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**Taxonomic reassessment of the Japanese Histeroidea (Coleoptera) and
phylogenetic reconstruction based on female genitalia characters**

**日本産エンマムシ上科(昆虫綱鞘翅目)の分類学的再検討と
雌生殖器形質に基づく系統構築**

北海道大学 大学院農学院
農学専攻 環境フロンティアコース 博士後期課程

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**Taxonomic reassessment of the Japanese Histeroidea (Coleoptera) and
phylogenetic reconstruction based on female genitalia characters**

**A thesis submitted to the Graduate School of Agriculture, Hokkaido
University for the degree of Doctor of Philosophy**

**by
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Abstract

The superfamily Histeroidea (Coleoptera) is a group of beetles that gather around decaying organic matter such as animal feces, decomposed animal carcasses, compost, and decaying plants. They prey on various insect larvae and other organisms inhabiting organic matter. Known as predators of agricultural and forestry pests, they are particularly recognized for their use in biological control, notably in controlling order Diptera within poultry houses and reducing the population of family Scolytinae. The predator-prey relationship in biological pest control often exhibits species specificity, hence the necessity for fundamental information on the classification, feeding habits, and life cycle of the superfamily Histeroidea for its effective application. Furthermore, the taxonomic and systematic information for the superfamily Histeroidea remains insufficiently developed. The superfamily Histeroidea consists of three families: Sphaeritidae with seven species, Synteliidae with eight species, and Histeridae with approximately 5,000 species known worldwide. In Japan, one species, one species, and 121 species were recorded for each respective family. A reevaluation of each group was conducted in the late 1980s, resulting in a comprehensive understanding of the taxonomic description of the superfamily Histeroidea in Japan. Previous descriptive studies primarily emphasized external morphology and male genitalia, neglecting detailed comparisons of traits related to the complex structures of mouthparts and female genitalia. Furthermore, in phylogenetic analyses within the superfamily, traits primarily focusing on adult external morphology and male genitalia, along with DNA sequences, have been used, with only a few studies incorporating other characteristics. Female genitalia have generally been considered to evolve more slowly with fewer morphological changes compared to male genitalia (Eberhard, 1985), hence not recognized for providing phylogenetic information

and have not been utilized in phylogenetic analyses. However, studies targeting the subfamily Saprinae and tribe Exosternini within the family Histeridae conducted phylogenetic analyses including traits of mouthparts and female genitalia, reporting that both mouthparts and female genitalia possess useful character states for phylogenetic analysis (Caterino & Tishechkin, 2015; Lackner & Tarasov, 2019).

In this study, we aimed to: 1) conduct detailed morphological observations of adult external morphology using scanning electron microscope (SEM) images and describe the mouthparts and female genitalia, 2) explore novel traits effective for taxonomic description and phylogenetic analysis, 3) focus on the female copulatory organs suggested to be effective in phylogenetic analysis, attempting to construct the phylogeny within the superfamily by extracting new traits and character states, and 4) accumulate and enrich new taxonomic and phylogenetic insights specific to the superfamily Histeroidea in Japan.

For the organization of fundamental descriptive taxonomic information, detailed descriptions were conducted for two genera found in Japan (*Hypocacculus* with one species and *Hypocaccus* with four species) within the family Histeridae, subfamily Saprinae, where previous studies (Lackner, 2010; Lackner & Tarasov, 2019) had standardized the morphological similarities and terminology of mouthparts and female genitalia. Through comparison with prior research, a thorough confirmation and redefinition of the external morphology, mouthparts, and female genitalia detailed morphology and terminology were carried out. Additionally, previously unidentified traits and their states were newly identified.

For comparison with the family Histeridae, detailed descriptions were conducted for one species from family Sphaeritidae and one species from family Synteliidae, which are considered more primitive lineages. Particularly, observations were made using

scanning electron microscope (SEM) images of adult specimens and detailed anatomical dissections of their mouthparts and female genitalia. Numerous new character states in the morphology of family Sphaeritidae and family Synteliidae were identified, allowing for the recognition of distinguishing character states between each family when compared to the family Histeridae. Notably, distinct differences in the traits of female genitalia among these families were observed, suggesting that these traits might be useful for phylogenetic analysis.

Given the suggested utility of female copulatory organ traits in phylogenetic analysis, additional observations were conducted on the female genitalia of family Sphaeritidae, family Synteliidae, and family Histeridae (one species of *Hypocacculus* and four species of *Hypocaccus*), as well as 19 species spanning 18 genera across six subfamilies within family Histeridae. These observations were conducted using recognized and defined terminology for the identified homologous traits, and the outcomes were meticulously documented through detailed descriptions and schematic diagrams.

In the construction of phylogenetic relationships, observations of the female genitalia from 26 species across three families of the superfamily Histeroidea led to the extraction and classification of 39 useful character states for phylogenetic analysis. These states were categorized and used to create a data matrix. Using this matrix, phylogenetic trees were constructed with PAUP* 4.0b1 and Mesquite.3.81. The resulting trees broadly supported the findings of previous studies that used both external morphology and DNA sequence information for phylogenetic analysis. This highlighted distinct differences in the traits of female genitalia among taxonomic groups, confirming their utility as valuable traits for phylogenetic analysis.

From this, our study confirmed numerous new traits and character states in the female genitalia of the superfamily Histeroidea, demonstrating their utility as valuable traits for phylogenetic analysis. The outcomes of this research have significantly enhanced the accuracy of understanding the phylogenetic relationships within the three families of the superfamily Histeroidea. Moreover, the discovery of numerous new traits contributes to accumulating descriptive taxonomic information, enhancing the reliability of taxonomic recognition and species identification, while also fostering advancements in applied entomology.

Chapter 1. General introduction

The superfamily Histeroidea is composed of three families, Sphaeritidae, Synteliidae and Histeridae. The Sphaeritidae and the Synteliidae are small families, comprising seven and eight known species, respectively. The Histeridae or histerid beetles form a fairly large group, containing about 5,000 described species, and are broadly distributed over the world. In Japan, there are currently one species known from Sphaeritidae, one species from Synteliidae, and 121 species from Histeridae.

Most Histeroidea species are predators, inhabiting various types of decaying organic matter such as animal feces, decomposed animal carcasses, compost, and other decaying plants, and preying on various larvae found within. According to Ôhara (1996b), *Niponius* from the family Histeridae is recognized as a natural enemy of the significant forestry pest, the Scolytidae family. Furthermore, research by Miwa (1938) utilizing *Presius javanus* of the family Histeridae demonstrated biological control against *Rhabdoscelus obscurus*, an invasive species of the family Dryophthoridae causing damage to bananas. Additionally, Ikeoka (2015) reported biological control of order Diptera larvae in poultry houses using *Merohister jekeli* and *Carcinops quatuordecimstriatus* of the family Histeridae. Predator-prey relationships in biological control often exhibit species specificity, necessitating fundamental information on the taxonomy, feeding habits, and life history of Histeroidea species for practical applications. The taxonomic research on the superfamily Histeroidea has long been overlooked in Japan outside of catalogs. They have long been overlooked in Japan. Although there have been modern reassessments of certain tribes and genera since the late 1980s (Ôhara & Nakane, 1986, 1989; Ôhara, 1986, 1989, 1991a, b, 1992a, b, c, 1993, 1994, 1999a, b), research on Japanese Histeroidea has advanced significantly, but many aspects such as

various taxonomic relationships and ecologies remain unresolved.

The monophyly of the three families within the superfamily Histeroidea is broadly supported, either as a sister group to Hydrophiloidea, as per McKenna *et al.* (2015), or as a clade within the superfamily Hydrophiloidea, as supported by Beutel (1999) and Bernhard *et al.* (2009). The distinction between the superfamilies Hydrophiloidea and Histeroidea was considered inadequate based on a reevaluation of beetle higher classification by Lawrence and Newton (1982). As a result, Bouchard *et al.* (2011) and Ślipiński *et al.* (2011) did not recognize the superfamily Histeroidea. However, analyses using DNA conducted by McKenna *et al.* (2015) and Cai *et al.* (2022) have distinguished between the superfamilies Hydrophiloidea and Histeroidea, as referenced in works by Lackner *et al.* (2023) and Ôhara (2023[2022]), among others. Newton (2016) and others have indicated that further investigation is necessary, emphasizing the need for expanded sampling in these discussions.

The analyses conducted so far have mainly focused on the external features of adult Histeroidea, morphological characteristics of the male genitalia, and DNA sequences. While analyses of smaller taxonomic groups like Exosternini (Caterino & Tishechkin, 2015) and Saprininae (Lackner & Tarasov, 2019) have included features of the female genitalia, these have not been employed in analyses covering the entire Histeroidea. Resolving the classification system within Histeridae, from genera to tribes and even subfamilies, requires substantial work. While there are intriguing suggestions regarding the ecological and morphological evolution within this diverse group, the low confidence in many major branches hinders definitive conclusions (Kovarík & Caterino, 2016).

In previous researches, the extraction and utilization of traits related to the female

genitalia in insect taxonomy were limited. The present study aims to enhance the reliability of phylogenetic analysis in Histeroidea by extracting new features based on detailed scanning electron microscope (SEM) images of adult external morphology, as well as detailed sketches and descriptions of both mouthparts and the female genitalia.

In Chapter 2, detailed descriptions are provided regarding the external morphology, mouthparts, and female genitalia of Sphaeritidae and Synteliidae, which are considered as outgroups in the phylogenetic analysis. Chapter 3 provides detailed descriptions of the external morphology, mouthparts, and female genitalia of *Hypocacculus* and *Hypocaccus*, belonging to the Saprinae, among the Histeridae considered as the ingroup for phylogenetic analysis. This is conducted to compare and examine these details with Saprinae, where Lackner (2010) and Lackner and Tarasov (2019) have conducted detailed descriptions and organized terminology regarding the external morphology, mouthparts, and female genitalia. Chapter 4, focusing on the results from Chapters 2 and 3, particular attention was given to the female genitalia. Detailed descriptions of the female genitalia were provided for two species in the outgroup and 24 species in the ingroup. Chapter 5, the characteristics of the female genitalia obtained in Chapter 4 are summarized. In Chapter 6, a phylogenetic analysis is conducted based on the summarized characteristics from Chapter 5, presenting the results and discussions derived from it.

Chapter 2. Detailed descriptions of representative species used as outgroups for the phylogenetic analyses

2-1. Introduction

In this chapter, detailed descriptions are provided for one species each from the family Sphaeritidae and the Synteliidae, treated as outgroups in the phylogenetic analysis of Japanese Histeroidea. Comprehensive descriptions of the external morphology, mouthparts, and female genitalia were conducted. Sphaeritidae and Synteliidae are characterized by more primitive body structures compared to Histeridae and have been utilized as outgroups in various phylogenetic analyses of Histeroidea. Previous studies on Sphaeritidae have focused on external morphology (Kryzhanovskij & Reichardt, 1976; Ôhara, 1994), mouthparts (Williams, 1936), tentorium (Stickney, 1923), male genitalia, female spermatheca (Ôhara, 1994), female genitalia (Hansen, 1997). Regarding Synteliidae, previous researches have included reports on larval morphology (Mamayev, 1974; Hayashi, 1986), studies on fossils (Jiang & Wang, 2021), external morphology (Kryzhanovskij & Reichardt, 1976; Ôhara, 1994; Zhou *et al.*, 2003), male genitalia, female spermatheca, and its glands (Ôhara, 1994). However, detailed illustrations or descriptions of the fine structures of external morphology and the detailed depiction of mouthparts and female genitalia were lacking for these families in previous studies.

In this study, detailed redescriptions of the external morphology and mouthparts using scanning electron microscopy (SEM) for *Sphaerites glabratus* and *Syntelia histeroides* were conducted, particularly focusing on detailed descriptions of the female genitalia.

2-2. Material and methods

Terminology. The terminology for mouthparts follows Williams (1936) and Lackner (2010) (Table 1), the terminology for tentorium follows Stickney (1923), and the terminology for female genitalia follows Ôhara (1994), Caterino and Tishechkin (2015), and Lackner and Tarasov (2019) (Table 2). In this study, the sequence of species names followed the arrangement by Ôhara (2023[2022]), with species not listed in Ôhara (2023[2022]) inserted alphabetically.

Genitalia dissection. All specimens were dry mounted and relaxed in warm water for several hours or overnight. The beetles were mounted on triangular points and observed under NIKON SMZ645 binocular microscope with diffuse light. Mouthparts were macerated in hot 10 % KOH solution for up to 45 minutes and cleared in 80 % ethanol. Observations of the female genitalia follows the methods described in Ôhara (1994): the female genitalia were first macerated in hot 10 % KOH solution for up to 45 minutes, cleared in 80 % ethanol, macerated in lactic acid with fuch sine and heated at 60 °C for an hour, and subsequently treated with acetyl salicylate heated at 60 °C for 15 minutes and cleared in xylene. The genitalia were then observed in α -terpineol in a small glass dish. The mouthparts and genitalia were subsequently mounted in Canada balsam on a small glass slide following the methods described by Maruyama (2004).

Digital photography. Digital photographs of the specimens were taken by NIKON 4500 Coolpix camera attached to a NIKON SMZ745T microscope and edited in Adobe Creative Cloud Photoshop (version 25.1), and were illustrated using an iPad Air APP Procreate. All illustrations were then adjusted using Adobe Illustrator.

Collection acronyms with curators (*: former curator). Specimens examined in this study are deposited in the following collections in Japan:

CITO – Private collection of Mr. Tateo Ito, Kyoto

CKIK – Private collection of Mr. Tomoki Kikuchi; Sapporo

CKIN – Private collection of Mr. Takeshi Kinoda; Miyakonojō

CNKT – Private collection of Mr. Masahiko Nakatani, Hokkaido

CSBT – Private collection of the late Mr. Taichi Shibata; Osaka

CTYS – Private collection of Mr. Kentaro Toyoshima, Gifu

CYMT – Private collection of Dr. Masanori Yamamoto, Shiga

CYSD – Private collection of Mr. Masataka Yoshida, Tokushima

EUM – Laboratory of Environmental Entomology, Ehime University Museum,
Matsuyama; Drs. Sadanari Hisamatsu*, Nobuo Ohbayashi*, Masahiro Sakai*,
Kazuhiko Konishi, Hiroyuki Yoshitomi

HMNH – Hiwa museum for Natural History, Shobara; Drs. Shingo Nakamura*, Yoshihiro
Senda

KMNH – Kanagawa Prefectural Museum of Natural History, Odawara; Dr. Kyohei
Watanabe

KUM – Kyushu University Museum, Fukuoka; Drs. Katsura Morimoto*, Osamu
Tadauchi*, Hiroaki Kojima*, Munetoshi Maruyama

OMNH – Osaka Museum of Natural History, Mr. Shigehiko Shiyake*, Dr. Shunpei Fujie

SEHU – Laboratory of Systematic Entomology, The Hokkaido University Museum,
Sapporo; Dr. Masahiro Ôhara

2-3. Results

Taxonomy

Superfamily **Histeroidea** Gyllenhal, 1808

Family **Sphaeritidae** Thomson, 1862

Genus *Sphaerites* Duftschmidt, 1805

Sphaerites glabratus (Fabricius, 1792)

[Japanese name: Emmamushi-damashi]

(Figs. 1, 27–32, 61, 107, 108)

Hister glabratus Fabricius, 1792: 73 [description; type locality: Germania Dom. (Germany)].

Sphaerites politus Mannerheim, 1846: 514; Adachi & Ohno 1962: 148 [misidentification Japan: Hokkaido, Mt. Kuro-dake]; Nakane 1963: 67, pl. 34, no. 1 [figured, with note]; Kryzhanovskij & Reichardt 1976: 22; Matsumoto 1981: 6 [Hokkaido, Hidaka Mountain Range]; Yasuda 1982: 76 [Hokkaido, Daisetsu-zan mountains]; Hisamatsu 1985: 219, pl. 40, no. 1 [figured, with note]; Yasuda 1988: 25; Ôhara 1994, 58 [redescription, male genitalia, spermatheca]; Ôhara 1996: 2.

Sphaerites glabratus: Löbl, 1996: 199; Ôhara, 1999: 77; Lackner *et al.*, 2015: 76 [catalogued]; Hongzhang *et al.*, 2022: 63 [note]; Ôhara, 2023[2022]: 59 [catalogued].

Description. Labrum (Fig. 27C, D) strongly transverse (width/length ratio 2.8, $n = 5$), with more than 10 pairs of lateral fringe and two pairs of labral setae. Mandibles (Figs. 27A, B, 32) with sharp apex, asymmetric, complete molae, dense small setae on dorsal of basal 1/6. Ventral side, one row of long setae on inner side. Ligula of labium (Fig. 28A, B) densely furnished with short setae on dorsal side. Paraglossa shaped slender (width/length ratio 0.2, $n = 5$), covered with setae. Mentum exhibits sexual dimorphism, with male mentum (Fig. 28D) being ovalshaped (width/length ratio 1.7, $n = 3$) and slightly concave, densely covered with setae on ventral side. Female mentum (Figs. 28C, 29E)

trapezoidal, highly transverse (width/length ratio 2.7, $n = 5$), slightly convex, smooth, with rows of punctures at base, and sparsely covered with setae on outer margin. Submentum (Fig. 29E) significantly swollen and with coarsely large punctures. Middle of gena (Fig. 29E) with constriction crosses ventral side of head, and surrounding area coarsely rugae. Several elongated palpal organs on outside of base and apical of the terminal labial palpomere (Fig. 28A, B, C), as well as on outside of base and apical of terminal maxillary palpomere (Figs. 27E, F, 31D). Maxilla (Fig. 27E, F) with developed lacinial hook. Membranous region between lacinia and palpifer densely covered with setae oriented towards tip. Mediostipes and palpifer with single row of setae. Tentorium (Fig. 28E, F) developed, and each arm thickened. Cervical sclerites (Fig. 28D, F, G) consist of cervepimeron and cervepisternum, with several setae at tip of cervepisternum. Proventriculus (Fig. 28H, I) without sutural teeth, consisting of eight slender longitudinal hairy bands, on posterior 1/4 of proventriculus.

Underside of elytron of simple structure, furnished with microsetae. Mesoscutum and abdominal tergites with micro rugae. Fifth abdominal tergite without groove to lock elytra.

Protarsus originates from ventral side of protibia, and without groove on dorsal surface of protibia to accommodate protarsus. (Fig. 31B, C). Apical spines (Fig. 31B, C) with two particularly large denticles.

Divided eighth tergite of female genitalia (Fig. 61). Eighth sternite undivided. Posterior end of the ninth tergite with three pairs of long setae. Ninth tergite in basal direction fused with ninth sternite in basal direction (valvifer) and ninth sternite in apical direction. Ninth tergite in apical direction absent. Ninth sternite in basal direction (valvifer) short. Anterior part of ninth sternite in basal direction (valvifer) not paddle-

shaped. Tenth tergite expanded posteriorly. Posterior end of tenth tergite with one pair of long setae. Tenth sternite absent. Articulating sclerite slender. Coxite short and robust, with a shovel-like shape, with external surface separated from internal surface by elevated lateral ridges. Coxite with two apical teeth. Both dorsal and ventral surfaces of coxite with sparse setae. Articular membrane closed, apical edge remote from apical emargination between teeth, and broad. Articular membrane with six setae. Stylus with eight setae at tip. Inside of oviduct densely covered with fine setae. Bursa copulatrix small and with a small expandable membrane. Spermatheca composed of one receptacle, not sclerotized. Spermathecal gland not sclerotized, extremely slender, and with numerous fine, round-tipped hairs on surface, attached posterior side of spermatheca. Length of spermathecal duct approximately four times length of spermatheca. spermathecal duct attached posterior end of oviduct. Membranous short protrusion present near ventral base of coxite.

Specimens examined. All specimens are deposited in SEHU. The collection locality of the specimen below is “Mt. Kuro-dake Daisetsuzan, Kamikawa-shichô, Hokkaido”, and the collector is “N. Yasuda”: 1 ex., 26.VI.1981; 1 ex., 21.VII.1977; 1 ♀ (TK-23-006), 3 exs., 29.VIII.1977; 1 ex., alt. over 1,800 m, 7.IX.1977; 4 exs., alt. 1,800 m, 18.VII.1981; 1 ♂ (TK-23-011), 7 exs., alt. 1,900 m, 23.VII.1981; 6 exs., alt. 1,800 m, 27.VII.1981; 1 ex., alt. 1,980 m, 27.VII.1981; 1 ex., 11.VIII.1981; 5 exs., alt. 1,900 m, 11.VIII.1981; 1 ♂, 2 exs., alt. 1,800 m, 15.VIII.1981; 1,900 m, 2 exs., 15.VIII.1981; 2 exs., 21.VIII.1981; 1 ex., alt. 1,800 m, 21.VIII.1981; 1 ex., 12.IX.1981; 1 ♀ (TK-23-013), 1 ♂ (TK-23-088), 5 exs., alt. 1,800 m, 28.VII.1982; 4 exs., 20.VII.1987, st. 1; 4 ♀♀ (TK-23-012, TK-23-017), 30.VII.1987; 3 ♀♀ (TK-23-008), 2 exs., 7.VIII.1987; 2 exs., 21.VIII.1987. 1 ex., Akaishi Renge, Daisetsuzan, 2.VIII.1977, N. Yasuda leg. (SEHU); 1

ex., Mt. Aka-dake, Daisetsuzan, 16.VIII.1984, N. Yasuda leg. (SEHU); 1 ex., Daisetsugenseirin, 4.VIII.1982, N. Yasuda leg., St. 2 (SEHU).

Distribution. Japan (Hokkaido, Rishiri Is.), Europe, Siberia, Russian Far East, China, Mongolia.

Biology. Regarding the biology of *Sphaerites glabratus* in Japan, there are reported the following: 1) They were found under rocks near mountaintops (Matsumoto, 1981), and 2) they were collected from pitfall traps in forests of *Pinus pumila* at elevations of 1800–1980 meters (Yasuda, 1982). Regarding the biology of *S. glabratus*, Newton (2000) summarizes as follows. “These usually rare beetles are generally associated with decaying organic matter such as dung, carrion, fungi, fermenting fruit, and sap of dying or dead trees and stumps, but their ecology is poorly known and the full life cycle has not been observed in detail. *S. glabratus* has been associated especially with northern conifer forests, sometimes at high altitudes; adults are attracted to sap flows on birch stumps, and have been observed to feed on the sap and mate there; females laid eggs in nearby sap-impregnated soil, and larvae developed quickly with the next generation of adults emerging within a month (Nikitsky, 1976).”

Remarks. Regarding the ninth tergite in the basal direction and the ninth tergite in the apical direction, this paper noted the absence of the latter. However, as a primitive characteristic within this family, there is a possibility that the ninth tergite remains undivided into basal and apical parts. Further examination is necessary concerning the structure of the female genitalia. Regarding the eighth sternite, Hansen (1997) reported it as divided, but in reality, there was a central translucent part that was sclerotized, and it was not actually divided.

In Newton (2016) and Ôhara (1994), traits of Sphaeritidae are summarized. The following traits are helpful in distinguishing Sphaeritidae from Synteliidae and Histeridae: 1) with developed molae, 2) a composite ventral plate that is flat, with a weakly convex median portion and a medioposterior portion projected as a narrow intercoxal process, and 3) exhibiting sexual dimorphism in character states of the mentum.

From the detailed description of *Sphaerites glabratus* in this study, additional features that could potentially aid in identifying the family have been identified: 4) a thick and elaborately developed tentorium, 5) a proventriculus comprising eight slender longitudinal hairy bands, located on the posterior 1/4, 6) tergite IV lacking a central groove to lock elytra (Kovarík & Caterino, 2016), and 7) protarsus originating from the ventral side of protibia, without a groove on the dorsal surface of protibia to accommodate the protarsus.

Taxonomy

Superfamily **Histeroidea** Gyllenhal, 1808

Family **Synteliidae** Lewis, 1882

Genus ***Syntelia*** Westwood, 1864

Syntelia Westwood, 1864, 11 [type species: *Syntelia indica* Westwood, 1864]; Kryzhanovskij & Reichardt, 1976: 414; Löbl, 2015: 76 [catalogued]; Newton, 2016: 277.

Syntelia histeroides Lewis, 1882

[Japanese name: Emmamushi-modoki]

(Figs. 2, 33–37, 62, 101, 102)

Syntelia histeroides Lewis, 1882, 137 [description; type locality: Japan: Yashiu, Southern Hokkaido, Kumakawa in Higo, Sado]; Kryzhanovskij & Reichardt, 1976: 414; Ôhara, 1994: 61 [redescription, male genitalia, spermatheca]; 1999: 77 [recorded]; Löbl, 2015: 76 [catalogued]; Kikuchi & Ôhara, 2023: 3 [redescription, mouthparts, female genitalia]; Ôhara & Ho, 2023: 39 [catalogued]; Ôhara, 2023[2022]: 59 [catalogued]; dela Cruz *et al.*, 2023: 245 [biological note].

Description. Labral disc of labrum (Fig. 33C, D) slightly visible from dorsal side, strongly transverse (width/length ratio 4, n=5), densely furnished with lateral fringe hair, without labral setae. Epipharynx densely covered with short setae, central part densely covered with longer setae. Mandibles (Fig. 33A, B) slightly asymmetrical with sharp apex, microscopic punctures on distal anterior half and outer edge, densely furnished with prothecal setae. Stipes of maxilla (Fig. 33E, F) shaped slender triangles (width/length ratio 0.15, n=5), with three to four long setae. Lacinia strongly longitudinal (width/length ratio 0.17, n=5), covered entirely and densely with short setae, without lacinial hook. Galea elongated (width/length ratio 0.22, n=5), covered with setae on inside, with setae becoming longer towards apical. Ligula of labium (Fig. 34A, B) densely furnished with short setae on inside. Paraglossa shaped slender (width/length ratio 0.2, n=5), covered with setae on inside. Mentum (Fig. 34C) strongly transverse (width/length ratio 3, n=5), sparsely with setae on outer margin. Outside of terminal maxillary palpomere and terminal labial palpomere (Figs. 33E, F, 34A–C, 35D), with approximately 15 elongated palpal organs. Tentorium (Fig. 34D, E) simple structure and with slightly developed dorsal arm. Proventriculus (Fig. 34F, G) without sutural teeth, composed of eight longitudinal hairy bands, the four bands short and located in posterior half of

proventriculus, while the other four longer and merge on anterior half of proventriculus, resulting two bands anterior portion (n=4), also another case where bands remain separate and continue to tip (n=1).

Underside of elytron (Fig. 37C) furnished with microsetae. Metanotum (Fig. 37A) coarsely punctate. Abdominal tergites (Fig. 37A) with dense punctures on basal area of each tergite; no groove on fifth abdominal tergite to lock elytra.

Protibia (Fig. 37D, E) with four to seven denticles on outer margin, three on apical margin; surface smooth. Median row of setae short and sparse. Outer row of setae long, only present basal and apical portions.

Undivided eighth tergite of female genitalia (Fig. 62). Posterior end of eighth tergite with several short setae. Eighth sternite undivided, and apical margin of eighth sternite extends. Basal baculi converge but separate, and basal baculi fused with lateral disk of eighth sternite. Posterior end of ninth tergite in basal direction with several short setae. Ninth tergite in basal direction fused with ninth sternite in basal direction (valvifer) and ninth sternite in apical direction. Ninth tergite in apical direction absent. Ninth sternite in basal direction (valvifer) short. Anterior part of ninth sternite in basal direction (valvifer) not paddle-shaped. Tenth tergite expands posteriorly and contacts ninth tergite. Tenth sternite elongates significantly and becomes long protrusion. Articulating sclerite absent. Coxite long and robust, with a shovel-like shape, with external surface separated from internal surface by elevated lateral ridges. Coxite without teeth at apical. Both dorsal and ventral surfaces of coxite densely covered with setae. Articular membrane closed, apical edge remote from apical emargination between teeth. Articular membrane with 14 to 15 setae. Stylus with six setae at tip. Inside of oviduct densely covered with fine setae. Bursa copulatrix small and with a little expandable membrane. Spermatheca composed

of one receptacle, not sclerotized. Spermathecal gland not sclerotized, extremely slender, and with numerous fine, round-tipped hairs on surface, attached posterior side of spermatheca. Length of spermathecal duct approximately six times length of spermatheca. spermathecal duct attached posterior end of oviduct.

Specimens examined. Hokkaido --- [Rumoi Dist.] 2 ♀♀, Hamanaka, Rumoi, 5.VII.1995, T. Kikuchi leg. (CKIK). [Kushiro Dist.] 1 ex., Futatsuyama, Shibechea, 30.VI.1966, K. Ijima leg. (SEHU); 1 ex., Shibechea, Kushiro, 8.VII.1958, M. Takahashi leg. (KUM). [Kamikawa Dist.] 1 ex., Eoroshi, Higashikawa, Kamikawa, 24.VIII.1991, T. Nishida leg. (SEHU); 1 ex., Inou, Asahikawa, 3.VI.1955, I. Tateyama leg. (SEHU); 1 ex., Kami-tawaramappu, 1.VII.1980, Y. Nishijima leg. (SEHU); 1 ex., Sôunkyô, Kamikawa, 18.VII.1981, N. Yasuda leg. (SEHU); 1 ex., same locality and collector but different date, 12.VI.1993 (SEHU); 2 exs., Mt. Esaushi-yama, Kamikawa, 29.V.1983, N. Yasuda leg. (SEHU). [Tokachi Dist.] 1 ex., Tokachi-damu, 17.VII.1998, A. Nakanishi leg., st. 1, pitfall trap (SEHU); 1 ♀, Satsunai-gawa Riv., Minamisatsunai, Nakasatsunai, 15.VI.2013, T. Kikuchi leg. (CKIK). [Hidaka Dist.] 1 ♂, Syunbetsu-kawa Riv., Shinhidaka, 4.VIII.2021, T. Kikuchi leg. (CKIK); 1 ♀, Hidakahoronai-kawa Riv., Urakawa, 14.VI.2021, T. Kikuchi leg. (CKIK). [Sorachi Dist.] 1 ♂, 1 ♀ (TK-22-037), 2 exs., Ôyûbari, Yûbari, 12.VII.2006, A. Ueda leg. (SEHU); 3 exs., same locality and collector but different date, 24.VII.2006 (SEHU); 1 ex., Syûparo-damu, Yûbari, 7.VII.1992, Y. Nishijima leg. (SEHU); 1 ex., Nokanan, Ashibetsu, 6.VI.1985, T. Nishida leg. (SEHU). [Ishikari Dist.] 1 ex., Mt. Maruyama, Sapporo, 21.VI.1972, A. Tanaka leg. (SEHU); 1 ex., same locality and collector but different date, 17.V.1992 (SEHU); 1 ex., Maruyama, Sapporo, 16.IX.1942, N. Aoyama leg. (SEHU); 1 ex., same locality, 20.V.1925, S. Matsumura leg. (SEHU); 2 exs., Moiwa, 15.VI.1904, no collector's name (SEHU); 1 ex.,

same locality, 4.VI.1905, no collector's name (SEHU); 1 ex., Mt. Shirahata-yama, Kiyota, Sapporo, 18.VII.2009, T. Toita leg. (SEHU); 1 ex., same locality, 7.VIII.1997, S. Hori leg. (SEHU); 1 ex., Nishino, Sapporo, 1.VII.1973, A. Tanaka leg. (SEHU); 1 ex., Jôzankei, 9.IX.1903, no collector's name (SEHU); 1 ex., Sapporo, 15.VI.1941, no collector's name (SEHU); 2 exs., same locality, 30.VI.1984, T. Kumata leg. (SEHU); 1 ex., same locality, 25.V.1975, A. Tanaka leg. (SEHU); 1 ex., same locality and collector but different date, 22.VIII.1977 (SEHU); 2 exs., same locality and collector but different date, 23.V.1981 (SEHU); 3 exs., same locality and collector but different date, 7.VI.1981 (SEHU); 1 ex., same locality, 6.VII.1967, M. Suwa leg. (SEHU); 3 exs., same locality but no date, S. Matsumura leg. (SEHU); 1 ex., Konopporo, Sapporo, 21.VIII.1985, S. Aoyama leg. (SEHU); 4 exs., Tokiwa, Sapporo, 16.VIII.1989, S. Aoyama leg. (SEHU); 3 exs., Bokusanai, Atsuta, 7.VI.1987, S. Aoyama leg. (SEHU); 2 ♀♀ (TK-22-013, TK-23-126), Isari-gawa (Izari-gawa) River, 16.VI.1986, M. Mori leg. (SEHU); 1 ex., Izarigawa-dam, Eniwa, 27.VIII.1996, Y. Nishijima leg. (SEHU); 1 ♀ (TK-23-127), Nopporo, 22.VI.1987, M. Ôhara leg. (SEHU); 2 ♀♀, Nopporo Forest Park, Ebetsu, 21.V.2009, T. Kikuchi leg. (CKIK); 1 ♂, Mt. Kana-yama, Teine, Sapporo, 17.VI.2012, T. Kikuchi leg. (CKIK); 1 ♀, Hoshioki Park, Hoshioki, Teine, Sapporo, 17.VII.2016, T. Kikuchi leg. (CKIK). [Iburi Dist.] 1 ex., Tomakomai, 21.VII.1989, Y. Nishijima leg. (SEHU); 1 ex., Shiraoi-dam, Morino, Shiraoi, 22.VIII.1980, no collector's name, bait trap, secondary forest (SEHU); 1 ex., Tachibanako, Noboribetsu, 29.VI.1988, Y. Nishijima leg. (SEHU); 5 exs., same locality and collector but different date, 22.VII.1988 (SEHU); 1 ex., Horobetsu, Noboribetsu, 23.VII.1988, Y. Nishijima leg. (SEHU); 1 ♂, 1 ♀, Takaoka, Tomakomai, 11.VII.2010, T. Kikuchi leg. (CKIK). [Shiribeshi Dist.] 1 ♀ (TK-22-007), Mt. Yôtei-zan, Hirafu, 22.VII.1991, M. Ôhara leg. (SEHU). [Oshima Dist.] 1 ex., Akagawa-rindô,

Hakodate, 1.VIII.1857, M. Munakata leg. (SEHU); 5 exs., same locality and collector but different date, 8.VIII.1957 (SEHU); 1 ex., Akanuma, Hakodate, 4.VII.1965, T. H. leg. (SEHU); 2 ♀♀, Kamiyakumo, Yakumo, 2.IX.2021 T. Kikuchi leg. (CKIK); 1 ex., Hokkaido, no date and collector's name (SEHU). Honshu --- [Fukushima Pref.] 1 ex., Akane-rindô, Haranomachi, 23.V.1981, N. Kobayashi leg. (SEHU); 1 ex., Hinoemata, Minami-Aizu, 6.VI.1977, K. Emoto leg. (SEHU). [Tochigi Pref.] 4 exs., Nikko, 12.VII.1956, M. Takahashi leg. (KUM); 1 ex., L. S. Chûzenji, Nikko, 6.VII.1942, A. Kira leg. (KUM). 4 exs., Chû-zenji, 9.VII.1917, E. Gallois leg. (SEHU); 2 exs., same locality and collector but different date, 11.VII.1917 (SEHU); 1 ex., same locality and collector but different date, 19.VII.1917 (SEHU); 1 ex., same locality and collector but different date, 20.VII.1917 (SEHU). [Tokyo Pref.] 1 ex., Okawadani, Okutama, 3.V.1969, T. Go leg. (SEHU). [Kanagawa Pref.] 2 exs., Dôdaira, Tanzawa, 1.VI.1993, Y. Hirano leg. (KMNH). [Gumma Pref.] 1 ex., Mt. Tanigawa-dake, 17.VII.1957, S. Hisamatsu leg. (EUM); 1 ex., same locality, 11.VI.1961, K. Kinugasa leg. (SEHU); 1 ex., Hohshi, 14–15.VI.1962, K. Kinugasa leg. (SEHU); 1 ex., Mt. Hotaka-yama, 21.VII.1991, K. Kinugasa leg. (SEHU). [Yamanashi Pref.] 1 ex., Hikawa-rindô, Daibosatsu Mts., 1.VII.1984, T. Kinoshita leg. (SEHU); 1 ex., Koganesawa-rindô, Ôtsuki, 12.VIII.1981, K. Emoto leg. (SEHU). [Nagano Pref.] 2 exs., Iwana-dome, 15.VII.1950, T. Nakane leg. (SEHU); 1 ex., Kamikôchi, 26.VII.1950, M. Kishi leg. (CSBT); 1 ex., Kiriake, Sakae, 26.VII.1996, M. Yamamoto leg. (CYMT); 1 ex., Shimashima, 18.VII.1974, K. Miwa leg. (CYMT). [Gifu Pref.] 1 ex., Nigori-go, Mt. On-take, 1,600–800 m, Osaka, Masuda, 25.VI.1989, Y. Imura leg. (SEHU); 1 ex., Hirayu, 20.VIII.1961, H. Yokoyama leg. (CSBT). [Nara Pref.] 1 ex., Kojin, Yamato, 22.IV.1975, T. Ito leg. (CSBT); 1 ex., Nabewari, Mt. Obako-dake, 9.VII.1982, M. Yamamoto leg. (CYMT). [Hiroshima Pref.]

1 ex., Mt. Hiba-yama, Bingo, 13.VIII.1971, T. Kosaka leg. (SEHU). Shikoku --- [Tokushima Pref.] 1 ex., Dosu-tôge, 2.VI.1974, M. Yoshida leg. (EUM); 6 exs., Takashiroyama-tôge, alt. ca. 1,500 m, 17.VII.1988, S. Hisamatsu leg. (EUM); 1 ex., Mt. Mimune, Higashi-Iya, 2 & 3.VIII.1969, S. Kinoshita leg. (EUM); 1 ex., Mt. Tsurugi-san, 12.VII.1976, S. Hisamatsu leg. (EUM). [Ehime Pref.] 2 exs., Omogo, 3.VI.1976, A. Oda leg. (EUM); 1 ex., Mt. Ishizuchi-san, 26.VII.1977, K. Mumaguchi leg. (EUM); 1 ex., Mt. Saragamine, 1.VI.1955, M. Miyatake & S. Ueda leg. (EUM); 1 ex., same locality, 28 & 29.V.1993, M. Kawanabe leg. (EUM). Kyushu --- [Ôita Pref.] 1 ex., Oika, Shônai, 9.VI.1994, Y. Sawada leg. (SEHU). [Miyazaki Pref.] 1 ex., Mt. Goyô-dake, Natsukiyama-one, Kitagawa, alt. 1,450 m, 27.VI.1993, T. Kinoda leg. (CKIN).

Distribution. Japan (Kunashir Is., Hokkaido, Honshu, Sado-ga-shima Is., Shikoku, Kyushu); Russia (Far East).

Biology. *Syntelia histeroides* has been collected under bark, in sap (*Fagus crenata*, *Quercus crispula* var. *crispula*, *Q. dentata*, *Acer* spp., *Ulmus davidiana* var. *japonica*, *U. laciniata*, *Pterocarya rhoifolia*, *Salix* spp., *Kalopanax saptemlobus*, *Aralia elata*, *Meliosma myriantha*, *Celastrus orbiculatus*, and *Phellodendron amurense*), and is also collected under cow dung, rotten mackerel, and trap with banana (Ohno, 2010). *S. histeroides* feed on larvae of Diptera and tenebionid beetles. Adults overwinter under the bark of trees and reappears around April. Adults generally emerged between May and August, with July being the most frequently recorded month (Ohno, 2010). *S. histeroides* is also collected by Madara-call-traps (Alpha-pinene and ethanol trap) (Takai, 2004) and bait trap with chicken (Suzuki, 2022). Regarding the egg-laying behavior of *Syntelia histeroides*, Haga *et al.* (2010) reported the following. "Observed under the bark of fallen hardwood tree with highly uneven bark as *Quercus variabilis*. The female floated on the

front half of her body with her front legs propped up, and the bark was firmly attached to the abdominal terminal. A fine white powdery substance was raised around the abdominal terminal. When we touched the female with our fingers, the bark seemed to be joined to the female's abdomen and did not move from that position. This situation suggests that the female was laying eggs and had somehow penetrated the bark and inserted her egg-laying tube into the hole, and that the powdery substance was wood dust from the fallen tree.”

Remarks. Regarding the ninth tergite in the basal direction and the ninth tergite in the apical direction, similar to *Sphaerites glabratus*, this paper noted the absence of the latter. However, as a primitive characteristic within this family, there is a possibility that the ninth tergite remains undivided into basal and apical parts. Further examination is necessary concerning the structure of the female genitalia. Kikuchi and Ohara (2023) Fig. 62 does not illustrate round-tipped hairs on the surface of the Spermathecal gland. However, upon closer observation, round-tipped hairs were found on the surface of the Spermathecal gland.

In Newton (2016) and Jiang and Wang (2016), the traits of Synteliidae are compiled. The following traits are helpful in distinguishing Synteliidae from Sphaeritidae and Histeridae: 1) a very short and nearly vertical labrum, immovably attached to the front of the head capsule, 2) prosternum completely and externally closing procoxal cavities, and 3) closely adjacent coxae.

This study has identified additional features from the detailed description of *Syntelia histeroides* that could potentially aid in the identification of the family: 4) a very simple structure of the tentorium, 5) absence of setae on the labrum, 6) proventriculus

with rows of setae fused on the anterior half, 7) tergite IV lacking a central groove to lock elytra (Kovarík & Caterino, 2016), 8) a long protrusion present around the base of coxite of the female genitalia, and 9) absence of an articulating sclerite between coxite.

2-4. Discussion

As a result of detailed descriptions of *Sphaerites glabratus* and *Syntelia histeroides*, several new trait states have been identified. For the female genitalia of Sphaeritidae, descriptions were limited to the simplified external appearance of *Sphaerites glabratus* as outlined by Hansen (1997) and only the female spermatheca described by Ôhara (1994). Similarly, for Synteliidae, the descriptions were confined to Ôhara (1994) portrayal of the female spermatheca and its glands in *Syntelia histeroides*. It became apparent that describing the entire female genitalia, encompassing the presence or absence as well as the shape variations of various organs, holds significant differences. This suggests that female genitalia possess traits suitable for appropriate utilization in phylogenetic analysis.

Chapter 3. Detailed descriptions of representative species used as ingroups for the phylogenetic analyses

3-1. Introduction

In this chapter, as part of the phylogenetic analysis of the Japanese Histeroidea, detailed descriptions were conducted for five species within the ingroup Histeridae. Specifically, attention was focused on *Hypacacculus* and *Hypocaccus*, detailing their external morphology, mouthparts, and female genitalia.

While Histeridae differs from the families Sphaeritidae and the Synteliidae in having detailed descriptions of mouthparts and female genitalia for some groups, the subfamily Sapriniinae stands out. The Sapriniinae has benefited significantly from detailed redescrptions of external morphology and mouthparts by Lackner (2010), as well as thorough descriptions of specific parts of the female genitalia by Lackner and Tarasov (2019). Leveraging these references for comprehensive descriptions, this study centered on *Hypocaccus* found in Japanese riverbank, detailing its external morphology, mouthparts, and female genitalia.

Further investigation revealed the necessity for a detailed assessment of *Hypocacculus*, closely related to *Hypocaccus*. Therefore, detailed descriptions of the external morphology, mouthparts, and female genitalia were conducted for *Hypocacculus* as well.

3-2. Material and methods

"Material and methods" are the same as in Chapter 2.

3-3. Results

Taxonomy

Subfamily **Saprininae** Blanchard, 1845

Tribe **Hipocaccini** Lackner, 2023

Genus ***Hypocacculus*** Bickhardt, 1914

Hypocacculus Bickhardt, 1914: 311 (Original designation adapted by ICZN Art. 11 & 12)

[type species: *Saprinus metallescens* Erichson, 1834: 192, designated in Bickhardt, 1916: 95]; Bickhardt, 1916: 95 [description]; Reichardt, 1926: 14 [key]; 1932: 28, 96 [redescription, with key]; 1941: 156, 280 [key]; Peyerimhoff, 1936: 228 [key]; Kryzhanovskij & Reichardt, 1976: 201 [key, figured, with note]; Mazur, 1984: 83 [catalogued]; Ôhara, 1994: 240 [synonymic list]; Mazur, 1997: 249 [catalogued]; Ôhara, 1999: 122 [recorded]; Lackner, 2010: 122 [key, figured, with note]; Mazur, 2011: 200 [catalogued]; Lackner *et al.*, 2015: 115 [catalogued]; Hongzhang *et al.*, 2022: 574 [note]; Lackner *et al.*, 2023: 1 [revised]; Kikuchi & Ôhara, 2023: 228 [note].

Diagnosis. Cuticle often metallic, elytra never with red maculae; body size between 1.20–3.00 mm, in most cases smaller than 2.5 mm. Antennal scape never extremely dilated and/or thickened; antennal club without visible articulation. Frontal stria never interrupted; supraorbital stria at times lacking; frontal disk punctate, never smooth and/or with several deep rugae (as in *Hypocaccus*). Eyes always visible from above. Pronotum without pronotal foveae, pronotal disk usually with punctuation at least laterally, never entirely smooth. Marginal pronotal stria usually complete, lateral pronotal stria always absent; disk of pronotum strongly convex, so that lateral margins are not

visible along their entire length (seen from dorsal view). Prosternum in most cases with pre-apical foveae; carinal prosternal and lateral prosternal striae present. Basal area of metaventrite rarely with two large tubercles. Protibia usually moderately dilated, outer margin with 6–16 teeth; meso- and metatibiae usually not particularly thickened (Lackner, 2010).

Subgenus *Nessus* Reichardt, 1932

Nessus Reichardt, 1932: 32 [type species: *Saprinus rubripes* Erichson, 1834: 193, original designation, as a subgenus of *Hypocacculus* Bickhardt, 1914]; Kryzhanovskij & Reichardt, 1976: 207 [redescription]; Mazur, 1984: 83 [catalogued]; 1997: 252 [catalogued]; Ôhara, 1994: 240 [synonymic list]; 1999: 122 [recorded]; Mazur, 2011: 208 [catalogued, as a subgenus of *Hypocaccus* Thomson, 1867]; Lackner *et al.*, 2015: 117 [catalogued]; Lackner & Seres, 2018: 420 [revision]; Hongzhang *et al.*, 2022: 588 [note]; Lackner *et al.*, 2023: 1 [revised, as a subgenus of *Hypocacculus* Bickhardt, 1914]; Ôhara, 2023[2022]: 63 [catalogued, as a subgenus of *Hypocaccus* Thomson, 1867]; Kikuchi & Ôhara, 2023: 208 [mouthparts].

Description of mouthparts. Mouthparts of *Hypocacculus* (*Nessus*) *asticus* are illustrated as a representative of the genus *Hypocacculus*.

Mentum and submentum (Figs. 39B, C, 40E) with branched setae. Terminal maxillary palpomere (Fig. 38E, F) and terminal labial palpomere (Fig. 39A–C) each with rows of palpal organs on outer surface of basal portion and apically.

Mandibles (Fig. 38A, B) asymmetric, with sharp apices and incomplete molae,

and densely with small setae on dorsal of basal 1/4. Ventral side with two rows of long setae on inner side. Labrum (Fig. 38C, D) strongly transverse (width/length ratio 2.5), with more than ten pairs of lateral fringes and two pairs of labral setae. Tentorium (Fig. 39D, E) without developed dorsal arm. Proventriculus (Fig. 39F, G) without sutural teeth, consisted by rather broad eight longitudinal hairy bands, the bands becoming narrower anteriorly.

***Hypocacculus (Nessus) asticus* Lewis, 1911**

[Japanese name: Hime-hamabe-emmamushi]

(Figs. 7, 38–42, 67)

Hypocaccus asticus Lewis, 1911: 89 [type locality: Japan: Enoshima]; Nakane, 1963: 67 [figured, with note]; Hisamatsu, 1985: 223 [figured, with note]; Hirano, 1986: 45 [biological note]; Tao, 1987: 34 [recorded, with biological note].

Hypocacculus asticus: Bickhardt, 1916: 96 [catalogued].

Hypocacculus (Nessus) asticus: Mazur, 1984: 83 [catalogued]; Ôhara, 1994: 240 [redescription, male genitalia]; Kim *et al.*, 1994: 136 [Korea]; Mazur, 1997: 252 [catalogued]; Ôhara & Paik, 1998: 29 [Jeju Is.]; Ôhara, 1998: 4 [figured, with note]; 1999: 122 [recorded]; Mazur, 2007: 68 [Taiwan]; Kikuchi & Ôhara, 2023: 208 [redescription, mouthparts, female genitalia].

Hypocaccus (Nessus) asticus: Hirano, 1995: 9 [recorded, with biological note]; 1997 b: 10 [recorded, with biological note]; Mazur, 2011: 208 [catalogued]; Lackner *et al.*, 2015: 117 [catalogued]; Hongzhang *et al.*, 2022: 588 [note]; Ôhara, 2023 [2022]: 63 [catalogued].

Description. Underside of elytron (Fig. 42A, B) furnished with microsetae, or sometimes with pairs of microsetae.

Protibia (Fig. 42C, D) with seven to eight denticles on outer margin, three on apical margin; dorsal surface smooth; outer row of setae divided into two portions: apical portion near on outer margin with short setae, basal portion rather near median row of setae with long setae; outer part of posterior surface areolate-rugose and bearing two to three short denticles.

Undivided eighth tergite of female genitalia (Fig. 67). Central portion of anterior margin of eighth tergite markedly truncate. Eighth sternite undivided. Basal baculi converge but separate, and basal baculi fused with lateral disk of eighth sternite. Ninth tergite in basal direction and ninth tergite in apical direction extremely small. Ninth sternite in basal direction (valvifer) linear, and anterior part not paddle-shaped. Ninth sternite in apical direction fuses with ninth sternite in basal direction (valvifer). Tenth tergite wide. Tenth sternite absent. Articulating sclerite oval shape. Coxite long and robust, not shovel-like, lacking differentiation between outer and inner surfaces, and devoid of teeth at the apex. Coxite very fine setae present on ventral side of coxite from anterior edge to central portion. Articular membrane closed, apical edge remote from apical emargination between teeth. Articulating membrane without a seta. Stylus not visible from dorsal side. Stylus with four setae at tip. Inside of oviduct densely covered with fine setae. Bursa copulatrix flat and not expanded. Spermatheca composed of one sclerotized receptacle. Spermathecal gland composed of one sclerotized receptacle, and with numerous fine, round-tipped hairs on surface, attached anterior side of spermatheca. Length of spermathecal duct approximately seven times length of spermatheca. Spermathecal duct attached near gonopore.

Specimens examined. Honshu --- [Kanagawa Pref.] 1 ♂ (TK-22-047), 1 ♀ (TK-22-001), Yuhiga-hama, Kamakura, 22.IV.1988, M. Tao leg. (SEHU) (Ôhara, 1994); 1 ex., Shichirigahama, Kamakura, 24.VIII.1989, K. Kawada leg. (SEHU); 1 ♂ (TK-22-019), 1 ex., same locality and collector but different date, 10.X.1989 (SEHU); 1 ex., same locality and collector but different date, 28.III.1994 (SEHU). [Shizuoka Pref.] 1 ♂ (TK-22-018), 2 ♀♀ (TK-22-002), 1 ex., Tadato-hama, Shimoda, 27.III.2006, Y. Kaneko leg. (SEHU). [Mie Pref.] 1 ex., Goen-hama, Tsu, 18.V.1997, M. Yamamoto leg. (CYMT). [Kyoto Pref.] 1 ex., Miyakawahara, 7.IV.1932, no collector's information (SEHU); 1 ex., Kotanbashi-kaigan, Kumihama, 13.X.1996, S. Yamashita leg. (SEHU). [Wakayama Pref.] 1 ex., Wakayama, 10.II.1957, M. Yoshida leg. (SEHU). [Shimane Pref.] 1 ♀, 1 ex., Izumo, Koryo, 5.VI.2007, T. Hayama leg. (SEHU); 2 exs., Chikumi-hama, Kitaura, Mihonoseki, Matsue, 1 & 2.VI.2008, T. Hayama leg., Yellow pan trap (SEHU). Shikoku --- [Tokushima Pref.] 1 ex., Asahino, Komatsu-kaigan, 20 & 21.VIII.1984, Y. Ito leg., body broken, only parts remained (EUM). Kyushu --- [Nagasaki Pref.] 1 ♀, Kazusa, Maehama, 28.III.1979, S. Imasaka leg. (SEHU).

Distribution. Japan (Honshu, Shikoku, Kyushu), Korean Peninsula, Jeju Island, Taiwan.

Biology. *Hypocacculus (Nessus) asticus* is reported to be a littoral species (Hirano, 1986), and it is obtained from the sand in coastal grasslands (Tao, 1987), from the vicinity of coastal plants' roots (Hirano, 1995, 1997 b).

Remarks. Kikuchi and Ohara (2023) illustrated the female genitalia of several species of *Hypocacculus* and *Hypocaccus*. However, they did not depict the ninth tergite in the basal direction and the ninth tergite in the apical direction. Additionally, they did not portray the fusion of the ninth tergite in the apical direction with the ninth tergite in

the basal direction (valvifer), the fine hairs located on the ventral anterior edge of the coxite, nor the round-tipped hairs on the surface of the spermathecal gland.

Genus *Hypocaccus* Thomson, 1867

Hypocaccus Thomson, 1867: 400 [type species: *Hister quadristriatus* Hoffmann, 1803: 85, subsequent designation by Lewis, 1899: 3]; Bickhardt, 1916: 82 [catalogued]; Kryzhanovskij & Reichardt, 1976: 217 [key, with note]; Mazur, 1984: 92 [catalogued]; Lackner & Seres, 2018: 420 [revision]; Hongzhang *et al.*, 2022: 574 [note]; Kikuchi & Ôhara, 2023: 205 [Key, with note].

Rhytidoprinus Houlbert et Monnot, 1923: 46 [type species: *Hister rugiceps* Duftschmid, 1805, by Mazur, 2004: 94 [catalogued].] Synonymized by Cooman, 1947: 428 [note].

Diagnosis. Cuticle often metallic and lustrous, at times matt, black or dark-brown; frontal stria carinate, in most cases straight or only slightly curved outwardly (rarely weakened medially with traces prolonged onto clypeus); frontal disk marked by single or double chevron, sometimes with longitudinal rugae or granulose structures. Pronotal disk punctate (at times rugulose-lacunose) or entirely smooth (subgenus *Baeckmanniolus*); pronotal foveae absent; pronotal hypomera glabrous. Prosternal process concave, compressed; carinal prosternal striae usually running parallel or subparallel, occasionally united in front; lateral prosternal striae united anteriorly under a sharp angle; pre-apical foveae present, usually moderate in size. Lateral sides of meso- and metaventriles occasionally short setae, often smooth. Outer margin of metatibia with two or three rows of short denticles (Lackner, 2010).

Subgenus *Hypocaccus* Thomson, 1867

Description of mouthparts. Mouthparts of *Hypocaccus* (*Hypocaccus*)

subaeneus are illustrated as a representative of the subgenus *Hypocaccus*.

Mentum and submentum (Figs. 51B, C, 52E) with branched setae. Terminal maxillary palpomere (Fig. 50E, F) and terminal labial palpomere (Fig. 51A–C) each with rows of palpal organs on outer surface of basal 1/3 and with a few rows of palpal organs on apical portion. Mandibles (Fig. 50A, B) asymmetric, with sharp apices, incomplete molae, and densely with small setae on dorsal of basal 1/4; ventral side with two rows of long setae on inner side. Labrum (Fig. 50C, D) strongly transverse (width/length ratio 2), with more than 10 pairs of lateral fringes (= fringed setae) and two pairs of labral setae. Tentorium (Fig. 51D, E) with developed dorsal arm. Proventriculus (Fig. 51F, G) without sutural teeth, consisted by rather broad eight longitudinal hairy bands.

Hypocaccus (*Hypocaccus*) *akanensis* Ôhara, 1994

[Japanese name: Akan-hamabe-emmamushi]

(Figs. 10, 43–46, 70, 88)

Hypocaccus (*Hypocaccus*) *akanensis* Ôhara, 1994: 255 [description, male genitalia; type locality: Japan: Hokkaido]; Haga, 1995: 74 [catalogued]; Mazur, 1997: 257 [catalogued]; Ôhara, 1998: 5 [key, figured, with note]; Kikuchi & Ôhara, 2023: 214 [female genitalia].

Hypocaccus (*Nessus*) *asticus*: Mazur, 2011: 208 [catalogued]; Lackner *et al.*, 2015: 117 [catalogued]; Ôhara, 2023 [2022]: 63 [catalogued].

Redescription. [At the time of describing this species, only the holotype (Fig. 46) was available and it was worn, making it difficult to describe detailed characteristics. In this study, we were able to obtain multiple fresh specimens, so we redescribe the species.] Body length (n = 29): PPL: 2.13–2.83 mm; PEL: 1.90–2.43 mm; APW: 0.67–0.80 mm; PPW: 1.43–1.87 mm; PL: 0.76–1.00 mm; EL: 1.23–1.50 mm; EW: 1.52–2.07 mm; ProW: 0.88–1.30 mm; ProL: 0.23–0.37 mm; PyL: 0.70–0.90 mm; PTL: 0.53–0.70 mm; MSTL: 0.55–0.70 mm; MTTL: 0.61–0.80 mm.

Body (Figs. 10C, 43A, C) oval, convex; cuticle shining and black or copper with brassy luster; antennae dark piceous with club black; legs black. Frontal stria (Fig. 43D) of head complete, carinate and straight on each side. Supraorbital stria complete. Disk of frons with rudimentary transverse rugae. Epistome more or less roughened.

Pronotal (Figs. 10C, 43A, C) sides convergent forward on basal 1/6, thence strongly arcuate and convergent apically. Apical angles round. Marginal stria carinate and complete laterally and anteriorly. Disk coarsely and densely punctate, the punctures becoming more rugose in lateral region and absent mediobasally; base with two or three transverse rows of large and oblong punctures, the rows being broadest at middle and becoming narrower laterally.

Marginal epipleural stria (Figs. 10C, 43A, C, F) complete and clearly impressed. Marginal elytral stria complete, broadly impressed in basal 1/3, the apical end extending inwards, reaching to near lateral 1/4 of elytral posterior margin. External subhumeral stria absent. Internal subhumeral stria impressed on median 1/3. Oblique humeral stria present on basal 1/3; area around the stria with several short rugae. First dorsal elytral stria completely present, but sometimes reduced on apical 1/4–1/8 in a short distance. Second to fourth dorsal striae well impressed on basal 1/2, the basal end of fourth extending

inwards and united with the base of sutural stria. Sutural stria completely impressed. Surface of elytra smooth on basal 1/2, and densely covered with coarse and deep punctures on apical 1/2, which are often united to longitudinal rugae; extreme apex of elytron and flank sparsely and finely punctate. Underside of elytron (Fig. 45A, B) furnished with microsetae.

Propygidium (Fig. 44C) densely covered with coarse and round punctures, which become finer and sparser toward the base, but mostly are separated by their own diameter. Pygidium densely covered with coarse punctures with weak rugae-appearance, which are a little smaller than those of the propygidium and separated by 0.3–0.5 times their diameter; punctures becoming finer and sparser on apical portion.

Anterior margin (Fig. 44A) of prosternum weakly obtuse-angulate in median portion. Pre-apical foveae deeply and distinctly present. Keel narrow, strongly compressed. Descending lateral striae carinate and convergent to apex, but their apical portions nearly parallel. Carinal striae completely impressed, divergent apically and basally, the anterior ends united with descending lateral striae. Lateral side of keel coarsely punctate, the punctures separated by about 1.5 (1–2) times of their diameter.

Anterior margin of mesoventrite (Figs. 43B, 44A) feebly emarginate; marginal stria carinate and complete. Disk of mesoventrite smooth. Meso-metaventricle suture (Figs. 43B, 44A) lightly impressed, accompanied with a coarsely crenated parallel line. Intercoxal disk of metaventricle (Figs. 43B, 44D) smooth. Lateral metaventricle stria (Figs. 43B, 44B) well impressed and carinate, obliquely extending posteriorly and reaching near hind coxa. Lateral disk (Figs. 43B, 44B) densely covered with coarse, round and shallow punctures which are gradually becoming smaller and sparser; impunctate along the lateral stria. Metepisternum densely and coarsely punctate.

Intercoxal disk of first abdominal (Figs. 43B, 44D) sternum smooth, and completely striate on each side.

Protibia (Fig. 45C, D) with seven to eight denticles on outer margin, two on apical margin; dorsal surface smooth; outer part of posterior surface areolate-rugose and bearing three to four short denticles.

Mentum and submentum (Fig. 43E) with branch setae. Terminal maxillary palpomere and terminal labial palpomere each with rows of palpal organs on outer surface of basal and apical portions.

Undivided eighth tergite of female genitalia (Fig. 70). Central portion of anterior margin of eighth tergite markedly truncate. Eighth sternite undivided. Basal baculi converge but separate, and basal baculi fused with lateral disk of eighth sternite. Ninth tergite in basal direction and ninth tergite in apical direction extremely small. Anterior part of ninth sternite in basal direction (valvifer) paddle-shaped. Ninth sternite in apical direction fuses with ninth sternite in basal direction (valvifer). Tenth tergite well-developed. Tenth sternite absent. Articulating sclerite oval shape. Coxite long and robust, not shovel-like, lacking differentiation between outer and inner surfaces, and devoid of teeth at the apex. Coxite very fine setae present on ventral side of coxite from anterior edge to central portion. Articular membrane closed, apical edge remote from apical emargination between teeth. Articulating membrane without a seta. Stylus visible from dorsal side. Stylus with six setae at tip. Inside of oviduct densely covered with fine setae. Bursa copulatrix flat and not expanded. Spermatheca composed of one sclerotized receptacle. Spermathecal gland composed of one sclerotized receptacle, and with numerous fine, round-tipped hairs on surface, attached anterior side of spermatheca. Length of spermathecal duct approximately seven times length of spermatheca.

Spermathecal duct attached near gonopore.

Type specimen examined. Holotype: ♂, labeled: 1. “♂”; 2. “Mount. AKAN, / prov Kushiro H- / okkaido 5-8-1918 / by M. SUZUKI.”; 3. “A379 2”; 4. “No- / 9044 / on slide. / M. ÔHARA”; 5. “Holo-type / Hypocaccus / akanensis / M. Ôhara”. [Red label] (Kyushu University Museum, Fukuoka) (Fig. 46).

Specimens examined. Hokkaido --- [Hidaka Dist.] 1 ♀, Riv. Saru-gawa, Biratori, Saru, 28.IX.2021, T. Kikuchi leg. (SEHU); 1 ♀, same locality and collector but different date, 24.X.2021 (SEHU); 2 ♂♂, same locality and collector but different date, 15.V.2022 (SEHU); 4 ♂♂ (TK-23-015), 6 ♀♀ (TK-23-003, TK-23-004, TK-23-014), Riv. Shunbetsu-gawa, Shinhidaka, 25.IV.2021, T. Kikuchi leg. (SEHU); 7 ♂♂, 7 ♀♀, same locality and collector but different date, 29.IV.2023 (SEHU); 2 ♂♂, same locality and date but different collector, M. Ôhara leg. (SEHU); 1 ex., same locality but different collector and date, 5.V.2023, T. Kikuchi leg. (SEHU).

Distribution. Japan (Hokkaido).

Biology. *Hypocaccus (Hypocaccus) akanensis* coexisted with *H. (H.) axeli* and *H. (H.) subaeneus* in the Riv. Shunbetsu-gawa, and with *H. (H.) subaeneus* in the Riv. Saru-gawa in Hokkaido, Japan. They inhabited fine riverbank sandy areas and burrowed into the sand. They were observed between April and May, and on sunny warm days, they could be seen flying above around the riverbank sandy areas.

***Hypocaccus (Hypocaccus) axeli* Kryzhanovskij, 1976**

[Japanese name: Arame-hamabe-emmamushi]

(Figs. 11, 47–49, 71)

Hypocaccus (Hypocaccus) axeli Kryzhanovskij, in Kryzhanovskij & Reichardt, 1976:

223 [type locality: Primorskij Kray; Japan: Harima (= Hyôgo)]; Ôhara, 1994: 245 [redescription, male genitalia, Japan: Hokkaido, Honshu]; Mazur, 1997: 257 [catalogued]; Ôhara, 1998: 4 [key, figured, with note]; Mazur, 2011: 205 [catalogued]; Lackner *et al.*, 2015: 116 [catalogued]; Ôhara, 2023[2022]: 63 [catalogued]; Kikuchi & Ôhara, 2023, 208 [female genitalia].

Hypocaccus axeli: Toyoshima, 2021: 50 [biological note].

Description. Elytral sutural stria united with marginal stria, but in Ôhara (1994), his specimens of this species were worn out, and described as “not united with marginal stria”. Underside of elytron (Fig. 48E, F) furnished with microsetae.

Protibia (Fig. 49A, B) with seven to nine denticles on outer margin, two on apical margin; dorsal surface smooth; outer part of posterior surface areolate-rugose and bearing three to five short denticles, with few smooth areas.

Mentum and submentum with unbranched setae. Terminal maxillary palpomere and terminal labial palpomere (Fig. 49 E) each with rows of palpal organs on outer surface of basal 1/4 and apical portions.

Undivided eighth tergite of female genitalia (Fig. 71). Central portion of anterior margin of eighth tergite markedly truncate. Eighth sternite undivided. Basal baculi converge but separate, and basal baculi fused with lateral disk of eighth sternite. Ninth tergite in basal direction and ninth tergite in apical direction extremely small. Anterior part of ninth sternite in basal direction (valvifer) paddle-shaped. Ninth sternite in apical direction fuses with ninth sternite in basal direction (valvifer). Tenth tergite well-developed. Tenth sternite absent. Articulating sclerite oval shape. Coxite long and robust, not shovel-like, lacking differentiation between outer and inner surfaces, and devoid of

teeth at the apex. Coxite very fine setae present on ventral side of coxite from anterior edge to central portion. Articular membrane closed, apical edge remote from apical emargination between teeth. Articulating membrane without a seta. Stylus visible from dorsal side. Stylus with six setae at tip. Inside of oviduct densely covered with fine setae. Bursa copulatrix flat and not expanded. Spermatheca composed of one sclerotized receptacle. Spermathecal gland composed of one sclerotized receptacle, and with numerous fine, round-tipped hairs on surface, attached anterior side of spermatheca. Length of spermathecal duct approximately seven times length of spermatheca. Spermathecal duct attached near gonopore.

Additional specimens examined. Hokkaido --- [Hidaka Dist.] 3 ♂♂, 3 ♀♀, Riv. Shunbetsu-gawa, Shinhidaka, 25.IV.2021, T. Kikuchi leg. (SEHU); 2 ♂♂, same locality and collector but different date, 29.IV.2023 (SEHU); 2 ♀♀, same locality and collector but different date, 5.V.2023 (SEHU). Honshu --- [Tochigi Pref.] 1 ♂, 2 ♀♀ (TK-22-004), Motegi, 22.V.1994, H. Takizawa leg. (SEHU). [Gifu Pref.] 2 ♂♂ (TK-22-006, TK-22-044), 2 ♀♀ (TK-21-027, TK-22-043), 2 exs., Taniguminagase, Ibigawa, Ibi, 1–11.VI.2017, K. Toyoshima leg. (SEHU) (Toyoshima, 2021).

Distribution. Japan (Hokkaido, Honshu); Russia (Far East).

Biology. *Hypocaccus (Hypocaccus) axeli* coexisted with *H. (H.) subaeneus* and *H. (H.) akanensis* in the Riv. Shunbetsu-gawa in Hokkaido, Japan. They inhabited fine riverbank sandy areas and burrowed into the sand. They were observed between April and May, and on sunny warm days, they could be seen flying around above the riverbank sandy areas.

***Hypocaccus (Hypocaccus) subaeneus* (Schmidt, 1890)**

[Japanese name: Yama-hamabe-emmamushi]

(Figs. 12, 50–54, 72)

Saprinus subaeneus Schmidt, 1890: 53 [type locality: Japan: Nikko].

Hypocaccus subaeneus: Schleicher, 1930: 137 [note]; Toyoshima, 2021: 49 [biological note].

Hypocaccus (? *Hypocaccus*) *subaeneus*: Kryzhanovskij & Reichardt, 1976: 229 [Japan: Honshu].

Hypocaccus (*Hypocaccus*) *subaenus* [sic]: Ôhara, 1994: 252 [redescription, male genitalia, Japan: Hokkaido, Honshu]; Hirano, 1995: 9 [catalogued]; Ôhara, 1998: 5 [key, figured, with note].

Hypocaccus subaenus [sic]: Hirano, 1985: 12 [catalogued]; 1997 a: 131 [catalogued].

Hypocaccus (*Hypocaccus*) *subaeneus*: Kim *et al.*, 1994: 136 [Korea]; Mazur, 1997: 261 [catalogued]; 2011: 207 [catalogued]; Ôhara & Yamamoto, 2000: 239 [Japan: Sikoku]; Lackner *et al.*, 2015: 117 [catalogued]; Ôhara, 2023[2022]: 64 [catalogued]; Kikuchi & Ôhara, 2023: 208 [mouthparts, female genitalia].

Hypocaccus akanensis: Nakatani & Kashizaki, 2019: 18, 103 [catalogued, misidentification].

Description. Underside of elytron (Fig. 54A, B) furnished with microsetae.

Protibia (Fig. 54C, D) with seven to nine denticles on outer margin, two to three on apical margin; dorsal surface smooth; outer part of posterior surface areolate-rugose and bearing four to five short denticles.

Undivided eighth tergite of female genitalia (Fig. 72). Central portion of anterior margin of eighth tergite markedly truncate. Eighth sternite undivided. Basal baculi

converge but separate, and basal baculi fused with lateral disk of eighth sternite. Ninth tergite in basal direction and ninth tergite in apical direction extremely small. Ninth sternite in basal direction (valvifer) linear, and anterior part not paddle-shaped. Ninth sternite in apical direction fuses with ninth sternite in basal direction (valvifer). Tenth tergite well-developed. Tenth sternite absent. Articulating sclerite oval shape. Coxite long and robust, not shovel-like, lacking differentiation between outer and inner surfaces, and devoid of teeth at the apex. Coxite very fine setae present on ventral side of coxite from anterior edge to central portion. Articular membrane closed, apical edge remote from apical emargination between teeth. Articulating membrane without a seta. Stylus visible from dorsal side. Stylus with six setae at tip. Inside of oviduct densely covered with fine setae. Bursa copulatrix flat and not expanded. Spermatheca composed of one sclerotized receptacle. Spermathecal gland composed of one sclerotized receptacle, and with numerous fine, round-tipped hairs on surface, attached anterior side of spermatheca. Length of spermathecal duct approximately seven times length of spermatheca. Spermathecal duct attached near gonopore.

Specimens examined. Hokkaido --- [Kamikawa Dist.] 3 exs., Riv. Ishikari-gawa (KP194.6), 27.VIII.2020, D. Sumikawa leg. (SEHU). [Ishikari Dist.] 1 ex., Riv. Ishikari-gawa, Atsuta, 8.V.2021, T. Kikuchi leg. (SEHU); 1 ex., Toyotaki, Sapporo, 10.VI.1987, M. Ôhara leg. (SEHU); 1 ex., Jôzankei, Sapporo, 7.VI.1986, M. Ôhara leg. (SEHU); 1 ex. (TK-22-038), same locality and collector but different date, 1.V.1987 (Ôhara, 1994), 1 ♀ (TK-22-046), same locality and collector but different date, 18.VI.1987 (Ôhara, 1994), 2 ♂♂ (TK-21-010), 3 ♀♀, 10 exs., Riv. Toyohira-gawa, Sapporo, 4.IV.2020, T. Kikuchi leg. (SEHU). [Kushiro Dist.] 1 ♂, Wakoto Peninsula, Lake Kussharo, Teshikaga, 26.VI.2012, M. Nakatani leg. (CNKT). [Tokachi Dist.] 1 ex., Shihoroshinbashi, Shihoro,

Chikaisuiko, 24.VII.2004, K. Ijima leg. (SEHU). [Hidaka Dist.] 4 exs., Riv. Saru-gawa, Biratori, Saru, 24.X.2021, T. Kikuchi leg. (SEHU); 2 exs., Riv. Saru-gawa, 15.V.2021, T. Kikuchi leg. (SEHU); 1 ex., same locality and collector but different date, 22.VII.2021 (SEHU); 1 ♀, same locality and collector but different date, 24.X.2021 (SEHU); 3 ♀♀ (TK-21-020, TK-21-021), same locality and collector but different date, 25.X.2021 (SEHU); 1 ex., same locality and collector but different date, 27.XI.2021 (SEHU); 2 ♂♂, 2 ♀♀, Riv. Shunbetsu-gawa, Shinhidaka, 29.V.2023, M. Ôhara leg. (SEHU). [Iburi Dist.] 1 ex., Riv. Shiraoui-gawa, Shiraoui, 24.IV.2021, T. Kikuchi leg. (SEHU). [Oshima Dist.] 1 ♂, 2 exs., Riv. Torizaki-gawa, Mori, Kayabe, 13.VI.2021, T. Kikuchi leg. (SEHU). Honshu --- [Aomori Pref.] 1 ex., Yagen-onsen, Ôhata, 16.V.1999, K. Emoto leg. (SEHU); 1 ♀, Riv. Akaishi-gawa, Ajigasawa, 12.VI.1988, H. Sawada leg. (SEHU). [Fukushima Pref.] 2 exs., Funamata-rindô, Hinoemata, Minamiaizu, 31.V.1993, K. Emoto leg. (SEHU). 1 ex., same locality and collector but different date, 29.V.1994 (SEHU). [Tochigi Pref.] 1 ♂, Tyûzen-ji, Nikkô, 6–31.VI.1911, S. Matsumura leg. (SEHU); 7 exs., Riv. Naka-gawa, Makino, Motegi, Haga, 22.V.1994, S. Ohmomo leg. (SEHU); 4 exs., Motegi, 22.V.1994, H. Takizawa leg. (SEHU). [Saitama Pref.] 3 exs., Riv. Gonotsubo-gawa, Yorii, 20–22.IV.1994, B. I. Collection (SEHU). [Kanagawa Pref.] 1 ex., Hokizawa, Tanzawa, 11.IV.1981, Y. Hirano leg. (EUM). [Nagano Pref.] 5 exs., Hatouchi-rindô, Iida, 30.VI.1998, T. Shimada leg. (SEHU). [Gifu Pref.] 1 ex., Ôura, Masaki, Hashima, 21.VII.2001, K. Emoto leg. (SEHU); 2 ♀♀, Enjô-ji, Kasamatsu, Hashima, 24–28.VI.2018, M. Ishiguro leg. (SEHU); 2 exs., same locality and collector but different date, 14.VIII.2018 (SEHU). [Shiga Pref.] 2 exs., Miyagahama, Ômihachiman, 5.VI.1994, S. Shiyake leg. (SEHU). [Kyoto Pref.] 3 exs. Riv. Kidu-gawa (left bank), Yawata City, 17.VII.2010, T. & A. Tani leg. Fit trap (CITO); 4 exs., same locality and collector but

different date, 5–9.V.2015, Fit trap (CITO); 2 exs., same locality and collector but different date, 17.V.2015, Pit trap (CITO); 1 ex., same locality and collector but different date, 21–28.V.2015, Fit trap (CITO); 4 exs., same locality and collector but different date, 23.V.2015, Pit trap (SEHU). [Hiroshima Pref.] 1 ex., Riv. Oze-gawa, Saeki, 16.V.1996, S. Nakamura leg. (HMHN). Shikoku --- [Tokushima Pref.] 4 exs., Ikeda-dam, Ueno, Ikeda, 9.IX.1979, M. Yoshida leg., light trap (CYSD).

Distribution. Japan (Hokkaido, Honshu, Shikoku); Korean Peninsula.

Biology. *Hypocaccus (Hypocaccus) subaeneus* is reported to inhabit sandy areas in mountainous riverbanks (Hirano, 1985, 1995, 1997 a), and it can also be found in the midstream regions of rivers, where it may hide among rocks and fallen trees (Nakayama, 2017). In Hokkaido, it is widely distributed, and the author occasionally collects it in the downstream areas of rivers. Nakatani and Kashizaki (2019) reported collecting it in sandy areas along the shores of Lake Kussharo. In regions where *H. (H.) axeli* and *H. (H.) akanensis* inhabit, they may coexist together.

***Hypocaccus (Hypocaccus) toyoshimai* Kikuchi et Ôhara, 2023.**

[Japanese name: Gifu-hamabe-emmamushi]

(Figs. 13, 55–58, 73, 94, 105, 107)

Hypocaccus (Hypocaccus) toyoshimai Kikuchi et Ôhara, 2023: 222 [description, male & female genitalia; type locality: Japan: Gifu Pref.].

Hypocaccus akanensis: Toyoshima, 2021: 49 [misidentification by Ôhara, Japan: Gifu Pref., biological note].

Description. Body length: PPL: 2.27–2.93 mm (n = 19); PEL: 2.00–2.63 mm (n

= 19); APW: 0.70–0.90 mm (n = 26); PPW: 1.57–2.03 mm (n = 26); PL: 0.87–1.07 mm (n = 26); EL: 1.33–1.67 mm (n = 26); EW: 2.20–1.70 mm (n = 19); ProW: 0.97–1.23 mm (n = 26); ProL: 0.23–0.43 mm (n = 26); PyL: 0.73–0.87 mm (n = 20); PTL: 0.60–0.67 mm (n = 26); MSTL: 0.63–0.73 mm (n = 26); MTTL: 0.70–0.90 mm (n = 26).

Body (Figs. 13, 55A, C) oval, convex; cuticle shining and black or copper with brassy luster; antennae dark piceous with club black; legs black. Frontal stria (Fig. 55D) of head complete, carinate and straight on each side. Supraorbital stria complete. Disk of frons with rudimentary transverse rugae. Surface of epistome rough.

Pronotal (Figs. 13, 55A, C) sides convergent forward to apical 1/6, thence strongly arcuate and convergent apically. Apical angles round. Marginal stria carinate and complete laterally and anteriorly. Disk coarsely and densely punctate, the punctures becoming more rugose in lateral region and absent mediobasally; basal area with two or three transverse rows of large and oblong punctures, almost shallowly depressed in central part.

Marginal epipleural stria (Figs. 13, 55A, C, F) complete and clearly impressed. Marginal elytral stria complete, broadly impressed in basal 1/3, the apical end extending inwards, reaching to near lateral 1/4 of posterior margin of elytron. External subhumeral stria absent. Internal subhumeral stria impressed on median 1/3. Oblique humeral stria present on basal 1/3, the area around the stria with several short rugae. First dorsal elytral stria completely present, but sometimes reduced on apical 1/4–1/8. Second to fourth dorsal striae well impressed on basal 1/2; the basal end of fourth extending inwards and united with the base of sutural stria. Sutural stria completely impressed. Surface of elytra smooth on basal 1/2, and densely covered with coarse and deep punctures on apical 1/2, which are often united and forming longitudinal rugae; extreme apex of elytron and flank

sparsely and finely punctate. Underside of elytron (Fig. 56E, F) furnished with microsetae.

Propygidium (Fig. 56C) densely covered with coarse and round punctures, which become finer and sparser toward the base, but mostly separated by their own diameter. Pygidium densely covered with coarse punctures with weak rugae appearance, which are a little smaller than those of the propygidium and separated by 0.3–0.5 times their diameter; punctures on the apex becoming finer and sparser.

Anterior margin (Figs. 55B, 56A) of prosternum weakly obtuse-angulate in median portion. Preapical foveae deep, distinctly present. Keel narrow, strongly compressed. Descending lateral striae carinate and convergent to apex, but nearly parallel on their apical portions. Carinal striae completely impressed, divergent apically and basally; anterior ends of the striae united with descending lateral striae. Lateral side of keel coarsely punctate, the punctures separated by about 1.5 (1–2) times the diameter.

Anterior margin of mesoventrite (Figs. 55B, 56A) feebly emarginate; marginal stria carinate and complete. Disk of mesoventrite smooth. Meso-metaventricle suture (Figs. 55B, 56A) lightly impressed, accompanied with a coarsely crenated parallel line. Intercoxal disk of metaventricle (Figs. 55B, 56B, D) smooth, and posterior margin bordered by 2–3 rows of punctures. Lateral metaventricle stria (Figs. 55B, 56 B) distinctly impressed and carinate, extending obliquely and reaching near hind coxa. Lateral disk densely covered with coarse, round and shallow punctures with fine punctures on basal 1/2, the punctures gradually becoming smaller and sparser; area along the lateral stria and on posterior 1/2 impunctate. Metepisternum densely and coarsely punctate.

Intercoxal disk of first abdominal (Figs. 55B, 56D) sternum smooth, and completely striate on each side.

Protibia (Fig. 57) with six to seven denticles on outer margin, two on apical

margin; dorsal surface smooth; outer part of posterior surface areolate-rugose and bearing three to four short denticles.

Mentum and submentum (Fig. 55E) with branch setae. Terminal maxillary palpomere and terminal labial palpomere each with rows of palpal organs on outer surface of basal and apical portions.

Aedeagus (Fig. 58A, B) slender, curved ventrad at middle; parameres long, about as long as four times the length of phallobase; median lobe sclerotized; base of ninth tergite elongate and curved downward.

Undivided eighth tergite of female genitalia (Fig. 73). Central portion of anterior margin of eighth tergite markedly truncate. Eighth sternite undivided. Basal baculi converge but separate, and basal baculi fused with lateral disk of eighth sternite. Ninth tergite in basal direction and ninth tergite in apical direction extremely small. Ninth sternite in basal direction (valvifer) linear, and anterior part not paddle-shaped. Ninth sternite in apical direction fuses with ninth sternite in basal direction (valvifer). Tenth tergite well-developed. Tenth sternite absent. Articulating sclerite oval shape. Coxite long and robust, not shovel-like, lacking differentiation between outer and inner surfaces, and devoid of teeth at the apex. Coxite very fine setae present on ventral side of coxite from anterior edge to central portion. Articular membrane closed, apical edge remote from apical emargination between teeth. Articulating membrane without a seta. Stylus visible from dorsal side. Stylus with six setae at tip. Inside of oviduct densely covered with fine setae. Bursa copulatrix flat and not expanded. Spermatheca composed of one sclerotized receptacle. Spermathecal gland composed of one sclerotized receptacle, and with numerous fine, round-tipped hairs on surface, attached anterior side of spermatheca. Length of spermathecal duct approximately seven times length of spermatheca.

Spermathecal duct attached near gonopore.

Type specimens. Holotype (SEHU): ♂, labeled: 1. “Gifu-ken Hashima-gun / Kasamatsu-chô Enjô-ji / 14. Aug. 2018 / Masaki Ishiguro saisyû” (in Chinese characters); 2. “Himehamabe / emmamushi” (in Katakana); 3. “Hypocaccus / (Hypocaccus) / subaeneus (Schmidt, 1890) / Det. M. Ôhara, 2021”; 4. “MO-20-013 / Ex. by Dr M. Ohara / SEHU, Japan”; 5. “Holo-type / Hypocaccus / (Hypocaccus) toyoshimai / T. Kikuchi & M. Ôhara, 2023” [Red label]. Paratypes: 1 ♂ (TK-22-016), 2 ♀♀ (TK-22-015), 4 exs., same data as the holotype (SEHU); 10 exs., Motegi, Tochigi, 22.V.1994, H. Takizawa leg. (SEHU); 1 ex. Shingai-hama, Hikone, Shiga, 1.VI.1994, S. Shiyake leg. (OMNH); 7 exs. same locality and collector but different date, 12.VII.2001 (OMNH); 1 ex. Riv. Kidugawa (left bank), Yawata City, Kyoto Prefecture, 28.X–4.XI.2017, T. & A. Tani leg. Fit trap (After Typhoon 22nd has passed) (CITO).

The type specimens collected by M. Ishiguro were recorded as *Hypocaccus* (*Hypocaccus*) *akanensis* in Toyoshima (2021).

Distribution. Japan (Honshu).

Biology. *Hypocaccus* (*Hypocaccus*) *toyoshimai* were collected by pitfall traps from the river bank sandy areas.

3-4. Discussion

The detailed descriptions of the external morphology, mouthparts, and female genitalia of *Hypocacculus* and *Hypocaccus* revealed trait states such as densely covered fine setae on the dorsal base of the mandibles and the presence of molae, features not recognized by Lackner (2010). Particularly within the female genitalia, distinct species-

specific differences were observed in trait states not extensively described by Lackner and Tarasov (2019), revealing several new characteristics, like the structure of hairs on the surface of the spermathecal duct junction and the spermathecal gland surface. These findings suggest that the female genitalia possess traits suitable for comprehensive utilization in phylogenetic analysis.

Chapter 4. The detailed description of female genitalia of the ingroup representative species used in phylogenetic analysis

4-1. Introduction

As the descriptions for *Sphaerites glabratus* and *Syntelia histeroides* from Chapter 2 continued alongside *Hypocacculus* and the riverine *Hypocaccus* in Chapter 3, notable differences in various traits of female genitalia among species were observed. Recognizing the utility of female genitalia traits in phylogenetic analysis, detailed descriptions for the female genitalia of 19 species within the ingroup were additionally provided. In Chapter 4, descriptions for the female genitalia of two species in the outgroup and 24 species in the ingroup were presented. New morphological terms were created and defined for the newly identified traits confirmed in this chapter.

4-2. Material and methods

Terminology. The terminology of female genital follows Ohara (1994), Lackner (2010), Caterino and Tishechkin (2015) and Lackner and Tarasov (2019). In this study, the sequence of species names followed the arrangement by Ôhara, 2023[2022], with species not listed in Ôhara, 2023[2022] inserted alphabetically.

Abbreviation. The following abbreviation is used in the figure for the female genitalia (Figs. 59, 60).

8t: eighth tergite

8s: eighth sternite

8ass: small sclerites on the lateral side of the eighth abdominal segment

The eighth abdominal segment bifurcates into the eighth tergite and the eighth

sternite, occasionally bearing small sclerotized on the lateral side between eighth tergite and eighth sternite.

9ta: ninth tergite located in the apical direction

9tb: ninth tergite located in the basal direction

9sa: ninth sternite located in the apical direction

9sb (v): ninth sternite located in the basal direction, referred to as valvifer

The ninth abdominal segment divides into the ninth tergite and the ninth sternite, each of which may further subdivide into two parts. The ninth sternite located in the basal direction becomes the valvifer and remains consistent across all species, but other parts may undergo reduction or complete disappearance in certain instances.

10t: tenth tergite

10s: tenth sternite

The tenth abdominal segment divides into the tenth tergite (10t) and the tenth sternite (10s). While 10t is present in all species, 10s may disappear in certain species.

am: articular membrane

as: articulating sclerite

Coxite with an articular membrane and a stylus, with the left and right coxites connected by an articulating sclerite, resembling a hinge-like structure.

bc: bursa copulatrix

bcs: bursa copulatrix sclerites

ov: common oviduct

Gonopore is often located on the ventral side of the base of the coxite and connects to the vagina, bursa copulatrix, and common oviduct. The bursa copulatrix and common oviduct may have sclerotized. The anus and rectum originate from the posterior margin of the 10t, but they are not depicted in the figures of this study.

sp: spermatheca

spg: spermathecal gland

The spermatheca serves as an organ responsible for storing and preserving sperm until fertilization (Snodgrass, 1935), connecting to the gonopore and bursa copulatrix via the spermathecal duct. While the spermathecal gland typically connects to the spermatheca, there are species where it is absent.

4-3. Results

Taxonomy

Superfamily **Histeroidea** Gyllenhal, 1808

Family **Sphaeritidae** Thomson, 1862

Genus *Sphaerites* Duftschmidt, 1805

Sphaerites glabratus (Fabricius, 1792)

[Japanese name: Emmamushi-damashi]

(Figs. 1, 27–32, 61, 107, 108)

Description of female genitalia, and specimens examined. See pages 13–15, in Chapter 2.

Family **Synteliidae** Lewis, 1882

Genus *Syntelia* Westwood, 1864

Syntelia histeroides Lewis, 1882

[Japanese name: Emmamushi-modoki]

(Figs. 2, 33–37, 62, 101, 102)

Description of female genitalia, and specimens examined. See pages 18–22, in Chapter 2.

Family **Histeridae** Gyllenhal, 1808

Subfamily **Niponiinae** Fowler, 1912

Genus *Niponius* Lewis, 1885

Niponius osorioceps Lewis, 1885

[Japanese name: Hime-hoso-emmamushi]

(Figs. 3, 63, 93)

Description of female genitalia. Eighth tergite undivided. Eighth sternite divided into two lateral plates and one central plate. Basal baculi converge but separate, and basal baculi articulated with lateral disk of eighth sternite. Ninth tergite in basal direction wide and covers sides. Ninth tergite in apical direction situated on lateral side. Ninth sternite in basal direction (valvifer) long. Anterior part of ninth sternite in basal direction (valvifer) paddle-shaped. Ninth sternite in basal direction (valvifer) oriented with ventral side facing slightly inward. Ninth sternite in apical direction elongates slender shape. Tenth tergite extremely large and wide. Tenth sternite absent. Articulating sclerite oval shape. Coxite short and robust, with a shovel-like shape, with external surface separated from internal surface by elevated lateral ridges, and they slightly directed inward on

ventral side. Coxite with four apical teeth. Apical teeth of coxite strengthened by a radial ridge on inner face. Articular membrane closed, apical edge remote from apical emargination between teeth. Articulating membrane without a seta. Stylus absent, but 6 setae at tip of stylus originating from articular membrane. Inside of oviduct densely covered with fine setae. Bursa copulatrix small and with a little expandable membrane. Sclerites of bursa copulatrix single, elongated in shape, with three pairs of setae on anterior side, and there a dorsal membrane. Spermatheca composed of one receptacle, sclerotized. Spermathecal gland not sclerotized, slender, and with numerous fine, round-tipped hairs on surface, attached anterior side of spermatheca. Spermathecal duct emerging from hole of spermatheca and attached near sclerites of bursa copulatrix.

Specimens examined. Honshu --- [Fukushima Pref.] 1 ex. (TK-23-129), Minami-Aizu, Tateiwa v., Yunohana, 20.VII.1947, Y. K. leg. (SEHU). [Gifu Pref.] 4 ♀♀ (TK-23-070, TK-23-073, TK-23-075, TK-23-078), Danahira-rindô, Miya-mura, 2-15.VI.2002, Y. Takai leg., α -pinene (SEHU).

Subfamily **Abraeinae** W. S. Macleay, 1819

Tribe **Plegaderini** Portevin, 1929

Genus **Plegaderus** Erichson, 1834

Subgenus *Plegaderus* Erichson, 1834

Plegaderus (Plegaderus) marseuli Reitter, 1877

[Japanese name: Munemizo-tsubu-emmamushi]

(Figs. 4, 64, 87, 92, 93, 102)

Description of female genitalia. Eighth tergite undivided. Eighth sternite undivided. Basal baculi converge but separate, and basal baculi fused with lateral disk of

eighth sternite. Ninth tergite in basal direction absent. Ninth tergite in apical direction situated on lateral side. Ninth sternite in basal direction (valvifer) long. Anterior part of ninth sternite in basal direction (valvifer) paddle-shaped. Ninth sternite in apical direction absent. Tenth tergite wide and markedly truncate. Tenth sternite absent. Articulating sclerite long, triangular shape. Coxite long and robust, with a pointed shape, not a shovel-like shape, and with three apical teeth. Articular membrane closed, apical edge remote from apical emargination between teeth. Articulating membrane with a seta. Stylus with a seta at tip. Inside of oviduct densely covered with fine setae. Bursa copulatrix small and with a little expandable membrane. Spermatheca composed of one receptacle, sclerotized. Spermathecal gland not sclerotized, slender, and with numerous fine, round-tipped hairs on surface, attached posterior side of spermatheca. Spermathecal duct attached posterior end of oviduct.

Specimens examined. Hokkaido --- [Kushiro Dist.] 1 ♀ (TK-23-094), Mt. Mokoto-yama, near Lake Kushyaro-ko, 6.VI.1992, M, Ôhara leg., under bark (*Abies sachalinensis*) (SEHU). [Tokachi Dist.] 1 ♀ (TK-23-095), Nukabira, 12.VII.1966, Y. Nishijima leg. (SEHU). [Ishikari Dist.] 1 ♀ (TK-23-133), Jôzankei, 16.VII.1988, M, Ôhara leg. (SEHU); 1 ♀ (TK-23-132), Jôzankei, 11.VI.1990, M, Ôhara leg. (SEHU). Honshu --- [Wakayama Pref.] 1 ♀ (TK-23-093), Mt. Ryûmon-zan, 4.I.1950, M. Aoyagi leg. (SEHU). [Okayama Pref.] 1 ♀ (TK-23-134), Jyôshimatsu, 23.VI.1948, M. Inouye leg. (SEHU).

Tribe **Abraeini** W. S. Macleay, 1819

Genus *Chaetabraeus* Portevin, 1929

Subgenus *Chaetabraeus* Portevin, 1929

***Chaetabraeus (Chaetabraeus) bonzicus* (Marseul, 1873)**

[Japanese name: Kuro-tsubu-emmamushi]

(Figs. 5, 65, 90, 99, 101)

Description of female genitalia. Eighth tergite divided. Eighth sternite undivided. Posterior end of eighth sternite with a deep notch. Basal baculi converge but separate, and basal baculi fused with lateral disk of eighth sternite. Ninth tergite in basal direction absent. Ninth sternite in basal direction (valvifer) long. Anterior part of ninth sternite in basal direction (valvifer) paddle-shaped. Ninth sternite in apical direction absent. Tenth tergite elongated anteriorly, with half of located inside female genitalia. Tenth sternite small. Articulating sclerite long, triangular shape. Coxite long and robust, not shovel-like, without differentiation of external and internal faces, and with three apical teeth. Articular membrane closed, apical edge remote from apical emargination between teeth. Articulating membrane with a seta. Stylus long with two setae at tip. Inside of oviduct densely covered with fine setae. Bursa copulatrix with considerable expandable membrane. Sclerite of bursa copulatrix at junction with oviduct. Spermatheca composed of one receptacle, sclerotized. Spermathecal gland sclerotized only in posterior part, extremely slender, and with numerous fine, round-tipped hairs on surface, attached posterior side of spermatheca. Spermathecal duct attached posterior end of oviduct.

Specimens examined. Hokkaido --- [Ishikari Dist.] 1 ♂ (TK-23-135), Hitsujigaoka, Sapporo, 20.VII.1985, M. Ôhara leg. (SEHU). Honshu --- [Tokyo Pref.] 2 ♀♀ (TK-23-097, TK-23-098), Sakahama, Inagi, 4.V.1988, A. Izumi leg. (SEHU). [Hyogo Pref.] 1 ♀ (TK-23-096), Motoyama-mura near Kobe, 16.XI.1937, K. Kurosa leg. (SEHU).

Subfamily **Saprininae** C. É. Blanchard, 1845

Tribe **Hypocaccini** Lackner, 2023

Genus *Eopachylopus* Reichardt, 1926

Eopachylopus ripae (Lewis, 1885)

[Japanese name: Tsuya-hamabe-emmamushi]

(Figs. 6, 66, 90, 92, 106, 108, 110)

Description of female genitalia. Eighth tergite divided. Eighth sternite undivided. Basal baculi parallel and separate, and basal baculi fused with lateral disk of eighth sternite. Ninth tergite in basal direction extremely small. Ninth tergite in apical direction absent. Ninth sternite in basal direction (valvifer) linear, and anterior part not paddle-shaped. Ninth sternite in apical direction fuses with ninth sternite in basal direction (valvifer). Tenth tergite wide. Tenth sternite absent. Articulating sclerite oval shape. Coxite long and robust, not shovel-like, without differentiation of external and internal faces, and with two apical teeth. Apical edge of articular membrane open and with a seta. Stylus absent, but a seta at tip of stylus originating from articular membrane. Inside of oviduct densely covered with fine setae. Bursa copulatrix flat and not expanded. Spermatheca composed of one receptacle, sclerotized. Spermathecal gland composed of one receptacle, sclerotized. Length of spermathecal duct approximately seven times length of spermatheca. Spermathecal duct attached near gonopore.

Specimens examined. Honshu --- [Aomori Pref.] 1 ♀ (TK-23-092), Tanakubo, Same, Hachinohe, alt. 0 m, 26.V.2022, T. Kikuchi leg., sand beach (CKIK). [Iwate Pref.] 2 ♀♀ (TK-23-081, TK-23-082), Taneichi, Hirono, Kunohe, alt. 0 m, 26.V.2022, T. Kikuchi leg., sand beach (CKIK). [Miyagi Pref.] 2 ♀♀ (TK-23-083, TK-23-084), Watanoha, Ishinomaki, alt. 0 m, T. Kikuchi leg., sand beach (CKIK).

Genus *Hypocacculus* Bickhardt, 1914

Subgenus *Nessus* Reichardt, 1932

Hypocacculus (Nessus) asticus Lewis, 1911

[Japanese name: Hime-hamabe-emmamushi]

(Figs. 7, 38–42, 67)

Description of female genitalia, and specimens examined. See pages 29–30, in Chapter3.

Genus *Hypocaccus* Thomson, 1867

Subgenus *Baeckmanniolus* Reichardt, 1926

Hypocaccus (Baeckmanniolus) varians hatsune (Nakane, 1977)

[Japanese name: Ogasawara-nami-hamabe-emmamushi]

(Figs. 8, 68)

Description of female genitalia. Eighth tergite undivided. Central portion of anterior margin of eighth tergite markedly truncate, with two pairs of long setae on posterior margin. Eighth sternite undivided. Basal baculi converge but separate, and basal baculi fused with lateral disk of eighth sternite. Ninth tergite in basal direction and ninth tergite in apical direction extremely small. Anterior part of ninth sternite in basal direction (valvifer) paddle-shaped. Ninth sternite in apical direction fuses with ninth sternite in basal direction (valvifer). Tenth tergite wide. Tenth sternite absent. Articulating sclerite oval shape. Coxite long and robust, not shovel-like, lacking differentiation between outer and inner surfaces, and devoid of teeth at the apex. Coxite very fine setae present on ventral side of coxite from anterior edge to central portion. Articular membrane closed, apical edge remote from apical emargination between teeth. Articulating membrane

without a seta. Stylus not visible from dorsal side. Stylus with four setae at tip. Inside of oviduct densely covered with fine setae. Bursa copulatrix flat and not expanded. Spermatheca composed of one sclerotized receptacle. Spermathecal gland composed of one sclerotized receptacle, and with numerous fine, round-tipped hairs on surface, attached anterior side of spermatheca. Length of spermathecal duct approximately seven times length of spermatheca. Spermathecal duct attached near gonopore.

Specimens examined. Honshu --- [Tokyo Pref.] 1 ♂ (TK-22-022), 4 ♀♀ (TK-22-021, TK-22-023, TK-22-024, TK-22-025), Hatsuneura, ChiChi-jima Is., Ogasawara, 13.II.1992, T. Kawashita leg. (SEHU); 2 ♂♂ (TK-22-020, TK-23-053), 1 ♀ (TK-23-054), 1 ex. (TK-23-052), same locality and collector but different date, 25.IV.1997, T. Kishimoto leg. (SEHU).

***Hypocaccus (Baeckmanniolus) varians varians* (Schmidt, 1890)**

[Japanese name: Nami-hamabe-emmamushi]

(Figs. 9, 69, 91)

Description of female genitalia. Eighth tergite undivided. Central portion of anterior margin of eighth tergite markedly truncate, with three pairs of long setae on posterior margin. Eighth sternite undivided. Basal baculi converge but separate, and basal baculi fused with lateral disk of eighth sternite. Ninth tergite in basal direction and ninth tergite in apical direction extremely small. Anterior part of ninth sternite in basal direction (valvifer) paddle-shaped. Ninth sternite in apical direction fuses with ninth sternite in basal direction (valvifer). Tenth tergite well-developed. Tenth sternite absent. Articulating sclerite oval shape. Coxite long and robust, not shovel-like, lacking differentiation between outer and inner surfaces, and devoid of teeth at the apex. Coxite very fine setae

present on ventral side of coxite from anterior edge to central portion. Articular membrane closed, apical edge remote from apical emargination between teeth. Articulating membrane without a seta. Stylus visible from dorsal side. Stylus with six setae at tip. Inside of oviduct densely covered with fine setae. Bursa copulatrix flat and not expanded. Spermatheca composed of one sclerotized receptacle. Spermathecal gland composed of one sclerotized receptacle, and with numerous fine, round-tipped hairs on surface, attached anterior side of spermatheca. Length of spermathecal duct approximately seven times length of spermatheca. Spermathecal duct attached near gonopore.

Specimens examined. Hokkaido --- [Iburi Dist.] 1 ♀ (TK-22-030), Zenibako, 30.VIII.1985, M. Ôhara leg. (SEHU); 2 ♀♀ (TK-23-021, TK-23-022), Tomakomai-kaigan Beach, 9.VI.1979, H. Onodera leg. (SEHU). Honshu --- [Chiba Pref.] 4 ♀♀ (TK-22-028, TK-23-019, TK-23-020, TK-23-049), 2 exs. (TK-23-050, TK-23-051), Ôami, 1.V.1990, M. Ôhara leg. (SEHU). [Nagasaki Pref.] 1 ♀ (TK-22-029), Kuchinostu, Shimabara, 20.IX.1977, S. Imasaka leg. (SEHU). Kyushu --- [Kagoshima Pref.] 2 ♀♀ (TK-22-026, TK-22-027), Hamada, Tanega-shima Is., Ôsumi-shotô Iss., 31. VII.1984, Y. Harada leg. (SEHU).

Subgenus *Hypocaccus* C. G. Thomson, 1867

Hypocaccus (Hypocaccus) akanensis Ôhara, 1994

[Japanese name: Akan-hamabe-emmamushi]

(Figs. 10, 43–46, 70, 88)

Description of female genitalia, and specimens examined. See pages 35–36, in Chapter3.

***Hypocaccus (Hypocaccus) axeli* Kryzhanovskij, 1976**

[Japanese name: Arame-hamabe-emmamushi]

(Figs. 11, 47–49, 71)

Description of female genitalia, and specimens examined. See pages 37–38, in Chapter3.

***Hypocaccus (Hypocaccus) subaeneus* (Schmidt, 1890)**

[Japanese name: Yama-hamabe-emmamushi]

(Figs. 12, 50–54, 72)

Description of female genitalia, and specimens examined. See pages 39–42, in Chapter3.

***Hypocaccus (Hypocaccus) toyoshimai* Kikuchi et Ôhara, 2023**

[Japanese name: Gifu-hamabe-emmamushi]

(Figs. 13, 55–58, 73, 94, 105, 107)

Description of female genitalia, and specimens examined. See pages 45–46, in Chapter3.

Tribe **Saprinini** Mazur, 1973

Genus ***Saprinus*** Erichson, 1834

Subgenus ***Saprinus*** Erichson, 1834

***Saprinus (Saprinus) niponicus* Dahlgren, 1962**

[Japanese name: Nise-dôgane-emmamushi]

(Figs. 14, 74)

Description of female genitalia. Eighth tergite undivided. Eighth sternite undivided and with several short setae. Basal baculi converge but separate, and basal baculi fused with lateral disk of eighth sternite. sclerotized plate between eighth tergite and eighth sternite exists. Ninth tergite in apical direction is large. Anterior part of ninth sternite in basal direction (valvifer) paddle-shaped. Ninth tergite in basal direction and ninth sternite in apical direction on ventral side and fuse with the ninth sternite in basal direction (valvifer). Tenth tergite anchor-like shape. Tenth sternite absent. Articulating sclerite oval shape. Coxite long and robust, with a shovel-like shape, with external surface separated from internal surface by elevated lateral ridges. Coxite without teeth at apical. Setae on ventral side regularly arranged, while setae on dorsal side randomly distributed. Articular membrane closed, apical edge remote from apical emargination between teeth. Articulating membrane with a seta. Stylus long with six setae at tip. Inside of oviduct densely covered with fine setae. Bursa copulatrix flat and not expanded. Spermatheca composed of one sclerotized receptacle. Spermathecal gland composed of one sclerotized receptacle, and with numerous fine, round-tipped hairs on surface, attached anterior side of spermatheca. Length of spermathecal duct approximately seven times length of spermatheca. Spermathecal duct attached near gonopore.

Specimens examined. Hokkaido --- [Kamikawa Dist.] 1 ♀ (TK-23-080), Otoineppu, 13.VII.2023, T. Kikuchi leg., bait trap (chicken carcass) (CKIK). [Ishikari Dist.] 1 ♀ (TK-23-079), Mt. Teine-yama, alt. 150 m, T. Kikuchi leg., bait trap (chicken carcass) (CKIK).

Subfamily **Dendrophilinae** Reitter, 1909

Tribe **Anapleini** Olexa, 1982

Genus *Anapleus* Horn, 1873

Anapleus nakanei Ôhara, 1994

[Japanese name: Nara-tsubu-emmamushi]

(Figs. 15, 75, 88, 101, 103)

Description of female genitalia. Eighth tergite divided. Posterior end of eighth tergite with several short setae. Eighth sternite undivided. Basal baculi converge but separate, and basal baculi fused with lateral disk of eighth sternite. Ninth tergite in apical direction small and covers only posterior half of hole in coxite cavity. Ninth sternite in basal direction (valvifer) linear, and anterior part not paddle-shaped. Central portion of anterior margin of tenth tergite markedly truncate. Tenth sternite elongated, and central portion of anterior margin markedly truncated. Articulating sclerite small. Coxite long and robust, with a shovel-like shape at apical end, and external surface separated from internal surface by elevated lateral ridges. Setae randomly distributed. Articular membrane closed, apical edge remote from apical emargination between teeth. Articulating membrane with a seta. Stylus long with seven setae at tip. Inside of oviduct densely covered with fine setae. Bursa copulatrix flat and not expanded. Spermatheca composed of one sclerotized receptacle. Spermathecal gland not sclerotized, slender, and with numerous fine, round-tipped hairs on surface, attached anterior side of spermatheca. Spermathecal duct attached posterior end of oviduct.

Specimens examined. Shikoku --- [Tokushima Pref.] 2 ♀♀ (TK-23-099, TK-23-103) 1 ex., Sagata-hama Beach, Ôshimada, Sato, Naruto, alt. 3 m, 5–11.V.2008, K. Tanaka leg., Underground trap (40 cm), pupa powder (SEHU); 1 ♀ (TK-23-104), Munakê-dani, Ôtani, Ôsawa, Naruto, alt. 50 m, 5–11.V.2008, K. Tanaka leg., Underground trap (40 cm), pupa powder (SEHU); 1 ex. (TK-23-136), Kitadomari, Seto, Naruto, alt. 4 m, 1–

29.VI.2008, M. Yoshida leg. Underground trap (50 cm), pupa powder (SEHU); 2 ♀♀ (TK-23-105, TK-23-106), Nagate, Hosonoi, Anan, alt. 60 m, 30.III–27.IV.2008, M. Yoshida leg., Underground trap (50 cm), pupa powder (SEHU); 1 ♀ (TK-23-102), Mt. Ryûô-zan, Nishitani, Ôsaka, Itano, alt. 350 m, 1–29.VI.2008, M. Yoshida leg., Underground trap (50 cm), pupa powder (SEHU); 2 ♀♀ (TK-23-100, TK-23-101), Mt. Ryûô-zan, Mima, Mima, alt. 990 m, 26.V–22.VI.2008, M. Yoshida leg., Underground trap (50 cm), chicken carcass (SEHU).

Tribe **Dendrophilini** Reitter, 1909

Genus *Dendrophilus* Leach, 1817

Subgenus *Dendrophilus* Leach, 1817

Dendrophilus (Dendrophilus) xavieri Marseul, 1873

[Japanese name: Ô-mame-emmamushi]

(Figs. 16, 76, 94, 96, 110)

Description of female genitalia. Eighth tergite divided and articulates at center. Eighth sternite undivided. Basal baculi converge but separate, and basal baculi fused with lateral disk of eighth sternite. Posterior part of eighth sternite deeply truncate, with fine setae densely growing along posterior margin and long setae sparsely distributed. sclerotized plate between eighth tergite and eighth sternite exists. Ninth tergite in basal direction fused with ninth sternite(A) and ninth sternite in apical direction. Tenth tergite long, weakly fused at center, and sparsely covered with setae at the posterior end. Tenth sternite absent. Articulating sclerite oval shape. Coxite long and robust, with a shovel-like shape, and external surface separated from internal surface by elevated lateral ridges. Setae on ventral side densely distributed. Articular membrane closed, apical edge remote

from apical emargination between teeth. Articulating membrane with a seta. Stylus with six setae at tip. Inside of oviduct densely covered with fine setae. Bursa copulatrix small and with a little expandable membrane. Spermatheca composed of one receptacle, not sclerotized. Spermathecal gland not sclerotized, extremely slender, and with numerous fine, round-tipped hairs on surface, attached anterior side of spermatheca. Spermathecal duct attached posterior end of oviduct.

Specimens examined. Shikoku --- [Ehime Pref.] 5 ♂♂, 5 ♀♀ (TK-23-107, TK-23-108, TK-23-109, TK-23-114, TK-23-115) 1 ex. (TK-23-137), Yanaidani, Matsuyama, 7.VII.2022, H. Saito leg., poultry manure (SEHU).

Tribe **Paromalini** Reitter, 1909

Genus ***Carcinops*** Marseul, 1855

Subgenus ***Carcinops*** Marseul, 1855

Carcinops (Carcinops) pumilio (Erichson, 1834)

[Japanese name: Kuro-chibi-emmamushi]

(Figs. 17, 59, 77)

Description of female genitalia. Eighth tergite divided. Eighth sternite undivided. Anterior part of eighth sternite broadly membranous, and posterior part deeply incised from two directions. Basal baculi converge but separate, and basal baculi fused with lateral disk of eighth sternite. sclerotized plate between eighth tergite and eighth sternite exists. Ninth tergite in basal direction wide and covers lateral sides. Anterior part of ninth sternite in basal direction (valvifer) paddle-shaped. Ninth sternite in basal direction (valvifer) oriented with ventral side facing slightly inward. Ninth sternite in apical direction extremely slender. Tenth tergite extremely large, with a slight truncate on

posterior margin. Tenth sternite absent. Coxite long and robust, with a shovel-like shape, with external surface separated from internal surface by elevated lateral ridges, and slightly directed inward on ventral side. Coxite with four apical teeth. Apical teeth of coxite strengthened by a radial ridge on inner face. Articular membrane with a seta. Stylus with two setae at tip. Inside of oviduct densely covered with fine setae. Bursa copulatrix small and with a little expandable membrane. Sclerite of bursa copulatrix at junction with oviduct. Spermatheca composed of one sclerotized receptacle. Spermathecal gland not sclerotized, extremely slender, and with numerous fine, round-tipped hairs on surface, attached anterior side of spermatheca. Spermathecal duct attached near sclerites of oviduct.

Specimens examined. Kyushu --- [Kagoshima Pref.] 2 ♂♂, 4 ♀♀ (TK-23-110, TK-23-111, TK-23-112, TK-23-113), 4 exs., Iriki-bokujyo, 17.III.1985, K. Tomiyama leg. (SEHU). Okinawa --- [Okinawa Pref.] 1 ex. (TK-23-138), Sumuide, Nago, YagachijimaIs., Ryukyus, 30.V.2022, Y. Tamadera leg. (SEHU).

Genus *Paromalus* Erichson, 1834

Subgenus *Paromalus* Erichson, 1834

Paromalus (Paromalus) parallelepipedus (Herbst, 1791)

[Japanese name: Hosochibi-hirata-emmamushi]

(Figs. 18, 78, 90, 99, 109)

Description of female genitalia. Eighth tergite undivided. Eighth sternite divided into two lateral plates and one central plate. Basal baculi converge but separate, and basal baculi fused with lateral disk of eighth sternite. Ninth tergite in basal direction wide and covers lateral sides. Ninth tergite in apical direction situated on lateral side. Ninth sternite

in basal direction (valvifer) extremely long, with a paddle-shaped anterior part. Ninth sternite in basal direction (valvifer) oriented with ventral side facing slightly inward. Ninth sternite in apical direction extremely small. Tenth tergite extremely large. Tenth sternite absent. Coxite long and robust, not shovel-like, without differentiation of external and internal faces, and slightly directed inward on ventral side, with two apical teeth. Articular membrane with a seta. Stylus absent, but 2 setae at tip of stylus originating from articular membrane. Inside of oviduct densely covered with fine setae. Bursa copulatrix with considerable expandable membrane. Sclerite of bursa copulatrix at junction with oviduct. Spermatheca composed of one sclerotized receptacle. Spermathecal gland not sclerotized, round, and with numerous fine, round-tipped hairs on surface, attached posterior side of spermatheca. Length of spermathecal duct approximately 10 times length of spermatheca. Spermathecal duct attached near sclerites of oviduct.

Specimens examined. Honshu --- [Tokyo Pref.] 1 ♀ (TK-23-139), Ômaru, Inagi, 10.IV.1998, K. Sawada leg. (SEHU). [Hyogo Pref.] 6 ♀♀ (TK-23-116, TK-23-117, TK-23-118, TK-23-119, TK-23-120, TK-23-121), Yunohana, 8.V.1949, S. Eda leg. (SEHU).

Subfamily **Onthophilinae** W. S. Macleay, 1819

Genus ***Epiechinus*** Lewis, 1891

Epiechinus arboreus (Lewis, 1884)

[Japanese name: Chibike-sesuji-emmamushi]

(Figs. 19, 79, 87, 92, 97, 100, 107–109)

Description of female genitalia. Many thick setae on ventral side surface of female genitalia. Eighth tergite divided. Eighth sternite divided into two lateral plates and one central plate. Basal baculi fused into basal bridge. Ninth tergite in basal direction

fuses with ninth sternite in basal direction (valvifer). Anterior half of Ninth tergite in basal direction embedded within membranous tissue. Ninth sternite in basal direction (valvifer) linear, and anterior part not paddle-shaped. Ninth sternite in apical direction absent. Tenth tergite wide, tapering towards anterior side. Tenth sternite absent. Coxite long and robust, not shovel-like, without differentiation of external and internal faces, with four apical teeth. Articular membrane with a seta. Stylus with five setae at tip. Inside of oviduct densely covered with fine setae. Bursa copulatrix with considerable expandable membrane. Anterior half of bursa copulatrix with numerous fine, round-tipped hairs on surface. Bursa copulatrix with single median sclerite in dorsal membrane. Spermatheca composed of one sclerotized receptacle. Spermathecal gland not sclerotized, short and attached to anterior side of spermatheca. Spermathecal duct attached near sclerites of bursa copulatrix.

Specimens examined. Honshu --- [Nara Pref.] 1 ex. (TK-23-061), Mt. Kasugayama, 8.I.1954, M. Ohtake leg. (SEHU); 4 ♀♀ (TK-23-122, TK-23-123, TK-23-124, TK-23-125), same locality but different date and collector, 12.VII.1959, M. Goto leg. (OMNH); 2 ♀♀ (TK-23-039, TK-23-040), Mt. Kasuga-yama, Nara, alt.120–220 m, 16.VII.2000, K. Akita leg. (SEHU); 2 exs. (TK-23-058, TK-23-059), Kasugano–Byakugouji, 16.XII.2007, S. Fujie leg. (SEHU); 2 ♀♀ (TK-23-027, TK-23-28), 5 exs. (TK-23-035, TK-23-036, TK-23-037, TK-23-060), Yagyû-kaidô, Nara, 13.III.2007, Y. Kawakami leg. (SEHU).

Genus *Onthophilus* Leach, 1817

Onthophilus ostreatus Lewis, 1879

[Japanese name: Ô-sesuji-emmamushi]

(Figs. 20, 80, 96, 104, 105)

Description of female genitalia. Eighth tergite divided and with short setae sparsely. Eighth sternite undivided, and both anterior and posterior parts shallowly incised from two directions. Apical margin protrudes sharply, and sparse setae on lateral side. Basal baculi converge but separate, and fuse with lateral disk of eighth sternite. Posterior end of ninth tergite, with a few extremely fine setae. Ninth tergite in basal direction fused with ninth sternite(A) and ninth sternite in apical direction, with anterior one-third penetrating into membranous tissue. Ninth tergite in apical direction absent. Ninth sternite in basal direction (valvifer) linear, and anterior part not paddle-shaped. Anterior half of ninth sternite in apical direction with short setae, while posterior half with long setae. Tenth tergite long, with short setae scattered on posterior side. Posterior margin of tenth tergite noticeably truncated, and anterior margin extends into membranous tissue. Tenth sternite slender. Coxite short and robust, with a shovel-like shape, with external surface separated from internal surface by elevated lateral ridges. Coxite with two apical teeth. Articular membrane with a seta. Stylus with five setae at tip. Inside of oviduct densely covered with fine setae. Bursa copulatrix small and with a little expandable membrane. Spermatheca composed of one receptacle, not sclerotized. Spermathecal gland not sclerotized, and with numerous fine, round-tipped hairs on surface, attached posterior side of spermatheca. Spermathecal duct attached posterior end of oviduct.

Specimens examined. Honshu --- [Chiba Pref.] 2 ♀♀ (TK-23-031, TK-23-032), Kashiwa, 5.XI.1994. K. Masumoto leg. (SEHU). [Mie Pref.] 3exs. (TK-23-055, TK-23-056, TK-23-057), Mizusawa, Yokkaichi, 23.X.1993, H. Otobe leg. (SEHU). Kyushu --- [Kagoshima Pref.] 2 ♀♀ (TK-23-023, TK-23-024), Meinô-bokujyô, Kanoya, 7.XII.1984, M. Ôhara leg. (SEHU).

***Onthophilus silvae* Lewis, 1884**

[Japanese name: Shinano-sesuji-emmamushi]

(Figs. 21, 81, 106)

Description of female genitalia. Eighth tergite divided. Eighth sternite undivided, and both anterior and posterior parts shallowly incised from two directions. Apical margin protrudes. Basal baculi converge but separate, and fuse with lateral disk of eighth sternite. Ninth tergite, with a few extremely fine setae. Ninth tergite in basal direction fused with ninth sternite(A) and ninth sternite in apical direction, with anterior one-second penetrating into membranous tissue. Ninth tergite in apical direction absent. Ninth sternite in basal direction (valvifer) linear, and anterior part not paddle-shaped. Anterior half of ninth sternite in apical direction densely covered with short setae, while posterior half densely covered with long setae. Tenth tergite long, with short setae scattered on posterior side. Posterior margin of tenth tergite noticeably truncated, and anterior margin extends into membranous tissue. Tenth sternite square. Coxite short and robust, with a shovel-like shape, with external surface separated from internal surface by elevated lateral ridges. Coxite with three apical teeth. Articular membrane with a seta. Stylus with five setae at tip. Inside of oviduct densely covered with fine setae. Bursa copulatrix small and with a little expandable membrane. Spermatheca composed of one sclerotized receptacle. Spermathecal gland not sclerotized, and with numerous fine, round-tipped hairs on surface, attached posterior side of spermatheca. Spermathecal duct attached posterior end of oviduct.

Specimens examined. Hokkaido --- [Ishikari Dist.] 1 ♀ (TK-23-063), 2 exs., Iseki-hozen-kôen in Hokkaido university, Sapporo, 23.V.1997, M. Ôhara & K. Mizota leg.

hand picking from nest of *Lasius* (#960608) (SEHU); 2 ♀♀ (TK-23-007, TK-23-025), Nopporo forest park, Sapporo (64414359), 6–8.VII.2000, S. Hori leg., PT (SEHU); 1 ex., (TK-23-140), Okusawa-suigen-chi, Otaru, 12.VII.1996, M. Ôhara leg., from ant nest (960614) (SEHU). [Shiribeshi Dist.] 1 ♀ (TK-23-038), 1ex. (TK-23-026), Yahata, Kutchan, 19.VIII.1994, M. Ôhara leg. (SEHU); 1 ♀ (TK-23-062), Utsai, Kuromatsunai, 26.V.1996, M. Ôhara leg., from nest (960526) of ant, *Lasius* sp. (SEHU). Honshu --- [Kanagawa Pref.] 2 ♂♂, 5 ♀♀ (TK-23-030, TK-23-043, TK-23-044, TK-23-045, TK-23-046), Tama, Kawasaki, 15.VI.1996, K. Kawada leg. (SEHU); 1 ♀ (TK-23-029), Mt. Masukata-yama, Tama, Kawasaki, 14.VII.1996, K. Kawada leg. (SEHU).

Subfamily **Histerinae** Gyllenhal, 1808

Tribe **Exosternini** Bickhardt, 1914

Genus ***Baconia*** Lewis, 1885

Baconia chujoi (Cooman, 1941)

[Japanese name: Chûjô-chibi-emmamushi]

(Figs. 22, 82, 97, 103)

Description of female genitalia. Eighth tergite undivided. Eighth sternite divided into two lateral plates and one central plate. Basal baculi converge but separate, and basal baculi fused with lateral disk of eighth sternite. Ninth tergite in apical direction large. Anterior part of ninth sternite in basal direction (valvifer) paddle-shaped. Tenth tergite extremely wide. Tenth sternite slender. Coxite long and robust, not shovel-like, without differentiation of external and internal faces, with five apical teeth. Articular membrane with a seta. Stylus with seven setae at tip. Inside of oviduct densely covered with fine setae. Bursa copulatrix reduced, with a little expandable membrane. Bursa copulatrix with

paired sclerites in dorsal membrane. Spermatheca composed of one sclerotized receptacle, and bent shaped. Spermathecal gland not sclerotized, and with numerous fine, round-tipped hairs on surface, attached around middle of spermatheca. Spermathecal duct attached near sclerites of bursa copulatrix.

Specimens examined. Honshu --- [Tokyo Pref.] 1 ex. (TK-23-130), Hatuzawamachi, Hachiôji, 19.V.2001, K. Sakai leg. (SEHU). [Kanagawa Pref.] 1 ex., Jinumuji temple, Takatori, Miura Peninsula, 26.IV.1981, K. Emoto leg. (SEHU); 2 ♀♀ (TK-23-071, TK-23-072), Mt. Masukata-yama, Tama, Kawasaki, 13.V.1995, K. Kawada leg. (SEHU).

Genus *Notodoma* Lacordaire, 1854

Notodoma fungorum Lewis, 1884

[Japanese name: Kinoko-aka-maru-emmamushi]

(Figs. 23, 83, 88, 89)

Description of female genitalia. Eighth tergite undivided. Eighth sternite undivided. Basal baculi converge but separate, and basal baculi fused with lateral disk of eighth sternite. Ninth tergite in apical direction large. Ninth sternite in basal direction (valvifer) extremely long, with a paddle-shaped anterior part. Ninth sternite in basal direction (valvifer) oriented with ventral side facing slightly inward. Ninth sternite in apical direction slender. Tenth tergite extremely long. Tenth sternite extremely slender. Coxite long and robust, not shovel-like, without differentiation of external and internal faces, and slightly directed inward on ventral side, with four apical teeth. Articular membrane with a seta. Stylus slender with five setae at tip. Inside of oviduct densely covered with fine setae. Bursa copulatrix small and with a little expandable membrane.

Spermatheca composed of one receptacle, not sclerotized. Spermathecal gland not sclerotized, and with numerous fine, round-tipped hairs on surface, attached posterior side of spermatheca. Spermathecal duct attached posterior end of oviduct.

Specimens examined. Honshu --- [Tokyo Pref.] 2 ♀♀ (TK-23-076, TK-23-077), Mt. Takao, Tokyo Municipal, 1.VI.1948, K. Kinugasa leg. (SEHU); 1 ♂ (TK-23-129), same locality and collector but different date, 29.IV.1963 (SEHU). Kyushu --- [Nagasaki Pref.] 1 ♂ (TK-23-074-2), 1 ♀ (TK-23-074-1), Mt. Tatsura (Tatera), Is. Tsushima, 25.V.1991, H. Ebihara leg. (SEHU). Okinawa --- [Okinawa Pref.] 1 ♀ (TK-23-069), Yona, Kunigami-son, Ryukyus, 12.IV.1997, Y. Sawada leg. (SEHU).

Tribe **Histerini** Gyllenhal, 1808

Genus *Atholus* C. G. Thomson, 1859

Atholus duodecimstriatus quatuordecimstriatus (Gyllenhal, 1808)

[Japanese name: Ko-tsuya-emmamushi]

(Figs. 24, 60, 84, 89–100, 102)

Description of female genitalia. Eighth tergite undivided and longitudinally strigose on surface. Eighth sternite divided into two lateral plates, and basal baculi converge but remain separate. Basal baculi fused with lateral disk of eighth sternite. Ninth tergite in basal direction contacts tenth tergite. Ninth tergite in apical direction large. Anterior part of ninth sternite in basal direction (valvifer) paddle-shaped. Ninth sternite in apical direction absent. Tenth tergite long. Central portion of posterior margin of tenth tergite markedly truncate. Tenth sternite extremely small. Articulating sclerite oval shape. Coxite long and robust, not shovel-like, without differentiation of external and internal faces, with two apical teeth. Articular membrane with a seta. Stylus slender with four

setae at tip. Inside of oviduct densely covered with fine setae. Bursa copulatrix flat and not expanded. Sclerotized plate extremely large and covers spermatheca. Spermatheca composed of four slender, tubular structures and not sclerotized. Spermatheca located near gonopore. Spermathecal gland absent. Spermathecal duct absent.

Specimens examined. Hokkaido --- [Ishikari Dist.] 1 ♂ (No.-9115), Jôzankei, 29.VI.1985, M. Ôhara leg. (SEHU). [Shiribeshi Dist.] 1 ♀ (TK-23-086), Kamishihoro, 7.VII.1990, M. Ôhara leg. (SEHU); 4 ♂♂, 1 ♀ (TK-23-085), Akaigawa, Ônuma, 13.VII.1990, M. Ôhara leg. (SEHU).

Genus *Margarinotus* Marseul, 1854

Subgenus *Grammostethus* Lewis, 1906

Margarinotus (Grammostethus) niponicus (Lewis, 1895)

[Japanese name: Ko-emmamushi]

(Figs. 25, 85)

Description of female genitalia. Eighth tergite undivided. Eighth sternite undivided, and apical margin protrudes. Basal baculi converge but separate, and basal baculi articulated with lateral disk of eighth sternite. Ninth tergite in basal direction fuses on both sides and extends to cover ventral surface. Ninth tergite in apical direction extremely large and extends to lateral side. Anterior part of ninth sternite in basal direction (valvifer) paddle-shaped. Tenth tergite an extremely large triangle, with a slight indentation at posterior side. Tenth sternite slender and with slight indentations at both anterior and posterior. Articulating sclerite oval shape. Coxite long and robust, not shovel-like, without differentiation of external and internal faces, with two apical teeth. Articular membrane with a seta. Stylus slender with five setae at tip. Inside of oviduct densely

covered with fine setae. Bursa copulatrix reduced, with a little expandable membrane. Spermatheca composed of seven slender tubular structures and not sclerotized. Spermathecal gland not sclerotized, and with numerous fine, round-tipped hairs on surface. Spermathecal duct absent.

Specimens examined. Hokkaido --- [Ishikari Dist.] 1 ♀ (TK-23-131), Nopporo, 3.VI.1988, M. Ôhara leg. (SEHU); 3 ♀♀ (TK-23-089, TK-23-090, TK-23-091), Hokkaido University, Sapporo, 7.VII.2023, T. Kikuchi leg., sap (*Ulmus davidiana*) (SEHU).

Tribe **Hololeptini** Hope, 1840

Genus *Hololepta* Paykull, 1811

Subgenus *Hololepta* Paykull, 1811

Hololepta (Hololepta) amurensis Reitter, 1879

[Japanese name: Ô-hirata-emmamushi]

(Figs. 26, 86, 91, 104)

Description of female genitalia. Eighth tergite undivided, and posterior margin slightly incised. Eighth sternite undivided. Apical margin protrudes sharply. Basal baculi converge but separate, and fuse with lateral disk of eighth sternite. Ninth tergite in basal direction absent. Ninth tergite in apical direction extremely large and extends to ventral side. Anterior part of ninth sternite in basal direction (valvifer) paddle-shaped. Ninth sternite in basal direction (valvifer) oriented with ventral side facing slightly inward. Ninth sternite in apical direction absent. Tenth tergite develops extremely large. Tenth tergite somewhat slender, with a rugose surface at posterior end. Articulating sclerite oval shape. Coxite long and robust, not shovel-like, without differentiation of external and

internal faces, with a notch at anterior part of ventral side, and ventral side slightly facing inward. Articular membrane with a seta. Stylus slender with nine setae at tip. Inside of oviduct densely covered with fine setae. Bursa copulatrix reduced, with a little expandable membrane. Spermatheca composed of seven slender tubular structures and not sclerotized. Spermathecal gland not sclerotized, and with numerous fine, round-tipped hairs on surface, attached posterior side of spermatheca. Spermathecal duct attached posterior end of oviduct.

Specimens examined. Hokkaido --- [Shiribeshi Dist.] 1 ♀ (TK-23-067), Mt. Yôtei, Hirafu, Kucchan, 15-16.VII.1991, M. Ôhara leg. (SEHU); 1 ♀ (TK-23-068), same locality and collector but different date, 22.VII.1991 (SEHU). Honshu --- [Gunma Pref.] 1 ♀ (TK-23-128), Ôsawa, 15.VII.1963, S. Kondo leg. (SEHU).

4-4. Discussion

The genitalia of insects vary significantly at the levels of order, family, genus, and species, particularly in terms of the internal interactions during mating and the morphological involvement of male and female genitalia. As a result, they are frequently utilized as essential tools for classification and identification (Eberhard, 1985). Specifically, the male genitalia are recognized as the most morphologically diverse and variable structures in the insect body (Eberhard, 1985), and they have been extensively studied throughout the insect world, primarily for species identification purposes (Tuxen, 1970). According to Song and Bucheli (2010), the majority of research on insect genitalia has focused on male genitalia. On the other hand, research on female genitalia is extremely limited. There are primarily three reasons why the female genitalia have not been extensively studied.

1. The female genitalia have less sclerotization and are mostly membranous, making their investigation challenging. For example, in certain insect families, the posterior end of the male abdomen is more heavily sclerotized and has been more thoroughly studied, while the membranous region with low transparency between the copulatory opening and the ovaries is often overlooked (Lackner & Tarasov, 2019).
2. Another explanation is that researchers generally believe there is little variation in female genitalia (Eberhard, 1985).
3. They consider them to evolve at a slower rate than male genitalia, thus assuming that they do not provide as much phylogenetic information.

The latest study (Ah-King *et al.*, 2014) focuses on the bias against the significance of female genitalia, challenging the old assumption that female genitalia are not crucial in the study of evolutionary processes. Research on female genitalia is limited in terms of extensive phylogenetic scales. For example, Miller (2008) and Miller and Bergsten (2012) reconstructed the phylogeny of the Noteridae and Gyrinidae families within the Coleoptera order using features of female genitalia. Liebherr and Will (1998) demonstrated some informativeness of female genitalia in phylogenetic estimation of Carabidae. Özgül-Siemund and Ahrens (2015) provided compelling evidence for the high taxonomic and phylogenetic importance of female genitalia in the Scarabaeidae family, specifically the Sericini beetles. A notable exception to the principle of disregarding female genitalia within the Coleoptera order is found in the Tenebrionoidea superfamily. In this study, I conclude that "comparative morphological studies of female genitalia are

highly useful for determining the phylogenetic relationships among members of this superfamily" (Iwan & Kamiński, 2016).

Research on the female genitalia within the superfamily Histeroidea has been documented by Ôhara (1989), describing the female genitalia of Japanese *Margarinotus*, focusing solely on the spermatheca and bursa copulatrix. Ôhara (1994) covered numerous taxa but provided only schematic diagrams of the female genitalia, highlighting the spermatheca, spermathecal gland, and bursa copulatrix. Caterino and Tishechkin (2015) displayed various female genitalia, yet their scope was limited to Exoxterinini. Lackner and Tarasov (2019) focused on the female genitalia of Saprininae, presenting solely the coxite, spermatheca, and spermathecal gland. Bichevoy (2022) sketched female genitalia across multiple genera, but it was limited to the coxite, ninth sternite in basal direction (valvifer), and spermatheca. dela Cruz and Ôhara (2022, 2023a, b), dela Cruz *et al.* (2023) described the female genitalia of *Atholus*, showcasing solely the coxite, ninth sternite in basal direction (valvifer), and spermatheca. In separate works, Kikuchi and Ôhara (2023a) detailed female genitalia of *Syntelia histeroides*, and Kikuchi and Ôhara (2023b) detailed parts of the female genitalia of *Hypocacculus* and *Hypocaccus* found in Japan, yet their focus remained limited to a few specific taxa.

Therefore, research on the female genitalia within the superfamily Histeroidea is still considered incomplete. In this study, sketches of female genitalia for other species within the superfamily Histeroidea revealed various previously unknown features. These features will be addressed in the following section as "Morphological characters and states."

Chapter 5. Extracting the character states of female genitalia

5-1. Introduction

This chapter explains 39 morphological characteristics extracted from the descriptions of female genitalia of 26 Japanese Histeroidea species presented in Chapter 4. These morphological characteristics will be utilized in the phylogenetic analysis in Chapter 6.

5-2. Materials and methods

Of the 39 morphological characteristics extracted from various parts of the female genitalia, different trait states considered homologous within each morphological characteristic were separated.

5-3. Results

Morphological characters and states

Female genitalia

1. membranous region between coxite and eighth tergite, surface (Fig. 87): (0) without long setae; (1) with long setae.

The membranous part of the female genitalia in the species addressed in this paper typically displayed very fine hairs, irregularities, and rugae. However, *Epiechinus arboreus* stood out with numerous long setae on the ventral side of its female genitalia, which was a distinctive feature unique to this species.

2. eighth tergite, unity (Fig. 88): (0) single plate; (1) two separate plates; (2) not divided

but with a deep incision.

In this study, the eighth tergite of the observed species was developed in all cases. While the shapes varied, they could be broadly categorized into three types: those consisting of a single plate, those divided into left and right parts, and those undivided but with a deep longitudinal incision.

3. eighth tergite, texture (Fig. 89): (0) smooth; (1) longitudinally strigose.

The texture of the eighth tergite was similar across many species, featuring numerous small punctures. *Atholus duodecimstriatus* *quatuordecimstriatus* displayed longitudinally striated features across its entire surface.

4. eighth tergite, setae: (0) absent; (1) with setae along posterior margin; (2) sparse setae overall.

Most species without setae on the eighth tergite, although some with setae along the posterior margin of the eighth tergite, while others exhibit sparse setae overall.

5. eighth sternite, main plate, unity (Fig. 90): (0) disk undivided; (1) disk undivided but with deep notches; (2) disk divided into two lateral plates; (3) disk divided into two lateral and one central plate.

The shapes and patterns of incisions on the main plate of the eighth sternite vary,

but this study focused on the number of divisions and the presence of incisions on the eighth sternite.

6. eighth sternite, apical margin (Fig. 91): (0) no protrudes; (1) protrudes.

In many species, the posterior margin of the eighth sternite is smooth, but there are species where it protrudes significantly. While shapes vary, this study focused on the trait of whether it protrudes or not.

7. eighth sternite, basal baculi, form (Fig. 92): (0) basal baculi parallel and separate; (1) basal baculi convergent but separate; (2) basal baculi fused into basal bridge.

In many species, the basal baculi at the base of the eighth sternite either converge and remain separate or are parallel and separate. *Epiechinus arboreus* is the only species where the basal baculi are fused into a basal bridge.

8. eighth sternite, basal baculi, distal articulation (Fig. 93): (0) basal baculi articulated with lateral disk of eighth sternite; (1) basal baculi fused with lateral disk of eighth sternite.

The eighth sternite, basal baculi, and distal articulation are fused with the lateral disk of the eighth sternite in many species, but in *Niponius osorioceps* and *Margarinotus niponicus*, the basal baculi are articulated with the lateral disk of the eighth sternite.

9. eighth sternite, setae: (0) absent; (1) with short setae on posterior margin; (2) with long setae on posterior margin; (3) with short and long setae on posterior margin; (4) with short setae on lateral edges.

In many species observed in this study, there are no setae on the eighth sternite, but there are a few species where setae are present on the eighth sternite.

10. sclerites, between eighth tergite and eighth sternite (Fig. 94): (0) absent; (1) present.

Only three species — *Saprinus* (*Saprinus*) *niponicus*, *Dendrophilus* (*Dendrophilus*) *xavieri*, and *Carcinops* (*Carcinops*) *pumilio* — exhibit sclerotized fragments on the lateral side between the eighth tergite and eighth sternite. The function of this organ remains unclear; however, its distinctive trait lies in the evident cornification, a character not observed in other species, drawing attention to its unique character.

11. ninth tergite in basal direction (Fig. 95): (0) absent; (1) present; (2) fuses with ninth sternite in basal direction (valvifer); (3) positions of each sclerite remain largely unchanged, fusing with the ninth sternite in basal direction (valvifer) and ninth sternite in apical direction; (4) Left and right ninth tergite in basal direction fuse together; (5) position of ninth tergite in basal direction shifts to ventral side and fuses with ninth sternite in basal direction (valvifer) and ninth sternite in apical direction.

The characteristics of the ninth tergite in basal direction vary considerably. Not only in terms of shapes, but also in their presence or absence, fusion with the ninth sternite,

and instances where the typically bilaterally divided ninth tergite is fused together.

12. ninth tergite in basal direction, setae: (0) with short setae; (1) with long setae.

Most species without setae on the ninth tergite in basal direction, but there are species with short and long setae on it.

13. ninth tergite in apical direction (Fig. 96): (0) absent; (1) present.

There are species observed both with and without the ninth tergite in apical direction, and in some cases, the ninth tergite in apical direction was arranged to cover the hole on the dorsal base of the coxite.

14. ninth sternite in basal direction (valvifer), basal shape (Fig. 97): (0) paddle-shaped; (1) narrow, not enlarged at base.

The ninth sternite in basal direction (valvifer) varied in size and finer details, but a major characteristic was the variation in the base shape, with some expanding to form a paddle-like structure, while others remained not enlarged.

15. ninth sternite in apical direction (Fig. 98): (0) absent; (1) present; (2) present, fused with ninth sternite in basal direction (valvifer).

In the species observed in this study, there were species with and without the ninth

sternite in apical direction. The size and shape of the ninth sternite in apical direction varied, ranging from being barely present to being exceptionally long. In this study, the presence of the ninth sternite in apical direction, whether it possessed long setae, and whether it fused with the ninth sternite in basal direction (valvifer) were observed as characteristic traits.

16. ninth sternite in apical direction, setae: (0) absent; (1) with short setae; (2) with short and long setae.

Most species without setae on the ninth sternite in apical direction, but there are species with short and long setae on it.

17. tenth tergite, position (Fig. 99): (0) only on surface; (1) penetrates inward.

The tenth tergite is located near the posterior end of the female genitalia and was confirmed in all species observed in this study. However, its size and shape varied, including those elongated vertically or horizontally, those with distinct incisions forming V or anchor shapes, and those with long setae. Especially noteworthy were cases where the anterior edge of the tenth tergite extended, recessing into the female genitalia (*Chaetabraeus* (*Chaetabraeus*) *bonzicus*, *Onthophilus* *ostreatus*, *O. silvae*). From these observations, the study focused on whether the tenth tergite invaginates into the female genitalia as a characteristic trait.

18. tenth tergite, setae: (0) absent; (1) with short setae; (2) with long setae.

Most species without setae on the tenth tergite, but there are species with short and long setae on it.

19. tenth tergite, distinct incisions (Fig. 100): (0) absent; (1) present.

The shape of the tenth tergite varies, ranging from being Oval-shaped to some species having distinct incisions.

20. tenth sternite (Fig. 101): (0) absent; (1) present; (2) horn-like shape.

In the species observed in this study, there were species with and without the tenth sternite. In the case of *Syntelia histeroides*, the tenth sternite took on a horn-like shape and extended posteriorly. The tenth sternite of *Anapleus nakanei* with distinct incisions. These were observed as characteristic traits in this study.

21. articulating sclerite (Fig. 102): (0) absent; (1) round shape; (2) triangular shape, long.

The articulating sclerite showed variations in size and fine shape, but generally appeared elliptical. Conversely, *Syntelia histeroides* lacked this sclerite, while *Plegaderus* (*Plegaderus*) *marseuli* and *Chaetabraeus* (*Chaetabraeus*) *bonzicus* had an elongated triangular-shaped articulating sclerite. This study focused on the presence or absence as well as the shape of the articulating sclerite as characteristic traits.

22. coxite, shape: (0) less than 1.5× as long as broad; (1) elongate, more than 1.5× as long as broad.

The shape of coxite varies among taxonomic groups and is considered an important trait by Caterino and Tishechkin (2014), Lackner and Tarasov (2019), Caterino and Vogler (2002), and Bichevoy (2022). characters-19 focuses on the length of coxite.

23. coxite, angle: (0) flat; (1) ventral side faces inward.

The coxite of many species are oriented flat on both sides. However, in *Niponius osorioceps*, *Carcinops* (*Carcinops*) *pumilio*, *Paromalus* (*Paromalus*) *parallelepipedus*, and *Notodoma fungorum*, there are variations in the degree, with the ventral side facing inward. These were observed as characteristic traits.

24. coxite, apical teeth: (0) apical teeth undifferentiated; (1) with two apical teeth; (2) with three apical teeth; (3) with four apical teeth; (4) with five apical teeth.

The apical teeth of coxite exhibited variation, ranging from undifferentiated apical teeth to having two to five apical teeth. These were observed as characteristic traits.

25. coxite, median ridge from apical tooth (Fig. 103): (0) apical tooth not strengthened by a longitudinal ridge along inner surface; (1) apical tooth strengthened by radial ridge on inner face.

In most species, the median ridge from the apical tooth of the coxite was not reinforced by a longitudinal ridge along the inner surface. However, only *Niponius osorioceps* and *Anapleus nakanei* exhibited the apical tooth being reinforced by a radial ridge on the inner face. These were observed as distinctive traits.

26. coxite, anterior edge (Fig. 104): (0) anterior edge with a notch; (1) anterior edge without a notch.

In the species observed in this study, three species (*Atholus duodecimstriatus* *quatuordecimstriatus*, *Margarinotus* (*Grammostethus*) *niponicus*, and *Hololepta* (*Hololepta*) *amurensis*) exhibited a notch on the anterior edge of the ventral side of the coxite. Individuals with this feature were not found in other species, so it was observed as a characteristic trait.

27. coxite, setae on ventral base (Fig. 105): (0) absent; (1) very fine setae present from the anterior edge towards the center.

In the genera *Hypocacculus* and *Hypocaccus*, a range of very fine setae was observed on the ventral side of the coxite, observed as a distinctive characteristic.

28. coxite, differentiation of inner and outer surfaces: (0) shovel-like, external face separated from internal face by elevated lateral ridges; (1) not shovel-like, without differentiation of external and internal faces.

Variations were observed in the inner and outer surfaces of the coxite. Some showed a shovel-like structure with the outer surface separated from the inner surface by raised lateral ridges, while others lacked distinction between the inner and outer surfaces, exhibiting a shovel-like structure. These were observed as characteristic traits.

29. coxite, articulation of style (Fig. 106): (0) closed, posterior edge remote from apical emargination between teeth; (1) open, posterior edge confluent with apical margin of coxite.

In the species observed in this study, differences in the shape of the articulation of the style were observed. In most species, the articulation of the style was closed, and the apical edge was distant from the apical emargination, with an open space between the teeth. Only in *Eopachylopus ripae* was it confirmed that the apical edge is integrated with the apical margin of the coxite. These were observed as characteristic traits.

30. articular membrane, setae (Fig. 107): (0) without seta; (1) one seta present; (2) two or more setae.

There were differences observed in the number of setae on the articular membrane. Most species had one seta on the articular membrane, but the genera *Hypocaccus* and *Anapleus nakanei* did not have setae on the articular membrane. Conversely, *Sphaerites glabratus* and *Syntelia histeroides* had two or more setae on the articular membrane. These were observed as distinctive traits.

31. stylus (Fig. 108): (0) absent; (1) present, located in posterior; (2) present, located in center.

Differences were observed in the state of the stylus. While in many species the stylus is positioned posteriorly to the coxite, in the case of *Sphaerites glabratus*, the stylus was centrally located. However, species like *Niponius osorioceps*, *Eopachylopus ripae*, and *Paromalus* (*Paromalus*) *parallelepipedus* were characterized by the absence of the stylus. Typically, the tip of the stylus bears one or more setae, but in species without a stylus, setae were directly present on the articular membrane. These were observed as distinctive traits.

32. bursa copulatrix, lumen, size: (0) reduced, with little expandable membrane; (1) with considerable expandable membrane; (2) flattened, unexpanded.

Differences were observed in the size of the bursa copulatrix. In many species, the bursa copulatrix exhibited a slightly smaller size with a less expandable membrane. Some species, however, showed a considerably more expandable bursa copulatrix, while others displayed a flattened, non-expanded bursa copulatrix. These were noted as distinctive traits.

33. bursa copulatrix, round-tipped hairs on surface (Fig. 109): (0) absent; (1) present.

Differences were observed in the surface structure of the bursa copulatrix. In many species, the surface of the bursa copulatrix appeared wrinkled. However, in the case of

Epiechinus arboreus, the surface of the bursa copulatrix was characterized by being densely covered with round-tipped hairs. These were observed as distinctive characteristics.

34. bursa copulatrix, sclerites: (0) completely membranous; (1) with paired sclerites bearing setae on the dorsal membrane; (2) with a single central sclerite on the dorsal membran; (3) with a single central sclerite bearing setae on the dorsal membrane; (4) with single median sclerite at junction with oviduct.

In the species observed in this study, there were species with sclerites in the bursa copulatrix. While many species were completely membranous, those with sclerites differed in their position, number, and presence of setae, which were observed as distinctive characteristics.

35. spermatheca, texture: (0) sclerotized; (1) not sclerotized.

The spermatheca (an organ that stores and maintains the viability of sperm until fertilization; itself an invagination of the eighth abdominal segment – Snodgrass (1935)) in the Histeridae is known to exhibit two basic forms: 1 Consisting of four to nine sessile receptacles lacking a distinct spermathecal gland. 2 Consisting of a single receptacle with a distinct spermathecal gland (Lackner & Tarasov, 2019).

A single receptacle spermatheca may sclerotize. In the species used in this study, there were instances where the spermatheca had sclerotized. Therefore, we focused on whether the spermatheca is sclerotized or not as a crucial trait in this research.

36. spermatheca, number: (0) single; (1) multiple.

The spermatheca has two forms: one with 'four to nine sessile receptacles' and the other with 'a single receptacle.' We highlighted these as distinctive traits. In this study, it was found that *Atholus duodecimstriatus quatuordecimstriatus* and *Margarinotus (Grammostethus) niponicus* consist of multiple spermathecae.

37. spermathecal gland: (0) absent; (1) not sclerotized; (2) sclerotized; (3) partially sclerotized.

The spermathecal gland is typically an organ derived from the spermatheca, and there are species where it is sclerotized or not sclerotized.

In Ôhara (2003), there was a sketch suggesting hairs on the spermathecal gland of *Saprinus optabilis*, but Lackner and Tarasov (2019) described this as a state damaged by chemical treatment. Among the species observed in this study, all except *Epiechinus arboreus* showed rounded-tipped hairs on the surface of the spermathecal gland. Similar structures have been reported in the spermathecal glands of Hydrophilidae, a taxonomic group close to Histeridae, by authors Minoshima (2009) and Nasserzadeh (2020), suggesting that it might not be a state damaged by chemical treatment as described by Lackner and Tarasov (2019). However, in the case of *Epiechinus arboreus* observed in this study (n=8), the tip of the spermathecal gland appeared as a structure that looked thin and torn, making it difficult to determine whether it was a normal morphology or had

been damaged. Hence, this study did not make a judgment based on the presence or absence of similar structures.

Lackner and Tarasov (2019) stated that species with multiple spermathecae lack a spermathecal gland. However, *Margarinotus* (*Grammostethus*) *niponicus*, despite having multiple spermathecae, had a spermathecal gland. Additionally, *Chaetabraeus* (*Chaetabraeus*) *bonzicus* showed sclerotization only at the base of the spermathecal gland. These were observed as characteristic traits.

38. spermathecal duct: (0) absent; (1) length less than five times spermatheca; (2) length more than five times spermatheca.

The spermathecal duct is a tubular organ connecting the spermatheca with the vagina or bursa copulatrix. It exhibits a wide range of lengths. Species with multiple spermathecae, such as *Atholus duodecimstriatus quatuordecimstriatus* and *Margarinotus* (*Grammostethus*) *niponicus*, do not possess a spermathecal duct. These were observed as characteristic traits.

39. spermathecal duct, attachment (Fig. 110); (1) attached near gonopore; (2) attaches to other than near gonopore.

In the species observed in this study, the attachment of the spermathecal duct was broadly classified into two patterns. One is where the spermathecal duct is attached to the posterior end of the vagina. This is a characteristic observed in subfamily Saprinae. The other is where the spermathecal duct is attached to the base of the bursa copulatrix

or oviduct. This is a characteristic found in many Histeridae. These were observed as characteristic traits.

From the descriptions of female genitalia of 26 Japanese Histeroidea species in Chapter 4, 39 morphological characteristics of the female genitalia were extracted. Among these, 19 were multistate, and the rest were binary. Several trait states believed to be specific to each taxonomic group have been identified.

Chapter 6. Construction and Discussion of Phylogenetic Trees

6-1. Introduction

In this chapter, a phylogenetic analysis of the female genitalia of 26 Japanese Histeroidea species was conducted based on the 39 morphological characteristics extracted in Chapter 5, demonstrating the relationships within the superfamily Histeroidea. The results were compared with existing phylogenetic analyses, exploring the utility of female genitalia in phylogenetic studies.

6-2. Material and methods

Analysis Methodology. The character matrix is shown in Table 3. All characters were equally weighted. Based on this matrix, most parsimonious trees were searched using PAUP* 4.0b1 (Swofford, 1998). A Heuristic search was performed with the addition sequence ‘random’ option (100 replications) chosen. Character states were optimized using Mesquite.3.81 (Maddison & Maddison, 2023).

6-3. Results and discussion

In this study, several intriguing new hypotheses regarding the relationships within the major Histeridae are being proposed. Perhaps the only significant disappointment is that the analysis conducted solely on female genitalia structures does not strongly support the appropriate resolution of the Histeridae. Nevertheless, some previously overlooked fundamental candidate groups have been identified.

Previous studies have widely supported the three families within Histeroidea as the sister group to Hydrophiloidea. Most have favored the relationship as (Sphaeritidae

(Synteliidae, Histeridae)) (Ôhara 1994; Hansen 1997; Ślipiński & Mazur 1999; Caterino & Vogler 2002; Caterino *et al.* 2005). However, McKenna *et al.* (2015) concluded that the sister group relationship between Sphaeritidae and Histeridae is more strongly supported. In this study, we assumed *Syntelia histeroides* belonging to Synteliidae as the root of the tree.

As a result of the analysis, 405 trees were generated, and through successive weighting, four trees emerged. Among those four trees, we used the one that was closest to the known cladograms for our considerations (Figs. 111, 112).

The analysis resulted in *Sphaerites glabratus* being designated as an outgroup in addition to the originally set outgroup, *Syntelia histeroides*. This rendered Histeridae as monophyletic. The unique derived trait in Histeridae is the absence of two or more setae on character 30 (Fig. 115) of the articular membrane. Both *S. glabratus* and *S. histeroides* possess two or more setae on the articular membrane. While the setae on the articular membrane have been highlighted by Bichevoy (2022), Kikuchi and Ôhara (2023a), and Kikuchi and Ôhara (2023b), there has been minimal focus on this in other papers.

Niponius osorioceps has been considered a candidate taxon for the most basal Histeroidea in Ôhara (1994) and Ślipiński and Mazur (1999). However, in this study, this species is not considered a candidate taxon for the most basal Histeroidea. Caterino and Vogler (2002) seriously questioned the notion of Niponiinae being positioned at the base of Histeroidea. While acknowledging the need for caution until molecular data for *Niponius* are analyzed, sister to the rest of Histeridae on the traits of male genitalia structures, it's positioned as closer to *Paromalus*. This placement is supported in the phylogenetic analysis based on female genitalia structures as well.

The *Plegaderus* (*Plegaderus*) *marseuli* and *Chaetabraeus* (*Chaetabraeus*)

bonzicus, belonging to the subfamily Abraeinae, were found to form a monophyletic group. This grouping is supported by characters 21 (Fig. 113). Character 21 describes the shape of the articulating sclerite. While most Histeridae species possess a round or elliptical three-dimensional structure, *P. (P.) marseuli* and *C. (C.) bonzicus* exhibit thin, flat, elongated triangular shapes.

The subfamily Saprinae was found to be monophyletic. There are distinctive traits within subfamily Saprinae observed in characters 37 (Fig. 116) and 39 (Fig. 117), both related to the spermatheca. Character 37 indicates the sclerotization of the spermathecal gland. In all taxa outside of the subfamily Saprinae used in this study, the spermathecal gland is membranous, while in the subfamily Saprinae, the spermathecal gland was distinctly sclerotized. Character 39 indicates the connection point of the spermathecal duct. Among the species used in this study, it is noteworthy that species belonging to the subfamily Saprinae possess particularly long spermathecal ducts. While in other groups with a spermathecal duct, its connection is to the bursa copulatrix or common oviduct, in subfamily Saprinae, the spermathecal duct connects near the gonopore. Character 11 indicates the state of the ninth tergite in the basal direction. In *Saprinus (Saprinus) niponicus*, the ninth tergite in basal direction moves to the ventral side, fusing with the ninth sternite (A)(valvifer) and ninth sternite in apical direction, a unique characteristic of *S. (S.) niponicus* alone. Character 29 indicates the condition of the articular membrane. In many species, the posterior edge of the articular membrane is closed, yet in *Eopachylopus ripae*, it remains open—a trait unique to *E. ripae* in this study. However, according to Caterino and Tishechkin (2015), species such as *Lacrimorpha balbina*, *Anaglymma congois*, and *Yarmister barberi* are reported to possess a similar character state. Character 27 (Fig. 114) indicates the structure on the ventral anterior part

of the coxite. Species belonging to the genera *Hypocacculus* and *Hypocaccus* exhibit very fine hairs from the ventral anterior to the central part. This was a shared derived trait in *Hypocacculus* and *Hypocaccus*. Character 9 addresses the situation of setae on the posterior margin of the eighth sternum. In the *Baeckmanniolus*, a subgenus of *Hypocaccus*, there are one to three long setae on the posterior margin of the eighth sternum — a shared derived trait within *Baeckmanniolus*. The subfamily Sapriniinae exhibited numerous shared derived traits, strongly supporting the monophyly of the subfamily, as identified through this study.

The subfamily Dendrophilinae did not show monophyly in studies by Caterino and Vogler (2002), Zhou *et al.* (2020), and Pražák *et al.* (2023) utilizing morphological analysis and molecular analysis, as well as in the study by McKenna *et al.* (2015) using molecular analysis. The species selected from the subfamily Dendrophilinae (*Anapleus nakanei*, *Dendrophilus* (*Dendrophilus*) *xavieri*, *Carcinops* (*Carcinops*) *pumilio*, and *Paromalus* (*Paromalus*) *parallelepipedus*) were phylogenetically distant, therefore indicating the lack of monophyly within the subfamily, prompting a reevaluation of these findings. As no traits supporting the monophyly of subfamily Dendrophilinae were obtained even through ancestral reconstruction, it suggests a need for reconsideration regarding this classification.

In the morphological analysis by Pražák *et al.* (2023), the subfamily Onthophilinae, which includes *Epiechinus* and *Onthophilus*, demonstrates monophyly. However, this study suggests that *Epiechinus* and *Onthophilus* are phylogenetically distant, indicating a lack of monophyly within the subfamily Onthophilinae. Examining the traits of the female reproductive structures in *Epiechinus* and *Onthophilus*, significant differences were observed, including the presence or absence of the ninth tergite in apical direction,

sclerites in the bursa copulatrix, among others. Specifically, the abundance of setae on the membranous surface between the coxite and eighth tergite (Character 1), fusion of the basal baculi of the eighth sternite at the basal bridge (Character 7), fusion of only the ninth tergite in the basal direction with the ninth sternite (valvifer) (Character 11), round-tipped hairs on the surface of the bursa copulatrix (Character 33), and the absence of round-tipped hairs on the surface of the spermathecal gland (Character 37). These were unique to *E. arboreus* in this study. These results raise serious doubts about the close relationship between *Epiechinus* and *Onthophilus*. This hypothesis should be tested molecularly. Furthermore, significant differences were confirmed between *O. ostreatus* and *O. silvae*. Despite many shared characteristics, a crucial difference was noted in character 35, concerning the sclerotization of the spermatheca — *O. ostreatus* lacked sclerotization while *O. silvae* showed it. Additionally, slight differences were observed in the adult appearance between *O. ostreatus* and *O. silvae*. Though not illustrated in this study, since the spermatheca of the congener *O. flavicornis* also lacked sclerotization, it necessitates a reconsideration of the classification of *O. silvae* as well.

In this study, the subfamily Histerinae was paraphyletic. Studies by Caterino and Vogler (2002), Caterino and Tishechkin (2015), Mckenna *et al.* (2015), Zhou *et al.* (2020), and Pražák *et al.* (2023) have indicated the polyphyly of subfamily Histerinae. In Ôhara (1994), sketches of the spermathecae of the tribe Histerini are presented. The tribe Histerini includes *Hister*, *Atholus*, *Margarinotus*, and *Merohister*, all of which have multiple spermathecae. In this study, the tribe Histerini (including *Atholus* and *Margarinotus* in this research) appears to form a monophyletic, characterized by the presence of multiple spermathecae as described in character 36. However, further reassessment of the entire subfamily Histerinae seems necessary.

I conducted analyses based on female genital traits across taxonomic groups, including Sphaeritidae, Synteliidae, and six subfamilies of Histeridae. Some groups, like the Abraeinae and Sapriniinae subfamilies, exhibited monophyly, supporting previous findings. However, other groups challenged previous research outcomes, warranting reevaluation. While detailed studies on female genitalia were previously limited, this study extracted numerous characters, yielding valuable insights. Future endeavors should focus on extracting characters from a wider range of taxonomic groups and integrating them into analyses alongside adult morphology, larval appearance, male genitalia, and DNA. Moreover, reports from Kikuchi and Ôhara (2023a) and Kikuchi and Ôhara (2023b) have highlighted intergroup differences in mouthparts like the tentorium and proventriculus, indicating potential for enhancing analytical precision by further exploring these characters for analysis.

Chapter 7. General discussion

Firstly, the aim is to accumulate and enrich new taxonomic and phylogenetic insights specific to the superfamily Histeroidea in Japan, thereby enhancing the accuracy of phylogenetic analysis within the superfamily Histeroidea. The subject species covered in this study consist of 26 species of the superfamily Histeroidea found in Japan. While this selection does not encompass all the species within the Japanese superfamily Histeroidea, detailed descriptions of the external morphology of several adult specimens, intricate observations of the mouthparts, and thorough descriptions of the female genitalia among the 26 species have allowed for the discovery of previously unknown traits. It specifically identified 39 characters related to the female genitalia, indicating their usefulness in phylogenetic analysis.

This study focused on the detailed descriptions of the female genitalia, which have not received much attention in previous research, and discovered 39 character states. These characters were then used for phylogenetic analysis. The resulting trees broadly supported the findings of previous studies that used both external morphology and DNA sequence information for phylogenetic analysis. This highlighted distinct differences in the traits of female genitalia among taxonomic groups, confirming their utility as valuable traits for phylogenetic analysis. Existing studies on female genitalia have predominantly focused on only a few aspects, such as coxites, spermathecae, and spermathecal glands, with few addressing the overall traits of the female genitalia, as in this study. Traits such as the eighth to tenth abdominal segments, articulating sclerites, non-sclerotized membranous parts, and bursa copulatrix, which have received little attention in existing

research, exhibit various characteristics. It is believed that these traits, previously overlooked in the female genitalia, could be highly valuable for phylogenetic analysis. Moreover, conducting more extensive and detailed research, even on aspects with some detailed descriptions like the spermatheca and spermathecal gland, has led to new discoveries. Taxonomic groups that have consistently been supported as monophyletic in both existing phylogenetic analyses and this study, such as the subfamily Sapriniinae, displayed highly similar trait states. Among the six species of *Hypocaccus* within the subfamily Sapriniinae scrutinized in this study, the differences in the spermatheca and spermathecal gland were very minimal, making it challenging to discern traits. It is presumed that the spermatheca and spermathecal gland represent stable trait states at the genus level. However, focusing on *Onthophilus ostreatus* and *O. silvae* from the subfamily Onthophilinae, a remarkably significant difference was observed in the traits of the spermatheca. Clarifying the stability of each trait state and extracting crucial trait states for each taxonomic group are essential for future research. Eberhard (1985) stated, "Researchers generally believe that female genitalia evolve slower than male genitalia and exhibit little change, therefore providing limited phylogenetic information." However, based on the results of this study, significant differences exist in the female genitalia among taxonomic groups. At present, I believe that they can be effectively used not only for species identification but also for distinguishing taxonomic groups higher than the genus level.

In terms of appearance, previously unknown trait states have been found. For instance, in families Synteliidae and Histeridae, the front tibiae arise from the dorsal side of the front femora, while in family Sphaeritidae, they arise from the ventral side, a characteristic not previously recognized. Regarding mouthparts, there are some

descriptions by Lackner (2010) and others, but they have been scarcely investigated. The shapes of individual parts are intricate, making dissection quite challenging. However, significant differences have been observed in the shapes of structures like the tentorium and proventriculus. There are substantial variations in the development of the molae as well, indicating that there are still many traits useful for phylogenetic analysis yet to be explored.

From this, our study confirmed numerous new traits and character states in the female genitalia of the superfamily Histeroidea, demonstrating their utility as valuable traits for phylogenetic analysis. The outcomes of this research have significantly enhanced the accuracy of understanding the phylogenetic relationships within the three families of the superfamily Histeroidea. Moreover, the discovery of numerous new traits contributes to accumulating descriptive taxonomic information, enhancing the reliability of taxonomic recognition and species identification, while also fostering advancements in applied entomology.

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Figures and Tables



Figure 1. *Sphaerites glabratus* (Fabricius, 1792), [TK-23-011], dorsal habitus, male. Scale bars: 1.0 mm.



Figure 2. *Syntelia histeroides* Lewis, 1882, [TK-22-007], dorsal habitus. Scale bars: 5.0 mm.



Figure 3. *Niponius osorioceps* Lewis, 1885, [TK-23-129], dorsal habitus. Scale bars: 1.0 mm.



Figure 4. *Plegaderus (Plegaderus) marseuli* Reitter, 1877, [TK-23-132], dorsal habitus. Scale bars: 1.0 mm.



Figure 5. *Chaetabraeus (Chaetabraeus) bonzicus* (Marseul, 1873), [TK-23-135], dorsal habitus. Scale bars: 0.5 mm.



Figure 6. *Eopachylopus ripae* (Lewis, 1885), [TK-23-083], dorsal habitus. Scale bars: 1.0 mm.



Figure 7. *Hypocacculus (Nessus) asticus* Lewis, 1911, [TK-22-047], dorsal habitus. Scale bars: 1.0 mm.



Figure 8. *Hypocaccus (Baeckmanniolus) varians hatsune* (Nakane, 1977), [TK-23-052], dorsal habitus. Scale bars: 1.0 mm.



Figure 9. *Hypocaccus (Baeckmanniolus) varians varians* (Schmidt, 1890), [TK-23-050], dorsal habitus. Scale bars: 1.0 mm.



Figure 10. *Hypocaccus (Hypocaccus) akanensis* Ôhara, 1994, [TK-23-003], dorsal habitus. Scale bars: 1.0 mm.



Figure 11. *Hypocaccus (Hypocaccus) axeli* Kryzhanovskij, 1976, [TK-21-027], dorsal habitus. Scale bars: 1.0 mm.



Figure 12. *Hypocaccus (Hypocaccus) subaeneus* (Schmidt, 1890), [TK-22-046], dorsal habitus. Scale bars: 1.0 mm.



Figure 13. *Hypocaccus (Hypocaccus) toyoshimai* Kikuchi et Ôhara 2023, [MO-22-013], dorsal habitus. Scale bars: 1.0 mm.



Figure 14. *Saprinus (Saprinus) niponicus* Dahlgren, 1962, [TK-23-079], dorsal habitus. Scale bars: 2.5 mm.



Figure 15. *Anapleus nakanei* Ôhara, 1994, [TK-23-136], dorsal habitus. Scale bars: 1.0 mm.



Figure 16. *Dendrophilus (Dendrophilus) xavieri* Marseul, 1873, [TK-23-137], dorsal habitus. Scale bars: 1.0 mm.



Figure 17. *Carcinops (Carcinops) pumilio* (Erichson, 1834), [TK-23-138], dorsal habitus. Scale bars: 1.0 mm.



Figure 18. *Paromalus (Paromalus) parallelepipedus* (Herbst, 1791), [TK-23-139], dorsal habitus. Scale bars: 1.0 mm.



Figure 19. *Epiechinus arboreus* (Lewis, 1884), [TK-23-058], dorsal habitus. Scale bars: 1.0 mm.



Figure 20. *Onthophilus ostreatus* Lewis, 1879, [TK-23-055], dorsal habitus. Scale bars: 1.0 mm.



Figure 21. *Onthophilus silvae* Lewis, 1884, [TK-23-140], dorsal habitus. Scale bars: 1.0 mm.



Figure 22. *Baconia chujoi* (Cooman, 1941), [TK-23-130], dorsal habitus. Scale bars: 1.0 mm.



Figure 23. *Notodoma fungorum* Lewis, 1884, [TK-23-074-2], dorsal habitus, male. Scale bars: 1.0 mm.



Figure 24. *Atholus duodecimstriatus quatuordecimstriatus* (Gyllenhal, 1808), [No. -9115], dorsal habitus. Scale bars: 1.0 mm.



Figure 25. *Margarinotus* (*Grammostethus*) *niponicus* (Lewis, 1895), [TK-23-131], dorsal habitus. Scale bars: 1.0 mm.



Figure 26. *Hololepta* (*Hololepta*) *amurensis* Reitter, 1879, [TK-23-128], dorsal habitus, female. Scale bars: 5.0 mm.

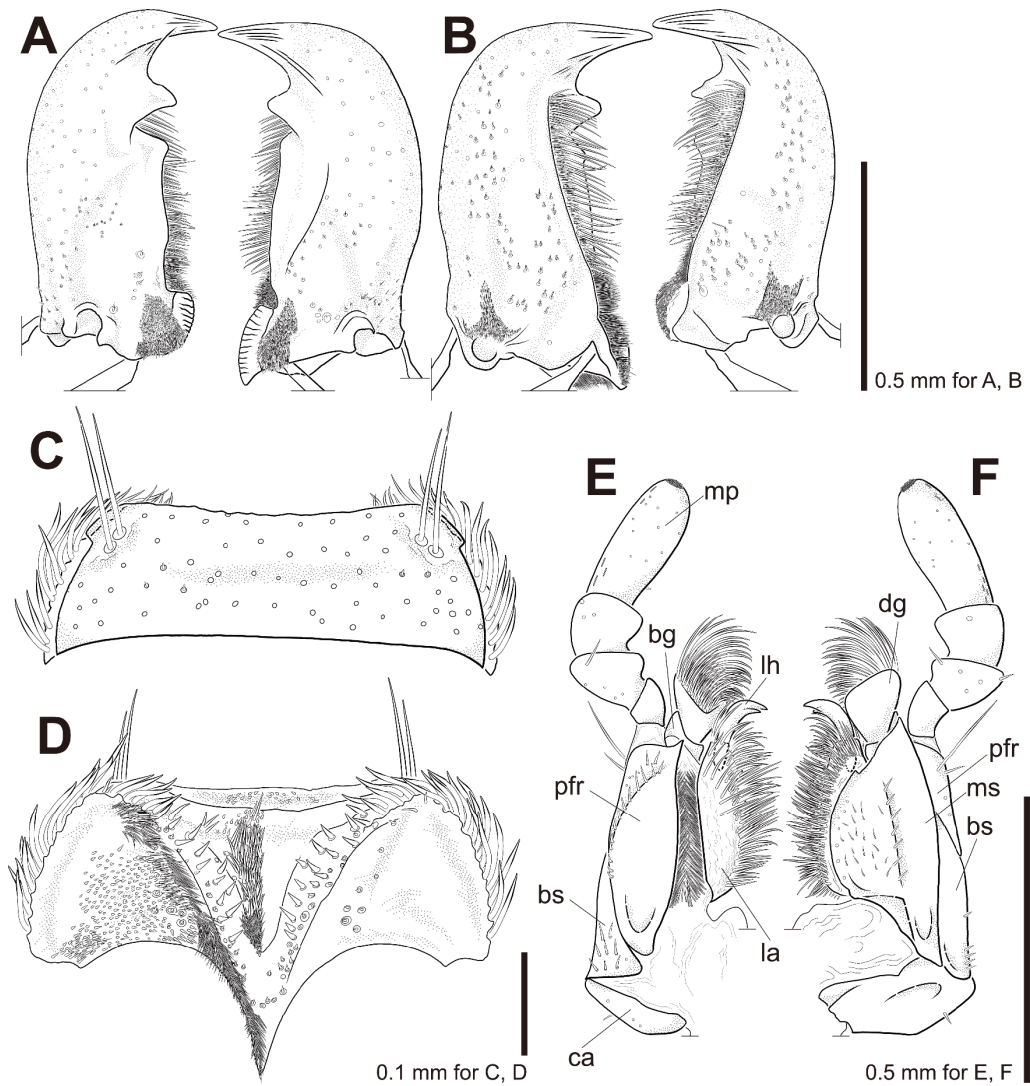


Figure 27. Mouthparts of *Sphaerites glabratus* (Fabricius, 1792), [TK-22-008]. — A, Mandibles, dorsal view; B, ditto, ventral view; C, labrum, dorsal view; D, ditto, ventral view; E, left maxilla, dorsal view; F, ditto, ventral view. — bg, basigalea; bs, basistipes; ca, cardo; dg, distigalea; la, lacinia; lh, lacinial hook; mp, maxillary palpus; ms, mediostipes; pfr, palpifer.

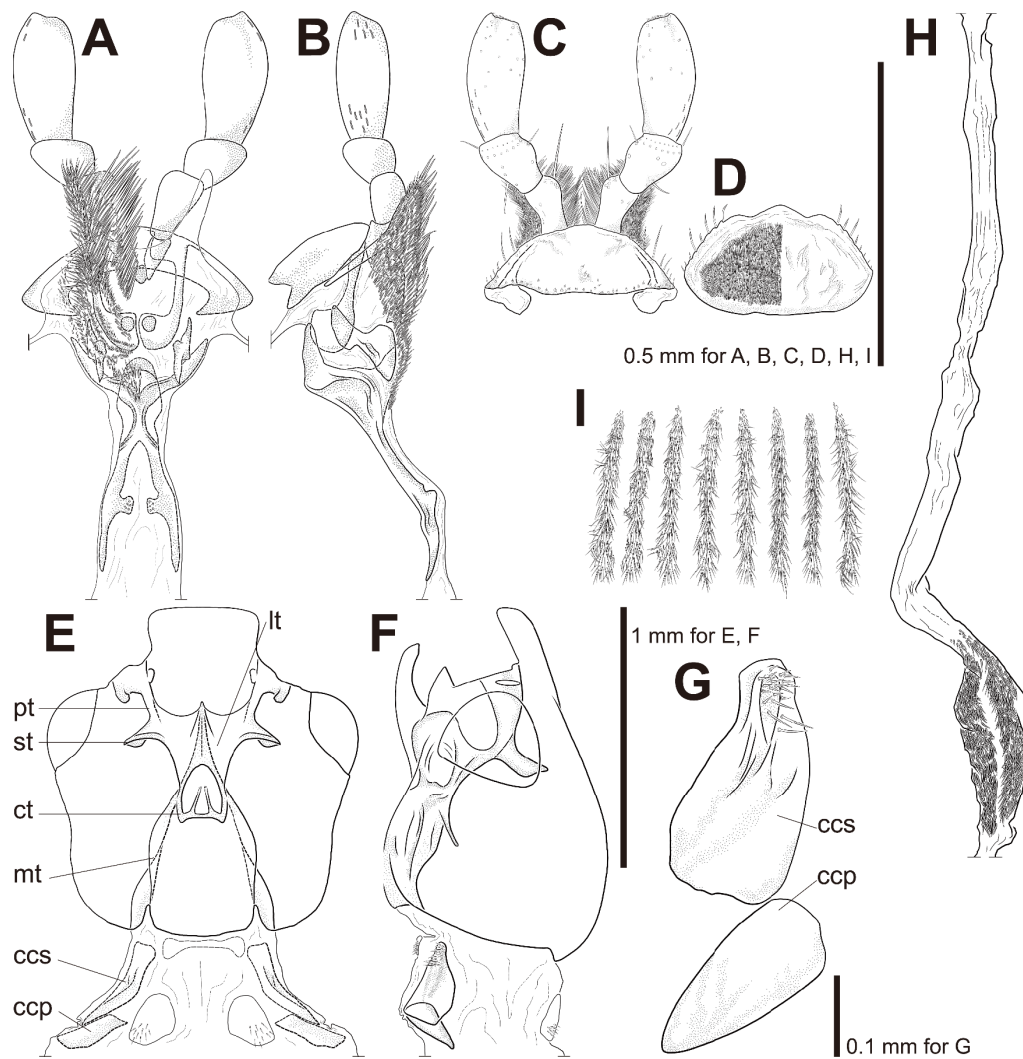


Figure 28. Mouthparts of *Sphaerites glabratus* (Fabricius, 1792), A–C, E–I [TK-22-008], D [TK-23-88]. — A, Female labium and hypopharynx, dorsal view; B, ditto, lateral view; C, female labium, ventral view; D, male mentum; ventral view; E, tentorium, dorsal view; F, ditto, lateral view; G, left cervical sclerite; H, proventriculus; I, ditto, inner surface. — ccp, cervepimeron; ccs, cervepisternum; ct, corpotentorium; lt, laminatentorium; mt, metatentorium; pt, pretentorium; st, supratentorium.

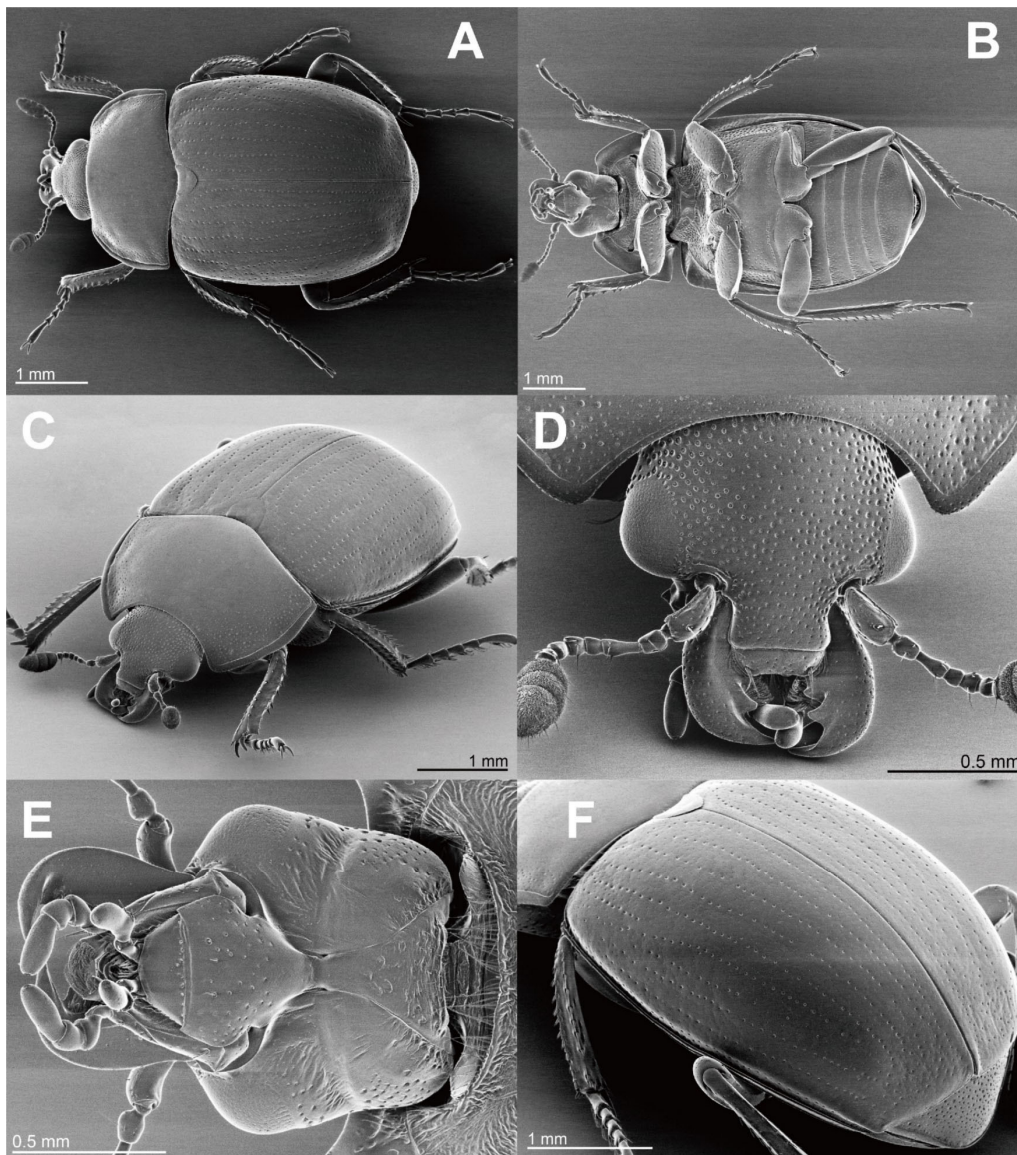


Figure 29. *Sphaerites glabratus* (Fabricius, 1792), SEM micrographs, A, C, D, F [TK-23-011, male], B, E [TK-23-013, female]. — A, Habitus, dorsal view; B, ditto, ventral view; C, ditto, oblique view; D, head, frontal view; E, ditto, ventral view; F, left elytron, oblique view.

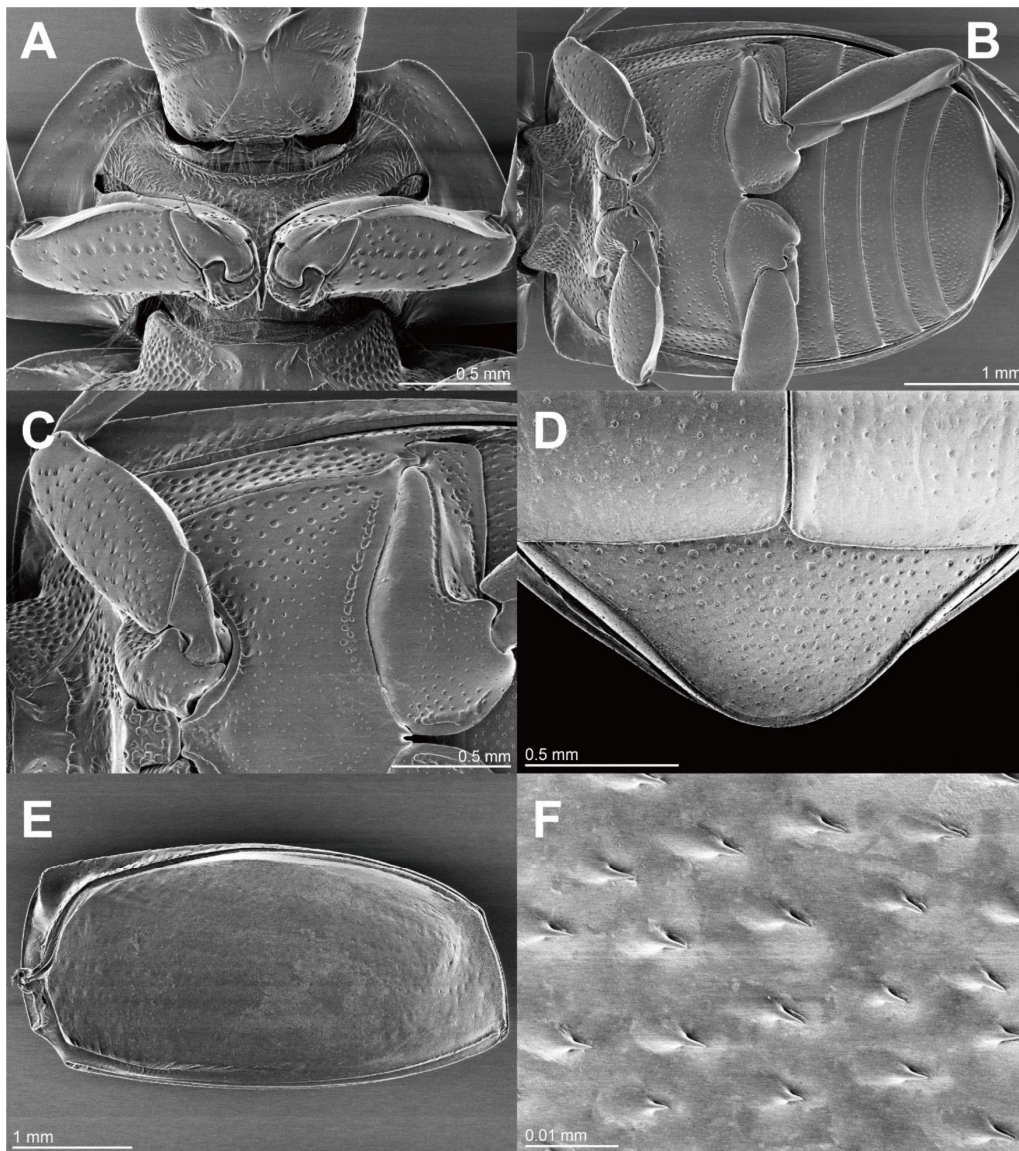


Figure 30. *Sphaerites glabratus* (Fabricius, 1792), SEM micrographs, A–C [TK-23-013], D [TK-23-011], E, F [TK-23-012]. — A, Prosternum, ventral view; B, metaventricle and abdominal sterna, ventral view; C, lateral side of metaventricle, ventral view; D, pygidium, caudal view; E, left elytron, ventral view; F, microsetae of left elytron, ventral side.

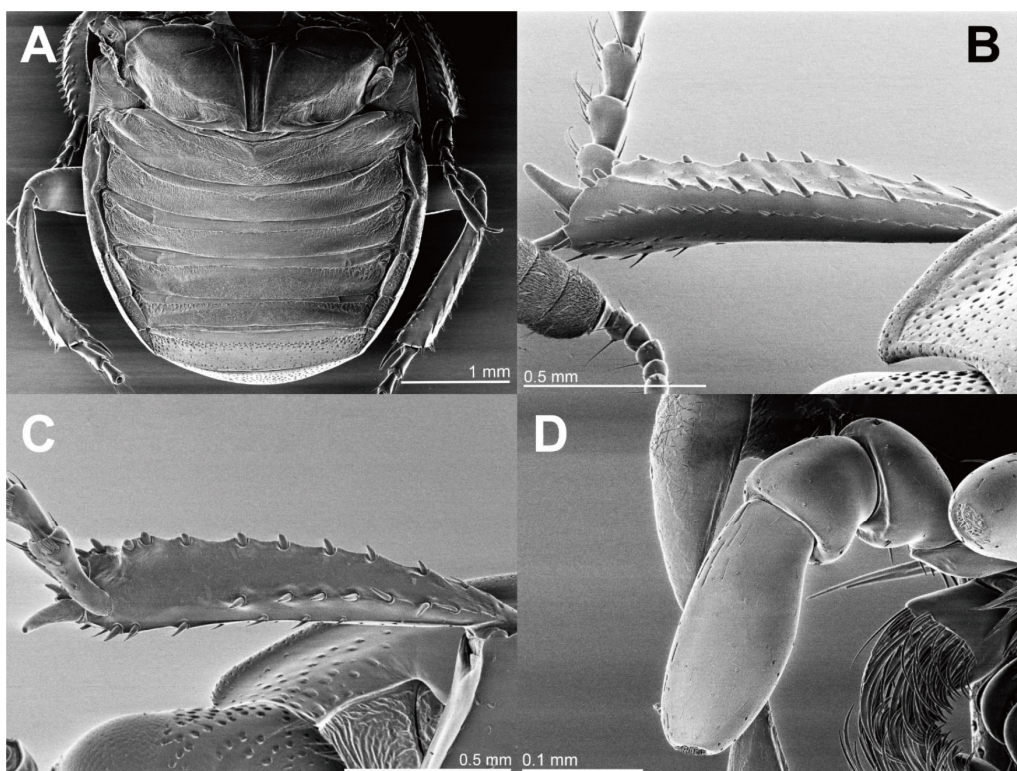


Figure 31. *Sphaerites glabratus* (Fabricius, 1792), SEM micrographs, A [TK-23-012], B [TK-23-011], C, D [TK-23-013]. — A, Meso- and metanotum, and abdominal tergites, dorsal view; B, right protibia, dorsal view; C, left protibia, ventral view; D, palpal organ of left labial palpus.

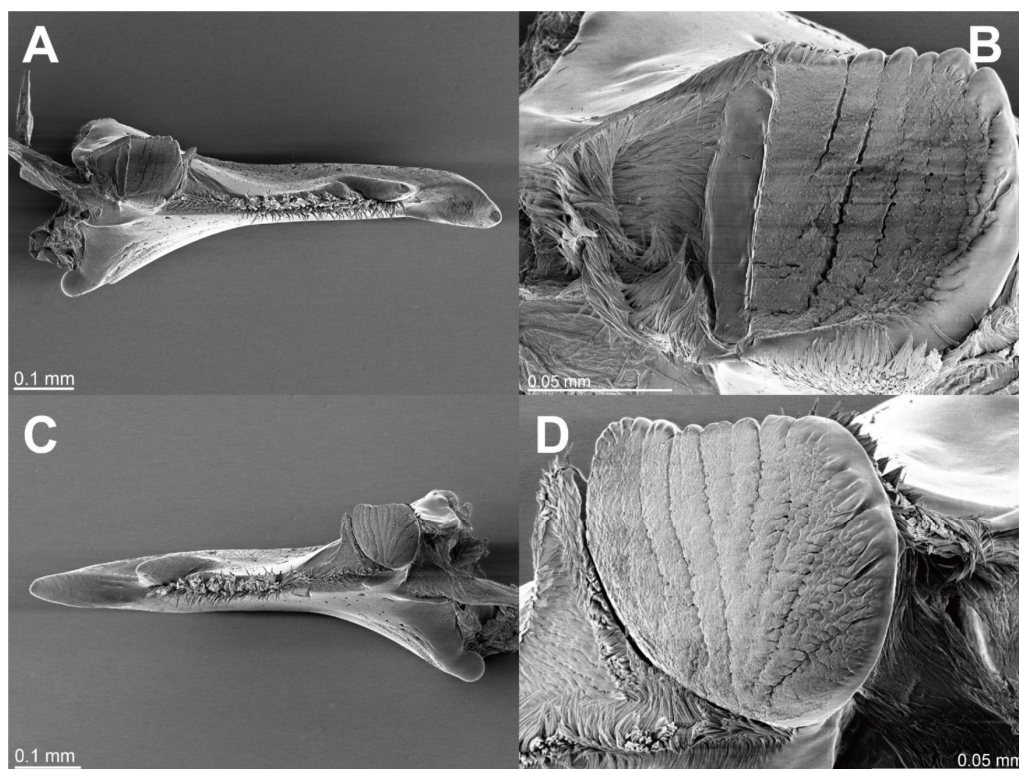


Figure 32. *Sphaerites glabratus* (Fabricius, 1792), SEM micrographs, [TK-23-017]. — A, Left mandible, inside view; B, mola of left mandible, inside view; C, right mandible, inside view; D, mola of right mandible, inside view.

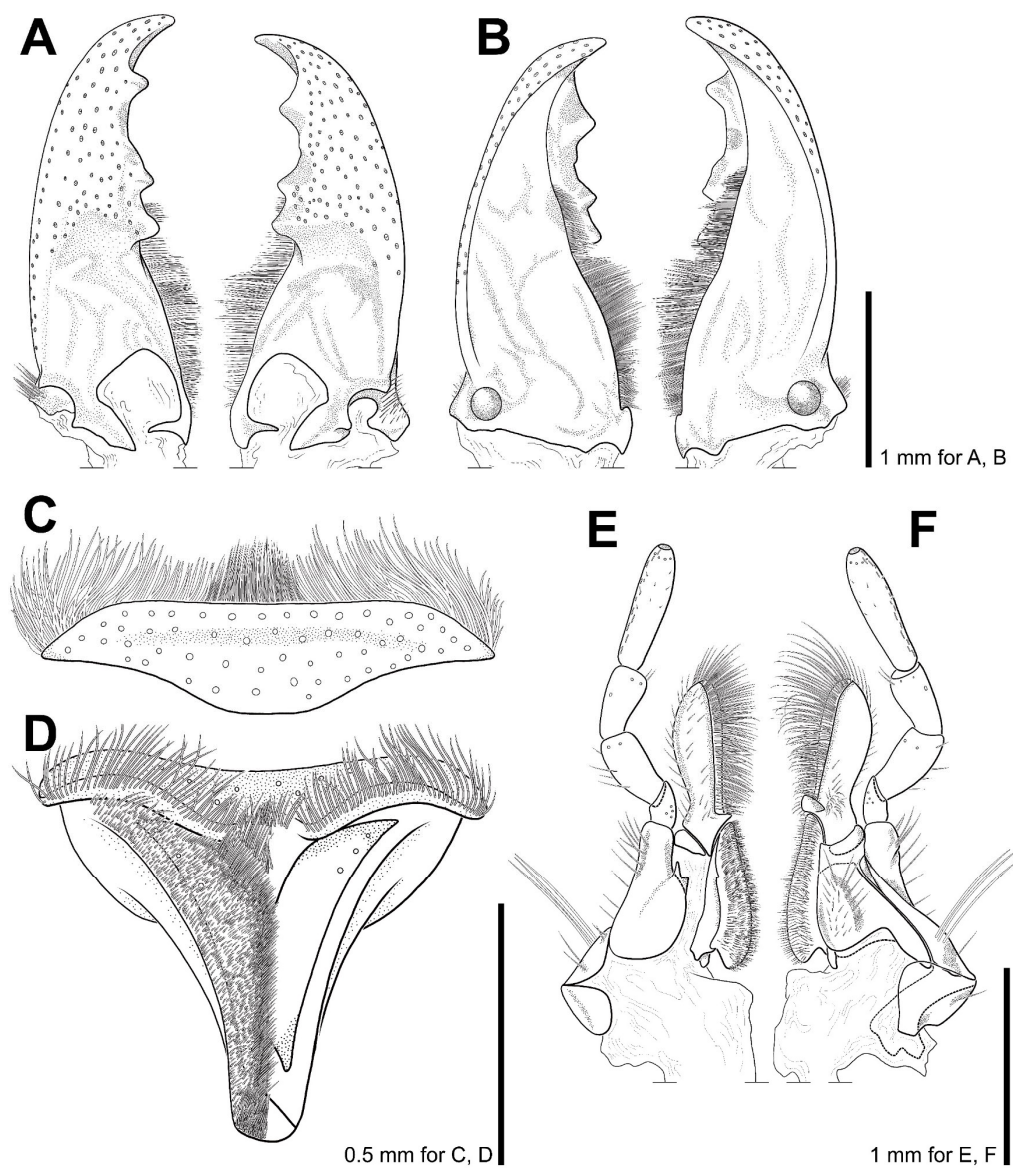


Figure 33. Mouthparts of *Syntelia histeroides* Lewis, 1882, [TK-22-013]. — A, Mandibles, dorsal view; B, ditto, ventral view; C, labrum, dorsal view; D, ditto, frontal view; E, left maxilla, dorsal view; F, ditto, ventral view.

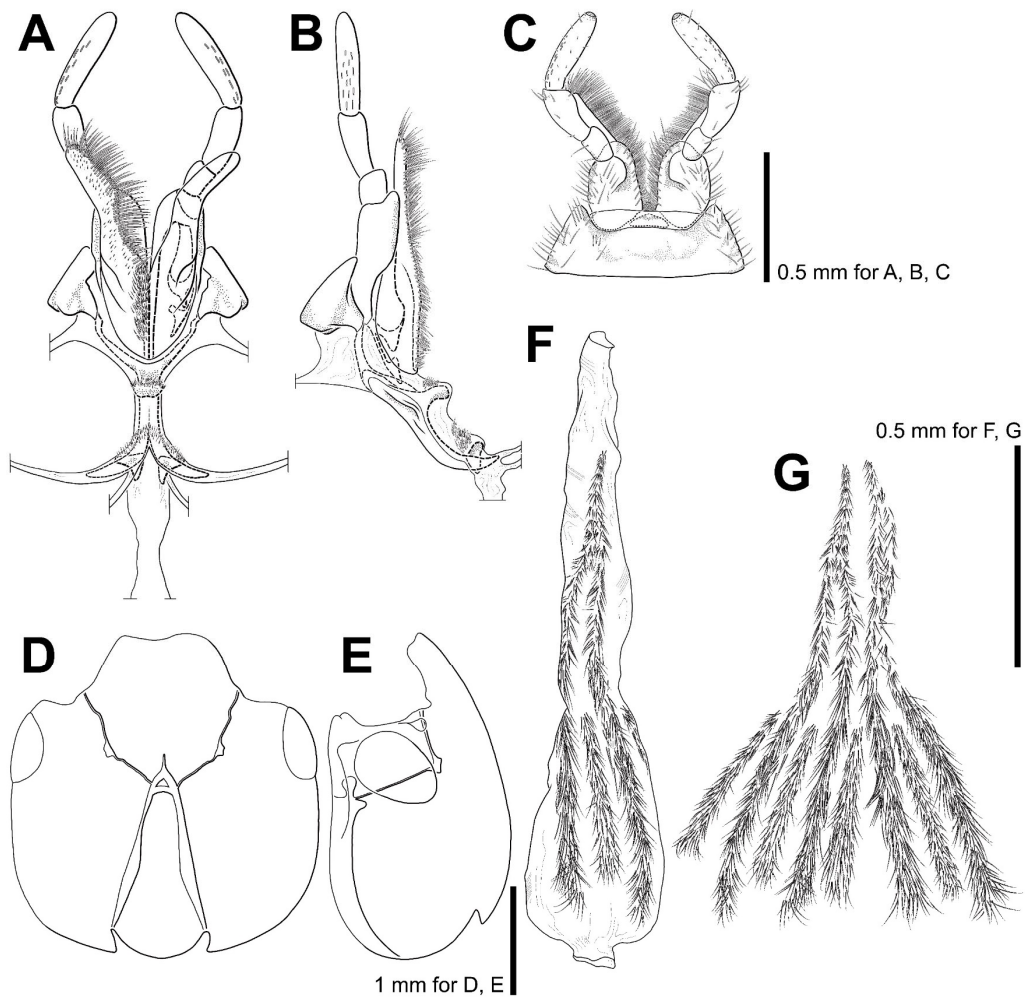


Figure 34. Mouthparts of *Syntelia histeroides* Lewis, 1882, A–C [TK-22-037], D–G [TK-22-013]. — A, Labium & hypopharynx, dorsal view; B, ditto, lateral view; C, labium, ventral view; D, tentorium, dorsal view; E, ditto, lateral view; F, proventriculus; G, ditto, inner surface.

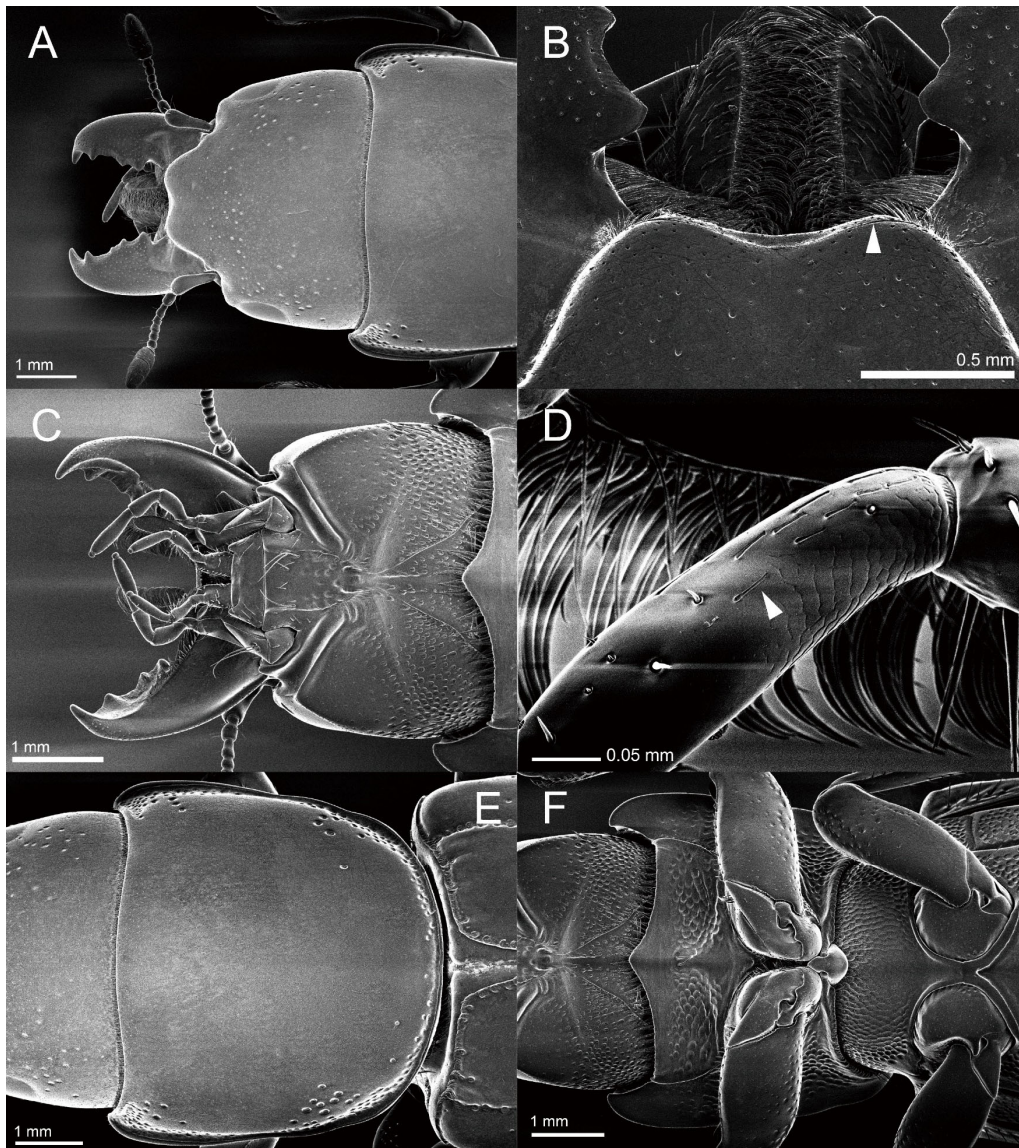


Figure 35. *Syntelia histeroides* Lewis, 1882, SEM micrographs, [TK-22-013]. — A, Head, dorsal view; B, labrum, dorsal view; C, mouthparts, ventral view; D, palpal organ of left labial palpus; E, pronotum, dorsal view; F, pro- & mesosternal, ventral view.

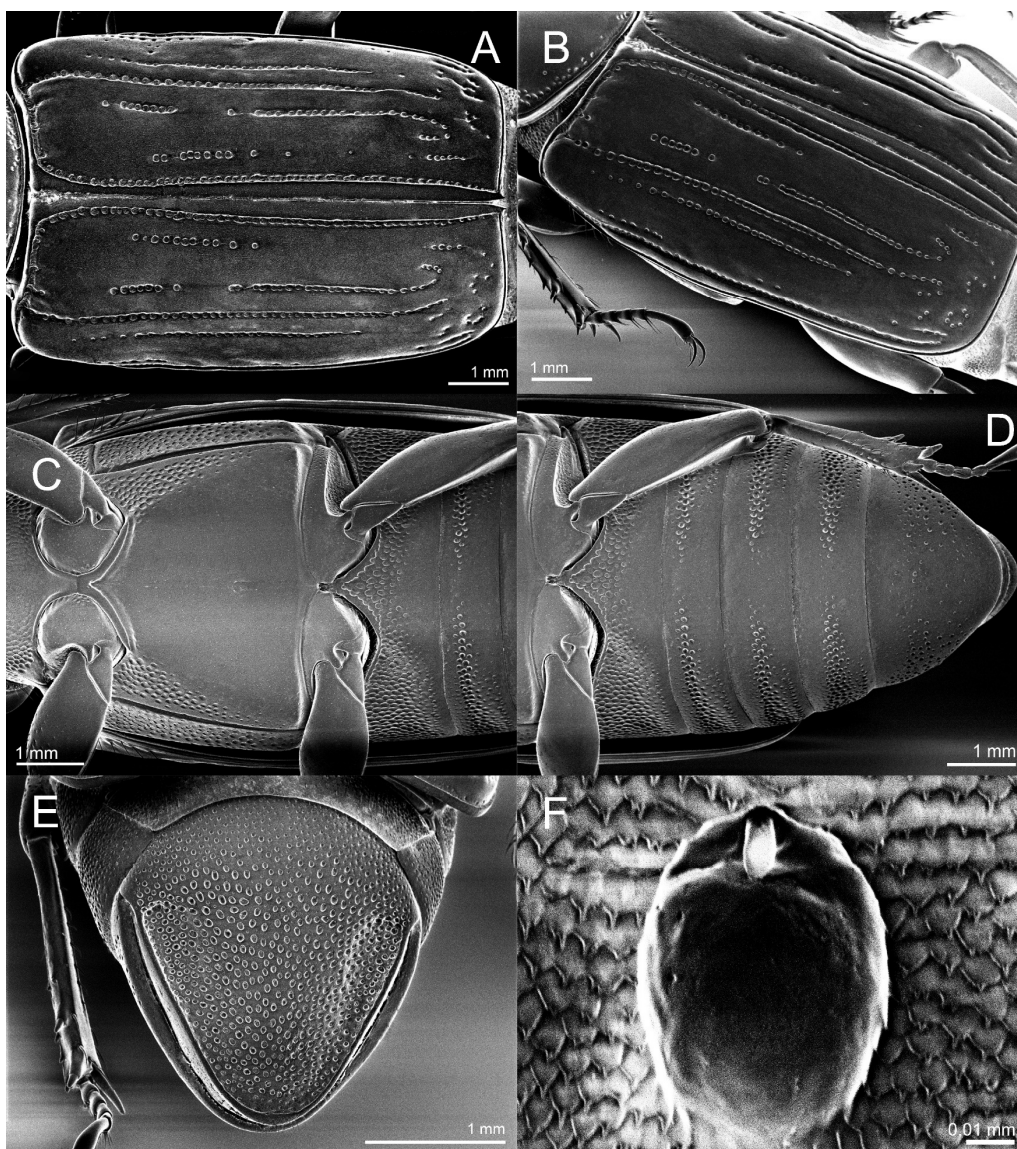


Figure 36. *Syntelia histeroides* Lewis, 1882, SEM micrographs, [TK-22-013]. — A, Elytra, dorsal view; B, left elytron, oblique view; C, metaventrите, ventral view; D, abdominal sterna, ventral view; E, pygidium, caudal view; F, punctation of pygidium.

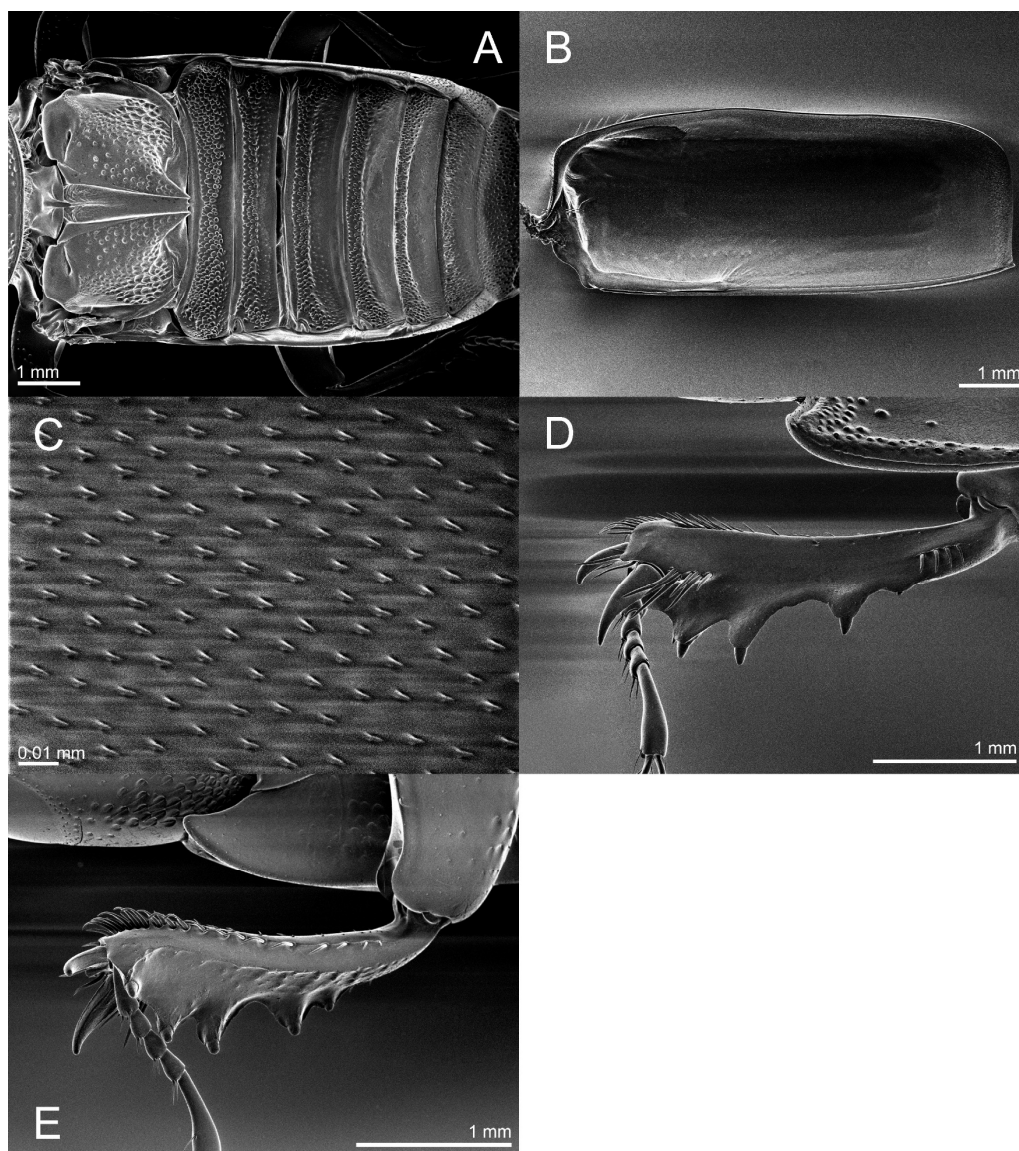


Figure 37. *Syntelia histeroides* Lewis, 1882, SEM micrographs, [TK-22-013]. — A, Meso- & metanotum, & abdominal tergites, dorsal view.; B, left elytron, ventral view; C, microsetae of left elytron, ventral side; D, protibia, dorsal view; E, ditto, ventral view.

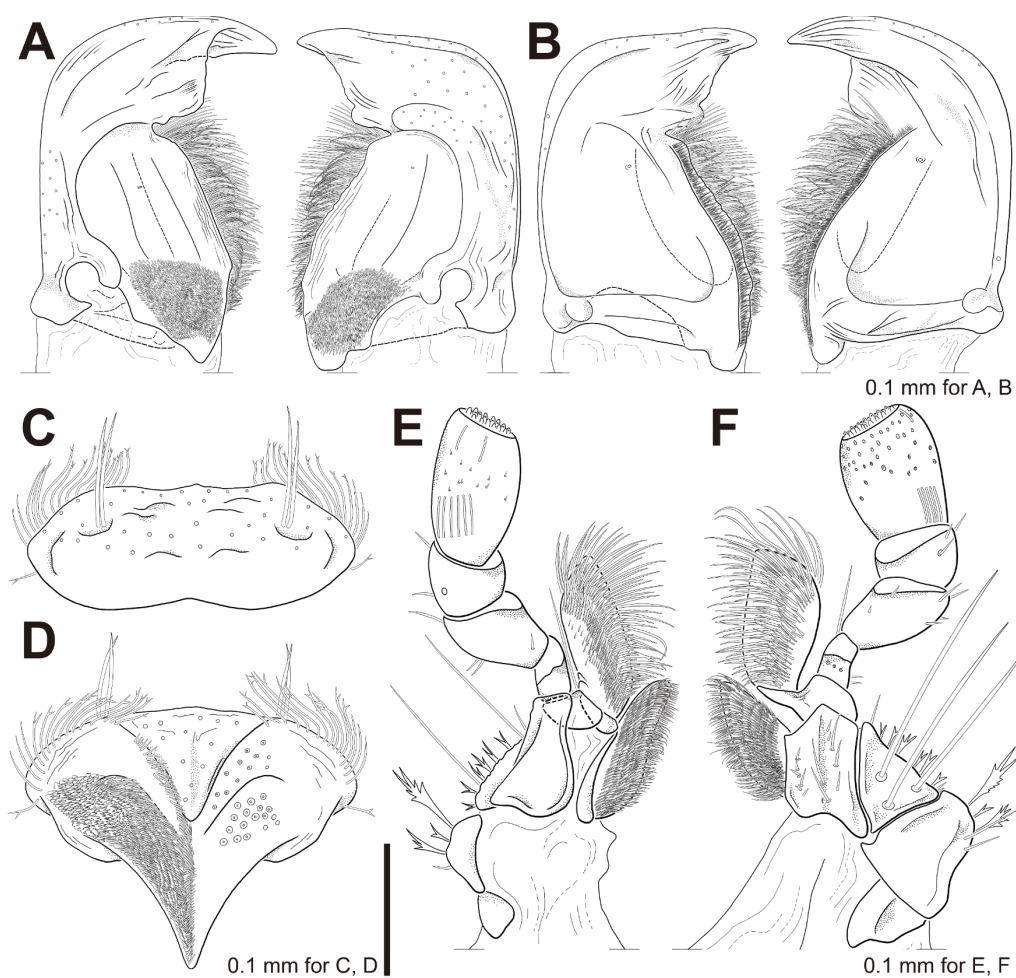


Figure 38. Mouthparts of *Hypocacculus (Nessus) asticus* Lewis, 1911, [TK-22-001]. — A, Mandibles, dorsal view; B, ditto, ventral view; C, labrum, dorsal view; D, ditto, frontal view; E, left maxilla, dorsal view; F, ditto, ventral view.

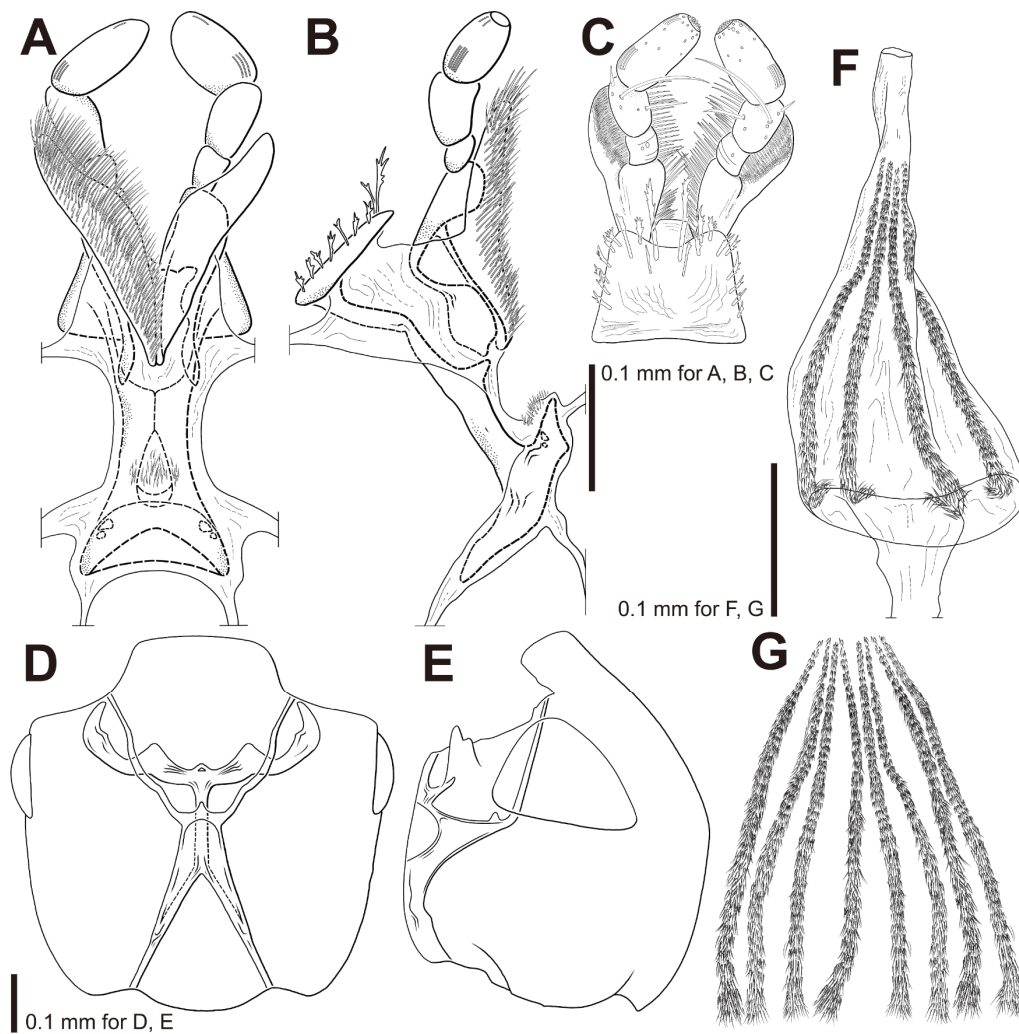


Figure 39. Mouthparts of *Hypocacculus (Nessus) asticus* Lewis, 1911, [TK-22-001]. — A, Labium and hypopharynx, dorsal view; B, ditto, lateral view; C, labium, ventral view; D, tentorium, dorsal view; E, ditto, lateral view; F, proventriculus; G, ditto, inner surface.

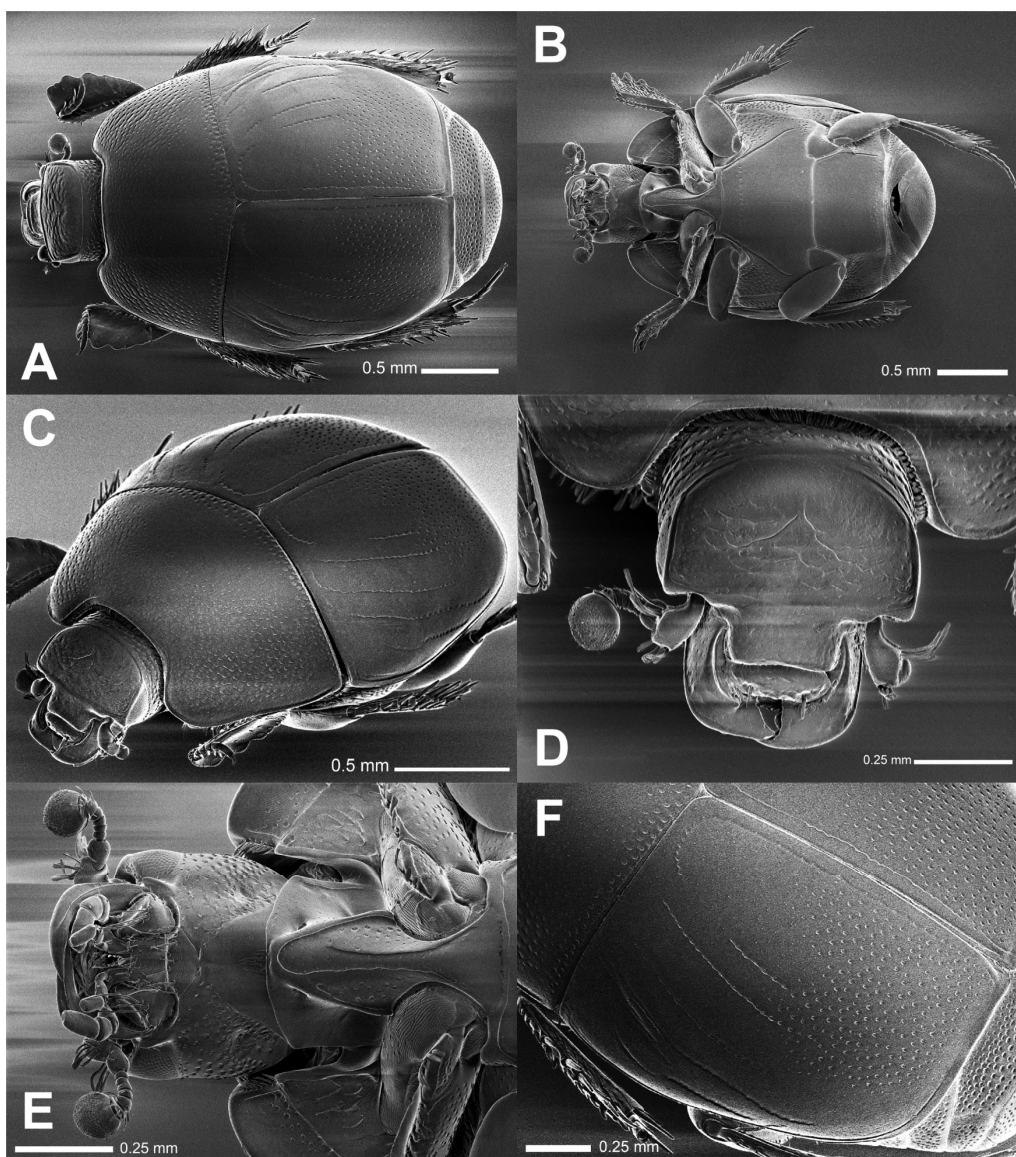


Figure 40. *Hypocacculus (Nessus) asticus* Lewis, 1911, SEM micrographs, A, C, D and F [TK-22-019], B and E [TK-22-047]. — A, Habitus, dorsal view; B, ditto, ventral view; C, ditto, oblique view; D, head, frontal view; E, ditto, ventral view; F, left elytron, oblique view.

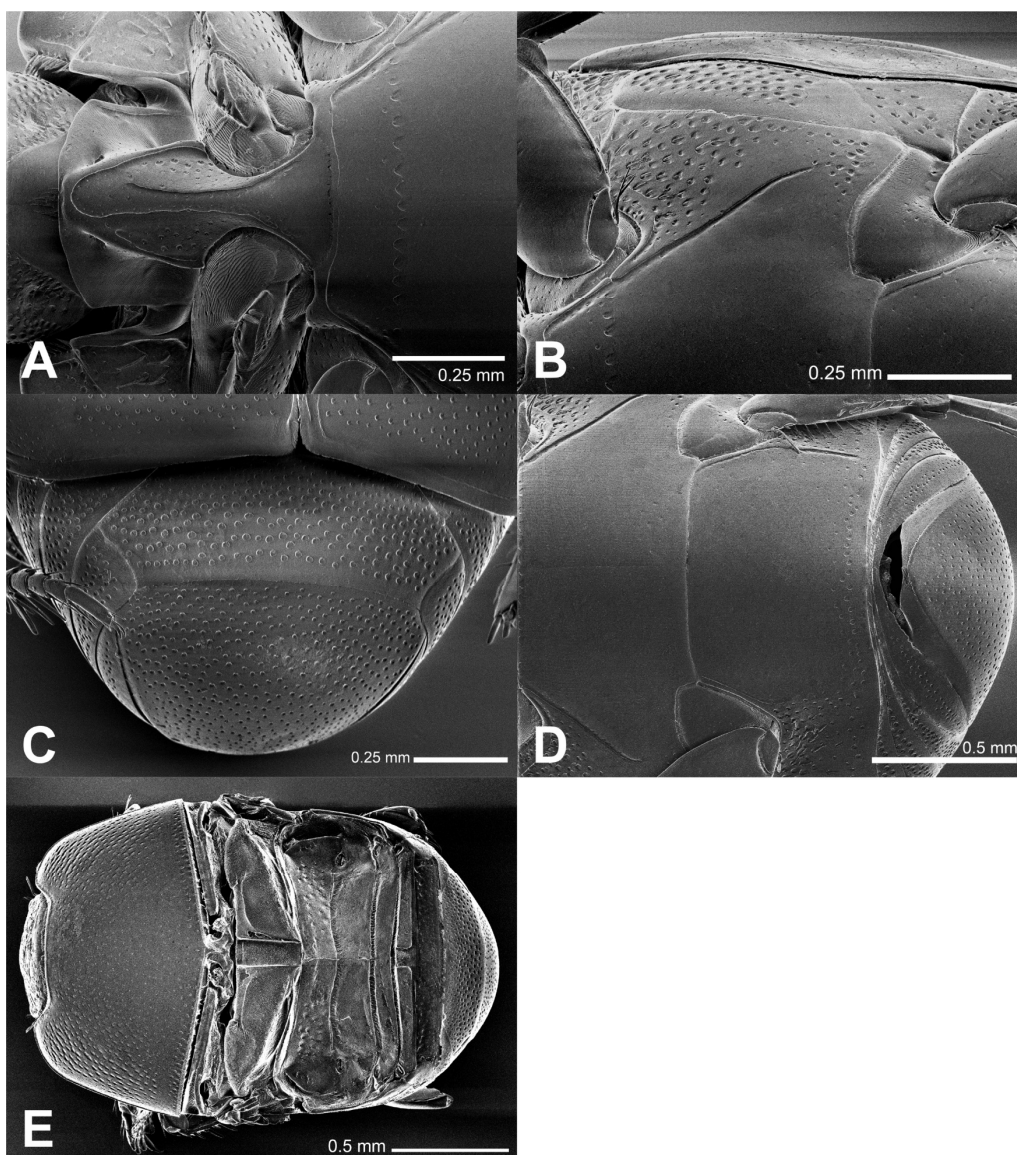


Figure 41. *Hypocacculus (Nessus) asticus* Lewis, 1911, SEM micrographs, A, B and D [TK-22-047], C [TK-22-019], E [TK-22-018]. — A, Prosternum, ventral view; B, lateral side of metaventricle, ventral view; C, propygidium and pygidium, caudal view; D, abdominal sterna, ventral view; E, mesonotum, metanotum and abdominal tergites, dorsal view.

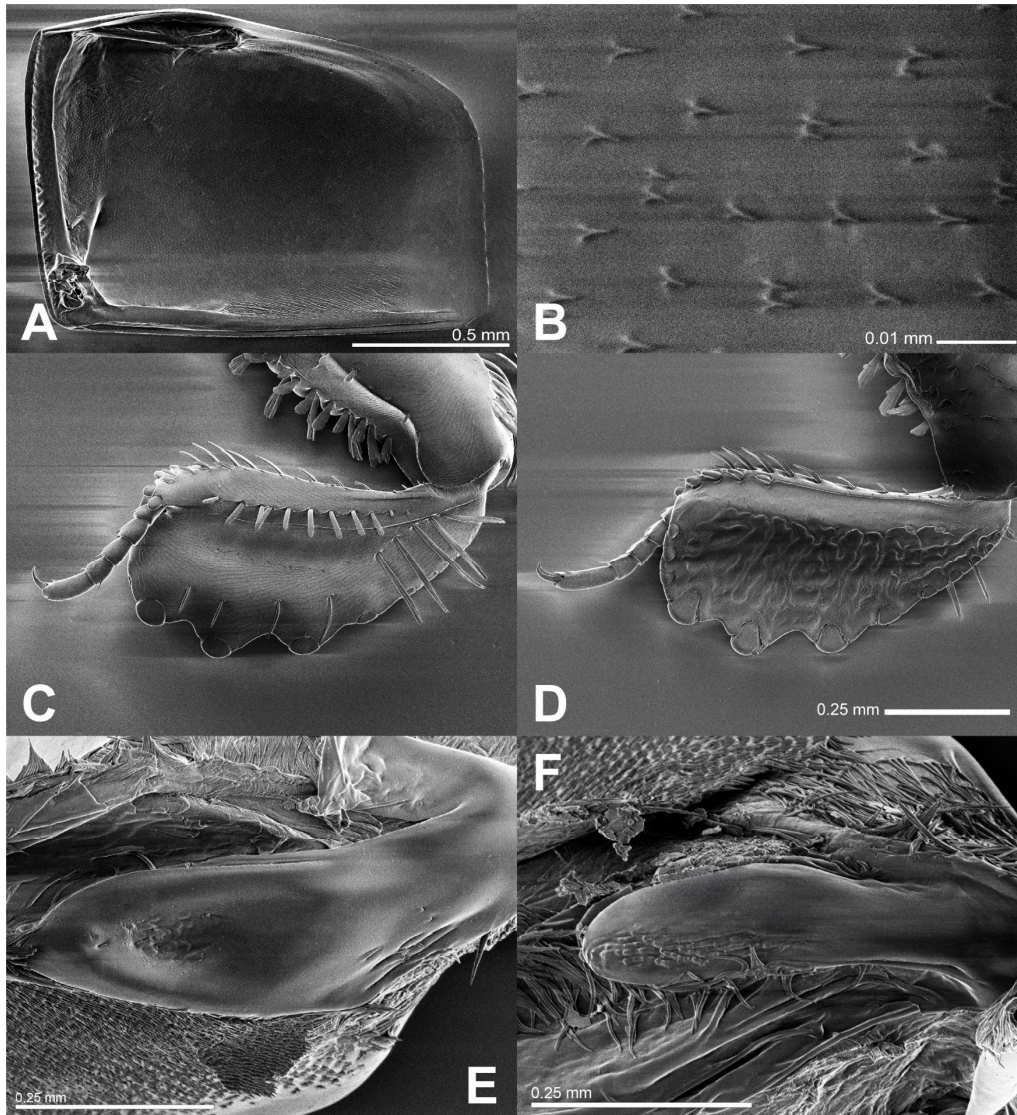


Figure 42. *Hypocacculus (Nessus) asticus* Lewis, 1911, SEM micrographs, A and B [TK-22-018], C and D [TK-22-019]. — A, Left elytron, ventral view; B, microsetae of left elytron, ventral side; C, left protibia, dorsal view; D, right protibia, ventral view; E, mola of left mandible; F, mola of right mandible.

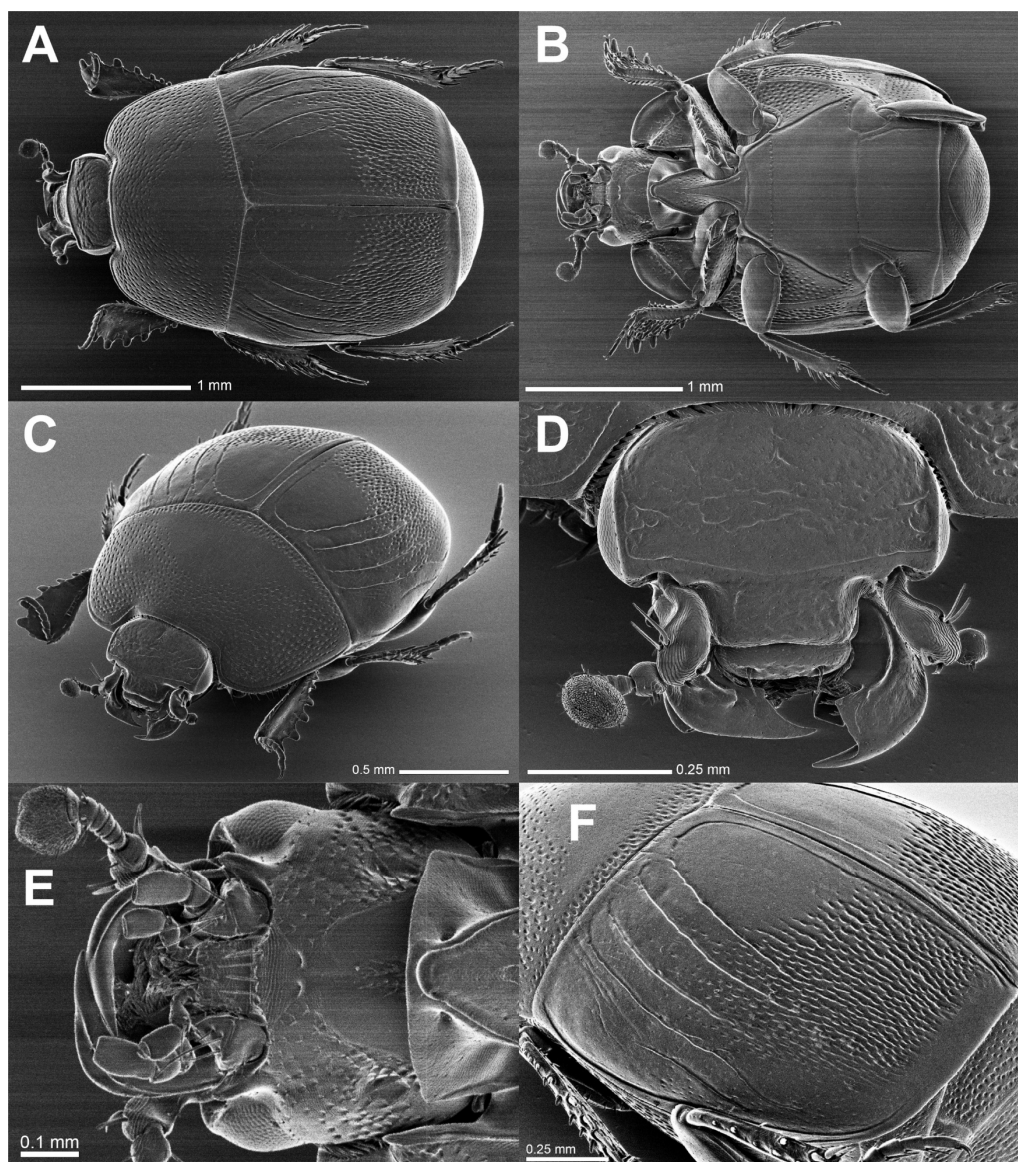


Figure 43. *Hypocaccus (Hypocaccus) akanensis* Ôhara, 1994, SEM micrographs, A, C, D and F [TK-23-003], B and E [TK-23-014]. — A, Habitus, dorsal view; B, ditto, ventral view; C, ditto, oblique view; D, head, frontal view; E, ditto, ventral view; F, left elytron, oblique view.

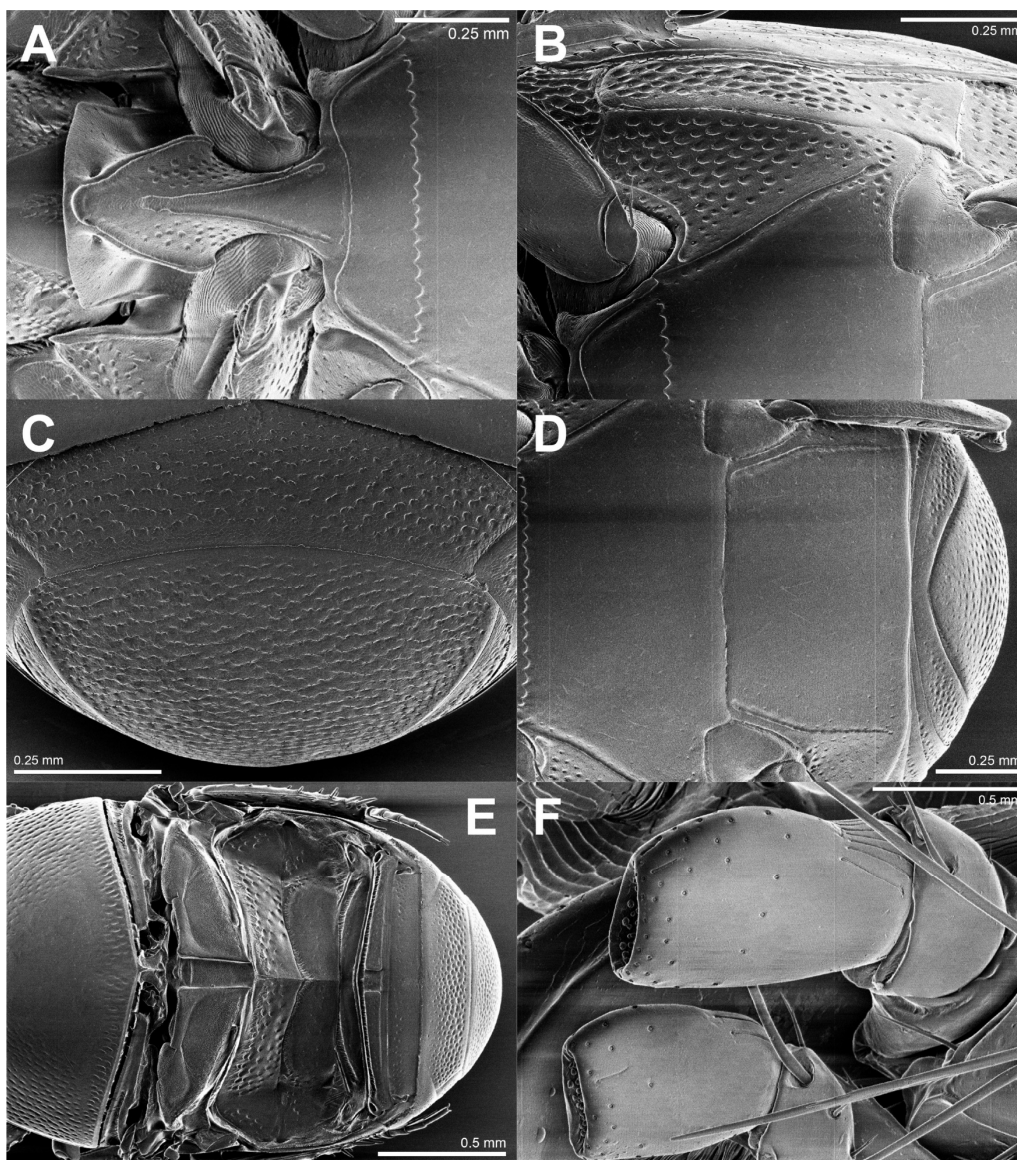


Figure 44. *Hypocaccus (Hypocaccus) akanensis* Ôhara, 1994, SEM micrographs, A, B and D [TK-23-014], C [TK-23-003], E [TK-23-015]. — A, Prosternum, ventral view; B, lateral side of metaventricle, ventral view; C, propygidium and pygidium, caudal view; D, abdominal sterna, ventral view; E, meso- and metanotum and abdominal tergites, dorsal view; F, palpal organ of left maxilla and labial palpus.

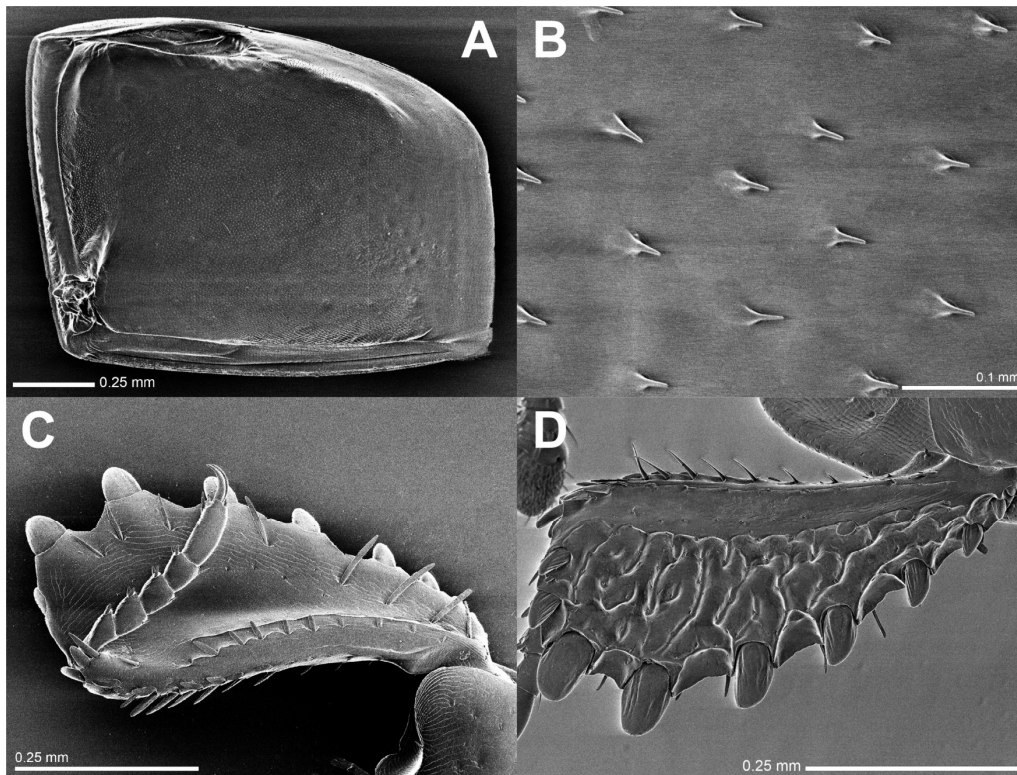


Figure 45. *Hypocaccus (Hypocaccus) akanensis* Ôhara, 1994, SEM micrographs, A and B [TK-23-015], C [TK-23-003], D and E [TK-23-014]. — A, Left elytron, ventral view; B, microsetae of left elytron, ventral side; C, right protibia, dorsal view; D, ditto, ventral view.



Figure 46. *Hypocaccus (Hypocaccus) akanensis* Ôhara, 1994 [Holotype]. — A, Habitus, dorsal view; B, ditto, ventral view; C, holotype with labels; D, labels.

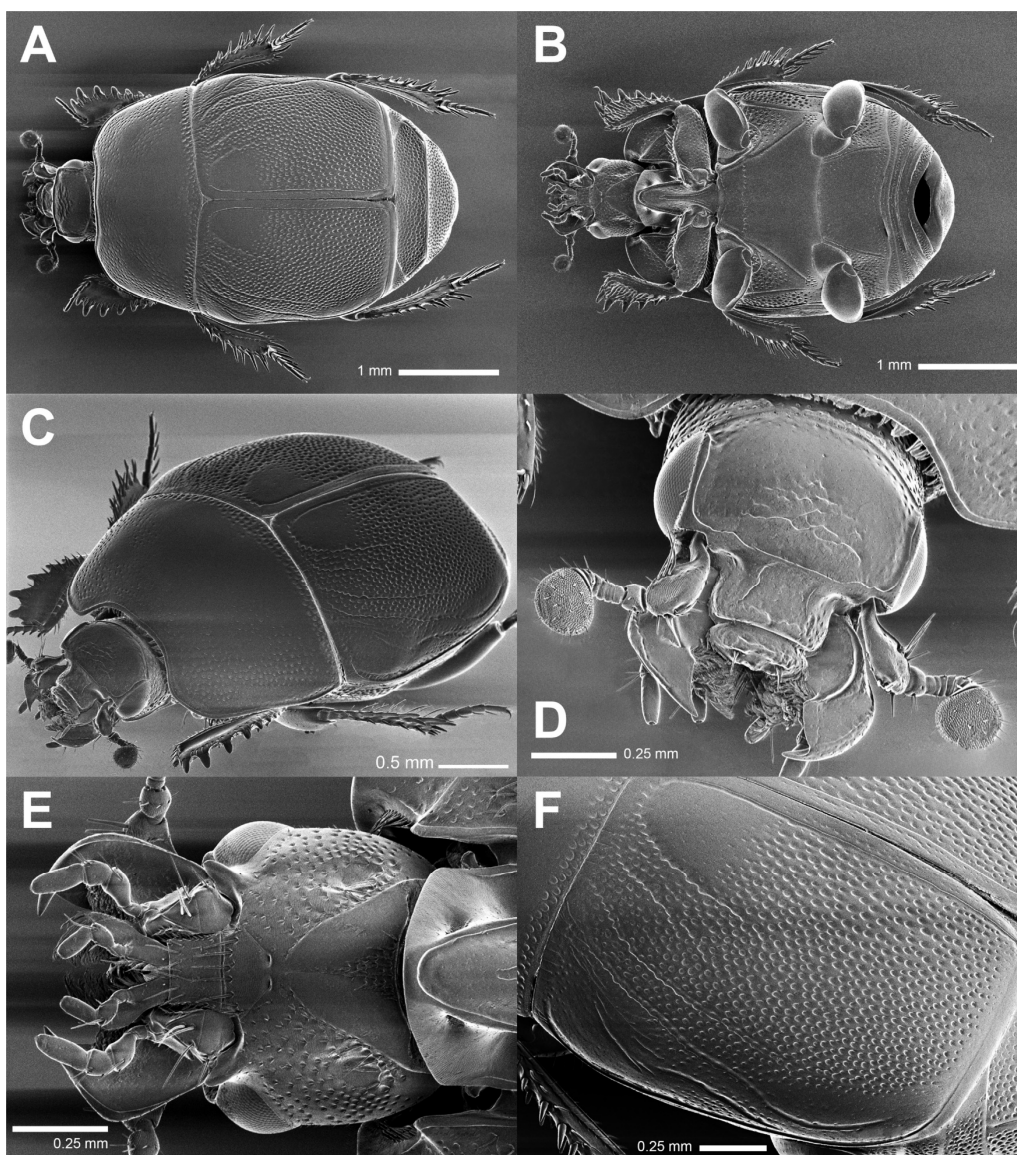


Figure 47. *Hypocaccus (Hypocaccus) axeli* Kryzhanovskij, 1976, SEM micrographs [TK-21-027]. — A, Habitus, dorsal view; B, ditto, ventral view; C, ditto, oblique view; D, head, frontal view; E, ditto, ventral view; F, left elytron, oblique view.

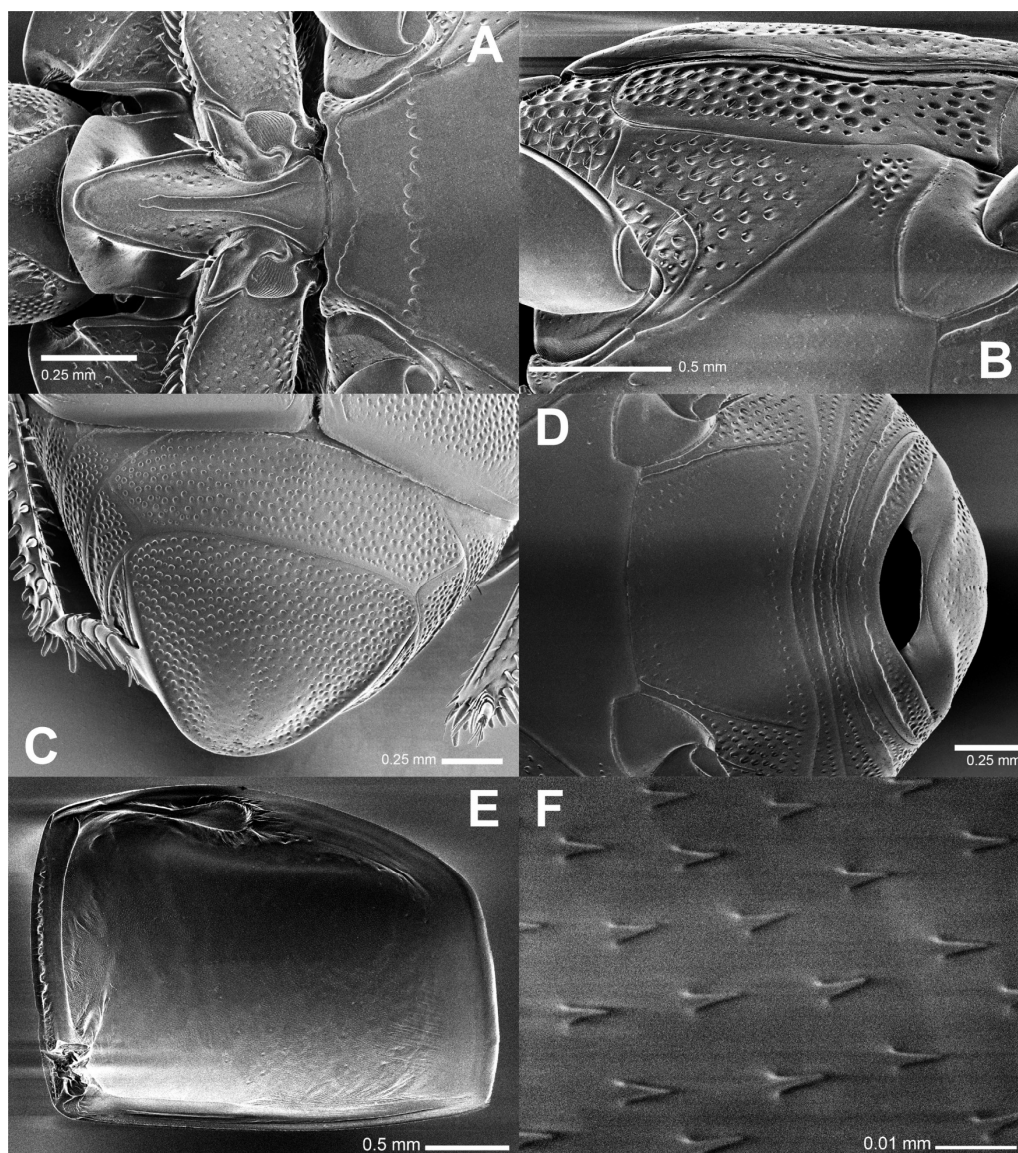


Figure 48. *Hypocaccus (Hypocaccus) axeli* Kryzhanovskij, 1976, SEM micrographs, A–D [TK-21-027], E and F [TK-22-006]. — A, Prosternum, ventral view; B, lateral side of metaventricle, ventral view; C, propygidium and pygidium, caudal view; D, abdominal sterna, ventral view; E, left elytron, ventral view; F, microsetae of left elytron

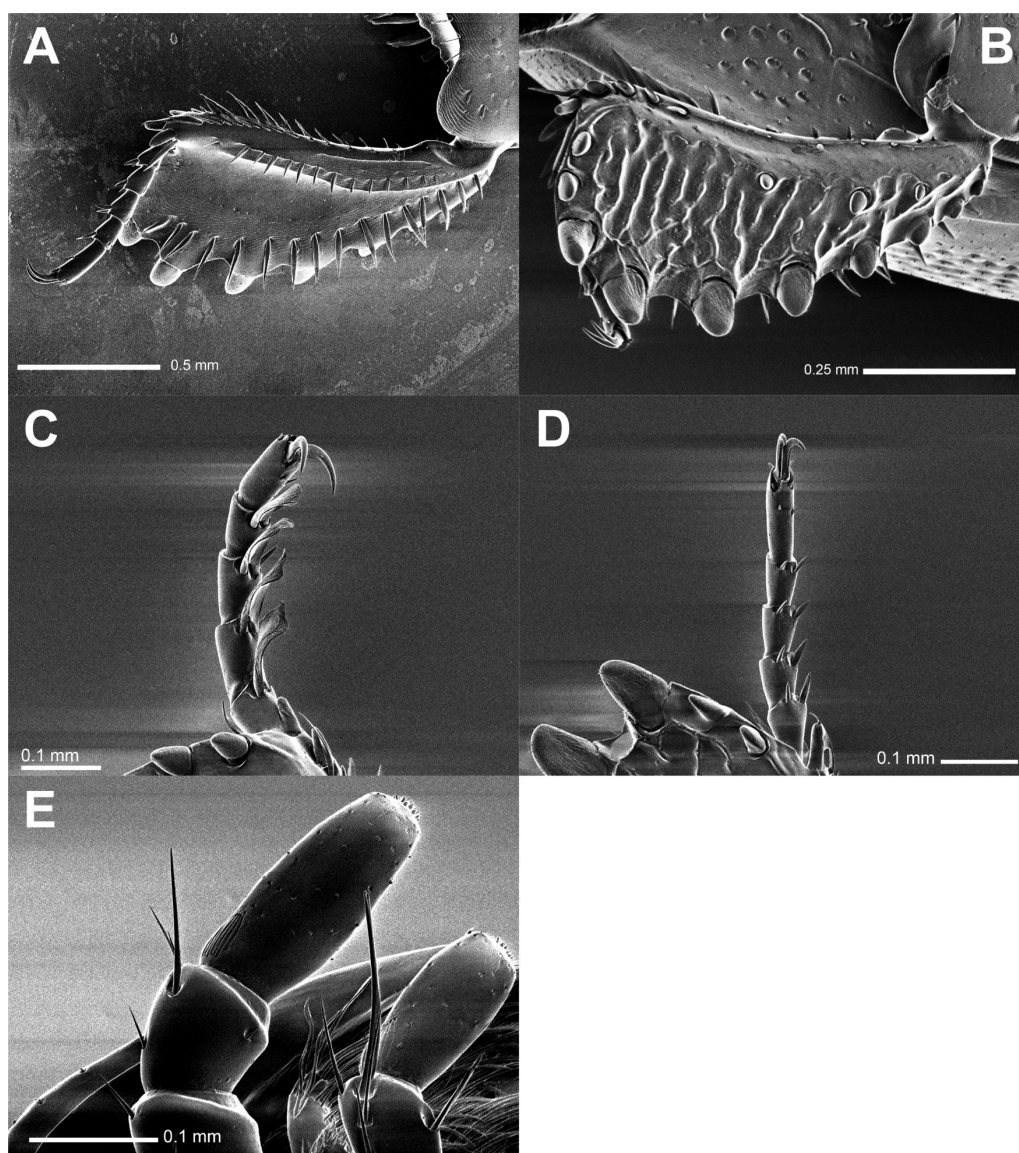


Figure 49. *Hypocaccus* (*Hypocaccus*) *axeli* Kryzhanovskij, 1976, SEM micrographs, A and B [TK-21-027], C [TK-22-044], D [TK-22-043], E [TK-22-006]. — A, Left protibia, dorsal view; B, right protibia, ventral view; C, anterior tarsus, male; D, ditto, female; E, palpal organ of right maxilla.

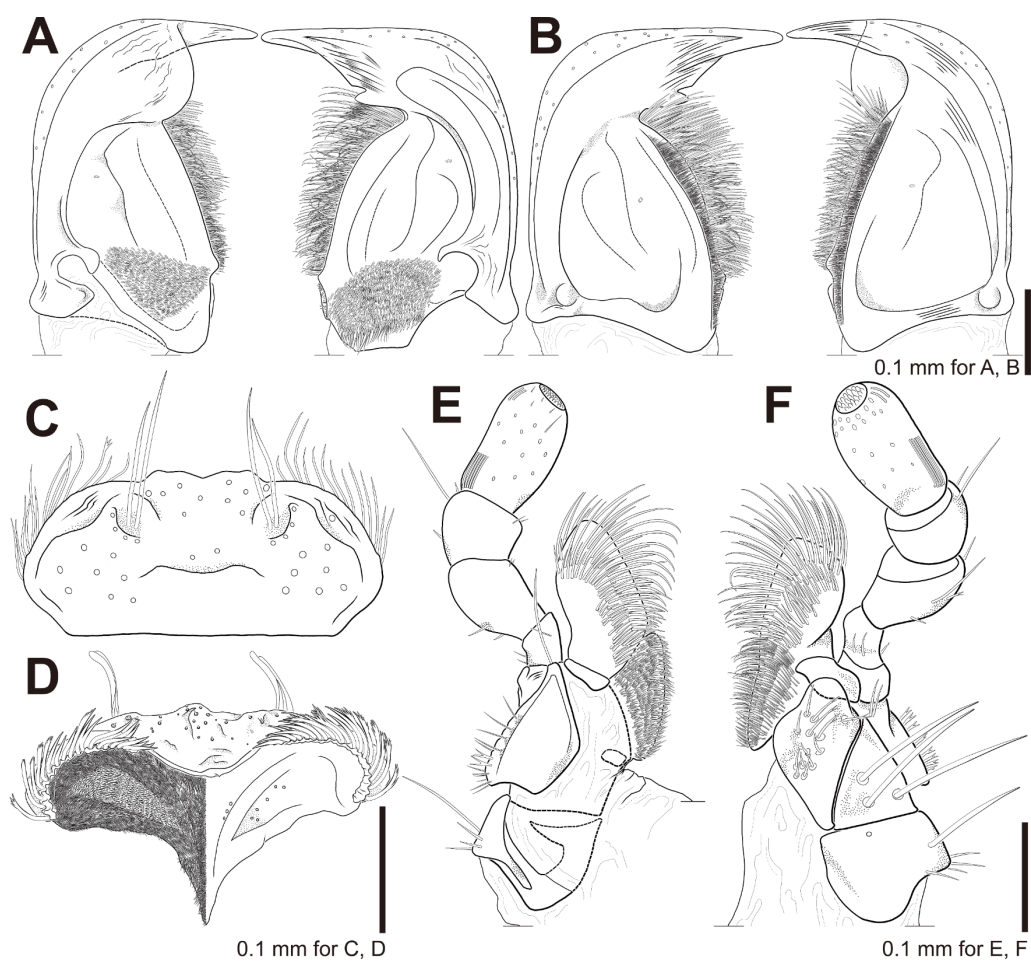


Figure 50. *Hypocaccus (Hypocaccus) subaeneus* (Schmidt, 1890), [TK-21-010]. — A, Mandibles, dorsal view; B, ditto, ventral view; C, labrum, dorsal view; D, ditto, frontal view; E, left maxilla, dorsal view; F, ditto, ventral view.

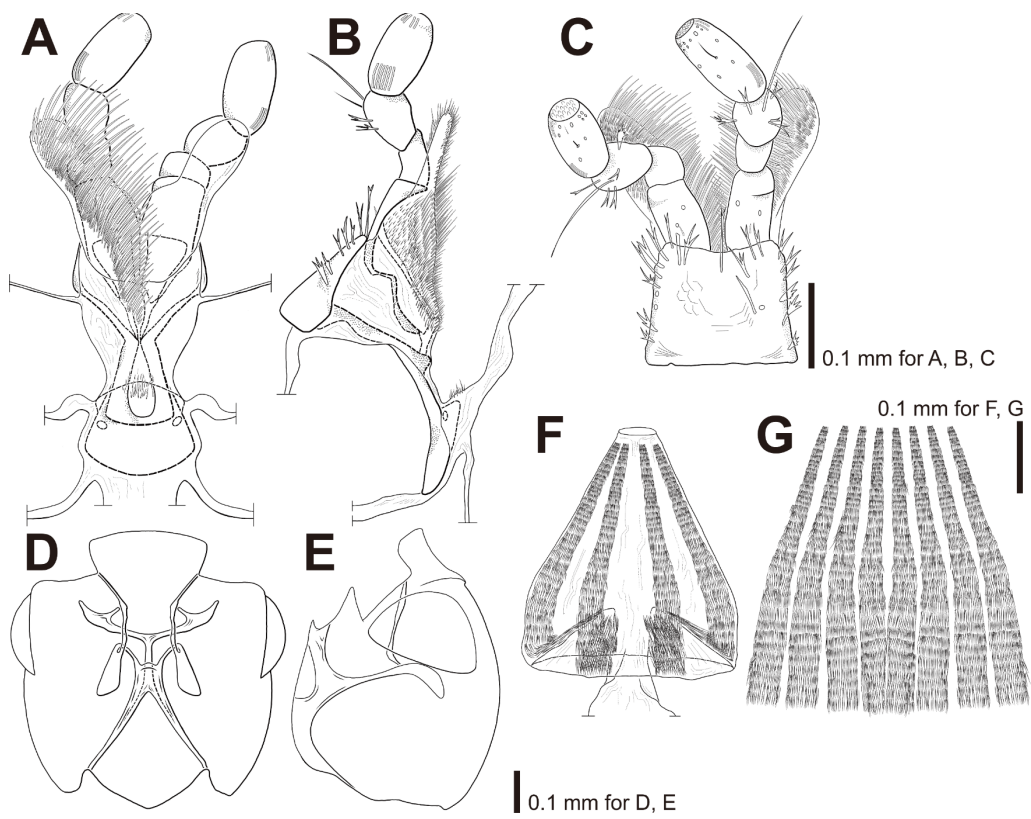


Figure 51. *Hypocaccus (Hypocaccus) subaeneus* (Schmidt, 1890), [TK-21-010]. — A, Labium and hypopharynx, dorsal view; B, ditto, lateral view; C, labium, ventral view; D, tentorium, dorsal view; E, ditto, lateral view; F, proventriculus; G, ditto, inner surface.

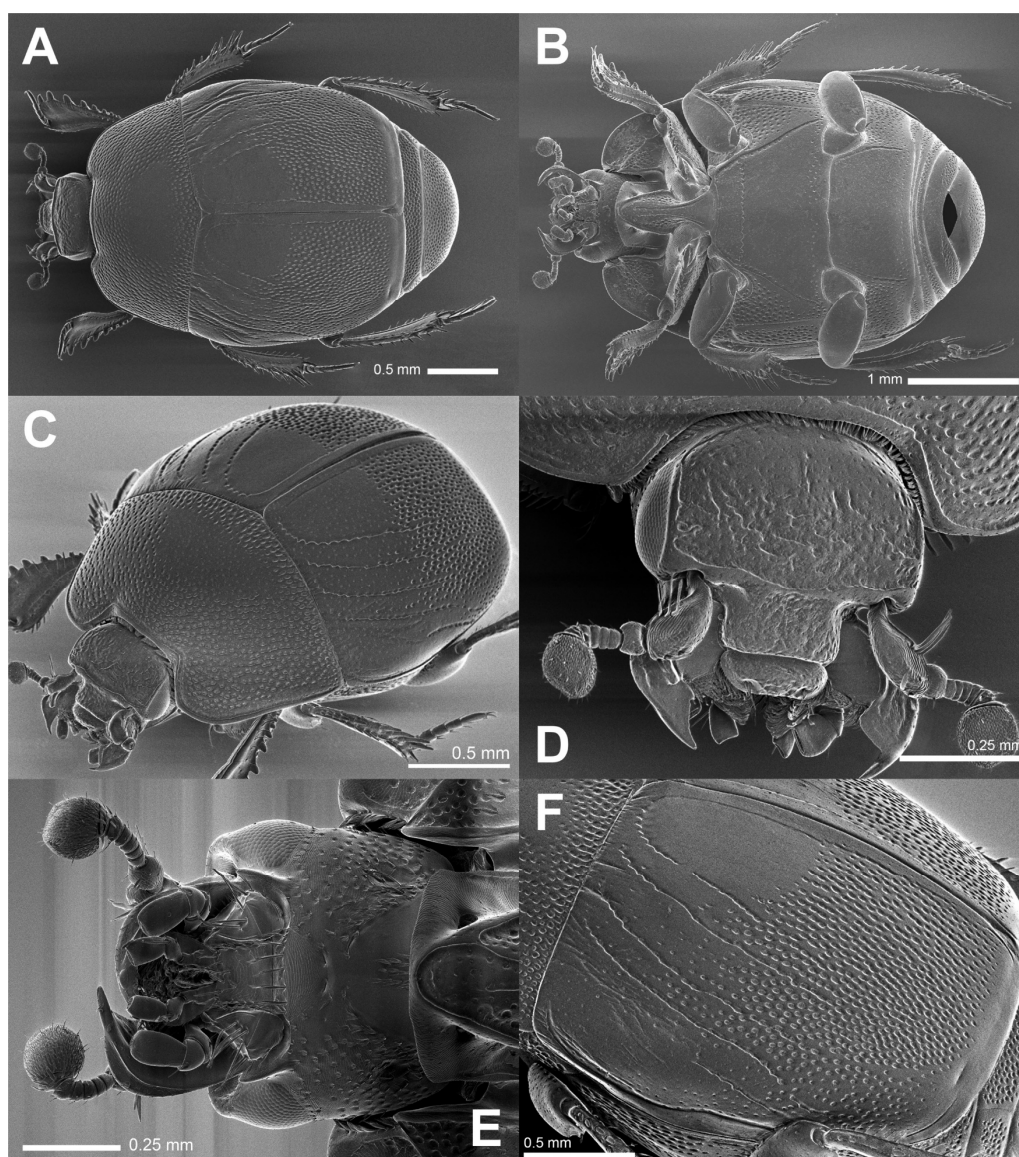


Figure 52. *Hypocaccus (Hypocaccus) subaeneus* (Schmidt, 1890), SEM micrographs, A, B and D–F [TK-22-046], C [TK-21-020]. — A, Habitus, dorsal view; B, ditto, ventral view; C, ditto, oblique view; D, head, frontal view; E, ditto, ventral view; F, left elytron, oblique view.

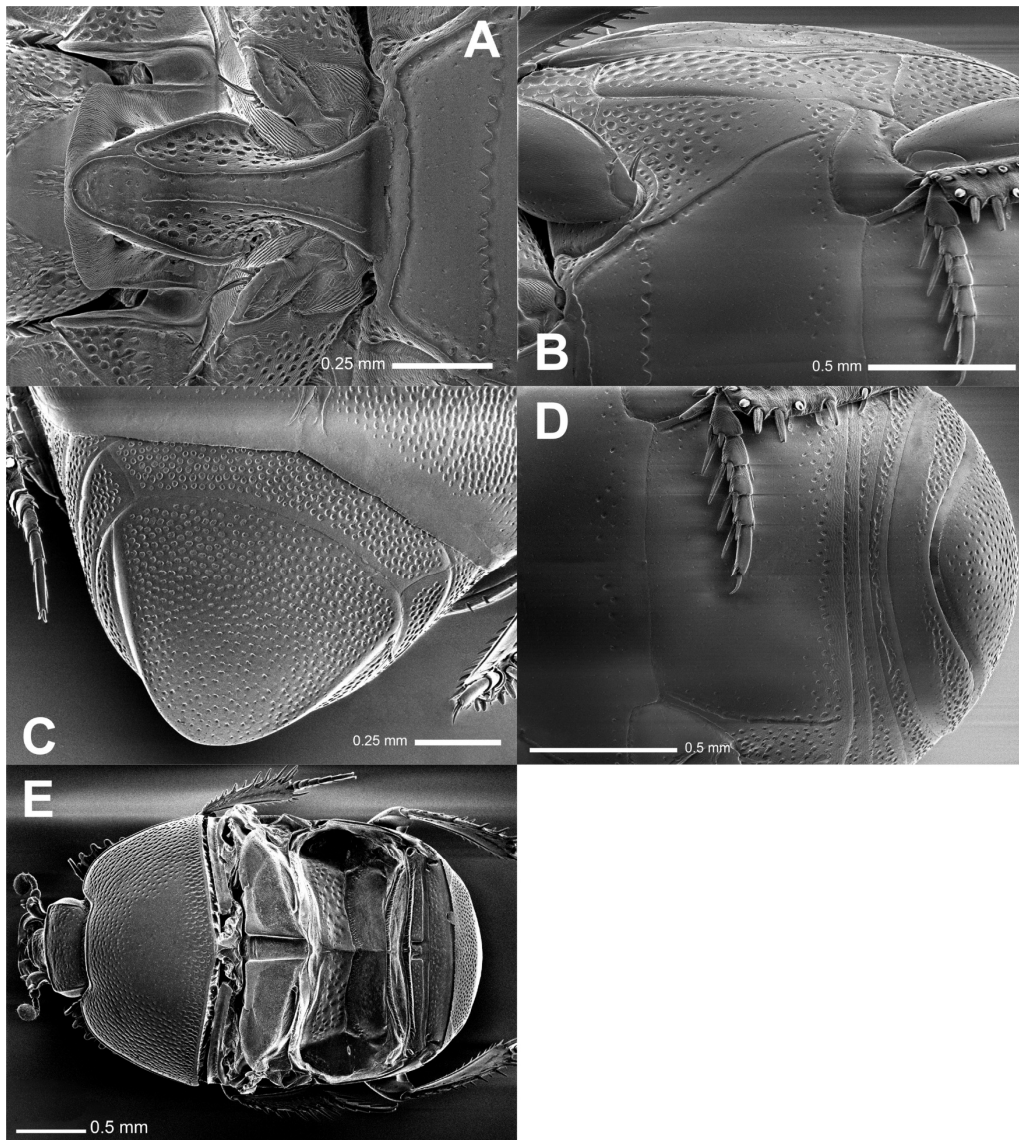


Figure 53. *Hypocaccus (Hypocaccus) subaeneus* (Schmidt, 1890), SEM micrographs, A–D [TK-22-046], E [TK-22-038]. — A, Prosternum, ventral view; B, lateral side of metaventricle, ventral view; C, propygidium and pygidium, caudal view; D, abdominal sterna, ventral view; E, meso- and metanotum and abdominal tergites, dorsal view.

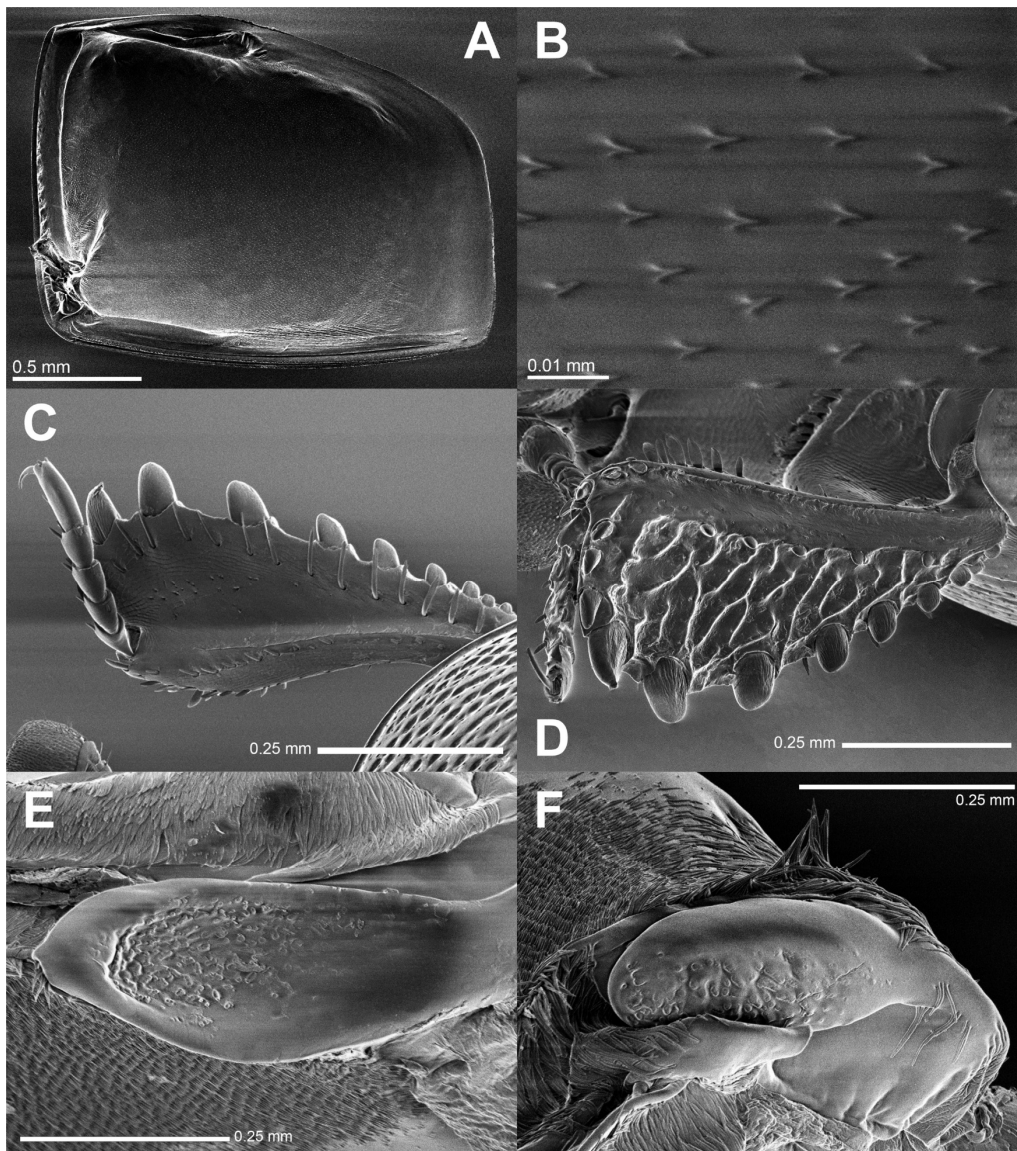


Figure 54. *Hypocaccus (Hypocaccus) subaeneus* (Schmidt, 1890), SEM micrographs, A and B [TK-22-038], C and D [TK-22-046]. — A, Left elytron, ventral view; B, microtrichiae of left elytron, ventral side; C, right protibia, dorsal view; D, ditto, ventral view; E, mola of left mandible; F, mola of right mandible.

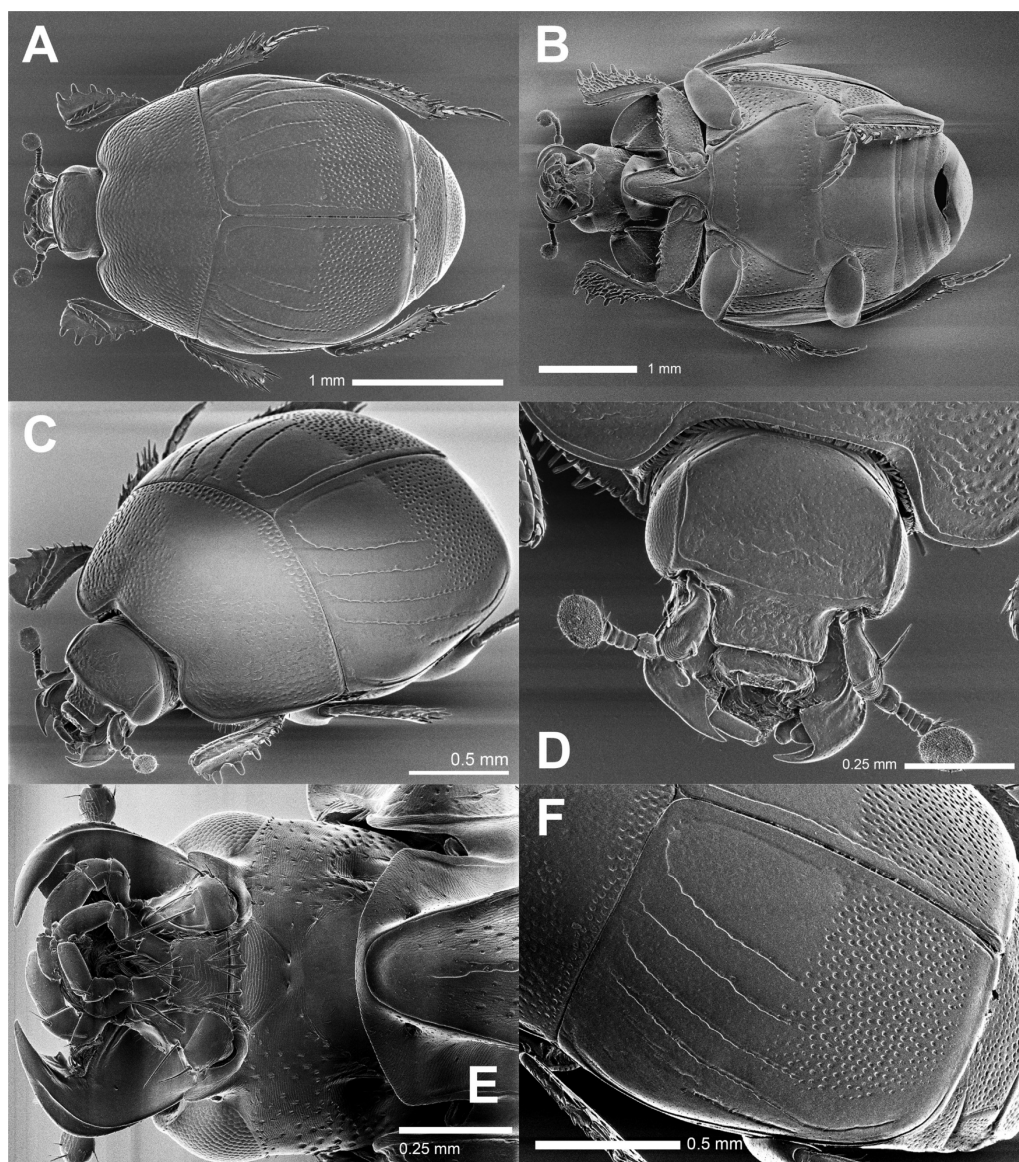


Figure 55. *Hypocaccus (Hypocaccus) toyoshimai* Kikuchi et Ôhara 2023, SEM micrographs, [MO-20-013].
 — A, Habitus, dorsal view; B, ditto, ventral view; C, ditto, oblique view; D, head, frontal view; E, ditto, ventral view; F, left elytron, oblique view.

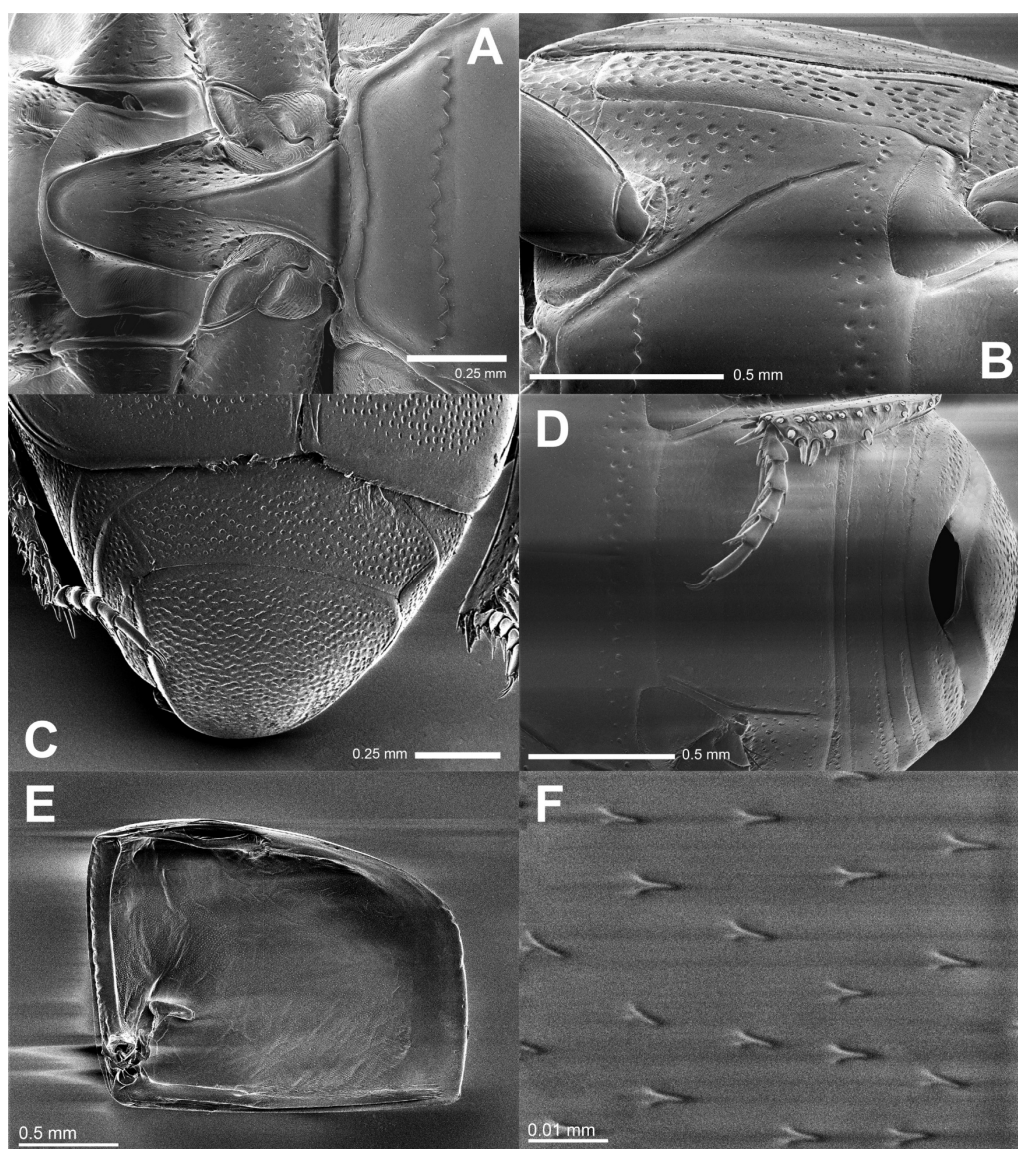


Figure 56. *Hypocaccus (Hypocaccus) toyoshimai* Kikuchi et Ôhara 2023, SEM micrographs, A–D [MO-20-013], E and F [TK-22-016]. — A, Prosternum, ventral view; B, lateral side of metaventrite, ventral view; C, propygidium and pygidium, caudal view; D, abdominal sterna, ventral view; E, left elytron, ventral view; F, microsetae of left elytron, ventral side.

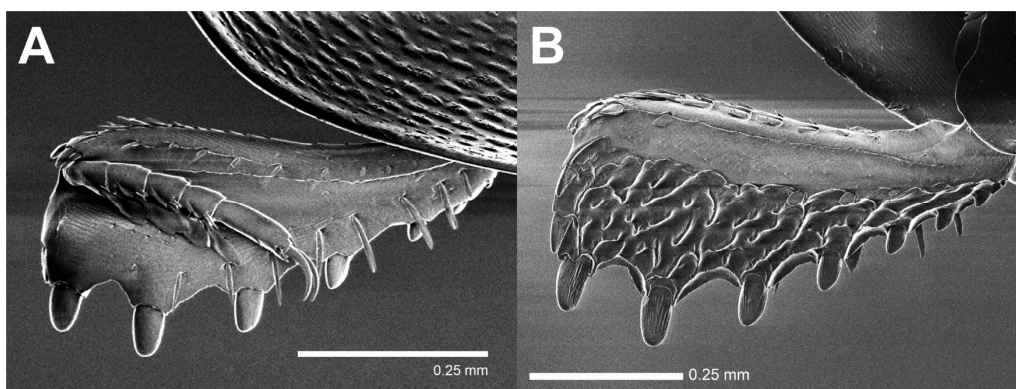


Figure 57. *Hypocaccus (Hypocaccus) toyoshimai* Kikuchi et Ôhara 2023, SEM micrographs, [MO-20-013].

— A, Left protibia, dorsal view; B, right protibia, ventral view.

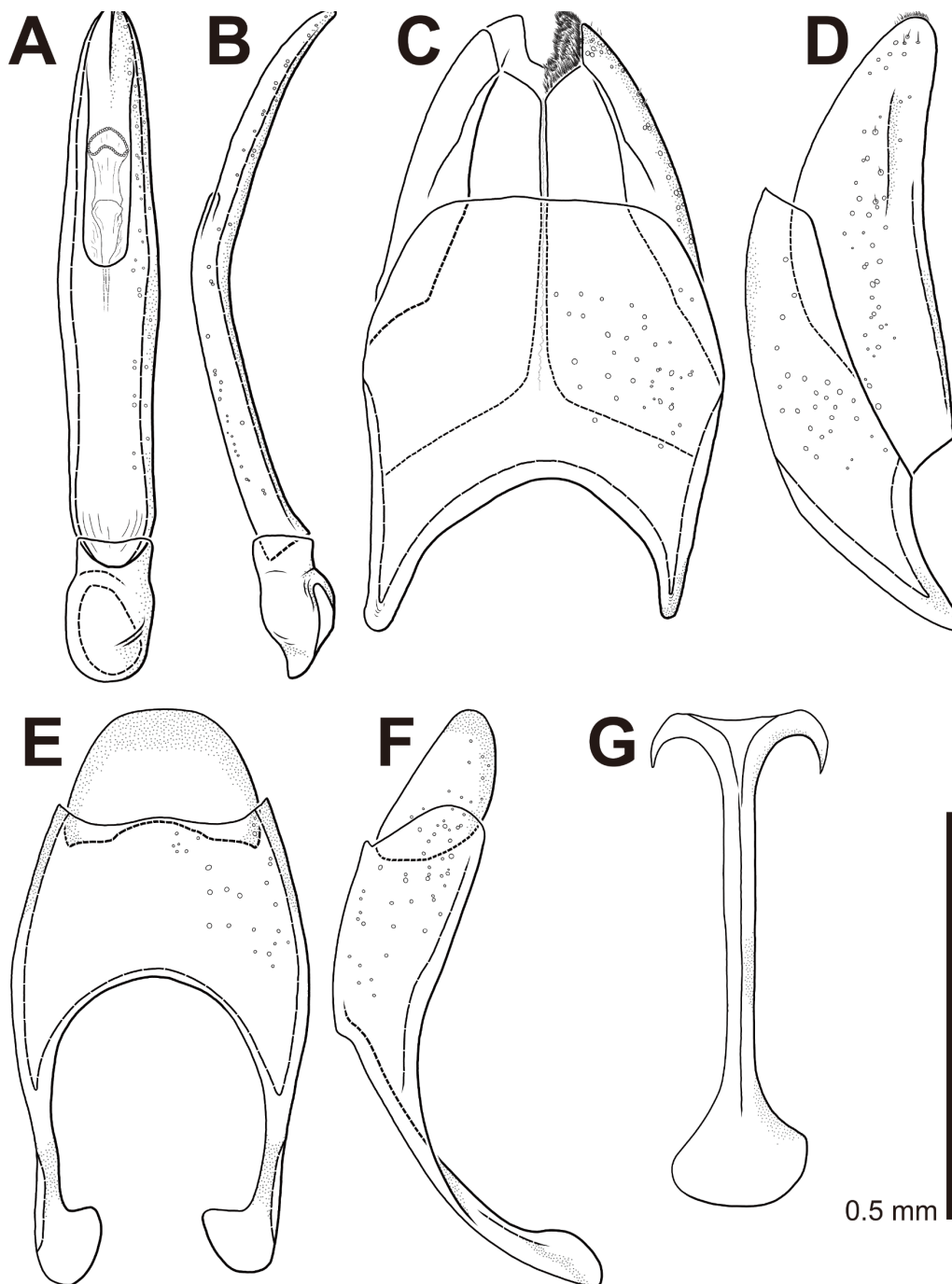


Figure 58. *Hypocaccus (Hypocaccus) toyoshimai* Kikuchi et Ôhara 2023, [MO-20-013]. — A, Aedeagus, dorsal view; B, ditto, lateral view; C, eighth tergite and sternum; D, ditto, lateral view; E, ninth and tenth tergites, dorsal view; F ditto lateral view; G, ninth sternum (spicule), dorsal view.

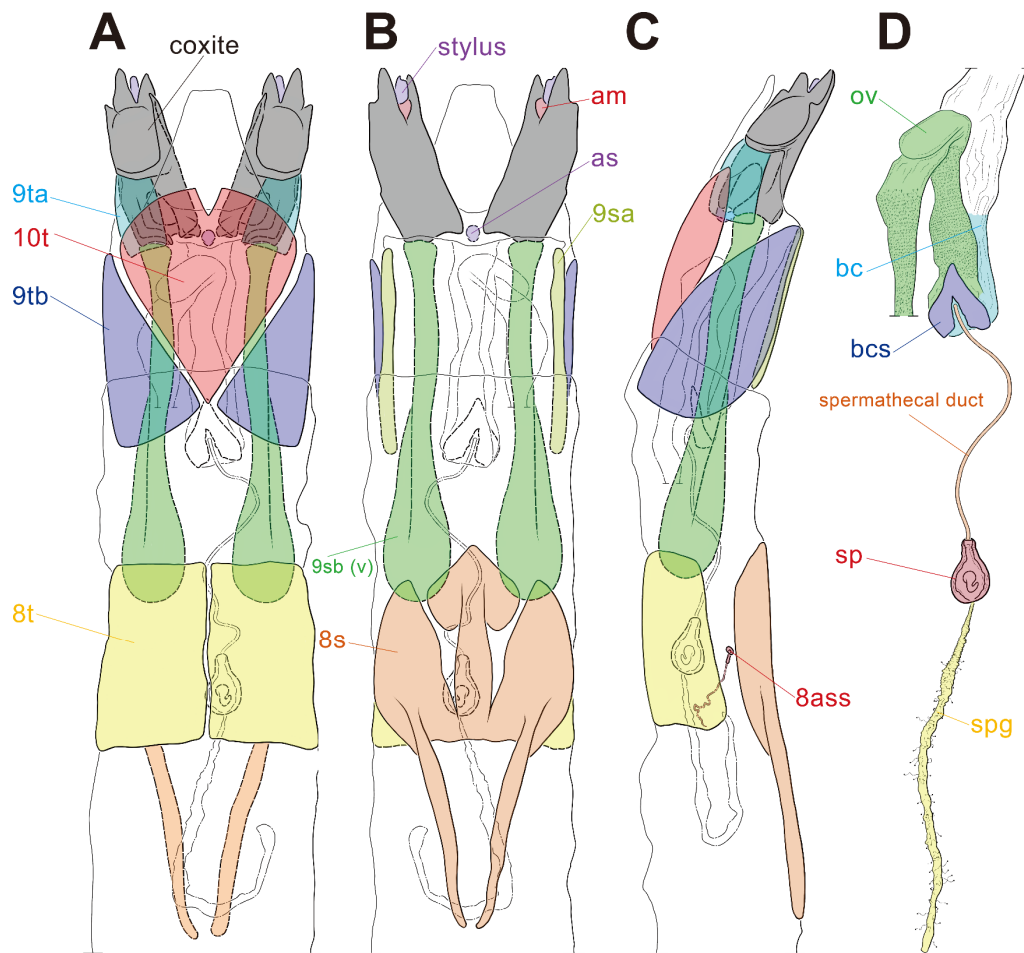


Figure 59. Schematic diagram of the female genitalia in Histeroidea. — *Carcinops (Carcinops) pumilio*, [TK-23-110].

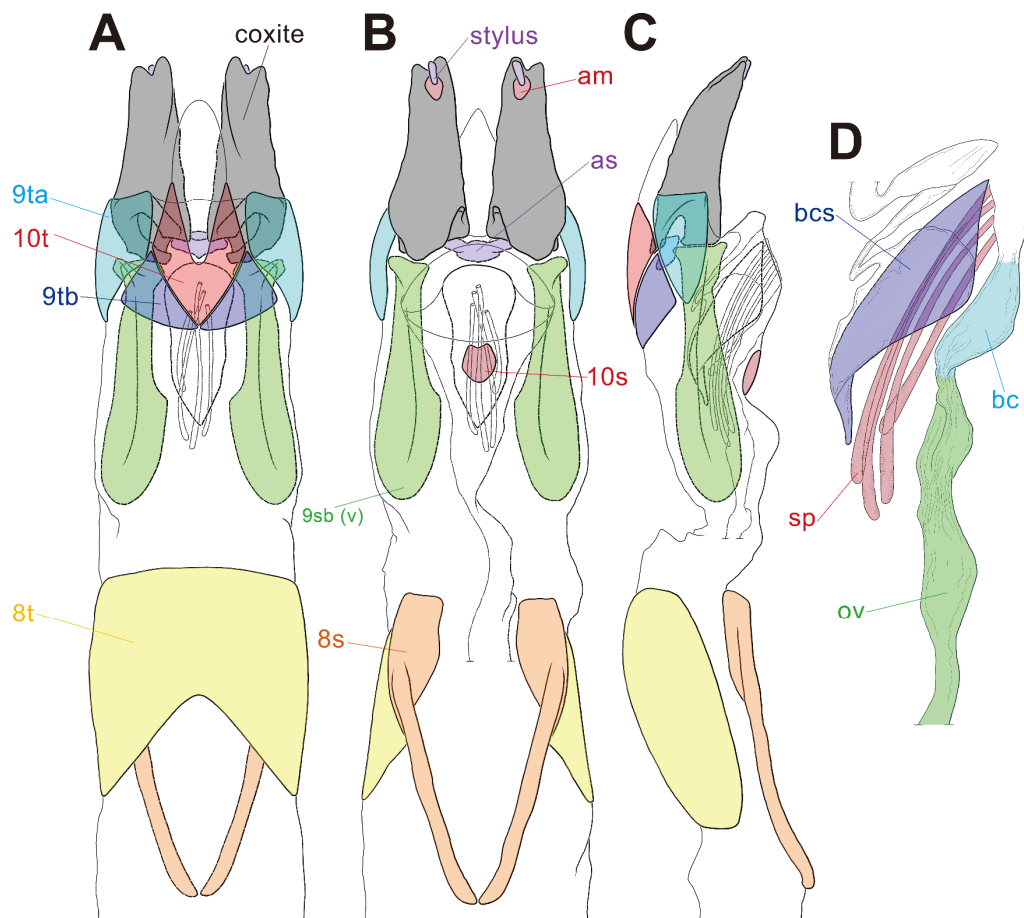


Figure 60. Schematic diagram of the female genitalia in Histeroidea. — *Atholus duodecimstriatus quatuordecimstriatus*, [TK-23-085].

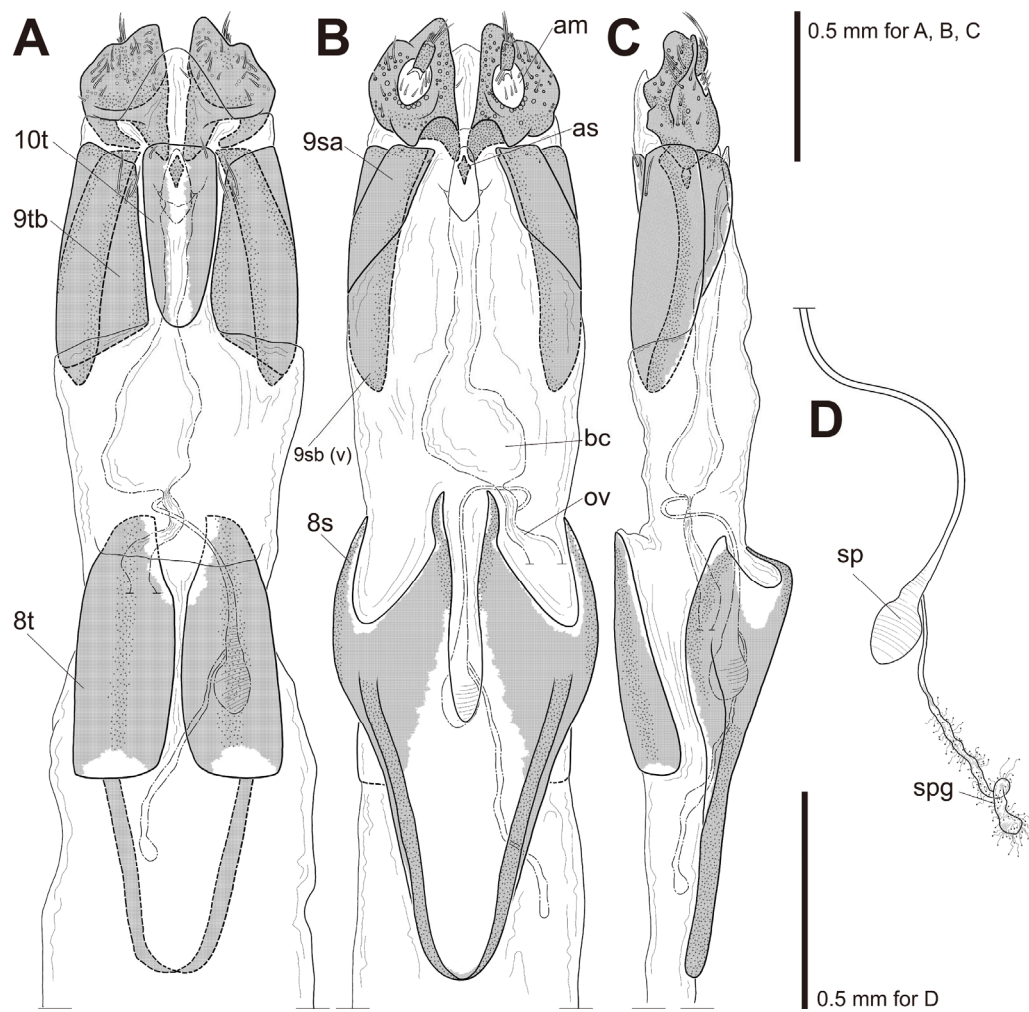


Figure 61. Female genitalia of *Sphaerites glabratus* (Fabricius, 1792), [TK-23-006]. — A, Dorsal view; B, ventral view; C, left lateral view; D, spermatheca and spermathecal gland.

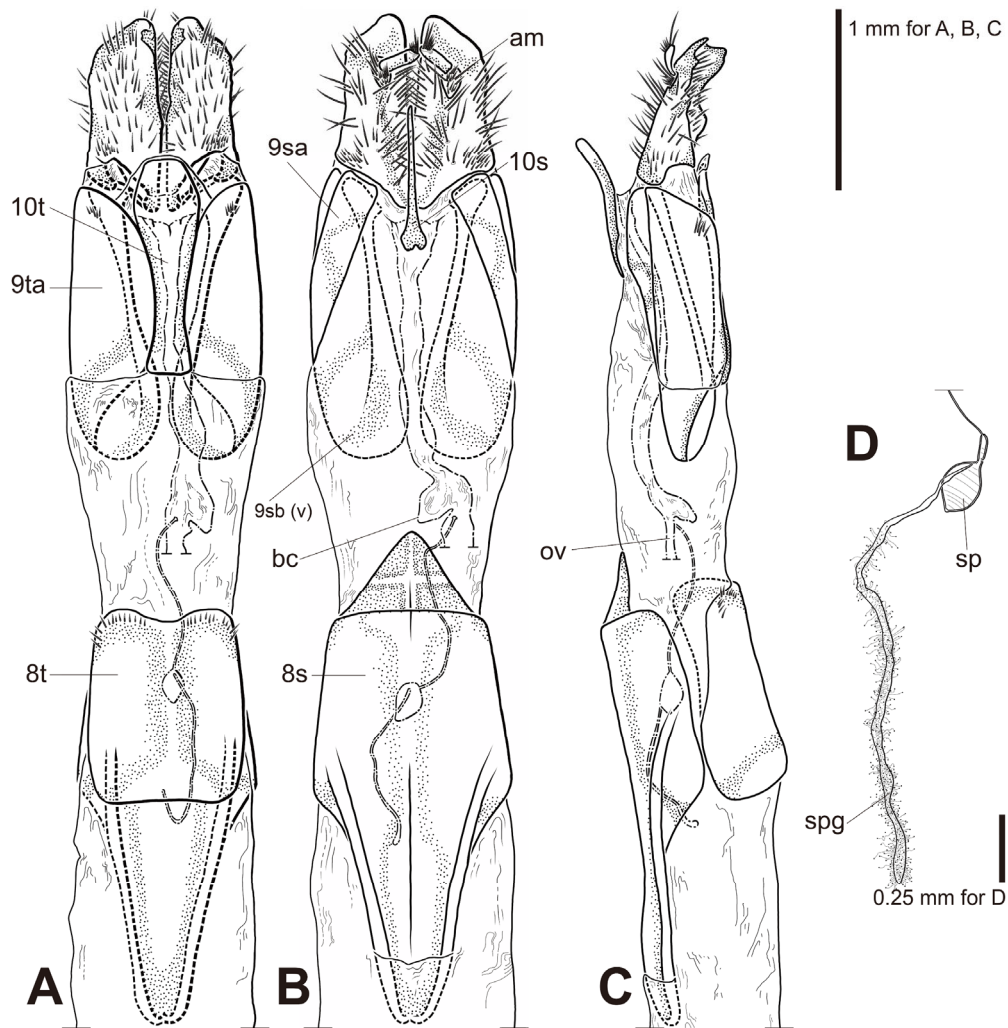


Figure 62. *Syntelia histeroides* Lewis, 1882, [TK-22-007]. — A, Dorsal view; B, ventral view; C, right lateral view; D, spermatheca and spermathecal gland.

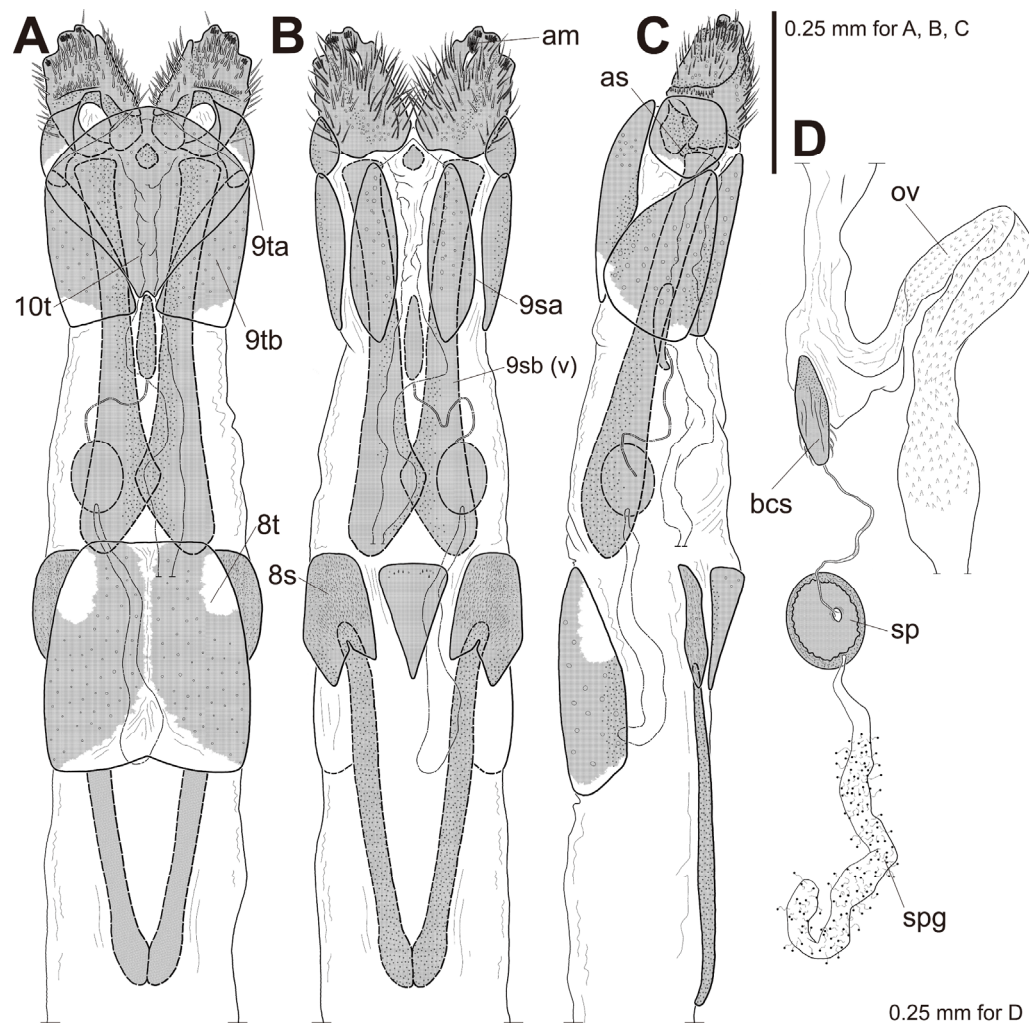


Figure 63. *Niponius osorioceps* Lewis, 1885, [TK-23-075]. — A, Dorsal view; B, ventral view; C, left lateral view; D, spermatheca and spermathecal gland.

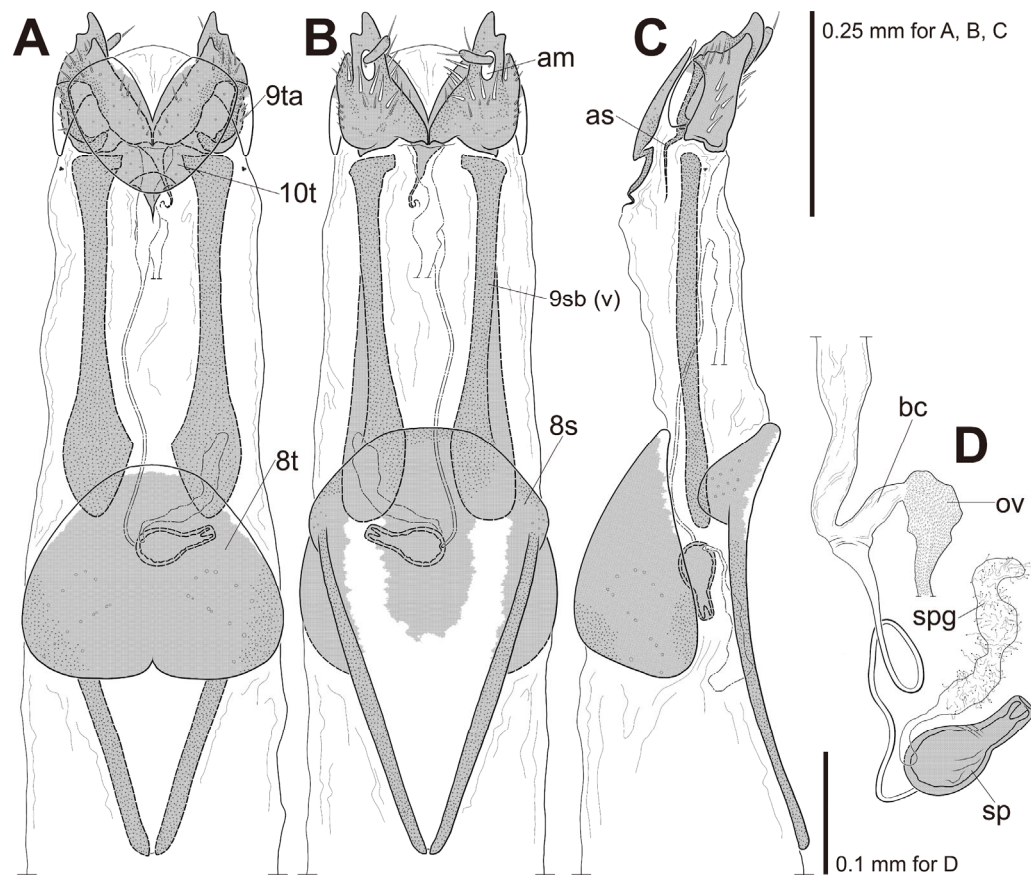


Figure 64. *Plegaderus (Plegaderus) marseuli* Reitter, 1877, [TK-23-094]. — A, Dorsal view; B, ventral view; C, left lateral view; D, spermatheca and spermathecal gland.

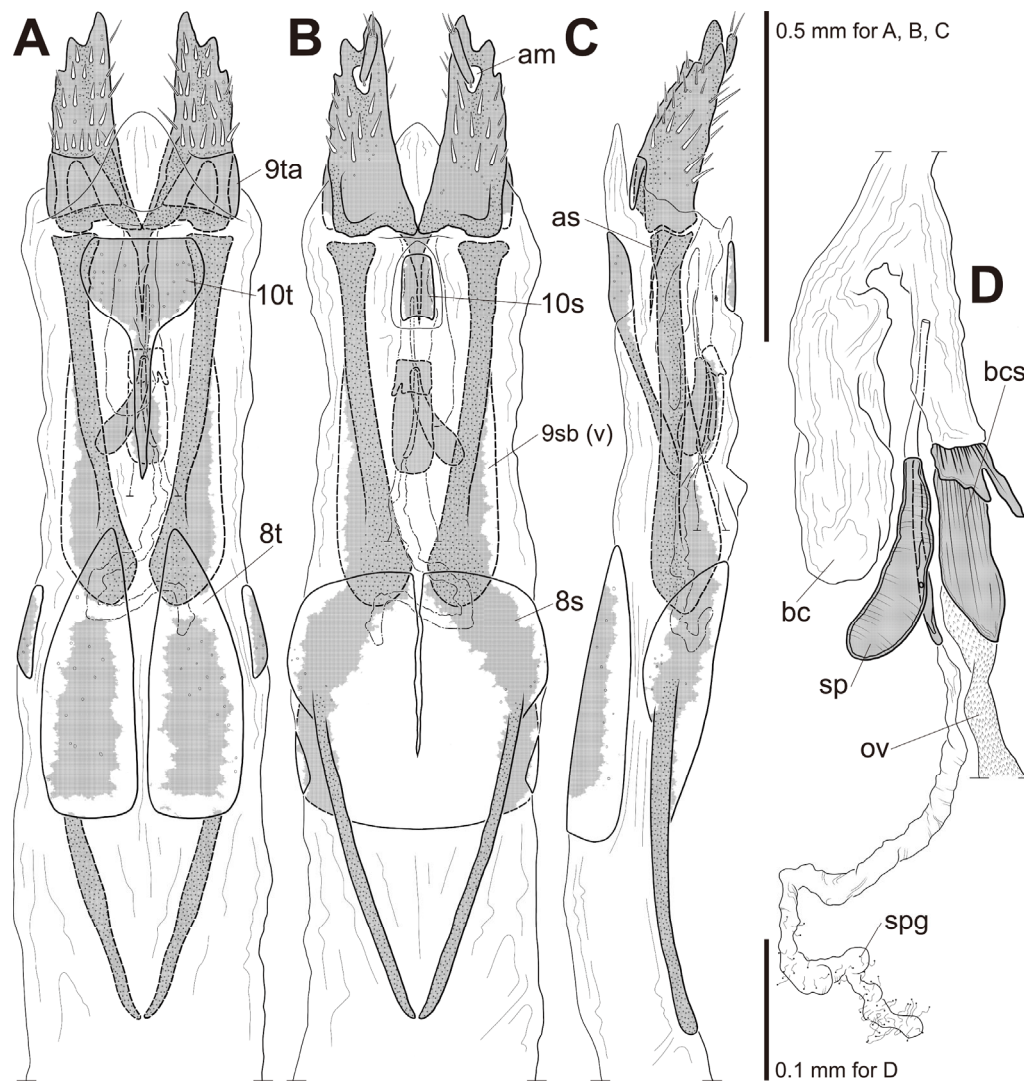


Figure 65. *Chaetabraeus (Chaetabraeus) bonzicus* (Marseul, 1873), [TK-23-097]. — A, Dorsal view; B, ventral view; C, left lateral view; D, spermatheca and spermathecal gland.

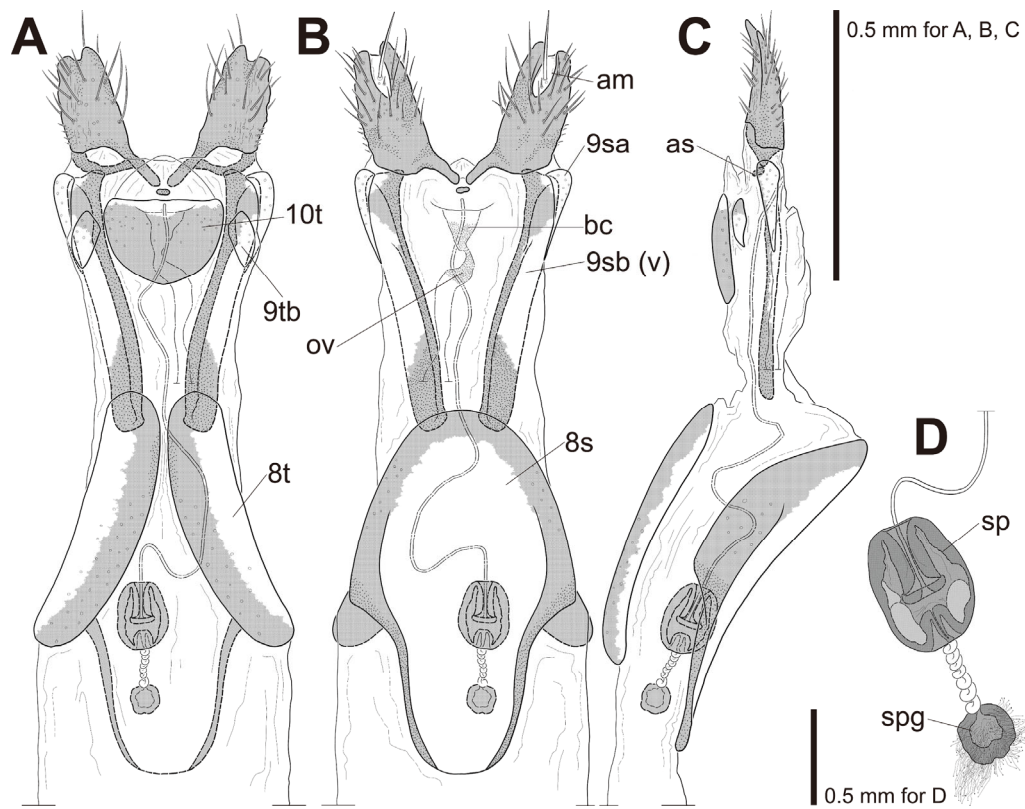


Figure 66. *Eopachylopus ripae* (Lewis, 1885), [TK-23-084]. — A, Dorsal view; B, ventral view; C, left lateral view; D, spermatheca and spermathecal gland.

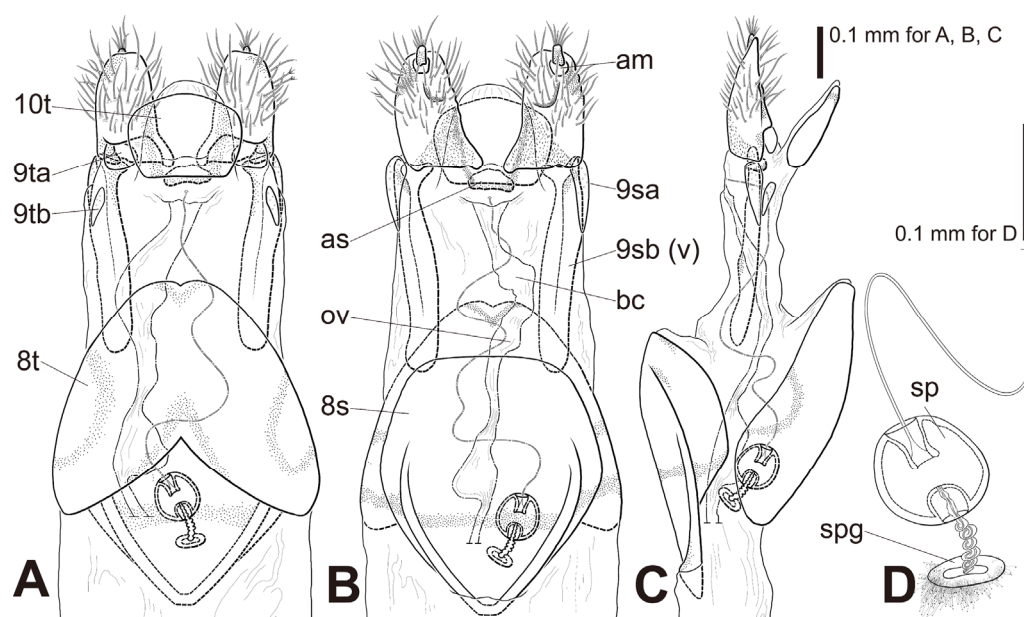


Figure 67. *Hypocacculus (Nessus) asticus* Lewis, 1911, [TK-22-002]. — A, Dorsal view; B, ventral view; C, right lateral view; D, spermatheca and spermathecal gland.

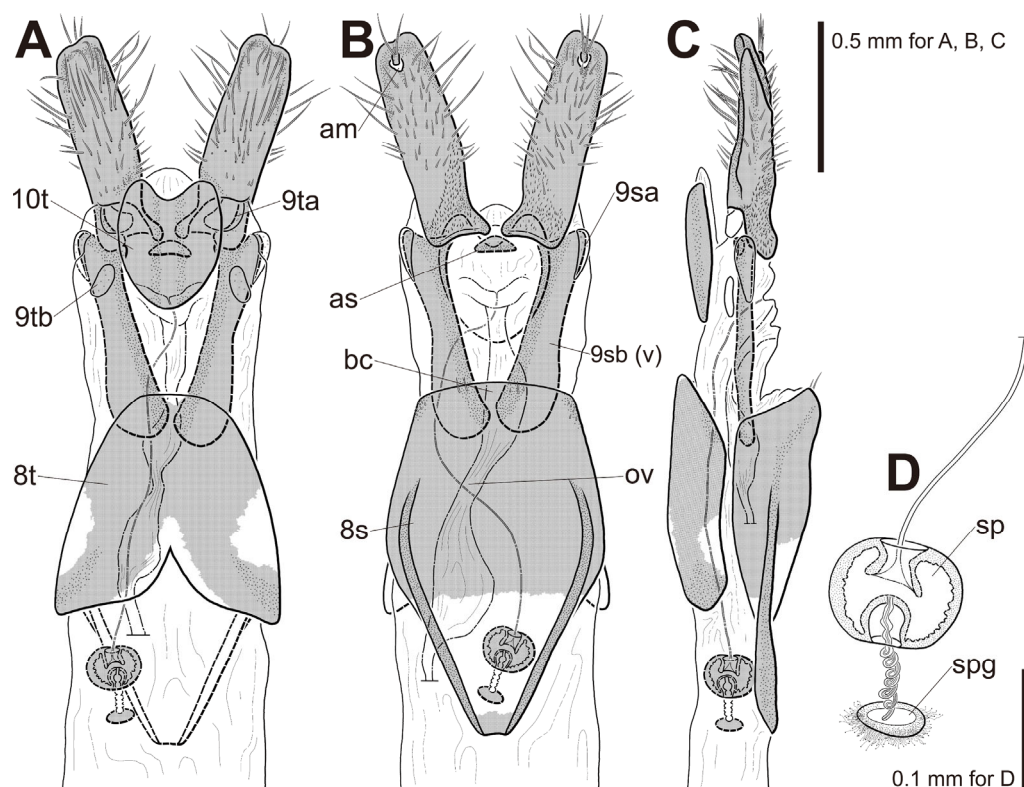


Figure 68. *Hypocaccus (Baeckmanniolus) varians hatsune* (Nakane, 1977), [TK-23-023]. — A, Dorsal view; B, ventral view; C, left lateral view; D, spermatheca and spermathecal gland.

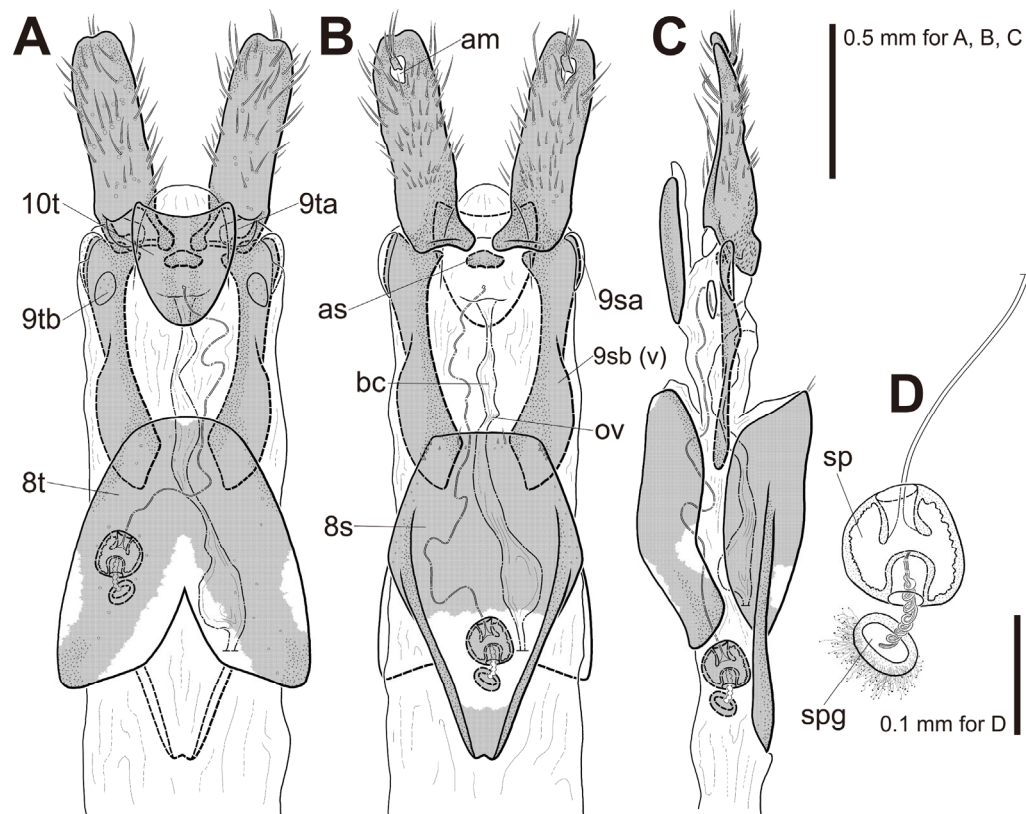


Figure 69. *Hypocaccus (Baeckmanniolus) varians varians* (Schmidt, 1890), [TK-23-019]. — A, Dorsal view; B, ventral view; C, left lateral view; D, spermatheca and spermathecal gland.

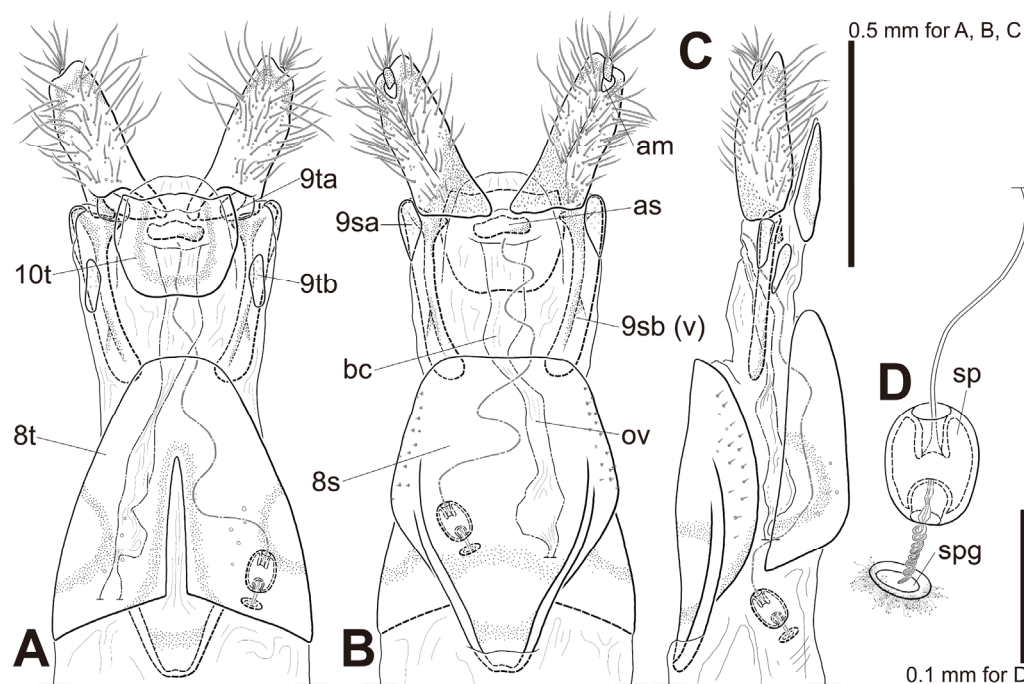


Figure 70. *Hypocaccus (Hypocaccus) akanensis* Ôhara, 1994, [TK-23-004]. — A, Dorsal view; B, ventral view; C, right lateral view; D, spermatheca and spermathecal gland.

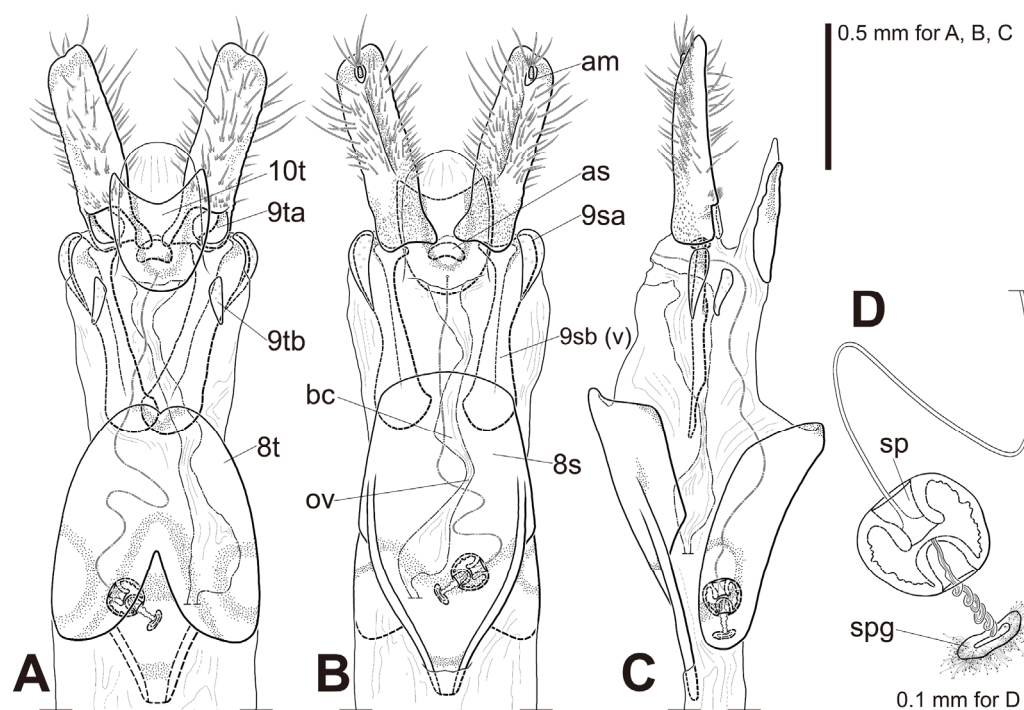


Figure 71. *Hypocaccus (Hypocaccus) axeli* Kryzhanovskij, 1976, [TK-22-004]. — A, Dorsal view; B, ventral view; C, right lateral view; D, spermatheca and spermathecal gland.

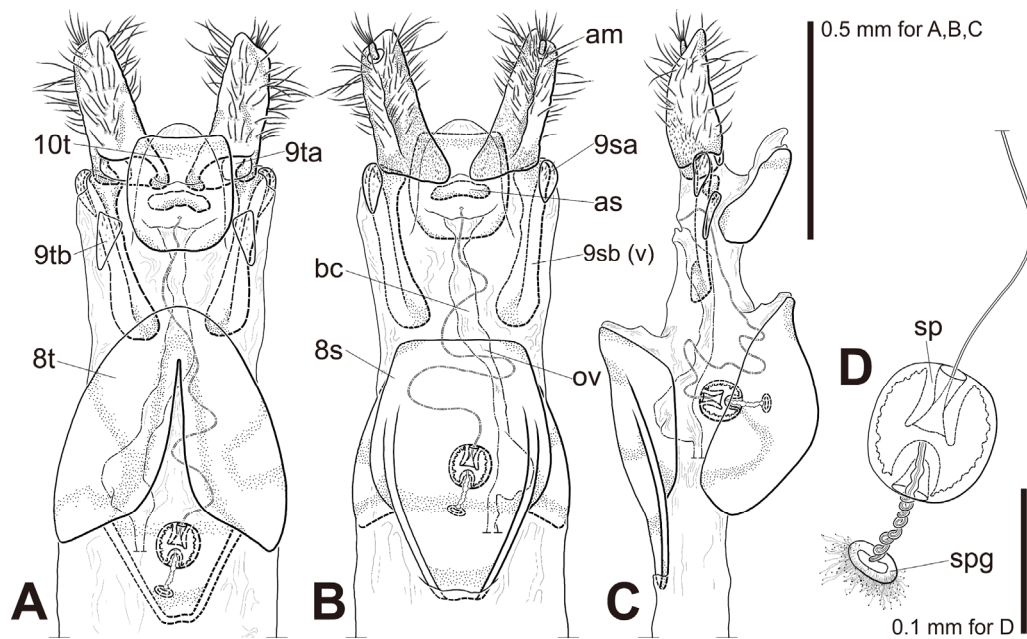


Figure 72. *Hypocaccus (Hypocaccus) subaeneus* (Schmidt, 1890), [TK-21-021]. — A, Dorsal view; B, ventral view; C, right lateral view; D, spermatheca and spermathecal gland.

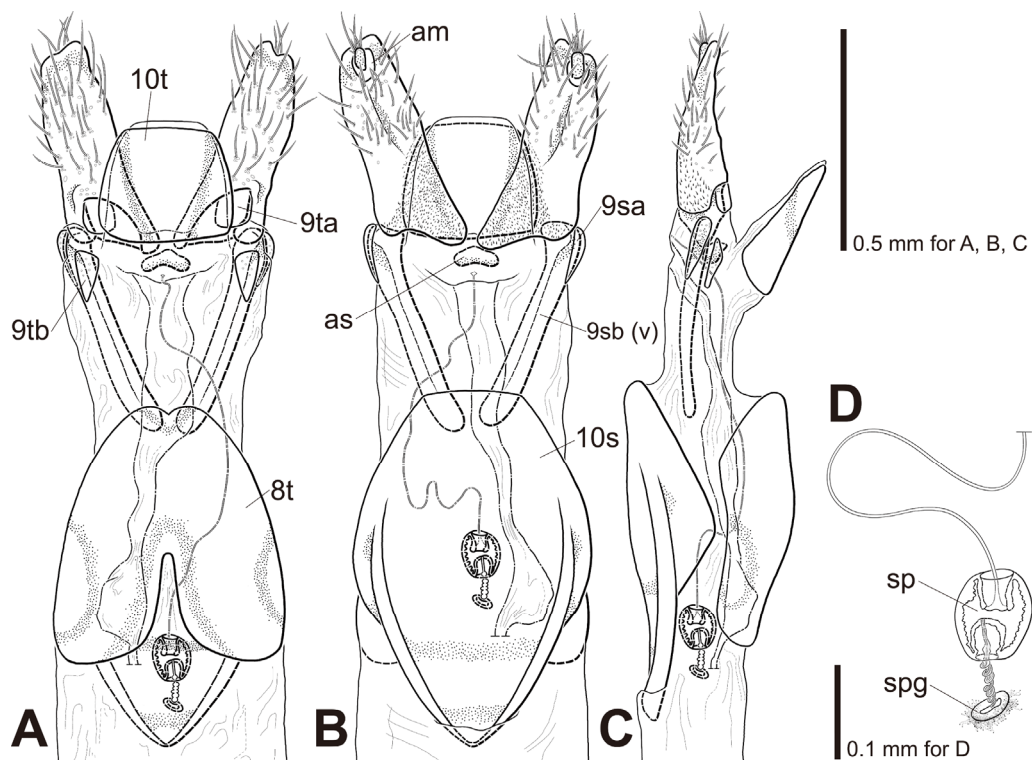


Figure 73. *Hypocaccus (Hypocaccus) toyoshimai* Kikuchi et Ôhara 2023, [TK-22-015]. — A, Dorsal view; B, ventral view; C, right lateral view; D, spermatheca and spermathecal gland.

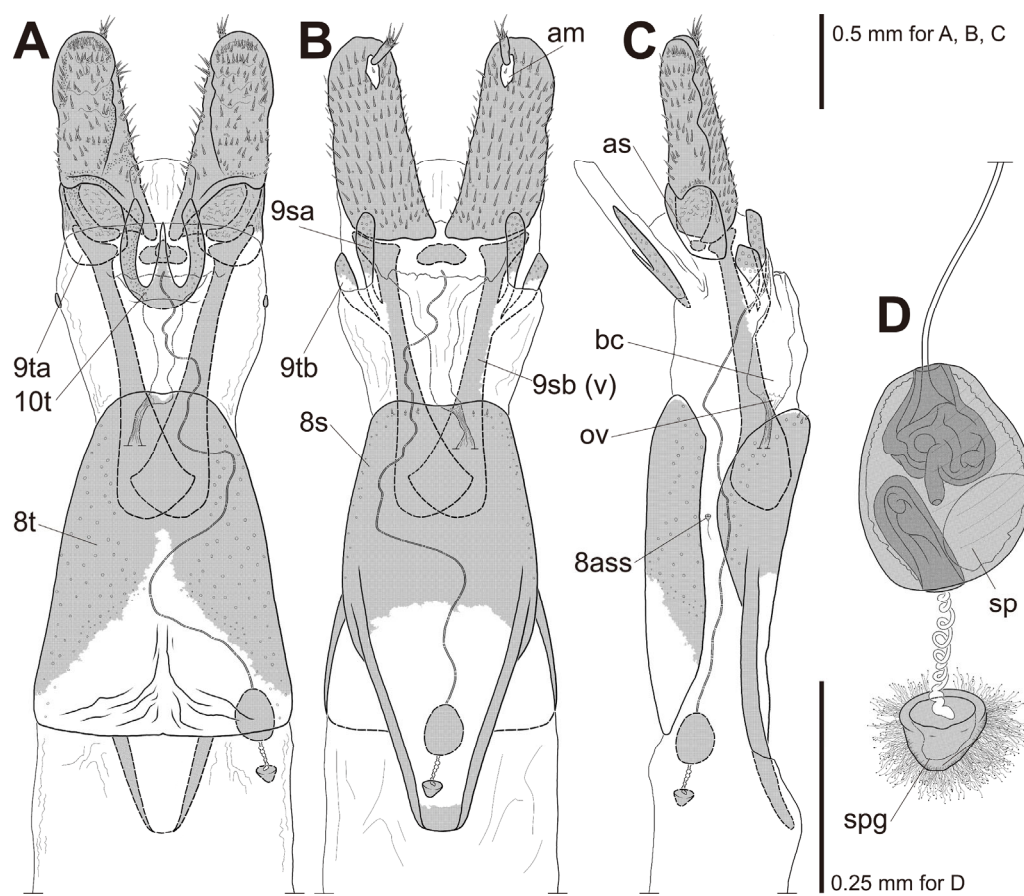


Figure 74. *Saprinus (Saprinus) niponicus* Dahlgren, 1962, [TK-23-080]. — A, Dorsal view; B, ventral view; C, left lateral view; D, spermatheca and spermathecal gland.

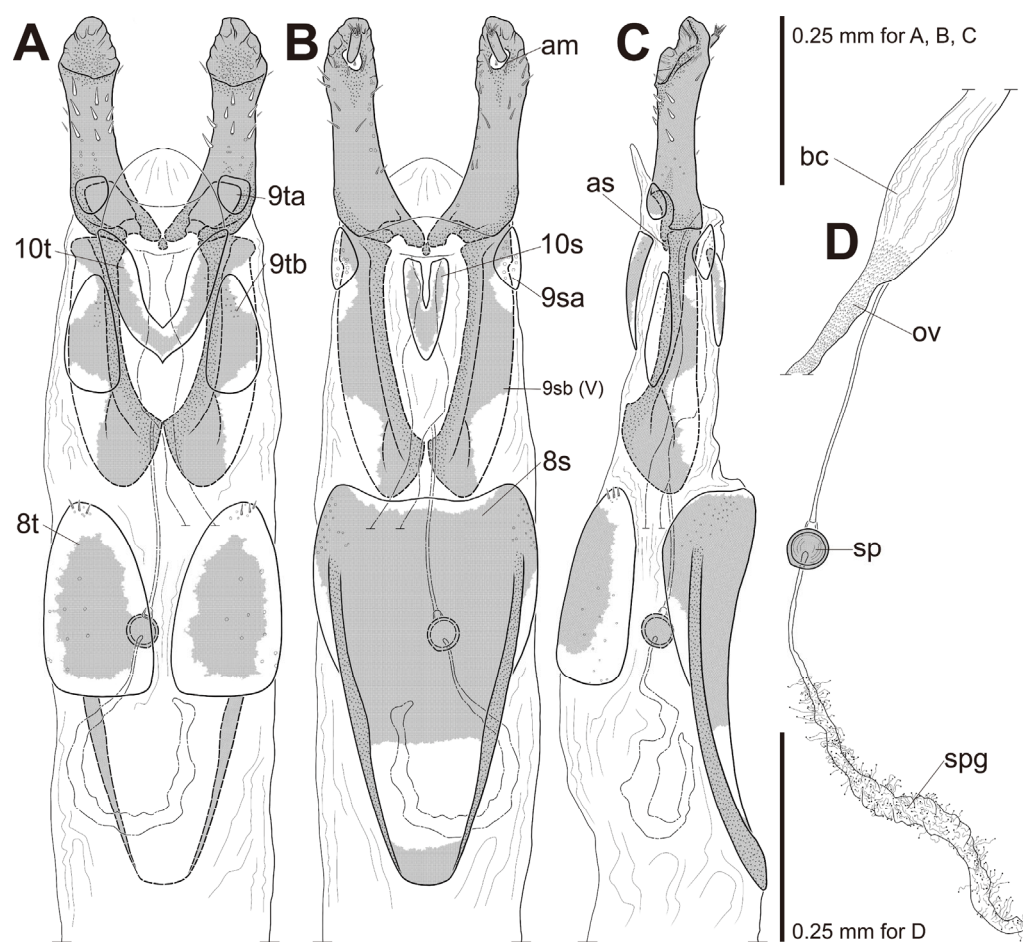


Figure 75. *Anapleus nakanei* Ôhara, 1994, [TK-23-100]. — A, Dorsal view; B, ventral view; C, left lateral view; D, spermatheca and spermathecal gland.

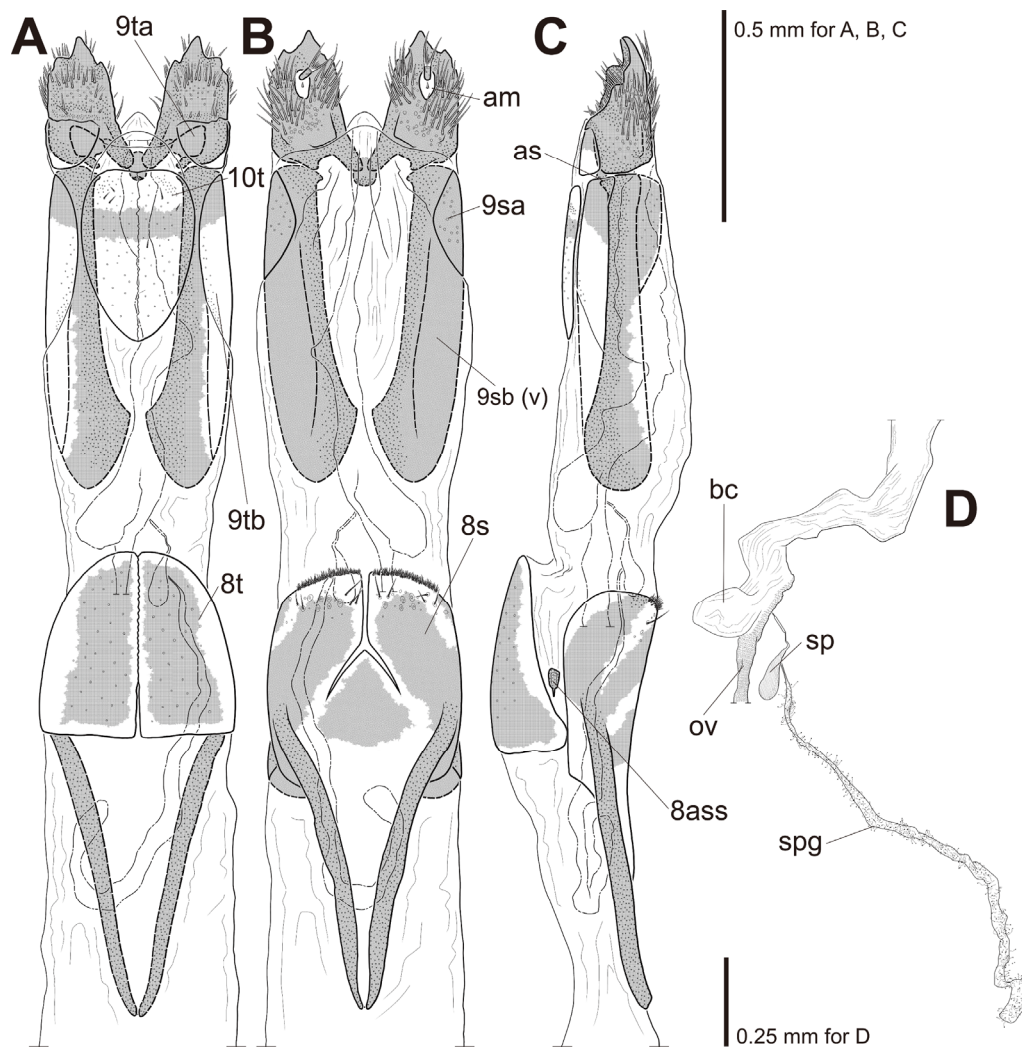


Figure 76. *Dendrophilus (Dendrophilus) xavieri* Marseul, 1873, [TK-23-109]. — A, Dorsal view; B, ventral view; C, left lateral view; D, spermatheca and spermathecal gland.

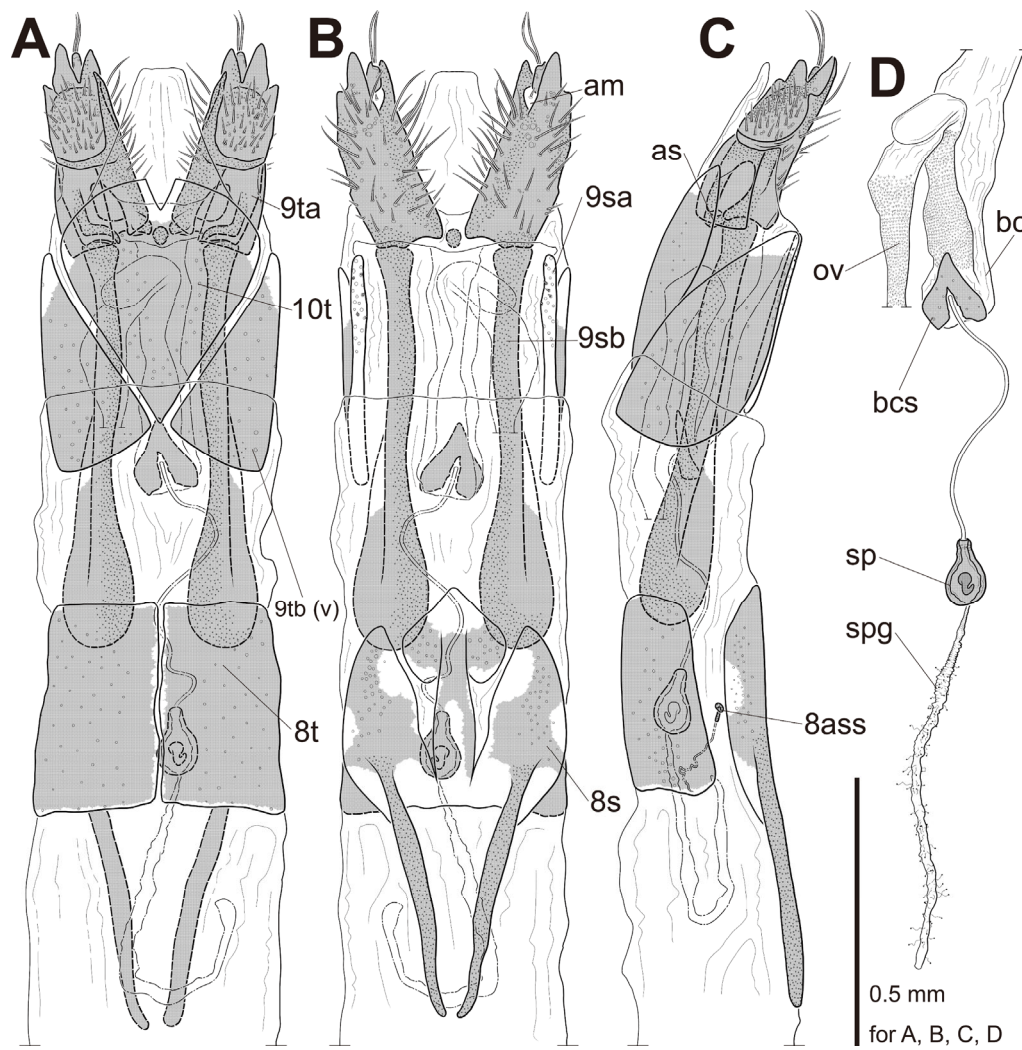


Figure 77. *Carcinops (Carcinops) pumilio* (Erichson, 1834), [TK-23-110]. — A, Dorsal view; B, ventral view; C, left lateral view; D, spermatheca and spermathecal gland.

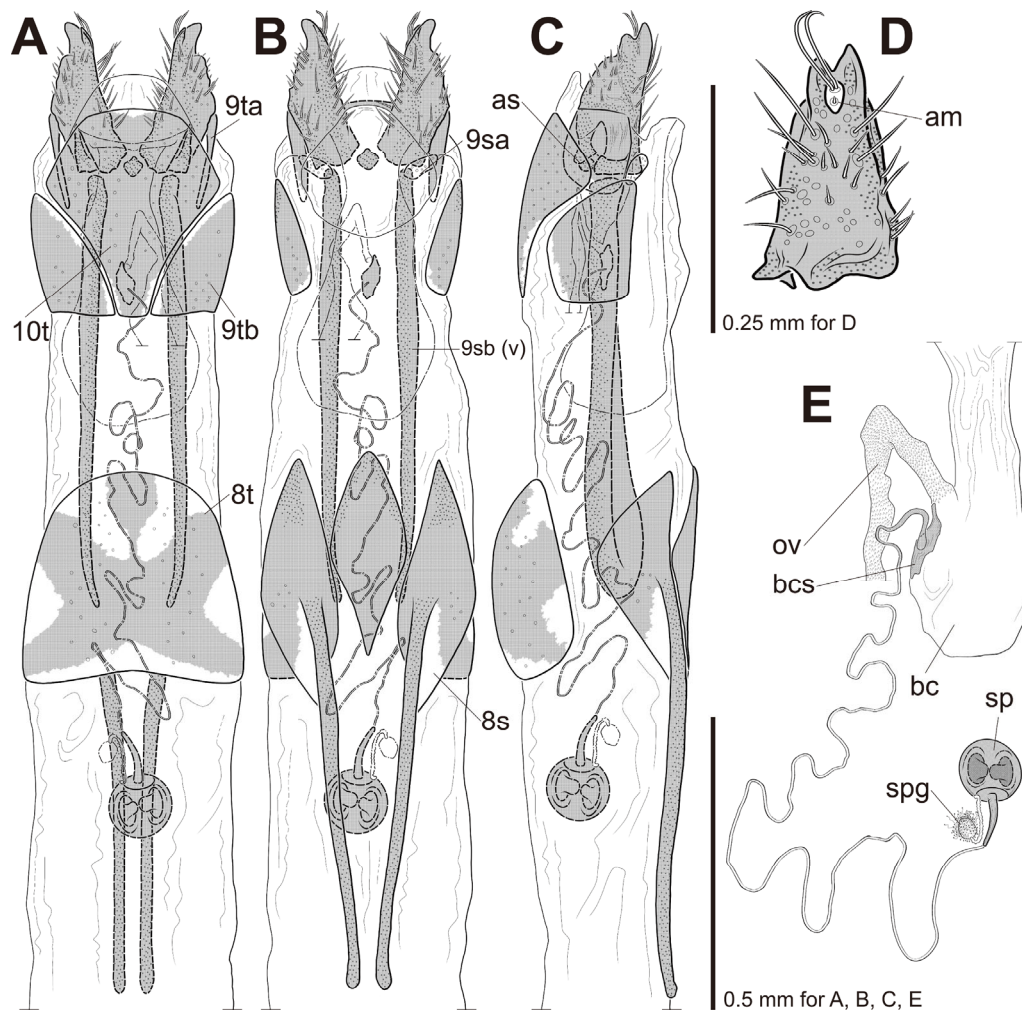


Figure 78. *Paromalus (Paromalus) parallelepipedus* (Herbst, 1791), [TK-23-121]. — A, Dorsal view; B, ventral view; C, left lateral view; D, inner side of coxite; E, spermatheca and spermathecal gland.

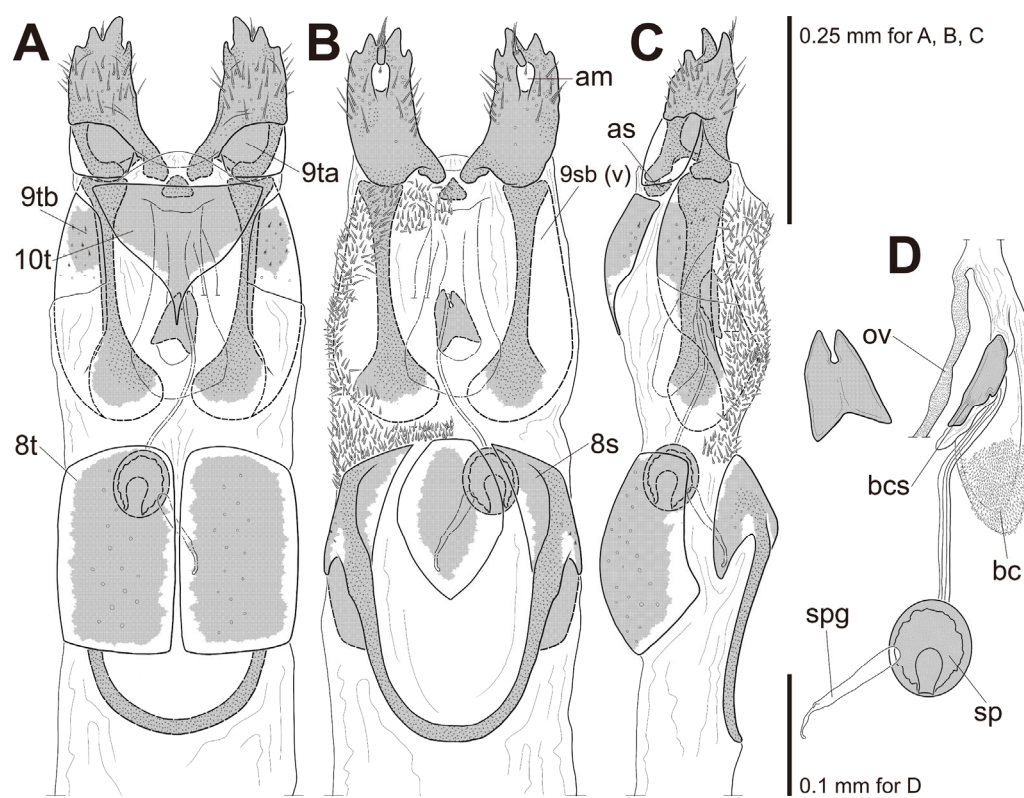


Figure 79. *Epiechinus arboreus* (Lewis, 1884), [TK-23-124]. — A, Dorsal view; B, ventral view; C, left lateral view; D, spermatheca and spermathecal gland.

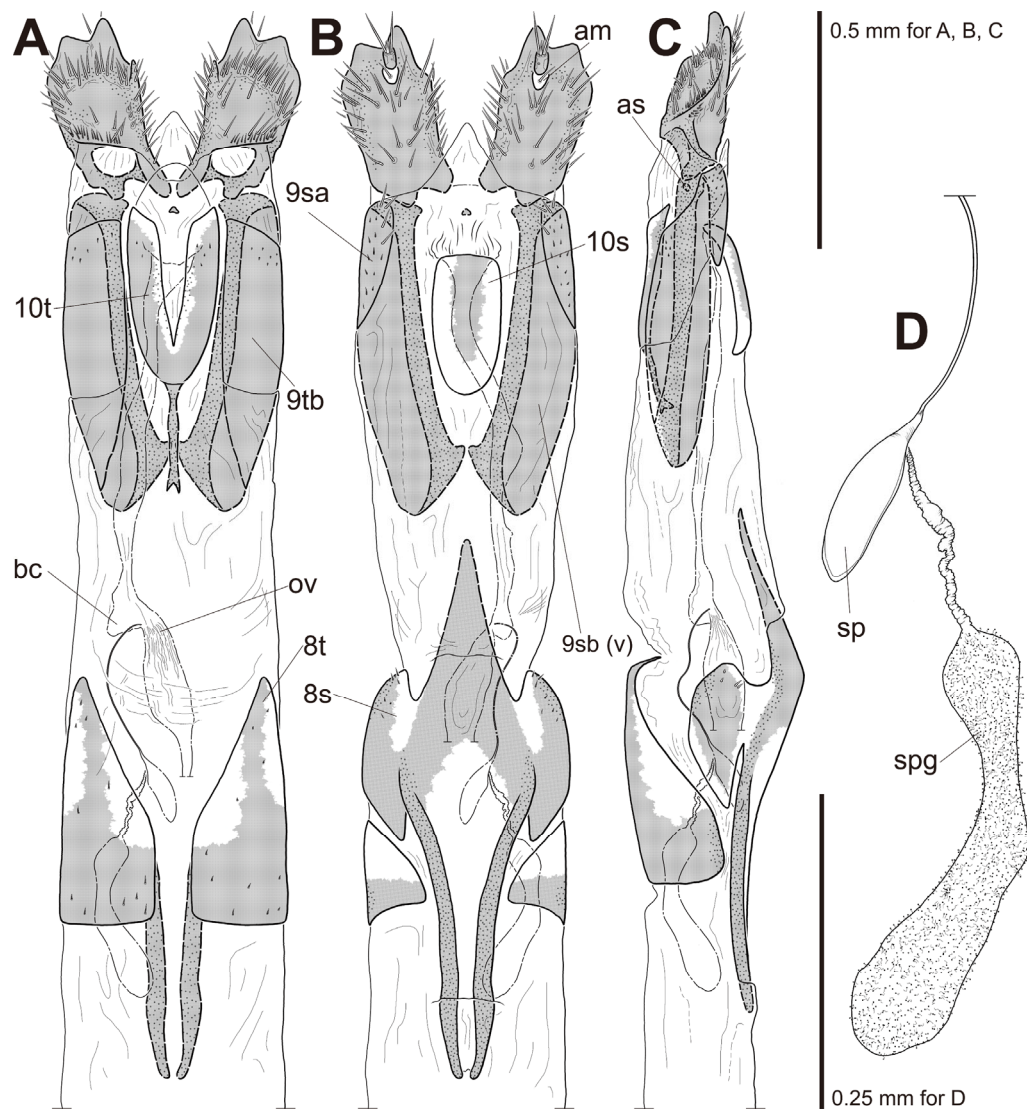


Figure 80. *Onthophilus ostreatus* Lewis, 1879, [TK-23-031]. — A, Dorsal view; B, ventral view; C, left lateral view; D, spermatheca and spermathecal gland.

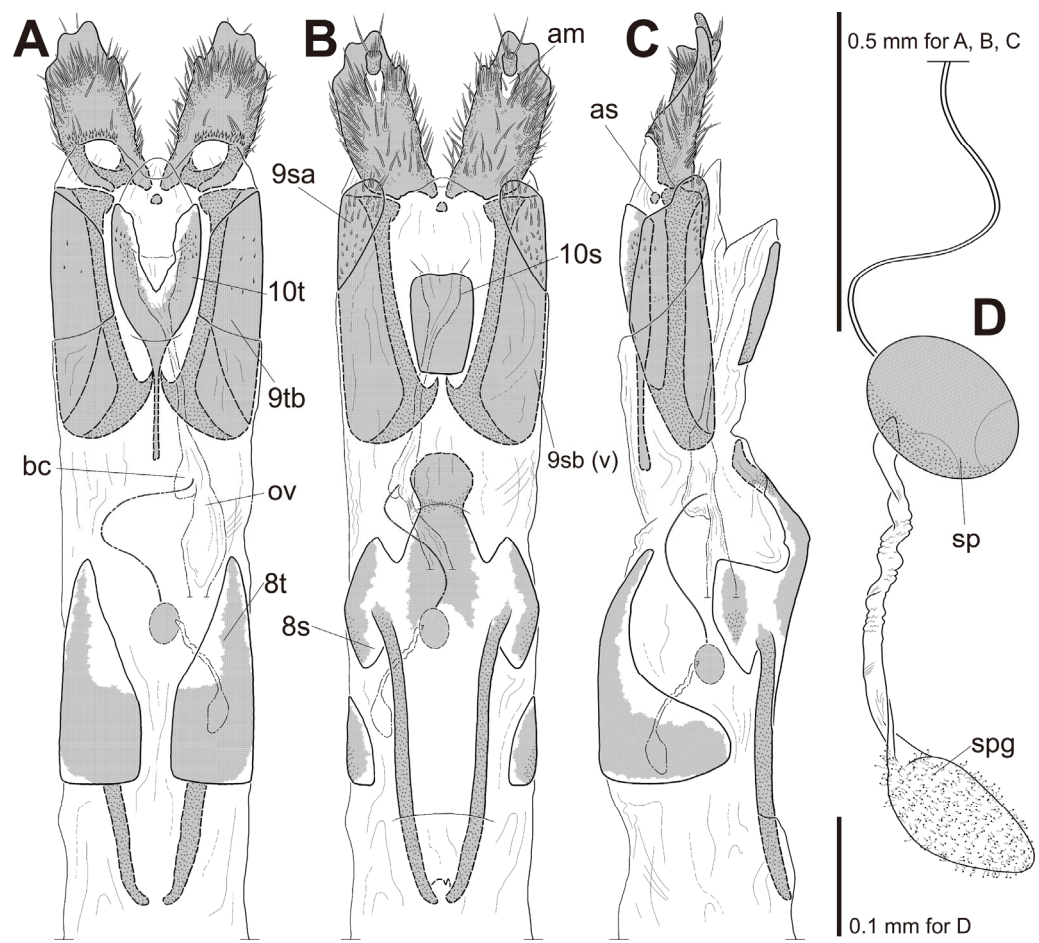


Figure 81. *Onthophilus silvae* Lewis, 1884, [TK- 23-044]. — A, Dorsal view; B, ventral view; C, left lateral view; D, spermatheca and spermathecal gland.

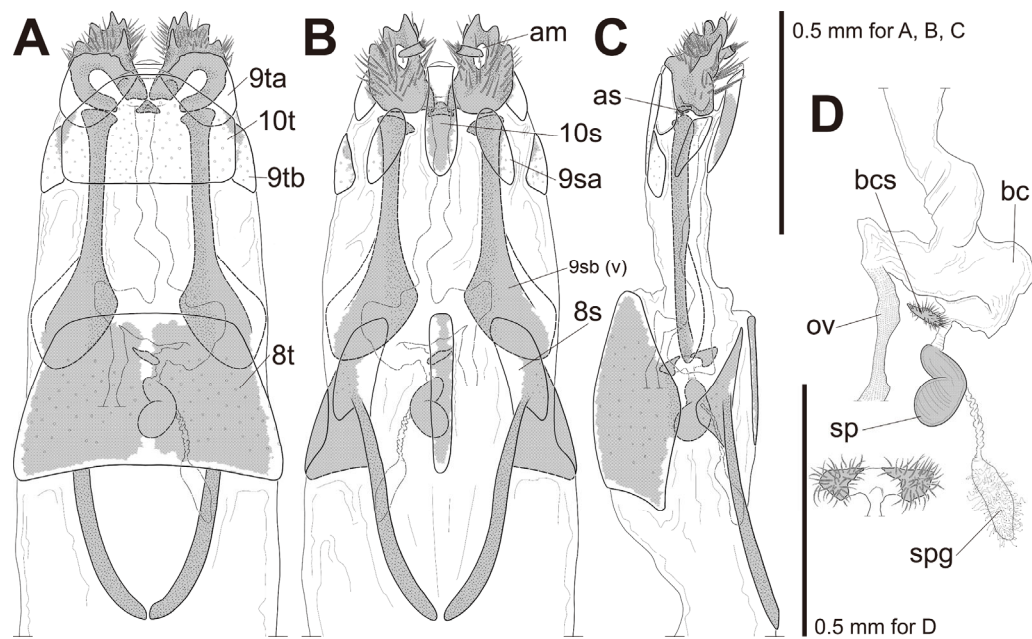


Figure 82. *Baconia chujoi* (Cooman, 1941), [TK-23-071]. — A, Dorsal view; B, ventral view; C, left lateral view; D, spermatheca and spermathecal gland.

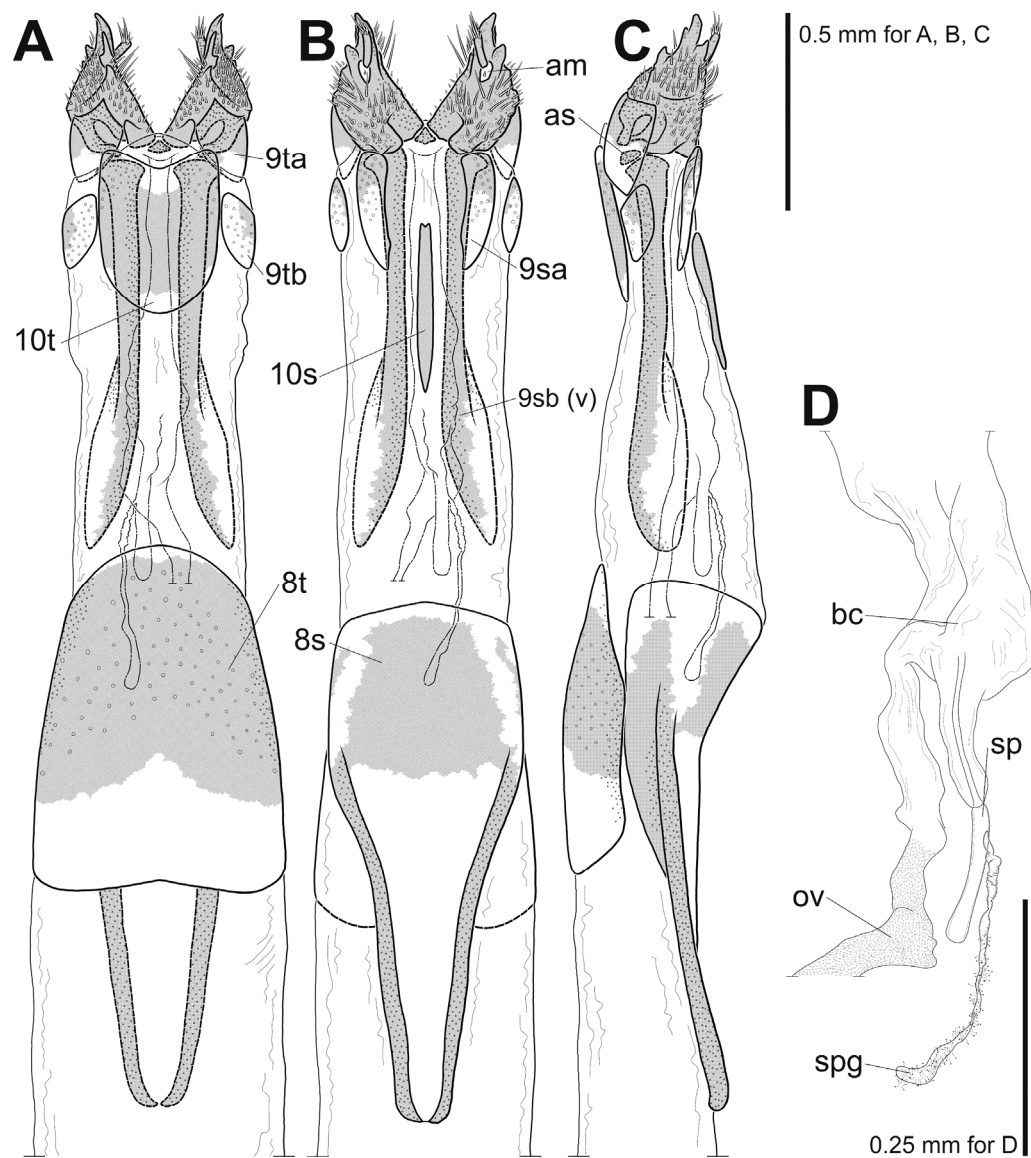


Figure 83. *Notodoma fungorum* Lewis, 1884, [TK-23-076]. — A, Dorsal view; B, ventral view; C, left lateral view; D, spermatheca and spermathecal gland.

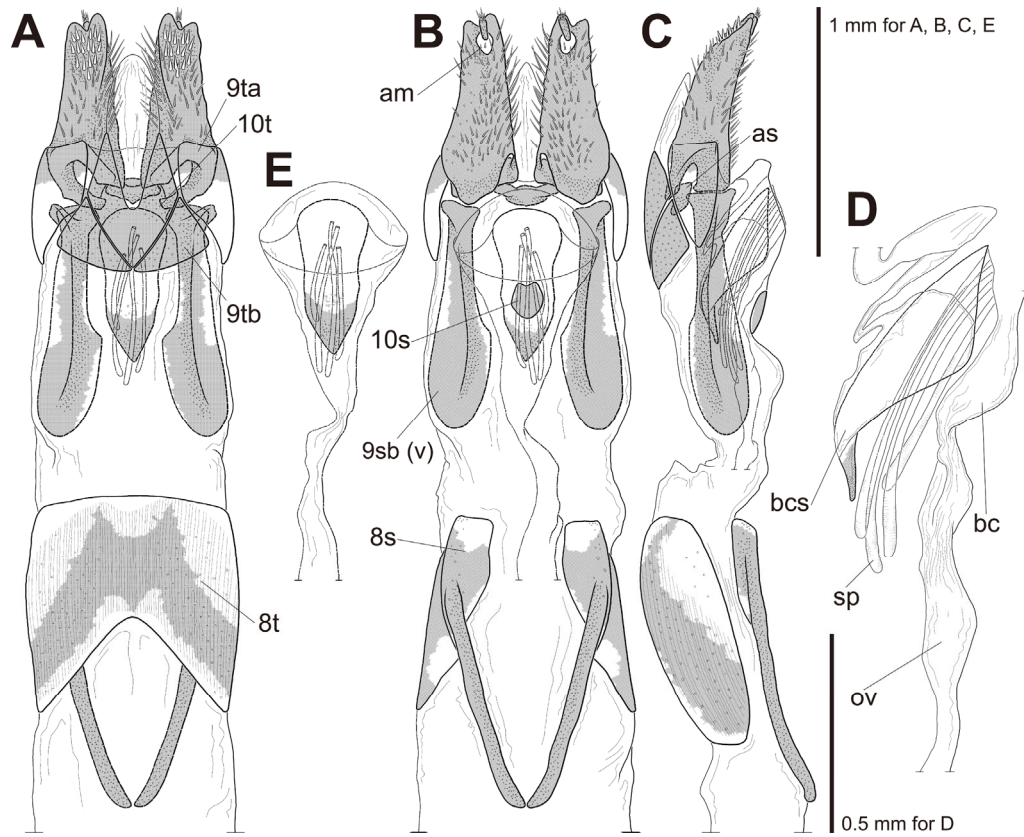


Figure 84. *Atholus duodecimstriatus quatuordecimstriatus* (Gyllenhal, 1808), [TK-23-085]. — A, Dorsal view; B, ventral view; C, left lateral view; D, spermatheca and spermathecal gland, lateral view; E, spermatheca and spermathecal gland, dorsal view.

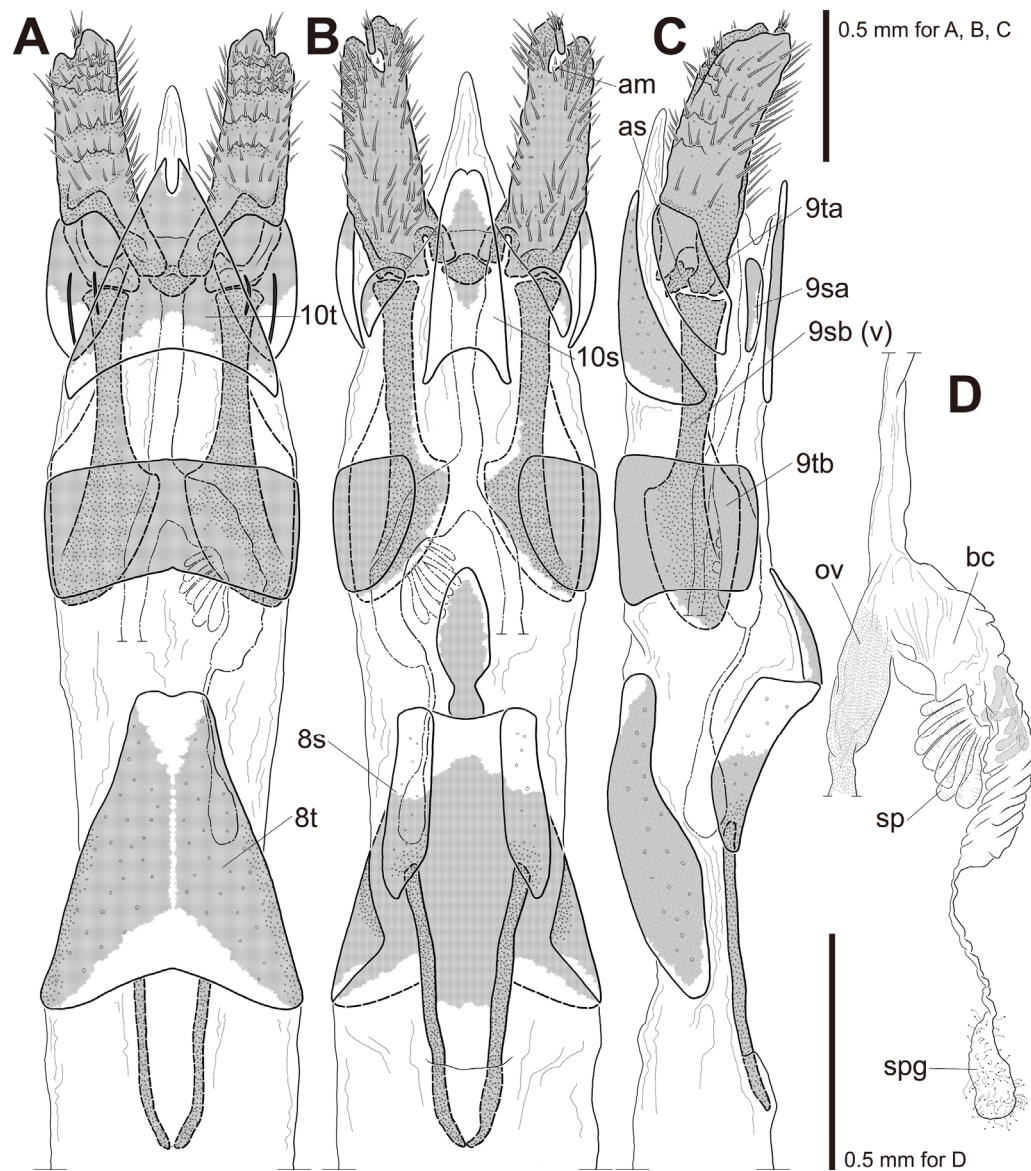


Figure 85. *Margarinotus (Grammostethus) niponicus* (Lewis, 1895), [TK-23-091]. — A, Dorsal view; B, ventral view; C, left lateral view; D, spermatheca and spermathecal gland.

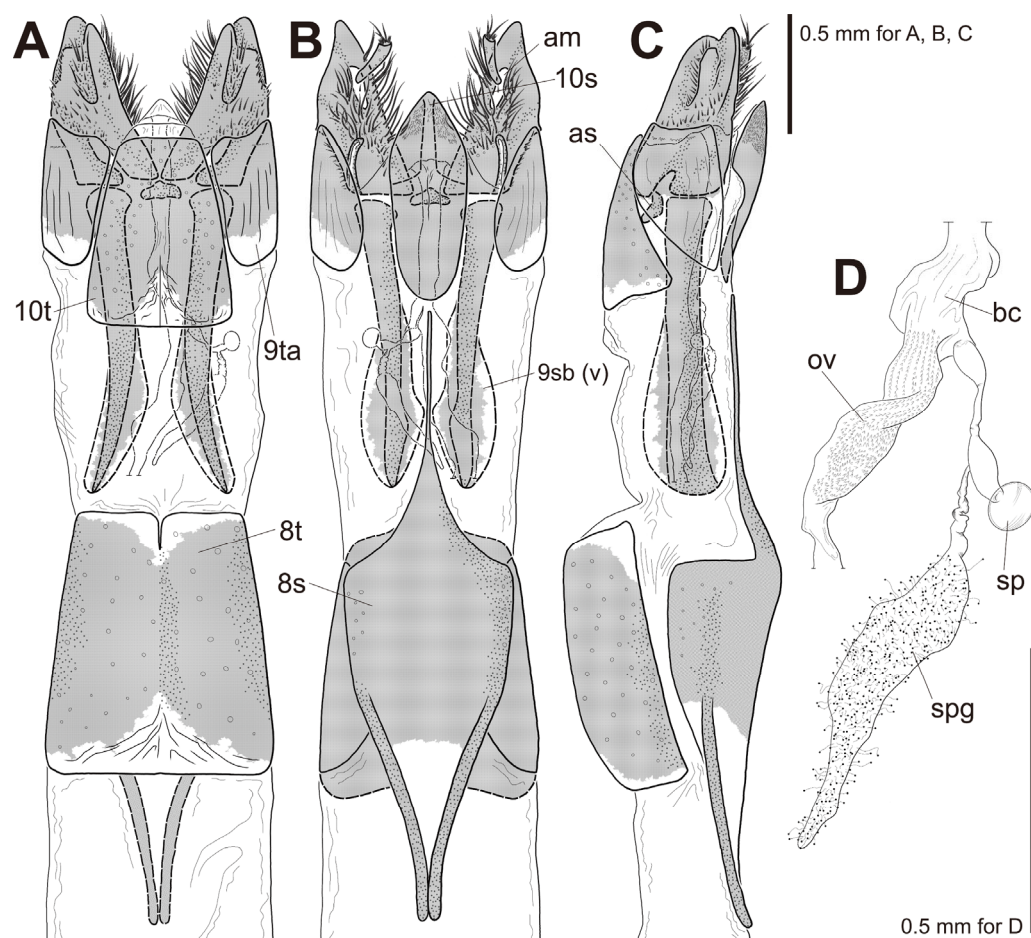


Figure 86. *Hololepta (Hololepta) amurensis* Reitter, 1879, [TK-23-068]. — A, Dorsal view; B, ventral view; C, left lateral view; D, spermatheca and spermathecal gland.

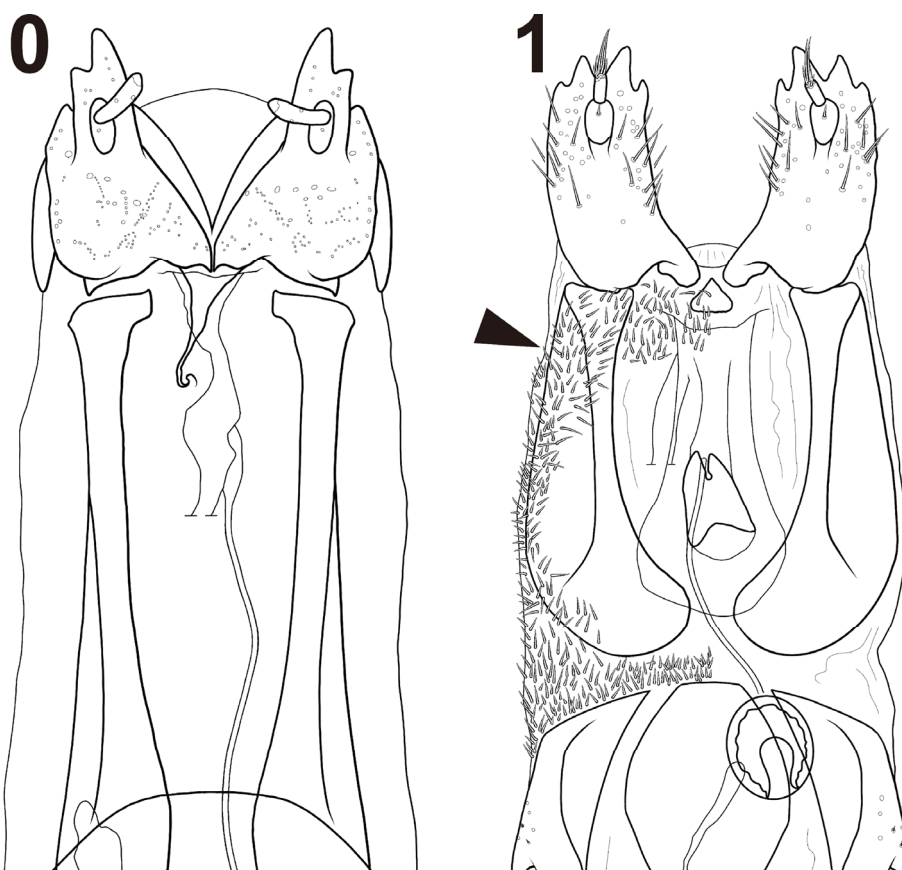


Figure 87. Morphological characters and states used in the analysis. — character 1, membranous region between coxite and eighth tergite, surface: (0) *Plegaderus marseuli*; (1) *Epiechinus arboreus*.

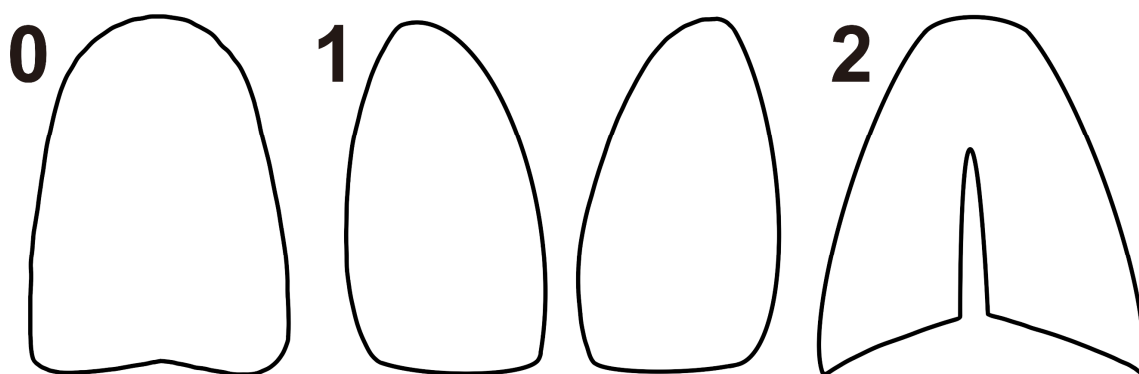


Figure 88. Morphological characters and states used in the analysis. — character 2, eighth tergite, unity: (0) *Notodoma fungorum*; (1) *Anapleus nakanei*; (2) *Hypocaccus* (*Hypocaccus*) *akanensis*.

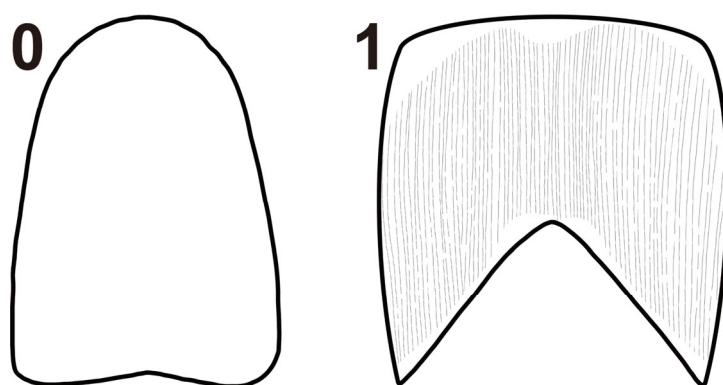


Figure 89. Morphological characters and states used in the analysis. — character 3, eighth tergite, texture: (0) *Notodoma fungorum*; (1) *Atholus duodecimstriatus quatuordecimstriatus*.

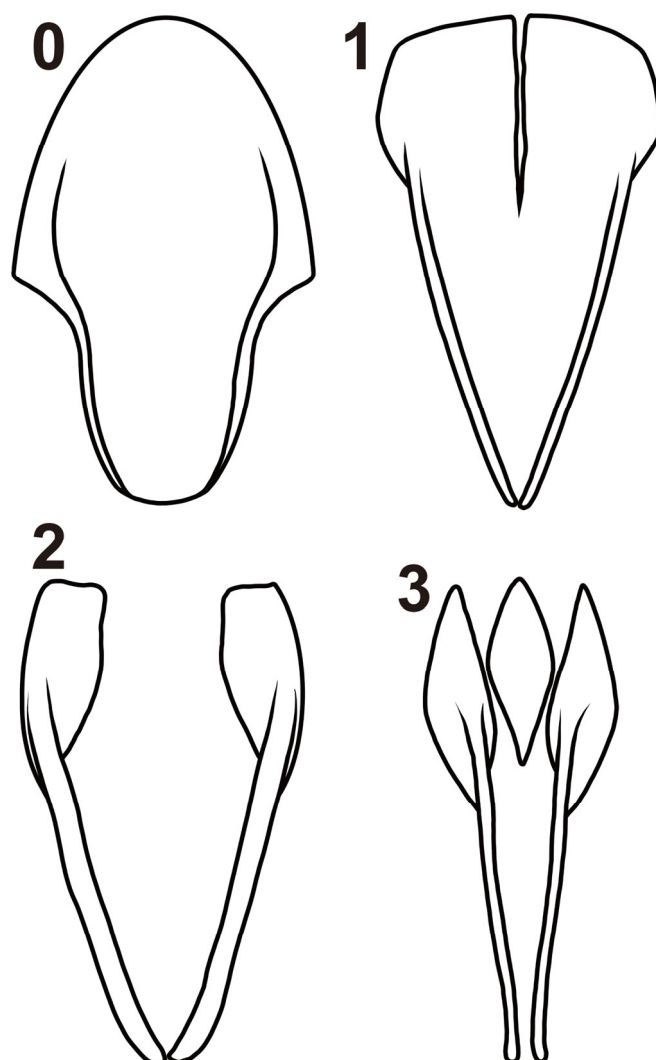


Figure 90. Morphological characters and states used in the analysis. — character 5, eighth sternite, main plate, unity: (0) *Eopachylopus ripae*; (1) *Chaetabraeus* (*Chaetabraeus*) *bonzicus*; (2) *Atholus duodecimstriatus quatuordecimstriatus*; (3) *Paromalus* (*Paromalus*) *parallelepipedus*.

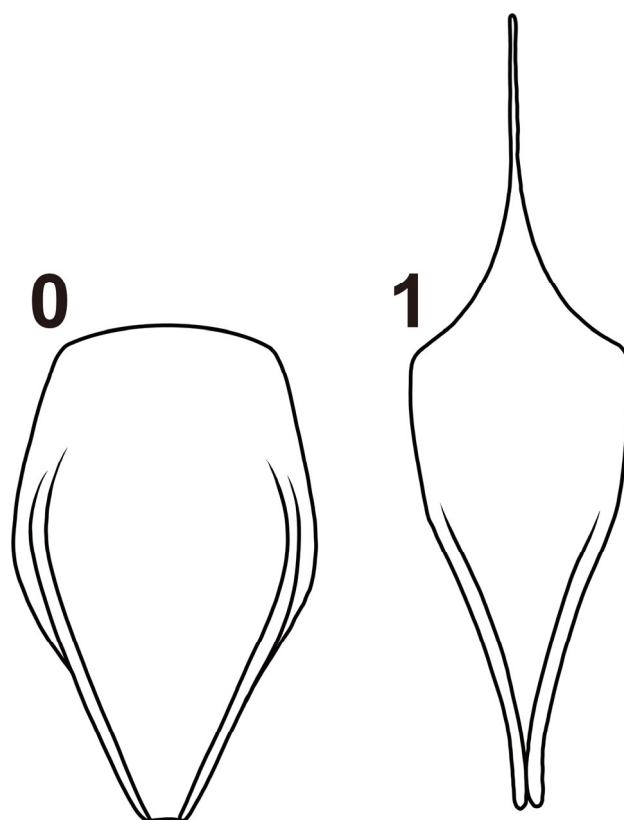


Figure 91. Morphological characters and states used in the analysis. — character 6, eighth sternite, apical margin: (0) *Hypocaccus (Baeckmanniolus) varians varians*; (1) *Hololepta (Hololepta) amurensis*.

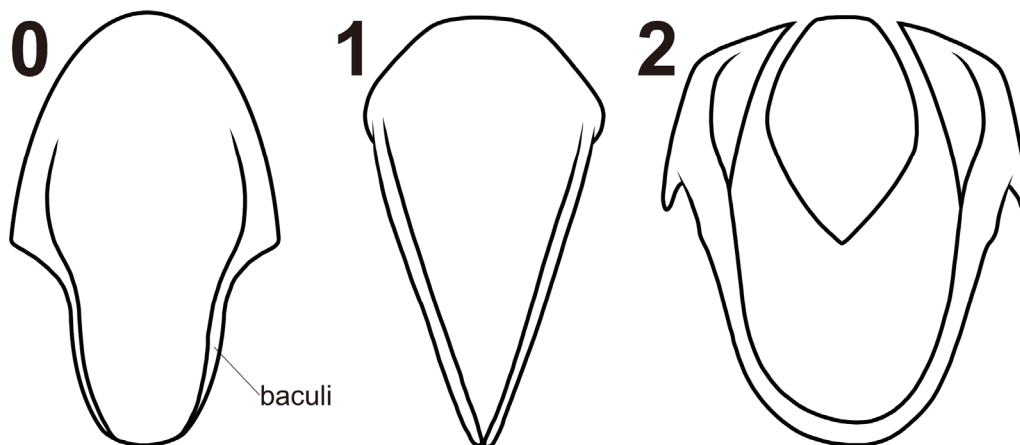


Figure 92. Morphological characters and states used in the analysis. — character 7, eighth sternite, basal baculi, form: (0) *Eopachylopus ripae*; (1) *Plegaderus (Plegaderus) marseuli*; (0) *Epiechinus arboreus*.

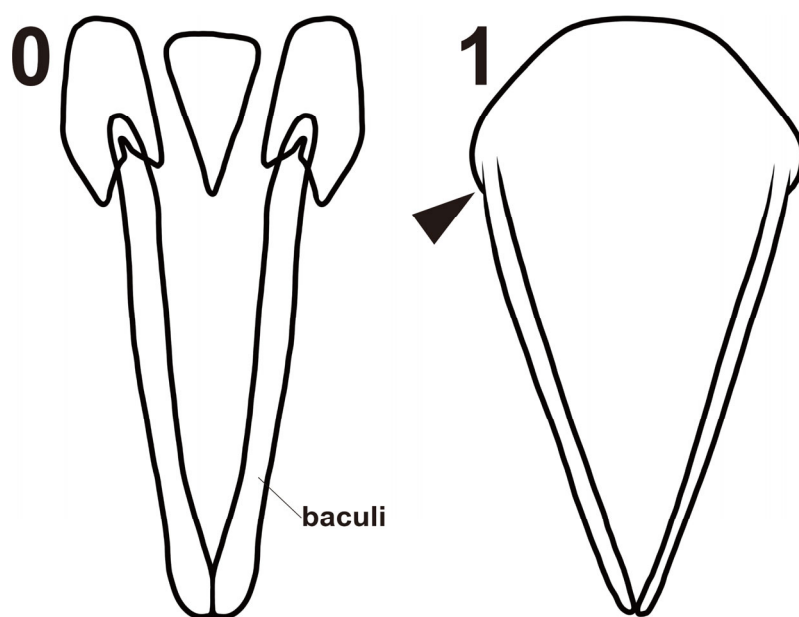


Figure 93. Morphological characters and states used in the analysis. — character 8, eighth sternite, basal baculi: (0) *Niponius osorioceps*; (1) *Plegaderus (Plegaderus) marseuli*.

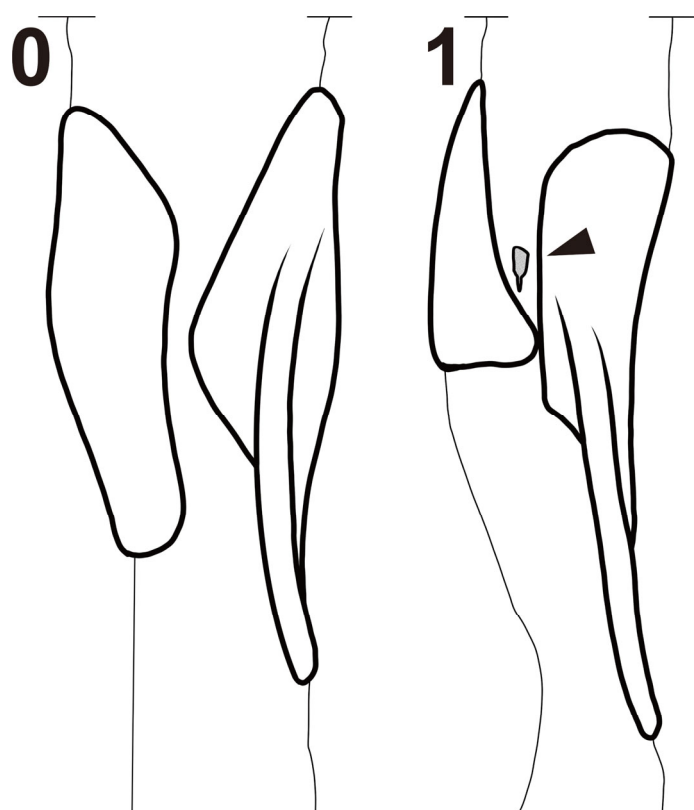


Figure 94. Morphological characters and states used in the analysis. — character 10, sclerites, between eighth tergite and eighth sternite: (0) *Hypocaccus (Hypocaccus) toyoshimai*; (1) *Dendrophilus (Dendrophilus) xavieri*.

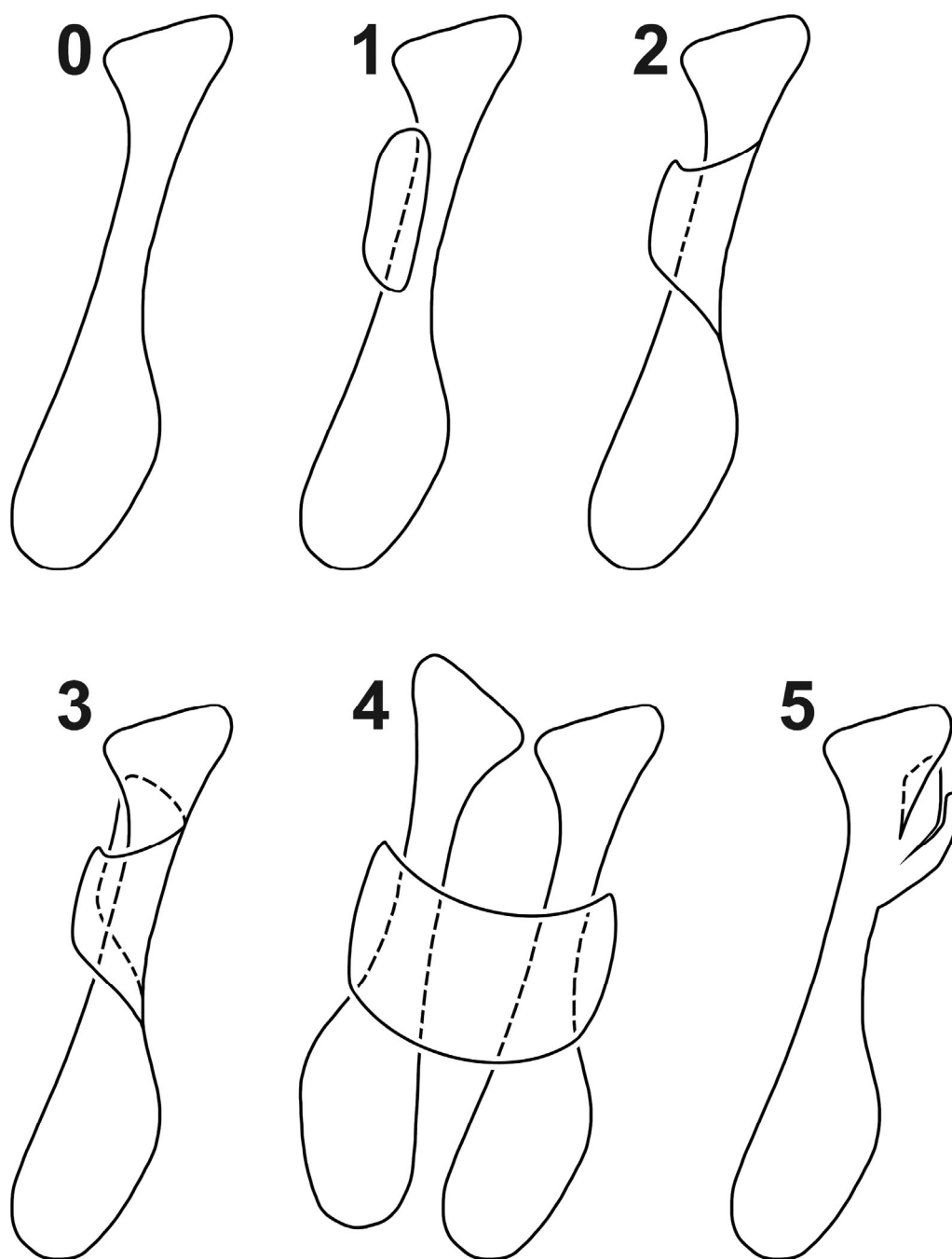


Figure 95. Morphological characters and states used in the analysis. — character 11, ninth tergite in basal direction: Reference image.

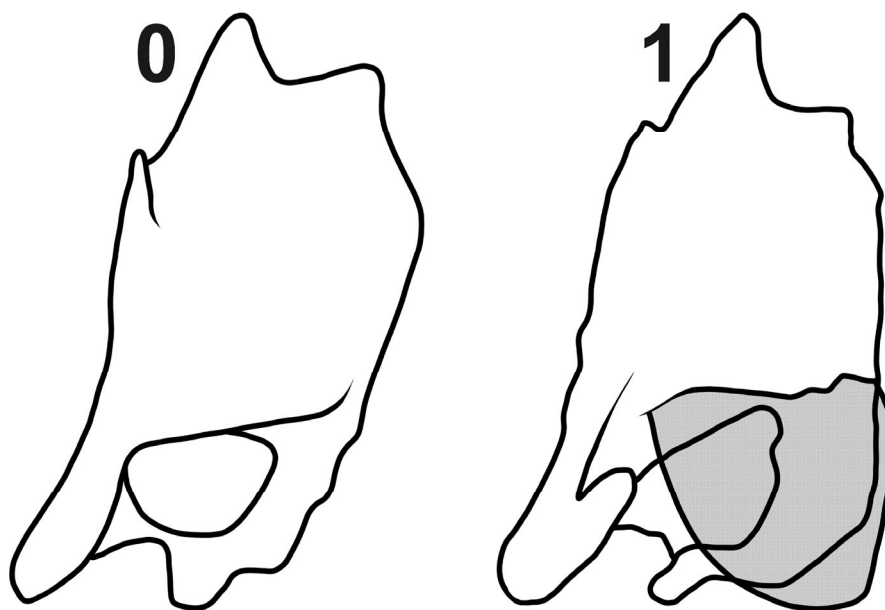


Figure 96. Morphological characters and states used in the analysis. — character 13, ninth tergite in apical direction: (0) *Onthophilus ostreatus*; (1) *Dendrophilus (Dendrophilus) xavieri*.

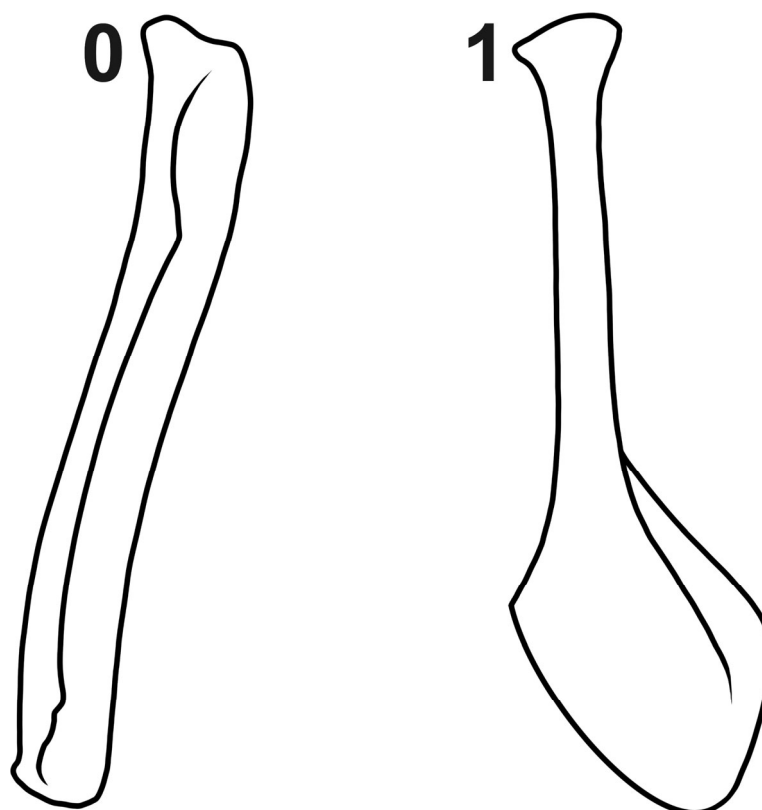


Figure 97. Morphological characters and states used in the analysis. — character 14, ninth sternite in basal direction (valvifer), basal shape: (0) *Epiechinus arboreus*; (1) *Baconia chujoi*.

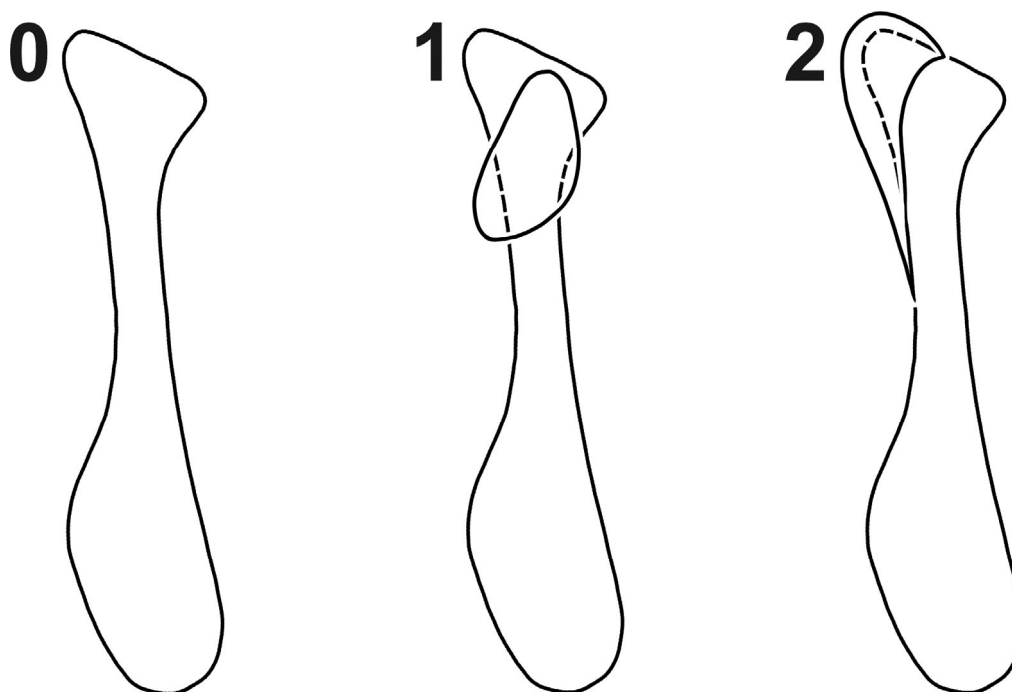


Figure 98. Morphological characters and states used in the analysis. — character 15, ninth sternite in apical direction: Reference image.

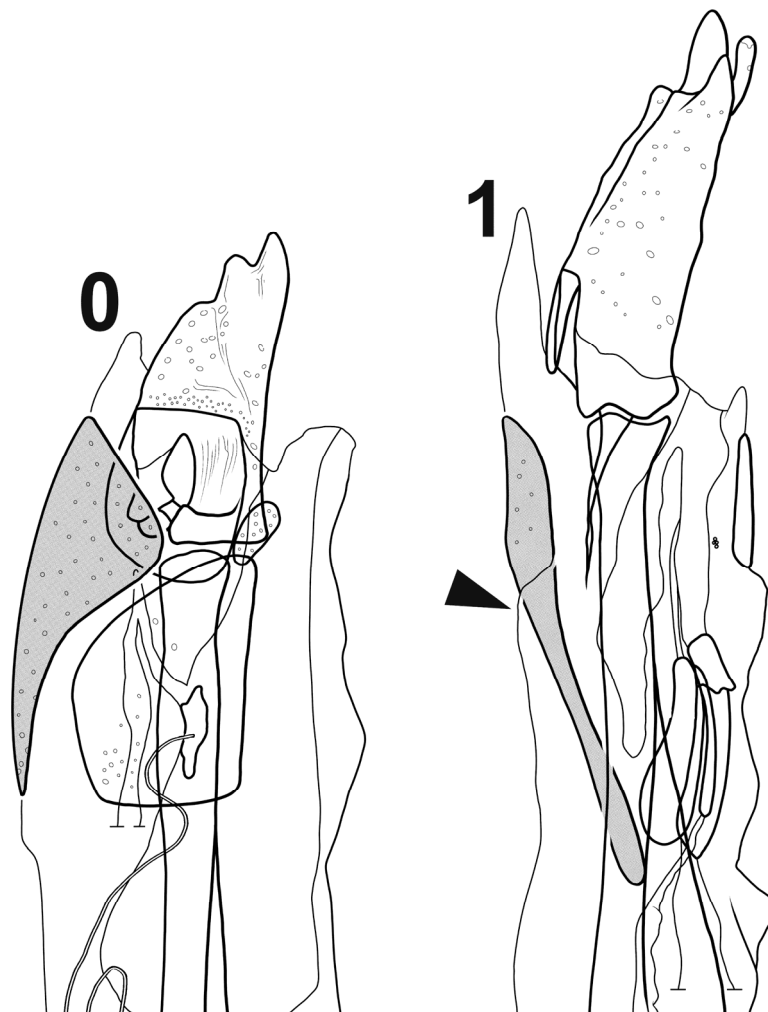


Figure 99. Morphological characters and states used in the analysis. — character 17, tenth tergite, position: (0) *Paromalus (Paromalus) parallelepipedus*; (1) *Chaetabraeus (Chaetabraeus) bonzicus*.

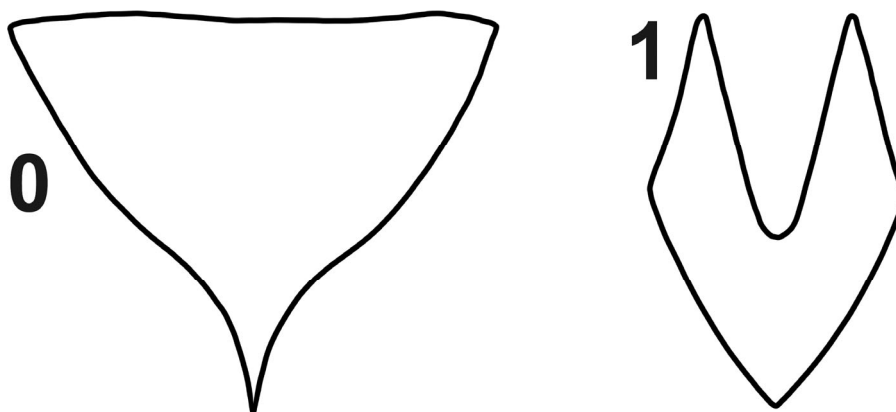


Figure 100. Morphological characters and states used in the analysis. — character 19, tenth tergite, distinct incisions: (0) *Epiechinus arboreus*; (1) *Atholus duodecimstriatus quatuordecimstriatus*.

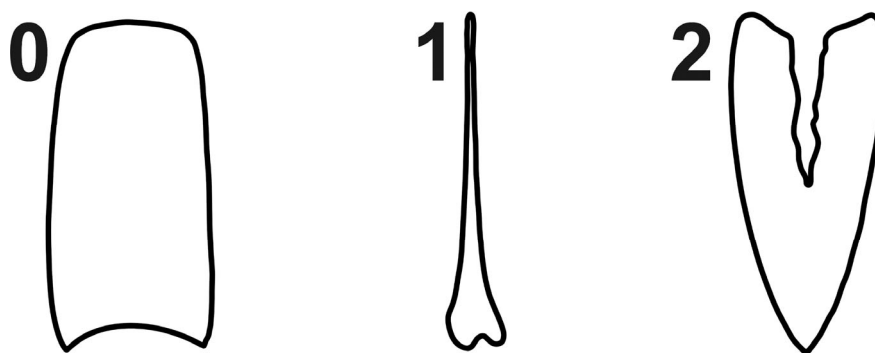


Figure 101. Morphological characters and states used in the analysis. — character 20, tenth sternite: (0) *Chaetabraeus (Chaetabraeus) bonzicus*; (1) *Syntelia histeroides*; (2) *Anapleus nakanei*.

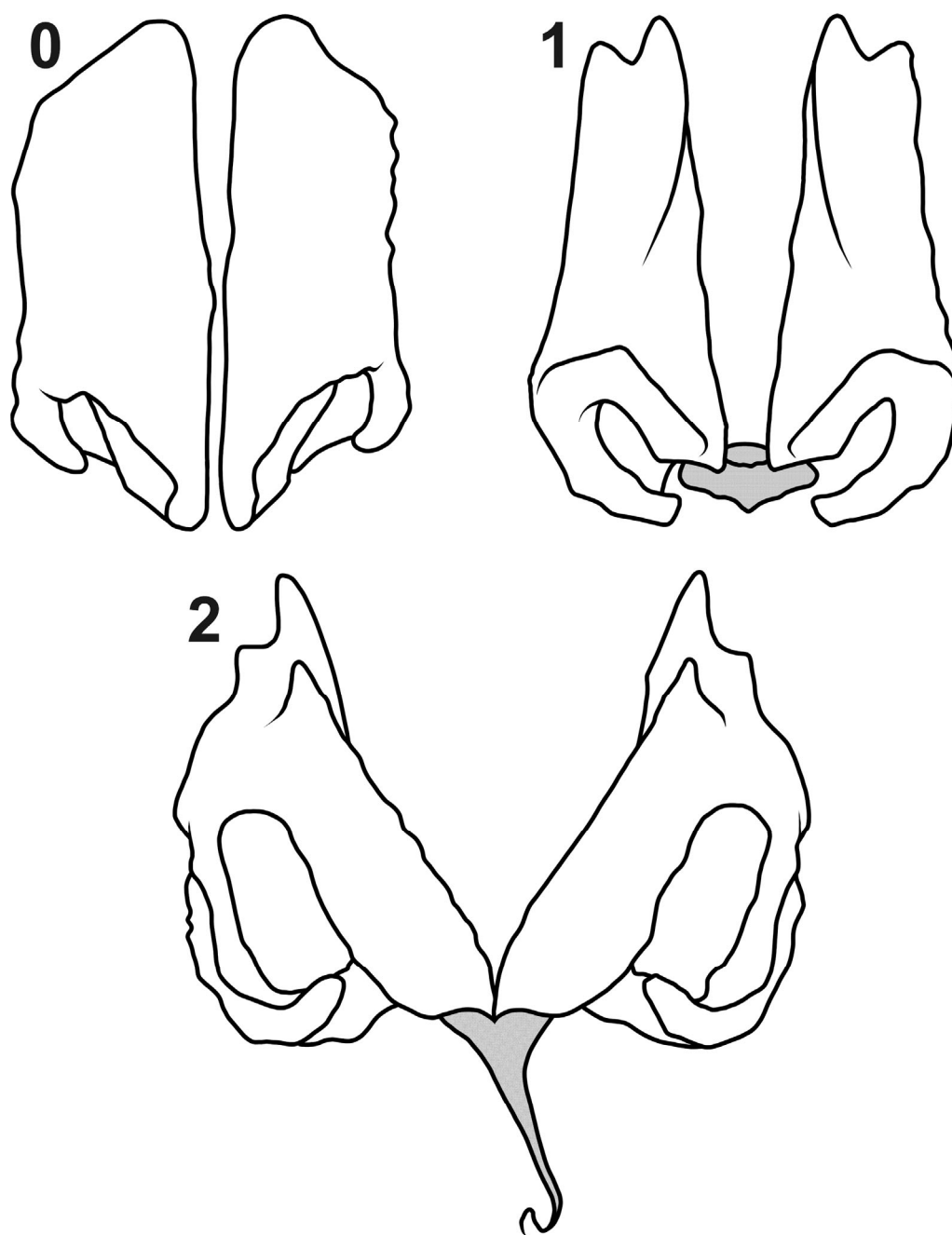


Figure 102. Morphological characters and states used in the analysis. — character 21, articulating sclerite: (0) *Syntelia histeroides*; (1) *Atholus duodecimstriatus quatuordecimstriatus*; (2) *Plegaderus (Plegaderus) marseuli*.

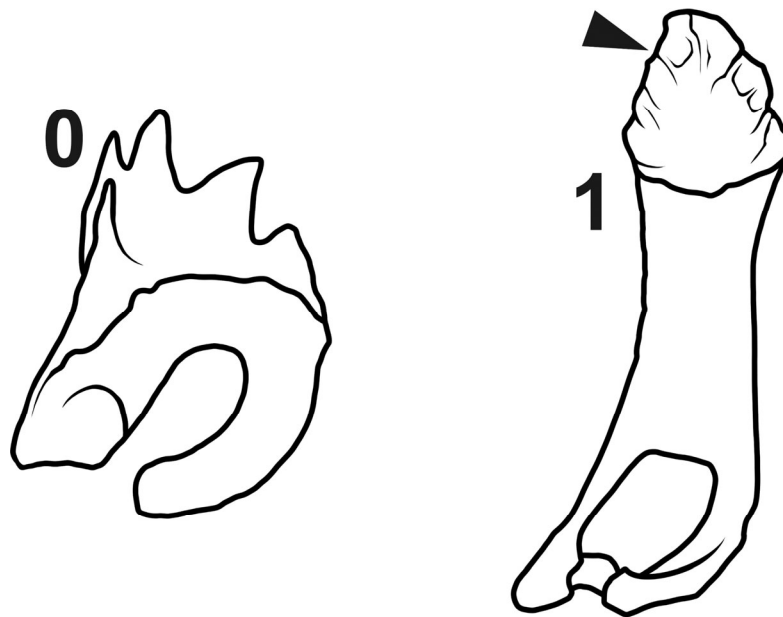


Figure 103. Morphological characters and states used in the analysis. — character 25, coxite, median ridge from apical tooth: (0) *Baconia chujoi*; (1) *Anapleus nakanei*.

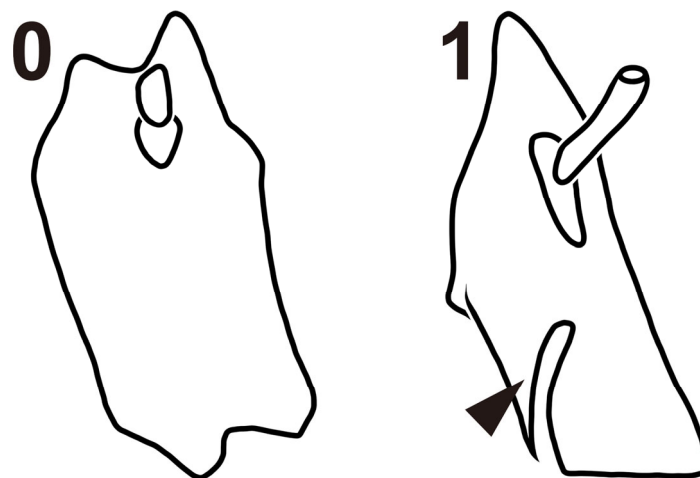


Figure 104. Morphological characters and states used in the analysis. — character 26, coxite, anterior edge: (0) *Onthophilus ostreatus*; (1) *Hololepta (Hololepta) amurensis*.

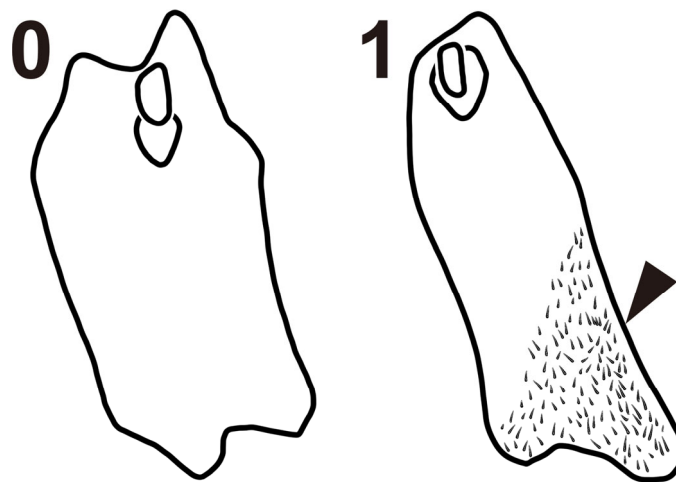


Figure 105. Morphological characters and states used in the analysis. — character 27, coxite, setae on ventral base: (0) *Onthophilus ostreatus*; (1) *Hypocaccus* (*Hypocaccus*) *toyoshimai*.

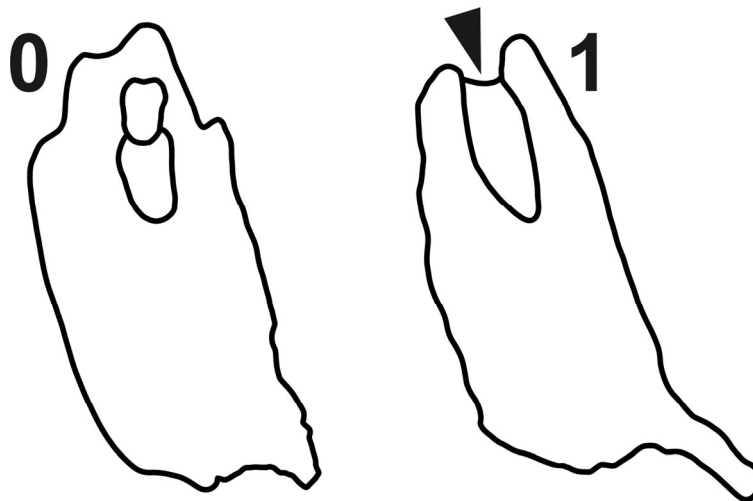


Figure 106. Morphological characters and states used in the analysis. — character 29, coxite, articulation of style: (0) *Onthophilus silvae*; (1) *Eopachylopus ripae*.

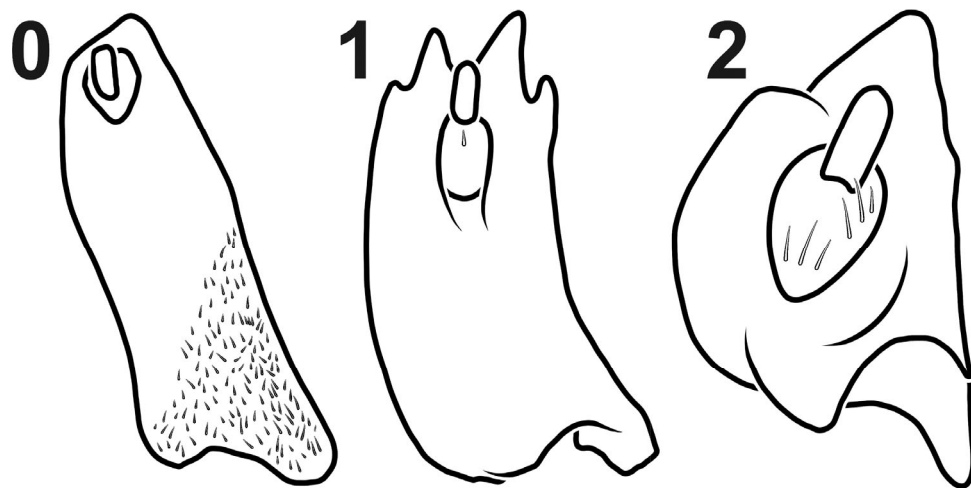


Figure 107. Morphological characters and states used in the analysis. — character 30, articular membrane, setae: (0) *Hypocaccus* (*Hypocaccus*) *toyoshimai*; (1) *Epiechinus arboreus*; (2) *Sphaerites glabratus*.

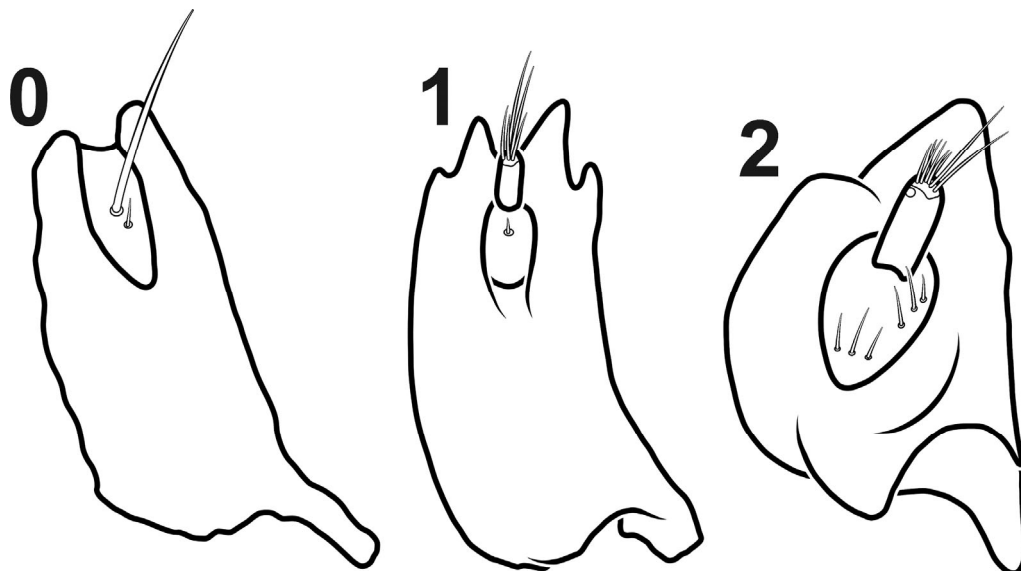


Figure 108. Morphological characters and states used in the analysis. — character 31, stylus: (0) *Eopachylopus ripae*; (1) *Epiechinus arboreus*; (2) *Sphaerites glabratus*.

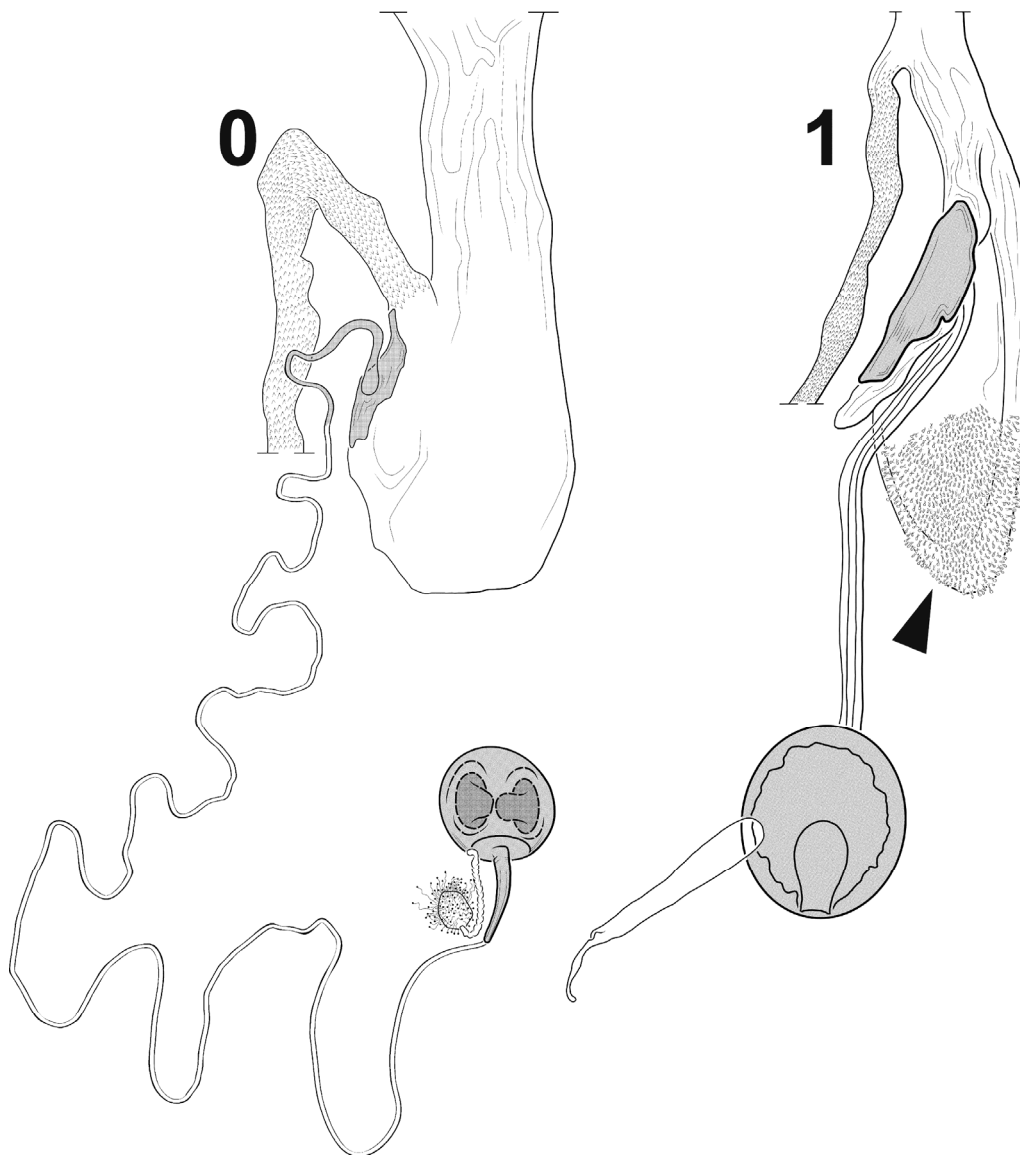


Figure 109. Morphological characters and states used in the analysis. — character 33, bursa copulatrix, round-tipped hairs on surface: (0) *Paromalus (Paromalus) parallelepipedus*; (1) *Epiechinus arboreus*.

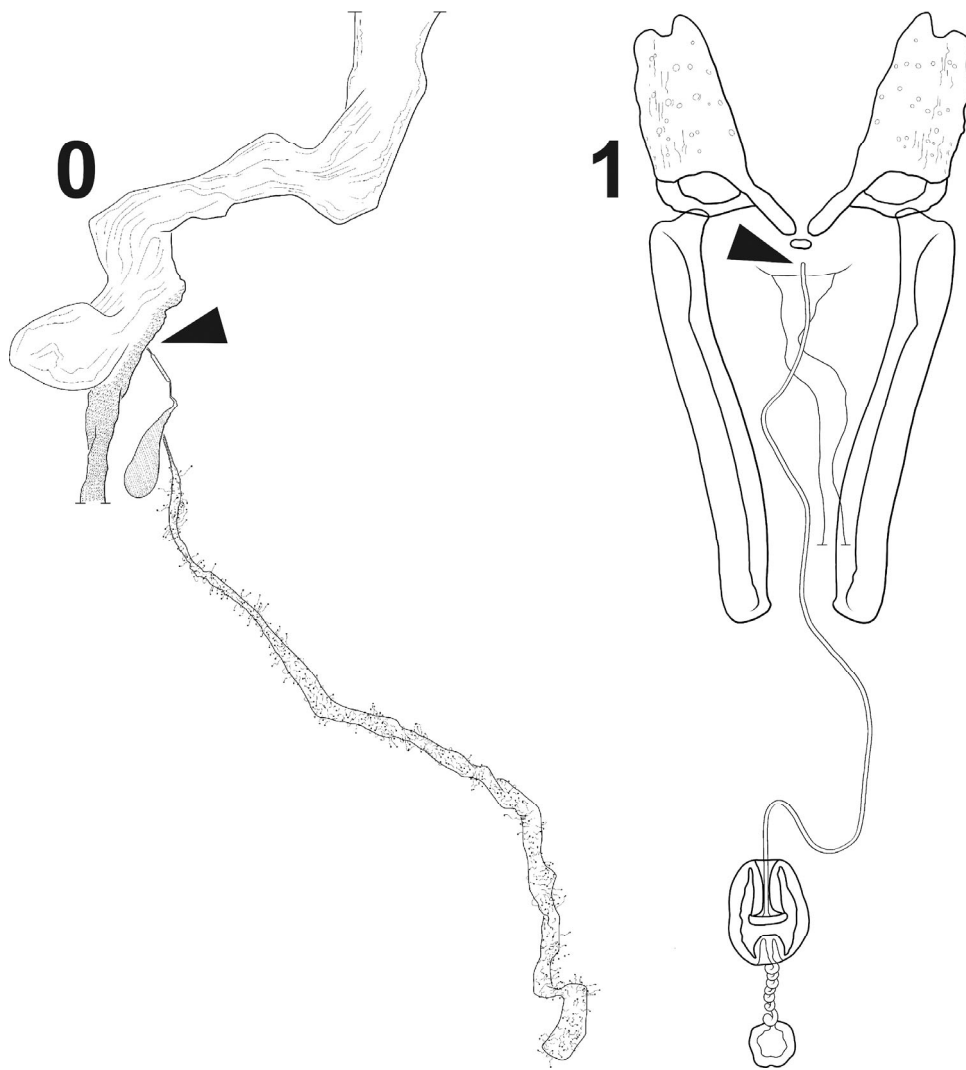


Figure 110. Morphological characters and states used in the analysis. — character 39, spermathecal duct, attachment: (0) *Dendrophilus* (*Dendrophilus*) *xavieri*; (1) *Eopachylopus ripae*.

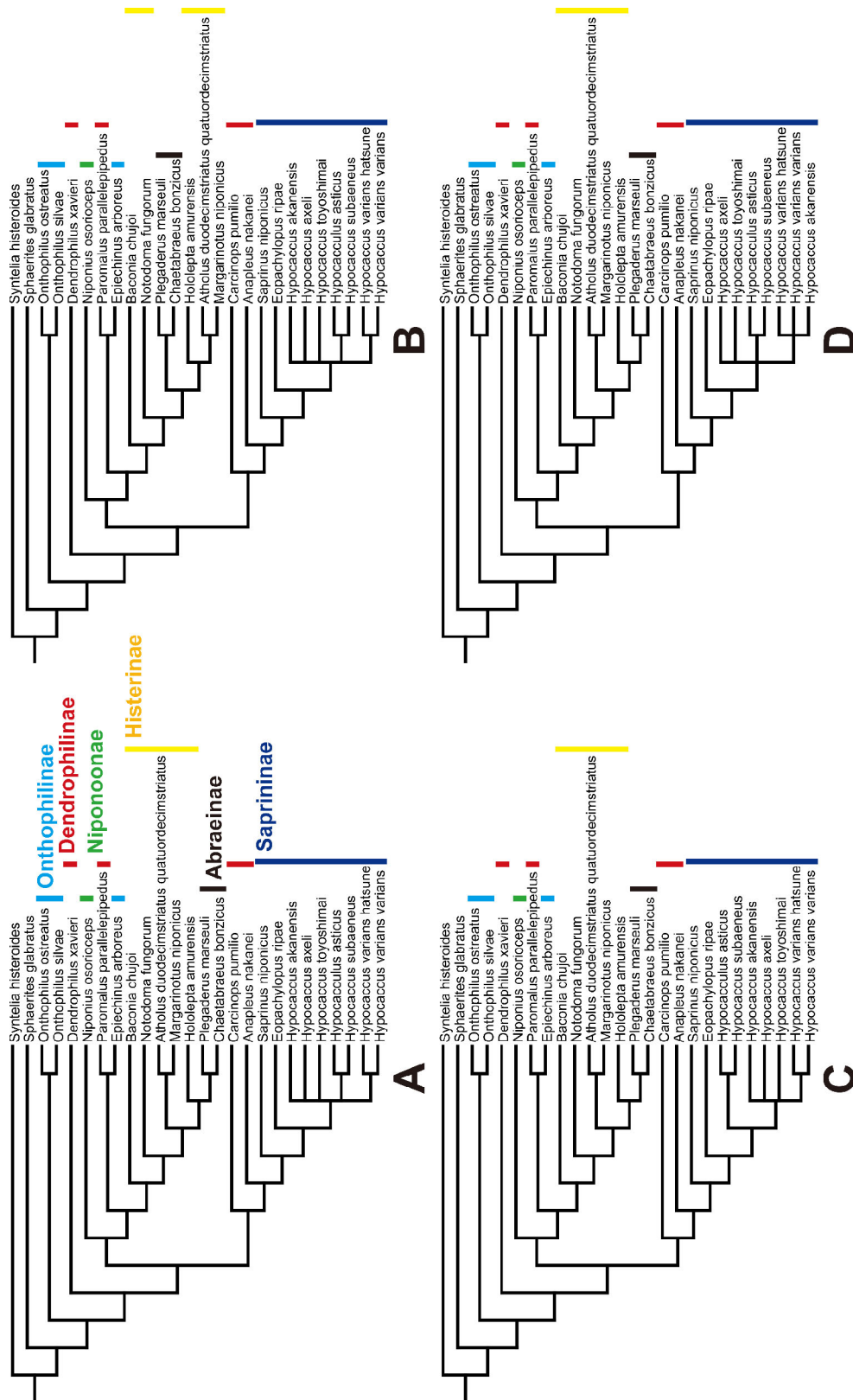


Figure 111. Four trees obtained from cladistic analysis for intergeneric relationships of female genitalia.

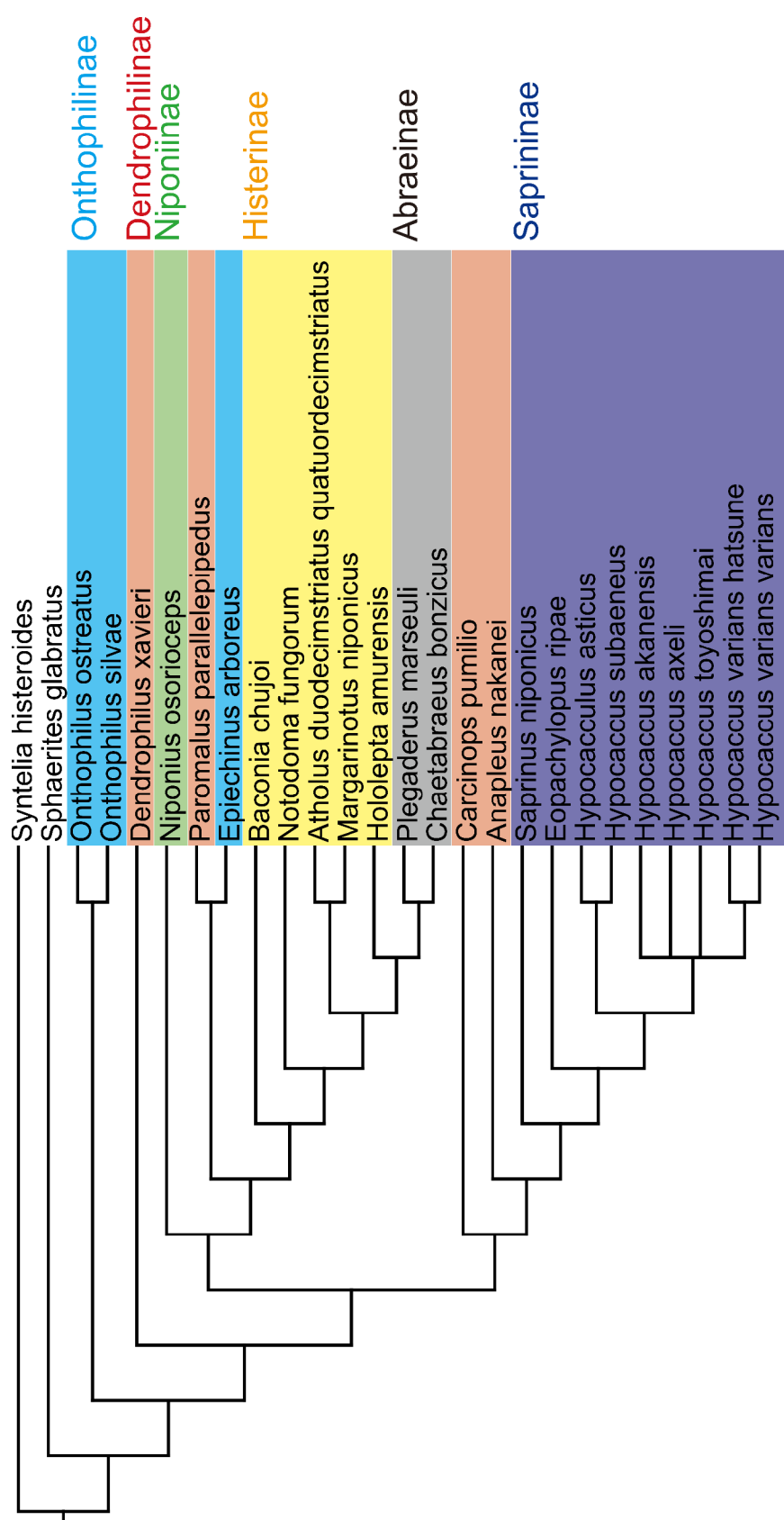


Figure 112. Preferred cladogram of female genitalia.



Figure 113. The cladogram processed for trace character history. — Character 21.

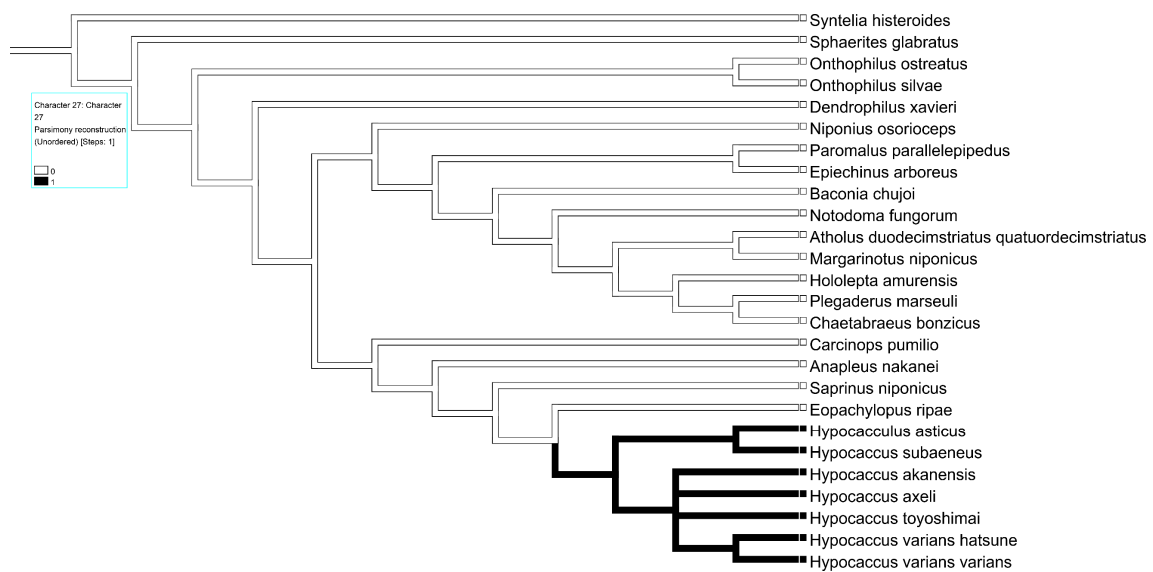


Figure 114. The cladogram processed for trace character history. — Character 27.

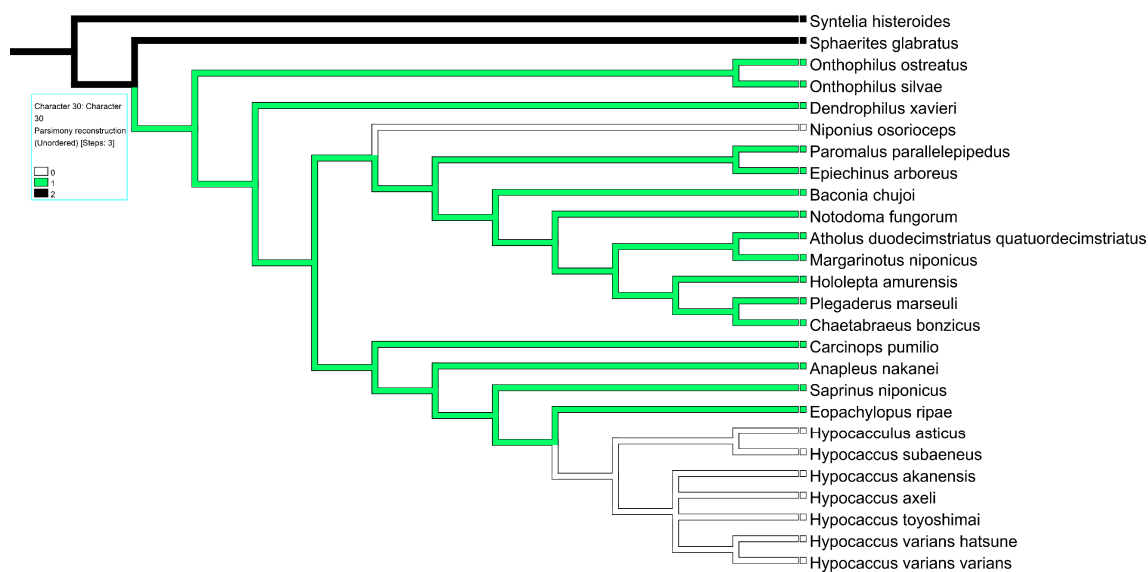


Figure 115. The cladogram processed for trace character history. — Character 30.

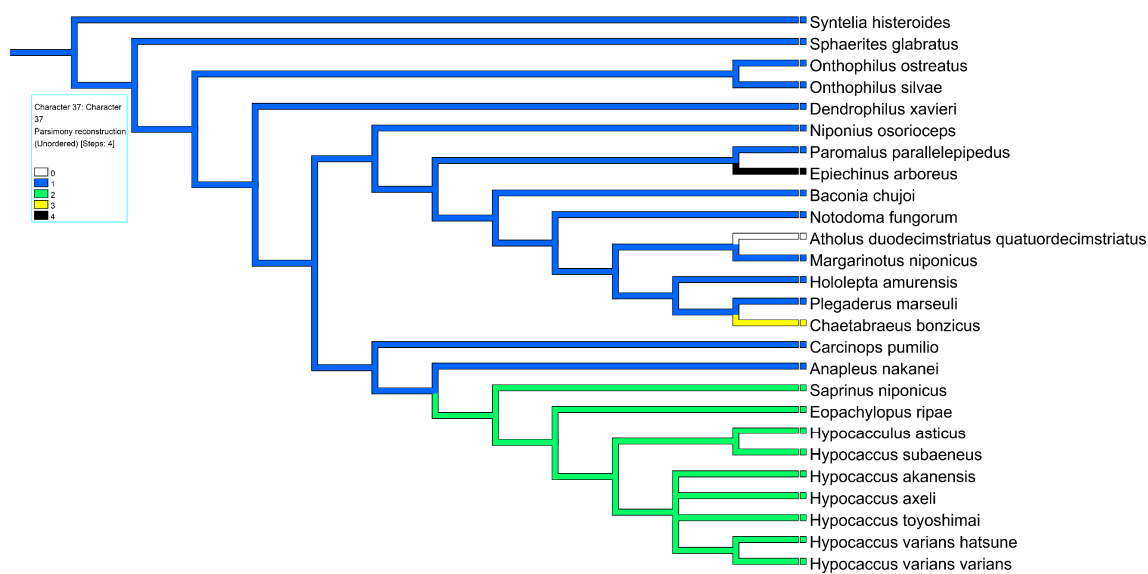


Figure 116. The cladogram processed for trace character history. — Character 37.

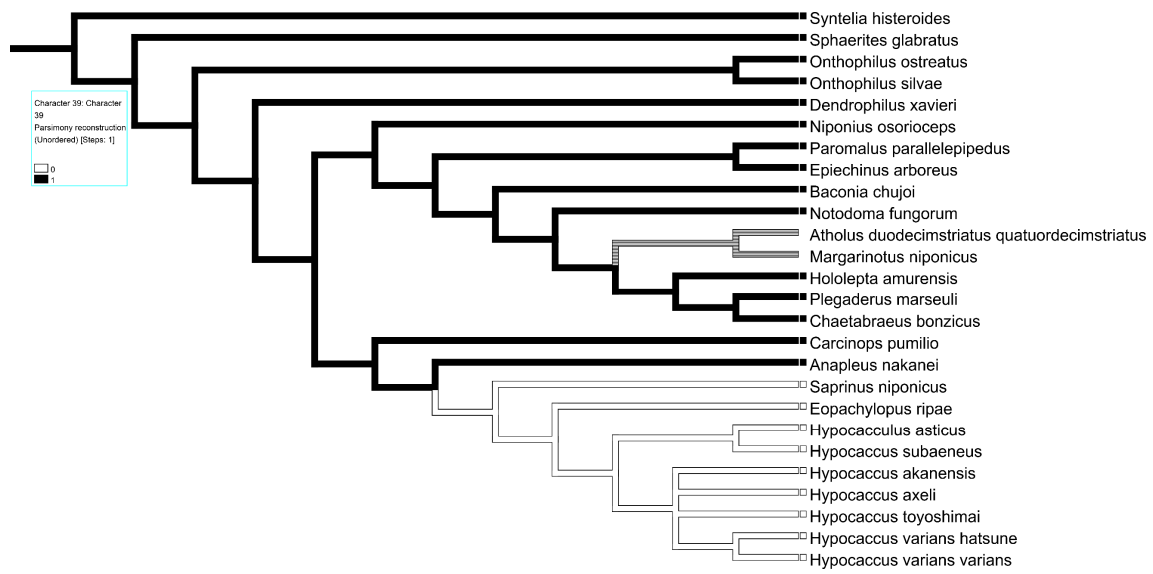


Figure 117. The cladogram processed for trace character history. — Character 39.

Table 1. Terminology used by multiple authors regarding mouthparts within the superfamily Histeroidea.

Williams, 1936	Lackner, 2010	Kikuchi, 2023
-	labrum	labrum
-	labral fold	-
-	labral process	-
-	mandibles	mandibles
mentum	mentum	mentum
submentum	submentum	submentum
labium	labium	labium
-	basal extension	-
labial palp	-	labial palp
palpiger	labial palpiger	-
ligula	ligula	ligula
-	paraglossa	-
-	terminal labial palpomere	-
maxilla	maxilla	maxilla
cardo	cardo	cardo
basigalea	-	basigalea
basistipes	stipes	basistipes
distigalea	galea	distigalea
lacinia	lacinia	lacinia
-	lacinial hook	lacinial hook
maxillary palpus	-	maxillary palpus
mediostipes	-	mediostipes
-	palpal organ	palpal organ
palpifer	-	palpifer
-	terminal maxillary palpomere	-
-	-	hypopharynx

Table 2. Terminology used by multiple authors regarding female genitalia within the superfamily Histeroidea.

Óhara, 1989	Óhara, 1994	Caterino & Tishechkin, 2015	Lackner & Tarasov, 2019 B	В настоящей работе, 2022	Kikuchi, 2023
-	-	eighth tergite	eighth tergite	-	eighth tergite
-	-	eighth sternite	eighth sternite	-	eighth sternite
-	-	median plate of eighth sternite	-	-	-
vagina	vagina	basal baculi of eighth sternite	basal baculi of eighth sternite	-	basal baculi
-	ovary	-	-	-	eighth abdominal sternite sclerites
-	-	-	-	-	ninth tergite located in basal direction
-	-	-	-	-	ninth tergite located in apical direction
valvifer	-	valvifer	valvifer	valvifer	ninth sternite located in basal direction (valvifer)
-	-	-	-	-	ninth sternite located in apical direction
-	-	basal attachment of ninth sternite	-	-	-
-	-	paraproct	-	-	tenth tergite
-	-	-	-	ventral-medial plate	tenth sternite
coxite	-	-	-	articular membrane	articular membrane
-	-	coxite	gonocoxite	gonocoxite	coxite
-	-	-	-	outskirts of coxite	-
-	-	-	-	apical excision of coxite	-
stylus	-	gonostylus	gonostylus	stylus	stylus
-	-	coxite articulating sclerite	articulating sclerite	articulating sclerite	articulating sclerite
-	-	common oviduct	-	-	common oviduct
spermatheca	spermatheca	spermatheca	spermatheca	spermatheca	spermatheca
-	spermatheca gland	spermatheca gland	spermatheca gland	-	spermatheca gland
-	-	-	spermatheca duct	-	spermatheca duct
bursa copulatrix	bursa copulatrix	bursa copulatrix	bursa copulatrix	bursa copulatrix	bursa copulatrix
-	-	-	-	-	bursa copulatrix sclerite
vulva	-	-	-	-	-

Table 3. Morphological data for the taxa included in this study

Table 6: Morphological characters for the taxa included in this study																																									
Character:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39		
<i>Sphaerites glabratus</i>	0	1	0	0	1	0	1	1	0	0	3	2	0	1	1	1	0	2	0	0	1	0	0	1	0	0	0	1	0	2	2	0	0	0	0	0	0	1	1	1	
<i>Syntelia histeroides</i>	0	0	0	1	0	1	1	1	0	0	3	1	0	1	1	0	1	0	2	0	1	0	2	0	0	0	0	0	0	0	2	1	0	0	0	0	0	1	1	1	
<i>Nipontius osorioceps</i>	0	0	0	0	3	0	1	0	1	0	1	0	1	0	1	0	0	0	0	0	1	0	1	3	1	0	0	0	0	0	0	0	0	0	3	1	0	1	1	1	
<i>Plegaderus marseuli</i>	0	0	0	0	0	0	1	1	0	0	0	-	1	0	0	-	0	0	1	0	2	1	0	2	0	0	0	0	1	0	1	1	0	0	1	0	1	0	1	1	
<i>Chaetabraeus bonzius</i>	0	1	0	0	1	0	1	1	0	0	0	-	1	0	0	-	1	0	0	1	2	1	0	2	0	0	0	0	1	0	1	1	1	0	4	1	0	3	1	1	
<i>Eopachylopus ripae</i>	0	1	0	0	0	0	1	0	0	1	0	0	1	2	0	0	0	0	0	1	1	0	1	0	1	0	0	1	1	1	0	2	0	0	1	0	2	2	0	0	
<i>Hypocacculus asticus</i>	0	2	0	0	0	0	1	1	0	0	1	1	1	2	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	0	0	1	2	0	0	1	0	2	2	0	
<i>Hypocacculus varians hatsune</i>	0	2	0	0	0	0	1	1	2	0	1	0	1	0	2	0	0	0	0	0	1	1	0	0	0	0	0	1	1	0	0	1	2	0	0	1	0	2	2	0	
<i>Hypocacculus varians varians</i>	0	2	0	0	0	0	1	1	2	0	1	0	1	0	2	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	0	1	2	0	0	1	0	2	2	0	
<i>Hypocacculus akanensis</i>	0	2	0	0	0	0	1	1	4	0	1	0	1	0	2	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	0	1	2	0	0	1	0	2	2	0	
<i>Hypocacculus axeli</i>	0	2	0	0	0	0	1	1	0	1	0	1	0	1	0	2	0	0	0	0	1	1	0	0	0	0	0	1	1	0	0	1	2	0	0	1	0	2	2	0	
<i>Hypocacculus subaeneus</i>	0	2	0	0	0	0	1	1	0	0	1	1	1	1	2	1	0	0	0	0	1	1	0	0	0	0	0	1	1	0	0	1	2	0	0	1	0	2	2	0	
<i>Hypocacculus toyoshimai</i>	0	2	0	0	0	0	1	1	0	0	1	0	1	0	2	0	0	0	0	0	1	1	0	0	0	0	0	1	1	0	0	1	2	0	0	1	0	2	2	0	
<i>Saprinus niponicus</i>	0	0	0	0	0	0	1	1	1	5	0	1	0	1	0	0	0	1	0	1	0	1	1	0	0	0	0	0	0	0	0	1	2	0	0	1	0	2	2	0	
<i>Anapleus nakanei</i>	0	1	0	1	0	0	0	1	0	0	1	0	1	1	0	0	0	0	1	3	1	1	0	0	1	0	0	0	0	0	0	1	2	0	0	1	0	1	2	1	
<i>Dendrophilus xavieri</i>	0	2	0	0	1	0	1	1	3	1	3	0	1	1	0	1	0	0	1	0	0	1	1	0	2	0	0	0	0	0	0	1	1	0	0	0	0	1	1	1	
<i>Carcinops pumilio</i>	0	1	0	0	1	1	1	1	0	1	1	0	1	0	1	0	0	0	0	1	0	1	1	1	3	0	0	0	0	0	0	1	1	0	0	2	1	0	1	2	1
<i>Paromalus parallelepipatus</i>	0	0	0	0	3	0	1	1	0	0	1	0	1	0	1	0	0	0	0	0	1	1	1	1	1	0	0	0	1	0	1	0	1	0	2	1	0	1	2	1	
<i>Epiechinus arboreus</i>	1	1	0	0	3	0	2	1	4	0	2	1	1	0	0	-	0	0	0	0	1	1	0	3	0	0	0	0	1	0	1	1	1	1	1	2	1	0	4	1	1
<i>Onthophilus ostreatus</i>	0	1	0	2	1	1	1	1	4	0	3	1	0	1	1	2	1	1	1	1	1	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0	0	1	1	1	
<i>Onthophilus silvae</i>	0	1	0	0	1	1	1	0	0	3	1	0	1	0	1	2	1	1	1	1	1	0	2	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	1	1	
<i>Bacontia chuioi</i>	0	0	0	0	3	0	1	1	0	0	1	0	1	0	1	0	0	0	0	1	1	0	0	4	0	0	0	0	1	0	1	1	0	0	1	1	0	1	1	1	
<i>Notodoma fungorum</i>	0	0	0	0	0	1	1	0	0	1	0	1	0	1	0	1	0	0	0	1	1	1	1	3	0	0	0	0	1	1	1	0	0	0	0	0	0	1	1	1	
<i>Atholus duodecimstriatus</i>	0	0	1	0	2	0	1	1	0	0	1	0	1	0	0	0	0	0	0	1	1	1	1	0	1	0	1	0	1	0	1	1	2	0	2	0	0	1	0	-	
<i>Margarinotus niponicus</i>	0	0	0	0	0	1	1	0	0	0	4	0	1	0	1	0	0	0	1	1	1	0	1	0	1	0	1	0	1	0	1	1	0	0	0	0	1	1	0	-	
<i>Hololepta amurensis</i>	0	0	0	0	0	1	1	1	0	0	0	-	1	0	0	-	0	0	0	1	1	1	1	1	1	0	1	0	1	0	1	1	0	0	0	0	0	0	1	1	