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1 **First fossil trichophyine rove beetle from mid-Cretaceous amber of**
2 **northern Myanmar (Coleoptera: Staphylinidae: Trichophyinae)**

3

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13

14 **Abstract.**

15 Trichophyinae is one of the smallest subfamilies of the megadiverse rove-beetle family
16 Staphylinidae, with only 18 species in the single extant genus *Trichophya* Mannerheim. Here
17 we describe the first fossil representative of Trichophyinae in mid-Cretaceous amber from
18 Kachin, northern Myanmar. †*Trichophya minor* **sp. nov.** is unusual in having non-filiform
19 thick antennae, similar to *T. antennalis* Cameron, 1932 from India, but this new species can
20 readily be distinguished from the latter by having much smaller and smoother body. Our
21 finding indicates that the subfamily had been originated by the Albian–Cenomanian
22 boundary, also showing a potential Gondwanan distribution at that time. We also briefly
23 discuss a miniaturization trend in the Burmese amber beetles.

24

25 *Key words:* Staphylinidae; Trichophyinae; *Trichophya*; Kachin amber; Cenomanian; new
26 species

27

28 **1. Introduction**

29

30 With over 65,000 species in one extinct and 33 extant subfamilies (Bouchard et al., 2011;
31 Tihelka et al., 2020; Yamamoto, 2021), the rove beetles (Staphylinidae) are the largest animal
32 and metazoan family, showing amazing morphological and ecological diversity in terrestrial
33 ecosystems (Grebennikov and Newton, 2009; Thayer, 2016). Fossil records are vital

34 information for understanding the origin and evolutionary history of each taxonomic category.
35 In rove beetles, fossils are known for most subfamilies, with only a few exceptions.

36 Trichophyinae and its presumably sister subfamily Habrocerinae are among the few
37 subfamilies without any fossil record until now (Ashe and Newton, 1993; Ashe, 2005; Cai et
38 al., 2017: supplemental information; Yamamoto and Maruyama, 2018; Orlov et al., 2020).
39 The trichophyines are one of the smallest subfamilies in the mega-diverse Staphylinidae. In
40 fact, it contains only a single genus *Trichophya* Mannerheim with 18 extant species native to
41 the Northern Hemisphere. Although the biology and ecology are largely unknown in
42 Trichophyinae, they are found in various forest environments, e.g., in forest leaf litter, under
43 bark and in squirrel middens (Legner and Moore, 1977; Newton et al., 2000; Shibata, 2001),
44 or on fungi (Newton, 1984; Miyashita, 1997). They are typically small beetles, usually 2–3
45 millimetres in body length. Among the rove beetles, one of the morphological characters
46 which define adult Trichophyinae is the presence of extremely slender, filiform, and
47 verticillate antennae (Newton et al., 2000). This feature is known only in or within a very
48 limited number of other staphylinid groups, namely: Dasycerinae, Habrocerinae, and
49 Scaphidiinae (tribe Scaphisomatini only). Further notable adult characters include the
50 presence of a strong neck constriction, five-segmented maxillary palpus including a minute
51 and aciculate pseudosegment mounted on the spindle-shaped fourth maxillary palpomere,
52 elytral epipleural keel or ridge absent, protrochantin exposed, mesothoracic spiracle in large
53 well-sclerotized triangular peritreme, and two pairs of abdominal paratergites present on most
54 segments (Ashe and Newton, 1993; Newton et al., 2000; Ashe, 2005).

55 The mid-Cretaceous amber Kachin amber, previously known as Burmese amber, from
56 northern Myanmar is well known for exceptionally diverse and abundant inclusions of
57 organisms. In fact, it currently encompasses the richest biota in Mesozoic amber by far, with
58 nearly 1,900 named taxa (Ross, 2019, 2020, 2021), despite the fact that most studies have
59 only been made in the last decade. In Staphylinidae, a total of 19 subfamilies have currently
60 been recorded including recently reported subfamilies such as Piestinae (Yamamoto et al.,
61 2019), Paederinae (Żyła et al., 2019), Pseudopsinae (Liu et al., 2020c), and Protopselaphinae
62 (Liu et al., 2020a, d). Here we report the first fossil occurrence of Trichophyinae from Kachin
63 amber. Our finding sheds new light on the Mesozoic origin and morphological evolution of
64 the subfamily, and this discovery eliminates a huge gap in the fossil record of rove beetles.

65

66

67 **2. Material and methods**

68 Amber material here studied was obtained from mines at the summit of Noiye Bum Hill
69 (26°20'N 96°36'E) in the Hukawng Valley, Kachin State, northern Myanmar (mapped in
70 Cruickshank and Ko 2003). The amber-bearing horizon has been dated with 98.8 ± 0.6 Ma
71 (earliest Cenomanian) as the minimum age based on the Uranium–lead dating of zircon
72 crystals in the volcanic sedimentary matrix (Shi et al., 2012). A slightly older age for Kachin
73 amber has been implied by Mao et al. (2018) and Balashov (2021). Based on these studies and
74 the discovery of an ammonite fossil in Kachin amber (Yu et al., 2019), a mid-Cretaceous age
75 is adopted here. The fossil resin was most likely formed by *Metasequoia* trees (Cupressaceae)
76 in a tropical forest located near a seashore (Grimaldi and Ross 2017; Mao et al., 2018; Yu et
77 al., 2019).

78 The amber specimen was cut using a hand saw, ground with emery papers of different
79 grain sizes, and finally polished with a polishing cloth. Observation was conducted with a
80 Leica MZ16 stereomicroscope. Photographs (Figs 1–4, Supplementary Figs 1–3) were taken
81 with three different methods. The habitus and body parts of the fossil and extant material
82 (Figs 1, 2F, 4, Supplementary Figs 1–2) were photographed using a Canon EOS 80D digital
83 camera, mounted on a Canon MP-E 65 mm macro lens (F2.8, 1–5X), and with an attached
84 Canon MT-24EX twin flash as a light source. In addition, the images of several body parts of
85 the fossil and slide specimen of the extant material (Figs 2B, E, 3, Supplementary Fig. 3) were
86 acquired with an Olympus DP26 digital camera mounted on an Olympus BX50
87 stereomicroscope. Finally, a few images of the enlarged body parts of the fossil (Fig. 2A, C,
88 D) were obtained using a Dun Ink BK PLUS Lab System, mounted on a Canon EOS 6D
89 digital camera with a 10× lens. During the imaging sessions, the amber specimen was
90 completely submerged in clove oil to enhance the quality of the outputs. The software Helicon
91 Focus 7.5.4 was used for focus stacking based on the acquired images. All images were
92 edited, arranged, and assembled with Adobe Photoshop Elements 15 software. The sole
93 specimen is deposited in the entomological collection of the Gantz Family Collections Center,
94 Field Museum of Natural History (FMNH), Chicago, IL, USA, under the registered number
95 FMNHINS-4357787. All the examined extant specimens are deposited in FMNH, and listed
96 in Appendix 1. The Appendix 2 includes the supplementary figures used in the texts cited as
97 Supplementary Figs 1–3. The supplementary data comprised of Appendices 1 and 2 have
98 been deposited in the Zenodo repository (<https://doi.org/10.5281/zenodo.4784783>; accessed
99 on 25 May 2021). This published work and the nomenclatural acts it contains have been
100 registered in ZooBank, the proposed online registration system for the International Code of
101 Zoological Nomenclature (ICZN). The ZooBank LSIDs (Life Science Identifiers) can be

102 resolved and the associated information viewed through any standard web browser by
103 appending the LSID to the prefix 'http://zoobank.org/'. The LSIDs for this publication are:
104 [urn:lsid:zoobank.org:pub:5C59F363-D3DD-450C-BDC6-14A56A492865;](http://zoobank.org/urn:lsid:zoobank.org:pub:5C59F363-D3DD-450C-BDC6-14A56A492865)
105 [urn:lsid:zoobank.org:act:C375811E-115A-4D84-9647-E504799A8DB2.](http://zoobank.org/urn:lsid:zoobank.org:act:C375811E-115A-4D84-9647-E504799A8DB2)

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108 **3. Systematic paleontology**

109

110 Order Coleoptera Linnaeus, 1758.
111 Superfamily Staphylinoidea Latreille, 1802.
112 Family Staphylinidae Latreille, 1802.
113 Subfamily Trichophyinae Thomson, 1858.

114

115 **Genus *Trichophya* Mannerheim, 1830: 73.**

116 Type species: *Aleochara pilicornis* Gyllenhal, 1810.

117

118 *Remarks.* The native distribution of *Trichophya* seems to be the Palearctic, Oriental and
119 Nearctic regions, but several more undescribed species are known from Mexico through
120 Nicaragua (Newton et al., 2000).

121

122 †*Trichophya minor* sp. nov.

123 (Figs 1–3)

124 LSID: [urn:lsid:zoobank.org:act:C375811E-115A-4D84-9647-E504799A8DB2.](http://zoobank.org/urn:lsid:zoobank.org:act:C375811E-115A-4D84-9647-E504799A8DB2)

125

126 *Type material.* Holotype, FMNHINS-4357787, a complete, well-preserved female adult;
127 deposited in FMNH. The fossil specimen is embedded in an irregularly flattened, rectangular
128 piece of transparent yellowish amber (10.5 × 3.9 × 1.9 mm).

129

130 *Etymology.* Latin adjective *minor* meaning small, referring to the minute body of this extinct
131 species.

132

133 *Locality and horizon.* Burmese (Kachin) amber from the Hukawng Valley (26°20'N 96°36'E),
134 Kachin State, northern Myanmar; upper Albian to lower Cenomanian (mid-Cretaceous).

135

136 *Differential diagnosis.* †*Trichophya minor* sp. nov. is morphologically closely similar to *T.*
137 *antennalis* Cameron, 1932 (Fig. 4B, Supplementary Fig. 1B), known from northern India
138 (Shimla Hills), in having relatively short and thick antennae, in contrast to the very long and
139 slender, verticillate antennae of all other extant species of the genus, but it can be
140 distinguished from *T. antennalis* by the much smaller body (ca. 1.3 mm versus 2.2 mm),
141 shorter elytra, more strongly tapered abdomen, and smoother body surface (cf. Figs 1A and
142 4B).

143

144 *Description.* Female. Body small (1.28 mm, measured from dorsal view), narrowly elongate,
145 tachyporine-like. Color uniformly dark reddish brown; mouthparts, legs, and gonocoxites
146 slightly paler. Surface uniformly weakly punctate, densely pubescent with inconspicuous
147 microsetae.

148 Head (Figs 1, 2A, B) moderately deflexed, large (0.19 mm long, 0.23 mm wide),
149 slightly smaller than pronotum, widest across eyes, moderately produced anteriorly; clypeus
150 narrow, less than half width of maximum width of head; frontoclypeal suture (Fig. 2A, *fcs*)
151 gently arcuate, lacking midcranial suture; neck constriction (see Supplementary Fig. 2B, C)
152 slightly visible, with basal carina (Fig. 2A, *ch*). Labrum entire, transverse. Eyes (Figs 1, 2A,
153 B) large, bulging, strongly projecting laterally (Fig. 2A). Antennal insertions (Fig. 2A, B, *ai*)
154 partly exposed, distant from anterior margins of eyes (Fig. 2A). Antennae (Figs 1, 2A, B, 3A)
155 with 11 antennomeres, slender, fili-moniliform, slightly longer than head and pronotum
156 combined, each antennomere moderately setose with microsetae: antennomere 1 (*a1*) robust,
157 nearly subparallel sided, only weakly dilated apically, slightly curved, about 1.4 times longer
158 than *a2*; *a2* strongly dilated apically, thicker than *a1*; *a3* elongate, rather slender, much
159 narrower than *a2*, less wide than *a1*; *a4*–*a9* small, spherical, each antennomere similar in shape
160 and size; *a10* very slightly elongate, slightly longer than *a9*; *a11* elongate, nearly twice as long
161 as wide, widest near middle, much larger than *a10*. Mandibles inconspicuous, details not
162 visible. Maxillary palpi (Figs 2A, B, 3D) five-segmented including pseudosegment, moderate
163 in size and length; palpomere 1 (*mp1*) small; *mp2* narrowly elongate, slightly curved; *mp3*
164 robust, much shorter than *mp2*, strongly dilated apically; *mp4* spindle-shaped, much longer
165 than *mp3*, densely covered with microsetae (Fig. 3D); *mp5* (pseudosegment) minute,
166 aciculate, hyaline (Fig. 3D). Mentum trapezoidal, moderately transverse, with truncate
167 anterior margin. Labial palpi (Fig. 2A) inconspicuous, not well visible. Gular sutures
168 complete, widely separated, rather strongly widened toward base, each forming straight line.

169 Pronotum (Fig. 1A) small (0.22 mm long, 0.33 mm wide), slightly larger than head,
170 strongly transverse (width/length = 1.5), widest slightly before base; sides arcuate, relatively
171 strongly narrowed anteriorly; anterior margin nearly truncate; posterior margin gently
172 rounded; anterolateral angles obtusely rounded; posterolateral angles rounded; surface with
173 dense and fine microsetae. Prosternum (Fig. 2B, E, *ps*) small, transverse; prosternal process
174 short, sharply pointed. Pronotal hypomeron narrow (Fig. 2B, E), relatively weakly folded
175 inward; postcoxal process absent. Procoxal cavities opened behind. Mesoscutellum (Fig. 2C,
176 *sc*) sub-triangular, longer than wide, with pointed apex. Elytra (Figs 1A, 2C, D) short (right
177 elytron 0.32 mm long, 0.20 mm wide), but moderately longer than pronotum; each elytron
178 moderately elongate (width/length = 1.6), with sinuate posterior margin (Fig. 2D, *spe*), along
179 with a row of posteriorly directed setae (Fig. 2D). Elytral epipleural keel or ridge absent.
180 Hindwings (Figs 1, 2F) fully developed, probably functional, with setae forming fringe along
181 margin. Mesoventrite (Fig. 2E, *msv*) very short, strongly transverse; mesoventral process (Fig.
182 2E) short, sharply pointed. Metaventrite (Fig. 2E, *mtv*) large, weakly transverse; metaventral
183 process between mesocoxae (Fig. 2E) short, seemingly pointed.

184 Legs (Figs 1B, 2B, E) relatively short, slender, lacking spines on tibiae. Protrochantins
185 (Fig. 2B, E, *pt*) large, well exposed; procoxae (Fig. 2B, E, *pc*) conical, small, and contiguous;
186 protrochanters small; profemora clavate, robust; protibiae (Fig. 1B) rod-like, very slender;
187 protarsi 5-segmented, less than half length of protibiae, basal four protarsomeres small and
188 short, together as long as protarsomere 5. Mesocoxae (Fig. 2E, *msc*) obliquely oval, short, at
189 least partially contiguous with each other; mesofemora and mesotibiae similar to those of
190 forelegs in shape, but slightly longer; mesotarsi (Fig. 3C) 5-segmented, about half length of
191 mesotibiae, basal four mesotarsomeres combined moderately longer than mesotarsomere 5,
192 tarsomere 1 (Fig. 3C, *mst1*) much longer than mesotarsomere 2. Metacoxae (Fig. 2E, *mtc*)
193 transverse, sub-triangular, and contiguous; metacoxal lamella not developed; metatrochanters
194 (Fig. 2E) fusiform, large; metafemora clavate, longer than mesofemora; metatibiae rod-like,
195 very slender; metatarsi (Fig. 3E, *mtt*) 5-segmented, more than half length of metatibiae,
196 metatarsomere 1 (Fig. 3E, *mtt1*) longest and about twice as long as tarsomere 2, and therefore,
197 basal four metatarsomeres combined much longer than metatarsomere 5. Claws (Fig. 3C, E)
198 simple, lacking conspicuous basal teeth.

199 Abdomen (Figs 1, 2F) triangular, widest in segment 4, with six visible sterna; sides
200 evenly strongly tapering from segment 4 to apex. Tergites (Figs. 1A, 2F) lacking both
201 pruinose spots and basolateral ridges; tergite III (Fig. 2F, *t3*) partly visible; tergites IV–VI of
202 almost same length, each markedly transverse; tergite VII (Fig. 2F, *t7*) longest; tergite VIII

203 (Fig. 2F, *t8*) largely exposed, elongate, narrowing apically, with rounded posterior margin.
204 Abdominal segments III–VII each with paratergites (one or two pairs, undetermined).
205 Sternites III–VI (Fig. 1B) subequal in length; sternite VII slightly longer; sternite VIII (Fig.
206 3B, *s8*) elongate, narrowing apically, with narrowly rounded apex. Gonocoxites (Figs 1, 2F,
207 3B, *gc*) present, large, cylindrical; surface covered with scattered macrosetae. Styli minute,
208 inconspicuous, much smaller than gonocoxites.

209 Male. Unknown.

210

211

212 4. Discussion

213 Among one extinct and 33 extant subfamilies (Bouchard et al., 2011; Tihelka et al.,
214 2020; Yamamoto, 2021), †*Trichophya minor* sp. nov. can unambiguously be placed in the
215 subfamily Trichophyinae based on the following criteria (Newton et al., 2000): body compact
216 and fusiform, anteriorly located antennal insertion which is partly visible dorsally, head with
217 well-developed neck constriction, maxillary palpus 5-segmented (fourth maxillary palpomere
218 is large and spindle-shaped, whereas the fifth one is minute and hyaline), pronotum without
219 postcoxal processes, protrochantin well exposed, tarsal formula 5-5-5, and abdomen with six
220 visible sterna. One of the most distinctive morphological features is the presence of a
221 specialized antenna, i.e., extremely slender, filiform, and verticillate antennae (Figs 4A,
222 Supplementary Figs 1A, 3C; Newton et al., 2000). However, †*T. minor* sp. nov. lacks such a
223 peculiar antenna as figured (Figs 1, 2A, B, 3A). Interestingly, a single extant *Trichophya*
224 species, namely *T. antennalis* from northwestern India, is known to have a morphologically
225 similar antenna (Fig. 4B, Supplementary Fig. 1B; Ashe and Newton, 1993). In addition, this
226 species shares several important characters with †*T. minor* sp. nov. such as a smaller body,
227 shorter antennae, and somewhat strongly transverse pronotum. Despite their similarities in
228 morphology, †*T. minor* sp. nov. can be clearly differentiated from *T. antennalis* by having the
229 much smaller body and smoother body surface. In this study, we refrain from establishing a
230 new genus which contains these two species because of the general morphological similarities
231 with the other extant *Trichophya* members. The only notable difference between these two
232 species and the rest of others are the structure of the antennae, but it is considered here merely
233 a primitive and ancestral character state, rather than a distinctive derived generic feature.
234 Another remarkable feature of †*T. minor* sp. nov. is its markedly small body size; it is about
235 1.28 mm, whereas the remaining congeners range from 1.7 mm to 3.4 mm, with the exception
236 of *T. minuta* Cameron, 1950 (1.2 mm) from Peninsular Malaysia. Several fossil occurrences

237 have been documented that imply a miniaturization trend for the Kachin amber beetles (e.g.,
238 Yamamoto and Takahashi, 2019; Żyła et al., 2019; Liu et al., 2020d; Li et al., 2020).
239 Although it is difficult to assume a particular reason with evidence for this phenomenon, if
240 they are not just a taphonomic artefact, then there are two hypotheses for explanation: namely,
241 random variation, or paleoenvironmental effect (Liu et al., 2020a). In the latter case, higher
242 ambient temperature and/or lower atmospheric oxygen concentration could be one of the most
243 important factors for contributing to such a miniaturization (Liu et al., 2020a). Alternatively,
244 it could be possible to speculate that these fossils actually indicate a "maximization" trend in
245 comparison with the Recent fauna, since (if we accept the concept of linear time) the Burmese
246 fossils existed long before the modern fauna.

247 The paleofauna of the Kachin amber is considered to have an affinity with Gondwana.
248 Indeed, the West Burma Block where the amber producing forests in Kachin once located was
249 actually connected to a marginal area of the ancient Australian landmass and was gradually
250 uplifted northwards during the Late Triassic to Late Jurassic (Heine and Müller, 2005; Poinar,
251 2019; Westerweel et al. 2019). At the time of the mid-Cretaceous, when the amber was
252 formed, the Block was an isolated island in the Tethys Sea (Westerweel et al. 2019), resulting
253 in the presence of a rich Gondwanan fauna that is currently endemic to the Southern
254 Hemisphere, specifically Australasia or South America (e.g., Cai et al., 2019; Liu et al.,
255 2020b). Of note, the Indian endemic leiodid subgenus *Pentacolonellus* Peck, 1997 of the
256 genus *Colonellus* Szymczakowski (Peck, 1997) has been found from Kachin amber (Cai and
257 Huang, 2017). Thus, our finding of a *Trichophya* species with a possible affinity to India is
258 significant when considering such a Gondwanan association. The current distribution of
259 Trichophyinae, or *Trichophya*, is rather cosmopolitan, known from the Nearctic, northern
260 Neotropical, Palaeartic, Oriental, and Australian regions (Ashe and Newton, 1993; Thayer,
261 2016). However, the native range of this group is narrower and confined to the northern
262 hemisphere; the distribution in Australia should be considered as a result of human
263 introduction (Thayer, 2016). Our discovery shows that *Trichophya* was indigenous to the
264 northern part of Myanmar during the mid-Cretaceous, providing implications for the native
265 distribution of Trichophyinae. Finally, the extant members of *Trichophya* have usually been
266 found from mountaneous areas, whereas the Kachin amber species inhabited in a tropical
267 forest very close to a seashore (Mao et al., 2018; Yu et al., 2019). This may suggest a different
268 ecological strategy of *Trichophya* beetles at that time in comparison with the Recent ones.

269
270

271 **5. Conclusions**

272 A new species, †*Trichophya minor* sp. nov., is herein described from mid-Cretaceous
273 Burmese (Kachin) amber based on a well-preserved adult female. It represents the first fossil
274 record of the subfamily Trichophyinae and increases the total number of staphylinid
275 subfamilies known from Kachin amber from 19 to 20. Our finding also indicates that the
276 extant genus *Trichophya* had originated by the mid-Cretaceous. This new fossil species
277 provides insights into several trends known in Kachin amber, i.e., a long-term morphological
278 stability, Gondwanan affinity, and miniaturization (see Liu et al., 2020a), together with
279 evolutionary insight into a certain specialized body part, namely antennae in our case. The
280 discovery of †*T. minor* sp. nov. may be important as a key fossil calibration point for future
281 dating of molecular phylogenetic trees as there is no fossil record from the presumed sister
282 subfamily Habrocerinae (Cai et al., 2017: supplementary table 2).

283

284

285 **Declaration of interests**

286 The authors declare that they have no known competing financial interests or personal
287 relationships that could have appeared to influence the work reported in this paper.

288

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296

297

298 **References**

299

300 Ashe, J.S., 2005. Phylogeny of the tachyporine group subfamilies and ‘basal’ lineages of the
301 Aleocharinae (Coleoptera: Staphylinidae) based on larval and adult characteristics.
302 Systematic Entomology 30 (1), 3–37. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-3113.2004.00258.x)
303 [3113.2004.00258.x](https://doi.org/10.1111/j.1365-3113.2004.00258.x)

304 Ashe, J.S., Newton Jr., A.F., 1993. Larvae of *Trichophya* and phylogeny of the tachyporine
305 group of subfamilies (Coleoptera: Staphylinidae) with a review, new species and
306 characterization of the Trichophyinae. *Systematic Entomology* 18 (4), 267–286.
307 <https://doi.org/10.1111/j.1365-3113.1993.tb00666.x>

308 Balashov, I., 2021. The first records of mollusks from mid-Cretaceous Hkamti amber
309 (Myanmar), with the description of a land snail, *Euthema myanmarica* n. sp.
310 (Caenogastropoda, Cyclophoroidea, Diplommatinidae). *Journal of Paleontology*, 1–10
311 <https://doi.org/10.1017/jpa.2021.26>

312 Bouchard, P., Bousquet, Y., Davies, A.E., Alonso-Zarazaga, M.A., Lawrence, J.F., Lyal,
313 C.H.C., Newton, A.F., Reid, C.A.M., Schmitt, M., Ślipiński, A., Smith, A.B.T., 2011.
314 Family-group names in Coleoptera (Insecta). *ZooKeys* 88, 1–972.

315 Cai, C., Huang, D., 2017. First fossil Coloninae from Upper Cretaceous Burmese amber
316 (Coleoptera: Staphylinoidea: Leiodidae). *Cretaceous Research* 77, 69–74.
317 <https://doi.org/10.1016/j.cretres.2017.05.005>

318 Cai, C., Lawrence, J.F., Yamamoto, S., Leschen, R.A.B., Newton, A.F., Ślipiński, A., Yin, Z.,
319 Huang, D., Engel, M.S., 2019. Basal polyphagan beetles in mid-Cretaceous amber
320 from Myanmar: biogeographic implications and long-term morphological stasis.
321 *Proceedings of the Royal Society B* 286, 20182175.
322 <https://doi.org/10.1098/rspb.2018.2175>

323 Cai, C., Leschen, R.A., Hibbett, D.S., Xia, F., Huang, D., 2017. Mycophagous rove beetles
324 highlight diverse mushrooms in the Cretaceous. *Nature Communications* 8, 14894.
325 <https://doi.org/10.1038/ncomms14894>

326 Cameron, M., 1932. The fauna of British India including Ceylon and Burma. Coleoptera.
327 Staphylinidae. Volume 3. Taylor and Francis, London. xiii + 1–443 pp.

328 Cameron, M., 1950. New species of Staphylinidae (Col.) from the Malay Peninsula. *The*
329 *Annals and Magazine of Natural History* (series 12) 3, 1–40.

330 Cruickshank, R.D., Ko, K., 2003. Geology of an amber locality in the Hukawng Valley,
331 northern Myanmar. *Journal of Asian Earth Sciences* 21 (5), 441–455.
332 [https://doi.org/10.1016/S1367-9120\(02\)00044-5](https://doi.org/10.1016/S1367-9120(02)00044-5)

333 Grebennikov, V.V., Newton, A.F., 2009. Good-bye Scydmaenidae, or why the ant-like stone
334 beetles should become megadiverse Staphylinidae sensu latissimo (Coleoptera).
335 *European Journal of Entomology* 106 (2), 275–301.

336 Grimaldi, D., Ross, A.J., 2017. Extraordinary Lagerstätten in amber, with particular reference
337 to the Cretaceous of Burma. In: Fraser, N.C., Sues, H.-D. (Eds), *Terrestrial*

338 Conservation Lagerstätten: Windows into the Evolution of Life on Land. Dunedin
339 Academic Press, Edinburgh, pp. 287–342.

340 Gyllenhal, L., 1810. *Insecta Suecica descripta. Classis I. Coleoptera sive Eleuterata. Tomi I.*
341 *Pars II.* L.J. Levertz, Scaris. xix + [1] + 660 pp.

342 Heine, C., Müller, R.D., 2005. Late Jurassic rifting along the Australian North West Shelf:
343 margin geometry and spreading ridge configuration. *Australian Journal of Earth*
344 *Sciences* 52 (1), 27–39. <https://doi.org/10.1080/08120090500100077>

345 Latreille, PA., 1802. *Histoire naturelle, générale et particulière des crustacés et des insectes.*
346 *Tome troisième. Familles naturelles et genres.* F. Dufart, Paris. xii + 13–468 pp.

347 Legner, E.F., Moore, I., 1977. Staphylinidae from under bark and at sap of trees, a
348 preliminary survey of species possibly beneficial to forestry (Coleoptera). *The Great*
349 *Lakes Entomologist* 10 (4), 173–177.

350 Li, Y.-D., Yamamoto, S., Huang, D.-Y., Cai, C.-Y., 2020. A miniaturized ommatid beetle in
351 mid-Cretaceous Burmese amber (Coleoptera: Archostemata: Ommatidae). *Papéis*
352 *Avulsos de Zoologia* 60, e20206063. <https://doi.org/10.11606/1807-0205/2020.60.63>

353 Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera*
354 *species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata.*
355 *Tomus I. Laurentii Salvii, Holmiae.* iv + 824 pp.

356 Liu, Y., Tihelka, E., Huang, D., Tian, L., Cai, C., 2020a. A new fossil species of the rove
357 beetle subfamily Protopselaphinae (Coleoptera: Staphylinidae) from mid-Cretaceous
358 Burmese amber. *Historical Biology*, 1–6.
359 <https://doi.org/10.1080/08912963.2020.1762594>

360 Liu, Z., Tihelka, E., McElrath, T., Yamamoto, S., Ślipiński, A., Wang, B., Ren, D., Pang, H.,
361 2020b. New minute clubbed beetles (Coleoptera, Monotomidae, Lenacini) from mid-
362 Cretaceous amber of northern Myanmar. *Cretaceous Research* 107, 104255.
363 <https://doi.org/10.1016/j.cretres.2019.104255>

364 Liu, Y., Tihelka, E., Tian, L., Huang, D., Cai, C., 2020c. First fossil pseudopsine rove beetle
365 from mid-Cretaceous Burmese amber (Coleoptera: Staphylinidae: Pseudopsinae).
366 *Zootaxa*, 4885 (1), 76–82. <https://doi.org/10.11646/zootaxa.4885.1.4>

367 Liu, Y., Tihelka, E., Yamamoto, S., Yin, Z., Huang, D., Tian, L., Cai, C., 2020d. The first
368 fossil record of the rove beetle subfamily Protopselaphinae (Coleoptera:
369 Staphylinidae) from mid-Cretaceous Burmese amber. *Cretaceous Research* 110,
370 104416. <https://doi.org/10.1016/j.cretres.2020.104416>

371 von Mannerheim, C. G., 1830. Précis d'un nouvel arrangement de la famille des brachélytres
372 de l'ordre des insectes coléoptères. St. Petersburg. 87 pp.

373 Mao, Y., Liang, K., Su, Y., Li, J., Rao, X., Zhang, H., Xia, F., Fu, Y., Cai, C., Huang, D.,
374 2018. Various amber ground marine animals on Burmese amber with discussions on
375 its age. *Palaeoentomology* 1 (1), 91–103.
376 <https://doi.org/10.11646/palaeoentomology.1.1.11>

377 Miyashita, K., 1997. On the male of *Trichophya japonica* (Coleoptera, Staphylinidae). *Elytra*,
378 Tokyo 25 (1), 84.

379 Newton Jr., A. F., 1984. Mycophagy in Staphylinidea (Coleoptera). In: Wheeler, Q.,
380 Blackwell, M. (Eds.), *Fungus-insect relationships: perspectives in ecology and*
381 *evolution*. Columbia University Press, New York, pp. 302–353.

382 Newton, A. F., Thayer, M. K., Ashe, J. S., Chandler, D. S., 2000. Staphylinidae Latreille,
383 1802. In: Arnett, R. H., Thomas, M. C. (Eds.), *American Beetles*. CRC Press, Boca
384 Raton, pp. 272–418.

385 Orlov, I., Leschen, R. A., Żyła, D., Solodovnikov, A., 2020. Total-evidence backbone
386 phylogeny of Aleocharinae (Coleoptera: Staphylinidae). *Cladistics*, 1–32.
387 <https://doi.org/10.1111/cla.12444>

388 Peck, S. B., 1997. *Colonellus (Pentacolonellus) gilli*, new subgenus and new species from
389 India (Coleoptera: Leiodidae: Coloninae). *Elytron*, Barcelona 11, 63–70.

390 Poinar Jr., G., 2019. Burmese amber: evidence of Gondwanan origin and Cretaceous
391 dispersion. *Historical Biology* 31 (10), 1304–1309.
392 <https://doi.org/10.1080/08912963.2018.1446531>

393 Ross, A. J., 2019. Burmese (Myanmar) amber checklist and bibliography 2018.
394 *Palaeoentomology* 2 (1), 22–84. <https://doi.org/10.11646/palaeoentomology.2.1.5>

395 Ross, A. J., 2020. Supplement to the Burmese (Myanmar) amber checklist and bibliography,
396 2019. *Palaeoentomology* 3 (1), 103–118.
397 <https://doi.org/10.11646/palaeoentomology.3.1.14>

398 Ross, A. J., 2021. Supplement to the Burmese (Myanmar) amber checklist and bibliography,
399 2020. *Palaeoentomology* 4 (1), 57–76.
400 <https://doi.org/10.11646/palaeoentomology.4.1.11>

401 Shi, G., Grimaldi, D. A., Harlow, G. E., Wang, J., Wang, J., Yang, M., Lei, W., Li, Q., Li, X.,
402 2012. Age constraint on Burmese amber based on U–Pb dating of zircons. *Cretaceous*
403 *Research* 37, 155–163. <https://doi.org/10.1016/j.cretres.2012.03.014>

404 Shibata, Y., 2001. A new species of the genus *Trichophya* (Coleoptera, Staphylinidae) from
405 Taiwan. *Elytra*, Tokyo 29 (2), 352–357.

406 Thayer, M. K., 2016. Staphylinidae Latreille, 1802. In: Beutel, R. G., Leschen, R. A. B.
407 (Eds.), *Handbook of Zoology; Arthropoda: Insecta, Coleoptera, Beetles. Volume 1:*
408 *Morphology and systematics (Archostemata, Adephaga, Myxophaga, Polyphaga*
409 *partim)*. 2nd edition. De Gruyter, Berlin/Boston, pp. 394–442.

410 Thomson, C. G., 1858. Försök till uppställning af Sveriges Staphyliner. Öfversigt af Kongliga
411 Vetenskaps-Akademiens Förhandlingar 15, 27–40.

412 Tihelka, E., Thayer, M. K., Newton, A. F., Cai, C., 2020. New data, old story: molecular data
413 illuminate the tribal relationships among rove beetles of the subfamily Staphylininae
414 (Coleoptera: Staphylinidae). *Insects* 11 (3), 164.
415 <https://doi.org/10.3390/insects11030164>

416 Westerweel, J., Roperch, P., Licht, A., Dupont-Nivet, G., Win, Z., Poblete, F., Ruffet, G.,
417 Swe, H. H., Thi, M. K., Aung, D. W., 2019. Burma Terrane part of the Trans-Tethyan
418 arc during collision with India according to palaeomagnetic data. *Nature Geoscience*
419 12, 863–868. <https://doi.org/10.1038/s41561-019-0443-2>

420 Yamamoto, S., 2021. Tachyporinae revisited: Phylogeny, evolution, and higher classification
421 based on morphology, with recognition of a new rove beetle subfamily (Coleoptera:
422 Staphylinidae). *Biology*, 10 (4): 323. <https://doi.org/10.3390/biology10040323>

423 Yamamoto, S., Caron, E., Bortoluzzi, S., 2019. *Propiestus archaicus*, the first Mesozoic
424 amber inclusion of piestine rove beetles and its evolutionary and biogeographical
425 significance (Coleoptera: Staphylinidae: Piestinae). *Journal of Systematic*
426 *Palaeontology* 17 (15), 1037–1050. <https://doi.org/10.1080/14772019.2018.1517282>

427 Yamamoto, S., Maruyama, M., 2018. Phylogeny of the rove beetle tribe Gymnusini sensu n.
428 (Coleoptera: Staphylinidae: Aleocharinae): Implications for the early branching events
429 of the subfamily. *Systematic Entomology* 43 (1), 183–199.
430 <https://doi.org/10.1111/syen.12267>

431 Yamamoto, S., Takahashi, Y., 2019. First and oldest Leptochirini rove beetles illuminate
432 diverse cephalic structures in the Cretaceous (Coleoptera: Staphylinidae:
433 Osoriinae). *Systematic Entomology* 44 (3), 588–611.
434 <https://doi.org/10.1111/syen.12342>

435 Yu, T., Kelly, R., Mu, L., Ross, A., Kennedy, J., Broly, P., Xia, F., Zhang, H., Wang, B.,
436 Dilcher, D., 2019. An ammonite trapped in Burmese amber. *Proceedings of the*

437 National Academy of Sciences of the United States of America 116 (23), 11345–
438 11350. <https://doi.org/10.1073/pnas.1821292116>
439 Żyła, D., Yamamoto, S., Jenkins Shaw, J., 2019. Total-evidence approach reveals an extinct
440 lineage of Paederinae rove beetles from the Cretaceous Burmese amber. *Palaeontology*
441 62 (6), 935–949. <https://doi.org/10.1111/pala.12435>

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443 Appendix A. Supplementary data

444 Supplementary data to this article can be found online at <https://doi.org/>

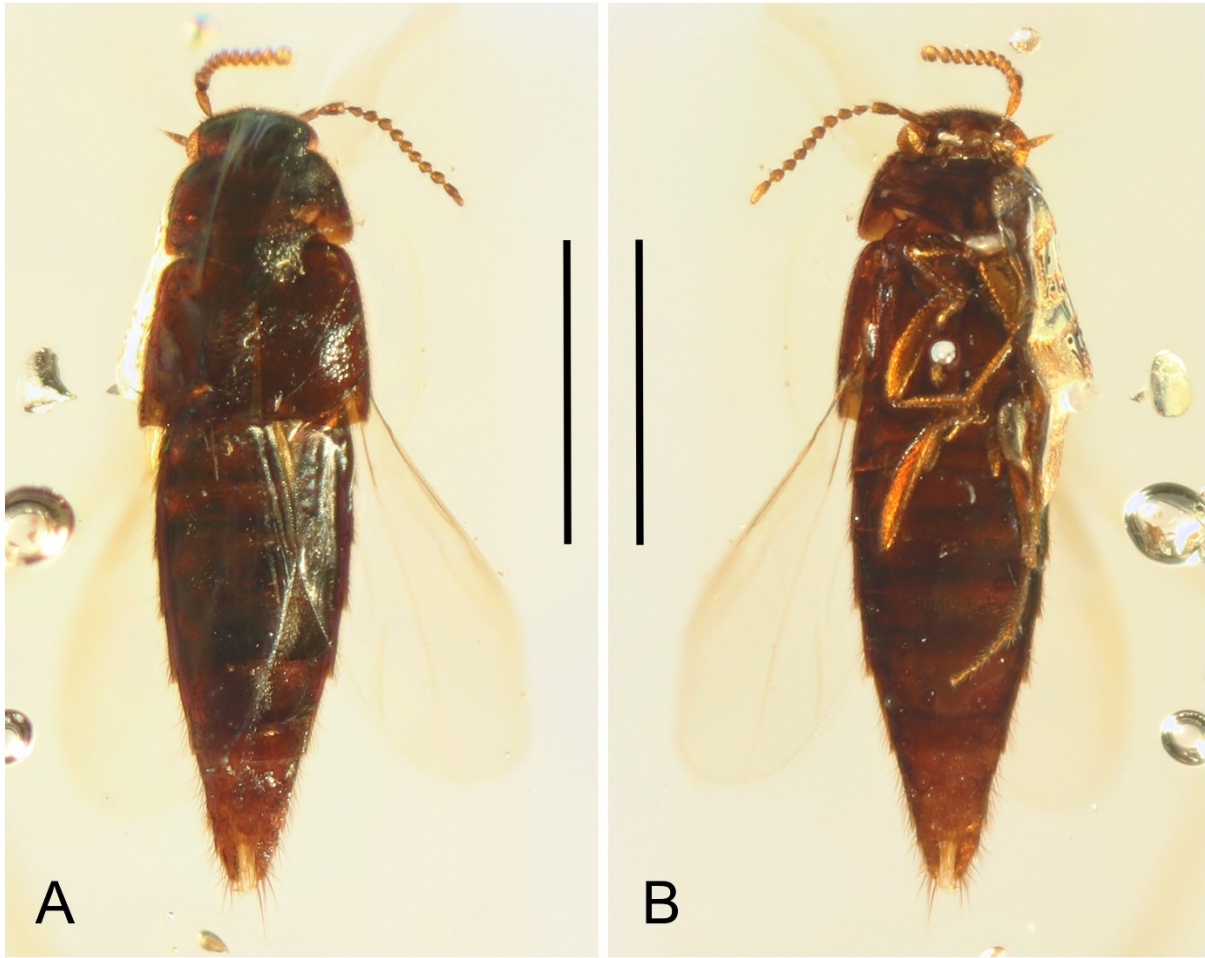
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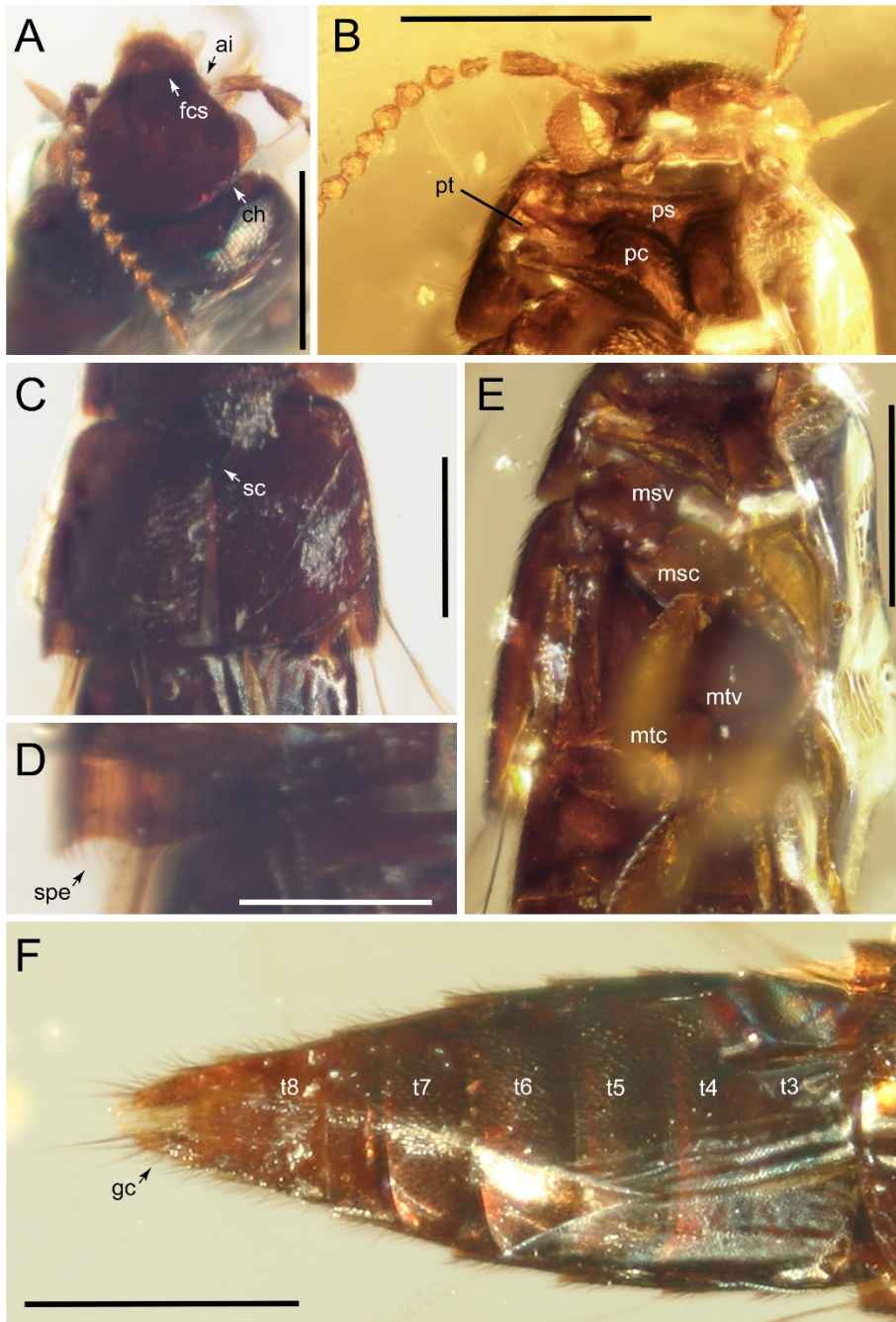
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452 **Fig. 1.** Habitus photographs of holotype (FMNHINS-4357787) of †*Trichophya minor* sp. nov.
453 in mid-Cretaceous Kachin amber from northern Myanmar. A. dorsal view; B. ventral view.

454 Scale bars: 0.5 mm.

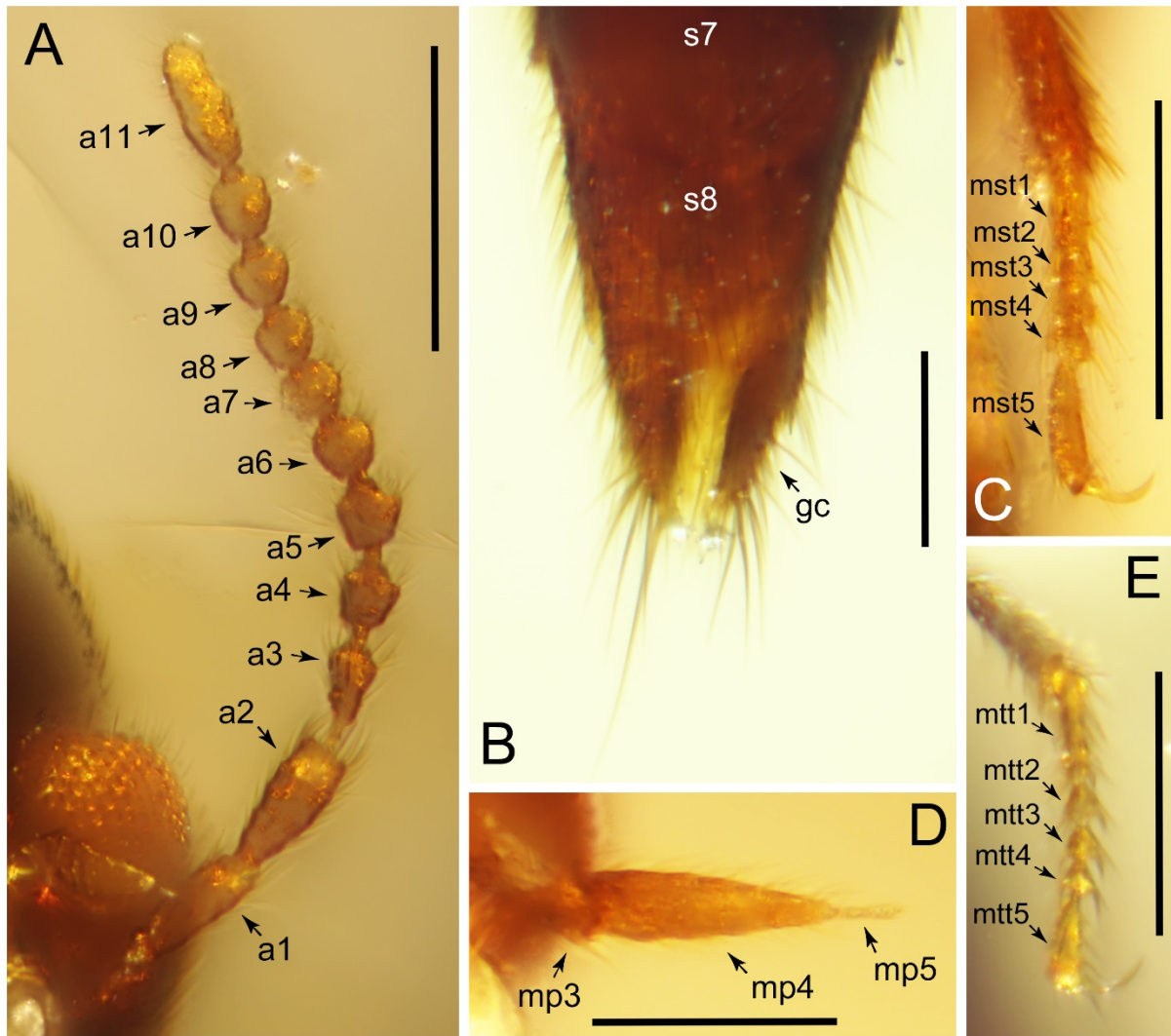
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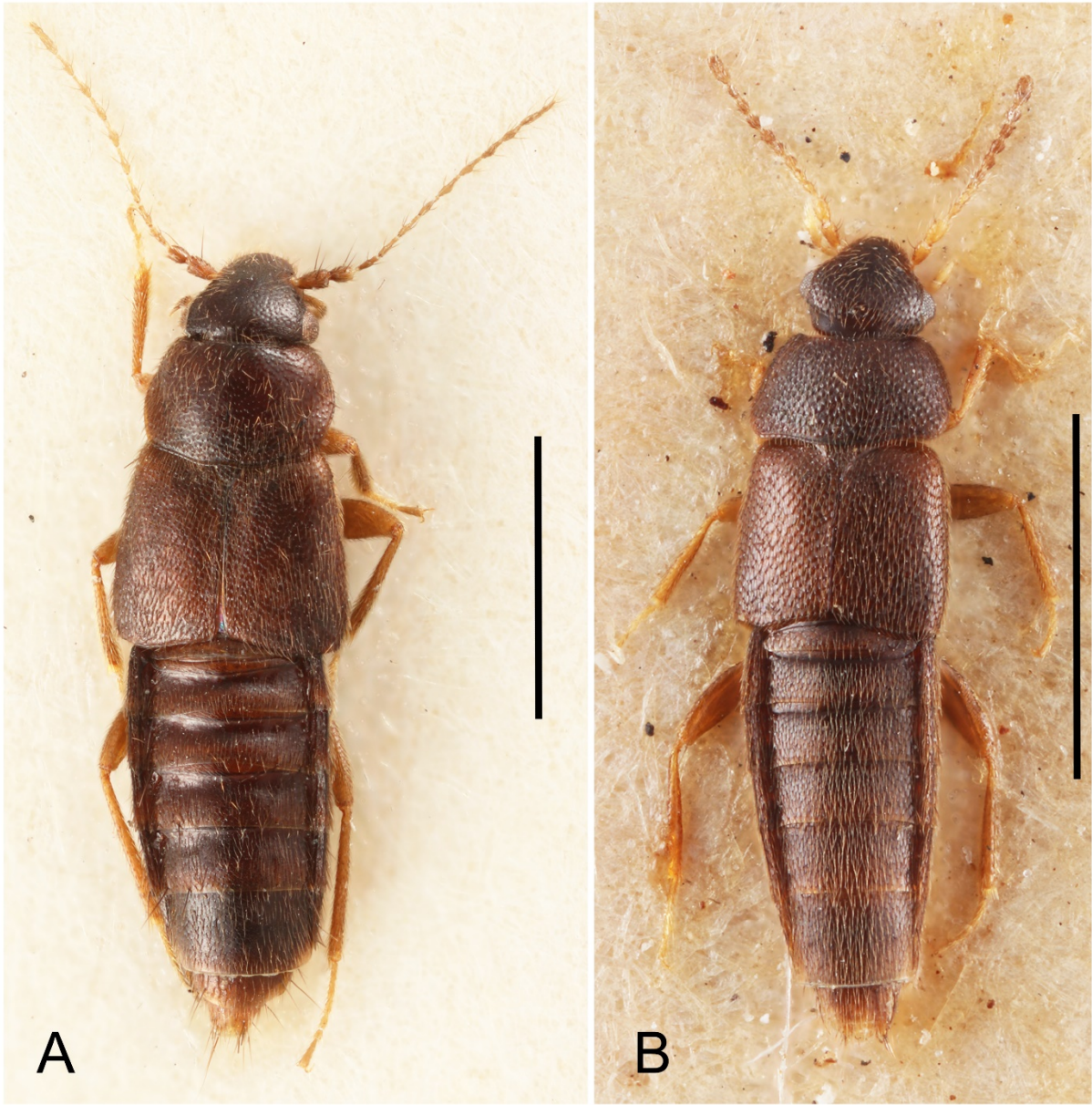
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458 **Fig. 2.** Morphological details of holotype (FMNHINS-4357787) of †*Trichophya minor* sp.
 459 nov. in mid-Cretaceous Kachin amber from northern Myanmar. A. head and left antenna,
 460 dorsal view; B. head, prothorax, and procoxae, ventral view; C. Elytra and mesoscutellum,
 461 dorsal view; D. posterior margin of left elytron, dorsal view; E. Meso- and metathorax,
 462 ventral view; F. Abdomen, dorsal view. Abbreviations: ai, antennal insertion; ch, basal carina
 463 on head; fcs, frontoclypeal suture; gc, gonocoxite; msc, mesocoxa; msv, mesoventrite; mtc,
 464 metacoxa; mtv, metaventrite; pc, procoxa; ps, prosternum; pt, protrochantin; sc,
 465 mesoscutellum; spe, sinuate posterior margin of elytron; t3–8, tergites 3–8. Scale bars: 0.2
 466 mm (A–C, E), 0.1 mm (D), 0.3 mm (F).



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 468 **Fig. 3.** Morphological details of holotype (FMNHINS-4357787) of †*Trichophya minor* sp.
 469 nov. in mid-Cretaceous Kachin amber from northern Myanmar. A. right antenna, ventral
 470 view; B. abdominal terminalia, ventral view; C. left mesotarsus, ventral view; D. left
 471 maxillary palpus; E. left metatarsus, ventral view. Abbreviations: a1–11, antennomeres 1–11;
 472 gc, gonocoxite; mp3–5, maxillary palpomeres 3–5; mst1–5, mesotarsomeres 1–5; mtt1–5,
 473 metatarsomeres 1–5; s7–8, sternites 7–8. Scale bars: 0.1 mm (A–C, E), 0.05 mm (D).

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477 **Fig. 4.** Extant species of Trichophyinae. A. *Trichophya pilicornis* (Gyllenhal) from Austria;

478 B. *T. antennalis* Cameron from northwestern India. Scale bars: 1.0 mm.

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488 **Highlights**

489 • The first fossil Trichophyinae is described from mid-Cretaceous Burmese amber and placed
490 in the extant genus *Trichophya*.

491

492 • †*Trichophya minor* sp. nov. is closely related to the extant species *T. antennalis* from India
493 based on antennae and body size.

494

495 • Our finding indicates that Trichophyinae had originated by the mid-Cretaceous.

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497 • Our discovery is also congruent with the hypothesis of the Gondwanan origin of Burmese
498 (Kachin) amber.

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