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Systematics, diversity, and evolution of the East Asian velvet ants (Insecta: Hymenoptera: Mutillidae & Myrmosidae)

東アジア産アリバチの体系学・多様性・進化

By

JURIYA OKAYASU

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Contents

Abstract … 1
Acknowledgments … 3
Chapter 1. General introduction: Biological reviews of previous studies … 4
Sexual dimorphism … 5
Host choice … 11
Parasitism … 13
Diversity and abundance … 15
Mating … 16
Defense … 18
Study subjects and chapter outline … 23
References … 27
Figures and tables … 63
Chapter 2. Review of *Eotrogaspidia* Lelej (Hymenoptera: Mutillidae: Trogaspidiini) ... 78
Abstract … 78
Introduction … 78
Material and methods … 79
Eotrogaspidia Lelej, 1996 … 80
Eotrogaspidia adhabar **sp. nov.** … 81
Eotrogaspidia amans (André, 1909) … 84
Eotrogaspidia auroguttata (Smith, 1855) … 85
Eotrogaspidia buddha **sp. nov.** … 88
Eotrogaspidia hauseri **sp. nov.** … 91
Eotrogaspidia lena (Cameron, 1899), **comb. nov.** … 93
Eotrogaspidia melanopleura **sp. nov.** … 94
Eotrogaspidia oryzae (Pagden, 1934) … 96
Eotrogaspidia rubripes (André, 1901), **comb. nov.** … 97
Eotrogaspidia saussurei (Lelej, 2005), **comb. nov.** … 98
Trogaspidia Ashmead, 1899 … 100
Trogaspidia acidalia (Cameron, 1897), **stat. resurr.** … 100
Trogaspidia mackieae (Cockerell, 1928) … 101
Key to species of *Eotrogaspidia* and species easily confused with *Eotrogaspidia* … 102
Discussion … 104
Acknowledgments … 105
References … 105
Figures … 111
Chapter 3. A new velvet ant genus *Arkaditilla* (Hymenoptera, Mutillidae, Trogaspidiini) from the Oriental Region, with review of species … 126
Abstract … 126
Introduction … 126
Material and methods … 127
Results … 127
Arkaditilla **gen. nov.** … 127
Key to species of *Arkaditilla* … 129
Arkaditilla bagrada (Cameron, 1902), **comb. nov.** … 130
Arkaditilla depressicornis (Mickel, 1935), **comb. nov.** … 131
Arkaditilla frim **sp. nov.** … 131

Arkaditilla gibba **sp. nov.** … 134
Arkaditilla leleji **sp. nov.** … 136
Arkaditilla nallinia (Zavattari, 1914), **comb. nov.** … 138
Acknowledgments … 139
References … 140
Figures … 142
Chapter 4. Review of female *Andreimyrme* Lelej (Hymenoptera: Mutillidae: Smicromyrmini) … 150
Abstract … 150
Introduction … 150
Taxonomic history and limits of this study … 151
Material and methods … 151
Andreimyrme Lelej, 1995 … 152
Key to females of *Andreimyrme* … 154
Andreimyrme auricoma **sp. nov.** … 155
Andreimyrme borkenti (Williams, 2019), **comb. nov.** … 157
Andreimyrme laminatihumeralis **sp. nov.** … 158
Andreimyrme matsumotoi **sp. nov.** … 161
Andreimyrme naturalis **sp. nov.** … 163
Andreimyrme neaera (Mickel, 1935) … 165
Andreimyrme paniya Terine, Lelej & Kumar, 2021 … 166
Andreimyrme rong **sp. nov.** … 166
Andreimyrme sarawakensis Lelej, 1996 … 169
Andreimyrme silvorientalis **sp. nov.** … 169
Andreimyrme substriolata (Chen, 1957) … 171
Andreimyrme takensis **sp. nov.** … 173
Andreimyrme ursasolaris **sp. nov.** … 175
Andreimyrme yotoi **sp. nov.** … 177
Discussion … 179
Acknowledgments … 180
References … 181
Figures … 185
Chapter 5. Love is in the air and beyond the ocean: Taxonomic review of *Neotrogaspidia* Lelej (Hymenoptera: Mutillidae: Trogaspidiini) in Northeast Asia highlights its unique distributional pattern ... 200
Abstract ... 200
Introduction ... 200
Material and methods ... 201
Results ... 202
Neotrogaspidia Lelej, 1996 ... 202
Key to species of *Neotrogaspidia* ... 204
Neotrogaspidia circumcincta (André, 1896), **comb. nov.** ... 205
Neotrogaspidia elpinice (Mickel, 1933), **stat. resurr. et comb. nov.** ... 207
Neotrogaspidia pustulata (Smith, 1873) ... 211
Neotrogaspidia recticarinata (Chen, 1957), **comb. nov.** ... 218
Discussion ... 219
Genus limits ... 219
Phoretic copulation ... 220
Biogeography ... 221
Acknowledgments ... 222

References ... 222
Figures … 233
Chapter 6. New data on female velvet ants of the genus *Mickelomyrme* Lelej (Hymenoptera: Mutillidae: Smicromyrmini) … 248
Abstract ... 248
Introduction ... 248
Material and methods ... 248
Taxonomy … 249
Mickelomyrme athalia (Pagden, 1949) … 249
Mickelomyrme autonoe (Mickel, 1934), **comb. nov.** … 250
Mickelomyrme grandiguttata **sp. nov.** … 251
Mickelomyrme semperi semperi (Ashmead, 1904) … 253
Mickelomyrme verticalis **sp. nov.** … 254
Mickelomyrme vietnaminix **sp. nov.** … 256
Mickelomyrme zebina (Smith, 1860) … 259
Key to the females of *Mickelomyrme* … 260
Acknowledgments ... 261
References ... 261
Figures … 264
Chapter 7. Current knowledge on velvet ants (Hymenoptera: Mutillidae, Myrmosidae) of Vietnam: Faunal review and new country records … 268
Abstract … 268
Introduction … 268
Material and methods … 269
Historical review … 270
Checklist … 271
Family Myrmosidae Fox, 1894 … 271
Subfamily Kudakruminae Krombein, 1979 … 272
Genus *Kudakrumia* Krombein, 1979 … 272
Kudakrumia loaibonho Williams, Lelej & Thaochan, 2019 … 272
Subfamily Myrmosinae Fox, 1894 … 272
Genus *Krombeinella* Pate, 1947 … 272
Krombeinella brothersi Williams, Lelej & Thaochan, 2019 … 273
Family Mutillidae Latreille, 1802 … 273
Subfamily Rhopalomutillinae Schuster, 1949 … 273
Genus *Pherotilla* Brothers, 2015 … 273
Pherotilla brothersi Zhou, Lelej & Xu, 2017 … 274
Pherotilla striganovae (Lelej, 2012) … 274
Subfamily Sphaeropthalminae Schuster, 1949 … 275
Tribe Sphaeropthalmini Schuster, 1949 … 275
Genus *Hemutilla* Lelej, Tu & Chen, 2014 … 275
Hemutilla bifurcata (Chen, 1957) … 275
Subfamily Dasylabrinae Invrea, 1964 … 276
Genus *Orientilla* Lelej, 1979 … 276
Orientilla desponsa (Smith, 1855) … 277
Orientilla krombeini Lelej, 1996 … 278
Orientilla vietnamica Lelej, 1979 … 278
Subfamily Odontomutillinae Lelej, 1983 … 279
Genus *Odontomutilla* Ashmead, 1899 … 279
Odontomutilla cordigera (Sichel & Radoszkowski, 1869) … 279

Odontomutilla sinensis (Smith, 1855) … 280
Odontomutilla uranioides Mickel, 1933 … 281
Genus *Yamanetilla* Lelej, 1996 … 281
Yamanetilla pedaria (Mickel, 1934) … 281
Subfamily Myrmillinae Bischoff, 1920 … 282
Genus *Bischoffitilla* Lelej, 2002 … 282
Bischoffitilla cambrai Williams, 2019 … 283
Bischoffitilla lamellata (Mickel, 1933) … 283
Bischoffitilla perakensis (Pagden, 1934) … 284
Subfamily Mutillinae Latreille, 1802 … 284
Tribe Ctenotillini Brothers & Lelej, 2017 … 285
Genus *Williamstilla* Lelej, 2023 … 285
Williamstilla guangdongensis (Lelej, 1992) … 285
Tribe Mutillini Latreille, 1802 … 286
Genus *Kurzenkotilla* Lelej, 2005 … 286
Kurzenkotilla annamensis Lelej, 2005 … 286
Kurzenkotilla harmandi (André, 1898) … 286
Tribe Smicromyrmini Bischoff, 1920 … 287
Genus *Andreimyrme* Lelej, 1995 … 287
Andreimyrme borkenti (Williams, 2019) … 287
Andreimyrme matsumotoi Okayasu, 2021 … 288
Andreimyrme rong Williams, 2021 … 288
Andreimyrme substriolata (Chen, 1957) … 289
Andreimyrme yotoi Okayasu, 2021 … 290
Genus *Ephucilla* Lelej, 1995 … 290
Ephucilla bacbo (Lelej, 1995) … 290
Ephucilla viet (Lelej, 1995) … 291
Genus *Mickelomyrme* Lelej, 1995 … 291
Mickelomyrme abnorma (Chen, 1957) … 291
Mickelomyrme athalia (Pagden, 1949) … 292
Mickelomyrme chinensis (Smith, 1855) … 292
Mickelomyrme kuznetsovi Lelej, 1996 … 293
Mickelomyrme pusillaeformis (Hammer, 1962) … 294
Mickelomyrme puttasoki Williams, 2019 … 294
Genus *Nemka* Lelej, 1985 … 295
Nemka limi (Chen, 1957) … 295
Genus *Promecilla* André, 1902 … 296
Promecilla decora (Smith, 1879) … 296
Genus *Sinotilla* Lelej, 1995 … 297
Sinotilla belokobylskiji Lelej, 1995 … 297
Sinotilla boheana (Chen, 1957) … 298
Genus *Smicromyrme* Thomson, 1870 … 298
Smicromyrme thaochani Williams, 2019 … 299
Smicromyrme triguttatus Mickel, 1933 … 299
Tribe Trogaspidiini Bischoff, 1920 … 300
Genus *Eotrogaspidia* Lelej, 1996 … 300
Eotrogaspidia auroguttata (Smith, 1855) … 300
Eotrogaspidia oryzae (Pagden, 1934) … 302
Genus *Krombeinidia* Lelej, 1996 … 302
Krombeinidia chang Williams, 2019 … 302

Krombeinidia griseomaculata (André, 1898) … 303
Krombeinidia subfossata (Chen, 1957) … 303
Genus *Neotrogaspidia* Lelej, 1996 … 304
Neotrogaspidia circumcincta (André, 1896) … 304
Genus *Nonveilleridia* Lelej, 1996 … 305
Nonveilleridia bataviana (André, 1909) … 305
Genus *Orientidia* Lelej, 1996 … 306
Orientidia thoawanae Williams, 2019 … 306
Genus *Petersenidia* Lelej, 1992 … 306
Petersenidia dorsispinata (Chen, 1957) … 307
Petersenidia leleji Williams, 2019 … 307
Petersenidia scaphella (Chen, 1957) … 308
Genus *Promecidia* Lelej, 1996 … 308
Promecidia birmanica (Dalla Torre, 1897) … 308
Promecidia ninnii (Magretti, 1892) … 309
Genus *Trogaspidia* Ashmead, 1899 … 309
Trogaspidia formosana (Matsumura, 1911) … 310
Trogaspidia fuscipennis fuscipennis (Fabricius, 1804) … 310
Trogaspidia mackieae (Cockerell, 1928) … 311
Trogaspidia rhea gaea Chen, 1957 … 312
Genus *Wallacidia* Lelej & Brothers, 2008 … 312
Wallacidia oculata (Fabricius, 1804) … 313
Wallacidia retinula (Chen, 1957) … 314
Genus *Zavatilla* Tsuneki, 1993 … 315
Zavatilla xuzaifui Zhou, Lelej & Williams, 2018 … 315
Tribe Zeugomutillini Waldren, 2023 … 316
Genus *Zeugomutilla* Chen, 1957 … 316
Zeugomutilla angkorensis Williams, 2017 … 316
Additional species potentially occurring in Vietnam … 316
Discussion … 318
Acknowledgments … 319
References … 319
Figures and tables … 331

Chapter 8. Preliminary assessment of the velvet ant fauna in Nepal, with description of new species of the genera *Strangulotilla* Nonveiller and *Zeugomutilla* Chen (Hymenoptera: Mutillidae) … 356
Abstract … 356
Introduction … 356
Material and methods … 357
Taxonomy … 357
Tribe Zeugomutillini Waldren, 2023 … 358
Genus *Strangulotilla* Nonveiller, 1979 … 358
Strangulotilla dubia **sp. nov.** … 358
Key to males of *Strangulotilla* … 361
Genus *Zeugomutilla* Chen, 1957 … 362
Zeugomutilla curvicarinata **sp. nov.** … 362
Key to females of *Zeugomutilla* … 364
Synoptic list of velvet ant species known from Nepal … 364
List of SEHU velvet ant specimens from Nepal … 365
Discussion … 366

Acknowledgments ... 367
References ... 367
Figures … 373
Chapter 9. Far Eastern velvet ants of the genus *Nemka* Lelej (Hymenoptera: Mutillidae): Systematics and ecological character displacement … 384
Abstract … 384
Introduction … 384
Material and methods … 386
Material … 386
Morphological study … 387
Body size analysis … 387
Systematics … 388
Nemka limi (Chen, 1957) … 388
Nemka taiwanensis (Mickel, 1933) … 390
Nemka wotani (Zavattari, 1913) … 393
Nemka yasumatsui (Mickel, 1936) … 394
Key to East Asian species of *Nemka* … 397
Body size analysis … 398
Discussion … 398
Acknowledgments ... 401
References ... 401
Figures and tables … 411
Chapter 10. Systematics of the male velvet ants of the tribe Smicromyrmini Bischoff (Hymenoptera: Mutillidae) of East Asia: Critical review of the genera and morphological phylogenetics … 430
Abstract … 430
Introduction … 431
Material and methods … 433
Taxon sampling … 433
Material … 433
Taxonomic work … 434
Phylogenetic analysis … 435
Phylogenetic results … 437
Characters and states for phylogenetic analysis … 437
Phylogenetic relationship … 442
Systematic results … 443
Tribe Smicromyrmini Bischoff, 1920 … 443
Key to the East Asian genera of Smicromyrmini based on the male morphology … 444
Key to the East Asian genera of Smicromyrmini based on the female morphology … 446
Genus *Andreimyrme* Lelej, 1995 … 446
Andreimyrme long Lelej, 1995 … 448
Genus *Chenmyrme* **nov.** … 448
Chenmyrme undata (Chen, 1957), **comb. nov.** … 450
Genus *Ephucilla* Lelej, 1995 … 450
Key to the East Asian species of *Ephucilla* based on the male morphology … 453
Key to the species of *Ephucilla* based on the female morphology … 453
Ephucilla aequatoris **sp. nov.** … 454

Ephucilla brevitegula Okayasu, 2020 … 457
Ephucilla calacuasana (Tsuneki, 1993), **comb. nov.** … 458
Ephucilla cheni Lelej, 1995 … 459
Ephucilla cyaneiventris cyaneiventris (André, 1896), **comb. nov.** … 459
Ephucilla cyaneiventris gobiana (Chen, 1957), **comb. nov.** … 461
Ephucilla drupa (Zavattari, 1913) … 461
Ephucilla guentheri (Zavattari, 1913) … 462
Ephucilla naja (Zavattari, 1913) … 463
Ephucilla panfilovi Lelej, 1995 … 464
Ephucilla retorta **sp. nov.** … 465
Ephucilla suginoi Okayasu, 2020 … 467
Ephucilla yoshitakei Okayasu, 2020 … 468
Female-based species of *Ephucilla* … 469
Ephucilla bacbo (Lelej, 1995) … 469
Ephucilla bicolor **sp. nov.** … 470
Ephucilla bifida **sp. nov.** … 472
Ephucilla hejunhuai Lelej, 2020 … 474
Ephucilla nigrothoracica (Okayasu, 2018), **comb. nov.** … 474
Ephucilla okajimai **sp. nov.** … 475
Ephucilla petina (Mickel, 1937), **comb. nov.** … 477
Ephucilla poonaensis (Cameron, 1892) … 478
Ephucilla subparallela (Chen, 1957), **comb. nov.** … 479
Ephucilla viet (Lelej, 1995) … 479
Genus *Ephutomma* Ashmead, 1899 … 480
Ephutomma mongolensis (Suárez, 1974) … 481
Genus *Hadrodontilla* **nov.** … 482
Hadrodontilla davidi (André, 1898), **comb. nov.** … 484
Hadrodontilla pekiniana (André, 1905), **comb. nov.** … 485
Genus *Mickelomyrme* Lelej, 1995 … 486
Key to the East Asian species of *Mickelomyrme* based on the male morphology … 488
Mickelomyrme athalia (Pagden, 1949) … 489
Mickelomyrme atrata (Mickel, 1934), **comb. nov.** … 491
Mickelomyrme bakeri (Mickel, 1934) … 491
Mickelomyrme bidentata (Tsuneki, 1993) … 492
Mickelomyrme caecina (Cameron, 1903), **comb. nov.** … 493
Mickelomyrme carinata **sp. nov.** … 494
Mickelomyrme chinensis (Smith, 1855) … 497
Mickelomyrme cristaticauda **sp. nov.** … 498
Mickelomyrme exiloides (Magretti, 1892) … 501
Mickelomyrme hageni (Zavattari, 1913) … 502
Mickelomyrme isora (Cameron, 1900) … 504
Mickelomyrme lavinia (Mickel, 1934), **comb. nov.** … 504
Mickelomyrme meator (Mickel, 1935), **comb. nov.** … 505
Mickelomyrme nigrogastra (Mickel, 1934) … 505
Mickelomyrme norna (Zavattari, 1913) … 506
Mickelomyrme palacala (Tsuneki, 1993), **comb. nov.** … 508
Mickelomyrme palawanensis (Mickel, 1934) … 508
Mickelomyrme pusillaeformis (Hammer, 1962) … 509
Mickelomyrme recondita **sp. nov.** … 510

Mickelomyrme semperi (Ashmead, 1904) … 513
Mickelomyrme zebina (Smith, 1860) … 513
Genus *Nemka* Lelej, 1985 … 514
Key to the East Asian species of *Nemka* based on the male morphology … 516
Nemka conjungenda (Magretti, 1892) … 516
Nemka kellyi (Pagden, 1934) … 517
Nemka limi (Chen, 1957) … 517
Nemka pagdeni Lelej, 1995 … 519
Nemka taiwanensis (Mickel, 1933) … 520
Nemka wotani (Zavattari, 1913) … 521
Nemka yasumatsui (Mickel, 1936) … 523
Genus *Nordeniella* Lelej, 2005 … 524
Genus *Physetopoda* Schuster, 1949 … 525
Physetopoda oratoria (Chen, 1957) … 527
Genus *Promecilla* André, 1902 … 528
Key to the East Asian species of *Promecilla* based on the male morphology … 529
Promecilla annexa (Cameron, 1909), **comb. nov.** … 530
Promecilla decora (Smith, 1879) … 530
Promecilla levinaris (Chen, 1957) … 532
Genus *Sinotilla* Lelej, 1995 … 533
Key to the East Asian species of *Sinotilla* based on the male morphology … 535
Sinotilla ansula (Chen, 1957) … 536
Sinotilla columnata (Chen, 1957) … 537
Sinotilla complanata **sp. nov.** … 537
Sinotilla dardanus (Smith, 1857), **comb. nov.** … 540
Sinotilla drola drola (Zavattari, 1913), **comb. nov.** … 542
Sinotilla drola lodra (Chen, 1957), **comb. nov.** … 543
Sinotilla gracillima (Smith, 1857) … 544
Sinotilla hong Lelej, 1995 … 545
Sinotilla ilerda (Cameron, 1902), **comb. nov.** … 545
Sinotilla jambar Okayasu, 2020 … 546
Sinotilla nitela (Mickel, 1934), **comb. nov.** … 547
Sinotilla runcina (Zavattari, 1914) … 548
Sinotilla scitula (Mickel, 1935), **comb. nov.** … 548
Sinotilla serpa (Zavattari, 1913) … 549
Sinotilla sparsilis (Mickel, 1934), **comb. nov.** … 550
Sinotilla trisecta (Chen, 1957) … 550
Sinotilla unica **sp. nov.** … 551
Sinotilla viriata (Mickel, 1934), **comb. nov.** … 554
Sinotilla volupia (Mickel, 1935), **comb. nov.** … 555
Genus *Smicromyrme* Thomson, 1870 … 555
Key to the subgenera of *Smicromyrme* based on the male morphology … 557
Key to the East Asian species of *Smicromyrme* based on the male morphology … 557
Subgenus *Erimyrme* Lelej, 1985 … 557
Smicromyrme (*Erimyrme*) *bidenticulatus* (Chen, 1957) … 558
Subgenus *Smicromyrme* Thomson, 1870 … 559
Smicromyrme (*Smicromyrme*) *australis* **sp. nov.** … 560

Smicromyrme (*Smicromyrme*) *lewisi* Mickel, 1935 … 562
Smicromyrme (*Smicromyrme*) *strandi* (Zavattari, 1913) … 569
Species tentatively placed in *Smicromyrme* … 569
Smicromyrme caeruleus Mickel, 1934 … 569
Smicromyrme devius (Cameron, 1909) … 570
Smicromyrme electra Mickel, 1935 … 570
Smicromyrme herophile Mickel, 1935 … 571
Smicromyrme jacobsoni (André, 1907) … 572
Smicromyrme minahassae (Zavattari, 1914) … 572
Genus *Tsunekimyrme* Lelej, 1995 … 573
Tsunekimyrme fluctuata (Smith, 1865) … 573
Discussion … 574
Acknowledgments … 575
References … 576
Figures and tables … 596
Chapter 11. General discussion … 690
References … 692
Figures … 695

Abstract

Velvet ants are characteristic wasps with extreme sexual dimorphism, with males usually being winged and females being wingless. They possess unique biological features resulting from flightless nature of females, which make them a useful model system in comparative biology. Most species are known as parasitoids of nest-provisioning wasps and bees. Given the high species richness and abundance, particularly in tropical or arid habitats, they potentially play an important role in natural and agricultural ecosystems. However, our knowledge on their systematics and natural history is fragmentary. Specifically, the East Asian velvet ants have been paid less attention comparing to other regions, despite of the potential diversity in this region. To fill these gaps, the present dissertation attempts to critically review the systematics of the East Asian velvet ants through examination of museum specimens and field surveys. Following a review of the velvet ant biology (Chapter 1), this dissertation includes: taxonomic review of the genus *Eotrogaspidia* Lelej, 1996 (Chapter 2), description a new genus previously confused with the genus *Krombeinidia* Lelej, 1996 (Chapter 3), taxonomic review of the genus *Andreimyrme* Lelej, 1995 based on the female morphology (Chapter 4), taxonomic review of Northeast Asian species of the genus *Neotrogaspidia* Lelej, 1996 (Chapter 5), taxonomic additions to the genus *Mickelomyrme* Lelej, 1995 (Chapter 6), faunal review and taxonomic additions to the velvet ants of Vietnam (Chapter 7) and Nepal (Chapter 8), taxonomic review and analysis of character displacement of the Far Eastern species of the genus *Nemka* Lelej, 1985 (Chapter 9), phylogenetic systematics of the East Asian genera of the tribe Smicromyrmini Bischoff, 1920 based on the male morphology (Chapter 10), and discussion on the utility of systematics within the context of comparative biology (Chapter 11).

Based on over 3,500 specimens, I recognized many new taxa and taxonomic changes for East Asian velvet ants. Three new genera and 32 new species were described: *Arkaditilla* **gen. nov.** (type species: *A. leleji* **sp. nov.**), *Chenmyrme* **gen. nov.** (type species: *Smicromyrme undata* Chen, 1957), and *Hadrodontilla* **gen. nov.** (type species: *Mutilla davidi* André, 1898); *Andreimyrme auricoma* **sp. nov.**, ♀ (Malaysia), *An. laminatihumeralis* **sp. nov.**, ♀ (Indonesia, Malaysia), *An. matsumotoi* **sp. nov.**, ♀ (Vietnam), *An. naturalis* **sp. nov.**, ♀ (Indonesia), *An. rong* **sp. nov.**, ♀ (Thailand, Vietnam), *An. silvorientalis* **sp. nov.**, ♀ (Indonesia), *An. takensis* **sp. nov.**, ♀ (Thailand), *An. ursasolaris* **sp. nov.**, ♀ (Indonesia), *An. yotoi* **sp. nov.**, ♀ (Laos, Vietnam), *Ephucilla aequatoris* **sp. nov.**, ♂ (Indonesia), *E. bicolor* **sp. nov.**, ♀ (Vietnam), *E. bifida* **sp. nov.**, ♀ (Indonesia), *E. okajimai* **sp. nov.**, ♀ (Thailand), *E. retorta* **sp. nov.**, ♂ (Laos, Vietnam), *Mickelomyrme carinata* **sp. nov.**, ♂ (Indonesia), *Mi. cristaticauda* **sp. nov.**, ♂ (Vietnam), *Mi. grandiguttata* **sp. nov.**, ♀ (Laos), *Mi. recondita* **sp. nov.**, ♂ (Thailand), *Mi. verticalis* **sp. nov.**, ♀ (Philippines), *Mi. vietnaminix* **sp. nov.**, ♀ (Vietnam), *Sinotilla complanata* **sp. nov.**, ♂ (Thailand), *Si. unica* **sp. nov.**, ♂ (China, Vietnam), *Smicromyrme* (*Smicromyrme*) *australis* **sp. nov.**, ♂ (Thailand) (Smicromyrmini), *Arkaditilla frim* **sp. nov.**, ♂ (Malaysia), *Ar. gibba* **sp. nov.**, ♂ (Indonesia), *Ar. leleji* **sp. nov.**, ♂ (Indonesia), *Eotrogaspidia adhabar* **sp. nov.**, ♂ (Nepal), *Eo. buddha* **sp. nov.**, ♂ ((India, Nepal, Pakistan, Sri Lanka), *Eo. hauseri* **sp. nov.**, ♂ (India, Nepal), *Eo. melanopleura* **sp. nov.**, ♀ (China), (Trogaspidiini), *Strangulotilla dubia* **sp. nov.**, ♂ (Nepal), and *Zeugomutilla curvicarinata* **sp. nov.**, ♀ (Nepal) (Zeugomutillini). The following 36 new combinations and 28 new synonymies were proposed: *An. borkenti* (Williams, 2019), **comb. nov.** (from *Smicromyrme*), *C. undata* (Chen, 1957), **comb. nov.** (from *Ephucilla*), *Ep. calacuasana* (Tsuneki, 1993), **comb. nov.** (from *Smicromyrme*), *Ep. cyaneiventris cyaneiventris* (André, 1896), **comb. nov.** (from *Sinotilla*), *Ep. cyaneiventris gobiana* (Chen, 1957), **comb. nov.** (from *Sinotilla*), *Ep. nigrothoracica* (Okayasu, 2018), **comb. nov.** (from *Sinotilla*), *Ep. petina* (Mickel, 1937), **comb. nov.** (from *Sinotilla*), *Ep. subparallela* (Chen, 1957), **comb. nov.**

(from *Sinotilla*), *H. davidi* (André, 1898), **comb. nov.** (from *Andreimyrme*), *H. pekiniana* (André, 1905), **comb. nov.** (from *Sinotilla*), *Mi. atrata* (Mickel, 1934), **comb. nov.** (from *Smicromyrme*), *Mi. autonoe* (Mickel, 1934), **comb. nov.** (from *Smicromyrme*), *Mi. caecina* (Cameron, 1903), **comb. nov.** (from *Smicromyrme*), *Mi. meator* (Mickel, 1935), **comb. nov.** (from *Smicromyrme*), *Mi. lavinia* (Mickel, 1934), **comb. nov.** (from *Smicromyrme*), *Mi. palacala* (Tsuneki, 1993), **comb. nov.** (from *Smicromyrme*), *Promecilla annexa* (Cameron, 1909), **comb. nov.** (from *Andreimyrme*), *Si. dardanus* (Smith, 1857), **comb. nov.** (from *Smicromyrme*), *Si. drola drola* (Zavattari, 1913), **comb. nov.** (from *Ephucilla*), *Si. drola lodra* (Chen, 1957), **comb. nov.** (from *Ephucilla*), *Si. ilerda* (Cameron, 1902), **comb. nov.** (from *Smicromyrme*), *Si. nitela* (Mickel, 1934), **comb. nov.** (from *Andreimyrme*), *Si. scitula* (Mickel, 1935), **comb. nov.** (from *Smicromyrme*), *Si. sparsilis* (Mickel, 1934), **comb. nov.** (from *Smicromyrme*), *Si. viriata* (Mickel, 1934), **comb. nov.** (from *Andreimyrme*), *Si. volupia* (Mickel, 1935), **comb. nov.** (from *Andreimyrme*) (Smicromyrmini), *Ar. bagrada* (Cameron, 1902), **comb. nov.** (from *Krombeinidia*), *Ar. depressicornis* (Mickel, 1935), **comb. nov.** (from *Krombeinidia*), *Ar. nallinia* (Zavattari, 1914), **comb. nov.** (from *Krombeinida*), *Eo. lena* (Cameron, 1899), **comb. nov.** (from *Trogaspidia*), *Eo. rubripes* (André, 1901), **comb. nov.** (from *Trogaspidia*), *Eo. saussurei* (Lelej, 2005), **comb. nov.** (from *Trogaspidia*), *Neotrogaspidia circumcincta* (André, 1896), **comb. nov.** (from *Orientidia*), *N. elpinice* (Mickel, 1933), **comb. nov.** (from *Trogaspidia*), *N. recticarinata* (Chen, 1957), **comb. nov.** (from *Trogaspidia*), and *Vanhartenidia ekka* (Nurse, 1902), **comb. nov.** (from *Eotrogaspidia*) (Trogaspidiini); *C. undata* (= *Sm. yuliana* Tsuneki, 1972, **syn. nov.**), *Ep. naja* (Zavattari, 1913) (= *Sm. thalia* Mickel, 1933, **syn. nov.**), *Ep. petina* (Mickel, 1937) (= *Sm. spinicauda* Chen, 1957, **syn. nov.**, *Si. lambirensis* Lelej, 1996, **syn. nov.**, *Si. belokobylskiji* Lelej, 1995, **syn. nov.**, *Si. calopoda* Okayasu, 2017, **syn. nov.**, and *Si. ohbayashii* Okayasu, 2017, **syn. nov.**), *Mi. athalia* (Pagden, 1949) (= *Sm. bicristata* Chen, 1957, **syn. nov.**), *Mi. bakeri* (Mickel, 1934) (= *Sm. tanoi* Tsuneki, 1972, **syn. nov.**), *Mi. caecina* (= *Sm. punctinotus* Mickel, 1935, **syn. nov.**), *Mi. norna* (Zavattari, 1913) (= *Sm. norna abnorma* Chen, 1957, **syn. nov.**), *Mi. zebina* (Smith, 1860) (= *Sm. aborlana aborlana* Tsuneki, 1993, **syn. nov.** and *Sm. aborlana zamboangae* Tsuneki, 1993, **syn. nov.**), *Nemka taiwanensis* (= *Sm. curvisquamata* Chen, 1957, **syn. nov.** and *Sm. ilanica* Tsuneki, 1972, **syn. nov.**), *P. decora* (Smith, 1879) (= *Sm. contractula* Chen, 1957, **syn. nov.**), *Si. dardanus* (= *Sm. dardanus salacia* Mickel, 1935, **syn. nov.**, *Sm. gribodoana* Invrea, 1943, **syn. nov.**, and *Sm. cyaneiventris boheana* Chen, 1957, **syn. nov.**), *Si. drola drola* (= *Sm. hombuceiana* Tsuneki, 1982, **syn. nov.**), *Si. nitela* (= *Sm. aponis* Tsuneki, 1993, **syn. nov.**), and *Si. viriata* (= *Sm. mindanaonis* Tsuneki, 1993, **syn. nov.**) (Smicromyrmini), *Eo. auroguttata* (Smith, 1855) (= *T. vallicola* Tsuneki, 1993, **syn. nov.**), *Neo. elpinice* (= *T. aestivalis* Hammer, 1949, **syn. nov.** and *T. maritima* Chen, 1957, **syn. nov.**), *Neo. circumcincta* (= *T. yuliensis* Tsuneki, 1972, **syn. nov.** and *K. agricola* Williams, 2019, **syn. nov.**), and *T. mackieae* (Cockerell, 1928) (= *T. pacifica* Tsuneki, 1972, **syn. nov.**) (Trogaspidiini). Two species were resurrected as full species: *Neo. elpinice*, **stat. resurr.** from the synonym of *Neo. pustulata* and *T. acidalia* (Cameron, 1897), **stat. resurr.** from the synonym of *T. villosa* (Fabricius, 1775). The type species of *Sinotilla* is replaced by *Si. dardanus* under Article 70.3.2 of the International Code of Zoological Nomenclature 4th edition.

Systematic and phylogenetic results of this study suggest that: 1) the diversity of East Asian velvet ants is much higher than currently recognized, but sampling efforts are inadequate and biased; 2) the generic assignment of many previously described species is inappropriate and should be critically revised based on reexamination of voucher specimens; and 3) the East Asian genera of the Smicromyrmini are defined only by a unique combination of character states due to high level of homoplasy.

(x + 696 pages)

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Chapter 1

General introduction: Biological review of previous studies

"*More often than not, biologists identify themselves as entomologists*
if they work with insects, or as botanists if plants are their things.
Or even as copepodologists, coleopterologists, or cecidomyiidologists
(if their creed be copepods, beetles, or cecidomyiid gnats, respectively)."
Menno Schilthuizen, "*Nature's nether regions*" (2014)

Velvet ants, or families Mutillidae Latreille, 1802 and Myrmosidae Fox, 1894, are groups of parasitoid stinging wasps (Hymenoptera: Aculeata) with remarkable morphology, diversity, ecology, and behavior. This group of insects has been fascinating naturalists from all around the world for centuries. The first written mention of velvet ants is found in the Greek poem "*Theriaca*" (second century BC) by Nicander of Colophon, which deals with venomous creatures and antidotes:

"*The antlet - now mark - which in truth resembles the ant, has a fiery neck, though its body is dust-coloured; its broad and spangled back is all speckled, and its dusky head is raised but little on its neck, yet it inflicts as much pain as the spiders aforenamed.*" (translation by Gow & Scholfield, 1953).

Two millennia later, scientific treatments of velvet ants officially started with Carl Linnaeus, who proposed the formal scientific name for velvet ants, *Mutilla* Linnaeus, 1758, in his iconic work "*Systema naturae*" (tenth edition) (Linnaeus, 1758). The name originates from the Latin adjective *mutilus*, mutilated, in reference to the wingless females (Tschuch, 2000). Thousands of species were discovered and named since then; 3,500 to 4,000 valid species had already been recognized when Mickel (1928) summarized the earliest literature on velvet ants. In this book, he dealt with almost every known aspect of the velvet ant biology and provided a reliable starting point for later workers. After Mickel (1928), entomologists drastically increased our knowledge on the natural history and systematics of velvet ants. Instead of describing many new species, systematists sought to revise the classification system step by step.

Velvet ants possess unique features, providing a fascinating model system to address questions in general biology. Nevertheless, they have seldom been analyzed in comparative approaches, presumably due to fragmentary knowledge of their natural history and systematics. In fact, velvet ants are not so easy to observe in the field. Important observations are scattered in a significant number of taxonomic papers that are usually unfamiliar to non-systematists. Complete life histories have been documented for only a few species. Systematic basis for velvet ants is quite incomplete, due to, in part, their enormous diversity.

Recently, the situation has changed dramatically. Substantial advances were made in systematics and some authors sought to synthesize natural history data in a comparative way, like phylogeny (Brothers & Lelej, 2017; Waldren *et al*., 2023; Williams, 2012), identification guide (Bogusch, 2006; Brothers, 2006; Gogala, 2017; József & Zoltán, 2011; Williams *et al*., 2024), systematic catalogs (Brothers, 2022; Lelej, 2002, 2005, 2007; Lo Cascio, 2015; Nonveiller, 1990; Pagliano *et al*., 2020), biological reviews (Brothers, 1989; Brothers *et al*., 2000; Luz *et al*., 2016a; Ronchetti & Polidori, 2020; Waldren *et al*., 2020a), and molecular technique for associating dimorphic sexes (Pilgrim & Pitts, 2006), leading to empirical studies of broad interest (e.g., Lopez *et al*., 2021; Pitts *et al*., 2010b; Wilson *et al*., 2012a, 2015, 2020). These studies shed new light on the peculiar nature of velvet ants. There remain,

however, many uninvestigated aspects of biology of velvet ants, which will undoubtedly yield useful data to understand the diversity of life. Further, their parasitoid lifestyle and abundance in various habitats (reviewed below) suggest velvet ants are important natural enemies regulating populations of beneficial or pest insects in natural and agricultural ecosystems. As an introduction to this dissertation, key features to understand velvet ants are reviewed below.

Sexual dimorphism

Insects acquired functional wings much earlier than any other animal taxa, probably 320 to 420 million years before present (Grimaldi & Engel, 2005; Misof *et al*., 2014; Ross, 2017). Flight ability provides improved dispersal ability to insects, enabling them to seek novel resources and mates effectively and to retreat from predators rapidly (Grimaldi & Engel, 2005). This key innovation is considered a major driving force of the massive diversification of insects (Mayhew, 2007; Nicholson *et al*., 2014). However, many insects, scattered in numerous orders and families, secondarily lost flight ability and wings despite of apparent disadvantage (Roff, 1990).

Wing reduction is a widespread phenomenon in Aculeata (stinging wasps), except for most families of apoid wasps. Many families of chrysidoid and "vespoid" families have at least a few wingless or short-winged members: Bethylidae, Bradynobaenidae, Chrysididae, Chyphotidae, Drynidae, Embolemidae, Formicidae, Heterogynaidae, Mutillidae, Plumariidae, Pompilidae, Rhopalosomatidae, Sclerogibbidae, Sierolomorphidae, Thynnidae, Tiphiidae (Fig. 1; Argaman, 1990; Azevedo *et al*., 2018; Bischoff, 1927; Boni Bartalucci, 2004, 2011; Evans, 1966; Goulet & Huber, 1993; Kimsey, 1991, 2006; Kimsey & Bohart, 1991; Kimsey & Wasbauer, 2006; Krogmann *et al*., 2009; Ohl & Bleidorn, 2006; Olmi, 1984, 1996, 2005; Pagliano & Romano, 2018; Peeters *et al*., 2020; Reid, 1941; Stubblefield & Seger, 1994; Townes, 1977). In some groups (e.g., Bradynobaenidae and tiphiid subfamily Brachycistidinae), all or most species show wing reduction. This phenomenon is generally restricted to female individuals and is likely associated with subterranean habitats or oviposition in a limited space.

The most striking feature of velvet ants is the prominent sexual dimorphisms. Females are always wingless (apterous) and give an ant-like appearance, while males look like normal wasps with functional wings (alate, macropterous) (Brothers, 1989). This nature is particularly important in mutillidology, because various biological characteristics of this group of insects stem from the female aptery and behavioral differences between sexes.

All known velvet ant females are wingless, lacking any traces of wings. Additionally, various morphological specializations associated with this wing reduction are observed in females. The ocelli (simple eyes) are obliterated in most females, except that females of the Myrmosinae (Myrmosidae) have functional ocelli, and the sole genus within the Pseudophotopsidinae, *Pseudophotopsis* André, shows three states: functional, rudimentary, and obliterated ocelli (Brothers & Lelej, 2017). The mesosomal segments (pterothoracic segments plus an anterior abdominal segment) are fused, and mesosomal sutures are obliterated or at most represented by a slight transverse furrow, carina, or row of tubercles, making the mesosoma a strongly sclerotized box (Reid, 1941). The myrmosid females, however, have the freely articulated and movable pronotum, while other mesosomal sutures are obliterated (Fig. 2A; Brothers & Lelej, 2017; Reid, 1941). Females in the Pseudophotopsidinae have the evident pro-mesonotal and meso-metanotal sutures although mesosomal segments are fused (Fig. 2B; Brothers & Lelej, 2017). The tegula, a sclerotized evagination on the mesosoma of Hymenoptera, is located on the lateral margin of mesoscutum and covers the wing base in males. This sclerite is totally absent in females

throughout the families. As well as wings, indirect flight muscles and sutures or apodemes which provide the attachment sites of those muscles, the notaulus and the parapsidal signum (Menke, 1993), are obliterated in females (Peeters *et al*., 2020). The dorsum of velvet ant females is evenly convex, lacking the meso- and metascutellum, medial domed subdivisions on the mesonotum and metanotum, which accommodate pulsating circulatory organs connected to posterior wing veins and facilitate circulation of hemolymph through the wings (Pass, 2018).

Flight loss is observed in various insect taxa (Roff, 1990). This suggests repeated evolution and selective advantage of apterous forms. In velvet ants, this is reasonable because females crawl into the limited space made by hosts, which may cause damage to wings (Brothers, 1989; Evans, 1969; Vivallo, 2020). Roff (1990) argued that wings are not always impediments to underground movement, because some insects have a high degree of modifications to cope with both active flight and underground movement (e.g., mole crickets). In the Hymenoptera, however, wings are formed by thin layers of membrane and cannot be folded tightly as in cockroaches and crickets. These features make hymenopterans vulnerable to subterranean lifestyle without wing reduction.

Males generally have functional wings like most wasps. They can be, however, brachypterous or apterous despite of disadvantages in mate searching and escaping from predators (Fig. 3). This phenomenon is uncommon, but widely scattered across five subfamilies: Dasylabrinae, Mutillinae, Myrmillinae, Sphaeropthalminae, and Ticoplinae (Table 1). This suggests multiple origins of male aptery. The geographical distribution of apterous males is restricted to Mediterranean region, Middle East, eastern and southern Sub-Saharan Africa, southern India, Sri Lanka, southwestern North America, and northern Chile (Table 1; Manley & Pitts, 2002; Nonveiller, 1996), where arid and semiarid habitats are dominant (Burgess *et al*., 2004; Campbell *et al*., 2021; Dinerstein *et al*., 2017; Olson *et al*., 2001; Ricketts *et al*., 1999; Wikramanayake *et al*., 2002). Few species may occur in their surrounding regions. This might suggest male aptery is an adaptation to such extreme environment. Powered flight requires costs to maintain flight apparatus and higher energy and oxygen consumption rate for flight itself (Edwards & Ruska, 1955; Harrison & Roberts, 2000; Roff, 1990; Wigglesworth & Lee, 1982). Wing reduction and flight loss reduces the size and density of tracheal system (Raś *et al*., 2022), regulating water loss in arid environment.

Three types of variation in male wing reduction are observed. First, various forms of reduction have been detected (morphological variation), from brachypterous males to totally apterous ones lacking tegula and mesosomal sutures (see Pagliano *et al*., 2020: figs 21, 153, 164, 166, 169, 184, 196, 201, 204, 206, 214, 224, 226, 227, 229, 232, 269, 271). Second, some genera which include apterous/brachypterous males also include winged males (intrageneric variation). Third, few species have both macropterous and apterous/brachypterous individuals (intraspecific variation), like *Dasymutilla hector* (Blake), *D. waco* (Blake), *Morsyma ashmeadii* Fox, *Sphaeropthalma brachyptera* (Schuster) (Ferguson, 1967; Mickel, 1928, 1936a; Pitts, 2007; Schuster, 1945). Furthermore, it is known that adult males of *Odontophotopsis melicausa melicausa* (Blake) and *Sphaeropthalma unicolor* (Cresson) chew their wings off (Manley & Pitts, 2002; Schuster, 1958), although no detailed description of this behavior is available in the literature.

Because of the extreme sexual dimorphism, it is almost impossible to associate the male and female sexes based on morphology. This is the major source of taxonomic confusion in this group. Many species and even some genera are known from one sex only, making recognition of the border of each genus and estimation of species diversity difficult (Zhou *et al*., 2018b). For example, Bischoff's (1920–1921) monograph dealt with as many as 1287 African species, of which only 5.5% were known from both sexes at that time

(Nonveiller, 1980ab). Male-female association has been a challenge in velvet ant systematics. There are potentially a number of species-level or genus-level synonyms. Sometimes the male and female of a single species are subsequently found to belong to different genera, suggesting wrongly associated sexes (e.g., Mickel, 1935a). This further complicates the situation. The following six lines of evidence have been used by systematists to associate the sexes of a particular species. In short, none of the presently available techniques is perfect in practice; it is usually necessary to use multiple lines of evidence to increase the likelihood of sex association.

Mating

Historically, the most widely used method is examination of pairs *in copula*. Sometimes mating pairs remain in copulation even after death and are found in museum collections (Fig. 4). Mating events can be rapidly terminated by human interference, but in this case, the collector is able to associate the male and the female by mounting them on a same pin (Figs 4C–4F). Mating events are spatio-temporarily unpredictable and are not frequently observed in the field. Therefore, entomologists often use caged females to attract conspecific males in the field (e.g., Brothers, 2018; Cambra & Quintero, 2003a; Cambra *et al*., 2020; Fattig, 1943; Hurd, 1951ab; József & Zoltán, 2011; Manley, 1999ab; Quintero & Cambra, 1996b, 2001a) or observe mating attempts in captivity (e.g., Bergamaschi *et al*., 2010, 2011, 2012; Cambra & Quintero, 1993, 2003a; Cambra *et al*., 2020; Garcia *et al*., 2006; Mickel, 1924b; Quintero & Cambra, 1994; Remington, 1944). Alternatively, Manley & Radke (2002) cited three occasions when a female of *Dasymutilla intermixta* Mickel and one or eight males of *D. sicheliana* (de Saussure) were collected in a single pitfall trap. They based the synonymy of these two *Dasymutilla* species on this observation, because the males were likely attracted by the female to the traps. Likewise, coincidental capture of males and females in Malaise trap samples may suggest that the females were carried by the males during copulation (e.g., Lelej, 2016).

In captivity, males attempt to mate with every virgin female (Quintero & Cambra, 1996b). Quintero & Cambra (1996b) found that males were not able to mate with unreceptive female and females were always unreceptive to non-conspecific males. They concluded that observation of mating attempts in captivity is a reliable method to associate sexes. Additionally, Garcia *et al*. (2006) observed males of *Anomophotopsis quinteroi* Cambra and *Pseudomethoca melanocephala* (Perty) displaying courtship behavior only toward conspecific females in multi-female mating trials. However, observations suggest that males sometimes try to mate with non-conspecific females or non-congeneric ones (Bartholomay *et al*., 2019a; Ferguson, 1962; Manley, 1977; Manley & Pitts, 2007; Rau, 1922; VanderSal-Jensen *et al*., 2016). Mating in captivity can be different from that in natural conditions (Manley & Pitts, 2007; Waldren *et al*., 2020a) and the evidence of non-conspecific mating in the field is scarce, with O'Toole (1975) being the only reported case. Also, velvet ant females are likely monandrous (e.g., Brothers, 1972), so females collected in the field generally refuse to mate (Garcia *et al*., 2006). These suggest that sex association cannot be reliably made unless successful mating events, not pre-copulatory interactions, are observed.

In addition to the unpredictability of mating events, another impediment in obtaining pairs in copulation is that mating may take place very rapidly. For example, mating in *Dasymutilla* Ashmead and *Pseudomethoca* Ashmead species lasts less than two minutes (Waldren *et al*., 2020a). Contrarily, velvet ants practicing phoretic copulation, in which the male transports the female by flight during mating (see below), are more frequently found *in copula* in the field than any other species, presumably because of the long mating duration (Mickel, 1937a; Nonveiller, 1980b; Saxton, 2010; Shappirio, 1947; Waldren *et al*., 2020a).

The most obvious example of this situation is the subfamily Rhopalomutillinae. The females of this subfamily are mostly found *in copula* and most species are known from both sexes (Brothers, 2015). Therefore, sex association might be highly skewed for such taxa when based solely on examination of mating pairs.

Host association

Less frequently used biological information to associate sexes is coincidental emergence from the same hosts (rearing experiment; Cambra *et al*., 2005; Cameron, 1902c; Garcia *et al*., 2006; Gôukon, 1993; Hearn *et al*., 2019; Linsley & MacSwain, 1952; Lopez *et al*., 2019; Manley, 2003; Mickel, 1924ab; Nonveiller, 1996d; Péringuey, 1898; Pitts & Parker, 2005; Quintero & Cambra, 2001a, 2005). This kind of data is sometimes obtained by entomologists who are not specialized in velvet ants. Quintero & Cambra (2001a) observed emergence of males of *Dasymutilla melanogaster* (Cameron) from the host *Microbembex monodonta* (Say) pupae experimentally parasitized by females of *D. araneoides* (Smith) under the laboratory condition. Instead of rearing records obtained in the field, some authors used correlation of body size (large females for large males), which is determined by the host size (Mickel, 1924b), as supplementary evidence for sex association (e.g., Luz & Williams, 2014; Zhou *et al*., 2018b).

This method requires much more efforts in the field than any other methods for sex association. Although museum specimens with rearing data are rare, they can be easily obtained. Rearing records are sometimes referred to as reliable evidence of sex association. However, those data should be viewed with caution, because velvet ants usually utilize a wide variety of host species presumably to reduce costs for host search. It has been known that the host spectrum of this group of wasps is situation-specific rather than species-specific (see below). Therefore, host ranges of closely related species can largely overlap. Inexplicitly, sex association using coincidental emergence is based on the assumption that brood chambers from a single nest or a single nesting site of the host are parasitized by a single female or, at least, by a single species of velvet ants. Emergence of multiple velvet ant species from a single host nest has never been observed, but this assumption must be empirically tested. Also, sex association based on host-parasitoid relationship can be complicated because velvet ant females may allocate fertilized (female) eggs and unfertilized (male) eggs to different host species (Matthews, 1997; Pitts *et al*., 2010a), in order to produce sexual dimorphism in body size (see below). Therefore, for instance, females and non-conspecific males of comparable size can be bred from a single host species.

Co-occurrence

Distributional and occurrence data are frequently used to infer sex association. Based on museum specimens, many taxonomic papers have tried to establish sex association of male-based and female-based species collected in a single collecting event (at same place and time) (e.g., Cambra & Quintero, 2003b; Cambra *et al*., 2018, 2020; Deyrup & Manley, 1986b; Krombein, 1954; Lelej, 1976, 1995c; Lelej & Osten, 2004; Lelej *et al*., 2016; Pitts, 2007; Quintero & Cambra, 1996b, 2001a, 2005). Specifically, a species with geographically isolated distribution from other congeners is confidently associated (e.g., Brabant *et al*., 2010; Brothers, 1971b; Cambra *et al*., 2014; Luz *et al*., 2016b; Okayasu, 2020; Pitts, 2007; Williams *et al*., 2022; Zhou *et al*., 2018b). Recent studies argue that repeated sampling of males and females in an overlapping range is adequate evidence (Bartholomay *et al*., 2019ab, 2022; Luz & Williams, 2014; Luz *et al*., 2016b; Williams *et al*., 2022). Field works may yield important supplementary data for male-female association. Males are sometimes observed

flying low over nesting sites of potential hosts, presumably to locate mates because mating can take place soon after the emergence of females at nesting sites (see below). Females are found walking in the same sites to search for hosts. Observation of both sexes in a nesting site implies that they are conspecific. An interesting case is that Williams *et al*. (2019a) regarded males and females feeding together on flower nectar as a single species. No additional biological data were available for associating sexes.

Because velvet ants are generally restricted to certain habitats, several congeneric species can be found sympatrically. Co-occurrence records from multiple collecting sites are usually necessary for reliable sex association. Therefore, co-existence evidence is difficult to adopt if specimens from only a small number of localities are available. Another difficulty is that the sex ratio of collected specimens can be highly skewed depending on the collecting methods. Often only one sex is found during a single collecting event because, stemming from the sexual dimorphism, the behavioral habits are different between sexes. Males are usually collected in sweep nets or in Malaise traps, while females are manually collected or trapped in pitfall or yellow pan traps.

Morphology

Although males and females share almost nothing in common anatomically, some authors referred to morphological similarities between sexes to corroborate sex association based on other evidence. In addition to morphological characters associated with flight, there are a number of differences between male and female individuals, like body shape, coloration, setation, and punctation (Fig. 4). Universally useful characters, which are species-specific and shared by both sexes, have never been discovered. It is, however, uncertain if there are no shared morphological traits, because sex association has been made for only 2–3% of total species richness (Brothers, 1989). Various parts of the body have been used, e.g., body coloration and setae orientation (Brabant *et al*., 2010; Cambra & Quintero, 2003b, 2004; Lelej, 1995c; Lelej & van Harten, 2006; Pitts, 2007; Williams *et al*., 2011a), head shape (Lelej, 1992), presence of a spine on the hypostoma (Cambra & Quintero, 2003a), mouthparts (Brothers, 1971b), mandibular shape (Lelej, 1992, 1995a; Lelej & van Harten, 2006), oral foramen (Quintero & Cambra, 2001a), presence of denticles on mesosoma (Lelej & van Harten, 2006), tibial spurs (Brothers, 1971b; Quintero & Cambra, 2001a), first metasomal segment (Quintero & Cambra, 2001a), and pygidium (Quintero & Cambra, 2001a; Williams *et al*., 2022). Recently, Zhou *et al*. (2018b) extensively compared male and female morphology of the genus *Zavatilla* Tsuneki, which had one species in Taiwan, two species in southern China to northern Vietnam, and one species in Nepal. They argued that no male traits were found analogous to the female traits that were useful to define the genus, and *vice versa*. Contrarily, they recognized that the coarse sculpture on the head and mesonotum, presence of a narrow pale fringe or band on the posterior margin of the second metasomal tergum, and presence of a wide complete pale band on the third metasomal tergum are shared by both sexes of *Zavatilla*, in addition to the large body size. Zhou *et al*. (2018b) suggested that these three traits may potentially be useful in other genera. This idea should be tested based on more in-depth morphological analyses with broader taxon sampling.

Sex association on morphological basis should be viewed with caution, because there seems no apparent logical link between male and female morphology. An exceptional case would be sex association in taxa with apterous males (André, 1901–1902; Cambra & Quintero, 2007; Lelej & Brothers, 2008; Quintero & Cambra, 2001b). Another possibility is the similarity in the mandibular shape. Both males and females use mandibles to chew holes when emergence (Batra, 1965). Therefore, velvet ants parasitizing hosts in a hard capsule may have the robust mandibles in both sexes. However, the functional morphology of

mandibles in relation to host utilization is mostly unknown. Generally, males have more robust mandibles than females, presumably to hold a female during copulation. Contrarily, females have slender mandibles to tear host cells for oviposition (Brothers, 1972; Dodson, 1966; Krombein, 1964, 1967; Linsley & MacSwain, 1942; Matthews, 1997). It is also expected that related species share morphological similarities both in males and females. Therefore, a potentially useful application of morphological characters is to infer sex association from resemblance to a related, preferably sister species of which both sexes are known (e.g., Lelej & Osten, 2004; Luz & Williams, 2014; Okayasu, 2020; Pagden, 1949; Williams, 2023; Zhou *et al*., 2018b).

Gynandromorphic specimens

The most infrequently used method is examination of gynandromorphs. Gynandromorphs are defined as chimeric individuals of genetically male and genetically female tissues, displaying both male and female traits simultaneously (Narita *et al*., 2010). Gynandromorphic specimens, therefore, can be useful sources to associate sexes based on morphology. This phenomenon has been recorded for only 19 specimens of 17 species (Table 2), although some authors did not describe or illustrate the referred specimen. The apparent difficulty of this method is the rarity of gynandromorphic specimens; Nonveiller (1973) found two gynandromorphs out of 100,000 velvet ant specimens; Quintero & Cambra (1994) found two out 15,000 velvet ant specimens; József & Zoltán (2011) found two in 3,800 *Myrmilla calva* (Villers) specimens. Previous studies suggest that gynandromorphs possess reduced wings and an abnormal male genital organ instead of a sting, suggesting that they are vulnerable to predators. This makes gynandromorphic specimens even rarer. Additionally, gynandromorphs exhibit male and female traits in a mosaic pattern. Thus, their morphology can be different from normal specimens in some properties, making species identification difficult.

Molecular data

Molecular-based sex association is now widely adopted. For velvet ants, a molecular method was made available by Pilgrim & Pitts (2006) based on the internal spacer regions 1 and 2 (*ITS1* and *ITS2*) sequences in the nuclear ribosomal cistron. *ITS1* and *ITS2* regions were amplified with polymerase chain reaction (PCR) method using the PCR primers modified from Pilgrim *et al*. (2002) and Weekers *et al*. (2002). This method has been successfully employed in subsequent studies by Lelej *et al*. (2023), Pilgrim *et al*. (2008), Pitts & Wilson (2009), Pitts *et al*. (2007), William (2012), and Williams *et al*. (2011b, 2012, 2022). These studies found different morpho-species show genetic distances above 2%. Also, *ITS1* and *ITS2* regions have been used for molecular phylogenetic analyses and species delimitations (Pitts *et al*., 2010b; Williams, 2012; Wilson & Pitts, 2008, 2009, 2010ab, 2011; Wilson *et al*., 2012a).

In the DNA barcoding framework for German wasps, Schmid-Egger & Schmidt (2021) described two new velvet ant species, *Smicromyrme burgeri* Schmid-Egger (replaced by *S. frankburgeri* Schmid-Egger; Schmid-Egger & Schmidt, 2022) and *S. langobardensis* Schmid-Egger. These two species were described from both sexes associated on the basis of the mitochondrial cytochrome c oxidase I (*COI*) gene sequences. The *COI* gene is widely used DNA barcode region across animal taxa (Hebert *et al*., 2003). Schmid-Egger & Schmidt (2021) adopted standardized protocols developed by Ivanova *et al*. (2006) for PCR amplification. Their results, however, indicated primer mismatch.

Molecular sex association is believed to be the most reliable method. The major limitation of this method is the requirement of fresh samples for experiments. Historical type

specimens are generally too old and fragile to be included in molecular works. However, sadly, many velvet ant species are known from type series or old taxonomic papers only (Williams *et al*., 2019b). For example, velvet ants are represented by some 700 species in the Oriental Region, but roughly 70% of them were described before 1970 and have never been illustrated or included in modern keys (Okayasu *et al*., 2021a). Therefore, identification of newly collected materials often requires examination of historical types or direct comparison with authoritatively identified specimens based on morphology. Additionally, velvet ants are, despite of their species richness and population density (see below), usually collected in small numbers (Schmidt & Buchmann, 1986), presumably because of their cryptic habitats. Forest-inhabiting velvet ants are specifically rare in collections. Also, there may be a large gap in the number of specimens between sexes as discussed above. Application of multiple collecting methods makes field surveys time-consuming and effortful. These impediments inevitably limit the geographical extent and number of focused taxa for molecular sex associations.

Host choice

Velvet ants are parasitoids of immature insects. Parasitoids lay their eggs on or in the bodies of the hosts. Larvae consume a single host to develop, unlike many predators, and they eventually kill the host, unlike parasites (Godfray, 1994). Additionally, the female parasitoid wasp does not transport the hosts over a long distance and construct their own nests, while the female hunting (predatory) wasp prepares a concealed place or modifies an existing refuge to deposit prey items (O'Neill, 2001). This definition distinguishes parasitoids from predators, like most Pompilidae and a few apoid wasps, whose larva feeds on a single prey item (Evans & West Eberhard, 1970; O'Neill, 2001).

Although hosts are known for only limited number of species (Brothers, 1989), it is likely that most velvet ants utilize larvae, prepupae, and pupae of aculeate hymenopterans, including solitary hunting wasps (Apoidea: Astatidae, Bembicidae, Crabronidae, Pemphredonidae, Philanthidae, Sphecidae; Pompiloidea: Pompilidae; Vespoidea: Vespidae), solitary, subsocial, or eusocial bees (Apoidea: Andrenidae, Apidae, Colletidae, Halictidae, Megachilidae, Melittidae, Stenotritidae), and ectoparasitoids (hyperparasitism; Chrysidoidea: Chrysididae; Pompiloidea: Sapygidae; Scolioidea: Scoliidae; Tiphioidea: Tiphiidae) (Brothers *et al*., 2000; Lelej, 1985; Luz *et al*., 2016a; Ronchetti & Polidori, 2020). Additionally, some species utilize case-bearing leaf beetle larvae and pupae (Coleoptera: Chrysomelidae: Cryptocephalinae), oothecae of cockroaches (Blattodea: Corydiidae), moth pupae within hard cocoons (Lepidoptera: Limacodidae), and pupae and puparia of flies (Diptera: Glossinidae, Rhinophoridae, Sarcophagidae, Syrphidae, Tachinidae, Tephritidae) (Table 3). The common feature of those hymenopteran and other insect hosts is that immature individuals are enclosed in some kinds of packages, like brood chambers, cocoons, puparia, and oothecae (Brothers, 1989). Mickel (1974) reared three males of *Odontophotopsis eubule* (Cameron) from three cockroach oothecae. Mickel (1974) and Brothers *et al*. (2000) suggested that the larva of this velvet ant was a likely hyperparasitoid of an ensign wasp (Hymenoptera Evaniidae), because Mickel (1974) reared six individuals of *Evaniella neomexicana* (Cameron) from oothecae obtained in the same collecting event. This assumption is reasonable because velvet ants basically attack concealed hosts.

Because female velvet ants are wingless, they have a relatively narrow host searching range (Evans & Miller, 1969; Evans *et al*., 1973). Their major hosts are nest-provisioning wasps and bees, which exhibit great diversity in nesting ecology. Therefore, the host preference of velvet ants seems situation-specific, rather than host-specific; previous host records suggested that velvet ants utilize wide variety of host species sharing similar ecological properties and occurring in a certain habitat (Brothers, 1989; Taylor *et al*., 2019).

This is presumably an adaptation to reduce costs for host searching (Brothers, 1989). Additionally, the hosts should be at resting stages; complicated manipulation and nest-provisioning behavior is unnecessary to utilize them, unlike hunting wasps which show a wide array of foraging strategies (O'Neill, 2001). For instance, a nocturnal velvet ant, *Sphaeropthalma amphion* (Fox), was reared from various cavity-nesting wasps and bees of Crabronidae, Megachilidae, Vespidae, and their cleptoparasites and parasitoids of Chrysididae, Megachilidae, Sapygidae (Hymenoptera), and Sarcophagidae (Diptera), all of which are found in xeric regions of southwestern North America (Pitts *et al*., 2004). A common western Palaearctic species, *Mutilla europaea* Linnaeus, attacks 21 species of eusocial bees of the genus *Bombus* Latreille (Apidae) that construct their nest in the ground (Brothers *et al*., 2000; Lelej, 1985; Ronchetti & Polidori, 2020). The polyphagous host utilization inevitably results in large overlaps in host range among multiple velvet ant species sharing the same geographic ranges and habitats. A single host species can be parasitized by several species of velvet ants (Mickel, 1928; Taylor *et al*., 2019).

The ecology of velvet ant hosts is indeed variable. Many species utilize immatures of nest-provisioning wasps and bees in their underground nests. Few species in *Dasymutilla* Ashmead, *Myrmosa* Latreille, *Pagdenidia* Lelej, *Smicromyrme* Thomson, *Timulla* Ashmead, and *Trogaspidia* Ashmead were reared from cocoons of parasitoid wasps (Hymenoptera: Scoliidae, Tiphiidae, and Thynnidae) on scarab beetle larvae (Coleoptera: Scarabaeidae) in soil (Table 4). Species in some genera of Mutillinae and Sphaeropthalminae parasitize on nest-provisioners and their cleptoparasites or parasitoids in cavities in twigs or rotten woods, or mud-dauber wasps constructing arboreal nests. Most hymenopteran host records involve solitary wasps and bees. However, species in the Mutillini, Myrmillinae, and Pseudomethocini penetrate into social nests of bumble bees and sweat bees (Apidae: *Bombus* Latreille; Halictidae: *Lasioglossum* Curtis; Brothers *et al*., 2000; Luz *et al*., 2016a; Ronchetti & Polidori, 2020). Three species in *Stenomutilla* André utilize solitary bees constructing multicellular nests in empty snail shells (Megachilidae: *Hoplitis* Klug; Bogusch *et al*., 2020; Ferton, 1908, 1921).

Non-hymenopteran hosts belong to three holometabolous orders, Coleoptera, Diptera, and Lepidoptera. They are generally found in soil or in nests of bees and wasps as parasitoids. The *Seyrigilla* Krombein and *Stenomutilla* species were reared from hard cocoons of limacodid moth in soil or on a twig (Table 3). Five species in the *Physetopoda* Schuster, *Smicromyrme*, and *Stenomutilla* (species identification not confirmed; Brothers *et al*., 2000) are known as parasitoids of case-bearing larvae and pupae of camptosomate leaf beetles (Coleoptera: Chrysomelidae: Cryptocephalinae). The larvae of this beetle group construct a hard case made mainly of their own feces, which serves as a predator avoidance device and a pupation chamber (Chaboo *et al*., 2016). This condition makes them acceptable hosts for velvet ants. The cryptocephaline larvae and pupae are generally found in leaf litter and in ant nests (Agrain *et al*., 2015; Brown & Funk, 2005; Erber, 1988), both of which are parasitized by velvet ants. Additionally, Argaman (1988) observed a female of *Nanomutilla parila* (Nagy) carrying a prepupal case of *Pachybrachis scripticolis* Faldermann (Chryptocephalini). Argaman noted that this mutillid is "definitely associated to *Pachybrachys scripticollis* Faldane [sic!]", but he did not observe oviposition or rearing. Another *Nanomutilla* species, *N. vaucheri* (Tournier), is found in leaf litter (Romano, 2012). These records suggest parasitism of the *Nanomutilla* species to chrysomelid pupae in leaf litter. Dipteran hosts involve both primary parasitoid and hyperparasitoid species. In the course of intensive surveys of parasitoids of tsetse flies (Diptera: Glossinidae: *Glossina* Wiedmann) in southern Africa, three species of velvet ants were reared from puparia in soil (Brothers, 1971a): *Chrestomutilla auxilaris* (Turner), *C. glossinae* (Turner), and *Smicromyrme benefactrix* (Turner). The *Chrestomutilla* species are likely obligate parasitoids of tsetse flies. Similarly,

three *Smicromyrme* species, *S. ausonius* Invrea, *S. nikolskajae* Lelej, and *S. tekensis* Skorikov, were reared from puparia of plant-infesting flies, the ber fruit fly *Carpomya vesuviana* Costa (Tephritidae) and small bulb fly *Eumerus strigatus* (Fallén) (Syrphidae), which were found in soil (Amini *et al*., 2014, 2024; Lelej, 1978). Other dipteran hosts known to date belong to the Rhinophoridae, Sarcophagidae, and Tachinidae. They are parasitoids of as diverse as the true bug (Hemiptera: Pentatomidae), leaf beetle (Coleoptera: Chrysomelidae), weevil (Coleoptera: Curculionidae), nest-provisioning bee or wasp (Hymenoptera), and even woodlouse (Isopoda: Armadillidiidae). Non-hymenopteran host records are generally based on by-chance rearing. Host-searching and oviposition behavior is mostly unknown, presumably because of cryptic and unexpectable nature of non-hymenopteran hosts. Confirmed records, although restricted to the Dasylabrinae, Smicromyrmini, and Sphaeropthalmini (Table 3), suggest that a wide range of case-bearing hosts can be acceptable for velvet ants, irrespective of their feeding habits.

Uncovering host-parasitoid association is another challenge in velvet ant biology. Although female velvet ants are generally found running on the ground or tree branches, oviposition and development of immature stages take place in a hidden space. It is often necessary to excavate an underground nest or dissect a tree to collect parasitized hosts. Direct evidence of parasitism, i.e., emergence of an adult from a host or observation of actual oviposition by a female, are often obtained by entomologists working on nesting habits of wasps and bees (e.g., Batra, 1965; Evans, 1957; Evans & O'Neill, 1988, 2007; Ferton, 1923; Krombein, 1967). Such solid evidence is available for roughly 2.6% of valid species worldwide (Ronchetti & Polidori, 2020, updated). Hosts of the rest of species were inferred from observation of adult behavior or temporal and spatial distribution of adult individuals. Specifically, observation of females intruding host nests has been considered strong evidence of parasitism; host records based on such observation were even regarded as confirmed ones in the recent review by Ronchetti & Polidori (2020). In addition to observation of nest intrusion *per se*, remnants adhering to the body surface of adults may imply the potential hosts. For example, pollens and dirt suggest parasitism on bees and ground-nesting hosts, respectively (Krombein, 1992). Table 5 summarizes known host-parasitoid associations and evidence for East Asian velvet ants.

Parasitism

Even within parasitoid wasps, there is great variation in their strategy, e.g., the number of immatures developing on a single host (solitary or gregarious), location of the larva (ectoparasitoid or endoparasitoid), timing when the larva starts consumption (idiobiont or koinobiont), and selection of parasitoids as hosts (primary parasitoid or hyperparasitoid) (Gauld & Bolton, 1988; Godfray, 1994; Polaszek & Vilhelmsen, 2023). Typically, velvet ants are solitary, idiobiont, and primary ectoparasitoids; an adult female lays a single egg on the outside of each host body to feed her offspring. When utilizing wasp or bee immatures as hosts, females select fully fed (post-defaecating) immatures, which finished consumption of provisions in the brood chamber (Hook & Evans, 1991; Houston & Thorp, 1984). However, Ordway (1964) found a velvet ant larva parasitizing on a pre-defaecating host. Velvet ant larvae crawl within the brood chamber (Batra, 1965; Janvier, 1933). Therefore, they are able to consume the entire contents, including the provisions; Wille & Orozco (1970) observed a larva of *Pseudomethoca willei* Mickel feeding on pollen deposited by the host adult. In laboratory settings, the larvae of *Dasymutilla* Ashmead and *Sphaeropthalma* Blake feed on additional food after consumption of the host (Cottrell in Brothers, 1972; Ferguson, 1962), but this was not the case for *Pseudomethoca* Ashmead (Brothers, 1972).

An exceptional mode of parasitism was reported by Krombein & Norden (1996). An

adult female of *Ephuta slossonae slossonae* (Fox) fed on the egg of the host spider wasp (Pompilidae) and placed an egg on the host's prey spider. Although the egg was killed for observation, the larva of this species would utilize the provision of its host, i.e., cleptoparasitism. The egg of this species was inserted between layers of muscle tissue of the spider. Other *Ephuta* species are also associated with pompilid hosts (Cambra *et al*., 2017; Deus *et al*., 2023; Evans & Yoshimoto, 1962; Kimsey, 1980; Loyola & Martins, 2006; Schuster, 1951, 1957; Zanette *et al*., 2004). However, it is unknown if they are obligate cleptoparasites.

Females generally detect a host that has already been parasitized (Cottrell in Brothers, 1972), but Katayama (2008) observed a female of *Mutilla mikado* which was unable to recognize parasitized hosts and laid an additional egg on them. Several eggs can be laid on a single host at the same time probably in error (Batra, 1965; Brothers, 1972; Ferguson, 1962; Heaversedge, 1969c; Katayama, 2008; Su *et al*., 2019; Wille & Orozco, 1970; Williams, 1919). In this case, the earliest hatching larva consumes the entire host and siblings (Brothers, 1972; Ferguson, 1962; Heaversedge, 1969c). Exceptions are three species of the genus *Aglaotilla* Brothers from Australia, *A*. *chalcea* Taylor, Murphy, Hitchen & Brothers, *A*. *ignita* (Smith), and *A*. *submetallescens* (Turner). Brothers (1984) and Taylor *et al*. (2019) reported that up to four individuals of these species had completed their development on a single host wasp (gregarious parasitism).

Most velvet ants directly utilize non-parasitoid insects (primary parasitoid). Some species have been recorded as hyperparasitoids of insect parasitoids, including velvet ants (hyperparasitoid; Table 4). The species in the genera *Ephucilla* Lelej (or *Promecilla* André), *Pseudomethoca* Ashmead, and *Sphaeropthalma* Blake are facultative ("accidental") hyperparasitoids. They are basically primary parasitoids of wasps and bees, but they act as hyperparasitoids only when the host had already been parasitized by a larva of a cleptoparasitic or parasitoid bee (Apidae and Megachilidae) or wasp (Chrysididae and Sapygidae). If a velvet ant larva is attacked by another individual of the same species, this phenomenon is specifically called superparasitism (Gauld & Bolton, 1988; Godfray, 1994). Contrarily, some species in the genera *Dasymutilla* Ashmead, *Myrmosa* Latreille, *Odontophotopsis* Viereck, *Pagdenidia* Lelej, *Physetopoda* Schuster, *Smicromyrme* Thomson, *Timulla* Ashmead, and *Trogaspidia* Ashmead are obligate ("intentional") hyperparasitoids of ectoparasitic wasps or endoparasitic flies (Table 4). Unlike facultative hyperparasitoids, those species and their hosts do not share the same primary hosts species. Most of the obligate hyperparasitoid records involve parasitoid wasps of the families Scoliidae, Tiphiidae, and Thynnidae on scarab beetles (Coleoptera: Scarabaeidae). Three species, *Physetopoda pusilla* (Klug), *Smicromyrme asiaticus* Lelej, and *S*. *ausonius* Invrea, are hyperparasitoids of endoparasitic flies of the families Rhinophoridae and Tachinidae on a stink bug (Hemiptera: Pentatomidae), a leaf beetle (Coleoptera: Chrysomelidae), a weevil (Coleoptera: Curculionidae), and a terrestrial isopod (Isopoda: Armadillidiidae). *Odontophotopsis eubule* is a likely hyperparasitoid of an ensign wasp in a cockroach oothecae as mentioned above. The situation-specific host choice is probably the case for hyperparasitic velvet ants, because *D*. *bioculata* (Cresson), *P*. *pusilla*, and *Trogaspidia castellana* (Mercet) prey upon primary parasitoids from two families. Interestingly, primary parasitoids in those genera are associated with nest-provisioning wasps and bees, and *D*. *bioculata* and *D*. *quadriguttata* (Say) utilize both nest-provisioners and parasitoids (Ronchetti & Polidori, 2020). Likewise, some species in *Physetopoda* and *Smicromyrme* attack leaf beetle immatures and puparia of fruit-infesting flies (Table 3). This suggests that hyperparasitism is not mandatory for those velvet ants. Rather, they more likely choose parasitoids encountered in their host-searching range and located by odors which are similar to their "normal" hosts.

Obtaining parasitism rate is not an easy task but is important to evaluate the impact of

velvet ants on hosts. Records suggest velvet ants intensively utilize host individuals found in a habitat, leading to high parasitism rate up to 79% (Abe, 1932; Bergamaschi *et al*., 2011; Brothers, 1978; Chorley, 1929; Garófalo *et al*., 2011; Gôukon, 1993; Hearn *et al*., 2019; Katayama *et al*., 1996; Lamborn, 1916; Markham, 1986; Roubik, 1990; Sakagami & Katayama, 1977; Schmidt & Buchmann, 1986; Su *et al*., 2019). They may even collapse a nest aggregation of the host species (Brothers *et al*., 2000; Evans, 1974; Gôukon, 1993; Lin & Michener, 1972; Michener, 1966), and Lin (1964) hypothesized that parasitism by velvet ants was a major driving force of social behavior in halictine bees (Hymenoptera: Halictidae).

Diversity and abundance

Velvet ants are comprised of approximately 4600 species in 225 genera worldwide (Pagliano *et al*., 2020, updated). Most species are classified in the Mutillidae, making it one of the largest aculeate families (Aguiar *et al*., 2013; Pulawski, 2016). However, as noted above, a majority of velvet ant species is known from only one sex because of difficulties in sex association caused by extreme sexual dimorphism, and thus many species might eventually be synonymized after sex association. Yet, the true species diversity of velvet ants is likely much higher than presently recognized. Brothers (1989) estimated the total number of species to be 8,000. Systematists often recognize undescribed species that exceeds the described species in number (Okayasu, 2020, 2021; Okayasu *et al*., 2021ab; Tu *et al*., 2014a; Waldren *et al*., 2020b; Williams *et al*., 2019b; Zhou *et al*., 2018b). The late Guido Nonveiller undertook intensive field surveys in Cameroon during 1962 to 1975, which resulted in 120,000 specimens representing 420 species. Of the 420 species recognized, at least 60% were undescribed (Nonveiller, 1980ab). This is surprising given that only 37 species had been recorded from that country before 1962 even though Bischoff (1920–1921) extensively reviewed the African fauna of velvet ants. Similarly, the Australian fauna has been poorly surveyed, with 230 species and subspecies (Brothers, 2022, including Tasmania). However, at least 700 species had been collected by 1983 and about 70% of them were undescribed (Brothers in Taylor, 1983). These examples clearly indicate that the diversity of velvet ants is much higher than presently recognized. To be fair, it should be noted that recent taxonomic revisions demonstrated many named forms were mere color variants of a single polymorphic species in the Dasymutillini (Bartholomay *et al*., 2019ab, 2020, 2021, 2022; Pilgrim *et al*., 2008, 2009; Williams *et al*., 2011b). Actually, velvet ants often vary considerably in size and color (Brothers, 1989). Multifaceted assessment of species validity is needed to elucidate the true diversity of velvet ants (e.g., Williams *et al*., 2011b).

Although the species richness of velvet ants has been long appreciated, the population density has been underestimated (Pitts *et al*., 2010b; Schmidt & Buchmann, 1986). The nests of aculeate wasps and bees, which are the main hosts of velvet ants, are widely dispersed in the field (Brothers, 1989; O'Neill, 2001). Velvet ants had been considered rare and sparsely distributed insects (Manley & Pitts, 2007; Pitts *et al*., 2010b; Schmidt & Buchmann, 1986). It is, however, evidential that the abundance and density of velvet ants, as well as the species richness, are likely much higher than generally assumed (da Cunha, 2004; Evans, 1957; Fattig, 1936; Flores *et al*., 2004; Jellison, 1982; Linsley *et al*., 1955; Manley & Pitts, 2007; Manley & Taber, 1978; Mickel, 1928, 1938; Nonveiller, 1987; Pitts *et al*., 2010b; Remington, 1944; Riddick, 1991; Schmidt & Buchman, 1986; Schmidt & Hook, 1979).

Schmidt & Buchman (1986) collected parasitoids of the ground-nesting bee *Diadasia rinconis rinconis* Cockerell (Hymenoptera: Apidae) using three 90 × 90 cm emergence traps in a nest aggregation in Arizona, USA. In total, 92 males and one female of *Dasymutilla foxi* (Cockerell) (Sphaeropthalminae: Dasymutillini) were trapped. Because females can flee from the trap by crawling or digging under the trap rim, the true number of individuals would be

184 in 2.4 m^2 trap area, assuming the sex ratio to be 1:1. A single nest of *Diadasia rinconis rinconis* contained seven brood chambers on average and the average nesting density was 25 nests/m^2. Therefore, a 2.4 m^2 trap area included roughly 420 brood chambers of the host bee, of which 184 (43.8%) were parasitized by *D. foxi*. The nest aggregation covered 446 m^2, which produced approximately 78,000 chambers in 11,150 nests. Thus, this study site potentially contained 34,000 velvet ant individuals, or 76 individuals/m^2.

Although quantitative accounts of velvet ant density are rare, additional collecting records suggest high population density and abundance in various habitats. In southwestern USA, a single light trap attracts 500 to 1,000 male specimens of nocturnal velvet ants (Pitts *et al*., 2010b; Wilson *et al*., 2010b). Schmidt & Hook (1979) collected 263 females of *Pseudomethoca simillima* (Smith) in 1.5 hours. In Kenya, Nonveiller (1987) collected 200 females of two species in a few square meters area on a beach of Lake Nakuru in one to two hours. Jellison (1982) located 4,000 to 10,000 velvet ants in a vacant lot. Jellison in Krombein (1992) located 6,000 to 7,000 males of *P. propinqua* (Cresson) and, more surprisingly, females outnumbered the males ten to one. Manley & Taber (1978) estimated the population size of *Dasymutilla foxi* in a 1,300 m^2 study site to be approximately 6,000. All these observations were made in open habitats, like deserts, beaches, or vacant lots, where ground-dwelling females and mate-searching males are readily noticeable. This gives impression that velvet ants are more abundant in dry open environments (Brothers, 1995, 2006). Contrarily, velvet ants are difficult to collect in forested habitats, because females can be arboreal or found in leaf litter and males can be collected by sweeping the bushes. Additionally, host bees and wasps generally do not form large nesting aggregations in forests. These hamper quantitative observation, collecting, and estimation of parasitism rate in forests. However, velvet ants seem greatly abundant and species-rich in forested habitats as well (Brothers, 1995; Okayasu *et al*., 2021b).

Host bees and wasps for velvet ants are important agents for pollination and pest control (Brock *et al*., 2021; Klatt *et al*., 2014; Klein *et al*., 2007). In some cases, velvet ants utilize plant or medical pest dipterans, like ber fruit flies and tsetse flies (Table 3). Velvet ants thus potentially play an important role in ecosystem (Pitts *et al*., 2010b). It is thus desired to assess diversity and abundance of velvet ants and their effects to other organisms through quantitative collecting methods, like yellow pans, pitfalls, and Malaise traps (e.g., Aranda & Graciolli, 2016; Vieira *et al*., 2017).

Mating

Reproductive success is a vital part of fitness. Male wasps and other insects employ various strategies in response to intrinsic and extrinsic conditions (O'Neill, 2001; Thornhill & Alcock, 1983). Even though mating behavior in velvet ants has ever been observed for the sake of sex association, comprehensive accounts have never been done until Brothers (1989) and Waldren *et al*. (2020a).

Female solitary wasps are receptive to mating soon after emergence (O'Neil, 2001). Generally, female velvet ants are monandrous (monogamous); a single mating event is enough to pass sperm that a female needs for an oviposition (or ovipositions throughout her life). Many authors observed that attractiveness of a female to males diminished rapidly after mating and males could not force an unreceptive female to mate (Bayliss & Brothers, 1996, 2001; Bergamaschi *et al*., 2011; Brothers, 1972, 1978; Callan, 1977; Deyrup & Manley, 1990; Garcia *et al*., 2006; Linsley *et al*., 1955; Manley & Neff, 1989; Mickel, 1938; Quintero & Cambra, 1996b; Tomberlin, 1997; Tormos *et al*., 2010), although multiple mating cannot be ruled out yet (Bergamaschi *et al*., 2010; Cambra *et al*., 2020; Ferguson, 1962). Male velvet ants, therefore, search and compete for females at an emergence site (Brothers, 1972; Callan,

1977; Jellison, 1982; Manley & Neff, 1989; Manley & Taber, 1978; Mickel, 1938; Pouvreau, 1973; Rocha-Filho & Melo, 2011; Saxton, 2010; Zillikens & Steiner, 2019). Males fly low over the emergence site (Alicata *et al*., 1974; Bergamaschi *et al*., 2010, 2012; Bohart & MacSwain, 1939; Brothers, 1972; da Cunha, 2004; Dubitzky *et al*., 2005; Dutt, 1912; Evans, 1957; Evans & Rubink, 1978; József & Zoltán, 2011; Krombein, 1954; Krombein & Evans, 1955; Manley & Neff, 1989; Rau, 1922; Rocha-Filho & Melo, 2011) and detect receptive females by chemical cues (Cambra & Quintero, 1993; Quintero & Cambra, 1996b; VanderSal-Jensen *et al*., 2016). In close proximity, visual cues may be also used (Linsley *et al*., 1955; Manley, 1977). Upon mating, multiple males can be attracted to a single female, resulting in intensive male-male competition (scramble competition: Brothers, 1989; Fattig, 1936; Jellison, 1982; Krombein, 1992; Matteini Palmerini, 2013; Polidori *et al*., 2013a; Quintero & Cambra, 2001a; Tormos *et al*., 2010).

Copulation modes of velvet ants are classified into two major categories, namely in-situ copulation and phoretic copulation (Waldren *et al*., 2020a). In-situ copulation occurs at or near the site of initial contact between a male and a female, and completes very rapidly (few seconds to five minutes) (Batra, 1965; Brothers, 1975, 1995; Cambra *et al*., 2020; Cazier & Mortenson, 1965; Hurd, 1951a; Krombein & Evans, 1954; Manley, 1977; Manley & Deyrup, 1989; Manley & Pitts, 2007; Mickel, 1938; Miyamoto, 1959; Rau, 1922; Remington, 1944; Shappirio 1947, 1948; Tomberlin, 1997). An alternative mode of copulation is phoretic copulation, in which a male transports a female counterpart (phoront) in flight or by foot during copulation (Azevedo *et al*., 2016; Brothers, 1989; Evans, 1969; Osten, 1999; Vivallo, 2020; Waldren *et al*., 2020a). Two subtypes of phoretic copulation are found in velvet ants: terminalic phoretic copulation and mandibular phoretic copulation (Waldren *et al*. 2020a). In terminalic phoretic copulation, phoresy is activated by holdfast mechanism of the male genitalia and surrounding structures (e.g., sternum). This subtype is found in the Myrmosidae and Rhopalomutillinae only. Male velvet ants practicing mandibular phoretic copulation seize the female in her pronotal neck with their mandibles prior to copulation; then holdfast mechanism is reinforced by the male genitalia and by legs (Alicata *et al*., 1974; Cambra & Quintero, 1993; Cambra *et al*., 2018; Crèvecoeur, 1930; Krombein & Norden, 1996; Linsley, 1960; Pagden, 1934a; Polidori *et al*., 2013a; Sheldon, 1970; Tormos *et al*., 2010; Waldren *et al*., 2020a). Phoretic copulation is a splendid male tactics and known from four subfamilies in the Mutillidae and one subfamily in the Myrmosidae. However, the adaptive value of this behavior is not fully elucidated. Phoretic copulation is analogous to mating flight in apoid wasps and bees, in which both male and female individuals have functional wings and attempt to disperse by flight (Vivallo, 2020). Phoretic copulation and mating flight are likely adaptations to avoid interference by predators and rival males during copulation (Lin, 1966; Rutowski & Alcock, 1980; O'Neill & Evans, 1983; Roig-Alsina, 1993; Thornhill & Alcock, 1983; see Chapter 5).

For species practicing phoretic copulation, male adults need to be larger than females to efficiently carry them (Brothers, 1989; Deyrup & Manley, 1986a). Velvet ants, like other hymenopterans, have haplodiploid sex determination system (Gauld & Bolton, 1988; Heimpel & de Boer, 2008), in which diploid females develop from fertilized eggs and haploid males develop from unfertilized eggs. This system allows female wasps to choose which sex to produce. Body size of adult velvet ants correlates with the amount of food supplied to the larva, that is, the size of the host individual (Brothers, 1989; Ferguson, 1962; Fiedler & Kluge, 1954; Hearn *et al*., 2021; Heaversedge, 1968; Mickel, 1924b), a common pattern across the animal kingdom known as Harrison's rule (Harrison, 1915; Lim *et al*., 2022; Salt, 1941). Consequently, female velvet ants can control the size of her offspring through host choice. Clear examples were given by Matthews (1997) and Pitts *et al*. (2010a) using *Sphaeropthalma pensylvanica* (Lepeletier) as a model system. In their studies, male

individuals were reared from larger hosts and female individuals from smaller hosts, suggesting facultative size-dependent sex allocation.

Defense

Predation offers strong selective force to prey animals, as it may greatly decrease future fitness and even eliminate the local prey population (Brodie *et al*., 1991; Edmunds, 1974; Lima & Dill, 1990). Natural selection imbues prey with a broad range of defensive behavioral, physiological, and morphological adaptations in response to predation (Sugiura, 2020). Six stages are recognized in a predation process: (1) encounter, (2) detection, (3) identification, (4) approach, (5) subjugation, and (6) consumption (Endler, 1991; Ruxton *et al*., 2018). The former four are called pre-contact predation sequence and the latter two are called post-contact predation sequence (Ruxton *et al*., 2018). Defense mechanisms are classified into two categories, namely the primary defense, which functions during pre-contact predation sequence and is present irrespectively of the presence of a predator, and the secondary defense, which is activated during post-contact predation sequence (Edmunds, 1974; Ruxton *et al*., 2018). A similar concept was proposed by Brodie *et al*. (1991), who separated defense mechanisms into the predator avoidance mechanisms, which reduce the probability that the prey is targeted by a predator, and the antipredator mechanisms, which reduce the probability that the predatory sequence is completed.

Female velvet ants likely spend a long time searching for the hosts throughout their lifespan (Batra, 1965; Mickel, 1928). Most species are diurnal, and fast-moving females may be salient to predators. Nevertheless, they are unable to escape from predators by flight. Further, females are long-lived but have low fecundity (Brothers, 1972, 1989; Danforth, 1991; Evans & Miller, 1969; Heaversedge, 1969c; Knerer & Atwood, 1967; Schmidt, 1978). These features make velvet ant females susceptible to predation (Schmidt, 2016; Schmidt *et al*., 2021). Investment in defense mechanisms against predators may significantly increase their fitness. Actually, they are endowed with a large repertoire of primary and secondary defense mechanisms, deserving the name “the indestructible insect” (Gall *et al*., 2018). This feature inspired the late Justin Schmidt (1947–2023), a naturalist enthusiastic about the defensive mechanisms of wasps and bees, resulting in a classic paper “Adaptations and responses of *Dasymutilla occidentalis* (Hymenoptera: Mutillidae) to predators” (Schmidt & Blum, 1977). Ever since Schmidt, the female defense against potential predators has been one of the major research topics in velvet ant biology. Contrarily, males have been neglected in this context. Therefore, the review presented below is mostly dedicated to antipredator and predator avoidance mechanisms in females.

Sting and venom injection

The principal defense mechanism is the stinger to inject venoms. This organ is a weaponized ovipositor and functions as a venom-injection apparatus to paralyze prey (for nest-provisioning wasps) and deter predator attacks (Kumpanenko *et al*., 2019). Venoms of aculeate wasps exert multiple functions; a wide variety of components, like peptides, proteins, etc., inflict pain and cause cellular toxicity to predators or produce paralysis to prey (O’Neill, 2001; Schmidt, 2019). The ability to induce pain plays a key role in antipredator defense (Schmidt, 1990). Pain warns the envenomated animal of the potential damage and compels it to release the prey or to flee (Schmidt, 1990, 2019).

Even though toxicity (measured as LD_{50}) of venoms produced by velvet ants is low when compared to social wasps (Sadler *et al*., 2018, 2021; Schmidt *et al*., 1980, 1984, 1986, 2021), the sting of female velvet ants is notoriously painful (Schmidt, 2016, 2019; Starr,

1985). It causes physical damage and injects membrane-targeting peptides (Jensen *et al*., 2021). The sting apparatus of velvet ants is the longest amongst stinging wasps, ants, and bees in relation to their body size (Sadler *et al*., 2018; Fig. 5) and additional morphological changes permit to accommodate it in the metasoma (Hermann, 1968; Kumpanenko *et al*., 2022). Because the stinger only shallowly penetrates the skin, the long sting of velvet ants has likely been selected to facilitate active resistance against predators.

Experiments using vertebrate predators have repeatedly shown that the stinger is an effective antipredator device (Carpenter, 1921; Gall *et al*., 2018; Manley, 1984, 2000; Schmidt & Blum, 1977; Schmidt *et al*., 2021; Vitt & Cooper, 1988). Even after swallowed by toads, female velvet ants can trigger regurgitation and return to normal activities (Mergler & Gall, 2020).

Biting

When distressed, female velvet ants actively resist using their sting as a primary weapon (Gall *et al*., 2018; Manley, 1984, 2000; Mergler & Gall, 2020; Schmidt & Blum, 1977; Vitt & Cooper, 1988), but Manley (2000) noted that the strongly sclerotized mandibles are also capable of breaking the human skin and causing pain.

Exoskeleton

The exoskeleton of females is heavily sclerotized and extraordinarily tough. Schmidt & Blum (1977) measured the force required to crush various body parts of dried insect specimens belonging to the families Apidae, Mutillidae, Scoliidae, Vespidae (Hymenoptera), Curculionidae, Lucanidae, and Scarabaeidae (Coleoptera). They found that the thorax is the toughest part of the body and compared crushing forces applied dorso-ventrally to that region. They demonstrated that the velvet ant *Dasymutilla occidentalis* (Linnaeus) was the toughest insect utilized in this trial, which required 11 times more force than the honeybee (27.8 ± 5.3 N vs. 2.44 ± 0.36 N). Comparing the force per gm dry weight, *D. occidentalis* was the second toughest, falling just short of the pitch eating weevil *Pachylobius picivorus* (Germar) (247.0 ± 47.0 N/gm vs. 284.0 ± 73.0 N/gm). The exoskeleton of *D. occidentalis* is strong enough to resist against bite-force of most insectivorous birds and lizards (Corbin *et al*., 2015; Isip *et al*., 2022; Masson *et al*., 2023; Tan *et al*., 2021). Schmidt & Blum (1977) further suggested that the external integumentary parts of this velvet ant species were rounded and slippery, which offers protection by making the manipulation by predators (and entomologists) difficult. The tough and slippery exoskeleton provides a chance for subjugated females to stridulate and sting in the predator's mouth (Schmidt & Blum, 1977). This feature was recently termed "capture tolerance" and considered a potentially important component of aposematism (Sherratt & Stefan, 2024).

It is obscure which properties contribute to the strong exoskeleton of velvet ant females. Females seem to have the exoskeleton thicker than other wasps of comparable size. They generally lack the mesosomal sutures, forming a strongly sclerotized box-like mesosoma (Reid, 1941). The integuments are intensively sculptured with numerous punctures, reticulations, rugosities, ridges, and carinae. Deyrup (1988) considered surface sculpturing reinforces the exoskeleton without adding extra weight. These features undoubtedly serve to strengthen the exoskeleton.

Tonic immobility

Tonic immobility, also known as thanatosis or death feigning, is a defense mechanism in

which a prey individual adopts a motionless posture triggered by physical contact or close proximity of a predator (Humphreys & Ruxton, 2018). Deyrup (1988) stated, somewhat anecdotally, that "At least some species in these genera [*Dasymutilla*, *Timulla*, *Pseudomethoca*, and *Ephuta*] and in the genus *Photomorphus* feign death, curling up motionless when the sand or litter is sifted." (square brackets by me). Additionally, this behavior has been observed in diurnal velvet ants *Ephuta scrupea* (Say), *E. spinifera* Schuster, *Odontomutilla jaferpaloti* Terine & Kumar, *Smicromyrme lewisi* Mickel, and *S. rufipes* (Fabricius) (Krombein, 1958; Krombein & Evans, 1955; Oehlke, 1974; Terine & Kumar, 2024; Yoshikawa, 1965). Contrarily, Krombein & Evans (1955) noted that *Ephuta sabaliana sabaliana* Schuster did not adopt tonic immobility when approached or disturbed by the collector. This is indicative of interspecific variation of this behavior. Wilson *et al*. (2010b) observed some nocturnal females of the genera *Odontophotopsis* Viereck and *Sphaeropthalma* Blake were induced to immobile state when lights were shone on them. Williams *et al*. (2024) illustrated *Sphaeropthalma* females immobilized on the ground. Tonic immobility is thus known from nine Old World or New World genera in three subfamilies (Mutillinae, Odontomutillinae, and Sphaeropthalminae). This suggests that this behavior is likely widespread taxonomically and geographically within the Mutillidae.

Tonic immobility involves several defensive mechanisms (Humphreys & Ruxton, 2018; Miyatake *et al*., 2009; Rogers & Simpson, 2014). As is always the case with adaptive evolution, tonic immobility reflects conditions where cost-benefit trade-off favors it over alternative defenses, most obviously fleeing (Humphreys & Ruxton, 2018). Although tonic immobility is likely a simple defense to evolve since it does not need specialized morphological adaptations (Humphreys & Ruxton, 2018), recent studies demonstrated that tonic immobility was subject to trade-offs (e.g., Nakayama & Miyatake, 2010). Regarding cost-benefit relationships, it is notable that velvet ants employ tonic immobility, because this may hinder fleeing or active resistance against predators by delaying behavioral responses or by reducing the effectiveness of the defenses as a result of evolutionary trade-offs. In theory, organisms (species or certain life stages) that are less able to use fleeing or active resistance are more likely to use tonic immobility (Humphreys & Ruxton, 2018). It is unclear how tonic immobility confers protection on velvet ants, because this behavioral response has never been observed in previous experiments using predators (Carpenter, 1921; Gall *et al*., 2018; Manley, 1984, 2000; Manley & Sherbrooke, 2001; Masters, 1979; Mergler & Gall, 2020; Punzo, 1991; Schmidt & Blum, 1977; Schmidt & Schmidt, 2022; Schmidt *et al*., 2021; Sexton, 1964; Vitt & Cooper, 1988).

Stridulation

Stridulation is sound emission by arthropods activated by rubbing two specialized surfaces of the exoskeleton (stridulatory organ; Ewing, 1989; Tschuch & Brothers, 1999). Both male and female velvet ants can produce audible sound by stridulation. The stridulatory organ in velvet ants consists of a file, a transversely striated region located antero-medially on the third tergum, and a scraper, a thicker portion of the posterior edge of the second tergum. Some earliest authors recognized that velvet ants emit sound from the metasoma (reviewed by Mickel, 1928). Detailed descriptions of this device and stridulatory sound appeared only after appropriate equipment was made available (Genise & Straneck, 1991; Hermann & Mullen, 1974; Hinton *et al*., 1969; Masters, 1979; Polidori *et al*., 2013bc; Schmidt & Blum, 1977; Spangler & Manley, 1978; Torrico-Bazoberry & Muñoz, 2019; Tschuch, 1993, 1994; Tschuch & Brothers, 1999, 2000). The stridulatory organ is present in most velvet ants. However, this structure is secondarily lost in some myrmosids and rhopalomutilline females (Brothers & Lelej, 2017; Krombein, 1979; Tschuch & Brothers, 2000). Comparative analyses by above

mentioned authors revealed sexual dimorphism and inter-specific variation in the file morphology and acoustical traits. Velvet ants stridulate when distressed (Bohart & MacSwain, 1939; Mickel, 1928; Osten, 1992; Rau, 1922; Schmidt & Blum, 1977), during copulation (Alicata *et al*., 1974; Bergamaschi *et al*., 2010; Oehlke, 1974; Spangler & Manley, 1978; Tomberlin, 1997; Tormos *et al*., 2010; Tschuch & Burger, 1994), and even while walking on the ground (Bohart & MacSwain, 1939; Shappirio, 1948, 1949; Swinton, 1878), suggesting functions as warning signal and inter-sexual communication.

Some experimental studies demonstrated defensive function of stridulation. Masters (1979), Schmidt & Blum (1977), and Schmidt *et al*. (2021) observed predator-prey interactions in captivity using arthropod and vertebrate predators. They found that velvet ants successfully interrupted predation events by stridulating. Pekár *et al*. (2020) tested if stridulation of the nocturnal spider *Palpimanus gibbulus* Dufour (Araneae: Palpimantidae), a potential Batesian visual mimic of velvet ants, was used as an anti-predator defense due to acoustic mimicry of co-occurring velvet ants. Their results showed that 1) stridulation positively influenced survival rates of the spiders against potential predators and 2) the spiders and velvet ants shared acoustic characteristics. Cambra *et al*. (2021) suggested that stridulation is a defensive strategy to warn potential predators during mating and host searching.

Fleeing

Females lack the flight muscles as well as the wings, which accounts for 23–26% of body mass in spider wasps (Marden, 1987) and 10–20% for most insects (Greenewalt, 1962). The reduction of flight muscles may allow investment in ambulatory muscles, providing better digging ability (Evans, 1969; Vivallo, 2020) and fleeing ability (as in tiger beetles: Kamoun & Hogenhout, 1996). Velvet ant females are thus generally fast-moving (ca. 0.33–0.50 km/hour; Mellor, 1927; Schmidt & Blum, 1977) and employ erratic dash to escape (Deyrup, 1988; Manley, 2000; Schmidt & Blum, 1977). Also, the lack of flight muscles provides more space for muscles that are inserted into the metasoma (Peeters *et al*., 2020: Fig. 8), which enables more flexible movement of the metasoma in order to lay an egg in a limited space and to actively resist an attack of predators with a stinger.

Lurking

When approached by predators, velvet ants often lurk in substrates (Bayliss & Brothers, 1996; Deyrup, 1988; Oehlke, 1974), such as an existing hole like the underground nest of bees and wasps (Bayliss & Brothers, 1996; Nagy, 1968; Rau, 1922), and under the bush (Janvier, 1933; Oehlke, 1974; Williams *et al*., 2024).

Alarm chemical secretion

Female velvet ants release alarm chemicals from the mandibular gland into the air (Fales *et al*., 1980; Schmidt & Blum, 1977), which elicit a pungent odor (Manley, 2000). Alarm chemicals include 4-methyl-3-heptanone, 4,6-dimethyl-3-nonanone, and 4,6-dimethyl-3-octanone, ketons known as alarm pheromones of ants (Blum & Brand, 1972; Blum *et al*., 1968; Crewe & Blum, 1972; Duffield & Blum, 1973; Fales *et al*., 1972; McGurk *et al*., 1966; Moser *et al*., 1968; Riley *et al*., 1974), aversive chemicals of harvestmen (Opiliones: Phalangiidae) (Blum & Edgar, 1971; Jones *et al*., 1976, 1977; Meinwald *et al*., 1971), or structurally similar to those ketons (Fales *et al*., 1980). An aversive chemical (4-methyl-3-heptanone) of harvestmen was found to be effective in avoiding ants (Blum & Edgar, 1971),

so Fales *et al*. (1980) speculated that alarm chemicals of velvet ants were used against ants. In fact, ants did exhibit aversion or alarm behavior to filter paper flags impregnated with 4-methyl-3-heptanone and 4,6-dimethyl-3-nonanone (Fales *et al*., 1980; Schmidt & Blum, 1977). The latter authors also found that 4-methyl-3-heptanone generally elicited aversion of vertebrate predators. Alarm chemicals are present at least in species from two subfamilies, Sphaeropthalminae (*Dasymutilla*, *Pappognatha*, and *Traumatomutilla*) and Mutillinae (*Smicromyrme* and *Timulla*) (Fales *et al*., 1980).

Aposematic coloration and Müllerian mimicry

The effectiveness of secondary defenses in velvet ants is well founded. However, defense mechanisms used at earlier stage during predation sequence are generally less costly and preferrable (Broom *et al*., 2010; Endler, 1991; Ruxton *et al*., 2018) because: (1) the failure of a later defense may be lethal for the prey; (2) the performance of the prey would get weaker or exhausted after implementing defenses early in the sequence; (3) even if the prey would survive the predation events the time and energy are lost; (4) the defense mechanisms employed at later stages are less frequently used. Organisms with effective secondary defense frequently possess to advertise they are unpalatable prey. This phenomenon is called aposematism, defined as a combination of aposematic (= warning) signal and secondary defense (Poulton, 1890; Rojas *et al*., 2015; Ruxton *et al*., 2018). Many diurnal female velvet ants have bright and contrasting patterns of red, orange, or yellow pheomelanin-based cuticles and white, silvery, or golden setal markings, usually on the black integument (Gall *et al*., 2018; Hines *et al*., 2017). Aposematically colored females may be neglected by vertebrate predators under experimental conditions (Gall *et al*., 2018; Manley, 1984, 2000; Manley & Sherbrooke, 2001; Schmidt *et al*., 2021; Sexton, 1964; Vitt & Cooper 1988).

Distantly related velvet ants often share surprisingly similar color patterns, suggesting convergent or parallel evolution (color syndromes). Contrarily, some species also show great geographical variation in coloration (Williams *et al*., 2011b), which makes identification of this insect further difficult. Ferguson (1966) recognized five geographically delimited color patterns of North American velvet ant females. These facts imply presence of geographically delimited Müllerian mimicry rings. Müllerian mimicry, originally suggested by Müller (1878, 1879), refers to warning signals shared by defended organisms (Ruxton *et al*., 2018). Recently, substantial advances have been made in this topic, and velvet ant mimicry is now known as one of the world's largest known mimicry complexes (Wilson *et al*., 2015).

Wilson *et al*. (2012b) analyzed seven integumental and setal color traits (Table 6) quantified from 65 out of 113 North American *Dasymutilla* Ashmead species known at the time, recognizing six morphologically distinct, geographically delimited mimicry rings. Furthermore, they found nearly random distribution of color patterns on the phylogenetic tree of the genus based on *ITS1*, *ITS2*, and *wingless* DNA markers. This suggests repeated evolution of color patterns irrelevant of phylogeny. A follow-up study by Wilson *et al*. (2015) expanded their analyses to include 16 color traits (Table 6) from 302 of 361 described species, 16 polymorphic color forms, and 33 undescribed species in all of the 21 North American diurnal velvet ant genera. Most species analyzed were clustered into eight mimicry rings, with 15 species that did not fit to any color patterns. Wilson *et al*. (2018) then applied similar methods to African fauna (both Palaearctic and Afrotropical parts). With 304 African taxa scored based on specimens or published descriptions, they recognized lower mimetic diversity; four mimicry rings in a continent approximately 1.7 times larger than North America. They ascribed it to lower environmental heterogeneity and lower diversity of insectivorous lizards, given the potential importance of lizards as predators (Pan *et al*., 2017). Upon description of a novel color form for East Asian velvet ants, Okayasu *et al*. (2018)

reviewed female color diversity of East Asian taxa based on the specimens (163 taxa) and literature (83 taxa). They found two color patterns, both of which occur in North America and Africa also, despite of the diversity of vertebrates and ecoregional heterogeneity in this region (Campbell *et al*., 2021; Dinerstein *et al*., 2017; Jenkins *et al*., 2013; Olson *et al*., 2001; Roll *et al*., 2017; Wikramanayake *et al*., 2002). Later, Lelej (2020b) described a new species with unique coloration that approximates Eastern females color syndrome in North America. Similarly colored females occur in South Asia (Lelej, 2020b; Williams *et al*., 2024). He also pointed out that females of the genus *Taiwanomyrme* Tsuneki, which could not be assigned to any color syndrome in Okayasu *et al*. (2018), are superficially similar to Texan color syndrome of North America. These suggest presence of unrecognized mimicry rings in East Asia.

To summarize, Müllerian mimicry is one of the hottest topics in the velvet ant research. Latest papers by Lopez *et al*. (2021) and Wilson *et al*. (2020) highlighted significant effects of thermal ecology in color diversity. Further studies are needed for better understanding of phenotypic diversity and its determinant of this beautiful insect.

Study subjects and chapter outline

As discussed above, velvet ants have unique biological features, which make them an unalterable model organism in comparative biology. Their broad diet makes them promising biocontrol agents or, conversely, harmful pests of beneficial pollinators. Low dispersal ability and strict habitat preference are useful properties for biogeographic studies addressing conservation issues. Still, our knowledge on velvet ants is disproportionately inadequate, due to their hidden diversity, sex association, and cryptic behavior. Specifically, in tropical regions, there is enormous diversity to be discovered (Brothers in Taylor, 1983; Nonveiller, 1980ab). Even though substantial advances have been made in the systematics (Brothers & Lelej, 2017; Waldren *et al*., 2023), phylogenetic relationship is unknown for most groups. It is, therefore, urgent to describe, analyze, and document the biodiversity of velvet ants in a systematic manner.

In this dissertation, I addressed the phylogenetic systematics of the East Asian velvet ants and explored its implications in comparative biology. East Asia is known as a biodiversity hotspot, harboring world's highest potential of new species discovery and endemism of terrestrial organisms (Kass *et al*., 2022; Kier *et al*., 2009; Moura & Jetz, 2021; Myers *et al*., 2000; Wikramanayake *et al*., 2002). Presently, approximately 400 velvet ant species in 44 genera have been recorded from this region. However, the fauna of this region has been paid less attention comparing to, e.g., Europe and North America, with only a few experts over the history.

History of the East Asian velvet ant systematics

The history of the velvet ant systematics in East Asia (as defined by Okayasu *et al*., 2018) was initiated by Fabricius (1804) who described *Mutilla fuscipennis* Fabricius, 1804 (now *Trogaspidia fuscipennis*) and *Mutilla oculata* Fabricius, 1804 (now *Wallacidia oculata*) from China. During the earliest period (~1932), systematists published many isolated new species descriptions from East Asia based on the specimens collected by European explorers and settlers, like Alfred Russel Wallace (André, 1896ab, 1898, 1905, 1907b, 1908, 1909; Ashmead, 1904b, 1905; Brown, 1906; Cameron, 1900, 1901, 1902ab, 1903, 1905, 1909; Cockerell, 1927, 1928; Kohl, 1883; Lepeletier, 1845; Mercet, 1903; Rohwer, 1910; de Saussure, 1867; Smith, 1855, 1857–1858 1860ab, 1865, 1873, 1874, 1879; Zavattari, 1910, 1913, 1914, 1922). Few species were described by Japanese authors (Matsumura, 1911, Yano,

1932; Yasumatsu, 1931) from Japan and Taiwan. Those new species were placed in the sole genus *Mutilla* and authors largely depended on written descriptions for identification. Type specimens were rarely reexamined (but see André, 1899; Sichel & Radoszkowski, 1869–1870). Therefore, their new species were inevitably poorly diagnosed. South Asian species were often mistakenly recorded from East Asia (e.g., *Mutilla analis* Lepeletier, *M. dimidiata* Lepeletier, and *M. repraesentans* Smith; Mickel, 1933ab, 1935a). Few attempts to review and catalog the Old World velvet ant fauna were made by André (1902a), Bischoff (1920–1921), Dalla Torre (1897), Radoszkowski (1885), and Sichel & Radoszkowski (1869–1870). However, East Asian taxa were not treated comprehensively. Regarding the genus-level classification, Ashmead (1899, 1900–1904) presented a revised system for the world Mutillidae and Myrmosidae. André (1904) criticized and rejected many genera recognized by Ashmead. In his catalog, André (1902a) used the genera *Dasylabris* Radoszkowski, *Myrmosa* Latreille, *Odontomutilla* Ashmead, *Promecilla* André, *Stenomutilla* André for the East Asian velvet ants, but most species were left in *Mutilla*.

This situation was totally changed by Clarence Mickel, the most significant mutillidologist in the mid-19th century. In his serial studies (Mickel, 1933abcd, 1934, 1935a, 1936b, 1937b, 1939), he reexamined most type specimens of the East Asian velvet ants, revised the genus-level classification, and described a number of new species. Most significantly, he published three comprehensive accounts of the velvet ant fauna of Taiwan (Mickel, 1933b), Philippines (Mickel, 1934), and islands of the Pacific Ocean (Mickel, 1935a). Based on the types and additional material, he corrected misidentifications by previous authors and provided identification keys to all known species. He applied concepts of the African or western Palaearctic genera to the East Asian species: *Cystomutilla* André, *Odontomutilla* Ashmead, *Rhopalomutilla* André, *Smicromyrme* Thomson, *Squamulotilla* Bischoff, and *Trogaspidia* Ashmead (as the subgenus of the New World genus *Timulla* Ashmead). Sadly, after 1937, his research interest shifted to the Neotropical fauna, leaving continental East Asia as a gap in the velvet ant systematics.

Soon after Mickel, several authors published new species descriptions and distributional records from East Asia. Their studies were based on fewer specimens and thus less comprehensive than those of Mickel. Yasumatsu (1934, 1936, 1937, 1938abc, 1939, 1947ab, 1948, 1951) and Yasumatsu & Kumashiro (1940) dealt with a small collection from China (mostly northern part), Korean Peninsula, and Japan. Hammer (1949) identified specimens collected in China by Kjell Kolthoff and published a list, where three new species were described. Based on field works and loaned material, Pagden (1934abc, 1938, 1949) provided meaningful contributions to the fauna of Indonesia and Malaysia. In addition to taxonomic and faunal contributions, he presented biological data obtained during his field works in Malay Peninsula. Also, in his 1949 paper, he reviewed the *Timulla* (*Trogaspidia*) *erato* group and the subspecies-complex of *Timulla* (*Trogaspidia*) *philippinensis* (Smith). Those species and subspecies complexes largely overlap with the future genus *Pagdenidia* Lelej and *Wallacidia* Lelej & Brothers, respectively.

Another significant progress was made in a single paper by Chin-wen Chen (1957), who revised the velvet ants of China and Taiwan. In this paper, he incorporated more than 1,600 specimens deposited in multiple institutes. With one new genus, 45 new species, and 13 new subspecies, the number of known Chinese taxa were nearly doubled. Moreover, he critically revised the status of Chinese genera and species and modified Mickel's classification system.

During the late 20th century, Katsuji Tsuneki studied specimens collected in Japan, Taiwan, Malaysia, and Philippines by Japanese entomologists. His first paper dealing with velvet ants was a revision of the Japanese species (Tsuneki, 1972a). However, the rest of his works was dedicated to isolated new species descriptions and distributional records (Tsuneki,

1972bc, 1973, 1982, 1993ab; Tsuneki *et al*., 1993). In his 1993 paper, he described two new subgenera for Taiwanese *Smicromyrme* species, namely *Taiwanomyrme* Tsuneki, 1993 and *Zavatilla* Tsuneki, 1993. O'Toole (1975) reviewed the subspecies-complex of *Timulla* (*Trogaspidia*) *oculata*, group compatible to the *Timulla philippinensis* subspecies-complex sensu Pagden. O'Toole's study was substantially an extended version of Pagden (1949) but was superior to it in terms of broader geographical sampling and morphological character recognition. Furthermore, O'Toole discussed the biogeography, subspeciation scenario, and functional morphology of the male genitalia. Haneda (1979) described a new species of the Myrmosidae from Japan.

A new era was initiated by Arkady Lelej. His critical revisions of the genus-level classification constitute modern bases for the East Asian velvet ant systematics. Although Mickel used the concepts of Afrotropical and western Palaearctic genera, Lelej recognized that the East Asian species were morphologically distinct from true members of those genera. Many new genera were erected to accommodate them, e.g., *Orientilla* Lelej, 1979 for the East Asian *Stenomutilla* species (Lelej, 1979, 1996a) and *Bischoffitilla* Lelej, 2002 for the East Asian *Squamulotilla* species (Lelej, 2002). Two major components of the East Asian velvet ants, *Smicromyrme* and *Trogaspidia*, were reclassified. The East Asian *Smicromyrme* and *Trogaspidia* species sensu Chen and Mickel are now included in 22 genera (including *Smicromyrme* and *Trogaspidia* themselves), many of which were described or redefined by him (Lelej, 1985, 1995ab, 1996bcd; Lelej & Yamane, 1992). In addition to those large taxa, Lelej dealt with some minor groups (Lelej, 1992; Lelej & Krombein, 1999, 2001) and local fauna of Japan and South Korea (Lelej & Yamane, 1992; Lelej *et al*., 2001), clarifying the outline of the fauna of this region. The East Asian velvet ant systematics marked milestone afterward; Lelej compiled exhaustive catalogs of the Mutillidae and Myrmosidae of the Oriental and Palaearctic Regions (Lelej, 2002, 2005). In these contributions, the genus-placement of all described East Asian species was reviewed and many taxonomic changes were made. Furthermore, identifications keys to the genera were given. Lelej's catalogs provided a good starting point for subsequent studies. Later, Lelej (2012) added a new species of the *Rhopalomutilla* from Vietnam.

Following Lelej's classification system, the East Asian velvet ant systematics has been developed so rapidly during the last decade. Recent studies are often done in collaboration and incorporate a number of specimens from various collecting localities. Useful systematic revisions were attempted for some small genera: Tu *et al*. (2014a) for the *Cystomutilla* and the new genus *Hemutilla* Lelej, Tu & Chen, 2014; Tu *et al*. (2015) for the *Taiwanomyrme*; Lelej *et al*. (2016) for the *Promecidia* Lelej; Lelej *et al*. (2017) for the *Zeugomutilla* Chen; Zhou *et al*. (2018b) for the *Zavatilla*; Okayasu *et al*. (2021a) for the *Eotrogaspidia* Lelej; Okayasu (2021) for the new genus *Arkaditilla* Okayasu, 2021; Okayasu *et al*. (2021b) for the female *Andreimyrme* Lelej; Okayasu (2023a) for the Northeast Asian *Neotrogaspidia* Lelej. Local faunal reviews were also published (Barthélémy *et al*., 2018 for Hong Kong; Okayasu, 2020 for the Japanese Smicromyrmini; Sutanto *et al*., 2021 for the Indonesian *Bischoffitilla*). Most notably, Williams *et al*. (2019a) addressed a comprehensive treatment of the female velvet ants of southern Thailand. Before this study, thirty-three species had been known from Thailand. Based on museum specimens and 592 females collected during two expeditions, they discovered 17 new species and 12 described species newly recognized from that country, suggesting greater diversity of the East Asian velvet ants. Additionally, Williams *et al*. (2019a) presented a key to the eastern Oriental genera based on the female morphology. This paper effectively works as an updated version of Lelej's (2005) key.

In an attempt to broader systematic revisions, some papers included East Asian taxa. Brothers (2015) arranged the genera of the subfamily Rhopalomutillinae Schuster of the world. All East Asian species, together with three Afrotropical or South Asian species, were

transferred to the new genus *Pherotilla* Brothers, 2015 from the *Rhopalomutilla*. Brothers (2022) provided a photographic and annotated catalog of all nominal taxa from the Australasian Region, in which the species known from the Wallacean part of East Asia were illustrated based on type specimens. Three important works were published by Lelej and coauthors in 2023. Lelej *et al*. (2023) revised the Oriental Mutillini, with three species of the *Kurzenkotilla* Lelej, 2005 being only East Asian representatives. Lelej & Williams (2023) reviewed the genera of the Smicromyrmini including 10 genera known from East Asia. Lastly, Lelej (2023) critically examined the Oriental and Palearctic genera of the Ctenotillini. The only East Asian species, *Ctenotilla guangdongensis* Lelej, 1992, was assigned to the new genus *Williamstilla* Lelej, 2023.

Considerable progress was made by studies reporting miscellaneous taxonomic and distributional data as well. Isolated new species descriptions concentrated more than 10 species (Lelej, 2020ab, 2021; Okayasu, 2017, 2022, 2023b; Okayasu *et al*., 2018; Thaochan *et al*., 2022; Williams *et al*., 2019b; Zhou *et al*., 2017). Identification keys were provided for certain taxa: Tu *et al*. (2014b) for the Chinese *Dasylabris*; Okayasu (2017) for the female *Sinotilla*; Okayasu (2023b) for the female *Orientilla*; Williams *et al*. (2019b) for the Old World genera of the Myrmosidae and males of the *Krombeinella* Pate and *Kudakrumia* Krombein. Taxonomic changes of some described species were proposed by Okayasu (2018) and Zhou *et al*. (2018a).

Even after the dramatic growth of the East Asian velvet ant systematics, there are many issues to be addressed. Nearly 70% of the known East Asian species were described more than 50 year ago (Pagliano *et al*., 2020). The identity of those old species should be revisited based on examination of the types and other identified specimens, because their descriptions hardly achieve modern taxonomic standards for precise species recognition (illustrations, keys, and comparative diagnoses). Given that the number of recorded species from each East Asian country varies greatly, sampling efforts by previous systematists might be biased toward easily accessible areas. This suggests broader sampling will yield many more unrecognized species. Although the genus-classification systems were largely reconstructed by Lelej's studies, identification of the East Asian genera is surprisingly difficult, presumably due to the small number of species and characters used to define them. Thus, I attempted a series of systematic revisions of the East Asian taxa as outlined below.

Chapter outline

In the Chapters 2 to 5, I revised the taxonomy of the *Andreimyrme* Lelej, 1995, *Eotrogaspidia* Lelej, 1996, *Krombeinidia bagrada* (Cameron, 1902) and kin, and Northeast Asian species of *Neotrogaspidia* Lelej, 1996. Where necessary, South Asian species were also examined for comparison. In the Chapter 6, previous treatments of the females of the genus *Mickelomyrme* Lelej, 1995 were critically reviewed and new data are presented. These genera belong to the tribes Smicromyrmini Bischoff, 1920 and Trogaspidiini Bischoff, 1920, two major components of the Old World fauna. For the Chapter 7, I explored the potential diversity and current knowledge on the East Asian velvet ants using Vietnam as a model region. Contrarily, in the Chapter 8, I investigated the diversity of Nepalese fauna based on the collection that has never been studied in the context of velvet ant systematics. By doing so, I obtained appropriate comparative material for the Chapter 10. In the Chapter 9, I reviewed Northeast Asian species of *Nemka* Lelej, 1985. Along with this, I addressed the following question: Is there ecological character displacement in velvet ants? This is particularly important to ask, given the abundance and wide host range of this insect. Lastly, in the Chapter 10, I critically reviewed the East Asian genera of the Smicromyrmini based on phylogenetic analyses using the male morphology.

References

Abe, S. (1932) [The nest of *Bombus diversus* Smith]. *Kontyû* 5 (5–6): 245–247. (in Japanese)

Agrain, F.A., Buffington, M.L., Chaboo, C.S., Chamorro, M.L. & Schöller, M. (2015) Leaf beetles are ant-nest beetles: the curious life of the juvenile stages of case-bearers (Coleoptera, Chrysomelidae, Cryptocephalinae). *ZooKeys* 547: 133–164. https://doi.org/10.3897/zookeys.547.6098

Aguiar, A.P., Deans, A.R., Engel, M.S., Forshage, M., Huber, J.T., Jennings, J.T., Johnson, N.F., Lelej, A.S., Longino, J.T., Lohrmann, V., Mikó, I., Ohl, M., Rasmussen, C., Taeger, A. & Yu, D.S.K. (2013) Order Hymenoptera. *In*: Zhang, Z.-Q. (ed.) Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness (addenda 2013). *Zootaxa* 3703 (1): 51–62. https://doi.org/10.11646/zootaxa.3703.1.12

Alicata, P., Caruso, D., Costa, G. & Mota, S. (1974) Ricerche eco-etologiche sulla fauna delle dune costiere di Porto Palo (Siracusa). — I. *Smicromyrme viduata* (Pall.) (Hymenoptera, Mutillidae): Ritmi di attivita, migrazioni e accoppiamnto. *Animalia* 1 (1/3): 89–108.

Amini, A., Lelej, A.S., Sadeghi, H. & Karimi, J. (2014) First record of the velvet ants (Hymenoptera: Mutillidae) reared from puparia of the ber fruit fly *Carpomya vesuviana* Costa (Diptera: Tephritidae) in Iran. *Zootaxa* 3861 (6): 585–590. http://dx.doi.org/10.11646/zootaxa.3861.6.5

Amini, A., Lotfalizadeh, H., Peris-Felipo, F.J. & Rasplus, J.-Y. (2024) Potential parasitoids for biocontrol of the ber fruit fly, *Carpomya vesuviana* Costa (Diptera: Tephritidae). *Life* 14 (1): 50. https://doi.org/10.3390/life14010050

André, E. (1896a) Mutillides nouveaux ou imparfaitement connus faisant partie des collections du musée National de Hongrie. *Termeszetraizi fuzetek* 19 (1): 9–25.

André, E. (1896b) Étude sur les Mutillides existant dans les collections du Musée civique de Gênes. *Annali del Museo Civico di Storia Naturale di Genova*, Serie 2 17: 66–104.

André, E. (1898) Étude sur les mutillides du Muséum de Paris. *Annales de la Société Entomologique de France* 67: 1–79.

André, E. (1899) Les types des mutillides de la collection O. Radoszkowski. *Annales de la Société Entomologique de France* 68: 1–43.

André, E. (1902a [1903]) Family Mutillidae. *In*: Wytsman, P. (ed.) *Genera Insectorum*. *Fascicles 11*. L. Desmet-Verteneuil, Bruxelles, pp. 1–77 + 3 pls.

André, E. (1901–1902) Matériaux pour servir à la connaissance des Mutillides d'Afrique. (Hym.). *Zeitschrift für Systematische Hymenopterologie und Dipterologie* 1 (5): 279–288 (1901a); 1 (6): 305–352 (1901); 2 (1): 17–48 (1902b).

André, E. (1904) Examen critique d'une nouvelle classification proposée par M. le Dr W. H. Ashmead pour la famille des Mutillidae. *Revue d'Entomologie publiée par la Société Française d'Entomologie* 23 (1): 27–32; 23 (2–3): 33–41.

André, E. (1905) Mutillides nouveaux ou peu connus de l'Ancien Monde et de l'Australie. (Hym.). *Zeitschrift für systematische Hymenopterologie und Dipterologie* 5 (4): 201–216; 5 (5): 265–277.

André, E. (1907a) Liste des Mutillides recueillis à Ceylan par M. le Dr. Walther Horn et description des espèces nouvelles. (Hym.). *Deutsche Entomologische Zeitschrift* 3: 251–258.

André, E. (1907b) Description d'une nouvelle espèce de Mutillide, de Java (Hym.). *Zeitschrift für Systematische Hymenopterologie und Dipterologie* 7 (3): 207–208.

André, E. (1908) Description de quelques nouveaux Mutillides du Musée National de

Hongrie. *Annales Historico-Naturales Musei Nationalis Hungarici* 6: 375–383.
André, E. (1909) Mutillides nouveaux ou imparfaitement connus du Musée royal d'histoire naturelle de Leide. *Notes from the Leyden Museum* 31: 171–180.
André, E. (1910) Révision monographique des Mutillides de l'Egypye. *Mémoires de la Société Entomologique d'Egypte* 1 (2): 1–94 + 3 pls.
Aranda, R. & Graciolli, G. (2016) Protocol for collecting Mutillidae (Hymenoptera, Aculeata) in ecological studies: species-area effects on Mutillidae communities. *Revista Brasileira de Entomologia* 60 (4): 312–318. https://doi.org/10.1016/j.rbe.2016.08.003
Argaman, Q. (1988) Description of the female of *Ticopla*, with biological and taxonomic notes (Hymenoptera, Mutillidae). *Fragmenta Balcanica Musei Macedonici Scientiarum Naturalium* 14 (5): 33–46.
Argaman, Q. (1990) Generic synopsis of Sierolomorphidae (Hymenoptera). *Israel Journal of Entomology* 24: 29–33.
Arnold, G. (1946) New species of African Hymenoptera No. 6. *Occasional Papers of the National Museum of Southern Rhodesia* 2 (12): 49–55.
Arnold, G. (1956) New species of African Hymenoptera No. 12. *Occasional Papers of the National Museum of Southern Rhodesia* 3 (21B): 52–77.
Arnold, G. (1960) New species of African Hymenoptera No. 15. *Occasional Papers of the National Museum of Southern Rhodesia* 3 (24B): 452–488.
Ashmead, W.H. (1899) Superfamilies in the Hymenoptera and generic synopses of the families Thynnidae, Myrmosidae, and Mutillidae. *Journal of the New York Entomological Society* 7: 45–60.
Ashmead, W.H. (1900–1904) Classification of the fossorial, predaceous and parasitic wasps, or the superfamily Vespoidea. *The Canadian Entomologist* 32: 145–155, 185–188, 295–296 (1900); 34: 79–88, 131–137, 163–166, 203–210, 219–231, 268–273, 287–291 (1902); 35: 3–8, 39–44, 95–107, 155–158, 199–205, 303–310, 323–332 (1903); 36: 5–9 (1904a).
Ashmead, W.H. (1904b) Descriptions of new genera and species of Hymenoptera from the Philippine Islands. *Proceedings of the United States National Museum* 28 (1387): 127–158. https://doi.org/10.5479/si.00963801.28-1387.127
Ashmead, W.H. (1905) Additions to the recorded hymenopterous fauna of the Philippine Islands, with descriptions of new species. *Proceedings of the United States National Museum* 28 (1413): 957–971.
Azevedo, C.O., Alencar, I.D.C.C., Ramos, M.S., Barbosa, D.N., Colombo, W.D., Vargas J.M.R. & Lim, J. (2018) Global guide of the flat wasps (Hymenoptera, Bethylidae). *Zootaxa* 4489 (1): 1–294. https://doi.org/10.11646/zootaxa.4489.1.1
Azevedo, C.O., Colombo, W.D., Alencar I.D.C.C., de Brito, C.D. & Waichert, C. (2016) Couples in phoretic copulation, a tool for male-female association in highly dimorphic insects of the wasp genus *Dissomphalus* Ashmead (Hymenoptera: Bethylidae). *Zoologia* 33 (6): e20160076. https://doi.org/10.1590/S1984-4689zool-20160076
Barbier, J. (1976) Note sur le parasitisme de Clytrinae (Col. Chrysomelidae) par des Mutillidae (Hym.). *L'Entomologiste* 32: 163–165.
Barthélémy, C., Lelej, A.S. & Loktionov, V.M. (2018) A contribution to the Mutillidae (Hymenoptera) of Hong Kong. *Zootaxa* 4514 (2): 230–242. https://doi.org/10.11646/zootaxa.4514.2.6
Bartholomay, P.R., Williams, K.A., Cambra, R.A. & Oliveira, M.L. (2020) Revision of the *Traumatomutilla juvenilis* species group (Hymenoptera, Mutillidae). *Journal of Natural History* 53 (43–44): 2639–2683. https://doi.org/10.1080/00222933.2020.1715501
Bartholomay, P.R., Williams, K.A., Cambra, R.A. & Oliveira, M.L. (2021) Revision of the

Traumatomutilla gemella species-group (Hymenoptera, Mutillidae) with the description of its hitherto unknown males. *Zoosystema* 43 (1): 1–28. https://doi.org/10.5252/zoosystema2021v43a1

Bartholomay, P.R., Williams, K.A., Cambra, R.A. & Oliveira, M.L. (2022) Revision of the *Traumatomutilla indica* species-group (Hymenoptera: Mutillidae). *Zootaxa* 5108 (1): 1–97. https://doi.org/10.11646/zootaxa.5108.1.1

Bartholomay, P.R., Williams, K.A., Lopez, V.M. & Oliveira, M.L. (2019a) Revision of the *Traumatomutilla americana* species group (Hymenoptera: Mutillidae). *Zootaxa* 4608 (1): 1–34. https://doi.org/10.11646/zootaxa.4608.1.1

Bartholomay, P.R., Williams, K.A., Luz, D.R., Cambra, R.A. & Oliveira, M.L. (2019b) *Traumatomutilla* André miscellanea: Revision of the bellica, bifurca, diabolica, and vitelligera species groups, and a new group for the new species *T. pilkingtoni* Bartholomay and Williams (Hymenoptera: Mutillidae: Sphaeropthalminae: Dasymutillini). *Insecta Mundi* 0709: 1–37.

Batra, S.W.T. (1965) Organisms associated with *Lasioglossum zephyrum* (Hymneoptera: Halictidae). *Journal of the Kansas Entomological Society* 38 (4): 367–389. https://www.jstor.org/stable/25083474

Bayliss, P.S. & Brothers, D.J. (1996) Biology of *Tricholabiodes* Radoszkowski in Southern Africa, with a new synonymy and review of recent biological literature (Hymenoptera: Mutillidae). *Journal of Hymenoptera Research* 5: 249–258.

Bayliss, P.S. & Brothers, D.J. (2001) Behaviour and host relationships of *Dolichomutilla sycorax* (Smith) (Hymenoptera: Mutillidae, Sphecidae). *Journal of Hymenoptera Research* 10 (1): 1–9.

Bergamaschi, A.C.B., Cambra, R.A., Brothers, D.J. & Melo, G.A.R. (2012) *Lynchiatilla* Casal, 1963 (Hymenoptera: Mutillidae): a new species from Brazil associated with *Paroxystoglossa spiloptera* Moure (Hymenoptera: Apidae: Halictinae), and notes on other species. *Zootaxa* 3548 (1): 55–64. https://doi.org/10.11646/zootaxa.3548.1.3

Bergamaschi, A.C.B., Cambra, R. & Melo, G.A.R. (2010) Male description and host record for *Lophomutilla corupa* Casal, 1968 (Hymenoptera: Mutillidae), with behavioural notes on mating behaviour and host nest attacks. *Journal of Natural History* 44 (43–44): 2597–2607. https://doi.org/10.1080/00222933.2010.499574

Bergamaschi, A.C.B., Cambra, R. & Melo, G.A.R. (2011) New combinations, sex association, behavioural notes and potential host record for two Neotropical species of *Pseudomethoca* Ashmead, 1896 (Hymenoptera: Mutillidae). *Zootaxa* 3062 (1): 55–63. https://doi.org/10.11646/zootaxa3062.1.6

Berland, L. (1925) *Fauna de France 10. Hyménoptères vespiformes. I (Sphegidae, Pompilidae, Scoliidae, Sapygidae, Mutillidae)*. Paul Lechevalier, Paris, viii + 364 pp.

Bezzi, M. (1924) *The Bombyliidae of the Ethiopian region based on material in the British museum (Natural History)*. British Museum (Natural History), London, 390 pp.

Bischoff, H. (1913) Ein interessanter Hymenopterenzwitter. *Zeitschrift für wissenschaftliche Insektenbiologie* 9 (2): 53–54.

Bischoff, H. (1920–1921) Monographie der Mutilliden Afrikas. *Archiv für Naturgeschichte* 86A (1–3): 1–480 (1920); 86A (4–5): 481–830 (1921).

Bischoff, H. (1927) *Biologie der Hymenopteren: Eine Naturgeschichte der Hautflügler*. Julius Springer, Berlin, viii + 598 pp.

Bischoff, H. (1931) Der Typus der *Mutilla dubia* F. — ein Gynander — *Mitteilungen der Deutschen Entomologischen Gesellschaft* 2 (4): 54–56.

Blake, C.A. (1872) Additions to the “Synopsis of N. Am. Mutillidae”. *Transactions of the American Entomological Society* 4: 71–76.

Blum, M.S. & Brand, J.M. (1972) Social insect pheromones: Their chemistry and function.

American Zoologist 12 (3): 553–576. https://doi.org/10.1093/icb/12.3.553
Blum, M.S. & Edgar, A.L. (1971) 4-Methyl-3-heptanone: Identification and role in opilionid exocrine secretions. *Insect Biochemistry* 1 (2): 181–188. https://doi.org/10.1016/0020-1790(71)90071-0
Blum, M.S., Padovani, F. & Amante, E. (1968) Alkanones and terpenes in the mandibular glands of *Atta* species (Hymenoptera: Formicidae). *Comparative Biochemistry and Physiology* 26 (1): 291–299. https://doi.org/10.1016/0010-406X(68)90333-2
Bogusch, P. (2006) The velvet ants (Hymenoptera: Mutillidae) of the Czech Republic and Slovakia: an identification key and annotated checklist. *Acta Musei Moraviae, Scientiae biologicae* 91: 103–148.
Bogusch, P., Hlaváčková, L., Petr, L. & Bosch, J. (2020) Nest structure, pollen utilization and parasites associated with two West-Mediterranean bees (Hymenoptera, Apiformes, Megachilidae) nesting in empty snail shells. *Journal of Hymenoptera Research* 76: 113–125. https://doi.org/10.3897/jhr.76.49579
Bohart, G.E. & MacSwain, J.W. (1939) The life history of the sand wasp, *Bembix occidentalis beutenmuelleri* Fox and its parasites. *Bulletin of the Southern California Academy of Sciences* 38 (2): 84–97.
Boni Bartalucci, M. (2004) Tribe-groups of the Myzininae with special regard to the Palaearctic taxa of the tribe Meriini (Hymenoptera, Tiphiidae). *Linzer biologische Beiträge* 36 (2): 1205–1308.
Boni Bartalucci, M. (2011) Myzininae of the Old World. The subtribe Braunsomeriina (Hymenoptera; Tiphiidae). *Linzer biologische Beiträge* 43 (1): 363–380 + 893–899.
Bowden, J. (1962) Bombyliidae (Diptera Brachycera). *Parc National de la Garamba — Mission H. de Saeger* 32 (2): 47–60.
Bowden, J. (1967) Studies in African Bombyliidae. VI. A provisional classification of the Ethiopian Systropinae with descriptions of new and little known species. *Journal of the Entomological Society of Southern Africa* 30 (2): 126–173. https://hdl.handle.net/10520/AJA00128789_2611
Brabant, C.M., Williams, K.A. & Pitts, J.P. (2010) True females of the subgenus *Photomorphina* Schuster (Hymenoptera: Mutillidae). *Zootaxa* 2559 (1): 58–68. https://doi.org/10.11646/zootaxa.2559.1.5
Brauns, A. (1964) *Taschenbuch der Waldinsekten: Grundriß einer terrestrischen Bestandes- und Standort-Entomologie*. Fischer, Stuttgart, 817 pp.
Brock, R.E., Cini, A. & Sumner, S. (2021) Ecosystem services provided by aculeate wasps. *Biological Reviews* 96 (4): 1645–1675. https://doi.org/10.1111/brv.12719
Brodie, E.D. Jr., Formanowicz, D.R. Jr. & Brodie, E.D. III (1991) Predator avoidance and antipredator mechanisms: distinct pathways to survival. *Ethology Ecology & Evolution* 3 (1): 73–77. https://doi.org/10.1080/08927014.1991.9525390
Brothers, D.J. (1971a) The genera of Mutillidae (Hymenoptera) parasitic of tsetse flies (*Glossina*, Diptera). *Journal of the Entomological Society of South Africa* 34 (1): 101–102. https://hdl.handle.net/10520/AJA00128789_2439
Brothers, D.J. (1971b) *Ascetotilla*, a new genus of Mutillidae from New Guinea (Hymenoptera). *Pacific Insects* 13 (3–4): 471–485.
Brothers, D.J. (1972) Biology and immature stages of *Pseudomethoca f. frigida*, with notes on other species (Hymenoptera: Mutillidae). *The University of Kansas Science Bulletin* 50 (1): 1–38.
Brothers, D.J. (1975) Phylogeny and classification of the aculeate Hymenoptera, with special reference to Mutillidae. *The University of Kansas Science Bulletin* 50 (11): 483–648.
Brothers, D.J. (1978) Biology and immature stages of *Myrmosula parvula* (Hymenoptera: Mutillidae). *Journal of the Kansas Entomological Society* 51 (4): 698–710.

https://www.jstor.org/stable/25083861
Brothers, D.J. (1984) Gregarious parasitoidism in Australian Mutillidae (Hymenoptera). *Australian Entomological Magazine* 11 (1): 8–10.
Brothers, D.J. (1989) Alternative life-history styles of mutillid wasps (Insecta, Hymenoptera). *In*: Bruton, M. N. (ed.) *Alternative life-history styles of animals*. *Perspectives in vertebrate sciences 6*. Springer, Dordrecht, pp. 279–291. https://doi.org/10.1007/978-94-009-2605-9_14
Brothers, D.J. (1995) Mutillidae. *In*: Gauld, I. & Hansen, P. (eds) *The Hymenoptera of Costa Rica*. Oxford University Press, Oxford, pp. 541–548.
Brothers, D.J. (2006) Familia Mutillidae. *In*: Fernández, F. & Sharkey, M.J. (eds) *Introducción a los Hymenoptera de la Región Neotropical*. Sociedad Colombiana de Entomología y Universidad Nacional de Colombia, Bogotá, D.C., pp. 577–594.
Brothers, D.J. (2015) Revision of the Rhopalomutillinae (Hymenoptera, Mutillidae): 1, generic review with descriptions of three new genera. *Journal of Hymenoptera Research* 46: 1–24. https://doi.org/10.3897/JHR.46.5733
Brothers, D.J. (2018) *Aglaotilla*, a new genus of Australian Mutillidae (Hymenoptera) with metallic coloration. *Zootaxa* 4415 (2): 357–368. https://doi.org/10.11646/zootaxa.4415.2.6
Brothers, D.J. (2022) Critical analysis of the type material of Mutillidae described from the Australasian Region (Hymenoptera). *Zootaxa* 5140 (1): 1–215. https://doi.org/10.11646/zootaxa.5140.1.1
Brothers, D.J. & Lelej, A.S. (2017) Phylogeny and higher classification of Mutillidae (Hymenoptera) based on morphological reanalyses. *Journal of Hymenoptera Research* 60: 1–97. https://doi.org/10.3897/jhr.60.20091
Brothers, D.J., Tschuch, G. & Burger, F. (2000) Associations of mutillid wasps (Hymenoptera, Mutillidae) with eusocial insects. *Insectes Sociaux* 47: 201–211. https://doi.org/10.1007/PL00001704
Brown, C.G. & Funk, D.J. (2005) Aspects of the natural history of Neochlamisus (Coleoptera: Chrysomelidae): Fecal case-associated life history and behavior, with a method for studying insect constructions. *Annals of the Entomological Society of America* 98 (5): 711–725. https://doi.org/10.1603/0013-8746(2005)098[0711:AOTNHO]2.0.CO;2
Brown, R.E. (1906) A catalogue of Philippine Hymenoptera, with description of new species. *The Philippine Journal of Science* 1 (6–10): 683–704.
Burgess, N., Hales, J.D., Underwood, E., Dinerstein, E., Olson, D., Itoua, I., Schipper, J., Ricketts, T. & Newman, K. (2004) *Terrestrial ecoregions of Africa and Madagascar: A conservation assessment*. Island Press, Washington DC, 550 pp.
Bürgis, H. (1990) Parasitische Hymenopteren aus puparien der in Asseln schmarotzenden Rhinophoridae (Diptera). *Deutsche Gesellschaft für allgemeine und angewandte Entomologie* e.V. 4 (2): 41–42.
Burrell, R.W. (1935) Notes on the habits of certain Australian Thynnidae. *Journal of the New York Entomological Society* 43 (1): 19–29. https://www.jstor.org/stable/25004587
Callan, E.M. (1977) Observations on *Centris rufosuffusa* Cockerell (Hymenoptera: Anthophoridae) and its parasites. *Journal of Natural History* 11 (2): 127–135. https://doi.org/10.1080/00222937700770101
Cambra, R.A., Brothers, D.J. & Quintero A., D. (2020) Review of *Calomutilla* Mickel, 1952, a new species, and comparison with *Pertyella* Mickel, 1952 (Hymenoptera: Mutillidae). *Zootaxa* 4789 (2): 466–480. https://doi.org/10.11646/zootaxa.4789.2.6
Cambra, R.A., Gonzalez, V.H. & Wcislo, W.T. (2005) Description of the male, host associations, and new distribution records for *Lophostigma cincta* (Du Buysson)

(Hymenoptera: Mutillidae). *Proceedings of the Entomological Society of Washington* 107 (1): 229–234.

Cambra, R.A., Queiros, C.N., Alves De Deus, J.P., Williams, K.A., Bartholomay, P.R., Iantas, J., Nether, M.C., Nishida, K., Añino, Y.J., Saavedra, D. & Tunes Buschini, M.L. (2021) Description of the male of *Xystromutilla bucki* Suárez, 1960 (Hymenoptera, Mutillidae), including new information on the biology of the genus. *ZooKeys* 1011: 73–84. https://doi.org/10.3897/zookeys.1011.60944

Cambra, R.A. & Quintero A., D. (1993) Studies on *Timulla* Ashmead (Hymenoptera: Mutillidae): New distributional records and synonymies, and descriptions of previously unknown allotypes. *The Pan-Pacific Entomologist* 69 (4): 299–313.

Cambra, R.A. & Quintero A., D. (2003a) Description of the previously unknown male of the Neotropical genus *Hoplognathoca* Suarez and new distributional records (Hymenoptera: Mutillidae: Sphaeropthalminae). *Transactions of the American Entomological Society* 129 (3–4): 487–495. https://www.jstor.org/stable/25078824

Cambra, R.A. & Quintero A., D. (2003b) *Tallium lattkei* n. sp. (Hymenoptera: Mutillidae) from Venezuela and Colombia, the northernmost distribution record for this Neotropical genus. *Transactions of the American Entomological Society* 129 (3–4): 497–502. https://www.jstor.org/stable/25078825

Cambra, R.A. & Quintero A., D. (2004) New species of *Xystromutilla* Andre (Hymenoptera: Mutillidae) and the first illustrated key for the males of the genus. *Transactions of the American Entomological Society* 130 (4): 463–478. https://www.jstor.org/stable/25078866

Cambra, R.A. & Quintero A., D. (2007) *Chilemutilla*, a new genus of Mutillidae (Hymenoptera) from Chile, and description of the first wingless mutillid male from South America. *Transactions of the American Entomological Society* 133 (1): 167–180. https://doi.org/10.3157/0002-8320(2007)133[167:CANGOM]2.0.CO;2

Cambra, R.A. & Quintero A., D. (2017) *Sphaeropthalma pinedai* sp. nov.: primer registro de un mutílido braquíptero para América del sur (Hymenoptera: Mutillidae). *Boletín Científico del Museo de Historia Natural (Centro de Museos)* 21 (2): 220230. https://doi.org/10.17151/bccm.2017.21.2.15

Cambra T., R.A., Quintero A., D. & Brothers, D.J. (2014) A new species of *Hoplognathoca* Suárez, 1962 from Central America and description of male of *Hoplognathoca costarricensis* Suárez, 1962 (Hymenoptera: Mutillidae). *Zootaxa* 3884 (3): 295–300. https://doi.org/10.11646/zootaxa.3884.3.9

Cambra, R.A., Quintero A., D. & Pagliano, G. (2016) Revision of *Limaytilla* Casal, 1964 (Hymenoptera: Mutillidae: Sphaeropthalmini), including the description of the first apterous male in the genus. *Il Naturalista Valtellinese, Atti Museo civ. Storia naturale Morbegno* 27: 37–70.

Cambra, R.A., Quintero A., D., Waldren, G.C., Bartholomay, P.R. & Williams, K.A. (2018) Taxonomic revision of the genus *Timulla* Ashmead, 1899 of Panama (Hymenoptera: Mutillidae). *Tecnociencia* 20 (2): 23–57.

Cambra, R.A., Tunes Buschini, M.L., Quintero A., D., Brozoski, F. & Rudiak Lustosa, P. (2017) *Ephuta icema* Casal, 1969 and its host *Auplopus subaurarius* Dreisbach, 1963 (Hymenoptera: Mutillidae, Pompilidae) from Brazil. *Zootaxa* 4272 (2): 285–290. https://doi.org/10.11646/zootaxa.4272.2.9

Cameron, P. (1900) Hymenoptera Orientalia, or contributions to the knowledge of the Hymenoptera of the Oriental zoological region. Part IX. The Hymenoptera of the Khasia Hills. Part II. Section I. *Memoirs and Proceedings of the Manchester Literary and Philosophical Society* 44 (15): 1–114.

Cameron, P. (1901) On the Hymenoptera collected during the “Skeat Expedition” to the

Malay Peninsula, 1899–1900. *Proceedings of the Zoological Society of London* 2: 16–44.
Cameron, P. (1902a) On the Hymenoptera collected by Mr. Robert Shelford at Sarawak, and on the Hymenoptera of the Sarawak Museum. *Journal of the Straits Branch of the Royal Asiatic Society* 37: 29–131.
Cameron, P. (1902b) On some new genera and species of Hymenoptera (Ichneumonidae, Chrysididae, Fossores, and Apidae). *The Entomologist* 35: 108–111, 179–183, 206–208, 237–241, 263–264, 312–315.
Cameron, P. (1902c) Descriptions of new genera and species of Hymenoptera collected by Major C. S. Nurse at Deesa, Sima and Ferozepore. *The Journal of the Bombay Natural History Society* 14 (2): 267–293 + pl. 9; 14 (3): 419–449.
Cameron, P. (1903) Descriptions of new genera and species of Hymenoptera taken by Mr. Robert Shelford at Sarawak, Borneo. *Journal of the Straits Branch of the Royal Asiatic Society* 39: 89–181.
Cameron, P. (1905) On the Malay fossorial Hymenoptera and Vespidae of the museum of the R. Zool. Soc. "Natura Artis Magistra" at Amsterdam. *Tijdschrift voor Entomologie* 48: 48–78.
Cameron, P. (1909) Descriptions of two new species of *Mutilla* from Kuching, Borneo. *The Entomologist* 42: 146–147.
Campbell, I., Behrens, K., Hesse, C. & Chaon, P. (2021) *Habitats of the world: A field guide for birders, naturalists and ecologists*. Princeton University Press, Princeton.
Carpenter, G.D.H. (1921) Experiments on the relative edibility of insects, with special reference to their coloration. *Transactions of the Entomological Society of London* 1921 (1–2): 1–105.
Cazier, M.A. & Mortenson, M.A. (1965) Studies on the bionomics of sphecoid wasps. II. *Philanthus gibbosus* (Fabricius) and *Philanthus anna* Dunning (Hymenoptera: Sphecidae). *Bulletin of the Southern California Academy of Sciences* 64 (4): 171–206.
Ćetković, A. & Nonveiller, G. (1992) First record of male apterity in the genus *Stenomutilla*. *Stenomutilla multilata* a new species from Ethiopia. Studies on African mutillids (Hymenoptera, Mutillidae) XV. *Bolletino del Museo Regionale di Scienze naturali di Torino* 10 (2): 393–399.
Chaboo, C.S., Chamorro, M.L. & Schöller, M. (2016) Catalogue of known immature stages of camptosomate leaf beetles (Coleoptera, Chrysomelidae, Cryptocephalinae and Lamprosomatinae). *Proceedings of the Entomological Society of Washington* 118 (2): 150–217. https://doi.org/10.4289/0013-8797.118.1.150
Chen, C.-w. (1957) A revision of the velvety ants or Mutillidae of China (Hymenoptera). *Quarterly Journal of the Taiwan Museum* 10 (3–4): 135–224 + 6 pls.
Chorley, J.K. (1929) The bionomics of *Glossina morsitans* in the Umniati Fly Belt, Southern Rhodesia, 1922–1923. *Bulletin of Entomological Research* 20 (3): 279–301. https://doi.org/10.1017/S000748530002126X
Clausen, C.P., Gardner, T.R. & Sato, K. (1932) Biology of some Japanese and Chosenese grub parasites (Scoliidae). *United States Department of Agriculture Technical Bulletin* 308: 1–27.
Cockerell, T.D.A. (1927) Hymenoptera from Lucban, Philippine Islands. *The Philippine Journal of Science* 33 (3): 271–277.
Cockerell, T.D.A. (1928) Mutillidae from Siam. *The Annals and Magazine of Natural History*, Series 10 2: 596–600. https://doi.org/10.1080/00222932808672926
Corbin, C.E., Lowenberger, L.K. & Gray, B.L. (2015) Linkage and trade-off in trophic morphology and behavioural performance of birds. *Functional Ecology* 29 (6): 808–815. https://doi.org/10.1111/1365-2435.12385

Crèvecoeur, A. (1930) Recherches biologiques sur *Smicromyrme* (*Mutilla*) *rufipes* F. (Hym. Mutillidae). *Bulletin & Annales de la Société entomologique de Belgique* 70: 271–284.

Crewe, R.M. & Blum, M.S. (1972) Alarm pheromones of the Attini: Their phylogenetic significance. *Journal of Insect Physiology* 18 (1): 31–42. https://doi.org/10.1016/0022-1910(72)90062-5

da Cunha, R. (2004) *Monoeca xanthopyga* (Hymenoptera, Apoidea, Tapinotaspidini), first host registration for parasitoids of the genus *Traumatomutilla* (Hymenoptera: Mutillidae) at the Serra Geral of Rio Grande do Sul, Brazil. *Acta Scientiae* 6 (2): 35–40.

Dalla Torre, C.G. de (1897) *Catalogus Hymenopterorum hucusque Descriptorum Systematicus et Synonimicus*. *Volumen VIII: Fossores (Sphegidae)*. Guilelmi Engelmann, Lipsiae, [4] + viii + 750 pp. https://doi.org/10.5962/bhl.title.10348

Danforth, B.N. (1991) Female foraging and intranest behavior of a communal bee, *Perdita portalis* (Hymenoptera: Andrenidae). *Annals of the Entomological Society of America* 84 (5): 537–548. https://doi.org/10.1093/aesa/84.5.537

Davidson, A. (1897) California bees and their parasites. *Proceedings of the Southern California Academy of Sciences* 1 (3): 3–7.

Davis, J.J. (1919) Contributions to a knowledge of the natural enemies of *Phyllophaga*. *Bulletin of the Illinois State Natural History Survey* 13: 53–138.

de Saeger, H. (1956) *Exploration du Parc National de la Garamba*. *Mission H. de Saeger*. *Fascicule 5*. *Entomologie, renseignements éco-biologiques*. Institut des Parcs Nationaux du Congo Belge, Bruxelles, 556 pp.

Deus, J.P.A., Noga, A., Brozoski, F., Dias, A.M.P. & Buschini, M.L.T. (2023) Trap-nesting biology of an ectoparasitoid spider wasp, *Auplopus subaurarius* (Hymenoptera: Pompilidae): the importance of wooded environments for niche generalist species. *Brazilian Journal of Biology* 83: e269165. https://doi.org/10.1590/1519-6984.269165

Deyrup, M. (1988) Review of adaptations of velvet ants (Hymenoptera: Mutillidae). *The Great Lakes Entomologist* 21 (1): 1–4. https://scholar.valpo.edu/tgle/vol21/iss1/1

Deyrup, M. & Manley, D. (1986a) Sex-biased size variation in velvet ants (Hymenoptera: Mutillidae). *Florida Entomologist* 69 (2): 327–335.

Deyrup, M. & Manley, D. (1986b) Description of the male of *Pseudomethoca oculata* (Banks) (Hymenoptera: Mutillidae). *Florida Entomologist* 69 (4): 658–661.

Deyrup, M. & Manley, D. (1990) Seasonal flight activity of male velvet ants (Hymenoptera: Mutillidae) in Southern Florida. *Entomological News* 101 (2): 99–108.

Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N.D., Wikramanayake, E., Hahn, N., Palminteri, S., Hedao, P., Noss, R., Hansen, M., Locke, H., Ellis, E.C., Jones, B., Barber, C.V., Hayes, R., Kormos, C., Martin, V., Crist, E., Sechrest, W., Price, L., Baillie, J.E.M., Weeden, D., Suckling, K., Davis, C., Sizer, N., Moore, R., Thau, D., Birch, T., Potapov, P., Turubanova, S., Tyukavina, A., De Souza, N., Pintea, L., Brito, J.C., Llewellyn, O.A., Miller, A.G., Patzelt, A., Ghazanfar, S.A., Timberlake, J., Klöser, H., Shennan-Farpón, Y., Kindt, R., Lillesø, J.B., Van Breugel, P., Graudal, L., Voge, M., Al-Shammari, K.F. & Saleem, M. (2017) An ecoregion-based approach to protecting half the terrestrial realm. *BioScience* 67 (6): 534–545. https://doi.org/10.1093/biosci/bix014

Dodson, C.H. (1966) Ethology of some bees of the tribe Euglossini (Hymenoptera: Apidae). *Journal of Kansas Entomological Society* 39 (4): 607–629. https://www.jstor.org/stable/25083566

Dollman, H.C. (1915) *Glossina morsitans*, Westw.: Some notes on the parasitisation of its pupae. *Transactions of the Entomological Society of London* 1915: 394–396 + pl.

LXIV.
Dubitzky, A., Blank, S.M. & Schönitzer, K. (2005) Die hymenopterenfauna (Symphyta, Aculeata) im norden von Dachau, Bayern. *Linzer biologische Beiträge* 37 (1): 235–314.
Duffield, R.M. & Blum, M.S. (1973) 4-Methyl-3-Heptanone: Identification and function in *Neoponera villosa* (Hymenoptera: Formicidae). *Annals of the Entomological Society of America* 66 (6): 1357. https://doi.org/10.1093/aesa/66.6.1357
Dutt, G.R. (1912) Life histories of Indian insects — IV (Hymenoptera). *Memoirs of the Department of Agriculture in India*, *Entomological Series* 12 (4): 183–267.
Edmunds, M. (1974) *Defence in animals: A survey of anti-predator defences*. Longman, Harlow, xviii + 358 pp.
Edwards, G.A. & Ruska, H. (1955) The function and metabolism of certain insect muscles in relation to their structure. *The Quarterly Journal of Microscopical Science* 96 (2): 151–159. https://doi.org/10.1242/jcs.s3-96.34.151
Eminson, R.A.F. (1915) Observations on *Glossina morsitans* in Northern Rhodesia. *Bulletin of Entomological Research* 5 (4): 381–382. https://doi.org/10.1017/S0007485300030388
Endler, J.A. (1991) Interactions between predators and prey. *In*: Krebs, J.A. & Davies, N.B. (eds) *Behavioural ecology: An evolutionary approach*. Blackwell Scientific, Oxford, pp. 169–196.
Erber, D. (1988) Biology of Camptosomata Clytrinae - Cryptocephalinae - Chlamisinae – Lamprosomatinae. *In*: Jolivet, P., Petitpierre, E. & Hsiao, T.H. (eds) *Biology of Chrysomelidae*. Series Entomologica, vol. 42. Kluwer Academic Publishers, Boston, pp. 513–552. https://doi.org/10.1007/978-94-009-3105-3_30
Evans, D.A. & Miller, B.R. (1969) A note on adult overwintering of *Dasymutilla nigripes* in Michigan (Hymenoptera: Mutillidae). *The Michigan Entomologist* 2 (3–4): 74.
Evans, D.A., Miller, B.R. & Bartlett, C.B. (1973) Host searching range of *Dasymutilla nigripes* (Fabricius) as investigated by tagging (Hymenoptera: Mutillidae). *Journal of the Kansas Entomological Society* 46 (3): 343–346. https://www.jstor.org/stable/25082582
Evans, H.E. (1957) *Studies on the comparative ethology of digger wasps of the genus* Bembix. Comstock Publishing Associates, Ithaca, x + 248 pp.
Evans, H.E. (1966) Discovery of the female *Plumarius* (Hymenoptera, Plumariidae). *Psyche* 74 (4): 229–237. https://doi.org/10.1155/1966/31937
Evans, H.E. (1969) Phoretic copulation in Hymenoptera. *Entomological News* 80 (5): 113–124.
Evans, H.E. (1974) Digger wasps as colonizers of new habitat (Hymenoptera: Aculeata). *Journal of the New York Entomological Society* 82 (4): 259–267. https://www.jstor.org/stable/25008941
Evans, H.E. & O'Neill, K.M. (1988) *The natural history and behavior of North American beewolves*. Comstock Publishing Associates, Ithaca, x + 278 pp.
Evans, H.E. & O'Neill, K.M. (2007) *The sand wasps: Natural history and behavior*. Harvard University Press, Cambridge, xx + 340 pp.
Evans, H.E. & Rubink, W.L. (1978) Observations on the prey and nests of seven species of *Cerceris* (Hymenoptera: Sphecidae). *The Great Basin Naturalist* 38 (1): 59–63. https://www.jstor.org/stable/41711615
Evans, H.E. & West Eberhard, M.J. (1970) *The wasps*. University of Michigan Press, Ann Arbor, vi + 265 pp.
Evans, H.E. & Yoshimoto, C.M. (1962) The ecology and nesting behavior of the Pompilidae (Hymenoptera) of the Northeastern United States. *Miscellaneous Publications of the*

Entomological Society of America 3: 66–119.
Ewing, A.W. (1989) *Arthropod bioacoustics: Neurobiology and behaviour*. Edinburgh University Press, Edinburgh, x + 260 pp.
Fabricius, J.C. (1804) *Systema Piezatorum secundum Ordines, Genera, Species adjectis Synonymis, Locis, Observationibus, Descriptionibus*. Carolum Reichard, Brunsvigae, pp. i–xiv + 15–440 + 1–30. https://doi.org/10.5962/bhl.title.10490
Fales, H.M., Blum, M.S., Crewe, R.M. & Brand, J.M. (1972) Alarm pheromones in the genus *Manica* derived from the mandibular gland. *Journal of Insect Physiology* 18 (6): 1077–1088. https://doi.org/10.1016/0022-1910(72)90142-4
Fales, H.M., Jaouni, T.M., Schmidt, J.O. & Blum, M.S. (1980) Mandibular gland allomones of *Dasymutilla occidentalis* and other mutillid wasps. *Journal of Chemical Ecology* 6: 895–903. https://doi.org/10.1007/BF00990473
Fattig, P.W. (1936) An unusual mating of velvet ants (Hymen.: Mutillidae). *Entomological News* 47 (2): 51–52.
Fattig, P.W. (1943) The Mutillidae or velvet ants of Georgia. *Emory University Museum Bulletin* 1: 1–24.
Ferguson, W.E. (1962) Biological characteristics of the mutillid subgenus *Photopsis* Blake and their systematic values. *University of California Publications in Entomology* 27: 1–92.
Ferguson, W.E. (1966) Distribution of diurnal Mutillidae in Western North America. *Bulletin of the Entomological Society of America* 12 (2): 113–114. https://doi.org/10.1093/besa/12.2.113a
Ferguson, W.E. (1967) Male sphaeropthalmine mutillid wasps of the Nevada Test Site. *Brigham Young University Science Bulletin*, *Biological Series* 8 (4): 1–26.
Ferton, C. (1908) Notes détachées sur l'instinct des hyménoptères mellifères et ravisseurs (4^{e} série) avec la description de quelques espèces et la planche 14. *Annales de la Société Entomologique de France* 77: 535–586 + pl. 14.
Ferton, C. (1921) Notes détachées sur l'instinct des hyménoptères mellifères et ravisseurs (9^{e} série) avec la description de deux espèces nouvelles. *Annales de la Société Entomologique de France* 89: 329–375.
Ferton, C. (1923) *La Vie des Abeilles et des Guêpes*. Étienne Chiron, Paris, xvi + 376 pp.
Fiedler, O.G.H. & Kluge, E.B. (1954) The parasites of tsetse flies in Zululand with special reference to the influence of the hosts upon them. *Onderstepoort Journal of Veterinary Research* 26 (3): 399–404.
Flores, G.E., Lagos, S.J. & Roig-Juñent, S. (2004) Artrópodos epígeos que viven bajo la copa del algarrobo (*Prosopis flexuosa*) en la Reserva Telteca (Mendoza, Argentina). *Multequina* 13 (2): 71–90.
Fox, W.J. (1899) The North American Mutillidae. *Transactions of the American Entomological Society* 25: 219–300. https://www.jstor.org/stable/25076689
Gall, B.G., Spivey, K.L., Chapman, T.L., Delph, R.J., Brodie, E.D. Jr. & Wilson, J.S. (2018) The indestructible insect: Velvet ants from across the United States avoid predation by representatives from all major tetrapod clades. *Ecology and Evolution* 8 (11): 5852–5862. https://doi.org/10.1002/ece3.4123
Garcia, E.Q., Cambra, R. & Melo, G.A.R. (2006) Sexual associations for two species of mutillid wasps (Hymenoptera, Mutillidae), with description of a new species of *Anomophotopsis*. *Revista Brasileira de Entomologia* 50 (3): 379–384.
Garófalo, C.A., Camillo, E. & Serrano, J.C. (2011) Reproductive aspects of *Meloetyphlus fuscatus* a meloid beetle cleptoparasite of the bee *Eulaema nigrita* (Hymenoptera, Apidae, Euglossini). *Apidologie* 42 (3): 337–348. https://doi.org/10.1007/s13592-011-0023-y

Gauld, I. & Bolton, B. (1988) *The Hymenoptera*. Oxford University Press, Oxford, xii + 332 pp.
Genise, J.F. & Straneck, R. (1991) Preliminary studies on the taxonomic value of stridulation and the stridulatory organ in the Mutillidae. *Sphecos* 21: 7–11.
Giner Marí, J. (1944) *Himenópteros de España*. *Fams. Apterogynidae y Mutillidae*. Instituto Español de Entomologia, Madrid, 124 pp.
Godfray, H.C.J. (1994) *Parasitoids: Behavioral and evolutionary ecology*. Princeton University Press, Princeton, x + 473 pp.
Gogala, A. (2017) Velvet ants of Slovenia (Hymenoptera: Mutillidae). *Scopolia* 90: 1–39.
Gôukon, K. (1993) Host records and some bionomical notes on mutillid wasps in Japan (Hymenoptera, Mutillidae). *Chugoku Kontyu* 7: 35–40. (in Japanese)
Gôukon, K., Sakagami, S.F. & Maeta, Y. (1986) Bionomic comparison of two populations of a eusocial halictine bee, *Lasioglossum duplex*, in northern Japan. Bionomics of the eusocial halictine bee *Lasioglossum duplex* VIII. *Japanese Journal of Ecology* 35 (5): 587–600. https://doi.org/10.18960/seitai.35.5_587
Goulet, H. & Huber, J.T. (1993) *Hymenoptera of the world: An identification guide to families*. Agriculture Canada, Ottawa, viii + 668 pp.
Gow, A.S.F. & Scholfield, A.F. (1953) *Nicander: The poems and poetical fragments*. Cambridge University Press, Cambridge.
Greenewalt, C.H. (1962) Dimensional relationships for flying animals. *Smithsonian Miscellaneous Collections* 144 (2): 1–46.
Grimaldi, D. & Engel, M.S. (2005) *Evolution of the insects*. Cambridge University Press, Cambridge, xvi + 755 pp.
Hammer, K. (1949) Über einige von Kjell Kolthoff und anderen in China gesammelten Hymenoptera. Chrysididae, Cleptidae, Mutillidae. *Arkiv för zoologi* 42A (8): 1–12.
Haneda, Y. (1979) A new species of *Myrmosa* (Hymenoptera: Tiphiidae) from Japan. *Kontyû* 47 (4): 540–542.
Harris, R.H.T.P. (1930) *Report on the bionomics of the tsetse fly (*Glossina pallidipes *Aust.) and a preliminary report on a new method of control, presented to the Provincial Administration of Natal*. Natal Witness, Pietermaritzburg, 75 pp.
Harrison, J.F. & Roberts, S.P. (2000) Flight respiration and energetics. *Annual Review of Physiology* 62: 179–205. https://doi.org/10.1146/annurev.physiol.62.1.179
Harrison, L. (1915) Mallophaga from *Apteryx*, and their significance; with a note on the genus *Rallicola*. *Parasitology* 8 (1): 88–100. https://doi.org/10.1017/S0031182000010428
Hayes, W.P. (1924) Two mutillids (Hym.) hyperparasitic on white grubs (Scarab., Col.). *Bulletin of the Brooklyn Entomological Society* 19 (4): 153.
Hearn, L.R., Williams, K.A., Stevens, M.I., Schwarz, M.P., Davies, O.K. & Parslow, B.A. (2019) Description and novel host records for a new species of Australian mutillid wasp (Hymenoptera: Mutillidae) from hylaeine bee nests (Hymenoptera: Colletidae). *Austral Entomology* 58 (3): 524–532. https://doi.org/10.1111/aen.12414
Hearn, L.R., Stevens, M.I., Schwarz, M.P. & Parslow, B.A. (2021) Parasitoids of the uniquely social colletid bee *Amphylaeus morosus* (Hymenoptera: Colletidae) in Victoria. *Memoirs of Museum Victoria* 80: 183–191. https://doi.org/10.24199/j.mmv.2021.80.10
Heaversedge, R.C. (1968) Variation in the size of insect parasites of puparia of *Glossina* spp. *Bulletin of Entomological Research* 28 (1): 153–158. https://doi.org/10.1017/S0007485300055930
Heaversedge, R.C. (1969a) Insect parasites of *Glossina pallidipes* Aust. puparia in Rhodesia. *Journal of the Entomological Society of Southern Africa* 32 (1): 225–229.

https://hdl.handle.net/10520/AJA00128789_4005
Heaversedge, R.C. (1969b) Levels of insect parasitism in puparia of *Glossina morsitans orientalis* Vanderplank (Diptera) in Rhodesia. *Journal of the Entomological Society of Southern Africa* 32 (1): 231–235. https://hdl.handle.net/10520/AJA00128789_4006
Heaversedge, R.C. (1969c) Brief notes on the reproductive morphology of *Mutilla glossinae* Turner (Hymenoptera) and the development of its immature stages. *Journal of the Entomological Society of Southern Africa* 32 (2): 485–488. https://hdl.handle.net/10520/AJA00128789_3592
Heaversedge, R.C. (1970) Developmental periods of insect parasites of *Glossina morsitans orientalis* Vanderplank (Diptera: Muscidae). *Journal of the Entomological Society of Southern Africa* 33 (2): 351–354. https://hdl.handle.net/10520/AJA00128789_3142
Hebert, P.D.N., Cywinska, A., Ball, S.L. & deWaard, J. R. (2003) Biological identifications through DNA barcodes. *Proceedings of the Royal Society B* 270 (1512): 313–321. https://doi.org/10.1098/rspb.2002.2218
Heimpel, G.E. & de Boer, J.G. (2008) Sex determination in the Hymenoptera. *Annual Review of Entomology* 53: 209–230. https://doi.org/10.1146/annurev.ento.53.103106.093441
Hermann, H.R. (1968) The hymenopterous poison apparatus IV. *Dasymutilla occidentalis* (Hymenoptera: Mutillidae). *Journal of the Georgia Entomological Society* 3 (1): 1–10.
Hermann, H.R. & Mullen, M.A. (1974) Stridulatory structures in *Dasymutilla occidentalis* (Hymenoptera: Mutillidae). *Journal of the Georgia Entomological Society* 9 (3): 204–205.
Hesse, A.J. (1935) Scientific results of the Vernay-Lang Kalahari Expedition, March to September, 1930. Mutillidae (Hymenoptera). *Annals of the Transvaal Museum* 16 (4): 507–524. https://hdl.handle.net/10520/AJA00411752_581
Hines, H.M., Witkowski, P., Wilson, J.S. & Wakamatsu, K. (2017) Melanic variation underlies aposematic color variation in two hymenopteran mimicry systems. *PLoS ONE* 12 (7): e0182135. https://doi.org/10.1371/journal.pone.0182135
Hinton, H.E., Gibbs, D.F. & Silberglied, R. (1969) Stridulatory files as diffraction gratings in mutillid wasps. *Journal of Insect Physiology* 15 (4): 549–550. https://doi.org/10.1016/0022-1910(69)90253-4
Hook, A.W. & Evans, H.E. (1991) Prey and parasites of *Cerceris fumipennis* (Hymenoptera: Sphecidae) from central Texas, with description of the larva of *Dasymutilla scaevola* (Hymenoptera: Mutillidae). *Journal of the Kansas Entomological Society* 64 (3): 257–264. https://www.jstor.org/stable/25085285
Houston, T.F. & Thorp, R.W. (1984) Bionomics of the bee *Stenotritus greavesi* and ethological characteristics of Stenotritidae (Hymenoptera). *Records of the Western Australian Museum* 11 (4): 375–385.
Humphreys, R.K. & Ruxton, G. (2018) A review of thanatosis (death feigning) as an anti-predator behaviour. *Behavioral Ecology and Sociobiology* 72 (2): 22. https://doi.org/10.1007/s00265-017-2436-8
Hurd, P. (1951a) The California velvet ants of the genus *Dasymutilla* Ashmead (Hymenoptera: Mutillidae). *Bulletin of the California Insect Survey* 1 (4): 89–118.
Hurd, P. (1951b) The female of *Pseudomethoca anthracina* (Fox) (Hymenoptera: Mutillidae). *The Pan-Pacific Entomologist* 27 (4): 156.
Invrea, F. (1950) Mutillidi nuovi o notevoli del Bacino Mediterraneo (Hymenoptera, Mutillidae). *Memorie della Società Entomologica Italiana* 29: 19–27.
Invrea, F. (1951) Mutillidi nuovi o notevoli del Bacino Mediterraneo (Hymenoptera, Mutillidae). II Parte. *Bolletino della Società Entomologica Italiana* 81 (3–4): 34–43.
Invrea, F. (1964) *Mutillidae-Myrmosidae*. *Fauna d'Italia 5*. Edizioni Calderini, Bologna, xii

+ 302 pp. + 1 p.
Isip, J.E., Jones, M.E.H. & Cooper, N. (2022) Clade-wide variation in bite-force performance is determined primarily by size, not ecology. *Proceedings of the Royal Society B* 289 (1969): 20212493. https://doi.org/10.1098/rspb.2021.2493
Ivanova, N.V., deWaard, J.R. & Hebert, P.D.N. (2006) An inexpensive, automation-friendly protocol for recovering high-quality DNA. *Molecular Ecology Notes* 6 (4): 998–1002. https://doi.org/10.1111/j.1471-8286.2006.01428.x
Janvier, H. (1933) Étude biologique de quelques hyménoptères du Chili. *Annales des sciences naturelles Zoologie* dixième série 16 (14): 209–356.
Jellison, W.L. (1982) Concentrations of mutillid wasps (Hymenoptera: Mutillidae). *Entomological News* 93 (1): 27–28.
Jenkins, C.N., Pimm, S.L. & Joppa, L.N. (2013) Global patterns of terrestrial vertebrate diversity and conservation. *Proceedings of the National Academy of Sciences* 110 (28): E2602–E2610. https://doi.org/10.1073/pnas.1302251110
Jones, T.H., Conner, W.E., Kluge, A.F., Eisner, T. & Meinwald, J. (1976) Defensive substances of opilionids. *Experientia* 32: 1234–1235. https://doi.org/10.1007/BF01953066
Jones, T.H., Meinwald, J., Hicks, K. & Eisner, T. (1977) Characterization and synthesis of volatile compounds from the defensive secretions of some "daddy longlegs" (Arachnida: Opiliones: *Leiobunum* spp.). *Proceedings of the National Academy of Sciences* 74 (2): 419–422. https://doi.org/10.1073/pnas.74.2.419
József, M. & Zoltán, G. (2011) Velvet ants of Hungary (Hymenoptera: Mutillidae). *Natura Somogyiensis* 18: 1–198.
Kamoun, S. & Hogenhout, S.A. (1996) Flightlessness and rapid terrestrial locomotion in tiger beetles of the *Cicindela* L. subgenus *Rivacindela* van Nidek from saline habitats of Australia (Coleoptera: Cicindelidae). *The Coleopterists Bulletin* 50 (3): 221–230. https://www.jstor.org/stable/4009161
Kass, J.M., Guénard, B., Dudley, K.L., Jenkins, C.N., Azuma, F., Fisher, B.L., Parr, C.L., Gibb, H., Longino, J.T., Ward, P.S., Chao, A., Lubertazzi, D., Weiser, M., Jetz, W., Guralnick, R., Blatrix, R., Lauriers, J.D., Donoso, D.A., Georgiadis, C., Gomez, K., Hawkes, P.G., Johnson, R.A., Lattke, J.E., MacGown, J.A., Mackay, W., Robson, S., Sanders, N.J., Dunn, R.R. & Economo, E.P. (2022) The global distribution of known and undiscovered ant biodiversity. *Science Advances* 8 (31): eabp9908. https://doi.org/10.1126/sciadv.abp9908
Katayama, E. (1966) Observations on the nests of *Bombus ardens* Smith and *B. diversus* Smith. *Insect* 17 (2–3): 1–6. (in Japanese)
Katayama, E. (2008) Oviposition behavior of *Mutilla mikado* Cameron (Hymenoptera, Mutillidae), an ectoparasitoid of bumblebees (Hymenoptera, Apidae). *Japanese Journal of Entomology* 11 (2): 57–68. (in Japanese)
Katayama, E., Ochiai, H. & Takamizawa, K. (1990) Supplementary notes on nests of some Japanese bumblebees. II. *Bombus ussurensis*. *Japanese Journal of Entomology* 58 (2): 335–346.
Katayama, E. & Takamizawa, K. (2004) Supplementary observations on the nests of *Bombus* (*Bombus*) *hypocrita hypocrita* Pérez (Hymenoptera, Apidae), with special reference to the nest architecture and colony size. *Japanese Journal of Entomology* 7 (3): 105–118. (in Japanese)
Katayama, E., Takamizawa, K. & Ochiai, H. (1993) Supplementary notes on the nests of some Japanese bumblebees. III. *Bombus* (*Thoracobombus*) *deuteronymus maruhanabachi*. *Japanese Journal of Entomology* 61 (4): 749–761.
Katayama, E., Takamizawa, K. & Ochiai, H. (1996) Nests of the Japanese bumblebee,

Bombus (*Diversobombus*) *diversus diversus*: Supplementary observations. *New Entomologist* 45 (1–2): 23–33.
Kawashima, I. & Suzuki, Y. 2002. [The Hymenoptera of Miura Peninsula, second report]. *Kanagawa-Chûhô* 140: 1–31. (in Japanese)
Kier, G., Kreft, H., Lee, T.M., Jetz, W., Ibisch, P.L., Nowicki, C., Mutke, J. & Barthlott, W. (2009) A global assessment of endemism and species richness across island and mainland regions. *Proceedings of the National Academy of Sciences* 106 (3): 9322–9327. https://doi.org/10.1073/pnas.0810306106
Kimsey, L.S. (1980) Notes on the biology of some Panamanian Pompilidae, with a description of a communal nest (Hymenoptera). *The Pan-Pacific Entomologist* 56 (2): 98–100.
Kimsey, L.S. (1991) Relationships among the tiphiid wasp subfamilies (Hymenoptera). *Systematic Entomology* 16 (4): 427–438. https://doi.org/10.1111/j.1365-3113.1991.tb00677.x
Kimsey, L.S. (2006) Competing taxonomies: Reexamination of the female-based genera of Brachycistidinae (Hymenoptera: Tiphiidae). *Zootaxa* 1211: 21–34. https://doi.org/10.11646/zootaxa.1211.1.2
Kimsey, L.S. & Bohart, R.M. (1991 [1990]) *The chrysidid wasps of the world*. Oxford Science Publications, New York, xii + 652 pp.
Kimsey, L.S. & Wasbauer, M.S. (2006) Phylogeny and checklist of the nocturnal tiphiids of the Western Hemisphere (Hymenoptera: Tiphiidae: Brachycistidinae). *Journal of Hymenoptera Research* 15 (1): 9–25.
Klatt, B.K., Holzschuh, A., Westphal, C., Clough, Y., Smit, I., Pawelzik, E. & Tscharntke, T. (2014) Bee pollination improves crop quality, shelf life and commercial value. *Proceedings of the Royal Society B* 281 (1775): 20132440. https://doi.org/10.1098/rspb.2013.2440
Klein, A.-M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C. & Tscharntke, T. (2007) Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B* 274 (1608): 303–313. https://doi.org/10.1098/rspb.2006.3721
Knerer, G. & Atwood, C.E. (1967 [1966]) Parasitization of social halictine bees in Southern Ontario. *Proceedings of the Entomological Society of Ontario* 97: 103–110.
Kohl, F.F. (1883 [1882]) Neue Hymenopteren in den Sammlungen des k. k. zoolog. Hof-Cabinetes zu Wien. I. *Verhandlungen der kaiserlich-königlichen Zoologisch-Botanischen Gesellschaft in Wien* 32: 475–498 + Tab. XXIII.
Krogmann, L., Austin, A.D. & Naumann, I.D. (2009) Systematics and biogeography of Australian rhopalosomatid wasps (Hymenoptera: Rhopalosomatidae) with a global synopsis of the enigmatic genus *Olixon* Cameron. *Systematic Entomology* 34 (2): 222–251. https://doi.org/10.1111/j.1365-3113.2008.00460.x
Krombein, K.V. (1940 [1939]) Studies in the Tiphiidae (Hymenoptera Aculeata) IV. A revision of the Myrmosinae of the New World with a discussion of the Old World species. *Transactions of the American Entomological Society* 65 (4): 415–465. https://www.jstor.org/stable/25077448
Krombein, K.V. (1948) The identity of the male of *Pseudomethoca simillima* (Smith). (Hymenoptera: Mutillidae). *Entomological News* 59 (7): 187–189.
Krombein, K.V. (1949) Two new gynandromorphs, with a list of previously recorded sexual aberrations in the scolioid wasps. *Proceedings of the United States National Museum* 100 (3257): 55–59.
Krombein, K.V. (1954) Taxonomic notes on some wasps from Florida with descriptions of new species and subspecies (Hymenoptera, Scolioidea and Sphecoidea). *Transactions*

of the American Entomological Society 80 (1): 1–27. https://www.jstor.org/stable/25077676

Krombein, K.V. (1958) Miscellaneous prey records of solitary wasps. III (Hymenoptera, Aculeata). *Proceedings of the Biological Society of Washington* 71: 21–26.

Krombein, K.V. (1964) Results of the Archbold Expeditions. No. 87. Biological notes of some Floridan wasps (Hymenoptera, Aculeata). *American Museum Novitates* 2201: 1–27.

Krombein, K.V. (1967) *Trap-nesting wasps and bees: Life histories, nests and associates*. Smithsonian Institution Press, Washington DC, vi + 570 pp.

Krombein, K.V. (1971) A monograph of the Mutillidae of New Guinea, Bismarck Archipelago and Solomon Islands. Part 1: Mutillinae (Hymenoptera Aculeata). *In*: Asahinas, S., Linsley Gressitt, J., Hidaka, Z., Nishida, T. & Nomura, K. (eds) *Entomological essays to commemorate the retirement of Professor K. Yasumatsu*. Hokuryukan, Tokyo, pp. 25–60.

Krombein, K.V. (1972) Monograph of the Madagascan Mutillidae (Hymenoptera). Part I: Myrmillini, Mutillini and Smicromyrmini. *Annales, Musée Royal de l'Afrique Centrale*, Série in 8°, Sciences Zoologiques 199: I–X + 1–61.

Krombein, K.V. (1978) Biosystematic studies of Ceylonese wasps, III. Life history, nest and associates of *Paraleptomenes mephitis* (Cameron) (Hymenoptera, Eumenidae). *Journal of the Kansas Entomological Society* 51 (4): 721–734. https://www.jstor.org/stable/25083863

Krombein, K.V. (1979) Biosystematic studies of Ceylonese wasps, IV. Kudakrumiinae, a new subfamily of primitive wasps (Hymenoptera, Mutillidae). *Transactions of the American Entomological Society* 105 (1): 67–83. https://www.jstor.org/stable/25078234

Krombein, K.V. (1992) Host relationships, ethology and systematics of *Pseudomethoca* Ashmead (Hymenoptera: Mutillidae, Andrenidae, Halictidae and Anthophoridae). *Proceedings of the Entomological Society of Washington* 94 (1): 91–106.

Krombein, K.V. & Evans, H.E. (1954) A list of wasps collected in Florida, March 29 to April 5, 1953, with biological annotations (Hymenoptera, Aculeata). *Proceedings of the Entomological Society of Washington* 56 (5): 225–236.

Krombein, K.V. & Evans, H.E. (1955) An annotated list of wasps collected in Florida, March 20 to April 3, 1954 (Hymenoptera, Aculeata). *Proceedings of the Entomological Society of Washington* 57 (5): 223–235.

Krombein, K.V. & Lelej, A.S. (1999) Biosystematic studies of Ceylonese wasps, XXII: *Bethsmyrmilla*, a new genus of mutillid wasps (Hymenoptera: Mutillidae: Myrmillinae). *Proceedings of the Entomological Society of Washington* 101 (1): 143–148.

Krombein, K.V. & Norden, B.B. (1996) Behavior of nesting *Episyron conterminus posterus* (Fox) and its cleptoparasite *Ephuta s. slossonae* (Fox) (Hymenoptera: Pompilidae, Mutillidae). *Proceedings of the Entomological Society of Washington* 98 (2): 188–194.

Kumpanenko, A., Gladun, D. & Vilhelmsen, L. (2019) Functional morphology and evolution of the sting sheaths in Aculeata (Hymenoptera). *Arthropod Systematics & Phylogeny* 77 (2): 325–338. https://doi.org/10.26049/ASP77-2-2019-08

Kumpanenko, A., Gladun, D. & Vilhelmsen, L. (2022) Morphology of the sting apparatus in velvet ants of the subfamilies Myrmosinae, Dasylabrinae, Myrmillinae and Mutillinae (Hymenoptera: Mutillidae). *Zoomorphology* 141 (1): 81–94. https://doi.org/10.1007/s00435-022-00552-w

Lamborn, W.A. (1916) Third report on *Glossina* investigations in Nyasaand. *Bulletin of*

Entomological Research 7 (1): 29–50. https://doi.org/10.1017/S0007485300017053
Lamborn, W.A. (1920) Some further notes on the tsetse-flies of Nyasaland. *Bulletin of Entomological Research* 11 (2): 101–104. https://doi.org/10.1017/S0007485300044503
Lamborn, W.A. (1925) An attempt to control *Glossina morsitans* by means of *Syntomosphyrum glossinae*, Waterston. *Bulletin of Entomological Research* 15 (3): 303–309. https://doi.org/10.1017/S0007485300046277
Lelej, A.S. (1976) Velvet ants of the genus *Dasylabris* Rad. (Hymenoptera, Mutillidae) in the Soviet fauna. *Entomologicheskoe Obozrenie* 55 (1): 189–204. (in Russian). [English translation (1976) in *Entomological Review* 55 (1): 136–146]
Lelej, A.S. (1978) Superfamily Mutilloidea. *In*: Tobias, V.I. (ed.) *Keys to the insects of the European part of the USSR Vol. 3, pt 1*. Nauka, Leningrad, pp. 71–84. (in Russian)
Lelej, A.S. (1979) A new genus of velvet ants (Hymenoptera, Mutillidae) from south-east Asia. *Zoologicheskiy Zhurnal* 58 (7): 1065–1067. (in Russian)
Lelej, A.S. (1985) *Osy-nemki (Hymenoptera, Mutillidae) Fauny SSSR i Sopredelnykh Stran* [*The velvet ants (Hymenoptera, Mutillidae) of the USSR and neighboring countries*]. Nauka, Leningrad, 268 pp. (in Russian)
Lelej, A.S. (1992) Two interesting species of velvet ants from China (Hymenoptera, Mutillidae). *Entomofauna* 13 (19): 281–288.
Lelej, A.S. (1993) A new genus of velvet ants from Sri Lanka (Insecta, Hymenoptera, Mutillidae). *Spixiana* 16 (3): 233–236.
Lelej, A.S. (1995a) A review of Palaearctic and Oriental species of genus *Nemka* Lelej with description of Oriental genus *Mickelomyrme* gen. n. (Hymenoptera, Mutillidae). *Far Eastern Entomologist* 6: 1–20.
Lelej, A.S. (1995b) To the knowledge of East Asian species of the tribe Smicromyrmini Bischoff, 1920 (Hymenoptera, Mutillidae) with description of four new genera and eight new species. *Far Eastern Entomologist* 13: 1–28.
Lelej, A.S. (1995c) To the knowledge of the velvet ants (Hymenoptera, Mutillidae) of Rajasthan, Western India. *Far Eastern Entomologist* 20: 1–11.
Lelej, A.S. (1996a) A review of the East Asian species of *Orientilla* (Hymenoptera, Mutillidae). *Memoirs of the Entomological Society of Washington* 17: 103–107.
Lelej, A.S. (1996b) To the knowledge of the East Asian species of the tribe Trogaspidiini Bischoff, 1920 (Hymenoptera, Mutillidae) with description of eight new genera and two new species. *Far Eastern Entomologist* 30: 1–24.
Lelej, A.S. (1996c) Mutillid wasps collected in Malaysia and Indonesia by Dr. Sk. Yamane (Hymenoptera, Mutillidae). *Tropics* 6 (1–2): 91–104. https://doi.org/10.3759/tropics.6.91
Lelej, A.S. (1996d) A review of the East Asian species of *Mickelomyrme* Lelej, 1995 (Hymenoptera, Mutillidae). *Entomofauna* 17 (15): 277–292.
Lelej AS (2002) *Catalogue of the Mutillidae (Hymenoptera) of the Palaearctic Region*. Dalnauka, Vladivostok, 172 pp.
Lelej AS (2005) *Catalogue of the Mutillidae (Hymenoptera) of the Oriental Region*. Dalnauka, Vladivostok, 252 pp.
Lelej, A.S. (2007) Biogeography of mutillid wasps (Hymenoptera, Mutillidae). *In*: Rasnitsyn, A.P. & Gokhman, V.E. (eds) *Studies on hymenopterous insects*. *Collection of scientific papers*. KMK Scientific Press Ltd., Moscow, pp. 82–111. (in Russian)
Lelej, A.S. (2012) A new species of *Rhopalomutilla* André, 1901 (Hymenoptera: Mutillidae) from South Vietnam. *Russian Entomological Journal* 21 (2): 143–145.
Lelej, A.S. (2016) The new synonymy of *Physetopoda* species (Hymenoptera: Mutillidae) from the United Arab Emirates. *Far Eastern Entomologist* 311: 7–8.

Lelej, A.S. (2020a) To the knowledge of velvet ants of the genera *Artiotilla* Invrea, *Radoszkowskitilla* Lelej and *Taiwanomyrme* Tsuneki (Hymenoptera: Mutillidae). *Far Eastern Entomologist* 410: 1–10. https://doi.org/10.25221/fee.410.1

Lelej, A.S. (2020b) Three new species of velvet ants from the tribe Smicromyrmini (Hymenoptera: Mutillidae) with unusual color syndrome. *Far Eastern Entomologist* 421: 1–9. https://doi.org/10.25221/fee.421.1

Lelej, A.S. (2021) A new species of the genus *Petersenidia* Lelej (Hymenoptera: Mutillidae) from Indonesia, eastward of Wallace's line. *Zootaxa* 5006 (1): 101–105. https://doi.org/10.11646/zootaxa.5006.1.13

Lelej, A.S. (2023) Review of the tribe Ctenotillini (Hymenoptera: Mutillidae) from Oriental and Palaearctic Regions. *Far Eastern Entomologist* 480: 1–22. https://doi.org/10.25221/fee.480.1

Lelej, A.S. & Brothers, D.J. (2008) The genus-group names of Mutillidae (Hymenoptera) and their type species, with a new genus, new name, new synonymies, new combinations and lectotypifications. *Zootaxa* 1889 (1): 1–79. https://doi.org/10.11646/zootaxa.1889.1.1

Lelej, A.S., Choi J.-Y. & Tripotin, P. (2001) Review of the mutillid wasps (Hymenoptera, Mutillidae) of Korea. *Far Eastern Entomologist* 96: 1–15.

Lelej, A.S. & Krombein, K.V. (1999) Two remarkable new genera of mutillid wasps (Hymenoptera: Mutillidae, Sphaeropthalminae, Pseudomethocini) from Thailand. *Far Eastern Entomologist* 79: 1–8.

Lelej, A.S. & Krombein, K.V. (2001) Review of the Oriental mutillid wasps of the subfamily Ticoplinae (Hymenoptera, Mutillidae). *Far Eastern Entomologist* 99: 1–18.

Lelej, A.S. & Osten, T. (2004) To the knowledge of the mutillid and bradynobaenid wasps of Iran (Hymenoptera: Mutillidae, Bradynobaenidae). *Proceedings of the Russian Entomological Society* 75 (1): 253–262.

Lelej, A.S., Proshchalykin, M. Yu. & Loktionov, V.M. (2014) To the knowledge of velvet ants (Hymenoptera, Mutillidae) of East Siberia. *Euroasian Entomological Journal* 13 (4): 388–394. (in Russian)

Lelej, A.S. & van Harten, A. (2006) A review of the Mutillidae (Hymenoptera) of Yemen. *Zootaxa* 1226 (1): 1–50. https://doi.org/10.11646/zootaxa.1226.1.1

Lelej, A.S. & Williams, K.A. (2023) Review of the tribe Smicromyrmini Bischoff, 1920 (Hymenoptera: Mutillidae). *Zootaxa* 5231 (2): 101–140. https://doi.org/10.11646/zootaxa.5231.2.1

Lelej, A.S., Williams, K.A., Loktionov, V.M., Pang, H. & Xu, Z.-f. (2017) Review of the genus *Zeugomutilla* Chen, 1957 (Hymenoptera, Mutillidae, Mutillini), with description of two new species. *Zootaxa* 4247 (1): 1–15. https://doi.org/10.11646/zootaxa.4247.1.1

Lelej, A.S., Williams, K.A., Terine, J.B., Okayasu, J., Parikh, G. & Kumar, G.P. (2023) Review of the tribe Mutillini (Hymenoptera: Mutillidae) from the Oriental Region. *Zootaxa* 5228 (4): 455–476. https://doi.org/10.11646/zootaxa.5228.4.5

Lelej, A.S. & Yamane, Sk. (1992) Interesting velvet ants (Hymenoptera, Mutillidae) from Japan and Korea. *Japanese Journal of Entomology* 60 (3): 625–632.

Lelej, A.S., Zhou, H.-t., Loktionov, V.M. & Xu, Z.-f. (2016) Review of the genus *Promecidia* Lelej, 1996, with description of two new species from China (Hymenoptera, Mutillidae, Trogaspidiini). *ZooKeys* 641: 103–120. https://doi.org/10.3897/zookeys.641.10765

Lepeletier de Saint-Fargeau, A. (1845) *Histoire naturelle des Insectes. Hyménoptères*. *Tome Troisième*. Roret, Paris, [4] + 646 pp. https://doi.org/10.5962/bhl.title.9005

Lim, K., Lee, S., Orr, M. & Lee, S. (2022) Harrison's rule corroborated for the body size of

cleptoparasitic cuckoo bees (Hymenoptera: Apidae: Nomadinae) and their hosts. *Scientific Reports* 12: 10984. https://doi.org/10.1038/s41598-022-14938-9

Lima, S.L. & Dill, L.M. (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68 (4): 619–640. https://doi.org/10.1139/z90-092

Lin, N. (1964) Increased parasitic pressure as a major factor in the evolution of social behavior in halictine bees. *Insectes Sociaux* 11: 187–192. https://doi.org/10.1007/BF02222936

Lin, N. (1966) Copulatory behaviour of the cicada killer wasp, *Sphecius speciosus*. *Animal Behaviour* 14 (1): 130–131. https://doi.org/10.1016/S0003-3472(66)80021-0

Lin, N. & Michener, C.D. (1972) Evolution of sociality in insects. *The Quarterly Review of Biology* 47 (2): 131–159. https://doi.org/10.1086/407216

Linnaeus, C. (1758) *Systema Naturae per Regna Tria Naturae, secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis*. *Tomus I. Editio Decima Reformata*. Laurentii Salvii, Holmiae, [4] + 823 pp. + [5]. https://doi.org/10.5962/bhl.title.559

Linsley, E.G. (1960) A fragmentary observation on the mating behavior of *Timulla*. *The Pan-Pacific Entomologist* 36 (1): 36.

Linsley, E.G. & MacSwain, J.W. (1942) The parasites, predators, and inquiline associates of *Anthophora linsleyi*. *The American Midland Naturalist* 27 (2): 402–417. https://doi.org/10.2307/2421008

Linsley, E.G. & MacSwain, J.W. (1952) Notes on some effects of parasitism upon a small population of *Diadasia bituberculata* (Cresson) (Hymenoptera: Anthophoridae). *The Pan-Pacific Entomologist* 28 (3): 131–135.

Linsley, E.G., MacSwain, J.W. & Smith, R.F. (1955) Observations on the mating habits of *Dasymutilla formicalia* Rohwer (Hymenoptera: Mutillidae). *The Canadian Entomologist* 87 (9): 411–413. https://doi.org/10.4039/Ent87411-9

Lloyd, L. (1917) Report on the investigation into the bionomics of *Glossina morsitans* in northern Rhodesia, 1915. *Bulletin of Entomological Research* 7 (1): 67–79. https://doi.org/10.1017/S0007485300017089

Lo Cascio, P. (2015) Worldwide checklist of the island mutillid wasps (Hymenoptera Mutillidae). *Biodiversity Journal* 6 (2): 529–592.

Lo Cascio, P. & Romano, M. (2004) Mutillid wasps of the Italian minor islands (Hymenoptera Mutillidae). *Bolletino della Società Entomologica Italiana* 136 (3): 227–250.

Lopez, A.W. (1931) Annual report of the Entomological Research Bureau, Philippine Sugar Association 1930-1931. *In*: Annual Report of the Research Bureau, Philippine Sugar Association, pp. 227–273.

Lopez, V.M., Bartholomay, P.R., Lima, F.V.O. & Silvestre, R. (2019) Male description of *Horcomutilla projectifrons* (Cresson, 1902) (Hymenoptera, Mutillidae) and the first host record for the genus. *Zootaxa* 4559 (3): 573–576. https://doi.org/10.11646/zootaxa.4559.3.8

Lopez, V.M., Tosta, T.A.A., da Silva, G.G., Bartholomay, P.R., Williams, K.A. & Ferreira, G.F. (2021) Color lightness of velvet ants (Hymenoptera: Mutillidae) follows an environmental gradient. *Journal of Thermal Biology* 100: 1–9. https://doi.org/10.1016/j.jtherbio.2021.103030

Loyola, R.D. & Martins, R.P. (2006) Trap-nest occupation by solitary wasps and bees (Hymenoptera: Aculeata) in a forest urban remanent. *Neotropical Entomology* 35 (1): 41–48. https://doi.org/10.1590/S1519-566X2006000100006

Luz, D.R. & Williams, K.A. (2014) The first sexual associations in the genus *Darditilla*

Casal, 1965 (Hymenoptera, Mutillidae). *ZooKeys* 454: 41–68. https://doi.org/10.3897/zookeys.454.8558
Luz, D.R., Waldren, G.C. & Melo, G.A.R. (2016a) Bees as hosts of mutillid wasps in the Neotropical region (Hymenoptera, Apidae, Mutillidae). *Revisita Brasileira de Entomologia* 60 (4): 302–307. https://doi.org/10.1016/j.rbe.2016.06.001
Luz, D.R., Williams, K.A. & Bartholomay, P.R. (2016b) The mutillid wasps of the *Dasymutilla paradoxa* species-group (Hymenoptera, Mutillidae). *Zootaxa* 4193 (2): 361–372. http://doi.org/10.11646/zootaxa.4193.2.10
Mäklin, F.W. (1856) Om hermafroditism bland insekterne, samt beskrifning öfver en i Helsingfors funne hermafrodit af *Mutilla obscura* Nyl. *Övfersigt af Förhandlingar, Finska Vetenskaps-Societeten, Helsingfors* 3: 106–112.
Manley, D.G. (1977) Notes on the courtship and mating of *Dasymutilla* Ashmead (Hymenoptera: Mutillidae) in California. *The Southwestern Naturalist* 21 (4): 552–554. https://www.jstor.org/stable/30054044
Manley, D.G. (1984) Predation upon velvet ants of the genus *Dasymutilla* in California (Hymenoptera: Mutillidae). *The Pan-Pacific Entomologist* 60 (3): 219–226.
Manley, D.G. (1999a) Synonymy of *Dasymutilla nocturna* Mickel (Hymenoptera: Mutillidae). *The Pan-Pacific Entomologist* 75 (1): 18–22.
Manley, D.G. (1999b) A synonymy for *Pseudomethoca donaeanae* (Cockerell & Fox) (Hymenoptera: Mutillidae). *The Pan-Pacific Entomologist* 75 (1): 32–34.
Manley, D.G. (2000) Defense adaptations in velvet ants (Hymenoptera: Mutillidae) and their possible selective pressures. *In*: Austin, A.D. & Dowton, M. (eds) *Hymenoptera: Evolution, biodiversity and biological control*. CSIRO Publishing, Collingwood, pp. 285–289.
Manley, D.G. (2003) *Dasymutilla jalisco*, a new species of velvet ant (Hymenoptera: Mutillidae) plus new synonymy for *Dasymutilla canina* (Smith). *Proceedings of the Entomological Society of Washington* 105 (3): 697–684.
Manley, D.G. & Deyrup, M.A. (1989) Notes on the biology of *Dasymutilla pyrrhus* (Fox) (Hymenoptera: Mutillidae). *Journal of Entomological Science* 24 (1): 53–56. https://doi.org/10.18474/0749-8004-24.1.53
Manley, D.G. & Neff, J.L. (1989) *Pseudomethoca ilione* (Fox), a new synonym of *P. gila* (Blake) (Hymenoptera: Mutillidae). *The Pan-Pacific Entomologist* 65 (1): 12–14.
Manley, D.G. & Pitts, J.P. (2002) A key to genera and subgenera of Mutillidae (Hymenoptera) in America north of Mexico with description of a new genus. *Journal of Hymenoptera Research* 11 (1): 72–100.
Manley, D.G. & Pitts, J.P. (2007) Tropical and subtropical velvet ants of the genus *Dasymutilla* Ashmead (Hymenoptera: Mutillidae) with descriptions of 45 new species. *Zootaxa* 1487 (1): 1–128. https://doi.org/10.11646/zootaxa.1487.1.1
Manley, D.G. & Radke, W.R. (2002) Synonymy of *Dasymutilla sicheliana* (Saussure) (Hymenoptera: Mutillidae). *The Pan-Pacific Entomologist* 78 (4): 230–234.
Manley, D.G. & Sherbrooke, W.C. (2001) Predation on velvet ants (Hymenoptera: Mutillidae) by Texas horned lizards (*Phrynosoma cornutum*). *The Southwestern Naturalist* 46 (2): 221–222. https://doi.org/10.2307/3672534
Manley, D.G. & Taber, S. III (1978) A mating aggregation of *Dasymutilla foxi* in Southern Arizona. *The Pan-Pacific Entomologist* 54 (3): 231–235.
Mann, W.M. (1915) A gynandromorphous mutillid from Montana. *Psyche* 22: 178–180. https://doi.org/10.1155/1915/54201
Marden, J.H. (1987) Maximum lift production during takeoff in flying animals. *The Journal of Experimental Biology* 130 (1): 235–258. https://doi.org/10.1242/jeb.130.1.235
Markham, R.H. (1986) Biological control of tsetse: Prospects and progress in the use of pupal

parasites. *Insect Science and Its Application* 7 (1): 1–4. https://doi.org/10.1017/S1742758400003015

Masson, R.S., Daoues, K., Measey, J. & Herrel, A. (2023) The evolution of bite force and head morphology in scincid lizards: diet and habitat use as possible drivers. *Biological Journal of the Linnean Society* 140 (1): 58–73. https://doi.org/10.1093/biolinnean/blad052

Masters, W.M. (1979) Insect disturbance stridulation: Its defensive role. *Behavioral Ecology and Sociobiology* 5 (2): 187–200. https://doi.org/10.1007/BF00293305

Matsumura, S. (1911) *Thousand insects of Japan supplement III*. Keiseisha-shoten, Tokyo, 147 pp. + pls 30–41. https://doi.org/10.5962/bhl.title.50811

Matteini Palmerini, M. (2013) Remarks on the behavior of the velvet ant *Nemka viduata viduata* (Pallas, 1773) (Insecta Hymenoptera Mutillidae). *Quaderno di Studi e Notizie di Storia Naturale della Romagna* 37: 237–260.

Matthews, R.W. (1997) Unusual sex allocation in a solitary parasitoid wasp, *Sphaeropthalma pensylvanica* (Hymenoptera: Mutillidae). *The Great Lake Entomologist* 30 (1–2): 51–54.

Mayhew, P.J. (2007) Why are there so many insect species? Perspectives from fossils and phylogenies. *Biological Reviews* 82 (3): 425–454. https://doi.org/10.1111/j.1469-185X.2007.00018.x

McGurk, D.J., Frost, J., Eisenbraun, E.J., Vick, K., Drew, W.A. & Young, J. (1966) Volatile compounds in ants: Identification of 4-methyl-3-heptanone from *Pogonomyrmex* ants. *Journal of Insect Physiology* 12 (11): 1435–1441. https://doi.org/10.1016/0022-1910(66)90157-0

Meinwald, J., Kluge, A.F., Carrel, J.E. & Eisner, T. (1971) Acyclic ketones in the defensive secretion of a "daddy longlegs" (*Leiobunum vittatum*). *Proceedings of the National Academy of Sciences* 68 (7): 1467–1468. https://doi.org/10.1073/pnas.68.7.1467

Mellor, J.E.M. (1927) A note on the mutillid *Ephutomma continua* Fabr. and *Bembex mediterranea* Hdl. in Egypt with a summary of the distribution and of some previously recorded habits of the Mutillidae. *Bulletin de la Société Royale Entomologique d'Egypte* 11: 69–79.

Mellor, J.E.M. (1933) Observations on insects from Mount Troodos in Cyprus. *Proceedings of the Entomological Society of London* 7: 62–63.

Menozzi, C. (1947) *Animali e vegetali dannosi alla barbabietola da zucchero e mezzi per combatterlli*. Società Approvvigionamento Bietole e Vendita Zucchero, Genova.

Mercet, R.G. (1903) Un Mutilido nuevo de España. *Boletín de la Real Sociedad Española de Historia Natural* 3: 173–175.

Mergler, C.J. & Gall, B.G. 2020. Has the indestructible insect met its match? Velvet ants as prey to bufonid toads. *Ethology Ecology & Evolution* 33 (1): 15–24. https://doi.org/10.1080/03949370.2020.1789747

Michener, C.D. 1966. The bionomics of a primitively social bee, *Lasioglossum versatum* (Hymenoptera: Halictidae). *Journal of the Kansas Entomological Society* 39 (2): 193–217. https://www.jstor.org/stable/25083507

Mickel, C.E. (1924a) A revision of the mutillid wasps of the genera *Myrmilloides* and *Pseudomethoca* occurring in America north of Mexico. *Proceedings of the United States National Museum* 64 (15): 1–52 + pls 1–4.

Mickel, C.E. (1924b) An analysis of a bimodal variation in size of the parasite *Dasymutilla bioculata* Cresson (Hymen.: Mutillidae). *Entomological News and Proceedings of the Academy of Natural Sciences of Philadelphia* 35 (7): 236–242.

Mickel, C.E. (1928) Biological and taxonomic investigations on the mutillid wasps. *United States National Museum Bulletin* 143: ix + 1–351 + 5 pls.

https://doi.org/10.5479/si.03629236.143.1
Mickel, C.E. (1933a) A new name for *Mutilla dimidiata* Lepeletier, with a redescription of the type specimen. *Annals of the Entomological Society of America* 26 (2): 377–380.
Mickel, C.E. (1933b) The Mutillidae of Formosa. *Annals of the Entomological Society of America* 26 (2): 381–423. https://doi.org/10.1093/aesa/26.2.381
Mickel, C.E. (1933c) A new species and subspecies from the Orient. *Lingnan Science Journal* 12 (3): 283–288
Mickel, C.E. (1933d) The Mutillidae of Eastern Asia. *Lingnan Science Journal* 12 (3): 289–325.
Mickel, C.E. (1934) Mutillidae of the Philippine Islands. *Philippine Journal of Science* 54 (1): 91–219 + 1 pl.
Mickel, C.E. (1935a) The mutillid wasps of the islands of the Pacific Ocean (Hymenoptera, Mutillidae). *Transactions of the Royal Entomological Society of London* 83 (2): 177–312. https://doi.org/10.1111/j.1365-2311.1935.tb01207.x
Mickel, C.E. (1935b) Descriptions and records of Nearctic mutillid wasps of the genera *Myrmilloides* and *Pseudomethoca* (Hymenoptera: Mutillidae). *Transactions of the American Entomological Society* 61 (4): 383–398. https://www.jstor.org/stable/25077360
Mickel, C.E. (1936a) New species and records of Nearctic mutillid wasps of the genus *Dasymutilla* (Hymenoptera). *Annals of the Entomological Society of America* 29 (1): 29–60. https://doi.org/10.1093/aesa/29.1.29
Mickel, C.E. (1936b) A new species of *Smicromyrme* from Japan (Mutillidae, Hymenoptera). *Mushi* 9 (1): 52–54.
Mickel, C.E. (1937a) The mutillid wasps of the genus *Timulla* which occur in North America north of Mexico. *Entomological Americana* 17 (1–2): 1–113 + pls 1–3.
Mickel, C.E. (1937b) New species and records of Mutillidae (Hymenoptera) from Borneo and the Solomon Islands. *The Annals and Magazine of Natural History*, Series 10 19: 441–456. https://doi.org/10.1080/00222933708655284
Mickel, C.E. (1938) Photopsoid mutillids collected by Dr. K. A. Salman at Eagle Lake, California (Hymenoptera). *The Pan-Pacific Entomologist* 14 (4): 178–185.
Mickel, C.E. (1939) Correction of type locality for two species of Mutillidae described by Frederick Smith (Hymenoptera). *Proceeding of the Royal Entomological Society of London*, Ser. B 8: 192–194. https://doi.org/10.1111/j.1365-3113.1939.tb00514.x
Mickel, C.E. (1952) The Mutillidae (wasps) of British Guiana. *Zoologia* 37 (11): 105–150.
Mickel, C.E. (1974) Mutillidae miscellanea: Taxonomy and distribution. *Annals of the Entomological Society of America* 67 (3): 461–471. https://doi.org/10.1093/aesa/67.3.461
Misof, B., Liu, S., Meusemann, K., Peters, R.S., Donath, A., Mayer, C., Frandsen, P.B., Ware, J., Flouri, T., Beutel, R.G., Niehuis, O., Petersen, M., Izquierdo-Carrasco, F., Wappler, T., Rust, J., Aberer, A.J., Aspöck, U., Aspöck, H., Bartel, D., Blanke, A., Berger, S., Böhm, A., Buckley, T.R., Calcott, B., Chen, J., Friedrich, F., Fukui, M., Fujita, M., Greve, C., Grobe, P., Gu, S., Huang, Y., Jermiin, L.S., Kawahara, A.Y., Krogmann, L., Kubiak, M., Lanfear, R., Letsch, H., Li, Y., Li, Z., Li, J., Lu, H., Machida, R., Mashimo, Y., Kapli, P., McKenna, D.D., Meng, G., Nakagaki, Y., Navarrete-Heredia, J.L., Ott, M., Ou, Y., Pass, G., Podsiadlowski, L., Pohl, H., von Reumont, B.M., Schütte, K., Sekiya, K., Shimizu, S., Slipinski, A., Stamatakis, A., Song, W., Su, X., Szucsich, N.U., Tan, M., Tan, X., Tang, M., Tang, J., Timelthaler, G., Tomizuka, S., Trautwein, M., Tong, X., Uchifune, T., Walzl, M.G., Wiegmann, B.M., Wilbrandt, J., Wipfler, B., Wong, T.K.F., Wu, Q., Wu, G., Xie, Y., Yang, S., Yang, Q., Yeates, D.K., Yoshizawa, K., Zhang, Q., Zhang, R., Zhang, W., Zhang, Y., Zhao, J., Zhou, C., Zhou,

L., Ziesmann, T., Zou, S., Li, Y., Xu, X., Zhang, Y., Yang, H., Wang, J., Wang, J., Kjer, K.M. & Zhou, X. (2014) Phylogenomics resolves the timing and pattern of insect evolution. *Science* 346 (6210): 763–767. https://doi.org/10.1126/science.1257570

Mitchell, A. & Brothers, D.J. (2002) Phylogeny of the genera of Ticoplinae (Hymenoptera: Mutillidae). *Journal of Hymenoptera Research* 11 (2): 312–325.

Miyamoto, S. (1959) On the nest of *Bombus diversus* Smith which collapsed before completion (biological studies on Japanese bees XI). *Akitsu* 8 (4): 85–90. (in Japanese)

Miyamoto, S. (1963) Biology of *Bombus ignitus* Smith. *Kontyû* 31 (1): 91–98.

Miyatake, T., Nakayama, S., Nishi, Y. & Nakajima, S. (2009) Tonically immobilized selfish prey can survive by sacrificing others. *Proceedings of the Royal Society B* 276 (1668): 2763–2767. https://doi.org/10.1098/rspb.2009.0558

Moser, J.C., Brownlee, R.C. & Silverstein, R. (1968) Alarm pheromones of the ant *Atta texana*. *Journal of Insect Physiology* 14 (4): 529–530. https://doi.org/10.1016/0022-1910(68)90068-1

Moura, M.R. & Jetz, W. (2021) Shortfalls and opportunities in terrestrial vertebrate species discovery. *Nature Ecology & Evolution* 5: 631–639. https://doi.org/10.1038/s41559-021-01411-5

Müller, F. (1878) Über die vortheile der mimicry bei schmetterlingen. *Zoologischer Anzeiger* 1: 54–55.

Müller, F. (1879) *Ituna* und *Thyridia*: Ein merkwürdiges Beispiel von Mimicry bei Schmetterlingen. *Kosmos* 5: 100–108.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858. https://doi.org/10.1038/35002501

Nagase, H. & Kawashima, I. (2012) On a gynandromorph specimen of *Bischoffitilla pungens* (Smith), which reveals two synonyms in Japanese mutillid wasps (Hymenoptera, Mutillidae). *Japanese Journal of Systematic Entomology* 18 (1): 31–33.

Nagy, C.G. (1968) Observations ecologiques sur l'espèce *Smicromyrme septentrionalis* Hffr. (Hymenoptera, Mutillidae). *Acta entomologica Bohemoslovaca* 62: 375–378.

Nakayama, S. & Miyatake, T. (2010) Genetic trade-off between abilities to avoid attack and to mate: a cost of tonic immobility. *Biology Letters* 6 (1): 18–20. https://doi.org/10.1098/rsbl.2009.0494

Narita, S., Pereira, R.A.S., Kjellberg, F. & Kageyama, D. (2010) Gynandromorphs and intersexes: potential to understand the mechanism of sex determination in arthropods. *Terrestrial Arthropod Reviews* 3 (1): 63–96. https://doi.org/10.1163/187498310X496190

Nonveiller, G. (1973) Recherches sur les Mutillides de l'Afrique (Mutillidae, Hymenoptera) IV. Deux gynandromorphes chez des Mutillides capturées au Cameroun. *Annales de la Facultes des Sciences du Cameroun* 15–16: 75–80.

Nonveiller, G. (1980a) Studies on African mutillids (Hymenoptera, Mutillidae) IX. The history and the present status of our knowledge of the Mutillidae fauna of Africa south of the Sahara (excluding Madagascar). *Acta entomologica Jugoslavica* 16 (1–2): 29–41.

Nonveiller, G. (1980b) Recherches sur les Mutillides de l'Afrique (Hymenoptera, Mutillidae) X. Bref aperçu des résultats des recherches sur la faune des Mutillides du Cameroun effectuées au cours de la période 1962–1975. *Memoires publies par l'Institut pour la Protection des Plantes*, Beograd 14: 11–68.

Nonveiller, G. (1987) Collecting Mutillidae in Kenya and Somalia (September 1986). *Sphecos* 15: 21–24.

Nonveiller, G. (1990) *Catalogue of the Mutillidae, Myrmosidae and Bradynobaenidae of the Neotropical Region including Mexico (Insecta: Hymenoptera)*. Hymenopterorum catalogus (nova editio). Pars 18. SPB Academic Publishing, The Hague, 150 pp.
Nonveiller, G. (1996) Révision du genre Afrotropical *Odontotilla* Bischoff, 1920 (mâle et femelle) (Hymenoptera: Mutillidae). *Annales de la Société entomologique de France* (N. S.) 32 (3): 299–357.
Oehlke, J. (1974) Beiträge zur Insektenfauna der DDR: Hymenoptera — Scolioidea. *Beiträge zur Entomologie* 24 (5–8): 279–300. https://doi.org/10.21248/contrib.entomol.24.5-8.279-300
Okayasu, J. (2017) Two new species of the genus *Sinotilla* Lelej, 1995 (Hymenoptera: Mutillidae), with notes on taxonomic characters. *Zootaxa* 4294 (2): 151–169. https://doi.org/10.11646/zootaxa.4294.2.1
Okayasu, J. (2018) Taxonomic review of Chin-wen Chen's species described in the genus *Smicromyrme* (Hymenoptera: Mutillidae: Smicromyrmini). *Acta Entomologica Musei Nationalis Pragae* 58 (2): 479–494. https://doi.org/10.2478/aemnp-2018-0036
Okayasu, J. (2020) Velvet ants of the tribe Smicromyrmini Bischoff (Hymenoptera: Mutillidae) of Japan. *Zootaxa* 4723 (1): 1–110. https://doi.org/10.11646/zootaxa.4723.1.1
Okayasu, J. (2021) A new velvet ant genus *Arkaditilla* (Hymenoptera, Mutillidae, Trogaspidiini) from the Oriental Region, with review of species. *Journal of Hymenoptera Research* 84: 145–168. https://doi.org/10.3897/jhr.84.68709
Okayasu, J. (2022) Remarkable range extension of the genus *Nordeniella* Lelej, 2005 (Hymenoptera: Mutillidae: Smicromyrmini): Description of a new species from Sumbawa, Indonesia. *Journal of Insect Biodiversity* 32 (2): 56–63. https://doi.org/10.12976/jib/2022.32.2.3
Okayasu, J. (2023a) Love is in the air and beyond the ocean: Taxonomic review of *Neotrogaspidia* Lelej (Hymenoptera: Mutillidae: Trogaspidiini) in Northeast Asia highlights its unique distributional pattern. *Entomological Science* 26 (1): e12532. https://doi.org/10.1111/ens.12532
Okayasu, J. (2023b) Discovery of the velvet ant genus *Orientilla* Lelej from Laos (Hymenoptera, Mutillidae, Dasylabrinae), with description of a related new species from India. *Journal of Hymenoptera Research* 96: 817–834. https://doi.org/10.3897/jhr.96.110590
Okayasu, J., Lelej, A.S. & Williams, K.A. (2021a) Review of *Eotrogaspidia* Lelej (Hymenoptera: Mutillidae: Trogaspidiini). *Zootaxa* 4920 (1): 56–90. https://doi.org/10.11646/zootaxa.4920.1.2
Okayasu, J., Williams, K.A. & Lelej, A.S. (2018) A remarkable new species of the genus *Sinotilla* Lelej (Hymenoptera: Mutillidae: Smicromyrmini) from Taiwan and an overview of color diversity in East Asian mutillid females. *Zootaxa* 4446 (3): 301–324. http://dx.doi.org/10.11646/zootaxa.4446.3.1
Okayasu, J., Williams, K.A. & Lelej, A.S. (2021b) Review of female *Andreimyrme* Lelej (Hymenoptera: Mutillidae: Smicromyrmini). *Zootaxa* 5061 (1): 1–38. https://doi.org/10.11646/zootaxa.5061.1.1
Olmi, M. (1984) A revision of the Dryinidae (Hymenoptera). *Memoirs of the American Entomological Institute* 37: I–XII + 1–1913.
Olmi, M. (1996 [1995]) A revision of the world Embolemidae (Hymenoptera Chrysidoidea). *Frustula entomologica*, nuova serie 18 (31): 85–146.
Olmi, M. (2005 [2003–2004]). A revision of the world Sclerogibbidae (Hymenoptera Chrysidoidea). *Frustula entomologica*, nuova serie 26–27 (39–40): 46–193.
Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N.,

Underwood, E.C., D'amico, J.A., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Lamoreux, J.F., Ricketts, T.H., Itoua, I., Wettengel, W.W., Kura, Y., Hedao, P. & Kassem, K. (2001) Terrestrial ecoregions of the world: A new map of life on Earth. *BioScience* 51(11): 933–938. https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2

O'Neill, K.M. (2001) *Solitary wasps: Behavior and natural history*. Comstock Publishing Associates, Ithaca, xvi + 406 pp.

O'Neill, K.M. & Evans, H.E. (1983) Alternative male mating tactics in *Bembecinus quinquespinosus* (Hymenoptera: Sphecidae): Correlations with size and color variation. *Behavioral Ecology and Sociobiology* 14 (1): 39–46. https://doi.org/10.1007/BF00366654

Ono, H. & Kawashima, I. (2013) Host records on two species of mutillid wasps (Hymenoptera, Mutillidae) in Japan. *Tsunekibachi* 23: 41–42. (in Japanese)

Ordway, E. (1964) *Sphecodes pimpinellae* and other enemies of *Augochlorella* (Hymenoptera: Halictidae). *Journal of the Kansas Entomological Society* 37 (2): 139–152. https://www.jstor.org/stable/25083373

Osten, T. (1992) Remarks on stridulatory organs in mutillids. *Sphecos* 23: 4–5.

Osten T. (1999) The phoretic copulation of Thynninae in an ecological and evolutionary perspective (Hymenoptera, Tiphiidae). *Linzer biologische Beiträge* 31 (2): 755–762.

O'Toole, C. (1975) The systematics of *Timulla oculata* (Fabricius) (Hymenoptera, Mutillidae). *Zoologica Scripta* 4 (1): 229–251. https://doi.org/10.1111/j.1463-6409.1975.tb00733.x

Pagden, H.T. (1934a) New species of Mutillidae (Hymenoptera, Vespoidea) from the Malay Peninsula . *Journal of the Federated Malay States Museums* 17: 419–457.

Pagden, H.T. (1934b) Biological notes on some Malayan aculeate Hymenoptera I. *Journal of the Federated Malay States Museums* 17: 458–466.

Pagden, H.T. (1934c) Biological notes on some Malayan aculeate Hymenoptera II, with descriptions of new species. *Journal of the Federated Malay States Museums* 17: 467–486.

Pagden, H.T. (1938) On a new species of Rophalomutilla (Hym. Mutillidae) from Java. *Journal of the Federated Malay States Museums* 18: 213–217.

Pagden, H.T. (1949) Descriptions and records of Austro-Malaysian Methocidae and Mutillidae (Hymenoptera). *Transactions of the Royal Entomological Society of London* 100 (8): 191–231. https://doi.org/10.1111/j.1365-2311.1949.tb01431.x

Pagliano, G. (2019) Una nuova specie di *Stenomutilla* con maschio attero (Hymenoptera Mutillidae). *Bolletino del Museo di Storia Naturale di Venezia* 70: 17–19.

Pagliano, G., Brothers, D.J., Cambra, R., Lelej, A.S., Lo Cascio, P., Matteini Palmerini, M., Scaramozzino, P.L., Williams, K.A. & Romano, M. (2020) Checklist of names in Mutillidae (Hymenoptera), with illustrations of selected species. *Bollettino del Museo Regionale di Scienze Naturali di Torino* 36 (1–2): 5–425.

Pagliano, G. & Romano, M. (2018) World list of all known species of Bradynobaenidae (Hymenoptera). *Il Naturalista Valtellinse* 28: 15–46.

Pan, A.D., Williams, K.A. & Wilson, J.S. (2017) Are diurnal iguanian lizards the evolutionary drivers of New World female velvet ant (Hymenoptera: Mutillidae) Müllerian mimicry rings? *Biological Journal of the Linnean Society* 120 (2): 436–447. https://doi.org/10.1111/bij.12894

Pass, G. (2018) Beyond aerodynamics: The critical roles of the circulatory and tracheal systems in maintaining insect wing functionality. *Arthropod Structure & Development* 47 (4): 391–407. https://doi.org/10.1016/j.asd.2018.05.004

Paulian, R. (1950) Recherches sur les insectes d'importance biologique de Madagascar. IX.

Stenomutilla splendida OLS. (Hymen. Mutill.). *Mémoires de l'Institut Scientifique de Madagascar*, Série A 3 (3): 389–391.

Peeters, C., Keller, R.A., Khalife, A., Fischer, G., Katzke, J., Blanke, A. & Economo, E.P. (2020) The loss of flight in ant workers enabled an evolutionary redesign of the thorax for ground labour. *Frontiers in Zoology* 17: 33. https://doi.org/10.1186/s12983-020-00375-9

Pekár, S., GarcÍa, L.F. & Bulbert, M.W. (2020) Spiders mimic the acoustic signalling of mutillid wasps to avoid predation: startle signalling or Batesian mimicry? *Animal Behaviour* 170: 157–166. https://doi.org/10.1016/j.anbehav.2020.10.015

Péringuey, L. (1898) Description of some new or little known South African Mutillidae in the collection of the South African Museum. *Annals of the South African Museum* 1: 33–94.

Péringuey, L. (1899) A contribution to the knowledge of South African Mutillidae (order Hymenoptera). *Annals of the South African Museum* 1: 352–378 + pl. 8.

Péringuey, L. (1909) New or little known South African Mutillidae (Hymenoptera). *Annals of the South African Museum* 5: 385–409.

Péringuey, L. (1914) Notes on South African Mutillidae (Hymenoptera) with descriptions of new or little known species. *Annals of the South African Museum* 10: 323–358.

Petersen, B. (1988) The Palaearctic Mutillidae of I.C. Fabricius and some related material (Insecta, Hymenoptera, Aculeata). *Steenstrupia* 14 (6): 129–224.

Pilgrim, E.M. & Pitts, J.P. (2006) A molecular method for associating the dimorphic sexes of velvet ants (Hymenoptera: Mutillidae). *Journal of the Kansas Entomological Society* 79 (3): 222–230. https://doi.org/10.2317/0511.09.1

Pilgrim, E.M., Williams, K.A., Manley, D.G. & Pitts, J.P. (2009) Addressing the *Dasymutilla quadriguttata* species-group and species-complex (Hymenoptera: Mutillidae): Several distinct species or a single, morphologically variable species? *Journal of the Kansas Entomological Society* 82 (3): 231–249. https://doi.org/10.2317/JKES08.11.1

Pilgrim, E.M., Williams, K.A. & Pitts, J.P. (2008) Sex association and synonymy in southwestern U.S. species of *Dasymutilla* (Hymenoptera: Mutillidae). *The Pan-Pacific Entomologist* 84 (1): 57–68. https://doi.org/10.3956/2007-13.1

Pilgrim, E.M., Roush, S.A. & Krane, D.E. (2002) Combining DNA sequences and morphology in systematics: testing the validity of the dragonfly species *Cordulegaster bilineata*. *Heredity* 89 (3): 184–190. https://doi.org/10.1038/sj.hdy.6800112

Pilgrim, E.M., Williams, K.A. & Pitts, J.P. (2008) Sex association and synonymy in southwestern U.S. species of *Dasymutilla* (Hymenoptera: Mutillidae). *The Pan-Pacific Entomologist* 84 (1): 57–68. https://doi.org/10.3956/2007-13.1

Pitts, J.P. (2007) Description of the female of *Sphaeropthalma galapagensis* Williams and notes on *Morsyma* Fox and *Caenotilla* Pitts and Manley (Hymenoptera: Mutillidae). *The Pan-Pacific Entomologist* 83 (2): 95–100.

Pitts, J.P., Boud, T.J. & Pilgrim, E.M. (2007) Molecular sex associations of three species of nocturnal velvet ant (Hymenoptera: Mutillidae). *Journal of the Kansas Entomological Society* 80 (2): 136–145. https://doi.org/10.2317/0022-8567(2007)80[136:MSAOTS]2.0.CO;2

Pitts, J.P. & McHugh, J.V. (2000) *Stethophotopsis*, a new genus of Sphaeropthalmini (Mutillidae: Sphaeropthalminae) with a brachypterous male from Arizona. *Journal of Hymenoptera Research* 9 (1): 29–33.

Pitts, J.P. & Parker, F.D. (2005) Description of the female, redescription of the male, and host associations of the Nearctic species *Sphaeropthalma jacala* Schuster (Hymenoptera: Mutillidae). *Zootaxa* 1011 (1): 55–64. https://doi.org/10.11646/zootaxa.1011.1.2

Pitts, J.P., Parker, F.D. & Pitts-Singer, T.L. (2004) A review of the *Sphaeropthalma uro*

species-group (Hymenoptera: Mutillidae), with taxonomic changes. *Journal of the Kansas Entomological Society* 77 (3): 222–234. https://doi.org/10.2317/0308.11.1

Pitts, J.P., Tanner, D., Waldren, G.C. & Paker, F.D. 2010a. Facultative size-dependent sex allocation in *Sphaeropthalma pensylvanica* Lepeletier (Hymenoptera: Mutillidae) with further host records. *Journal of the Kansas Entomological Society* 83 (1): 68–75. https://doi.org/10.2317/JKES0812.15.1

Pitts, J.P. & Wilson, J.S. (2009) Description of the female of *Acrophotopsis* (Hymenoptera: Mutillidae) with synonymy of *Sphaeropthalma dirce*. *Journal of Hymenoptera Research* 18 (2): 205–211.

Pitts, J.P., Wilson, J.S. & von Dohlen, C.D. (2010b) Evolution of the nocturnal Nearctic Sphaeropthalminae velvet ants (Hymenoptera: Mutillidae) driven by Neogene orogeny and Pleistocene glaciation. *Molecular Phylogenetics and Evolution* 56 (1): 134–145. https://doi.org/10.1016/j.ympev.2010.03.033

Pitts, J.P., Wilson, J.S., Williams, K.A. & Boehme, N.F. (2010c) Nocturnal velvet ant males (Hymenoptera: Mutillidae) of Deep Canyon, California including four new species and a fifth new species from Owens Lake Valley, California. *Zootaxa* 2553 (1): 1–34. https://doi.org/10.11646/zootaxa.2553.1.1

Polaszek, A. & Vilhelmsen, L. (2023) Biodiversity of hymenopteran parasitoids. *Current Opinion in Insect Science* 56: 101026. https://doi.org/10.1016/j.cois.2023.101026

Polidori, C., Beneitez, A., Asís, J.D. & Tormos, J. (2013a) Scramble competition by males of the velvet ant *Nemka viduata* (Hymenoptera: Mutillidae). *Behavior* 150: 23–37. https://www.jstor.org/stable/23434979

Polidori, C., Pavan, G., Ruffato, G., Asís, J.D. & Tormos, J. (2013b) Common features and species-specific differences in stridulatory organs and stridulation patterns of velvet ants (Hymenoptera: Mutillidae). *Zoologischer Anzeiger* 252 (4): 457–468. https://doi.org/10.1016/j.jcz.2013.01.003

Polidori, C., Ruffato, G., Borruso, L., Settanni, C. & Pavan, G. (2013c) Stridulatory organ and distress call in males and females of a small velvet ants (Hymenoptera: Mutillidae). *Bioacoustics* 22 (2): 121–135. https://doi.org/10.1080/09524622.2012.736241

Poulton, E.B. (1890) *The colours of animals: Their meaning and use, especially considered in the case of insects*. D. Appleton and Company, New York, xvi + 360 pp.

Pouvreau, A. (1973) Les ennemis des Bourdons. I – Étude d'une zoocé-nose: le nid de Bourdons. *Apidologie* 4 (2): 103–148. https://doi.org/10.1051/apido:19730202

Pulawski, W.J. (2016) Catalog of Sphecidae *sensu lato* (= Apoidea excluding Apidae). https://www.calacademy.org/scientists/projects/catalog-of-sphecidae (accessed 22 February 2024)

Punzo, F. (1991) Field and laboratory observations on prey items taken by the wolf spider, *Lycosa lenta* Hentz (Araneae, Lycosidae). *Bulletin of the British Arachnological Society* 8 (8): 261–264.

Quintero A., D. & Cambra, R.A. (1994) Systematics of *Pseudomethoca areta* (Cameron): Sex association, description of the male and a gynandromorph, and a new synonymy (Hymenoptera: Mutillidae). *Journal of Hymenoptera Research* 3: 303–308.

Quintero A., D. & Cambra T., R.A. (1996a) *Timulla centroamericana* (Dalla Torre) (Hymenoptera: Mutillidae), a parasitoid of *Liris* (Hymenoptera: Sphecidae). *Southwestern Entomologist* 21 (2): 205–207.

Quintero A., D. & Cambra T., R.A. (1996b) *Horcomutilla* Casal: Description of previously unknown males, new distribution records, and comments on the genus (Hymenoptera: Mutillidae). *Journal of Hymenoptera Research* 5: 53–63.

Quintero A., D. & Cambra T., R.A. (2001a) On the identity of *Scaptopoda* F. Lynch

Arribálzaga, new taxonomic changes and new distribution records for Neotropical Mutillidae (Hymenoptera), with notes on their biology. *Transactions of the American Entomological Society* 127 (3): 291–304. https://www.jstor.org/stable/25078749

Quintero A., D. & Cambra T., R.A. (2001b) On the endemic genus *Morsyma* Fox (Hymenoptera: Mutillidae: Sphaeropthalminae), with a description of the previously unknown female. *Transactions of the American Entomological Society* 127 (4): 451–458. https://www.jstor.org/stable/25078755

Quintero A., D. & Cambra, R.A. (2005) *Pappognatha* Mickel (Hymenoptera: Mutillidae: Sphaeropthalminae): New species, sex associations, hosts, and new distribution records. *Journal of Hymenoptera Research* 14 (2): 191–199.

Radoszkowski, O. (1885) Revision des armures copulatrices des mâles de la famille de Mutillides. *Horae Societatis Entomologicae Rossicae* 19 (1–2): 3–49 + 9 pls.

Raś, M., Wipfler, B., Dannenfeld, T. & Iwan, D. (2022) Postembryonic development of the tracheal system of beetles in the context of aptery and adaptations towards an arid environment. *PeerJ* 10: e13378. https://doi.org/10.7717/peerj.13378

Rau, P. (1922) Ecological and behavior notes on Missouri insect. *Transactions of the Academy of Science of St. Louis* 24 (7): 1–71 + pls V–VIII.

Reid, J.A. (1941) The thorax of the wingless and short-winged Hymenoptera. *Transaction of the Royal Entomological Society of London* 91 (8): 367–446. https://doi.org/10.1111/j.1365-2311.1941.tb01046.x

Remington, C.L. (1944) The relationship of *Dasymutilla permista* Mickel to *Dasymutilla quadriguttata* (Say) and behavior notes on the species. *Annals of the Entomological Society of America* 37 (2): 198–200. https://doi.org/10.1093/aesa/37.2.198

Ricketts, T.H., Dinerstein, E., Olson, D.M., Loucks, C.J., Eichbaum, W., DellaSala, D., Kavanagh, K., Hedao, P., Hurley, P.T., Carney, K.M., Abell, R. & Walters, S. (1999) *Terrestrial ecoregions of North America: A conservation assessment*. Island Press, Washington DC.

Riddick, E.W. (1991) *Pseudomethoca simillima* (Smith) (Hymenoptera: Mutillidae), a newly discovered parasitoid of *Andrena macra* Mitchell (Hymenoptera: Andrenidae). *Proceedings of the Entomological Society of Washington* 93 (1): 208–209.

Riley, R.G., Silverstein, R.M. & Moser, J.C. (1974) Isolation, identification, synthesis and biological activity of volatile compounds from the heads of *Atta* ants. *Journal of Insect Physiology* 20 (8): 1629–1637. https://doi.org/10.1016/0022-1910(74)90092-4

Rocha-Filho, L.C. da & Melo, G.A.R. (2011) Nesting biology and behavioural ecology of the solitary bee *Monoeca haemorrhoidalis* (Smith) and its cleptoparasite *Protosiris gigas* Melo (Hymenoptera: Apidae: Tapinotaspidini; Osirini). *Journal of Natural History* 45 (4–6): 2815–2840. https://doi.org/10.1080/00222933.2011.616271

Roff, D.A. (1990) The evolution of flightlessness in insects. *Ecological Monographs* 60 (4): 389–421. https://doi.org/10.2307/1943013

Rogers, S.M. & Simpson, S.J. (2014) Thanatosis. *Current Biology* 24 (21): R1031–R1033. https://doi.org/10.1016/j.cub.2014.08.051

Rohwer, S.A. (1910) Some new hymenopterous insects from the Philippine Islands. *Proceedings of the United States National Museum* 37 (1722): 657–660.

Roig-Alsina, A. (1993) The evolution of the apoid endophallus, its phylogenetic implications, and functional significance of the genital capsule (Hymenoptera, Apoidea). *Bollettino di zoologia* 60 (2): 169–183. https://doi.org/10.1080/11250009309355807

Rojas, B., Valkonen, J. & Nokelainen, O. (2015) Aposematism. *Current Biology* 25 (9): R345–R361. https://doi.org/10.1016/j.cub.2015.02.015

Roll, U., Feldman, A., Novosolov, M., Allison, A., Bauer, A.M., Bernard, R., Böhm, M., Castro-Herrera, F., Chirio, L., Collen, B., Colli, G.R., Dabool, L., Das, I., Doan, T.M.,

Grismer, L.L., Hoogmoed, M., Itescu, Y., Kraus, F., LeBreton, M., Lewin, A., Martins, M., Maza, E., Meirte, D., Nagy, Z.T., Nogueira, C. de C., Pauwels, O.S.G., Pincheira-Donoso, D., Powney, G.D., Sindaco, R., Tallowin, O.J.S., Torres-Carvajal, O., Trape, J.-F., Vidan, E., Uetz, P., Wagner, P., Wang, Y., Orme, C.D.L., Grenyer, R. & Meiri, S. (2017) The global distribution of tetrapods reveals a need for targeted reptile conservation. *Nature Ecology & Evolution* 1: 1677–1682. https://doi.org/10.1038/s41559-017-0332-2

Romano, M. (2012) *Nanomutilla vaucheri* in Sardegna, prima segnalazione per l'Italia (Hymenoptera Mutillidae). *Bolletino della Società Entomologica Italiana* 144 (1): 23–27.

Ronchetti, F. & Polidori, C. (2020) A sting affair: A global quantitative exploration of bee, wasp and ant hosts of velvet ants. *PLoS ONE* 15 (9): e0238888. https://doi.org/10.1371/journal.pone.0238888

Rosenhauer, W.G. (1852) *Über die Entwicklung und Fortpflanzung der Clythren und Cryptocephalen, einer Insektengruppe aus der Ordnung Coleoptera*. Theodor Blaesing, Erlangen, 34 pp.

Rosenhauer, W.G. (1856) *Die Thiere Andalusiens nach dem Resultate einer Reise zusammengestellt, nebst den Beschreibungen von 249 neuen oder bis jetzt noch unbeschriebenen Gattungen und Arten*. Theodor Blaesing, Erlangen, viii + 429 pp.

Ross, A. (2017) Insect evolution: The origin of wings. *Current Biology* 27 (3): R113–R115. https://doi.org/10.1016/j.cub.2016.12.014

Roubik, D.W. (1990) A mixed colony of *Eulaema* (Hymenoptera: Apidae), natural enemies, and limits to sociality. *Journal of the Kansas Entomological Society* 63 (1): 150–157. https://www.jstor.org/stable/25085155

Rutowski, R.L. & Alcock, J. (1980) Temporal variation in male copulatory behaviour in the solitary bee *Nomadopsis puellae* (Hymenoptera: Andrenidae). *Behaviour* 73 (3–4): 175–188. https://www.jstor.org/stable/4534039

Ruxton, G.D., Allen, W.L., Sherratt, T.N. & Speed, M.P. (2018) *Avoiding attack: The evolutionary ecology of crypsis, aposematism, and mimicry*. Second edition. Oxford University Press, Oxford, xii + 279 pp.

Sadler, E.A., Pitts, J.P. & Wilson, J.S. (2018) Stinging wasps (Hymenoptera: Aculeata), which species have the longest sting? *PeerJ* 6: e4743. https://doi.org/10.7717/peerj.4743

Sakagami, S., Ebmer, A.W., Matsumura, T. & Maeta, Y. (1982) Bionomics of the halictine bees in northern Japan II. *Lasioglossum* (*Evylaeus*) *sakagamii* (Hymenoptera, Apoidea, Halictidae), with taxonomic notes on allied species. *Kontyû* 50 (2): 198–211.

Sakagami, S. & Katayama, E. (1977) Nests of some Japanese bumblebees (Hymenoptera, Apidae). *Journal of the Faculty of Science*, *Hokkaido University*, Series 6, Zoology 21 (1): 92–153. http://hdl.handle.net/2115/27633

Salt, G. (1941) The effects of hosts upon their insect parasites. *Biological Reviews* 16 (4): 239–264. https://doi.org/10.1111/j.1469-185X.1941.tb01103.x

de Saussure, H. (1867) *Reise der österreichschen Fregatte Novara um die Erde in den Jahren 1857, 1858, 1859 unter den Befehlen des Commodore B. von Wüllerstorf-Urbair*. *Zoologischer Theil*. *Zweiter Band*. *Hymenoptera*. *Familien der Vespiden, Sphegiden, Pompiliden, Crabroniden und Heterogynen*. C. Gerold's Sohn, Wien, 138 pp. + 4 pls.

Saxton, S.M. (2010) Mating behaviour of *Myrmosa atra* (Hymenoptera: Mutillidae) with a consideration of the adaptive significance of long copulation duration. *British Journal of Entomology and Natural History* 23: 33–38 + pl. 4.

Schmidt, J.O. (1978) *Dasymutilla occidentalis*: A long-lived aposematic wasp (Hymenoptera: Mutillidae). *Entomological News* 89 (5–6): 135–136.

Schmidt, J.O. (1990) Hymenopteran venoms: Striving toward the ultimate defense against

vertebrates. *In*: Evans, D.L. & Schmidt, J.O. (eds) *Insect defenses: Adaptive mechanisms and strategies of prey and predators*. SUNY Press, Albany, pp. 387–419.
Schmidt, J.O. (2016) *The sting of the wild*. Johns Hopkins University Press, Baltimore, xiii + 257 pp. + 8 pls.
Schmidt, J.O. (2019) Pain and lethality induced by insect stings: An exploratory and correlational study. *Toxins* 11 (7): 427. https://doi.org/10.3390/toxins11070427
Schmidt, J.O. & Blum, M.S. (1977) Adaptations and responses of *Dasymutilla occidentalis* (Hymenoptera: Mutillidae) to predators. *Entomologia Experimentalis et Applicata* 21 (2): 99–111. https://doi.org/10.1111/j.1570-7458.1977.tb02663.x
Schmidt, J.O. & Buchmann, S.L. (1986 Are mutillids scarce? (Hymenoptera: Mutillidae). *The Pan-Pacific Entomologist* 62 (2): 103–104.
Schmidt, J.O. & Hook, A.W. (1979) A record population of *Pseudomethoca simillima* (Smith) (Hymenoptera: Mutillidae). *The Florida Entomologist* 62 (2): 152.
Schmidt, J.O. & Schmidt, L.S. (2022) Vinegaroons (Uropygi: *Mastigoproctus tohono*) in a multi-predator/multi-prey system: Prey, predators, and cannibalism. *Journal of Arachnology* 50 (3): 267–276. https://doi.org/10.1636/JoA-S-21-005
Schmidt, J.O., Schmidt, L.S. & Schmidt, D.K. (2021) The paradox of the velvet-ant (Hymenoptera, Mutillidae). *Journal of Hymenoptera Research* 84: 327–337. https://doi.org/10.3897/jhr.84.68795
Schmid-Egger, C. & Schmidt, C. (2021) Unexpected diversity in Central European Vespoidea (Hymenoptera, Mutillidae, Myrmosidae, Sapygidae, Scoliidae, Tiphiidae, Thynnidae, Vespidae), with description of two species of *Smicromyrme* Thomson, 1870. *ZooKeys* 1062: 49–72. https://doi.org/10.3897/zookeys.1062.70763
Schmid-Egger, C. & Schmidt, C. (2022) *Smicromyrme frankburgeri* Schmid-Egger (Hymenoptera, Mutillidae), a replacement name for *S. burgeri* Schmid-Egger, 2021, preoccupied by *S. burgeri* Lelej, 2020. *ZooKeys* 1097: 133–134. https://doi.org/10.3897/zookeys.1097.83215
Schuster, R.M. (1945) An interesting new brachypterous species of *Photopsis* (Hymenoptera, Mutillidae). *The Pan-Pacific Entomologist* 21 (4): 149–151.
Schuster, R.M. (1951) A revision of the genus *Ephuta* (Mutillidae) in America north of Mexico. *Journal of the New York Entomological Society* 59 (1): 1–43. https://www.jstor.org/stable/25005387
Schuster, R.M. (1957 [1956]) A revision of the genus *Ephuta* (Mutillidae) in America north of Mexico. Part II. Species group grisea. *Journal of the New York Entomological Society* 64: 7–84. https://www.jstor.org/stable/25005598
Schuster, R.M. (1958) A revision of the sphaeropthalmine Mutillidae of America north of Mexico. II. *Entomologica Americana* 37: 1–130.
Sergeev, M.E. & Lelej, A.S. 2011. [On the parasitism of the velvet ant *Physetopoda halensis* (Hymenoptera, Mutillidae) on the larva of leaf beetle *Labidostomis hummeralis* (Coleoptera, Chrysomelidae, Clytrinae) in south-eastern Ukraine]. *Vestnik Zoologii* 45 (2): 144. (in Russian)
Serkova, L.G. (1962) To the natural history of desert pasture pest leaf beetle (*Theone silphoides*). *Proceedings of the Institute of Plant Protection of Kazakh Soviet Socialist Republic* 7: 83–108. (in Russian)
Sexton, O.J. (1964) Differential predation by the lizard, *Anolis carolinensis*, upon unicoloured and polycoloured insects after interval of no contact. *Animal Behaviour* 12 (1): 101–110. https://doi.org/10.1016/0003-3472(64)90110-1
Seyrig, A. (1936) Un Mutillide parasite d'un Lépidoptère: *Stenomutilla freyi*. *In*: *Livre Jubilaire de M. Eugène-Louis Bouvier, membre de l'Institut, professor honoraire au Muséum*. Firmin-Didot, Paris, pp. 313–316 + pl. 14.

Shappirio, D.G. (1947) Observations on wasps. *The Scientific Monthly* 64 (4): 348–350.
Shappirio, D.G. (1948 [1947]) Observations on the biology of some mutillid wasps (Hymenoptera, Mutillidae). *Bulletin of the Brooklyn Entomological Society* 42 (5): 162–163.
Sheldon, J.K. (1970) Sexual dimorphism in the head structure of Mutillidae Hymenoptera: A possible behavioral explanation. *Entomological News* 81 (3): 57–61.
Sherratt, T.N. & Stefan, A. (2024) Capture tolerance: A neglected third component of aposematism? *Evolutionary Ecology*: https://doi.org/10.1007/s10682-024-10289-1
Sichel, J. & Radoszkowski, O. (1869–1870) Essai d'une monographie des Mutilles de l'ancien continent. *Horae Socieratis Entomologicae Rossicae* 6 (3): 139–172 + pl. 6–8 (1869); 6 (4): 173–309 + pl. 9–11 (1870).
Smith, F. (1855) *Catalogue of hymenopterous insects in the collection of the British Museum*. *Part III*. *Mutillidae and Pompilidae*. Taylor and Francis, London, [4] + 206 pp. + pl. A + 5 pls. https://doi.org/10.5962/bhl.title.20858
Smith, F. (1857–1858) Catalogue of the hymenopterous insects collected at Sarawak, Borneo; Mount Ophir, Malacca; and at Singapore, by A.R. Wallace. *Journal of the Proceedings of the Linnean Society*, Zoology 2 (6): 42–88 + pls. 1–2 (1857); 2 (7): 89–130 (1858). https://doi.org/10.1111/j.1096-3642.1857.tb01759.x; https://doi.org/10.1111/j.1096-3642.1858.tb02548.x
Smith, F. (1860 [1861]) Descriptions of new species of hymenopterous insects collected by Mr. A. R. Wallace at Celebes. *Journal of the Proceedings of the Linnean Society*, Zoology 5: 57–93. https://doi.org/10.1111/j.1096-3642.1860.tb01021.x
Smith, F. (1860b [1861]) Catalogue of hymenopterous insects collected by Mr. A.R. Wallace in the islands of Bachian, Kaisaa, Amboyna, Gilolo, and at Dory in New Guinea. *Journal of the Proceedings of the Linnean Society*, Zoology, 5: 93–143. https://doi.org/10.1111/j.1096-3642.1860.tb01022.x
Smith, F. (1865) Descriptions of new species of hymenopterous insects from the islands of Sumatra, Sula, Gilolo, Salwatty, and New Guinea, collected by Mr. A. R. Wallace. *Journal of the Proceedings of the Linnean Society*, Zoology 8 (30): 61–94 + pl. 4. https://doi.org/10.1111/j.1096-3642.1865.tb02422.x
Smith, F. (1873) Description of aculeate Hymenoptera of Japan, collected by Mr. George Lewis at Nagasaki and Hiogo. *The Transactions of the Entomological Society of London* 21 (2): 181–206. https://doi.org/10.1111/j.1365-2311.1873.tb00641.x
Smith, F. (1874) Description of new species of Tenthredinidae, Ichneumonidae, Chrysididae, Formicidae, &c. of Japan. *The Transactions of the Entomological Society of London* 1874: 373–409. https://doi.org/10.1111/j.1365-2311.1874.tb00867.x
Smith, F. (1879) *Descriptions of new species of Hymenoptera in the collection of the British Museum*. Taylor and Francis, London, XXI + 240 pp. https://doi.org/10.5962/bhl.title.60089
Spangler, H.G. & Manley, D.G. (1978) Sounds associated with the mating behavior of a mutillids wasp. *Annals of the Entomological Society of America* 71 (3): 389–392. https://doi.org/10.1093/aesa/71.3.389
Starr, C.K. (1985) A simple pain scale for field comparison of hymenopteran stings. *Journal of Entomological Science* 20 (2): 225–232. https://doi.org/10.18474/0749-8004-20.2.225
Stubblefield, J.W. & Seger, J. (1994) Sexual dimorphism in the Hymenoptera. *In*: Short, R.V. & Balaban, E. (eds) *The differences between the sexes*. Cambridge University Press, Cambridge, pp. 71–103.
Su, W., Liang, C., Ding, G., Jiang, Y., Huang, J. & Wu, J. (2019) First record of the velvet ant *Mutilla europaea* (Hymenoptera: Mutillidae) parasitizing the bumblebee *Bombus*

breviceps (Hymenoptera: Apidae). *Insects* 10 (4): 104. https://doi.org/10.3390/insects10040104
Sugiura, S. (2020) Predators as drivers of insect defenses. *Entomological Science* 23 (3): 316–337. https://doi.org/10.1111/ens.12423
Sutanto, D.D., Williams, K.A., Nugroho, H. & Lelej, A.S. (2021) To the knowledge of the velvet ant genus *Bischoffitilla* Lelej (Hymenoptera: Mutillidae) in Indonesia. *Treubia* 48 (1): 1–12. http://dx.doi.org/10.14203/treubia.v46i0.3795
Swezey, O.H. (1915) Some hyperparasites of white grubs. *Proceedings of the Hawaiian Entomological Society* 3 (2): 71–72.
Swinton, A.H. (1878) On the stridulation of some Hemiptera, Hymenoptera, and Coleoptera. *The Entomologist's Monthly Magazine* 15: 117–118.
Tan, W.C., Measey, J., Vanhooydonck, B. & Herrel, A. (2021) The relationship between bite force, morphology, and diet in southern African agamids. *BMC Ecology and Evolution* 21: 126. https://doi.org/10.1186/s12862-021-01859-w
Taylor, C.K., Murphy, M.V., Hitchen, Y. & Brothers, D.J. (2019) Four new species of Australian velvet ants (Hymenoptera: Mutillidae, *Aglaotilla*) reared from bee and wasp nests, with a review of Australian mutillid host records. *Zootaxa* 4609 (2): 201–224. https://doi.org/10.11646/zootaxa.4609.2.1
Taylor, R.W. (1983) Descriptive taxonomy: past, present, and future. *In*: Highley, E. & Taylor, R.W. (eds) *Australian systematic entomology: A bicentenary perspective*. CSIRO, Melbourne, pp. 93–134.
Terine, J.B. & Kumar, G.P. (2024) Three new species of the genus *Odontomutilla* Ashmead, 1899 (Hymenoptera: Mutillidae) from India. *Zootaxa* 5405 (1): 131–141. https://doi.org/10.11646/zootaxa.5405.1.6
Thaochan, N., Williams, K.A., Thoawan, K., Jeenthong, T. & Sittichaya, W. (2022) Three new species and one new country record of velvet ants (Hymenoptera, Mutillidae) from Thailand. *Journal of Hymenoptera Research* 93: 151–165. https://doi.org/10.3897/jhr.93.94727
Thompson, W.R. (1950) *A catalogue of the parasites and predators of insect pests*. *Section 1*. *Parasitic host catalogue*. *Part 4*. *Parasites of the Hymenoptera, Isopoda and Isoptera*. 2nd edition. The Imperial Parasite Service, Belleville.
Thompson, W.R. (1958) *A catalogue of the parasites and predators of insect pests*. *Section 2*. *Host parasite catalogue*. *Part 5*. *Hosts of the Hymenoptera (Miscogasteridae to Trigonalidae), Lepidoptera and Strepsiptera*. The Commonwealth Institute of Biological Control, Ottawa.
Thornhill, R. & Alcock, J. (1983) *The evolution of insect mating system*. Harvard University Press, Cambridge and London, ix + 547 pp.
Thorp, R.W. (1969a) Ecology and behavior of *Anthophora edwardsii* (Hymenoptera: Anthophoridae). *The American Midland Naturalist* 82 (2): 321–337. https://doi.org/10.2307/2423781
Thorp, R.W. (1969b) Ecology and behavior of *Melecta separata callura* (Hymenoptera: Anthophoridae). *The American Midland Naturalist* 82 (2): 338–345. https://doi.org/10.2307/2423782
Togashi, I. (1991) Distribttional [sic!] notes of bees of *Colletes* Latreille occurring in Ishikawa Prefecture, Japan. *Entomological Journal of Fukui* 8: 21–25. (in Japanese)
Tomberlin, J.K. (1997) Mating behavior of *Dasymutilla occidentalis* (Hymenoptera: Mutillidae). *Entomological News* 108 (4): 310, 317.
Tormos, J., Asís, J.D., Polidori, C., Benéitez, A. & Storino, G. (2010) The mating behaviour of the velvet ant, *Nemka viduata* (Hymenoptera: Mutillidae). *Journal of Insect Behavior* 23 (2): 117–127. https://doi.org/10.1007/s10905-009-9200-5

Torrico-Bazoberry, D. & Muñoz, M. (2019) High-frequency components in the distress stridulation of Chilean endemic velvet ants (Hymenoptera: Mutillidae). *Revista Chilena de Entomología* 45 (1): 5–13. https://www.biotaxa.org/rce/article/view/45599
Townes, H.K. (1977) A revision of the Rhopalosomatidae (Hymenoptera). *Contributions of the American Entomological Institute* 15: 1–34.
Tschuch, G. (1993) Sound production in mutillid wasps (Mutillidae, Hymenoptera). *Bioacoustics* 5 (1–2): 123–129. https://doi.org/10.1080/09524622.1993.9753234
Tschuch, G. (1994) Stridulationsorgane der Mutilliden (Hymenoptera). *Mitteilungen der Deutschen Gesellschaft für Allgemeine und Angewandte Entomologie* 9 (1–3): 427–429.
Tschuch, G. (2000) Ameisenwespen in ethnologischer und angewandter Entomologie (Hymenoptera: Vespoidea: Mutillidae). *Entomologia Generalis* 25 (1): 67–74. https://doi.org/10.1127/entom.gen/25/2000/67
Tschuch, G. & Brothers, D.J. (1999) Modeling vibration and sound production in insects with nonresonant stridulatory organs. *The Journal of the Acoustical Society of America* 106 (6): 3706–3710. https://doi.org/10.1121/1.428227
Tschuch, G. & Brothers, D.J. (2000) Stridulatory organs in solitary aculeate Hymenoptera (Insecta). *Zoologischer Anzeiger* 239: 319–327.
Tsuneki, K. (1965) The biology of east-Asiatic *Cerceris* (Hym., Sphecidae) with special reference to the peculiar social relationships and return to the nest in *Cerceris hortivaga* Kohl. *Etizenia* 9: 1–46.
Tsuneki, K. (1972a) Studies on the Mutillidae of Japan (Hymenoptera). *Etizenia* 61: 1–26.
Tsuneki, K. (1972b) Two new species of Mutillidae from Borneo (Hym.). *The Life Study* 16 (1–2): 17–21.
Tsuneki, K. (1972c) Mutillidae collected in Formosa in 1966 and 68 (Hymenoptera). *Etizenia* 64: 1–25.
Tsuneki, K. (1973) New and the first recorded species and subspecies of Sphecidae and Mutillidae from Japan, with taxonomic notes on some species (Hymenoptera). *Etizenia* 65: 1–28.
Tsuneki, K. (1982) Studies on the new material of Sphecidae, Chrysididae and Mutillidae of Formosa and the southern Ryukyus (Hymenoptera). *Special Publications of the Japan Hymenopterists Association* 23: 15–45.
Tsuneki, K. (1993a) On some Taiwanese Mutillidae, collected in 1976 by Mr. T. Murota, with description of new taxa (Hymenoptera). *Special Publications of the Japan Hymenopterists Association* 41: 39–50.
Tsuneki, K. (1993b) A new and an undescribed species of Mutillidae from Is. Okinawa, the Ryukyus (Hymenoptera). *Special Publications of the Japan Hymenopterists Association* 41: 51–55.
Tsuneki, K., Nozaka, C., Tano, T., Kurokawa, H. & Murota, T. (1993) Mutillidae recently collected in the Philippines (Hymenoptera). *Special Publications of the Japan Hymenopterists Association* 41: 1–38.
Tu, B.-B., Lelej, A.S. & Chen, X.-X. (2014a) Review of the genus *Cystomutilla* André, 1896 (Hymenoptera: Mutillidae: Sphaeropthalminae: Sphaeropthalmini), with description of the new genus *Hemutilla* gen. nov. and four new species from China. *Zootaxa* 3889 (1): 71–91. http://dx.doi.org/10.11646/zootaxa.3889.1.4
Tu, B.-B., Lelej, A.S. & Chen, X.-X. (2014b) Five newly recorded species of *Dasylabris* (Hymenoptera: Mutillidae) from China. *Entomotaxonomia* 36 (4): 300–310.
Tu, B.-B., Lelej, A.S. & Chen, X.-X. (2015) Review of the genus *Taiwanomyrme* Tsuneki, 1993 (Hymenoptera, Mutillidae, Mutillinae), with description of two new species from China. *Zootaxa* 4020 (3): 588–600. https://doi.org/10.11646/zootaxa.4020.3.10

Turner, R.E. (1915) A new species of *Mutilla* parasitic on *Glossina morsitans*. *Bulletin of Entomological Research* 5 (4): 383. https://doi.org/10.1017/S000748530003039X
Turner, R.E. (1916) On Mutillidae parasitic on *Glossina morsitans*. *Bulletin of Entomological Research* 7 (1): 93–95. https://doi.org/10.1017/S0007485300017119
Turner, R.E. (1920) On a new mutillid parasite of *Glossina morsitans*. *Bulletin of Entomological Research* 10 (3): 327–328. https://doi.org/10.1017/S0007485300044187
Turrisi, G.F. (1999) Un caso di ginandromorfismo in *Myrmilla bison* (A. Costa 1887) (Hymenoptera Mutillidae). *Bollettino dell'Accademia Gioenia di Scienze Naturali di Catania* 31 (354): 331–334.
Turrisi, G.F. & Foucart, A. (2008) Description of a gynandromorphic *Myrmilla calva* (Villiers 1789), with a summary on gynandromorphism phenomenon within Mutillidae (Hymenoptera: Scolioidea). *Linzer biologische Beiträge* 40 (2): 1873–1880.
Turrisi, G.F., Matteini Palmerini, M. & Brothers, D.J. (2015) Systematic revision and phylogeny of the genera *Blakeius* Ashmead, 1903 and *Liomutilla* André, 1907, with description of two new genera (Hymenoptera: Mutillidae, Myrmillinae). *Zootaxa* 4010 (1): 1–78. http://dx.doi.org/10.11646/zootaxa.4010.1.1
Turrisi, G.F., Matteini Palmerini, M., Demetriou, J., Matteini Palmerini, M. & Forbicioni, L. (2022) Description of new teratological cases including chromatic aberrations in Mutillidae (Hymenoptera Vespoidea). *Redia* 105: 145–162. http://dx.doi.org/10.19263/REDIA-105.22.19
VanderSal-Jensen, N.D., Crews, S.C. & Gillespie, R.G. (2016) Is love in the air or at first sight? Mate finding cues used by sympatric male velvet ants (Hymenoptera: Mutillidae). *Invertebrate Biology* 135 (3): 200–210. https://doi.org/10.1111/ivb.12128
Vieira, C.R., Waichert, C., Williams, K.A. & Pitts, J.P. (2017) Evaluation of Malaise and yellow pan trap performance to assess velvet ants (Hymenoptera: Mutillidae) diversity in a Neotropical savanna. *Environmental Entomology* 46 (2): 353–361. https://doi.org/10.1093/ee/nvx046
Vitt, L.J. & Cooper, W.E. (1988) Feeding responses of skinks (*Eumeces laticeps*) to velvet ants (*Dasymutilla occidentalis*). *Journal of Herpetology* 22 (4): 485–488. https://doi.org/10.2307/1564347
Vivallo, F. (2020) Phoretic copulation in Aculeata (Insecta: Hymenoptera): A review. *Zoological Journal of the Linnean Society* 191 (3): 627–636. https://doi.org/10.1093/zoolinnean/zlaa069
Waldren, G.C., Roberts, J.D. & Pitts, J.P. (2020a) Phoretic copulation in the velvet ant *Sphaeropthalma pensylvanica* (Lepeletier) (Hymenoptera, Mutillidae): A novel behavior for Sphaeropthalminae with a synthesis of mating strategies in Mutillidae. *Journal of Hymenoptera Research* 78: 69–89. https://doi.org/10.3897/jhr.78.55762
Waldren, G.C., Sadler, E.A., Murray, E.A., Bossert, S., Danforth, B.N. & Pitts, J.P. (2023) Phylogenomic inference of the higher classification of velvet ants (Hymenoptera: Mutillidae). *Systematic Entomology* 48 (3): 463–487. https://doi.org/10.1111/syen.12588
Waldren, G.C., Williams, K.A., Cambra, R.A. & Pitts, J.P. (2020b) Systematic revision of the North American velvet ant genus *Invreiella* Suárez (Hymenoptera: Mutillidae) with description of eleven new species. *Zootaxa* 4894 (2): 151–205. https://doi.org/10.11646/zootaxa.4894.2.1
Weekers, P.H.H., de Jonckheere, J.F. & Dummont, H.J. (2001) Phylogenetic relationships inferred from ribosomal ITS sequences and biogeographic patterns in representatives of the genus *Calopteryx* (Insecta: Odonata) of the west Mediterranean and adjacent west European zone. *Molecular Phylogenetics and Evolution* 20 (1): 89–99.

https://doi.org/10.1006/mpev.2001.0947
Wheeler, W.M. (1910) A gynandromorphous mutillid. *Psyche* 17: 186–190. https://doi.org/10.1155/1910/97518
Wigglesworth, V.B. & Lee, W.M. 1982. The supply of oxygen to the flight muscles of insects: A theory of tracheole physiology. *Tissue & Cell* 14 (3): 501–518. https://doi.org/10.1016/0040-8166(82)90043-X
Wikramanayake, E., Dinerstein, E., Loucks, C.J., Olson, D.M., Morrison, J., Lamoreux, J., McKnight, M. & Hedao, P. (2002) *Terrestrial ecoregions of the Indo-Pacific: A conservation assessment*. Island Press, Washington DC, xxix + 643 pp.
Wille, A. & Orozco, E. (1970) The life cycle and behavior of the social bee *Lasioglossum* (*Dialictus*) *umbripenne* (Hymenoptera: Halictidae). *Revista de Biología Tropical* 17 (2): 199–245.
Williams, F.X. (1919) Philippine wasp studies Part 2. Descriptions of new species and life history studies. *Report of Work of the Experiment Station of the Hawaiian Sugar Planters' Association, Entomological Series Bulletin* 14: 19–180.
Williams, K.A. (2012) *Systematics of Mutillidae (Hymenoptera) with special emphasis on* Dasymutilla *and their allies*. Ph.D. Thesis, Utah State University. https://doi.org/10.26076/ef6b-f9fa
Williams, K.A. (2023) Taxonomic updates for diurnal velvet ants (Hymenoptera: Mutillidae) in the United States of America. *Zootaxa* 5301 (1): 105–123. https://doi.org/10.11646/zootaxa.5301.1.5
Williams, K.A., Bartholomay, P.B., Cambra, R.A., Pitts, J.P. & Oliveira, M.L. (2022) Revision of *Cephalomutilla* André (Hymenoptera: Mutillidae) including one new species, three new sex associations, and nine new synonymies. *Austral Entomology* 61 (2): 137–155. https://doi.org/10.1111/aen.12596
Williams, K.A., Brothers, D.J. & Pitts, J.P. (2011a) New species of *Tobantilla* Casal, 1965 and a new genus and species, *Gogoltilla chichikovi* gen. et sp. nov., from Argentina (Hymenoptera: Mutillidae). *Zootaxa* 3064 (1): 41–68. https://doi.org/10.11646/zootaxa.3064.1.2
Williams, K.A., Cambra, R.A., Bartholomay, P.R., Luz, D.R., Quintero A., D. & Pitts, J.P. (2019a) Review of the genus *Lomachaeta* Mickel, 1936 (Hymenoptera: Mutillidae) with new species and sex associations. *Zootaxa* 4564 (1): 101–136. https://doi.org/10.11646/zootaxa.4564.1.4
Williams, K.A., Lelej, A.S., Okayasu, J., Borkent, C.J., Malee, R., Thoawan, K. & Thaochan, N. (2019b) The female velvet ants (aka modkhong) of southern Thailand (Hymenoptera: Mutillidae), with a key to the genera of southeast Asia. *Zootaxa* 4602 (1): 1–69.
Williams, K.A., Manley, D.G., Deyrup, M., von Dohlen, C. & Pitts, J.P. (2012) Systematic review of the *Dasymutilla monticola* species-group (Hymenoptera: Mutillidae): using phylogenetics to address species-group placement and sex associations. *Zootaxa* 3554 (1): 1–29. https://doi.org/10.11646/zootaxa.3554.1.1
Williams, K.A., Manley, D.G., Pilgrim, E.M., von Dohlen, C. & Pitts, J.P. (2011b) Multifaceted assessment of species validity in the *Dasymutilla bioculata* species group (Hymenoptera: Mutillidae). *Systematic Entomology* 36 (1): 180–191. https://doi.org/10.1111/j.1365-3113.2010.00555.x
Williams, K.A., Pan, A.D. & Wilson, J.S. (2024) *Velvet ants of North America*. Princeton University Press, Princeton and Oxford, 440 pp.
Wilson, J.S., Jahner, J.P., Forister, M.L., Sheehan, E.S., Williams, K.A. & Pitts, J.P. (2015) North American velvet ants form one of the world's largest known Müllerian mimicry complexes. *Current Biology* 25 (16): R704–R706.

https://doi.org/10.1016/j.cub.2015.06.053
Wilson, J.S., Clark, S.L., Williams, K.A. & Pitts, J.P. (2012a) Historical biogeography of the arid-adapted velvet ant *Sphaeropthalma arota* (Hymenoptera: Mutillidae) reveals cryptic species. *Journal of Biogeography* 39: 336–352. https://doi.org/10.1111/j.1365-2699.2011.02580.x
Wilson, J.S., Pan, A.D., Limb, E.S. & Williams, K.A. (2018) Comparison of African and North American velvet ant mimicry complexes: Another example of Africa as the 'odd man out'. *PLoS ONE* 13 (1): e0189482. https://doi.org/10.1371/journal.pone.0189482
Wilson, J.S. & Pitts, J.P. (2008) Revision of velvet ant genus *Dilophotopsis* Schuster (Hymenoptera: Mutillidae) by using molecular and morphological data, with implications for desert biogeography. *Annals of the Entomological Society of America* 101 (3): 514–524. https://doi.org/10.1603/0013-8746(2008)101[514:ROVAGD]2.0.CO;2
Wilson, J.S. & Pitts, J.P. (2009) Species boundaries of *Sphaeropthalma unicolor* (Hymenoptera: Mutillidae): Is color useful for differentiating species? *Journal of Hymenoptera Research* 18 (2): 212–226.
Wilson, J.S. & Pitts, J.P. (2010a) Pleistocene diversification of the *Odontophotopsis unicornis* species-group (Hymenoptera: Mutillidae). *Annals of the Entomological Society of America* 103 (4): 555–565. https://doi.org/10.1603/AN09177
Wilson, J.S. & Pitts, J.P. (2010b) Phylogeographic analysis of the nocturnal velvet ant genus *Dilophotopsis* (Hymenoptera: Mutillidae) provides insights into diversification in the Nearctic deserts. *Biological Journal of the Linnean Society* 101 (2): 360–375. https://doi.org/10.1111/j.1095-8312.2010.01526.x
Wilson, J.S., Sidwell, J.S., Forister, M.L., Williams, K.A. & Pitts, J.P. (2020) Thistledown velvet ants in the Desert Mimicry Ring and the evolution of white coloration: Müllerian mimicry, camouflage and thermal ecology. *Biology Letters* 16: 20200242. https://doi.org/10.1098/rsbl.2020.0242
Wilson, J.S., Williams, K.A., Forister, M.L., von Dohlen, C.D. & Pitts, J.P. (2012b) Repeated evolution in overlapping mimicry rings among North American velvet ants. *Nature Communications* 3: 1272. https://doi.org/10.1038/ncomms2275
Wilson, J.S., Williams, K.A., Tanner, D.A. & Pitts, J.P. (2010b) Nectaring by nocturnal velvet ants (Hymenoptera: Mutillidae). *The Southwestern Naturalist* 55 (3): 441–443. https://doi.org/10.1894/JC-33.1
Yano, M. (1932) Mutillidae. *In*: Uchida, S. (ed.) *Iconographia Insectorum Japonicorum Editio Prima*. Hokuryukan, Tokyo, pp. 325–327 + 1 pl. (in Japanese)
Yasumatsu, K. (1931) Description of a new species of *Myrmosa* from Japan (Hym. Myrmosidae). *Transactions of the Sapporo Natural History Society* 11 (4): 221–226 + pl. III.
Yasumatsu, K. (1934) Les Hyménoptères de l'ile Yakushima. *Mushi* 7 (2): 61–67.
Yasumatsu, K. (1936) Hymenoptera of the Bonin Islands. *Transactions of the Natural History Society of Formosa* 26 (157): 356–363.
Yasumatsu, K. (1937) Hymenoptera of Tsushima (first report). *Journal of Natural History Society in Fukuoka* 2 (2): 59–74. (in Japanese)
Yasumatsu, K. (1938a) Les Mutillides de Coree et de la Mandschourie du Sud. *Transactions of the Natural History Society of Formosa* 28 (175): 83–87.
Yasumatsu, K. (1938b) Hyménoptères trouvées dans les environs de Nanking et de Changsha du bassin Yang-tse (Chine) par M. Kwo-Mo Ho. *Transactions of the Natural History Society of Formosa* 28 (180–181): 345–347. (in Japanese)
Yasumatsu, K. (1938c) Beitrage zur synonymie einiger Hymenopterenarten von den Ryukyu-

Inseln. *Transactions of the Natural History Society of Formosa* 28 (183): 446–447.
Yasumatsu, K. (1939) Notes on *Squamulotilla strangulata* (Smith). (Hym., Mutillidae). *Transactions of the Natural History Society of Formosa* 29 (193): 245.
Yasumatsu, K. (1944) [Hymenoptera]. *In*: Furukawa, H. (ed.) *Nihon Seibutsushi. Konchu 1*. Kenkyû-sha, Tokyo, pp. 405–527. (in Japanese)
Yasumatsu, K. (1947a) Über einige Mutilliden aus Chekiang, Ost-China, gesammelt von Herrn Y. Ouchi. *Matsumushi* 2 (1): 25–27.
Yasumatsu, K. (1947b) Some wasps and bees of the desert Kunshan-Tagh in Inner Mongolia. *Mushi* 18: 29–33.
Yasumatsu, K. (1948) Records of East Chinese Mutillidae (Hymenoptera). Lingnan Science Journal 22 (1–4): 71–73.
Yasumatsu, K. (1951) Mutillidae of Shansi, North China (Hymenoptera). *Mushi* 22 (12): 69–72.
Yasumatsu, K. & Kumashiro, S. (1940) [Two mutillid species from North Korea]. *Kontyû* 14 (1): 43. (in Japanese)
Yoshikawa, Y. (1965) [Studies on stridulation of velvet ants (*Smicromyrme lewisi yanoi* Mickel stridulates)]. *Insect* 15 (2–3): 12–13. (in Japanese)
Zanette, L.R.S., Soares, L.A., Pimenta, H.C., Conçalves, A.M. & Martins, R.P. (2004) Nesting biology and sex ratios of *Auplopus militaris* (Lynch-Arribálzaga 1873) (Hymenoptera Pompilidae). *Tropical Zoology* 17 (2): 145–154. https://doi.org/10.1080/03946975.2004.10531204
Zavattari, E. (1910) Catalogo delle Mutille del Museo Zoologico di Napoli. *Annuario del Museo Zoologico dell'Università di Napoli*, New Series 3 (9): 1–16.
Zavattari, E. (1913) H. Sauter's Formosa-Ausbeute. Mutillidae (Hym.). *Archiv für Naturgeschichte* 79A (3): 19–42.
Zavattari, E. (1914) Mutille Austro-Malesi. *Bolletino della Societa Entomologica Italiana* 45: 61–114.
Zavattari, E. (1922) Eine neue Mutille von China (Hym). *Entomologische Mitteilungen* 11(4): 192. https://doi.org/10.5962/bhl.part.3338
Zhou, H.-t., Lelej, A.S. & Liu, J.-x. (2018a) New records of velvet ants (Hymenoptera: Mutillidae) from China with taxonomic notes. *Far Eastern Entomologist* 354: 23–28. http://doi.org/10.25221/fee.354.4
Zhou, H.-t., Lelej, A.S., Williams, K.A. & Liu, J.-x. (2018b) Revision of the Oriental genus *Zavatilla* Tsuneki (Hymenoptera, Mutillidae, Trogaspidiini), with descriptions of two new species. *Zootaxa* 4418 (2): 101–120. https://doi.org/10.11646/zootaxa.4418.2.1
Zhou, H.-T., Lelej, A.S. & Xu, Z.-F. (2017) Discovery of the subfamily Rhopalomutillinae (Hymenoptera: Mutillidae) in China and description of *Pherotilla brothersi* sp. nov. *Zootaxa* 4273 (4): 587–594. https://doi.org/10.11646/zootaxa.4273.4.8
Zillikens, A. & Steiner, J. (2019) Nest sites, breeding cycle and possible cleptoparasites of *Monoeca catarina* Aguiar (Hymenoptera, Apidae, Tapinotaspidini) from Santa Catarina Island, southern Brazil. *Studies on Neotropical Fauna and Environment* 55 (1): 29–35. https://doi.org/10.1080/01650521.2019.1681087

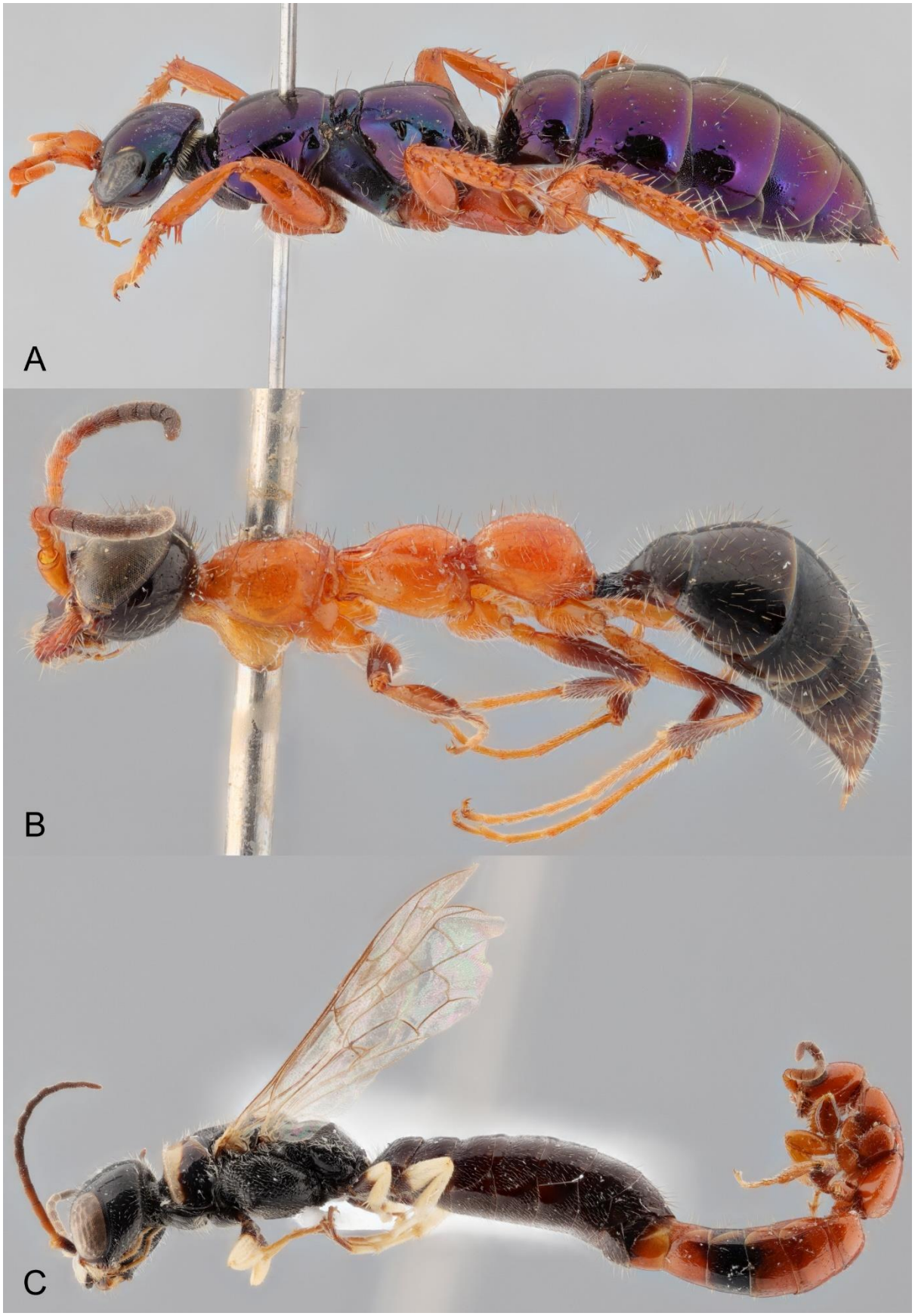

Figure 1. Wingless wasps. A. *Diamma bicolor* Westwood, Australia; B. *Methocha priorrecta* Lin, Taiwan; C. *Zythynnus* sp., Australia.

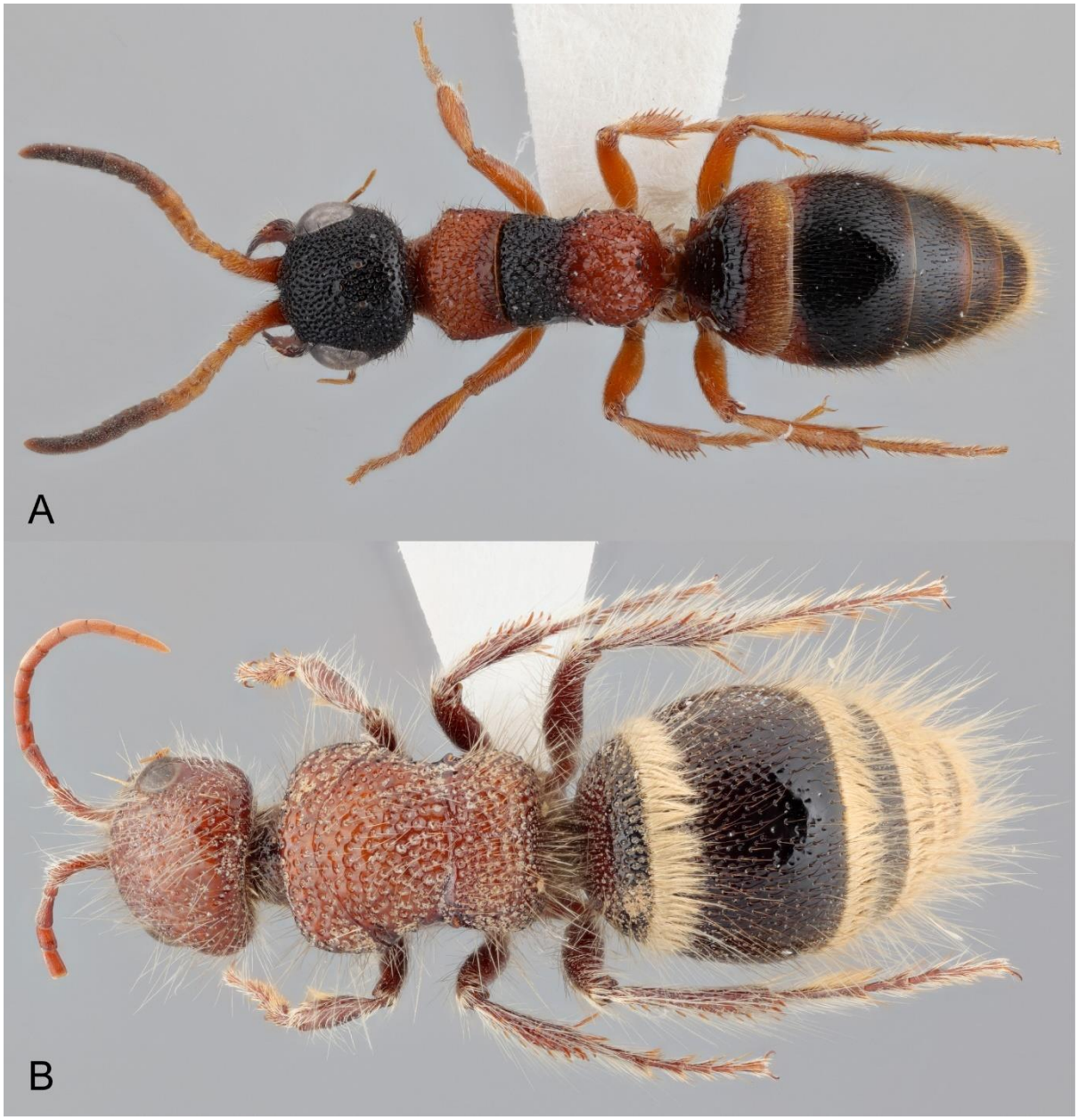

Figure 2. Velvet ants with traces on the mesosoma. A. *Taimyrmosa nigrofasciata* (Yasumatsu) (Myrmosidae), Japan; B. *Pseudophotopsis caspica* (Radoszkowski) (Pseudophotopsidinae), Turkmenistan.

Figure 3. Wingless males. A. *Myrmilla capitata* (Lucas), France; B. *Spilomutilla* sp., India.

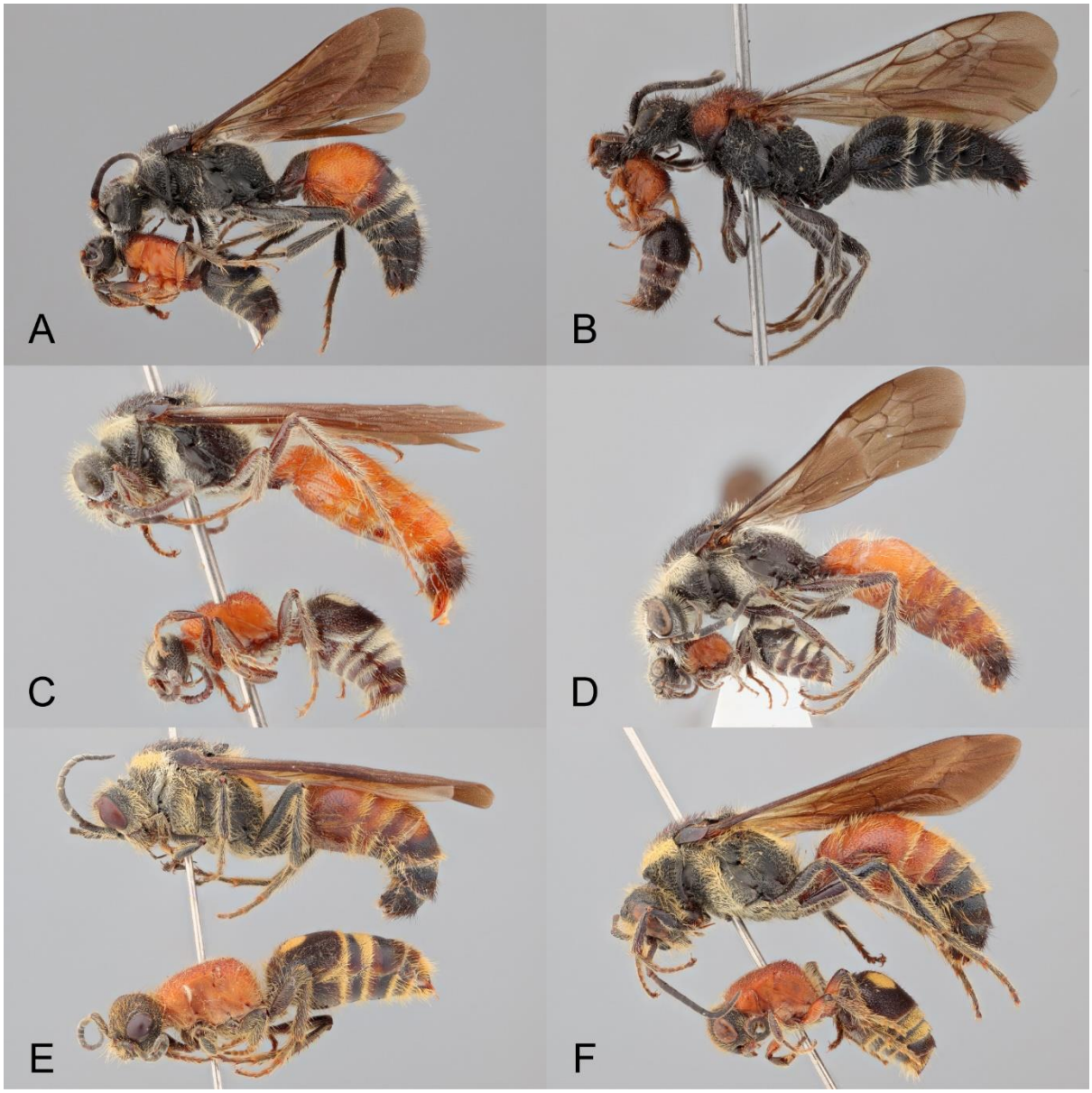

Figure 4. Pinned specimens of mating pairs. A. *Neotrogaspidia pustulata* (Smith), Japan; B. *Smicromyrme lewisi* Mickel, Japan; C. *Trogaspidia formosana* (Matsumura), Taiwan; D. *T. fuscipennis* (Fabricius), Taiwan; E. *T. lingnani* (Mickel), China; F. *T. rhea gaea* Chen, China.

Figure 5. Female velvet ants with their stinger extruded. A. *Sinotilla calopoda* Okayasu, Indonesia; B. *Tropidotilla litoralis* (Petagna), Greece.

Table 1. Velvet ant genera including apterous or brachypterous males.

Genus	Geographic distribution of aptery	Variation	Reference
Ticoplinae: Smicromyrmillini			
Hindustanilla Lelej	Oriental	Apterous.	Brothers & Lelej, 2017; Lelej & Krombein, 2001; Pagliano *et al*., 2020
Smicromyrmilla Suárez	Afrotropical	Macropterous, brachypterous, apterous.	Brothers, 1975; Brothers & Lelej, 2017; Ćetković & Nonveiller, 1992; Mitchell & Brothers, 2002
Dasylabrinae: Apteromutillini			
Apteromutilla Ashmead	Afrotropical	Apterous.	Ashmead, 1900–1904; Brothers & Lelej, 2017; Ćetković & Nonveiller, 1992; Pagliano *et al*., 2020; Péringuey, 1899, 1909
Brachymutilla André	Afrotropical	Apterous.	André, 1901–1902; Ashmead, 1900–1904; Bischoff, 1920–1921; Brothers, 1975; Brothers & Lelej, 2017; Ćetković & Nonveiller, 1992; Hesse, 1935; Pagliano *et al*., 2020
Liotilla Bischoff	Afrotropical	Apterous.	Brothers & Lelej, 2017; Pagliano *et al*., 2020
Dasylabrinae: Dasylabrini			
Dasylabroides André	Afrotropical	Macropterous, brachypterous.	Brothers & Lelej, 2017; Hesse, 1935; Pagliano *et al*., 2020; Péringuey, 1898, 1914
Stenomutilla André	Afrotropical	Macropterous, apterous.	Ćetković & Nonveiller, 1992; Pagliano, 2019
Sphaeropthalminae: Dasymutillini			
Dasymutilla Ashmead	Nearctic	Macropterous, brachypterous, apterous. Intraspecific variation.	Mickel, 1928, 1936a; Schuster, 1945
Sphaeropthalminae: Pseudomethocini			
Myrmilloides André	Nearctic	Brachypterous.	Ashmead, 1900–1904; Blake, 1872; Brothers & Lelej, 2017; Manley & Pitts, 2002; Pagliano *et al*., 2020; Schuster, 1945; Williams *et al*., 2024
Sphaeropthalminae: Sphaeropthalmini			
Chilemutilla Cambra & Quintero	Neotropical	Macropterous, apterous.	Cambra & Quintero, 2007
Limaytilla Casal	Neotropical	Macropterous, apterous.	Cambra & Quintero, 2007; Cambra *et al*., 2016
Morsyma Fox	Nearctic	Macropterous, apterous. Intraspecific variation.	Ashmead, 1900–1904; Fox, 1899; Krombein, 1940; Manley & Pitts, 2002; Pitts, 2007; Quintero & Cambra, 2001b; Schuster, 1958; Williams *et al*., 2024
Odontophotopsis Viereck	Nearctic	Macropterous male chewing off wings.	Manley & Pitts, 2002
Sphaeropthalma Blake	Nearctic, Neotropical	Macropterous, brachypterous, apterous. Macropterous male chewing off wings.	Cambra & Quintero, 2007, 2017; Ferguson, 1967; Manley & Pitts, 2002; Pitts & McHugh, 2000; Pitts *et al*., 2010c; Schuster, 1945, 1958
Stethophotopsis Pitts	Nearctic	Brachypterous.	Pitts & McHugh, 2000; Williams *et al*., 2024
Myrmillinae			
Arnoldtilla Nonveiller	Afrotropical	Apterous.	Arnold, 1956; Nonveiller, 1996; Pagliano *et al*., 2020
Bidecoloratilla Turrisi & Matteini Palmerini	Palaearctic	Apterous.	Bischoff, 1920–1921; Giner Marí, 1944; Invrea, 1964; Turrisi *et al*., 2015; Williams *et al*., 2024
Bimaculatilla Turrisi & Matteini Palmerini	Palaearctic	Apterous.	Turrisi *et al*., 2015
Ceratotilla Bischoff	Afrotropical	Brachypterous, apterous.	Bischoff, 1920–1921; Brothers & Lelej, 2017; Pagliano *et al*., 2020
Labidomilla André	Afrotropical	Macropterous, apterous.	Brothers & Lelej, 2017; Ćetković &

			Nonveiller, 1992; Pagliano *et al*., 2020
Myrmilla Wesmael	Afrotropical, Palaearctic	Macropterous, brachypterous, apterous.	André, 1910; Arnold, 1960; Ashmead 1900–1904; Berland, 1925; Bischoff, 1920–1921; Brothers & Lelej, 2017; Ćetković & Nonveiller, 1992; Invrea, 1964; Pagliano *et al*., 2020; Péringuey, 1898; Turrisi *et al*., 2015; Williams *et al*., 2024
Odontotilla Bischoff	Afrotropical	Brachypterous, apterous.	Brothers & Lelej, 2017; Ćetković & Nonveiller, 1992; Nonveiller, 1996; Pagliano *et al*., 2020
Omotilla Invrea	Afrotropical	Apterous.	Brothers & Lelej, 2017; Ćetković & Nonveiller, 1992
Spilomutilla Ashmead	Oriental	Apterous.	André, 1907a; Ashmead, 1900–1904; Brothers *et al*., 2019; Krombein & Lelej, 1999; Lelej, 2005; Sichel & Radoszkowski, 1869–1870
Viereckia Ashmead	Afrotropical	Macropterous, apterous.	Ashmead, 1900–1904; Brothers & Lelej, 2017; Lelej & Brothers, 2008; Péringuey, 1899
Mutillinae: Smicromyrmini			
Gynandrotilla Arnold	Afrotropical	Apterous.	Arnold, 1946; Lelej & Williams, 2023
Indratilla Lelej	Oriental	Apterous.	Lelej, 1993, 2005; Lelej & Williams, 2023; Williams *et al*., 2024

Table 2. Records of gynandromorphs.

Species	Reference
Myrmosinae: Myrmosini	
Myrmosa atra Panzer	Bischoff, 1913
Sphaeropthalminae: Dasymutillini	
Dasymutilla gloriosa (de Saussure)	Mickel, 1936a; Williams *et al*., 2024
Dasymutilla quadriguttata (Say)	Mickel, 1928
Dasymutilla vestita (Lepeletier)	Mann, 1915
Traumatomutilla americana (Linnaeus)	Bartholomay *et al*., 2019a; Bischoff, 1931; Mickel, 1952
Sphaeropthalminae: Pseudomethocini	
Pseudomethoca areta (Cameron)	Quintero & Cambra, 1994
Pseudomethoca frigida (Smith)	Wheeler, 1910
Pseudomethoca frigida (Smith)	Krombein, 1949
Pseudomethoca propinqua (Cresson)	Mickel, 1935b
Pseudomethoca simillima (Smith)	Krombein, 1948
Myrmillinae	
Bischoffitilla pungens (Smith)	Nagase & Kawashima, 2012
Myrmilla (*Myrmilla*) *calva* (Villers)	Turrisi & Foucart, 2008
Myrmilla (*Myrmilla*) *calva* (Villers)	József & Zoltán, 2011
Myrmilla (*Myrmilla*) *erythrocephala* (Latreille)	Turrisi, 1999
Mutillinae: Mutillini	
Mutilla europaea Linnaeus	Mäklin, 1856
Mutillinae: Smicromyrmini	
Nemka viduata viduata (Pallas)	Lo Cascio & Romano, 2004
Smicromyrme giarabubensis Invrea	Turrisi *et al*., 2022
Smicromyrme varians (André)	Nonveiller, 1973
Mutillinae: Trogaspidiini	
Trogaspidia niveitegulata Bischoff	Nonveiller, 1973

Table 3. Non-hymenopteran hosts of velvet ants.

Host species	Host stage	Velvet ant species	Velvet ant higher classification	Reference
Blattodea: Corydiidae				
Arenivaga genitalis Caudell	ootheca	*Odontophotopsis eubule* (Cameron)	Sphaeropthalminae: Sphaeropthalmini	Mickel, 1974
Lepidoptera: Limacodidae				
Coenobasis amoena Felder	cocoon	Mutillidae sp.	Unknown	Bowden, 1962
Fletcherodes brunneus (Viette)	cocoon	*Seyrigilla splendida* Olsoufieff	Dasylabrinae: Dasylabrini	Krombein, 1972; Paulian, 1950
Macrosemyra sp.	cocoon	*Stenomutilla lavaudeni lavaudeni* Olsoufieff	Dasylabrinae: Dasylabrini	Krombein, 1972
Parasa reginula Saalmüller	cocoon	*Stenomutilla freyi* (Brancsik)	Dasylabrinae: Dasylabrini	Seyrig, 1936
Parasa vivida Walker	cocoon	Mutillidae sp.	Unknown	Bowden, 1962
Coenobasis sp. or *Parasa* sp.	cocoon	Mutillidae sp.	Mutillidae	Bowden, 1962; de Saeger, 1956
Limacodidae sp.	cocoon	*Stenomutilla beroe* (Péringuey)	Dasylabrinae: Dasylabrini	Bezzi, 1924; Bowden, 1967
Coleoptera: Chrysomelidae				
Clytra quadripunctata (Linnaeus)	cocoon	*Physetopoda halensis* (Fabricius)	Mutillinae: Smicromyrmini	Brauns, 1964; Petersen, 1988
Cryptocephalus sp.	unknown	*Smicromyrme rufipes* (Fabricius)	Mutillinae: Smicromyrmini	Giner Marí, 1944
Labidostomis hummeralis (Schneider)	larva	*Physetopoda halensis* (Fabricius)	Mutillinae: Smicromyrmini	Sergeev & Lelej, 2011
Lachnaia tristigma (Lacordaire)?	pupa	*Stenomutilla argentata* (Smith)?	Dasylabrinae: Dasylabrini	Brothers *et al*., 2000; Rosenhauer, 1852, 1856
Pachybrachis scripticolis Faldermann	larva	*Nanomutilla parila* (Nagy)	Ticoplinae: Ticoplini	Argaman, 1988
Tituboea sp.	cocoon	*Physetopoda punctata* (Latreille)	Mutillinae: Smicromyrmini	Barbier, 1976
Clythrid beetle	cocoon	*Smicromyrme thyone* (Péringuey)	Mutillinae: Smicromyrmini	Péringuey, 1898
Diptera: Glossinidae				
Glossina austeni Newstead	puparium	*Chrestomutilla auxilaris* (Turner)	Dasylabrinae: Dasylabrini	Fiedler & Kluge, 1954
Glossina brevipalpis Newstead	puparium	*Chrestomutilla auxilaris* (Turner)	Dasylabrinae: Dasylabrini	Fiedler & Kluge, 1954
Glossina morsitans Westwood	puparium	*Chrestomutilla glossinae* (Turner)	Dasylabrinae: Dasylabrini	Chorley, 1929; Dollman, 1915; Eminson, 1915; Heaversedge, 1968; Lamborn, 1916, 1920, 1925; Lloyd, 1917; Turner, 1915
Glossina morsitans Westwood	puparium	*Chrestomutilla auxilaris* (Turner)	Dasylabrinae: Dasylabrini	Turner, 1920
Glossina morsitans Westwood	puparium	*Smicromyrme benefactrix* (Turner)	Mutillinae: Smicromyrmini	Chorley, 1929; Turner, 1916
Glossina morsitans orientalis Vanderplank	puparium	*Chrestomutilla glossinae* (Turner)	Dasylabrinae: Dasylabrini	Heaversedge, 1969b, 1970
Glossina pallidipes Austen	puparium	*Chrestomutilla auxilaris* (Turner)	Dasylabrinae: Dasylabrini	Harris, 1930
Glossina pallidipes Austen	puparium	*Chrestomutilla glossinae* (Turner)	Dasylabrinae: Dasylabrini	Heaversedge, 1969a
Diptera: Rhinophoridae				
Stevenia signata (Mik)	puparium	*Physetopoda pusilla* (Klug)	Mutillinae: Smicromyrmini	Bürgis, 1990
Diptera: Syrphidae				
Eumerus strigatus (Fallén)	puparium	*Smicromyrme ausonius* Invrea	Mutillinae: Smicromyrmini	Lelej, 1978
Diptera: Tachinidae				
Erythrocera sp.	puparium	*Smicromyrme asiaticus* Lelej	Mutillinae: Smicromyrmini	Lelej, 1985; Serkova, 1962
Gymnosoma rotundata (Linnaeus)	?	*Physetopoda pusilla* (Klug)	Mutillinae: Smicromyrmini	Mellor, 1933

Zeuxia cinerea Meigen	puparium	*Smicromyrme ausonius* Invrea	Mutillinae: Smicromyrmini	Invrea, 1950, 1951; Menozzi, 1947
Diptera: Tephritidae				
Carpomya vesuviana Costa	puparium	*Smicromyrme nikolskajae* Lelej	Mutillinae: Smicromyrmini	Amini *et al*., 2014, 2024
Carpomya vesuviana Costa	puparium	*Smicromyrme tekensis* Skorikov	Mutillinae: Smicromyrmini	Amini *et al*., 2014, 2024

Table 4. Hyperparasitic velvet ants and their hosts.

Velvet ant species	Host species	Host ecology	Primary host	Reference
Myrmosinae: Myrmosini				
Myrmosa unicolor Say	*Tiphia* sp.	ectoparasitoid	Unknown	Krombein, 1940
Sphaeropthalminae: Dasymutillini				
Dasymutilla bioculata (Cresson)	*Myzinum quinquecincta* (Fabricius)	ectoparasitoid	*Lachnosterna* sp.	Swezey, 1915
Dasymutilla bioculata (Cresson)	*Myzinum quinquecincta* (Fabricius)	ectoparasitoid	*Phyllophaga* sp.	Davis, 1919
Dasymutilla quadriguttata (Say)	*Myzinum obscurum* (Fabricius)	ectoparasitoid	Scarabaeidae sp.	Fattig, 1943
Dasymutilla quadriguttata (Say)	*Myzinum quinquecincta* (Fabricius)	ectoparasitoid	*Lachnosterna* sp.	Swezey, 1915
Dasymutilla quadriguttata (Say)	*Myzinum quinquecincta* (Fabricius)	ectoparasitoid	*Phyllophaga* sp.	Davis, 1919; Hayes, 1924; Remington, 1944
Sphaeropthalminae: Pseudomethocini: Pseudomethocina				
Pseudomethoca simillima (Smith)	*Nomada* sp.	cleptoparasite	*Andrena macra* Mitchell	Riddick, 1991
Sphaeropthalminae: Sphaeropthalmini				
Odontophotopsis eubule (Cameron)	*Evaniella neomexicana* (Ashmead)	endoparasitoid	*Arenivaga genitalis* Caudell	Mickel, 1974
Sphaeropthalma abdominalis (Blake)	*Ceratochrysis enhuycki* (Cooper)	ectoparasitoid	Unknown	Pitts *et al*., 2004
Sphaeropthalma abdominalis (Blake)	*Sapyga pumila* Cresson	ectoparasitoid	Unknown	Pitts *et al*., 2004
Sphaeropthalma abdominalis (Blake)	*Stelis lateralis* Cresson?	cleptoparasite	Unknown	Pitts *et al*., 2004
Sphaeropthalma abdominalis (Blake)	*Stelis* sp.	cleptoparasite	*Ashmeadiella gillettei* Titus	Pitts *et al*., 2004
Sphaeropthalma abdominalis (Blake)	*Stelis* sp.	cleptoparasite	*Hoplitis grinnelli* (Cockerell)	Pitts *et al*., 2004
Sphaeropthalma amphion (Fox)	*Chrysis derivata* du Buysson	ectoparasitoid	Unknown	Pitts *et al*., 2004
Sphaeropthalma amphion (Fox)	*Sapyga aculeata* Cresson	ectoparasitoid	*Hoplitis sambuci* Titus	Pitts *et al*., 2004
Sphaeropthalma amphion (Fox)	*Sapyga elegans* Cresson	ectoparasitoid	*Hoplitis fulgida* (Cresson),	Pitts *et al*., 2004
Sphaeropthalma amphion (Fox)	Sarcophagidae sp.	endoparasitoid	Unknown	Pitts *et al*., 2004
Sphaeropthalma amphion (Fox)	*Stelis* sp.	cleptoparasite	*Hoplitis bullifacies* (Michener)	Pitts *et al*., 2004
Sphaeropthalma amphion (Fox)	*Stelis* spp.	cleptoparasite	Unknown	Pitts *et al*., 2004
Sphaeropthalma jacala Schuster	*Chrysis derivata* du Buysson	ectoparasitoid	*Trypoxylon tenoctitlan* Richards	Pitts & Parker, 2005
Sphaeropthalma unicolor (Cresson)	*Melecta separata callura* (Cockerell)	cleptoparasite	*Anthophora edwardsii* Cresson	Thorp, 1969ab
Sphaeropthalma unicolor (Cresson)	*Xeromelecta californica* (Cresson)	cleptoparasite	*Anthophora linsleyi* Timberlake	Linsley & MacSwain, 1942
Sphaeropthalma unicolor (Cresson)	*Xeromelecta californica* (Cresson)	cleptoparasite	*Anthophora montana* Cresson	Davidson, 1897
Sphaeropthalma uro (Blake)	*Chrysis derivata* du Buysson	ectoparasitoid	Unknown	Pitts *et al*., 2004
Sphaeropthalma uro (Blake)	*Chrysis* sp.	ectoparasitoid	*Parancistrocerus* sp.	Pitts *et al*., 2004
Sphaeropthalma uro (Blake)	*Chrysis* spp.	ectoparasitoid	Unknown	Pitts *et al*., 2004
Sphaeropthalma uro (Blake)	*Sapyga pumila* Cresson	ectoparasitoid	Unknown	Pitts *et al*., 2004
Sphaeropthalma uro (Blake)	*Stelis* spp.	cleptoparasite	Unknown	Pitts *et al*., 2004
Mutillinae: Smicromyrmini				
Ephucilla ludovica (Cameron), *E. poonaensis* (Cameron), or *Promecilla yerburghi* (Cameron)	*Chrysis* sp.	ectoparasitoid	*Paraleptomenes mephitis* (Cameron)	Krombein, 1978

Physetopoda pusilla (Klug)	*Gymnosoma rotundata* (Linnaeus)	endoparasitoid	*Dolycoris baccarum* (Linnaeus)	Mellor, 1933
Physetopoda pusilla (Klug)	*Stevenia signata* (Mik)	endoparasitoid	*Armadillidium vulgare* (Latreille)	Bürgis, 1990
Smicromyrme nr. *antennatus* (Smith)	*Tiphia* sp.	ectoparasitoid	Unknown	Clausen *et al*., 1932
Smicromyrme asiaticus Lelej	*Erythrocera* sp.	endoparasitoid	*Theone silphoides* (Dalman)	Lelej, 1985; Serkova, 1962
Smicromyrme ausonius Invrea	*Zeuxia cinerea* Meigen	endoparasitoid	*Conorhynchus mendicus* Gyllenhall	Invrea, 1950, 1951; Menozzi, 1947
Mutillinae: Trogaspidiini				
Pagdenidia hymalajensis (Radoszkowski)	*Tiphia simlaensis* Cameron	ectoparasitoid	Unknown	Clausen *et al*., 1932
Timulla ocellaria ocellaria Mickel	Scoliidae or Tiphiidae sp.	ectoparasitoid	*Ligyrus gibbosus* (DeGeer)	Fattig, 1943; Quintero & Cambra, 1996a
Trogaspidia castellana castellana (Mercet)	*Campsomeriella collaris quadrifasciata* (Fabricius)	ectoparasitoid	Unknown	Thompson, 1950, 1958
Trogaspidia castellana castellana (Mercet)	*Campsomeris annulata* (Fabricius)	ectoparasitoid	Unknown	Thompson, 1950, 1958
Trogaspidia castellana castellana (Mercet)	*Liacos analis* (Fabricius)	ectoparasitoid	Unknown	Thompson, 1950, 1958
Trogaspidia castellana castellana (Mercet)	*Megacampsomeris asiatica* (de Saussure)	ectoparasitoid	Unknown	Thompson, 1950, 1958
Trogaspidia castellana castellana (Mercet)	*Megacampsomeris reticulata* (Cameron)	ectoparasitoid	Unknown	Thompson, 1950, 1958
Trogaspidia castellana castellana (Mercet)	*Megascolia scutellaris* (Gribodo)	ectoparasitoid	Unknown	Thompson, 1950, 1958
Trogaspidia castellana castellana (Mercet)	*Micromeriella marginella modesta* (Smith)	ectoparasitoid	Unknown	Thompson, 1950, 1958
Trogaspidia castellana castellana (Mercet)	*Phalerimeris aurulenta* (Smith)	ectoparasitoid	Unknown	Thompson, 1950, 1958
Trogaspidia castellana castellana (Mercet)	*Seriocampsomeris stygia* (Illiger)	ectoparasitoid	Unknown	Thompson, 1950, 1958
Trogaspidia castellana castellana (Mercet)	*Tiphia lucida* Crawford	ectoparasitoid	*Adoretus* sp.	Williams, 1919; Mickel, 1934
Trogaspidia castellana castellana (Mercet)	*Tiphia segregata* Crawford	ectoparasitoid	Unknown	Thompson, 1950, 1958
Trogaspidia castellana visayensis (Mercet)	*Campsomeris* sp. or *Scolia* sp.	ectoparasitoid	Scarabaeidae sp.	Lopez, 1931; Mickel, 1934
Mutillidae *incerta sedis*				
Mutillidae sp.	Thynnidae sp.	ectoparasitoid	Unknown	Burrell, 1935
Mutillidae sp.	*Melecta separata callura* (Cockerell)	cleptoparasite	*Anthophora edwardsii* Cresson	Thorp, 1969a

Table 5. Host records for East Asian velvet ants. Abbreviations: **C**, co-occurrence of adults and potential hosts; **E**, emergence of adults; **I**, intrusion of females into host nests; **N**, observation of adults in nesting sites; **O**, observation of oviposition or larvae; **?**, not specified.

Velvet ant species	Host species	Host affiliation	Evidence	Reference
Sphaeropthalminae: Sphaeropthalmini				
Cystomutilla teranishii Mickel	*Ectemnius iridifrons* (Pérez)	Crabronidae	E	Gôukon, 1993
Dasylabrinae				
Dasylabris (*Baltilla*) *adversa* Skorikov	*Anthophora* sp.	Apidae	N	Lelej *et al*., 2014
Dasylabris (*Baltilla*) *adversa* Skorikov	*Colletes* sp.	Colletidae	N	Lelej *et al*., 2014
Dasylabris (*Baltilla*) *adversa* Skorikov	*Hylaeus* sp.	Colletidae	N	Lelej *et al*., 2014
Dasylabris (*Baltilla*) *gobicola* Skorikov	*Anthophora* sp.	Apidae	N	Lelej *et al*., 2014
Dasylabris (*Baltilla*) *gobicola* Skorikov	*Colletes* sp.	Colletidae	N	Lelej *et al*., 2014
Dasylabris (*Baltilla*) *gobicola* Skorikov	*Hylaeus* sp.	Colletidae	N	Lelej *et al*., 2014
Dasylabris (*Baltilla*) *kozlovi* Skorikov	*Anthophora* spp.	Apidae	I, N	Lelej *et al*., 2014
Dasylabris (*Baltilla*) *kozlovi* Skorikov	*Colletes* sp.	Colletidae	N	Lelej *et al*., 2014
Dasylabris (*Baltilla*) *kozlovi* Skorikov	*Hylaeus* sp.	Colletidae	N	Lelej *et al*., 2014
Dasylabris (*Dasylabris*) *siberica* (Christ)	*Anthophora* sp.	Apidae	N	Lelej *et al*., 2014
Dasylabris (*Dasylabris*) *siberica* (Christ)	*Colletes* sp.	Colletidae	N	Lelej *et al*., 2014
Dasylabris (*Dasylabris*) *siberica* (Christ)	*Hylaeus* sp.	Colletidae	N	Lelej *et al*., 2014
Myrmillinae				
Bischoffitilla ardescens (Smith)	*Tetraloniella mitsukurii* (Cockerell)	Apidae	E	Gôukon, 1993
Bischoffitilla ardescens (Smith)	*Lasioglossum duplex* (Dalla Torre)	Halictidae	E	Gôukon, 1993
Bischoffitilla ardescens (Smith)	*Lasioglossum sakagamii* Ebmer	Halictidae	E, N, O	Sakagami *et al*., 1982
Bischoffitilla pungens (Smith)	*Colletes esakii* Hirashima	Colletidae	E, I, N	Kawashima & Suzuki, 2002; Nagase & Kawashima, 2012; Ono & Kawashima, 2013
Bischoffitilla pungens (Smith)	*Lasioglossum duplex* (Dalla Torre)	Halictidae	E, O	Gôukon, 1993; Gôukon *et al*., 1986
Mutillinae: Mutillini				
Mutilla mikado Cameron	*Bombus breviceps* Smith	Apidae	E, I, O	Lelej *et al*., 2023; Su *et al*., 2019
Mutilla mikado Cameron	*Bombus deuteronymus maruhanabachi* Sakagami & Ishikawa	Apidae	I, O	Katayama, 2008; Katayama *et al*., 1993
Mutilla mikado Cameron	*Bombus diversus diversus* Smith	Apidae	E, I, O	Abe, 1932; Katayama, 1966, 2008; Katayama *et al*., 1996; Miyamoto, 1959; Sakagami & Katayama, 1977; Tsuneki, 1972a
Mutilla mikado Cameron	*Bombus haemorrhoidalis* Smith	Apidae	I, O	Su *et al*., 2019
Mutilla mikado Cameron	*Bombus hypocrita hypocrita* Pérez	Apidae	I	Katayama & Takamizawa, 2004
Mutilla mikado Cameron	*Bombus ignitus* Smith	Apidae	E, I	Miyamoto, 1963; Sakagami & Katayama, 1977
Mutilla mikado Cameron	*Bombus ussurensis* Radoszkowski	Apidae	O	Katayama *et al*., 1990
Mutillinae: Smicromyrmini				
Ephucilla brevitegula Okayasu	*Phimenes flavopictus formosanus* (Zimmermann)	Vespidae	E	Okayasu, 2020

Mickelomyrme hageni (Zavattari)	*Lasioglossum subtropicum* Sakagami, Miyanaga & Maeta	Halictidae	N	Brothers *et al*., 2000
Nemka kellyi (Pagden)	Stizine wasp	Bembicidae	I	Pagden, 1934c
Nemka kellyi (Pagden)	*Cerceris bidentula* Maidl	Philanthidae	I	Pagden, 1934c
Nemka yasumatsui (Mickel)	*Bembecinus hungaricus* (Frivaldszky)	Bembicidae	C	Okayasu, 2020
Nemka yasumatsui (Mickel)	*Bembix niponica* Smith	Bembicidae	E	Ono & Kawashima, 2013
Nemka yasumatsui (Mickel)	*Stizus perrisi* Dufour	Bembicidae	C	Okayasu, 2020
Promecilla decora (Smith)	*Pison argentatum* Shuckard	Crabronidae	E	Pagden, 1934b
Smicromyrme (*Smicromyrme*) *lewisi* Mickel	*Gorytes tricinctus* (Pérez)	Bembicidae	E	Gôukon, 1993
Smicromyrme (*Smicromyrme*) *lewisi* Mickel	*Oxybelus bipunctatus* Olivier	Crabronidae	N	Lelej, 1985
Smicromyrme (*Smicromyrme*) *lewisi* Mickel	*Tachysphex nigricolor nigricolor* (Dalla Torre)	Crabronidae	E	Gôukon, 1993
Smicromyrme (*Smicromyrme*) *lewisi* Mickel	*Cerceris hortivaga* Kohl	Philanthidae	E, N	Tsuneki, 1965
Smicromyrme (*Smicromyrme*) *lewisi* Mickel	*Cerceris* sp.	Philanthidae	N	Lelej *et al*., 2001
Smicromyrme (*Smicromyrme*) *lewisi* Mickel	*Colletes esakii* Hirashima	Colletidae	I	Togashi, 1991
Smicromyrme (*Smicromyrme*) *lewisi* Mickel	*Colletes* sp.	Colletidae	N	Lelej *et al*., 2014
Smicromyrme (*Smicromyrme*) *lewisi* Mickel	*Hylaeus* sp.	Colletidae	N	Lelej *et al*., 2014
Smicromyrme (*Smicromyrme*) *lewisi* Mickel	Apoidea sp.	Apoidea	I	Lelej *et al*., 2001
Mutillinae: Trogaspidiini				
Neotrogaspidia pustulata (Smith)	*Cerceris albofasciata* (Rossi)	Philanthidae	?	Yasumatsu, 1944
Neotrogaspidia pustulata (Smith)	*Dasypoda japonica* Cockerell	Melittidae	N	Okayasu, 2023a
Pagdenidia hymalajensis (Radoszkowski)	*Tiphia simlaensis* Cameron	Tiphiidae	E	Clausen *et al*., 1932
Trogaspidia castellana castellana (Mercet)	*Campsomeriella collaris quadrifasciata* (Fabricius)	Scoliidae	?	Thompson, 1950, 1958
Trogaspidia castellana castellana (Mercet)	*Campsomeris annulata* (Fabricius)	Scoliidae	?	Thompson, 1950, 1958
Trogaspidia castellana castellana (Mercet)	*Liacos analis* (Fabricius)	Scoliidae	?	Thompson, 1950, 1958
Trogaspidia castellana castellana (Mercet)	*Megacampsomeris asiatica* (de Saussure)	Scoliidae	?	Thompson, 1950, 1958
Trogaspidia castellana castellana (Mercet)	*Megacampsomeris reticulata* (Cameron)	Scoliidae	?	Thompson, 1950, 1958
Trogaspidia castellana castellana (Mercet)	*Megascolia scutellaris* (Gribodo)	Scoliidae	?	Thompson, 1950, 1958
Trogaspidia castellana castellana (Mercet)	*Micromeriella marginella modesta* (Smith)	Scoliidae	?	Thompson, 1950, 1958
Trogaspidia castellana castellana (Mercet)	*Phalerimeris aurulenta* (Smith)	Scoliidae	?	Thompson, 1950, 1958
Trogaspidia castellana castellana (Mercet)	*Seriocampsomeris stygia* (Illiger)	Scoliidae	?	Thompson, 1950, 1958
Trogaspidia castellana castellana (Mercet)	*Tiphia lucida* Crawford	Tiphiidae	E	Williams, 1919; Mickel, 1934
Trogaspidia castellana castellana (Mercet)	*Tiphia segregata* Crawford	Tiphiidae	?	Thompson, 1950, 1958
Trogaspidia castellana visayensis (Mercet)	*Campsomeris* sp. or *Scolia* sp.	Tiphiidae	E	Lopez, 1931; Mickel, 1934
Trogaspidia oceanica oceanica (André)	*Bembecinus papuanus* (Cameron)	Bembicidae	N	Krombein, 1971

Table 6. Color traits analyzed to infer Müllerian mimicry rings.

Body parts	**Wilson *et al*. (2012b)**	**Wilson *et al*. (2015)**	**Wilson *et al*. (2018)**
Head		head primary (background) color	head primary (background) color
		head secondary color	head secondary color
Mesosoma	percent black of mesosoma	mesosoma background color	mesosoma background color
		mesosoma secondary color	mesosoma secondary color
Metasoma		petiole color	petiole color
		presence or absence of a contrasting setal spot on petiole	presence or absence of a contrasting setal coloration on petiole
	percent black of metasoma	metasoma background color	metasoma background color
	pattern on metasoma	metasoma secondary color	metasoma secondary color
	non-black metasomal color	presence of a third color on the second tergum of metasoma	presence of a third color on the second tergum of metasoma
		contrasting dark and light pattern on the second tergum of metasoma	contrasting dark and light pattern on the second tergum of metasoma
		presence or absence of light setal fringe on the third to fifth tergum	presence or absence of light setal fringe on the third to fifth tergum
Legs		leg primary color	leg primary color
Whole body	integument color	integument color	integument color
	setal length in five categories	setal color in four categories	hairness: hair length or density in four categories

Chapter 2

Review of *Eotrogaspidia* Lelej (Hymenoptera: Mutillidae: Trogaspidiini)

Disclaimer: *This chapter has already been published as a peer-reviewed paper as follows: Okayasu, J., Lelej, A.S. & Williams, K.A. (2021) Zootaxa 4920 (1): 56–90 (https://doi.org/10.11646/zootaxa.4920.1.2). New nomenclatural acts appearing in this chapter have already been made in this publication and, thus, this dissertation chapter is not considered a published work within the meaning of the International Code of Zoological Nomenclature 4th edition (Article 8.2).*

Abstract
Ten species of *Eotrogaspidia* Lelej, 1996, two related species of *Trogaspidia* Ashmead, 1899 and one related species of *Vanhartenidia* Lelej in Lelej & van Harten, 2006 are revised. Before this study, *Eotrogaspidia* included the following four species: *E. amans* (André, 1909) (♂♀), *E. auroguttata* (Smith, 1855) (♂♀), *E. ekka* (Nurse, 1902) (♀) and *E. oryzae* (Pagden, 1934) (♂♀). In the present paper, four new species are described: *E. adhabar* **sp. nov.** (♂) (India, Nepal), *E. buddha* **sp. nov.** (♂♀) (India, Nepal, Pakistan, Sri Lanka), *E. hauseri* **sp. nov.** (♂) (India, Nepal) and *E. melanopleura* **sp. nov.** (♀) (China). Three species are transferred to *Eotrogaspidia* from *Trogaspidia*: *E. lena* (Cameron, 1899), **comb. nov.** (♂), *E. rubripes* (André, 1901), **comb. nov.** (♀) and *E. saussurei* (Lelej, 2005), **comb. nov.** (♂♀). *Mutilla ekka* Nurse, 1902 from India is transferred from *Eotrogaspidia* to *Vanhartenidia ekka*, **comb. nov.** The male of *E. saussurei* is described. New synonymies are proposed for *E. auroguttata* (= *T. vallicola* Tsuneki, 1993, **syn. nov.**) and *Trogaspidia mackieae* (Cockerell, 1928) (= *T. pacifica* Tsuneki, 1972, **syn. nov.**). Eight new country records are presented: one from China, two from Laos, one from Vietnam, two from India, one from Iran, and one from Afghanistan. Female specimens of *E. buddha* **sp. nov.** were formerly misidentified as *T. acidalia* (Cameron, 1897), **stat. resurr.** by the late B. Petersen. The lectotype of *T. acidalia* is designated and illustrated to clarify its identity. Diagnoses and illustrations for reviewed species and a key to all known *Eotrogaspidia* species and related genera are provided for males and females.

Key words
Aculeata, velvet ants, taxonomy, Oriental region, Palaearctic region, Asia.

Introduction

In the Oriental region, Mutillidae are represented by ca. 650 species in 63 genera (Brothers *et al*., 2019; Lelej, 2005, 2007; Lelej & Brothers, 2008; ; Pagliano *et al*., 2020; Williams *et al*., 2019b). Of these, almost 90% were described before 1970 and, of the species described more than half a century ago, only roughly 20% were included in modern keys or were illustrated in modern papers (e.g., Lelej, 1995, 1996ab, 2005; Lelej & Krombein, 1999, 2001; Lelej *et al*., 2016, 2017; Terayama, 2005; Terayama *et al*., 2011, 2016; Tu *et al*., 2014, 2015; Okayasu, 2017, 2018, 2020; Okayasu *et al*. 2018; Pagliano *et al*., 2020; Williams *et al*., 2019a; Zhou *et al*., 2017, 2018). The remaining species were included in older keys (Chen, 1957; Mickel, 1933ab, 1934, 1935) or known only from their original descriptions. Therefore, identification of most Oriental mutillids largely depends on outdated literature (Williams *et al*., 2019a), leaving many potential synonyms for subsequent names proposed by recent authors.

The genus *Eotrogaspidia* Lelej, 1996c is a small group of Trogaspidiini Bischoff,

1920, and presently includes four species that are predominantly distributed in the Oriental region: *E. amans* (André, 1909) (♂♀), *E. auroguttata* (Smith, 1855) (♂♀), *E. ekka* (Nurse, 1902) (♀) and *E. oryzae* (Pagden, 1934) (♂♀). These species had been long known from their original descriptions and Mickel's (1933a, 1935) keys only. Recently, *E. auroguttata* and *E. oryzae* were illustrated and diagnosed (Terayama *et al*., 2011; Williams *et al*., 2019a). However, the genus, as a whole, has not been revised so far. Below, based on museum specimens from various localities in Asia, including unrevised types from Katsuji Tsuneki in Museum of Nature and Human Activities, I review ten species of *Eotrogaspidia*, with descriptions of new species from China, India, Nepal, Pakistan and Sri Lanka, new synonymies, new combinations and new distributional records.

Material and methods

The following abbreviations are used for institutions housing the material discussed in this study.

BMNH The Natural History Museum, London, UK.
CASC California Academy of Sciences, San Francisco, California, USA.
CSCA California State Collection of Arthropods, Sacramento, California, USA.
ELKU Entomological Laboratory, Faculty of Agriculture, Kyushu University, Fukuoka, Japan.
EUM Ehime University Museum, Matsuyama, Japan.
HUM Hokkaido University Museum, Sapporo, Japan.
IBSS Federal Scientific Center of the East Asia Terrestrial Biodiversity (formerly Institute of Biology and Soil Science), Vladivostok, Russia.
MNHAH Museum of Nature and Human Activities, Sanda, Japan.
MNHN Muséum National d'Histoire Naturelle, Paris, France.
MSNF Museo di Zoologia della Specola, Sezione del Museo di Storia Naturale, Firenze, Italy.
MTC Mamoru Terayama Collection in Laboratory of Applied Entomology, Department of Agricultural and Environmental Biology, The University of Tokyo, Tokyo, Japan.
QSBG Queen Sirikit Botanic Gardens, Mae Rim, Chiang Mai, Thailand,
RMNH Naturalis Biodiversity Center, Leiden, South Holland, the Netherlands.
SEMC Snow Entomological Museum, University of Kansas, Lawrence, Kansas, USA.
SMNS Staatliches Museum für Naturkunde Stuttgart, Germany.
TARI Taiwan Agricultural Research Institute, Taichung, Taiwan.
TFRI Taiwan Forestry Research Institute, Taipei, Taiwan.
TUA Laboratory of Entomology, Tokyo University of Agriculture, Atsugi, Japan.
UCDC Bohart Museum of Entomology, University of California, Davis, California, USA.
UMMZ University of Michigan Museum of Zoology, Ann Arbor, Michigan, USA.
USNM National Museum of Natural History, Smithsonian Institution, Washington DC, USA.
ZMMU Zoological Museum of Moscow State University, Russia.
ZSM Zoologische Staatsammlung, München, Germany.

Specimens were examined with various stereomicroscopes in multiple laboratories. Most habitus photographs were taken using a Leica MC170 HD camera through a Leica M165C stereomicroscope. Photo processing was done using Adobe Photoshop software and Adobe Illustrator software. Terminology follows the Hymenoptera Anatomy Ontology (2013). Integument sculpture terminology follows Harris (1979). In the synonymic lists and material examined sections, abbreviations for depository and additional or corrected data by

the authors are given in square brackets. New records are asterisked (*). Old names of insect collecting localities in Taiwan were translated into the present names using Chu & Yamanaka (1973–1975) and Kojima *et al*. (2011).

Male genitalia were extracted after softening specimens by soaking in 70 % ethanol. Muscles of the genitalia were removed in a 10 % potassium hydroxide (KOH) solution without heating for one to three hours, and subsequently soaked in a 25 % acetic acid solution to neutralize. Lastly, genitalia were observed in 70 % ethanol under a stereomicroscope. After examination, genitalia were stored in micro vials filled with glycerin and pinned with their respective specimens. Terminology follows Snodgrass (1941).

Specimens were measured twice in order to reduce measurement errors, and the mean value was indicated in the description. Body length was measured as the sum of head length, mesosomal length and metasomal length in dorsal view. Head length was measured in dorsal view excluding antennal tubercle. Mesosomal length was measured between posterior margin of head and posterior margin of propodeum. In males, mesosomal width was measured at antero-lateral angle of dorsum of pronotum (humeral width), pronotal spiracles (pronotal width) and mesonotum including tegulae (mesonotal width).

Abbreviations are: F = flagellomere; LOD = longitudinal lateral ocellar diameter; MOD = longitudinal medial ocellar diameter; OD = interocellar distance between medial and lateral ocelli; OOD = ocular-ocellar distance between lateral ocellus and eye; POD = interocellar distance between lateral ocelli; S = sternum; T = tergum; MT = Malaise trap; YPT = yellow pan trap.

***Eotrogaspidia* Lelej, 1996**

(Figs 1–15)

Eotrogaspidia Lelej, 1996c: 21, ♂♀.
Type species: *Mutilla auroguttata* Smith, 1855, by original designation.

Extended diagnosis

MALE. Post genal bridge without medial projection; hypostomal carina not dentate. Clypeus polished, concave or gibbous in pentagonal shape (Figs 5–6). Mandible apically bidentate, ventrally excised into large basal tooth, without inner subbasal denticle. Prementum not tuberculate. Scape with one strong or two parallel longitudinal carinae ventrally; scape punctate or smooth between two carinae (Figs 5A, 6C); F1 compressed, 3 × longer than pedicel. Parascutal carina well developed; mesopleuron ventrally with precoxal swelling; mesoscutellum with medial longitudinal carina posteriorly elevated or tuberculate; propodeum laterally without denticles. Metacoxa evenly convex with sparse long recumbent setae (Fig. 7A), or flattened with dense erect microsetae (Figs 7B–G). S2 evenly convex, without lateral felt line; T7 with medial longitudinal impunctate line; S5–6 without lateral carinae; S8 with strong longitudinal lateral ridge posteriorly tuberculate; cuspis stick-like (Figs 10A, 10D), spatulate (Figs 10B, 11B), narrowed posteriorly (Fig. 10C), or lamellate (Figs 11A, 11C); digitus slender, apparently smaller than cuspis; paracuspis stick-like; penis valves weakly asymmetrical, posteriorly with ventral hook (Figs 10E–H, 11D–F). FEMALE. Mesosoma broadest at propodeum; scutellar scale developed. Procoxa armed with rounded tubercle. T2 with two large pale setal spots, distance between them 0.3–0.5 × spot diameter; T3–T4 with complete or medially interrupted band of pale setae; if T2 spots small and distance between them 1.0 × or more than spot diameter, then T3–T4 with two small spots of pale setae widely separated from lateral margin of terga (Figs 2C–D, 4B–C); pygidial plate sub-convex, laterally defined by weak longitudinal carinae; surface of pygidial plate irregularly rugose on anterior 1/3–1/2 and smooth posteriorly, transversely rugose entirely, or

micro-reticulate entirely with irregular sub-rugae anteriorly (Fig. 12).

Species included
Eotrogaspidia includes 10 species: *E. adhabar* **sp. nov.**, ♂ (India, Nepal), *E. amans* (André, 1909), ♂♀ (Indonesia), *E. auroguttata* (Smith, 1855), ♂♀ (China, India*, Indonesia, Japan, Laos*, Thailand, Vietnam), *E. buddha* **sp. nov.**, ♂♀ (India, Nepal, Pakistan, Sri Lanka), *E. hauseri* **sp. nov.**, ♂ (India, Nepal), *E. lena* (Cameron, 1899), **comb. nov.**, ♂ (India), *E. melanopleura* **sp. nov.**, ♀ (China), *E. oryzae* (Pagden, 1934), ♂♀ (Laos*, Malaysia, Thailand, Vietnam), *E. rubripes* (André, 1901), **comb. nov.**, ♀ (Afghanistan*, Iran*, Palestine, Syria) and *E. saussurei* (Lelej, 2005), **comb. nov.**, ♂♀ (India, Sri Lanka). Every new combination proposed herein involves species that were previously placed in the genus *Trogaspidia* Ashmead, 1899 (*T. lena*, *T. rubripes*, *T. saussurei*). Also, we propose the reallocation of *Mutilla ekka* Nurse, 1902, ♀ (India) from *Eotrogaspidia* to *Vanhartenidia* Lelej in Lelej & van Harten, 2006 (**new combination**) because this species is closely related and potentially synonymous with *V. dives* (Smith, 1855).

Distribution
Oriental region. Only *E. auroguttata* and *E. rubripes* are distributed in the Palaearctic region (Palaearctic China and Middle East, respectively).

Remarks
The male of this genus is similar to that of *Trogaspidia* by having the mandible ventrally excised with a large tooth, the mesoscutellum with a longitudinal medial carina, S2 without a felt line, the paracuspis well-developed and the digitus straight, but it differs by having F1 compressed (cylindrical in *Trogaspidia*), the digitus small (usually larger in *Trogaspidia*) and the penis valves weakly asymmetrical (right penis valve usually more strongly modified in *Trogaspidia*). The male of this genus is also similar to that of *Vanhartenidia* by having the metacoxa conspicuously flattened and covered with dense erect pale microsetae ventrally, but differs by having a stick-like digitus (lamellate in *Vanhartenidia*) and a well-developed stick-like paracuspis (paracuspis tuberculate coarctate in *Vanhartenidia*). The female of this genus is similar to that of *Trogaspidia* by having the mesosoma broadest at the propodeum and the pygidial plate posteriorly smooth or micro-reticulate, but differs by having the pygidial plate irregularly rugose on anterior 1/3–1/2 and smooth posteriorly or micro-reticulate entirely (longitudinally striate, longitudinally rugose, or irregularly rugose on basal 3/4 in *Trogaspidia*). The female of *Eotrogaspidia* also resembles that of *Vanhartenidia* by having T2 with large baso-lateral golden spots, but can be distinguished from the latter by having the protarsus weakly pectinate (strongly pectinate in *Vanhartenidia*) and the pygidial plate weakly sculptured, irregularly or transversely rugose, or micro-reticulate throughout, with lateral carina not widened posteriorly (pygidial plate with well-developed longitudinal rugae and lateral carina widened posteriorly in *Vanhartenidia*).

***Eotrogaspidia adhabar* sp. nov.**
(Figs 1A, 1E, 5A, 7A, 8A–B, 10A, 10E)

Diagnosis
MALE. Clypeus medially gibbous in pentagonal shape (Fig. 5A); scape with one strong longitudinal carina ventrally (Fig. 5A). Metacoxa evenly convex with long sparse setae (Fig. 7A). FEMALE. Unknown.

Description

MALE. Body length: 13.0 mm. Forewing length: 10.9 mm.

Color and setae. Black with mandible medially, premetum, stipes, palpi, scape except apex and pedicel dark brown, apex od scape yellow, tegula brownish black, protibial spur pale brown, meso- and metatibial spurs yellowish, T1–4 and S1–4 yellowish red except medial carina on S1 black, T5–7 and S5–8 brownish black. Frons, vertex and gena entirely covered with sparse long erect silvery setae, dense on antennal scrobe, malar space and clypeus laterally; frons with dense long appressed silvery setae; vertex behind ocellar region with dense short appressed silvery setae; anterior margin of clypeus fringed with long erect golden setae; prementum, stipes and palpi with sparse very short erect pale golden setae; scape with sparse long recumbent and sparse long erect silvery setae; pedicel and F1 with dense short sub-appressed silvery setae; F2–11 with dense very short erect pale golden setae. Mesosoma mostly with sparse erect silvery setae; pronotal collar posteriorly glabrous; dorsum of pronotum, mesopleuron and dorsum of propodeum between sublateral carinae with dense long appressed silvery setae; mesoscutum with sparse short recumbent and sparser long erect black setae; tegula with sparse short recumbent black setae; mesoscutellum with sparse long erect black setae on anterior half, with sparse long erect yellowish setae on posterior half; axilla and metanotal trough with dense short recumbent silvery setae; lateral face of pronotum, metapleuron and propodeum except dorsum with sparse short recumbent silvery setae. Wings pale brown, veins brown, with short erect black, regularly distributed setae. Legs entirely with sparse long erect silvery setae; procoxa with dense short appressed silvery setae; meso- and metatrochanters, femora and tibiae with sparse short appressed silvery setae; tarsi with dense long recumbent silvery setae, ventrally more or less yellowish. T1, T2–5 laterally and S1–8 with sparse long erect white setae; T2–5 medially with sparse long erect golden setae; T6–7 with sparse long recumbent black and sparser long erect white setae; T1–4 with posterior fringe of sparse long golden setae; S2–4 with posterior fringe of sparse long white setae; S5–8 with posterior fringe of sparse long pale golden setae; T2 with lateral golden felt line.

Structure. Head 1.79 × wider than long; lateral margins strongly convergent behind eye; vertex rounded posteriorly; POD/OOD = 0.68; OD:MOD:LOD = 1.00:1.38:1.00; ocellar region slightly convex, each ocellus without posterior carina; antennal tubercle and antennal scrobe with weak continuous dorsal carina not reaching inner eye margin; genal carina absent; frons and gena with minute sparse and large dense punctures; ocellar region and vertex laterally to it with large sparse punctures; vertex posteriorly to ocelli with minute dense and large sparse punctures; post genal bridge without medial projection; hypostomal carina weakly developed. Clypeus medially gibbous in pentagonal shape, laterally flattened; anterior margin medially widely protruding anteriorly; medial protruding part depressed ventrally, laterally not defined by carina; surface of clypeus impunctate, polished, except anterior margin and posterior margin of medial convexity with minute dense punctures. Mandible slender, narrowed to apex, apically bidentate, without subbasal denticle; inner denticle smaller than apex; ventral margin excised into large basal tooth; outer face of mandible with minute dense punctures. Scape bending medially, with one strong carina beneath not widened apically; surface of scape with small dense punctures dorsally, impunctate and polished ventrally; surface of pedicel with minute sparse punctures; F1 compressed; ration between length and width of pedicel, F1 and F2 = 1.00:1.18:3.53:1.59:2.29:1.47; F2–11 almost equal in width; F11 as long as F10, conical; surface of flagellum with minute dense punctures. Prementum flattened, micro-reticulate, with posterior impunctate convex line; stipes with minute sparse punctures.

Mesosoma broadest at mesonotum including tegulae; ratio between head width, humeral width, pronotal width, mesonotal width = 88:75:84:100; humeral angle rounded, with weak humeral carina ventrally; propodeum abruptly convergent posteriorly; mesoscutal

width 1.17 × its length, 0.70 × mesonotal width; tegula short rounded, posteriorly reaching mesoscuto-scutellar articulation, 1.38 × longer than wide; mesoscutum distinctly convex; notaulus evenly wide, reaching anterior 3/8 of mesoscutum, subparallel; parapsidal line length 0.2 × mesoscutal length; parascutal carina forming wide, apically rounded, weakly elevated process on postero-lateral angle of mesoscutum; mesoscutellum gibbous with medial longitudinal carina posteriorly elevated; mesopleuron laterally with distinct transverse mesopleural suture, ventrally with precoxal swelling; precoxal ridge absent; pronotal collar anteriorly with minute dense punctures, posteriorly with small sparse punctures; dorsum of pronotum with minute dense and large dense punctures; mesoscutum and mesoscutellum with large confluent punctures; tegula impunctate polished except anterior and inner margins with small sparse punctures; axilla with minute sparse punctures; metascutellum medially with minute sparse punctures, laterally with small confluent punctures; metanotal trough striate; posterior propodeal face reticulate, with sublateral carina, antero-medially with long triangular cell posteriorly forming small process; dorsal and lateral propodeal faces not separated by carina; lateral face of pronotum transversely striate; anterior part of lateral face of mesopleuron, dorsal half of metapleuron and ventral half of lateral propodeal face with minute dense punctures; medial part of lateral face of mesopleuron and ventral face of mesopleuron with large confluent punctures; posterior part of lateral face of mesopleuron and ventral half of metapleuron with minute dense and small sparse punctures; dorsal half of lateral propodeal face reticulate.

Wings well developed; distance between origin of RS on vein SC and the base of stigmatic cell equal to stigmatic cell length and first abscissa RS length.

Procoxa with minute dense punctures; meso- and metacoxae with minute sparse and small sparse punctures, ventro-medially largely impunctate polished; femora and tarsi with minute dense and small sparse punctures; tarsi with small sparse punctures; metacoxa with weak inner carina throughout; tibiae without outer spines; claws simple, without inner denticles.

T1 with distinct dorsum and anterior slope; T1 spiracle weakly tuberculate; T2 evenly convex, 1.33 × wider than long; S1 with straight medial longitudinal carina with its outer margin emarginate medially and elevated posteriorly forming sharp tooth; S2 evenly convex without medial swelling or carina; T1, T2 laterally and S1–2 with large dense punctures; T2 disc with small sparse punctures; T3–7 and S3–8 with small dense punctures except T7 medially with narrow longitudinal impunctate carina not forming tubercle posteriorly; S7 with lateral rounded tubercle; S8 with lateral pointed tubercle reaching posterior 1/2 of sternum. Paramere down-curved posteriorly, without inner protuberance; inner margin of paramere dorsally with row of short erect golden setae; ventral lobe posteriorly projecting, pointed; parapenial lobe large, rounded; cuspis long slender, apex pointed, posteriorly up-curved, clearly surpassing apex of penis valve, ventrally with dense long erect golden setae; digitus S-shaped, posteriorly with dense short erect golden setae on outer face; paracuspis tuberculate with dense long erect golden setae; penis valves slender, weakly asymmetrical, right penis valve slightly longer than left, with posterior ventral hook and subapical short erect setae.

FEMALE. Unknown.

Type material

3♂. Holotype, ♂, **Nepal:** BARA DISTRICT: Adhabar, 21.X.1975, S. Takagi leg. [HUM]. Paratypes: **India:** KERALA: 2♂, Walayar Forests, 700 ft., X.1959, P.S. Nathan [CASC].

Distribution

India: Kerala. Nepal: Bara.

Etymology
This new species is named after the type locality in Nepal. Treat as a noun in apposition.

Remarks
This new species is readily recognized in *Eotrogaspidia* by having the clypeus gibbous and the metacoxa evenly convex with long sparse setae; in these features, it is similar to *Trogaspidia*. The genitalia, however, are consistent with other *Eotrogaspidia* males.

***Eotrogaspidia amans* (André, 1909)**
(Figs 1B, 1F, 2A, 2E, 5B, 7B, 8C–D, 10B, 10F, 12A)

Mutilla amans André, 1909: 173, ♂♀, lectotype ♀ (Tandjong Priok, Java, Indonesia) [RMNH], designated by Mickel (1935: 236).
Timulla (*Trogaspidia*) *amans*: Mickel, 1935: 220, 226, 236, ♂♀.
Timulla (*Trogaspidia*) *amans amans*: Pagden, 1949: 228, ♂♀.
Eotrogaspidia amans amans: Lelej, 1996c: 22; Lelej, 2005: 77; Lo Cascio, 2015: 548; Okayasu *et al*., 2018: 304, ♀.
Eotrogaspidia amans: Williams *et al*., 2019a: 32, ♀.

Diagnosis
MALE. Clypeus deeply concave (Fig 5B); scape ventrally with two parallel carinae; F1 weakly compressed, not wider than F2. Pronotum and propodeum dorsally with dense pale setae obscuring cuticular sculpture (Fig. 1B). Metacoxa flattened with dense erect pale microsetae (Fig. 7B). T2 laterally with large dense punctures; T7 with medial triangular impunctate line not forming tubercle posteriorly; cuspis robust, spatulate in inner view (Fig. 10B). FEMALE. T2 pale setal spots large, densely setose, well defined (Fig. 2A); distance between T2 spots 0.3–0.5 × spot diameter; pale setal bands on T3–4 complete (Fig. 2A); pygidial plate entirely with coarser micro-reticulation and with irregular sub-rugae anteriorly (Fig. 12A); lateral margins of pygidial plate convergent posteriorly.

Material examined
5♂2♀. **Indonesia:** Java: 1♂, Bantam Paroaseram, 23.V.1931, Luftnick [RMNH]; 1♂, Buitenzorg, W. Roepke [RMNH]; 2♂, same place, XII.1936, E. Fransen [CSCA, RMNH]; 1♀, Karangandoel, G. Slamat, 150 m, X.1940, F.C. Drescher [RMNH]; 1♂, Malang, IV.1933, Betrem [RMNH]; 1♀, Nglirip, Djati-Bosch by Bodjonegoro, I.1936, Walsch [RMNH].

Distribution
Indonesia: Java, Kangean Islands (Pagden, 1949).

Remarks
Morphologically, both sexes of this species are quite similar to *E. oryzae*, suggesting recent speciation. In males, *E. amans* and *E. oryzae* are recognized in the genus by having the following combination of character states: F1 as wide as F2; both pronotum and propodeum clothed with dense appressed golden setae; T7 with longitudinal triangular impunctate line; cuspis widened posteriorly. In females, both species are recognized by having the following combination of character states: T2 with large basal spots of golden setae; both T3 and T4 with complete band of golden setae; pygidial plate entirely micro-reticulate. However, *E. amans* differs from *E. oryzae* by having the male T2 laterally with large dense punctures (with small sparse punctures in *E. oryzae*), female T2 spots densly setose (sparsely setose in

E. oryzae), female pygidial plate with coarse microreticulation (with finer microreticulation in *E. oryzae*) and female pygidial plate with lateral carinae convergent posteriorly (subparallel in *E. oryzae*). These two species are distributed in allopatry; *E. amans* has been recorded from Java only, while *E. oryzae* is widespread in Indochina.

***Eotrogaspidia auroguttata* (Smith, 1855)**

(Figs 1C, 1G, 2B, 2F, 4D, 4H, 5C, 7C, 8E–F, 10C, 10G, 12B, 12H)

Mutilla auroguttata Smith, 1855: 53, ♀, holotype ♀ ("Brasil", actually Xianggang [= Hong Kong, China] according to Mickel, 1939) [BMNH]; Dalla Torre, 1897: 14; André, 1902: 72.

Mutilla repraesentans: Zavattari, 1913: 29, ♀, misidentification.

Mutilla analis: Zavattari, 1913: 41, ♂, in part, misidentification.

Timulla (*Trogaspidia*) *disparilis* Mickel, 1933a: 398, ♂, holotype ♂ (Taihorin [= Dalin], Taiwan) [Museum für Naturkunde, Humbolt Universität, Berlin, Germany]; Mickel, 1933b: 314, ♂; Mickel, 1935: 234, ♂. Synonymized by Lelej (1996c: 22) under *Eotrogaspidia auroguttata* (Smith).

Timulla (*Trogaspidia*) *repraesentoides* Mickel, 1933a: 411, ♀, holotype ♀ (Hoozan [= Fengshan], Taiwan) [Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany]; Mickel, 1933b: 309, ♀; Mickel, 1935: 254, ♀. Synonymized by Mickel (1939: 192) under *Timulla auroguttata* (Smith).

Timulla (*Trogaspidia*) *auroguttata*: Mickel, 1939: 192, ♀.

Trogaspidia disparilis: Chen, 1957: 168, ♂, examined; Tsuneki, 1972: 6, ♂; Murota, 1973: 119, ♂; Tsuneki, 1993: 48, ♂.

Trogaspidia auroguttata auroguttata: Chen, 1957: 171, ♀, examined.

Trogaspidia auroguttata repraesentoides: Chen, 1957: 172, ♀, examined; Tsuneki, 1972: 8, ♀.

Trogaspidia vallicola Tsuneki, 1993, **syn. nov.**: 48, ♀, holotype ♀ (Ssuchungchi, Taiwan) [MNHAH], examined; Hashimoto & Nakanishi, 1997: 31; Lelej, 2005: 104; Pagliano *et al*., 2020: 292.

Eotrogaspidia auroguttata: Lelej, 1996c: 22, ♂♀; Lelej, 2002: 81; Lelej, 2005: 78; Pagliano, 2011: 44, ♀; Terayama *et al*., 2011: 22, ♂♀; Lo Cascio, 2015: 548; Okayasu, 2016: 61, ♀, examined; Terayama *et al*., 2016: 169, ♂♀; Barthélémy *et al*., 2018: 237, ♂ non ♀; Okayasu *et al*., 2018: 309, ♀; Ito, 2018: 25, ♂; Williams *et al*., 2019a: 32, ♀, examined; Pagliano *et al*., 2020: 245.

Diagnosis

MALE. Clypeus deeply concave (Fig. 5C); scape ventrally with two parallel carinae; F1 weakly compressed, not wider than F2. Pronotum and propodeum dorsally with dense pale setae obscuring cuticular sculpture (Fig. 1C). Metacoxa flattened with dense erect pale microsetae (Fig. 7C). T7 with narrow elongate impunctate line forming weak tubercle posteriorly; cuspis narrowed posteriorly in inner view (Fig. 10C). FEMALE. T2 pale setal spots large, densely setose, well defined (Fig. 2B); distance between T2 spots 0.3–0.5 × spot diameter; pale setal bands on T3–4 medially widely interrupted by black setae (Fig. 2B); pygidial plate coarsely irregularly rugose on anterior half, smooth posteriorly (Fig. 12B).

Material examined

84♂199♀. Holotype, *T. vallicola*, ♀, **China:** Taiwan: Pingtung, Ssuchungchi, 2.VIII.1976, T. Murota leg. [MNHAH (B1-288593)]. **China:** Fujian: Chungan, Bohea Hills, 1♀, 11.I.1939, 2♀, 10.III.1939, 1♀, 25.VI.1939, 1♀, 4.VII.1939, 1♀, 10.VII.1939, 3♀,

12.IX.1939, 1♀, 15.IX.1939, 4♀, 25.IX.1939, 4♀, 30.IX.1939, 1♀, IX.1939, 2♀, 6.X.1939, 25♀, 7.X.1939, 1♀, 8.IV.1940, 2♀, 20.IV.1940, 1♀, 24.IV.1940, 1♀, 30.IV.1940, T.C. Maa leg., *Trogaspidia auroguttata* (Smith), B. Petersen det. 1982 [TARI]; Chungan, Bohea Hills, 2♂, 12.IX.1939, 1♂, 15.IX.1939, 2♂, 25.IX.1939, 1♂, 30.IX.1939, 1♀, 24.IV.1940, T.C. Maa leg. [TARI]; Yungan, Siyingpan, 2♀, 20.IX.1939, 1♀, 16.II.1940, 1♀, 7.V.1940, 1♀, 23.VI.1940, 2♀, 7.VII.1940, 1♀, 30.XII.1940, 1♀, 20.I.1941, 1♀, 21.I.1941, 1♀, 2.II.1941, 1♀, 19.III.1941, 1♀, 9.IV.1941, 1♀, 10.IV.1941, 2♀, 17.IV.1941, 1♀, 30.I.1945, T.C. Maa leg., *Trogaspidia auroguttata* (Smith), B. Petersen det. 1982 [TARI]; Yungan, Siyingpan, 2♂, 20.IX.1939, 1♂, 21.IX.1939, 1♂, 28.VI.1940, T.C. Maa leg. [TARI]; Hotien, Changting, 1♀, 4.VI.1940, 1♀, 15.IV.1941, 2♀, 19.IV.1941, 1♀, 1.V.1941, 2♀, 2.V.1941, T.C. Maa leg., *Trogaspidia auroguttata* (Smith), B. Petersen det. 1982 [TARI]; 1♀, Fengshih, Shanghan, 7.VIII.1940, T.C. Maa leg. [TARI]; Haiteng [= Haicheng], Hungkung, 1♂, 1.IX.1940, 2♂, 6.IX.1940, T.C. Maa leg. [TARI]; 1♂, Taining, 3.IX.1940, T.C. Maa leg. [TARI]; 2♀, Tungan, 4.X.1940, T.C. Maa leg., *Trogaspidia auroguttata* (Smith), B. Petersen det. 1982 [TARI]; Shaowu, Shuipeikieh [= Shui Pei Kai], 1♀, 2.VI.1941, 1♀, 8.IX.1941, 2♀, 1.X.1941, 1♀, 16.III.1942, 1♀, 26.III.1942, 1♀, XI.1942, 1♀, 21.III.1943, 1♀, 29.IV.1943, 2♀, 12.V.1943, 1♀, 2.VI.1943, 1♀, 20–24.VII.1943, 1♀, 25–27.VII.1943, 1♀, 5.VIII.1943, 1♀, 1–10.IX.1943, 2♀, 12.V.1944, 1♀, X.1944, T.C. Maa leg., *Trogaspidia auroguttata* (Smith), B. Petersen det. [TARI]; Shaowu, Shuipeikieh [= Shui Pei Kai], 2♂, 9.VII.1941, 1♂, 10–12.VII.1943, T.C. Maa leg. [TARI]; 1♀, Kienyang [= Jianyang], Aotow, 15.X.1941, T.C. Maa leg., *Trogaspidia auroguttata* (Smith), B. Petersen det. 1982 [TARI]; Shaowu, Kuhsienkieh, 1♀, 30.IV.1944, 2♀, 2.V.1944, 1♀, X.1944, 6♀, 1944, T.C. Maa leg., *Trogaspidia auroguttata* (Smith), B. Petersen det. 1982 [TARI]; 3♂, Shaowu, Kuhsienkieh, 1944, T.C. Maa leg. [TARI]; 1♀, Shaowu, Kaoyany, 29.IV.1945, T.C. Maa leg., *Trogaspidia auroguttata* (Smith), B. Petersen det. 1982 [TARI]; 1♀, Kienyang [= Jianyang], Hwangkeng, 27.VIII.1945, T.C. Maa leg., *Trogaspidia auroguttata* (Smith), B. Petersen det. 1982 [TARI]; 1♀, Shaowu, Wuko, 30.VIII.1945, T.C. Maa leg., *Trogaspidia auroguttata* (Smith), B. Petersen det. 1982 [TARI]; 1♂, Shaowu, North Street, 25–27.VII.1983 [TARI]; GUANGDONG: 1♀, Kwangtung [= Guangdong], Lobushan, 25.V.1937, T.C. Maa leg., *Trogaspidia auroguttata* (Smith), B. Petersen det. 1982 [TARI]; 4♀, Chebaling National Nature Reserves, 20–21.VI.1990, A. Lelej [IBSS]; HAINAN: 1♀, Ryosui [Lingshui], 23.XI.1940, M. Chujo leg. [TARI]; HUNAN: 1♀, Changte, Yangshan, 18.XI.1938, T.C. Maa leg. [TARI]; JIANGSU: 1♀, ChoeiTong, 11.VII.1920, *Trogaspidia auroguttata* (Smith), B. Petersen det. 1982 [TARI]; 1♀, Chemu, 11.V.1935, O. Piel leg., *Trogaspidia auroguttata* (Smith), B. Petersen det. 1982 [TARI]; Sichuan: 1♂, Chengtu [= Chengdu], 17.VII.1938, K.F. Chen leg. [TARI]; TAIWAN: 1♂, Taichung, 27.VI.1907, S. Matsumura leg. [HUM]; 1♀, Taihorin [= Dalin], VI.[19]11, H. Sauter leg., *Mutilla representans* Smith, E. Zavattari det. [1913] [SMNS]; 1♂, same place, VII.1914, Inamura leg. [TARI]; Tainan, Sugar Ex. st., 1♂, 10.IV.1916, 1♀, 15.IV.1916 [TARI]; 1♂, Ako [= Pingtung], 17.XI.1916, T. Shiraki leg. [TARI]; 1♀, [Pingtung], Chyoshu [= Chaozhou], 18.XI.1916, T. Shiraki leg. [TARI]; 1♂, Tainan, IV.1918, T. Shiraki leg., *Mutilla analis* Lepeletier, T. Shiraki det. [TARI]; 1♀, same place, IV.1918, T. Shiraki leg., *Mutilla repraesentans* Smith, T. Shiraki det. [TARI]; 1♂1♀, same place, Tsuru leg. [TARI]; 1♂, same place, Ishida leg. [TARI]; 1♀, [Pintung], Koshun [= Hengchun], 25.IV–25.V.1918, J. Sonan, K. Miyake & M. Yoshino leg. [TARI]; 1♀, Taito [= Taitung], 25.II–27.III.1919, S. Inamura, J. Sonan & M. Yoshino leg. [TARI]; 1♂, [Nantou], [Hsinyi], Namakaban [= Luona], 19.IX.1924, T. Shiraki & J. Sonan leg., *Mutilla repraesentans* Smith, T. Shiraki det. [TARI]; 1♀, Taihoku [= Taipei], VIII.1926, K. Fukuda leg. [TARI]; 1♀, same place, 28.X.1943, J. Sonan leg. [TARI]; Taipei, 1♀, 6.IX.1958, 1♂, 18.IX.1958, 1♂, 8.IX.1958, 1♂, 18.IX.1958, S.C. Chiu leg. [TARI]; 1♂, Taipei, 3.X.1968, S.C. Chiu leg., *Trogaspidia auroguttata* (Smith), B. Petersen det. 1988 [TARI]; 1♀, [Chiayi], Takezaki [= Chuchi], 15.XI.1926, J.

Sonan leg. [TARI]; 1♂, Takao [= Kaohsiung], 27.VIII.1927, J. Sonan & K. Shibata leg. [TARI]; 1♀, [Pintung], Raisha [= Laiyi], 30.VIII.1927, J. Sonan & K. Shibata leg. [TARI]; Tainan, Xinhua, 1♀, 20.VI.1930, 1♀, 23.VI.1930, 1♀, 10.XII.1930 [TARI]; 1♀, Hsinchu, Pairan, 30.VI.1930, J. Sonan leg. [TARI]; 1♂, Yangmingshan, 29.VIII.1932, S. Okagaki leg. [HUM]; 1♂, Kagi [= Chiayi], 15.IX.1933, J. Sonan leg. [TARI]; 1♂, same place, 25.VIII.1949, C.T. Lin leg. [TARI]; 1♀, [Taipei], Hokuto [= Peitou], 3.IV.1934, S. Sakamoto leg. [TARI]; 2♂, Taijong [= Taichung], Ta-Nan-Juang, 6–12.VIII.1948, T.C. Maa leg. [TARI]; 1♀, Taipeh [Taipei], Shoeiyuandih, 15.III.1949, K.S. Lin leg. [TARI]; 1♀, Taipei, Chiaochi, 5.V.1950, T.C. Maa leg., *Trogaspidia auroguttata* (Smith), B. Petersen det. 1982 [TARI]; 1♂, Kangtsui [= Jiangchu], 18.I.1963, H.H. Tseng leg., *Trogaspidia auroguttata* (Smith), B. Petersen det. 1988 [TARI]; 1♀, [New Taipei], Sintien [= Xindian], 21.VIII.1963, K.H. Liu leg. [TARI]; 1♂, [Taipei], Sanchangli [= Songshan], 1.VIII.1964, H.R. Cheng leg. [TARI]; 1♀, [Hsinchu], Kuanhsi, IX.1968, MT [TARI]; 1♂, Lan Hsu, Yehyu, 17.VI.1970, Y. Hori leg. [EUM]; 1♀, Taoyuan, near Palin, Sankuan, 800 m alt., 15.V.1978, M. Yashiro leg. [EUM]; 1♂, Nanshan Xi, 15.VIII.1980 [MTC]; 1♂, Kaohsiung, Liukuei, 27–28.VI.1981, L.Y. Chou & C.H. Yang leg. [TARI]; 1♂, Kaohsiung, Maolin, 26.III.1982, K.C. Chou & C.C. Pan leg., *Trogaspidia auroguttata* (Smith), B. Petersen det. 1988 [TARI]; 1♂, Taitung, Lanyu, 4–9.V.1982, K.S. Lin, K.C. Chou, S.C. Lin & C.C. Pan leg., *Trogaspidia auroguttata* (Smith), B. Petersen det. 1988 [TARI]; 1♂, Taichung, Tatushan, V.1982, T.C. Maa leg. [TARI]; 1 ♀, Taipei, Shih ting, 28.III.1993, K. Okajima leg. [TUA]; 1♂, Changhua County, Chiuche, 8.V.1980, Sk. Yamane leg., *Trogaspidia auroguttata* (Smith), B. Petersen det. 1988 [IBSS]; 1♂, Shinka [= Sinhua], 24.V.1929, K. Sato leg. [IBSS]; 1♂, Daoyazhuang, Yuanli, Miaoli, 26.X.2017, W.-C. Yeh leg. [TFRI]; 1♂, Lishanshu, Yuanli, Miaoli, 8.V.2018, S.-S. Lu leg. [TFRI]; YUNNAN: 30 km SW Jinpin, 1♀, 370 m, 16.IV.1956, 1♀, 500 m, 2.V.1956, Huang Ke-ren et al. [ZMMU]; 30 km SW Jinpin, 1♀, 400–500 m, 23.V.1956, 1♀, 900 m, 27.V.1957, D. Panfilov [ZMMU]; 1♀, "1260 B" [= South Yunnan, V–VI.1956, D. Panfilov] [ZMMU]; 30 km SE Cheli, 450 m, 1♂1♀, 18.IV.1957, 1♀, 19.IV.1957, D. Panfilov [ZMMU]; 1♀, 25 km NE Cheli, 7.V.1957, D. Panfilov [ZMMU]; Jingdong, 1♀, 1300 m, 9.III.1957, 1♀, 1450 m, 23.III.1957, D. Panfilov [ZMMU]; 1♀, Simao, 1300 m, 5.IV.1957, D. Panfilov [ZMMU]; 1♀, Yuanjiang, 500 m, 12.V.1957, Zang Ling-chao [ZMMU]; ZHEJIANG: 1♂, Hangehow [= Hangzhou], 8.VI.1928 [TARI]. India: Uttarkhand: 1♀, Mussoorie, VII.1992, K. Werner leg. [MSNF]. **Indonesia**, JAVA: 13♂1♀, Bandoeng, 700 m, various dates in 1940, J. Olthof [RMNH]; 1♂1♀, G. Megamendoeng, 700 m, IV–VI.1936, M.A. Lieftinck [RMNH]; 12♂13♀, additional handwritten localities on Java [RMNH]. **Japan:** RYÛKYÛ:1♀, Okinawa-jima Island, Higashison, 5.IV.1998, K. Yamada leg. [TUA]; 1♀, Iriomote-jima Island, Taketomi, Haeminaka, 24°17′27″N 123°53′2″E, 30 m alt., 25.X.2015, J. Okayasu leg. [EUM]; 1♂, Okinawa-jima Island, Kunigami, Sate, Gaji-Sate II Forest Road, 26.78°N 128.25°E, 200 m alt., 4–5.VII.2016, Y. Komeda leg., YPT [ELKU]; 1♀, Okinawa-jima Island, Onna-son, Kenmin-no-mori, 8.VII.2018, H. Yoshitake leg. [EUM]; 1♀, Okinawa-jima Island, Kunigami-son, Okuma, 5.V.2019, H. Yoshitake leg. [EUM]. **Laos:** HOUA PHAN: 2♂, Ban Saleui, 1400–1500 m alt., 20–24.VI.2003, N. Ohbayashi leg. [EUM]; LUANG PHABANG: 2♀, Phou-vieng Gnai, 19.284470°N 102.355703°E, 1319 m alt., 22.IV.2018, H. Yoshitomi leg. [EUM]; XIENG KHOUANG: 1♀, 21 km west of Phongsawang, 19.311431°N 103.030361°E, 1104 m alt., 22.IV.2018, H. Yoshitomi leg. [EUM]. **Thailand:** CHIANG MAI: 1♂2♀, 7 km NW of Fang, Horticular Experimental Station, 30.X–2.XI.1979, Zool. Muz. Copenhagen Exped., *Trogaspidia disparilis* Mickel, B. Petersen det. 1980 [IBSS]; 1♀, Mae Rim, Mae Sa, 400–450 m alt., 15.V.2002, T. Ishikawa leg. [TUA]; Kanchanaburi: 1♀, Sai Yok, Prasat Mueange Sing Park, 19.V.2018, 50m, K.A. Williams [CSCA]; Krabi: 1♀, 12.4 km NNW Krabi, Oil palm farm, 8.193°N 98.876°E, 50 m, 29.III.2017, K.A. Williams [CSCA]; 14 km NNE Krabi, Phnom Bencha Mountain Resort, 8.208°N 98.937°E, 80 m, 1♀,

31.III.2017, 1♂1♀, 2.IV.2017, K.A. Williams [CSCA]; Phuket: 2♀, Patong Beach, 5–9.III.1986, T. and M. Simon Thomas [RMNH]; 2♀, Phuket Island, 50 m, 7°47'N 98°19'E, 1.VIII.1986, R. Hensen [RMNH]. **Vietnam:** Bac Can: 3♀, Ba Be National Park, 31.VII–2.VIII.2000, K. Okajima leg. [TUA]; Hoa Binh: 1♀, 14.VII.2010, H. Kurokawa leg. [MTC]; 1♀, A. de Cooman leg. [TARI]; Nghe An: 1♀, Ky Son, Cao Phong, forest, 27.X.1990, S. Belokobylskij [IBSS]; Quang Ninh: 1♀, Phong Vong, 25.III.1987, V. Kuznetsov [IBSS]; 1♀, same place, 10.X.1990, V. Kuznetsov [IBSS].

Distribution

China: Fujian, Guangdong, Hainan, Hong Kong, Hunan, Jiangsu, Sichuan*, Taiwan, Yunnan*, Zhejiang* (Smith, 1855; Barthélémy *et al*., 2018). India*: Uttarakhand. Indonesia: Java (Williams *et al*., 2019a). Japan: Ryûkyû Islands. Laos*: Houa Phan, Luang Phabang, Xieng Khouang. Thailand: Chaiyaphum, Chiang Mai, Kanchanaburi, Krabi, Phuket, Sakho Nakhon (Williams *et al*., 2019a). Vietnam: Bac Can*, Dak Lak, Hoa Binh*, Nghe An*, Quang Ninh* (Williams *et al*., 2019a).

Remarks

Photos of the holotype of *E. auroguttata* and *T. auroguttata repraesentoides* are available from Okayasu *et al*. (2018) and "Integrated insect types database of Taiwanese species" (http://twinsecttype.nmns.edu.tw/, accessed 21 August 2020). In Iriomote-jima Island, Japan, this species was collected on a road through sugarcane field (Okayasu, 2016; Fig. 15) and by sweeping of low grass on dry forest edge (Ito, 2018).

Tsuneki (1993) separated *T. vallicola* from *E. auroguttata* by the setal color on the frons, shape of the clypeus, setal pattern on the mesosomal dorsum, surface sculpturing on the posterior propodeal face, color of the legs, setal color of the metasoma, distance between the setal spots on T2, and surface sculpturing on the pygidial plate. Each of these diagnostic features, however, is regarded as variation, since many intermediate forms were examined from throughout the range of this widespread species. The holotype of *T. vallicola* (Figs 4D, 4H, 12H) matches all the diagnostic characteristics of *E. auroguttata*.

Barthélémy *et al*. (2018) examined three males and four females of *E. auroguttata* from Hong Kong, China. However, the photographed female (Barthélémy *et al*., 2018) probably belongs to *T. fuscipennis* (Fabricius, 1804) based on the mesosomal shape and setal pattern. This species is similar to *E. auroguttata* in having the T2 with large pale setal spots, T3–4 with pale setal band and pygidial plate irregularly rugose anteriorly, but differs by having the humeral angle projecting, T3–4 with pale setal band only narrowly interrupted medially by black setae and the pygidial plate rugose on anterior 3/4.

***Eotrogaspidia buddha* sp. nov.**

(Figs 1D, 1H, 2C, 2G, 5D, 7D, 8G–H, 10D, 10H, 12C)

Diagnosis

MALE. Clypeus basally elevated, medial depression on anterior margin laterally defined by carinae (Fig. 5D); F1 strongly compressed, wider than F2. Pronotum with narrow lateral spot of pale setae (Fig. 1D); propodeum dorsally with sparse pale setae (Fig. 1D). Metacoxa flattened with dense erect pale microsetae on inner third (Fig. 7D). Cuspis stick-like. FEMALE. Frons, vertex, and gena punctures dense to confluent. Mesosoma uniformly yellowish red (Fig. 2G); dorsum with coarse confluent punctures (Fig. 2C); posterolateral propodeal margin distinctly dentate. T2 pale setal spots small, distance between them 1.0 × or more than spot diameter (Fig. 2C); T3–4 with a pair of small lateral pale setal spots, distance between spots and that between spot and lateral margin of tergum approximately equal to

spot diameter (Fig. 2C); pygidial plate irregularly rugose on anterior 1/3 and smooth posteriorly (Fig. 12C).

Description

MALE. Body length: 10.4–12.0 mm. Forewing length: 9.2 mm.

Color and setae. Black with metasomal T1–6 and S1–7 ferruginous. Frons, lateral area of clypeus, with silvery, dense, subappressed setae; gena with silvery, dense, erect and subappressed setae; base of mandible and vertex with silvery dense appressed and sparse long erect setae; vertex behind ocelli with silvery dense recumbent and sparse long erect setae; scape with silvery sparse long recumbent and erect setae; pedicel and F1 inside with silvery dense appressed pubescence, outside with sparse recumbent short setae; F2–11 with white dense pubescence; pronotum dorsally with lateral triangle spot of silvery dense recumbent setae; mesopleuron with silvery dense recumbent and sparse erect setae; mesoscutum, mesoscutellum and tegula (anteriorly and mesally) with black recumbent setae; propleuron, lateral area of metanotum and dorsum of propodeum with grayish, sparse, appressed setae; posterior and lateral propodeal slope with grayish, sparse, erect setae; legs with grayish, dense, suberect setae. Metasomal terga with golden appressed and subappressed setae, forming fringe on T1–6, sterna with sparse subappressed and erect yellow-gray setae, forming fringe on S2–6. T2 with lateral felt line, S2 without lateral felt line.

Structure. Relation of head width and mesosoma width including tegula about 68:80. Mandible bidentate at apex, without subbasal tooth on inner border and dorsal carina extending from base to subapical tooth; outer margin beneath with large subbasal tooth. Clypeus with medial concave area raised, defined laterally and anteriorly by carina. Scape slightly curved beneath, shiny, with two obscure carinae, F1 flattened, 1.2 × F2; antennal scrobe dorsally carinate. Ocelli small, POD:OOD = 0.74. Distance between outer ocellar margins 1.1 × distance between posterior ocelli and dorsoposterior occipital border. Frons and vertex with dense separated punctures, frons with interspaces setose, vertex with interspaces simple; gena with fine, dense punctures.

Notauli and parapsids developed and not touching anterior border of mesoscutum.Tegula large, blackish, smooth and shiny with few punctures anteriorly and mesally. Mesoscutellum convex with medial longitudinal carina ending by tubercle. Metanotum densely punctate, with medial glabrous narrow area. Pronotum and mesopleuron with moderately fine, confluent punctures; mesoscutum and mesoscutellum with moderately coarse, somewhat confluent punctures; propleuron transversally striate; inferior portions of metapleuron glabrous and shiny. Mesopleuron beneath with precoxal smooth, shiny, swollen area. Metacoxa beneath flattened, mesal half with golden dense short erect setae; pro- and mesocoxa beneath with smooth shiny area. Propodeum reticulate, with larger cells laterally and dorsomedially; anterodorsally with large medial longitudinal and lateral transversal cells.

Forewings fuscous, submarginal cell 1 large, subtriangular, approximately equal in length to marginal cell; submarginal cell 2 receiving recurrent vein at midpoint; submarginal cell 3 less distinct than submarginal cell 2 and receiving recurrent vein at midpoint.

Longitudinal carina on S1 well developed, 3/4 × as long as S1 in profile, medially emarginated. T1–6 and posterior halves of S3–S6 with moderately fine, well separated punctures, much sparser on T2 disc; S1–2 with moderately coarse, separated punctures; S6–7 with lateral tubercle; S8 (hypopygium) with oblique, oriented mesally carina, 1/2 × as long as S8 in profile; T7 with moderately coarse, dense punctures. Pygidial plate on T7 medially with narrow widened apically chagrined area. Paramere down-curved posteriorly with pointed apex, inner margin of paramere dorsally with row of short erect golden setae; parapenial lobe large, rounded; cuspis long slender, lamellate, apically rounded setose, posteriorly up-curved, clearly surpassing apex of penis valve, ventrally with dense long erect golden setae; digitus

S-shaped long but shorter than cuspis, dorsally carinate, with capitate setose apex; paracuspis stick-like setose, shorter than digitus, apical part with dense long erect golden setae; penis valves slender, weakly asymmetrical, right penis valve slight longer that left, with posterior ventral hook and subapical short erect setae; left valve with ventral apical sharp tooth and preapical emargination ending by pointed tooth.

FEMALE. Body length 4.8–6.4 mm.

Color and setae. Head black, except antennal tubercle, mandible, scape, pedicel and clypeus largely red-brown, and venter of flagellum largely red-brown. Mesosoma ferruginose-red, legs brownish-red, palps pale brown. Metasoma black, ventrally red-brown. Body setae generally sparse and silvery, except frons, vertex, and mesosomal dorsum with sub- erect blackish and red-brown setae; T2 disc and T3–5 setae dense black; and T2 disc lateral spots, T3–4 lateral spots, and T6 basal tuft with dense whitish-silver setae; T2 lateral spot diameter 0.6 × distance between spots, T3–4 lateral spot width 1.0 × distance between spots; T2 with sparse apical fringe of black setae.

Structure. Width behind eye 0.98 × maximal (propodeal) mesosoma width. Frons, vertex, and gena punctures dense to confluent. Mandible apex apparently unidentate. Clypeus apically bidentate, teeth connected by arcuate carina; basomedial portion with robust tubercle. Antennal scrobe with arcuate dorsal carina and straight lateral carina. Antennal tubercle with scattered micropunctures. Genal carina weak, forming tooth at hypostomal carina and extending posteriorly to occipital carina. F1 1.2 × F2 and 2.0 × pedicel length, F2 1.5 × pedicel length.

Mesosomal length (including propodeum) 1.4 × propodeal width. Dorsum of mesosoma with coarse confluent punctures; obscure interrupted carina separating dorsal and lateral faces of pronotum and mesonotum. Side of mesosoma with dense micropunctures and short setae. Mesopleural lamella an obscure carina. Humeral carina weak, incomplete; anterodorsal pronotal setose area tuberculate. Ratio of width of humeral angle, anterior spiracle, narrowest point of mesonotum, propodeal spiracle, and propodeum posteriorly 60:67:67:70:73. Scutellar scale well developed, ~1.5 punctures wide. Posterior propodeal face reticulate with many interspaces obliterated leaving apparent striae. Lateral and posterior propodeal faces separated by carina with few short teeth. Metatibio-tarsal ratio 65:29:20:15:11:12.

T1 anterior face with sparse punctures, posterior with confluent punctures. T2 with moderate separated pits, smaller on disc interspaces micropunctate and setose. T3–5 and S3–5 with small dense punctures. S1 with simple longitudinal lamella. S2 with sparse punctures, interspaces smooth. T2 felt line 0.25 × T2 total length. T6 with long sub-ovate pygidium, widest medially with well developed lateral carina; weak irregularly rugose in basal third and smooth posteriorly. S6 posterior margin truncate.

Type material

10♂47♀. Holotype, ♂, **Sri Lanka:** COLOMBO DISTRICT: Ratmalana, 19–21.I.1975, K.V. Krombein, P.B. Karunaratne, P. Fernando, N.V.T.A. Weragoda / *Trogaspidia acidalia* (Cameron), B. Petersen det. 1995 [USNM]. Paratypes: **India:** KARNATAKA: 1♂, 15 km SE Bangalore, KT, 23–24.VII.1996, K. Werner & L. Lorenz leg. [IBSS]; TAMIL NADU: 1♀, Coimbatore, VII.1958, P. Susi Nathan leg. [CASC]; 1♀, same place, X.1959, P. Susi Nathan leg. [CASC]; 1♀, same place, III.1961, P. Susi Nathan leg. [RMNH]; 1♀, same place, VI.1963, P. Susi Nathan leg. [RMNH]; Tiruchirappalli, Pudukottai, XI.1997, T. Susi Nathan [SEMC]; 1♀. Pondicherry, 10 km N Alankuppam, 18.II.2010, F. Burger leg. [IBSS]; 1♀, Pondicherry, 10 km N Auroville, 2.II–2.III.2011, F. Burger leg. [IBSS]; UTTARAKHAND: 1♀, Dehra Dun, 5.V.1944 [UMMZ]. Nepal: Chitwan District: 1♂, Chitwan, N[ational] P[ark] Sauraha, 150 m, 31.V–4.VI 1997, M. Hauser leg. [IBSS]. **Pakistan:** PUNJAB PROVINCE: 1♀,

12 mi NW Rawalpindi, 16.XII.1961, E.S. Ross and D.Q. Cavagnaro [CASC]. **Sri Lanka:** AMPARAI DISTRICT: 1♀, Dehiattekandiya, 23–24.VII.1993, K.V. Krombein et al. [USNM]; 2♀, Ekgal Aru, 9–11.VI.1976, 19–22.II.1977, K.V. Krombein et al. [USNM]; 1♀, Lahugala Sanctuary, 15.VI 1976, K.V. Krombein et al. [USNM]; ANURADHAPURA DISTRICT: 1♂, Padaviya, 18.V.1976, MT, Karunaratne et al. [USNM]; COLOMBO DISTRICT: 1♂1♀, Ratmalana, Zoo farm, 19.I.1975 K.V. Krombein et al. / *Trogaspidia acidalia* (Cameron), B. Petersen det. 1995 [IBSS]; 2♀, Ratmalana, 15.II.1975, K.V. Krombein et al. [USNM]; 2♂2♀, Ratmalana, airport, 19.II.1975, K.V. Krombein et al. [USNM]; 2♀, Colombo, 8–14.II.1975, K.V. Krombein et al. [USNM]; 1♀, Colombo, 24–28.II.1975, K.V. Krombein et al. [USNM]; 1♀, Katunayaka, 16.I. 1977, K.V. Krombein et al. [USNM]; GALLE DISTRICT: 1♀ Kanneliya Jungle, 11–16.I 1975, MT, K.V. Krombein et al. [USNM]; HAMBANTOTA DISTRICT: 1♀, Palatupana, 21–22.VI 1976, K.V. Krombein et al. [USNM]; KANDY DISTRICT: 1♂, Vict. Redenigala Rantembe Sanct., 07°13'N 80°57'E, 23–30.VIII.1999, MT, M. and J. Wasbauer [UCDC]; MANNAR DISTRICT: 2♀, Ma Villu, 23–27.I.1978, P. Karunaratne et al. [USNM]; 1♀, 0.8 km NE Kokmotte Bungalow, Wilpattu National Park, 50–100 ft [15–30 m], 22–23.I 1977, K.V. Krombein et al. [USNM]; 1♀, same place, 22–23.I.1977, MT, K.V. Krombein et al. [USNM]; 1♀, same place, 21–25.V 1976, K.V. Krombein et al. [USNM]; 6♀, same place, 5–8.X 1977, K.V. Krombein et al. [USNM]; 7♀, same place, 15–16.II.1979, K.V. Krombein et al. [USNM]; 1♀, Ma Villu, a tank, 16–19.IX 1980, K.V. Krombein et al. [USNM]; 1♀, Marichchukkaddi, 26.I.1978, P. Karunaratne et al. [USNM]; Monaragala District: 2♀, Angunakolapelessa, 21–23.I 1979, K.V. Krombein et al. [USNM]; 1♀, same place, 8–9.X 1980, K.V. Krombein et al. [USNM]; RATNAPURA DISTRICT: 1♀, Gilimale, Induruwa, 19–22.VII.1976, K.V. Krombein et al. [USNM]; 1♂, Ratnapura, 18.X.1969 [USNM]; VAVUNIYA DISTRICT: 1♂, Parayanalankulam, 40 km NW of Medawachchiya, 20–25.III.1970, D. Davis, W. Rowe [USNM].

Distribution
India: Karnataka, Tamil Nadu, Uttarakhand. Nepal: Chitwan. Pakistan: Punjab. Sri Lanka: Amparai, Anuradhapura, Colombo, Galle, Hambantota, Kandy, Mannar, Monaragala, Ratnapura, Vavuniya.

Etymology
The Buddha was religious leader who lived in ancient India and founder of the world religion of Buddhism, which is widely practiced on the Indian subcontinent. The specific epithet *buddha* is a noun in apposition.

Remarks
This species was wrongly identified by Børge Petersen as *Trogaspidia acidalia* (Cameron, 1897) in the USNM collection. I found, among his series, some females that correspond to the original description (Cameron, 1897). Thanks to Gavin Broad (BMNH), I studied photos of the lectotype of *Mutilla acidalia* Cameron, 1897 (Fig. 14) and found it to be identical to the female specimens examined herein. Therefore, both sexes of *Trogaspidia acidalia sensu* Petersen are described here as *Eotrogaspidia buddha* **sp. nov.**

***Eotrogaspidia hauseri* sp. nov.**
(Figs 3A, 3E, 6A, 7E, 9A–B, 11A, 11D)

Diagnosis
MALE. Clypeus deeply concave, shiny, with sculptured narrow anterior border (Fig. 6A); scape strongly widened apically; F1 strongly compressed, wider than F2. Pronotum with

sparse subappressed and erect pale setae; propodeum dorsally with dense pale setae obscuring cuticular sculpture (Fig. 3A). Metacoxa flattened with dense erect pale microsetae (Fig. 7E). Hypopygium (S8) with longitudinal ridge reaching posterior 1/3 of sternum; cuspis lamellate, reaching paramere apex. FEMALE. Unknown.

Description

MALE. Body length: 8.8–9.6 mm. Forewing length: 6.0 mm.

Color and setae. Black with metasomal T1–5 and S1–5 ferruginous. Frons, lateral area of clypeus, with silvery, dense, subappressed setae; gena with silvery, dense, erect and subappressed setae; anterior clypeal border with few geyish erect setae; base of mandible, malar space, and vertex with silvery dense appressed and sparse long erect setae; vertex behind ocelli with silvery dense recumbent and sparse long erect setae; scape dorsally and pedicel with silvery recumbent and erect setae; F1 inside with silvery dense appressed pubescence, outside with sparse recumbent short setae; F2–11 with white dense pubescence; pronotum dorsally with silvery sparse subappressed and erect setae; mesopleuron with silvery dense recumbent and sparse erect setae; mesoscutum and tegula (anteriorly and mesally) with black recumbent setae; propleuron, mesoscutellum and lateral area of metanotum with grayish, sparse, appressed and erect setae; dirsum of propodeum with silvery dense recumbent setae; posterior and lateral propodeal slope with grayish, sparse, erect setae; legs with silvery, dense, suberect setae. Metasomal terga with yellowish appressed and subappressed setae, forming fringe on T1–6, sterna with sparse subappressed and erect yellow-gray setae, forming fringe on S2–6. T2 with lateral felt line, S2 without lateral felt line.

Structure. Relation of head width and mesosoma width including tegula about 90:95. Mandible bidentate at apex, without subbasal tooth on inner border and dorsal carina extending from base to subapical tooth; outer margin beneath with large subbasal tooth. Clypeus concave, shiny area defined anteriorly by carina, basal medial triangle punctate, setose. Scape slightly curved, strongly widened apically, beneath shiny with two obscure carinae. F1 strongly compressed, wider than F2, F1 length 1.25 × F2. Ocelli small, POD:OOD = 0.72. Distance between outer ocellar margins 1.2 × distance between posterior ocelli and dorsoposterior occipital border. Frons and vertex with separated punctures, gena with fine, dense punctures.

Notauli developed and almost touching anterior border of mesoscutum; parapsids less developed ½ mesoscutal length. Tegula large, blackish, smooth and shiny with few punctures anteriorly and mesally. Mesoscutellum convex with medial longitudinal carina not ending posteriorly by tubercle. Metanotum densely punctate. Pronotum and mesopleuron with moderately fine, confluent punctures; mesoscutum and mesoscutellum with moderately coarse, somewhat confluent punctures; propleuron obscurely transversally striate; inferior portions of metapleuron glabrous, microstriate and shiny. Mesopleuron beneath with precoxal smooth shiny swollen area. Metacoxa beneath flattened, carinated mesally, microsetose; mesocoxa beneath with smooth shiny area. Propodeum reticulate, dorsally with hidden sculpture.

Forewing fuscous, submarginal cell 1 large, apically subovate, approximately equal in length to marginal cell; submarginal cell 2 receiving recurrent vein at midpoint; submarginal cell 3 less distinct than submarginal cell 2 and receiving recurrent vein at midpoint.

Longitudinal carina on S1 well developed, 3/4 × as long as S1 in profile, straight. T1–6 and posterior halves of S3–6 with moderately fine, well separated punctures, sparser on T2 disc; S1–2 with moderately coarse, separated punctures; S6–7 with lateral tubercle; hypopygium (S8) with oblique lateral carina oriented mesally, 3/4 × as long as S8 in profile; T7 and S8 with moderately coarse, dense punctures; T7 medially with rather wide smooth,

shiny area.

Paramere down-curved posteriorly, with pointed apex, dorsally carinate with row of short erect golden setae; parapenial lobe large, rounded; cuspis widely lamellate, apically rounded, densely setose, clearly surpassing apex of penis valve, with dense long erect golden setae oriented mesally; digitus stick-like setose, much shorter than cuspis; paracuspis stick-like setose, shorter than digitus; penis valves weakly asymmetrical, right penis valve slightly longer that left, with strong posterior ventral hook; left valve with strong ventral posterior hook.

FEMALE. Unknown.

Type material

3♂. Holotype, ♂, **Nepal:** CHITWAN DISTRICT: Chitwan, N[ational] P[ark] Sauraha, 200 m, 27°34'N 84°29'E, 31.V.1997, M. Hauser leg. [ZSM]. Paratypes: **India:** TAMIL NADU: 1♂, Coimbatore, V.1947, P. Susi Nathan [UMMZ]. **Nepal:** CHITWAN DISTRICT: 1♂, same data as holotype [IBSS].

Distribution

India: Tamil Nadu. Nepal: Chitwan.

Etymology

The specific epithet is a patronym honoring Martin Hauser who collected the type series, recognized the significance of the wasps, and generously made the material available for study.

Remarks

Among the males of *Eotrogaspidia*, *E. hauseri*, *E. lena* and *E. saussurei* are recognized by the lamellate cuspis. *Eotrogaspidia hauseri* is rather similar to *E. lena* by having the cuspis reaching paramere apex, but differs by having the scape widened apically (not widened in *E. lena*), the propodeum densely covered with pale setae (cuticular sculpture visible in *E. lena*) and the hypopygium (S8) with longitudinal lateral ridge reaching posterior 1/3 of the sternum (reaching posterior margin in *E. lena*).

***Eotrogaspidia lena* (Cameron, 1899), comb. nov.**

(Figs 3B, 3F, 6B, 9C)

Mutilla lena Cameron, 1899: 64, ♂, holotype ♂ (Barrackpore, West Bengal, India) [BMNH].
Trogaspidia lena: Lelej, 2005: 96; Pagliano *et al*., 2020: 285.

Diagnosis

MALE. Clypeus deeply concave, shiny, with sculptured narrow anterior border (Fig. 6B); scape not widened apically; F1 strongly compressed, wider than F2. Pronotum with sparse subappressed and erect fuscous setae; propodeum dorsally with more or less dense pale setae and partly hidden cuticular sculpture (Fig. 3B). Metacoxa ventrally flattened on mesal half with short dense setae. Hypopygium (S8) with longitudinal lateral ridge along entire length of sternum; cuspis lamellate, reaching paramere apex. FEMALE. Unknown.

Material examined

1♂. **India:** GOA: 1♂, Goa, Mormugao, Aug. 1925, J.C. Bridwell, *Trogaspidia lena* (Cameron), B. Petersen det. 1978 [USNM].

Distribution
India: Goa*, West Bengal (Cameron 1899).

Remarks
The detailed original description of this species (Cameron, 1899) closely matches the examined specimen. In the original description, Cameron mentioned that "Scutellum scarecely raised above the level of the mesonotum, strongly punctured, the middle on the basal part smooth and shining, the smooth part slightly depressed in the middle at the base". Contrarily, the males of *Trogaspidia* have the mesoscutellum conical and distinctly raised above the level of mesonotum, as described for species of the group ii-a in Cameron (1899) like *T. fortinata* (Cameron, 1899) and *T. selma* (Cameron, 1899). I thus accept the unpublished identification by B. Petersen and propose a new combination here.

***Eotrogaspidia melanopleura* sp. nov.**
(Figs 2D, 2H, 12D)

Diagnosis
FEMALE. Head with large coarse punctures. Mesosoma dark reddish brown, mesopleuron, metapleuron, antero-dorsal angle of lateral propodeal face and ventral half of posterior propodeal face blackish (Fig. 2H); thoracic dorsum with larger coarser punctures than on head, giving foveate-alveolate appearance (Fig. 2D); posterolateral propodeal margin distinctly dentate. T2 pale setal spots small, distance between them 1.43 × spot diameter (Fig. 2D); T3–4 with a pair of small lateral pale setal spots, distance between spots and that between spot and lateral margin of tergum approximately equal to spot diameter (Fig. 2D); pygidial plate irregularly rugose on anterior 1/2 and smooth posteriorly (Fig. 12D). MALE. Unknown.

Description. FEMALE. Body length: 6.72 mm.

Color and setae. Black with antennal tubercle, mandible on basal 2/3 yellowish brown, clypeus, postgenal bridge, scape, pedicel and metasomal sterna reddish brown, flagellum ventrally and legs dark brown, palpi yellow, mesosoma dark reddish brown except pronotal collar, meso- and metapleuron, antero-dorsal angle of lateral propodeal face and ventral half of posterior propodeal face black, tibial spurs yellow. Head entirely covered with sparse long erect golden setae; frons, postgenal bridge, scape, prementum and stipes with sparse short recumbent golden setae; vertex and gena with dense short appressed golden setae; antennal scrobe with sparse long appressed golden setae; clypeus and mandible with sparse long erect pale golden setae; pedicel, flagellum and palpi with dense extremely short recumbent pale golden setae. Mesosoma dorsally with sparse long golden setae; thoracic dorsum with sparse short recumbent golden setae; lateral face of mesosoma with short appressed pale golden setae, sparse on pronotum, dorsal half of meso- and metapleuron and propodeum, and dense on ventral half of meso- and metapleuron, with few long erect pale golden setae on propodeum. Legs entirely covered with sparse long pale golden setae, erect on procoxa, trochanters, femora and tibiae, recumbent on meso- and metacoxa and tarsi; procoxa with dense short appressed pale golden setae; femora and tibiae with sparse short recumbent pale golden setae. T1, T3–5 laterally, T6 and S1–2 with sparse long erect pale golden setae; T2 disc and T3–5 with dense short recumbent black setae; T2 laterally with sparse long recumbent and sparser long erect pale golden setae; S3–6 with sparse short erect pale golden setae; T1 with posterior sparse fringe of black setae; T2 with two transversely aligned small spots of dense appressed pale golden setae, with distance between spots 1.43 × spot diameter; T2 laterally with golden felt line 0.4 × T2 length; T3 and T4 with lateral spot

of dense appressed pale golden setae, separated from lateral margin of terga; T6 with sparse lateral pygidial fringe of pale golden setae; S2–S6 with posterior sparse fringe of pale golden setae.

Structure. Head 1.41 × wider than long; posterior margin truncate in dorsal view; gena wide; minimum distance between eyes 1.31 × eye height; eye height 2.03 × malar distance; frons and vertex with large confluent punctures, intervals smooth; gena with large dense punctures, intervals densely micropunctate; post genal bridge with large sparse punctures; genal carina sharp, reaching ventral half of gena; hypostomal tooth dentiform; antennal scrobe with distinct dorsal carina and dense micropunctures; antennal tubercle transversely wrinkled; eye oval, slightly protruding from head capsule. Clypeus with subapical transverse ridge and medial longitudinal ridge; transverse ridge medially interrupted and laterally connected with clypeus itself as large tooth; longitudinal ridge apically forming wide truncate tubercle; surface of clypeus with dense micropuntures. Mandible slender, apically pointed with one subapical inner denticle; ventral margin straight. Scape medially bending with small sparse punctures; surface of pedicel with minute sparse punctures; ration between length and width of pedicel, F1 and F2 = 1.00:1.71:3.14:2.29:2.14:2.14; F2–9 almost same in length and width; F10 slightly longer than F9, conical; surface of flagellum with minute dense punctures. Prementum flattened; prementum and stipes with dense micropunctures.

Mesosoma broadest at propodeum in dorsal view; ration between head width:humeral width:pronotal width:mesonotal width:propdeal width:metasomal width = 100:74:82:78:83:118; dorsal thoracic length 1.00 × pronotal width; anterior margin of dorsum of pronotum strongly arcuate, without dorsal tooth; pronotum laterally weakly projecting, forming weak rounded angle at pronotal spiracle; lateral margin of mesosoma weakly crenulate, divergent posteriorly; posterolateral margin of propodeum dentate; humeral angle rounded, with humeral carina weak, reaching dorsum of pronotum; mesopleuron concave; scutellar scale small, well defined with posterior margin truncate; scutellar scale width 1.33 × its length, 0.13 × propodeal width, and approximately 1.5 × diameter of nearby punctures; prescutellar scales absent; metanoto-propodeal suture obliterated; pronotal collar transversely wrinkled; thoracic dorsum with large confluent punctures, giving foveate-alveolate appearance; posterior propodeal face coarsely reticulate; propleuron and lateral face of mesosoma with dense micropunctures.

Procoxa with dense micropunctures; meso- and metacoxa, trochanters, femora, tibiae and tarsi with small sparse punctures; protarsus with weak outer spines; metacoxa with weak inner carina throughout; meso- and metatibiae with two rows of 4–5 longitudinal spines; claws simple, without inner denticle.

T1 without distinct dorsum; T2 evenly convex, dorsal T2 length 0.83 × T2 width; S1 with medial straight longitudinal carina with its outer margin slightly bi-notched; S2 evenly convex, without basomedial carina; T1, T2 laterally and S1 with mixed small and minute sparse punctures; T2 disc with small sparse and minute dense punctures; T3–5, T6 laterally and S3–6 with minute dense punctures; S2 with sparse large punctures; pygidial plate subconvex, laterally well defined by carina on posterior half; surface of pygidial plate coarsely irregularly rugose on anterior half and smooth on posterior half.

MALE. Unknown.

Type material

1♀. Holotype, ♀, **China:** GUANGDONG: Lofoushan [= Mt. Luofushan], 18.VII.1937, T.C. Maa leg. [TARI].

Distribution

China: Guangdong.

Etymology
The specific epithet *melanopleura* is a combination of a Greek adjective μελαν (black, brown), and a Greek noun πλευρον, pl. πλευρα (pleuron, pleura) with reference to the blackish mesopleuron and metapleuron of this new species. Treat as a noun in apposition.

Remarks
This species is readily separated from females of the three East Asian species, *E. auroguttata*, *E. amans* and *E. oryzae* by having the T2 pale setal spots small and T3–4 with a pair of lateral pale setal spots. *Eotrogaspidia buddha*, *E. rubripes* and *E. saussurei* have similarly maculated metasomal terga, but this new species is recognized by having the frons and vertex punctures large and confluent (smaller and separated in others), the mesosoma dark reddish brown with partially blackish markings (uniformly yellowish red in others), the thoracic dorsum with large confluent punctures (with finer punctation in others), the lateral margin of posterior propodeal face dentate (at most tuberculate in *E. rubripes*), the width of pale spots on T3 and T4 equal to the distance between them and that between the spot and lateral margin of the terga (twice larger in *E. rubripes*), and the pygidial plate irregularly rugose on the anterior half and smooth on the posterior half (irregularly rugose on anterior 1/3 in *E. buddha*; transversely rugose throughout in *E. saussurei*).

***Eotrogaspidia oryzae* (Pagden, 1934)**
(Figs 3C, 3G, 4A, 4E, 6C, 7F, 9D–E, 11B, 11E, 12E)

Timulla (*Trogaspidia*) *oryzae* Pagden, 1934: 426, ♂♀, holotype ♂ (Simpang Lima, Perak, Malaysia) [BMNH]; Mickel, 1935: 236, ♂♀.
Timulla (*Trogaspidia*) *amans oryzae*: Pagden, 1949: 229, ♂♀.
Eotrogaspidia amans oryzae: Lelej, 1996c: 22, ♂♀; Lelej, 2005: 78; Okayasu *et al*., 2018: 306, ♀.
Eotrogaspidia oryzae: Williams *et al*., 2019a: 32, ♀, examined; Pagliano *et al*., 2020: 245.

Diagnosis
MALE. Clypeus deeply concave (Fig. 6C); scape ventrally with two parallel carinae; F1 weakly compressed, not wider than F2. Metacoxa flattened with dense erect pale microsetae (Fig. 7F). Pronotum and propodeum dorsally with dense pale setae obscuring cuticular sculpture (Fig. 3C). T2 laterally with small sparse punctures; T7 with medial triangular impunctate line not forming tubercle posteriorly; cuspis robust, spatulate in inner view (Fig. 11B). FEMALE. T2 pale setal spots large, sparsely setose, obscurely defined (Fig. 4A); distance between T2 spots 0.3–0.5 × spot diameter; pale setal bands on T3–4 complete (Fig. 4A); pygidial plate entirely with finer micro-reticulation and with irregular sub-rugae anteriorly (Fig. 12E); lateral margins of pygidial plate subparallel posteriorly.

Material examined
4♂9♀. **Laos:** Bolikhamxai: 1♀, Ban Thabok, 6.III.2003, J. Kantoh leg. [TUA]. **Thailand:** Chiang Mai: 3♂, Chiang Mai, 21.IV.1988, W.J. Pulawski [CASC, CSCA]; Kanchanaburi: Lam Ta Pen River, 5 km NW Lat Ya, 13–16.IV.1989, W.J. Pulawski [CASC]; Khon Kaen: 1♀, Ubol, 20.XII.1962, A. Nagatomi leg. [MNHAH]; 1♀, Nampong, 11.X.1972, M. Sato leg. [EUM]; Nakhon Si Thammarat: 1♀, Pakpanang, 14.VII.1961, K. Iwata leg. [MNHAH]; Prachaub Khiri Khan: 1♀, Khao Sam Roi Yot National Park, malaise, 17–24.V.2009, Yai Amnad, T4831 [QSBG]. **Vietnam:** Hanoi: 1♂, Tu Liem Co Nhue, 13.XII.2015, P.H. Pham [CASC]; 1♀, Hanoi, park, 8.X.1990, S. Belokobylskij leg. [IBSS]; 2♀, same place, meadow,

7.X.1990, S. Belokobylskij leg. [IBSS]; HOA BINH: 1♀, Yen Thuy District, Lac Thinh, Cuc Phuong National Park, 20°23'N 105°34'E, h=300 m, 5–6.V.2002, S. Belokobylskij leg. [IBSS].

Distribution
Laos*: Bolikhamxai. Malaysia: Perak (Pagden 1934). Thailand: Chiang Mai, Kanchanaburi*, Khon Kaen, Nakhon Si Thammarat*, Prachaub Khiri Khan. Vietnam: Hanoi, Hoa Binh*.

Remarks
This species was erected as species by Pagden (1934) from Malaysia. Later, Pagden (1949) regarded it as a continental subspecies of *E. amans* because no difference in male genitalia was found and other morphological differences were "too slight to have specific significance". Recently, Williams *et al*. (2019a) resurrected *E. oryzae* to full species status on the basis of female morphology, together with the difference in punctation of male T2 included in Mickel's (1935) key. Here, I follow this treatment and diagnostic characters recognized by Mickel (1935) and Williams *et al*. (2019a) are included in the key below.

Eotrogaspidia rubripes (André, 1901), comb. nov.
(Figs 4B, 4F, 12F)

Mutilla catanensis var. *rubripes* André, 1901: 287, ♀, syntypes ♀ (Syrie [= Syria]; Jéricho, [Palestine]) [MNHN]; André, 1902: 33.
Trogaspidia rubripes: Invrea, 1950: 21, ♀; Invrea, 1965: 80, ♀; Lelej, 2002: 85; Pagliano *et al*., 2020: 289.

Diagnosis
FEMALE. Posterolateral propodeal margin at most tuberculate (Fig. 4B). T2 pale setal spots small, distance between them 1.0 × or more than spot diameter (Fig. 4B); T3–4 with a pair of small lateral pale setal spots, distance between spots and that between spot and lateral margin of tergum 0.5 × spot diameter (Fig. 4B); pygidial plate irregularly rugose on anterior 1/2 and smooth posteriorly (Fig. 12F). MALE. Unknown.

Material examined
2♀. **Afghanistan:** LAGHMAN PROVINCE: 1♀, Shamakat, 2.IV.1972, O. Kabakov leg. [IBSS]. **Iran:** MAZANDERAN: 1♀, coastal plain between Chalus and Shahsavar, 20 m, 12.V.1965, D.B. Baker [SEMC].

Distribution
Afghanistan*: Laghman. Iran*: Mazanderan. Palestine (André, 1901; Invrea, 1950, 1965). Syria (André, 1901).

Remarks
The female of *Eotrogaspidia rubripes* resembles that of *Neotrogaspidia hammeri* (Suárez, 1959) described from Cyprus (Suárez, 1959) and currently known from Cyprus, Greece, Palestine, Iran, Armenia, Azerbaijan, South-West Turkmenistan (Lelej, 2002). Suárez (1959) and Invrea (1965) considered that the male of *N. hammeri* was the opposite sex of *E. rubripes*. The true female of *N. hammeri* was associated with a male by Lelej (1985). The female of *E. rubripes* differs from that of *N. hammeri* by the shape and sculpture of the pygidial plate.

***Eotrogaspidia saussurei* (Lelej, 2005), comb. nov.**
(Figs 3D, 3H, 4C, 4G, 6D, 7G, 9F–G, 11C, 11F, 12G)

Mutilla luxuriosa Cameron, 1897: 67, ♀ (Ceylon [= Sri Lanka], specifically Trincomali [= Trincomalee] because most of the material collected by Yerbury originates from this place) [Oxford University Museum of Natural History, Oxford, UK], nom. praeocc. non Smith, 1879, objectively invalid name; André, 1902: 40.

Trogaspidia saussurei Lelej, 2005: 101; Pagliano *et al*. 2020: 290. Replacement name for *Mutilla luxuriosa* Cameron, 1897. Secondary junior homonym in *Trogaspidia*, non *Trogaspidia saussurei* Olsoufieff, 1938, currently in the genus *Chrysotilla* Bischoff, 1920. According to Article 59.2 of ICZN (1999), *Eotrogaspidia saussurei* (Lelej, 2005) is a valid specific name.

Diagnosis

MALE. Clypeus deeply concave, shiny, with sculptured narrow anterior border (Fig. 6D); scape not widened apically; F1 strongly compressed, wider than F2. Pronotum with sparse subappressed and erect pale setae; propodeum dorsally with sparse pale setae and visible sculpture (Fig. 3D). Metacoxa beneath totally flattened and closed with very short dense pubescence (Fig. 7G). Hypopygium (S8) with short longitudinal lateral ridge reaching posterior 1/2 of sternum; cuspis lamellate, reaching posterior 1/2 of paramere. FEMALE. T2 pale setal spots small, distance between them 1.0 × or more than spot diameter (Fig. 4C); T3–4 with a pair of small lateral pale setal spots, distance between spots and that between spot and lateral margin of tergum approximately equal to spot diameter (Fig. 4C); pygidial plate with weak transversal curved rugae laterally oriented to apex (Fig. 12G).

Description

MALE (hitherto unknown). Body length: 8.0–10.4 mm. Forewing length: 6.4–8.0 mm.

Color and setae. Black with metasomal T1–6 and S2–6 ferruginous, S1, S7, S8 brownish. Frons, lateral and basal area of clypeus, with silvery, dense, subappressed setae; gena with silvery, dense, erect and subappressed setae; base of mandible and vertex with silvery dense appressed and sparse long erect setae; vertex behind ocelli with silvery dense recumbent and sparse long erect brownish setae; scape with silvery sparse long recumbent and erect setae; pedicel, F1 inside and F2 inside with silvery dense appressed pubescence, outside with sparse recumbent short setae; F2–11 with white dense pubescence; pronotum dorsally with sparse erect whitish and blackish setae; mesopleuron with silvery dense recumbent and sparse erect setae; mesoscutum, mesoscutellum and tegula (anteriorly and mesally) with black recumbent setae; propleuron, lateral area of metanotum and dorsum of propodeum with grayish, sparse, appressed setae with not hidden sculpture; posterior and lateral propodeal slope with grayish, sparse, erect setae; legs with whitish, dense, suberect setae. Metasomal terga with golden appressed and subappressed setae, forming fringe on T1–6, sterna with sparse subappressed and erect yellow-gray setae, forming fringe on S2–6. T2 with lateral felt line, S2 without lateral felt line.

Structure. Relation of head width and mesosoma width including tegula about 64:75. Mandible bidentate at apex, without subbasal tooth on inner border and with dorsal carina extending from base to subapical tooth; outer margin beneath with large subbasal tooth. Clypeus concave shiny, raised and sculptured madiobasally. Scape slightly curved, beneath shiny, with two obscure carinae, F1 strongly compressed, wider than F2, F1 length 1.5 × F2; antennal scrobe dorsally carinate. Ocelli small, POD:OOD = 0.61. Distance between outer ocellar margins 0.93 × distance between posterior ocelli and dorsoposterior occipital border. Frons, vertex and gena with dense separated punctures, frons with interspaces setose, vertex

with interspaces simple.

Notauli and parapsids developed but not touching anterior border of mesoscutum.Tegula large, blackish, smooth and shiny with few punctures anteriorly and mesally. Mesoscutellum convex with medial longitudinal carina ending by obtuse tubercle. Metanotum densely punctate, with medial chagrined narrow area. Pronotum with moderately fine, confluent punctures; mesopleuron with dense punctures; mesoscutum and mesoscutellum with moderately coarse, somewhat confluent punctures; propleuron transversally striate; inferior portions of metapleuron glabrous. Mesopleuron beneath with precoxal smooth, swollen area. Metacoxa mesally carinated, beneath flattened, with dense erect microsetae; procoxa beneath with smooth area; mesocoxa beneath with oblique carina. Propodeum reticulate, with larger cells dorsally; anterodorsally with large medial longitudinal and lateral transversal cells.

Forewings fuscous, submarginal cell 1 large, approximately equal in length to marginal cell; submarginal cell 2 receiving recurrent vein at midpoint; submarginal cell 3 less distinct than submarginal cell 2 and receiving recurrent vein in apical third.

Longitudinal carina on S1 well developed, 3/4 × as long as S1 in profile. T1–6 and posterior halves of S3–6 with moderately fine, well separated punctures, much sparser on T2 disc; S2 with moderately coarse, separated punctures; S7 with lateral tubercle; S8 (hypopygium) laterally with longitudinal carina oriented mesally, 1/2 × as long as S8 in profile; T7 with moderately coarse, dense punctures; T7 medially with narrow widened apically shiny area. Paramere down-curved posteriorly with pointed apex; inner margin of paramere dorsally with row of short erect golden setae; parapenial lobe large, rounded; cuspis long lamelliform, apex rounded, clearly surpassing apex of penis valve, ventrally with dense long erect golden setae; digitus stick-like setose, much shorter than cuspis; paracuspis stick-like setose, shorter than digitus; penis valves weakly asymmetrical, right penis valve slightly longer that left, with posterior ventral hook; left valve with ventral apical hook.

Material examined

15♂34♀. **India:** KARNATAKA: 16♀, 18 km E Bangalore, Madras Rd., 2.X.1985, C.W. and L.B. O'Brien, under stones [CASC, CSCA]; KERALA: 2♀, S. Malabar, Walayar Forest, 1000 ft., 13.X.1947, P. Susi Nathan [UMMZ]; PUDUCHERRY: 1♀, Karikal, I.1962, P. Susi Nathan leg. [RMNH]; 1♀, same place, VII.1962, P. Susi Nathan leg. [RMNH]; 1♀, Nedungadu, P.O. Tanjore, 16.II.1938, P. Susi Nathan [RMNH]; TAMIL NADU: 1♀, Coimbatore, 29.XI.1939, P. Susi Nathan leg. [RMNH]; 1♀, same place, P. Susi Nathan leg., V.1947 [UMMZ]; 1♂, same place, P. Susi Nathan leg., XI.1960 [RMNH]; 2♂, same place, P. Susi Nathan leg., IV.1962 [CSCA, RMNH]; 3♂, Poonamallee, VI.1962, P. Susi Nathan [CSCA, RMNH]; 1♀, South India, [Tamil Nadu], Tranquebar [= Tharangambadi], May 1953, P.S. Nathan [USNM]. **Sri Lanka:** AMPARAI DISTRICT: 1♀, Lahugala Sanctuary, 13–14.VI.1976, K.V. Krombein et al. [USNM]; 1♀, same place, 15.VI.1976, K.V. Krombein et al. [USNM]; ANURADHAPURA DISTRICT: 1♂, Padaviya, 13–20.III.1976, MT, P. Karunaratne et al. [USNM]; COLOMBO DISTRICT: 1♀, Gampaha Botanical Garden, 27.IX.1980, K.V. Krombein et al. [USNM]; 1♀, Ratmalana, 11.IV.1970, 10 m, R.T. Simon Thomas [RMNH]; 1♀, same place, 6.VI.I976, K.V. Krombein et al. [USNM]; HAMBANTOTA DISTRICT: 1♀, Palatupana, 29.III–2.IV.1981, K.V. Krombein et al. [USNM]; JAFFNA DISTRICT: 1♀, 16 km S of Pooneryn, 24–26.I.1977, K.V. Krombein et al. [USNM]; KANDY DISTRICT: 1♂, Vict. Redenigala Rantembe Sanct., 07°13'N 80°57'E, 23–30.VIII.1999, MT, M. and J. Wasbauer [UCDC]; MANNAR DISTRICT: 2♂1♀, Ma Villu, 23–27.I.1978, P. Karunaratne et al. [USNM]; 1♂, same place, 17–21.II.1979, MT, K.V. Krombein et al. [USNM]; 1♂, 0.8 km NE Kokmotte Bungalow, Wilpattu National Park, 5–8.X.1977, K.V. Krombein et al. [USNM]; 1♀, Ma Villu, a tank, 11–12.IV.1981, K.V. Krombein et al. [USNM]; MONARAGALA DISTRICT: 1♂, Angunakolapelessa, 27–28.III.1981,

MT, K.V. Krombein et al. [USNM]; 1♀, 15 km E of Uda Walawe, 31.VII–3.VIII.1993, K.V. Krombein et al. [USNM]; POLONNARUWA DISTRICT: 1♂, Mannampitiya, 24–26.XII 1969, N. Karunaratne [USNM]; RATNAPURA DISTRICT: 1♂, Gilimale, Induruwa, 2.II.1979, MT [USNM].

Distribution
India*: Karnataka, Kerala, Puducherry, Tamil Nadu. Sri Lanka: Amparai*, Anuradhapura*, Colombo*, Hambantota*, Jaffna*, Kandy*, Mannar*, Monaragala*, Polonnaruwa*, Ratnapura*, Trincomalee (Cameron 1897).

Remarks
Both sexes of this species were collected at the same place in Sri Lanka (Mannar District, Ma Villu) in the same collecting event.

Trogaspidia Ashmead, 1899

Trogaspidia acidalia (Cameron, 1897), stat. resurr.
(Fig. 14)

Mutilla acidalia Cameron, 1897: 56, ♂♀, lectotype ♀ (Ceylon [= Sri Lanka], specifically Trincomali [= Trincomalee] according to Cameron, 1903) [BMNH], designated here; André, 1902: 38, ♂; Cameron, 1903: 331; André, 1907: 256, ♀.
Mutilla hexaops var. *acidalia*: André, 1899: 34, ♀.
Trogaspidia acidalia: Hammer, 1962: 9, ♀.
Trogaspidia villosa: Lelej, 2005: 105, ♀, in part.

Diagnosis
MALE (adopted from Cameron, 1897). Head black, frons covered with thick long white setae; mesosoma black, pronotum thickly covered with long white setae; flagellum ventrally covered with sparse white setae, F2 nearly twice as long as F3; Metasoma ferruginous, except apical segment. FEMALE. Mesosoma brownish-red, dorsally ferruginous-red (Fig. 14B). T2 pale setal spots small, distance between spots 2.0 × spot diameter (Fig. 14D); T3–4 with a pair of lateral pale setal spots (Fig. 14D); pygidial plate flattened, longitudinally striate (Fig. 14D).

Material examined
11♀. Lectotype, *M. acidalia*, ♀, **Sri Lanka:** TRINCOMALEE: Type / Cameron Coll. 1902-289 / *Mutilla acidalia* Cam. Type Ceylon / B.M.TYPE HYM. 15-52 [BMNH]. **India:** KARNATAKA: 4♀, 15 km SE Bangalore, KT, 23–24.VII.1996, K. Werner & L. Lorenz leg. [IBSS, MSNF]; TAMIL NADU: 1♀, Pondicherry, 10 km N Auroville, 14.I.2007, F. Burger leg. [IBSS]; 1♀, same place, 2.II–2.III.2011, F. Burger leg. [IBSS]; 1♀, Pudukkottai District, 29 km N Pudukkottai. 20.X.1997, A. Sforzi & L. Bartalozzi leg. [MSNF]; 1♀, near Vellore, 30.X.1997, TN [MSNF]; **Sri Lanka:** AMPARAI DISTRICT: 1♀, Dehiattekandiya, 7°38′N 81°04′E, 23–24.VII.1993, K.V. Krombein et al. [IBSS]; HAMBANTOTA DISTRICT: 1♀, Palatupana, 6°55′N 81°24′E, 27–29.IV.1997, K.V. Krombein et al. [USNM].

Distribution
India: Karnataka*, Tamil Nadu*, West Bengal (Hammer, 1962). Sri Lanka: Amparai*, Hambantota*, Trincomalee (André, 1907).

Remarks
Lelej (2005) treated *Mutilla acidalia* Cameron, 1897 as a synonym of *M. villosa* Fabricius, 1775, since the former was considered a variety of *M. hexaops* de Saussure, 1867 based on André (1899), which was synonymized with *M. villosa* by Lelej (2005). The late B. Petersen studied the type material of P. Cameron's species described from the Oriental region, including syntypes of *M. acidalia* (pers. comm. to A. Lelej), and regarded this species as a distinct species in the genus *Trogaspidia*. However, the male and female of *T. acidalia* sensu Petersen actually belongs to a new species, *E. buddha* **sp. nov.** I found among the specimens from Sri Lanka two females which correspond to the original description of *M. acidalia*. Thanks to Gavin Broad (BMNH), I studied the photos of the female lectotype, especially the pygidial plate (Fig. 14) and found it to be identical to said specimens. The male of *M. acidalia* associated by Cameron (1897) (not found in BMNH) with unmodified mesoscutellum probably belongs to the genus *Krombeinidia* Lelej, 1996 or *Petersenidia* Lelej, 1992.

Trogaspidia mackieae (Cockerell, 1928)
(Fig. 13)

Mutilla mackieae Cockerell, 1928: 597, ♂♀, holotype, ♂ (Nan River, Cajun, Siam [Nan Province, Thailand]) [USNM].
Trogaspidia mackieae: Lelej, 2005: 97; Pagliano *et al*., 2020: 285.
Trogaspidia pacifica Tsuneki, 1972, **syn. nov.**: 10, ♂, holotype ♂ (Chihpenchi, Taitung, Formosa [= Taiwan]) [USNM]; Lelej, 2005; 98; Pagliano *et al*., 2020: 288.
Trogaspidia wilsoni: Williams *et al*., 2019a: 43, ♀, in part, examined.

Diagnosis
MALE. F1 cylindrical, ~ 2 × longer than pedicel. Metacoxa flattened with dense erect pale microsetae (Fig. 7H). Penis valves strongly asymmetrical (Figs 13E–G). FEMALE. Mesosoma ferruginous-red; humeral carina weakly developed, providing rounded humeral angle (Fig. 13B). T2 pale setal spots large, distance between spots slightly less than spot diameter (Fig. 13B); T3–4 with pale setal band (Fig. 13B); pygidial plate flattened, longitudinally striate anteriorly and micro-reticulate on posterior 1/5 (Fig. 13I).

Material examined
17♂24♀. **China:** YUNNAN: 1♀, Yuanjiang, 400 m, 23.III.1955, O. Kryzhanovskij [ZMMU]; 2♀, Nanji River, 200 m, 10, 12.VI.1956, D. Panfilov [ZMMU]; 1♂, 30 km SW Jinpin, 370 m, 22.IV.1956, Huang Ke-ren et al. [ZMMU]; 2♂1♀, same place, 400 m, 28.IV.1956, Huang Ke-ren et al. [ZMMU]; 1♀, same place, 340–400 m, 22.V.1956, D. Panfilov [ZMMU]; 1♂, "1260 B" [South Yunnan, V–VI.1956, D. Panfilov] [ZMMU]; 1♀, "1271 Б" [South Yunnan, V–VI.1956, D. Panfilov] [ZMMU]; 1♂, "1020 A" [South Yunnan, V–VI.1956, D. Panfilov] [ZMMU]; 1♂, Xiaomonyang, 940 m, 5.V.1957, Liu Da-hua [ZMMU]; 1♂, Ganglangba, 650 m, 20.III.1957, Zang Ling-chao [ZMMU]; 1♂, same place, 18.III.1957, Liang Qiu-zhen [ZMMU]; 1♂, Cheli, 500 m, 8.IV.1955, V. Popov [ZMMU]; 2♀, same place, 500 m, 8.IV.1955, Xue Yu-feng [ZMMU]; 1♀, same place, 550 m, 6.IV.1957, D. Panfilov [ZMMU]; 2♀, Cheli, bank of Mekong River, 550 m, 22.IV.1957, D. Panfilov [ZMMU]; 5♀, same place, 24.IV.1957, D. Panfilov [ZMMU]. **Thailand:** CHAIYAPHUM: 1♂, Pa Hin Ngam National Park, ecotone between mix deciduous and dipterocarp forest, 15°38.132'N 101°23.922'E, 698 m, MT, 7–13.II.2007, K. Sa-Nog and B. Adnadai [QSBG]; CHIANG MAI: 2♂, Chiang Khan, 17°52'N 101°36'E, 17.VII.1986, R. Hensen [RMNH]; 1♂, Mae Rim, Mae Sa, 400–500 m alt., 16.V.2002, T. Ishizaki leg. [TUA]; 1♂2♀, same place, 26.V.2002, T. Ishizaki leg. [TUA];

KANCHANABURI: 1♂, Kanchanaburi, 12.IV.1989, W.J. Pulawski [CASC]; 4♀, Thong Pha Phum, Vimarndin farm stay, 14.656°N 98.521°E, 200 m, 17–18.V.2018, K.A. Williams, K. Yah, R. Malee, and N. Thaochan [CSCA]; LOEI: 2♀, Waranya Resort, Phu Ruea district, 17.460°N 101.355°E, 650 m, K.A. Williams, K. Yah, R. Malee, and N. Thaochan [CSCA]. **Vietnam:** HANOI: 1♂, Tu Lien, 13.XII.2015, P.H. Phaum [CASC]; Son La: 1♂, Son La, 3–15.V.1986, A. Gorochov [IBSS].

Distribution

China*: Taiwan, Yunnan (Tsuneki, 1972). Thailand: Chaiyaphum*, Chiang Mai*, Kanchanaburi*, Loei*, Nan (Cockerell, 1928). Vietnam*: Hanoi, Son La.

Remarks. Photos of the holotype of *T. pacifica* are available from the "Integrated insect types database of Taiwanese species" (http://twinsecttype.nmns.edu.tw/, accessed 21 August 2020). They perfectly match the type of *T. mackieae* from USNM, allowing me to synonymize *T. pacifica* with *T. mackieae*.

The male of this species is similar to that of *Eotrogaspidia* in having the clypeus concave, the metacoxa flattened and clothed with dense erect microsetae ventrally, and the digitus small, but differs by having F1 cylindrical, 2 × longer than pedicel and the right penis valve with an inner projection (Fig. 13E), whereas *Eotrogaspidia* males have F1 compressed, 3 × longer than pedicel and the penis valves simple and weakly asymmetrical. The female of *T. mackieae* has the pygidial plate striate (Fig. 13I), like most *Trogaspidia* females. We retain this species in *Trogaspidia*, but the male is included in the key below because it is easily confused with *Eotrogaspidia*. Originally, the female was associated with the male holotype by Cockerell (1928), though this description was inadequate for reliable identification. Later, based on overlapping distribution and preliminary DNA analysis of specimens collected in Thailand by K. Williams, I confirmed Cockerell's (1928) association and was able to examine additional diagnostic features. Finally, I examined a long series of females of *T. mackieae* collected along with males in Yunnan (China).

When *Trogaspidia wilsoni* Williams, 2019 was described, some females were discussed that apparently belonged to *T. wilsoni* but differed in pronotal morphology. For this reason, they were not included in the paratype series of *T. wilsoni*. These females are here recognized as belonging to *T. mackieae*, not *T. wilsoni*. Females of *T. wilsoni* differ from *T. mackieae* by having the humeral angle sharp (weakly rounded in *T. mackieae*) and the pygidial apex usually smooth (pygidial apex micro-reticulate in *T. mackieae*).

Key to species of *Eotrogaspidia* and species easily confused with *Eotrogaspidia*

Males (unknown in *E. melanopleura* **sp. nov.**, *E. rubripes* and *T. acidalia*)

1. Metacoxa conspicuously flattened with erect dense pale microsetae ventrally (Figs 7B–H) … 2
- Metacoxa convex with long sparse setae ventrally (Fig. 7A) … 10
2. F1 cylindrical; penis valves strongly asymmetrical (Fig. 13E). South China, North Thailand, Vietnam … ***Trogaspidia mackieae*** (Cockerell)
- F1 more or less compressed; penis valves weakly asymmetrical (Figs 8–9) … 3
3. Digitus lamellate; paracuspis tuberculate coarctate (Lelej & van Harten 2006: Fig. 27). South Asia, Middle East, Africa … ***Vanhartenidia*** **Lelej**—not treated here
- Digitus stick-like; paracuspis stick-like (Figs 10A, 11B) (*Eotrogaspidia*) … 4
4. F1 weakly compressed, not wider than F2; pronotum and propodeum dorsally with dense pale setae obscuring cuticular sculpture (Figs 1B, 1C, 3C) … 5

- F1 strongly compressed, wider than F2; pronotum dorsally with sparse pale setae (Figs 3A–B, 3D) (in *E. buddha* **sp. nov.** with lateral white spots; Fig. 1D); propodeum dorsally with sparse pale setae and visible sculpture (Figs 1D, 3B, 3D) (in *E. hauseri* **sp. nov.** with dense pale setae and invisible sculpture; Fig. 3A) … 7

5. T7 with narrow elongate impunctate line forming weak tubercle posteriorly; cuspis narrowed posteriorly in inner view (Fig. 10C). China, India, Indonesia, Japan, Laos, Thailand, Vietnam. … ***E. auroguttata*** (Smith)
- T7 with medial triangular impunctate line not forming tubercle posteriorly; cuspis robust, spatulate in inner view (Figs 10B, 11B) … 6

6. T2 lateral punctures large dense, separated by less than puncture diameter. Indonesia. … ***E. amans*** (André)
- T2 lateral punctures small sparse, separated by approximate puncture diameter. Laos, Malaysia, Thailand, Vietnam. … ***E. oryzae*** (Pagden)

7. Clypeus basally elevated, medial depression on anterior margin laterally defined by carinae (Fig. 5D); pronotum with narrow lateral spot of pale setae (Fig. 1D); cuspis stick-like (Fig. 10D). India, Nepal, Pakistan, Sri Lanka. … ***E. buddha*** **sp. nov.**
- Clypeus deeply concave, mostly smooth with narrow sculptured anterior border (Figs 6A–B, 6D); pronotum without lateral spot of pale setae (Figs 3A-B, 3D); cuspis lamellate; cuspis lamellate … 8

8. Scape strongly widened apically; propodeum dorsally with dense pale setae obscuring cuticular sculpture (Fig. 3A). India, Nepal. … ***E. hauseri*** **sp. nov.**
- Scape not widened apically; propodeum dorsally mostly with more or less sparse pale setae and visible sculpture (Fig. 3B, 3D) … 9

9. Metacoxa ventrally flattened in mesal half with short dense setae; propodeum dorsally with denser setae and partly hidden sculpture (Fig. 3B); hypopygium (S8) with longitudinal lateral ridge along entire length; cuspis reaching paramere apex (Fig. 9C). India. … ***E. lena*** (Cameron)
- Metacoxa ventrally totally flattened with very short dense setae (Fig. 7G); propodeum dorsally with sparser setae and visible sculpture (Fig. 3D); hypopygium (S8) with short longitudinal lateral ridge on anterior half; cuspis reaching posterior 1/2 of paramere (Fig. 9G). India, Sri Lanka. … ***E. saussurei*** (Lelej, 2005)

10. Penis valves highly asymmetrical, with right penis valve larger and bearing various projections (Figs 13E–G). Widespread. … ***Trogaspidia*** **Ashmead**—not treated here
- Penis valves similar in shape, with right penis valve only slightly longer than left (Figs 8A–B, 10E) … 11

11. Clypeus basally gibbous, medial depression on anterior margin laterally not carinate (Fig. 5A); scape with one strong carina (Fig. 5A); mesoscutellum with medial carina. India, Nepal. … ***E. adhabar*** **sp. nov.**
- Clypeus predominantly flattened or concave, anterior margin usually with distinct carina; scape with two carinae; mesoscutellum with medial impunctate line. Widespread. … ***Neotrogaspidia*** **Lelej**—not treated here

Females (unknown in *E. adhabar* **sp. nov.**, *E. lena* and *E. hauseri* **sp. nov.**)

1. Protarsus strongly pectinate (Lelej & van Harten 2006: Fig. 24); lateral carina of pygidial plate widened posteriorly (Lelej & van Harten 2006: Fig. 29) … ***Vanhartenidia*** **Lelej**—not treated here
- Protarsus weakly pectinate (Fig. 4D); lateral carina of pygidial plate not widened posteriorly (Fig. 12) … 2

2. Pygidial plate flattened, longitudinally striate, longitudinally rugose or irregularly rugose

on basal 3/4, at most with apical fifth micro-reticulate (Figs 13I, 14D) … ***Trogaspidia* Ashmead**—not treated here
- Pygidial plate subconvex, irregularly rugose on basal half or third and smooth apically, or entirely micro-reticulate (Fig. 12) … 3
3. Setal pale spots on T2 large, distance between them 0.3–0.5 × their diameter (Figs 2A–B, 4A); T3–4 with pale setal band at most medially interrupted by black setae (Figs 2A–B, 4A) (*Eotrogaspidia*) … 4
- Setal pale spots on T2 small or absent, distance between them, when present, 1.0 × or more than their diameter (Figs 2C–D, 4B–C); metasoma with a pair of lateral pale setal spots on T3–4 or with pale setal band on T3 or T3–4 (Figs 2C–D, 4B–C) … 6
4. Pale setal bands on T3–4 widely interrupted by black setae (Fig. 2B); pygidial plate irregularly rugose on anterior half and smooth posteriorly (Fig. 12B) … ***E. auroguttata*** (Smith)
- Pale setal bands on T3–4 complete (Figs 2A, 4A); pygidial plate entirely micro-reticulate with sub-rugae anteriorly (Figs 12A, 12E) … 5
5. Pale spots on T2 densely setose, well defined (Fig. 2A); pygidial plate with coarser microreticulation (Fig. 12A); lateral margins of pygidial plate convergent posteriorly … ***E. amans*** (André)
- Pale spot on T2 sparsely setose, obscurely defined (Fig. 4A); pygidial plate with finer microreticulation (Fig. 12E); lateral margins of pygidial plate subparallel posteriorly … ***E. oryzae*** (Pagden)
6. Pale setal band of T3 extending nearly to lateral margin of T3 (Okayasu 2020: Figs 48C–D) … ***Neotrogaspidia* Lelej**—not treated here
- Pale setal band of T3 reduced to small spot, widely separated from lateral margin of T3 (Figs 2C–D, 4B–C) (*Eotrogaspidia*) … 7
7. Pygidial plate with weak transverse curved rugae laterally oriented to apex (Fig. 12G) … ***E. saussurei*** (Lelej)
- Pygidial plate weakly irregularly rugose on anterior 1/3–1/2 and smooth posteriorly (Figs 12C–D, 12F) … 8
8. Posterolateral propodeal margin at most tuberculate; pale setal spots on T3–4 wide, 2 × more than distance between spot and lateral border (Fig. 4B). Afghanistan, Iran, Palestine, Syria. … ***E. rubripes*** (André)
- Posterolateral propodeal margin distinctly dentate; pale setal spots on T3–4 narrow, equal to distance between spot and lateral border (Figs 2C–D) … 9
9. Mesosoma dorsally with coarse confluent punctures (Fig. 2C); mesosoma entirely yellowish red (Fig. 2G); pygidial plate rugose on anterior 1/3 (Fig. 12C) … ***E. buddha* sp. nov.**
- Mesosoma dorsally foveate-alveolate (Fig. 2D); mesosoma dark reddish brown, with mesopleuron, metapleuron and ventral half of posterior propodeal face blackish (Fig. 2H); pygidial plate rugose on anterior 1/2 (Fig. 12D). China. … ***E. melanopleura* sp. nov.**

Discussion

Before I conducted this revision, *Eotrogaspidia* included four species that were predominantly distributed in East and Southeast Asia. In the present paper, I found the true species diversity of this genus was higher than formerly recognized with 10 species found throughout Asia, three from males only, two from females only and five from both sexes. Discovery of additional species also highlighted the morphological diversity within *Eotrogaspidia*. Within the Trogaspidiini, the males of this genus are readily recognized by having the metacoxa conspicuously flattened with dense erect microsetae (Lelej, 1996c,

2005). The females are defined by having the T2 setal spots much larger than the distance between them and the pygidial plate irregularly rugose anteriorly (Lelej, 1996c, 2005; Williams *et al*., 2019a). Some exceptions were found in this study, namely *Eotrogaspidia adhabar* **sp. nov.**, *E. buddha* **sp. nov.**, *E. melanopleura* **sp. nov.**, *E. rubripes*, *E. saussurei*, and *Trogaspidia mackieae*.

The metacoxal shape of *Eotrogaspidia* males was initially regarded as an autapomorphy of the genus. *Trogaspidia mackieae*, however, has a similar metacoxal shape, although the strongly asymmetrical penis valve of the male and the striated pygidial plate of the female support the current generic placement. Likewise, *Vanhartenidia* has a similar condition of the male metacoxa, but differs in male genitalia and female pygidial sculpture. Contrarily, *E. adhabar* **sp. nov.** has the metacoxa convex like most species of Mutillinae, but we placed this species in *Eotrogaspidia* based on the weakly asymmetrical penis valves, which only scarcely differ in length.

The females of *Eotrogaspidia* and *Neotrogaspidia* were separated by the relative size of T2 spots to the distance between them (0.3–0.4 in *Eotrogaspidia* vs. 1.0–2.0 in *Neotrogaspidia*; Lelej, 1996c, 2005). In the present review, four species with small T2 spots, *E. buddha* **sp. nov.**, *E. melanopleura* **sp. nov.**, *E. rubripes* and *E. saussurei*, are reliably placed in *Eotrogaspidia* based on the sex association of *E. buddha* **sp. nov.** and *E. saussurei*. Therefore, we used the T3 and T4 maculated with a pair of lateral pale setal spots to separate them from *Neotrogaspidia* females which have a combination of small T2 spots and a pale setal band on T3 or T3–4.

Overall, genus identification of Trogaspidiini is still difficult because of the high morphological variation; many apparently diagnostic external morphological features appear to be subject to convergent evolution and male genitalic features, especially penis valve shape, appear to more closely track with phylogenetic relationships that should be used to define genus limits. A phylogenetic framework, especially if based on molecular data, will likely help to reveal the limits of the genera within this tribe.

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References

André, E. (1899) Les types des mutillides de la collection O. Radoszkowski. *Annales de la Société Entomologique de France* 68: 1–43.

André, E. (1901) *Species des Hyménoptères d'Europe & d'Algérie*. *Tome Huitième*. *Les*

Mutillides. Vve Dubosclard and A. Hermann, Paris, pp. 145–304.
André, E. (1902 [1903]) Family Mutillidae. *In*: Wytsman, P. (ed.) *Genera Insectorum*. *Fascicles 11*. L. Desmet-Verteneuil, Bruxelles, pp. 1–77 + 3 pls.
André, E. (1907). Liste des Mutillides recueillis à Ceylan par M. le Dr. Walter Horn et description des espèces nouvelles. (Hym.). *Deutsche Entomologische Zeitschrift* 3: 251–258. https://doi.org/10.1002/mmnd.48019070305
André, E. (1909) Mutillides nouveaux ou imparfaitement connus du Musée royal d'histoire naturelle de Leide. *Notes from the Leyden Museum* 31: 171–180.
Ashmead, W.H. (1899) Superfamilies in the Hymenoptera and generic synopses of the families Thynnidae, Myrmosidae, and Mutillidae. *Journal of the New York Entomological Society* 7: 45–60.
Barthélémy, C., Lelej, A.S. & Loktionov, V.M. (2018) A contribution to the Mutillidae (Hymenoptera) of Hong Kong. *Zootaxa* 4514 (2): 230–242. https://doi.org/10.11646/zootaxa.4514.2.6
Bischoff, H. (1920–1921) Monographie der Mutilliden Afrikas. *Archiv für Naturgeschichte* 86A(1–3): 1–480 (1920); 86A(4–5): 481–830 (1921).
Brothers, D.J., Lelej, A.S. & Williams, K.A. (2019) Genus-group names of Mutillidae (Hymenoptera): corrections and updates since 2008. *Zootaxa* 4651 (3): 578–588. https://doi.org/10.11646/zootaxa.4651.3.10
Cameron, P. (1897) Hymenoptera Orientalia, or Contributions to a knowledge of the Hymenoptera of the Oriental Zoological Region. Part V. *Memoirs and Proceedings of the Manchester Literary and Philosophical Society* 41 (4): 1–144 + pls 3–4.
Cameron, P. (1899) Description of a new genus and some new species of fossorial Hymenoptera from the Oriental Zoological Region. *The Annals and Magazine of Natural History*, Series 7 4 (19): 52–69. https://doi.org/10.1080/00222939908678162
Cameron, P. (1903) On some new genera and species of parasitic and fossorial Hymenoptera from the Khasia Hills, Assam. *The Annals and Magazine of Natural History*, Series 7 11 (62, 63, 68, 69, 72): 173–185, 313–331, 266–273, 363–371 & 565–583. https://doi.org/10.1080/00222930309487036; https://doi.org/10.1080/00222930308678748; https://doi.org/10.1080/00222930308678869; https://doi.org/10.1080/00222930308678869; https://doi.org/10.1080/00222930308678775
Chen, C.-w. (1957) A revision of the velvety ants or Mutillidae of China (Hymenoptera). *Quarterly Journal of the Taiwan Museum* 10 (3–4): 135–224 + 6 pls.
Chu, Y.-I. & Yamanaka, T. (1973–1975) A check list of the present and old name of insect collected localities in Taiwan. *Journal of the National Taiwan Museum* 16: 31–72 (1973); 17: 51–75 (1974); 18: 121–150 (1975).
Cockerell, T.D.A. (1928) Mutillidae from Siam. *The Annals and Magazine of Natural History*, Series 10 2: 596–600. https://doi.org/10.1080/00222932808672926
Dalla Torre, C.G. de (1897) *Catalogus Hymenopterorum hucusque Descriptorum Systematicus et Synonimicus*. *Vol. VIII*. *Fossores (Sphegidae)*. Guilelmi Engelmann, Lipsiae, [4] + viii + 750 pp.
Fabricius, J.C. (1775) *Systema entomologiae, systens Insectorum classes, ordines, genera, species, adjectis synonymis, locis, descriptionibus, observationibus*. In Officina Libraria Kortii, Flensburgi et Lipsiae, 832 pp. https://doi.org/10.5962/bhl.title.36510
Fabricius, J.C. (1804) *Systema Piezatorum secundum Ordines, Genera, Species adjectis Synonymis, Locis, Observationibus, Descriptionibus*. Carolum Reichard, Brunsvigae, pp. i–xiv + 15–440 + 1–30. https://doi.org/10.5962/bhl.title.10490
Hammer, K. (1962 [1960]) Mutilliden (Insecta: Hymenoptera) aus dem Indischen Museum in

Calcutta. *Records of the Indian Museum* 58 (1): 1–51.
Harris, R.A. (1979) A glossary of surface sculpturing. *Occasional Papers in Entomology* 28: 1–31.
Hashimoto, Y. & Nakanishi, A. (1997) *A list of the type-specimens of Hymenoptera described by K. Tsuneki in the Museum of Nature and Human Activities, Hyogo (MNHAH)*. Catalogue of Collections in the Museum of Nature and Human Activities, Hyogo No. 2. Museum of Nature and Human Activities, Sanda, 47 pp. + 8 pls.
Hymenoptera Anatomy Ontology (2013) Hymenoptera glossary. Available from: http://glossary.hymao.org (accessed 1 August 2020)
International Commission on Zoological Nomenclature (ICZN) (1999) *International Code of Zoological Nomenclature*. *4th edition*. ITZN, London, xxx + 306 pp.
Invrea, F. (1950) Mutillidi nuovi o notevoli del Bacino Mediterraneo (Hymenoptera, Mutillidae). *Memorie della Società Entomologica Italiana* 29: 19–27.
Invrea, F. (1965) Studi sugli Apterogynidi e Mutillidi della Palestina. *Memorie della Società Entomologica Italiana* 44: 53–93.
Ito, R. (2018) A second record of *Eotrogaspidia auroguttata* (Smith, 1855) (Hymenoptera, Mutillidae, Mutillinae) from the Yaeyama Islands, Japan. *Tsunekibachi* 32: 25–26. (in Japanese)
Kojima, J., Saito, F. & Nguyen, L.T.P. (2011) On the species-group taxa of Taiwanese social wasps (Hymenoptera: Vespidae) described and/or treated by J. Sonan. *Zootaxa* 2920 (1): 42–64. https://doi.org/10.11646/zootaxa.2920.1.2
Lelej, A.S. (1985) *Osy-nemki (Hymenoptera, Mutillidae) Fauny SSSR i Sopredelnykh Stran [The Velvet Ants (Hymenoptera, Mutillidae) of the USSR and Neighboring Countries]*. Nauka, Leningrad, 268 pp. (in Russian)
Lelej, A.S. (1995) A review of Palaearctic and Oriental species of genus *Nemka* Lelej with description of Oriental genus *Mickelomyrme* gen. n. (Hymenoptera, Mutillidae). *Far Eastern Entomologist* 6: 1–20.
Lelej, A.S. (1996a) A review of the East Asian species of *Mickelomyrme* Lelej, 1995 (Hymenoptera, Mutillidae). *Entomofauna* 17 (15): 277–292.
Lelej, A.S. (1996b) A review of the East Asian species of *Orientilla* (Hymenoptera, Mutillidae). *Memoirs of the Entomological Society of Washington* 17: 103–107.
Lelej, A.S. (1996c) To the knowledge of the East Asian species of the tribe Trogaspidiini Bischoff, 1920 (Hymenoptera, Mutillidae) with description of eight new genera and two new species. *Far Eastern Entomologist* 30: 1–24.
Lelej, A.S. (2002) *Catalogue of the Mutillidae (Hymenoptera) of the Palaearctic Region*. Dalnauka, Vladivostok, 172 pp.
Lelej, A.S. (2005) *Catalogue of the Mutillidae (Hymenoptera) of the Oriental Region*. Dalnauka, Vladivostok, 252 pp.
Lelej, A.S. (2007) Biogeography of mutillid wasps (Hymenoptera, Mutillidae). *In*: Rasnitsyn, A.P. & Gokhman, V.E. (eds) *Studies on hymenopterous insects*. *Collection of scientific papers*. KMK Scientific Press Ltd., Moscow, pp. 82–111. (in Russian)
Lelej, A.S. & Brothers, D.J. (2008) The genus-group names of Mutillidae (Hymenoptera) and their type species, with a new genus, new name, new synonymies, new combinations and lectotypifications. *Zootaxa* 1889 (1): 1–79. https://doi.org/10.11646/zootaxa.1889.1.1
Lelej, A.S. & Krombein, K.V. (1999) Two remarkable new genera of mutillid wasps (Hymenoptera: Mutillidae, Sphaeropthalminae, Pseudomethocini) from Thailand. *Far Eastern entomologist* 79: 1–8.
Lelej, A.S. & Krombein, K.V. (2001) Review of the Oriental mutillid wasps of the subfamily Ticoplinae (Hymenoptera, Mutillidae). *Far Eastern Entomologist* 99: 1–18.

Lelej, A.S. & van Harten, A. (2006) A review of the Mutillidae (Hymenoptera) of Yemen. *Zootaxa* 1226 (1): 1–50. https://doi.org/10.11646/zootaxa.1226.1.1
Lelej, A.S. & Yamane, Sk. (1992) Interesting velvet ants (Hymenoptera, Mutillidae) from Japan and Korea. *Japanese Journal of Entomology* 60 (3): 625–632.
Lelej, A.S., Williams, K.A., Loktionov, V.M., Pang, H. & Xu, Z.-F. (2017) Review of the genus *Zeugomutilla* Chen, 1957 (Hymenoptera, Mutillidae, Mutillini), with description of two new species. *Zootaxa* 4247 (1): 1–15. https://doi.org/10.11646/zootaxa.4247.1.1
Lelej, A.S., Zhou, H.-T., Loktionov, V.M. & Xu, Z.-F. (2016) Review of the genus *Promecidia* Lelej, 1996, with description of two new species from China (Hymenoptera, Mutillidae, Trogaspidiini). *ZooKeys* 641: 103–120. https://doi.org/10.3897/zookeys.641.10765
Lo Cascio, P. (2015) Worldwide checklist of the island mutillid wasps (Hymenoptera Mutillidae). *Biodiversity Journal* 6 (2): 529–592.
Mickel, C.E. (1933a) The Mutillidae of Formosa. *Annals of the Entomological Society of America* 26 (2): 381–423. https://doi.org/10.1093/aesa/26.2.381
Mickel, C.E. (1933b) The Mutillidae of Eastern Asia. *Lingnan Science Journal* 12 (3): 289–325.
Mickel, C.E. (1934) Mutillidae of the Philippine Islands. *Philippine Journal of Science* 54 (1): 91–219 + 1 pl.
Mickel, C.E. (1935) The mutillid wasps of the islands of the Pacific Ocean (Hymenoptera, Mutillidae). *Transactions of the Royal Entomological Society of London* 83 (2): 177–312. https://doi.org/10.1111/j.1365-2311.1935.tb01207.x
Mickel, C.E. (1939) Correction of type locality for two species of Mutillidae described by Frederick Smith (Hymenoptera). *Proceeding of the Royal Entomological Society of London*, Series B 8: 192–194. https://doi.org/10.1111/j.1365-3113.1939.tb00514.x
Murota, T. (1973) Sphecidae, Mutillidae, Scoliidae and Chrysididae collected in Formosa in 1972. *Life Study* 17 (3–4): 115–120. (in Japanese)
Nurse, C.G. (1902) New species of Indian Hymenoptera. *Journal of the Bombay Natural History Society* 14: 79–92.
Okayasu, J. (2016) [First record of *Eotrogaspidia auroguttata* (Smith) from Yaeyama Islands, Japan]. *Gekkan-Mushi* 543: 61–62. (in Japanese)
Okayasu, J. (2017) Two new species of the genus *Sinotilla* Lelej, 1995 (Hymenoptera: Mutillidae), with notes on taxonomic characters. *Zootaxa* 4294 (2): 151–169. https://doi.org/10.11646/zootaxa.4294.2.1
Okayasu, J. (2018) Taxonomic review of Chin-wen Chen's species described in the genus *Smicromyrme* (Hymenoptera: Mutillidae: Smicromyrmini). *Acta Entomologica Musei Nationalis Pragae* 58 (2): 479–494. https://doi.org/10.2478/aemnp-2018-0036
Okayasu, J. (2020) Velvet ants of the tribe Smicromyrmini Bischoff (Hymenoptera: Mutillidae) of Japan. *Zootaxa* 4723 (1): 1–110. https://doi.org/10.11646/zootaxa.4723.1.1
Okayasu, J., Williams, K.A. & Lelej, A.S. (2018) A remarkable new species of the genus *Sinotilla* Lelej (Hymenoptera: Mutillidae: Smicromyrmini) from Taiwan and an overview of color diversity in East Asian mutillid females. *Zootaxa* 4446 (3): 301–324. https://doi.org/10.11646/zootaxa.4446.3.1
Olsoufieff, G. (1938 [1937]) Revision systématique des Mutilles de Madagascar. *Bulletin de l'Academie Malgache*, New Series 20: 171–217 + pls. 27–28.
Pagden, H.T. (1934) New species of Mutillidae (Hymenoptera, Vespoidea) from the Malay Peninsula. *Journal of the Federated Malay States Museums* 17 (3): 419–457.
Pagden, H.T. (1949) Descriptions and records of Austro-Malaysian Methocidae and

Mutillidae (Hymenoptera). *Transactions of the Royal Entomological Society of London* 100 (8): 191–231. https://doi.org/10.1111/j.1365-2311.1949.tb01431.x

Pagliano, G. (2011) I Mutillidae (Hymenoptera) della collezione Zavattari le collezioni del Museo Regionale di Scienze Naturali di Torino. *Bolletino del Musei Regionale di Scienze Naturali di Torino* 28 (1): 37–60.

Pagliano, G., Brothers, D.J., Cambra, R., Lelej, A.S., Lo Cascio, P., Matteini Palmerini, M., Scaramozzino, P.L., Williams, K.A. & Romano, M. (2020) Checklist of names in Mutillidae (Hymenoptera), with illustrations of selected species. *Bollettino del Museo Regionale di Scienze Naturali di Torino* 36 (1–2): 5–425.

de Saussure, H. (1867) *Reise der österreichschen Fregatte Novara um die Erde in den Jahren 1857, 1858, 1859 unter den Befehlen des Commodore B. von Wüllerstorf-Urbair. Zoologischer Theil. Zweiter Band. Hymenoptera. Familien der Vespiden, Sphegiden, Pompiliden, Crabroniden und Heterogynen*. C. Gerold‘s Sohn, Wien, 138 pp. + 4 pls.

Smith, F. (1855) *Catalogue of hymenopterous insects in the collection of the British Museum. Part III. Mutillidae and Pompilidae*. Taylor and Francis, London, 206 pp. + 5 pls.

Smith, F. (1879) *Descriptions of new species of Hymenoptera in the collection of the British Museum*. Taylor and Francis, London, XXI + 240 pp.

Snodgrass, R.E. (1941) The male genitalia of Hymenoptera. *Smithsonian Miscellaneous Collections* 99 (14): 1–86, 33 pls.

Suárez, F.J. (1959) Especies nuevas o poco conocidas de la fauna mediterranea. II nota (Hym. Myrmosidae, Mutillidae). *EOS*, *Revista Española de Entomologia*, *Madrid* 35 (3): 283–300.

Terayama, M. (2005) Taxonomic guide to the Japanese aculeate wasps, 2. Family Mutillidae. *Tsunekibachi* 4: 1–13. (in Japanese)

Terayama, M., Suda, H., Murota, T., Haneda, Y. & Tano, T. (2011) The velvet ants (Mutillidae) of Japan. *Gekkan-Mushi* 481: 12–25. (in Japanese)

Terayama, M., Suda, H., Murota, T. & Tano, T. (2016) Family Mutillidae. *In*: Terayama, M. & Suda, H. (eds) *A guide to the aculeate wasps of Japan*. Tokai University Press, Hiratsuka, pp. 161–174. (in Japanese)

Tsuneki, K. (1972) Mutillidae collected in Formosa in 1966 and 68 (Hymenoptera). *Etizenia* 64: 1–25.

Tsuneki, K. (1993) On some Taiwanese Mutillidae, collected in 1976 by Mr. T. Murota, with description of new taxa (Hymenoptera). *Special Publications of the Japan Hymenopterists Association* 41: 39–50.

Tu, B.-B., Lelej, A.S. & Chen, X.-X. (2014) Review of the genus *Cystomutilla* André, 1896 (Hymenoptera: Mutillidae: Sphaeropthalminae: Sphaeropthalmini), with description of the new genus *Hemutilla* gen. nov. and four new species from China. *Zootaxa* 3889 (1): 71–91. https://doi.org/10.11646/zootaxa.3889.1.4

Tu, B.-B., Lelej, A.S. & Chen, X.-X. (2015) Review of the genus *Taiwanomyrme* Tsuneki, 1993 (Hymenoptera, Mutillidae, Mutillinae), with description of two new species from China. *Zootaxa* 4020 (3): 588–600. https://doi.org/10.11646/zootaxa.4020.3.10

Williams, K.A., Lelej, A.S., Okayasu, J., Borkent, C.J., Malee, R., Thoawan, K. & Thaochan, N. (2019a) The female velvet ants (aka modkhong) of southern Thailand (Hymenoptera: Mutillidae), with a key to the genera of southeast Asia. *Zootaxa* 4602 (1): 1–69. https://doi.org/10.11646/zootaxa.4602.1.1

Williams, K.A., Lelej, A.S. & Thoawan, K. (2019b) New species of Myrmosinae (Hymenoptera: Mutillidae) from Southeastern Asia. *Zootaxa* 4656 (3): 525–534. https://doi.org/10.11646/zootaxa.4656.3.9

Zavattari, E. (1913) H. Sauter’s Formosa-Ausbeute. Mutillidae (Hym.). *Archiv für Naturgeschichte* 79A (3): 19–42.

Zhou, H.-T., Lelej, A.S. & Xu, Z.-F. (2017) Discovery of the subfamily Rhopalomutillinae (Hymenoptera: Mutillidae) in China and description of *Pherotilla brothersi* sp. nov. *Zootaxa* 4273 (4): 587–594. https://doi.org/10.11646/zootaxa.4273.4.8

Zhou, H.-T., Lelej, A.S., Williams, K.A. & Liu, J.-X. (2018) Revision of the Oriental genus *Zavatilla* Tsuneki (Hymenoptera, Mutillidae, Trogaspidiini), with descriptions of two new species. *Zootaxa* 4418 (2): 101–120. https://doi.org/10.11646/zootaxa.4418.2.1

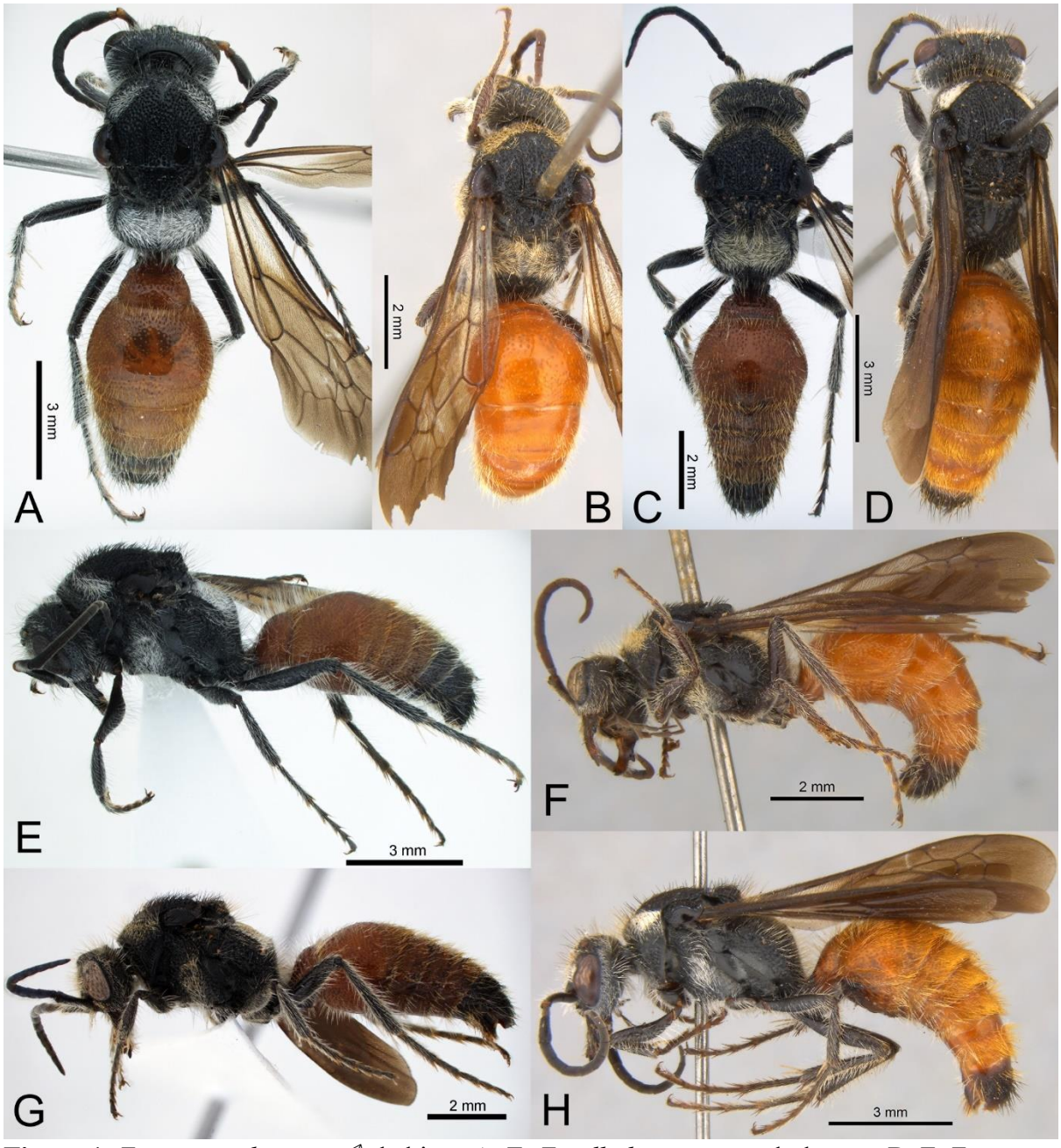

Figure 1. *Eotrogaspidia* spp., ♂, habitus. A, E. *E. adhabar* **sp. nov.**, holotype; B, F. *E. amans* (André); C, G. *E. auroguttata* (Smith); D, H. *E. buddha* **sp. nov.**, paratype; A–D. dorsal view; E–H. lateral view.

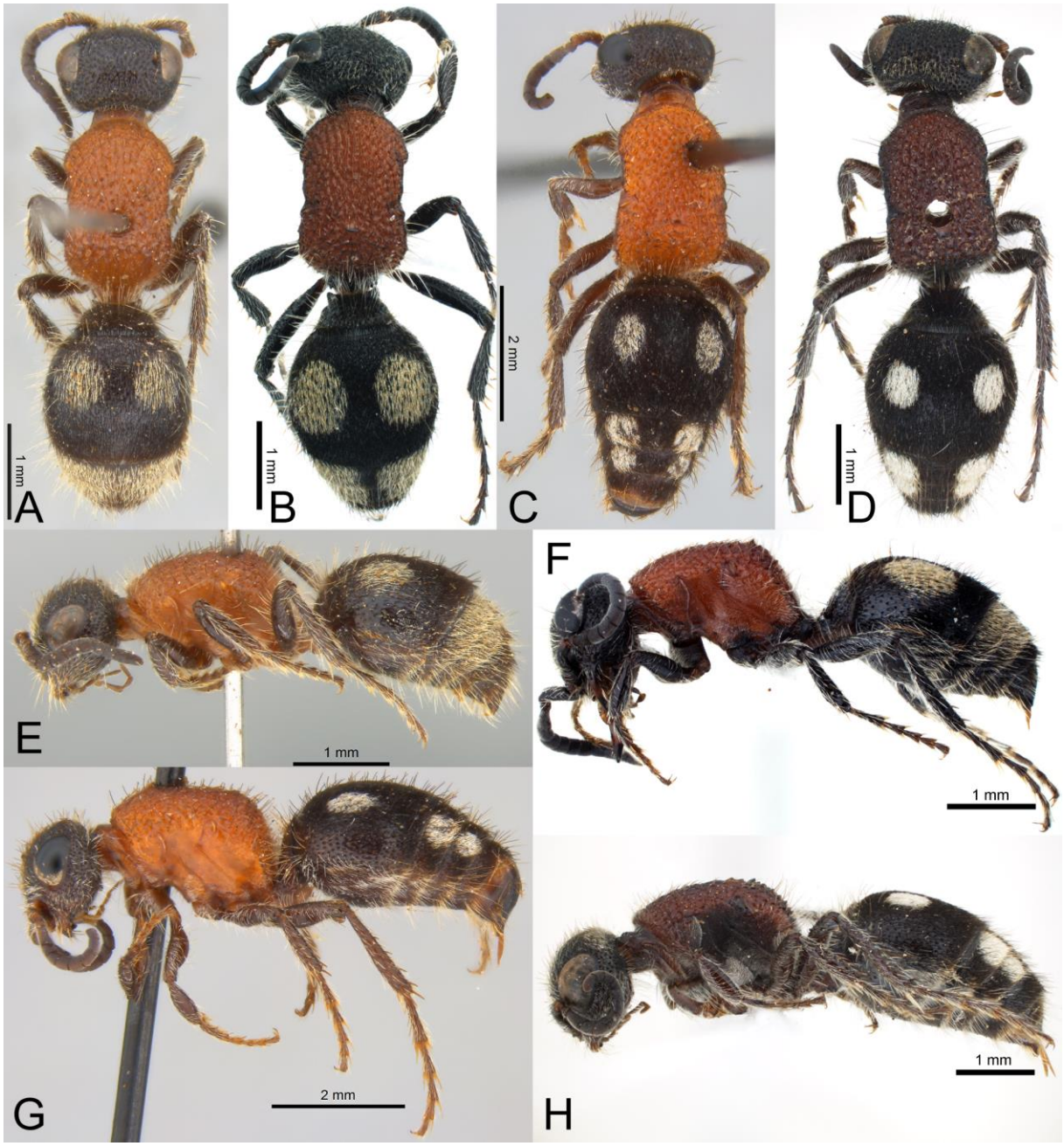

Figure 2. *Eotrogaspidia* spp., ♀, habitus. A, E. *E. amans* (André); B, F. *E. auroguttata* (Smith); C, G. *E. buddha* **sp. nov.**, paratype; D, H. *E. melanopleura* **sp. nov.**, holotype; A–D. dorsal view; E–H. lateral view.

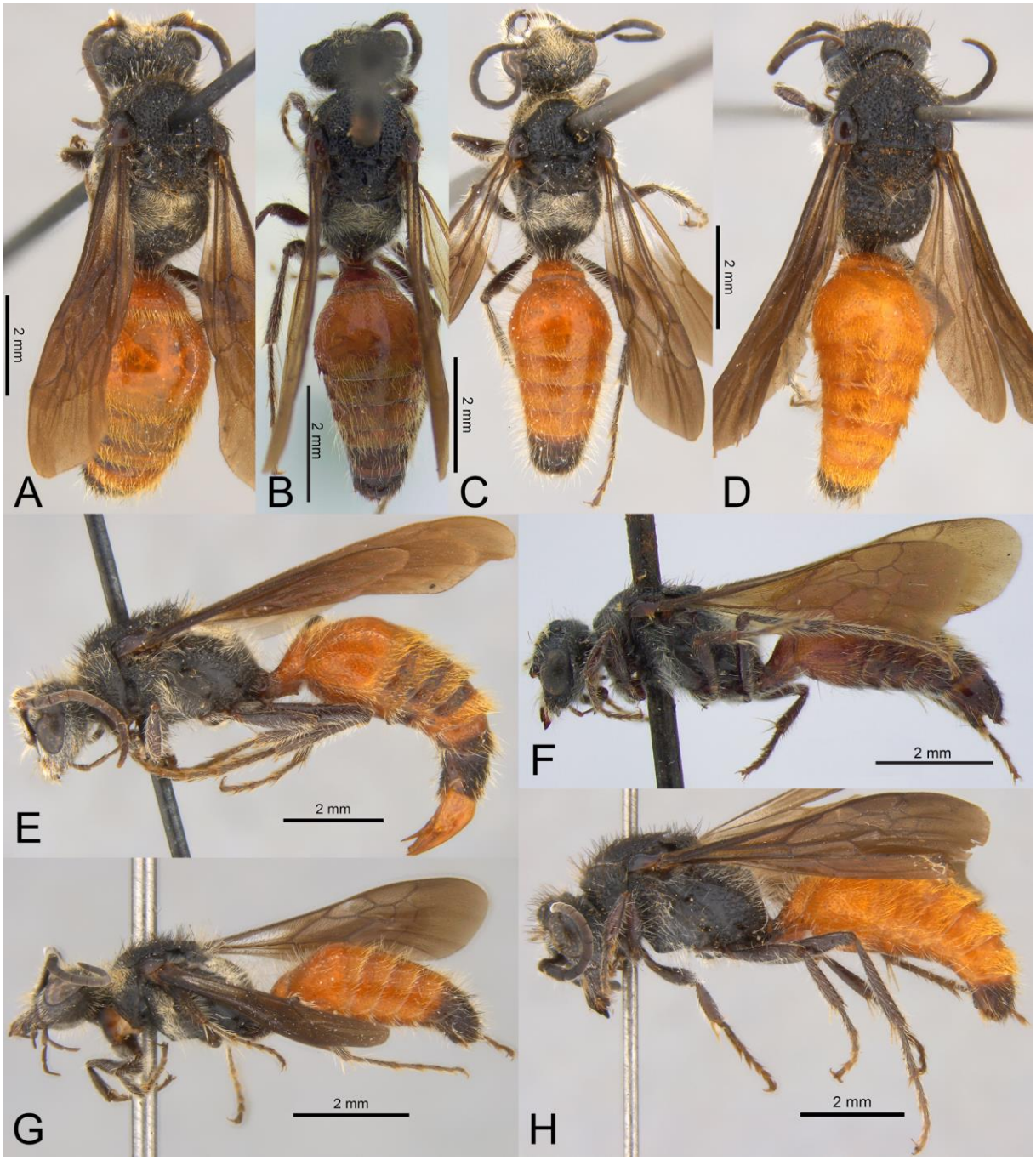

Figure 3. *Eotrogaspidia* spp., ♂, habitus. A, E. *E. hauseri* **sp. nov.**, paratype; B, F. *E. lena* (Cameron); C, G. *E. oryzae* (Pagden); D, H. *E. saussurei* (Lelej); A–D. dorsal view; E–H. lateral view.

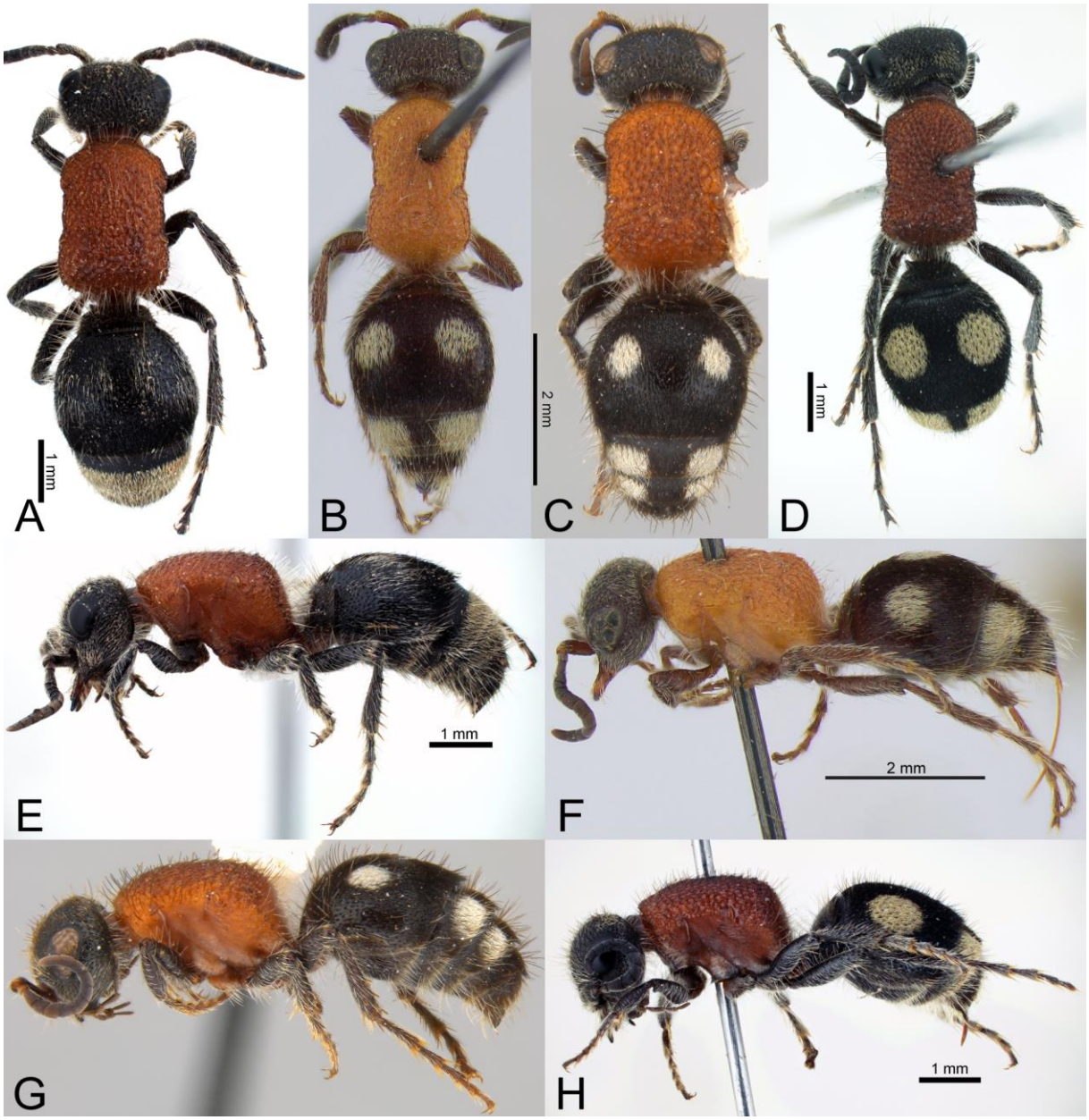

Figure 4. *Eotrogaspidia* spp., ♀, habitus. A, E. *E. oryzae* (Pagden); B, F. *E. rubripes* (André); C, G. *E. saussurei* (Lelej); D, H. *Trogaspidia vallicola* Tsuneki, holotype; A–D. dorsal view; E–H. lateral view.

Figure 5. *Eotrogaspidia* spp., ♂, face view. A. *E. adhabar* **sp. nov.**, holotype; B. *E. amans* (André); C. *E. auroguttata* (Smith); D. *E. buddha* **sp. nov.**, paratype.

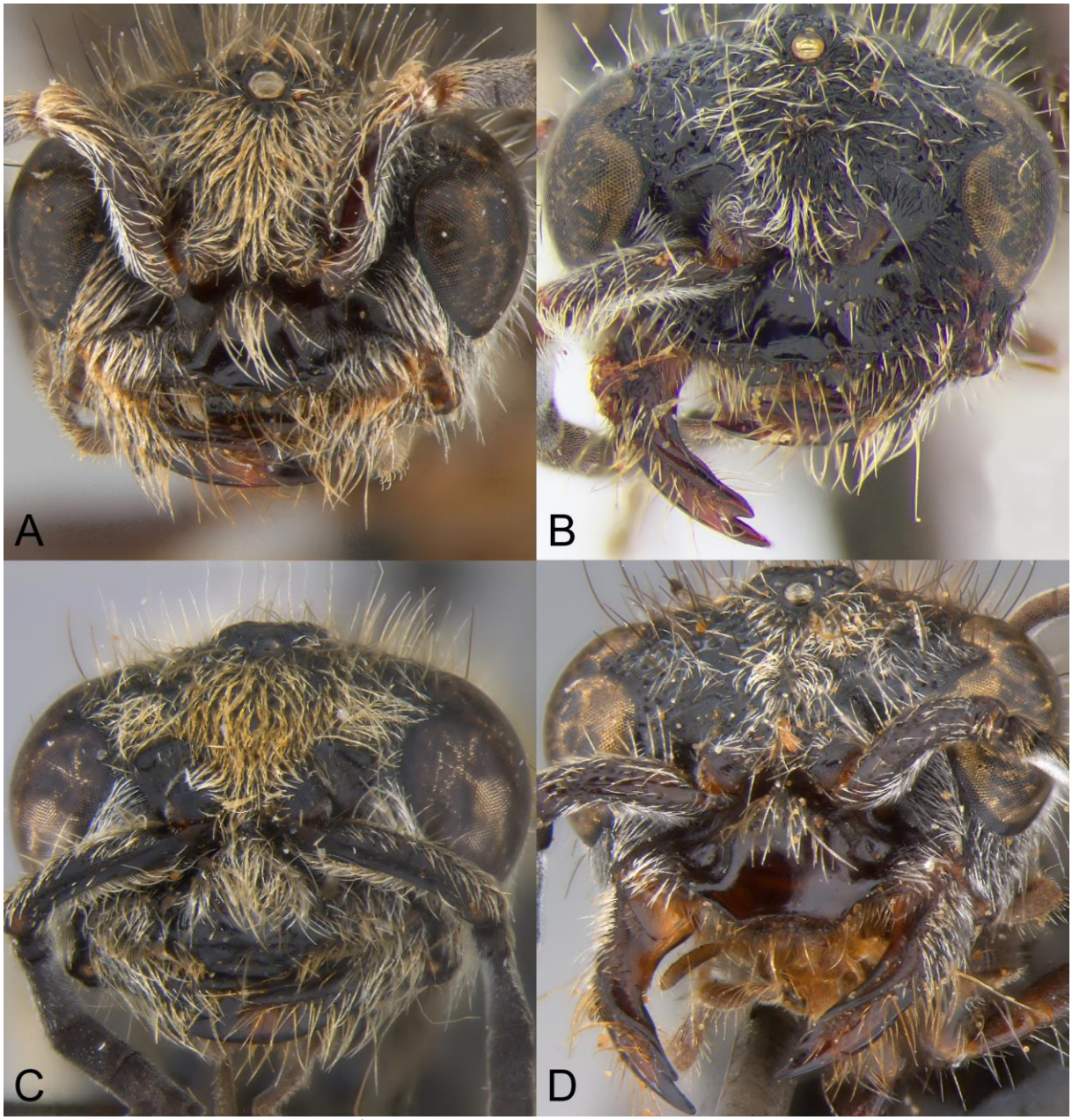

Figure 6. *Eotrogaspidia* spp., ♂, face view. A. *E. hauseri* **sp. nov.**, paratype; B. *E. lena* (Cameron); C. *E. oryzae* (Pagden); D. *E. saussurei* (Lelej).

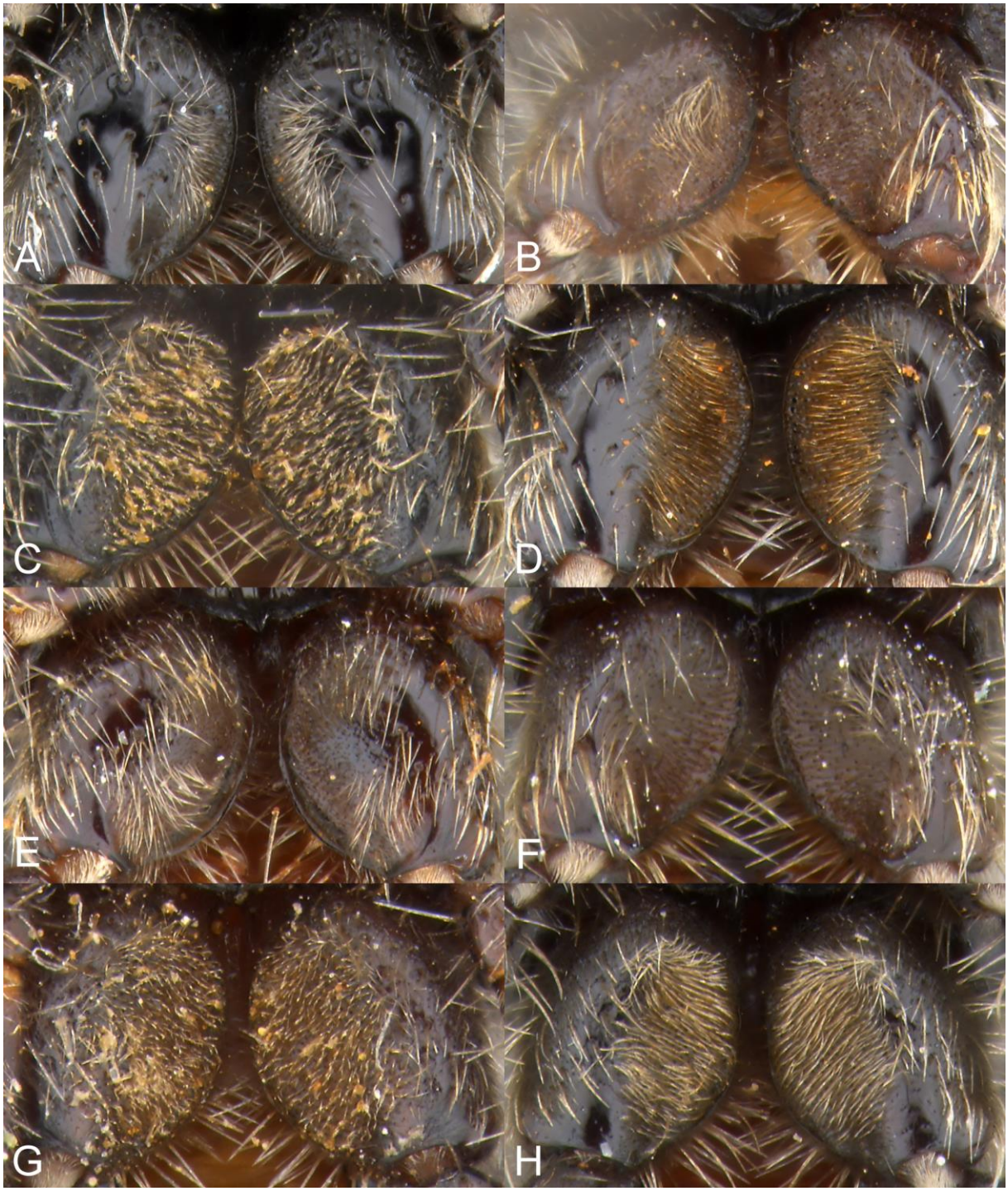

Figure 7. *Eotrogaspidia* and *Trogaspidia* spp., ♂, metacoxa. A. *E. adhabar* **sp. nov.**, paratype; B. *E. amans* (André); C. *E. auroguttata* (Smith); D. *E. buddha* **sp. nov.**, paratype; E. *E. hauseri* **sp. nov.**, paratype; F. *E. oryzae* (Pagden); G. *E. saussurei* (Lelej); H. *T. mackieae* (Cockerell).

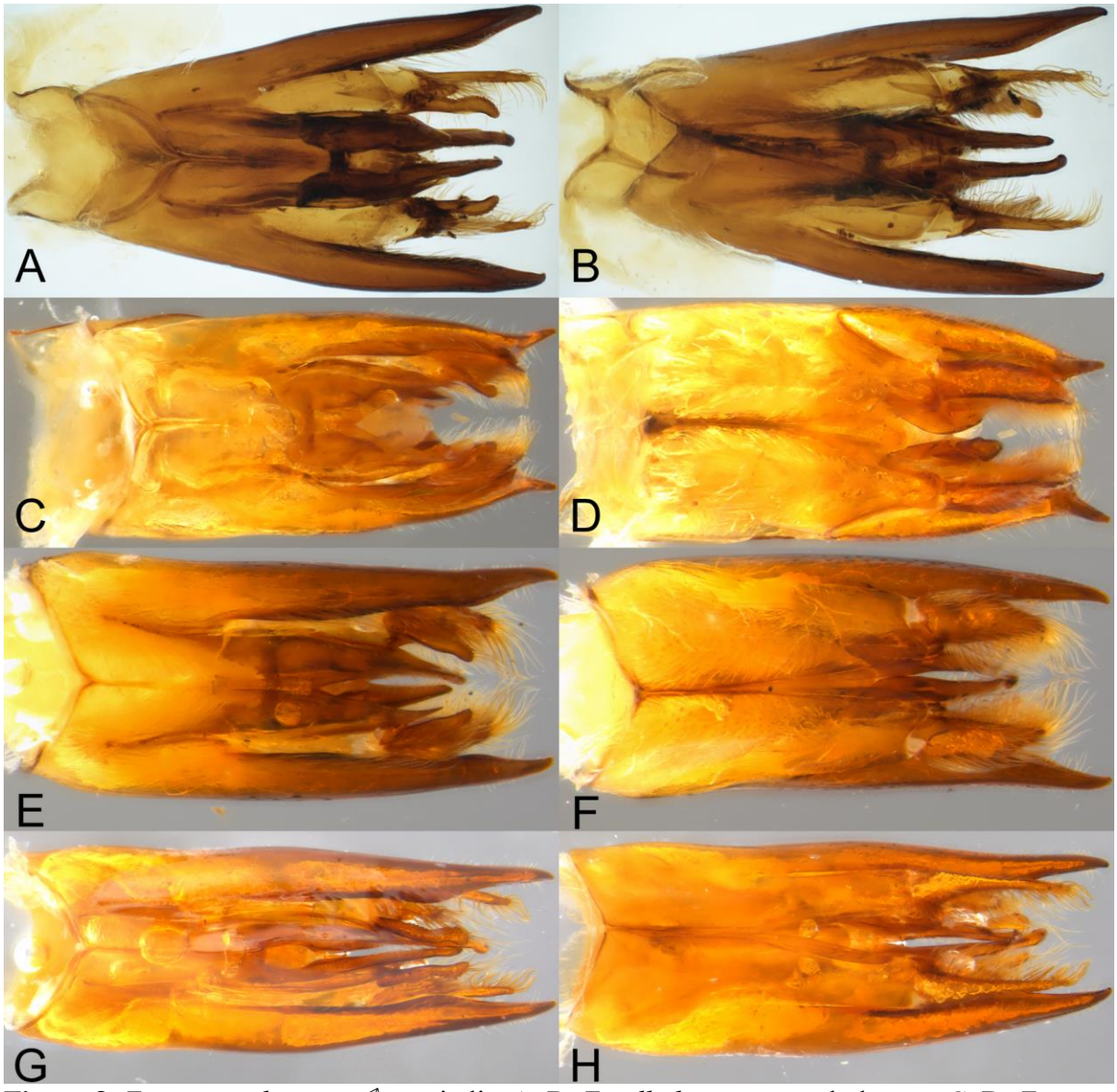

Figure 8. *Eotrogaspidia* spp., ♂, genitalia. A–B. *E. adhabar* **sp. nov.**, holotype; C–D. *E. amans* (André); E–F. *E. auroguttata* (Smith); G–H. *E. buddha* **sp. nov.**, paratype; A, C, E, G. dorsal view; B, D, F, H. ventral view.

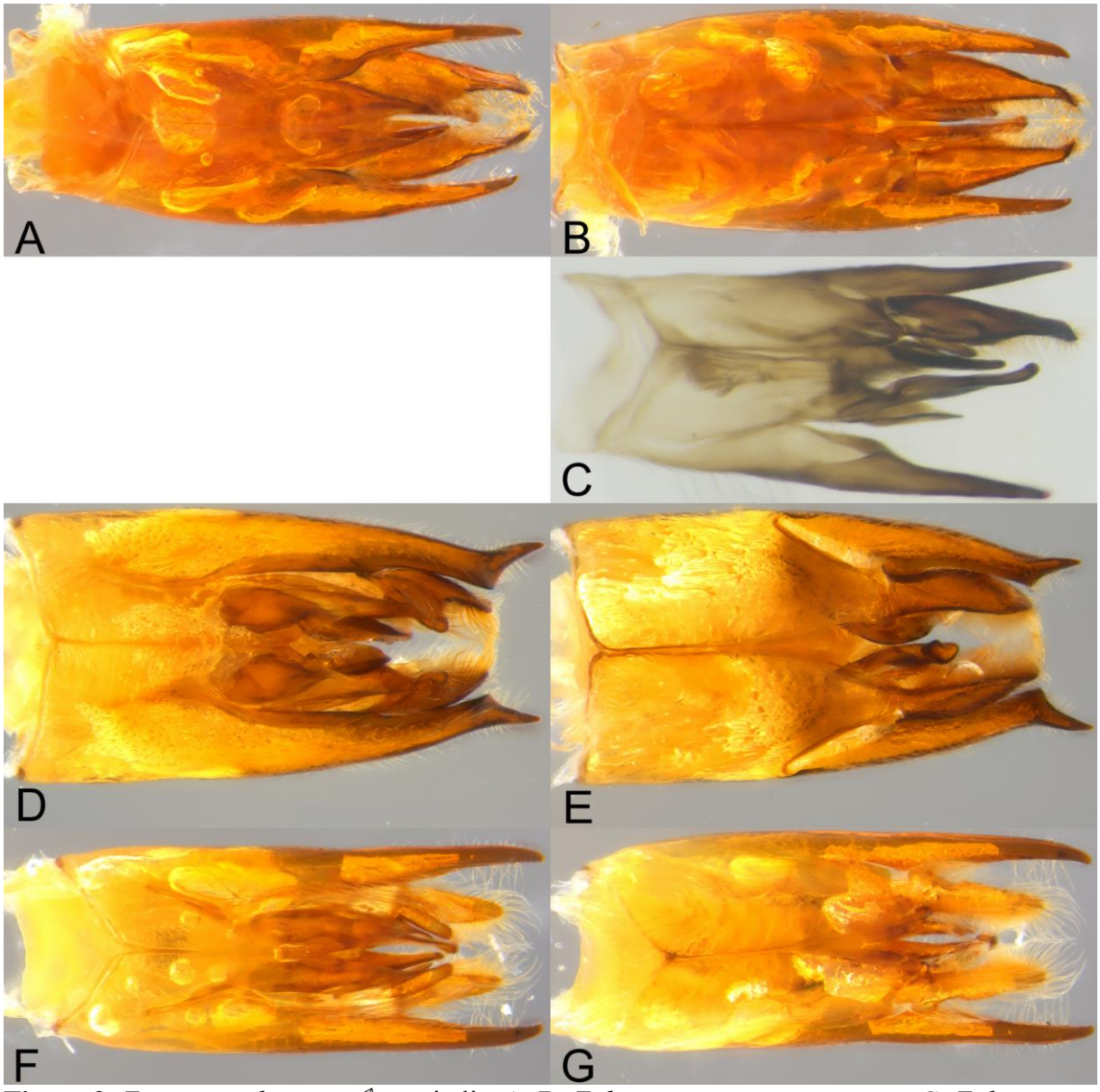

Figure 9. *Eotrogaspidia* spp., ♂, genitalia. A–B. *E. hauseri* **sp. nov.**, paratype; C. *E. lena* (Cameron); D–E. *E. oryzae* (Pagden); F–G. *E. saussurei* (Lelej); A, D, F. dorsal view; B–C, E, G. ventral view.

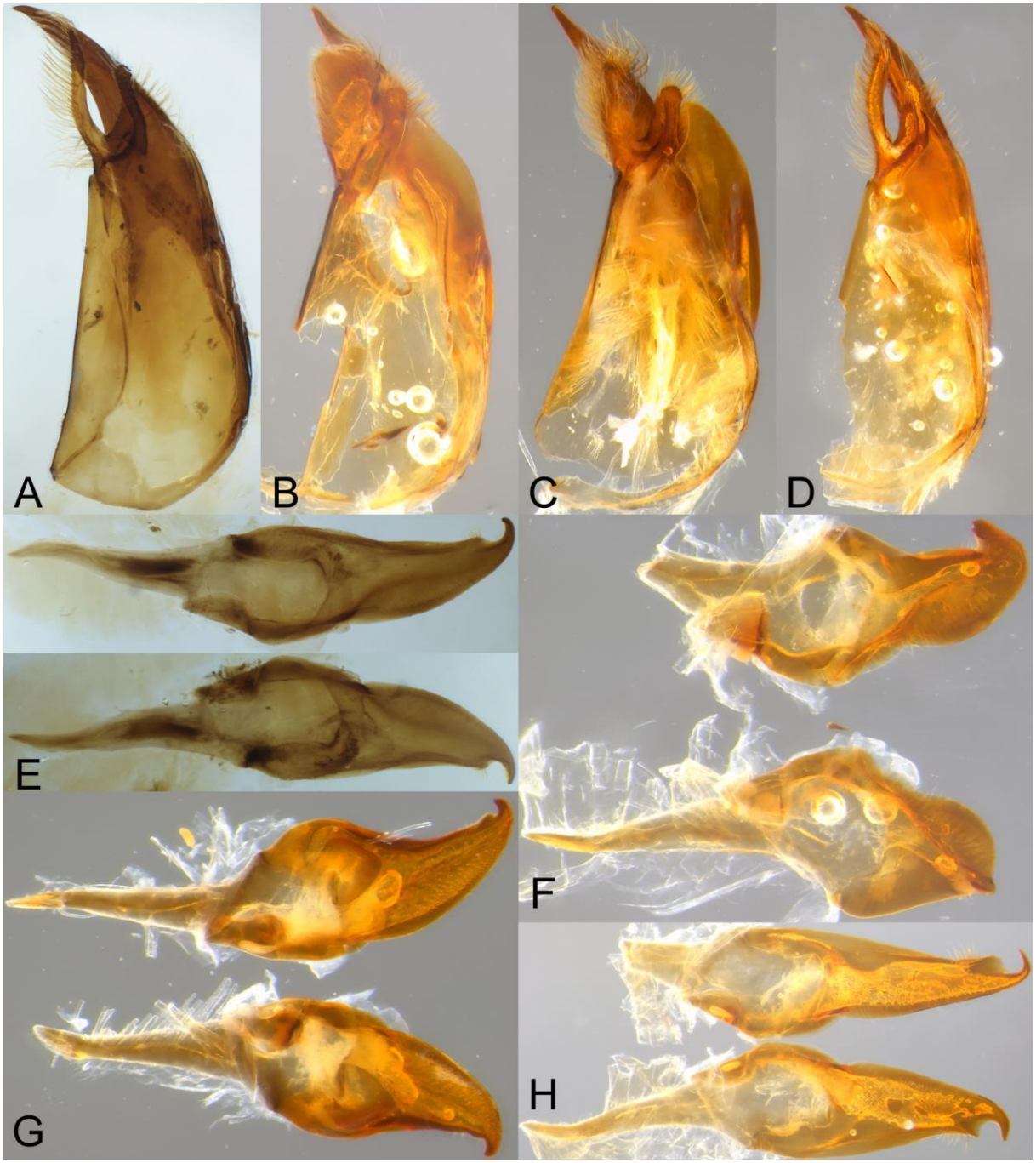

Figure 10. *Eotrogaspidia* spp., ♂, genitalia. A, E. *E. adhabar* **sp. nov.**, holotype; B, F. *E. amans* (André); C, G. *E. auroguttata* (Smith); D, H. *E. buddha* **sp. nov.**, paratype; A–D. paramere, basiparamere and volsella, inner view; E–H. right (above) and left (below) penis valves.

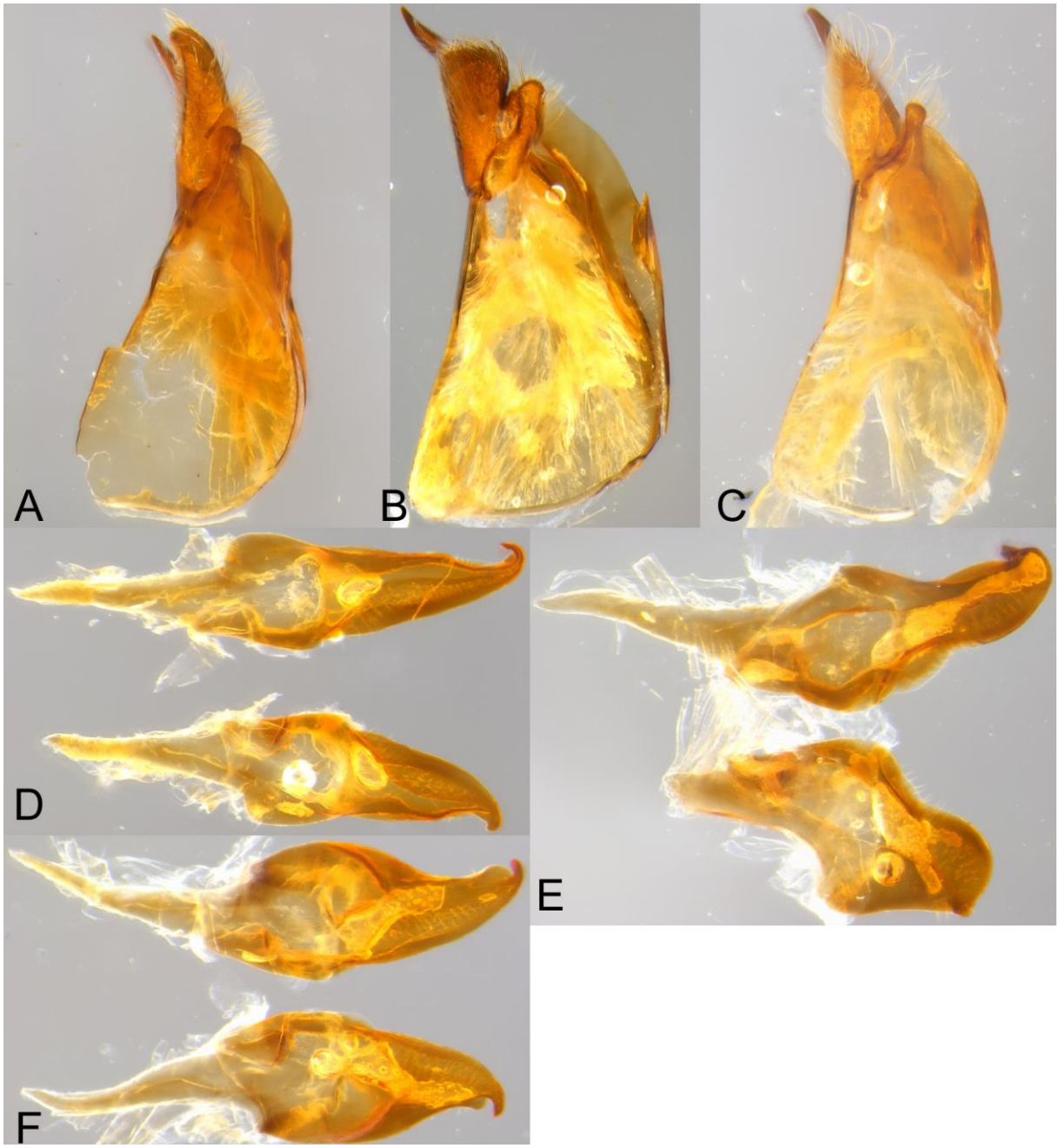

Figure 11. *Eotrogaspidia* spp., ♂, genitalia. A, D. *E. hauseri* **sp. nov.**, paratype; B, E. *E. oryzae* (Pagden); C, F. *E. saussurei* (Lelej); A–C. paramere, basiparamere and volsella, inner view; D–F. right (above) and left (below) penis valves.

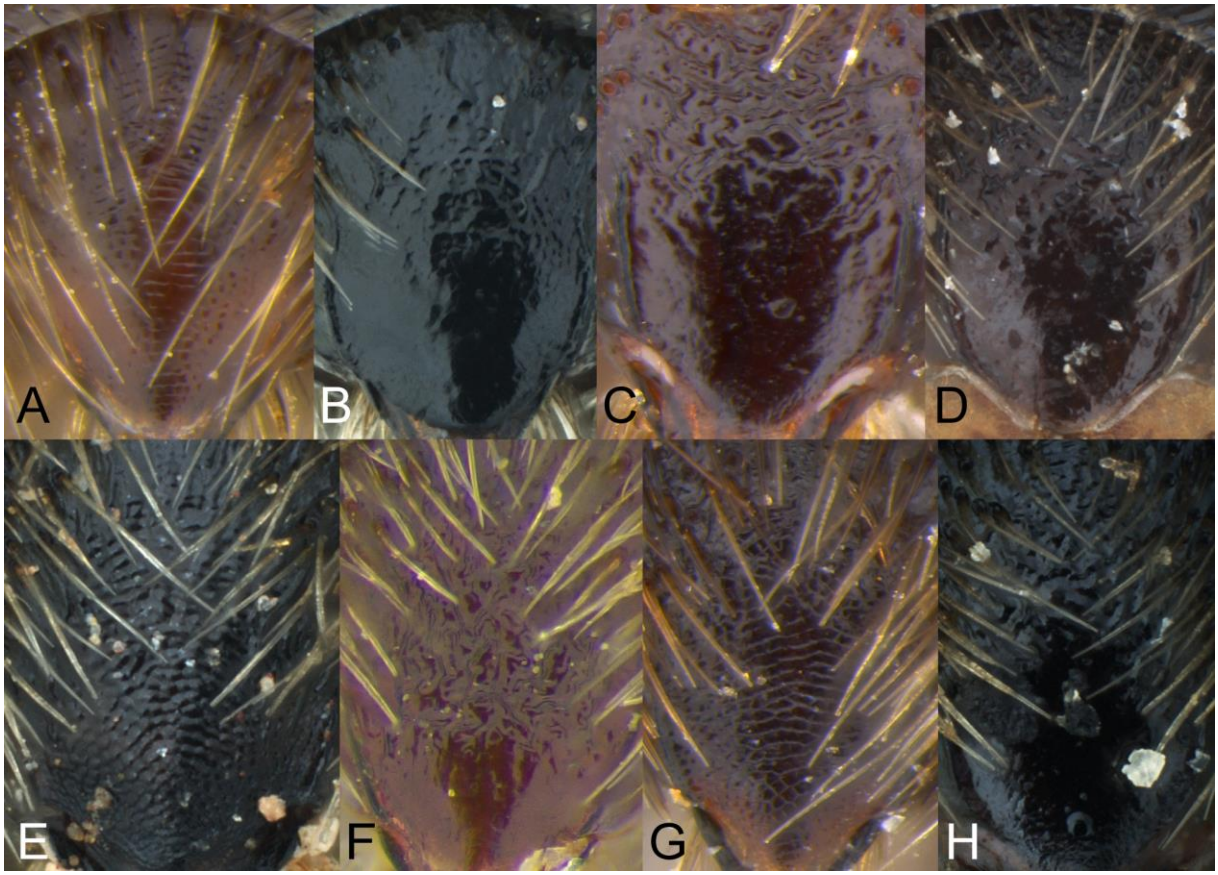

Figure 12. *Eotrogaspidia* spp., ♀, pygidial plate. A. *E. amans* (André); B. *E. auroguttata* (Smith); C. *E. buddha* **sp. nov.**, paratype; D. *E. melanopleura* **sp. nov.**, holotype; E. *E. oryzae* (Pagden); F. *E. rubripes* (André); G. *E. saussurei* (Lelej); H. *Trogaspidia vallicola* Tsuneki, holotype.

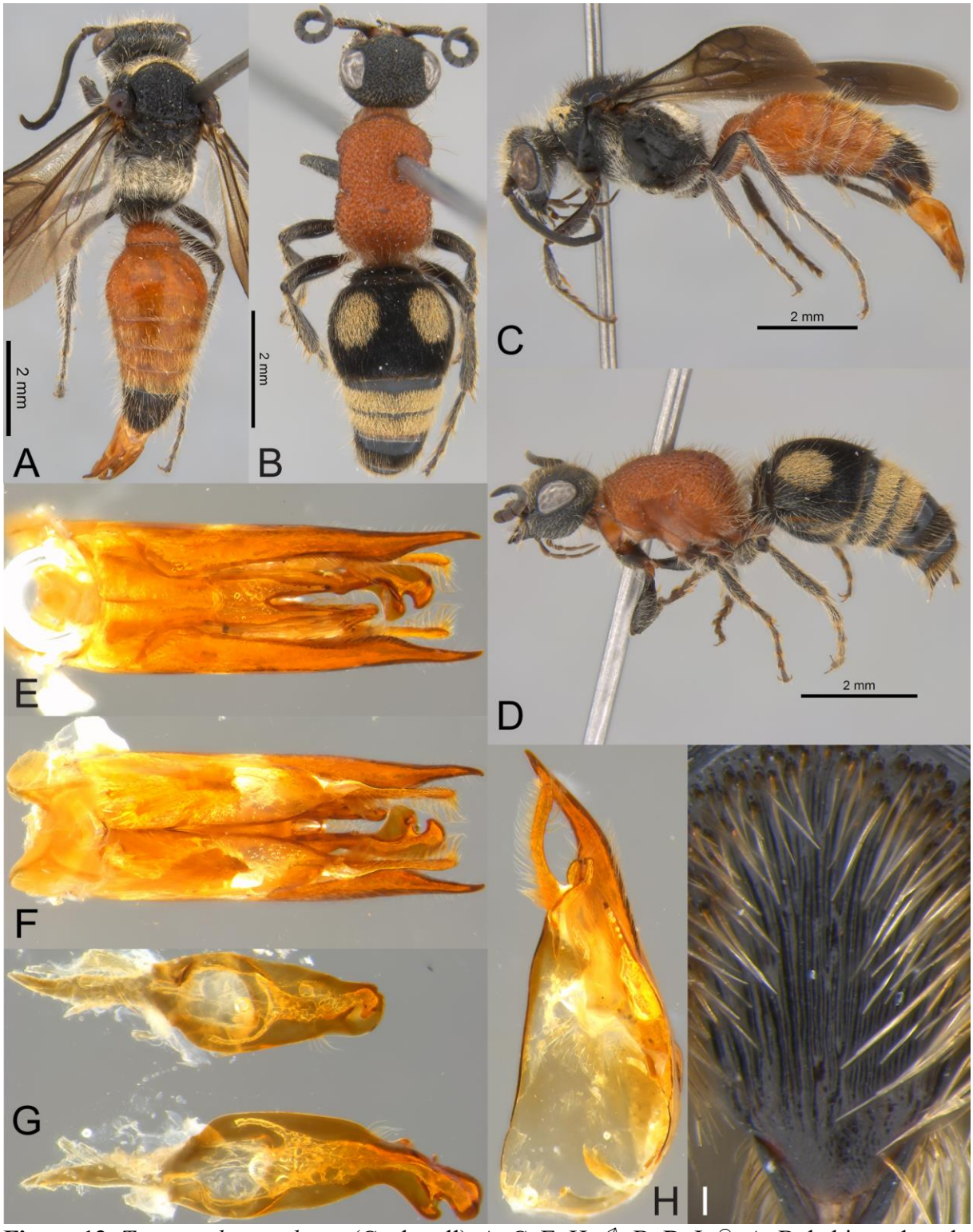

Figure 13. *Trogaspidia mackieae* (Cockerell). A, C, E–H. ♂; B, D, I. ♀; A–B. habitus, dorsal view; C–D. habitus, lateral view; E. genitalia, dorsal view; F. genitalia, ventral view; G. left (above) and right (below) penis valves; H. paramere, basiparamere and volsella, inner view; I. pygidial plate.

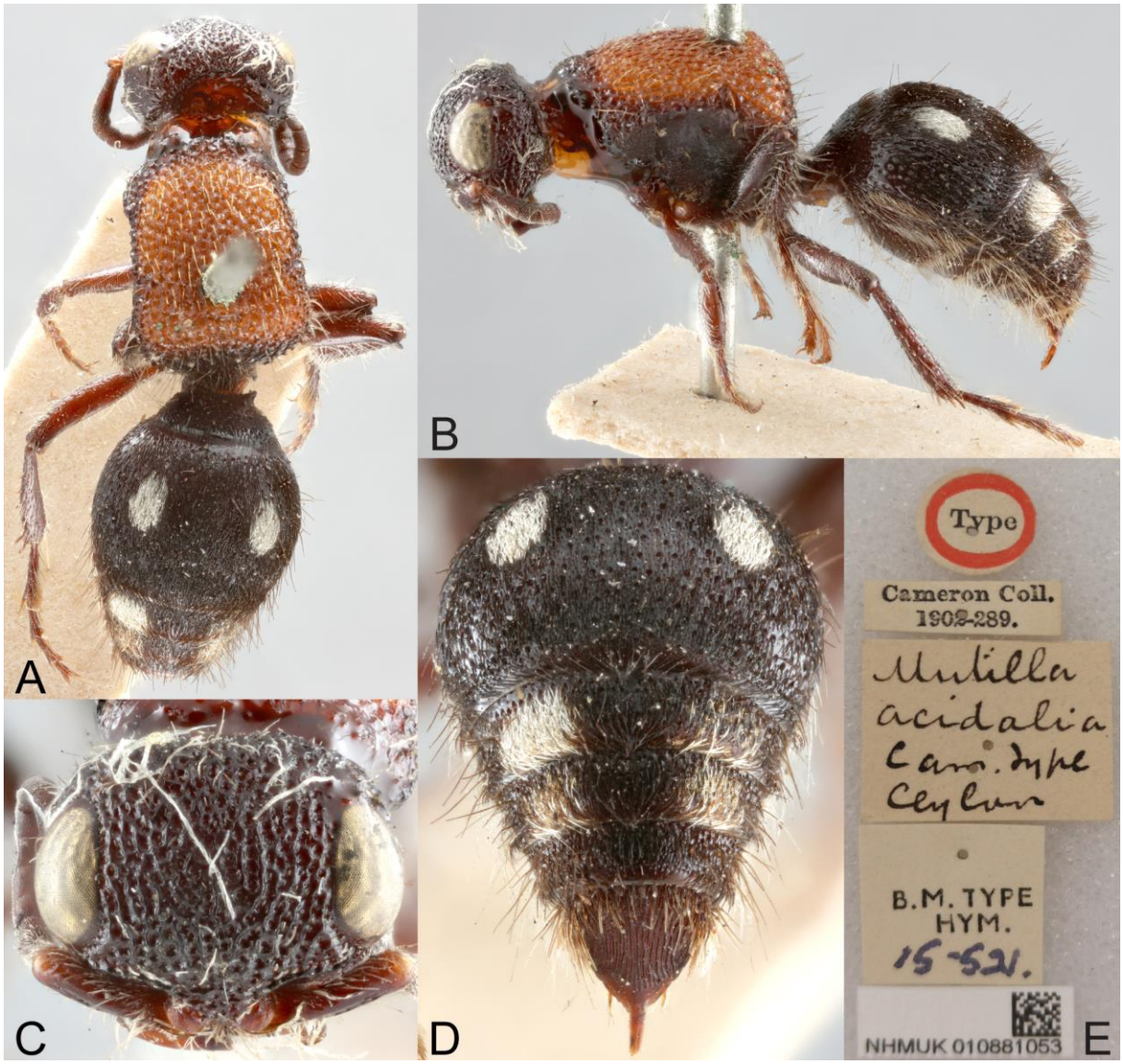

Figure 14. *Trogaspidia acidalia* (Cameron), ♀, lectotype. A. habitus, dorsal view; B. habitus, lateral view; C. head, dorsal view; D. metasoma, posterior view; E. labels. (Photos by G. Broad).

Figure 15. Sugar cane field in Iriomote-jima Island, Japan, where one female of *E. auroguttata* (Smith) was collected.

Chapter 3

A new velvet ant genus *Arkaditilla* (Hymenoptera, Mutillidae, Trogaspidiini) from the Oriental Region, with review of species

Disclaimer: *This chapter has already been published as a peer-reviewed paper as follows: Okayasu, J. (2021) Journal of Hymenoptera Research 84: 145–168 (https://doi.org/10.3897/jhr.84.68709). New nomenclatural acts appearing in this chapter have already been made in this publication and, thus, this dissertation chapter is not considered a published work within the meaning of the International Code of Zoological Nomenclature 4th edition (Article 8.2).*

Abstract
A new Old World genus in the tribe Trogaspidiini Bischoff, 1920, *Arkaditilla* **gen. nov.**, is described based on male morphology. Six species are recognized in this genus: *A. bagrada* (Cameron, 1902), **comb. nov.** (Indonesia, Malaysia), *A. depressicornis* (Mickel, 1935), **comb. nov.** (Malaysia), *A. frim* **sp. nov.** (Malaysia), *A. gibba* **sp. nov.** (Indonesia), *A. leleji* **sp. nov.** (Indonesia), and *A. nallinia* (Zavattari, 1914), **comb. nov.** (Indonesia). The species of this new genus were formerly placed in the genus *Krombeinidia* Lelej, 1996, but they are differentiated from it and other genera by having a unique set of morphological character states, such as the mandible inner margin expanded, forming subbasal tooth; the paramere antero-ventrally serrate; and the digitus dorsal margin lamellate. A key to species of *Arkaditilla* is provided.

Key words
Aculeata, distribution, new species, Southeast Asia, taxonomy.

Introduction

The tribe Trogaspidiini Bischoff, 1920 has the greatest species diversity of the four tribes of the subfamily Mutillinae (Pagliano *et al*., 2020). The eastern Oriental species of this tribe were assigned to the subgenus *Trogaspidia* Ashmead, 1899 of the New World genus *Timulla* Ashmead, 1899 by Mickel (1933a, b, 1934, 1935), but Invrea (1954) resurrected *Trogaspidia* to full genus status. Chen (1957) transferred some species of *Trogaspidia* sensu Mickel to *Smicromyrme* Thomson, 1870. Lelej (1995, 1996a) and Lelej & Yamane (1992) reclassified the *Smicromyrme-Trogaspidia* assemblage, recognized new genera for species of *Smicromyrme* sensu Chen, and arranged them in the subtribe Petersenidiina Lelej, 1996. Along with this, East Asian members of *Trogaspidia* sensu Chen were divided into five genera constituting Trogaspidiina Bischoff, 1920. Those two subtribes were included in Trogaspidiini, but later regarded as separate tribes by Lelej & Nemkov (1997). However, Brothers & Lelej (2017) found that Petersenidiini was a paraphyletic group and synonymized it with Trogaspidiini. Consequently, Trogaspidiini is now represented by 13 genera in the eastern Oriental Region (Brothers & Lelej 2017; Pagliano *et al*., 2020). The species of this tribe are sometimes difficult to place in those previously established genera, because the "petersenidiine" genera exhibit various intermediate character states between Petersenidiini and Trogaspidiini (Brothers & Lelej, 2017). Also, the species of Trogaspidiini show great interspecific morphological variations, making genus delimitation difficult (e.g., Okayasu *et al*., 2021). Revision of genus-level classification is thus required, and generic placement of described species, which are mostly known from the old literature only (Okayasu *et al*., 2021), needs to be extensively reviewed.

In this study, I present a review of the *Krombeinidia* Lelej, 1996 species with male flagellomere 1 depressed, *K. depressicornis* (Mickel, 1935) and *K. nallinia* (Zavattari, 1914), because Mickel's (1935) key suggests they are the only species with that trait in the former Petersenidiini. I also examined *K. bagrada* (Cameron, 1902), which was placed near those two species by Mickel (1935) although it has the flagellomere 1 cylindrical, and three undescribed species that are similar to *K. depressicornis* and *K. nallinia*. As discussed below, those "*Krombeinidia*" species share additional character states that are their potential synapomorphies, so the new genus *Arkaditilla* is proposed to accommodate them.

Material and methods

The following abbreviations are used to denote institutes housing the material discussed in this study.

EUM Ehime University Museum, Matsuyama, Japan.
FRIM Forest Research Institute Malaysia, Selangor, Malaysia.
NARO Insect Museum, National Agriculture and Food Research Organization, Tsukuba, Japan (former Institute for Agro-Environmental Sciences).
TKPM Tokushima Prefectural Museum, Tokushima, Japan.
TUA Laboratory of Entomology, Tokyo University of Agriculture, Atsugi, Japan.

In the synonymic lists and the material examined sections, abbreviations for depository and additional or corrected data by the author are given in square brackets. New records are asterisked (*).

Specimens were observed under a Leica S8APO stereomicroscope (10–80× magnification). Photo images were taken with a Nikon Digital Sight DS-Fi1 camera attached to a Leica S8APO, and stacked using CombineZM software (Hadley, 2008). Measurements of specimens were taken twice, in order to reduce measurement errors, and the mean value was indicated in the description. The distributional maps (Figs 73–76) were generated using SimpleMappr (Shorthouse, 2010). Figures were edited with Adobe Photoshop software and Adobe Illustrator software. Terminology mostly follows the Hymenoptera Anatomy Consortium (2021) for the general morphology, and Harris (1979) for the integument sculpture. The following abbreviations are used: F, flagellomere; LOD, lateral ocellus diameter; MOD, median ocellus diameter; OD, interocellar distance (between median and lateral ocellus); OOD, ocular-ocellar distance (between lateral ocellus and eye); POD, posterior ocellar distance (between lateral ocelli); S, metasomal sternum; T, metasomal tergum.

Prior to observation, the male genitalia were soaked in a 10% potassium hydroxide (KOH) solution without heating for one to three hours to dissolve muscles, and subsequently soaked in a 25% acetic acid solution to neutralize. Then, the genitalia were observed in a Petri dish filled with 70% ethanol under a stereomicroscope. Further dissection was done using forceps and a minuten pin attached to a handle. Dissected parts were photographed under incident light in a Petri dish filled with glycerin except that the penis valves were placed on a glass slide with a drop of glycerin and a cover glass. After examination, all dissected parts were stored in micro vials filled with glycerin and pinned with their respective specimens.

Results

Arkaditilla gen. nov.

(Figs 1–76)

Diagnosis.
MALE. Frons punctate; vertex roundly sloping posteriorly; postgenal bridge flattened; hypostomal carina simple, without denticle; clypeus dorsally elevated; prementum without tubercle. Mandible apically bidentate, ventrally excised into basal tooth (Figs 19–24); inner margin expanded, forming subbasal tooth (Figs 13–18); dorso-lateral carina sharp, not crooked. Scape ventrally with two longitudinal carinae, densely punctate or mostly smooth with sparse punctures apically between carinae (Figs 25, 27, 29, 31, 33, 35); flagellum with yellow or reddish brown ventral markings; F1 longer than F2, depressed (Figs 28, 30, 32, 34, 36) except A. bagrada with F1 cylindrical (Fig. 26). Mesosoma black; notaulus present, reaching anterior 1/3 to 1/2 of mesoscutum; parascutal carina forming weakly elevated, rounded tubercle posteriorly; tegula posterior margin slightly protruding over transscutal articulation, not recurved; mesoscutellum evenly convex, puncto-reticulate; mesopleuron divided into dorsal and ventral convexities by transverse groove; propodeum gradually sloping posteriorly, without sublateral longitudinal carina; propodeal dorso-lateral margin without denticles. Pterostigma length subequal to distance between origin of RS on vein SC and proximal base of pterostigma. Protibial spur slender; mesocoxa evenly convex; metacoxa evenly convex with long sparse recumbent setae, without tubercle on inner margin. Metasoma black with segments 1–2 or 3 orange; S2 swollen anteriorly, without lateral felt line (Figs 2, 4, 6, 8, 10, 12); T7 medially with slender longitudinal smooth convex line; S6–S8 without lateral carina; S7 entirely exposed, 0.75× as long as S8; S8 mostly sclerotized with posterior membranous area evenly convex posteriorly; left and right basiparameres ventro-medial margins connected to form postero-medial tongue-like tubercle (Figs 38, 40, 42, 46, 48); parapenial lobe spatulate, not flexed; ventral portion of basiparamere strongly projecting posteriorly to connect volsella (Figs 49, 52, 55, 58, 61, 64); paramere antero-ventrally serrate (Figs 49, 52, 55, 58, 61, 64); digitus straight, dorsal margin lamellate (Figs 67–72); paracuspis absent, tuberculate or stick-like; penis valves symmetrical, with posterior hook (Figs 50, 51, 53, 54, 56, 57, 59, 60, 62, 63, 65, 66). FEMALE. Unknown.

Type species
Arkaditilla leleji gen. et sp. nov., designated here.

Species included
This genus includes the following six species: *Arkaditilla bagrada* (Cameron, 1902), **comb. nov.**, ♂ (Indonesia, Malaysia); *A. depressicornis* (Mickel, 1935), **comb. nov.**, ♂ (Malaysia); *A. frim* **sp. nov.**, ♂ (Malaysia); *A. gibba* **sp. nov.**, ♂ (Indonesia); *A. leleji* **sp. nov.**, ♂ (Indonesia); *A. nallinia* (Zavattari, 1914), **comb. nov.**, ♂ (Indonesia).

Distribution
Widespread in Sundaland, the Oriental Region (Figs 73–76).

Etymology
I am delighted to name this new genus in honor of Arkady Stepanovich Lelej, a fellow mutillidologist, pioneer of Old World mutillid systematics, and friend, to celebrate his 75th birthday and 50th anniversary of his career since the publication of Lelej (1971), with a common suffix for mutillid genera. Gender feminine.

Biology
This genus is rare in collections; only twelve specimens of *A. bagrada*, nine specimens of *A.*

depressicornis, and seven specimens of *A*. *nallinia* have been reported by previous authors (Cameron, 1902; Lelej, 1996b; Mickel, 1935, 1937; Zavattari, 1914). In this study, however, a series of 28 specimens collected in Malaise traps placed in a lowland rain forest at Pasoh Forest Reserve was examined, suggesting greater abundance in forested habitats. See Maetô *et al*. (1999) for sampling sites.

Remarks

This new genus belongs to the former Petersenidiini Lelej, 1996 by having the penis valves symmetrical, and the species of this genus were formerly placed in *Krombeinidia* Lelej, 1996 (Lelej, 1996a) or *Petersenidia* Lelej, 1992 (Lelej, 1996b). However, the males of *Arkaditilla* differ from those of *Krombeinidia* and *Petersenidia* by having the mandible with a subbasal inner tooth (mandibular inner margin entire in *Krombeinidia* and *Petersenidia*), the basiparamere antero-ventrally serrate (entire in *Krombeinidia* and *Petersenidia*), and the digitus dorsal margin lamellate (digitus cylindrical in *Krombeinidia* and *Petersenidia*). Within Trogaspidiini, the males of this new genus and *Serendibiella* Lelej, 2005 share the mandible with subbasal inner tooth, but the former differs from the latter by having the hypostomal carina without a tubercle (present in *Serendibiella*), the mesocoxa evenly convex (laterally swollen in *Serendibiella*), S2 without a lateral felt line (present in *Serendibiella*), S8 flattened (with sublateral longitudinal carina in *Serendibiella*), and the penis valves symmetrical (right penis valve longer than left in *Serendibiella*).

Key to species of *Arkaditilla*

1. Scape ventral carinae subparallel (Fig. 25), mostly smooth between them; flagellum at most with F1 apical 1/3 and F2 basal 1/2 yellow; F1 cylindrical (Fig. 26); paracuspis stick-like (Fig. 67). Indonesia, Malaysia. … ***A. bagrada*** (Cameron)
- Scape ventral carinae divergent apically (Figs 27, 29, 31, 33, 35), densely punctate between them; flagellum at least with F1 apical 1/3 and F2 entirely whitish yellow ventrally; F1 depressed (Figs 28, 30, 32, 34, 36); paracuspis absent or slightly tuberculate (Figs 68–72) … 2
2. Mandible ventrally slightly excised with small basal tooth (Fig. 23); mandible inner margin lamellately expanded near apex (Fig. 17); F1 weakly depressed, F1 height subequal to pedicel diameter (Fig. 34); T3 black; penis valve strongly expanded ventrally on posterior half (Figs 62, 63). Indonesia. … ***A. leleji*** **sp. nov.**
- Mandible ventrally deeply excised with large basal tooth (Figs 20, 21, 23, 24); mandible inner margin expanded subbasally (Figs 14–16, 18); F1 strongly depressed, F1 height ~0.8× pedicel diameter (Figs 28, 30, 32, 36); T3 orange; penis valve weakly expanded ventrally (Figs 53, 54, 56, 57, 59, 60, 65, 66) … 3
3. Digitus posteriorly slender stick-like (Fig. 39); paracuspis absent (Fig. 68). Malaysia. … ***A. depressicornis*** (Mickel)
- Digitus posteriorly expanded, forming triangular projection (Figs 41, 43, 47); paracuspis slightly tuberculate (Figs 69–72) … 4
4. Clypeus medially strongly elevated even ventrally; cuspis widened near apex, forming oblique posterior margin (Figs 58, 70). Indonesia. … ***A. gibba*** **sp. nov.**
- Clypeus dorsally elevated, sloping ventrally; cuspis widened on posterior 1/3 with rounded apex (Figs 55, 64, 69, 72) … 5
5. Mandible with weak subapical and subbasal teeth (Fig. 15); cuspis weakly widened on posterior 1/3 (Figs 55, 69). Malaysia. … ***A. frim*** **sp. nov.**
- Mandible with sharp subapical tooth and large inner subbasal tooth (Fig. 18); cuspis strongly widened on posterior 1/3 (Figs 64, 72). Indonesia. … ***A. nallinia*** (Zavattari)

Arkaditilla bagrada (Cameron, 1902), comb. nov.

(Figs 1, 2, 13, 19, 25, 26, 37, 38, 49–51, 67, 73)

Mutilla bagrada Cameron, 1902: 76, ♂, holotype ♂ (Kuching, Sarawak, [Malaysia]) [Natural History Museum, London, UK].
Timulla (*Trogaspidia*) *bagrada*: Mickel, 1935: 263, ♂; Mickel, 1937: 449, ♂.
Krombeinidia bagrada: Lelej, 1996a: 11; 2005: 65; Lo Cascio, 2015: 550; Pagliano *et al*., 2020: 250.
Petersenidia bagrada: Lelej, 1996b: 95, ♂.

Diagnosis

MALE. Clypeus dorsally elevated, sloping ventrally. Mandible with sharp subapical and large inner subbasal teeth (Fig. 13), ventrally deeply excised with large basal tooth (Fig. 19). Scape ventral carinae subparallel, mostly smooth between them (Fig. 25); F1 apical 1/3 and F2 basal 1/2 yellow, F2 apical 1/2 and F3–F11 with ventral reddish brown patch; F1 cylindrical (Fig. 26). T3 orange (Fig. 2); cuspis strongly widened on posterior 1/3 with rounded apex (Figs 49, 67); digitus posteriorly slender stick-like (Fig. 37); paracuspis stick-like (Fig. 67); penis valve weakly expanded ventrally (Figs 50, 51). FEMALE. Unknown.

Material examined

24♂. **Malaysia:** NEGERI SEMBILAN: Pasoh Forest Reserve, 25.III–2.IV.1993, K. Konishi & K. Maeto leg., coarse Malaise trap, plot 2 [2♂ FRIM, NARO], 2–8.IV.1993 [1♂ FRIM], 8–15.IV.1993 [1♂ NARO]; Pasoh Forest Reserve, 25.III–2.IV.1993, K. Konishi & K. Maeto leg., fine Malaise trap, plot 2 [2♂ FRIM, NARO]; Pasoh Forest Reserve, 26.III–3.IV.1993, K. Konishi & K. Maeto leg., coarse Malaise trap, plot 4 [1♂ FRIM], 9–16.IV.1993 [1♂ NARO]; Pasoh Forest Reserve, 3–9.IV.1993, K. Konishi & K. Maeto leg., fine Malaise trap, plot 4 [1♂ FRIM]; Pasoh Forest Reserve, 26.XI–3.XII.1993, K. Maeto leg., coarse Malaise trap, plot 1 [2♂ FRIM, NARO]; Pasoh Forest Reserve, 26.XI–3.XII.1993, K. Maeto leg., coarse Malaise trap, plot 4 [2♂ FRIM, NARO]; Pasoh Forest Reserve, 26.XI–3.XII.1993, K. Maeto leg., fine Malaise trap, plot 1 [2♂ FRIM, NARO], 10–17.XII.1993 [1♂ FRIM]; Pasoh Forest Reserve, 26.XI–3.XII.1993, K. Maeto leg., fine Malaise trap, plot 3 [1♂ NARO], 10–17.XII.1993 [1♂ FRIM]; Pasoh Forest Reserve, 26.XI–3. XII.1993, K. Maeto leg., fine Malaise trap, plot 4 [1♂ NARO], 3–10.XII.1993 [1♂ NARO]; Pasoh Forest Reserve, 3–10.XII.1993, K. Maeto leg., coarse Malaise trap, plot 6 [1♂ NARO]; Pasoh Forest Reserve, 10–17.XII.1993, K. Maeto leg., coarse Malaise trap, plot 2 [1♂ FRIM]; Pasoh Forest Reserve, 10–17.XII.1993, K. Maeto leg., fine Malaise trap, plot 2 [2♂ FRIM, NARO].

Identification source

Keyed using Mickel (1935) and compared with the original description. No differences were found between the specimens examined herein and Cameron's description.

Distribution

Indonesia: Kalimantan Timur (Lelej, 1996b). Malaysia: Negeri Sembilan*, Sarawak (Cameron, 1902; Mickel, 1937).

Remarks

This is the only species in *Arkaditilla* with F1 cylindrical, like most species of Mutillinae. Similarly, the species of East Asian genera of the former Petersenidiini, like *Krombeinidia*, *Orientidia* Lelej, 1996, *Pagdenidia* Lelej, 1996, *Petersenidia*, *Taiwanomyrme* Tsuneki, 1993,

and *Zavatilla* Tsuneki, 1993, have the F1 cylindrical. I presume that this is a plesiomorphic state in *Arkaditilla*, and *A. bagrada* is sister to the remaining members of the genus.

Arkaditilla depressicornis (Mickel, 1935), comb. nov.

(Figs 3, 4, 14, 20, 27, 28, 39, 40, 52–54, 68, 74)

Timulla (*Trogaspidia*) *depressicornis* Mickel, 1935: 264, ♂, holotype ♂ (Sandakan, [Sabah], Borneo, [Malaysia]) [National Museum of Natural History, Washington D.C., USA]; Mickel, 1937: 449, ♂.
Krombeinidia depressicornis: Lelej, 1996a: 11; Lelej, 2005: 66; Lo Cascio, 2015: 550; Pagliano *et al*., 2020: 251.
Petersenidia depressicornis: Lelej, 1996b: 94, ♂.

Diagnosis
MALE. Clypeus dorsally elevated, sloping ventrally. Mandible with sharp subapical and large inner subbasal teeth (Fig. 14), ventrally deeply excised with large basal tooth (Fig. 20). Scape ventral carinae divergent apically (Fig. 27), densely punctate between them; F1 apical 1/3, F2–F3, F2–F4, or F2–F5 whitish yellow on ventral half, F5 or F5–F6 with ventral whitish yellow patch, F6–F11 or F7–F11 with ventral dark brown patch; F1 strongly depressed, F1 height ~0.8× pedicel diameter (Fig. 28). T3 orange (Fig. 4); cuspis weakly widened on posterior 1/3 with rounded apex (Figs 52, 68); digitus posteriorly slender stick-like (Fig. 39); paracuspis absent (Fig. 68); penis valve weakly expanded ventrally (Figs 53, 54). FEMALE. Unknown.

Material examined.
3♂. **Malaysia:** NEGERI SEMBILAN: Pasoh Forest Reserve, 31.III.1993, K. Konishi leg. [1♂ NARO]; Pasoh Forest Reserve, 26.XI–3.XII.1993, K. Maeto leg., fine Malaise trap, plot 6 [1♂ FRIM]; PAHANG: Cameron Highland, 19 mile, 15.III.2006, K. Takasuka leg. [1♂ EUM].

Identification source
Keyed using Mickel (1935) and compared with the original description. Mickel (1935) described this species as having the F1 apical 1/2 and F2–F4 ventrally “pale ferruginous”, but the specimens examined herein have the F2–F3, F2–F4, or F2–F5 entirely whitish yellow ventrally.

Distribution
Malaysia: Negeri Sembilan*, Pahang*, Sabah, Sarawak (Mickel, 1935, 1937; Lelej, 1996b).

Remarks
This species was originally described from Borneo (Mickel, 1935) and is newly recorded from Peninsular Malaysia. In this study, this species was primarily recognized by having the F2–F4 ventrally entirely yellow as included in Mickel’s (1935) key.

Arkaditilla frim sp. nov.

(Figs 5, 6, 15, 21, 29, 30, 41, 42, 55–57, 69, 75)

Diagnosis
MALE. Clypeus dorsally elevated, sloping ventrally. Mandible with weak subapical and subbasal teeth (Fig. 15), ventrally deeply excised with large basal tooth (Fig. 21). Scape

ventral carinae divergent apically (Fig. 29), densely punctate between them; F1 apical 1/3, F2, F3 basal half whitish yellow on ventral half, F5–F11 with ventral yellow to reddish brown patch; F1 strongly depressed, F1 height ~0.8× pedicel diameter (Fig. 30). T3 orange (Fig. 6); cuspis weakly widened on posterior 1/3 with rounded apex (Figs 55, 69); digitus posteriorly expanded, forming triangular projection (Fig. 41); paracuspis slightly tuberculate (Fig. 69); penis valve weakly expanded ventrally (Figs 56, 57). FEMALE. Unknown.

Description

MALE. Body length: 11.2–15.0 mm (holotype: 15.0 mm; mean: 13.1 mm); forewing length: 8.09–10.7 mm (holotype: 10.7 mm; mean: 9.37 mm).

Color and setae. Frons, vertex, gena, clypeus, pedicel, flagellum mostly, prementum, stipes, mesosoma, T4–T7, S4–S8 black; mandible brown to black, with apex always black and medial 1/5–1/2 yellowish brown; labrum, protibial spur yellow; scape, tegula brownish black; F1 apical 1/3, F2, F3 basal half whitish yellow on ventral half; F5–F11 yellow to reddish brown ventrally; trochanters brown to dark brown; coxae, femora, tibiae, tarsi dark brown to brownish black; meso- and metatibial spurs pale yellow; T1–T3, S1–S3 orange; wings pale brown on proximal 1/3, brown on distal 2/3, with veins dark brown. Upper frons, vertex, trochanters, T1, S1 with sparse long erect pale golden setae; lower frons, dorsal propodeal face, dorsal half of lateral propodeal face with dense short appressed and sparse long erect pale golden setae; eye dorsal margin with long erect black setae; gena, pronotal dorsum, metascutellum with sparse short recumbent and sparse long erect pale golden setae; clypeus with dense long recumbent pale golden setae; mandible, tibiae, tarsi, T2–T5 with sparse long recumbent pale golden setae; scape, femora, S2 with sparse long recumbent and sparse long erect pale golden setae; pedicel, F1, tegula anterior portion with sparse short recumbent pale golden setae; F2–F11 with sparse erect pale golden microsetae; pronotal collar anteriorly, T2 disc, T3–T5 medially, S3–S6 with sparse short erect pale golden setae; pronotal collar posteriorly glabrous; pronotal lateral face meso- and metacoxae with sparse long appressed pale golden setae; propleuron with sparse long appressed and sparse long erect pale golden setae; mesoscutum with sparse short recumbent black and sparse short erect pale golden to black setae; tegula inner margin with sparse short recumbent pale golden and sparse short erect pale golden to black setae; mesoscutellum with sparse short recumbent pale golden, sparse long erect black, sparse long erect pale golden setae; anterior and posterior parts of mesopleuron, metapleuron, ventral half of lateral propodeal face with sparse short appressed pale golden setae; axilla, metanotal trough, medial and ventral parts of mesopleuron, procoxa with dense long appressed and sparse long erect pale golden setae; T6–T7, S7–S8 with sparse long recumbent and sparse long erect black setae; T2 with lateral golden felt line; T1–T5, S2–S5 with posterior fringe of sparse pale golden setae; S6–S8 with posterior fringe of sparse black setae.

Structure. Head 1.82–2.00× as wide as long (holotype: 2.00); lateral margins strongly convergent behind eye; vertex rounded posteriorly; POD/OOD = 0.56–0.58 (holotype: 0.56); OD:MOD:LOD = 1.00:1.08–1.12:0.94–1.00 (holotype: 1.00:1.12:0.94); ocellar region slightly convex, ocelli without posterior carina; antennal scrobe with weak inverted V-shaped dorsal carina not reaching inner eye margin; genal carina absent; postgenal bridge flattened; hypostomal carina weakly developed; clypeus dorsally elevated, sloping ventrally, with subventral transverse groove laterally not defined by carina; anterior clypeal margin projecting medially; mandible robust, narrowed to apex with inner margin expanded forming small subbasal tooth; mandible apex bidentate; mandible ventral margin excised into large basal tooth; mandible dorsal carina sharp; prementum flattened; scape curved medially, with two longitudinal ventral carinae divergent apically; F1 depressed, F1 height 0.67–0.80× pedicel diameter (holotype: 0.67); relative length of pedicel, F1 and F2 = 1.00:2.85–

3.06:1.92–2.29 (holotype: 1.00:3.06:2.29); F2–F11 almost equal in width; F11 as long as F2, conical.

Mesosoma widest at mesonotum including tegulae; head width:humeral width:pronotal width:mesonotal width = 88:62:91:100; humeral angle rounded, with sharp humeral carina on ventral half; mesoscutum strongly convex; mesoscutal width 1.12× its length; tegula short rounded, posteriorly reaching mesoscuto-scutellar articulation, 1.44–1.53× as long as wide (holotype: 1.53); notaulus evenly wide, reaching anterior 1/2 of mesoscutum, subparallel; parapsidal line length 0.25× mesoscutal length; parascutal carina forming rounded, weakly elevated process on postero-lateral angle of mesoscutum; mesoscutellum convex without medial carina, tubercle or impunctate line; mesopleuron divided into dorsal and ventral convexities by distinct transverse mesopleural groove, ventrally without transverse precoxal ridge, longitudinal impunctate line, or precoxal swelling; dorsal propodeal face without distinct dorsum and sublateral carina, with anterior inverted triangular cell and semicircular sublateral cell; lateral margins of propodeum gradually convergent posteriorly; dorsal and lateral propodeal faces not separated by carina.

Wings well developed; distance between origin of RS on vein SC and base of stigmatic cell equal to stigmatic cell length and first abscissa of RS length; cell 2RS present.

Meso- and metacoxae evenly convex; metacoxa with weak complete inner longitudinal carina; protibial spur slender; tibiae without outer spines.

T1 without distinct dorsum; T1 spiracle weakly tuberculate; T2 evenly convex, 1.28× as wide as long; S1 with straight medial longitudinal carina with its ventral margin slightly elevated posteriorly; S2 swollen anteriorly; T7 medially with longitudinal impunctate convex line, posteriorly not forming tubercle; S6–S8 without lateral carina or tubercle; S7 entirely exposed, 0.75× as long as S8; S8 mostly sclerotized with posterior membranous area evenly convex posteriorly. Paramere down-curved posteriorly, with weak inner protuberance on posterior 1/2 of dorso-inner margin; inner margin of paramere dorsally with short erect golden setae; ventral lobe posteriorly projecting, pointed; parapenial lobe large, with posterior margin slightly concave; cuspis long slender, weakly widened on posterior 1/3 with rounded apex, slightly surpassing apex of penis valve, with dense long erect setae ventrally and posteriorly; digitus straight, posteriorly expanded, forming triangular projection, with dense erect golden setae posteriorly; paracuspis slightly tuberculate with few erect golden setae; penis valves symmetrical slender, weakly expanded ventrally, with posterior ventral hook, without setae.

Frons, vertex, gena, pronotal dorsum, mesoscutum, medial part of mesopleuron with large dense punctures; postgenal bridge, clypeus lateral portion, mandible outer face, scape between ventral carinae, flagellum, pronotal lateral face, propleuron, axilla, metanotal trough, anterior and posterior parts of mesopleuron, metapleuron, ventral half of lateral propodeal face, procoxa, tarsi with minute dense punctures; clypeus medial convexity with large sparse punctures; mandible mostly, pronotal collar posteriorly smooth; scape mostly, trochanters, femora, tibiae, T1 medially, T2 disc, T3–T6, S1–S2 with small sparse punctures; pedicel, pronotal collar anteriorly, meso- and metacoxa with minute sparse punctures; mesoscutellum with large confluent punctures; metascutellum with small confluent punctures; dorsal propodeal face, dorsal half of lateral propodeal face reticulate; T1–T2 laterally, T7, S3–S8 with small dense punctures; tegula mostly microreticulate with few small punctures anteriorly, postero-inner portion with minute sparse punctures.

FEMALE. Unknown.

Type material

2♂. Holotype ♂: **Malaysia:** NEGERI SEMBILAN: Pasoh Forest Reserve, 3–10.XII.1993, K. Maeto leg., coarse Malaise trap, plot 6 [FRIM]. Paratype: **Malaysia:** NEGERI SEMBILAN:

Pasoh Forest Reserve, 25.III–2.IV.1993, K. Konishi & K. Maeto leg., fine Malaise trap, plot 2 [1♂ NARO].

Distribution
Malaysia: Negeri Sembilan.

Etymology
This new species is named after FRIM, Forest Research Institute Malaysia, which was the Malaysian counterpart of the Japan-Malaysia joint research project in 1993 funded by the Ministry of the Environment of Japan. Treat as a noun in apposition.

Remarks
This species occurs sympatrically with *A. depressicornis*, but this new species differs from it by having the mandible with weakly developed subbasal and subapical teeth (subbasal and subapical teeth large in *A. depressicornis*), the digitus posteriorly expanded (digitus slender in *A. depressicornis*), and the paracuspis tuberculate (paracuspis absent in *A. depressicornis*).

***Arkaditilla gibba* sp. nov.**
(Figs 7, 8, 16, 22, 31, 32, 43, 44, 58–60, 70, 75)

Diagnosis
MALE. Clypeus medially strongly elevated even ventrally. Mandible with sharp subapical and large inner subbasal teeth (Fig. 16), ventrally deeply excised with large basal tooth (Fig. 22). Scape ventral carinae divergent apically (Fig. 31), densely punctate between them; F1 apical 1/3 and F2 whitish yellow on ventral half; F1 strongly depressed, F1 height ~0.8× pedicel diameter (Fig. 32). T3 orange (Fig. 8); cuspis widened near apex, forming oblique posterior margin (Figs 58, 70); digitus posteriorly expanded, forming triangular projection (Fig. 43); paracuspis slightly tuberculate (Fig. 70); penis valve weakly expanded ventrally (Figs 59, 60). FEMALE. Unknown.

Description
MALE. Body length: 12.4–15.1 mm (holotype: 12.4 mm; mean: 13.8 mm); forewing length: 10.6–11.0 mm (holotype: 10.6 mm; mean: 10.8 mm).

Color and setae. Frons, vertex, gena, clypeus, mandible mostly, scape, pedicel, flagellum mostly, prementum, stipes, mesosoma, coxae, femora, tibiae, tarsi, T4–T7, S1 medial carina, S4–S8 black; mandible medial 1/4 reddish brown; F1 apical 1/3, F2 whitish yellow on ventral half; labrum, tegula brownish black; trochanters, protibial spur dark brown; meso- and metatibial spurs pale yellow; T1–T3, S1 except medial carina, S2–S3 orange; wings pale brown, with veins dark brown. Upper frons, vertex, T1, S1 with sparse long erect pale golden setae; lower frons, pronotal dorsum, dorsal propodeal face, dorsal half of lateral propodeal face with dense short appressed and sparse long erect pale golden setae; gena, femora, tibiae with sparse short recumbent and sparse long erect pale golden setae; eye dorsal margin with long erect black setae; clypeus with dense long recumbent pale golden setae; mandible, trochanters, T2 lateral margin with sparse long recumbent pale golden setae; scape with sparse long recumbent and sparse long erect pale golden setae; pedicel, F1 with sparse short recumbent pale golden setae; F2–F11 with sparse erect pale golden microsetae; pronotal collar anteriorly, T2 disc, T3–T5, S3–S6 with sparse short erect pale golden setae; pronotal collar posteriorly glabrous; pronotal lateral face, coxae with sparse long appressed pale golden setae; propleuron with sparse long appressed and sparse long erect pale golden setae; mesoscutum with sparse short recumbent and sparse short erect goldish black setae;

mesoscutellum, metascutellum with sparse short recumbent pale golden and sparse long erect pale golden to blackish golden setae; axilla, metanotal trough with dense long appressed pale golden setae; anterior and posterior parts of mesopleuron, metapleuron, ventral half of lateral propodeal face with sparse short appressed pale golden setae; medial and ventral parts of mesopleuron with dense long appressed and sparse long erect pale golden setae; tegula anterior portion, tarsi with sparse long recumbent pale golden setae; tegula inner margin with sparse short recumbent and sparse short erect golden setae; S2 with sparse short recumbent and sparse short erect pale golden setae; T6–T7, S7–S8 with sparse short erect black setae; T2 with lateral golden felt line; T1–T5, S2–S5 with posterior fringe of sparse pale golden setae; S6–S8 with posterior fringe of sparse black setae.

Structure. Head 1.89–1.92× as wide as long (holotype: 1.92); lateral margins strongly convergent behind eye; vertex rounded posteriorly; POD/OOD = 0.56–0.77 (holotype: 0.77); OD:MOD:LOD = 1.00:1.15–1.58:0.92–1.08 (holotype: 1.00:1.58:0.92); ocellar region slightly convex, ocelli without posterior carina; antennal scrobe with weak inverted V-shaped dorsal carina not reaching inner eye margin; genal carina absent; postgenal bridge flattened; hypostomal carina weakly developed; clypeus medially strongly elevated even ventrally, without subventral transverse groove; anterior clypeal margin projecting medially; mandible robust, narrowed to apex with inner margin expanded forming large subbasal tooth; mandible apex bidentate; mandible ventral margin excised into large basal tooth; mandible dorsal carina sharp; prementum flattened; scape curved medially, with two longitudinal ventral carinae divergent apically; F1 depressed, F1 height 0.75× pedicel diameter; relative length of pedicel, F1 and F2 = 1.00:3.00–3.05:1.84–2.26 (holotype: 1.00: 3.05:1.84); F2–F11 almost equal in width; F11 as long as F2, conical.

Mesosoma widest at mesonotum including tegulae; head width:humeral width:pronotal width:mesonotal width = 87:60:93:100; humeral angle rounded, with sharp humeral carina not reaching pronotal dorsum; mesoscutum strongly convex; mesoscutal width 1.20× its length; tegula short rounded, posteriorly reaching mesoscuto-scutellar articulation, 1.43–1.44× as long as wide (holotype: 1.44); notaulus evenly wide, reaching anterior 1/2 of mesoscutum, subparallel; parapsidal line length 0.25× mesoscutal length; parascutal carina forming rounded, weakly elevated process on postero-lateral angle of mesoscutum; mesoscutellum convex without medial carina, tubercle or impunctate line; mesopleuron divided into dorsal and ventral convexities by distinct transverse mesopleural groove, ventrally without transverse precoxal ridge, longitudinal impunctate line, or precoxal swelling; dorsal propodeal face without distinct dorsum and sublateral carina, with anterior inverted triangular cell and semicircular sublateral cell; lateral margins of propodeum gradually convergent posteriorly; dorsal and lateral propodeal faces not separated by carina.

Wings well developed; distance between origin of RS on vein SC and base of stigmatic cell equal to stigmatic cell length and first abscissa of RS length; cell 2RS present.

Meso- and metacoxae evenly convex; metacoxa with weak complete inner longitudinal carina; protibial spur slender; tibiae without outer spines.

T1 without distinct dorsum; T1 spiracle weakly tuberculate; T2 evenly convex, 1.25× as wide as long; S1 with straight medial longitudinal carina with its ventral margin convex; S2 swollen anteriorly; T7 medially with longitudinal impunctate convex line, posteriorly not forming tubercle; S6–S8 without lateral carina or tubercle; S7 entirely exposed, 0.75× as long as S8; S8 mostly sclerotized with posterior membranous area evenly convex posteriorly. Paramere down-curved posteriorly, with weak inner protuberance on posterior 1/2 of dorso-inner margin; inner margin of paramere dorsally with short erect golden setae; ventral lobe posteriorly projecting, pointed; parapenial lobe large, with posterior margin concave; cuspis long slender, widened near apex, forming oblique posterior margin, apparently surpassing apex of penis valve, with dense long erect setae ventrally and posteriorly; digitus straight,

posteriorly expanded, forming triangular projection, with dense erect golden setae posteriorly; paracuspis slightly tuberculate with few erect golden setae; penis valves symmetrical slender, weakly expanded ventrally, with posterior ventral hook, without setae.

Frons, vertex, gena, pronotal dorsum, mesoscutum, medial part of mesopleuron with large dense punctures; postgenal bridge, trochanters, femora, tibiae, T1 medially, T2 disc, S2 with small sparse punctures; clypeus lateral portion, mandible outer and dorsal faces, scape between ventral carinae, flagellum, pronotal lateral face, propleuron, axilla, metanotal trough, anterior and posterior parts of mesopleuron, metapleuron, ventral half of lateral propodeal face, coxae, tarsi with minute dense punctures; clypeus medial convexity, scape mostly, pedicel, T1–T2 laterally, T3–T7, S1, S3–S8 with small dense punctures; mesoscutellum with large confluent punctures; metascutellum with small confluent punctures; dorsal propodeal face, dorsal half of lateral propodeal face reticulate; pronotal collar anteriorly with minute sparse punctures; pronotal collar posteriorly smooth; tegula mostly microreticulate with few small punctures anteriorly, postero-inner portion with minute sparse punctures.

FEMALE. Unknown.

Type material

2♂. Holotype ♂: **Indonesia:** EAST JAVA: Mt. Argopuro, 31.VII.1995 [TKPM]. Paratype: **Indonesia:** EAST JAVA: Mt. Argopuro, 31.VII.1995 [1♂ TKPM].

Distribution

Indonesia: East Java.

Etymology

The specific name *gibba* is a Latin noun meaning gibbosity. It refers to the strongly elevated clypeus of this new species.

Remarks

This species and *A. nallinia* are recognized in *Arkaditilla* by having the mandible with sharp subapical and large inner subbasal teeth, the mandible ventral margin deeply excised with large basal tooth, the scape ventral carinae divergent apically, F1 strongly depressed, the cuspis widened posteriorly, the digitus posteriorly expanded, the paracuspis tuberculate, and the penis valve weakly expanded ventrally, but the former differs from the latter by having the clypeus strongly elevated even ventrally (clypeus elevated dorsally in *A. nallinia*), and the cuspis widened near apex (cuspis widened on posterior 1/3 in *A. nallinia*).

Arkaditilla leleji **sp. nov.**

(Figs 9, 10, 17, 23, 33, 34, 45, 46, 61–63, 71, 75)

Diagnosis

MALE. Clypeus dorsally elevated, sloping ventrally. Mandible with sharp subapical and large inner subbasal teeth lamellately expanded near apex (Fig. 17), ventrally slightly excised with small basal tooth (Fig. 23). Scape ventral carinae divergent apically (Fig. 33), densely punctate between them; F1 apical half and F2–F6 whitish yellow on ventral half, F7–F11 with ventral dark brown patch; F1 weakly depressed, F1 height subequal to pedicel diameter (Fig. 34). T3 black (Fig. 10); cuspis weakly widened on posterior 1/3 with rounded apex (Figs 61, 71); digitus posteriorly slender stick-like (Fig. 45); paracuspis slightly tuberculate (Fig. 71); penis valve strongly expanded ventrally on posterior half (Figs 62, 63). FEMALE. Unknown.

Description

MALE. Body length: 15.9 mm; forewing length: 13.0 mm.

Color and setae. Frons, vertex, gena, clypeus, mandible mostly, pedicel, flagellum mostly, prementum, stipes, mesosoma, meso- and metacoxae, T3–T7, S1 medial carina, S4–S8 black; mandible medial 1/3 brown; labrum, protibial spur yellow; scape, F7–F11 ventrally, trochanters dark brown; F1 apical half, F2–F6 whitish yellow on ventral half; tegula, procoxa, femora, tibiae, tarsi, S3 lateral portion brownish black; meso- and metatibial spurs pale yellow; T1–T2, S1 except medial carina, S2–S3 mostly orange; wings brown, with veins dark brown. Upper frons, vertex, T1, S1 with sparse long erect pale golden setae; lower frons, gena, pronotal dorsum, dorsal propodeal face, dorsal half of lateral propodeal face, coxae with dense short appressed and sparse long erect pale golden setae; eye dorsal margin with long erect black setae; clypeus with dense long recumbent pale golden setae; mandible with sparse short recumbent and sparse long erect pale golden setae; scape with sparse long recumbent and sparse long erect pale golden setae; pedicel, F1, trochanters, T2 lateral margin with sparse short recumbent pale golden setae; F2–F11 with sparse erect pale golden microsetae; pronotal collar anteriorly, T2 disc, T3–T5, S3–S6 with sparse short erect pale golden setae; pronotal collar posteriorly glabrous; pronotal lateral face with sparse long appressed pale golden setae; propleuron with sparse long appressed and sparse long erect pale golden setae; mesoscutum with sparse short recumbent and sparse short erect dark golden setae; meso- and metascutellum, femora with sparse short recumbent pale golden and sparse long erect golden setae; anterior and posterior parts of mesopleuron, metapleuron, ventral half of lateral propodeal face with sparse short appressed pale golden setae; axilla, metanotal trough, medial and ventral parts of mesopleuron with dense long appressed and sparse long erect pale golden setae; tegula anterior portion, tarsi with sparse long recumbent golden setae; tegula inner margin with sparse short recumbent and sparse short erect golden setae; tibiae with sparse short recumbent golden and sparse long erect golden setae; T6–T7, S7–S8 with sparse short erect black setae; S2 with sparse short recumbent and sparse short erect pale golden setae; T2 with lateral golden felt line; T1–T5, S2–S5 with posterior fringe of sparse pale golden setae; S6–S8 with posterior fringe of sparse black setae.

Structure. Head 2.00× as wide as long; lateral margins strongly convergent behind eye; vertex rounded posteriorly; POD/OOD = 0.54; OD:MOD:LOD = 1.00:1.29:1.00; ocellar region slightly convex, ocelli without posterior carina; antennal scrobe with weak inverted V-shaped dorsal carina not reaching inner eye margin; genal carina absent; postgenal bridge flattened; hypostomal carina weakly developed; clypeus dorsally elevated, sloping ventrally, without subventral transverse groove; anterior clypeal margin projecting medially; mandible robust, narrowed to apex with inner margin expanded forming large subbasal tooth; mandible apex bidentate; mandible ventral margin slightly excised into small basal tooth; mandible dorsal carina sharp; prementum flattened; scape curved medially, with two longitudinal ventral carinae divergent apically; F1 depressed, F1 height 0.91× pedicel diameter; relative length of pedicel, F1 and F2 = 1.00:3.00:2.37; F2–F11 almost equal in width; F11 as long as F2, conical.

Mesosoma widest at mesonotum including tegulae; head width:humeral width:pronotal width:mesonotal width = 83:62:85:100; humeral angle rounded, with sharp humeral carina not reaching pronotal dorsum; mesoscutum strongly convex; mesoscutal width 1.11× its length; tegula short rounded, posteriorly reaching mesoscuto-scutellar articulation, 1.54× as long as wide; notaulus evenly wide, reaching anterior 1/2 of mesoscutum, subparallel; parapsidal line length 0.3× mesoscutal length; parascutal carina forming rounded, weakly elevated process on postero-lateral angle of mesoscutum; mesoscutellum convex without medial carina, tubercle or impunctate line; mesopleuron divided into dorsal and ventral convexities by distinct transverse mesopleural groove,

ventrally with transverse precoxal ridge, without longitudinal impunctate line, or precoxal swelling; dorsal propodeal face without distinct dorsum and sublateral carina, with anterior inverted triangular cell and semicircular sublateral cell; lateral margins of propodeum gradually convergent posteriorly; dorsal and lateral propodeal faces not separated by carina.

Wings well developed; distance between origin of RS on vein SC and base of stigmatic cell equal to stigmatic cell length and first abscissa of RS length; cell 2RS present.

Meso- and metacoxae evenly convex; metacoxa with weak complete inner longitudinal carina; protibial spur slender; tibiae without outer spines.

T1 without distinct dorsum; T1 spiracle weakly tuberculate; T2 evenly convex, 1.15× as wide as long; S1 with straight medial longitudinal carina with its ventral margin convex; S2 swollen anteriorly; T7 medially with longitudinal impunctate convex line, posteriorly not forming tubercle; S6–S8 without lateral carina or tubercle; S7 entirely exposed, 0.75× as long as S8; S8 mostly sclerotized with posterior membranous area evenly convex posteriorly. Paramere down-curved posteriorly, without inner protuberance on dorso-inner margin; inner margin of paramere dorsally with short erect golden setae; ventral lobe posteriorly projecting, pointed; parapenial lobe large, with posterior margin slightly concave; cuspis long slender, weakly widened on posterior 1/3 with rounded apex, apparently surpassing apex of penis valve, with dense long erect setae ventrally and posteriorly; digitus straight, posteriorly not expanded, with dense erect golden setae posteriorly; paracuspis slightly tuberculate with few erect golden setae; penis valves symmetrical slender, strongly expanded ventrally on posterior half, with posterior ventral hook, without setae.

Frons, vertex, gena, pronotal dorsum, mesoscutum, medial part of mesopleuron with large dense punctures; postgenal bridge, trochanters, femora, tibiae, T1 medially, T2 disc with small sparse punctures; clypeus mostly, mandible outer and dorsal faces, scape between ventral carinae, flagellum, pronotal lateral face, propleuron, axilla, metanotal trough, anterior and posterior parts of mesopleuron, metapleuron, ventral half of lateral propodeal face, coxae, tarsi with minute dense punctures; clypeus anterior margin with few large punctures; scape mostly, pedicel, T1–T2 laterally, T3–T7, S1–S8 with small dense punctures; pronotal collar anteriorly with minute sparse punctures; pronotal collar posteriorly smooth; mesoscutellum with large confluent punctures; metascutellum with small confluent punctures; dorsal propodeal face, dorsal half of lateral propodeal face reticulate; tegula mostly microreticulate with few small punctures anteriorly, postero-inner portion with minute sparse punctures.

FEMALE. Unknown.

Type material

1♂. **Holotype** ♂: **Indonesia:** KALIMANTAN TIMUR: Bukit Soeharto, 13–17.III.1994, K. Matsumoto & K. Konishi leg. [NARO].

Distribution

Indonesia: Kalimantan Timur.

Etymology

This new species is dedicated to Arkady Lelej as is the genus itself.

Remarks

This new species is unique in *Arkaditilla* by having the mandible ventral margin slightly excised with small basal tooth, F1 weakly depressed, T3 black, and the penis valve strongly expanded ventrally on posterior half.

***Arkaditilla nallinia* (Zavattari, 1914), comb. nov.**

(Figs 11, 12, 18, 24, 35, 36, 47, 48, 64–66, 72, 76)

Mutilla nallinia Zavattari, 1914: 100, ♂, syntypes ♂ (Giava [= Java], [Indonesia]; Bali, [Indonesia]) [Museo Regionale di Scienze Naturali, Torino, Italy].
Timulla (*Trogaspidia*) *nallinia*: Mickel, 1935: 263, ♂.
Krombeinidia nallinia: Lelej, 1996a: 11; Lelej, 2005: 66; Lo Cascio, 2015: 551; Pagliano *et al*., 2020: 251.
Petersenidia nallinia: Lelej, 1996b: 94, ♂.

Diagnosis
MALE. Clypeus dorsally elevated, sloping ventrally. Mandible with sharp subapical and large inner subbasal teeth (Fig. 18), ventrally deeply excised with large basal tooth (Fig. 24). Scape ventral carinae divergent apically (Fig. 35), densely punctate between them; F1 apical 1/3, F2 and F3 basal 1/3 whitish yellow on ventral half; F1 strongly depressed, F1 height ~0.8× pedicel diameter (Fig. 36). T3 orange (Fig. 12); cuspis strongly widened on posterior 1/3 with rounded apex (Figs 64, 72); digitus posteriorly expanded, forming triangular projection (Fig. 47); paracuspis slightly tuberculate (Fig. 72); penis valve weakly expanded ventrally (Figs 65, 66). FEMALE. Unknown.

Material examined
2♂. **Indonesia:** BALI: Tabanan, Bengkel, Pura Batu Salahan, 08°23'31.8"S, 115°05'E, 682 m alt., 12.VIII.2006, K. Watanabe leg. [1♂ TUA].

Identification source
Keyed using Mickel (1935) and compared with the original description. No differences were found between the specimen examined herein and Zavattari's description.

Distribution
Indonesia: Bali, Java (Lelej, 1996b; Mickel, 1935; Zavattari, 1914).

Remarks
Only three mutillid species have been recorded from Bali, namely *Arkaditilla nallinia*, *Krombeinidia griseomaculata* (André, 1898), and *Mickelomyrme pusillaeformis* (Hammer, 1962) (Zavattari 1914; Lelej 2005; Okayasu 2020; current data), although Zavattari's record of *K. griseomaculata* was not accepted by Lelej (2005) and Mickel (1935). Field surveys in this small island will be useful for discovery of the female of *Arkaditilla*.

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References

Brothers, D.J. & Lelej, A.S. (2017) Phylogeny and higher classification of Mutillidae (Hymenoptera) based on morphological reanalyses. *Journal of Hymenoptera Research* 60: 1–97. https://doi.org/10.3897/jhr.60.20091

Cameron, P. (1902) On the Hymenoptera collected by Mr. Robert Shelford at Sarawak, and on the Hymenoptera of the Sarawak Museum. *Journal of the Straits Branch of the Royal Asiatic Society* 37: 29–131.

Chen, C.-w. (1957) A revision of the velvety ants or Mutillidae of China (Hymenoptera). *Quarterly Journal of the Taiwan Museum* 10 (3–4): 135–224 + 6 pls.

Hadley, A. (2008) CombineZM software. https://combinezm.en.lo4d.com/ (accessed 15 May 2021)

Harris, R.A. (1979) A glossary of surface sculpturing. *Occasional Papers in Entomology* 28: 1–31.

Hymenoptera Anatomy Consortium (2021) The Hymenoptera Glossary. http://glossary.hymao.org/ (accessed 15 May 2021)

Invrea, F. (1954) Mutillidi della Dalmazia e del litorale Montenegrino. Nota prima. *Memorie della Societa Entomologica Italiana* 32: 143–159 + 2 figs.

Lelej, A.S. (1971) New and little-known species of velvet ants (Hymenoptera, Mutillidae) from Middle Asia and Kazakhstan. *Entomologicheskoe Obozrenie* 50 (3): 676–680 + 5 figs. (in Russian)

Lelej, A.S. (1995) To the knowledge of East Asian species of the tribe Smicromyrmini Bischoff, 1920 (Hymenoptera, Mutillidae) with description of four new genera and eight new species. *Far Eastern Entomologist* 13: 1–28.

Lelej, A.S. (1996a) To the knowledge of the East Asian species of the tribe Trogaspidiini Bischoff, 1920 (Hymenoptera, Mutillidae) with description of eight new genera and two new species. *Far Eastern Entomologist* 30: 1–24.

Lelej, A.S. (1996b) Mutillid wasps collected in Malaysia and Indonesia by Dr. Sk. Yamane (Hymenoptera, Mutillidae). *Tropics* 6 (1–2): 91–104. https://doi.org/10.3759/tropics.6.91

Lelej, A.S. (2005) *Catalogue of the Mutillidae (Hymenoptera) of the Oriental Region*. Dalnauka, Vladivostok, 252 pp.

Lelej, A.S. & Nemkov, P.G. (1997) Phylogeny, evolution and classification of Mutillidae (Hymenoptera). *Far Eastern Entomologist* 46: 1–24.

Lelej, A.S. & Yamane, Sk. (1992) Interesting velvet ants (Hymenoptera, Mutillidae) from Japan and Korea. *Japanese Journal of Entomology* 60 (3): 625–632.

Lo Cascio, P. (2015) Worldwide checklist of the island mutillid wasps (Hymenoptera Mutillidae). *Biodiversity Journal* 6 (2): 529–592.

Maetô, K., Fukuyama, K. & Kirton, L.G. (1999) Edge effects on ambrosia beetle assemblages in a lowland rain forest, bordering oil palm plantations, in peninsular Malaysia. *Journal of Tropical Forest Science* 11 (3): 537–547.

Mickel, C.E. (1933a) The Mutillidae of Formosa. *Annals of the Entomological Society of America* 26 (2): 381–423. https://doi.org/10.1093/aesa/26.2.381

Mickel, C.E. (1933b) The Mutillidae of Eastern Asia. *Lingnan Science Journal* 12 (3): 289–325.

Mickel, C.E. (1934) Mutillidae of the Philippine Islands. *Philippine Journal of Science* 54 (1): 91–219 + 1 pl.

Mickel, C.E. (1935) The mutillid wasps of the islands of the Pacific Ocean (Hymenoptera,

Mutillidae). *Transactions of the Royal Entomological Society of London* 83 (2): 177–312. https://doi.org/10.1111/j.1365-2311.1935.tb01207.x

Mickel, C.E. (1937) New species and records of Mutillidae (Hymenoptera) from Borneo and the Solomon Islands. *The Annals and Magazine of Natural History* 10 (19): 441–456. https://doi.org/10.1080/00222933708655284

Okayasu, J. (2020) Velvet ants of the tribe Smicromyrmini Bischoff (Hymenoptera: Mutillidae) of Japan. *Zootaxa* 4723 (1): 1–110. https://doi.org/10.11646/zootaxa.4723.1.1

Okayasu, J., Lelej, A.S. & Williams, K.A. (2021) Review of *Eotrogaspidia* Lelej (Hymenoptera: Mutillidae: Trogaspidiini). *Zootaxa* 4920 (1): 56–90. https://doi.org/10.11646/zootaxa.4920.1.2

Pagliano, G., Brothers, D.J., Cambra, R., Lelej, A.S., Lo Cascio, P., Matteini Palmerini, M., Scaramozzino, P.L., Williams, K.A. & Romano, M. (2020) Checklist of names in Mutillidae (Hymenoptera), with illustrations of selected species. *Bollettino del Museo Regionale di Scienze Naturali di Torino* 36 (1–2): 5–425.

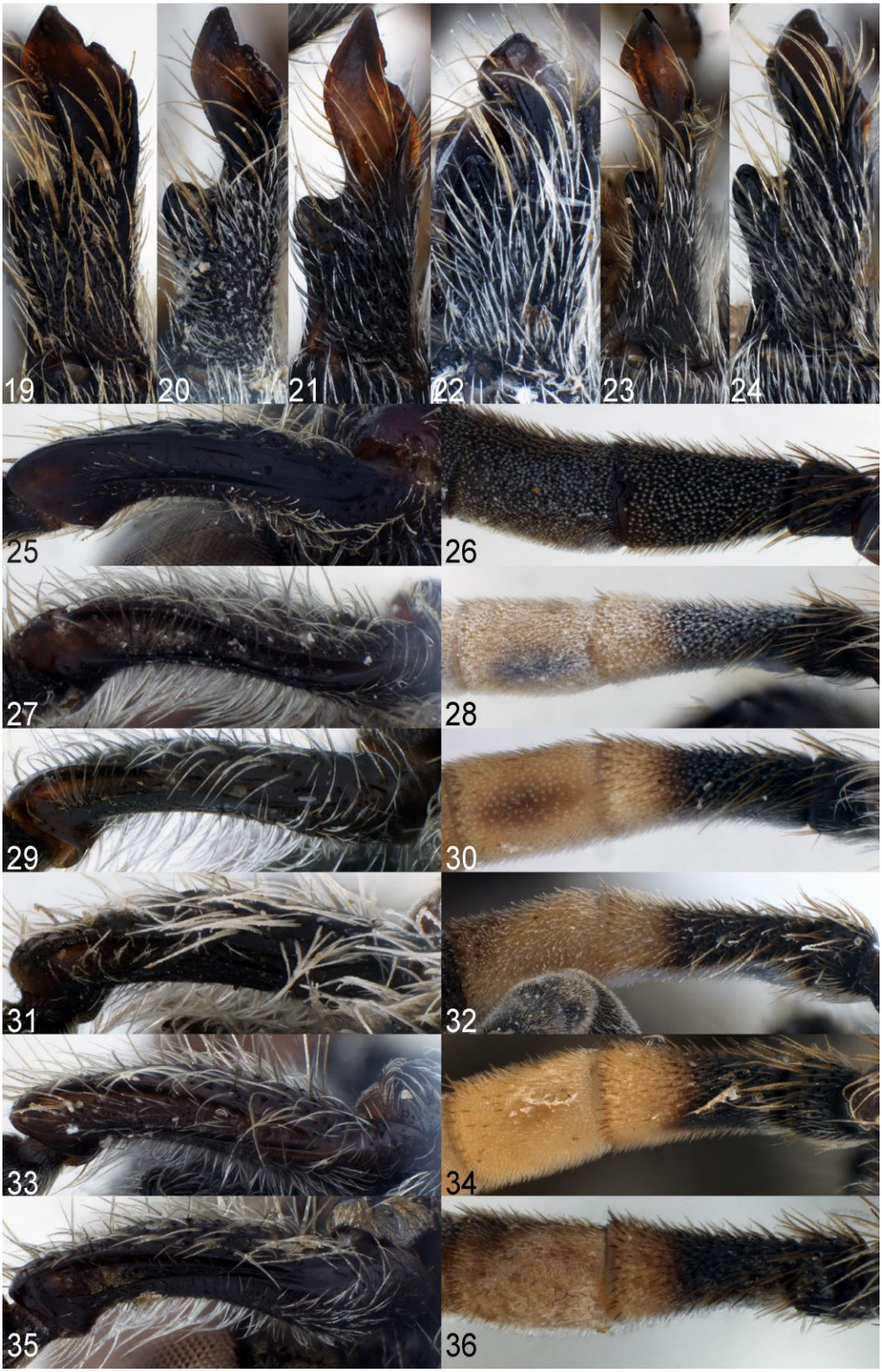
Shorthouse, D.P. (2010) SimpleMappr, an online tool to produce publication-quality point maps. http://www.simplemappr.net (accessed 15 May 2021)

Zavattari, E. (1914) Mutille Austro-Malesi. *Bollettino della Societa Entomologica Italiana* 45: 61–114.

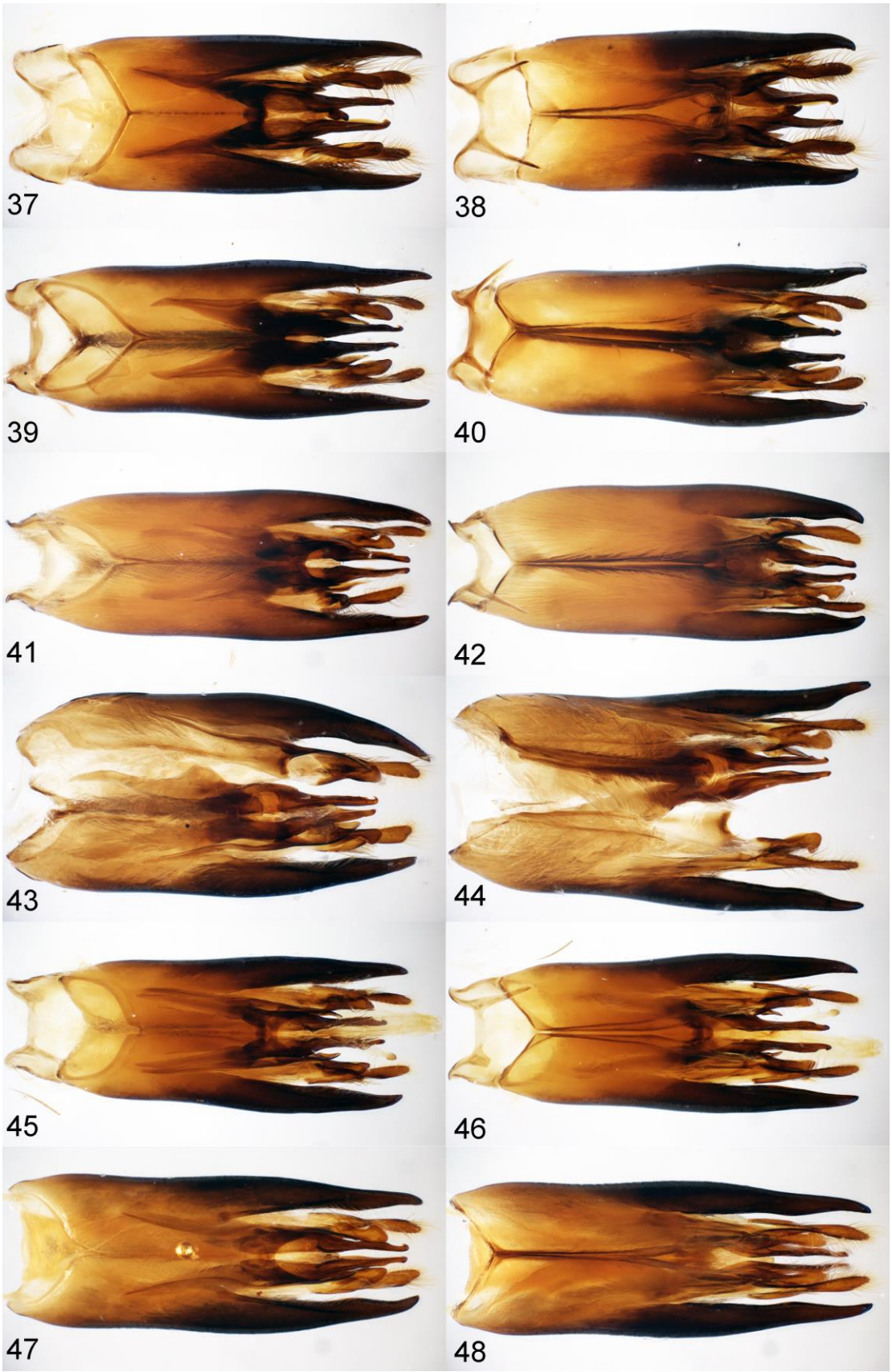
Figures 1–6. *Arkaditilla* spp., ♂, habitus. 1, 2. *A. bagrada* (Cameron); 3, 4. *A. depressicornis* (Mickel); 5, 6. *A. frim* **sp. nov.**, holotype; 1, 3, 5. dorsal view; 2, 4, 6. lateral view. Scale bars: 3 mm.

Figures 7–12. *Arkaditilla* spp., ♂, habitus. 7, 8. *A. gibba* **sp. nov.**, holotype; 9, 10. *A. leleji* **sp. nov.**, holotype; 11, 12. *A. nallinia* (Zavattari); 7, 9, 11. dorsal view; 8, 10, 12. lateral view. Scale bars: 3 mm.

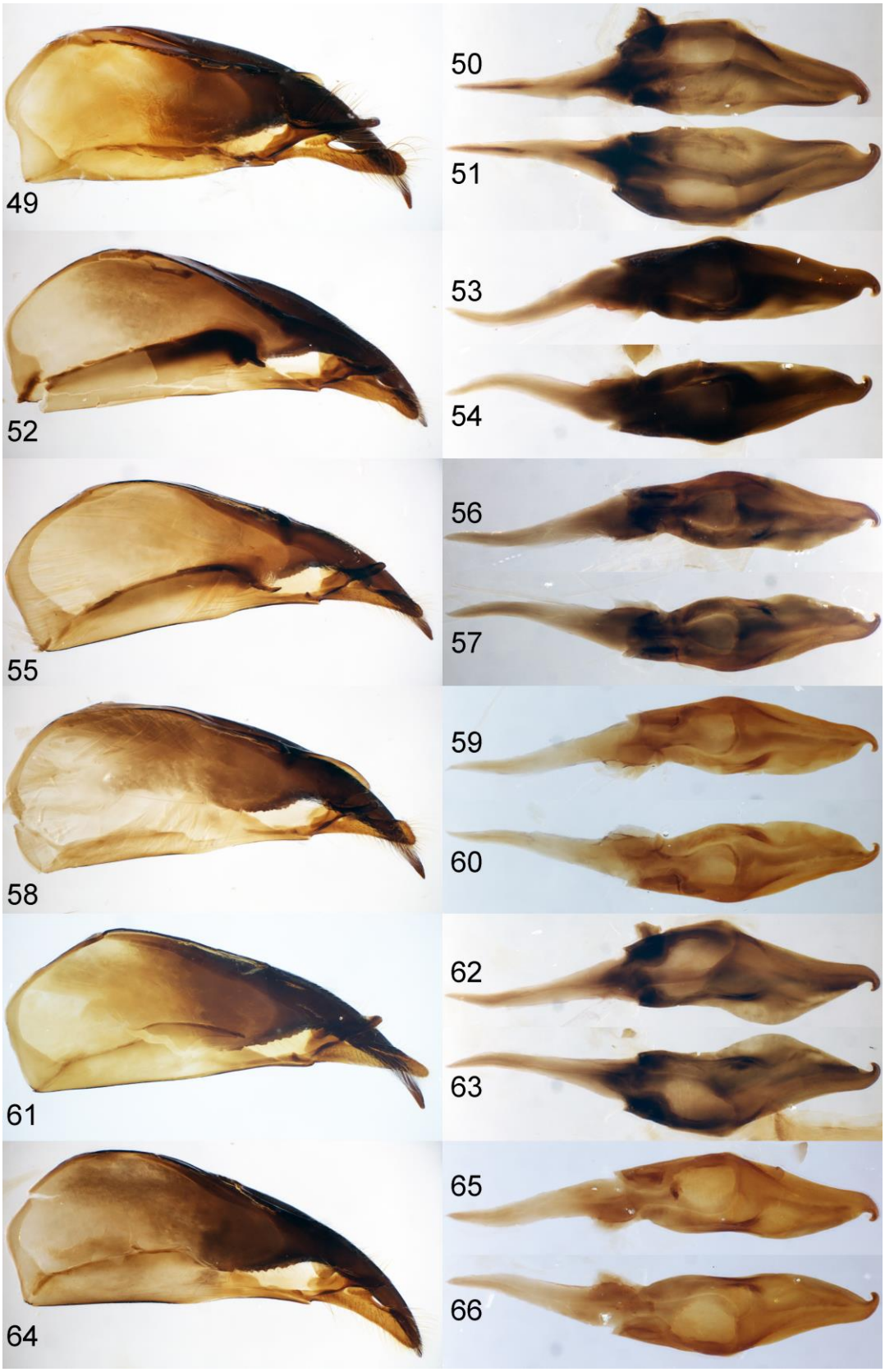
Figures 13–18. *Arkaditilla* spp., ♂, face. 13. *A. bagrada* (Cameron); 14. *A. depressicornis* (Mickel); 15. *A. frim* **sp. nov.**, holotype; 16. *A. gibba* **sp. nov.**, paratype; 17. *A. leleji* **sp. nov.**, holotype; 18 *A. nallinia* (Zavattari).



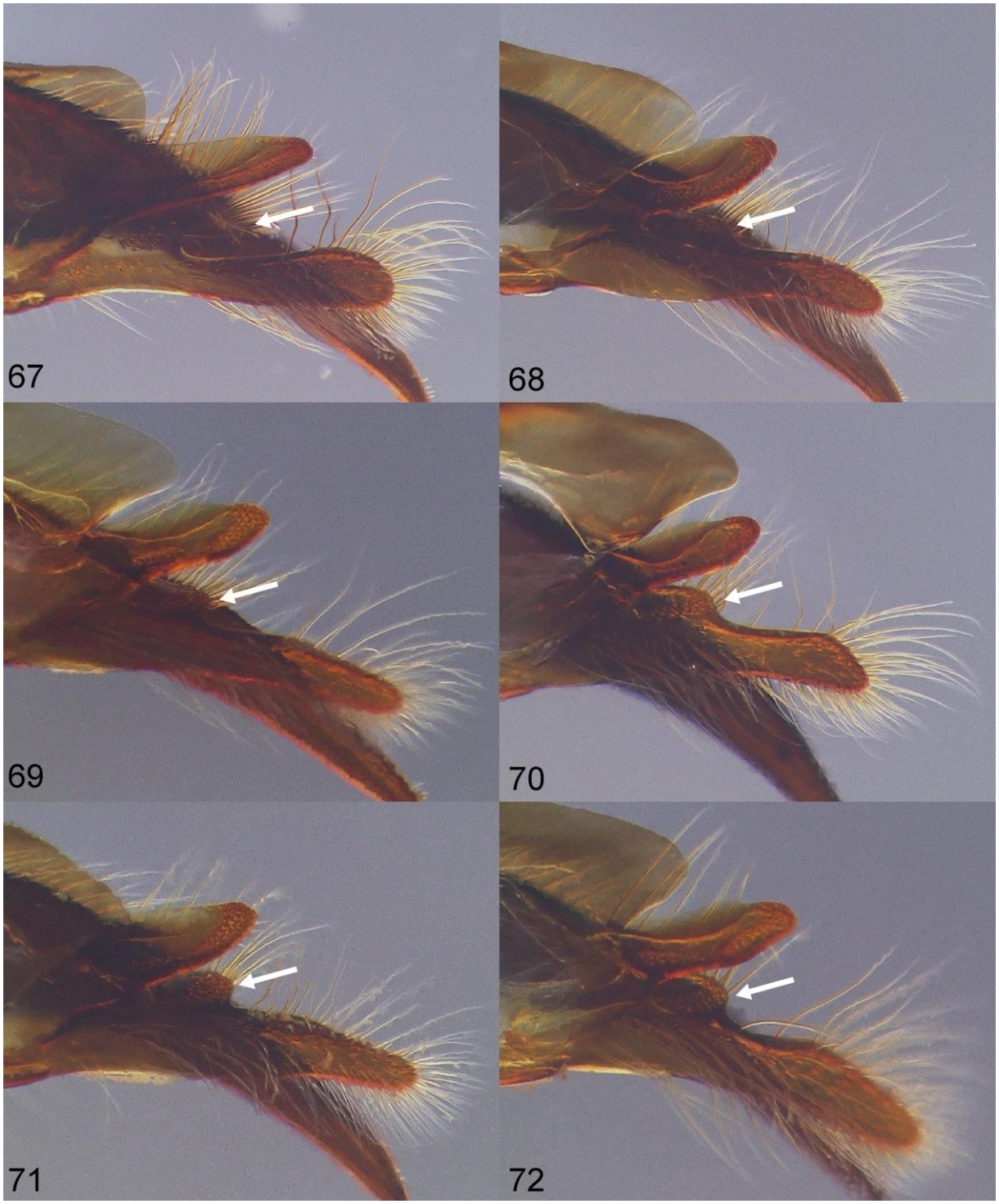
Figures 19–36. *Arkaditilla* spp., ♂. 19, 25, 26. *A. bagrada* (Cameron); 20, 27, 28. *A. depressicornis* (Mickel); 21, 29, 30. *A. frim* **sp. nov.**, holotype; 22, 31, 32. *A. gibba* **sp. nov.**, holotype; 23, 33, 34. *A. leleji* **sp. nov.**, holotype; 24, 35, 36. *A. nallinia* (Zavattari); 19–24. mandible, lateral view; 25, 27, 29, 31, 33, 35. scape, ventral view; 26, 28, 30, 32, 34, 36. pedicel, F1, and F2, lateral view.



Figures 37–48. *Arkaditilla* spp., ♂, genitalia. 37, 38. *A. bagrada* (Cameron); 39, 40. *A. depressicornis* (Mickel); 41, 42. *A. frim* **sp. nov.**, holotype; 43, 44. *A. gibba* **sp. nov.**, holotype; 45, 46. *A. leleji* **sp. nov.**, holotype; 47, 48. *A. nallinia* (Zavattari); 37, 39, 41, 43, 45, 47. dorsal view; 38, 40, 42, 44, 46, 48. ventral view.



Figures 49–66. *Arkaditilla* spp., ♂, genitalia. 49–51. *A. bagrada* (Cameron); 52–54. *A. depressicornis* (Mickel); 55–57. *A. frim* **sp. nov.**, holotype; 58–60. *A. gibba* **sp. nov.**, holotype; 61–63. *A. leleji* **sp. nov.**, holotype; 64–66. *A. nallinia* (Zavattari); 49, 52, 55, 58, 61, 64. genital capsule and volsella, inner view; 50, 53, 56, 59, 62, 65. left penis valve; 51, 54, 57, 60, 63, 66. right penis valve.



Figures 67–72. *Arkaditilla* spp., ♂, genital volsella, ventro-inner view. 67. *A. bagrada* (Cameron); 68. *A. depressicornis* (Mickel); 69. *A. frim* **sp. nov.**, holotype; 70. *A. gibba* **sp. nov.**, holotype; 71. *A. leleji* **sp. nov.**, holotype; 72. *A. nallinia* (Zavattari). White arrows indicate the paracuspis.

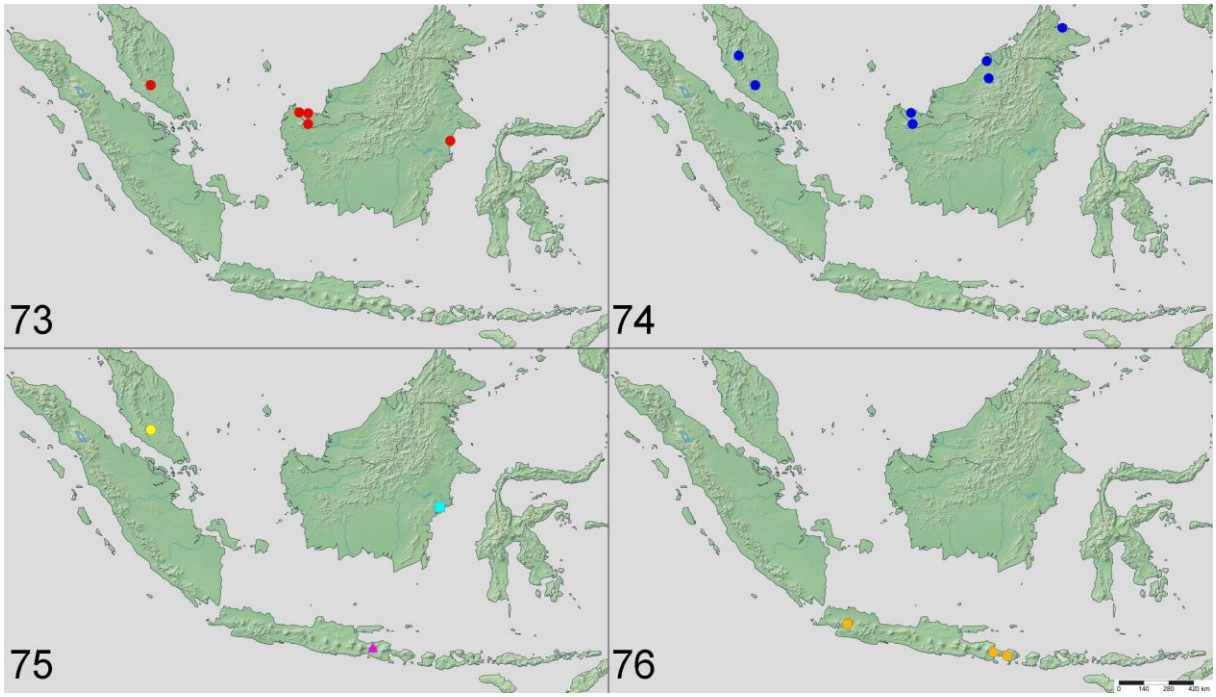


Figure 73–76. Distributional map of *Arkaditilla* spp. based on specimens examined herein and the literature (Cameron, 1902; Lelej, 1996b; Mickel, 1935, 1937; Zavattari, 1914). 73. *A. bagrada* (Cameron) (red circle); 74. *A. depressicornis* (Mickel) (blue circle); 75. *A. frim* **sp. nov.** (yellow circle), *A. gibba* **sp. nov.** (purple triangle), and *A. leleji* **sp. nov.** (light blue square); 76. *A. nallinia* (Zavattari) (orange circle).

Chapter 4

Review of female *Andreimyrme* Lelej (Hymenoptera: Mutillidae: Smicromyrmini)

Disclaimer: *This chapter has already been published as a peer-reviewed paper as follows: Okayasu, J., Williams, K.A., Lelej, A.S. & Pham, T.H. (2021) Zootaxa 5061 (1): 1–38 (https://doi.org/10.11646/zootaxa.5061.1.1). New nomenclatural acts appearing in this chapter have already been made in this publication and, thus, this dissertation chapter is not considered a published work within the meaning of the International Code of Zoological Nomenclature 4th edition (Article 8.2).*

Abstract
Females of the East Asian velvet-ant genus *Andreimyrme* Lelej, 1995 are reviewed. The genus definition is extended to accommodate *A. borkenti* (Williams, 2019), **comb. nov.** (from *Smicromyrme* Thomson, 1870), and nine new species: *A. auricoma* Okayasu, **sp. nov.** (Malaysia), *A. laminatihumeralis* Okayasu, **sp. nov.** (Indonesia, Malaysia), *A. matsumotoi* Okayasu, **sp. nov.** (Vietnam), *A. naturalis* Williams, **sp. nov.** (Indonesia), *A. rong* Williams, **sp. nov.** (Thailand, Vietnam), *A. silvorientalis* Okayasu, **sp. nov.** (Indonesia), *A. takensis* Okayasu, **sp. nov.** (Thailand), *A. ursasolaris* Williams, **sp. nov.** (Indonesia), and *A. yotoi* Okayasu, **sp. nov.** (Laos, Vietnam). Diagnoses, distributional records, and illustrations are provided for these and four previously recognized species, *A. neaera* (Mickel, 1935), *A. paniya* Terine, Lelej & Kumar, 2021, *A. sarawakensis* Lelej, 1996, and *A. substriolata* (Chen, 1957). *Andreimyrme borkenti* is newly recorded from Vietnam. A key to species known from females is provided. Habitat preference of this genus is discussed based on collecting records.

Key words
Aculeata, velvet ant, taxonomy, new species, Asia, Oriental Region.

Introduction

Wasps of the family Mutillidae are extremely dimorphic; males are usually winged and females are wingless. Morphology alone is insufficient for associating males and females of particular species (Brothers, 1989). Observation of mating couples, examination of gynandromorphs, rearing experiments, or repeated sampling of males and females in the same ranges are often necessary for sex association (Bartholomay *et al*., 2019; Brothers, 1989; Turrisi & Foucart, 2008). Many species or even genera are therefore known from one sex only (Brothers, 1989).

The tribe Smicromyrmini Bischoff, 1920 includes 26 valid genera (Brothers & Lelej, 2017), 13 of these are present in the Eastern Palaearctic and Oriental Regions (Lelej, 2002, 2005; Pagliano *et al*., 2020). The largest genus *Smicromyrme* Thomson, 1870 has been used as a place-holder for many species that cannot be reliably placed in the modern generic construct, suggesting that many species need to be transferred out of *Smicromyrme* (Williams *et al*., 2019b). Lelej (1985, 1995ab, 2002, 2005) classified East Asian members of this genus into many new genera of the tribe (Okayasu, 2017). Identification of these genera largely depends on the male morphology, especially male genitalia (Williams *et al*., 2019b). Identification of females is sometimes difficult because of the high intra-generic variation, the similarity in general appearance as a result of convergence related to Müllerian mimicry, and the easily overlooked key features (Okayasu *et al*., 2018; Williams *et al*., 2019b).

The genus *Andreimyrme* Lelej, 1995b is a rather small Asian smicromyrmine genus. Ten species are currently placed in *Andreimyrme*; of these, six are known from males only

and the remaining four are known from females only (Lelej, 2005; Lelej *et al*., 2007; Okayasu, 2020; Terine *et al*., 2021). As implied from this outline, none is known from both sexes. The rarity of *Andreimyrme* specimens makes sex associations difficult. Despite intensive collecting efforts in southern Thailand by Williams *et al*. (2019b), none was recognized during their 2017–2018 expeditions except for one possible species representing only eight of 592 total female specimens collected.

Taxonomic history and limits of this study

The *Andreimyrme* was described by Lelej (1995b) with the type species *A. long* Lelej, 1995 (♂). An additional species, *A. davidi* (André, 1898) (♂) was placed in this genus at the same time. The males of *Andreimyrme*, together with those of *Dentilla* Lelej in Lelej & Kabakov, 1980, *Ephutomma* Ashmead, 1899, and *Tsunekimyrme* Lelej, 1995b, were recognized in Smicromyrmini by having the mandible apically widened and tridentate. *Andreimyrme* was easily separated from those genera by having the mandible ventral margin straight (excised into large tooth or lobe in others), the flagellomere 1 0.7× as long as wide (1.5–1.6× as long as wide in *Ephutomma*), and the metasomal sternum 2 without a felt line (present in *Dentilla* and *Tsunekimyrme*) except for *A. davidi*. *Dentilla* and *Ephutomma* already had confirmed females, while sex associations for *Andreimyrme* and *Tsunekimyrme* were unknown. *Andreimyrme davidi* and *A. long* were recorded from China and Taiwan, and the only species of *Tsunekimyrme*, *T. fluctuata* (Smith, 1865) was known from Indonesia and The Philippines. In the continental East Asian region, two females, *Smicromyrme substriolatus* Chen, 1957 (♀) and *Smicromyrme tridentiens* Chen, 1957 (♀), were characterized by having the mandible wide and tridentate. Lelej (1995b) suggested the former as the potential female of *A. davidi* and the latter as that of *A. long*. The genus definition for female *Andreimyrme* was based on these species.

Lelej (1996a) further added *A. sarawakensis* Lelej, 1996 (♀) and *A. neaera* (Mickel, 1935) (♀, from *Smicromyrme*) to *Andreimyrme*. In his catalog, Lelej (2005) suggested that three additional species, one subdivided into two subspecies, *A. annexa* (Cameron, 1909) (♂), *A. v. viriata* (Mickel, 1934) (♂), *A. v. nitela* (Mickel, 1934) (♂), and *A. volupia* (Mickel, 1935) (♂), were potentially members of this genus because they lacked the ventral mandibular tooth of most other Asian Smicromyrmini genera. Lelej *et al*. (2007) described *A. pakistanensis* Lelej & Ullah, 2007 (♂) from Pakistan. Okayasu (2020) synonymized *A. tridentiens* under *A. substriolata* after examination of types and additional material. Terine *et al*. (2021) recorded this genus from India and described *A. paniya* Terine, Lelej & Kumar, 2021 (♀).

As described above, there is no female that has been definitively associated with a male in *Andreimyrme*. The characters used by Lelej (1995b) to diagnose the females of *Andreimyrme* are diagnostic for an apparently natural group of species that likely constitutes the same genus as males of *Andreimyrme*. Given the difficulty of sex association in mutillids, I consider it is important to document the diversity of this genus for future analyses, even if based solely on female sex. In this study, I aimed to review *Andreimyrme* species based on females through examination of specimens collected in various localities in the Oriental Region and obtained from various museum collections.

Material and methods

The following abbreviations are used to denote institutes housing types and specimens examined herein.

CSCA California State Collection of Arthropods, Sacramento, California, USA.
ELKU Entomological Laboratory, Faculty of Agriculture, Kyushu University, Fukuoka, Japan.
EUM Ehime University Museum, Matsuyama, Japan.
FRIM Forest Research Institute Malaysia, Selangor, Malaysia.
HUM Hokkaido University Museum, Sapporo, Japan.
IBSS Federal Scientific Center of the East Asia Terrestrial Biodiversity (formerly Institute of Biology and Soil Science), Vladivostok, Russia.
NMB Natural History Museum of Basel, Basel, Basel-Stadt, Switzerland.
NSMT National Museum of Nature and Science, Tsukuba, Japan.
QSBG Queen Sirikit Botanic Gardens, Chiang Mai, Chiang Mai, Thailand.
RMNH Naturalis Biodiversity Center, Leiden, South Holland, the Netherlands.
RUMF Ryukyu University Museum "Fujukan", Nakagami, Okinawa, Japan.
SKYC Department of Biology, Kagoshima University, Kagoshima, Japan.
TARI Taiwan Agricultural Research Institute, Taichung, Taiwan.
TUA Laboratory of Entomology, Tokyo University of Agriculture, Atsugi, Japan.
USNM National Museum of Natural History, Smithsonian Institution, Washington DC, USA.
VNMN Vietnam National Museum of Nature, Vietnam Academy of Science and Technology, Hanoi, Vietnam.
ZMUC Zoological Museum, University of Copenhagen, Universitetsparken, Denmark.
ZSIK National Zoological Collections, Western Ghat Regional Centre, Zoological Survey of India, Kozhikode, India.

Specimens were examined with various stereomicroscopes in multiple labs. Most photographs were taken with a Nikon Digital Sight DS-Fi1 camera attached to a Leica S8APO stereomicroscope, and stacked using CombineZM software (Hadley, 2008). The distributional maps (Figs 90–92) were generated by SimpleMappr (Shorthouse, 2010). Figures were edited using Adobe Photoshop and Adobe Illustrator software. In the synonymic lists and the material examined sections, abbreviations for depository and additional or corrected data by the authors are given in square brackets. New records are asterisked (*). Terminology mostly follows the Hymenoptera Anatomy Consortium (2021) for the general morphology, and Harris (1979) for the integument sculpture. Additionally, I used the term "prescutellar scales" to refer to the scales located anterolaterally in the scutellar area (Bartholomay *et al*., 2018), which are virtually subdivided "anterolateral carinae" of Bartholomay *et al*. (2018). Measurement methods follow Bartholomay *et al*. (2019). Abbreviations are: F = flagellomere; GOI = geno-orbital index: maximum breadth of eye in profile/maximum breadth of gena in same line (Gauld & Mitchell, 1981); S = metasomal sternum; T = metasomal tergum.

Andreimyrme Lelej, 1995

Andreimyrme Lelej, 1995b: 5, ♂♀; Lelej, 1996a: 100, ♀; Lelej, 2002: 50; Lelej, 2005: 38; Lelej, 2007: 88; Lelej *et al*., 2007: 56, ♂; Lelej & Brothers, 2008: 7; Lo Cascio, 2015: 544; Brothers & Lelej, 2017: 95, ♂♀; Okayasu *et al*., 2018: 303, ♀; Williams *et al*., 2019b: 16, ♀; Okayasu, 2020: 56, ♂♀; Pagliano *et al*., 2020: 169; Terine *et al*., 2021: 185, ♀.

Type species
Andreimyrme long Lelej, 1995b, ♂, by original designation.

Diagnosis
FEMALE. Genal carina distinct, forming sharp hypostomal tooth (Figs 40, 42, 47); clypeus with subventral transverse ridge; mandible slender tridentate (Figs 36, 37, 46), wide tridentate (Figs 38–41, 43, 45, 47, 48), or broadly expanded (Figs 42, 44); prementum armed with posterior rounded tubercle (Fig. 49). Mesosomal lateral margins subparallel or convergent posteriorly (Figs 50–62); prescutellar scales absent; scutellar scale obliterated; metanotal-propodeal suture obliterated. Protarsus with external comb of long spines; protarsomere 1 apically protruding outward to receive spines. T2 with posterior band of pale setae (Figs 63–76); pygidial plate subconvex with lateral margins defined by weak carinae, subparallel or slightly convergent anteriorly (Figs 77–89); surface of pygidial plate smooth or longitudinally rugose (Figs 77–89). MALE. Frons punctate; clypeus deeply concave. Mandible robust, widened apically, tridentate at apex with additional large inner tooth; ventral margin not emarginate basally. Scape bicarinate ventrally; F1 0.7× as long as wide. Notaulus complete, reaching anterior margin of mesoscutum; parapsidal signum scarcely visible; mesoscutellum punctate; mesopleuron anteriorly with medial deep glabrous depression, without or with precoxal denticle ventrally. S2 without basomedial carina and without lateral felt line (except *A. davidi* with trace of felt line); S8 (hypopygium) without tubercle or carina; genital volsella wide, without basal external lobe, with long setae on inner and ventral margins.

Species included
This genus includes 20 valid species, including the new ones, one of which is divided into two subspecies: *Andreimyrme annexa* (Cameron, 1909), ♂ (Malaysia); *A. auricoma* Okayasu, **sp. nov.**, ♀ (Malaysia); *A. borkenti* (Williams, 2019), **comb. nov.**, ♀ (Thailand, Vietnam); *A. davidi* (André, 1898), ♂ (China, Taiwan); *A. laminatihumeralis* Okayasu, **sp. nov.**, ♀ (Indonesia, Malaysia); *A. long* Lelej, 1995, ♂ (China); *A. matsumotoi* Okayasu, **sp. nov.**, ♀ (Vietnam); *A. naturalis* Williams, **sp. nov.**, ♀ (Indonesia); *A. neaera* (Mickel, 1935), ♀ (Malaysia); *A. pakistanensis* Lelej & Ullah, 2007, ♂ (Pakistan); *A. paniya* Terine, Lelej & Kumar, 2021, ♀ (India); *A. rong* Williams, **sp. nov.**, ♀ (Thailand, Vietnam); *A. sarawakensis* Lelej, 1996, ♀ (Malaysia); *A. silvorientalis* Okayasu, **sp. nov.**, ♀ (Indonesia); *A. substriolata* (Chen, 1957), ♀ (China, Taiwan, Indonesia, Japan, Laos, Malaysia, Thailand, Vietnam); *A. takensis* Okayasu, **sp. nov.**, ♀ (Thailand); *A. ursasolaris* Williams, **sp. nov.**, ♀ (Indonesia); *A. v. viriata* (Mickel, 1934), ♂ (Philippines); *A. v. nitela* (Mickel, 1934), ♂ (Philippines); *A. volupia* (Mickel, 1935), ♂ (Malaysia); *A. yotoi* Okayasu, **sp. nov.**, ♀ (Laos, Vietnam).

Gender
Feminine (Lelej & Brothers 2008).

Sex association
The possible female of the type species was associated and identified as *Smicromyrme tridentiens* Chen, 1957 (= *A. substriolata* (Chen, 1957)) by Lelej (1995b: 7). Based on the overlapping distribution and the shared mandibular shape, we assume *A. rong* **sp. nov.** to be the potential female of *A. long*.

Distribution
Predominantly from the Oriental Region, but two species penetrate to Palaearctic China and *A. pakistanensis* is known from Pakistan (Islamabad) westward of India.

Remarks
Females of *Andreimyrme* are recognized by having the mandible tridentate or broadly expanded, the prementum with a rounded posterior tubercle, and the scutellar scale

obliterated, while those of other smicromyrmine genera have the mandible edentate or bidentate, the prementum unarmed, and the scutellar scale spinulose, naillike, or transverse, except *Promecilla* André, 1902 which lacks developed scutellar scale. Originally, female *Andreimyrme* were defined by having the mandible wide and robust (Fig. 45), like *A. substriolata* which was the first female assigned to this genus. *Smicromyrme borkenti* Williams, 2019 was described in Williams *et al*. (2019b) from southern Thailand. This species is similar to *Andreimyrme* by having the mandible tridentate, the scutellar scale obliterated, and the pygidial plate sub-trapezoidal, laterally delimited by carinae, but was differentiated from it by having the mandible slender, tapering to apex (Fig. 37). Considering the large variability of *Smicromyrme*, *S. borkenti* was described in that genus. In this study, however, I found that all *Andreimyrme* females with the wide mandible and *S. borkenti* share the prementum with posterior rounded tubercle. I used this trait to reallocate *S. borkenti* to *Andreimyrme*, because *Smicromyrme* females have the prementum flattened, at most with medial carina.

Key to females of *Andreimyrme*

1. Mandible with subapical teeth obliterated, forming blunt expansion (Fig. 44); humeral angle rounded, lacking humeral carina. Indonesia. … ***A. silvorientalis*** Okayasu, **sp. nov.**
- Mandible with distinct acute subapical teeth (Figs 37, 45); humeral angle sharp, with developed humeral carina … 2
2. Mandible dilated apically, with dorsal subapical tooth larger and longer than minute middle subapical tooth (Fig. 42). Thailand, Vietnam. … ***A. rong*** Williams, **sp. nov.**
- Mandible parallel-sided or converging to apex, with two distinct subapical teeth, middle subapical tooth as large or larger than dorsal subapical tooth (Figs 37, 45) … 3
3. T3 with sparse black setae (Figs 68, 70); pygidial plate mostly smooth (Figs 82, 84) … 4
- T3 with pale setal band (Fig. 63); pygidial plate longitudinally rugose (Fig 77) … 6
4. Head dark red ventrally; mesosoma dark red with large black spot on posterior propodeal face; metasoma dark red; T2 posterior band narrow, white, medially interrupted. India. … ***A. paniya*** Terine, Lelej & Kumar
- Head entirely black; mesosoma entirely red; metasoma metallic blue; T2 posterior band wide, pale golden, entire … 5
5. Head punctures large confluent (Fig. 41); T2 disc with elongate pale setal spot (Fig. 68); lateral margin of pygidial plate carinate on posterior half (Fig. 82). Malaysia. … ***A. neaera*** (Mickel)
- Head punctures small sparse (Fig. 43); T2 disc without setal spot (Fig. 70); lateral margin of pygidial plate carinate throughout (Fig. 84). Malaysia. … ***A. sarawakensis*** Lelej
6. Mandible wide, height at dorsal subapical tooth subequal to height at midlength of mandible (Figs 38–40, 45, 47, 48) … 7
- Mandible slender, tapering to apex, height at dorsal subapical tooth greater than height at midlength of mandible (Figs 36, 37, 46) … 12
7. T2 metallic blue, discal spot reduced to few whitish setae (Fig. 75). Indonesia. … ***A. ursasolaris*** Williams, **sp. nov.**
- T2 black, discal spot elongate or ovate, well-defined (Figs 65, 72, 73, 76) … 8
8. T2 broadly depressed medially, with large ovate pale setal spot (Figs 67, 76) … 9
- T2 disc flattened or narrowly depressed medially, with medium elongate pale setal spot (Figs 65, 66, 72, 73) … 10
9. F1 dark brown (Fig. 40); legs orange basally, femoral apices, tibiae, and tarsi blackish (Fig. 5); posterior propodeal face with distinct medial longitudinal carina with sharp tubercle at anterior edge. Indonesia. … ***A. naturalis*** Williams, **sp. nov.**

- F1 orange (Fig. 48); legs entirely orange (Fig. 18); posterior propodeal face without longitudinal carina, at most with some puncture intervals aligned to form irregular apparent carina. Laos, Vietnam. … ***A. yotoi*** Okayasu, **sp. nov.**

10. Mandible apically oblique (Fig. 38); humeral carina lamellately projecting; T2 disc depressed medially; T2 punctures large (Fig. 65). Malaysia, Indonesia. … ***A. laminatihumeralis*** Okayasu, **sp. nov.**
- Mandible apically vertical (Figs 39, 45); humeral carina weakly developed; T2 disc scarcely flattened medially; T2 punctures small (Figs 66, 72, 73) … 11

11. S2 punctures separated by less than puncture diameter, postero-laterally confluent; lateral margins of pygidial plate convergent anteriorly, carinate on posterior half (Fig. 80); larger species (12 mm). Vietnam. … ***A. matsumotoi*** Okayasu, **sp. nov.**
- S2 punctures separated by more than 1.5× puncture diameter, evenly distributed; lateral margins of pygidial plate subparallel, carinate throughout (Fig. 86); smaller species (~9.7 mm). Widespread in East Asia. … ***A. substriolata*** (Chen)

12. Metasoma with bluish metallic luster (Fig. 63); T2 disc narrowly depressed medially, with very small anteromedial elongate whitish setal spot (Fig. 63); S1 black (Fig. 19); lateral margins of pygidial plate carinate on posterior half (Fig. 77). Malaysia. … ***A. auricoma*** Okayasu, **sp. nov.**
- Metasoma black (Figs 64, 74); T2 disc flattened medially, with moderate to large anteromedial pale golden setal spot (Figs 64, 74); S1 reddish (Figs 20, 33); lateral margins of pygidial plate carinate throughout (Figs 78, 87) … 13

13. Frons and vertex punctures confluent (Fig. 37); vertex with medial longitudinal carina; clypeus with medial tubercle; mesosoma elongate (Fig. 51), dorsal thoracic length 0.9× mesosomal width; T2 roughly as long as wide, length 0.96× width (Fig. 64); T2 discal spot elongate (Fig. 64). Thailand, Vietnam. … ***A. borkenti*** (Williams)
- Frons and vertex punctures dense (Fig. 46); vertex merely punctate; clypeus medially elevated but lacking tubercle; mesosoma compact (Fig. 60), dorsal thoracic length 0.8× mesosomal width; T2 wider than long, length 0.88× width (Fig. 74); T2 discal spot ovate (Fig. 74). Thailand. … ***A. takensis*** Okayasu, **sp. nov.**

Andreimyrme auricoma sp. nov.

(Figs 1, 19, 36, 50, 63, 77, 90)

Diagnosis

FEMALE. Head black; frons, vertex, and gena punctures large confluent; vertex with medial longitudinal carina; clypeus medially elevated but lacking tubercle. Mandible slender tridentate, tapering to apex, dorsal subapical tooth smaller than middle subapical tooth, middle subapical tooth smaller than apical tooth. F1 black. Mesosoma entirely red; dorsal thoracic length 0.9× mesosomal width; humeral carina lamellately projecting; posterior propodeal face without medial carina. Legs black with profemur basally yellow and mesofemur basally dark brown. Metasoma with bluish metallic luster; T2 length 0.88× width; T2 disc narrowly depressed medially, with anteromedial elongate spot of pale golden setae; T2 punctures large confluent; T2 posterior band wide, pale golden, complete; T3 with wide uniform band of pale golden setae; S1 black; S2 punctures large sparse; surface of pygidial plate longitudinally rugose anteriorly and smooth posteriorly; lateral margins of pygidial plate slightly convergent anteriorly, carinate on posterior half. MALE. Unknown.

Description

FEMALE. Body length 8.7 mm.

Color and setae. Head black with antennal rim, mandible basal 3/4, and scape apex

reddish brown; prementum and stipes dark brown; palpi dark yellow; pedicel brownish black; F2–10 ventrally dark brown; mesosoma yellowish red; procoxa brownish red; meso- and metacoxal anterior halves yellowish red; meso- and metacoxal posterior halves and trochanters dark brown; profemur mostly yellow; profemur apex brown; mesofemur mostly dark brown; mesofemur apex, metafemur, tibiae, and tarsi black; tibial spurs yellowish white; metasoma black with T1–2 and S2 metallic blue. Lower frons, meso-and metacoxa with sparse long recumbent and sparse long erect golden setae; upper frons and vertex with sparse short recumbent orange-golden and sparse long erect dark golden setae; antennal scrobe with sparse long appressed golden setae; eye dorsal margin with long erect black setae; gena, clypeus, mandible, and scape with sparse long recumbent golden setae; prementum, stipes, and palpi with sparse extremely short erect golden setae; pedicel and F1 with sparse short recumbent golden setae; F2–10 with dense extremely short recumbent golden setae; thoracic dorsum with sparse short recumbent orange-golden and sparser long erect black setae; posterior propodeal face and trochanters with sparse long erect golden setae; lateral face of mesosoma with sparse short appressed pale golden setae and with sparser long erect pale golden setae on mesopleural ventral half; procoxa with dense short appressed and sparse long recumbent golden setae; femora and tibiae with sparse short recumbent and sparser long erect golden setae; tarsi with sparse long appressed golden setae; T1, T2 around margins, T3, T4–6 laterally, S1–6 with sparse long erect pale golden setae; T2 disc and T4–5 medially with dense short recumbent and sparse long erect black setae; pygidial plate glabrous with thickened lateral pygidial fringe of long erect pale golden setae; T1 and S4–5 with posterior fringe of sparse long pale golden setae; T2 with narrow elongate (1.75× as long as wide) anteromedial spot of dense appressed pale golden setae not reaching anterior margin of T2, and with posterior narrow band of dense appressed pale golden setae slightly widened medially; minimum distance between spot and band on T2 2.66× spot length; T2 with lateral golden felt line; T3 with wide uniform band of dense appressed pale golden setae; S2–3 and S6 with posterior fringe od dense long pale golden setae.

Structure. Head 1.39× as wide as long in dorsal view; lateral margins strongly convergent behind eye; posterior margin truncate; vertex rounded posteriorly in lateral view; GOI = 1.30; vertex with medial longitudinal carina reaching upper frons; lower frons with short medial longitudinal groove; genal carina distinct; hypostomal tooth sharp; antennal scrobe with dorsal carina reaching mandibular base; eye oval, slightly protruding from head capsule; minimum distance between eyes 1.04× eye height; eye height 2.47× malar distance; vertex width 1.03× pronotal width; clypeus medially elevated but not forming tubercle, with subventral transverse ridge; anterior margin of transverse ridge medially shallowly emarginate. Mandible slender tridentate, dorsal subapcial tooth smaller than middle subapical tooth, middle subapical tooth smaller than apical tooth; ventral margin straight. Prementum with posterior rounded tubercle. Scape bending medially; F1 length 1.17× its width and 1.4× F2 length; F2–9 almost same in length and width; F10 slightly longer than F9, conical and weakly depressed.

Mesosoma broadest at pronotal spiracles, with lateral margins weakly convergent; ratio between head width:humeral width:pronotal width:mesonotal width:propodeal width:metasomal width = 100:80:86:79:80:116; dorsal thoracic length 0.90× pronotal width; thoracic dorsum posteriorly sloping in lateral view; anterior margin of dorsum of pronotum nearly straight, with a pair of very weak rounded sublateral tubercles; pronotum laterally weakly projecting but not forming distinct angle at pronotal spiracle; lateral margin of mesosoma weakly crenulate; humeral angle angulate; humeral carina lamellately projecting; prescutellar scales and metanotal-propodeal suture obliterated; dorsal and lateral propodeal faces not separated by carina; posterior propodeal face without medial longitudinal carina.

Metacoxa with weak complete inner longitudinal carina; meso- and metatibiae with a

pair of longitudinal rows of five spines on outer face; protarsus with external comb of long spines.

T1 without distinct dorsum; T2 disc medially narrowly depressed; dorsal T2 length 0.88× T2 width; S1 with straight medial longitudinal carina; S2 with anteromedial short inconspicuous longitudinal carina; posterior margin of S6 bidentate; pygidial plate slightly convex, elongate; lateral margins of pygidial plate slightly convergent anteriorly, weakly carinate on posterior half.

Frons, vertex, gena, thoracic dorsum, T1 posterior half, and T2 disc with large confluent punctures; clypeus, scape, pedicel, pronotal collar, coxae, and trochanters with minute sparse punctures; flagellum and mesosomal lateral face with minute dense punctures; posterior propodeal face reticulate; femora with minute sparse and small sparse punctures; tibiae, tarsi, and S3–5 with small sparse punctures; T1 anterior half, T2 laterally, S1–2 with large sparse puncture; T3–5, T6 laterally, and S6 with small confluent punctures; pygidial plate finely longitudinally rugose on anterior 2/3, smooth posteriorly.

MALE. Unknown.

Type material

1♀. Holotype ♀: **Malaysia:** NEGERI SEMBILAN: Pasoh Forest Reserve, 1.IV.1993, K. Konishi leg. [FRIM].

Distribution

Malaysia: Negeri Sembilan.

Etymology

The specific name *auricoma*, meaning “golden-haired”, is a Latin singular feminine adjective in the nominative case and refers to the orange-golden setae on the vertex and thoracic dorsum of this new species.

Remarks

This new species is similar to *A. borkenti* and *A. takensis* by having the mandible tapering to apex, but differs by having the frons and vertex with large confluent punctures (dense but separated in *A. takensis*), the vertex with medial carina (lacking in *A. takensis*), the clypeus medially elevated but lacking tubercle (with medial tubercle in *A. borkenti*), the metasoma with bluish metallic luster (metasomal integument black in *A. borkenti* and *A. takensis*), the S1 black (more or less reddish in *A. borkenti* and *A. takensis*), the T2 length 0.88× its width (subequal in *A. borkenti*), the T2 disc depressed medially (flattened in *A. borkenti* and *A. takensis*), the T2 spot small elongate (medium-sized in *A. borkenti*; large ovate in *A. takensis*), the pygidial plate finely longitudinally rugose (coarsely rugose in *A. takensis*), and the lateral margins of the pygidial plate carinate on the posterior half (carinate throughout in *A. borkenti* and *A. takensis*). This species was collected from a primary lowland forest during a field survey by Kazuhiko Konishi, probably by sweeping bushes (K. Konishi personal communication), as a part of Japan-Malaysia joint research project. The collecting site was described by Maetô *et al*. (1999).

***Andreimyrme borkenti* (Williams, 2019), comb. nov.**

(Figs 2, 20, 37, 51, 64, 78, 90)

Smicromyrme borkenti Williams in Williams *et al*., 2019b: 28, ♀, holotype ♀ (Phnom Bencha Mountain Resort, 14 km NNE Krabi, Krabi, Thailand) [CSCA], examined; Pagliano *et al*., 2020: 193.

Diagnosis.
FEMALE. Head black; frons, vertex, and gena punctures large confluent; vertex with medial longitudinal carina; clypeus with medial tubercle. Mandible slender tridentate, tapering to apex, dorsal subapical tooth smaller than middle subapical tooth, middle subapical tooth smaller than apical tooth. F1 black. Mesosoma entirely red; dorsal thoracic length 0.90× mesosomal width; humeral carina lamellately projecting; posterior propodeal face without medial carina. Legs yellowish red with femoral apices, tibiae, and tarsi dark brown to black. Metasoma black; T2 length 0.96× width; T2 disc flattened medially, with anteromedial elongate spot of golden setae; T2 punctures small confluent; T2 posterior band wide, pale golden, complete; T3 with wide uniform band of golden setae; S1 dark brown; S2 punctures large sparse; surface of pygidial plate finely longitudinally rugose on anterior 2/3 and smooth posteriorly; lateral margins of pygidial plate subparallel, carinate throughout. MALE. Unknown.

Material examined
8♀. Holotype ♀: **Thailand:** KRABI: 14 km NNE Krabi, Phnom Bencha Mountain Resort, 8.208°N 98.937°E, 80 m, 2.IV.2017, K. Williams et al. leg. [CSCA]. Paratypes: **Thailand:** KRABI: 14 km NNE Krabi, Phnom Bencha Mountain Resort, 8.208°N 98.937°E, 80 m, 3.IV.2017, K. Williams et al. leg. [2♀ CSCA]; NAKHON SI THAMMARAT: 4.4 km N Hin Tok, Mountainside rubber farm, 8.303°N 99.849°E, 7–8.IV.2017, K. Williams et al. leg. [3♀ CSCA, QSBG]; TRANG: Trang, 50 m, 7°33′N 99°36′E, 27.VII.1986, R. Hensen leg. [1♀ RMNH]. **Vietnam:** HANOI: Ba Vi, Mt. Tan Vien, 500 m, 15.X.1995, M. Tomokuni leg. [1♀ NSMT].

Distribution
Thailand: Krabi, Nakhon Si Thammarat, Trang. Vietnam*: Hanoi.

Remarks
Two of the paratypes of *A. borkenti* from Nakhon Si Thammarat have a broader mandible than the rest and actually belong to *A. substriolata*. A single female from Vietnam was identical to Thai specimens.

Andreimyrme laminatihumeralis sp. nov.
(Figs 3, 21, 38, 52, 65, 79, 90)

Diagnosis
FEMALE. Head black; frons, vertex, and gena punctures large confluent; vertex with medial longitudinal carina; clypeus with medial tubercle. Mandible wide tridentate, oblique to apex, dorsal subapical tooth distinct but smaller than middle subapical tooth, middle subapical tooth subequal to apical tooth. F1 black. Mesosoma red; dorsal thoracic length 0.91–0.95× mesosomal width; humeral carina lamellately projecting; posterior propodeal face without medial longitudinal carina. Legs largely yellowish red with apices of meso- and metafemora, meso- and metatibiae, and tarsi dark brown to black. Metasoma black; T2 length 0.89–0.92× width; T2 disc narrowly depressed medially, with anteromedial elongate spot of pale golden setae; T2 punctures large confluent; T2 posterior band wide, pale golden, complete; T3 with wide uniform band of pale golden to golden setae; S1 brown; S2 punctures large dense; surface of pygidial plate longitudinally rugose anteriorly and granulate posteriorly; lateral margins of pygidial plate subparallel, carinate throughout. MALE. Unknown.

Description

FEMALE. Body length 5.9 mm–8.1 mm (holotype: 8.1 mm; mean: 6.9 mm).

Color and setae. Head black with antennal rim yellowish brown to dark brown; mandible basal 2/3 yellowish brown: palpi brownish yellow; scape and pedicel brown; flagellum dark brown to black; F2–10 ventrally yellow to brown; mesosoma yellowish red; legs yellowish red with protibia yellowish red to dark brown; meso- and metafemoral apices, meso- and metatibiae, and tarsi dark brown to black; metasoma black with S1 brown. Frons and vertex with sparse short recumbent and sparser long erect golden-tinged black setae; antennal scrobe with sparse short recumbent golden setae; eye dorsal margin with long erect black setae; gena, clypeus, and scape with sparse long recumbent pale golden to golden setae; mandible, posterior propodeal face, T1, T2 around margins, T3, T4–5 laterally, T6, and S1–6 with sparse long erect pale golden to golden setae; prementum, stipes and palpi with extremely short erect golden setae; pedicel and F1 with sparse short recumbent golden setae; F2–10 with dense extremely short recumbent pale golden to golden setae; thoracic dorsum with sparse short recumbent golden to black and sparser long erect black setae; propleuron, mesopleuron posterior half, coxae and trochanters with sparse short appressed and sparser long erect pale golden setae; lateral face of mesosoma with sparse short appressed pale golden setae; femora and tibiae with sparse short recumbent and sparser long erect pale golden to golden setae; tarsi with sparse long appressed pale golden to golden setae; T2 disc with dense short recumbent and sparse short erect black setae; T4–5 medially with dense short recumbent and sparse long erect black setae; pygidial plate glabrous with thickened lateral pygidial fringe of long erect golden setae; T1 and S2–6 with posterior fringe of sparse long pale golden to golden setae; T2 with narrow elongate (2.06–2.92× as long as wide; holotype: 2.00; mean: 2.33) anteromedial spot of dense appressed pale golden to golden setae reaching anterior margin of T2, and with posterior narrow band of dense appressed pale golden to golden setae slightly widened medially; minimum distance between spot and band on T2 1.85–2.14× (holotype: 1.85; mean: 2.00) spot length; T2 with lateral golden felt line; T3 with wide uniform band of dense appressed pale golden to golden setae.

Structure. Head 1.37–1.47× (holotype: 1.37; mean: 1.43) as wide as long in dorsal view; lateral margins strongly convergent behind eye; posterior margin truncate; vertex rounded posteriorly in lateral view; gena narrow with GOI = 1.50–1.74 (holotype: 1.74; mean: 1.59); vertex with short medial longitudinal carina reaching upper frons; lower frons without medial groove; genal carina distinct; hypostomal tooth sharp; antennal scrobe with dorsal carina reaching mandibular base; eye oval, slightly protruding from head capsule; minimum distance between eyes 0.97–1.00× (holotype: 0.97; mean: 0.98) eye height; eye height 2.60–2.96× (holotype: 2.96; mean: 2.73) malar distance; vertex width 1.04–1.12 × (holotype: 1.09; mean: 1.08) pronotal width; clypeus medially elevated and forming short longitudinal tubercle not reaching anterior margin, with subventral transverse ridge; anterior margin of transverse ridge medially shallowly emarginated. Mandible wide tridentate, oblique to apex, dorsal subapical tooth distinct but smaller than middle subapical tooth, middle subapical tooth subequal to apical tooth; ventral margin straight. Prementum with posterior rounded tubercle. Scape bending medially; F1 length 1.14–1.27× (holotype: 1.24; mean: 1.21) its width and 1.33–1.40× (holotype: 1.40; mean: 1.36) F2 length; F2–10 almost same in length and width; F10 conical and weakly depressed.

Mesosoma broadest at pronotal spiracles, with lateral margins subparallel; ratio between head width:humeral width:pronotal width:mesonotal width:propodeal width:metasomal width (mean in parenthesis) = 100:71–75 (73):76–79 (77):71–75 (73):75–76 (75.7):109–111 (110), 100:75:79:75:76:111 in holotype; dorsal thoracic length 0.91–0.95× (holotype: 0.91; mean: 0.94) pronotal width; thoracic dorsum evenly convex in lateral view; anterior margin of dorsum of pronotum nearly straight, with a pair of small rounded

sublateral tubercles; pronotum laterally weakly projecting but not forming distinct angle at pronotal spiracle; lateral margin of mesosoma weakly crenulate; humeral angle angulate; humeral carina lamellately projecting; prescutellar scales and metanotal-propodeal suture obliterated; dorsal and lateral propodeal faces not separated by carina; posterior propodeal face without medial longitudinal carina.

Metacoxa with weak complete inner longitudinal carina; meso- and metatibiae with a pair of longitudinal rows of five spines on outer face; protarsus with external comb of long spines.

T1 without distinct dorsum; T2 disc medially narrowly depressed; dorsal T2 length 0.89–0.92 × (holotype: 0.89; mean: 0.91) T2 width; S1 with straight medial longitudinal carina; S2 with anteromedial short inconspicuous longitudinal carina; posterior margin of S6 bidentate; pygidial plate slightly convex, elongate; lateral margins of pygidial plate subparallel, weakly carinate throughout.

Frons, vertex, gena, thoracic dorsum, T1 posterior half, and T2 disc with large confluent punctures; clypeus, pedicel, F1 with minute sparse punctures; scape, pronotal collar, propleuron, femora, tibiae, tarsi, T1 anterior half, and S1 with small sparse punctures; F2–10, lateral face of pronotum, mesopleuron, metapleuron, lateral propodeal face, coxae, trochanters with minute dense punctures; posterior propodeal face reticulate; mesopleuron with minute dense punctures, with few large punctures on posterior half; T2 laterally and S2 with large dense punctures; T3–6 and S3–6 with small dense punctures; pygidial plate finely longitudinally rugose on anterior 4/9, obscurely granulate posteriorly.

MALE. Unknown.

Type material

3♀. Holotype ♀: **Malaysia:** TERENGGANU: Kuala Terengganu, near Kenyir Lake, 4.III.2003, T. Tsuru leg. [TUA]. Paratypes: **Indonesia:** ACEH: Sumatra Island, Aceh, Kota Cane, 28.IV.1998, H. Takizawa leg. [2♀ TUA].

Distribution

Indonesia: Aceh. Malaysia: Terengganu.

Etymology

The specific name *laminatihumeralis* is from a Latin singular feminine adjective *laminata*, meaning “lamellate”, and a Latin singular feminine adjective *humeralis*, meaning “humeral”, a compound Latin adjective in the nominative case referring to the lamellately projecting humeral carina of this new species, which is a key feature to separate it from *A. matsumotoi* and *A. substriolata*.

Remarks

This new species is similar to *A. matsumotoi* **sp. nov.** and *A. substriolata* by having the combination of the mandible wide, F1 black, the T2 spot elongate, the T3 with a pale setal band, and the pygidial plate finely longitudinally rugose, but differs by having the mandible apically oblique (vertical in *A. matsumotoi* and *A. substriolata*), the humeral carina lamellately projecting (weakly developed in *A. matsumotoi* and *A. substriolata*), the T2 disc narrowly depressed medially (flattened in *A. matsumotoi* and *A. substriolata*), the T2 punctures large confluent (small confluent in *A. substriolata*), the S2 punctures evenly distributed and separated by approximate puncture diameter (S2 punctures postero-laterally denser in *A. matsumotoi*; S2 punctures separated by more than 1.5× puncture diameter in *A. substriolata*), and the lateral margins of pygidial plate subparallel (convergent anteriorly in *A. matsumotoi*). By having the mandible apically oblique, *A. laminatihumeralis* **sp. nov.** is

similar to *A. neaera*, *A. paniya*, and *A. sarawakensis*, but this new species differs from these by having the mandible wider, the T2 coarsely punctate, and the T3 with a pale setal band. Although this species is distributed in Peninsular Malaysia and Sumatra, no differences were found between the continental and island populations.

***Andreimyrme matsumotoi* sp. nov.**

(Figs 4, 22, 39, 53, 66, 80, 90)

Diagnosis

FEMALE. Head black; frons, vertex, and gena punctures large confluent; vertex with medial longitudinal carina; clypeus with medial tubercle. Mandible wide tridentate, vertical to apex, dorsal subapical tooth distinct but smaller than middle subapical tooth, middle subapical tooth subequal to apical tooth. F1 black. Mesosoma entirely red; dorsal thoracic length 0.92× mesosomal width; humeral carina weakly developed; posterior propodeal face with medial longitudinal carina. Legs black with femoral bases yellowish red. Metasoma black; T2 length 0.92× width; T2 disc flattened medially, with anteromedial elongate spot of golden setae; T2 punctures small confluent; T2 posterior band wide, pale golden, complete; T3 with wide uniform band of golden setae; S1 dark brown; S2 punctures large dense; surface of pygidial plate longitudinally rugose anteriorly and granulate posteriorly, with many granule coalescing and forming longitudinally rugose surface; lateral margins of pygidial plate convergent anteriorly, carinate on posterior half. MALE. Unknown.

Description

FEMALE. Body length 12.1 mm.

Color and setae. Head black with antennal rim, mandible medial 1/4, scape apex, and pedicel dark brown; palpi yellowish brown; F2–7 ventrally yellow; mesosoma yellowish red; legs black with coxae, trochanters, and femoral bases yellowish red; tibial spurs yellow; metasoma black with S1 dark brown. Lower frons, gena, femora, tibiae, and S2 with sparse long recumbent and sparse long erect golden setae; upper frons and vertex with sparse short recumbent and sparser long erect black setae; antennal scrobe with sparse long appressed golden setae; eye dorsal margin with long erect black setae; clypeus with sparse long recumbent golden setae; mandible, posterior propodeal face, propleuron, procoxa, T1, T2 around margins, T3, T4–5 laterally, T6, S1, and S3–6 with sparse long erect golden setae; prementum, stipes and palpi with sparse extremely short erect golden setae; scape with sparse long recumbent golden setae; pedicel and F1 with sparse short recumbent golden setae; F2–10 with dense extremely short recumbent golden setae; thoracic dorsum with sparse short recumbent and sparser long erect black setae; lateral face of mesosoma with sparse short appressed golden setae; mesopleuron posterior half, lateral propodeal face, meso- and metacoxa, and trochanters with sparse short appressed and sparser long erect golden setae; tarsi with sparse long appressed golden setae; T2 disc with dense short recumbent and sparse short erect black setae; T4–5 with dense short recumbent and sparse long erect black setae; pygidial plate glabrous with thickened lateral pygidial fringe of long erect golden setae; T1 and S2–6 with posterior fringe of sparse long golden setae; T2 with narrow elongate (1.96× as long as wide) anteromedial spot of dense appressed golden setae reaching anterior margin of T2, and with posterior narrow band of dense appressed golden setae slightly widened medially; minimum distance between spot and band on T2 1.30× spot length; T2 with lateral golden felt line; T3 with wide uniform band of dense appressed golden setae.

Structure. Head 1.32× as wide as long in dorsal view; lateral margins strongly convergent behind eye; posterior margin truncate. vertex rounded posteriorly in lateral view; gena wide with GOI = 0.85; vertex with medial longitudinal carina reaching lower frons;

lower frons with short medial longitudinal groove; genal carina distinct; hypostomal tooth angulate; antennal scrobe with dorsal carina reaching mandibular base; eye oval, slightly protruding from head capsule; minimum distance between eyes 1.05× eye height; eye height 2.38× malar distance; vertex width 1.04× pronotal width; clypeus medially elevated and forming short longitudinal tubercle not reaching anterior margin, with subventral transverse ridge; anterior margin of transverse ridge medially deeply emarginate. Mandible wide tridentate, vertical to apex, dorsal subapical tooth distinct but smaller than middle subapical tooth, middle subapical tooth subequal to apical tooth; ventral margin straight. Prementum with posterior rounded tubercle. Scape bending medially; F1 length 1.12× its width and F2 length; F2–9 almost same in length and width; F10 slightly longer than F9, conical and weakly depressed.

Mesosoma broadest at pronotal spiracles, with lateral margins weakly convergent posteriorly; ratio between head width:humeral width:pronotal width:mesonotal width:propodeal width:metasomal width = 100:83:87:76:79:125; dorsal thoracic length 0.92× pronotal width; thoracic dorsum evenly convex in lateral view; anterior margin of dorsum of pronotum nearly straight, with a pair of small pointed sublateral teeth; pronotum laterally weakly projecting but not forming distinct angle at pronotal spiracle; lateral margin of mesosoma weakly crenulate; humeral angle angulate; humeral carina weakly developed; prescutellar scales and metanotal-propodeal suture obliterated; dorsal and lateral propodeal faces not separated by carina; posterior propodeal face with medial longitudinal carina reaching thoracic dorsum;

Metacoxa with weak complete inner longitudinal carina; meso- and metatibiae with a pair of longitudinal rows of eight spines on outer face; protarsus with external comb of long spines.

T1 without distinct dorsum; T2 disc medially flattened; dorsal T2 length 0.92× T2 width; S1 with straight medial longitudinal carina; S2 with anteromedial short inconspicuous longitudinal carina; posterior margin of S6 bidentate; pygidial plate slightly convex, elongate; lateral margins of pygidial plate convergent anteriorly, weakly carinate on posterior half.

Frons, vertex, gena, and thoracic dorsum with large confluent punctures; clypeus, pedicel, F1, tibiae, and tarsi with minute sparse punctures; scape, pronotal collar, propleuron, T1 anterior half, and S1 with small sparse punctures; F2–10, metapleuron, and lateral propodeal face with minute dense punctures; posterior propodeal face reticulate; lateral face of pronotum with minute dense and large dense punctures; mesopleuron with minute dense punctures, with few large punctures on ventral half; coxae, trochanters, and femora with minute dense and small sparse punctures; T1 posterior half and T2 disc with small confluent punctures; T2 laterally with large dense punctures; S2 with large dense punctures medially, confluent postero-laterally; T3–6 and S3–6 with small dense punctures; pygidial plate finely longitudinally rugose on anterior 7/8, granulate posteriorly, with many granule coalescing and forming longitudinally rugose surface.

MALE. Unknown.

Type material

1♀. Holotype ♀: **Vietnam:** VINH PHUC: Tam Dao, 900–1200 m, 6.V.1998, R. Matsumoto leg. [VNMN].

Distribution

Vietnam: Vinh Phuc.

Etymology

The specific name *matsumotoi* is dedicated to the type collector Rikio Matsumoto.

Remarks
This new species is superficially similar to *A. substriolata*, and these two species are separated by minor morphological differences, namely the density of S2 punctures and the shape of pygidial plate. *Andreimyrme matsumotoi* is, however, more than 1.2 times larger than *A. substriolata*, suggesting utilization of larger hosts because the body size of mutillids correlates to that of the hosts (Ferguson, 1962; Mickel, 1924). Additional specimens will enable formal analyses to test this hypothesis.

***Andreimyrme naturalis* sp. nov.**
(Figs 5, 23, 40, 54, 67, 81, 90)

Diagnosis
FEMALE. Head black; frons, vertex, and gena punctures large confluent; vertex with medial longitudinal carina; clypeus with medial tubercle. Mandible wide tridentate, vertical to apex, dorsal subapical tooth distinct but smaller than middle subapical tooth, middle subapical tooth subequal to apical tooth. F1 dark brown. Mesosoma entirely red; dorsal thoracic length 1.01× mesosomal width; humeral carina lamellately projecting; posterior propodeal face with medial longitudinal carina with sharp tubercle at anterior edge. Legs largely black. Metasoma black; T2 length 0.87× width; T2 disc depressed medially, with anteromedial large ovate spot of golden setae; T2 punctures small confluent; T2 posterior band wide, pale golden, complete; T3 with wide uniform band of pale golden setae; S1 yellowish red; S2 punctures large dense; surface of pygidial plate longitudinally rugose anteriorly and smooth posteriorly; lateral margins of pygidial plate weakly convergent anteriorly, carinate on posterior half.
MALE. Unknown.

Description
FEMALE. Body length 9.5 mm.

Color and setae. Head black with antennal rim, palpi, scape mostly, F1, and F2–10 dorsally dark brown; mandible except apical 1/4 and basal outer face yellowish brown; scape apex and pedicel orange-brown; F2–10 ventrally yellow-brown; mesosoma yellowish red; legs black with coxae, trochanters, and femoral bases yellowish red; tibial spurs yellow; metasoma black. Frons with sparse long recumbent golden and sparser long erect black setae; vertex with sparse short golden and sparser long erect black setae; antennal scrobe and lateral face of mesosoma with sparse short appressed pale golden setae; eye dorsal margin with long erect black setae; gena, femora, tibiae, and S2 with sparse long recumbent and sparser long erect pale golden setae; clypeus, pedicel and F1 with sparse short recumbent golden setae; mandible, posterior propodeal face, trochanters, T1, T2 around margins, T3, T6, S1, and S3–6 with sparse long erect golden setae; prementum, stipes and palpi with sparse extremely short erect golden setae; scape and procoxa with sparse long recumbent golden setae; F2–10 with dense extremely short recumbent golden setae; pronotal dorsum with sparse short recumbent orange and sparser long erect brown setae; thoracic dorsum posterior to pronotum with sparse short recumbent golden and sparser long erect brown setae; propleuron with sparse short recumbent and sparser long erect pale golden setae; mesopleuron ventral half and lateral propodeal face with sparse short appressed and sparser long erect pale golden setae; meso- and metacoxae with sparse short appressed and sparser short erect golden setae; tarsi with sparse long appressed golden setae; T2 disc with dense short recumbent and sparse short erect black setae; T4–5 with sparse long recumbent and sparser long erect black setae; pygidial plate glabrous with thickened lateral pygidial fringe of long erect golden setae; T1 and S2–6 with posterior fringe of sparse long golden setae; T2 with lateral golden felt line; T2 with

large ovate anteromedial spot of dense appressed pale golden setae; T2 posteriorly and T3 entirely with wide uniform band of dense appressed golden setae.

Structure. Head 1.22× as wide as long in dorsal view; lateral margins strongly convergent behind eye; posterior margin truncate; vertex rounded posteriorly in lateral view; gena wide with GOI = 1.17; vertex with medial longitudinal carina reaching middle frons; lower frons with short medial longitudinal groove; genal carina distinct; hypostomal tooth sharp; antennal scrobe with dorsal carina reaching mandibular base; eye oval, slightly protruding from head capsule; minimum distance between eyes 1.12× eye height; eye height 3.0× malar distance; vertex width 1.05× pronotal width; clypeus medially elevated and having short longitudinal tubercle dorsally, with subventral transverse ridge; anterior margin of transverse ridge medially shallowly emarginated. Mandible wide tridentate, vertical to apex, dorsal subapical tooth distinct but smaller than middle subapical tooth, middle subapical tooth subequal to apical tooth; ventral margin straight. Prementum with posterior rounded tubercle. Scape bending medially; F1 length 1.00× its width, 1.10× F2 length; F2–9 almost same in length and width; F10 slightly longer than F9, conical and weakly depressed.

Mesosoma broadest at humeral angle, with lateral margins weakly convergent; ratio between head width:humeral width:pronotal width:mesonotal width:propodeal width:metasomal width = 99:84:84:82:80:121; dorsal thoracic length 1.01× pronotal width; thoracic dorsum not posteriorly sloping; anterior margin of dorsum of pronotum relatively straight, with a pair of rounded sublateral tubercles; pronotum laterally not projecting; lateral margin of mesosoma weakly crenulate; humeral angle sharp angulate; humeral carina lamellate; prescutellar scales and metanotal-propodeal suture obliterated; dorsal and lateral propodeal faces separated by apparent wavy carina; posterior propodeal face with strong medial longitudinal carina and sharp tubercle anteriorly.

Metacoxa with weak complete inner longitudinal carina; meso- and metatibiae with a pair of longitudinal rows of six spines on outer face; protarsus with external comb of long spines.

T1 without distinct dorsum; T2 disc with broad medial depression; dorsal T2 length 0.87× T2 width; S1 with straight medial longitudinal carina; S2 with obscure anteromedial short inconspicuous longitudinal carina; posterior margin of S6 bidentate; pygidial plate slightly convex, elongate; lateral margins of pygidial plate weakly converging anteriorly, carinate on posterior half.

Frons, vertex, gena, and thoracic dorsum with large confluent punctures; clypeus, pedicel, F1, pronotal collar, meso- and metacoxae, trochanters, femora, tibiae, and tarsi with minute sparse punctures; scape and T1 anterior half with small sparse punctures; F2–10, lateral face of pronotum, metapleuron, and procoxa with minute dense punctures; posterior propodeal face reticulate; propleuron with minute sparse and small sparse punctures; mesopleuron and lateral propodeal face with minute dense punctures, with small sparser punctures; T1 posterior half and T2 disc with small confluent punctures; T2 laterally and S1–2 with large dense punctures; T3–6 and S3–6 with small dense punctures; pygidial plate finely longitudinally rugose on anterior 2/3, smooth posteriorly.

MALE. Unknown.

Type material

1♀. Holotype ♀: **Indonesia:** EAST JAVA: G[unung]. Raoeng [= Mt. Raung], “Bajoekidoel”, 450–700 m, XI.1931, H. Lucht leg. [RMNH].

Distribution

Indonesia: East Java.

Etymology
With special gratitude to Frederique Bakker, this species is named for the Naturalis Biodiversity Center in Leiden, the Netherlands. They have graciously facilitated the study of roughly 10,000 mutillid specimens from around the World by the author.

Remarks
This new species is similar to *A. yotoi* **sp. nov.** by having the mandible wide and the T2 disc broadly depressed, but differs from that species by having the antenna and legs darker and the propodeum with distinct longitudinal carina. *Andreimyrme naturalis* **sp. nov.** has a small sharp tubercle in the scutellar area, at the anterior edge of the longitudinal propodeal carina, which resembles a small scale.

Andreimyrme neaera **(Mickel, 1935)**
(Figs 6, 24, 41, 55, 68, 82, 90)

Smicromyrme neaera Mickel, 1935: 278, ♀, holotype ♀ (Sandakan, [Sabah], Borneo, [Malaysia]) [USNM].
Andreimyrme neaera: Lelej, 1996a: 100, ♀; Lelej, 2005: 38; Lo Cascio, 2015: 544; Okayasu *et al*., 2018: 303, ♀; Williams *et al*., 2019b: 16, ♀; Okayasu, 2020: 61, ♀, examined; Pagliano *et al*., 2020: 169.

Diagnosis
FEMALE. Head black; frons, vertex, and gena punctures large confluent; vertex without medial longitudinal carina; clypeus medially elevated but lacking tubercle. Mandible wide tridentate, oblique to apex, dorsal subapical tooth distinct but smaller than middle subapical tooth, middle subapical tooth subequal to apical tooth. F1 dark brown. Mesosoma entirely red; dorsal thoracic length 0.98× mesosomal width; humeral carina lamellately projecting; posterior propodeal face with medial longitudinal carina. Legs yellowish red with meso- and metafemoral apices, tibiae, and tarsi black. Metasoma with bluish metallic luster; T2 length 0.93× width; T2 disc flattened medially, with anteromedial elongate spot of pale golden setae; T2 punctures small confluent; T2 posterior band wide, pale golden, complete; T3 with black setae; S1 reddish; S2 punctures large sparse; surface of pygidial plate smooth; lateral margins of pygidial plate slightly convergent anteriorly, carinate on posterior half. MALE. Unknown.

Material examined
1♀. **Malaysia:** SABAH: Kalabakan, 3–11.IV.1973, K.M. Guichard leg., B. Petersen det. [1♀ ZMUC].

Distribution
Malaysia: Sabah.

Remarks
Andreimyrme neaera, *A. paniya*, and *A. sarawakensis* are recognized within *Andreimyrme* by lacking a pale setal band on T3 and having the pygidial plate smooth, but this species differs from the latter two by having the head black (ventrally reddish in *A. paniya*), the frons, vertex, and gena with large confluent punctures (with small sparse punctures in *A. sarawakensis*), the mesosoma entirely red (posterior propodeal face with black spot in *A. paniya*), the metasoma metallic blue (dark red in *A. paniya*), the T2 spot present (absent in *A. paniya* and *A. sarawakensis*), and the T2 posterior band wide and complete (narrow and interrupted in *A. paniya*). The specimen examined herein has the antennal rim, mandible, and

scape dark brown (ferruginous in holotype) and thoracic dorsum with black setae (ferruginous in holotype).

Andreimyrme paniya Terine, Lelej & Kumar, 2021
(Fig. 91)

Andreimyrme paniya Terine, Lelej & Kumar, 2021: 185, ♀, holotype ♀ (Periya, Wayanad District, Kerala, India) [ZSIK], examined.

Diagnosis
FEMALE. Head ventrally dark red; frons and vertex punctures large dense; gena punctures large confluent; vertex without medial longitudinal carina; clypeus with medial tubercle. Mandible wide tridentate, oblique to apex, dorsal subapical tooth distinct but smaller than middle subapical tooth, middle subapical tooth subequal to apical tooth. F1 black. Mesosoma dark red with large black spot on posterior propodeal face; dorsal thoracic length 0.94× mesosomal width; humeral carina lamellately projecting; posterior propodeal face without medial longitudinal carina. Legs yellowish red with femoral apices, tibiae, and tarsi black. Metasoma dark red; T2 length 1.05× width; T2 disc flattened medially, without anteromedial pale spot; T2 punctures small confluent; T2 posterior band narrow, white, medially interrupted; T3 with black setae; S2 punctures large sparse; surface of pygidial plate smooth; lateral margins of pygidial plate slightly convergent anteriorly, carinate on posterior half.
MALE. Unknown.

Material examined
Holotype ♀: **India:** KERALA: Wayanad district, Periya, Camp shed, 11°51′5.06″N 75°47′22.55″E, 594 m, 10.II.2021, K.A. Subramanian & party, ZSI/WGRC/IR/INV. 17336 [ZSIK].

Distribution
India: Kerala.

Remarks
This species is recognized in *Andreimyrme* by having the head ventrally and metasoma reddish, the posterior propodeal face with black spot, and the T2 posterior band medially interrupted. Although we added nine East Asian species to *Andreimyrme* based on females, *A. paniya* is still the sole member with the mesosoma and metasoma reddish, providing additional support to recognition of a color syndrome for *A. paniya* and similarly colored mutillids discovered in India (Lelej, 2020; Terine *et al*., 2021).

Andreimyrme rong sp. nov.
(Figs 7, 8, 25, 42, 56, 69, 83, 91)

Diagnosis
FEMALE. Head black; frons, vertex, and gena punctures large confluent; vertex with medial longitudinal carina; clypeus with medial tubercle. Mandible wide tridentate, vertical to apex, dorsal subapical tooth acute, larger than middle subapical or apical tooth, middle subapical tooth minute, sometimes obliterated. F1 blackish. Mesosoma entirely red; dorsal thoracic length 0.83× mesosomal width; humeral carina weakly developed; posterior propodeal face with medial longitudinal carina. Legs black with femoral bases yellowish red. Metasoma black; T2 length 0.88× width; T2 disc obscurely flattened medially, with anteromedial setal

spot variable in size, color, and shape; T2 punctures small confluent; T2 posterior band wide, pale golden, complete; T3 with wide uniform band of pale golden setae; S1 yellowish red; S2 punctures large dense; surface of pygidial plate obscurely imbricate; lateral margins of pygidial plate subparallel, carinate throughout. MALE. Unknown.

Description

FEMALE. Body length 4.5 mm–7.3 mm (holotype: 7.3 mm; mean: 5.6 mm).

Color and setae. Head black with antennal rim and palpi dark brown; mandible except apical 1/4 and basal outer face yellowish brown; scape and pedicel orange; F2–10 ventrally yellow-brown; mesosoma yellowish red; legs yellowish red with femoral apices, tibiae, and tarsi black; tibial spurs yellow; metasoma black. Frons with sparse long recumbent golden and sparser long erect black setae; vertex with sparse short blackish golden and sparser long erect black setae; antennal scrobe with sparse short appressed pale golden setae; eye dorsal margin with long erect black setae; gena, femora, tibiae, and S2 with sparse long recumbent and sparser long erect pale golden setae; clypeus, pedicel, and F1 with sparse short recumbent golden setae; mandible, posterior propodeal face, trochanters, T1, T2 around margins, T3, T6, S1, and S3–6 with sparse long erect golden setae; prementum, stipes and palpi with sparse extremely short erect golden setae; scape and procoxa with sparse long recumbent golden setae; F2–10 with dense extremely short recumbent golden setae; pronotal dorsum with sparse short recumbent orange and sparser long erect brown setae; thoracic dorsum posterior to pronotum with sparse short recumbent golden and sparser long erect brown setae; propleuron with sparse short recumbent and sparser long erect pale golden setae; lateral face of mesosoma with sparse short appressed pale golden setae; ventral half of mesopleuron and lateral propodeal face with sparse short appressed and sparser long erect pale golden setae; meso- and metacoxae with sparse short appressed and sparser short erect golden setae; tarsi with sparse long appressed golden setae; T2 disc with dense short recumbent and sparse short erect black setae; T4–5 with sparse long recumbent and sparser long erect black setae; pygidial plate glabrous with thickened lateral pygidial fringe of long erect golden setae; T1 and S2–6 with posterior fringe of sparse long golden setae; T2 with lateral golden felt line; T2 with large ovate anteromedial spot of dense appressed pale golden setae; T2 posteriorly and T3 entirely with wide uniform band of dense appressed golden setae.

Structure. Head 1.11× as wide as long in dorsal view; lateral margins strongly convergent behind eye; posterior margin truncate; vertex rounded posteriorly in lateral view; gena wide with GOI = 0.85; vertex with medial longitudinal carina reaching lower frons; lower frons with short medial longitudinal groove; genal carina distinct; hypostomal tooth sharp; antennal scrobe with dorsal carina reaching mandibular base; eye oval, slightly protruding from head capsule; minimum distance between eyes 1.32× eye height; eye height 2.10× malar distance; vertex width 1.15× pronotal width; clypeus medially elevated with rounded dorsal tubercle, with subventral transverse ridge; anterior margin of transverse ridge medially shallowly emarginated medially, trituberculate laterally. Mandible wide tridentate, vertical to apex, dorsal subapical tooth acute, larger than middle subapical or apical tooth, middle subapical tooth minute, sometimes obliterated; ventral margin straight. Prementum with posterior rounded tubercle. Scape bending medially; F1 length 1.33× its width, 1.50× F2 length; F2–9 almost same in length and width; F10 slightly longer than F9, conical and weakly depressed.

Mesosoma broadest at pronotal spiracles, with lateral margins subparallel; ratio between head width:humeral width:pronotal width:mesonotal width:propodeal width:metasomal width = 85:67:73:73:73:100; dorsal thoracic length 0.83× pronotal width; thoracic dorsum not posteriorly sloping; anterior margin of dorsum of pronotum rounded, with a pair of weak sublateral tubercles; pronotum laterally weakly projecting but not

forming distinct angle at pronotal spiracle; lateral margin of mesosoma weakly crenulate; humeral angle rounded; humeral carina present; prescutellar scales and metanotal-propodeal suture obliterated; dorsal and lateral propodeal faces separated by apparent wavy carina; posterior propodeal face with medial longitudinal carina.

Metacoxa with weak complete inner longitudinal carina; meso- and metatibiae with a pair of longitudinal rows of six spines on outer face; protarsus with external comb of long spines.

T1 without distinct dorsum; T2 disc medially flattened; dorsal T2 length 0.88× T2 width; S1 with straight medial longitudinal carina; S2 with angular posteromedial protuberance; posterior margin of S6 bidentate; pygidial plate slightly convex, elongate; lateral margins of pygidial plate subparallel, weakly carinate throughout but not enclosed.

Frons, vertex, gena, and thoracic dorsum with large confluent punctures; clypeus, pedicel, F1, pronotal collar, meso- and metacoxae, trochanters, femora, tibiae, and tarsi with minute sparse punctures; scape and T1 anterior half with small sparse punctures; F2–10, lateral face of pronotum, metapleuron, and procoxa with minute dense punctures; posterior propodeal face reticulate; propleuron with minute sparse and small sparse punctures; mesopleuron and lateral propodeal face with minute dense punctures, with small sparser punctures; T1 posterior half and T2 disc with small confluent punctures; T2 laterally and S1–2 with large dense punctures; T3–6 and S3–6 with small dense punctures; pygidial plate obscure imbricate.

MALE. Unknown.

Type material

5♀. Holotype ♀: **Vietnam:** DAK LAK: Chu Yang Sin National Park, Krong K'Mar, 740–900 m, 2–10.VI.2007, Malaise traps, C. v. Achterberg & R. de Vries leg. [RMNH]. Paratypes: **Thailand:** CHAIYAPHUM: Tat Tone National Park, 280 m, 15°58.538′N 102°02.153′E, 9–10.I.2007, pan trap, T1555, T. Jaruphan & O. Budasawong leg. [1♀ QSBG]; CHIANG MAI: Doi Intanon National Park, Campground pond, 1200 m, 18°32.40′N 98°31.80′E, 2–9.III.2007, Malaise trap, T1779, A. Areeluck leg. [1♀ QSBG]; PHETCHABURI: Kaeng Krachan National Park, 970 m, 12°47.83′N 99°27.37′E, 1–8.VIII.2008, malaise, T4357, Sirichai & Chusak leg. [1♀ QSBG]; SARABURI: Mai Ngerm Mai Thong Resort, 7 km NW Muak Lek, 14.711°N 101.165°E, 273 m, 15.III.2019, K. Williams et al. leg. [1♀ CSCA].

Distribution

Thailand: Chaiyaphum, Chiang Mai, Phetchaburi, Saraburi. Vietnam: Dak Lak.

Etymology

The specific name *rong* is from the Vietnamese *rồng* meaning "dragon" and is treated as a noun in apposition. The type species of *Andreimyrme*, *A. long*, is named using a Chinese word for dragon. These species have similar mandibles and may be eventually recognized as belonging to the same species.

Remarks

The mandibular shape of this new species is unique among females in the genus; only *A. silvorientalis* **sp. nov.** has a similar apically dilated mandible. *Andreimyrme rong* **sp. nov.** overlaps with the male genotype, *A. long*, in Chiang Mai, Thailand, although the latter species has not been formally recorded. The extremely dilated mandible shape of this female superficially resembles that of *A. long*. For this reason, I suspect that *A. rong* may eventually be recognized as the female for that species, which is why I provided a similar name.

Andreimyrme sarawakensis Lelej, 1996
(Figs 9, 26, 43, 57, 70, 84, 91)

Andreimyrme sarawakensis Lelej, 1996a: 100, ♀, holotype ♀ (Tower Region, Lambir National Park, Miri, Sarawak, Malaysia) [SKYC]; Lelej, 2005: 38; Lo Cascio, 2015: 544; Okayasu *et al*., 2018: 303, ♀; Okayasu, 2020: 61, ♀, examined; Pagliano *et al*., 2020: 169.

Diagnosis
FEMALE. Head black; frons, vertex, and gena punctures small sparse; vertex without medial carina; clypeus with medial tubercle. Mandible wide tridentate, oblique to apex, dorsal subapical tooth distinct but smaller than middle subapical tooth, middle subapical tooth subequal to apical tooth. F1 brown to black. Mesosoma entirely red; dorsal thoracic length 0.90–0.95× mesosomal width; humeral carina lamellately projecting; posterior propodeal face without medial carina. Legs yellowish red with tibiae and tarsi brown to black. Metasoma with bluish metallic luster; T2 length 0.94–1.0× width; T2 disc flattened medially, without anteromedial pale spot; T2 punctures small sparse; T2 posterior band wide, pale golden, complete; T3 with black setae; S1 reddish; S2 punctures small sparse; surface of pygidial plate obscurely longitudinally coarsely rugose anteriorly and smooth posteriorly; lateral margins of pygidial plate subparallel, carinate throughout. MALE. Unknown.

Material examined
3♀. **Malaysia:** KUALA LUMPUR: near Lake Gardens, H.M. Pendlebury leg., *Promecilla neaera* (Mickel), B. Petersen det. [1♀ ZMUC]; SABAH: 17 km west from Sandakan, Spilog, 200 m, 28.XI.1978, S. Nagai leg. [1♀ EUM]; SARAWAK: Kuching, K. Astana, 1–2, IX-8-’66 [1♀ HUM].

Distribution
Malaysia: Kuala Lumpur, Sabah*, Sarawak.

Remarks
This species is recognized in *Andreimyrme* by having the frons, vertex and gena with small sparse punctures (with large, dense to confluent punctures in others). This species was originally described based on a single specimen from Sarawak. In this study, we examined three additional specimens from Kuala Lumpur, Sabah, and Sarawak, and minor color variation was recognized: frons, vertex, and gena with golden to black setae; gena and clypeus dark brown; scape orange to black; protibia orange to black; T2 posterior margin dark brown to black with bluish metallic luster; T3–5 with brown to black recumbent setae; metasomal sterna reddish brown to black.

Andreimyrme silvorientalis sp. nov.
(Figs 10, 27, 44, 58, 71, 85, 91)

Diagnosis
FEMALE. Head black; frons, vertex, and gena punctures large confluent; vertex with medial longitudinal carina; clypeus with medial tubercle. Mandible wide, subapical teeth obliterated, replaced by blunt expansion. F1 black. Mesosoma entirely red; dorsal thoracic length 0.98× mesosomal width; humeral carina obliterated; posterior propodeal face without medial carina. Legs black with femoral bases yellowish red. Metasoma black; T2 length 0.90× width; T2 disc medially flattened, with anteromedial spot reduced to few golden setae; T2 punctures

small confluent; T2 posterior band wide, pale golden, complete; T3 with wide uniform band of golden setae; S1 black; S2 punctures large dense; surface of pygidial plate longitudinally rugose anteriorly and granulate posteriorly; lateral margins of pygidial plate subparallel, carinate throughout. MALE. Unknown.

Description

FEMALE. Body length 10.5 mm.

Color and setae. Head black with antennal rim, palpi, scape apex, and pedicel dark brown; mandible except apical 1/4 and basal outer face yellowish brown; F2–10 ventrally brown; mesosoma yellowish red; legs yellowish red with femoral apices, tibiae, and tarsi black; tibial spurs yellow; metasoma black. Frons with sparse long recumbent golden and sparser long erect black setae; vertex with sparse short blackish golden and sparser long erect black setae; antennal scrobe with sparse short appressed pale golden setae; eye dorsal margin with long erect black setae; gena, femora, tibiae, and S2 with sparse long recumbent and sparser long erect golden setae; clypeus, pedicel, and F1 with sparse short recumbent golden setae; mandible, posterior propodeal face, trochanters, T1, T2 around margins, T3, T6, S1, and S3–6 with sparse long erect golden setae; prementum, stipes, and palpi with sparse extremely short erect golden setae; scape and procoxa with sparse long recumbent golden setae; F2–10 with dense extremely short recumbent golden setae; pronotal dorsum with sparse short recumbent and sparser long erect black setae; thoracic dorsum posterior to pronotum with sparse short recumbent golden and sparser long erect black setae; propleuron with sparse short recumbent and sparser long erect pale golden setae; lateral face of mesosoma with sparse short appressed pale golden setae; ventral half of mesopleuron and lateral propodeal face with sparse short appressed and sparser long erect pale golden setae; meso- and metacoxae with sparse short appressed and sparser short erect golden setae; tarsi with sparse long appressed golden setae; T2 disc with dense short recumbent and sparse short erect black setae; T4–5 with sparse long recumbent and sparser long erect black setae; pygidial plate glabrous with thickened lateral pygidial fringe of long erect golden setae; T1 and S2–6 with posterior fringe of sparse long golden setae; T2 anteromedial spot reduced to few golden setae; T2 with lateral golden felt line; T3 with wide uniform band of dense appressed golden setae.

Structure. Head 1.28× as wide as long in dorsal view; lateral margins strongly convergent behind eye; posterior margin truncate; vertex rounded posteriorly in lateral view; gena wide with GOI = 1.08; vertex with medial longitudinal carina reaching lower frons; lower frons with short medial longitudinal groove; genal carina distinct; hypostomal tooth sharp; antennal scrobe with dorsal carina reaching mandibular base; eye oval, slightly protruding from head capsule; minimum distance between eyes 0.93× eye height; eye height 2.86× malar distance; vertex width 1.00× pronotal width; clypeus medially elevated and forming short longitudinal tubercle not reaching anterior margin, with subventral transverse ridge; anterior margin of transverse ridge medially shallowly emarginated. Mandible wide, inner teeth obliterated, replaced by blunt expansion; ventral margin straight. Prementum with posterior rounded tubercle. Scape bending medially; F1 length 1.13× its width, 1.08× F2 length; F2–9 almost same in length and width; F10 slightly longer than F9, conical and weakly depressed.

Mesosoma broadest at pronotal spiracles, with lateral margins subparallel; ratio between head width:humeral width:pronotal width:mesonotal width:propodeal width:metasomal width = 100:78:88:80:81:119; dorsal thoracic length 0.98× pronotal width; thoracic dorsum posteriorly sloping; anterior margin of dorsum of pronotum nearly straight, with a pair of very weak rounded sublateral tubercles; pronotum laterally weakly projecting but not forming distinct angle at pronotal spiracle; lateral margin of mesosoma weakly

crenulate; humeral angle rounded; humeral carina absent; prescutellar scales and metanotal-propodeal suture obliterated; dorsal and lateral propodeal faces not separated by carina; posterior propodeal face without medial longitudinal carina.

Metacoxa with weak complete inner longitudinal carina; meso- and metatibiae with a pair of longitudinal rows of six spines on outer face; protarsus with external comb of long spines.

T1 without distinct dorsum; T2 disc medially flattened; dorsal T2 length 0.90× T2 width; S1 with straight medial longitudinal carina; S2 with anteromedial short inconspicuous longitudinal carina; posterior margin of S6 bidentate; pygidial plate slightly convex, elongate; lateral margins of pygidial plate subparallel, weakly carinate throughout but not enclosed.

Frons, vertex, gena, and thoracic dorsum with large confluent punctures; clypeus, scape, pedicel, F1, pronotal collar, meso- and metacoxae, trochanters, femora, tibiae, and tarsi with minute sparse punctures; F2–10, lateral face of pronotum, metapleuron, and procoxa with minute dense punctures; posterior propodeal face reticulate; propleuron with minute sparse and small sparse punctures; mesopleuron and lateral propodeal face with minute dense punctures, with small sparser punctures; T1 anterior half with small sparse punctures; T1 posterior half and T2 disc with small confluent punctures; T2 laterally and S1–2 with large dense punctures; T3–6 and S3–6 with small dense punctures; pygidial plate finely longitudinally rugose on anterior 2/3, granulate posteriorly.

MALE. Unknown.

Type material

1♀. Holotype ♀: **Indonesia:** GOLONTALO: North Sulawesi, Pegunungan Tilongkabila [= Mts Tilongkabila], 500–800 m, 14–17.III.2009, K. Takasuka leg. [EUM].

Distribution

Indonesia: Golontalo.

Etymology

The specific name *silvorientalis* is from a Latin singular feminine noun *silva*, meaning "forest", and a Latin singular feminine adjective *orientalis*, meaning "eastern", a compound Latin adjective in the nominative case, indicating that this new species is the easternmost record of *Andreimyrme* in Southeast Asia, with an additional reference to its similarity to the Neotropical genus *Silvorientilla* Williams & Cambra, 2019 in the mandibular shape (Williams *et al*., 2019a).

Remarks

This new species is recognized in *Andreimyrme* by having the dorsal and middle subapical mandibular teeth and the humeral carina obliterated (more or less developed in others). This species was collected by Keizo Takasuka during a field survey in Sulawesi. The collecting site was described by Takasuka *et al*. (2011).

***Andreimyrme substriolata* (Chen, 1957)**

(Figs 11–15, 28–32, 45, 49, 59, 72, 73, 86, 92, 95)

Smicromyrme substriolata Chen, 1957: 209, ♀, holotype ♀ (Kuling [= Guling], Kiangsi [= Jiangxi], China) [TARI], examined.

Smicromyrme tridentiens Chen, 1957: 213, ♀, holotype ♀ (Tachulan [= Dazhulan], Shaowu, Fukien [= Fujian], China) [TARI], examined. Synonymized by Okayasu (2020: 58) under *Andreimyrme substriolata* (Chen).

Andreimyrme tridentiens: Lelej, 1995b: 8, ♀, examined; Lelej, 2005: 38; Okayasu *et al*., 2018: 303, ♀; Pagliano *et al*., 2020: 169.

Andreimyrme substriolata: Lelej, 1995b: 9, ♀, examined; Lelej, 2002: 50; Lelej, 2005: 38; Lo Cascio, 2015: 544; Okayasu *et al*., 2018: 303, ♀; Okayasu, 2020: 58, ♀, examined; Pagliano *et al*., 2020: 169.

Diagnosis

FEMALE. Head black; frons, vertex, and gena punctures large and confluent; vertex with medial longitudinal carina; clypeus with medial tubercle. Mandible wide tridentate, vertical to apex, dorsal subapical tooth distinct but smaller than middle subapical tooth, middle subapical tooth subequal to apical tooth. F1 black. Mesosoma entirely red; dorsal thoracic length 0.95–1.18× mesosomal width; humeral carina weakly developed; posterior propodeal face without medial carina. Legs variable, entirely red, mostly black with femoral bases red, or entirely black. Metasoma black, sometimes with bluish metallic luster; T2 length 0.88–0.98× width; T2 disc flattened medially, with anteromedial elongate spot of pale golden to golden setae; T2 punctures small confluent; T2 posterior band wide, pale golden, complete; T3 with wide uniform band of pale golden to golden setae; S1 yellowish red; S2 punctures large sparse; surface of pygidial plate longitudinally rugose anteriorly and smooth posteriorly; lateral margins of pygidial plate subparallel, carinate throughout. MALE. Unknown.

Material examined

29♀. Holotype ♀, *Smicromyrme substriolata* Chen, 1957: **China:** JIANGXI: Kuling [= Guling], 7.VIII.1935, O. Piel leg. [TARI]. Paratypes, *Smicromyrme substriolata* Chen, 1957: **China:** ANHUI: Anhwei [= Anhui], Ningkwo, 20.VII.1920 [1♀ TARI]; Wangshan [= Huangshan], 11.VII.1936 K.F. Chen leg. [1♀ TARI]; JIANGXI: Kuling [= Guling], 4.VII.1919 [1♀ TARI]; ZHEJIANG: [Lin'an, Hangzhou], Tienmushan [= Tianmushan], 6.VI.1936, O. Piel leg. [1♀ TARI]. Holotype ♀, *Smicromyrme tridentiens* Chen, 1957: **China:** FUJIAN: Shaowu, Tachulan [= Dazhulan], 26.IV.1942 [TARI]. **China:** FUJIAN: Fukien [= Fujian], Kuatun [= Guadun], 2300 m, 27.40°N 117.405°E, 11.V.1938, J. Kiapporich leg., *Smicromyrme substriolata* Chen, B. Petersen det. 1995 [1♀ ZMUC]; TAIWAN: Nantou, Lienwhachi, 25.III.1979, A. Shinohara leg., *Andreimyrme substriolata* (Chen), A.S. Lelej det. 1995 [1♀ NSMT]; Kaohsiung, Taoyuan, Paolai, 3.V.1996, H. Takizawa leg. [1♀ HUM]; Nantou, Tuchhsiang, Sun Moon Lake, Mt. Shuisho, 9.IV.2004, T. Mita leg. [1♀ TUA]; Taipei, Pinglin, Chenshanfu, 24.V.2010, N. Ohbayashi leg. [1♀ EUM]; ZHEJIANG: Hangzhou, Linan, Mt. West Tianmu-shan, 20–22.VIII.2001, N. Ohbayashi, L.-Z. Li & K. Kasahara leg. [1♀ EUM]. **Indonesia:** SUMATRA UTARA: Sumatra, Sibolangit, Urung Tame, 24.IV.1998, H. Takizawa leg. [1♀ TUA]. **Japan:** AMAMI ISLANDS: Amami-ôshima, Naze, Koshuku, Amami-chûô Forest Road, 200 m, 28.361°N 129.466°E, 3–7.VII.2017, Y. Komeda leg., yellow pan trap [2♀ ELKU]; Amami-ôshima, Naze, Koshuku, 28°21′45.0″N 129°27′50.0″E, 270 m alt., trail through forest, small gap, on forest floor, 3.VII.2021, 9:45 AM, J. Okayasu leg. [1♀ HUM]; OKINAWA ISLANDS: Okinawa-jima, Kunigami-son, Ie-rindô, 8.IV.2003, S. Arai leg. [1♀ TUA]. **Laos:** HOUA PHANH: Sam Neua, Mt. Pan, v.2013 [1♀ EUM]; XIENGKHOUANG: Ban Tha, 1200 m, 19°44′N 103°24′E, 4.V.2011, H. Sawada leg. [1♀ ELKU]. **Malaysia:** TERENGGANU: Kuala Terengganu, Kampung Pasil Dula, 1.III.2002, T. Tsuru leg. [1♀ TUA]. **Thailand:** CHIANG MAI: Doi Suthep, Chang Khian, 800–900 m, 8–11.V.2000, K. Okajima leg. [1♀ TUA]; NAKHON SI THAMMARAT: 4.4 km N Hin Tok, Mountainside rubber farm, 8.303°N 99.849°E, 7–8.IV.2017, K. Williams et al. leg. [2♀ CSCA]; PHETCHABUN: Nam Nao, 1.I.1955 [1♀ RUMF]. **Vietnam:** GIA LAI: Buon Luoi, 40 km N An Khe, 22–27.VI.1983, L.

Medvedev leg., *Andreimyrme tridentiens* (Chen), A.S. Lelej det. 1995 [1♀ IBSS]; HANOI: Mt. Bavi, 800–1000 m, VII.1941, A. De Cooman leg. [1♀ TARI]; HOA BINH: Da Bac, Tuly, forest, 20°52'17"N 105°15'13"E, 23.X.1990, S. Belokobylskij leg., *Andreimyrme tridentiens* (Chen), A.S. Lelej det. 1995 [2♀ IBSS]; THUA THIEN-HUE: 19 km point, Bach Ma National Park, 1400 m, 16.198°N 107.860°E, 3–6.VIII.2016, Y. Komeda & T. Mita leg., yellow pan trap [1♀ VNMN].

Distribution
China: Anhui, Fujian, Jiangxi, Zhejiang. Taiwan: Kaohsiung, Nantou, Taipei. Indonesia: Sumatra Utara. Japan: Amami Islands, Okinawa Islands. Laos: Houa Phanh, Xiengkhouang. Malaysia: Terengganu. Thailand: Chiang Mai, Nakhon Si Thammarat*, Phetchabun*. Vietnam: Gia Lai, Hanoi, Hoa Binh, Thua Tien-Hue.

Remarks
This species is similar to *A. laminatihumeralis* **sp. nov.** and *A. matsumotoi* **sp. nov.** as discussed above. The specific name of this species was originally spelled as *substriolata*, but should be masculine since the gender of *Smicromyrme* was subsequently regarded as masculine following Article 30.2.4 of ICZN (1999) (Lelej & Brothers, 2008). A redescription of *A. substriolata* was provided by Okayasu (2020). Taiwanese specimens differ from those of continental Asia and Sumatra by their entirely black legs and larger T2 spot (Fig. 14). Three females from Amami-ôshima Island are identical to the continental form, while a single female from Okinawa-jima Island is intermediate, with entirely black legs, and the T2 spot small (Fig. 15). Therefore, it is premature to describe the Taiwanese population as a separate species. Molecular experiments or discovery of the male are required to answer if these color variants are good species.

***Andreimyrme takensis* sp. nov.**
(Figs 16, 33, 46, 60, 74, 87, 91)

Diagnosis
FEMALE. Head black; frons and vertex punctures large dense; gena punctures large confluent; vertex without medial carina; clypeus medially elevated but lacking tubercle. Mandible slender tridentate, tapering to apex, dorsal subapical tooth smaller than middle subapical tooth, middle subapical tooth smaller than apical tooth. F1 pale brown. Mesosoma entirely red; dorsal thoracic length 0.82× mesosomal width; humeral carina lamellately projecting; posterior propodeal face without medial carina. Legs brown with femoral bases orange. Metasoma black; T2 length 0.88× width; T2 disc flattened medially, with anteromedial large ovate spot of golden setae; T2 punctures small confluent; T2 posterior band wide, pale golden, complete; T3 with wide uniform band of golden setae; S1 yellowish red; S2 punctures large dense; surface of pygidial plate coarsely longitudinally rugose anteriorly and granulate posteriorly; lateral margins of pygidial plate subparallel, carinate throughout. MALE. Unknown.

Description
FEMALE. Body length 5.2 mm.

Color and setae. Head black with gena, prementum, and stipes brownish black; antennal rim yellowish brown; clypeus except anterior margin of transverse ridge and F2–10 dorsally dark brown; mandible basal half yellow; palpi brownish yellow; scape and pedicel orange; F1 and F2–10 ventrally brown; mesosoma yellowish red; coxae, trochanters, and femora except femoral apices orange; femoral apices, tibiae, and apical tarsomere pale

brown; other tarsomeres brownish yellow; tibial spurs pale yellow; metasoma black with S1 yellowish red; S2 brownish black. Frons and vertex with sparse short recumbent golden and sparser long erect black setae; antennal scrobe with sparse long appressed pale golden setae; eye dorsal margin with long erect black setae; gena, coxae, trochanters, femora and tibiae with sparse long recumbent and sparse long erect pale golden setae; clypeus and scape with sparse long recumbent pale golden setae; mandible, posterior propodeal face, propleuron, T1, T2 around margins, T3, T6, and all sterna with sparse long erect pale golden setae; prementum, stipes and palpi with sparse extremely short erect pale golden setae; pedicel and F1 with sparse short recumbent pale golden setae; F2–10 with dense extremely short recumbent pale golden setae; thoracic dorsum with sparse short recumbent and sparser long erect black setae; lateral face of mesosoma with sparse short appressed pale golden setae; ventral half of mesopleuron with sparse short appressed and sparser long erect pale golden setae; tarsi with sparse long appressed pale golden setae; T2 disc with dense short recumbent and sparse long erect black setae; T4–5 with dense long recumbent and sparse long erect black setae; pygidial plate glabrous with thickened lateral pygidial fringe of long erect golden setae; T1 and S2–6 with posterior fringe of sparse long golden setae; T2 with large ovate (1.11× as long as wide) anteromedial spot of dense appressed golden setae reaching anterior margin of T2, and with posterior narrow band of dense appressed golden setae slightly widened medially; minimum distance between spot and band on T2 0.70× spot length; T2 with lateral golden felt line; T3 with wide uniform band of dense appressed golden setae.

Structure. Head 1.45× as wide as long in dorsal view; lateral margins strongly convergent behind eye; posterior margin truncate; vertex rounded posteriorly in lateral view; gena narrow with GOI = 2.00; vertex without medial longitudinal carina; lower frons with short medial longitudinal groove; genal carina distinct; hypostomal tooth sharp; antennal scrobe with dorsal carina reaching mandibular base; eye oval, slightly protruding from head capsule; minimum distance between eyes 1.02× eye height; eye height 2.62× malar distance; vertex width 1.04× pronotal width; clypeus medially elevated but not forming tubercle, with subventral transverse ridge; anterior margin of transverse ridge medially shallowly emarginated. Mandible slender tridentate, dorsal subapical tooth smaller than middle subapical tooth, middle subapical tooth smaller than apical tooth; ventral margin straight. Prementum with posterior rounded tubercle. Scape bending medially; F1 length 1.25× its width and F2 length; F2–9 almost same in length and width; F10 slightly longer than F9, conical and weakly depressed.

Mesosoma broadest at pronotal spiracles, with lateral margins weakly convergent posteriorly; ratio between head width:humeral width:pronotal width:mesonotal width:propodeal width:metasomal width = 100:78:88:80:81:119; dorsal thoracic length 0.82× pronotal width; thoracic dorsum evenly convex in lateral view; anterior margin of dorsum of pronotum nearly straight, without sublateral tooth or tubercle; pronotum laterally weakly projecting but not forming distinct angle at pronotal spiracle; lateral margin of mesosoma weakly crenulate; humeral angle angulate; humeral carina lamellately projecting; prescutellar scales and metanotal-propodeal suture obliterated; dorsal and lateral propodeal faces not separated by carina; posterior propodeal face without medial longitudinal carina.

Metacoxa with weak complete inner longitudinal carina; meso- and metatibiae with a pair of longitudinal rows of five spines on outer face; protarsus with external comb of long spines.

T1 without distinct dorsum; T2 disc medially flattened; dorsal T2 length 0.88× T2 width; S1 with straight medial longitudinal carina; S2 with anteromedial short inconspicuous longitudinal carina; posterior margin of S6 bidentate; pygidial plate slightly convex, elongate; lateral margins of pygidial plate subparallel, weakly carinate throughout but not enclosed.

Frons, vertex, T2 laterally, and S2 with large dense punctures; gena and thoracic

dorsum with large confluent punctures; clypeus, pedicel, F1, pronotal collar, propleuron, coxae, trochanters, femora, tibiae, and tarsi with minute sparse punctures; scape, T1, S1, and S3–6 with small sparse punctures; F2–10, lateral face of pronotum, metapleuron, and lateral propodeal face with minute dense punctures; posterior propodeal face reticulate; mesopleuron with minute dense punctures, with few large punctures on ventral half; T2 disc with small confluent punctures; T3–6 with small dense punctures; pygidial plate coarsely longitudinally rugose on anterior 2/3, granulate posteriorly.

MALE. Unknown.

Type material

1♀. Holotype ♀: **Thailand:** TAK: Sam Nagao, Bhumibol Dam, 6–8.XI.1979, Zool. Mus. Copenhagen Exped. [ZMUC].

Distribution

Thailand: Tak.

Etymology

The specific name *takensis* is a Latin singular feminine adjective in the nominative case and derived from Tak, the Thai province where the type locality of this new species is located.

Remarks

This new species is similar to *A. auricoma* **sp. nov.** and *A. borkenti* as discussed above. Given the wide distribution of *A. rong* **sp. nov.** in northern Thailand, *A. takensis* **sp. nov.** may share the overlapping geographical range with this species. These two species are potentially confusing because of the overall body color, specifically the scape orange, the legs basally yellowish red, and the T2 with a ovate setal spot. However, *A. takensis* differs from *A. rong* by having the mandible slender with two acute subapical teeth (mandible wide and apically dilated in *A. rong*).

Andreimyrme ursasolaris sp. nov.

(Figs 17, 34, 47, 61, 75, 88, 91)

Diagnosis

FEMALE. Head black; frons, vertex, and gena punctures large confluent; vertex without medial carina; clypeus with medial tubercle. Mandible wide tridentate, vertical to apex, dorsal subapical tooth distinct but smaller than middle subapical tooth, middle subapical tooth subequal to apical tooth. F1 blackish. Mesosoma entirely red; dorsal thoracic length 0.92× mesosomal width; humeral carina weakly developed; posterior propodeal face without medial carina. Legs black with femoral bases yellowish red. T1–2 metallic blue, T3–6 blackish; T2 length 0.95× width; T2 disc obscurely flattened medially, with anteromedial spot mostly obliterated, represented by few appressed anteromedial silvery setae; T2 punctures small confluent; T2 posterior band wide, pale golden, complete; T3 with wide uniform band of golden setae; S1 yellowish red; S2 punctures large sparse; surface of pygidial plate finely longitudinally rugose anteriorly and smooth posteriorly; lateral margins of pygidial plate weakly convergent anteriorly, carinate throughout. MALE. Unknown.

Description

FEMALE. Body length 6.3 mm.

Color and setae. Head black with antennal rim and palpi dark brown; mandible except apical 1/4 and basal outer face yellowish brown; scape and pedicel dark red-brown; F2–10

ventrally brown; mesosoma yellowish red; legs yellowish red with femoral apices, tibiae, and tarsi black; tibial spurs yellow; metasoma black with T1–2 and S2 metallic blue; S1 orange. Frons with sparse long recumbent golden and sparser long erect black setae; vertex with sparse short blackish golden and sparser long erect black setae; antennal scrobe with sparse short appressed pale golden setae; eye dorsal margin with long erect black setae; gena, femora, tibiae and S2 with sparse long recumbent and sparser long erect pale golden setae; clypeus with sparse short recumbent golden setae; mandible, trochanters, T1, T2 around margins, T3, T6, S1, and S3–6 with sparse long erect golden setae; prementum, stipes and palpi with sparse extremely short erect golden setae; scape and procoxa with sparse long recumbent golden setae; pedicel and F1 with sparse short recumbent golden setae; F2–10 with dense extremely short recumbent golden setae; pronotal dorsum with sparse suberect blackish setae; thoracic dorsum posterior to pronotum with sparse short and long suberect blackish setae; posterior propodeal face with sparse long erect interspersed blackish and golden setae; propleuron with sparse short recumbent and sparser long erect pale golden setae; lateral face of mesosoma with sparse short appressed pale golden setae; ventral half of mesopleuron and lateral propodeal face with sparse short appressed and sparser long erect pale golden setae; meso- and metacoxae with sparse short appressed and sparser short erect golden setae; tarsi with sparse long appressed golden setae; T2 disc with dense short recumbent and sparse short erect black setae; T4–5 with sparse long recumbent and sparser long erect black setae; pygidial plate glabrous with thickened lateral pygidial fringe of long erect golden setae; T1 and S2–6 with posterior fringe of sparse long golden setae; T2 anteromedial spot reduced to few silvery setae; T2 with lateral golden felt line; T3 with wide uniform band of dense appressed golden setae.

Structure. Head 1.11× as wide as long in dorsal view; lateral margins strongly convergent behind eye; posterior margin truncate; vertex rounded posteriorly in lateral view; gena wide with GOI = 1.1; vertex without medial longitudinal carina but with many intervals aligned to form apparent parallel striae; lower frons without medial longitudinal groove; genal carina distinct; hypostomal tooth sharp; antennal scrobe with dorsal carina reaching mandibular base; eye oval, slightly protruding from head capsule; minimum distance between eyes 1.03× eye height; eye height 2.22× malar distance; vertex width 1.05× pronotal width; clypeus medially elevated and forming short longitudinal tubercle not reaching anterior margin, with subventral transverse ridge; anterior margin of transverse ridge medially shallowly emarginated, laterally wavy. Mandible wide tridentate, vertical to apex, dorsal subapical tooth distinct but smaller than middle subapical tooth, middle subapical tooth subequal to apical tooth; ventral margin straight. Prementum with posterior rounded tubercle. Scape bending medially; F1 length 1.0× its width, 1.17× F2 length; F2–9 almost same in length and width; F10 slightly longer than F9, conical and weakly depressed.

Mesosoma broadest at pronotal spiracles, with lateral margins subparallel; ratio between head width:humeral width:pronotal width:mesonotal width:propodeal width:metasomal width = 81:66:74:71:71:100; dorsal thoracic length 0.92× pronotal width; thoracic dorsum not posteriorly sloping; anterior margin of dorsum of pronotum rounded, with a pair of very weak rounded sublateral tubercles; pronotum laterally weakly projecting but not forming distinct angle at pronotal spiracle; lateral margin of mesosoma weakly crenulate; humeral angle angulate; humeral carina present; prescutellar scales and metanotal-propodeal suture obliterated; dorsal and lateral propodeal faces not separated by carina; posterior propodeal face without medial longitudinal carina.

Metacoxa with weak complete inner longitudinal carina; meso- and metatibiae with a pair of longitudinal rows of six spines on outer face; protarsus with external comb of long spines.

T1 without distinct dorsum; T2 disc obscurely flattened; dorsal T2 length 0.95× T2

width; S1 with straight medial longitudinal carina; S2 without anteromedial longitudinal carina; posterior margin of S6 bidentate; pygidial plate slightly convex, elongate; lateral margins of pygidial plate weakly convergent anteriorly, weakly carinate throughout but not enclosed.

Frons, vertex, gena, and thoracic dorsum with large confluent punctures; clypeus, pedicel, F1, pronotal collar, meso- and metacoxae, trochanters, femora, tibiae, and tarsi with minute sparse punctures; scape and T1 with small sparse punctures; F2–10, lateral face of pronotum, metapleuron, and procoxa with minute dense punctures; posterior propodeal face reticulate; propleuron with minute sparse and small sparse punctures; mesopleuron and lateral propodeal face with minute dense punctures, with small sparser punctures; T2 disc with small confluent punctures; T2 laterally and S1–2 with large sparse punctures; T3–6 and S3–6 with small dense punctures; pygidial plate with obscure longitudinal scratches anterolaterally, smooth posteriorly.

MALE. Unknown.

Type material

1♀. Holotype ♀: **Indonesia:** ACEH: Sumatra, Aceh, Ketambe, 400 m, I.1995, Malaise trap near rainforest edge, Y. v. Nierop & C. v. Achterberg leg. [RMNH].

Distribution

Indonesia: Aceh.

Etymology

The specific name *ursasolaris* is from a Latin singular feminine noun *ursa*, meaning “female bear”, and a Latin singular feminine adjective *solaris*, meaning “of the sun”, a compound Latin adjective in the nominative case. This species is named in honor of the Sun Bear, *Helarctos malayanus* (Raffles, 1821), a charismatic mammal species native to southeast Asia, including Sumatra.

Remarks

Like the Bornean species, *A. neaera* and *A. sarawakensis*, this new species has the metasoma metallic blue and the mandible wide, but it can be recognized by having a silvery setal band on T3 (T3 setae blackish in *A. neaera* and *A. sarawakensis*). The only other species with a metallic blue metasoma, *A. auricoma* **sp. nov.**, has the mandible slender, unlike *A. ursasolaris* **sp. nov.**

***Andreimyrme yotoi* sp. nov.**

(Figs 18, 35, 48, 62, 76, 89, 91)

Diagnosis

FEMALE. Head black; frons, vertex, and gena punctures large confluent; vertex with medial longitudinal carina; clypeus with medial tubercle. Mandible wide tridentate, vertical to apex, dorsal subapical tooth distinct but smaller than middle subapical tooth, middle subapical tooth subequal to apical tooth. F1 orange. Mesosoma entirely red; dorsal thoracic length 0.89× mesosomal width; humeral carina lamellately projecting; posterior propodeal face without medial longitudinal carina. Legs entirely orange. Metasoma black; T2 length 0.85× width; T2 disc widely depressed medially, with anteromedial large ovate spot of golden setae; T2 punctures large confluent; T2 posterior band wide, golden, complete; T3 with wide uniform band of golden setae; S1 yellowish red; S2 punctures large dense; surface of pygidial plate longitudinally rugose anterolaterally, smooth medially and granulate posterolaterally;

lateral margins of pygidial plate subparallel. MALE. Unknown.

Description

FEMALE. Body length 9.2 mm.

Color and setae. Head black with antennal rim yellowish brown; mandible basal 3/4 reddish yellow; prementum and stipes dark brown; palpi brownish yellow; scape, pedicel, F1, and F2–10 ventrally orange; mesosoma yellowish red; legs orange with apical tarsomere black; tibial spurs reddish yellow; metasoma black with T1 anterior 2/3 and S1 yellowish red; S2 dark brown. Frons, vertex, thoracic dorsum, coxae, and trochanters with sparse short recumbent and sparser long erect golden setae; antennal scrobe and tarsi with sparse long appressed golden setae; eye dorsal margin with long erect black setae; gena, clypeus and scape with sparse long recumbent golden setae; mandible, posterior propodeal face, T1, T2 around margins, T3, T6, S1, and S3–6 with sparse long erect golden setae; prementum, stipes and palpi with sparse extremely short erect pale golden setae; pedicel and F1 with sparse short recumbent golden setae; F2–10 with dense extremely short recumbent golden setae; propleuron and mesopleural ventral half with sparse short appressed and sparser long erect golden setae; lateral face of mesosoma with sparse short appressed golden setae; femora, tibiae, and S2 with sparse long recumbent and sparser long erect golden setae; T2 disc with dense short recumbent and sparse short erect black setae; T4–5 with dense short recumbent and sparse long erect golden setae; pygidial plate glabrous with thickened lateral pygidial fringe of long erect golden setae; T1 and S2–6 with posterior fringe of sparse long golden setae; T2 with large ovate (1.24× as long as wide) anteromedial spot of dense appressed golden setae reaching anterior margin of T2, and with posterior narrow band of dense appressed golden setae slightly widened medially; minimum distance between spot and band on T2 0.83× spot length; T2 with lateral golden felt line; T3 with wide uniform band of dense appressed golden setae.

Structure. Head 1.43× as wide as long in dorsal view; lateral margins strongly convergent behind eye; posterior margin truncate; vertex rounded posteriorly in lateral view; gena narrow with GOI = 1.56; vertex with medial longitudinal carina reaching upper frons; lower frons without medial groove; genal carina distinct; hypostomal tooth sharp; antennal scrobe with dorsal carina reaching mandibular base; eye oval, slightly protruding from head capsule; minimum distance between eyes 1.10× eye height; eye height 3.08× malar distance; vertex width 1.05× pronotal width; clypeus medially elevated and forming short longitudinal tubercle not reaching anterior margin, with subventral transverse ridge; anterior margin of transverse ridge medially shallowly emarginated. Mandible wide tridentate, vertical to apex, dorsal subapical tooth distinct but smaller than middle subapical tooth, middle subapical tooth subequal to apical tooth; ventral margin straight. Prementum with posterior rounded tubercle. Scape bending medially; F1 length 1.12× its width and F2 length; F2–9 almost same in length and width; F10 slightly longer than F9, conical and weakly depressed.

Mesosoma broadest at pronotal spiracles, with lateral margins subparallel; ratio between head width:humeral width:pronotal width:mesonotal width:propodeal width:metasomal width = 100:74:81:72:74:116; dorsal thoracic length 0.89× pronotal width; thoracic dorsum posteriorly sloping in lateral view; anterior margin of dorsum of pronotum nearly straight, with a pair of small pointed sublateral teeth; pronotum laterally weakly projecting but not forming distinct angle at pronotal spiracle; lateral margin of mesosoma weakly crenulate; humeral angle angulate; humeral carina lamellately projecting; prescutellar scales and metanotal-propodeal suture obliterated; dorsal and lateral propodeal faces not separated by carina; posterior propodeal face without medial longitudinal carina.

Metacoxa with weak complete inner longitudinal carina; meso- and metatibiae with a pair of longitudinal rows of four spines on outer face; protarsus with external comb of long

spines.

T1 without distinct dorsum; T2 disc medially widely depressed; dorsal T2 length 0.85× T2 width; S1 with straight medial longitudinal carina; S2 with anteromedial short inconspicuous longitudinal carina; posterior margin of S6 bidentate; pygidial plate slightly convex, elongate; lateral margins of pygidial plate subparallel, weakly carinate throughout but not enclosed.

Frons, vertex, gena, thoracic dorsum, T1 posterior half, and T2 disc with large confluent punctures; clypeus, scape, pedicel, pronotal collar, propleuron, coxae, trochanters, femora, tibiae, and tarsi with minute sparse punctures; flagellum, mesopleuron, metapleuron, and lateral propodeal face with minute dense punctures; posterior propodeal face reticulate; lateral face of pronotum, T2 laterally, and S2 with large dense punctures; T1 anterior half and S1 with large sparse punctures; T3–6 with small dense punctures; S3–6 with small sparse punctures; pygidial plate finely longitudinally rugose laterally on anterior 2/3, granulate posterolaterally, unsculptured medially.

MALE. Unknown.

Type material

2♀. Holotype ♀: **Vietnam:** NINH BINH: Nho Quan, Cuc Phuong National Park, 500 m, 20.348°N 105.598°E, 9–11.VIII.2016, yellow pan trap, Y. Komeda & T. Mita leg. [VNMN]. Paratype: **Laos**: ATTAPEU: Thong Kai Ohk, Ban Kachung, (Mai) env., 1200–1450 m, 15°01–02′N 107°26–27′E, 10–23.VI.2011, M. Brancucci, M. Geier, D. Hauck, Z. Kraus, A. Phantala & E. Vongphachan leg. [1♀ NMB].

Distribution

Laos: Attapeu. Vietnam: Ninh Binh.

Etymology

The specific name *yotoi* is dedicated to the type collector Yôto Komeda.

Remarks

This new species is most similar to *A*. *naturalis* **sp. nov.** as discussed above. The holotype of this species was collected in a yellow pan trap together with males of *Odontomutilla* Ashmead, 1899 (Mutillinae: Mutillini) and *Krombeinidia* Lelej, 1996 (Mutillinae: Trogaspidiini), and females of *Hemutilla* Lelej, Tu & Chen, 2014 (Sphaeropthalminae), *Bischoffitilla* Lelej, 2002 (Myrmillinae), *Mickelomyrme* Lelej, 1995, and *Smicromyrme* (Mutillinae: Smicromyrmini). However, no potential male was found.

Discussion

Female mutillids have limited ability in host searching due to aptery. Mark-recapture analysis undertook by Evans *et al*. (1973) found that females of *Dasymutilla nigripes* (Fabricius, 1787) were restricted in an area within 400 feet (little over 120 m) from the initial collecting site. Therefore, mutillids exhibit situation-specific host choice, i.e. utilization of various host species with similar ecological traits that are found in particular environment (Brothers, 1989; Ronchetti & Polidori, 2020). However, explicit mention of habitats is generally rare in the literature.

I recently visited Amami-ôshima where two females of *A*. *substriolata* had been collected previously. One female was collected from a small gap in a dense and humid subtropical secondary forest (Figs 93, 94). This female specimen was found walking on a forest floor. Likewise, the holotypes of *A*. *auricoma* and *A*. *silvorientalis* were collected from

tropical forests (Maetô *et al*., 1999; Takasuka *et al*., 2011). Those collecting records suggest forested habitats of *Andreimyrme*. Although no host information is presently available, we assume that *Andreimyrme* species parasitize ground-nesting hosts, because females of this genus have the protarsal rake and the pygidial plate flattened, bounded by lateral carinae (Krombein, 1972; Williams *et al*., 2011). Additionally, a female of *A. substriolata* ran more quickly and confidently than a female of an arboreal mutillid *Petersenidia fukudai* (Tsuneki, 1972) collected from the same place (personal observation; http://movspec.mus-nh.city.osaka.jp/ethol/showdetail-e.php?movieid=momo210725as01b&home=0; http://movspec.mus-nh.city.osaka.jp/ethol/showdetail-e.php?movieid=momo210725pf01b&home=0), further suggesting the ground-dwelling nature of *A. substriolata*.

The tridentate mandible of *Andreimyrme* females is unique among Smicromyrmini. More interestingly, this genus shows great variation in this character. *Andreimyrme auricoma*, *A. borkenti*, and *A. takensis* have the mandible slender, tapering to the apex (Figs 36, 37, 46). *Andreimyrme substriolata* and eight additional species have the mandible wide, with the apical teeth arranged vertically (*A. matsumotoi*, *A. naturalis*, *A. ursasolaris*, and *A. yotoi*; Figs 39, 40, 45, 47) or obliquely (*A. laminatihumeralis*, *A. neaera*, *A. paniya*, and *A. sarawakensis*; Figs 38, 41, 43). *Andreimyrme rong* and *A. silvorientalis* have the middle or both dorsal and middle preapical teeth obliterated, with an apically dilated shape (Figs 42, 44). Contrarily, females of other smicromyrmine genera exhibit little mandibular variation; the mandible is slender with one or no subapical teeth. The mandible of *Andreimyrme* is likely an adaptation to ecological traits of hosts which are found in forested habitats, because *A. silvorientalis* and females of the Neotropical genus *Silvorientilla* (Sphaeropthalminae) share the apically dilated mandible, suggesting convergent evolution. Both genera were collected from subtropical or tropical forests. However, evidence for the potential advantage of the mandibles of most of *Andreimyrme* species has not been studied.

Mutillids can be difficult to collect in forested habitats (Williams *et al*., 2019b), so females of forest-inhabiting mutillids are rarely found in museum collections (e.g., Okayasu 2021). Overall, I could examine only 58 *Andreimyrme* specimens from South and Southeast Asia through this study (Figs 90–92). Of the 14 *Andreimyrme* species based on the female sex, 13 are recognized from fewer than 10 specimens, and, six of the nine new species described herein are singletons. Despite of the limited number of material, however, the species diversity of female *Andreimyrme* was expanded by 350% in the present paper. This implies the greater abundance and diversity of mutillids in tropical and subtropical forests of Southeast Asia. I emphasize the urgent need to elucidate the biodiversity of mutillids in Southeast Asian tropical forests, that are recently threatened by deforestation (Sodhi *et al*., 2010; Hughes, 2017). I hope this paper will facilitate discovery of additional specimens and even more new species of *Andreimyrme* and other forest-inhabiting mutillids in Southeast Asia.

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References

André, E. (1898) Étude sur les mutillides du Muséum de Paris. *Annales de la Société Entomologique de France* 67: 1–79.

André, E. (1902 [1903]) Family Mutillidae. *In*: Wytsman, P. (ed.) *Genera Insectorum*. *Fascicles 11*. L. Desmet-Verteneuil, Bruxelles, pp. 1–77 + 3 pls.

Ashmead, W.H. (1899) Superfamilies in the Hymenoptera and generic synopses of the families Thynnidae, Myrmosidae, and Mutillidae. *Journal of the New York Entomological Society* 7: 45–60.

Bartholomay, P.R., Williams, K.A., Lopez, V.M. & Oliveira, M.L. (2019) Revision of the *Traumatomutilla americana* species group (Hymenoptera: Mutillidae). *Zootaxa* 4608 (1): 1–34. https://doi.org/10.11646/zootaxa.4608.1.1

Bartholomay, P.R., Williams, K.A., Luz, D.R. & Oliveira, M.L. (2018) New species of *Traumatomutilla* André in the *T. tabapua* and *T. integella* species-groups (Hymenoptera, Mutillidae). *Zootaxa* 4433 (2): 361–385. https://doi.org/10.11646/zootaxa.4433.2.7

Bischoff, H. (1920–1921) Monographie der Mutilliden Afrikas. *Archiv für Naturgeschichte* 86A(1–3): 1–480 (1920); 86A(4–5): 481–830 (1921).

Brothers, D.J. (1989) Alternative life-history styles of mutillid wasps (Insecta, Hymenoptera). *In*: Bruton, M.N. (ed.) *Alternative life-history styles of animals*. *Perspectives in vertebrate sciences 6*. Springer, Dordrecht, pp. 279–291. https://doi.org/10.1007/978-94-009-2605-9_14

Brothers, D.J. & Lelej, A.S. (2017) Phylogeny and higher classification of Mutillidae (Hymenoptera) based on morphological reanalyses. *Journal of Hymenoptera Research* 60: 1–97. https://doi.org/10.3897/jhr.60.20091

Cameron, P. (1909) Descriptions of two new species of *Mutilla* from Kuching, Borneo. *The Entomologist* 42: 146–147. https://doi.org/10.1002/mmnd.48019090204

Chen, C.-w. (1957) A revision of the velvety ants or Mutillidae of China (Hymenoptera). *Quarterly Journal of the Taiwan Museum* 10 (3–4): 135–224 + 6 pls.

Evans, D.A., Miller, B.R. & Bartlett, C.B. (1973) Host searching range of *Dasymutilla nigripes* (Fabricius) as investigated by tagging (Hymenoptera: Mutillidae). *Journal of the Kansas Entomological Society* 46 (3): 343–346.

Fabricius, J.C. (1787) *Mantissa insectorum sistens eorum species nuper detecta, adjectis characteribus genericis, differentiis specificis, emendationibus, observationibus*. *Tom. I*. Impensis Christ. Gottl. Proft, Hafniae, 348 pp. https://doi.org/10.5962/bhl.title.36471

Ferguson, W.E. (1962) Biological characteristics of the mutillid subgenus *Photopsis* Blake and their systematic values. *University of California Publications in Entomology* 27: 1–92.

Gauld, I.D. & Mitchell, P.A. (1981) *The taxonomy, distribution and host preferences of Indo-Papuan parasitic wasps of the subfamily Ophioninae (Hymenoptera: Ichneumonidae)*. CAB: Slough. Commonwealth Institute of Entomology, London, 611 pp.

Hadley, A. (2008) CombineZM software. Available from: https://combinezm.en.lo4d.com/ (accessed 10 September 2021)

Harris, R.A. (1979) A glossary of surface sculpturing. *Occasional Papers in Entomology* 28: 1–31.

Hughes, A.C. (2017) Understanding the drivers of Southeast Asian biodiversity loss. *Ecosphere* 8 (1): e01624. https://doi.org/10.1002/ecs2.1624

Hymenoptera Anatomy Consortium (2021) Hymenoptera glossary. Available from: http://glossary.hymao.org/ (accessed 10 September 2021)

International Commission on Zoological Nomenclature (ICZN) (1999) *International Code of Zoological Nomenclature*. *4th edition*. ITZN, London, xxx + 306 pp.

Krombein, K.V. (1972) Monograph of the Madagascan Mutillidae (Hymenoptera). Part I: Myrmillini, Mutillini and Smicromyrmini. *Annales, Musée Royal de l'Afrique Centrale*, Série in 8°, Sciences Zoologiques 199: I–X + 1–61.

Lelej, A.S. (1985) *Osy-nemki (Hymenoptera, Mutillidae) Fauny SSSR i Sopredelnykh Stran* [*The velvet ants (Hymenoptera, Mutillidae) of the USSR and neighboring countries*]. Nauka, Leningrad, 268 pp. (in Russian)

Lelej, A.S. (1995a) A review of Palaearctic and Oriental species of genus *Nemka* Lelej with description of Oriental genus *Mickelomyrme* gen. n. (Hymenoptera, Mutillidae). *Far Eastern Entomologist* 6: 1–20.

Lelej, A.S. (1995b) To the knowledge of East Asian species of the tribe Smicromyrmini Bischoff, 1920 (Hymenoptera, Mutillidae) with description of four new genera and eight new species. *Far Eastern Entomologist* 13: 1–28.

Lelej, A.S. (1996a) Mutillid wasps collected in Malaysia and Indonesia by Dr. Sk. Yamane (Hymenoptera, Mutillidae). *Tropics* 6 (1–2): 91–104. https://doi.org/10.3759/tropics.6.91

Lelej, A.S. (1996b) To the knowledge of the East Asian species of the tribe Trogaspidiini Bischoff, 1920 (Hymenoptera, Mutillidae) with description of eight new genera and two new species. *Far Eastern Entomologist* 30: 1–24.

Lelej, A.S. (2002) *Catalogue of the Mutillidae (Hymenoptera) of the Palaearctic Region*. Dalnauka, Vladivostok, 172 pp.

Lelej, A.S. (2005) *Catalogue of the Mutillidae (Hymenoptera) of the Oriental Region*. Dalnauka, Vladivostok, 252 pp.

Lelej, A.S. (2007) Biogeography of mutillid wasps (Hymenoptera, Mutillidae). *In*: Rasnitsyn, A.P. & Gokhman, V.E. (eds) *Studies on hymenopterous insects*. *Collection of scientific papers*. KMK Scientific Press Ltd., Moscow, pp. 82–111. (in Russian)

Lelej, A.S. (2020) Three new species of velvet ants from the tribe Smicromyrmini (Hymenoptera: Mutillidae) with unusual color syndrome. *Far Eastern Entomologist* 421: 1–9. https://doi.org/10.25221/fee.421.1

Lelej, A.S. & Brothers, D.J. (2008) The genus-group names of Mutillidae (Hymenoptera) and their type species, with a new genus, new name, new synonymies, new combinations and lectotypifications. *Zootaxa* 1889 (1): 1–79. https://doi.org/10.11646/zootaxa.1889.1.1

Lelej, A.S. & Kabakov, O.N. (1980) On Bradynobaenidae and Mutillidae (Hymenoptera) of Afghanistan. *Entomologicheskoe Obozrenie* 59 (1): 181–196. (in Russian). [English translation (1981) in *Entomological Review* 59 (1): 141–156]

Lelej, A.S., Ullah, M. & Mahmood, K. (2007) Additions to the knowledge of the Mutillidae (Hymenoptera) of Pakistan. *Zootaxa* 1444 (1): 53–60. https://doi.org/10.11646/zootaxa.1444.1.4

Lo Cascio, P. (2015) Worldwide checklist of the island mutillid wasps (Hymenoptera Mutillidae). *Biodiversity Journal* 6 (2): 529–592.

Maetô, K., Fukuyama, K. & Kirton, L.G. (1999) Edge effects on ambrosia beetle assemblages in a lowland rain forest, bordering oil palm plantations, in peninsular Malaysia. *Journal of Tropical Forest Science* 11 (3): 537–547.

Mickel, C.E. (1924) An analysis of a bimodal variation in size of the parasite *Dasymutilla*

bioculata Cresson (Hymen.: Mutillidae). *Entomological News* 35: 236–242.
Mickel, C.E. (1933) The Mutillidae of Eastern Asia. *Lingnan Science Journal* 12 (3): 289–325.
Mickel, C.E. (1934) Mutillidae of the Philippine Islands. *Philippine Journal of Science* 54 (1): 91–219 + 1 pl.
Mickel, C.E. (1935) The mutillid wasps of the islands of the Pacific Ocean (Hymenoptera, Mutillidae). *Transactions of the Royal Entomological Society of London* 83 (2): 177–312. https://doi.org/10.1111/j.1365-2311.1935.tb01207.x
Okayasu, J. (2017) Two new species of the genus *Sinotilla* Lelej, 1995 (Hymenoptera: Mutillidae), with notes on taxonomic characters. *Zootaxa* 4294 (2): 151–169. https://doi.org/10.11646/zootaxa.4294.2.1
Okayasu, J. (2020) Velvet ants of the tribe Smicromyrmini Bischoff (Hymenoptera: Mutillidae) of Japan. *Zootaxa* 4723 (1): 1–110. https://doi.org/10.11646/zootaxa.4723.1.1
Okayasu, J. (2021) A new velvet ant genus *Arkaditilla* (Hymenoptera, Mutillidae, Trogaspidiini) from the Oriental Region, with review of species. *Journal of Hymenoptera Research* 84: 145–168. https://doi.org/10.3897/jhr.84.68709
Okayasu, J., Williams, K.A. & Lelej, A.S. (2018) A remarkable new species of the genus *Sinotilla* Lelej (Hymenoptera: Mutillidae: Smicromyrmini) from Taiwan and an overview of color diversity in East Asian mutillid females. *Zootaxa* 4446 (3): 301–324. https://doi.org/10.11646/zootaxa.4446.3.1
Pagliano, G., Brothers, D.J., Cambra, R., Lelej, A.S., Lo Cascio, P., Matteini Palmerini, M., Scaramozzino, P.L., Williams, K.A. & Romano, M. (2020) Checklist of names in Mutillidae (Hymenoptera), with illustrations of selected species. *Bollettino del Museo Regionale di Scienze Naturali di Torino* 36 (1–2): 5–425.
Raffles, T.S. (1821) XVII. Descriptive catalogue of a zoological collection, made on account of the honourable East India Company, in the island of Sumatra and its vicinity, under the direction of Sir Thomas Stamford Raffles, lieutenant- governor of Fort Marlborough; with additional notices illustrative of the natural history of those countries. *Transactions of the Linnean Society of London* 13 (1): 239–274. https://doi.org/10.1111/j.1095-8339.1821.tb00064.x
Ronchetti, F. & Polidori, C. (2020) A sting affair: A global quantitative exploration of bee, wasp and ant hosts of velvet ants. *PLoS ONE* 15 (9): e0238888. https://doi.org/10.1371/journal.pone.0238888
Shorthouse, D.P. (2010) SimpleMappr, an online tool to produce publication-quality point maps. Available from: http://www.simplemappr.net (accessed 5 August 2021)
Smith, F. (1865) Descriptions of new species of hymenopterous insects from the islands of Sumatra, Sula, Gilolo, Salwatty, and New Guinea, collected by Mr. A. R. Wallace. *Journal of the Proceedings of the Linnean Society*, Zoology 8: 61–94 + pl. 4. https://doi.org/10.1111/j.1096-3642.1865.tb02422.x
Sodhi, N.S., Koh, L.P., Clements, R., Wanger, T.C., Hill, J.K., Hamer, K.C., Clough, Y., Tscharntke, T., Posa, M.R.C. & Lee, T.M. (2010) Conserving Southeast Asian forest biodiversity in human-modified landscape. *Biological Conservation* 143 (10): 2375–2384. https://doi.org/10.1016/j.biocon.2009.12.029
Takasuka, K., Watanabe, K. & Konishi, K. (2011) Genus *Cryptopimpla* Taschenberg new to Sulawesi, Indonesia, with description of a new species (Hymenoptera, Ichneumonidae, Banchinae). *Journal of Hymenoptera Research* 23: 65–75. https://doi.org/10.3897/jhr.23.1595
Terine, J.B., Lelej, A.S. & Kumar, G.P. (2021) Discovery of the genus *Andreimyrme* Lelej, 1995 (Hymenoptera: Mutillidae) in India and description of a new species from the

Western Ghats. *Zootaxa* 5020 (1): 184–190. https://doi.org/10.11646/zootaxa.5020.1.10

Thomson, C.G. (1870) Öfversigt af Sveriges rofsteklar. *Opuscula Entomologica*, Lund 1 (2): 202–251.

Tsuneki, K. (1972) Studies on the Mutillidae of Japan (Hymenoptera). *Etizenia* 61: 1–26.

Tu, B.-B., Lelej, A.S. & Chen, X.-X. (2014) Review of the genus *Cystomutilla* André, 1896 (Hymenoptera: Mutillidae: Sphaeropthalminae: Sphaeropthalmini), with description of the new genus *Hemutilla* gen. nov. and four new species from China. *Zootaxa* 3889 (1): 71–91. https://doi.org/10.11646/zootaxa.3889.1.4

Turrisi, G.F. & Foucart, A. (2008) Description of a gynandromorphic *Myrmilla calva* (Villiers 1789), with a summary on gynandromorphism phenomenon within Mutillidae (Hymenoptera: Scolioidea). *Linzer biologische Beiträge* 40 (2): 1873–1880.

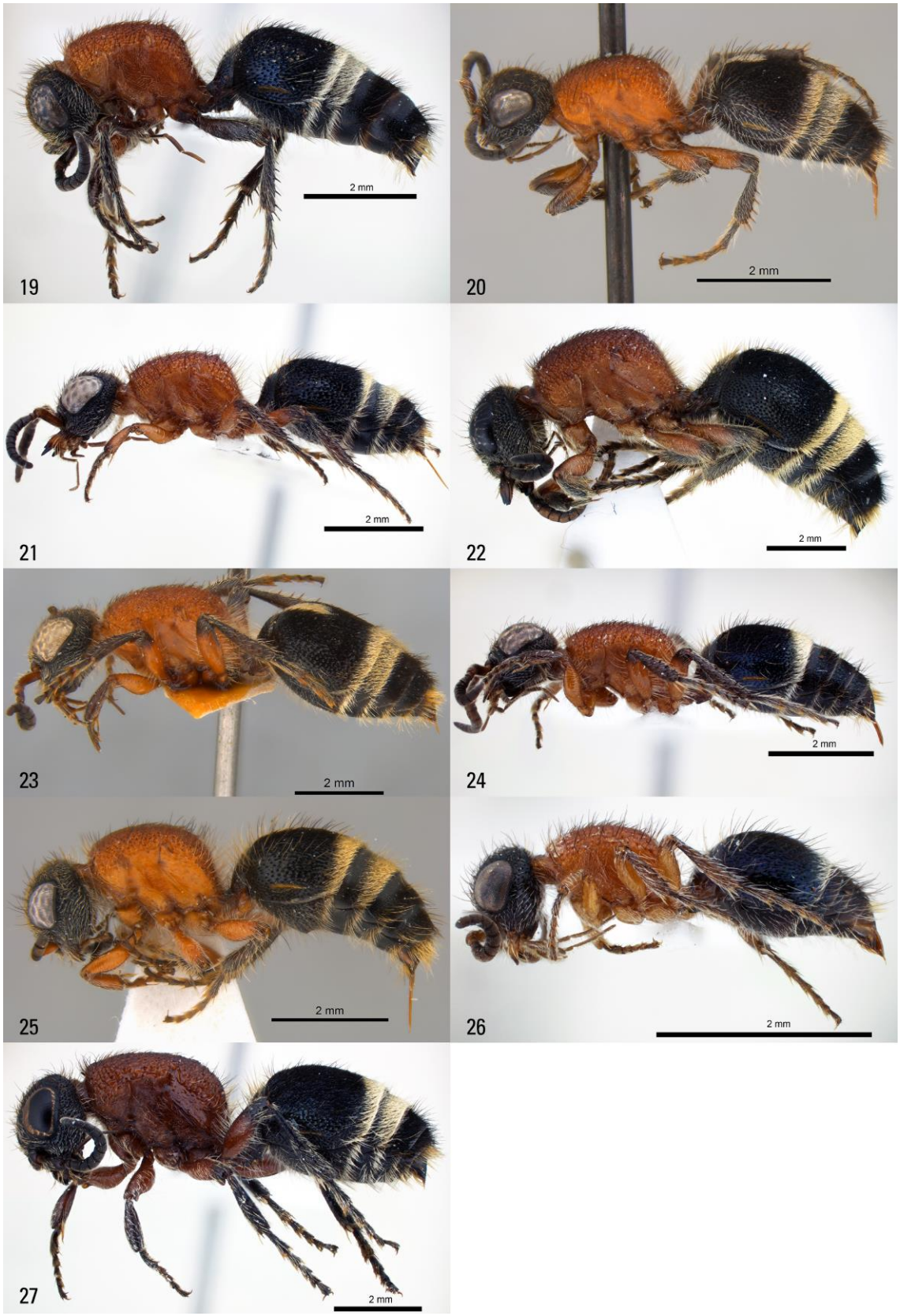
Williams, K.A., Brothers, D.J. & Pitts, J.P. (2011) New species of *Tobantilla* Casal, 1965 and a new genus and species, *Gogoltilla chichikovi* gen. et sp. nov., from Argentina (Hymenoptera: Mutillidae). *Zootaxa* 3064 (1): 41–68. https://doi.org/10.11646/zootaxa.3064.1.2

Williams, K.A., Cambra, R.A., Waldren, G.C., Quintero, D. & Pitts, J.P. (2019a) *Silvorientilla*, gen. nov. a new Neotropical velvet ant genus (Hymenoptera: Mutillidae). *Folia Entomológica Mexicana*, Nueva Serie 4 (3): 91−109.

Williams, K.A., Lelej, A.S., Okayasu, J., Borkent, C.J., Malee, R., Thoawan, K. & Thaochan, N. (2019b) The female velvet ants (aka modkhong) of southern Thailand (Hymenoptera: Mutillidae), with a key to the genera of southeast Asia. *Zootaxa* 4602 (1): 1–69. https://doi.org/10.11646/zootaxa.4602.1.1

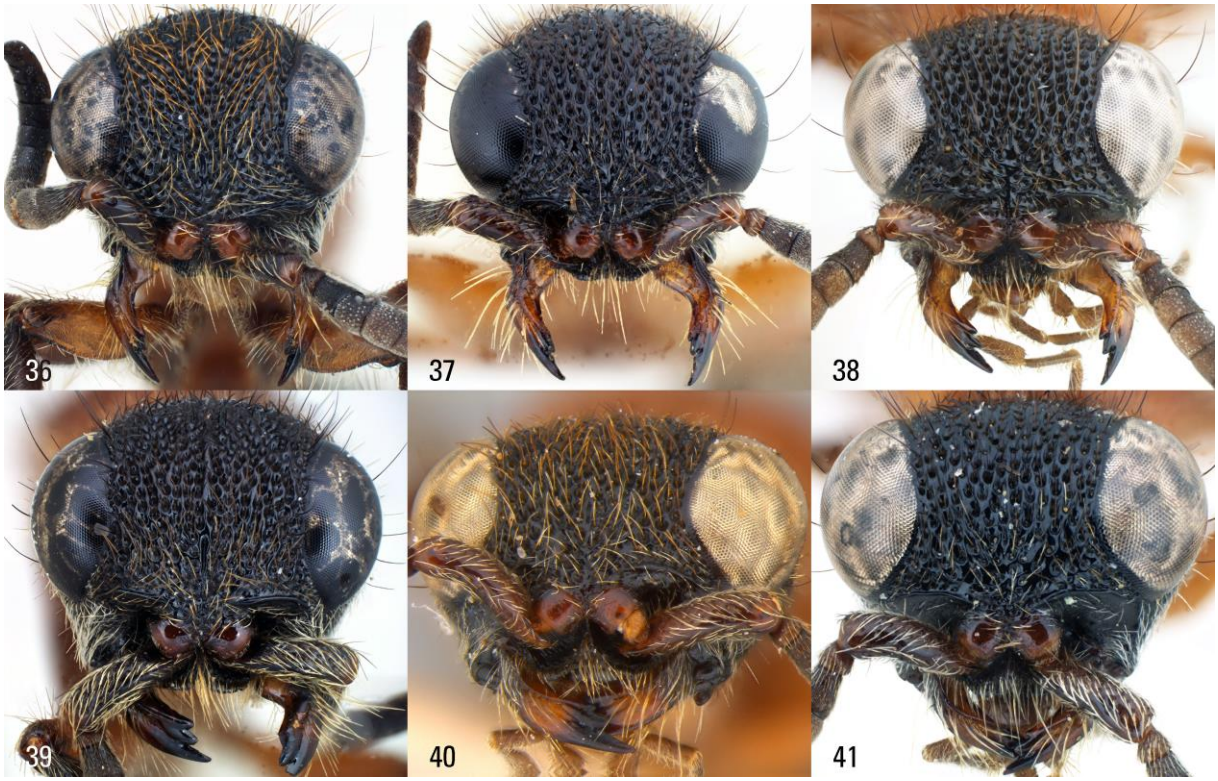
Figures 1–10. *Andreimyrme* spp., ♀, dorsal habitus. 1. *A. auricoma* **sp. nov.**, holotype; 2. *A. borkenti* (Williams), holotype; 3. *A. laminatihumeralis* **sp. nov.**, holotype; 4. *A. matsumotoi* **sp. nov.**, holotype; 5. *A. naturalis* **sp. nov.**, holotype; 6. *A. neaera* (Mickel); 7. *A. rong* **sp. nov.**, holotype; 8. *A. rong* **sp. nov.**, paratype; 9. *A. sarawakensis* Lelej; 10. *A. silvorientalis* **sp. nov.**, holotype.

Figures 11–18. *Andreimyrme* spp., ♀, dorsal habitus. 11. *A. substriolata* (Chen), holotype; 12. *A. tridentiens* (Chen), holotype; 13. *A. substriolata* (Chen), Laos; 14. *A. substriolata* (Chen), Taiwan; 15. *A. substriolata* (Chen), Japan (Okinawa); 16. *A. takensis* **sp. nov.**, holotype; 17. *A. ursasolaris* **sp. nov.**, holotype; 18. *A. yotoi* **sp. nov.**, holotype.



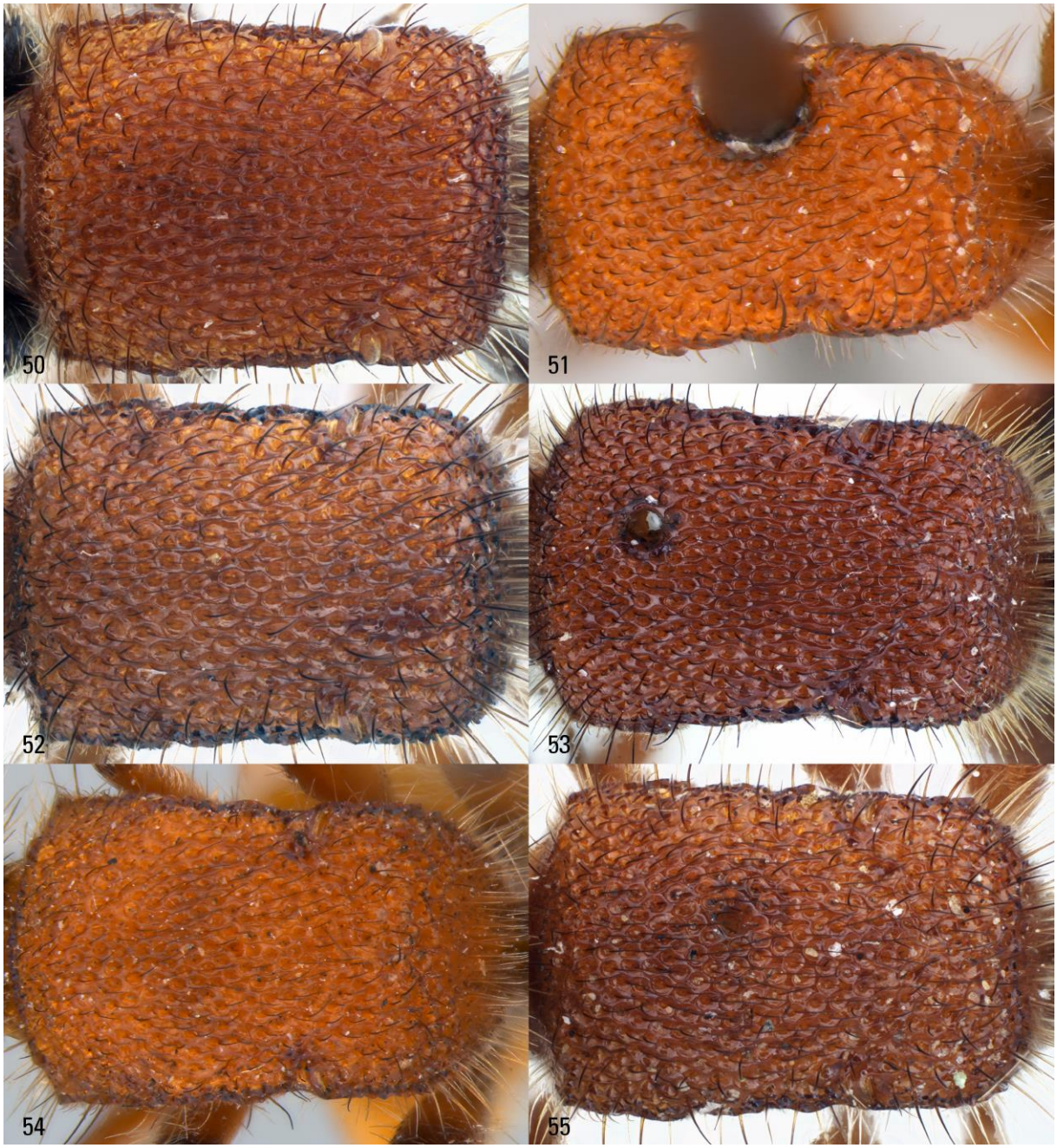
Figures 19–27. *Andreimyrme* spp., ♀, lateral habitus. 19. *A. auricoma* **sp. nov.**, holotype; 20. *A. borkenti* (Williams), holotype; 21. *A. laminatihumeralis* **sp. nov.**, holotype; 22. *A. matsumotoi* **sp. nov.**, holotype; 23. *A. naturalis* **sp. nov.**, holotype; 24. *A. neaera* (Mickel); 25. *A. rong* **sp. nov.**, holotype; 26. *A. sarawakensis* Lelej; 27. *A. silvorientalis* **sp. nov.**, holotype.

Figures 28–35. *Andreimyrme* spp., ♀, lateral habitus. 28. *A. substriolata* (Chen), holotype; 29. *A. tridentiens* (Chen), holotype; 30. *A. substriolata* (Chen), Laos; 31. *A. substriolata* (Chen), Taiwan; 32. *A. substriolata* (Chen), Japan (Okinawa); 33. *A. takensis* **sp. nov.**, holotype; 34. *A. ursasolaris* **sp. nov.**, holotype; 35. *A. yotoi* **sp. nov.**, holotype.

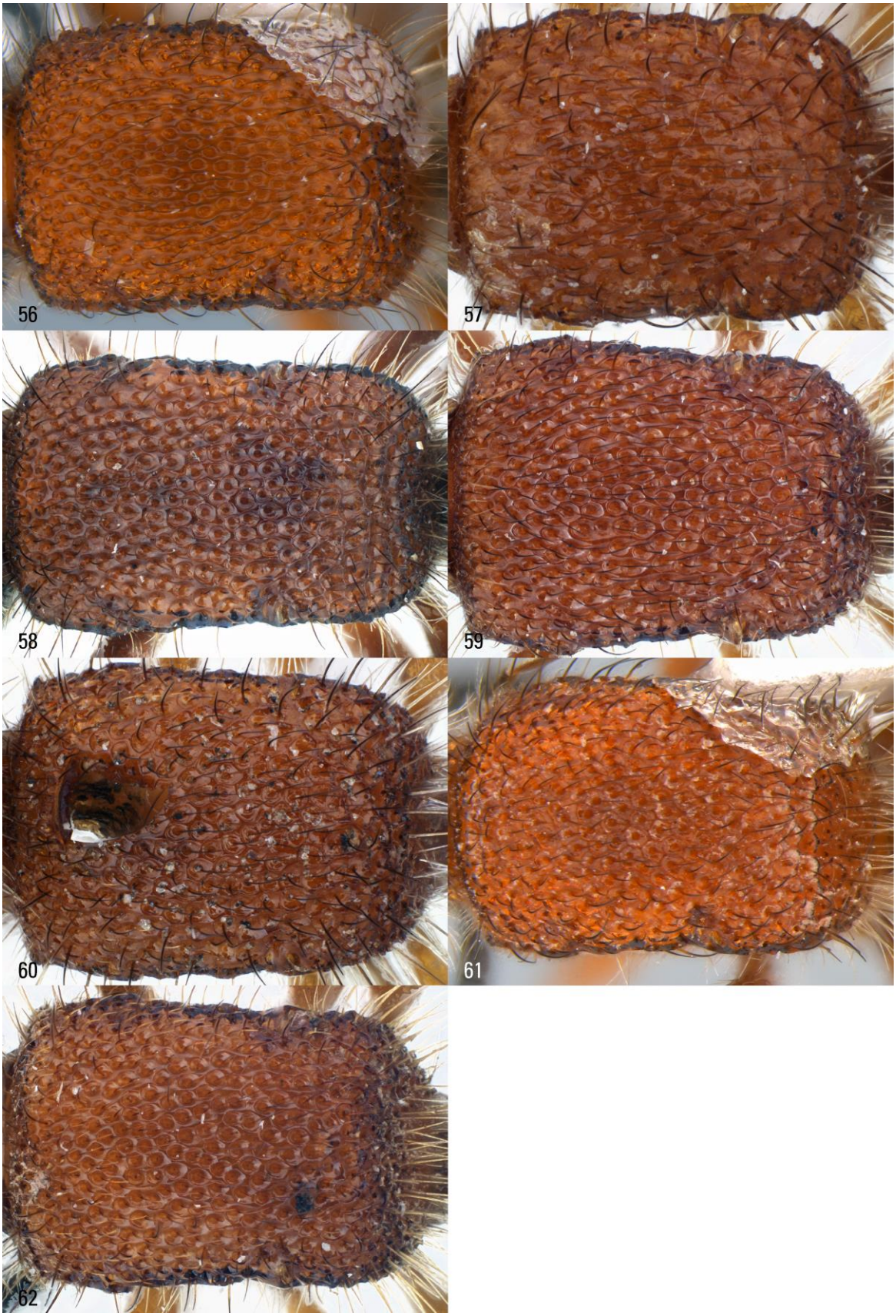


Figures 36–41. *Andreimyrme* spp., ♀, face. 36. *A. auricoma* **sp. nov.**, holotype; 37. *A. borkenti* (Williams), Vietnam; 38. *A. laminatihumeralis* **sp. nov.**, holotype; 39. *A. matsumotoi* **sp. nov.**, holotype; 40. *A. naturalis* **sp. nov.**, holotype; 41. *A. neaera* (Mickel).

Figures 42–49. *Andreimyrme* spp., ♀, head. 42–48. Face; 49. prementum and stipes, with an arrow indicating the premental tubercle; 42. *A. rong* **sp. nov.**, holotype; 43. *A. sarawakensis* Lelej; 44. *A. silvorientalis* **sp. nov.**, holotype; 45, 49. *A. substriolata* (Chen), Laos; 46. *A. takensis* **sp. nov.**, holotype; 47. *A. ursasolaris* **sp. nov.**, holotype; 48. *A. yotoi* **sp. nov.**, holotype.

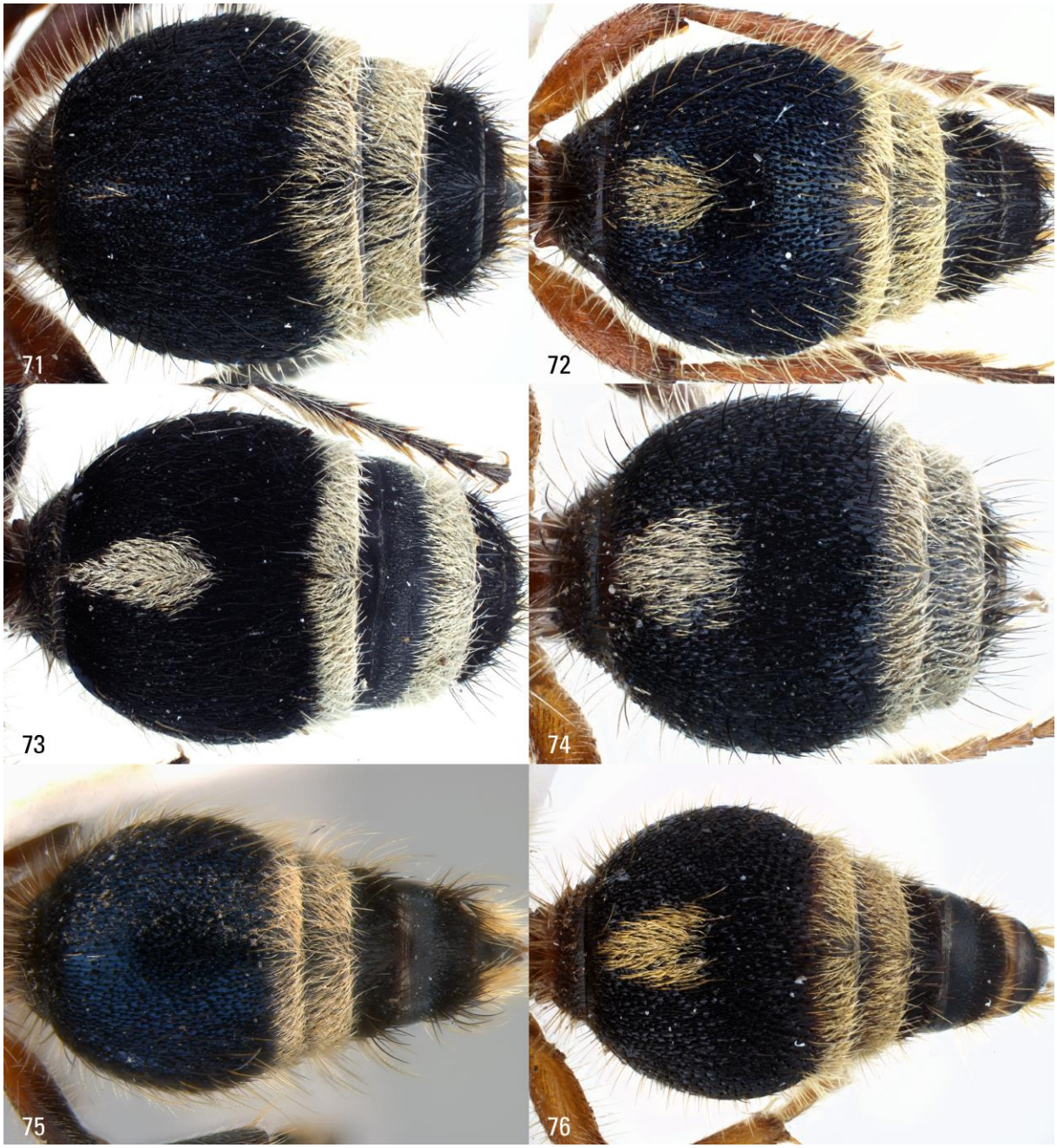


Figures 50–55. *Andreimyrme* spp., ♀, mesosoma. 50. *A. auricoma* **sp. nov.**, holotype; 51. *A. borkenti* (Williams), holotype; 52. *A. laminatihumeralis* **sp. nov.**, holotype; 53. *A. matsumotoi* **sp. nov.**, holotype; 54. *A. naturalis* **sp. nov.**, holotype; 55. *A. neaera* (Mickel).

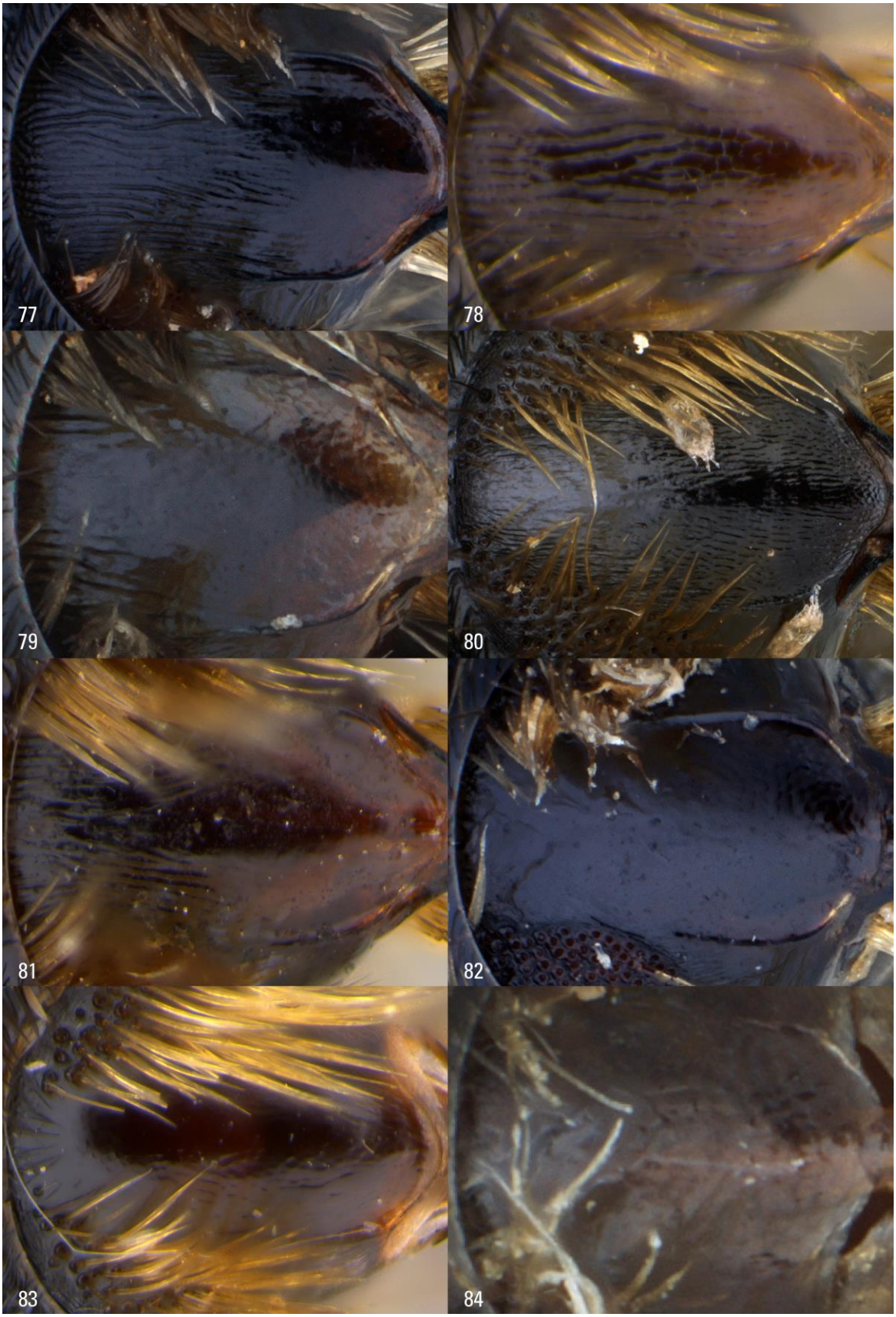


Figures 56–62. *Andreimyrme* spp., ♀, mesosoma. 56. *A. rong* **sp. nov.**, holotype; 57. *A. sarawakensis* Lelej; 58. *A. silvorientalis* **sp. nov.**, holotype; 59. *A. substriolata* (Chen), Laos; 60. *A. takensis* **sp. nov.**, holotype; 61. *A. ursasolaris* **sp. nov.**, holotype; 62. *A. yotoi* **sp. nov.**, holotype.

Figures 63–70. *Andreimyrme* spp., ♀, metasoma. 63. *A. auricoma* **sp. nov.**, holotype; 64. *A. borkenti* (Williams), holotype; 65. *A. laminatihumeralis* **sp. nov.**, holotype; 66. *A. matsumotoi* **sp. nov.**, holotype; 67. *A. naturalis* **sp. nov.**, holotype; 68. *A. neaera* (Mickel); 69. *A. rong* **sp. nov.**, holotype; 70. *A. sarawakensis* Lelej.

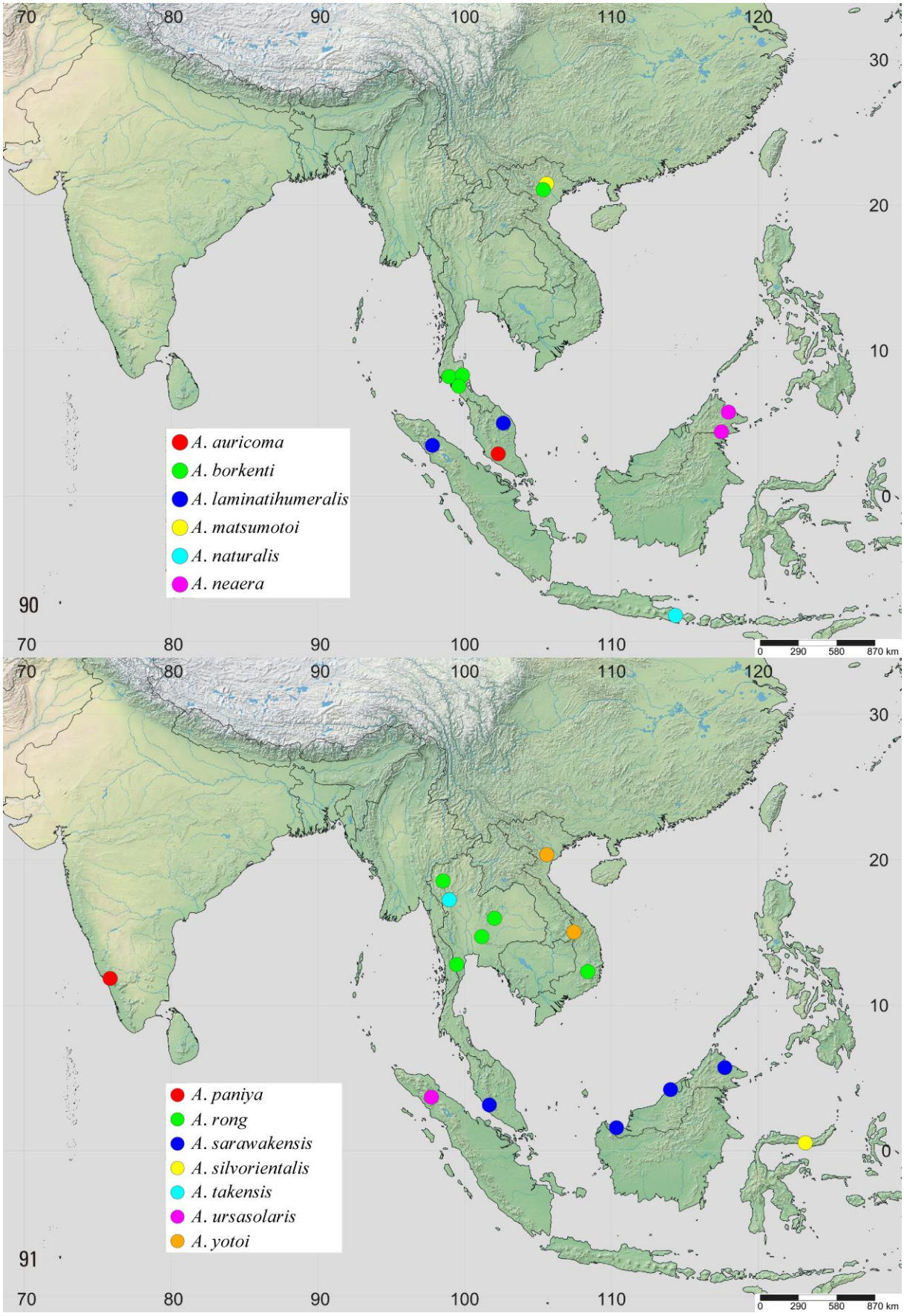


Figures 71–76. *Andreimyrme* spp., ♀, metasoma.71. *A. silvorientalis* **sp. nov.**, holotype; 72. *A. substriolata* (Chen), Laos; 73. *A. substriolata* (Chen), Taiwan; 74. *A. takensis* **sp. nov.**, holotype; 75. *A. ursasolaris* **sp. nov.**, holotype; 76. *A. yotoi* **sp. nov.**, holotype.



Figures 77–84. *Andreimyrme* spp., ♀, pygidial plate. 77. *A. auricoma* **sp. nov.**, holotype; 78. *A. borkenti* (Williams), holotype; 79. *A. laminatihumeralis* **sp. nov.**, holotype; 80. *A. matsumotoi* **sp. nov.**, holotype; 81. *A. naturalis* **sp. nov.**, holotype; 82. *A. neaera* (Mickel); 83. *A. rong* **sp. nov.**, holotype; 84. *A. sarawakensis* Lelej.

Figures 85–89. *Andreimyrme* spp., ♀, pygidial plate.85. *A. silvorientalis* **sp. nov.**, holotype; 86. *A. substriolata* (Chen), Laos; 87. *A. takensis* **sp. nov.**, holotype; 88. *A. ursasolaris* **sp. nov.**, holotype; 89. *A. yotoi* **sp. nov.**, holotype.



Figures 90–91. Distributional maps of *Andreimyrme* spp. based on the material examined and the literature (Lelej 1995b, 1996a; Mickel 1935).

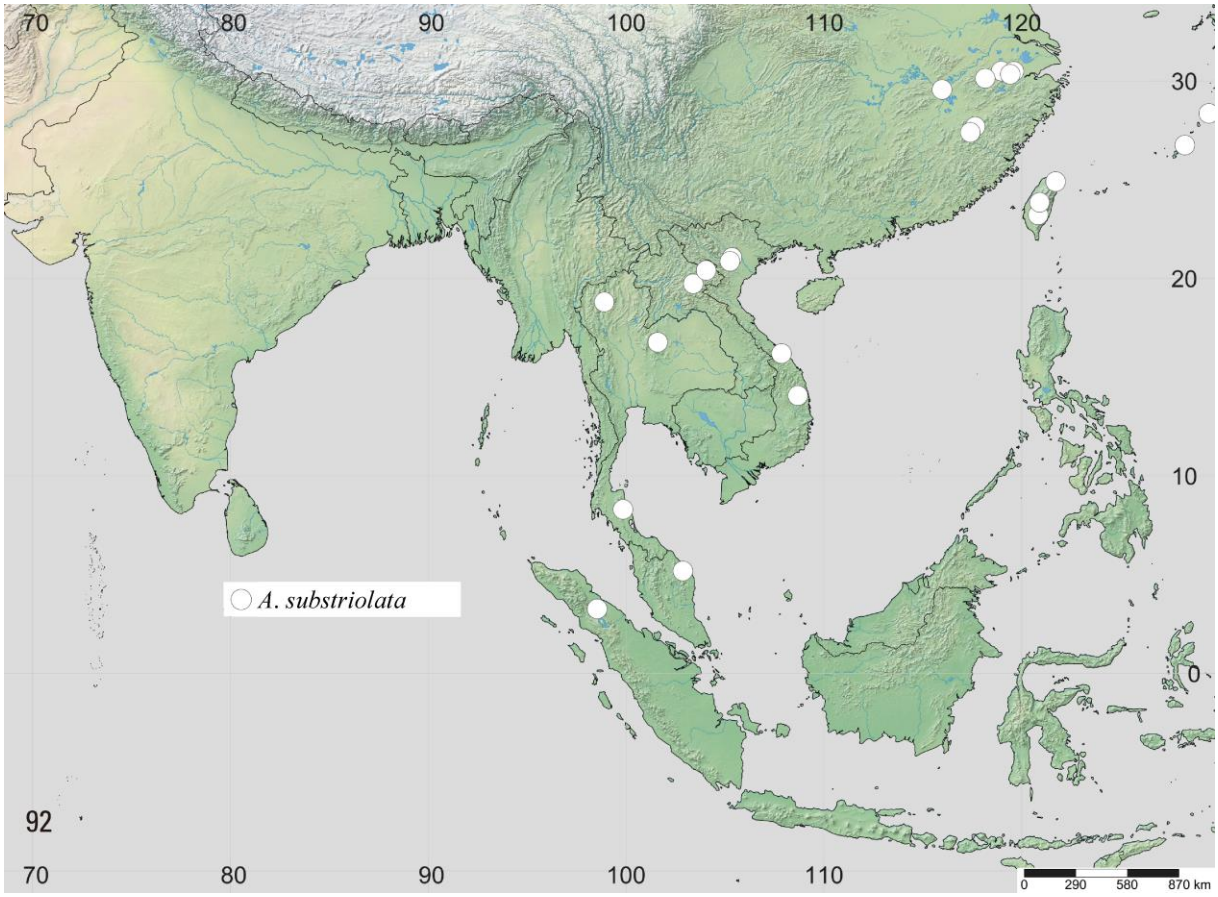


Figure 92. Distributional map of *Andreimyrme substriolata* (Chen) based on the material examined.

Figures 93–95. Koshuku, Amami-ôshima Island where one female of *Andreimyrme substriolata* (Chen) was collected. 93. Subtropical secondary forest at Koshuku; 94. small gap in the forest; 95. living female of *A. substriolata* in an insect net.

Chapter 5

Love is in the air and beyond the ocean: Taxonomic review of *Neotrogaspidia* Lelej (Hymenoptera: Mutillidae: Trogaspidiini) in Northeast Asia highlights its unique distributional pattern

Disclaimer: *This chapter has already been published as a peer-reviewed paper as follows: Okayasu, J. (2023) Entomological Science 26 (1): e12532 (https://doi.org/10.1111/ens.12532). New nomenclatural acts appearing in this chapter have already been made in this publication and, thus, this dissertation chapter is not considered a published work within the meaning of the International Code of Zoological Nomenclature 4th edition (Article 8.2).*

Abstract
The genus *Neotrogaspidia* Lelej, 1996 is a small group of velvet ants with five species from the Australasian, Oriental and Palearctic Regions. The type species, *N. pustulata* (Smith, 1873) (♂♀), is the only Northeast Asian species known at present. In this paper, *N. elpinice* (Mickel, 1933), **stat. resurr. et comb. nov.** (♂♀) is resurrected from the junior synonym of *N. pustulata*. Two new combinations are proposed for *N. circumcincta* (André, 1896), **comb. nov.** (♂♀) from *Orientidia* Lelej, 1996 and *N. recticarinata* (Chen, 1957), **comb. nov.** (♂) from *Trogaspidia* Ashmead, 1899. New synonymies are proposed for *N. elpinice* with *T. aestivalis* Hammer, 1949, **syn. nov.** and *T. maritima* Chen, 1957, **syn. nov.**, and *N. circumcincta* with *T. yuliensis* Tsuneki, 1972, **syn. nov.** and *Krombeinidia agricola* Williams, 2019, **syn. nov.** An updated genus diagnosis and a key to all described species are provided. New records include *N. circumcincta* from Laos and Vietnam, *N. pustulata* from North Korea, and *N. recticarinata* from Taiwan. The inflated endophallus of the male genitalia of *N. pustulata* is illustrated. A potential host record, habitat records and mating observations of *Neotrogaspidia* are presented. The historical process of formation of the distributional patterns of this genus in Northeast Asia is discussed.

Key words
Aculeata, biogeography, dispersal, Oriental Region, Palearctic Region, phoretic copulation.

Introduction

Velvet ants, or the family Mutillidae, are characteristic wasps exhibiting strong sexual dimorphism. All female individuals are wingless and lack flight ability, while males have developed wings and are capable of flight in most species (Brothers, 1989). Because of the flightless nature of females, mutillids have strict preference to certain environments and show situation-specific host choice, that is, utilization of a wide variety of host species found in a particular habitat, presumably as an adaptation to reduce costs for host searching (Brothers, 1989; Taylor *et al*., 2019). Additionally, female mutillids tend to move only over short distances (Evans & Miller, 1969; Evans *et al*., 1973). Therefore, mutillids can be useful indicators of past environmental and geographic changes (Pitts *et al*., 2010b; Wilson *et al*., 2012).

Some groups of mutillids practice phoretic copulation, in which the male transports the female counterpart by flight during copulation (Evans, 1969; Vivallo, 2020; Waldren *et al*., 2020). This behavior is considered a method to overcome geographic barriers for females (Evans, 1969), although the adaptive merit of phoretic copulation has not been fully elucidated. An alternative mating strategy is in situ copulation, in which mating events take

place at or near the site of initial contact between a male and a female (Waldren *et al*., 2020). In particular groups of mutillids, males are as large as or even smaller than females and are physically unable to carry females (Waldren *et al*., 2020). Alternative mating strategies may provide varied dispersal ability to females, resulting in incongruent distributional patterns across taxa.

The genus *Neotrogaspidia* Lelej, 1996 is a small taxon of the tribe Trogaspidiini Bischoff, 1920 (*sensu* Brothers & Lelej, 2017), with five valid species from the Australasian, Oriental and Palearctic Regions (Brothers 2022; Lelej, 2005; Pagliano *et al*., 2020). The type species, *N. pustulata* (Smith, 1873), is the only species distributed in Northeast Asia. Although a recent taxonomic revision highlighted the mutillid endemism in Japanese islands (Okayasu, 2020), *N. pustulata* is widely distributed throughout China, Taiwan, Japan and South Korea. This species was even recorded from oceanic Hachijyô-jima Island (Izu Islands), Chichi-jima Island and Nishi-jima Island (Ogasawara Islands) (Nambu & Shimizu, 1984; Sugiura *et al*., 2013; Takahashi, 1993; Tsuneki, 1984; Yasumatsu, 1936). Considering the low dispersal ability of mutillids, I hypothesized some separate species would be subsequently recognized within this widespread species. In this paper, Northeast Asian species of *Neotrogaspidia* are reviewed based on museum specimens using the morphology.

Material and methods

The following abbreviations are used to denote institutes housing types and specimens examined herein.

BMNH The Natural History Museum, London, UK.
CSCA California State Collection of Arthropods, Sacramento, California, USA.
ELKU Entomological Laboratory, Faculty of Agriculture, Kyushu University, Fukuoka, Japan.
EUM Ehime University Museum, Matsuyama, Japan.
HMNH Hiwa Museum for Natural History, Shôbara, Japan.
MNHAH Museum of Nature and Human Activities, Sanda, Japan.
MSNG Museo Civico di Storia Naturale "G. Doria", Genoa, Italy.
NARO Insect Museum, National Agriculture and Food Research Organization, Tsukuba, Japan (former Institute for Agro-Environmental Sciences).
NHRS Naturhistoriska riksmuseet, Stockholm, Sweden.
NSMT National Museum of Nature and Science, Tsukuba, Japan.
OMNH Osaka Museum of Natural History, Osaka, Japan.
SEHU Hokkaido University Insect Collection, Sapporo, Japan.
TARI Taiwan Agricultural Research Institute, Taichung, Taiwan.
TMUZ Systematic Zoology Laboratory, Tokyo Metropolitan University, Tokyo, Japan.
TUA Laboratory of Entomology, Tokyo University of Agriculture, Atsugi, Japan.
USNM National Museum of Natural History, Smithsonian Institution, Washington D.C., USA.
ZMNB Museum für Naturkunde, Humbolt Universität, Berlin, Germany.

Specimens were examined under a Leica M205C stereomicroscope (7.8–160× magnification). Most habitus photographs were taken using a Canon EOS 6D Mark II digital camera equipped with a Canon MP-E 65 mm f/2.8 1–5× Macro Photo lens. External morphological features were imaged with a Canon EOS 6D Mark II attached to a Leica M205C. Focus stacking was done using Zerene Stacker software (Zerene Systems). The map figures were generated by SimpleMappr (Shorthouse, 2010). Figures were edited with Adobe

Photoshop and Adobe Illustrator software.

In the synonymic lists and the material examined sections, abbreviations for material depositories and additional or corrected data by the author are given in square brackets. Old names of insect collecting localities in Taiwan were translated into the present names using Chu & Yamanaka (1973–1975) and Kojima *et al*. (2011). The geographic coordinates were obtained from Google Earth. New country records are asterisked (*).

Morphological terminology mostly follows the Hymenoptera Anatomy Consortium (2022). Abbreviations are: F, flagellomere; S, metasomal sternum; T, metasomal tergum.

Results

Neotrogaspidia Lelej, 1996

Neotrogaspidia Lelej, 1996: 20, ♂♀; Lelej & Nemkov, 1997: 4; Lelej, 2002: 82; Lelej, 2005: 79; Lelej & Brothers, 2008: 39; Lo Cascio, 2015: 553; Brothers & Lelej, 2017: 96; Okayasu *et al*., 2018: 304, ♀; Pagliano *et al*., 2020: 253; Okayasu *et al*., 2021: 86, ♂♀; Brothers, 2022: 145, ♂♀.
Neptrogaspidia: Tsurusaki *et al*., 2012: 71. Incorrect subsequent spelling.

Type species
Mutilla pustulata Smith, 1873, by original designation.

Extended diagnosis
MALE. Frons punctate; vertex rounded; postgenal bridge flattened, lacking tubercle; hypostomal carina simple, without denticle; clypeus dorsally elevated with surface predominantly concave, subventrally with transverse carina (except *N*. hammeri and probably *N*. *tricarinata*). Mandible slender, apically bidentate; ventral margin excised into basal tooth; inner margin without subbasal tooth; dorso-lateral carina sharp, not crooked. Prementum not tuberculate. Scape with two longitudinal carinae ventrally, punctate between them; F1 weakly depressed, 2.0–2.5× longer than pedicel and 1.0–1.25× longer than F2. Mesosoma black; notaulus present, reaching anterior 1/2–1/3 of mesoscutum; parascutal carina forming weakly elevated, rounded tubercle posteriorly; tegula posterior margin slightly protruding over transscutal line, not recurved; mesoscutellum subgibbous, punctate, with medial longitudinal impunctate line, sometimes posteriorly elevated into carina but never tuberculate or forming conical apex; mesopleuron divided into dorsal and ventral convexities by transverse groove; mesopleuron with precoxal smooth rounded tubercle ventrally; propodeum with distinct dorsal and posterior faces; propodeal dorso-lateral margin without denticles. Distance between origin of RS on vein SC and proximal base of pterostigma 1.0–1.5× pterostigma length. Protibial spur slender; mesocoxa evenly convex; metacoxa evenly convex with long sparse recumbent setae, without tubercle on inner margin. Metasoma with some anterior segments red and remaining segments black (except *N*. *haemarrhoa* with segments 1–3 black and remaining segments red; Brothers 2022: fig. 141); T2 postero-lateral margin abruptly terminating (except *N*. *haemarrhoa*, *N*. *hammeri* and *N*. *tricarinata* with T2 posterolateral margin evenly convex); S2 evenly convex, medially with obscure longitudinal ridge; lateral felt line present on T2 but absent on S2; T7 medially with triangular convex impunctate space or slender convex impunctate line, sometimes posteriorly elevated into carina; T7 posterior margin truncate; S6 with weak lateral tubercle, represented by smooth convexity or minute sharp tubercle; S7 entirely exposed, 0.6× as long as S8, with lateral rounded tubercle; S8 mostly sclerotized with posterior membranous area evenly convex posteriorly; S8 with lateral longitudinal carina; left and right basiparameres ventro-medial margins connected to form

postero-medial tongue-like tubercle; parapenial lobe spatulate, not flexed; ventral portion of basiparamere strongly projecting posteriorly to connect volsella; cuspis stick-like or short robust; digitus straight stick-like, smaller than cuspis; paracuspis present, stick-like; penis valve long slender, surpassing posterior 1/2 of paramere; right penis valve longer than left, posteriorly with hook-like apex or with inner projection (*N. tricarinata*; Brothers 2022: fig. 305); left penis valve posteriorly with rounded or hooklike apex. FEMALE. Genal carina largely obliterated, not connected with hypostomal carina; hypostomal tooth present; clypeus with dorsal transverse carina and medial longitudinal tubercle; dorsal clypeal carina and clypeus laterally connected by tubercle. Mandible slender, without inner subbasal tooth. Prementum without tubercle. Mesosoma compact, broadest at propodeum or pronotum as wide as propodeum; scutellar scale weakly developed; mesopleural lamella present. Procoxa armed with rounded tubercle; protarsus pectinate; protarsomere1 apically truncate, not projecting outward. T2 evenly convex; T2 pale setal spots small or absent (*N. serafica*), distance between them, when present, subequal to spot diameter; T3 with complete pale setal band and T4 with black setae, or both T3 and T4 with complete (*N. serafica*) or medially interrupted (*N. hammeri*) pale setal band; T3 and T4 setal bands extending nearly to lateral margin of terga; pygidial plate subconvex, laterally defined by weak longitudinal carinae not widened posteriorly; surface of pygidial plate entirely shagreened or irregularly rugose on anterior 1/2 and shagreened or smooth on posterior 1/2.

Diversity and distribution

This genus includes the following eight species: *N. circumcincta* (André, 1896), ♂♀ (China, Taiwan, Indonesia, Laos, Malaysia, Thailand, Vietnam); *N. elpinice* (Mickel, 1933), ♂♀ (China, Taiwan); *N. haemarrhoa* (Zavattari, 1914), ♂ (Indonesia: Lombok, Sumbawa); *N. hammeri* (Suárez, 1959), ♂♀ (Armenia, Azerbaijan, Cyprus, Greece, Iran, Palestine, Russia, Turkmenistan); *N. pustulata* (Smith, 1873), ♂♀ (Japan, North Korea, South Korea); *N. recticarinata* (Chen, 1957), ♂ (China, Taiwan); *N. serafica* (Zavattari, 1914), ♀ (Indonesia: Ambon, Lombok, Solor, Sumbawa); *N. tricarinata* (Zavattari, 1907), ♂ (Indonesia: Aru or Kei). Based on the overlapping distribution (Indonesia: Lombok and Sumbawa), *N. serafica* was suggested as the female of *N. haemarrhoa* (Lelej, 2005).

Biology

Label data and observations made by Japanese entomologists suggest that *N. circumcincta* and *N. pustulata* are found from meadows, like grassland, riversides, backshore vegetations, paddy fields or sesame fields (Imai, 2019; Nakamura & Matsuda, 2005; Nomura, 1978; Tsuneki, 1972c; Yamamoto, 2010; Suda, 2018; Sugiura *et al*., 2013; T. Mita, pers. comm., 2022). Matsumura (1932) noted that larvae of *N. pustulata* parasitized on “bee larvae”. Yasumatsu (1944) listed the ground-nesting solitary wasp *Cerceris navitatis* Smith, 1873 [= *C. albofasciata* (Rossi, 1790)] (Apoidea: “Crabronidae”: Philanthinae) as a host of *N. pustulata*. However, no evidence was indicated for these records. A female of *N. pustulata* was observed in a nest aggregation of *Dasypoda japonica* Cockerell, 1911 (Apoidea: Melittidae), together with small bees, *Liris* Fabricius, 1804 species (Crabronidae) and pompilids (R. Matsumoto, pers. comm., 2022). These potential host records may be supported by the presence of the protarsal rake and the defined pygidial plate in females, which are associated with utilization of ground-nesting hosts (Krombein, 1972; Williams *et al*., 2011). Takahashi (1993) recorded a male of *N. pustulata* visiting a flower of Vitaceae species. Several pairs of *N. pustulata* were observed practicing mandibular phoretic copulation (Figs 92–98), and males are capable of carrying females by flight (Mimura, 2019; T. Kawabe, T. Mita, pers. comm., 2022). Despite of the ground-dwelling habits of females of this species, those previously observed mating pairs were found on plant leaves (Mimura,

2019; Figs 93–98).

Remarks

The diagnostic features of *Neotrogaspidia* within Trogaspidiini are discussed below. Some females of this genus, like *N. circumcincta* and *N. pustulata* (as *Smicromyrme yakushimensis*), were originally described as lacking the defined pygidial plate (André, 1896; Chen, 1957; Yasumatsu, 1934). These species were previously placed in *Orientidia* Lelej, 1996 (Trogaspidiini) or *Sinotilla* Lelej, 1995 (Smicromyrmini) (Lelej, 2005), genera characterized by having the pygidium smooth and convex without lateral carinae (Okayasu, 2017: figs 6,14). Additionally, *Neotrogaspidia* females have the pronotum as wide as the propodeum, unlike most females of Trogaspidiini *sensu* Lelej & Nemkov (1997). *Krombeinidia agricola* Williams in Williams *et al*., 2019, which is considered a synonym of *N. circumcincta* here, was therefore originally described under that genus. However, *Neotrogaspidia* females differ from those genera by having the dorsal transverse clypeal carina laterally connected with clypeus by a tubercle (clypeus with a dorsal transverse carina but lacking lateral tubercles in *Orientidia* and *Sinotilla*), the procoxa armed with a rounded tubercle (procoxa lacking a tubercle in *Krombeinidia*, *Orientidia* and *Sinotilla*) and the pygidial plate slightly convex, rugose or shagreened, laterally delimited by carinae on posterior 1/2 (surface smooth in *Krombeinidia*; convex, smooth, and lacking lateral carinae in *Orientidia* and *Sinotilla*).

Key to species of *Neotrogaspidia*

1. Male: head with ocelli; 11 flagellomeres; winged ... 2
- Female: head without ocelli; 10 flagellomeres; wingless ... 8
2. Metasomal segments 1–3 and anterior half of segment 4 black and the remaining segments red (Brothers, 2022: fig. 141). Indonesia (Australasian part) ... ***N. haemarrhoa*** (Zavattari)
- Metasoma with some anterior segments red and the remaining segments black (Figs 1–8) ... 3
3. Right penis valve with inner hook-like projection, giving posteriorly bifid appearance (Brothers, 2022: fig. 305). Indonesia (Australasian part) ... ***N. tricarinata*** (Zavattari)
- Right penis valve incurved, without inner projection (Figs 54–61) ... 4
4. Clypeus without transverse carina; T2 posterolateral margin gradually curved; cuspis short robust, 2.5× longer than wide and 1.5× longer than digitus. Western Palearctic ... ***N. hammeri*** (Suárez)
- Clypeus subventrally with transverse carina reaching lateral margin of clypeus (Figs 38–41); T2 posterolateral margin abruptly terminating (Fig. 5); cuspis long slender, much longer than wide and 2.0× longer than digitus (Figs 62,64,66,68) ... 5
5. Scape with two closely located sharp carinae (Figs 42,45); pronotum and propodeum dorsally with dense appressed setae (Figs 1,2,7,8); mesoscutellum with medial impunctate line posteriorly elevated into carina (Figs 7,8); propodeal dorsum with sublateral longitudinal carina; T2 abruptly convex (Figs 46,49); S8 lateral carinae subparallel and tuberculate posteriorly, reaching posterior 1/2 of the sternum (Figs 50,53); penis valves long slender (Figs 63,69), apparently surpassing posterior 1/2 of cuspis (Figs 55,61); right penis valve posteriorly sharp (Figs 63,69); left penis valve posteriorly with rounded apex (Figs 63,69) ... 6
- Scape with two widely separated obscure carinae, recognizable only apically (Figs 43,44); pronotum and propodeum dorsally with sparse suberect setae (Figs 3–6); mesoscutellum with medial impunctate line posteriorly not elevated (Figs 3–6); propodeal dorsum without sublateral carina; T2 evenly convex (Figs 47,48); S8 lateral carinae convergent posteriorly

and not tuberculate, reaching posterior margin of the sternum (Figs 51,52); penis valves short robust (Figs 65,67), reaching posterior 1/2 of cuspis (Figs 57,59); right penis valve apically robust (Figs 65,67); left penis valve posteriorly with hook-like apex (Figs 65,67) ... 7

6. Clypeus concave throughout (Fig. 38); penis valves with short sparse setae on inner face (Figs 55,63). China, Taiwan, Indonesia (Oriental part), Laos, Malaysia, Thailand, Vietnam ... ***N. circumcincta*** (André)
- Clypeus concave with medial longitudinal ridge (Fig. 41); penis valves with long dense setae on inner face (Figs 61,69). China, Taiwan …… ***N. recticarinata*** (Chen)
7. S1 red (Fig. 47); T3 and S3 red (Fig. 47). China, Taiwan ... ***N. elpinice*** (Mickel)
- S1 dark brown to black (Fig. 48); T3 and S3 variable, at least T3 medially largely black (Fig. 48). Japan, North Korea, South Korea ... ***N. pustulata*** (Smith)
8. T2 without pale setal spots (Brothers, 2022: fig. 281). Indonesia (Australasian part) … ***N. serafica*** (Zavattari)
- T2 with two anterior pale setal spots (Figs 80–85) ... 9
9. T3–T4 with pale setal band medially widely interrupted by black setae ... ***N. hammeri*** (Suárez)
- T3 with complete pale setal band (Figs 80–85) and T4 with black setae (Figs 80–85) ... 10
10. Frons longitudinally puncto-striate (Fig. 74); T2 posterior margin with narrow band of golden setae reaching lateral margins of the tergum and interrupted medially (Figs 80,81); S2 with large sparse punctures, interspaces micropunctate and setose (Fig. 10); T3 and S3 red (Fig. 10), rarely black (Fig. 81) ... ***N. circumcincta*** (André)
- Frons merely punctate (Figs 75,76); T2 posterior margin with black setae (Figs 82–85); S2 with large sparse punctures, interspaces smooth and asetose (Figs 12,14,16); T3 and S3 black (Figs 11–16) ... 11
11. T2 spots circular, densely setose and well defined (Figs 82,83) ... ***N. elpinice*** (Mickel)
- T2 spots transverse, sparsely setose and obscurely defined (Figs 84,85) ... ***N. pustulata*** (Smith)

Neotrogaspidia circumcincta (André, 1896), comb. nov.

(Figs 1,2,9,10,38,42,46,50,54,55,62,63,74,77,80,81,99)

Mutilla circumcincta André, 1896: 71, ♀, lectotype ♀ (Balighe [= Balige], [Sumatra Utara], Sumatra, Indonesia) [MSNG], designated by Mickel (1933b: 314); André, 1902: 38; André, 1905: 212, ♂♀.

Timulla (*Trogaspidia*) *circumcincta*: Mickel, 1933b: 314, ♀; Mickel, 1935: 267, ♀; Wu, 1941: 136.

Trogaspidia circumcincta: Chen, 1957: 171, ♀; He *et al*., 2004: 962, ♀.

Trogaspidia yuliensis Tsuneki, 1972b, **syn. nov.**: 12, ♂, holotype (Yuli [玉里鎮], Hualien Pref., Formosa [= Taiwan]) [USNM]; Lelej, 2005: 105; Hua, 2006: 301; Pagliano *et al*., 2020: 293.

Trogaspidia tethys: Tsuneki, 1993: 48, ♂.

Orientidia circumcincta: Lelej, 2005: 68; Hua, 2006: 300; Okayasu *et al*., 2018: 304, ♀; Pagliano *et al*., 2020: 254.

Krombeinidia agricola Williams in Williams *et al*., 2019, **syn. nov.**: 34, ♀, holotype ♀ (Vimarndin farm stay, Thong Pha Phum, Kanchanaburi, Thailand) [CSCA]; Pagliano *et al*. 2020: 250.

Diagnosis

MALE. Clypeus concave throughout (Fig. 38); scape with two closely located sharp carinae

(Fig. 42); pronotum with dense appressed golden setae (Fig. 2); mesoscutellum with medial impunctate line posteriorly elevated into carina (Fig. 1); propodeal dorsum with dense appressed golden setae, sublaterally delimited by longitudinal carinae; metasomal segments 1–5 red and 6–8 black (Fig. 46); T2 abruptly convex (Fig. 46); S8 lateral carinae subparallel and tuberculate posteriorly, reaching posterior 1/2 of S8 (Fig. 50); penis valve long slender, incurved, without inner projection (Figs 54,55,63); penis valves with short sparse setae on inner face (Figs 55,63); cuspis slender stick-like, 2.0× longer than digitus (Fig. 62). FEMALE. Frons with large confluent punctures with many transverse intervals obliterated, leaving puncto-striate surface (Fig. 74); T2 spots subcircular, densely setose and well defined (Figs 80,81); T2 posterior margin with narrow band of dense appressed golden setae reaching lateral margins of T2 and interrupted medially (Figs 80,81); S2 with large sparse punctures, interspaces micropunctate and setose (Fig. 10); T3 and S3 usually with red cuticle (Figs 10,80), rarely black (Fig. 81); T3 with complete band of dense appressed golden setae (Figs 80,81); T4 with black setae (Figs 80,81).

Material examined

3♂15♀. **China:** FUJIAN: Fukien [= Fujian], Chungan, Bohea Hills, 23.VII.1939, T.C. Maa leg., *Timulla circumcincta* [probably Chen's hand], *Trogaspidia circumcincta* (André) [probably Chen's hand], *Trogaspidia circumcincta circumcincta* (André), B. Petersen det. 1982 [1♀ TARI]; Fukien [= Fujian], Chungan, Bohea Hills, 12.IX.1939, T.C. Maa leg., *Timulla* sp. n. 2 [probably Chen's hand], *Trogaspidia recticarinata* Chen? [unknown hand], *Trogaspidia circumcincta circumcincta* (André), B. Petersen det. 1982 [1♂ TARI]; Fukien [= Fujian], Yungan [= Yong'an], Siyingpan, 29.VI.1940, T.C. Maa leg., *T. circumcincta* [probably Chen's hand], *Trogaspidia circumcincta circumcincta* (André), B. Petersen det. 1982 [1♀ TARI]; Fukien [= Fujian], Changting, Hotien, 1.V.1941, T.C. Maa leg., *T. circumcincta* [probably Chen's hand], *Trogaspidia circumcincta circumcincta* (André), B. Petersen det. 1982 [1♀ TARI]. **Taiwan:** TAIPEI: Taipei, Changho, 20.X.1970, K.S. Lin leg., *Trogaspidia circumcincta circumcincta* (André), B. Petersen det. 1988 [1♂ TARI], 28.X.1970 [1♂ TARI]. **Laos:** HOUA PHAN: Ban Saleui, alt. ca 1,400 m, 16.VI.2003, N. Ohbayashi leg. [1♀ EUM]; XAISOMBOUN: Saisombun [= Xaisomboun], Nam Ja River, 21.III.2005, M. Sato leg. [1♀ EUM]; XIENG KHOUANG: Ban Muang, 27.IV.2018, K. Yasuda leg. [1♀ EUM]. **Malaysia:** SARAWAK: Kuching, Paddy field, 28.XI.1969, H. Hasegawa leg. [1♀ NARO]; TERENGGANU: Kenyir Lake, Nr. Tekak Riv., Trengganu-St., 3.III.2002, K. Matsumoto leg. [1♀ TUA], 5.III.2002 [1♀ TUA]. **Thailand:** CHIANG MAI: Mae Sa, Mae Rim, 400–450 m alt., 15.V.2002, T. Tsuru leg. [1♀ TUA]; Mae Sa, Mae Rim, 400–450 m alt., 4.VIII.2001, T. Ishikawa leg. [2♀ TUA]. Vietnam: HANOI: Hanoi capital island in Red River, 21°30′N 105°51′E, 24.XI.2014 [1♀ EUM]; HOA BINH: Tonkin [= North Vietnam], Hoa Binh, VIII.1940, A. de Cooman leg. [2♀ TARI].

Sex association

This species was initially described from the female sex only. The male was associated and described by André (1905) based on a pair *in copula*.

Distribution

China: Fujian, Guangdong (Mickel, 1933b). Taiwan: Hualien, Taipei (Tsuneki, 1972b). Indonesia: "Java", Sumatra Utara (André, 1896; Chen, 1957). Laos*: Houa Phan, Xaisomboun, Xieng Khouang. Malaysia: Kuala Lumpur, Sarawak, Terengganu (André, 1905). Thailand: Chiang Mai, Kanchanaburi (Williams *et al*., 2019). Vietnam*: Hanoi, Hoa Binh.

Remarks

This is the most widely distributed *Neotrogaspidia* species, from southern China to Java, Indonesia. One female specimen from Laos has the metasomal segment 3 entirely black (Fig. 81), and one female from China has the S4 red. No additional characters implying species-level status of these females were recognized.

Tsuneki described or recorded mutillid species from Taiwan by merely comparing with published descriptions (Chen, 1957; Mickel, 1933a, 1935) and specimens at his hand. Therefore, most of his species are inadequately diagnosed and potentially synonymous with previously established taxa. In the original description, *Trogaspidia yuliensis* Tsuneki, 1972 was discussed as being similar to *N. pustulata*, but was not compared with *N. circumcincta* because the male of *N. circumcincta* was lacked in Tsuneki's identification sources. The original description, illustrations, and photos of the holotype of *T. yuliensis* (available in Chan *et al*., 2022) match the character states of *N. circumcincta*.

Krombeinidia agricola Williams, 2019 was described based on a single female from Thailand. Here, this species is recognized as a synonym of *N. circumcincta* by having the T2 posterior band medially interrupted, T3 with orange cuticle, and the pygidial plate shagreened.

Tsuneki (1993) recorded *Trogaspidia tethys* (Mickel, 1934) from Pingtung, Taiwan based on a single male specimen. This male-based taxon, including three subspecies, is predominantly distributed in Southeast Asia (Indonesia, Malaysia, Philippines; Mickel, 1934, 1935; Pagden, 1934) but has never been recorded from East Asia adjacent to Taiwan. Tsuneki's record is therefore doubtful. *Trogaspidia tethys* and *Neotrogaspidia* species share some diagnostic characters (see Discussion section below). This species is a good candidate for *Neotrogaspidia*, and *N. circumcincta* keys to *T. tethys* in Mickel (1935) by having the clypeus concave with transverse carina, metasomal segments 1–5 red, and S8 carinae tuberculate posteriorly. Although the voucher specimen (probably in USNM) was not examined, Tsuneki's (1993) record of *T. tethys* is here considered a misidentification of *N. circumcincta*.

***Neotrogaspidia elpinice* (Mickel, 1933), stat. resurr. et comb. nov.**

(Figs 3,4,11–14,19,20,24,39,43,47,51,56,57,64,65,75,78,82,83,100)

Mutilla analis (non Lepeletier 1845): Zavattari, 1913: 41, ♂, part.

Timulla (*Trogaspidia*) *elpinice* Mickel, 1933a: 395, ♂, holotype ♂ (Takao [= Kaohsiung 高雄], Formosa [= Taiwan]) [ZMNB]; Mickel, 1935: 250, ♂. Synonymized by Chen (1957: 165) under *Trogaspidia pustulata* (Smith, 1873).

Trogaspidia aestivalis Hammer, 1949, **syn. nov.**: 8, ♂, holotype male (Kiangsu [= Jiangsu], China) [NHRS]. Synonymized by Chen (1957: 164) under *Trogaspidia pustulata* (Smith, 1873).

Trogaspidia pustulata: Chen, 1957: 164, ♂♀; Lelej & Yamane, 1992: 628, ♂, part; He *et al*., 2004: 966, ♂♀.

Trogaspidia maritima Chen, 1957, **syn. nov.**: 177, ♀, holotype ♀ (Mokanshan [= Mt. Moganshan 莫干山], Chekiang [= Zhejiang], China) [TARI]; Lelej, 2005: 97; Hua, 2006: 301; Okayasu *et al*., 2018: 307, ♀; Pagliano *et al*., 2020: 286.

Trogaspidia pustulata elpinice: Tsuneki, 1972b: 7, ♂; Murota, 1973b: 119, ♂; Tsuneki, 1993: 47, ♂.

Neotrogaspidia pustulata: Lelej, 1996: 21, part; Lelej, 2002: 82, part; Lelej, 2005: 79, part; Hua, 2006: 300, part; Pagliano *et al*., 2020: 253, part.

Trogaspidia maritime: He *et al*., 2004: 965, ♀. Incorrect subsequent spelling.

Diagnosis

MALE. Clypeus concave throughout (Fig. 39); scape with two widely separated obscure carinae, recognizable only apically (Fig. 43); pronotum with sparse suberect golden setae (Fig. 4); mesoscutellum with medial impunctate line posteriorly not elevated into carina (Fig. 3); propodeal dorsum with sparse suberect golden setae, sublaterally without carina; metasomal segments 1–3 or 1–4 red (Fig. 47); T2 evenly convex (Fig. 47); S8 lateral carinae convergent posteriorly and not tuberculate, reaching posterior margin of S8 (Fig. 51); penis valve short robust, incurved, without inner projection (Figs 56,57,65); penis valves with short sparse setae on inner face (Figs 57,65); cuspis slender stick-like, 2.0× longer than digitus (Fig. 64). FEMALE. Frons with large confluent punctures (Fig. 75); T2 spots subcircular, densely setose and well defined (Fig. 82,83); T2 posterior margin with black setae (Fig. 82,83); S2 with large sparse punctures, interspaces smooth and asetose (Fig. 12); T3 and S3 with black cuticle (Figs 12,82,83); T3 with complete band of dense appressed golden setae (Figs 82,83); T4 with black setae (Figs 82,83).

Material examined

88♂72♀. Holotype ♀, *Trogaspidia maritima* Chen: **China:** ZHEJIANG: Mokan Shan [= Mt. Moganshan], Musée Heude, 22.V.[19]36, O. Piel, coll., *Trogaspidia maritima* Chen [probably Chen's hand], *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1982 [TARI]. Paratypes, *Trogaspidia maritima* Chen: **China:** ANHUI: Prov. Anhwei [= Anhui], Ningkwo [= Ningguo], Yui Wau Kiai, 18.VII.[19]20, *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1982 [1♀ TARI]; JIANGSU: Kiangsu [= Jiangsu], Chenmo, 11.V.[19]35, O. Piel, coll., *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1982 [1♀ TARI], 21.V.[19]35 [1♀ TARI]; ZHEJIANG: Hangchow [= Hangzhou], 20.V.1929, *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1982 [1♀ TARI], 17.IV.1930 [1♀ TARI], 193 [1♀ TARI]; Chekiang [= Zhejiang], Tien-Mu-Shan [= Mt. Tianmushan], 193, Col., *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1982 [1♀ TARI]; Chekiang [= Zhejiang], Chusan [= Zhoushan], 22.IV.[19]31, O. Piel, coll., *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1982 [1♀ TARI], 14.VIII.[19]36 [1♀ TARI], 21.VIII.[19]31 [1♀ TARI], 5.IX.[19]31 [1♀ TARI]; Mokan Shan [= Mt. Moganshan], 28.V.[19]36, O. Piel, coll., *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1982 [1♀ TARI]. **China:** ANHUI: Anhwei [= Anhui], Ningkwo [= Ningguo], 6.VII.[19]20, *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1982 [1♂ TARI]; Anhwei [= Anhui], Ningkwo [= Ningguo], Yui-Wau-Kiai, 17.VII.1920, *Trogaspidia pustulata* (F. Sm.), C.W. Chen det. [1♂ TARI]; FUJIAN: Chungan, Bohea Hills, 23.VII.1939, T.C. Maa leg., *Timulla insidiator* [probably Chen's hand], *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1982 [1♀ TARI], 1.XI.1939 [1♂ TARI]; Chungan, Bohea Hills, 1.X.1939, T.C. Maa leg., *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1982 [1♂ TARI], 1939 [1♀ TARI]; Fukien [= Fujian], Shaowu, Tachulan [= Dazhulan], 10.VI.1942, T.C. Maa leg. [1♀ TARI]; Fukien [= Fujian], Shaowu, Tachulan [= Dazhulan], 11–17.VIII.1943, T.C. Maa leg., *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1982 [1♂ TARI], 30–31.VIII.1943 [1♂ TARI], 21–30.IX.1943 [1♂ TARI], 29.IX.1947 [1♂ TARI]; Fukien [= Fujian], Shaowu, Tachulan [= Dazhulan], 12.VIII.1945, T.C. Maa leg., *Timulla elpinice* ♂ [probably Chen's hand], *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1982 [1♂1♀ (*in copula*) TARI]; Fukien [= Fujian], Shaowu, Tachulan [= Dazhulan], 13–17.VIII.1945, T.C. Maa leg., *Timulla* sp. n. ♀ [probably Chen's hand] [1♀ TARI]; Fukien [= Fujian], Shaowu, Shuipeikieh [= Shui Pei Kai], 16.VIII.1942, T.C. Maa leg., *T. insidiator* [probably Chen's hand], *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1982 [1♀ TARI], 12.V.1943 [2♀ TARI]; Fukien [= Fujian], Shaowu, Shuipeikieh [= Shu Pei Kai], V.1944, T.C. Maa leg., *Trogaspidia pustulata = insidiator* [probably Chen's hand], *Trogaspidia pustulata aestivalis* Hammer, B.

Petersen det. 1982 [1♀ TARI]; Fukien [= Fujian], Kienyang [= Jianyang], 8.VI.1942, T.C. Maa leg., *T. insidiator*? [probably Chen's hand], *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1982 [1♀ TARI]; Fukien [= Fujian], Kienyang [= Jianyang], 8.VI.1942, T.C. Maa leg., *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1982 [1♀ TARI]; Fukien [= Fujian], Shaowu, Kaoyany, 12.V.1942, T.C. Maa leg. [2♀ TARI], 30.VII.1945 [1♀ TARI]; Fukien [= Fujian], Chungan, Kwatun, 3.V.1942, T.C. Maa leg., *Timulla* sp. n. [probably Chen's hand] [1♀ TARI]; Fukien [= Fujian], Chungan, Kwatun, 21–25.VIII.1943, T.C. Maa leg., *Timulla elpinice* [probably Chen's hand], *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1982 [1♂ TARI]; Fukien [= Fujian], Kienyang [= Jianyang], Hwangkeng, 11.X.1943, T.C. Maa leg., *Timulla elpinice* [probably Chen's hand], *Trogaspidia pustulata* (F. Smith) [probably Chen's hand], *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1982 [1♂ TARI]; Fukien [= Fujian], Kienyang [= Jianyang], Hwangkeng, 17.IV.1945, T.C. Maa leg., *Timulla* sp. [probably Chen's hand] [1♂ TARI]; Fukien [= Fujian], Shaowu, Wuko, 30.VIII.1944, T.C. Maa leg., *Timulla elpinice* [probably Chen's hand], *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1982 [1♂ TARI]; HUNAN: Yuanling, Yuanwangtan, 7.VI.1939, T.C. Maa leg., *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1982 [1♀ TARI]; JIANGSU: Nanking [= Nanjing], 21.VII.[19]17, *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1982 [1♂ TARI], 20.VII.[19]18 [1♂ TARI], 16.IX.[19]18 [1♀ TARI]; Prov. Kiangsu [= Jiangsu], Chinkiang [= Zhenjiang], 30.VI.[19]18, *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1982 [1♂ TARI]; Prov. Kiangsu [= Jiangsu], Chinkiang [= Zhenjiang], Tchenkiang [= Zhenjiang], 24.VII.[19]18, *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1982 [1♂ TARI], 25.IV.[19]19 [1♀ TARI]; Kiangsu [= Jiangsu], [additional locality unrecognizable], 6.VIII.[19]33, O. Piel leg., *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1982 [1♂ TARI]; Kiangsu [= Jiangsu], Chenmo, 13.V.[19]35, O. Piel leg., *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1982 [2♀ TARI]; JIANGXI: [Lushan, Jiujiang], Kuling [= Guling], 10.VII.[19]35, O. Piel leg., *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1982 [1♀ TARI], 12.VII.[19]35 [1♀ TARI], 7.IX.[19]35 [1♂ TARI]; SHANGHAI: Prov. Kiangsu [= Jiangsu], Shanghai, Zi-ka-wei, IX.[19]19, *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1982 [1♂ TARI], 4.X.[19]19 [1♂ TARI], 31.V.[19]24 [1♀ TARI], 3.VI.[19]24 [1♀ TARI], 8.VI.[19]24 [1♀ TARI]; Prov. Kiangsu [= Jiangsu], Shanghai, Zi-ka-wei, 16.VI.[19]25 [1♀ TARI]; Prov. Kiangsu [= Jiangsu], Shanghai, Zô-Sè [= Sheshan], 1.VIII.[19]21, *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1982 [1♀ TARI], 20.VII.[19]24 [1♀ TARI], 25.VII.[19]24 [1♂ TARI], 8.VII.[19]25 [2♀ TARI], 15.VII.[19]25 [1♂ TARI], 19.VII.[19]25 [1♀ TARI]; Prov. Kiangsu [= Jiangsu], Shanghai, Zô-Sè [= Sheshan], 10.VII.[19]25 [1♀ TARI], 22.VII.[19]25 [1♀ TARI], 4.VIII.[19]25 [1♂ TARI]; Prov. Kiangsu [= Jiangsu], Shanghai, Zô-Sè [= Sheshan], 24.V.[19]30, O. Piel leg., *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1982 [1♀ TARI], 7.VII.[19]30 [1♂1♀ TARI], 8.VII.[19]30 [2♂ TARI], 11.VII.[19]30 [1♂ TARI], 18.VII.[19]30 [1♀ TARI], 20.VII.[19]30 [1♀ TARI], 21.VII.[19]30 [1♀ TARI], 22.VII.[19]30 [1♂ TARI], 23.VII.1930 [1♂1♀ TARI], 24.VII.[19]30 [1♂ TARI], 26.VII.[19]30 [1♂1♀ TARI], 11.VIII.[19]30 [1♂ TARI, 22.VIII.[19]30 [2♂ TARI], 23.VIII.[19]30 [2♂1♀ TARI], 25.VIII.[19]30 [1♂ TARI], 26.VIII.[19]30 [2♂ TARI], 1.IX.[19]30 [1♀ TARI]; Prov. Kiangsu [= Jiangsu], Shanghai, Zô-Sè [= Sheshan], 13.V.[19]30, O. Piel leg., *Trogaspidia pustulata* (F. Sm.), C.W. Chen det. [1♀ TARI]; Prov. Kiangsu [= Jiangsu], Shanghai, Zô-Sè [= Sheshan], 26.VII.[19]30, O. Piel leg., *Timulla insidiator* [probably Chen's hand], *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1982 [1♀ TARI]; Prov. Kiangsu [= Jiangsu], Shanghai, Zô-Sè [= Sheshan], 29.VII.[19]30, O. Piel leg., *Trogaspidia pustulata* (F. Sm.), C.W. Chen det., *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1982 [1♂ TARI]; Prov. Kiangsu [= Jiangsu], Shanghai [1♀ TARI]; Prov. Kiangsu [= Jiangsu], Shanghai, 7.V.[19]30, O. Piel leg.,

Trogaspidia pustulata aestivalis Hammer, B. Petersen det. 1982 [1♀ TARI], 9.V.[19]30 [1♀ TARI], 2.VI.[19]30 [1♀ TARI], 24.VI.[19]30 [1♀ TARI], 26.IX.[19]30 [1♂ TARI]; Prov. Kinagsu [= Jiangsu], Shanghai, 4.VIII.[19]31, *in copula*, *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1982 [1♂1♀ (*in copula*) TARI]; Poudong [= Pudong], Aoui, 1999, *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1982 [1♂ TARI]; SICHUAN: Mt. OMei [= Emei], 22.VII.1941, T.T. Chuh leg., *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1982 [1♂ TARI]; ZHEJIANG: Hangchow [= Hangzhou], 21.VII.1928, *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1982 [1♂ TARI]; Chekiang [= Zhejiang], Chusan [= Zhoushan], 29.VIII.[1930], O. Piel leg., *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1982 [1♂ TARI], 1.VIII.[19]31 [1♂ TARI], 8.VIII.[19]31 [1♂ TARI], 11.VIII.[19]31 [1♂ TARI], 13.VIII.[19]31 [1♂ TARI], 18.VIII.[19]31 [1♂ TARI], 27.VIII.[19]31 [1♂ TARI], 28.VIII.[19]31 [1♂ TARI], 29.VIII.[19]31 [4♂ TARI], 31.VIII.[19]31 [6♂ TARI], 1.IX.[19]31 [4♂ TARI], 7.IX.[19]31 [2♂ TARI], 8.IX.[19]31 [3♂ TARI], 23.VII.[19]34 [1♂ TARI]; Fuyang, 9.VII.1933, *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1982 [1♂ TARI]; Wenchou [= Wenzhou], 16.VII.[19]34, *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1982 [1♂ TARI]; Chekiang [= Zhejiang], Chusan [= Zhoushan], 28.VII.[19]35, *Trogaspidia pustulata* (F. Smith) [probably Chen's hand], *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1982 [1♀ TARI]; Province Unknown: chow [probably Hangchow = Hangzhou], 1935, T.C. Ma leg., *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1982 [1♀ TARI]; Buo-hwa-shan, 12.VII.1943, *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1982 [1♂ TARI], 15.VII.1943 [1♂ TARI]. **Taiwan:** KEELUNG: Agincourt [= Pengjia], 1.V.1927, K. Shibata leg., *Timulla insidiator* [probably Chen's hand] [1♀ TARI]; NANTOU: Hori [= Puli], 2599, 2–5, J. Yoshioka Collection [1♀ NSMT]; New Taipei: Zhonghe, 21.VIII.1958, S.C. Chiu leg. [1♀ TARI]; Sintien [= Xindian], 26.VIII.1968, K.H. Chang leg., *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1988 [1♂ TARI]; Taipei: [Wulai], Rimogan [= Fushan], 8.XI.1923, J. Sonan leg., *Timulla elpinice* [probably Chen's hand] [1♂ TARI]; Taihoku [= Taipei], 18.III.1925, T. Yoshida leg. [1♂ TARI]; Taihoku [= Taipei], 18.VI.1925, J. Sonan leg., *Trogaspidia pustulata* (F. Sm.), C.W. Chen det. [1♂ TARI]; Taihoku [= Taipei], 20.IX.1927, K. Sato leg., *Neotrogaspidia pustulata* (Smith), A.S. Lelej det. 1996 [1♂ NSMT]; Taihoku [= Taipei], 16.XI.1929, J. Sonan leg., *Timulla elpinice* [probably Chen's hand] [1♂ TARI]; Taihoku [= Taipei], 13.XI.1933, S. Sakamoto leg., *Trogaspidia pustulata* (Smith) [probably Chen's hand] [1♂ TARI]; Taihoku [= Taipei], 7.IV.1941, J. Sonan leg. [1♀ TARI]; Taipei, 10.VIII.1968, K.H. Chang leg., *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1988 [1♂ TARI]; Taipei, 3.X.1968, S.C. Chiu leg.], *Trogaspidia pustulata aestivalis* Hammer, B. Petersen det. 1988 [2♂ TARI]; Taipei, Sungshan [= Songshan], 18.V.1972, M. Sakai leg. [1♀ EUM]; TAOYUAN: Haihu, III, *Mutilla insidiator* Smith, T. Shiraki det. [1♀ TARI].

Sex association

This species was initially described from the male sex only. The female was associated and diagnosed as *Trogaspidia pustulata* by Chen (1957) based on a pair *in copula*.

Distribution

China: Anhui, Fujian, Guangdong, Hunan, Jiangsu, Jiangxi, Shanghai, Sichuan, Zhejiang (Lelej, 1996). Taiwan: Chiayi, Hualien, Keelung, Nantou, New Taipei, Pingtung, Taichung, Taipei, Taitung, Taoyuan, Yilan (Chen, 1957; Tsuneki, 1972b; Murota, 1973b).

Remarks

Neotrogaspidia elpinice was originally separated from the male of *N. pustulata* by having the

S8 with lateral carinae rounded posteriorly (terminating as teeth in *N. pustulata*), last two metasomal segments black (metasomal segments 3–7 black in *N. pustulata*), and T4 and T5 with a pale setal band (T3 and T4 with a pale setal band in *N. pustulata*) (Mickel, 1933a). Chen (1957) examined a number of males from China and Taiwan, and regarded these traits as variation. Additionally, Chen identified a female collected *in copula* with a male from China as *Timulla insidiator* using Mickel's (1935) key. Chen (1957) concluded that *T. elpinice* and *T. insidiator* are synonyms of *N. pustulata*. By contrast, Tsuneki (1972b) compared male specimens of *N. elpinice* from Taiwan and those of *N. pustulata* from Japan, and resurrected the former as a subspecies of the latter. In Tsuneki's treatment, the male of *N. elpinice* was separated from that of *N. pustulata* by the metasomal segments 1–3, 1–4, or 1–5 red (metasomal segments 1–2 red and T3 at least medially black in *N. pustulata*) and metasoma with a pale setal band on T3, T4 and sometimes on T5 (metasoma with a pale setal band on T3 and T4, and never on T5 in *N. pustulata*). Tsuneki also used the clypeus with ventral portion smooth and dorsal punctate area smaller to distinguish *N. elpinice* (clypeus with ventral portion transversely microrugulose and dorsal punctate area larger in *N. pustulata*), while corrected Mickel's interpretation of hypopygial ridges. Lelej & Yamane (1992) examined a male of *N. elpinice* from China and both sexes of *N. pustulata* from Japan and South Korea. They regarded those two species as synonymous following Chen's treatment.

Here, I examined a large series of male and female specimens of both species from China, Taiwan, Japan, North Korea and South Korea. In males, *N. elpinice* is separated from *N. pustulata* by having the metasomal segments 1–3, 1–4, or 1–5 red (metasomal segments 1–3 red except S1 dark brown to black and medial portion of T3 largely black in *N. pustulata*) as Tsuneki (1972b) stated, although Tsuneki (1972c) recorded a single male of *N. pustulata* with the metasomal segment 3 entirely red. Additionally, the males of *N. pustulata* never have a pale setal band on T5, unlike *N. elpinice*. The microsculpture of the male clypeus was subject to variation and not useful in most cases. In females, *N. elpinice* is differentiated from *N. pustulata* by having the T2 pale spots subcircular and densely setose (transverse and sparsely setose in *N. pustulata*). These morphological differences suggest *N. elpinice* and *N. pustulata* belong to genetically isolated clades. Although species-level status can be controversial, I prefer to treat these nominal taxa as separate species.

In the original description, *Trogaspidia maritima* was separated from the female of *N. pustulata* by the pronotal collar almost flattened (posteriorly constricted in *N. pustulata*) and the T2 spots subcircular ("transversely aligned" in *N. pustulata*) (Chen 1957). I compared type specimens of *T. maritima* with *N. pustulata* specimens identified by Chen (here considered as *N. elpinice*) and found that they were synonymous. Chen correctly distinguished *N. pustulata* by having the T2 spots transverse. However, no females with this character state were found in Chen's specimens identified as such.

***Neotrogaspidia pustulata* (Smith, 1873)**

(Figs 5,6,15–18,23,26–37,40,44,48,52,58,59,66,67,70–72,76,79,84,85,86–98,100)

Mutilla pustulata Smith, 1873: 182, ♂, holotype ♂ (Hiogo [= Hyôgo 兵庫], Japan) lost (Mickel, 1935); Dalla Torre, 1897: 75; André, 1902: 71.

Mutilla insidiator Smith, 1873: 182, ♀, holotype ♀ (Hiogo [= Hyôgo 兵庫], Japan) [BMNH]; Dalla Torre, 1897: 50; André, 1902: 39; Matsumura, 1931: 29; Yano, 1932: 327, ♀; The Natural History Society of Fukui, 1938: 5–35. Synonymized by Chen (1957: 164) under *Trogaspidia pustulata* (Smith, 1873).

Mutilla insidiator Smith, 1874: 408, ♀, holotype ♀ (Hiogo [= Hyôgo 兵庫], Japan) [BMNH]. Synonymized by Mickel (1935: 255) under *Timulla* (*Trogaspidia*)

insidiator (Smith, 1873).

Mutilla petulans Smith, 1874: 408, ♂, holotype ♂ (Hiogo [= Hyôgo 兵庫], Japan) [BMNH]; Dalla Torre, 1897: 72; André, 1902: 71; Matsumura, 1931: 29; Matsumura, 1932: 8. Synonymized by Mickel (1935: 248) under *Timulla* (*Trogaspidia*) *pustulata* (Smith, 1873).

Mutilla japonica Dalla Torre, 1897: 48, ♀, new name for *Mutilla insidiator* Smith, 1874; André, 1902: 39. Synonymized by Mickel (1935: 255) under *Timulla* (*Trogaspidia*) *insidiator* (Smith, 1873).

Mutilla insidiatrix Schulz, 1906: 158, ♀, unjustified emendation for *Mutilla insidiator* Smith, 1874. Synonymized by Mickel (1935: 255) under *Timulla* (*Trogaspidia*) *insidiator* (Smith, 1873).

Stenomutilla petulans: Uchida, 1925: 334, ♂.

Smicromyrme yakushimensis Yasumatsu, 1934: 65, ♀, holotype ♀ (Anbô-Funayuki [安房–船行], Yakushima Island [屋久島], Japan) [ELKU]; Tsuneki, 1972a: 20, ♀; Tsuneki, 1982a: 70; Tsuneki, 1982b: 100; Nagase, 1982: 61; Yoshida, 1989: 651. Synonymized by Okayasu (2020: 95) under *Neotrogaspidia pustulata* (Smith, 1873).

Timulla (*Trogaspidia*) *pustulata*: Mickel, 1935: 248, ♂; Yasumatsu, 1936: 361, ♂; Yasumatsu, 1938a: 84, ♂.

Timulla (*Trogaspidia*) *insidiator*: Mickel, 1935: 255, ♀; Yasumatsu, 1938b: 351, ♀; Yasumatsu, 1944: 519; Yasumatsu, 1950: 1448, ♀; Ohgushi & Yoshida, 1960: 53.

Smicromyrme lewisi yanoi: Yasumatsu, 1938b: 351, ♂ non ♀.

Timulla pustulata: Kim, 1963: 340; Kim, 1970: 512, ♂.

Trogaspidia pustulata: Tsuneki, 1972a: 13, ♂♀; Tsuneki, 1972c: 59; Murota, 1973a: 100, ♂; Nomura, 1978: 16; Nagase, 1980: 5; Haneda, 1982: 51, ♀; Nagase, 1982: 61; Terayama, 1982: 26; Tsuneki, 1982a: 70; Tsuneki, 1982b: 100; Tsuneki, 1984: 9, ♂; Nambu & Shimizu, 1984: 24, ♂; Tsuneki, 1985: 9, ♂♀; Tano *et al*., 1985: 31, ♂; Lelej & Yamane, 1992: 628, ♂♀; Gôukon, 1993: 38, ♂♀; Takahashi, 1993: 3, ♂♀; Kim *et al*., 1994: 255; Takahashi, 1996: 29, ♂♀; Hisamatsu, 2004: 135; Nakamura & Matsuda, 2005: 149, ♂; Fukasawa & Miyano, 2010: 25; Takahashi, 2010: 18; Sugiura *et al*., 2013: 162.

Timulla insidiator: Tsuneki, 1959: 79, ♂; Tsuneki, 1962: 1, ♂; Tano, 1964: 37, ♂♀; Ishikawa, 1965: 289, ♂♀.

Sinotilla yakushimensis: Yamane, 1999: 379, ♀; Lelej, 2005: 56; Terayama, 2005: 8, ♀; Terayama *et al*., 2011: 21, ♀; Lo Cascio, 2015: 557; Terayama *et al*., 2016: 168, ♀; Okayasu, 2017: 162, ♀; Okayasu *et al*., 2018: 304, ♀; Pagliano *et al*., 2020: 187.

Neotrogaspidia pustulata: Lelej, 1996: 21; Yamane, 1999: 378, ♂♀; Lelej *et al*., 2001: 12, ♂♀; Waki, 2001: 35, ♀; Azuma *et al*., 2002: 322; Iwata *et al*., 2002: 122, ♀; Lelej, 2002: 82; Haneda, 2003: 1; Haneda & Tano, 2003: 9, ♀; Tano *et al*., 2003: 24, ♂; Kurokawa, 2003: 59, ♀; Nakamura, 2003: 287, ♂♀; Katô *et al*., 2004: 56, ♂♀; Nagase, 2004: 1280, ♂♀; Haneda *et al*., 2005: 57, ♂; Lelej, 2005: 79; Terayama, 2005: 7, ♂♀; Haneda *et al*., 2006a: 5, ♀; Haneda *et al*., 2006b: 40, ♂; Hua, 2006: 300; Ohkusa, 2007: 30, ♂♀; Takahashi & Shimizu, 2007: 11, ♂; Haneda *et al*., 2007: 50, ♂; Ikudome & Yamane, 2007: 6, ♂♀; Ohkusa & Tajima, 2008: 69, ♂; Ikudome & Yamane, 2009: 3, ♂♀; Ohkusa & Tajima, 2010: 7, ♂; Yamamoto, 2010: 25, ♂♀; Sato & Tsurusaki, 2010: 68; Terayama *et al*., 2011: 21, ♂♀; Suda, 2011: 137, ♀; Mimura, 2014: 16, ♂; Murao, 2014: 644, ♀; Lo Cascio, 2015: 553; Murao, 2015: 36, ♀; Terayama *et al*., 2016: 169, ♂♀; Inoue, 2018: 27, ♀; Okayasu *et al*., 2018: 304, ♀; Suda, 2018: 39, ♀; Imai, 2019: 2, ♂♀; Kim & Kwon, 2019: 94; Mimura, 2019: 57, ♂♀; Okayasu, 2020: 95, ♂♀; Pagliano *et al*., 2020: 253; Akiyama *et al*., 2021: 141, ♀; Ôtsui *et al*., 2021: 35, ♂♀; Kan, 2022: 178, ♂.

Neptrogaspidia [sic!] *pustulata*: Tsurusaki *et al*., 2012: 71.
Neotrogaspidia pusfulata: Kawazoe, 2013: 15, female. Incorrect subsequent spelling.

Diagnosis
MALE. Clypeus concave throughout (Fig. 40); scape with two widely separated obscure carinae, recognizable only apically (Fig. 44); pronotum with sparse suberect golden setae (Fig. 6); mesoscutellum with medial impunctate line posteriorly not elevated into carina (Fig. 5); propodeal dorsum with sparse suberect golden setae, sublaterally without carina; T1–2 and S2 red, T1 sometimes black (Fig. 48); S1 dark brown to black (Fig. 48); T3 and S3 black or red, at least T3 medially largely black (Fig. 48); T4 black (Fig. 48); T2 evenly convex (Fig. 48); S8 lateral carinae convergent posteriorly and not tuberculate, reaching posterior margin of S8 (Fig. 52); penis valve short robust, incurved, without inner projection (Figs 58,59,67); penis valves with short sparse setae on inner face (Figs 59,67); cuspis slender stick-like, 2.0× longer than digitus (Fig. 66). FEMALE. Frons with large confluent punctures (Fig. 76); T2 spots transverse, sparsely setose and obscurely defined (Figs 84,85); T2 posterior margin with black setae (Figs 84,85); S2 with large sparse punctures, interspaces smooth and asetose (Fig. 16); T3 and S3 with black cuticle (Figs 16,84,85); T3 with complete band of dense appressed golden setae (Figs 84,85); T4 with black setae (Figs 84,85).

Material examined
150♂171♀. Holotype ♀, *Smicromyrme yakushimensis* Yasumatsu: **Japan:** ÔSUMI ISLANDS: Yakushima, Ambô-Funayuki, 7.VIII.1929, H. Hori leg. [ELKU]. **Japan:** AICHI: Nagoya, 1933, M. Baba leg. [1♂ SEHU]; Mt. Hongusan, 1.VI.1956, M. Sato leg. [1♀ EUM]; AMAMI ISLANDS: Toku No Shima [= Tokunoshima Island], Sumiyo, 3.IV.1954, T. Oku leg. [1♀ SEHU]; Amami-Ohshima, [Amami-shi], Shinmura, 18.VII.1954, T. Edashige leg. [1♂ EUM]; Amami-Oshima, Ookawa, 22.VII.1963, Y. Kurosawa leg., *Trogaspidia pustulata* Sm., Lelej det. 1991 [1♂ NSMT]; Amami-Oshima, Shinmura, 29.VII.1972, T. Nambu leg. [1♂ NSMT]; Ryukyu, Tokunoshima Is., Amagi-cho, Matsubara, 24.VI.2017, Y. Tamadera leg. [1♀ EUM]; Amami-Oshima Isl., Amami-shi, Kasari-cho, Manya, 28°26′35.9″N 129°42′07.6″E, 10 m alt., 13.IX.2020, T. Mita leg. [1♂ ELKU]; Tokuno-shima Isl., Tokunoshima-cho, Tete, rice paddy, 27°53′10.3″N 128°55′23.2″E, 10 m alt., 23.VII.2021, Y. Tatsumi leg. [1♀ ELKU]; Oshima-gun, Tokunoshima-cho, Tete, 27°53′02.9″N 128°55′37.2″E, 23.VII.2021, Y. Tatsumi leg. [1♂ ELKU]; CHIBA: Yachimata-shi, Yachimatahe, 27.IX.2021, K. Yoshida leg. [1♂ EUM]; Matsudo, 2601, 8–25 [2♂ NSMT]; EHIME: Iyo [= Ehime], 20.X.1914, Arakawa, Matsumura [1♀ SEHU], 2.VII.[19]38 [1♀ SEHU]; Iyo [= Ehime], Sasayama, 21.VIII.1916, Matsumura [1♂ SEHU]; Matsuyama, Kumanodai, 13.V.1947, M. Miyatake leg., *Timulla insidiator* Smith, S. Ueda det. 1953 [2♀ EUM]; Matsuyama, Tarumi, 31.VII.1947, T. Kobayashi leg. [1♀ EUM]; Matsuyama, Tarumi, 16.IV.1950, M. Miyatake leg. [1♀ EUM]; [Matsuyama-shi], Sugitate, 12.IX.1951, T. Ishihara leg. [1♂ EUM]; nr. Matsuyama, Hoshino-oka, 2.VII.1953, M. Miyatake leg. [1♀ EUM]; Matsuyama, Fune, 17.V.1953, F. Takechi leg. [1♀ EUM], 4.VII.1953 [1♀ EUM], 17.VII.1953 [1♀ EUM], 20.IV.1954 [1♀ EUM]; Matsuyama, Higashino, 11.IX.1953, S. Ueda leg. [1♂ EUM]; Matsuyama, Kumanodai, 24.V.1955, F. Takechi leg. [1♀ EUM]; [Kumakôgen-chô], Mt. Ishizuchi, Jyojusha, 29.VII.1955, S. Ueda leg. [1♂ EUM]; Matsuyama, 30.VII.1957, M. Miyatake leg. [1♀ EUM]; [Matsuyama-shi], Mt. Takanawa, 11.VIII.1959, F. Takechi leg. [1♂ EUM]; Uchiumi-mura [= Ainan-chô], Nec of Yura Pen., 3.IX.1995, H. Ono leg. [1♀ EUM]; [Kita-gun], Oda-cho [= Uchiko-chô], 20.VI.1996, E. Yamamoto leg. [1♀ EUM], 7.VI.1997 [1♀ EUM]; Ôzu-shi, Matsugahana, 21.IX.1996, T. Befu leg. [1♀ EUM]; Sugesawa-machi, Kawauchi-jinjya, 9.V.2006, K. Takasuka leg. [1♀ EUM]; Shikokuchûô-shi, Kanada-chô, Handa, Asakura-ike, 24.V.2006, T. Kurihara leg. [1♀

EUM]; Kumakogen, Yurano, 11.IX.2007, E. Yamamoto leg. [1♂ EUM]; [Kitauwa-gun], Kihoku-chô, Okufujikawa, 6.IX.2008, Y. Kawakami leg. [1♂ EUM]; Seiyo-shi, Shirokawa-cho, Takanoko, 27.V.2016, H. Ikeda leg. [1♀ EUM]; Matsuyama-shi, Takanoko-machi, 8.X.2016, K. Yasuda leg. [1♀ EUM], 28.VI.2017 [1♀ EUM]; Minami-Uwa-gun, Ainan-cho, Cape Komo, 21.IX.2017, Y. Hisasue leg. [1♂ EUM]; Matsuyama-shi, Tarumi, Ehime University Faculty of Agriculture Campus, 33°50′22″N 132°47′38.3″E, 41 m alt., meadow, 5.VII.2019, K. Yasuda leg. [1♂ EUM]; Saijyô, Kurodani, 13.VIII.2020, K. Kuroda leg. [1♀ EUM]; FUKUI: [Fukui-shi], Sanri-hama, 12.IX.1972, K. Tsuneki leg., *Trogaspidia pustulata* (Smith), K. Tsuneki det. 1983 [1♂ NSMT]; FUKUOKA: Fukuokashi, Nishi-ku, Motooka, Kyushu Univ., 3.VI.2019, Y. Tatsumi leg. [1♀ ELKU]; Nishi-ku, Kuwabara, 11.VI.2019, J. Abe leg. [1♀ ELKU]; Fukuoka-shi, Nishi-ku, Motooka, Ito-Campus [= Kyushu University], 19.VI.2019, K. Nishiya leg. [1♀ ELKU]; Itoshima-shi, Shito, 25.VI.2019, K. Nishiya leg. [1♀ ELKU], 28.VIII.2019 [1♂ ELKU]; Kasuya-gun, Umi-machi, Mt. Shioji, 31.VII.2020, Y. Hisasue leg. [1♂ ELKU]; Itoshima-shi, Zuibaiji, 33°30′10.8″N 130°14′49.2″E, 200 m [alt.], 30.VIII.2020, K. Nishiya leg. [1♂ ELKU]; Fukuoka-shi, Sawara-ku, Higashiirube, Muromi Riv. (Riverside), 33.5117°N 130.3350°E, 1.IV.2021, Y. Hisasue leg. [ELKU]; GOTÔ ISLANDS: Fukue-jima, Minamimatsuura-gun, Miirakuchô, Takasaki, 19.V.1997, K. Toriyama leg. [1♀ TUA]; HIROSHIMA: Hiroshima, 10.IX.1955, T. Ishihara leg. [1♂ EUM]; [Miyoshi-shi], Kisa-chô, Kisa, 24.VII.1996, S. Nakamura leg. [1♂ HMNH]; Miyoshi-shi, Mukouetamachi, 25.VII.1996, S. Nakamura leg. [1♂ HMNH]; Kôzan-chô [= Sera-chô], Higashiuehara, 26.IX.1996, S. Nakamura leg. [1♂ HMNH]; Ôta-gawa, st. 6, 8.x.1998, S. Nakamura leg. [1♀ HMNH], 27.VII.2003 [1♂ HMNH]; [Ôtake-shi, Ogata-chô, Ogata], Yasaka-dam, 10.V.2000, S. Nakamura leg. [1♀ HMNH]; Ôta-gawa, st. 4, 2.X.2007, S. Nakamura leg. [1♂ HMNH]; HYÔGO: Harima [= Hyôgo], 2.VII.1912, Iyo, Arakawa [1♂ SEHU]; IBARAKI: Hitachiôta-shi, Shimoose, 3.VIII.2021, K. Yoshida leg. [1♀ EUM]; IZU ISLANDS: Hachijyô-jima Island, Mt. Kandoyama, 28.V.[19]80 [1♀ EUM]; KAGAWA: Vil. Sakamoto [= Hanzan-chô], 19.VIII.1947, T. Kobayashi leg. [1♀ EUM]; KAGOSHIMA: Satsuma [= Kagoshima], [Minamikyûshû-shi], Chiran, 28.VII.’1908 [1♀ NSM]; Takakuma-yama, 29.VIII.1975, K. Kushigemati leg. [1♂ SEHU]; KANAGAWA: [Kawasaki-shi], [Tama-ku], Higashiikuta, 4.VI.1933, A.Y. [1♀ NSMT]; Ohiso, 9.VI.1940, H. Hasegawa leg. [1♀ NSMT]; [Fujisawa-shi], C. Katase, 5.XI.[19]34, H.K. [1♀ NSMT]; [Fujisawa-shi], Katase, 11.XI.1934, A. Yoshida leg. [1♀ NSMT]; Shinohara-cho, Yokohama, 8.VI.1941, K. Sato leg. [1♀ NSMT]; [Atsugi-shi], Ogino, 27.IX.1991, H. Takizawa leg. [1♀ SEHU], 9.XI.1991 [1♀ SEHU]; Atsugi-City, Funako, T[okyo].U[niversity of].A[griculture]. Campus, 5.IX.2001, T. Ishizaki leg. [1♂ TUA]; Ebina-shi, Sagami-gawa Riv., 28.IX.2006, St. 5, YPT, M. Ooishi & R. Watanabe leg. [1♂ TUA]; Yokosuka, Nagasawa, 1.VIII.2013, H. Nagase leg. [1♂ NSMT]; KÔCHI: [Kôchi-shi], Mt. Kodakasa, 10.IX.1929 [1♂ SEHU]; Okinoshima, 11.VI.1952, K. Kojima leg. [1♀ SEHU]; [Shimanto-shi], Nakamura, 12.VIII.1955, S. Hisamatsu leg. [2♂ EUM]; [Tosashimizu-shi], Cape Ashizuri, 24.VII.1960, N. Ohbayashi leg., *Neotrogaspidia pustulata*, M. Terayama det. 2010 [1♀ EUM]; [Takaokagun], Kubokawa Cho [= Shimanto-chô], 4.VII.1965, Y. Kawakami leg. [1♀ EUM], 15.V.1968 [1♀ EUM]; Kochi Shi, Asakura, 13.XI.1983, Y. Kawakami leg. [1♀ EUM]; Muroto-shi, Sakiyama, 18.IX.1988, Y. Kawakami leg. [1♂ EUM], 19.X.2003 [1♀ EUM]; [Aki-gun], Tôyô-chô, Ikumi, 9.X.1990, T. Befu leg. [1♀ EUM], 28.IV.1991 [1♀ EUM]; Nankoku-shi, Mt. Kotohira-san, 12.VIII.1991, T. Befu leg. [1♀ EUM]; [Tosashimizu-shi], Ashizuri-misaki, 18.IX.1994, Y. Kawakami leg. [1♂1♀ EUM]; [Agawa-gun], Ino Cho, Ôchi, 31.V.1995, Y. Kawakami leg. [1♀ EUM]; Aki-shi, Higashiyama-kôen, 20.VIII.1995, Y. Kawakami leg. [1♂ EUM]; Muroto C[ity]. [= Muroto-shi], Sakihama, 13.VIII.1995, Y. Kawakami leg. [1♂ EUM], 23.VIII.1995 [2♂ EUM], 3.IX.1995 [1♂ EUM], 15.IX.1995 [2♂1♀ EUM], 6.V.1996 [1♀ EUM]; [Kônan-shi], Akaoka-chô, Hiraiyama, 21.IX.1995, T. Befu leg. [1♀ EUM];

Muroto C[ity]. [= Muroto-shi], Sakiyama, 5.V.1996, Y. Kawakami leg. [3♀ EUM]; Kochi C[ity]. [= Kôchi-shi], Mt. Hitsuzan, 25.V.1996, Y. Kawakami leg. [1♀ EUM], 24.IV.1997 [1♀ EUM], 14.VII.1997 [2♂ EUM], 8.X.1997 [1♂ EUM], 1.VI.1998 [1♀ EUM], 8.VIII.1998 [1♂ EUM], 14.VIII.1998 [1♂ EUM], 19.VIII.2000 [1♂ EUM]; Kôchi-shi, Mt. Hitsuzan, 29.VIII.2005, Y. Kawakami leg. [1♂ EUM], 31.V.2006 [1♀ EUM], 4.VI.2006 [2♀ EUM]; [Hata-gun], Mihara Vil[lage]. [= Mihara-mura], 1.IX.1996, Y. Kawakami leg. [2♂ EUM]; Nishitosa [= Shimanto-shi], Egawasaki, 8.IX.1996, Y. Kawakami leg. [1♀ EUM]; Nishitosa V[illage]. [= Shimanto-shi], Egawasaki, 15.IX.1996, Y. Kawakami leg. [1♂ EUM], 11.V.1997 [1♀ EUM], 12.V.1997 [1♀ EUM], 3.VIII.1997 [1♂ EUM], 13.IX.1998 [1♂ EUM], 15.IX.1998 [1♂ EUM]; Hata G[un]. [currently Takaoka-gun], Touwa V[illage]. [= Shimanto-chô], Mishima, 22.IX.1996, Y. Kawakami leg. [2♂ EUM], 18.V.1997 [1♀ EUM], 28.IX.1997 [1♂ EUM], 4.X.1998 [1♂ EUM]; [Takaoka-gun], Tôwa-son [= Shimanto-chô], Mishima, 9.VIII.1998, Y. Kawakami leg. [1♂ EUM], 13.IX.1998 [1♀ EUM], 8.X.2001 [1♂ EUM], 19.V.2002 [2♀ EUM], 4.VIII.2002 [1♂ EUM], 11.VIII.2002 [3♂ EUM], 16.IX.2002 [2♂ EUM], 14.IX.2004 [1♂ EUM], 19.IX.2004 [1♀ EUM], 25.IX.2004 [2♂ EUM], 27.IX.2004 [1♂ EUM], 25.VIII.2005 [1♂ EUM]; [Takaoka-gun], Shimanto-chô, Mishima, 14.IX.2006, Y. Kawakami leg. [2♂ EUM], 30.IX.2006 [1♂ EUM]; Nakamura C[ity]. [= Shimanto-shi], Nyûta, 10.X.1996, Y. Kawakami leg. [3♂ EUM]; Nankoku-shi, Hisaeda, 25.V.1997, T. Befu leg. [1♀ EUM]; [Agawa-gun], Ino-chô, Kashiki, 29.VII.1997, Y. Kawakami leg. [1♂ EUM]; [Agawa-gun], Ino-chô, Kagechi, 28.VIII.1997, Y. Kawakami leg. [1♂ EUM]; Nakamura-shi [= Shimanto-shi], Kawanobori, 15.IX.1999, Y. Kawakami leg. [3♂ EUM], 2.X.1999 [1♀ EUM], 29.IX.2002 [1♂ EUM], 9.VI.2002 [1♀ EUM]; Tosayamada-chô [= Kami-shi], golf course, 20.IX.2000, Y. Kawakami leg. [1♀ EUM]; Tosashimizushi, Matsuo, 23.XI.2000, Y. Kawakami leg. [1♀ EUM]; Nankoku-shi, Kaita, 8.IX.2001, T. Befu leg. [1♀ EUM]; Agawa-mura [= Niyodogawa-chô], Moriyama, 21.V.2002, T. Befu leg. [1♀ EUM]; Nankoku-shi, Inabu, 28.V.2002, T. Befu leg. [1♀ EUM]; Nankoku-shi, Inabu, Hayashidani, 22.VIII.2001, T. Befu leg. [1♀ EUM], 3.VII.2002 [1♀ EUM]; Nakamura-shi [= Shimanto-shi], Takeshima, 29.IX.2002, Y. Kawakami leg. [1♀ EUM], 6.X.2002 [1♀ EUM]; Tosashimizu-shi, Ôhama, 5.X.2003, Y. Kawakami leg. [1♂ EUM]; [Aki-gun], Yasuda T[own]., Tohhama [= Tônohama], 5.VI.2004, Y. Kawakami leg. [1♂ EUM]; [Takaoka-gun], Tôwa-son [= Shimanto-chô], Tsuga, 19.IX.2004, Y. Kawakami leg. [1♂2♀ EUM]; Tosashimizu-shi, Nakanohama, 2.X.2004, Y. Kawakami leg. [1♂ EUM]; Muroto-shi, Sakihamachô, Iruki, 19.IX.2005, Y. Kawakami leg. [1♀ EUM]; Tosashimizu-shi, Shimonokae, 2.X.2005, Y. Kawakami leg. [1♂1♀ EUM], 8.VII.2007 [1♂ EUM]; Tosa-shi, Mt. Hageyama, 21.X.2005, Y. Kawakami leg. [1♀ EUM], 22.IX.2008 [1♂ EUM]; [Hata-gun], Saga-chô [= Kuroshio-chô], Suzu, 30.X.2005, Y. Kawakami leg. [1♂ EUM]; Kôchi-shi, Kôda, Mt. Kashio-yama, 4.VII.2006, Y. Kawakami leg. [1♀ EUM], 6.VIII.2006 [1♂ EUM], 24.VII.2007 [1♂1♀ EUM]; [Takaoka-gun], Nakatosa-chô, [Kaminokae], Sasaba, 16.VII.2007, Y. Kawakami leg. [1♀ EUM], 18.VII.2007 [2♂ EUM], 19.VII.2007 [1♂ EUM], 23.VII.2007 [2♂ EUM], 24.VII.2008 [1♂ EUM], 12.VII.2009 [1♂ EUM], 27.VII.2009 [1♂1♀ EUM], 30.VII.2009 [1♂1♀ EUM]; [Takaoka-gun], Ochi-chô, Kurose, 21.IX.2007, Y. Kawakami leg. [1♀ EUM]; Muroto-shi, Mitsu, 17.VII.2008, Y. Kawakami leg. [1♀ EUM]; Muroto-shi, Hane[-chô], Kuromi, 17.VIII.2008, Y. Kawakami leg. [1♂ EUM]; Aki-shi, Nakagô, Ioki, 8.IX.2008, Y. Kawakami leg. [2♂ EUM]; [Takaoka-gun], Shimanto-chô, Okitsu, 25.IX.2008, Y. Kawakami leg. [1♂ EUM]; KUMAMOTO: Kumamoto, 20.VII.1907, H. Kawamura leg., *Mutilla insidiator* Sm. [unknown hand], *Mutilla insidiator* Sm. [unknown hand] [1♀ SEHU]; Kumamoto, 10.X.1907, H. Kawamura leg., *Mutilla petulans* Sm. [unknown hand], *Mutilla petulans* Sm. [unknown hand] [1♂ SEHU]; Kumamoto, 12.VIII.1907, H. Kawamura leg. [1♂ SEHU], 25.VIII.1907 [1♂ SEHU], 4.X.1907 [1♀ SEHU], 10.X.1907 [1♀ SEHU]; Fune, 10.X.1907, H. Kawamura leg. [1♀ SEHU];

MIYAZAKI: Kobayashi, 15.IX.1931, K. Sato leg. [1♂ NSMT]; Ebino-shi, Yaeno, Sawahara, 25.VI.2016, S. Koiwaya leg. [1♀ EUM]; Miyazaki-shi, Aoshima, 4.XI.2016, R. Ito leg. [1♀ EUM]; NAGANO: Mt. Ontake, 19.VII.1998, S. Maru leg., *Neotrogaspidia pustulata*, M. Terayama det. 2010 [1♀ EUM]; NARA: Tenri, 17.VIII.1957, I. Miyagi leg. [1♂ EUM], 19.VIII.[19]58 [1♂ EUM], 24.VII.1959 [1♂1♀ EUM]; Nara-shi, Zoushi-chou, Mt. Kasuga-yama, 22.VIII.2003, T. Tsuru leg. [1♀ TUA]; Nara-shi, Mt. Wakakusa-yama, 25.VIII.2003, T. Tsuru leg. [1♀ TUA]; OGASAWARA ISLANDS: Chichijima, II–V.1918, A. Nohira leg. [1♂ OMNH]; Ogasawara ins., Chichijima, A. Nohira leg. [2♂ OMNH]; Ogasawara, Chichijima Is., Mt. Mikazukiyama, 10.VII.1975, A. Shimizu leg., *Trogaspidia pustulata*, K. Tsuneki det. 1983 [3♂ TMUZ]; ÔITA: Beppu, 10.VII.1916, Matsumura leg. [1♂ SEHU], VII.1916 [1♀ SEHU]; Hayami-gun, Hiji, 3.IX.2002, Y. Mimura leg. [1♀ TUA]; Bungotakada-shi, Mizusaki, 8.V.2017, Y. Miyamoto leg. [1♀ EUM]; Takeda-shi, Udo, 6.V.2018, D. Tsuneishi leg. [1♀ EUM]; ÔSAKA: [Ôsaka-shi], Sumiyoshi, 6.VII.1932 [1♀ NSMT]; [Ôsaka-shi], Sumiyoshi, 25.VII.[19]32, H.K. [1♀ NSMT]; ÔSUMI ISLANDS: Tanegashima, Syogayama, 31.V.1960 [1♀ MNHAH]; Is. Yakushima, Nagata, Nagata rindo, 9.V.2001, H. Ohshima leg. [4♀ TUA]; SAGA: Saga-shi, Yamato-cho, Kawakami, 18.V.2022, J. Abe leg. [1♀ ELKU]; SAITAMA: Kodama, Jyûniten-ike, 14.VIII.1971, T. Nambu leg. [1♀ NSMT]; Kodama, Jyûniten-ike, 14.VIII.1971, T. Nambu leg., *Trogaspidia pustulata* (Smith), K. Tsuneki det. 1972 [1♂ NSMT]; Yorii, Sakurazawa, 1.V.1972, T. Nambu leg. [1♀ NSMT]; Hanyû, Kamimurakimi, 8.VI.1974, T. Nambu leg. [1♀ NSMT]; Ogose, high school, 14.X.1978, T. Nambu leg. [1♀ NSMT], 26.V.1979 [1♀ NSMT]; Satte-shi, Nishisekiyado, near Asama-jinjya, 20.VII.1997, M. Uchida leg. [1♀ NSMT]; Kawajima town, Kami-Ôyashiki, Old Ara River, 20.VII.1998, K. Toyoda leg. [1♀ TUA]; [Hiki-gun], Ranzan-machi, Sugaya, 5.VI.2001, K. Toyoda leg. [1♀ NSMT]; Ranzan[-machi], Syogunzawa, 9.VI.2001, K. Toyoda leg. [1♀ NSMT]; Ranzan town, Shiga, Suwanoiri, 60 m alt., 5.VII.2002, K. Toyoda leg. [1♀ TUA]; SHIMANE: Takatsu-gawa, st. 1, 28.IX.2000, S. Nakamura leg. [1♂ HMNH]; Takatsu-gawa, st. 2, 27.VII.2005, S. Nakamura leg. [1♂ HMNH]; Iishi-gun, Iinan-chô, Shitsumi, meadow, 35°08′N 132°41′E, 23.IX.2020, H. Yoshitomi leg. [3♀ EUM]; SHIZUOKA: Shimoda, 20.VIII.[19]40, Yamamoto leg. [1♂ SEHU]; [Kakegawa-shi], Ôsuka, 12.VIII.1970, T. Nambu leg. [1♂ NSMT]; TOKARA ISLANDS: Is. Takara, 17.VII.1964, M. Nishikawa leg. [2♀ ELKU, 1♀ TUA]; Nakanoshima Is., Mt. Nanatsuyama, 5.VI.2004, J. Kanto leg. [1♀ TUA]; Toshima-mura, Takara Is., 2.VII.2004, J. Yamasako leg. [1♀ EUM]; TOKUSHIMA: Awa, [Mima-shi], Koyadaira, 2.VIII.1913, E. Gallois leg. [1♀ SEHU]; [Kaifu-gun], Kaifu T[own]. [= Kaifu-chô], Yoshida, 24.VIII.1997, Y. Kawakami leg. [1♂ EUM]; Itano, Aizumi, Otoze, Nishi-Aoki-Danchi, 29.IV.1998, M. Nishikawa leg. [2♀ EUM]; Yamakawa-chô, Kawata-kitajima, 23–26.VIII.1999, T. Doi & K. Aita leg. [1♀ EUM]; TOKYO: Hirayama, Matsumura [1♂ SEHU]; Meguro, 4.VI.1915 [1♀ NSMT], 8.VI.1915 [1♀ NSMT]; [Nishitama-gun], [Okutama-machi], Hikawa, 23.IX.1934, A. Yoshida leg. [1♀ NSMT]; Mizumoto, 2996, 8–7 [1♀ NSMT]; Kanamachi, 2612, 10–5 [2♂ NSMT]; TOTTORI: Iwami, Kawakudari, 9.VIII.[19]51, S. Ueda leg. [1♀ EUM]; TSUSHIMA: [Kamiagata-machi], Sasuna, 7.VI.1968, K. Kurosawa [1♀ NSMT]; [Kamiagata-machi], Sasuna, 11–16.IX.1968, R. Ishikawa leg. [2♂1♀ (1♂1♀ *in copula*) NSMT]; Atsusaki, 30.VII.2001, R. Oomuta leg. [2♂ TUA]; WAKAYAMA: Wakayama, 1904, Nakawata leg. [1♂ SEHU]; Hamanaka-mura [= Kainan-shi], VIII.1928, F. Wada leg. [1♂ SEHU]; Wakayama, 1930, Sakaguchi leg. [1♂ SEHU]; YAEYAMA ISLANDS: Ishigaki Is., Omoto, 7.IV.1997, T. Ishikawa leg. [1♀ TUA]; Is. Ishigaki, Ohtake, 2.VI.2001, T. Tsuru leg. [1♀ TUA]; Yaeyama-gun, [Iriomote-jima], Haimida, 11.IV.2013, Y. Hikosaka leg. [1♂ TUA]; Okinawa, Yaeyama-gun, Iriomote-jima, Nakamagawa trail, 21.III.2016, T. Ito leg. [1♀ EUM]; YAMAGUCHI: Kusunoki-machi [= Ube-shi], Nishimagura, 30.V.2000, T. Kishimoto leg. [1♀ TUA]; PREFECTURE UNKNOWN: [probably Tokyo], Arakawa, 5.VII.[19]10 [1♀ SEHU], 2.X.1910 [1♀ SEHU];

Suidou-yama, 24.VII.1962, S. Ookusa leg. [1♀ TUA]. Probably Japan: Shirono [3♀ NSMT], 15.VIII.'1908 [1♀ NSMT], VIII.1927 [1♂ NSMT], VIII.1929 [2♂ NSMT]; Joga, 21.X.1937, Adati leg. [1♀ NSMT]; no locality label [1♂ NSMT]. **North Korea:** HAMGYEONGBUK-DO: Corea [= Korea], Ranan [= Ranam], 14–15.VIII.1933, K. Nomura leg., *T. elpinice*? ♀ [probably Chen's hand] [1♀ TARI]. **South Korea:** GYEONGGI-DO: Chosen [= Korea], Suigen [= Suwon], 9.VII.1923, K. Sato leg., *Trogaspidia pustulata* (Sm.), Lelej det. 1991 [1♂ NSMT]; Chosen [= Korea], Suigen [= Suwon], 25.VII.1923, K. Sato leg. [2♂1♀ NSMT]; Korea, Suigen [= Suwon], 10.VI.1925, K. Sato leg. [1♀ NSMT]; Corea [= Korea], Suigen [= Suwon], 1.VIII.1929, H. Furukawa leg. [1♀ NSMT]; Chosen [= Korea], Keikido [= Gyeonggi-do], Hosen, Koryo, 17–19.VII.1930, T. Shiraki leg. [1♀ TARI]; GYEONGSANGNAM-DO: Kyungan, Koje city, Sinhyun-Up, Jangpyung-Ri, 30.VII.2001, H. Ohshima leg. [1♀ TUA]; SEOUL: Corea [= Korea], Keijo [= Seoul], 7.VIII.1933, K. Nomura leg. [1♂ TARI]; PROVINCE UNKNOWN: Corea [= Korea], Okamoto leg. [1♂ SEHU].

Sex association

This species was initially described from the male sex only. The female was described as *Mutilla insidiator* by Smith (1873) and associated by Chen (1957) based on a pair *in copula*. However, Chen's specimens belonged to *N. elpinice* as discussed above. Lelej and Yamane (1992) examined a pair *in copula* and confirmed the sex association. In this study, additional mating pairs were examined (Figs 92–98).

Distribution

Japan: Honshû (Aichi, Chiba, Fukui, Fukushima, Gifu, Gunma, Hiroshima, Hyôgo, Ibaraki, Ishikawa, Kanagawa, Kyôto, Mie, Miyagi, Nagano, Nara, Ôsaka, Saitama, Shiga, Shimane, Shizuoka, Tochigi, Tokyo, Tottori, Toyama, Wakayama, Yamaguchi), Shikoku (Ehime, Kagawa, Kôchi, Tokushima), Kyûshû (Fukuoka, Kagoshima, Kumamoto, Miyazaki, Nagasaki, Ôita, Saga), Tsushima, Gotô Islands (Fukue-jima), Ôsumi Islands (Iô-jima, Kuchinoerabu-jima, Take-shima, Tanega-shima, Yaku-shima), Tokara Islands (Kuchino-shima, Nakanoshima, Takara-jima), Amami Islands (Amami-ôshima, Tokuno-shima), Miyako Islands (Miyako-jima), Yaeyama Islands (Iriomote-jima, Ishigaki-jima), Izu Islands (Hachijyô-jima), Ogasawara Islands (Chichi-jima, Nishijima) (Gôukon, 1993; Haneda *et al*., 2005, 2006a; Ikudome & Yamane, 2009; Imai, 2019; Kurokawa, 2003; Lelej & Yamane, 1992; Mickel, 1935; Nakamura, 2003; Sugiura *et al*., 2013; Takahashi, 1996; Terayama *et al*., 2011; Tsuneki, 1972ac, 1985; Yamamoto, 2010). North Korea*: Hamgyeongbuk-do. South Korea: Chungcheongnam-do, Daejeon-Gwangyeoksi, Gyeonggido, Gyeongsangnam-do, Hamgyeonbuk-do, Jeju-do, Jeollanam-do, Seoul (Lelej *et al*., 2001; Yasumatsu, 1938a).

Remarks

Neotrogaspidia pustulata is one of the most frequently encountered mutillids in Japan, because of its wide distribution, from temperate mainland to subtropical islands, and long activity period, from April to November. This is the only species known from the oceanic Ogasawara Islands. Ogasawara Islands have volcanic origin and have never been connected with other lands since their formation (Shimizu, 2003). This group of islands is located 1000 km southeast of the Japan mainland and 700 km southeast of Hachijyô-jima Island, which is the nearest island where *N. pustulata* occurs. Many alien animals and plants have been introduced to Ogasawara Islands either intentionally or unintentionally by human activities (Shimizu, 2003); it is uncertain whether the Ogasawara population of *N. pustulata* is native and Sugiura *et al*. (2013) regarded this species as alien. Morphologically, specimens from Ogasawara and those from Japan mainland are congruent. However, future DNA analyses

might find that the Ogasawara population belongs to a new species.

One male specimen was dropped into 80% ethanol and picked up immediately to observe the movement of the male genitalia under a stereomicroscope. Soon after salvaged from ethanol, this male extruded his genitalia and inflated the endophallus (Figs 70–72). This is the third published observation record of the endophallus of mutillids, since O'Toole (1975) illustrated the endophallus of "*Wallacidia oculata* (Fabricius, 1804)" (*W. oculata sensu* O'Toole is now classified into 14 species: Lelej, 2005) and Cambra and Quintero (1993) illustrated that of *Timulla nisa* Mickel, 1938. The endophallus of *N. pustulata* has the apical inflated sac, which is probably homologous with the distal bulb of O'Toole (1975), and two dorsal sacs, while it lacks lateral inflatable sacs observed in *W. oculata* by O'Toole (1975). The endophallus structure of mutillids is undescribed for most species, so it is unclear whether morphological differences between the endophalli of *N. pustulata* and *W. oculata* recognized here represent genus-level diagnostics. I have also observed the inflated endophallus of *Trogaspidia fuscipennis* (Fabricius, 1804) (Fig. 73).

***Neotrogaspidia recticarinata* (Chen, 1957), comb. nov.**

(Figs 7,8,21,22,25,41,45,49,53,60,61,68,69,99)

Trogaspidia recticarinata Chen, 1957: 167, ♂, holotype ♂ (Lungchi, Fukien [= Fujian], China) [TARI]; Lelej, 2005: 99; Hua, 2006: 301; Pagliano *et al*., 2020: 289.
Trogaspidia circumcincta: He *et al*., 2004: 962.

Diagnosis

MALE. Clypeus concave with medial longitudinal ridge (Fig. 41); scape with two closely located sharp carinae (Fig. 45); pronotum with dense appressed golden setae (Fig. 8); mesoscutellum with medial impunctate line posteriorly elevated into carina (Figs 7,8); propodeal dorsum with dense appressed golden setae, sublaterally delimited by longitudinal carinae; metasomal segments 1–5 red and 6–8 black (Fig. 49); T2 abruptly convex (Fig. 49); S8 lateral carinae subparallel and tuberculate posteriorly, reaching posterior 1/2 of S8 (Fig. 53); penis valve long slender, incurved, without inner projection (Figs 60,61,69); penis valves with long dense setae on inner face (Figs 61,69); cuspis slender stick-like, 2.0× longer than digitus (Fig. 68). FEMALE. Unknown.

Material examined

3♂. Holotype ♂: locality label missing, *Trogaspidia recticarinata* Chen, Chen det., *Trogaspidia circumcincta circumcincta* (André), B. Petersen det. 1982 [TARI]. Paratype: locality label missing, *Trogaspidia recticarinata* Chen, Chen det., *Trogaspidia circumcincta circumcincta* (André), B. Petersen det. 1982 [1♂ TARI]. **Taiwan:** TAIPEI: Taihoku [= Taipei], 20.IX.1927, K. Sato leg., *Trogaspidia recticarinata* Chen, A.S. Lelej det. 1996 [1♂ NSMT].

Distribution

China: Fujian. Taiwan*: Taipei.

Sex association

This species is known from the male sex only.

Remarks

This species shares many diagnostic character states with *N. circumcincta*. Identification labels suggest that B. Petersen regarded these two species as synonyms. He *et al*. (2004) even

listed *N. recticarinata* as a junior synonym of *N. circumcincta*, although they did not present the evidence. However, *N. recticarinata* has the clypeus with medial portion raised and forming a longitudinal ridge and the penis valves with long dense setae on inner face, while *N. circumcincta* has the clypeus concave even medially and the penis valves with short sparse setae on inner face. Therefore, I retain them as separate species. Despite intensive collecting by T.C. Maa in Fujian, no potential female was found in his collection (TARI).

Discussion

Genus limits

The genera of Trogaspidiini are morphologically diverse and difficult to diagnose (e.g., Okayasu *et al*., 2021). The four Northeast Asian species treated in this study, including the type species, are recognized by having a unique combination of character states within Trogaspidiini, suggesting the monophyly of *Neotrogaspidia*. These four species can be easily confused with the predominantly Oriental genus *Eotrogaspidia* Lelej, 1996 by having the male mesoscutellum subgibbous (not tuberculate or conical), the male volsella with stick-like digitus and paracuspis, the male penis valve weakly asymmetrical, and the female pygidial plate subconvex with obscure shagreened or rugose surface sculpture. However, the male clypeus with a subventral transverse carina and the male T2 postero-lateral margin abruptly terminating are useful to separate them from other trogaspidiine genera. Females are diagnosed by having the T3 with a complete pale setal band and T4 with black setae, while *Eotrogaspidia* females have both T3 and T4 maculated with a pale setal band or spots (Okayasu *et al*., 2021). Some Southeast Asian species in *Trogaspidia* Ashmead, 1899, like *T. tethys*, have the male characteristics of *Neotrogaspidia* (Mickel, 1935; Tsuneki *et al*., 1993; J. Okayasu, pers. obs., 2022), suggesting greater diversity of this genus in the Oriental Region. The genus placement of Southeast Asian species is, however, beyond the aim of this study.

Despite the likely monophyly of *Neotrogaspidia* in the strict sense, the species from the Australasian and western Palearctic Regions partially lack the diagnostic features discussed above. This makes genus delimitation difficult. The male of *N. haemarrhoa* has the clypeus with a transverse subventral carina (Mickel, 1935), but this structure is absent in *N. hammeri* and probably in *N. tricarinata*. These three species have the male T2 postero-laterally evenly convex, like most males of Trogaspidiini. The penis valve of *N. tricarinata* possesses a large hook-like projection on apico-inner margin, giving strongly asymmetrical appearance like the males of *Trogaspidia* and *Wallacidia* Lelej & Brothers, 2008. In females, *N. hammeri* and *N. serafica* have T3 and T4 maculated with either complete or medially interrupted pale setal bands. Consequently, the following combination of character states is currently used to separate *Neotrogaspidia* from most species of *Eotrogaspidia* (Okayasu *et al*., 2021): the male metacoxa convex with long sparse setae ventrally (flattened with erect microsetae in *Eotrogaspidia*), the female T2 spots separated by approximate spot diameter, and the female T3 or both T3 and T4 with a pale setal band extending nearly to lateral margins of terga (T2 spots large, separated by 0.3–0.5× their diameter, and both T3 and T4 with a complete or medially interrupted setal band; if T2 spots small, then both T3 and T4 maculated with a pair of setal spots widely separated from lateral margins of the terga). *Eotrogaspidia adhabar* Okayasu, Lelej & Williams, 2021 have the male metacoxa convex with sparse setae, but this species differs from *Neotrogaspidia* males by having the clypeus gibbous and the scape with a single ventral carina.

The metacoxa of most *Eotrogaspidia* males and the clypeus and the scape of *E. adhabar* show apparently apomorphic states in Trogaspidiini. Contrarily, *Neotrogaspidia* in current concept is defined by lacking those unique features. Therefore, various trogaspidiines

with the male mesoscutellum subgibbous and the female pygidial plate with obscure sculpture may eventually be transferred to *Neotrogaspidia*, and some species that are currently placed in *Neotrogaspidia* may be transferred to different genera. Future in-depth morphological or phylogenetic analyses will possibly find that *Neotrogaspidia* is, in fact, restricted to the eastern Oriental and Palearctic Regions.

Phoretic copulation

The mating biology, habitats and hosts have been largely unknown for *Neotrogaspidia*, even though *N. pustulata* is one of the most commonly encountered mutillids in Japan. Observations by Japanese entomologists revealed that this species practices mandibular phoretic copulation (Waldren *et al*., 2020). The *Neotrogaspidia* males have the morphological traits associated with prolonged phoretic copulation, like the concaved clypeus and the baso-ventral mandibular tooth (Crèvecoeur, 1930; Sheldon, 1970). Based on the morphological examination of mating pairs and comparison of mating behavior, O'Toole (1975) and Quintero and Cambra (1994) further speculated that the developed endophallus and the asymmetric penis valve work as the holdfast mechanism during copulation. The presence of these morphological traits in *Neotrogaspidia* and *Trogaspidia* (Figs 70–73) provides additional support for this hypothesis.

Neotrogaspidia species meet the size prerequisite for phoretic copulation with males being larger than females (Deyrup & Manley, 1986; Evans, 1969; Waldren *et al*., 2020). The body length of *N. pustulata* examined here, 7.53–16.7 (11.5 ± 1.39) mm for males and 4.17–9.94 (7.28 ± 1.21) mm for females (n = 122♂130♀), suggests utilization of multiple host species with variable body size and size-dependent sex allocation (Pitts *et al*., 2010a). Deyrup & Manley (1986) associated the large body size in female individuals (in relation to males) to utilization of aggregated hosts. Because aggregated hosts offer numerous individuals with uniform size, sex determination based on host size results in highly skewed sex ratio (Deyrup & Manley, 1986). Also, females gain better fitness by ovipositing a large number of eggs in a single occasion (Deyrup & Manley, 1986); in this case, females with larger clutch size are more advantageous. Therefore, Deyrup (1988) considered utilization of non-aggregated hosts with various size to be a preadaptation for phoretic copulation. Contrarily, the present observation implies *N. pustulata*, while practicing phoretic copulation, utilize aggregated *Dasypoda* bees as a host. The sexual dimorphism in body size also suggests that this species utilize alternative hosts, presumably other aggregated bees or non-aggregated ground-nesting bees and wasps with variable body size.

The adaptive value of phoretic copulation is unclear. It has been suggested that this behavior enables dispersal of wingless females to a novel place where an unexploited host population is found (Evans, 1969; O'Toole, 1975; Vivallo, 2020). In this case, however, phoretic copulation offer benefits only stochastically. No evidence to corroborate this hypothesis has been provided, at least for mutillids. Contrarily, the mating flight in apoid wasps and bees, of which multiple males compete for a single female at the emergence site, was discussed as having evolved as an escape mechanism from interference by predators and rival males (Lin, 1966; O'Neill & Evans, 1983; Roig-Alsina, 1993; Rutowski & Alcock, 1980). Mating flight is similar to phoretic copulation in that the genital coupling may take place in the air but differs from it because both male and female individuals have functional wings and attempt to disperse by flight (Vivallo, 2020).

Similar to apoid wasps and bees, male–male competition for a single female has been documented for several mutillid species (Brothers, 1989; Fattig, 1936; Jellison, 1982; Matteini Palmerini, 2013; Polidori *et al*., 2013; Tormos *et al*., 2010). In this circumstance, one male can avoid competition by carrying the female via phoretic copulation (Brothers,

1989; Deyrup & Manley, 1986). Additionally, ground-dwelling mutillids are usually found in open habitats where host bees and wasps are abundant (Brothers, 1995) and mating pairs of mutillids can be easily located by predators. This hypothesis might be supported by the fact that the male mutillid practicing mandibular phoretic copulation intentionally carries the female counterpart and copulation takes place on a tree or under a bush (Bartholomay *et al*., 2017; Crèvecoeur, 1930; Lamborn, 1916; Linsley, 1960; Matteini Palmerini, 2013; Polidori *et al*., 2013; Rothney, 1903; Tormos *et al*., 2010; Waldren *et al*., 2020). The present observations showed that the male of *N. pustulata* carries the female higher up to the tree to copulate (Figs 93–98), despite the ground-dwelling habits of females. Also, this species is found in open habitats (e.g., Fig. 90) where a mating pair can be salient on the substrate to predators and rival males. Although male–male competition has not been observed for *Neotrogaspidia* species, this phenomenon is known in trogaspidiine genus *Timulla* Ashmead, 1899 (Fattig, 1936). These data support the hypothesis suggesting the function of phoretic copulation as predation and male–male competition avoidance. Additional observations are needed to elucidate the correlation of open habitats, increased predation and competition pressures, and phoretic copulation.

Biogeography

Japanese islands are known for their high endemism of terrestrial organisms, formed by paleogeographic and paleoclimatic dynamics (Motokawa, 2017). Mutillids may be greatly affected by such changes because of their low dispersal ability. As discussed above, the Northeast Asian *Neotrogaspidia* species are probably monophyletic. Based on the morphology, it is likely that *N. circumcincta* is sister to *N. recticarinata* and *N. elpinice* to *N. pustulata*. *Neotrogaspidia circumcincta* and *N. recticarinata* overlap geographically (Fig. 99), while *N. elpinice* and *N. pustulata* are distributed allopatrically (Fig. 100). The distribution of the latter two species mostly matches that of the Sino-Japanese realm (Holt *et al*. 2013). In this realm, *N. elpinice* is restricted to southern China, and the geographic range of this species is congruent with the Chinese transition zone in the strict sense (He *et al*., 2017; Hermogenes De Mendonça & Ebach, 2020; Morrone, 2015; Proches & Ramdhani, 2012). *Neotrogaspidia pustulata* has more island-biased distribution, covering most groups of Japanese islands and the Korean Peninsula. This species is morphologically consistent throughout its distributional range (Figs 26–37) and regarded as a single species, opposing the initial anticipation.

Okayasu (2020) recognized three distributional patterns of Japanese mutillids, but *N. pustulata* matches none of them. The geographic range of *Neotrogaspidia* covers warm temperate to tropical regions in East Asia. In Japan, *N. pustulata* is restricted to south of 40°N. Therefore, the Korean population of *N. pustulata* probably represents relict distribution in northern refugia (e.g., Bao *et al*., 2015 and references therein). Currently, no *Neotrogaspidia* species has been recorded from northern China, implying a vicariant speciation event in the Korean Peninsula (*N. pustulata*) and southern China (*N. elpinice*), which subsequently led to a dispersal event of the former species to Japan via Tsushima Island (Tojo *et al*., 2017).

Previous studies demonstrated faunal similarity in southern Ryûkyû and Taiwan (e.g., Ota, 1998, 2000). Two mutillid species, *Eotrogaspidia auroguttata* (Smith, 1855) and *Mickelomyrme hageni* (Zavattari, 1913), are distributed throughout central to southern Ryûkyû and Taiwan (Okayasu, 2020; Okayasu *et al*., 2021). Contrarily, *Neotrogaspidia* populations in the Ryûkyû–Taiwan Arc are separated by the Yonaguni Strait, which is located between the southern Ryûkyû and Taiwan (Fig. 100). This suggests, despite their close proximity, that the southern Ryûkyû and Taiwan had been long separated, negating the Pleistocene land bridge hypothesis (Kimura, 1996, 2002; Kizaki & Ohshiro, 1977; Oshiro &

Nohara, 2000; Ujiie, 1990). Alternatively, this distributional pattern might be formed by low fitness of *N. pustulata* in an overlapping range of *N. elpinice* and *N. pustulata* after secondary contact in Taiwan, due to the competition for common resources (competitive exclusion; Hardin, 1960) or reproductive interference (sexual exclusion; Hochkirch *et al*., 2007; Gröning & Hochkirch, 2008).

The presence of *N. pustulata* in Iô-jima Island and Take-shima Island (Ikudome & Yamane, 2007, 2009) suggests dispersal events over 40 km, because the fauna and flora of those islands had been largely devastated by the huge eruption of Kikai Caldera 7300 years before present (Kimura *et al*., 1996; Machida & Arai, 2003). Moreover, this species is known from oceanic Izu Islands and Ogasawara Islands. Although it is unclear whether *N. pustulata* populations in oceanic islands are native, this species likely possesses much higher dispersal ability than generally assumed. The wide distributional range of *N. pustulata* had probably been established by overseas dispersal events via mandibular phoretic copulation. Unlike *Neotrogaspidia*, the genus *Ephucilla* Lelej, 1995 has three endemic species in forested habitats of the Amami, Okinawa and Yaeyama Islands (Okayasu, 2020). *Ephucilla* species have the clypeus subconvex and they lack the developed endophallus, suggesting in situ copulation. The low dispersal ability of *Ephucilla* species had hypothetically contributed to the high endemism of this genus in the Ryûkyû Islands.

The data presented herein suggest that alternative mating strategies can result in incongruent speciation and distribution patterns in mutillids. This study is solely based on morphological evidence, but molecular analyses will elucidate historical dispersal process of mutillids in East Asian islands. Mating behavior has been recorded for only 62 species, or roughly 1.3% of global species diversity (Waldren *et al*., 2020). Observation attempts of mating events in the field are particularly important, although spatio-temporarlly unpredictable, because mating behavior and duration in captivity might differ in some aspects from behavior in natural conditions (Waldren *et al*., 2020). Additionally, morphological adaptations associated with phoretic copulation are not fully understood; there are few speculative interpretations based on museum specimens or fragmentary observations (e.g., O'Toole, 1975; Sheldon, 1970). Overall, this study emphasizes that the functional morphology and taxonomic distribution of phoretic copulation are vital to address mutillid biogeography, because mating strategies may ultimately determine the distributional patterns of these insects.

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References

Akiyama, Y., Enoki, J. & Nakamura, S. (2021) Insects from Hiroshima Prefecture collected by Mr. Takashi Shintani preserved in Hiwa Museum for Natural History. *Hiwa Museum for Natural History Material Reports* 21: 1–144. (in Japanese)

André, E. (1896) Étude sur les Mutillides existant dans les collections du Musée civique de Gênes. *Annali del Museo Civico di Storia naturale di Genova* 37: 66–104.

André, E. (1902 [1903]) Family Mutillidae. *In*: Wytsman, P. (ed.) *Genera Insectorum*. *Fascicles 11*. L. Desmet-Verteneuil, Bruxelles, pp. 1–77 + 3 pls.

André, E. (1905) Mutillides nouveaux ou peu connues de l'Ancien Monds et de l'Australie. *Zeitschrift für systematische Hymenopterologie und Dipterologie* 5 (1–6): 201–216 + 265–277.

Ashmead, W.H. (1899) Superfamilies in the Hymenoptera and generic synopses of the families Thynnidae, Myrmosidae, and Mutillidae. *Journal of the New York Entomological Society* 7: 45–60.

Azuma, S., Yafuso, M., Kinjo, M., Hayashi, M., Kohama, T., Sasaki, T., Kimura, M. & Kawamura, F. (2002) *Check list of the insect of the Ryukyu Islands*. *Second edition*. The Biological Society of Okinawa, Okinawa, 570 pp. (in Japanese)

Bao, L., Kudureti, A., Bai, W., Chen, R., Wang, T., Wang, H. & Ge, J. (2015) Contributions of multiple refugia during the last glacial period to current mainland populations of Korean pine (*Pinus koraiensis*). *Scientific Reports* 5: 18608. https://doi.org/10.1038/srep18608

Bartholomay, P.R., Waldren, G.C. & Oliveira, M.L. (2017) Observation of a mixed-sex, mixed-species aggregation of velvet ants, genus *Timulla* Ashmead, 1899 (Hymenoptera: Mutillidae) in the Brazilian Amazon, Roraima, with a new synonymy. *Zootaxa* 4362 (1): 135–140. https://doi.org/10.11646/zootaxa.4362.1.8

Bischoff, H. (1920–1921) Monographie der Mutilliden Afrikas. *Archiv für Naturgeschichte* 86A (1–3): 1–480 (1920); 86A (4–5): 481–830 (1921).

Brothers, D.J. (1989) Alternative life-history styles of mutillid wasps (Insecta, Hymenoptera). *In*: Bruton, M.N. (ed.) *Alternative life-history styles of animals*. *Perspectives in vertebrate sciences 6*. Springer, Dordrecht, pp. 279–291. https://doi.org/10.1007/978-94-009-2605-9_14

Brothers, D.J. (1995) Mutillidae. *In*: Gauld, I. & Hansen, P. (eds) *The Hymenoptera of Costa Rica*. Oxford University Press, Oxford, pp. 541–548.

Brothers, D.J. (2022) Critical analysis of the type material of Mutillidae described from the Australasian Region (Hymenoptera). *Zootaxa* 5140 (1): 1–215. https://doi.org/10.11646/zootaxa.5140.1.1

Brothers, D.J. & Lelej, A.S. (2017) Phylogeny and higher classification of Mutillidae (Hymenoptera) based on morphological reanalyses. *Journal of Hymenoptera Research* 60: 1–97. https://doi.org/10.3897/jhr.60.20091

Cambra, R.A. & Quintero A., D. (1993) Studies on *Timulla* Ashmead (Hymenoptera: Mutillidae): New distributional records and synonymies, and descriptions of previously unknown allotypes. *The Pan-Pacific Entomologist* 69 (4): 299–313.

Chan, M.-L., Yeh, J.-Y., Jeng, M.-L., Tsai, J.-F., Chen, Y.-L., Chen, L.-H. & Lin, S.-R. (2021) Integrated insect types database of Taiwanese species. Available from: http://twinsecttype.nmns.edu.tw/ (accessed 8 September 2022)

Chen, C.-w. (1957) A revision of the velvety ants or Mutillidae of China (Hymenoptera). *Quarterly Journal of the Taiwan Museum* 10 (3–4): 135–224 + 6 pls.

Chu, Y.-i. & Yamanaka, T. (1973–1975) A check list of the present and old name of insect collected localities in Taiwan. *Journal of the National Taiwan Museum* 16: 31–72 (1973); 17: 51–75 (1974); 18: 121–150 (1975).

Cockerell, T.D.A. (1911) Bees in the collection of the United States National Museum 2.

Proceedings of the United States National Museum 40 (1818): 241–264.
Crèvecoeur, A. (1930) Recherches biologiques sur *Smicromyrme* (*Mutilla*) *rufipes* F. (Hym. Mutillidae). *Bulletin & Annales de la Société entomologique de Belgique* 70: 271–284.
Dalla Torre, C.G. de (1897) *Catalogus Hymenopterorum hucusque Descriptorum Systematicus et Synonimicus*. *Volumen VIII: Fossores (Sphegidae)*. Guilelmi Engelmann, Lipsiae, [4] + viii + 750 pp. https://doi.org/10.5962/bhl.title.10348
Deyrup, M. (1988) Review of adaptations of velvet ants (Hymenoptera: Mutillidae). *The Great Lakes Entomologist* 21 (1): 1–4.
Deyrup, M. & Manley, D. (1986) Sex-biased size variation in velvet ants (Hymenoptera: Mutillidae). *Florida Entomologist* 69 (2): 327–335.
Evans, D.A. & Miller, B.R. (1969) A note on adult overwintering of *Dasymutilla nigripes* in Michigan (Hymenoptera: Mutillidae). *The Michigan Entomologist* 2 (3–4): 74.
Evans, D.A., Miller, B.R. & Bartlett, C.B. (1973) Host searching range of *Dasymutilla nigripes* (Fabricius) as investigated by tagging (Hymenoptera: Mutillidae). *Journal of the Kansas Entomological Society* 46 (3): 343–346.
Evans, H.E. (1969) Phoretic copulation in Hymenoptera. *Entomological News* 80 (5): 113–124.
Fabricius, J.C. (1804) *Systema Piezatorum secundum Ordines, Genera, Species adjectis Synonymis, Locis, Observationibus, Descriptionibus*. Carolum Reichard, Brunsvigae, pp. i–xiv + 15–440 + 1–30. https://doi.org/10.5962/bhl.title.10490
Fattig, P.W. (1936) An unusual mating of velvet ants (Hymen.: Mutillidae). *Entomological News* 47 (2): 51–52.
Fukasawa, S. & Miyano, S. (2010) Fauna of aculeate Hymenoptera (Insecta) from the Izu Islands, Japan. *Journal of the Natural History Museum and Institute, Chiba* 11 (1): 11–28.
Gôukon, K. (1993) Host records and some bionomical notes on mutillid wasps in Japan (Hymenoptera, Mutillidae). *Chugoku Kontyu* 7: 35–40. (in Japanese)
Gröning, J. & Hochkirch, A. (2008) Reproductive interference between animal species. *The Quarterly Review of Biology* 83 (3): 257–282. https://doi.org/10.1086/590510
Hammer, K. (1949) Über einige von Kjell Kolthoff und anderen in China gesammelten Hymenoptera. Chrysididae, Cleptidae, Mutillidae. *Arkiv för zoologi* 42A (8): 1–12.
Haneda, Y. (1982) [Aculeate Hymenoptera of the Island of Amami-Ohshima collected in 1981]. *Hymenopterists' Communication* 14: 51–54. (in Japanese)
Haneda, Y. (2003) The aculeate Hymenoptera recorded from Tsushima, Nagasaki Prefecture before the year 2003. *Tsunekibachi* 1: 1–7. (in Japanese)
Haneda, Y., Inoue, S., Nozaka, C., Tano, T., Kurokawa, H. & Murota, T. (2005) The Hymenoptera recorded at Mt. Monju, Fukui Prefecture, Central Japan. *Tsunekibachi* 4: 53–75. (in Japanese)
Haneda, Y., Nozaka, C., Tano, T., Kurokawa, H. & Murota, T. (2006a) Aculeate Hymenoptera collected from Toyama Prefecture in 2005. *Tsunekibachi* 8: 1–48. (in Japanese)
Haneda, Y., Nozaka, C., Tano, T., Kurokawa, H. & Murota, T. (2006b) The aculeate Hymenoptera collected at Tsushima, Nagasaki Prefecture in August of 2006. *Tsunekibachi* 10: 39–52. (in Japanese)
Haneda, Y., Nozaka, C., Tano, T., Kurokawa, H. & Murota, T. (2007) The Hymenoptera collected from Amami-Oshima, Kagoshima Prefecture in August of 2007. *Tsunekibachi* 12: 49–59. (in Japanese)
Haneda, Y. & Tano, T. (2003) The aculeate Hymenoptera collected at Tsushima, Nagasaki Prefecture in May of 2003. *Tsunekibachi* 1: 8–22. (in Japanese)
Hardin, G. (1960) The competitive exclusion principle. *Science* 131 (3409): 1292–1297.

https://doi.org/10.1126/science.131.3409.1292
He, J., Kreft, H., Gao, E., Wang, Z. & Jiang, H. (2017) Patterns and drivers of zoogeographical regions of terrestrial vertebrates in China. Journal of Biogeography 44 (5): 1172–1184. https://doi.org/10.1111/jbi.12892
He, J.-H., Chen, X.-X., Fan, J.-J., Li, Q., Liu, C.-M., Lou, X.-M., Ma, Y., Wang, S.-F., Wu, Y.-R., Xu, Z.-H., Xu, Z.-F. & Yao, J. (2004) *Hymenopteran insect fauna of Zhejiang*. Science Press, Beijing, lvi + 1373 pp. + xliii pls. (in Chinese)
Hermogenes De Mendonça, L. & Ebach, M.C. (2020) A review of transition zones in biogeographical classification. *Biological Journal of the Linnean Society* 131 (4): 717–736. https://doi.org/10.1093/biolinnean/blaa120
Hisamatsu, M. (2004) List of Hymenoptera recorded in Ibaraki Prefecture. *Bulletin of Ibaraki Nature Museum* 7: 125–164. (in Japanese)
Hochkirch, A., Gröning, J. & Bücker, A. (2007) Sympatry with the devil: reproductive interference could hamper species coexistence. *Journal of Animal Ecology* 76 (4): 633–642. https://doi.org/10.1111/j.1365-2656.2007.01241.x
Holt, B.E., Lessard, J.-P., Borregaard, M.K., Fritz, S.A., Araújo, M.B., Dimitrov, D., Fabre, P.-H., Graham, C.H., Graves, G.R., Jønsson, K.A., Nogués-Bravo, D., Wang, Z., Whittaker, R.J., Fjeldså, J. & Rahbek, C. (2013) An update of Wallace's zoogeographical regions of the world. *Science* 339 (6115): 74–78. https://doi.org/10.1126/science.1228282
Hua, L.-z. (2006) *List of Chinese insects Vol. IV*. Sun Yat-sen University Press, Guangzhou, 540 pp.
Hymenoptera Anatomy Consortium (2022) Hymenoptera glossary. Available from: http://glossary.hymao.org/ (accessed 8 September 2022)
Ikudome, S. & Yamane, Sk. (2007) Ants, wasps and bees of Iwo-jima, Northern Ryukyus, Japan (Hymenoptera, Aculeata). *The Bulletin of the Institute of Minami-Kyûshû Regional Science, Kagoshima Women's Junior College* 23: 1–7.
Ikudome, S. & Yamane, Sk. (2009) Ants, wasps and bees of Take-shima, Northern Ryukyus, Japan (Hymenoptera, Aculeata). *The Bulletin of the Institute of Minami-Kyûshû Regional Science, Kagoshima Women's Junior College* 25: 1–8.
Imai, Y. (2019) [Records and biology of mutillids in Gunma Prefecture]. *Gekkan-Mushi* 581: 2–3. (in Japanese)
Inoue, H. (2018) A list of Hymenoptera species of Itami City, Hyogo Prefecture. *Bulletin of the Itami City Museum of Insects* 6: 23–35. (in Japanese)
Ishikawa, R. (1965) Family Mutillidae. *In*: Asahina, S., Ishihara, T. & Yasumatsu, K. (eds) *Iconographia insectorum Japonicorum colore naturali edita volumen III*. Hokuryu-kan Publishing, Tokyo, p. 289 + 1 pl. (in Japanese)
Iwata, Y., Nagase, H., Waki, I. & Nakajima, H. (2002) A list of insects collected by Mr. S. Nakayama. *Bulletin of the Kawasaki Municipal Science Museum for Youth* 13: 119–131. (in Japanese)
Jellison, W.L. (1982) Concentrations of mutillid wasps (Hymenoptera: Mutillidae). *Entomological News* 93 (1): 27–28.
Kan, T. (2022) [Records of Mutillidae]. *Yamaguchi-no-mushi* 21: 178. (in Japanese)
Katô, M., Aihara, I., Enju, M. & Waki, I. (2004) [Hymenoptera of Nanasawa and Ohyama, Atsugi-shi]. [Fauna and flora of Nanasawa, Atsugi-shi]. *Atsugi-shi kyôdo shiryôkan shiryôshû* 17: 49–69. (in Japanese)
Kawazoe, A. (2013) [Hymenoptera collection of Jitsuzo Makita]. *Hirakura* 57 (1): 15–19. (in Japanese)
Kim, C.W. (1963) Catalogue of Hymenoptera from Korea. *Humanities & Sciences (Natural Sciences), Korea University* 6: 243–374. (in Korean)

Kim, C.W. (1970) *Illustrated encyclopedia of fauna and flora of Korea*. *Vol. 11 Insecta (III)*. Samwha-Chulpansa, Seoul, 892 pp. (in Korean)

Kim, C.W., Lee, J.W., Park, J.S., Kim, B.J. & Park, J.C. (1994) Hymenoptera. *In*: Shin, Y.H. & Yoon, I.B. (eds) *Check list of insects from Korea*. Kon-Kuk University Press, Seoul, pp. 216–269.

Kim, J.-K. & Kwon, O.-C. (2019) Insect fauna of Mt. Chilbo in Gyeonggi-do. *Korean Journal of Nature Conservation* 18 (1): 85–102. (in Korean) https://doi.org/10.30960/kjnc.2019.18.1.85

Kimura, K., Ooi, N. & Suzuki, S. (1996) Evidence of vegetation recovery on Yakushima Island after the major Holocene eruption at the Kikai Caldera, as revealed by the pollen record of buried soils under the old-growth Cryptomeria japonica forest. *Japanese Journal of Historical Botany* 4 (1): 13–23.

Kimura, M. (1996) Quaternary paleogeography of the Ryukyu Arc. *Journal of Geography* 105 (3): 259–285. https://doi.org/10.5026/jgeography.105.3_259

Kimura, M. (2002) The formation and paleogeography of Ryukyu Arc. *In*: Kimura, M. (ed.) *The formation of the Ryukyu Arc and migration of biota to the arc*. Okinawa Times, Naha, pp. 19–54. (in Japanese)

Kizaki, K. & Oshiro, I. (1977) Paleogeography of the Rytkyu [sic!] Islands. *Marine Science Monthly* 9: 542–549. (in Japanese)

Kojima, J., Saito, F. & Nguyen, L.T.P. (2011) On the species-group taxa of Taiwanese social wasps (Hymenoptera: Vespidae) described and/or treated by J. Sonan. *Zootaxa* 2920 (1): 42–64. http://dx.doi.org/10.11646/zootaxa.2920.1.2

Krombein, K.V. (1972) Monograph of the Madagascan Mutillidae (Hymenoptera). Part I: Myrmillini, Mutillini and Smicromyrmini. *Annales, Musée Royal de l'Afrique Centrale*, Série in 8°, Sciences Zoologiques 199: I–X + 1–61.

Kurokawa, H. (2003) The aculeate Hymenoptera recorded at Egamichou, Fukui City, Fukui Prefecture, Central Japan. *Tsunekibachi* 1: 59–62. (in Japanese)

Lamborn, W.A. (1916) Third report on *Glossina* investigations in Nyasaland. *Bulletin of Entomological Research* 7 (1): 29–50. https://doi.org/10.1017/S0007485300017053

Lelej, A.S. (1995) To the knowledge of East Asian species of the tribe Smicromyrmini Bischoff, 1920 (Hymenoptera, Mutillidae) with description of four new genera and eight new species. *Far Eastern Entomologist* 13: 1–28.

Lelej, A.S. (1996) To the knowledge of the East Asian species of the tribe Trogaspidiini Bischoff, 1920 (Hymenoptera, Mutillidae) with description of eight new genera and two new species. *Far Eastern Entomologist* 30, 1–24.

Lelej, A.S. (2002) *Catalogue of the Mutillidae (Hymenoptera) of the Palaearctic Region*. Dalnauka, Vladivostok, 172 pp.

Lelej, A.S. (2005) *Catalogue of the Mutillidae (Hymenoptera) of the Oriental Region*. Dalnauka, Vladivostok, 252 pp.

Lelej, A.S. & Brothers, D.J. (2008) The genus-group names of Mutillidae (Hymenoptera) and their type species, with a new genus, new name, new synonymies, new combinations and lectotypifications. *Zootaxa* 1889: 1–79.

Lelej, A.S., Choi, J.-Y. & Tripotin, P. (2001) Review of the mutillid wasps (Hymenoptera, Mutillidae) of Korea. *Far Eastern Entomologist* 96: 1–15.

Lelej, A.S. & Nemkov, P.G. (1997) Phylogeny, evolution and classification of Mutillidae (Hymenoptera). *Far Eastern Entomologist* 46: 1–24.

Lelej, A.S. & Yamane, Sk. (1992) Interesting velvet ants (Hymenoptera, Mutillidae) from Japan and Korea. *Japanese Journal of Entomology* 60 (3): 625–632.

Lepeletier de Saint-Fargeau, A. (1845) *Histoire Naturelle des Insectes*. *Hyménoptères*. Tome Troisième. Roret, Paris, [4] + 646 pp. https://doi.org/10.5962/bhl.title.9005

Lin, N. (1966) Copulatory behaviour of the cicada killer wasp, *Sphecius speciosus*. *Animal Behaviour* 14 (1): 130–131. https://doi.org/10.1016/S0003-3472(66)80021-0
Linsley, E.G. (1960) A fragmentary observation on the mating behavior of *Timulla*. *The Pan-Pacific Entomologist* 36 (1): 36.
Lo Cascio, P. (2015) Worldwide checklist of the island mutillid wasps (Hymenoptera Mutillidae). *Biodiversity Journal* 6 (2): 529–592.
Machida, H. & Arai, F. (2003) *Atlas of Tephra in and around Japan*. University of Tokyo Press, Tokyo, 336 pp. (in Japanese)
Matsumura, S. (1931) *6000 illustrated insects of Japan-Empire*. Tôkô Shoin, Tokyo, 3 pp. + 1497 pp. + 23 pp. + 10 pls. (in Japanese)
Matsumura, S. (1932) *Illustrated common insects of Japan*. *Vol. IV*. *Hymenoptera, Diptera, Rhynchota*. Shunyodo, Tokyo, 99 pp. + 145 pp. + 9 pp. + 23 pls.
Matteini Palmerini, M. (2013) Remarks on the behavior of the velvet ant *Nemka viduata viduata* (Pallas, 1773) (Insecta Hymenoptera Mutillidae). *Quaderno di Studi e Notizie di Storia Naturale della Romagna* 37: 237–260.
Mickel, C.E. (1933a) The Mutillidae of Formosa. *Annals of the Entomological Society of America* 26 (2): 381–423. https://doi.org/10.1093/aesa/26.2.381
Mickel, C.E. (1933b) The Mutillidae of Eastern Asia. *Lingnan Science Journal* 12 (3): 289–325.
Mickel, C.E. (1934) Mutillidae of the Philippine Islands. *Philippine Journal of Science* 54 (1): 91–219 + 1 pl.
Mickel, C.E. (1935) The mutillid wasps of the islands of the Pacific Ocean (Hymenoptera, Mutillidae). *Transactions of the Royal Entomological Society of London* 83 (2): 177–312. https://doi.org/10.1111/j.1365-2311.1935.tb01207.x
Mickel, C.E. (1938) The Neotropical mutillid wasps of the genus *Timulla* Ashmead (Hymenoptera: Mutillidae). *Transactions of the Royal Entomological Society of London* 87 (22): 529–679. https://doi.org/10.1111/j.1365-2311.1938.tb00728.x
Mimura, Y. (2014) [Record of the male of *Neotrogaspidia pustulata* (Smith, 1873) in Ôita Prefecture]. *Gekkan-Mushi* 526: 16. (in Japanese)
Mimura, Y. (2019) [A mating pair and a case of phoretic copulation of *Neotrogaspidia pustulata* (Smith, 1873)]. *Gekkan-Mushi* 578, 57. (in Japanese)
Morrone, J.J. (2015) Biogeographical regionalisation of the world: a reappraisal. *Australian Systematic Botany* 28 (2–3): 81–90. https://doi.org/10.1071/SB14042
Motokawa, M. (2017) "Land Emergence" and "Elevation Shift" affect diversification: A new perspective toward understanding the high species diversity of terrestrial animals in Japan. *In*: Motokawa, M. & Kajihara, H. (eds) *Species diversity of animals in Japan*. Springer Japan, Tokyo, pp. 3–23. https://doi.org/10.1007/978-4-431-56432-4_1
Murao, R. (2014) [Mutillidae of Mt. Hiko-san (Hym.: Mutillidae)]. *Pulex* 93: 643–645. (in Japanese)
Murao, R. (2015) Records of aculeate wasps and bees in the coast of northwestern part of Fukuoka Prefecture, Kyushu, Japan. *Tsunekibachi* 27: 33–50. (in Japanese)
Murota, T. (1973a) Some aculeate Hymenoptera collected in the Amami Group of the Ryukyus. *The Life Study* 17 (3–4): 100–102. (in Japanese)
Murota, T. (1973b) Sphecidae, Mutillidae, Scoliidae and Chrysididae collected in Formosa in 1972. *The Life Study* 17 (3–4): 115–120. (in Japanese)
Nagase, H. (1980) [Hymenoptera of southern Kyushu —2—]. *Hymenopterists' Communication* 10: 4–8. (in Japanese)
Nagase, H. (1982) [Hymenoptera of southern Kyushu —4—]. *Hymenopterists' Communication* 14: 57–78. (in Japanese)
Nagase, H. (2004) Hymenoptera (excl. Formicidae). *In*: Kanagawa Konchû Danwakai (ed.)

Insect fauna of Kanagawa III. Kanagawa Konchû Danwakai, Kanagawa, pp. 1241–1326. (in Japanese)

Nakamura, K. (2003) Hymenoptera. *In*: Inaizumi, M., Sato, K., Nakamura, T., Takahashi, S. & Kagawa, K. (eds) [*Insects of Tochigi I*]. Tochigi Prefecture Government, Utsunomiya, pp. 249–336. (in Japanese)

Nakamura, S. & Matsuda, S. (2005) The insects in the riverside of Takatsu River, Shimane Prefecture, a result of survey in 2000. *Bulletin of the Hoshizaki Green Foundation* 8: 99–172. (in Japanese)

Nambu, T. & Shimizu, A. (1984) [Visits to Ogasawara (Chichi-jima, Haha-jima)]. *Hymenopterists' Communication* 19: 11–25. (in Japanese)

Nomura, Y. (1978) [On the insect fauna of Tottori sand dune]. *Tottori Seibutsu* 10–13: 13–19. (in Japanese)

Ohgushi, R. & Yoshida, M. (1960) Insect-fauna of Kohshima, Miyazaki Pref. *The Life Study* 4 (4): 49–56. (in Japanese)

Ohkusa, S. (2007) Hymenoptera collected from north-west at Aichi Prefecture. *Tsunekibachi* 12: 26–38. (in Japanese)

Ohkusa, S. & Tajima, T. (2008) Hymenoptera collected from north-west at Aichi Prefecture. *Tsunekibachi* 13: 63–81. (in Japanese)

Ohkusa, S. & Tajima, T. (2010) Hymenoptera of eastern part Shiga Prefecture. *Tsunekibachi* 17: 1–20. (in Japanese)

Okayasu, J. (2017) Two new species of the genus *Sinotilla* Lelej, 1995 (Hymenoptera: Mutillidae), with notes on taxonomic characters. *Zootaxa* 4294 (2): 151–169. https://doi.org/10.11646/zootaxa.4294.2.1

Okayasu, J. (2020) Velvet ants of the tribe Smicromyrmini Bischoff (Hymenoptera: Mutillidae) of Japan. *Zootaxa* 4723 (1): 1–110. https://doi.org/10.11646/zootaxa.4723.1.1

Okayasu, J., Lelej, A.S. & Williams, K.A. (2021) Review of *Eotrogaspidia* Lelej (Hymenoptera: Mutillidae: Trogaspidiini). *Zootaxa* 4920 (1): 56–90. https://doi.org/10.11646/zootaxa.4920.1.2

Okayasu, J., Williams. K.A. & Lelej, A.S. (2018) A remarkable new species of the genus *Sinotilla* Lelej (Hymenoptera: Mutillidae: Smicromyrmini) from Taiwan and an overview of color diversity in East Asian mutillid females. *Zootaxa* 4446 (3): 301–324. http://dx.doi.org/10.11646/zootaxa.4446.3.1

O'Neill, K.M. & Evans, H.E. (1983) Alternative male mating tactics in *Bembecinus quinquespinosus* (Hymenoptera: Sphecidae): correlations with size and color variation. *Behavioral Ecology and Sociobiology* 14 (1): 39–46. https://doi.org/10.1007/BF00366654

Oshiro, I. & Nohara, T. (2000) Distribution of Pleistocene terrestrial vertebrates and their migration to the Ryukyus. *Tropics* 10 (1): 41–50. https://doi.org/10.3759/tropics.10.41

Ota, H. (1998) Geographic patterns of endemism and speciation in amphibians and reptiles of the Ryukyu Archipelago, Japan, with special reference to their Paleogeographical implications. *Researches on Population Ecology* 40 (2): 189–204. https://doi.org/10.1007/BF02763404

Ota, H. (2000) The current geographic faunal pattern of reptiles and amphibians of the Ryukyu Archipelago and adjacent regions. *Tropics* 10 (1): 51–62. https://doi.org/10.3759/tropics.10.51

O'Toole, C. (1975) The systematics of *Timulla oculata* (Fabricius) (Hymenoptera, Mutillidae). *Zoologica Scripta* 4 (1): 229–251. https://doi.org/10.1111/j.1463-6409.1975.tb00733.x

Ôtsui, K., Uemori, K. & Murao, R. (2021) [Records of aculeate Hymenoptera from

Nakagawa-shi, Fukuoka Prefecture]. *Korasana* 97: 33–48. (in Japanese)
Pagden, H.T. (1934) New species of Mutillidae (Hymenoptera, Vespoidea) from the Malay Peninsula. *Journal of the Federated Malay States Museums* 17 (3): 419–457.
Pagliano, G., Brothers, D.J., Cambra, R., Lelej, A.S., Lo Cascio, P., Matteini Palmerini, M., Scaramozzino, P.L., Williams, K.A. & Romano, M. (2020) Checklist of names in Mutillidae (Hymenoptera), with illustrations of selected species. *Bollettino del Museo Regionale di Scienze Naturali di Torino* 36 (1–2): 5–425.
Pitts, J.P., Tanner, D., Waldren, G.C. & Paker, F.D. (2010a) Facultative size-dependent sex allocation in *Sphaeropthalma pensylvanica* Lepeletier (Hymenoptera: Mutillidae) with further host records. *Journal of the Kansas Entomological Society* 83 (1): 68–75. https://doi.org/10.2317/JKES0812.15.1
Pitts, J.P., Wilson, J.S. & von Dohlen, C.D. (2010b) Evolution of the nocturnal Nearctic Sphaeropthalminae velvet ants (Hymenoptera: Mutillidae) driven by Neogene orogeny and Pleistocene glaciation. *Molecular Phylogenetics and Evolution* 56 (1): 134–145. https://doi.org/10.1016/j.ympev.2010.03.033
Polidori, C., Beneitez, A., Asís, J.D. & Tormos, J. (2013) Scramble competition by males of the velvet ant *Nemka viduata* (Hymenoptera: Mutillidae). *Behaviour* 150: 23–37.
Procheş, S. & Ramdhani, S. (2012) The world's zoogeographical regions confirmed by cross-taxon analyses. *BioScience* 62 (3): 260–270. https://doi.org/10.1525/bio.2012.62.3.7
Quintero A., D. & Cambra, R.A. (1994) Systematics of *Pseudomethoca areta* (Cameron): Sex association, description of the male and a gynandromorph, and a new synonymy (Hymenoptera: Mutillidae). *Journal of Hymenoptera Research* 3: 303–308.
Roig-Alsina, A. (1993) The evolution of the apoid endophallus, its phylogenetic implications, and functional significance of the genital capsule (Hymenoptera, Apoidea). *Bollettino di zoologia* 60 (2): 169–183. https://doi.org/10.1080/11250009309355807
Rossi, P. (1790) *Fauna Etrusca sistens insecta quae in Provinciis Florentina et Pisana praesertim collegit Petrus Rossius*. *Tomus Secundus*. Thomae Masi & Sociorum, Liburni [= Livorno], 348 pp. + 10 pls.
Rothney, G.A.J. (1903) The aculeate Hymenoptera of Barrackpore, Bengal. *Transactions of the Entomological Society of London* 1903: 93–116.
Rutowski, R.L. & Alcock, J. (1980) Temporal variation in male copulatory behaviour in the solitary bee *Nomadopsis puellae* (Hymenoptera: Andrenidae). *Behaviour* 73 (3–4): 175–188.
Sato, T. & Tsurusaki, N. (2010) Preliminary report of insect fauna occurring in the Tottori Sand Dunes. *Bulletin of the Tottori Prefectural Museum* 47: 45–81. (in Japanese)
Schulz WA (1906) *Spolia Hymenopterologica*. Albert Pape, Paderborn, 356 pp. + 1 pl. https://doi.org/10.5962/bhl.title.59757
Sheldon, J.K. (1970) Sexual dimorphism in the head structure of Mutillidae Hymenoptera: A possible behavioral explanation. *Entomological News* 81 (3): 57–61.
Shimizu, Y. (2003) The nature of Ogasawara and its conservation. *Global Environmental Research* 7 (1): 3–14.
Shorthouse, D.P. (2010) SimpleMappr, an online tool to produce publication-quality point maps. Available from: http://www.simplemappr.net (accessed 7 September 2022)
Smith, F. (1855) *Catalogue of hymenopterous insects in the collection of the British Museum*. *Part III*. *Mutillidae and Pompilidae*. Taylor and Francis, London, [4] + 206 pp. + pl. A + 5 pls. https://doi.org/10.5962/bhl.title.20858
Smith, F. (1873) Description of aculeate Hymenoptera of Japan, collected by Mr. George Lewis at Nagasaki and Hiogo. *The Transactions of the Entomological Society of London* 1873: 181–206. https://doi.org/10.1111/j.1365-2311.1873.tb00641.x
Smith, F. (1874) Description of new species of Tenthredinidae, Ichneumonidae, Chrysididae,

Formicidae, &c. of Japan. *The Transactions of the Entomological Society of London* 1874: 373–409. https://doi.org/10.1111/j.1365-2311.1874.tb00867.x
Suárez, F.J. (1959) Especies nuevas o poco conocidas de la fauna mediterranea. II nota (Hym. Myrmosidae, Mutillidae). *EOS, Revista Española de Entomologia*, Madrid 35 (3): 283–300.
Suda, T. (2011) [Collecting data of Mutillidae including new records]. *Rambu* 20: 136–138. (in Japanese)
Suda, T. (2018) [Additional records of Mutillidae from Gunma prefecture]. *Rambu* 24: 39. (in Japanese)
Sugiura, S., Tsuru, T. & Yamaura, Y. (2013) Effects of an invasive alien tree on the diversity and temporal dynamics of an insect assemblage on an oceanic island. *Biological Invasions* 15 (1): 157–169. https://doi.org/10.1007/s10530-012-0275-0
Takahashi, H. (1993) Flower-visiting activities of the aculeate wasps on Hachijo-jima Island of the Izu Islands. *The Biological Magazine Okinawa* 31: 1–6. (in Japanese)
Takahashi, H. (1996) [Collecting records of Mutillidae]. *Gekkan-Mushi* 310: 28–29. (in Japanese)
Takahashi, H. (2010) A tentative list of the Hymenoptera (excluding Formicidae) of the Ogasawara (Bonin) Islands. *Tsunekibachi* 18: 15–20. (in Japanese)
Takahashi, H. & Shimizu, A. (2007) Notes on a collection of Hymenoptera, from the Ogasawara Islands, in the insect collections of the Laboratory of Systematic Zoology, Tokyo Metropolitan University. *Ogasawara Research* 32: 9–20. (in Japanese)
Tano, T. (1964) The aculeate Hymenoptera collected on the island of Yakushima. *The Life Study* 8 (3): 37–39. (in Japanese)
Tano, T., Kurokawa, H., Murota, T. & Nozaka, C. (2003) The Hymenoptera collected at Tsushima, Nagasaki Prefecture in July of 2003. *Tsunekibachi* 1: 23–40. (in Japanese)
Tano, T., Murota, T. & Nozaka, C. (1985) [On the Hymenoptera of Sakishima Islands]. *Hymenopterists' Communication* 23: 27–36. (in Japanese)
Taylor, C.K., Murphy, M.V., Hitchen, Y. & Brothers, D.J. (2019) Four new species of Australian velvet ants (Hymenoptera: Mutillidae, *Aglaotilla*) reared from bee and wasp nests, with a review of Australian mutillid host records. *Zootaxa* 4609 (2): 201–224. https://doi.org/10.11646/zootaxa.4609.2.1
Terayama, M. (1982) [Distributional records of Hymenoptera of Kanagawa Prefecture]. *Kanagawa-Chûhô* 67: 25–31. (in Japanese)
Terayama, M. (2005) Taxonomic guide to the Japanese aculeate wasps, 2. Family Mutillidae. *Tsunekibachi* 4: 1–13. (in Japanese)
Terayama, M., Suda, H., Murota, T., Haneda, Y. & Tano, T. (2011) The velvet ants (Mutillidae) of Japan. *Gekkan-Mushi* 481: 12–25. (in Japanese)
Terayama, M., Suda, H., Murota, T. & Tano, T. (2016) Family Mutillidae. *In*: Terayama, M. & Suda, H. (eds) *A guide to the aculeate wasps of Japan*. Tokai University Press, Hiratsuka, pp. 161–174. (in Japanese)
The Natural History Society of Fukui (1938) [*Illustrated insects of Fukui Prefecture*]. The Natural History Society of Fukui, Fukui. (in Japanese)
Tojo, K., Sekiné, K., Takenaka, M., Isaka, Y., Komaki, S., Suzuki, T. & Schoville, S.D. (2017) Species diversity of insects in Japan: Their origins and diversification processes. *Entomological Science* 20 (1): 357–381. https://doi.org/10.1111/ens.12261
Tormos, J., Asís, J.D., Polidori, C., Benéitez, A. & Storino, G. 2010. The mating behaviour of the velvet ant, *Nemka viduata* (Hymenoptera: Mutillidae). *Journal of Insect Behavior* 23 (2): 117–127. https://doi.org/10.1007/s10905-009-9200-5
Tsuneki, K. (1959) [Collecting Hymenoptera in Ashizuri and Sata]. *The Life Study* 3 (4): 78–82. (in Japanese)

Tsuneki, K. (1962) The aculeate Hymenoptera collected on the island of Amami-Ohshima, the Riukius. *The Life Study* 6 (1): 1–8. (in Japanese)
Tsuneki, K. (1972a) Studies on the Mutillidae of Japan (Hymenoptera). *Etizenia* 61: 1–26.
Tsuneki, K. (1972b) Mutillidae collected in Formosa in 1966 and 68 (Hymenoptera). *Etizenia* 64: 1–25.
Tsuneki, K. (1972c) [Collecting records of velvet ants in Fukui Prefecture in 1972]. *The Life Study* 16 (3–4): 59. (in Japanese)
Tsuneki, K. (1982a) A referenced list of the species of the Sphecidae, Chrysididae, Scoliidae and Mutillidae hitherto known from the Ryukyu Archipelago, with the distribution table (Hymenoptera). *Special Publications of the Japan Hymenopterists Association* 23: 53–77.
Tsuneki, K. (1982b) [Solitary wasps of the Ryukyu Archipelago and their distribution]. *Hymenopterists' Communication* 14: 79–107. (in Japanese)
Tsuneki, K. (1984) Solitary wasps newly collected in the Ogasawaras or the Bonin Island (Hymenoptera). *Special Publications of the Japan Hymenopterists Association* 28: 1–12.
Tsuneki, K. (1985) [Distributional records of Hymenoptera]. *Hymenopterists' Communication* 23: 7–16. (in Japanese)
Tsuneki, K. (1993) On some Taiwanese Mutillidae, collected in 1976 by Mr. T. Murota, with description of new taxa (Hymenoptera). *Special Publications of the Japan Hymenopterists Association* 41: 39–50.
Tsuneki, K., Nozaka, C., Tano, T., Kurokawa, H. & Murota, T. (1993) Mutillidae recently collected in the Philippines (Hymenoptera). *Special Publications of the Japan Hymenopterists Association* 41: 1–38.
Tsurusaki, N., Hayashi, M., Miyanaga, R., Ichisawa, K. & Kawakami, Y. (2012) Catalogue of the insects of Tottori Sand Dunes, Honshu, Japan. *Natural History Research of San'in* 7: 47–82. (in Japanese)
Uchida, T. (1925) A list of known species of the Corean Hymenoptera which I collected in 1922, and their geographical distributions. *Insect World* 29: 328–337. (in Japanese)
Ujiie, H. (1990) Geological history of the Ryukyu Arc. *In*: Ujiie, H. (ed.) *Nature of Okinawa; Geomorphology and geology*. Hirugisha, Naha, pp. 251–255. (in Japanese)
Vivallo, F. (2020) Phoretic copulation in Aculeata (Insecta: Hymenoptera): A review. *Zoological Journal of the Linnean Society* 191 (3): 627–636. https://doi.org/10.1093/zoolinnean/zlaa069
Waki, I. (2001) [Collecting records of Hymenoptera in Chigasaki]. *Chigasaki City Museum of Heritage Research Report* 9: 33–39. (in Japanese)
Waldren, G.C., Roberts, J.D. & Pitts, J.P. (2020) Phoretic copulation in the velvet ant *Sphaeropthalma pensylvanica* (Lepeletier) (Hymenoptera, Mutillidae): A novel behavior for Sphaeropthalminae with a synthesis of mating strategies in Mutillidae. *Journal of Hymenoptera Research* 78: 69–89. https://doi.org/10.3897/jhr.78.55762
Williams, K.A., Brothers, D.J. & Pitts, J.P. (2011) New species of *Tobantilla* Casal, 1965 and a new genus and species, *Gogoltilla chichikovi* gen. et sp. nov., from Argentina (Hymenoptera: Mutillidae). *Zootaxa* 3064 (1): 41–68. https://doi.org/10.11646/zootaxa.3064.1.2
Williams, K.A., Lelej, A.S., Okayasu, J., Borkent, C.J., Malee, R., Thoawan, K. & Thaochan, N. (2019) The female velvet ants (aka modkhong) of southern Thailand (Hymenoptera: Mutillidae), with a key to the genera of southeast Asia. *Zootaxa* 4602 (1): 1–69. http://dx.doi.org/10.11646/zootaxa.4602.1.1
Wilson, J.S., Clark, S.L., Williams, K.A. & Pitts, J.P. (2012) Historical biogeography of the arid-adapted velvet ant *Sphaeropthalma arota* (Hymenoptera: Mutillidae) reveals

cryptic species. *Journal of Biogeography* 39: 336–352. https://doi.org/10.1111/j.1365-2699.2011.02580.x

Wu, C.F. (1941) *Catalogus Insectorum Sinensium Volume VI*. The Department of Biology, Yenching University, Peiping, vi + 333 pp. + xv.

Yamamoto, N. (2010) Records of Mutillidae from Nagasaki Prefecture. *Tsunekibachi* 17: 25–27. (in Japanese)

Yamane, Sk. (1999) Family Mutillidae. *In*: Yamane, Sk., Ikudome, S. & Terayama, M. (eds) *Identification guide to the Aculeata of the Nansei Islands, Japan*. Hokkaido University Press, Sapporo, pp. 369–381.

Yano, M. (1932) Mutillidae. *In*: Uchida, S. (ed.) *Iconographia Insectorum Japonicorum Editio Prima*. Hokuryukan, Tokyo, pp. 325–327 + 1 pl. (in Japanese)

Yasumatsu, K. (1934) Les Hyménoptères de l'ile Yakushima. *Mushi* 7 (2): 61–67.

Yasumatsu, K. (1936) Hymenoptera of the Bonin Islands. *Transactions of the Natural History Society of Formosa* 26 (157): 356–363.

Yasumatsu, K. (1938a) Les Mutillides de Coree et de la Mandschourie du Sud. *Transactions of the Natural History Society of Formosa* 28 (75): 83–87.

Yasumatsu, K. (1938b) Mutillidae. *In*: Esaki, T., Hori, H. & Yasumatsu, K. (eds) *Insectorum Japonicorum Illastratio Iconographica Coloribus ad Naturam Depicta*. Sanseidô, Tokyo, p. 351 + pl. 158.

Yasumatsu, K. (1944) [Hymenoptera]. *In*: Furukawa, H. (ed.) *Nihon Seibutsushi, Konchu 1*. Kenkyû-sha, Tokyo, pp. 405–527. (in Japanese)

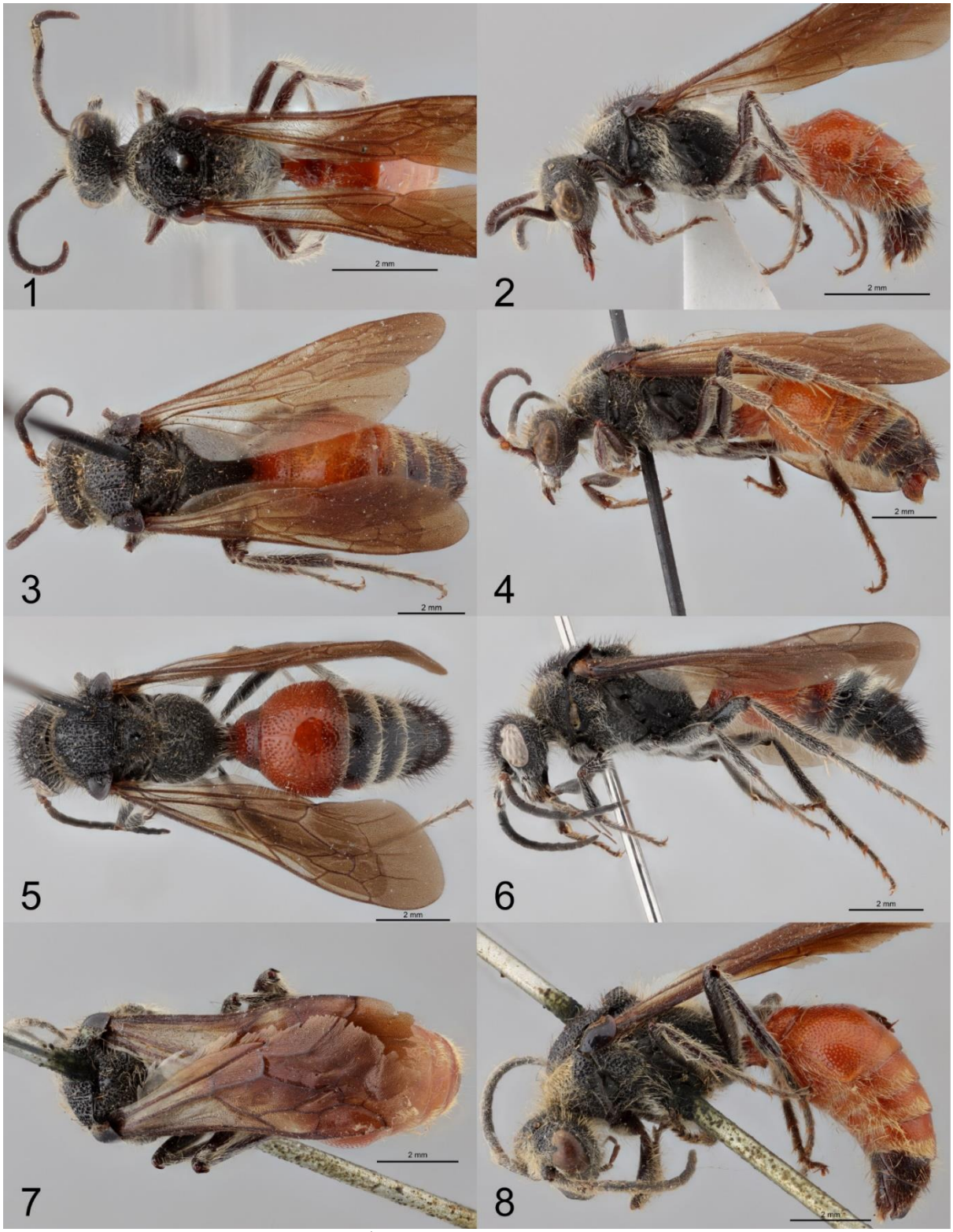
Yasumatsu, K. (1950) *Timulla insidiator* Smith. *In*: Ishii, T., Easki, T., Kinoshita, S., Shiraki, T., Uchida, S., Kawamura, T., Kuwayama, S. & Yuasa, H. (eds) *Iconographia Insectorum Japonicorum Edito Secunda*. Hokuryukan, Tokyo, p. 1448.

Yoshida, M. (1989) Family Mutillidae. *In*: Entomological Laboratory, Faculty of Agriculture, Kyushu University & Japan Wildlife Research Center (eds) *A check list of Japanese insects*. Entomological Laboratory, Faculty of Agriculture, Kyushu University, Fukuoka, pp. 650–651. (in Japanese)

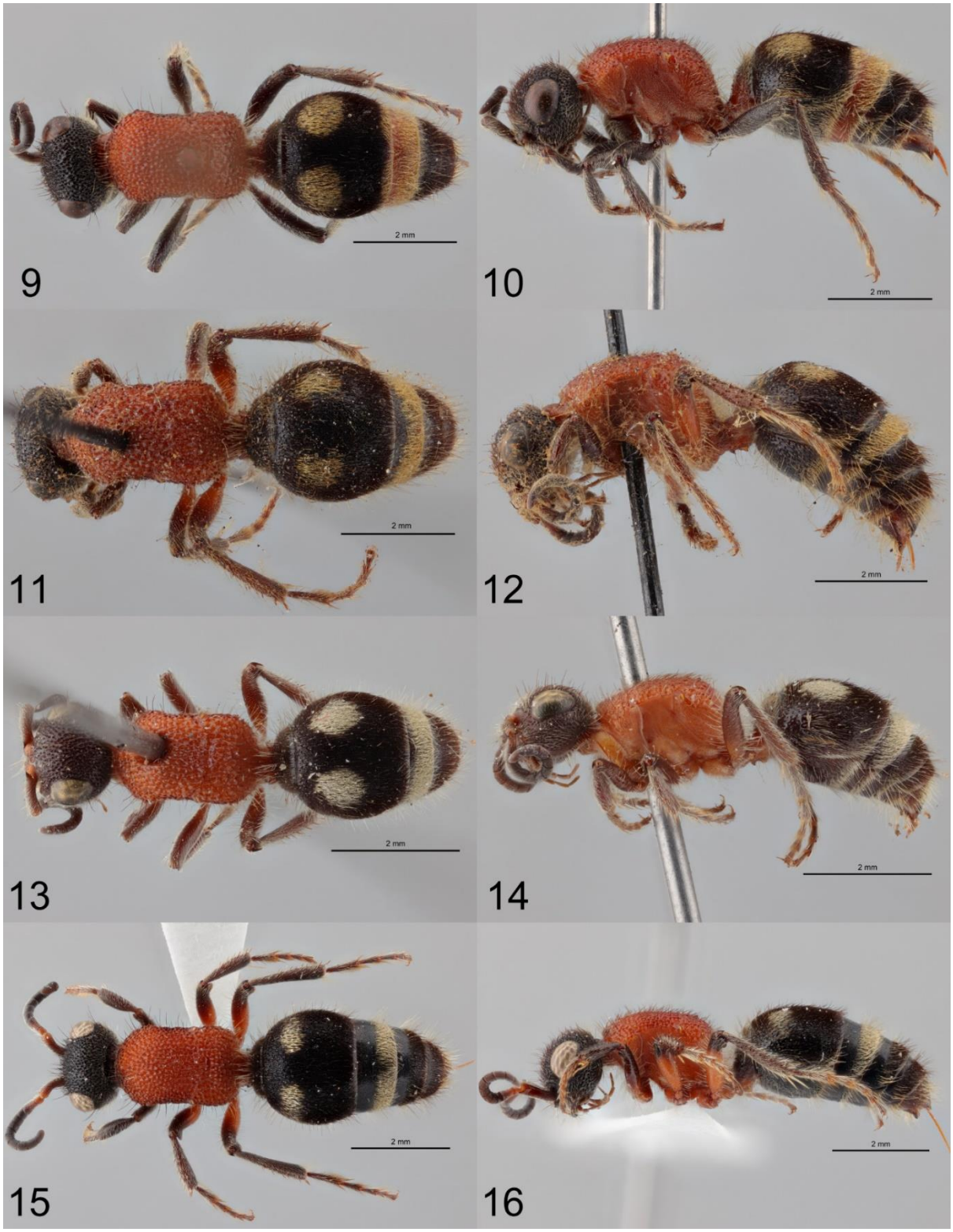
Zavattari, E. (1907) Nuovo o poco note Mutille dell'Australia. *Bollettino dei Musei di Zoologia ed Anatomia Comparata della R. Università di Torino* 22: 1–4.

Zavattari, E. (1913) H. Sauter's Formosa-Ausbeute. Mutillidae (Hym.). *Archiv für Naturgeschichte* 79A (3): 19–42. https://doi.org/10.5962/bhl.part.7709

Zavattari, E. (1914) Mutille Austro-Malesi. *Bolletino della Societa Entomologica Italiana* 45: 61–114.

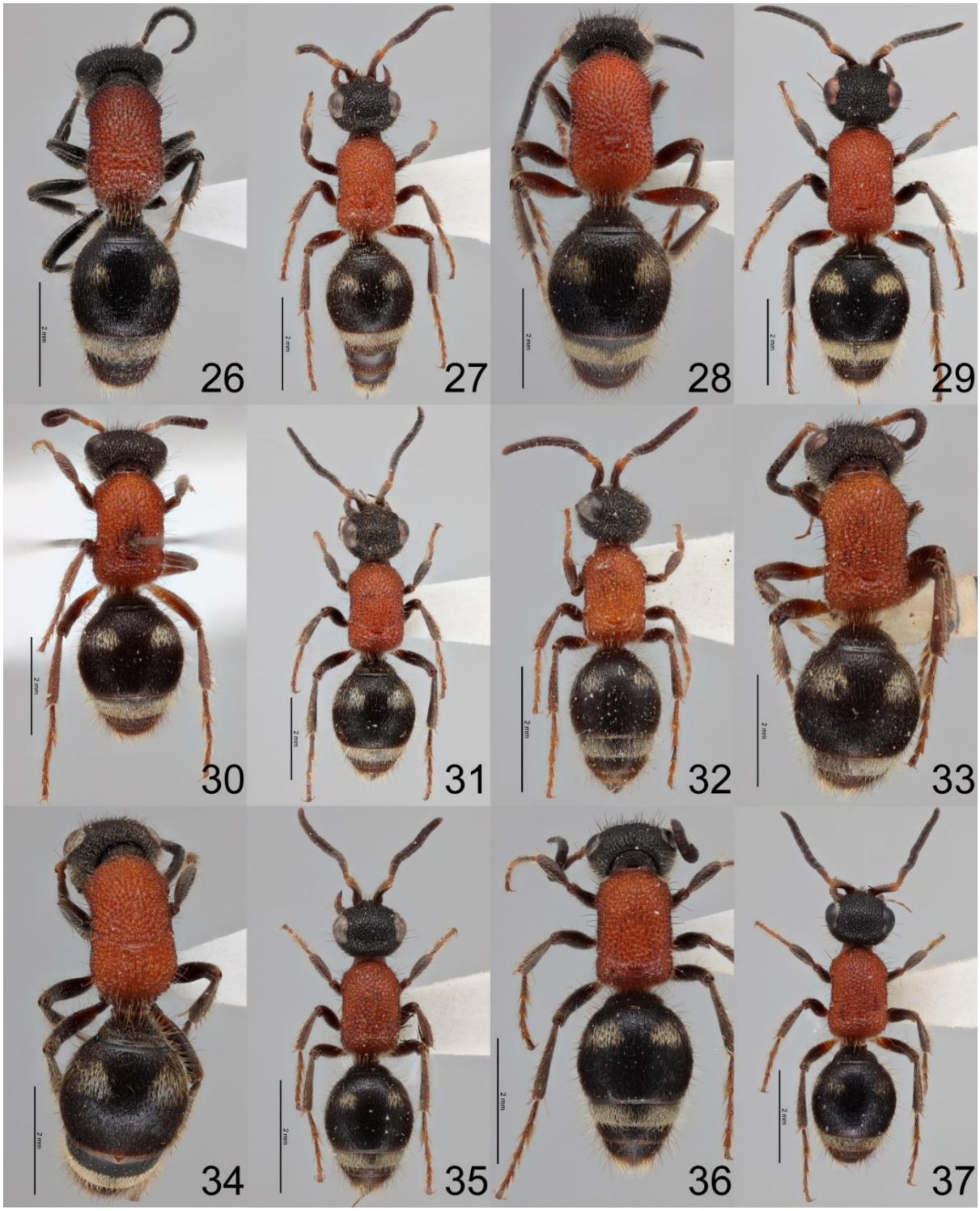


Figures 1–8. *Neotrogaspidia* spp., ♂, habitus. 1, 2. *N. circumcincta* (André); 3, 4. *N. elpinice* (Mickel); 5, 6. *N. pustulata* (Smith); 7, 8. *N. recticarinata* (Chen), paratype; 1, 3, 5, 7. Dorsal view; 2, 4, 6, 8. lateral view.



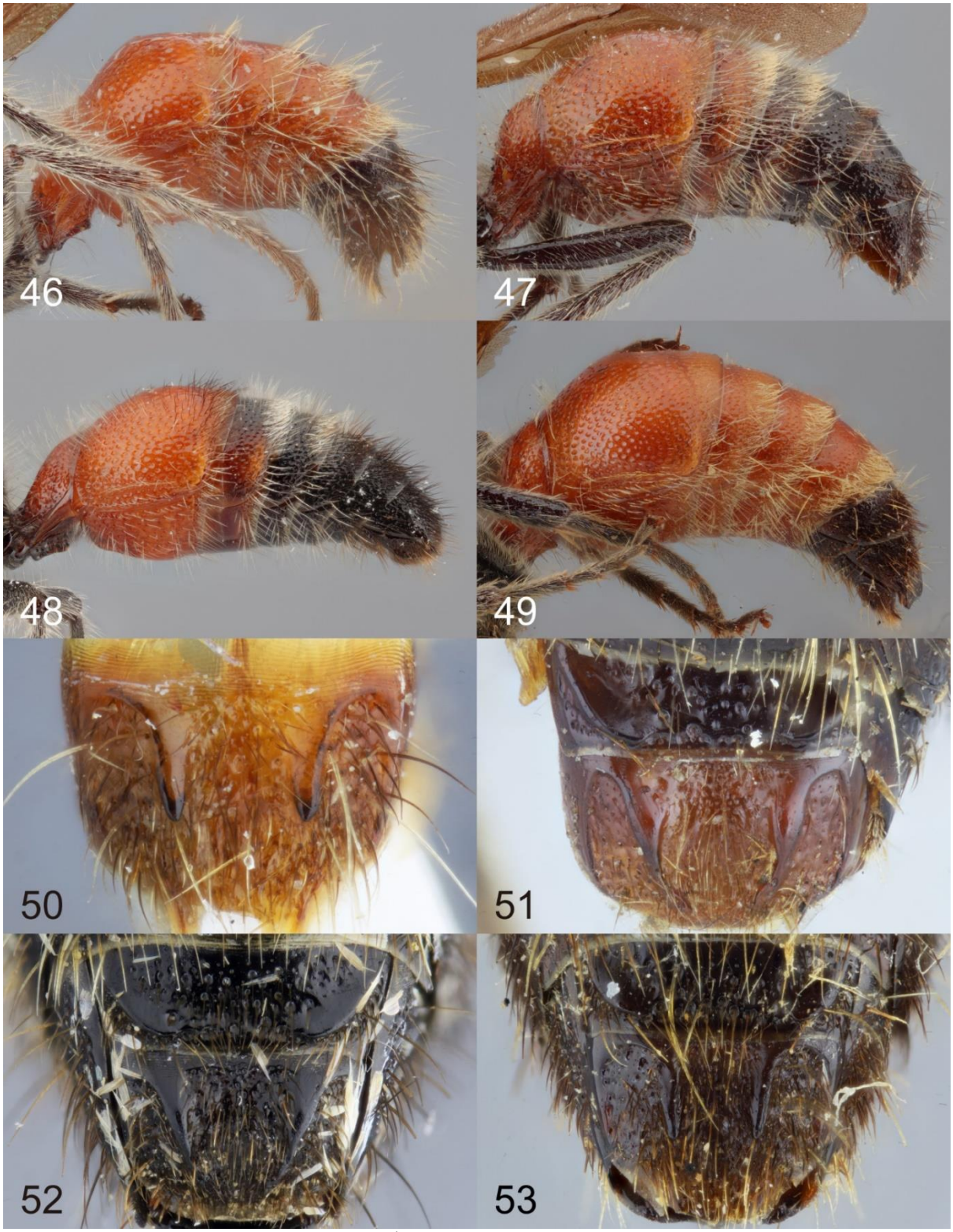
Figures 9–16. *Neotrogaspidia* spp., ♀, habitus. 9, 10. *N. circumcincta* (André); 11, 12. *Trogaspidia maritima* Chen, paratype; 13, 14. *N. elpinice* (Mickel), Taiwan; 15, 16. *N. pustulata* (Smith), Japan; 9, 11, 13, 15. dorsal view; 10, 12, 14, 16. lateral view.

Figures 17–25. *Neotrogaspidia* spp., ♂♀, holotype. 17, 18, 23. *Smicromyrme yakushimensis* Yasumatsu; 19, 20, 24. *Trogaspidia maritima* Chen; 21, 22, 25. *T. recticarinata* Chen; 17, 19, 21. dorsal habitus; 18, 20, 22. lateral habitus; 23–25. labels.

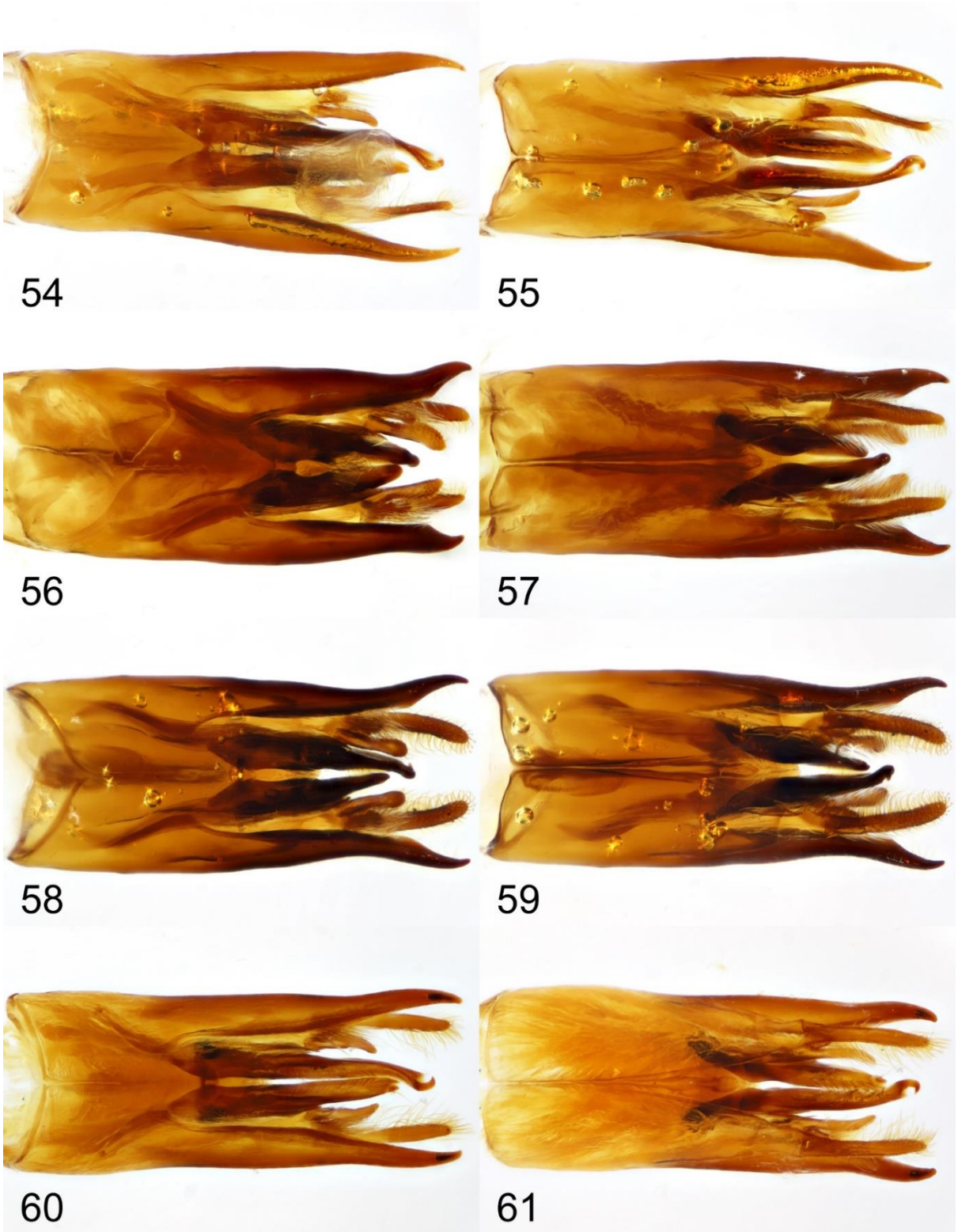


Figures 26–37. *Neotrogaspidia pustulata* (Smith), ♀, dorsal habitus. 26. Japan: Honshû (Chiba); 27. Japan: Honshû (Nara); 28. Japan: Shikoku (Ehime); 29. Japan: Kyûshû (Ôita); 30. Japan: Izu Islands (Hachijyô-jima); 31. Ôsumi Islands (Yakushima); 32. Japan: Tokara Islands (Nakano-shima); 33. Japan: Tokara Islands (Takara-jima); 34. Japan: Amami Islands (Tokuno-shima); 35. Japan: Yaeyama Islands (Ishigaki-jima); 36. Japan: Yaeyama Islands (Iriomote-jima); 37. South Korea.

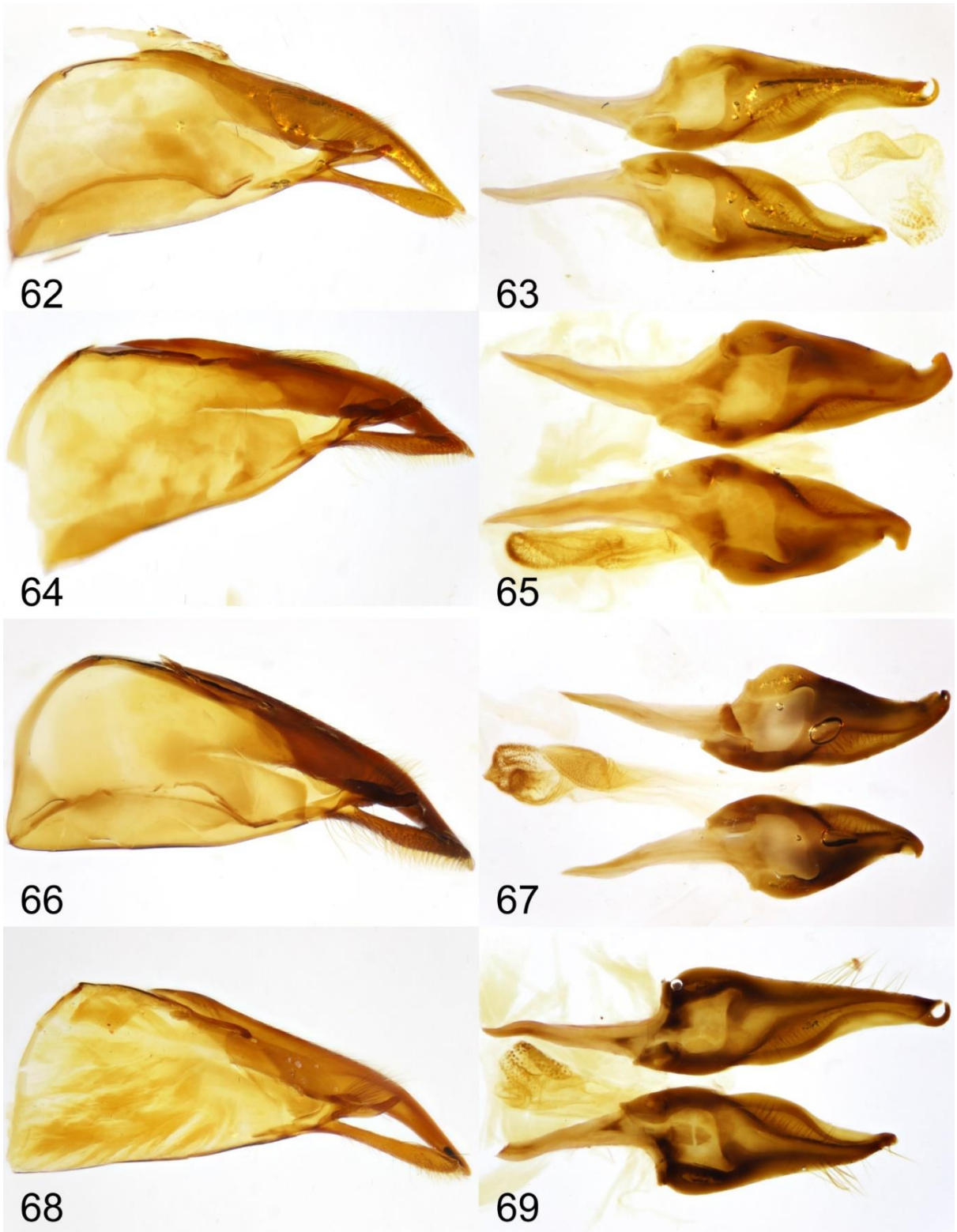
Figures 38–45. *Neotrogaspidia* spp., ♂, head. 38, 42. *N. circumcincta* (André); 39, 43. *N. elpinice* (Mickel); 40, 44. *N. pustulata* (Smith); 41, 45. *N. recticarinata* (Chen), paratype; 38–41. face; 42–45. scape, ventral view.



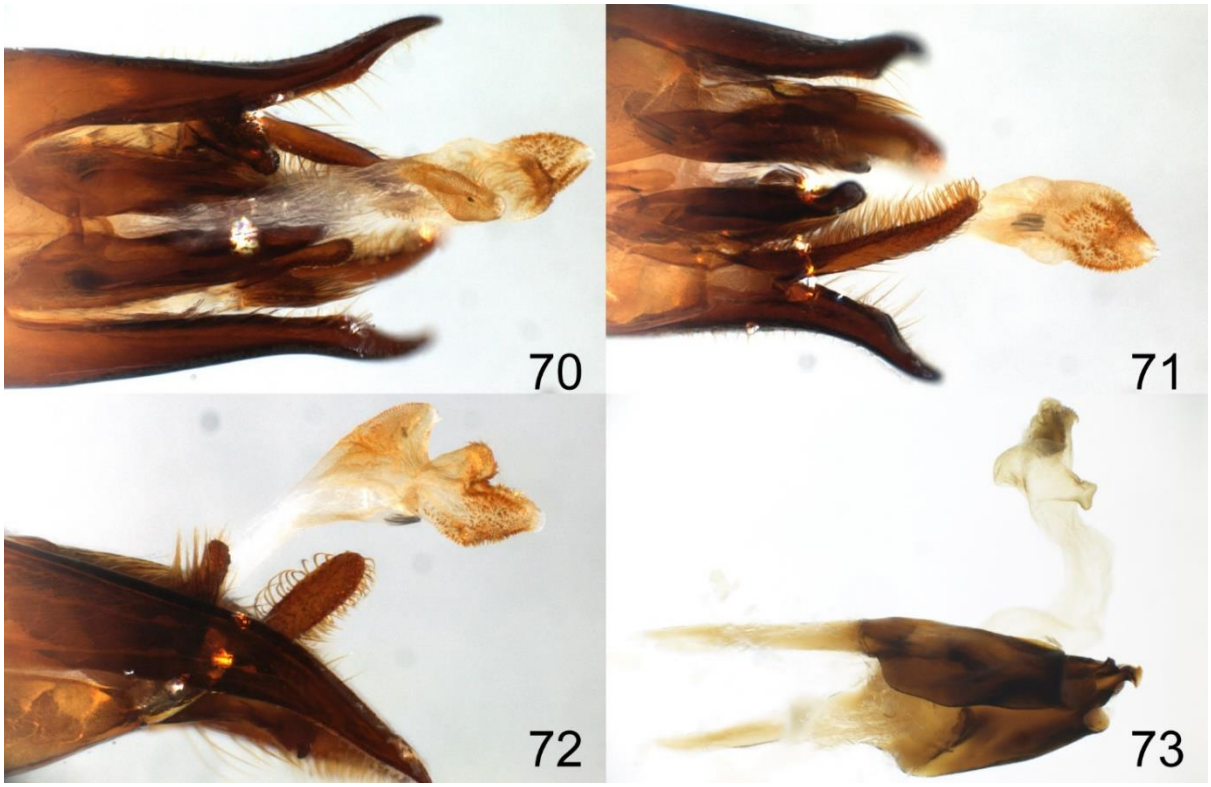
Figures 46–53. *Neotrogaspidia* spp., ♂, metasoma. 46, 50. *N. circumcincta* (André); 47, 51. *N. elpinice* (Mickel); 48, 52. *N. pustulata* (Smith); 49, 53. *N. recticarinata* (Chen), paratype; 46–49. metasoma, lateral view; 50–53. S7 and S8, ventral view.



Figures 54–61. *Neotrogaspidia* spp., ♂, genitalia. 54, 55. *N. circumcincta* (André); 56, 57. *N. elpinice* (Mickel); 58, 59. *N. pustulata* (Smith); 60, 61. *N. recticarinata* (Chen), paratype; 54, 56, 58, 60. dorsal view; 55, 57, 59, 61. ventral view.

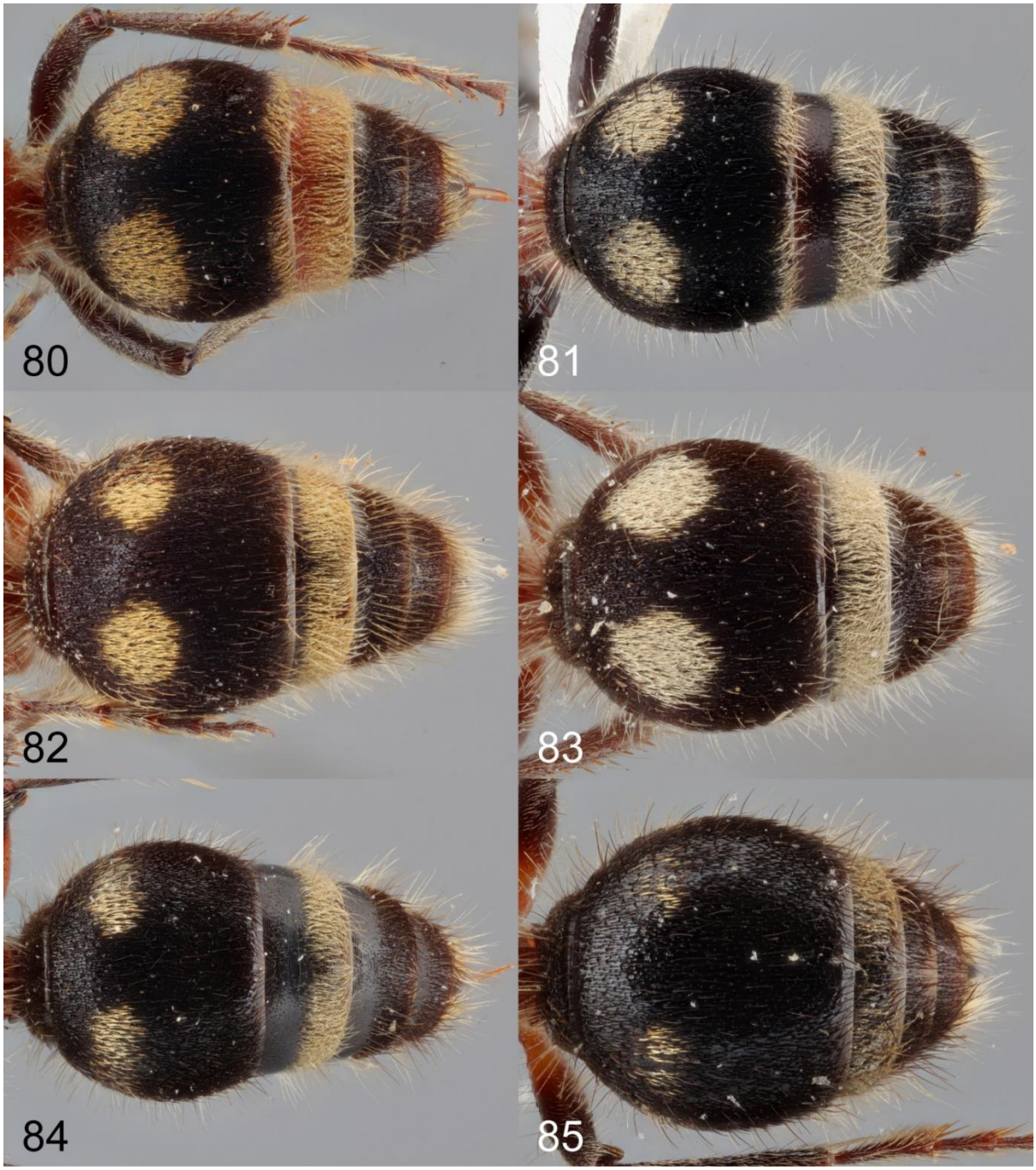


Figures 62–69. *Neotrogaspidia* spp., ♂, genitalia. 62, 63. *N. circumcincta* (André); 64, 65. *N. elpinice* (Mickel); 66, 67. *N. pustulata* (Smith); 68, 69. *N. recticarinata* (Chen), paratype; 62, 64, 66, 68. genital capsule, inner view; 63, 65, 67, 69. right (upper) and left (lower) penis valves.



Figures 70–73. Trogaspidiini spp., ♂, genitalia. 70–72. *Neotrogaspidia pustulata* (Smith); 73. *Trogaspidia fuscipennis* (Fabricius); 70. endophallus, dorsal view; 71. endophallus, ventral view; 72. endophallus, lateral view; 73. penis valves and endophallus.

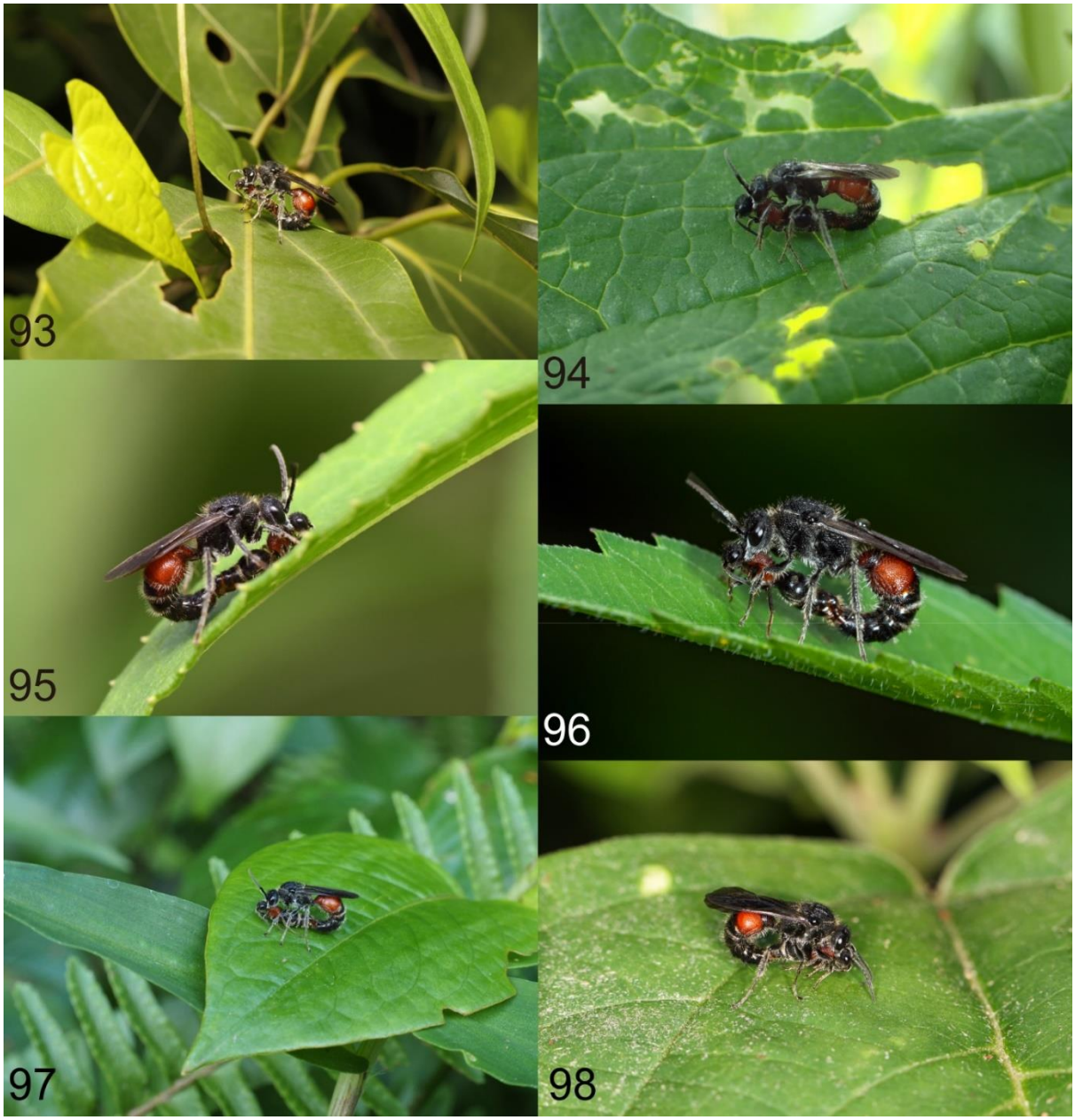
Figures 74–79. *Neotrogaspidia* spp., ♀, head and metasoma. 74, 77. *N. circumcincta* (André); 75, 78. *N. elpinice* (Mickel); 76, 79. *N. pustulata* (Smith); 74–76. face; 77–79. pygidial plate.



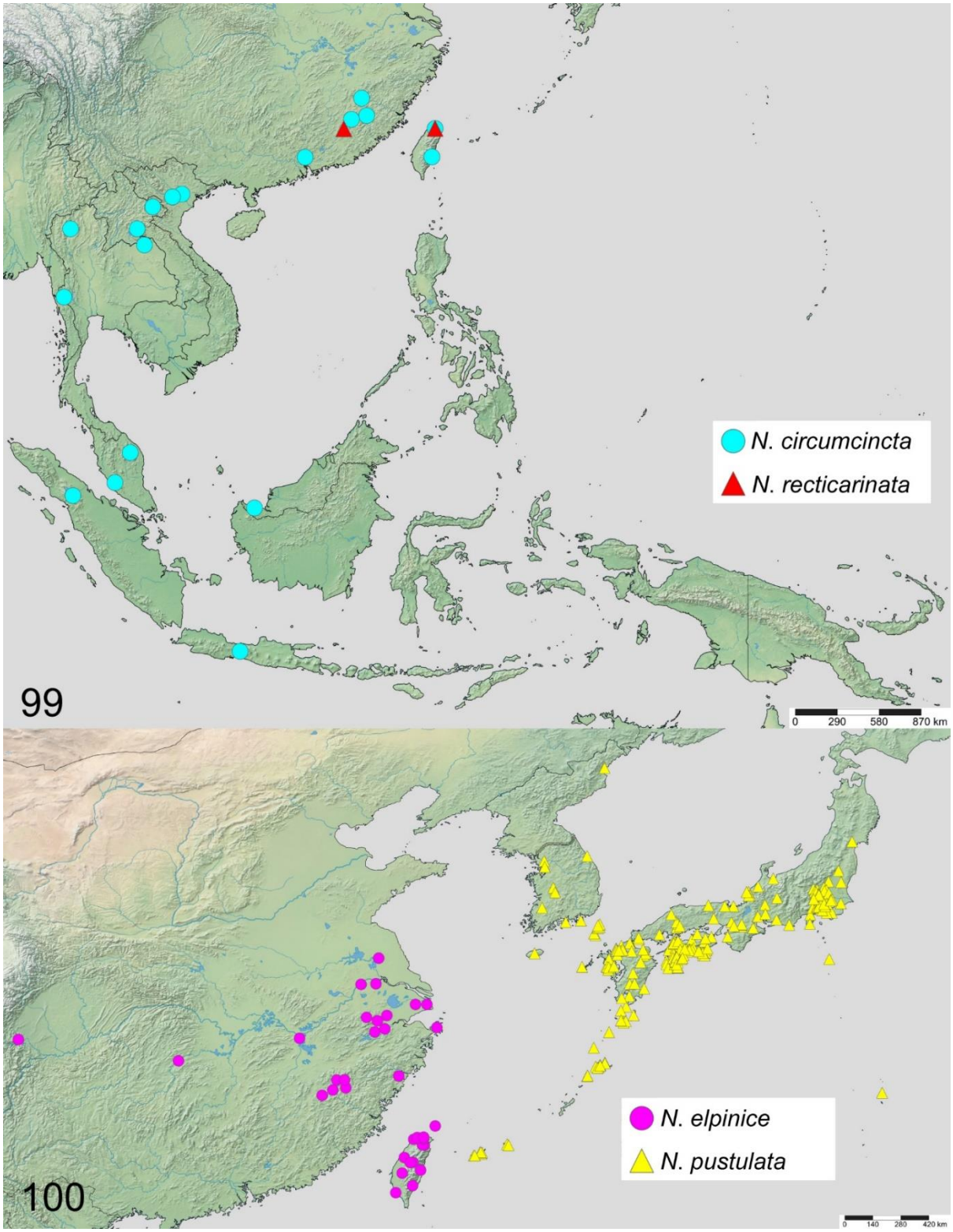
Figures 80–85. *Neotrogaspidia* spp., ♀, metasoma, dorsal view. 80. *N. circumcincta* (André) with segment 3 red; 81. *N. circumcincta* (André) with segment 3 black; 82. *N. elpinice* (Mickel), China; 83. *N. elpinice* (Mickel), Taiwan; 84. *N. pustulata* (Smith), Japan; 85. *N. pustulata* (Smith), South Korea.

Figures 86–91. *Neotrogaspidia pustulata* (Smith), ♀ in a nest aggregation of *Dasypoda japonica* Cockerell. 86–89. A living female of *N. pustulata*; 90, 91. nest aggregation of *D. japonica*. Photographs by Rikio Matsumoto.

Figure 92. *Neotrogaspidia pustulata* (Smith), ♂♀ *in copula* (NSMT).



Figures 93–98. *Neotrogaspidia pustulata* (Smith), ♂♀ *in copula*. 93. Photograph by Toru Kawabe; 94. photograph by Toshiharu Mita; 95. photograph by Tomohiro Nagata; 96. photograph by Akira Ozono; 97. photograph by Noriyoshi Shimura; 98. photograph by Takuro Tsukiji from Mushi Navi (https://mushinavi.com).



Figures 99–100. Distributional maps of *Neotrogaspidia* spp. based on specimens examined and previous works. 99. Distribution of *N. circumcincta* (André) (blue circle) and *N. recticarinata* (Chen) (red triangle); 100. distribution of *N. elpinice* (Mickel) (purple circle) and *N. pustulata* (Smith) (yellow triangle).

Chapter 6

New data on female velvet ants of the genus *Mickelomyrme* Lelej (Hymenoptera: Mutillidae: Smicromyrmini)

Disclaimer: *This work is not issued for the purposes of zoological nomenclature and is not considered a published work within the meaning of the International Code of Zoological Nomenclature 4th edition (Article 8.2).*

Abstract
New data on the taxonomy of *Mickelomyrme* Lelej, 1995 are presented. *Mickelomyrme autonoe* (Mickel, 1934), **comb. nov.** is transferred from *Smicromyrme* Thomson, 1870. New synonymies are proposed for *M. athalia* (Pagden, 1949) (= *S. bicristata* Chen, 1957, **syn. nov.**) and *M. zebina* (Smith, 1860) (= *S. aborlana aborlana* Tsuneki, 1993, **syn. nov.** and *S. aborlana zamboangae* Tsuneki, 1993, **syn. nov.**) The female of *M. semperi semperi* (Ashmead, 1904) sensu Lelej (1996) is described as *M. verticalis* **sp. nov.** (Philippines). Two additional new species, *M. grandiguttata* **sp. nov.** (♀) from Laos and *M. vietnaminix* **sp. nov.** (♀) from Vietnam are described. New distributional records include *M. athalia* from Sarawak, Malaysia and *M. s. semperi* from Bohol, Philippines.

Key words
Aculeata, distribution, Oriental Region. Southeast Asia, taxonomy, velvet ants.

Introduction

Velvet ant fauna of the eastern Oriental Region, especially continental countries, are still poorly understood (Okayasu *et al*., 2021; Williams *et al*., 2019). There remain large gaps in the number of recorded species among countries (Pagliano *et al*., 2020). Furthermore, many species are included in older keys only or known from the original descriptions, so available information for identifying named species is very limited. The genus *Mickelomyrme* Lelej, 1995 currently includes 23 species and two subspecies distributed throughout the eastern Palaearctic and Oriental Regions (Lelej, 2005; Thaochan *et al*., 2022; Williams *et al*., 2019). The species of this genus are generally small-sized and are abundant in Southeast Asia (Williams *et al*., 2019). This genus was reviewed by Lelej (1996b), but additional new species and synonyms may be found because of the small body size and high morphological diversity and variability in *Mickelomyrme* species. The aim of this chapter is to provide new data on *Mickelomyrme* through examination of museum specimens collected in Southeast Asia, including Chen's (1957) voucher specimens.

Material and methods

The following abbreviations are used for institutes housing the types and material discussed in this paper.

EUMJ Ehime University Museum, Matsuyama, Japan.
IEBR Institute of Ecology and Biological Resources, Vietnam Academy of Science and Technology, Hanoi, Vietnam.
KUM Kyushu University Museum, Fukuoka, Japan.
NARO Insect Museum, National Agriculture and Food Research Organization, Tsukuba, Japan (former Institute for Agro-Environmental Sciences).

NHMUK The Natural History Museum, London, UK.
NMNH National Museum of Natural History, Smithsonian Institution, Washington D.C., USA.
NSMT National Museum of Nature and Science, Tsukuba, Japan.
OUMNH Oxford University Museum of Natural History, Oxford, UK.
SEHU Hokkaido University Insect Collection, Sapporo, Japan.
SKYC Seiki Yamane Collection in Kagoshima University, Kagoshima, Japan.
TARI Taiwan Agricultural Research Institute, Taichung, Taiwan.
THNHM Thailand Natural History Museum, National Science Museum, Pathum Thani, Thailand.
TUA Laboratory of Entomology, Tokyo University of Agriculture, Atsugi, Japan.
ZMUC Zoological Museum, University of Copenhagen, Universitetsparken, Denmark.

Specimens were observed under a Leica M205C stereomicroscope (7.8–160× magnification). Habitus photographs were taken using a Canon EOS 6D Mark II digital camera equipped with a Canon MP-E 65mm f/2.8 1–5× Macro Photo lens. External morphological features were imaged with a Canon EOS 6D Mark II attached to a Leica M205C. Focus stacking was done using Zerene Stacker (Zerene Systems LLC, Richland, WA, USA). Photo processing was done using Adobe Photoshop and Adobe Illustrator. Terminology mostly follows Hymenoptera Anatomy Consortium (2024). Measurement methods follow Bartholomay *et al*. (2019) and Okayasu (2020). The antennal flagellomeres, metasomal terga and sterna are abbreviated as F, T and S, respectively. In the synonymic lists and material examined sections, abbreviations for depository and additional or corrected data by the author are given in square brackets. New records are asterisked (*).

Taxonomy

Mickelomyrme athalia (Pagden, 1949)

(Figs 1–6)

Smicromyrme athalia Pagden, 1949: 219, ♂♀, holotype ♂ (Kuala Lumpur, Federated Malay States [= Malaysia]) [NHMUK].
Smicromyrme bicristata Chen, 1957, **syn. nov.**: 211, ♀, holotype ♀ (Ryosui [= Lingshui], Hainan, China) [TARI], examined.
Mickelomyrme athalia: Lelej, 1995: 17; Lelej 1996b: 280, ♂♀; Lelej, 2005: 43; Okayasu *et al*., 2018: 303, ♀; Williams *et al*., 2019: 18, ♂♀, examined; Okayasu, 2020: 44, ♂; Pagliano *et al*., 2020: 174.
Mickelomyrme bicristata: Lelej, 1996b: 284, ♀; Lelej, 2005: 43; Hua, 2006: 300; Lo Cascio, 2015: 551; Okayasu *et al*., 2018: 303, ♀; Williams *et al*., 2019: 18; Okayasu, 2020: 44; Pagliano *et al*., 2020: 174.
Mickelomyrme hageni (non Zavattari, 1913): Barthélémy *et al*., 2018: 235, ♂.

Diagnosis
FEMALE. Head color variable; vertex and gena punctures dense but separated; antenna black with scape and some basal flagellomeres orange to reddish brown; mesosoma red, sometimes with black spot on lateral face; pronotal dorsum with lateral white setal patch; metanotum and propodeum lacking pale setal patch; posterior propodeal face vertical; legs reddish brown with femoral and tibial apices dark brown; T2 length 0.98–1.00× width; T2 with two or three transversely aligned pale setal spots, separated by approximate medial spot diameter; T2 medial spot, when present, more yellow-tinted than lateral spot and located on black cuticle;

T2 disc flat, with small sparse punctures; T2 lateral margin with dense but separated punctures; T2 posterior margin with black setae; T4–5 with black recumbent and pale golden erect setae, T4 often with appressed pale golden setae laterally; pygidial plate slender with lateral margins subparallel; pygidial striae short, leaving posterior portion smooth. MALE. See Lelej (1996b).

Material examined

Holotype ♀, *Smicromyrme bicristata* Chen: **China:** HAINAN: Ryosui [= Lingshui], 10.XI.1942, Miwa & Mitono leg. [TARI]. Paratype, *Smicromyrme bicristata* Chen: **China:** HAINAN: Kaikô [= Haikou], IX.1942, Miwa & Mitono leg. [1♀ TARI]. **Malaysia:** KUALA LUMPUR: Spooner Road, 1.IV.1940, H.T. Pagden leg., *Smicromyrme athalia* Pagden, B. Petersen det. 1989 [1♀ ZMUC]; PAHANG: Kuala Tahan, 12.IV.1940, M. W.F. Tweedie leg., *Smicromyrme athalia* Pagden, B. Petersen det. 1989 [1♀ ZMUC]; SARAWAK: Kuching, K. Ast[ana]., 1–4, IX-8-'66 [1♀ SEHU]. **Thailand:** CHIANG MAI: Omkoi, Dry dipterocarp forest, 17°50′49.9″N 98°22′33.0″E, 950–1010 m alt., 23.VI.2017, R. Mizuno leg. [1♀ THNHM], 24.VI.2017 [1♀ THNHM], 7.VII.2017 [1♀ THNHM], 9.VIII.2017 [1♀ THNHM], 13.VIII.2022 [1♀ THNHM]. **Vietnam:** BA RIA VUNG TAU: Binh Chau, Xuyen Moc, 4.I.2002, K. Okajima leg. [3♀ TUA]; Binh Chau, Xuyen Moc, 4.I.2002, S. Okajima leg. [1♀ TUA], 5.I.2002 [7♀ TUA]; Binh Chau, Xuyen Moc, 5.I.2002, T. Ishikawa leg. [3♀ TUA]; Binh Chau, Xuyen Moc, 5.I.2002, H. Mizushima leg. [2♀ TUA].

Distribution

China: Fujian, Guangdong, Hainan, Hong Kong, Yunnan (Barthélémy *et al*., 2018; Okayasu, 2020). Laos (Lelej, 2005). Malaysia: Kuala Lumpur, Negeri Sembilan, Pahang, Penang, Sarawak*, Selangor (Okayasu, 2020; Pagden, 1949; Williams *et al*., 2019). Thailand: Chiang Mai, Kanchanaburi, Khonkaen, Krabi, Nakhon Nayok, Nakhon Si Thammarat, Phatthalung, Songkhla, Surat Thani, Trang (Williams *et al*., 2019). Vietnam: Ba Ria Vung Tau, Hoa Binh (Okayasu, 2020).

Remarks

The synonymy of *M. bicristata* with *M. athalia* was initially suggested by Williams *et al*. (2019) and confirmed here. Lelej (1996b) compared these two species and distinguished *M. bicristata* from *M. athalia* by the anterolateral pale setal patch on the pronotum (at most with small "wedge" of pale setae in *M. athalia*). Williams *et al*. (2019) examined a series of 46 females of *M. athalia* collected in Malaysia and Thailand. They found that the key feature recognized by Lelej (1996b) was inadequate to separate them because the pronotal setal patch is variable in intensity and *M. athalia* frequently has such patches too. They included the more yellow-tinted medial T2 spot as an additional diagnostic feature of *M. athalia*, while *M. bicristata* had the lateral and medial T2 spots concolorous according to the original description (Chen, 1957). However, type specimens of *M. bicristata* have the lateral spots little paler than the medial one (Figs 1, 5). This species is therefore synonymized with *M. athalia* here.

Mickelomyrme autonoe (Mickel, 1934), comb. nov.

Smicromyrme autonoe Mickel, 1934: 208, ♀, holotype ♀ (Puerto Princesa, Palawan, Philippines) [NMNH]; Mickel, 1935: 293, ♀; Lelej, 2005: 56; Lo Cascio, 2015: 558; Okayasu *et al*., 2018: 304, ♀; Pagliano *et al*., 2020:192, ♀.

Diagnosis

FEMALE. Head black; vertex and gena punctures dense but separated; antenna black; mesosoma red; pronotal dorsum, metanotum, and propodeum lacking pale setal patch; posterior propodeal face vertical; legs black; T2 length approximately equal to T2 width; T2 with three transversely aligned pale setal spots, separated by approximate medial spot diameter; T2 medial spot concolorous with lateral spot and located on black cuticle; T2 disc flat, with small confluent punctures; T2 lateral margin with dense but separated punctures;T2 posterior margin with narrow pale golden setal band; T4–5 with black recumbent and pale golden erect setae; pygidial striae short, leaving posterior portion smooth. MALE. Unknown.

Material examined
Holotype ♀: **Philippines:** PALAWAN: Palawan, P. Princesa, Baker [NMNH].

Distribution
Philippines: Palawan (Mickel, 1934).

Remarks
Photos of the holotype of this species are available from: http://n2t.net/ark:/65665/3f6d85b6e-2430-4b3d-937d-00d25193991b (accessed 13 February 2024). This species has the T2 spots disposed in a horizontal line, which is the key feature to separate *Mickelomyrme* from *Smicromyrme*.

***Mickelomyrme grandiguttata* sp. nov.**
(Figs 7, 8, 11, 17–19)

Diagnosis
FEMALE. Head black with vertex or both frons and vertex largely with reddish brown; vertex and gena punctures confluent; antenna dark brown to black; mesosoma red; pronotal dorsum, metanotum, and propodeum lacking pale setal patch; posterior propodeal face vertical; legs brown to black; T2 length 0.83–0.88× width; T2 with three transversely aligned pale setal spots, separated by 0.157–0.188× medial spot diameter; T2 medial spot concolorous with lateral spot and located on black cuticle; T2 disc flat, with intermixed small sparse and minute dense punctures; T2 lateral margin with dense but separated punctures; T2 posterior margin with black setae; T4 with wide complete golden setal band; T5 with black recumbent and golden erect setae; pygidial plate slender with lateral margins subparallel; pygidial striae short, leaving posterior portion smooth. MALE. Unknown.

Description
FEMALE. Body length: 7.65–8.05 mm (holotype: 7.65 mm).

Color and setae. Frons dark brown to reddish brown; gena, mandible apical 1/3, flagellum dorsally, meso- and metalegs mostly, T2 mostly, T3–6, and S2–6 black; vertex, antennal rim, mandible basal 2/3, and meso- and metacoxae reddish brown; postgenal bridge, clypeus, scape, pedicel, flagellum ventrally, proleg, and trochanters dark brown; mesosoma, T1, S1, and T2 below pale setal spots yellowish red; mesofemur, meso- and metatibiae basal halves, and metafemur basal 2/3 brown; tibial spurs pale yellow. Frons and vertex with sparse short appressed and sparse short erect golden setae; gena, clypeus, and S2 with sparse long recumbent pale golden setae; postgenal bridge with sparse short erect pale golden setae; antennal scrobe with sparse short appressed golden setae; mandible, propleuron, posterior propodeal face, T1, T2 lateral margin, T3–4, T6, S1, and S3–6 with sparse long erect pale golden setae; scape with sparse long recumbent and sparse short erect golden setae; pedicel and F1 with sparse short recumbent setae; F2–10 with dense erect pale golden microsetae;

thoracic dorsum with sparse short recumbent and sparse long erect golden setae; lateral pronotal face, dorsal halves of meso- and metapleura, and lateral propodeal face with sparse short appressed pale golden setae; ventral halves of meso- and metapleura with dense long appressed golden setae; T2 disc with dense short recumbent and sparse short erect black setae; T5 with sparse short recumbent black and sparse long erect pale golden setae; T1 and S2–S6 with posterior fringe of sparse long golden setae; T2 with three broad, oval spots of dense appressed golden setae, aligned transversely; distance between medial and lateral spots 0.157–0.188× (holotype: 0.157) medial spot width; distance between medial spot and T2 posterior margin 0.40–0.54× (holotype: 0.40) medial spot length; T2 posterior margin medially with posterior fringe of sparse long golden setae; T2 with golden lateral felt line; T3–4 with wide complete band of dense appressed golden setae; T6 with lateral pygidial fringe of golden setae.

Structure. Head width 1.49–1.58× (holotype 1.49) length; gena wide, 0.96–1.08× (holotype 0.96) eye breadth in lateral view; frons and vertex without medial carina or groove; occipital carina complete; genal carina and hypostomal absent; postgenal bridge flat; dorsal scrobal carina wavy, extending nearly to inner eye margin; eye oval, slightly protruding from head capsule; minimum distance between eyes 1.04–1.09× (holotype 1.09) eye height; eye height 1.91–2.02× (holotype 1.91) malar distance; clypeus with subventral transverse ridge and medial longitudinal ridge apically not terminating as tubercle; anterior margin of transverse ridge medially weakly emarginate; apex of medial longitudinal tubercle reaching anterior margin of transverse ridge; mandible slender without inner tooth; mandibular ventral margin straight; prementum flat without medial carina or tubercle; scape bending medially; length and width of pedicel:F1:F2 = 1.00:0.93–1.10:1.79–2.20:1.50:1.57–1.60:1.43–1.50 (holotype 1.00:1.10:2.20:1.50:1.60:1.50); F2–F9 almost same in length and width; F10 as long as F1, conical.

Mesosoma broadest at pronotum; lateral margins subparallel, weakly crenulate; head width:humeral width:pronotal width:mesonotal width:propodeal width:metasomal width = 100:83:89–92:80–81:86–88:127–128 (holotype 100:83:89:80:86:127); dorsal thoracic length 0.95–0.96× (holotype 0.96) pronotal width; anterior margin of pronotal dorsum arcuate, without tooth or tubercle; pronotum laterally projecting; humeral angle rounded without humeral carina; metanotum with prescutellar row of pointed tubercles; scutellar scale laterally without scales; scutellar scale moderately elevated, rounded; scutellar scale width 0.93–3.00× its length, 0.12–0.20× propodeal width, 2.0–4.5× puncture diameter; metanoto-propodeal suture indistinct; postero-lateral margin of propodeum without tubercles; posterior propodeal face oblique.

Metacoxa with weak inner longitudinal carina; meso- and metatibiae with two longitudinal rows of spines on outer face; protarsus with external comb of long spines.

T1 subsessile, without distinct dorsum; T2 dorsally flat; dorsal T2 length 0.83–0.88× (holotype 0.88) T2 width; S1 with medial longitudinal carina on anterior 2/3, its ventral margin straight; S2 evenly convex, without anteromedial carina; S6 posterior margin bidentate; pygidial plate flat, slender, elongate; lateral margins of pygidial plate delimited by sharp longitudinal carinae throughout, subparallel.

Upper frons with large dense punctures; lower frons and thoracic dorsum with large confluent punctures; vertex and gena with small confluent punctures; postgenal bridge transversely rugose; clypeus except medial ridge, propleuron, lateral pronotal face, meso- and metapleuron, lateral propodeal face, and T1 antero-medial portion with minute sparse punctures; clypeal medial ridge with small confluent punctures; scape, femora, tibiae, and tarsi with small sparse punctures; pedicel, flagellum, prementum, stipes, and S1 with minute dense punctures; posterior propodeal face reticulate; ventral half of mesopleuron with vertical row of small punctures; coxae, trochanters, and T2 disc with small sparse and minute dense

punctures; T1 mostly, T2 lateral margin, T3–5, T6 laterally, and S3–6 with small dense punctures; S2 with large sparse punctures; pygidial plate densely striate on anterior 2/3, with 12–13 striae diverging posteriorly, leaving medial and posterior portions smooth.

MALE. Unknown.

Type material

Holotype ♀: **Laos:** XIENG KHOUANG: Phou Samsoum, 2200 m alt., 22.IV.2007, M. Sato leg. [EUMJ]. Paratype: **Laos:** HUA PHAN: Mt. Phu Pane, 900–1600 m, 20°12′N 100°59′E, 10–21.VI.2010, St. Jaki and Lao collectors leg. [1♀ KUM]; XIENG KHOUANG: Phou Samsoum, 2200 m alt., 22.IV.2007, M. Sato leg. [1♀ EUMJ].

Distribution

Laos: Hua Phan, Xieng Khouang.

Etymology

The specific name *grandiguttata* is the combination of the Latin adjective *grandis*, large, and the Latin feminine adjective *guttata*, spotted, in the nominative case. It refers to the enlarged T2 spots of this new species.

Remarks

The paratype from Phou Samsoum lacks the head, prolegs, and right mesoleg except coxa. The dorsal face of mesosoma and T1 of this specimen are densely covered with dirt. This, together with the presence of protarsal rake and flattened pygidial plate, suggests utilization of hosts in soil.

This new species is similar to the female of *M. athalia*, *M. kinguri* Williams, 2019, *M. kuznetsovi*, *M. puttasoki* Williams, 2019, *M. semperi semperi*, *M. zebina*, and *M. vietnaminix* **sp. nov.** by having the T2 posterior margin with black setae and T4 with pale setal band, but differs by having the head black with medially reddish vertex (head uniformly red in *M. kinguri*), vertex with confluent punctures (dense but separated in *M. kinguri*, *M. puttasoki*, and *M. vietnaminix* **sp. nov.**), antenna mostly black (largely or entirely reddish yellow in *M. puttasoki* and *M. vietnaminix* **sp. nov.**), mesosoma without setal patches (with white setal patch on pronotum in *M. athalia*, *M. kinguri* and *M. puttasoki*, on pronotum and propodeum in *M. vietnaminix* **sp. nov.**), pronotum uniformly yellowish red (with anteromedial black spot in *M. kinguri* and *M. puttasoki*), legs black (largely reddish yellow in *M. kinguri*, *M. puttasoki* and *M. vietnaminix* **sp. nov.**), T2 wider than long (T2 longer than wide in *M. semperi semperi*), T2 spots larger, separated by ~0.188 × medial spot diameter (smaller and separated by approximate spot diameter in others except *M. kinguri*), T2 medial and lateral spots concolorous (medial spot more yellow-tinted in *M. athalia*, *M. kinguri*, *M. kuznetsovi* and *M. puttasoki*), T2 medial spot subcircular (elongate oval in *M. kinguri* and *M. vietnaminix* **sp. nov.**), T2 disc evenly convex (medially depressed in *M. s. semperi*), T2 disc with small sparse punctures interspaced with minute dense punctures (T2 with small dense to confluent punctures only, with intervals impunctate in others), pygidial plate slender with lateral margins subparallel (broad and triangular in *M. puttasoki*), and striae on pygidial plate reaching posterior 1/4 (many striae reaching posterior margin in *M. kinguri* and *M. puttasoki*).

***Mickelomyrme semperi semperi* (Ashmead, 1904)**

(Figs 24, 25, 28, 29)

Mutilla semperi Ashmead, 1904: 135, ♂, holotype ♂ (Manila, [Luzon, Philippines]) [NMNH]; Brown, 1906: 689.

Smicromyrme semperi semperi: Mickel, 1934: 210, ♂♀; Mickel, 1935: 291, ♂♀; Baltazar, 1966: 210; Tsuneki *et al*., 1993: 13, ♂.
Mickelomyrme semperi semperi: Lelej, 1996b: 284, ♂; Lelej, 2005: 44; Lo Cascio, 2015: 551; Okayasu, 2020: 44; Pagliano *et al*., 2020: 175.
Mickelomyrme semperi: Pagliano, 2011: 41, ♂.

Diagnosis
FEMALE. Head black; vertex punctures confluent; gena punctures dense but separated; antenna black; mesosoma red; pronotal dorsum, metanotum, and propodeum lacking pale setal patch; posterior propodeal face oblique; legs black; T2 length 1.10× width; T2 with three transversely aligned pale setal spots, separated by approximate medial spot diameter; T2 medial spot concolorous with lateral spot and located on black cuticle; T2 disc anteriorly concave, with small confluent punctures; T2 lateral margin with dense but separated punctures; T2 posterior margin with black setae; T4–5 with black recumbent and pale golden erect setae; pygidial plate slender with lateral margins subparallel; pygidial striae short, leaving posterior portion smooth. MALE. See Lelej (1996b).

Material examined
Philippines: BOHOL: Bilar, 23.VII.1970, T. Okadome leg., *Smicromyrme semperi semperi* Mick. [probably Petersen's hand] [1♂1♀ TUA]; LUZON: Bacnotan, 18–19.III.1974, S. Ueda leg., *Smicromyrme semperi semperi* Mick. [probably Petersen's hand] [1♂ TUA].

Distribution
Philippines: Bohol*, Luzon, Negros, Panay (Ashmead, 1904; Mickel, 1934).

Remarks
Lelej (1996b) recognized *M. s. semperi* as having a pale setal band on T4. However, Mickel's (1934) description of the female of *M. s. semperi* states that this species has the T4 clothed with black setae. The female specimen examined in this study, which was collected with one male at same place and time, supports Mickel's identification. *Mickelomyrme s. semperi* sensu Lelej (1996b) is described as new below.

Mickelomyrme verticalis **sp. nov.**
(Figs 26, 27, 30, 31)

Mickelomyrme semperi semperi (non Ashmead, 1904): Lelej, 1996b: 284, ♀.

Diagnosis
FEMALE. Head black; vertex and gena punctures confluent; antenna black; mesosoma red; pronotal dorsum, metanotum, and propodeum lacking pale setal patch; posterior propodeal face vertical; legs black; T2 length 0.95× width; T2 with three transversely aligned pale setal spots, separated by approximate medial spot diameter; T2 medial spot concolorous with lateral spot and located on black cuticle; T2 disc anteriorly concave, with small confluent punctures; T2 lateral margin with confluent punctures; T2 posterior margin with pale golden setal fringe medially; T4 with wide complete pale golden setal band; T5 with black recumbent and pale golden erect setae; pygidial plate slender with lateral margins subparallel; pygidial striae short, leaving posterior portion smooth. MALE. Unknown.

Description
FEMALE. Body length: 5.92 mm.

Color and setae. Frons, vertex, gena, postgenal bridge, clypeus, mandible apical 1/2, flagellum, prementum, stipes, T1–6, S2, and S6 black; antennal rim, mandible basal 1/2, and S3–5 brown; scape and pedicel dark brown; mesosoma and S1 yellowish red; legs brownish black. Frons with sparse long recumbent pale golden and sparse long erect blackish golden setae; vertex with sparse long appressed golden and sparse long erect blackish golden setae; gena with sparse long recumbent pale golden setae; antennal scrobe with sparse long appressed golden setae; clypeus with sparse long erect golden setae; scape with sparse long recumbent golden setae; pedicel and flagellum with dense erect golden microsetae; pronotal collar with sparse short recumbent pale golden setae; thoracic dorsum except pronotum and T2 disc with sparse short recumbent and sparse long erect black setae; pronotal dorsum and S2 with sparse short recumbent and sparse long erect pale golden setae; propleuron, mesopleuron anterior 1/2, posterior propodeal face, T1, T2 lateral margin, T3–4, S1, and S3–6 with sparse long erect pale golden setae; lateral pronotal face, mesopleuron posterior 1/2, and metapleuron with sparse short appressed pale golden setae; lateral propodeal face with sparse short appressed and sparse long erect pale golden setae; coxae, trochanters, femora, and tibiae with sparse long recumbent and sparse long erect pale golden setae; tarsi with sparse long appressed pale golden setae; T5 with sparse short recumbent black and sparse long erect pale golden setae; T2 with three subcircular spots of dense appressed pale golden setae, lateral spots located slightly posteriorly to medial one; distance between medial and lateral spots 0.81× medial spot width; distance between medial spot and T2 posterior margin 1.19× medial spot length; T2 posterior margin medially with small triangular patch of golden setae; T2 with golden lateral felt line; T3 and T4 with wide complete band of dense appressed pale golden setae reaching lateral margin of terga; S2–S6 with posterior sparse fringe of pale golden setae; T6 with lateral pygidial fringe of pale golden setae.

Structure. Head width 1.45× length; gena wide, 0.76× eye breadth in lateral view; frons and vertex without medial carina or groove; occipital carina complete; genal carina and hypostomal absent; postgenal bridge flat; dorsal scrobal carina obliterated; eye oval, slightly protruding from head capsule; minimum distance between eyes 1.09× eye height; eye height 2.2× malar distance; clypeus with subventral transverse ridge and medial longitudinal ridge apically not terminating as tubercle; anterior margin of transverse ridge medially incised; apex of medial longitudinal tubercle reaching anterior margin of transverse ridge; mandible slender without inner tooth; mandibular ventral margin straight; prementum flat without medial carina or tubercle; scape bending medially; length and width of pedicel:F1:F2 = 1.00:1.00:1.50:1.30:1.40:1.50; F2–F9 almost same in length and width; F10 as long as F1, conical.

Mesosoma broadest at pronotum; lateral margins subparallel, weakly crenulate; head width:humeral width:pronotal width:mesonotal width:propodeal width:metasomal width = 100:73:82;73:78:115; dorsal thoracic length 1.03× pronotal width; anterior margin of pronotal dorsum arcuate, without tooth or tubercle; pronotum laterally slightly projecting; humeral angle rounded with weak vertical humeral carina; metanotum with prescutellar row of scales; scutellar scale laterally with few scales; scutellar scale moderately elevated, wide; scutellar scale width 1.67× its length, 0.18× propodeal width, 5.00× puncture diameter; metanoto-propodeal suture indistinct; postero-lateral margin of propodeum with few tubercles dorsally; posterior propodeal face vertical.

Metacoxa with weak inner longitudinal carina; meso- and metatibiae with two longitudinal rows of spines on outer face; protarsus with external comb of long spines.

T1 subsessile, without distinct dorsum; T2 medially longitudinally concave; dorsal T2 length 0.95× T2 width; S1 with medial longitudinal carina on anterior 2/3, its ventral margin straight; S2 with weak anteromedial longitudinal carina; S6 posterior margin bidentate; pygidial plate flat, slender, elongate; lateral margins of pygidial plate delimited by sharp

longitudinal carinae throughout, subparallel.

Frons, vertex, gena, thoracic dorsum, T2 disc, and T2 posterolateral portion with small confluent punctures; clypeus, propleuron, lateral pronotal face, metapleuron, trochanters, femora, tibiae, tarsi, T1 except posterior margin, and S3–5 with minute sparse punctures; prementum, stipes, pedicel, flagellum, coxae, T3–5, T6 laterally, S1, and S6 with minute dense punctures; scape with small sparse punctures; posterior propodeal face reticulate; mesopleuron and lateral propodeal face with minute sparse punctures and few small punctures; T1 posterior margin and T2 anterolateral portion with small dense punctures; S2 with large dense punctures; pygidial plate sparsely striate on anterior 3/4, with 14 striae and smooth posteriorly.

MALE. Unknown.

Type material
Holotype ♀: **Philippines:** LUZON: Bacnotan, 18–19.III.1974, S. Ueda leg. [TUA].

Distribution
Philippines: Luzon.

Etymology
The specific name *verticalis*, vertical, is the Latin feminine adjective in the nominative case. It refers to the vertical posterior propodeal face that distinguishes this new species from *M. semperi*.

Remarks
Mickelomyrme verticalis **sp. nov.** matches the diagnostic character sates of *M. s. semperi* included in Lelej's (1996b) key. This new species differs from the latter by having the gena with confluent punctures (dense but separated in *M. s. semperi*), posterior propodeal face vertical (oblique in *M. s. semperi*), T2 length 0.95× width (1.1 in *M. s. semperi*), T2 posterior margin with a pale golden setal fringe medially (with black setae in *M. s. semperi*), T2 punctures small confluent even laterally (confluent on T2 disc, separated on lateral margin in *M. s. semperi*), and T4 with a wide pale band of setae (with black recumbent and pale golden erect setae in *M. s. semperi*).

Mickelomyrme s. nigrogastra (Mickel, 1934) was described from Luzon and later recorded from Palawan by Tsuneki *et al*. (1993). This subspecies may be the male of *M. verticalis* **sp. nov.** based on the morphological similarity to *M. s. semperi* in both sexes. However, there is no direct evidence to associate them.

Mickelomyrme vietnaminix **sp. nov.**

(Figs 9, 10, 12, 20, 21)

Diagnosis
FEMALE. Head black with vertex dark reddish brown; vertex punctures sparse; gena punctures dense but separated; antenna reddish yellow; mesosoma red; pronotal dorsum, metanotum, and propodeum with lateral white setal patch; posterior propodeal face vertical; legs reddish yellow with femoral and tibial apices brown; T2 length 0.94–0.97× width; T2 with three transversely aligned pale setal spots, separated by 1.32–1.88× medial spot diameter; T2 medial spot concolorous lateral spot and located on orange-brown cuticle; T2 disc evenly convex, with small dense but separated punctures; T2 lateral margin with sparse punctures; T2 posterior margin with black setae; T4 with wide complete white setal band; T5 medially with sparse long erect dark golden setae and laterally with sparse long appressed

and sparse long erect white setae; pygidial plate narrow triangular with lateral margins convergent posteriorly; pygidial striae short, leaving posterior portion smooth. MALE. Unknown.

Description

FEMALE. Body length: 3.37–4.93 mm (holotype 4.93 mm; mean 4.22 mm).

Color and setae. Upper frons and gena dark brown to black; lower frons above antennal rim reddish brown; vertex and clypeus dark reddish brown; antennal rim, mandible basal 2/3, antenna, and legs except tibial apices reddish yellow; antennal scrobe dark reddish brown to black; postgenal bridge yellowish brown to dark reddish brown; mandible apical 1/3, T2 mostly, T3–6, and S2–6 black; mesosoma and T1 yellowish red; tibial apices brown; tibial spurs yellow; S1 dark brown; T2 below setal spots orange-brown; rarely T2 largely brownish on anterior half. Frons with sparse short recumbent black and sparse long erect dark golden setae; vertex with sparse short recumbent golden and sparse long erect dark golden setae; gena, tarsi, and S2 with sparse long recumbent white setae; postgenal bridge glabrous; antennal scrobe with sparse long appressed pale golden setae; clypeus with sparse long erect golden setae; mandible, T2 lateral margin, and T6 with sparse long erect pale golden setae; scape and coxae with sparse long recumbent white setae; pedicel and lateral pronotal face with sparse short recumbent white setae; flagellum with dense erect white microsetae; pronotal collar with sparse short erect pale golden setae; thoracic dorsum, propleuron, femora, and tibiae with sparse short recumbent and sparse long erect white setae; posterior and lateral propodeal faces, T1, T3–4 lateral margins, S1, and S3–6 with sparse long erect white setae; meso- and metapleura dorsal half with sparse appressed white microsetae; meso- and metapleura ventral halves with long dense appressed white setae; trochanters with sparse short erect white setae; T2 disc with sparse short recumbent black and sparse long erect pale golden setae; T3–5 medially with sparse long erect dark golden setae; T5 lateral margin with sparse long appressed and sparse long erect white setae; pronotum with lateral patch of dense appressed white setae; metanotum with lateral obscurely defined patch of appressed white setae; propodeum with lateral patch of sparse to dense appressed white setae; T2 with anteromedial, elongate, oval spot of dense appressed white setae and lateral oval spots of dense appressed white setae located slightly posteriorly to medial one; distance between medial and lateral spots 1.32–1.88× (holotype 1.32; mean 1.52) medial spot width; distance between medial spot and T2 posterior margin 1.20–1.35× (holotype: 1.20; mean 1.28) medial spot length; T3–4 with wide band of dense appressed white setae not reaching lateral margin of terga, medially interrupted by black setae; S2–6 with posterior sparse fringe of white setae.

Structure. Head width 1.29–1.34× (holotype: 1.29; mean 1.32) length; gena wide, 1.12–1.36× (holotype 1.22; mean 1.26) eye breadth in lateral view; frons and vertex without medial carina or groove; occipital carina complete; genal carina and hypostomal absent; postgenal bridge flat; dorsal scrobal carina wavy, extending nearly to inner eye margin; eye oval, slightly protruding from head capsule; minimum distance between eyes 1.37–1.46× (holotype 1.37; mean 1.41) eye height; eye height 1.40–1.52× (holotype: 1.52; mean 1.45) malar distance; clypeus with subventral transverse ridge and medial longitudinal ridge apically terminating as rounded tubercle; anterior margin of transverse ridge truncate; apex of medial longitudinal tubercle reaching anterior margin of transverse ridge; mandible slender without inner tooth; mandibular ventral margin straight; prementum flat without medial carina or tubercle; scape bending medially; length and width of pedicel:F1:F2 (mean in parentheses) = 1.00:0.88–1.00 (0.97):1.38–1.50 (1.47):1.17–1.25 (1.23):1.00–1.17 (1.10):1.25–1.33 (1.27) (holotype 1.00:1.00:1.50:1.25:1.13:1.25); F2–9 almost same in length and width; F10 as long as F1, conical.

Mesosoma broadest at pronotum; lateral margins subparallel, weakly crenulate; head

width:humeral width:pronotal width:mesonotal width:propodeal width:metasomal width (mean in parentheses) = 100:77.8–83.3 (80.5):85.7–94.0 (90.0):80.5–85.5 (82.6):85.7–90.4 (87.8):114.3–119.3 (117.0) (holotype 100:83.3:91.7:83.3:89.3:119.0); dorsal thoracic length 0.94–0.96× (holotype 0.95; mean 0.96) pronotal width; anterior margin of pronotal dorsum arcuate, without tooth or tubercle; pronotum laterally slightly projecting; humeral angle rounded with weak vertical humeral carina; metanotum with prescutellar row of spinulose scales; scutellar scale laterally with few spinulose scales; scutellar scale moderately elevated, small; scutellar scale width 1.00–1.86× (holotype 1.86; mean 1.31) its length, 0.08–0.17× (holotype 0.17; mean 0.11) propodeal width, 1.00–3.25× (holotype 3.25; mean 1.88) puncture diameter; metanoto-propodeal suture indistinct; postero-lateral margin of propodeum with few tubercles; posterior propodeal face vertical.

Metacoxa with weak inner longitudinal carina; meso- and metatibiae with two longitudinal rows of spines on outer face; protarsus with external comb of long spines.

T1 subsessile, without distinct dorsum; T2 evenly convex; dorsal T2 length 0.94–0.97×(holotype 0.94; mean 0.95) T2 width; S1 with medial longitudinal carina on anterior 2/3, its ventral margin straight or weakly emarginate; S2 evenly convex, without anteromedial carina; S6 posterior margin bidentate; pygidial plate flat, slender, triangular; lateral margins of pygidial plate delimited by sharp longitudinal carinae throughout, convergent posteriorly.

Frons and vertex with large sparse punctures; gena with large dense but separated punctures; postgenal bridge transversely rugose; clypeus, pedicel, meso- and metapleura dorsal halves, trochanters, femora, tibiae, tarsi, T1, S1, and S3–6 with minute sparse punctures; prementum, stipes, flagellum, propleuron, lateral pronotal face, meso- and metapleura ventral halves, coxae, T3–5, and T6 laterally with minute dense punctures; scape, lateral propodeal face, T2 lateral margin, and S2 with small sparse punctures; thoracic dorsum with large confluent punctures; posterior propodeal face reticulate; T2 disc with small dense punctures; pygidial plate sparsely longitudinally striate on anterior 3/4 with 10–15 striae and smooth posteriorly.

MALE. Unknown.

Type material

Holotype ♀: **Vietnam:** BA RIA VUNG TAU: Xuyen Moc, Binh Chau, 5.I.2002, T. Ishikawa leg. [TUA]. Paratypes: Vietnam: BA RIA VUNG TAU: Xuyen Moc, Binh Chau, 5.I.2002, T. Ishikawa leg. [2♀ TUA]; Xuyen Moc, Binh Chau, 5.I.2002, H. Mizushima leg. [1♀ TUA].

Distribution

Vietnam: Ba Ria Vung Tau.

Etymology

The specific name *vietnaminix* is the combination of Vietnam and the Latin noun *nix*, snow, in the genitive case. It refers to the snowy white markings on mesosomal dorsum and metasomal terga of this new species, with indication to the country of origin.

Remarks

The lateral setal spot on metanotum and propodeum varies in intensity (Figs 9, 10). This new species is unique in the *Mickelomyrme* by having the entirely reddish yellow and metanotum and propodeum with a lateral white setal patch. By having lateral setal spots on the pronotum, this species may be confused with *M. athalia*, *M. kinguri*, and *M. puttasoki*. However, this new species can be distinguished from them by having the head entirely dark (head uniformly red in *M. kinguri*), vertex with dense but separated punctures (confluent in *M. athalia*),

pronotum uniformly yellowish red (with anteromedial black spot in *M. kinguri* and *M. puttasoki*), T2 medial and lateral spots concolorous (medial spot more yellow-tinted in *M. athalia*, *M. kinguri*, and *M. puttasoki*), T2 medial spot oval (subcircular in *M. athalia* and *M. puttasoki*), pygidial plate slender with lateral margins subparallel (broad and triangular in *M. puttasoki*), and striae on pygidial plate sparse, reaching posterior 1/4 (dense and reaching posterior margin in *M. kinguri* and *M. puttasoki*).

***Mickelomyrme zebina* (Smith, 1860)**

(Figs 13–16, 22, 23)

Mutilla zebina Smith, 1860: 115, ♀, holotype ♀ (Bachian [= Bacan], Indonesia) [OUMNH]; Dalla Torre, 1897: 99; André, 1902: 41.
Smicromyrme zebina: Mickel, 1934: 204, ♂♀; Mickel, 1935: 292, ♂♀; Baltazar, 1966: 211; Tsuneki *et al*., 1993: 21, ♀.
Smicromyrme aborlana Tsuneki in Tsuneki *et al*., 1993, **syn. nov.**: 23, ♀, holotype ♀ (Aborlan, Palawan, Philippines) [NMNH].
Smicromyrme aborlana zamboangae Tsuneki in Tsuneki *et al*., 1993, **syn. nov.**: 24, ♀, holotype ♀ (Pasonanka Park, Zamboanga, Mindanao, Philippines) [NMNH].
Mickelomyrme zebina: Lelej, 1996a: 97, ♂♀, examined; Lelej, 2005: 45; Lo Cascio, 2015: 551; Okayasu *et al*., 2018: 303, ♀; Okayasu, 2020: 44, ♂; Pagliano *et al*., 2020: 175.
Mickelomyrme aborlana aborlana: Lelej, 2005: 43; Okayasu *et al*., 2018: 306, ♀; Okayasu, 2020: 44; Pagliano *et al*., 2020: 174
Mickelomyrme aborlana zamboangae: Lelej, 2005: 43; Okayasu *et al*., 2018: 306, ♀; Okayasu, 2020: 44; Pagliano *et al*., 2020: 174.

Diagnosis

FEMALE. Head black; vertex and gena punctures dense but separated; antenna dark brown to black; mesosoma red; pronotal dorsum, metanotum, and propodeum lacking pale setal patch; posterior propodeal face vertical; legs black with femoral bases sometimes red; T2 length 0.89–0.92× width; T2 with three pale setal spots, lateral spot located posteriorly to medial one; medial and lateral T2 spots separated by 1.13–1.33× medial spot diameter; T2 medial spot concolorous with lateral spot and located on black cuticle; T2 disc flat, with small sparse punctures; T2 lateral margin with sparse punctures; T2 posterior margin with black setae; T4 with wide pale golden setal band, sometimes medially interrupted by black setae; T5 with black recumbent and pale golden erect setae; pygidial plate wide triangular with lateral margins convergent posteriorly; pygidial striae reaching posterior margin of pygidial plate.
MALE. See Okayasu (2020).

Material examined

Indonesia: KALIMANTAN TIMUR: E. Kalimantan, Kutai N. P., Sangkimah, 14.IX.1993, Sk. Yamane leg., *Mickelomyrme zebina* (Smith), A. Lelej det. 1995 [1♂1♀ (in copula) SKYC]; E. Kalimantan, Kutai N. P., Teluk Kabah, 18.IX.1993, Sk. Yamane leg., *Mickelomyrme zebina* (Smith), Lelej det. 1995 [1♀ IEBR]. **Malaysia:** SABAH: Borneo, 10 mile NW of Keningau, 900 m alt., 30.V.1980, S. Nagai leg. [1♀ EUMJ]; Luasong, 16.XI.1997, K. Matsumoto leg. [2♀ NARO]. **Philippines:** LUZON: Bacnotan, 18–19.III.1974, S. Ueda leg. [1♀ TUA], 7.IV.1974 [1♀ TUA]; Baguio, Asin Hot Spring, 21–25.III.1974, S. Ueda leg. [1♀ TUA]; Pullmell Cr. 300 m, Colorado Ralls, Benguet, 14.VI.1977, S. Ueno leg. [1♀ NSMT]; PALAWAN: Matalangao, 25 km W. of Roxas, 300 m alt., 20–22.XI.1978, S. Nagai leg. [2♀ EUMJ].

Distribution
Brunei (Lelej, 2005). Indonesia: Kalimantan Timur, Maluku Utara (Smith, 1860). Malaysia: Sabah, Sarawak (Lelej, 1996a). Philippines: Cebu, Luzon, Mindanao, Negros, Palawan (Mickel, 1934; Tsuneki *et al*., 1993).

Remarks
Photos of the holotype of *Smicromyrme aborlana zamboangae* are available from: http://n2t.net/ark:/65665/385767ac6-4818-4edd-92de-81c13de3df98 (accessed 13 February 2024). This species is widespread in islands of Philippines, Sundaland, and Wallacea. In the original description, *M. aborlana* was separated from *M. zebina* by having the frons, vertex, and thoracic dorsum with erect black setae (whitish in *M. zebina*), mandible with a minute tooth on inner margin (without inner tooth in *M. zebina*), trochanters and femoral bases clear ferruginous (dark brown in *M. zebina*), and T4 with a pale setal band medially interrupted (complete in *M. zebina*). *Mickelomyrme aborlana zamboangae* was recognized by the pygidial striae reaching posterior margin of pygidial plate (pygidial plate with posterior 1/4 or 1/5 smooth in the nominotypical subspecies). However, these character states are variable within a species. The inner tooth of mandible is variable in females, unlike males. Also, it may be sometimes worn down in old specimens, making evaluation of this character difficult. Other setal or cuticular color characters are subjects of variation (Figs 13, 15, 16). The striae on pygidial plate are diverged posteriorly in *M. zebina*, sometimes leaving posterior portion unsculptured. Many intermediate forms were examined for the characters listed above. Thus, I propose the synonymy of *M. aborlana* and its subspecies with *M. zebina*.

Key to the females of *Mickelomyrme*

1. T2 with one anteromedial golden setal spot; T2 posterior margin with wide complete golden setal band. China, Laos, Vietnam … ***M. chinensis*** (Smith, 1855)
- T2 with two or three transversely aligned pale setal spots; T2 posterior margin with black setae, medial pale setal patch or spot, or narrow pale setal fringe or band … 2
2 (1). Mesosoma black with dorso-medial portion red; T2 posterior margin with medial pale setal spot. India ... ***M. vincula*** (Nurse, 1903)
- Mesosoma largely red; T2 posterior margin with black setae or pale setal fringe ... 3
3 (2). T2 disc with small confluent punctures … 4
- T2 disc with small separated or intermixed small sparse and minute dense punctures … 6
4 (3). T2 dorsally flat; T2 posterior margin with narrow pale golden setal band. Philippines … ***M. autonoe*** (Mickel, 1934)
- T2 anteromedial portion concave; T2 posterior margin with black setae … 5
5 (4). Gena punctures dense but separated; posterior propodeal face oblique; T2 length 1.1× width; T2 posterior margin with black setae; T2 lateral margin with dense but separated punctures; T4 with black recumbent and pale golden erect setae. Philippines … ***M. semperi semperi*** (Ashmead, 1904)
- Gena punctures confluent; posterior propodeal face vertical; T2 length 0.95× width; T2 posterior margin with pale golden setal fringe medially; T2 lateral margin with confluent punctures; T4 with pale golden setal band. Philippines … ***M. verticalis*** **sp. nov.**
6 (3). T2 posterior margin with medial pale setal patch … 7
- T2 posterior margin predominantly with black setae … 9
7 (6). T4–5 with pale golden setal band; pygidial striae reaching posterior margin of pygidial plate. Thailand … ***M. leleji*** Sittichaya & Williams, 2022
- T4–5 with black setae; pygidial striae short, leaving posterior portion smooth … 8
8 (7). Vertex with dense but separated punctures. Japan, Taiwan … ***M. hageni*** (Zavattari,

1913)
- Vertex with confluent punctures. China, Indonesia, Laos, Myanmar, Thailand, Vietnam … ***M. pusillaeformis*** (Hammer, 1962)
9 (6). Antenna entirely reddish yellow; metanotum and propodeum with lateral white setal patch. Vietnam … ***M. vietnaminix*** **sp. nov.**
- At least flagellum largely blackish; metanotum and propodeum with sparse setae … 10
10 (9). Pygidial plate slender with lateral margins subparallel; pygidial striae short, leaving posterior portion smooth … 11
- Pygidial plate wide triangular with lateral margins convergent posteriorly; pygidial striae reaching posterior margin of pygidial plate … 13
11 (10). T2 spots large, separated by ~0.2× medial spot width; T2 disc with intermixed small sparse and minute dense punctures. Laos … ***M. grandiguttata*** **sp. nov.**
- T2 spots small, separated by approximate medial spot diameter or medial spot obliterated; T2 disc with small sparse punctures … 12
12 (11). Pronotal dorsum with lateral white setal patch. China, Laos, Malaysia, Thailand, Vietnam … ***M. athalia*** (Pagden, 1949)
- Pronotum with sparse setae. China, Laos, Thailand. Vietnam … ***M. kuznetsovi*** Lelej, 1996
13 (10). Head entirely orange; T2 medial spot composed of orange setae on orange cuticle. Thailand … ***M. kinguri*** Williams, 2019
- Head largely black, at least with reddish spot on vertex; T2 medial spot composed of white to pale golden setae on black cuticle … 14
14 (13). Antenna and legs orange; pronotal dorsum with lateral white setal patch. Thailand … ***M. puttasoki*** Williams, 2019
- Antenna and legs dark brown to black; pronotum with sparse setae. Brunei, Indonesia, Philippines … ***M. zebina*** (Smith, 1860)

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References

André, E. (1902 [1903]) Family Mutillidae. *In*: Wytsman, P. (ed.) *Genera Insectorum*. *Fascicles 11*. L. Desmet-Verteneuil, Bruxelles, pp. 1–77 + 3 pls.

Ashmead, W.H. (1904) Descriptions of new genera and species of Hymenoptera from the Philippine Islands. *Proceedings of the United States National Museum* 28 (1387): 127–158.

Baltazar, C.R. (1966) A catalogue of Philippine Hymenoptera (with a bibliography, 1758–1963). *Pacific Insects Monograph* 8: 1–488.

Barthélémy, C., Lelej, A.S. & Loktionov, V.M. (2018) A contribution to the Mutillidae (Hymenoptera) of Hong Kong. Zootaxa 4514 (2): 230–242. https://dx.doi.org/10.11646/zootaxa.4514.2.6

Bartholomay, P.R., Williams, K.A., Lopez, V.M. & Oliveira, M.L. (2019) Revision of the *Traumatomutilla americana* species group (Hymenoptera: Mutillidae). Zootaxa 4608

(1): 1–34. https://doi.org/10.11646/zootaxa.4608.1.1
Brown, R.E. (1906) A catalogue of Philippine Hymenoptera, with description of new species. *The Philippine Journal of Science* 1: 683–704. https://doi.org/10.5962/bhl.part.13887
Chen, C.-w. (1957) A revision of the velvety ants or Mutillidae of China (Hymenoptera). *Quarterly Journal of the Taiwan Museum* 10 (3–4): 135–224 + 6 pls.
Dalla Torre, C.G. de (1897) *Catalogus Hymenopterorum hucusque Descriptorum Systematicus et Synonimicus*. *Volumen VIII: Fossores (Sphegidae)*. Guilelmi Engelmann, Lipsiae, [4] + viii + 750 pp.
Hua, L.-z. (2006) *List of Chinese insects Vol. IV*. Sun Yat-sen University Press, Guangzhou, 540 pp.
Hymenoptera Anatomy Consortium (2023) Hymenoptera glossary. Available from: http://glossary.hymao.org (accessed 8 November 2023)
Lelej, A.S. (1995) A review of Palaearctic and Oriental species of genus *Nemka* Lelej with description of Oriental genus *Mickelomyrme* gen. n. (Hymenoptera, Mutillidae). *Far Eastern Entomologist* 6: 1–20.
Lelej, A.S. (1996a) Mutillid wasps collected in Malaysia and Indonesia by Dr. Sk. Yamane (Hymenoptera, Mutillidae). *Tropics* 6 (1–2): 91–104. https://doi.org/10.3759/tropics.6.91
Lelej, A.S. (1996b) A review of the East Asian species of *Mickelomyrme* Lelej, 1995 (Hymenoptera, Mutillidae). *Entomofauna* 17 (15): 277–292.
Lelej, A.S. (2005) *Catalogue of the Mutillidae (Hymenoptera) of the Oriental Region*. Dalnauka, Vladivostok, 252 pp.
Lo Cascio, P. (2015) Worldwide checklist of the island mutillid wasps (Hymenoptera Mutillidae). *Biodiversity Journal* 6 (2): 529–592.
Mickel, C.E. (1934) Mutillidae of the Philippine Islands. *Philippine Journal of Science* 54 (1): 91–219 + 1 pl.
Mickel, C.E. (1935) The mutillid wasps of the islands of the Pacific Ocean (Hymenoptera, Mutillidae). *Transactions of the Royal Entomological Society of London* 83 (2): 177–312. https://doi.org/10.1111/j.1365-2311.1935.tb01207.x
Okayasu, J. (2020) Velvet ants of the tribe Smicromyrmini Bischoff (Hymenoptera: Mutillidae) of Japan. *Zootaxa* 4723 (1): 1–110. https://doi.org/10.11646/zootaxa.4723.1.1
Okayasu, J., Lelej, A.S. & Williams, K.A. (2021) Review of *Eotrogaspidia* Lelej (Hymenoptera: Mutillidae: Trogaspidiini). *Zootaxa* 4920 (1): 56–90. https://doi.org/10.11646/zootaxa.4920.1.2
Okayasu, J., Williams, K.A. & Lelej, A.S. (2018) A remarkable new species of the genus *Sinotilla* Lelej (Hymenoptera: Mutillidae: Smicromyrmini) from Taiwan and an overview of color diversity in East Asian mutillid females. *Zootaxa* 4446(3): 301–324. http://dx.doi.org/10.11646/zootaxa.4446.3.1
Pagden, H.T. (1949) Descriptions and records of Austro-Malaysian Methocidae and Mutillidae (Hymenoptera). *Transactions of the Royal Entomological Society of London* 100 (8): 191–231. http://doi.org/10.1111/j.1365-2311.1949.tb01431.x
Pagliano, G. (2011) I Mutillidae (Hymenoptera) della collezione Zavattari le collezioni del Museo Regionale di Scienze Naturali di Torino. *Bolletino del Musei Regionale di Scienze Naturali di Torino* 28 (1): 37–60.
Pagliano, G., Brothers, D.J., Cambra, R., Lelej, A.S., Lo Cascio, P., Matteini Palmerini, M., Scaramozzino, P.L., Williams, K.A. & Romano, M. (2020) Checklist of names in Mutillidae (Hymenoptera), with illustrations of selected species. *Bollettino del Museo Regionale di Scienze Naturali di Torino* 36 (1–2): 5–425.
Smith, F. (1860 [1861]) Catalogue of hymenopterous insects collected by Mr. A.R. Wallace in

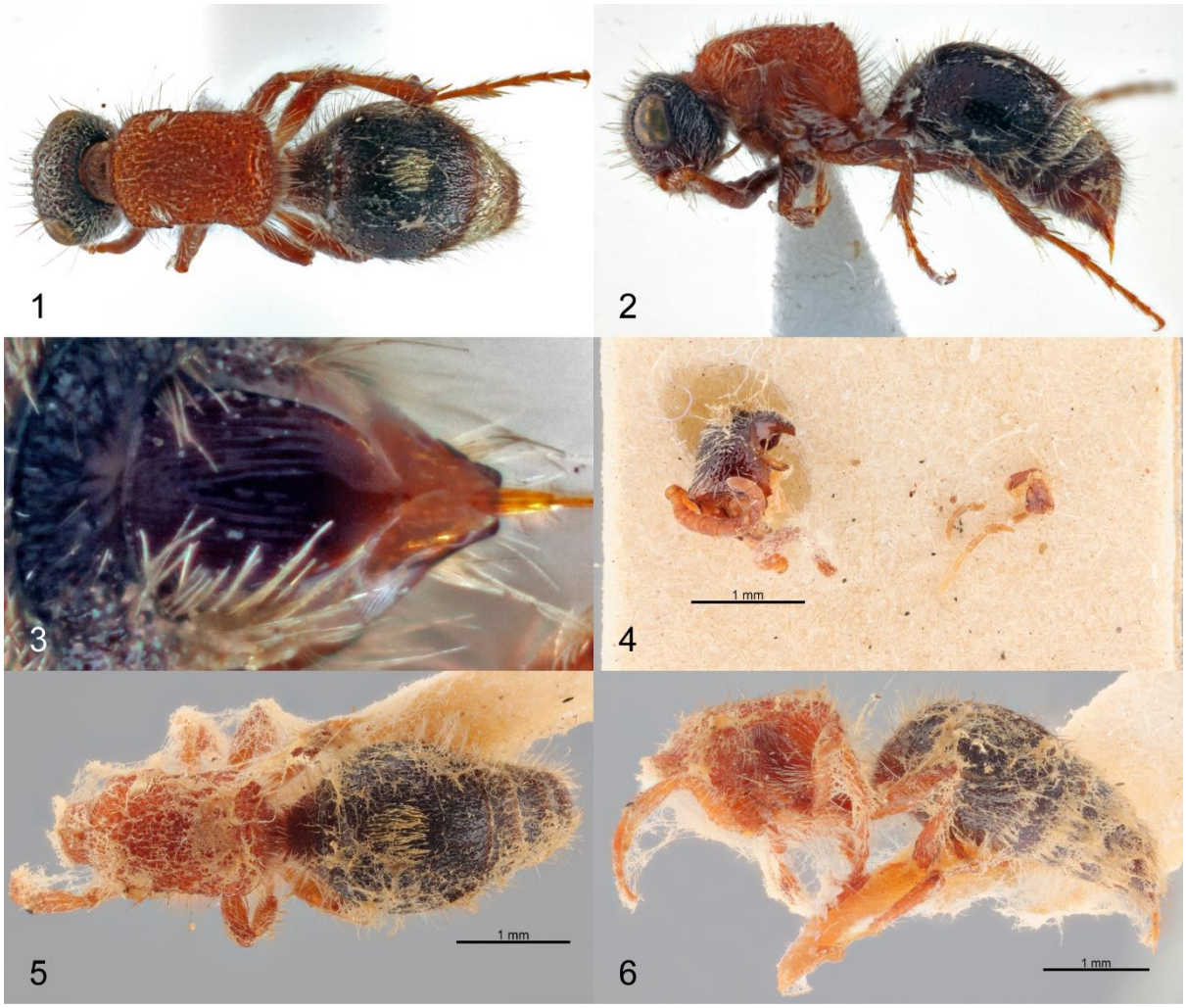
the islands of Bachian, Kaisaa, Amboyna, Gilolo, and at Dory in New Guinea. *Journal of the Proceedings of the Linnean Society*, *Zoology* 5: 93–143. https://doi.org/10.1111/j.1096-3642.1860.tb01022.x

Thaochan, N., Williams, K.A., Thoawan, K., Jeenthong, T. & Sittichaya, W. (2022) Three new species and one new country record of velvet ants (Hymenoptera, Mutillidae) from Thailand. *Journal of Hymenoptera Research* 93: 151–165. https://doi.org/10.3897/jhr.93.94727

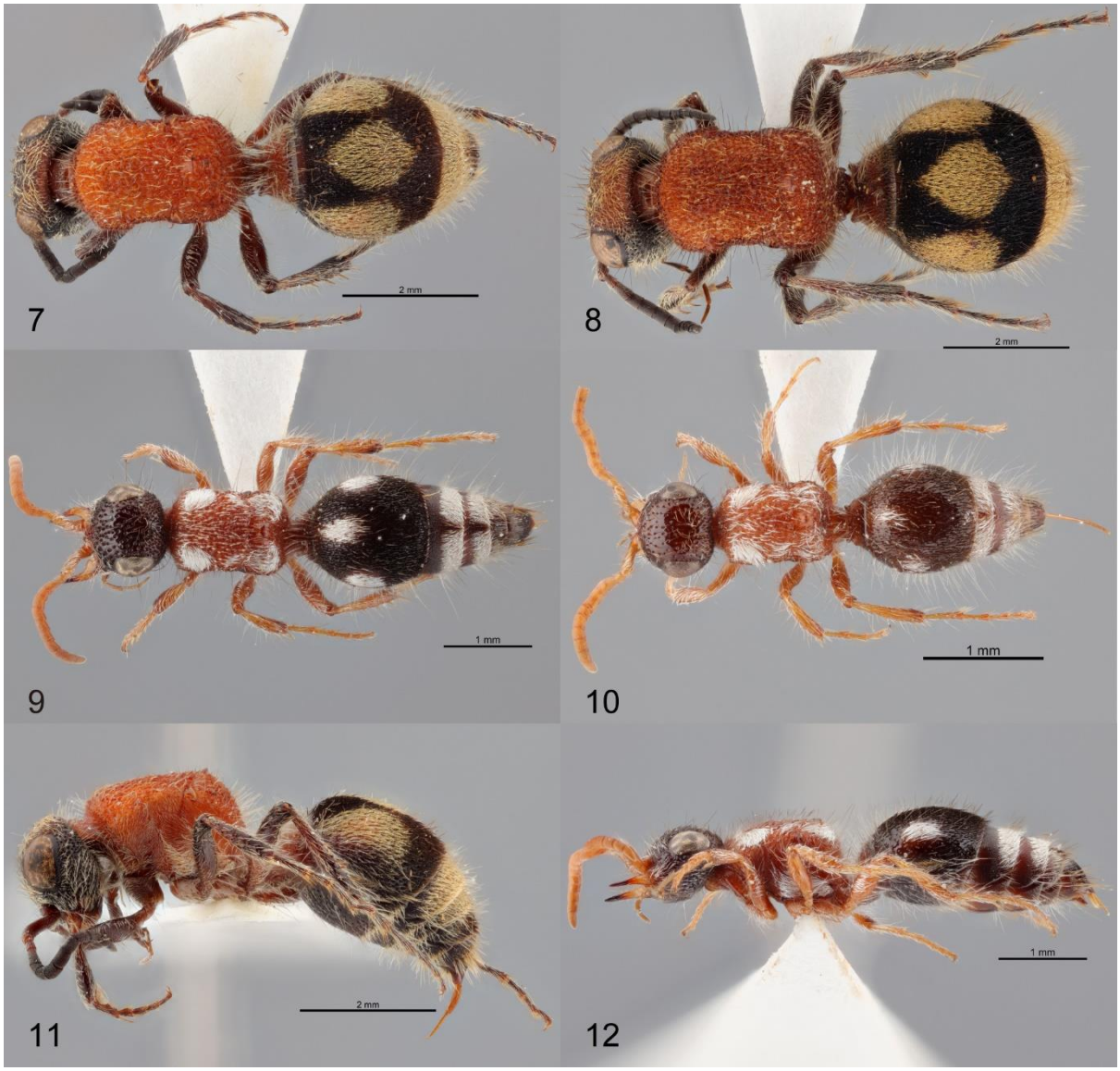
Tsuneki, K., Nozaka, C., Tano, T., Kurokawa, H. & Murota, T. (1993) Mutillidae recently collected in the Philippines (Hymenoptera). *Special Publications of the Japan Hymenopterists Association* 41: 1–38.

Williams, K.A., Lelej, A.S., Okayasu, J., Borkent, C.J., Malee, R., Thoawan, K. & Thaochan, N. (2019) The female velvet ants (aka modkhong) of southern Thailand (Hymenoptera: Mutillidae), with a key to the genera of southeast Asia. *Zootaxa* 4602 (1): 1–69. http://dx.doi.org/10.11646/zootaxa.4602.1.1

Zavattari, E. (1913) H. Sauter's Formosa-Ausbeute. Mutillidae (Hym.). *Archiv für Naturgeschichte* 79A (3): 19–42.



Figures 1–6. *Smicromyrme bicristata* Chen, ♀, type specimens. 1–3. Holotype; 4–6. paratype; 1, 5. dorsal habitus; 2, 6. lateral habitus; 3. pygidial plate; 4. head mounted on a card.



Figures 7–12. *Mickelomyrme* spp., ♀, type specimens. 7, 11. *M. grandiguttata* **sp. nov.**, holotype; 8. *M. grandiguttata* **sp. nov.**, paratype; 9, 12. *M. vietnaminix* **sp. nov.**, holotype; 10. *M. vietnaminix* **sp. nov.**, paratype; 7–10. dorsal habitus; 11, 12. lateral habitus.

Figures 13–16. *Mickelomyrme zebina* (Smith), ♀. 13, 14. Malaysia (Sabah); 15. Philippines (Palawan); 16. Philippines (Luzon); 13, 15, 16. dorsal habitus; 14. lateral habitus.

Figures 17–23. *Mickelomyrme* spp., ♀. 17, 19. *M. grandiguttata* **sp. nov.**, holotype; 18. *M. grandiguttata* **sp. nov.**, paratype; 20, 21. *M. vietnaminix* **sp. nov.**, holotype; 22, 23. *M. zebina* (Smith), Malaysia; 17, 18, 20, 22. face; 19, 21, 23. pygidial plate.

Figures 24–31. *Mickelomyrme* spp., ♀. 24, 25, 28, 29. *M. semperi semperi* (Ashmead), Philippines; 26, 27, 30, 31. *M. verticalis* **sp. nov.**, holotype; 24, 26. dorsal habitus; 25, 27. lateral habitus; 28, 30. face; 29, 31. pygidial plate.

Chapter 7

Current knowledge on velvet ants (Hymenoptera: Mutillidae, Myrmosidae) of Vietnam: Faunal review and new country records

Disclaimer: *This work is not issued for the purposes of zoological nomenclature and is not considered a published work within the meaning of the International Code of Zoological Nomenclature 4th edition (Article 8.2).*

Abstract

The velvet ant fauna of Vietnam is reviewed based on the literature and specimens from various museum collections. Before this study, forty-eight species have been recorded, and the following ten species are newly recorded: *Pherotilla brothersi* Zhou, Lelej & Xu, 2017 (Rhopalomutillinae), *Hemutilla bifurcata* (Chen, 1957) (Sphaeropthalminae), *Bischoffitilla perakensis* (Pagden, 1934) (Myrmillinae), *Kurzenkotilla harmandi* (André, 1898) (Mutillinae: Mutillini), *Mickelomyrme puttasoki* Williams, 2019, *Promecilla decora* (Smith, 1897), *Smicromyrme thaochani* Williams, 2019 (Mutillinae: Smicromyrmini), *Krombeinidia chang* Williams, 2019, *Orientidia thoawanae* Williams, 2019, and *Wallacidia retinula* (Chen, 1957) (Mutillinae: Trogaspidiini). Additional 37 new provincial records are presented. As a supplement to previously published works, specimen-based records are given for species recorded without reference to voucher specimens. Synonymies, geographical distribution, sex association, seasonal occurrence, and habitats are reviewed for all 58 species in 26 genera. The number of recorded species from each province was greatly variable, and 56% of the provinces currently have no velvet ant record. Twenty-two of 58 recorded species are known from both sexes. The host is known for only one species. These data highlight the need of intensive field surveys in Vietnam to elucidate the true biodiversity of velvet ants in this country, which is likely much higher than documented to date.

Key words

Aculeata, biodiversity, distribution, Oriental Region, Southeast Asia, taxonomy.

Introduction

Velvet ants currently comprise two aculeate families Mutillidae Latreille, 1802 and Myrmosidae Fox, 1894 (Waldren *et al*., 2023). There are about 4600 species in 225 genera worldwide (Pagliano *et al*., 2020, updated). Velvet ants show extreme sexual dimorphism: males have developed wings (alate), while females are wingless (apterous) and exhibit an ant-like appearance. Males rarely show wing reduction and mesosomal modification related with aptery (Brothers & Lelej, 2017). Recent studies have been revealing the weird ecology of velvet ants as a consequence of females' limited mobility, such as highly structural geographical populations and Müllerian mimicry complexes (Wilson *et al*., 2012ab, 2015, 2018).

Southeast Asia is known for the diversity and endemism of terrestrial organisms (Jenkins *et al*., 2013; Kier *et al*., 2009; Myers *et al*., 2000; Roll *et al*., 2017; Wikramanayake *et al*., 2002). Velvet ants of this region are still poorly understood because of the high species richness, lack of material, and unrevised historical type specimens. Further information on this insect, like hosts, behavior, phenology, etc., is even more incomplete. Continental Southeast Asian countries, specifically Cambodia, Laos, Thailand, and Vietnam, had not been covered by older taxonomic works (e.g., Chen, 1957; Mickel, 1933abc, 1934, 1935; Pagden, 1934a, 1949).

Vietnam is located on the eastern margin of the Indochina Peninsula and mostly covered by tropical dry or moist broadleaf forest biomes (Campbell *et al*., 2021; Dinerstein *et al*., 2017; Olson *et al*., 2001; Wikramanayake *et al*., 2002). This country is included in the Indo-Burma biodiversity hotspot (Myers *et al*., 2000) with many key biodiversity areas (Tordoff *et al*., 2012). In addition to the known diversity, this country harbors enormous undiscovered diversity of terrestrial organisms (Kass *et al*., 2022; Moura & Jetz, 2021).

Until 1995, only four species had been recorded from Vietnam (André, 1898; Lelej, 1979; O'Toole, 1975; Sichel & Radoszkowski, 1869–1870). Recent publications in Asian velvet ant taxonomy added 44 species (see the historical review section below). Thus, the velvet ant fauna of this country includes 48 species. Similar number of species had been recorded from Thailand by 2019 (Lelej, 2005; Lelej *et al*., 2016, 2017; Okayasu *et al*., 2018). However, a comprehensive treatment of female velvet ants of southern Thailand (Williams *et al*., 2019a) nearly doubled that number, from 33 to 63, by adding 17 new species and 12 new country records. This suggests that the true diversity of Vietnamese velvet ants is likewise much higher than presently recognized.

To facilitate the study of velvet ants of Vietnam, I aimed to review the current status of the faunal survey in this country. Furthermore, I sought to obtain new country and provincial records based on museum specimens to investigate their potential diversity in this country. Also, some of the Vietnamese species were recorded without reference to voucher specimens and their collecting data. Specimen-based records are provided for such species.

Material and methods

The list below is primarily based on distributional and taxonomic records of Vietnamese mutillids and myrmosids obtained from the literature and arranged following the recent higher classification of the family (Brothers & Lelej, 2017; Waldren *et al*., 2023). As a supplement to Lelej (2005) and Williams *et al*. (2019a), I present label data for species recorded without reference to voucher specimens in these publications. Additional specimens were loaned from various museums (listed below) and examined under various stereomicroscopes in multiple labs. Newly recorded species were identified using modern taxonomic papers (Barthélémy *et al*., 2018; Lelej, 1996a; Lelej *et al*., 2023; Tu *et al*., 2014; Williams *et al*., 2019a; Zhou *et al*., 2017) or through comparison with voucher or type specimens as specified in the identification source section. New records are asterisked (*). If available, occurrence data (altitude, seasons, and habitats) of Vietnamese velvet ants were reviewed based on the literature and label data. Ecoregions of each collecting locality were identified using the map developed by Dinerstein *et al*. (2017).

Most photographs were taken with a Canon EOS 6D Mark II digital camera equipped with a Canon MP-E 65mm f/2.8 1-5x Macro Photo macro lens. Photo stacking was done using Zerene Stacker (Zerene Systems LLC, Richland, WA, USA). The map figures were generated by SimpleMappr (Shorthouse, 2010). Figures were edited with Adobe Photoshop and Adobe Illustrator (Adobe Inc., San Jose, CA, USA). In the synonymic lists and the material examined sections, abbreviations for material depositories and additional or corrected data by the authors are given in square brackets.

The following abbreviations are used to denote institutes housing type specimens and the material examined in this paper.

CSCA California State Collection of Arthropods, Sacramento, California, USA.
ELKU Entomological Laboratory, Faculty of Agriculture, Kyushu University, Fukuoka, Japan.
EUMJ Ehime University Museum, Matsuyama, Ehime, Japan.

IBSS Federal Scientific Center of the East Asia Terrestrial Biodiversity (formerly Institute of Biology and Soil Science), Vladivostok, Russia.
IEBR Institute of Ecology and Biological Resources, Vietnam Academy of Science and Technology, Hanoi, Vietnam.
IMK Indian Museum, Kolkata, India.
MNHAH Museum of Nature and Human Activities, Sanda, Japan.
MNHN Muséum national d'histoire naturelle, Paris, France.
MSNG Museo Civico di Storia Naturale "G. Doria", Genoa, Italy.
MTC Mamoru Terayama Collection in Laboratory of Applied Entomology, Department of Agricultural and Environmental Biology, The University of Tokyo, Tokyo, Japan.
NHMUK The Natural History Museum, London, UK.
NHMW Naturhistorisches Museum Wien, Wien, Austria.
NMNH National Museum of Natural History, Smithsonian Institution, Washington D.C., USA.
NSMT National Museum of Nature and Science, Tsukuba, Japan.
OMNH Osaka Museum of Natural History, Osaka, Japan.
RMNH Naturalis Biodiversity Center, Leiden, South Holland, the Netherlands.
SCAU Hymenopteran Collection of South China Agricultural University, Guangzhou, China.
SDEI Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany.
SEHU Hokkaido University Insect Collection, Sapporo, Japan.
TARI Taiwan Agricultural Research Institute, Taichung, Taiwan.
THNHM Thailand Natural History Museum, National Science Museum, Pathum Thani, Thailand.
TUA Laboratory of Entomology, Tokyo University of Agriculture, Atsugi, Kanagawa, Japan.
UMSP University of Minnesota Insect Collection, St. Paul, Minnesota, USA.
VNMN Vietnam National Museum of Nature, Vietnam Academy of Science and Technology, Hanoi, Vietnam.
ZISP Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia.
ZJUH Parasitic Hymenoptera Collection of Zhejiang University, Hangzhou, China.
ZMMU Zoological Museum of Moscow State University, Moscow, Russia.
ZMNB Museum für Naturkunde, Humbolt Universität, Berlin, Germany.
ZMUC Zoological Museum, University of Copenhagen, Universitetsparken, Denmark.

Historical review

The first Vietnamese species, *Mutilla cordigera* Sichel & Radoszkowski, 1869, was described in a comprehensive treatment of the velvet ants of the Old World by Sichel & Radoszkowski (1869–1870). André (1898) then described the second species, *Mutilla griseomaculata* André, 1898. Those earliest species were described based on a single individual with rough collecting data (stating "Chine" or "Cochinchine" only, both regarded as southern Vietnam) deposited in MNHN. Mickel (1933c) reexamined their type specimens and reallocated the former to the *Odontomutilla* Ashmead, 1899 and the latter to *Timulla* (*Trogaspidia*) Ashmead, 1899.

After more than 70 years since André's (1898) paper, O'Toole (1975) recorded *Timulla* (*Trogaspidia*) *oculata* (Fabricius, 1804) from three localities in Vietnam based on four specimens. Lelej (1979) described the new genus *Orientilla* Lelej, 1979 with *O. vietnamica* Lelej, 1979 as the type species. As its name implies, this species was described from southern Vietnam, but a single female was recognized. Consequently, during 1869 to 1979, only four species were recorded from Vietnam based on seven specimens.

Remarkable progress was made in a series of taxonomic treatments of East Asian

velvet ants by Lelej (1995ab, 1996abcd, 2005, 2012). In these publications, he examined museum specimens collected by Russian and Japanese entomologists and added 24 species to the Vietnamese fauna, 17 as new country records and seven as new species originally described from Vietnam. Along with this, he revised the genus-level classification for East Asian velvet ants.

Following Lelej's classification system, recent works drastically increased the number of Vietnamese species. With about 70 specimens from various institutes, Lelej *et al*. (2016, 2017), Okayasu (2018, 2020, 2023a), Okayasu *et al*. (2018, 2021ab), Williams *et al*. (2019ac), and Zhou *et al*. (2018ab) newly recorded 21 species, including nine new species described from Vietnam. They also provided useful resources like identification keys and illustrations. Some of those works attempted to review small East Asian genera (Lelej *et al*., 2016, 2017; Okayasu, 2023a; Okayasu *et al*., 2021ab; Zhou *et al*., 2018b) or local fauna of East Asian countries (Okayasu, 2020; Williams *et al*., 2019a). However, no comprehensive treatment specifically focusing on the Vietnamese fauna has not been done.

Checklist

Before this study, two species in two genera of two myrmosid subfamilies and 46 species in 23 genera of 5 mutillid subfamilies have been recorded from Vietnam (Table 1). After examination of museum specimens, I recognized ten species, three genera, and one mutillid subfamily new to Vietnamese fauna, bringing the total diversity to 58 species in 28 genera (Tables 1–2).

Family Myrmosidae Fox, 1894

Myrmosids are morphologically distinct from mutillids (Krombein, 1940; Kumpanenko *et al*., 2020; Reid, 1941; Waldren *et al*., 2023). The status of this taxon has been controversial (Brothers & Lelej, 2017; Waldren *et al*., 2023). Previous cladistic frameworks generally treated it as a subfamily of Mutillidae (Brothers, 1975; Brothers & Carpenter, 1993; Brothers & Lelej, 2017; Lelej & Nemkov, 1997). However, recent molecular phylogenetic and phylogenomic analyses often suggest their independent family-level status (Branstetter *et al*., 2017; Debevec *et al*., 2012; Pilgrim *et al*., 2008), although the placement of Myrmosidae within Pompiloidea is unstable. With extended taxon sampling and ultraconserved element phylogenomic approach, Waldren *et al*. (2023) concluded that the full-family status of Myrmosidae was reasonable and well-supported since this taxon was recovered as sister to Sapygidae or Pompilidae + Sapygidae. I followed this treatment and regarded myrmosids a distinct family, with Kudakruminae Krombein, 1979 and Myrmosinae as its subfamilies. See Brothers & Lelej (2017) and Waldren *et al*. (2023) for further discussion on this issue.

This family is exclusively distributed in the Holarctic Region. In the Oriental Region, myrmosids had been recorded from South Asia only and represented by two kudakrumine genera, *Kudakrumina* Krombein, 1979 and *Nothomyrmosa* Krombein, 1979 (Krombein, 1979; Lelej, 2005), except *Taimyrmosa* Lelej, 2005 (Myrmosinae) which was known from Taiwan (Lelej, 2005). However, surprisingly, Williams *et al*. (2019b) discovered the *Kudakrumina* and the Palaearctic genus *Krombeinella* Pate, 1947 (Myrmosinae) from Southeast Asia including Vietnam. Because myrmosids lack many diagnostic features of velvet ants (e.g., felt line on the second metasomal segment), males can be easily confused with tiphiid and thynnid wasps (Williams *et al*., 2019b). Therefore, diverse elements of this family might eventually be found after careful examination of Malaise trap and yellow pan trap samples from Southeast Asia.

Subfamily Kudakruminae Krombein, 1979

Genus *Kudakrumia* Krombein, 1979

urn:lsid:zoobank.org:act:34DA23A6-4DFF-473E-B943-202A579D0673

Kudakrumia Krombein, 1979: 74, ♂♀. Type species: *Kudakrumia mirabilis* Krombein, 1979 (♂♀), by original designation.

Diversity and distribution
This genus is restricted to the Oriental Region, with two species from South Asia (India and Sri Lanka) and two from Southeast Asia (Thailand and Vietnam) (Krombein, 1979; Kumar *et al*., 2019; Williams *et al*., 2019).

Remarks
Identification keys to the Old World genera and species of Kudakruminae were provided by Kumar *et al*. (2019) and Williams *et al*. (2019b).

Kudakrumia loaibonho Williams, Lelej & Thaochan, 2019

urn:lsid:zoobank.org:act:EFF272C7-EC74-4A45-BBC7-3754D0E20051

Kudakrumia loaibonho Williams, Lelej & Thaochan, 2019b: 527, ♂, holotype ♂ (Nui Chua National Park, Ninh Thuan, Vietnam) [RMNH].

Distribution
Vietnam: Ninh Thuan (Williams *et al*., 2019b).

Occurrence in Vietnam
May. Southern Vietnam lowland dry forests ecoregion. ca. 150 m alt.

Sex association
Female unknown.

Remarks
This species is one of four described species of *Kudakrumia*. In East Asia, two species, *K. loaibonho* and *K. malaenglek* Williams, Lelej & Thaochan, 2019 (Thailand), are known. Both species have been collected from dry habitats during dry season and are likely arid-adapted species (Williams *et al*., 2019b).

Subfamily Myrmosinae Fox, 1894

Genus *Krombeinella* Pate, 1947

urn:lsid:zoobank.org:act:04C11BAA-B70F-45B4-AD15-7BCE770A550B

Myrmosa (*Krombeinella*) Pate, 1947: 197, ♂♀. Type species: *Hylaeus thoracicus* Fabricius, 1793 (♂), by original designation.
Krombeinella: Lelej, 1985: 57.

Diversity and distribution
This genus includes 19 species, most of which are Palaearctic in distribution (Lelej, 1985, 2002; Parejo-Pulido & Romano, 2022; Suárez & Nonveiller, 1988; Williams *et al*., 2019a).

Williams *et al*. (2019a) discovered the first Oriental species from southern Vietnam.

Remarks
Williams *et al*. (2019b) provided a key to all known males.

Krombeinella brothersi Williams, Lelej & Thaochan, 2019
urn:lsid:zoobank.org:act:53FB1C86-10BB-497F-83CC-11165365CE88

Krombeinella brothersi Williams, Lelej & Thaochan, 2019b: 529, ♂, holotype ♂ (Dong trail, Cat Tien National Park, Dong Nai, Vietnam) [RMNH].

Distribution
Vietnam: Dong Nai (Williams *et al*., 2019b).

Occurrence in Vietnam
April. Southeast Indochina dry evergreen forests ecoregion. ca. 100 m alt.

Sex association
Female unknown.

Remarks
The genus *Krombeinella* is predominantly occurs in the western Palaearctic Region (Lelej, 2002), and *K. brothersi* is the only species known from East Asia. This species, like two *Kudakrumia* species known from Southeast Asia, was collected from dry habitat during dry season (Williams *et al*., 2019b).

Family Mutillidae Latreille, 1802

Unlike the Myrmosidae, this family is widespread in the world, except arctic regions. Brothers & Lelej (2017) recognized eight subfamilies (including the Myrmosinae) within it. Waldren *et al*. (2023) proposed a different higher classification system, with eight subfamilies.

Subfamily Rhopalomutillinae Schuster, 1949

This subfamily is widespread in the Afrotropical and Oriental Regions. Brothers (2015) reviewed the genus-level classification of this subfamily, recognizing four genera. The genus *Pherotilla* Brothers, 2015 is distributed in both regions, while other three genera are known from the Afrotropical Region only (Brothers, 2015). Hosts and other ecological features are unknown for entire subfamily. However, the body shape and color of rhopalomutilline females are suggestive of subterranean habitats and potential myrmecophily (Brothers, 1989, 2015). Although rhopalomutillines are generally rarely sampled, males can be abundant in East Asian tropical forests and collected in Malaise traps in large number (personal observation).

Genus *Pherotilla* Brothers, 2015
urn:lsid:zoobank.org:act:B716E7F3-C2A0-4CF9-81A3-10F101AE05CD

Pherotilla Brothers, 2015: 10, ♂♀. Type species: *Rhopalomutilla mlanjeana* Bischoff, 1920 (♂♀), by original designation.

Diversity and distribution
This genus includes six species, two from the Afrotropical Region and the rest four from the Oriental Region (Brothers, 2015; Zhou *et al*., 2017). Brothers (2015) recognized additional five undescribed species.

Remarks
An identification key to the Oriental species was provided by Zhou *et al*. (2017).

***Pherotilla brothersi* Zhou, Lelej & Xu, 2017**
urn:lsid:zoobank.org:act:39D34F6D-D41E-46F4-9A37-A2E3E5ACA331
(Figs 1A, 1B)

Pherotilla brothersi Zhou, Lelej & Xu, 2017: 588, ♂, holotype ♂ (Nabanhe National Nature Reserve, Xishuangbanna, Yunnan, China) [SCAU]; Pagliano *et al*., 2020: 25.

Material examined.
Vietnam: BA RIA VUNG TAU: Xuyen Moc, Binh Chau, 4–5.I.2002, Malaise trap, K. Okajima leg. [4♂ TUA].

Identification source
Keyed using Zhou *et al*. (2017) and compared with the original description.

Distribution
China. Vietnam*: Ba Ria Vung Tau.

Occurrence in Vietnam
January. Southern Vietnam lowland dry forests ecoregion.

Sex association
Female unknown.

Remarks
This species was described from southern China and is newly recorded from Vietnam.

***Pherotilla striganovae* (Lelej, 2012)**
urn:lsid:zoobank.org:act:04726A7E-09D5-4B87-84BE-3FA81C2C721C

Rhopalomutilla striganovae Lelej, 2012: 144, ♀, holotype ♀ (Cat Tien National Park, Nam Cat Tien sector, Dong Nai, Vietnam) [ZISP].
Pherotilla striganovae: Brothers, 2015: 13; Okayasu *et al*., 2018: 312, ♀; Williams *et al*., 2019a: 11, ♀; Pagliano *et al*., 2020: 25.

Distribution
Thailand. Vietnam: Dong Nai (Lelej, 2012).

Occurrence in Vietnam
January, February. Southeast Indochina dry evergreen forests ecoregion.

Sex association

This species was initially described from female sex only. The male of this species was recognized by Williams *et al*. (2019a) based on a pair *in copula* but has not been formally associated and described yet.

Remarks
The holotype of this species was collected from the litter of a semi-deciduous forests in southern Vietnam.

Subfamily Sphaeropthalminae Schuster, 1949

This subfamily was classified into three tribes by Brothers & Lelej (2017), namely Dasymutillini Brothers & Lelej, 2017, Pseudomethocini Brothers, 1975 (subdivided into Euspinoliina Brothers & Lelej, 2017 and Pseudomethocina), and Sphaeropthalmini Schuster, 1949. However, based on phylogenomic analyses, Waldren *et al*. (2023) recognized Dasymutillini, Ephutini Ashmead, 1903 (transferred from Mutillinae: Mutillini), Euspinoliini, Pseudomethocini, Sphaeropthalmini, and six unnamed clades within this subfamily.

This is apparently the most diverse group in the New World (Pagliano *et al*., 2020; Williams *et al*., 2024). In the Old World, this subfamily is represented by the genera *Cystomutilla* André, 1896, *Hemutilla* Lelej, Tu & Chen, 2014 (Sphaeropthalmini), *Ephutomorpha* André, 1902, and *Eurymutilla* Ashmead, 1899 (not assigned to a tribe yet). The latter two genera are predominantly distributed in the Australasian Region, and few species are known from Wallacea (Brothers, 2022; Lelej, 2005). In East Asia, one *Cystomutilla* species and six *Hemutilla* species have been recorded from China, South Korea, and Japan (Tu *et al*., 2014; Zhou *et al*., 2018a). The first record of *Hemutilla* given below represents the southernmost range of this genus. Formerly, the genera *Cockerellidia* Lelej & Krombein, 1999 and *Karlidia* Lelej in Lelej & Krombein, 1999 known from Southeast Asia were placed in Pseudomethocini (Lelej & Krombein, 1999). They were assigned to the subtribe Ephutina of Mutillini Latreille, 1802 (Brothers & Lelej, 2017) and now to Odontomutillinae (Waldren *et al*., 2023).

Tribe Sphaeropthalmini Schuster, 1949

Genus *Hemutilla* Lelej, Tu & Chen, 2014

urn:lsid:zoobank.org:act:3770A069-74D3-4EC3-9EBF-D04C6A31BEED

Hemutilla Lelej, Tu & Chen in Tu *et al*., 2014: 76, ♂♀. Type species: *Hemutilla granulata* Tu, Lelej & Chen, 2014 (♂), by original designation.

Diversity and distribution
This genus includes six species known from China (both Palaearctic and Oriental parts) and Taiwan. One species, *H. bifurcata* (Chen, 1957), is here newly recognized from Vietnam.

Remarks
This genus was reviewed by Tu *et al*. (2014).

Hemutilla bifurcata (Chen, 1957)

urn:lsid:zoobank.org:act:C38A8AA6-162E-4420-A0C4-1DBA6CF68445
(Figs 1C, 1D)

Cystomutilla bifurcata Chen, 1957: 152, ♀, holotype ♀ (Tachulan [= Dazhulan], Showu,

Fukien [= Fujian], China) [TARI]; Lelej, 2005: 107; Hua, 2006: 299.
Hemutilla bifurcata: Tu *et al*., 2014: 87, ♀; Okayasu *et al*., 2018: 306, ♀; Pagliano *et al*., 2020: 28.

Material examined
Vietnam: LAM DONG: Bao Loc, Dambri, 26.XII.2001, K. Okajima leg. [1♀ TUA]; THUA THIEN HUE: near Bach Ma National Park., 19 km point, 253/BTTNVN, 16.198°N 107.860°E, 1400 m alt., 3–6.VIII.2016, yellow pan trap, Y. Komeda & T. Mita leg. [1♀ VNMN].

Identification source
Keyed using Tu *et al*. (2014) and compared with the original description.

Distribution
China. Vietnam*: Lam Dong, Thua Thien Hue.

Occurrence in Vietnam
August, December. Southern Annamites montane rain forests and Northern Vietnam lowland rain forests ecoregions. 1400 m alt.

Sex association
Male unknown.

Remarks
This is the first record of the genus and the subfamily from Vietnam. Hosts are unknown for this genus. The species of another Old World sphaeropthalmine genus *Cystomutilla* are known to parasitize on cavity-nesting apoid wasps (Hymenoptera: Crabronidae) (Borries, 1892; Ferton, 1908; Gôukon, 1993; Lelej, 1985).

Subfamily Dasylabrinae Invrea, 1964

This subfamily was classified into two tribes (Brothers & Lelej, 2017), namely Apteromutillini Brothers & Lelej, 2017 and Dasylabrini Invrea, 1964. The former is restricted to South Africa, while the latter is widespread in the Old World (Pagliano *et al*., 2020). Waldren *et al*. (2023) examined seven out of ten dasylabrine genera and found that the Apteromutillini was nested in the Dasylabrini, making the latter a paraphyletic group. Therefore, there is presently no tribal distinction in this subfamily. Dasylabrines are predominantly found in arid regions (Pagliano *et al*., 2020). In the Oriental Region, this subfamily is represented by the genera *Dasylabris* Radoszkowski, 1885, *Orientilla* Lelej, 1979, and *Tricholabiodes* Radoszkowski, 1885. The genus *Orientilla* is the only Southeast Asian taxon; the *Dasylabris* and *Tricholabiodes* are known from India and Sri Lanka only (Lelej, 2005).

Genus *Orientilla* Lelej, 1979
urn:lsid:zoobank.org:act:479EFED7-DAAD-4157-871C-F799FC7BFF4B

Orientilla Lelej, 1979: 1066, ♀; Lelej, 1996a: 103, ♂♀. Type species: *Orientilla vietnamica* Lelej, 1979 (♀), by original designation.

Diversity and distribution

This genus includes 15 species widely distributed in the Australasian, Oriental, and eastern Palaearctic Regions.

Remarks
This genus was reviewed by Lelej (1996a). An updated key to females was provided by Okayasu (2023b). This genus is closely related to the Afrotropical and western Palaearctic genus *Stenomutilla* André, 1896 (Brothers & Lelej, 2017; Lelej, 1996a; Waldren *et al*., 2023). The *Stenomutilla* species are known as parasitoids of bees and wasps constructing their nests with mud or in pre-existing cavities or limacodid moth cocoons (Lepidoptera) in the soil or on twigs (Okayasu, 2023b and references therein).

***Orientilla desponsa* (Smith, 1855)**
urn:lsid:zoobank.org:act:D8A0B4BA-9EBC-40CB-9D58-719DBBCC8100
urn:lsid:zoobank.org:act:1EB23ADE-BE84-4141-932C-7E21C60708BA
(Figs 2A–2D)

Mutilla desponsa Smith, 1855: 38, ♂, syntypes ♂ (North China) [NHMUK]; Dalla Torre, 1897: 31.
Mutilla variegata Smith, 1855: 39, ♀, syntypes ♀ (North China) [NHMUK]; Dalla Torre, 1897: 95. Synonymized by André (1909: 179) under *Stenomutilla desponsa* (Smith).
Stenomutilla desponsa: André, 1909: 179, ♂♀; Mickel, 1933b: 324, ♂; Wu, 1941: 135; Yasumatsu, 1948: 73, ♂; Chen, 1957: 220, ♂; Murota, 1973: 119, ♂; He *et al*., 2004: 961, ♂.
Stenomutilla variegata: Mickel, 1933b: 323, ♀; Wu, 1941: 135; Chen, 1957: 220, ♀; Murota, 1973: 119, ♂; He *et al*., 2004: 961, ♀.
Orientilla variegata: Lelej, 1979: 1067, ♀; Lelej, 1996a: 106, ♂♀, part.
Orientilla desponsa: Lelej, 2005: 111, part; Hua, 2006: 300; Lo Cascio, 2015: 554; Brothers & Lelej, 2017: 59, ♂♀; Okayasu *et al*., 2018: 308, ♀; Williams *et al*., 2019a: 11; Pagliano *et al*., 2020: 131.

Material examined
Vietnam: BAC KAN: Ba Be, 22°25′29.39″N 105°38′19.09″E, ca 277 m alt., 5.VII.2014, H. Yoshitomi leg. [1♂ EUMJ]; GIA LAI: Mang Yang, Kon Ka Kinh National Park, 14°12′11.6″N 108°18′58″E, ca 830 m alt., 19.V–3.VI.2022, Malaise trap, Lam V Tinh leg. [1♂ IEBR]; PHU THO: Viet Tri, 21°22′02.6″N 105°19′15.6″E, 20.X.2018, Ngat T. Tran, Minh P. Nguyen, Tuan V. Luong leg. [1♂ IEBR]; QUANG TRI: Dak Rong, A Ngo, ca 150–200 m alt., 31.V.2006, ISD's collectors leg. [1♂ IEBR]; THAI NGUYEN: Dai Tu, Cat Ne, 21°31′54.4″N 105°39′51.1″E, 20–25.VIII.2007, Malaise trap [2♂ IEBR]; Minh Tien, 25.V.2007, Malaise trap [1♂ IEBR]; VINH PHUC: Ngoc Thanh, Me Linh, 20.VIII.2001, Lam X. Truong leg. [1♂ IEBR]; 22°16′51″N, 105°71′54″E, 1–10.X.2020, Malaise trap, IED's collectors leg. [3♂ IEBR]; 21°23′01.7″N 105°42′40.7″E, ca 70 m alt., 11–20.V.2021, Malaise trap, IED's collectors leg. [6♂ IEBR].

Identification source
Keyed using Lelej (1996a) and compared with the original description.

Distribution
China. Taiwan. Vietnam: Bac Kan*, Gia Lai*, Phu Tho*, Quang Tri*, Thai Nguyen*, Vinh Phuc*, Hoa Binh (Lelej, 1996a, as Ha Son Binh). This species was also recorded from Myanmar (Bingham, 1897: 30, as *M. variegata*), but Bingham's description differs from the

true *O. desponsa* in the body color (Lelej, 1979, 1996a).

Occurrence in Vietnam
May to August, October. South China-Vietnam subtropical evergreen forests, Northern Indochina subtropical forests, Red River freshwater swamp forests, Luang Prabang montane rain forests, and Southern Annamites montane rain forests ecoregions. 70–830 m alt.

Sex association
This species was initially described from the male only. The female of this species was described as *Mutilla variegata* Smith, 1855 and associated by André (1909), but the evidence of this synonymy was not indicated. This treatment was confirmed by Lelej (1996a) based on males and females collected at same place.

Orientilla krombeini **Lelej, 1996**

urn:lsid:zoobank.org:act:C539EA3D-9104-4CB2-8319-53D3A6FE37CA
(Figs 2E–2F)

Orientilla krombeini Lelej, 1996a: 105, ♂♀, holotype ♀ (Culao Cham, Quangnam-Danang, Vietnam) [IBSS]; Lelej, 2005: 112; Brothers & Lelej, 2017: 59, ♂♀; Okayasu *et al*., 2018: 302, ♀; Pagliano *et al*., 2020: 131.

Material examined
Vietnam: BA RIA VUNG TAU: Xuyen Moc, Bung Rieng, 3.I.2002, K. Okajima leg. [1♂ TUA]; THUA THIEN HUE: Bach Ma, ca. 800 m alt.,10.VI.2002, Y. Arita leg. [1♂ TUA].

Identification source
Keyed using Lelej (1996a) and compared with the original description.

Distribution
Vietnam: Ba Ria Vung Tau*, Thua Thien Hue*, Quang Nam (Lelej, 1996a).

Occurrence in Vietnam
January, March, June. Northern Vietnam lowland rain forests, Southern Annamites montane rain forests, and Southern Vietnam lowland dry forests ecoregions. ca. 800 m alt.

Sex association
This species was described from both sexes collected at the same place and time.

Orientilla vietnamica **Lelej, 1979**

urn:lsid:zoobank.org:act:FB75D0A2-9C1E-4122-A55D-3A04FAD7E539
(Figs 2G, 2H)

Orientilla vietnamica Lelej, 1979: 1066, ♀, holotype ♀ (Nha Trang, S. Annam, Vietnam) [ZISP]; Lelej, 1996a: 105, ♀; Lelej, 2005: 113; Okayasu *et al*., 2018: 309, ♀; Williams *et al*., 2019a: 11, ♀; Pagliano *et al*., 2020: 132; Pagliano & Scaramozzino, 2021: 96, ♀; Thaochan *et al*., 2022: 164, ♂♀; Okayasu, 2023b: 822, ♀.

Distribution
Laos. Myanmar. Thailand. Vietnam: Khanh Hoa (Lelej, 1979; Williams *et al*., 2019a).

Occurrence in Vietnam
September. Southern Vietnam lowland dry forests ecoregion.

Sex association
This species was initially described from the female only. The male of this species was recognized by Thaochan *et al*. (2022) but not described.

Subfamily Odontomutillinae Lelej, 1983

The taxonomic status of this subfamily has been drastically changed over years. The genus *Odontomutilla* Ashmead, 1899 was placed in the Mutillina by Brothers (1975). Later, Lelej (1983) established the tribe Odontomutillini within the Dasylabrinae to include the *Odontomutilla* and Australian *Odontomyrme* Lelej, 1983. Lelej (1996c) added the genus *Yamanetilla* Lelej, 1996 to this tribe, which was composed of East Asian species once assigned to the *Odontomutilla*. Lelej & Nemkov (1997) recognized the separate subfamily Ephutinae sister to the Dasylabrinae, with the Ephutini (composed of the New World genus *Ephuta* Say, 1836 and related genera) and the Odontomutillini as tribes within it. However, Brothers & Lelej (2017) found close relationship of the Ephutinae to the Mutillini and downgraded it to the subtribal status (Ephutina). The *Odontomyrme* was transferred to the Dasymutillini at the same time, leaving the *Ephuta* group of genera (Nearctic and Neotropical) and *Odontomutilla* group of genera (Afrotropical, Australasian, Oriental, and Palaearctic) within the Ephutina. Waldren *et al*. (2023) regarded them as separate taxa, the former as Ephutini in the Sphaeropthalminae and the latter as a distinct subfamily. The Odontomutillinae was found to be sister to (Mutillinae + Myrmillinae). This subfamily now includes the following four genera: *Cockerellidia*, *Karlidia*, *Odontomutilla*, and *Yamanetilla*. The *Cockerelidia* and *Karlidia* are extremely rare genera and include one species each distributed in Myanmar and Thailand.

Genus *Odontomutilla* Ashmead, 1899
urn:lsid:zoobank.org:act:87077B9B-02C0-498C-818A-AE7704196C10

Odontomutilla Ashmead, 1899: 55, ♂♀. Type species: *Odontomutilla abbottii* Ashmead, 1899 (♂♀), by original designation = *Mutilla saussurei* Sichel & Radoszkowski, 1869 (♂) (syn. by André, 1901).
Peringueya Ashmead, 1903: 327, ♂♀. Synonymized by Bischoff (1920: 245). Type species: *Mutilla erinnys* Péringuey, 1898 (♂), by original designation.
Radoszkowskius Ashmead, 1903: 327, ♂♀. Synonymized by André (1904: 36). Type species: *Mutilla simplicifascia* Sichel & Radoszkowski, 1869 (♂♀).

Diversity and distribution
This genus includes roughly 80 species known from the Afrotropical, Australasian, Oriental, and southern Palaearctic Regions (Brothers, 2022; Lelej, 2002, 2005; Pagliano *et al*., 2020). Twenty species are recorded from East Asia.

Remarks
This genus was reviewed based on the species from China (Chen, 1957), India (Lelej *et al*., 2020), and the islands of Pacific Ocean (Mickel, 1935). However, no comprehensive study has been conducted for the continental Southeast Asian species.

Odontomutilla cordigera (Sichel & Radoszkowski, 1869)

urn:lsid:zoobank.org:act:90F421C3-CF5B-497D-A75D-030366300007

Mutilla cordigera Sichel & Radoszkowski, 1869: 155, 202, ♀, holotype ♀ (Chine [actually Cochin China = southern Vietnam]) [MNHN]; Dalla Torre, 1897: 27, ♀; André, 1902b: 29.
Odontomutilla cordigera: Zavattari, 1914: 64, ♀; Mickel, 1933b: 302, ♀; Chen, 1957: 222; Lelej, 2005: 114; Lo Cascio, 2015: 553; Okayasu *et al*., 2018: 311, ♀; Williams *et al*., 2019a: 30; Pagliano *et al*., 2020: 219.

Material examined
Vietnam: GIA LAI: K Bang, Son Lang, Kon Chu Rang Natural Reserve, 14°31′08″N, 108°28′24″E, ca 840 m alt., 25.VII.2017, Lien T.P. Nguyen, Tam T.T. Vu, Cuong Q. Nguyen, Tuong X. Ngo leg. [1♀ IEBR].

Identification source
Keyed using Mickel (1933b) and compared with the original description.

Distribution
Thailand. Vietnam: additional data unavailable (Lelej, 2005; Sichel & Radoszkowski, 1870), Gia Lai*. According to Mickel (1933b), the records of this species from Indonesia and Malaysia were based on misidentified material.

Occurrence in Vietnam
July. Southern Annamites montane rain forests ecoregion. ca 840 m alt.

Sex association
Male unknown.

Odontomutilla sinensis (Smith, 1855)

urn:lsid:zoobank.org:act:1FCF7E3A-5901-4BB9-AA6C-17F024EEF595
(Figs 3A–3D)

Mutilla sinensis Smith, 1855: 39, ♂♀, holotype ♀ (North China) [NHMUK]; Dalla Torre, 1897: 86; André, 1898: 31.
Odontomutilla sinensis: André, 1902b: 30; Zavattari, 1914: 65, ♀; Mickel, 1933b: 301, ♂♀; Wu, 1941: 134; Yasumatsu, 1948: 72, ♂♀; Hammer, 1949: 3, ♂♀; Chen, 1957: 154, ♂♀; Lelej, 2002: 106; He *et al*., 2004: 944, ♂♀; Lelej, 2005: 116; Hua, 2006: 300; Okayasu *et al*., 2018: 304, ♀; Pagliano *et al*., 2020: 223; Pagliano & Scaramozzino, 2021: 119, ♀.

Material examined
Vietnam: VINH PHUC: Tam Dao, IV.1995, M. Sato leg. [1♀ EUMJ]; Tam Dao, 960–1230 m [alt.], 20.V.1995, A. Shinohara leg. [1♀ NSMT].

Identification source
Compared with voucher specimens (Chen, 1957) [TARI].

Distribution
China. Vietnam: additional data unavailable (Lelej, 2005), Vinh Phuc*.

Occurrence in Vietnam
April, May. South China-Vietnam subtropical evergreen forests ecoregion.

Sex association
This species was described from both sexes, but the evidence of this association was not indicated.

Odontomutilla uranioides Mickel, 1933

urn:lsid:zoobank.org:act:D739AFDB-E7A5-4A9B-9635-CC2770CBE8D6
(Figs 3E, 3F)

Odontomutilla urania: Dover, 1926: 234.
Odontomutilla uranioides Mickel, 1933b: 304, ♀, holotype ♀ (Hong Kong, China) [UMSP]; Wu, 1941: 134; Chen, 1957: 155, ♀; Lelej, 2005: 117; Hua, 2006: 300; Barthélémy *et al*., 2018: 237, ♀; Okayasu *et al*., 2018: 310, ♀; Williams *et al*., 2019a: 31, ♀; Pagliano *et al*., 2020: 224.

Material examined
Vietnam: VINH PHUC: Tam Dao, IV–7.V.1996, native collector leg. [1♀ TUA]; Tam Dao, 930 m alt., 1–7.V.1996, Y. Arita leg. [2♀ EUMJ].

Identification source
Keyed using Chen (1957) and Mickel (1933b) and compared with the original description.

Distribution
China. Laos. Thailand. Vietnam: additional data unavailable (Lelej, 2005), Lam Dong, Vinh Phuc* (Okayasu *et al*., 2018).

Occurrence in Vietnam
April, May. South China-Vietnam subtropical evergreen forests ecoregion. 930 m alt.

Sex association
Male unknown.

Genus *Yamanetilla* Lelej, 1996

urn:lsid:zoobank.org:act:096BAD40-ECB6-4FBA-B541-737D0AA6E572

Yamanetilla Lelej, 1996c: 101, ♂♀. Type species: *Odontomutilla taiwaniana nipponica* Tsuneki, 1972 (♂♀), by original designation.

Diversity and distribution
This genus includes seven species. The type species occurs in the Palaearctic part of Japan, but other species are Oriental in distribution (Lelej, 1996c, 2002, 2005; Pagliano *et al*., 2020).

Remarks
This genus was nested in the widespread and speciose *Odontomutilla* in phylogenetic analyses by Brothers & Lelej (2017) and Waldren *et al*. (2023).

Yamanetilla pedaria (Mickel, 1934)

urn:lsid:zoobank.org:act:D26393D2-C247-49E6-BEDA-3889CDCDCC39

Odontomutilla pedaria Mickel, 1934: 135, ♂♀, holotype ♂ (Iligan, Mindanao, Philippines) [NMNH]; Mickel, 1935: 216, ♂♀; Baltazar, 1966: 209.
Yamanetilla pedaria: Lelej, 1996c: 102, ♀; Lelej, 2005: 118; Lo Cascio, 2015: 565; Brothers & Lelej, 2017: 62, ♂♀; Okayasu *et al*., 2018: 304, ♀; Pagliano *et al*., 2020: 224.

Distribution
Malaysia. Philippines. Vietnam: Ba Ria Vung Tau (Lelej, 1996c, as Hau Giang).

Occurrence in Vietnam
April. Southern Vietnam lowland dry forests ecoregion.

Sex association
This species was described from both sexes, but the evidence of this association was not indicated.

Remarks
Photos of the holotype of this species are available from: http://n2t.net/ark:/65665/38569db63-a96b-45cb-bc97-e6d47a29afc3 (accessed 11 October 2023).

Subfamily Myrmillinae Bischoff, 1920

This subfamily is widespread in the Old World, and few species occur in Wallacea (Brothers, 2022; Lelej, 2005, 2005; Pagliano *et al*., 2020). In the Oriental Region, it is represented by the genera *Bethsmyrmilla* Krombein & Lelej, 1999, *Bischoffitilla* Lelej, 2002, *Brahmatilla* Lelej, 2005, *Myrmilla* Wesmael, 1851, and *Spilomutilla* Ashmead, 1903. Many East Asian species of this subfamily were described in the Afrotropical genus *Squamulotilla* Bischoff, 1920 by previous authors (e.g., Chen, 1957; Mickel, 1933ab, 1934, 1935; Pagden, 1934a, 1949). They were reallocated to *Bischoffitilla* by Lelej (2002, 2005), leaving only one myrmilline genus in that region. Other four genera are known from India and Sri Lanka only (Lelej, 2005).

Genus *Bischoffitilla* Lelej, 2002
urn:lsid:zoobank.org:act:609C107C-9382-4156-889A-23D7A40AC27C

Bischoffitilla Lelej, 2002: 28, ♂♀. Type species: *Squamulotilla exilipunctata* Chen, 1957 (♀), by original designation.

Diversity and distribution
This is the largest genus of the subfamily with 75 described species (Lelej, 2002, 2005; Pagliano *et al*., 2020; Williams *et al*., 2019a). They are distributed throughout the Oriental Region and reach the Palaearctic part of China, Korean Peninsula, and Japan in the north and Afghanistan and Pakistan in the west (Lelej, 2002, 2005; Lelej *et al*., 2013).

Remarks
The *Bischoffitilla* species are tiny wasps and hard to identify. Identification keys to the species from China, Taiwan, the islands of Pacific Ocean, and southern Thailand were provided by Chen (1957), Mickel (1935) (supplemented by Tsuneki *et al*., 1993), and Williams *et al*. (2019a). However, many morphospecies that cannot be readily identified with

those references are recognized in Vietnam and neighboring countries (personal observation).

Bischoffitilla cambrai Williams, 2019

urn:lsid:zoobank.org:act:CCD60BD9-4D5C-458A-9B23-EB15067CDF8D

(Figs 4A, 4B)

Bischoffitilla cambrai Williams in Williams *et al*., 2019a: 13, ♀, holotype ♀ (Khlong Sok, Surat Thani, Thailand) [CSCA]; Pagliano *et al*., 2020: 141.

Distribution

Thailand. Vietnam: Lao Cai (Williams *et al*., 2019a).

Occurrence in Vietnam

September. Northern Indochina subtropical forests ecoregion. 300–650 m alt.

Sex association

Male unknown.

Remarks

This species is widely distributed in Thailand and occurs in northern Vietnam.

Bischoffitilla lamellata (Mickel, 1933)

urn:lsid:zoobank.org:act:7F1DE646-0676-4D50-8D69-FAF6A113D84D

urn:lsid:zoobank.org:act:7F169B49-306E-46A1-9BCC-776A36F44774

(Figs 4C–4F)

Squamulotilla lamellata Mickel, 1933b: 295, ♀, holotype ♀ (Honan Island [= Haizhu], Canton [= Guangzhou], [Guangdong], China) [UMSP]; Wu, 1941: 135; Chen, 1957: 145, ♀.

Squamulotilla arundinacea Pagden, 1934a: 445, ♀, holotype ♀ (Parit Buntar, Perak, Federated Malay States [= Malaysia]) [NHMUK]; Mickel, 1935: 196, ♀. Synonymized by Williams *et al*. (2019a: 12) under *Bischoffitilla lamellata* (Mickel).

Bischoffitilla arundinacea: Lelej, 2002: 127; Lelej, 2005: 24; Okayasu *et al*., 2018: 302, ♀; Pagliano *et al*., 2020: 140, ♀.

Bischoffitilla lamellata: Lelej, 2002: 127; Lelej, 2005: 27; Hua, 2006: 299; Barthélémy *et al*., 2018: 232, ♂♀; Okayasu *et al*., 2018: 303, ♀; Williams *et al*., 2019a: 12, ♀; Pagliano *et al*., 2020: 142.

Material examined

Vietnam: BA RIA VUNG TAU: Xuyen Moc, Binh Chau, 5.I.2002, K. Okajima leg. [1♂7♀ TUA]; Xuyen Moc, Binh Chau, 5.I.2002, T. Ishikawa leg. [3♀ TUA]; Xuyen Moc, Binh Chau, 5.I.2002, H. Mizushima leg. [1♀ TUA]; BAC KAN: Ba Be Nat[ional]. Park, 31.VII–2.VIII.2000, K. Okajima leg. [2♀ TUA]; THUA THIEN HUE: Bach Ma N[ational]P[ark], Entrance, 253/BTTNVN, 16.250°N 107.873°E, 50 m alt., Yellow pan trap, 2–6.VIII.2016, T. Mita leg. [1♂ VNMN].

Identification source

Compared with voucher specimens (Chen, 1957) [TARI] and description in Barthélémy *et al*. (2018).

Distribution
China. Malaysia. Thailand. Vietnam: additional data unavailable (Lelej, 2005), Ba Ria Vung Tau*, Bac Kan*, Thua Thien Hue*.

Occurrence in Vietnam
January, July, August. South China-Vietnam subtropical evergreen forests, Northern Vietnam lowland rain forests, and Southern Vietnam lowland dry forests ecoregions. 50 m alt.

Sex association
This species was initially described from the female only. The male of this species was associated and described by Barthélémy *et al*. (2018) based on males and females collected at same place.

Remarks
This species is the most widely distributed and commonest *Bischoffitilla* species in Indochina.

Bischoffitilla perakensis **(Pagden, 1934)**
urn:lsid:zoobank.org:act:2E2FF3BB-1024-4B75-8E51-75F7D17510FA
(Figs 4G, 4H)

Squamulotilla perakensis Pagden, 1934a: 448, ♀, holotype ♀ (Parit Buntar, Perak, Federated Malay States [= Malaysia]) [NHMUK]; Mickel, 1935: 196, ♀.
Bischoffitilla perakensis: Lelej, 2002: 127; Lelej, 2005: 28; Okayasu *et al*., 2018: 306; Williams *et al*., 2019a: 13, ♀; Pagliano *et al*., 2020: 142; Thaochan *et al*., 2022: 163, ♀.

Material examined
Vietnam: HANOI: Hanoi University of Agriculture, 16.VIII.2000, K. Okajima leg. [1♀ TUA].

Identification source
Compared with a voucher specimen (Williams *et al*., 2019a) [THNHM].

Distribution
Malaysia. Thailand. Vietnam*: Hanoi.

Occurrence in Vietnam
August. Red River freshwater swamp forests ecoregion.

Sex association
Male unknown.

Subfamily Mutillinae Latreille, 1802

This is the largest mutillid subfamily in the Old World (Pagliano *et al*., 2020). Four tribes were recognized in this subfamily by Brothers & Lelej (2017): Ctenotillini Brothers & Lelej, 2017, Mutillini Latreille, 1802 (subdivided into Ephutina and Mutillina), Smicromyrmini Bischoff, 1920, and Trogaspidiini Bischoff, 1920. Waldren *et al*. (2023) further added three tribes, Psammothermini Waldren, 2023 (separated from Smicromyrmini sensu Brothers &

Lelej, 2017), Pristomutillini Waldren, 2023, and Zeugomutillini Waldren, 2023 (separated from Ctenotillini sensu Brothers & Lelej, 2017). One genus of Ctenotillini, two genera of Mutillini, 10 genera of Smicromyrmini, 14 genera of Trogaspidiini, and one genus of Zeugomutillini have been recorded from the eastern Oriental Region (Lelej, 2005, 2023; Lelej *et al*., 2023; Okayasu, 2021; Pagliano *et al*., 2020).

Tribe Ctenotillini Brothers & Lelej, 2017

Genus *Williamstilla* Lelej, 2023

urn:lsid:zoobank.org:act:A27D4891-3152-4CA1-AB82-A285AC584781

Williamstilla Lelej, 2023: 16, ♂♀. Type species: *Ctenotilla guangdongensis* Lelej, 1992 (♀), by original designation.

Diversity and distribution
This genus includes the type species only.

Remarks
The type species was previously included in *Ctenotilla* Bischoff, 1920 (Lelej, 1992). Identification keys to distinguish the Oriental ctenotilline genera and species were provided by Lelej (2023).

Williamstilla guangdongensis (Lelej, 1992)

urn:lsid:zoobank.org:act:9AEF624E-509D-4A4D-AB7D-AA6A281D2C50
(Figs 5A, 5B)

Ctenotilla guangdongensis Lelej, 1992: 282, ♀, holotype ♀ (Ding Hu Shan, Guangdong, China) [SCAU]; Lelej, 2005: 34; Brothers & Lelej, 2017: 56, ♂♀; Okayasu *et al*., 2018: 303, ♀; Williams *et al*., 2019a: 15, ♀; Pagliano *et al*., 2020: 161; Thaochan *et al*., 2022: 163, ♀.
Williamstilla guangdongensis: Lelej, 2023: 18, ♂♀.

Material examined
Vietnam: BAC KAN: Ba Be National Park, 31.VII–2.VIII.2000, K. Okajima leg. [1♀ TUA]; VINH PHUC: Ngoc Thanh, Me Linh, 22°16′51″N 105°71′54″E, 10.IV.2021, Malaise trap, IED's collectors leg. [1♂ IEBR].

Identification source
Keyed using Lelej (2023) and compared with voucher specimens (Williams *et al*., 2019a) [THNHM].

Distribution
Cambodia. China. Laos. Thailand. Vietnam: additional data unavailable (Williams *et al*., 2019a), Bac Kan*, Vinh Phuc*.

Occurrence in Vietnam
April, July, August. South China-Vietnam subtropical evergreen forests ecoregion.

Sex association
This species was initially described from the female only. The male of this species was

recognized by Brothers & Lelej (2017) and later described and illustrated by Lelej (2023). However, the evidence of this association was not indicated in any of these publications. Williams *et al*. (2019a) examined a pair *in copula* from Thailand.

Tribe Mutillini Latreille, 1802

Genus *Kurzenkotilla* Lelej, 2005

urn:lsid:zoobank.org:act:78E724C0-6D12-45B8-A3EE-B1099578F97E

Kurzenkotilla Lelej, 2005: 34, ♀; Lelej *et al*., 2023: 458, ♂♀. Type species: *Artiotilla ariana* Lelej in Lelej & Kabakov, 1980 (♀), by original designation.

Diversity and distribution

This genus includes nine species (Lelej *et al*., 2023). The type species is the only Palaearctic member of the genus. In East Asia, this genus is represented by two species, both of which occur in Vietnam. Other six species are known from South Asia.

Remarks

This genus, together with other Oriental mutilline genera, was recently reviewed by Lelej *et al*. (2023).

Kurzenkotilla annamensis Lelej, 2005

urn:lsid:zoobank.org:act:A86110FB-27A9-42C4-A22A-E5B7FF476C6A

(Figs 5C, 5D)

Kurzenkotilla annamensis Lelej, 2005: 171, ♀, holotype ♀ (Naca, Con River, Nghe An, Vietnam) [IBSS]; Zhou *et al*., 2018a: 25, ♀; Pagliano *et al*., 2020: 225; Lelej *et al*., 2023: 459, ♂♀.

Distribution

China. Thailand. Vietnam: Hoa Binh, Nghe An, Ninh Thuan (Lelej, 2005; Lelej *et al*., 2023).

Occurrence in Vietnam

May, September. Northern Indochina subtropical forests and Southern Vietnam lowland dry forests ecoregions. 90–200 m alt.

Sex association

This species was initially described from the female only. The male of this species was associated and described by Lelej *et al*. (2023) based on overlapping distribution and morphological similarity to *K. harmandi* in both sexes.

Kurzenkotilla harmandi (André, 1898)

urn:lsid:zoobank.org:act:F55B5071-8EBA-4467-95A3-0A6EEE5CC664

(Figs 5E, 5F)

Mutilla harmandi André, 1898: 29, ♂, holotype ♂ (Lakhon [= Laos or Thailand]) [MNHN]; André, 1902b: 39; Lelej, 2005: 35; Williams *et al*., 2019a: 31; Pagliano *et al*., 2020: 229; Thaochan *et al*., 2022: 163, ♀; Waldren *et al*., 2023: 469.
Kurzenkotilla annamensis (non Lelej, 2005): Williams *et al*., 2019a: 31.
Kurzenkotilla harmandi: Lelej *et al*., 2023: 461, ♂♀.

Material examined
Vietnam: DAK LAK: Dak Lak Prov., Krong Bong District, Chu Yang Sin National Park, 12°29′00.1″N 108°20′21.4″E, 520 m alt., 13.III.2013, T. Mita et al. leg. [1♀ VNMN].

Identification source
Compared with voucher specimens (Lelej *et al*., 2023) [THNHM].

Distribution
Laos. Thailand. Vietnam*: Dak Lak.

Occurrence in Vietnam
March. Southern Annamites montane rain forests ecoregion. 520 m alt.

Sex association
This species was initially described from the male only. The female of this species was associated and described by Lelej *et al*. (2023) based on identical ITS1 sequences.

Remarks
Two Southeast Asian species of the *Kurzenkotilla*, *K. annamensis* and *K. harmandi*, are apparently closely related and distinguished only by the setal color and markings on the male metasoma, female mesosomal shape, and size of setal spots on the female metasomal tergum 2 (Lelej *et al*., 2023).

Tribe Smicromyrmini Bischoff, 1920

Genus *Andreimyrme* Lelej, 1995
urn:lsid:zoobank.org:act:591352DA-D3B9-4B61-8210-9C26B1FF9643

Andreimyrme Lelej, 1995b: 5, ♂♀; Okayasu *et al*., 2021b: 3, ♀; Lelej & Williams, 2023: 108, ♂♀. Type species: *Andreimyrme long* Lelej, 1995 (♂), by original designation.

Diversity and distribution
This genus includes 20 species and one subspecies. Most species are distributed in Southeast Asia. Two species also reach the Palaearctic part of China and one species is known from a single locality in India.

Remarks
This genus was recently reviewed by Okayasu *et al*. (2021b) based on the female morphology. Many species are known only from the female and discovery of males is awaited.

Andreimyrme borkenti (Williams, 2019)
urn:lsid:zoobank.org:act:5208A335-E3C0-4D78-8072-D7AE91A8079B
(Figs 6A, 6B)

Smicromyrme borkenti Williams in Williams *et al*., 2019a: 28, ♀, holotype ♀ (Phnom Bencha Mountain Resort, 14 km NNE Krabi, Krabi, Thailand) [CSCA]; Pagliano *et al*., 2020: 193.
Andreimyrme borkenti: Okayasu *et al*., 2021b: 11, ♀; Thaochan *et al*., 2022: 163, ♀.

Material examined
Vietnam: HANOI: Ba Vi, Mt. Tan Vien, 500 m [alt.], 15.X.1995, M. Tomokuni leg. [1♀ NSMT].

Identification source
Voucher specimen (Okayasu *et al*., 2021b).

Distribution
Thailand. Vietnam: Hanoi (Okayasu *et al*., 2021b).

Occurrence in Vietnam
October. Red River freshwater swamp forests ecoregion. 500 m alt.

Sex association
Male unknown.

Andreimyrme matsumotoi Okayasu, 2021

urn:lsid:zoobank.org:act:F1B7AF0E-D87A-46F9-BCA2-D714CA0763CC
(Figs 6C, 6D)

Andreimyrme matsumotoi Okayasu in Okayasu *et al*., 2021b: 13, ♀, holotype ♀ (Tam Dao, Vinh Phuc, Vietnam) [VNMN].

Material examined
Holotype ♀: **Vietnam:** VINH PHUC: Tam Dao, 900–1200 m [alt.], 6.V.1998, R. Matsumoto leg. [VNMN].

Identification source
Voucher specimen (Okayasu *et al*., 2021b).

Distribution
Vietnam: Vinh Phuc (Okayasu *et al*., 2021b).

Occurrence in Vietnam
May. South China-Vietnam subtropical evergreen forests ecoregion. 900–1200 m alt.

Sex association
Male unknown.

Andreimyrme rong Williams, 2021

urn:lsid:zoobank.org:act:C4ED6FC7-5C7C-4553-8337-7C6EB9F55E43
(Figs 6E, 6F)

Andreimyrme rong Williams in Okayasu *et al*., 2021b: 17, ♀, holotype ♀ (Chu Yang Sin National Park, Krong K'Mar, Dak Lak, Vietnam) [RMNH]; Lelej & Williams, 2023: 104, ♀.

Distribution
Thailand. Vietnam: Dak Lak (Okayasu *et al*., 2021b).

Occurrence in Vietnam
June. Southern Annamites montane rain forests ecoregion. 740–900 m alt.

Sex association
Male unknown.

***Andreimyrme substriolata* (Chen, 1957)**
urn:lsid:zoobank.org:act:7858997B-0A13-4D21-B748-922114BA2618
urn:lsid:zoobank.org:act:E44C59A0-5F97-4CBE-9DE5-01A839934014
(Figs 6G, 6H)

Smicromyrme substriolata Chen, 1957: 209, ♀, holotype ♀ (Kuling [= Guling], Kiangsi [= Jiangxi], China) [TARI]; He *et al*., 2004: 958, ♀.
Smicromyrme tridentiens Chen, 1957: 213, ♀, holotype ♀ (Tachulan [= Dazhulan], Fukien [= Fujian], China) [TARI]. Synonymized by Okayasu (2020: 58) under *Andreimyrme substriolata* (Chen).
Andreimyrme tridentiens: Lelej, 1995b: 8, ♀; Lelej, 2005: 38; Hua, 2006: 299; Okayasu *et al*., 2018: 303, ♀; Pagliano *et al*., 2020: 169.
Andreimyrme substriolata: Lelej, 1995b: 9, ♀; Lelej, 2002: 50; Lelej, 2005: 38; Hua, 2006: 299; Lo Cascio, 2015: 544; Okayasu *et al*., 2018: 303, ♀; Okayasu, 2020: 58, ♀; Pagliano *et al*., 2020: 169; Okayasu *et al*., 2021b: 22, ♀; Thaochan *et al*., 2022: 163, ♀; Terine *et al*., 2024.

Material examined
Vietnam: HANOI: Mt. Bavi, 800–1000 m [alt.], VII.1941, A. De Cooman leg. [1♀ TARI]; SON LA: Sop Cop, Sop Cop N[ature]R[eserve], 20°58′57″N 103°35′11″E, 812 m, 25.VI.2022, NTP L, TTN, NQC [1♀ IEBR]; THUA THIEN-HUE: Bach Ma N[ational]P[ark], 19 km point, 253/BTTNVN, 1400 m [alt.], 16.198°N 107.860°E, 6.VIII.2016, Y. Komeda leg. [1♀ VNMN].

Identification source
Voucher specimens (Okayasu *et al*., 2021b).

Distribution
China. Taiwan. India. Indonesia. Japan. Laos. Malaysia. Thailand. Vietnam: Gia Lai, Hanoi, Hoa Binh, Son La*, Thua Tien Hue (Lelej, 1995b; Okayasu, 2020; Okayasu *et al*., 2021b).

Occurrence in Vietnam
June, July, August, October. Northern Indochina subtropical forests, Red River freshwater swamp forests, Northern Vietnam lowland rain forests, and Southern Vietnam lowland dry forests ecoregions. 800–1400 m alt. Forest.

Sex association
Male unknown.

Remarks
This is the most widespread *Andreimyrme* species and is variable in color and setation (Okayasu *et al*., 2021b).

Andreimyrme yotoi Okayasu, 2021

urn:lsid:zoobank.org:act:97F67DB2-0766-4DA1-B02F-0F58250BA4EA

(Figs 6I. 6J)

Andreimyrme yotoi Okayasu in Okayasu *et al*., 2021b: 29, ♀, holotype ♀ (Cuc Phuong National Park, Nho Quan, Ninh Binh, Vietnam) [VNMN].

Material examined

Holotype ♀: **Vietnam:** NINH BINH: Nho Quan, Cuc Phuong N[ational]. P[ark]., 314/BTTNVN, 500 m [alt.], 20.348°N 105.598°E, 9–11.VIII.2016, yellow pan trap, Y. Komeda & T. Mita leg. [VNMN].

Identification source

Voucher specimen (Okayasu *et al*., 2021b).

Distribution

Laos. Vietnam: Ninh Binh (Okayasu *et al*., 2021b).

Occurrence in Vietnam

August. Northern Vietnam lowland rain forests ecoregion. 500 m alt.

Sex association

Male unknown.

Genus *Ephucilla* Lelej, 1995

urn:lsid:zoobank.org:act:41652F68-54AD-400A-A3D0-D8391509984C

Ephucilla Lelej, 1995b: 10, ♂; Lelej, 2005: 39, ♂♀; Okayasu, 2020: 62, ♂♀; Lelej & Williams, 2023: 112, ♂♀. Type species: *Mutilla naja* Zavattari, 1913 (♂), by original designation.

Diversity and distribution

This genus includes 17 Oriental species (Lelej, 2005, 2020b; Okayasu, 2020).

Remarks

Three specie-groups are recognized within *Ephucilla* based on the male morphology by Lelej (1995b). Identification keys to males of the *naja* group and all females of the genus were provided by Okayasu (2020).

Ephucilla bacbo (Lelej, 1995)

urn:lsid:zoobank.org:act:1D7326D1-18A5-460D-A12A-73EA5801DE13

(Figs 7A, 7B)

Sinotilla bacbo Lelej, 1995b: 24, ♀, holotype ♀ (Trung Trang, Haiphong, North Vietnam) [ZISP]; Lelej, 1996c: 98, ♀.

Ephucilla bacbo: Lelej, 2005: 39; Lo Cascio, 2015: 548; Okayasu *et al*., 2018: 309, ♀; Okayasu, 2020: 64; Pagliano *et al*., 2020: 171.

Distribution

Indonesia. Vietnam: Hai Phong (Lelej, 1995b).

Occurrence in Vietnam
January. Red River freshwater swamp forests ecoregion.

Sex association
Male unknown.

Ephucilla viet (Lelej, 1995)

urn:lsid:zoobank.org:act:4B896FBA-7FDA-4325-9F2B-2159CB4CD7E6
(Figs 7C, 7D)

Sinotilla viet Lelej, 1995b: 25, ♀, holotype ♀ (Dong Kho, Quang Ninh, Vietnam) [IBSS].
Ephucilla viet: Lelej, 2005: 41; Lo Cascio, 2015: 548; Okayasu *et al*., 2018: 303, ♀; Williams *et al*., 2019a: 17, ♀; Okayasu, 2020: 65; Pagliano *et al*., 2020: 172.

Distribution
Malaysia. Thailand. Vietnam: Quang Ninh, Vinh Phuc (Lelej, 1995b; Williams *et al*., 2019a).

Occurrence in Vietnam
March, May. South China-Vietnam subtropical evergreen forests ecoregion.

Sex association
Male unknown.

Genus *Mickelomyrme* Lelej, 1995

urn:lsid:zoobank.org:act:18E1B55F-1A03-4FAC-AA77-CAEFCF661142

Mickelomyrme Lelej, 1995a: 17, ♂♀; Lelej, 1996d: 278, ♂♀; Lelej & Williams, 2023: 116, ♂♀. Type species: *Mutilla hageni* Zavattari, 1913 (♂), by original designation.

Diversity and distribution
This genus includes 23 Oriental species (Lelej, 1996d, 2005; Thaochan *et al*., 2022; Williams *et al*., 2019a). Two of them also occur in the Palaearctic part of China.

Remarks
This genus was reviewed by Lelej (1996d). However, many species were subsequently recognized (Lelej, 2005; Thaochan *et al*., 2022; Williams *et al*., 2019a). The *Mickelomyrme* species are generally small and are abundant in Southeast Asia (Williams *et al*., 2019a).

Mickelomyrme abnorma (Chen, 1957)

urn:lsid:zoobank.org:act:6E185071-C3C6-4585-BA6D-8AA4C00BEC29

Smicromyrme norna abnorma Chen, 1957: 203, ♂, holotype ♂ (Kuling [= Guling], [Lushan, Jiujiang], Kiangsi [= Jiangxi], China) [TARI].
Smicromyrme norna alnorma: He *et al*., 2004: 953, ♂. Incorrect subsequent spelling.
Mickelomyrme abnorma: Lelej, 1996d: 285, ♂; Lelej, 2002: 54; Lelej, 2005: 43; Hua, 2006: 300; Okayasu, 2020: 44; Pagliano *et al*., 2020: 174.

Distribution
China. Thailand. Vietnam: Son La (Lelej, 1996d).

Occurrence in Vietnam
May. Northern Indochina subtropical forests ecoregion. 400–600 m alt.

Sex association
Female unknown.

Mickelomyrme athalia (Pagden, 1949)

urn:lsid:zoobank.org:act:AD804EF8-B945-4B9E-8129-B5FE7CDFBDA7
(Figs 8A–8D)

Smicromyrme athalia Pagden, 1949: 219, ♂♀, holotype ♂ (Kuala Lumpur, Malaysia) [NHMUK].
Mickelomyrme athalia: Lelej, 1995a: 17; Lelej, 1996d: 280, ♂♀; Lelej, 2005: 43; Okayasu *et al*., 2018: 303, ♀; Williams *et al*., 2019a: 18, ♂♀; Okayasu, 2020: 44, ♂; Pagliano *et al*., 2020: 174.
Mickelomyrme hageni (non Zavattari, 1913): Barthélémy *et al*., 2018: 235, ♂.

Material examined
Vietnam: BA RIA VUNG TAU: Xuyen Moc, Binh Chau, 4.I.2002, K. Okajima leg. [3♀ TUA]; Xuyen Moc, Binh Chau, 4.I.2002, S. Okajima leg. [1♀ TUA]; Xuyen Moc, Binh Chau, 5.I.2002, T. Ishikawa leg. [3♀ TUA]; Xuyen Moc, Binh Chau, 5.I.2002, H. Mizushima leg. [2♀ TUA]; Xuyen Moc, Binh Chau, 5.I.2002, S. Okajima leg. [7♀ TUA].

Identification source
Compared with voucher specimens (Williams *et al*., 2019a) [THNHM].

Distribution
China. Laos. Malaysia. Thailand. Vietnam: Ba Ria Vung Tau*, Hoa Binh (Okayasu, 2020).

Occurrence in Vietnam
January, July. Northern Indochina subtropical forests and Southern Vietnam lowland dry forests ecoregions.

Sex association
This species was described from both sexes collected at same place and time.

Mickelomyrme chinensis (Smith, 1855)

urn:lsid:zoobank.org:act:0A34468C-70F8-47C6-82C6-ACC4805AA38C
urn:lsid:zoobank.org:act:223CAAB6-C68D-4DFF-AC86-7C7678BFD5FA
(Figs 8E–8H)

Mutilla chinensis Smith, 1855: 38, ♀, holotype ♀ (North China) [NHMUK]; Dalla Torre, 1897: 23; André, 1902b: 38.
Mutilla exacta Smith, 1879: 201, ♂, holotype ♂ (Shanghai, China) [NHMUK]; Dalla Torre, 1897: 38; André, 1902b: 39. Synonymized by Zhou *et al*. (2018a: 25) under *Mickelomyrme chinensis* (Smith).
Smicromyrme chinensis: Mickel, 1933b: 318, ♀; Wu, 1941: 134; Hammer, 1949: 11, ♀; Yasumatsu, 1951: 70, ♀; Chen, 1957: 208, ♀; Lelej, 2002: 73; He *et al*., 2004: 948; Lelej, 2005: 58; Hua, 2006: 301.

Smicromyrme exacta: Mickel, 1933b: 323, ♂; Yasumatsu, 1948: 73, ♂; Chen, 1957: 201, ♂; He *et al*., 2004: 950, ♂.
Mickelomyrme exacta: Lelej, 1995a: 17; Lelej, 1996d: 285, ♂; Lelej, 2002: 54; Lelej, 2005: 43; Hua, 2006: 300; Brothers & Lelej, 2017: 58.
Mickelomyrme chinensis: Zhou *et al*., 2018a: 25, ♂♀; Okayasu *et al*., 2018: 303, ♀; Williams *et al*., 2019a: 7, ♀; Okayasu, 2020: 44; Pagliano *et al*., 2020: 175.

Material examined
Vietnam: NINH BINH: Cuc Phuong, 200–300 m alt., 25.IV.1998, R. Matsumoto leg. [1♀ OMNH]; Cuc Phuong N[ational]. P[ark]., Nho Quan, 500 m, 20.348°N 105.598°E, (314/BTTNVW), 9–11.VIII.2016, Y. Komeda & T. Mita leg., YPT [1♀ ELKU]. VINH PHUC: Phúc Yên, Ngọc Thanh, Melinh Biodiversity Station, 21.3884995°N 105.712599695°E, 68 m alt., 6.VI.2023, L.T.P. Nguyen et al. leg. [1♀ IEBR].

Identification source
Compared with voucher specimens (Chen, 1957) [TARI].

Distribution
China. Laos. Vietnam: Ninh Binh, Vinh Phuc* (Zhou *et al*., 2018a).

Occurrence in Vietnam
April, May, June, August. South China-Vietnam subtropical evergreen forests and Northern Vietnam lowland rain forests ecoregions. 68–500 m alt.

Sex association
This species was initially described from the female only. The male of this species was described as *Mutilla exacta* Smith, 1879 and was associated by Zhou *et al*. (2018a) based on males and females collected at same place and time.

Mickelomyrme kuznetsovi Lelej, 1996
urn:lsid:zoobank.org:act:333496C6-F099-441A-B613-181E4D54D350

Smicromyrme triguttata latisquamula: Chen, 1957: 209, ♀, part.
Mickelomyrme kuznetsovi Lelej, 1996d: 283, ♀, holotype ♀ (Il. Phong Vong, Quang Ninh, North Vietnam) [ZISP]; Lelej, 2005: 44; Brothers & Lelej, 2017: 58, ♀; Okayasu, 2018: 481, ♀; Okayasu *et al*., 2018: 303, ♀; Williams *et al*., 2019a: 19, ♀; Okayasu, 2020: 44.

Distribution
China. Laos. Thailand. Vietnam: Quang Ninh (Lelej, 1996d).

Occurrence in Vietnam
October. South China-Vietnam subtropical evergreen forests ecoregion. 185 m alt. “Open glade with rare grass”.

Sex association
Male unknown.

Remarks
This species is likely a synonym of *M. athalia*, because the diagnostic features of *M.*

kuznetsovi (Lelej, 1996d) are inadequate to separate it from *M. athalia* (Williams *et al*., 2019a).

Mickelomyrme pusillaeformis (Hammer, 1962)

urn:lsid:zoobank.org:act:3DF335AE-89E4-472B-81C7-8AB701C51968
urn:lsid:zoobank.org:act:1AFAA2AE-0326-4146-87BD-566B0915D525
(Figs 9A, 9B)

Smicromyrme pusillaeformis Hammer, 1962: 34, ♀, holotype ♀ (Mergui, [Myanmar]) [IMK]; Lelej, 2005: 63.
Smicromyrme (*Nemka*) *hageni*: Lelej & Yamane, 1992: 631, ♂♀, part.
Mickelomyrme yunnanensis Lelej, 1996d: 280, ♂♀, holotype ♂ (Niner-Dajie, Yunnan, China) [ZMMU]; Lelej, 2005: 45; Brothers & Lelej, 2017: 58, ♂; Okayasu, 2018: 480, ♀; Okayasu *et al*., 2018: 303, ♀. Synonymized by Williams *et al*. (2019a: 19) under *Mickelomyrme pusillaeformis* (Hammer).
Mickelomyrme pusillaeformis: Williams *et al*., 2019a: 19, ♀; Okayasu, 2020: 44, ♀; Pagliano *et al*., 2020: 175; Thaochan *et al*., 2022: 163, ♀.

Distribution
China. Indonesia. Laos. Myanmar. Thailand. Vietnam: Dong Nai (Okayasu *et al*., 2018; Williams *et al*., 2019a).

Occurrence in Vietnam
May. Southeast Indochina dry evergreen forests ecoregion. 100 m alt.

Sex association
This species was initially described from the female only. The male was associated and described as *M. yunnanensis* Lelej, 1996 based on a pair *in copula* (Lelej, 1996d; Lelej & Yamane, 1992; Williams *et al*., 2019a).

Mickelomyrme puttasoki Williams, 2019

urn:lsid:zoobank.org:act:A7F3B42B-4251-46FD-9EE0-94F912AA3FF3
(Figs 9C, 9D)

Mickelomyrme puttasoki Williams in Williams *et al*., 2019: 20, ♀, holotype ♀ (Vimarnin farm stay, Thong Pha Phum, Kanchanaburi, Thailand) [CSCA]; Okayasu, 2020: 44; Pagliano *et al*., 2020: 175.

Material examined
Vietnam: BA RIA VUNG TAU: Xuyen Moc, Binh Chau, 4.I.2002, K. Okajima leg. [2♀ TUA], 5.I.2002 [7♀ TUA]; Xuyen Moc, Binh Chau, 4.I.2002, S. Okajima leg. [2♀ TUA], 5.I.2002 [1♀ TUA]; Xuyen Moc, Binh Chau, 5.I.2002, T. Ishikawa leg. [3♀ TUA]; Xuyen Moc, Binh Chau, 5.I.2002, H. Mizushima leg. [3♀ TUA].

Identification source
Keyed using Williams *et al*. (2019a) and compared with the original description.

Distribution
Thailand. Vietnam*: Ba Ria Vung Tau.

Occurrence in Vietnam
January. Southern Vietnam lowland dry forests ecoregion.

Sex association
Male unknown.

Remarks
This species was described from southern Thailand and is newly recorded from Vietnam. At Vimardin farm stay in Thailand and Binh Chau in Vietnam, *M. athalia* and *M. puttasoki* were collected at same time (Williams *et al*., 2019a).

Genus *Nemka* Lelej, 1985

urn:lsid:zoobank.org:act:FABE9198-1559-4438-A6E2-4F2D8291C919
urn:lsid:zoobank.org:act:E9BF1217-9DD6-40C7-9E11-D067B9BAE086

Smicromyrme (*Nemka*) Lelej, 1985: 240, ♂♀. Type species: *Mutilla viduata* Pallas, 1773 (♂), by original designation.
Nemka: Lelej, 1995a: 2, ♂♀; Lelej & Williams, 2023: 118, ♂♀.
Smicromyrme (*Horaia*) Tsuneki, 1993 (non Tonnoir, 1930): 43, ♂. Synonymized by Lelej (1995a: 2). Type species: *Smicromyrme* (*Horaia*) *chihpenchius* Tsuneki, 1993 (♂) (misspelled as "*chihpenchia*"), by original designation = *Mutilla wotani* Zavattari, 1913 (♀) (syn. by Okayasu, 2020).

Diversity and distribution
This genus is widely distributed throughout the Palaearctic Region, from western Europe and North Africa to the Palaearctic part of China and Japan, and also occurs in the continental Oriental Region. Eighteen species are included (Lelej, 1995a, 2005; Okayasu, 2020).

Remarks
Only one *Nemka* species has been recorded from Vietnam. However, there are additional three species occurring in Indochina, which might eventually be found in Vietnam.

Nemka limi (Chen, 1957)

urn:lsid:zoobank.org:act:B7B76A3A-3785-489D-9645-B0AD37568B78
urn:lsid:zoobank.org:act:46E9C74D-3B42-4FD4-ABD3-1E28774ECFFA
(Figs 9E–9H)

Smicromyrme wotani (non Zavattari, 1913): Yasumatsu, 1938: 85, ♀; Yasumatsu, 1951: 70, ♀.
Smicromyrme limi limi Chen, 1957: 215, ♀, holotype ♀ (Chusan [= Zhoushan], Chekiang [= Zhejiang], China) [TARI]; He *et al*., 2004: 952, ♀.
Smicromyrme limi nanhai Chen, 1957: 216, ♀, holotype ♀ (San-ah [= Sanya], Hainan, China) [TARI]. Synonymized by Okayasu (2020: 33) under *N. limi* (Chen).
Nemka wotani (non Zavattari, 1913): Lelej, 1995a: 10, ♂♀, part; Lelej *et al*., 2001: 12, ♀; Lelej, 2002: 57, part; Lelej, 2005: 48, part; Hua, 2006: 300; Lo Cascio, 2015: 553.
Nemka limi limi: Lelej, 1995: 11, ♀; Lelej, 2005: 46; Hua, 2006: 300; Okayasu *et al*., 2018: 303, ♀; Pagliano *et al*., 2020: 176.
Nemka limi nanhai: Lelej, 1995: 11, ♀; Lelej, 2005: 46; Hua, 2006: 300; Lo Cascio, 2015: 553; Okayasu *et al*., 2018: 303, ♀; Pagliano *et al*., 2020: 176.
Nemka limi: Okayasu, 2020: 33, ♂♀.

Material examined
Vietnam: CAO BANG: Phia Oac Phia Den N[ational]P[ark] station, 30.VI.2022, Nguyen D Hiep leg. [1♀ IEBR]; LANG SON: [Lôc Binh], Montes Mauson [= Mt. Mau Son], Mai 2–3000, IV, H. Fruhstorfer leg., *Smicromyrme wotani wotani* (Zavattari), B. Petersen det. 1983 [1♂ ZMUC]; VINH PHUC: Ngoc Thanh, Me Linh Biodiversity station, 70 m, 21°23′03″N 105°42′40″E, 18.VIII.2022, NTPL, TTN [2♀ IEBR]; Phúc Yên, Ngọc Thanh, Melinh Biodiversity Station, 21.3884995°N 105.712599695°E, 68 m alt., 6.VI.2023, L.T.P. Nguyen et al. leg. [1♀ IEBR].

Identification source
Voucher specimen (Okayasu, 2020). Compared with types [TARI].

Distribution
China. South Korea. Vietnam: Cao Bang*, Lang Son, Quang Ninh, Vinh Phuc* (Lelej, 1995a; Okayasu, 2020).

Occurrence in Vietnam
April, June, August, October. South China-Vietnam subtropical evergreen forests ecoregion. 68–70 m alt.

Sex association
This species was initially described from the female only. The male of this species was associated and diagnosed by Okayasu (2020) based on males and females collected at same place and time and morphological similarities to related species in both sexes.

Genus *Promecilla* André, 1902

urn:lsid:zoobank.org:act:8CA9A025-EFE4-4894-8628-67E7FEF60DDF

Promecilla André, 1902b: 30, ♂♀; Lelej & Williams, 2023: 122, ♂♀. Type species: *Mutilla regia* Smith, 1855 (♀), by original designation.

Diversity and distribution
This genus includes 29 species, five in the Afrotropical Region, four in the southern Palaearctic Region (Central Asia and Pakistan), and 20 in the Oriental Region (Lelej, 2002, 2005, 2020b; Pagliano *et al*., 2020).

Promecilla decora (Smith, 1879)

urn:lsid:zoobank.org:act:256F9F95-ABE6-4A6B-AEB1-20DAB1086C1A
(Figs 10A–10D)

Mutilla decora Smith, 1879: 200, ♀, holotype ♀ (Pulo Penang [= Penang Island], [Penang], [Malaysia]) [NHMUK]; Dalla Torre, 1897: 30; André, 1902b: 39.
Smicromyrme decora: Pagden, 1934b: 465, ♂♀; Mickel, 1935: 288, ♀; Pagden, 1949: 222, ♂♀; Chen, 1957: 213, ♀; Lelej, 1995b: 19.
Sinotilla decora: Lelej, 2005: 55; Hua, 2006: 301; Okayasu, 2017: 152, ♀; Okayasu *et al*., 2018: 303, ♀.
Promecilla decora: Brothers & Lelej, 2017: 59, ♂♀; Barthélémy *et al*., 2018: 237, ♀; Williams *et al*., 2019a: 25, ♀; Pagliano *et al*., 2020: 183; Thaochan *et al*., 2022: 164, ♀.

Material examined
Vietnam: BAC KAN: Ba Be, Ba Be National Park, 22.23°N 105.37°E, 200 m alt., 2.V.2006, R. Matsumoto leg. [1♀ OMNH]; HOA BINH: Tonkin [= North Vietnam], Hoa Binh, A. de Cooman leg. [2♀ TARI]; VINH PHUC: Ngoc Thanh, Me Linh Biodiversity station, 21°23′01.7″N 105°42′40.7″E, 21–30.V.2020, MT, IED's coll. [1♂ IEBR]; Ngoc Thanh, Me Linh Biodiversity station, 22°16′51″N 105°71′54″E, 10.IV.2021, MT, IED [1♂ IEBR], 20.VIII.2021 [1♂ IEBR], 20.XI.2021 [1♂ IEBR]; Ngoc Thanh, Me Linh Biodiversity station, 21°23′03″N 105°42′40″E, 18.VIII.2022, NTPL, TTN [1♀ IEBR].

Identification source
Compared with voucher specimens (Williams *et al*., 2019a) [THNHM]. Compared with description in Pagden (1949).

Distribution
China. Malaysia. Thailand. Vietnam*: Bac Kan, Hoa Binh, Vinh Phuc. This species was also recorded from Myanmar (Kachin, Shan, Yangon; Magretti, 1892: 213) and Indonesia (Java; Zavattari, 1910: 9), but these records have not been verified (Mickel, 1935).

Occurrence in Vietnam
April, May, August, November. South China-Vietnam subtropical evergreen forests and Northern Indochina subtropical forests ecoregions. 200 m alt.

Sex association
This species was initially described from the female only. The male of this species was associated by Pagden (1934b) based on males and females reared from the same host and a pair *in copula*, and was described by Pagden (1949).

Remarks
This is the only Vietnamese species whose host has been recorded; Pagden (1934b) reared both sexes from the nest cells of a mud-daubing solitary wasp *Pison argentatum* Shuckard (Hymenoptera: Crabronidae). See Starr (2004) for the nesting biology of the host species.

Genus *Sinotilla* Lelej, 1995

urn:lsid:zoobank.org:act:00A7AEE2-AB00-4546-8686-1450DCB792CA

Sinotilla Lelej, 1995b: 18, ♂♀; Lelej & Williams, 2023: 125, ♂♀. Type species:
Smicromyrme cyaneiventris boheanus Chen, 1957 (♂), by original designation.

Diversity and distribution
This genus predominantly occurs in the Oriental Region and reaches the Palaearctic part of China. Twenty-one species are included.

Remarks
Identification keys to the males with a ventral mandibular lobe and to females were provided by Okayasu (2017, 2020).

Sinotilla belokobylskiji Lelej, 1995

urn:lsid:zoobank.org:act:6BCD81AA-6452-4476-BB50-DA49E10F0658
(Figs 10E, 10F)

Sinotilla belokobylskiji Lelej, 1995b: 22, ♀, holotype ♀ (Tam Dao, Vinh Phuc, Vietnam) [ZISP]; Lelej, 2005: 54; Okayasu, 2017: 152, ♀; Okayasu *et al*., 2018: 303, ♀; Williams *et al*., 2019a: 26, ♀; Okayasu, 2020: 89; Pagliano *et al*., 2020: 186; Lelej & Williams, 2023: 105, ♀.

Material examined
Vietnam: HOA BINH: Tonkin [= North Vietnam], Hoa Binh, A. de Cooman leg., *Smicr. decora* (Smith) (?) [probably Chen's hand] [1♀ TARI].

Identification source
Compared with voucher specimens (Williams *et al*., 2019a) [THNHM].

Distribution
China. Thailand. Vietnam: Hanoi, Hoa Binh, Vinh Phuc (Lelej, 1995b).

Occurrence in Vietnam
October, November. South China-Vietnam subtropical evergreen forests, Red River freshwater swamp forests, and Northern Indochina subtropical forests ecoregions. 1000 m alt. Forest, bamboo.

Sex association
Male unknown.

Sinotilla boheana (Chen, 1957)
urn:lsid:zoobank.org:act:D561B471-694C-4251-8F4D-EDFBCD3BE4E8

Smicromyrme cyaneiventris boheana Chen, 1957: 204, ♂, holotype ♂ (Tachulan [= Dazhulan], Shaowu, Fukien [= Fujian], China) [probably ZMUC].
Sinotilla boheana: Lelej, 1995b: 19, ♂; Lelej, 2005: 54; Hua, 2006: 300; Okayasu, 2017: 152; Okayasu, 2020: 89; Pagliano *et al*., 2020: 186; Lelej & Williams, 2023: 105, ♂.

Distribution
China. Vietnam: Hoa Binh (Lelej, 1995b, as Ha Son Binh).

Occurrence in Vietnam
October. Northern Indochina subtropical forests ecoregion. Forest.

Sex association
Female unknown.

Remarks
A single male specimen from Vietnam was illustrated by Lelej & Williams (2023: Fig. 74).

Genus *Smicromyrme* Thomson, 1870
urn:lsid:zoobank.org:act:B761D778-D7AB-4154-ADC0-85B065A325A6

Smicromyrme Thomson, 1870: 208, ♂♀; Lelej & Williams, 2023: 128, ♂♀. Type species: *Mutilla rufipes* Fabricius, 1787 (♀), by monotypy.

Diversity and distribution
This is the largest smicromyrmine genus with 272 species from the Afrotropical, Palaearctic, and Oriental Regions (Lelej & Williams, 2023). Thirty-six species are distributed in East Asia (Lelej, 2002, 2005; Pagliano *et al*., 2020; Thaochan *et al*., 2022). Five subgenera are recognized for the Palaearctic species. Only few East Asian species are assigned to those subgenera.

Remarks
This genus is apparently an assemblage of heterogeneous species that cannot be reliably assigned to any other genera of the Smicromyrmini. Extensive taxonomic revision is needed for South and Southeast Asian species.

Smicromyrme thaochani Williams, 2019

urn:lsid:zoobank.org:act:FC8E183E-12AF-4733-AF1E-147BBE59CA0E
(Figs 11A, 11B)

Smicromyrme thaochani Williams in Williams *et al*., 2019a: 29, ♀, holotype ♀ (Baan Maka Nature Lodge, Krachan, Kaeng, Phetchaburi, Thailand) [CSCA]; Pagliano *et al*., 2020: 203.

Material examined
Vietnam: BA RIA VUNG TAU: Xuyen Moc, Binh Chau, 4.I.2002, H. Mizushima leg. [1♀ TUA]; Xuyen Moc, Binh Chau, 4.I.2002, S. Okajima leg. [1♀ TUA]; VINH PHUC: Melinh, 21°23′N 105°42′E, alt. 56 m, 20.VII.2010, J. Kantoh leg. [1♀ ELKU]; Phúc Yên, Ngọc Thanh, Melinh Biodiversity Station, 21.3884995°N 105.712599695°E, 68 m alt., 6.VI.2023, L.T.P. Nguyen et al. leg. [2♀ IEBR].

Identification source
Keyed using Williams *et al*. (2019a) and compared with the original description.

Distribution
Thailand. Vietnam*: Ba Ria Vung Tau, Vinh Phuc.

Occurrence in Vietnam
January, June, July. South China-Vietnam subtropical evergreen forests and Southern Vietnam lowland dry forests ecoregions. 56–68 m alt.

Sex association
Male unknown.

Smicromyrme triguttatus Mickel, 1933

urn:lsid:zoobank.org:act:CA6FD63D-EBA9-4FD3-AE6C-DDB8A08B2198
urn:lsid:zoobank.org:act:A32593B6-9480-4B86-B7F9-92DC9F63593D
(Figs 11C, 11D)

Mutilla pandora (non Smith, 1857): Zavattari, 1913: 31, ♀.
Smicromyrme triguttata Mickel, 1933a: 421, ♀, holotype ♀ (Taihorin [= Dalin], [Chiayi], Formosa [= Taiwan]) [ZMNB]; Suzuki, 1934: 25; Mickel, 1935: 293, ♀.
Smicromyrme triguttata triguttata: Chen, 1957: 209, ♀; Lelej, 2005: 64; Hua, 2006: 301.
Smicromyrme triguttata latisquamula Chen, 1957: 209, ♀, holotype (Kuling [= Guling],

Kiangsi [= Jiangxi], China) [TARI]; Lelej, 1995b: 27, ♀; Lelej, 2005: 64; Hua, 2006: 301; Okayasu *et al*., 2018: 304, ♀. Synonymized by Okayasu (2018: 481) under *Smicromyrme triguttatus* Mickel.

Smicromyrme triguttatus: Okayasu *et al*., 2018: 306; Williams *et al*., 2019a: 29, ♀; Pagliano *et al*., 2020: 190; Thaochan *et al*., 2022: 164, ♀.

Smicromyrme (*Erimyrme*) *triguttatus*: Okayasu, 2018: 481, ♀.

Material examined

Vietnam: THUA THIEN HUE: Bach Ma NP, Entrance, 253/BTTNVN, 16.250°N 107.873°E, 50 m alt., Yellow pan trap, 2–6.VIII.2016, T. Mita leg. [1♀ VNMN]; near Bach Ma National Park, 19 km point, 253/BTTNVN, 16.198°N 107.860°E, 1400 m alt., 3–6.VIII.2016, Y. Komeda & T. Mita leg., Yellow pan trap [2♀ VNMN].

Identification source

Voucher specimens (Okayasu, 2018).

Distribution

China. Taiwan. Laos. Thailand. Vietnam: Thua Thien Hue, Vinh Phuc (Lelej, 1995b; Okayasu, 2018).

Occurrence in Vietnam

August, November. South China-Vietnam subtropical evergreen forests and Northern Vietnam lowland rain forests ecoregions. 50–1400 m alt.

Sex association

Male unknown.

Tribe Trogaspidiini Bischoff, 1920

Genus *Eotrogaspidia* Lelej, 1996

urn:lsid:zoobank.org:act:7CC8609D-DDEC-4B8E-BCD7-6244FBCE784D

Eotrogaspidia Lelej, 1996b: 21, ♂♀; Okayasu *et al*., 2021a: 58, ♂♀. Type species: *Mutilla auroguttata* Smith, 1855 (♀), by original designation.

Diversity and distribution

This genus includes one Palaearctic and nine Oriental species (Okayasu *et al*., 2021a). In East Asia, it is represented by four species.

Remarks

This genus was reviewed by Okayasu *et al*. (2021a).

Eotrogaspidia auroguttata (Smith, 1855)

urn:lsid:zoobank.org:act:7DBC9CA9-FCC1-45AB-9A0C-3991FD25C166
urn:lsid:zoobank.org:act:3CAD83BC-E625-49C7-92A8-D794626D5F0B
urn:lsid:zoobank.org:act:CFB0F7E2-7E71-49D9-9869-9AE3023A5E02
urn:lsid:zoobank.org:act:153492DD-30CE-49A4-BE6D-64976D4EB20D
(Figs 12A–12D)

Mutilla auroguttata Smith, 1855: 53, ♀, holotype ♀ ("Brasil", actually Xianggang [= Hong

Kong, China] according to Mickel, 1939) [NHMUK]; Dalla Torre, 1897: 14; André, 1902b: 72.

Mutilla repraesentans (non Smith, 1855): Zavattari, 1913: 29, ♀.

Mutilla analis (non Lepeletier, 1845): Zavattari, 1913: 41, ♂, part.

Timulla (*Trogaspidia*) *disparilis* Mickel, 1933a: 398, ♂, holotype ♂ (Taihorin [= Dalin], [Chiayi], Formosa [= Taiwan]) [ZMNB]; Mickel, 1933b: 314, ♂; Suzuki, 1934: 23; Mickel, 1935: 234, ♂; Wu, 1941: 136. Synonymized by Lelej (1996b: 22) under *Eotrogaspidia auroguttata* (Smith).

Timulla (*Trogaspidia*) *repraesentoides* Mickel, 1933a: 411, ♀, holotype ♀ (Hoozan [= Fengshan], [Kaohsiung], Formosa [= Taiwan]) [SDEI]; Mickel, 1933b: 309, ♀; Suzuki, 1934: 24; Mickel, 1935: 254, ♀; Wu, 1941: 136. Synonymized by Mickel (1939: 192) under *Timulla auroguttata* (Smith).

Timulla (*Trogaspidia*) *auroguttata*: Mickel, 1939: 192, ♀.

Trogaspidia disparilis: Chen, 1957: 168, ♂; Tsuneki, 1972: 6, ♂; Murota, 1973: 119, ♂; Nambu & Tano, 1983: 21, ♂; Tsuneki, 1993: 48, ♂.

Trogaspidia auroguttata auroguttata: Chen, 1957: 171, ♀.

Trogaspidia auroguttata repraesentoides: Chen, 1957: 172, ♀; Tsuneki, 1972: 8, ♀.

Trogaspidia vallicola Tsuneki, 1993: 48, ♀, holotype ♀ (Ssuchungchi, Taiwan) [MNHAH]; Hashimoto & Nakanishi, 1997: 31. Synonymized by Okayasu *et al*. (2021a: 64) under *Eotrogaspidia auroguttata* (Smith).

Eotrogaspidia auroguttata: Lelej, 1996b: 22, ♂♀; Lelej, 2002: 81; Lelej, 2005: 78; Hua, 2006: 299; Pagliano, 2011: 44, ♀; Terayama *et al*., 2011: 22, ♂♀; Lo Cascio, 2015: 548; Okayasu, 2016: 61, ♀; Terayama *et al*., 2016: 168, ♂♀; Barthélémy *et al*., 2018: 237, ♂; Okayasu *et al*., 2018: 309, ♀; Ito, 2018: 25, ♂; Williams *et al*., 2019a: 32, ♀; Pagliano *et al*., 2020: 245; Pagliano & Scaramozzino, 2021: 122, ♂♀; Okayasu *et al*., 2021a: 63, ♂♀; Thaochan *et al*., 2022: 163, ♀.

Material examined

Vietnam: BAC KAN: Ba Be Nat[ional]. Park, 31.VII–2.VIII.2000, K. Okajima leg. [3♀ TUA]; VINH PHUC: Tam Dao, 21.440811°N 105.616088°E, 383 m alt., 7.VI.2023, L.T.P. Nguyen leg. [1♀ IEBR].

Identification source

Voucher specimens (Okayasu *et al*., 2021a).

Distribution

China. Taiwan. India. Indonesia. Japan. Laos. Myanmar. Thailand. Vietnam: additional data unavailable (Pagliano & Scaramozzino, 2021), Bac Kan, Dak Lak, Hoa Binh, Nghe An, Quang Ninh, Vinh Phuc* (Okayasu *et al*., 2021a; Williams *et al*., 2019a).

Occurrence in Vietnam

March, June to August, October. South China-Vietnam subtropical evergreen forests, Northern Indochina subtropical forests, and Luang Prabang montane rain forests ecoregions. 383 m alt. Forest.

Sex association

This species was initially described from the female only. The male of this species was described as *Timulla disparilis* Mickel, 1933 and associated by Lelej (1996b) based on the sex association made by Børge Petersen. This association is supported by males and females repeatedly collected at the same place (Okayasu *et al*., 2021a; Williams *et al*., 2019a).

Remarks
Photos of the holotype of *Timulla repraesentoides* are available from: http://twinsecttype.nmns.edu.tw/specimen/?id=NMNS-SDEI-01391 (accessed 11 October 2023).

Eotrogaspidia oryzae (Pagden, 1934)

urn:lsid:zoobank.org:act:11BEEAB7-CE24-468B-BC0D-526C6DFF85B8
(Figs 12E–12H)

Timulla (*Trogaspidia*) *oryzae* Pagden, 1934a: 426, ♂♀, holotype ♂ (Simpang Lima, Alor Pongsu, Krian, Perak, Federated Malay States [= Malaysia]) [NHMUK]; Mickel, 1935: 236, ♂♀.
Timulla (*Trogaspidia*) *amans oryzae*: Pagden, 1949: 229, ♂♀.
Eotrogaspidia amans oryzae: Lelej, 1996b: 22, ♂♀; Lelej, 2005: 78.
Eotrogaspidia oryzae: Williams *et al*., 2019a: 32, ♀; Pagliano *et al*., 2020: 245; Okayasu *et al*., 2021a: 79, ♂♀; Thaochan *et al*., 2022: 163, ♀.

Distribution
Laos. Malaysia. Thailand. Vietnam: Hanoi, Hoa Binh (Okayasu *et al*., 2021a; Williams *et al*., 2019a).

Occurrence in Vietnam
May, October, December. Red River freshwater swamp forests and Northern Vietnam lowland rain forests ecoregions. 300 m alt. Meadow.

Sex association
This species was described from both sexes collected *in copula*.

Genus *Krombeinidia* Lelej, 1996

urn:lsid:zoobank.org:act:FB9E89E8-5A8D-4AA2-8C9F-F7D150DB6158

Krombeinidia Lelej, 1996b: 11, ♂♀. Type species: *Krombeinidia peterseni* Lelej, 1996 (♂♀), by original designation.

Diversity and distribution
This Oriental genus is widespread in this region with 23 species (Lelej, 2005; Okayasu, 2021, 2023; Williams *et al*., 2019).

Krombeinidia chang Williams, 2019

urn:lsid:zoobank.org:act:9A5A4C53-C44F-4C12-9780-F66B024249D3
(Figs 13A, 13B)

Krombeinidia chang Williams in Williams *et al*., 2019a: 35, ♀, holotype ♀ (Baan Maka Nature Lodge, Krachan, Kaeng, Phetchaburi, Thailand) [CSCA]; Pagliano *et al*., 2020: 250.

Material examined
Vietnam: BA RIA VUNG TAU: Xuyen Moc, Binh Chau, 5.I.2002, S. Okajima leg. [2♀ TUA].

Identification source
Keyed using Williams *et al*. (2019a) and compared with the original description.

Distribution
Thailand. Vietnam*: Ba Ria Vung Tau.

Occurrence in Vietnam
January. Southern Vietnam lowland dry forests ecoregion.

Sex association
Male unknown.

***Krombeinidia griseomaculata* (André, 1898)**
urn:lsid:zoobank.org:act:5A2D5DAD-26E7-489C-8DED-C02D1BE18F3A

Mutilla griseomaculata André, 1898: 22, ♀, holotype ♀ (Cochinchine [= south Vietnam]) [MNHN]; André, 1902b: 39.
Timulla (*Trogaspidia*) *griseomaculata*: Mickel, 1933b: 316, ♀; Yasumatsu, 1948: 72, ♀.
Smicromyrme griseomaculata: Chen, 1957: 190, ♀; He *et al*., 2004: 950, ♀.
Krombeinidia griseomaculata: Lelej, 1996b: 15, ♀; Lelej, 2005: 66; Hua, 2006: 300; Lo Cascio, 2015: 551; Pagliano *et al*., 2020: 251; Pagliano & Scaramozzino, 2021: 123, ♀.

Distribution
China. Indonesia. Thailand. Vietnam: additional data unavailable (André, 1898), Ba Ria Vung Tau, Kien Giang (Lelej, 1996b).

Occurrence in Vietnam
April. Southern Vietnam lowland dry forests ecoregion.

Sex association
Male unknown.

***Krombeinidia subfossata* (Chen, 1957)**
urn:lsid:zoobank.org:act:1ABBDE75-246A-40FC-8BC3-CBB313D4D957
(Figs 13C, 13D)

Smicromyrme subfossata Chen, 1957: 188, ♂, holotype ♂ (Suipeichieh [= Shui Pei Kai], Shaowu, Fukien [= Fujian], China) [TARI].
Petersenidia subfossata: Lelej & Yamane, 1992: 629.
Krombeinidia subfossata: Lelej, 1996b: 14, ♂; Lelej, 2005: 67; Hua, 2006: 300; Lo Cascio, 2015: 551; Pagliano *et al*., 2020: 251; Pagliano & Scaramozzino, 2021: 123, ♂; Thaochan *et al*., 2022: 163, ♂.

Distribution
China. Malaysia. Thailand. Vietnam: Gia Lai (Lelej, 1996b).

Occurrence in Vietnam
July. Southern Vietnam lowland dry forests ecoregion.

Sex association
Female unknown.

Genus *Neotrogaspidia* Lelej, 1996

urn:lsid:zoobank.org:act:ABD6AFA5-BC36-4E14-A791-FCBFD406DEC4

Neotrogaspidia Lelej, 1996b: 20, ♂♀; Okayasu, 2023a: 2, ♂♀. Type species: *Mutilla pustulata* Smith, 1873 (♀), by original designation.

Diversity and distribution
This genus includes eight species (Brothers, 2022; Lelej, 2002, 2005; Okayasu, 2023a). Seven species occur in East Asia including Wallacea and one species is known from Central Asia.

Remarks
Northeast Asian species of this genus were reviewed by Okayasu (2023a), in which an identification key to all *Neotrogaspidia* species was provided.

Neotrogaspidia circumcincta (André, 1896)

urn:lsid:zoobank.org:act:F557AD50-261A-44A6-BCAA-F1D5FEFCA3A2
urn:lsid:zoobank.org:act:3EF19E76-01EE-4CBE-A92E-37EFBD3C7FEA
urn:lsid:zoobank.org:act:E9303B87-40E6-4717-B512-45272E20255C
(Figs 13E–13H)

Mutilla circumcincta André, 1896b: 71, ♀, lectotype ♀ (Balighe [= Balige], [Sumatra Utara], Sumatra, Indonesia) [MSNG], designated by Mickel (1933b: 314); André, 1902b: 38; André, 1905: 212, ♂♀.
Timulla (*Trogaspidia*) *circumcincta*: Mickel, 1933b: 314, ♀; Mickel, 1935: 267, ♀; Wu, 1941: 136.
Trogaspidia circumcincta: Chen, 1957: 171, ♀; He *et al*., 2004: 962, ♀.
Trogaspidia yuliensis Tsuneki, 1972: 12, ♂, holotype ♂ (Yuli, Hualien Pref., Formosa [= Taiwan]) [NMNH]; Lelej, 2005: 105; Hua, 2006: 301; Pagliano *et al*., 2020: 293. Synonymized by Okayasu (2023a: 5) under *Neotrogaspidia circumcincta* (André).
Trogaspidia tethys: Tsuneki, 1993: 48, ♂.
Orientidia circumcincta: Lelej, 2005: 68; Hua, 2006: 300; Okayasu *et al*., 2018: 304, ♀; Pagliano *et al*., 2020: 254; Pagliano & Scaramozzino, 2021: 124, ♀.
Krombeinidia agricola Williams in Williams *et al*., 2019: 34, ♀, holotype ♀ (Vimarndin farm stay, Thong Pha Phum, Kanchanaburi, Thailand) [CSCA]; Pagliano *et al*., 2020: 250. Synonymized by Okayasu (2023a: 6) under *Neotrogaspidia circumcincta* (André).
Neotrogaspidia circumcincta: Okayasu, 2023a: 5, ♂♀.

Material examined
Vietnam: HANOI: Hanoi capital island in Red River, 21°3'N, 105°51'E, 24.XI.2014 [1♀ EUMJ]; HOA BINH: Tonkin [= North Vietnam], Hoa Binh, VIII.1940, A. de Cooman leg. [2♀ TARI].

Identification source
Voucher specimens (Okayasu, 2023a).

Distribution
China. Taiwan. Indonesia. Laos. Malaysia. Thailand. Vietnam: Hanoi, Hoa Binh (Okayasu, 2023a).

Occurrence in Vietnam
August, November. Red River freshwater swamp forests and Northern Indochina subtropical forests ecoregions.

Sex association
This species was initially described from the female only. The male of this species was associated and described by André (1905) based on a pair *in copula*.

Remarks
Photos of the holotype of *Trogaspidia yuliensis* are available from: http://twinsecttype.nmns.edu.tw/specimen/?id=NMNS-USNM-00083 (accessed 11 October 2023).

Genus *Nonveilleridia* Lelej, 1996

urn:lsid:zoobank.org:act:3EDBF019-C8CA-4AFA-BFC0-5E47B8013BAF

Nonveilleridia Lelej, 1996b: 20, ♂. Type species: *Mutilla bataviana* André, 1909 (♂), by original designation.

Diversity and distribution
This genus includes the type species only.

Remarks
This genus is morphologically unique and easily recognized. Discovery of the female is still awaited. Williams *et al*. (2019a) suspected that this genus might be associated with a female currently included in *Krombeinidia* or *Trogaspidia*.

Nonveilleridia bataviana (André, 1909)

urn:lsid:zoobank.org:act:ABEFADF6-CDA2-4B2D-B2C3-A3D924394D81
(Figs 14A, 14B)

Mutilla bataviana André, 1909: 177, ♂, syntypes ♂ (Moeara Antjol, [Jakarta, Indonesia]; Batavia [= Jakarta], [Indonesia]) [RMNH].
Timulla (*Trogaspidia*) *bataviana*: Mickel, 1935: 250, ♂; Pagden, 1949: 217, ♂.
Nonveilleridia bataviana: Lelej, 1996b: 20, ♂; Lelej, 2005: 80; Lo Cascio, 2015: 553; Zhou *et al*., 2018a: 27, ♂; Williams *et al*., 2019a: 37; Pagliano *et al*., 2020: 254.

Material examined
Vietnam: THUA THIEN HUE: Bach Ma N[ational]P[ark], Entrance, 16.250N, 107.873E, 50 m alt., Yellow pan trap, 2–6.VIII.2016, T. Mita leg., (253/BTTNVN) [1♂ VNMN].

Identification source
Keyed using Lelej (2005) and Mickel (1935) and compared with the original description.

Distribution
China. Indonesia. Thailand. Vietnam: Gia Lai, Hanoi, Thua Thien Hue* (Lelej, 1996b;

Williams *et al*., 2019a).

Occurrence in Vietnam
August. Red River freshwater swamp forests, Northern Vietnam lowland rain forests, and Southern Vietnam lowland dry forests ecoregions. 50 m alt.

Sex association
Female unknown.

Genus *Orientidia* Lelej, 1996

urn:lsid:zoobank.org:act:127C21B8-988D-45FB-8D0D-74CB8EBA0A90

Orientidia Lelej, 1996b: 10, ♂♀. Type species: *Mutilla proserpina* Smith, 1858 (♀), by original designation.

Diversity and distribution
This genus includes nine East Asian species.

Remarks
There is no useful key to identify *Orientidia* species.

Orientidia thoawanae Williams, 2019

urn:lsid:zoobank.org:act:5011918C-07A3-49C4-9D8A-9A13A3C31E4B
(Figs 14C, 14D)

Orientidia thoawanae Williams in Williams *et al*., 2019a: 38, ♀, holotype ♀ (Prince of Songkhla University, Hat Yai, Songkhla, Thailand) [CSCA]; Thaochan *et al*., 2022: 163, ♀.
Orientidia thoawani: Pagliano *et al*., 2020: 254. Incorrect subsequent spelling.

Material examined
Vietnam: NINH BINH: Cuc Phuong, 27.IV.1996, Y. Okushima leg. [1♀ TUA]; Nho Quan, Cuc Phuong National Park, 314/BTTNVN, 20.354N, 105.588E, 500 m alt., 8.VIII.2016, T. Mita leg. [1♀ VNMN].

Identification source
Keyed using Williams *et al*. (2019a) and compared with the original description.

Distribution
Malaysia. Thailand. Vietnam*: Ninh Binh.

Occurrence in Vietnam
April, August. Northern Vietnam lowland rain forests ecoregion. 500 m alt.

Sex association
Male unknown.

Genus *Petersenidia* Lelej, 1992

urn:lsid:zoobank.org:act:0922C40C-C9F8-4249-97B6-453953E0A270

Petersenidia Lelej in Lelej & Yamane, 1992: 628, ♂♀. Type species: *Smicromyrme fukudai* Tsuneki, 1972 (♂), by original designation.

Diversity and distribution
This genus is widespread in the Oriental Region and reaches the Palaearctic part of Japan. Forty-four species are included.

Remarks
Many species of the former Petersenidiini Lelej, 1996, whose systematic position is uncertain, are now placed in this genus (Williams *et al*., 2019a). Of the 44 *Petersenidia* species, 22 are doubtfully assigned to this genus at present.

Petersenidia dorsispinata (Chen, 1957)

urn:lsid:zoobank.org:act:2E5E791C-1710-4A1E-88DD-AE3726EE0401
(Figs 15A, 15B)

Smicromyrme dorsispinata Chen, 1957: 192, ♀, holotype ♀ (Hwangkeng, Kienyang [= Jianyang], Fukien [= Fujian], China) [TARI].
Petersenidia dorsispinata: Lelej, 2005: 70; Hua, 2006: 300; Okayasu *et al*., 2018: 304, ♀; Pagliano *et al*., 2020: 255.

Material examined
Vietnam: GIA LAI: Gia Lai Con Tum Prov. [= Gia Lai], 20 km N Buon Luoi, Tram Lap, 13.II.1993, A. Gorochov leg. [1♀ ZISP]; HOA BINH: Ha Son Binh Prov. [= Hoa Binh], Da Bac, Tuly, forest, 19.X.1990, S. Belokobylskij leg. [1♀ ZISP]; LAM DONG: South Annam Lam Dong Prov. [= Lam Dong], Cat Tien, III.2004, A. Anichkin & A. Evsyunin leg. [1♀ ZISP].

Identification source
Compared with types [TARI].

Distribution
China. Vietnam: Gia Lai, Hoa Binh, Lam Dong (Lelej, 2005; Okayasu *et al*., 2018).

Occurrence in Vietnam
February, March, October. Northern Indochina subtropical forests, Southern Annamites montane rain forests, and Southeast Indochina dry evergreen forests ecoregions. Forest.

Sex association
Male unknown.

Petersenidia leleji Williams, 2019

urn:lsid:zoobank.org:act:3A3564FB-C26C-4166-8817-22D6DD4B39B0

Petersenidia leleji Williams in Williams *et al*., 2019a: 40, ♀, holotype ♀ (2.4 km S Ban Na, Farm, Phatthalung, Thailand) [CSCA]; Pagliano *et al*., 2020: 256.

Distribution
Thailand. Vietnam: Hoa Binh, Quang Ninh, Vinh Phuc (Williams *et al*., 2019a).

Occurrence in Vietnam
March, April, October, November. South China-Vietnam subtropical evergreen forests and Northern Indochina subtropical forests ecoregions. 1120 m alt. Forest.

Sex association
Male unknown.

Petersenidia scaphella (Chen, 1957)

urn:lsid:zoobank.org:act:1F5412AA-5AD9-4B3F-AC82-E78D85461290
(Figs 15C, 15D)

Smicromyrme scaphella Chen, 1957: 187, ♂, holotype ♂ (Tachulan [= Dazhulan], Shaowu, Fukien [= Fujian], China) [TARI]; He *et al*., 2004: 956, ♂.
Petersenidia scaphella: Lelej & Yamane, 1992: 629; Lelej, 1996b: 10, ♂; Lelej, 2005: 72; Hua, 2006: 300; Pagliano *et al*., 2020: 257.

Material examined
Vietnam: LAO CAI: Sapa, Tram Ton, 1926 m alt., 22°21.182′N 103°46.49′E, 23.VI.2012, T. Mita leg. [1♂ VNMN].

Identification source
Compared with types [TARI].

Distribution
China. Vietnam: Hoa Binh, Lao Cai* (Lelej, 1996b).

Occurrence in Vietnam
June, October. Northern Indochina subtropical forests. 1926 m alt. Forest.

Sex association
Female unknown.

Genus *Promecidia* Lelej, 1996

urn:lsid:zoobank.org:act:D6565E4B-194B-4686-80F1-8371EA601CF6

Promecidia Lelej, 1996b: 15, ♀; Lelej, 2005: 80, ♂♀; Lelej *et al*., 2016: 105, ♂♀. Type species: *Promecidia yamanei* Lelej, 1996 (♀), by original designation.

Diversity and distribution
This genus is widespread in the Oriental Region with 11 species (Lelej *et al*., 2016; Williams *et al*., 2019a).

Remarks
This genus was reviewed by Lelej *et al*. (2016). Females of the *Orientidia* and *Promecidia* are easily confused by having two pale setal spots on the metasomal tergum 2 and pygidial plate smooth and convex (Williams *et al*., 2019a). However, they are clearly distinguished by the male morphology.

Promecidia birmanica (Dalla Torre, 1897)

urn:lsid:zoobank.org:act:254143AB-5358-4B50-B8C4-2A0CE5C78230

urn:lsid:zoobank.org:act:19DB50E9-9439-4302-A6D4-A874F2EA54AF

Mutilla schlettereri Magretti, 1892 (non Morawitz, 1890): 230, ♂, holotype ♂ (Monti dei Carin–Chebá [= mountain area in Karen Hills], [Myanmar]) [MSNG]; Bingham, 1897: 43, ♂.
Mutilla birmanica Dalla Torre, 1897: 16. New name for *Mutilla schlettereri* Magretti.
Promecidia birmanica: Lelej, 2005: 80, ♂; Lelej *et al*., 2016: 109, ♂; Thaochan *et al*., 2022: 164, ♂.
Promecidia ninnii: Lelej, 2005: 81, ♂, part.

Distribution
India. Laos. Myanmar. Vietnam: Dong Nai (Lelej *et al*., 2016).

Occurrence in Vietnam
August. Southeast Indochina dry evergreen forests ecoregion.

Sex association
Female unknown.

Promecidia ninnii (Magretti, 1892)

urn:lsid:zoobank.org:act:8A90104C-DDF7-4C69-9115-9AAE832F044B
(Figs 15E, 15F)

Mutilla ninnii Magretti, 1892: 211, ♀, holotype ♀ (Monti dei Carin–Chebà (900–1100 m. s./m.) [= mountain area in Karen Hills], [Myanmar]) [MSNG]; Bingham, 1897: 11, ♀; Dalla Torre, 1897: 66.
Promecidia ninnii: Lelej, 2005: 81, ♀, part; Lelej *et al*., 2016: 116, ♀; Williams *et al*., 2019a: 41, ♂♀; Pagliano *et al*., 2020: 257; Pagliano & Scaramozzino, 2021: 125, ♂.

Distribution
Cambodia. Laos. Myanmar. Thailand. Vietnam: Dong Nai (Lelej *et al*., 2016).

Occurrence in Vietnam
June. Southeast Indochina dry evergreen forests ecoregion. Forest.

Sex association
This species was initially described from the female only. The male of this species was recognized by Williams *et al*. (2019a) based on a pair *in copula*, but has not been formally associated and described.

Genus *Trogaspidia* Ashmead, 1899

urn:lsid:zoobank.org:act:BDF8410F-AC2B-410C-88F8-21FA2656E3AF

Trogaspidia Ashmead, 1899: 58, ♂♀. Type species: *Mutilla medon* Smith, 1855 (♂), by original designation.

Diversity and distribution
This is one of the most speciose and widespread mutillid genera in the Old World, with about 330 species from the Afrotropical, Australasian, Oriental, and Palaearctic Regions (Okayasu, 2023a; Okayasu *et al*., 2021a; Pagliano *et al*., 2020). Fifty-one species have been recorded

from East Asia. Although six subgenera are recognized for some of the Afrotropical species, the Oriental species are not assigned to any subgenera.

Remarks
Because of the species richness and morphological diversity, the *Trogaspidia* species are difficult to identify. Even though there are already more than 50 species, many potential new species are recognized from East Asia (personal observation).

Trogaspidia formosana (Matsumura, 1911)

urn:lsid:zoobank.org:act:F29170F5-797D-48A3-9A29-97582982E625
urn:lsid:zoobank.org:act:B526B981-CC9A-46D2-BA85-317459EE0FF0
(Figs 16A–16D)

Mutilla formosana Matsumura, 1911: 140, ♂♀, lectotype ♀ (Formosa [= Taiwan]) [SEHU], designated by Lelej (2005: 93); Matsumura, 1930: 6, pl. 14, ♂♀; Matsumura, 1931: 29, ♂♀.
Mutilla analis (non Lepeletier, 1845): Zavattari, 1913: 41, ♂, part.
Timulla (*Trogaspidia*) *formosana*: Mickel, 1935: 270.
Timulla (*Trogaspidia*) *denotata* Mickel, 1933a: 400, ♂, holotype ♂ (Formosa [= Taiwan]) [ZMNB]; Suzuki, 1934: 23; Mickel, 1935: 239, ♂. Synonymized by Chen (1957: 170) under *Trogaspidia formosana* (Matsumura).
Trogaspidia formosana: Chen, 1957: 170, ♂♀; Tsuneki, 1972: 4, ♂♀; Murota, 1973: 119, ♂; Nambu & Tano, 1983: 21, ♂; Tsuneki, 1993: 48, ♂; Lelej, 2005: 93; Hua, 2006: 301; Pagliano, 2011: 45, ♂; Lo Cascio, 2015: 562; Okayasu *et al*., 2018: 305, ♀; Pagliano *et al*., 2020: 283; Pagliano & Scaramozzino, 2021: 129, ♂.

Distribution
China. Taiwan. Vietnam: additional data unavailable (Lelej, 2005).

Sex association
This species was described from both sexes, but the evidence of this association was not indicated. Chen (1957) examined five pairs *in copula* and confirmed this treatment.

Trogaspidia fuscipennis fuscipennis (Fabricius, 1804)

urn:lsid:zoobank.org:act:92EA4EC4-5792-45C6-B9C4-30596AFB2E9E
(Figs 16E–16H)

Mutilla fuscipennis Fabricius, 1804: 436, ♂, lectotype ♂ (China) [ZMUC], designated by Mickel (1933b: 306); Olivier, 1811: 63; Dalla Torre, 1897: 42; André, 1902: 39.
Timulla (*Trogaspidia*) *fuscipennis*: Mickel, 1933b: 306, ♂♀; Wu, 1941: 136.
Trogaspidia fuscipennis fuscipennis: Chen, 1957: 169, ♂♀; He *et al*., 2004: 964, ♂♀; Lelej, 2005: 93; Hua, 2006: 301; Pagliano *et al*., 2020: 283.
Trogaspidia fuscipennis: Okayasu *et al*., 2018: 305, ♀; Williams *et al*., 2019a: 44, ♀; Thaochan *et al*., 2022: 164, ♀; Okayasu, 2023a: 18, ♂.
Eotrogaspidia auroguttata (non Smith, 1855): Barthélémy *et al*., 2018: 237, ♀.

Material examined
Vietnam: BA RIA VUNG TAU: Xuyen Moc, Binh Chau, 4.I.2002, K. Okajima leg. [3♂6♀ TUA], 5.I.2002 [6♂8♀ TUA]; Xuyen Moc, Binh Chau, 4.I.2002, T. Ishikawa leg. [2♂4♀ TUA], 5.I.2002 [12♂19♀ TUA]; Xuyen Moc, Binh Chau, 4.I.2002, H. Mizushima leg. [1♀

TUA], 5.I.2002 [16♂23♀ TUA]; Xuyen Moc, Binh Chau, 5.I.2002, S. Okajima leg. [6♀ TUA]; BAC KAN: Ba Be Nat[ional]. Park, 31.VII–2.VIII.2000, K. Okajima leg. [1♀ TUA]; HANOI: Hanoi University of Agriculture, 28.VII.2000, K. Okajima leg. [1♀ TUA]; Mt. Bavi National Park, 29.VII.2000, K. Okajima leg. [1♀ TUA]; HA TINH: Vu Quang National Park, Co Ranger Station, 18°17′45″N 105°22′30″E, ca 78 m alt., 21.IV.2022, Lien T.P Nguyen, Ngat T. Tran leg. [1♀ IEBR]; HOA BINH: Hoa Binh, 14.VII.2010, H. Kurokawa leg. [2♀ MTC].

Identification source
Compared with voucher specimens (Chen, 1957) [TARI].

Distribution
China. Thailand. Vietnam: Ba Ria Vung Tau*, Bac Kan, Hanoi*, Ha Tinh*, Hoa Binh*, Ho Chi Minh (Williams *et al*., 2019a).

Occurrence in Vietnam
January, April, July, August. South China-Vietnam subtropical evergreen forests, Red River freshwater swamp forests, Northern Indochina subtropical forests, Northern Annamites rain forests, and Southern Vietnam lowland dry forests ecoregions. ca 78 m alt.

Sex association
This species was initially described from the male only. The female of this species was associated and diagnosed by Mickel (1933b) based on a pair *in copula*.

Trogaspidia mackieae **(Cockerell, 1928)**

urn:lsid:zoobank.org:act:D4D8308E-2589-4C26-BE4E-6142A184140F
urn:lsid:zoobank.org:act:CF0E2C2B-9A10-4A2C-994F-E7032E3764AC
(Figs 17A–17D)

Mutilla mackieae Cockerell, 1928: 597, ♂♀, holotype, ♂ (Nan River, Cajun, Siam [= Thailand]) [NMNH].
Trogaspidia mackieae: Lelej, 2005: 97; Pagliano *et al*., 2020: 285; Okayasu *et al*., 2021a: 82, ♂♀.
Trogaspidia pacifica Tsuneki, 1972: 10, ♂, holotype ♂ (Chihpenchi, Taitung, Formosa [= Taiwan]) [NMNH]; Lelej, 2005; 98; Hua, 2006: 301; Pagliano *et al*., 2020: 288. Synonymized by Okayasu *et al*. (2021a: 82) under *Trogaspidia mackieae* (Cockerell).
Trogaspidia wilsoni: Williams *et al*., 2019a: 43, ♀, part.

Distribution
China. Taiwan. Thailand. Vietnam: Hanoi, Son La (Okayasu *et al*., 2021a).

Occurrence in Vietnam
May, December. Red River freshwater swamp forests and Northern Indochina subtropical forests ecoregions.

Sex association
This species was described from both sexes collected “together”.

Remarks
Photos of the holotype of *Trogaspidia pacifica* are available from:

http://twinsecttype.nmns.edu.tw/species/orig/?id=581B6C5D742EE29579E73F1A5727EF71 (accessed 11 October 2023). Morphologically, the male of this species can be confused with *Eotrogaspidia* males (Okayasu *et al*., 2021a). However, they are distinguished by the shape of male genitalia.

Trogaspidia rhea gaea Chen, 1957

urn:lsid:zoobank.org:act:EC37FB30-0E99-4E49-B8D6-521EB378D2ED

(Figs 17E–17H)

Trogaspidia rhea gaea Chen, 1957: 168, ♂♀, holotype ♂ (Wuku, Shaowu, Fukien [= Fujian], China) [TARI]; He *et al*., 2004: 968, ♂♀; Lelej, 2005: 100; Hua, 2006: 301; Okayasu *et al*., 2018: 305, ♀; Pagliano *et al*., 2020: 289.
Trogaspidia rhea: Thaochan *et al*., 2022: 164, ♀.

Material examined
Vietnam: BAC KAN: Ba Be National Park, 31.VII–2.VIII.2000, K. Okajima leg. [1♀ TUA]; CAO BANG: Pac Bo, 3.VIII.2000, S. Okajima leg. [1♀ TUA]; HANOI: Tonkin [= North Vietnam], Mont Bavi, 900 à 1000 m, VIII.1940, P.A. de Cooman leg. [1♀ TARI]; NINH BINH: Cuc Phuong N[ational]. P[ark]. Bong, 20°21′N 105°35′E, 370 m alt., 23–27.VII.2010, H. Sawada leg. [1♂ TUA]; THUA THIEN HUE: Bach Ma, ca. 800 m alt., 10.VI.2002, Y. Arita leg. [1♀ TUA].

Identification source
Compared with types [TARI].

Distribution
China. Vietnam: Bac Kan*, Cao Bang*, Ha Tinh, Hanoi*, Ninh Binh*, Thua Thien Hue* (Okayasu *et al*., 2018).

Occurrence in Vietnam
June to October. South China-Vietnam subtropical evergreen forests, Red River freshwater swamp forests, Northern Vietnam lowland rain forests, and Northern Annamites rain forests ecoregions. 98–1000 m alt.

Sex association
This species was described from both sexes collected *in copula*.

Remarks
The nominotypical subspecies is distributed in Taiwan.

Genus *Wallacidia* Lelej & Brothers, 2008

urn:lsid:zoobank.org:act:6E07EA14-51B6-4799-98C3-51B0C654B5B8

Radoszkowskius (non Ashmead, 1903): Lelej, 1996b: 17, ♂♀; Lelej, 2005: 82, ♂♀.
Wallacidia Lelej & Brothers, 2008: 64, ♂♀. Type species: *Mutilla oculata* Fabricius, 1804 (♀), by original designation.

Diversity and distribution
This genus is predominantly Oriental in distribution and reaches Palaearctic part of China. Twenty-two species are currently known (Lelej, 2005; Pagliano *et al*., 2020).

Remarks
This genus was erected to accommodate *Timulla* (*Trogaspidia*) *oculata* (Fabricius, 1804) (now *W. oculata*), *Timulla* (*Trogaspidia*) *philippinensis* (Smith, 1855) (now *W. philippinensis*), and their subspecies. O'Toole (1975) and Pagden (1949) provided keys to those subspecies, covering about a half species of the present *Wallacidia*.

***Wallacidia oculata* (Fabricius, 1804)**
urn:lsid:zoobank.org:act:9D5F453D-DEFA-49D4-A94D-844C27009D8E
urn:lsid:zoobank.org:act:050A9B97-B0C1-466E-B998-9C2A0DF8AEA1
urn:lsid:zoobank.org:act:D6CE4207-144E-4C3A-9653-58552D649359
urn:lsid:zoobank.org:act:B7D54F46-61AF-43FF-A96E-CE29759D3378
urn:lsid:zoobank.org:act:EEEA8093-A825-4BC7-999A-8EBB3D3B93F8
(Figs 18A–18D)

Mutilla oculata Fabricius, 1804: 432, ♀, holotype ♀ (China) [ZMUC]; Olivier, 1811: 60, ♀; Sichel & Radoszkowski, 1869: 229, ♀; Dalla Torre, 1897: 68; André, 1902b: 40; Bingham, 1903: iii, ♂; Bingham, 1905: 35.
Mutilla novarae de Saussure, 1867: 106, ♀, holotype ♀ (Hong Kong, China) [NHMW]; Dalla Torre, 1897: 67; André, 1902b: 40. Synonymized by Mickel (1933b: 308) under *Timulla oculata* (Fabricius).
Mutilla malayana Cameron, 1901: 16, ♂, holotype ♂ (Bukit Besar, Jalor, District of Patani State, Malay Peninsula, [Malaysia]) [NHMUK]; André, 1902b: 71. Synonymized by O'Toole (1975: 232) under *Timulla oculata oculata* (Fabricius).
Mutilla skeati Cameron, 1901: 17, ♀, holotype ♀ (Kuala Aring, State of Kelantan, Malay Peninsula, [Malaysia]) [NHMUK]; André, 1902b: 41. Synonymized by Mickel (1933a: 395) under *Timulla philippinensis malayana* (Cameron) and resurrected to full species status by Mickel (1935: 230). Synonymized by O'Toole (1975: 232) under *Timulla oculata oculata* (Fabricius).
Mutilla dimidiata (non Lepeletier, 1845): Bingham, 1905: 35.
Mutilla amartana Zavattari, 1913: 28, ♂♀, lectotype ♀ (Taihanroku [Taipan], Taiwan) [ZMNB], designated by Mickel (1933a: 391); Yano, 1932: 327, ♂♀; Hirayama, 1937: 114, pl. 56, ♂ non ♀. Synonymized by Hammer (1949: 4) under *Trogaspidia oculata* (Fabricius).
Timulla (*Trogaspidia*) *philippinensis amartana*: Mickel, 1933a: 391, ♂♀; Suzuki, 1934: 24; Mickel, 1935: 229, ♂♀.
Timulla (*Trogaspidia*) *philippinensis malayana*: Mickel, 1933a: 395, ♂♀; Mickel, 1935: 230, ♂.
Mutille [sic!] *amartana*: Kato, 1934: pl. 42, ♂♀.
Timulla (*Trogaspidia*) *philippinensis skeati*: Mickel, 1935: 230, ♀.
Timulla (*Trogaspidia*) *oculata*: Mickel, 1933b: 308, ♀; Yasumatsu, 1938b: 346, ♂; Wu, 1941: 136; Yasumatsu, 1948: 83, ♀.
Trogaspidia oculata: Hammer, 1949: 4, ♀; Hill, 1982: 84, ♀.
Trogaspidia oculata oculata: Chen, 1957: 164, ♂♀; He *et al*., 2004: 966, ♂♀.
Trogaspidia oculata amartana: Chen, 1957: 164, ♂♀; Tsuneki, 1972: 6, ♂♀; Murota, 1973: 119, ♂; Tsuneki, 1993: 47, ♂♀.
Timulla oculata oculata: O'Toole, 1975: 232, ♂♀.
Trogaspidia oculata amortana: Sabi *et al*., 1977: 42, ♂. Incorrect subsequent spelling.
Radoszkouskius oculata: Lelej, 1996b: 17, ♂♀; Lelej, 2005: 84.
Radoszkouskius oculatus: Hua, 2006: 300.

Wallacidia oculata: Lelej & Brothers, 2008: 64; Pagliano, 2011: 46, ♀; Lo Cascio, 2015: 564; Barthélémy *et al*., 2018: 239, ♂♀; Okayasu *et al*., 2018: 305: ♀; Williams *et al*., 2019a: 47, ♀; Pagliano *et al*., 2020: 295; Thaochan *et al*., 2022: 164, ♂♀.

Material examined
Vietnam: DONG NAI: Bien Hoa, 14.VII.1924, R. Vitalis de Salvaza leg. [1♂ TARI]; LAO CAI: Sapa, ca. 1500 m [alt.], 18.V.2003, Y. Arita leg. [1♀ TUA]; THUA THIEN HUE: Bach Ma, ca. 800 m [alt.], 10.VI.2002, Y. Arita leg. [1♀ TUA]; VINH PHUC: Tam Dao, 21.440811°N 105.616088°E, 383 m alt., 7.VI.2023, L.T.P. Nguyen leg. [2♀ IEBR].

Identification source
Compared with voucher specimens (Chen, 1957) [TARI].

Distribution
Cambodia. China. Taiwan. Laos. Malaysia. Myanmar. Thailand. Vietnam: Dong Nai*, Hai Phong, Hoa Binh, Khanh Hoa, Lao Cai*, Quang Ninh, Thua Thien Hue*, Vinh Phuc* (Lelej, 1996b; O'Toole, 1975).

Occurrence in Vietnam
March, May to July, September, October, December. South China-Vietnam subtropical evergreen forests, Red River freshwater swamp forests, Northern Indochina subtropical forests, Northern Vietnam lowland rain forests, Southeast Indochina dry evergreen forests, and Southern Vietnam lowland dry forests ecoregions. 383–1500 m alt.

Sex association
This species was initially described from the female only. The male of this species was associated and diagnosed by Chen (1957), but the evidence of this association was not indicated.

Remarks
Many subspecies were recognized by O'Toole (1975) from South and Southeast Asia. Lelej (1996b, 2005), however, regarded them as distinct species.

***Wallacidia retinula* (Chen, 1957)**

urn:lsid:zoobank.org:act:5011918C-07A3-49C4-9D8A-9A13A3C31E4B
(Figs 18E, 18F)

Trogaspidia retinula Chen, 1957:174, ♀, holotype ♀ (Taipei, Taiwan) [TARI].
Radoszkowskius retinulus: Lelej, 2005 85; Hua, 2006: 300.
Wallacidia retinula: Lelej & Brothers, 2008: 65; Lo Cascio, 2015: 564; Okayasu *et al*., 2018: 307, ♀; Pagliano *et al*., 2020: 295.

Material examined
Vietnam: VINH PHUC: Melinh, 21°23′N 105°42′E, alt. 56 m, 20.VII.2010, J. Kantoh leg. [1♀ ELKU].

Identification source
Compared with types [TARI].

Distribution

China. Taiwan. Vietnam*: Vinh Phuc.

Occurrence in Vietnam
July. South China-Vietnam subtropical evergreen forests ecoregion. 56 m alt.

Sex association
Male unknown. Lelej (2005) suggested that this species could be the female of *Wallacidia conversa* (Chen, 1957). This association is likely because *W. conversa* and *W. retinula* are only species of the genus occurring in China and Taiwan aside from *W. oculata*.

Remarks
This species was described based on seven females from China and Taiwan (Chen, 1957). The Vietnamese female was compared with the type specimens, and no noticeable variation was observed.

Genus *Zavatilla* Tsuneki, 1993

urn:lsid:zoobank.org:act:E7B51D45-C193-49BE-A9C8-D1EDA9421926

Smicromyrme (*Zavatilla*) Tsuneki, 1993: 42, ♂. Type species: *Mutilla gutrunae* Zavattari, 1913 (♂), by original designation.
Zavatilla: Lelej, 1995a: 2; Lelej, 2005: 77, ♂♀; Zhou *et al*., 2018b: 102, ♂♀.

Diversity and distribution
This genus includes four Oriental species. Three species, *Z. gutrunae* (Zavattari, 1913), *Z. flavotegulata* (Chen, 1957), and *Z. nepalensis* Zhou & Lelej, 2018, are tentatively endemic to Taiwan, southern China, and Nepal, respectively. *Zavatilla xuzaifui* Zhou, Lelej & Williams, 2018 is the only species occurring in Southeast Asia.

Remarks
This genus was reviewed by Zhou *et al*. (2018b).

Zavatilla xuzaifui Zhou, Lelej & Williams, 2018

urn:lsid:zoobank.org:act:54E9A955-7E1C-4EA8-9D5C-7F4C96A291A9

Zavatilla xuzaifui Zhou, Lelej & Williams in Zhou *et al*., 2018b: 111, ♂♀, holotype ♂ (Shimen Forest Park, Guangzhou, Guangdong, China) [SCAU]; Pagliano *et al*., 2020: 295.

Distribution
China. Vietnam: Hoa Binh, Tuyen Quang, Vinh Phuc (Zhou *et al*., 2018b).

Occurrence in Vietnam
April, May, October, November. South China-Vietnam subtropical evergreen forests, Northern Indochina subtropical forests, and Northern Vietnam lowland rain forests ecoregions. 300–1000 m alt. Forest.

Sex association
This species was described from both sexes because this is the only *Zavatilla* species occurring in Vietnam.

Remarks
This species represents the southernmost record of the *Zavatilla* and occurs in the northern part of Vietnam. It is unclear if this suggests the southern limits of the distribution of this genus.

Tribe *Zeugomutillini* Waldren, 2023

Genus *Zeugomutilla* Chen, 1957
urn:lsid:zoobank.org:act:1703E994-4215-4402-8E07-BFD603A7EF13

Zeugomutilla Chen, 1957: 157, ♂; Lelej, 1992: 284, ♂♀; Lelej, 2005: 37, ♂♀; Lelej *et al*., 2017: 2, ♂♀. Type species: *Zeugomutilla pycnopyga* Chen, 1957 (♂), by original designation.

Diversity and distribution
This genus includes nine Oriental species, five from South Asia and the rest four from East Asia.

Remarks
This genus was reviewed by Lelej *et al*. (2017). One additional species was recently described and an updated key was provided by Okayasu (2023c).

Zeugomutilla angkorensis Williams, 2017
urn:lsid:zoobank.org:act:FCBD211A-F555-4A05-9017-ED7710DC2813

Zeugomutilla angkorensis Williams in Lelej *et al*., 2017: 4, ♂, holotype ♂ (Cát Tiên N.P., Đồng Nai, Vietnam) [RMNH]; Pagliano *et al*., 2020: 168.

Distribution
Cambodia. Thailand. Vietnam: Dong Nai (Lelej *et al*., 2017).

Occurrence in Vietnam
May, October. Southeast Indochina dry evergreen forests ecoregion. ca. 100 m alt.

Sex association
Female unknown.

Additional species potentially occurring in Vietnam

Ticoplinae: Smicromyrmillini

Eosmicromyrmilla spp.

Remarks
The subfamily Ticoplinae Nagy, 1970 is represented by eight species in two genera of the tribe Smicromyrmillini Argaman, 1988 in South and Southeast Asia (Brothers *et al*., 2019; Lelej, 2005; Lelej & Krombein, 2001; Lelej *et al*., 2021). The genus *Hindustanilla* Lelej, 2001 occurs in India only. Contrarily, the genus *Eosmicromyrmilla* Lelej & Krombein, 2001 has four species in India and Sri Lanka, one species in Pakistan, and one species in China (Yunnan). Given its wide distribution, the latter genus might be found in Vietnam as well.

Lelej *et al*. (2021) provided identification keys to the Old World genera of Smicromyrmillini and to *Eosmicromyrmilla* species.

Mutillinae: Smicromyrmini

Mickelomyrme exiloides (Magretti, 1892)

Remarks
This species is known from China (Yunnan), northern Laos, and Myanmar (Lelej, 1996d; Magretti, 1892; Zhou *et al*., 2018a).

Nemka pagdeni Lelej, 1995

Remarks
This species was described based on four males and two females from Yunnan, China (Lelej, 1995a). Later, it was recorded from Thailand by Lelej (2005).

Nordeniella spp.

Remarks
This genus was erected for five species known from India and Sri Lanka (Lelej, 2005). Additional three species were subsequently discovered in Thailand and Indonesia (Sumbawa), suggesting wider distribution of the genus in Southeast Asia (Okayasu, 2022; Thaochan *et al*., 2022; Williams *et al*., 2019a).

Physetopoda thai Lelej, 1995

Remarks
This species is fairly widespread in Thailand and also found in Laos and Myanmar (Lelej, 1995b; Thaochan *et al*., 2022; Williams *et al*., 2019a).

Mutillinae: Trogaspidiini

Pagdenidia hymalajensis (Radoszkowski, 1885)

Remarks
Males and females of *Pagdenidia* are characteristic in their morphology (Lelej, 1996b; Pagden, 1949). However, this genus includes only seven species represented by few specimens. Of the seven described species, *P. hymalajensis* is the most widely distributed one: China (Yunnan), India, Myanmar, and Thailand (Lelej, 2005).

Taiwanomyrme spp.

Remarks
This genus is currently restricted to the Oriental part of China and Taiwan (Lelej, 2020a; Tu *et al*., 2015). This genus, however, may be found in northern Vietnam, Laos, and Thailand, given its wide distribution and faunal similarity between southern China and northern Indochina (Williams *et al*., 2019a).

Trogaspidia lingnani (Mickel, 1933)

Remarks
Like *T. pagdeni*, this species is widespread in China and occurs in Laos and Thailand (Chen, 1957; Mickel, 1933b; Williams *et al*., 2019a).

Trogaspidia pagdeni (Mickel, 1933)

Remarks
This species is widespread in China and Indochina (Laos, Malaysia, and Thailand) (Chen, 1957; Mickel, 1933b; Thaochan *et al*., 2022; Williams *et al*., 2019a). Future studies will certainly confirm occurrence of this species in Vietnam.

Mutillinae: Zeugomutillini

Zeugomutilla pycnopyga Chen, 1957

Remarks
This species is known from southern China (Fujian and Yunnan) and various places in Thailand (Chen, 1957; Lelej *et al*., 2017; Thaochan *et al*., 2022).

Zeugomutilla saepes (Chen, 1957)

Remarks
Like the preceding species, this species may be widespread in Indochina. Presently, this species has been recorded from southern China (Fujian and Guangdong) and a single locality each in Cambodia and Thailand (Chen, 1957; Lelej *et al*., 2017; Thaochan *et al*., 2022; Williams *et al*., 2019a).

Discussion

Before the present study, forty-eight velvet ant species have been recorded from Vietnam (Table 1). Historical review of taxonomic studies of the Vietnamese velvet ants revealed three major inputs (Fig. 19). The first input was made during 1870 to 1979 (André, 1898; Lelej, 1979; O'Toole, 1975; Sichel & Radoszkowski, 1869–1870). During this period, only one species was recorded by each study. The second input was made in eight publications by Arkady Lelej (1995–2012), with 24 species recorded based on the specimens collected in expeditions by Russian and Japanese entomologists. The third input, from 2016 to present, drastically increased the number of Vietnamese species. In their 12 publications on velvet ant systematics, Arkady Lelej, Juriya Okayasu, Kevin Williams, and Hu-ting Zhou recorded 21 species including nine new species originally described from this country. This period is also characterized by international cooperation of systematists in multiple countries.

Unlike Thailand, no comprehensive study focusing on Vietnamese local fauna was made until the present study was conducted. Here, I added ten species based on the specimens from various collections, expanding the velvet ant fauna of Vietnam by 21%. The distribution and sex associations of all 58 Vietnamese species are reviewed in Table 2. Of these, 18 species (32.7%) are known from both sexes, and host information is available for one species, *P. decora*. Despite of the high endemism of terrestrial organisms in Vietnam (Sterling & Hurley, 2005), only four putatively endemic species have been described.

The number of species recorded from each province was listed in Table 3 and mapped in Fig. 20. This suggests that most provinces are undersampled; 35 (55.6%) of 63 provinces

presently have no velvet ant records, and 15 (23.8%) have only one or two records. Most notably, only one species has been recorded from the Mekong River Delta region, which occupies the southernmost part of the country. Additionally, most species were recorded based on less than ten specimens. The total number of known Vietnamese specimens is no more than 400 (~0.12 specimen records per 100 km^2; Fig. 21).

Overall, this review reveals that Vietnamese velvet ant fauna is largely undersampled, and the true species richness is likely much higher than currently documented. Ecological data are mostly unavailable. Recent papers have demonstrated the usefulness of repeated sampling in a limited area to associate dimorphic sexes (Bartholomay *et al*., 2019; Williams *et al*., 2019a) and to infer potential hosts from correlated occurrence of velvet ants with other insects (Añino *et al*., 2020; Aranda & Graciolli, 2016; Polidori *et al*., 2010). Intensive collecting in Vietnam is therefore desired to uncover the biodiversity and ecology of this insect.

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References

André, E. (1896a) Notes pour servir à la connaissance de mutilles paléarctiques et description de quelques espèces nouvelles. Deuxieme partie. *Mémoires de la Société Zoologique de France* 9: 261–277.

André, E. (1896b) Étude sur les Mutillides existant dans les collections du Musée civique de Gênes. *Annali del Museo Civico di Storia Naturale di Genova* 37: 66–104.

André, E. (1898) Étude sur les Mutillides du Muséum de Paris. *Annales de la Société Entomologique de France* 67: 1–79.

André, E. (1901–1902) Matériaux pour servir à la connaissance des Mutillides d'Afrique. *Zeitschrift für Systematische Hymenopterologie und Dipterologie* 1: 279–288, 305–352 (1901); 2: 17–48 (1902a).

André, E. (1902b [1903]) Family Mutillidae. *In*: Wytsman, P. (ed.) *Genera Insectorum*. *Fascicles 11*. L. Desmet-Verteneuil, Bruxelles, pp. 1–77+ 3 pls.

André, E. (1904) Examen critique d'uen nouvelle classification proposée par M. le Dr. W. H. Ashmead pour la famille des Mutillidae. *Revue d'Entomologie* 23 (1): 27–41.

André, E. (1905) Mutillides nouveaux ou peu connues de l'Ancien Monds et de l'Australie. *Zeitschrift für systematische Hymenopterologie und Dipterologie* 5: 265–277.

André, E. (1909) Mutillides nouveaux ou imparfaitement connus du Musée royal d'histoire naturelle de Leide. *Notes from the Leyden Museum* 31: 171–180.

Añino, Y.J., Cambra, R.A., Windsor, D.M., Williams, K.A., Bartholomay, P.R., Sánchez, V. & Quintero, D. (2020) Seasonal and annual abundance of *Ephuta* wasp (Hymenoptera: Mutillidae) in Panama. *Revista de Biología Tropical* 68 (2): 573–579. http://dx.doi.org/10.15517/rbt.v68i2.38876

Aranda, R. & Graciolli, G. (2016) Environmental heterogeneity in parasitoid-host interaction for Mutillidae (Hymenoptera: Apocrita). *Environmental Entomology* 45 (5): 1146–1153. https://doi.org/10.1093/ee/nvw098

Argaman, Q. (1988) Description of the female of *Ticopla*, with biological and taxonomic notes (Hymenoptera, Mutillidae). *Fragmenta Balcanica Musei Macedonici Scientiarum Naturalium* 14: 33–45.

Ashmead, W.H. (1899) Superfamilies in the Hymenoptera and generic synopses of the families Thynnidae, Myrmosidae, and Mutillidae. *Journal of the New York Entomological Society* 7: 45–60.

Ashmead, W.H. (1900–1904) Classification of the fossorial, predaceous and parasitic wasps, or the superfamily Vespoidea. *The Canadian Entomologist* 32: 145–155, 185–188, 295–296 (1900); 34: 79–88, 131–137, 163–166, 203–210, 219–231, 268–273, 287–291 (1902); 35: 3–8, 39–44, 95–107, 155–158, 199–205, 303–310, 323–332 (1903); 36: 5–9 (1904).

Baltazar, C.R. (1966) A catalogue of Philippine Hymenoptera (with a bibliography, 1758–1963). *Pacific Insects Monograph* 8: 1–488.

Barthélémy, C., Lelej, A.S. & Loktionov, V.M. (2018) A contribution to the Mutillidae (Hymenoptera) of Hong Kong. *Zootaxa* 4514 (2): 230–242. https://doi.org/10.11646/zootaxa.4514.2.6

Bartholomay, P.R., Williams, K.A., Lopez, V.M. & Oliveira, M.L. (2019) Revision of the *Traumatomutilla americana* species group (Hymenoptera: Mutillidae). *Zootaxa* 4608 (1): 1–34. https://doi.org/10.11646/zootaxa.4608.1.1

Bingham, C.T. (1897) *The fauna of British India including Ceylon and Burma: Hymenoptera, I. Wasps and Bees*. Taylor and Francis, London, 608 pp. + 4 pls.

Bingham, C.T. (1903) Diagnoses of aculeate Hymenoptera. *Fasciculi Malayenses*, *Zoology* 1 (2): appendix, iii–vii.

Bingham, C.T. (1905) Report on the aculeate Hymenoptera. *Fasciculi Malayenses*, *Zoology* 1 (3): 19–60 + pl. A.

Bischoff, H. (1920–1921) Monographie der Mutilliden Afrikas. *Archiv für Naturgeschichte* 86A (1–3): 1–480 (1920); 86A (4–5): 481–830 (1921).

Borries, H. (1892) *Mutilla erythrocephala* Fabr. som parasit hos *Crabro* (*Solenius*) *rubicola* D. & P. *Entomologisk Tidskrift* 13: 247–249.

Branstetter, M.G., Danforth, B.N., Pitts, J.P., Faircloth, B.C., Ward, P.S., Buffington, M.L., Gates, M.W., Kula, R.R. & Brady, S.G. (2017) Phylogenomic insights into the evolution of stinging wasps and the origin of ants and bees. *Current Biology* 27 (7): 1019–1025. https://doi.org/10.1016/j.cub.2017.03.027

Brothers, D.J. (1975) Phylogeny and classification of the aculeate Hymenoptera, with special reference to Mutillidae. *The University of Kansas Science Bulletin* 50 (11): 483–648.

Brothers, D.J. (1989) Alternative life-history styles of mutillid wasps (Insecta, Hymenoptera). *In*: Bruton, M.N. (ed.) *Alternative life-history styles of animals. Perspectives in vertebrate sciences 6*. Springer, Dordrecht, pp. 279–291. https://doi.org/10.1007/978-94-009-2605-9_14

Brothers, D.J. (2015) Revision of the Rhopalomutillinae (Hymenoptera, Mutillidae): 1, generic review with descriptions of three new genera. *Journal of Hymenoptera Research* 46: 1–24. https://doi.org/10.3897/JHR.46.5733

Brothers, D.J. (2022) Critical analysis of the type material of Mutillidae described from the Australasian Region (Hymenoptera). *Zootaxa* 5140 (1): 1–215. https://doi.org/10.11646/zootaxa.5140.1.1

Brothers, D.J. & Carpenter, J.M. (1993) Phylogeny of Aculeata: Chrysidoidea and Vespoidea (Hymenoptera). *Journal of Hymenoptera Research* 2 (1): 227–302.

Brothers, D.J. & Lelej, A.S. (2017) Phylogeny and higher classification of Mutillidae (Hymenoptera) based on morphological reanalyses. *Journal of Hymenoptera Research* 60: 1–97. https://doi.org/10.3897/jhr.60.20091

Brothers, D.J., Lelej, A.S. & Williams, K.A. (2019) Genus-group names of Mutillidae (Hymenoptera): corrections and updates since 2008. *Zootaxa* 4651 (3): 578–588. https://doi.org/10.11646/zootaxa.4651.3.10

Cameron, P. (1901) On the Hymenoptera collected during the "Skeat Expedition" to the Malay Peninsula, 1899–1900. *Proceedings of the Zoological Society of London* 2: 16–44.

Campbell, L., Behrens, K., Hesse, C. & Chaon, P. (2021) *Habitats of the world*. Princeton University Press, Princeton, 568 pp.

Chen, C.-w. (1957) A revision of the velvety ants or Mutillidae of China (Hymenoptera). *Quarterly Journal of the Taiwan Museum* 10 (3–4): 135–224 + 6 pls.

Cockerell, T.D.A. (1928) Mutillidae from Siam. *The Annals and Magazine of Natural History*, Series 10 2: 596–600. https://doi.org/10.1080/00222932808672926

Dalla Torre, C.G. de (1897) *Catalogus Hymenopterorum hucusque Descriptorum Systematicus et Synonimicus*. *Volumen VIII: Fossores (Sphegidae)*. Guilelmi Engelmann, Lipsiae, [4] + viii + 750 pp. https://doi.org/10.5962/bhl.title.10348

Debevec, A.H., Cardinal, S. & Danforth, B.N. (2012) Identifying the sister group to the bees: a molecular phylogeny of Aculeata with an emphasis on the superfamily Apoidea. *Zoologica Scripta* 41 (5): 527–535. https://doi.org/10.1111/j.1463-6409.2012.00549.x

Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N.D., Wikramanayake, E., Hahn, N., Palminteri, S., Hedao, P., Noss, R., Hansen, M., Locke, H., Ellis, E.C., Jones, B., Barber, C.V., Hayes, R., Kormos, C., Martin, V., Crist, E., Sechrest, W., Price, L., Baillie, J.E.M., Weeden, D., Suckling, K., Davis, C., Sizer, N., Moore, R., Thau, D., Birch, T., Potapov, P., Turubanova, S., Tyukavina, A., de Souza, N., Pintea, L., Brito, J.C., Llewellyn, O.A., Miller, A.G., Patzelt, A., Ghazanfar, S.A., Timberlake, J., Klöser, H., Shennan-Farpón, Y., Kindt, R., Lillesø, J.B., van Breugel, P., Graudal, L., Voge, M., Al-Shammari, K.F. & Saleem, M. (2017) An ecoregion-based approach to protecting half the terrestrial realm. *BioScience* 67 (6): 534–545. https://doi.org/10.1093/biosci/bix014

Dover, C. (1926) A contribution to a list of the aculeate Hymenoptera (excepting ants) of Hongkong. *The China Journal of Science & Arts* 4: 233–235.

Fabricius, J.C. (1787) *Mantissa insectorum sistens eorum species nuper detecta, adjectis characteribus genericis, differentiis specificis, emendationibus, observationibus*. *Tom. 1*. Impensis Christ. Gottl. Proft, Hafniae [= Copenhagen], 348 pp. https://doi.org/10.5962/bhl.title.11657

Fabricius, J.C. (1793) *Entomologica Systematica emendata et aucta, secundum Classes, Ordines, Genera, Species adjectis Synonymis, Locis, Observationibus, Descriptionibus*. *T. 2*. Christ. Gottl. Proft, Hafniae [= Copenhagen], viii + 519 pp. https://doi.org/10.5962/bhl.title.125869

Fabricius, J.C. (1804) *Systema Piezatorum secundum Ordines, Genera, Species adjectis Synonymis, Locis, Observationibus, Descriptionibus*. Carolum Reichard, Brunsvigae, pp. i–xiv + 15–440 + 1–30. https://doi.org/10.5962/bhl.title.10490

Ferton, C. (1908) Notes détachées sur l'instinct des hyménoptères mellifères et ravisseurs (4^{e} Série). *Annales de la Société entomologique de France* 70: 535–586.

Fox, W.J. (1894) A proposed classification of the fossorial Hymenoptera of North America. *Proceedings of the Academy of Natural Sciences of Philadelphia* 1894: 292–307.

Gôukon, K. (1993) Host records and some bionomical notes on mutillid wasps in Japan (Hymenoptera, Mutillidae). *Chugoku Kontyu* 7: 35–40. (in Japanese)

Hammer, K. (1949) Über einige von Kjell Kolthoff und anderen in China gesammelten Hymenoptera. Chrysididae, Cleptidae, Mutillidae. *Arkiv för zoologi* 42A (8): 1–12.

Hammer, K. (1962 [1960]). Mutilliden (Insecta: Hymenoptera) aus dem Indischen Museum

in Calcutta. *Records of the Indian Museum* 58 (1): 1–51.
He, J.-H., Chen, X.-X., Fan, J.-J., Li, Q., Liu, C.-M., Lou, X.-M., Ma, Y., Wang, S.-F., Wu, Y.-R., Xu, Z.-H., Xu, Z.-F. & Yao, J. (2004) *Hymenopteran insect fauna of Zhejiang*. Science Press, Beijing, lvi + 1373 pp. + xliii pls. (in Chinese)
Hill, D.C. (1982) *Hong Kong insects*. *Vol. 2*. Urban Council Publication, Hong Kong, 144 pp.
Hirayama, S. (1937) [*The illustrated thousand insects of Japan*. *Vol. 2*]. Sanseidô, Tokyo, 194 pp. + 88 pls. + 28 pp. + 3 pp. + 40 pp. (in Japanese)
Hua, L.-z. (2006) *List of Chinese insects Vol. IV*. Sun Yat-sen University Press, Guangzhou, 540 pp.
Invrea, F. (1964) *Mutillidae-Myrmosidae*. *Fauna d'Italia 5*. Edizioni Calderini, Bologna, xii + 302 pp. + 1 p.
Ito, R. (2018) A second record of *Eotrogaspidia auroguttata* (Smith, 1855) (Hymenoptera, Mutillidae, Mutillinae) from the Yaeyama Islands, Japan. *Tsunekibachi* 32: 25–26. (in Japanese)
Jenkins, C.N., Pimm, S.L. & Joppa, L.N. (2013) Global patterns of terrestrial vertebrate diversity and conservation. *Proceedings of the National Academy of Sciences* 110 (28): E2602–E2610. https://doi.org/10.1073/pnas.1302251110
Kass, J.M., Guénard, B., Dudley, K.L., Jenkins, C.N., Azuma, F., Fisher, B.L., Parr, C.L., Gibb, H., Longino, J.T., Ward, P.S., Chao, A., Lubertazzi, D., Weiser, M., Jetz, W., Guralnick, R., Blatrix, R., Lauriers, J.D., Donoso, D.A., Georgiadis, C., Gomez, K., Hawkes, P.G., Johnson, R.A., Lattke, J.E., MacGown, J.A., Mackay, W., Robson, S., Sanders, N.J., Dunn, R.R. & Economo, E.P. (2022) The global distribution of known and undiscovered ant biodiversity. *Science Advances* 8 (31): eabp9908. https://doi.org/10.1126/sciadv.abp9908
Kato, M. (1934) *Three colour illustrated insects of Japan*. *Fasc. X*. Kôseikaku, Tokyo, 15 pp. + 22 pp. + 50 pls. (in Japanese)
Kier, G., Kreft, H., Lee, T.M., Jetz, W., Ibisch, P.L., Nowicki, C., Mutke, J. & Barthlott, W. (2009) A global assessment of endemism and species richness across island and mainland regions. *Proceedings of the National Academy of Sciences* 106 (3): 9322–9327. https://doi.org/10.1073/pnas.0810306106
Krombein, K.V. (1940 [1939]) Studies in the Tiphiidae (Hymenoptera Aculeata) IV. A revision of the Myrmosinae of the New World with a discussion of the Old World species. *Transactions of the American Entomological Society* 65 (4): 415–465. https://www.jstor.org/stable/25077448
Krombein, K.V. (1979) Biosystematic studies of Ceylonese wasps, IV. Kudakrumiinae, a new subfamily of primitive wasps (Hymenoptera, Mutillidae). *Transactions of the American Entomological Society* 105 (1): 67–83.
Krombein, K.V. & Lelej, A.S. (1999) Biosystematic studies of Ceylonese wasps, XXII: *Bethsmyrmilla*, a new genus of mutillid wasps (Hymenoptera: Mutillidae: Myrmillinae). *Proceedings of the Entomological Society of Washington* 101 (1): 143–148.
Kumar, G.P., Lelej, A.S., Das, D., Raveendran, H.K.P. & Loktionov, V.M. (2019) Discovery of the genus *Kudakrumia* Krombein, 1979 (Hymenoptera: Mutillidae) in India and description of a new species. *Zootaxa* 4612 (2): 260–266. https://doi.org/10.11646/zootaxa.4612.2.8
Kumpanenko, A., Gladun, D. & Vilhelmsen, L. (2022) Morphology of the sting apparatus in velvet ants of the subfamilies Myrmosinae, Dasylabrinae, Myrmillinae and Mutillinae (Hymenoptera: Mutillidae). *Zoomorphology* 141 (1): 81–94. https://doi.org/10.1007/s00435-022-00552-w
Latreille, [P.A.] (1796) *Précis des Charactères Génériques des Insectes, disposés dans un*

Ordre Naturel. Brive, Paris, xiv + 201 pp. https://doi.org/10.5962/bhl.title.58411
Latreille, P.A. (1802) *Histoire naturelle, générale et particulière des Crustacés et des Insectes*. *3*. F. Dufart, Paris, xii + 467 pp. https://doi.org/10.5962/bhl.title.15764
Lelej, A.S. (1979) A new genus of velvet ants (Hymenoptera, Mutillidae) from south-east Asia. *Zoologicheskiy Zhurnal* 58 (7): 1065–1067. (in Russian)
Lelej, A.S. (1983) Contributions to the knowledge of the velvet ants (Hymenoptera, Mutillidae) of Australia. *Entomologicheskoe Obozrenie* 62 (3): 612–619. (in Russian). [English translation (1984) in: *Entomological Review* 62 (3): 152–160]
Lelej, A.S. (1985) *Osy-nemki (Hymenoptera, Mutillidae) Fauny SSSR i Sopredelnykh Stran* [*The velvet ants (Hymenoptera, Mutillidae) of the USSR and neighboring countries*]. Nauka, Leningrad, 268 pp. (in Russian)
Lelej, A.S. (1992) Two interesting species of velvet ants from China (Hymenoptera, Mutillidae). *Entomofauna* 13 (19): 281–288.
Lelej, A.S. (1995a) A review of Palaearctic and Oriental species of genus *Nemka* Lelej with description of Oriental genus *Mickelomyrme* gen. n. (Hymenoptera, Mutillidae). *Far Eastern Entomologist* 6: 1–20.
Lelej, A.S. (1995b) To the knowledge of East Asian species of the tribe Smicromyrmini Bischoff, 1920 (Hymenoptera, Mutillidae) with description of four new genera and eight new species. *Far Eastern Entomologist* 13: 1–28.
Lelej, A.S. (1996a) A review of the East Asian species of *Orientilla* (Hymenoptera, Mutillidae). *Memoirs of the Entomological Society of Washington* 17: 103–107.
Lelej, A.S. (1996b) To the knowledge of the East Asian species of the tribe Trogaspidiini Bischoff, 1920 (Hymenoptera, Mutillidae) with description of eight new genera and two new species. *Far Eastern Entomologist* 30: 1–24.
Lelej, A.S. (1996c) Mutillid wasps collected in Malaysia and Indonesia by Dr. Sk. Yamane (Hymenoptera, Mutillidae). *Tropics* 6 (1–2): 91–104. https://doi.org/10.3759/tropics.6.91
Lelej, A.S. (1996d) A review of the East Asian species of *Mickelomyrme* Lelej, 1995 (Hymenoptera, Mutillidae). *Entomofauna* 17 (15): 277–292.
Lelej, A.S. (2002) *Catalogue of the Mutillidae (Hymenoptera) of the Palaearctic Region*. Dalnauka, Vladivostok, 172 pp.
Lelej, A.S. (2005) *Catalogue of the Mutillidae (Hymenoptera) of the Oriental Region*. Dalnauka, Vladivostok, 252 pp.
Lelej, A.S. (2012) A new species of *Rhopalomutilla* André, 1901 (Hymenoptera: Mutillidae) from South Vietnam. *Russian Entomological Journal* 21 (2): 143–145.
Lelej, A.S. (2020a) To the knowledge of velvet ants of the genera *Artiotilla* Invrea, *Radoszkowskitilla* Lelej and *Taiwanomyrme* Tsuneki (Hymenoptera: Mutillidae). *Far Eastern Entomologist* 410: 1–10. https://doi.org/10.25221/fee.410.1
Lelej, A.S. (2020b) Three new species of velvet ants from the tribe Smicromyrmini (Hymenoptera: Mutillidae) with unusual color syndrome. *Far Eastern Entomologist* 421: 1–9. https://doi.org/10.25221/fee.421.1
Lelej, A.S. (2023) Review of the tribe Ctenotillini (Hymenoptera: Mutillidae) from Oriental and Palaearctic Regions. *Far Eastern Entomologist* 480: 1–22. https://doi.org/10.25221/fee.480.1
Lelej, A.S. & Brothers, D.J. (2008) The genus-group names of Mutillidae (Hymenoptera) and their type species, with a new genus, new name, new synonymies, new combinations and lectotypifications. *Zootaxa* 1889: 1–79. https://doi.org/10.11646/zootaxa.1889.1.1
Lelej, A.S., Choi, J.Y. & Tripotin, P. (2001) Review of the mutillid wasps (Hymenoptera, Mutillidae) of Korea. *Far Eastern Entomologist* 96: 1–15.
Lelej, A.S. & Kabakov, O.N. (1980) On Bradynobaenidae and Mutillidae (Hymenoptera) of

Afghanistan. *Entomologicheskoe Obozrenie* 59 (1): 181–196. (in Russian). [English translation (1981) in *Entomological Review* 59 (1): 141–156]
Lelej, A.S. & Krombein, K.V. (1999) Two remarkable new genera of mutillid wasps (Hymenoptera: Mutillidae, Sphaeropthalminae, Pseudomethocini) from Thailand. *Far Eastern Entomologist* 79: 1–8.
Lelej, A.S. & Krombein, K.V. (2001) Review of the Oriental mutillid wasps of the subfamily Ticoplinae (Hymenoptera, Mutillidae). *Far Eastern Entomologist* 99: 1–18.
Lelej, A.S. & Nemkov, P.G. (1997) Phylogeny, evolution and classification of Mutillidae (Hymenoptera). *Far Eastern Entomologist* 46: 1–24.
Lelej, A.S., Ovchinnikov, S.V. & Inayatullah, M. (2013) Velvet ants of the subfamily Myrmillinae (Hymenoptera: Mutillidae) of Pakistan. *Russian Entomological Journal* 22 (3): 197–199.
Lelej, A.S., Terine, J.B. & Kumar, G.P. (2021) New species of Ticoplinae (Hymenoptera: Mutillidae) from India. *Zootaxa* 5052 (4): 567–578. https://doi.org/10.11646/zootaxa.5052.4.6
Lelej, A.S., Terine, J.B., Kumar, G.P., Das, D. & Sureshan, P.M. (2020) Review of the genus *Odontomutilla* Ashmead, 1899 (Hymenoptera: Mutillidae) of the Indian subcontinent, with description of two new species. *Zootaxa* 4822 (2): 191–208. https://doi.org/10.11646/zootaxa.4822.2.3
Lelej, A.S. & Williams, K.A. (2023) Review of the tribe Smicromyrmini Bischoff, 1920 (Hymenoptera: Mutillidae). *Zootaxa* 5231 (2): 101–140. https://doi.org/10.11646/zootaxa.5231.2.1
Lelej, A.S., Williams, K.A., Loktionov, V.M., Pang, H. & Xu, Z.-F. (2017) Review of the genus *Zeugomutilla* Chen, 1957 (Hymenoptera, Mutillidae, Mutillini), with description of two new species. *Zootaxa* 4247 (1): 1–15. https://doi.org/10.11646/zootaxa.4247.1.1
Lelej, A.S., Williams, K.A., Terine, J.B., Okayasu, J., Parikh, G. & Kumar, G.P. (2023) Review of the tribe Mutillini (Hymenoptera: Mutillidae) from the Oriental Region. *Zootaxa* 5228 (4): 455–476. https://doi.org/10.11646/zootaxa.5228.4.5
Lelej, A.S. & Yamane, Sk. (1992) Interesting velvet ants (Hymenoptera, Mutillidae) from Japan and Korea. *Japanese Journal of Entomology* 60 (3): 625–632.
Lelej, A.S., Zhou, H.-T., Loktionov, V.M. & Xu, Z.-F. (2016) Review of the genus *Promecidia* Lelej, 1996, with description of two new species from China (Hymenoptera, Mutillidae, Trogaspidiini). *ZooKeys* 641: 103–120. https://doi.org/10.3897/zookeys.641.10765
Lepeletier de Saint-Fargeau, A. (1845) *Histoire Naturelle des Insectes*. *Hyménoptères*. *Tome Troisième*. Roret, Paris, [4] + 646 pp. https://doi.org/10.5962/bhl.title.9005
Lo Cascio, P. (2015) Worldwide checklist of the island mutillid wasps (Hymenoptera Mutillidae). *Biodiversity Journal* 6 (2): 529–592.
Magretti, P. (1892) Viaggio di Leonardo Fea in Birmania e regioni vicine XLIII. Imenotteri. Parte prima. Mutillidei, Scoliidei, Tifiidei, Tinnidei colla descrizione di parecchie nuove specie. *Annali del Museo Civico di Storia Naturale di Genova* Serie 2 12 (32): 197–266 + pl. V.
Matsumura, S. (1911) *Thousand insects of Japan supplement III*. Keiseisha-shoten, Tokyo, 147 pp. + pls 30–41. https://doi.org/10.5962/bhl.title.50811
Matsumura, S. (1930) *The illustrated thousand insects of Japan Vol. 2 (Hymenoptera)*. Tôkô Shoin, Tokyo, 198 pp. + 18 pls. + 89 pp. + 8 pp. (in Japanese)
Matsumura, S. (1931) *6000 illustrated insects of Japan-Empire*. Tôkô Shoin, Tokyo, 3pp. + 1497 pp. + 23 pp. + 10 pls. (in Japanese)
Mickel, C.E. (1933a) The Mutillidae of Formosa. *Annals of the Entomological Society of*

America 26 (2): 381–423. https://doi.org/10.1093/aesa/26.2.381
Mickel, C.E. (1933b) The Mutillidae of Eastern Asia. *Lingnan Science Journal* 12 (3): 289–325.
Mickel, C.E. (1934) Mutillidae of the Philippine Islands. *Philippine Journal of Science* 54 (1): 91–219 + 1 pl.
Mickel, C.E. (1935) The mutillid wasps of the islands of the Pacific Ocean (Hymenoptera, Mutillidae). *Transactions of the Royal Entomological Society of London* 83 (2): 177–312. https://doi.org/10.1111/j.1365-2311.1935.tb01207.x
Mickel, C.E. (1939) Correction of type locality for two species of Mutillidae described by Frederick Smith (Hymenoptera). *Proceeding of the Royal Entomological Society of London*, Ser. B 8: 192–194. https://doi.org/10.1111/j.1365-3113.1939.tb00514.x
Morawitz, F. (1890) Hymenoptera Fossoria Transcaspica nova. *Horae Societatis Entomologicae Rossicae* 24: 570–645.
Moura, M.R. & Jetz, W. (2021) Shortfalls and opportunities in terrestrial vertebrate species discovery. *Nature Ecology & Evolution* 5: 631–639. https://doi.org/10.1038/s41559-021-01411-5
Murota, T. (1973) Sphecidae, Mutillidae, Scoliidae and Chrysididae collected in Formosa in 1972. *Life Study* 17 (3–4): 115–120. (in Japanese)
Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858. https://doi.org/10.1038/35002501
Nagy, C.G. (1970) Further investigations on the heterogynoid wasps. *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg* 4 (69): 83–86.
Nambu, T. & Tano, T. (1983) [Wasps and ants collected in Taiwan in 1980]. *Hymenopterists' Communication* 16: 11–23. (in Japanese)
Nonveiller, G. (1995) A preliminary approach to a revision of the Afrotropical representatives of the genus *Trogaspidia* Ashmead, 1899 (*sensu* Bischoff, 1920) (Hymenoptera, Mutillidae). Studies on African Mutillidae: Note XXI. (Third contribution to the knowledge of the Afrotropical *Trogaspidia*). *Annales de la Societé Entomologique de France (N.S.)* 31 (4): 349–368.
Okayasu, J. (2016) [First record of *Eotrogaspidia auroguttata* (Smith) from Yaeyama Islands, Japan]. *Gekkan-Mushi* 543: 61–62. (in Japanese)
Okayasu, J. (2017) Two new species of the genus *Sinotilla* Lelej, 1995 (Hymenoptera: Mutillidae), with notes on taxonomic characters. *Zootaxa* 4294 (2): 151–169. https://doi.org/10.11646/zootaxa.4294.2.1
Okayasu, J. (2018) Taxonomic review of Chin-wen Chen's species described in the genus *Smicromyrme* (Hymenoptera: Mutillidae: Smicromyrmini). *Acta Entomologica Musei Nationalis Pragae* 58 (2): 479–494. https://doi.org/10.2478/aemnp-2018-0036
Okayasu, J. (2020) Velvet ants of the tribe Smicromyrmini Bischoff (Hymenoptera: Mutillidae) of Japan. *Zootaxa* 4723 (1): 1–110. https://doi.org/10.11646/zootaxa.4723.1.1
Okayasu, J. (2021) A new velvet ant genus *Arkaditilla* (Hymenoptera, Mutillidae, Trogaspidiini) from the Oriental Region, with review of species. *Journal of Hymenoptera Research* 84: 145–168. https://doi.org/10.3897/jhr.84.68709
Okayasu, J. (2022) Remarkable range extension of the genus *Nordeniella* Lelej, 2005 (Hymenoptera: Mutillidae: Smicromyrmini): Description of a new species from Sumbawa, Indonesia. *Journal of Insect Biodiversity* 32 (2): 56–63. https://doi.org/10.12976/jib/2022.32.2.3
Okayasu, J. (2023a) Love is in the air and beyond the ocean: Taxonomic review of *Neotrogaspidia* Lelej (Hymenoptera: Mutillidae: Trogaspidiini) in Northeast Asia

highlights its unique distributional pattern. *Entomological Science* 26 (1): e12532. https://doi.org/10.1111/ens.12532

Okayasu, J. (2023b) Discovery of the velvet ant genus *Orientilla* Lelej from Laos (Hymenoptera, Mutillidae, Dasylabrinae), with description of a related new species from India. *Journal of Hymenoptera Research* 96: 817–834. https://doi.org/10.3897/jhr.96.110590

Okayasu, J. (2023c) Preliminary assessment of the velvet ant fauna in Nepal, with description of new species of the genera *Strangulotilla* Nonveiller and *Zeugomutilla* Chen (Hymenoptera: Mutillidae). *Insecta matsumurana*, New Series 79: 1–27.

Okayasu, J., Lelej, A.S. & Williams, K.A. (2021a) Review of *Eotrogaspidia* Lelej (Hymenoptera: Mutillidae: Trogaspidiini). *Zootaxa* 4920 (1): 56–90. https://doi.org/10.11646/zootaxa.4920.1.2

Okayasu, J., Williams, K.A. & Lelej, A.S. (2018) A remarkable new species of the genus *Sinotilla* Lelej (Hymenoptera: Mutillidae: Smicromyrmini) from Taiwan and an overview of color diversity in East Asian mutillid females. *Zootaxa* 4446 (3): 301–324. http://dx.doi.org/10.11646/zootaxa.4446.3.1

Okayasu, J., Williams, K.A., Lelej, A.S. & Pham, T.H. (2021b) Review of female *Andreimyrme* Lelej (Hymenoptera: Mutillidae: Smicromyrmini). *Zootaxa* 5061 (1): 1–38. https://doi.org/10.11646/zootaxa.5061.1.1

Olivier, [A.G.] (1811) Mutille. *Encyclopédie Methodique*. *Histoire Naturelle*. *Insectes* 8: 49–66.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'Amico, J.A., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Lamoreux, J.F., Ricketts, T.H., Itoua, I., Wettengel, W.W., Kura, Y., Hedao, P. & Kassem, K. (2001) Terrestrial ecoregions of the world: A new map of life on Earth. *BioScience* 51 (11): 933–938. https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2

O'Toole, C. (1975) The systematics of *Timulla oculata* (Fabricius) (Hymenoptera, Mutillidae). *Zoologica Scripta* 4 (1): 229–251. https://doi.org/10.1111/j.1463-6409.1975.tb00733.x

Pagden, H.T. (1934a) New species of Mutillidae (Hymenoptera, Vespoidea) from the Malay Peninsula. *Journal of the Federated Malay States Museums* 17: 419–457.

Pagden, H.T. (1934b) Biological notes on some Malayan aculeate Hymenoptera I. (Sphecoidea and Vespoidea). *Journal of the Federated Malay States Museums* 17 (3): 458–466.

Pagden, H.T. (1949) Descriptions and records of Austro-Malaysian Methocidae and Mutillidae (Hymenoptera). *Transactions of the Royal Entomological Society of London* 100 (8): 191–231. https://doi.org/10.1111/j.1365-2311.1949.tb01431.x

Pagliano, G. (2011) I Mutillidae (Hymenoptera) della collezione Zavattari le collezioni del Museo Regionale di Scienze Naturali di Torino. *Bolletino del Musei Regionale di Scienze Naturali di Torino* 28 (1): 37–60.

Pagliano, G., Brothers, D.J., Cambra, R., Lelej, A.S., Lo Cascio, P., Matteini Palmerini, M., Scaramozzino, P.L., Williams, K.A. & Romano, M. (2020) Checklist of names in Mutillidae (Hymenoptera), with illustrations of selected species. *Bollettino del Museo Regionale di Scienze Naturali di Torino* 36 (1–2): 5–425.

Pagliano, G. & Scaramozzino, P. L. (2021) La collezione di Mutillidae e di Bradynobaenidae (Hymenoptera) di Guido Pagliano. *Bollettino del Museo Regionale di Scienze Naturali di Torino* 38 (1–2): 63–147.

Pallas, P.S. (1773) *Reisen durch verschiedene Provinzen des Russischen Reichs*. *Zweiter Theil*. *Zweites Buch vom Jahr 1771*. Kayserlichen Academie der Wissenschaften, St.

Petersburg, [12] + 744 pp.
Parejo-Pulido, D. & Romano, M. (2022) A new species of *Krombeinella* from Turkey (Hymenoptera: Mutillidae). *Boletín de la Sociedad Entomológica Aragonesa* 70: 75–78.
Pate, V.S.L. (1947 [1946]) A minute on *Paramyrmosa* Saussure (Hymenoptera, Tiphiidae). *The Canadian Entomologist* 78 (11–12): 196–197.
Péringuey, L. (1898) Description of some new or little known South African Mutillidae in the collection of the South African Museum. *Annals of the South African Museum* 1 (1): 33–94.
Pilgrim, E.M., von Dohlen, C.D. & Pitts, J.P. (2008) Molecular phylogenetics of Vespoidea indicate paraphyly of the superfamily and novel relationships of its component families and subfamilies. *Zoologica Scripta* 37 (5): 539–560. https://doi.org/10.1111/j.1463-6409.2008.00340.x
Polidori, C., Mendiola, P., Asís, J.D., Tormos, J. & Selfa, J. (2010) Temporal asynchrony and spatial co-occurrence with the host: the foraging patterns of *Nemka viduata*, a parasitoid of digger wasps (Hymenoptera: Mutillidae and Crabronidae). *Journal of Ethology* 28: 353–361. https://doi.org/10.1007/s10164-009-0196-2
Radoszkowski, O. (1885) Revision des armures copulatrices des mâles de la famille de Mutillides. *Horae Societatis Entomologicae Rossicae* 19 (1–2): 3–49 + 9 pls.
Reid, J.A. (1941) The thorax of the wingless and short-winged Hymenoptera. *Transaction of the Royal Entomological Society of London* 91 (8): 367–446. https://doi.org/10.1111/j.1365-2311.1941.tb01046.x
Roll, U., Feldman, A., Novosolov, M., Allison, A., Bauer, A.M., Bernard, R., Böhm, M., Castro-Herrera, F., Chirio, L., Collen, B., Colli, G.R., Dabool, L., Das, I., Doan, T.M., Grismer, L.L., Hoogmoed, M., Itescu, Y., Kraus, F., LeBreton, M., Lewin, A., Martins, M., Maza, E., Meirte, D., Nagy, Z.T., Nogueira, C. de C., Pauwels, O.S.G., Pincheira-Donoso, D., Powney, G.D., Sindaco, R., Tallowin, O.J.S., Torres-Carvajal, O., Trape, J.-F., Vidan, E., Uetz, P., Wagner, P., Wang, Y., Orme, C.D.L., Grenyer, R. & Meiri, S. (2017) The global distribution of tetrapods reveals a need for targeted reptile conservation. *Nature Ecology & Evolution* 1: 1677–1682. https://doi.org/10.1038/s41559-017-0332-2
de Saussure, H. (1867) *Reise der österreichschen Fregatte Novara um die Erde in den Jahren 1857, 1858, 1859 unter den Befehlen des Commodore B. von Wüllerstorf-Urbair*. *Zoologischer Theil*. *Zweiter Band*. *Hymenoptera*. *Familien der Vespiden, Sphegiden, Pompiliden, Crabroniden und Heterogynen*. C. Gerold's Sohn, Wien, 138 pp. + 4 pls.
Sabi, K., Nozaka, C., Kurokawa, H. & Tano, T. (1977) [Insect collecting trip to Taiwan]. *Hymenopterists' Communication* 5: 34–42. (in Japanese)
Say, T. (1836) Descriptions of new species of North American Hymenoptera, and observation on some already described. *Boston Journal of Natural History* 1 (3): 209–305.
Schuster, R.M. (1949) Contribution towards a monograph of the Mutillidae of the Neotropical region. III. A key to the subfamilies represented and descriptions of several new genera (Hymenoptera). *Entomologica Americana,* New Series 29 (3–4): 59–140.
Shorthouse, D.P. (2010) SimpleMappr, an online tool to produce publication-quality point maps. Available from: http://www.simplemappr.net (accessed 11 October 2023)
Sichel, J. & Radoszkowski, O. (1869–1870) Essai d'une monographie des Mutilles de l'Ancion Continent. *Horae Societatis Entomologicae Rossicae* 6 (3): 139–172 (1869); 6 (4): 173–309 + tabs. 6–11 (1870).
Smith, F. (1855) *Catalogue of hymenopterous insects in the collection of the British Museum*. *Part III*. *Mutillidae and Pompilidae*. Taylor and Francis, London, 206 pp. + 5 pls.

https://doi.org/10.5962/bhl.title.20858
Smith, F. (1857–1858) Catalogue of the hymenopterous insects collected at Sarawak, Borneo; Mount Ophir, Malacca; and at Singapore, by A.R. Wallace. *Journal of the Proceedings of the Linnean Society, Zoology* 2: 42–88 + pls. 1–2 (1857); 89–130 (1858). https://doi.org/10.1111/j.1096-3642.1857.tb01759.x; https://doi.org/10.1111/j.1096-3642.1858.tb02548.x
Smith, F. (1879) *Descriptions of new species of Hymenoptera in the collection of the British Museum*. Taylor and Francis, London, XXI + 240 pp. https://doi.org/10.5962/bhl.title.60089
Starr, C.K. (2004) Nesting biology of the solitary wasp *Pison argentatum* (Hymenoptera: Sphecidae) in Borneo and the Philippines. *Journal of the Kansas Entomological Society* 77 (4): 565–572. https://doi.org/10.2317/E32.1
Sterling, E.J. & Hurley, M.M. (2005) Conserving biodiversity in Vietnam: applying biogeography to conservation research. *Proceedings of the California Academy of Sciences* 56 (supplement 1): 98–118.
Suárez, F. J. & Nonveiller, G. (1988) Mirmosidos de la Peninsula Iberica (Hymenoptera, Myrmosidae). *Graellsia* 44: 81–158.
Suzuki, M. (1934) A list of Japanese Mutillidae. *Kansai Konchu Zasshi* 2 (1): 23–25. (in Japanese)
Terayama, M., Suda, H., Murota, T., Haneda, Y. & Tano, T. (2011) The velvet ants (Mutillidae) of Japan. *Gekkan-Mushi* 481: 12–25. (in Japanese)
Terayama, M., Suda, H., Murota, T. & Tano, T. (2016) Family Mutillidae. *In*: Terayama, M. & Suda, H. (eds) *A guide to the aculeate wasps of Japan*. Tokai University Press, Hiratsuka, pp. 161–174. (in Japanese)
Terine, J.B., Das, D. & Kumar, G.P. (2024) Occurrence of *Andreimyrme substriolata* (Chen, 1957) and *Odontomutilla fletcheri* Lelej, Terine & Girish Kumar, 2020 (Hymenoptera, Mutillidae) in India, with note on their geographical affinities. *Journal of Insect Biodiversity and Systematics* 10 (1): 81–89.
Thaochan, N., Williams, K.A., Thoawan, K., Jeenthong, T. & Sittichaya, W. (2022) Three new species and one new country record of velvet ants (Hymenoptera, Mutillidae) from Thailand. *Journal of Hymenoptera Research* 93: 151–165. https://doi.org/10.3897/jhr.93.94727
Thomson, C.G. (1870) Öfversigt af Sveriges rofsteklar. *Opuscula Entomologica*, Lund 1 (2): 202–251.
Tonnoir, A.L. (1930) Notes on Indian blepharocerid larvae and pupae with remarks on the morphology of Blepharocerid larvae and pupae in general. *Records of the Indian Museum* 32: 161–214.
Tordoff, A.W., Baltzer, M.C., Fellowes, J.R., Pilgrim, J.D. & Langhammer, P.F. (2012) Key biodiversity areas in the Indo-Burma Hotspot: Process, progress and future directions. *Journal of Threatened Taxa* 4 (8): 2779–2787. https://doi.org/10.11609/JoTT.o3000.2779-87
Tsuneki, K. (1972) Mutillidae collected in Formosa in 1966 and 68 (Hymenoptera). *Etizenia* 64: 1–25.
Tsuneki, K. (1993) On some Taiwanese Mutillidae, collected in 1976 by Mr. T. Murota, with description of new taxa (Hymenoptera). *Special Publications of the Japan Hymenopterists Association* 41: 39–50.
Tsuneki, K., Nozaka, C., Tano, T., Kurokawa, H. & Murota, T. (1993) Mutillidae recently collected in the Philippines (Hymenoptera). *Special Publications of the Japan Hymenopterists Association* 41: 1–38.
Tu, B.-B., Lelej, A.S. & Chen, X.-X. (2014) Review of the genus *Cystomutilla* André, 1896

(Hymenoptera: Mutillidae: Sphaeropthalminae: Sphaeropthalmini), with description of the new genus *Hemutilla* gen. nov. and four new species from China. *Zootaxa* 3889 (1): 71–91. http://dx.doi.org/10.11646/zootaxa.3889.1.4

Tu, B.-B., Lelej, A.S. & Chen, X.-X. (2015) Review of the genus *Taiwanomyrme* Tsuneki, 1993 (Hymenoptera, Mutillidae, Mutillinae), with description of two new species from China. *Zootaxa* 4020 (3): 588–600. http://dx.doi.org/10.11646/zootaxa.4020.3.10

Waldren, G.C., Sadler, E.A., Murray, E.A., Bossert, S., Danforth, B.N. & Pitts, J. P. (2023) Phylogenomic inference of the higher classification of velvet ants (Hymenoptera: Mutillidae). *Systematic Entomology* 48 (3): 463–487. https://doi.org/10.1111/syen.12588

Wesmael, M. (1851) Revue critique des Hyménoptères fouisseurs de Belgique. *Bulletin de l'Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique* 18 (2): 362–384, 451–493.

Wikramanayake, E., Dinerstein, E., Loucks, C.J., Olson, D.M., Morrison, J., Lamoreux, J., McKnight, M. & Hedao, P. (2002) *Terrestrial ecoregions of the Indo-Pacific: A conservation assessment*. Island Press, Washington DC, xxix + 643 pp.

Williams, K.A., Pan, A.D. & Wilson, J.S. (2024) *Velvet ants of North America*. Princeton University Press, Princeton and Oxford, 440 pp.

Williams, K.A., Lelej, A.S., Okayasu, J., Borkent, C.J., Malee, R., Thoawan, K. & Thaochan, N. (2019a) The female velvet ants (aka modkhong) of southern Thailand (Hymenoptera: Mutillidae), with a key to the genera of southeast Asia. *Zootaxa* 4602 (1): 1–69. http://dx.doi.org/10.11646/zootaxa.4602.1.1

Williams, K.A., Lelej, A.S. & Thaochan, N. (2019b) New species of Myrmosinae (Hymenoptera: Mutillidae) from Southeastern Asia. *Zootaxa* 4656 (3): 525–534. https://doi.org/10.11646/zootaxa.4656.3.9

Wilson, J.S., Clark, S.L., Williams, K.A. & Pitts, J.P. (2012a) Historical biogeography of the arid-adapted velvet ant *Sphaeropthalma arota* (Hymenoptera: Mutillidae) reveals cryptic species. *Journal of Biogeography* 39: 336–352. https://doi.org/10.1111/j.1365-2699.2011.02580.x

Wilson, J.S., Williams, K.A., Forister, M.L., von Dohlen, C.D. & Pitts, J.P. (2012b) Repeated evolution in overlapping mimicry rings among North American velvet ants. *Nature Communications* 3: 1272. https://doi.org/10.1038/ncomms2275

Wilson, J.S., Jahner, J.P., Forister, M.L., Sheehan, E.S., Williams, K.A. & Pitts, J.P. (2015) North American velvet ants form one of the world's largest known Müllerian mimicry complexes. *Current Biology* 25: R704–R706. https://doi.org/10.1016/j.cub.2015.06.053

Wilson, J.S., Pan, A.D., Limb, E.S. & Williams, K.A. (2018) Comparison of African and North American velvet ant mimicry complexes: Another example of Africa as the 'odd man out'. *PLoS ONE* 13 (1): e0189482. https://doi.org/10.1371/journal.pone.0189482

Wu, C.F. (1941) *Catalogus Insectorum Sinensium*. *Volume VI*. The Department of Biology, Yenching University, Peiping, vi + 333 pp. + xv.

Yasumatsu, K. (1938a) Les Mutillides de Coree et de la Mandschourie du Sud. *Transactions of the Natural History Society of Formosa* 28 (175): 83–87.

Yasumatsu, K. (1938b) Hyménoptères trouvées dans les environs de Nanking et de Changsha du bassin Yang-tse (Chine) par M. Kwo-Mo Ho. *Transactions of the Natural History Society of Formosa* 28 (180–181): 345–347. (in Japanese)

Yasumatsu, K. (1948) Records of East Chinese Mutillidae (Hymenoptera). *Lingnan Science Journal* 22 (1–4): 71–73.

Yasumatsu, K. (1951) Mutillidae of Shansi, North China (Hymenoptera). *Mushi* 22 (12): 69–72.

Yano, M. (1932) Mutillidae. *In*: Uchida, S. (ed.) *Iconographia Insectorum Japonicorum Editio Prima*. Hokuryukan, Tokyo, pp. 325–327 + 1 pl. (in Japanese)

Zavattari, E. (1910) Catalogo delle Mutille del Museo Zoologico di Napoli. *Annuario del Museo Zoologico dell'Università di Napoli*, New Series 3 (9): 1–16.

Zavattari, E. (1913) H. Sauter's Formosa-Ausbeute. Mutillidae (Hym.). *Archiv für Naturgeschichte* 79A (3): 19–42. https://doi.org/10.5962/bhl.part.7709

Zavattari, E. (1914) Mutille Austro-Malesi. *Bolletino della Societa Entomologica Italiana* 45: 61–114.

Zhou, H.-T., Lelej, A.S. & Liu, J.-X. (2018a) New records of velvet ants (Hymenoptera: Mutillidae) from China with taxonomic notes. *Far Eastern Entomologist* 354: 23–28. https://doi.org/10.25221/fee.354.4

Zhou, H.-t., Lelej, A.S., Williams, K.A. & Liu, J.-x. (2018b) Revision of the Oriental genus *Zavatilla* Tsuneki (Hymenoptera, Mutillidae, Trogaspidiini), with descriptions of two new species. *Zootaxa* 4418 (2): 101–120. http://dx.doi.org/10.11646/zootaxa.4418.2.1

Zhou, H.-T., Lelej, A.S. & Xu, Z.-F. (2017) Discovery of the subfamily Rhopalomutillinae (Hymenoptera: Mutillidae) in China and description of *Pherotilla brothersi* sp. nov. *Zootaxa* 4273 (4): 587–594. https://doi.org/10.11646/zootaxa.4273.4.8

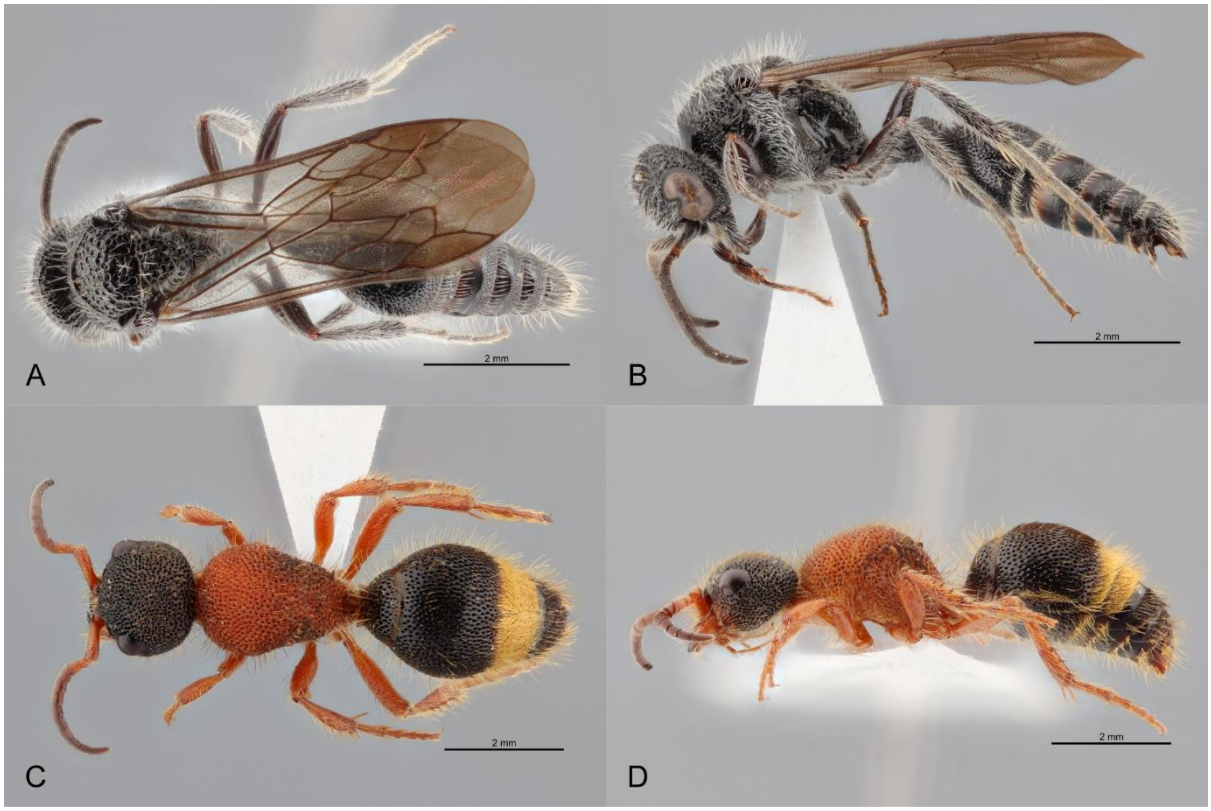

Figure 1. Rhopalomutillinae and Sphaeropthalminae spp., habitus. A, B. *Pherotilla brothersi* Zhou, Lelej & Xu, ♂, Vietnam; C, D. *Hemutilla bifurcata* (Chen), ♀, Vietnam; A, C. dorsal view; B, D. lateral view.

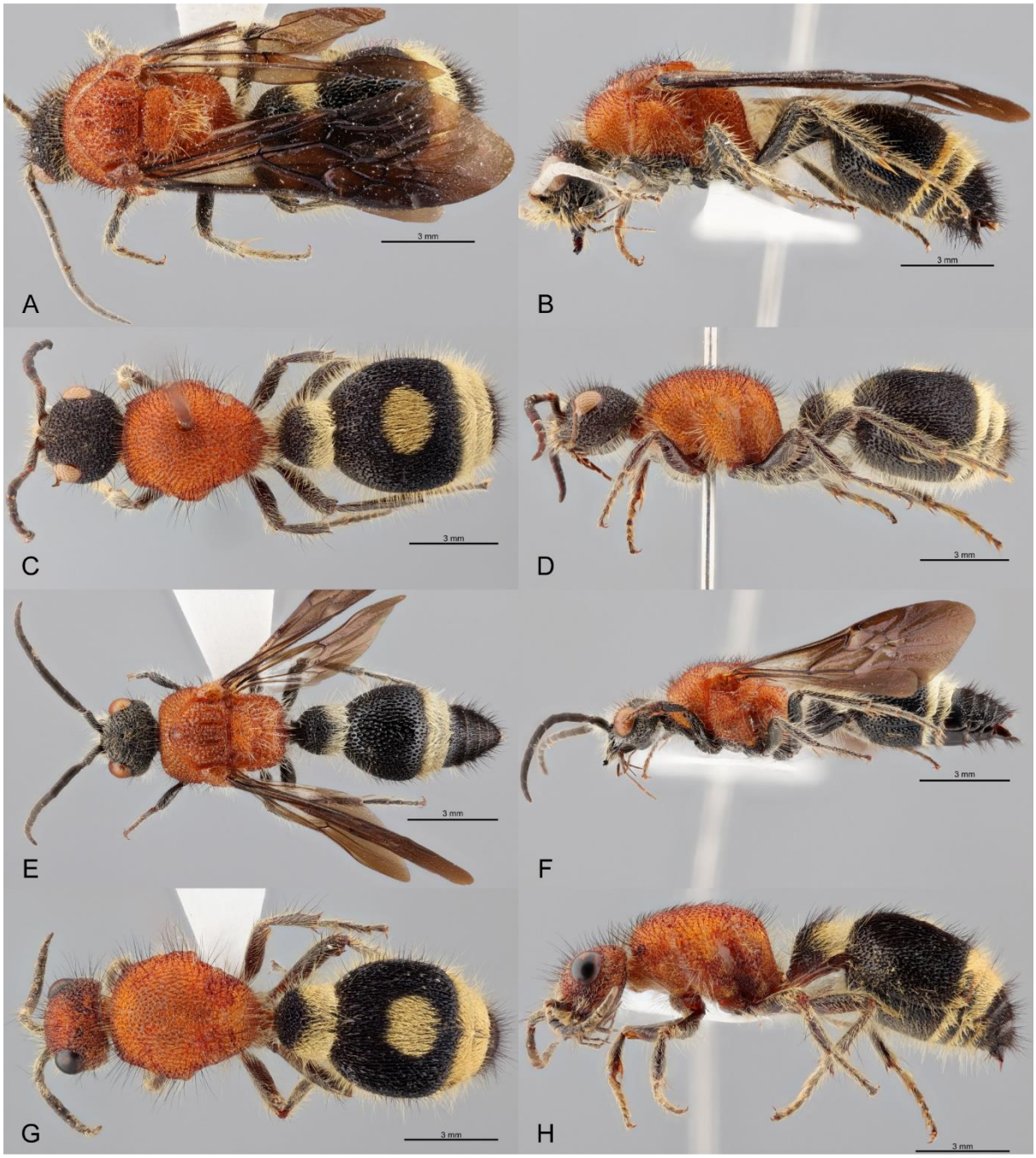

Figure 2. *Orientilla* spp., habitus. A, B. *O. desponsa* (Smith), ♂, Vietnam; C, D. *O. desponsa* (Smith), ♀, Taiwan; E, F. *O. krombeini* Lelej, ♂, Vietnam; G, H. *O. vietnamica* Lelej, ♀, Thailand; A, C, E, G. dorsal view; B, D, F, H. lateral view.

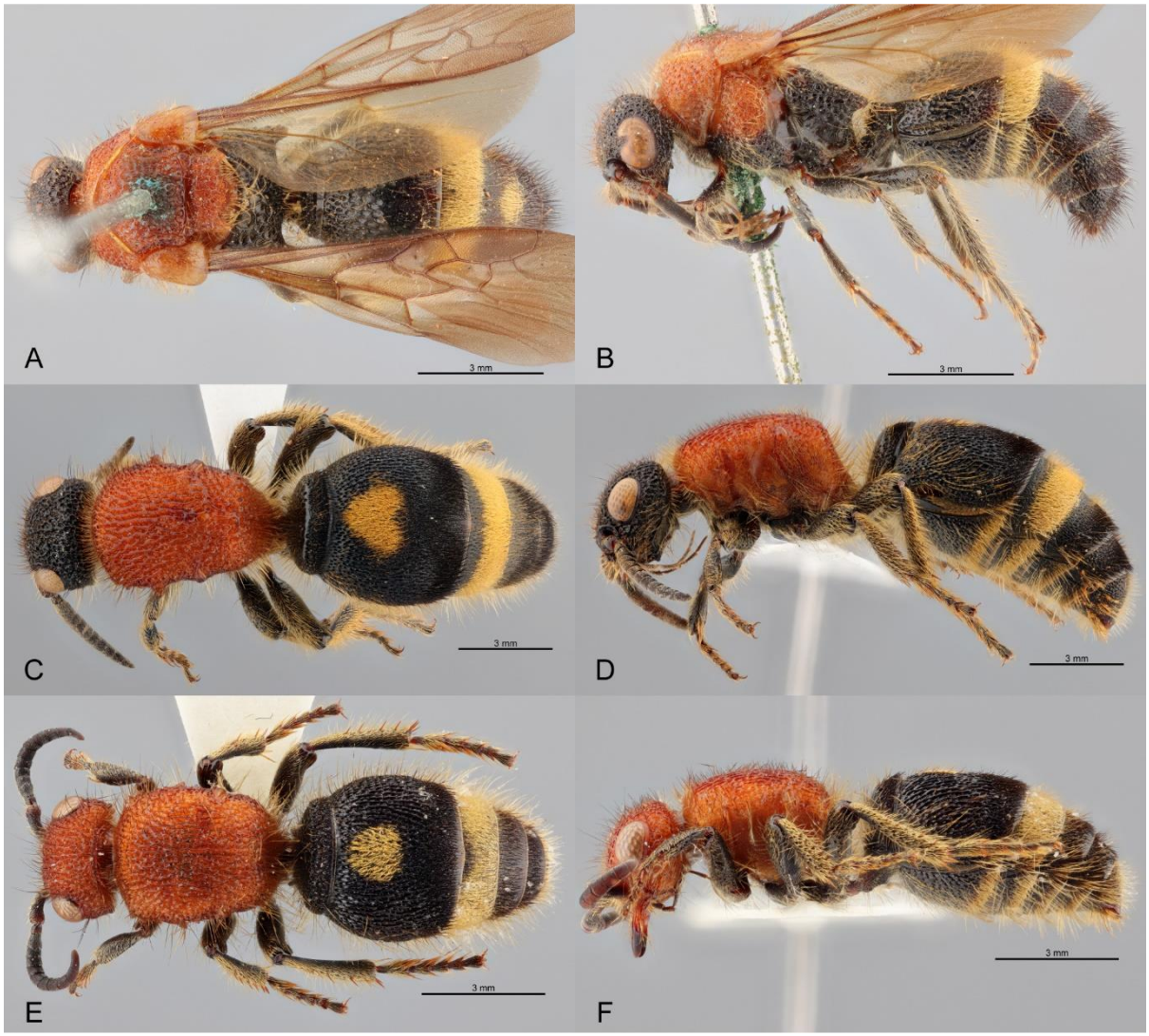

Figure 3. *Odontomutilla* spp., habitus. A, B. *O. sinensis* (Smith), ♂, China; C, D. *O. sinensis* (Smith), ♀, Vietnam; E, F. *O. uranioides* Mickel, ♀, Vietnam; A, C, E. dorsal view; B, D, F. lateral view.

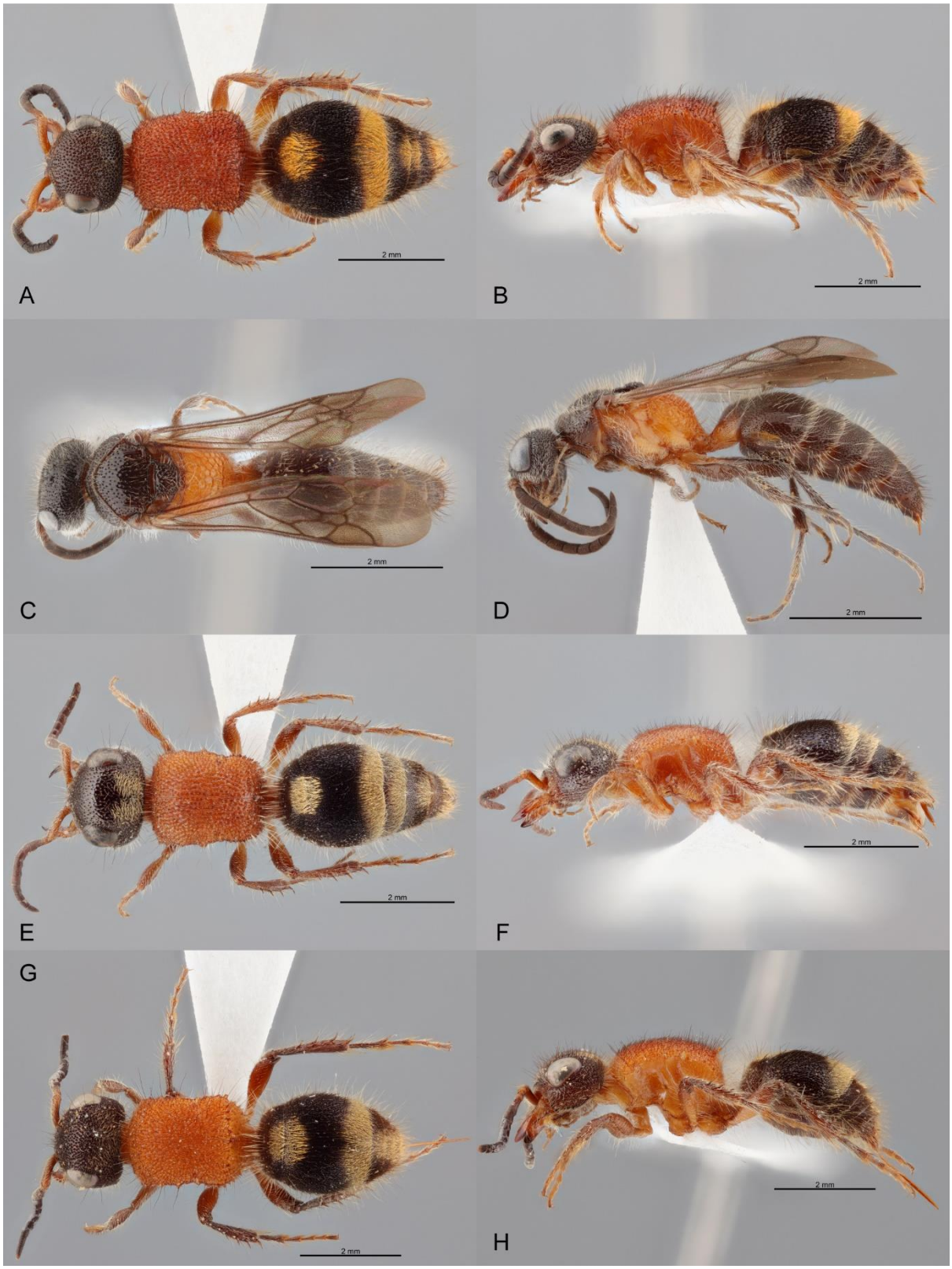

Figure 4. *Bischoffitilla* spp., habitus. A, B. *B. cambrai* Williams, ♀, Thailand; C, D. *B. lamellata* (Mickel), ♂, Vietnam; E, F. *B. lamellata* (Mickel), ♀, Vietnam; G, H. *B. perakensis* (Pagden), ♀, Vietnam; A, C, E, G. dorsal view; B, D, F, H. lateral view.

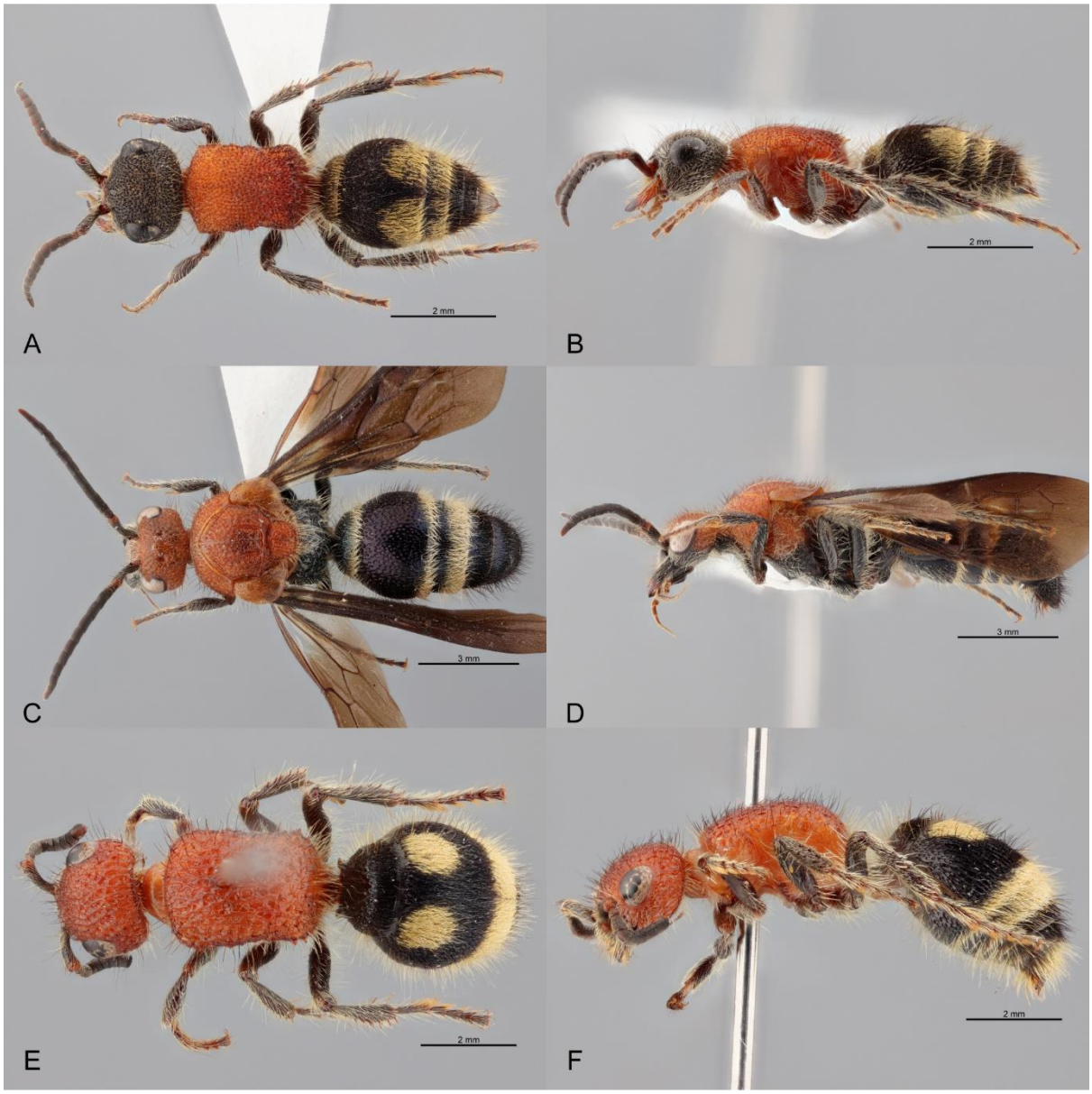

Figure 5. Ctenotillini and Mutillini spp., habitus. A, B. *Williamstilla guangdongensis* (Lelej), ♀, Vietnam; C, D. *Kurzenkotilla annamensis* Lelej, ♂, Thailand; E, F. *K. harmandi* (André), ♀, Vietnam; A, C, E. dorsal view; B, D, F. lateral view.

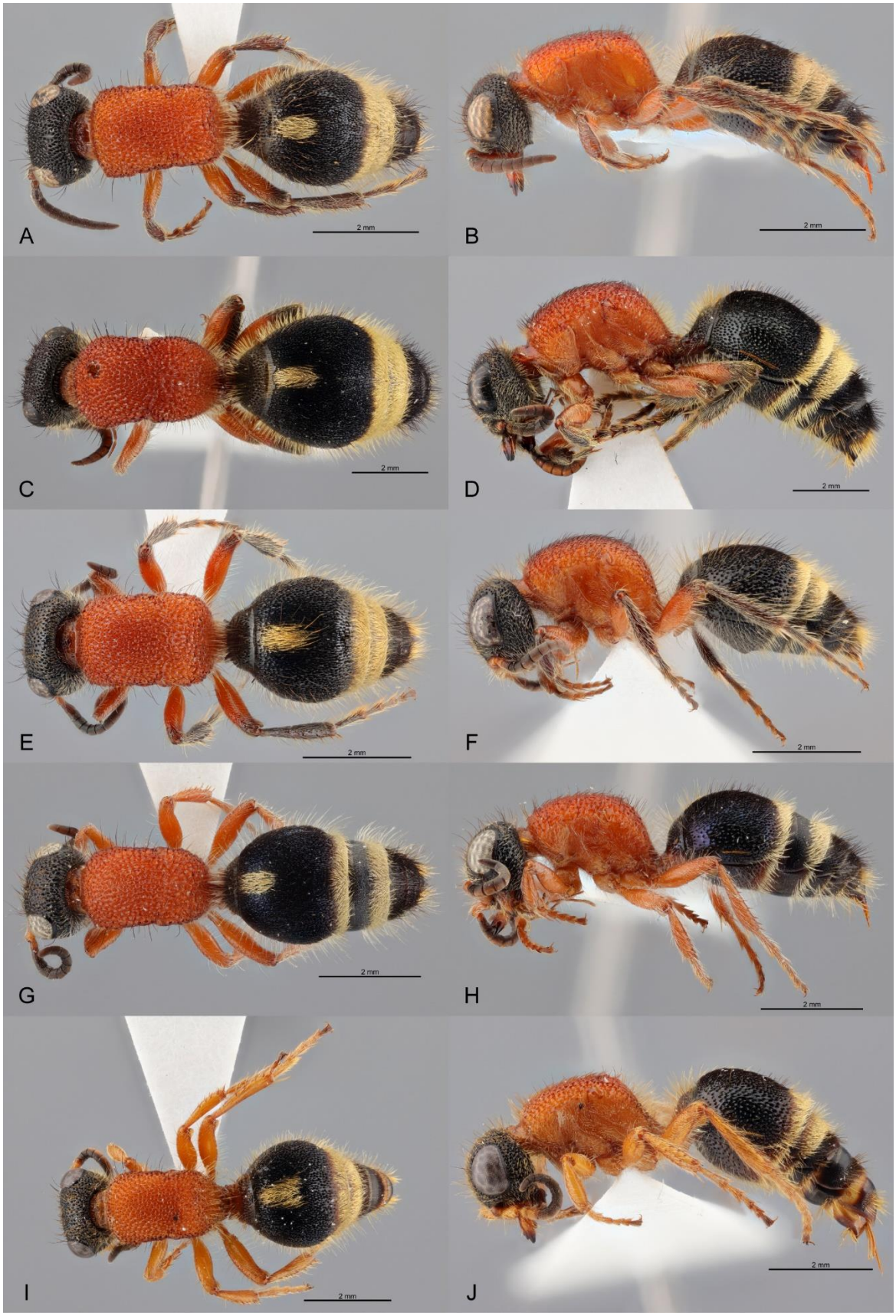

Figure 6. *Andreimyrme* spp., habitus. A, B. *A. borkenti* (Williams), ♀, Vietnam; C, D. *A. matsumotoi* Okayasu, ♀, holotype, Vietnam; E, F. *A. rong* Williams, ♀, Laos; G, H. *A. substriolata* (Chen), ♀, Vietnam; I, J. *A. yotoi* Okayasu, ♀, holotype, Vietnam; A, C, E, G, I. dorsal view; B, D, F, H, J. lateral view.

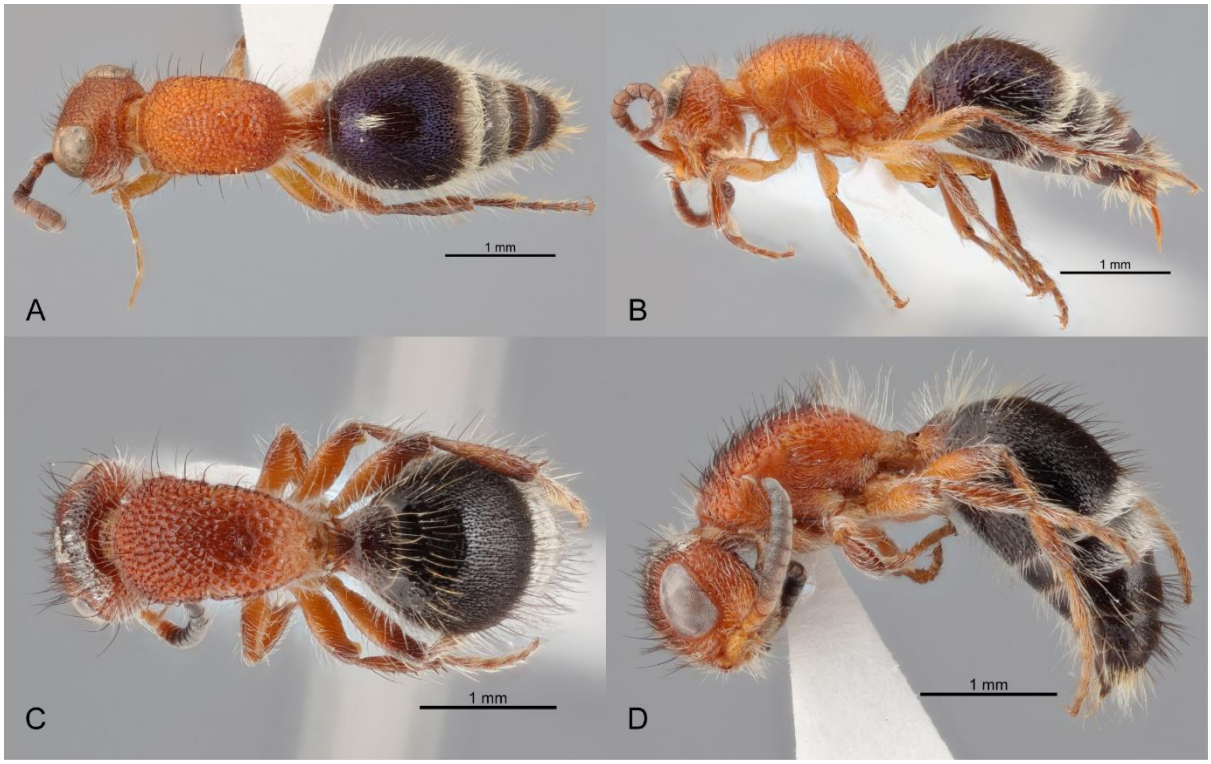

Figure 7. *Ephucilla* spp., habitus. A, B. *E. bacbo* (Lelej), ♀, Indonesia; C, D. *E. viet* (Lelej), ♀, Thailand; A, C. dorsal view; B, D. lateral view.

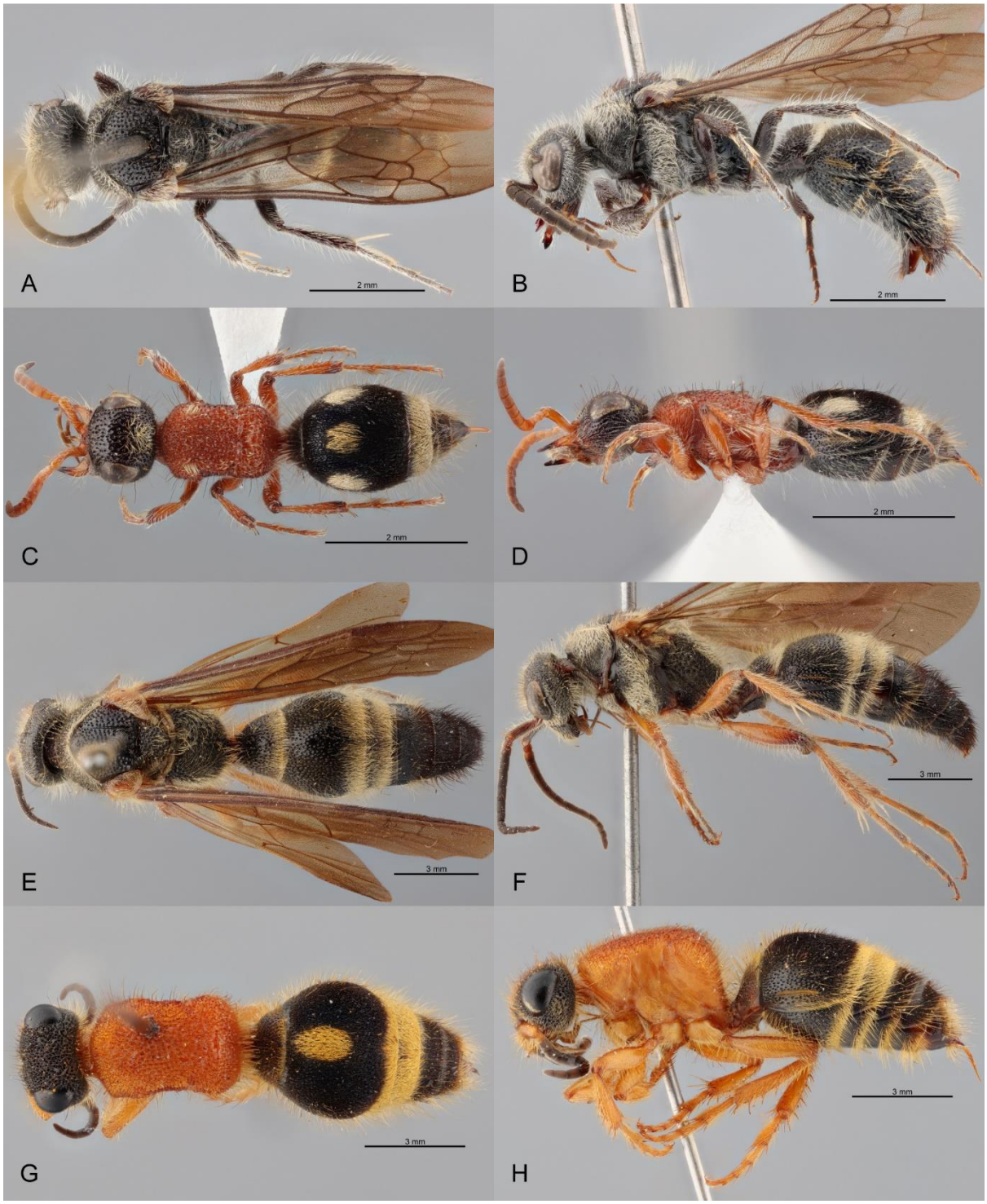

Figure 8. *Mickelomyrme* spp., habitus. A, B. *M. athalia* (Pagden), ♂, Malaysia; C, D. *M. athalia* (Pagden), ♀, Vietnam; E, F. *M. chinensis* (Smith), ♂, China; G, H. *M. chinensis* (Smith), ♀, Vietnam; A, C, E, G. dorsal view; B, D, F, H. lateral view.

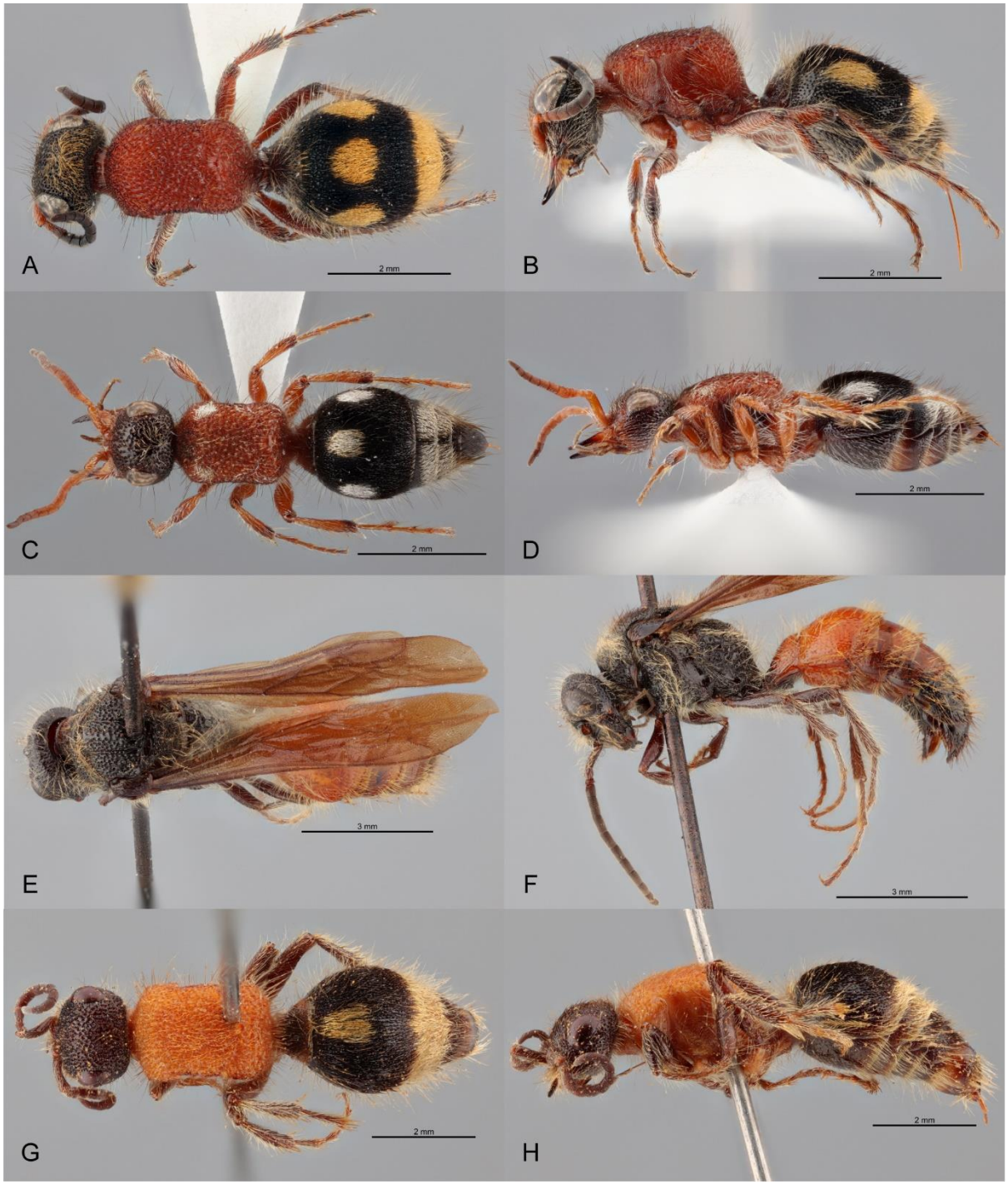

Figure 9. *Mickelomyrme* and *Nemka* spp., habitus. A, B. *M. pusillaeformis* (Hammer), ♀, Laos; C, D. *M. puttasoki* Williams, ♀, Vietnam; E, F. *N. limi* (Chen), ♂, Vietnam; G, H. *N. limi* (Chen), ♀, China; A, C, E, G. dorsal view; B, D, F, H. lateral view.

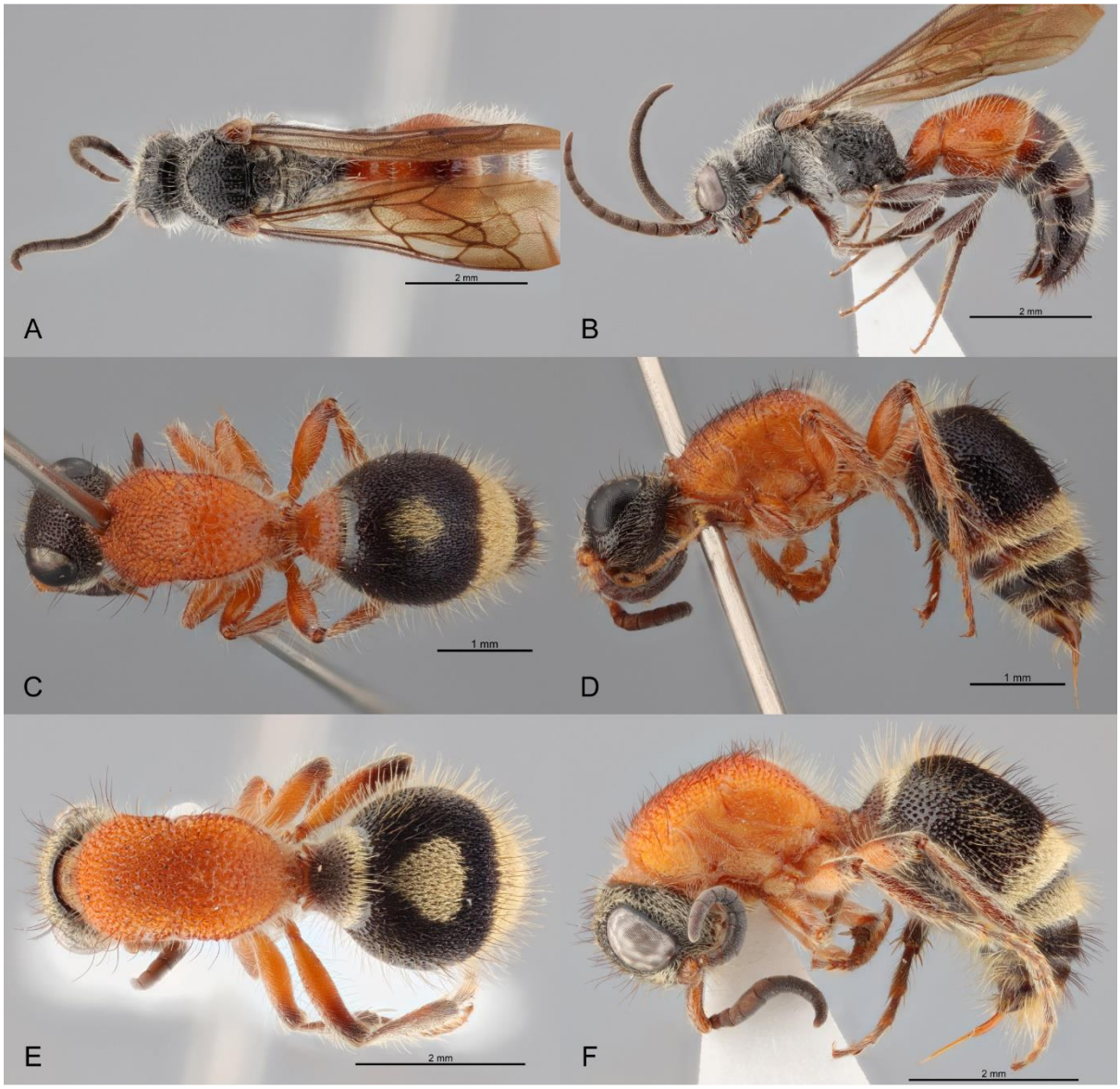

Figure 10. *Promecilla* and *Sinotilla* spp., habitus. A, B. *P. decora* (Smith), ♂, Malaysia; C, D. *P. decora* (Smith), ♀, Vietnam; E, F. *S. belokobylskiji* Lelej, ♀, Thailand; A, C, E. dorsal view; B, D, F. lateral view.

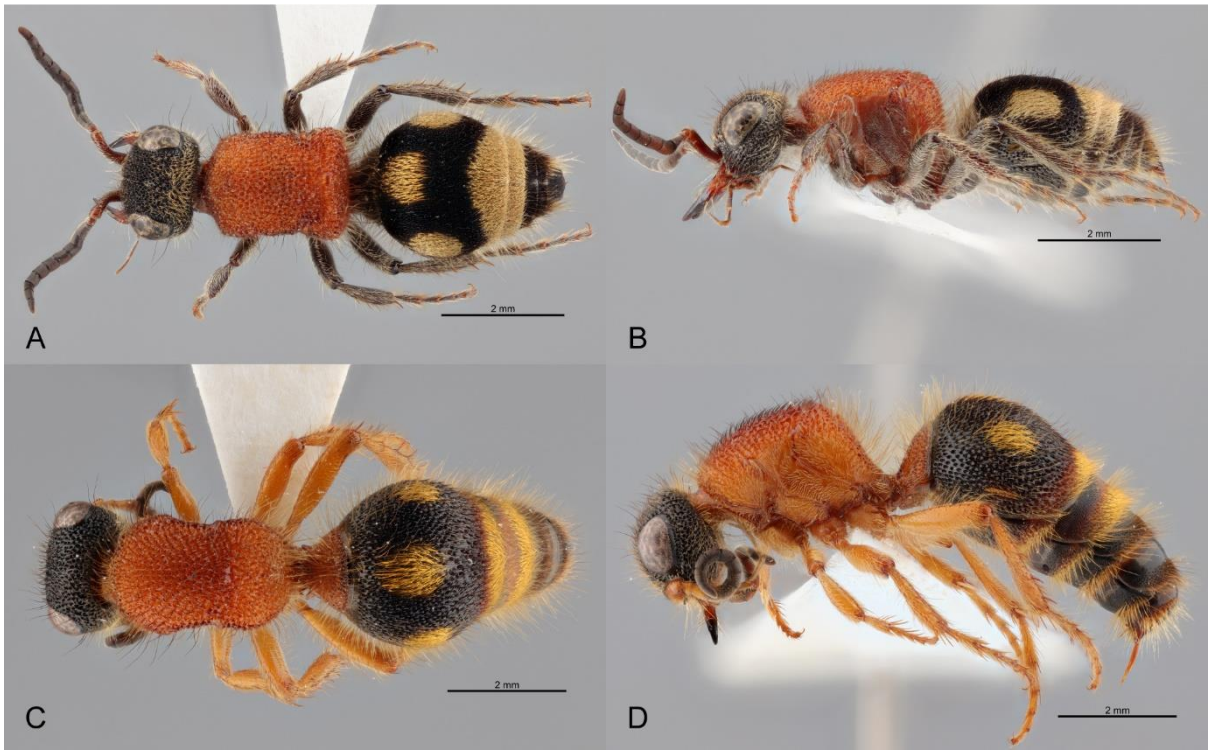

Figure 11. *Smicromyrme* spp., habitus. A, B. *S. thaochani* Williams, ♀, Vietnam; C, D. *S. triguttatus* Mickel, ♀, Vietnam; A, C. dorsal view; B, D. lateral view.

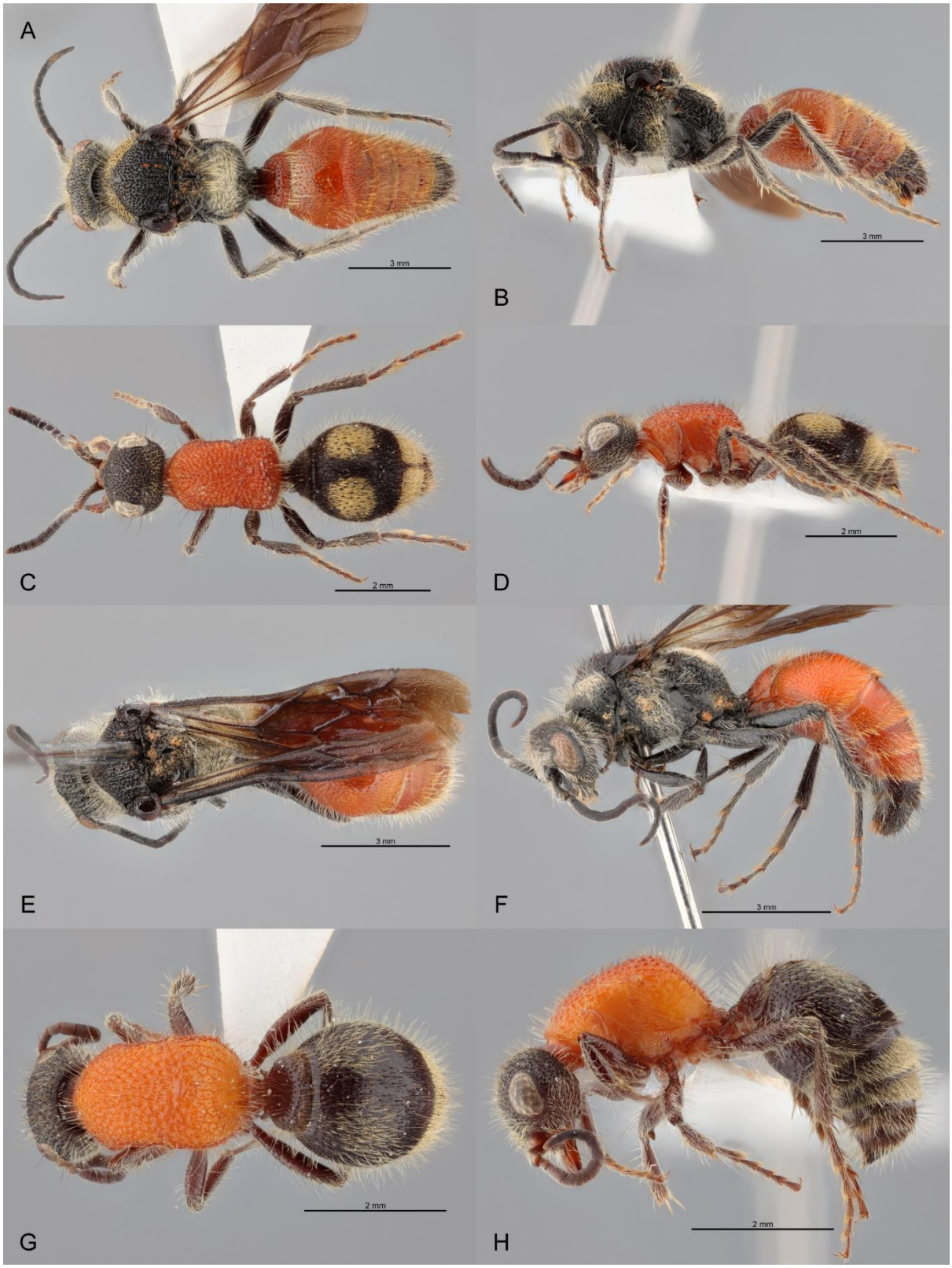

Figure 12. *Eotrogaspidia* spp., habitus. A, B. *E. auroguttata* (Smith), ♂, Laos; C, D. *E. auroguttata* (Smith), ♀, Vietnam; E, F. *E. oryzae* (Pagden), ♂, Laos; G, H. *E. oryzae* (Pagden), ♀, Thailand; A, C, E, G. dorsal view; B, D, F, H. lateral view.

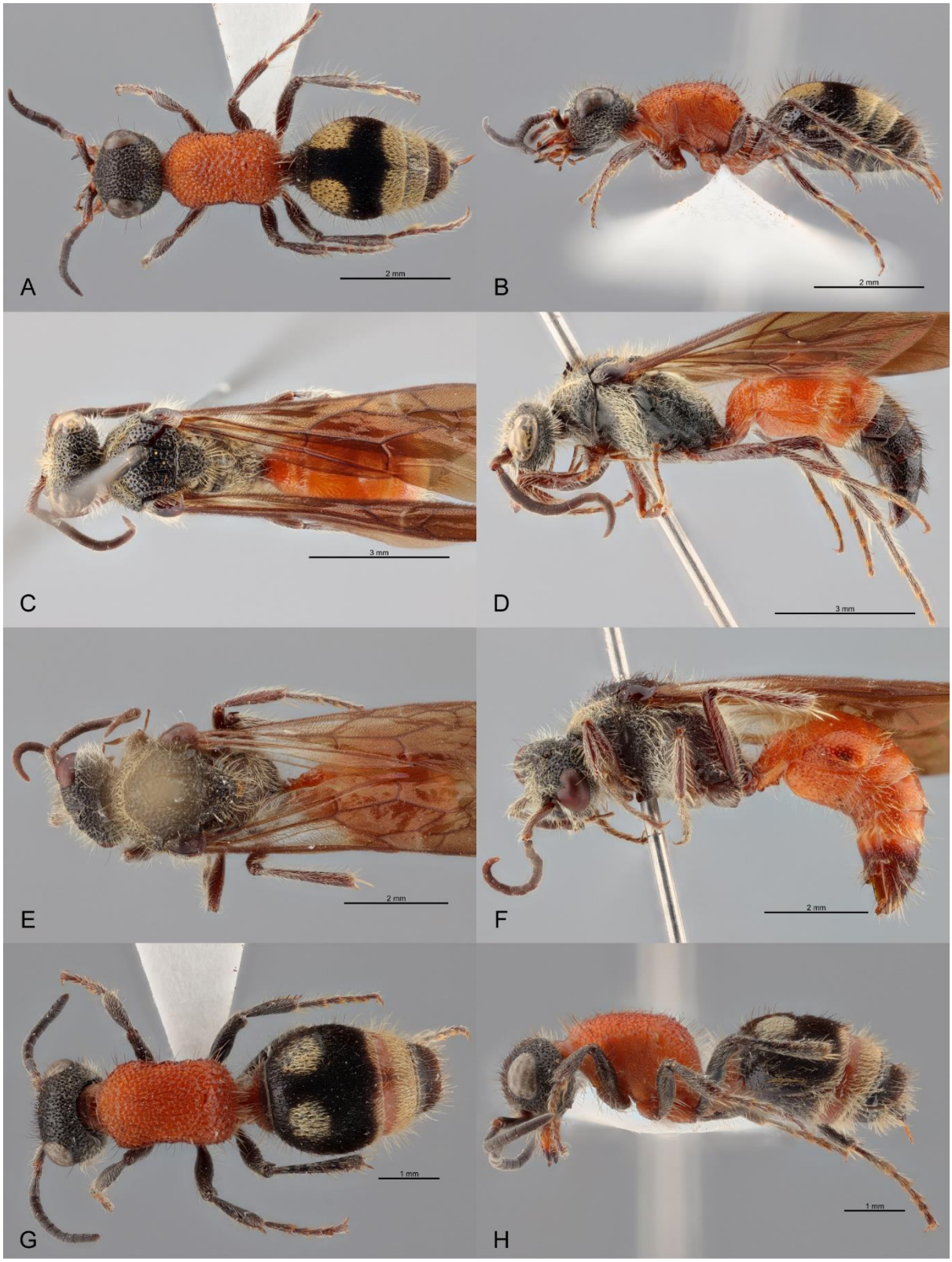

Figure 13. *Krombeinidia* and *Neotrogaspidia* spp., habitus. A, B. *K. chang* Williams, ♀, Vietnam; C, D. *K. subfossata* (Chen), ♂, Thailand; E, F. *N. circumcincta* (André), ♂, China; G, H. *N. circumcincta* (André), ♀, Vietnam; A, C, E, G. dorsal view; B, D, F, H. lateral view.

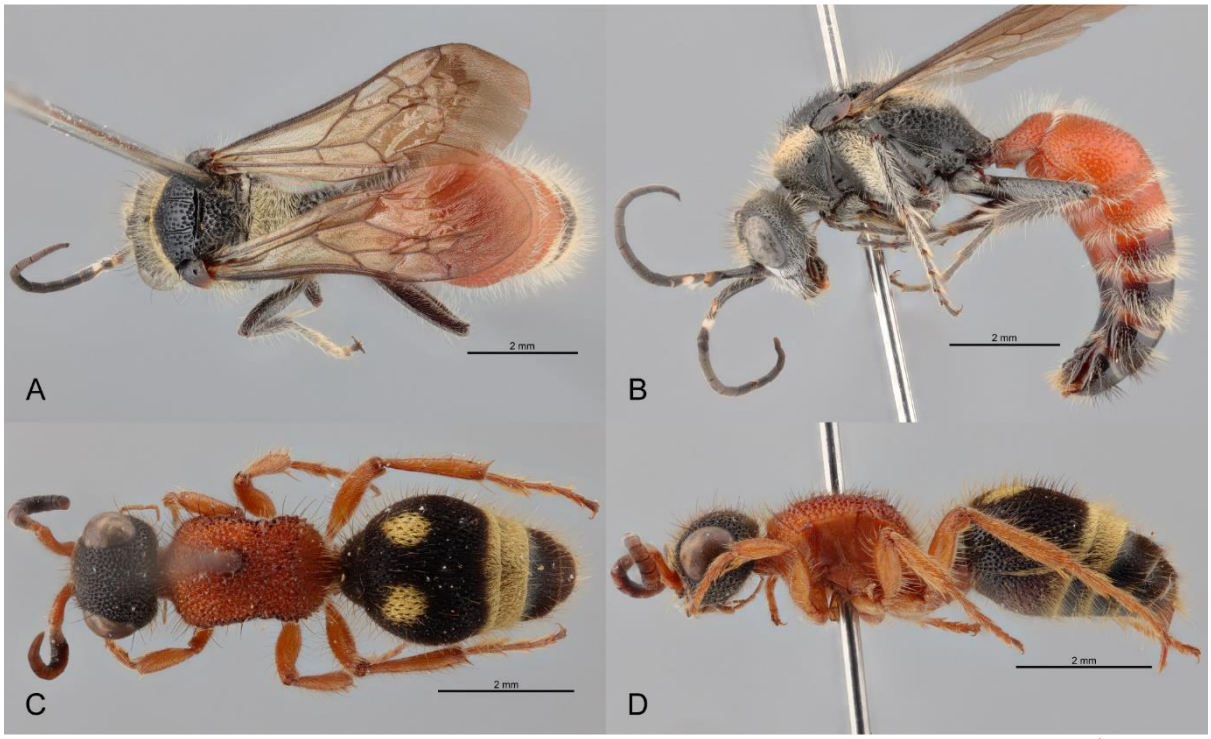

Figure 14. *Nonveilleridia* and *Orientidia* spp., habitus. A, B. *N. bataviana* (André), ♂, Vietnam; C, D. *O. thoawanae* Williams, ♀, Vietnam; A, C. dorsal view; B, D. lateral view.

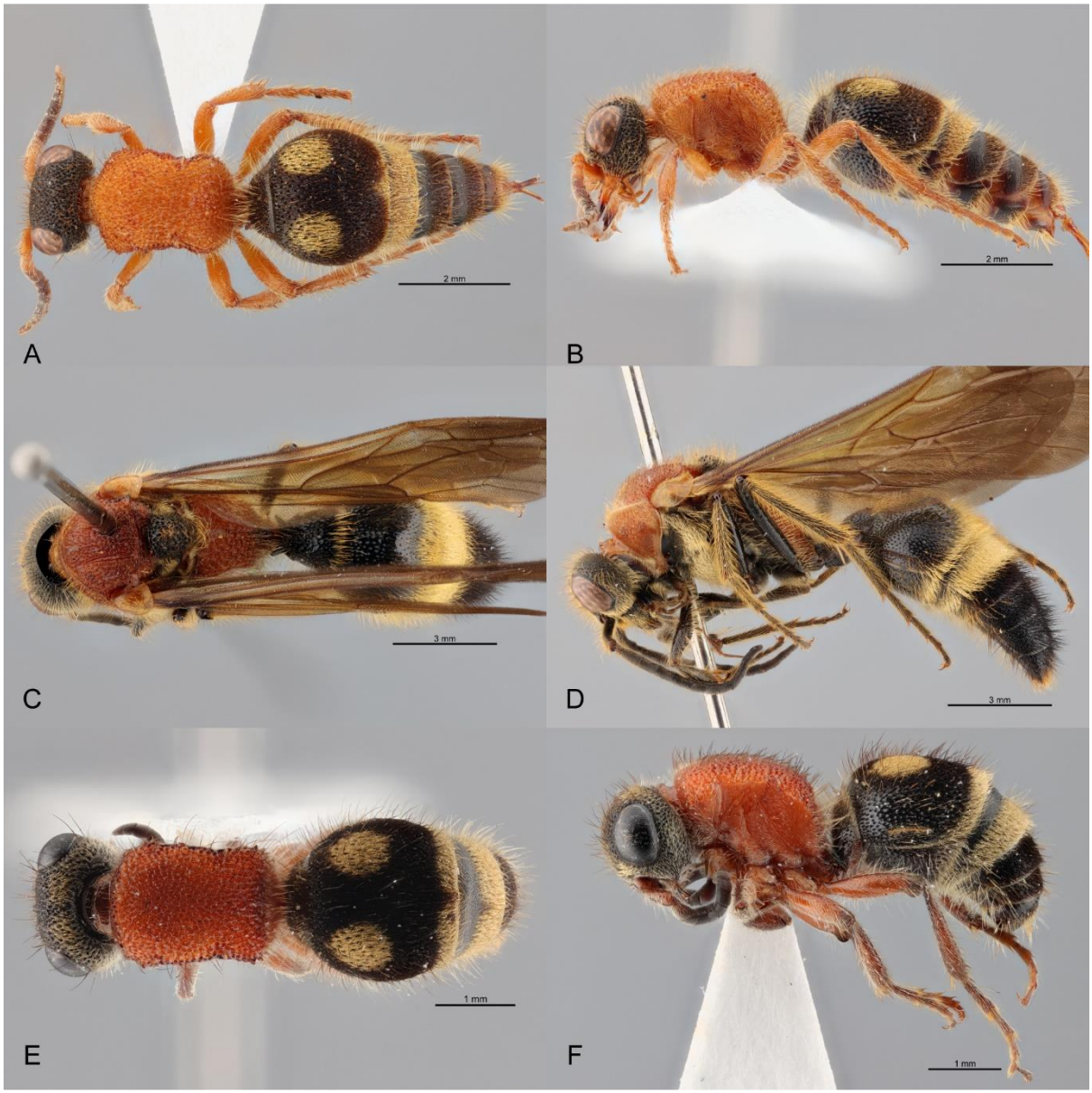

Figure 15. *Petersenidia* and *Promecidia* spp., habitus. A, B. *Pe. dorsispinata* (Chen), ♀, China; C, D. *Pe. scaphella* (Chen), ♂, Vietnam; E, F. *Pr. ninnii* (Magretti), ♀, Thailand; A, C, E. dorsal view; B, D, F. lateral view.

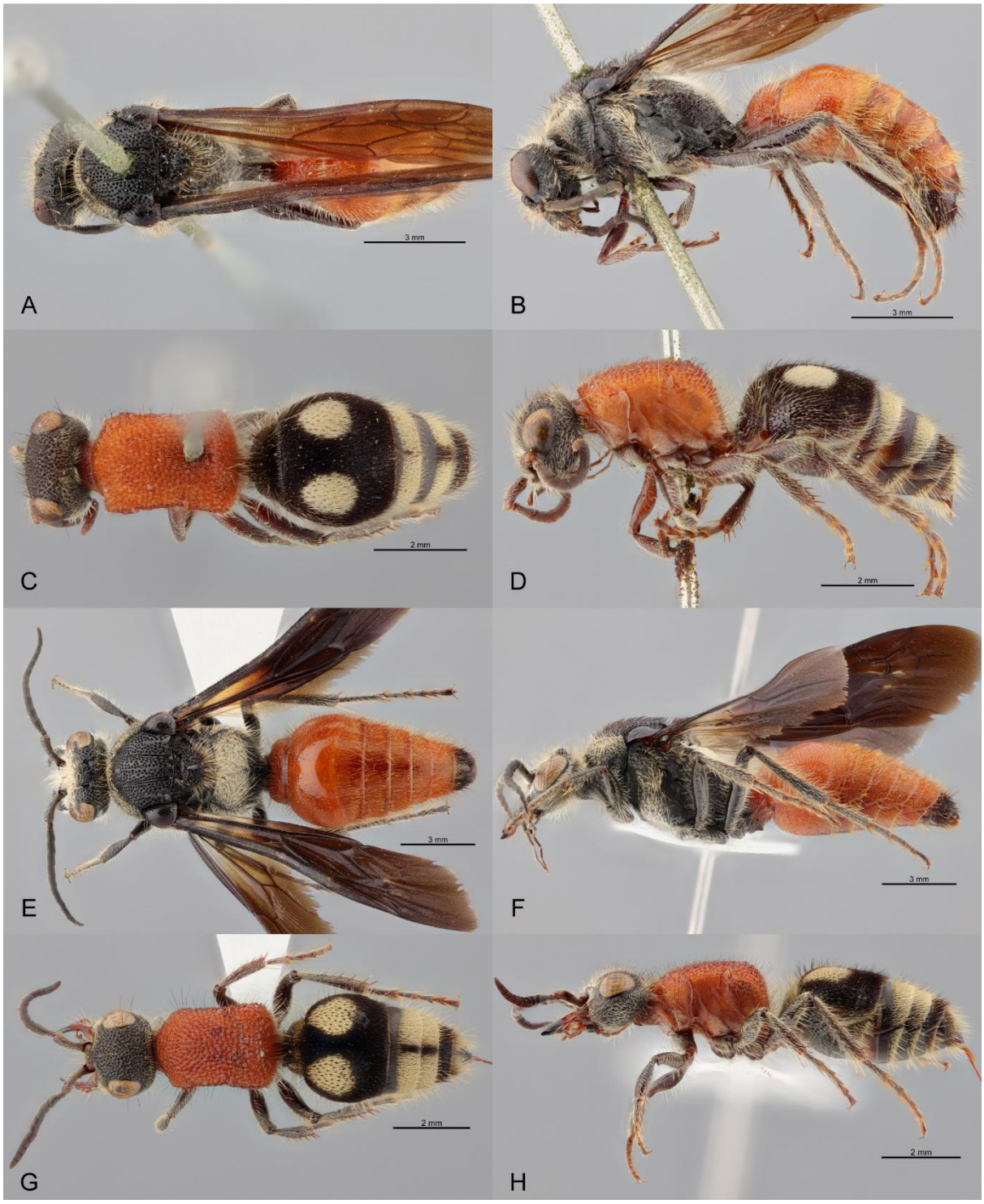

Figure 16. *Trogaspidia* spp., habitus. A, B. *T. formosana* (Matsumura), ♂, Taiwan; C, D. *T. formosana* (Matsumura), ♀, paralectotype, Taiwan; E, F. *T. fuscipennis fuscipennis* (Fabricius), ♂, Vietnam; G, H. *T. fuscipennis* (Fabricius), ♀, Vietnam; A, C, E, G. dorsal view; B, D, F, H. lateral view.

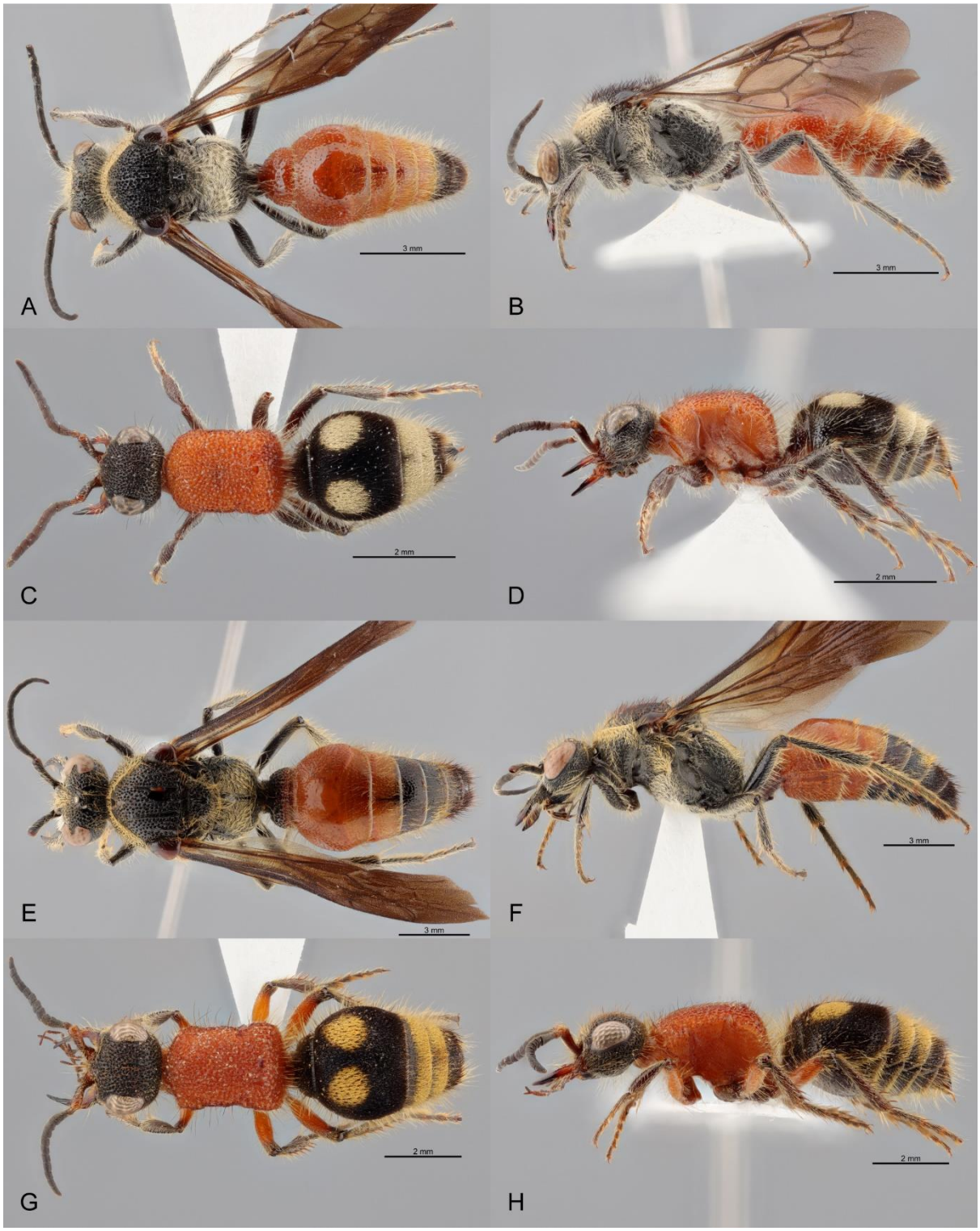

Figure 17. *Trogaspidia* spp., habitus. A, B. *T. mackieae* (Cockerell), ♂, Thailand; C, D. *T. mackieae* (Cockerell), ♀, Thailand; E, F. *T. rhea gaea* (Chen), ♂, Vietnam; G, H. *T. rhea gaea* (Chen), ♀, Vietnam; A, C, E, G. dorsal view; B, D, F, H. lateral view.

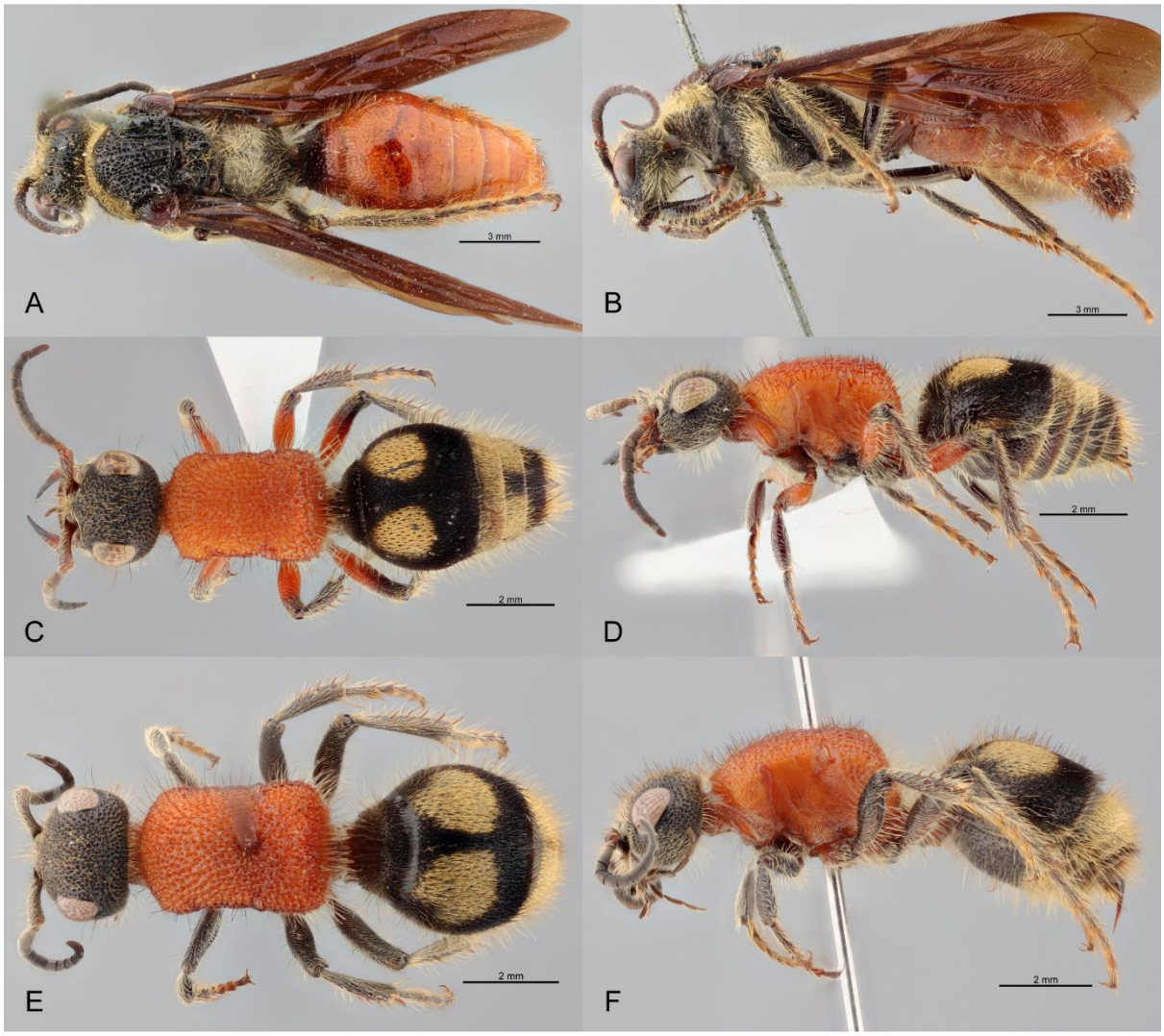

Figure 18. *Wallacidia* spp., habitus. A, B. *W*. *oculata* (Fabricius), ♂, Taiwan; C, D. *W*. *oculata* (Fabricius), ♀, Vietnam; E, F. *W*. *retinula* (Chen), ♀, Vietnam; A, C, E. dorsal view; B, D, F. lateral view.

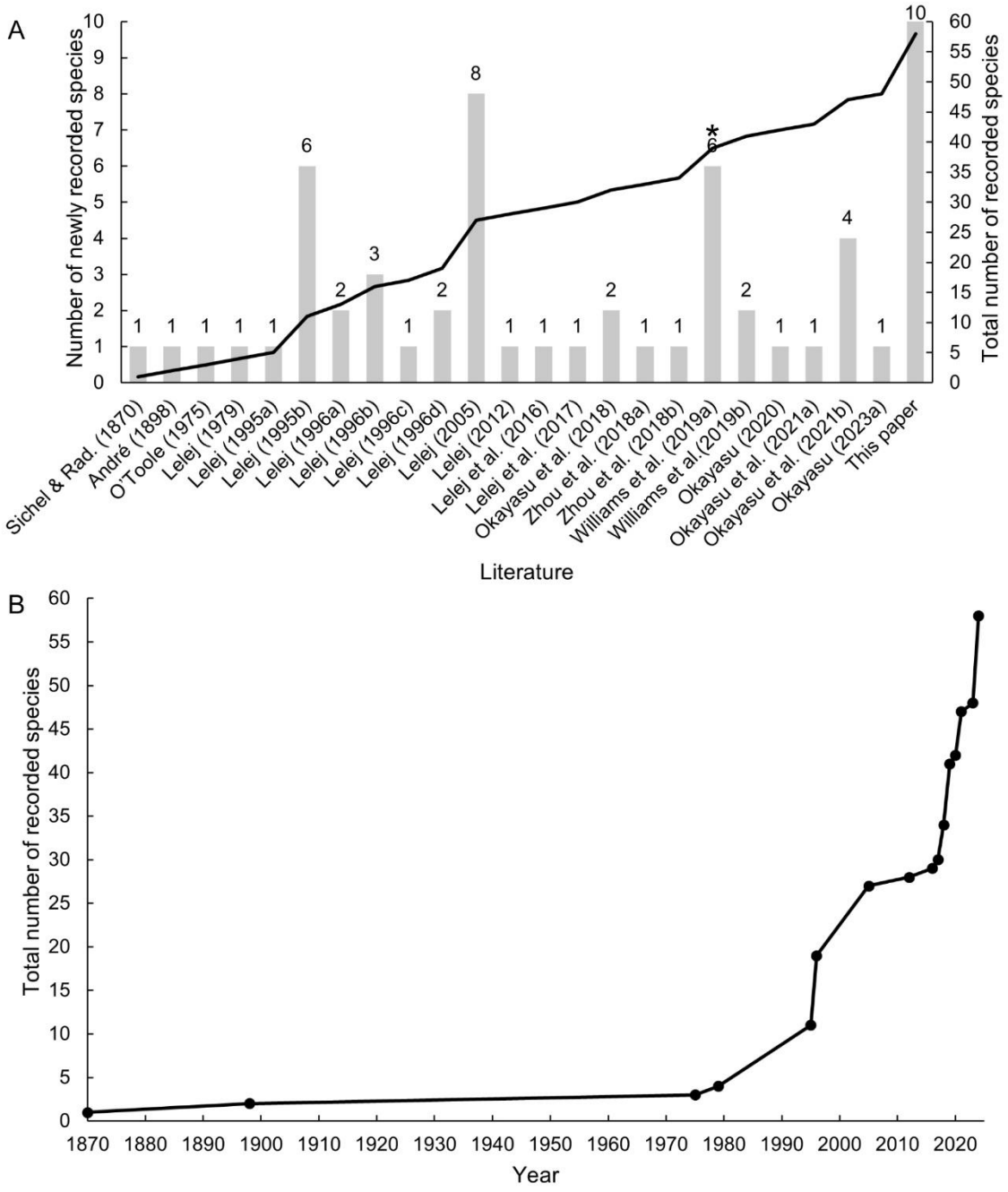

Figure 19. History of described or recorded species from Vietnam including the present work. A. Number of newly described and recorded species in each taxonomic paper and cumulative number of species; B. cumulative number of species. An asterisk indicates that a new synonymy for Vietnamese species was proposed.

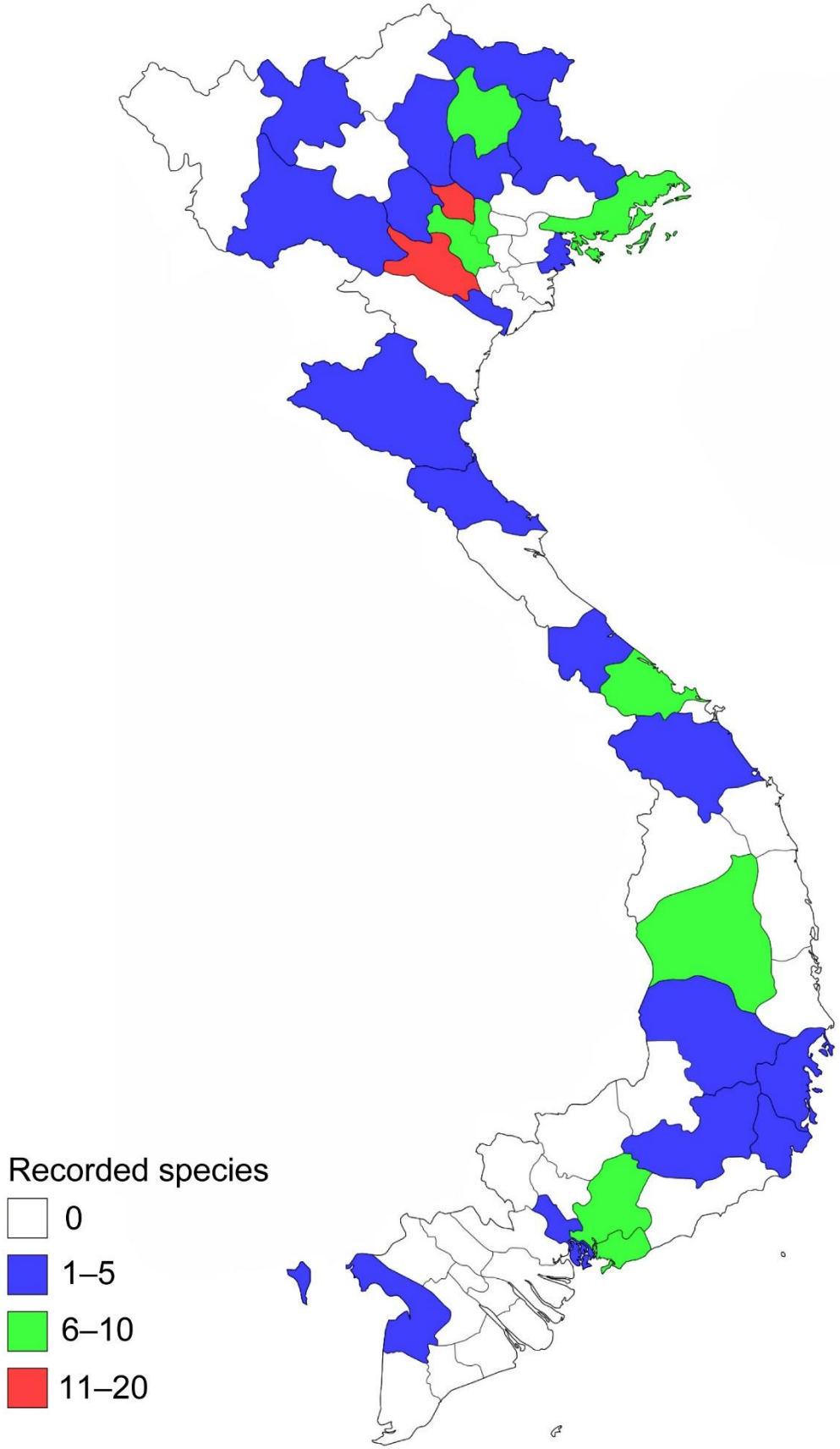

Figure 20. Number of recorded species in provincial level. White: 0; blue: 1–5; green 6–10; red: 11–20.

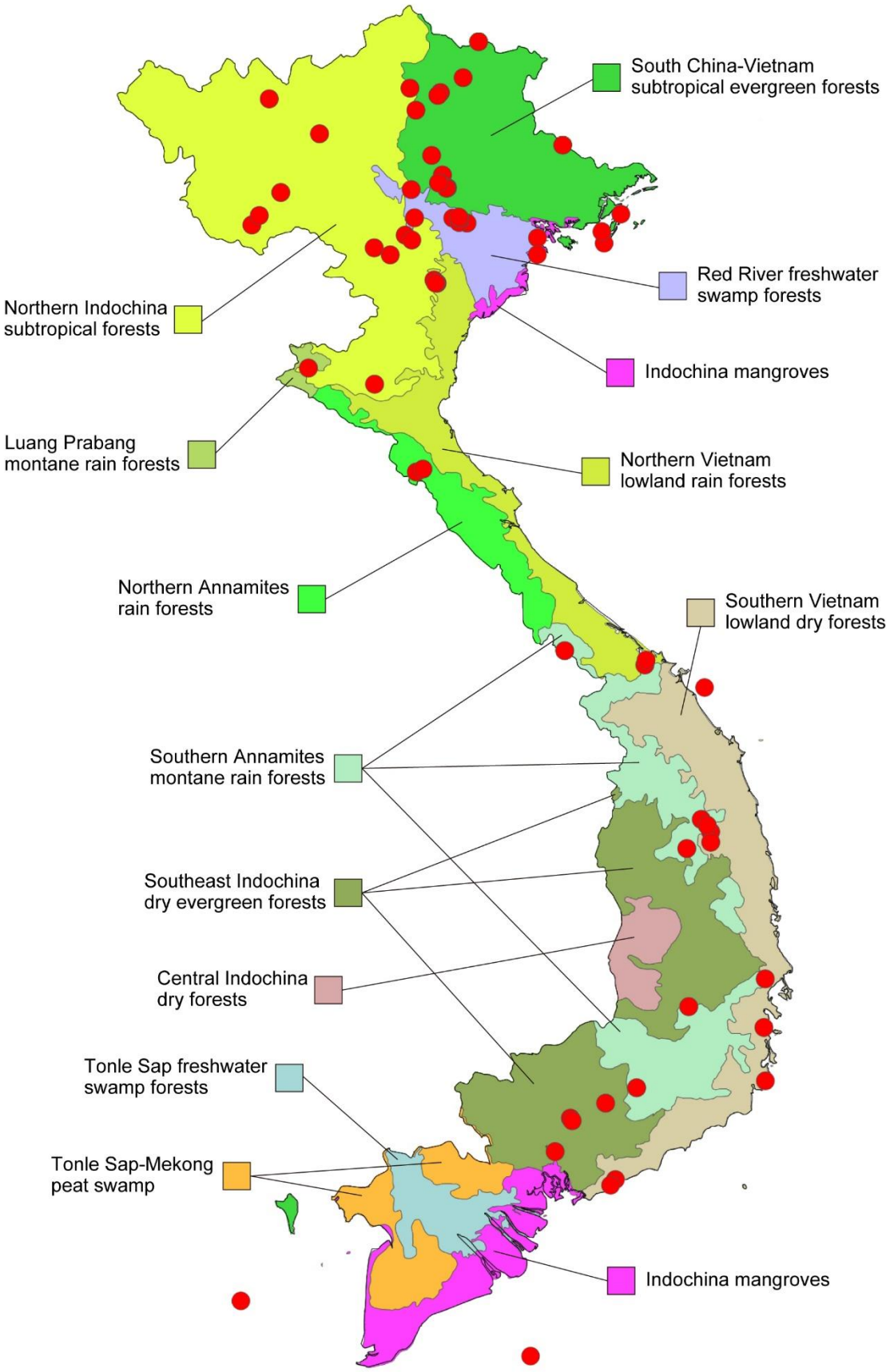

Figure 21. Terrestrial ecoregions of Vietnam. Red circles designate collecting localities.

Table 1. Number of recorded species from Vietnam.

Higher classification		Genus	Number of recorded species	Reference
Myrmosidae				
Kudakruminae		*Kudakrumia*	1	Williams *et al*. 2019b
Myrmosinae		*Krombeinella*	1	Williams *et al*. 2019b
Mutillidae				
Rhopalomutillinae		*Pherotilla*	2	Lelej 2012; this study
Sphaeropthalminae	Sphaeropthalmini	*Hemutilla*	1	This study
Dasylabrinae		*Orientilla*	3	Lelej 1979, 1996a
Odontomutillinae		*Odontomutilla*	3	Lelej 2005; Okayasu *et al*. 2018
		Yamanetilla	1	Lelej 1996c
Myrmillinae		*Bischoffitilla*	3	Lelej 2005; Williams *et al*. 2019a; this study
Mutillinae	Ctenotillini	*Williamstilla*	1	Williams *et al*. 2019a
	Mutillini	*Kurzenkotilla*	2	Lelej 2005; Lelej *et al*. 2023; this study
	Smicromyrmini	*Andreimyrme*	5	Lelej 1995b; Okayasu 2020; Okayasu *et al*. 2021b
		Ephucilla	2	Lelej 1995b; Williams *et al*. 2019a
		Mickelomyrme	6	Lelej 1996d; Okayasu 2020; Okayasu *et al*. 2018; Zhou *et al*. 2018a; this study
		Nemka	1	Lelej 1995a; Okayasu 2020
		Promecilla	1	This study
		Sinotilla	2	Lelej 1995b
		Smicromyrme	2	Okayasu 2018; this study
	Trogaspidiini	*Eotrogaspidia*	2	Okayasu *et al*. 2021a; Williams *et al*. 2019a
		Krombeinidia	3	André 1898; Lelej 1996b; this study
		Neotrogaspidia	1	Okayasu 2023a
		Nonveilleridia	1	Lelej 1996b
		Orientidia	1	This study
		Petersenidia	3	Lelej 1996b, 2005; Williams *et al*. 2019a
		Promecidia	2	Lelej *et al*. 2016
		Trogaspidia	4	Lelej 2005; Okayasu *et al*. 2018, 2021a; Williams *et al*. 2019a
		Wallacidia	2	Lelej 1996b; O'Toole 1975; this study
		Zavatilla	1	Zhou *et al*. 2018b
	Zeugomutillini	*Zeugomutilla*	1	Lelej *et al*. 2017
Total number			58	

Table 2-1. Occurrence of Vietnamese velvet ants across countries (+ – present; - – absent; ? – doubtfully recorded).

Species/country	Vietnam	South Korea	Japan	China & Taiwan	Laos	Cambodia	Thailand	Malaysia	Myanmar	India	Indonesia	Philippines
Kudakrumia loaibonho (♂)	+	-	-	-	-	-	-	-	-	-	-	-
Krombeinella brothersi (♂)	+	-	-	-	-	-	-	-	-	-	-	-
Pherotilla brothersi (♂)	+	-	-	+	-	-	-	-	-	-	-	-
Pherotilla striganovae (♀)	+	-	-	-	-	-	+	-	-	-	-	-
Hemutilla bifurcata (♀)	+	-	-	+	-	-	-	-	-	-	-	-
Orientilla desponsa (♂♀)	+	-	-	+	-	-	-	-	-	-	?	-
Orientilla krombeini (♂♀)	+	-	-	-	-	-	-	-	-	-	-	-
Orientilla vietnamica (♀)	+	-	-	-	+	-	+	-	+	-	-	-
Odontomutilla cordigera (♀)	+	-	-	-	-	-	+	+	-	-	+	-
Odontomutilla sinensis (♂♀)	+	-	-	+	-	-	-	-	-	-	-	-
Odontomutilla uranioides (♀)	+	-	-	+	+	-	+	-	-	-	-	-
Yamanetilla pedaria (♂♀)	+	-	-	-	-	-	-	+	-	-	-	+
Bischoffitilla cambrai (♀)	+	-	-	-	-	-	+	-	-	-	-	-
Bischoffitilla lamellata (♂♀)	+	-	-	+	-	-	+	+	-	-	-	-
Bischoffitilla perakensis (♀)	+	-	-	-	-	-	+	+	-	-	-	-
Williamstilla guangdongensis (♂♀)	+	-	-	+	+	+	+	-	-	-	-	-
Kurzenkotilla annamensis (♂♀)	+	-	-	+	-	-	+	-	-	-	-	-
Kurzenkotilla harmandi (♂♀)	+	-	-	-	+	-	+	-	-	-	-	-
Andreimyrme borkenti (♀)	+	-	-	-	-	-	+	-	-	-	-	-
Andreimyrme matsumotoi (♀)	+	-	-	-	-	-	-	-	-	-	-	-
Andreimyrme rong (♀)	+	-	-	-	-	-	+	-	-	-	-	-
Andreimyrme substriolata (♀)	+	-	+	+	+	-	+	+	-	+	+	-
Andreimyrme yotoi (♀)	+	-	-	-	+	-	-	-	-	-	-	-
Ephucilla bacbo (♀)	+	-	-	-	-	-	-	-	-	-	+	-
Ephucilla viet (♀)	+	-	-	-	-	-	+	+	-	-	-	-
Mickelomyrme abnorma (♂)	+	-	-	+	-	-	+	-	-	-	-	-
Mickelomyrme athalia (♂♀)	+	-	-	+	+	-	+	+	-	-	-	-
Mickelomyrme chinensis (♂♀)	+	-	-	+	+	-	-	-	-	-	-	-
Mickelomyrme kuznetsovi (♀)	+	-	-	+	+	-	+	-	-	-	-	-
Mickelomyrme pusillaeformis (♂♀)	+	-	-	+	+	-	+	-	+	-	+	-
Mickelomyrme puttasoki (♀)	+	-	-	-	-	-	+	-	-	-	-	-
Nemka limi (♂♀)	+	+	-	+	-	-	-	-	-	-	-	-
Promecilla decora (♂♀)	+	-	-	+	-	-	+	+	?	-	?	-

Table 2-2. Occurrence of Vietnamese velvet ants across countries (+ – present; - – absent; ? – doubtfully recorded).

Species/country	Vietnam	South Korea	Japan	China & Taiwan	Laos	Cambodia	Thailand	Malaysia	Myanmar	India	Indonesia	Philippines
Sinotilla belokobylskiji (♀)	+	-	-	+	-	-	+	-	-	-	-	-
Sinotilla boheana (♂)	+	-	-	+	-	-	-	-	-	-	-	-
Smicromyrme thaochani (♀)	+	-	-	-	-	-	+	-	-	-	-	-
Smicromyrme triguttatus (♀)	+	-	-	+	+	-	+	-	-	-	-	-
Eotrogaspidia auroguttata (♂♀)	+	-	+	+	+	-	-	-	-	+	+	-
Eotrogaspidia oryzae (♂♀)	+	-	-	-	+	-	+	+	-	-	-	-
Krombeinidia chang (♀)	+	-	-	-	-	-	+	-	-	-	-	-
Krombeinidia griseomaculata (♀)	+	-	-	+	-	-	+	-	-	-	+	-
Krombeinidia subfossata (♂)	+	-	-	+	-	-	+	+	-	-	-	-
Neotrogaspidia circumcincta (♂♀)	+	-	-	+	+	-	+	+	-	-	+	-
Nonveilleridia bataviana (♂)	+	-	-	+	-	-	+	-	-	-	+	-
Orientidia thoawanae (♀)	+	-	-	-	-	-	+	+	-	-	-	-
Petersenidia dorsispinata (♀)	+	-	-	+	-	-	-	-	-	-	-	-
Petersenidia leleji (♀)	+	-	-	-	-	-	+	-	-	-	-	-
Petersenidia scaphella (♂)	+	-	-	+	-	-	-	-	-	-	-	-
Promecidia birmanica (♂)	+	-	-	-	+	-	-	-	+	+	-	-
Promecidia ninnii (♀)	+	-	-	-	-	+	+	-	+	-	-	-
Trogaspidia formosana (♂♀)	+	-	-	+	-	-	-	-	-	-	-	-
Trogaspidia fuscipennis fuscipennis (♂♀)	+	-	-	+	-	-	+	-	-	-	-	-
Trogaspidia mackieae (♂♀)	+	-	-	+	-	-	+	-	-	-	-	-
Trogaspidia rhea gaea (♂♀)	+	-	-	+	-	-	-	-	-	-	-	-
Wallacidia oculata (♂♀)	+	-	-	+	+	+	+	+	+	-	-	-
Wallacidia retimula (♀)	+	-	-	+	-	-	-	-	-	-	-	-
Zavatilla xuzaifui (♂♀)	+	-	-	+	-	-	-	-	-	-	-	-
Zeugomutilla angkorensis (♂)	+	-	-	-	-	+	+	-	-	-	-	-
Number of shared species with Vietnam	58	1	2	33	15	4	36	13	5	3	8	1

Table 3. Number of recorded species from each province in Vietnam.

Region	Province	Number of recorded species	Region	Province	Number of recorded species
Northeast	Bac Giang	0	South Central Coast	Binh Dinh	0
	Bac Kan	7		Binh Thuan	0
	Cao Bang	2		Danang	0
	Ha Giang	0		Khanh Hoa	2
	Lang Son	1		Ninh Thuan	2
	Phu Tho	1		Phu Yen	0
	Thai Nguyen	1		Quang Nam	1
	Tuyen Quang	1		Quang Ngai	0
	Quang Ninh	6		Subtotal	5
	Subtotal	13	Central Highlands	Dak Lak	3
Northwest	Dien Bien	0		Dak Nong	0
	Hoa Binh	16		Gia Lai	6
	Lai Chau	0		Kon Tum	0
	Lao Cai	3		Lam Dong	2
	Son La	3		Subtotal	11
	Yen Bai	0	Southeast	Ba Ria Vung Tau	10
	Subtotal	18		Binh Duong	0
Red River Delta	Bac Ninh	0		Binh Phouc	0
	Ha Nam	0		Dong Nai	7
	Hai Duong	0		Ho Chi Minh	1
	Hai Phong	2		Tay Ninh	0
	Hanoi	10		Subtotal	17
	Hung Yen	0	Mekong River Delta	An Giang	0
	Nam Dinh	0		Bac Lieu	0
	Ninh Binh	4		Ben Tre	0
	Thai Binh	0		Ca Mau	0
	Vinh Phuc	17		Can Tho	0
	Subtotal	29		Dong Thap	0
North Central Coast	Ha Tinh	2		Hau Giang	0
	Nghe An	2		Kien Giang	1
	Thanh Hoa	0		Long An	0
	Thua Thien Hue	8		Soc Trang	0
	Quang Binh	0		Tien Giang	0
	Quang Tri	1		Tra Vinh	0
	Subtotal	12		Vinh Long	0
				Subtotal	1

Chapter 8

Preliminary assessment of the velvet ant fauna in Nepal, with description of new species of the genera *Strangulotilla* Nonveiller and *Zeugomutilla* Chen (Hymenoptera: Mutillidae)

Disclaimer: *This chapter has already been published as a peer-reviewed paper as follows: Okayasu, J. (2023) Insecta matsumurana, New Series 79: 1–27 (http://hdl.handle.net/2115/90642). New nomenclatural acts appearing in this chapter have already been made in this publication and, thus, this dissertation chapter is not considered a published work within the meaning of the International Code of Zoological Nomenclature 4th edition (Article 8.2).*

Abstract
During 1965 to 1983, Hokkaido University undertook several entomological expeditions to various parts of Nepal. Specimens are preserved in the Hokkaido University Insect Collection (SEHU), providing valuable resources for better understanding of the velvet ant fauna of this rarely explored country with only eight recorded species in seven genera. This collection included 49 velvet ant specimens. The aim of this paper is to present its outline as the first attempt to assess the potential diversity of velvet ants in this country. Two genera of the tribe Zeugomutillini Waldren, 2023, *Strangulotilla* Nonveiller, 1979 and *Zeugomutilla* Chen, 1957, are newly recorded from Nepal. Two new species, *S. dubia* **sp. nov.** (♂) and *Z. curvicarinata* **sp. nov.** (♀), are described from Chitwan, Bagmati. These new species are similar to Indian and Sri Lankan congeners but can be distinguished based on morphology. A list of Nepalese specimens in SEHU is given. This collection included 24 morphospecies in 15 genera, exceeding the known diversity by three times.

Key words
Aculeata, biodiversity, Oriental Region, South Asia, taxonomy.

Introduction

Velvet ants (Mutillidae and Myrmosidae) are a large group of parasitoid stinging wasps with approximately 650 species recorded in the Oriental Region (Lelej, 2005, 2007; Pagliano *et al*., 2020). In this region, South Asia is known for its unique but rarely explored velvet ant fauna (Lelej, 1995; Okayasu, 2022).

Nepal is located just south of the Himalayan mountains, extending approximately one third of this mountain range (Paudel *et al*., 2012). Although Nepal occupies only 0.1% of the global land mass, the geography of this country is disproportionately complicated, from lowlands to world's highest peak, and a variety of terrestrial ecoregions is found (Fig. 1; Dinerstein *et al*., 2017; Olson *et al*., 2001; Paudel *et al*., 2012; Wikramanayake *et al*., 2002). It is, therefore, not surprising that Nepal harbors the highest richness and endemism of terrestrial organisms in South Asia (Myers *et al*., 2000; Paudel *et al*., 2012; Roll *et al*., 2017; Wikramanayake *et al*., 2002). However, the velvet ant fauna of Nepal is largely unsampled and only eight species have been recorded in six publications (Hammer, 1962; Lelej, 2005; Lelej *et al*., 2007, 2023; Okayasu *et al*., 2021; Zhou *et al*., 2018).

Hokkaido University conducted entomological expeditions to Nepal in 1965, 1967, 1968, 1972, 1975, and 1983 (Kumata, 1973; Suwa, 1984; Yamane & Yamane, 1979). Many entomologists were involved in this project; a vast number of specimens representing various insect orders were collected. The material collected in the expeditions has been fruitfully

discussed by expert systematists over half a century in more than 50 papers (e.g., Kimoto & Takizawa, 1972, 1973, 1981; Kumata, 1973, 1985, 1989; Miyatake, 1985; Ôhara, 1989; Okushima, 1999; Suwa, 1977, 1984, 1994; Takagi, 1975, 1977, 2019, 2020; Takizawa, 1988; Williams *et al*., 2010; Yamane & Yamane, 1979). Those contributions provide basic knowledge of the insect fauna of Nepal, like new species descriptions, checklists, identification keys, and illustrations.

I explored the Nepalese collection in the Hokkaido University Insect Collection and found 49 velvet ant specimens, which will provide valuable resources for better understanding of the Nepalese fauna. This paper attempts to assess the potential diversity of velvet ants in this country based on the results of the Hokkaido University expeditions. A list of the specimens and description of two new species of Zeugomutillini Waldren, 2023, tribe new to Nepal, are given.

Material and methods

Nepalese velvet ant specimens collected through the Hokkaido University expeditions are deposited in the Hokkaido University Insect Collection, Sapporo, Japan (SEHU). Those specimens were sorted into genera using recent keys to Old World velvet ants (Lelej, 2002, 2005; Lelej & Williams, 2023; Turrisi *et al*., 2015; Williams *et al*., 2019). Some specimens were further identified to species-level. However, this paper is limited to present new species descriptions in Zeugomutillini and a list of morphospecies, because accurate identification of South Asian species often requires reexamination of types or identified specimens. Exceptions are the following two species that were described or recorded from Nepal in previous papers (Lelej *et al*., 2023; Okayasu *et al*., 2021) based on SEHU specimens: *Eotrogaspidia adhabar* Okayasu, Lelej & Williams, 2021 and *Kurzenkotilla scrobiculata* (Hammer, 1962). Voucher specimens were so labelled and linked with the names appearing in the list below. Two female specimens of *Zeugomutilla recondita* (Cameron, 1900) were examined for comparison: Udawattekele Sanctuary, Kandy District, Sri Lanka, 22.V.1973 & 4.I.1974, beating, A. Ôtake leg. [Insect Museum, National Agriculture and Food Research Organization, Tsukuba, Japan]. They were identified using the key in Lelej *et al*. (2017).

Morphological observation was done under a Leica M205C stereomicroscope (7.8–160× magnification). Measurement methods follow Bartholomay *et al*. (2019) and Okayasu (2020). Habitus photographs were taken using a Canon EOS 6D Mark II digital camera equipped with a Canon MP-E 65mm f/2.8 1–5× Macro Photo lens. External morphological features were imaged with a Canon EOS 6D Mark II attached to a Leica M205C. Focus stacking was done using Zerene Stacker (Zerene Systems LLC, Richland, WA, USA). The map figure (Fig. 1) was generated using SimpleMappr (Shorthouse, 2010); the geographic coordinates were obtained from Google Earth (Google LLC, Mountain View, CA, USA). Terminology for ecoregions follows Dinerstein *et al*. (2017) and Olson *et al*. (2001). Figures were edited with Adobe Photoshop and Adobe Illustrator software (Adobe Inc., San Jose, CA, USA). The label data of the new species were transcribed as they were and placed in quotation marks; slashes (/) separate lines on the same label. Morphological terminology mostly follows the Hymenoptera Anatomy Consortium (2023). Abbreviations are: F = flagellomere; LOD = lateral ocellus diameter; MOD = medial ocellus diameter; OD = interocellar distance between medial and lateral ocelli; OOD = ocular-ocellar distance between lateral ocellus and eye; POD = posterior ocellar distance between lateral ocelli; S = sternum; T = tergum.

Taxonomy

Tribe Zeugomutillini Waldren, 2023

This tribe was established by Waldren *et al*. (2023) to accommodate three genera previously included in Ctenotillini Brothers & Lelej, 2017, namely *Montanomutilla* Nonveiller, 1979 (♀), *Strangulotilla* Nonveiller, 1979 (♂♀), and *Zeugomutilla* Chen, 1957 (♂♀).

Genus *Strangulotilla* Nonveiller, 1979

This genus includes 21 species (Lelej, 2005; Lo Cascio *et al*., 2012; Nonveiller, 1979; Terine *et al*., 2021). Most species are distributed in the Afrotropical and southern Palaearctic Regions. This genus was recorded from the Oriental Region by Lelej (2005) based on the Sri Lankan species *S. krombeini* Lelej, 2005 (♂♀). Terine *et al*. (2021) further added *S. sureshani* Terine, Lelej & Kumar, 2021 (♂) from India.

Strangulotilla dubia sp. nov.

(Figs 2–9)

Type material

Holotype ♂: "NEPAL: NARAYANI / Chitwan, alt. 300 m / 24–25.vii.1983 / Ent. Inst. Hokk. Univ." [SEHU].

Diagnosis

MALE. Head, pronotal dorsum, mesoscutum, and mesoscutellum with small sparse punctures (Figs 2, 4); antennal scrobe with dorsal transverse carina (Fig. 4); dorso-medial portion of occipital carina projecting posteriorly and flexed (Fig. 3); clypeus concave, lacking medial longitudinal and subventral transverse carinae (Fig. 4); notaulus reaching anterior 1/2 of mesoscutum (Fig. 2); tegula entirely punctate and setose (Fig. 2); T1–5, T6 anterior half, and S1–6 with sparse long erect white setae (Fig. 3); T6 posterior half and T7 with sparse short recumbent and sparse long erect black setae (Fig. 3); metasomal segments 3–6 not constricted (Fig. 2); S8 lacking sublateral carina (Fig. 5); digitus short broad (Fig. 8); penis valve broad, with subapical ventral tooth weakly developed (Fig. 9). FEMALE. Unknown.

Description

MALE. Body length: 8.01 mm; forewing length: 5.95 mm.

Color and setae. Frons, vertex, gena, clypeus, scape except apex, and flagellum brownish black; postgenal bridge, mandible basal 1/2 and apex, prementum, stipes, mesosoma including tegula, legs except trochanters, and metasoma dark brown; antennal rim, mandible medial 1/4, scape apex, pedicel, maxillary and labial palpi, trochanters, and protibial spur brown; wings pale brown; meso- and metatibial spurs yellowish white. Frons with sparse short recumbent white and sparse long erect dark golden setae; vertex, gena, scape mostly, pronotal dorsum, dorsal 1/2 of dorsal propodeal face, mesopleuron, femora, and tibiae with sparse short recumbent and sparse long erect white setae; postgenal bridge, mandible, pronotal neck, mesoscutellum, metascutellum, ventral 1/2 of dorsal propodeal face, T1–5, T6 anterior half, and S1–6 with sparse long erect white setae; malar space, clypeus, and propleuron with sparse long appressed white setae; scape apex and pedicel with sparse short recumbent dark golden setae; flagellum with dense erect golden microsetae; prementum, stipes, and maxillary and labial palpi with sparse short erect pale golden setae; mesoscutum with sparse long erect blackish golden setae; tegula inner margin with sparse short recumbent white setae; tegula mostly and S8 with sparse long recumbent blackish golden setae; axilla and metanotal trough with dense short appressed white setae; lateral

pronotal face, metapleuron, and lateral propodeal face with sparse short appressed white setae; coxae, trochanters, and tarsi with sparse long recumbent white setae; T2 lateral portion with long white felt line; S2 lacking felt line; T6 posterior half and T7 with sparse short recumbent and sparse long erect black setae; S7 glabrous.

Structure. Head 1.54× wider than long; lateral margins weakly convergent behind eye, postero-lateral angle rounded; vertex rounded posteriorly; POD/OOD = 0.48; OD:POD:MOD:LOD = 11:19:10:8; ocellar region slightly convex; ocelli without posterior carina; occipital carina complete, with dorso-medial portion projecting posteriorly and flexed; eye inner margin deeply emarginate; antennal scrobe dorsally with transverse carina extending nearly to eye and widely separated from antennal rim; genal carina absent; postgenal bridge flattened; hypostomal carina sharp, not projecting; clypeus concave, lacking medial longitudinal and subventral transverse carinae; dorsomedial portion of clypeus elevated into ridge; ventral portion of clypeus medially raised, forming ventral grooved space; mandible robust, narrowed to apex; mandible apex bidentate, subapical tooth smaller than apex; mandibular dorsal carina elevated, ending as subbasal rounded angle; mandible ventral margin basally widened, forming pointed triangular process; prementum flattened; scape ventrally with one sharp and one obscure longitudinal subparallel carinae, separated by 0.63× scape width; F1 cylindrical; length and width of pedicel:F1:F2 = 12:13:20:17:32:17; F2–4 similar in length; F5–10 slightly shorter than F2; F11 conical as long as F2.

Mesosoma widest at mesonotum including tegulae; head width:humeral width:pronotal width:mesonotal width:propodeal width:T2 width = 89:70:83:98:77:100; anterior margin of pronotal dorsum arcuate; anterior face of pronotum vertical; humeral angle rounded, with weak humeral carina reaching ventral 1/2 of pronotal lateral face; mesoscutum weakly convex; mesoscutal width 1.19× its length; tegula oval, 1.5× longer than wide; tegula oval, posterior margin rounded and not flexed, surpassing mesoscutoscutellar articulation and reaching mesoscutellum; notaulus not widened posteriorly, reaching anterior 1.2 of mesoscutum, subparallel; parapsidal line obliterated; parascutal carina weakly developed, slighted raised on postero-lateral angle of mesoscutum; mesoscutellum 1.39× wider than long, slightly convex; mesopleuron divided into dorsal and ventral convexities by shallow transverse groove, ventrally without transverse precoxal ridge, longitudinal impunctate line, or precoxal swelling; dorsal propodeal face oblique, without distinct dorsum; propodeal dorso-lateral margin lacking carina; lateral margins of propodeum convergent posteriorly.

Wings well developed; distance between origin of RS on vein SC and base of stigmatic cell equal to stigmatic cell length; cell 2RS present.

Meso- and metacoxae evenly convex; metacoxa with weak complete inner longitudinal carina; tibiae without outer spines.

T1 slender, subpetiolate but not constricted posteriorly, without distinct dorsum; T1 spiracle weakly tuberculate; T2 evenly convex, 1.27× wider than long; S1 with low medial longitudinal carina on anterior 2/3, it ventral margin straight; S2 flattened with obscure anteromedial longitudinal carina; S7–8 flat without lateral carina or tubercle; S8 mostly sclerotized with posterior membranous area evenly convex posteriorly. Paramere depressed dorsally and ventrally, down-curved with posterior part flexed dorsally; paramere inner margin lacking projection; paramere ventrally face with short erect setae; ventral lobe rounded, projecting posteriorly; parapenial lobe curved ventrally, apically truncate; basiparamere slightly shorter than paramere; cuspis shape elongate, expanded ventrally on anterior 2/3 and narrowed on posterior 1/3, anteriorly with dorsal rod-like process; cuspis apex apparently surpassing posterior 1/3 of paramere; cuspis densely setose on apex, inner face, and antero-dorsal process, with large seta-filled pit on inner face; digitus 1/2× longer than cuspis, depressed, broad, densely setose on outer face; penis valve symmetrical, broad, expanded dorsally, with posterior ventral hook and small projection anteriorly to it;

endophallus membranous.

Frons, vertex, gena, postgenal bridge, scape, pronotal dorsum, propleuron, mesoscutum, tegula, metascutellum, T1–6, S1, S3–6, and S8 with small sparse punctures; clypeus, axilla, and metanotal tough with minute dense punctures; mandible outer face with small sparse and minute sparse punctures; pedicel, flagellum, prementum, stipes, and maxillary and labial palpi with dense micropunctures; mesoscutellum laterally with small dense punctures, medially with small sparse punctures; metanotal trough striate; dorsal propodeal face reticulate, anteriorly with medial elongate and sublateral semicircular cells; lateral pronotal face, mesopleuron anteriorly, and metapleuron dorsally with minute sparse punctures; mesopleuron medially with large confluent punctures; lateral propodeal face dorsally reticulate, ventrally with minute sparse punctures; S2 with large dense punctures; T7 with small dense punctures, medially with slender longitudinal smooth line; T1 lateral portion and S7 smooth.

FEMALE. Unknown.

Distribution

Nepal: Bagmati.

Etymology

The specific name *dubia*, dubious, is a Latin feminine adjective in the nominative case. It suggests that this species, together with other Oriental members, is questionably placed in *Strangulotilla* as discussed below.

Remarks

Upon description of the first Oriental species, B. Petersen pointed out the differences between *S. krombeini* and other *Strangulotilla* species from the Afrotropical Region in the shape of mandibles, clypeus, occipital carina, S8, and genitalia (Petersen in litt. to A. Lelej; Lelej, 2005: 37), casting doubt on the genus-placement of *S. krombeini*. Petersen suggested to treat this and related species from South Asia as a separate “in between” taxon of *Strangulotilla* and *Zeugomutilla*. Within *Strangulotilla*, three Oriental species, *S. krombeini*, *S. sureshani*, and *S. dubia*, are recognized by having the mandibular ventral margin with a basal triangular process (incised into a basal tooth in Afrotropical species), notaulus reaching anterior 1/2 of mesoscutum (reaching anterior margin of mesoscutum in Afrotropical species), metasomal segments 3–6 not constricted (constricted in Afrotropical species; Nonveiller, 1979: fig. 4), S8 flat (armed with sublateral carinae in Afrotropical species; Nonveiller, 1979: figs 6a, 6c), and penis valve broad with a weakly developed subapical ventral tooth (slender with a long sharp subapical ventral tooth in Afrotropical species; Nonveiller, 1979: fig. 7d). They are distinguished from males of *Zeugomutilla* by having the mandibular ventral margin with a basal triangular process (basally widened and rounded in *Zeugomutilla*; Lelej *et al*., 2017: fig. 12), notaulus reaching anterior 1/2 of mesoscutum (reaching anterior margin of mesoscutum in *Zeugomutilla*), S2 evenly convex (with a medial longitudinal carina in *Zeugomutilla*; Lelej *et al*., 2017: figs 4, 38), S8 flat (anterior portion raised, trituberculate in *Zeugomutilla*; Lelej *et al*., 2017: figs 4, 38), and penis valve broad with a weakly developed subapical ventral tooth (penis valve slender, with a long sharp subapical ventral tooth in *Zeugomutilla*; Lelej *et al*., 2017: figs 9, 42). The placement of the Oriental members of *Strangulotilla* is thus tentative. Furthermore, *S. dubia* possesses an anterior rod-like process on the dorsal margin of cuspis (Fig. 8), rare trait in Mutillinae by which this new species can be separated from Afrotropical *Strangulotilla* and *Zeugomutilla* males. However, the descriptions and illustrations of *S. krombeini* and *S. sureshani* are not detailed enough to determine if this structure is present in these species. A separated genus might be eventually erected for

Oriental *Strangulotilla* species after extensive morphological comparison.

Strangulotilla dubia differs from other Oriental species by having the head, pronotal dorsum, mesoscutum, and mesoscutellum with small sparse punctures (with large dense punctures in *S. krombeini* and *S. sureshani*), antennal scrobe with dorsal transverse carina (absent in *S. sureshani*), clypeus lacking medial longitudinal and subventral transverse carinae (present in *S. krombeini*), tegula entirely punctate and setose (outer portion smooth and glabrous in *S. krombeini* and *S. sureshani*), metasoma covered with sparse recumbent to erect setae (T2–7 with dense appressed golden setae in *S. sureshani*), and digitus broad (stick-like in *S. krombeini* and *S. sureshani*).

Key to males of *Strangulotilla* (modified from Nonveiller, 1979 and Terine *et al*., 2021)

1. Mandibular ventral margin with basal triangular process (Fig. 3); notaulus reaching anterior 1/2 of mesoscutum (Fig. 2); S8 flat (Fig. 5) … 2
- Mandibular ventral margin incised, forming basal tooth; notaulus reaching anterior margin of mesoscutum; S8 with sublateral carina (Nonveiller, 1979: figs 6a, 6c) … 4
2. Head and mesosoma dorsally with small sparse punctures (Figs 2, 4); tegula entirely punctate and setose (Fig. 2); digitus expanded (Fig. 8). Nepal … ***S. dubia*** Okayasu
- Head and mesosoma dorsally with large dense punctures (Terine *et al*., 2021: figs 6, 8); tegula outer portion smooth and glabrous (Terine *et al*., 2021: fig. 8); digitus stick-like … 3
3. Clypeus with medial longitudinal and subventral transverse carinae; metasoma black, dorsally with sparse recumbent and suberect white setae. Sri Lanka … ***S. krombeini*** Lelej
- Clypeus with medial longitudinal depression and lacking transverse carina (Terine *et al*., 2021: fig. 6); metasoma brownish black and T2–7 covered with dense appressed golden and sparse erect pale golden setae (Terine *et al*., 2021: fig. 9). India ... ***S. sureshani*** Terine, Lelej & Kumar
4. S8 lateral margin flat, with sublateral carina apparently surpassing S8 lateral margin in lateral view (Nonveiller, 1979: fig. 6b) … 5
- S8 lateral margin elevated on anterior half, with sublateral carina partially or entirely concealed by elevation of S8 lateral margin in lateral view (Nonveiller, 1979: figs 6d, 6e) ... 9
5. Mandibular subbasal inner tooth rectangular, right-angled to mandibular inner margin (Nonveiller, 1979: fig. 6f); penis valve with posterior ventral tooth flexed outward (Nonveiller, 1979: fig. 7a) ... 6
- Mandibular subbasal inner tooth narrowed apically, directed obliquely to mandibular inner margin (Nonveiller, 1979: fig. 6g); penis valve with posterior ventral tooth straight (Nonveiller, 1979: fig. 7e) ... 8
6. Tegua slender, strongly convex, entirely punctate and densely setose. Central, eastern, and western Africa ... ***S. samharica*** (Magretti)
- Tegula broad, weakly convex anteriorly, with outer margin smooth and glabrous ... 7
7. Head black with vertex yellowish red. Namibia ... ***S. thoracosulcata damarana*** (Bischoff)
- Head entirely black. Central and eastern Africa ... ***S. thoracosulcata thoracosulcata*** (Magretti)
8. T2 punctures large, deep, and dense, separated by less than puncture diameter. Democratic Republic of the Congo ... ***S. kisantuana*** Nonveiller
- T2 punctures small, shallow, and sparse, separated by more than puncture diameter. Republic of the Congo ... ***S. tenuipunctata*** Nonveiller
9. Mesosoma red except darkened tegula; S8 lateral margin strongly elevated, entirely concealing sublateral carina in lateral view (Nonveiller, 1979: fig. 6d). Botswana ... ***S. dayi*** Nonveiller

- Body entirely black; S8 lateral margin weakly elevated, with sublateral carina partially concealed and visible in lateral view (Nonveiller, 1979: fig. 6e). Angola ... ***S. unicolorata*** Nonveiller

Genus *Zeugomutilla* Chen, 1957

This genus was recently reviewed by Lelej *et al*. (2017). Eight species are recognized in this genus, of which four are known from East Asia and the rest four are known from South Asia. In South Asia, this genus has been recorded from India and Sri Lanka only.

Zeugomutilla curvicarinata sp. nov.

(Figs 10–16)

Type material

Holotype ♀: "NEPAL: NARAYANI / Chitwan, alt. 300 m / 24–25.vii.1983 / Ent. Inst. Hokk. Univ." [SEHU].

Diagnosis

FEMALE. Head black except gena dark brown (Figs 11, 14); genal carina strongly curved toward mandibular base (Fig. 15); scape dark brown (Fig. 14); propodeal dorsum armed with row of six teeth (Fig. 12); T2 with paired pale golden setal spots, separated by 1.89× spot diameter (Fig. 13); T3–4 with sparse appressed pale golden setae (Fig. 13); pygidial plate smooth (Fig. 16). MALE. Unknown.

Description

FEMALE. Body length: 5.40 mm.

Color and setae. Frons, vertex, flagellum, and T1–6 brownish black; clypeus, gena, scape, mandible apex, prementum, stipes, femora, tibiae, and S2–6 dark brown; antennal rim, postgenal bridge, pedicel, labrum, maxillary and labial palpi, and tarsi brown; mandible except apex and trochanters yellow; mesosoma, procoxa anterior 1/3, and S1 orange. Frons, vertex, pronotal anterior margin, and femora with sparse short recumbent and sparse long erect pale golden setae; gena, scape, coxae, tibiae, and tarsi with sparse long recumbent pale golden setae; clypeus, postgenal bridge, mandible, propleuron, dorsal propodeal face, trochanters, T1, T2 anterior and lateral margins, T5–6 lateral portions, and S1–6 with sparse long erect pale golden setae; pedicel, and flagellum with dense appressed pale golden microsetae; prementum, stipes, labrum, and maxillary and labial palpi with sparse short erect golden setae; pronotal collar with sparse short erect pale golden setae; thoracic dorsum, T2 disc, and T5–6 medial portions with sparse short recumbent and sparse long erect black setae; mesosomal lateral face with sparse short appressed pale golden setae; T3–4 with sparse long appressed and sparse long erect pale golden setae; T2 with a pair of small sublateral circular spots of dense appressed pale golden setae disposed in horizontal line; T2 spot diameter:distance between T2 spots:distance between T2 spot and T2 anterior margin:distance between T2 spot and T2 posterior margin = 28:53:45:48; T2 posterior margin and metasomal sterna lacking setal fringe or band.

Structure. Head 1.39× wider than long with lateral margins strongly convergent behind eye; gena wide, 1.06× eye breadth in lateral view; frons and vertex without medial carina or groove; occipital carina complete; genal carina sharp, dorsally separated from occipital carina, ventrally strongly curved reaching mandibular base; hypostomal tooth absent; hypostomal carina sharp and raised; postgenal bridge medially projecting; antennal scrobe with dorsal carina wavy, nearly straight, widely separated from inner eye margin; eye

oval, slightly protruding from head capsule; minimum distance between eyes 1.40× eye height; eye height 2.60× malar distance; clypeus medially elevated with subventral transverse crenulate ridge; clypeal ventrally with lateral rounded tubercle; mandible slender, narrowed to apex; mandible apically bidentate, inner tooth smaller than apex, with small subbasal inner tooth; mandibular ventral margin straight; prementum flattened, medially with sharp longitudinal carina extending along its entire length; length and width of pedicel:F1:F2 = 10:10:17:15:13:15; F2–9 almost same in length and width; F10 as long as F1, conical and weakly depressed.

Mesosoma broadest at propodeum; lateral margins weakly crenulate, divergent posteriorly; head width:humeral width:pronotal width:mesonotal width:propodeal width:metasomal width = 93:68:73:73:80:100; dorsal thoracic length 0.86× pronotal width; anterior margin of pronotal dorsum nearly straight; pronotum laterally not projecting; pronotal lateral margin with sharp tooth; humeral carina sharp, complete, dorsally terminating as sharp tooth; scutellar scale absent; scutellar area without scales; propodeal dorsum with transverse row of six sharp tooth, longest medially; metanotal-propodeal suture obliterated; dorsal propodeal face vertical, without medial carina; propodeal lateral margin weakly dentate on dorsal half, crenulate on ventral half; mesopleural lamella short.

Procoxa with projecting lamella on antero-inner margin; metacoxa with sharp complete inner longitudinal carina; meso- and metatibiae with one row of spines; protarsus with short outer spines; protarsomere 1 apically truncate, not protruding outward.

T1 subsessile, without distinct dorsum; T2 evenly convex, dorsally flattened; dorsal T2 length 0.98× T2 width; S1 with low medial longitudinal carina on anterior 2/3, it ventral margin straight; S2 evenly convex with obscure anteromedial longitudinal carina; S6 posterior margin notched; pygidial plate slender, subconvex, lateral margins subparallel delimited by sharp longitudinal carina.

Frons and vertex with large dense punctures, separated by approximate puncture diameter, intervals distinct and smooth; gena with large confluent shallow punctures, making puncto-reticulate surface; postgenal bridge transversely rugose; clypeus medial elevated part, propleuron, procoxa, and tarsi with minute dense punctures; clypeal lateral portion, mandible, mesosomal lateral face, meso- and metacoxae, trochanters, femora, and tibiae with minute sparse punctures; scape, T1, T2 lateral margin, T3–5, and S1 with small sparse punctures; pedicel, flagellum, prementum, stipes, and labial and maxillary palpi with dense micropunctures; pronotal collar with minute sparse punctures; thoracic dorsum with large confluent punctures; dorsal propodeal face reticulate on dorso-lateral portion and with minute sparse punctures medially and ventrally; T2 disc, T6, and S3–6 with small dense punctures; S2 with large sparse punctures; pygidial plate smooth.

MALE. Unknown.

Distribution

Nepal: Bagmati.

Etymology

The specific name *curvicarinata* is the combination of a Latin prefix *curvi*, curved, and a Latin feminine adjective in the nominative case *carinata*, carinate. It refers to the curved genal carina of this new species.

Remarks

This new species is similar to *Z. recondita* (Cameron, 1900) and *Z. spinulosa* (André, 1898) by having the T2 spots separated by more than spot diameter and pygidial plate smooth, but differs by having the head black except gena dark brown (orange to brown in *Z. recondita*;

dark brown with a medial reddish spot on frons in *Z. spinulosa*), genal carina curved ventrally, extending nearly to mandibular base (straight and separated from mandibular base in *Z. recondita*), propodeal dorsum with six teeth (with eight to twelve teeth in *Z. recondita* and *Z. spinulosa*), T2 spots small, separated by 1.89× spot diameter (T2 spots separated by ~1.5× spot diameter in *Z. recondita*), and T3–4 with sparse appressed pale golden setae (with golden setal bands in *Z. recondita*; with medial setal spots in *Z. spinulosa*).

Key to females of *Zeugomutilla* (modified from Lelej *et al*., 2017)

1. T2 pale setal spots large, separated by 0.25–1.0× spot diameter or spots conjugated … 2
- T2 pale setal spots small, separated by 1.3–2.0× spot diameter … 5
2. Head yellowish orange (Lelej *et al*., 2017: figs 27, 31); T2 spots conjugated (Lelej *et al*., 2017: fig. 27). India, Sri Lanka … ***Z. horni*** (André)
- Head reddish to black; T2 spots separated (Lelej *et al*., 2017: figs 6, 16, 17, 28) … 3
3. Body length 4.4–5.4 mm; head reddish brown to dark brown (Lelej *et al*., 2017: figs 28, 32). India, Sri Lanka … ***Z. recondita*** (Cameron), part
- Body length 8.0–9.6 mm; head black (Lelej *et al*., 2017: figs 1, 16) … 4
4. Scape black; T2 spots larger, separated by roughly 0.25× spot diameter (Lelej *et al*., 2017: figs 16, 17). China … ***Z. pangi*** Lelej
- Scape yellowish orange to brown; T2 spots smaller, separated by approximate spot diameter (Lelej *et al*. 2017: fig. 6). Cambodia, China, Thailand … ***Z. saepes*** (Chen)
5. Pygidial plate longitudinally striate anteriorly, smooth posteriorly (Lelej *et al*., 2017: fig. 34). India, Sri Lanka … ***Z. bainbriggei*** (Turner)
- Pygidial plate sculpture obscure, mostly smooth (Lelej *et al*., 2017: fig. 35) … 6
6. Frons dark brown with reddish spot; T3–4 with medial pale setal spot. India, Pakistan ... ***Z. spinulosa*** (André)
- Frons uniformly orange to black; T3–4 entirely covered with golden setal band or sparse pale golden setae … 7
7. Head orange to brown; genal carina straight, separated from mandibular base; T2 spots larger, separated by ~1.5× spot diameter; T3–4 with golden setal band. Sri Lanka ... ***Z. recondita*** (Cameron), part.
- Frons and vertex black, gena dark brown (Figs 11, 14); genal carina curved ventrally, extending nearly to mandibular base (Fig. 15); T2 spots smaller, separated by 1.89× spot diameter (Fig. 13); T3–4 with sparse pale golden setae (Fig. 13). Nepal … ***Z. curvicarinata*** Okayasu

Synoptic list of velvet ant species known from Nepal

Mutillinae: Mutillini

1. *Kurzenkotilla rufodorsata* (Cameron, 1897): Bagmati, Karnali (Lelej *et al*., 2023). Also known from northern India.
2. *Kurzenkotilla scrobiculata* (Hammer, 1962): Karnali, Sudurpashchim (Lelej *et al*., 2023). Also known from northern India.

Mutillinae: Smicromyrmini

3. *Ephutomma himalayana* Lelej & Ullah, 2007: Bagmati (Lelej *et al*., 2007). Also known from northeastern Pakistan.
4. *Smicromyrme nepalensis* Hammer, 1962: Bagmati (Hammer, 1962).

Mutillinae: Trogaspidiini

5. *Eotrogaspidia adhabar* Okayasu, Lelej & Williams, 2021: Madhesh (Okayasu *et al*., 2021). Also known from southern India.
6. *Karlissaidia sexmaculata* (Swederus, 1787): additional data unavailable (Lelej, 2005). Widespread in India and known from eastern Pakistan.
7. *Zavatilla nepalensis* Zhou & Lelej, 2018: Koshi (Zhou *et al*., 2018).

Mutillinae: Zeugomutillini
8. *Strangulotilla dubia* Okayasu, 2023: Bagmati (this study).
9. *Zeugomutilla curvicarinata* Okayasu, 2023: Bagmati (this study).

Odontomutillinae
10. *Yamanetilla taiwaniana* (Zavattari, 1913): additional data unavailable (Lelej, 2005). Also known from Taiwan.

List of SEHU velvet ant specimens from Nepal

Overall, 49 Nepalese specimens (30♂19♀) collected from 13 localities in 20 days were found in SEHU. They represented 24 morphospecies in 15 genera of four subfamilies.

Dasylabrinae
1. *Dasylabris* sp. (Figs 17, 18): Madhesh: 1♀, Adhabar, Terai Forest, 27.VI.1968, T. Kumata leg. In coloration, this species matches *D. argentipes* (Smith, 1855) known from southern India (Bingham, 1897; Lelej, 2005; Terine *et al*., 2015).

Mutillinae: Mutillini
2. *Kurzenkotilla scrobiculata* (Hammer, 1962) (Figs 19, 20): 1♀, Nepal, YB, I. Yoneta leg.

Mutillinae: Smicromyrmini
3. *Promecilla* sp. 1 (Figs 21, 22): Bagmati: 1♂, Napal valley [= Nepal Valley], Godavari, 15.VI.1968, T. Kumata leg.; 1♂, same data except 11.VII.1968; 8♂, Godavari, Phulchoki, 17.VIII.1975, S. Takagi leg.; 1♂, same data except 19.VIII.1975. This species matches the description and illustrations of the male of *P. regia* (Smith, 1855) in Lelej & Williams (2023) and Nurse (1903).
4. *Promecilla* sp. 2 (Figs 23, 24): Madhesh: 1♀, Janakpur, Malipu–Suri Dhoban, 1000–1100 m alt., 29.VIII.1983, Ent. Inst. Hokk. Univ.
5. *Smicromyrme* sp. 1 (Figs 25, 26): Bagmati: 1♂, Napal valley [= Nepal Valley], Godavari, 11.VII.1968, T. Kumata leg.
6. *Smicromyrme* sp. 2 (Figs 27, 28): Madhesh: 1♀, Adhabar, Terai Forest, 27.VI.1968, T. Kumata leg.

Mutillinae: Trogaspidiini
7. *Eotrogaspidia adhabar* Okayasu, Lelej & Williams, 2021 (Figs 29, 30): Madhesh: holotype ♂, Narayani, Adhabar, 21.X.1975, S. Takagi leg. This species was described based on a male from SEHU and two additional males collected in southern India (Okayasu *et al*., 2021).
8. *Karlissaidia* sp. 1 (Figs 31, 32): Madhesh: 1♂, Narayani, Adhabar, 21.X.1975, S. Takagi leg.
9. *Karlissaidia* sp. 2 (Figs 33, 34): Madhesh: 2♂, Adhabar, Terai Forest, 27.VI.1968, T. Kumata leg.
10. *Petersenidia* sp. (Figs 35, 36): Bagmati: 1♀, Kathmandu, Balaju, Kj-2, 23.IV.1968, T.

Matsumura leg.
11. *Radoszkowskitilla* sp. (Figs 37, 38): Madhesh: 1♂, Adhabar, Terai Forest, 27.VI.1968, T. Kumata leg. According to published descriptions and keys, this species does not match any described species of the genus (Lelej, 2005, 2020).
12. *Trogaspidia* sp. 1 (Figs 39, 40): Bagmati: 1♀, Sundarijal, 22–25.X.1983, S. Takagi leg.; Madhesh: 1♀, Janakpur, Suri Dhoban–Gongar, 1100–1300 m alt., 27.VIII.1983, Ent. Inst. Hokk. Univ.
13. *Trogaspidia* sp. 2 (Figs 41, 42): Bagmati: 1♀, No. 3 West, Rupakot Tal, Pv-2, 20.V.1968, T. Matsumura leg.; Gandaki: 1♀, Marsyandi Valley, Syange–Chyamche, 1200–1400 m alt., 7.VI.1988, M. Suwa leg.; Madhesh: 1♀, No. 2 East, Namuto, Nj, 15.VII.1968, T. Matsumura leg.
14. *Trogaspidia* sp. 3 (Figs 43, 44): Bagmati: 1♀, No. 3 West, Pokhara, 21.V.1968, T. Matsumura leg.; 2♀, Narayani, Chitwan, alt. 300 m, 24–25.VII.1983, Ent. Inst. Hokk. Univ.
15. *Trogaspidia* sp. 4 (Figs 45, 46): Bagmati: 1♀, Kathmandu, MN-3, 20.II.1968, T. Kawamichi leg.
16. *Trogaspidia* sp. 5 (Figs 47, 48): Bagmati: 1♂, No. 3 West, Pokhara, Pw, 21.V.1968, T. Matsumura leg.; 1♂, Narayani, Chitwan, alt. 300 m, 24–25.VII.1983, Ent. Inst. Hokk. Univ.; Madhesh: 1♂, Janakpur, Malipu–Suri Dhoban, 1000–1100 m alt., 10.VIII.1983, Ent. Inst. Hokk. Univ.
17. *Wallacidia* sp. 1 (Figs 49, 50): Madhesh: 3♂, Adhabar, Terai Forest, 24.VI.1968, T. Kumata leg.; 1♂, same data except 15.VII.1968; 4♂, Adhabar, Terai Forest, 3000 m, 27.VI.1968, T. Kumata leg.
18. *Wallacidia* sp. 2 (Figs 51, 52): 1♀, Nepal, VI.1968, T. Kumata leg.

Mutillinae: Zeugomutillini
19. *Strangulotilla dubia* Okayasu, 2023 (Figs 2–9): Bagmati: holotype ♂, Narayani, Chitwan, 300 m alt., 24–25.VII.1983, Ent. Inst. Hokk. Univ.
20. *Zeugomutilla curvicarinata* Okayasu, 2023 (Figs 10–16): Bagmati: holotype ♀, Narayani, Chitwan, 300 m alt., 24–25.VII.1983, Ent. Inst. Hokk. Univ.

Myrmillinae
21. *Bischoffitilla* sp. 1 (Figs 53, 54): Bagmati: 1♀, Kathmandu V[alley]., Godawari, 13, 14, 17.IX.1987, H. Takizawa leg.
22. *Bischoffitilla* sp. 2 (Figs 55, 56): Bagmati: 1♀, Napal valley [= Nepal Valley], Godavari, 1450 m alt., 16.VI.1968, T. Kumata leg.

Odontomutillinae
23. *Odontomutilla* sp. (Figs 57, 58): Madhesh: 1♀, Adhabar, Terai Forest, 24.VI.1968, T. Kumata leg. This species does not match any described species known from the Indian subcontinent (Lelej *et al*., 2020).
24. *Yamanetilla* sp. (Figs 59, 60): Madhesh: 1♂, Janakpur, Malipu–Suri Dhoban, 1000–1100 m alt., 10.VIII.1983, Ent. Inst. Hokk. Univ. This species does not match *Y. taiwaniana*, the only *Yamanetilla* species known from Nepal.

Discussion

The SEHU collection included 24 morphospecies listed above, exceeding the known diversity by three times. The genera *Dasylabris* Radoszkowski, 1885 (Dasylabrinae), *Petersenidia* Lelej, 1992, *Promecilla* André, 1902, *Radoszkowskitilla* Lelej, 2005, *Strangulotilla*,

Trogaspidia Ashmead,1899, *Wallacidia* Lelej & Brothers, 2008, *Zeugomutilla* (Mutillinae), *Bischoffitilla* Lelej, 2002 (Myrmillinae), and *Odontomutilla* Ashmead, 1899 (Odontomutillinae) are new to Nepal. Even though the SEHU specimens were collected in only a limited number of places, this fraction shows that the diversity of velvet ants in Nepal is much higher than currently documented. Additional evidence may also imply the hidden diversity of Nepalese velvet ants. First, the Himalayan region is known for the high concentration of bee species contrasting to India (Orr *et al*., 2021; Williams *et al*., 2010). Because bees are important hosts for velvet ants (Luz *et al*., 2016; Ronchetti & Polidori, 2020), I anticipate that the number of species per unit area in Nepal exceeds that in India, the South Asian country with more than 200 velvet ant species. Secondly, Müllerian mimicry diversity of velvet ants is likely positively correlated with the predator diversity (e.g., lizards) and habitat heterogeneity (Wilson *et al*., 2018). This indicates that higher morphological diversity will be found after extensive collection from wider range of Napal, since the collecting localities of Hokkaido University expeditions cover only four out of 12 ecoregions found in Nepal (Fig. 1).

The shortage of material is the major limitation of taxonomic studies dedicated to velvet ants of Nepal. Most morphospecies identified in this study are known from one or two specimens. The western and eastern parts are mostly unsampled. Given that the climate, fauna, and flora greatly vary within this country along altitude and latitude (Rawat, 2017; Williams *et al*., 2010), broader sampling is apparently needed.

The complex geography and species richness in Nepal provide an ideal setting to elucidate factors shaping geographical patterns of species richness and distribution (Williams *et al*., 2010). Previous phylogeographic studies revealed the strong connection of velvet ants and habitats, suggesting their usefulness in biogeography (Pitts *et al*., 2010; Wilson & Pitts, 2011; Wilson *et al*., 2012). It is crucial to document the local velvet ant fauna for this scarcely studied yet notable country. I hope the lists, illustrations, and descriptions in this paper will be a starting point for better understanding of Nepalese velvet ant fauna.

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References

André, E. (1898) Étude sur les Mutillides du Muséum de Paris. *Annales de la Société Entomologique de France* 67: 1–79.

André, E. (1902 [1903]). Family Mutillidae. *In*: Wytsman, P. (ed.) *Genera Insectorum. Fascicles 11*. L. Desmet-Verteneuil, Bruxelles, pp. 1–77 + 3 pls.

Ashmead, W.H. (1899) Superfamilies in the Hymenoptera and generic synopses of the families Thynnidae, Myrmosidae, and Mutillidae. *Journal of the New York Entomological Society* 7: 45–60.

Bartholomay, P.R., Williams, K.A., Lopez, V.M. & Oliveira, M.L. (2019) Revision of the *Traumatomutilla americana* species group (Hymenoptera: Mutillidae). *Zootaxa* 4608 (1): 1–34. https://doi.org/10.11646/zootaxa.4608.1.1

Bingham, C.T. (1897) *The fauna of British India including Ceylon and Burma: Hymenoptera, I. Wasps and bees*. Taylor and Francis, London, 608 pp. + 4 pls.

Brothers, D.J. & Lelej, A.S. (2017) Phylogeny and higher classification of Mutillidae

(Hymenoptera) based on morphological reanalyses. *Journal of Hymenoptera Research* 60: 1–97. https://doi.org/10.3897/jhr.60.20091

Cameron, P. (1897) Hymenoptera Orientalia, or contributions to a knowledge of the Hymenoptera of the Oriental Zoological Region. Part V. *Memoirs and Proceedings of the Manchester Literary and Philosophical Society* 41 (4): 1–144 + pls 3–4.

Cameron, P. (1900) Hymenoptera Orientalia, or contributions to the knowledge of the Hymenoptera of the Oriental Zoological Region. Part IX. The Hymenoptera of the Khasia Hills. Part II. Section I. *Memoirs and Proceedings of the Manchester Literary and Philosophical Society* 44 (15): 1–114.

Chen, C.-W. (1957) A revision of the velvety ants or Mutillidae of China (Hymenoptera). *Quarterly Journal of the Taiwan Museum* 10 (3–4): 135–224 + 6 pls.

Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N.D., Wikramanayake, E., Hahn, N., Palminteri, S., Hedao, P., Noss, R., Hansen, M., Locke, H., Ellis, E.C., Jones, B., Barber, C.V., Hayes, R., Kormos, C., Martin, V., Crist, E., Sechrest, W., Price, L., Baillie, J.E. M., Weeden, D., Suckling, K., Davis, C., Sizer, N., Moore, R., Thau, D., Birch, T., Potapov, P., Turubanova, S., Tyukavina, A., De Souza, N., Pintea, L., Brito, J.C., Llewellyn, O.A., Miller, A.G., Patzelt, A., Ghazanfar, S.A., Timberlake, J., Klöser, H., Shennan-Farpón, Y., Kindt, R., Lillesø, J.B., Van Breugel, P., Graudal, L., Voge, M., Al-Shammari, K.F. & Saleem, M. (2017) An ecoregion-based approach to protecting half the terrestrial realm. *BioScience* 67 (6): 534–545. https://doi.org/10.1093/biosci/bix014

Hammer, K. (1962 [1960]). Mutilliden (Insecta: Hymenoptera) aus dem Indischen Museum in Calcutta. *Records of the Indian Museum* 58 (1): 1–51.

Hymenoptera Anatomy Ontology (2023) Hymenoptera glossary. Available from: http://glossary.hymao.org (accessed 29 July 2023)

Kimoto, S. & Takizawa, H. (1972) Chrysomelid-beetles of Nepal, collected by the Hokkaido University Scientific Expedition to Nepal Himalaya, 1968. Part I. *Kontyû* 40 (4): 215–223.

Kimoto, S. & Takizawa, H. (1973) The chrysomelid-beetles of Nepal, collected by the Hokkaido University Scientific Expedition to Nepal Himalaya, 1968. Part II. *Kontyû* 41 (2): 170–180.

Kimoto, S. & Takizawa, H. (1981) Chrysomelid-beetles of Nepal, collected by the Hokkaido University Scientific Expeditions to Nepal Himalaya, 1968 and 1975. Part III (Coleoptera). *The Entomological Review of Japan* 35 (1/2): 51–65 + pls 2–4.

Kumata, T. (1973) On the genus *Phyllonorycter* or *Lithocolletis* from central Nepal, with description of twelve new species. Notes on Gracillariidae (Lepidoptera) of Nepal, I. *Insecta matsumurana*, New Series 1: 1–45.

Kumata, T. (1985) A new genus of Gracillariidae, with three new species from Asia (Lepidoptera). *Insecta matsumurana*, New Series 32: 109–137.

Kumata, T. (1989) Two new genera related to *Acrocercops* (Gracillariidae, Lepidoptera), with five new species from the Oriental Region. *Insecta matsumurana*, New Series 42: 47–82.

Lelej, A.S. (1995) To the knowledge of the velvet ants (Hymenoptera, Mutillidae) of Rajasthan, western India. *Far Eastern Entomologist* 20: 1–11.

Lelej, A.S. (2002) *Catalogue of the Mutillidae (Hymenoptera) of the Palaearctic Region*. Dalnauka, Vladivostok, 172 pp.

Lelej, A.S. (2005) *Catalogue of the Mutillidae (Hymenoptera) of the Oriental Region*. Dalnauka, Vladivostok, 252 pp.

Lelej, A.S. (2007) Biogeography of mutillid wasps (Hymenoptera, Mutillidae). *In*: Rasnitsyn, A.P. & Gokhman, V.E. (eds) *Studies on hymenopterous insects*. *Collection of scientific*

papers. KMK Scientific Press Ltd., Moscow, pp. 82–111. (in Russian)
Lelej, A.S. (2020) To the knowledge of velvet ants of the genera *Artiotilla* Invrea, *Radoszkowskitilla* Lelej and *Taiwanomyrme* Tsuneki (Hymenoptera: Mutillidae). *Far Eastern Entomologist* 410: 1–10. https://doi.org/10.25221/fee.410.1
Lelej, A.S. & Brothers, D.J. (2008) The genus-group names of Mutillidae (Hymenoptera) and their type species, with a new genus, new name, new synonymies, new combinations and lectotypifications. *Zootaxa* 1889: 1–79. https://doi.org/10.11646/zootaxa.1889.1.1
Lelej, A.S., Terine, J.B., Kumar, G.P., Das, D. & Sureshan, P. M. (2020) Review of the genus *Odontomutilla* Ashmead, 1899 (Hymenoptera: Mutillidae) of the Indian subcontinent, with description of two new species. *Zootaxa* 4822 (2): 191–208. https://doi.org/10.11646/zootaxa.4822.2.3
Lelej, A.S., Ullah, M. & Mahmood, K. (2007) Additions to the knowledge of the Mutillidae (Hymenoptera) of Pakistan. *Zootaxa* 1444 (1): 53–60. https://doi.org/10.11646/zootaxa.1444.1.4
Lelej, A.S. & Williams, K.A. (2023) Review of the tribe Smicromyrmini Bischoff, 1920 (Hymenoptera: Mutillidae). *Zootaxa* 5231 (2): 101–140. https://doi.org/10.11646/zootaxa.5231.2.1
Lelej, A.S., Williams, K.A., Loktionov, V.M., Pang, H. & Xu, Z.-F. (2017) Review of the genus *Zeugomutilla* Chen, 1957 (Hymenoptera, Mutillidae, Mutillini), with description of two new species. *Zootaxa* 4247 (1): 1–15. https://doi.org/10.11646/zootaxa.4247.1.1
Lelej, A.S., Williams, K.A., Terine, J.B., Okayasu, J., Parikh, G. & Kumar, G.P. (2023) Review of the tribe Mutillini (Hymenoptera: Mutillidae) from the Oriental Region. *Zootaxa* 5228 (4): 455–476. https://doi.org/10.11646/zootaxa.5228.4.5
Lelej, A.S. & Yamane, Sk. (1992) Interesting velvet ants (Hymenoptera, Mutillidae) from Japan and Korea. *Japanese Journal of Entomology* 60 (3): 625–632.
Lo Cascio, P., Romano, M. & Grita, F. (2012) New species and new records of mutillid wasps from the Socotra Archipelago (Hymenoptera: Mutillidae). *Acta Entomologica Musei Nationalis Pragae* 52 (supplementum 2): 525–544.
Luz, D.R., Waldren, G.C. & Melo, G.A.R. (2016) Bees as hosts of mutillid wasps in the Neotropical region (Hymenoptera, Apidae, Mutillidae). *Revisita Brasileira de Entomologia* 60 (4): 302–307. https://doi.org/10.1016/j.rbe.2016.06.001
Miyatake, M. (1985) Coccinellidae collected by the Hokkaido University expedition to Nepal Himalaya, 1968 (Coleoptera). *Insecta matsumurana*, New Series 30: 1–33.
Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858. https://doi.org/10.1038/35002501
Nonveiller, G. (1979 [1978]) Recherches sur les Mutillides de l'Afrique (Hymenoptera, Mutillidae) VIII. Révision des genres *Ctenotilla*, *Cephalotilla* et *Pseudocephalotilla* sensu Bischoff. *Memoires publies par l'Institut pour la Protection des Plantes*, Beograd 13: 1–184.
Nurse, C.G. (1903) New species of Indian aculeate Hymenoptera. *The Annals and Magazine of Natural History*, Series 7 11: 393–403, 511–526, 528–549. https://doi.org/10.1080/00222930308678815
Ôhara, M. (1989) Notes on six histerid beetles from southern Asia (Coleoptera: Histeridae). *Insecta matsumurana*, New Series 42: 31–46.
Okayasu, J. (2020) Velvet ants of the tribe Smicromyrmini Bischoff (Hymenoptera: Mutillidae) of Japan. *Zootaxa* 4723 (1): 1–110. https://doi.org/10.11646/zootaxa.4723.1.1
Okayasu, J. (2022) Remarkable range extension of the genus *Nordeniella* Lelej, 2005

(Hymenoptera: Mutillidae: Smicromyrmini): Description of a new species from Sumbawa, Indonesia. *Journal of Insect Biodiversity* 32 (2): 56–63. https://doi.org/10.12976/jib/2022.32.2.3

Okayasu, J., Lelej, A.S. & Williams, K.A. (2021) Review of *Eotrogaspidia* Lelej (Hymenoptera: Mutillidae: Trogaspidiini). *Zootaxa* 4920 (1): 56–90. https://doi.org/10.11646/zootaxa.4920.1.2

Okushima, Y. (1999) Cantharidae collected by the Hokkaido University expeditions to Nepal Himalaya (Coleoptera). *Insecta matsumurana*, New Series 56: 51–68.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'amico, J.A., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Lamoreux, J.F., Ricketts, T.H., Itoua, I., Wettengel, W.W., Kura, Y., Hedao, P. & Kassem, K. (2001) Terrestrial ecoregions of the world: A new map of life on Earth. *BioScience* 51 (11): 933–938. https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2

Orr, M.C., Hughes, A.C., Chesters, D., Pickering, J., Zhu, C.-D. & Ascher, J.S. (2021) Global patterns and drivers of bee distribution. *Current Biology* 31 (3): 451–458. https://doi.org/10.1016/j.cub.2020.10.053

Pagliano, G., Brothers, D.J., Cambra, R., Lelej, A.S., Lo Cascio, P., Matteini Palmerini, M., Scaramozzino, P.L., Williams, K.A. & Romano, M. (2020) Checklist of names in Mutillidae (Hymenoptera), with illustrations of selected species. *Bollettino del Museo Regionale di Scienze Naturali di Torino* 36 (1–2): 5–425.

Paudel, P.K., Bhattarai, B.P. & Kindlmann, P. (2012) An overview of the biodiversity in Nepal. *In*: Kindlmann, P. (ed.) *Himalayan biodiversity in the changing world*. Springer, Dordrecht, pp. 1–40. https://doi.org/10.1007/978-94-007-1802-9_1

Pitts, J.P., Wilson, J.S. & von Dohlen, C.D. (2010) Evolution of the nocturnal Nearctic Sphaeropthalminae velvet ants (Hymenoptera: Mutillidae) driven by Neogene orogeny and Pleistocene glaciation. *Molecular Phylogenetics and Evolution* 56 (1): 134–145. https://doi.org/10.1016/j.ympev.2010.03.033

Radoszkowski, O. 1885. Revision des armures copulatrices des mâles de la famille de Mutillides. *Horae Societatis Entomologicae Rossicae* 19 (1–2): 3–49 + 9 pls.

Rawat, G.S. (2017) The Himalayan vegetation along horizontal and vertical gradients. *In*: Prins, H.T. & Namgail, T. (eds) *Bird migration in the Himalaya: Wetland functioning amidst mountains and glaciers*. Cambridge University Press, Cambridge, pp. 189–204. https://doi.org/10.1017/9781316335420.015

Roll, U., Feldman, A., Novosolov, M., Allison, A., Bauer, A.M., Bernard, R., Böhm, M., Castro-Herrera, F., Chirio, L., Collen, B., Colli, G.R., Dabool, L., Das, I., Doan, T.M., Grismer, L.L., Hoogmoed, M., Itescu, Y., Kraus, F., LeBreton, M., Lewin, A., Martins, M., Maza, E., Meirte, D., Nagy, Z.T., Nogueira, C. de C., Pauwels, O.S.G., Pincheira-Donoso, D., Powney, G.D., Sindaco, R., Tallowin, O.J.S., Torres-Carvajal, O., Trape, J.-F., Vidan, E., Uetz, P., Wagner, P., Wang, Y., Orme, C.D.L., Grenyer, R. & Meiri, S. (2017) The global distribution of tetrapods reveals a need for targeted reptile conservation. *Nature Ecology & Evolution* 1: 1677–1682. https://doi.org/10.1038/s41559-017-0332-2

Ronchetti, F. & Polidori, C. (2020) A sting affair: A global quantitative exploration of bee, wasp and ant hosts of velvet ants. *PLoS ONE* 15 (9): e0238888. https://doi.org/10.1371/journal.pone.0238888

Shorthouse, D.P. (2010) SimpleMappr, an online tool to produce publication-quality point maps. Available from: http://www.simplemappr.net (accessed 27 July 2023)

Smith, F. (1855) Catalogue of hymenopterous insects in the collection of the British Museum. Part III. Mutillidae and Pompilidae. Taylor and Francis, London, 206 pp. + 5 pls.

https://doi.org/10.5962/bhl.title.20858
Suwa, M. (1977) Anthomyiidae collected by the Hokkaido University expeditions to Nepal Himalaya, 1968 and 1975 (Diptera). *Insecta matsumurana*, New Series 10: 17–51.
Suwa, M. (1984) The *Alticola* group of *Pegomya*, with descriptions of some new species from Taiwan and Nepal (Diptera: Anthomyiidae). *Insecta matsumurana*, New Series 29: 1–38.
Suwa, M. (1994) The genus *Phorbia* in Nepal, with descriptions of five new species (Diptera: Anthomyiidae). *Insecta matsumurana*, New Series 50: 1–52.
Swederus, N.S. (1787) Et nytt genus, och femtio nya species af insekter beskrifne. *Kongliga Vetenskaps Academiens nya Handlingar* 8: 181–201.
Takagi, S. (1975) Coccoidea collected by the Hokkaido University expedition to Nepal Himalaya, 1968 (Homoptera). *Insecta matsumurana*, New Series 6: 1–33.
Takagi, S. (1977) Five species of Diaspididae associated with Pinaceae in central Nepal (Homoptera: Coccoidea). *Insecta matsumurana*, New Series 11: 1–30.
Takagi, S. (2019) *Chionaspis* in the tropics (Sternorrhyncha: Coccoidea: Diaspididae). *Insecta matsumurana*, New Series 75: 29–79.
Takagi, S. (2020) The scale insect genus *Myrtaspis* (Sternorrhyncha: Coccoidea: Diaspididae). *Insecta matsumurana*, New Series 76: 23–89.
Takizawa, H. (1988) Chrysomelid beetles of Nepal, collected by the Hokkaido University Scientific Expeditions to Nepal Himalaya. Part IV (Coleoptera: Chrysomelidae). *The Entomological Review of Japan* 43 (1): 1–16 + pls 1–2.
Terine, J.B., Kumar, G.P. & Adithya, Y.B. (2023) A new species of *Dasylabris* Radoszkowski, 1885 (Hymenoptera: Mutillidae) from India. *Zootaxa* 5263 (1): 135–140. https://doi.org/10.11646/zootaxa.5263.1.8
Terine, J.B., Lelej, A.S. & Kumar, G.P. (2021) Discovery of the genus *Strangulotilla* Nonveiller, 1979 (Hymenoptera, Mutillidae) in India and description of a new species from the Western Ghats. *Zootaxa* 5057 (3): 429–436. https://doi.org/10.11646/zootaxa.5057.3.7
Turrisi, G.F., Matteini Palmerini, M. & Brothers, D.J. (2015) Systematic revision and phylogeny of the genera *Blakeius* Ashmead, 1903 and *Liomutilla* André, 1907, with description of two new genera (Hymenoptera: Mutillidae, Myrmillinae). *Zootaxa* 4010 (1): 1–78. http://dx.doi.org/10.11646/zootaxa.4010.1.1
Waldren, G.C., Sadler, E.A., Murray, E.A., Bossert, S., Danforth, B.N. & Pitts, J.P. (2023) Phylogenomic inference of the higher classification of velvet ants (Hymenoptera: Mutillidae). *Systematic Entomology* 48 (3): 463–487. https://doi.org/10.1111/syen.12588
Wikramanayake, E., Dinerstein, E., Loucks, C.J., Olson, D.M., Morrison, J., Lamoreux, J., McKnight, M. & Hedao, P. (2002) *Terrestrial ecoregions of the Indo-Pacific: A conservation assessment*. Island Press, Washington DC, xxix + 643 pp.
Williams, K.A., Lelej, A.S., Okayasu, J., Borkent, C.J., Malee, R., Thoawan, K. & Thaochan, N. (2019) The female velvet ants (aka modkhong) of southern Thailand (Hymenoptera: Mutillidae), with a key to the genera of southeast Asia. *Zootaxa* 4602 (1): 1–69. http://dx.doi.org/10.11646/zootaxa.4602.1.1
Williams, P.H., Ito, M., Matsumura, T. & Kudo, I. (2010) The bumblebees of the Nepal Himalaya (Hymenoptera: Apidae). *Insecta matsumurana*, New Series 66: 115–151.
Wilson, J.S., Clark, S.L., Williams, K.A. & Pitts, J.P. (2012) Historical biogeography of the arid-adapted velvet ant *Sphaeropthalma arota* (Hymenoptera: Mutillidae) reveals cryptic species. *Journal of Biogeography* 39: 336–352. https://doi.org/10.1111/j.1365-2699.2011.02580.x
Wilson, J.S., Pan, A.D., Limb, E.S. & Williams, K.A. (2018) Comparison of African and

North American velvet ant mimicry complexes: Another example of Africa as the 'odd man out'. *PLoS ONE* 13 (1): e0189482. https://doi.org/10.1371/journal.pone.0189482

Wilson, J.S. & Pitts, J.P. (2011) Pleistocene connection between the Nearctic Mediterranean and desert regions in the *Sphaeropthalma unicolor* species-complex (Hymenoptera: Mutillidae). *Insect Conservation and Diversity* 4 (3): 222–234. https://doi.org/10.1111/j.1752-4598.2010.00124.x

Yamane, S. & Yamane, Sk. (1979) Polistine wasps from Nepal (Hymenoptera, Vespidae). *Insecta matsumurana*, New Series 15: 1–37.

Zavattari, E. (1913) H. Sauter's Formosa-Ausbeute. Mutillidae (Hym.). *Archiv für Naturgeschichte* 79A (3): 19–42.

Zhou, H.-t., Lelej, A.S., Williams, K.A. & Liu, J.-x. (2018) Revision of the Oriental genus *Zavatilla* Tsuneki (Hymenoptera, Mutillidae, Trogaspidiini), with descriptions of two new species. *Zootaxa* 4418 (2): 101–120. http://dx.doi.org/10.11646/zootaxa.4418.2.1

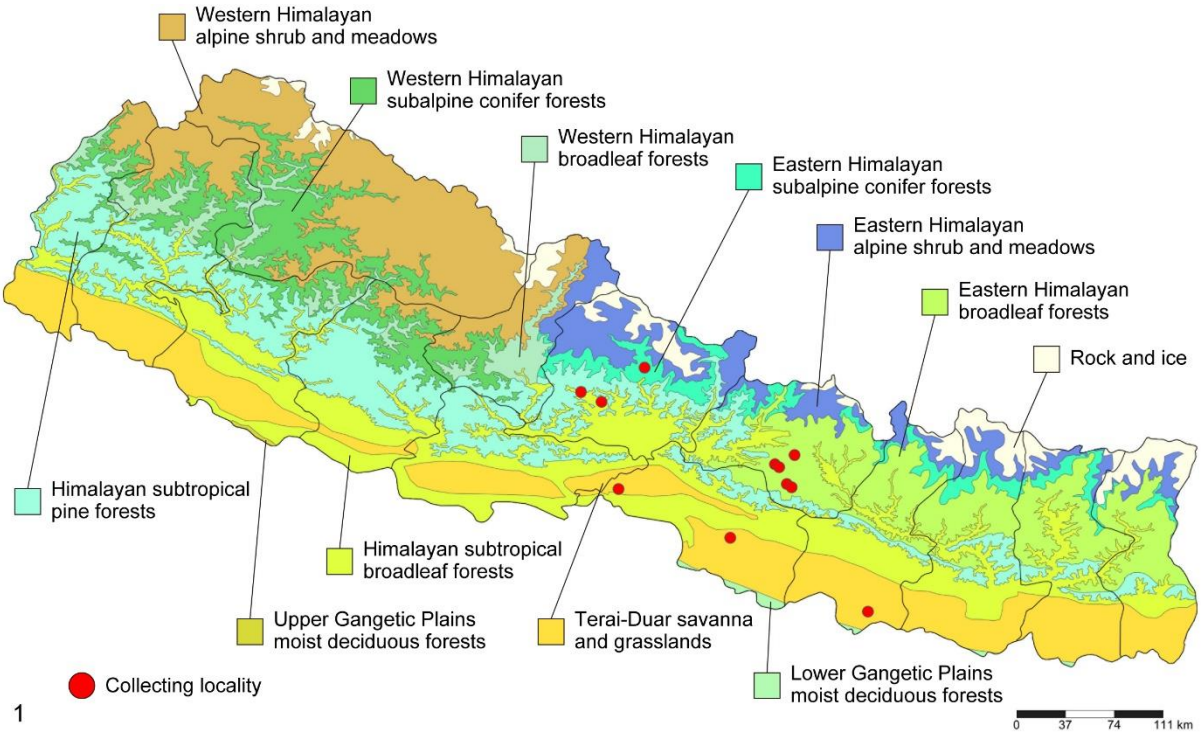


Figure 1. The terrestrial ecoregions of Nepal and collecting localities of velvet ants of Hokkaido University expeditions.

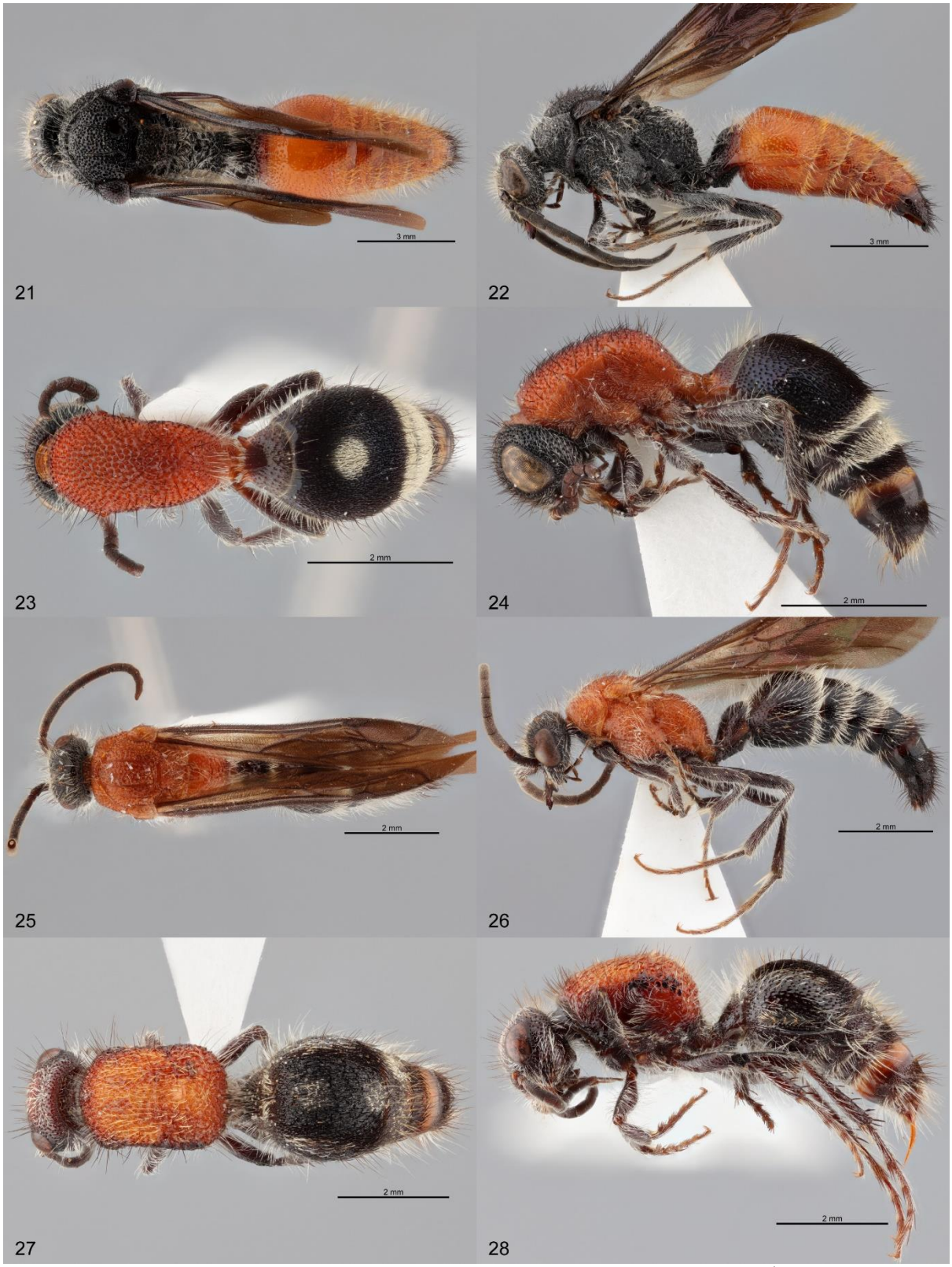
Figures 2–3. *Strangulotilla dubia* Okayasu, holotype ♂. 2. Dorsal habitus; 3. lateral habitus.

Figures 4–9. *Strangulotilla dubia* Okayasu, holotype ♂. 4. Face; 5. S7–8; 6. genitalia, dorsal view (right paramere and basiparamere removed); 7. genitalia, ventral view; 8. genitalia, inner view; 9. penis valve . Arrow indicates the antero-dorsal process on the cuspis.

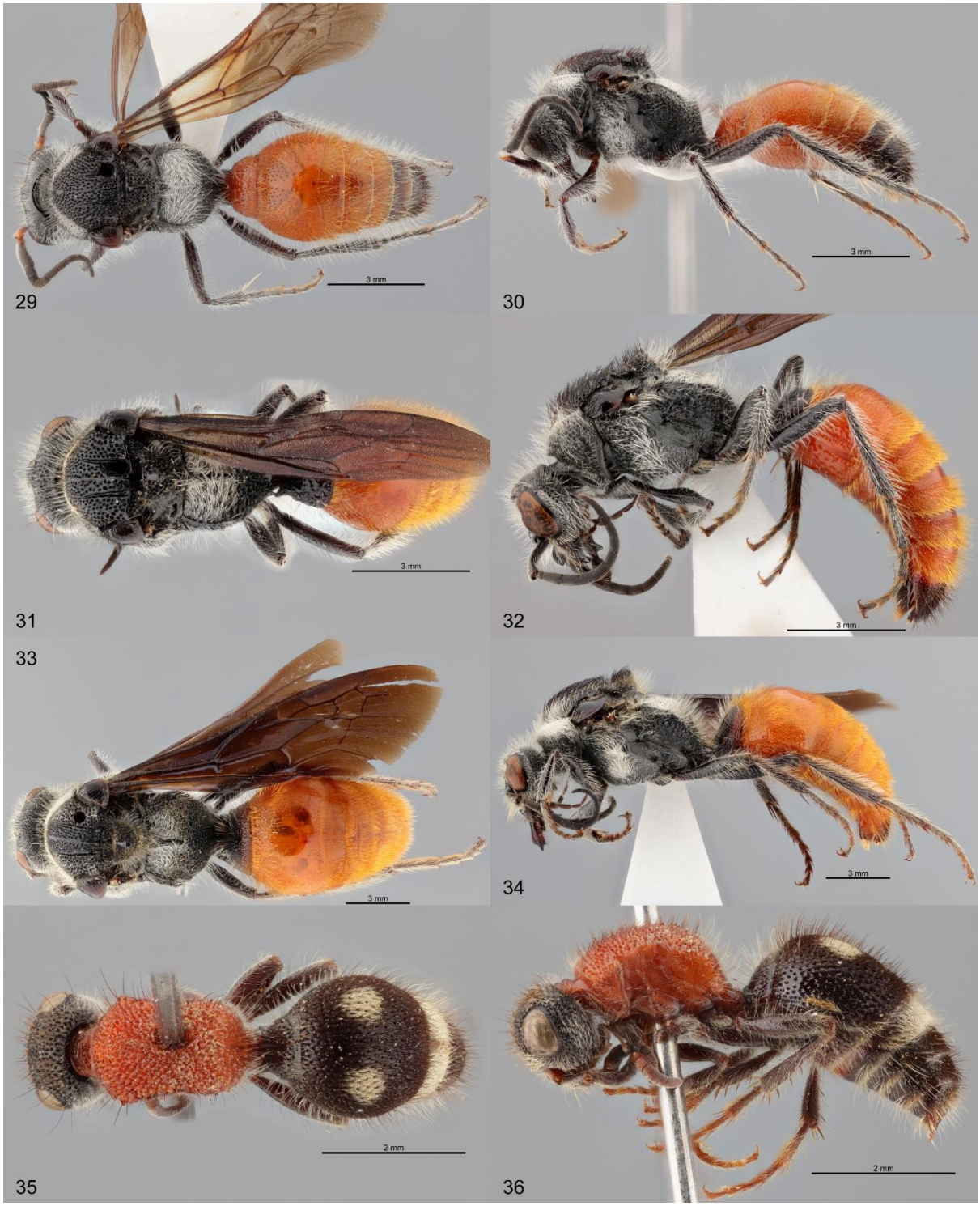
Figures 10–11. *Zeugomutilla curvicarinata* Okayasu, holotype ♀. 10. Dorsal habitus; 11. lateral habitus.

Figures 12–16. *Zeugomutilla curvicarinata* Okayasu, holotype ♀. 12. Mesosoma, dorsal view; 13. metasoma, dorsal view; 14. face; 15. gena, ventro-lateral view; 16. pygidial plate.

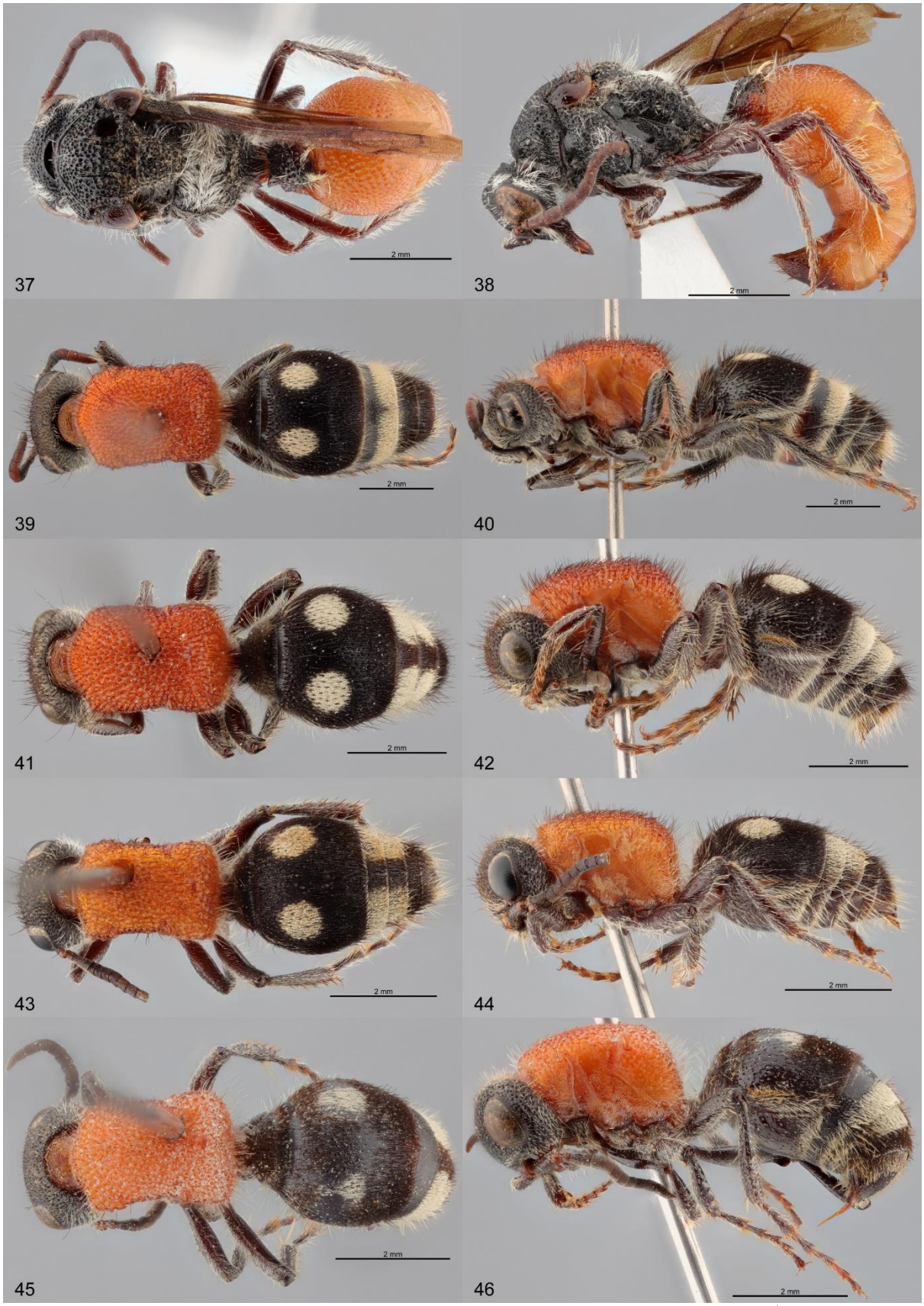
Figures 17–20. Dasylabrinae and Mutillini spp. from Nepal. 17, 18. *Dasylabris* sp., ♀; 19, 20. *Kurzenkotilla scrobiculata* (Hammer), ♀; 17, 19. dorsal habitus; 18, 20. lateral habitus.



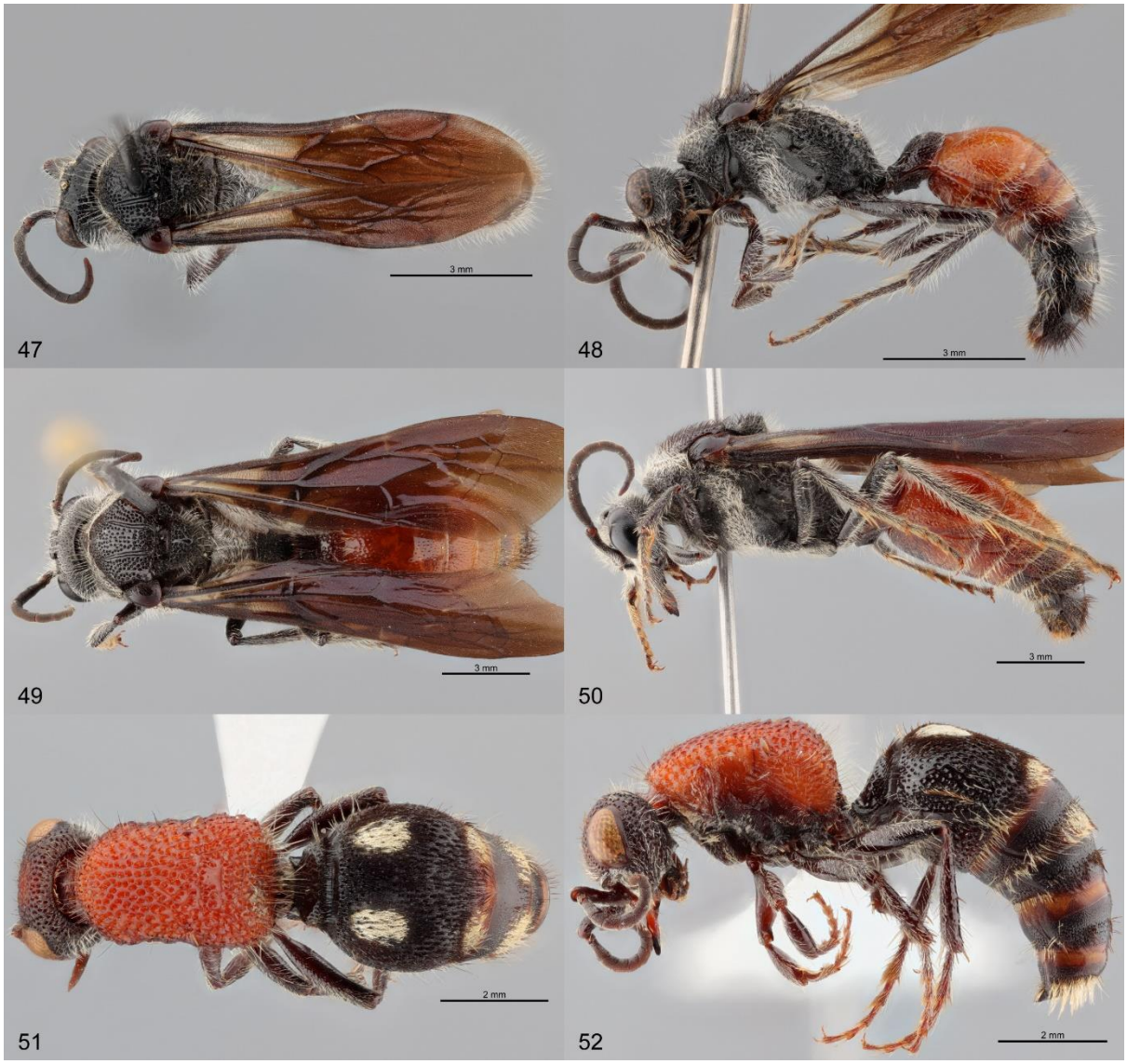
Figures 21–28. Smicromyrmini spp. from Nepal. 21, 22. *Promecilla* sp. 1, ♂; 23, 24. *Promecilla* sp. 2, ♀; 25, 26. *Smicromyrme* sp. 1, ♂; 27, 28. *Smicromyrme* sp. 2, ♀; 21, 23, 25, 27. dorsal habitus; 22, 24, 26, 28. lateral habitus.



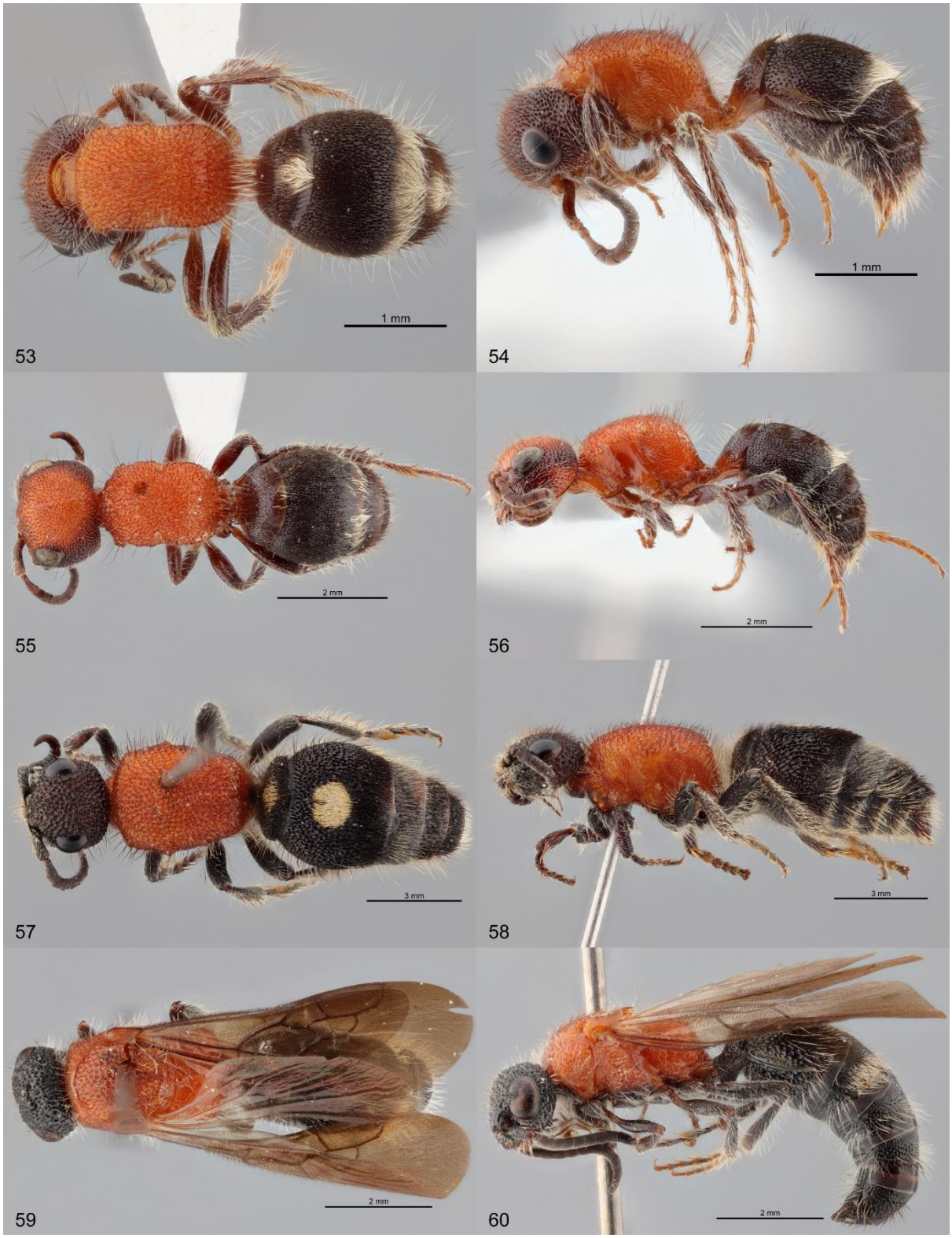
Figures 29–36. Trogaspidiini spp. from Nepal. 29, 30. *Eotrogaspidia adhabar* Okayasu *et al*., holotype ♂; 31, 32. *Karlissaidia* sp. 1, ♂; 33, 34. *Karlissaidia* sp. 2, ♂; 35, 36. *Petersenidia* sp., ♀; 29, 31, 33, 35. dorsal habitus; 30, 32, 34, 36. lateral habitus.



Figures 37–46. Trogaspidiini spp. from Nepal. 37, 38. *Radoszkowskitilla* sp., ♂; 39, 40. *Trogaspidia* sp. 1, ♀; 41, 42. *Trogaspidia* sp. 2, ♀; 43, 44. *Trogaspidia* sp. 3, ♀; 45, 46. *Trogaspidia* sp. 4, ♀; 37, 39, 41, 43, 45. dorsal habitus; 38, 40, 42, 44, 46. lateral habitus.



Figures 47–52. Trogaspidiini spp. from Nepal. 47, 48. *Trogaspidia* sp. 5, ♂; 49, 50. *Wallacidia* sp. 1, ♂; 51, 52. *Wallacidia* sp. 2, ♀; 47, 49, 51. dorsal habitus; 48, 50, 52. lateral habitus.



Figures 53–60. Myrmillinae and Odontomutillinae spp. from Nepal. 53, 54. *Bischoffitilla* sp. 1, ♀; 55, 56. *Bischoffitilla* sp. 2, ♀; 57, 58. *Odontomutilla* sp., ♀; 59, 60. *Yamanetilla* sp., ♂; 53, 55, 57, 59. dorsal habitus; 54, 56, 58, 60. lateral habitus.

Chapter 9

Far Eastern velvet ants of the genus *Nemka* Lelej (Hymenoptera: Mutillidae): Systematics and ecological character displacement

Disclaimer: *This work is not issued for the purposes of zoological nomenclature and is not considered a published work within the meaning of the International Code of Zoological Nomenclature 4th edition (Article 8.2).*

Abstract

Five species of the velvet ant genus *Nemka* Lelej, 1985 distributed in eastern China, Taiwan, and Japan were reviewed. Four species were recognized from both sexes, diagnosed, and illustrated: *N. limi* (Chen, 1957) (Eastern China), *N. taiwanensis* (Mickel, 1933) (Taiwan), *N. wotani* (Zavattari, 1913) (Taiwan), and *N. yasumatsui* (Mickel, 1936) (Japan). The female of *N. taiwanensis* was associated with the male. *Smicromyrme curvisquamata* (Chen, 1957) (♀) and *S. ilanica* Tsuneki, 1972 (♂) are proposed as **new junior synonyms** of *N. taiwanensis*. An identification key to all eight East Asian species of *Nemka*, including *N. conjungenda* (Magretti, 1892), *N. kellyi* (Pagden, 1934), *N. pagdeni* Lelej, 1995, and *N. viduata* (Pallas, 1773), is presented. Host records of the *Nemka* were reviewed. A single velvet ant species utilizes various hosts occurring in a particular habitat, and body size of velvet ants strongly correlates with size of the hosts. Here, I compared body size of those four *Nemka* species to infer their host choices. As a result, the body size of *N. limi* and *N. yasumatsui*, which are only *Nemka* species in eastern China and Japan, respectively, exhibited wide variation in both sexes with bimodal distribution in males, suggesting utilization of multiple hosts. In contrast, the body size of *N. taiwanensis* and *N. wotani*, which coexist in Taiwan, was less variable with unimodal distribution; *N. taiwanensis* was significantly larger than *N. wotani*. This implies strict preference to host size between these Taiwanese species. The specialized host choice is the potential factor that enables sympatric distribution of two *Nemka* species in Taiwan.

Key words

Host-parasitoid association, new synonymy, Oriental Region, Palaearctic Region, resource competition, niche partitioning, sex association.

Introduction

One of the major goals of evolutionary ecology is to discover the underlying mechanisms of formation and maintenance of species diversity and distribution. Phylogenetically related species are expected to have similar resource requirements and similar manners of mating interaction. In the sympatric zone of two related species, one can reduce fitness of another by competing for common resources (resource competition) and by interacting for mates (reproductive interference). As a consequence, these species may experience strong selection to evolve different traits in resource useage and reproduction — ecological and reproductive character displacements, respectively (Brown & Wilson, 1956; Gröning & Hochkirch, 2008; Pfennig & Pfennig, 2009; Slatkin, 1980). Otherwise, they cannot stably coexist and either may be extinct — competitive exclusion (Hardin, 1960) or sexual exclusion (Gröning & Hochkirch, 2008; Hochkirch *et al*., 2007). Resource competition had been considered a major driving force of phenotypic divergence in coexisting organisms (Losos, 2000; Schluter, 2000), while reproductive interference had been regarded as an unusual phenomenon (Gröning & Hochkirch, 2008). Recent theoretical and empirical studies, however,

demonstrated that reproductive interference can also lead to ecological character displacement when the character is related with both resource useage and reproduction (Konuma & Chiba, 2007; Pfennig & Pfennig, 2005, 2009). The effect of resource competition in character displacement is not fully understood yet.

Wasps of the family Mutillidae, also known as velvet ants, are composed of more than 4600 valid species worldwide (Pagliano *et al*., 2020). Velvet ants generally exhibit extreme sexual dimorphism; males are fully winged (rarely short-winged or wingless), while females are always wingless (Brothers, 1989), resulting in reduced mobility in female individuals. This nature is particularly important for their ecology. Because of the limited ability in host searching, dispersal, and escape from predators, females show many ecological and morphological specializations, including situation-specific host preference (Brothers, 1989; Taylor *et al*., 2019), highly structural geographical populations (Pitts *et al*., 2010b; Wilson & Pitts, 2008, 2010ab; Wilson *et al*., 2012a), long painful stings (Sadler *et al*., 2018; Schmidt, 2016, 2019; Schmidt & Blum, 1977; Starr, 1985), stridulation (Hinon *et al*., 1969; Polidori *et al*., 2013bc; Schmidt & Blum, 1977; Torrico-Bazoberry & Muñoz, 2019; Tschuch, 1993; Tschuch & Brothers, 1999), strong and slippery exoskeletons (Schmidt & Blum, 1977), alarm chemical secretion (Fales *et al*., 1980; Schmidt & Blum, 1977), aposematic coloration (Gall *et al*., 2018), and Müllerian mimicry complexes (Okayasu *et al*., 2018; Pan *et al*., 2016; Wilson *et al*., 2012b, 2015, 2018).

The published host records of velvet ants, only about 190 species (4% of valid species worldwide) studied to date (Ronchetti & Polidori, 2020), suggest that their host preference is generally situation-specific rather than host-specific (Brothers, 1989; Mickel, 1928; Taylor *et al*., 2019). This phenomenon is believed to be an adaptation to the low dispersal ability in wingless females, which makes it easier to find suitable hosts for them (Brothers, 1989). Some species, for which host-parasitoid associations have been investigated in detail, are apparently polyphagous and utilize multiple host species from various higher taxa sharing similar nesting habits; the nocturnal velvet ant *Sphaeropthalma amphion* (Fox, 1899) was reared from 27 dipteran and hymenopteran host species (Pitts *et al*., 2004); *Mutilla europaea* Linnaeus, 1758 attacks 21 species of the bee genus *Bombus* Latreille (Apidae; see Lelej, 1985 and Ronchetti & Polidori, 2020 for review). Similarly, one host species can be parasitized by several species of Mutillidae (Mickel, 1928; Taylor *et al*., 2019).

Temporal and spatial co-occurrence of multiple congeneric velvet ants is frequently observed, especially in tropical and subtropical regions. Williams *et al*. (2019) reported that three species of *Bischoffitilla* Lelej, 2002, three species of *Mickelomyrme* Lelej, 1995, and two species of *Trogaspidia* Ashmead, 1899 were collected at Vimarndin farm stay in Southern Thailand during May 17th to 20th, 2018. According to the recent taxonomic revision of *Eotrogaspidia* Lelej, 1996 by Okayasu *et al*. (2021), *E. buddha* Okayasu, Lelej & Williams, 2021 and *E. saussurei* (Lelej, 2005) were collected at various places in Sri Lanka at same time. This is noteworthy considering that their ecological niches are presumed to be largely overlapping given the wide host range and the preference to certain environment in velvet ants. Also, predation pressure by velvet ants to the hosts seems to be extremely high; during the three-year (1988–1990) survey of an aggregation of hundreds of nests of a ground-nesting wasp *Gorytes tricinctus* (Pérez) (Bembicidae) by Gôukon (1993) in Japan, the parasitism rate of the velvet ant *S. lewisi* Mickel, 1935 had drastically increased from 15.4 % (1988) to 55.2 % (1989), and the aggregation collapsed in 1990 probably due to the high parasitism rate. Likewise, high parasitism rates of velvet ants up to 79% have been recorded for species scattered in various subfamilies (Brothers, 1978; Sakagami & Katayama, 1977; Schmidt & Buchmann, 1986). Such high predation pressure was even regarded as a major factor in the evolution of aggregation-forming and nest-guarding behavior of bees of the family Halictidae (Lin, 1964).

Historically, velvet ants had been thought to exist in low population densities (Manley & Pitts, 2007; Pitts *et al*., 2010; Schmidt & Buchmann, 1986) because velvet ants were rarely found in large numbers (Schmidt & Buchmann, 1986) and their host bees and wasps were usually dispersed in their habitats (Brothers 1989). This assumption, however, likely stems from our inadequate knowledge, and the true abundance could be much greater than previously thought, as suggested by Manley & Pitts (2007), Manley & Taber (1978), Pitts *et al*. (2010), Schmidt & Buchmann (1986), and Schmidt & Hook (1979) (and references therein). For example, Schmidt & Buchmann (1986) estimated that 43% of approximately 78,000 brood chambers in 11,150 nests of *Diadasia rincornis* Cockerell (Hymenoptera: Apidae) at their 446 m^2 study site were parasitized by *Dasymutilla foxi* (Cockerell, 1894). Due to the overlapping host range, abundance, density, and high parasitism rate, interspecific competition among coexisting velvet ants can be great. Species interactions in such velvet ant communities have not been understood at all. However, some sorts of niche differentiation are expected based on the competitive exclusion principle (Boehme *et al*., 2012).

The genus *Nemka* Lelej, 1985 includes 17 species and five subspecies from the Oriental and Palaearctic Regions (Okayasu, 2020; Pagliano *et al*., 2020). In eastern margin of China mainland, Taiwan, and Japan, this genus had been represented by five species and one subspecies with one subsequent synonym (Lelej, 2005). Taxonomic status of these species has been confused because of unknown sex association, misidentification by previous authors, and poorly diagnosed species. Recently, Okayasu (2020) resurrected *N. yasumatsui* (Mickel, 1936) to full species status, and synonymized *N. limi nanhai* (Chen, 1957) under *N. limi limi* (Chen, 1957) and *N. chihpenchia* (Tsuneki, 1993) under *N. wotani* (Zavattari, 1913), leaving five valid species in that region. However, there still remain several species for which sex association and taxonomic validity are unknown. The primary focus of the present study was to review the species of *Nemka* occurring in eastern China, Taiwan, and Japan.

After the taxonomic review of *Nemka* (Okayasu, 2020 and this study), I recognized *N. limi* from China mainland, *N. taiwanensis* (Mickel, 1933) and *N. wotani* from Taiwan, and *N. yasumatsui* from Japan. Interestingly, two Taiwanese species showed sympatric distribution. These four *Nemka* species are considered monophyletic based on morphology, providing perfect usefulness to test if there is character displacement in tropical velvet ants.

Body size of adult velvet ants generally varies considerably even in one species and one sex, correlating with the amount of food supplied to the larva, namely the size of the host (Brothers, 1989; Ferguson, 1962; Heaversedge, 1968; Mickel, 1924). Mickel (1924) carried out a rearing experiment of *Dasymutilla bioculata* (Cresson, 1865). He reared larger specimens of this species from the larger host *Bembix pruinosa* Fox and smaller specimens from the smaller host *Microbembex monodonta* (Say) (Bembicidae). Body length of *D. bioculata* measured for 150 male and 232 female museum specimens exhibited bimodal distribution in both sexes (Mickel, 1924: Pl. VI). Mickel (1924) concluded that the amount of food supply determined the body size of *D. bioculata*. Consequently, the wide variation and multimodal distribution of body size in a velvet ant species may imply choice of different-sized hosts by females.

Here, I used this species-complex of *Nemka* to test the hypotheses: 1) *N. limi* and *N. yasumatsui* from eastern China and Japan, where only one species of *Nemka* is distributed, have wide host preference, resulting in wider variation of body size; 2) two Taiwanese *Nemka* species utilize different host species, resulting in narrower range of body size distribution.

Material and methods

Material

This study is based on the museum specimens obtained from the following institutes.

ELKU Entomological Laboratory, Faculty of Agriculture, Kyushu University, Fukuoka, Japan.
EUMJ Ehime University Museum, Matsuyama, Japan.
MNHAH Museum of Nature and Human Activities, Sanda, Japan.
NMNH National Museum of Natural History, Smithsonian Institution, Washington D.C., USA.
NSMT National Museum of Nature and Science, Tsukuba, Japan.
OMNH Osaka Museum of Natural History, Osaka, Japan.
SDEI Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany.
SEHU Hokkaido University Insect Collection, Sapporo, Japan.
TARI Taiwan Agricultural Research Institute, Taichung, Taiwan.
TFRI Taiwan Forestry Research Institute, Taipei, Taiwan.
TUA Laboratory of Entomology, Tokyo University of Agriculture, Atsugi, Japan.
ZMUC Zoological Museum, University of Copenhagen, Universitetsparken, Denmark.

Old locality names of insect collecting sites in Taiwan were translated into the present names using Chu & Yamanaka (1973–1975) and Kojima *et al*. (2011). In the synonymic lists and the Material examined sections, abbreviations for depository and additional or corrected data by the authors are given in square brackets.

Morphological study

Specimens were examined with a Leica M205C stereomicroscope (10–160× magnification). Most habitus photographs were taken using a Canon EOS 6D Mark II DSLR camera equipped with a Canon MP-E 65mm f/2.8 1–5× Macro Photo lens. External morphological features were imaged with a Canon EOS 6D Mark II attached to a Leica M205C. Focus stacking was done using Zerene Stacker (Zerene Systems LLC, Richland, WA, USA). The map figure was generated by SimpleMappr (Shorthouse, 2010). Figures were edited using Adobe Photoshop and Adobe Illustrator (Adobe Inc., San Jose, CA, USA). Terminology follows the Hymenoptera Anatomy Consortium (2024). Abbreviations are: S = metasomal sternum; T = metasomal tergum.

Male genitalia were extracted after softening specimens by soaking in 80% ethanol. Muscles of the genitalia were removed in a 10% potassium hydroxide (KOH) solution without heating for one to three hours, and subsequently soaked in a 25% acetic acid solution to neutralize. Lastly, genitalia were observed in 80% ethanol under a stereomicroscope. After examination, genitalia were stored in micro vials filled with glycerin and pinned with their respective specimens.

Body size analysis

Specimens were measured twice in order to reduce measurement errors, and the mean value was used in analyses. Measurements were taken using an ocular micrometer attached to a stereomicroscope. Body size was measured for *N. limi* (10♂9♀), *N. taiwanensis* (8♂2♀), *N. wotani* (5♂13♀), and *N. yasumatsui* (123♂91♀). Total body length was measured as the sum of head length, mesosomal length and metasomal length in dorsal view (Okayasu, 2020). Multimodality of body size distribution was tested by Silverman's test (Silverman, 1981, 1983) with 1,000 replicates of bootstrapping using VISUAL-SILVERMAN program developed by Kusuhashi & Okamoto (2015). Due to the lack of enough material, statistical

tests were performed for *N. yasumatsui* only.

Systematics

Nemka limi (Chen, 1957)

(Figs 1A–1D, 2A, 2B, 3A, 3E, 4A, 5A, 5B, 6A, 6E, 6I, 7A, 7E, 8A, 8E, 9A, 9E)

Smicromyrme wotani (non Zavattari, 1913): Yasumatsu, 1938: 85, ♀; Yasumatsu, 1951: 70, ♀.

Smicromyrme orientalis taiwanensis (non Mickel, 1933): Chen, 1957: 197, ♂, part; He *et al*., 2004: 955, ♂.

Smicromyrme limi limi Chen, 1957: 215, ♀, holotype ♀ (Chusan [= Zhoushan 舟山], Chekiang [= Zhejiang], China) [TARI], examined; He *et al*., 2004: 952, ♀.

Smicromyrme limi nanhai Chen, 1957: 216, ♀, holotype ♀ (San-ah [= Sanya 三亜], Hainan, China) [TARI], examined. Synonymized by Okayasu (2020: 33) under *Nemka limi* (Chen).

Nemka wotani (non Zavattari, 1913): Lelej, 1995: 10, ♂♀, part; Lelej *et al*., 2001: 12, ♀; Lelej, 2002: 57, part; Lelej, 2005: 48, part; Hua, 2006: 300; Lo Cascio, 2015: 553.

Nemka limi limi: Lelej, 1995: 11, ♀; Lelej, 2005: 46; Hua, 2006: 300; Okayasu *et al*., 2018: 303, ♀; Pagliano *et al*., 2020: 176.

Nemka limi nanhai: Lelej, 1995: 11, ♀; Lelej, 2005: 46; Hua, 2006: 300; Lo Cascio, 2015: 553; Okayasu *et al*., 2018: 303, ♀; Pagliano *et al*., 2020: 176.

Nemka taiwanensis (non Mickel, 1933): Lelej, 2002: 55, part; Lelej, 2005: 47, part; Hua, 2006: 300, part; Okayasu, 2020: 24, part; Pagliano *et al*., 2020: 177, part.

Nemka limi: Okayasu, 2020: 33, ♂♀, examined.

Zoobank LSID

urn:lsid:zoobank.org:act:B7B76A3A-3785-489D-9645-B0AD37568B78
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Diagnosis

MALE. Gena with large dense to confluent punctures (Fig. 7E); clypeus basomedially elevated forming basal and subbasal denticles, and with a pair of subapical rounded tubercles (Figs 7A, 8A). Mesosoma black; dense recumbent pale golden setae on dorsum of pronotum anteriorly short and posteriorly long, mixed with sparse long erect pale golden setae (Fig. 9A); lateral face of pronotum entirely rugoso-punctate (Fig. 9E); meso- and metascutellum with sparse long erect pale golden setae; ventral tubercle on mesopleuron laterally largely depressed (Fig. 8E). Metasomal segments 1–4 yellowish red; T3–4 with sparse golden setae; S7 with medial triangular low tubercle; cuspis reaching anterior 1/2 of paramere (Fig. 6E). FEMALE. Frons punctures close even medially (Fig. 3A); frons setae sparse, recumbent, golden to black; vertex with large dense but separated punctures; eye length ~2× malar distance. Scutellar scale posterior margin truncate to convex (Fig. 4A). T2 posterior margin with narrow band of pale golden to golden setae, medially slightly widened triangularly; T6 with thickened lateral pygidial fringe of pale golden setae; pygidial plate rugoso-striate anteriorly, unsculptured on posterior 1/6–1/5 (Fig. 3E).

Type material examined

Holotype ♀, *Smicromyrme limi limi* Chen: **China:** ZHEJIANG: Chusan [= Zhoushan], 20.VIII.1931, O. Piel leg. [TARI]. Paratypes, *Smicromyrme limi limi* Chen: **China:** SHANGHAI: Shanghai, 23.VII.1930, O. Piel leg. [1♀ TARI]; [Songjiang], Zô-Sè [=

Sheshan], 31.VII.1930, O. Piel leg. [1♀ ZMUC], 4.VIII.1930, [1♀ TARI], 11.VIII.1930 [1♀ TARI], 15.VIII.1930 [1♀ TARI], 31.VIII.1930 [1♀ TARI]; ZHEJIANG: Chusan [= Zhoushan], 25.II.1931, O. Piel leg. [1♀ TARI], 16.VIII.1931 [1♀ TARI], 5.IX.1931 [1♀ TARI]; [Lin'an, Hangzhou], Tienmushan [= Tianmushan], 15.VII.1905 [1♀ TARI]. Holotype ♀, *Smicromyrme limi nanhai* Chen: **China:** HAINAN: San-ah [= Sanya], 21.XI.1940, M. Chûjyô leg. [TARI]. Paratype, *Smicromyrme limi nanhai* Chen: **China:** HAINAN: [Sanya], Yurin [= Yulin], 21.XI.1940, M. Chûjyô leg. [1♀ TARI].

Additional material examined

China: ANHUI: Ningkwo [= Ningguo], Yui-Wáu-Kiai, 22.VII.1920, *Smicromyrme wotani limi* Chen, B. Petersen det. 1987 [1♂ TARI], 24.VII.1920 [2♂ TARI]; FUJIAN: Chungan, Bohea Hills, 10.IX.1939, T.C. Maa leg., *Smicromyrme wotani limi* Chen, B. Petersen det. 1987 [1♀ TARI], 12.IX.1939 [2♀ TARI], 25.IX.1939 [2♀ TARI, 1♀ ZMUC], 2.X.1939 [1♀ TARI], 16.X.1939 [1♀ TARI], 13–17.VIII.1943 [1♀ TARI]; Changting, Tsingshanpu, 12.VI.1940, T.C. Maa leg., "*Timulla orientalis taiwanensis*" [probably Chen's hand] [1♂ TARI]; Changting, Hotien, 25.VII.1940, T.C. Maa leg., *Smicromyrme wotani limi* Chen, B. Petersen det. 1987 [1♀ TARI]; Hwa-an, W. Gate, 23.IX.1940, T.C. Maa leg., *Smicromyrme wotani limi* Chen, B. Petersen det. 1987 [1♂ ZMUC]; Yungan [= Yong'an], Siyingpan, 1940, T.C. Maa leg., *Smicromyrme wotani limi* Chen, B. Petersen det. 1987 [1♀ TARI]; Shaowu, Shuipeikieh [= Shui Pei Kai], 4.VIII.1941, T.C. Maa leg., *Smicromyrme wotani limi* Chen, B. Petersen det. 1987 [1♀ TARI], 25.VI.1942 [1♂ ZMUC], 10–12.VII.1943 [1♀ TARI], 20–24.VII.1943 [2♀ TARI, 1♀ ZMUC], 5.VIII.1943 [2♀ ZMUC], 1–2.IX.1943 [1♂ TARI]; Shaowu, W Gate, 22.IX.1942, T.C. Maa leg., *Smicromyrme wotani limi* Chen, B. Petersen det. 1987 [1♀ TARI]; Shaowu, Kuhsienkieh, 8.VII.1944, T.C. Maa leg., *Smicromyrme wotani limi* Chen, B. Petersen det. 1987 [1♀ TARI], 1944 [5♀ TARI, 1♀ ZMUC]; Shaowu, Kaoyany, 30.VII.1945, T.C. Maa leg., *Smicromyrme wotani limi* Chen, B. Petersen det. 1987 [1♀ TARI]; Shaowu, Tachulan [= Dazhulan], 8–12.VIII.1945, T.C. Maa leg., *Smicromyrme wotani limi* Chen, B. Petersen det. 1987 [1♀ ZMUC]; GUANGDONG: Loufoushan [= Mt. Luofushan], 29.V.1937, T.C. Maa leg., *Smicromyrme wotani limi* Chen, B. Petersen det. 1987 [1♀ TARI]; JIANGXI: [Lushan, Jiujiang], Kuling [= Guling], 21.VIII.1935, O. Piel leg., *Smicromyrme wotani limi* Chen, B. Petersen det. 1987 [1♂ TARI]; SHANGHAI: [Songjiang], Zô-Sè [= Sheshan], 4.VIII.1924, O. Piel leg., *Smicromyrme wotani limi* Chen, B. Petersen det. 1987 [1♂ TARI], 17.VII.1930 [1♂ ZMUC], 19.VII.1930 [1♂ TARI], 23.VII.1930 [1♂ TARI, 1♂ ZMUC], 24.VII.1930 [3♂ TARI], 25.VII.1930 [1♂ TARI], 31.VII.1930 [1♂ TARI], 1.VIII.1930 [1♂ TARI], 4.VIII.1930 [2♂ TARI]; ZHEJIANG: Hangchow [= Hangzhou], 15.VI.1925, H.A. Jaynes leg., *Nemka wotani* (Zavattari), B. Petersen det. 1995 [1♂ NMNH]; Zô-Póu, VII.1930, *Smicromyrme wotani limi* Chen, B. Petersen det. 1987 [1♂ TARI]; Chusan [= Zhoushan], Ohekiano, 7.IX.1931, O. Piel leg., *Smicromyrme wotani limi* Chen, B. Petersen det. 1987 [1♂ ZMUC]. **Vietnam:** CAO BANG: Phia Oac Phia Den NP station, 30.VI.2022, Nguyen D Hiep leg. [1♀ IEBR]; LANG SON: [Lôc Binh], Montes Mauson [= Mt. Mau Son], Mai 2–3000, IV, H. Fruhstorfer leg., *Smicromyrme wotani wotani* (Zavattari), B. Petersen det. 1983 [1♂ ZMUC]; VINH PHUC: Ngoc Thanh, Me Linh Biodiversity station, 70 m, 21°23′03″N 105°42′40″E, 18.VIII.2022, NTPL, TTN [2♀ IEBR].

Distribution

China: Anhui, Fujian, Guangdong, Hainan, Jiangxi, Shanghai, Shanxi (Yasumatsu, 1951), Zhejiang. South Korea: Chungcheongnam-do (Lelej *et al*., 2001). Vietnam: Cao Bang, Lang Son, Quang Ninh, Vinh Phuc (Lelej, 1995).

Sex association

This species was initially described from the female only. The male was associated by Okayasu (2020) based on males and females collected at Zô-Sè [= Sheshan], Shanghai in China at the same time.

Remarks
Records of *N. wotani* from China mainland (Yasumatsu, 1938, 1951) and South Korea (Lelej *et al*., 2001) are assigned to *N. limi* (Okayasu, 2020), and records of *N. taiwanensis* from China mainland (Chen, 1957) are also assigned to this species (see below), leaving only one *Nemka* species in the eastern margin of the Eurasian continent. One additional species, *N. pagdeni* Lelej, 1995, is known from China mainland (Yunnan). However, *N. pagdeni* has not been not discovered in *Nemka* specimens from eastern China, and, therefore, *N. limi* and *N. pagdeni* do not share same geographical ranges.

***Nemka taiwanensis* (Mickel, 1933)**
(Figs 1E, 1F, 2C, 2D, 3B, 3F, 4B, 5C, 5D, 6B, 6F, 6J, 7B, 7F, 8B, 8F, 9B, 9F)

Mutilla dimidiata (non Lepeletier, 1845): Zavattari, 1913: 42, ♂; Matsumura, 1931: 29, ♂.
Mutilla gribodoi (non Magretti, 1892): Zavattari, 1913: 42, ♂, part.
Timulla (*Trogaspidia*) *orientalis taiwanensis* Mickel, 1933: 408, ♂, holotype ♂ (Taihanroku 大板鹿[= Taipan 台板], [Taitung], Formosa [= Taiwan]) [Museum für Naturkunde, Humbolt Universität, Berlin, Germany]; Mickel, 1935: 267, ♂.
Smicromyrme orientalis taiwanensis: Chen, 1957: 197, ♂, part, examined; Tsuneki, 1972b: 16, ♂, part.
Smicromyrme curvisquamata Chen, 1957, **syn. nov.**: 214, ♀, holotype ♀ (Chipon [= Chihpen 知本], Taitung, Taiwan) [TARI], examined.
Smicromyrme ilanica Tsuneki, 1972b, **syn. nov.**: 16, ♂, holotype ♂ (Tsukeng, Ilan [= Yilan 宜蘭], Formosa [= Taiwan]) [NMNH].
Nemka curvisquamata: Lelej, 1995: 10, ♀; Lelej, 2005: 46; Hua, 2006: 300; Lo Cascio, 2015: 553; Okayasu *et al*., 2018: 306; Okayasu, 2020: 24; Pagliano *et al*., 2020: 176.
Nemka taiwanenis: Lelej, 1995: 14, ♂; Lelej, 2002: 55; Lelej, 2005: 47; Hua, 2006: 300; Pagliano, 2011: 41, ♂; Lo Cascio, 2015: 553; Okayasu, 2020: 24; Pagliano *et al*., 2020: 177.
Mickelomyrme ilanica: Lelej, 1995: 17; Lelej, 1996b: 287, ♂; Lelej, 2005: 44; Hua, 2006: 300; Lo Cascio, 2015: 551; Okayasu, 2020: 44; Pagliano *et al*., 2020: 175.

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Diagnosis
MALE. Gena with large dense to confluent punctures (Fig. 7F); clypeus basomedially elevated forming basal and subbasal denticles, and with a pair of subapical narrow tubercles (Figs 7B, 8B). Mesosoma black; dense recumbent pale golden setae on dorsum of pronotum anteriorly short and posteriorly long, mixed with sparse long erect pale golden setae (Fig. 9B); lateral face of pronotum entirely rugoso-punctate (Fig. 9F); meso- and metascutellum with sparse long erect pale golden setae; ventral tubercle on mesopleuron laterally largely depressed (Fig. 8F). Metasomal segments 1–3 or 4 yellowish red; T3–4 with sparse pale golden to golden setae; S7 with medial triangular low tubercle; cuspis reaching anterior 1/2 of paramere (Fig. 6F). FEMALE. Frons punctures close even medially (Fig. 3B); frons setae

sparse, recumbent, golden to black; vertex with large dense but separated punctures; eye length ~2× malar distance. Scutellar scale posterior margin emarginate medially (Fig. 4B). T2 posterior margin with narrow band of pale golden to golden setae, medially slightly widened triangularly; T6 with thickened lateral pygidial fringe of pale golden setae; pygidial plate rugoso-striate anteriorly, unsculptured on posterior 1/5 (Fig. 3F).

Type material examined
Holotype ♀, *Smicromyrme curvisquamata* Chen: **Taiwan:** TAITUNG: Chipon [= Chihpen], 1.VII.1927, S. Issiki leg. [TARI]. Paratype, *Smicromyrme curvisquamata* Chen: **Taiwan:** YILAN: Taipin [= Mt. Taiping], 12.IX.1910, T. Shiraki leg., *Mutilla dimidiata* Lepeletier, T. Shiraki det., *Smicromyrme wotani limi* Chen, B. Petersen det. 1987, *Smicromyrme wotani*? [probably Chen's hand], *Smicr. curvisquamata* Chen [unknown hand] [1♀ TARI].

Additional material examined
Taiwan: CHIAYI: Kagi [= Chiayi], 30.IX.1933, J. Sonan leg. [1♂ TARI]; HSINCHU: Shinchiku [= Hsinchu], 18.VII.1930, J. Sonan & K. Miyake leg., *Timulla* (*Trogaspidia*) *orientalis taiwanensis* Mickel, J. Sonan det., *Timulla orientalis taiwanensis* [probably Chen's hand] [1♂ TARI]; NANTOU: Formosa, Horisha [= Puli], 30.IV.07, Matsumura leg. [1♂ SEHU]; TAICHUNG: Taichû-shû [= Taichung], Taikôkei [= Tahuchi], Urai [= Chingshan]-Pisutan [Tachien]-Saramao [= Lishan], 16.VII.1932, T. Esaki leg., *Smicromyrme wotani* (Zavattari), B. Petersen det. 1981 [1♀ ELKU]; TAINAN: Tainan, 30.IV.1925, J. Sonan leg. [1♂ TARI]; TAIPEI: Yangmingshan, 12.VII.1977, H. Takizawa leg. [1♀ SEHU]; YILAN: Taipin [= Mt. Taiping], 12.IX.1910, T. Shiraki leg., *Timulla* (*Trogaspidia*) *orientalis taiwanensis* Mickel, J. Sonan det. [1♂ TARI]; Taipin [= Mt. Taiping], 12.IX.1910, *Mutilla dimidiata* Lepeletier, T. Shiraki det., *Timulla orientalis taiwanensis* [probably Chen's hand] [1♂ TARI]; Taipin [= Mt. Taiping], 12.IX.1910, T. Shiraki leg., *Timulla orientalis taiwanensis* [probably Chen's hand] [1♂ TARI].

Distribution
Taiwan: Chiayi, Hsinchu, Nantou, Tainan, Taichung*, Taitung, Yilan.

Sex association
This species was initially described from the male only. The female was described as *Smicromyrme curvisquamata* and associated herein based on three males of *N. taiwanensis* and the paratype of *N. curvisquamata* collected at Taiping, Yilan in Taiwan at the same time.

Remarks
Nemka taiwanensis had been variously misidentified by previous authors (Table 1). Voucher specimens of *S. orientalis taiwanensis* identified by Chen (1957), although most of them are not labeled as such, were reexamined. They actually included three species, *N. limi*, *N. wotani* and true *N. taiwanensis*. Specimens from China mainland were assigned to *N. limi* (see above). *Nemka taiwanensis* is consequently distributed in Taiwan only. One male specimen of *N. wotani* in Chen's collection was labeled as "*Timulla orientalis taiwanensis* (4–7 black)", indicating that Chen regarded this species as a color variant of *N. taiwanensis*. Actually, two out of six males of *N. taiwanensis* examined here have the metasomal segments 1–3 red and the following segments black. However, males of *N. taiwanensis* and those of *N. wotani* are separated by the punctation on gena, shape of clypeal tubercle, setation on pronotal dorsum, surface sculpturing of lateral pronotal face and shape of mesopleural tubercle (Table 2).

Smicromyrme curvisquamata Chen, 1957 was described based on two females from Taiwan, and subsequently transferred to *Nemka* by Lelej (1995). The pygidial plate of this

species was described as "delicately finger-printedly punctate throughout" (Chen, 1957). This has been accepted as the primary basis to separate *N. curvisquamata* from *N. kellyi*, *N. limi*, *N. pagdeni* and *N. wotani* by Lelej (1995) and Okayasu (2020). However, type specimens of *N. curvisquamata* has the pygidial plate striate on anterior 4/5 and smooth on posterior 1/5 (Fig. 3F). Chen (1957) distinguished *N. curvisquamata* from *N. limi* by the stronger clypeal medial carina and the shape of scutellar scale. The clypeal medial carina is highly variable, and *N. limi*, *N. yasumatsui* and *N. wotani* sometimes have a strong carina. This character is therefore considered to be inappropriate to diagnose the *Nemka* species.

Tsuneki (1972b) examined 11 males of *S. orientalis taiwanensis*. Of these, nine were described as having metasomal segments 1–3 red and identified as *N. wotani* by Okayasu (2020). The remaining two was reexamined by Lelej (1995) and identified as an unknown species of *Mickelomyrme*. However, Tsuneki (1972b) illustrated the subbasal tooth and subapical narrow tubercles on clypeus (Tsuneki, 1972b: figs 62–64). This justifies Tsuneki's identification for these two specimens.

Tsuneki (1972b) also described *S. ilanica* from Taiwan comparing it with *N. taiwanensis*. *Smicromyrme ilanica* was later transferred to *Mickelomyrme* by Lelej (1995). This species, however, has the antennal tubercles well separated (Tsuneki, 1972b: fig. 65; closely located in *Mickelomyrme*) and clypeus with subbasal tooth (Tsuneki, 1972: fig. 66; absent in *Mickelomyrme*), and thus is considered to belong to *Nemka*. Tsuneki (1972b) distinguished *S. ilanica* from *N. taiwanensis* by the following combination of character states:

"*(1) Vestiture: On upper frons and vertex brownish black, on abdomen except anterior portion of tergite 1 golden, on ventral side slightly paler, on tergites and sternites 6 and 7 blackish brown, otherwise as in* S. o. taiwanensis*. (2) Clypeus: Fig. 65, in the lateral view: Fig. 66 (left mandible removed), markedly depressed below the level of mandible (in this respect similar), on upper medial region provided with a triangular process and a stout tubercle longitudinally arranged (Fig. 66), lower flattened area longitudinally, irregularly coarsely rugose, with a transverse line of hair-bearing punctures towards middle, the surface without short, fine greyish white pudescenee* [sic!]*, also a pair of raised line on medio-anterior portion lacking. (3) Ocellr* [sic!] *area and the vertex behind it much strongly raised, interocellar area in taiwanensis slightly but distinctly impressed, in this species not impressed; punctures on vertex more or less longitudinally confluent and on culocellar area distinctly rugoso-punctate. (4) Ocelli relatively larger, OOD approximately thrice as great as the diameter of postocellus. (5) Tegulae with apex more weakly reflected, with the surface coarsely, strongly and fairly closely punctured, on medio-external area alone punctures fine and sparse. (6) Basal enclosed area of propodeum distinctly larger (Fig. 67, cf. Fig. 68, in* S. o. taiwanensis*, the form is variable more or less, but the general size is rather constant). (7) Punctures on abdomen comparatively finer and closer, the difference is on tergite 2 very conspicuous. (8) Medial lunate platform of sternite 6 broader and with the surface excavated. (9) Sternite 7 not impressed medially.*

Length 16.5 mm. The dissected right half of genitalia seen from inside: Fig. 69 (p: penis, v: volsella), volsella consisted of two part, the outer lengthened part at base provided with a very striking tuft of long hair, the portion seen from apex: Fig. 70. Black, with basal 4 segments of abdomen except the extreme base ferruginous."

Tsuneki (1972b) apparently confused males of *N. wotani* with those of *N. taiwanensis*, and provided little information on the character states of *N. taiwanensis*. Therefore, most of Tsuneki's diagnosis for *S. ilanica* does not make sense. Also, only one specimen of *S. ilanica* was available for Tsuneki's study. After examination of series of six males of *N. taiwanensis*, diagnostic features for *S. ilanica* listed above were found inadequate since some of the

specimens exhibited intermediate forms. *Smicromyrme ilanica* is thus proposed as a junior synonym of *N. taiwanensis*. Photos of the holotype of *S. ilanica* are available in Chan *et al*. (2024) and http://n2t.net/ark:/65665/370037bca-dab8-4053-95f8-c89cfa0ab906 (accessed 19 February 2024).

Nemka wotani (Zavattari, 1913)

(Figs 1G, 1H, 3C, 3G, 4C, 5E, 5F, 6C, 6G, 6K, 7C, 7G, 8C, 8G, 9C, 9G)

Mutilla wotani Zavattari, 1913: 27, ♀, lectotype ♀ (Tainan 台南, Formosa [= Taiwan]) [SDEI], designated by Mickel (1933: 420), examined; Sonan, 1931: 7, ♀, examined.
Smicromyrme wotani: Mickel, 1933: 420, ♀; Mickel, 1935: 291, ♀; Chen, 1957: 207, ♀, examined; Tsuneki, 1972b: 18, ♀, examined; Tsuneki, 1993: 40, ♀.
Smicromyrme orientalis taiwanensis (non Mickel, 1933): Chen, 1957: 197, ♂, part; Tsuneki, 1972b: 16, ♂, part, examined.
Smicromyrme (*Horaia*) *chihpenchia* Tsuneki, 1993: 43, ♂, holotype ♂ (Chihpenchi 知本, Taitung, Taiwan) [MNHAH], examined. Synonymized by Okayasu (2020: 31) under *Nemka wotani* (Zavattari).
Nemka wotani: Lelej, 1995: 10, ♂♀, part, examined; Lelej, 2002: 57; Lelej, 2005: 48; Hua, 2006: 300, part; Pagliano, 2011: 41, ♂; Lo Cascio, 2015: 553; Okayasu *et al*., 2018: 303, ♀; Okayasu, 2020: 31, ♂♀, examined; Pagliano *et al*., 2020: 177.
Nemka chihpenchia: Lelej, 1995: 11, ♂; Lelej, 2005: 45; Lo Cascio, 2015: 552; Pagliano *et al*., 2020: 176.
Smicromyrme chihpenchia: Hashimoto & Nakanishi, 1997: 31, ♂.

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Diagnosis

MALE. Gena with large sparse punctures (Fig. 7G); clypeus basomedially elevated forming basal and subbasal denticles, and with a pair of subapical rounded tubercles (Figs 7C, 8C). Mesosoma black; dense recumbent pale golden setae on dorsum of pronotum short, mixed with sparse long erect pale golden setae (Fig. 9C); lateral face of pronotum anteriorly rugoso-punctate and posteriorly transversely puncto-striate (Fig. 9G); meso- and metascutellum with sparse long erect pale golden setae; ventral tubercle on mesopleuron laterally flattened (Fig. 8G). Metasomal segments 1–3 yellowish red; T3–4 with sparse pale golden setae; S7 with medial triangular low tubercle; cuspis reaching anterior 1/2 of paramere (Fig. 6G). FEMALE. Frons punctures laterally close and medially separated (Fig. 3C); frons setae sparse, recumbent, golden to black; vertex with large dense but separated punctures; eye length ~2× malar distance. Scutellar scale posterior margin truncate to convex (Fig. 4C). T2 posterior margin narrow band of pale golden setae, medially slightly widened triangularly; T6 with thickened lateral pygidial fringe of pale golden setae; pygidial plate rugoso-striate anteriorly, unsculptured on posterior 1/6–1/5 (Fig. 3G).

Type material examined

Lectotype ♀, *Mutilla wotani* Zavattari: **Taiwan:** TAINAN: Tainan, VIII.1909, H. Sauter leg. [SDEI (DEI-GISHym 16749)]. Holotype ♂, *Smicromyrme chihpenchia* Tsuneki: **Taiwan:** TAITUNG: Chihpenchi, 12.VIII.1976, T. Murota leg. [MNHAH (B1-288585)].

Additional material examined

Taiwan: CHIAYI: Takezaki [= Chuchi], 15.XI.1926, J. Sonan leg. [1♀ SEHU]; Takezaki [= Chuchi], 15.XI.1926, *Smicromyrme wotani wotani* Zavattari, B. Petersen det. 1987 [1♀ TARI]; Chuchi, 18.VI.1941, Y. Yano leg. [1♀ ELKU]; Chuchi, 24–25.VII.1968, K. Tsuneki leg. [1♀ NMNH]; Chuchi, 24–25.VII.1968, K. Tsuneki leg., *Smicromyrme orientalis taiwanensis* (Mickel), K. Tsuneki det. 1972 [probably Petersen's hand] [1♂ ZMUC]; Chuchi, 24–25.VII.1968, K. Tsuneki leg., *Smicromyrme wotani* (Zavattari), K. Tsuneki det. 1972 [1♀ ZMUC]; Chuchi, 26.VII.1968, K. Tsuneki leg., *Smicromyrme wotani* (Zavattari), K. Tsuneki det. 1972 [1♀ ZMUC]; Kagi [= Chiayi], 30.IX.1933, J. Sonan leg., *Smicromyrme wotani wotani* Zavattari, B. Petersen det. 1987 [1♀ TARI]; NEW TAIPEI: Hsintien [= Xindian], VIII.1920, S. Inamura leg., *Mutilla wotani* Zavattari, T. Shiraki det., *Smicromyrme wotani wotani* (Zavattari), B. Petersen det. 1987 [1♀ ZMUC]; Hsintien [= Xindian], VIII.1920, S. Inamura leg., *Smicromyrme wotani wotani* (Zavattari), B. Petersen det. 1987 [1♀ TARI]; PENGHU: Pengfutao, VII.1930, S. Minowa leg., *Smicromyrme wotani wotani* Zavattari, B. Petersen det. 1987 [1♀ TARI]; PINGTUNG: Hengchun, 17.VII.1968, K. Tsuneki leg., *Smicromyrme wotani* (Zavattari), K. Tsuneki det. 1972 [1♀ ZMUC]; TAICHUNG: Tulan, 5.VII.1968, K. Tsuneki leg., *Smicromyrme wotani* (Zavattari), K. Tsuneki det. 1972 [1♀ ZMUC]; TAINAN: Xinhua, 5.V.1925, S. Takano leg. [1♀ SEHU]; Yujing, 2.VII.1937, J. Sonan leg., *Smicromyrme wotani wotani* (Zavattari), B. Petersen det. 1987 [1♀ TARI]; TAIPEI: Taipei, 25.IX.1927, J. Sonan leg., *Smicromyrme wotani wotani* (Zavattari), B. Petersen det. 1987 [5♀ TARI]; TAITUNG: Taitô-chô [= Taitung], Kanzangoe, Suzuka-Shinpuro [=Hsinwulu], 10.VIII.1932, T. Esaki leg., *Smicromyrme wotani* (Zavattari), B. Petersen det. 1981 [1♀ ELKU]; Beinan, Chihpen, 15.VIII.1936, K. Iida leg., *Nemka wotani* (Zavattari), A. Lelej det. 1995 [1♂ NSMT (NSMT-Hym No. 3350)], 18.VIII.1936 [1♀ NSMT (NSTM-Hym No. 3323)]; Chihpenchi, 30.VI.1968, K. Tsuneki leg., *Smicromyrme orientalis taiwanensis* (Mickel), K. Tsuneki det. 1972 [probably Petersen's hand] [1♂ ZMUC]; Fangliao, 24.IV.1941, Nitobe leg., *Mutilla suspiciosa* (Smith), T. Shiraki det., *Timulla orientalis taiwanensis* (4–7 black) [probably Chen's hand] [1♂ TARI].

Distribution

Taiwan: Chiayi, Hualien (Tsuneki, 1972b), New Taipei, Penghu, Pingtung, Taichung, Tainan, Taipei, Taitung, Taoyuan (Tsuneki, 1972b).

Sex association

This species was initially described from the female only. The male was associated by Lelej (1995) and Lelej & Yamane (1992) based on males and females collected at the same place and time in Japan. However, their specimens, including females, were later identified as *N. yasumatsui* (Okayasu, 2020). Based on the Japanese specimens, Lelej (1995) correctly identified the true male of *N. wotani* from Taiwan. Okayasu (2020) examined one male and two females of *N. wotani* collected at Chuchi, Chiayi in Taiwan at the same time.

Remarks

This is the only velvet ant species ever recorded from Penghu Island.

Nemka yasumatsui (Mickel, 1936)

(Figs 2E, 2F, 3D, 3H, 4D, 5G, 5H, 6D, 6H, 6L, 7D, 7H, 8D, 8H, 9D, 9H)

Smicromyrme yasumatsui Mickel, 1936: 52, ♀, holotype ♀ (Chikuzen 筑前, Fukuoka, Japan) [University of Minnesota, St. Paul, Minnesota, USA]; Tsuneki, 1972a: 17, ♀; Murota, 1977: 6, ♀; Yoshida, 1989: 651; Takahashi, 1996: 28, ♀. Synonymized by Lelej (1995: 10) under *Nemka wotani* (Zavattari) and resurrected to full species status

by Okayasu (2020: 25).
Smicromyrme (*Nemka*) *wotani* (non Zavattari, 1913): Lelej & Yamane, 1992: 631, ♂♀.
Nemka wotani (non Zavattari, 1913): Lelej, 1995: 10, ♂♀, part, examined; Yamane, 1999: 381, ♂♀; Lelej, 2002: 57; Lelej, 2005: 48; Terayama, 2005: 8, 11, 17, ♂♀; Hua, 2006: 300, part; Terayama *et al*., 2011: 13, 21, ♂♀; Suda, 2011: 137, ♀; Tsurusaki *et al*., 2012: 70, ♂; Nagase *et al*., 2014: 132, ♀; Ono & Kawashima, 2013: 41, ♂; Lo Cascio, 2015: 553; Terayama *et al*., 2016: 167, ♂♀.
Smicromyrme lewisi (non Mickel, 1935): Sato & Tsurusaki, 2010: 68, ♀.
Nemka yasumatsui: Okayasu, 2020: 25, ♂♀, examined.

Zoobank LSID
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Diagnosis
MALE. Gena with large dense to confluent punctures (Fig. 7H); clypeus basomedially elevated forming basal and subbasal denticles, and with a pair of subapical rounded tubercles (Figs 7D, 8D). Mesosoma black; dense recumbent pale golden setae on dorsum of pronotum short, mixed with sparse long erect pale golden setae (Fig. 9D); lateral face of pronotum entirely rugoso-punctate (Fig. 9H); meso- and metascutellum with sparse long erect pale golden setae; ventral tubercle on mesopleuron laterally largely depressed (Fig. 8H). Metasomal segments 1–3 yellowish red; T3–T4 with sparse pale golden setae; S7 with medial triangular low tubercle; cuspis reaching anterior 1/2 of paramere (Fig.6H). FEMALE. Frons punctures laterally close and medially separated (Fig. 3D); frons setae sparse, recumbent, golden to black; vertex with large dense but separated punctures; eye length ~2 × malar distance. Scutellar scale posterior margin truncate to convex (Fig. 4D). T2 posterior margin with narrow band of pale golden setae, medially slightly widened triangularly; T6 with thickened lateral pygidial fringe of pale golden setae; pygidial plate rugoso-striate anteriorly, unsculptured on posterior 1/6–1/5 (Fig. 3H).

Type material examined
Paratype: **Japan:** FUKUOKA: Chikuzen, 3.IX.1930, K. Yasumatsu leg., *Smicromyrme wotani* (Zavattari), B. Petersen det. 1981 [1♀ ELKU].

Additional material examined
Japan: AICHI: Toyohashi-shi, Hosoya-chô, Omotehama, 17.IX.2006, N. Toda leg. [1♀ EUMJ]; CHIBA: Futtsu-shi, Futtsu, 26.VII.1972, H. Suda leg. [1♀ HSC]; Futtsu-shi, Minato, Kazusaminato, 3.IX.2017 [7♀ EUMJ]; Futtsu City, Shinmaiko-kaigan beach, 35°14′54″N 139°52′04″E, 24.VII.2021, T. Yoshida leg. [2♀ SEHU]; EHIME: Matsuyama, 21.IX.1950, H. Kusunoki leg. [1♀ EUMJ]; FUKUOKA: Chikuzen, 3.IX.1930, K. Yasumatsu leg. [2♀ ELKU, 1♀ TARI]; Chikuzen, 3.IX.1930, K. Yasumatsu leg., *Smicromyrme wotani* (Zavattari), B. Petersen det. 1981 [2♀ ELKU]; Chikuzen, 3.IX.1930, K. Yasumatsu leg., compared with type by B. Petersen in 1968, *Smicromyrme wotani* (Zavattari), B. Petersen det. 1981 [1♀ ZMUC]; GOTÔ ISLANDS: Nozaki-jima Island, 26.VII.1971, T. Okadome leg., *Smicromyrme wotani wotani* (Zavattari), B. Petersen det. 1983 [1♂ TUA]; Nozaki-jima Island, 31.VII.1971, S. Okadome leg., *Smicromyrme wotani* (Zavattari), B. Petersen det. 1981 [1♀ ZMUC]; Fukue-jima Island, Takahama, 32.7084°N 128.6618°E, 27.VII.2013, R. Matsumoto leg. [1♀ OMNH]; HYÔGO: Awaji-shima Island, Minamiawaji-shi, Nandan-chô, Fukiage-hama, 17.VII.2000, R. Matsumoto leg. [1♀ OMNH]; IKI ISLANDS: Iki-shi, Ikino-shima Island, Katsumoto-chô, Kushiyama camp site, 33°51'N 129°42'E, 16–17.VII.2016, R. Itô leg. [1♂3♀ ELKU]; Iki-shi, Ikino-shima Island, Katsumoto-chô, Kushiyama beach,

33°51'N129°41'E, 17.VII.2016, R. Itô leg. [1♀ ELKU]; KAGOSHIMA: Kimotsuki-chô, Futamata, Forest road, 3.VII.2011, T. Kawano leg. [1♀ ELKU]; KÔCHI: Tosashimizu-shi, Shimonokae, 4.VII.1999, Y. Kawakami leg. [1♂ EUMJ], 10.VII.1999 [1♀ EUMJ], 19.VIII.2000 [4♀ EUMJ], 20.VIII.2000 [1♀ EUMJ], 16.VI.2001 [18♂7♀ EUMJ], 16.VI.2002 [21♂1♀ EUMJ], 21.IX.2003 [3♀ EUMJ], 5.X.2003 [1♀ EUMJ], 4.VII.2004 [4♀ EUMJ], 16.VI.2006 [1♀ EUMJ], 5.VII.2007 [16♂5♀ EUMJ], 8.VII.2007 [1♂3♀ EUMJ], 12.VII.2007 [5♂ EUMJ], 11.VII.2009 [18♂5♀ EUMJ], 13.VII.2009 [3♂1♀ EUMJ]; Tosashimizu-shi, Shimonokae, 15.VI.2002, T. Befu leg. [1♂1♀ OMNH]; Tosashimizu-shi, Shimonokae, beach, 32.861°N 132.953°E, 10.VIII.2020, J. Okayasu leg. [1♀ EUMJ]; Tosashimizu-shi, Shimonokae-kaigan Beach, 32°51'42.8"N 132°57'16.7"E, 6.VII.2022, 18:35, J. Okayasu leg. [1♀ SEHU], 7.VII.2022, 7:45–13:45, J. Okayasu leg. [18♂41♀ SEHU]; Shimanto-shi, Nashishi, 29.VIII.1999, Y. Kawakami leg. [2♀ EUMJ], 17.VI.2001 [4♂2♀ EUMJ]; Kuroshio-chô, Ideguchi, 25.VI.2000, Y. Kawakami leg. [1♂2♀ EUMJ], 1.X.2000 [2♀ EUMJ], 10.VI.2001 [1♂ EUMJ], 17.VI.2001 [1♂ EUMJ]; Shimanto-chô, Okitsu, 20.VII.2014, Y. Kawakami leg. [6♂1♀ EUMJ]; KUMAMOTO: Amakusa, Tomioka–Shiki, 16.VI.1931, Esaki & Hori leg. [3♀ ELKU]; Amakusa, Tomioka–Shiki, Esaki & Hori leg., 19.VI.1931, *Smicromyrme wotani* (Zavattari), B. Petersen det. 1981 [7♀ ELKU, ZMUC]; Amakusa, Tomioka–Tororo, 18.VI.1931, Esaki & Hori leg. [1♀ ELKU]; KYÔTO: Kyôtango-shi, Amino-chô, Kotobiki-hama, 35°42′14″N 135°3′23″E, 5.VIII.2007, R. Matsumoto leg. [4♂2♀ OMNH]; MIYAZAKI: Aoshima, on the grassland, 12.VIII.1953, H. Nagase leg. [1♂ MNHAH]; Kushima-shi, Ichiki, Ishinami-kaigan, 31.4702°N 131.3619°E, 9.VII.2018, R. Matsumoto leg. [4♂ OMNH]; NIIGATA: Shibata-shi [1♂ NSMT]; OSAKA: Osaka Prefectural Nature Park, 28.IX.2007, R. T. leg. [1♀ OMNH]; ÔSUMI ISLANDS: Tanegashima Island, Nakatane-chô, estuary of Ôura-gawa river, on the sandy ground, 30.VII.1982, H. Kaburaki leg. [1♂ MNHAH]; Tanegashima Island, Hamada, 2.VIII.1984, Sk. Yamane leg. [1♂ IEBR, 2♀ MTC]; SAGA: Karatsu, 14.IX.1937, E. Sueusou leg. [2♀ ZMUC]; SHIMANE: Hamada-shi, Iwami seaside park, 19.VIII.2015, H. Yoshitomi leg. [1♀ EUMJ]; Hamada-shi, 14.VIII.2016, T. Miyamoto leg. [1♀ EUMJ]; Izumo, Sashiumi, 18.VIII.2016, H. Yoshitomi leg. [1♀ EUMJ]; Izumo-shi, Sashiumi, 35°20.234′N 132°39.909′E, 16–17.VII.2017, H. Yoshitomi leg. [1♂2♀ EUMJ]; SHIZUOKA: Hamamatsu-shi, Nakatajima-sakyû, on sandy ground, 26.IX.1985, N. Toda leg. [1♀ EUMJ]; TOTTORI: Tottori-shi, Hamasaka, 30 m alt., VIII.1946, H. Aoki leg. [1♀ OMNH (N000003301)], 34.5402°N 134.1992°E, 14.VII.2013, R. Matsumoto leg. [1♂ OMNH]; Sand hill, 13.VII.1983, T. Ishikawa leg. [2♀ EUMJ]; Tottori-city, Tottori sand dunes, 27.VI.2011, Y. Fukuda leg. [1♀ EUMJ]; Tottori-shi, Hamasaka, Tottori Sand Dune, Ichirimatsu, 35°32'08.9"N 134°13'23.3"E, 67 m alt., dune with sparse vegetation, 1.VII.2022, 19:10–19:45, J. Okayasu leg. [8♀ SEHU], 2.VII.2022, 6:45–9:00 [4♀ SEHU], 2.VII.2022, 18:05–19:45, J. Okayasu leg. [1♂10♀ SEHU].

Distribution

Japan: Aichi, Chiba, Ehime, Fukui (Tsuneki, 1972a; Lelej, 1995), Fukuoka, Gotô Islands, Hyôgo, Iki Islands, Kagoshima, Kôchi, Kumamoto, Kyôto, Miyazaki, Niigata, Osaka, Ôsumi Islands, Saga, Shimane, Shizuoka, Tochigi (Tsuneki, 1972a), Tottori.

Sex association

This species was initially described from the female only. The male was associated by Lelej (1995) and Lelej & Yamane (1992) based on males and females collected at the same place and time in Japan. Mating pairs were obtained in captivity and in the field in the present study.

Remarks

The main habitats of this species are beaches and sand dunes with scattered low vegetation (Figs 10B–10D). Okayasu (2020) examined four potential paratypes with an identical locality label deposited in ELKU, TARI, and ZMUC. After this study, true paratype with appropriate labels was discovered from ELKU.

Key to East Asian species of *Nemka*

The following eight species of *Nemka* are recognized in East Asia: *N. conjungenda* (Magretti, 1892) (Myanmar, Thailand), *N. kellyi* (Pagden, 1934) (Malaysia), *N. limi* (Chen, 1957) (China), *N. pagdeni* Lelej, 1995 (China, Thailand), *N. taiwanensis* (Mickel, 1933) (Taiwan), *N. viduata* (Pallas, 1773) (northern Africa, Europe, Middle East, Central Asia, western Russia, and reaches Mongolia and Xingjiang, China; see Pagliano *et al*., 2020), *N. wotani* (Zavattari, 1913) (Taiwan) and *N. yasumatsui* (Mickel, 1936) (Japan). All of these species are now known from both sexes. *Nemka viduata* is classified into six subspecies: *N. v. andalusiana* (Skorikov, 1935), *N. v. bartholomaei* (Radoszkowski, 1865), *N. v. insulae* (Invrea, 1940), *N. v. macquarti* (Lepeletier, 1845), *N. v. tunensis* (Fabricius, 1804), and the nominotypical subspecies (see Lelej, 1985, 2002 and Petersen, 1988 for review). The East Asian population is assigned to the nominotypical subspecies (Lelej, 1995).

Most of the diagnostic characters for females of *N. pagdeni* recognized by Lelej (1995) are not included in the key because they are considered as intraspecific variation. The absence of pale setal spots on T4 and T5 is used to separate *N. pagdeni* from *N. kellyi* here. Sex association for *N. pagdeni* was made based on males and females collected in Yunnan, China, where only one species of this genus has been discovered (Lelej, 1995). Additional sampling or molecular studies might identify the true female of *N. pagdeni* and find that *N. pagdeni* females sensu Lelej (1995) are identical with *N. kellyi*.

Males of the East Asian species are recognized in *Nemka* by having the metasoma with some posterior segments black or entirely black except *N. conjungenda* which is the only species with the mesosoma red and metasoma black. Females are recognized by the T2 with posterior band medially triangularly widened.

1. Male: head with ocelli; 11 flagellomeres; alate … 2
- Female: head without ocelli; 10 flagellomeres; apterous ... 9
2 (1). Mesosoma black … 3
- Mesosoma red and ventrally black … ***N. conjungenda*** (Magretti)
3 (2). Clypeus without subapical tubercles and basal and subbasal denticles … 4
- Clypeus with a pair of subapical tubercles (Figs 8A–8D) and basal and subbasal denticles … 5
4 (3). Metasomal segments 2–3 or T4 red; T3–4 with pale setal fringes; cuspis as long as paramere … ***N. pagdeni*** Lelej
- Metasomal segment 2 red or entirely black; T3–4 with pale setal bands; cuspis shorter than paramere … ***N. viduata*** (Pallas)
5 (3). Meso- and metascutellum with sparse pale golden to golden setae; metasomal segments 1–3 or 4 red … 6
- Meso- and metascutellum with dense appressed and sparse erect pale golden setae; metasomal segments 2–6 red … ***N. kellyi*** (Pagden)
6 (5). Clypeus with subapical tubercle rounded (Figs 8A, 8C, 8D) … 7
- Clypeus with subapical tubercle narrow (Fig. 8B) … ***N. taiwanensis*** (Mickel)
7 (6). Gena with dense punctures (Figs 8E, 8H); lateral face of pronotum entirely rugoso-punctate (Figs 9E, 9H); mesopleural ventral tubercle laterally depressed (Figs 8E, 8H) … 8

- Gena with sparse punctures (Fig. 7G); lateral face of pronotum posteriorly puncto-striate (Fig. 9G); mesopleural ventral tubercle laterally flattened (Fig. 8G) … ***N. wotani*** (Zavattari)

8 (7). Dorsal pronotal face with recumbent pale setae anteriorly short and posteriorly long, providing thicker setation on posterior half (Fig. 9A); metasomal segments 1–4 yellowish red … ***N. limi*** (Chen)

- Dorsal pronotal face with recumbent pale setae short throughout, providing sparser setation (Fig. 9D); metasomal segments 1–3 yellowish red … ***N. yasumatsui*** (Mickel)

9 (1). Pygidial plate striate throughout … 10

- Pygidial plate striate on anterior 4/5–5/6 and smooth or granulate posteriorly (Figs 3–3H) … 11

10 (9). Frons with sparse setae; T2 with confluent punctures; T6 with pale setae … ***N. conjungenda*** (Magretti)

- Frons with pale spot of dense appressed setae; T2 with dense but separated punctures; T6 with black setae … ***N. viduata*** (Pallas)

11 (9). Vertex puncto-reticulate; eye length more than 2× malar distance; pygidial plate posterior portion granulate … 12

- Vertex with dense but separated punctures; eye length ~2× malar distance; pygidial plate posterior portion smooth … 13

12 (11). T4–5 with lateral patch of golden setae … ***N. kellyi*** (Pagden)

- T4–5 with few pale setae laterally … ***N. pagdeni*** Lelej

13 (12) Frons punctures close even medially (Figs 3A, 3B) … 14

- Frons punctures laterally close and medially separated (Figs 3C, 3D) … 15

14. Scutellar scale posterior margin truncate (Fig. 4A) … ***N. limi*** (Chen)

- Scutellar scale posterior margin emarginate medially (Fig. 4B) … ***N. taiwanensis*** (Mickel)

15 (14). Species from Taiwan … ***N. wotani*** (Zavattari)

- Species from Japan … ***N. yasumatsui*** (Mickel)

Body size analysis

Body length of the paratype of *N. curvisquamata* measured here was 13.3 mm, and the length of the holotype was obtained from Chen (1957). Body size distribution and range were different between species and also sexes (Table 3). Intraspecific seasonal or geographical variation of body size was not observed. *Nemka limi* and *N. yasumatsui* exhibited wide range of variation, with bimodal distribution in males and unimodal distribution in females (Figs 11–14, 18. 19). Silverman's test could not reject bimodality of male body size and unimodality of female body size with *p* values of over 0.4 (Table 4; Izenman & Sommer, 1988). In contrast, *N. taiwanensis* and *N. wotani* were less variable and exhibited unimodal distribution in both sexes (Figs 11, 12, 15–17). *Nemka taiwanensis* was larger than *N. wotani* in both sexes, with little overlap in body size range.

Discussion

The species of *Nemka* are known to inhabit sandy areas like beaches and sand dunes (Alicata *et al*., 1974; Bogusch, 2006; József & Zoltán, 2011; Lelej, 1995; Matteini Palmerini, 2013; Okayasu, 2020; Pagden, 1934b; Polidori *et al*., 2010; Figs 10B–10E). Hosts of only two species, *N. viduata* and *N. yasumatsui*, have been confirmed, while the biology of other species of *Nemka* is mostly unknown, except that potential hosts of *N. aurantiaca* (Skorikov, 1935) and *N. kellyi* were detected (Table 5). Nevertheless, published host records, together with the pectinate protarsus and the defined pygidial plate of females (Krombein, 1972;

Williams *et al*., 2011), suggest that *Nemka* species are likely to utilize various ground-nesting apoid wasps as their hosts.

Four species of *Nemka* treated in the present study and *N. kellyi* are considered to form a monophyletic group. The subapical paired tubercles and basomedial denticles on the clypeus, and S7 with medial tubercle of the males are unique synapomorphies supporting this hypothesis. Females of *N. limi*, *N. taiwanensis*, *N. wotani*, and *N. yasumatsui* have the pygidial plate posteriorly smooth. This is probably a derived character state in *Nemka*, because other species of the genus have the pygidial plate striate throughout, or striate anteriorly and guranulate or subrugulose posteriorly. These character states suggest that those four species form a monophyletic group.

Of these four *Nemka* species, *N. yasumatsui* is the only species for which the host was recorded (Table 5). Ono & Kawashima (2013) reared one male of this species (misidentified as *N. wotani*) from a cocoon of *Bembix niponica* Smith (Crabronidae). Therefore, *N. limi*, *N. taiwanensis*, and *N. wotani* probably parasitize on immature stages of sand wasps of the genera *Bembecinus* Costa, *Bembix* Fabricius, *Gorytes* Latreille, or *Stizus* Latreille. Hypothetically, those *Nemka* species are ecological equivalents occupying similar ecological niches.

Given that velvet ants are normally solitary parasitoids (Brothers, 1989), bimodal distribution and wide range of body size in males of *N. limi* and *N. yasumatsui* suggest utilization of multiple hosts with different body size rather than occasional gregarious parasitism. Larger individuals probably had emerged from *Bembix* sand wasps, specifically *Bembix niponica*. At Shimonokae Beach (Figs 10B, 10C), Japan, where numerous specimens of *N. yasumatsui* had been collected, the following sand-nesting wasps and bees were also collected by me and Y. Kawakami: *Anoplius* (*Arachnophroctonus*) *reflexus* (Smith), *Pompilus cinereus* (Fabricius) (Pompilidae), *Bembecinus hungaricus* (Frivaldsky), *Cerceris albofasciata* (Rossi), *C. arenaria yanoi* Tsuneki, *Tachysphex nigricolor nigricolor* (Dalla Torre) (Crabronidae), *Megachile* (*Eutricharaea*) *kobensis* Cockerell (Megachilidae) with a number of *Bembix niponica* specimens (voucher specimens in EUMJ). At Kotobiki-hama Beach, Japan, where four males and two females of *N. yasumatsui* were collected, the following potential hosts were also recorded: *A. reflexus*, *P. cinereus*, *Bembecinus hungaricus*, *Bembix niponica*, *T. n. nigricolor*, and *M. kobensis* (Nakao *et al*., 2014). At Tottori Sand Dune, Tsurusaki *et al*. (2012) recorded *N. yasumatsui* (as *N. wotani*) together with the following potential hosts: *A. reflexus*, *P. cinereus*, *Bembecinus hungaricus*, *Bembix niponica*, *C. japonica* Ashmead, and *M. kobensis*.

Contrarily to males, *N. limi* and *N. yasumatsui* exhibited unimodal distribution of body size in females. Small body size of female velvet ants is regarded as an adaptation to utilization of variable hosts since large females may have difficulty when intruding into the nests of burrowing hosts (Deyrup & Manley, 1986). On the other hand, larger females have an advantage in the amount of egg production and storage (Honěk, 1993; Hurlbutt, 1987; Lawrence, 1981; Narasimham, 1984; O'Neill, 1985; van den Assem *et al*., 1989). Therefore, unimodal distribution of female body size is considered to be formed by the relatively low fitness of too small or too large individuals (i.e., stabilizing selection). Judging from the male size variation depending on the size of utilized hosts, female unimodal size distribution implies facultative host-size dependent sex allocation by egg-lying females (Pitts *et al*., 2010a). In males, larger individuals are advantageous in patrolling for mate searching, displacing smaller males and carrying females during scramble competition and mating, while smaller males are advantageous in rapid allocation of mates (Polidori *et al*., 2013a; Stone *et al*., 1995). Overall, body size distribution of *N. limi* and *N. yasumatsui* suggests that females more frequently emerge from smaller hosts and males from both smaller and larger hosts.

Unimodal distribution and narrow range of body size of *N. taiwanensis* and *N. wotani* in both sexes imply strict preference to particular hosts with similar body size, despite of the wide host range common in velvet ants. The larger species, *N. taiwanensis* likely parasitizes on larger hosts than those of *N. wotani*.

Nemka limi and *N. yasumatsui* are distributed in eastern margin of China mainland and Japan, respectively, where only one species of the genus has been recorded. *Nemka wotani* is widespread in Taiwan, while *N. taiwanensis* has fewer distributional records (Fig. 10A). However, interestingly, these Taiwanese species apparently share same geographical ranges since both of them were collected at Chihpen, Taitung. Therefore, they are potential competitors occupying similar ecological niches. The diverged host usage is the approximate factor that enables sympatric distribution of *N. taiwanensis* and *N. wotani*. This phenotypic divergence is regarded as ecological character displacement and also resource partitioning.

Body size variation is sometimes connected with mate recognition and mechanical function during mating in animals (Okuzaki *et al*., 2010; Pfennig & Pfennig, 2005). Pfennig & Pfennig (2005) provided empirical evidence that reproductive interference can invoke body size divergence in animals. In velvet ants (especially in *Nemka*), scramble competition by multiple males (up to 16) for only one female is sometimes observed (Brothers, 1989; Fattig, 1936; Matteini Palmerini, 2013; Polidori *et al*., 2013a). Additionally, female velvet ants are likely monandrous (Bayliss & Brothers, 1996, 2001; Bergamaschi *et al*., 2010; Brothers, 1972; Linsley *et al*., 1955; Mickel, 1938; Tormos *et al*., 2010). Reproductive interference can thus largely reduce females' fitness when sexually interacting species occur sympatrically. However, body size is unlikely to work as a signal for mate recognition, because visual cues are not used for female detection by males (VanderSal-Jensen *et al*., 2016). Additionally, body size does not seem to possess a mechanical function to hinder interspecific copulation, since two allopatric *Nemka* species (*N. limi* and *N. yasumatsui*) show wide range of variation in both sexes. In general, copulation can be done between a male and a female with totally different body size of the same species (Brothers, 1989), and no empirical evidence that large males preferentially mate with large females (or *vice versa*) has been known (Brothers, 2015).

Also, differentiation in host choice, which determines body size of adult velvet ants, cannot mitigate reproductive interference, because strict preference of *Nemka* species to sandy environment does not allow parapatric or allopatric distribution. In actuality, *N. taiwanensis* and *N. wotani* exhibit perfect sympatry in Taiwan. Given that their morphological differences are maintained, *N. taiwanensis* and *N. wotani* are considered to be completely isolated reproductively.

I conclude that 1) body size divergence in *N. taiwanensis* and *N. wotani* is a consequence of resource competition and 2) biochemical or behavioral factors, like pheromone, cuticular hydrocarbons, and stridulation (Matteini Palmerini, 2013; Polidori *et al*., 2013bc; Tormos *et al*., 2010; VanderSal-Jensen *et al*., 2016), probably enable reproductive isolation of these two species. Future studies should confirm 1) actual hosts, 2) facultative size-dependent sex allocation, (3) sexual interactions between two Taiwanese *Nemka* species, and (4) mate recognition cues. Field observation of mating and oviposition, rearing experiments, and analyses of gene flow and cuticular hydrocarbons would be also useful.

According to Schluter (2000), at least 25 cases of ecological character displacement caused by resource competition between sympatric but distantly related organisms were reported (e.g. Schluter, 1986; Yom-Tov, 1993). Recently, Komine *et al*. (2019) tested the effect of competition for food resource on character displacement by using sympatric and allopatric populations of two non-congeneric frogs to exclude an influence of reproductive interference. They emphasized the usefulness of non-congeners to evaluate ecological

character displacement. In the present paper, I demonstrated that resource competition between congeneric species can lead to ecological character displacement when 1) reproductive isolation is completed (including subsequent reinforcement after secondary contact), 2) two sympatric species have strict adherence to particular environment or spatial location, and 3) ancestral populations of sympatric species have high plasticity to resource use, namely wide preference and alternative resources.

Currently, we know little about host-parasitoid association and interspecific interactions in velvet ants. Coexistence of congeneric species is still a mystery of this insect. Many of the published host records are based on Nearctic or Palaearctic species; our knowledge on the parasitism of tropical and subtropical velvet ants is even more inadequate. Brothers (1989) stated that "Many species have been recorded from a single host only, but that may be more a function of our inadequate knowledge than a reflection of the true situation." This might be true in many cases. However, I anticipate that ecological character displacement, accompanied with resource partitioning, may be more common in coexisting tropical velvet ants like two Taiwanese *Nemka* species. Another type of negative species interaction, reproductive interference, can also have great influence on the formation of biogeographical patterns of velvet ants, given the severe mating competition by males. Many factors affecting this interaction are mostly unknown for velvet ants, such as sex ratio, relative population size, mechanism of reproductive isolation, frequency and intensity of interspecific sexual interaction, and sterility of hybrid offspring. Finally, I emphasize that systematic bases are essential to elucidate the formation of biogeographical patterns observed in related species-complex of organisms.

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References

Alicata, P., Caruso, D., Costa, G. & Mota, S. (1974) Ricerche eco-etologiche sulla fauna delle dune costiere di Porto Palo (Siracusa). — I. *Smicromyrme viduata* (Pall.) (Hymenoptera, Mutillidae): Ritmi di attivita, migrazioni e accoppiamnto. *Animalia* 1 (1/3): 89–108.

André, E. (1899–1903) *Species des Hyménoptères d'Europe & d'Algérie*. *Tome Huitième*. *Les Mutillides*. Vve Dubosclard and A. Hermann, Paris, 480 pp. + 15 pls. [1–64 + pl. 1–8 (1899); 65–144 (1900); 145–304 (1901); 305–384 (1902a); 385–478 (1903); pl. 9–15 (date unknown).

Ashmead, W.H. (1899) Superfamilies in the Hymenoptera and generic synopses of the families Thynnidae, Myrmosidae, and Mutillidae. *Journal of the New York Entomological Society* 7: 45–60.

Bayliss, P.S. & Brothers, D.J. (1996) Biology of *Tricholabiodes* Radoszkowski in Southern Africa, with a new synonymy and review of recent biological literature (Hymenoptera: Mutillidae). *Journal of Hymenoptera Research* 5: 249–258.

Bayliss, P.S. & Brothers, D.J. (2001) Behaviour and host relationships of *Dolichomutilla sycorax* (Smith) (Hymenoptera: Mutillidae, Sphecidae). *Journal of Hymenoptera Research* 10 (1): 1–9.

de Beaumont, J. (1951) Hyménoptères récoltés par une mission suisse au Maroc (1947). Sphecidae 1. *Bulletin de la Société des Sciences Naturelles et Physiques du Maroc* 29: 259–284.

Bergamaschi, A.C.B., Cambra, R. & Melo, G.A.R. (2010) Male description and host record for *Lophomutilla corupa* Casal, 1968 (Hymenoptera: Mutillidae), with behavioural notes on mating behaviour and host nest attacks. *Journal of Natural History* 44 (43): 2597–2607. https://doi.org/10.1080/00222933.2010.499574

Boehme, N.F., Tanner, D.A., Williams, K.A. & Pitts, J.P. (2012) Faunal study of velvet ants (Hymenoptera: Mutillidae) and their activity patterns and habitat preference at Ash Meadows National Wildlife Refuge, Nye County, Nevada, USA. *Zootaxa* 3587 (1): 1–45. https://doi.org/10.11646/zootaxa.3587.1.1

Bogusch, P. (2006) The velvet ants (Hymenoptera: Mutillidae) of the Czech Republic and Slovakia: an identification key and annotated checklist. *Acta Musei Moraviae, Scientiae biologicae* 91: 103–148.

Brothers, D.J. (1972) Biology and immature stages of *Pseudomethoca f. frigida*, with notes on other species (Hymenoptera: Mutillidae). *The University of Kansas Science Bulletin* 50 (1): 1–38.

Brothers, D.J. (1978) Biology and immature stages of *Myrmosula parvula* (Hymenoptera: Mutillidae). *Journal of the Kansas Entomological Society* 51 (4): 698–710.

Brothers, D.J. (1989) Alternative life-history styles of mutillid wasps (Insecta, Hymenoptera). *In*: Bruton, M.N. (ed.) *Alternative life-history styles of animals. Perspectives in vertebrate sciences 6*. Springer, Dordrecht, pp. 279–291. https://doi.org/10.1007/978-94-009-2605-9_14

Brothers, D.J. (2015) Revision of the Rhopalomutillinae (Hymenoptera, Mutillidae): 1, generic review with descriptions of three new genera. *Journal of Hymenoptera Research* 46: 1–24. https://doi.org/10.3897/JHR.46.5733

Brown, W.L. & Wilson, E.O. (1956) Character displacement. *Systematic Zoology* 5 (2): 49–64. https://doi.org/10.2307/2411924

Chen, C.-w. (1957) A revision of the velvety ants or Mutillidae of China (Hymenoptera). *Quarterly Journal of the Taiwan Museum* 10 (3-4): 135–224 + 6pls.

Chu, Y.-i. & Yamanaka, T. (1973–1975) A check list of the present and old name of insect collected localities in Taiwan. *Journal of the National Taiwan Museum* 16: 31–72 (1973); 17: 51–75 (1974); 18: 121–150 (1975).

Cockerell, T.D.A. (1894) Descriptions of new Hymenoptera. *Entomological News* 5: 199–201.

Cresson, E.T. (1865) Catalogue of Hymenoptera in the collection of the Entomological Society of Philadelphia, from Colorado Territory. *Proceedings of the Entomological Society of Philadelphia* 4: 428–442.

Deyrup, M. & Manley, D. (1986) Sex-biased size variation in velvet ants (Hymenoptera: Mutillidae). *Florida Entomologist* 69 (2): 327–335.

Fabricius, J.C. (1804) *Systema Piezatorum secundum Ordines, Genera, Species adjectis Synonymis, Locis, Observationibus, Descriptionibus*. Carolum Reichard, Brunsvigae, pp. i–xiv + 15–440 + 1–30. https://doi.org/10.5962/bhl.title.10490

Fales, H.M., Jaouni, T.M., Schmidt, J.O. & Blum, M.S. (1980) Mandibular gland allomones

of *Dasymutilla occidentalis* and other mutillid wasps. *Journal of Chemical Ecology* 6: 895–903. https://doi.org/10.1007/BF00990473
Fattig, P.W. (1936) An unusual mating of velvet ants (Hymen.: Mutillidae). *Entomological News* 47: 51–52.
Ferguson, W.E. (1962) Biological characteristics of the mutillid subgenus *Photopsis* Blake and their systematic values. *University of California Publications in Entomology* 27: 1–92.
Fox, W.J. (1899) The North American Mutillidae. *Transactions of the American Entomological Society* 25: 219–300.
Gall, B.G., Spivey, K.L., Chapman, T.L., Delph, R.J., Brodie, E.D. Jr. & Wilson, J.S. (2018) The indestructible insect: Velvet ants from across the United States avoid predation by representatives from all major tetrapod clades. *Ecology and Evolution* 8 (11): 5852–5862. https://doi.org/10.1002/ece3.4123
Gôukon, K. (1993) Host records and some bionomical notes on mutillid wasps in Japan (Hymenoptera, Mutillidae). *Chugoku Kontyu* 7: 35–40. (in Japanese)
Grandi, G. (1961) Studi di un Entomologo Sugli Imenotteri Superiori. *Bolletino dell'Instituto di Entomologia della Università Degli Studi di Bologna* 25: i–xv + 1–659.
Gröning, J. & Hochkirch, A. (2008) Reproductive interference between animal species. *The Quarterly Review of Biology* 83 (3): 257–282. https://doi.org/10.1086/590510
Hardin, G. (1960) The competitive exclusion principle. *Science* 131 (3409): 1292–1297. https://doi.org/10.1126/science.131.3409.1292
Hashimoto, Y. & Nakanishi, A. (1997) *A list of the type-specimens of Hymenoptera described by K. Tsuneki in the Museum of Nature and Human Activities, Hyogo (MNHAH)*. Catalogue of collections in the Museum of Nature and Human Activities, Hyogo No. 2. Museum of Nature and Human Activities, Sanda, 47 pp. + 8 pls.
He, J.-H., Chen, X.-X., Fan, J.-J., Li, Q., Liu, C.-M., Lou, X.-M., Ma, Y., Wang, S.-F., Wu, Y.-R., Xu, Z.-H., Xu, Z.-F. & Yao, J. (2004) *Hymenopteran insect fauna of Zhejiang*. Science Press, Beijing, lvi + 1373 pp. + 43 pls. (in Chinese)
Heaversedge, R.C. (1968) Variation in the size of insect parasites of puparia of *Glossina* spp. *Bulletin of Entomological Research* 28 (1): 153–158. https://doi.org/10.1017/S0007485300055930
Hochkirch, A., Gröning, J. & Bücker, A. (2007) Sympatry with the devil: reproductive interference could hamper species coexistence. *Journal of Animal Ecology* 76 (4): 633–642. https://doi.org/10.1111/j.1365-2656.2007.01241.x
Honěk, A. (1993) Intraspecific variation in body size and fecundity in insects: a general relationship. *Oikos* 66: 483–492.
Hua L-z (2006) *List of Chinese insects Vol. IV*. Sun Yat-sen University Press, Guangzhou, 540 pp.
Hurlbutt, B. (1987) Sexual size dimorphism in parasitoid wasps. *Biological Journal of the Linnean Society* 30 (1): 63–89. https://doi.org/10.1111/j.1095-8312.1987.tb00290.x
Hymenoptera Anatomy Consortium (2024) Hymenoptera glossary. Available from: http://glossary.hymao.org (accessed on 19 February 2024)
Invrea, F. (1940) Mutillidi dell'isola di Cipro raccolti dal Sig. G.A. Mauromoustakis. *Bollettino della Società entomologica italiana* 72: 118–122.
Izenman, A.J. & Sommer, C.J. (1988) Philatelic mixtures and multimodal densities. *Journal of the American Statistical Association* 83: 941–953. https://doi.org/10.2307/2290118
József, M. & Zoltán, G. (2011) Velvet ants of Hungary (Hymenoptera: Mutillidae). *Natura Somogyiensis* 18: 1–198.
Kojima, J., Saito, F. & Nguyen, L.T.P. (2011) On the species-group taxa of Taiwanese social wasps (Hymenoptera: Vespidae) described and/or treated by J. Sonan. *Zootaxa* 2920:

42–64. http://dx.doi.org/10.11646/zootaxa.2920.1.2
Komine, H., Watari, Y. & Kaji, K. (2019) Ecological character displacement in non-congeneric frogs. *Zoological Science* 36: 410–416. https://doi.org/10.2108/zs190037
Konuma, J. & Chiba, S. (2007) Ecological character displacement caused by reproductive interference. *Journal of Theoretical Biology* 247 (2): 354–364. https://doi.org/10.1016/j.jtbi.2007.03.013
Krombein, K.V. (1972) Monograph of the Madagascan Mutillidae (Hymenoptera). Part I: Myrmillini, Mutillini and Smicromyrmini. *Annales, Musée Royal de l'Afrique Centrale*, Série in 8°, Sciences Zoologiques 199: I–X + 1–61.
Krombein, K.V. (1981) Biosystematic studies of Ceylonese wasps, VIII: A monograph of the Philanthidae (Hymenoptera: Sphecoidea). *Smithsonian Contributions to Zoology* 343: i–iii + 1–75. https://doi.org/10.5479/si.00810282.343
Kusuhashi, N. & Okamoto, T. (2015) A nonparametric multimodality test —Silverman's test— and its introduction into paleontology. *Fossils* 97: 23–37. (in Japanese)
Lawrence, P.L. (1981) Interference competition and optimal host selection in the parasitic wasp, *Biosteres longicaudatus*. *Annals of the Entomological Society of America* 74 (6): 540–544. https://doi.org/10.1093/aesa/74.6.540
Lelej, A.S. (1985) *Osy-nemki (Hymenoptera, Mutillidae) Fauny SSSR i Sopredelnykh Stran* [*The velvet ants (Hymenoptera, Mutillidae) of the USSR and neighboring countries*]. Nauka, Leningrad, 268 pp. (in Russian)
Lelej, A.S. (1995) A review of Palaearctic and Oriental species of genus *Nemka* Lelej with description of Oriental genus *Mickelomyrme* gen. n. (Hymenoptera, Mutillidae). *Far Eastern Entomologist* 6: 1–20.
Lelej, A.S. (1996a) To the knowledge of the East Asian species of the tribe Trogaspidiini Bischoff, 1920 (Hymenoptera, Mutillidae) with description of eight new genera and two new species. *Far Eastern Entomologist* 30: 1–24.
Lelej, A.S. (1996b) A review of the East Asian species of *Mickelomyrme* Lelej, 1995 (Hymenoptera, Mutillidae). *Entomofauna* 17 (15): 277–292.
Lelej AS (2002) *Catalogue of the Mutillidae (Hymenoptera) of the Palaearctic Region*. Dalnauka, Vladivostok, 172 pp.
Lelej AS (2005) *Catalogue of the Mutillidae (Hymenoptera) of the Oriental Region*. Dalnauka, Vladivostok, 252 pp.
Lelej, A.S., Choi, J.Y. & Tripotin, P. (2001) Review of the mutillid wasps (Hymenoptera, Mutillidae) of Korea. *Far Eastern Entomologist* 96: 1–15.
Lelej, A.S. & Yamane, Sk. (1992) Interesting velvet ants (Hymenoptera, Mutillidae) from Japan and Korea. *Japanese Journal of Entomology* 60 (3): 625–632.
Lepeletier de Saint-Fargeau, A. (1845) *Histoire naturelle des Insectes*. *Hyménoptères*. Tome Troisième. Roret, Paris, [4] + 646 pp. https://doi.org/10.5962/bhl.title.9005
Lichtenstein, J. (1878) Lucilia bufonivora. *La feuille des jeunes naturalistes: revue mensuelle d'histoire naturelle* 8: 35.
Lin, N. (1964) Increased parasitic pressure as a major factor in the evolution of social behavior in halictine bees. *Insectes Sociaux* 11: 187–192.
Linnaeus C (1758) *Systema Naturae per Regna Tria Naturae, secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis*. *Tomus I. Editio Decima Reformata*. Laurentii Salvii, Holmiae, [4] + 823 pp. + [5]. https://doi.org/10.5962/bhl.title.559
Linsley, E.G., MacSwain, J.W. & Smith, R.F. (1955) Observations on the mating habits of *Dasymutilla formicalia* Rohwer (Hymenoptera: Mutillidae). *The Canadian Entomologist* 87 (9): 411–413. https://doi.org/10.4039/Ent87411-9
Lo Cascio, P. (2015) Worldwide checklist of the island mutillid wasps (Hymenoptera

Mutillidae). *Biodiversity Journal* 6 (2): 529–592.
Losos, J.B. (2000) Ecological character displacement and the study of adaptation. *Proceedings of the National Academy of Sciences* 97 (11): 5693–5695. https://doi.org/10.1073/pnas.97.11.5693
Magretti, P. (1892) Viaggio di Leonardo Fea in Birmania e regioni vicine XLIII. Imenotteri. Parte prima. Mutillidei, Scoliidei, Tifiidei, Tinnidei colla descrizione di parecchie nuove specie. *Annali del Museo Civico di Storia Naturale di Genova* 2 (12): 197–266 + 1 pl.
Manley, D.G. & Pitts, J.P. (2007) Tropical and subtropical velvet ants of the genus *Dasymutilla* Ashmead (Hymenoptera: Mutillidae) with descriptions of 45 new species. *Zootaxa* 1487: 1–128. https://doi.org/10.11646/zootaxa.1487.1.1
Manley, D.G. & Taber, S. III (1978) A mating aggregation of *Dasymutilla foxi* in Southern Arizona. *The Pan-Pacific Entomologist* 54 (3): 231–235.
Marikovskaya, T.P. (1968) [New data on the biology of some species of social bees (Hymenoptera, Megachilidae) from southeast Kazakhstan]. *Entomologicheskoe Obozrenie* 47 (4): 796–805. (in Russian). [English translation (1968) in *Entomological Review* 47: 487–491]
Martynova, K.V. & Martynov, A.V. (2021) New records of *Cerceris tuberculata* (Villers, 1787) (Hymenoptera: Crabronidae) from Ukraine, with notes on its parasitoids and prey. *Ukrainian Entomological Journal* 19 (1–2): 77–84. https://doi.org/10.15421/282105
Matsumura, S. (1931) *6000 illustrated insects of Japan-Empire*. Tôkô Shoin, Tokyo, 3pp. + 1497 pp. + 23 pp. + 10 pls. (in Japanese)
Matteini Palmerini, M. (2013) Remarks on the behavior of the velvet ant *Nemka viduata viduata* (Pallas, 1773). *Quaderno di studi e Notizie di Storia Naturale della Romagna* 37: 237–260.
Mickel, C.E. (1924) An analysis of a bimodal variation in size of the parasite *Dasymutilla bioculata* Cresson (Hymen.: Mutillidae). *Entomological News* 35: 236–242.
Mickel, C.E. (1928) Biological and taxonomic investigations on the mutillid wasps. *United States National Museum Bulletin* 143: ix + 1–351 + 5 pls. https://doi.org/10.5479/si.03629236.143.1
Mickel, C.E. (1933) The Mutillidae of Formosa. *Annals of the Entomological Society of America* 26 (2): 381–423. https://doi.org/10.1093/aesa/26.2.381
Mickel, C.E. (1935) The mutillid wasps of the islands of the Pacific Ocean (Hymenoptera, Mutillidae). *Transactions of the Royal Entomological Society of London* 83 (2): 177–312. https://doi.org/10.1111/j.1365-2311.1935.tb01207.x
Mickel, C.E. (1936) A new species of *Smicromyrme* from Japan (Mutillidae, Hymenoptera). *Mushi* 9 (1), 52–54.
Mickel, C.E. (1938) Photopsoid mutillids collected by Dr. K. A. Salman at Eagle Lake, California (Hymenoptera). *The Pan-Pacific Entomologist* 14 (4): 178–185.
Murota, T. (1977) [Wasps of Fukui Prefecture]. *Hymenopterists' Communication* 5: 5–7. (in Japanese)
Nagase, H. (2014) Family Megachilidae. *In*: Tadauchi, O. & Murao, R. (eds) *An illustrated guide to Japanese bees*. Bun-ichi Sogo Shuppan Co., Tokyo, pp. 269–331. (in Japanese)
Nagase, H., Harada, K., Ito, H. & Yago, M. (2014) Catalogue of the Masayo Kato insect collection, the University Museum, the University of Tokyo Part I. Hymenoptera. *The University Museum, The University of Tokyo Material Reports* 104: 5–189.
Nakao, S., Gôukon, K., Miyanaga, R., Shimizu, A., Masuda, R., Kawamura, T., Qian, C.C. & Haneda, T. (2014) Records of the aculeate wasps and bees living in Kotohikihama,

Kyoto Prefecture, Japan. *The scientific reports of Kyoto Prefectural University*. *Life and environmental sciences* 66: 25–29.
Narasimham, A.U. (1984) Comparative studies on *Tetrastichus hagenowii* (Ratzeburg) and *T. asthenogmus* (Waterston), two primary parasites of cockroach oothecae, and on their hyperparasite *Tetrastichus* sp. (*T. miser* (Nees) group) (Hymenoptera: Eulophidae). *Bulletin of Entomological Research* 74 (2): 175–189. https://doi.org/10.1017/S0007485300011329
Okayasu, J. (2020) Velvet ants of the tribe Smicromyrmini Bischoff (Hymenoptera: Mutillidae) of Japan. *Zootaxa* 4723 (1): 1–110. https://doi.org/10.11646/zootaxa.4723.1.1
Okayasu, J., Lelej, A.S. & Williams, K.A. (2021) Review of *Eotrogaspidia* Lelej (Hymenoptera: Mutillidae: Trogaspidiini). *Zootaxa* 4920 (1): 56–90. https://doi.org/10.11646/zootaxa.4920.1.2
Okayasu, J., Williams, K.A. & Lelej, A.S. (2018) A remarkable new species of the genus *Sinotilla* Lelej (Hymenoptera: Mutillidae: Smicromyrmini) from Taiwan and an overview of color diversity in East Asian mutillid females. *Zootaxa* 4446 (3): 301–324. https://doi.org/10.11646/zootaxa.4446.3.1
Okuzaki, Y., Takami, Y. & Sota, T. (2010) Resource partitioning or reproductive isolation: the ecological role of body size differences among closely related species in sympatry. *Journal of Animal Ecology* 79: 383–392. https://doi.org/10.1111/j.1365-2656.2009.01645.x
O'Neil, K.M. (1985) Egg size, prey size, and sexual size dimorphism in digger wasps (Hymenoptera: Sphecidae). *Canadian Journal of Zoology* 63 (9): 2187–2193. https://doi.org/10.1139/z85-323
Ono, H. & Kawashima, I. (2013) Host records on two species of mutillid wasps (Hymenoptera, Mutillidae) in Japan. *Tsunekibachi* 23: 41–42. (in Japanese)
Pagden, H.T. (1934a) New species of Mutillidae (Hymenoptera, Vespoidea) from the Malay Peninsula. *Journal of the Federated Malay States Museum* 17: 419–457.
Pagden, H.T. (1934b) Biological notes on some Malayan aculeate Hymenoptera II. with descriptions of new species. *Journal of the Federated Malay States Museums* 17: 467–486.
Pagden, H.T. (1949) Descriptions and records of Austro-Malaysian Methocidae and Mutillidae (Hymenoptera). *Transactions of the Royal Entomological Society of London* 100 (8): 191–231. http://doi.org/10.1111/j.1365-2311.1949.tb01431.x
Pagliano, G. (2011) I Mutillidae (Hymenoptera) della collezione Zavattari le collezioni del Museo Regionale di Scienze Naturali di Torino. *Bolletino del Musei Regionale di Scienze Naturali di Torino* 28 (1): 37–60.
Pagliano, G., Brothers, D.J., Cambra, R., Lelej, A.S., Lo Cascio, P., Matteini Palmerini, M., Scaramozzino, P.L., Williams, K.A. & Romano, M. (2020) Checklist of names in Mutillidae (Hymenoptera), with illustrations of selected species. *Bollettino del Museo Regionale di Scienze Naturali di Torino* 36 (1–2): 5–425.
Pallas, P.S. (1773) *Reisen durch verschiedene Provinzen des Russischen Reichs*. *Zweiter Theil*. *Zweites Buch vom Jahr 1771*. Kayserlichen Academie der Wissenschaften, St. Petersburg, [12] + 744 pp.
Pan, A.D., Williams, K.A. & Wilson, J.S. (2016) Are diurnal iguanian lizards the evolutionary drivers of New World female velvet ant (Hymenoptera: Mutillidae) Müllerian mimicry rings? *Biological Journal of the Linnean Society* 120 (2): 436–447. https://doi.org/10.1111/bij.12894
Petersen, B. (1988) The Palaearctic Mutillidae of I.C. Fabricius and some related material (Insecta, Hymenoptera, Aculeata). *Steenstrupia* 14 (6): 129–224.

Pfennig, K.S. & Pfennig, D.W. (2005) Character displacement as the ‘‘Best of a bad situation’’: fitness trade-offs resulting from selection to minimize resource and mate competition. *Evolution* 59 (10): 2200–2208.

Pfennig, K.S. & Pfennig, D.W. (2009) Character displacement: ecological and reproductive responses to a common evolutionary problem. *The Quarterly Review of Biology* 84 (3): 253–276. https://doi.org/10.1086/605079

Pitts, J.P., Parker, F. & Pitts-Singer, T.L. (2004) A review of the *Sphaeropthalma uro* species-group (Hymenoptera: Mutillidae), with taxonomic changes. *Journal of the Kansas Entomological Society* 77 (3): 222–234. https://doi.org/10.2317/0308.11.1

Pitts, J.P., Tanner, D., Waldren, G.C. & Paker, F.D. (2010a) Facultative size-dependent sex allocation in *Sphaeropthalma pensylvanica* Lepeletier (Hymenoptera: Mutillidae) with further host records. *Journal of the Kansas Entomological Society* 83 (1), 68–75. https://doi.org/10.2317/JKES0812.15.1

Pitts, J.P., Wilson, J.S. & von Dohlen, C.D. (2010b) Evolution of the nocturnal Nearctic Sphaeropthalminae velvet ants (Hymenoptera: Mutillidae) driven by Neogene orgeny and Pleistocene glaciation. *Molecular Phylogenetics and Evolution* 56 (1): 134–145. https://doi.org/10.1016/j.ympev.2010.03.033

Polidori, C., Beneitez, A., Asís, J.D. & Tormos, J. (2013a) Scramble competition by males of the velvet ant *Nemka viduata* (Hymenoptera: Mutillidae). *Behavior* 150: 23–37.

Polidori, C., Mendiola, P., Asís, J.D., Tormos, J. & Selfa, J. (2010) Temporal asynchrony and spatial co-occurrence with the host: the foraging patterns of *Nemka viduata*, a parasitoid of digger wasps (Hymenoptera: Mutillidae and Crabronidae). *Journal of Ethology* 28: 353–361. https://doi.org/10.1007/s10164-009-0196-2

Polidori, C., Pavan, G., Ruffato, G., Asís, J.D. & Tormos, J. (2013b) Common features and species-specific differences in stridulatory organs and stridulation patterns of velvet ants (Hymenoptera: Mutillidae). *Zoologischer Anzeiger* 252: 457–468. https://doi.org/10.1016/j.jcz.2013.01.003

Polidori, C., Ruffato, G., Borruso, L., Settanni, C. & Pavan, G. (2013c) Stridulatory organ and distress call in males and females of a small velvet ants (Hymenoptera: Mutillidae). *Bioacoustics* 22 (2): 121–135. https://doi.org/10.1080/09524622.2012.736241

Praz, C.J. (2017) Subgeneric classification and biology of the leafcutter and dauber bees (genus *Megachile* Latreille) of the western Palearctic (Hymenoptera, Apoidea, Megachilidae). *Journal of Hymenoptera Research* 55: 1–54. https://doi.org/10.3897/jhr.55.11255

Radoszkowski, O. (1865) Les mutilles russes. *Bulletin de la Société Impériale des Naturalistes de Moscou* 38: 422–467 + tabs. 7–9.

Radoszkowski, O. (1885) Revision des armures copulatrices des mâles de la famille de Mutillides. *Horae Societatis Entomologicae Rossicae* 19 (1–2): 3–49, + 9 pls.

Ronchetti, F. & Polidori, C. (2020) A sting affair: A global quantitative exploration of bee, wasp and ant hosts of velvet ants. *PLoS ONE* 15 (9): e0238888. https://doi.org/10.1371/journal.pone.0238888

Sadler, E.A., Pitts, J.P. & Wilson, J.S. (2018) Stinging wasps (Hymenoptera: Aculeata), which species have the longest sting? *PeerJ* 6: e4743. https://doi.org/10.7717/peerj.4743

Sakagami, S. & Katayama, E. (1977) Nests of some Japanese bumblebees (Hymenoptera, Apidae). *Journal of the Faculty of Science, Hokkaido University*, Series 6, Zoology 21 (1): 92–153.

Sato, T. & Tsurusaki, N. (2010) Preliminary report of insect fauna occurring in the Tottori Sand Dunes. *Bulletin of the Tottori Prefectural Museum* 47: 45–81. (in Japanese)

Schluter, D. (1986) Character displacement between distantly related taxa – finches and bees

in the Galapagos. *American Naturalist* 127: 95–102. https://doi.org/10.1086/284470
Schluter, D. (2000) *The ecology of adaptive radiation*. Oxford University Press, Oxford, 300 pp.
Schmid-Egger, C. (2004) Revision of *Bembecinus* (Hymenoptera: Crabronidae) of the Palaearctic region. *Notes fauniques de Gembloux* 54: 3–69.
Schmidt, J.O. (2016) *The sting of the wild*. Johns Hopkins University Press, Baltimore, xiii + 257 pp. + 8 pls.
Schmidt, J.O. (2019) Pain and lethality induced by insect stings: An exploratory and correlational study. *Toxins* 11 (7): 427. https://doi.org/10.3390/toxins11070427
Schmidt, J.O. & Blum, M.S. (1977) Adaptations and responses of *Dasymutilla occidentalis* (Hymenoptera: Mutillidae) to predators. *Entomologia Experimentalis et Applicata* 21 (2): 99–111. https://doi.org/10.1111/j.1570-7458.1977.tb02663.x
Schmidt, J.O. & Buchmann, S.L. (1986) Are mutillids scarce? (Hymenoptera: Mutillidae). *The Pan-Pacific Entomologist* 62 (2): 103–104.
Schmidt, J.O. & Hook, A.W. (1979) A record population of *Pseudomethoca simillima* (Smith) (Hymenoptera: Mutillidae). *The Florida Entomologist* 62 (2): 152.
Shorthouse, D.P. (2010) SimpleMappr, an online tool to produce publication-quality point maps. Available from: http://www.simplemappr net (accessed 19 February 2024)
Sichel, J. & Radoszkowski, O. (1869–1870) Essai d'une monographie des Mutilles de l'ancien continent. *Horae Socieratis Entomologicae Rossicae* 6 (3): 139–172 + pl. 6–8 (1869); 6 (4): 173–309 + pl. 9–11 (1870).
Silverman, B.W. (1981) Using kernel density estimates to investigate multimodality. J*ournal of Royal Statistical Society B* 43: 97–99.
Silverman, B.W. (1983) Some properties of a test for multimodality based on kernel density estimates. *In*: Kingman, J.F.C. & Reuter, G.E.H. (eds) *Probability, statistics and analysis*. London Mathematical Society Lecture Note Series 79. Cambridge University Press, London, pp. 248–259. https://doi.org/10.1017/CBO9780511662430.015
Skorikov, A.S. (1935) Zur Mutilliden-Fauna Zentralasiens. *Trudy Tadzhikskoi Basy Akademii Nauk SSSR* 5: 257–349 + 7 pls. (in Russian)
Slatkin, M. (1980) Ecological character displacement. *Ecology* 61 (1): 163–177. https://doi.org/10.2307/1937166
Sonan, J. (1931) Some wasps and bees of Hokoto (Pescadores). *Transactions of the Natural History Society of Formosa* 21 (112): 6–8. (in Japanese)
Starr, C.K. (1985) A simple pain scale for field comparison of hymenopteran stings. *Journal of Entomological Science* 20 (2): 225–232. https://doi.org/10.18474/0749-8004-20.2.225
Stone, G.N., Loder, P.M.J. & Blackburn, T.M. (1995) Foraging and courtship behaviour in males of the solitary bee *Anthophora plumipes* (Hymenoptera: Anthophoridae): thermal physiology and the roles of body size. *Ecological Entomology* 20 (2): 169–183. https://doi.org/10.1111/j.1365-2311.1995.tb00443.x
Suda, T. (2011) [Collecting data of Mutillidae including new records]. *Rambu* 20: 136–138. (in Japanese)
Takahashi, H. (1996) [Collecting records of Mutillidae]. *Gekkan-Mushi* 310: 28–29. (in Japanese)
Taylor, C.K., Murphy, M.V., Hitchen, Y. & Brothers, D.J. (2019) Four new species of Australian velvet ants (Hymenoptera: Mutillidae, *Aglaotilla*) reared from bee and wasp nests, with a review of Australian mutillid host records. *Zootaxa* 4609 (2): 201–224. https://doi.org/10.11646/zootaxa.4609.2.1
Templado, J. (1958) *Smicromyrme viduata* Pall. parasito de *Bembix mediterranea* Handl.

Graellsia 16 (1–3): 45–47.
Terayama, M. (2005) Taxonomic guide to the Japanese aculeate wasps, 2. Family Mutillidae. *Tsunekibachi* 4: 1–13. (in Japanese)
Terayama, M., Suda, H., Murota, T., Haneda, Y. & Tano, T. (2011) The velvet ants (Mutillidae) of Japan. *Gekkan-Mushi* 481: 12–25. (in Japanese)
Terayama, M., Suda, H., Murota, T. & Tano, T. (2016) Family Mutillidae. *In*: Terayama, M. & Suda, H. (eds) *A guide to the aculeate wasps of Japan*. Tokai University Press, Hiratsuka, pp. 161–174. (in Japanese)
Tormos, J., Asis, J.D., Beneitez, A. & Gayubo, S.F. (2009) Description of the mature larva of the sand wasp *Bembix bidentata* and its parasitoids (Hymenoptera: Crabronidae, Chrysididae, Mutillidae). *Florida Entomologist* 92 (1): 43–53. http://doi.org/10.1653/024.092.0108
Tormos, J., Asis, J.D. & Gayubo, S.F. (2003) Description of the mature larva of *Nemka viduata* (Pallas) (Hymenoptera: Multillidae: Mutillinae), a parasitoid of *Stizus continuus* (Klug) (Hymenoptera: Crabronidae: Bemibicinae). *Journal of Entomological Science* 38 (4): 502–510. https://doi.org/10.18474/0749-8004-38.4.502
Tormos, J., Asis, J.D., Polidori, C., Benéitez, A. & Storino, G. (2010) The mating behavior of the velvet ant, *Nemka viduata* (Hymenoptera: Mutillidae). *Journal of Insect Behavior* 23: 117–127. https://doi.org/10.1007/s10905-009-9200-5
Torrico-Bazoberry, D. & Muñoz, M.I. (2019) High-frequency components in the distress stridulation of Chilean endemic velvet ants (Hymenoptera: Mutillidae). *Revista Chilena de Entomologia* 45 (1): 5–13.
Tschuch, G. (1993) Sound production in mutillid wasps (Mutillidae, Hymenoptera). *Bioacoustics* 5 (1–2): 123–129. https://doi.org/10.1080/09524622.1993.9753234
Tschuch, G. & Brothers, D.J. (1999) Modeling vibration and sound production in insects with nonresonant stridulatory organs. *The Journal of the Acoustical Society of America* 106 (6): 3706–3710. https://doi.org/10.1121/1.428227
Tsuneki, K. (1972a) Studies on the Mutillidae of Japan (Hymenoptera). *Etizenia* 61: 1–26.
Tsuneki, K. (1972b) Mutillidae collected in Formosa in 1966 and 68 (Hymenoptera). *Etizenia* 64: 1–25.
Tsuneki, K. (1993) On some Taiwanese Mutillidae, collected in 1976 by Mr. T. Murota, with description of new taxa (Hymenoptera). *Special Publications of the Japan Hymenopterists Association* 41: 39–50.
Tsurusaki, N., Hayashi, M., Miyanaga, R., Ichisawa, K. & Kawakami, Y. (2012) Catalogue of the insects of Tottori Sand Dunes, Honshu, Japan. *Natural History Research of San'in* 7: 47–82. (in Japanese)
van den Assem, J., van Iersel, J.J.A. & Los-den Hartogh, R.L. (1989) Is being large more important for female than for male parasitic wasps? *Behaviour* 108 (1–2): 160–195. https://doi.org/10.1163/156853989X00114
VanderSal-Jensen, N.D., Crews, S.C. & Gillespie, R.G. (2016) Is love in the air or at first sight? Mate finding cues used by sympatric male velvet ants (Hymenoptera: Mutillidae). *Invertebrate Biology* 135 (3): 200–210. https://doi.org/10.1111/ivb.12128
Williams, K.A., Brothers, D.J. & Pitts, J.P. (2011) New species of *Tobantilla* Casal, 1965 and a new genus and species, *Gogoltilla chichikovi* gen. et sp. nov., from Argentina (Hymenoptera: Mutillidae). *Zootaxa* 3064 (1): 41–68. https://doi.org/10.11646/zootaxa.3064.1.2
Williams, K.A., Lelej, A.S., Okayasu, J., Borkent, C.J., Malee, R., Thoawan, K. & Thaochan, N. (2019) The female velvet ants (aka modkhong) of southern Thailand (Hymenoptera: Mutillidae), with a key to the genera of southeast Asia. *Zootaxa* 4602 (1): 1–69. https://doi.org/10.11646/zootaxa.4602.1.17

Wilson, J.S., Clark, S.L., Williams, K.A. & Pitts, J.P. (2012a) Historical biogeography of the arid-adapted velvet ant *Sphaeropthalma arota* (Hymenoptera: Mutillidae) reveals cryptic species. *Journal of Biogeography* 39: 336–352. https://doi.org/10.1111/j.1365-2699.2011.02580.x

Wilson, J.S., Jahner, J.P., Forister, M.L., Sheehan, E.S., Williams, K.A. & Pitts, J.P. (2015) North American velvet ants form one of the world's largest known Müllerian mimicry complexes. *Current Biology* 25: R704–R706. https://doi.org/10.1016/j.cub.2015.06.053

Wilson, J.S., Pan, A.D., Limb, E.S. & Williams, K.A. (2018) Comparison of African and North American velvet ant mimicry complexes: Another example of Africa as the 'odd man out'. *PLoS ONE* 13 (1): e0189482. https://doi.org/10.1371/journal.pone.0189482

Wilson, J.S. & Pitts, J.P. (2008) Revision of velvet ant genus *Dilophotopsis* Schuster (Hymenoptera: Mutillidae) by using molecular and morphological data, with implications for desert biogeography. *Annals of the Entomological Society of America* 101 (3): 514–524. https://doi.org/10.1603/0013-8746(2008)101[514:ROVAGD]2.0.CO;2

Wilson, J.S. & Pitts, J.P. (2010a) Pleistocene diversification of the *Odontophotopsis unicornis* species-group (Hymenoptera: Mutillidae). *Annals of the Entomological Society of America* 103 (4): 555–565. https://doi.org/10.1603/AN09177

Wilson, J.S. & Pitts, J.P. (2010b) Phylogeographic analysis of the nocturnal velvet ant genus Dilophotopsis (Hymenoptera: Mutillidae) provides insights into diversification in the Nearctic deserts. *Biological Journal of the Linnean Society* 101 (2): 360–375. https://doi.org/10.1111/j.1095-8312.2010.01526.x

Wilson, J.S., Williams, K.A., Forister, M.L., von Dohlen, C.D. & Pitts, J.P. (2012b) Repeated evolution in overlapping mimicry rings among North American velvet ants. *Nature Communications* 3: 1272. https://doi.org/10.1038/ncomms2275

Yamane, Sk. (1999) Family Mutillidae *In*: Yamane, Sk., Ikudome, S. & Terayama, M. (eds) *Identification guide to the Aculeata of the Nansei Islands, Japan*. Hokkaido University Press, Sapporo, pp. 369–381.

Yasumatsu, K. (1938) Les Mutillides de Coree et de la Mandschourie du Sud. *Transactions of the Natural History Society of Formosa* 28 (175): 83–87.

Yasumatsu, K. (1951) Mutillidae of Shansi, North China (Hymenoptera). *Mushi* 22 (12): 69–72.

Yom-Tov, Y. (1993) Size variation in *Rhabdomys pumilio*: A case of character release? *Zeitschrift für Säugetierkunde* 58: 48–53.

Yoshida, M. (1989) Family Mutillidae. *In*: Entomological Laboratory, Faculty of Agriculture, Kyushu University & Japan Wildlife Research Center (eds) *A check list of Japanese insects*. Entomological Laboratory, Faculty of Agriculture, Kyushu University, Fukuoka, pp. 650–651. (in Japanese)

Zavattari, E. (1913) H. Sauter's Formosa-Ausbeute. Mutillidae (Hym.). *Archiv für Naturgeschichte* 79A (3): 19–42. https://doi.org/10.5962/bhl.part.7709

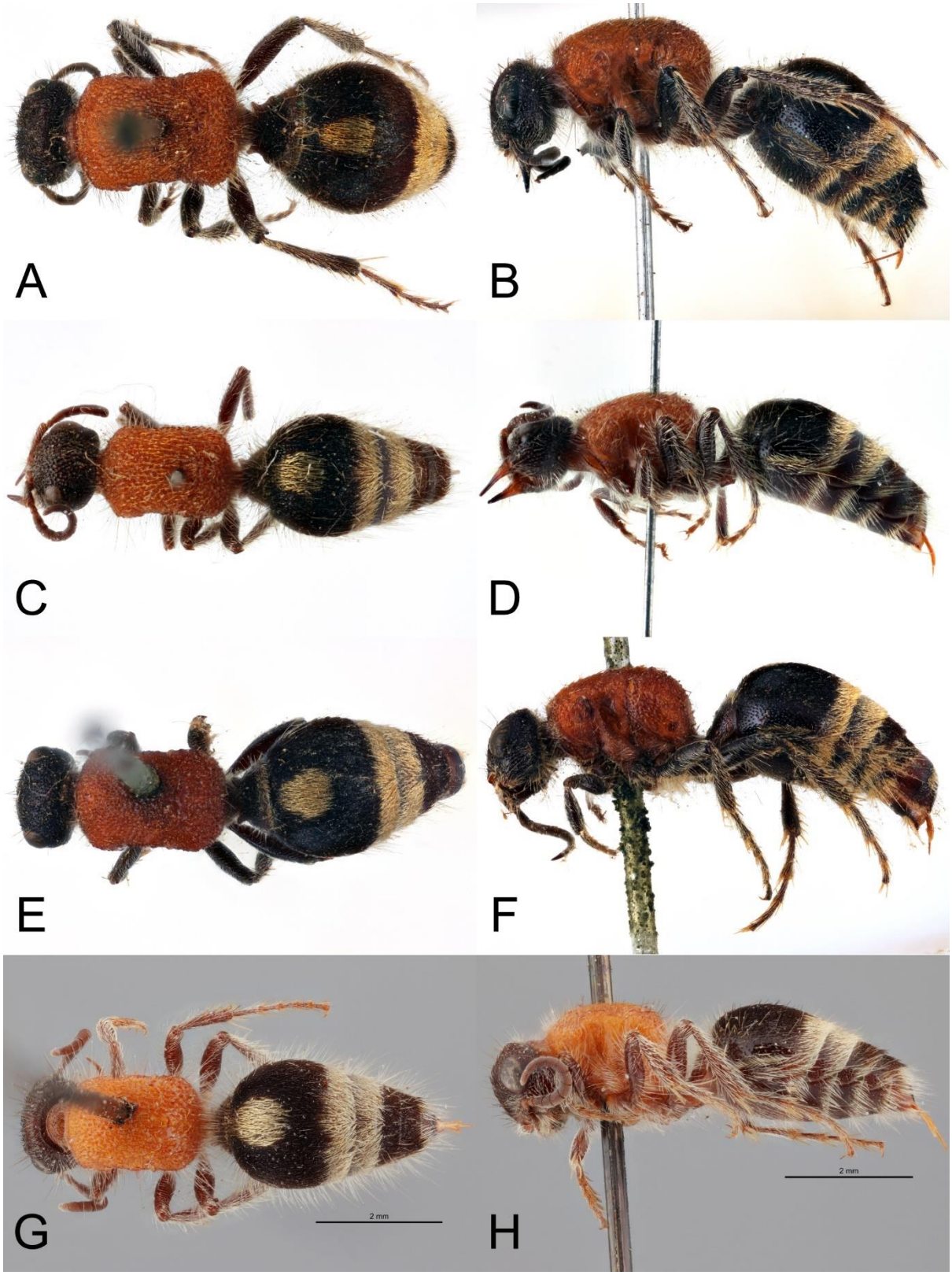

Figure 1. *Nemka* spp., ♀, habitus. A, B. *N. limi* (Chen), holotype; C, D. *N. limi nanhai* (Chen), holotype; E, F. *N. curvisquamata* Chen, holotype; G, H. *N. wotani* (Zavattari), lectotype; A, C, E, G. dorsal view; B, D, F, H. lateral view.

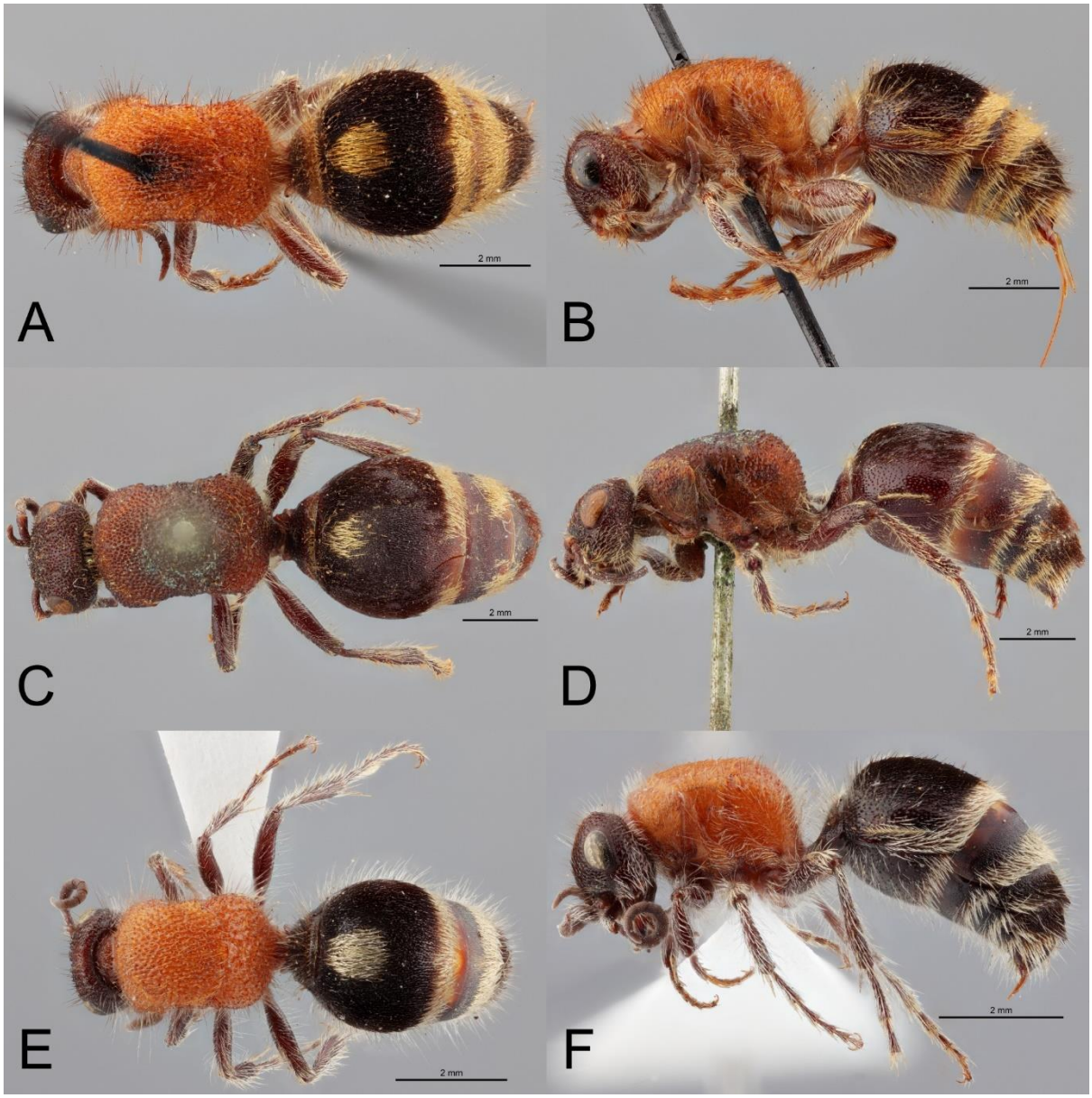

Figure 2. *Nemka* spp., ♀, habitus. A, B. *N. limi* (Chen), paratype; C, D. *N. curvisquamata* (Chen), paratype; E, F. *N. yasumatsui* (Mickel); A, C, E. dorsal view; B, D, F. lateral view.

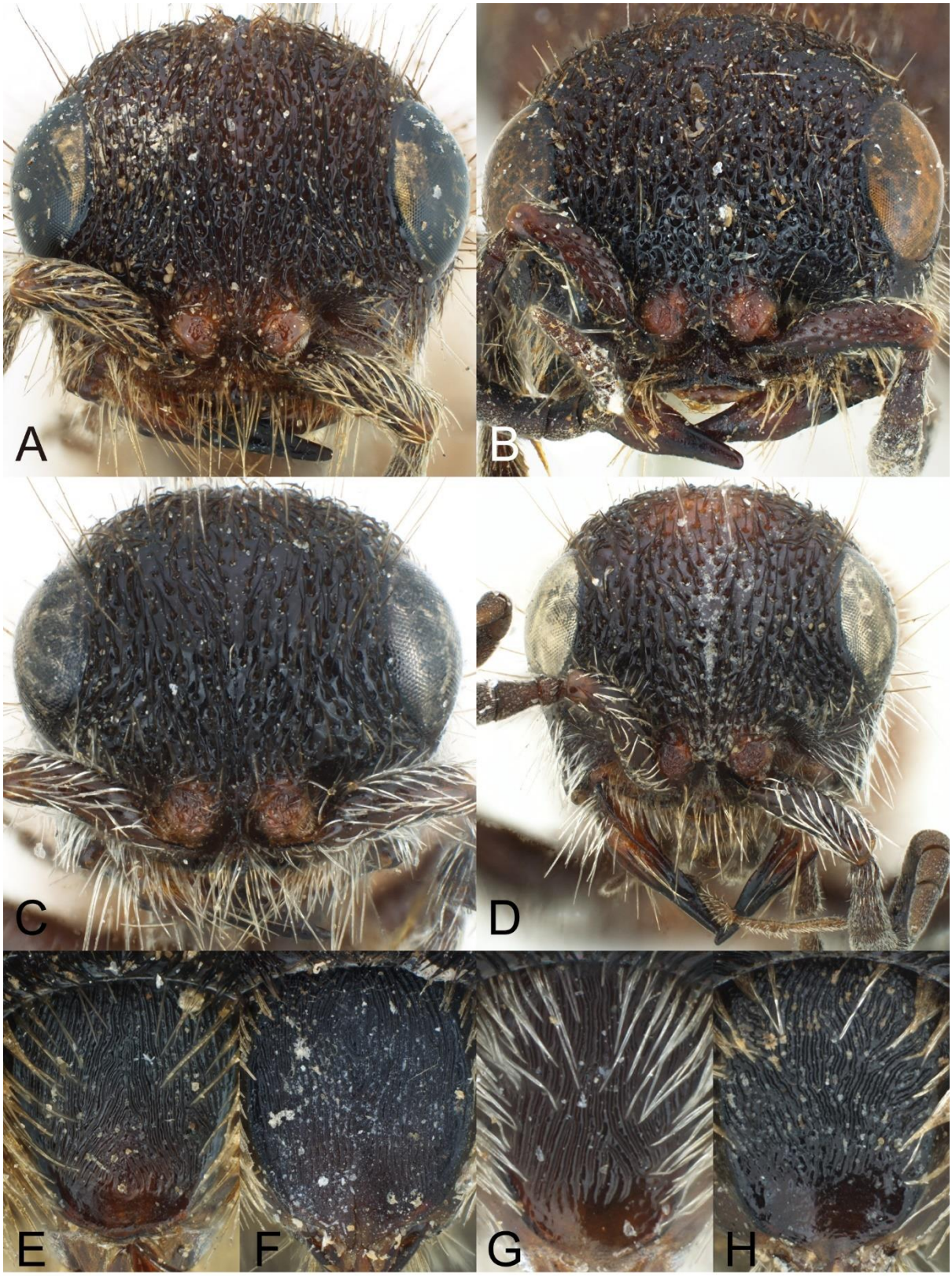

Figure 3. *Nemka* spp., ♀. A, E, *N. limi* (Chen), paratype; B, F. *N. curvisquamata* (Chen), paratype; C, G. *N. wotani* (Zavattari), lectotype; D, H. *N. yasumatsui* (Mickel); A–D. head, face view; E–H. pygidial plate.

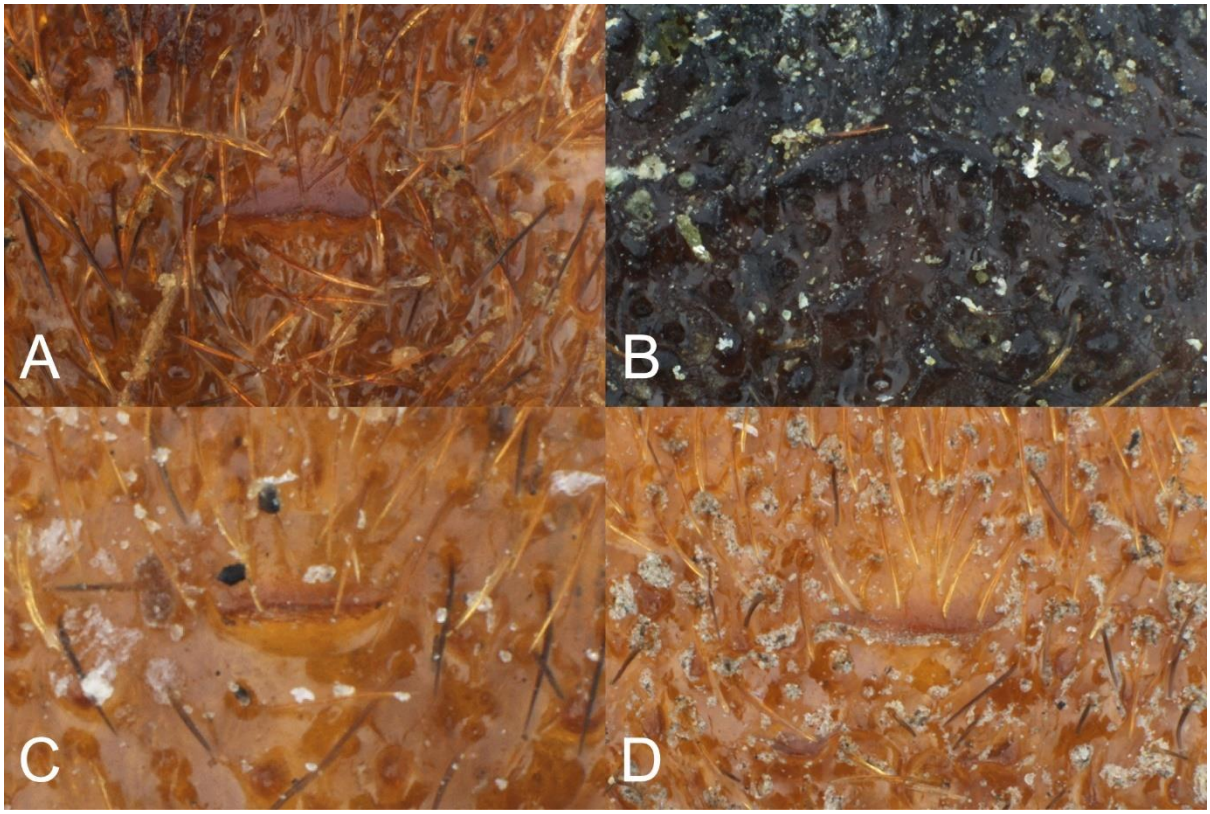

Figure 4. *Nemka* spp., ♀, scutellar scale. A. *N. limi* (Chen), paratype; B. *N. curvisquamata* (Chen), paratype; C. *N. wotani* (Zavattari), lectotype; D. *N. yasumatsui* (Mickel).

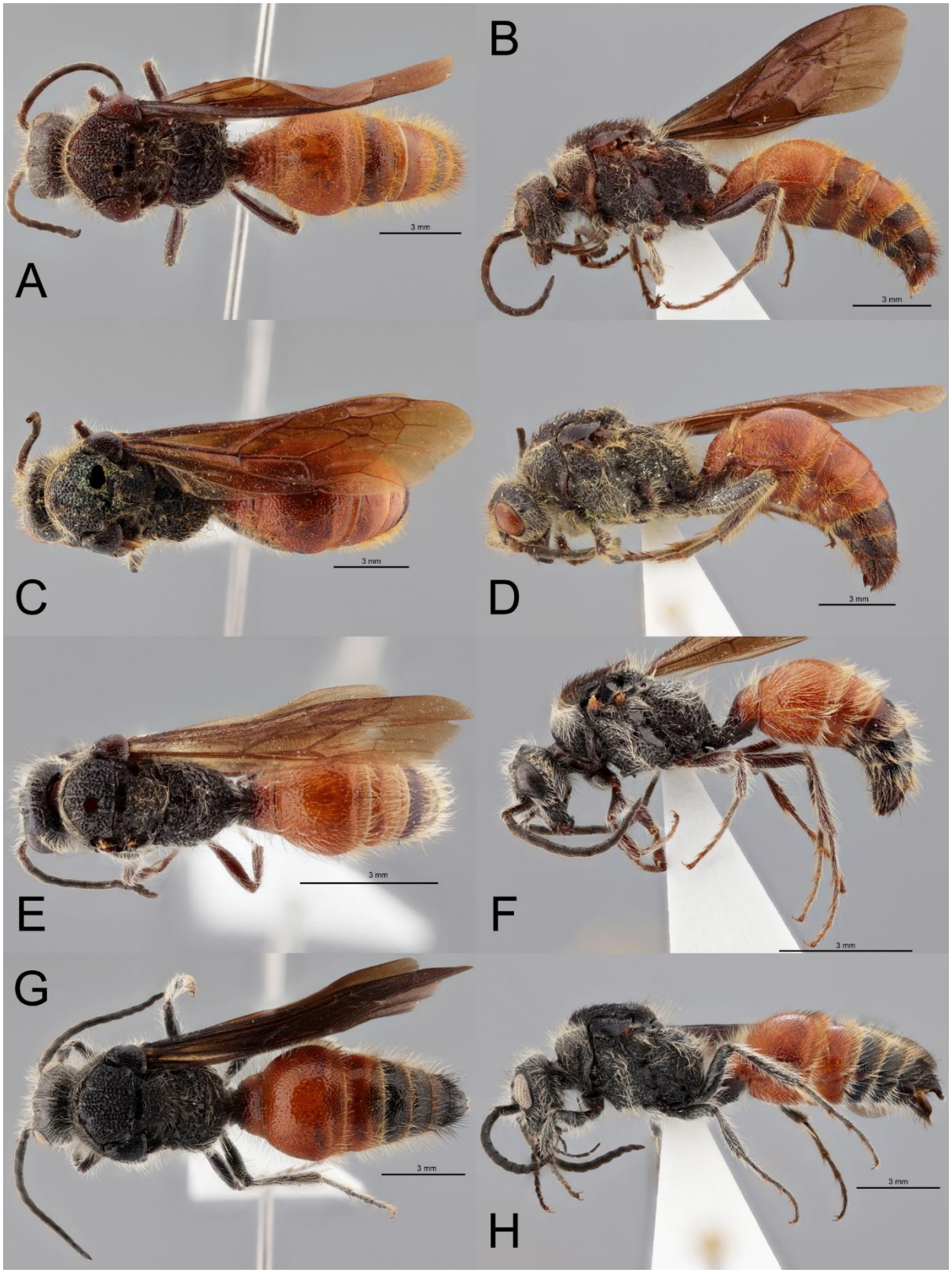

Figure 5. *Nemka* spp., ♂, habitus. A, B. *N. limi* (Chen); C, D. *N. taiwanensis* (Mickel); E, F. *N. wotani* (Zavattari); G, H. *N. yasumatsui* (Mickel); A, C, E, G. dorsal view; B, D, F, H. lateral view.

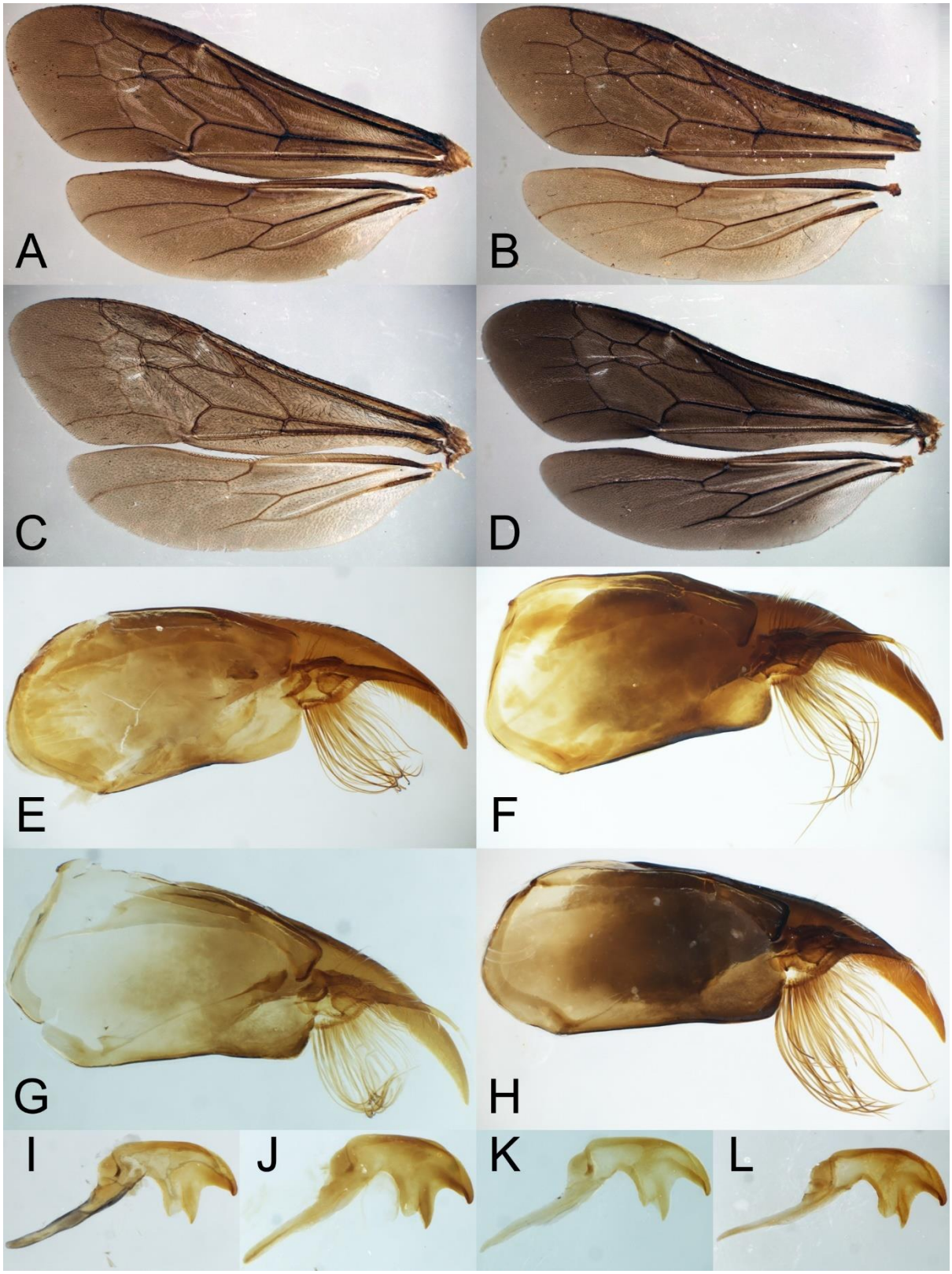

Figure 6. *Nemka* spp., ♂. A, E, I. *N. limi* (Chen); B, F, J. *N. taiwanensis* (Mickel); C, G, K. *N. wotani* (Zavattari); D, H, L. *N. yasumatsui* (Mickel); A–D. wings; E–H. genitalia, inner view; I–L. penis valve.

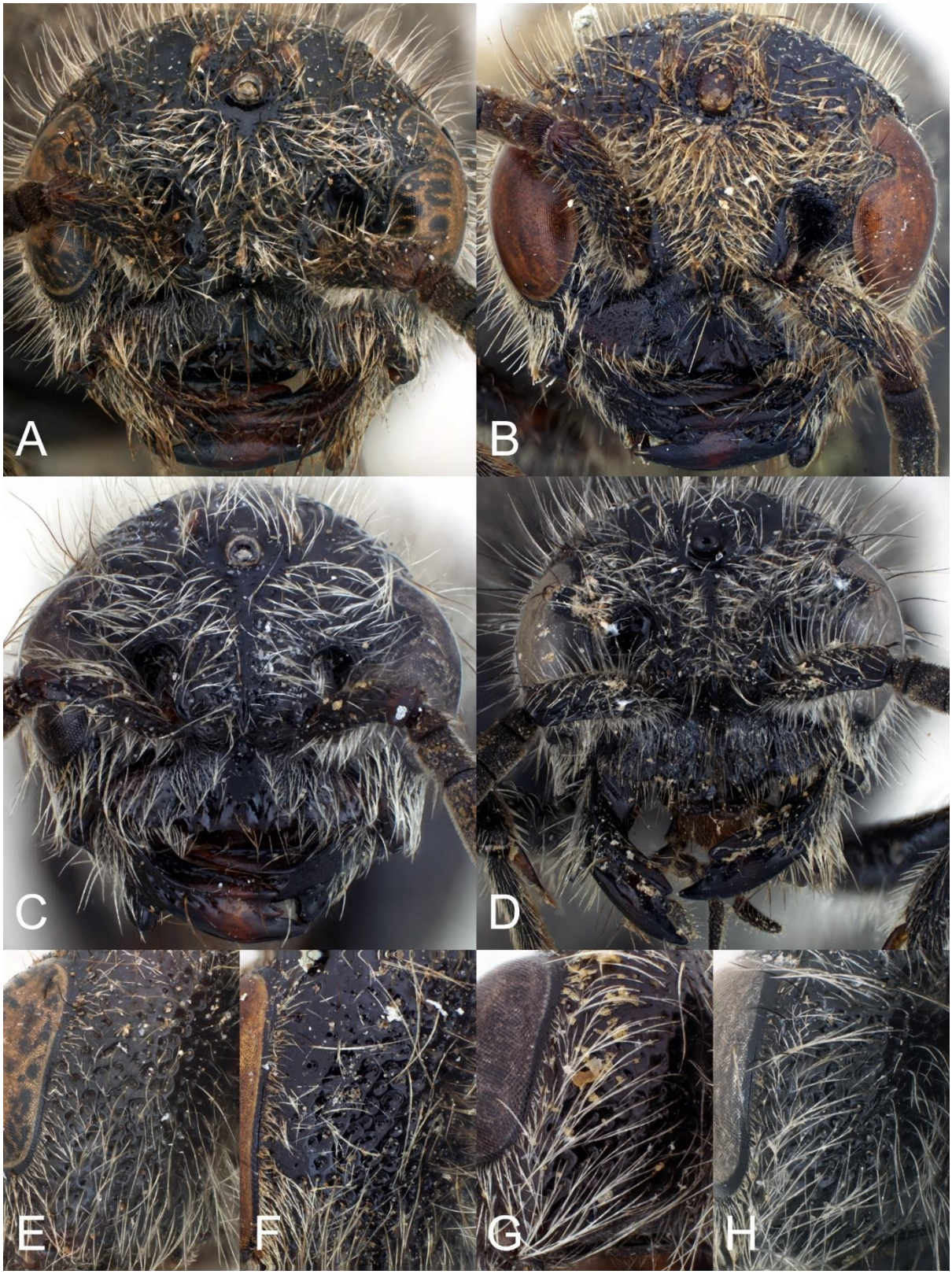

Figure 7. *Nemka* spp., ♂, head. A, E. *N. limi* (Chen); B, F. *N. taiwanensis* (Mickel); C, G. *N. wotani* (Zavattari); D, H. *N. yasumatsui* (Mickel); A–D. face view; E–H. gena.

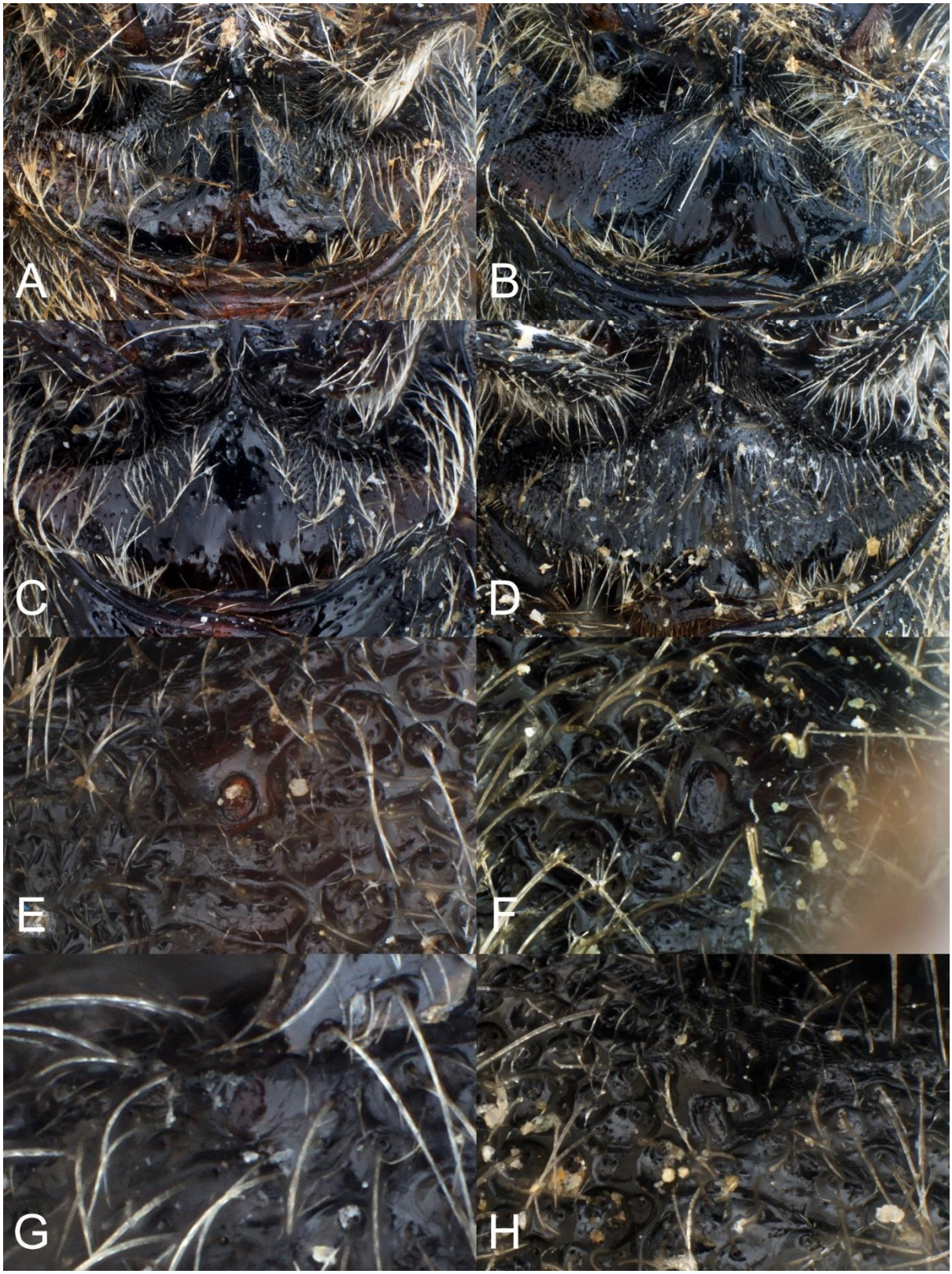

Figure 8. *Nemka* spp., ♂. A, E. *N. limi* (Chen); B, F. *N. taiwanensis* (Mickel); C, G. *N. wotani* (Zavattari); D, H. *N. yasumatsui* (Mickel); A–D. clypeus; E–H. mesopleural tubercle.

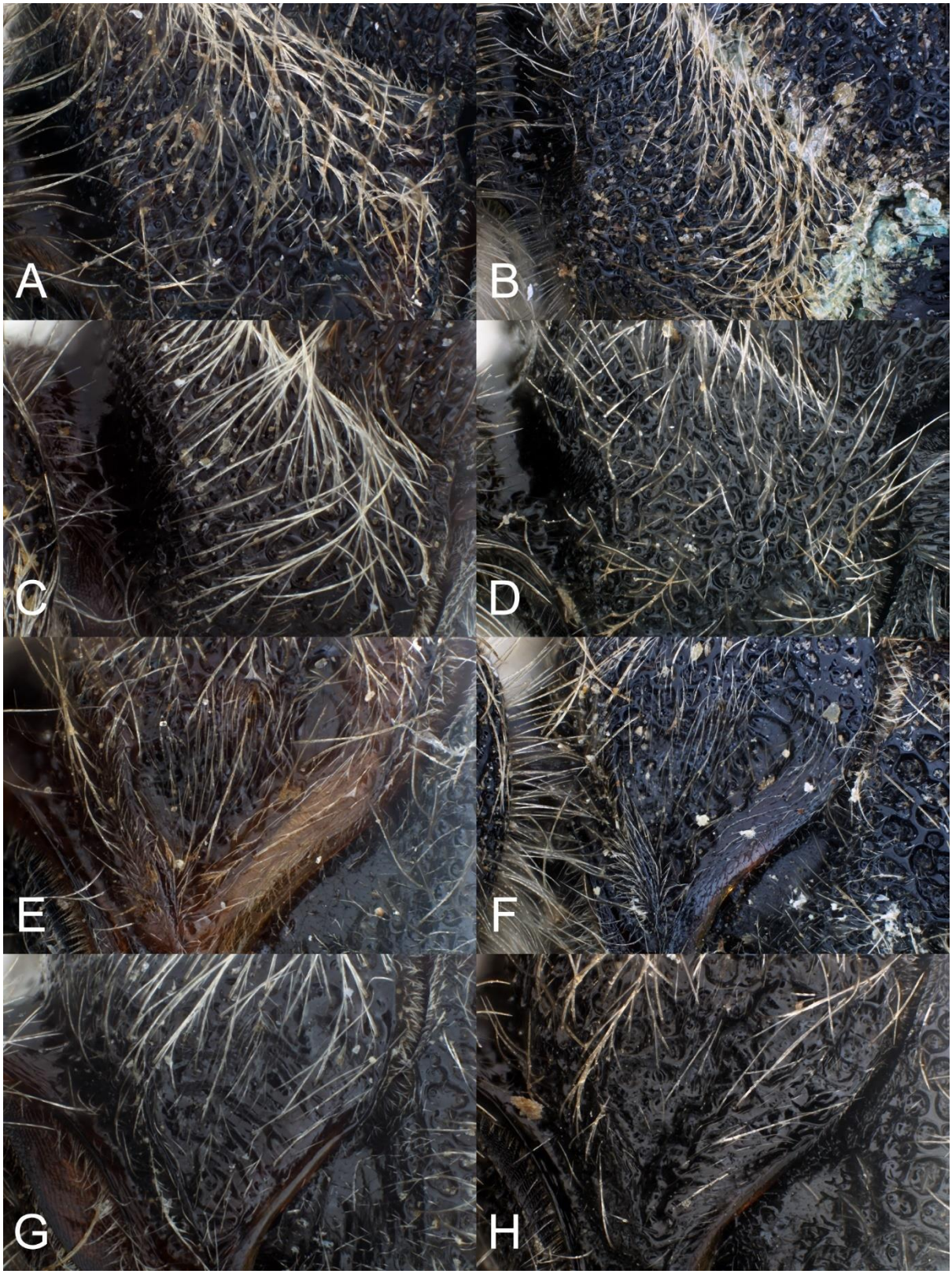

Figure 9. *Nemka* spp., ♂, pronotum. A, E. *N. limi* (Chen); B, F. *N. taiwanensis* (Mickel); C, G. *N. wotani* (Zavattari); D, H. *N. yasumatsui* (Mickel); A–D. dorso-lateral view; E–H. lateral view.

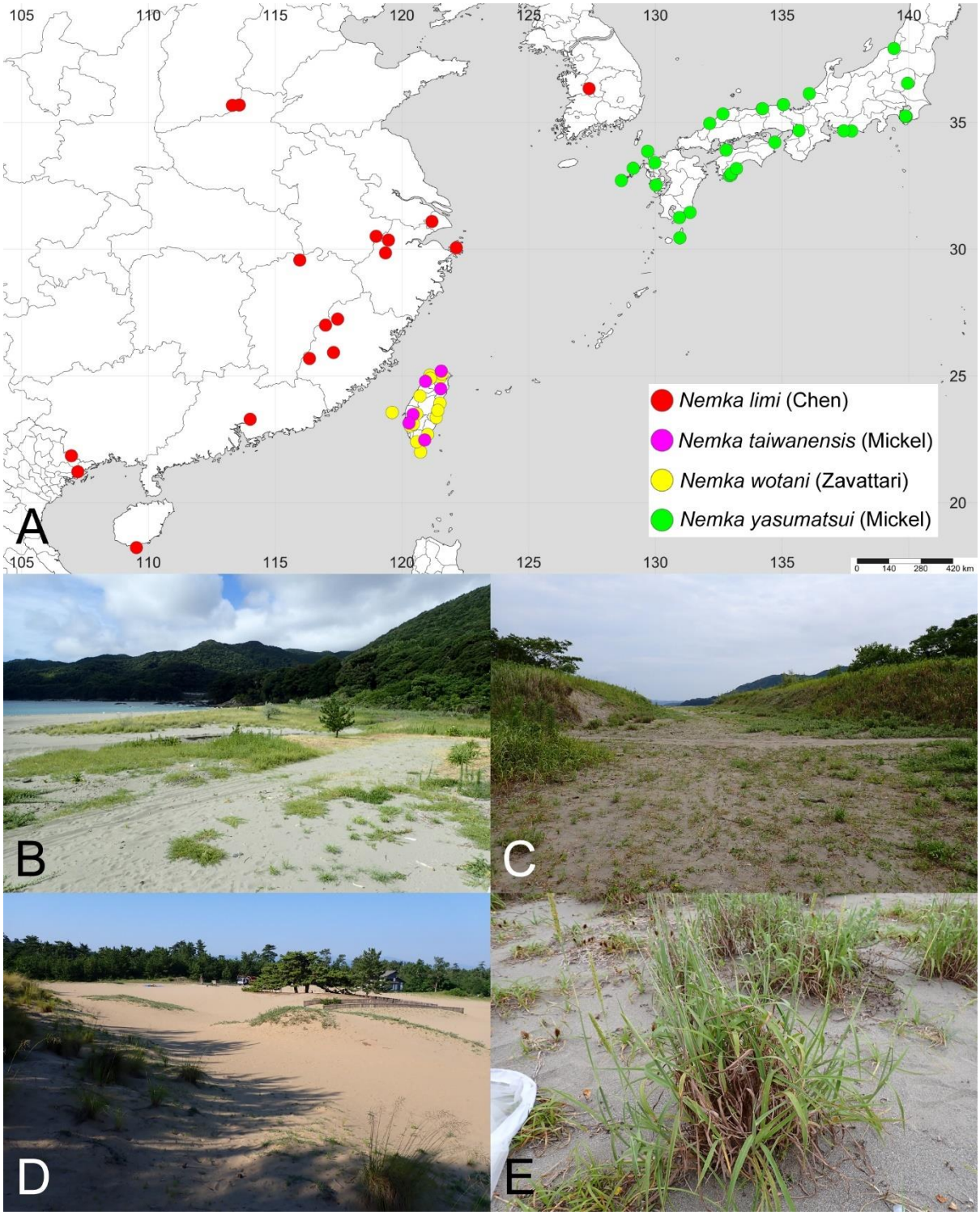

Figure 10. Distribution and habitats of *Nemka* spp. A. Distributional map of *Nemka* spp. based on the material examined and the literature (Lelej, 1995; Lelej *et al*., 2001; Mickel, 1933; Tsuneki, 1972ab; Yasumatsu, 1951); B, C. habitat of *N. yasumatsui* (Mickel) in Japan (Kôchi: Shimonokae Beach); D. habitat of *N. yasumatsui* (Mickel) in Japan (Tottori: Tottori Sand Dune); E. coastal plant on which a female of *N. yasumatsui* was found.

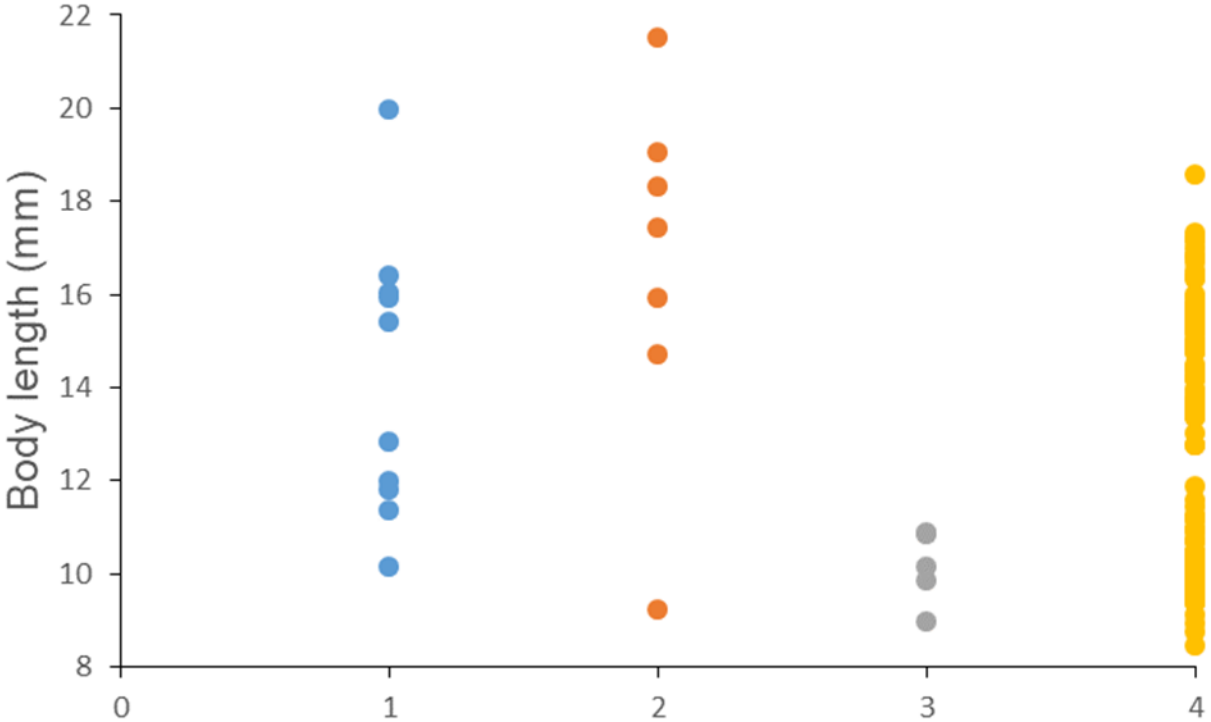

Figure 11. Body length distribution of *Nemka* spp. (♂). 1. *N. limi* (Chen); 2. *N. taiwanensis* (Mickel); 3. *N. wotani* (Zavattari); 4. *N. yasumatsui* (Mickel).

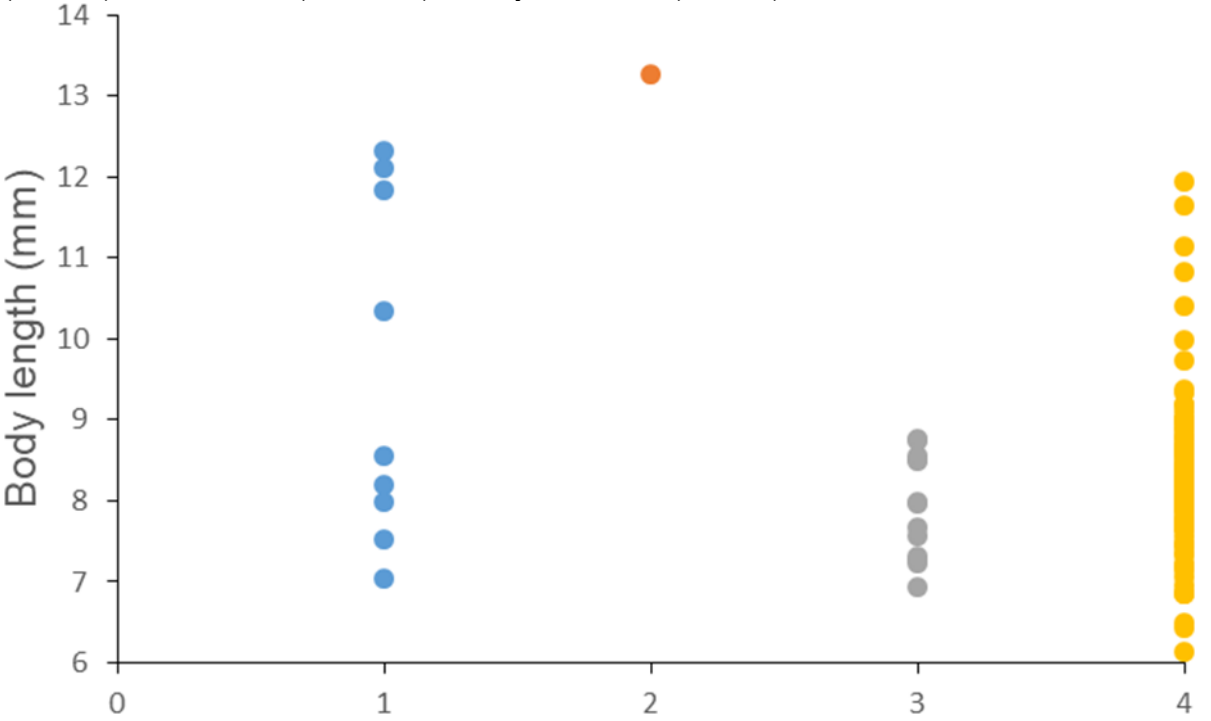

Figure 12. Body length distribution of *Nemka* spp. (♀). 1. *N. limi* (Chen); 2. *N. taiwanensis* (Mickel); 3. *N. wotani* (Zavattari); 4. *N. yasumatsui* (Mickel).

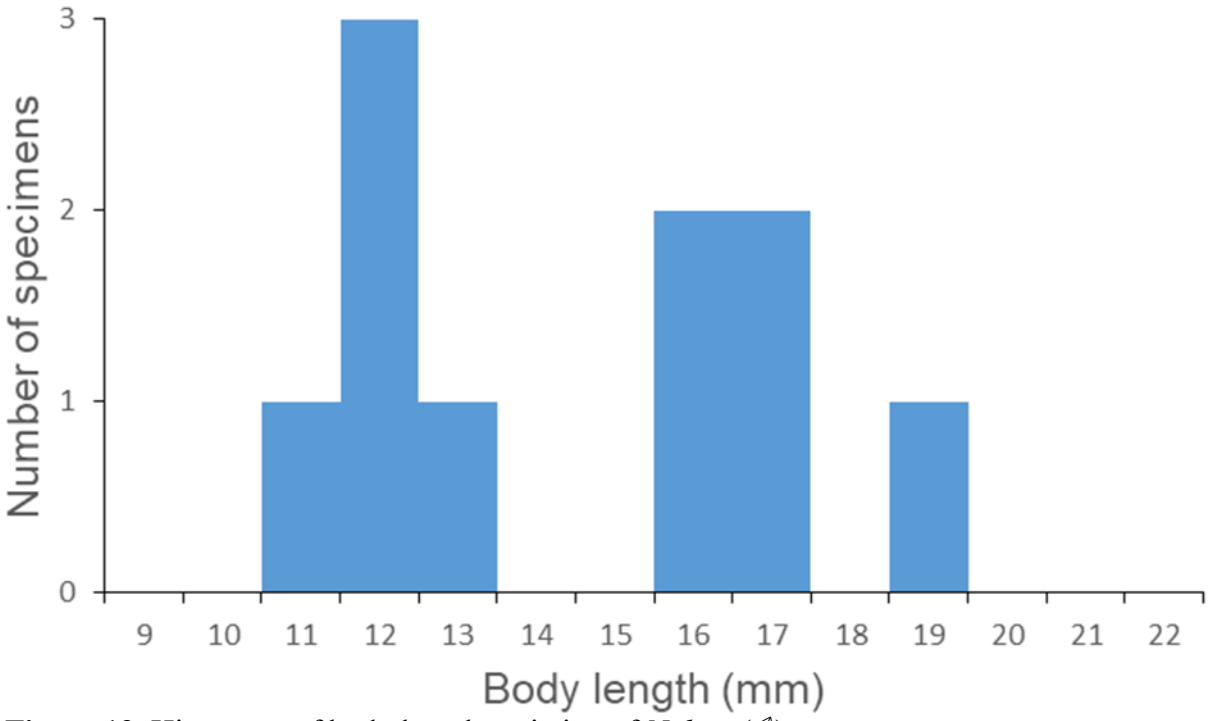

Figure 13. Histogram of body length variation of *N. limi* (♂).

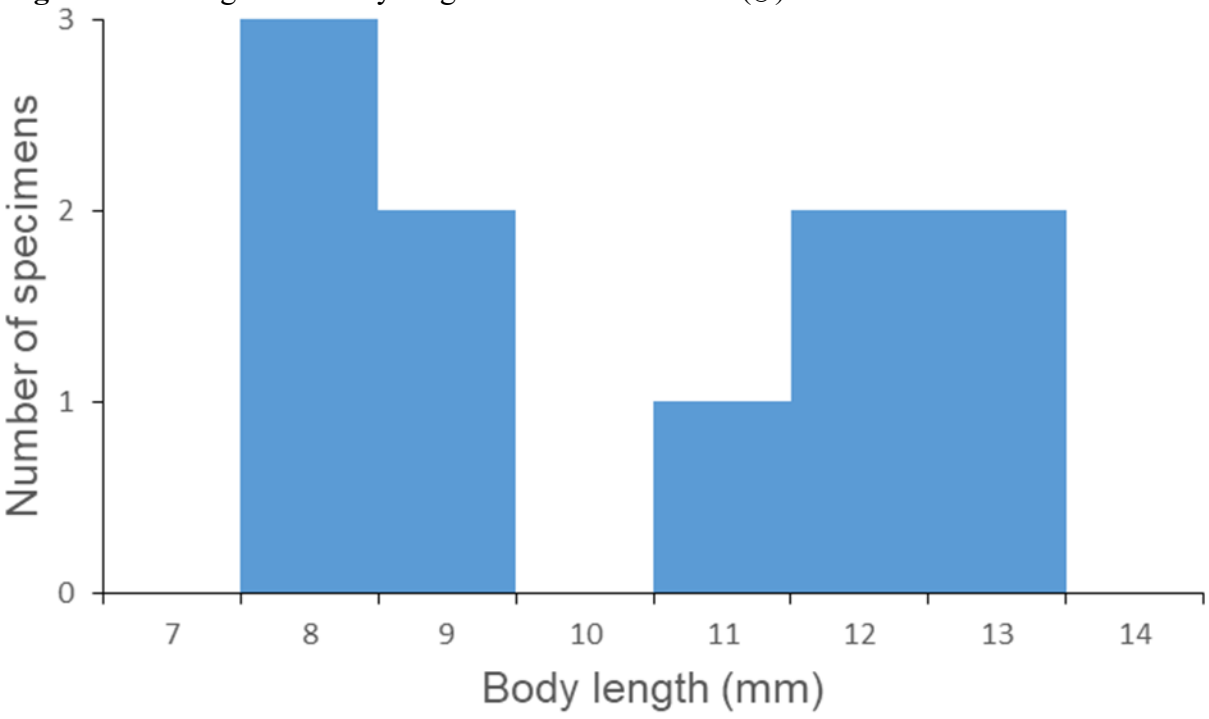

Figure 14. Histogram of body length variation of *N. limi* (♀).

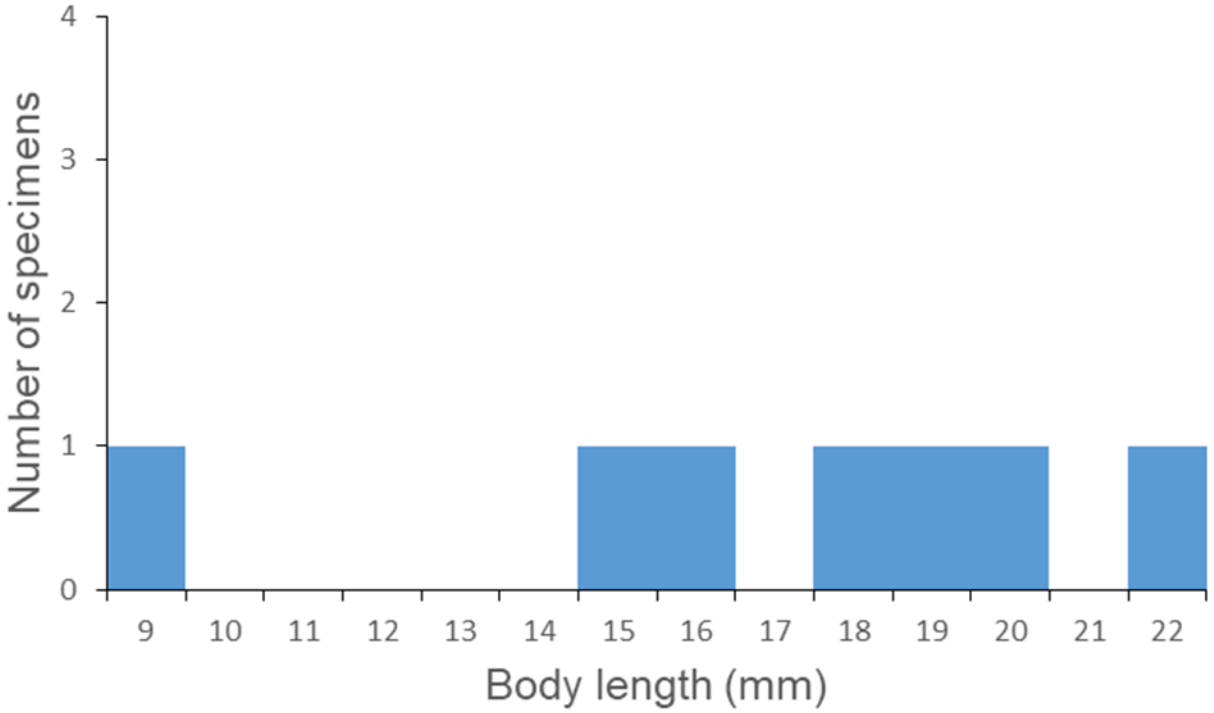

Figure 15. Histogram of body length variation of *N. taiwanensis* (♂).

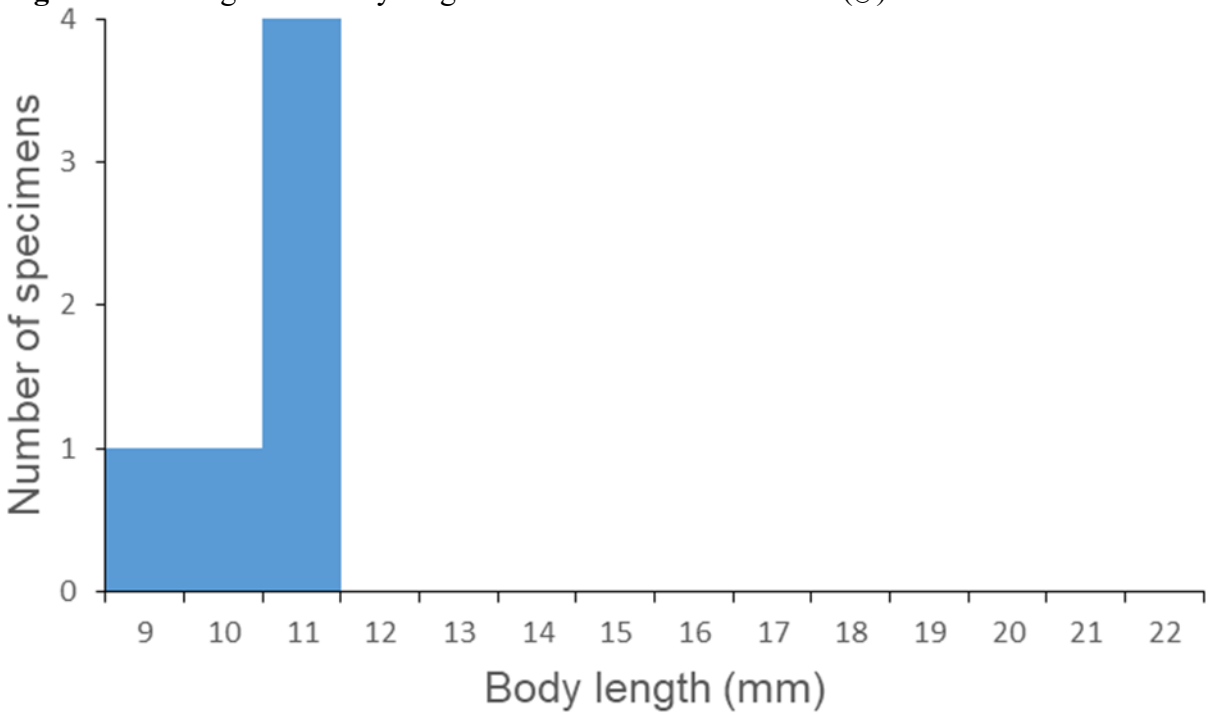

Figure 16. Histogram of body length variation of *N. wotani* (♂).

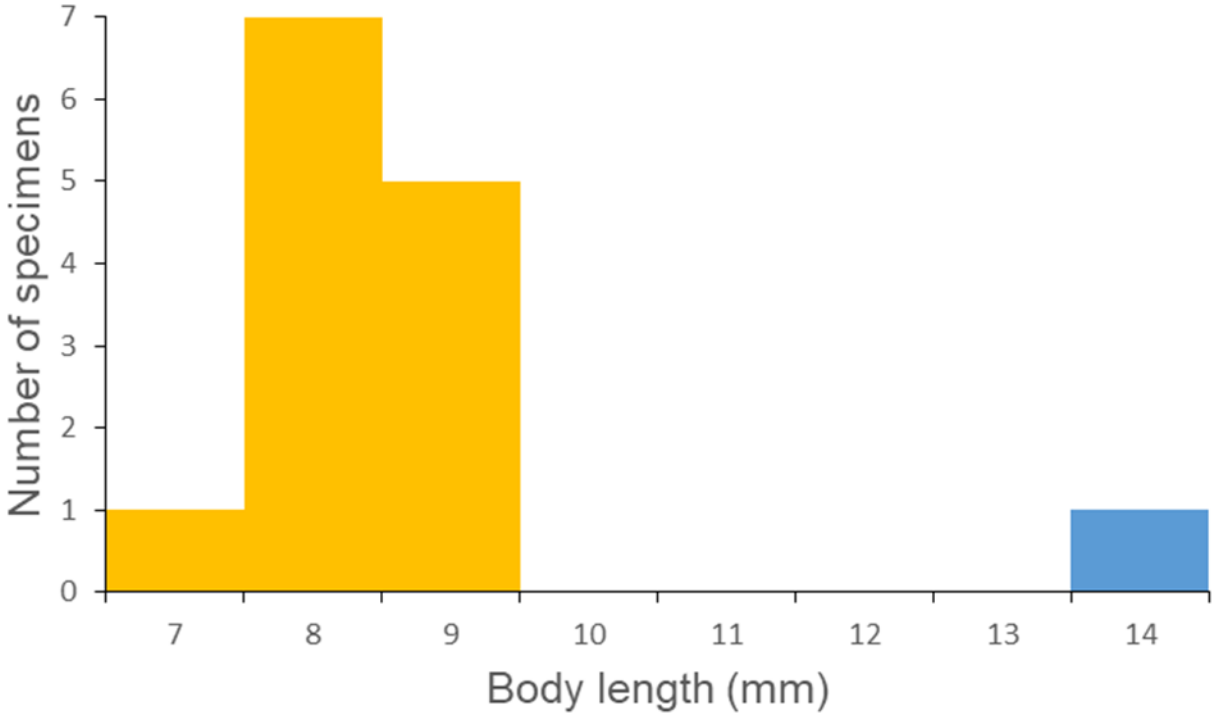

Figure 17. Histogram of body length variation of *N. taiwanensis* (blue) and *N. wotani* (orange) (♀).

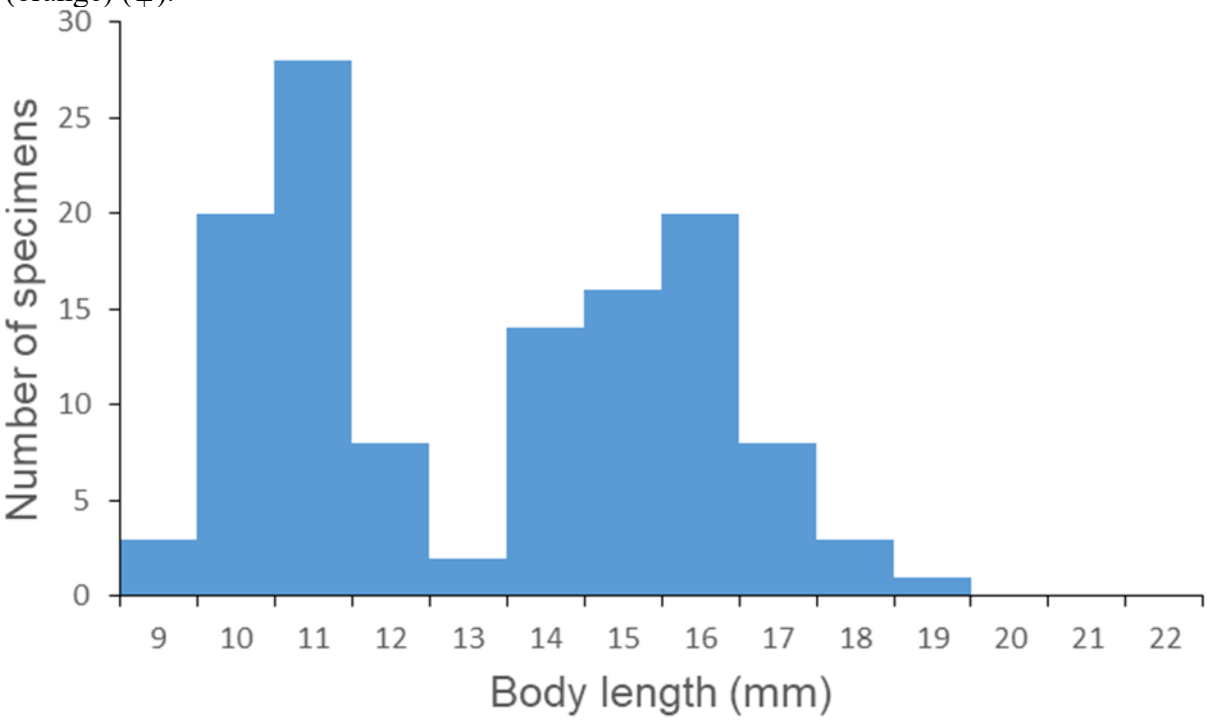

Figure 18. Histogram of body length variation of *N. yasumatsui* (♂).

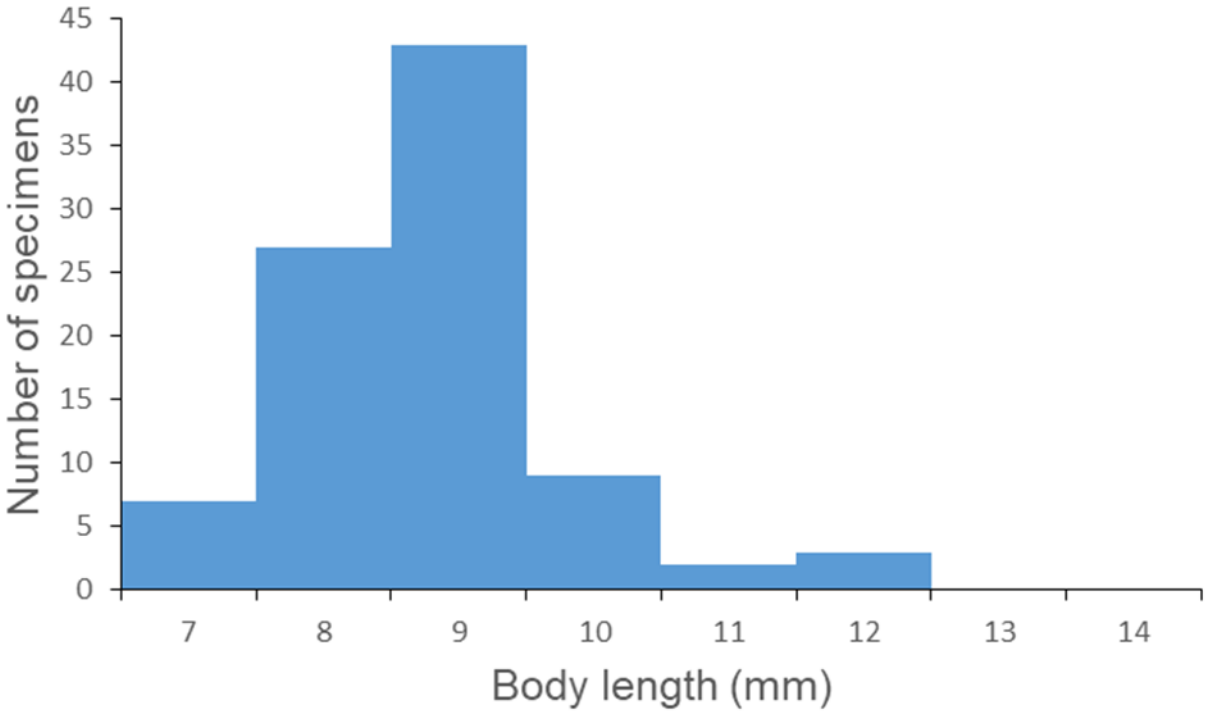

Figure 19. Histogram of body length variation of *N. yasumatsui* (♀).

Table 1. Scientific names applied to *Nemka* spp. in the literature.

	***N. limi* (Chen)**		***N. taiwanensis* (Mickel)**		***N. wotani* (Zavattari)**		***N. yasumatsui* (Mickel)**	
	♂	♀	♂	♀	♂	♀	♂	♀
Zavattari (1913)			*Mu. dimidiata* *Mu. gribodoi*			*Mu. wotani*		
Mickel (1933, 1935)			*Ti.* (*Tr.*) *orientalis taiwanensis*			*S. wotani*		
Mickel (1936)								*S. yasumatsui*
Yasumatsu (1938, 1951)		*S. wotani*						
Chen (1957)	*S. orientalis taiwanensis*	*S. limi limi* *S. limi nanhai*	*S. orientalis taiwanensis*	*S. curvisquamata*	*S. orientalis taiwanensis*	*S. wotani*		
Tsuneki (1972a)								*S. yasumatsui*
Tsuneki (1972b)			*S. ilanica* *S. orientalis taiwanensis*		*S. orientalis taiwanensis*	*S. wotani*		
Tsuneki (1993)					*S. chihpenchia*	*S. wotani*		
Lelej (1995)		*N. limi* *N. wotani*	*N. taiwanensis* *Mi. ilanica*	*N. curvisquamata*	*N. wotani*	*N. wotani*	*N. wotani*	*N. wotani*
Lelej *et al.* (2001)		*N. wotani*						
Okayasu (2020)	*N. limi*	*N. limi*			*N. wotani*	*N. wotani*	*N. yasumatsui*	*N. yasumatsui*

Table 2. Diagnostic characters and distribution of *Nemka* spp.

	***N. limi* (Chen)**	***N. taiwanensis* (Mickel)**	***N. wotani* (Zavattari)**	***N. yasumatsui* (Mickel)**
Distribution	China mainland, South Korea, Vietnam	Taiwan	Taiwan	Japan
Male: gena punctation	dense (Fig. 7E)	dense (Fig. 7F)	sparse (Fig. 7G)	dense (Fig. 7H)
Male: clypeal tubercle	rounded (Fig. 8A)	narrow (Fig. 8B)	rounded (Fig. 8C)	rounded (Fig. 8D)
Male: dense recumbent setae on dorsal face of pronotum	anteriorly short and posteriorly long (Fig. 9A)	anteriorly short and posteriorly long (Fig. 9B)	short (Fig. 9C)	short (Fig. 9D)
Male: surface sculpturing of lateral face of pronotum	rugoso-punctate (Fig. 9E)	rugoso-punctate (Fig. 9F)	anteriorly rugoso-punctate and posteriorly transversely puncto-striate (Fig. 9G)	rugoso-punctate (Fig. 9H)
Male: mesopleural tubercle	depressed (Fig. 8E)	depressed (Fig. 8F)	flattened (Fig. 8G)	depressed (Fig. 8H)
Male: metasomal color	segments 1–4 red (Figs 5A, 5B)	segments 1–3 or 4 red (Figs 5C, 5D)	segments 1–3 red (Figs 5E, 5F)	segments 1–3 red (Figs 5G, 5H)
Female: frons punctation	entirely close (Fig. 3A)	entirely close (Fig. 3B)	laterally close and medially separated (Fig. 3C)	laterally close and medially separated (Fig. 3D)
Female: scutellar scale posterior margin	truncate to convex (Fig. 4A)	emarginate medially (Fig. 4B)	truncate to convex (Fig. 4C)	truncate to convex (Fig. 4D)

Table 3. Body size variation, mean, standard error (SD) and median of *Nemka* spp.

	N. limi		***N. taiwanensis***		***N. wotani***		***N. yasumatsui***	
	♂	♀	♂	♀	♂	♀	♂	♀
Minimum body size	10.15	7.037	9.230	12	8.982	6.942	8.473	6.147
Maximum body size	19.98	12.31	21.52	13.26	10.87	8.760	18.56	11.95
Mean	14.19	9.542	16.60	N/A	10.14	7.923	12.70	8.337
SD	3.036	2.111	3.923	N/A	0.7865	0.6372	2.639	1.034
Median	14.13	8.545	17.45	N/A	10.15	7.960	13.02	8.245

Table 4. Silverman's test of multimodality.

	H0: one mode; H1: more than one mode	H0: two modes; H1: more than two modes
Nemka yasumatsui ♂	$p = 0$	$p = 0.54$
Nemka yasumatsui ♀	$p = 0.636$	-

Table 5. Recorded or suspected hosts of *Nemka* spp. Abbreviations: C, co-occurrence; E, emerged; I, intruded into host nests; O, observed in nest aggregation; U, unknown.

Host family	Host species	Velvet ant species	Evidence	Reference	Remarks
Pompilidae	*Anoplius reflexus* (Smith)	*N. yasumatsui* (Mickel)	C	This study	
	Pompilus cinereus (Fabricius)	*N. yasumatsui* (Mickel)	C	This study	
Bembicidae	*Bembecinus acanthomerus* (Morice)	*N. aurantiaca* (Skorikov)	O	Lelej (1995)	Recorded as *B. dentipes* (Gussakovskij) (syn. by Schmid-Egger, 2004).
	Bembecinus hungaricus (Frivaldsky)	*N. yasumatsui* (Mickel)	C	This study	
	Bembecinus tridens (Fabricius)	*N. v. viduata* (Pallas)	E	Grandi (1961)	
	Bembix bidentata Vander Linden	*N. v. viduata* (Pallas)	E	Tormos *et al*. (2009)	
	Bembix niponica Smith	*N. yasumatsui* (Mickel)	E	Ono & Kawashima (2013)	
	Bembix olivacea Fabricius	*N. viduata andalusiana* (Skorikov)	E	Templado (1958)	Recorded as *B. mediterranea* Handlirsch (syn. by de Beaumont, 1951).
	Gorytes sp.	*N. v. viduata* (Pallas)	U	André (1899–1903)	
	Stizus continuus (Klug)	*N. v. viduata* (Pallas)	E	Tormos *et al*. (2003); Polidori *et al*. (2010)	
	Stizine wasp	*N. kellyi* (Pagden)	I	Pagden (1934b)	
Crabronidae	*Tachysphex n. nigricolor* (Dalla Torre)	*N. yasumatsui* (Mickel)	C	This study	
Philanthidae	*Cerceris albofasciata* (Rossi)	*N. yasumatsui* (Mickel)	C	This study	
	Cerceris arenaria yanoi Tsuneki	*N. yasumatsui* (Mickel)	C	This study	
	Cerceris bidentula Maidl	*N. kellyi* (Pagden)	I	Pagden (1934b)	Recorded as *C. langkasukae* Pagden (syn. by Krombein, 1981).
	Cerceris japonica Ashmead	*N. yasumatsui* (Mickel)	C	This study	
	Cerceris tuberculata (Villers)	*N. v. viduata* (Pallas)	O	Martynova & Martynov (2021)	
	Larra anathema (Rossi)	*N. v. viduata* (Pallas)	U	Sichel & Radoszkowski (1869–1870)	
Megachilidae	*Megachile communis* Morawitz	*N. viduata luctuosa* (Radoszkowski)	O	Marikovskaya (1968)	Recorded as *M. leucomalla* Gerstäcker (corrected by Praz, 2017).
	Megachile kobensis Cockerell	*N. yasumatsui* (Mickel)	C	This study	
Melittidae	*Dasypoda hiritipes* (Fabricius)	*N. v. viduata* (Pallas)	I	Lichtenstein (1878)	

Chapter 10

Systematics of the male velvet ants of the tribe Smicromyrmini Bischoff (Hymenoptera: Mutillidae) of East Asia: Critical review of the genera and morphological phylogenetics

Disclaimer: *This work is not issued for the purposes of zoological nomenclature and is not considered a published work within the meaning of the International Code of Zoological Nomenclature 4th edition (Article 8.2).*

Abstract

Systematic of the East Asian genera of the Old World tribe Smicromyrmini Bischoff, 1920 are reviewed based on phylogenetic analyses using the male morphology. Genericplacement of the East Asian species of this tribe known from males is discussed. The following 12 genera were recognized: *Andreimyrme* Lelej, 1995, ♂♀; *Chenmyrme* **gen. nov.**, ♂; *Ephucilla* Lelej, 1995, ♂♀; *Ephutomma* Ashmead, 1899, ♂♀; *Hadrodontilla* **gen. nov.**, ♂♀; *Mickelomyrme* Lelej, 1995, ♂♀; *Nemka* Lelej, 1985, ♂♀; *Physetopoda* Schuster, 1949, ♂♀; *Promecilla* André, 1902, ♂♀; *Sinotilla* Lelej, 1995, ♂; *Smicromyrme* Thomson, 1870, ♂♀; *Tsunekimyrme* Lelej, 1995, ♂. Updated genus diagnoses, a key to the East Asian genera of Smicromyrmini, and keys to the East Asian species of those genera are provided. Sex associations for the species of *Ephucilla*, *Hadrodontilla*, and *Sinotilla* are discussed. Keys to female-based species of *Ephucilla* are provided. Eleven new species are described: *Ephuc. aequatoris* **sp. nov.**, ♂ (Indonesia), *Ephuc. bicolor* **sp. nov.**, ♀ (Vietnam), *Ephuc. bifida* **sp. nov.**, ♀ (Indonesia), *Ephuc. okajimai* **sp. nov.**, ♀ (Thailand), *Ephuc. retorta* **sp. nov.**, ♂ (Laos, Vietnam), *M. carinata* **sp. nov.**, ♂ (Indonesia), *M. cristaticauda* **sp. nov.**, ♂ (Vietnam), *M. recondita* **sp. nov.**, ♂ (Thailand), *Si. complanata* **sp. nov.**, ♂ (Thailand, Vietnam), *Si. unica* **sp. nov.**, ♂ (China, Vietnam), and *Sm.* (*Sm.*) *australis* **sp. nov.**, ♂ (Thailand). New combinations are proposed for the following 22 species and two subspecies: *C. undata* (Chen, 1957), **comb. nov.** (from *Ephucilla*), *Ephuc. calacuasana* (Tsuneki, 1993), **comb. nov.** (from *Smicromyrme*), *Ephuc. cyaneiventris cyaneiventris* (André, 1896), **comb. nov.** (from *Sinotilla*), *Ephuc. cyaneiventris gobiana* (Chen, 1957), **comb. nov.** (from *Sinotilla*), *Ephuc. nigrothoracica* (Okayasu, 2018), **comb. nov.** (from *Sinotilla*), *Ephuc. petina* (Mickel, 1937), **comb. nov.** (from *Sinotilla*), *Ephuc. subparallela* (Chen, 1957), **comb. nov.** (from *Sinotilla*), *H. davidi* (André, 1898), **comb. nov.** (from *Andreimyrme*), *H. pekiniana* (André, 1905), **comb. nov.** (from *Sinotilla*), *M. atrata* (Mickel, 1934), **comb. nov.** (from *Smicromyrme*), *M. caecina* (Cameron, 1903), **comb. nov.** (from *Smicromyrme*), *M. lavinia* (Mickel, 1934), **comb. nov.** (from *Smicromyrme*), *M. meator* (Mickel, 1935), **comb. nov.** (from *Smicromyrme*), *M. palacala* (Tsuneki, 1993), **comb. nov.** (from *Smicromyrme*), *Pr. annexa* (Cameron, 1909), **comb. nov.** (from *Andreimyrme*), *Si. dardanus* (Smith, 1857), **comb. nov.** (from *Smicromyrme*), *Si. drola drola* (Zavattari, 1913), **comb. nov.** (from *Ephucilla*), *Si. drola lodra* (Chen, 1957), **comb. nov.** (from Ephucilla), *Si. ilerda* (Cameron, 1902), **comb. nov.** (from *Smicromyrme*), *Si. nitela* (Mickel, 1934), **comb. nov.** (from *Andreimyrme*), *Si. scitula* (Mickel, 1935), **comb. nov.** (from *Smicromyrme*), *Si. sparsilis* (Mickel, 1934), **comb. nov.** (from *Smicromyrme*), *Si. viriata* (Mickel, 1934), **comb. nov.** (from *Andreimyrme*), and *Si. volupia* (Mickel, 1935), **comb. nov.** (from *Andreimyrme*). Five subspecies are raised to full species status: *M. atrata* (formerly *M. lavinia atrata*), *M. nigrogastra* (Mickel, 1934) (formerly *M. semperi nigrogastra*), *Si. columnata* (Chen, 1957) (formerly *Si. serpa columnata*), *Si. nitela* (formerly *Sm. viriata nitela*), and *Si. sparsilis* (formerly *Sm. ilerda sparsilis*). Seventeen new synonymies are proposed for *C. undata* (= *Sm. yuliana* Tsuneki, 1972, **syn. nov.**), *Ephuc. naja* (Zavattari, 1913) (= *Sm. thalia* Mickel, 1933, **syn. nov.**), *Ephuc. petina* (Mickel, 1937) (= *Sm. spinicauda* Chen, 1957, **syn. nov.**, *Si. lambirensis* Lelej,

1996, **syn. nov.**, *Si. belokobylskiji* Lelej, 1995, **syn. nov.**, *Si. calopoda* Okayasu, 2017, **syn. nov.**, and *Si. ohbayashii* Okayasu, 2017, **syn. nov.**), *M. bakeri* (Mickel, 1934) (= *Sm. tanoi* Tsuneki, 1972, **syn. nov.**), *M. caecina* (= *Sm. punctinotus* Mickel, 1935, **syn. nov.**), *M. norna* (Zavattari, 1913) (= *Sm. norna abnorma* Chen, 1957, **syn. nov.**), *P. decora* (Smith, 1879) (= *Sm. contractula* Chen, 1957, **syn. nov.**), *Si. dardanus* (= *Sm. dardanus salacia* Mickel, 1935, **syn. nov.**, *Sm. gribodoana* Invrea, 1943, **syn. nov.**, and *Sm. cyaneiventris boheana* Chen, 1957, **syn. nov.**), *Si. drola drola* (= *Sm. hombuceiana* Tsuneki, 1982, **syn. nov.**), *Si. nitela* (= *Sm. aponis* Tsuneki, 1993, **syn. nov.**), and *Si. viriata* (= *Sm. mindanaonis* Tsuneki, 1993, **syn. nov.**) *Hadrodontilla pekiniana* is regarded as the female of *H. davidi*, but formal synonymization is postponed until more evidence is obtained. The originally designated type species of *Sinotilla*, *Si. boheana* (Chen, 1957), is here regarded a new junior synonym of *Si. dardanus*. The latter species is designated as the type species of *Sinotilla* under Article 70.3.2 of ICZN. Phylogenetic analyses based on 123 morphological characters provided support for the monophyly of most genera. However, potential paraphyly or polyphyly of *Ephucilla* and *Promecilla* was suggested. The East Asian smicromyrmine genera were generally defined only by combination of plesiomorphic and/or homoplastic characters with few unique synapomorphies.

Key words
Aculeata, morphological evolution, Mutillinae, nomenclature, Oriental Region, Palaearctic Region, taxonomy.

Introduction

Velvet ants are cosmopolitan groups of parasitoid stinging wasps including some 4600 species in 225 genera of the families Mutillidae Latreille, 1802 and Myrmosidae Fox, 1894 (Brothers & Lelej, 2017; Brothers *et al*., 2019; Lelej & Brothers, 2008; Pagliano *et al*., 2020; Waldren *et al*., 2023). Despite of their usefulness in biogeography and evolutionary ecology (Wilson *et al*., 2012ab, 2015, 2018), systematic basis of velvet ants is disproportionately incomplete.

East Asia is known as a biodiversity hotspot of terrestrial ecosystem (Jenkins *et al*., 2013; Myers *et al*., 2000; Roll *et al*., 2017), with the world's highest discovery potential of terrestrial animal new species and endemism (Kass *et al*., 2022; Kier *et al*., 2009; Moura & Jetz, 2021; Wikramanayake *et al*., 2002). The East Asian velvet ant fauna includes 401 species and 39 subspecies in 44 genera; the number of recorded species for each country is disparate: 120 species are known from China mainland, 59 from Taiwan, three from North Korea, nine from South Korea, 20 from Japan, 48 from Vietnam, 24 from Laos, six from Cambodia, 69 from Thailand, 98 from Malaysia, three from Singapore, 92 from Indonesia, four from Brunei, 60 from Philippines, and one from Timor-Leste (Pagliano *et al*., 2020, corrected and updated following Lelej, 2020ab, 2021, 2023; Lelej *et al*., 2023; Okayasu, 2018, 2020, 2021, 2022, 2023ab; Okayasu *et al*. 2021ab; Thaochan *et al*., 2022; Williams *et al*., 2019bc). Biased sampling by the previous researchers is the most conceivable cause of this situation. The true diversity of velvet ants can be much higher than currently recognized in most of those regions, given the high species diversity and the rate of undescribed species in tropics (e.g., Brothers in Taylor, 1983; Nonveiller, 1980; Okayasu *et al*., 2021b). In fact, during about 30 field days in two expeditions in 2017 and 2018 to southern Thailand, Williams *et al*. (2019b) collected 592 female specimens that were classified into 38 species, of which 17 were new to science and 12 represented new country records, doubling the number of known mutillid species in Thailand. Discovery of even more new species from East Asia is expected. A systematic basis for genus-level classification of East Asian velvet

ants is required to appropriately compare them with close congeners including previously described species.

The tribe Smicromyrmini Bischoff, 1920 includes 26 genera and four subgenera from the Afrotropical, Oriental, and Palaearctic Regions, with the type genus *Smicromyrme* Thomson, 1870 (Brothers & Lelej, 2017; Lelej & Williams, 2023). After C. E. Mickel regarded many of the East Asian species of *Mutilla* Linnaeus, 1758 as *Smicromyrme* (Mickel, 1933ab, 1934, 1935), a large number of eastern Palaearctic and Oriental species had been described in or transferred to that genus by some authorities such as Mickel himself (1933a, 1934, 1935, 1936, 1937), C.-w. Chen (1957), K. Hammer (1962), H. T. Pagden (1934a, 1949), K. Tsuneki (1972abc, 1973, 1982, 1993a), and Tsuneki *et al*. (1993), making *Smicromyrme* a "wastebasket" taxon (Gould, 1985). For the last three decades, A.S. Lelej (1985, 1993, 1995ab, 1996bc, 2002, 2005) and collaborators (Brothers & Lelej, 2017; Lelej & Nemkov, 1997; Lelej & Yamane, 1992; Lelej *et al*., 2001) sorted *Smicromyrme* species into other genera including new ones, and arranged them into Smicromyrmini and Trogaspidiini Bischoff, 1920 based on morphological phylogenetic analyses. His taxonomic concepts have been followed by recent taxonomic papers and catalogs (Lelej, 2007; Lelej & Williams, 2023; Lo Cascio, 2015; Okayasu, 2017, 2018, 2020; Okayasu *et al*., 2018; Pagliano *et al*., 2020; Williams *et al*., 2019b; Zhou *et al*., 2018ab). However, reclassification of *Smicromyrme* is still ongoing; 32 out of 35 East Asian species are only tentatively placed in the *Smicromyrme*. This genus is widely distributed throughout the Old World, and Afrotropical members of this genus should be revised as well. Besides, the phylogenetic relationship among the genera within Smicromyrmini is largely unknown.

To facilitate the study of this insect in East Asia, construction of clear generic classification is a top priority. However, because of the strong sexual dimorphism observed in velvet ants (Brothers, 1989), many East Asian species are known from one sex only (Lelej, 2005). Systematic and phylogenetic treatments of the Smicromyrmini genera are thus difficult. Generic and subgeneric concepts in this tribe depend exclusively on the male morphology due to the relative usefulness of the male genitalia (Williams *et al*., 2019b), leaving many female-based species that cannot be reliably placed in any genera. Also, most of the East Asian species are included in the outdated literature only and have never been revised since then (Okayasu *et al*., 2021a; Williams *et al*., 2019b). Therefore, reliable identification of newly collected material often depends on direct comparison with types or identified specimens, hampering molecular studies to associate dimorphic sexes (e.g., Pilgrim & Pitts, 2006).

Two practical solutions of this situation would be: 1) to conduct intensive field surveys in limited areas to obtain fresh specimens feasible for DNA analyses and associate both sexes using molecular technique (e.g., Williams *et al*., 2019b); 2) to arrange the smicromyrmine genera based solely on the male morphology using museum specimens, specifically types, and subsequently associate females to males that are reliably placed in the revised classification system. The first approach is particularly useful in that it enables reassessment of the genus-level classification simultaneously for both males and females. The drawback is the cost and time required for field trips and molecular experiments. More importantly, in the first approach, taxon sampling is inevitably limited due to the geographical settings, which can lead to poor recognition of genus-limits and inaccurate phylogenetic inference (Bernot *et al*., 2023; Branstetter *et al*., 2017; Nabhan & Sarkar, 2012; Plazzi *et al*., 2010). In the present study, the second approach is adopted to comprehensively search for diagnostic morphological characters. Below, I review the East Asian genera of the Smicromyrmini and analyzed the phylogenetic relationship among them using the male morphology. The current status of sex association is reviewed.

Material and methods

Taxon sampling

This chapter focuses on the smicromyrmine genera and species occurring in East Asia as defined by Okayasu *et al*. (2018). In order to improve the accuracy of phylogenetic analyses, taxon sampling was intended to be as extensive as possible and several smicromyrmine taxa that are known from outside of East Asia were included. Terminal taxa included 63 species and one subspecies in 12 smicromyrmine genera including new ones described herein. Outgroup taxa included species from three tribes in Mutillinae, Mutillini Latreille, 1802 (seven species in three genera), Trogaspidiini Bischoff, 1920 (64 species and subspecies in 16 genera), Zeugomutillini Waldren, 2023 (two species in two genera), and the subfamily Myrmillinae Bischoff, 1920 (six species in two genera) which was found to be sister to Mutillinae by Brothers & Lelej (2017) and Waldren *et al*. (2023). Taxa included and the sources of material are listed in Table 1.

Although phylogenetic analyses were based solely on the male morphology, the females of the genera *Ephucilla* Lelej, 1995 and *Sinotilla* Lelej, 1995 in the current concepts are taxonomically reviewed to solve the confusion in sex association of these genera. As a supplement, a key to East Asian smicromyrmine genera based on the female morphology was compiled using the published information (Lelej, 1985, 1995b, 2002, 2005; Lelej & Williams, 2023) and female specimens examined in this and previous studies (Okayasu, 2018, 2022; Okayasu *et al*., 2018, 2021b; Williams *et al*., 2019b).

Material

The present study is primarily based on 1,057 male specimens from East Asia. Additional 571 female specimens were examined to review sex association and distribution of East Asian smicromyrmines. The material for all ingroup and outgroup taxa was obtained from the following institutes.

ELKU Entomological Laboratory, Faculty of Agriculture, Kyushu University, Fukuoka, Japan.
EUMJ Ehime University Museum, Matsuyama, Japan.
FFPRI Forestry and Forest Products Research Institute, Tsukuba, Japan.
FRIM Forest Research Institute Malaysia, Selangor, Malaysia.
HMNH Hiwa Museum for Natural History, Shôbara, Japan.
HSC Hirohisa Suda Personal Collection, Sakura, Japan.
IBSS Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far East Branch of the Russian Academy of Sciences, Vladivostok, Russia (formerly Institute of Biology and Soil Science).
IEBR Institute of Ecology and Biological Resources, Vietnam Academy of Science and Technology, Hanoi, Vietnam.
KMNH Kitakyushu Museum of Natural History and Human History, Kitakyushu, Japan.
KUM Kyushu University Museum, Fukuoka, Japan.
MNHAH Museum of Nature and Human Activities, Sanda, Japan.
MTC Mamoru Terayama Collection in Laboratory of Applied Entomology, Department of Agricultural and Environmental Biology, The University of Tokyo, Tokyo, Japan.
NARO Insect Museum, National Agriculture and Food Research Organization, Tsukuba, Japan (formerly Institute for Agro-Environmental Sciences).
NHMUK The Natural History Museum, London, UK.

NMNH National Museum of Natural History, Smithsonian Institution, Washington D.C., USA.
NSMT National Museum of Nature and Science, Tsukuba, Japan.
OMNH Osaka Museum of Natural History, Osaka, Japan.
RUMF Ryukyu University Museum "Fujukan", Nakagami, Okinawa, Japan.
SDEI Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany.
SEHU Hokkaido University Insect Collection, Sapporo, Japan.
SKYC Seiki Yamane Collection in Kagoshima University, Kagoshima, Japan.
TARI Taiwan Agricultural Research Institute, Taichung, Taiwan.
THNHM Thailand Natural History Museum, National Science Museum, Pathum Thani, Thailand.
TKPM Tokushima Prefectural Museum, Tokushima, Japan.
TMUZ Systematic Zoology Laboratory, Tokyo Metropolitan University, Tokyo, Japan.
TPM Tochigi Prefectural Museum, Utsunomiya, Japan.
TUA Laboratory of Entomology, Tokyo University of Agriculture, Atsugi, Japan.
VNMN Vietnam National Museum of Nature, Vietnam Academy of Science and Technology, Hanoi, Vietnam.
ZMNB Museum für Naturkunde, Humbolt Universität, Berlin, Germany.
ZMUC Natural History Museum of Denmark, University of Copenhagen, Universitetsparken, Denmark.

The following acronyms are also used to denote institutes housing type specimens that were not personally examined for the present study.

HNHM Magyar Természettudományi Múzeum, Budapest, Hungary.
HNMB Magyar Nemzeti Múzeum, Budapest, Hungary.
IMK Indian Museum, Kolkata, India.
MNHN Muséum national d'Histoire naturelle, Paris, France.
MSNG Museo Civico di Storia Naturale "G. Doria", Genoa, Italy.
OUMNH Oxford University Museum of Natural History, Oxford, UK.
RMNH Naturalis Biodiversity Center, Leiden, South Holland, the Netherlands.
UMSP University of Minnesota, St. Paul, Minnesota, USA.
ZISP Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia.
ZMMU Zoological Museum of Moscow University, Moscow, Russia.

Old names of insect collecting localities in Taiwan were translated into the present names using Chu & Yamanaka (1973–1975) and Kojima *et al*. (2011). In the synonymic lists and material examined sections, acronyms for depository and additional or corrected data by the author are given in square brackets. New distributional records are indicated by an asterisk (*).

Taxonomic work

Specimens were mostly examined with a Leica M205C stereomicroscope (10–160× magnification). Comparative measurements were taken directly from specimens using an ocular micrometer on the stereomicroscope. Most habitus photographs were taken using a Canon EOS 6D Mark II DSLR camera equipped with a Canon MP-E 65mm f/2.8 1–5× Macro Photo lens. External morphological features were imaged with a Canon EOS 6D Mark II attached to a Leica M205C. A semitransparent plastic cup was placed around the specimen to disperse the light. Focus stacking was done using Zerene Stacker (Zerene Systems LLC,

Richland, WA, USA). Images were post-processed using Adobe Photoshop and assembled into plates using Adobe Illustrator (Adobe Inc., San Jose, CA, USA).

Specimens were identified based on examination of types or other identified specimens, identification keys (Lelej, 1985, 1995a; Mickel, 1933ab, 1934, 1935), and published descriptions, as specified in Identification source sections. Some species were recognized from photographs provided by NHMUK, NMNH, and ZMNB for online databases (Chan *et al*., 2024; National Museum of Natural History, 2024; Natural History Museum, 2014).

Regarding the morphological terminology in the context of insect systematics, researchers have historically employed disparate, often incompatible, repertoires of terms (Das Pol *et al*., 2023; Girón *et al*., 2023; Yoder *et al*., 2010). In the present study, I follow the standardized frameworks by the Hymenoptera Anatomy Ontology (Hymenoptera Anatomy Consortium, 2024; Yoder *et al*., 2010) and Das Pol *et al*. (2023) with slight modification for the male genitalia (Figs 1, 2), even though their terminologies are partially incongruent with those traditionally used to describe velvet ant morphology (e.g., André, 1899; Berland, 1925; Bingham, 1897; Brothers, 1975; Giner Marí, 1944; Invrea, 1965; Lelej, 1985; Osten, 1982; O'Toole, 1975; Radoszkowski, 1885; Snodgrass, 1941). The following abbreviations are used: F = flagellomere; LOD = lateral ocellus diameter; LOL = lateral ocellar line (distance between median and lateral ocelli); MOD = median ocellus diameter; OOL = ocular-ocellar line (distance between lateral ocellus and compound eye); POL = posterior ocellar line (distance between lateral ocelli); S = metasomal sternum; T = metasomal tergum.

Prior to dissection, dried specimens were relaxed by soaking in 80% ethanol for several hours. Male genitalia were extracted from the bodies by carefully pulling the harpe or holding the whole genitalia with forceps. Extracted genitalia were soaked in a 10% potassium hydroxide (KOH) solution without heating for one to three hours to dissolve the muscles, and subsequently soaked in a 25% acetic acid solution to neutralize. Then, genitalia were placed and observed in a Petri dish filled with 80% ethanol under a stereomicroscope. In the Petri dish, cleaned genitalia were further dissected by the following procedure: 1) remove the cupula by pulling it with forceps; 2) cut the membrane between right and left gonostipes using a point of a minutien pin attached to a handle; 3) remove muscles in genital capsule and extract paired penisvalvae with forceps; 4) detach the spatha to separate right and left penisvalvae. Dissected parts were photographed under the incident light in a Petri dish filled with glycerin except that the penisvalvae were placed on a glass slide with a drop of glycerin and a cover slip. After examination, all dissected parts were stored in micro vials filled with glycerin and pinned with their respective bodies.

Phylogenetic analysis

The phylogenetic relationship among East Asian smicromyrmine genera was analyzed using male morphological characters under maximum parsimony criterion. Species were used as terminal taxa to assess monophyly of the genera, thus I scored characters that were useful for both species-level and genus-level classification. A total of 123 characters comprising 325 different states (84 binary and 39 multistate) was coded, of which one is obtained from the general body color, 43 from the head (including appendages), 21 from the mesosoma, two from the wings, six from the legs, 28 from the metasoma, and 22 from the male genitalia. Autapomorphies of species are parsimony-uninformative and behave as if they were missing entries (Goloboff, 2022a). However, they were included in the data matrix to facilitate future identification. Characters and states defining the Trogaspidiini genera were also scored to get better resolution of phylogeny, because the Trogaspidiini was nested within the Smicromyrmini in the preliminary analyses. Observed variation in character states within

terminal taxa was treated as polymorphism. Inapplicable and unobserved states were coded with a hyphen (-) and a question mark (?), respectively, although both are interpreted as missing data (gap) by the software. The final data matrix (Table 2) was built using Mesquite version 3.81 (Maddison & Maddison, 2023) and saved as NEXUS and TNT format files.

The heuristic searches of the most parsimonious or best-fitting tree were performed with the Willi Hennig Society edition of TNT version 1.6 (Goloboff & Catalano, 2016; Goloboff & Morales, 2023; Goloboff *et al*., 2003b, 2008b) using the traditional search and the following settings: general RAM of 1,000 Mbytes, memory holding 500,000 trees (*hold 500000*), collapsing rule as TBR, Wagner trees (Farris, 1970) as starting trees, one random seed, 10,000 replications, branch swapping algorithm as TBR, and 10 trees saved per replication. Other settings were retained in default mode. *Myrmilla calva* (Villers, 1789) was designated as the outgroup to root the trees. All characters were treated as discrete and nonadditive/unordered (Fitch parsimony; Fitch, 1971). Minimum and maximum possible steps were calculated using TNT (*minmax*), which were 199 and 3507, respectively. If multiple equally parsimonious trees were recovered, monophyletic groups that are present in all of the trees are summarized as a strict consensus tree. Clade supports were evaluated as frequency differences (Group present/Contradicted, or GC scores) from symmetric resampling (Goloboff *et al*., 2003a) based on the most parsimonious trees recovered under equal weights. Resampling was done using TNT with 33% change probability, 1,000 pseudoreplicates, cut = 0, and traditional search in default setting (*resample sym gc replications 1000*). After phylogenetic analyses, the morphological data matrix and tree files were imported into WinClada-ASADO version 1.61 (Nixon, 2002, 2004) for unambiguous character optimization and calculation of consistency and retention indices (ci and ri) for characters and ensemble consistency and retention indices (CI and RI) for trees (Farris, 1989; Kluge & Farris, 1969). Phylogenetic trees and character-state changes were visualized with WinClada and assembled into plates with Adobe Illustrator. Unique changes and homoplastic changes were mapped onto trees with solid and open rectangles, respectively.

An initial analysis was performed with all characters equally weighted. Subsequently, implied weighting scheme was employed to down-weight characters in relation to their degrees of homoplasy (Goloboff, 1993; Goloboff *et al*., 2008a). With implied weighting, characters with more homoplasy (thus less reliable) are given lower weights during tree search. This method tends to generate more resolved trees (Goloboff, 1993, 1995, 2022b; Ramírez, 2003; Turner & Zandee, 1995). The extent to which the homoplastic characters are down-weighted is defined by the concavity constant *k*. Under implied weighting, TNT searches the tree that maximizes the sum of character fits (*F*). The fit of the character *i* is defined as $f_i = k/(h_i + k)$, where *h* refers to a number of homoplastic (extra) steps defined as *h* = (number of observed steps based on the most parsimonious tree under equal weights) – (minimum possible steps); thus, a perfectly hierarchical (homoplasy-free) character has a $f = 1$. The optimal tree has the maximum possible *F*, which is $\Sigma f_i = \Sigma k/(h_i + k)$. Characters with high level of homoplasy have smaller *f* value and poorly contribute to the resulting tree. The formula suggests that the higher the *k* value is, the lower the strength against homoplasy is. Even though this parameter greatly influences the results of analyses, specifically for large datasets (Goloboff, 2022b), the "optimal" *k* value cannot be determined due to, in part, our ignorance of true phylogeny and homoplasy (Congreve & Lamsdell, 2016; Goloboff, 2022b; Goloboff *et al*., 2008a). Alternatively, a range of *k* values should be explored. Because of the concave function of implied weighting, higher *k* values tend to produce more similar results (Goloboff, 1993; Mirande, 2009). Therefore, Mirande (2009) pointed out that regularly distributed *k* values provide artificially biased results towards higher values (milder weights). Instead, appropriate intervals of *k* values are defined in a way that a character with average homoplasy has the character fit of regular intervals of 50, 60, 70%, etc., comparing to the

perfectly hierarchical character (Mirande, 2009, further explained by Reemer & Ståhls, 2013 and Weiler *et al*., 2016). To calculate the *k* value, the formula is rewritten as $k = (f \times h_m)/(1 - h_m)$, where h_m represents the average homoplasy per character defined as h_m = (observed tree length of the most parsimonious tree under equal weights) – (minimum possible length)/(number of characters). Various *f* values (0.5, 0.6, 0.7, etc.) are assigned to this formula. In the present study, a range of *k* values was determined to result in average character fits of 50, 53, 56, 59, 62, 65, 68, 71, 74, 77, 80, 83, 86, 89, 92, 95, 98% of the perfectly hierarchical one, with $h_m = 4.992$. The *k* values were computed using the TNT script *aaa.run* (Mirande, 2009) with the following settings (*aaa 10 17 50 98 7*): hits 10 times, 17 distortion groups, minimum value of distortion in an average character 50, maximum value of distortion in an average character 98, and searching level 7.

In contrast to the above argument, Goloboff *et al*. (2008a) proposed that the *k* value should be calculated as the function of *N*, which is defined as *N* = (cost of adding the first extra step to a character without homoplasy)/(cost of adding the last step of homoplasy to the most homoplastic character), to avoid overweighting while down-weighing homoplastic characters. With *N* = 15, Goloboff *et al*. (2008a) acquired clearly improved results over those for equal weights. The TNT script *setk.run* was written by J. Salvador Arias (Instituto Miguel Lillo, San Miguel de Tucumán, Argentina) to calculate the *k* value under *N* ~15. This script has been widely used by systematists (e.g., Brothers & Lelej, 2017; Hermes *et al*., 2014; Santos *et al*., 2015; Troya *et al*., 2022), although theoretical and empirical supports for this method have not been addressed in further detail. In the present study, the TNT script *setk_trans.run*, an English translation of *setk.run* by Wilson & Shaik (2022), was used to find an "appropriate" *k* value for the dataset.

The resulting *k* values (Table 3) were used in heuristic searches of the best-fitting tree outlined above. They substantially cover the default setting of implied weighting (*k* = 3) and half the number of terminal taxa (Goloboff & Arias, 2019), allowing exploration of an adequate range of parameters. In the present study, however, I attempt to manually examine reference trees resulted from implied weighing for topological comparison only; the optimal *k* value for the dataset is not discussed like some systematists do in sensitivity analysis (Giribet, 2003; Mirande, 2009; Ramírez, 2003; Wheeler, 1995).

Phylogenetic results

Characters and states for phylogenetic analysis

Values between square brackets are length (number of steps for state changes), ci, and ri for the characters based on the most parsimonious trees recovered by an equally weighted analysis. Multiple values may be obtained depending on the topology of equally parsimonious trees.

General color pattern

1. Body color excluding head: (0) mesosoma partially or entirely red, metasoma black or bluish; (1) mesosoma black, metasoma partially or entirely red; (2) entirely black; (3) both mesosoma and metasoma partially red. [length = 23, 24, 25; ci = 12, 13; ri = 68, 70, 71]

Head and appendages

2. Head color: (0) black; (1) red. [length = 2; ci = 50; ri = 50]
3. Head size: (0) small, distance between eyes ~1.2× eye height; (1) enlarged, distance between eyes more than 1.3× eye height. [length = 5; ci = 20; ri = 83]
4. Vertex: (0) rounded; (1) apparently elevated beyond ocellar region with distinct anterior

and posterior faces. [length = 3, 4; ci = 25, 33; ri = 94, 96]
5. Vertex posterolateral margin: (0) slightly convergent posteriorly, leaving transverse posterior margin; (1) strongly convergent posteriorly. [length = 2; ci = 50; ri = 96]
6. Median and lateral ocelli: (0) small, median and lateral ocelli separated by approximate median ocellus diameter; (1) enlarged, median and lateral ocelli separated by ~1/2× median ocellus diameter. [length = 4; ci = 25; ri = 25]
7. Ocellar region convexity: (0) only slightly convex; (1) gibbose; (2) convex, vertex posteriorly to ocellar region also convex. [length = 3, 4; ci = 50, 66; ri = 97, 98]
8. Internal eye margin: (0) straight; (1) slightly emarginate; (2) deeply emarginate. [length = 2; ci = 100; ri = 100]
9. Median ocellus posterior longitudinal carina: (0) absent; (1) present. [length = 7; ci = 14; ri = 77]
10. Frons surface sculpture: (0) punctate; (1) longitudinally striate. [length = 2; ci = 50; ri = 97]
11. Frons carina: (0) without carina; (1) with longitudinal wide carina anteriorly to lateral ocellus. [length = 6, 7; ci = 14, 16; ri = 76, 80]
12. Frons setae: (0) sparse suberect; (1) apparently denser than vertex setae and recumbent to appressed. [length = 12; ci = 8; ri = 69]
13. Frons longitudinal sulcus: (0) without medial sulcus: (1) with shallow sulcus; (2) with deep sulcus. [length = 14, 15; ci = 13, 14; ri = 72, 74]
14. Antennal scrobal carina: (0) arcuate; (1) inverted V-shaped; (2) absent. [length = 8; ci = 12; ri = 53]
15. Antennal rim: (0) convex; (1) flat, leaving lateral carina. [length = 3; ci = 33; ri = 93]
16. Minimum distance between antennal rims: (0) 2× antennal rim width; (1) subequal to antennal rim width. [length = 3, 4; ci = 25, 33; ri = 75, 83]
17. Malar distance: (0) long, ventral eye margin and mandibular base well separated; (1) ventral eye margin and mandibular base closely located. [length = 4; ci = 25; ri = 25]
18. Occipital carina shape: (0) sharp; (1) wide (2) projecting over pronotal collar. [length = 6; ci = 33; ri = 20]
19. Occiput dorso-lateral margin: (0) with internal process; (1) entire. [length = 4; ci = 25; ri = 85]
20. Postgenal bridge: (0) flat; (1) concave; (2) projecting. [length = 4; ci = 50; ri = 71]
21. Postgenal bridge dorso-lateral margin: (0) flat; (1) delimited with sharp elevation. [length = 10, 11, 12; ci = 8, 9, 10; ri = 71, 73, 76]
22. Clypeus convexity: (0) deeply concave; (1) subconvex; (2) dorsally elevated; (3) gibbose. [length = 9; ci = 33; ri = 92]
23. Clypeus dorso-medial carina: (0) simple; (1) forming process dorsally. [length = 2; ci = 50; ri = 87]
24. Clypeus subventral transverse line: (0) without carina, flange, or process; (1) highly crooked; (2) with medial paired teeth; (3) medially concave, leaving sublateral rounded tubercles; (4) with transverse flange overhanging ventral clypeal margin; (5) medially projecting ventrad in rectangular shape; (6) medially projecting ventrad in rectangular shape, with dorsal transverse carina; (7) medially projecting ventrad in rectangular shape, with robust process. [length = 12, 13; ci = 53, 58; ri = 92, 93]
25. Clypeus subventral transverse flange (- if clypeus without transverse flange): (0) complete, well defined; (1) medially interrupted, leaving lateral rounded tubercles. [length = 2; ci = 50; ri = 75]
26. Clypeus ventral margin: (0) without teeth; (1) medially emarginate leaving lateral teeth; (2) with medial paired teeth. [length = 3, 4; ci = 25, 33; ri = 0, 33]
27. Clypeus subventral transverse impression: (0) absent; (1) present. [length = 11, 12; ci = 8,

9; ri = 63, 66]
28. Mandible width: (0) narrowed distally; (1) widened distally. [length = 4, 5; ci = 20, 25; ri = 55, 66]
29. Mandible apex: (0) bidentate; (1) tridentate. [length = 8, 9; ci = 11, 12; ri = 79, 82]
30. Mandible subdistal internal tooth: (0) absent; (1) present. [length = 4; ci = 25; ri = 25]
31. Mandible subproximal internal tooth: (0) present; (1) absent. [length = 2; ci = 50; ri = 90]
32. Mandible dorso-lateral carina: (0) weakly developed; (1) highly elevated only proximally; (2) highly elevated, extending to subapical tooth; (3) absent. [length = 9; ci = 33; ri = 70]
33. Mandible ventral margin: (0) straight; (1) emarginate proximally, forming large tooth; (2) not emarginate with small rounded proximal lobe; (3) not emarginate with large rounded proximal lobe; (4) virtually straight with small triangular process. [length = 14, 15; ci = 26, 28; ri = 76, 78]
34. Mandible additional ventral process on proximo-ventral tooth (- if mandible ventral margin straight): (0) absent; (1) present. [length = 1; ci = 100; ri = 100]
35. Scape ventral carina: (0) 0; (1) 1; (2) 2. [length = 10, 11, 12; ci = 16, 18, 20; ri = 52, 57, 61]
36. Scape between two ventral carinae (- if scape with one ventral carina or without it): (0) punctate; (1) smooth, polished. [length = 4, 5; ci = 20, 25; ri = 42, 57]
37. F1 length: (0) as long as wide; (1) shorter than wide; (2) longer than wide but shorter than F2; (3) as long as or longer than F2. [length = 15, 16; ci = 18, 20; ri = 84, 85]
38. F1 shape: (0) cylindrical; (1) compressed. [length = 5; ci = 20; ri = 73]
39. Flagellomeres apices: (0) truncate; (1) bifid. [length = 1; uninformative]
40. Hypostomal carina posterior portion: (0) weakly developed; (1) lamellately projecting over proboscidial fossa. [length = 5; ci = 20; ri = 20]
41. Prementum convexity: (0) convex; (1) flat. [length = 2, 3; ci = 33, 50; ri = 0, 50]
42. Prementum carina or process: (0) without carina; (1) unicarinate; (2) bicarinate; (3) with dorsal rounded process. [length = 27, 28; ci = 10, 11; ri = 59, 61]
43. Prementum surface sculpture: (0) mostly smooth; (1) punctate; (2) striate. [length = 6; ci = 33; ri = 55]
44. Maxillary palpus length: (0) much shorter than antenna; (1) 0.5–1.0× antenna length. [length = 5; ci = 20; ri = 83]

Mesosoma and appendages
45. Pronotum humeral carina: (0) absent; (1) weakly developed; (2) sharp. [length = 18, 19, 20; ci = 10, 11; ri = 25, 29, 33]
46. Mesoscutum convexity: (0) strongly convex; (1) weakly convex. [length = 3; ci = 33; ri = 94]
47. Notaulus: (0) reaching posterior margin of pronotum; (1) present on posterior 1/3–2/3 of mesoscutum; (2) very short; (3) obliterated. [length = 11; ci = 27; ri = 75]
48. Notaulus width (- if absent): (0) equally wide; (1) apparently widened posteriorly. [length = 4; ci = 25; ri = 84]
49. Parapsidal signum: (0) projecting dorsad; (1) linear. [length = 2; ci = 50; ri = 0]
50. Parascutal carina: (0) absent; (1) weakly developed; (2) strongly developed, forming elevated process on postero-lateral angle of mesoscutum. [length = 8, 9; ci = 22, 25; ri = 78, 81]
51. Tegula length: (0) elongate; (1) short rounded. [length = 6, 7; ci = 14, 16; ri = 80, 83]
52. Forewing distance between origin of RS on vein SC and proximal margin of pterostigma: (0) apparently less than pterostigma length; (1) subequal to pterostigma length; (2) 1.15–2.0× pterostigma length. [length = 9; ci = 22; ri = 87]
53. Forewing cell 2RS: (0) absent; (1) present. [length = 1; ci = 100; ri = 100]

54. Transscutal impression shape: (0) slender; (1) oval. [length = 8, 9; ci = 11, 12; ri = 81, 84]
55. Mesoscutellum convexity: (0) strongly convex; (1) weakly convex, slightly exceeding the level of mesoscutellum. [length = 8, 9; ci = 11, 12; ri = 88, 90]
56. Mesoscutellum modification: (0) punctate; (1) with medial impunctate line; (2) with medial carina; (3) with medial process. [length = 11; ci = 27; ri = 78]
57. Metascutellum surface sculpture: (0) medially interrupted by impunctate line; (1) punctate throughout. [length = 6, 7; ci = 14, 16; ri = 66, 72]
58. Mesopleural transverse impression: (0) lateral mesopleural face divided into dorsal and ventral convexities by transverse impression; (1) lateral mesopleural face evenly convex. [length = 4; ci = 25; ri = 93]
59. Mesopleural ventral process or swelling: (0) without ventral process or swelling; (1) with ventral triangular process; (2) with rounded swelling. [length = 3; ci = 66; ri = 97]
60. Mesopleural ventral impunctate line: (0) absent; (1) present. [length = 25, 26, 27; ci = 3, 4; ri = 61, 63, 64]
61. Mesopleural precoxal transverse carina: (0) absent; (1) present. [length = 17; ci = 5; ri = 67]
62. Metathoracic spiracle: (0) circular; (1) oval. [length = 9; ci = 22; ri = 56]
63. Metasternum: (0) shorter than coxal height; (1) longer than coxal height. [length = 1; uninformative]
64. Propodeum length in dorsal view: (0) half as long as pronotum + mesoscutum length; (1) as long as or longer than pronotum + mesoscutum length. [length = 2; ci = 50; ri = 85]
65. Propodeum: (0) with distinct dorsum and posterior slope; (1) gradually sloping. [length = 10; ci = 10; ri = 80]
66. Propodeum antero-medial elongate cell: (0) short; (1) long, reaching posterior half of propodeum. [length = 4, 5; ci = 20, 25; ri = 91, 93]
67. Propodeum sublateral longitudinal carina: (0) absent; (1) present. [length = 5; ci = 20; ri = 89]
68. Leg color: (0) uniformly dark; (1) dark, with femora, tibiae, and tarsi partially yellowish red; (2) uniformly yellowish red. [length = 5, 6; ci = 33, 40; ri = 33, 50]
69. Procoxa posterior process: (0) absent; (1) present. [length = 1; uninformative]
70. Protibial spur: (0) simple; (1) spatulate. [length = 1; ci = 100; ri = 100]
71. Mesocoxa ventral face: (0) evenly convex; (1) laterally swollen. [length = 2; ci = 50; ri = 50]
72. Metacoxa internal carina: (0) weak; (1) lamellately projecting; (2) absent. [length = 6, 7; ci = 14, 16; ri = 45, 54]
73. Metacoxa ventral face: (0) evenly convex; (1) laterally swollen; (2) flat with dense erect microsetae. [length = 5; ci = 40; ri = 25]

Metasoma and male genitalia

74. T1 lateral margins: (0) weakly convergent anteriorly, providing sessile appearance; (1) strongly convergent anteriorly, providing subsessile appearance. [length = 2, 3; ci = 33, 50; ri = 87, 93]
75. T1 spiracle: (0) flat; (1) projecting. [length = 4; ci = 25; ri = 40]
76. T1 posterior margin: (0) with setal fringe; (1) with setal band. [length = 6; ci = 16; ri = 50]
77. T1 ventro-lateral margin: (0) with few punctures only; (1) densely punctate. [length = 1; ci = 100; ri = 100]
78. S1 carina: (0) without carina; (1) with medial longitudinal carina. [length = 2; ci = 50; ri = 87]
79. T2 width: (0) as wide as mesonotal width including tegulae; (1) apparently wider than

mesonotal width including tegulae. [length = 4; ci = 25; ri = 83]
80. T2 disc convexity: (0) evenly convex; (1) abruptly convex. [length = 15; ci = 6; ri = 65]
81. T2 posterolateral angle convexity: (0) evenly convex; (1) abruptly terminating. [length = 1; ci = 100; ri = 100]
82. T2 posterior margin: (0) with setal fringe; (1) with setal band. [length = 6, 7, 8; ci = 12, 14, 16; ri = 58, 64, 70]
83. S2 antero-medial portion: (0) without carina; (1) with longitudinal carina; (2) swollen. [length = 16; ci = 12; ri = 80]
84. S2 lateral portion: (0) evenly convex; (1) longitudinally gibbose. [length = 1; uninformative]
85. S2 posterior process: (0) 0; (1) 1; (2) 2. [length = 4; ci = 50; ri = 50]
86. S2 felt line: (0) present; (1) absent. [length = 8, 9; ci = 11, 12; ri = 84, 86]
87. T3–4 shape: (0) not constricted; (1) anteriorly and posteriorly constricted. [length = 1, 2; ci = 50, 100; ri = 0, 100]
88. T3 setae: (0) with sparse setae; (1) with setal band. [length = 16, 17; ci = 5, 6; ri = 60, 62]
89. T4 setae: (0) with sparse setae; (1) with setal band. [length = 8; ci = 12; ri = 22]
90. S6: (0) flat; (1) with lateral process. [length = 4; ci = 25; ri = 66]
91. T7 surface sculpture: (0) punctate throughout; (1) with slender impunctate line; (2) with triangular impunctate line; (3) with medial narrow impunctate convex line; (4) with medial rounded impunctate convexity. [length = 30, 31, 32; ci = 12, 13; ri = 72, 73, 74]
92. T7 posterior region: (0) flat; (1) laterally concave, leaving medial process. [length = 3; ci = 33; ri = 50]
93. T7 posterior margin: (0) truncate or rounded; (1) medially concave. [length = 1; ci = 100; ri = 100]
94. S7 length: (0) much shorter than S6; (1) less than 1/2× S6; (2) more than 1/2× S6. [length = 6, 7; ci = 28, 33; ri = 93, 94]
95. S7 shape: (0) flat; (1) with medial process; (2) with transverse carina; (3) with lateral process. [length = 4; ci = 50; ri = 95]
96. S7 posterior margin: (0) concave; (1) truncate. [length = 1; ci = 100; ri = 100]
97. S8 sclerotization: (0) mostly sclerotized with posterior membranous area evenly convex posteriorly; (1) mostly sclerotized with posterior membranous area medially projecting posteriorly; (2) S8 sclerite medially incised and replaced by membranous area. [length = 8, 9; ci = 22, 25; ri = 65, 70]
98. S8 shape: (0) flat; (1) with sublateral longitudinal carina. [length = 2; ci = 50; ri =97]
99. S8 lateral margin: (0) flat; (1) elevated into carina. [length = 1; ci = 100; ri = 100]
100. S8 antero-medial process: (0) present; (1) absent. [length = 5, 6, 7; ci = 14, 16, 20; ri = 14, 28, 42]
101. S8 postero-lateral process: (0) absent; (1) present. [length = 3, 4; ci = 25, 33; ri = 25, 50]
102. Harpe internal process: (0) present; (1) absent. [length = 14, 15; ci = 6, 7; ri = 51, 55]
103. Harpe ventral margin: (0) with dense long setae; (1) without setae. [length = 1; ci = 100; ri = 100]
104. Harpe antero-ventral margin: (0) entire; (1) serrate. [length = 1; ci = 100; ri = 100]
105. Gonostipes length: (0) short, slightly longer than wide; (1) long, much longer than wide. [length = 1; ci = 100; ri = 100]
106. Gonostipes ventro-medial lobe: (0) weakly sclerotized, without posterior process; (1) strongly sclerotized, with posterior process. [length = 3; ci = 33; ri = 96]
107. Parapenis shape: (0) flexed inward, posterior margin truncate; (1) bifid; (2) with straight ventral process; (3) oblong; (4) slender, down-curved posteriorly; (5) spatulate; (6) projecting posterad. [length = 9, 10; ci = 60, 66; ri = 94, 95]
108. Parapenis dorsal margin: (0) without tubercles; (1) with tubercles. [length = 1; ci = 100;

ri = 100]
109. Gonostipes ventral lobe: (0) projecting posterad; (1) projecting dorsad; (2) truncate; (3) bifid. [length = 12, 13; ci = 23, 25; ri = 80, 82]
110. Cupula length: (0) longer than 1/2× gonostyle length; (1) much shorter than gonostyle length. [length = 1; ci = 100; ri = 100]
111. Basivolsella setae: (0) with short setae; (1) with extremely long wavy setae much longer than basivolsella. [length = 5; ci = 20; ri = 85]
112. Paracuspis: (0) absent; (1) present, connected with basivolsella via conjunctiva. [length = 6; ci = 16; ri = 90]
113. Basivolsella seta-filled pit: (0) present; (1) absent. [length = 10, 11, 12; ci = 8, 9, 10; ri = 75, 77, 79]
114. Parossiculus shape: (0) basivolsella elongate, convex externally and flat internally; (1) basivolsella elongate, depressed; (2) basivolsella expanded ventrad with long slender cuspis distally; (3) basivolsella subovate or rectangular; (4) basivolsella elongate, with internal and ventral faces; (5) basivolsella elongate, posteriorly depressed and anteriorly expanded ventrad; (6) basivolsella short, expanded ventrad; (7) basivolsella rod-like; (8) basivolsella lamellate. [length = 17; ci = 47; ri = 88]
115. Basiura shape: (0) elongate anterad; (1) small rounded; (2) small, expanded ventrad; (3) plate-like. [length = 8; ci = 37; ri = 93]
116. Apiceps shape: (0) apiceps convergent and pointed posterad; (1) slender; (2) robust; (3) minute; (4) obliterated; (5) robust, strongly curved; (6) lamellate; (7) broad, rounded. [length = 16, 17, 18; ci = 38, 41, 43; ri = 77, 79, 81]
117. Penisvalvae: (0) symmetrical; (1) slightly asymmetrical, only differing in length; (2) asymmetrical. [length = 3, 4; ci = 50, 66; ri = 95, 97]
118. Penisvalva shape: (0) strongly expanded ventrad, bidentate; (1) slender, bidentate; (2) slender, bidentate, with external process; (3) slender, unidentate; (4) slender, unidentate with external lobe; (5) capitate; (6) ventral margin posteriorly emarginate, leaving hook-like process, left penisvalva simple; (7) with capitate apex projecting internally, left penisvalva with capitate apex; (8) with two apical hooks, left penisvalva with apical hook. [length = 16; ci = 50; ri = 87]
119. Penisvalva external face (- if penisvalva is not bidentate): (0) flat; (1) armed with vertical carina along anterior process. [length = 3; ci = 33; ri = 93]
120. Penisvalva subdorsal margin (- if penisvalva is not bidentate): (0) flat; (1) longitudinally carinate; (2) with longitudinal flange expanded dorsad. [length = 4; ci = 50; ri = 86]
121. Penisvalva posterior setae: (0) present; (1) absent. [length = 3; ci = 33; ri = 77]
122. Penisvalva internal setae: (0) absent; (1) present. [length = 2; ci = 50; ri = 0]
123. Penisvalva ventral cuticular piece: (0) absent; (1) present. [length = 4, 5; ci = 20, 25; ri = 91, 93]

Phylogenetic relationship

An initial analysis based on equal weights recovered 60 equally parsimonious trees (length = 813), resulting in a poorly resolved strict consensus tree (Fig. 3; Table 3). The Smicromyrmini was found paraphyletic with the Trogaspidiini sister to *Ephucilla-Mickelomyrme-Promecilla-Sinotilla* group. Monophyly of most smicromyrmine genera was supported, except that *Ephucilla* Lelej, 1995 and *Smicromyrme* were recovered as paraphyletic in some of the equally parsimonious trees. The symmetric resampling analysis recovered all presently recognized genera as monophyletic with moderate to low GC scores (GC = 11–52) for most genera. Monophyly of the genera *Dentilla* Lelej, 1980, *Ephutomma* Ashmead, 1899, and *Nemka* Lelej, 1985 was supported by unique synapomorphies and high

GC scores (GC = 78–99).

Using implied weighting, tree topology varied drastically depending on the *k* value (Figs 4–21). Monophyly of the Smicromyrmini was recovered only when higher *k* values (k12, k15, and k16) were used (Figs 16-1, 19-1, 20-1). The genera *Dentilla*, *Ephutomma*, *Nemka*, and *Physetopoda* Schuster, 1949 are found monophyletic under all settings. Two species, "*Andreimyrme*" *davidi* (André, 1896) and "*Ephucilla*" *undata* (Chen, 1957), constituted a monotypic clade. Contrarily, the status of the genera *Ephucilla* Lelej, 1995, *Mickelomyrme* Lelej, 1995, *Promecilla* André, 1902, and *Smicromyrme* is unstable under different *k* values (Table 4). The *Mickelomyrme* and *Smicromyrme* were monophyletic in most analyses. Three monophyletic groups were recognized in *Ephucilla*. With lower *k* values (k0–k5), a clade composed of *E. aequatoris* **sp. nov.** and *E. retorta* **sp. nov.** was recovered as sister to *Sinotilla*, making the *Ephucilla* paraphyletic (Figs 4–9). However, their sister relationship was supported only by reduction of characters: carinae on the prementum and penisvalva obliterated (42:0; 119:0). Similarly, the *Promecilla* was consistently divided into two monophyletic clades. One of them includes *P. annexa* (Cameron, 1909), *P. decora* (Smith, 1879), and *P. yerburghi* (Cameron, 1892). This group was found sister to or nested in *Ephucilla-Mickelomyrme-Sinotilla*, with *Promecilla* s. str. outside of them, suggesting paraphyly or polyphyly of *Promecilla* (Figs 4–19, 21)). Two non-homoplastic synapomorphies support this grouping (10:1; 46:1). Even though several groups of species were recognized in *Sinotilla* based on the morphology, no clear distinction was recognized for them from the trees.

Below, the East Asian smicromyrmine genera were arranged based on the phylogenetic trees estimated from the male morphology. Taxonomic arrangements were intended to be conservative, specifically for *Ephucilla-Mickelomyrme-Promecilla-Sinotilla* group of genera, given the inconsistency of the phylogenetic results. Under k16, the resulting trees are only one step longer than those under equal weights, with the Smicromyrmini and all genera recovered as monophyletic. This setting is thus preferred for the purpose of the present study. Intra- and intergeneric relationship is further discussed in each section.

Systematic results

Tribe Smicromyrmini Bischoff, 1920

Smicromyrmini Bischoff, 1920: 23; Lelej, 1985: 180; Lelej, 1995b: 2; Lelej & Nemkov, 1997: 18; Lelej, 2002: 50; Lelej, 2005: 38; Brothers & Lelej, 2017: 47; Pagliano *et al*., 2020: 169; Lelej & Williams, 2023: 103; Waldren *et al*., 2023: 476.
Smicromyrminae: Skorikov, 1935: 312; Invrea, 1964: 151.
Smicromyrmina: Brothers, 1975: 626, part; Brothers, 1999: 244, part.

Diagnosis

MALE. The Smicromyrmini was generally recovered as a paraphyletic group in the present phylogenetic analyses and thus this tribe is not defined by unique synapomorphies. The males of this tribe are characterized by the following combination of plesiomorphic or highly homoplastic characters: internal eye margin emarginate; antennal rims separated, convex; gena lacking vertical carina; occipital carina not projecting posterad; clypeus concave or subconvex; mandible without subproximal internal tooth; F1 cylindrical; mesoscutellum punctate, without medial impunctate line, carina, or process; mesoscutellum without postero-lateral tooth; mesopleuron lacking ventral swelling; propodeum with short antero-medial elongate cell and without sublateral longitudinal carina; propodeum dorso-lateral margin rounded; meso- and metacoxae evenly convex; metacoxa without internal setose pit;

metasomal segment 1 subsessile; T1 without distinct dorsal and anterior faces; S1 with medial longitudinal carina; T2 postero-lateral angle evenly convex; T2 ventro-lateral margin below felt line with sparse setae only; S2 antero-medial portion not swollen; S2 lateral portion evenly convex; S2 without posterior process; S6 flat, lacking lateral process; T7 punctate throughout or with medial impunctate line, lacking medial convexity; T7 posterior portion flat; T7 posterior margin convex or truncate; S7 length less than 1/2× S6; S7 flat or with medial process; S8 flat, mostly sclerotized with posterior membranous area evenly convex posteriorly, without postero-lateral process; cupula much shorter than gonostyle length; harpe down-curved; harpe ventral margin with sparse setae; gonostipes much longer than wide; gonostipes ventro-medial lobe weakly sclerotized, without posterior process; parapenis dorsal margin without tubercles; penisvalvae symmetrical, bidentate.

FEMALE. See Brothers & Lelej (2017) and Lelej & Williams (2023).

Genera included

A total of 26 genera and four subgenera are classified in this tribe. Of these, the following 13 genera are distributed in East Asia: *Andreimyrme* Lelej, 1995, ♂♀; *Chenmyrme* **gen. nov.**, ♂; *Ephucilla* Lelej, 1995, ♂♀; *Ephutomma* Ashmead, 1899, ♂♀; *Hadrodontilla* **gen. nov.**, ♂♀; *Mickelomyrme* Lelej, 1995, ♂♀; *Nemka* Lelej, 1985, ♂♀; *Nordeniella* Lelej, 2005, ♂♀; *Physetopoda* Schuster, 1949, ♂♀; *Promecilla* André, 1902, ♂♀; *Sinotilla* Lelej, 1995, ♂; *Smicromyrme* Thomson, 1870, ♂♀; *Tsunekimyrme* Lelej, 1995, ♂.

Distribution

Afrotropical, Oriental, and Palaearctic Regions.

Key to the East Asian genera of Smicromyrmini based on the male morphology

1. Mandibular dorso-lateral carina highly elevated, terminating as large internal tooth … 2
- Mandibular dorso-lateral carina weakly developed, if elevated then frons longitudinally striate, mandible apically bidentate, or basivolsella expanded ventrally with long slender cuspis … 4
2 (1). Mandible without subdistal internal tooth; mandibular ventral margin emarginate with large proximal tooth … ***Ephutomma*** Ashmead
- Mandible with subdistal internal tooth; mandibular ventral margin straight … 3
3 (2). Flagellomere apices truncate; tegula posteriorly reaching transscutal articulation; mesopleuron with ventral process; procoxa without posterior process; S2 without lateral felt line; harpe dorso-internal margin with proximal process; parapenis posteriorly truncate with sharp process projecting posterad; gonostipes ventral lobe truncate; basivolsella without seta-filled pit; apiceps obliterated … ***Andreimyrme*** Lelej
- Flagellomere apices bifid; tegula posteriorly surpassing transscutal articulation; mesopleuron without ventral process; procoxa with sharp posterior process; S2 with lateral felt line; harpe dorso-internal margin entire; parapenis bifid; gonostipes ventral lobe projecting dorsad; basivolsella with seta-filled pit; apiceps distinct … ***Hadrodontilla*** **gen. nov.**
4 (1). Mesopleuron divided into dorsal and ventral convexities by transverse impression … 5
- Mesopleuron evenly convex, lacking transverse impression … 9
5 (4). Mesopleuron with ventral process; basivolsella expanded ventrad with long slender cuspis … ***Nemka*** Lelej
- Mesopleuron without ventral process; basivolsella slender, lacking cuspis … 6
6 (5). Clypeal ventral margin with paired teeth medially; mandible ventrally not emarginate with small proximal lobe … ***Nordeniella*** Lelej

- Clypeal ventral margin entire, lacking teeth; mandible ventrally emarginate with large proximal tooth … 7
7 (6). Mandibular dorso-lateral carina highly elevated proximally; gonostipes ventral lobe projecting dorsad; penisvalva internal face with setae along anterior process … ***Chenmyrme*** **gen. nov.**
- Mandibular dorso-lateral carina weakly developed; gonostipes ventral lobe truncate or projecting posterad; penisvalva internal face lacking setae … 8
8 (7). Vertex rounded; S2 lacking lateral felt line; basivolsella elongate with long wavy setae ventrally; basivolsella internal face without seta-filled pit … ***Physetopoda*** Schuster
- Vertex elevated beyond ocellar region; S2 with lateral felt line; basivolsella short subovate with short setae ventrally; basivolsella internal face with seta-filled pit … ***Smicromyrme*** Thomson
9 (4). Parascutal carina forming elevated process (except *M. chinensis*); basivolsella expanded ventrad with long slender cuspis … 10
- Parascutal carina forming weak process; basivolsella short subovate, rectangular, or elongate, lacking cuspis … 11
10 (9). Mandible apically bidentate; mandibular dorso-lateral carina weakly developed or highly elevated only proximally … ***Mickelomyrme*** Lelej
- Mandible apically tridentate; mandibular dorso-lateral carina highly elevated, terminating as internal tooth … ***Tsunekimyrme*** Lelej
11 (9). Mandibular ventral margin emarginate with large proximal tooth … 12
- Mandibular ventral margin not emarginate with rounded proximal lobe … 16
12 (11). Mandible apically bidentate; F1 apparently shorter than wide … 13
- Mandible apically tridentate; F1 as long as wide … 15
13 (12). Notaulus obliterated; T1 lateral margin densely micropunctate; parapenis oblong; basivolsella elongate depressed, at most with shallow pit; penisvalva slender, weakly expanded ventrad; penisvalva posterior process with external process … ***Sinotilla*** Lelej, s. str.
- Notaulus present; T1 lateral margin smooth; parapenis bifid; basivolsella subovate, with deep seta-filled pit; penisvalva strongly expanded ventrad; penisvalva posterior process lacking external process … 14
14 (13). Metacoxal internal carina lamellately projecting posteriorly; harpe laterally weakly convex; penisvalva external face lacking carina … ***Sinotilla*** Lelej, part
- Metacoxal internal carina weakly developed; harpe laterally strongly convex on anterior 1/3; penisvalva external face with vertical carina along anterior process … ***Sinotilla*** Lelej, part
15 (12). Parapenis down-curved posteriorly with small lobe on posterior margin; penisvalva strongly expanded ventrad … ***Ephucilla*** Lelej, s. str.
- Parapenis bifid, lacking posterior lobe; penisvalva slender, weakly expanded ventrad… ***Ephucilla*** Lelej, part
16 (11) Parapenis flexed outward; basivolsella slender, lacking seta-filled pit and ventral long wavy setae; apiceps obliterated; penisvalva slender, weakly expanded ventrad … ***Ephucilla*** Lelej, part
- Parapenis flat; basivolsella subovate or rectangular with seta-fill pit, or elongate with long wavy setae; apiceps distinct; penisvalva strongly expanded ventrad … 17
17 (16). F1 apparently shorter than wide; S2 with lateral felt line; parapenis bifid, sometimes anterior process obliterated; basivolsella short subovate or rectangular with short setae; basiura expanded ventrad … ***Sinotilla*** Lelej, part
- F1 as long as wide; S2 without lateral felt line; parapenis down-curved posteriorly or truncate with slender vertical process ventrally; basivolsella elongate with long wavy setae

ventrally; basiura small … 18
18 (17). Frons punctate; mandible apically bidentate, ventrally with large proximal lobe; parapenis slender down-curved … ***Promecilla*** André, s. str.
- Frons longitudinally striate; mandible apically tridentate, ventrally with small proximal lobe; parapenis with straight ventral process … ***Promecilla*** André, part

Key to the East Asian genera of Smicromyrmini based on the female morphology

1. Pygidial plate smooth, convex … 2
- Pygidial plate longitudinally striate or rugose, flat to subconvex … 4
2 (1). Mesosomal lateral margins divergent posteriorly … ***Nordeniella*** Lelej
- Mesosomal lateral margins convergent posteriorly … 3
3 (2). Scutellar scale present … ***Ephucilla*** Lelej
- Scutellar scale obliterated … ***Promecilla*** André
4 (1). Genal carina sharp; prementum with dome-like process; scutellar scale obliterated … ***Andreimyrme*** Lelej
- Genal carina absent; prementum subconvex; scutellar scale developed … 5
5 (4). Mandible broad, with two subdistal teeth as large as apex; T1 broad, sessile with T2; pygidial plate broad, triangular … ***Hadrodontilla*** **gen. nov.**
- Mandible slender, with one or two subdistal teeth much smaller than apex; T1 slender, subsessile with T2; pygidial plate parallel-sided, oval, subovate, or distinctly convergent posteriorly … 6
6 (5). Pygidial plate convergent anteriorly, broadest subposteriorly … 7
- Pygidial plate parallel-sided, oval, or distinctly convergent posteriorly, broadest at midpoint or anterior portion … 8
7 (6). Minimal distance between eyes 1.1–1.3× eye height; scutellar scale weakly developed … ***Ephutomma*** Ashmead
- Minimal distance between eyes 1.6–1.8× eye height; scutellar scale elevated … ***Physetopoda*** Schuster
8 (6). Pygidial plate oval … ***Nemka*** Lelej
- Pygidial plate parallel-sided or convergent posteriorly … 9
9 (8). T2 with two or three pale setal spots … 10
- T2 with one antero-medial pale setal spot … 11
10 (9). T2 with two or three pale setal spots aligned horizontally; T2 posterior margin with narrow pale setal fringe, small medial pale setal spot, or sparse black setae … ***Mickelomyrme*** Lelej, part
- T2 with three pale setal spots, with anterior margin of lateral spot not surpassing midpoint of medial spot; T2 posterior margin with broad pale setal band … ***Smicromyrme*** Thomson, part
11 (9). Eye height at least 3.0× distance between posterior eye border and posterior head border … ***Mickelomyrme*** Lelej, part
- Eye height 1.5–2.0× distance between posterior eye border and posterior head border … ***Smicromyrme*** Thomson, part

Genus *Andreimyrme* Lelej, 1995

Andreimyrme Lelej, 1995b: 5, ♂♀; Lelej, 2002: 50; Lelej, 2005: 38; Lelej, 2007: 88; Lelej *et al*., 2007: 56, ♂; Lelej & Brothers, 2008: 7; Brothers & Lelej, 2017: 95; Okayasu *et al*., 2018: 303, ♀; Williams *et al*., 2019b: 16, ♀; Okayasu, 2020: 56, ♂♀; Pagliano *et al*., 2020: 169; Okayasu *et al*., 2021b: 3, ♀; Lelej & Williams, 2023: 108, ♂♀. Gender

feminine.

Zoobank LSID
urn:lsid:zoobank.org:act:591352DA-D3B9-4B61-8210-9C26B1FF9643

Type species
Andreimyrme long Lelej, 1995, ♂, by original designation.

Diagnosis
MALE. Frons punctate; vertex rounded; ventral clypeal margin entire; mandible apex tridentate, internal teeth as large as apex, with subdistal internal tooth; mandible dorso-lateral carina highly elevated, terminating as internal tooth; mandible ventral margin straight; flagellomere apices truncate; F1 length 0.7× width; notaulus reaching posterior margin of pronotum; parascutal carina forming weak process; tegula rounded posteriorly, reaching transscutal articulation; mesopleuron divided into dorsal and ventral convexities by transverse impression; mesopleuron ventral face with sharp process; procoxa lacking posterior process; metacoxal internal carina weakly developed; S2 lacking lateral felt line; harpe dorso-internal margin with proximal process; parapenis posteriorly truncate with sharp process projecting posterad; gonostipes ventral lobe truncate; basivolsella elongate with long wavy setae on ventral margin; basivolsella internal face lacking seta-filled pit; basiura small rounded; apiceps obliterated; penisvalva strongly expanded ventrad; penisvalva posterior process lacking external process.

FEMALE. See Okayasu *et al*. (2021b).

Species included
A total of 16 species is recognized in this genus: *A*. *auricoma* Okayasu, 2021, ♀ (Malaysia); *A*. *borkenti* (Williams, 2019), ♀ (Thailand, Vietnam); *A*. *laminatihumeralis* Okayasu, 2021, ♀ (Indonesia, Malaysia); *A*. *long* Lelej, 1995, ♂ (China); *A*. *matsumotoi* Okayasu. 2021, ♀ (Vietnam); *A*. *naturalis* Williams, 2021, ♀ (Indonesia); *A*. *neaera* (Mickel, 1935), ♀ (Malaysia); *A*. *pakistanensis* Lelej & Ullah, 2007, ♂ (Pakistan); *A*. *paniya* Terine, Lelej & Kumar, 2021, ♀ (India); *A*. *rong* Williams, 2021, ♀ (Thailand, Vietnam); *A*. *sarawakensis* Lelej, 1996, ♀ (Malaysia); *A*. *silvorientalis* Okayasu, 2021, ♀ (Indonesia); *A*. *substriolata* (Chen, 1957), ♀ (China, Taiwan, India, Indonesia, Japan, Laos, Malaysia, Thailand, Vietnam); *A*. *takensis* Okayasu, 2021, ♀ (Thailand); *A*. *ursasolaris* Williams, 2021, ♀ (Indonesia); *A*. *yotoi* Okayasu, 2021, ♀ (Laos, Vietnam).

Sex association
The type species was described from the male only. Originally, this genus had two male-based species, *A*. *davidi* and *A*. *long*. Lelej (1995b) associated *A*. *substriolata* and *A*. *tridentiens* as the females of this genus, because these females had the wide robust mandible analogous to that of males. Based on the overlapping distribution and body size, Lelej (1995b) suggested sex association for the larger *A*. *davidi* with *A*. *substriolata* and the smaller *A*. *long* with *A*. *tridentiens*. Later, *A*. *tridentiens* was considered a color variant of *A*. *substriolata* by Okayasu (2020). Okayasu *et al*. (2021b) assumed *A*. *rong* to be the potential female of the type species.

Distribution
Oriental and Palaearctic Regions.

Remarks

Lelej (2005) placed *Smicromyrme annexa* (Cameron, 1909), *S. viriata* Mickel, 1934, and *S. volupia* Mickel, 1935 in *Andreimyrme* by having the mandible without proximo-ventral tooth. However, those species are reallocated to *Sinotilla* in this study. *Andreimyrme davidi* was included in this genus and associated with *A. substriolata* by Lelej (1995b). Although *A. davidi* possesses the similarly shaped mandible, this species shows additional character states to separate it from *Andreimyrme* as discussed below, leaving only two male-based species in this genus (Lelej, 1995b; Lelej *et al*., 2007). The females were reviewed by Okayasu *et al*. (2021b).

Andreimyrme long Lelej, 1995

Andreimyrme long Lelej, 1995b: 7, ♂, holotype ♂ (Mangshi, West Yunnan, China) [ZMMU]; Lelej, 2005: 38; Lelej & Brothers, 2008: 7; Okayasu, 2020: 56; Pagliano *et al*., 2020: 169; Okayasu *et al*., 2021b: 4; Lelej & Williams, 2023: 104, ♂.

Zoobank LSID
urn:lsid:zoobank.org:act:870D87B0-47B8-41F0-B55C-00FB2836545A

Material examined
No material examined.

Sex association
Female unknown.

Distribution
China: Yunnan (Lelej, 1995b).

Remarks
This species is known from only two males collected in the mountainous region of Yunnan, China.

Genus *Chenmyrme* nov.

Zoobank LSID
Unavailable.

Type species
Smicromyrme undatus Chen, 1957, ♂ (misspelled as *undata*), designated here.

Diagnosis
MALE. Frons punctate; vertex rounded; ventral clypeal margin entire; mandible apex bidentate, internal tooth smaller than apex, without subdistal internal tooth; mandible dorso-lateral carina highly elevated proximally; mandible ventral margin emarginate with large proximal tooth; flagellomere apices truncate; F1 longer than wide; notaulus reaching posterior margin of pronotum; parascutal carina forming weak process; tegula rounded posteriorly, reaching transscutal articulation; mesopleuron divided into dorsal and ventral convexities by transverse impression; mesopleuron ventral face lacking process; procoxa lacking posterior process; metacoxal internal carina weakly developed; S2 with lateral felt line; harpe dorso-internal margin lacking proximal process; parapenis bifid; gonostipes ventral lobe projecting dorsad; basivolsella elongate with convex external face and flat

internal face, with short setae on ventral margin; basivolsella internal face lacking seta-filled pit; basiura small rounded; apiceps long; penisvalva strongly expanded ventrad; penisvalva posterior process lacking external process; penisvalva internal face with setae along anterior process.

FEMALE. Unknown.

Species included
One species, *C. undata* (Chen, 1957), ♂ (Taiwan).

Sex association
Female unknown.

Distribution
Oriental Region.

Etymology
The generic name *Chenmyrme* is dedicated to Chin-wen Chen, who revised the Chinese and Taiwanese Mutillidae in his 1957 paper, with a common suffix for smicromyrmine genera derived from *Smicromyrme*. Gender feminine.

Remarks
Phylogenetic analyses generally recovered sister relationship of *Smicromyrme undatus* and *Ephutomma* (but with very low GC score of 1; Fig. 22-1). Synapomorphies supporting *S. undatus* + *Ephutomma* included: pronotal humeral carina weakly developed (45:1), mesoscutellum strongly convex (55:0), T2 apparently wider than mesonotal width including tegulae (79:1), basivolsella with short setae (111:0), basivolsella lacking seta-filled pit (113:1), and penisvalva subdorsal margin with longitudinal flange expanded dorsad (120:1). Most of these character states also occur elsewhere in the Smicromyrmini. The subdorsal flange on the penisvalva is shared with *Nemka* males and recovered as a unique synapomorphy of (*Nemka* + (*S. undatus* + *Ephutomma*)) under k13 and k14. *Smicromyrme undatus* is distinguished from *Ephutomma* and *Nemka* by having the mandible apex bidentate (tridentate in *Ephutomma* and *Nemka*), mandible dorso-lateral carina elevated only proximally (terminating as internal tooth in *Ephutomma* and *Nemka*), mesopleuron lacking ventral process (present in *Nemka*), gonostipes ventral lobe projecting dorsad (truncate in *Ephutomma* and *Nemka*), parossiculus lacking ventral lobe and cuspis (present in *Nemka*), and penisvalva internal face with setae along anterior process (absent in *Ephutomma* and *Nemka*). Thus, a new genus is necessary for this species.

The species of this new genus was formerly placed in the *undata* group of *Ephucilla* (Lelej, 1995b), but it differs from that genus by having the frons punctate (longitudinally striate in *Ephucilla*), ocelli enlarged (small in *Ephucilla*), mesopleural transverse impression present (mesopleuron evenly convex in *Ephucilla*), gonostipes ventral lobe projecting dorsad (projecting posterad in *Ephucilla*), basivolsella with convex external face and flat internal face (elongate depressed in *Ephucilla*), and penisvalva internal face with setae along anterior process (absent in *Ephucilla*).

This new genus is known from only two male specimens collected in Taiwan. Contrarily, the *Ephutomma* species are mostly nocturnal and found in arid and semiarid regions of the Old World (Lelej, 2002, 2005; Lelej & Williams, 2023; Pagliano *et al*., 2020). In the Oriental Region, the latter genus never occurs in the eastern part; the only Oriental species, *E. himalayana* Lelej & Ullah, 2007, is distributed in the lowland of Nepal and northern Pakistan (Lelej *et al*., 2007). The male of *C. undata* has the ocelli enlarged like those

of Ephutomma, suggesting nocturnal habits.

Chenmyrme undata (Chen, 1957), comb. nov.

Smicromyrme undata Chen, 1957: 198, ♂, holotype ♂ (Pingtung, Taiwan) [TARI], examined.
Smicromyrme yuliana Tsuneki, 1972c, **syn. nov.**: 23, ♂, holotype ♂ (Yuli, Hualien, Formosa [= Taiwan]) [NMNH], photo examined.
Ephucilla undata: Lelej, 1995b: 14; Lelej, 2005: 41; Hua, 2006: 300; Lo Cascio, 2015: 548; Okayasu, 2020: 65; Pagliano *et al*., 2020: 172.
Ephucilla yuliana: Lelej, 2005: 41; Hua, 2006: 300; Lo Cascio, 2015: 549; Okayasu, 2020: 65; Pagliano *et al*., 2020: 172.

Zoobank LSID
urn:lsid:zoobank.org:act:82A4C772-16C6-4292-86EE-0DA26EF71389

Material examined
1♂. Holotype ♂, *Smicromyrme undata* Chen: **Taiwan:** PINGTUNG: Pingtung, 18.IV.1938 [TARI].

Identification source
Primary type. Photos of the holotype of *S. yuliana* are available in Chan *et al*. (2024) and National Museum of Natural History (2024).

Sex association
Female unknown.

Distribution
Taiwan: Hualien, Pingtung (Tsuneki, 1972c).

Remarks
The holotype of this species is deposited in TARI and has appropriate labels. This species and *S. yuliana* share the mandible dorsally crooked, and the original description by Tsuneki (1972c) matches the holotype of *C. undata*. *Smicromyrme yuliana* is thus regarded as a junior synonym of *C. undata*. The head of the holotype of *C. undata* is missing, so character states of head morphology were obtained from holotype photos of *S. yuliana* and supplemented by descriptions in Chen (1957) and Tsuneki (1972c).

Genus *Ephucilla* Lelej, 1995

Ephucilla Lelej, 1995b: 10, ♂; Lelej, 2005: 39, ♂♀; Lelej, 2007: 88; Lelej & Brothers, 2008: 21; Brothers & Lelej, 2017: 95; Okayasu *et al*., 2018: 303, ♀; Williams *et al*., 2019b: 17, ♀; Okayasu, 2020: 62, ♂♀; Pagliano *et al*., 2020: 171; Lelej & Williams, 2023: 112, ♂♀. Gender feminine.

Zoobank LSID
urn:lsid:zoobank.org:act:41652F68-54AD-400A-A3D0-D8391509984C

Type species
Mutilla naja Zavattari, 1913, ♂, by original designation.

Diagnosis

MALE. Frons longitudinally striate; vertex elevated beyond ocellar region; ventral clypeal margin entire; mandible apex bidentate or tridentate, internal teeth smaller than apex, without subdistal internal tooth; mandible dorso-lateral carina weakly developed or highly elevated proximally; mandible ventral margin emarginate with large proximal tooth or not emarginate with small proximal lobe; flagellomere apices truncate; F1 length subequal to width; notaulus present on posterior part of mesoscutum or reaching posterior margin of pronotum; parascutal carina forming weak process; tegula rounded posteriorly or projecting postero-laterad, slightly surpassing transscutal articulation; mesopleuron evenly convex, lacking transverse impression; mesopleuron ventral face lacking process; procoxa lacking posterior process; metacoxal internal carina weakly developed; S2 lacking lateral felt line; harpe dorso-internal margin lacking proximal process; parapenis bifid or slender down-curved; gonostipes ventral lobe projecting posterad; basivolsella elongate depressed with short setae on ventral margin; basivolsella internal face lacking seta-filled pit; basiura small rounded; apiceps minute or obliterated; penisvalva strongly expanded ventrad or slender; penisvalva posterior process lacking external process; penisvalva internal face lacking setae.

FEMALE. Head size moderate; minimum distance between eyes 0.75–1.20× eye height; genal carina and hypostomal tooth present; clypeus medially elevated, often forming ventral tubercle; clypeus with subventral transverse flange; mandible slender, apically bidentate or tridentate with internal teeth smaller than apex; prementum flat, lacking posterior rounded process; F1 length 1.0–1.4× F1 width and 1.0–1.6× F2 length; mesosoma broadest at pronotal spiracle; mesosomal lateral margins subparallel or convergent posteriorly; antero-dorsal pronotal margin arcuate; humeral carina sharp; scutellar scale small, weakly elevated; mesopleural lamella absent; propodeum laterally rounded; procoxa lacking rounded tubercle; protarsus with weak external spines; T1 slender, subsessile with T2; T2 dorsally flat or anteriorly concave; pygidial plate convex, laterally at most defined by obscure longitudinal carinae; surface of pygidial plate smooth; lateral pygidial margins strongly convergent anteriorly.

Species included

A total of 22 species and one subspecies is recognized in this genus: *E. aequatoris* **sp. nov.**, ♂ (Indonesia); *E. bacbo* (Lelej, 1995), ♀ (Indonesia, Vietnam); *E. bicolor* **sp. nov.**, ♀ (Vietnam); *E. bifida* **sp. nov.**, ♀ (Indonesia); *E. brevitegula* Okayasu, 2020, ♂♀ (Japan); *E. calacuasana* (Tsuneki, 1993), ♂ (Philippines); *E. cheni* Lelej, 1995, ♂ (China); *E. cyaneiventris cyaneiventris* (André, 1896), ♂♀ (China, Thailand); *E. cyaneiventris gobiana* (Chen, 1957), ♂ (China); *E. drupa* (Zavattari, 1913), ♂ (Taiwan); *E. guentheri* (Zavattari, 1913), ♂ (Taiwan); *E. hejunhuai* Lelej, 2020, ♀ (China); *E. ludovica* (Cameron, 1900), ♂ (India); *E. naja* (Zavattari, 1913), ♂♀ (Taiwan); *E. nigrothoracica* (Okayasu, 2018), ♀ (Taiwan); *E. okajimai* **sp. nov.**, ♀ (Thailand); *E. panfilovi* Lelej, 1995, ♂ (China); *E. petina* (Mickel, 1937), ♀ (China, Indonesia, Malaysia, Thailand, Vietnam); *E. poonaensis* (Cameron, 1892), ♀ (India, Sri Lanka); *E. retorta* **sp. nov.**, ♂ (Laos, Vietnam); *E. subparallela* (Chen, 1957), ♀ (China); *E. suginoi* Okayasu, 2020, ♂♀ (Japan); *E. viet* (Lelej, 1995), ♀ (Malaysia, Thailand, Vietnam); *E. yoshitakei* Okayasu, 2020, ♂♀ (Japan).

Sex association

The type species was initially described from the male only. The female of this species was described as *Smicromyrme thalia* Mickel, 1933 and associated by Okayasu (2020) based on the morphological similarity to related species.

Distribution

Oriental and Palaearctic Regions.

Remarks

The males of this genus were divided into three groups by Lelej (1995b). Of these, the *undata* group is recognized as a separate genus in the present phylogenetic analyses except *E. cheni*. Analyses also found that the *Ephucilla* species were separated into three monophyletic clades (Fig. 3–19, 21). The *Ephucilla* s. str. includes the type species, *E. naja*, and *E. brevitegula*, *E. cyaneiventris*, *E. suginoi*, and *E. yoshitakei*. *Ephucilla drupa* and *E. guentheri* form a monophyletic group sister to *Ephucilla* s. str. under equal weights and lower *k* values (k0–k7). Two new species, *E. aequatoris* and *E. retorta*, were found sister species with high GC score (GC = 89; Fig. 22-2) characterized by the mandible with a proximo-ventral lobe (33:2), apiceps obliterated (116:4), and penisvalva lacking external vertical carina (119:0). Phylogenetic placement of this group was variable depending on the *k* values. Under lower *k* values (k0–k5), sister relationship of this group and *Sinotilla* were recovered, with two homoplastic synapomorphies: prementum lacking a medial carina (42:0) and penisvalva flat, lacking external vertical carina (119:0). With higher *k* values, this group is either the earliest diverging lineage within *Ephucilla* (k6, k7, setk) or sister to (*E. drupa* + *E. guentheri*) (k8–k15). Monophyly of the *Ephucilla* was moderately supported (GC = 46; Fig. 22-2) with several synapomorphies: mandible apex tridentate (29:1), T7 with a triangular impunctate line (91:2), basivolsella lacking a seta-filled pit (113:1), apiceps minute (116:3), and penisvalva lacking a ventral cuticular piece (123:1). It is worth noting that sister relationship of (*E. aequatoris* + *E. retorta*) and (*E. drupa* + *E. guentheri*) is supported by a unique synapomorphy: penisvalva slender, bidentate (118:1).

Ephucilla aequatoris, *E. drupa*, *E. guentheri*, and *E. retorta* differ from *Ephucilla* s. str. by having the mesosoma black (at least partially red in *Ephucilla* s. str.), parapenis bifid without posterior lobe (down-curved with small lobe on posterior margin in *Ephucilla* s. str.), and penisvalva slender (strongly expanded ventrad in *Ephucilla* s. str.). This genus may be eventually separated into several genera, given the inconsistency of the male morphology and phylogenetic relationship within it. In the present study, the genus diagnosis is expanded so as to include those dubious species, because females are unknown for them. Contrarily, all species of the *Ephucilla* s. str. have associated males and females.

Phylogenetic analyses and morphological reexamination revealed that some males of *Ephucilla* and closely related *Sinotilla* had been wrongly assigned to each genus by previous papers (e.g., *E. cyaneiventris* and *S. drola*). Along with this, the sex associations for these genera appeared problematic. The *Ephucilla* was initially described from males only (Lelej, 1995b). The *Sinotilla* was recognized from both sexes based on the sex association of *S. cyaneiventris*, although the type species was known from the male only. The female of *Ephucilla* was subsequently described by Lelej (2005) based on the potential sex association of *E. ludovica* (♂) and *E. poonaensis* (♀). In this treatment, the *Ephucilla* female was distinguished from that of the *Sinotilla* by having the pygidial plate delimited by weak longitudinal carinae postero-laterally (pygidial plate lacking lateral carinae in *Sinotilla*). Accordingly, three female-based species of *Sinotilla*, *S. bacbo*, *S. thalia*, and *S. viet*, were reallocated to *Ephucilla*. This concept was followed by recent works (Lelej & Williams, 2023; Okayasu, 2017, 2020; Williams *et al*., 2019b). However, reexamination of voucher specimens and phylogenetic analyses demonstrated that *S. cyaneiventris* certainly belongs to the *Ephucilla*. The remaining species in the *Sinotilla* are known from one sex only; there is no evidence to associate the female-based species to that genus anymore. It is true that females of *Ephucilla* and *Sinotilla* in the current concept are separated by the presence of lateral pygidial carinae, but this character is too obscure and often hard to observe. Thus, I prefer to treat all *Ephucilla* and *Sinotilla* females as a single genus until further evidence for

sex association becomes available.

Key to the East Asian species of *Ephucilla* based on the male morphology

1. Mandible apically bidentate; mandibular dorso-lateral carina highly elevated. China … ***E. cheni*** Lelej
- Mandible apically tridentate; mandibular dorso-lateral carina weakly developed … 2
2 (1). Mesosoma more or less red; metasoma blue metallic; parapenis down-curved posteriorly, with small lobe on posterior margin; penisvalva strongly expanded ventrad … 3
- Mesosoma black; metasoma black or with some anterior segments orange; parapenis bifid, without posterior lobe; penisvalva slender … 8
3 (2). Parapsidal signum short; basivolsella slender … 4
- Parapsidal signum long; basivolsella broader … 6
4 (3). Mesosoma entirely red; basivolsella gradually narrowed posteriorly. Japan … ***E. yoshitakei*** Okayasu
- Mesosoma red with propleuron and mesopleuron ventrally black; basivolsella sharply narrowed posteriorly … 5
5 (4). Mesopleuron black on ventral face; mesoscutellum mostly with golden setae. China … ***E. cyaneiventris cyaneiventris*** (André)
- Mesopleuron black on ventral half; mesoscutellum mostly with black setae. China …***E. cyaneiventris gobiana*** (Chen)
6 (3). Tegula projecting postero-laterad, surpassing transscutal articulation, more than 1.54× longer than wide; T2–3 with dense posterior fringes. Taiwan … ***E. naja*** (Zavattari)
- Tegula rounded posteriorly, hardly reaching transscutal articulation, ~1.53× longer than wide; T2–3 with sparse posterior fringes … 7
7 (6). Metanotum black. Japan … ***E. brevitegula*** Okayasu
- Metanotum yellowish red. Japan … ***E. suginoi*** Okayasu
8 (2). Mandibular ventral margin not emarginate with small proximal lobe; tegula predominantly yellow; parapenis with posterior process slender; gonossiculus lacking apiceps; basivolsella dorsal margin lacking process … 9
- Mandibular ventral margin emarginate with large proximal tooth; tegula dark brown; parapenis with posterior process widened; gonossiculus with apiceps; basivolsella dorsal margin with proximal process projecting posterad … 11
9 (8). Mandibular ventral lobe rounded. Laos, Vietnam … ***E. retorta*** **sp. nov.**
- Mandibular ventral lobe anteriorly incised, subdentate ... 10
10 (9). Posterior propodeal face mostly with erect pale setae; T1 with small sparse punctures. Indonesia … ***E. aequatoris*** **sp. nov.**
- Posterior propodeal face dorsally with appressed pale setae; T1 with large dense punctures. Philippines ... ***E. calacuasana*** (Tsuneki)
11 (8). Notaulus reaching posterior margin of pronotum; T2 evenly convex (Lelej, 1995b: Fig. 12). China … ***E. panfilovi*** Lelej
- Notaulus present on posterior 1/2 of mesoscutum; T2 abruptly convex … 12
12 (11). Metasomal segments 1–2 red. Taiwan … ***E. drupa*** (Zavattari)
- Metasoma black. Taiwan … ***E. guentheri*** (Zavattari)

Key to the species of *Ephucilla* based on the female morphology

1. Frons and vertex with medial longitudinal carina; T2 disc antero-dorsally concave; T2 punctures large confluent, intervals reduced. China, Indonesia, Malaysia, Thailand,

Vietnam … ***E. petina*** (Mickel)
- Frons and vertex lacking medial carina; T2 disc dorsally flat; T2 punctures small, intervals distinct … 2
2 (1). Lower gena and malar space with sparse punctures, separated by approximate puncture diameter … 3
- Lower gena and malar space with dense punctures, separated by ~0.5× puncture diameter … 6
3 (2). Body mostly black; humeral carina obscure. Taiwan … ***E. nigrothoracica*** (Okayasu)
- At least mesosoma red; humeral carina sharp … 4
4. (3) Propodeum abruptly convergent posteriorly; T2 punctures confluent. China … ***E. subparallela*** (Chen)
- Propodeum evenly convergent posteriorly; T2 punctures sparse … 5
5 (4). Head yellowish red; mesosoma entirely yellowish red; humeral carina lamellately projecting; T2 blue metallic, with antero-medial pale golden setal spot and posterior band. Indonesia, Vietnam … ***E. bacbo*** (Lelej)
- Head black; pronotal dorsum and propleuron black, and lateral mesosomal face and propodeum with black spot; humeral carina sharp but not lamellate; T2 black, lacking pale setal spot and posterior band. Vietnam … ***E. bicolor*** **sp. nov.**
6 (2). Genal carina bifid ventrally, extending toward hypostomal carina and mandibular base. Indonesia … ***E. bifida*** **sp. nov.**
- Genal carina extending toward hypostomal carina … 7
7 (6). Frons punctures dense but separated, intervals distinct … 8
- Frons punctures confluent, intervals reduced … 9
8 (7). Pronotal dorsum with sublateral white setal spot; T1 orange; T2 with antero-medial white setal spot; S2 punctures large. India, Sri Lanka … ***E. poonaensis*** (Cameron)
- Pronotal dorsum with sparse setae only; T1 black; T2 lacking pale setal spot; S2 punctures small. Malaysia, Thailand, Vietnam … ***E. viet*** (Lelej)
9 (7). Head red … 10
- Head black … 11
10 (9). T2 anteriorly red and posteriorly black, with antero-medial golden setal spot. China … ***E. hejunhuai*** Lelej
- T2 blue metallic, without pale setal spot. Thailand … ***E. okajimai*** **sp. nov.**
11 (9). Pronotal dorsum lacking sublateral tooth; T1 yellowish red. China, Thailand … ***E. cyaneiventris cyaneiventris*** (André)
- Pronotal dorsum with sublateral tooth; T1 black … 12
12 (11). Frons and vertex longitudinally punctate-striate, intervals micro-punctate; humeral carina weakly developed; scutellar scale width 1.0× its length and puncture diameter. Japan … ***E. yoshitakei*** Okayasu
- Frons and vertex punctate, interval smooth; humeral carina lamellately projecting; scutellar scale width more than 2.0× its length and puncture diameter … 13
13 (12). Dorsal pronotal tooth small rounded; humeral carina dorsally rounded. Taiwan … ***E. naja*** (Zavattari)
- Dorsal pronotal tooth pointed; humeral carina dorsally projecting … 14
14 (13). Dorsal pronotal tooth large. Japan … ***E. brevitegula*** Okayasu
- Dorsal pronotal tooth small. Japan … ***E. suginoi*** Okayasu

Ephucilla aequatoris sp. nov.

Zoobank LSID
Unavailable.

Diagnosis

MALE. Mandible apically tridentate; mandibular dorso-lateral carina weakly developed; mandibular ventral margin with small proximal lobe anteriorly incised, subdentate; mesosoma black; notaulus present on posterior 1/3 of mesoscutum; tegula predominantly dark yellow; tegula short, rounded posteriorly; posterior propodeal face mostly with erect pale golden setae; metasomal segments 1–2 orange; T1 with small sparse punctures; T2–3 lacking posterior setal fringe; parapenis bifid with posterior process slender, lacking posterior lobe; basivolsella slender, depressed; apicps obliterated; penisvalva slender.

FEMALE. Unknown.

Description

MALE. Body length: 8.47–9.37 mm (holotype 9.37 mm); forewing length: 5.47–6.25 mm (holotype 6.25 mm).

Color and setae. Frons, vertex, gena, postgenal bridge, clypeus, mandible except subdistal 1/4, and mesosoma except tegula black; antennal rim, mandible subdistal 1/4, pedicel, maxillary and labial palpi, and protibial spur brown; scape, flagellum ventrally, prementum, stipes, tegula internal margin, and legs dark brown; flagellum dorsally, T3–7, and S3–8 brownish black; tegula except internal margin dark yellow; meso- and metatibial spurs white; T1–2 and S1–2 orange. Frons with sparse long recumbent and sparse long erect pale golden setae; vertex, mandible, profemur, T1–3, S1, and S3–5 with sparse long erect pale golden setae; gena, postgenal bridge, scape, pronotal dorsum, propleuron, metascutellum, metapleuron ventral 1/3, propodeum, meso- and metafemora, trochanters, tibiae, and S2 with sparse short recumbent and sparse long erect pale golden setae; clypeus with sparse long appressed and sparse long erect pale golden setae; pedicel with sparse short recumbent pale golden setae; flagellum with dense erect pale golden microsetae; prementum, stipes, and maxillary and labial palpi with sparse short erect pale golden setae; lateral pronotal face and metapleuron dorsal 2/3 with sparse short appressed pale golden setae; mesoscutum, mesoscutellum, and S6–8 with sparse long erect golden setae; tegula and coxae with sparse long recumbent pale golden setae; meso- and metanotal troughs with dense short appressed pale golden setae; mesopleuron with dense long appressed and sparse long erect pale golden setae; tarsi with sparse long appressed pale golden setae; T4–5 with sparse long erect pale golden and sparse long erect black setae; T6–7 with sparse long erect black setae; T2 lateral felt line golden, 0.4× T2 length; S2 lacking lateral felt line; S2–3 with sparse posterior fringe of pale golden setae; S4–6 with sparse posterior fringe of black setae.

Structure. Head width 1.72–1.75× length (holotype 1.75); lateral margins strongly convergent behind eye, postero-lateral angle rounded; vertex elevated, sharply sloping posteriorly; minimum distance between eyes 0.986–1.00× eye height (holotype 1.00); POL/OOL = 0.475–0.488 (holotype 0.488); MOD:LOD:LOL:POL = 1.00:0.769–0.900:0.846–1.00:1.62–1.90 (holotype 1.00:0.769:0.846:1.62); ocellar region convex; median ocellus lacking posterior longitudinal carina; frons with shallow medial longitudinal sulcus, lacking longitudinal carina anteriorly to lateral ocellus; occipital carina sharp, complete; internal eye margin deeply emarginate; antennal scrobal carina V-shaped, extending nearly to internal eye margin; antennal rim convex; antennal rims separated by approximate antennal rim width; gena lacking vertical carina; postgenal bridge flat; hypostomal carina sharp, not projecting; malar space developed, ventral eye margin and mandibular base separated; clypeus subconvex, with subventral complete transverse flange overhanging ventral clypeal margin; clypeal dorso-medial portion elevated into simple carina; mandible slender, narrowed to apex; mandibular apex tridentate, vertical, first internal tooth smaller than apex, second internal tooth as large as first; mandibular internal margin entire; mandibular dorso-lateral

carina sharp; mandibular ventral margin not emarginate with small rounded proximal lobe; mandibular ventral lobe anteriorly incised, subdentate; prementum flat; scape with two sharp subparallel carinae, separated by 0.5× scape width; F1 cylindrical; length and width of pedicel:F1:F2 = 1.00:1.20–1.36:2.30–2.36:1.80–1.82:2.82–2.90:1.90–2.00 (holotype 1.00:1.36:2.36:1.82:2.82:2.00); flagellomere apices truncate.

Mesosoma widest at mesonotum including tegulae; antero-dorsal pronotal margin nearly straight; humeral angle weakly angulate; humeral carina sharp, reaching pronotal dorsum; mesoscutum weakly convex; tegula short, rounded posteriorly, not flex, slightly surpassing transscutal articulation; tegula length 1.46–1.49× width (holotype 1.49); notauli subparallel, present on posterior 1/3 of mesoscutum, posteriorly widened; parapsidal signum short, linear; parascutal carina forming weak process on postero-lateral angle of mesoscutum; transscutal impression arcuate; mesoscutellum weakly convex; mesopleuron convex, lacking transverse impression; ventral mesopleural face with longitudinal impunctate line and without process and swelling; mesocoxal foramen armed with transverse precoxal carina; metathoracic spiracle oval; metasternum much shorter than coxal height; propodeal length 1.13–1.25× pronotal + mesoscutal length (holotype 1.13); posterior propodeal face oblique, without distinct dorsum; propodeal sublateral longitudinal carina absent; propodeal dorso-lateral margin rounded, lacking longitudinal carina; lateral margins of propodeum convergent posteriorly.

Wings fully developed; distance between origin of RS on vein SC and proximal margin of pterostigma 1.68–2.40× pterostigma length (holotype 2.40); forewing cell 2RS present.

Procoxa lacking posterior process; meso- and metacoxae evenly convex; metacoxa with internal longitudinal carina weakly developed; protibial spur slender; tibiae without external spines.

Metasomal segment 1 slender, subsessile; T1 width:T2 width:T2 length = 0.58–0.59:1.00:0.83–0.90 (holotype 0.58:1.00:0.83); T1 oblique, without distinct dorsum; T1 spiracle projecting; T2 evenly convex; S1 with medial longitudinal carina on anterior 3/4, straight in profile; S2 evenly convex with obscure antero-medial longitudinal carina; T3–6 not constricted; T7 evenly convex, with posterior margin truncate; S6–8 flat, lacking lateral carina or process; S7 posterior margin truncate; S8 mostly sclerotized with posterior membranous area evenly convex posteriorly. Harpe depressed laterally, down-curved; harpe dorso-internal margin lacking process; harpe dorsal margin with sparse short erect setae; gonostipes much longer than wide and as long as harpe; gonostipes ventro-medial lobe not forming posterior process; gonostipes ventral lobe projecting posteriorly; parapenis bifid with posterior process slender, flexed outward; parapenis dorsal margin lacking tubercles; cupula much shorter than gonostipes; basivolsella depressed, slender, incurved, without cuspis; basivolsella apex hardly reaching posterior 1/2 of harpe and surpassing penisvalva by 1/4× basivolsella length; basivolsella lacking seta-filled pit, with sparse long erect setae on internal face and antero-dorsal and ventral margins; basiura weakly sclerotized, lacking apiceps; basiura glabrous; penisvalvae symmetrical; penisvalva slender, weakly expanded ventrally, with distinct anterior and posterior ventral processes; penisvalva lacking setae; endophallus membranous.

Frons and vertex densely longitudinally striate; gena with small sparse and minute sparse punctures; postgenal bridge transversely rugose; clypeus, lateral pronotal face, metapleuron dorsal 2/3, meso- and metacoxae, trochanters, femora, tibiae, and tarsi with minute sparse punctures; scape, propleuron, tegula, T1–6, and S1–8 with small sparse punctures; pedicel, flagellum, prementum, stipes, maxillary and labial palpi, meso- and metanotal troughs, and procoxa with minute dense punctures; pronotal dorsum, mesoscutellum, and metapleuron ventral 1/3 with large confluent punctures; mesoscutum and

mesopleuron with large dense punctures, separated by ~0.5× puncture diameter; metascutellum with small confluent punctures; propodeum reticulate, with medial subtriangular and sublateral semicircular cell on anterior margin; T7 with small dense punctures and postero-medial triangular impunctate line.

FEMALE. Unknown.

Material examined

2♂. Holotype, ♂: **Indonesia:** KALIMANTAN TIMUR: Bukit Soeharto, 17–26.III.1994, Malaise trap, K. Konishi leg. [NARO]. Paratype: **Indonesia:** KALIMANTAN TIMUR: Bukit Soeharto, 17–26.III.1994, Malaise trap, K. Konishi leg. [1♂ NARO].

Sex association

Female unknown.

Distribution

Indonesia: Kalimantan Timur.

Etymology

The specific name *aequatoris*, of equator, is the Latin singular noun in the genitive case. It suggests that this new species originates from equatorial Borneo.

Remarks

This species, together with *E. calacuasana* and *E. retorta* **sp. nov.**, are characterized in *Ephucilla* by having the mandible apically tridentate with weak dorso-ventral carina and small proximo-ventral lobe, parapenis bifid with posterior process slender, flexed outward, basivolsella slender and depressed, apiceps obliterated, and penisvalva slender. However, this new species can be distinguished from them by having the mandible with a proximo-ventral lobe anteriorly incised (rounded in *E. retorta*), tegula dark (bright orange in *E. calacuasana* and *E. retorta*), posterior propodeal face with erect setae (dorsally with appressed setae, obscuring surface sculpture in *E. calacuasana*), and T1 with small sparse punctures (with large dense punctures in *E. calacuasana*).

Ephucilla brevitegula Okayasu, 2020

Ephutomma naja (non Zavattari, 1913): Lelej & Yamane, 1992: 631, ♂.

Ephucilla naja (non Zavattari, 1913): Lelej, 1995b: 11, ♂, part; Yamane, 1999: 380, ♂; Azuma *et al*., 2002: 322; Terayama, 2004: 13; Lelej, 2005: 40; Terayama, 2005: 11, 17, ♂ non Fig. 6K; Hua, 2006: 300, part; Terayama *et al*., 2011: 13, 21, ♂, part; Lo Cascio, 2015: 548, part; Terayama *et al*., 2016: 166, ♂, part.

Ephucilla brevitegula Okayasu, 2020: 76, ♂♀, holotype ♂ (Urauchi, Iriomote-jima Island, Yaeyama Islands, Japan) [EUMJ], examined.

Zoobank LSID

urn:lsid:zoobank.org:act:7605308E-D0F2-4796-A7ED-BFDC8B38DBE7

Material examined

17♂4♀. Holotype ♂: **Japan:** YAEYAMA ISLANDS: Iriomote-jima Island, Urauchi, 24°21'N 123°48'E, sweeping, 30.X.2017, K. Kuroda leg. [EUMJ]. Paratypes: **Japan:** YAEYAMA ISLANDS: Ishigaki-jima Island, Mt. Omotodake, 17.VI.1932, S. Asahina collection [1♂ NSMT]; Iriomote-jima Island, 2.VI.1935 [1♂ TARI]; Ishigaki-jima Island, Omoto-dake,

22.VIII.1992, A. Lelej leg. [1♂ IBSS]; Iriomote-jima Island, Mariyudo-falls, 8.XII.1993, R. Matsumoto leg. [1♂ OMNH]; Ishigaki-jima Island, Bunatabaru, light trap, 21.XI.1996, K. Yasuda leg. [1♂ NARO]; Iriomote-jima Island, Nakamagawa-rindô, 16.V.2001, T. Tsuru leg. [1♂ TUA], 17.V.2001, T. Tsuru leg. [1♂ TUA]; Iriomote-jima Island, Shirahama-rindô, 8.V.2002, T. Tsuru leg. [4♂ TUA]; Ishigaki-jima Island, Mt. Omotodake, collected 28.IV.2012, emerged V.2012, T. Kawano leg. [1♀ ELKU]; Ishigaki-jima Island, Takeda-trail, 14–16.VI.2013, T. Itô leg. [1♀ EUMJ]; Ishigaki-jima Island, Mt. Nosoko-dake, 31.V.2014, T. Nakata leg. [1♂ EUMJ]; Iriomote-jima Island, Shirahama, 24.3630°N 123.7662°E, 25.VI.2015, R. Matsumoto leg. [1♂ OMNH]; Ishigaki-jima Island, Miyara–Sokobaru, 19.XII.2015, T. Nakata leg. [1♀ EUMJ]; Iriomote-jima Island, Taketomi-chô, Mt. Tedô-san, 200 m alt., 24.3808°N 123.3804°E, FIT with light, 1–5.X.2017, K. Narita leg. [1♂ EUMJ]; Iriomote-jima Island, Urauchi, 24°21'N 123°48'E, sweeping, 30.X.2017, K. Kuroda leg. [1♀ EUMJ]. **Japan:** YAEYAMA ISLANDS: Iriomote Is., Shiramizu, 29.7.1973, S. Azuma leg. [1♂ RUMF]; Iriomote-jima, Ôtomi, 4.VI.1977, A. Nagatomi leg. [1♂ SEHU].

Identification source
Primary type.

Sex association
This species was described from both sexes collected at same place and time (Okayasu, 2020).

Distribution
Japan: Yaeyama Islands.

Remarks
This species inhabits moist subtropical forests of Yaeyama Islands and utilize the potter wasp *Phimenes flavopictus formosanus* (Zimmermann, 1931) (Hymenoptera: Vespidae: Eumeninae) as a host (Okayasu, 2020).

Ephucilla calacuasana (Tsuneki, 1993), comb. nov.

Smicromyrme calacuasana Tsuneki in Tsuneki *et al*., 1993: 16, ♂, holotype ♂ (Calacuasan, Palawan, Philippines) [NMNH], photo examined; Lelej, 2005: 57; Lo Cascio, 2015: 558.
Smicromyrme calacuasanus: Pagliano *et al*., 2020: 193.

Zoobank LSID
urn:lsid:zoobank.org:act:16C8C3E0-D109-421A-B1F7-C18C53C67CC4

Material examined
No material examined.

Sex association
Female unknown.

Distribution
Philippines: Palawan (Tsuneki *et al*., 1993).

Remarks

Photos of the holotype of this species are available in National Museum of Natural History (2024). This species is here assigned to *Ephucilla* by having the frons striate, vertex elevated, mandible apically tridentate with a small ventral lobe, and basivolsella elongate depressed without seta-filled pit (Tsuneki *et al*., 1993).

Ephucilla cheni Lelej, 1995

Ephucilla cheni Lelej, 1995b: 14, ♂, holotype ♂ (W Dali, Mt. Qiangshan, Yunnan, China) [ZMMU]; Lelej, 2005: 40; Okayasu, 2020: 64; Pagliano *et al*., 2020: 171.

Zoobank LSID
urn:lsid:zoobank.org:act:7624D42C-7846-46CF-BBC7-5B942D35CDFE

Material examined
No material examined.

Sex association
Female unknown.

Distribution
China: Yunnan (Lelej, 1995b).

Remarks
In Lelej (1995b), *E. cheni* and *E. undata* (now *Chenmyrme*) were characterized in the *Ephucilla* by having the mandible apically bidentate and mandibular dorso-lateral carina highly elevated. However, *E. cheni* has the frons longitudinally striate, clypeus with a subventral transverse flange, and S2 lacking a felt line. These traits justify its placement in *Ephucilla*.

Ephucilla cyaneiventris cyaneiventris (André, 1896), comb. nov.

Mutilla cyaneiventris André, 1896: 18, ♂, holotype ♂ (Nord de la Chine [= North China]) [HNMB]; André, 1902b: 39.
Smicromyrme cyaneiventris: Mickel, 1933b: 320, ♂; Wu, 1941: 134; Yasumatsu, 1948: 73, ♂; Hammer, 1949: 11, ♂.
Smicromyrme cyaneiventris cyaneiventris: Chen, 1957: 203, ♂♀, examined.
Sinotilla cyaneiventris: Lelej, 1995b: 20, ♀, examined; Lelej, 2002: 63; Lelej, 2005: 54; Okayasu, 2017: 164, ♀; Williams *et al*., 2019b: 26, ♀; Okayasu, 2020: 89; Pagliano *et al*., 2020: 186; Thaochan *et al*., 2022: 164, ♀.
Sinotilla cyaneiventris cyaneiventris: He *et al*., 2004: 948, ♂; Hua, 2006: 301.

Zoobank LSID
urn:lsid:zoobank.org:act:5AF197AA-01A9-43B4-ACE6-7B086D98E091

Material examined
49♂6♀. **China:** BEIJING: Peping [= Beijing], *Smicromyrme cyan. cyaneiventris* (André), B. Petersen det. 1982 [1♂ TARI]; HAINAN: no data [1♂ MTC]; JIANGSU: Kiangsu [= Jiangsu], Chinking, 16.VI.18, O. Piel leg., *Smicromyrme cyan. cyaneiventris* (André), B. Petersen det. 1982 [2♂ TARI], 19.VI.18 [1♂ TARI]; Kiangsu [= Jiangsu], Chinking, Tchenkiang, 16.6.18, *Smicromyrme cyaneiventris cyaneiventris* (André), B. Petersen det.

1988 [1♀ TARI]; JIANGXI: [Lushan, Jiujiang], Kuling [= Guling], 18.9.34, O. Piel leg., *Smicromyrme cyan*. *cyaneiventris* (André), B. Petersen det. 1982 [1♂ TARI], 24.7.35 [1♂ TARI], 25.7.35 [1♂ TARI], 28.7.35 [2♂ TARI], 29.7.35 [2♂ TARI], 30.7.35 [1♂ TARI], 3.8.35 [2♂ TARI], 4.8.35 [1♂ TARI], 5.8.35 [2♂ TARI], 7.8.35 [2♂ TARI], 13.8.35 [4♂ TARI], 16.9.35 [1♂ TARI], 31.9.35 [1♂ TARI]; [Lushan, Jiujiang], Kuling [= Guling], 27.7.35, O. Piel leg., *Smicromyrme cyan*. *cyaneiventris* (André), B. Petersen det. 1982, *Smicromyrme cyaneiventris cyaneiventris* (André) [unknown hand] [1♂ TARI]; [Lushan, Jiujiang], Kuling [= Guling], 5.8.35, O. Piel leg., *Smicromyrme cyan*. *cyaneiventris* (André), B. Petersen det. 1982, *Smicromyrme strandi* [probably Chen's hand] [1♂ TARI]; [Lushan, Jiujiang], Kuling [= Guling], 16.9.35, O. Piel leg., *Smicromyrme cyaneiventris cyaneiventris* (André), B. Petersen det. 1988, *Smicromyrme cyaneiventris cyaneiventris* (André) [unknown hand] [1♂1♀ (*in copula*) TARI]; Kiang-si [= Jiangxi], Lushan, Lienhwa-tung, 24.V.1941, S. Asahina collection, *Sinotilla cyaneiventris* (André), A. Lelej det. 1995 [1♀ NSMT (NSMT-I-Hym No. 23579)]; ZHEJIANG: Chekiang [= Zhejiang], Chusan [= Zhoushan], 19.6.31, O. Piel leg., *Smicromyrme cyan*. *cyaneiventris* (André), B. Petersen det. 1982 [1♂ TARI], 21.6.31 [1♂ TARI], 28.6.31 [1♂ TARI], 5.8.31 [1♂ TARI], 11.8.31, [1♂ TARI], 31.8.31 [2♂ TARI], 1.9.31 [2♂ TARI], 2.9.31 [3♂ TARI], 9.9.31 [1♂ TARI]; Chekiang [= Zhejiang], Chusan [= Zhoushan], 27.6.31, O. Piel leg., *Smicromyrme cyan*. *cyaneiventris* (André), B. Petersen det. 1982, *Smicromyrme cyaneiventris* (André) [unknown hand] [1♂ TARI]; Chekiang [= Zhejiang], Chusan [= Zhoushan], 30.6.31, O. Piel leg., *Smicromyrme cyaneiventris cyaneiventris* (André), B. Petersen det. 1988 [1♀ TARI]; [Lin'an, Hangzhou], Tienmushan [= Tianmushan], 15.VI.1935, *Smicromyrme cyan*. *cyaneiventris* (André), B. Petersen det. 1982 [1♂ TARI], 21.VII.36 [1♂ TARI], 27.VIII.1936 [1♂ TARI], 4.9.1942 [1♂ TARI]; [Lin'an, Hangzhou], Tienmushan [= Tianmushan], 8.6.36, *Smicromyrme cyaneiventris cyaneiventris* (André), B. Petersen det. 1988 [1♀ TARI], 23.4.37 [1♀ TARI]; Chekiang [= Zhejiang], [Lin'an, Hangzhou], W. Tien-Mu-shan [= West Tianmushan], 17.VIII.1936, T.C. Maa leg., *Smicromyrme cyan*. *cyaneiventris* (André), B. Petersen det. 1982 [1♂ TARI]; [Lin'an, Hangzhou], West Tianmushan, 17.VII.1937, Y. Ôuchi leg., *Smicromyrme cyaneiventris cyaneiventris* (André), C.W. Chen det. [1♂ ELKU].

Identification source
Voucher specimens (Chen, 1957).

Sex association
This species was initially described from the male only. The female was associated and described (as a key) by Chen (1957) based on a pair *in copula*.

Distribution
China: Beijing, Hainan*, Jiangsu, Jiangxi, Zhejiang. Thailand: Kanchanaburi, Pathun Thani, Phetchabun (Thaochan *et al*., 2022; Williams *et al*., 2019b).

Remarks
Lelej (1995b) examined a female specimen and placed this species in *Sinotilla*. However, this species belongs to *Ephucilla* and is closely related to *E*. *brevitegula*, *E*. *naja*, *E*. *suginoi*, and *E*. *yoshitakei* by having the parapenis slender, down-curved with a small lobe on posterior margin, basivolsella slender, and penisvalva strongly expanded ventrad. Williams *et al*. (2019b) recorded this species from Thailand based on two females. However, the Thai females differ from those from China by having the pedicel, scape, femoral apices, tibiae, and tarsi black. Discovery of male individuals from Thailand might reveal that the Thai population belongs to a separate species.

Ephucilla cyaneiventris gobiana (Chen, 1957), comb. nov.

Smicromyrme cyaneiventris gobiana Chen, 1957: 204, ♂, holotype ♂ (Yangkiaping [= Yangkiaping], Chahar, [Inner Mongolia], China) [unknown].
Sinotilla cyaneiventris gobiana: Lelej, 2002: 63; Lelej, 2005: 54; Hua, 2006: 301; Okayasu, 2020: 89; Pagliano *et al*., 2020: 186.

Zoobank LSID
urn:lsid:zoobank.org:act:AF0E5AF5-07C6-4583-AD31-44818D894A46

Material examined
No material examined

Sex association
Female unknown.

Distribution
China: Inner Mongolia (Chen, 1957).

Remarks
This subspecies is known from the holotype male and a single paratype male. Both specimens were not found in TARI. This subspecies was separated from the nominotypical one by having the mesoscutellum mostly with black setae (golden in *S. c. cyaneiventris*) and mesopleuron red on dorsal half and black on ventral half (only ventral face black in *S. c. cyaneiventris*). This subspecies is probably a color variant of *S. cyaneiventris*, but reexamination of types or additional specimens from northern China is necessary to propose a new synonymy because all *E. cyaneiventris* males examined herein had the mesoscutellum with golden setae and mesopleuron mostly red.

Ephucilla drupa (Zavattari, 1913)

Mutilla drupa Zavattari, 1913: 41, ♂, lectotype ♂ (Kankau, Koshun [= Hengchun], [Pingtung], Formosa [= Taiwan]) [SDEI], designated by Mickel (1933a: 417), examined.
Smicromyrme drupa: Mickel, 1933a: 417, ♂; Suzuki, 1934: 25; Mickel, 1935: 288, ♂; Chen, 1957: 202, ♂; Tsuneki, 1972c: 18, ♂, examined; Tsuneki, 1982: 43, ♂; Nambu & Tano, 1983: 21, ♂; Tsuneki, 1993a: 40, ♂; Pagliano, 2011: 41, ♂.
Ephucilla drupa: Lelej, 1995b: 11, ♂; Lelej, 2005: 40; Hua, 2006: 300; Lo Cascio, 2015: 548; Okayasu, 2020: 64; Pagliano *et al*., 2020: 171; Pagliano & Scaramozzino, 2021: 108, ♂.

Zoobank LSID
urn:lsid:zoobank.org:act:6BBDF51F-E3DE-4A40-8726-5B6F4A0B7418

Material examined
6♂. Lectotype ♂: **Taiwan:** PINGTUNG: Koshun [= Hengchun], Kankau, 7.IV.1912, H. Sauter leg. [SDEI (DEI-GISHym 16740)]. **Taiwan:** NANTOU: Penpuchi, 600 m, 10.VIII.1968, K. Tsuneki leg., *Smicromyrme drupa* (Zavattari) [probably Tsuneki's hand] [1♂ NMNH]; PINGTUNG: Kuraru [= Sheding Nature Park, Kenting National Park, Hengchun],

6.V.1926, T. Kano leg., *Ephucilla drupa* (Zavattari), A. Lelej det. 1995 [1♂ NSMT (NSMT-I-Hym No. 1087)], 8.V.1928 [1♂ NSMT (NSMT-I-Hym No. 1095)]; Gaoshifo Shan, 22.1317°N 120.7959°E, 230 m [alt.], 8.V.2017, T. Mita leg. [1♂ ELKU]; Shihzih, Fenglin, Mt. Beililongshan, 28.IV.2019, T. Saeki leg. [1♂ TUA].

Identification source
Primary type.

Sex association
Female unknown.

Distribution
Taiwan: Nantou, New Taipei, Pingtung (Nambu & Tano, 1983).

Remarks
Within *Ephucilla*, *E. drupa*, E. *guentheri*, and *E. panfilovi* are characterized by the basivolsella dorsal margin armed with a small proximal process projecting posterad (Lelej, 1995b: Fig. 14), which could be confused with the paracuspis of some trogaspidiines (O'Toole, 1975). However, this process is not considered paracuspis, because the paracuspis is subdivided from basivolsella via conjunctiva.

Ephucilla guentheri (Zavattari, 1913)

Mutilla güntheri Zavattari, 1913: 33, ♂, lectotype ♂ (Taihorinsho [= Dalin], [Chiayi], Formosa [= Taiwan]) [SDEI], designated by Mickel (1933a: 417), examined.
Smicromyrme guntheri: Mickel, 1933a: 417, ♂; Suzuki, 1934: 25; Mickel, 1935: 287, ♂; Chen, 1957: 202, ♂. Incorrect subsequent spelling.
Smicromyrme güntheri: Tsuneki, 1972c: 20, ♂, examined.
Ephucilla guentheri: Lelej, 1995b: 10; Lelej, 2005: 40; Hua, 2006: 300; Pagliano, 2011: 40, ♂; Lo Cascio, 2015: 548; Okayasu, 2020: 65, ♂; Pagliano *et al*., 2020: 171; Pagliano & Scaramozzino, 2021: 108, ♂.

Zoobank LSID
urn:lsid:zoobank.org:act:5362F2D6-10A5-4A0D-872C-B1563666CCAE

Material examined
2♂. Lectotype ♂: **Taiwan:** CHIAYI: Taihorinsho [= Dalin], X.1909, H. Sauter leg. [SDEI (DEI-GISHym 16741)]. **Taiwan:** CHIAYI: Kuanhua, 1100 m, 1–2.VIII.1968, K. Tsuneki leg., *Smicromyrme güntheri* (Zavattari, 1913) [probably Tsuneki's hand] [1♂ NMNH].

Identification source
Primary type.

Sex association
Female unknown.

Distribution
Taiwan: Chiayi, Taichung, Tainan (Chen, 1957).

Remarks

This species and *E. drupa* are similar in structural features and distinguished only by the metasomal color. Future analyses of molecular data, color variation, and female morphology might find that these two species are conspecific.

Ephucilla naja (Zavattari, 1913)

Mutilla naja Zavattari, 1913: 38, ♂, lectotype ♂ (Taihorin [= Dalin], [Chiayi], Formosa [= Taiwan]) [SDEI], designated by Mickel (1933a: 417), examined.
Promecilla calliope (non Smith, 1857): Zavattari, 1913: 23, ♀.
Smicromyrme naja: Mickel, 1933a: 417, ♂; Suzuki, 1934: 25; Mickel, 1935: 275, ♂; Chen, 1957: 202, ♂, examined; Tsuneki, 1972c: 19, ♂, examined; Sabi *et al*., 1977: 42, ♂; Nambu & Tano, 1983: 21, ♂; Tsuneki, 1993a: 39, ♂.
Smicromyrme thalia Mickel, 1933a, **syn. nov.**: 417, ♀, holotype ♀ (Taihorin [= Dalin], Chiayi, Formosa [= Taiwan]) [SDEI], examined; Suzuki, 1934: 25; Mickel, 1935: 283, ♀; Chen, 1957: 208, ♀, examined.
Ephucilla naja: Lelej, 1995b: 11, ♂, part; Lelej, 2005: 40; Hua, 2006: 300, part; Lelej & Brothers, 2008: 21; Pagliano, 2011: 40, ♂; Lo Cascio, 2015: 548, part; Okayasu, 2020: 83, ♂; Pagliano *et al*., 2020: 172; Pagliano & Scaramozzino, 2021: 108, ♂; Lelej & Williams, 2023: 104, ♂.
Sinotilla thalia: Lelej, 1995b: 19.
Ephucilla thalia: Lelej, 2005: 41; Okayasu, 2020: 65, ♀, examined; Pagliano *et al*., 2020: 172; Lelej & Williams, 2023: 104, ♀.

Zoobank LSID
urn:lsid:zoobank.org:act:23A93F44-1B4B-45F4-8993-AE86DD44C8A3
urn:lsid:zoobank.org:act:2A08253E-3DDD-4721-AEA5-73BCD128144C

Material examined
44♂6♀. Lectotype ♂, *Mutilla naja* Zavattari: **Taiwan:** CHIAYI: Taihorin [= Dalin], 7.VIII.1911, H. Sauter leg. [SDEI (DEI-GISHym 16746)]. Paralectotype, *Mutilla naja* Zavattari: **Taiwan:** CHIAYI: Taihorin [= Dalin], 7.VIII.1911, H. Sauter leg. [1♂ SDEI]. Holotype ♀, *Smicromyrme thalia* Mickel: **Taiwan:** CHIAYI: Taihorin [= Dalin], 7.VIII.1911, H. Sauter leg., *Promecilla calliope* (Smith), E. Zavattari det. 1913 [SDEI (DEI-GISHym 16736)]. **Taiwan:** CHIAYI: Taihorin [= Dalin], VIII.1909, H. Sauter leg., *Smicromyrme naja* (Zavattari), B. Petersen det. 1981 [1♂ ZMUC], IX.1909 [1♂ ZMUC], XI.1909 [1♂ ZMUC]; HUALIEN: Juisui, 1.V.1980, Sk. Yamane leg., *Smicromyrme cyaneiventris naja* (Zavattari), B. Petersen det. 1988 [1♂ ZMUC]; KAOHSIUNG: Hoozan [= Fengshan], IV.1910, H. Sauter leg., *Smicromyrme naja* (Zavattari), B. Petersen det. 1981 [1♂ ZMUC]; Liukei, 29.VII.1985, H. Takizawa leg. [1♂ SEHU]; Liukuei, Paolai, 21.III.1995, H. Takizawa leg. [1♂ SEHU]; Liouguei, Colors Butterfly Valley, 25–27.V.2006, T. Tsuru leg. [1♂ SEHU]; NANTOU: Ren'ai, Wushe, 18.V–15.VI.1919, T. Okuni, J. Sonan, K. Miyake & M. Yoshino leg. [1♂ TARI]; Baibara [= Hsinseng], 25.IV.1929, K. Sato leg., *Ephucilla naja* (Zavattari), A. Lelej det. 1995 [1♂ NSMT]; Hori [= Puli], 28.IV.1929, K. Sato leg., *Ephucilla naja* (Zavattari), A. Lelej det. 1995 [1♂ NSMT]; Puli, Pen-pu Hsi, 600 m alt., 11.VIII.1968, K. Tsuneki leg. [1♂ NMNH]; Puli, Pen-pu Hsi, 600 m alt., 26.VIII.1968, K. Tsuneki leg., *Smicromyrme naja* (Zavattari), K. Tsuneki det. 1972, 1973 [2♂ ZMUC]; KwantauShih, 6.VIII.1972, S. Yamane leg., *Smicromyrme cyaneiventris naja* Zavattari, B. Petersen det. 1988 [1♂ IBER]; Puli, Pen-pu Hsi, 700 m alt., 24.00N 121.06E, 2.V.2012, Y. Komeda leg. [1♂ ELKU]; Mushe, 1150 m alt., 21–23.VI.1983, K.S. Lin & S.C. Lin leg. [1♂ TARI]; Tungpu, 1200 m alt., 23–27.VII.1984, K.C. Chou & C.H. Yang leg. [3♂ TARI]; Tungpu, 1200 m alt., IX.1985, Malaise

trap, K.S. Lin leg. [1♂ TARI]; PINGTUNG: Koshun [= Hengchun], 25.IV–25.V.1918, J. Sonan, K. Miyake & M. Yoshino leg. [1♂ TARI]; Koshun [= Hengchun], 25.IV–25.V.1918, J. Sonan, K. Miyake & M. Yoshino leg., *Promecilla calliope* Smith, T. Shiraki det., *Smicromyrme cyaneiventris naja* Zavattari, B. Petersen det. 1988 [1♀ TARI]; Koshun [= Hengchun], Kueitzuchiao, 12.X.1926, J. Sonan leg., *Smicromyrme cyaneiventris naja* Zavattari, B. Petersen det. 1988 [1♀ TARI], 13.X.1926 [1♂ TARI]; Koshun [= Hengchun], Kueitzuchiao, 1–4.III.1956, K.S. Lin leg. [1♀ TARI]; Koshun [= Hengchun], Kueitzuchiao, 21.III, J. Yoshioka collection [1♂ NSMT], 27.III [1♀ NSMT]; Kusukusu [= Kaoshih], 16.IV.1937, T. Shiraki & M. Chujo leg. [2♂ TARI], 16.VI.1937 [1♂ TARI]; Kankao [= Changkou], 23.IV.1941, Nitobe leg. [1♂ TARI], 23.V.1941 [1♂ TARI]; Kenting Park, 22.VI.1970, Y. Hori leg. [1♂ EUMJ]; Kenting Park, 22–26.III.1982, T. Lin & S.C. Lin leg. [1♂ TARI]; Chilushui, 4.VIII.1982, K.C. Chou & C.N. Lin leg. [1♂ TARI]; Shihzih, Fenglin, Mt. Beililongshan, 28.IV.2019, T. Saeki leg. [1♂ TUA]; TAICHUNG: Maling, 10.VI.1941, J. Sonan leg. [1♂ TARI]; Lieng, Mt. Tangmadan-shan, 24°09'N 120°57'E, 22.X.2017, K. Narita leg. [1♂ TARI]; Lieng, Mt. Tangmadan-shan, 24°09'N 120°57'E, 28.X.2017, fogging to a hollow of a pine tree at night, K. Yoshida leg. [1♀ TARI]; Lieng, Mt. Tangmadan-shan, 24°09'N 120°57'E, 1.XI.2017, J. Okayasu leg. [1♂ TARI]; Heping, Dongmao-shan, 24°10'N 120°58'E, 1.XI.2017, K. Narita leg. [1♂ TARI]; TAINAN: Kuantyling, 11.IV.1941, Nitobe leg., *Mutilla naja* Zavattari, T. Shiraki det. [1♂ TARI]; TAIPEI: Yangmingshan, 25.X.1965, K.H. Chang leg. [1♂ TARI]; YILAN: Tucheng, 19.VII.1935, J. Sonan leg. [1♂ TARI]; UNKNOWN PREFECTURE: Hogan, IV.1918, T. Shiraki leg., *Mutilla naja* Zavattari, T. Shiraki det. [1♂ TARI]; Kaushirei, 20.XI.1926, J. Sonan leg. [1♂ TARI].

Identification source
Primary type.

Sex association
This species was initially described from the male only. Okayasu (2020) suggested *E. thalia* was the potential female, because *E. naja* was similar to *E. brevitegula*, *E. suginoi* and *E. yoshitakei* from Japan in the male morphology and females of these species were similar to *E. thalia*. Similarly, *E. cyaneiventris* is similar to *E. naja* in males and *E. thalia* in females. These five *Ephucilla* species were found to be monophyletic in phylogenetic analyses. *Ephucilla thalia* is thus formally recognized as the female of *E. naja* herein.

Distribution
Taiwan: Chiayi, Hualien, Kaohsiung, Nantou, Pingtung, Taichung, Tainan, Taipei, Taitung, Yilan (Chen, 1957).

Remarks
This species is fairly common in forested habitats of Taiwan.

Ephucilla panfilovi Lelej, 1995

Ephucilla panfilovi Lelej, 1995b: 13, ♂, holotype (vicinities of Kunmin, Yunnan, China) [ZMMU]; Lelej, 2005: 40; Okayasu, 2020: 65; Pagliano *et al*., 2020: 172.

Zoobank LSID
urn:lsid:zoobank.org:act:409792A9-25D2-4E8F-9205-016869218BE3

Material examined

No material examined.

Sex association
Female unknown.

Distribution
China: Yunnan (Lelej, 1995b).

Remarks
This species was not available in this study. However, this species is recognized by the mandibular apex tridentate, mandibular ventral margin emarginate with a proximal tooth, notaulus reaching posterior margin of pronotum, T2 evenly convex, and basivolsella dorsal margin with a proximal process projecting posterad (Lelej, 1995b: Fig. 14).

Ephucilla retorta sp. nov.

Zoobank LSID
Unavailable.

Diagnosis
MALE. Mandible apically tridentate; mandibular dorso-lateral carina weakly developed; mandibular ventral margin with small rounded proximal lobe; mesosoma black; notaulus present on posterior 1/3 of mesoscutum; tegula yellow; tegula short, rounded posteriorly; posterior propodeal face mostly with erect pale golden setae; metasomal segments 1–3 orange; T1 with large sparse punctures; T2–3 lacking posterior pale setal fringe; parapenis bifid with posterior process slender, lacking posterior lobe; basivolsella slender, depressed; apiceps obliterated; penisvalva slender.

FEMALE. Unknown.

Description
MALE. Body length: 8.48–11.1 mm (holotype 11.1 mm); forewing length: 6.48–7.57 mm (holotype 7.57 mm).

Color and setae. Frons, vertex, gena, postgenal bridge, clypeus, mandible except subdistal 1/4, flagellum dorsally, mesosoma except tegula, T4–7, and S4–8 black; antennal rim, mandible subdistal 1/4, flagellum ventrally, protrochanter, and protibial spur brown; scape, pedicel, prementum, stipes, meso- and metacoxae, and meso- and metatrochanters brownish black; maxillary and labial palpi dark brown; tegula yellow; procoxa, femora, tibiae, and tarsi brownish black to black; meso- and metatibial spurs white; T1–2 and S1–2 orange; T3 reddish brown to orange; S3 orange with medial portion black. Frons and scape with sparse long recumbent and sparse long erect pale golden setae; vertex, postgenal bridge, pronotal dorsum, trochanters, T1–3, T4 except posterior margin, S1, and S3–5 with sparse long erect pale golden setae; gena, propodeum, femora, tibiae, and S2 with sparse short recumbent and sparse long erect pale golden setae; clypeus and propleuron with sparse long appressed and sparse long erect pale golden setae; mandible, mesoscutum, and mesoscutellum with sparse long erect golden setae; pedicel with dense short recumbent pale golden setae; flagellum with dense erect pale golden microsetae; prementum, stipes, and maxillary and labial palpi with sparse short erect pale golden setae; lateral pronotal face and metapleuron with sparse short appressed pale golden setae; tegula and coxae with sparse long recumbent pale golden setae; metascutellum with sparse short appressed and sparse long erect golden setae; meso- and metanotal troughs with dense short appressed pale golden setae;

mesopleuron with dense long appressed and sparse long erect pale golden setae; tarsi with sparse long appressed pale golden setae; T4 posterior margin, T5–7, and S6–8 with sparse long erect black setae; T2 lateral felt line golden, 0.45× T2 length; S2 lacking lateral felt line; T1–3 and S2 with sparse posterior fringe of pale golden setae.

Structure. Head width 1.54–1.67× length (holotype 1.54); lateral margins strongly convergent behind eye, postero-lateral angle rounded; vertex elevated, sharply sloping posteriorly; minimum distance between eyes 0.957–0.988× eye height (holotype 0.957); POL/OOL = 0.509–0.5111 (holotype 0.509); MOD:LOD:LOL:POL = 1.00:0.857–0.917:1.00–1.14:1.92–2.00 (holotype: 1.00:0.857:1.14:2.00); ocellar region convex; median ocellus lacking posterior longitudinal carina; frons with shallow medial longitudinal sulcus, lacking longitudinal carina anteriorly to lateral ocellus; occipital carina sharp, complete; internal eye margin deeply emarginate; antennal scrobal carina V-shaped, widely separated from internal eye margin; antennal rim convex; antennal rims separated by approximate antennal rim width; gena lacking vertical carina; postgenal bridge flat; hypostomal carina sharp, not projecting; malar space developed, ventral eye margin and mandibular base separated; clypeus subconvex, with subventral complete transverse flange overhanging ventral clypeal margin; clypeal dorso-medial portion elevated into simple carina; mandible slender, narrowed to apex; mandible apex tridentate, first internal tooth smaller than apex, second internal tooth as large as first; mandibular internal margin entire; mandibular dorso-lateral carina sharp; mandibular ventral margin not emarginate with small rounded proximal lobe; prementum flat; scape with two sharp subparallel carinae, separated by 0.5× scape width; F1 cylindrical; length and width of pedicel:F1:F2 = 1.00:1.07–1.25:1.80–1.83:1.47–1.50:2.20–2.25:1.53–1.67 (holotype 1.00:1.07:1.80:1.47:2.20:1.53); flagellomere apices truncate.

Mesosoma widest at mesonotum including tegulae; antero-dorsal pronotal margin nearly straight; humeral angle weakly angulate; humeral carina sharp, reaching pronotal dorsum; mesoscutum weakly convex; tegula short, rounded posteriorly, not flex, slightly surpassing transscutal articulation; tegula length 1.35–1.53× width (holotype 1.53); notauli subparallel, present on posterior 1/3 of mesoscutum, posteriorly widened; parapsidal signum short, linear; parascutal carina forming weak process on postero-lateral angle of mesoscutum; transscutal impression arcuate; mesoscutellum weakly convex; mesopleuron convex, lacking transverse impression; ventral mesopleural face with longitudinal impunctate line and without process and swelling; mesocoxal foramen armed with transverse precoxal carina; metathoracic spiracle oval; metasternum much shorter than coxal height; propodeal length 1.10–1.18× pronotal + mesoscutal length (holotype 1.10); posterior propodeal face oblique, without distinct dorsum; propodeal sublateral longitudinal carina absent; propodeal dorso-lateral margin rounded, lacking longitudinal carina; lateral margins of propodeum convergent posteriorly.

Wings fully developed; distance between origin of RS on vein SC and proximal margin of pterostigma 1.67–1.75× pterostigma length (holotype 1.75); forewing cell 2RS present.

Procoxa lacking posterior process; meso- and metacoxae evenly convex; metacoxa with internal longitudinal carina weakly developed; protibial spur slender; tibiae without external spines.

Metasomal segment 1 slender, subsessile; T1 width:T2 width:T2 length = 0.56–0.58:1.00:0.78–0.80 (holotype 0.58:1.00:0.80); T1 oblique, without distinct dorsum; T1 spiracle projecting; T2 evenly convex; S1 with medial longitudinal carina on anterior 3/4, straight in profile; S2 evenly convex with obscure antero-medial longitudinal carina; T3–6 not constricted; T7 evenly convex, with posterior margin truncate; S6–8 flat, lacking lateral carina or process; S7 posterior margin truncate; S8 mostly sclerotized with posterior

membranous area evenly convex posteriorly. Harpe depressed laterally, down-curved; harpe dorso-internal margin lacking process; harpe dorsal margin with sparse short erect setae; gonostipes much longer than wide and as long as harpe; gonostipes ventro-medial lobe not forming posterior process; gonostipes ventral lobe projecting posterad; parapenis bifid with posterior process slender, flexed outward; parapenis dorsal margin lacking tubercles; cupula much shorter than gonostipes; basivolsella depressed, slender, incurved, without cuspis; basivolsella apex hardly reaching posterior 1/2 of harpe and surpassing penisvalva by 1/3× basivolsella length; basivolsella lacking seta-filled pit, with sparse long erect setae on internal face and antero-dorsal and ventral margins; basiura weakly sclerotized, lacking apiceps; basiura glabrous; penisvalvae symmetrical; penisvalva slender, weakly expanded ventrad, with distinct anterior and posterior ventral processes; penisvalva lacking setae; endophallus membranous.

Frons and vertex densely longitudinally striate; gena with large sparse and minute sparse punctures; postgenal bridge transversely rugose; clypeus, lateral pronotal face, metapleuron dorsal 2/3, coxae, trochanters, meso- and metafemora, tibiae, and tarsi with minute sparse punctures; scape, tegula, and profemur with small sparse punctures; pedicel, flagellum, prementum, stipes, maxillary and labial palpi, and meso- and metanotal troughs with minute dense punctures; pronotal dorsum, mesopleuron, metascutellum, and metapleuron ventral 1/3 with large confluent punctures; propleuron and S3–8 with small dense punctures; mesoscutum and T2 posterolateral margin with large dense punctures, separated by ~0.5× puncture diameter; metascutellum with small confluent punctures; propodeum reticulate, with medial subtriangular and sublateral semicircular cell on anterior margin; T1, T2 except posterolateral margin, T3–6, and S1–2 with large sparse punctures; T7 with large sparse punctures and posteromedial triangular impunctate line.

FEMALE. Unknown.

Material examined

2♂. Holotype ♂: **Laos:** XIENG KHOUANG: 25 km Southeast Ban Ban, Hot Spring, 19°33'24.09"N 103°41'26.1"E, 568 m alt., 29.IV.2015, T. Mita leg. [ELKU]. Paratype: **Vietnam:** LAO CAI: Sa Pa, 1.XI.2001, U. Jinbo leg. [1♂ TUA].

Sex association

Female unknown.

Distribution

Laos: Xieng Khouang. Vietnam: Lao Cai.

Etymology

The specific name *retorta*, twisted, is the Latin, singular, feminine perfect passive participle in the nominative case. It refers to the parapenis flexed outward which distinguishes this new species from most *Ephucilla* species.

Remarks

This new species is similar to but distinguishable from *E. aequatoris* **sp. nov.** and *E. calacuasana* as discussed above.

Ephucilla suginoi Okayasu, 2020

Ephucilla naja (non Zavattari, 1913): Terayama *et al*., 2011: 13, 21, ♂, part; Lo Cascio, 2015: 548, part; Terayama *et al*., 2016: 166, ♂, part.

Ephucilla sp.: Terayama, 2019: 48, ♀.
Ephucilla suginoi Okayasu, 2020: 71, ♂♀, holotype ♂ (Sashiki, Nanjyô-shi, Okinawa-jima Island, Okinawa Islands, Japan) [SEHU], examined.

Zoobank LSID
urn:lsid:zoobank.org:act:0F00D5AD-B920-40B3-89AC-884055961270

Material examined
8♂1♀. Holotype ♂: **Japan:** OKINAWA ISLANDS: Okinawa-jima Island, Nanjyô-shi, Sashiki, 1.VIII.1976, S. Yamauchi leg. [SEHU]. Paratypes: **Japan:** OKINAWA ISLANDS: Okinawa-jima Island, Kunigami Village, Oku, 24.VII.2003, Malaise trap, H. Makihara leg. [1♂ TPM], 13.V.2011, K. Sugino leg. [1♀ EUMJ]. **Japan:** OKINAWA ISLANDS: [Okinawa-jima Island], Yona, 30.VII.[19]72, T. Teruya leg. [1♂ RUMF]; Okinawa Is., [Kunigami], Benoki, 9.IX.1972, T. Teruya leg. [1♂ RUMF]; Okinawa-jima, Hyakuna, 30.IV.1976, H. Takizawa leg. [1♂ SEHU]; Okinawa-jima, Chinen, 6.V.1976, H. Takizawa leg. [1♂ SEHU]; [Okinawa-jima Island, Nakagami-gun, Nishihara-chô, Sembaru], Ryukyu University, 1994.5.16 [1♂ RUMF]; Okinawa-jima, Kunigami-gun, Nakijin-son, Tamashiro, 30.V.2022, Y. Tamadera leg. [1♂ SEHU].

Identification source
Primary type.

Sex association
This species was described from both sexes because this is the only species of *Ephucilla* in Okinawa Island, Japan.

Distribution
Japan: Okinawa Islands.

Remarks
This species is quite similar to *E. brevitegula* from Yaeyama Islands and distinguished only by having the metanotum red (black in *E. brevitegula*).

Ephucilla yoshitakei Okayasu, 2020

Ephucilla naja (non Zavattari, 1913): Terayama *et al*., 2011: 13, 21, ♂, part, examined; Lo Cascio, 2015: 548, part; Terayama *et al*., 2016: 166, ♂, part.
Ephucilla yoshitakei Okayasu, 2020: 66, ♂♀, holotype ♂ (Amami-chûô Forest Road, Naze, Amami-ôshima Island, Amami Islands, Japan) [NARO], examined; Okayasu, 2021b: 27, ♂♀, examined.

Zoobank LSID
urn:lsid:zoobank.org:act:F8A7CAE7-9540-4037-AE56-A57BE18CAAB3

Material examined
9♂5♀. Holotype ♂: **Japan:** AMAMI ISLANDS: Amami-ôshima Island, Naze, Amami-chûô Forest Road, 250–300 m alt., 28°20'–22'N 129°26'–29'E, 10–12.VII.2014, S. Shimizu leg. [NARO]. Paratypes: **Japan:** AMAMI ISLANDS: Amami-ôshima Island, Yamato-son, Ongachi, 1.VII.2000, H. Suda leg. [1♂ HSC]; Amami-ôshima Island, Kasari, Yani, Gamôzaki-kankô-kôen park, 28°29'N 129°38'E, 25–26.V.2016, H. Yoshitake leg. [1♀

EUMJ]. **Japan:** AMAMI ISLANDS: Amami-ôshima Island, Amami-shi, Naze, Koshuku, 28°21'45.0"N 129°27'50.0"E, 270 m alt., trail through forest, sweeping bush, 1.VII.2021, 13:30, J. Okayasu leg. [1♂ SEHU], 3.VII.2021, 9:30–14:25 [1♂1♀ SEHU], 4.VII.2021, 11:25 [1♀ SEHU], 5.VII.2021, 8:25 [1♂ SEHU], 6.VII.2021, 9:30–16:15 [4♂ SEHU]; Amami-ôshima Island, Amami-shi, Naze, Koshuku, 28°21'45.0"N 129°27'50.0"E, 270 m alt., trail through forest, yellow pan trap, 7.VII.2021, J. Okayasu leg. [2♀ SEHU].

Identification source
Primary type.

Sex association
This species was described from both sexes because this is the only species of *Ephucilla* in Amami-ôshima Island, Japan.

Distribution
Japan: Amami Islands.

Remarks
This species was consistently placed as sister to *E. naja* by the present phylogenetic analyses, with a single homoplastic synapomorphy: tegula elongate, surpassing transscutal articulation (51:0).

Female-based species of *Ephucilla*

Ephucilla bacbo (Lelej, 1995)

Sinotilla bacbo Lelej, 1995b: 24, ♀, holotype ♀ (Trung Trang, Haiphong, North Vietnam) [ZISP]; Lelej, 1996b: 98, ♀, examined.
Ephucilla bacbo: Lelej, 2005: 39; Lo Cascio, 2015: 548; Okayasu *et al*., 2018: 309, ♀; Okayasu, 2020: 64; Pagliano *et al*., 2020: 171.

Zoobank LSID
urn:lsid:zoobank.org:act:1D7326D1-18A5-460D-A12A-73EA5801DE13

Material examined
1♀. **Indonesia:** KALIMANTAN TIMUR: Kutai N[ational]. P[ark]., Sangkimah, 15.IX.1993, Sk. Yamane leg., *Sinotilla bacbo* Lelej, A. Lelej det. 1995 [1♀ SKYC].

Identification source
Voucher specimen (Lelej, 1996b).

Sex association
Male unknown.

Distribution
Indonesia: Kalimantan Timur. Vietnam: Hai Phong (Lelej, 1995b).

Remarks
This species is known from two remote places in eastern Oriental Region, northern Vietnam and Borneo. Even after examination of hundreds of velvet ant specimens from Indochina

(Williams *et al*., 2019b; this study), the distributional gap has not been filled. Small body size, arboreal habits, and forested habitats of the *Ephucilla* species (Okayasu, 2020) likely hinder extensive sampling of this insect in Southeast Asia.

***Ephucilla bicolor* sp. nov.**

Zoobank LSID
Unavailable.

Diagnosis
FEMALE. Head black; frons and vertex lacking medial carina; frons with large dense punctures, intervals distinct; lower gena and malar space with large sparse punctures; genal carina extending to hypostomal carina; mesosoma red with various portions black; pronotal dorsum with sparse setae only; pronotal dorsum lacking sublateral tooth; humeral carina sharp, not terminating as tooth; propodeum evenly convergent posteriorly; T1 dark brown; T2 black, lacking antero-medial pale setal spot; T2 disc with small sparse punctures; T2 antero-dorsal portion flat; T2 posterior margin with sparse pale golden setae; S2 with small sparse punctures; pygidial plate laterally delimited by weak longitudinal carina on posterior 1/3.

MALE. Unknown.

Description
FEMALE. Body length: 6.78 mm.

Color and setae. Frons, vertex, gena, postgenal bridge, mandible distal 1/3, flagellum dorsally, prementum, stipes, pronotal dorsum, mesonotum lateral portion, propodeum medial portion, propleuron, mesopleuron dorsal 1/2, metapleuron dorsal 2/3, lateral propodeal face anterior 1/2, procoxa, T2–5, S2 around margins, and S3–4 black; antennal rim, clypeus, mandible basal 2/3, pedicel, protrochnater, profemur ventrally, metatibia, and S2 posteromedial portion brown; scape and pronotal anteriorly brownish black; flagellum ventrally and maxillary and labial palpi pale brown; pronotal color posteriorly, lateral pronotal face, mesonotum medial portion, metanotum, propodeum around margins, mesopleuron ventral 1/2, metapleuron ventral 1/3, lateral propodeal face posterior 1/2, meso- and metacoxae, meso- and metatrochanters, meso- and metafemora ventrally, and S1 orange; femora dorsally, pro- and mesotibiae, tarsi, T1, T6, and S5–6 dark brown; tibial spurs yellow. Frons, vertex, mesonotum, metanotum, and propodeum dorsally with sparse short recumbent pale golden and sparse long erect golden setae; gena, scape, femora, tibiae, and S2 with sparse long recumbent and sparse long erect pale golden setae; postgenal bridge, posterior propodeal face, trochanters, T1, T2 around margins, T3, T4–5 lateral margins, T6, and S3–5 with sparse long erect pale golden setae; clypeus, mandible, and S6 with sparse long erect golden setae; pedicel and F1 with sparse short recumbent pale golden setae; F2–10 with dense erect pale golden microsetae; prementum, stipes, and maxillary and labial palpi with sparse short erect golden setae; pronotal dorsum with sparse short recumbent and sparse long erect pale golden setae; propleuron, coxae, and S1 with sparse short appressed and sparse long erect pale golden setae; lateral mesosomal face with sparse short appressed pale golden setae; tarsi with sparse long appressed pale golden setae; T2 disc with sparse short recumbent and sparse long erect black setae; T4–5 medially with sparse long erect black setae; T2 lateral felt line golden, 0.35× T2 length; T2 posterior margin lacking pale setal band; T3 wide uniform band of pale golden setae; S2 with sparse posterior fringe of pale golden setae.

Structure. Head width 1.39× length; genal width 0.700× eye breadth in lateral view; frons and vertex without medial carina or sulcus; occipital carina sharp, complete; malar space lacking vertical carina; genal carina obscurely developed, present on ventral 1/2 of

gena, ventrally reaching hypostomal carina but not forming hypostomal tooth; hypostomal carina sharp; postgenal bridge flat; antennal scrobal carina sharp, arcuate, extending nearly to internal eye margin; eye oval, slightly projecting from head capsule; minimum distance between eyes 0.768× eye height; eye height 2.34× malar distance; clypeus medially elevated, ventrally forming small rounded tooth; clypeus with subventral complete transverse flange, with its ventral margin truncate; clypeus lacking lateral tooth below subventral flange; mandible slender, narrowed to apex; mandible apically with one internal tooth smaller than apex; mandibular internal margin entire; mandibular ventral margin straight; prementum flat, medially with sharp longitudinal carina extending along its entire length; length and width of pedicel:F1:F2 = 1.00:1.20:2.00:1.80:1.50:1.70.

Mesosoma broadest at mesonotum; lateral margins crenulate, evenly convergent posteriorly; head width:humeral width:pronotal width:mesonotal width:propodeal width:metasomal width = 91:69:78:78:73:100; dorsal thoracic length 1.02× pronotal width; antero-dorsal pronotal margin weakly arcuate, lacking sublateral tooth; pronotum laterally not projecting; humeral angle angulate; humeral carina sharp, reaching pronotal dorsum but not terminating as tooth; metanotal-propodeal suture obliterated; prescutellar scales absent; scutellar scale weakly elevated, obscured by insect pin; propodeum lacking scales; posterior propodeal face vertical, without medial carina; lateral propodeal margin crenulate; mesopleural lamella absent.

Procoxa lacking process; metacoxa with sharp complete internal longitudinal carina; meso- and metatibiae with two rows of external spines; protarsus with short external spines; protarsomere 1 apically truncate, not protruding outward.

T1 subsessile, without distinct dorsum; T2 disc dorsally flat; dorsal T2 length 1.02× T2 width; S1 with medial longitudinal carina on anterior 3/4, straight in profile; S2 evenly convex, lacking antero-medial carina; S6 posterior margin distinctly bidentate; pygidial plate slender, convex; lateral pygidial carina weakly developed, present on posterior 1/3.

Frons, vertex, and gena dorsally half with large dense punctures, separated by ~0.5× puncture diameter; gena ventral 1/2, and malar space with large sparse punctures; postgenal bridge transversely rugose; antennal rim smooth; clypeal medial elevated portion, mesopleuron ventral 1/2, T3, T6 laterally, and S3–6 with small dense punctures; clypeus laterally, prementum, and stipes with minute sparse punctures; scape, meso- and metacoxae, trochanters, femora, tibiae, T1, T2, T4–5, S1, and S2 with small sparse punctures; pedicel, flagellum, maxillary and labial palpi, propleuron, lateral pronotal face, mesopleuron dorsal 1/2, metapleuron, lateral propodeal face, procoxa, and tarsi with minute dense punctures; thoracic dorsum densely punctate-reticulate; posterior propodeal face reticulate; pygidial plate smooth.

MALE. Unknown.

Material examined

1♀. Holotype ♀: **Vietnam:** HOA BINH: Ha Son Binh Prov. [= Hoa Binh], Cuc Phuong, 200–300 m alt., 24.IV.1998, R. Matsumoto leg. [VNMN].

Sex association

Male unknown.

Distribution

Vietnam: Hoa Binh.

Etymology

The specific name *bicolor*, two-colored, is the Latin, singular, feminine adjective in the

nominative case. It refers to the two-colored mesosoma of this new species.

Remarks
This species is similar to *E. bacbo* by having the frons and vertex lacking a medial carina, lower gena and malar space with separated punctures, humeral carina sharp, propodeum evenly convergent posteriorly, and T2 evenly convex with small sparse punctures. However, this new species is distinguished from it by having the head black, mesosoma partially black, humeral carina sharp but not lamellate, and T2 black with sparse setae only.

Ephucilla bifida sp. nov.

Zoobank LSID
Unavailable.

Diagnosis
FEMALE. Head black; frons and vertex lacking medial carina; frons with large dense punctures, intervals distinct; lower gena and malar space with large confluent punctures; genal carina bifid ventrally, extending to hypostomal carina and mandibular base; mesosoma red; pronotal dorsum with sparse setae only; pronotal dorsum lacking sublateral tooth; humeral carina sharp, not terminating as tooth; propodeum wider than metanotum; T1 black; T2 black, lacking antero-medial pale setal spot; T2 disc with small sparse and minute dense punctures; T2 antero-dorsal portion flat; T2 posterior margin with pale golden setal band; S2 with small sparse punctures; pygidial plate laterally delimited by weak longitudinal carina on posterior 1/2.

MALE. Unknown.

Description
FEMALE. Body length: 4.44 mm.

Color and setae. Frons, vertex, gena, and T1–5 black; postgenal bridge, clypeus, mandible distal and proximal 1/3, scape, pedicel, flagellum dorsally, prementum, stipes, femora dorsally, tibiae, tarsi, and S6 brownish black; antennal rim, T6, and S3–5 dark brown; mandible medial 1/3 reddish yellow; flagellum ventrally and maxillary and labial palpi pale brown; mesosoma, coxae, trochanters, femora ventrally, and S1 orange; tibial spurs pale brown; S2 brown. Frons, vertex, thoracic dorsum, T2 disc, and T4–5 medially with sparse short recumbent and sparse long erect black setae; gena and scape with sparse long recumbent pale golden setae; postgenal bridge, clypeus, mandible, posterior propodeal face, T1, T2 around margins, T3, T4–5 lateral margins, T6, and S1–6 with sparse long erect pale golden setae; pedicel, F1, and lateral mesosomal face with sparse short appressed pale golden setae; F2–10 with dense erect pale golden microsetae; prementum, stipes, and maxillary and labial palpi with sparse short erect pale golden setae; propleuron with sparse short appressed and sparse long erect pale golden setae; coxae, trochanters, femora, tibiae, and T2 lateral margin with sparse long recumbent and sparse long erect pale golden setae; tarsi with sparse long appressed pale golden setae; T2 lateral felt line golden, 0.3× T2 length; T2 with narrow dense posterior band of pale golden setae, medially slightly widened; T3 with wide uniform band of pale golden setae; S2–5 with sparse posterior fringe of pale golden setae.

Structure. Head width 1.43× length; genal width 0.722× eye breadth in lateral view; frons and vertex without medial carina or sulcus; occipital carina sharp, complete; malar space anteriorly delimited by vertical carina; genal carina wavy, dorsally extending nearly to vertex; genal carina ventrally bifid, one reaching hypostomal carina and forming small hypostomal tooth and one reaching mandibular base; hypostomal carina sharp; postgenal

bridge flat; antennal scrobal carina sharp, arcuate, extending nearly to ventral eye margin; eye oval, slightly projecting from head capsule; minimum distance between eyes 1.20× eye height; eye height 2.17× malar distance; clypeus medially elevated, not forming tooth; clypeus with subventral complete transverse flange, with its ventral margin truncate; clypeus lacking lateral tooth below subventral flange; mandible slender, narrowed to apex; mandible apically with one internal tooth smaller than apex; mandibular internal margin entire; mandibular ventral margin straight; prementum flat, medially with sharp longitudinal carina extending along its entire length; length and width of pedicel:F1:F2 = 1.00:1.29:2.00:1.86:1.43:1.86.

Mesosoma broadest at pronotum; lateral margins crenulate, constricted at propodeal spiracle; head width:humeral width:pronotal width:mesonotal width:propodeal width:metasomal width = 92:67:79:73:75:100; dorsal thoracic length 0.915× pronotal width; antero-dorsal pronotal margin weakly arcuate, lacking sublateral tooth; pronotum laterally slightly projecting; humeral angle weakly angulate; humeral carina sharp, reaching pronotal dorsum but not terminating as tooth; metanotal-propodeal suture obliterated; prescutellar scales absent; scutellar scale weakly elevated, its width 0.146× propodeal width, 4.00× puncture diameter; propodeum dorsally with spinulose scales; posterior propodeal face oblique, without medial carina; lateral propodeal margin weakly dentate on dorsal half, crenulate on ventral half; mesopleural lamella absent.

Procoxa lacking process; metacoxa with sharp complete internal longitudinal carina; meso- and metatibiae with one row of external spines; protarsus with short external spines; protarsomere 1 apically truncate, not protruding outward.

T1 subsessile, without distinct dorsum; T2 disc dorsally flat; dorsal T2 length 0.930× T2 width; S1 with medial longitudinal carina on anterior 3/4, elevated posteriorly; S2 evenly convex, lacking antero-medial carina; S6 posterior margin truncate; pygidial plate slender, convex; lateral pygidial carina weakly developed, present on posterior 1/2.

Frons and vertex with large dense punctures, separated by 0.5–1× puncture diameter; gena and thoracic dorsum with large confluent punctures; postgenal bridge transversely rugose; antennal rim and clypeus laterally smooth; clypeal medial elevated portion, T1 posterior margin, T3–5, and T6 laterally with small dense punctures; scape, meso- and metacoxae, trochanters, femora, tibiae, T1 anteriorly, S1, and S3–6 with small sparse punctures; pedicel, flagellum, maxillary and labial palpi, propleuron, lateral mesosomal face, procoxa, and tarsi with minute dense punctures; prementum and stipes with minute sparse punctures; posterior propodeal face sparsely longitudinally striate; T2 disc with small sparse and minute dense punctures; T2 lateral margin and S2 with large sparse punctures; pygidial plate smooth.

MALE. Unknown.

Material examined

1♀. Holotype ♀: **Indonesia:** NUSA TENGGARA BARAT: Propinsi Nusa Tenggara Barat, Kabuoaten Lombok Barat, Kecamatan Anyar, Desa Senaru, Taman Nasional Gunung Rinjani, 08°18'19"S 116°23'59"E, alt. 550 m, LO-00-MO-020, 2.XI.2000, M. Ohara leg. [SEHU].

Sex association

Male unknown.

Distribution

Indonesia: Nusa Tenggara Barat.

Etymology

The specific name *bifida*, bifid, is the Latin, singular, feminine adjective in the nominative case. It refers to the bifid genal carina which distinguishes this new species from other *Ephucilla* females.

Remarks
This new species is unique in *Ephucilla* females by having the genal carina bifid, extending to both hypostomal carina and mandibular base. This species represents the first record of the genus from Wallacea.

Ephucilla hejunhuai Lelej, 2020

Ephucilla hejunhuai Lelej, 2020: 2, ♀, holotype ♀ (Xiang Tai Shan near Guangzhou, Guangdong, China) [IBSS].

Zoobank LSID
urn:lsid:zoobank.org:act:BB574DEA-C989-429C-974A-FBB37AF053C6

Material examined
No material examined.

Sex association
Male unknown.

Distribution
China: Guangdong.

Remarks
This species is unique in *Ephucilla* by having the T2 anteriorly reddish.

Ephucilla nigrothoracica (Okayasu, 2018), comb. nov.

Sinotilla nigrothoracica Okayasu in Okayasu *et al*., 2018: 313, ♀, holotype ♀ (Lienhuachih, Nantou Co., Taiwan) [SEHU], examined; Okayasu, 2020: 89; Pagliano *et al*., 2020: 186.

Zoobank LSID
urn:lsid:zoobank.org:act:D0FDA3E6-C6A5-47F4-9977-EF2E7287E10E

Material examined
3♀. Holotype ♀: **Taiwan:** NANTOU: Lienhuachih, 5.V.1996, H. Takizawa leg. [SEHU]. **Taiwan:** TAITUNG: Pilan, Chihpen-Wanchuan, 5–7.IV.2001, K. Okajima leg. [1♀ TUA]; Peinan Hsiang, Chihpen spa, 1.IV.2004, T. Tsuru leg. [1♀ TUA].

Identification source
Primary type.

Sex association
Male unknown.

Distribution

Taiwan: Nantou, Pingtung, Taipei, Taitung (Okayasu *et al*., 2018).

Remarks
This species was initially described in *Sinotilla* because it lacks the lateral pygidial carinae. Two additional specimens examined herein have the T2 posterior band only medially, while the holotype has theT2 posterior band extending early to lateral T2 margin.

Ephucilla okajimai **sp. nov.**

Zoobank LSID
Unavailable.

Diagnosis
FEMALE. Head red; frons and vertex lacking medial carina; frons with large confluent punctures, intervals reduced; lower gena and malar space with large confluent punctures; genal carina extending to hypostomal carina; mesosoma red; pronotal dorsum with sparse setae only; pronotal dorsum with small rounded sublateral tooth; humeral carina lamellately projecting, not terminating as tooth; propodeum evenly convergent posteriorly; T1 orange; T2 blue metallic, lacking antero-medial pale setal spot; T2 disc with small confluent punctures; T2 antero-dorsal portion flat; T2 posterior margin with golden setal band; S2 with large sparse punctures; pygidial plate laterally delimited by weak longitudinal carina on posterior 3/4.

MALE. Unknown.

Description
FEMALE. Body length: 6.08 mm.

Color and setae. Frons, vertex, gena, postgenal bridge, antennal rim, clypeus, mesosoma, procoxa anterior 1/3, meso- and metacoxae, trochanters, meso- and metafemora proximal 3/4, T1, and S1 orange; mandible proximal 2/3 reddish yellow; mandible distal 1/3, F1, F2–10 dorsally, meso- and metafemora apical 1/4, and T3–5 black; scape brown; pedicel, prementum, stipes, profemur, tibiae dorsally, and tarsi dark brown; F2–10 ventrally, maxillary and labial palpi, and tibial spurs pale brown; tibiae ventrally brown; T2 blue metallic; T6 and S2–6 brownish black. Frons and vertex with sparse short recumbent and sparse long erect golden setae; gena and scape with sparse long recumbent pale golden setae; postgenal bridge, mandible, posterior propodeal face, trochanters, and S2 with sparse long erect pale golden setae; clypeus, T1, T2 lateral margin, T2 around margins, T3, T4–5 lateral margins, T6, and S3–6 with sparse long erect golden setae; pedicel and F1 with sparse short appressed pale golden setae; F2–10 with dense erect pale golden microsetae; prementum, stipes, and maxillary and labial palpi with sparse short erect pale golden setae; thoracic dorsum with sparse short recumbent and sparse long erect dark golden setae; propleuron, mesopleuron, lateral propodeal face, and S1 with sparse short appressed and sparse long erect pale golden setae; lateral pronotal face and metapleuron with sparse short appressed pale golden setae; coxae, femora, and tibiae with sparse long recumbent and sparse long erect pale golden setae; tarsi with sparse long appressed pale golden setae; T2 disc with sparse short recumbent black and sparse long erect golden setae; T4–5 medially with sparse short recumbent and sparse long erect black setae; T2 lateral felt line golden, 0.3× T2 length; T2 with narrow dense posterior band of golden setae, medially strongly widened; T3 with wide uniform band of golden setae; S2–5 with sparse posterior fringe of golden setae.

Structure. Head width 1.35× length; genal width 0.875× eye breadth in lateral view; frons and vertex without medial carina or sulcus; occipital carina sharp, complete; malar

space lacking vertical carina; genal carina wavy, dorsally extending to midpoint of gena, ventrally reaching hypostomal carina and forming small hypostomal tooth; hypostomal carina sharp; postgenal bridge flat; antennal scrobal carina sharp, straight, distantly separated from internal eye margin; eye oval, slightly projecting from head capsule; minimum distance between eyes 1.16× eye height; eye height 1.80× malar distance; clypeus medially elevated, ventrally forming small rounded tooth; clypeus with complete subventral transverse flange, with its anterior margin truncate; clypeus lacking lateral tooth below subventral flange; mandible slender, narrowed to apex; mandible apically with two internal teeth smaller than apex; mandibular internal margin entire; mandibular ventral margin straight; prementum flat, medially with sharp longitudinal carina extending along its entire length; length and width of pedicel:F1:F2 = 1.00:1.09:1.91:1.36:1.18:1.36.

Mesosoma broadest at pronotum; lateral margins crenulate, evenly convergent posteriorly; head width:humeral width:pronotal width:mesonotal width:propodeal width:metasomal width = 79:64:67:65:63:100; dorsal thoracic length 1.02× pronotal width; antero-dorsal pronotal margin nearly straight, with small rounded sublateral tooth; pronotum laterally not projecting; humeral angle angulate; humeral carina sharp, dorsally lamellately projecting and reaching pronotal dorsum but not terminating as tooth; metanotal-propodeal suture obliterated; prescutellar scales absent; scutellar scale weakly elevated, its width 0.210× propodeal width, 2.86× puncture diameter; propodeum lacking scales; posterior propodeal face vertical, without medial carina; lateral propodeal margin crenulate; mesopleural lamella absent.

Procoxa lacking process; metacoxa with sharp complete internal longitudinal carina; mesotibia lacking external spines; metatibia with two rows of external spines; protarsus with short external spines; protarsomere 1 apically truncate, not protruding outward.

T1 subsessile, without distinct dorsum; T2 disc dorsally flat; dorsal T2 length 1.06× T2 width; S1 with medial longitudinal carina on anterior 3/4, slightly emarginate at posterior 1/3; S2 evenly convex, lacking antero-medial carina; S6 posterior margin emarginate medially; pygidial plate slender, subconvex; lateral pygidial carina sharp, present on posterior 3/4.

Frons, vertex, gena, and thoracic dorsum with large confluent punctures; postgenal bridge transversely rugose; antennal rim smooth; clypeus medial elevated portion, mesopleuron ventral 1/2, T3–5, T6 laterally, S1, and S3–6 with small dense punctures; clypeus laterally with minute sparse punctures; scape, meso- and metacoxae, trochanters, femora, tibiae, and T1 with small sparse punctures; pedicel, flagellum, maxillary and labial palpi, propleuron, mesopleuron dorsal 1/2, metapleuron, lateral propodeal face, procoxa, and tarsi with minute dense punctures; prementum and stipes with minute sparse punctures; posterior propodeal face reticulate; T2 disc with small confluent punctures; T2 lateral margin with large dense punctures, separated by less than puncture diameter; S2 with large sparse punctures; pygidial plate longitudinally rugose on anterior 1/3 and smooth posteriorly.

MALE. Unknown.

Material examined

1♀. Holotype ♀: **Thailand:** CHIANG MAI: Chiang Dao, Pakia, 1500 m alt., 6.V.2002, K. Okajima leg. [TUA].

Sex association

Male unknown.

Distribution

Thailand: Chiang Mai.

Etymology
The specific name *okajimai* is dedicated to the type collector, Kentaro Okajima.

Remarks
Based on the body coloration, this new species was initially confused with *E. bacbo* and *E. viet*. However, this species has denser and coarser punctures on the head and T2, by which it can be distinguished from them.

Ephucilla petina (Mickel, 1937), comb. nov.

Smicromyrme petina Mickel, 1937: 451, ♀, holotype ♀ (Mt. Matang, W. Sarawak, Borneo, [Malaysia]) [NHMUK].
Smicromyrme spinicauda Chen, 1957, **syn. nov.**: 210, ♀, holotype ♀ (Tienmushan [= Mt. Tianmu-shan], Chekiang [= Zhejiang], China) [TARI], examined; He *et al*., 2004: 957, ♀; Lelej, 2005: 64; Okayasu *et al*., 2018: 306, ♀; Pagliano *et al*., 2020: 202.
Sinotilla belokobylskiji Lelej, 1995b, **syn. nov.**: 22, ♀, holotype ♀ (Tam Dao, Vinh Phuc, Vietnam) [ZISP]; Lelej, 2005: 54; Okayasu, 2017: 152, ♀; Okayasu *et al*., 2018: 303, ♀; Williams *et al*., 2019b: 26, ♀, examined; Okayasu, 2020: 89; Pagliano *et al*., 2020: 186; Lelej & Williams, 2023: 105, ♀.
Sinotilla lambirensis Lelej, 1996b, **syn. nov.**: 98, ♀, holotype ♀ (Tower Region, Lambir National Park, Miri, Sarawak, Malaysia) [SKYC], examined; Lelej, 2005: 55; Lo Cascio, 2015: 557; Okayasu, 2017: 159, ♀; Okayasu, 2018: 493, ♀; Okayasu, 2020: 89; Pagliano *et al*., 2020: 186.
Sinotilla petina: Lelej, 2005: 55; Okayasu, 2017: 152, ♀; Okayasu *et al*., 2018: 306; Okayasu, 2020: 89; Pagliano *et al*., 2020: 186.
Sinotilla calopoda Okayasu, 2017, **syn. nov.**: 152, ♀, holotype ♀ (Sukabumi, Kabandungan, Mekarjaya, Pasirgede, Jawa Barat, Indonesia) [EUMJ], examined; Okayasu, 2018: 493, ♀; Okayasu, 2020: 89; Pagliano *et al*., 2020: 186.
Sinotilla ohbayashii Okayasu, 2017, **syn. nov.**: 156, ♀, holotype ♀ (Wuyishan, Dujia, Fujian, China) [EUMJ], examined; Okayasu *et al*., 2018: 317, ♀; Okayasu, 2018: 493, ♀; Okayasu, 2020: 89; Pagliano *et al*., 2020: 186.
Sinotilla lambiriensis: Okayasu *et al*., 2018: 304, ♀. Incorrect subsequent spelling.
Sinotilla spinicauda: Okayasu, 2018: 492, ♀; Okayasu, 2020: 89.

Zoobank LSID
urn:lsid:zoobank.org:act:E6CF1A30-4C6A-415D-8787-8442A550D5E1
urn:lsid:zoobank.org:act:7963896F-EF35-4645-96D2-EE1E0EA5E2FD
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urn:lsid:zoobank.org:act:B685E7AD-E7E6-4F54-A4F1-BC38CBE67C95

Material examined
13♀. Holotype ♀, *Sinotilla labirensis* Lelej: **Malaysia:** SARAWAK: Miri, Lambir National Park, Tower Region, 22.I.1993, Sk. Yamane leg. [SKYC]. Holotype ♀, *Smicromyrme spinicauda* Chen: **China:** ZHEJIANG: Chekiang [= Zhejiang], Tien-Mu-Shan [= Mt. Tianmu-shan], 17.VIII.1936, T.C. Maa leg., *Smicr. spinicauda* Chen [unknown hand] [TARI]. Holotype ♀, *Sinotilla calopoda* Okayasu: **Indonesia:** JAWA BARAT: Sukabumi, Kabandungan, Mekarjaya, Pasirgede, Jangkar, 1163 m alt., by beating, 06°49'46.6"S

106°34'43.4"E, 27.X.2009, H. Yoshitake leg. [EUMJ]. Holotype ♀, *Sinotilla ohbayashii* Okayasu: **China:** FUJIAN: Wuyishan, Dujia, 31.V.2002, N. Ohbayashi & L. Li leg. [EUMJ]. **Malaysia:** NEGERI SEMBILAN: Pasoh Forest, 27.IX.1986, Y. Miyatake leg. [1♀ OMNH]. **Thailand:** CHIANG MAI: Chiang Dao, Pa Kia, 6.V.2000, T. Tsuru leg. [1♀ TUA]; Doi Suthep, Chang Khian, 8–11.V.2000, K. Okajima leg. [1♀ TUA]; Omkoi District, dry dipterocarp forest, 17°50'49.9"N 98°22'33.0"E, 950–1010 m alt., 12.IX.2016, R. Mizuno leg. [1♀ THNHM], 14.XII.2016 [2♀ THNHM], 14.VII.2019 [1♀ THNHM]. **Vietnam:** HOA BINH: Tonkin [= North Vietnam], Hoa Binh, A. de Cooman leg., *Smicr. decora* (Smith) (?) [probably Chen's hand] [1♀ TARI]; VINH PHUC: Tam Dao, V.1997 [1♀ TUA].

Identification source
Voucher specimens (Chen, 1957; Lelej, 1996b; Okayasu, 2017; Williams *et al*., 2019b).

Sex association
Male unknown.

Distribution
China: Fujian, Zhejiang, Yunnan (Lelej, 2005). Indonesia: Jawa Barat. Malaysia: Negeri Sembilan, Sarawak. Thailand: Chiang Mai, Phetchaburi, Songkhla (Williams *et al*., 2019b). Vietnam: Hanoi, Hoa Binh, Vinh Phuc.

Remarks
After examination of 13 females from throughout East Asia, *S. belokobylskiji*, *S. calopoda*, *S. lambiensis*, *S. ohbayashii*, and *S. spinicauda* were found synonymous because of overlapping variation of characters previously used to separate them. Even though the type specimens of *S. petina* were not available for this study, I could not find any significant differences between the original description of *S. petina* and specimens examined herein.

Ephucilla poonaensis (Cameron, 1892)

Mutilla poonaensis Cameron, 1892: 129, ♀, syntypes ♀ (Poona, [Maharashtra], India) [NHMUK]; André 1894: 482, ♀; Dalla Torre 1897: 73; Bingham 1897: 39, ♀; Maxwell-Lefroy, 1909: 187, ♀; Dutt, 1912: 184, ♀.
Mutilla hesitata Cameron, 1900: 42, ♀, syntypes ♀ (Ceylon [= Sri Lanka]) [NHMUK]. Synonymized by Lelej (2005: 41) under *Ephucilla poonaensis* (Cameron).
Promecilla poonaensis: André, 1902b: 31; Hammer, 1962: 48, ♀; Pagliano & Scaramozzino, 2021: 111, ♀.
Promecilla hesitata: André, 1902b: 31; Krombein, 1978: 729, ♀; Krombein 1991: 9.
Ephucilla poonaensis: Lelej, 2005: 40; Lo Cascio, 2015: 548; Okayasu, 2020: 65, ♀; Pagliano *et al*., 2020: 172.

Zoobank LSID
urn:lsid:zoobank.org:act:3D9D2949-5FE9-47D3-9696-90F6ED2FDF1E

Material examined
2♀. **India:** WEST BENGAL: Bengal, Birbhum Distr., Santiniketan, VII.1938, T.C. Maa leg. [1♀ TARI]. **Sri Lanka:** KANDY: Udawattakele Sanct., on standing dead tree trunk, 25–27.IV.1981, K.V. Krombein, T. Wijesinhe, L. Weeratunge leg., *Promecilla poonaensis* (Cameron), B. Petersen det. 1984 [1♀ NMNH].

Identification source
Identified specimen.

Sex association
This species was described from the female only. The potential male of this species is *E. ludovica*, because these two species share the same host (Krombein, 1978, 1991).

Distribution
India: Maharashtra, West Bengal (Cameron, 1892). Sri Lanka: Kandy.

Remarks
This species was reared from arboreal mud nests of the potter wasp *Paraleptomenes mephitis* (Cameron, 1901) (Krombein, 1978, 1991) and an unidentified eumenine species (Dutt, 1912; Maxwell-Lefroy, 1909).

Ephucilla subparallela (Chen, 1957), comb. nov.

Smicromyrme subparallela Chen, 1957: 214, ♀, holotype ♀ (Wencheng, Liencheng, Fukien [= Fujian], China) [TARI], examined.
Sinotilla subparallela: Lelej, 1995b: 19; Lelej, 2005: 56; Okayasu, 2017: 152, ♀; Okayasu *et al*., 2018: 304, ♀; Okayasu, 2020: 89; Pagliano *et al*., 2021: 187.

Zoobank LSID
urn:lsid:zoobank.org:act:D95A663A-9291-4BB4-B5F4-2AB9F9B9A78B

Material examined
1♀. Holotype ♀: **China:** FUJIAN: Fukien [= Fujian], Liencheng, Wencheng, 11.VI.1939, T.C. Maa leg., *Smicr*. *subparallela* Chen [unknown hand] [TARI].

Identification source
Primary type.

Sex association
Male unknown.

Distribution
China: Fujian.

Remarks
The holotype of this species is deposited in TARI and has appropriate labels. However, this specimen is badly damaged and setal patterns cannot be recognized. Some appendages are mounted on a card.

Ephucilla viet (Lelej, 1995)

Sinotilla viet Lelej, 1995b: 25, ♀, holotype ♀ (Island Dong Kho, Prov. Quang Ninh, North Vietnam) [IBSS].
Ephucilla viet: Lelej, 2005: 41; Lo Cascio, 2015: 548; Okayasu *et al*., 2018: 303, ♀; Williams *et al*., 2019b: 17, ♀, examined; Okayasu, 2020: 65; Pagliano *et al*., 2020: 172.

Zoobank LSID
urn:lsid:zoobank.org:act:4B896FBA-7FDA-4325-9F2B-2159CB4CD7E6

Material examined
1♀. **Thailand:** CHIANG MAI: Omkoi District, dry dipterocarp forest, 17°50'49.9"N 98°22'33.0"E, 950–1010 m alt., 23.VI.2017, R. Mizuno leg. [1♀ THNHM].

Identification source
Voucher specimen (Williams *et al*., 2019b).

Sex association
Male unknown.

Distribution
Malaysia: Pahang (Williams *et al*., 2019b). Thailand: Chiang Mai, Phetchaburi (Williams *et al*., 2019b). Vietnam: Quang Ninh, Vinh Phuc (Lelej, 1995b; Williams *et al*., 2019b).

Remarks
Despite of intensive sampling in southern Thailand by Williams *et al*. (2019b), only a single specimen was collected by chance in that region collected by chance. Like *E. bacbo*, this species is widely distributed in Indochina but huge distributional gaps are still present, probably due to its cryptic nature.

Genus *Ephutomma* Ashmead, 1899

Ephutomma Ashmead, 1899: 52, ♂; André, 1902b: 19, ♂, part; Bischoff, 1920: 144, ♂; Mickel, 1928: 32; Skorikov, 1935: 321, ♂; Lelej & Kabakov, 1980: 192, ♂♀; Lelej, 1985: 183, ♂♀; Lelej, 1995c: 209, ♂♀; Lelej, 2002: 52; Lelej, 2005: 41; Lelej, 2007: 88; Lelej & Brothers, 2008: 22; Brothers & Lelej, 2017: 95; Pagliano *et al*., 2020: 172; Lelej & Williams, 2023: 112, ♂♀. Gender feminine.
Mutilla (*Ephutomma*): André, 1900: 136, ♂.
Eremomyrme Suárez, 1965: 51, ♂; Brothers, 1975: 592, ♂; Lelej, 1976: 277, ♂♀. Synonymized by Lelej & Kabakov (1980: 192) under *Ephutomma* Ashmead. Gender feminine.

Zoobank LSID
urn:lsid:zoobank.org:act:7A528526-C489-4633-9955-8193F32FE251
urn:lsid:zoobank.org:act:0CE1F7C5-40A0-49B1-AE8E-C4685B2FFBA2

Type species
Ephutomma: *Mutilla incerta* Radoszkowski, 1877 (non Spinola, 1841) (replaced by *Mutilla turcestanica* Dalla Torre, 1897), ♂, by original designation.
Eremomyrme: *Mutilla turcestanica* Dalla Torre, 1897, ♂, by automatic designation.

Diagnosis
MALE. Frons punctate; vertex rounded; ventral clypeal margin entire or with medial paired teeth medially; mandible apex tridentate, internal teeth as large as apex, without subdistal internal tooth; mandible dorso-lateral carina highly elevated, terminating as internal tooth; mandible ventral margin emarginate with large proximal tooth; flagellomere apices truncate; F1 longer than wide; notaulus reaching posterior margin of pronotum; parascutal carina

forming elevated process; tegula rounded posteriorly, slightly surpassing transscutal articulation; mesopleuron divided into dorsal and ventral convexities by transverse impression; mesopleuron ventral face lacking sharp process; procoxa lacking posterior process; metacoxal internal carina weakly developed; S2 lacking lateral felt line; harpe dorso-internal margin lacking proximal process; parapenis bifid; gonostipes ventral lobe truncate; basivolsella elongate with long wavy setae on ventral margin; basivolsella internal face lacking seta-filled pit; basiura small rounded; apiceps long slender; penisvalva strongly expanded ventrad; penisvalva posterior process lacking external process; penisvalva internal face lacking setae.

FEMALE. See Lelej & Williams (2023).

Species included

A total of 18 species is recognized in this genus. The following one species is distributed in East Asia: *E. mongolensis* (Suárez, 1974), ♂♀ (China, Mongolia, Russia).

Sex association

The type species was initially described from the male only. The female of this species was described as *Smicromyrme semenovi* Skorikov, 1935 and associated by Lelej & Kabakov (1980).

Distribution

Afrotropical, Oriental, and Palaearctic Regions.

Remarks

This genus was recovered as a monophyletic group by the present phylogenetic analyses under all setting, although *E. mongolensis* differs from the type species, *E. turcestanica*, by having the head enlarged, ocelli small, and cuspis short robust. Monophyly was well supported (GC = 83; Fig. 22-1) by a unique synapomorphy and several homoplastic synapomorphies: frons with a medial shallow sulcus (13:1), mandible widened distally (28:1), mandibular proximo-ventral tooth armed with an additional ventral process (34:1), distance between origin of RS on vein SC and proximal margin of pterostigma exceeding pterostigma length (52:2), S2 with an antero-medial carina (83:1), S2 lacking lateral felt line (86:1), and penisvalva lacking ventral cuticular piece (123:0).

Ephutomma mongolensis (Suárez, 1974)

Smicromyrme mongolensis Suárez, 1974: 14, ♂, holotype ♂ (Ulaan chodag, 16 km S von Somon Öndörschireet, [Töv], Mongolia) [HNHM]; Lelej, 1975: 324.
Eremomyrme mongolensis: Lelej, 1977b: 534, ♂.
Smicromyrme kozlovi: Lelej, 1976: 273, ♀; Lelej, 1981: 78, ♂.
Smicromyrme (*Paramyrme*) *kozlovi*: Lelej, 1977b: 534, ♀.
Ephutomma mongolensis: Lelej, 1985: 188, ♂♀; Lelej, 1995c: 210, ♂♀; Lelej, 2002: 53; Lelej *et al*., 2014: 390; Lelej, 2017: 65; Pagliano *et al*., 2020: 173; Pagliano & Scaramozzino, 2021: 108, ♂.

Zoobank LSID

urn:lsid:zoobank.org:act:F2297337-9CAB-460E-96CA-22B025E15203

Material examined

2♂. **China:** INNER MONGOLIA: Apaka, 5.VII.1939, K. Tsuneki leg. [1♂ MNHAH],

16.VII.1939 [1♂ MNHAH].

Identification source
Keyed using Lelej (1985) and compared with the original description.

Sex association
Female unknown.

Distribution
China*: Inner Mongolia. Mongolia: Bayanhongor, Dornod, Govĭ-Altay, Sükhbaatar, Töv, Zavhan (Lelej, 1976, 1977b; Suárez, 1974). Russia: Zabaykalsky (Lelej, 1981).

Remarks
Most species of the *Ephutomma* are found in arid areas of the Palaearctic Region, like Central Asia and Northern Africa (Lelej, 2002, 2005; Pagliano *et al*., 2020). This is the only species of the genus in East Asia.

Genus *Hadrodontilla* nov.

Type species
Mutilla davidi André, 1898, ♂, designated here.

Zoobank LSID
Unavailable.

Diagnosis
MALE. Frons punctate; vertex rounded; ventral clypeal margin entire; mandible apex tridentate, internal teeth as large as apex, with subdistal internal tooth; mandible dorso-lateral carina highly elevated, terminating as internal tooth; mandible ventral margin straight; flagellomere apices bifid; F1 longer than wide; notaulus reaching posterior margin of pronotum; parascutal carina forming weak process; tegula projecting posterad, surpassing transscutal articulation; mesopleuron divided into dorsal and ventral convexities by transverse impression; mesopleuron ventral face lacking sharp process; procoxa with sharp posterior process; metacoxal internal carina weakly developed; S2 with lateral felt line; harpe dorso-internal margin lacking proximal process; parapenis bifid; gonostipes ventral lobe projecting dorsad; basivolsella elongate with long wavy setae on ventral margin; basivolsella internal face with seta-filled pit; basiura small rounded; apiceps long slender; penisvalva strongly expanded ventrad; penisvalva posterior process lacking external process; penisvalva internal face lacking setae.

FEMALE. Head size large; minimum distance between eyes 1.32–1.46× eye height; minimum distance between posterior margin of head and posterodorsal angle of eye 0.625–0.724× eye height; genal carina and hypostomal tooth absent; clypeus medially elevated but not forming tubercle; clypeus with subventral transverse flange; mandible broad, apically tridentate with internal teeth as large as apex; prementum convex, lacking posterior rounded process; F1 length 1.53–1.83× F1 width and 1.28–1.67× F2 length; mesosoma broadest at pronotal spiracle; mesosomal lateral margins slightly convergent posteriorly; antero-dorsal pronotal margin nearly straight; humeral carina sharp; scutellar scale wide, elevated; mesopleural lamella absent; propodeum laterally rounded; procoxa lacking rounded tubercle; protarsus pectinate; T1 broad, sessile with T2; T2 dorsally flat; T2 length 0.75–0.87× T2 width; pygidial plate flat, ovate, laterally defined by sharp longitudinal carinae; surface of

pygidial plate feebly longitudinally rugose on anterior 2/3 and shagreened on posterior 1/3; lateral pygidial margins strongly convergent anteriorly.

Species included
Two species: *H. davidi* (André, 1898), ♂ (China, Taiwan, Vietnam); *H. pekiniana* (André, 1905), ♀ (China, Taiwan, Thailand).

Sex association
The type species is known from the male only. The potential female of the type species is associated below.

Distribution
Oriental Region.

Etymology
The generic name *Hadrodontilla* is the combination of the Greek adjective *hadro*, robust, and the Greek prefix *odonto*, having teeth, with a common suffix for mutillid genera derived from *Mutilla*. It refers to the wide robust mandible of the type species. Gender feminine.

Remarks
The male of this genus was formerly placed in *Andreimyrme* (Lelej, 1995b). However, the type species of this new genus, *H. davidi*, differs from *Andreimyrme* by having the unique set of characters: the flagellomere apices bifid (truncate in *Andreimyrme*), tegula surpassing transscutal articulation (not surpassing in *Andreimyrme*), mesopleuron without ventral process (present in *Andreimyrme*), procoxa armed with a posterior triangular process (without process in *Andreimyrme*), S2 with a lateral felt line (absent in *Andreimyrme*), parapenis bifid (posteriorly truncate in *Andreimyrme*), gonostipes ventral lobe projecting dorsad (truncate in *Andreimyrme*), and basivolsella with a seta-filled pit (absent in *Andreimyrme*).

In phylogenetic analyses, this new genus was supported by two unique and a number of homoplastic states, most notably: mandible widened distally (28:1), mandible armed with a subdistal internal tooth (30:1), flagellomere apices bifid (39:1), propodeum half as long as pronotum + mesoscutum length (64:0), procoxa armed with a posterior triangular process (69:1), and gonostipes ventral lobe projecting dorsad (109:1). Phylogenetic placement of this new genus was unstable. Generally, the *Hadrodontilla* is grouped with *Dentilla*, *Nemka*, and *Physetopoda* (k0–k7, k12, k15, k16), with two homoplastic synapomorphies: T2 width subequal to mesonotal width including tegulae (79:0) and basivolsella with long wavy setae anteriorly (111:1). Under k8–k11, k13, k14, and setk, the *Dentilla*, *Hadrodontilla*, *Nemka*, and *Physetopoda* are, together with (*Chenmyrme* + *Ephutomma*) and *Skorikovia*, sequentially distal to (Smicromyrmini s. str. + Trogaspidiini). In some analyses, the sister relationship of *Dentilla* and *Hadrodontilla* is supported by the mandible widened distally (28:1), mandible armed with a subdistal internal tooth (30:1), and S7 mostly concealed, much shorter than S6 (94:0). However, the *Hadrodontilla* is separated from *Dentilla* by having the internal eye margin deeply emarginate (shallow in *Dentilla*), clypeal dorso-medial carina simple (forming a process in *Dentilla*), mandible ventral margin straight (emarginate with a proximal tooth in *Dentilla*), F1 length subequal to F2 length (shorter in *Dentilla*), tegula elongate, apparently surpassing transscutal articulation (short, slightly surpassing transscutal articulation in *Dentilla*), procoxa armed with a posterior triangular process (absent in *Dentilla*), parapenis bifid (truncate in *Dentilla*), and gonostipes ventral lobe projecting dorsad (truncate in *Dentilla*).

Hadrodontilla davidi (André, 1898), comb. nov.

Mutilla davidi André, 1898: 28, ♂, holotype ♂ (Kiang-Si [= Jiangxi], China) [MNHN]; André, 1902b: 39.
Smicromyrme davidi: Mickel, 1933b: 321, ♂; Wu, 1941: 134; Chen, 1957: 201, ♂, examined; He *et al*., 2004: 948, ♂.
Andreimyrme davidi: Lelej, 1995b: 8; Lelej, 2005: 38; Hua, 2006: 299; Lo Cascio, 2015: 544; Okayasu, 2020: 56; Pagliano *et al*., 2020: 169; Okayasu *et al*., 2021b: 4.

Zoobank LSID
urn:lsid:zoobank.org:act:A5EDAD08-F30D-4455-985F-851531397B04

Material examined
23♂. **China:** FUJIAN: Chungan, Bohea Hills, 30.IX.1939, T.C. Maa leg., *Smicromyrme davidi* (André), B. Petersen det. 1983, *Smicromyrme davidi* [probably Chen's hand] [1♂ TARI]; Chungan, Bohea Hills, 30.IX.1939, T.C. Maa leg., 25.X.1939, *Smicromyrme davidi* (André), B. Petersen det. 1983 [1♂ TARI]; Shaowu, Shuipeikieh [= Shui Pei Kai], 28.VII.1943, T.C. Maa leg., *Smicromyrme davidi* (André), B. Petersen det. 1983, *Smicromyrme davidi* (And.) [probably Chen' hand] [1♂ TARI], 1–10.IX.1943 [1♂ TARI], 13.IX.1943 [1♂ TARI], 6.XI.1943 [1♂ TARI], 24.V.1944 [2♂ TARI]; Shaowu, Kuhsienkieh, 1944, T.C. Maa leg., *Smicromyrme davidi* (André), B. Petersen det. 1983 [1♂ TARI]; Chungan, Sankang, 11–12.VIII.1945. T.C. Maa leg., *Smicromyrme davidi* (André), B. Petersen det. 1983, *Smicromyrme davidi* (And.) [probably Chen' hand] [1♂ TARI]; Shaowu, Tachulan [= Dazhulan], 13–17.VIII.1945, *Smicromyrme davidi* (André), B. Petersen det. 1983 [2♂ TARI]; Shaowu, Tachulan [= Dazhulan], 13–17.VIII.1945, *Smicromyrme davidi* (André), B. Petersen det. 1983, *Smicromyrme davidi* (André) [probably Chen's hand] [1♂ ZMUC]; JIANGSU: Chinkiang, Sia Shu, 21.VI.18, O. Piel leg., *Smicromyrme davidi* (André), B. Petersen det. 1983, *Mutilla davidi* And. [unknown hand] [1♂ TARI]. **Taiwan:** NANTOU: Horisha [= Puli], 18.V–VIII., H. Kawamura leg., *Smicromyrme davidi* (André), B. Petersen det. 1983 [2♂ TARI]. **Probably China:** UNKNOWN PROVINCE: locality data unrecognizable, 7.14.1949, *Smicromyrme davidi* (André), B. Petersen det. 1983, *Smicr. davidi* (André) [probably Chen's hand] [1♂ TARI], 7.14.1949 [4♂ TARI]; locality data unrecognizable, 7.14.1949, *Mutilla davidi* André, compared with type, B. Petersen 1983, *Smicromyrme davidi* (André), B. Petersen det. 1983 [1♂ ZMUC]. **Vietnam:** UNKNOWN PROVINCE: no data [1♂ IEBR].

Identification source
Voucher specimens (Chen, 1957).

Sex association
This species was described from the male only. The most likely female is *H. pekiniana* (André, 1905) (see below).

Distribution
China: Fujian, Jiangsu, Jiangxi (André, 1898). Taiwan: Nantou. Vietnam*: additional data unavailable.

Remarks
Previously, this species and *H. pekiniana* have been recorded from China and Taiwan only. Additional specimens revealed wider distribution of these species in East Asia, from northern

China to Vietnam and northern Thailand.

Hadrodontilla pekiniana (André, 1905), comb. nov.

Mutilla pekiniana André, 1905: 214, ♀, lectotype ♀ (Pékin [= Beijing], Chiue [= China]) [MNHN], designated by Mickel (1933b: 319).
Smicromyrme pekiniana: Mickel, 1933b: 319, ♀; Hammer, 1949: 11, ♀; Chen, 1957: 208, ♀, examined.
Smicromyrme cyaneiventris: Yasumatsu, 1951: 71, ♀.
Sinotilla pekiniana: Lelej, 1995b: 22, ♀; Lelej, 2002: 63; Lelej, 2005: 55; Okayasu, 2017: 152, ♀; Okayasu *et al*., 2018: 304, ♀; Pagliano *et al*., 2020: 186.

Zoobank LSID
urn:lsid:zoobank.org:act:C8F78BF9-1274-4074-85B2-2DAA689227E0

Material examined
15♀. **China:** FUJIAN: Fukien [= Fujian], Chungan, Bohea Hills, 29.VII.1939, T.C. Maa leg., *Smicromyrme pekiniana* [probably Chen's hand], *Smicromyrme pekiniana* André, B. Petersen det. 1983 [1♀ TARI], 15.IX.1939 [2♀ TARI, ZMUC]; Fukien [= Fujian], Chungan, Bohea Hills, 21.VI.1941, T.C. Maa leg., *Smicromyrme pekiniana* André, B. Petersen det. 1983 [1♀ TARI]; Fukien [= Fujian], Yungan [= Yong'an], Siyingpan, 7.VII.1940, T.C. Maa leg., *Smicromyrme pekiniana* [probably Chen's hand], *Smicr*. *pekiniana* (André) [probably Chen's hand], *Smicromyrme pekiniana* André, B. Petersen det. 1983 [1♀ TARI]; Fukien [=Fujian], Chungan, Chenmou, 8.VIII.1943, T.C. Maa leg., *Smicromyrme pekiniana* [probably Chen's hand], *Smicromyrme pekiniana* André, B. Petersen det. 1983 [1♀ TARI]; Fukien [= Fujian], Chungan, Sankang, 11–12.VIII.1945, T.C. Maa leg., *Smicromyrme pekiniana* [probably Chen's hand], *Smicromyrme pekiniana* André, B. Petersen det. 1983 [1♀ TARI]; Fukien [= Fujian], Shaowu, Tachulan [= Dazhulan], 13–17.VIII.1945, T.C. Maa leg., *pekiniana* [probably Chen's hand], *Smicromyrme pekiniana* André, B. Petersen det. 1983 [1♀ TARI]; Fukien [= Fujian], Chungan, Tsilikiao, 21–25.VIII.1945, T.C. Maa leg., *Smicromyrme pekiniana* [probably Chen's hand], *Smicromyrme pekiniana* André, B. Petersen det. 1983 [1♀ ZMUC]; JIANGSU: Kiangsu [= Jiangsu], Chinking, *Smicromyrme pekiniana* André, B. Petersen det. 1983 [1♀ TARI]; ZHEJIANG: [Huzhou], [Deqing], Mokanshan [= Mt. Mogan-shan], N. Gist Gee., *Mutilla pekiniana* A., Compared with type, B. Petersen 1988, *Smicromyrme pekiniana* André, B. Petersen det. 198 [1♀ ZMUC]. **Taiwan:** NANTOU: Kwantaushih, 14.VIII.1972, S. Yamane leg., *Smicromyrme pekiniana* André, B. Petersen det. 1988 [1♀ IEBR]; Ren-ai Township, Huisun Forest Protection Area, on lawn, N24.091 E121.035, 12.VII.2023, native collector leg. [1♀ TARI], 13.VII.2023 [1♀ TARI]. **Thailand:** CHIANG MAI: Chiang Mai, 20.V.1942, C. Tongyai leg., *Smicromyrme pekiniana* (André), B. Petersen det. 1983 [1♀ ZMUC].

Identification source
Voucher specimens (Chen, 1957).

Sex association
This species was originally described from the female only. This species and *H*. *davidi* were collected at "Sankang" and "Tachulan", Fujian, China at same time. They share the wide robust mandible which is presumably used to emerge from a hard cell or cocoon of the host. Here, *H*. *pekiniana* is tentatively regarded as the female of *H*. *davidi*. However, I prefer to treat them as separate taxa until additional evidence for sex association is available.

Distribution
China: Beijing, Fujian, Jiangsu, Shanxi (André, 1905; Yasumatsu, 1951). Taiwan*: Nantou. Thailand*: Chiang Mai.

Remarks
Similarly to some *Neotrogaspidia* females (Okayasu, 2023), this species was described as having the pygidial plate convex and smooth (André, 1905; Yasumatsu, 1951) unlike the actual condition, except for Chen (1957). Lelej (1995b) placed this species in *Sinotilla* whose females (now placed in *Ephucilla*) are characterized by the pygidial plate convex and smooth without lateral carinae. This species, however, differs from *Ephucilla* females by the genal carina absent (present in *Ephucilla*), mandible broad with internal teeth as large as apex (slender with minute internal teeth in *Ephucilla*), scutellar scale elevated (weakly developed in *Ephucilla*), protarsus with long external spines (with short delicate spines in *Ephucilla*), and pygidial plate rugose with lateral margins delimited by distinct carinae (smooth and at most with obscure lateral carinae in *Ephucilla*). This species is similar to *Andreimyrme* females by having the mandible broad and tridentate, but it differs from the latter by the genal carina absent (present in *Andreimyrme*), prementum lacking a rounded process (present in *Andreimyrme*), scutellar scale present (absent in *Andreimyrme*), and lateral margins of the pygidial plate strongly convergent anteriorly (subparallel in *Andreimyrme*). Therefore, this species does not match any described genera. I place this species in *Hadrodontilla* because the type species and *H. pekinaina* are likely belong to the same species.

Although the female specimen of *Smicromyrme cyaneiventris* identified by Yasumatsu (1951) is missing in ELKU where it should be, his description matches *H. pekiniana*.

Genus *Mickelomyrme* Lelej, 1995

Mickelomyrme Lelej, 1995a: 17, ♂♀; Lelej, 2002: 54; Lelej, 2005: 43; Lelej, 2007: 88; Lelej & Brothers, 2008: 34; Brothers & Lelej, 2017: 95; Okayasu *et al*., 2018: 303, ♀; Zhou *et al*., 2018a: 25, ♂♀; Williams *et al*., 2019b: 16, ♀; Okayasu, 2020: 42, ♂♀; Pagliano *et al*., 2020: 174; Lelej & Williams, 2023: 116, ♂♀.

Zoobank LSID
urn:lsid:zoobank.org:act:18E1B55F-1A03-4FAC-AA77-CAEFCF661142

Type species
Mutilla hageni Zavattari, 1913, ♂, by original designation.

Diagnosis
MALE. Frons longitudinally striate; vertex elevated beyond ocellar region; ventral clypeal margin entire; mandible apex bidentate, internal tooth smaller than apex, without subdistal internal tooth; mandible dorso-lateral carina weakly developed or highly elevated proximally; mandible ventral margin emarginate with large proximal tooth; flagellomere apices truncate; F1 length subequal to width; notaulus present on posterior part of mesoscutum or reaching posterior margin of pronotum; parascutal carina forming elevated process (except *M. chinensis*); tegula rounded posteriorly or projecting postero-laterad, slightly surpassing transscutal articulation; mesopleuron evenly convex, lacking transverse impression; mesopleuron ventral face lacking process; procoxa lacking posterior process; metacoxal internal carina weakly developed or lamellately projecting posteriorly; S2 with lateral felt line; harpe dorso-internal margin lacking proximal process; parapenis posteriorly truncate;

gonostipes ventral lobe projecting posterad; basivolsella expanded ventrad with long slender cuspis, with long wavy setae on ventral margin; basivolsella internal face with or without seta-filled pit; basiura small rounded; apiceps long slender; penisvalva strongly expanded ventrad; penisvalva posterior process lacking external process; penisvalva internal face lacking setae.

FEMALE. See Lelej & Williams (2023).

Species included

A total of 31 species is recognized in this genus: *M. athalia* (Pagden, 1949), ♂♀ (China, Laos, Malaysia, Thailand, Vietnam); *M. atrata* (Mickel, 1934), ♂ (Philippines); *M. autonoe* (Mickel, 1934), ♀ (Philippines); *M. bakeri* (Mickel, 1934), ♂ (Indonesia, Malaysia, Philippines); *M. bidentata* (Tsuneki, 1993), ♂♀ (Philippines); *M. caecina* (Cameron, 1903), ♂ (China, Indonesia, Malaysia, Thailand, Vietnam); *M. carinata* **sp. nov.**, ♂ (Indonesia); *M. chinensis* (Smith, 1855), ♂♀ (China, Laos, Vietnam); *M. cristaticauda* **sp. nov.**, ♂ (Vietnam); *M. exiloides* (Magretti, 1892), ♂ (China, Laos, Malaysia, Myanmar, Thailand); *M. grandiguttata* Okayasu, ♀ (Laos); *M. hageni* (Zavattari, 1913), ♂♀ (Japan, Taiwan); *M. handlirschi* (Magretti, 1892), ♂ (Myanmar); *M. isora* (Cameron, 1900), ♂ (India, Thailand); *M. kinguri* Williams, 2019, ♀ (Thailand); *M. kuznetsovi* Lelej, 1996, ♀ (China, Laos, Vietnam); *M. lavinia* (Mickel, 1934), ♂ (Philippines); *M. leleji* Sittichaya & Williams, 2022, ♀ (Thailand); *M. meator* (Mickel, 1935), ♂ (Malaysia); *M. nigrogastra* (Mickel, 1934), ♂ (Philippines); *M. norna* (Zavattari, 1913), ♂ (China, Taiwan, Thailand); *M. palacala* (Tsuneki, 1993), ♂ (Philippines); *M. palawanensis* (Mickel, 1934), ♂ (Philippines); *M. pusillaeformis* (Hammer, 1962), ♂♀ (China, Indonesia, Myanmar, Laos, Thailand, Vietnam); *M. puttasoki* Williams, 2019, ♀ (Thailand, Vietnam); *M. recondita* **sp. nov.**, ♂ (Thailand); *M. semperi* (Ashmead, 1904), ♂♀ (Philippines); *M. verticalis* Okayasu, ♀ (Philippines); *M. vietnaminix* Okayasu, ♀ (Vietnam); *M. vincula* (Nurse, 1903), ♀ (India); *M. zebina* (Smith, 1860), ♂♀ (Brunei, Indonesia, Malaysia, Philippines).

Sex association

The type species was initially described from the male only. The female of this species was described as *Mutilla alberici* Zavattari, 1913 and associated by Lelej & Yamane (1992).

Gender

Feminine.

Distribution

Oriental and Palaearctic Regions.

Remarks

This genus was recovered as a monophyletic group in the present phylogenetic analyses, except when characters with average homoplasy were assigned 50% or 53% of weights comparing to perfectly hierarchical ones (k0, k1). However, no unique synapomorphy supports its monophyly, and the GC score was low (GC = 22; Fig. 22-2). This genus was generally found sister to (*Ephucilla* + *Sinotilla*) or (*Promecilla*, part + (*Ephucilla* + *Sinotilla*)), depending on the placement of *P. decora* and associated species. Monophyly of these genera is likely well founded by two unique synapomorphies: frons longitudinally striate (10:1) and mesoscutum weakly convex (46:1).

The males of this genus were divided into two groups by Lelej (1996c). The *hageni* group is characterized by having the metacoxa armed with internal carina lamellately projecting posteriorly (72:1), while males of the *chinensis* group (originally referred to as the

exacta group) have the metacoxa with simple internal carina. Using implied weighting (k2 or more), both groups were found monophyletic. Females of the species of the *hageni* group are known for most species (*M. athalia*, *M. hageni*, *M. pusillaeformis*, *M. semperi*, and *M. zebina*). Contrarily, *M. chinensis* is the only species known from both sexes in the *chinensis* group. The female of this species is exceptional in *Mickelomyrme* by having the T2 with a single antero-medial pale setal spot, like most species of Smicromyrmini. Future studies focusing on molecular sex association and phylogenetic relationship within the *Mickelomyrme* could find the *chinensis* group to be a separate genus. However, I retain the *Mickelomyrme* as a single genus. Although the *hageni* group was supported by the developed metacoxal carina that is unique to this group within the *Mickelomyrme*, the *chinensis* group was supported by a single homoplastic synapomorphy: T7 with a slender impunctate line (91:1). This character is, however, secondarily reversed or transformed in the genus (*M. chinensis*: 91:0; *M. zebina*: 91:1) and variable intraspecifically (*M. athalia* and *M. hageni*; 91:0 & 1). Additionally, the female T2 spot of *M. chinensis* likely shows plesiomorphic state, because most smicromyrmine species have the T2 with one antero-medial spot in females. Monophyly of the *chinensis* group should be considered weakly supported.

Key to the East Asian species of *Mickelomyrme* based on the male morphology

1. Metacoxal internal carina weakly developed … 2
- Metacoxal internal carina lamellately projecting posteriorly … 10
2 (1). Frons with deep medial sulcus; clypeal subventral transverse flange medially interrupted; posterior propodeal face mostly with erect pale setae; basivolsella strongly expanded ventrad … 3
- Frons with shallow medial sulcus; clypeal subventral transverse flange at most medially emarginate; posterior propodeal face dorsally with appressed pale setae; basivolsella weakly expanded ventrad ... 4
3 (2). Clypeus with medial process; clypeal subventral transverse flange reduced, medially widely interrupted, leaving sublateral rounded tubercle; posterior margin of anterior process on penisvalva nearly straight; penisvalva with ventral margin strongly expanded anteriorly to anterior process. China, Taiwan, Thailand … ***M. norna*** (Zavattari)
- Clypeus lacking medial process; clypeal subventral transverse flange overhanging ventral clypeal margin, medially narrowly interrupted, giving bidentate appearance; posterior margin of anterior process on penisvalva angulate; penisvalva with ventral margin slightly expanded anteriorly to anterior process. Thailand … ***M. recondita*** **sp. nov.**
4 (2). Basivolsella incised posteriorly … 5
- Basivolsella rounded posteriorly … 6
5 (4). Parascutal carina weakly developed; legs orange; T2 laterally with large confluent punctures; cuspis shorter than basivolsella. China, Laos, Vietnam … ***M. chinensis*** (Smith)
- Parascutal carina forming elevated process; legs black; T2 laterally with large sparse punctures; cuspis longer than basivolsella. China, Laos, Malaysia, Myanmar, Thailand … ***M. exiloides*** (Magretti)
6 (4). Pronotal dorsum with confluent punctures … 7
-Pronotal dorsum with dense but separated punctures ... 8
7 (6). Metasoma entirely black. Philippines ... ***M. atrata*** (Mickel)
- Metasomal segments 1–2 orange. Philippines ... ***M. lavinia*** (Mickel)
8 (6) F2 length 2.5× width; notaulus reaching posterior margin of pronotum; propodeum with sparse pale setae. Malaysia … ***M. meator*** (Mickel)
- F2 length 2.0× width; notaulus present on posterior 1/3 of mesoscutum; propodeum dorsally with appressed pale setae … 9

9 (8). T2 lateral margin with small sparse punctures, generally separated by 2× puncture diameter; T2 posterior margin and T3 with sparse erect pale golden setae. China, Indonesia, Malaysia, Thailand, Vietnam … ***M. caecina*** (Cameron)
- T2 lateral margin with large dense punctures, separated by less than puncture diameter; T2 posterior margin and T3 medially with dense appressed golden setae. Vietnam … ***M. cristaticauda*** **sp. nov.**
10 (1). Clypeal subventral transverse flange medially widely interrupted, leaving sublateral rounded tubercle … 11
- Clypeal subventral transverse flange complete … 13
11 (10). Clypeal medial carina robust, highly elevated, extending over midpoint of clypeus; metacoxal internal carina dentate posteriorly; S1 medial carina posteriorly spinose. Indonesia … ***M. carinata*** **sp. nov.**
- Clypeal medial carina sharp, limited on dorsal portion of clypeus; metacoxal internal carina truncate posteriorly; S1 medial carina posteriorly angulate … 12
12 (11). Mandibular dorso-lateral carina weakly developed, terminating as small rounded sub-denticle. Philippines … ***M. bidentata*** (Tsuneki)
- Mandibular dorso-lateral carina highly elevated, not terminating as sub-denticle. Philippines … ***M. palawanensis*** (Mickel)
13 (10). T3–4 or T3–6 anteriorly and posteriorly constricted ... 14
- T3–6 not constricted … 16
14 (13). T1 posterior margin with pale setal band; S1 medial carina posteriorly angulate; T2–6 with large confluent punctures; T3–6 constricted. Japan, Taiwan … ***M. hageni*** (Zavattari)
- T1 posterior margin with pale setal fringe; S1 medial carina posteriorly spinose; T2–6 with small sparse punctures; T3–4 constricted and T5–6 not constricted … 15
15 (14). Metasoma black; T1 and T2 posterior margins with pale setal bands. Philippines … ***M. nigrogastra*** (Mickel)
- Metasomal segments 1–2 red; T1 and T2 posterior margins with pale setal fringe. Philippines … ***M. semperi*** (Ashmead)
16 (13). Cuspis with setae along entire length. China, Indonesia, Laos, Myanmar, Thailand, Vietnam … ***M. pusillaeformis*** (Hammer)
- Cuspis with setae only posteriorly … 17
17 (16). Pronotal dorsum with small sparse punctures and T2 with minute sparse punctures. Philippines ... ***M. palacala*** (Tsuneki)
- Pronotal dorsum and T2 with small dense punctures ... 18
18 (17). Penisvalva with ventral margin strongly expanded anteriorly to anterior process. Indonesia, Malaysia, Philippines … ***M. bakeri*** (Mickel)
- Penisvalva with ventral margin slightly expanded anteriorly to anterior process … 19
19 (18). Frons without longitudinal sulcus; pronotal dorsum with confluent punctures; lateral pronotal face micropunctate. China, Laos, Malaysia, Thailand, Vietnam … ***M. athalia*** (Pagden)
- Frons with deep longitudinal sulcus on ventral 1/2; pronotal dorsum with sparse punctures; lateral pronotal face longitudinally striate. Brunei, Indonesia, Malaysia, Philippines … ***M. zebina*** (Smith)

Mickelomyrme athalia (Pagden,1949)

Smicromyrme athalia Pagden, 1949: 219, ♂♀, holotype ♂ (Kuala Lumpur, Federated Malay States [= Malaysia]) [NHMUK].
Smicromyrme bicristata Chen, 1957: 211, ♀, holotype ♀ (Ryosui [= Lingshui], Hainan,

China) [TARI], examined. Synonymized in the Chapter 6.
Smicromyrme hageni (non Zavattari, 1913): Chen, 1957: 202, ♂, part.
Mickelomyrme athalia: Lelej, 1995a: 17; Lelej, 1996c: 280, ♂♀; Lelej, 2005: 43; Okayasu *et al*., 2018: 303, ♀; Williams *et al*., 2019b: 18, ♂♀, examined; Okayasu, 2020: 44, ♂, examined; Pagliano *et al*., 2020: 174.
Mickelomyrme bicristata: Lelej, 1996c: 284, ♀; Lelej, 2005: 43; Hua, 2006: 300; Lo Cascio, 2015: 551; Okayasu *et al*., 2018: 303, ♀; Williams *et al*., 2019b: 18; Okayasu, 2020: 44; Pagliano *et al*., 2020: 174.
Mickelomyrme hageni (non Zavattari, 1913): Barthélémy *et al*., 2018: 235, ♂.

Zoobank LSID
urn:lsid:zoobank.org:act:AD804EF8-B945-4B9E-8129-B5FE7CDFBDA7
urn:lsid:zoobank.org:act:80F959E5-0986-4678-9B8C-7EFE09666C75

Material examined
17♂25♀. Holotype ♀, *Smicromyrme bicristata* Chen: **China:** HAINAN: Ryosui [= Lingshui], 10.XI.1942, Miwa & Mitono leg. [TARI]. Paratype, *Smicromyrme bicristata* Chen: **China:** HAINAN: Kaikô [= Haikou], IX.1942, Miwa & Mitono leg. [1♀ TARI]. **China:** FUJIAN: Shaowu, Shuipeikieh [= Shui Pei Kai], 25.VI.1942, T.C. Maa leg., *Smicromyrme athalia* Pagden, B. Petersen det. 1987 [1♂ TARI], 4–6.VII.1943 [1♂ TARI], 13–14.VII.1943 [1♂ TARI], 1–2.IX.1943 [1♂ TARI]; GUANGDONG: Lofoushan [= Mt. Luofushan], 24.V.1937, T.C. Maa leg., *Smicromyrme athalia* Pagden, B. Petersen det. 1987 [1♂ TARI]; YUNNAN: Xishuangbanna, 13.III.1958, Z. Yiran leg., *Smicromyrme hageni* (Zavattari), B. Petersen det. 1982 [1♂ ZMUC]. **Malaysia:** KUALA LUMPUR: Spooner Road, 1.IV.1940, H. T. Pagden leg., *Smicromyrme athalia* Pagden, B. Petersen det. 1989 [1♀ ZMUC]; NEGERI SEMBILAN: Pasoh Forest Reserve, 26.III–3.IV.1993, K. Konishi & K. Maeto leg., Fine Malaise trap at plot 4 [1♂ FRIM]; PAHANG: Kuala Tahan, 12.IV.1940, M.W.F. Tweedie leg., *Smicromyrme athalia* Pagden, B. Petersen det. 1989 [1♀ ZMUC]; Fraser Hill, X.1948, NLHK rauss, *Smicromyrme athalia* Pagden, B. Petersen det. 1995 [1♂ NMNH]; PENANG: Batu Feringgi catchment area, 23.XII.1956, H.T. Pagden leg. [1♂ ZMUC]. **Thailand:** CHIANG MAI: Fang Horticult. Exp. Station, 550–600 m alt., 20.X.1981, Zool. Museum Copenhagen leg. [1♂ ZMUC], 22.X.1981 [1♂ ZMUC]; Mae Rim, Nong Hoi, 970–1000 m alt., 21.V.2002, K. Okajima leg. [1♂ TUA], 22.V.2002 [1♂ TUA]; Mae Rim, Nong Hoi, 970–1000 m alt., 22.V.2002, T. Ishizaki leg. [1♂ TUA], 30.V.2002 [1♂ TUA]; Mae Rim, Nong Hoi, 970–1000 m alt., 30.V.2002, T. Tsuru leg. [1♂ TUA]; Omkoi District, Dry dipterocarp forest, 17°50'49.9"N 98°22'33.0"E, 950–1010 m alt., 23.VI.2017, R. Mizuno leg. [1♀ THNHM], 24.VI.2017 [1♀ THNHM], 7.VII.2017 [1♀ THNHM], 9.VIII.2017 [1♀ THNHM], 13.VIII.2022 [1♀ THNHM]. **Vietnam:** BA RIA VUNG TAU: Xuyen Moc, Binh Chau, 4.I.2002, K. Okajima leg. [3♀ TUA]; Xuyen Moc, Binh Chau, 4.I.2002, S. Okajima leg. [1♀ TUA], 5.I.2002 [7♀ TUA]; Xuyen Moc, Binh Chau, 5.I.2002, T. Ishikawa leg. [3♀ TUA]; Xuyen Moc, Binh Chau, 5.I.2002, H. Mizushima leg. [2♀ TUA]; HOA BINH: Hoa Binh village, 14.VII.2010, H. Kurokawa leg. [1♂ MTC].

Identification source
Voucher specimens (Okayasu, 2020).

Sex association
This species was described from both sexes collected at same place and time (Pagden, 1949).

Distribution

China: Fujian, Guangdong, Hainan, Hong Kong, Yunnan (Barthélémy *et al*., 2018; Chen, 1957). Laos: additional data unavailable (Lelej, 2005). Malaysia: Kuala Lumpur, Negeri Sembilan, Pahang, Penang, Selangor (Pagden, 1949). Thailand: Chiang Mai, Kanchanaburi, Khonkaen, Krabi, Nakhon Nayok, Nakhon Si Thammarat, Phatthalung, Songkhla, Surat Thani, Trang (Williams *et al*., 2019b). Vietnam: Ba Ria Vung Tau, Hoa Binh.

Remarks
The collecting sites of this species, Pasoh Forest Reserve and Omkoi District, was described by Maetô *et al*. (1999) and Mizuno *et al*. (2019).

Mickelomyrme atrata (Mickel, 1934), comb. nov.

Smicromyrme lavinia atrata Mickel, 1934: 216, ♂, holotype ♂ (Samar, Philippines) [NMNH], photo examined; Mickel, 1935: 287, ♂; Baltazar, 1966: 210; Lelej, 2005: 61; Lo Cascio, 2015: 558.
Smicromyrme lavinia atratus: Pagliano *et al*., 2020: 197.

Zoobank LSID
urn:lsid:zoobank.org:act:A77C709E-B9FD-41C3-AB7F-C3C90F0B7A4E

Material examined
No material examined.

Sex association
Female unknown.

Distribution
Philippines: Samar (Mickel, 1934).

Remarks
Photos of the holotype of this species are available in National Museum of Natural History (2024). This species was initially described as a subspecies of *M. lavinia*. This species differs from the latter by having the metasoma entirely black (metasomal segments 1–2 red in *M. l. lavinia*). The nominotypical subspecies is widely distributed in the Philippine islands and *M. l. atrata* is known from a single locality in Samar, the Central Philippines. This is suggestive of overlapping distribution of those subspecies. Therefore, they are treated as distinct species.

Mickelomyrme bakeri (Mickel, 1934)

Smicromyrme bakeri Mickel, 1934: 212, ♂, holotype ♂ (Puerto Princesa, Palawan, Philippines) [NMNH], photo examined; Mickel, 1935: 291, ♂; Baltazar, 1966: 209.
Smicromyrme tanoi Tsuneki, 1972a, **syn. nov.**: 19, ♂, holotype ♂ (Mt. Kinabalu, [Sabah], Borneo, [Malaysia]) [OMNH], examined.
Mickelomyrme bakeri: Lelej, 1995a: 17; Lelej, 1996c: 284, ♂; Lelej, 2005: 46; Lo Cascio, 2015: 551; Okayasu, 2020: 44, ♂, part, examined; Pagliano *et al*., 2020: 174.
Mickelomyrme tanoi: Lelej, 1995a: 17; Lelej, 1996c: 284, ♂; Lelej, 2005: 45; Lo Cascio, 2015: 551; Okayasu, 2020: 44, ♂; Pagliano *et al*., 2020: 175.

Zoobank LSID
urn:lsid:zoobank.org:act:708E2975-7E07-4DD2-AA4D-11E0BB66014A

urn:lsid:zoobank.org:act:0212C36E-B096-49AB-B347-D72C8F461D2A

Material examined
3♂. Holotype ♂, *Smicromyrme tanoi* Tsuneki: **Malaysia:** SABAH: Mt. Kinabalu, 19.VIII.1971, T. Tano leg. [OMNH]. **Indonesia:** SULAWESI SELATAN: near Bantimung, 40 m alt., 24.VI.2005, T. Tano leg. [1♂ MTC]. **Philippines:** PALAWAN: Balabac, Dalawan Bay, 13.X.1961, Malaise trap, Noona Dan Exp. leg., *Smicromyrme bakeri* Mickel, B. Petersen det. 1972 [1♂ NARO].

Identification source
Identified specimen. Photos of the holotype of this species are available in National Museum of Natural History (2024).

Sex association
Female unknown.

Distribution
Indonesia: Sulawesi Selatan. Malaysia: Labuan, Sabah (Mickel, 1935). Philippines: Palawan.

Remarks
In the original description, *M. tanoi* was compared with *M. hageni* and *M. zebina* only. Reexamination of the holotype revealed that this species keys to *M. bakeri* in Mickel's (1935) treatment, as Lelej (1996c) associated them. Lelej (1996c) separated *M. tanoi* from *M. bakeri* by the clypeus with subventral triangular cell delimited by carinae (absent in *M. bakeri*) and POL 0.8× OOL (0.9 in *M. bakeri*). The clypeal cell of *M. tanoi* (Tsuneki, 1972a: Fig. 12) is, in fact, a large puncture which is also present in *M. bakeri*. The POL/OOL ratio is often variable in male velvet ants, and it does not serve as the sole evidence for species validity. *Mickelomyrme tanoi* is thus considered a junior synonym of *M. bakeri*.

Mickelomyrme bidentata (Tsuneki, 1993)

Smicromyrme bidentata Tsuneki in Tsuneki *et al*., 1993: 19, ♂, holotype ♂ (Hidden Valey [sic!] Springs, Alaminor, Pr. Laguna, Luzon, Philippines) [NMNH], photo examined.
Mickelomyrme bidentata: Lelej, 2005: 43; Lo Cascio, 2015: 551; Okayasu, 2020: 44; Pagliano *et al*., 2020: 174.

Zoobank LSID
urn:lsid:zoobank.org:act:8F6D136F-88A4-413B-8BC5-5B381D8CC065

Material examined
No material examined.

Sex association
This species was described from both sexes collected at same place and time. The female was recognized from a single specimen and distinguished from *M. zebina* only by the erect setae on head and thoracic dorsum black (whitish in *M. zebina*) and T3 and T4 setal bands subinterrupted medially (complete or only T4 band subinterrupted in *M. zebina*). However, *M. zebina* females are variable in setation as discussed in the Chapter 6. The *M. bidentata* female cannot be separated from *M. zebina*.

Distribution
Philippines: Luzon (Tsuneki *et al*., 1993).

Remarks
Photos of the holotype of this species are available in National Museum of Natural History (2024). This species has the mandibular dorso-lateral carina terminating as a small rounded sub-denticle. Tsuneki *et al*. (1993) interpreted this as an internal tooth and stated that "Mandible on dorsal inner margin near apex distinctly bidentate, basal one of which smaller and weaker" (Tsuneki *et al*., 1993: 4). This is the key feature to distinguish this species from *M. zebina* as discussed in Tsuneki *et al*. (1993). Additionally, this species differs from *M. zebina* by having the clypeal subventral flange medially interrupted.

Mickelomyrme caecina (Cameron, 1903), comb. nov.

Mutilla caecina Cameron, 1903: 153, ♂, holotype ♂ (Lingga, Sarawak, Borneo, [Malaysia]) [NHMUK].
Smicromyrme caecina: Mickel, 1935: 285, ♂; Lelej, 2005: 57; Lo Cascio, 2015: 558.
Smicromyrme punctinota Mickel, 1935, **syn. nov.**: 286, ♂, holotype ♂ (Bettotan, near Sandakan, [Sabah], Borneo, [Malaysia]) [NHMUK]; Mickel, 1937: 450, ♂; Lelej, 2005: 63; Lo Cascio, 2015: 559.
Mickelomyrme abnorma (non Chen, 1957): Lelej, 1996c: 285, ♂; Lelej, 2002: 54, part; Lelej, 2005: 43, part; Hua, 2006: 300, part; Okayasu, 2020: 44, part; Pagliano *et al*., 2020: 174, part.
Smicromyrme caecinus: Pagliano *et al*., 2020: 193.
Smicromyrme punctinotus: Pagliano *et al*., 2020: 201.

Zoobank LSID
urn:lsid:zoobank.org:act:84EAA0D4-4CFE-49CB-99BE-53FDB2B5A9EA
urn:lsid:zoobank.org:act:DA2EB321-D69A-442B-A364-0C202E5577CF

Material examined
33♂. **Indonesia:** KALIMANTAN TIMUR: Bukit Soeharto, 17–26.III.1994, Malaise trap, K. Konishi leg. [3♂ NARO]; SUMATRA BARAT: Muko Muko, Maninjau, 31.VII.1983, S. Yamane leg. [1♂ SEHU]; Mt. Sanggul, 1250–1400 m alt., 19.XII.2004 [1♂ SEHU]. **Malaysia:** KUALA LUMPUR: Kepong, FRIM [= Forest Research Institute Malaysia], 14–21.I.1992, Coarse Malaise trap, T. Matsumura leg. [1♂ NARO]; NEGERI SEMBILAN: Pasoh Forest Reserve, 18–25.I.1992, Coarse Malaise trap, T. Matsumura leg. [1♂ NARO]; Pasoh Forest Reserve, 25.III–2.IV.1993, Fine Malaise trap, plot 1, K. Konishi & K. Maeto leg. [1♂ FRIM]; Pasoh Forest Reserve, 2–8.IV.1993, Coarse Malaise trap, plot 2, K. Konishi & K. Maeto leg. [1♂ NARO]; Pasoh Forest Reserve, 26.XI–3.XII.1993, Coarse Malaise trap, plot 1, K. Maeto leg. [4♂ FRIM, NARO]; Pasoh Forest Reserve, 26.XI–3.XII.1993, Fine Malaise trap, plot 1, K. Maeto leg. [1♂ FRIM]; Pasoh Forest Reserve, 3–10.XII.1993, Coarse Malaise trap, plot 1, K. Maeto leg. [1♂ NARO]; Pasoh Forest Reserve, 26.XI–3.XII.1993, Coarse Malaise trap, plot 5, K. Maeto leg. [1♂ FRIM]; Pasoh Forest Reserve, 26.XI–3.XII.1993, Fine Malaise trap, plot 1, K. Maeto leg. [2♂ FRIM, NARO]; Pasoh Forest Reserve, 26.XI–3.XII.1993, Fine Malaise trap, plot 2, K. Maeto leg. [1♂ FRIM]; Pasoh Forest Reserve, 10–17.XII.1993, Coarse Malaise trap, plot 6, K. Maeto leg. [2♂ FRIM, NARO]; Pasoh Forest Reserve, 10–17.XII.1993, Fine Malaise trap, plot 1, K. Maeto leg. [4♂ FRIM, NARO]; SABAH: Borneo, Papan, 50 km SW of Kota Kinabalu, 15.XI.1975, S. Shinonaga leg. [1♂ EUMJ]; SELANGOR: Ulu Gombak, FIT, 21.V–3.VI.2003, M.

Maruyama leg. [7♂ TUA].

Identification source
Keyed using Mickel (1935) and compared with the original description. Photos of this species are available in Natural History Museum (2014).

Sex association
Female unknown.

Distribution
China: Yunnan (Lelej, 1996c). Indonesia*: Kalimantan Timur, Sumatra Barat. Malaysia: Kuala Lumpur*, Negeri Sembilan*, Sabah, Sarawak (Cameron, 1903; Mickel, 1935, 1937). Thailand: additional data unavailable (Lelej, 2005). Vietnam: Son La (Lelej, 1996c).

Remarks
This species was placed in *Smicromyrme* by Mickel (1935), and its systematic placement has not been revised. This species is here assigned to *Mickelomyrme* by having the frons longitudinally striate, mandible bidentate apically and with a proximo-ventral tooth, parascutal carina forming a distinct posterior tooth, mesopleuron evenly convex, S2 with a lateral felt line, and basivolsella with a long slender cuspis and long wavy setae ventrally.

In Mickel's (1935) key, this species was diagnosed by having the clypeal subventral flange deeply emarginate. However, this character was revealed to be variable after examination of a series of 33 specimens, obscuring species boundary of *S. caecinus* and *S. punctinotus*. The latter species is here proposed as a new junior synonym.

The specimens examined herein are generally consistent in morphology. However, the seta-filled pit on basivolsella varies in development and sometimes obliterated. One of the collecting sites of this species, Pasoh Forest Reserve, was described by Maetô *et al*. (1999).

***Mickelomyrme carinata* sp. nov.**

Mickelomyrme bakeri (non Mickel, 1934): Okayasu, 2020: 44, ♂, part, examined.

Zoobank LSID
Unavailable.

Diagnosis
MALE. Frons with shallow medial sulcus; clypeus lacking medial process; clypeal medial carina robust, highly elevated, extending over midpoint of clypeus; clypeal subventral transverse flange medially widely interrupted, leaving sublateral rounded tubercle; mandibular dorso-lateral carina highly elevated, not terminating as sub-denticle; F2 length 1.94× width; pronotal dorsum with large confluent punctures; lateral pronotal face minute dense punctures; notaulus present on posterior 3/4 of mesoscutum; posterior propodeal face mostly with erect pale golden setae; legs dark; metacoxal internal carina lamellately projecting, dentate posteriorly; metasoma black; T1 posterior margin with narrow pale golden setal band; S1 medial carina posteriorly spinose; T2 with large sparse punctures; T2 posterior margin with narrow pale golden setal band; T3 with sparse erect pale golden setae; T3–6 with small sparse punctures; T3–6 not constricted; basivolsella strongly expanded ventrad and rounded; cuspis longer than basivolsella; cuspis with setae only posteriorly; posterior margin of anterior process on penisvalva straight; penisvalva with ventral margin strongly expanded anteriorly to anterior process.

FEMALE. Unknown.

Description

MALE. Body length: 10.7 mm; forewing length: 7.26 mm.

Color and setae. Body black except: mandible subdistal 1/5 dark brown; maxillary and labial palpi brown; tegula external and posterior margins pale brown; protrochanter, tibiae, and tarsi brownish black. Frons, pronotal dorsum, and mesopleuron with dense long appressed and sparse long erect pale golden setae; vertex, gena, and lateral propodeal face with sparse short erect and sparse long erect pale golden setae; postgenal bridge, mandible, mesoscutellum, T1–5, and S1–6 with sparse long erect pale golden setae; clypeus with sparse long appressed and sparse long erect pale golden setae; scape with sparse long recumbent and sparse long erect pale golden setae; pedicel with dense short recumbent pale golden setae; flagellum with dense erect pale golden microsetae; prementum, stipes, and maxillary and labial palpi with sparse short erect pale golden setae; lateral pronotal face and metapleuron with sparse short appressed pale golden setae; propleuron and metascutellum with sparse short recumbent and sparse long erect pale golden setae; mesoscutum and T6–7 with sparse long erect black setae; tegula anterior 1/3 with sparse long recumbent golden setae; tegula posterior 2/3 and coxae with dense long recumbent pale golden setae; meso- and metanotal troughs with dense short appressed pale golden setae; posterior propodeal face with sparse long erect pale golden setae and with dense long appressed pale golden setae on anterior margin; trochanters, femora, and tibiae with dense short recumbent and sparse long erect pale golden setae; tarsi with sparse long appressed pale golden setae; S7 glabrous; S8 with sparse long erect golden setae; T2 lateral felt line golden, 0.5× T2 length; S2 lateral felt line golden, 0.35× S2 length; T1–2 with narrow dense posterior band of pale golden setae; T3 and S3–5 with sparse posterior fringe of pale golden setae; S2 with dense posterior fringe of pale golden setae; S6 with sparse posterior fringe of golden setae.

Structure. Head width 1.53× length; lateral margins strongly convergent behind eye, posterolateral angle rounded; vertex elevated, sharply sloping posteriorly; minimum distance between eyes 1.15× eye height; POL/OOL = 0.896; MOD:LOD:LOL:POL = 1.00:0.833:1.83:3.58; ocellar region convex; median ocellus lacking posterior longitudinal carina; frons with shallow medial longitudinal sulcus, lacking longitudinal carina anteriorly to lateral ocellus; occipital carina wide, complete; internal eye margin deeply emarginate; antennal scrobal carina V-shaped, separated from internal eye margin; antennal rim convex; antennal rims separated by approximate antennal rim width; gena lacking vertical carina; postgenal bridge flat; hypostomal carina sharp, not projecting; malar space developed, ventral eye margin and mandibular base separated; clypeus subconvex, with subventral transverse flange medially widely interrupted, leaving sublateral rounded tubercle; clypeus with medial highly elevated carina extending from dorso-medial portion to ventral 1/3 of clypeus; mandible slender, narrowed to apex; mandible apex bidentate, internal tooth smaller than apex; mandibular internal margin entire; mandibular dorso-lateral carina highly elevated proximally; mandibular ventral margin emarginate with large proximal tooth; prementum flat; scape with one lamellate and one weak wavy carinae, separated by 0.5× scape width; F1 cylindrical; length and width of pedicel:F1:F2 = 1.00:1.33:2.00:1.50:2.91:1.50; flagellomere apices truncate.

Mesosoma widest at mesonotum including tegulae; antero-dorsal pronotal margin slightly arcuate; humeral angle weakly angulate; humeral carina sharp, reaching pronotal dorsum; mesoscutum weakly convex; tegula short, rounded posteriorly, not flex, slightly surpassing transscutal articulation; tegula length 1.57× width; notauli subparallel, present on posterior 3/4 of mesoscutum, posteriorly widened; parapsidal signum short, linear; parascutal carina forming elevated process on posterolateral angle of mesoscutum; transscutal

impression arcuate; mesoscutellum weakly convex; mesopleuron convex, lacking transverse impression; ventral mesopleural face without longitudinal impunctate line, process, and swelling; mesocoxal foramen without transverse precoxal carina; metathoracic spiracle oval; metasternum much shorter than coxal height; propodeal length 1.04× pronotal + mesoscutal length; posterior propodeal face oblique, without distinct dorsum; propodeal sublateral longitudinal carina absent; propodeal dorso-lateral margin rounded, lacking longitudinal carina; lateral margins of propodeum convergent posteriorly.

Wings fully developed; distance between origin of RS on vein SC and proximal margin of pterostigma 1.71× pterostigma length; forewing cell 2RS present.

Procoxa lacking posterior process; meso- and metacoxae evenly convex; metacoxa with internal longitudinal carina lamellately projecting, posteriorly forming tooth; protibial spur slender; tibiae without external spines.

Metasomal segment 1 slender, subsessile; T1 width:T2 width:T2 length = 0.62:1.00:0.70; T1 oblique, without distinct dorsum; T1 spiracle projecting; T2 evenly convex; S1 with medial longitudinal carina on anterior 3/4, posteriorly spinose; S2 evenly convex, lacking antero-medial carina; T3–6 not constricted; T7 evenly convex, with posterior margin truncate; S6–8 flat, lacking lateral carina or process; S7 posterior margin truncate; S8 mostly sclerotized with posterior membranous area evenly convex posteriorly. Harpe depressed laterally, down-curved; harpe dorso-internal margin lacking process; harpe dorsal margin with sparse short erect setae; gonostipes much longer than wide and as long as harpe; gonostipes ventro-medial lobe not forming posterior process; gonostipes ventral lobe projecting posteriorly; parapenis flexed inward, posterior margin truncate; parapenis dorsal margin lacking tubercles; cupula much shorter than gonostipes; basivolsella depressed, oval, strongly expanded ventrad, with long slender cuspis; cuspis 2× longer than basivolsella; cuspis apex reaching posterior 1/5 of harpe; basivolsella with large seta-filled pit on internal face, with dese long erect wavy setae on ventral margin, and with sparse long erect setae on dorsal margin; basiura weakly sclerotized with distinct apiceps; apiceps apex with sparse long erect setae; penisvalvae symmetrical; penisvalva broad, expanded ventrad, with long anterior and posterior ventral processes; penisvalva lacking setae; endophallus weakly sclerotized.

Frons densely longitudinally striate; vertex, gena, mesoscutum, and S1 with large dense punctures; postgenal bridge transversely rugose; clypeus, pedicel, flagellum, prementum, stipes, maxillary and labial palpi, lateral pronotal face, meso- and metanotal troughs, coxae, trochanters, femora, tibiae, and tarsi with minute dense punctures; scape, tegula posterior 1/2, T1–2 posterior margins, and S3–8 with small dense punctures; pronotal dorsum, mesopleuron, and metapleuron ventral 1/3 with large confluent punctures; mesoscutellum with large confluent punctures and posteromedial subtriangular impunctate space; metascutellum and T7 with small confluent punctures; tegula anterior 1/2, T1–2 except posterior margins, and S2 with large sparse punctures; metapleuron dorsal 2/3 with minute sparse punctures; propodeum reticulate, with medial subtriangular and sublateral semicircular cell on anterior margin; T3–6 with small sparse punctures.

FEMALE. Unknown.

Material examined

1♂. Holotype ♂: **Indonesia:** GORONTALO: Pegunungan Tilongkabila, Bogani Nani Warta Bone N[ational]. P[ark]., 100 m alt., Malaise trap, 9–20.II.2009, K. Takasuka leg. [EUMJ].

Sex association

Female unknown.

Distribution

Indonesia: Gorontalo.

Etymology
The specific name *carinata*, carinate, is the Latin, singular, feminine adjective in the nominative case. It refers to the clypeus of this new species with a strong medial carina.

Remarks
This new species was previously confused with *M. bakeri* by Okayasu (2020). However, this species differs from it by having the clypeus with a distinct medial longitudinal carina (absent in *M. bakeri*), clypeal subventral transverse flange medially interrupted (complete in *M. bakeri*), mandibular dorso-lateral carina elevated (weakly developed in *M. bakeri*), and metacoxal internal carina posteriorly dentate (truncate in *M. bakeri*). By sharing the clypeal flange interrupted, mandibular dorso-lateral carina elevated, and metacoxal internal carina lamellate, this new species is similar to *M. bidentata* and *M. palawanensis*. In phylogenetic analyses, this new species was found sister to the rest of the *hageni* group.

Mickelomyrme chinensis (Smith, 1855)

Mutilla chinensis Smith, 1855: 38, ♀, holotype ♀ (North China) [NHMUK]; Dalla Torre, 1897: 23; André, 1902b: 38.
Mutilla exacta Smith, 1879: 201, ♂, holotype ♂ (Shanghai, [China]) [NHMUK]; Dalla Torre, 1897: 38; André, 1902b: 39. Synonymized by Zhou *et al*. (2018a: 25) under *Mickelomyrme chinensis* (Smith).
Smicromyrme chinensis: Mickel, 1933b: 318, ♀; Wu, 1941: 134; Hammer, 1949: 11, ♀; Yasumatsu, 1951: 70, ♀; Chen, 1957: 208, ♀, examined; Lelej, 2002: 73; He *et al*., 2004: 948, ♀; Lelej, 2005: 58; Hua, 2006: 301.
Smicromyrme exacta: Mickel, 1933b: 323, ♂; Wu, 1941: 135; Yasumatsu, 1948: 73, ♂; Chen, 1957: 201, ♂, examined; He et al., 2004: 950, ♂.
Mickelomyrme exacta: Lelej, 1995a: 17; Lelej, 1996c: 285, ♂; Lelej, 2002: 54; Lelej, 2005: 43; Hua, 2006: 300; Brothers & Lelej, 2017: 58.
Mickelomyrme chinensis: Zhou *et al*., 2018a: 25, ♂♀; Okayasu *et al*., 2018: 303, ♀; Williams *et al*., 2019b: 7, ♀; Okayasu, 2020: 44; Pagliano *et al*., 2020: 175.

Zoobank LSID
urn:lsid:zoobank.org:act:0A34468C-70F8-47C6-82C6-ACC4805AA38C
urn:lsid:zoobank.org:act:223CAAB6-C68D-4DFF-AC86-7C7678BFD5FA

Material examined
8♂8♀. **China:** ANHUI: Wangshan [= Huangshan], 5.VIII.1935, *Smicromyrme chinensis* (Smith), B. Petersen det. 1983 [1♀ TARI]; FUJIAN: Yanping, [Nanping], 14.VI.1917, compared with type by B. Petersen in 1982 [1♂ ZMUC]; Fukien [= Fujian], Kuatun, 15.VII.1946, Tschung-Sen leg., *Smicromyrme chinensis* (Smith), B. Petersen det. 1990 [1♂ TARI]; GUANGXI: Jinxiu, Dayao Mountain, 1–26.VIII.1994, W. Kitawaki leg. [1♀ TUA]; SICHUAN: Mt. Emei-shan, 27.VI.1955, *Smicromyrme exacta* (Smith), B. Petersen det. 1983 [2♂ ZMUC], 1.VII.1955 [1♂ ZMUC]. **Laos:** ATTAPEU: Attapeau prov. [= Attapeu], Annam Highlands, Mts Dong Amphan N[ational]B[iodiversity]C[onservation]A[rea], NONG FA (crater lake) env., ca. 1160 m, 15°05.9'N 107°25.6'E, 30.IV–6.V.2010, St. Jaki leg. [1♀ KUM]; HOUA PHAN: Ban Saleui, ca 1400–1500 m alt., 20–24.VI.2003, N. Ohbayashi leg. [1♂ EUMJ]; Hua Phan Prov. [= Houa Phan], MT. PHU PANE, 900–1600 m, 10–21.VI.2010, 20°12'N 103°59'E, St. Jaki and Lao collectors leg. [1♀ KUM]; Hua Phan Prov. [= Houa

Phan], MT. PHU PANE, 1200–1600 m, 31.V–11.VI.2011, 20°12'N 103°59'E, St. Jaki and Lao collectors leg. [1♀ KUM]; VIENTIANE: Ban Van Eue, 31.V.1966, Malaise trap, native collector, Rondon-Bishop Mus. Collection, *Smicromyrme exacta* (Smith), B. Petersen det. 1982 [2♂ ZMUC]. **Vietnam:** NINH BINH: Cuc Phuong, 200–300 m alt., 25.IV.1998, R. Matsumoto leg. [1♀ OMNH]; Nho Quan, Cuc Phuong N[ational]. P[ark]., 500 m, 20.348°N 105.598°E, 314/BTTNVW, Yellow pan trap, 9–11.VIII.2016, Y. Komeda & T. Mita leg. [1♀ ELKU]; VINH PHUC: Phúc Yên, Ngọc Thanh, Melinh Biodiversity Station, 21.3884995°N 105.712599695°E, 68 m alt., 6.VI.2023, L.T.P. Nguyen et al. leg. [1♀ IEBR].

Identification source
Identified specimens.

Sex association
This species was initially described from the female only. The male was described as *Mutilla exacta* and associated by Zhou *et al*. (2018a) based on males and females repeatedly collected at same place and time.

Distribution
China: Anhui, Fujian, Guangdong, Guangxi, Hainan, Henan, Jiangsu, Jiangxi, Shanxi, Shanghai, Sichuan, Yunnan, Zhejiang (Chen, 1957; Hammer, 1949; Smith, 1879; Yasumatsu, 1948, 1951; Zhou *et al*., 2018a). Laos: Attapeu*, Houa Phan, Vientiane. Vietnam: Ninh Binh, Vinh Phuc.

Brothers & Lelej (2017) included doubtfully identified male specimen (number not mentioned) of this species from Laos in their phylogenetic analysis. This record was not followed by Zhou *et al*. (2018) and Pagliano *et al*. (2020). In the present study, three males and three females from Laos were examined.

Remarks
The female of this species is exceptional in *Mickelomyrme* by having a single antero-medial pale setal spot on T2. Contrarily, the male morphology reliably places this species in *Mickelomyrme*. The sister relationship of (*M. chinensis* + *M. exiloides*) was supported at least by four homoplastic synapomorphies: postgenal bridge dorso-lateral margin lacking elevation (21:0), notaulus reaching posterior margin of pronotum (47:0), tegula elongate (51:0), and T1 posterior margin with a setal band (76:1).

Mickelomyrme cristaticauda sp. nov.

Zoobank LSID
Unavailable.

Diagnosis
MALE. Frons with shallow medial sulcus; clypeus lacking medial process; clypeal medial carina sharp, limited on dorsal portion of clypeus; clypeal subventral transverse flange complete, overhanging ventral clypeal margin; mandibular dorso-lateral carina weakly developed, not terminating as sub-denticle; F2 length 1.99× width; pronotal dorsum with large confluent punctures; lateral pronotal longitudinally striate; notaulus present on posterior 1/3 of mesoscutum; posterior propodeal face dorsally with appressed golden setae; legs dark; metacoxal internal carina weakly developed; metasomal segment 1–2 orange; T1 posterior margin with dense golden setal fringe; S1 medial carina posteriorly angulate; T2 disc with large sparse punctures; T2 lateral margin with large dense punctures; T2 posterior margin and

T3 medially with dense appressed golden setae; T3–6 medially with small sparse punctures and laterally with small dense punctures; T3–6 not constricted; basivolsella weakly expanded and rounded ventrad; cuspis slightly shorter than basivolsella; cuspis with setae only posteriorly; posterior margin of anterior process on penisvalva straight; penisvalva with ventral margin slightly expanded anteriorly to anterior process.

FEMALE. Unknown.

Description

MALE. Body length: 11.9 mm; forewing length: 9.53 mm.

Color and setae. Frons, vertex, gena, postgenal bridge, clypeus, mandible except subapical 1/4, F1 dorsally, F2–11, stipes, mesosoma except tegula, coxae except apex, T3–7, and S3–8 black; antennal rim, scape apex, F1 ventrally, coxal apices, trochanters, and protibial spur brown; mandible subdistal 1/4 and prementum dark brown; scape except apex, pedicel, maxillary and labial palpi, femora, tibiae, and tarsi brownish black; tegula yellow; meso- and metatibial spurs yellowish white; T1–2 and S1–2 orange. Frons with sparse long recumbent and sparse long erect golden setae; vertex and S2 with sparse short recumbent and sparse long erect golden setae; gena, postgenal bridge, propleuron, posterior propodeal face ventral 1/2, lateral propodeal face, trochanters, and femora with dense short recumbent and sparse long erect golden setae; clypeus and mesopleuron with dense long appressed and sparse long erect golden setae; mandible, scape, T1–4, S1, and S3–5 with sparse long erect golden setae; pedicel with dense short recumbent golden setae; flagellum with dense erect blackish golden microsetae; prementum, stipes, and maxillary and labial palpi with sparse short erect golden setae; pronotal dorsum with dense short appressed and sparse long erect golden setae; lateral pronotal face and metapleuron with sparse short appressed golden setae; mesoscutum with sparse long recumbent and sparse long erect golden setae; tegula with sparse long recumbent golden setae; mesoscutellum and metascutellum with dense short appressed and sparse long erect golden setae; meso- and metanotal troughs with dense short appressed golden setae; posterior propodeal face dorsal 1/2 with dense long appressed and sparse long recumbent golden setae; coxae and tibiae with dense long recumbent and sparse long erect golden setae; tarsi with sparse long appressed golden setae; T5–6 with sparse long erect black setae; T7 with sparse long recumbent and sparse long erect black setae; S6–8 with intermixed sparse long erect golden and sparse long erect black setae; T2 lateral felt line golden, 0.4× T2 length; S2 lateral felt line golden, 0.25× S2 length; T1 with dense posterior fringe of golden setae; T2 posterior margin and T3 medially with dense appressed golden setae; S2 with sparse posterior fringe of golden setae.

Structure. Head width 1.59× length; lateral margins strongly convergent behind eye, posterolateral angle rounded; vertex elevated, sharply sloping posteriorly; minimum distance between eyes 0.970× eye height; POL/OOL = 0.517; MOD:LOD:LOL:POL = 1.00:0.609:0.783:1.30; ocellar region convex; median ocellus lacking posterior longitudinal carina; frons with deep medial longitudinal sulcus, lacking longitudinal carina anteriorly to lateral ocellus; occipital carina sharp, complete; internal eye margin deeply emarginate; antennal scrobal carina V-shaped, extending nearly to internal eye margin; antennal rim convex; antennal rims separated by approximate antennal rim width; gena lacking vertical carina; postgenal bridge flat; hypostomal carina sharp, not projecting; malar space developed, ventral eye margin and mandibular base separated; clypeus subconvex, with subventral complete transverse flange overhanging ventral clypeal margin; clypeal dorso-medial portion elevated into simple carina; mandible slender, narrowed to apex; mandible apex bidentate, internal tooth smaller than apex; mandibular internal margin entire; mandibular dorso-lateral carina sharp; mandibular ventral margin emarginate with large proximal tooth; prementum flat; scape with one lamellate and one weak wavy carinae, separated by 0.65× scape width;

F1 cylindrical; length and width of pedicel:F1:F2 = 1.00:1.43:1.50:1.79:3.57:1.79; flagellomere apices truncate.

Mesosoma widest at mesonotum including tegulae; antero-dorsal pronotal margin slightly arcuate; humeral angle weakly angulate; humeral carina sharp, reaching pronotal dorsum; mesoscutum weakly convex; tegula short, projecting posterad, not flex, reaching mesoscutellum; tegula length 1.59× width; notauli subparallel, present on posterior 1/3 of mesoscutum, posteriorly widened; parapsidal signum short, linear; parascutal carina forming elevated process on posterolateral angle of mesoscutum; transscutal impression arcuate; mesoscutellum weakly convex; mesopleuron convex, lacking transverse impression; ventral mesopleural face with longitudinal impunctate line and without process and swelling; mesocoxal foramen without transverse precoxal carina; metathoracic spiracle oval; metasternum much shorter than coxal height; propodeal length 1.15× pronotal + mesoscutal length; posterior propodeal face oblique, without distinct dorsum; propodeal sublateral longitudinal carina absent; propodeal dorso-lateral margin rounded, lacking longitudinal carina; lateral margins of propodeum convergent posteriorly.

Wings fully developed; distance between origin of RS on vein SC and proximal margin of pterostigma 1.88× pterostigma length; forewing cell 2RS present.

Procoxa lacking posterior process; meso- and metacoxae evenly convex; metacoxa with internal longitudinal carina weakly developed; protibial spur slender; tibiae without external spines.

Metasomal segment 1 slender, subsessile; T1 width:T2 width:T2 length = 0.60:1.00:0.80; T1 oblique, without distinct dorsum; T1 spiracle projecting; T2 evenly convex; S1 with medial longitudinal carina on anterior 3/4, straight in profile; S2 evenly convex, lacking antero-medial carina; T3–6 not constricted; T7 evenly convex, with posterior margin truncate; S6–8 flat, lacking lateral carina or process; S7 posterior margin truncate; S8 mostly sclerotized with posterior membranous area evenly convex posteriorly. Harpe depressed laterally, down-curved; harpe dorso-internal margin lacking process; harpe dorsal margin with sparse short erect setae; gonostipes much longer than wide and as long as harpe; gonostipes ventro-medial lobe not forming posterior process; gonostipes ventral lobe projecting posteriorly; parapenis flexed inward, posterior margin truncate; parapenis dorsal margin lacking tubercles; cupula much shorter than gonostipes; basivolsella depressed, oval, weakly expanded ventrad, with long slender cuspis; cuspis slightly shorter than basivolsella; cuspis apex reaching posterior 1/2 of harpe; basivolsella with large seta-filled pit on internal face, with dese long erect wavy setae on ventral margin, and with sparse long erect setae on dorsal margin; basiura weakly sclerotized with distinct apiceps; apiceps apex with sparse long erect setae; penisvalvae symmetrical; penisvalva broad, expanded ventrad, with distinct anterior and posterior ventral processes; penisvalva lacking setae; endophallus membranous.

Frons and vertex densely longitudinally striate; gena, pronotal dorsum, mesoscutum between notauli, and mesoscutellum with large confluent punctures; postgenal bridge transversely rugose; clypeus with minute dense punctures; scape, T1, and T3–6 medially with small sparse punctures; pedicel, flagellum, prementum, stipes, maxillary and labial palpi, meso- and metanotal troughs, metapleuron dorsal 2/3, and coxae with minute dense punctures; lateral pronotal face obscurely longitudinally striate; propleuron with small sparse and minute dense punctures; mesoscutum laterally to notaulus and T2 lateral margin with large dense punctures, separated by ~0.5× puncture diameter; tegula, trochanters, femora, tibiae, and tarsi with minute sparse punctures; mesopleuron and metapleuron ventral 1/3 with large dense and minute dense punctures; metascutellum with small dense and minute dense punctures; propodeum reticulate, with medial subtriangular and sublateral semicircular cell on anterior margin; T2 disc and S1–2 with large sparse punctures; T3–6 laterally and S3–8 with small dense punctures; T7 with small confluent punctures and medial slender impunctate

line.

FEMALE. Unknown.

Material examined
1♂. Holotype ♂: **Vietnam:** THUA THIEN HUE: Bach Ma N[ational]P[ark], Pheasant trail, 16.231°N 107.852°E, 500 m alt., 253/BTTNVN, 4.VIII.2016, T. Mita leg. [VNMN].

Sex association
Female unknown.

Distribution
Vietnam: Thua Thien Hue.

Etymology
The specific name *cristaticauda* is the combination of the Latin adjective *cristata*, crested, and the Latin singular noun *cauda*, tail, in the genitive case. This name is the direct translation of the Oriental gallopheasant genus *Lophura* Fleming, which includes *L. edwardsi* (Oustalet) endemic to central Vietnam. It hints the type locality of this new species, Pheasant trail in Bach Ma National Park, and loosely refers to the T2 and T3 medially ornamented with appressed golden setae.

Remarks
This new species and *M. caecina* share many morphological features. This new species is distinguished only by the T2 laterally with large dense punctures (small sparse in *M. caecina*) and T2 posterior margin and T3 medially with dense appressed golden setae (with sparse erect setae in *M. caecina*). However, phylogenetic analyses recovered sister relationship of *M. cristaticauda* to (*M. chinensis* + *M. exiolides*), likely because the T2 and T3 setae are coded as state 1 (82:1; 88:1).

Mickelomyrme exiloides (Magretti, 1892)

Mutilla exiloides Magretti, 1892: 36, ♂, syntypes ♂ (Monti dei Carin-Chebà [= mountain area in Karen Hills], [Myanmar]) [MSNG]; Bingham, 1897: 48, ♂; Dalla Torre, 1897: 39; André, 1902b: 39.
Mickelomyrme exiloides: Lelej, 1995a: 17; Lelej, 1996c: 285, ♂; Lelej, 2005: 44; Zhou *et al*., 2018a: 26, ♂; Okayasu, 2020: 44; Pagliano *et al*., 2020: 175; Pagliano & Scaramozzino, 2021: 109, ♂.

Zoobank LSID
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Material examined
23♂. **Laos:** CHAMPASAK: Paksong, 6 km south Paksong, 15°04'10"N 106°12'09"E, 1221 m [alt.], Yellow pan trap, 18–19.III.2016, T. Mita leg. [1♂ ELKU]; XIENG KHOUANG: Huay La Ngoy, 19°28'58.34"N 102°42'48.77"E, 838 m alt., 5.V.2015, T. Mita leg. [1♂ ELKU]. **Malaysia:** NEGERI SEMBILAN: Pasoh Forest Reserve, 22–23.III.1979, M. Wong & P. Becker leg., *Smicromyrme exiloides* (Magretti), B. Petersen det. 1988 [1♂ ZMUC]; Pasoh Forest Reserve, Fine Malaise trap, plot 5, 26.III–3.IV.1993, K. Konishi & K. Maeto leg. [1♂ FRIM]; Pasoh Forest Reserve, Coarse Malaise trap, plot 6, 26.XI–3.XII.1993, K. Maeto leg. [2♂ FRIM, NARO], 10–17.XII.1993 [2♂ FRIM, NARO]; PERAK: Batang,

Padang, 19 mile, 4°22'5.11"N 101°20'0.92"E, 605 m alt., FIT, 17–21.X.2016, H. Ikeda leg. [1♂ FRIM]; SELANGOR: Hulu Langat, Sungai Lui, 3.V.1936, H.T. Pagden leg. [1♂ ZMUC]. **Thailand:** CHIANG MAI: Mae Ya, Doi Inthanon N. P., 600–700 m alt., 11.X.1981, Zool. Museum Copenhagen leg. [1♂ ZMUC]; Doi Suthep-Pui N[ational]. P[ark]., Konthathan waterfall area, 600 m alt., 20–27.X.1979, Zool. Museum Copenhagen leg. [1♂ ZMUC]; Mae Rim, Nong Hoi, 970–1000 m alt., 21.V.2002, T. Tsuru leg. [1♂ TUA], 30.V.2002 [1♂ TUA]; Mae Rim, Nong Hoi, 970–1000 m alt., 22.V.2002, K. Okajima leg. [5♂ TUA]; Mae Rim, Nong Hoi, 970–1000 m alt., 22.V.2002, T. Ishizaki leg. [2♂ TUA], 30.V.2002 [1♂ TUA]; Omkoi District, Dry dipterocarp forest, 17°50'49.9"N 98°22'33.0"E, 950–1010 m alt., 6.V.2017, R. Mizuno leg. [1♂ THNHM].

Identification source
Identified specimens.

Sex association
Female unknown.

Distribution
China: Yunnan (Zhou *et al*., 2018a). Laos: Champasak*, Vientiane, Xieng Khouang* (Lelej, 1996c). Malaysia*: Negeri Sembilan, Perak, Selangor. Myanmar: Kayah (?) (Magretti, 1892). Thailand*: Chiang Mai.

Remarks
The collecting sites of this species, Pasoh Forest Reserve and Omkoi District, was described by Maetô *et al*. (1999) and Mizuno *et al*. (2019). In previous studies, fourteen males from three localities in China, Laos, and Myanmar were examined (Lelej, 1996c; Magretti, 1892; Zhou *et al*., 2018a). Additional specimens examined herein revealed intraspecific variation; body setae vary from whitish to golden; T2–4 setal bands can be sparse or obliterated; the seta-filled pit on basivolsella varies in development and sometimes obliterated.

Mickelomyrme hageni (Zavattari, 1913)

Mutilla hageni Zavattari, 1913: 32, ♂, lectotype ♂ (Kankau, Koshun [= Hengchun], [Pingtung], Formosa [= Taiwan]) [SDEI], designated by Mickel (1933a: 417), examined.
Mutilla alberici Zavattari, 1913: 31, ♀, lectotype ♀ (Tainan, Formosa [= Taiwan]) [SDEI], designated by Mickel (1933a: 421), examined. Synonymized by Lelej & Yamane (1992: 631) under *Smicromyrme hageni* (Zavattari).
Mutilla discreta (non Cameron, 1897): Matsumura & Uchida, 1926: 50, ♂, examined.
Smicromyrme hageni: Mickel, 1933a: 417, ♂; Suzuki, 1934: 25; Mickel, 1935: 291, ♂; Yasumatsu, 1938b: 447, ♂; Chen, 1957: 202, ♂, part; Tsuneki, 1972b: 20, ♂; Tsuneki, 1972c: 220, ♂, examined; Kuribayashi, 1973: 181; Nambu & Tano, 1983: 21, ♂; Yoshida, 1989: 651.
Smicromyrme alberici: Mickel, 1933a: 421, ♀; Suzuki, 1934: 24; Mickel, 1935: 293, ♀; Chen, 1957: 208, ♀; Tsuneki, 1972c: 19, ♀; Tsuneki, 1973: 23, ♀; Yoshida, 1989: 651; Tsuneki, 1993a: 40, ♀; Azuma *et al*., 2002: 322.
Smicromyrme (*Nemka*) *hageni*: Lelej & Yamane, 1992: 631, ♂♀, part.
Mickelomyrme hageni: Lelej, 1995a: 17; Lelej, 1996c: 280, ♂♀, examined; Yamane, 1999: 381, ♂♀; Brothers *et al*., 2000: 210; Azuma *et al*., 2002: 322; Terayama, 2004: 13; Lelej, 2005: 44; Terayama, 2005: 7, 11, 16, ♂♀; Hua, 2006: 300; Lelej & Brothers,

2008: 34; Pagliano, 2011: 40, ♂; Terayama *et al*., 2011: 13, 20, ♂♀; Lo Cascio, 2015: 551; Terayama *et al*., 2016: 167, ♂♀; Brothers & Lelej, 2017: 58, ♂♀; Okayasu *et al*., 2018: 303, ♀; Okayasu, 2020: 44, ♂♀, examined; Pagliano *et al*., 2020: 175; Lelej & Williams, 2023: 104, ♂♀.

Zoobank LSID
urn:lsid:zoobank.org:act:2BE6CD8B-F900-480A-A092-5924FBA52B6D
urn:lsid:zoobank.org:act:7EB72997-2A55-4E9F-9240-6D41DD71DF9A

Material examined
34♂5♀. Lectotype ♂, *Mutilla hageni* Zavattari: **Taiwan:** PINGTUNG: Koshun [= Hengchun], Kankau, 7.IV.1912, H. Sauter leg. [SDEI (DEI-GISHym 16743)]. Paralectotypes, *Mutilla hageni* Zavattari: **Taiwan:** PINGTUNG: Koshun [= Hengchun], Kankau, IV.1912, H. Sauter leg. [1♂ ZMUC], VII.1912 [2♂ ZMUC]. Lectotype ♀, *Mutilla alberici* Zavattari: **Taiwan:** TAINAN: Tainan, VIII.1911, H. Sauter leg. [SDEI (DEI-GISHym 16739)]. **Japan:** MIYAKO ISLANDS: Irabu-jima Island, Ikemasoe, 6.XII.2004, H. Suda leg. [1♂ HSC]; YAEYAMA ISLANDS: Ishigaki-jima Island, H. Kuroiwa leg., *Mutilla discreta* Cameron, S. Matsumura det. 1926, *Smicromyrme hageni* (Zavattari), K. Yasumatsu det. 1938 [1♂ SEHU]; Ishigaki-jima Island, Takeda, 8–10.V.1973, S. Ueda leg., *Smicromyrme hageni* (Zavattari), B. Petersen det. 1979 [1♂ ZMUC], 18.V.1973 [1♂ ZMUC]; Iriomote-jima, Ueharu, 27.V.1975, Y. Yoshiyasu leg. [1♂ SEHU]; Yonaguni-jima Island, Mt. Kuburatake, 10.VIII.1979, M. Terayama leg. [1♂ MTC]; Ishigaki-jima Island, Ishigaki, 28.VIII.1998, H. Suda leg. [1♂ HSC]; Taketomi-jima Island, Higashiyashiki, 29.VIII.1998, H. Suda leg. [1♂ HSC]; Yonaguni-jima Island, Sonai, 28.VII.1999, R. Matsumoto leg. [1♂ OMNH]; Iriomote-jima Island, Funaura, 1.VIII.1999, R. Matsumoto leg. [1♂ OMNH]; Iriomote-jima Island, Ôhara, Husatoruba, 12.VI.2002, T. Tsuru leg. [1♂ TUA]; Yonaguni-jima Island, Minami-bokujyô, 28.V.2003, T. Ishikawa leg. [1♀ TUA]; Yonaguni-jima Island, Mantabaru, 100 m alt., 24.46N 122.97E, 13.VIII.2012, Y. Komeda leg. [2♂ ELKU]; Ishigaki-jima Island, Yoshihara, 18.VII.2014, T. Nakata leg. [1♂ EUMJ]; Yonaguni-jima Island, Kubura, 24.4543°N 122.9482°E, 21.VI.2015, R. Matsumoto leg. [1♀ OMNH]; Ishigaki-jima Island, Kabira, Sukuji Beach, 24.4647°N 124.1235°E, 26.VI.2015, R. Matsumoto leg. [2♂ OMNH]; Ishigaki-jima Island, Hirakubo, 25.XI.2016, R. Itô leg. [1♀ ELKU]. **Taiwan:** HSINCHU: Hsinchu, 8.VIII.1968, S.C. Chiu leg. [1♂ TARI]; NANTOU: Hori [= Puli], 28.IV.1929, A. Saito leg., *Mickelomyrme hageni* (Zavattari), A. Lelej det. 1995 [3♂ NSMT]; Puli, Penpuchi, 26.VIII.1966, K. Tsuneki leg. [1♂ NMNH]; PINGTUNG: Koshun [= Hengchun], IV.1918, T. Shiraki leg., *Mutilla hageni* Zavattari, T. Shiraki det. [1♂ TARI]; Koshun [= Hengchun], Kueitzuchiao, 20.V.1934, Asada leg. [1♂ NARO]; Oluampi, Eluanbi, 18.VII.1968, K. Tsuneki leg. [1♀ NMNH]; Ouluanpi Coast Forest, 27.VI.1981, T. Lin & C. C. Pan leg. [1♂ TARI]; Koshun [= Hengchun], Kueitzuchiao, VIII, *Mutilla hageni* Zavattari, T. Shiraki det. [1♂ TARI]; TAINAN: Tainan, V.1918. T. Shiraki leg., *Mutilla alberici* Zavattari, T. Shiraki det. [1♀ TARI]; TAOYUAN: Kuangyin, 14.VI.1968, K. Tsuneki leg., *Smicromyrme hageni* (Zavattari), K. Tsuneki det. 1972 [4♂ ZMUC]; UNKNOWN PREFECTURE: Kuaru, 17.IV.1937, K. Iwata leg., *Mickelomyrme hageni* (Zavattari), A. Lelej det. 1995 [1♂ NSMT].

Identification source
Primary type.

Sex association
This species was initially described from the male only. The female was described as *Mutilla alberici* and associated by Lelej & Yamane (1992) based on a pair *in copula* although this

pair actually belonged to *Mi*. *yunnanensis* Lelej, 1996 (= *Mi*. *pusillaeformis*) (Lelej, 1996c). Lelej (1996c), however, retained *Mu*. *alberici* as a junior synonym of *Mi*. *hageni* because they were only species of *Mickelomyrme* occurring in Ryûkyû Islands, Japan.

Distribution
Japan: Miyako Islands, Okinawa Islands, Yaeyama Islands (Lelej & Yamane, 1992). Taiwan: Hsinchu, Nantou, Pingtung, Tainan, Taoyuan.

Remarks
This species was originally described from Taiwan and later recorded from China by Chen (1957) based on six male specimens. His voucher specimens were reexamined by Okayasu (2020) and were revealed to be *M*. *athalia*. The male of *M*. *hageni* differs from that of *M*. *athalia* by having the T3–6 constricted (not constricted in *M*. *athalia*) and penisvalva with ventral margin strongly expanded anteriorly to anterior process (slightly expanded in *M*. *athalia*). A subsequent record of *M*. *hageni* from Hong Kong by Barthélémy *et al*. (2018) is also considered to be misidentification of *M*. *athalia*.

Mickelomyrme isora (Cameron, 1900)

Mutilla isora Cameron, 1900: 8, ♂, holotype ♂ (Khasia Hills, [Meghalaya, India]) [OUMNH]; André 1902b: 39.
Mickelomyrme isora: Lelej, 2005: 44; Okayasu, 2020: 44; Pagliano *et al*., 2020: 175; Thaochan *et al*., 2022: 163, ♂.

Zoobank LSID
urn:lsid:zoobank.org:act:8ED6A976-1160-4585-969C-89D668FF1294

Material examined
No material examined.

Sex association
Female unknown.

Distribution
India: Meghalaya (Cameron, 1900). Thailand: Chiang Mai (Thaochan *et al*., 2022), additional data unavailable (Lelej, 2005).

Remarks
This species was not available for the present study. Cameron's original description is inadequate to recognize the diagnostic traits and this species is omitted from the key above.

Mickelomyrme lavinia (Mickel, 1934), comb. nov.

Smicromyrme lavinia lavinia Mickel, 1934: 214, ♂, holotype ♂ (Mount Banahao, Luzon, Philippines) [NMNH], photo examined; Mickel, 1935: 287, ♂; Baltazar, 1966: 210; Tsuneki *et al*., 1993: 15, ♂; Lelej, 2005: 61; Lo Cascio, 2015: 558; Pagliano *et al*., 2020: 197.

Zoobank LSID
urn:lsid:zoobank.org:act:FE35F025-6375-400B-82A4-607BAC27E1D0

Material examined
No material examined.

Sex association
Female unknown.

Distribution
Philippines: Luzon, Mindanao, Palawan (Mickel, 1934; Tsuneki *et al*., 1993).

Remarks
Photos of the holotype of this species are available in National Museum of Natural History (2024). This species, together with its previous subspecies *Sm*. *lavinia atrata*, is here assigned to *Mickelomyrme* by having the frons longitudinally striate, mandible bidentate apically and emarginate ventrally, F1 length 1/2× F2 length, parascutal carina forming a distinct posterior tooth, mesopleuron evenly convex, S2 with a lateral felt line, and basivolsella with a long slender cuspis and long wavy setae ventrally (Mickel, 1934).

Mickelomyrme meator (Mickel, 1935), comb. nov.

Smicromyrme meator Mickel, 1935: 285, ♂, holotype ♂ (Sandakan, [Sabah], Borneo, [Malaysia]) [NMNH], photo examined; Mickel, 1937: 450, ♂; Lelej, 2005: 62; Lo Cascio, 2015: 558; Pagliano *et al*., 2020: 198.

Zoobank LSID
urn:lsid:zoobank.org:act:45C24C38-EBBF-4778-BAA7-F8AFD7E42F5F

Material examined
No material examined.

Sex association
Female unknown.

Distribution
Malaysia: Sabah, Sarawak (Mickel, 1935, 1937).

Remarks
Photos of the holotype of this species are available in National Museum of Natural History (2024). This species is here assigned to *Mickelomyrme* by having the frons striate, mandible bidentate apically and emarginate ventrally, parascutal carina forming a distinct posterior process, mesopleuron evenly convex, and S2 with a lateral felt line.

Mickelomyrme nigrogastra (Mickel, 1934)

Smicromyrme semperi nigrogastra Mickel, 1934: 212, ♂, holotype ♂ (Zambales Province, Luzon, Philippines) [NMNH], photo examined; Mickel, 1935: 291, ♂; Baltazar, 1966: 210; Tsuneki *et al*., 1993: 13, ♂.
Mickelomyrme semperi nigrogastra: Lelej, 1996c: 284, ♂; Lelej, 2005: 45; Lo Cascio, 2015: 551; Okayasu, 2020: 44; Pagliano *et al*., 2020: 175.

Zoobank LSID
urn:lsid:zoobank.org:act:D8CA1801-494D-46E9-970C-303A53D7646E

Material examined
No material examined.

Sex association
Female unknown.

Distribution
Philippines: Luzon, Palawan (Mickel, 1934; Tsuneki *et al*., 1993).

Remarks
Photos of the holotype of this species are available in National Museum of Natural History (2024). This species was initially described as a subspecies of *M*. *semperi*. However, this species differs from *M*. *semperi* by having the metasoma entirely black (metasomal segments 1–2 red in *M*. *semperi*) and T1 and T2 posterior margins with a distinct pale setal band (T1 and T2 posterior margins with a pale setal fringe in *M*. *semperi*). Both *M*. *nigrogastra* and *M*. *semperi* occur in Luzon, suggesting overlapping distribution. These data support full species status of *M*. *nigrogastra*.

Mickelomyrme norna (Zavattari, 1913)

Mutilla norna Zavattari, 1913: 40, ♂, lectotype ♂ (Taihorinsho [= Dalin], [Chiayi], Formosa [= Taiwan]) [ZMNB], designated by Mickel (1933a: 417).
Smicromyrme norna: Mickel, 1933a: 417, ♂; Suzuki, 1934: 25; Mickel, 1935: 288, ♂; Tsuneki, 1982: 44, ♂.
Smicromyrme norna norna: Chen, 1957: 203, ♂.
Smicromyrme norna abnorma Chen, 1957, **syn. nov.**: 203, ♂, holotype ♂ (Kuling [= Guling], [Lushan, Jiujiang], Kiangsi [= Jiangxi], China) [TARI], examined.
Mickelomyrme norna: Lelej, 1995a: 17; Lelej, 1996c: 285, ♂, examined; Lelej, 2005: 44; Hua, 2006: 300; Pagliano, 2011: 41, ♂; Lo Cascio, 2015: 551; Okayasu, 2020: 44; Pagliano *et al*., 2020: 175.
Mickelomyrme abnorma: Lelej, 2002: 54, part; Lelej, 2005: 43, part; Hua, 2006: 300, part; Okayasu, 2020: 44; Pagliano *et al*., 2020: 174.
Smicromyrme norna alnorma: He *et al*., 2004: 953, ♂. Incorrect subsequent spelling.

Zoobank LSID
urn:lsid:zoobank.org:act:9AF86CAB-34AC-423C-B573-E5FF0D3D1FA1
urn:lsid:zoobank.org:act:6E185071-C3C6-4585-BA6D-8AA4C00BEC29

Material examined
73♂. Holotype ♂, *Smicromyrme norna abnorma* Chen: **China:** JAINGXI: [Lushan, Jiujiang], Kuling [= Guling], 13.8.35, O. Piel leg. [TARI]. Paratypes, *Smicromyrme norna abnorma* Chen: **China:** ANHUI: Anhwei [= Anhui], Ningkwo, Yue Wan Kiai, 17.7.20, *Smicromyrme isola abnorma* Chen, B. Petersen det. 1983 [10♂ TARI], 18.7.20 [2♂ TARI], 23.7.20 [1♂ TARI], 24.7.20 [1♂ TARI], 19.7.20 [1♂ TARI]; JIANGSU: Hwangshan, 7.8.36, *Smicromyrme isola abnorma* Chen, B. Petersen det. 1983 [2♂ TARI]; JAINGXI: [Lushan, Jiujiang], Kuling [= Guling], 8.9.34, O. Piel leg., *Smicromyrme isola abnorma* Chen, B. Petersen det. 1983 [1♂ TARI], 18.9.34 [2♂ TARI], 27.7.35 [1♂ TARI], 29.7.35 [2♂ TARI],

31.7.35 [1♂ TARI], 3.8.35 [3♂ TARI], 4.8.35 [1♂ TARI], 10.8.35 [1♂ TARI], 11.8.35 [2♂ TARI], 13.8.35 [7♂ TARI], 14.8.35 [1♂ TARI], 16.8.35 [1♂ TARI], 17.8.35 [3♂ TARI]; Wuyuan, 1934, *Smicromyrme isola abnorma* Chen, B. Petersen det. 1983 [1♂ TARI]; ZHEJIANG: [Lin'an, Hangzhou], Tianmu-shan, 14.VII.1935, *Smicromyrme isola abnorma* Chen, B. Petersen det. 1983 [1♂ TARI]; [Lin'an, Hangzhou], West Tianmu-shan, 8.8.1937, *Smicromyrme isola abnorma* Chen, B. Petersen det. 1983 [1♂ TARI]; UNKNOWN PROVINCE: Kikow [= Xikow], 8.VII.1935, *Smicromyrme isola abnorma* Chen, B. Petersen det. 1983 [1♂ TARI]. **China:** ANHUI: Huangshan, 7.VIII.36, *Smicromyrme norna abnorma* Chen, subsp. nov. [probably Chen's hand] [1♂ ELKU]; FUJIAN: Fukien [= Fujian], Shaowu, Tachulan [= Dazhulan], 25.VII.1942, T.C. Maa leg. [1♂ TARI], 8–12.VIII.1943 [1♂ TARI], 16–20.VIII.1944 [1♂ TARI], 20–23.VII.1945 [1♂ TARI], VII.1945 [3♂ TARI], 9.IX.1945 [1♂ TARI]. **Taiwan:** NANTOU: [Ren'ai], Tatungtsun, 9.IX.1928, T. Kano leg., *Mickelomyrme norna* (Zavattari), A. Lelej det. 1995 [1♂ NSMT (NSMT-I-Hym No. 1091)]; Nanshanchi, 800 m alt., 30.VI.1965, R. Ishikawa leg., *Mickelomyrme norna* (Zavattari), A. Lelej det. 1995 [1♂ NSMT (NSMT-I-Hym No. 4706)]; Tungpu, 1200 m alt., 20–24.VI.1983, K.C. Chou & C.Y. Wong leg. [1♂ TARI]; Lienhuachih, 350 m alt., Malaise trap, VI.1984, K.S. Lin & K.C. Chou leg. [1♂ TARI]; NEW TAIPEI: Wulai, VI.1931, J. Sonan leg. [1♂ TARI]; PINGTUNG: Mudan, Gaoshi Vil., 22°07'59"N 120°51'02"E, ca. 300 m alt., sweeping, 12.V.2016, S. Shimizu leg. [3♂ NARO]; TAITUNG: Taitung County, Jingping forest Rd. [= road], 23.139751N 121.170509E, FIT, 26.II–26.VI.2022, Y. Ho & M. Liu leg. [3♂ TARI]; UNKNOWN PREFECTURE: Ryuganrim, 11.VII.1937, J. Sonan leg. [1♂ TARI]. **Thailand:** CHIANG MAI: Doi Suthep, 750–850 alt., 20.VIII.2001, T. Ishizaki leg. [1♂ TUA]; Mae Rim, Nong Hoi, 970–1000 m alt., 21.V.2002, T. Ishizaki leg. [2♂ TUA]; Mae Rim, Nong Hoi, 970–1000 m alt., 22.V.2002, K. Okajima leg. [1♂ TUA].

Identification source
Voucher specimens (Chen, 1957; Lelej, 1996c).

Sex association
Female unknown.

Distribution
China: Anhui, Fujian, Jiangsu, Jiangxi, Zhejiang. Taiwan: Chiayi, Nantou, New Taipei, Pingtung. Thailand*: Chiang Mai.

Remarks
Mickelomyrme abnorma was described as the continental subspecies of *M. norna* known from Taiwan (Chen, 1957). Lelej (1996c) revised this subspecies to full species status based on morphological differences in the clypeus, forewing venation, T2 punctures, and male genitalia. Reexamination of type specimens, however, revealed that *M. abnorma* sensu Lelej (1996c) was conspecific with *M. caecina*. Chen (1957) distinguished *S. n. abnorma* from *S. n. norna* by having the metasomal segments 1–3 with deep golden setae (white in *M. n. norna*) and T3 predominantly or entirely black (T3 red in *S. n. norna*). However, those characters are greatly variable and often overlap in both subspecies. They are thus considered synonymous.

The late B. Petersen who studied Cameron's types regarded *M. norna* and *M. abnorma* as subspecies of *M. isora* according to his identification labels. *Mickelomyrme isora* is known from India and Thailand (Lelej, 2005), and *M. norna* is newly recorded from Chiang Mai, Thailand here, suggesting overlapping distribution. It seems likely that *M. norna* is a junior synonym of *M. isora*, but reexamination of Cameron's syntypes and lectotype designation are required.

Mickelomyrme palacala (Tsuneki, 1993), comb. nov.

Smicromyrme palacala Tsuneki in Tsuneki *et al*., 1993: 15, ♂, holotype ♂ (Calacuasan, Palawan, Philippines) [NMNH], photo examined; Lelej, 2005: 63; Lo Cascio, 2015: 559; Pagliano *et al*., 2020: 200.

Zoobank LSID
urn:lsid:zoobank.org:act:83DB082A-98B5-4301-9672-7169777C8DA5

Material examined
No material examined.

Sex association
Female unknown.

Distribution
Philippines: Palawan (Tsuneki *et al*., 1993).

Remarks
Photos of the holotype of this species are available in National Museum of Natural History (2024). This species is here assigned to *Mickelomyrme* by having the frons longitudinally striate, clypeus with a subventral transverse flange, mandible bidentate apically and emarginate ventrally, and parascutal carina forming a distinct process (Tsuneki *et al*., 1993). Although the original description of this species is too short and inadequate, the small body size, measuring only 4 mm, and abbreviated surface sculpture aid in recognizing this species.

Mickelomyrme palawanensis (Mickel, 1934)

Smicromyrme palawanensis Mickel, 1934: 206, ♂, holotype ♂ (Puerto Princesa, Palawan, Philippines) [NMNH], photo examined; Mickel, 1935: 292, ♂; Baltazar, 1966: 210; Tsuneki *et al*., 1993: 20, ♂.
Mickelomyrme palawanensis: Lelej, 2005: 44; Lo Cascio, 2015: 551; Okayasu, 2020: 44; Pagliano *et al*., 2020: 175.

Zoobank LSID
urn:lsid:zoobank.org:act:58100A60-72E5-4A87-B83E-29F27C50E04D

Material examined
No material examined

Sex association
Female unknown.

Distribution
Philippines: Palawan (Mickel, 1934; Tsuneki *et al*., 1993).

Remarks
Photos of the holotype of this species are available in National Museum of Natural History (2024).

Mickelomyrme pusillaeformis (Hammer, 1962)

Smicromyrme pusillaeformis Hammer, 1962: 34, ♀, holotype ♀ (Mergui, [Tanintharyi, Myanmar]) [IMK]; Lelej, 2005: 63.
Smicromyrme (*Nemka*) *hageni* (non Zavattari, 1913): Lelej & Yamane, 1992: 631, ♂♀, part.
Mickelomyrme yunnanensis Lelej, 1996c: 280, ♂♀, holotype ♂ (Niner (Puer)-Dajie (Jinggu), Yunnan, China); Lelej, 2005: 45; Okayasu, 2018: 480, ♀; Okayasu *et al*., 2018: 303, ♀, examined. Synonymized by Williams *et al*. (2019b: 19) under *Mickelomyrme pusillaeformis* (Hammer).
Mickelomyrme pusillaeformis: Williams *et al*., 2019b: 19, ♀, examined; Okayasu, 2020: 44, ♂♀, examined; Pagliano *et al*., 2020: 175; Thaochan *et al*., 2022: 163, ♀.

Zoobank LSID
urn:lsid:zoobank.org:act:3DF335AE-89E4-472B-81C7-8AB701C51968
urn:lsid:zoobank.org:act:1AFAA2AE-0326-4146-87BD-566B0915D525

Material examined
17♀. Paratype, *Mickelomyrme yunnanensis* Lelej: **Thailand:** CHIANG MAI: Fang, 12.VI.1965, Japan-U.S. Cooperative Sci. Program [1♀ NSMT]. **Indonesia:** BALI: West Bali, Dusun PK Jelati, 7.V.1998, IKT Ginarsa leg. [1♀ EUMJ]. **Laos:** HOUA PHAN: Hua Phan Prov. [= Houa Phan], MT. PHU PANE, 1200–1600 m, 10–22.V.2011, 20°12'N 103°59'E, St. Jaki and Lao collectors leg. [1♀ KUM], 31.V–11.VI.2011 [2♀ KUM]; LUANG PHABANG: Phou-vieng Gnai, 19.284470°N 102.355703°E, 1319 m alt., 22.IV.2018, H. Yoshitomi leg. [1♀ EUMJ]. **Thailand:** CHIANG MAI: Chiang Mai, 4.V.1939, C. Tongyai leg. [1♀ ZMUC]; Fang Horticult. Exp. Station, 550–600 m alt., 19.X.1981, Zool. Museum Copenhagen leg. [1♀ ZMUC], 20.X.1981 [2♀ ZMUC]; Mae Sa, 25–28.IV.2000, K. Okajima leg. [1♀ TUA]; Mae Rim, Nong Hoi, 970–1000 m alt., 30.V.2002, T. Ishizaki leg. [1♀ TUA]; Omkoi District, Dry dipterocarp forest, N17°50'49.9" E98°22'33.0", 950–1010m alt., 19.VI.2017, R. Mizuno leg. [2♀ THNHM], VI.2017 [1♀ THNHM], 20.VIII.2022 [1♀ THNHM]; TRANG: Yan Ta Khao District, Thung Khai, Peninsular Botanic Garden, 3.IV.2005, T. Kurihara leg. [1♀ EUMJ].

Identification source
Identified specimens.

Sex association
This species was initially described from the female only. The male was associated and described as *Mi*. *yunnanensis* based on a pair *in copula* (Lelej & Yamane, 1992; Lelej, 1996c). Later, Williams *et al*. (2019b) synonymized *Mi*. *yunnanensis* under *Mi*. *pusillaeformis*.

Distribution
China: Yunnan (Lelej, 1996c). Indonesia: Bali. Laos: Attapeu, Bolikhamsay, Houa Phan*, Luang Phabang (Okayasu, 2018; Williams *et al*., 2019b). Myanmar: Tanintharyi (Hammer, 1962). Thailand: Chaiyaphum, Chiang Mai, Kanchanaburi, Krabi, Lampang, Phatthalung, Phetchaburi, Songkhla, Surat Thani, Trang (Williams *et al*., 2019b). Vietnam: Dong Nai (Williams *et al*., 2019b).

Remarks

One of the collecting sites of this species, Omkoi District, was described by Mizuno *et al*. (2019).

Mickelomyrme recondita sp. nov.

Zoobank LSID
Unavailable.

Diagnosis
MALE. Frons with deep medial sulcus; clypeus lacking medial process; clypeal medial carina sharp, limited on dorsal portion of clypeus; clypeal subventral transverse flange overhanging ventral clypeal margin, medially narrowly interrupted, giving bidentate appearance; mandibular dorso-lateral carina weakly developed, not terminating as sub-denticle; F2 length 2.31–2.45× width; pronotal dorsum with large confluent punctures; lateral pronotal face longitudinally striate; notaulus reaching posterior margin of pronotum; posterior propodeal face mostly with erect golden setae; legs dark; metacoxal internal carina weakly developed; metasomal segment 1–3 orange; T1–2 posterior margins with sparse golden setal fringe; S1 medial carina posteriorly angulate; T2 with small sparse punctures; T3 with sparse erect golden setae; T3–6 with small dense punctures; T3–6 not constricted; basivolsella strongly expanded and rounded ventrad; cuspis longer than basivolsella; cuspis with setae only posteriorly; posterior margin of anterior process on penisvalva angulate; penisvalva with ventral margin slightly expanded anteriorly to anterior process.

FEMALE. Unknown.

Description
MALE. Body length: 6.25–10.1 mm; forewing length: 5.53–8.19 mm.

Color and setae. Frons, vertex, gena, clypeus, mandible except subdistal 2/3, flagellum, mesosoma except propleuron and tegula, T4–7, and S4–8 black; postgenal bridge and antennal rim brownish black; mandible subdistal 1/3, maxillary and labial palpi, and protibial spur brown; scape, pedicel, prementum, stipes, trochanters, femora, tibiae, and tarsi dark brown; propleuron and coxae dark brown to brownish black; tegula yellow; meso- and metatibial spurs yellowish white; T1–3 and S1–3 orange. Frons and scape with sparse long recumbent and sparse long erect golden setae; vertex, mandible, T1–5, S1, and S3–6 with sparse long erect golden setae; gena, postgenal bridge, pronotal dorsum, mesoscutellum, metascutellum, propodeum, trochanters, femora, and S2 with sparse short recumbent and sparse long erect golden setae; clypeus with sparse long appressed and sparse long erect golden setae; pedicel and flagellum with dense erect golden microsetae; prementum, stipes, and maxillary and labial palpi with sparse short erect golden setae; propleuron and procoxa with sparse short appressed and sparse long erect golden setae; lateral pronotal face and metapleuron with sparse short appressed golden setae; mesoscutum and S7–8 with sparse long erect dark golden setae; tegula with sparse long recumbent golden setae; meso- and metanotal troughs with dense short appressed golden setae; mesopleuron with dense long appressed and sparse long erect golden setae; meso- and metacoxae with sparse long appressed golden setae; tibiae with dense long recumbent and sparse long erect golden setae; tarsi with dense long appressed golden setae; T6–7 with sparse long erect black setae; T2 lateral felt line golden, 0.5× T2 length; S2 lateral felt line golden, 0.3× S2 length; T1–2 and S2–5 with sparse posterior fringe of golden setae; S6 with sparse posterior fringe of dark golden setae.

Structure. Head width 1.43–1.56× length (holotype 1.56); lateral margins strongly convergent behind eye, posterolateral angle rounded; vertex elevated, sharply sloping

posteriorly; minimum distance between eyes 1.02–1.17× eye height (holotype 1.02); POL/OOL = 0.559–0.676 (holotype 0.605); MOD:LOD:LOL:POL = 1.00:0.714–0.900:1.00–1.10:1.86–2.30 (holotype 1.00:0.714:1.00:1.86); ocellar region convex; median ocellus with posterior longitudinal carina; frons with deep medial longitudinal sulcus, lacking longitudinal carina anteriorly to lateral ocellus; occipital carina sharp, complete; internal eye margin deeply emarginate; antennal scrobal carina V-shaped, extending nearly to internal eye margin; antennal rim convex; antennal rims separated by approximate antennal rim width; gena lacking vertical carina; postgenal bridge flat; hypostomal carina sharp, not projecting; malar space developed, ventral eye margin and mandibular base separated; clypeus subconvex, with subventral transverse flange overhanging ventral clypeal margin, medially narrowly interrupted; clypeal dorso-medial portion elevated into simple carina; mandible slender, narrowed to apex; mandible apex bidentate, internal tooth smaller than apex; mandibular internal margin entire; mandibular dorso-lateral carina sharp; mandibular ventral margin emarginate with large proximal tooth; prementum flat; scape with two sharp subparallel carinae, separated by 0.6× scape width; F1 cylindrical; length and width of pedicel:F1:F2 = 1.00:1.13–1.42:1.93–2.00:1.36–1.67:3.00–4.08:1.50–1.75 (holotype 1.00:1.42:2.00:1.67:4.08:1.75); flagellomere apices truncate.

Mesosoma widest at mesonotum including tegulae; antero-dorsal pronotal margin slightly arcuate; humeral angle weakly angulate; humeral carina sharp, reaching pronotal dorsum; mesoscutum weakly convex; tegula short, projecting posterad, not flex, reaching mesoscutellum; tegula length 1.56–1.69× width (holotype 1.65); notauli weakly convergent posteriorly, reaching posterior margin of pronotum, posteriorly widened; parapsidal signum short, linear; parascutal carina forming elevated process on posterolateral angle of mesoscutum; transscutal impression arcuate; mesoscutellum weakly convex; mesopleuron convex, lacking transverse impression; ventral mesopleural face with longitudinal impunctate line and without process and swelling; mesocoxal foramen armed with transverse precoxal carina; metathoracic spiracle oval; metasternum much shorter than coxal height; propodeal length 1.25–1.38× pronotal + mesoscutal length (holotype 1.25); posterior propodeal face oblique, without distinct dorsum; propodeal sublateral longitudinal carina absent; propodeal dorso-lateral margin rounded, lacking longitudinal carina; lateral margins of propodeum convergent posteriorly.

Wings fully developed; distance between origin of RS on vein SC and proximal margin of pterostigma 1.60–2.20× pterostigma length (holotype 2.07); forewing cell 2RS present.

Procoxa lacking posterior process; meso- and metacoxae evenly convex; metacoxa with internal longitudinal carina weakly developed; protibial spur slender; tibiae without external spines.

Metasomal segment 1 slender, subsessile; T1 width:T2 width:T2 length = 0.55–0.60:1.00:0.72–0.82 (holotype 0.60:1.00:0.72); T1 oblique, without distinct dorsum; T1 spiracle projecting; T2 evenly convex; S1 with medial longitudinal carina on anterior 3/4, straight in profile; S2 evenly convex, with obscure antero-medial carina; T3–6 not constricted; T7 evenly convex, with posterior margin truncate; S6–8 flat, lacking lateral carina or process; S7 posterior margin truncate; S8 mostly sclerotized with posterior membranous area evenly convex posteriorly. Harpe depressed laterally, down-curved; harpe dorso-internal margin lacking process; harpe dorsal margin with sparse short erect setae; gonostipes much longer than wide and as long as harpe; gonostipes ventro-medial lobe not forming posterior process; gonostipes ventral lobe projecting posterad; parapenis flexed inward, posterior margin truncate; parapenis dorsal margin lacking tubercles; cupula much shorter than gonostipes; basivolsella depressed, rounded, strongly expanded ventrad, with long slender cuspis 2× longer than basivolsella; cuspis apex reaching posterior 1/3 of harpe;

basivolsella with large seta-filled pit on internal face, with dese long erect wavy setae on ventral margin, and with sparse long erect setae on dorsal margin; basiura weakly sclerotized with distinct apiceps; apiceps apex with sparse long erect setae; penisvalvae symmetrical; penisvalva broad, expanded ventrad, with distinct anterior and posterior ventral processes; posterior margin of anterior process projecting; penisvalva ventral margin weakly expanded anteriorly to anterior process; penisvalva lacking setae; endophallus membranous.

Frons and vertex densely longitudinally striate; gena, pronotal dorsum, mesoscutum, and mesoscutellum with large confluent punctures; postgenal bridge and propleuron with minute sparse punctures; clypeus, scape, and T3–6 with small dense punctures; pedicel, flagellum, prementum, stipes, maxillary and labial palpi, and meso- and metanotal troughs with minute dense punctures; lateral pronotal face longitudinally coarsely striate; tegula, meso- and metacoxae, T1–2, and S1–8 with small sparse punctures; metascutellum with small confluent punctures; mesopleuron and metapleuron ventral 1/3 with large dense and minute sparse punctures; metapleuron dorsal 2/3, procoxa, trochanters, femora, tibiae, and tarsi with minute sparse punctures; propodeum reticulate, with medial subtriangular and sublateral semicircular cell on anterior margin; T7 with small confluent punctures and medial subtriangular impunctate line.

FEMALE. Unknown.

Material examined

4♂. Holotype ♂: **Thailand:** CHIANG MAI: Mae Rim, Nong Hoi, 970–1000 m alt., 23.V.2002, K. Okajima leg. [TUA]. Paratypes: **Thailand:** CHIANG MAI: Mae Rim, Nong Hoi, 10.V.2002, T. Ishizaki leg. [1♂ TUA]; Doi Suthep, Chang Khian, 800–900 m alt., 13.V.2002, K. Okajima leg. [1♂ TUA]; Mae Rim, Nong Hoi, 970–1000 m alt., 22.V.2002, T. Tsuru leg. [1♂ TUA].

Sex association

Female unknown.

Distribution

Thailand: Chiang Mai.

Etymology

The specific name *recondita*, hidden, is the Latin, singular, feminine perfect passive participle in the nominative case. It suggests that this new species was initially confused with *M. norna* by the author.

Remarks

This species and *M. norna* are easily recognized in *Mickelomyrme* by having the frons with a deep sulcus, clypeal subventral flange medially interrupted, notaulus reaching posterior margin of pronotum, metacoxal internal carina weakly developed, and basivolsella strongly expanded ventrad. However, this new species is distinguished by having the clypeus lacking a medial process (present in *M. norna*), clypeal subventral flange overhanging ventral clypeal margin and medially narrowly interrupted (subventral flange reduced and medially widely interrupted in *M. norna*), and penisvalva weakly expanded ventrad anteriorly to anterior process (strongly expanded in *M. norna*). As implied from their similarity, phylogenetic analyses found sister relationship of *M. norna* and *M. recondita* with moderate GC score (GC = 49), with *M. caecina* proximal to them. Interestingly, *M. norna* and *M. recondita* were collected sympatrically in Thailand (Nong Hoi).

Mickelomyrme semperi (Ashmead, 1904)

Mutilla semperi Ashmead, 1904b: 135, ♂, holotype ♂ (Manila, [Luzon], Philippines) [NMNH]; Brown, 1906: 689, ♂.
Smicromyrme semperi semperi: Mickel, 1934: 210, ♂♀; Mickel, 1935: 291, ♂♀; Baltazar, 1966: 210; Tsuneki *et al*., 1993: 13, ♂.
Mickelomyrme semperi semperi: Lelej, 1996c: 284, ♂♀; Lelej, 2005: 44; Lo Cascio, 2015: 551; Okayasu, 2020: 44; Pagliano *et al*., 2020: 175.
Mickelomyrme semperi: Pagliano, 2011: 41, ♂.

Zoobank LSID
urn:lsid:zoobank.org:act:9DDBA5E9-3854-41A2-8668-315551812AC7

Material examined
2♂1♀. **Philippines:** BOHOL: Bilar, 23.VII.1970, T. Okadome leg., *Smicromyrme semperi semperi* Mick. [probably Petersen's hand] [1♂1♀ TUA]; LUZON: Bacnotan, 18–19.III.1974, S. Ueda leg., *Smicromyrme semperi semperi* Mick. [probably Petersen's hand] [1♂ TUA].

Identification source
Identified specimens.

Sex association
This species was initially described from the male only. The female was associated and described by Mickel (1934) based on a pair *in copula*.

Distribution
Philippines: Bohol, Luzon, Negros, Panay (Ashmead, 1904b; Mickel, 1934).

Remarks
This species shares the T3 and T4 constricted anteriorly and posteriorly with *M. hageni* (87:1). This is the unique synapomorphy supporting their sister relationship recovered using implied weighting (all *k* values).

Mickelomyrme zebina (Smith, 1860)

Mutilla zebina Smith, 1860: 115, ♀, holotype ♀ (Bachian [= Bacan], [Maluku Utara], Indonesia) [OUMNH]; Dalla Torre, 1897: 99; André, 1902b: 41.
Smicromyrme zebina: Mickel, 1934: 204, ♂♀; Mickel, 1935: 292, ♂♀; Baltazar, 1966: 211; Tsuneki *et al*., 1993: 21, ♂♀.
Smicromyrme bidentata: Tsuneki *et al*., 1993: 19, ♀.
Smicromyrme aborlana Tsuneki in Tsuneki *et al*., 1993: 23, ♀, holotype ♀ (Aborlan, Palawan, Philippines) [NMNH]. Synonymized in the Chapter 6 under *M. zebina* (Smith).
Smicromyrme aborlana zamboangae Tsuneki in Tsuneki *et al*., 1993: 24, ♀, holotype ♀ (Pasonanka Park, Zamboanga, Mindanao, Philippines) [NMNH]. Synonymized in the Chapter 6 under *M. zebina* (Smith).
Mickelomyrme zebina: Lelej, 1996b: 97, ♂♀, examined; Lelej, 2005: 45; Lo Cascio, 2015: 551; Okayasu *et al*., 2018: 303, ♀; Okayasu, 2020: 44, ♂, examined; Pagliano *et al*., 2020: 175; Brothers, 2022: 172, ♀.
Mickelomyrme aborlana aborlana: Lelej, 2005: 43; Lo Cascio, 2015: 551; Okayasu *et al*.,

2018: 306, ♀; Okayasu, 2020: 44; Pagliano *et al*., 2020: 174.
Mickelomyrme aborlana zamboangae: Lelej, 2005: 43; Lo Cascio, 2015: 551; Okayasu *et al*., 2018: 306, ♀; Okayasu, 2020: 44; Pagliano *et al*., 2020: 174.
Mickelomyrme bidentata: Lelej, 2005: 43, part; Lo Cascio, 2015: 551, part; Okayasu *et al*., 2018: 306, ♀; Okayasu, 2020: 44, part; Pagliano *et al*., 2020: 174, part.

Zoobank LSID
urn:lsid:zoobank.org:act:F71846E2-A495-4A94-B597-52748198529C
urn:lsid:zoobank.org:act:645E3452-4275-43B3-BA45-6A0DAF329521
urn:lsid:zoobank.org:act:178D189A-3754-4467-85E5-EAA0877C288F

Material examined
1♂10♀. **Indonesia:** KALIMANTAN TIMUR: E. Kalimantan, Sangkimah, Kutai N. P., 14.IX.1993, Sk. Yamane leg., *Mickelomyrme zebina* (Smith), A. Lelej det. 1995 [1♂1♀ (*in copula*) SKYC]. **Malaysia:** SABAH: Borneo, 10 mile NW of Keningau, 900 m alt., 30.V.1980, S. Nagai leg. [1♀ EUMJ]; Luasong, 16.XI.1997, K. Matsumoto leg. [2♀ NARO]. **Philippines:** LUZON: Bacnotan, 18–19.III.1974, S. Ueda leg. [1♀ TUA], 7.IV.1974 [1♀ TUA]; Baguio, Asin Hot Spring, 21–25.III.1974, S. Ueda leg. [1♀ TUA]; Benguet, Colorado Ralls, Pullmell Cr. 300 m, 14.VI.1977, S. Ueno leg. [1♀ NSMT]; PALAWAN: Matalangao, 25 km W. of Roxas, 300 m alt., 20–22.XI.1978, S. Nagai leg. [2♀ EUMJ].

Identification source
Voucher specimen (Lelej, 1996b).

Sex association
This species was initially described from the female only. The male was associated and described by Mickel (1934) based on a pair *in copula*.

Distribution
Brunei (Lelej, 2005). Indonesia: Kalimantan Timur, Maluku Utara (Smith, 1860). Malaysia: Sabah, Sarawak (Lelej, 1996b). Philippines: Cebu, Luzon, Mactan, Mindanao, Negros, Palawan (Mickel, 1934; Tsuneki *et al*., 1993).

Remarks
A photo of the holotype of this species are available in Brothers (2022: Fig. 336).

Genus *Nemka* Lelej, 1985

Smicromyrme (*Nemka*) Lelej, 1985: 240, ♂♀.
Smicromyrme (*Horaia*) Tsuneki, 1993a (non Tonnoir, 1930): 43, ♂. Synonymized by Lelej (1995a: 2) under *Nemka* Lelej.
Nemka: Lelej 1995a: 2, ♂♀; Lelej, 2002: 54; Lelej, 2005: 45; Lelej, 2007: 88; Pagliano & Strumia, 2007: 71, ♂♀; Lelej & Brothers, 2008: 39; Brothers & Lelej, 2017: 95; Okayasu *et al*., 2018: 303, ♀; Williams *et al*., 2019b: 22, ♀; Okayasu, 2020: 24, ♂♀; Pagliano *et al*., 2020: 176; Lelej & Williams, 2023: 118, ♂♀. Gender feminine.

Zoobank LSID
urn:lsid:zoobank.org:act:FABE9198-1559-4438-A6E2-4F2D8291C919
urn:lsid:zoobank.org:act:E9BF1217-9DD6-40C7-9E11-D067B9BAE086

Type species
Nemka: *Mutilla viduata* Pallas, 1773, ♂, by original designation.
Horaia: *Smicromyrme* (*Horaia*) *chihpenchius* Tsuneki, 1993, ♂ (misspelled as *chihpenchia*) (= *Mutilla wotani* Zavattari, 1913, ♀, syn. by Okayasu, 2020), by original designation.

Diagnosis
MALE. Frons punctate; vertex elevated beyond ocellar region; ventral clypeal margin entire; mandible apex tridentate, internal teeth as large as apex, without subdistal internal tooth; mandible dorso-lateral carina weakly developed or highly elevated proximally; mandible ventral margin emarginate with large proximal tooth; flagellomere apices truncate; F1 length subequal to width; notaulus reaching posterior margin of pronotum; parascutal carina forming elevated process; tegula rounded posteriorly or projecting posterad, slightly surpassing transscutal articulation; mesopleuron divided into dorsal and ventral convexities by transverse impression; mesopleuron ventral face with sharp process; procoxa lacking posterior process; metacoxal internal carina weakly developed; S2 with lateral felt line; harpe dorso-internal margin lacking proximal process; parapenis posteriorly truncate; gonostipes ventral lobe truncate; basivolsella expanded ventrad with long slender cuspis, with long wavy setae on ventral margin; basivolsella internal face with seta-filled pit; basiura small rounded; apiceps long slender; penisvalva strongly expanded ventrad; penisvalva posterior process lacking external process; penisvalva internal face lacking setae.

FEMALE. See Lelej & Williams (2023).

Species included
A total of 17 species and five subspecies is recognized in this genus. The following seven species are distributed in East Asia: *N. conjungenda* (Magretti, 1892), ♂♀ (Myanmar, Thailand); *N. kellyi* (Pagden, 1934), ♂♀ (Malaysia); *N. limi* (Chen, 1957), ♂♀ (China, South Korea, Vietnam); *N. pagdeni* Lelej, 1995, ♂♀ (China, Laos, Thailand); *N. taiwanensis* (Mickel, 1933), ♂♀ (Taiwan); *N. wotani* (Zavattari, 1913), ♂♀ (Taiwan); *N. yasumatsui* (Mickel, 1936), ♂♀ (Japan).

Sex association
The type species was initially described from the male only. The female of this species was described as *Mutilla coronata* Fabricius, 1793 and associated by Morawitz (1865).

Distribution
Oriental and Palaearctic Regions.

Remarks
This genus was recovered as a monophyletic group under all settings with high GC score (GC = 99; Fig. 22-1). One unique synapomorphy and a number of homoplastic synapomorphies support its monophyly, most notably: vertex elevated beyond ocellar region (4:1), tegula elongate (51:0), mesoscutellum strongly convex (55:0), mesopleuron with a triangular process ventrally (59:1), and basivolsella expanded ventrad with a slender cuspis (114:2). Under lower k values (k0–k11), this genus was found sister to *Dentilla*. Their sister relationship was supported by one unique synapomorphy and, at least, one homoplastic synapomorphy: clypeus dorso-medial carina forming a process (23:1) and parapenis truncate (107:0). With higher k values, the *Nemka* was sister to either ((*Physetopoda* + (*Dentilla* + *Hadrodontilla*)) with *Chenmyrme* and *Ephutomma* proximal to the *Nemka* (k12, k15, k16) or (*Chenmyrme* + *Ephutomma*) (k13, k14, setk).

Within the *Nemka*, phylogenetic relationship among species was consistent ((*N.*

viduata + (*N. pagdeni* + *N. wotani* and kin)), although only limited number of taxa was available for the present study. Four Northeast Asian species, *N. limi*, *N. taiwanensis*, *N. wotani*, and *N. yasumatsui*, constituted a monophyletic group supported by two unique synapomorphies: clypeus with paired subventral tubercles (24:3) and S7 with a medial process (95:1).

The males of *Mickelomyrme* and *Nemka* are characterized by the basivolsella expanded ventrad with a long slender cuspis. However, these two genera are distantly related, suggesting parallel evolution of this feature.

Key to the East Asian species of *Nemka* based on the male morphology

1. Mesosoma red and ventrally black; metasoma black. Myanmar, Thailand … ***N. conjungenda*** (Magretti)
- Mesosoma black; metasoma with some anterior segments orange … 2
2 (1). Clypeus without subventral tubercles and dorsal and subdorsal processes. China, Thailand … ***N. pagdeni*** Lelej
- Clypeus with paired subventral tubercles and dorsal and subdorsal processes … 3
3 (2). Meso- and metascutellum with dense appressed and sparse erect pale setae; metasomal segments 2–6 orange. Malaysia … ***N. kellyi*** (Pagden)
- Meso- and metascutellum with sparse pale setae only; metasomal segments 1–3 or 1–4 orange … 4
4 (3). Clypeus with subventral tubercle slender. Taiwan … ***N. taiwanensis*** (Mickel)
- Clypeus with subventral tubercle rounded … 5
5 (4). Gena with sparse punctures; lateral pronotal face posteriorly longitudinally punctate-striate; mesopleural ventral process laterally flat. Taiwan … ***N. wotani*** (Zavattari)
- Gena with dense punctures; lateral pronotal face of entirely punctate-rugose; mesopleural ventral process laterally concave … 6
6 (5). Pronotal dorsum with short recumbent pale setae anteriorly and long recumbent setae posteriorly, providing thicker setation on posterior half; metasomal segments 1–4 orange. China, Vietnam … ***N. limi*** (Chen)
- Pronotal dorsum with short recumbent pale setae only, providing sparser setation; metasomal segments 1–3 orange. Japan … ***N. yasumatsui*** (Mickel)

Nemka conjungenda (Magretti, 1892)

Mutilla conjungenda Magretti, 1892: 214, ♂♀, syntypes ♂♀ (Schwegoo [= Shwegu], [Kachin], [Myanmar]) [MSNG]; Bingham, 1897: 19, ♂♀; André, 1902b: 38.
Nemka tenasserimica (non Magretti, 1892): Lelej, 1995a: 19, ♀.
Nemka conjungenda: Lelej, 2005: 45; Okayasu *et al*., 2018: 303, ♀; Williams *et al*., 2019b: 22, ♀, examined; Okayasu, 2020: 24; Pagliano *et al*., 2020: 176; Thaochan *et al*., 2022: 163, ♀.

Zoobank LSID
urn:lsid:zoobank.org:act:C314FEC0-1A65-4BB6-AEAC-3AD65E1135F5

Material examined
4♀. **Thailand:** CHIANG MAI: Omkoi District, Dry dipterocarp forest, 17°50'49.9"N 98°22'33.0"E, 950–1010 m alt., 19.VI.2017, R. Mizuno leg. [1♀ THNHM]; 20.VI.2017 [1♀ THNHM]; 23.VI.2017 [2♀ THNHM].

Identification source
Voucher specimens (Williams *et al*., 2019b).

Sex association
This species was described from both sexes collected *in copula* (Magretti, 1892).

Distribution
Myanmar: Kachin (Magretti, 1892). Thailand: Chiang Mai, Lampang, Sisaket, Tak, Trang, Ubon Ratchathani (Lelej, 1995a; Thaochan *et al*., 2022; Williams *et al*., 2019b).

Remarks
One of the collecting sites of this species, Omkoi District, was described by Mizuno *et al*. (2019). The male of this species is exceptional in *Nemka* in that it has the mesosoma largely red and metasoma entirely black (Magretti, 1892).

Nemka kellyi (Pagden, 1934)

Smicromyrme kellyi Pagden, 1934a: 439, ♂♀, holotype ♂ (Bukit Panchor, Kedah, Unfederated Malay States [= Malaysia]) [NHMUK]; Pagden, 1934c: 481, ♂♀; Pagden, 1949: 218, ♂♀.
Timulla (*Trogaspidia*) *kellyi*: Mickel, 1935: 267, ♂.
Smicromyrme kedahensis Mickel, 1935: 290, ♀, holotype ♀ (Bukit Panchor, Kedah, Unfederated Malay States [= Malaysia]) [NHMUK]. Synonymized by Pagden (1949: 218) under *Smicromyrme kellyi* Pagden.
Nemka kellyi: Lelej, 1995a: 14, ♂♀; Lelej, 2005: 46; Okayasu *et al*., 2018: 303, ♀; Okayasu, 2020: 24; Pagliano *et al*., 2020: 176.

Zoobank LSID
urn:lsid:zoobank.org:act:26710B2B-6597-49F2-A2EB-30C94E09CD93

Material examined
No material examined.

Sex association
This species was described from both sexes collected at same place and time (Pagden, 1934a). Later, Pagden (1949) confirmed this association based on a pair *in copula*.

Distribution
Malaysia: Kedah, Kuala Lumpur, Melaka, Pahang, Selangor (Pagden, 1934a, 1949).

Remarks
Even though this species is unavailable for the present study, the original description and illustrations support its genus placement.

Nemka limi (Chen, 1957)

Smicromyrme wotani (non Zavattari, 1913): Yasumatsu, 1938a: 85, ♀; Yasumatsu, 1951: 70, ♀.
Smicromyrme orientalis taiwanensis (non Mickel, 1933a): Chen, 1957: 197, ♂, part, examined; He *et al*., 2004: 955, ♂.

Smicromyrme limi limi Chen, 1957: 215, ♀, holotype ♀ (Chusan [= Zhoushan], Chekiang [= Zhejiang], China) [TARI], examined; He *et al*., 2004: 952, ♀.
Smicromyrme limi nanhai Chen, 1957: 216, ♀, holotype ♀ (San-ah [= Sanya], Hainan, China) [TARI], examined. Synonymized by Okayasu (2020: 33) under *Nemka limi* (Chen).
Nemka wotani (non Zavattari, 1913): Lelej, 1995a: 10, ♂♀, part, examined; Lelej *et al*., 2001: 12, ♀; Lelej, 2002: 57, part; Lelej, 2005: 48, part; Hua, 2006: 300; Lo Cascio, 2015: 553.
Nemka limi limi: Lelej, 1995a: 11, ♀; Lelej, 2005: 46; Hua, 2006: 300; Okayasu *et al*., 2018: 303, ♀; Pagliano *et al*., 2020: 176.
Nemka limi nanhai: Lelej, 1995a: 11, ♀; Lelej, 2005: 46; Hua, 2006: 300; Lo Cascio, 2015: 553; Okayasu *et al*., 2018: 303, ♀; Pagliano *et al*., 2020: 176.
Nemka taiwanensis (non Mickel, 1933a): Lelej, 1995a: 14, ♂, part; Lelej, 2002: 55, part; Lelej, 2005: 47, part; Hua, 2006: 300, part; Okayasu, 2020: 24, part; Pagliano *et al*., 2020: 177, part.
Nemka limi: Okayasu, 2020: 33, ♂♀, examined.

Zoobank LSID
urn:lsid:zoobank.org:act:B7B76A3A-3785-489D-9645-B0AD37568B78
urn:lsid:zoobank.org:act:46E9C74D-3B42-4FD4-ABD3-1E28774ECFFA

Material examined
25♂46♀. Holotype ♀, *Smicromyrme limi limi* Chen: **China:** ZHEJIANG: Chusan [= Zhoushan], 20.8.31, O. Piel leg. [TARI]. Paratypes, *Smicromyrme limi limi* Chen: **China:** SHANGHAI: Shanghai, 23.7.30, O. Piel leg. [1♀ TARI]; [Songjiang], Zô-Sè [= Sheshan], 31.7.30, O. Piel leg. [1♀ ZMUC], 4.8.30, [1♀ TARI], 11.8.30 [1♀ TARI], 15.8.30 [1♀ TARI], 31.8.30 [1♀ TARI]; ZHEJIANG: Chusan [= Zhoushan], 25.2.31, O. Piel leg. [1♀ TARI], 16.8.31 [1♀ TARI], 5.9.31 [1♀ TARI]; [Lin'an, Hangzhou], Tienmushan [= Tianmushan], 15.VII.1905 [1♀ TARI]. Holotype ♀, *Smicromyrme limi nanhai* Chen: **China:** HAINAN: San-ah [= Sanya], 21.XI.1940, Michio Chûjyô leg. [TARI]. Paratype, *Smicromyrme limi nanhai* Chen: **China:** HAINAN: [Sanya], Yurin [= Yulin], 21.XI.1940, M. Chûjyô leg. [1♀ TARI]. **China:** ANHUI: Ningkwo [= Ningguo], Yui-Wáu-Kiai, 22.VII.1920, *Smicromyrme wotani limi* Chen, B. Petersen det. 1987 [1♂ TARI], 24.VII.1920 [2♂ TARI]; FUJIAN: Chungan, Bohea Hills, 10.IX.1939, T.C. Maa leg., *Smicromyrme wotani limi* Chen, B. Petersen det. 1987 [1♀ TARI], 12.IX.1939 [2♀ TARI], 25.IX.1939 [2♀ TARI, 1♀ ZMUC], 2.X.1939 [1♀ TARI], 16.X.1939 [1♀ TARI], 13–17.VIII.1943 [1♀ TARI]; Changting, Tsingshanpu, 12.VI.1940, T.C. Maa leg., "*Timulla orientalis taiwanensis*" [probably Chen's hand] [1♂ TARI]; Changting, Hotien, 25.VII.1940, T.C. Maa leg., *Smicromyrme wotani limi* Chen, B. Petersen det. 1987 [1♀ TARI]; Hwa-an, W. Gate, 23.IX.1940, T.C. Maa leg., *Smicromyrme wotani limi* Chen, B. Petersen det. 1987 [1♂ ZMUC]; Yungan [= Yong'an], Siyingpan, 1940, T.C. Maa leg., *Smicromyrme wotani limi* Chen, B. Petersen det. 1987 [1♀ TARI]; Shaowu, Shuipeikieh [= Shui Pei Kai], 4.VIII.1941, T.C. Maa leg., *Smicromyrme wotani limi* Chen, B. Petersen det. 1987 [1♀ TARI], 25.VI.1942 [1♂ ZMUC], 10–12.VII.1943 [1♀ TARI], 20–24.VII.1943 [2♀ TARI, 1♀ ZMUC], 5.VIII.1943 [2♀ ZMUC], 1–2.IX.1943 [1♂ TARI]; Shaowu, W Gate, 22.IX.1942, T.C. Maa leg., *Smicromyrme wotani limi* Chen, B. Petersen det. 1987 [1♀ TARI]; Shaowu, Kuhsienkieh, 8.VII.1944, T.C. Maa leg., *Smicromyrme wotani limi* Chen, B. Petersen det. 1987 [1♀ TARI], 1944 [5♀ TARI, 1♀ ZMUC]; Shaowu, Kaoyany, 30.VII.1945, T.C. Maa leg., *Smicromyrme wotani limi* Chen, B. Petersen det. 1987 [1♀ TARI]; Shaowu, Tachulan [= Dazhulan], 8–12.VIII.1945, T.C. Maa leg., *Smicromyrme wotani limi* Chen, B. Petersen det.

1987 [1♀ ZMUC]; GUANGDONG: Loufoushan [= Mt. Luofushan], 29.V.1937, T.C. Maa leg., *Smicromyrme wotani limi* Chen, B. Petersen det. 1987 [1♀ TARI]; JIANGXI: [Lushan, Jiujiang], Kuling [= Guling], 21.8.35, O. Piel leg., *Smicromyrme wotani limi* Chen, B. Petersen det. 1987 [1♂ TARI]; SHANGHAI: [Songjiang], Zô-Sè [= Sheshan], 4.8.24, O. Piel leg., *Smicromyrme wotani limi* Chen, B. Petersen det. 1987 [1♂ TARI], 17.7.30 [1♂ ZMUC], 19.7.30 [1♂ TARI], 23.7.30 [2♂ TARI, ZMUC], 24.7.30 [3♂ TARI], 25.7.30 [1♂ TARI], 31.7.30 [1♂ TARI], 1.8.30 [1♂ TARI], 4.8.30 [2♂ TARI]; ZHEJIANG: Hangchow [= Hangzhou], 15.VI.1925, H.A. Jaynes leg., *Nemka wotani* (Zavattari), B. Petersen det. 1995 [1♂ NMNH]; Zô-Póu, VII.1930, *Smicromyrme wotani limi* Chen, B. Petersen det. 1987 [1♂ TARI]; Chusan [= Zhoushan], Ohekiano, 7.9.31, O. Piel leg., *Smicromyrme wotani limi* Chen, B. Petersen det. 1987 [1♂ ZMUC]. **Vietnam:** CAO BANG: Phia Oac Phia Den N[ational]P[ark] station, 30.VI.2022, Nguyen D Hiep leg. [1♀ IEBR]; LANG SON: [Lôc Binh], Montes Mauson [= Mt. Mau Son], Mai 2–3000, IV, H. Fruhstorfer leg., *Smicromyrme wotani wotani* (Zavattari), B. Petersen det. 1983 [1♂ ZMUC]; VINH PHUC: Ngoc Thanh, Me Linh Biodiversity station, 70 m, 21°23'03"N 105°42'40"E, 18.VIII.2022, NTPL, TTN [2♀ IEBR]; Phúc Yên, Ngọc Thanh, Melinh Biodiversity Station, 21.3884995°N 105.712599695°E, 68 m alt., 6.VI.2023, L.T.P. Nguyen et al. leg. [1♀ IEBR].

Identification source
Voucher specimens (Okayasu, 2020).

Sex association
This species was initially described from the female only. The male was associated and diagnosed by Okayasu (2020) based on males and females repeatedly collected at same place and time.

Distribution
China: Anhui, Fujian, Guangdong, Hainan, Jiangxi, Shanghai, Shanxi, Zhejiang (Chen, 1957; Okayasu, 2020; Yasumatsu, 1951). South Korea: Chungcheongnam (Lelej *et al*., 2001). Vietnam: Cao Bang, Lang Son, Quang Ninh, Vinh Phuc (Lelej 1995a).

Remarks
This species is fairly widespread in eastern margin of China and also found in northern Vietnam. This species was previously confused with *N. taiwanensis* and *N. wotani*. The latter two species are in fact endemic to Taiwan.

Nemka pagdeni Lelej, 1995

Nemka pagdeni Lelej, 1995a: 11, ♂♀, holotype ♂ (30 km SW Jinping, Yunnan, China) [ZMMU]; Lelej, 2005: 46; Okayasu *et al*., 2018: 303, ♀; Okayasu, 2020: 24; Pagliano *et al*., 2020: 176.

Zoobank LSID
urn:lsid:zoobank.org:act:3F63B009-5618-493F-BF3C-23C7D1DF1F9B

Material examined
1♂. **Laos:** VIENTIANE: Vientiang, Mekong River, 17.9637°N 102.5960°E, 150 m alt., 14.III.2016, T. Mita leg. [1♂ ELKU].

Identification source

Keyed using Lelej (1995a) and compared with the original description.

Sex association
This species was described from both sexes collected in Yunnan, China, where only one *Nemka* species was distributed (Lelej, 1995a).

Distribution
China: Yunnan (Lelej, 1995a). Laos*: Vientiane. Thailand: additional data unavailable (Lelej, 2005).

Remarks
The only specimen examined herein was collected at the sandy riverside of Mekong River. Like other species of *Nemka* (Alicata *et al*., 1974; Bogusch, 2006; József & Zoltán, 2011; Lelej, 1995a; Matteini Palmerini, 2013; Okayasu, 2020; Pagden, 1934c; Polidori *et al*., 2010), this species likely prefers sandy environment.

Nemka taiwanensis (Mickel, 1933)

Mutilla dimidiata (non Lepeletier, 1845): Zavattari, 1913: 42, ♂.
Mutilla gribodoi (non Magretti, 1892): Zavattari, 1913: 42, ♂, part.
Timulla (*Trogaspidia*) *orientalis taiwanensis* Mickel, 1933a: 408, ♂, holotype ♂ (Taihanroku [= Taipan], [Taitung], Formosa [= Taiwan]) [ZMNB]; Suzuki, 1934: 24; Mickel, 1935: 267, ♂.
Smicromyrme orientalis taiwanensis: Chen, 1957: 197, ♂, part, examined; Tsuneki, 1972c: 16, ♂, part.
Smicromyrme curvisquamata Chen, 1957: 214, ♀, holotype ♀ (Chipon [= Chihpen], Taitung, Taiwan) [TARI], examined. Synonymized in the Chapter 9 under *N. taiwanensis* (Mickel).
Smicromyrme ilanica Tsuneki, 1972c: 16, ♂, holotype ♂ (Tsukeng, Ilan [= Yilan], Formosa [= Taiwan]) [NMNH]. Synonymized in the Chapter 9 under *N. taiwanensis* (Mickel).
Nemka curvisquamata: Lelej, 1995a: 10, ♀; Lelej, 2005: 46; Hua, 2006: 300; Lo Cascio, 2015: 553; Okayasu *et al*., 2018: 306; Okayasu, 2020: 24; Pagliano *et al*., 2020: 176.
Nemka taiwanenis: Lelej, 1995a: 14, ♂; Lelej, 2002: 55; Lelej, 2005: 47; Hua, 2006: 300; Pagliano, 2011: 41, ♂; Lo Cascio, 2015: 553; Okayasu, 2020: 24; Pagliano *et al*., 2020: 177.
Mickelomyrme ilanica: Lelej, 1995a: 17; Lelej, 1996c: 287, ♂; Lelej, 2005: 44; Hua, 2006: 300; Lo Cascio, 2015: 551; Okayasu, 2020: 44; Pagliano *et al*., 2020: 175.

Zoobank LSID
urn:lsid:zoobank.org:act:029C6004-535F-4037-8191-4318A0F9A5F0
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urn:lsid:zoobank.org:act:D69FC69B-59DE-4182-8735-026313DF5485

Material examined
7♂3♀. Holotype ♀, *Smicromyrme curvisquamata* Chen: **Taiwan:** TAITUNG: Chipon [= Chihpen], 1.VII.1927, S. Issiki leg. [TARI]. Paratype, *Smicromyrme curvisquamata* Chen: **Taiwan:** YILAN: Taipin [= Mt. Taiping], 12.IX.1910, T. Shiraki leg., *Mutilla dimidiata* Lepeletier, T. Shiraki det., *Smicromyrme wotani limi* Chen, B. Petersen det. 1987, *Smicromyrme wotani*? [probably Chen's hand], *Smicr. curvisquamata* Chen [unknown hand] [1♀ TARI]. **Taiwan:** CHIAYI: Kagi [= Chiayi], 30.IX.1933, J. Sonan leg. [1♂ TARI];

HSINCHU: Shinchiku [= Hsinchu], 18.VII.1930, J. Sonan & K. Miyake leg., *Timulla* (*Trogaspidia*) *orientalis taiwanensis* Mickel, J. Sonan det., *Timulla orientalis taiwanensis* [probably Chen's hand] [1♂ TARI]; NANTOU: Horisha [= Puli], 30.IV.07, Matsumura leg. [1♂ SEHU]; TAICHUNG: Taichû-shû [= Taichung], Taikôkei [= Tahuchi], Urai [= Chingshan]-Pisutan [Tachien]-Saramao [= Lishan], 16.VII.1932, T. Esaki leg., *Smicromyrme wotani* (Zavattari), B. Petersen det. 1981 [1♀ ELKU]; TAINAN: Tainan, 30.IV.1925, J. Sonan leg. [1♂ TARI]; YILAN: Taipin [= Mt. Taiping], 12.IX.1910, T. Shiraki leg., *Timulla* (*Trogaspidia*) *orientalis taiwanensis* Mickel, J. Sonan det. [1♂ TARI]; Taipin [= Mt. Taiping], 12.IX.1910, *Mutilla dimidiata* Lepeletier, T. Shiraki det., *Timulla orientalis taiwanensis* [probably Chen's hand] [1♂ TARI]; Taipin [= Mt. Taiping], 12.IX.1910, T. Shiraki leg., *Timulla orientalis taiwanensis* [probably Chen's hand] [1♂ TARI].

Identification source
Voucher specimens (Chen, 1957).

Sex association
This species was initially described from the male only. The female was described as *Smicromyrme curvisquamata* and associated in the Chapter 9 based on males and a female collected at same place and time.

Distribution
Taiwan: Chiayi, Hsinchu, Tainan, Taichung, Taitung, Yilan (Chen, 1957).

Remarks
This species is widely distributed in Taiwan but rarer than *N. wotani*.

Nemka wotani (Zavattari, 1913)

Mutilla wotani Zavattari, 1913: 27, ♀, lectotype ♀ (Tainan, Formosa [= Taiwan]) [SDEI], designated by Mickel (1933a: 420), examined; Sonan, 1931: 7, ♀.
Smicromyrme wotani: Mickel, 1933a: 420, ♀; Suzuki, 1934: 25; Mickel, 1935: 291, ♀; Chen, 1957: 207, ♀; Tsuneki, 1972c: 18, ♀, examined; Sabi *et al*., 1977: 42, ♀; Tsuneki, 1993a: 40, ♀.
Smicromyrme orientalis taiwanensis (non Mickel, 1933a): Chen, 1957: 197, ♂, part, examined; Tsuneki, 1972c: 16, ♂, part.
Smicromyrme (*Horaia*) *chihpenchia* Tsuneki, 1993a: 43, ♂, holotype ♂ (Chihpenchi, Taitung, Taiwan) [MNHAH], examined. Synonymized by Okayasu (2020: 31) under *Nemka wotani* (Zavattari).
Nemka wotani: Lelej, 1995a: 10, ♂♀, part, examined; Lelej, 2002: 57; Terayama, 2004: 13; Lelej, 2005: 48; Hua, 2006: 300, part; Pagliano, 2011: 41, ♂; Lo Cascio, 2015: 553; Okayasu *et al*., 2018: 303, ♀; Okayasu, 2020: 31, ♂♀, examined; Pagliano *et al*., 2020: 177.
Nemka chihpenchia: Lelej, 1995a: 11, ♂; Lelej, 2005: 45; Lo Cascio, 2015: 552; Pagliano *et al*., 2020: 176.
Smicromyrme chihpenchia: Hashimoto & Nakanishi, 1997: 31, ♂.

Zoobank LSID
urn:lsid:zoobank.org:act:C5E8A53B-D4C3-4CD7-95F6-E820F967E857
urn:lsid:zoobank.org:act:365F94BB-0183-4AAA-863D-24DB1C19212C

Material examined
5♂22♀. Lectotype ♀, *Mutilla wotani* Zavattari: **Taiwan:** TAINAN: Tainan, VIII.1909, H. Sauter leg. [SDEI (DEI-GISHym 16749)]. Holotype ♂, *Smicromyrme chihpenchia* Tsuneki: **Taiwan:** TAITUNG: Chihpenchi, 12.VIII.1976, T. Murota leg. [MNHAH (B1-288585)]. **Taiwan:** CHIAYI: Takezaki [= Chuchi], 15.XI.1926, J. Sonan leg. [1♀ SEHU]; Takezaki [= Chuchi], 15.XI.1926, *Smicromyrme wotani wotani* Zavattari, B. Petersen det. 1987 [1♀ TARI]; Chuchi, 18.VI.1941, Y. Yano leg. [1♀ ELKU]; Chuchi, 24–25.VII.1968, K. Tsuneki leg. [1♀ NMNH]; Chuchi, 24–25.VII.1968, K. Tsuneki leg., *Smicromyrme orientalis taiwanensis* (Mickel), K. Tsuneki det. 1972 [probably Petersen's hand] [1♂ ZMUC]; Chuchi, 24–25.VII.1968, K. Tsuneki leg., *Smicromyrme wotani* (Zavattari), K. Tsuneki det. 1972 [1♀ ZMUC]; Chuchi, 26.VII.1968, K. Tsuneki leg., *Smicromyrme wotani* (Zavattari), K. Tsuneki det. 1972 [1♀ ZMUC]; Kagi [= Chiayi], 30.IX.1933, J. Sonan leg., *Smicromyrme wotani wotani* Zavattari, B. Petersen det. 1987 [1♀ TARI]; NEW TAIPEI: Hsintien [= Xindian], VIII.1920, S. Inamura leg., *Mutilla wotani* Zavattari, T. Shiraki det., *Smicromyrme wotani wotani* (Zavattari), B. Petersen det. 1987 [1♀ ZMUC]; Hsintien [= Xindian], VIII.1920, S. Inamura leg., *Smicromyrme wotani wotani* (Zavattari), B. Petersen det. 1987 [1♀ TARI]; PENGHU: Pengfutao, VII.1930, S. Minowa leg., *Smicromyrme wotani wotani* Zavattari, B. Petersen det. 1987 [1♀ TARI]; PINGTUNG: Hengchun, 17.VII.1968, K. Tsuneki leg., *Smicromyrme wotani* (Zavattari), K. Tsuneki det. 1972 [1♀ ZMUC]; TAICHUNG: Tulan, 5.VII.1968, K. Tsuneki leg., *Smicromyrme wotani* (Zavattari), K. Tsuneki det. 1972 [1♀ ZMUC]; TAINAN: Xinhua, 5.V.1925, S. Takano leg. [1♀ SEHU]; Yujing, 2.VII.1937, J. Sonan leg., *Smicromyrme wotani wotani* (Zavattari), B. Petersen det. 1987 [1♀ TARI]; TAIPEI: Taipei, 25.IX.1927, J. Sonan leg., *Smicromyrme wotani wotani* (Zavattari), B. Petersen det. 1987 [5♀ TARI]; TAITUNG: Taitô-chô [= Taitung], Kanzangoe, Suzuka-Shinpuro [=Hsinwulu], 10.VIII.1932, T. Esaki leg., *Smicromyrme wotani* (Zavattari), B. Petersen det. 1981 [1♀ ELKU]; [Beinan], Chipon [= Chihpen], 15.VIII.1936, K. Iida leg., *Nemka wotani* (Zavattari), A. Lelej det. 1995 [1♂ NSMT (NSMT-Hym No. 3350)], 18.VIII.1936 [1♀ NSMT (NSTM-Hym No. 3323)]; Chihpenchi, 30.VI.1968, K. Tsuneki leg., *Smicromyrme orientalis taiwanensis* (Mickel), K. Tsuneki det. 1972 [probably Petersen's hand] [1♂ ZMUC]; Fangliao, 24.IV.1941, Nitobe leg., *Mutilla suspiciosa* (Smith), T. Shiraki det., *Timulla orientalis taiwanensis* (4–7 black) [probably Chen's hand] [1♂ TARI].

Identification source
Voucher specimens (Okayasu, 2020).

Sex association
This species was initially described from the female only. The male was associated by Lelej (1995a) and Lelej & Yamane (1992) based on a male and females collected at same place and time although those specimens actually belonged to *N. yasumatsui* (Okayasu, 2020). True male specimens of *N. wotani* were recognized and diagnosed by Okayasu (2020) using morphological similarities of *N. limi*, *N. wotani*, and *N. yasumatsui*.

Distribution
Taiwan: Chiayi, Hualien, New Taipei, Penghu, Pingtung, Taichung, Tainan, Taipei, Taitung, Taoyuan (Tsuneki, 1972c).

This species was recorded from Sumbawa, Indonesia by Zavattari (1914), but this record probably belongs to a separate species.

Remarks
This is the oldest name among Northeast Asian *Nemka* species. Many misidentifications were

involved with this species, which were clarified by Lelej (1995a) and Okayasu (2020).

Nemka yasumatsui (Mickel, 1936)

Smicromyrme yasumatsui Mickel, 1936: 52, ♀, holotype ♀ (Chikuzen, Fukuoka, Japan) [UMSP]; Tsuneki, 1972b: 17, ♀; Murota, 1977: 6, ♀; Yoshida, 1989: 651; Takahashi, 1996: 28, ♀. Synonymized by Lelej (1995a: 10) under *Nemka wotani* (Zavattari) and resurrected to full species status by Okayasu (2020: 25).
Smicromyrme (*Nemka*) *wotani* (non Zavattari, 1913): Lelej & Yamane, 1992: 631, ♂♀.
Nemka wotani (non Zavattari, 1913): Lelej, 1995a: 10, ♂♀, part; Haneda *et al*., 1998: 335; Yamane, 1999: 381, ♂♀; Lelej, 2002: 57; Lelej, 2005: 48; Terayama, 2005: 8, 11, 17, ♂♀; Hua, 2006: 300, part; Nishida & Kawazoe, 2011: 197, ♀; Terayama *et al*., 2011: 13, 21, ♂♀; Suda, 2011: 137, ♀; Tsurusaki *et al*., 2012: 70, ♂; Nagase *et al*., 2014: 132, ♀; Ono & Kawashima, 2013: 41, ♂; Lo Cascio, 2015: 553; Terayama *et al*., 2016: 167, ♂♀.
Smicromyrme lewisi (non Mickel, 1935): Sato & Tsurusaki, 2010: 68, ♀.
Nemka yasumatsui: Okayasu, 2020: 25, ♂♀, examined.

Zoobank LSID
urn:lsid:zoobank.org:act:2F7E340E-335E-4BBE-855C-B6968F63C9D0

Material examined
131♂168♀. Paratype: **Japan:** FUKUOKA: Chikuzen, 3.IX.1930, K. Yasumatsu leg., *Smicromyrme wotani* (Zavattari), B. Petersen det. 1981 [1♀ ELKU]. **Japan:** AICHI: Toyohashi-shi, Hosoya-chô, Omotehama, 17.IX.2006, N. Toda leg. [1♀ EUMJ]; CHIBA: Futtsu-shi, Futtsu, 26.VII.1972, H. Suda leg. [1♀ HSC]; Futtsu-shi, Minato, Kazusaminato, 3.IX.2017 [7♀ EUMJ]; Futtsu City, Shinmaiko-kaigan beach, 35°14'54"N 139°52'04"E, 24.VII.2021, T. Yoshida leg. [2♀ SEHU]; EHIME: Matsuyama, 21.IX.1950, H. Kusunoki leg. [1♀ EUMJ]; FUKUOKA: Chikuzen, 3.IX.1930, K. Yasumatsu leg. [2♀ ELKU, 1♀ TARI]; Chikuzen, 3.IX.1930, K. Yasumatsu leg., *Smicromyrme wotani* (Zavattari), B. Petersen det. 1981 [2♀ ELKU]; Chikuzen, 3.IX.1930, K. Yasumatsu leg., compared with type by B. Petersen in 1968, *Smicromyrme wotani* (Zavattari), B. Petersen det. 1981 [1♀ ZMUC]; GOTÔ ISLANDS: Nozaki-jima Island, 26.VII.1971, T. Okadome leg., *Smicromyrme wotani wotani* (Zavattari), B. Petersen det. 1983 [1♂ TUA]; Nozaki-jima Island, 31.VII.1971, S. Okadome leg., *Smicromyrme wotani* (Zavattari), B. Petersen det. 1981 [1♀ ZMUC]; Fukue-jima Island, Takahama, 32.7084°N 128.6618°E, 27.VII.2013, R. Matsumoto leg. [1♀ OMNH]; HYÔGO: Awaji-shima Island, Minamiawaji-shi, Nandan-chô, Fukiage-hama, 17.VII.2000, R. Matsumoto leg. [1♀ OMNH]; IKI ISLANDS: Iki-shi, Ikino-shima Island, Katsumoto-chô, Kushiyama camp site, 33°51'N 129°42'E, 16–17.VII.2016, R. Itô leg. [1♂3♀ ELKU]; Iki-shi, Ikino-shima Island, Katsumoto-chô, Kushiyama beach, 33°51'N129°41'E, 17.VII.2016, R. Itô leg. [1♀ ELKU]; KAGOSHIMA: Kimotsuki-chô, Futamata, Forest road, 3.VII.2011, T. Kawano leg. [1♀ ELKU]; KÔCHI: Tosashimizu-shi, Shimonokae, 4.VII.1999, Y. Kawakami leg. [1♂ EUMJ], 10.VII.1999 [1♀ EUMJ], 19.VIII.2000 [4♀ EUMJ], 20.VIII.2000 [1♀ EUMJ], 16.VI.2001 [18♂7♀ EUMJ], 16.VI.2002 [21♂1♀ EUMJ], 21.IX.2003 [3♀ EUMJ], 5.X.2003 [1♀ EUMJ], 4.VII.2004 [4♀ EUMJ], 16.VI.2006 [1♀ EUMJ], 5.VII.2007 [16♂5♀ EUMJ], 8.VII.2007 [1♂3♀ EUMJ], 12.VII.2007 [5♂ EUMJ], 11.VII.2009 [18♂5♀ EUMJ], 13.VII.2009 [3♂1♀ EUMJ]; Tosashimizu-shi, Shimonokae, 15.VI.2002, T. Befu leg. [1♂1♀ OMNH]; Tosashimizu-shi, Shimonokae, beach, 32.861°N 132.953°E, 10.VIII.2020, J. Okayasu leg. [1♀ EUMJ]; Tosashimizu-shi, Shimonokae-kaigan Beach, 32°51'42.8"N 132°57'16.7"E, 6.VII.2022, 18:35, J. Okayasu leg. [1♀ SEHU],

7.VII.2022, 7:45–13:45, J. Okayasu leg. [18♂41♀ (5♂5♀ *in copula*) SEHU]; Shimanto-shi, Nashishi, 29.VIII.1999, Y. Kawakami leg. [2♀ EUMJ], 17.VI.2001 [4♂2♀ EUMJ]; Kuroshio-chô, Ideguchi, 25.VI.2000, Y. Kawakami leg. [1♂2♀ EUMJ], 1.X.2000 [2♀ EUMJ], 10.VI.2001 [1♂ EUMJ], 17.VI.2001 [1♂ EUMJ]; Shimanto-chô, Okitsu, 20.VII.2014, Y. Kawakami leg. [6♂1♀ EUMJ]; KUMAMOTO: Amakusa, Tomioka–Shiki, 16.VI.1931, Esaki & Hori leg. [3♀ ELKU]; Amakusa, Tomioka–Shiki, Esaki & Hori leg., 19.VI.1931, *Smicromyrme wotani* (Zavattari), B. Petersen det. 1981 [7♀ ELKU, ZMUC]; Amakusa, Tomioka–Tororo, 18.VI.1931, Esaki & Hori leg. [1♀ ELKU]; KYÔTO: Kyôtango-shi, Amino-chô, Kotobiki-hama, 35°42'14"N 135°3'23"E, 5.VIII.2007, R. Matsumoto leg. [4♂2♀ OMNH]; MIYAZAKI: Aoshima, on the grassland, 12.VIII.1953, H. Nagase leg. [1♂ MNHAH]; Kushima-shi, Ichiki, Ishinami-kaigan, 31.4702°N 131.3619°E, 9.VII.2018, R. Matsumoto leg. [4♂ OMNH]; NIIGATA: Shibata-shi [1♂ NSMT]; OSAKA: Osaka Prefectural Nature Park, 28.IX.2007, R. T. leg. [1♀ OMNH]; ÔSUMI ISLANDS: Tanegashima Island, Nakatane-chô, estuary of Ôura-gawa river, on the sandy ground, 30.VII.1982, H. Kaburaki leg. [1♂ MNHAH]; Tanegashima Island, Hamada, 2.VIII.1984, Sk. Yamane leg. [1♂ IEBR, 2♀ MTC]; SAGA: Karatsu, 14.IX.1937, E. Sueusou leg. [2♀ ZMUC]; SHIMANE: Hamada-shi, Iwami seaside park, 19.VIII.2015, H. Yoshitomi leg. [1♀ EUMJ]; Hamada-shi, 14.VIII.2016, T. Miyamoto leg. [1♀ EUMJ]; Izumo, Sashiumi, 18.VIII.2016, H. Yoshitomi leg. [1♀ EUMJ]; Izumo-shi, Sashiumi, 35°20.234'N 132°39.909'E, 16–17.VII.2017, H. Yoshitomi leg. [1♂2♀ EUMJ]; SHIZUOKA: Hamamatsu-shi, Nakatajima-sakyû, on sandy ground, 26.IX.1985, N. Toda leg. [1♀ EUMJ]; TOTTORI: Tottori-shi, Hamasaka, 30 m alt., VIII.1946, H. Aoki leg. [1♀ OMNH (N000003301)], 34.5402°N 134.1992°E, 14.VII.2013, R. Matsumoto leg. [1♂ OMNH]; Sand hill, 13.VII.1983, T. Ishikawa leg. [2♀ EUMJ]; Tottori-city, Tottori sand dunes, 27.VI.2011, Y. Fukuda leg. [1♀ EUMJ]; Tottori-shi, Hamasaka, Tottori Sand Dune, Ichirimatsu, 35°32'08.9"N 134°13'23.3"E, 67 m alt., dune with sparse vegetation, 1.VII.2022, 19:10–19:45, J. Okayasu leg. [8♀ SEHU], 2.VII.2022, 6:45–9:00 [4♀ SEHU], 2.VII.2022, 18:05–19:45, J. Okayasu leg. [1♂10♀ (1♂1♀ *in copula*) SEHU].

Identification source
Voucher specimens (Okayasu, 2020).

Sex association
This species was initially described from the female only. The male was associated by Lelej & Yamane (1992) and Lelej (1995a) based on a male and females collected at same place and time although misidentified as *N. wotani* (Okayasu, 2020). Six pairs *in copula* were examined in this study.

Distribution
Japan: Gotô Islands, Honshu (Aichi, Chiba, Fukui, Hyôgo, Kyôto, Mie, Niigata, Osaka, Shimane, Shizuoka, Tochigi, Tottori), Iki Islands, Kyushu (Fukuoka, Kagoshima, Kumamoto, Miyazaki, Saga), Shikoku (Ehime, Kôchi), Ôsumi Islands (Nishida & Kawazoe, 2011; Lelej, 1995a; Tsuneki, 1972a).

Remarks
This species utilizes the sand-nesting wasp *Bembix niponica* Smith, 1873 as a host (Ono & Kawashima, 2013).

Genus *Nordeniella* Lelej, 2005

Nordeniella Lelej, 2005: 185, ♂♀; Lelej, 2007: 89; Lelej & Brothers, 2008: 40; Brothers & Lelej, 2017: 95; Williams *et al*., 2019b: 22, ♀; Pagliano *et al*., 2020: 177; Okayasu, 2022: 57, ♀; Thaochan *et al*., 2022: 158, ♀; Lelej & Williams, 2023: 118, ♂♀. Gender feminine.

Zoobank LSID
urn:lsid:zoobank.org:act:479C5956-8FEF-4F3A-A27A-677502B62680

Type species
Mutilla thermophila Turner, 1911, ♀, by original designation.

Diagnosis
MALE. Frons punctate; vertex rounded; ventral clypeal margin with paired teeth medially; mandible apex tridentate, internal teeth smaller than apex, without subdistal internal tooth; mandible dorso-lateral carina weakly developed; mandible ventral margin not emarginate with small proximal lobe; flagellomere apices truncate; F1 length subequal to width; notaulus present on posterior part of mesoscutum; parascutal carina forming elevated process; tegula rounded posteriorly, slightly surpassing transscutal articulation; mesopleuron divided into dorsal and ventral convexities by transverse impression; mesopleuron ventral face with sharp process; procoxa lacking posterior process; metacoxal internal carina weakly developed; S2 lacking lateral felt line.

FEMALE. See Lelej & Williams (2023).

Species included
A total of eight species is recognized in this genus. The following three species is distributed in East Asia: *N. dokbua* Sittichaya & Williams, 2022, ♀ (Thailand); *N. maleeae* Williams, 2019, ♀ (Thailand); *N. sumbawaensis* Okayasu, 2022, ♀ (Indonesia).

Sex association
The type species was initially described from the female only. The male of this species was associated and described by Lelej (2005).

Distribution
Oriental Region.

Remarks
Originally, five species from India and Sri Lanka were assigned to this genus (Lelej, 2005). Okayasu (2022), Thaochan *et al*. (2022), and Williams *et al*. (2019b) described three new species based on females from Indonesia and Thailand, so the male of this genus will eventually be discovered in East Asia.

Genus *Physetopoda* Schuster, 1949

Physetopoda Schuster, 1949: 112, ♂♀; Lelej, 1985: 197, ♂♀; Lelej, 1995b: 15, ♀; Lelej, 1995c: 210, ♂♀; Lelej *et al*., 2001: 14; Lelej, 2002: 57; Lelej, 2005: 49; Lelej, 2007: 89; Pagliano & Strumia, 2007: 72, ♂♀; Lelej & Brothers, 2008: 46; Brothers & Lelej, 2017: 96; Okayasu *et al*., 2018: 303, ♀; Williams *et al*., 2019b: 23, ♀; Pagliano *et al*., 2020: 178; Lelej & Williams, 2023: 120, ♂♀. Gender feminine.
Glossotilla: Chen, 1957: 159, ♀. Gender feminine.
Smicromyrme (*Paramyrme*) Lelej, 1977b: 531, ♂♀. Synonymized by Brothers (1983: 444)

under *Physetopoda* Schuster.
Smicromyrme (*Physetopoda*): Brothers, 1983: 441.
Paramyrme: Lelej, 1984: 101, ♂♀. Gender feminine.

Zoobank LSID
urn:lsid:zoobank.org:act:16AC1E37-4078-4228-B9F1-8A0CEDAEF96E
urn:lsid:zoobank.org:act:BC28F973-8200-4BAC-B672-0883FECA3A04

Type species
Physetopoda: *Physetopoda insularis* Schuster, 1949, ♂ (= *Mutilla rubrocincta* Lucas, 1849, ♂, syn. by Brothers, 1983), by original designation.
Paramyrme: *Mutilla montana* Panzer, 1805, ♀ (= *Mutilla halensis* Fabricius, 1787, ♀, syn. by Panzer 1806b), by original designation.

Diagnosis
MALE. Frons punctate; vertex rounded; ventral clypeal margin entire; mandible apex tridentate, internal teeth smaller than apex, without subdistal internal tooth; mandible dorso-lateral carina weakly developed; mandible ventral margin emarginate with large proximal tooth; flagellomere apices truncate; F1 longer than wide; notaulus reaching posterior margin of pronotum; parascutal carina forming elevated process; tegula rounded posteriorly, slightly surpassing transscutal articulation; mesopleuron divided into dorsal and ventral convexities by transverse impression; mesopleuron ventral face lacking process; procoxa lacking posterior process; metacoxal internal carina weakly developed; S2 lacking lateral felt line; harpe dorso-internal margin with or without proximal process; parapenis bifid; gonostipes ventral lobe projecting posterad; basivolsella elongate, posteriorly depressed and anteriorly expanded ventrad with long wavy setae on ventral margin; basivolsella internal face lacking seta-filled pit; basiura small rounded; apiceps long slender; penisvalva strongly expanded ventrad; penisvalva posterior process lacking external process; penisvalva internal face lacking setae.

FEMALE. See Lelej & Williams (2023).

Species included
A total of 46 species and seven subspecies is recognized in this genus. The following two species are distributed in East Asia: *P. oratoria* (Chen, 1957), ♂♀ (China, Mongolia, Russia); *P. thai* Lelej, 1995, ♀ (Laos, Myanmar, Thailand).

Sex association
The type species was initially described from the male only. The female of its senior synonym was associated and described by Lelej (1985).

Distribution
Afrotropical, Oriental, and Palaearctic Regions.

Remarks
This genus was recovered as a monophyletic group under all settings with moderate GC score (GC = 52; Fig. 22-1), supported by a combination of two to five homoplastic synapomorphies: antennal rims separated by 2× its width (16:0), clypeus subconvex (22:1), mandible dorso-latera carina elevated only proximally (32:1), S2 lacking a lateral felt line (86:1), harpe with an internal process (102:0), and basivolsella elongate, posteriorly depressed and anteriorly expanded ventrad (114:5).

Physetopoda oratoria (Chen, 1957)

Smicromyrme oratoria oratoria Chen, 1957: 197, ♂, holotype ♂ (Longtong, Tsinan [= Jinan], Shantung [= Shandong], China) [TARI], examined.
Smicromyrme oratoria vaticinia Chen, 1957: 198, ♂, holotype ♂ (Yangkikaping [= Yangkiaping], Chahar, [Inner Mongolia], China) [TARI], examined. Synonymized by Lelej (2002: 60) under *Physetopoda oratoria* (Chen).
Smicromyrme oratoria miscisis Chen, 1957: 198, ♂, holotype ♂ (Yangkiaping, Chahar, [Inner Mongolia], China) [TARI], examined. Synonymized by Lelej (2002: 60) under *Physetopoda oratoria* (Chen).
Glossotilla rectangulata Chen, 1957: 159, ♀, holotype ♀ (Tayintze, Linsi, Jehol [= Inner Mongolia], China) [TARI], examined. Synonymized by Lelej (2002: 60) under *Physetopoda oratoria* (Chen).
Smicromyrme montana f. *rubrocincta* (non Lucas, 1849): Lelej, 1975: 324, ♂.
Smicromyrme montana (non Panzer, 1806b): 273, ♂.
Smicromyrme (*Paramyrme*) *eoa* Lelej, 1977b: 531, ♂♀, holotype ♀ (Primorskii krai, Russia) [ZISP]. Synonymized by Lelej (2002: 60) under *Physetopoda oratoria* (Chen).
Paramyrme eoa: Lelej, 1984: 109, ♂♀.
Physetopoda eoa: Lelej, 1985: 206, ♂♀; Lelej, 1995c: 210, ♂♀; Lelej *et al*., 2001: 13.
Physetopoda oratoria: Lelej, 1995b: 15; Lelej *et al*., 2001: 14; Lelej, 2002: 60; Hua, 2006: 300; Lelej *et al*., 2014: 392, ♂; Kochetkov & Lelej, 2015: 261, ♂♀; Lelej, 2017: 155; Pagliano *et al*., 2020: 180; Lelej & Williams, 2023: 105, ♂.

Zoobank LSID
urn:lsid:zoobank.org:act:9AFFA561-87ED-4C05-854E-04D25E68F5AC
urn:lsid:zoobank.org:act:F16337CA-062F-4D87-B003-B76B099A0BAA
urn:lsid:zoobank.org:act:C5E9D3F1-255E-46C3-8554-D428582280DE
urn:lsid:zoobank.org:act:19C5D2A1-F058-4EDE-8875-0CBA3E2A3F3F
urn:lsid:zoobank.org:act:0942BFF0-9AEC-4E79-BAC9-6A0B97CAC84F

Material examined
9♂1♀. Holotype ♂, *Smicromyrme oratoria oratoria* Chen: **China:** SHANDONG: Tsinanfou [= Jinan], Long-tong, 500 à 700 m, *Smicromyrme oratoria or*. Chen [unknown hand] [TARI]. Holotype ♂, *Smicromyrme oratoria miscisis* Chen: **China:** INNER MONGOLIA: Chahar [= Inner Mongolia], Yangkiaping, 6.VII.37, O. Piel leg. [TARI]. Paratypes, *Smicromyrme oratoria miscisis* Chen: **China:** JILIN: Mandchourie, Prov. Kirin [= Jilin], Kao-lin-tze, 23.VII.39, M. Volkoff leg. [1♂ TARI]; **Mongolia:** Mong. E, Siaotihaeize, chan, Licent, 17.VII.27 [1♂ TARI]. Holotype ♂, *Smicromyrme oratoria vaticinia* Chen: **China:** INNER MONGOLIA: Chahar [= Inner Mongolia], Yangkiaping, 29.VII.37, O. Piel leg. [TARI]. Paratypes, *Smicromyrme oratoria vaticinia* Chen: **China:** INNER MONGOLIA: Chahar [= Inner Mongolia], Yangkiaping, 19.VII.31, O. Piel leg. [1♂ TARI], 29.VII.31 [1♂ TARI], 3.VIII.37 [1♂ TARI]; SHANDONG: Kiaocheu [= Kiaochow = Jiaozhou], Chau Si Sud, Licent, 22.VI.16 [1♂ TARI]. Holotype ♀, *Glossotilla rectangulata* Chen: **China:** INNER MONGOLIA: Manchoukuo, Ta-Yngtse [= Dayinzi], Linsisien [= Linxi], VII.[19]40, E. Bourgault leg., *Smicromyrme rectangulata* (Chen), B. Petersen det. 1982 [TARI].

Identification source
Primary type.

Sex association
This species was initially described from the male only. The female of its junior synonym was associated and described by Lelej (1977b), but the evidence of this association was not indicated. Chen (1957) described *G. rectangulata* and this species was also regarded as the female of *P. oratoria* (Lelej, 2002).

Distribution
China: Inner Mongolia, Jilin, Shandong. Mongolia (Lelej, 1975). Russia: Amur, Irkutsk, Khabarovsk, Khakassia, Primorsky, Sakha, Tuva, Zabaykalsky (Lelej, 1977b, 1985; Lelej *et al*., 2014).

Remarks
The holotypes of this species and its subspecies are deposited in TARI and have appropriate labels.

Genus *Promecilla* André, 1902

Promecilla André, 1902b: 30, ♀; Ashmead, 1903: 330, ♀; Bischoff, 1921: 715, ♀; Mickel, 1928: 35; Skorikov, 1935: 321; Hammer, 1962: 46, ♀; Brothers, 1975: 592, ♂♀; Krombein, 1978: 729, ♀, part; Lelej & Kabakov, 1980: 192, ♂; Lelej, 1985: 180, ♂♀; Krombein 1991: 9, part; Lelej, 2002: 63; Lelej, 2005: 51; Lelej, 2007: 89; Lelej & Brothers, 2008: 48; Brothers & Lelej, 2017: 96; Okayasu *et al*., 2018: 303, ♀; Zhou *et al*., 2018a: 26, ♂; Williams *et al*., 2019b: 24; Pagliano *et al*., 2020: 182; Lelej & Williams, 2023: 122, ♂♀. Gender feminine.
Smicromyrme (*Rhombotilla*): Nagy, 1972: 5, ♂.

Zoobank LSID
urn:lsid:zoobank.org:act:8CA9A025-EFE4-4894-8628-67E7FEF60DDF

Type species
Mutilla regia Smith, 1855, ♀, by original designation.

Diagnosis
MALE. Frons punctate or longitudinally striate; vertex elevated beyond ocellar region; ventral clypeal margin entire; mandible apex bidentate or tridentate, internal teeth smaller than apex, without subdistal internal tooth; mandible dorso-lateral carina weakly developed; mandible ventral margin not emarginate with large rounded or small proximal lobe; flagellomere apices truncate; F1 length subequal to width; notaulus present on posterior part of mesoscutum or reaching posterior margin of pronotum; parascutal carina forming weak process; tegula rounded posteriorly, slightly surpassing transscutal articulation; mesopleuron evenly convex, lacking transverse impression; mesopleuron ventral face lacking process; procoxa lacking posterior process; metacoxal internal carina weakly developed or lamellately projecting posteriorly; S2 lacking lateral felt line; harpe dorso-internal margin lacking proximal process; parapenis slender down-curved or with straight ventral process; gonostipes ventral lobe posteriorly truncate; basivolsella elongate, posteriorly depressed and anteriorly expanded ventrad with long wavy setae on ventral margin; basivolsella internal face with or without seta-filled pit; basiura small rounded; apiceps long slender; penisvalva strongly expanded ventrad; penisvalva posterior process lacking external process; penisvalva internal face lacking setae.

FEMALE. See Lelej & Williams (2023).

Species included
A total of 30 species is recognized in this genus. The following seven species are distributed in East Asia: *P. annexa* (Cameron, 1909), ♂ (Indonesia, Malaysia); *P. calliope* (Smith, 1857), ♀ (Malaysia); *P. decora* (Smith, 1879), ♂♀ (China, Malaysia, Thailand, Vietnam); *P. delia* (Mickel, 1935), ♀ (Indonesia, Malaysia); *P. hyale* (Mickel, 1934), ♀ (Philippines); *P. levinaris* (Chen, 1957), ♂ (China); *P. philippinensis* Lelej, 2005, ♀ (Philippines).

Sex association
The type species was initially described from the female only. The male of this species was associated and described by Cameron (1902b), and its junior synonym was described from both sexes by Nurse (1903).

Gender
Feminine.

Distribution
Afrotropical, Oriental, and Palaearctic Regions.

Remarks
Two clades were recognized in this genus, one includes the typical *Promecilla* species, like *P. levinaris* and *P. regia*, and another includes *P. annexa*, *P. decora*, and *P. yerburghi* (hereafter the *decora* group). The latter group differs from *Promecilla* s. str. by having the frons longitudinally striate (punctate in *Promecilla* s. str.), mandible apically tridentate with a small proximo-ventral lobe (apically bidentate with a large proximo-ventral lobe in *Promecilla* s. str.), and parapenis with a straight ventral process (down-curved posteriorly in *Promecilla* s. str.). Under equal weights, the *decora* group was recovered as paraphyletic due to sister relationship between *P. yerburghi* and (*P. levinaris* + *P. regia*) (Fig. 3-2). The *Promecilla* was monophyletic in this instance, supported by one unique synapomorphy and four homoplastic synapomorphies: S2 evenly convex (83:0), parapenis with a straight ventral process (107:2), gonostipes ventral lobe truncate (109:2), basivolsella with long wavy setae 111:1), and basivolsella elongate, posteriorly depressed and anteriorly expanded ventrad (114:5). Using implied weighting, the *Promecilla* s. str. and the *decora* group were dissociated except when k16 was used (Fig. 20-2). The *decora* group was sister to either (*Ephucilla* + *Sinotilla*) (k0–k7; Figs 4–11) or ((*Mickelomyrme* + (*Ephucilla* + *Sinotilla*)) (k8–k15, setk; Figs 12–19, 21), with *Promecilla* s. str. sister to them. Monophyly of the *decora* group-*Ephucilla*-*Mickelomyrme*-*Sinotilla* is supported by two unique synapomorphies: frons longitudinally striate (10:1) and mesoscutum weakly convex (46:1). The *decora* group might eventually be recognized as a separate genus. In the present study, this group is retained in *Promecilla*, given its uncertain placement. Luckily, females are known for both *Promecilla* s. str. and the *decora* group.

Key to the East Asian species of *Promecilla* based on the male morphology

1. Frons punctate; mandible apically bidentate, ventrally with large proximal lobe; metacoxa with weakly developed internal carina; parapenis curved ventrally … ***P. levinaris*** (Chen)
- Frons longitudinally striate; mandible apically tridentate, ventrally with small proximal lobe; metacoxa with internal carina lamellately projecting posteriorly; parapenis with straight ventral process … 2
2 (1). Lateral pronotal face micropunctate; basivolsella without seta-filled pit, posteriorly

oblique. Indonesia, Malaysia … ***P. annexa*** (Cameron)
- Lateral pronotal face longitudinally striate; basivolsella with seta-filled pit, posteriorly rounded. China, Malaysia, Thailand, Vietnam … ***P. decora*** (Smith)

Promecilla annexa (Cameron, 1909), comb. nov.

Mutilla annexa Cameron, 1909: 146, ♂, holotype ♂ (Kuching, [Sarawak], Borneo, [Malaysia]) [NHMUK].
Smicromyrme annexa: Mickel, 1935: 284, ♂.
Andreimyrme annexa: Lelej, 2005: 39; Lo Cascio, 2015: 544; Pagliano *et al*., 2020: 169.

Zoobank LSID
urn:lsid:zoobank.org:act:267C6BD1-22C3-4D05-BDF2-20A19F7AB2D6

Material examined
7♂. **Indonesia:** GORONTALO: Pegunungan Tilongkabila, Bogani Nani Warta Bone N. P., 100 m alt., Malaise trap, 26.I–9.II.2009, K. Takasuka leg. [2♂ EUMJ], 9–20.II.2009 [3♂ EUMJ], 20.II–3.III.2009 [1♂ EUMJ]; Pegunungan Tilongkabila, Bogani Nani Warta Bone N. P., 100–500 m alt., 6–9.II.2009, K. Takasuka leg. [1♂ EUMJ].

Identification source
Keyed using Mickel (1935) and compared with the original description.

Sex association
Female unknown.

Distribution
Indonesia*: Gorontalo. Malaysia: Sabah, Sarawak (Cameron, 1909; Mickel, 1935).

Remarks
This species was placed in *Andreimyrme* by having the mandibular ventral margin lacking proximal tooth (Lelej, 2005). However, this species is here assigned to *Promecilla* by having the frons longitudinally striate, mandible slender, mandibular dorso-lateral carina weakly developed, mandibular ventral margin with a small proximal lobe, and F1 as long as wide.

Promecilla decora (Smith, 1879)

Mutilla decora Smith, 1879: 200, ♀, holotype ♀ (Pulo Penang [= Penang Island], [Penang], [Malaysia]) [NHMUK]; Cameron, 1892: 118; Dalla Torre, 1897: 30; André, 1902b: 39.
Smicromyrme decora: Pagden, 1934b: 465, ♂♀; Mickel, 1935: 288, ♀; Pagden, 1949: 222, ♂♀; Chen, 1957: 213, ♀; Lelej, 1995b: 19.
Smicromyrme contractula Chen, 1957, **syn. nov.**: 212, ♀, holotype ♀ (Hotien, Changting, Fukien [= Fujian], China) [TARI], examined.
Sinotilla contractula: Lelej, 1995b: 19; Lelej, 2005: 54; Hua, 2006: 300; Okayasu, 2017: 152, ♀; Okayasu *et al*., 2018: 303, ♀; Okayasu, 2020: 89; Pagliano *et al*., 2020: 186.
Sinotilla decora: Lelej, 2005: 55; Hua, 2006: 301; Okayasu, 2017: 152, ♀; Okayasu *et al*., 2018: 303, ♀.
Promecilla decora: Brothers & Lelej, 2017: 59, ♂♀; Barthélémy *et al*., 2018: 237, ♀; Williams *et al*., 2019b: 25, ♀; Pagliano *et al*., 2020: 183; Thaochan *et al*., 2022: 164,

♀.

Zoobank LSID
urn:lsid:zoobank.org:act:256F9F95-ABE6-4A6B-AEB1-20DAB1086C1A
urn:lsid:zoobank.org:act:B663229D-CB43-49E4-B959-9010DE561781

Material examined
21♂8♀. Holotype ♀, *Smicromyrme contractula* Chen: **China:** FUJIAN: Fukien [= Fujian], Changting, Hotien, 1.V.1941, T.C. Maa leg., *Smicrom*. *contractula* sp. nov. TYPE [probably Chen's hand], *Smicr*. *contractula* Chen [unknown hand] [TARI]. **China:** HONG KONG: Hong Kong, 7.V.26 [1♂ SEHU]. **Malaysia:** NEGERI SEMBILAN: Pasoh Forest Reserve, Coarse Malaise trap, plot 6, 26.XI–3.XII.1993, K. Maeto leg. [5♂ FRIM, NARO], 3–10.XII.1993 [3♂ FRIM, NARO], 10–17.XII.1993 [1♂ FRIM]; Pasoh Forest Reserve, Fine Malaise trap, plot 6, 3–10.XII.1993, K. Maeto leg. [2♂ FRIM, NARO]; Pasoh Forest Reserve, Fine Malaise trap, 10–17.XII.1993, K. Maeto leg. [1♂ NARO]. **Vietnam:** BAC KAN: Ba Be, Ba Be National Park, 22.23°N 105.37°E, 200 m alt., 2.V.2006, R. Matsumoto leg. [1♀ OMNH]; HOA BINH: Tonkin [= North Vietnam], Hoa Binh, A. de Cooman leg. [2♀ TARI]; VINH PHUC: Ngoc Thanh, Me Linh Biodiversity station, 21°23'01.7"N 105°42'40.7"E, 21–30.V.2020, MT, IED's coll. [1♂ IEBR]; Ngoc Thanh, Me Linh Biodiversity station, 22°16'51"N 105°71'54"E, 10.IV.2021, MT, IED [1♂ IEBR], 20.VIII.2021 [1♂ IEBR], 20.XI.2021 [1♂ IEBR]; Ngoc Thanh, Me Linh Biodiversity station, 70 m, 21°23'03"N 105°42'40"E, 18.VIII.2022, NTPL, TTN [1♀ IEBR]. **Thailand:** CHIANG MAI: Mae Rim, Nong Hoi, Malaise trap, 9–10.V.2002 [1♂ TUA]; Mae La Nong, Phrao, 400 m alt., 8.VIII.2001, T. Ishizaki leg. [1♂1♀ TUA]; Doi Pui, Ban Maeo, 1000 m alt., 9.VIII.2001, T. Ishikawa leg. [1♀ TUA]; Doi Suhtep, 750–850 m alt., 19.VIII.2001, T. Ishizaki leg. [1♂ TUA]; Omkoi District, Dry dipterocarp forest, 17°50'49.9"N 98°22'33.0"E, 950–1010 m alt., 16.VII.2017, R. Mizuno leg. [1♂ THNHM], 20.VII.2019 [1♀ THNHM].

Identification source
Compared with the description in Pagden (1949).

Sex association
This species was initially described from the female only. The male was associated by Pagden (1934b) based on males and a female emerged from nest cells of *Pison argentatum* Shuckard (Hymenoptera: Crabronidae) and a pair *in copula*, and described by Pagden (1949).

Distribution
China: Fujian, Hong Kong, Yunnan (Lelej, 2005). Malaysia: Kelantan, Kuala Lumpur, Negeri Sembilan*, Penang, Perak, Selangor (Pagden, 1934b, 1949; Smith, 1879; Williams *et al*., 2019b). Thailand: Chonburi, Krabi, Nakhon Si Thammarat, Phatthalung, Phetchabun, Phetchaburi, Surat Thani (Thaochan *et al*., 2022; Williams *et al*., 2019b). Vietnam: Bac Kan, Hoa Binh, Vinh Phuc.

This species was recorded from Myanmar (Kachin, Shan, Yangon; Magretti, 1892: 213) and Indonesia (Java; Zavattari, 1910: 9). These records were not accepted by Mickel (1935), but reexamination of voucher specimens is needed. One of the collecting sites, Omkoi District, was described by Mizuno *et al*. (2019).

Remarks
By having the pygidial plate smooth and convex, *Sm*. *contractula* is potentially a member of the genera *Ephucilla* or *Promecilla*, or *Sinotilla*. Chen (1957) described this species as having

a small indistinct scutellar scale and pygidial plate lacking lateral carinae. The presence of the scutellar scale and absence of lateral pygidial carinae were key features to separate *Sinotilla* from *Ephucilla* and *Promecilla*, and thus *Sm*. *contractula* was placed in *Sinotilla* by Lelej (1995b). The holotype of *Sm*. *contractula* does possess a scale on the mesosoma. Here, this process is not regarded as homologous to the scutellar scale of *Sinotilla* (now *Ephucilla*) but is homologized with a scale-like process occasionally observed in females of *Promecilla* (Williams *et al*., 2019b). Therefore, *Sm*. *contractula* is here placed in *Promecilla*, and the following character states provide additional support for the present taxonomic treatment: genal carina weak, wavy; hypostomal tooth present; clypeus with a subventral transverse flange; mandible slender; F1 longer than wide; prementum flat; mesosomal lateral margins convergent posteriorly; protarsal rake absent.

Within *Promecilla*, *Sm*. *contractula* and *P*. *decora* are distinguished from other congeners by having the following combination of character states: head black with sparse setae; frons and vertex with small confluent punctures; clypeus and scape yellowish red; mesosoma yellowish red, dorsally with sparse setae; legs largely reddish; T1 yellowish red; T2 black or obscurely blue metallic with an antero-medial golden setal spot; T2 with a posterior complete band of golden setae, medially triangularly widened; T3 with a complete band of golden setae; T2–3 yellow beneath setal bands; T4–5 with sparse black setae; S2 punctures large dense, separated by less than puncture diameter. Both species were previously included in *Smicromyrme*, and Chen (1957) distinguished *Sm*. *contractula* from *P*. *decora* by the mesosoma less convergent posteriorly, pronotum with one tooth dorso-laterally, and S2 with denser punctures. I compared the holotype of *Sm*. *contractula* with female specimens of *P*. *decora* and concluded that those characters did not deserve diagnoses to separate these nominal taxa because of variation. The mesosomal shape of *Sm*. *contractula* and *P*. *decora* largely overlaps; the pronotum (measured at pronotal spiracles) 1.08–1.15× wider than propodeum (measured at propodeal spiracles) in *P*. *decora*, while 1.12 in *Sm*. *contractula*. The holotype of *Sm*. *contractula* has the pronotal spiracle forming a rounded process and has a sharp process anteriorly to it, while *P*. *decora* has one of the following states: both processes sharp; pronotal spiracle rounded and with a sharp anterior process; both processes rounded. The S2 punctures were mostly separated by less than a puncture diameter in both species. Accordingly, *Sm*. *contractula* cannot be delimited morphologically from *P*. *decora*. I thus consider them as synonymous.

In addition to the morphological variation discussed above, this widespread species shows considerable variation in color, which was not described in the previous treatments (Pagden, 1949; Williams *et al*., 2019b): pedicel yellowish red to brown; F1 yellowish red to black; thoracic dorsum with pale golden to black short recumbent setae intermixed with long erect black setae; femoral apices light brown to dark brown; tibiae dorsally brown to entirely dark brown; tarsi yellowish red to dark brown; T2 antero-medial spot circular and densely setose to subovate and obscure; S2–3 black, sometimes with posterior margin reddish on S2 or both S2 and S3.

The collecting sites of this species, Pasoh Forest Reserve and Omkoi District, was described by Maetô *et al*. (1999) and Mizuno *et al*. (2019).

Promecilla levinaris **(Chen, 1957)**

Smicromyrme levinaris Chen, 1957: 207, ♂, holotype ♂ (Yungan [= Yong'an], Fukien [= Fujian], China) [TARI], examined; Lelej, 2005: 61; Hua, 2006: 301.
Promecilla levinaris: Zhou *et al*., 2018a: 26, ♂; Pagliano *et al*., 2020: 183.

Zoobank LSID

urn:lsid:zoobank.org:act:99AB8A2B-15C3-48BB-9EF8-1B1596ADD59E

Material examined
1♂. Holotype ♂: **China:** FUJIAN: Fukien [= Fujian], Yungan [= Yong'an], Siyingpan, light, T.C. Maa leg., *Smicromyrme levinaris* Chen [unknown hand] [TARI].

Identification source
Primary type.

Sex association
Female unknown.

Distribution
China: Guangdong, Guizhou, Fujian, Yunnan (Zhou *et al*., 2018a).

Remarks
The holotype of this species is deposited in TARI and has appropriate labels. The paratype of this species is probably deposited in ZMUC. This is the only species of *Promecilla* s. str. in East Asia.

Genus *Sinotilla* Lelej, 1995

Sinotilla Lelej, 1995b: 18, ♂; Lelej, 2005: 54; Lelej, 2007: 89; Lelej & Brothers, 2008: 55; Brothers & Lelej, 2017: 96; Okayasu, 2020: 87, ♂; Pagliano *et al*., 2020: 186; Lelej & Williams, 2023: 125, ♂. Gender feminine.

Zoobank LSID
urn:lsid:zoobank.org:act:00A7AEE2-AB00-4546-8686-1450DCB792CA

Type species
Mutilla dardanus Smith, 1857, ♂, designated here. Lelej (1995b) originally designated *Smicromyrme cyaneiventris boheana* Chen, 1957 (currently *Si*. *boheana*) as the type species. However, this species is here synonymized with *Si*. *dardanus* (new combination), which is fixed as the type species of *Sinotilla* under Article 70.3.2 of the code (ICZN, 1999). The voucher specimen of *Si*. *boheana* identified by Lelej (1995b) was illustrated in Lelej & Williams (2023: Fig. 74). It was conspecific with *Si*. *dardanus*. The holotype of *Si*. *boheana* was not found despite of 15-day survey in TARI where Chen's holotypes are presently deposited. This species, however, is quite possibly a junior synonym of *Si*. *dardanus* because this is the only smicromyrmine species in China with the mesosoma mostly red and legs partially yellowish red.

Diagnosis
MALE. Frons longitudinally striate; vertex elevated beyond ocellar region; ventral clypeal margin entire; mandible apex bidentate, internal tooth smaller than apex, without subdistal internal tooth; mandible dorso-lateral carina weakly developed; mandible ventral margin emarginate with large proximal tooth or not emarginate with small proximal lobe; flagellomere apices truncate; F1 distinctly shorter than wide; notaulus present on posterior part of mesoscutum or obliterated; parascutal carina forming weak process; tegula rounded posteriorly or projecting posterad or postero-laterad, slightly surpassing transscutal articulation; mesopleuron evenly convex, lacking transverse impression; mesopleuron ventral

face lacking process; procoxa lacking posterior process; metacoxal internal carina weakly developed or lamellately projecting posteriorly; S2 with lateral felt line, sometimes obliterated; harpe dorso-internal margin lacking proximal process; parapenis bifid or oblong; gonostipes ventral lobe projecting posterad; basivolsella elongate depressed, subovate, or rectangular, with short setae on ventral margin; basivolsella internal face with or without seta-filled pit; basiura expanded ventrad; apiceps long slender; penisvalva strongly expanded ventrad or slender; penisvalva posterior process with or without external process; penisvalva internal face lacking setae.

FEMALE. Unknown.

Species included

A total of 19 species and one subspecies is recognized in this genus: *S. ansula* (Chen, 1957), ♂ (China); *S. coeruleotincta* (Cameron, 1900), ♂ (India); *S. columnata* (Chen, 1957), ♂ (China); *S. complanata* **sp. nov.**, ♂ (Thailand, Vietnam); *S. dardanus* (Smith, 1857), ♂ (China, Indonesia, Laos, Malaysia, Thailand, Vietnam); *S. drola drola* (Zavattari, 1913), ♂ (Taiwan); *S. drola lodra* (Chen, 1957), ♂ (China); *S. gracillima* (Smith, 1857), ♂ (Malaysia); *S. hong* Lelej, 1995, ♂ (China, Vietnam); *S. ilerda* (Cameron, 1902), ♂ (Malaysia); *S. jambar* Okayasu, 2020, ♂ (Japan); *S. nitela* (Mickel, 1934), ♂ (Indonesia, Philippines); *S. runcina* (Zavattari, 1914), ♂ (Indonesia, Malaysia); *S. scitula* (Mickel, 1935), ♂ (Malaysia); *S. serpa* (Zavattari, 1913), ♂ (Taiwan); *S. sparsilis* (Mickel, 1934), ♂ (Philippines); *S. trisecta* (Chen, 1957), ♂ (China); *S. unica* **sp. nov.**, ♂ (China, Vietnam); *S. viriata* (Mickel, 1934), ♂ (Philippines); *S. volupia* (Mickel, 1935), ♂ (Malaysia).

Sex association

The type species is known from the male only. The genus concept for female *Sinotilla* (Lelej, 1995b, 1996b, 2002, 2005; Lelej & Williams, 2023; Okayasu, 2017, 2020; Okayasu *et al*., 2018; Williams *et al*., 2019b) was based on the sex association of *Si. cyaneiventris*. This species is assigned to *Ephucilla* based on the male morphology. Remaining female-based species were transferred to *Ephucilla* as well.

Distribution

Oriental and Palaearctic Regions.

Remarks

This genus was recovered as a monophyletic group under all settings with low GC score (GC = 35; Fig. 22-3), supported by two unique synapomorphies: F1 length less than its width (37:1) and basiura expanded ventrad (115:2). Sister relationship of the *Ephucilla* and *Sinotilla* was suggested in most analyses.

Within *Sinotilla*, the type species, *S. dardanus*, and closely related *S. drola* and its subspecies possess a number of unique features showing apparent apomorphic states: occiput lacking an internal process (19:1), notaulus obliterated (47:3), T1 ventro-lateral margin densely micropunctate (77:1), parapenis oblong (107:3), basivolsella elongate, depressed (114:1), penisvalva slender, armed with an external process (118:2). This group was found monophyletic with high resampling support (GC = 99; Fig. 22-3) and three unique synapomorphies (77:1; 107:3; 118:2). Even though this group is clearly differentiated from others, those three species were consistently nested in *Sinotilla*, presumably because the rest *Sinotilla* species lacked shared apomorphic character states. Discovery of females for *Sinotilla* will aid in clarifying phylogenetic relationship within the genus and recognition of a separate genus.

The basivolsellar shape of the species of *Sinotilla* (excluding the type species and its

kin) and *Smicromyrme* is superficially similar. However, the basivolsella of *Sinotilla* is proximally expanded dorsad, while that of *Smicromyrme* has the dorsal and ventral margins subparallel. For phylogenetic analyses, the parossiculus shape of those genera was coded as identical state (114:3).

Key to the East Asian species of *Sinotilla* based on the male morphology

1. Notaulus obliterated; T1 ventro-lateral margin densely micropunctate; parapenis oblong; basivolsella elongate depressed; penisvalva slender; penisvalva posterior process with external process … 2
- Notaulus present; T1 ventro-lateral margin smooth; parapenis bifid; penisvalva strongly expanded ventrad; basivolsella subovate or rectangular; penisvalva posterior process lacking external process … 4
2 (1). Mesosoma red except propleuron and ventral portion of mesopleuon black. China, Indonesia, Laos, Malaysia, Thailand, Vietnam … ***S. dardanus*** (Smith)
- Mesosoma red except propleuron, ventral portion of mesopleuron, metapleuron, and propodeum black … 3
3 (2). Legs entirely dark brown to black. Taiwan … ***S. drola drola*** (Zavattari)
- Legs black with protibia and meso- and metatibial external faces orange. China … ***S. drola lodra*** (Chen)
4 (2). Mandible ventrally emarginate with large proximal tooth; basivolsella slender … 5
- Mandible ventrally with small proximal lobe; basivolsella broad … 7
5 (4). POL/OOL = 1.06–1.17; mesoscutellum black; metacoxal internal carina lamellately projecting posteriorly; tibiae black; harpe laterally weakly convex; parapenis with posterior process rectangular and anterior lobe broad, rounded; apiceps slender; penisvalva external face lacking flange. China, Vietnam … ***S. unica*** **sp. nov.**
- POL/OOL ≤ 0.65; mesoscutellum red; metacoxal internal carina weakly developed; protibia entirely and meso- and metatibiae basally orange; harpe laterally strongly convex on anterior 1/3; parapenis with posterior process slender and anterior process angulate; apiceps robust; penisvalva external face with vertical carina along anterior process … 6
6 (5). Clypeus with distinct medial longitudinal carina extending over midpoint of clypeus; anterior process of parapenis scarcely developed. China … ***S. ansula*** (Chen)
- Clypeus without medial carina; anterior process of parapenis triangular, pointed. Thailand, Vietnam … ***S. complanata*** **sp. nov.**
7 (4). Clypeal subventral transverse flange medially widely interrupted, leaving sublateral rounded tubercle … 8
- Clypeal subventral transverse flange complete … 11
8 (7). Mesosoma red except propleuron and mesopleural ventral face black; T3 entirely covered with dense appressed pale setae. China, Vietnam … ***S. hong*** Lelej
- Mesosoma at least with meso- and metapleura and propodeum black; T3 posteriorly fringed with appressed pale setae … 9
9 (8). Tegula weakly projecting postero-laterad, slightly surpassing transscutal articulation; metasoma blue metallic; T1–3 with sparse posterior pale setal fringe. Japan … ***S. jambar*** Okayasu
- Tegula projecting posterad, reaching posterior 1/2 of mesoscutellum; metasoma black; T1–3 with dense posterior pale setal fringe … 10
10 (9). Mesoscutellum red. China … ***S. columnata*** (Chen)
- Mesoscutellum black. Taiwan … ***S. serpa*** (Zavattari)
11 (7). POL/OOL ≥ 0.8; metacoxal internal carina lamellately projecting posteriorly … 12
- POL/OOL ≤ 0.75; metacoxal internal carina weakly developed … 13

12 (11). Metasoma blue metallic; parapenis with anterior process rounded. Indonesia, Philippines … ***S. nitela*** (Mickel)
- Metasomal segments 1–3 red and posteriorly black; parapenis with anterior process pointed. Philippines … ***S. viriata*** (Mickel)
13 (11). Frons with strong longitudinal carina anteriorly to lateral ocellus … 14
- Frons with obscure longitudinal carina … 17
14 (13). Mesosoma black, contrasting to orange tegula; metasomal segments 1–2 red. China … ***S. trisecta*** (Chen)
- Mesosoma partially red, nearly concolorous with tegula; metasoma blue metallic … 15
15 (14). Propodeum entirely black; T3 with sparse recumbent to erect pale setae. Malaysia … ***S. scitula*** (Mickel)
- Propodeum dorsally red; T3 with pale setal band … 16
16 (15). Pronotal dorsum with deep, confluent punctures, with puncture intervals reduced; mesoscutum with confluent punctures. Malaysia … ***S. ilerda*** (Cameron)
- Pronotal dorsum with shallow, obscurely defined punctures, with puncture intervals distinct; mesoscutum with dense but separated punctures. Philippines … ***S. sparsilis*** (Mickel)
17 (13). Scape, pedicel, profemur, protibia, and mesofemur orange; mesosoma entirely red; parapenis with anterior process reduced; basivolsella with seta-filled pit at midpoint. Malaysia … ***S. gracillima*** (Smith)
- Scape, pedicel, and legs dark; mesosoma at least ventrally black; parapenis deeply bifid, with developed anterior and posterior processes; basivolsella with seta-filled pit near apex … 18
18 (17). Propodeum black; metasoma black; basivolsella posteriorly sharp and widest near base, giving triangular appearance. Indonesia, Malaysia … ***S. runcina*** (Zavattari)
- Propodeum dorsally red and ventrally black; T1–2 and S2 blue metallic; basivolsella posteriorly rounded and widest at anterior 1/3, giving subovate appearance. Malaysia … ***S. volupia*** (Mickel)

Sinotilla ansula (Chen, 1957)

Smicromyrme ansula Chen, 1957: 204, ♂, holotype ♂ (Tienmushan [= Tianmushan], Chekiang [= Zhejiang], China) [TARI], examined; He *et al*., 2004: 944, ♂.
Sinotilla ansula: Lelej, 1995b: 19; Lelej, 2005: 56; Hua, 2006: 300; Pagliano *et al*., 2020: 186.

Zoobank LSID
urn:lsid:zoobank.org:act:0252C874-736C-4541-BD09-FEB7C6E7DE64

Material examined
3♂. Holotype ♂: **China:** ZHEJIANG: [Lin'an, Hangzhou], Tianmu-shan, 15.IX.1947 [TARI]. Paratypes: **China:** ZHEJIANG: [Lin'an, Hangzhou], Tianmu-shan, 15.IX.1947 [2♂ TARI].

Identification source
Primary type.

Sex association
Female unknown.

Distribution

China: Zhejiang.

Remarks
The holotype of this species is deposited in TARI and has appropriate labels.

Sinotilla columnata (Chen, 1957)

Smicromyrme columnata Chen, 1957: 205, ♂, holotype ♂ (Kuling [= Guling], [Lushan, Jiujiang], Kiangsi [= Jiangxi], China) [TARI], examined; Lelej, 2005: 58; Hua, 2006: 301.
Sinotilla serpa columnata: Okayasu, 2018: 490, ♂; Okayasu, 2020: 89, ♂; Pagliano *et al*., 2020: 187.

Zoobank LSID
urn:lsid:zoobank.org:act:30658FAF-7E4E-4738-A610-2B6193FD6A9C

Material examined
5♂. Holotype ♂: **China:** JIANGXI: Kiangsi [= Jiangxi], [Lushan, Jiujiang], Kuling [= Guling], 21.9.34, O. Piel leg. [TARI]. Paratypes: **China:** JIANGXI: Kiangsi [= Jiangxi], [Lushan, Jiujiang], Kuling [= Guling], 17.9.34, O. Piel leg. [1♂ TARI], 18.9.34 [1♂ TARI]; Kiangsi [= Jiangxi], Kwangche, Chien-Men, 22–23.VIII.1943, T.C. Maa leg. [1♂ TARI]. **China:** JIANGXI: Kiangsi [= Jiangxi], Kwangshe, Chienmen, 22–23.VIII.1945, T.C. Maa leg., *Smicromyrme columnata* [probably Chen's hand] [1♂ TARI].

Identification source
Primary type.

Sex association
Female unknown.

Distribution
China: Jiangxi.

Remarks
This species differs from *S. serpa* only by the mesoscutellum color and even the male genitalia are not useful to discriminate them. Okayasu (2018) downgraded this species as a subspecies of *S. serpa*. The color trait is consistent among the specimens examined herein and, in the present study, *S. columnata* is treated as a full species to simplify the taxonomy, approach adopted in recent taxonomic papers (e.g., Lelej, 2005; Williams *et al*., 2019b).

Sinotilla complanata sp. nov.

Zoobank LSID
Unavailable.

Diagnosis
MALE. Frons lacking longitudinal carina anteriorly to lateral ocellus; POL/OOL = 0.594–0.623; clypeus lacking medial carina; clypeal subventral transverse flange complete; mandible ventrally emarginate with large proximal tooth; scape and pedicel dark; mesosoma red with propleuron, mesopleuron ventral 1/2, metapleuron ventral 2/3, and propodeum

black; pronotal dorsum with large confluent punctures; mesoscutum with large dense punctures; notaulus present on posterior 1/4 of mesoscutum; tegula projecting posterad; legs dark with pro- and mesofemoral apices, protibia, and meso- and metatibiae basal 1/2 orange; metacoxal internal carina weakly developed; metasoma black; T1–3 with dense posterior golden setal fringe; T3 with sparse erect golden setae; parapenis with posterior process slender and anterior process triangular; basivolsella slender subovate, with deep seta-filled pit at midpoint; apiceps robust; penisvalva strongly expanded ventrad; penisvalva lacking external process on posterior process; penisvalva external face with vertical carina along anterior process.

FEMALE. Unknown.

Description

MALE. Body length: 5.94–11.3 mm (holotype 11.3 mm); forewing length: 4.31–8.19 mm (holotype 8.19 mm).

Color and setae. Frons, vertex, gena, clypeus, mandible except subdistal 1/4, F1 dorsally, F2–11, propleuron, mesopleuron ventral 1/2, metapleuron ventral 2/3, propodeum, and metasoma black; postgenal bridge, prementum, stipes, and coxae brownish black to black; antennal rim, mandible subdistal 1/4, pedicel dorsally, and trochanters dark brown; scape except apex dark brown to brownish black; scape apex, tegula, pro- and mesofemoral apices, protibia, and meso- and metatibiae proximal 1/2 orange; pedicel ventrally orange to brown; F1 ventrally orange to dark brown; maxillary and labial palpi and protibial spur brown; pronotum, mesoscutum, mesoscutellum, metascutellum, meso- and metanotal troughs, mesopleuron dorsal 1/2, and metapleuron dorsal 1/3 yellowish red; pro- and mesofemora except apices, metafemur, meso- and metatibiae distal 1/2, and tarsi dark brown to black; meso- and metatibial spurs yellowish white. Frons with sparse short appressed and sparse long erect golden setae; vertex, mandible, pronotal dorsum, mesoscutellum, metascutellum, T1–4, T5 except posterior margin, S1, and S3–5 with sparse long erect golden setae; gena, postgenal bridge, propodeum, trochanters, femora, tibiae, and S2 with sparse short recumbent and sparse long erect golden setae; clypeus, propleuron, and coxae with sparse long appressed pale golden and sparse long erect golden setae; scape with sparse long recumbent and sparse long erect golden setae; pedicel with dense short recumbent golden setae; flagellum with dense erect golden microsetae; prementum, stipes, and maxillary and labial palpi with sparse short erect golden setae; lateral pronotal face and metapleuron dorsal 2/3 with sparse short appressed pale golden setae; mesoscutum and tegula with sparse long erect dark golden setae; meso- and metanotal troughs with dense short appressed pale golden setae; mesopleuron and metapleuron ventral 1/3 with sparse short appressed pale golden and sparse long erect golden setae; tibiae with sparse long recumbent and sparse long erect golden setae; tarsi with sparse long appressed golden setae; T5 posterior margin, T6–7, and S6–8 with sparse long erect black setae; T2 lateral felt line golden, 0.45× T2 length; S2 lateral felt line golden, 0.15× S2 length; T1–3 with dense posterior fringe of golden setae; S2–4 with sparse posterior fringe of golden setae; S5 with sparse posterior fringe of black setae.

Structure. Head width 1.61–1.67× length (holotype 1.61); lateral margins strongly convergent behind eye, posterolateral angle rounded; vertex elevated, sharply sloping posteriorly; minimum distance between eyes 1.00–1.02× eye height (holotype 1.00); POL/OOL = 0.594–0.623 (holotype 0.608); MOD:LOD:LOL:POL = 1.00:0.6888–0.750:0.938–1.00:1.90–2.06 (holotype 1.00:0.688:0.938:1.94); ocellar region convex; median ocellus with posterior longitudinal carina; frons with shallow medial longitudinal sulcus, lacking longitudinal carina anteriorly to lateral ocellus; occipital carina sharp, complete; internal eye margin deeply emarginate; antennal scrobal carina V-shaped, widely separated from internal eye margin; antennal rim convex; antennal rims separated by approximate

antennal rim width; gena lacking vertical carina; postgenal bridge flat; hypostomal carina sharp, not projecting; malar space developed, ventral eye margin and mandibular base separated; clypeus subconvex, with subventral complete transverse flange overhanging ventral clypeal margin; clypeal dorso-medial portion elevated into simple carina; mandible slender, narrowed to apex; mandible apex bidentate, internal tooth as large as apex; mandibular internal margin entire; mandibular dorso-lateral carina sharp; mandibular ventral margin emarginate with large proximal tooth; prementum with two parallel carinae on dorsal 1/2; scape with two sharp subparallel carinae, separated by 0.6× scape width; F1 cylindrical; length and width of pedicel:F1:F2 = 1.00:1.22–1.54:1.11–1.40:1.56–1.90:2.33–2.90:1.67–2.00 (holotype 1.00:1.50:1.40:1.90:2.90:2.00); flagellomere apices truncate.

Mesosoma widest at mesonotum including tegulae; antero-dorsal pronotal margin nearly straight; humeral angle weakly angulate; humeral carina sharp, not reaching pronotal dorsum; mesoscutum weakly convex; tegula short, projecting posterad, not flex, reaching mesoscutellum; tegula length 1.59–1.79× width (holotype 1.67); notauli weakly convergent posteriorly, present on posterior 1/4 of mesoscutum, posteriorly widened; parapsidal signum short, linear; parascutal carina forming weak process on posterolateral angle of mesoscutum; transscutal impression arcuate; mesoscutellum weakly convex; mesopleuron convex, lacking transverse impression; ventral mesopleural face without longitudinal impunctate line, process, and swelling; mesocoxal foramen without transverse precoxal carina; metathoracic spiracle oval; metasternum much shorter than coxal height; propodeal length 1.06–1.15× pronotal + mesoscutal length (holotype 1.15); posterior propodeal face oblique, without distinct dorsum; propodeal sublateral longitudinal carina absent; propodeal dorso-lateral margin rounded, lacking longitudinal carina; lateral margins of propodeum convergent posteriorly.

Wings fully developed; distance between origin of RS on vein SC and proximal margin of pterostigma 1.22–1.54× pterostigma length (holotype 1.22); forewing cell 2RS present.

Procoxa lacking posterior process; meso- and metacoxae evenly convex; metacoxa with internal longitudinal carina weakly developed; protibial spur slender; tibiae without external spines.

Metasomal segment 1 slender, subsessile; T1 width:T2 width:T2 length = 0.54–0.62:1.00:0.67–0.73 (holotype 0.62:1.00:0.73); T1 oblique, without distinct dorsum; T1 spiracle projecting; T2 evenly convex; S1 with medial longitudinal carina on anterior 3/4, straight in profile; S2 evenly convex, lacking antero-medial longitudinal carina; T3–6 not constricted; T7 evenly convex, with posterior margin rounded; S6–8 flat, lacking lateral carina or process; S7 posterior margin truncate; S8 mostly sclerotized with posterior membranous area evenly convex posteriorly. Harpe depressed laterally, down-curved; harpe dorso-internal margin lacking process; harpe expanded laterally on anterior 1/2; harpe ventral margin with sparse short erect setae; gonostipes much longer than wide and as long as harpe; gonostipes ventro-medial lobe not forming posterior process; gonostipes ventral lobe projecting posterad; parapenis deeply bifid, with distinct anterior and posterior processes; anterior process of parapenis triangular, pointed; posterior process of parapenis slender, elongate, flexed outward; cupula much shorter than gonostipes; basivolsella slender subovate, depressed, without cuspis; basivolsella apex hardly reaching posterior 1/2 of harpe and surpassing penisvalva by 1/3× basivolsella length; basivolsella with large deep seta-filled pit, with sparse long erect setae on internal face and ventral margin; basiura strongly sclerotized with robust apiceps and few long erect setae; penisvalvae symmetrical; penisvalva broad, expanded ventrad, with distinct anterior and posterior ventral processes; penisvalva lacking setae; endophallus membranous.

Frons and vertex densely longitudinally striate; gena and pronotal dorsum with large

confluent punctures; postgenal bridge transversely rugose; clypeus, lateral pronotal face, metapleuron dorsal 2/3, procoxa, trochanters, meso- and metafemora, tibiae, and tarsi with minute sparse punctures; scape, metascutellum, T3–6, and S3–8 with small dense punctures; pedicel, flagellum, prementum, stipes, maxillary and labial palpi, and meso- and metanotal troughs with minute dense punctures; propleuron with minute dense and small sparse punctures; mesoscutum, mesoscutellum, mesopleuron, metapleuron ventral 1/3, and T2 lateral margin with large dense punctures, separated by ~0.5× puncture diameter; tegula, meso- and metacoxae, and profemur with small sparse punctures; propodeum reticulate, with medial subtriangular and sublateral semicircular cell on anterior margin; T1 except posterior margin, T2 disc, and S1–2 with large sparse punctures; T1 posterior margin with small dense and minute dense punctures; T7 with small dense punctures and posteromedial slender impunctate line.

FEMALE. Unknown.

Material examined

4♂. Holotype ♂: **Thailand:** CHIANG MAI: Mae Rim, Nong Hoi, 970–1000 m alt., 21.V.2002, T. Ishizaki leg. [TUA]. Paratypes: **Thailand:** CHIANG MAI: Doi Mae Tho, 20.V.2002, K. Okajima leg. [1♂ TUA]; Mae Rim, Nong Hoi, 970–1000 m alt., 22.V.2002, T. Ishizaki leg. [1♂ TUA]. **Vietnam:** GIA LAI: Mang Yang, Kon Ka Kinh NP, 14°12'11"N 108°18'58"E, 834 m, 19.V–3.VI.2022, MT, L.V. Tinh leg. [1♂ IEBR].

Sex association

Female unknown.

Distribution

Thailand: Chiang Mai. Vietnam: Gia Lai.

Etymology

The specific name *complanata*, flattened, is the Latin, singular, feminine perfect passive participle in the nominative case. It refers to the clypeus without a medial carina, which distinguishes this new species from the most closely related *S. ansula*.

Remarks

This species shares many diagnostic features with *S. ansula*. They were found sister in phylogenetic analyses under all settings. This new species is distinguished from *S. ansula* by having the clypeus lacking medial carina (with distinct medial carina in *S. ansula*) and parapenis with anterior process distinctly projecting (anterior process weakly developed in *S. ansula*).

Sinotilla dardanus (Smith, 1857), comb. nov.

Mutilla dardanus Smith, 1857: 86, ♂, holotype ♂ (Sarawak, Borneo, [Malaysia]) [OUMNH]; Cameron, 1892: 118; Dalla Torre, 1897: 30; André, 1896: 13, ♂; André, 1902b: 39.

Mutilla gracillima (non Smith, 1857): Zavattari 1914: 92, ♂.

Smicromyrme dardanus dardanus: Mickel, 1935: 282, ♂; Lelej, 2005: 58; Lo Cascio, 2015: 558; Pagliano *et al*., 2020: 194.

Smicromyrme dardanus salacia Mickel, 1935, **syn. nov.**: 282, ♂, holotype ♂ (Samawang, near Sandakan, [Sabah], N. Borneo, [Malaysia]) [NHMUK], examined; Lelej, 2005: 58; Lo Cascio, 2015: 558; Pagliano *et al*., 2020: 194.

Smicromyrme zavattarii Mickel, 1935 (non Invrea, 1932): 282, ♂, holotype ♂ (Bandjermasin

[= Banjarmasin], [Kalimantan Selatan], Borneo, [Indonesia]) [MSNG]; Mickel, 1937: 450, ♂.

Smicromyrme gribodoana Invrea, 1943, **syn. nov.**: 193, ♂; Hammer, 1962: 44. New name for *Smicromyrme zavattarii* Mickel.

Smicromyrme cyaneiventris boheana Chen, 1957, **syn. nov.**: 204, ♂, holotype ♂ (Tachulan [= Dazhulan], Shaowu, Fukien [= Fujian], China) [probably ZMUC].

Sinotilla boheana: Lelej, 1995b: 19, ♂; Lelej, 2005: 54; Hua, 2006: 300; Lelej & Brothers, 2008: 55; Okayasu, 2017: 152; Okayasu, 2020: 89; Pagliano *et al*., 2020: 186; Pagliano & Scaramozzino, 2021: 112, ♂; Lelej & Williams, 2023: 105, ♂.

Sinotilla gribodoana: Lelej, 1996b: 97, ♂, examined; Lelej, 2005: 55; Okayasu, 2017: 152; Lo Cascio, 2015: 557; Pagliano *et al*., 2020: 186.

Zoobank LSID

urn:lsid:zoobank.org:act:CA30956A-29DC-4C08-AB98-EAAE232399D3
urn:lsid:zoobank.org:act:1B09E583-D2A7-4022-9949-753FC21B62FB
urn:lsid:zoobank.org:act:E7C4FF05-0FCB-4A74-AAA2-85C07C9125D3
urn:lsid:zoobank.org:act:AF51DAD6-EA33-4441-B6B9-D801413920C5

Material examined

57♂. Holotype ♂, *Smicromyrme dardanus salacia* Mickel: **Malaysia:** SABAH: Samawang near Sandakan, 10.VII.1927 [NHMUK]. **China:** HAINAN: near Jianfengling, 19.V.2009, H. Kurokawa leg. [1♂ MTC]. **Indonesia:** BANGKA BELITUNG: Beliteng [= Belitung] Is. near Sumatra, 20–25.XII.2002, Y. Nishiyama leg. [1♂ KMNH]; KALIMANTAN TIMUR: Bukit Soeharto, 13–17.III.1994, K. Matsumoto & K. Konishi leg. [1♂ NARO]; Bukit Soeharto, Malaise trap, 13–17.III.1994, K. Konishi leg. [1♂ NARO], 17–26.III.1994 [1♂ NARO]; SUMATRA SELATAN: Benakat, Light trap, 13.XII.1992, S. Yoshimatsu & K. Matsumoto leg. [1♂ NARO]. **Laos:** XIENG KHOUANG: 25 km Southeast Ban Ban, Hot Spring, Yellow pan trap, 19°33'24.09"N 103°41'26.17"E, 568 m alt., 28.IV–4.V.2015, T. Mita leg. [1♂ ELKU]; 25 km Southeast Ban Ban, Hot Spring, 19°33'24.09"N 103°41'26.17"E, 568 m alt., 29.IV.2015, T. Mita leg. [1♂ ELKU]. **Malaysia:** NEGERI SEMBILAN: Pasoh Forest Reserve, 28.IX.1986, Y. Miyatake leg. [1♂ OMNH]; Pasoh Forest Reserve, Coarse Malaise trap, plot 1, 25.III–2.IV.1993, K. Konishi & K. Maeto leg. [1♂ FRIM], 2–8.IV.1993 [1♂ NARO]; Pasoh Forest Reserve, Coarse Malaise trap, plot 4, 26.III–3.IV.1993, K. Konishi & K. Maeto leg. [4♂ FRIM, NARO], 3–9.IV.1993 [2♂ FRIM, NARO], 9–16.IV.1993 [2♂ FRIM, NARO]; Pasoh Forest Reserve, Fine Malaise trap, plot 4, 26.III–3.IV.1993, K. Konishi & K. Maeto leg. [2♂ FRIM, NARO]; Pasoh Forest Reserve, Fine Malaise trap, plot 1, 2–8.IV.1993, K. Konishi & K. Maeto leg. [1♂ FRIM], 8–15.IV.1993 [1♂ NARO]; Pasoh Forest Reserve, Fine Malaise trap, plot 2, 2–8.IV.1993, K. Konishi & K. Maeto leg. [1♂ FRIM]; Pasoh Forest Reserve, Coarse Malaise trap, plot 5, 9–16.IV.1993, K. Konishi & K. Maeto leg. [1♂ NARO]; Pasoh Forest Reserve, Coarse Malaise trap, plot 1, 26.XI–3.XII.1993, K. Maeto leg. [4♂ FRIM, NARO], 3–10.XII.1993 [4♂ FRIM, NARO], 10–17.XII.1993 [1♂ FRIM]; Pasoh Forest Reserve, Coarse Malaise trap, plot 3, 26.XI–3.XII.1993, K. Maeto leg. [1♂ NARO]; Pasoh Forest Reserve, Coarse Malaise trap, plot 4, 26.XI–3.XII.1993, K. Maeto leg. [1♂ FRIM], 10–17.XII.1993 [1♂ NARO]; Pasoh Forest Reserve, Coarse Malaise trap, plot 6, 26.XI–3.XII.1993, K. Maeto leg. [2♂ FRIM, NARO], 3–10.XII.1993 [4♂ FRIM, NARO]; Pasoh Forest Reserve, Fine Malaise trap, plot 6, 26.XI–3.XII.1993, K. Maeto leg. [1♂ FRIM], 10–17.XII.1993 [1♂ NARO]; Pasoh Forest Reserve, Fine Malaise trap, plot 1, 3–10.XII.1993, K. Maeto leg. [1♂ FRIM]; Pasoh Forest Reserve, Coarse Malaise trap, plot 5, 3–10.XII.1993, K. Maeto leg. [1♂ NARO]; SARAWAK: Lambir, Miri, Canopy Biology Prog. Malaise trap Gap, 1–3.XII.1992, A0149, *Sinotilla gribodoana*

(Invrea), A. Lelej det. 1995 [1♂ SKYC]. **Thailand:** CHIANG MAI: Doi Mae Tho, 20.V.2002, T. Tsuru leg. [1♂ TUA]; Mae Rim, Nong Hoi, 970–1000 m alt., 22.V.2002, T. Ishizaki leg. [1♂ TUA]; Mae Rim, Nong Hoi, 970–1000 m alt., 23.V.2002, K. Okajima leg. [1♂ TUA]; Mae Rim, Nong Hoi, 970–1000 m alt., 30.V.2002, T. Tsuru leg. [1♂ TUA]. **Vietnam:** THUA THIEN HUE: Bach Ma N[ational]P[ark], Entrance, 16.250°N 107.873°E, 50 m alt., 253/BTTNVN, Yellow pan trap, 2–5.VIII.2016, T. Mita leg. [1♂ VNMN]; Bach Ma N[ational]P[ark], Rhododendron trail, 16.192°N 107.849°E, 1100 m alt., 253/BTTNVN, Yellow pan trap, 3–6.VIII.2016, Y. Komeda & T. Mita leg. [1♂ VNMN]; Bach Ma N[ational]P[ark], Rhododendron trail, 16.192°N 107.849°E, 1100 m alt., 253/BTTNVN, sweeping, 5.VIII.2016, Y. Komeda leg. [1♂ VNMN]; VINH PHUC: Tam Dao, 500 m alt., 24.V.1997, R. Matsumoto leg. [1♂ OMNH].

Identification source
Voucher specimen (Mickel, 1935).

Sex association
Female unknown.

Distribution
China: Fujian, Hainan*, Yunnan (Chen, 1957; Lelej, 1995b). Indonesia: Bangka Belitung*, Kalimantan Selatan, Kalimantan Timur, Sumatra Selatan* (Zavattari, 1914). Laos: additional data unavailable (Pagliano & Scaramozzino, 2021), Xieng Khouang*. Malaysia: Negeri Sembilan*, Sabah, Sarawak. Thailand*: Chiang Mai. Vietnam: Hoa Binh, Thua Thien Hue*, Vinh Phuc* (Lelej, 1995b).

Remarks
This species is here designated as the type species of *Sinotilla* as discussed above. Extensive museum surveys revealed that this species is fairly widespread in East Asia and morphologically variable. *Smicromyrme dardanus salacia* was separated from the nominotypical subspecies by having the scape entirely pale ferruginous. In Mickel's (1935) treatment, *Si*. *gribodoana* (as *Sm*. *zavattarii*) was separated from *Si*. *dardanus* by having the metasomal segments 1–2 dark blue metallic (black in *Si*. *dardanus*). However, these color traits appeared to be intraspecific variation of this widespread species after examination of 56 male specimens. No additional characters supporting the status of the color variants as separate taxa were found. Therefore, they are regarded as junior synonyms of *Si*. *dardanus*. Three specimens from Thailand and Vietnam have a seta-filled pit on basivolsella. This pit is also regarded as variation given the case of *M*. *caecina*, *M*. *exiloides*, and *S*. *drola lodra*.

One of the collecting sites of this species, Pasoh Forest Reserve, was described by Maetô *et al*. (1999).

Sinotilla drola drola (Zavattari, 1913), comb. nov.

Mutilla drola Zavattari, 1913: 37, ♂, lectotype ♂ (Taihorin [= Dalin], [Chiayi], Formosa [= Taiwan]) [ZMHB], designated by Mickel (1933a: 417), examined.
Smicromyrme drola: Mickel, 1933a: 417, ♂; Suzuki, 1934: 25; Mickel, 1935: 282, ♂; Tsuneki, 1993a: 39, ♂.
Smicromyrme drola drola: Chen, 1957: 203, ♂, examined.
Smicromyrme hombuceiana Tsuneki, 1982, **syn. nov.**: 43, ♂, holotype ♂ (Pempuchi valley, Nantou Pref., Formosa [= Taiwan]) [NMNH]; Lelej, 2005: 60; Hua, 2006: 301.
Ephucilla drola drola: Lelej, 1995b: 11, ♂; Lelej, 2005: 40; Hua, 2006: 299; Lo Cascio,

2015: 548; Pagliano *et al*., 2020: 171.
Smicromyrme hombucciana: Lo Cascio, 2015: 558. Incorrect subsequent spelling.

Zoobank LSID
urn:lsid:zoobank.org:act:DB2F9574-F664-4768-8A0F-33AD67BE9E00
urn:lsid:zoobank.org:act:45DACFFF-D4AA-45EE-805C-1EC171BFC99C

Material examined
21♂. Lectotype ♂, *Mutilla drola* Zavattari: **Taiwan:** CHIAYI: Taihorin [= Dalin], XI.1910, H. Sauter leg. [ZMHB]. **Taiwan:** CHANGHUA: Rengechi [= Cunshang, Dacun], 18.V.1926, J. Sonan leg. [1♂ TARI]; MIAOLI: Taiko [= Dahu] [1♂ TARI]; NANTOU: Tungpu, 1200 m. alt., 25–29.IX.1980, L.Y. Chou & T. Lin leg. [1♂ TARI]; Tungpu, 1200 m. alt., 5–8.X.1981, T. Lin & W.S. Tang leg. [1♂ TARI]; Tungpu, 1200 m. alt., 20–24.VI.1983, K.C. Chou & C.Y. Wong leg. [2♂ TARI]; Tungpu, 1200 m. alt., Malaise trap, X.1985, K.S. Lin leg. [3♂ TARI], XII.1985 [2♂ TARI]; Lienhuachi, 650 m alt., Malaise trap, V.1984, K.S. Lin & K.C. Chou leg. [1♂ TARI], VI.1984 [2♂ TARI]; Ren'ai, Yellow pan trap, 2–4.X.2016, S. Shimizu leg. [1♂ NARO], 4–6.X.2016 [1♂ NARO]; TAICHUNG: Wufeng, 1–7.IV.1980, K.C. Chou leg. [1♂ TARI]; Heping, Basianshan National Forest Recreation Area, 24°11'N 121°00'E, 850–980 m alt., Malaise trap, 6–10.VI.2010, T. Tsuru & M. Ôhara leg. [1♂ SEHU]; TAIPEI: Taipei, 16.IX.1934, M. Komatsu leg. [1♂ TARI]; Taipei City, Wenshuan Dist., Maekong, 5.VI.2023, S.-J. Hu leg. [1♂ TARI].

Identification source
Primary type. Photos of the holotype of *Sm*. *hombuceiana* are available in Chan *et al*. (2024).

Sex association
Female unknown.

Distribution
Taiwan: Changhua, Chiayi, Miaoli, Nantou, Taichung, Taipei.

This species was recorded from Sikkim, northeastern India by Hammer (1962: 44), but this record probably belongs to a separate species.

Remarks
Lelej (1995b) placed this species in the *Ephucilla*. However, this species shares many diagnostic features with *S*. *dardanus*: notaulus obliterated, T1 ventro-lateral margin densely micropunctate, parapenis oblong, and penisvalva posterior process with an external process.

Smicromyrme hombuceiana clearly belongs to *Sinotilla* s. str. by having the frons longitudinally striate, vertex elevated, mandible bidentate apically and emarginate ventrally, F1 shorter than F2, mesoscutum lacking notaulus, and tegula projecting posterad. It matches *Si*. *drola* in the body color. No additional differences were recognized from the original description and holotype photos, suggesting synonymy of *Si*. *drola* and *Sm*. *hombuceiana*.

Sinotilla drola lodra (Chen, 1957), comb. nov.

Smicromyrme drola lodra Chen, 1957: 203, ♂, holotype ♂ (Tienmushan [= Tianmushan], Chekiang [= Zhejiang], China) [TARI], examined; He *et al*., 2004: 949, ♂.
Ephucilla drola lodra: Lelej, 1995b: 11; Lelej, 2005: 40; Hua, 2006: 299; Okayasu, 2020: 64; Pagliano *et al*., 2020: 171.

Zoobank LSID
urn:lsid:zoobank.org:act:EDD5EB3E-3653-4186-9E9C-43C8FD31BE24

Material examined
8♂. Holotype ♂, *Smicromyrme drola lodra* Chen: **China:** ZHEJIANG: [Lin'an, Hangzhou], Tienmushan [= Tianmushan], 26.VII.36, O. Piel leg., *Smicromyrme dardanus lodra* Chen, B. Petersen det. 198, *Smicromyrme drola lodra* Chen [unknown hand] [TARI]. Paratypes, *Smicromyrme drola lodra* Chen: **China:** ZHEJIANG: [Lin'an, Hangzhou], Tienmushan [= Tianmushan], 27.VIII.1936 [1♂ TARI], 28.VIII.1936 [1♂ TARI], 4.IX.1943 [1♂ TARI], 7.IX.1943 [1♂ TARI], 2.IX.1947 [1♂ TARI], 3.IX.1947 [1♂ TARI], 15.IX.1947 [1♂ TARI].

Identification source
Primary type.

Sex association
Female unknown.

Distribution
China: Zhejiang.

Remarks
The holotype of this species is deposited in TARI and has appropriate labels. In the original description, this subspecies was diagnosed by having the tibiae and tarsi ferruginous (black in *S. drola drola*) and T2 and T3 setal bands golden yellow (whitish in *S. drola drola*) (Chen, 1957). Even though cuticular and setal color is generally variable in velvet ants, this subspecies can be recognized at least by the protibia and meso- and metatibial external faces orange. More data are needed to evaluate the status of this subspecies.

Like *M. caecina* and *M. exiloides*, this subspecies show variation in development of the seta-filled pit on basivolsella and some specimens totally lack this character.

Sinotilla gracillima (Smith, 1857)

Mutilla gracillima Smith, 1857: 84, ♂, holotype ♂ (Sarawak, Borneo, [Malaysia]) [OUMNH]; Cameron, 1892: 119; Dalla Torre, 1897: 44; André, 1902b: 70.
Smicromyrme gracillima: Mikel, 1935: 275, ♂.
Sinotilla gracillima: Lelej, 2005: 55; Lo Cascio, 2015: 557; Okayasu 2020: 89; Pagliano *et al*., 2020: 186.

Zoobank LSID
urn:lsid:zoobank.org:act:BDBF519E-2265-4C77-A59A-2B025DEAFD74

Material examined
1♂. **Malaysia:** NEGERI SEMBILAN: Pasoh Forest Reserve, Coarse Malaise trap, plot 4, 3–9.IV.1993, K. Konishi & K. Maeto leg. [1♂ FRIM].

Identification source
Keyed using Mickel (1935) and compared with the original description.

Sex association
Female unknown.

Distribution
Malaysia: Negeri Sembilan*, Sarawak (Smith, 1857).

Remarks
This species was often recovered as sister to *Sinotilla* s. str. or (*S. ansula* + *S. complanata*) by having the legs partially orange (68:1). One of the collecting sites of this species, Pasoh Forest Reserve, was described by Maetô *et al*. (1999).

Sinotilla hong Lelej, 1995

Sinotilla hong Lelej, 1995b: 20, ♂, holotype ♂ (Yuping, Yunnan, China) [ZMMU]; Lelej, 2005: 55; Okayasu, 2017: 152; Okayasu, 2020: 89, ♂; Pagliano *et al*., 2020: 186.

Zoobank LSID
urn:lsid:zoobank.org:act:49E0BA26-9E12-4A3D-9F92-7A9C01F8679E

Material examined
2♂. **Vietnam:** DIEN BIEN: Tua Chua, Xa Nhe, 21°52'35"N 103°24'46"E, 12.IV.2022, DTHoa [1♂ IEBR]; VINH PHUC: Ngoc Thanh, Me Linh Bio-Station, 22°16'51"N 105°71'54"E, 10.IV.2021, (MT), IED [1♂ IEBR].

Identification source
Compared with the original description.

Sex association
Female unknown.

Distribution
China: Yunnan (Lelej, 1995b). Vietnam*: Dien Bien, Vinh Phuc.

Remarks
Two Vietnamese specimens slightly differ in coloration: one male has legs entirely black while another male has pro- and mesofemora, pro- and mesotibiae, metafemur proximal 1/3, and metatibia proximal 2/3 red.

Sinotilla ilerda (Cameron, 1902), comb. nov.

Mutilla ilerda Cameron, 1902a: 78, ♂, holotype ♂ (Kuching, Sarawak, [Malaysia]) [NHMUK].
Smicromyrme ilerda ilerda: Mickel, 1935: 278, ♂; Lelej, 2005: 61; Lo Cascio, 2015: 558; Pagliano *et al*., 2020: 196.

Zoobank LSID
urn:lsid:zoobank.org:act:8DBB4E20-9CB9-4260-8139-CF7F7BC358C4

Material examined
3♂. **Malaysia:** NEGERI SEMBILAN: Pasoh Forest Reserve, Coarse Malaise trap, plot 6, 26.XI–3.XII.1993, K. Maeto leg. [1♂ FRIM], 3–10.XII.1993 [1♂ NARO], 10–17.XII.1993 [1♂ FRIM].

Identification source
Keyed using Mickel (1935) and compared with the original description. Photos of this species are available in Natural History Museum (2014).

Sex association
Female unknown.

Distribution
Malaysia: Negeri Sembilan*, Sabah, Sarawak (Camron, 1902a; Mickel, 1935).

Remarks
This species, together with its previous subspecies *Sm*. *ilerda sparsilis*, is here assigned to *Sinotilla* by having the frons longitudinally striate, vertex elevated, mandible apically bidentate with a small proximo-ventral lobe, F1 length 1/3× F2 length, T2–T3 with a pale setal band, and S2 with a lateral felt line (Cameron, 1902a; Mickel, 1934). *Sinotilla ilerda* and *Si*. *sparsilis* are distinguished from other *Sinotilla* species with ventral mandibular lobe by having the basivolsella expanded dorsad, giving rectangular appearance, with a shallow seta-filled pit represented by concavity bearing dense setae.

One of the collecting sites of this species, Pasoh Forest Reserve, was described by Maetô *et al*. (1999).

Sinotilla jambar Okayasu, 2020

Sinotilla jambar Okayasu, 2020: 89, ♂, holotype ♂ (Ôkuni Forest road, Yona, Kunigami, Okinawa-jima Island, Japan) [ELKU], examined.

Zoobank LSID
urn:lsid:zoobank.org:act:0B48E4CE-1057-49AE-86EA-5FE0249561BB

Material examined
25♂. Holotype ♂: **Japan:** OKINAWA ISLANDS: Okinawa-jima Island, Kunigami, Yona, Ôkuni Forest road, 300 m alt., 26.75°N 128.24°E, 3.VII.2016, Y. Komeda leg. [ELKU]. Paratypes: **Japan:** OKINAWA ISLANDS: Okinawa-jima Island, Kunigami Village, Uka, 11 years forest, Malaise trap, 22.VIII.2002, H. Makihara leg. [8♂ TPM]; Okinawa-jima Island, Kunigami Village, Oku, Malaise trap, 26.IX.2002, H. Makihara leg. [2♂ TPM], 10.X.2002 [1♂ TPM], 24.X.2002 [3♂ TPM], 10.VII.2003 [7♂ TPM], 24.VII.2003 [2♂ TPM], 14.IX.2003 [1♂ TPM].

Identification source
Primary type.

Sex association
Female unknown.

Distribution
Japan: Okinawa Island.

Remarks
This species is closely related to *S*. *columnata* and *S*. *serpa* and recognized by the tegula

weakly projecting postero-laterad (tegula projecting posterad and reaching posterior 1/2 of mesoscutellum in *S. columnata* and *S. serpa*), metasoma blue metallic (black in *S. columnata* and *S. serpa*), and T1–3 posterior margins with sparse pale setal fringes (dense in *S. columnata* and *S. serpa*). Again, the male genitalia are not useful to distinguish them.

Sinotilla nitela (Mickel, 1934), comb. nov.

Mutilla nigra (non Smith, 1859): Bingham, 1895: 440, ♂.
Smicromyrme viriata nitela Mickel, 1934: 197, ♂, holotype ♂ (Mt. Maquiling [= Mt. Makiling], Luzon, Philippines) [NMNH], photo examined; Mickel, 1935: 285, ♂; Baltazar, 1966: 211.
Smicromyrme aponis Tsuneki in Tsuneki *et al*., 1993, **syn. nov.**: 10, ♂, holotype ♂ (Mt. Apo, North Catabato, Mindanao, Philippines) [NMNH], photo examined; Lelej, 2005: 56; Lo Cascio, 2015: 557; Pagliano *et al*., 2020: 192.
Andreimyrme viriata nitela: Lelej, 2005: 39; Lo Cascio, 2015: 544; Pagliano *et al*., 2020: 169; Okayasu *et al*., 2021b: 4.

Zoobank LSID
urn:lsid:zoobank.org:act:190D3B13-4D46-4EEC-A3E2-D64A7AFC0BD0
urn:lsid:zoobank.org:act:A11779C3-C96A-4517-B675-E0FF5BAA1E37

Material examined
1♂. **Indonesia:** GORONTALO: Pegunungan Tilongkabila, 500–800 m alt., 14–17.III.2009, K. Takasuka leg. [1♂ EUMJ].

Identification source
Keyed using Mickel (1935), compared with holotype photos, and compared with the original description. Photos of the holotypes of *Si. nitela* and *Sm. aponis* are available in National Museum of Natural History (2024).

Sex association
Female unknown.

Distribution
Indonesia*: Gorontalo. Philippines: Luzon, Mindanao, Negros, Samar (Mickel, 1934; Tsuneki *et al*., 1993).

Remarks
This species is here assigned to the *Sinotilla* by having the frons longitudinally striate, clypeus with a subventral transverse flange, F1 shorter than F2, mandible apically bidentate with a small proximo-ventral lobe. mesopleuron evenly convex, parapenis bifid, and basivolsella subovate.

This species was initially described as the subspecies of *S. viriata* on the basis of the metasomal coloration. Furthermore, *S. viriata nitela* has the parapenis with anterior process rounded, while this process is pointed in *S. viriata viriata*. Both subspecies have been recorded from islands of Luzon, Mindanao, and Samar, suggesting overlapping distribution. These data support full species status of *S. nitela*.

In the original description, Tsuneki *et al*. (1993) used the head shape, clypeal shape and setation, mandibular shape, mesoscutellar setation, and propodeal sculpture to distinguish *Sm. aponis* from *Si. nitela*. However, these characters are apparent variation or artifact

depending on the condition of specimens. No additional differences were recognized from the holotype photos. Therefore, they are synonymized herein.

Sinotilla runcina (Zavattari, 1914)

Mutilla runcina Zavattari, 1914: 94, ♂, holotype ♂ (Bandjermasin [= Banjarmasin], [Kalimantan Selatan], Borneo, [Indonesia]) [MSNG].
Smicromyrme runcina: Mickel, 1935: 279, ♂; Mickel, 1937: 450, ♂.
Sinotilla runcina: Lelej, 1996b: 99, ♂, examined; Lo Cascio, 2015: 557; Okayasu, 2017: 152; Okayasu, 2018: 480, ♂, examined; Okayasu, 2020: 89, ♂; Pagliano *et al*., 2020: 186.

Zoobank LSID
urn:lsid:zoobank.org:act:18464F4C-A3B0-4242-AE20-3992AA35553B

Material examined
12♂. **Malaysia:** NEGERI SEMBILAN: Pasoh Forest Reserve, Coarse Malaise trap, plot 4, 26.III–3.IV.1993, K. Konishi & K. Maeto leg. [2♂ FRIM, NARO]; Pasoh Forest Reserve, Coarse Malaise trap, plot 5, 26.III–3.IV.1993, K. Konishi & K. Maeto leg. [1♂ FRIM], 9–16.IV.1993 [1♂ NARO]; Pasoh Forest Reserve, Coarse Malaise trap, plot 1, 2–8.IV.1993, K. Konishi & K. Maeto leg. [1♂ FRIM]; Pasoh Forest Reserve, Coarse Malaise trap, plot 4, 3–9.IV.1993, K. Konishi & K. Maeto leg. [1♂ NARO], 9–16.IV.1993 [1♂ FRIM]; Pasoh Forest Reserve, Fine Malaise trap, plot 1, 8–15.IV.1993, K. Konishi & K. Maeto leg. [1♂ NARO]; Pasoh Forest Reserve, Coarse Malaise trap, plot 3, 26.XI–3.XII.1993, K. Maeto leg. [1♂ FRIM]; Pasoh Forest Reserve, Coarse Malaise trap, plot 6, 3–10.XII.1993, K. Maeto leg. [2♂ FRIM, NARO]; SARAWAK: Lambir, Miri, 31.VIII–3.IX.1992, Canopy Biology Program Malaise trap T0, A0036, *Sinotilla runcina* (Zavattari), A. Lelej det. 1995 [1♂ SKYC].

Identification source
Voucher specimen (Lelej, 1996c; Okayasu, 2018).

Sex association
Female unknown.

Distribution
Indonesia: Kalimantan Selatan (Zavattari, 1914). Malaysia: Negeri Sembilan, Sabah, Sarawak (Mickel, 1935).

Remarks
This species shares many morphological features with *S. volupia*. They are separated by the body coloration and basivolsellar shape only and sometimes found sister in phylogenetic analyses using implied weighting. One of the collecting sites of this species, Pasoh Forest Reserve, was described by Maetô *et al*. (1999).

Sinotilla scitula (Mickel, 1935), comb. nov.

Smicromyrme scitula Mickel, 1935: 279, ♂, holotype ♂ (Sandakan, [Sabah], Borneo, [Malaysia]) [NMNH], photo examined; Lelej, 2005: 63; Lo Cascio, 2015: 559.
Smicromyrme scitulus: Pagliano *et al*., 2020: 201.

Zoobank LSID

urn:lsid:zoobank.org:act:323596EF-A63A-4A4F-9AA3-4BC5CDE1DE8C

Material examined
No material examined.

Sex association
Female unknown.

Distribution
Malaysia: Sabah (Mickel, 1935).

Remarks
Photos of the holotype of this species are available in National Museum of Natural History (2024). This species is here assigned to *Sinotilla* by having the frons longitudinally striate, mandible apically bidentate, and F1 length 1/3× F2 length (Mickel, 1935). *Sinotilla scitula*, *S. sparsilis*, and *S. volupia* were stated to have the mandibular ventral margin excised with a small blunt tooth (Mickel, 1934, 1935). However, this trait is not considered a tooth here. Instead, it is interpreted as the proximoventral lobe incised, subdentate, which is also observed in *S. columnata*, *S. runcina*, *S. serpa*, and *S. trisecta* with varying intensity.

Sinotilla serpa (Zavattari, 1913)

Mutilla serpa Zavattari, 1913: 39, ♂, lectotype ♂ (Taihorinsho [= Dalin], [Chiayi], Formosa [= Taiwan]) [ZMNB], designated by Mickel (1933a: 417), examined.
Smicromyrme serpa: Mickel, 1933a: 417, ♂; Suzuki, 1934: 25; Mickel, 1935: 275, ♂; Chen, 1957: 202, ♂; Tsuneki, 1972c: 20, ♂.
Sinotilla serpa: Lelej, 2005: 55; Hua, 2006: 301; Pagliano, 2011: 41, ♂; Lo Cascio, 2015: 557; Okayasu, 2017: 152.
Sinotilla serpa serpa: Okayasu, 2018: 480, ♂, examined; Okayasu, 2020: 89, ♂; Pagliano *et al*., 2020: 187.

Zoobank LSID
urn:lsid:zoobank.org:act:7FF4D9C3-863E-42FA-AABF-F559D62FA4DF

Material examined
8♂. Lectotype ♂: **Taiwan:** CHIAYI: Taihorinsho [= Dalin], VIII.1909, H. Sauter leg. [ZMHB]. **Taiwan:** NANTOU: Lienhuachih, 650 m, Malaise trap, VI.1984, K.S. Lin & K.C. Chou leg. [1♂ TARI], VII.1984 [1♂ TARI], IX.1984 [1♂ TARI]; Tungpu, 1200 m, Malaise trap, XII.1985, K.S. Lin leg. [1♂ TARI]; PINGTUNG: Mudan, Gaoshi, 300 m alt., 22°7'59"N 120°51'2"E, sweeping, 12.V.2016, S. Shimizu leg. [1♂ NARO]; TAICHUNG: Sunmoon Lake, Malaise trap, 20.X.1968 [1♂ TARI]; Wanfeng Hill, Malaise trap, VII.1984, K.S. Lin & K.C. Chou leg. [1♂ TARI].

Identification source
Primary type.

Sex association
Female unknown.

Distribution

Taiwan: Chiayi, Nantou, Pingtung, Taichung, Tainan, Yilan (Chen, 1957).

Remarks
This species shares the clypeal subventral flange medially interrupted (25:1) with *S. columnata* and *S. jambar*. This is a unique synapomorphy within *Sinotilla* but also found in *Mickelomyrme*. Those three species constitute a monophyletic group under all settings.

Sinotilla sparsilis (Mickel, 1934), comb. nov.

Smicromyrme ilerda sparsilis Mickel, 1934: 191, ♂, holotype ♂ (Dapitan, Mindanao, Philippines) [NMNH], photo examined; Mickel, 1935: 278, ♂; Baltazar, 1966: 210; Lelej, 2005: 61; Lo Cascio, 2015: 558; Pagliano *et al*., 2020: 196.

Zoobank LSID
urn:lsid:zoobank.org:act:69F0F166-02C0-40CA-A6FD-B2C6E0B20606

Material examined
No material examined.

Sex association
Female unknown.

Distribution
Philippines: Mindanao (Mickel, 1934).

Remarks
Photos of the holotype of this species are available in National Museum of Natural History (2024). Originally, this species was separated from *Si. ilerda* by having the pronotal punctures more separated and T2 punctures larger and coarser (Mickel, 1934). Later, Mickel (1935) used the T1 posterior margin with intermixed large and small punctures (with small punctures only in *Si. ilerda*) instead of T2 punctation. Although differences in T1 and T2 punctations cannot be recognized from the holotype photos, *Si. sparsilis* is distinguished by the pronotal dorsum with separated, obscurely defined punctures (with deep, confluent punctures in *Si. ilerda*) and mesoscutum with separated punctures (confluent in *Si. ilerda*). These diagnostic features provide evidence to treat *Si. sparsilis* as a full species.

Sinotilla trisecta (Chen, 1957)

Smicromyrme trisecta Chen, 1957: 206, ♂, holotype ♂ (Chusan [= Zhoushan], Chekiang [= Zhejiang], China) [TARI], examined; He *et al*., 2004: 958, ♂; Lelej, 2005: 64; Hua, 2006: 301.
Sinotilla trisecta: Okayasu, 2018: 493, ♂; Okayasu, 2020: 89, ♂; Pagliano *et al*., 2020: 203.

Zoobank LSID
urn:lsid:zoobank.org:act:D6B056D5-499E-4CB9-870E-9D611F05E817

Material examined
7♂. Holotype ♂: **China:** ZHEJIANG: Chusan [= Zhoushan], 1.9.31, O. Piel leg. [TARI]. Paratypes: **China:** ZHEJIANG: Chusan [= Zhoushan], 29.8.31, O. Piel leg. [1♂ TARI], 1.9.31 [1♂ TARI], 7.9.31 [2♂ TARI], 8.9.31 [1♂ TARI], 10.9.31 [1♂ TARI].

Identification source
Primary type.

Sex association
Female unknown.

Distribution
China: Zhejiang.

Remarks
In continental East Asia, this is the only species of *Sinotilla* with the metasomal segments 1 and 2 orange. This species shares the frons with a strong longitudinal carina anteriorly to lateral ocellus with *S. ilerda*. They were sometimes recovered as sister under equal weights and several *k* values.

Sinotilla unica sp. nov.

Zoobank LSID
Unavailable.

Diagnosis
MALE. Frons lacking longitudinal carina anteriorly to lateral ocellus; POL/OOL = 1.06–1.17; clypeus lacking medial carina; clypeal subventral transverse flange complete; mandible ventrally emarginate with large proximal tooth; scape and pedicel dark; mesosoma red with propleuron, mesoscutellum, metascutellum, meso- and metanotal troughs, mesopleuron, metapleuron, and propodeum black; pronotal dorsum and mesoscutum with large dense punctures; notaulus present on posterior 1/4 of mesoscutum; tegula rounded posteriorly; legs dark; metacoxal internal carina lamellately projecting posteriorly; metasoma black; T1 and T2 with dense posterior white setal fringe; T3 with sparse erect pale golden setae; parapenis with posterior process rectangular and anterior process broad, rounded; basivolsella slender subovate, with deep seta-filled pit at midpoint; apiceps slender; penisvalva strongly expanded ventrad; penisvalva lacking external process on posterior process; penisvalva external face lacking vertical carina.

FEMALE. Unknown.

Description
MALE. Body length: 6.99–10.4 mm (holotype 8.48 mm); forewing length: 4.65–7.03 mm (holotype 5.71 mm).

Color and setae. Frons, vertex, gena, postgenal bridge, clypeus, mandible apex and proximo-external face, propleuron, mesoscutellum, metascutellum, meso- and metanotal troughs, mesopleuron, metapleuron, propodeum, and metasoma black; antennal rim, femora, tibiae, and tarsi dark brown; mandible except apex and proximo-external face yellowish brown; scape, pedicel, flagellum, prementum, stipes, and coxae brownish black; maxillary and labial palpi and protibial spur yellow; pronotum and mesoscutum yellowish red; tegula reddish yellow to brown; trochanters brown; meso- and metatibial spurs yellowish white. Frons and scape with sparse long recumbent and sparse long erect pale golden setae; vertex, mandible, pronotal dorsum, and mesoscutellum with sparse long erect pale golden setae; gena, postgenal bridge, mesopleuron, metascutellum, metapleuron ventral 1/3, propodeum, trochanters, femora, and tibiae with sparse short recumbent and sparse long erect pale golden

setae; clypeus with sparse long appressed white and sparse long erect pale golden setae; pedicel with dense short recumbent pale golden setae; flagellum with dense erect pale golden microsetae; prementum, stipes, and maxillary and labial palpi with sparse short erect pale golden setae; lateral pronotal face and metapleuron dorsal 2/3 with sparse short appressed pale golden setae; propleuron with sparse short appressed and sparse long erect pale golden setae; mesoscutum with sparse long erect dark golden setae; tegula medially with sparse long recumbent dark golden setae; tegula around margins and coxae with sparse long recumbent pale golden setae; meso- and metanotal troughs with dense short appressed pale golden setae; tarsi with sparse long appressed pale golden setae; T1–5, S1, and S3–5 with sparse long erect white setae; T6 and S6–7 with sparse long erect white or black setae; T7 and S8 with sparse long erect black setae; S2 with sparse short recumbent and sparse long erect white setae; T2 lateral felt line golden, 0.5× T2 length; S2 lacking lateral felt line; T1 and T2 with dense posterior fringe of white setae.

Structure. Head width 1.58–1.72× length (holotype 1.64); lateral margins strongly convergent behind eye, posterolateral angle rounded; vertex elevated, sharply sloping posteriorly; minimum distance between eyes 0.91–0.99× eye height (holotype 0.99); POL/OOL = 1.06–1.17 (holotype 1.16); MOD:LOD:LOL:POL = 1.00:0.769–0.900:1.80–2.10:3.30–4.30 (holotype 1.00:0.900:2.10:4.30); ocellar region convex; median ocellus with posterior elevation and longitudinal carina; frons with shallow medial longitudinal sulcus, lacking longitudinal carina anteriorly to lateral ocellus; occipital carina sharp, complete; internal eye margin deeply emarginate; antennal scrobal carina V-shaped, widely separated from internal eye margin; antennal rim convex; antennal rims separated by approximate antennal rim width; gena lacking vertical carina; postgenal bridge flat; hypostomal carina sharp, not projecting; malar space developed, ventral eye margin and mandibular base separated; clypeus subconvex, with subventral complete transverse flange overhanging ventral clypeal margin; clypeal dorso-medial portion elevated into simple carina; mandible slender, narrowed to apex; mandible apex bidentate, internal tooth as large as apex; mandibular internal margin entire; mandibular dorso-lateral carina sharp; mandibular ventral margin emarginate with large proximal tooth; prementum flat; scape with two sharp subparallel carinae, separated by 0.5× scape width; F1 cylindrical; length and width of pedicel:F1:F2 = 1.00:1.25–1.40:1.22–1.40:1.67–1.83:2.78–3.00:1.78–2.00 (holotype 1.00:1.40:1.40:1.80:3.00:2.00); flagellomere apices truncate.

Mesosoma widest at mesonotum including tegulae; antero-dorsal pronotal margin nearly straight; humeral angle weakly angulate; humeral carina sharp, reaching pronotal dorsum; mesoscutum weakly convex; tegula short, rounded posteriorly, not flex, slightly surpassing transscutal articulation; tegula length 1.42–1.54× width (holotype 1.50); notauli subparallel, present on posterior 1/4 of mesoscutum, posteriorly widened; parapsidal signum short, linear; parascutal carina forming weak process on posterolateral angle of mesoscutum; transscutal impression arcuate; mesoscutellum weakly convex; mesopleuron convex, lacking transverse impression; ventral mesopleural face with longitudinal impunctate line and without process and swelling; mesocoxal foramen without transverse precoxal carina; metathoracic spiracle oval; metasternum much shorter than coxal height; propodeal length 0.917–0.968× pronotal + mesoscutal length; posterior propodeal face oblique, without distinct dorsum; propodeal sublateral longitudinal carina absent; propodeal dorso-lateral margin rounded, lacking longitudinal carina; lateral margins of propodeum convergent posteriorly.

Wings fully developed; distance between origin of RS on vein SC and proximal margin of pterostigma 1.15–1.54× pterostigma length; forewing cell 2RS present.

Procoxa lacking posterior process; meso- and metacoxae evenly convex; metacoxa with internal longitudinal carina lamellately projecting, posteriorly truncate; protibial spur slender; tibiae without external spines.

Metasomal segment 1 slender, subsessile; T1 width:T2 width:T2 length = 0.60–0.70:1.00:0.70–0.73 (holotype 0.65:1.00:0.70); T1 oblique, without distinct dorsum; T1 spiracle projecting; T2 abruptly convex; S1 with medial longitudinal carina on anterior 3/4, straight in profile; S2 evenly convex with antero-medial elevated; T3–6 not constricted; T7 evenly convex, with posterior margin truncate; S6–8 flat, lacking lateral carina or process; S7 posterior margin truncate; S8 mostly sclerotized with posterior membranous area evenly convex posteriorly. Harpe depressed laterally, down-curved; harpe dorso-internal margin lacking process; harpe dorsal margin with sparse short erect setae; gonostipes much longer than wide and as long as harpe; gonostipes ventro-medial lobe not forming posterior process; gonostipes ventral lobe projecting posterad; parapenis deeply bifid, with distinct anterior and posterior processes, not flexed; posterior process on parapenis with small rounded outer process; cupula much shorter than gonostipes; basivolsella slender subovate, depressed, without cuspis; basivolsella apex reaching posterior 1/2 of harpe and surpassing penisvalva by 2/3× basivolsella length; basivolsella with large deep seta-filled pit, with sparse long erect setae on internal face and ventral margin; basiura strongly sclerotized with slender apiceps and few long erect setae; penisvalvae symmetrical; penisvalva broad, expanded ventrad, with distinct anterior and posterior ventral processes; penisvalva lacking setae; endophallus membranous.

Frons obscurely longitudinally striate; vertex, pronotal dorsum, and mesoscutellum with large dense punctures, separated by ~0.5× puncture diameter; gena, mesopleuron, and metapleuron ventral 1/3 with large confluent punctures; postgenal bridge transversely rugose; clypeus, lateral pronotal face, metapleuron dorsal 2/3, procoxa, trochanters, femora, tibiae, and tarsi with minute sparse punctures; scape, tegula, meso- and metacoxae, T3–7, and S3–8 with small sparse punctures; pedicel, flagellum, prementum, stipes, maxillary and labial palpi, propleuron, and meso- and metanotal troughs with minute dense punctures; mesoscutum and T1 except posterior margin with large dense punctures, separated by 0.5–1.0 puncture diameter; metascutellum with small dense punctures; propodeum reticulate, with medial subtriangular and sublateral semicircular cell on anterior margin; T1 posterior margin with small dense punctures; T2 and S1–2 with large sparse punctures.

FEMALE. Unknown.

Material examined

4♂. Holotype ♂: **China:** HAINAN: near Riyue Bay, 17.V.2009, H. Kurokawa leg. [MTC]. Paratypes: **China:** GUANGDONG: Kwangtung [= Guangdong], Lofoushan [= Mt. Luofushan], 18.VII.1937, T.C. Maa leg. [1♂ TARI]; HAINAN: near Riyue Bay, 17.V.2009, H. Kurokawa leg. [1♂ MTC]. **Vietnam:** CAO BANG: Ha Lang, Duc Quang, 517 m, 19.V.2023, 22°45'39"N 106°37'36"E, NTPL, TTL, NQC [1♂ IEBR].

Sex association

Female unknown.

Distribution

China: Guangdong, Hainan. Vietnam: Cao Bang.

Etymology

The specific name *unica*, unique, is the Latin, singular, feminine adjective in the nominative case. It suggests that this new species constitutes a unique linage within *Sinotilla*.

Remarks

By having the mandible with a proximo-ventral tooth, notaulus present, penisvalva strongly

expanded ventrad, and penisvalva with posterior process lacking an external process, this species is similar to *S. ansula* and *S. complanata* **sp. nov.** This new species differs from them by having the POL 1.06–1.17× OOL (~0.65 in *S. ansula* and *S. complanata*), mesoscutellum black (red in *S. ansula* and *S. complanata*), metacoxal internal carina lamellately projecting (weakly developed in *S. ansula* and *S. complanata*), tibiae entirely black (protibia entirely and meso- and metatibiae proximally orange in *S. ansula* and *S. complanata*), posterior process on parapenis rectangular (slender in in *S. ansula* and *S. complanata*), anterior process on parapenis broad and rounded (angulate in in *S. ansula* and *S. complanata*), and penisvalva lacking an external carina (with vertical carina on external face in in *S. ansula* and *S. complanata*). In coloration, this new species is similar to *S. jambar* and *S. serpa*. However, *S. unica* **sp. nov.** is distinguished by having the clypeal subventral transverse flange complete (medially interrupted in *S. jambar* and *S. serpa*), mandible ventrally emarginate with large proximal tooth (with small proximal lobe in *S. jambar* and *S. serpa*), tegula rounded posteriorly (projecting posterad in *S. jambar* and *S. serpa*), metacoxal internal carina lamellately projecting (weakly developed in *S. jambar* and *S. serpa*), and basivolsella slender (broad, oval in *S. jambar* and *S. serpa*).

Sinotilla viriata (Mickel, 1934), comb. nov.

Smicromyrme viriata viriata Mickel, 1934: 195, ♂, holotype ♂ (Iligan, Mindanao, Philippines) [NMNH], photo examined; Mickel, 1935: 284, ♂; Baltazar, 1966: 211; Tsuneki *et al*., 1993: 11, ♂.

Smicromyrme mindanaonis Tsuneki in Tsuneki *et al*., 1993, **syn. nov.**: 12, ♂, holotype ♂ (Makahambus Cave, Bukidnon, Mindanao, Philippines) [NMNH], photo examined; Lelej, 2005: 62; Lo Cascio, 2015: 559; Pagliano *et al*., 2020: 198.

Andreimyrme viriata viriata: Lelej, 2005: 39; Lo Cascio, 2015: 544; Pagliano *et al*., 2020: 169; Okayasu *et al*., 2021b: 4.

Zoobank LSID
urn:lsid:zoobank.org:act:95D6887A-96A6-4E36-ACA5-73F484B2410D
urn:lsid:zoobank.org:act:27D30B0E-CA1B-4D9F-8AED-7E8DA7163218

Material examined
1♂. **Philippines:** LUZON: San Gabriel, 20.III.1974, S. Ueda leg., *Smicromyrme viriata* Mickel [probably Petersen's hand] [1♂ TUA].

Identification source
Identified specimen. Photos of the holotypes of *Si. viriata* and *Sm. mindanaonis* are available in National Museum of Natural History (2024).

Sex association
Female unknown.

Distribution
Philippines: Biliran, Luzon, Mindanao, Samar, Sibuyan, Panay (Mickel, 1934; Tsuneki *et al*., 1993).

Remarks
This species is here assigned to the *Sinotilla* by having the frons longitudinally striate, clypeus with a subventral transverse flange, F1 shorter than F2, mandible apically bidentate

with a small proximo-ventral lobe. mesopleuron evenly convex, parapenis bifid, and basivolsella subovate.

In the original description, Tsuneki *et al*. (1993) used the vertex sculpture, genal shape, clypeal setation, mandibular shape, and metasomal color to distinguish *Sm. mindanaonis* from *Si. viriata*. However, these characters are too slight or apparently variable and cannot be ascertained from the holotype photos. Therefore, they are synonymized herein.

Sinotilla volupia (Mickel, 1935), comb. nov.

Smicromyrme volupia Mickel, 1935: 277, ♂, holotype ♂ (Bettotan, near Sandakan, [Sabah], Borneo, [Malaysia]) [NHMUK].
Andreimyrme volupia: Lelej, 2005: 39; Lo Cascio, 2015: 544; Pagliano *et al*., 2020: 169; Okayasu *et al*., 2021b: 4.

Zoobank LSID
urn:lsid:zoobank.org:act:BEB36E62-14BE-4A71-8503-18F51D3EC1CA

Material examined
1♂. **Malaysia:** NEGERI SEMBILAN: Pasoh Forest Reserve, 1.IV.1993, K. Konishi leg. [1♂ FRIM].

Identification source
Keyed using Mickel (1935) and compared with the original description.

Sex association
Female unknown.

Distribution
Malaysia: Negeri Sembilan*, Sabah (Mickel, 1935).

Remarks
This species is here assigned to *Sinotilla* by having the frons longitudinally striate, vertex elevated, mandible apically bidentate with a small proximo-ventral lobe, F1 length 1/5× F2 length, T2–T3 with a pale setal band, and S2 with a lateral felt line (Mickel, 1935). At Pasoh Forest Reserve, as many as five *Sinotilla* species were collected, including closely related *S. runcina* and *S. volupia*.

Genus *Smicromyrme* Thomson, 1870

Smicromyrme Thomson, 1870: 208, ♂♀; Ashmead, 1903: 326, ♂♀; Bischoff, 1921: 556, ♂♀; Mickel, 1928: 36; Mickel, 1933a: 416, ♂♀; Mickel, 1935: 271, ♂♀; Skorikov, 1935: 312, ♂♀; Giner Marí, 1944: 75, ♂♀; Chen, 1957: 178, ♂♀; Invrea, 1964: 153, ♂♀; Brothers, 1975: 592, ♂♀; Lelej, 1985: 211, ♂♀; Lelej, 1995c: 210, ♂♀Lelej, 2002: 64; Lelej, 2005: 56; Lelej, 2007: 89; Pagliano & Strumia, 2007: 83, ♂♀; Lelej & Brothers, 2008:56; Brothers & Lelej, 2017: 96; Okayasu *et al*., 2018: 304, ♀; Williams *et al*., 2019b: 26, ♀; Okayasu, 2020: 8, ♂♀; Pagliano *et al*., 2020: 187; Lelej & Williams, 2023: 128, ♂♀. Gender masculine (Lelej & Brothers, 2008).
Mutilla (*Smicromyrme*): Dalla Torre, 1897: 6.

Zoobank LSID

urn:lsid:zoobank.org:act:B761D778-D7AB-4154-ADC0-85B065A325A6

Type species
Mutilla rufipes Fabricius, 1787, ♀, by monotypy.

Diagnosis
MALE. Frons punctate; vertex elevated beyond ocellar region; ventral clypeal margin entire; mandible apex bidentate or tridentate, internal teeth smaller than apex, without subdistal internal tooth; mandible dorso-lateral carina weakly developed; mandible ventral margin emarginate with large proximal tooth or not emarginate with small proximal lobe or tooth; flagellomere apices truncate; F1 length subequal to width; notaulus present on posterior part of mesoscutum or reaching posterior margin of pronotum; parascutal carina forming weak process; tegula rounded posteriorly, slightly surpassing transscutal articulation; mesopleuron divided into dorsal and ventral convexities by transverse impression; mesopleuron ventral face lacking process; procoxa lacking posterior process; metacoxal internal carina weakly developed or lamellately projecting posteriorly; S2 with lateral felt line; harpe dorso-internal margin with or without proximal process; parapenis bifid; gonostipes ventral lobe posteriorly truncate; basivolsella subovate, with short setae on ventral margin; basivolsella internal face with seta-filled pit; basiura small rounded; apiceps long slender; penisvalva strongly expanded ventrad; penisvalva posterior process with or without external process; penisvalva internal face lacking setae.

FEMALE. See Lelej & Williams (2023).

Species included
A total of 16 species and one subspecies are recognized in the *Astomyrme* Schwartz, 1984, 19 species in the *Eremotilla* Lelej, 1985, 11 species in the *Erimyrme* Lelej, 1985, one species in the *Rhombotilla* Nagy, 1966, 10 species and three subspecies in the *Smicromyrme* s. str., and 210 species and 14 subspecies that are not placed in any subgenera. The following four East Asian species are reliably placed in *Smicromyrme* based on the male morphology: *S.* (*Erimyrme*) *bidenticulatus* Chen, 1957, ♂♀ (China, Mongolia, Russia, South Korea); *S.* (*Smicromyrme*) *australis* **sp. nov.**, ♂ (Thailand); *S.* (*Smicromyrme*) *lewisi* Mickel, 1935, ♂♀ (China, Japan, Mongolia, North Korea, Russia, South Korea); *S.* (*Smicromyrme*) *strandi* (Zavattari, 1913), ♂♀ (China, Taiwan). Additional 20 species and two subspecies known from East Asia are tentatively placed in the *Smicromyrme*: *S. basalis annularis* Mickel, 1934, ♀ (Philippines); *S. basalis basalis* (Smith, 1879), ♀ (Indonesia, Malaysia, Philippines); *S. borneo* Lelej, 1996, ♀ (Malaysia); *S. caeruleus* Mickel, 1934, ♂ (Philippines); *S. chuchianus* Tsuneki, 1993, ♀ (Taiwan); *S. deidamia* (Smith, 1857), ♀ (Malaysia); *S. devius*: (Cameron, 1909), ♂ (Malaysia); *S. electra* Mickel, 1935, ♂ (Indonesia); *S. furus anthracipes* Mickel, 1934, ♀ (Philippines); *S. furus furus* Mickel, 1934, ♀ (Philippines); *S. helarctos* Williams, 2019, ♀ (Thailand); *S. herophile* Mickel, 1935, ♂ (Indonesia); *S. jacobsoni* (André, 1907), ♂ (Indonesia); *S. kuanfuanus* Tsuneki, 1972, ♀ (Taiwan); *S. lochius* Mickel, 1937, ♀ (Malaysia, Thailand); *S. minahassae* (Zavattari, 1914), ♂ (Indonesia); *S. songkhwae* Sittichaya & Williams, 2022, ♀ (Thailand); *S. substitutus* (André, 1896), ♀ (China, India); *S. tenasserimicus* (Magretti, 1892), ♀ (Myanmar, Thailand); *S. thaochani* Williams, 2019, ♀ (Thailand); *S. thia* Mickel, 1933, ♀ (Taiwan); *S. triguttatus* Mickel, 1933, ♀ (China, Taiwan, Laos, Thailand, Vietnam).

Sex association
The type species was initially described from the female only. The male of this species was associated and described by Spinola (1806) although misidentified as *Mutilla ephippium*

Fabricius, 1793. See Petersen (1988) and Lelej & Brothers (2008) also.

Distribution
Afrotropical, Oriental, and Palaearctic Regions.

Remarks
Under equal weights, this genus was found either monophyletic or paraphyletic due to *S. australis*. Monophyly was supported by low GC score (GC = 27; Fig. 22-2). Using implied weighting, monophyly of the *Smicromyrme* was recovered under most *k* values except when k12 was used (Fig. 16-1). Two or three homoplastic synapomorphies were recognized: frons with sparse setae (12:0), parascutal carina forming an elevated process (50:2), and basivolsella subovate (114:3). Of the four subgenera known from the male, only two subgenera, *Erimyrme* and *Smicromyrme* s. str., were examined for phylogenetic analyses. In most analyses where the *Smicromyrme* was recovered as monophyletic, the *Erimyrme* was found sister to the *Smicromyrme* s. str. With k0, k1, and k15, however, the *Erimyrme* was nested in the *Smicromyrme* s. str. (Figs 4-2, 5-2, 19-1). Further taxonomic sampling and reanalyses are apparently needed to evaluate monophyly of the subgenera of this morphologically diverse genus.

In the present study, six East Asian *Smicromyrme* species based on the male were not examined. I demonstrate, however, these species probably belong to the *Sinotilla* except *Sm. jacobsoni* which is a likely member of the Trogaspidiini. This suggests most of the female-based species known from Southeast Asia may also be transferred out of the *Smicromyrme* subsequently.

Key to the subgenera of *Smicromyrme* based on the male morphology

1. Mandible apically tridentate; mandibular ventral margin not emarginate, straight or with small proximal tooth … ***Astomyrme*** Schwartz
- Mandible apically bidentate or tridentate; mandibular ventral margin emarginate with large proximal tooth … 2
2 (1). Mandible apically tridentate … ***Erimyrme*** Lelej
- Mandible apically bidentate … 3
3 (2). Clypeus without subventral teeth … ***Eremotilla*** Lelej
- Clypeus with paired subventral teeth … ***Smicromyrme*** Thomson

Key to the East Asian species of *Smicromyrme* based on the male morphology

1. Mandible apically tridentate … China, Mongolia, South Korea … ***S.*** **(*Eri.*)** ***bidenticulatus*** (Chen)
- Mandible apically bidentate … 2
2 (2). Metacoxal internal carina lamellately projecting; parapenis shallowly bifid. Thailand … ***S.*** **(*S.*)** ***australis*** **sp. nov.**
- Metacoxal internal carina weakly developed; parapenis deeply bifid … 3
3 (2). Mesosoma red with pro-, meso- and metapleura and propodeum black; ventral mesopleural face with longitudinal impunctate line. China, Japan, Mongolia, North Korea, Russia, South Korea … ***S.*** **(*S.*)** ***lewisi*** Mickel
- Mesosoma red with propleuron and mesopleuron ventral 1/2 black; ventral mesopleural face lacking impunctate line. China, Taiwan … ***S.*** **(*S.*)** ***strandi*** (Zavattari)

Subgenus *Erimyrme* Lelej, 1985

Smicromyrme (*Erimyrme*) Lelej, 1985: 236, ♂♀; Lelej, 1995c: 210, ♂♀; Lelej, 2002: 68; Pagliano *et al*., 2020: 190; Lelej & Williams, 2023: 131, ♂♀.

Zoobank LSID
urn:lsid:zoobank.org:act:54EA40EF-863C-4535-838B-833494F00DDA

Type species
Smicromyrme pusilla septentrionalis Hoffer, 1936, ♀ (= *Mutilla ephippium* var. *sicana* De Stefani, 1887, ♂, syn. by Petersen, 1988), by original designation.

Diagnosis
MALE. Clypeus with paired subventral teeth; mandible apically tridentate; mandible ventral margin emarginate with large proximal tooth.

FEMALE. See Lelej & Williams (2023).

Species included
See above.

Sex association
The type species was initially described based on females only. The male of its senior synonym was described by De Stefani (1887).

Distribution
Palaearctic Region.

Remarks
In East Asia, this subgenus is restricted to the Palaearctic part of China and Korean Peninsula. Based on the female morphology, Okayasu (2018) assigned the Oriental species *S. triguttatus* to this subgenus. However, given the uncertain placement of the Oriental *Smicromyrme* species, subgeneric placement of this species is highly suspicious.

Smicromyrme (*Erimyrme*) *bidenticulatus* (Chen, 1957)

Smicromyrme bidenticulata Chen, 1957: 199, ♂, holotype ♂ (Longtong, Tsinan [= Jinan], China) [TARI], examined; Hua, 2006: 301.
Smicromyrme hasanensis Lelej, 1977a: 91, ♂♀, holotype ♀ (7 km E Khasan, Primorsky Krai, Russia) [ZISP]; Lelej, 1981: 78, ♂♀. Synonymized by Lelej (1985: 239) under *Smicromyrme bidenticulatus* Chen.
Smicromyrme hasanensis f. *apunctatus* Lelej, 1977a: 94, ♀. Unavailable name (ICZN, 1999: Article 15.2).
Smicromyrme hasanensis f. *monopunctatus* Lelej, 1977a: 94, ♀. Unavailable name (ICZN, 1999: Article 15.2).
Smicromyrme (*Smicromyrme*) *hasanensis*: Lelej, 1977b: 531, ♂.
Smicromyrme (*Erimyrme*) *bidenticulata*: Lelej, 1985: 239, ♂♀; Lelej, 1995c: 210, ♂♀; Lelej, 2000: 615; Lelej *et al*., 2001: 10, ♂♀; Lelej, 2002: 68.
Smicromyrme (*Erimyrme*) *bidenticulatus*: Lelej, 2017: 156; Okayasu, 2018: 480, ♂; Pagliano *et al*., 2020: 190; Pagliano & Scaramozzino, 2021: 109, ♂.

Zoobank LSID

urn:lsid:zoobank.org:act:FF7F8A81-BE53-4DED-84FD-FADEB53C02B5

Material examined
6♂1♀. Holotype ♂, *Smicromyrme bidenticulatus* Chen: **China:** SHANDONG: Tsinanfou [= Jinan], Long-tong, 500 à 700 m, *Smicromyrme bidenticulata* Chen [unknown hand] [TARI]. **South Korea:** GYEONGGI: Suigen [= Suwon], 25.VII.1923, K. Sato leg. [2♂ NSMT], 10.VI.1925 [1♀ NSMT]; Cheonmasan, 30.VIII.1942 [1♂ MNHAH]; Dongducheon, Mt. Soyosan, 3.IX.1942 [1♂ MNHAH], 3.IX.1943 [1♂ MNHAH].

Identification source
Primary type.

Sex association
This species was initially described from the male only. The female of its junior synonym was associated and described by Lelej (1977a).

Distribution
China: Inner Mongolia, Jiangsu Shandong (Chen, 1957; Lelej, 1985). Mongolia (Lelej, 1977b). Russia: Primorsky (Lelej, 1977a). South Korea: Gyeonggi, Seoul, South Chungcheong (Lelej *et al*., 2001).

Remarks
This species was described based on two male specimens. The holotype is deposited in TARI and has appropriate labels. However, the paratype was not found there.

Subgenus *Smicromyrme* Thomson, 1870

Smicromyrme Thomson, 1870: 208, ♂♀.
Smicromyrme (*Smicromyrme*): Lelej, 1985: 231, ♂♀; Lelej, 1995c: 210, ♂♀; Lelej, 2002: 69; Pagliano *et al*., 2020: 191; Lelej & Williams, 2023: 132, ♂♀.

Zoobank LSID
urn:lsid:zoobank.org:act:B761D778-D7AB-4154-ADC0-85B065A325A6

Type species
Mutilla rufipes Fabricius, 1787, ♀, by monotypy.

Diagnosis
MALE. Clypeus with paired subventral teeth; mandible apically bidentate; mandible ventral margin emarginate with large proximal tooth.
FEMALE. See Lelej & Williams (2023).

Species included
See above.

Sex association
See above.

Distribution
Oriental and Palaearctic Regions.

Remarks
Previously, this subgenus included two East Asian species. Their distribution is restricted to northeast part of the region, China, Taiwan, Korean Peninsula, and Japan. Discovery of *S. australis* confirmed that this subgenus occurs further south.

***Smicromyrme* (*Smicromyrme*) *australis* sp. nov.**

Zoobank LSID
Unavailable.

Diagnosis
MALE. MOD subequal to LOL; clypeus with subventral paired teeth; mandible apically bidentate; mandible ventrally emarginate with large proximal tooth; antenna mostly black; mesosoma orange with propleuron and mesopleuron ventral 1/2 black; ventral mesopleural face with longitudinal impunctate line; metacoxal internal carina lamellately projecting posteriorly; T7 with medial impunctate line, lacking carinae; harpe dorso-internal margin lacking process; parapenis shallowly bifid.

FEMALE. Unknown.

Description
MALE. Body length: 8.31 mm; forewing length: 6.33 mm.

Color and setae. Frons, vertex, gena, postgenal bridge, antennal rim, clypeus, mandible except subdistal 1/4, scape except apex, F2–11, stipes, propleuron, mesopleuron ventral 1/2, coxae, meso- and metatrochanters, femora, tibiae, and metasoma except T1 lateral margin and T2–4 posterior margins black; mandible subdistal 1/4, scape apex, prementum, protrochanter, tarsi, and T1 lateral margin dark brown; pedicel and F1 brownish black; maxillary and labial palpi brown; pronotum, mesoscutum, tegula, mesoscutellum, metascutellum, meso- and metanotal troughs, mesopleuron dorsal 1/2, metapleuron, and propodeum orange; protibial spur brown; meso- and metatibial spurs yellowish white; T2–4 posterior margins yellow. Frons, scape, pronotal dorsum, and mesopleuron with sparse long recumbent and sparse long erect pale golden setae; vertex, postgenal bridge, clypeus medially, mandible, mesoscutellum, metascutellum, propodeum, propleuron, procoxa, trochanters, T1–5, T6 lateral margin, and S1–5 with sparse long erect pale golden setae; gena, lateral pronotal face and metapleuron with sparse short appressed pale golden setae; tegula around margins, and meso- and metacoxae with sparse long recumbent pale golden setae; clypeus with sparse long appressed pale golden setae; pedicel with sparse short recumbent pale golden setae; flagellum with dense erect pale golden microsetae; prementum, stipes, and maxillary and labial palpi with sparse short erect pale golden setae; mesoscutum with intermixed sparse long erect pale golden and black setae; tegula medially with sparse long recumbent setae; meso- and metanotal troughs with sparse short appressed pale golden setae; femora and tibiae with sparse short recumbent and sparse long erect pale golden setae; tarsi with dense long appressed pale golden setae; T6 medially and S6–8 with sparse short recumbent black and sparse long erect pale golden setae; T6–7 with sparse short recumbent and sparse long erect black setae; T2 lateral felt line golden, 0.35× T2 length; S2 lateral felt line golden, 0.15× S2 length; T1–4 with dense posterior fringe of golden setae; S2–5 with sparse posterior fringe of pale golden setae.

Structure. Head width 1.43× length; lateral margins strongly convergent behind eye, posterolateral angle rounded; vertex elevated, sharply sloping posteriorly; minimum distance between eyes 1.14× eye height; POL/OOL = 0.682; MOD:LOD:LOL:POL =

1.00:0.733:0.933:2.00; ocellar region slightly convex; median ocellus lacking posterior longitudinal carina; frons lacking longitudinal carina and sulcus; occipital carina sharp, complete; internal eye margin deeply emarginate; antennal scrobal carina V-shaped, extending nearly to internal eye margin; antennal rim convex; antennal rims separated by approximate antennal rim width; gena lacking vertical carina; postgenal bridge flat; hypostomal carina sharp, not projecting; malar space developed, ventral eye margin and mandibular base separated; clypeus subconvex, with subventral paired teeth medially; clypeal dorso-medial portion elevated into simple carina; clypeal ventral margin medially projecting; mandible slender, narrowed to apex; mandible apex bidentate, internal tooth smaller than apex; mandibular internal margin entire; mandibular dorso-lateral carina sharp; mandibular ventral margin emarginate with large proximal tooth; prementum flat; scape with two sharp ventral carinae, separated by 0.6× scape width; F1 cylindrical; length and width of pedicel:F1:F2 = 1.00:0.857:1.43:1.29:1.79:1.36; flagellomere apices truncate.

Mesosoma widest at mesonotum including tegulae; antero-dorsal pronotal margin slightly arcuate; humeral angle weakly angulate; humeral carina sharp, reaching pronotal dorsum; mesoscutum strongly convex; tegula short, oval with posterior margin rounded, not flexed, and slightly surpassing transscutal articulation; tegula length 1.54× width; notauli subparallel, reaching anterior margin of mesoscutum, posteriorly widened; parapsidal signum short, linear; parascutal carina forming elevated process on posterolateral angle of mesoscutum; transscutal impression arcuate; mesoscutellum weakly convex; mesopleuron divided into dorsal and ventral convexities by shallow transverse impression; ventral mesopleural face with longitudinal impunctate line and without process and swelling; mesocoxal foramen without transverse precoxal carina; metathoracic spiracle oval; metasternum much shorter than coxal height; propodeal length 1.00× pronotal + mesoscutal length; posterior propodeal face oblique, without distinct dorsum; propodeal sublateral longitudinal carina absent; propodeal dorso-lateral margin rounded, lacking longitudinal carina; lateral margins of propodeum convergent posteriorly.

Wings fully developed; distance between origin of RS on vein SC and proximal margin of pterostigma 1.17× pterostigma length; forewing cell 2RS present.

Procoxa lacking posterior process; meso- and metacoxae evenly convex; metacoxa with internal longitudinal carina lamellately projecting, forming truncate posterior margin; protibial spur slender; tibiae without external spines.

Metasomal segment 1 slender, subsessile; T1 width:T2 width:T2 length = 0.55:1.00:0.67; T1 oblique, without distinct dorsum; T1 spiracle projecting; T2 evenly convex; S1 with medial longitudinal carina on anterior 3/4, straight in profile; S2 evenly convex, lacking antero-medial carina; T3–6 not constricted; T7 evenly convex, with posterior margin truncate; S6–8 flat, lacking lateral carina or process; S7 posterior margin truncate; S8 mostly sclerotized with posterior membranous area evenly convex posteriorly. Harpe depressed laterally, down-curved; harpe dorso-internal margin lacking process; harpe internal face and dorsal margin with sparse short erect setae; gonostipes much longer than wide and as long as harpe; gonostipes ventro-medial lobe not forming posterior process; gonostipes ventral lobe simple, posteriorly truncate; parapenis shallowly bifid; parapenis dorsal margin lacking tubercles; cupula much shorter than gonostipes; basivolsella depressed, short subovate, lacking cuspis posteriorly; basivolsella apex reaching anterior 1/3 of harpe and surpassing penisvalva by 1/2× basivolsella length; basivolsella with large seta-filled pit on internal face, with dense long erect setae on ventral margin, and with sparse long erect setae on dorsal margin; basiura weakly sclerotized with distinct apiceps; apiceps apex with sparse long erect setae; penisvalvae symmetrical; penisvalva broad, expanded ventrad, with distinct anterior and posterior ventral processes; penisvalva lacking setae; endophallus weakly sclerotized.

Frons, vertex, gena, pronotal dorsum, mesoscutum, mesoscutellum, lateral mesopleural face, and metapleuron ventral 1/3 with large confluent punctures; postgenal bridge transversely rugose; clypeus, metapleuron dorsal 2/3, lateral propodeal face ventral 1/2, trochanters, femora, and tarsi with minute sparse punctures; scape, tegula internal margin, metascutellum, T1 posterior margin, and T7 with small dense punctures; pedicel, flagellum, prementum laterally, stipes, and maxillary and labial palpi with minute dense punctures; prementum medially and tegula external margin smooth; propleuron, mesonotal trough, coxae, tibiae, T3–6, and S3–8 with small sparse punctures; metanotal trough longitudinally striate; posterior propodeal face and lateral propodeal face dorsal 1/2 reticulate, with medial subtriangular and sublateral semicircular cell on anterior margin; lateral pronotal face obscurely longitudinally striate; ventral mesopleural face, T1 except posterior margin, and T2 lateral margin with large dense punctures; T2 disc and S1–2 with large sparse punctures; T7 with medial slender impunctate line.

FEMALE. Unknown.

Material examined
1♂. Holotype ♂: **Thailand:** CHIANG MAI: Chiang Dao, Pakia, 1500 m alt., 8.V.2002, T. Ishizaki leg. [TUA].

Sex association
Female unknown.

Distribution
Thailand: Chiang Mai.

Etymology
The specific name *australis*, southern, is the Latin feminine adjective in the nominative case. It suggests that this new species represents the southernmost confirmed record of male *Smicromyrme* in East Asia.

Remarks
Within the *Smicromyrme* s. str., this species, together with *S. lewisi*, *S. rufipes*, and *S. strandi*, is characterized by having the following combination of character states: ocelli moderate, MOD subequal to LOD; antenna mostly black; T7 lacking longitudinal carinae; harpe dorso-internal margin entire, lacking proximal process. This new species differs from them by having the mesosoma orange except ventral face black (at least propodeum black in *S. lewisi* and *S. rufipes*), mesopleuron with ventral impunctate line (mesopleuron lacking impunctate line in *S. strandi*), metacoxal internal carina lamellately projecting (weakly developed in *S. lewisi*, *S. rufipes*, and *S. strandi*), and parapenis shallowly bifid (deeply bifid in *S. lewisi* and *S. strandi*).

Smicromyrme (*Smicromyrme*) *lewisi* Mickel, 1935

Mutilla japonica Cameron, 1900 (non Dalla Torre, 1897): 76, ♀, holotype ♀ (Hakodate, [Hokkaido], Japan) [NHMUK]; André, 1902b: 70, ♀; Schulz, 1906: 158, ♀.
Mutilla cameroni Yano, 1932 (non Schulz, 1906): 326, ♂♀, syntypes ♂♀ (Honshu and Kyushu, Japan) [unknown]; The Natural History Society of Fukui, 1938: 5-35; Kim, 1970: 511; Kim *et al*., 1994: 255.
Smicromyrme cameroni: Suzuki, 1934: 24.
Smicromyrme lewisi lewisi Mickel, 1935: 288, ♂♀, holotype ♀ (Hakodate, Hokkaido Island,

Japan) [NHMUK], examined; Yasumatsu, 1938a: 85, ♀; Kim, 1963: 341; Kim, 1970: 513. New name for *Mutilla japonica* Cameron.

Smicromyrme lewisi nigricula Mickel, 1935: 289, ♂, holotype ♂ (Jyozankei, Hokkaido Island, Japan) [UMSP]. Synonymized by Lelej (1985: 233) under *Smicromyrme lewisi* Mickel.

Smicromyrme lewisi yanoi Mickel, 1935: 289, ♂♀, holotype and allotype ♂♀ (islands of Honshu and Kyushu, Japan) [unknown]; Yasumatsu, 1937: 68; Yasumatsu, 1938a: 85, ♂; Yasumatsu, 1938c: 351, ♀ non ♂; Yasumatsu, 1951: 70, ♂; Kim, 1963: 341; Ishikawa, 1965: 289, ♂♀; Tsuneki, 1965: 12, ♂; Yoshikawa, 1965: 12, ♀; Kim, 1970: 513; Hisamatsu, 2004: 135. New name for *Mutilla cameroni* Yano. Synonymized by Tsuneki (1972b: 16) under *Smicromyrme rufipes lewisi* Mickel. Synonymized by Lelej (1985: 233) under *Smicromyrme lewisi* Mickel.

Smicromyrme rufipes rufipes (non Fabricius, 1787): Chen, 1957: 200, ♂♀.

Smicromyrme momidziyama Tsuneki, 1972b: 17, ♀, holotype ♀ (Momidziyama, Sapporo, [Hokkaidô], Japan) [MNHAH], examined; Yoshida, 1989: 651; Hashimoto & Nakanishi, 1997: 31, ♀. Synonymized by Lelej (2002: 70) under *Smicromyrme lewisi* Mickel.

Smicromyrme rufipes lewisi: Tsuneki, 1972b: 16, ♂♀, examined; Tsuneki 1972d: 59, ♂♀; Lelej, 1976: 272, ♂♀; Nomura, 1978: 16; Lelej, 1981: 78, ♂♀; Yoshida, 1989: 651; Yamada, 1990: 480; Gôukon, 1993: 37, ♂♀; Kim *et al*., 1994: 255; Matsuda & Nakamura, 1996: 57, ♂; Takahashi, 1996: 28, ♂♀; Nakamura & Haneda, 1997: 34, ♂♀; Nakamura & Haneda, 1998: 32, ♀; Togashi, 1998: 285; Matsuda & Nakamura, 1999: 111, ♀; Nakamura *et al*., 2001: 83, ♂; Yamada, 2001: 57, ♂♀; Inoue, 2003: 50; Nambu, 2005: 193, ♂; Kameyama *et al*., 2006: 74, ♀.

Smicromyrme rufipes lewisi f. *nigricula*: Tsuneki, 1972b: 16, ♂; Lelej, 1977a: 91, ♂.

Smicromyrme rufipes: Lelej, 1975: 324, ♂♀; Togashi, 1991: 22.

Smicromyrme (*Smicromyrme*) *rufipes lewisi*: Lelej, 1977b: 530, ♂♀.

Smicromyrme (*Smicromyrme*) *lewisi*: Lelej, 1985: 232, ♂♀; Lelej & Yamane, 1992: 630, ♂♀; Lelej, 1995c: 211, ♂♀; Lelej *et al*., 2001: 9, ♂♀; Lelej, 2002: 70; Lelej *et al*., 2014: 393, ♂♀; Kochetkov & Lelej, 2015: 262, ♂♀; Lelej, 2017: 156; Okayasu, 2020: 9, ♂♀, examined; Pagliano *et al*., 2020: 191.

Smicromyrme rufipes lewisi var. *nigricula*: Yoshida, 1989: 651; Yamada, 2001: 57.

Smicromyrme lewisi: Haneda *et al*., 1998: 335, ♂♀; Takahashi & Matsumoto, 1999: 23, ♀; Yamane, 1999: 380, ♂♀; Haneda & Yamamoto, 2000: 780, ♂♀; Nakamura & Haneda, 2000: 119, ♂; Tano *et al*., 2003: 16, ♂; Nagase, 2004: 1280, ♂♀; Terayama, 2004: 13; Haneda *et al*., 2005: 57, ♂♀; Kinota *et al*., 2005: 25, ♂; Kurokawa, 2005: 76, ♂♀; Negoro *et al*., 2005: 32, ♂♀; Terayama, 2005: 8, 11, ♂♀; Haneda *et al*., 2006a: 5, ♂♀; Haneda *et al*., 2006b: 40, ♂♀; Hua, 2006: 301; Ohkusa, 2006: 22, ♂; Ikudome & Yamane, 2007: 6; Ohkusa, 2007: 30, ♂♀; Yamamoto & Haneda, 2007: 15, ♂; Ohkusa & Tajima, 2008: 69, ♀; Ohkusa & Tajima, 2010: 7, ♂♀; Suda, 2011: 137, ♀; Terayama *et al*., 2011: 20, ♂♀; Ogawa *et al*., 2012: 38, ♀; Tsurusaki *et al*., 2012: 70; Hayashi *et al*., 2013: 25; Nagase *et al*., 2014: 56, ♂; Lo Cascio, 2015: 558; Terayama *et al*., 2016: 168, ♂♀; Notsu, 2019: 6, ♀; Okayasu *et al*., 2018: 304, ♀; Akiyama *et al*., 2021: 141, ♀; Ôtsui *et al*., 2021: 35, ♂; Pagliano & Scaramozzino, 2021: 113, ♂♀; Kan, 2022: 178, ♂♀; Mita *et al*., 2023: 51, ♀.

Smicromyrme lewisii: Kubo, 2000: 318, ♂. Incorrect subsequent spelling.

Smicromyrme rufipes Mickel (sic!): Nakamura *et al*., 2000: 61, ♀. Lapsus calami.

Smicromyrme alberici: Shintani, 2003: 17, ♀. Lapsus calami.

Smicromyrme lewisil: Fukasawa & Miyano, 2010: 25. Incorrect subsequent spelling.

Zoobank LSID

urn:lsid:zoobank.org:act:9B116630-AD12-4439-BB3A-F6A281DDF558
urn:lsid:zoobank.org:act:B3DFD6CF-D849-4C9D-A676-63FB33D570F4
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urn:lsid:zoobank.org:act:F404C19F-B0CC-4DFC-902D-D93AE9E6F2FC

Material examined

309♂188♀. Holotype ♀, *Smicromyrme lewisi* Mickel: **Japan:** HOKKAIDÔ: Hakodate, Lewis, Cameron coll. 1901-137., B.M. TYPE HYM. 15-720, *Mutilla japonica* Cam. Type, = *lewisi* Mickel [NHMUK]. Holotype ♀, *Smicromyrme momidziyama* Tsuneki: **Japan:** HOKKAIDÔ: Sapporo, Momiji-yama, 3–4.VIII.1958, K. Tsuneki leg. [MNHAH (B1-288588)]. **China:** BEIJING: Beijing, 30.V.1938, K. Tsuneki leg. [1♂ MNHAH]; HEILONGJIANG: Mandschurei, Charbin [= Harbin], 7.VII.1954, V. Alin leg., vend. Eing. Nr. 22, 1954, *Smicromyrme strandi lewisi* Mickel, B. Petersen det. 1987 [1♂ ZMUC]; INNER MONGOLIA: Apaka, 10.VI.1939, K. Tsuneki leg. [1♂ MNHAH], 28.VI.1939 [1♂ MNHAH]; LIAONING: Kwantung Prov., [Dalian, Jinzhou], Mt. Daiosho [Mt. Dahei], 4.VIII.1935, M. Hanano leg., *Smicromyrme rufipes rufipes* (Fabricius), C.W. Chen det. [1♀ ELKU]; SHANDONG: Jinan, Longtong, 700 m alt., *Smicromyrme rufipes* (Fabricius), C.E. Mickel det. [1♂1♀ TARI]; ZHEJIANG: Chekiang [= Zhejiang], Chusan [= Zhoushan], 7.9.31, O. Piel leg., *Smicromyrme cyan*. *cyaneiventris* (André), B. Petersen det. 1982 [1♂ TARI]. **Japan:** AICHI: Seto, Jokoji, 6.VI.1975, H. Yamada leg. [1♀ TUA]; Nagoya, Moriyama, Tokoku, 5.VII.1975, H. Yamada leg. [1♀ TUA]; Seto, Mt. Sanageyama, 17.VII.1975, H. Yamada leg. [1♀ TUA]; Sobue, 19.IX.1975, H. Yamada leg. [2♀ TUA]; Asahi, Yawata, 650 m, Decd. f., MT, 18–28.VII.1998, M. Ozawa leg. [1♂ TUA]; CHIBA: Narashino, 10.VII.1918, A. Kato leg. [1♀ TUA]; Kimitsu Dist., Amaha Town, Mt. Nokogiri-yama, 10.VIII.1958, H. Suda leg. [1♂ HSC]; Higashikatsushika, Shonan Town, Takayanagishinden, 25.VII.1966, H. & T. Suda leg. [1♂1♀ HSC]; Kimitsu Dist., Seiwa Vill., Mt. Kanô-zan, 9.VIII.1966, H. & T. Suda leg. [1♂1♀ HSC]; Sakura City, Usui, 6.VIII.1968, H. Suda leg. [2♂ HSC]; Chosei Dist., Chonan Town, Mt. Kasamori-yama, 16.VII.1970, H. Suda leg. [1♀ HSC]; Sakura City, Ohja-machi, 14.VIII.1970, H. Suda leg. [1♂1♀ HSC]; Sakura City, Iida, 15.X.1970, H. Suda leg. [1♀ HSC]; Sanbu Dist., Shibayama, 6.VIII.1971, H. Suda leg. [1♂ HSC]; Mabashi, 20.VIII.1973, S. Katsuya leg. [2♂ NARO], 21.VII.1974 [1♀ NARO], 28.VII.1974 [5♀ NARO], 26.VII.1975 [4♂5♀ NARO]; Kimitsu City, Kawamata-Kusagawara, Mt. Mitsuishi-yama, 28.VI.1980, H. Suda leg. [1♂ HSC]; Narita City, Narita, 25.VII.1980, H. Suda leg. [1♂ HSC]; Chiba City, Takada-cho, 5.VIII.1995, H. Suda leg. [1♂ HSC]; Sakura City, Yagi, 31.V.1998, H. Suda leg. [1♂ HSC]; Youkaichiba-shi [= Sousa-shi], Kagobeta, 21.VII.1999, T. Ito leg. [1♂ EUMJ]; Ichikawa City, Horinouchi, 6.VIII.2002, H. Suda leg. [1♂1♀ HSC], 3.IX.2003 [1♀ HSC]; Ichikawa City, Kitakokubun, Kotsukayama-kôen, 6.VIII.2002, H. Suda leg. [1♂ HSC], 3.IX.2003 [1♀ HSC]; Ichikawa City, Kounodai, Satomi-kôen, 4.IX.2002, H. Suda leg. [1♀ HSC]; Sakura City, Tsuchiuki, 4.VIII.2004, H. Suda leg. [1♂ HSC], 2.IX.2004 [1♀ HSC]; Chosei, Nagara, Ueno, 10.VIII.2004, H. Suda leg. [2♂1♀ HSC]; Shiroi City, Ki, 26.VII.2006, H. Suda leg. [1♂ HSC]; Shiroi City, Shishiba, 10.IX.2006, H. Suda leg. [1♀ HSC], 28.IX.2006 [1♀ HSC], 17.VIII.2009 [1♀ HSC]; EHIME: Matsuyama, Tarumi, 6.VIII.1948, M. Miyatake leg. [1♂ EUMJ]; Matsuyama, 3.VIII.1951, M. Miyatake leg. [1♂ EUMJ]; Matsuyama, 4.VII.1955, F. Takechi leg. [1♀ EUMJ]; Matsuyama, Dogo, 5.IX.1955, M. Miyatake leg. [1♀ EUMJ]; Oda-cho [= Uchiko-chô], 16.VI.1984, E. Yamamoto leg. [1♀ EUMJ], 10.VIII.1996 [1♀ EUMJ], 13.VIII.1996 [1♀ EUMJ], 7.VI.1997 [2♀ EUMJ], 21.VI.1997 [1♀ EUMJ], 15.VII.1999 [1♂

EUMJ]; Odamiyama, Koyayama, 22.VIII.1991, E. Yamamoto leg. [1♂ EUMJ]; Kumakogen, Yurano, 28.VI.2006, E. Yamamoto leg. [1♂ EUMJ]; Houjou-City [Matsuyama-shi], Mt. Takanawa, 2.X.2004, T. Kitano leg. [1♀ EUMJ]; Matsuyama-shi, Sugezawa, 21.V.2016, K. Kuroda leg. [1♂1♀ (*in copula*) EUMJ]; Matsuyama, Tsuwaji-shima Is., beach, 33°58'30"N 132°30'29"E, 14.VI.2020, K. Kuroda & K. Yasuda leg. [2♂2♀ EUMJ]; FUKUI: Monjusan, 12.VIII.1962, K. Tsuneki leg. [1♂ NMNH]; FUKUOKA: Buzen, Hikosan-Morizane, 18.VII.1929, Esaki &Fujino leg., *Smicromyrme rufipes lewisi* Mickel, B. Petersen det. 1981 [1♂ ZMUC]; Chikuzen, Fukuoka, 3.IX.1930, K. Yasumatsu leg., *Smicromyrme rufipes lewisi* Mickel, B. Petersen det. 1981 [1♀ ZMUC]; Chikuzen, Kugumiya, 23.VII.1947, N. Gyotoku leg. [1♂ KMNH]; Kugumiya, 28.VII.1948, N. Gyotoku leg. [2♂ KMNH], 9.VII.2002 [1♂ KMNH], 12.VII.2002 [1♂ KMNH]; Asakura, Kugumiya, 11.VI.1949, N. Gyotoku leg. [1♀ KMNH]; Chikushino-city, Yoshiki, at light, 11.VIII.1991, N. Gyotoku leg. [1♂ KMNH], 15.VIII.1990 [1♂ KMNH], 16.IX.1990 [1♂ KMNH], 8.VII.1993 [1♂ KMNH]; Chikushino-city, Yoshiki, 14.VIII.1993, N. Gyotoku leg. [1♂ KMNH]; Asakura-gun, Kugumiya-mura, at light, 27.VII.2001, N. Gyotoku leg., *Smicromyrme lewisi yanoi* Mickel, K. Yasumatsu leg. [1♂ KMNH]; Asakura-gun, Kugumiya-mura, 29.VII.2001, N. Gyotoku leg. [1♂ KMNH], 12.VII.2002 [1♂ KMNH]; Yame-gun, Shimohirokawa-mura, Fujita, 13.VI.2007, N. Gyotoku leg. [1♀ KMNH]; Fukuoka-shi, Noko Is., 3.VII.2015, S. Imada leg. [1♀ EUMJ]; Higashi-ku, Nata-kaigan, 9.VII.2017, T. Kawano leg. [1♂ ELKU]; Fukuoka-shi, Nishi-ku, Motooka, Kyushu Univ., 33.593°N 130.215°E, 8.VII.2019, Y. Hisasue leg. [1♀ ELKU]; Tagawa-gun, Soeda-machi, Mt. Hiko-san, 33°28'57"N 130°54'33"E, 30.VII.2019, Y. Hisasue leg [1♂ ELKU]; Itoshima-shi, Shimakeya, 22.V.2021, J. Abe leg. [1♂ ELKU]; Soeda-mchi, Hiko-san, alt. 679 m, 22.VII.2021, LT, S. Tomura leg. [2♂ ELKU]; Tagawa-gun, Soeda cho, Mt. Hiko, 33.482°N 130.909°E, alt. 650 m, MT [= Malaise trap], 23.VII.2021, Kyushu Univ. leg. [1♂ ELKU]; Fukuoka-shi, Nishi-ku, Imazu Beach, 33.610°N 130.258°E, 4.VII.2022, Y. Hisasue leg. [1♂ ELKU]; FUKUSHIMA: Iwabe, 26.VIII.1992, Y. Nishijima leg. [1♂ SEHU]; Tadami, Mt. Asakusa-dake, MT-D in area disturbed by debris flow, 782 m, 13.VIII–13.IV.2020, Y. Okatsu & Y. Nakano leg. [1♂ SEHU]; GIFU: Hirugano, 20.VII.1975, H. Yamada leg. [3♀ TUA]; GOTÔ ISLANDS: Is. Nozaki-shima, 30.VII.1971, T. Okadome leg. [1♀ ZMUC]; HIROSHIMA: Ôta-gawa, st. 5, 24.VII.1993, S. Nakamura leg. [4♂ HMNH], 2.X.2003 [1♀ HMNH]; Gôno-kawa, st. 5, 11.X.1994, S. Nakamura leg. [1♀ HMNH]; Ashida-gawa, st. 4, 16.VII.1997, S. Nakamura leg. [1♀ HMNH]; Gôno-kawa, st. 4, 10.VIII.1999, S. Nakamura leg. [1♂ HMNH]; Shôbara-shi, Honmura-chô, 19.VIII.1997, B. Maeto leg. [3♂ HMNH], 23.VII.2000 [1♂ HMNH]; [Akitakata-shi], Yachiyo-chô, Haji Dam, St. 2, 12.VII.2000, S. Nakamura leg. [1♂ HMNH]; Yamagata-gun, Akiôta-chô, Kake, Nukui Dam, 9.VIII.2007 [1♀ HMNH]; Hatsukaichi-shi, Miyauchi, Akashi, 13–15.VIII.2015, S. Imada leg. [1♀ EUMJ]; HOKKAIDÔ: Jyôzan, 3.VIII.1913 [1♂ SEHU]; Fujinosawa, 22.VII.1928, Uchida leg. [1♀ SEHU]; Zenibako, 26.VII.1938, Y. Sugihara leg. [1♂1♀ (*in copula*) SEHU]; Sounkyo, 17.VII.1953, T. Ishihara leg. [1♀ EUMJ]; Bankei, 23.IX.1958, F. Mochida leg. [1♂ SEHU]; Jyozankei, 16.VII.1959, K. Sato leg. [1♂ NSMT]; Ishikari, Momijiyama, 5.VIII.1968, T. Nambu leg. [1♂ NSMT]; Sapporo, 10.VII.1973, T. Kumata leg. [1♀ SEHU]; Shumarinai, 22.VII.1980, H. Nishino leg. [1♀ MTC]; Satsunai-gawa, Nananosawa, 17.VIII.1982, Y. Nishijima leg. [1♂ SEHU]; Okushiri Is., 10.VIII.'85, M. Munakata leg. [1♀ SEHU]; Jôzankei, 7.VIII.1987, Y. Nishijima leg. [1♂ SEHU]; Rumoi-shi, Horonuka, 10.VII.'90 [2♂ SEHU]; Kamikawa-gun, Nikyu near Simukappu, 4.VIII.1993, T. Munakata leg. [1♂1♀ SEHU]; Chitose-ko lake, 12.VIII.1994, S. Hori leg. [1♀ TUA]; Moiwa, 23.VII.1996, J. Kodaka leg. [1♂ SEHU]; Toubetsu, Aoyamaoku, 23.IX.2006, M. Ohara leg. [1♀ SEHU]; Hakodate City, Setogawa-cho, 1.VIII.2007, H. Suda leg. [3♂ HSC]; Kamishihoro-chô, Mitsumata, 43.507N 143.140E, 20.VII.2014, N. Kikuchi leg. [1♂1♀ SEHU]; Teshio-gun, Enbetsu-chô, Fujimi, 44.710N 141.787E, 29.VI.2015, N. Kikuchi leg.

[1♀ SEHU]; Ishikari-shi, Hama-machi, Hamanasu-no-oka kôen, 43°15'29"N 141°21'45"E, 7.VII.2017, J. Okayasu leg. [1♂ EUMJ]; Sapporo, Minami-ku, Toyama, large gap in forest, flying 15 cm above ground, 42°58'31.1"N 141°15'29.8"E, 270 m alt., 26.VI.2022, 10:45, J. Okayasu leg. [1♂ SEHU]; Kato-gun, Kamishihoro-cho, Mitsumata, 43.551N 143.155E, YPT, 27–28.VII.2022, J. Abe leg. [1♂ ELKU]; Jyôzan, 12.VII [1♂ SEHU]; Takasago, 24.VII [1♂ SEHU]; HYÔGO: Harima, 20.VI.1912 [1♂ SEHU]; Higami, Higakyokoku, 17.VII.1972, S. Ueda leg. [1♂ ZMUC]; Is. Awajishima, Mt. Senzan, 8.VIII.1974, S. Ohkusa leg. [1♂ ZMUC]; Awaji, Narutodai, 1.VIII.'98 [1♀ EUMJ]; Himeji City, Hiromineyama, 22.VII.1991, H. Suda leg. [1♂ HSC]; Harima, Kuzaki, M. Yamanaka leg. [1♂1♀ NSMT]; IBARAKI: Yatabe, 10–15.VII.1982, N. Fukuhara leg. [1♂ NARO]; 1 Hitachinaka City, Ajigaura, 23.VII.1997, K. Toyoda le. [1♀ TUA]; Hitachinaka-shi, Ibaraki Prefectural Seaside Park, 15.VIII.1999, T. Toba leg. [1♀ TUA]; Kitaibarakishi, Sadanami, 18–30.VII.2002, Malaise trap, H. Goto leg. [1♂ FFPRI], 30.VII–13.VIII.2002 [7♂ FFPRI], 13–27.VIII.2002 [1♂ FFPRI], 27.VIII–10.IX.2002 [1♂ FFPRI]; Satomi-mura, Okami, 12–26.VIII.2003, Malaise trap, S. Makino et al. leg. [1♂ FFPRI], 29.VII–12.VIII.2003 [2♂ FFPRI]; Hitachinaka-shi, Ajigaura-kaigan, 13.X.2002, H. Ono leg. [1♀ TUA]; Hitachinaka-shi, Ajigaura Coast, 18.VII.2003, H. Ono leg. [10♂2♀ TUA]; IWATE: Koiwai, 9.VIII.1975, T. Nambu leg. [1♂ NSMT]; IZU ISLANDS: Izu-oshima, Oshima-machi, Motomachi, 17.VIII.2012, K. Tsuji leg. [1♀ TUA]; Izu-oshima Isl., Oshima Town, Motomachi, Kamitatsu, 17.VIII.2012, YPT, K. Tsuji leg. [1♂ TUA]; KAGOSHIMA: Chiran, 12.VII.1963, Y. Kurosawa leg. [1♂ NSMT (NSMT-Hym No. 4871)]; Minami-ôsumi-chô, Satamagome, Tajiri, Sata-misaki, 16.VII.2011, H. Yoshitake leg. [1♀ EUMJ]; KANAGAWA: Mt. Tanzawa, Hinokiboramaru, 5.VIII.1985, N. Ohbayashi leg. [1♂1♀ (*in copula*) EUMJ]; Hatano [2♂ SEHU]; KÔCHI: Tosa [= Kôchi], Kuroson, 29.VII.1954, A. Kato leg. [1♂ TUA]; Muroto C., Sakihama, 3.IX.1995, Y. Kawakami leg. [4♂ EUMJ], 14.IX.1995 [2♂ EUMJ], 15.IX.1995 [2♂ EUMJ], 2.VI.1996 [1♂ EUMJ], 6.VI.1998 [1♂ EUMJ]; Mt. Kajigamori, 14.VII.1996, Y. Kawakami leg. [5♂ EUMJ]; Nishitosa V. [Shimanto-shi], Egawasaki, 3.VIII.1997, Y. Kawakami leg. [1♀ EUMJ]; Nankoku-shi, Inabu, Hayashidani, 4.IX.2001, T. Befu leg. [1♀ EUMJ]; Tôwa-son [= Shimanto-chô], Mishima, 28.VII.2002, Y. Kawakami leg. [2♀ EUMJ], 4.VIII.2002 [1♀ EUMJ], 14.IX.2004 [5♀ EUMJ]; Kochi-shi, Hitsuzan, 5.IX.2002, Y. Kawakami leg. [1♀ EUMJ], 4.VI.2006 [1♀ EUMJ], 6.VI.2006 [1♀ EUMJ]; Muroto-shi, Sakihama-chô, Irugi, 19.IX.2005, Y. Kawakami leg. [4♀ EUMJ], 19.IX.2005 [1♀ EUMJ]; Tosa-shi, Hageyama, 16.VII.2006, Y. Kawakami leg. [12♂ EUMJ], 24.VII.2006 [1♀ EUMJ], 21.VII.2007 [10♂ EUMJ]; Tosashimizu-shi, Shimonokae, 5.VII.2007, Y. Kawakami leg. [1♂ EUMJ]; Shimanto-chô, Mishima, 22.VII.2007, Y. Kawakami leg. [1♂ EUMJ]; Aki-shi, Nakagô, Ioki,, 8.IX.2008, Y. Kawakami leg. [1♀ EUMJ]; KUMAMOTO: Kumamoto, 23.VII.1909, H. Kawamura leg. [1♀ SEHU]; Kumamoto City, Kita Ward, Ueki Town, Koga, 26.VI.2016, K. Narita leg. [1♂ EUMJ]; KYÔTO: Shûgakuin, 8.VI.1959, T. Shyôji leg. [1♀ NSMT]; Aobasan, 28.VII.1970, K. Tsuneki leg. [1♀ NMNH]; MIYAZAKI: Hyûga [= Miyzaki], Takanake, VI.1945, T. Nakane leg. [1♀ SEHU]; NAGANO: Kitasaku Dist., Karuizawa Town, Asama-kôgen, 23.VIII.1967, T. & H. Suda leg. [1♂ HSC]; Kiso, Ohdaira-kohgen, 19.VII.1975, Y. Hori leg. [1♀ TUA]; Ohmachi City, Taira, Mt. Koguma-yama, 12.VIII.1976, H., T. & Y. Suda leg. [2♂ HSC]; Komagane City, Komagane-kohgen, Komagaike-Furujyô, 6.VIII.1980, H., T. & Y. Suda leg. [1♂ HSC]; Sanada-machi [= Ueda-shi], Torii-tôge, 23.VII.2005, K. Nakamura leg. [1♂ TPM]; NARA: Tenri City, 24.VII.1959, I. Miyagi leg. [1♀ EUMJ]; Yoshino, Miyataki, 9.VIII.1974, S. Ueda leg. [1♀ ZMUC]; Nara-shi, Zoushi-chou, Mt. Kasuga-yama, 21.VIII.2003, T. Tsuru leg. [2♀ TUA]; NIIGATA: Hime-kawa, 17.VIII.2001, T. Tsuru leg. [1♂ TUA], 18.VIII.2001 [1♀ TUA]; ÔITA: Bungo, Sobosan, 4.VIII.1931, K. Yasumatsu leg. [1♀ ELKU]; Ôita-gun, Hasama-machi, Furuno, 14.IX.2000, T. Miyake leg. [1♀ EUMJ]; OKAYAMA: [Maniwa-shi], Hiruzen Kohgen, 21.VII.1996, Y.

Kawakami leg. [7♂1♀ EUMJ]; Kasaoka-shi, Kitagi-jima Is., Ohura, 30.VI.2003, T. Ishikawa leg. [1♀ TUA]; OKI ISLANDS: Dôgo, Saigô, 16.VIII.1963, H. Kadowaki leg. [1♂ NARO]; SAITAMA: Togasaki, 21.VI.1945 [1♀ NARO]; Okutama, Kita-akikawa, 27.VIII.1965, S. Katsuya leg. [1♀ NARO]; Hodosan, 8.VIII.1966, T. Nambu leg. [1♂ NSMT]; Nagatoro, 21.VII.1968, T. Nambu leg. [1♂ NSMT]; Nagatoro, 22.VII.1969, T. Nambu leg., *Smicromyrme rufipes lewisi* Mickel, K. Tsuneki det. 1972 [2♂ NSMT]; Nakatsugawa, 17.VIII.1969, T. Nambu leg. [1♂ NSMT]; Konosu, Hikawa-jinjya, 28.VI.1970, T. Nambu leg. [1♂ NSMT]; Chichibu, Shinpukuji, 14.VII.1973, T. Nambu leg. [1♂ NSMT]; Minano, 3.VIII.1973, T. Nambu leg. [1♂ NSMT]; Hikigun, 14.VII.1974, M. Terayama leg. [1♂ MTC]; Ôtaki, Mizuba–Kawamata, 4.VIII.1974, T. Nambu leg. [1♂ NSMT]; Ogose, 23.VII.1981, T. Nambu leg. [4♂ NSMT, 1♂ TUA]; Kasayama, Ogawa, 13.VII.1994, M. Uchida leg. [3♂ NSMT]; Ranzan, Sugaya, 17.VII.1996, K. Toyoda leg. [1♀ TUA]; SHIMANE: Izumo-shi, Sashiumi, 35°20.234°N 132°39.909°E, 16–17.VII.2017, H. Yoshitomi leg. [1♂ EUMJ]; SHIZUOKA: Kanaya, 3.VIII.1947, J. Minamikawa leg. [3♂ NARO], 10.VIII.1947 [9♂ NARO], 13.VIII.1947 [2♂ NARO], 6.VIII.1948 [3♂ NARO], 24.VII.1950 [1♂ NARO], 25.VII.1950 [1♂ NARO], 21.IX.1952 [1♂ NARO], 19.VIII.1954 [2♂ NARO]; Mt. Hakkô-san, 24.VII.1948, J. Minamikawa leg. [2♂ NARO]; Kasuisai, 8.VIII.1948, J. Minamikawa leg. [1♂ NARO]; Ogasayama, 20.VIII.1948, J. Minamikawa leg. [1♂ NARO]; Mochimune, 15.VII.1950, J. Minamikawa leg. [2♂ NARO]; Izu, Shimoda, 21.VIII.1957, T. Nambu leg. [2♂ NSMT]; Izu, Shimoda, 21.VIII.1957, T. Nambu leg., *Smicromyrme rufipes lewisi* Mickel, K. Tsuneki det. 1972 [1♀ NSMT]; Izu, Shirahama, 21.VIII.1957, T. Nambu leg. [2♂ NSMT]; Abe-gun, Dainititoge, 5.VIII.1959, J. Minamikawa leg. [1♂ NARO]; Abe-tôge, 8.VIII.1960, J. Minamikawa leg. [1♂ NARO]; Fujinomiya-shi, Fumoto, 11.IX.2003, K. Iijima leg. [1♀ TUA]; Numazu-shi, Ita, 10–30.V.2013, MsT [= Malaise trap], H. Handa leg. [1♂ TUA], 30.V–29.VI.2013 [2♂ TUA], 29.VI–23.VIII.2013 [8♂ TUA]; TOCHIGI: Utsunomiya, Nagaoka, 21.IX.1980, K. Nakamura leg. [1♀ TPM], 10.VIII.1980 [2♀ TPM]; Nakakasuo, Awano, 15.VII.1981, K. Kubota leg. [1♂ TPM]; Nogi T., Watarase Marsh, 4.VII.1993, H. Ohkawa leg. [1♀ TPM]; Motegi-machi, Magino, 22.V.1994, K. Satoh leg. [1♀ TPM]; Kuroiso-shi, Nabekake, Nakagawa River, 2.VI.1994, K. Satoh leg. [1♀ TPM]; Fujiwara-machi [= Nikkô-shi], Yokokawa, 21.VII.1997, K. Sato leg. [1♀ TPM]; Takanezawa-machi, Fubasami, 3.VIII.2006, K. Kagawa leg. [1♂ TPM]; Nikkô-shi, Kamimiyori, Kamimiyori-shiobaraonsenguchi Station, 20.VII.2020, N. Kikuchi leg. [3♂3♀ (*in copula*) SEHU]; TOKUSHIMA: Awa [= Tokushima], Koyadaira, 25.VII.[19]13, E. Gallois leg. [1♀ SEHU]; Kaifu T. [= Kaifu-gun, Kaiyô-chô], Yoshida, 11.VII.1999, Y. Kawakami leg. [3♂ EUMJ]; TÔKYÔ: Meguro, IX.1914, M. Yamanaka leg. [1♀ NSMT], 21.VII.1916 [1♂ NSMT], 17.IX.1916 [1♀ NSMT], VII.1929 [2♂ NSMT], no date [1♂ NSMT]; Tachikawa, 1.VII.1928, K. Sato leg. [1♂ NSMT]; [Okutama-machi], Hikawa-mura, Kurasawa, on the ground, 21.VII.1935 [2♀ KMNH]; Totuka, 23.VII.1937 [1♀ NSMT], 22.VIII.1938 [1♀ NSMT]; Nishiogikubo, 5.VIII.1938, M. Kawai leg. [1♀ NARO], 15.VII.1939 [1♀ NARO], 3.VII.1940 [1♀ NARO], 4.VII.1940 [1♂1♀ NARO], 13.VII.1941 [1♂ NARO]; Fuchû, 11.VIII.1939, Nagasawa leg. [1♂1♀ NARO], 15.VIII.1939 [1♂ NARO], 18.VIII.1939 [1♂ NARO], 5.IX.1939 [1♂ NARO]; Yoyogi, 19.VIII.1952, A. Kato leg. [1♂ TUA]; Ôta-ku, Haramachi near Tamagawa, 26.VII.1953, S. Katsuya leg. [1♂ NAO]; Kanamachi, 30.VII.1953, S. Yoshioka leg. [1♀ NSMT], 20.VI [1♀ NSMT], 26.VI [1♀ NSMT], 2.VII [1♀ NSMT], 7.VII [1♀ NSMT], 21.VII [1♀ NSMT], 22.VII [1♀ NSMT], 25.VII [7♂5♀ NSMT], 26.VII [5♂ NSMT], 30.VII [1♂2♀ NSMT], 11.VIII [1♀ NSMT], 12 [1♀ NSMT]; Mt. Takao-san, 2.VIII.1953, J. Minamikawa leg. [4♂8♀ NARO]; Ôta-ku, Magome, Ômori, 24.VII.1955, S. Katsuya leg. [1♂ NARO]; Mt. Takao, 27.VII.1955, A. Habu leg. [1♀ NARO]; Yoyogi, 25.IX.1955 [1♀ TUA]; Setagaya, 18.VIII.1957, S. Katsuya leg. [1♀ NARO]; Hachiohji City, Takao-machi, Takao-san-Shiroyama, 16.VII.1975, H. Suda

leg. [1♂ HSC]; Hachiôji, Katakura, 2.VIII.1989, M. Tomokuni leg. [1♀ NSMT]; Hachio-ji, 3.VIII.1998, M. Terayama leg. [1♀ MTC]; Suginami, 25.VII, J. Yoshioka leg. [1♂ NSMT]; WAKAYAMA: Seto, 5.VII.1929, H. Katayama leg., *Smicromyrme lewisi yanoi* Mickel, C.E. Mickel det. 1934 [1♀ ELKU]; YAMAGUCHI: Iwakuni-shi, 5.IX.2004, M. Terayama leg. [1♀ MTC]; YAMANASHI: Kohfu City, Ikari-cho, Shôsenkyô, 24.VIII.1971, H. Suda leg. [1♂4♀ HSC], 10.VIII.1977 [1♂ HSC]; Ohtsuki City, Ohtsukimachi, Magi, Kuwanishi, 19.VII.1997, H. Suda leg. [1♂ HSC]. **North Korea:** NORTH PYONGAN: Around Habiro, Mt. Myohyang-San, Alt. ca. 200–550 m, 30.VI.2009, C. Han leg. [1♀ EUMJ]; SOUTH PYONGYANG: South Pyongyang, Pyongyang Hotel garden, 14.VIII.1971, S. Horvatovich & J. Papp leg. [2♂ MNHAH]. **Russia:** AMUR: Amur Oblast, Semenovka, 6.VII.1975, A.S. Lelej leg. [1♂1♀ ZMUC]. **South Korea:** DAEJEON: Corea [= Korea], Loc. Taiden [= Daejeon], Tiunan, 29.VIII.1933, K. Okazaki leg. [1♀ ELKU, 1♀ ZMUC]; GANGWON: Genzan [= Wonsan], 2.VIII.1919, E. Gallois leg., *Smicromyrme lewisi* Mickel, Lelej det. 2001 [1♀ SEHU]; GYEONGGI: Suigen [= Suwon], 10.VII.1924, K. Sato leg. [2♀ NSMT], 10.VI.1925 [2♂ NSMT], 1.VIII.1927 [1♂ NSMT], IX.1928 [1♀ NSMT], VI.1930 [1♂1♀ NSMT], VI.1931 [1♂ NSMT], no date [3♂ NSMT]; Suigen [= Suwon], VI.1930, K. Sato leg., *Smicromyrme rufipes lewisi* Mickel, B. Petersen det. 1981 [1♂ ZMUC]; Dongducheon, Soyosan, 15.VI.1941 [1♂ MNHAH], 18.VI.1943 [2♂1♀ (1♂1♀ *in copula*) MNHAH]; Seoul, 20.VIII.1942 [1♂ MNHAH]; GYEONGSANGBUK: Kyongsangpuk-do [= Gyeongsangbuk-do], Andong, 4.VI.1970, H. Yamada leg. [1♂ TUA]; Hwasan, 19.VII, Uchida leg. [1♂ SEHU].

Identification source
Voucher specimens (Okayasu, 2020).

Sex association
This species was initially described from the female only. The male was associated by Mickel (1935) based on males and females collected at same place and time.

Distribution
China: Anhui, Beijing, Fujian, Hebei, Heilongjiang, Inner Mongolia, Jiangsu, Jiangxi, Liaoning*, Shandong, Shanxi, Zhejiang* (Chen, 1957; Hammer, 1949; Yasumatsu, 1951). Mongolia (Lelej, 1976, 1977b). Japan: Awaji-shima Island, Gotô Islands (Nozaki-jima Island), Hokkaido, Honshu (Aichi, Aomori, Chiba, Fukui, Fukushima, Gifu, Gunma, Hiroshima, Hyôgo, Ibaraki, Ishikawa, Iwate, Kanagawa, Kyôto, Miyagi, Nagano, Nara, Niigata, Okayama, Saitama, Shiga, Shimane, Shizuoka, Tochigi, Tôkyô, Tottori, Toyama, Wakayama, Yamaguchi, Yamanashi), Izu Islands (Izu-ôshima Island), Kyûshû (Fukuoka, Kagoshima, Kumamoto, Miyazaki, Ôita), Oki Islands (Dôgo), Okushiri-tô Island, Ôsumi Islands (Tanega-shima Island, Iô-jima Island), Shikoku (Tokushima, Ehime, Kôchi), Tsushima Island (Gôukon, 1993; Haneda *et al*., 2006ab; Lelej & Yamane, 1992; Munakata, 1987; Negoro *et al*., 2005; Ogawa *et al*., 2012; Ohkusa & Tajima, 2010; Suda, 2011; Tano *et al*., 2003; Terayama *et al*., 2011; Togashi, 1991; Tsuneki, 1972b; Tsurusaki *et al*., 2012; Yamada, 2001; Yamane, 1999; Yasumatsu, 1937). Kuril Islands (Kunashir Island) (Lelej, 1985). North Korea: Kangwon, North Pyongan, South Pyongyang. Russia: Amur, Buryatia, Irkutsk, Khabarovsk, Khakassia, Krasnoyarsk, Primorsky, Sakhalin, Tuva, Zabaykalsky (Lelej, 1977a, 1981; Lelej *et al*., 2014). South Korea: Chungcheongnam, Daejeon, Gangwon, Gyeonggi, Gyeongsangbuk, Gyeongsangnam, Jeju, Jeollanam, Pyongyang (Lelej *et al*., 2001).

Remarks

This species was found sister to the type species, *S. rufipes*, by the present analyses. This species utilizes the ground-nesting wasps *Gorytes tricinctus* (Pérez, 1905), *Tachysphex nigricolor nigricolor* (Dalla Torre, 1897) (Hymenoptera: Crabronidae), and *Cerceris hortivaga* Kohl, 1880 (Hymenoptera: Philanthidae) (Gôukon, 1993; Tsuneki, 1965).

Smicromyrme (*Smicromyrme*) *strandi* (Zavattari, 1913)

Mutilla strandi Zavattari, 1913: 36, ♂, lectotype ♂ (Taihorin [= Dalin], [Chiayi], Formosa) [ZMNB], designated by Mickel (1933a: 416).
Smicromyrme strandi: Mickel, 1933a: 416, ♂; Suzuki, 1934: 25; Mickel, 1935: 275, ♂; Lelej, 1995b: 26, ♂♀; Lelej, 2002: 72; Lelej, 2005: 64; Hua, 2006: 301; Pagliano, 2011: 42, ♂; Lo Cascio, 2015: 559; Okayasu, 2020: 20; Pagliano *et al*., 2020: 192.
Smicromyrme rufipes strandi: Chen, 1957: 201, ♂♀, examined; Tsuneki, 1972c: 21, ♂♀; Tsuneki, 1993a: 39, ♂; He *et al*., 2004: 956, ♂.

Zoobank LSID
urn:lsid:zoobank.org:act:C28A9754-6D91-47DC-8A72-50991B809693

Material examined
6♂3♀. **China:** FUJIAN: Fukien [= Fujian], Shaowu, Shuipeikieh [= Shui Pei Kai], 24.V.1944, T.C. Maa leg., *Smicromyrme strandi strandi* (Zavattari), B. Petersen det. 1987 [1♂ TARI]; JIANGXI: [Lushan, Jiujiang], Kuling [= Guling], 3.8.35, O. Piel leg., *Smicromyrme strandi strandi* (Zavattari), B. Petersen det. 1987 [1♂ TARI], 6.8.35 [1♂ TARI], 10.8.35 [2♂ TARI]. **Taiwan:** PINGTUNG: Zhuitan, Donggang Riv., N22.5496 E120.5093, 40 m alt., 20.V.2017, T. Mita leg. [1♀ ELKU]; TAITUNG: [Beinan], Chipon [= Chihpen], 18.VIII.1936, K. Iida leg., *Smicromyrme strandi* (Zavattari), A. Lelej det. 1994 [1♀ NSMT (NSMT-Hym No. 3322)]; UNKNOWN PREFECTURE: Tnpim, 3.IV.07, Matsumura [1♂ SEHU]; Inoue, 14.VI.1925, T. Kano leg., *Smicromyrme strandi* (Zavattari), A. Lelej det. 1994 [1♀ NSMT (NSMT-Hym No. 1094)].

Identification source
Voucher specimens (Chen, 1957).

Sex association
This species was initially described from the male only. The female was associated by Tsuneki (1972c) based on males and females collected at same place and time.

Distribution
China: Fujian, Guangdong, Jiangxi, Zhejiang (Chen, 1957; Lelej, 1995b). Taiwan: Chiayi, Nantou, Pingtung*, Taichung, Tainan, Taipei, Taitung*, Taoyuan (Chen, 1957; Tsuneki, 1972c; Zavattari, 1913).

Remarks
The distributional range of this species and *S. lewisi* overlaps in southern China. In the male morphology, *S. strandi* is distinguished from *S. lewisi* only by the mesosoma mostly red and mesopleuron lacking ventral impunctate line.

Species tentatively placed in *Smicromyrme*

Smicromyrme caeruleus Mickel, 1934

Smicromyrme caerulea Mickel, 1934: 201, ♂, holotype ♂ (Samar, Philippines) [NMNH]; Mickel, 1935: 284, ♂; Baltazar, 1966: 209; Lelej, 2005: 57; Lo Cascio, 2015: 558.
Smicromyrme caeruleus: Pagliano *et al*., 2020: 193.

Zoobank LSID
urn:lsid:zoobank.org:act:488C1190-DB1E-4CAD-87B6-B536FDE7A434

Material examined
No material examined.

Sex association
Female unknown.

Distribution
Philippines: Samar (Mickel, 1934).

Remarks
This species probably belongs to the *Sinotilla* by having the frons longitudinally striate, mandible apically bidentate and not emarginate ventrally, and F1 length 1/4× F2 length (Mickel, 1934).

Smicromyrme devius (Cameron, 1909)

Mutilla devia Cameron, 1909: 147, ♂, holotype ♂ (Kuching, [Sarawak], Borneo, [Malaysia]) [NHMUK].
Smicromyrme devia: Mickel, 1935: 284, ♂; Lelej, 2005: 59; Lo Cascio, 2015: 558.
Smicromyrme devius: Pagliano *et al*., 2020: 195.

Zoobank LSID
urn:lsid:zoobank.org:act:D76983BD-E6D3-4AF2-A0B8-8B2CD7F0AEFB

Material examined
No material examined.

Sex association
Female unknown.

Distribution
Malaysia: Sarawak (Cameron, 1909).

This species was recorded from Simueloe Island (= Simeulue, Indonesia) by Zavattari (1914: 92). This record was not accepted by Mickel (1935), but reexamination of voucher specimens is needed.

Remarks
This species probably belongs to the *Sinotilla* by having the frons longitudinally striate and F1 length 1/4× F2 length (Cameron, 1909).

Smicromyrme electra Mickel, 1935

Mutilla unimaculata (non Smith, 1857): Smith, 1861: 75, ♂.
Smicromyrme fredericki Mickel, 1935: 203. Nomen nudum.
Smicromyrme electra Mickel, 1935: 280, ♂, holotype ♂ (Macassar, [Sulawesi Selatan], Celebes, [Indonesia]) [OUMNH]; Lelej, 2005: 59; Lo Cascio, 2015: 558; Pagliano *et al*., 2020: 195; Brothers, 2022: 62, ♂.

Zoobank LSID
urn:lsid:zoobank.org:act:BFD30FDC-00C8-4498-A48D-7EE70AFA158E

Material examined
No material examined.

Sex association
Female unknown.

Distribution
Indonesia: Sulawesi Selatan (Mickel, 1935).

Remarks
Photos of the holotype of this species are available in Brothers (2022: Fig. 112). This species probably belongs to *Sinotilla* by having the frons longitudinally striate, vertex elevated, mandible apically bidentate and emarginate ventrally, F1 length 2/5× F2 length, mesosoma mostly red, T2–3 with a posterior pale setal band, and S2 with a lateral felt line (Brothers, 2022; Mickel, 1935). According to the identification label by B. Petersen, this species is synonymous with *S. minahassae*. However, *S. minahassae* has the T1 with posterior setal band less developed and T4 with black setae (Brothers, 2022), and full species status is accepted here. Examination of the male genitalia is needed to test this synonymy.

Smicromyrme herophile Mickel, 1935

Smicromyrme herophile Mickel, 1935: 275, ♂, holotype ♂ (Pekalongan, [Jawa Tengah], Java, [Indonesia]) [UMSP]; Lelej, 2005: 60; Lo Cascio, 2015: 558; Pagliano *et al*., 2020: 196.

Zoobank LSID
urn:lsid:zoobank.org:act:94AC0D9A-5D98-45EE-B929-081A966ACDB1

Material examined
No material examined.

Sex association
Female unknown.

Distribution
Indonesia: Jawa Tengah (Mickel, 1935).

Remarks
This species probably belongs to the *Sinotilla* by having the frons longitudinally striate, mandible bidentate apically and emarginate ventrally, F1 length 4/9× F2, and T2–3 with a posterior pale setal band (Mickel, 1935).

Smicromyrme jacobsoni (André, 1907)

Mutilla jacobsoni André, 1907: 207, ♂, holotype ♂ (Semarang, [Jawa Tengah], Java, [Indonesia]) [RMNH]; André, 1909: 172, ♂.
Smicromyrme jacobsoni: Mickel, 1935: 284, ♂; Lelej, 2005: 61; Lo Cascio, 2015: 558; Pagliano *et al*., 2020: 197.

Zoobank LSID
urn:lsid:zoobank.org:act:5BD4699D-B047-485A-96B0-6AD148A204E3

Material examined
No material examined.

Sex association
Female unknown.

Distribution
Indonesia: Jawa Tengah (André, 1907).

Remarks
This species probably belongs to the Trogaspidiini (former Petersenidiini) by having the frons punctate, vertex roundly sloping posteriorly, and F1 as long as F2 (André, 1907).

Smicromyrme minahassae (Zavattari, 1914)

Mutilla minahassae Zavattari, 1914: 95, ♂, lectotype ♂ (Minahassa [= Minahasa], [Sulawesi Utara], Celebes [= Sulawesi], [Indonesia]) [MSNG], designated by Brothers (2022: 102).
Smicromyrme minahassae: Mickel, 1935: 276, ♂; Lelej, 2005: 62; Lo Cascio, 2015: 559; Pagliano *et al*., 2020: 198; Brothers, 2022: 102, ♂.

Zoobank LSID
urn:lsid:zoobank.org:act:83C16B06-454A-4359-8A52-23035297268E

Material examined
No material examined.

Sex association
Female unknown.

Distribution
Indonesia: Sulawesi Utara (Zavattari 1914).

Remarks
Photos of the lectotype of this species are available in Brothers (2022: Fig. 198). This species probably belongs to the *Sinotilla* by having the frons striate, vertex elevated, mandible bidentate apically and emarginate ventrally, F1 shorter than wide, mesosoma mostly red, T2–3 with a posterior pale setal band (Brothers, 2022; Zavattari, 1914).

Genus *Tsunekimyrme* Lelej, 1995

Tsunekimyrme Lelej, 1995b: 16, ♂; Lelej, 2005: 65; Lelej, 2007: 89; Lelej & Brothers, 2008: 63; Brothers & Lelej, 2017: 96; Pagliano *et al*., 2020: 204; Lelej & Williams, 2023: 135, ♂. Gender feminine.

Zoobank LSID
urn:lsid:zoobank.org:act:3AEE4C78-3E3E-4FA8-A9F7-B82E81E11152

Type species
Mutilla fluctuata Smith, 1865, ♂, by original designation.

Diagnosis
MALE. Frons longitudinally striate; vertex elevated beyond ocellar region; ventral clypeal margin entire; mandible apex tridentate, internal teeth as large as apex, without subdistal internal tooth; mandible dorso-lateral carina highly elevated, terminating as internal tooth; mandible ventral margin emarginate with large proximal tooth; flagellomere apices truncate; F1 length subequal to width; notaulus reaching posterior margin of pronotum; parascutal carina forming elevated process; tegula rounded posteriorly, slightly surpassing transscutal articulation; mesopleuron evenly convex, lacking transverse impression; mesopleuron ventral face lacking process; procoxa lacking posterior process; metacoxal internal carina lamellately projecting posteriorly; S2 with lateral felt line; harpe dorso-internal margin lacking proximal process; basivolsella expanded ventrad with long slender cuspis, with long wavy setae on ventral margin; basiura small rounded; apiceps long slender.

FEMALE. Unknown.

Species included
One species, *T. fluctuata* (Smith, 1865), ♂ (Brunei, Indonesia, Philippines).

Sex association
Female unknown.

Distribution
Oriental Region.

Remarks
This genus was not available for the present study. However, the unique mandibular and genitalic shape allows recognition of this genus.

Tsunekimyrme fluctuata (Smith, 1865)

Mutilla fluctuata Smith, 1865: 80, ♂, holotype ♂ (Morty Island [actually Mysol Island = Pulau Batanme], [Papua Barat, Indonesia]) [OUMNH]; Dalla Torre, 1897: 41; André, 1902b: 70.
Smicromyrme fluctuata: Mickel, 1934: 204, ♂; Mickel, 1935: 292, ♂; Baltazar, 1966: 209; Tsuneki *et al*., 1993: 17, ♂.
Tsunekimyrme fluctuata: Lelej, 1995b: 18, ♂; Lelej, 2005: 65; Lelej & Brothers, 2008: 64; Pagliano *et al*., 2020: 204; Brothers, 2022: 69, ♂; Lelej & Williams, 2023: 105, ♂.

Zoobank LSID

urn:lsid:zoobank.org:act:30657F86-2C30-430C-B4CD-7A9F0858AF80

Material examined
No material examined.

Sex association
Female unknown.

Distribution
Brunei (Lelej, 2005). Indonesia: Papua Barat (Smith, 1865). Philippines: Mindanao, Negros, Samar, Tawi Tawi (Lelej, 1995b; Mickel, 1934; Tsuneki *et al*., 1993).

Remarks
Photos of the holotype of this species are available in Brothers (2022: Fig. 127). The type locality of this species was indicated as Morty Island (Smith, 1865), but was corrected as Mysol Island by Brothers (2022).

Discussion

Phylogenetic analyses found the monophyly of most East Asian smicromyrmine genera. However, they were generally supported by low GC scores and few unique synapomorphies, specifically for "higher" smicromyrmine genera like *Ephucilla*, *Mickelomyrme*, *Promecilla*, *Sinotilla*, and *Smicromyrme*. Furthermore, inter-generic relationship was unstable, depending on the *k* values. This is apparently due to high level of homoplasy in the male morphological characters; eighty of 123 characters (ca. 65%) have ci of lower than 50 (Fig. 23) and the average homoplasy per character was 4.99. Nevertheless, the characters generally have high ri (50 or more), suggesting that shared character states more or less support certain monophyletic groups (Farris, 1989). Thus, the East Asian smicromyrmine genera are effectively defined and confidently identified using a unique set of character states.

An excellent case of homoplasy was observed in the parossiculus shape (character 114). This character is particularly useful in identifying smicromyrmine genera, because it exhibits complex, discrete states among the genera. Thus, one might consider the similarly shaped parossiculus as strong evidence for shared ancestry. However, phylogenetic analyses revealed multiple origins of character states. For example, the males of the *Mickelomyrme*, *Nemka*, and *Skorikovia* are seemingly similar by sharing the basivolsella armed with a large ventral lobe proximally and a slender cuspis distally (114:2). Yet, analyses never recovered monophyly of (*Mickelomyrme* + *Nemka* + *Skorikovia*). Most parsimonious reconstruction by ACCTRAN optimization (fast/accelerated character transformation; Farris, 1970) based on one of the best-fitting trees under k16 suggests character-state changes at three different nodes in phylogeny (Fig. 24). The same applies to the states 1 and 3. The parossiculus, together with the gonossiculus, is connected to muscles and works as a clasping device to hold the female counterpart during copulation (Das Pol *et al*., 2023; Gauld & Bolton, 1988; O'Toole, 1975; Schulmeister, 2011; Snodgrass, 1941; Fig. 25). Therefore, the parosicculus is likely subject to selection through, e.g., male-male competition, female choice, and predator avoidance via phoretic copulation (Okayasu, 2023a), resulting in parallel or convergent evolution.

Before the present study, the genus *Smicromyrme* included 35 East Aian species, 21 being known from males. After the review, this genus was recognized as a nearly empty wastebasket in this realm; only one species in the subgenus *Erimyrme* and three species in the subgenus *Smicromyrme* are genuine representatives of the genus (Table 5). The rest 12

species were transferred out of this genus and six likely belong to the genus *Sinotilla* or a different tribe. In East Asia, true *Smicromyrme* species are limited to northeastern part (China, Taiwan, Korean Peninsula, and Japan), except for *S. australis* discovered in northern Thailand. There are 14 species and two subspecies known only from females that are distributed in East Asia, mostly tropical regions. Those females would eventually be associated with males from other more commonly occurring genera. For instance, the *Ephucilla*, *Mickelomyrme*, and *Sinotilla* appeared three major components of the East Asian smicromyrmine fauna (Table 5). Many, if not all, of the species in those genera are known from one sex only. However, the female morphology alone is not enough to rule out the possibility that the East Asian "*Smicromyrme*" females are true members of that genus. In the current classification system, identification of the smicromyrmine genera largely relies upon the mandibular shape, presence/absence of the scutellar scale, setal markings on the metasoma, and the pygidial plate shape and sculpture in females (Lelej, 1995b; Lelej & Williams, 2023; Williams *et al*., 2019b). Apart from the scutellar scale, female morphological traits are disturbed by homoplasy resulting from parallel or convergent evolution. For example, the pygidial plate morphology is often associated with the host choice in velvet ants (Bartholomay *et al*., 2015ab; Bayliss & Brothers, 2001; Brothers, 2018; Krombein, 1972; Luz *et al*., 2016; Okayasu, 2020; Pitts & Manley, 2004; Taylor *et al*., 2019; Williams *et al*., 2011, 2019a). Another well-established example of convergent evolution in female velvet ants is the color patterns associated with Müllerian mimicry (Okayasu *et al*., 2018; Wilson *et al*., 2012b, 2015, 2018). Most female morphological traits cannot be readily linked with functional values. However, it is almost evident that characters traditionally used in genus-delimitation based on females are misleading or, at least, poorly informative. A comparative analysis of the female morphology is strongly encouraged.

To summarize, phylogenetic analyses conducted in the present study clearly suggest that both male and female morphological characters encompass a number of non-homologous state changes. Taxonomic difficulty in dealing with the Smicromyrmini is ascribed to homoplastic nature of morphology. Still, the East Asian genera can be precisely diagnosed by a combination of male morphological features when a multitude of characters are incorporated. Comparing to males, apterous females are anatomically simplified. It is advisable to start with the male characters as an initial step toward better systematic basis of velvet ants.

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References

Akiyama, Y., Enoki, J. & Nakamura, S. (2021) Insects from Hiroshima Prefecture collected by Mr. Takashi Shintani preserved in Hiwa Museum for Natural History. *Hiwa Museum for Natural History Material Reports* 21: 1–144. (in Japanese)

Alicata, P., Caruso, D., Costa, G. & Mota, S. (1974) Ricerche eco-etologiche sulla fauna delle dune costiere di Porto Palo (Siracusa). — I. *Smicromyrme viduata* (Pall.) (Hymenoptera, Mutillidae): Ritmi di attivita, migrazioni e accoppiamnto. *Animalia* 1 (1/3): 89–108.

André, E. (1894 [1893]) Contribution a la connaissance des mutilles de l'Inde. *Journal of the Bombay Natural History Society* 4 (8): 462–484.

André, E. (1896) Mutillides nouveaux ou imparfaitement connus faisant partie des collections du musée National de Hongrie. *Termeszetraizi fuzetek* 19 (1): 9–25.

André, E. (1898) Étude sur les mutillides du Muséum de Paris. *Annales de la Société Entomologique de France* 67: 1–79.

André, E. (1899–1903) *Species des Hyménoptères d'Europe & d'Algérie*. *Tome Huitième*. *Les Mutillides*. Vve Dubosclard and A. Hermann, Paris, 480 pp. + 15 pls. [1–64 + pl. 1–8 (1899); 65–144 (1900); 145–304 (1901); 305–384 (1902a); 385–478 (1903); pl. 9–15 (date unknown).

André, E. (1902b [1903]) Family Mutillidae. *In*: Wytsman, P. (ed.) *Genera Insectorum*. *Fascicles 11*. L. Desmet-Verteneuil, Bruxelles, pp. 1–77 + 3 pls.

André, E. (1905) Mutillides nouveaux ou peu connus de l'Ancien Monde et de l'Australie. (Hym.). *Zeitschrift für systematische Hymenopterologie und Dipterologie* 5 (4): 201–216; 5 (5): 265–277.

André, E. (1907) Description d'une nouvelle espèce de Mutillide, de Java (Hym.). *Zeitschrift für Systematische Hymenopterologie und Dipterologie* 7 (3): 207–208.

André, E. (1909) Mutillides nouveaux ou imparfaitement connus du Musée royal d'histoire naturelle de Leide. *Notes from the Leyden Museum* 31: 171–180.

Ashmead, W.H. (1899) Superfamilies in the Hymenoptera and generic synopses of the families Thynnidae, Myrmosidae, and Mutillidae. *Journal of the New York Entomological Society* 7: 45–60.

Ashmead, W.H. (1900–1904a) Classification of the fossorial, predaceous and parasitic wasps, or the superfamily Vespoidea. *The Canadian Entomologist* 32: 145–155, 185–188, 295–296 (1900); 34: 79–88, 131–137, 163–166, 203–210, 219–231, 268–273, 287–291 (1902); 35: 3–8, 39–44, 95–107, 155–158, 199–205, 303–310, 323–332 (1903); 36: 5–9 (1904a).

Ashmead, W.H. (1904b) Descriptions of new genera and species of Hymenoptera from the Philippine Islands. *Proceedings of the United States National Museum* 28 (1387): 127–158. https://doi.org/10.5479/si.00963801.28-1387.127

Azuma, S., Yafuso, M., Kinjo, M., Hayashi, M., Kohama, T., Sasaki, T., Kimura, M. & Kawamura, F. (2002) *Check list of the insect of the Ryukyu Islands*. *Second edition*. The Biological Society of Okinawa, Okinawa, 570 pp. (in Japanese)

Baltazar, C.R. (1966) A catalogue of Philippine Hymenoptera (with a bibliography, 1758–1963). *Pacific Insects Monograph* 8: 1–488.

Barthélémy, C., Lelej, A.S. & Loktionov, V.M. (2018) A contribution to the Mutillidae (Hymenoptera) of Hong Kong. *Zootaxa* 4514 (2): 230–242. https://doi.org/10.11646/zootaxa.4514.2.6

Bartholomay, P.R., Williams, K.A., Luz, D.R. & Morato, E.F. (2015a) *Frigitilla* gen. nov., a new genus of Amazonian Mutillidae (Hymenoptera). *Zootaxa* 3957 (1): 49–58. https://doi.org/10.11646/zootaxa.3957.1.3

Bartholomay, P.R., Williams, K.A., Waldren, G.C. & de Oliveira, M.L. (2015b) Corrections on the biology of *Traumatomutilla* André, 1901 (Hymenoptera: Mutillidae). *Zootaxa* 3920 (1): 198–200. http://dx.doi.org/10.11646/zootaxa.3920.1.10

Bayliss, P.S. & Brothers, D.J. (2001) Behaviour and host relationships of *Dolichomutilla sycorax* (Smith) (Hymenoptera: Mutillidae, Sphecidae). *Journal of Hymenoptera Research* 10 (1): 1–9.

Berland, L. (1925) *Fauna de France 10. Hyménoptères vespiformes. I (Sphegidae, Pompilidae, Scoliidae, Sapygidae, Mutillidae)*. Paul Lechevalier, Paris, viii + 364 pp.

Bernot, J.P., Owen, C.L., Wolfe, J.M., Meland, K., Olesen, J. & Crandall, K.A. (2023) Major revisions in pancrustacean phylogeny and evidence of sensitivity to taxon sampling. *Molecular Biology and Evolution* 40 (8): msad175. https://doi.org/10.1093/molbev/msad175

Bingham, C.T. (1895) On a collection of hymenopterous insects from the Philippines. *Annales and Magazines of Natural History*, Series 6 16 (96): 438–446. https://doi.org/10.1080/00222939508680303

Bingham, C.T. (1897) *The fauna of British India including Ceylon and Burma*. *Hymenoptera 1. Wasps and bees*. Taylor and Francis, London, 608 pp. + 4 pls. https://doi.org/10.5962/bhl.title.48423

Bischoff, H. (1920–1921) Monographie der Mutilliden Afrikas. *Archiv für Naturgeschichte* 86A (1–3): 1–480 (1920); 86A (4–5): 481–830 (1921).

Bogusch, P. (2006) The velvet ants (Hymenoptera: Mutillidae) of the Czech Republic and Slovakia: an identification key and annotated checklist. *Acta Musei Moraviae, Scientiae biologicae* 91: 103–148.

Branstetter, M.G., Danforth, B.N., Pitts, J.P., Faircloth, B.C., Ward, P.S., Buffington, M.L., Gates, M.W., Kula, R.R. & Brady, S.G. (2017) Phylogenomic insights into the evolution of stinging wasps and the origin of ants and bees. *Current Biology* 27 (7): 1019–1025. https://doi.org/10.1016/j.cub.2017.03.027

Brothers, D.J. (1975) Phylogeny and classification of the aculeate Hymenoptera, with special reference to Mutillidae. *The University of Kansas Science Bulletin* 50 (11): 483–648.

Brothers, D.J. (1983) Identity and classification of *Physetopoda*, *Chaetotilla* and *Paramyrme*. *Journal of the Kansas Entomological Society* 56 (3): 441–445.

Brothers, D.J. (1989) Alternative life-history styles of mutillid wasps (Insecta, Hymenoptera). *In*: Bruton, M.N. (ed.) *Alternative life-history styles of animals*. *Perspectives in vertebrate sciences 6*. Springer, Dordrecht, pp. 279–291. https://doi.org/10.1007/978-94-009-2605-9_14

Brothers, D.J. (1999) Phylogeny and evolution of wasps, ants and bees (Hymenoptera, Chrysidoidea, Vespoidea and Apoidea). *Zoologica Scripta* 28 (1–2): 233–250. https://doi.org/10.1046/j.1463-6409.1999.00003.x

Brothers, D.J. (2018) *Aglaotilla*, a new genus of Australian Mutillidae (Hymenoptera) with

metallic coloration. *Zootaxa* 4415 (2): 357–368. https://doi.org/10.11646/zootaxa.4415.2.6
Brothers, D.J. (2022) Critical analysis of the type material of Mutillidae described from the Australasian Region (Hymenoptera). *Zootaxa* 5140 (1): 1–215. https://doi.org/10.11646/zootaxa.5140.1.1
Brothers, D.J. & Lelej, A.S. (2017) Phylogeny and higher classification of Mutillidae (Hymenoptera) based on morphological reanalyses. *Journal of Hymenoptera Research* 60: 1–97. https://doi.org/10.3897/jhr.60.20091
Brothers, D.J., Lelej, A.S. & Williams, K.A. (2019) Genus-group names of Mutillidae (Hymenoptera): corrections and updates since 2008. *Zootaxa* 4651 (3): 578–588. https://doi.org/10.11646/zootaxa.4651.3.10
Brothers, D.J., Tschuch, G. & Burger, F. (2000) Associations of mutillid wasps (Hymenoptera, Mutillidae) with eusocial insects. *Insectes Sociaux* 47: 201–211. https://doi.org/10.1007/PL00001704
Brown, R.E. (1906) A catalogue of Philippine Hymenoptera, with description of new species. *The Philippine Journal of Science* 1 (6–10): 683–704.
Cameron, P. (1892) Hymenoptera Orientalis; or contributions to a knowledge of the Hymenoptera of the Indian Zoological Region. Part IV. *Memoirs and Proceedings of the Manchester Literary and Philosophical Society* 35: 97–137 + 1 pl.
Cameron, P. (1897) Hymenoptera Orientalia, or Contributions to a knowledge of the Hymenoptera of the Oriental Zoological Region. Part V. *Memoirs and Proceedings of the Manchester Literary and Philosophical Society* 41 (4): 1–144 + pls 3–4.
Cameron, P. (1900) Hymenoptera Orientalia, or contributions to the knowledge of the Hymenoptera of the Oriental zoological region. Part IX. The Hymenoptera of the Khasia Hills. Part II. Section I. *Memoirs and Proceedings of the Manchester Literary and Philosophical Society* 44 (15): 1–114.
Cameron, P. (1901) On the Hymenoptera collected during the "Skeat Expedition" to the Malay Peninsula, 1899–1900. *Proceedings of the Zoological Society of London* 1901 (2): 16–44. https://doi.org/10.1111/j.1469-7998.1901.tb08163.x
Cameron, P. (1902a) On the Hymenoptera collected by Mr. Robert Shelford at Sarawak, and on the Hymenoptera of the Sarawak Museum. *Journal of the Straits Branch of the Royal Asiatic Society* 37: 29–131.
Cameron, P. (1902b) Descriptions of new genera and species of Hymenoptera collected by Major C. S. Nurse at Deesa, Simla and Ferozepore. Part I. *Journal of the Bombay Natural History Society* 14 (2): 267–293 + 1 pl.
Cameron, P. (1903) Descriptions of new genera and species of Hymenoptera taken by Mr. Robert Shelford at Sarawak, Borneo. *Journal of the Straits Branch of the Royal Asiatic Society* 39: 89–181.
Cameron, P. (1909) Descriptions of two new species of *Mutilla* from Kuching, Borneo. *The Entomologist* 42 (553): 146–147.
Chan, M.-L., Yeh, J.-Y., Jeng, M.-L., Tsai, J.-F., Chen, Y.-L., Chen, L.-H. & Lin, S.-R. (2024) Integrated insect types database of Taiwanese species. Available from: http://twinsecttype.nmns.edu.tw/ (accessed 8 January 2024)
Chen, C.-w. (1957) A revision of the velvety ants or Mutillidae of China (Hymenoptera). *Quarterly Journal of the Taiwan Museum* 10 (3–4): 135–224 + 6 pls.
Chu, Y.-i. & Yamanaka, T. (1973–1975) A check list of the present and old name of insect collected localities in Taiwan. *Journal of the National Taiwan Museum* 16: 31–72 (1973); 17: 51–75 (1974); 18: 121–150 (1975).
Cockerell, T.D.A. (1928) Mutillidae from Siam. *The Annals and Magazine of Natural History*, Series 10 2: 596–600. https://doi.org/10.1080/00222932808672926

Congreve, C.R. & Lamsdell, J.C. (2016) Implied weighting and its utility in palaeontological datasets: A study using modelled phylogenetic matrices. *Palaeontology* 59 (3): 447–462. https://doi.org/10.1111/pala.12236

Das Pol, D., Mikó, I., Talamas, E.J., Vilhelmsen, L. & Sharanowski, B.J. (2023) A revised terminology for male genitalia in Hymenoptera (Insecta), with a special emphasis on Ichneumonoidea. *PeerJ* 11: e15874. https://doi.org/10.7717/peerj.15874

Dalla Torre, C.G. de (1897) *Catalogus Hymenopterorum hucusque Descriptorum Systematicus et Synonimicus*. *Volumen VIII: Fossores (Sphegidae)*. Guilelmi Engelmann, Lipsiae, [4] + viii + 750 pp. https://doi.org/10.5962/bhl.title.10348

De Stefani, T. (1887) Un nuovo genere di crabronidi ed altri imenotteri nuovi o poco cogniti raccolti in Sicilia. *Naturalista Siciliano* 6 (8): 59–62, 85–90, 110–114, 143–147 + tab. 2.

Dutt, G.R. (1912) Life histories of Indian insects — IV (Hymenoptera). *Memoirs of the Department of Agriculture in India*, Entomological Series 12 (4): 183–267.

Fabricius, J.C. (1787) *Mantissa insectorum sistens eorum species nuper detecta, adjectis characteribus genericis, differentiis specificis, emendationibus, observationibus. Tom. I*. Christ Gottl Proft, Hafniae, 348 pp.

Fabricius, J.C. (1793) *Entomologica Systematica emendata et aucta, secundum Classes, Ordines, Genera, Species adjectis Synonymis, Locis, Observationibus, Descriptionibus*. *Tom. II*. Christ Gottl Proft, Hafniae, viii + 519 pp. https://doi.org/10.5962/bhl.title.125869

Fabricius, J.C. (1804) *Systema Piezatorum secundum Ordines, Genera, Species adjectis Synonymis, Locis, Observationibus, Descriptionibus*. Carolum Reichard, Brunsvigae, pp. i–xiv + 15–440 + 1–30. https://doi.org/10.5962/bhl.title.10490

Farris, J.S. (1970) A method for computing Wagner trees. *Systematic Zoology* 19 (1): 83–92. https://doi.org/10.1093/sysbio/19.1.83

Farris, J.S. (1989) The retention index and the rescaled consistency index. *Cladistics* 5 (4): 417–419. https://doi.org/10.1111/j.1096-0031.1989.tb00573.x

Fitch, W.M. (1971) Toward defining the course of evolution: Minimum change for a specific tree topology. *Systematic Zoology* 20 (4): 406–416. https://doi.org/10.1093/sysbio/20.4.406

Fukasawa, S. & Miyano, S. (2010) Fauna of the aculeate Hymenoptera (Insecta) from the Izu Islands, Japan. *Journal of the Natural History Museum and Institute, Chiba* 11 (1): 11–28. (in Japanese)

Gauld, I. & Bolton, B. (1988) *The Hymenoptera*. Oxford University Press, Oxford, xii + 332 pp.

Giner Marí, J. (1944) *Himenópteros de España*. *Fams. Apterogynidae y Mutillidae*. Instituto Español de Entomologia, Madrid, 124 pp.

Giribet, G. (2003) Stability in phylogenetic formulations and its relationship to nodal support. *Systematic Biology* 52 (4): 554–564. https://doi.org/10.1080/10635150390223730

Girón, J.C., Tarasov, S., González Montaña, L.A., Matentzoglu, N., Smith, A.D., Koch, M., Boudinot, B.E., Bouchard, P., Burks, R., Vogt, L., Yoder, M., Osumi-Sutherland, D., Friedrich, F., Beutel, R. & Mikó, I. (2023) Formalizing invertebrate morphological data: A descriptive model for cuticle-based skeleto-muscular systems, an ontology for insect anatomy, and their potential applications in biodiversity research and informatics. *Systematic Biology* 72 (5): 1084–1100. https://doi.org/10.1093/sysbio/syad025

Goloboff, P.A. (1993) Estimating character weights during tree search. *Cladistics* 9 (1): 83–91. https://doi.org/10.1111/j.1096-0031.1993.tb00209.x

Goloboff, P.A. (1995) Parsimony and weighting: A reply to Turner and Zandee. *Cladistics* 11

(1): 91–104. https://doi.org/10.1111/j.1096-0031.1995.tb00006.x
Goloboff, P.A. (2022a) *Phylogenetic analysis of morphological data: Volume 1. From observations to optimal phylogenetic trees*. CRC Press, Boca Raton, xx + 277 pp.
Goloboff, P.A. (2022b) *Phylogenetic analysis of morphological data: Volume 2. Refining phylogenetic analyses*. CRC Press, Boca Raton, xx + 291pp.
Goloboff, P.A. & Arias, J.S. (2019) Likelihood approximations of implied weights parsimony can be selected over the Mk model by the Akaike information criterion. *Cladistics* 35 (6): 695–716. https://doi.org/10.1111/cla.12380
Goloboff, P.A. & Catalano, S.A. (2016) TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics* 32 (3): 221–238. https://doi.org/10.1111/cla.12160
Goloboff, P.A., Carpenter, J.M., Arias, J.S. & Miranda-Esquivel, D.R. (2008a) Weighting against homoplasy improves phylogenetic analysis of morphological data sets. *Cladistics* 24 (5): 758–773. https://doi.org/10.1111/j.1096-0031.2008.00209.x
Goloboff, P.A., Farris, J.S., Källersjö, M., Oxelman, B., Ramírez, M.J. & Szumik, C.A. (2003a) Improvements to resampling measures of group support. *Cladistics* 19 (4): 324–332. https://doi.org/10.1111/j.1096-0031.2003.tb00376.x
Goloboff, P.A., Farris, J.S. & Nixon, K.C. (2003b) T.N.T.: Tree analysis using new technology. Program and documentation. Available from: https://www.lillo.org.ar/phylogeny/tnt/ (accessed 8 January 2024)
Goloboff, P.A., Farris, J.S. & Nixon, K.C. (2008b) TNT, a free program for phylogenetic analysis. *Cladistics* 24 (5): 774–786. https://doi.org/10.1111/j.1096-0031.2008.00217.x
Goloboff, P.A. & Morales, M.E. (2023) TNT version 1.6, with a graphical interface for MacOS and Linux, including new routines in parallel. *Cladistics* 39 (2): 144–153. https://doi.org/10.1111/cla.12524
Gôukon, K. (1993) Host records and some bionomical notes on mutillid wasps in Japan (Hymenoptera, Mutillidae). *Chugoku Kontyu* 7: 35–40. (in Japanese)
Gould, S.J. (1985) Treasures in a taxonomic wastebasket. *Natural History* 94 (12): 22–33. http://hdl.handle.net/2246/6491
Hammer, K. (1949) Über einige von Kjell Kolthoff und anderen in China gesammelten Hymenoptera. Chrysididae, Cleptidae, Mutillidae. *Arkiv för zoologi* 42A (8): 1–12.
Hammer, K. (1960 [1962]). Mutilliden (Insecta: Hymenoptera) aus dem Indischen Museum in Calcutta. *Records of the Indian Museum* 58 (1): 1–51.
Haneda, Y., Inoue, S., Nozaka, C., Tano, T., Kurokawa, H. & Murota, T. (2005) The Hymenoptera recorded at Mt. Monju, Fukui Prefecture, Central Japan. *Tsunekibachi* 4: 53–75. (in Japanese)
Haneda, Y., Nozaka, C., Tano, T., Kurokawa, H. & Murota, T. (2006a) Aculeate Hymenoptera collected from Toyama Prefecture in 2005. *Tsunekibachi* 8: 1–48. (in Japanese)
Haneda, Y., Nozaka, C., Tano, T., Kurokawa, H. & Murota, T. (2006b) The aculeate Hymenoptera collected at Tsushima, Nagasaki Prefecture in August of 2006. *Tsunekibachi* 10: 39–52. (in Japanese)
Haneda, Y., Tano, T., Okuno, H., Nozaka, C., Murota, T., Kurokawa, H. & Inoue, S. (1998) Hymenoptera. *In*: Sasaji, H. (ed.) [*Catalog of insects of Fukui Prefecture, 2nd edition*]. Fukui Prefecture Government, Fukui, pp. 314–404. (in Japanese)
Haneda, Y. & Yamamoto, E. (2000) [Aculeata collected in Odamiyama and surrounding area (Hymenoptera)]. *In*: Yamamoto, E. (ed.) *Nature of Odamiyama II*. Oda-chô, Ehime, pp. 775–837. (in Japanese)
Hashimoto, Y. & Nakanishi, A. (1997) *A list of the type-specimens of Hymenoptera described by K. Tsuneki in the Museum of Nature and Human Activities, Hyogo (MNHAH)*.

Catalogue of collections in the Museum of Nature and Human Activities, Hyogo No. 2. Museum of Nature and Human Activities, Sanda, 47 pp. + 8 pls.
Hayashi, M., Kadowaki, H., Matsuda, T., Fukaya, H. & Chikami, Y. (2013) Research on insect distribution of Oki Islands, Shimane Prefecture, Japan. Part 3. *Special Bulletin of the Hoshizaki Green Foundation* 8: 1–73.
He, J.-H., Chen, X.-X., Fan, J.-J., Li, Q., Liu, C.-M., Lou, X.-M., Ma, Y., Wang, S.-F., Wu, Y.-R., Xu, Z.-H., Xu, Z.-F. & Yao, J. (2004) *Hymenopteran insect fauna of Zhejiang*. Science Press, Beijing, lvi + 1373 pp. + 43 pls. (in Chinese)
Hermes, M.G., Melo, G.A.R. & Carpenter, J.M. (2014) The higher-level phylogenetic relationships of the Eumeninae (Insecta, Hymenoptera, Vespidae), with emphasis on *Eumenes* sensu lato. *Cladistics* 30 (5): 453–484. https://doi.org/10.1111/cla.12059
Hisamatsu, M. (2004) List of Hymenoptera recorded in Ibaraki Prefecture. *Bulletin of Ibaraki Nature Museum* 7: 125–164. (in Japanese)
Hoffer, A. (1936) Diagnoses novae mulillidarum Čechosloveniae. *Časopis Československé společnosti entomologické* 33: 157–163 + 7 figs. (in Czech)
Hua, L.-z. (2006) *List of Chinese insects Vol. IV*. Sun Yat-sen University Press, Guangzhou, 540 pp.
Hymenoptera Anatomy Consortium (2024) Hymenoptera glossary. Available from: http://glossary.hymao.org (accessed 8 January 2024)
Ikudome, S. & Yamane, Sk. (2007) Ants, wasps and bees of Iwo-jima, Northern Ryukyus, Japan (Hymenoptera, Aculeata). *The Bulletin of the Institute of Minami-Kyûshû Regional Science, Kagoshima Women's Junior College* 23: 1–7.
Inoue, N. (2003) [Records of the Hymenoptera in Ibaraki, 1]. *Ruriboshi* 30: 50–53. (in Japanese)
International Commission on Zoological Nomenclature (ICZN) (1999) *International code of zoological nomenclature*. Fourth edition. ITZN, London, xxx + 306 pp.
Invrea, F. (1932) Una nuova *Smicromyrme* di Liguria. *Bollettino della Società Entomologica Italiana* 64: 144–146 + 1 fig.
Invrea, F. (1940) Mutillidi dell'isola di Cipro raccolti dal Sig. G.A. Mauromoustakis. *Bollettino della Società Entomologica Italiana* 72: 118–122.
Invrea, F. (1943) A proposito di una *Smicromyrme* del'Isola di Borneo nota tassonomica e combiamento di nome (Hymenoptera, Mutillidae). *Annali del Museo Civico di Storia Naturale di Genova* 61: 191–193.
Invrea, F. (1964) *Mutillidae-Myrmosidae*. *Fauna d'Italia 5*. Edizioni Calderini, Bologna, xii + 302 pp. + 1 p.
Ishikawa, R. (1965) Family Mutillidae. *In*: Asahina, S., Ishihara, T. & Yasumatsu, K. (eds) *Iconographia insectorum Japonicorum colore naturali edita Volumen III*. Hokuryu-kan Publishing, Tokyo, p. 289 + 1 pl. (in Japanese)
Jenkins, C.N., Pimm, S.L. & Joppa, L.N. (2013) Global patterns of terrestrial vertebrate diversity and conservation. *Proceedings of the National Academy of Sciences* 110 (28): E2602–E2610. https://doi.org/10.1073/pnas.1302251110
József, M. & Zoltán, G. (2011) Velvet ants of Hungary (Hymenoptera: Mutillidae). *Natura Somogyiensis* 18: 1–198.
Kameyama, T., Nishi, M. & Nakamura, S. (2006) Insects from Ohta River, Hiroshima Prefecture, A result of survey in 2003. *Miscellaneous Reports of the Hiwa Museum for Natural History* 47: 1–184. (in Japanese)
Kan, T. (2022) [Records of Mutillidae]. *Yamaguchi-no-mushi* 21: 178. (in Japanese)
Kass, J.M., Guénard, B., Dudley, K.L., Jenkins, C.N., Azuma, F., Fisher, B.L., Parr, C.L., Gibb, H., Longino, J.T., Ward, P.S., Chao, A., Lubertazzi, D., Weiser, M., Jetz, W., Guralnick, R., Blatrix, R., Lauriers, J.D., Donoso, D.A., Georgiadis, C., Gomez, K.,

Hawkes, P.G., Johnson, R.A., Lattke, J.E., MacGown, J.A., Mackay, W., Robson, S., Sanders, N.J., Dunn, R.R. & Economo, E.P. (2022) The global distribution of known and undiscovered ant biodiversity. *Science Advances* 8 (31): eabp9908. https://doi.org/10.1126/sciadv.abp9908

Kier, G., Kreft, H., Lee, T.M., Jetz, W., Ibisch, P.L., Nowicki, C., Mutke, J. & Barthlott, W. (2009) A global assessment of endemism and species richness across island and mainland regions. *Proceedings of the National Academy of Sciences* 106 (3): 9322–9327. https://doi.org/10.1073/pnas.0810306106

Kim, C.W. (1963) Hymenoptera of Korea. *Humanities and Sciences (Natural Science), Korea University* 6: 243–374. (in Korean)

Kim, C.W. (1970) *Illustrated encyclopedia of fauna and flora of Korea*. *Vol. 11 Insecta (III)*. Samwha-Chulpansa, Seoul, 892 pp. (in Korean)

Kim, C.W., Lee, J.W., Park, J.S., Kim, B.J. & Park, J.C. (1994) Hymenoptera. *In*: Shin, Y.H. & Yoon, I.B. (eds) *Check list of insects from Korea*. Kon-Kuk University Press, Seoul, pp. 216–269.

Kinota, K., Haneda, Y. & Tano, T. (2005) Aculeate wasps collected in Sapporo-shi, Otaru-shi and Ishikari-shi, Hokkaido. *Tsunekibachi* 5: 25–31. (in Japanese)

Kluge, A.G. & Farris, J.S. (1969) Quantitative phyletics and the evolution of anurans. *Systematic Zoology* 18 (1): 1–32. https://doi.org/10.1093/sysbio/18.1.1

Kochetkov, D.N. & Lelej, A.S. (2015) The velvet ants (Hymenoptera, Mutillidae) of Khinganskiy Reserve, Amur Region. *A.I. Kurentsov's Annual Memorial Meetings* 26: 259–263. (in Russian)

Kohl, F.F. (1880) Die Rauwespen Trirols nach ihrer horizontalen und verbreitung mit einen Anhange biologischen und kritischer Notizen. *Z. Ferdinandeums Tirol Vorariberg* 3 (24): 97–242.

Kojima, J., Saito, F. & Nguyen, L.T.P. (2011) On the species-group taxa of Taiwanese social wasps (Hymenoptera: Vespidae) described and/or treated by J. Sonan. *Zootaxa* 2920: 42–64. http://dx.doi.org/10.11646/zootaxa.2920.1.2

Krombein, K.V. (1972) Monograph of the Madagascan Mutillidae (Hymenoptera). Part I: Myrmillini, Mutillini and Smicromyrmini. *Annales, Musée Royal de l'Afrique Centrale*, Série in 8°, Sciences Zoologiques 199: I–X + 1–61.

Krombein, K.V. (1978) Biosystematic studies of Ceylonese wasps, III. Life history, nest and associates of *Paraleptomenes mephitis* (Cameron) (Hymenoptera, Eumenidae). *Journal of the Kansas Entomological Society* 51 (4): 721–734.

Krombein, K.V. (1991) Biosystematic studies of Ceylonese wasps, XIX: Natural history notes in several families (Hymenoptera: Eumenidae, Vespidae, Pompilidae, and Crabronidae). *Smithsonian Contributions to Zoology* 515: 1–41. https://doi.org/10.5479/si.00810282.515

Kubo, K. (2000) Order Hymenoptera. *In*: Iwase, K., Ohtsubo, H., Kubo, K., Shimura, T. & Watari, H. (eds) Insects of Mt. Enkai-zan and surrounding area. *Kanagawa-Chûhô* 130: 287–343. (in Japanese)

Kuribayashi, S. (1973) *Insects of Okinawa*. Gakushu-Kenkyu-sha, Tokyo, 184 pp. (in Japanese)

Kurokawa, H. (2005) Addition records of the Aculeata from Mt. Ashiwa-yama, Fukui. *Tsunekibachi* 4: 76. (in Japanese)

Latreille, P.A. (1802) *Histoire naturelle, générale et particulière des Crustacés et des Insectes*. *3*. F. Dufart, Paris, xii + 467 pp. https://doi.org/10.5962/bhl.title.15764

Lelej, A.S. (1971) [New and little-known species of velvet ants (Hymenoptera, Mutillidae) from Middle Asia and Kazakhstan]. *Entomologicheskoe Obozrenie* 50 (3): 676–680 + 5 figs. (in Russian). [English translation (1972) in *Entomological Review* 50 (3): 384–

386]
Lelej, A.S. (1975) [Apterogynidae, Myrmosidae, Mutillidae (Hymenoptera) of Mongolia]. *In*: Kerzhner, I.M. (ed.) *Nasekomye Mongolii 3* [*Insects of Mongolia 3*]. Nauka, Leningrad, pp. 320–325. (in Russian)
Lelej, A.S. (1976) [Addition to the fauna of velvet ants (Hymenoptera, Mutillidae) of Mongolia]. *In*: Kerzhner, I.M. & Kozlov, M.A. (eds) *Nasekomye Mongolii 4* [*Insects of Mongolia 4*]. Nauka, Leningrad, pp. 268–281 + 12 figs. (in Russian)
Lelej, A.S. (1977a [1976]) [Interesting data on Myrmosidae and Mutillidae (Hymenoptera) from the south of Primorye Territory]. *In*: Lehr, P.A. (ed.) *Nasekomye Dal'nego Vostoka* [*Insects of the Russian Far East*]. DVNTS AN SSSR, Vladivostok, pp. 88–95. (in Russian)
Lelej, A.S. (1977b) [New data on the velvet ant fauna of Mongolia (Hymenoptera: Mutillidae)]. *In*: Kerzhner, I.M. (ed.) *Nasekomye Mongolii 5* [*Insects of Mongolia 5*]. Nauka, Leningrad, pp. 526–536 + 5 figs. (in Russian)
Lelej, A.S. (1981 [1980]). [Wasps of the families Myrmosidae and Mutillidae (Hymenoptera) from Eastern Siberia and the Far East]. *In*: Lehr, P.A. (ed.) *Taksonomiya Dal'nego Vostoka* [*Taxonomy of insects of the Far East*]. DVNTS AN SSSR, Vladivostok, pp. 73–79. (in Russian)
Lelej, A.S. (1984) [The velvet ants of the genus *Paramyrme* (Hymenoptera, Mutillidae)]. *In*: Lehr, P.A. (ed.) *Sistematika Nasekomykh Dal'nego Vostoka* [*Systematics of the insects of the Russian Far East*]. DVNTS AN SSSR, Vladivostok, pp. 101–115 + 32 figs. (in Russian)
Lelej, A.S. (1985) *Osy-nemki (Hymenoptera, Mutillidae) Fauny SSSR i Sopredelnykh Stran* [*The velvet ants (Hymenoptera, Mutillidae) of the USSR and neighboring countries*]. Nauka, Leningrad, 268 pp. (in Russian)
Lelej, A.S. (1993) A new genus of velvet ants from Sri Lanka (Insecta, Hymenoptera, Mutillidae). *Spixiana* 16 (3): 233–236.
Lelej, A.S. (1995a) A review of Palaearctic and Oriental species of genus *Nemka* Lelej with description of Oriental genus *Mickelomyrme* gen. n. (Hymenoptera, Mutillidae). *Far Eastern Entomologist* 6: 1–20.
Lelej, A.S. (1995b) To the knowledge of East Asian species of the tribe Smicromyrmini Bischoff, 1920 (Hymenoptera, Mutillidae) with description of four new genera and eight new species. *Far Eastern Entomologist* 13: 1–28.
Lelej, A.S. (1995c) Sem. Mutillidae — Nemki, Ili Mutillidy [Family Mutillidae — Velvet ants, or mutillids]. *In*: Lehr, P.A. (ed.) *Opredelitel' Nasekomykh Dal'nego Vostoka Rossii* [*Keys to insects of the Russian Far East*]. Vol. 4. Neuropteroidea, Mecoptera, and Hymenoptera. Part 1. Nauka, St. Petersburg, 202–211. (in Russian)
Lelej, A.S. (1996a) To the knowledge of the East Asian species of the tribe Trogaspidiini Bischoff, 1920 (Hymenoptera, Mutillidae) with description of eight new genera and two new species. *Far Eastern Entomologist* 30: 1–24.
Lelej, A.S. (1996b) Mutillid wasps collected in Malaysia and Indonesia by Dr. Sk. Yamane (Hymenoptera, Mutillidae). *Tropics* 6 (1–2): 91–104. https://doi.org/10.3759/tropics.6.91
Lelej, A.S. (1996c) A review of the East Asian species of *Mickelomyrme* Lelej, 1995 (Hymenoptera, Mutillidae). *Entomofauna* 17 (15): 277–292.
Lelej, A.S. (2000) Family Mutillidae. Addition. *In*: Lelej, A.S., Kupianskaya, A.N., Nemkov, P.G. & Kholin, S.K. (eds) *Key to the insects of Russian Far East*. *Vol. IV*. *Neuropteroidea Mecoptera, Hymenoptera*. *Part 4*. Dalnauka, Vladivostok, p. 615. (in Russian)
Lelej, A.S. (2002) *Catalogue of the Mutillidae (Hymenoptera) of the Palaearctic Region*.

Dalnauka, Vladivostok, 172 pp.
Lelej, A.S. (2005) *Catalogue of the Mutillidae (Hymenoptera) of the Oriental Region*. Dalnauka, Vladivostok, 252 pp.
Lelej, A.S. (2007) Biogeography of mutillid wasps (Hymenoptera, Mutillidae). *In*: Rasnitsyn, A.P. & Gokhman, V.E. (eds) *Studies on hymenopterous insects*. *Collection of scientific papers*. KMK Scientific Press Ltd., Moscow, pp. 82–111. (in Russian)
Lelej, A.S. (2017) Family Mutillidae — Velvet ants. *In*: Belokobylskij, A.S. & Lelej, A.S. (eds) Annotated catalogue of the Hymenoptera of Russia. Volume I. Symphyta and Apocrita: Aculeata. *Proceedings of the Zoological Institute of the Russian Academy of Sciences*, Supplement 6: 152–158.
Lelej, A.S. (2020a) To the knowledge of velvet ants of the genera *Artiotilla* Invrea, *Radoszkowskitilla* Lelej and *Taiwanomyrme* Tsuneki (Hymenoptera: Mutillidae). *Far Eastern Entomologist* 410: 1–10. https://doi.org/10.25221/fee.410.1
Lelej, A.S. (2020b) Three new species of velvet ants from the tribe Smicromyrmini (Hymenoptera: Mutillidae) with unusual color syndrome. *Far Eastern Entomologist* 421: 1–9. https://doi.org/10.25221/fee.421.1
Lelej, A.S. (2021) A new species of the genus *Petersenidia* Lelej (Hymenoptera: Mutillidae) from Indonesia, eastward of Wallace's line. *Zootaxa* 5006 (1): 101–105. https://doi.org/10.11646/zootaxa.5006.1.13
Lelej, A.S. (2023) Review of the tribe Ctenotillini (Hymenoptera: Mutillidae) from Oriental and Palaearctic Regions. *Far Eastern Entomologist* 480: 1–22. https://doi.org/10.25221/fee.480.1
Lelej, A.S. & Brothers, D.J. (2008) The genus-group names of Mutillidae (Hymenoptera) and their type species, with a new genus, new name, new synonymies, new combinations and lectotypifications. *Zootaxa* 1889: 1–79. https://doi.org/10.11646/zootaxa.1889.1.1
Lelej, A.S., Choi, J.-Y. & Tripotin, P. (2001) Review of the mutillid wasps (Hymenoptera, Mutillidae) of Korea. *Far Eastern Entomologist* 96: 1–15.
Lelej, A.S. & Kabakov, O.N. (1980) On Bradynobaenidae and Mutillidae (Hymenoptera) of Afghanistan. *Entomologicheskoe Obozrenie* 59 (1): 181–196. (in Russian). [English translation (1981) in *Entomological Review* 59 (1): 141–156]
Lelej, A.S. & Nemkov, P.G. (1997) Phylogeny, evolution and classification of Mutillidae (Hymenoptera). *Far Eastern Entomologist* 46: 1–24.
Lelej, A.S., Proshchalykin, M.Y. & Loktionov, V.M. (2014) To the knowledge of velvet ants (Hymenoptera, Mutillidae) of East Siberia. *Euroasian Entomological Journal* 13 (4): 388–394. (in Russian)
Lelej, A.S. & Schmid-Egger, C. (2005) The velvet ants (Hymenoptera, Mutillidae) of Central Europe. *Linzer biologische Beiträge* 37 (2): 1505–1543.
Lelej, A.S., Ullah, M. & Mahmood, K. (2007) Additions to the knowledge of the Mutillidae (Hymenoptera) of Pakistan. *Zootaxa* 1444 (1): 53–60. https://doi.org/10.11646/zootaxa.1444.1.4
Lelej, A.S. & Williams, K.A. (2023) Review of the tribe Smicromyrmini Bischoff, 1920 (Hymenoptera: Mutillidae). *Zootaxa* 5231 (2): 101–140. https://doi.org/10.11646/zootaxa.5231.2.1
Lelej, A.S., Williams, K.A., Loktionov, V.M., Pang, H. & Xu, Z.-f. (2017) Review of the genus *Zeugomutilla* Chen, 1957 (Hymenoptera, Mutillidae, Mutillini), with description of two new species. *Zootaxa* 4247 (1): 1–15. https://doi.org/10.11646/zootaxa.4247.1.1
Lelej, A.S., Williams, K.A., Terine, J.B., Okayasu, J., Parikh, G. & Kumar, G.P. (2023) Review of the tribe Mutillini (Hymenoptera: Mutillidae) from the Oriental Region. *Zootaxa* 5228 (4): 455–476. https://doi.org/10.11646/zootaxa.5228.4.5

Lelej, A.S. & Yamane, Sk. (1992) Interesting velvet ants (Hymenoptera, Mutillidae) from Japan and Korea. *Japanese Journal of Entomology* 60 (3): 625–632.

Lelej, A.S., Zhou, H.-t., Loktionov, V.M. & Xu, Z.-f. (2016) Review of the genus *Promecidia* Lelej, 1996, with description of two new species from China (Hymenoptera, Mutillidae, Trogaspidiini). *ZooKeys* 641: 103–120. https://doi.org/10.3897/zookeys.641.10765

Lepeletier de Saint-Fargeau, A. (1845) *Histoire naturelle des Insectes*. *Hyménoptères*. *Tome Troisième*. Roret, Paris, [4] + 646 pp. https://doi.org/10.5962/bhl.title.9005

Linnaeus, C. (1758) *Systema Naturae per Regna Tria Naturae, secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis*. *Tomus I. Editio Decima Reformata*. Laurentii Salvii, Holmiae, [4] + 823 pp. + [5]. https://doi.org/10.5962/bhl.title.559

Lo Cascio, P. (2015) Worldwide checklist of the island mutillid wasps (Hymenoptera Mutillidae). *Biodiversity Journal* 6 (2): 529–592.

Lucas, H. (1849) *Exploration Scientifique de l'Algérie pendant des Années 1840, 1841, 1842. Sciences Physiques, Zoologie, III*. *Histoire Naturelle des Animaux Articulés, Troisieme Partie, Insectes*. Imprimerie Nationale, Paris, [6] + 527 pp. and *Zoologie, IV*. *Histoire Naturelle des Animaux Articulés, Atlas*. Imprimerie Nationale, Paris, 122 pls. https://doi.org/10.5962/bhl.title.112444

Luz, D.R., Waldren, G.C. & Melo, G.A.R. (2016) Bees as hosts of mutillid wasps in the Neotropical region (Hymenoptera, Apidae, Mutillidae). *Revisita Brasileira de Entomologia* 60 (4): 302–307. https://doi.org/10.1016/j.rbe.2016.06.001

Maddison, W.P. & Maddison, D.R. (2023) Mesquite: a modular system for evolutionary analysis. Version 3.81. Available from: http://www.mesquiteproject.org (accessed 8 January 2024)

Maetô, K., Fukuyama, K. & Kirton, L.G. (1999) Edge effects on ambrosia beetle assemblages in a lowland rain forest, bordering oil palm plantations, in peninsular Malaysia. *Journal of Tropical Forest Science* 11 (3): 537–547.

Magretti, P. (1892) Viaggio di Leonardo Fea in Birmania e regioni vicine XLIII. Imenotteri. Parte prima. Mutillidei, Scoliidei, Tifiidei, Tinnidei colla descrizione di parecchie nuove specie. *Annali del Museo Civico di Storia Naturale di Genova* 2 (12): 197–266 + 1 pl.

Matsuda, S. & Nakamura, S. (1996) Insects from the Ôta basin in Hiroshima Prefecture. *Hibakagaku* 173: 1–96. (in Japanese)

Matsuda, S. & Nakamura, S. (1999) The insects of the basin of the Gouno River, Hiroshima and Shimane Prefecture. *Miscellaneous Reports of the Hiwa Museum for Natural History* 37: 39–176. (in Japanese)

Matsumura, S. (1911) *Thousand insects of Japan supplement III*. Keiseisha-shoten, Tokyo, 147 pp. + pls 30–41. https://doi.org/10.5962/bhl.title.50811

Matsumura, S. & Uchida, T. (1926) Die Hymenopteren-Fauna von den Riukiu Inseln. *Insecta matsumurana* 1: 32–52, 63–77 + 3 pls.

Matteini Palmerini, M. (2013) Remarks on the behavior of the velvet ant *Nemka viduata viduata* (Pallas, 1773) (Insecta Hymenoptera Mutillidae). *Quaderno di Studi e Notizie di Storia Naturale della Romagna* 37: 237–260.

Maxwell-Lefroy, H. (1909) *Indian insect life: A manual of the insects of the plains (tropical India)*. Thacker, Spink & Company, Calcutta, xii + 786 pp. + 84 pls.

Mickel, C.E. (1928) Biological and taxonomic investigations on the mutillid wasps. *United States National Museum Bulletin* 143: ix + 1–351 + 5 pls. https://doi.org/10.5479/si.03629236.143.1

Mickel, C.E. (1933a) The Mutillidae of Formosa. *Annals of the Entomological Society of*

America 26 (2): 381–423. https://doi.org/10.1093/aesa/26.2.381
Mickel, C.E. (1933b) The Mutillidae of Eastern Asia. *Lingnan Science Journal* 12 (3): 289–325.
Mickel, C.E. (1934) Mutillidae of the Philippine Islands. *Philippine Journal of Science* 54 (1): 91–219 + 1 pl.
Mickel, C.E. (1935) The mutillid wasps of the islands of the Pacific Ocean (Hymenoptera, Mutillidae). *Transactions of the Royal Entomological Society of London* 83 (2): 177–312. https://doi.org/10.1111/j.1365-2311.1935.tb01207.x
Mickel, C.E. (1936) A new species of *Smicromyrme* from Japan (Mutillidae, Hymenoptera). *Mushi* 9 (1): 52–54.
Mickel, C.E. (1937) New species and records of Mutillidae (Hymenoptera) from Borneo and the Solomon Islands. *The Annals and Magazine of Natural History*, Series 10 19: 441–456. https://doi.org/10.1080/00222933708655284
Mirande, J.M, (2009) Weighted parsimony phylogeny of the family Characidae (Teleostei: Characiformes). *Cladistics* 25 (6): 574–613. https://doi.org/10.1111/j.1096-0031.2009.00262.x
Mita, T., Abe, J., Kudo, Y., Otsui, K., Murao, R. & Watanabe, K. (2023) Records of wasps and bees (Hymenoptera) collected in Hiraodai, Kyushu, Japan. *Sugare-oi* 3: 46–63. (in Japanese)
Mizuno, R., Suttiprapan, P., Jaitrong, W. & Ito, F. (2019) Daily and seasonal foraging activity of the Oriental non-army ant Doryline *Cerapachys sulcinodis* species complex (Hymenoptera: Formicidae). *Sociobiology* 66 (2): 239–246. https://doi.org/10.13102/sociobiology.v66i2.3775
Morawitz, A. (1865) Über eine neue, oder vielmehr verkannte Form von Männchen unter den Mutillen, nebst einer Übersicht der in Europa beobachteten Arten. *Bulletin de l'Académie Impériale des Sciences de St.-Pétersbourg* 8: 82–141.
Moura, M.R. & Jetz, W. (2021) Shortfalls and opportunities in terrestrial vertebrate species discovery. *Nature Ecology & Evolution* 5: 631–639. https://doi.org/10.1038/s41559-021-01411-5
Munakata, M. (1987) [Collecting records of bees and wasps in Okushiri Island]. *Hymenopterists' Communication* 27: 35–39. (in Japanese)
Murota, T. (1977) [Wasps of Fukui Prefecture]. *Hymenopterists' Communication* 5: 5–7. (in Japanese)
Murota, T. & Nozaka, C. (1987) Records of wasps from Yaeyama Islands. *Hymenopterists' Communication* 27: 106–116. (in Japanese)
Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858. https://doi.org/10.1038/35002501
Nabhan, A.R. & Sarkar, I.N. (2012) The impact of taxon sampling on phylogenetic inference: a review of two decades of controversy. *Briefings in Bioinformatics* 13 (1): 122–134. https://doi.org/10.1093/bib/bbr014
Nagase, H. (2004) Hymenoptera (excl. Formicidae). *In*: Kanagawa Konchû Danwakai (ed.) *Insect fauna of Kanagawa III*. Kanagawa Konchû Danwakai, Odawara, pp. 1241–1326. (in Japanese)
Nagase, H., Harada, K., Ito, H. & Yago, M. (2014) Catalogue of the Masayo Kato insect collection, the University Museum, the University of Tokyo Part I. Hymenoptera. *The University Museum, The University of Tokyo Material Reports* 104: 5–189.
Nagy, C.G. (1966) Ein neues Mutilliden-Subgenus aus Rumänien (Hymenoptera). *Reichenbachia* 6 (13–34): 113–117.
Nagy, C.G. (1972) Two new species of Mutillidae (Hymenoptera) from Asia Minor and

description of female *Mutilla erronea*. *Bulletin of the Iraq Natural History Museum* 5 (2): 4–9.
Nakamura, S. & Haneda, Y. (1997) Distributional notes on wasps (Apocrita: Hymenoptera) from Hiroshima Prefecture. *Miscellaneous Reports of the Hiwa Museum for Natural History* 35: 31–48. (in Japanese)
Nakamura, S. & Haneda, Y. (1998) Distributional notes on wasps (Apocrita: Hymenoptera) from Hiroshima Prefecture (2). *Miscellaneous Reports of the Hiwa Museum for Natural History* 36: 31–42. (in Japanese)
Nakamura, S. & Haneda, Y. (2000) Distributional notes on wasps and bees (Apocrita: Hymenoptera) from Hiroshima Prefecture (4). *Miscellaneous Reports of the Hiwa Museum for Natural History* 39: 117–136. (in Japanese)
Nakamura, S., Kameyama, T. & Katayama, S. (2001) The insects in the riverside of Gono-kawa River. *Bulletin of the Hoshizaki Green Foundation* 5: 17–114. (in Japanese)
Nakamura, S., Takayama, T. & Hamaguchi, K. (2000) Insects from Ashida River, Hiroshima Prefecture, a result of survey in 1997. *Journal of the Hiba Society of Natural History* 196: 1–144. (in Japanese)
Nambu, T. (2005) [The Hymenoptera of Ranzan City]. *In*: Yoshino, M., Sekine, S., Okudaira, F., Sekine, H., Shimazaki, M. & Kokubo, K. (eds) [*Reports of Ranzan City natural history survey, Volume 10*]. Ranzan City Board of Education, Ranzan, pp. 184–212. (in Japanese)
Nambu, T. & Tano, T. (1983) [Wasps and ants collected in Taiwan in 1980]. *Hymenopterists' Communication* 16: 11–23. (in Japanese)
National Museum of Natural History (2024) Department of Entomology collections. Available from: https://collections.nmnh.si.edu/search/ento/ (accessed 8 January 2024)
Natural History Museum (2014) Collection specimens [Data set]. Natural History Museum Data Portal (data.nhm.ac.uk). Available from: https://doi.org/10.5519/0002965 (accessed 8 January 2024)
Negoro, H., Haneda, Y. & Tano, T. (2005) The Aculeata of Toyama Prefecture. *Tsunekibachi* 4: 31–52. (in Japanese)
Nishida, E. & Kawazoe, A. (2011) [The Hymenoptera of Shima Peninsula]. *In*: Ikawa, N. (ed.) [*Insects of Shima Peninsula*]. Mie Entomology Club, Mie, 196–203.
Nixon, K.C. (2002) WinClada ver. 1.00.08. Published by the author, Ithaca.
Nixon, K.C. (2004) ASADO ver. 1.61. Published by the author, Ithaca. Available from: http://www.diversityoflife.org/winclada/ (accessed 8 January 2024)
Nomura, Y. (1978) [On the insect fauna of Tottori sand dune]. *Tottori Seibutsu* 10–13: 13–19. (in Japanese)
Nonveiller, G. (1980) Recherches sur les Mutillides de l'Afrique (Hymenoptera, Mutillidae) X. Bref aperçu des résultats des recherches sur la faune des Mutillides du Cameroun effectuées au cours de la période 1962–1975. *Memoires publies par l'Institut pour la Protection des Plantes*, Beograd 14: 11–68.
Nostu, Y. (2019) [Records of velvet ants collected in Tottori and Shimane]. *Sukashiba* 66: 5–7. (in Japanese)
Nurse, C.G. (1903) New species of Indian aculeate Hymenoptera. *The Annals and Magazine of Natural History*, Series 7 11: 393–403, 511–526, 528–549. https://doi.org/10.1080/00222930308678815
Ogawa, H., Nosaka, M., Hashii, N., Yokoyama, M. & Tsurusaki, N. (2012) Records of faunal survey of insects of Tottori Sand Dunes in 2011 with comments to the fauna of "Sakyu Oasis". *Natural History Research of San'in* 7: 31–40. (in Japanese)
Ohkusa, S. (2006) Hymenoptera collected from Gifu Prefecture. *Tsunekibachi* 9: 16–28. (in

Japanese)
Ohkusa, S. (2007) Hymenoptera collected from north-west at Aichi Prefecture. *Tsunekibachi* 12: 26–38. (in Japanese)
Ohkusa, S. & Tajima, T. (2008) Hymenoptera collected from north-west at Aichi Prefecture. *Tsunekibachi* 13: 63–81. (in Japanese)
Ohkusa, S. & Tajima, T. (2010) Hymenoptera of eastern part of Shiga Prefecture. *Tsunekibachi* 17: 1–20. (in Japanese)
Okayasu, J. (2017) Two new species of the genus *Sinotilla* Lelej, 1995 (Hymenoptera: Mutillidae), with notes on taxonomic characters. *Zootaxa* 4294 (2): 151–169. https://doi.org/10.11646/zootaxa.4294.2.1
Okayasu, J. (2018) Taxonomic review of Chin-wen Chen's species described in the genus *Smicromyrme* (Hymenoptera: Mutillidae: Smicromyrmini). *Acta Entomologica Musei Nationalis Pragae* 58 (2): 479–494. https://doi.org/10.2478/aemnp-2018-0036
Okayasu, J. (2020) Velvet ants of the tribe Smicromyrmini Bischoff (Hymenoptera: Mutillidae) of Japan. *Zootaxa* 4723 (1): 1–110. https://doi.org/10.11646/zootaxa.4723.1.1
Okayasu, J. (2021a) A new velvet ant genus *Arkaditilla* (Hymenoptera, Mutillidae, Trogaspidiini) from the Oriental Region, with review of species. *Journal of Hymenoptera Research* 84: 145–168. https://doi.org/10.3897/jhr.84.68709
Okayasu, J. (2021b) Exploring the final piece of Japanese mutillid fauna in Amami-Ôshima Island, the newest World Heritage site. *Hamuli* 12: 25–29.
Okayasu, J. (2022) Remarkable range extension of the genus *Nordeniella* Lelej, 2005 (Hymenoptera: Mutillidae: Smicromyrmini): Description of a new species from Sumbawa, Indonesia. *Journal of Insect Biodiversity* 32 (2): 56–63. https://doi.org/10.12976/jib/2022.32.2.3
Okayasu, J. (2023a) Love is in the air and beyond the ocean: Taxonomic review of *Neotrogaspidia* Lelej (Hymenoptera: Mutillidae: Trogaspidiini) in Northeast Asia highlights its unique distributional pattern. *Entomological Science* 26 (1): e12532. https://doi.org/10.1111/ens.12532
Okayasu, J. (2023b) Discovery of the velvet ant genus *Orientilla* Lelej from Laos (Hymenoptera, Mutillidae, Dasylabrinae), with description of a related new species from India. *Journal of Hymenoptera Research* 96: 817–834. https://doi.org/10.3897/jhr.96.110590
Okayasu, J. (2023c) Preliminary assessment of the velvet ant fauna in Nepal, with description of new species of the genera *Strangulotilla* Nonveiller and *Zeugomutilla* Chen (Hymenoptera: Mutillidae). *Insecta matsumurana*, New series 79: 1–27.
Okayasu, J., Lelej, A.S. & Williams, K.A. (2021a) Review of *Eotrogaspidia* Lelej (Hymenoptera: Mutillidae: Trogaspidiini). *Zootaxa* 4920 (1): 56–90. https://doi.org/10.11646/zootaxa.4920.1.2
Okayasu, J., Williams, K.A. & Lelej, A.S. (2018) A remarkable new species of the genus *Sinotilla* Lelej (Hymenoptera: Mutillidae: Smicromyrmini) from Taiwan and an overview of color diversity in East Asian mutillid females. *Zootaxa* 4446 (3): 301–324. http://dx.doi.org/10.11646/zootaxa.4446.3.1
Okayasu, J., Williams, K.A. & Lelej, A.S. (2021b) Review of female *Andreimyrme* Lelej (Hymenoptera: Mutillidae: Smicromyrmini). *Zootaxa* 5061 (1): 1–38. https://doi.org/10.11646/zootaxa.5061.1.1
Ono, H. & Kawashima, I. (2013) Host records on two species of mutillid wasps (Hymenoptera, Mutillidae) in Japan. *Tsunekibachi* 23: 41–42. (in Japanese)
Osten, T. (1982) Vergleichend-funktionsmorphologische Untersuchungen der Kopfkapsel und der Mundwerkzeuge ausgewählter "Scolioidea" (Hymenoptera, Aculeata). *Stuttgarter*

Beiträge zur Naturkunde, Serie A (Biologie) 354: 1–60.
O'Toole, C. (1975) The systematics of *Timulla oculata* (Fabricius) (Hymenoptera, Mutillidae). *Zoologica Scripta* 4 (1): 229–251. https://doi.org/10.1111/j.1463-6409.1975.tb00733.x
Ôtsui, K., Uemori, K. & Murao, R. (2021) [Records of aculeate Hymenoptera from Nakagawa-shi, Fukuoka Prefecture]. *Korasana* 97: 33–48. (in Japanese)
Pagden, H.T. (1934a) New species of Mutillidae (Hymenoptera, Vespoidea) from the Malay Peninsula. *Journal of the Federated Malay States Museums* 17 (3): 419–457.
Pagden, H.T. (1934b) Biological notes on some Malayan aculeate Hymenoptera I. (Sphecoidea, and Vespoidea). *Journal of the Federated Malay States Museum* 17 (3): 458–466.
Pagden, H.T. (1934c) Biological notes on some Malayan aculeate Hymenoptera II. with descriptions of new species. *Journal of the Federated Malay States Museums* 17 (3): 467–486.
Pagden, H.T. (1949) Descriptions and records of Austro-Malaysian Methocidae and Mutillidae (Hymenoptera). *Transactions of the Royal Entomological Society of London* 100 (8): 191–231. https://doi.org/10.1111/j.1365-2311.1949.tb01431.x
Pagliano, G. (2011) I Mutillidae (Hymenoptera) della collezione Zavattari le collezioni del Museo Regionale di Scienze Naturali di Torino. *Bolletino del Musei Regionale di Scienze Naturali di Torino* 28 (1): 37–60.
Pagliano, G., Brothers, D.J., Cambra, R., Lelej, A.S., Lo Cascio, P., Matteini Palmerini, M., Scaramozzino, P.L., Williams, K.A. & Romano, M. (2020) Checklist of names in Mutillidae (Hymenoptera), with illustrations of selected species. *Bollettino del Museo Regionale di Scienze Naturali di Torino* 36 (1–2): 5–425.
Pagliano, G. & Scaramozzino, P.L. (2021) La collezione di Mutillidae e di Bradynobaenidae (Hymenoptera) di Guido Pagliano. *Bollettino del Museo Regionale di Scienze Naturali di Torino* 38 (1–2): 63–147.
Pagliano, G. & Strumia, F. (2007) Contributo alla conoscenza dei Mutillidae italiani (Hymenoptera, Scolioidea). *Bollettino del Museo Regionale di Scienze Naturali di Torino* 24 (1): 25–110.
Pallas, P.S. (1773) *Reisen durch verschiedene Provinzen des Russischen Reichs*. *Zweiter Theil*. *Zweites Buch vom Jahr 1771*. Kayserlichen Academie der Wissenschaften, St. Petersburg, [12] + 744 pp.
Panzer, G.W.F. (1792–1844) *Faunae Insectorum Germaniae initia oder Deutschlands Insecten*. Nürnberg. 1797: Hf. 39–48; 1798: Hf. 49–60; 1799: Hf. 61–72; 1800: Hf. 73–79; 1801: Hf. 80–85; 1805: Hf. 97–99; 1806a–1809: Hf. 101–107. (Dates of publication after Sherborn, 1923). https://doi.org/10.5962/bhl.title.12432
Panzer, G.W.F. (1806b) *Entomologischer Versuch die Jürineschen Gattungen der Linnéschen Hymenopteren nach dem Fabriziusschen System zu prufen: im Bezug auf die in der Deutschen Insektenfaune bekannt gemachten Gattungen und Arten dieser Klasse*. *Kritische Revision der Insektenfaune Deutschlands nach dem System bearbeitet*. *I–C. Heft. II. Bändchen mit zwey illuminirten Kupfertafeln*. Felssekerschen Buchhandlung, Nürnberg, [14] + 270 pp. + 2 pls. https://doi.org/10.5962/bhl.title.6539
Pérez, J. (1905) Hyménoptères recueillis dans le Japon central, par M. Harmand, ministre plénipotentiaire de France à Tokio. Troisième partie. Pompilides, Pemphrédonides, Sphégides et Crabronides. *Bulletin de Muséum d'Histoire naturelle* 3: 148–158.
Petersen, B. (1988) The Palaearctic Mutillidae of I.C. Fabricius and some related material (Insecta, Hymenoptera, Aculeata). *Steenstrupia* 14 (6): 129–224.
Pilgrim, E.M. & Pitts, J.P. (2006) A molecular method for associating the dimorphic sexes of velvet ants (Hymenoptera: Mutillidae). *Journal of the Kansas Entomological Society*

79 (3): 222–230. https://doi.org/10.2317/0511.09.1
Pitts, J.P. & Manley, D.G. (2004) A revision of *Lomachaeta* Mickel, with a new species of *Smicromutilla* Mickel (Hymenoptera: Mutillidae). *Zootaxa* 474: 1–27. https://doi.org/10.11646/zootaxa.474.1.1
Plazzi, F., Ferrucci, R.R. & Passamonti, M. (2010) Phylogenetic representativeness: A new method for evaluating taxon sampling in evolutionary studies. *BMC Bioinformatics* 11: 209. https://doi.org/10.1186/1471-2105-11-209
Polidori, C., Mendiola, P., Asís, J.D., Tormos, J. & Selfa, J. (2010) Temporal asynchrony and spatial co-occurrence with host: the foraging patterns of *Nemka viduata*, a parasitoid of digger wasps (Hymenoptera: Mutillidae and Crabronidae). *Journal of Ethology* 28: 353–361. https://doi.org/10.1007/s10164-009-0196-2
Radoszkowski, O. (1877) Chrysidiformes, Mutillidae et Sphegidae. *In*: *Puteshestvie v Turkestan A.P. Fedtshenko* [*Voyage au Turkestan d'Alexis Fedtschenko*], (14)2(5), Sankt-Petersburg, pp. 1–87 + 3 pls. (in Russian)
Radoszkowski, O. (1885) Revision des armures copulatrices des mâles de la famille de Mutillides. *Horae Societatis Entomologicae Rossicae* 19 (1–2): 3–49 + 9 pls.
Ramírez, M.J. (2003) The spider subfamily Amaurobioidinae (Araneae, Anyphaenidae): A phylogenetic revision at the generic level. *Bulletin of the American Museum of Natural History* 277: 1–262. https://doi.org/10.1206/0003-0090(2003)277%3C0001:TSSAAA%3E2.0.CO;2
Reemer, M. & Ståhls, G. (2013) Phylogenetic relationships of Microdontinae (Diptera: Syrphidae) based on molecular and morphological characters. *Systematic Entomology* 38 (4): 661–688. https://doi.org/10.1111/syen.12020
Roll, U., Feldman, A., Novosolov, M., Allison, A., Bauer, A.M., Bernard, R., Böhm, M., Castro-Herrera, F., Chirio, L., Collen, B., Colli, G.R., Dabool, L., Das, I., Doan, T. M., Grismer, L.L., Hoogmoed, M., Itescu, Y., Kraus, F., LeBreton, M., Lewin, A., Martins, M., Maza, E., Meirte, D., Nagy, Z.T., Nogueira, C. de C., Pauwels, O.S.G., Pincheira-Donoso, D., Powney, G.D., Sindaco, R., Tallowin, O.J.S., Torres-Carvajal, O., Trape, J.-F., Vidan, E., Uetz, P., Wagner, P., Wang, Y., Orme, C.D.L., Grenyer, R. & Meiri, S. (2017) The global distribution of tetrapods reveals a need for targeted reptile conservation. *Nature Ecology & Evolution* 1: 1677–1682. https://doi.org/10.1038/s41559-017-0332-2
Sabi, K., Nozaka, C., Kurokawa, H. & Tano, T. (1977) [Insect collecting trip to Taiwan]. *Hymenopterists' Communication* 5: 34–42. (in Japanese)
Santos, B.F., Payne, A., Pickett, K.M. & Carpenter, J.M. (2015) Phylogeny and historical biogeography of the paper wasp genus *Polistes* (Hymenoptera: Vespidae): implications for the overwintering hypothesis of social evolution. *Cladistics* 31 (5): 535–549. https://doi.org/10.1111/cla.12103
Sato, T. & Tsurusaki, N. (2010) Preliminary report of insect fauna occurring in the Tottori Sand Dunes. *Bulletin of the Tottori Prefectural Museum* 47: 45–81. (in Japanese)
Schulmeister, S. (2011) Functional morphology of the male genitalia and copulation in lower Hymenoptera, with special emphasis on the Tenthredinoidea s. str. (Insecta, Hymenoptera, 'Symphyta'). *Acta Zoologica* 82 (4): 331–349. https://doi.org/10.1046/j.1463-6395.2001.00094.x
Schulz, W.A. (1906) *Spolia Hymenopterologica*. Albert Pape, Paderborn, 356 pp. + 1 pl. https://doi.org/10.5962/bhl.title.59757
Schuster, R.M. (1949) Contribution towards a monograph of the Mutillidae of the Neotropical region. III. A key to the subfamilies represented and descriptions of several new genera (Hymenoptera). *Entomologica Americana*, New Series 29 (3–4): 59–140.

Schwartz, F. (1984) Description d'un genre nouveau, disjoint de *Smicromyrme*, et d'une espèce nouvelle du sud de la France (Hymenoptera, Mutillidae). *L'Entomologiste* 40 (1): 21–25.

Sherborn, C.D. (1923) On the dates of G.W.F. Panzer's "Fauna Insect. German.", 1792–1844. *The Annals and Magazine of Natural History*, Series 9 11: 566–567. https://doi.org/10.1080/00222932308632887

Shintani, T. (2003) Distributional information on insects from Sera-plateau, Hiroshima Prefecture (1). *Journal of the Hiba Society of Natural History* 208: 13–19 + 1 pl. (in Japanese)

Sichel, J. & Radoszkowski, O. (1869–1870) Essai d'une monographie des Mutilles de l'ancien continent. *Horae Societatis Entomologicae Rossicae* 6 (3): 139–172 + pl. 6–8 (1869); 6(4): 173–309 + pl. 9–11 (1870).

Skorikov, A.S. (1935) Zur Mutilliden-Fauna Zentralasiens. *Trudy Tadzhikskoi Basy Akademii Nauk SSSR* 5: 257–349 + 7 pls. (in Russian)

Smith, F. (1855) *Catalogue of hymenopterous insects in the collection of the British Museum*. *Part III*. *Mutillidae and Pompilidae*. Taylor and Francis, London, [4] + 206 pp. + pl. A + 5 pls. https://doi.org/10.5962/bhl.title.20858

Smith, F. (1857–1858) Catalogue of the hymenopterous insects collected at Sarawak, Borneo; Mount Ophir, Malacca; and at Singapore, by A.R. Wallace. *Journal of the Proceedings of the Linnean Society*, Zoology 2 (6): 42–88 + pls. 1–2 (1857); 2 (7): 89–130 (1858). https://doi.org/10.1111/j.1096-3642.1857.tb01759.x; https://doi.org/10.1111/j.1096-3642.1858.tb02548.x

Smith, F. (1859) Catalogue of hymenopterous insects collected by Mr. A.R. Wallace at the islands of Aru and Key. *Journal of the Proceedings of the Linnean Society*, Zoology 3 (11): 132–178. https://doi.org/10.1111/j.1096-3642.1859.tb00077.x

Smith, F. (1860 [1861]) Catalogue of hymenopterous insects collected by Mr. A.R. Wallace in the islands of Bachian, Kaisaa, Amboyna, Gilolo, and at Dory in New Guinea. *Journal of the Proceedings of the Linnean Society*, Zoology 5: 93–143. https://doi.org/10.1111/j.1096-3642.1860.tb01022.x

Smith, F. (1865) Descriptions of new species of hymenopterous insects from the islands of Sumatra, Sula, Gilolo, Salwatty, and New Guinea, collected by Mr. A. R. Wallace. *Journal of the Proceedings of the Linnean Society*, Zoology 8 (30): 61–94 + pl. 4. https://doi.org/10.1111/j.1096-3642.1865.tb02422.x

Smith, F. (1873) Description of aculeate Hymenoptera of Japan, collected by Mr. George Lewis at Nagasaki and Hiogo. *The Transactions of the Entomological Society of London* 21 (2): 181–206. https://doi.org/10.1111/j.1365-2311.1873.tb00641.x

Smith, F. (1879) *Descriptions of new species of Hymenoptera in the collection of the British Museum*. Taylor and Francis, London, xxi + 240 pp. https://doi.org/10.5962/bhl.title.60089

Snodgrass, R.E. (1941) The male genitalia of Hymenoptera. *Smithsonian Miscellaneous Collections* 99 (14): 1–86 + 33 pls.

Sonan, J. (1931) Some wasps and bees of Hokoto (Pescadores). *Transactions of the Natural History Society of Formosa* 21 (112): 6–8. (in Japanese)

Spinola, M. (1806) *Insectorum Liguriae Species Novae aut Rariores, quas in Agro Ligustico nuper detexit, descripsit, et Iconibus illustravit Maximilianus Spinola, adjecto catalogo specierum auctoribus jam enumeratarum, quae in eadem regione passim occurrunt*. *Tom. I*. Yves Gravier, Genuae, xvii + 160 pp. + 2 pls.

Spinola, M. (1841) Hyménoptères recueillis à Cayenne en 1839 par M. Leprieur, pharmacien de la Marine Royale. *Annales de la Société Entomologique de France* 10: 86–149.

Suárez, F.J. (1965) Nota sinonímica preliminar y propuesta del nombre genérico

Eremomyrme nom. nov. (Hymenoptera, Mutillidae). *Memorie della Società Entomologica Italiana* 44: 51–52.
Suárez, F.J. (1974) Nuevas especies de mutilidos recogidos por la mision del Dr. Z. Kaszab en Mongolia, durante las campañas de 1963 a 1968 (Hymenoptera: Myrmosidae y Mutillidae). *Archivos del Instituto de Aclimatación* 19: 5–19 + 6 figs.
Suda, T. (2011) [Collecting data of Mutillidae including new records]. *Rambu* 20: 136–138. (in Japanese)
Suzuki, M. (1934) A list of Japanese Mutillidae. *Kansai Konchu Zasshi* 2 (1): 23–25. (in Japanese)
Swederus, N.S. (1787) Et nytt genus, och femtio nya species af insekter beskrifne. *Kongliga Vetenskaps Academiens nya Handlingar* 8: 181–201.
Takahashi, H. (1996) [Collecting records of Mutillidae]. *Gekkan-Mushi* 310: 28–29. (in Japanese)
Takahashi, H. & Matsumoto, Y. (1999) Some records of Hymenoptera from Izu Islands, Tokyo, Japan. *Gensei* 74: 23–26. (in Japanese)
Tano, T., Kurokawa, H., Murota, T. & Nozaka, C. (2003) The Hymenoptera collected at Tsushima, Nagasaki Prefecture in July of 2003. *Tsunekibachi* 1: 23–40. (in Japanese)
Taylor, C.K., Murphy, M.V., Hitchen, Y. & Brothers, D.J. (2019) Four new species of Australian velvet ants (Hymenoptera: Mutillidae, *Aglaotilla*) reared from bee and wasp nests, with a review of Australian mutillid host records. *Zootaxa* 4609 (2): 201–224. https://doi.org/10.11646/zootaxa.4609.2.1
Taylor, R.W. (1983) Descriptive taxonomy: past, present, and future. *In*: Highley, E. & Taylor, R.W. (eds) *Australian systematic entomology: A bicentenary perspective*. CSIRO, Melbourne, pp. 93–134.
Terayama, M. (2004) A catalogue of aculeate Hymenoptera of Japan. *Memoirs of the Myrmecological Society of Japan* 2: ii + 1–123. (in Japanese)
Terayama, M. (2005) Taxonomic guide to the Japanese aculeate wasps, 2. Family Mutillidae. *Tsunekibachi* 4: 1–13. (in Japanese)
Terayama, M. (2019) Record of a female velvet ant of the genus *Ephucilla* collected in Okinawa Island. *Gekkan-Mushi* 580: 48. (in Japanese)
Terayama, M., Suda, H., Murota, T., Haneda, Y. & Tano, T. (2011) The velvet ants (Mutillidae) of Japan. *Gekkan-Mushi* 481: 12–25. (in Japanese)
Terayama, M., Suda, H., Murota, T. & Tano, T. (2016) Family Mutillidae. *In*: Terayama, M. & Suda, H. (eds) *A guide to the aculeate wasps of Japan*. Tokai University Press, Hiratsuka, pp. 161–174. (in Japanese)
Terine, J.B., Lelej, A.S. & Kumar, G.P. (2021) Discovery of the genus *Andreimyrme* Lelej, 1995 (Hymenoptera: Mutillidae) in India and description of a new species from the Western Ghats. *Zootaxa* 5020 (1): 184–190. https://doi.org/10.11646/zootaxa.5020.1.10
Thaochan, N., Williams, K.A., Thoawan, K., Jeenthong, T. & Sittichaya, W. (2022) Three new species and one new country record of velvet ants (Hymenoptera, Mutillidae) from Thailand. *Journal of Hymenoptera Research* 93: 151–165. https://doi.org/10.3897/jhr.93.94727
The Natural History Society of Fukui (1938) [*Illustrated insects of Fukui Prefecture*]. The Natural History Society of Fukui, Fukui. (in Japanese)
Thomson, C.G. (1870) Öfversigt af Sveriges rofsteklar. *Opuscula Entomologica*, Lund 1 (2): 202–251.
Togashi, I. (1991) Distribttional [sic!] notes of bees of *Colletes* Latreille occurring in Ishikawa Prefecture, Japan. *Entomological Journal of Fukui* 8: 21–25. (in Japanese)
Togashi, I. (1998) Hymenoptera. *In*: Togashi, I. (ed.) [*Insects of Ishikawa*]. Ishikawa

Prefecture Government, Kanazawa, pp. 252–304. (in Japanese)
Tonnoir, A.L. (1930) Notes on Indian Blepharocerid larvae and pupae with remarks on the morphology of Blepharocerid larvae and pupae in general. *Records of the Indian Museum* 32: 161–214.
Troya, A., Marcineiro, F., Lattke, J.E. & Longino, J. (2022) *Igaponera curiosa*, a new ponerine genus (Hymenoptera: Formicidae) from the Amazon. *European Journal of Taxonomy* 823: 82–101. https://doi.org/10.5852/ejt.2022.823.1817
Tsuneki, K. (1965) The biology of east-Asiatic *Cerceris* (Hym., Sphecidae) with special reference to the peculiar social relationships and return to the nest in *Cerceris hortivaga* Kohl. *Etizenia* 9: 1–46.
Tsuneki, K. (1972a) Two new species of Mutillidae from Borneo (Hym.). *The Life Study* 16 (1–2): 17–21.
Tsuneki, K. (1972b) Studies on the Mutillidae of Japan (Hymenoptera). *Etizenia* 61: 1–26.
Tsuneki, K. (1972c) Mutillidae collected in Formosa in 1966 and 68 (Hymenoptera). *Etizenia* 64: 1–25.
Tsuneki, K. (1972d) [Collecting records of velvet ants in Fukui Prefecture in 1972]. *The Life Study* 16 (3–4): 59. (in Japanese)
Tsuneki, K. (1973) New and the first recorded species and subspecies of Sphecidae and Mutillidae from Japan, with taxonomic notes on some species (Hymenoptera). *Etizenia* 65: 1–28.
Tsuneki, K. (1982) Studies on the new material of Sphecidae, Chrysididae and Mutillidae of Formosa and the southern Ryukyus (Hymenoptera). *Special Publications of the Japan Hymenopterists Association* 23: 15–45.
Tsuneki, K. (1993a) On some Taiwanese Mutillidae, collected in 1976 by Mr. T. Murota, with description of new taxa (Hymenoptera). *Special Publications of the Japan Hymenopterists Association* 41: 39–50.
Tsuneki, K. (1993b) A new and an undescribed species of Mutillidae from Is. Okinawa, the Ryukyus (Hymenoptera). *Special Publications of the Japan Hymenopterists Association* 41: 51–55.
Tsuneki, K., Nozaka, C., Tano, T., Kurokawa, H. & Murota, T. (1993) Mutillidae recently collected in the Philippines (Hymenoptera). *Special Publications of the Japan Hymenopterists Association* 41: 1–38.
Tsurusaki, N., Hayashi, M., Miyanaga, R., Ichisawa, K. & Kawakami, Y. (2012) Catalogue of the insects of Tottori Sand Dunes, Honshu, Japan. *Natural History Research of San'in* 7: 47–82. (in Japanese)
Tu, B.-B., Lelej, A.S. & Chen, X.-X. (2015) Review of the genus *Taiwanomyrme* Tsuneki, 1993 (Hymenoptera, Mutillidae, Mutillinae), with description of two new species from China. *Zootaxa* 4020 (3): 588–600. https://doi.org/10.11646/zootaxa.4020.3.10
Turner, H. & Zandee, R. (1995) The behaviour of Goloboff's tree fitness measure *F*. *Cladistics* 11 (1): 57–72. https://doi.org/10.1111/j.1096-0031.1995.tb00004.x
Turner, R.E. (1911) New Hymenoptera from Ceylon. Mutillidae and Scoliidae. *Spolia Zeylanica* 7 (27): 141–154.
Waldren, G.C., Sadler, E.A., Murray, E.A., Bossert, S., Danforth, B.N. & Pitts, J.P. (2023) Phylogenomic inference of the higher classification of velvet ants (Hymenoptera: Mutillidae). *Systematic Entomology* 48(3): 463–487. https://doi.org/10.1111/syen.12588
Weiler, L., Ferrari, A. & Grazia, J. (2016) Phylogeny and biogeography of the South American subgenus *Euschistus* (*Lycipta*) Stål (Heteroptera: Pentatomidae: Carpocorini). *Insect Systematics and Evolution* 47 (4): 313–346. https://doi.org/10.1163/1876312X-47032145

Wheeler, W.C. (1995) Sequence alignment, parameter sensitivity, and the phylogenetic analysis of molecular data. *Systematic Biology* 44 (3): 321–331. https://doi.org/10.1093/sysbio/44.3.321

Wikramanayake, E., Dinerstein, E., Loucks, C.J., Olson, D.M., Morrison, J., Lamoreux, J., McKnight, M. & Hedao, P. (2002) *Terrestrial ecoregions of the Indo-Pacific: A conservation assessment*. Island Press, Washington DC, xxix + 643 pp.

Williams, K.A., Brothers, D.J. & Pitts, J.P. (2011) New species of *Tobantilla* Casal, 1965 and a new genus and species, *Gogoltilla chichikovi* gen. et sp. nov., from Argentina (Hymenoptera: Mutillidae). *Zootaxa* 3064 (1): 41–68. https://doi.org/10.11646/zootaxa.3064.1.2

Williams, K.A., Cambra, R.A., Waldren, G.C., Quintero A., D. & Pitts, J.P. (2019a) *Silvorientilla*, gen. nov. a new Neotropical velvet ant genus (Hymenoptera: Mutillidae). *Folia Entomológica Mexicana*, nueva serie 4 (3): 91−109.

Williams, K.A., Lelej, A.S., Okayasu, J., Borkent, C.J., Malee, R., Thoawan, K. & Thaochan, N. (2019b) The female velvet ants (aka modkhong) of southern Thailand (Hymenoptera: Mutillidae), with a key to the genera of southeast Asia. *Zootaxa* 4602 (1): 1–69. https://doi.org/10.11646/zootaxa.4602.1.1

Williams, K.A., Lelej, A.S. & Thaochan, N. (2019c) New species of Myrmosinae (Hymenoptera: Mutillidae) from Southeastern Asia. *Zootaxa* 4656 (3): 525–534. https://doi.org/10.11646/zootaxa.4656.3.9

Wilson, G.D. & Shaik, S. (2022) Evidence for Early Mesozoic diversification of Hypsimetopidae Nicholls, 1943 (Isopoda), with the description of a new genus from Andhra Pradesh and notes on threats to Indian cave environments. *Journal of Crustacean Biology* 42(4): ruac052. https://doi.org/10.1093/jcbiol/ruac052

Wilson, J.S., Clark, S.L., Williams, K.A. & Pitts, J.P. (2012a) Historical biogeography of the arid-adapted velvet ant *Sphaeropthalma arota* (Hymenoptera: Mutillidae) reveals cryptic species. *Journal of Biogeography* 39: 336–352. https://doi.org/10.1111/j.1365-2699.2011.02580.x

Wilson, J.S., Williams, K.A., Forister, M.L., von Dohlen, C.D. & Pitts, J.P. (2012b) Repeated evolution in overlapping mimicry rings among North American velvet ants. *Nature Communications* 3: 1272. https://doi.org/10.1038/ncomms2275

Wilson, J.S., Jahner, J.P., Forister, M.L., Sheehan, E.S., Williams, K.A. & Pitts, J.P. (2015) North American velvet ants form one of the world's largest known Müllerian mimicry complexes. *Current Biology* 25: R704–R706. https://doi.org/10.1016/j.cub.2015.06.053

Wilson, J.S., Pan, A.D., Limb, E.S. & Williams, K.A. (2018) Comparison of African and North American velvet ant mimicry complexes: Another example of Africa as the 'odd man out'. *PLoS ONE* 13(1): e0189482. https://doi.org/10.1371/journal.pone.0189482

Wu, C.F. (1941) *Catalogus Insectorum Sinensium Volume VI*. The Department of Biology, Yenching University, Peiping, vi + 333 pp. + xv.

Yamada, H. (1990) Mutillidae, Chrysididae, Sphecidae and Megachilidae of Aichi Prefecture. *In*: Natural Environment Division of Aichi Prefecture (ed.) *The insects of Aichi (the first volume)*. Aichi Prefecture Government, Aichi, pp. 480–487. (in Japanese)

Yamada, M. (2001) Aculeate Hymenoptera fauna of Aomori Prefecture, the northernmost Honshu, Japan. 10. Distributional records of mutillid, tephiid [sic!] and scoliid wasps. *Journal of the Natural History of Aomori* 6: 57–60. (in Japanese)

Yamamoto, E. & Haneda, Y. (2007) Aculeata collected in Odamiyama and the surrounding area (supplement 3). *Shikokukogera* 4: 15–27. (in Japanese)

Yamane, Sk. (1999) Family Mutillidae. *In*: Yamane, Sk., Ikudome, S. & Terayama, M. (eds)

Identification guide to the Aculeata of the Nansei Islands, Japan. Hokkaido University Press, Sapporo, pp. 369–381.
Yano, M. (1932) Mutillidae. *In*: Uchida, S. (ed.) *Iconographia Insectorum Japonicorum Editio Prima*. Hokuryukan, Tokyo, pp. 325–327 + 1 pl. (in Japanese)
Yasumatsu, K. (1937) Hymenoptera of Tsushima (first report). *Journal of Natural History Society in Fukuoka* 2 (2): 59–74. (in Japanese)
Yasumatsu, K. (1938a) Les Mutillides de Coree et de la Mandschourie du Sud. *Transactions of the Natural History Society of Formosa* 28 (175): 83–87.
Yasumatsu, K. (1938b) Beitrage zur synonymie einiger Hymenopterenarten von den Ryukyu-Inseln. *Transactions of the Natural History Society of Formosa* 28 (183): 446–447.
Yasumatsu, K. (1938c) Family Mutillidae. *In*: Esaki, T., Hori, H. & Yasumatsu, K. (eds) *Insectorum Japonicorum Illastratio Iconographica Coloribus ad Naturam Depicta*. Sanseidô, Tokyo, p. 351. (in Japanese)
Yasumatsu, K. (1948) Records of East Chinese Mutillidae (Hymenoptera). *Lingnan Science Journal* 22 (1–4): 71–73.
Yasumatsu, K. (1951) Mutillidae of Shansi, North China (Hymenoptera). *Mushi* 22 (12): 69–72.
Yoder, M.J., Mikó, I., Seltmann, K.C., Bertone, M.A. & Deans, A.R. (2010) A gross anatomy ontology for Hymenoptera. *PLoS ONE* 5 (12): e15991. https://doi.org/10.1371/journal.pone.0015991
Yoshida, M. (1989) Family Mutillidae. *In*: Entomological Laboratory, Faculty of Agriculture, Kyushu University, Japan Wildlife Research Center (eds) *A check list of Japanese insects*. Entomological Laboratory, Faculty of Agriculture, Kyushu University, Fukuoka, pp. 650–651. (in Japanese)
Yoshikawa, Y. (1965) [Studies on stridulation of velvet ants (*Smicromyrme lewisi yanoi* Mickel stridulates)]. *Insect* 15 (2–3): 12–13. (in Japanese)
Zavattari, E. (1910) Catalogo delle Mutille del Museo Zoologico di Napoli. *Annuario del Museo Zoologico dell'Università di Napoli*, New Series 3 (9): 1–16.
Zavattari, E. (1913) H. Sauter's Formosa-Ausbeute. Mutillidae (Hym.). *Archiv für Naturgeschichte* 79A (3): 19–42.
Zavattari, E. (1914) Mutille Austro-Malesi. *Bolletino della Societa Entomologica Italiana* 45: 61–114.
Zhou, H.-t., Lelej, A.S. & Liu, J.-x. (2018a) New records of velvet ants (Hymenoptera: Mutillidae) from China with taxonomic notes. *Far Eastern Entomologist* 354: 23–28. http://doi.org/10.25221/fee.354.4
Zhou, H.-t., Lelej, A.S., Williams, K.A. & Liu, J.-x. (2018b) Revision of the Oriental genus *Zavatilla* Tsuneki (Hymenoptera, Mutillidae, Trogaspidiini), with descriptions of two new species. *Zootaxa* 4418 (2): 101–120. https://doi.org/10.11646/zootaxa.4418.2.1
Zimmermann, K. (1931) Studien über individuelle und geographische variabilität paläarktischer *Polistes* und verwandter Vespiden. *Zeitschrift für Morphogie und Ökologie der Tiere* 22: 173–230. https://doi.org/10.1007/BF00417968

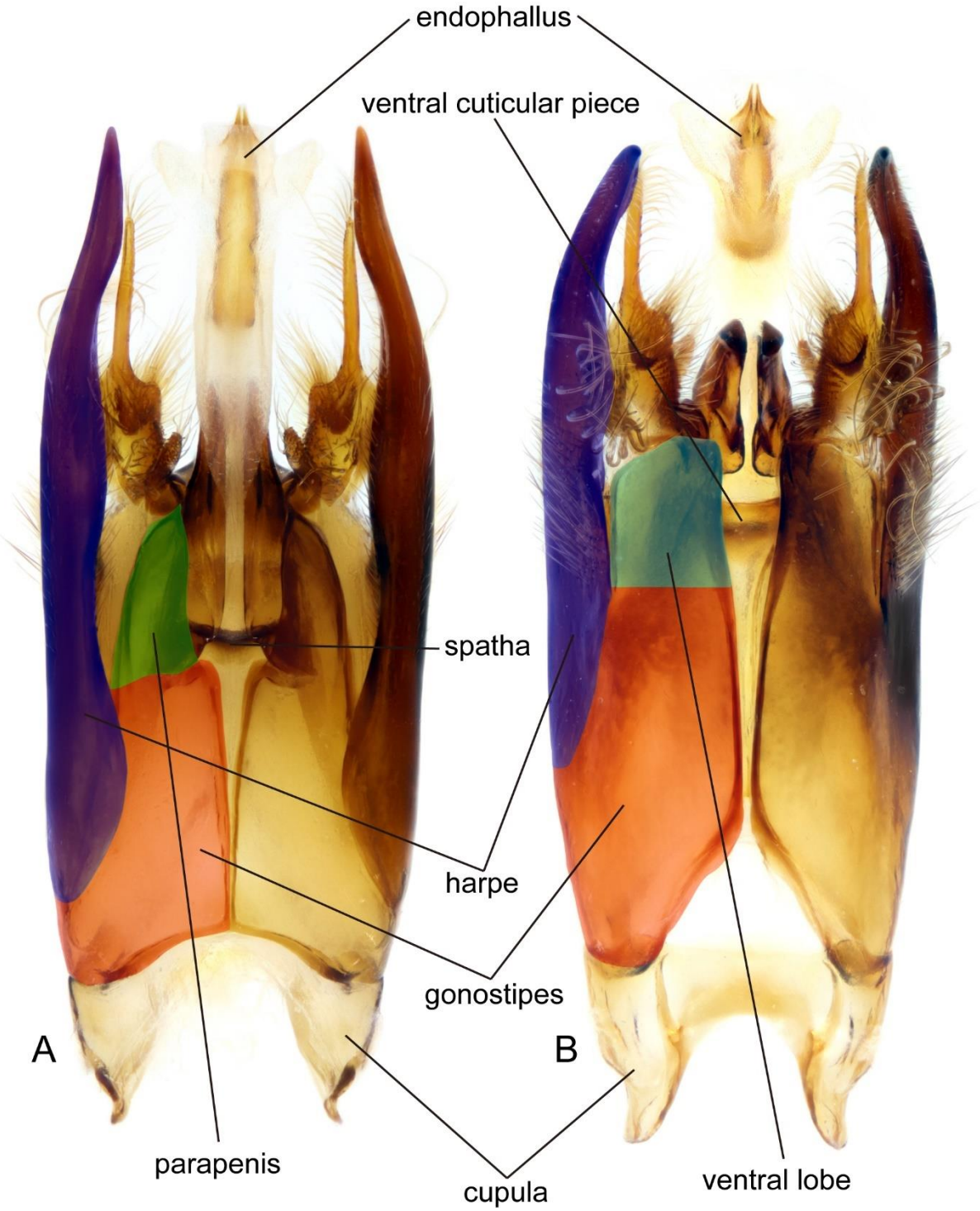


Figure 1. Male genitalia of *Nemka viduata* (Pallas). A. Dorsal aspect; B. ventral aspect.

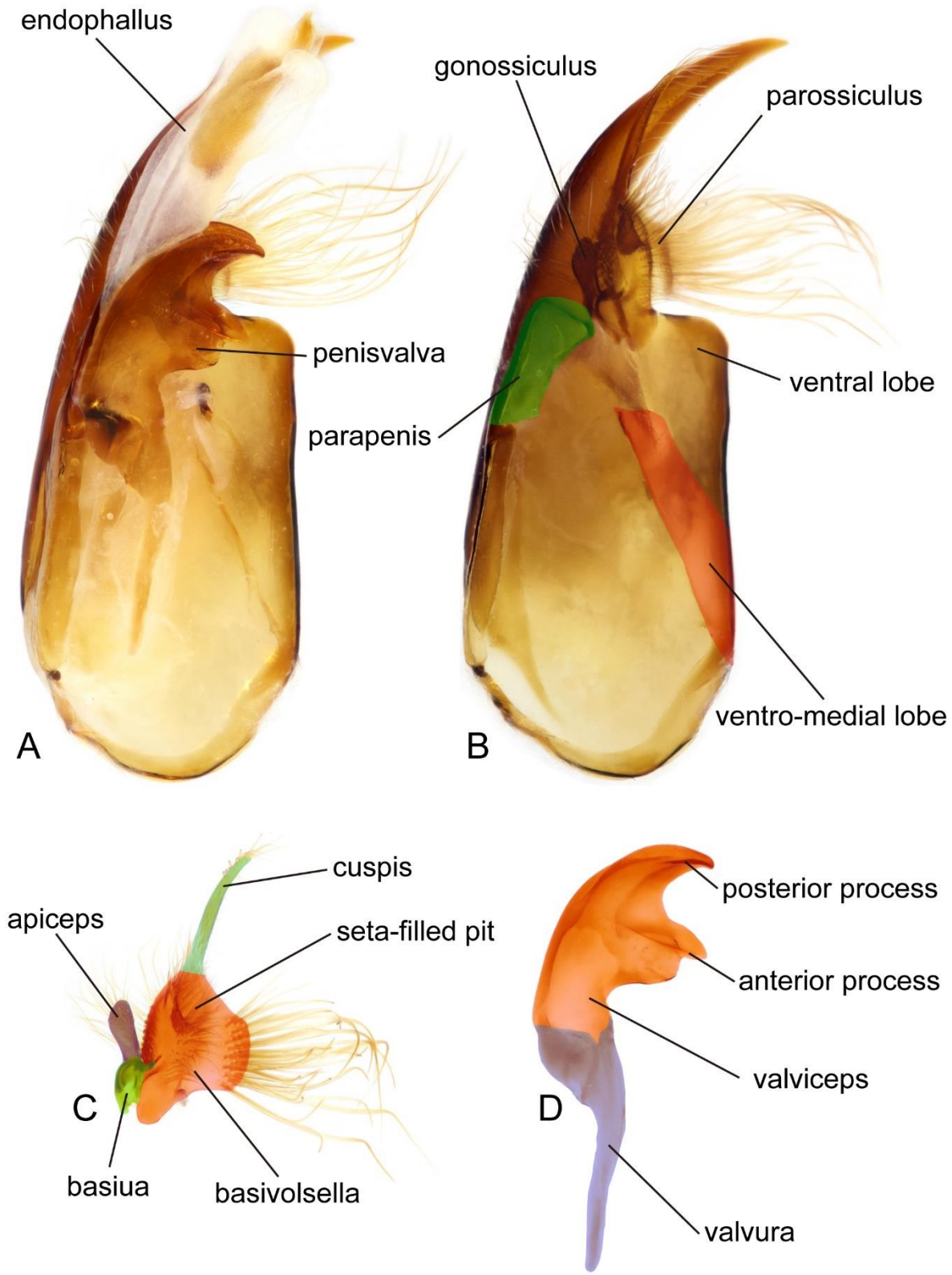


Figure 2. Male genitalia of *Nemka viduata* (Pallas). A. Internal aspect with penisvalvae; B. internal aspect of gonostyle and volsella; C. volsella; D. penisvalva.

Figure 3-1. Strict consensus tree of 60 most parsimonious trees under equal weights (length = 867; CI = 22; RI = 79). Type species are shown in **bold**.

Figure 3-2. Strict consensus tree of 60 most parsimonious trees under equal weights (length = 867; CI = 22; RI = 79). Type species are shown in **bold**.

Figure 3-3. Strict consensus tree of 60 most parsimonious trees under equal weights (length = 867; CI = 22; RI = 79). Type species are shown in **bold**.

Figure 3-4. Strict consensus tree of 60 most parsimonious trees under equal weights (length = 867; CI = 22; RI = 79). Type species are shown in **bold**.

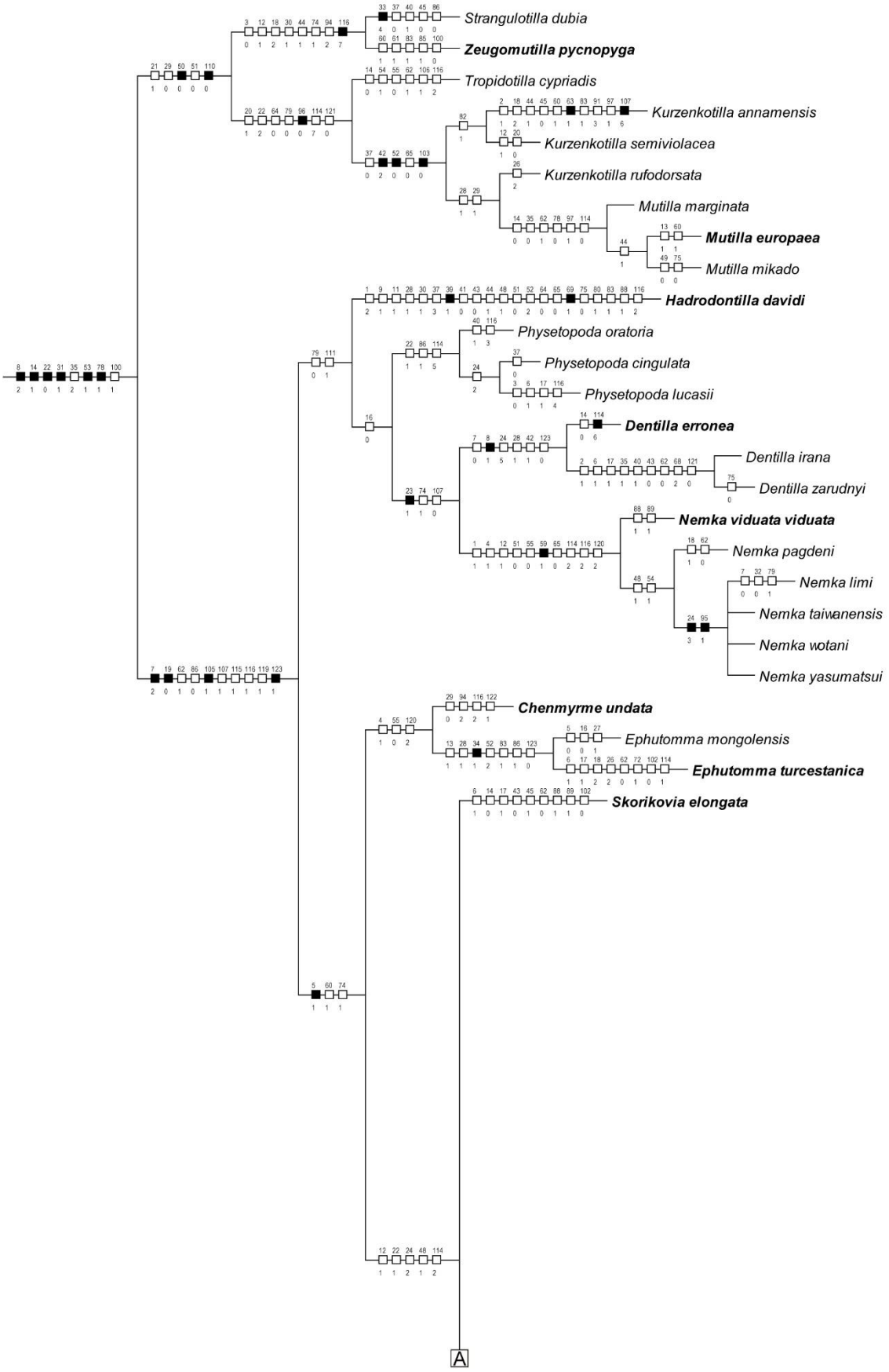


Figure 4-1. Strict consensus tree of 440 best-fitting trees under k0 (length = 871; CI = 22; RI = 79). Type species are shown in **bold**.

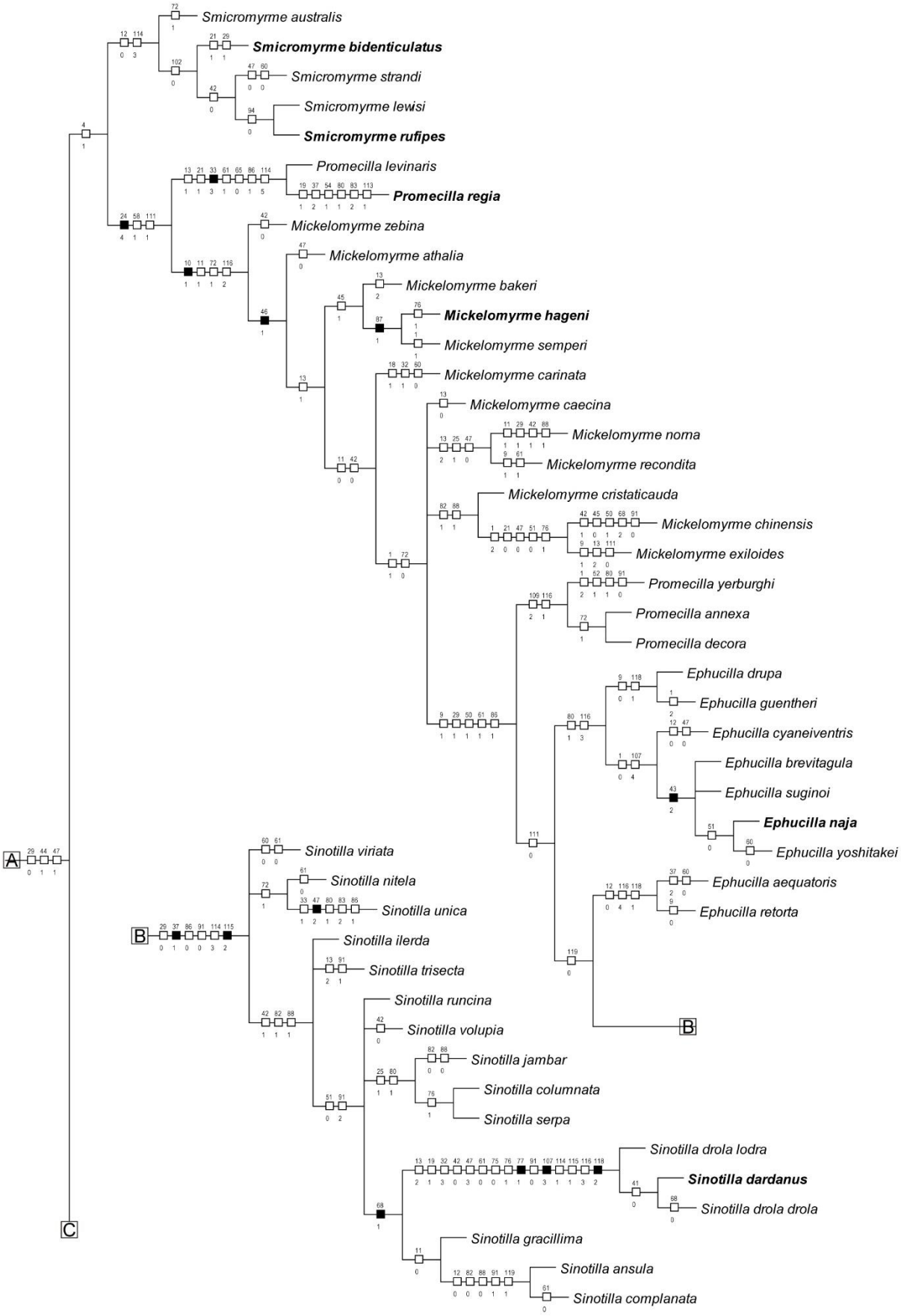


Figure 4-2. Strict consensus tree of 440 best-fitting trees under k0 (length = 871; CI = 22; RI = 79). Type species are shown in **bold**.

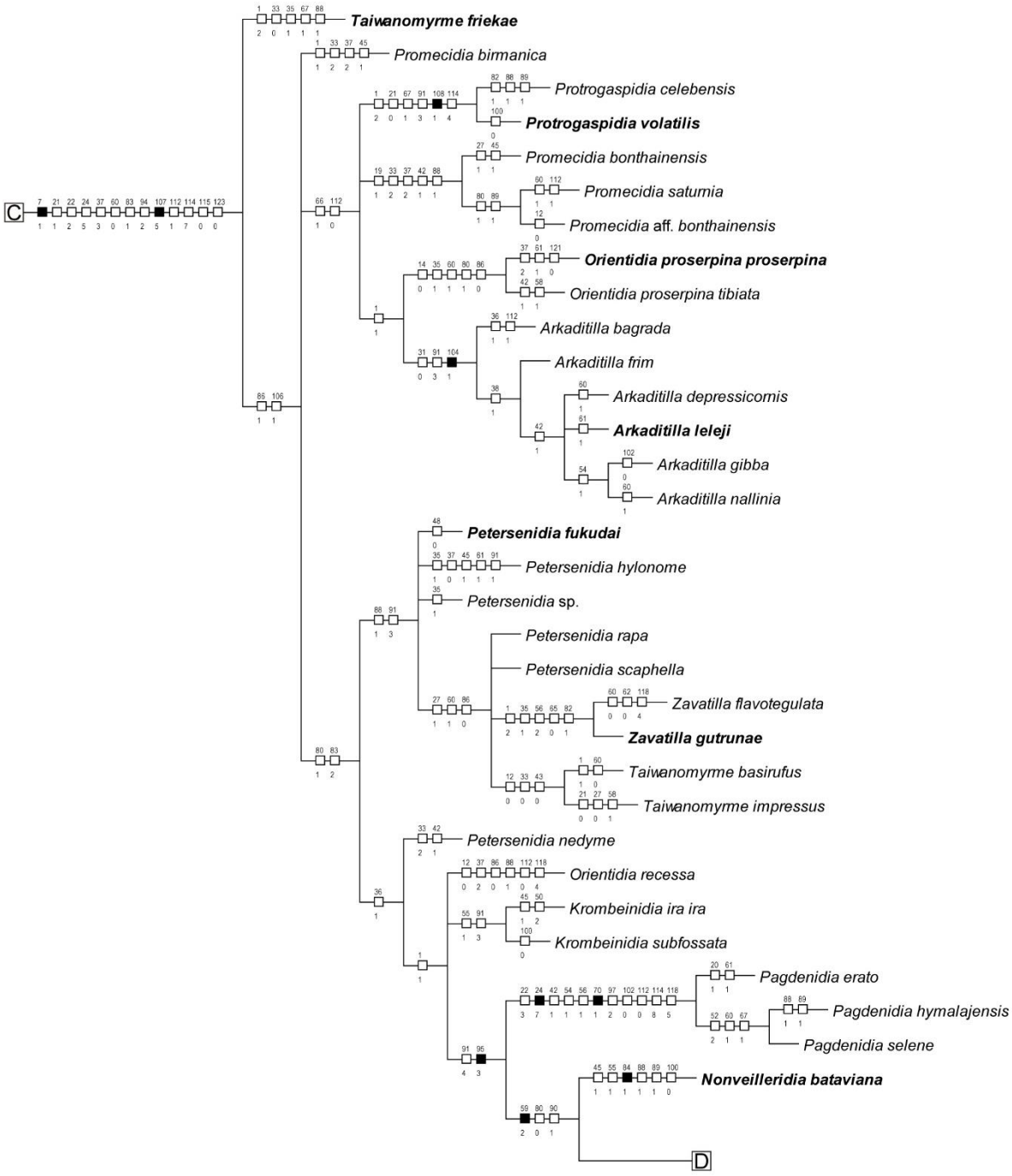


Figure 4-3. Strict consensus tree of 440 best-fitting trees under k0 (length = 871; CI = 22; RI = 79). Type species are shown in **bold**.

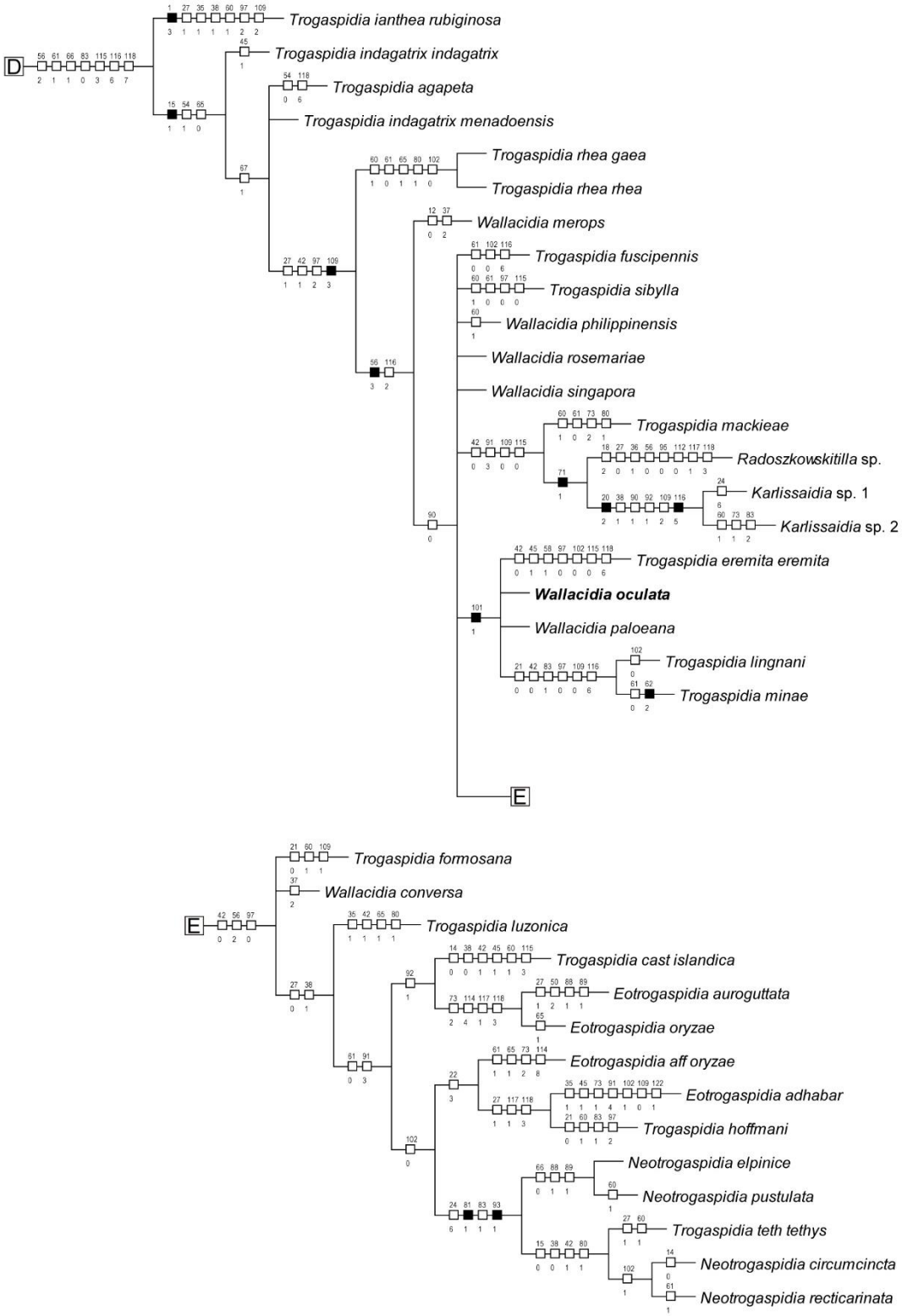


Figure 4-4. Strict consensus tree of 440 best-fitting trees under k0 (length = 871; CI = 22; RI = 79). Type species are shown in **bold**.

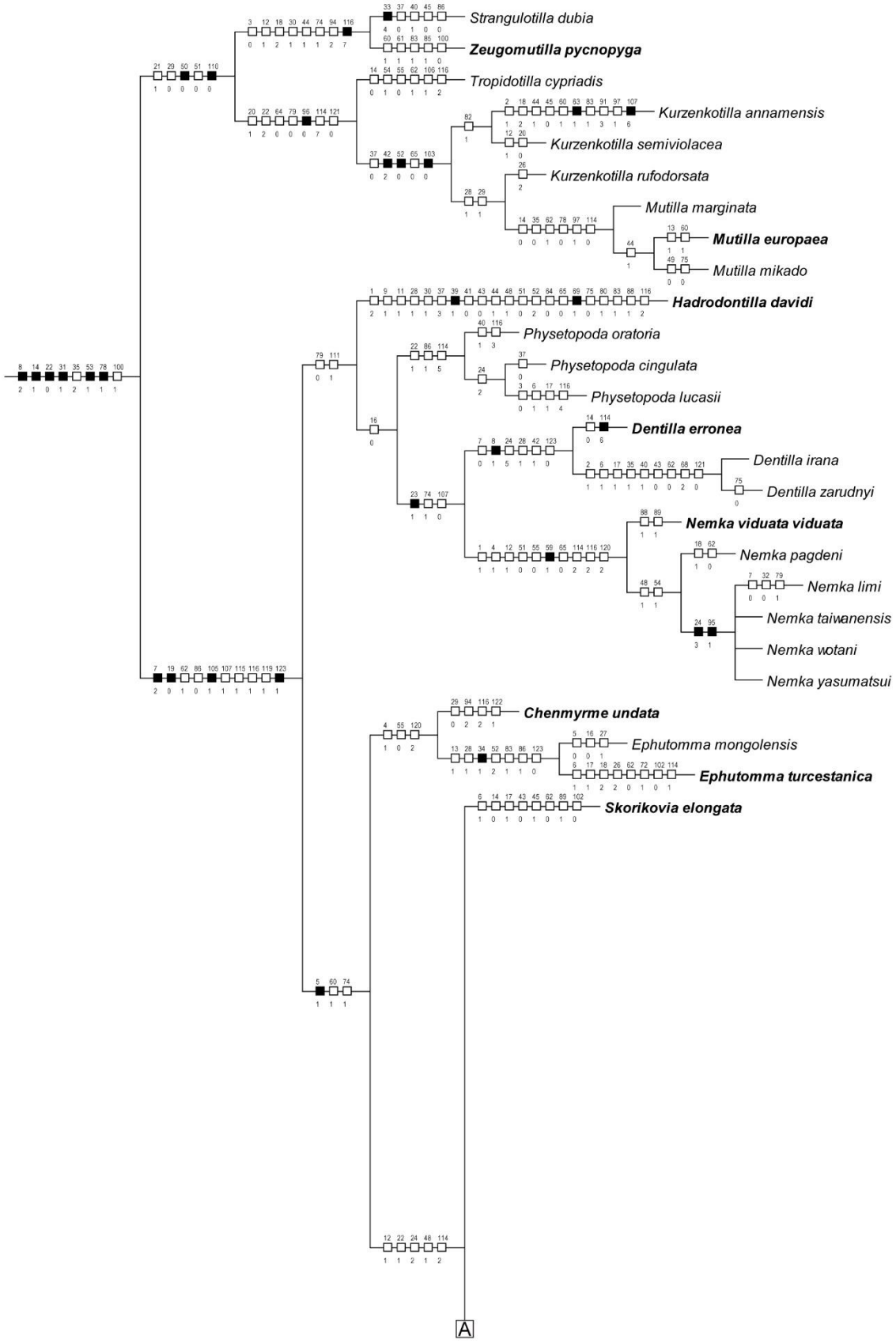


Figure 5-1. Strict consensus tree of 500 best-fitting trees under k1 (length = 868; CI = 22; RI = 79). Type species are shown in **bold**.

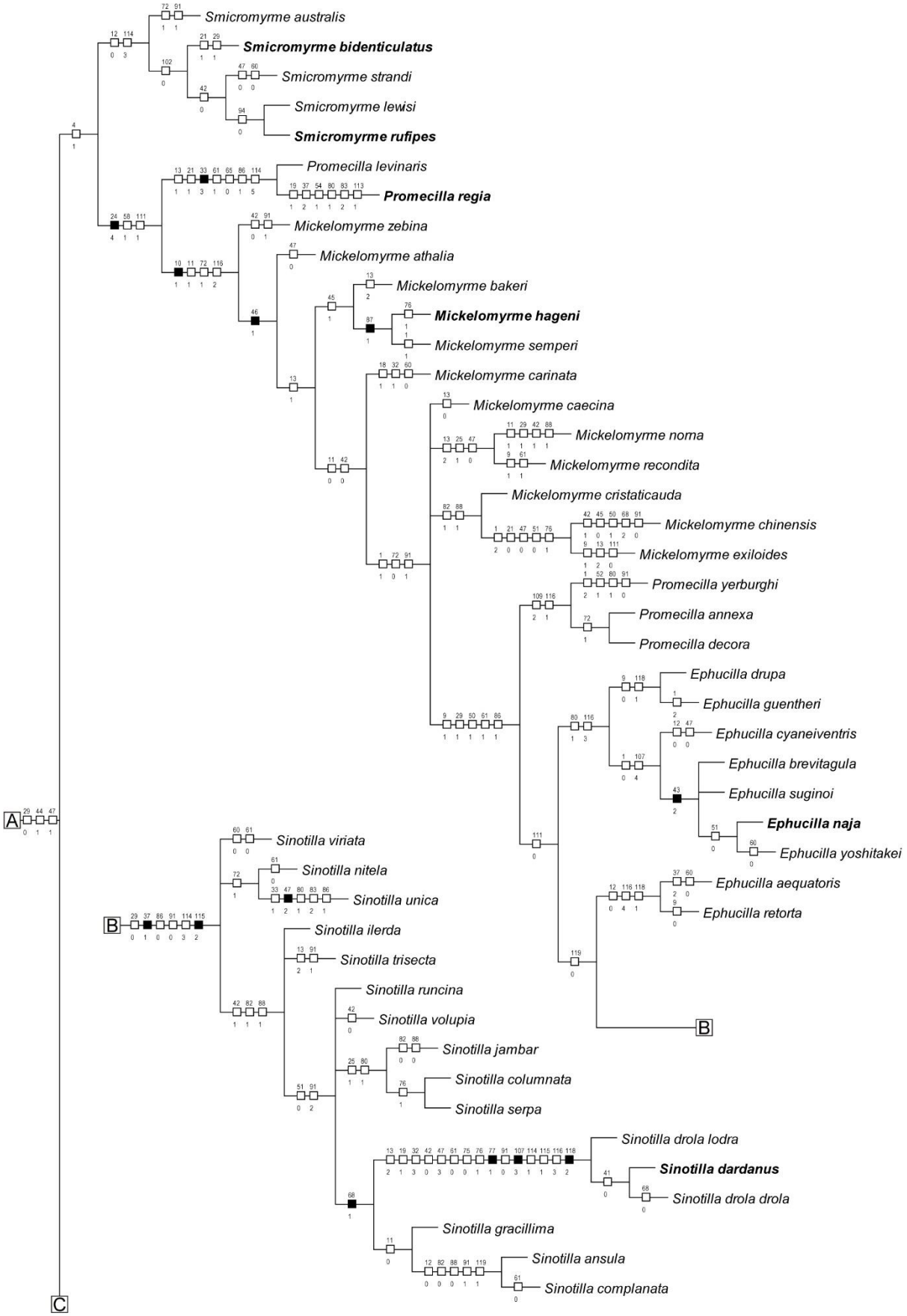


Figure 5-2. Strict consensus tree of 500 best-fitting trees under k1 (length = 868; CI = 22; RI = 79). Type species are shown in **bold**.

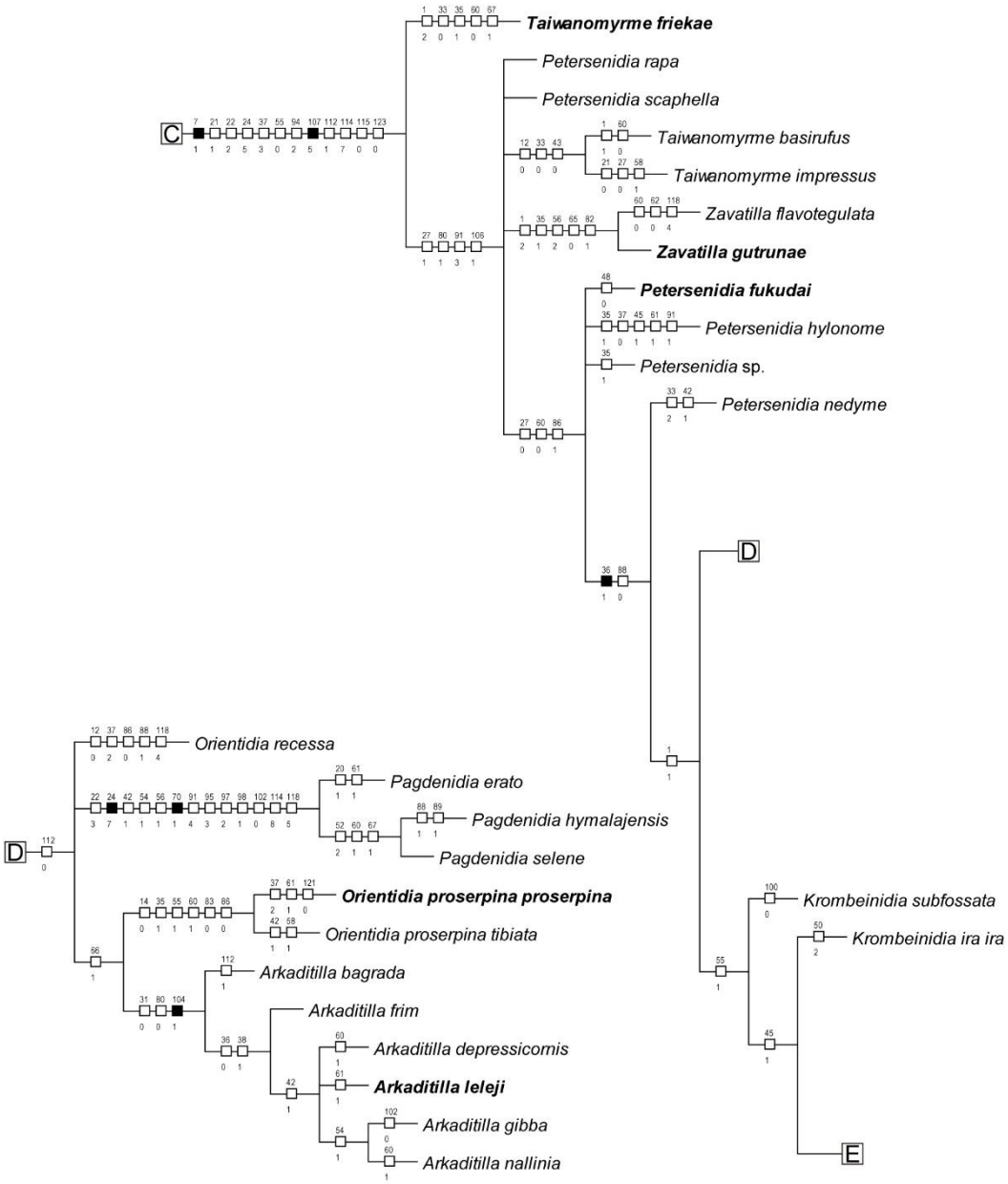


Figure 5-3. Strict consensus tree of 500 best-fitting trees under k1 (length = 868; CI = 22; RI = 79). Type species are shown in **bold**.

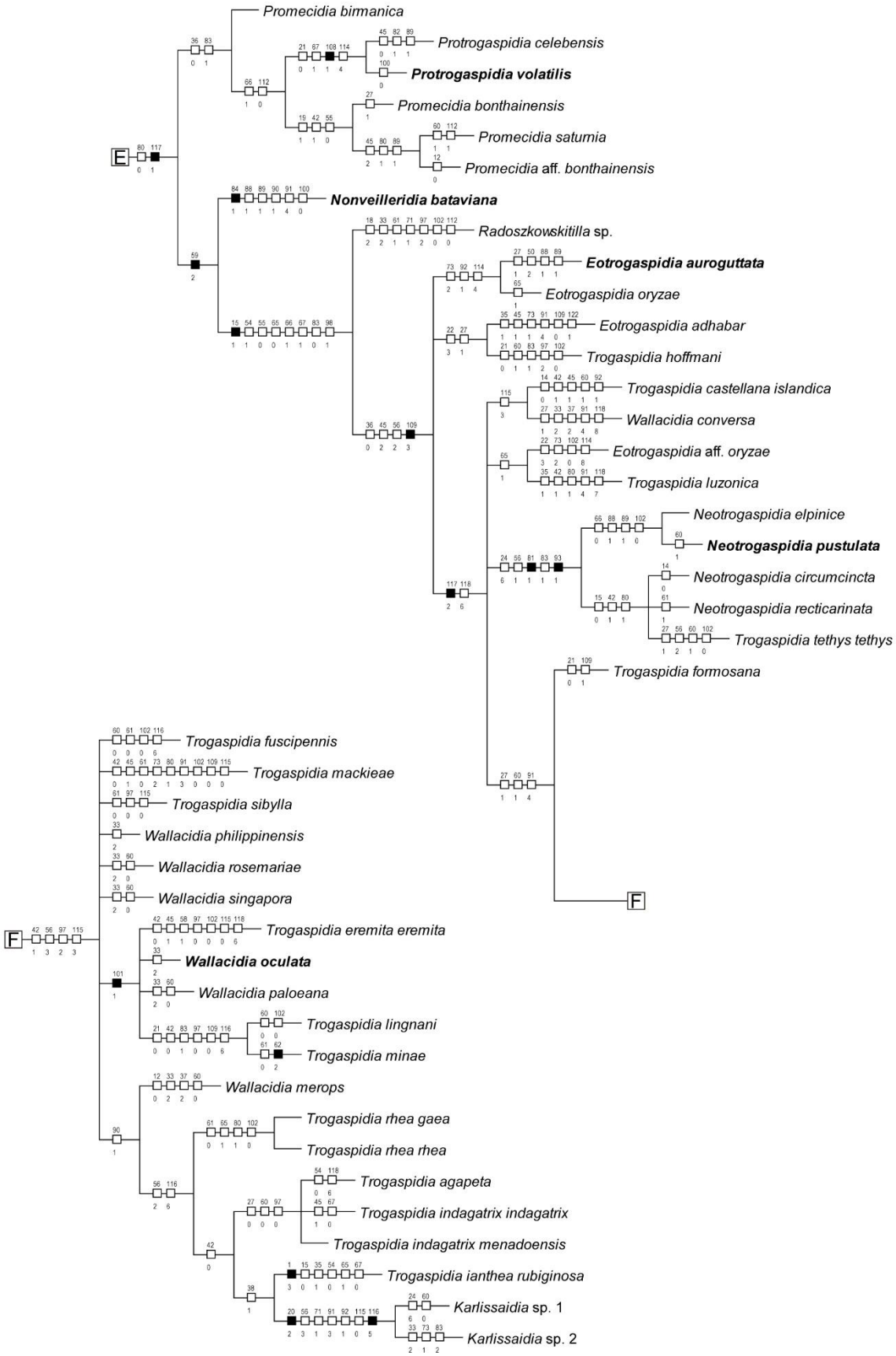


Figure 5-4. Strict consensus tree of 500 best-fitting trees under k1 (length = 868; CI = 22; RI = 79). Type species are shown in **bold**.

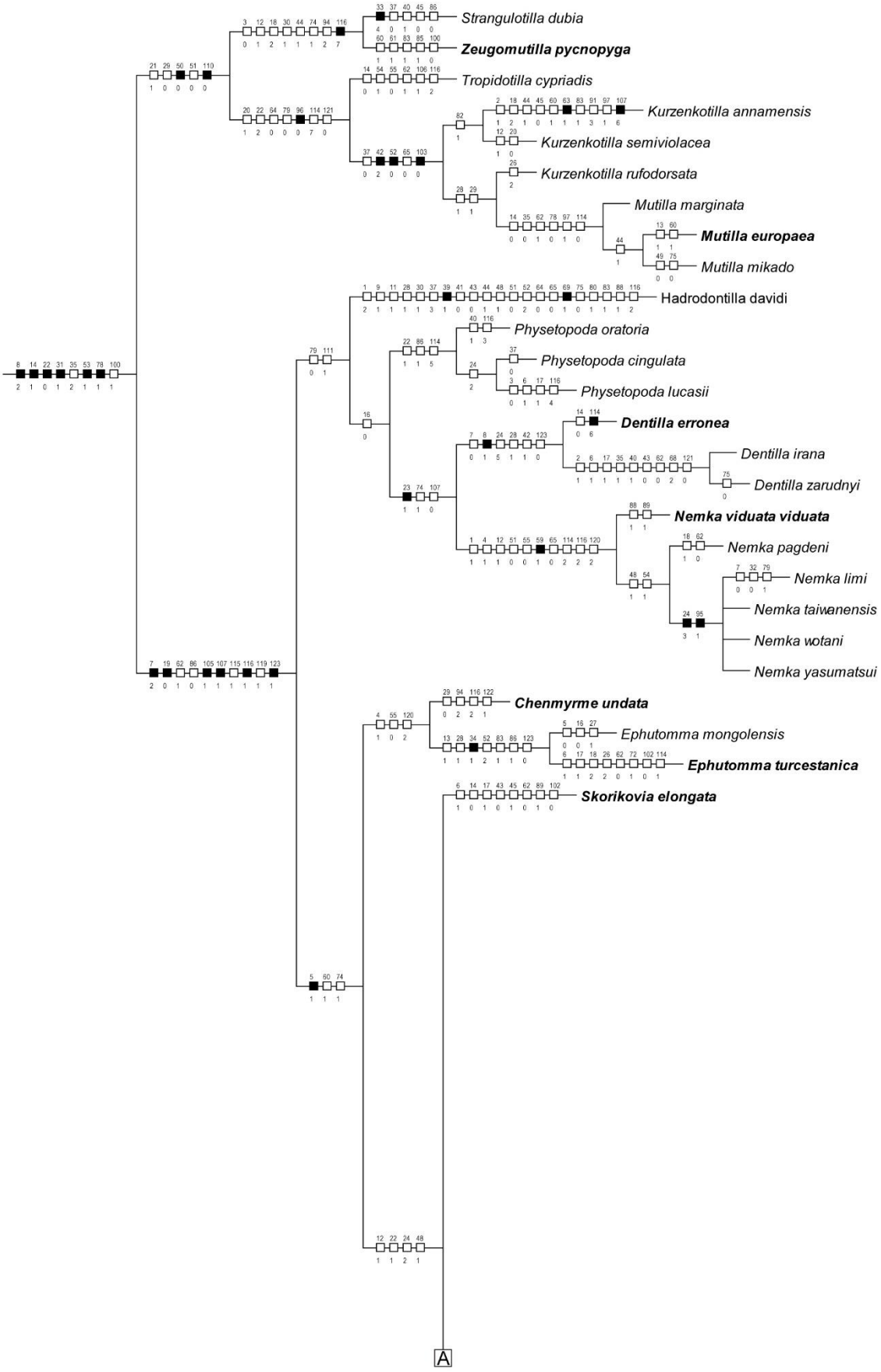


Figure 6-1. Strict consensus tree of 351 best-fitting trees under k2 (length = 863; CI = 23; RI = 79). Type species are shown in **bold**.

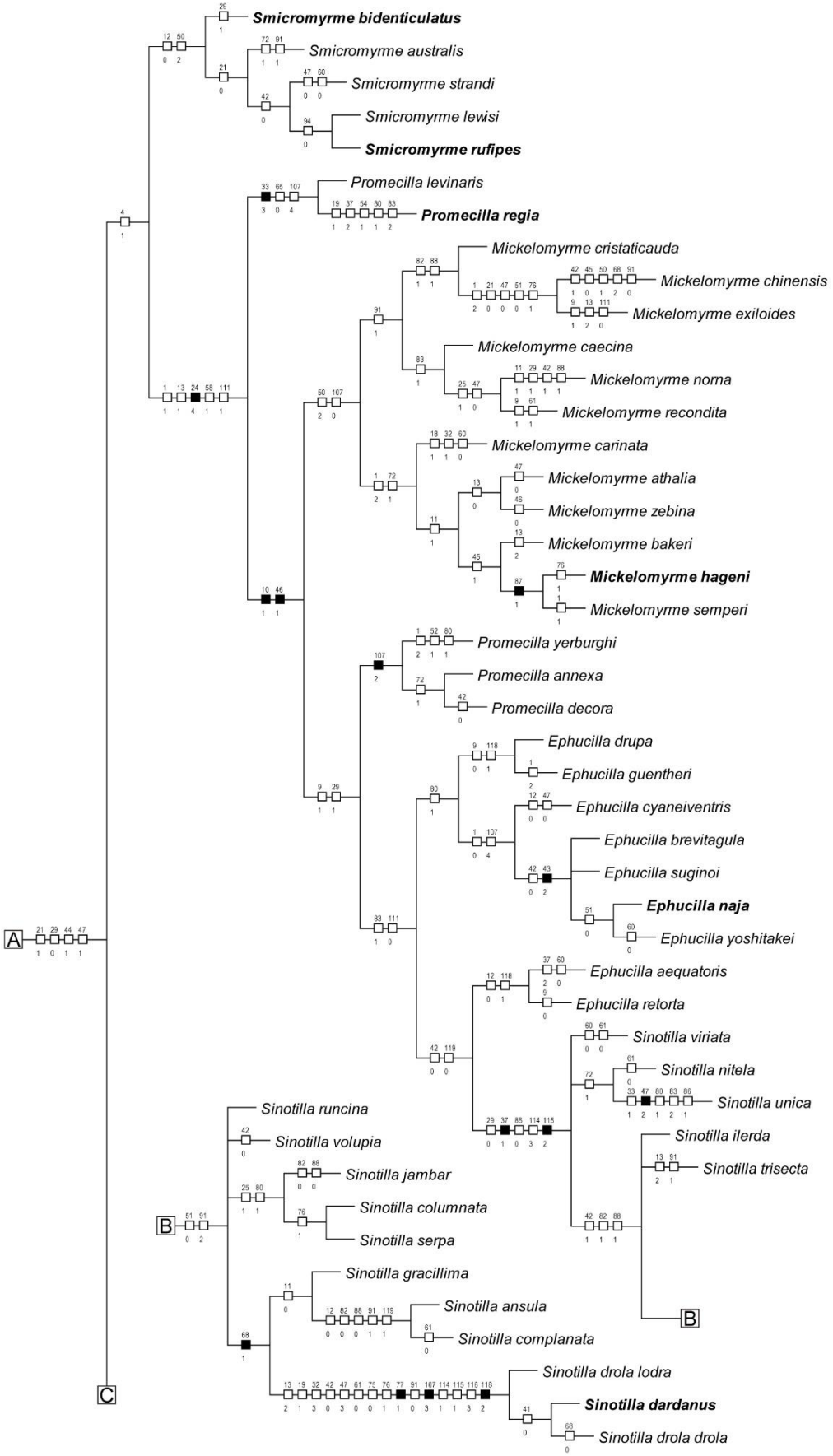
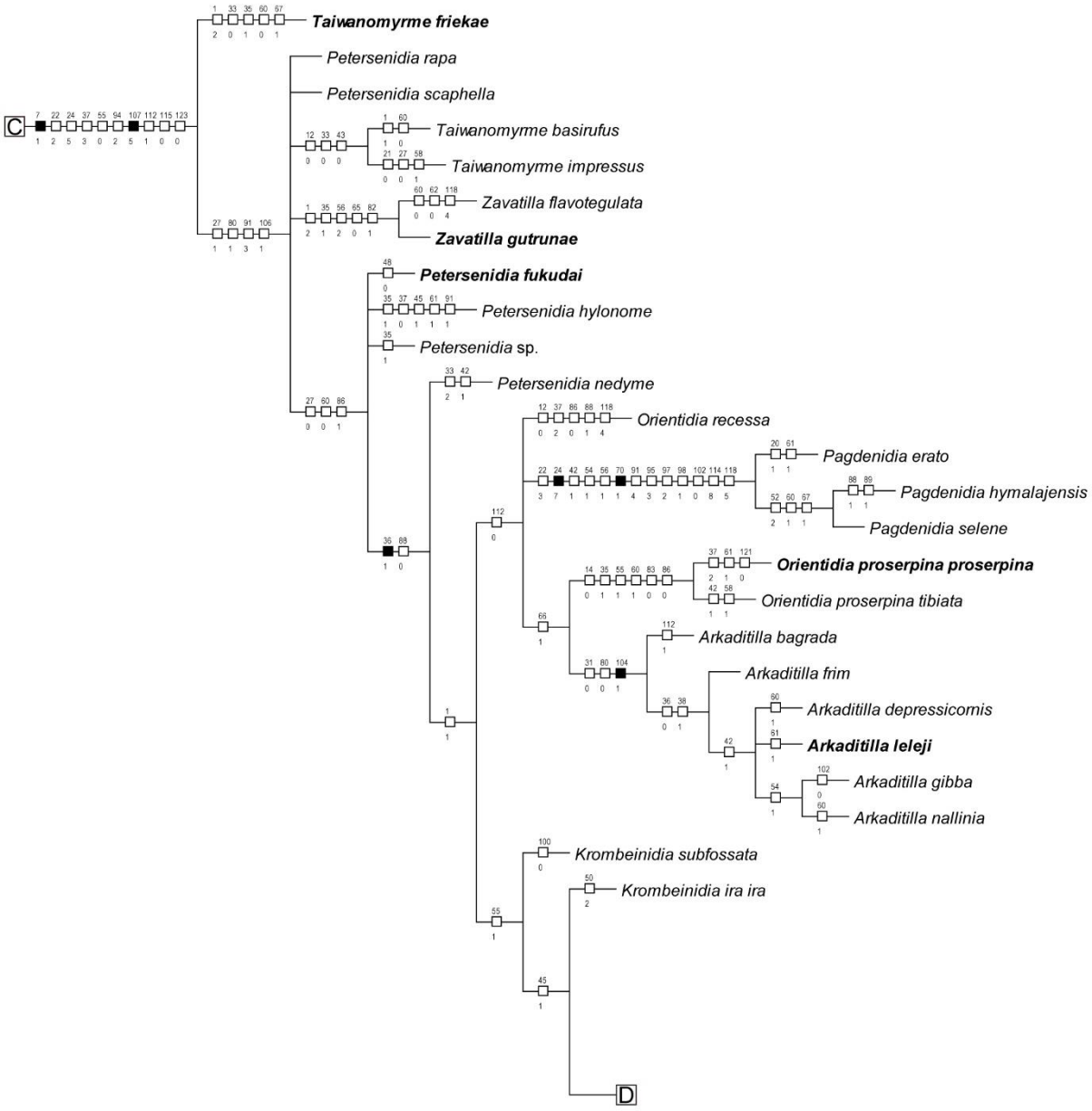


Figure 6-2. Strict consensus tree of 351 best-fitting trees under k2 (length = 863; CI = 23; RI = 79). Type species are shown in **bold**.



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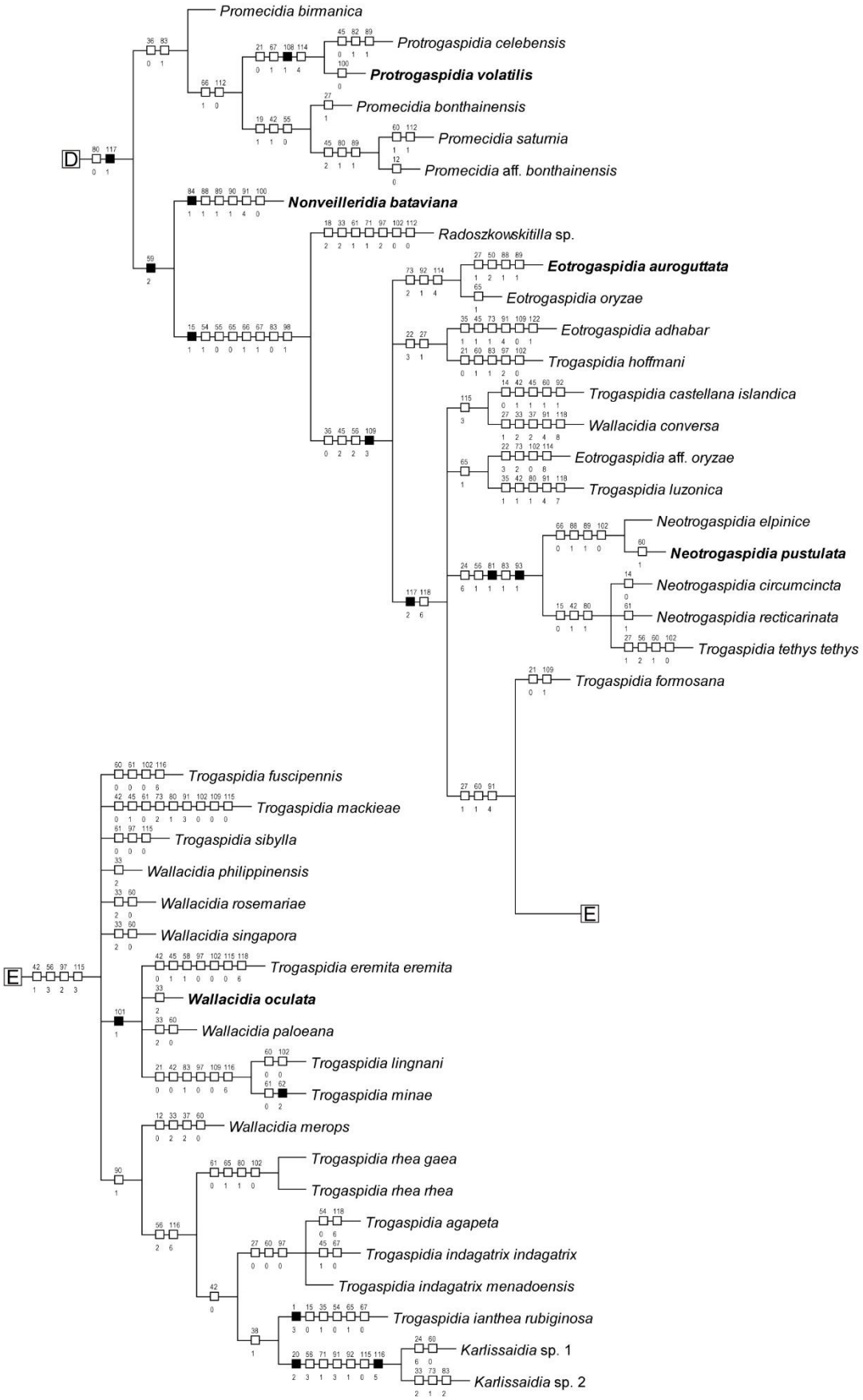

Figure 6-4. Strict consensus tree of 351 best-fitting trees under k2 (length = 863; CI = 23; RI = 79). Type species are shown in **bold**.

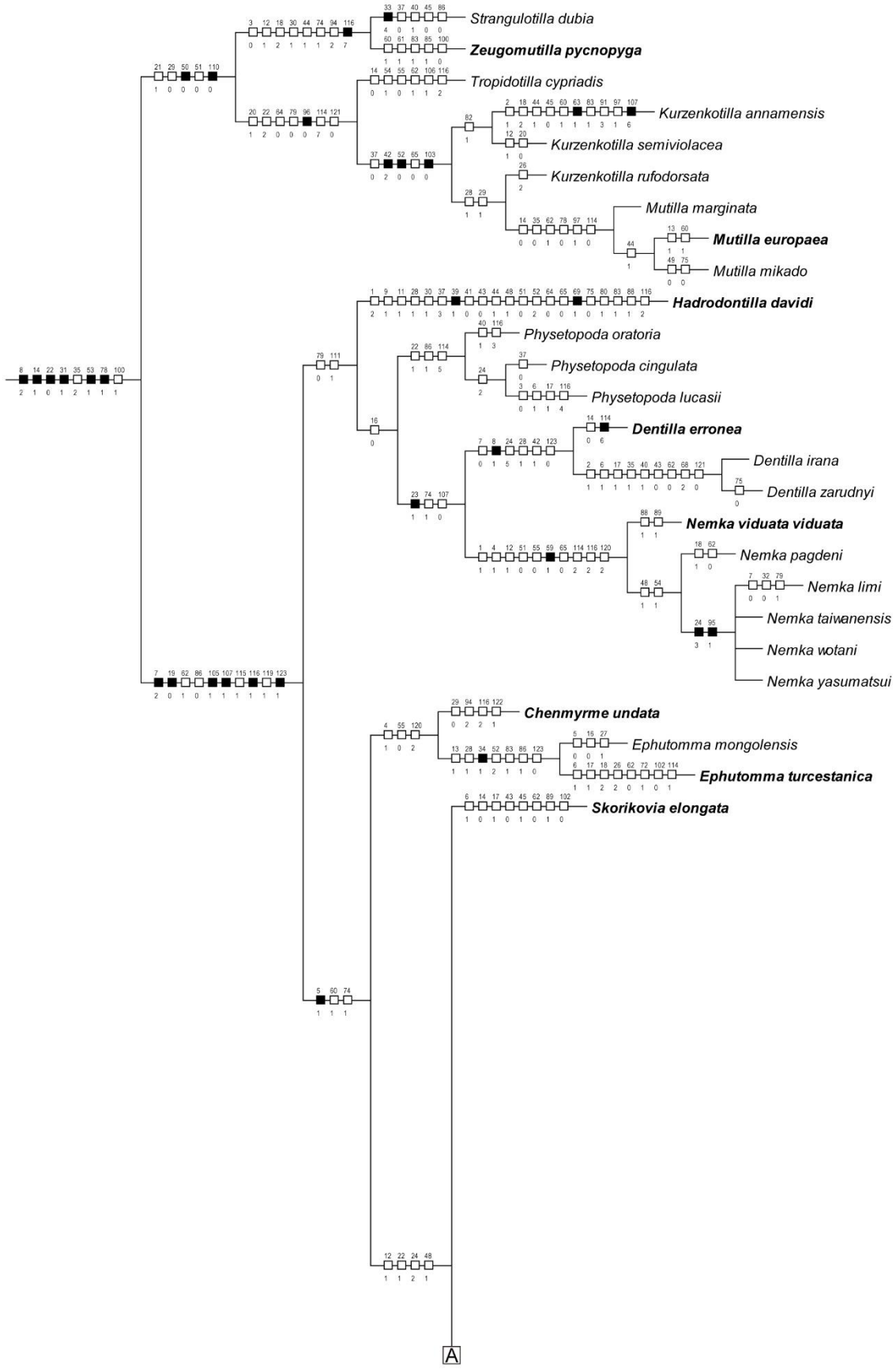

Figure 7-1. Strict consensus tree of 190 best-fitting trees under k3 (length = 864; CI = 23; RI = 79). Type species are shown in **bold**.

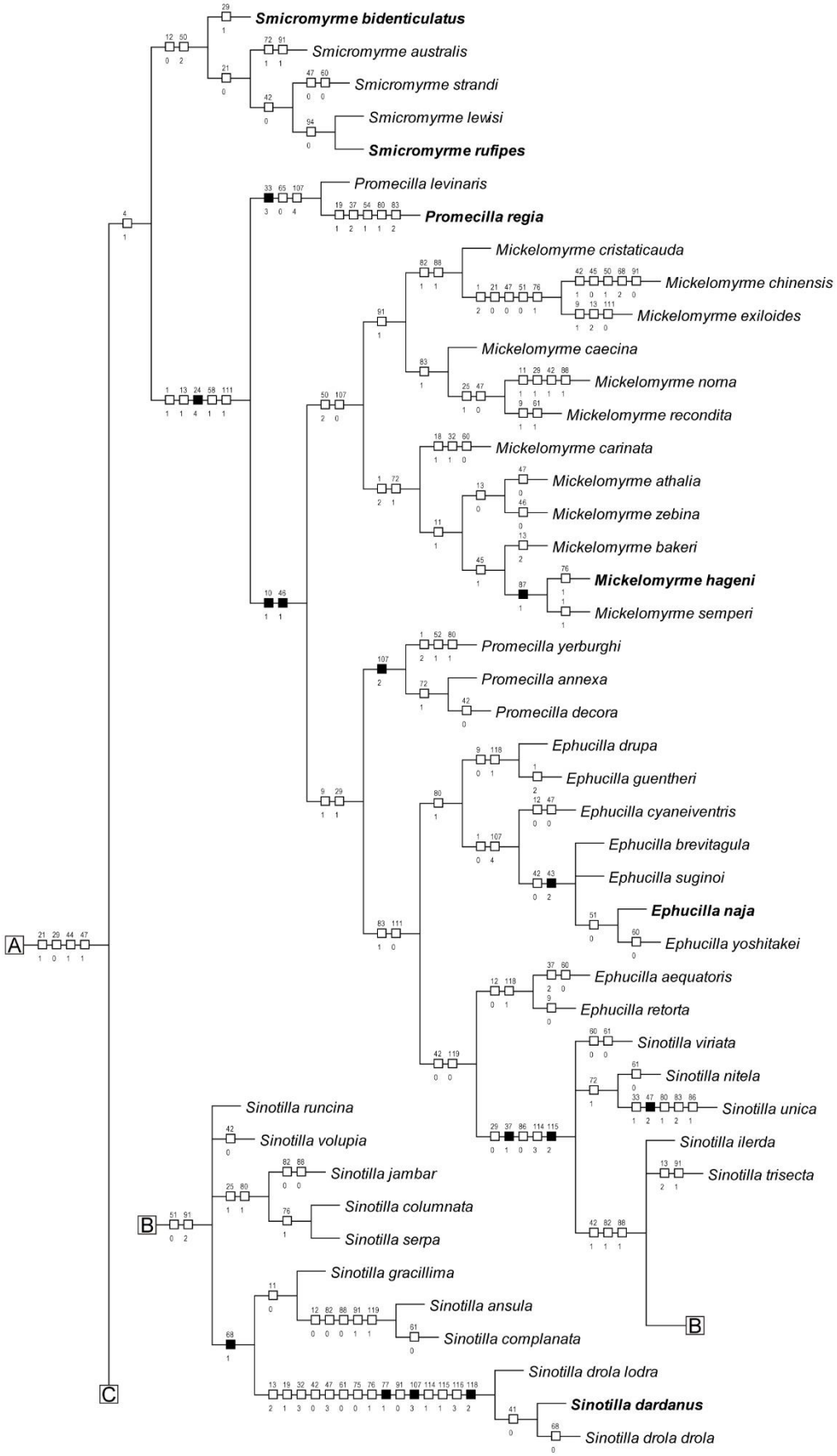

Figure 7-2. Strict consensus tree of 190 best-fitting trees under k3 (length = 864; CI = 23; RI = 79). Type species are shown in **bold**.

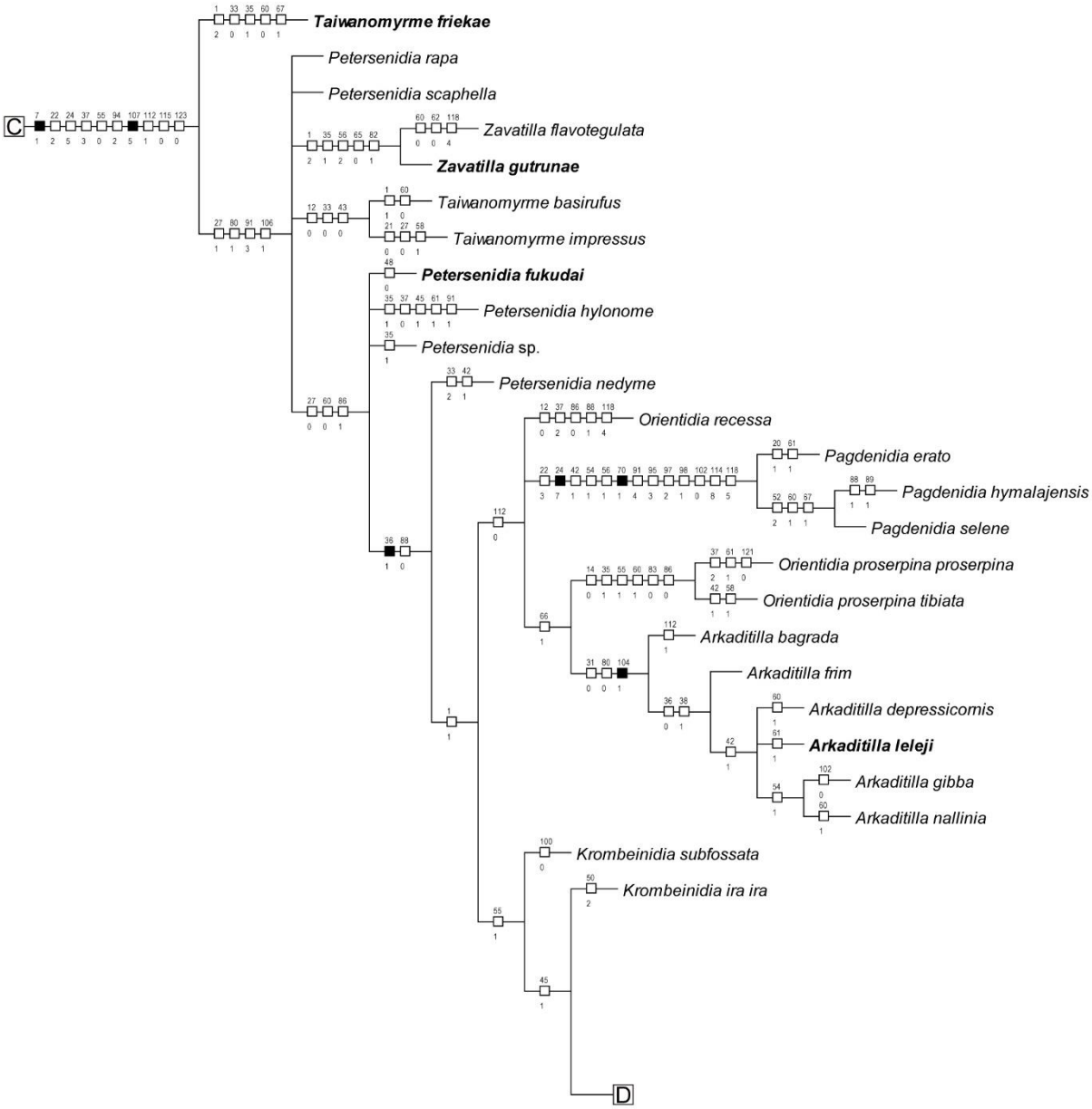

Figure 7-3. Strict consensus tree of 190 best-fitting trees under k3 (length = 864; CI = 23; RI = 79). Type species are shown in **bold**.

Figure 7-4. Strict consensus tree of 190 best-fitting trees under k3 (length = 864; CI = 23; RI = 79). Type species are shown in **bold**.

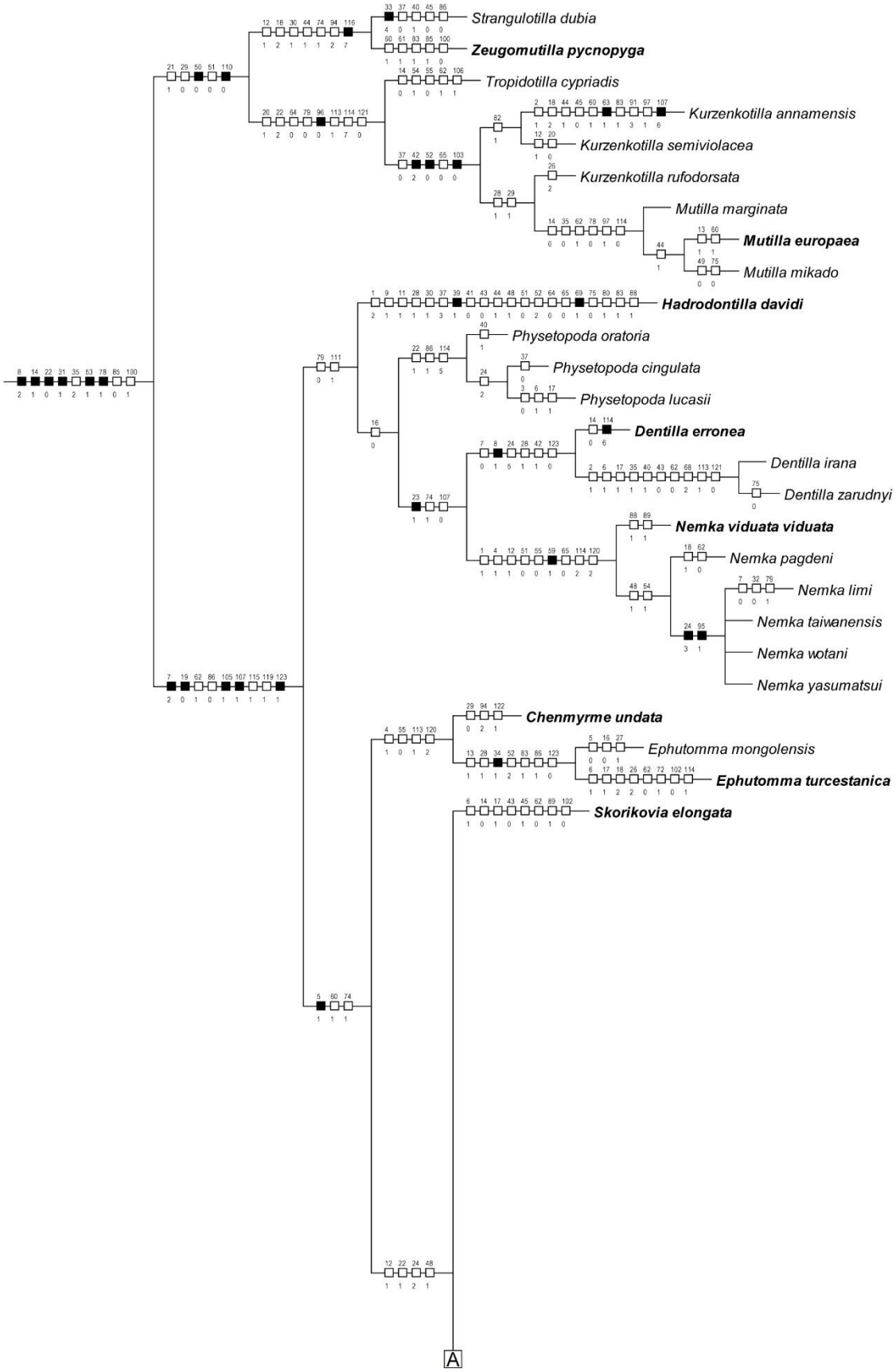

Figure 8-1. Strict consensus tree of 160 best-fitting trees under k4 (length = 863; CI = 23; RI = 79). Type species are shown in **bold**.

Figure 8-2. Strict consensus tree of 160 best-fitting trees under k4 (length = 863; CI = 23; RI = 79). Type species are shown in **bold**.

Figure 8-3. Strict consensus tree of 160 best-fitting trees under k4 (length = 863; CI = 23; RI = 79). Type species are shown in **bold**.

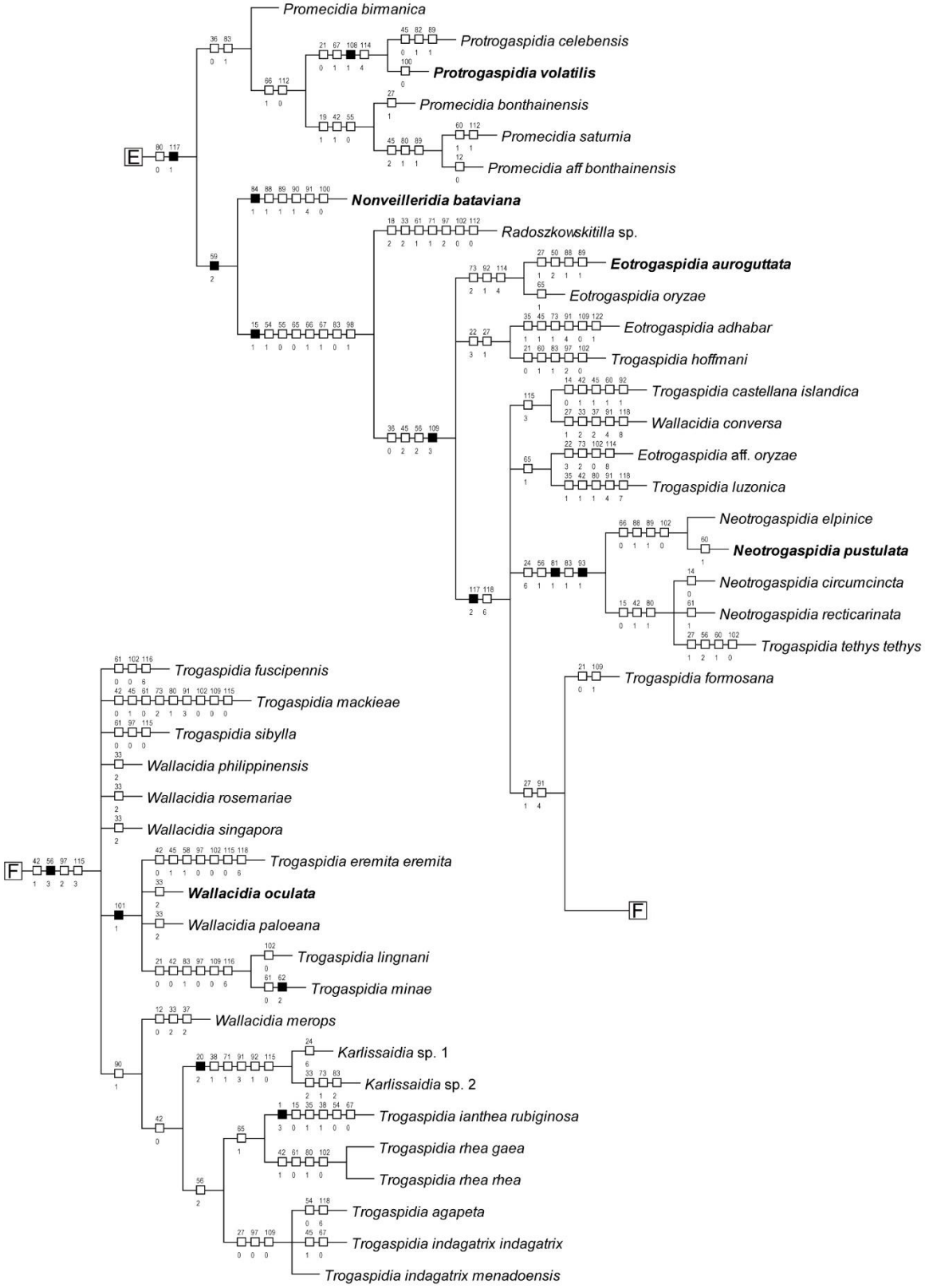

Figure 8-4. Strict consensus tree of 160 best-fitting trees under k4 (length = 863; CI = 23; RI = 79). Type species are shown in **bold**.

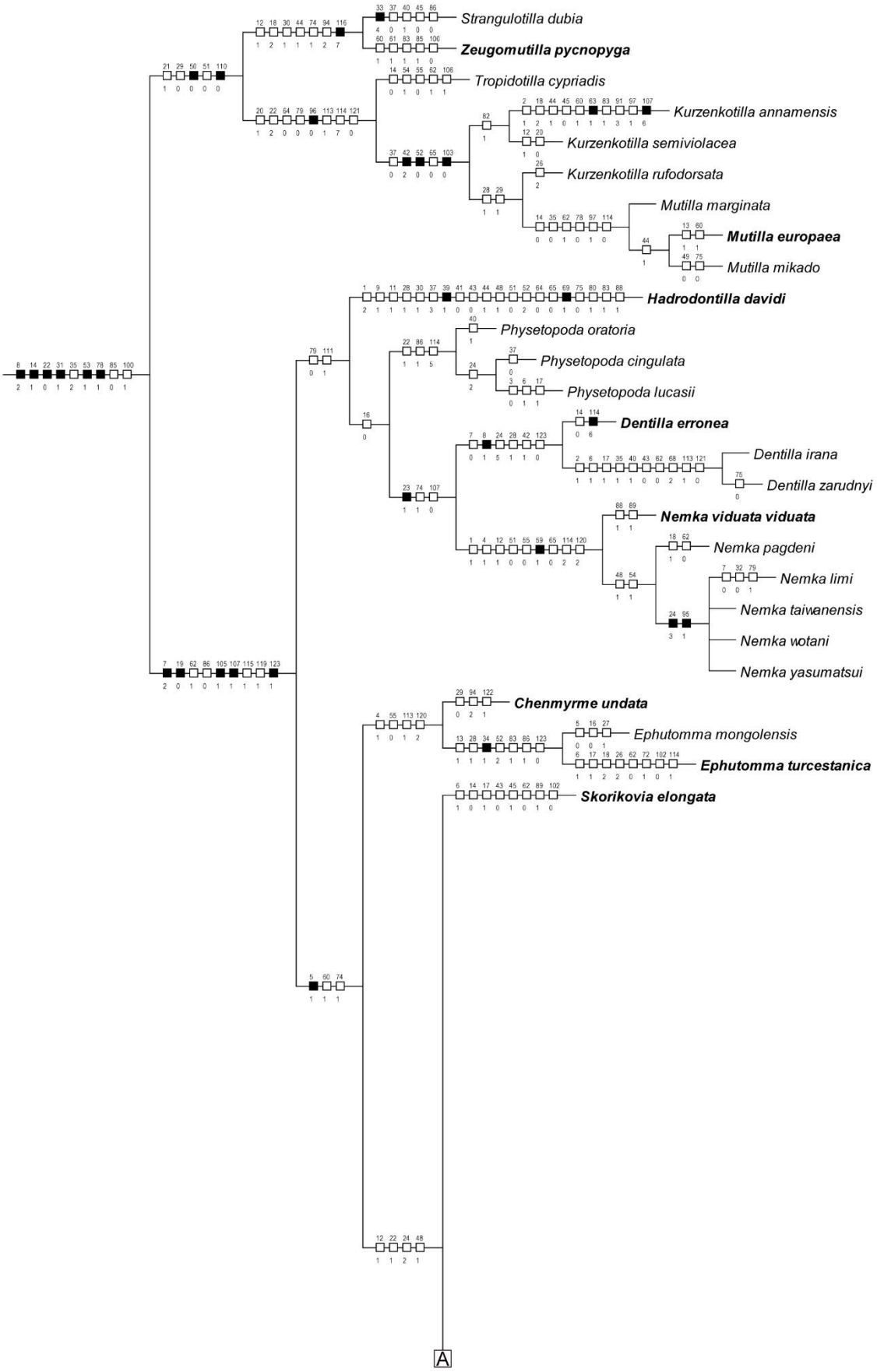

Figure 9-1. Strict consensus tree of 80 best-fitting trees under k5 (length = 863; CI = 23; RI = 79). Type species are shown in **bold**.

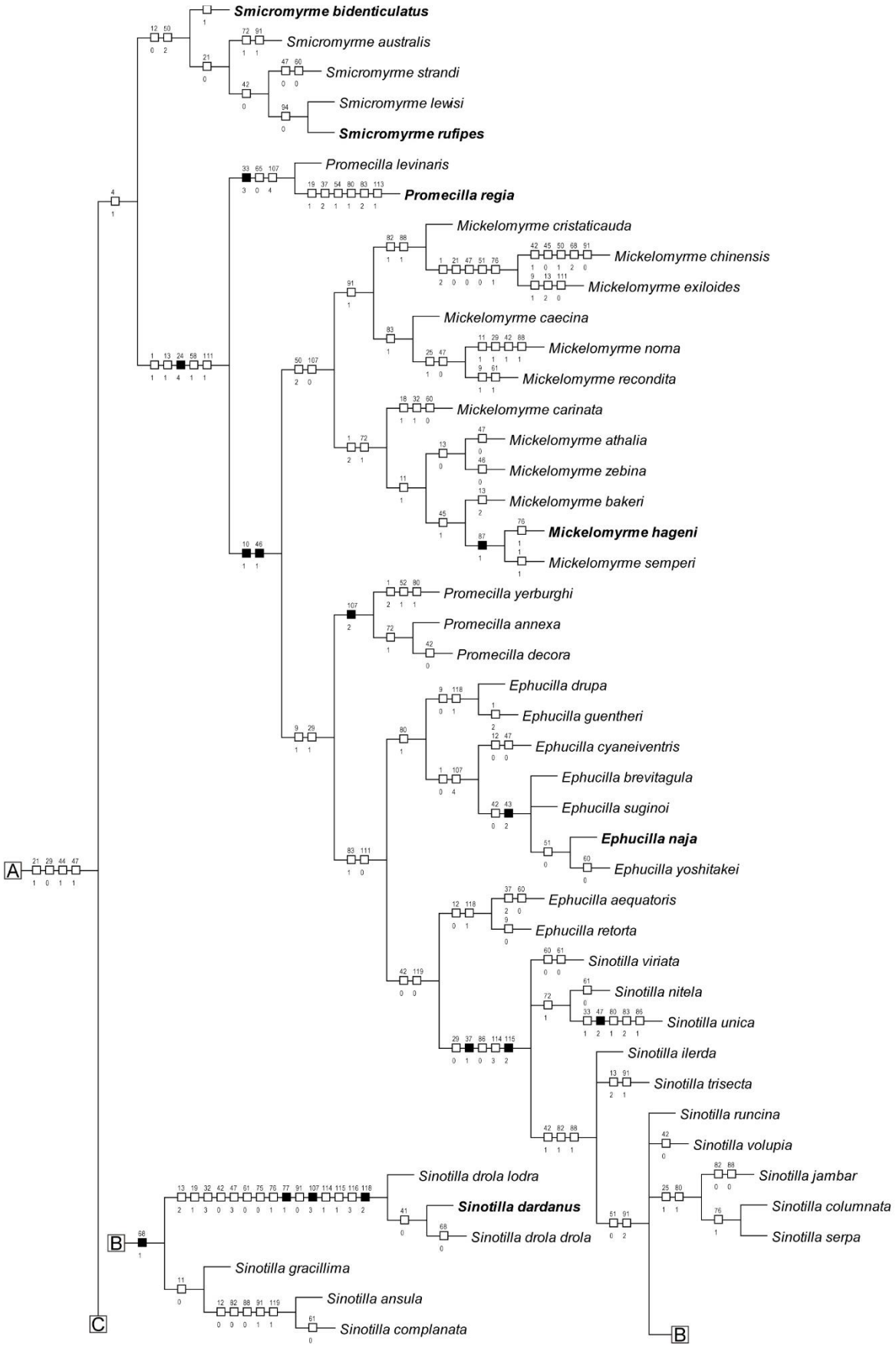

Figure 9-2. Strict consensus tree of 80 best-fitting trees under k5 (length = 863; CI = 23; RI = 79). Type species are shown in **bold**.

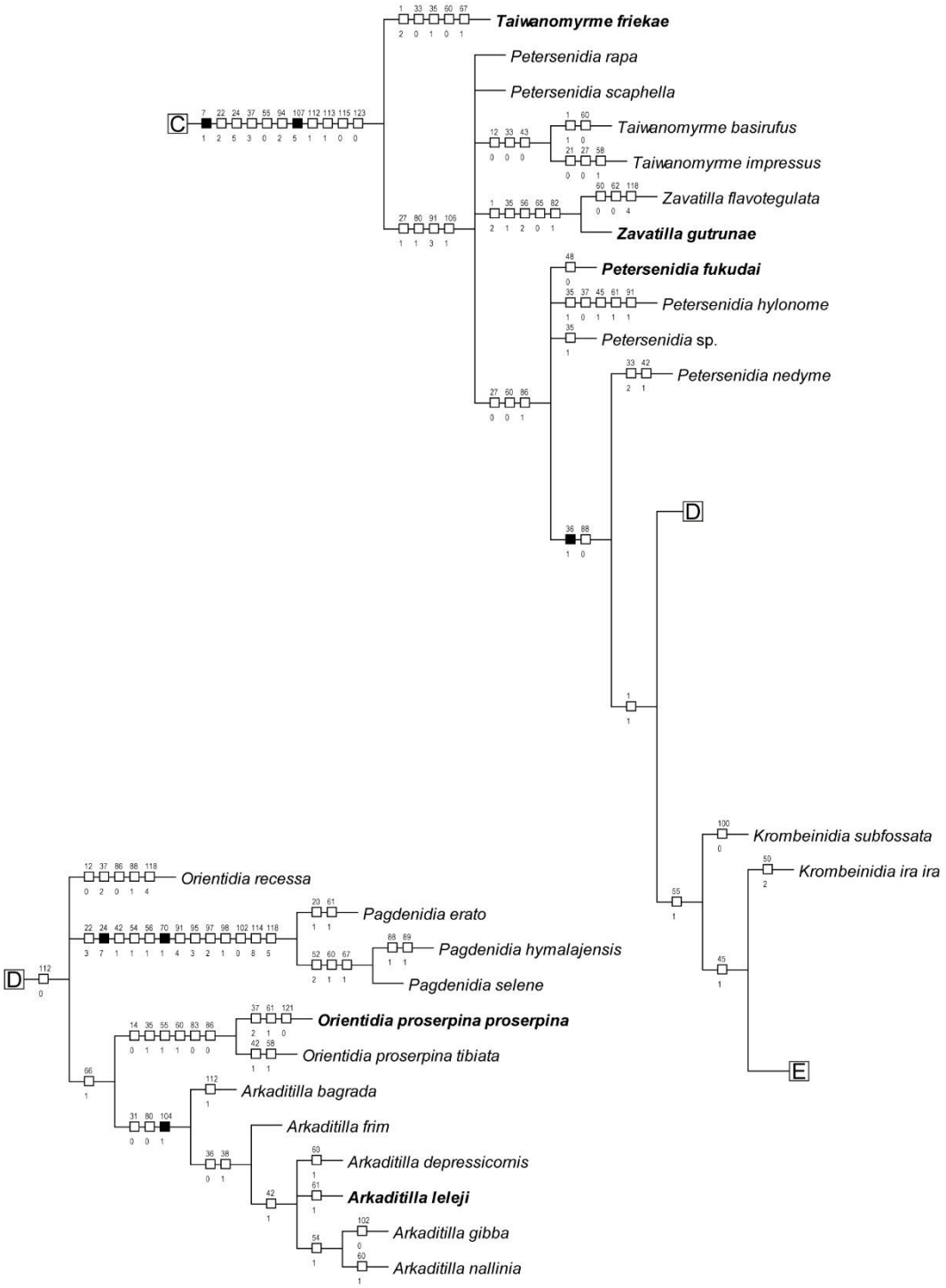

Figure 9-3. Strict consensus tree of 80 best-fitting trees under k5 (length = 863; CI = 23; RI = 79). Type species are shown in **bold**.

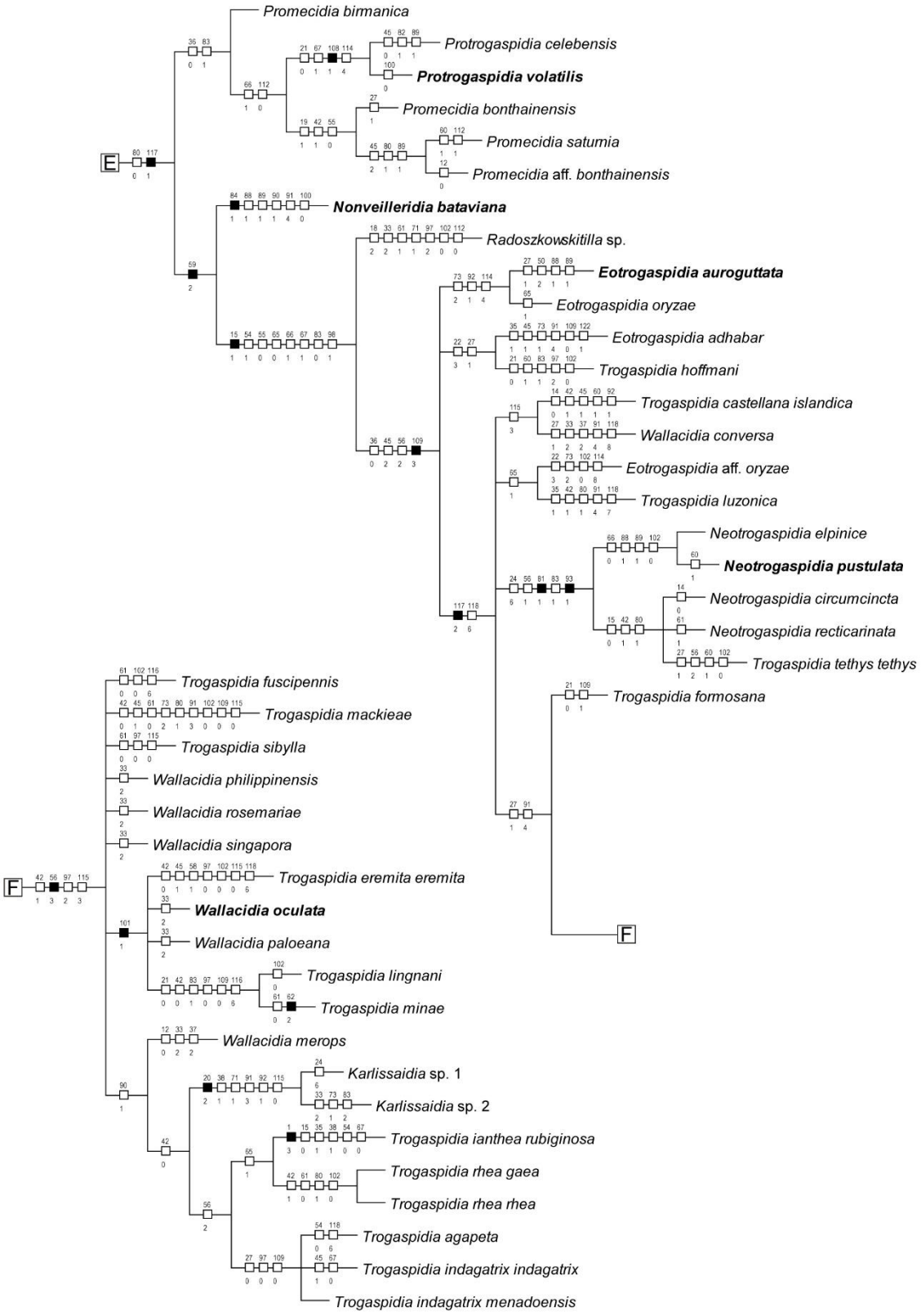

Figure 9-4. Strict consensus tree of 80 best-fitting trees under k5 (length = 863; CI = 23; RI = 79). Type species are shown in **bold**.

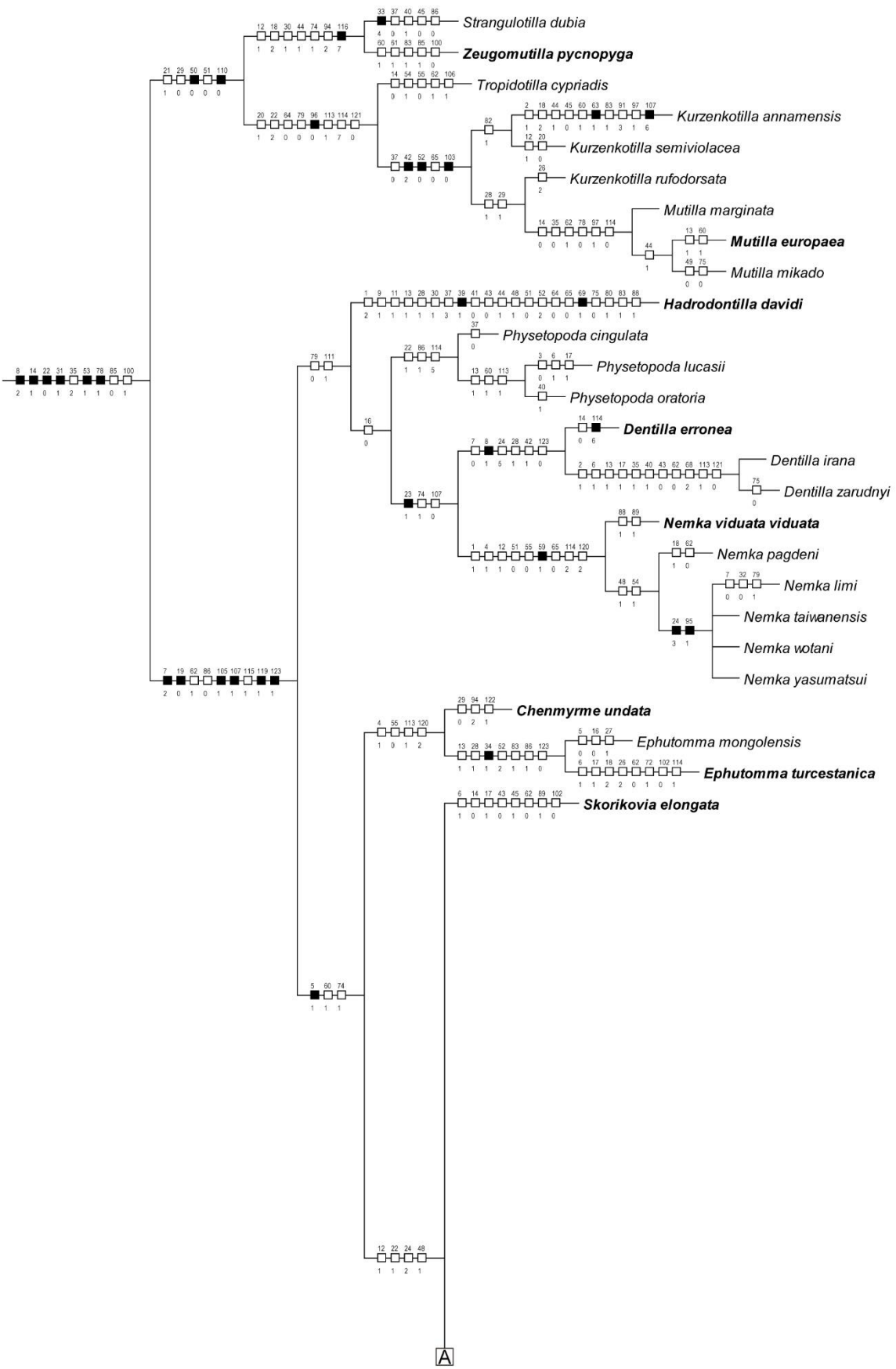

Figure 10-1. Strict consensus tree of 102 best-fitting trees under k6 (length = 857; CI = 23; RI = 80). Type species are shown in **bold**.

Figure 10-2. Strict consensus tree of 102 best-fitting trees under k6 (length = 857; CI = 23; RI = 80). Type species are shown in **bold**.

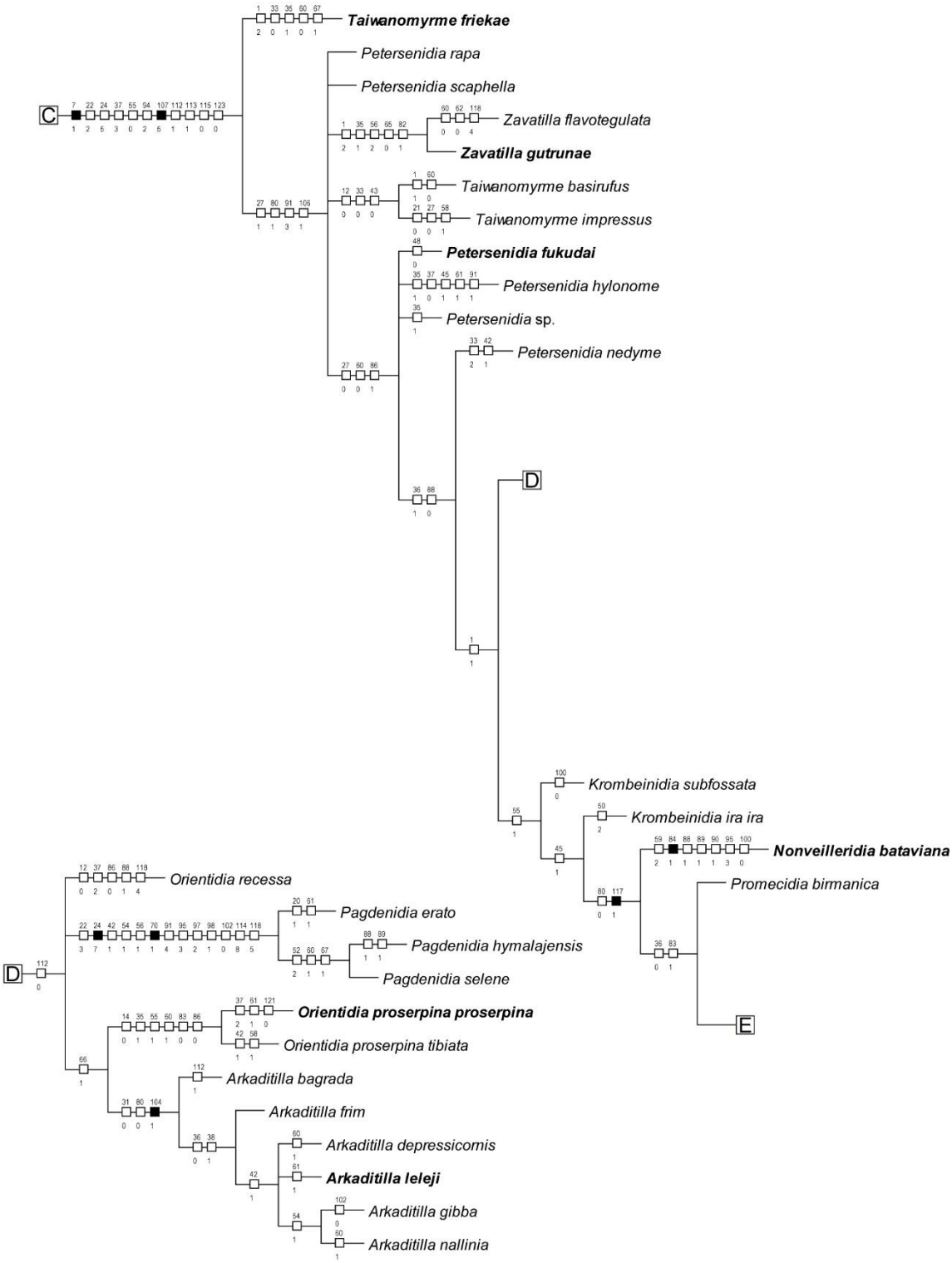

Figure 10-3. Strict consensus tree of 102 best-fitting trees under k6 (length = 857; CI = 23; RI = 80). Type species are shown in **bold**.

Figure 10-4. Strict consensus tree of 102 best-fitting trees under k6 (length = 857; CI = 23; RI = 80). Type species are shown in **bold**.

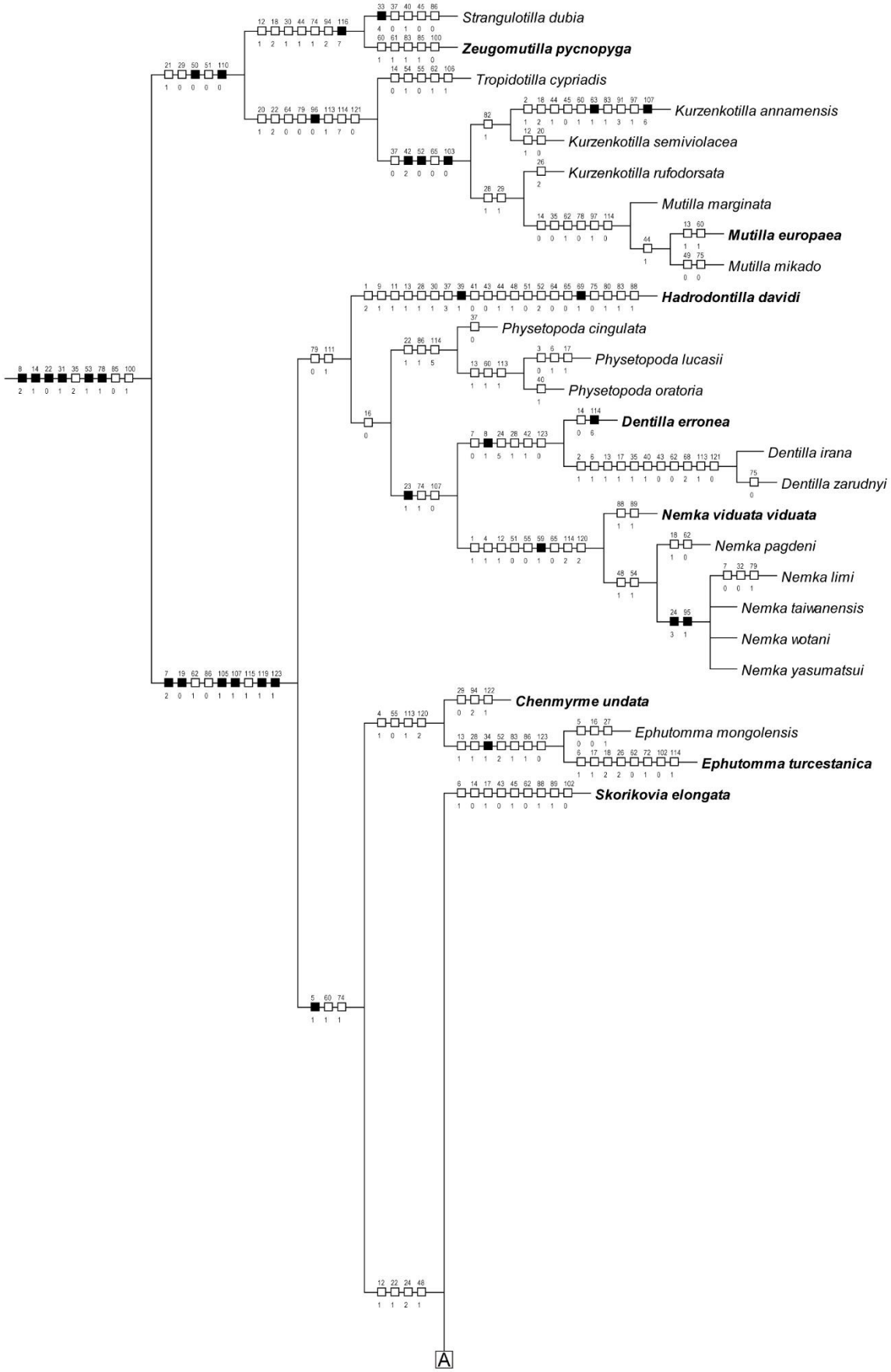

Figure 11-1. Strict consensus tree of 36 best-fitting trees under k7 (length = 840; CI = 23; RI = 80). Type species are shown in **bold**.

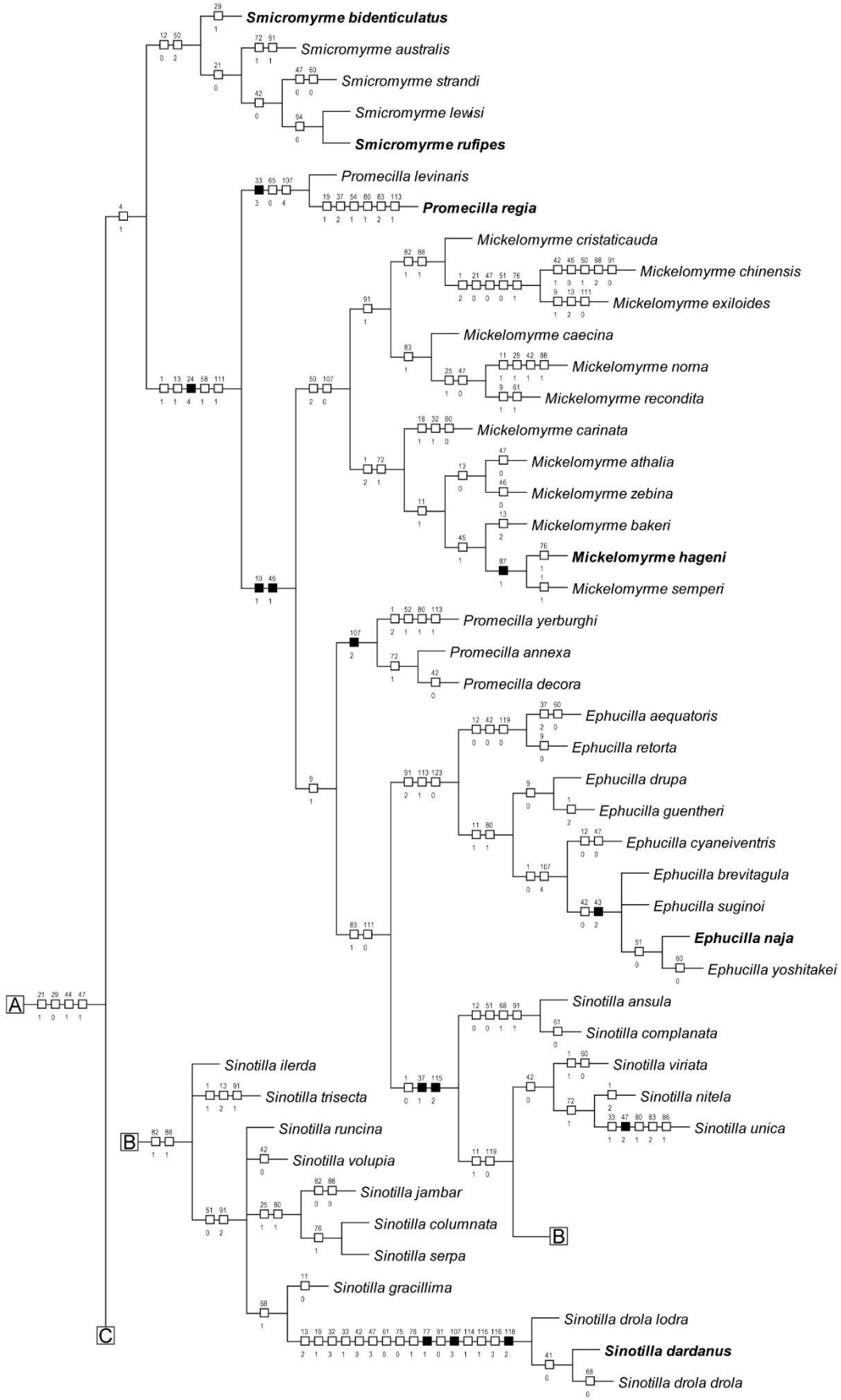

Figure 11-2. Strict consensus tree of 36 best-fitting trees under k7 (length = 840; CI = 23; RI = 80). Type species are shown in **bold**.

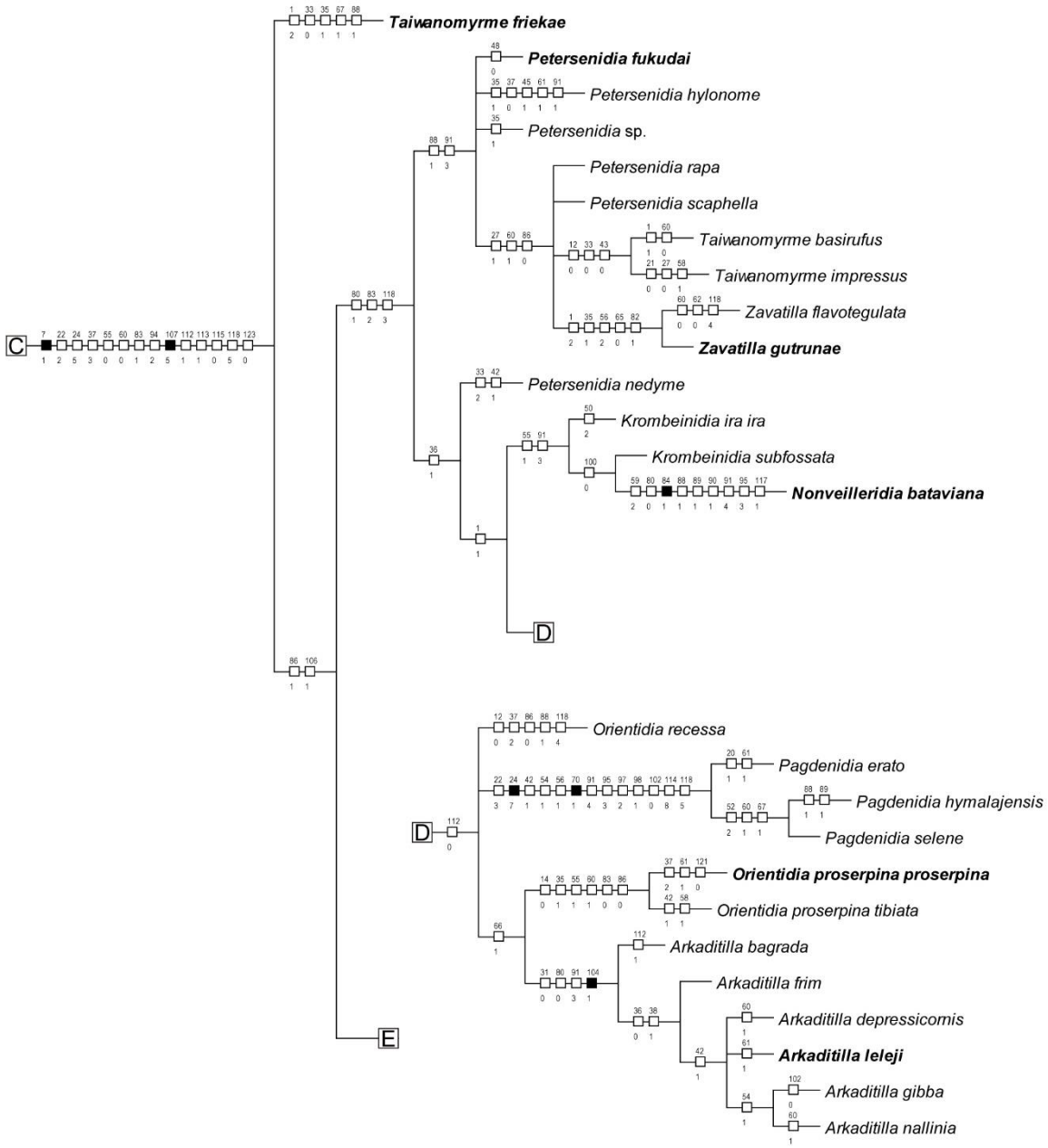

Figure 11-3. Strict consensus tree of 36 best-fitting trees under k7 (length = 840; CI = 23; RI = 80). Type species are shown in **bold**.

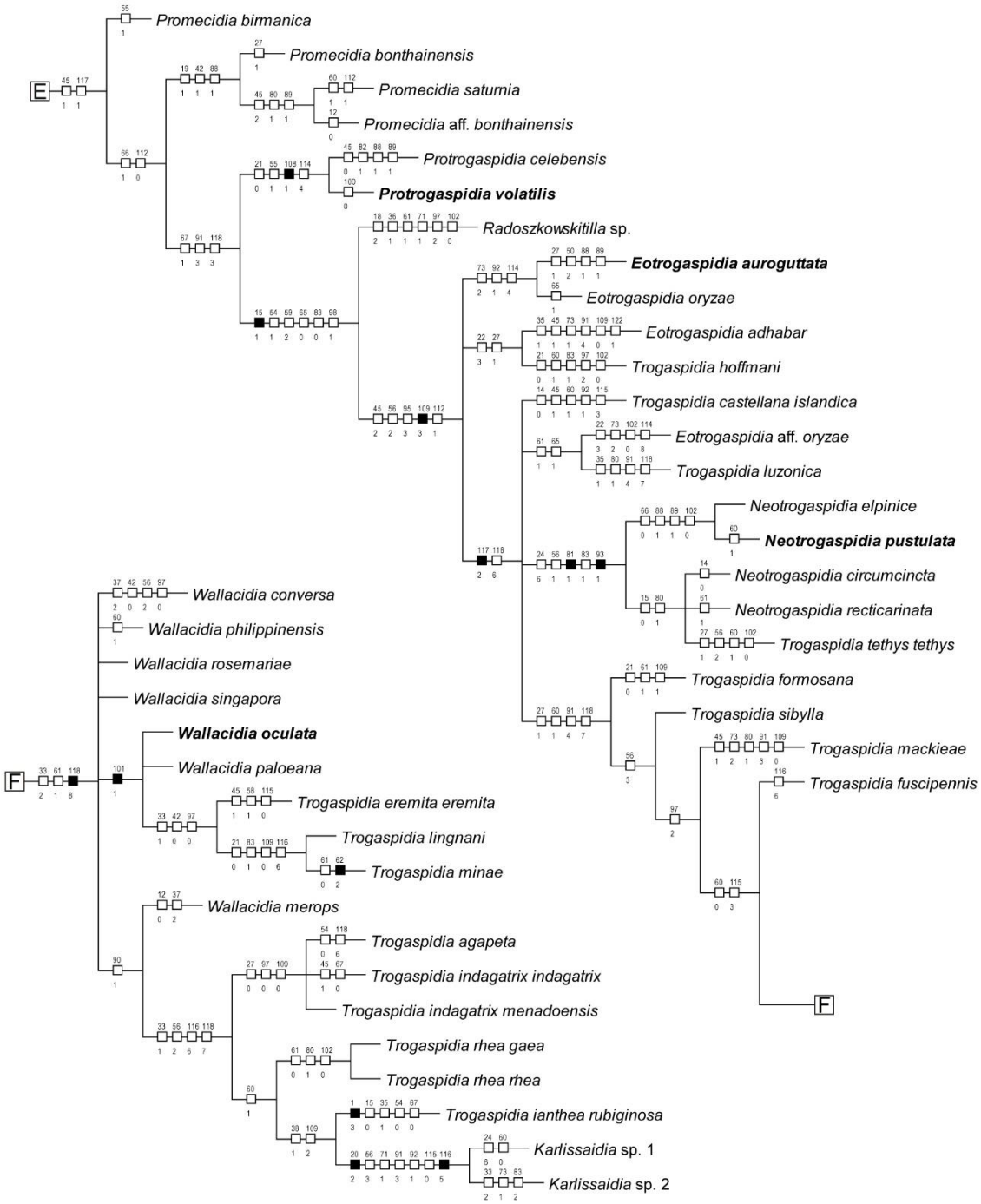

Figure 11-4. Strict consensus tree of 36 best-fitting trees under k7 (length = 840; CI = 23; RI = 80). Type species are shown in **bold**.

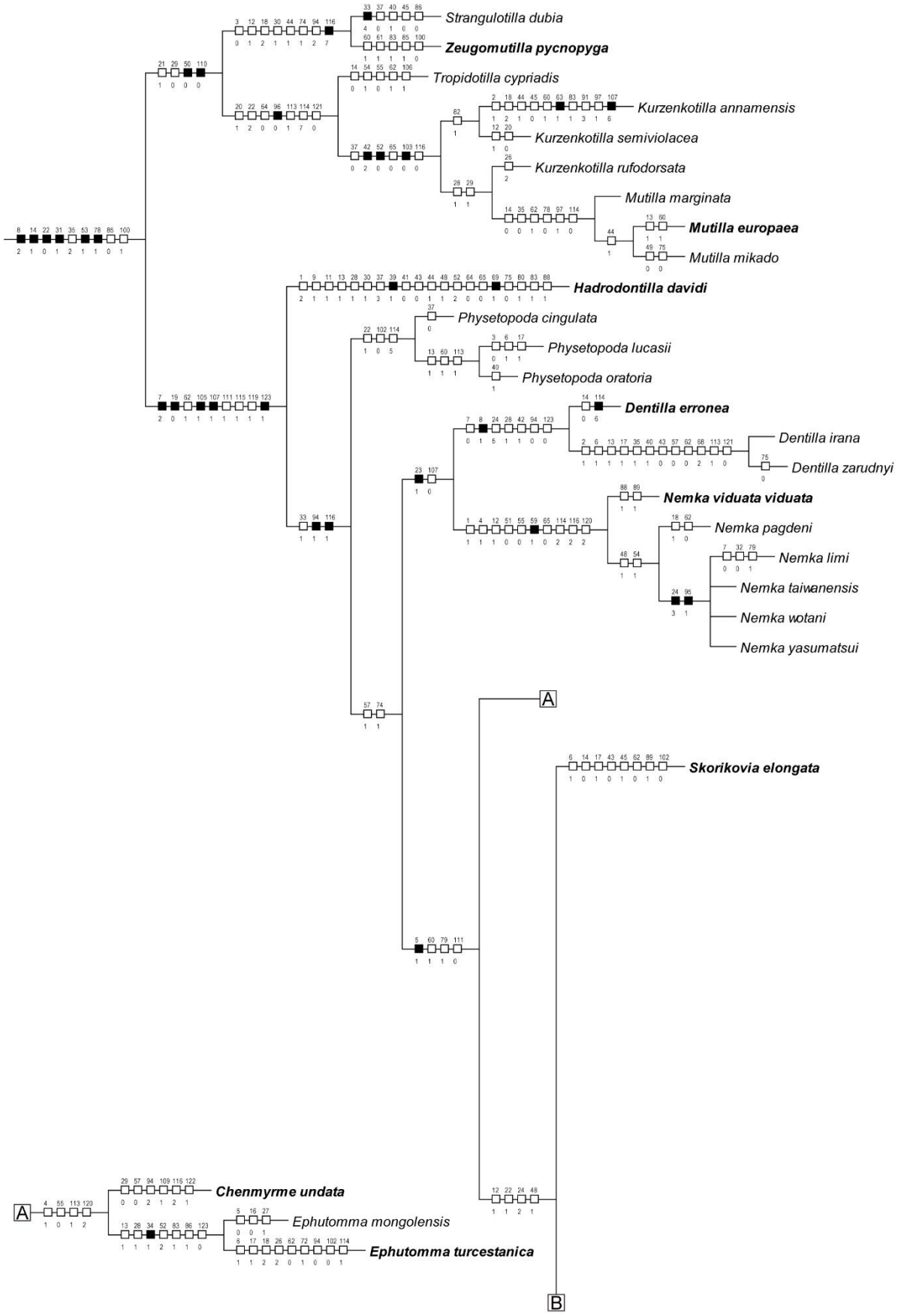

Figure 12-1. Strict consensus tree of 75 best-fitting trees under k8 (length = 830; CI = 23; RI = 80). Type species are shown in **bold**.

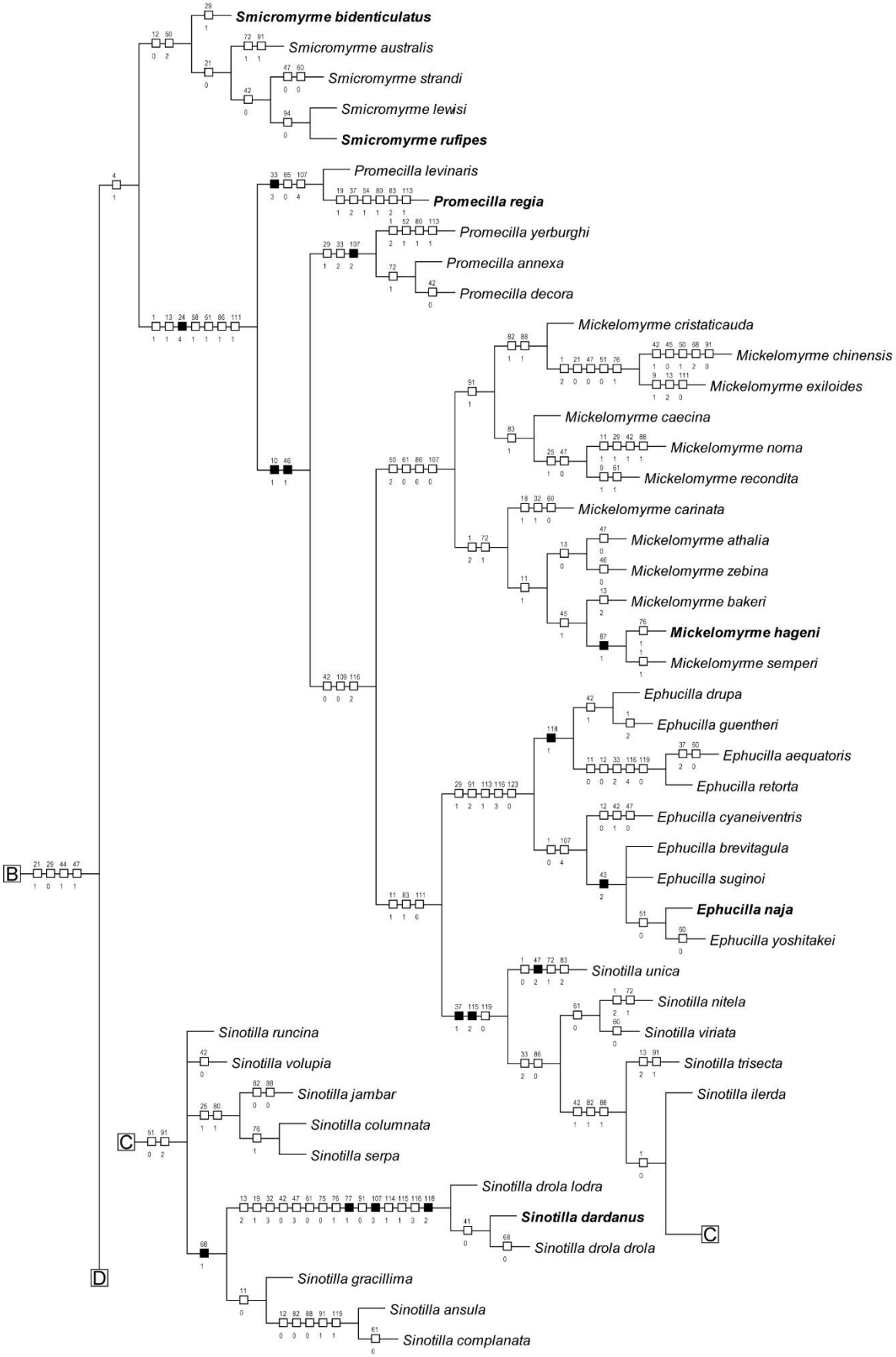

Figure 12-2. Strict consensus tree of 75 best-fitting trees under k8 (length = 830; CI = 23; RI = 80). Type species are shown in **bold**.

Figure 12-3. Strict consensus tree of 75 best-fitting trees under k8 (length = 830; CI = 23; RI = 80). Type species are shown in **bold**.

Figure 12-4. Strict consensus tree of 75 best-fitting trees under k8 (length = 830; CI = 23; RI = 80). Type species are shown in **bold**.

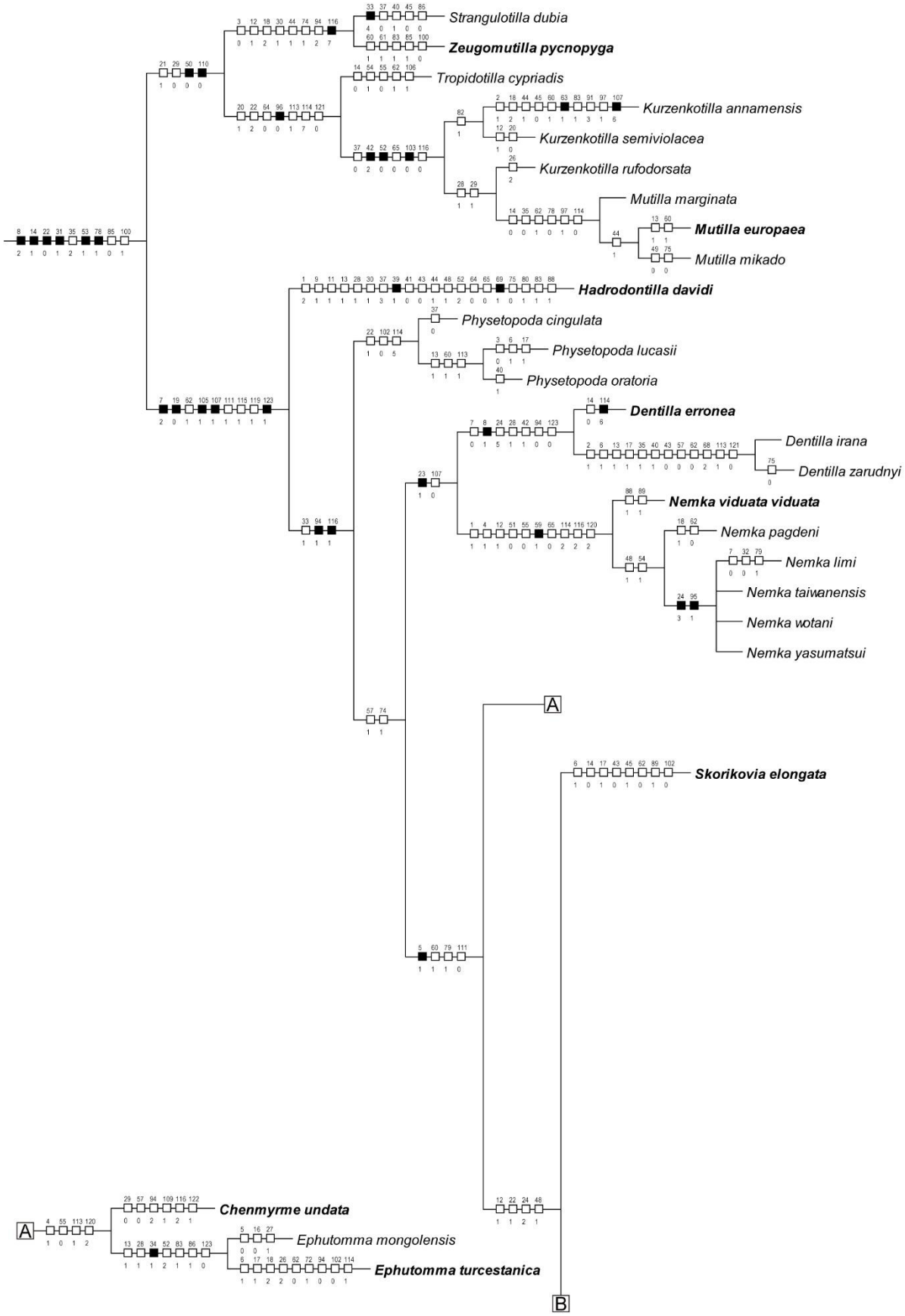

Figure 13-1. Strict consensus tree of 75 best-fitting trees under k9 (length = 830; CI = 23; RI = 80). Type species are shown in **bold**.

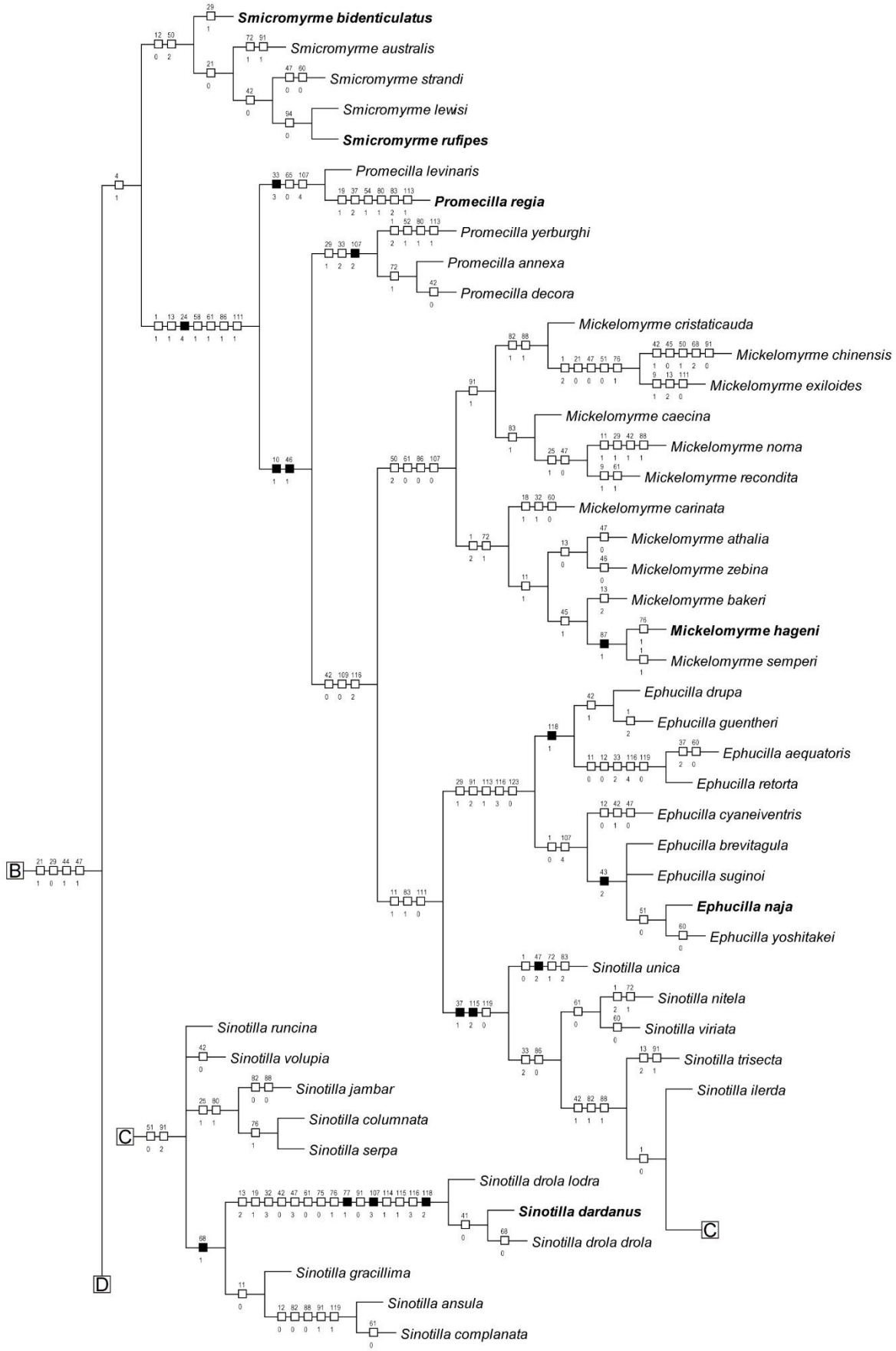

Figure 13-2. Strict consensus tree of 75 best-fitting trees under k9 (length = 830; CI = 23; RI = 80). Type species are shown in **bold**.

Figure 13-3. Strict consensus tree of 75 best-fitting trees under k9 (length = 830; CI = 23; RI = 80). Type species are shown in **bold**.

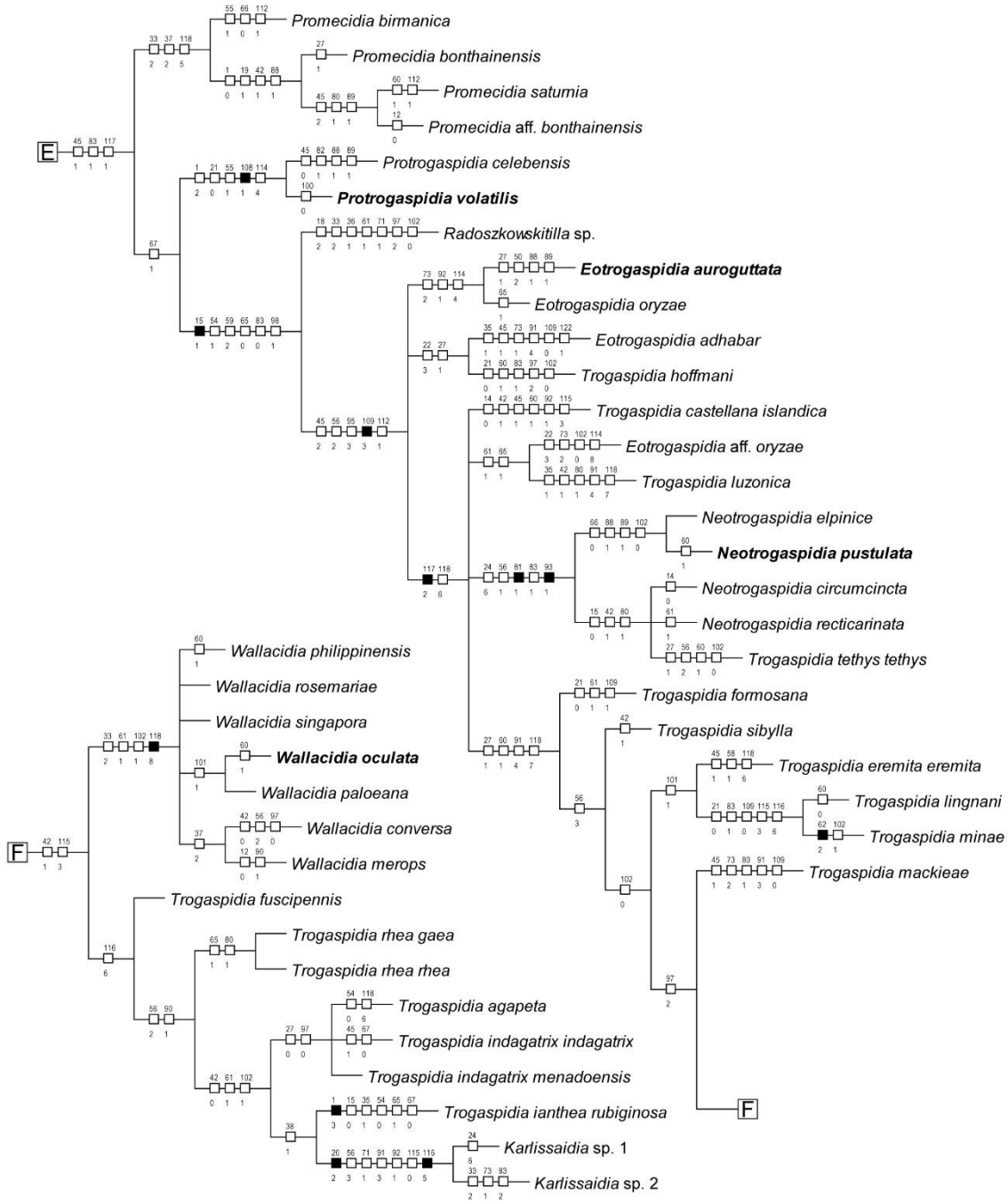

Figure 13-4. Strict consensus tree of 75 best-fitting trees under k9 (length = 830; CI = 23; RI = 80). Type species are shown in **bold**.

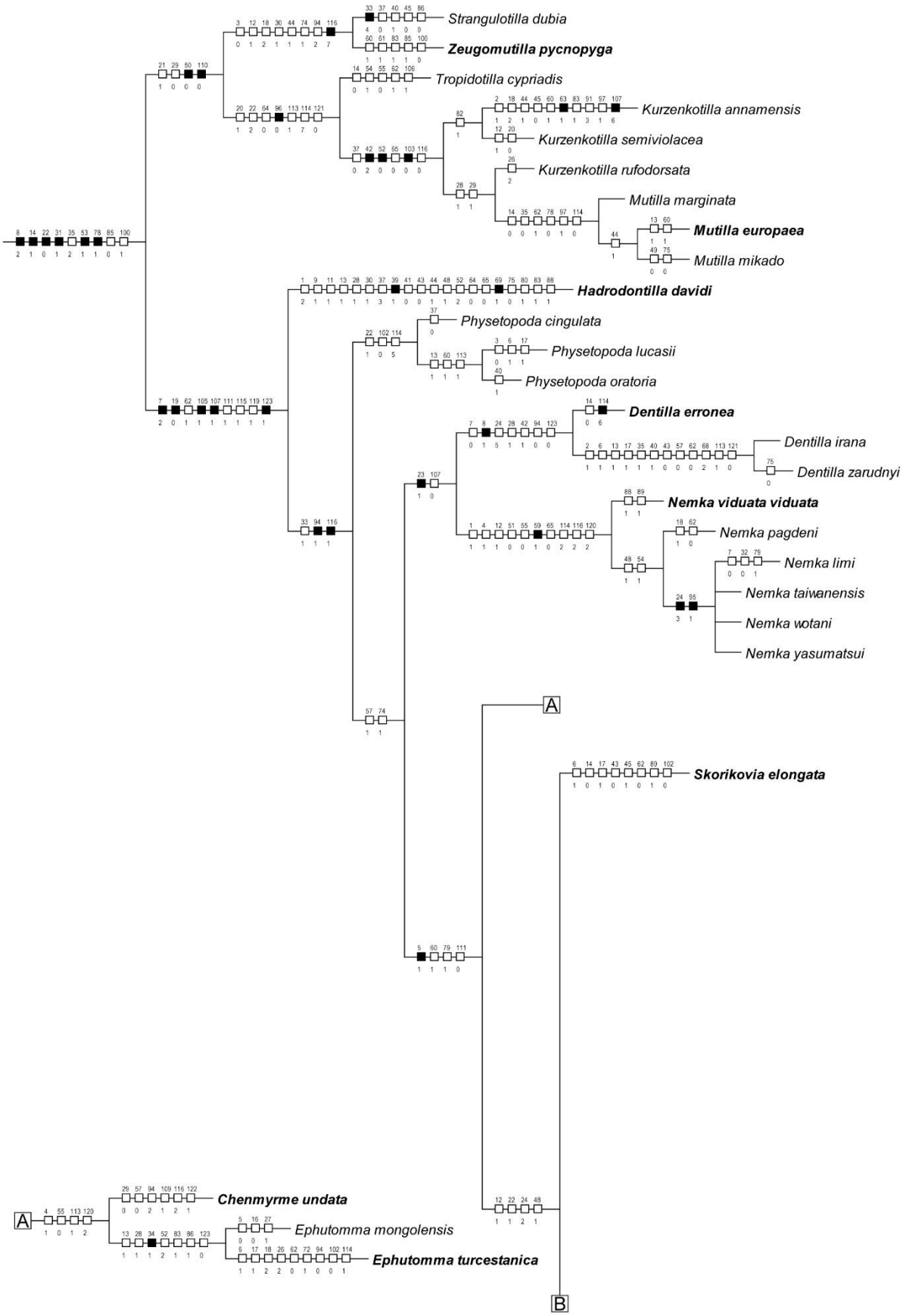

Figure 14-1. Strict consensus tree of 65 best-fitting trees under k10 (length = 830; CI = 23; RI = 80). Type species are shown in **bold**.

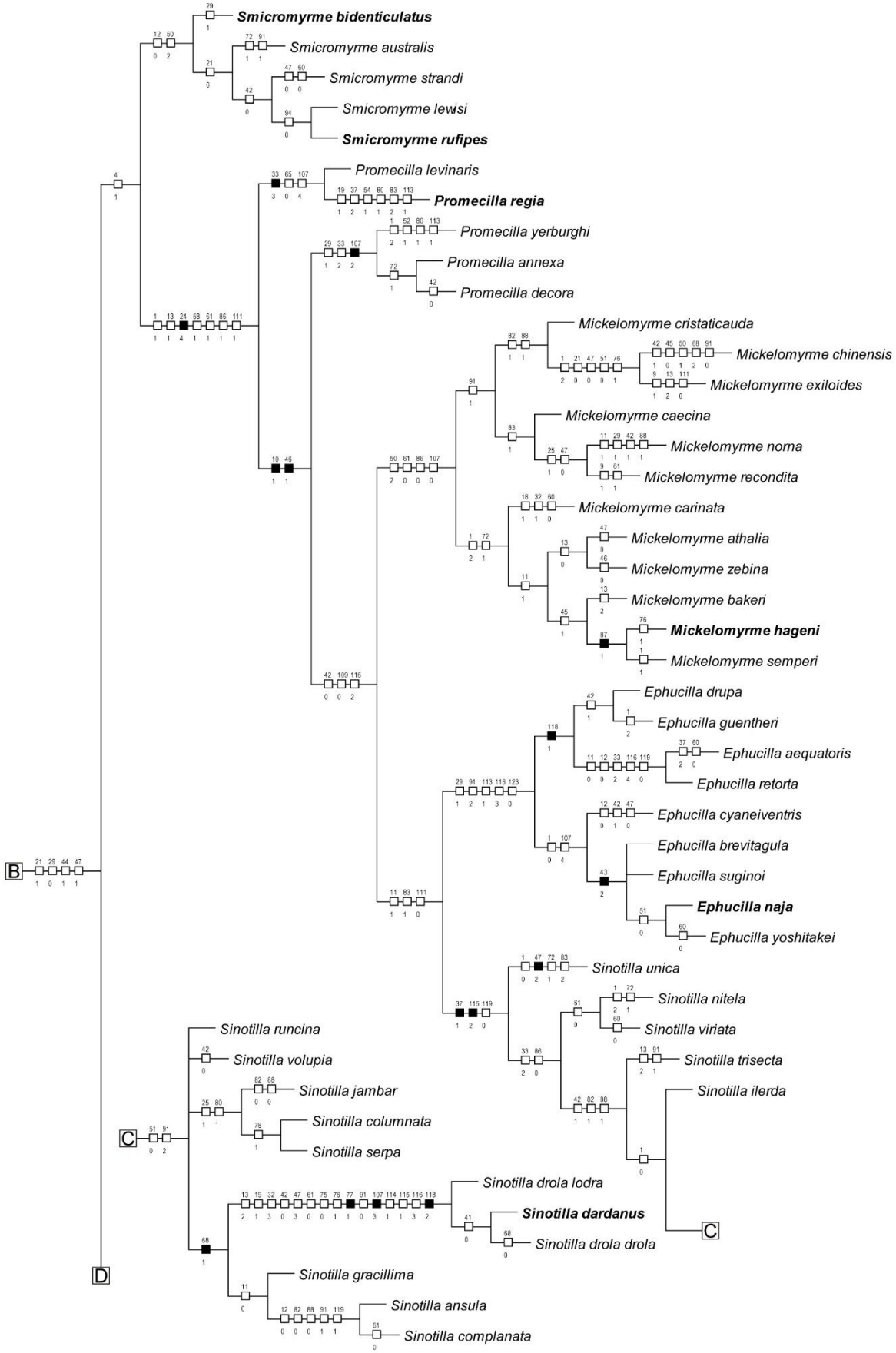

Figure 14-2. Strict consensus tree of 65 best-fitting trees under k10 (length = 830; CI = 23; RI = 80). Type species are shown in **bold**.

Figure 14-3. Strict consensus tree of 65 best-fitting trees under k10 (length = 830; CI = 23; RI = 80). Type species are shown in **bold**.

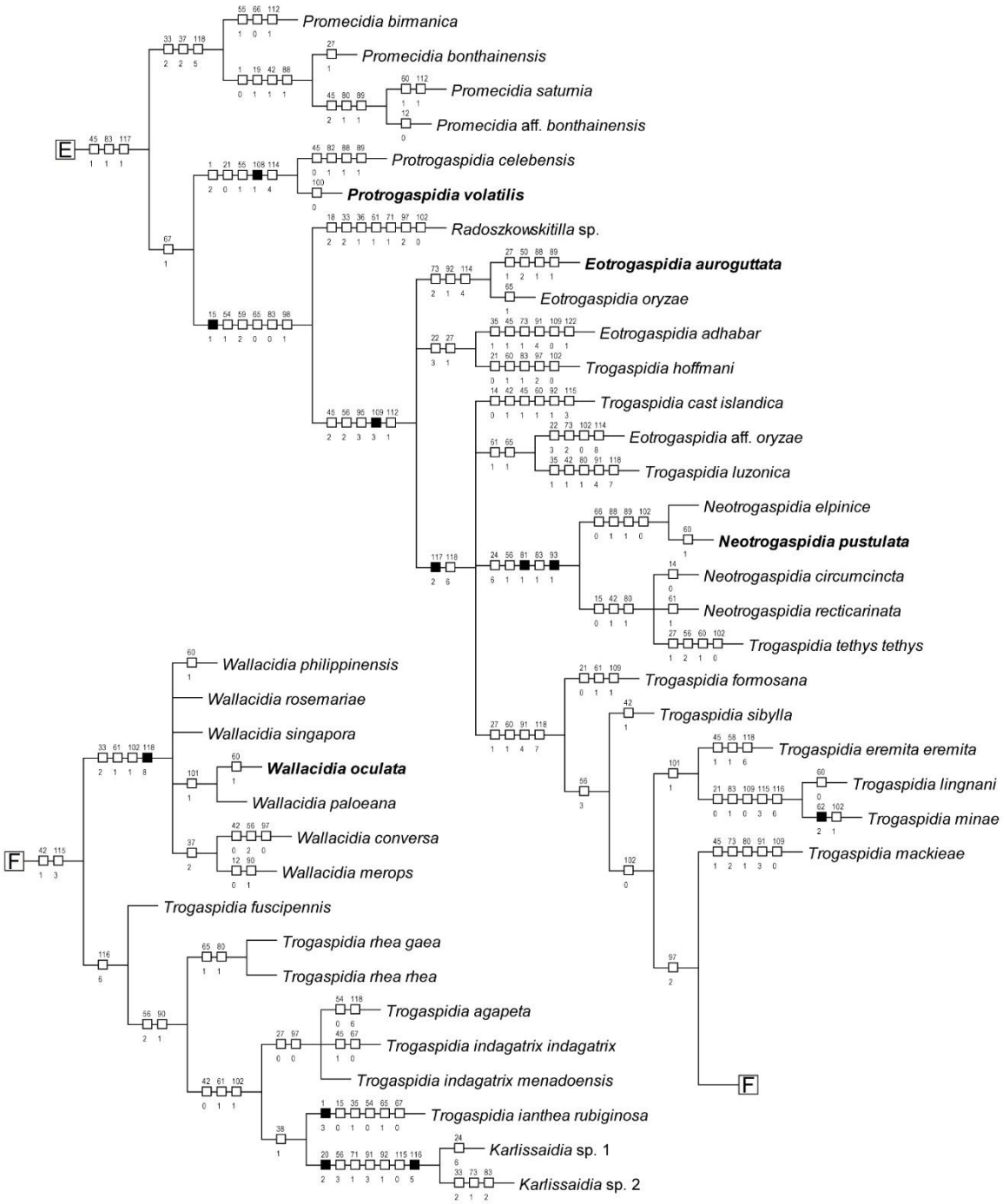

Figure 14-4. Strict consensus tree of 65 best-fitting trees under k10 (length = 830; CI = 23; RI = 80). Type species are shown in **bold**.

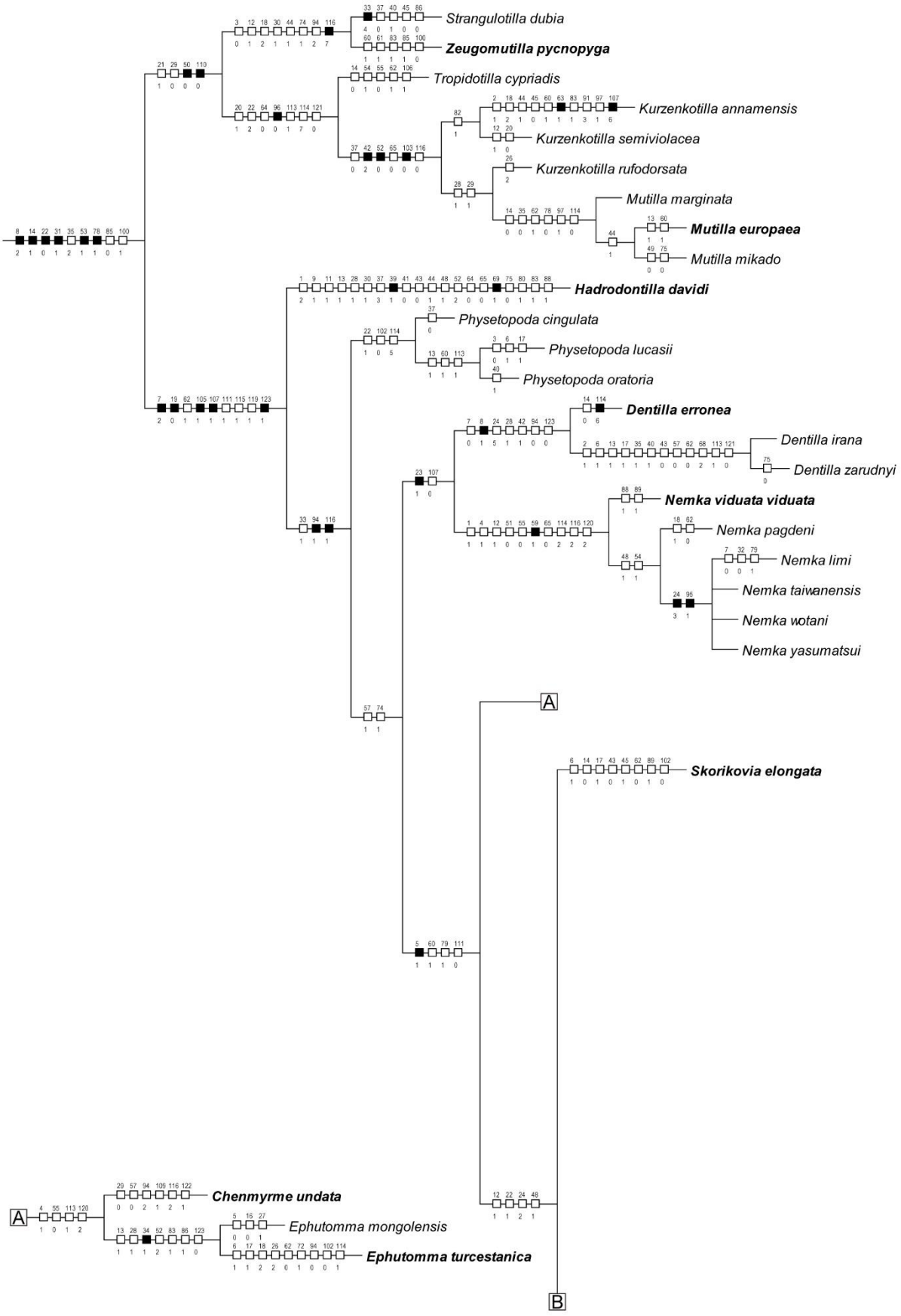

Figure 15-1. Strict consensus tree of 50 best-fitting trees under k11 (length = 830; CI = 23; RI = 80). Type species are shown in **bold**.

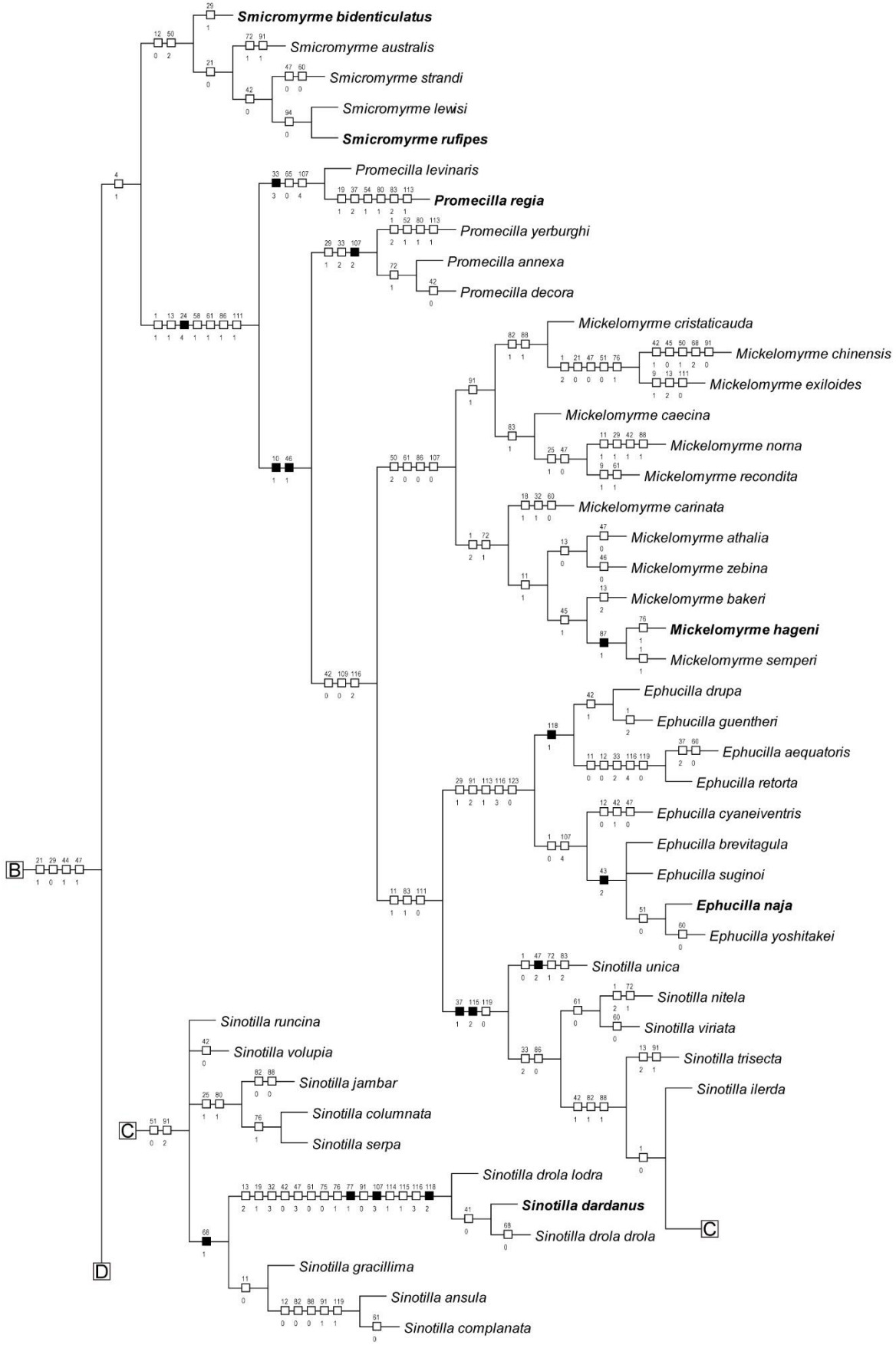

Figure 15-2. Strict consensus tree of 50 best-fitting trees under k11 (length = 830; CI = 23; RI = 80). Type species are shown in **bold**.

Figure 15-3. Strict consensus tree of 50 best-fitting trees under k11 (length = 830; CI = 23; RI = 80). Type species are shown in **bold**.

Figure 15-4. Strict consensus tree of 50 best-fitting trees under k11 (length = 830; CI = 23; RI = 80). Type species are shown in **bold**.

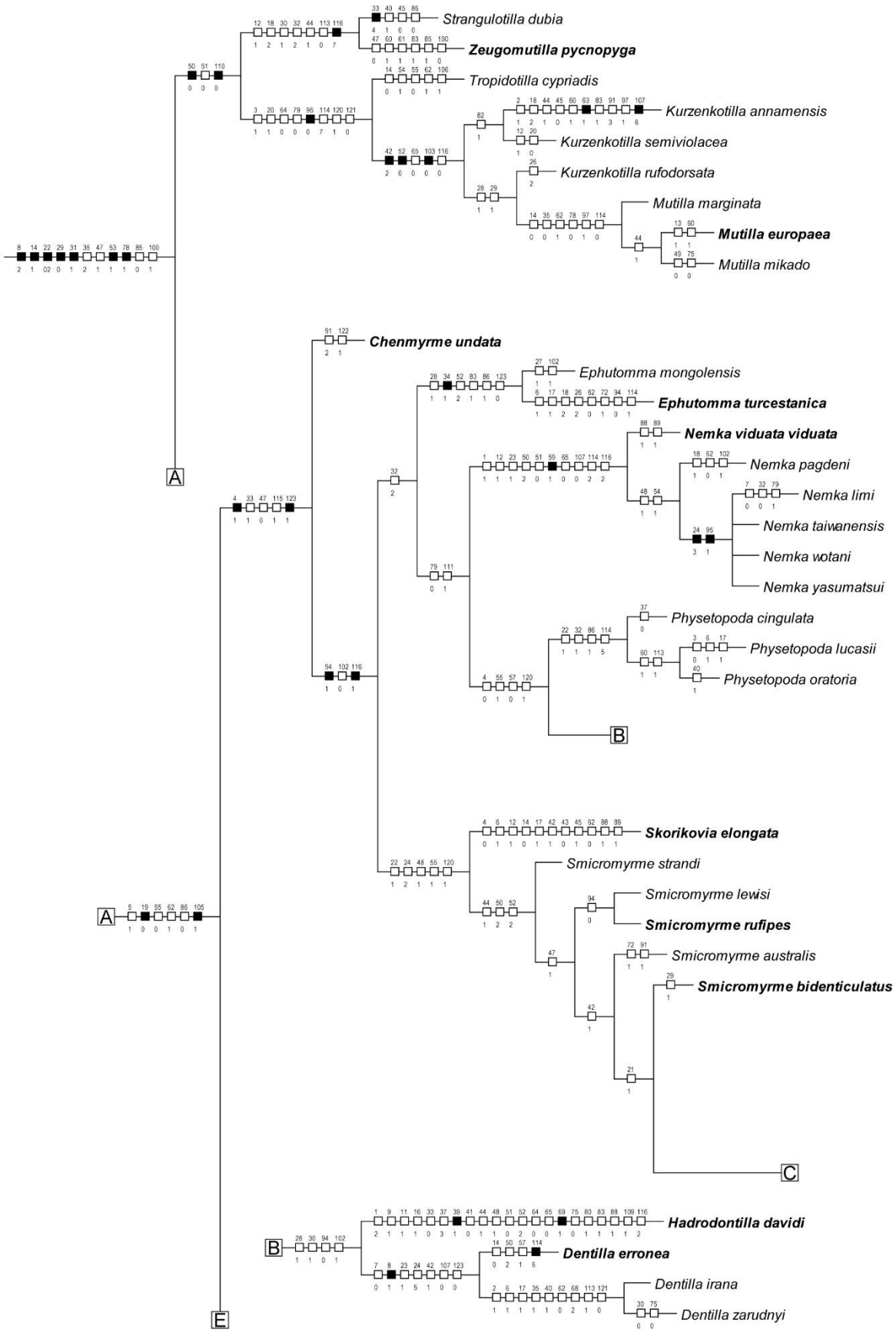

Figure 16-1. Strict consensus tree of nine best-fitting trees under k12 (length = 823; CI = 24; RI = 81). Type species are shown in **bold**.

Figure 16-2. Strict consensus tree of nine best-fitting trees under k12 (length = 823; CI = 24; RI = 81). Type species are shown in **bold**.

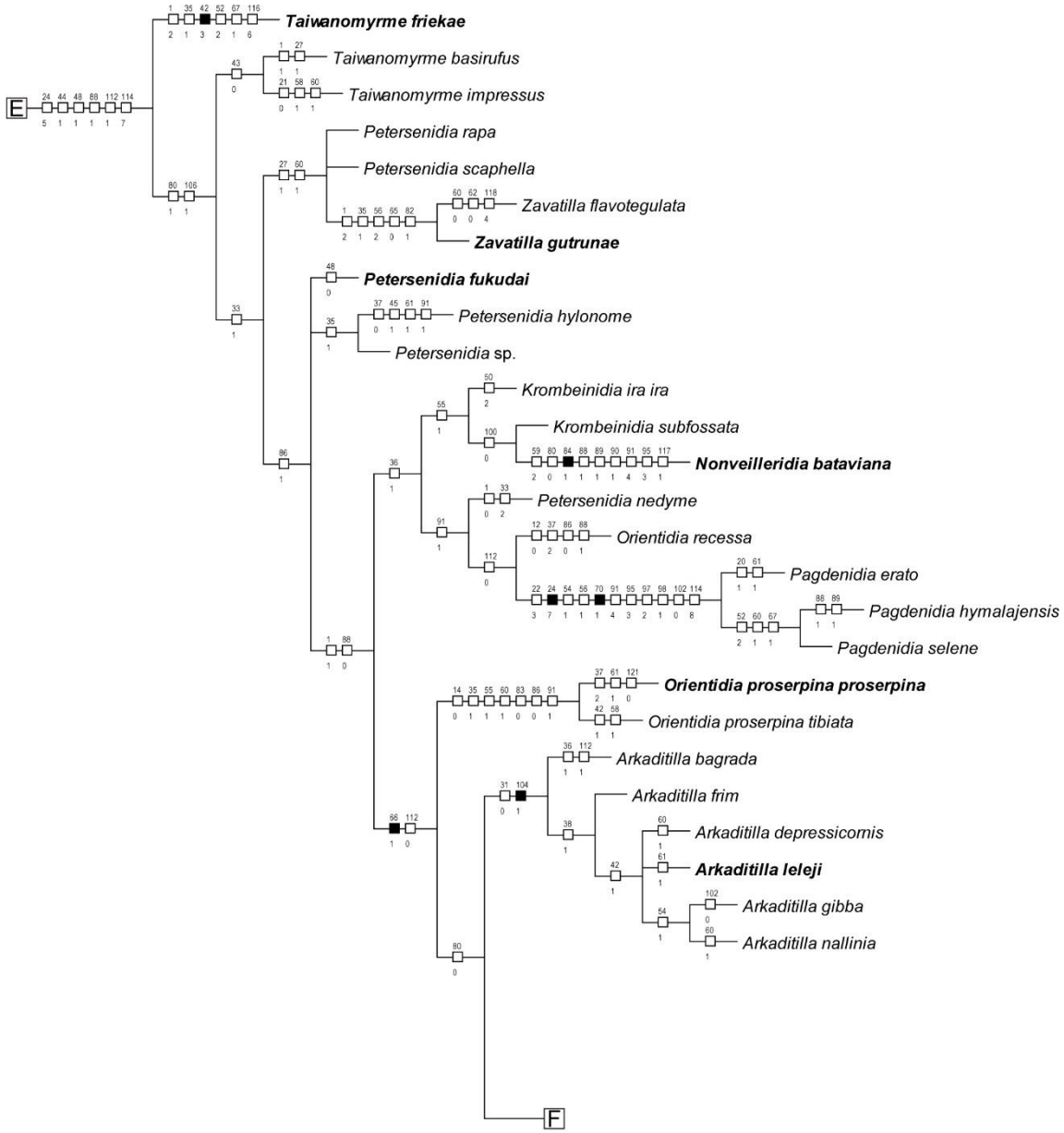

Figure 16-3. Strict consensus tree of nine best-fitting trees under k12 (length = 823; CI = 24; RI = 81). Type species are shown in **bold**.

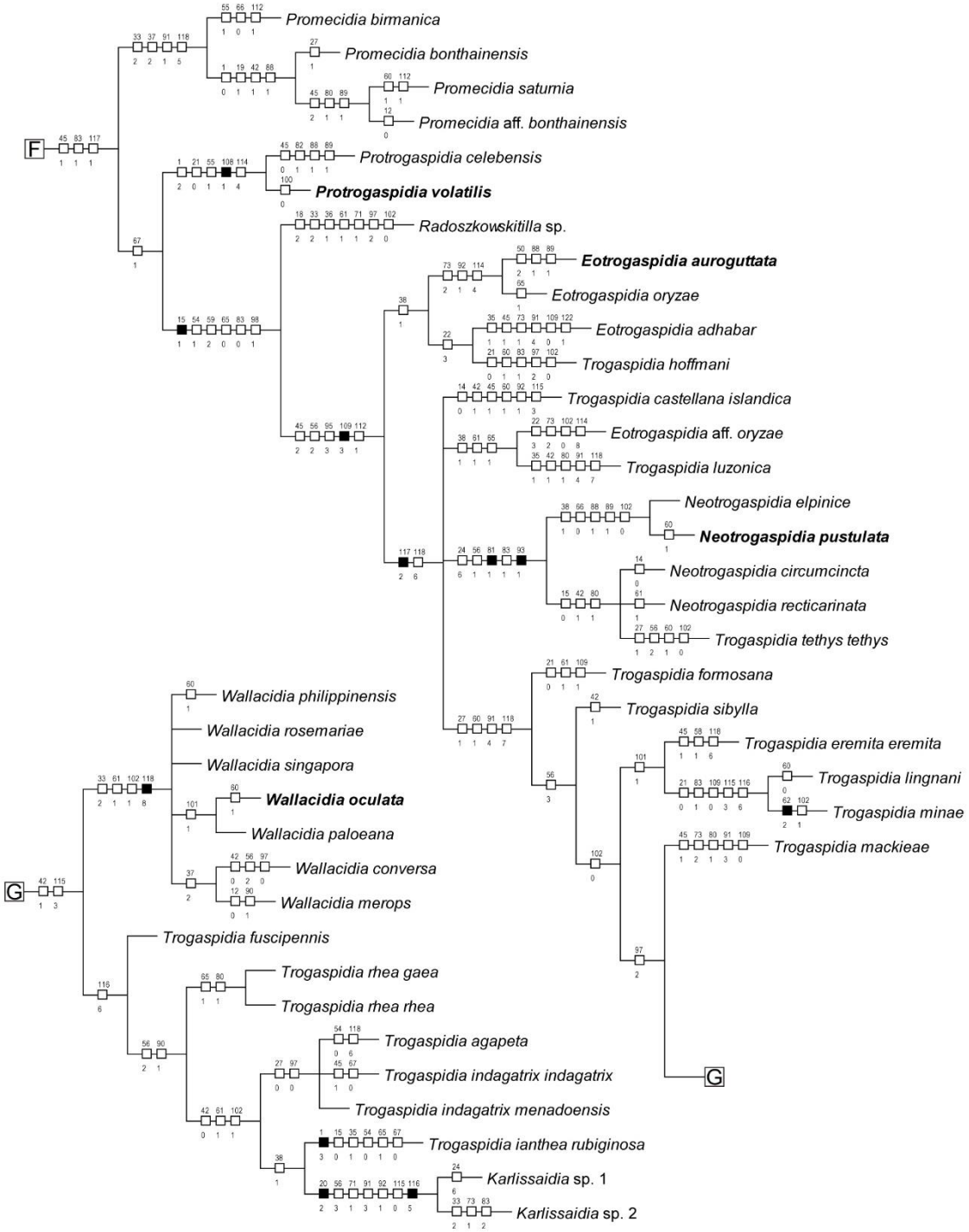

Figure 16-4. Strict consensus tree of nine best-fitting trees under k12 (length = 823; CI = 24; RI = 81). Type species are shown in **bold**.

Figure 17-1. Strict consensus tree of nine best-fitting trees under k13 (length = 821; CI = 24; RI = 81). Type species are shown in **bold**.

Figure 17-2. Strict consensus tree of nine best-fitting trees under k13 (length = 821; CI = 24; RI = 81). Type species are shown in **bold**.

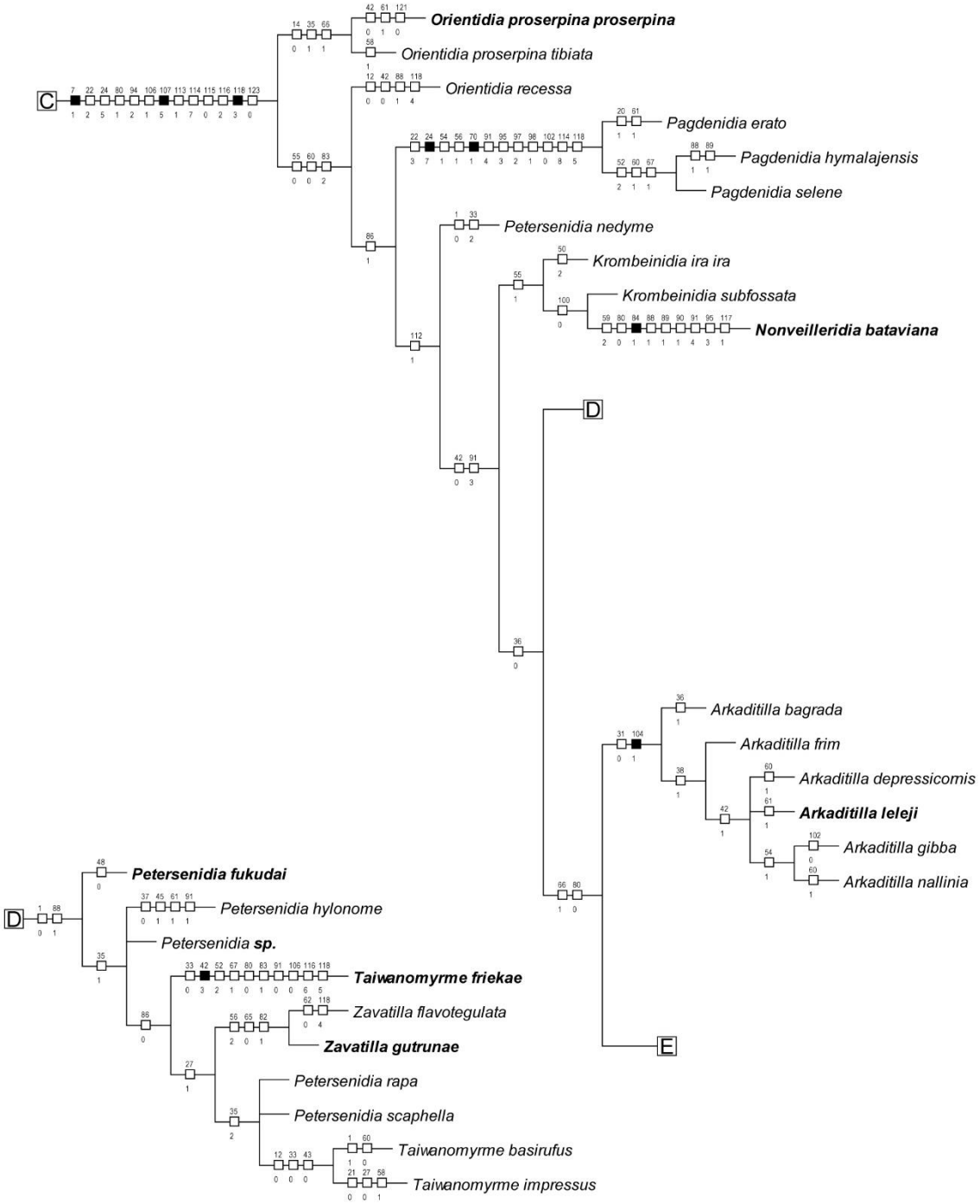

Figure 17-3. Strict consensus tree of nine best-fitting trees under k13 (length = 821; CI = 24; RI = 81). Type species are shown in **bold**.

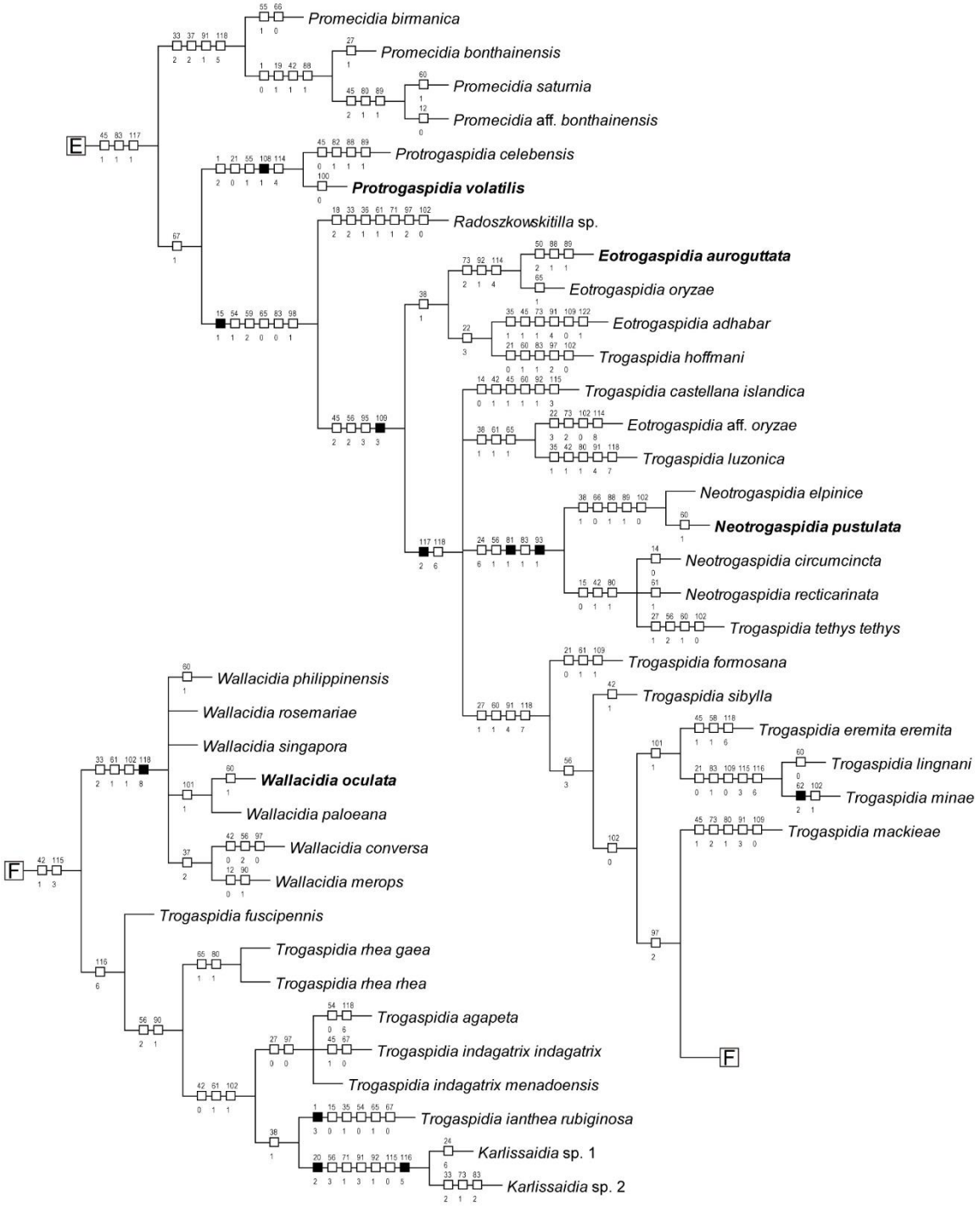

Figure 17-4. Strict consensus tree of nine best-fitting trees under k13 (length = 821; CI = 24; RI = 81). Type species are shown in **bold**.

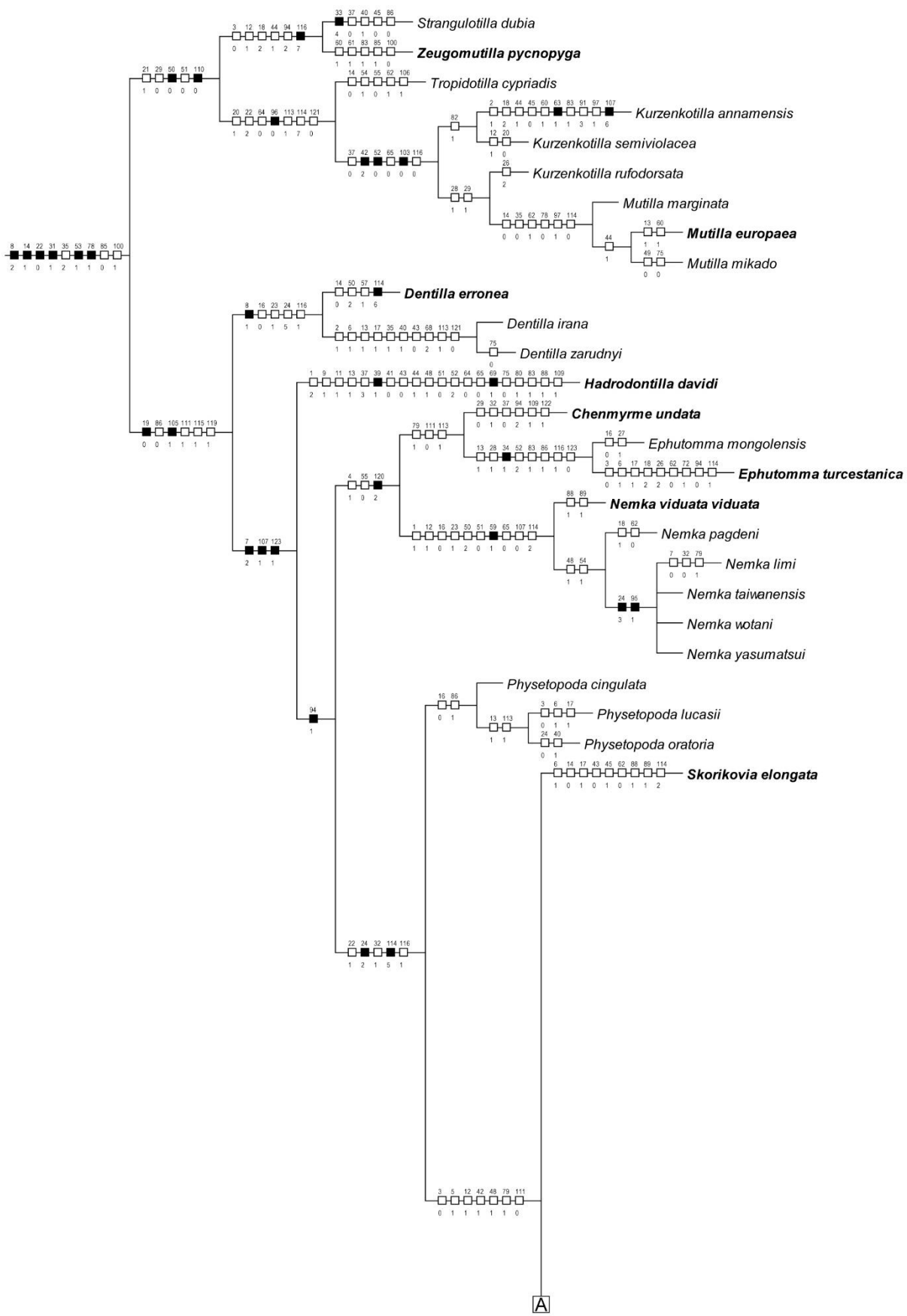

Figure 18-1. Strict consensus tree of nine best-fitting trees under k14 (length = 822; CI = 24; RI = 81). Type species are shown in **bold**.

Figure 18-2. Strict consensus tree of nine best-fitting trees under k14 (length = 822; CI = 24; RI = 81). Type species are shown in **bold**.

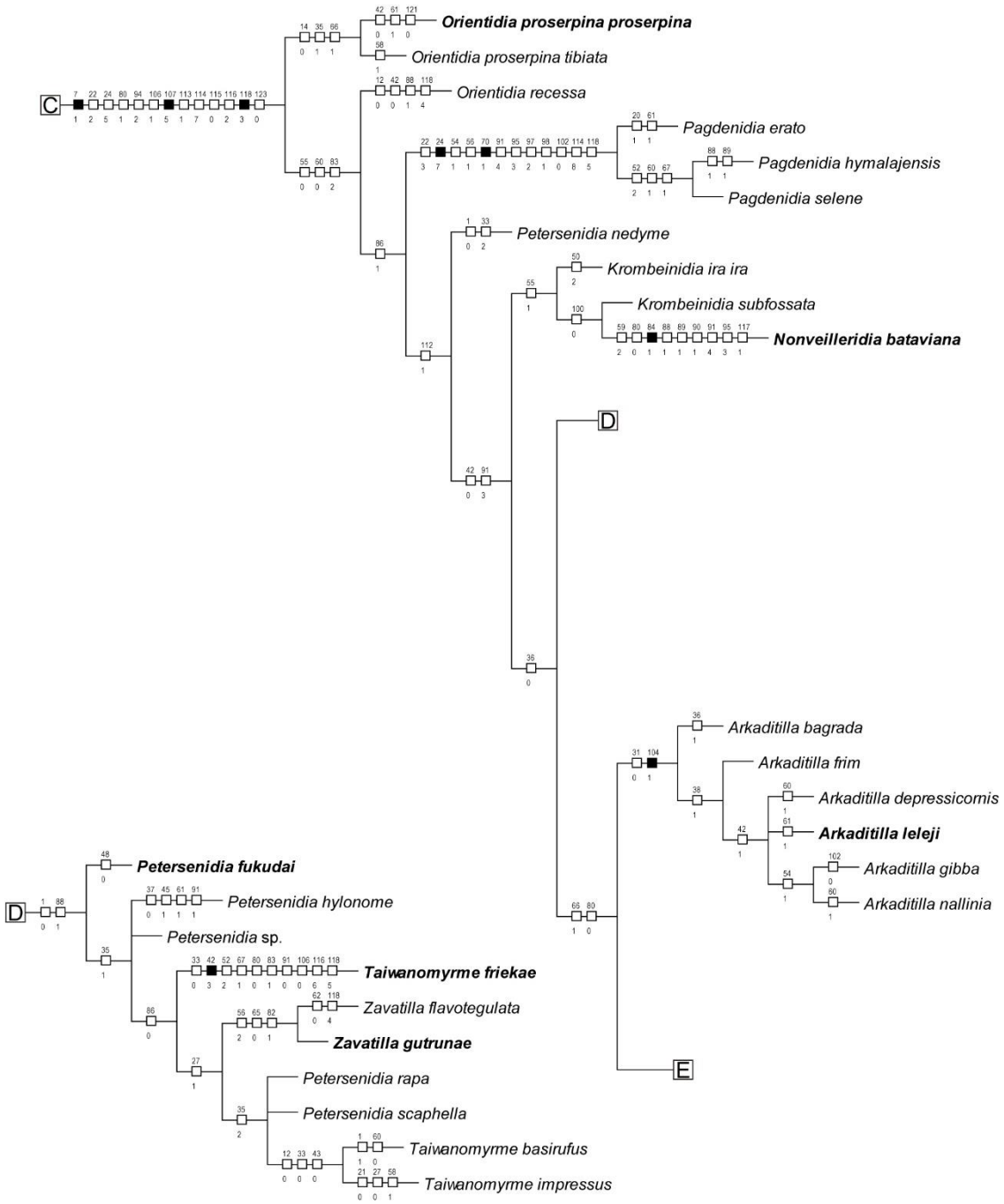

Figure 18-3. Strict consensus tree of nine best-fitting trees under k14 (length = 822; CI = 24; RI = 81). Type species are shown in **bold**.

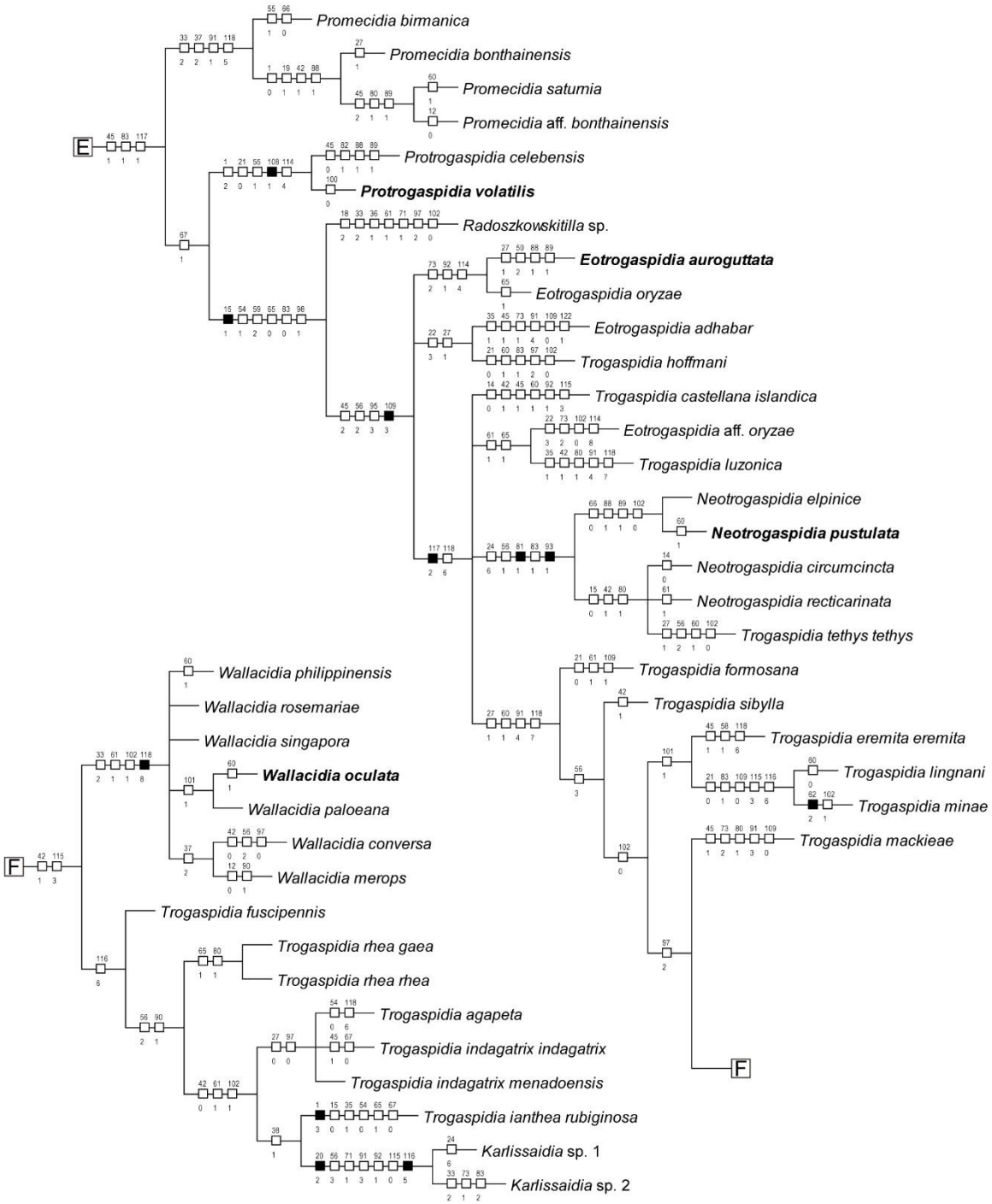

Figure 18-4. Strict consensus tree of nine best-fitting trees under k14 (length = 822; CI = 24; RI = 81). Type species are shown in **bold**.

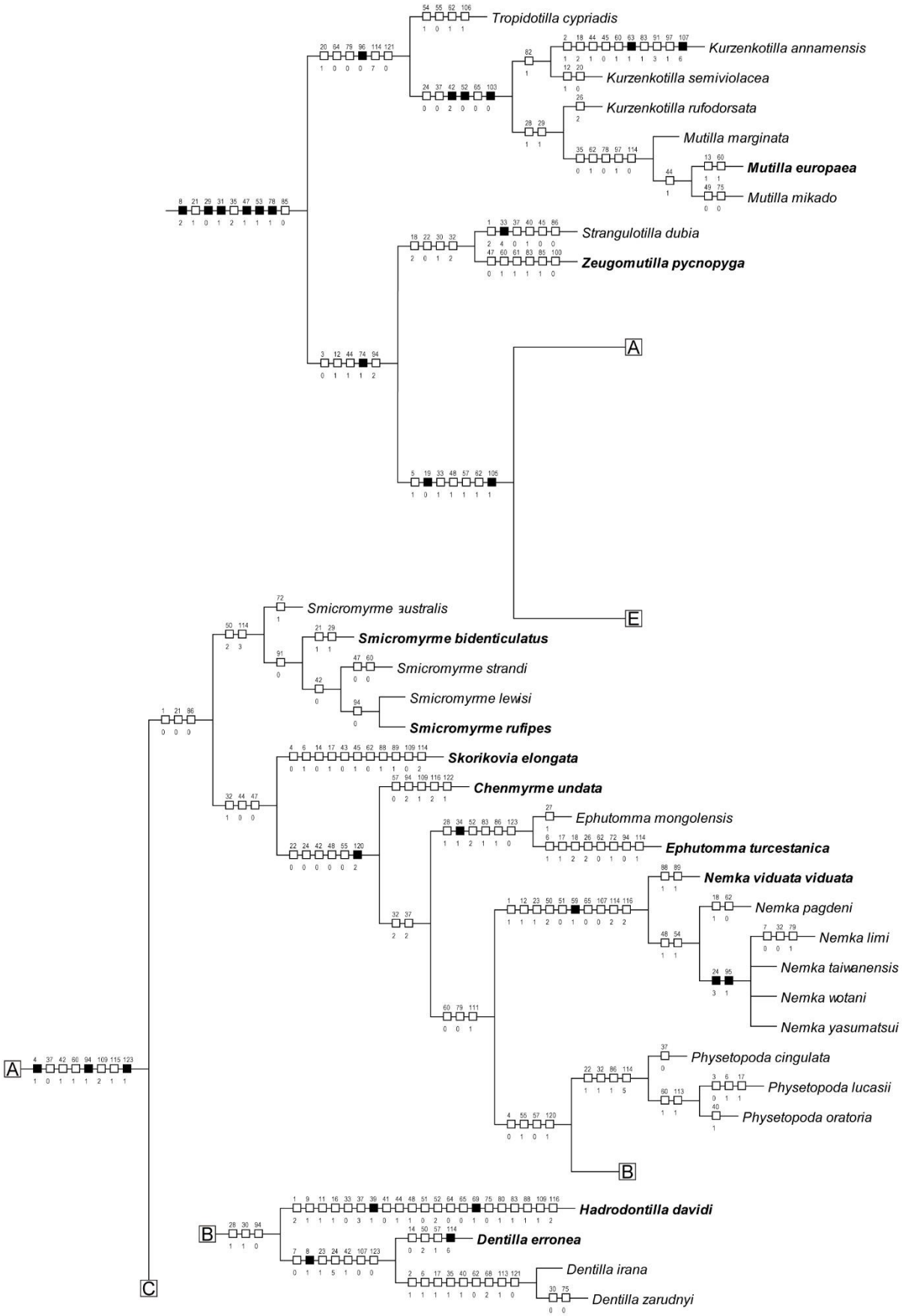

Figure 19-1. Strict consensus tree of nine best-fitting trees under k15 (length = 819; CI = 24; RI = 81). Type species are shown in **bold**.

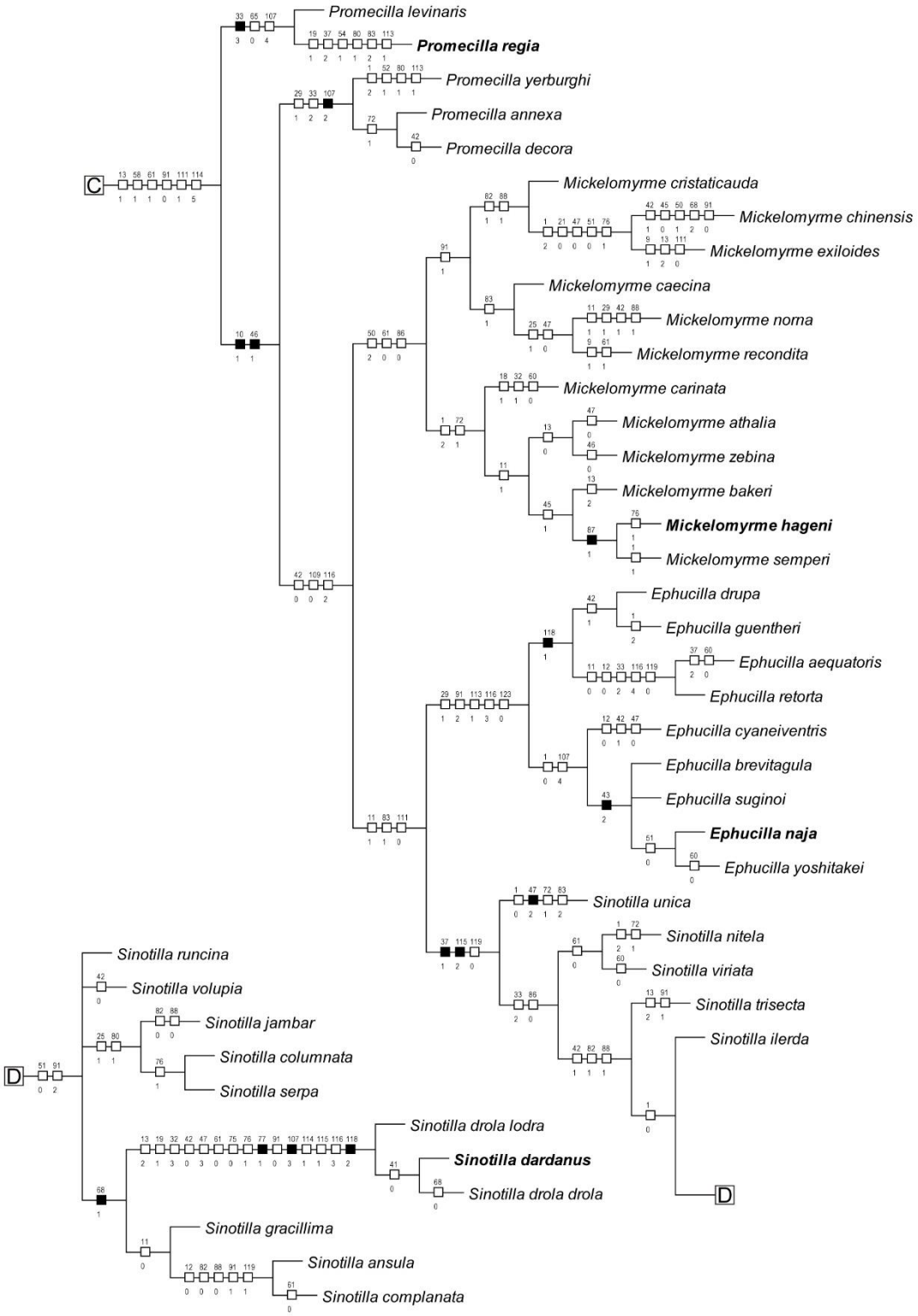

Figure 19-2. Strict consensus tree of nine best-fitting trees under k15 (length = 819; CI = 24; RI = 81). Type species are shown in **bold**.

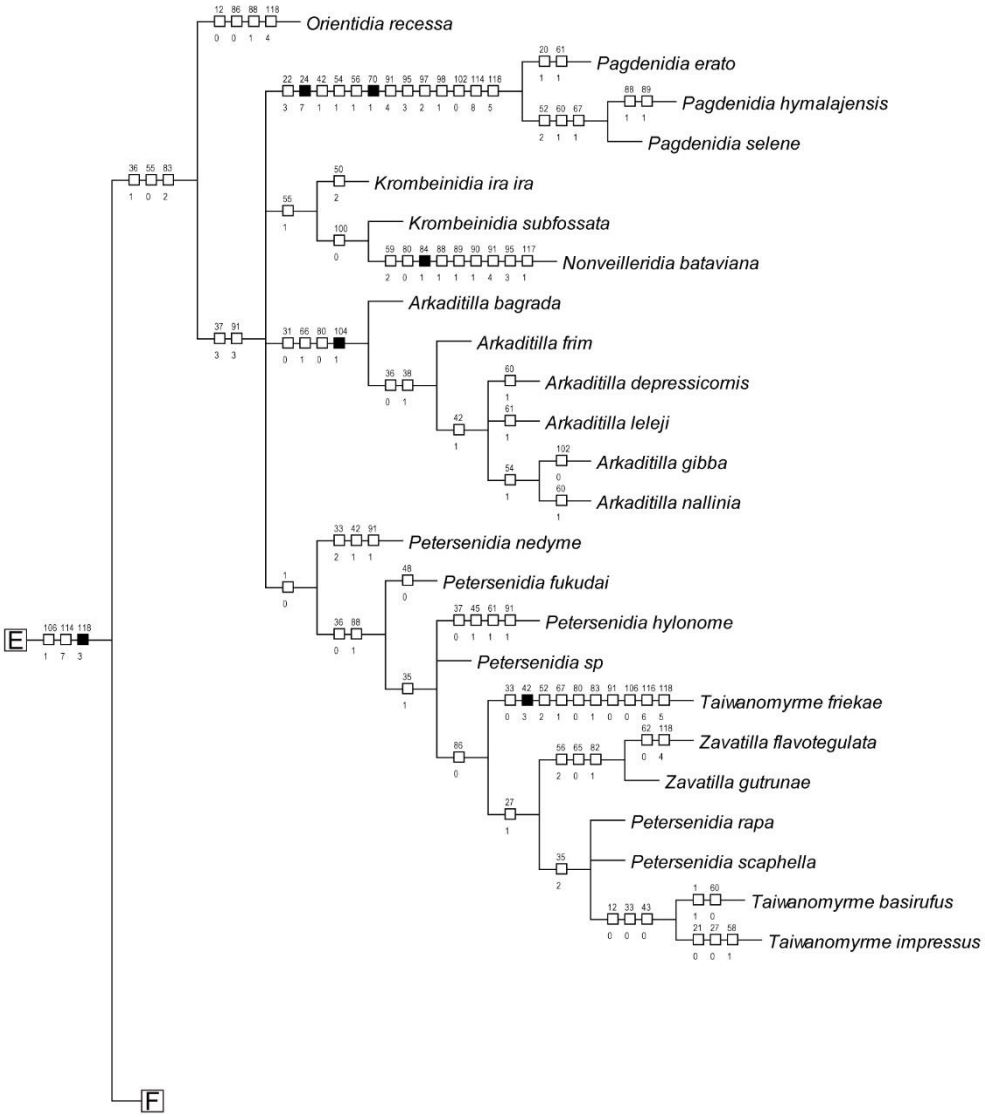

Figure 19-3. Strict consensus tree of nine best-fitting trees under k15 (length = 819; CI = 24; RI = 81). Type species are shown in **bold**.

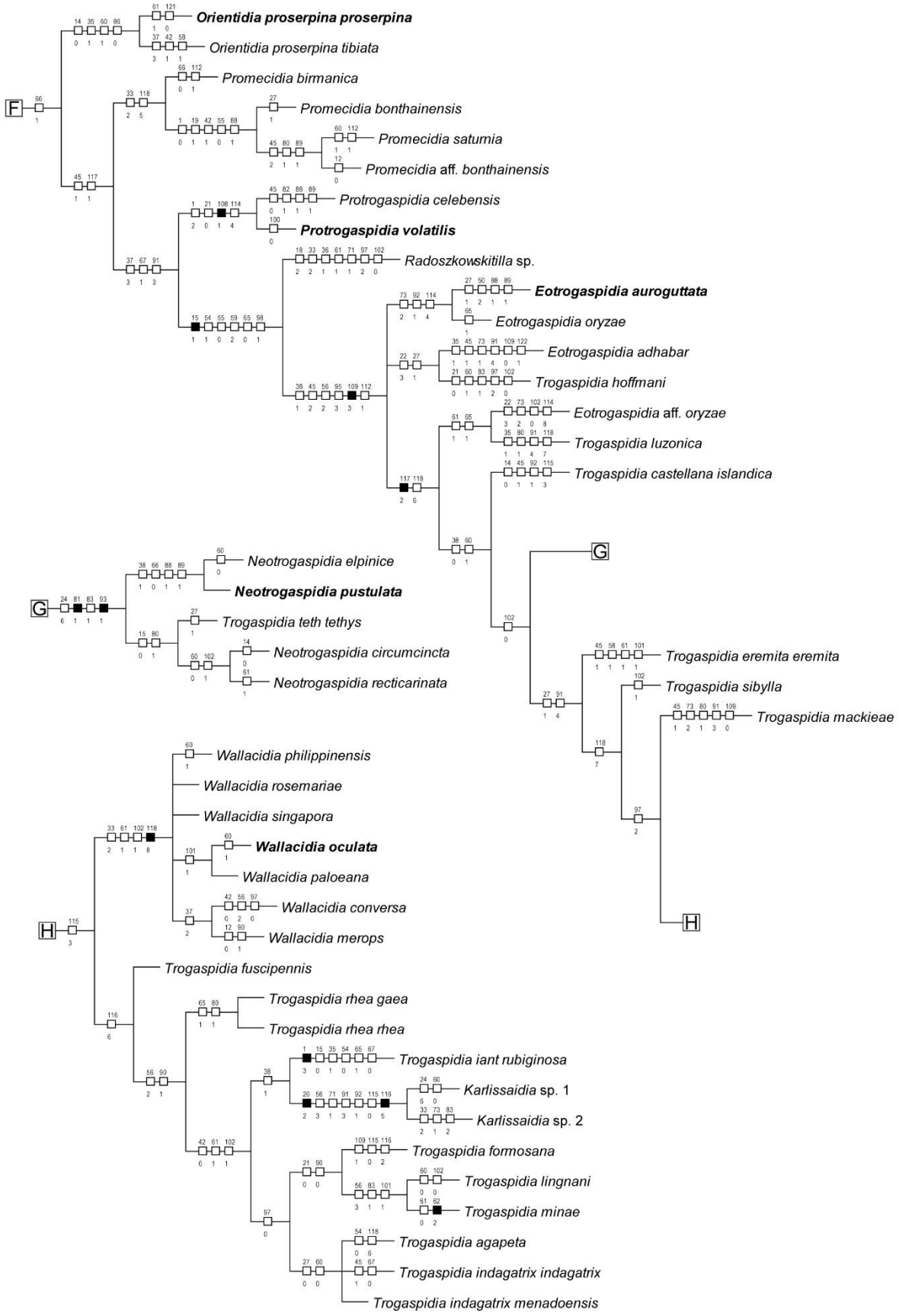

Figure 19-4. Strict consensus tree of nine best-fitting trees under k15 (length = 819; CI = 24; RI = 81). Type species are shown in **bold**.

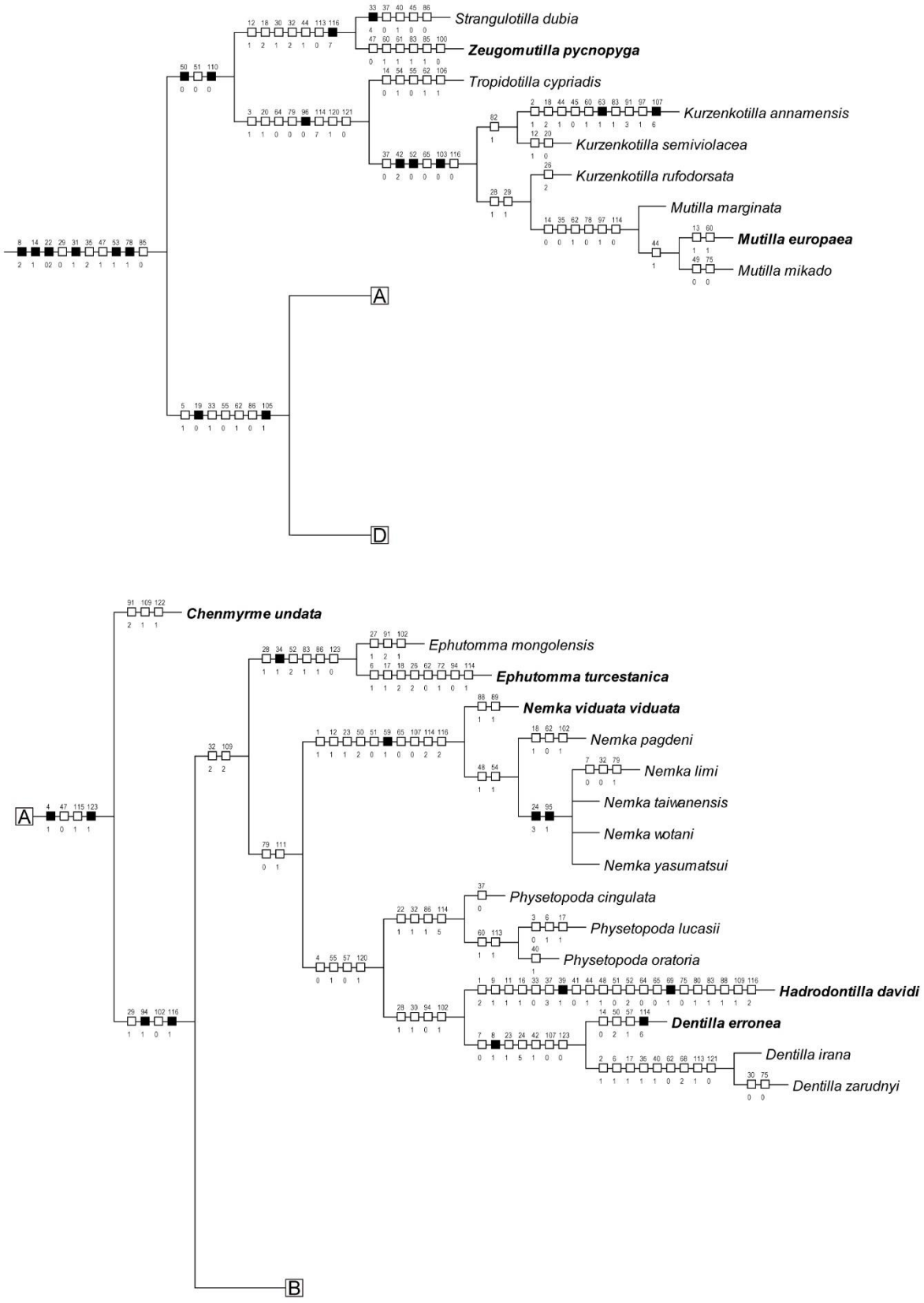

Figure 20-1. Strict consensus tree of 10 best-fitting trees under k16 (length = 818; CI = 24; RI = 81). Type species are shown in **bold**.

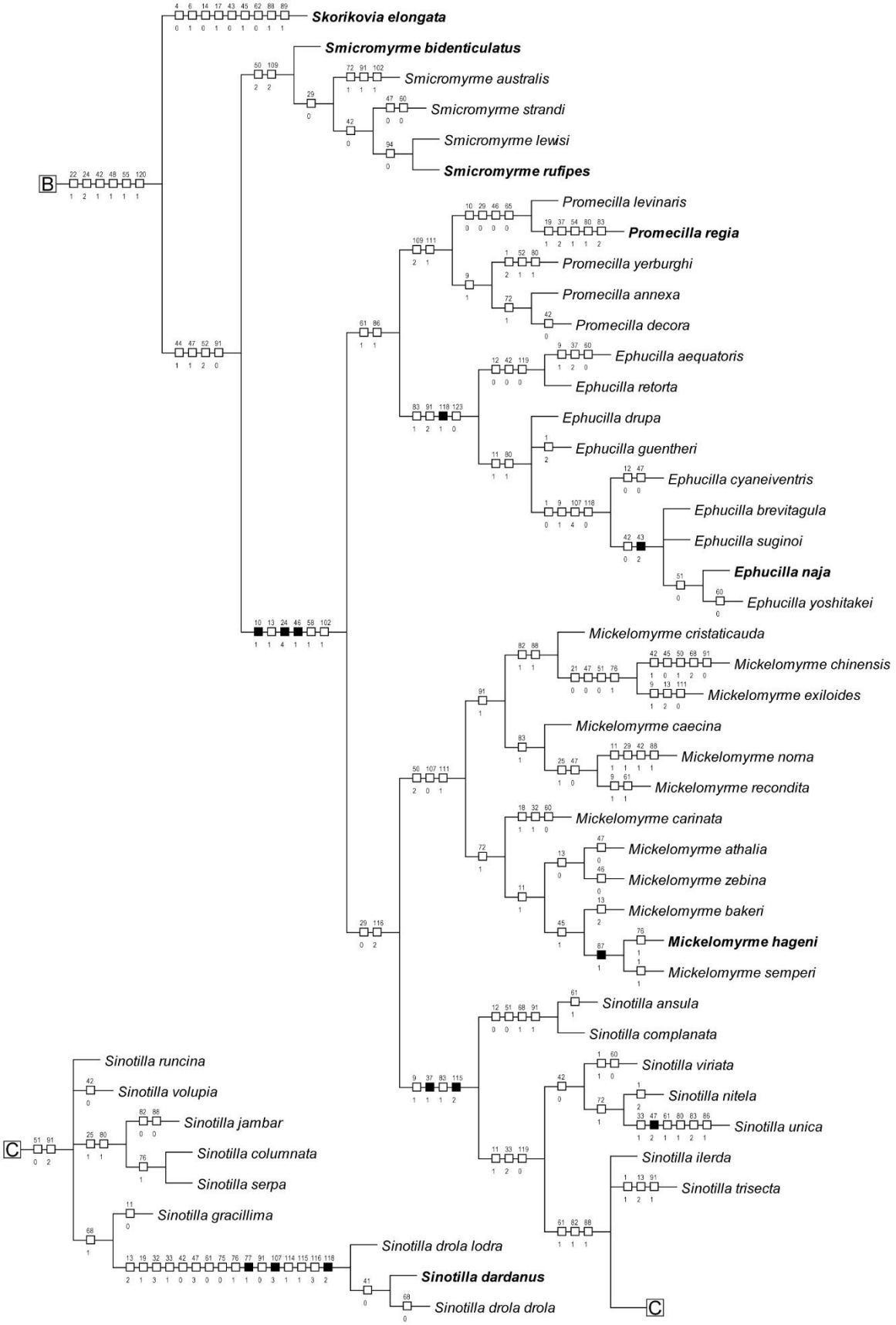

Figure 20-2. Strict consensus tree of 10 best-fitting trees under k16 (length = 818; CI = 24; RI = 81). Type species are shown in **bold**.

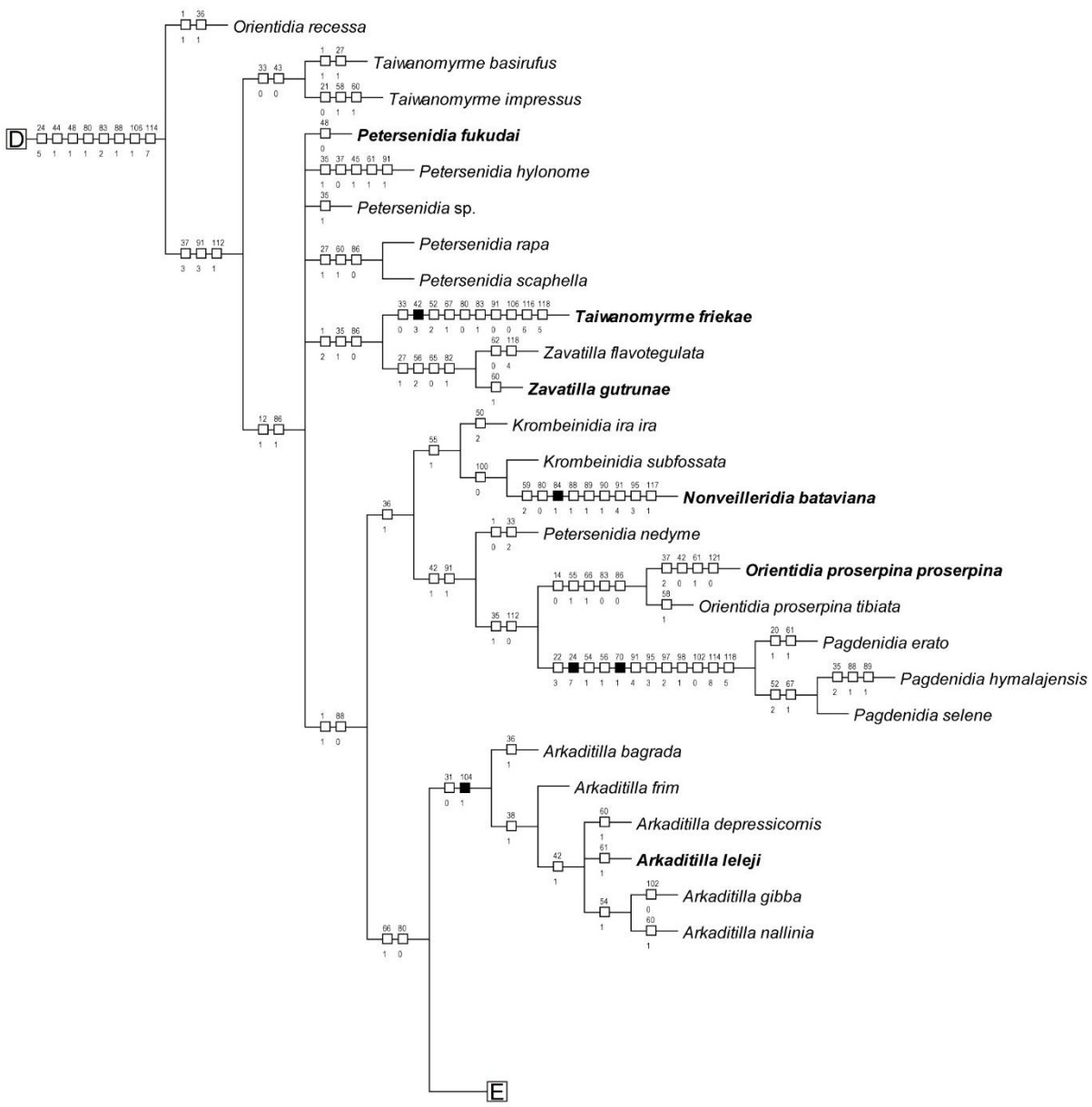

Figure 20-3. Strict consensus tree of 10 best-fitting trees under k16 (length = 818; CI = 24; RI = 81). Type species are shown in **bold**.

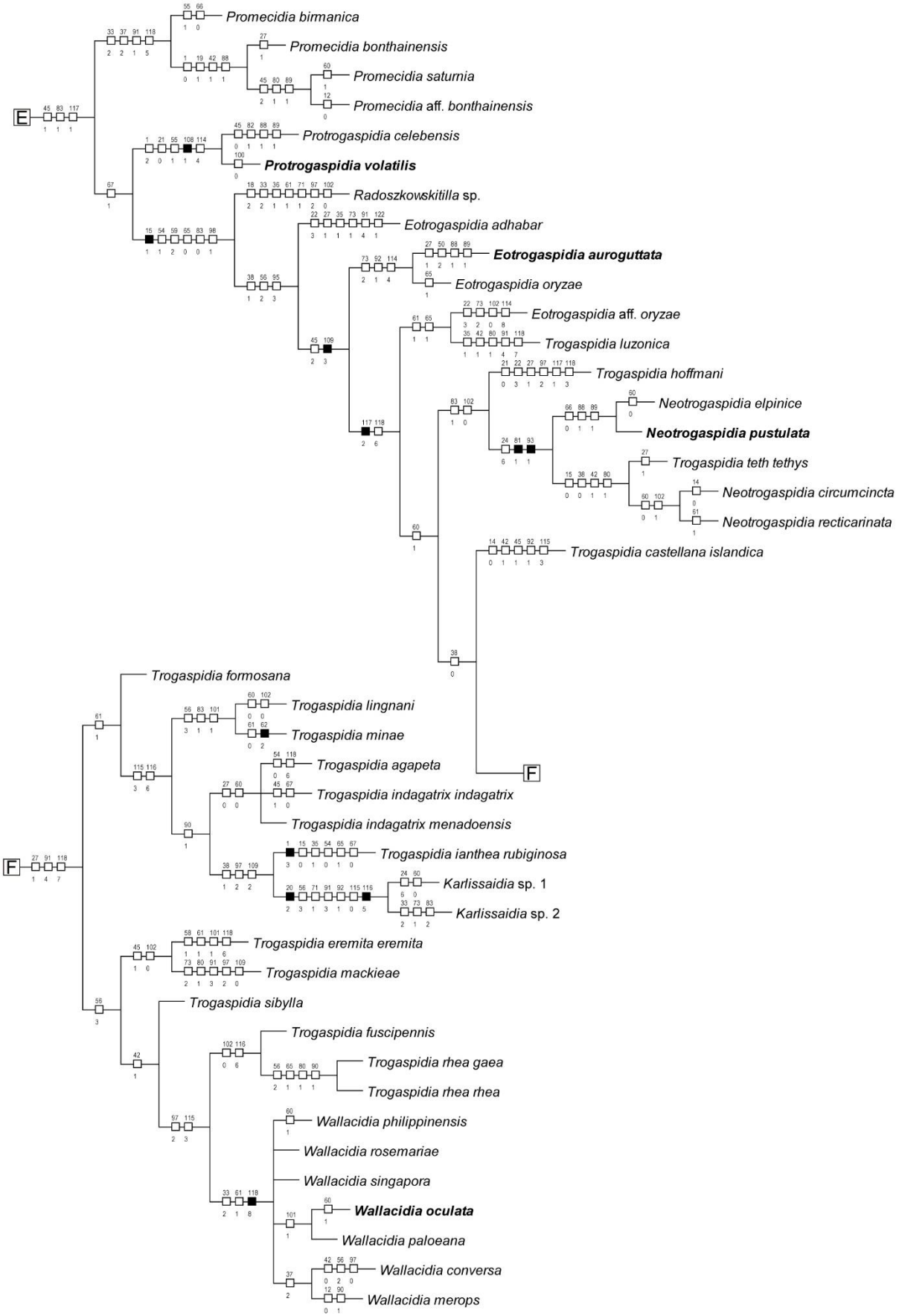

Figure 20-4. Strict consensus tree of 10 best-fitting trees under k16 (length = 818; CI = 24; RI = 81). Type species are shown in **bold**.

Figure 21-1. Strict consensus tree of nine best-fitting trees under setk (length = 822; CI = 24; RI = 81). Type species are shown in **bold**.

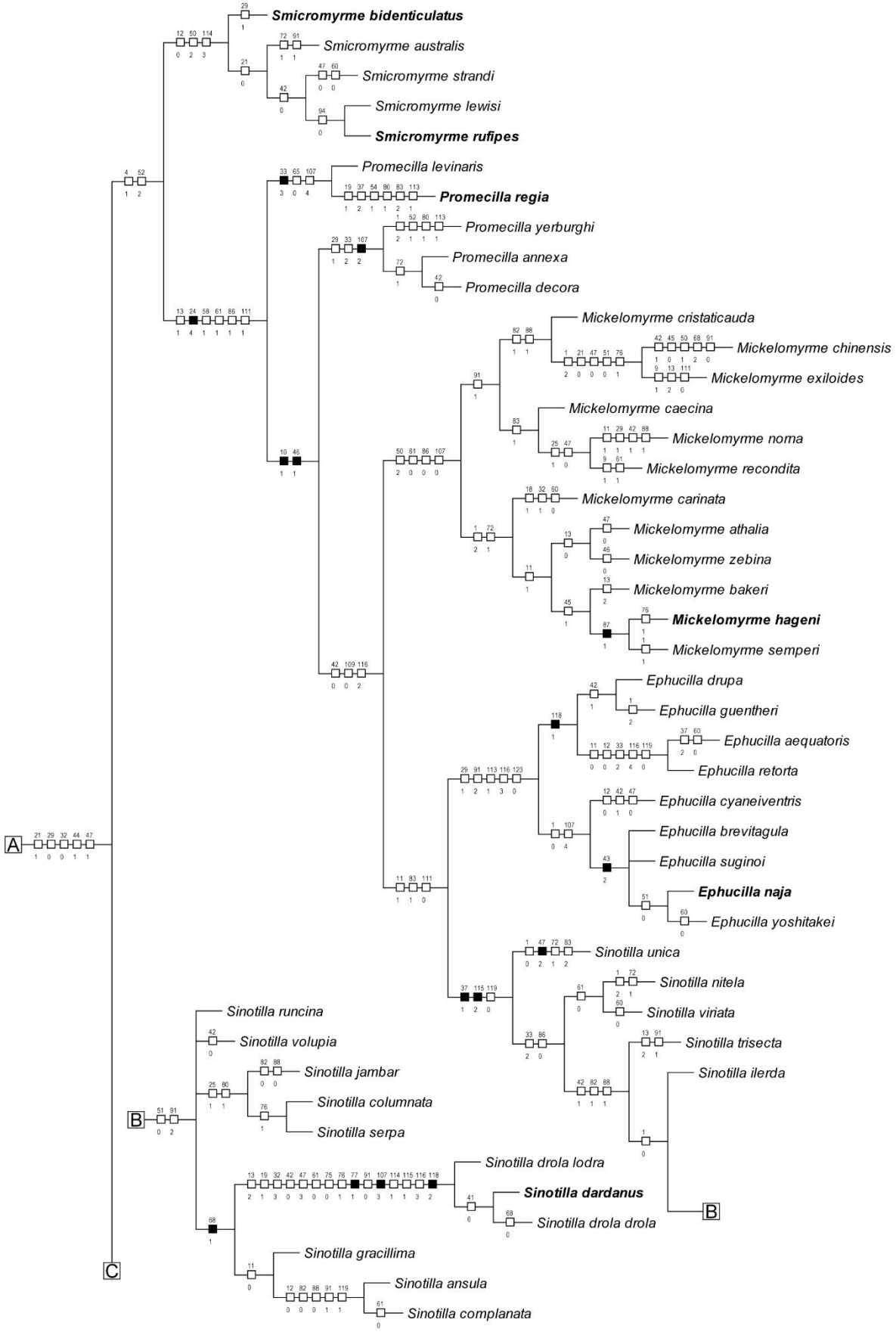

Figure 21-2. Strict consensus tree of nine best-fitting trees under setk (length = 822; CI = 24; RI = 81). Type species are shown in **bold**.

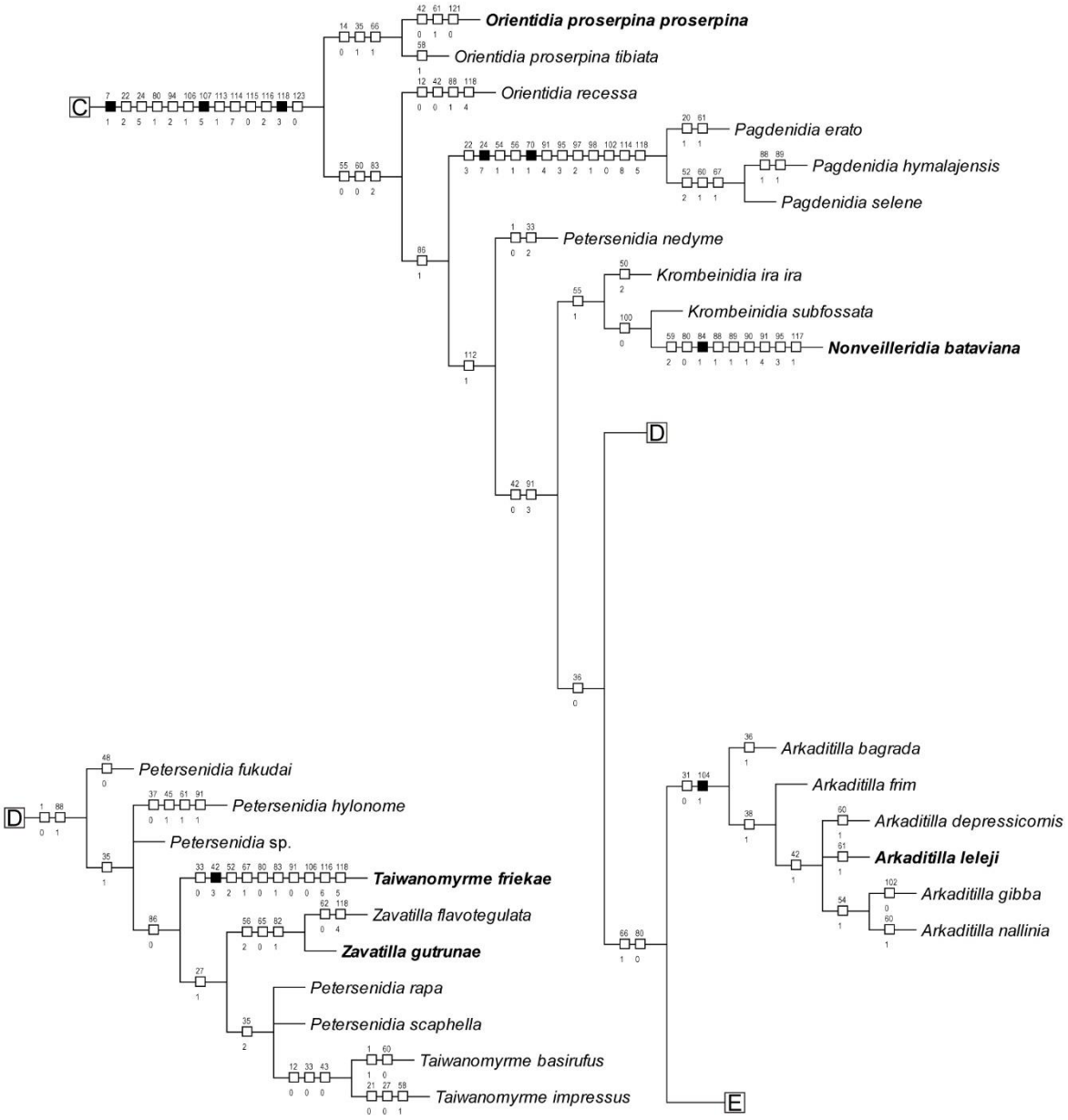

Figure 21-3. Strict consensus tree of nine best-fitting trees under setk (length = 822; CI = 24; RI = 81). Type species are shown in **bold**.

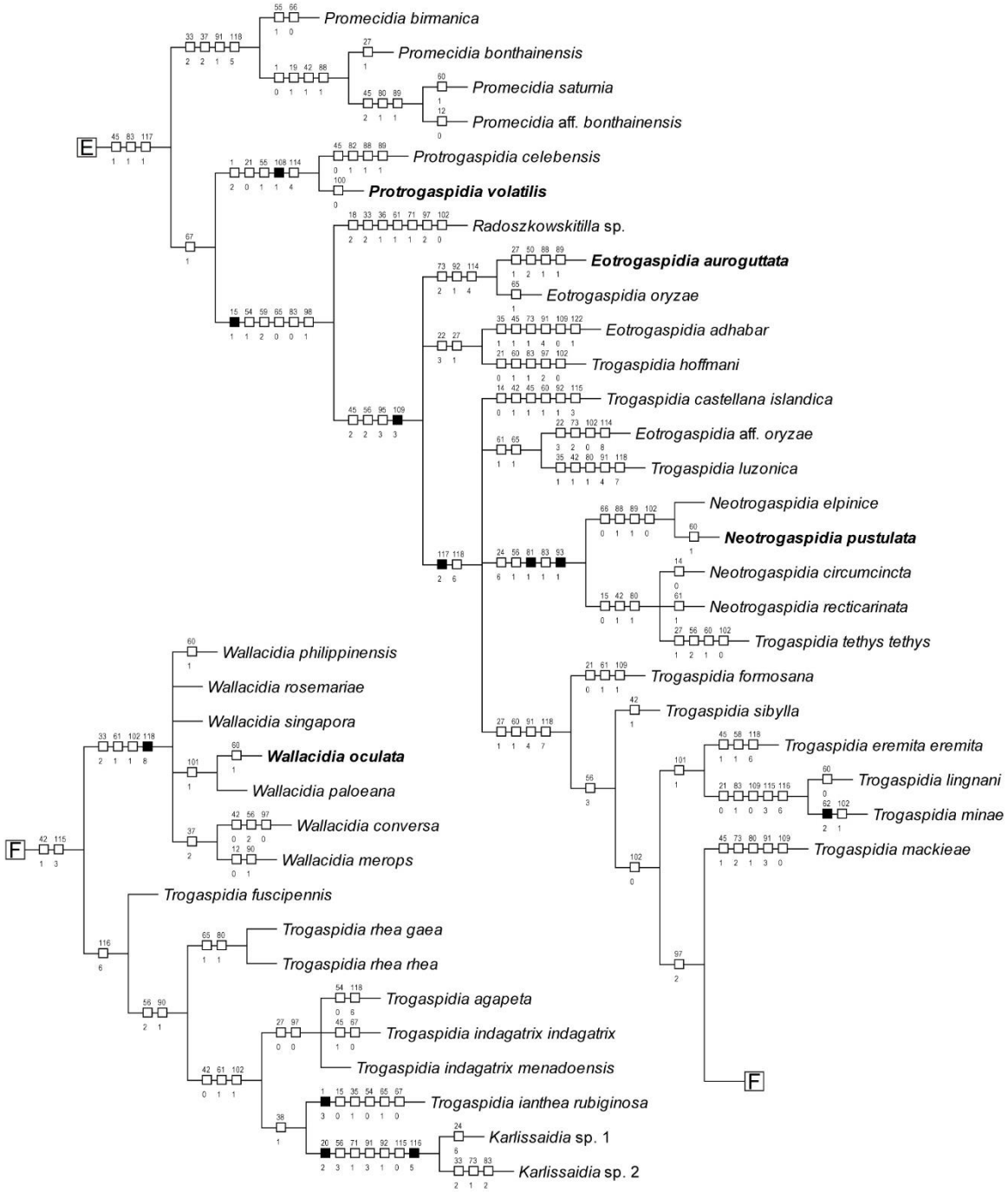

Figure 21-4. Strict consensus tree of nine best-fitting trees under setk (length = 822; CI = 24; RI = 81). Type species are shown in **bold**.

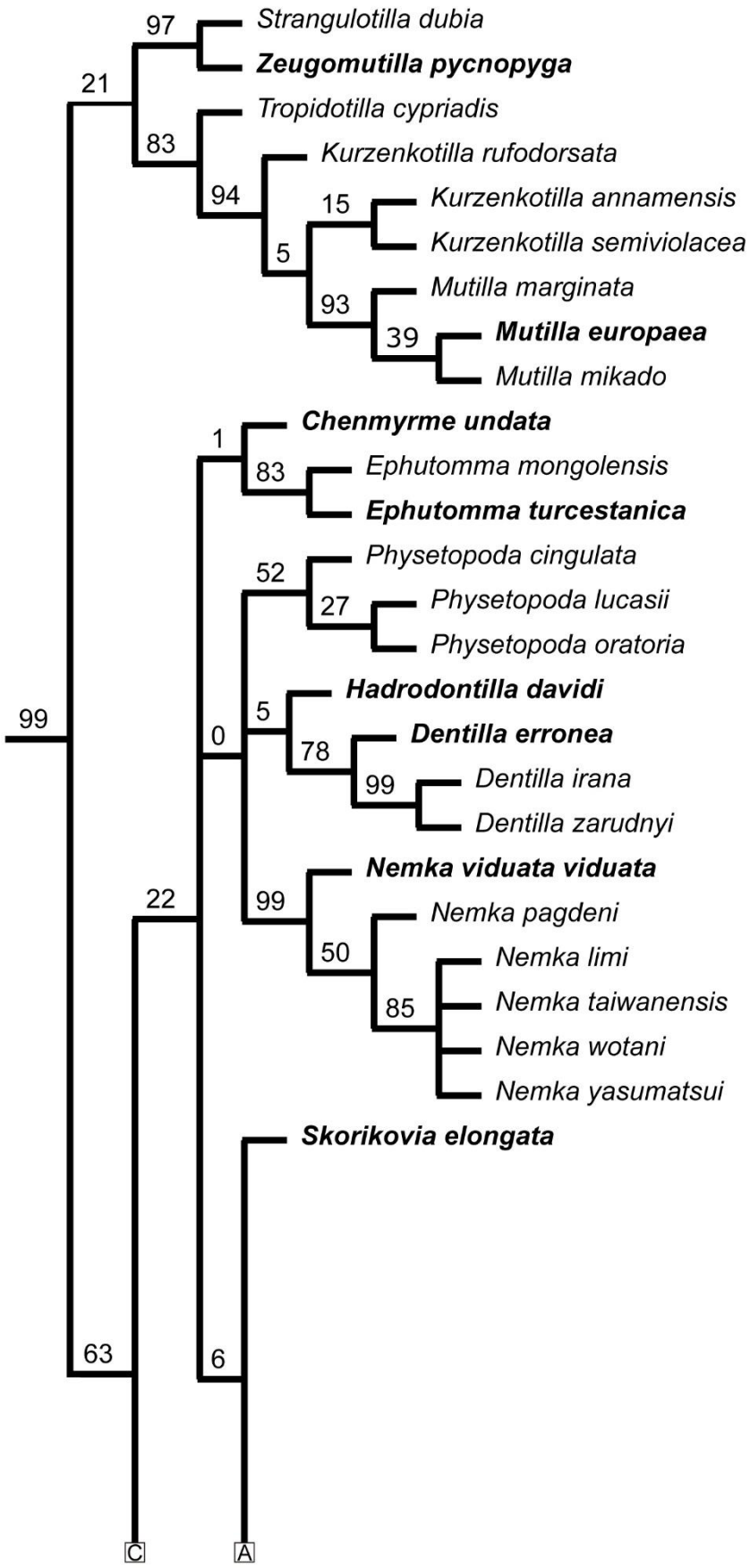

Figure 22-1. Resampling supports (GC scores) under equal weights. Type species are shown in **bold**.

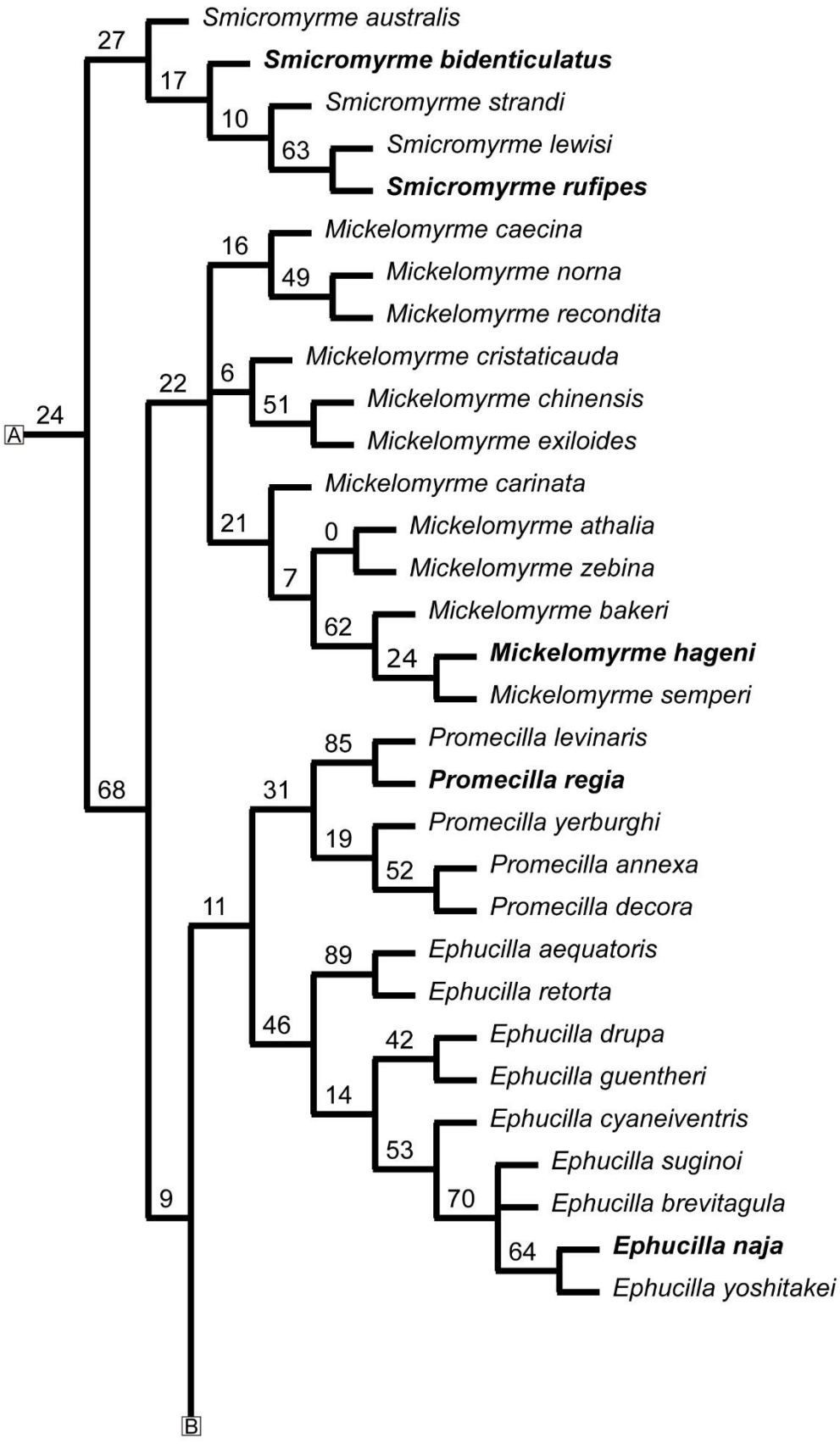

Figure 22-2. Resampling supports (GC scores) under equal weights. Type species are shown in **bold**.

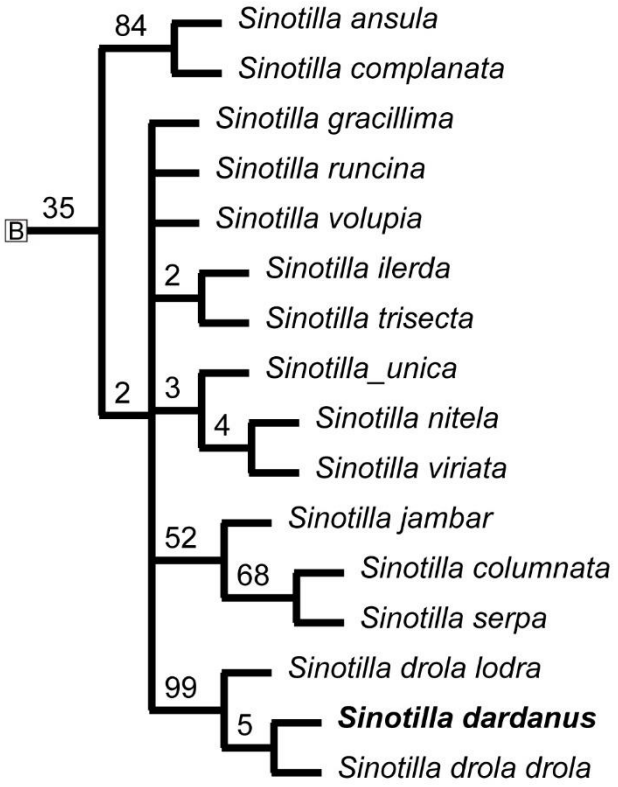

Figure 22-3. Resampling supports (GC scores) under equal weights. Type species are shown in **bold**.

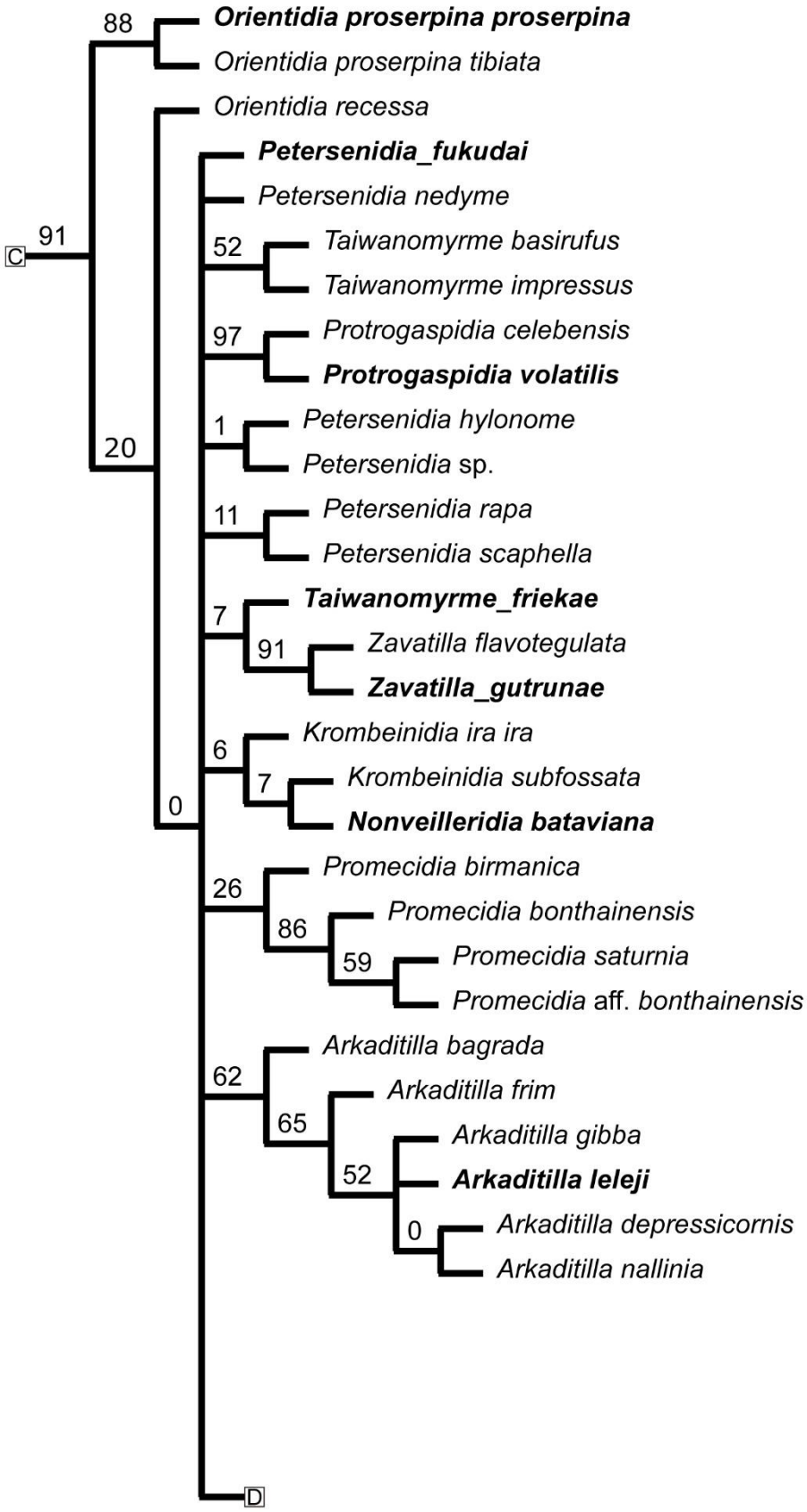

Figure 22-4. Resampling supports (GC scores) under equal weights. Type species are shown in **bold**.

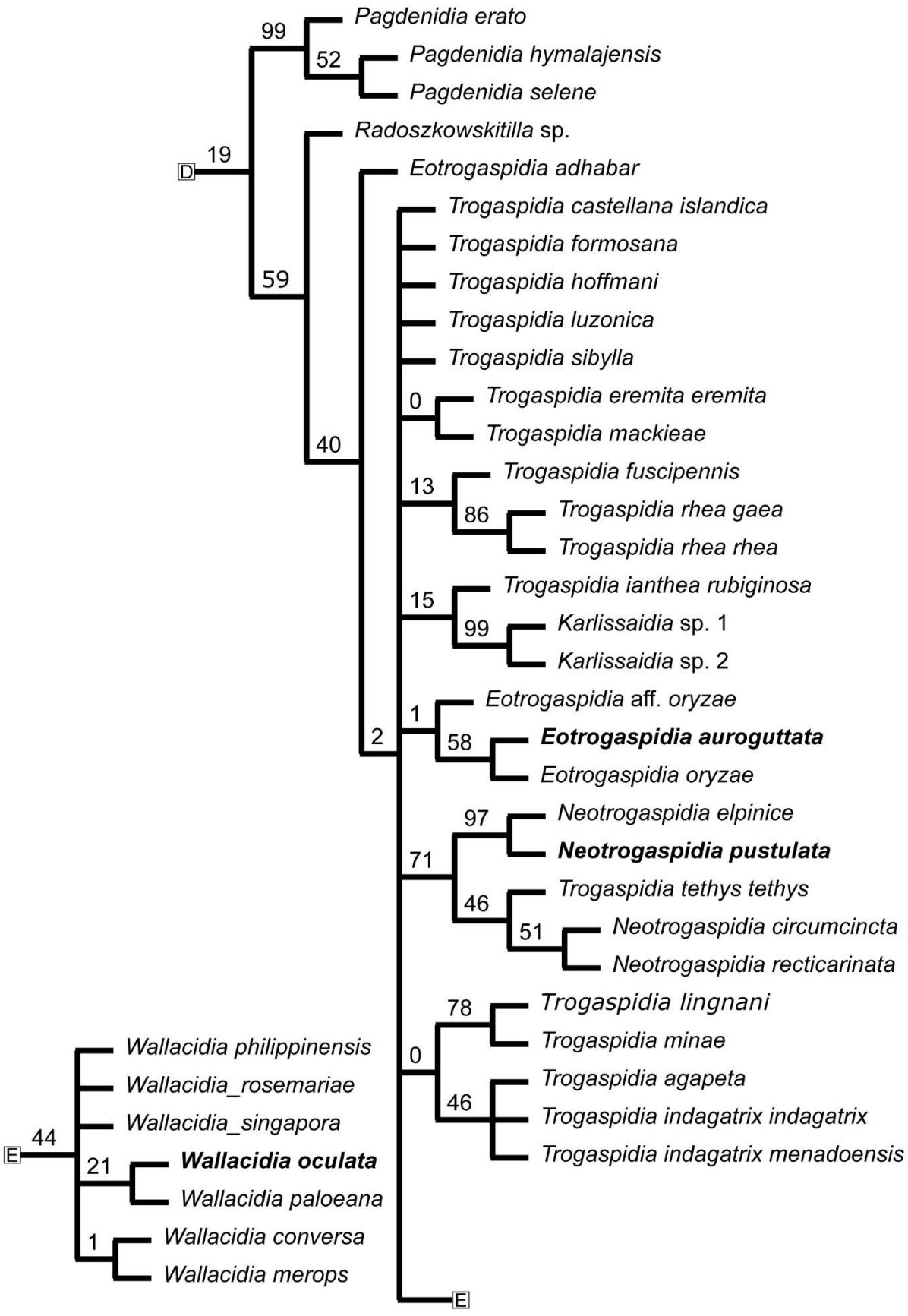

Figure 22-5. Resampling supports (GC scores) under equal weights. Type species are shown in **bold**.

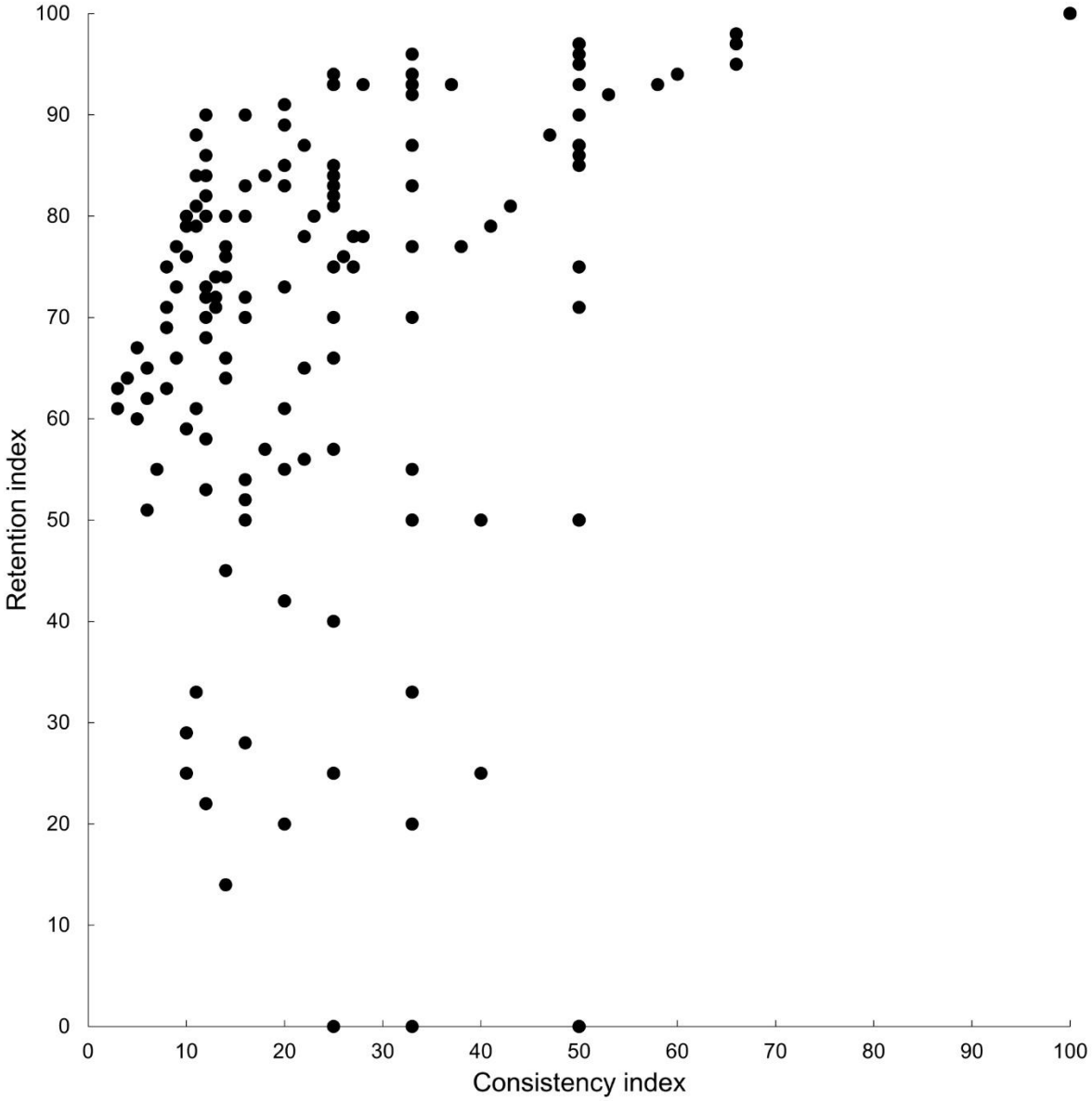

Figure 23. Distribution of consistency and retention indices for morphological characters analyzed in the present study.

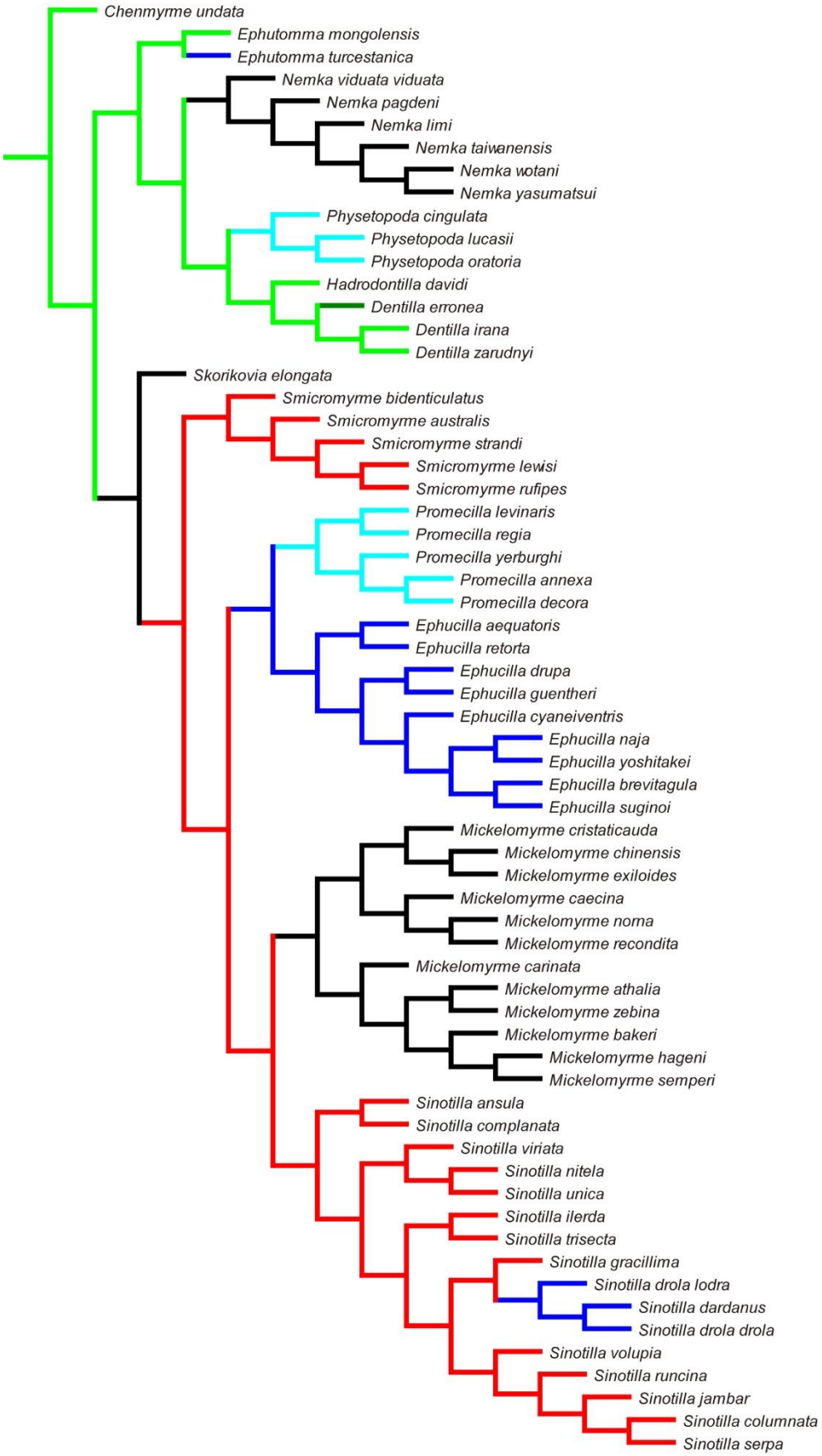

Figure 24. ACCTRAN optimization of the parossiculus shape (character 114) based on one of the best-fitting trees under k16. Light green: state 0; blue: state 1; black: state 2; red: state 3; light blue: state 5; green: state 6.

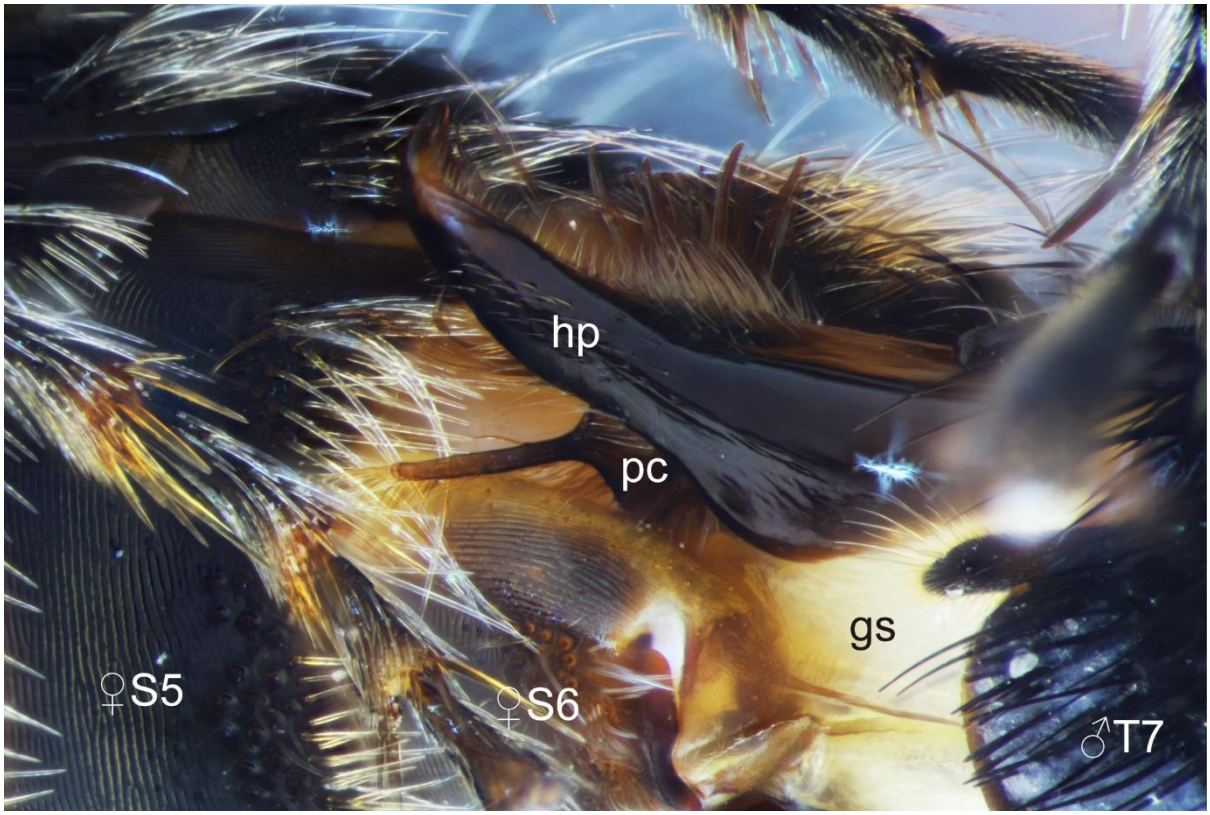

Figure 25. Male genitalia and surrounding body parts of a mating pair of *Nemka yasumatsui* (Mickel) fixed in boiling water. Abbreviations: gs = gonostipes; hp = harpe; pc = parossiculus; ♀S5 = female sternum 5; ♀S6 = female sternum 6; ♂T7 = male tergum 7.

Table 1. Additional taxa and specimens examined for phylogenetic analysis († = type species of the genus).

Taxon	Specimens examined	Locality	Identification source
Myrmillinae			
Bischoffitilla ardescens (Smith, 1873)	12♂ [ELKU, EUMJ]	**Japan:** EHIME, FUKUOKA, KAGOSHIMA, KOCHI.	Keyed using Terayama *et al*. (2016).
†*Bischoffitilla exilipunctata* (Chen, 1957)	1♂ [NSMT]	**South Korea:** GYEONGGI.	Voucher specimen (Lelej *et al*., 2001).
Bischoffitilla lamellata (Mickel, 1933)	2♂ [TUA, VNMN]	**Vietnam:** BA RIA VUNG TAU, THUA THIEN HUE.	Compared with description in Barthélémy *et al*. (2018).
Bischoffitilla murotai (Tsuneki, 1993)	11♂ [ELKU, SEHU, TPM]	**Japan:** AMAMI ISLANDS, OKINAWA ISLANDS.	Keyed using Terayama *et al*. (2016).
Bischoffitilla pungens (Smith, 1873)	9♂ [EUMJ]	**Japan:** EHIME, KOCHI.	Keyed using Terayama *et al*. (2016).
†*Myrmilla calva* (Villers, 1789)	1♂ [SEHU]	**France:** GIRONDE.	Keyed using Lelej & Schmid-Egger (2005).
Mutillinae: Mutillini			
Kurzenkotilla annamensis Lelej, 2005	2♂ [TUA]	**Thailand:** CHIANG MAI.	Voucher specimen (Lelej *et al*., 2023).
Kurzenkotilla rufodorsata (Cameron, 1897)	1♂ [NARO]	**Nepal:** BAGMATI.	Voucher specimen (Lelej *et al*., 2023).
Kurzenkotilla semiviolacea (André, 1896)	1♂ [NSMT]	**India:** UTTAR PRADESH.	Voucher specimen (Lelej *et al*., 2023).
†*Mutilla europaea* Linnaeus, 1758	6♂ [ELKU, EUMJ, SEHU]	**Austria:** TYROL. **Denmark. France:** VAR.	Identified specimens (B. Petersen, 1981).
Mutilla marginata Baer, 1848	3♂ [SEHU]	**Czech:** ÚSTECKÝ.	Keyed using Lelej & Schmid-Egger (2005).
Mutilla mikado Cameron, 1900	5♂ [EUMJ, SEHU]	**Japan:** HYÔGO, NAGANO, TOCHIGI.	Keyed using Terayama *et al*. (2016).
Tropidotilla cypriadis Invrea, 1940	1♂ [EUMJ]	**Georgia:** SHIDA KARTLI.	Keyed using Lelej (1985).
Mutillinae: Smicromyrmini			
†*Dentilla erronea* (André, 1902)	3♂ [KUM]	**Greece:** CHALKIDIKI.	Keyed using Lelej (1985) and compared with the original description.
Dentilla irana Lelej, 1985	3♂ [EUMJ]	**Iran:** HORMOZGAN. **Oman:** OHOFAR.	Keyed using Lelej (1985) and compared with the original description.
Dentilla zarudnyi Lelej, 1985	1♂ [EUMJ]	**Iran:** HORMOZGAN.	Keyed using Lelej (1985) and compared with the original description.
†*Ephutomma turcestanica* (Dalla Torre, 1897)	1♂ [NMNH]	**Turkmenistan:** LEBAP.	Voucher specimen (Lelej, 1985).
†*Nemka viduata viduata* (Pallas, 1773)	11♂ [EUMJ, KUM]	**Greece:** CHALKIDIKI. **Kazakhstan:** ALMATY.	Keyed using Lelej (1995a).
Physetopoda cingulata (Costa, 1858)	1♂ [SEHU]	**France:** GARD.	Keyed using Lelej & Schmid-Egger (2005).
Physetopoda lucasii (Smith, 1855)	1♂ [SEHU]	**France:** GARD.	Keyed using Lelej & Schmid-Egger (2005).
Promecilla regia (Smith, 1855)	11♂ [SEHU]	**Nepal:** BAGMATI.	Compared with description in Nurse (1903) and illustrations in Lelej & Williams (2023).
Promecilla yerburghi (Cameron, 1892)	1♂ [SEHU]	**India:** TAMIL NADU.	Keyed using Bingham (1897) and compared with the original description.
†*Skorikovia elongata* (Radoszkowski, 1885)	4♂ [TUA]	**Afghanistan:** PANJSHIR.	Keyed using Lelej (1985) and compared with the original description.
†*Smicromyrme rufipes* (Fabricius, 1787)	4♂ [ELKU, SEHU]	**Denmark. France:** GIRONDE. **Germany:** BERLIN, SACHSEN.	Identified specimen (B. Petersen, 1981).
Mutillinae: Trogaspidiini			
Arkaditilla bagrada (Cameron, 1902)	24♂ [FRIM, NARO]	**Malaysia:** NEGERI SEMBILAN.	Voucher specimens (Okayasu, 2021a).
Arkaditilla depressicornis (Mickel, 1935)	3♂ [EUMJ, NARO]	**Malaysia:** NEGERI SEMBILAN, PAHANG.	Voucher specimens (Okayasu, 2021a).

Arkaditilla frim Okayasu, 2021	Holotype ♂, paratype 1♂ [FRIM, NARO]	**Malaysia:** NEGERI SEMBILAN.	Primary type (Okayasu, 2021a).
Arkaditilla gibba Okayasu, 2021	Holotype ♂, paratype 1♂ [TKPM]	**Indonesia:** JAWA TIMUR.	Primary type (Okayasu, 2021a).
†*Arkaditilla leleji* Okayasu, 2021	Holotype ♂ [NARO]	**Indonesia:** KALIMANTAN TIMUR.	Primary type (Okayasu, 2021a).
Arkaditilla nallinia (Zavattari, 1914)	1♂ [TUA]	**Indonesia:** BALI.	Voucher specimen (Okayasu, 2021a).
Eotrogaspidia adhalar Okayasu *et al*, 2021	Holotype ♂ [SEHU]	**Nepal:** MADHESH.	Primary type (Okayasu *et al*., 2021a).
†*Eotrogaspidia auroguttata* (Smith, 1855)	16♂ [ELKU, EUMJ, MTC, NSMT, SEHU]	**Taiwan:** CHIAYI, NANTOU, TAICHUNG, TAINAN, TAIPEI. **Japan:** OKINAWA ISLANDS. **Laos:** HOUA PHAN.	Voucher specimens (Lelej, 1996a; Okayasu *et al*. 2021a).
Eotrogaspidia oryzae (Pagden, 1934)	2♂ [ELKU]	**Laos**: XIENG KHOUANG. **Thailand:** RAJBURI.	Identified specimens (B. Petersen, 1979).
Eotrogaspidia aff. *oryzae*	1♂ [ELKU]	**Thailand:** KHON KAEN.	
Karlissaidia sp. 1	1♂ [SEHU]	**Nepal:** MADHESH.	Voucher specimen (Okayasu, 2023c).
Karlissaidia sp. 2	2♂ [SEHU]	**Nepal:** MADHESH.	Voucher specimens (Okayasu, 2023c).
Krombeinidia ira ira (Cameron, 1902)	2♂ [EUMJ]	**Malaysia:** PAHANG.	Keyed using Mickel (1935) and compared with the original description.
Krombeinidia subfossata (Chen, 1957)	2♂ [NSMT, TARI]	**China:** FUJIAN. **Thailand:** TRANG.	Primary type (Chen, 1957).
Neotrogaspidia circumcincta (André, 1896)	3♂ [TARI]	**China:** FUJIAN. **Taiwan:** TAIPEI.	Voucher specimens (Okayasu, 2023a).
Neotrogaspidia elpinice (Mickel, 1933)	88♂ [NSMT, TARI]	**China:** ANHUI, FUJIAN, JIANGSU, JIANGXI, SHANGHAI, SICHUAN, ZHEJIANG. **Taiwan:** NEW TAIPEI, TAIPEI.	Voucher specimens (Okayasu, 2023a).
†*Neotrogaspidia pustulata* (Smith, 1873)	150♂ [ELKU, EUMJ, HMNH, NSMT, OMNH, SEHU, TMUZ, TARI, TUA]	**Japan:** AICHI, AMAMI ISLANDS, CHIBA, EHIME, FUKUI, FUKUOKA, HIROSHIMA, HYOGO, KAGOSHIMA, KANAGAWA, KOCHI, KUMAMOTO, MIYAZAKI, NARA, OGASAWARA ISLANDS, OITA, SAITAMA, SHIMANE, SHIZUOKA, TOKUSHIMA, TOKYO, TSUSHIMA, WAKAYAMA, YAEYAMA ISLANDS. **South Korea:** GYEONGGI, SEOUL.	Voucher specimens (Okayasu, 2023a).
Neotrogaspidia recticarinata (Chen, 1957)	Holotype ♂, paratype 1♂, 1♂ [NSMT, TARI]	**China:** FUJIAN. **Taiwan:** TAIPEI.	Primary type (Chen, 1957).
†*Nonveilleridia bataviana* (André, 1909)	2♂ [NARO, VNMN]	**Indonesia:** KALIMANTAN SELATAN. **Vietnam:** THUA THIEN HUE.	Keyed using Mickel (1935) and compared with the original description.
†*Orientidia proserpina* (Smith, 1857)	1♂ [NARO]	**Indonesia:** KALIMANTAN TIMUR.	Keyed using Mickel (1935) and compared with the description in Mickel (1935) (as *T. fortuita nebulosa* Mickel).
Orientidia tibiata (Mickel, 1934)	3♂ [EUMJ, TARI, TUA]	**Philippines:** LUZON, MINDANAO, NEGROS.	Identified specimens (B. Petersen, 1981, 1993).
Orientidia recessa (Chen, 1957)	Holotype ♂, paratypes 15♂ [TARI]	**China:** JIANGXI.	Primary type (Chen. 1957).
Pagdenidia erato (Mickel, 1935)	1♂ [FRIM]	**Malaysia:** NEGERI SEMBILAN.	Keyed using Pagden (1949) and compared with the original description.
Pagdenidia hymalajensis (Radoszkowski, 1885)	1♂ [TUA]	**Thailand:** CHIANG MAI.	Keyed using Pagden (1949) and compared with the original

			description.
Pagdenidia selene (Pagden, 1949)	2♂ [TUA]	**Malaysia:** SELANGOR.	Keyed using Pagden (1949) and compared with the original description.
†*Petersenidia fukudai* (Tsuneki, 1972)	Holotype ♂, holotype of *Smicromyrme fukudai tokunosimana* Tsuneki ♂, 145♂ [ELKU, EUMJ, IEBR, MNHAH, NSMT, SEHU, TARI, TUA]	**Japan:** AMAMI ISLANDS, EHIME, FUKUOKA, KAGOSHIMA, KÔCHI, ÔITA, ÔSUMI ISLANDS.	Primary type (Tsuneki, 1972b).
Petersenidia hylonome (Mickel, 1935)	29♂ [FRIM, NARO]	**Indonesia:** KALIMANTAN TIMUR. **Malaysia:** NEGERI SEMBILAN.	Keyed using Mickel (1935) and compared with the original description.
Petersenidia nedyme (Mickel, 1935)	6♂ [FRIM, NARO]	**Malaysia:** NEGERI SEMBILAN.	Keyed using Mickel (1935) and compared with the original description.
Petersenidia rapa (Zavattari, 1913)	17♂ [NSMT, SEHU, TARI]	**China:** ZHEJIANG. **Taiwan:** CHIAYI, NANTOU, NEW TAIPEI, PINGTUNG, TAIPEI, TAOYUAN, YILAN.	Voucher specimens (Chen, 1957; Lelej, 1996a).
Petersenidia scaphella (Chen, 1957)	Holotype ♂, paratypes 4♂, 14♂ [TARI, VNMN]	**China:** FUJIAN, JIANGXI, ZHEJIANG. **Vietnam:** LAO CAI.	Primary type (Chen, 1957).
Petersenidia sp.	9♂ [ELKU, EUMJ, NARO, RUMF, TKPM]	**Japan:** OKINAWA ISLANDS.	
Promecidia birmanica (Dalla Torre, 1897)	34♂ [FRIM, IEBR, NARO, NSMT]	**Malaysia:** NEGERI SEMBILAN, PENANG.	Keyed using Lelej *et al*. (2016).
Promecidia bonthainensis (André, 1896)	12♂ [EUMJ, MNHAH, TKPM]	**Indonesia:** GORONTALO, SULAWESI SELATAN.	Keyed using Lelej *et al*. (2016).
Promecidia saturnia (Mickel, 1935)	29♂ [FRIM, NARO, TUA]	**Malaysia:** NEGERI SEMBILAN, SARAWAK, SELANGOR.	Identified specimen (B. Petersen).
Promecidia aff. *bonthainensis*	1♂ [EUMJ]	**Indonesia:** GORONTALO.	
Protrogaspidia celebensis (André, 1905)	2♂ [EUMJ]	**Indonesia:** GORONTALO.	Keyed using Mickel (1935) and compared with the original description.
Protrogaspidia volatilis (Smith, 1858)	2♂ [EUMJ, NSMT]	**Indonesia:** GORONTALO, SULAWESI SELATAN.	Voucher specimen (Lelej, 1996b).
Radoszkowskitilla sp.	1♂ [SEHU]	**Nepal:** MADHESH.	Voucher specimen (Okayasu, 2023c).
Taiwanomyrme basirufus (Chen, 1957)	Holotype ♂, paratypes 3♂ [TARI]	**China:** FUJIAN, JIANGXI, ZHEJIANG.	Primary type (Chen, 1957).
†*Taiwanomyrme friekae* (Zavattari, 1913)	Holotype of *Smicromyrme taiwanus* Tsuneki ♂, 7♂ [ELKU, MNHAH, MTC, NSMT, SEHU]	**Taiwan**: NANTOU, TAICHUNG, TAIPEI, PINGTUNG.	Voucher specimen (Lelej, 1996a; Tsuneki, 1993a).
Taiwanomyrme impressus (Chen, 1957)	Holotype ♂, paratypes 2♂ [TARI]	**China:** JIANGXI.	Primary type (Chen, 1957).
Trogaspidia agapeta (Cameron, 1902)	4♂ [TUA]	**Indonesia:** SULAWESI TENGAH. **Malaysia:** PAHANG. **Philippines:** BOHOL.	Keyed using Mickel (1935) and compared with the original description.
Trogaspidia castellana islandica (Mickel, 1934)	5♂ [ELKU, TARI]	**Philippines:** BASILAN.	Identified specimen (B. Petersen, 1974, 1989).
Trogaspidia eremita eremita (Mickel, 1934)	1♂ [TUA]	**Philippines:** LUZON.	Identified specimen (B. Petersen, 1980).
Trogaspidia formosana (Matsumura, 1911)	23♂ [EUMJ, NSMT, TARI]	**Taiwan:** NANTOU, PINGTUNG, TAICHUNG, TAINAN, TAIPEI, TAITUNG.	Voucher specimens (Chen, 1957; Lelej, 1996a).
Trogaspidia fuscipennis	16♂ [ELKU,	**China:** ZHEJIANG. **Taiwan:**	Voucher specimens (Chen, 1957).

(Fabricius, 1804)	EUMJ, NSMT, TARI]	CHIAYI, NANTOU, TAINAN, TAIPEI, TAITUNG, PINGTUNG. **Laos:** VIENTIANE.	
Trogaspidia hoffmani (Mickel, 1933)	3♂ [TARI]	**China:** FUJIAN.	Voucher specimens (Chen, 1957).
Trogaspidia ianthea rubiginosa (André, 1896)	1♂ [EUMJ]	**Indonesia:** MALUKU.	Keyed using Mickel (1935) and compared with the original description.
Trogaspidia indagatrix indagatrix (Mickel, 1935)	2♂ [NARO]	**Indonesia:** MALUKU UTARA.	Keyed using Mickel (1935) and compared with the original description.
Trogaspidia indagatrix menadoensis (Mickel, 1935)	2♂ [EUMJ]	**Indonesia:** MALUKU.	Keyed using Mickel (1935) and compared with the original description.
Trogaspidia lingnani (Mickel, 1933)	8♂ [EUMJ, TARI]	**China:** FUJIAN, ZHEJIANG. **Laos:** HOUA PHAN.	Voucher specimens (Chen, 1957).
Trogaspidia luzonica (Radoszkowski, 1885)	2♂ [TARI]	**Philippines:** LUZON.	Identified specimens (B. Petersen, 1989).
Trogaspidia mackieae (Cockerell, 1928)	2♂ [TUA]	**Thailand:** CHIANG MAI.	Voucher specimens (Okayasu *et al*. 2021a).
Trogaspidia minae (Zavattari, 1913)	1♂ [TARI]	**Taiwan:** HSINCHU.	Voucher specimen (Chen, 1957).
Trogaspidia rhea gaea Chen, 1957	Holotype ♂, paratypes 7♂, 3♂ [EUMJ, TARI, TUA]	**China:** ANHUI, FUJIAN. **Laos:** HOUA PHAN. **Vietnam:** NINH BINH.	Primary type (Chen, 1957).
Trogaspidia rhea rhea (Mickel, 1933)	18♂ [ELKU, SEHU, TARI, TUA]	**Taiwan:** CHANGHUA, CHIAYI, NANTOU, TAINAN, TAICHUNG, TAITUNG, PINGTUNG, YILAN.	Voucher specimens (Chen, 1957).
Trogaspidia sibylla (Smith, 1857)	1♂ [TUA]	**Malaysia:** SARAWAK.	Identified specimen (B. Petersen, 1981).
Trogaspidia tethys tethys (Mickel, 1934)	1♂ [TARI]	**Philippines:** LUZON.	Identified specimen (B. Petersen, 1989).
Wallacidia conversa (Chen, 1957)	2♂ [NSMT]	**Taiwan:** TAIPEI.	Voucher specimen (Lelej, 1996a).
Wallacidia merops (Smith, 1860)	1♂ [NARO]	**Indonesia:** MALUKU UTARA.	Keyed using O'Toole (1975) and compared with the description in O'Toole (1975).
†*Wallacidia oculata* (Fabricius, 1804)	9♂ [EUMJ, TARI]	**China:** ZHEJIANG. **Taiwan:** KAOHSIUNG, PINGTUNG, TAINAN, TAIPEI. **Vietnam:** DONG NAI.	Voucher specimen (Chen, 1957; Lelej, 1996a). Identified specimens (C.O. O'Toole, 1976).
Wallacidia paloeana (Pagden, 1949)	1♂ [EUMJ]	**Indonesia:** SULAWESI TENGAH.	Keyed using O'Toole (1975) and compared with the original description.
Wallacidia philippinensis (Smith, 1855)	2♂ [NSMT, TUA]	**Philippines:** LUZON, PALAWAN.	Identified specimen (B. Petersen, 1976; A. Lelej, 1994).
Wallacidia rosemariae (O'Toole, 1975)	1♂ [EUMJ]	**Indonesia:** NUSA TENGGARA BARAT.	Keyed using O'Toole (1975) and compared with the original description.
Wallacidia singapora (Mickel, 1935)	4♂ [EUMJ, NARO, FRIM]	**Indonesia:** SUMATRA SELATAN. **Malaysia:** NEGERI SEMBILAN, SARAWAK.	Keyed using O'Toole (1975) and compared with the original description.
Zavatilla flavotegulata (Chen, 1957)	Holotype ♂, paratypes 2♂ [TARI]	**China:** JIANGXI.	Primary type (Chen, 1957).
†*Zavatilla gutrunae* (Zavattari, 1913)	18♂ [MTC, NSMT, TARI]	**Taiwan:** HSINCHU, NANTOU, TAITUNG, TAOYUAN.	Keyed using Zhou *et al*. (2018b) and compared with the original description.
Mutillinae: Zeugomutillini			
Strangulotilla dubia Okayasu, 2023	Holotype ♂ [SEHU]	**Nepal:** BAGMATI.	Primary type (Okayasu, 2023c).
†*Zeugomutilla pycnopyga* Chen, 1957	1♂ [ELKU]	**Laos:** LUANG PRABANG.	Keyed using Lelej *et al*. (2017) and compared with the original description.

Table 2. Morphological data matrix.

Chenmyrme undata 00?1102200000101002??000-0000011102?0???101?2000111110000000?01?1100000000110011000000000002002010001011010101100101200121111
Dentilla erronea 0010000100000000000000015-0011111210202000111010001211101010000101100000000011001000000000010000100010111010002110061100111100
Dentilla irana 0110010100001100100000015-0011112101-2001110000001111101000000001100200000110010000000000001000010001011010002110101100110000
Dentilla zarudnyi 0110010100001100100000015-0011012101-2001110000001111101000000001100200000100010000000000001000010001011010002110101100110000
Ephucilla aequatoris 1001102211001101000011040000101020202000101121111112101011001101100000000011001100010010000200101000101101010010011140101100
Ephucilla brevitagula 0001102211111101000011040000101010200000102121111112101011011011000000001100111001001000020010100010110104001001113001100
Ephucilla cyaneiventris 0001102211101101000011040000101010200000111121011112101011011011000000001100111001001000020010100010110104001001113001100
Ephucilla drupa 1001102201111101000011040000101010200000111121111112101011011011000000001100111001001000020010100010110104001001113011100
Ephucilla guentheri 2001102201111101000011040000101010200000111121111112101011011011000000001100111001001000020010100010110101001001113011100
Ephucilla naja 0001102211111101000011040000101010200000102121111102101011011011000000001100111001000002001010001011010040010011130011100
Ephucilla retorta 1001102201001101000011040000101020200000101121111112101011011011000000001100110010010000200101000101101010011140101100
Ephucilla suginoi 0001102211111101000011040000101010200000102121111112101011011011000000001100111001001000020010100010110104001001113001100
Ephucilla yoshitakei 0001102211111101000011040000101010200000102121111102101011001101100000000011001100100100002001010001011010040010011130011100
Ephutomma mongolensis 0011002200001100000000000-0111012112020??????020001112100010010110000000011001100100100002001010001011010102100101100120012100
Ephutomma turcestanica 0001112200001101120000000-2011012112020011000200011121000100100011000000101100110001001000010000100010010102100111100120012100
Hadrodontilla davidi 2010002210101101000000000-00111120-2030100001200111021010000001000000010000000010100100001000000010001011010111000120011101
Mickelomyrme athalia 2001102201110101000010400000010102000001111210112101011010111000000011001100000000000[0 1]0010100010110100001100212011101
Mickelomyrme bakeri 2001102201112101000011040000001010200000111111111212101011010111000000101100110000000000000010100010110100001100212011101
Mickelomyrme caecina 1001102201010101000011040000001010200000101121111212101011010110000000011001100100000001100110000100000010100010110100001100[0 1]2120011101
Mickelomyrme carinata 2001102201011010100010400000011102000001012111121210101100010110000001011001100000000000000010100010110100001100212011101
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Smicromyrme bidenticulatus 0001102200000101000001102-0001010102000001112011212101010010101100000000011001100000000000000010100010010102100031100 11101
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Bischoffitilla murotai 0010000000000001001001 00-20010000-0-20011010203-1111000010000001100000000010001000011000020000100000110000021001000000100
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Kurzenkotilla rufodorsata 0010000200000101001112 00-20110100-2000001210101010001010000000000000000001010000000100001000000001010000000001700001000
Kurzenkotilla semiviolacea 0010000200010101001200-00000100-2000001210201010001010000000000000000001010001000101001000000001010000000001700001000
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Mutilla mikado [0 2]0100002000000010011120 0-00110100-0-00001211201000001010000001000000000001000000000101003000001001010000000001000000100
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Arkaditilla depressicornis 1000101200010101000012 05-0000000102031001111201111111000100101011100000001100110002001000030020100010111115001 00170203--100
Arkaditilla frim 1000101200010101000012 05-0000000102031001101120111111100010000101110000000011001100020010000300201000101111150010 0170203--100
Arkaditilla gibba 1000101200010101000012 05-0000000102031001111201111111100100001011100000001100110002001000030020100010111115001 00170203--100
Arkaditilla leleji 1000101200010101000012 05-0000000102031001111201111111000100011011100000001100110002001000030020100010111115001 00170203--100
Arkaditilla nallinia 1000101200010101000012 05-0000000102031001111201111111001001010111000000011001100020010000300201000101111150010 0170213--100
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Eotrogaspidia auroguttata 1000101200010111000012 05-0100010102031001012011121111021020010101100000021100110000001011031023101010110115031 01140213--100
Eotrogaspidia oryzae 1000101200010111000012 05-0000010102031001012011111111021020010111100000211001100000010000310231010101101150310 1140213--100
Eotrogaspidia aff. oryzae 1000101200010111000013 05-0000010102031001012011111111021020110111100000211001100000010000300231010100101150310 1180226--100
Karlissaidia sp. 1 1000101200010111000212 06-0100010102031001012011111111031020110101100010011001100000010001310231210101101150210 1170527--100
Karlissaidia sp. 2 1000101200010111000212 05-0100010202031001012011111111031021110101100010011001100000010001310231210101101150210 1170527--100
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Krombeinidia subfossata 1000101200010101000012 05-0000010102130001012011111110101000010110000000011001100200010000300201000001101150010 1170203--100
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Neotrogaspidia recticarinata 1000101200010101000012 06-0000010102030001112011111111011020110101100000011001111010010000303231010101101150310 1170226--100
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Orientidia proserpina tibiata 1000101200010001000012 05-0000010101-3000111120111111110101101010111000000011001110000000000100201000101101150010 0170203--100

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Pagdenidia hymalajensis 100010120001010100001307-0000010102130001111201111121101100101011010010001100111002001011040023121010010115001001802O5--100
Pagdenidia selene 10001012000101010000130 7-0000010101-3000111120111112110100101011010010001100111002001000040023121010010115001001802O5--100
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Petersenidia hylonome 000010120001010100012O5-0000010101-0000101111011111100010001101100000000110011100200101001002010001011011500101702O3--100
Petersenidia nedyme 0000101200010101000012O5-0000010202130001111201111111000100001011000000001100111002000100030020100010110115001017020 3--100
Petersenidia rapa 0000101200010101000012O5-0100010102030001011201111111000100101011000000001100111002000010030020100010110115001017020 3--100
Petersenidia scaphella 0000101200010101000012O5-0100010102030001011201111111000100101011000000001100111002000010030020100010110115001017020 3--100
Petersenidia sp. 0000101200010101000012O5-0000010101-3000101120111111100010000101100000000110011100200101003002010001011011500101702O3--100
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Promecidia bonthainensis 0000101200010101001012O5-0100010202020001111011111111000100001011100000000110011000100100001002010001011011500100702 5--100
Promecidia saturnia 0000101200010101001012O5-0000010202020001111201111111000100101011100000000110011100100101100201000101101150010170215--100
Promecidia aff. bonthainensis 0000101200000101001012O5-0000010202020001111201111111000100001011100000000110011100100101100201000101101150010070215--100
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Protrogaspidia volatilis 2000101200010101000002O5-0000010102030001011011111111010100001011100000011001100010010000300201000001101151010014O213--100
Radoszkowskitilla sp. 1000101200010111020012O5-0000010202130001011101111111001020110101100010011001100000010000300201210100101150010017O213--100
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Taiwanomyrme impressus 0000101200000101000002O5-00000100-2030001001201111111000110101011000000001100111002000010030020100010110115001017020 3--100
Trogaspidia agapeta 1000101200010111000012O5-0000010102030001012011111110021020110101100000011001100000010001400231010101101150010173626--100
Trogaspidia castellana islandica 1000101200010011000012O5-0000010102030001111101111111102102101010110000001100110000001000031023101010110115031017322 6--100
Trogaspidia eremita eremita 1000101200010111000012O5-0100010102030001011011111111031121110101100000011001100000010000400231010110101150310101722 6--100
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Wallacidia paloeana 1000101200010111000012O5-0100010202030001111201111111031020110101100000001100110000001000040023121011110115031017322 8--100
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Wallacidia rosemariae 1000101200010111000012O5-0100010202030001111201111111031020110101100000001100110000001000040023121010110115031017322 8--100
Wallacidia singapora 1000101200010111000012O5-0100010202030001111201111111031020110101100000001100110000001000040023121010110115031017322 8--100
Zavatilla flavotegulata 2000101200010101000012O5-0100010101-3000101120111111100210000001000000000110011101200001003002010001011011500101702O4--100
Zavatilla gutrunae 2000101200010101000012O5-0100010101-3000101120111111100210010101000000000110011101200001003002010001011011500101702O3--100
Strangulotilla dubia 2000000200010101021010O1-0000112402000011011001010011010000000011000000001100110000000000010020100010110000000000070000100
Zeugomutilla pycnopyga 1000000200010101021010O1-00001120-2020001011200010011010000011001100000000011001100010110000100201000001100000000000070000100

Table 3. Settings and results of phylogenetic analyses.

Settings	*k* value	Length	Number of trees	CI	RI	Source
Equal weights	-	813	60	24	81	-
k0 (distref = 50)	3.085	854	440	23	80	*aaa.run*
k1 (distref = 53)	3.479	849	500	23	80	*aaa.run*
k2 (distref = 56)	3.927	845	351	23	80	*aaa.run*
k3 (distref = 59)	4.440	845	190	23	80	*aaa.run*
k4 (distref = 62)	5.034	844	160	23	80	*aaa.run*
k5 (distref = 65)	5.730	844	80	23	80	*aaa.run*
k6 (distref = 68)	6.557	839	102	23	80	*aaa.run*
k7 (distref = 71)	7.554	836	36	23	80	*aaa.run*
k8 (distref = 74)	8.782	823	75	24	81	*aaa.run*
k9 (distref = 77)	10.329	823	73	24	81	*aaa.run*
k10 (distref = 80)	12.342	823	65	24	81	*aaa.run*
k11 (distref = 83)	15.064	823	50	24	81	*aaa.run*
k12 (distref = 86)	18.953	821	9	24	81	*aaa.run*
k13 (distref = 89)	24.964	819	9	24	81	*aaa.run*
k14 (distref = 92)	35.482	819	9	24	81	*aaa.run*
k15 (distref = 95)	58.623	817	9	24	81	*aaa.run*
k16 (distref = 98)	151.186	814	10	24	81	*aaa.run*
setk (N = 15.022036)	33.925781	819	9	24	81	*setk_trans.run*

Table 4. Status of some unstable genera under different settings; non-monophyletic results are indicated in **bold**.

Settings	*Ephucilla*	*Mickelomyrme*	*Promecilla*	*Smicromyrme*
Equal weights	monophyletic or paraphyletic	monophyletic	monophyletic	monophyletic or paraphyletic
k0 (distref = 50)	**paraphyletic**	**paraphyletic**	**polyphyletic**	monophyletic
k1 (distref = 53)	**paraphyletic**	**paraphyletic**	**polyphyletic**	monophyletic
k2 (distref = 56)	**paraphyletic**	monophyletic	**polyphyletic**	monophyletic
k3 (distref = 59)	**paraphyletic**	monophyletic	**polyphyletic**	monophyletic
k4 (distref = 62)	**paraphyletic**	monophyletic	**polyphyletic**	monophyletic
k5 (distref = 65)	**paraphyletic**	monophyletic	**polyphyletic**	monophyletic
k6 (distref = 68)	monophyletic	monophyletic	**polyphyletic**	monophyletic
k7 (distref = 71)	monophyletic	monophyletic	**polyphyletic**	monophyletic
k8 (distref = 74)	monophyletic	monophyletic	**paraphyletic**	monophyletic
k9 (distref = 77)	monophyletic	monophyletic	**paraphyletic**	monophyletic
k10 (distref = 80)	monophyletic	monophyletic	**paraphyletic**	monophyletic
k11 (distref = 83)	monophyletic	monophyletic	**paraphyletic**	monophyletic
k12 (distref = 86)	monophyletic	monophyletic	**paraphyletic**	**paraphyletic**
k13 (distref = 89)	monophyletic	monophyletic	**paraphyletic**	monophyletic
k14 (distref = 92)	monophyletic	monophyletic	**paraphyletic**	monophyletic
k15 (distref = 95)	monophyletic	monophyletic	**paraphyletic**	monophyletic
k16 (distref = 98)	monophyletic	monophyletic	monophyletic	monophyletic
setk (N = 15.022036)	monophyletic	monophyletic	**paraphyletic**	monophyletic

Table 5. Number of known species/subspecies of East Asian Smicromyrmini.

Genus/country	China	Taiwan	North Korea	South Korea	Japan	Vietnam	Laos	Cambodia	Thailand	Malaysia	Singapore	Brunei	Indonesia	Philippines	Total
Andreimyrme	2/0	1/0	0/0	0/0	1/0	5/0	2/0	0/0	4/0	5/0	0/0	0/0	5/0	0/0	14/0
Chenmyrme	0/0	1/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	1/0
Ephucilla	6/1	4/0	0/0	0/0	3/0	5/0	1/0	0/0	4/0	2/0	0/0	0/0	4/0	1/0	20/1
Ephutomma	1/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	1/0
Hadrodontilla	2/0	2/0	0/0	0/0	0/0	1/0	0/0	0/0	1/0	0/0	0/0	0/0	0/0	0/0	2/0
Mickelomyrme	7/0	2/0	0/0	0/0	1/0	8/0	6/0	0/0	10/0	6/0	0/0	1/0	5/0	11/0	29/0
Nemka	2/0	2/0	0/0	1/0	1/0	1/0	1/0	0/0	2/0	1/0	0/0	0/0	0/0	0/0	7/0
Nordeniella	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	2/0	0/0	0/0	0/0	1/0	0/0	3/0
Physetopoda	1/0	0/0	0/0	0/0	0/0	0/0	1/0	0/0	1/0	0/0	0/0	0/0	0/0	0/0	2/0
Promecilla	2/0	0/0	0/0	0/0	0/0	1/0	0/0	0/0	1/0	4/0	0/0	0/0	2/0	0/0	7/0
Sinotilla	6/1	2/0	0/0	0/0	1/0	4/0	1/0	0/0	2/0	6/0	0/0	0/0	3/0	3/0	18/1
Smicromyrme	3/0	1/0	1/0	2/0	1/0	0/0	0/0	0/0	1/0	0/0	0/0	0/0	0/0	0/0	4/0
Tsunekimyrme	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	1/0	1/0	1/0	1/0
Incertae sedis	2/0	4/0	0/0	0/0	0/0	1/0	1/0	0/0	6/0	5/0	0/0	0/0	5/0	3/2	20/2
Total	34/2	19/0	1/0	3/0	8/0	26/0	13/0	0/0	34/0	30/0	0/0	2/0	26/0	21/2	129/4

Chapter 11

General discussion

"*La science est une, et vous l'avez partagée.*"
Étienne Geoffroy Saint-Hilaire, "*Notions synthétiques, historiques et physiologiques de philosophie naturelle*" (1838),
paraphrasing Honoré de Balzac, "*Louis Lambert*" (1832)

Velvet ants possess a number of unique features that make them useful and interesting models for comparative biology (Chapters 1, 5, 9, 10). As parasitoids, velvet ants are potentially influential to host insects, given their abundance, broad diet, and high parasitism rate (Chapter 1). The host repertoire of velvet ants includes pollinators (bees and hoverflies), pest control agents (hunting and parasitoid wasps exploiting pest insects), and agricultural or medical pests (ber fruit flies and tsetse flies). Recent studies focusing on their biogeography (Pitts *et al*., 2010; Wilson & Pitts, 2008, 2010ab, 2011; Wilson *et al*., 2012a), defense mechanisms (Gall *et al*., 2018; Mergler & Gall, 2020), mimicry (Wilson *et al*., 2012b, 2015, 2018), and thermal ecology (Lopez *et al*., 2021; Wilson *et al*.,2020) had wisely utilized biological characteristics of this insect to address issues in general biology. However, such works would have not been possible without more fundamental knowledge, like systematics, distribution, and natural history. For instance, Williams's (2012) study on the molecular phylogeny of North American *Dasymutilla* Ashmead, 1899 species has been repeatedly cited to prove phylogenetic independence of aposematic color traits in this genus (Wilson *et al*., 2012b, 2020).

Throughout the present dissertation, I examined over 3,500 specimens from East Asia, including historical type specimens of P. Cameron, C.-w. Chen, A.S. Lelej, C.E. Mickel, F. Smith, K. Tsuneki, and E. Zavattari. Based on the types and other identified material, I revised the systematic basis for the East Asian velvet ants, providing a robust reference system for future research. With 32 new species and 36 new combinations, the species richness of the genera *Andreimyrme* Lelej, 1995, *Arkaditilla* Okayasu, 2021, *Eotrogaspidia* Lelej, 1996, *Ephucilla* Lelej, 1995, *Mickelomyrme* Lelej, 1995, and *Neotrogaspidia* Lelej, 1996 drastically increased, suggesting hidden diversity of the East Asian velvet ants (Chapters 2–6, 10). Conversely, most male-based species presently included in the "wastebasket" genus *Smicromyrme* Thomson, 1870 (i.e., an apparently polyphyletic genus composed of heterogeneous species that could not be assigned to more appropriate genus) were sorted out into various smicromyrmine genera (Chapter 10). Another place-holder for the East Asian velvet ants, *Trogaspidia* Ashmead, 1899, of which monophyly is highly questionable, has not been treated similarly. Critical analysis and reexamination of this genus will be necessary.

Paradoxically to the potential diversity of East Asian velvet ants, I recognized as many as 28 new synonymies, leading to reduction of superficial diversity (Chapters 2, 5, 6, 9, 10). The large number of taxonomic changes (new combinations and new synonymies) is ascribed to inadequate morphological inspection and misidentification in the previous studies. Besides, taxonomic treatments of East Asian taxa often relied on geographically biased sampling (Williams *et al*., 2019; Chapter 7). In the present study, I managed these impediments by incorporating newly recognized characters and broadly extended specimen and taxon samplings (Chapters 2–5, 10), which greatly improved morphology-based generic classification systems of velvet ants. Still, the phylogenetic analyses demonstrated that morphological characters of this insect included a high level of homoplasy (Chapter 10). This does not necessarily mean that morphology is no longer necessary or not useful for

systematics, because a unique combination of character states can provide a reliable border for higher taxa (Chapters 2, 5, 10). In addition, incongruence of phylogeny and morphological traits offers a useful basis for hypothesizing parallelism or convergence resulting from functional selecting pressures.

Functional aspects of the velvet ant morphology are mostly unknown. However, we can assume that clasping function of cephalic and genitalic structures is subject to selection in males practicing mandibular phoretic copulation. Some authors proposed that the concaved clypeus, presence of a mandibular ventral tooth, asymmetric penisvalva, and developed endophallus work as holdfast mechanisms during copulation (Crèvecceur, 1930; O'Toole, 1975; Quintero & Cambra, 1994; Sheldon, 1970). Additionally, based on the examination of mating pairs (Chapter 1: fig. 4; Chapter 10: fig. 24), I further assume that the distally widened mandible, enlarged volsella, and elongate basivolsellar setae are adaptations to enhance the clasping function. Most parsimonious reconstruction of character states (Chapter 10) suggests multiple origins of the distally widened mandible, elongate basivolsellar setae, and asymmetric penisvalva (Fig. 1). This clearly suggests that those adaptive morphological traits evolved repeatedly synchronizing with phoretic copulation.

Then, what is the point to investigate phoretic copulation? It is evident from the lack of wings that female velvet ants possess low dispersal ability (Brothers, 1989; Evans & Miller, 1969; Evans *et al*., 1973), making them susceptible to geographical and habitat changes. This feature is particularly useful for understanding the biogeographical patterns of terrestrial organisms (Lo Cascio, 2015; Wilson & Pitts, 2011; Wilson *et al*., 2012a). However, one overlooked aspect is the male-aided dispersal ability of females. In contrast to in situ copulation, phoretic copulation takes much longer mating duration (Mickel, 1937; Nonveiller, 1980; Saxton, 2010; Shappirio, 1947; Waldren *et al*., 2020); a single mating event of *Timulla* species lasts up to 20 hours (Cambra *et al*., 2018). Therefore, phoretic copulation offers a chance of long-distance dispersal to females. Varied dispersal ability due to alternative mating strategies may result in varied distributional patterns among taxa. In Figure 2, the distribution of *Neotrogaspidia pustulata* (Smith, 1873) and three *Ephucilla* species in Ryûkyû Islands are compared. The former species has the concaved clypeus, asymmetric penisvalva, and developed endophallus and practices phoretic copulation (Chapter 5). Contrarily, the *Ephucilla* species have the reduced volsella and membranous endophallus, suggesting that they practice in situ copulation. Likely due to these biological features, their distributional patterns are contrasting: *Neotrogaspidia pustulata* occurs widely across islands with no noticeable morphological variations (Chapter 5), while distributional range of each morphospecies of the *Ephucilla* is restricted to a single island or an island-group (Okayasu, 2020). This implies that species practicing in situ copulation are more susceptible to geographic factors. In conclusion, velvet ants exhibit truly curious interactions of morphology, behavior, and biogeography. Morphological examination of museum specimens can also provide a cue for understanding such behavioral, evolutionary, and biogeographical aspects of velvet ants.

Overall, the present dissertation shows that basic knowledge on velvet ants is vital to fully utilize their biological characteristics. Specifically, systematics not only provides a useful reference system, but also synthesizes various aspects of organisms, like morphology, phylogeny, distribution, behavior, and host choice (Simpson, 1961). This research field is thus regarded as a process of hypothesis formation within the broader context of comparative biology. As systematists, our missions are to name, describe, and compare nominal taxa in an explicit way, and, additionally, to concentrate biological information under authoritatively curated taxon names. Further, we have to investigate to what extent uniformity (similarity) and diversity (difference) of life are explained by phylogeny. By doing so, we can expose a pattern that deserves an evolutionary hypothesis (e.g., a hypothesis of parallelism or

convergence and a hypothesis of speciation by vicariance or dispersal). I hope case studies presented in this dissertation will facilitate further basic research dedicated to velvet ants. An additional point to be emphasized is the usefulness of historical museum collections. The present study largely depends on specimens loaned from institutes around the world. They provided valuable comparative data which inspired and supported this dissertation. Future studies are encouraged to incorporate field data and museum specimens for better understanding of this fascinating creature.

References

Brothers, D.J. (1989) Alternative life-history styles of mutillid wasps (Insecta, Hymenoptera). *In*: Bruton, M.N. (ed.) *Alternative life-history styles of animals*. *Perspectives in vertebrate sciences 6*. Springer, Dordrecht, pp. 279–291. https://doi.org/10.1007/978-94-009-2605-9_14

Cambra, R.A., Quintero A., D., Waldren, G.C., Bartholomay, P.R. & Williams, K.A. (2018) Taxonomic revision of the genus *Timulla* Ashmead, 1899 of Panama (Hymenoptera: Mutillidae). *Tecnociencia* 20 (2): 23–57.

Crèvecoeur, A. (1930) Recherches biologiques sur *Smicromyrme* (*Mutilla*) *rufipes* F. (Hym. Mutillidae). *Bulletin & Annales de la Société entomologique de Belgique* 70: 271–284.

Evans, D.A. & Miller, B.R. (1969) A note on adult overwintering of *Dasymutilla nigripes* in Michigan (Hymenoptera: Mutillidae). *The Michigan Entomologist* 2 (3–4): 74.

Evans, D.A., Miller, B.R. & Bartlett, C.B. (1973) Host searching range of *Dasymutilla nigripes* (Fabricius) as investigated by tagging (Hymenoptera: Mutillidae). *Journal of the Kansas Entomological Society* 46 (3): 343–346. https://www.jstor.org/stable/25082582

Gall, B.G., Spivey, K.L., Chapman, T.L., Delph, R.J., Brodie, E.D. Jr. & Wilson, J.S. 2018. The indestructible insect: Velvet ants from across the United States avoid predation by representatives from all major tetrapod clades. *Ecology and Evolution* 8 (11): 5852–5862. https://doi.org/10.1002/ece3.4123

Lo Cascio, P. (2015) Worldwide checklist of the island mutillid wasps (Hymenoptera Mutillidae). *Biodiversity Journal* 6 (2): 529–592.

Lopez, V.M., Tosta, T.A.A., da Silva, G.G., Bartholomay, P.R., Williams, K.A. & Ferreira, G.F. (2021) Color lightness of velvet ants (Hymenoptera: Mutillidae) follows an environmental gradient. *Journal of Thermal Biology* 100: 1–9. https://doi.org/10.1016/j.jtherbio.2021.103030

Mergler, C.J. & Gall, B.G. 2020. Has the indestructible insect met its match? Velvet ants as prey to bufonid toads. *Ethology Ecology & Evolution* 33 (1): 15–24. https://doi.org/10.1080/03949370.2020.1789747

Mickel, C.E. (1937) The mutillid wasps of the genus *Timulla* which occur in North America north of Mexico. *Entomological Americana* 17 (1–2): 1–113 + pls 1–3.

Nonveiller, G. (1980) Recherches sur les Mutillides de l'Afrique (Hymenoptera, Mutillidae) X. Bref aperçu des résultats des recherches sur la faune des Mutillides du Cameroun effectuées au cours de la période 1962–1975. *Memoires publies par l'Institut pour la Protection des Plantes*, Beograd 14: 11–68.

Okayasu, J. (2020) Velvet ants of the tribe Smicromyrmini Bischoff (Hymenoptera: Mutillidae) of Japan. *Zootaxa* 4723 (1): 1–110. https://doi.org/10.11646/zootaxa.4723.1.1

O'Toole, C. (1975) The systematics of *Timulla oculata* (Fabricius) (Hymenoptera, Mutillidae). *Zoologica Scripta* 4 (1): 229–251. https://doi.org/10.1111/j.1463-6409.1975.tb00733.x

Pitts, J.P., Wilson, J.S. & von Dohlen, C.D. (2010) Evolution of the nocturnal Nearctic Sphaeropthalminae velvet ants (Hymenoptera: Mutillidae) driven by Neogene orogeny and Pleistocene glaciation. *Molecular Phylogenetics and Evolution* 56 (1): 134–145. https://doi.org/10.1016/j.ympev.2010.03.033

Quintero A., D. & Cambra, R.A. (1994) Systematics of *Pseudomethoca areta* (Cameron): Sex association, description of the male and a gynandromorph, and a new synonymy (Hymenoptera: Mutillidae). *Journal of Hymenoptera Research* 3: 303–308.

Saxton, S.M. (2010) Mating behaviour of *Myrmosa atra* (Hymenoptera: Mutillidae) with a consideration of the adaptive significance of long copulation duration. *British Journal of Entomology and Natural History* 23: 33–38 + pl. 4.

Shappirio, D.G. (1947) Observations on wasps. *The Scientific Monthly* 64 (4): 348–350.

Sheldon, J.K. (1970) Sexual dimorphism in the head structure of Mutillidae Hymenoptera: A possible behavioral explanation. *Entomological News* 81 (3): 57–61.

Simpson, G.G. (1961) *Principles of animal taxonomy*. Columbia University Press, New York, 247 pp.

Waldren, G.C., Roberts, J.D. & Pitts, J.P. (2020) Phoretic copulation in the velvet ant *Sphaeropthalma pensylvanica* (Lepeletier) (Hymenoptera, Mutillidae): A novel behavior for Sphaeropthalminae with a synthesis of mating strategies in Mutillidae. *Journal of Hymenoptera Research* 78: 69–89. https://doi.org/10.3897/jhr.78.55762

Williams, K.A. (2012) *Systematics of Mutillidae (Hymenoptera) with special emphasis on* Dasymutilla *and their allies*. Ph.D. Thesis, Utah State University. https://doi.org/10.26076/ef6b-f9fa

Williams, K.A., Lelej, A.S., Okayasu, J., Borkent, C.J., Malee, R., Thoawan, K. & Thaochan, N. (2019) The female velvet ants (aka modkhong) of southern Thailand (Hymenoptera: Mutillidae), with a key to the genera of southeast Asia. *Zootaxa* 4602 (1): 1–69. https://doi.org/10.11646/zootaxa.4602.1.1

Wilson, J.S., Jahner, J.P., Forister, M.L., Sheehan, E.S., Williams, K.A. & Pitts, J.P. (2015) North American velvet ants form one of the world's largest known Müllerian mimicry complexes. *Current Biology* 25 (16): R704–R706. https://doi.org/10.1016/j.cub.2015.06.053

Wilson, J.S., Clark, S.L., Williams, K.A. & Pitts, J.P. (2012a) Historical biogeography of the arid-adapted velvet ant *Sphaeropthalma arota* (Hymenoptera: Mutillidae) reveals cryptic species. *Journal of Biogeography* 39: 336–352. https://doi.org/10.1111/j.1365-2699.2011.02580.x

Wilson, J.S., Pan, A.D., Limb, E.S. & Williams, K.A. (2018) Comparison of African and North American velvet ant mimicry complexes: Another example of Africa as the 'odd man out'. *PLoS ONE* 13 (1): e0189482. https://doi.org/10.1371/journal.pone.0189482

Wilson, J.S. & Pitts, J.P. (2008) Revision of velvet ant genus *Dilophotopsis* Schuster (Hymenoptera: Mutillidae) by using molecular and morphological data, with implications for desert biogeography. *Annals of the Entomological Society of America* 101 (3): 514–524. https://doi.org/10.1603/0013-8746(2008)101[514:ROVAGD]2.0.CO;2

Wilson, J.S. & Pitts, J.P. (2010a) Pleistocene diversification of the *Odontophotopsis unicornis* species-group (Hymenoptera: Mutillidae). *Annals of the Entomological Society of America* 103 (4): 555–565. https://doi.org/10.1603/AN09177

Wilson, J.S. & Pitts, J.P. (2010b) Phylogeographic analysis of the nocturnal velvet ant genus *Dilophotopsis* (Hymenoptera: Mutillidae) provides insights into diversification in the Nearctic deserts. *Biological Journal of the Linnean Society* 101 (2): 360–375. https://doi.org/10.1111/j.1095-8312.2010.01526.x

Wilson, J.S. & Pitts, J.P. (2011) Pleistocene connection between the Nearctic Mediterranean and desert regions in the *Sphaeropthalma unicolor* species-complex (Hymenoptera: Mutillidae). *Insect Conservation and Diversity* 4 (3): 222–234. https://doi.org/10.1111/j.1752-4598.2010.00124.x

Wilson, J.S., Sidwell, J.S., Forister, M.L., Williams, K.A. & Pitts, J.P. (2020) Thistledown velvet ants in the Desert Mimicry Ring and the evolution of white coloration: Müllerian mimicry, camouflage and thermal ecology. *Biology Letters* 16: 20200242. https://doi.org/10.1098/rsbl.2020.0242

Wilson, J.S., Williams, K.A., Forister, M.L., von Dohlen, C.D. & Pitts, J.P. (2012b) Repeated evolution in overlapping mimicry rings among North American velvet ants. *Nature Communications* 3: 1272. https://doi.org/10.1038/ncomms2275

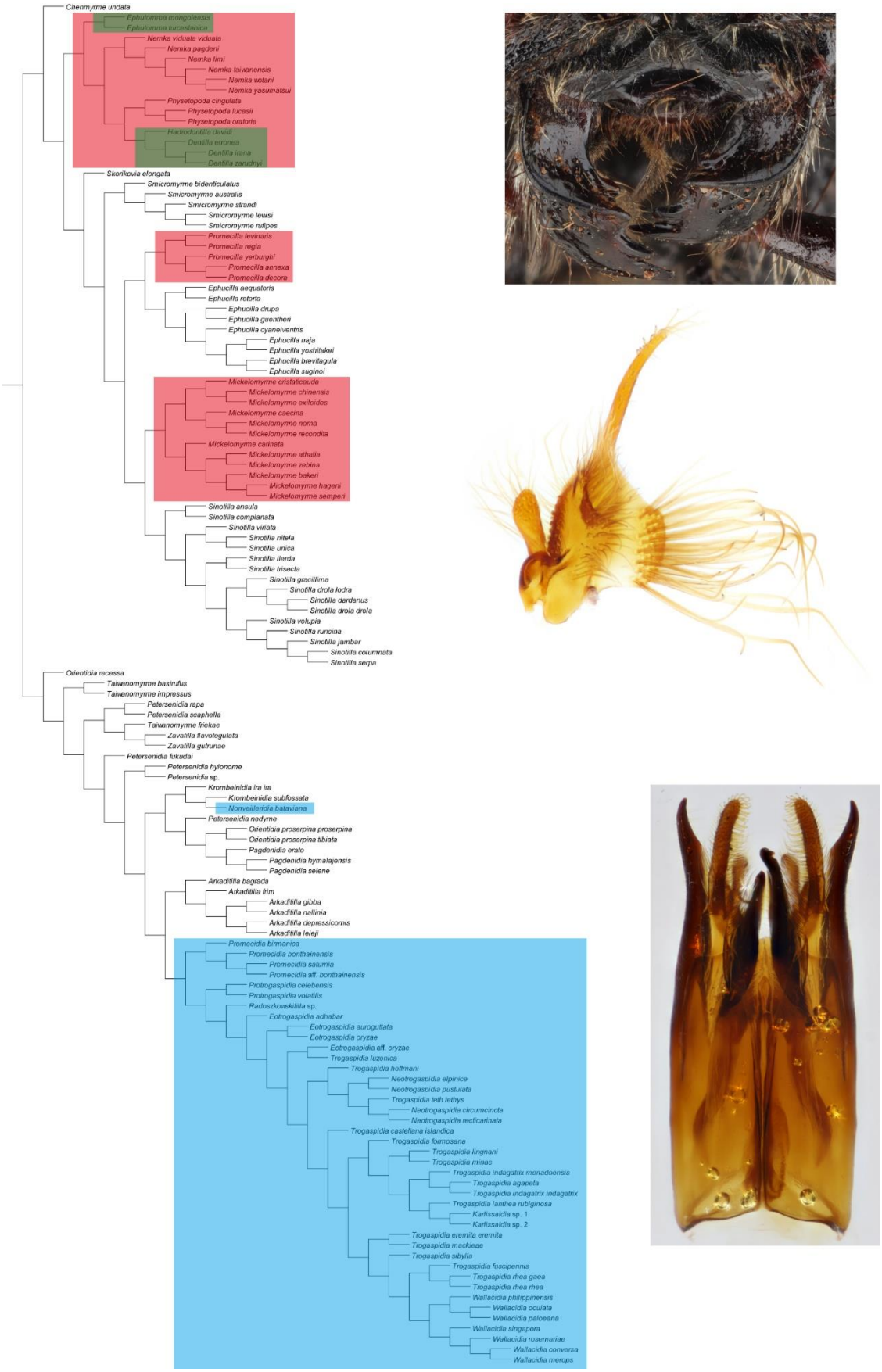

Figure 1. One of the best-fitting trees under k16 (Chapter 10). Distribution of the distally widened mandible (right above) is shown in green, elongate basivolsellar setae (right middle) in red, and asymmetric penisvalva (right below) in blue.

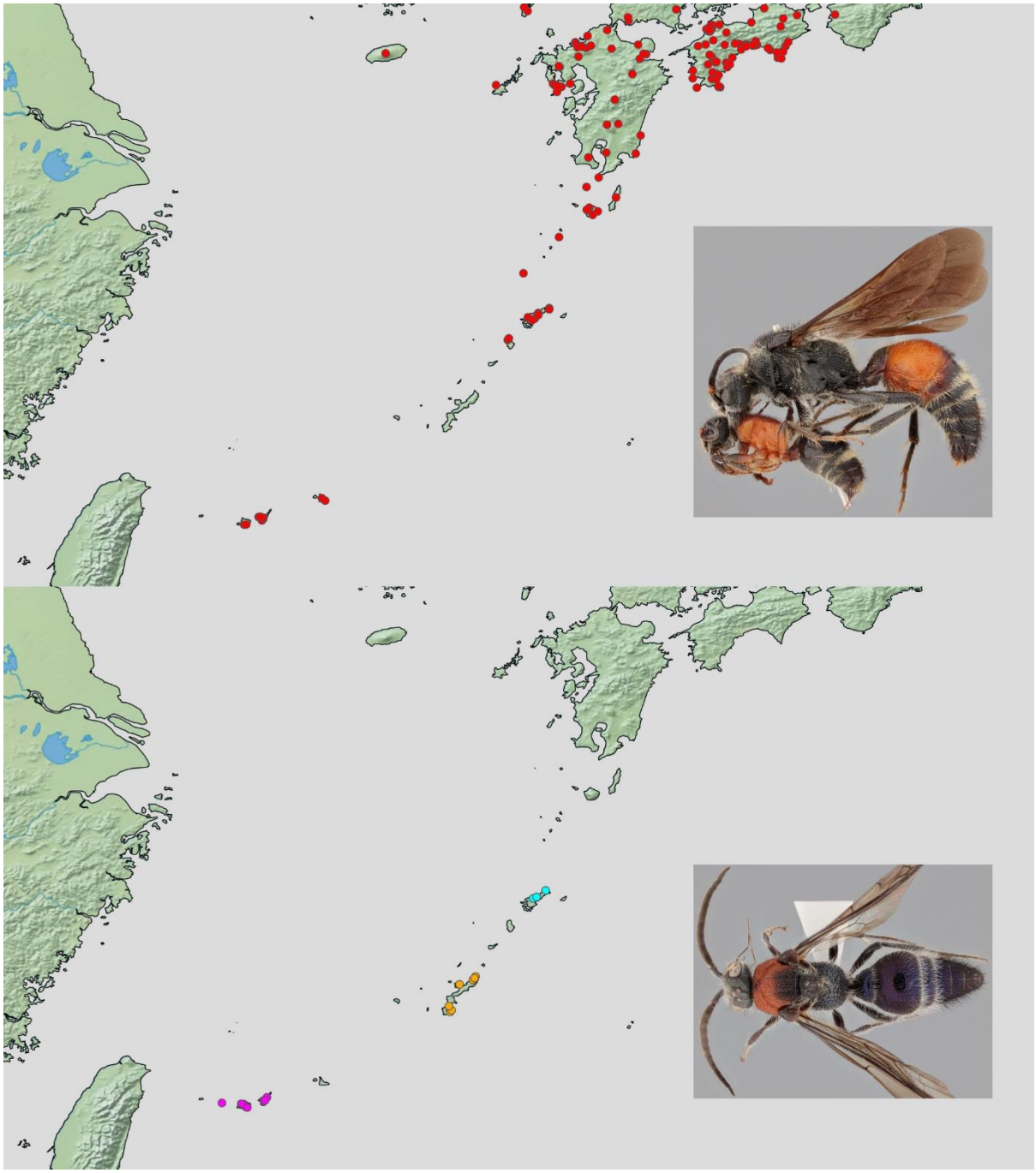

Figure 2. Distribution of *Neotrogaspidia pustulata* (Smith) (above) and *Ephucilla* spp. (below) in Ryûkyû Islands. Red: *N. pustulata*; pink: *E. brevitegula*; orange: *E. suginoi*; blue: *E. yoshitakei*. Data from the Chapters 5 and 10.