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Two new species and records of *Neoperla* (Plecoptera, Perlidae) from Yunnan, China

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Abstract

Two new species of the stonefly genus *Neoperla*, *N. gaoligongshana* **sp. nov.** and *N. hajeki* **sp. nov.** are described from Yunnan Province of southwestern China based on the morphological and distributional data, and the new species are compared with two congeners, *N. wuzhishana* Chen & Du, 2016 and *N. orissa* Stark & Sivec, 2015. *Neoperla hubleyi* Stark & Sivec, 2008 is recorded from Yunnan Province for the first time.

Keywords

New record, new species, Perlinae, stoneflies, Yunnan

Introduction

Neoperla Needham, 1905 is the largest genus in Perlinae, with more than 270 species worldwide. In China, there are at least 110 valid species described by Chen and Du (2015, 2016a, 2016b, 2016c, 2017, 2018), Chu (1929), Claassen (1940), Dewalt et al. (2021), Du (1998, 1999, 2000a, 2000b), Du et al. (1999, 2001), Du and Sivec (2004, 2005), Du and Wang (2005, 2007), Huo et al. (2021), Kong et al. (2014), Kong and Li (2016), Li et al. (2011a, 2011b, 2012a, 2012b, 2013a, 2013b, 2014a, 2014b, 2017, 2019, 2020), Li et al. (2021), Li and Li (2013a, 2013b), Li and Liu (2019), Li and Wang (2011), Li and Zhang (2014), Mo et al. (2019, 2020a, 2020b, 2021a, 2021b), Murányi et al. (2015), Needham (1905), Qin et al. (2013), Sivec et

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al. (1988), Sivec and Zwick (1987), Stark and Sivec (2008, 2015), Wang et al. (2013a, 2013b, 2014), Wu (1935, 1938, 1948, 1962, 1973), Wu and Claassen (1934), Yang et al. (2017), and Yang and Yang (1990, 1991, 1992, 1993, 1995a, 1995b, 1996, 1998), Yang and Li (2018), and Zwick (1973, 1977, 1983, 1986). Eight species of *Neoperla* are known from Yunnan Province: *N. cavaleriei* Navás, 1922, *N. diehli* Sivec, 1985, *N. lihuae* Li & Murányi, 2014, *N. limbatella* Navás, 1933, *N. lui* Du, 2004, *N. yanlii* Li & Wang, 2014, *N. yunnana* Li & Wang, 2014, and *N. obscurofulva* Wu, 1962. Yunnan Province is located in southwestern China. The region is adjacent to Guizhou and Guangxi in the east, Tibet to the northwest, Myanmar to the west, Sichuan to the north, and Laos and Vietnam to the south. The total area of Yunnan Province is 3941 million square kilometers.

We recently examined a collection of stonefly specimens received from the National Museum Prague of the Czech Republic, and some of the results of our investigations into this material have been already published (Mo et al. 2019, 2020b, 2021a, 2021b; Li and Kong 2020; Li et al. 2019, 2020). Herein, we report our results on the *Neoperla* from Yunnan Province in this collection, including two new species and one new record from the province.

Materials and methods

Types are kept in the Insect Collection of Henan Institute of Science and Technology (**HIST**), Xinxiang of China and the National Museum Prague (**NMP**) of the Czech Republic, and the Collection of Smaller Insect Orders, Department of Zoology, Hungarian Natural History Museum (**HNHM**), Budapest, as indicated in the text. Specimens used in this study were collected using a light trap and stored in 75% ethanol. Specimens were examined with the aid of a Leica M420 dissecting microscope and the color photographs were taken with a Leica S8APO stereo microscope. Aedeagi were everted using the cold-maceration technique of Zwick (1983). The morphological terminology follows that of Stark and Sivec (2008). The map (Fig. 7) was prepared using a base map of Yunnan Province downloaded from DataV.GeoAtlas (Alibaba, China) and ACME Mapper 2.2 (http://datav.aliyun.com/tools/atlas/index.html; http://mapper.acme.com/).

Results and discussion

***Neoperla gaoligongshana* sp. nov.**
http://zoobank.org/69D93D93-861F-4F64-98BC-0F01F862F255
Figs 1, 2

Material examined. *Holotype*: male (NMP), China: Yunnan Province, Baoshan City, Gaoligongshan National Nature Reserve, Baihualing Village, 6–8.VII.2016, 25°17.7'N, 98°48.1'E, 1535 m, light trap, leg. J. Hájek & J. Růžička.

Diagnosis. Males of this species are characterized by having the tergum 7 with a triangular process with sparse spines apically. The aedeagal tube is straight, and aedeagal sac is armed with spines.

Description. Adult habitus (Fig. 1). Body color brown. Head mostly yellowish brown, with a black marking covering ocellar triangle, the marking extended forward to pale M-line and getting brown, and a narrow triangular marking occurring forward of M-line. Head approximately as wide as the pronotum; compound eyes black; antenna and palpi yellow. Distance between ocelli slightly wider than the diameter of an ocellus. Pronotum disc brown, midline darker, margins pale (Fig. 1B, C). Wings subhyaline, veins brown; legs pale to yellowish brown, femorotibial joint dark brown. Abdomen brownish, cerci brownish (Fig. 1B, C).

Male (Figs 1, 2). Forewing length ca 10.9 mm, hindwing length ca 9.7 mm. Tergum 6 unmodified. Process of tergum 7 triangular, apex rounded and margined by sparse spines (Fig. 1B, D). Tergum 8 with a median sensilla basiconica patch on a trapezoidal sclerite. Tergum 9 with two lateral patches of several sensilla basiconica and long hairs. Hemitergal processes slender, straight in lateral aspect, apex obtuse (Fig. 1B, D).

Aedeagus (Fig. 2). Aedeagal tube weakly sclerotized ventrally and dorsally sclerotized strongly, apex with two ventral spinous lobes (Fig. 2A, B). Sac nearly straight, ca 2× as long as the tube. Spinose apex of sac slender, slightly ventrally curved, with an apical dorsolateral patch of black spines and a subapical ventral patch of spines (Fig. 2A, C); two wide rows of numerous smaller spines covering most of the dorsal surface of the sac, basal half of spinous rows interrupted medially (Fig. 2A, C).

Female. Unknown.

Etymology. The specific name refers to the Gaoligongshan National Nature Reserve in Yunnan Province, where the type locality is situated.

Distribution. China (Yunnan).

Ecology. Gaoligongshan National Nature Reserve is located in northwestern Yunnan Province and is the largest nature reserve of the province. At the same locality, accompanying stoneflies were *Neoperla hajeki* sp. nov. and *Tyloperla illiesi* Stark & Sivec, 2005.

Remarks. The new species is a member of the *N. montivaga* group. The aedeagal tube and terga 7–10 of the new species are similar to those of *Neoperla wuzhishana* Chen & Du, 2016, but *N. wuzhishana* can be distinguished from the new species primarily by the shape of the aedeagal sac and aedeagal armatures (Fig. 8C). In *N. wuzhishana*, the aedeagal sac is distinctly curved and expanded apically (Fig. 8C, present study) (which is obscure in the original drawing because of an apical damage in the type) and has at least four large dorsal spines subapically (see figs 7, 8 in Chen, Du 2016b); however, the aedeagal sac of *N. gaoligongshana* is nearly straight and the apex is constricted and has only small spines subapically on its dorsal side. In addition, the aedeagal sac of *N. wuzhishana* bears a dozen moderately long spines at mid-length which are absent in *N. gaoligongshana*. Besides, the color pattern including that of the head and legs of *N. wuzhishana* and *N. gaoligongshana* is different: *N. wuzhishana* has brown legs and the head is pale with a small dark spot between the posterior ocelli, while in *N. gaoligongshana*, the legs are pale to yellowish brown, the femorotibial joint is dark brown, and the head has a large, black marking covering the ocellar triangle, with this marking extending anterolaterally under the pale M-line (Fig. 1B).

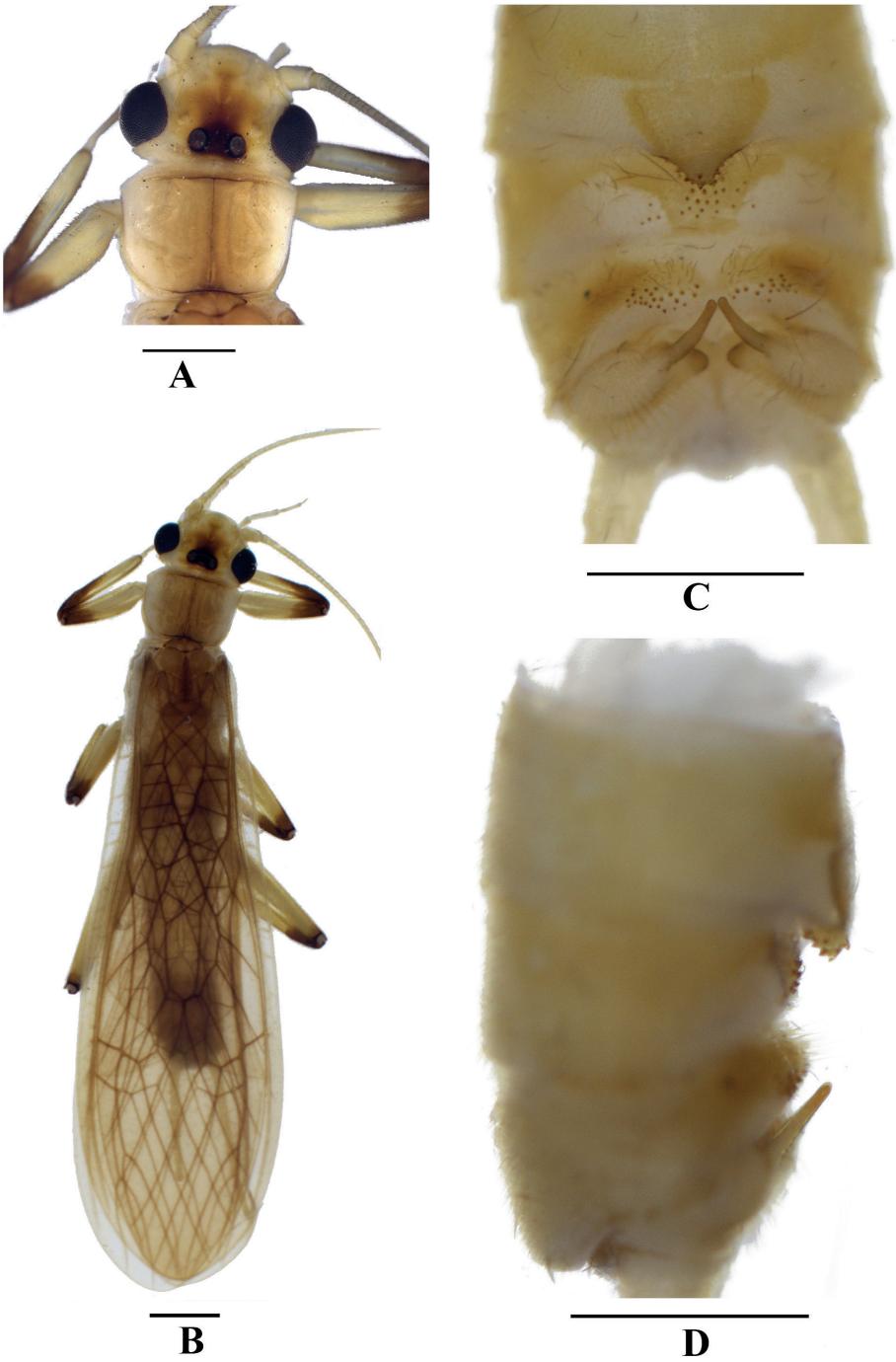

Figure 1. *Neoperla gaoligongshana* sp. nov. (male) **A** head and pronotum, dorsal view **B** adult habitus, dorsal view **C** terminalia, dorsal view **D** terminalia, lateral view. Scale bars: 1 mm.

Figure 2. *Neoperla gaoligongshana* sp. nov. (male) **A** aedeagus with everted sac, dorsal view **B** aedeagus with everted sac, ventral view **C** aedeagus with everted sac, dorsolateral view. Scale bars: 1 mm.

We examined specimens of *N. wuzhishana* from Yinggeling, Hainan Province, and found slight intraspecific variations of head pattern and armatures of the aedeagal sac: the dark area between ocelli in males was slightly smaller than in females, which in both sexes are quite small (Fig. 8A, B); four large spines in types (both in the original

illustrations and descriptions) (see figs 7, 8 in Chen, Du 2016b), which can number seven to nine in our specimens (Fig. 8C, D). Therefore, the absence of large aedeagal spines in *N. gaoligongshana* is regarded as a distinguishing character, separating it from *N. wuzhishana.*

***Neoperla hajeki* sp. nov.**
http://zoobank.org/2E0FD484-BE6F-4350-9C62-30AB5B651779
Figs 3–5

Type material. ***Holotype*:** male (NMP), China: Yunnan Province, Baoshan City, Zizhi Village, 29.VI–2.VII.2016, 25°43.7'N, 98°34.1'E, 1995 m, light trap, leg. J. Hájek and J. Růžička. ***Paratypes*:** 9 females (NMP), 1 male and 3 females (HIST), 1 male and 2 females (HNHM), same date as holotype.

Diagnosis. This species is characterized by a small dark marking over the ocellar area and a dark brown stigma before the M-line. The male of new species is characterized by an S-shaped aedeagal tube and by a sac bearing a subapical triangular patch of spinules in dorsal aspect.

Description. Adult habitus (Figs 3, 5). General body color brown. Head general pale brown, a small dark marking covers ocellar area, with a dark brown stigma before M-line. Head slightly wider than pronotum; compound eyes blackish, antenna dark brown except the basal segment yellowish (Figs 3A, 5A), palpi pale brown. Distance between ocelli narrower than the diameter of ocellus and a small marking between ocelli dark brown. Pronotum yellow, with rugosities and a strip-like midline (Figs 3A, 5A). Wings hyaline, veins brown; legs brown, basal part of femur dark brown, with wider yellow bands in mid- and hind legs (Figs 3B, 5B). Cerci yellowish (Figs 3D, 5B).

Male (Figs 3, 4). Forewing length 9.1–9.3 mm, hind wing length 7.9–8.1 mm. Process of tergum 7 sclerotized and triangular, with a nipple-like apex and covered with small sensilla basiconica (Fig. 3B, D). Tergum 8 with a median plump mound and a few sensilla basiconica, mostly covered by the process of tergum 7. Tergum 9 with two separated mesal projections covered by sensilla basiconica and hairs. Hemitergal processes of tergum 10 finger-like in shape, slightly curved medially in dorsal aspect, apex acute (Fig. 3B, D).

***Aedeagus*.** Aedeagal tube sclerotized, slightly S-shaped in lateral aspect. Sac short, ca 1/3 as long as the tube (Fig. 4). Aedeagal sac bearing a subapical triangular patch of spinules in dorsal aspect (Fig. 4A), remainder bald except a few ventral spinules (Fig. 4B, C).

Female (Fig. 5). Forewing length 9.3–9.6 mm, hind wing length 8.2–8.4 mm. General color pattern is similar to males. The subgential plate of sternum 8 is not produced posteriorly. Vagina large and apically slender, spiral and incurved, apical round, full of scaly spots. Spermatheca small, its origin in the terminal vagina.

Egg (Fig. 6). Chorion length 346–348 μm, width 173–177 μm. Micropyles 3 with rims, placed ca 1/3 length near opercullum, each located between striae (Fig. 6A, F). Collar not distinctly stalked, but slightly constricted at base; width ca 79.5 μm at collar

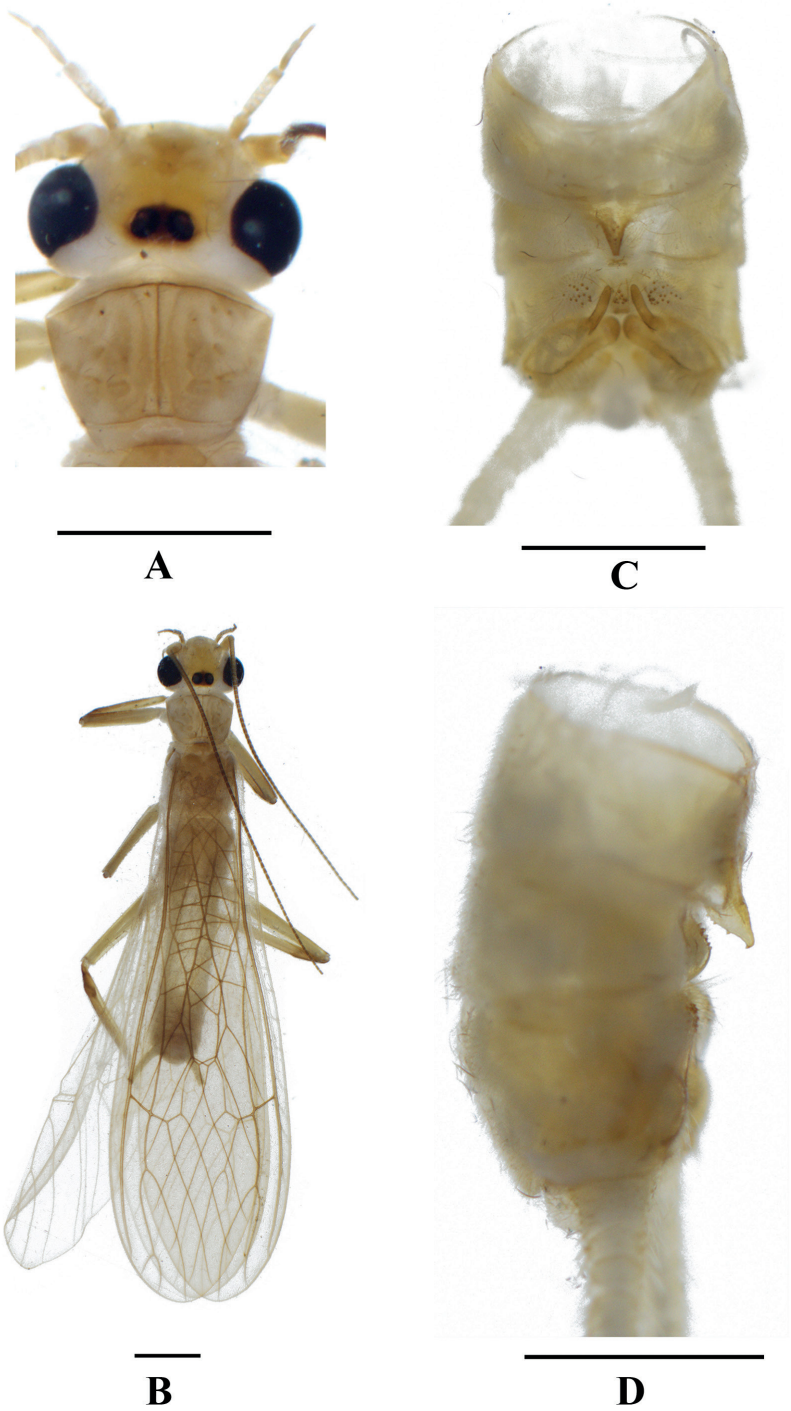

Figure 3. *Neoperla hajeki* sp. nov. (male) **A** head and pronotum, dorsal view **B** adult habitus, dorsal view **C** terminalia, dorsal view **D** terminalia, lateral view. Scale bars: 1 mm.

Figure 4. *Neoperla hajeki* sp. nov. (male) **A** aedeagus with everted sac, dorsal view **B** aedeagus with everted sac, ventral view **C** aedeagus with everted sac, lateral view. Scale bars: 1 mm.

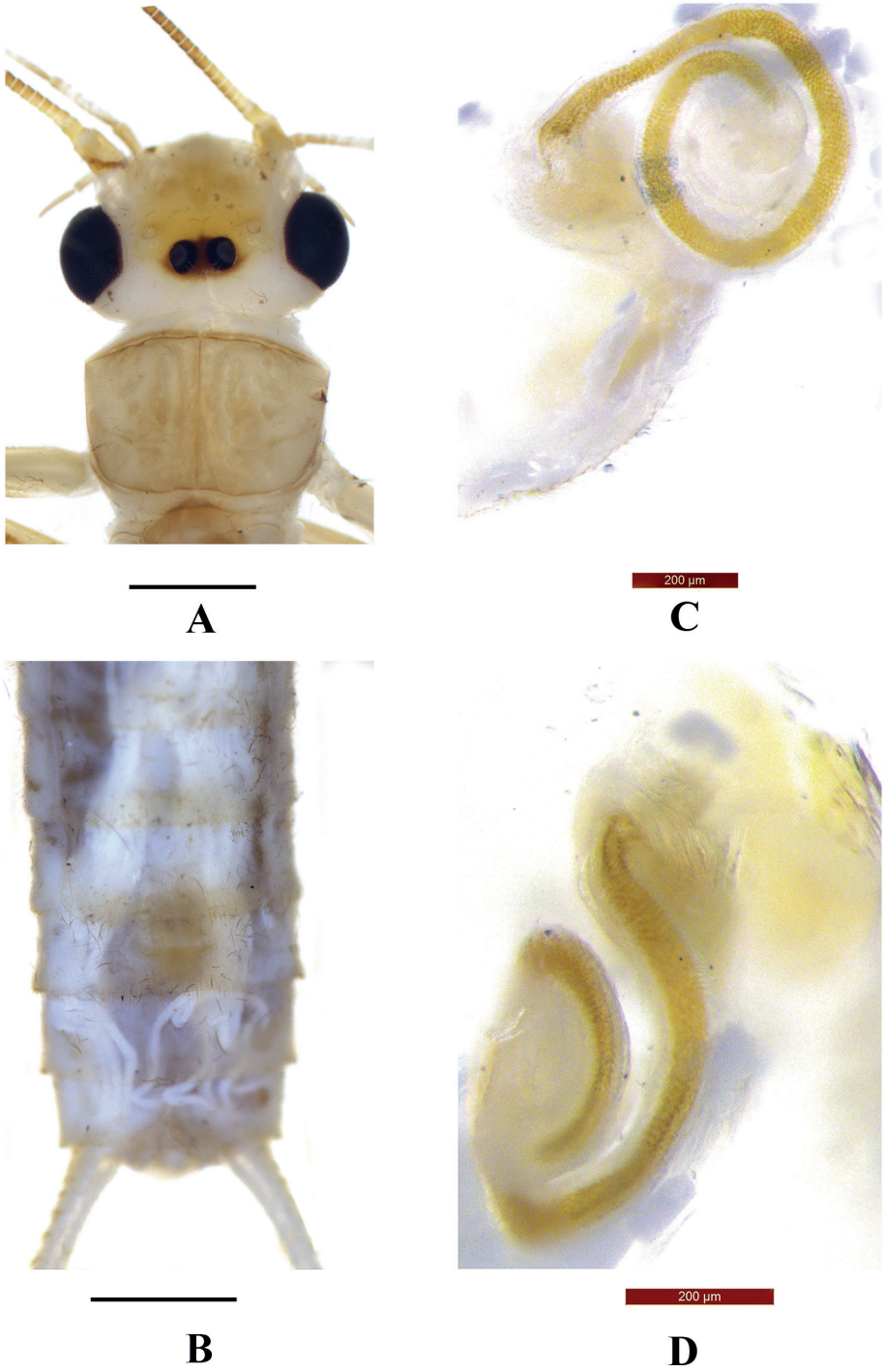

Figure 5. *Neoperla hajeki* sp. nov. (male) **A** head and pronotum, dorsal view **B** terminalia, dorsal view **C** vagina, dorsal view **D** vagina, lateral view. Scale bars: 1 mm (**A–B**); 0.2 mm (**C–D**).

(Fig. 6D). Collar short, irregular in shape (Fig. 6D). Rim slightly flanged, margin irregularly scalloped. Chorion with striate on lid and collar. FCIs on lid distinct; cells with thin, smooth walls and floors punctuated (Fig. 6B, E).

Etymology. The species is named after Dr Jiri Hájek for collecting the specimens.

Distribution. China (Yunnan).

Ecology. See ecology of *Neoperla gaoligongshana* sp. nov.

Remarks. The new species is a member of the *N. clymene* group. Color pattern, pronotum, and male genital features are similar to *Neoperla orissa* Stark & Sivec, 2015 from India. The new species can be easily separated from *N. orissa* by the projection of tergum 7 and detail of the aedeagal sac armature. In *N. hajeki*, the projection of tergum 7 is pointed in dorsal aspect, and the dorsal spines of the aedeagal sac are triangularly arranged. In *N. orissa*, the slender and median projection of tergum 7 appears truncate in dorsal aspect, and the spines of the sac are arranged in several close-set rows.

Neoperla lihuae Li & Murányi, 2014

Neoperla lihuae Li and Murányi 2014: 2 (original description).

Material examined. 1 male and 3 females (NMP), 1 male and 1 female (HIST), China: Yunnan Province, Yingjiang County, Dehong Dai and Jingpo Autonomous Prefecture, Tongbiguan Town, at light in village near river, 24–26.VI.2016, 24°36.7'N, 97°39.4'E, 1340 m, leg. J. Hájek & J. Růžička.

Distribution. China: Yunnan.

Ecology. Tongbiguan Town is located in southwestern Yingjiang County, and it also belongs to the Gaoligongshan region. At the same locality, accompanying stoneflies were *Neoperla hubleyi* Stark & Sivec, 2008 and one unidentified female *Neoperla* sp.

Remarks. *Neoperla lihuae* Li & Murányi, 2014 was originally described by Li et al. (2014a) from Xishuangbanna in Yunnan Province. Our specimens from Yingjiang County agree well with original description of the head pattern and terminalia, the aedeagal tube and sac.

Neoperla hubleyi Stark & Sivec, 2008

Neoperla hubleyi Stark and Sivec 2008: 30 (original description); Mo et al. 2020: 521 (new record for Guangxi Zhuang Autonomous Region).

Material examined. 1 male (HIST), China: Yunnan Province, Dehong Dai and Jingpo Autonomous Prefecture, Yingjiang County, Tongbiguan Town, at light in village near river, 24–26.VI.2016, 24°36.7'N, 97°39.4'E, 1340 m, leg. J. Hájek & J. Růžička.

Distribution. China: Yunnan and Guangxi Zhuang Autonomous Region; Vietnam.

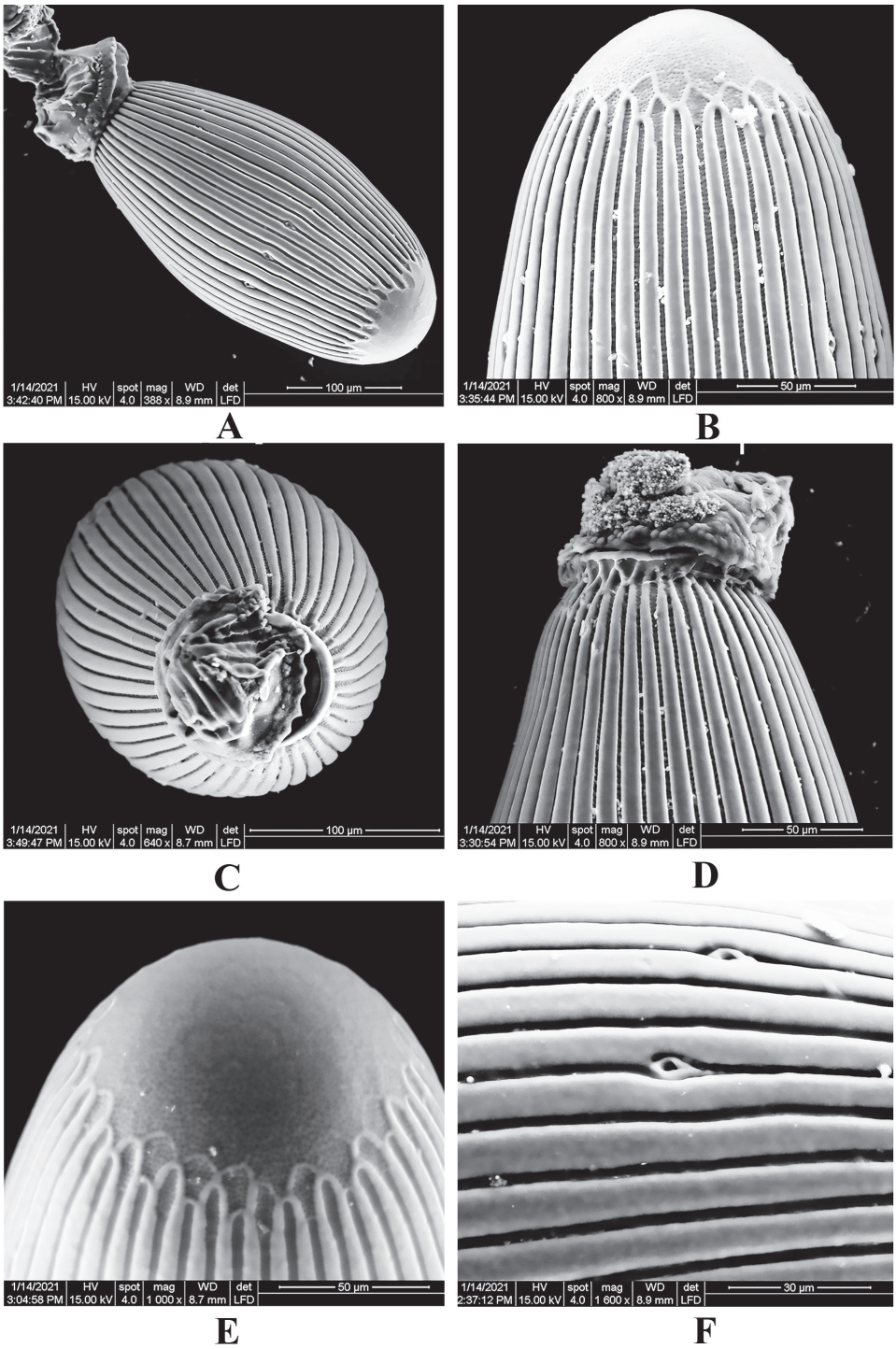

Figure 6. *Neoperla hajeki* sp. nov. (egg) **A** egg **B** lid **C** collar **D** collar and lid **E** FCIs and lid **F** micropyles.

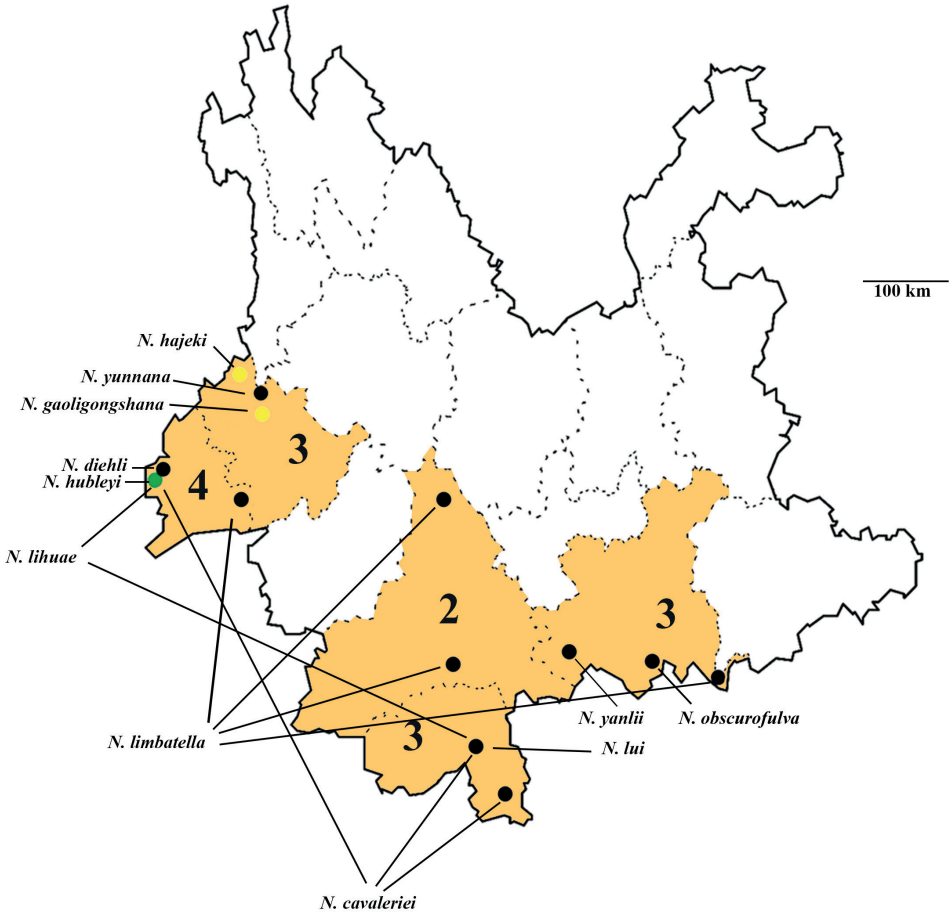

Figure 7. Distribution of *Neoperla* Needham, 1905 in cities of Yunnan. Yellow dots indicate location of the two new species, green dot indicates two new records.

Ecology. See ecology of *Neoperla lihuae* Li & Murányi, 2014.

Remarks. Stark and Sivec (2008) originally described this species from Vietnam, and Mo et al. (2020a) described a new record in Guangxi Zhuang Autonomous Region. The terminalia and aedeagus of our specimen fit the original description of Stark and Sivec (2008).

Concluding remarks

Neoperla was divided into the *Neoperla clymene* group and the *Neoperla montivaga* group by Zwick (1983). The *N. clymene* species group currently includes more than 150 species, and the *N. montivaga* species group includes over 123 species worldwide (Huo et al. 2021; Mo et al. 2021a).

So far 11 species of *Neoeprla* have been recorded from Yunnan Province, including the two new species and one species newly recorded in this paper. Among the six

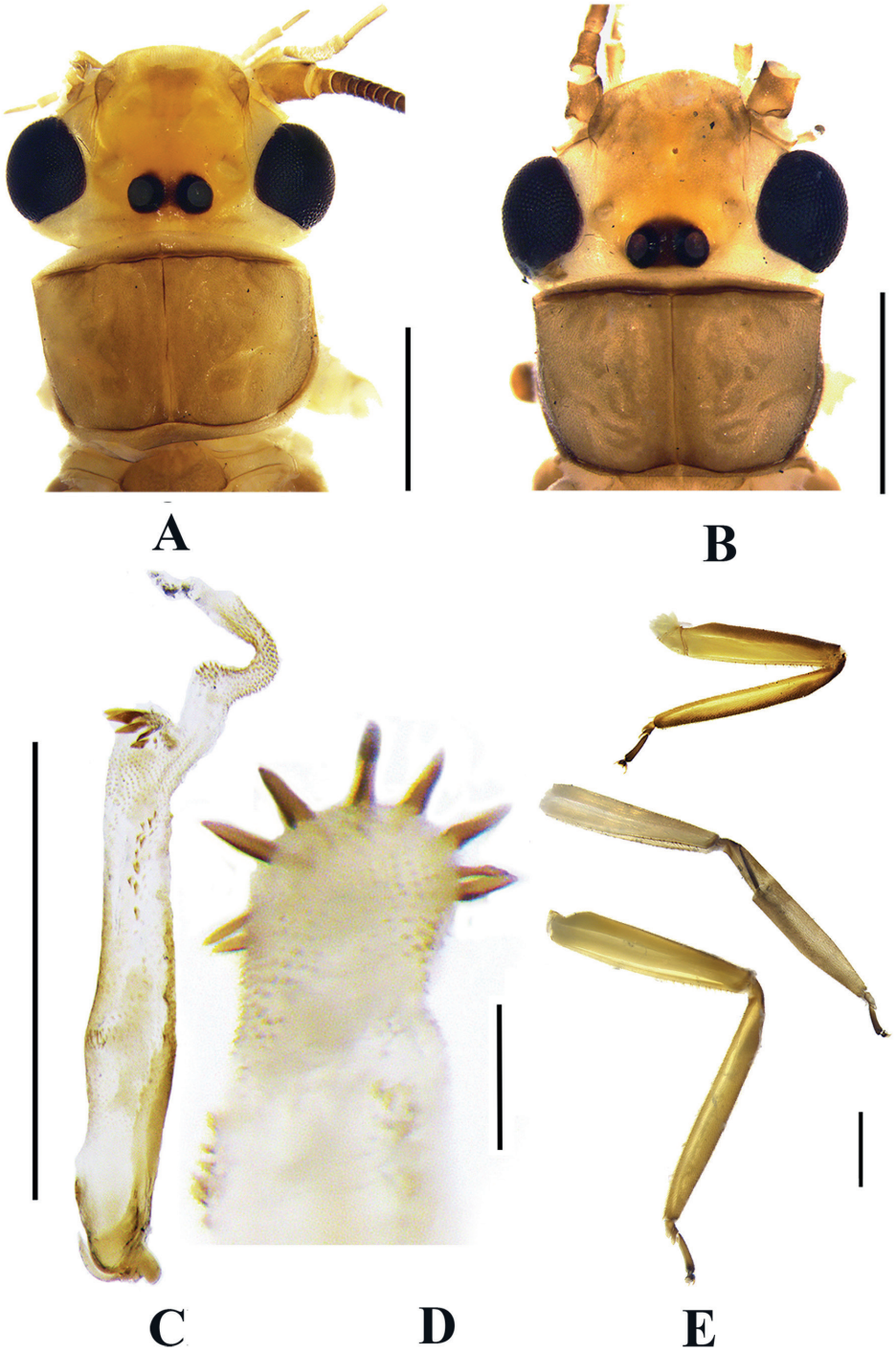

Figure 8. *Neoperla wuzhishana* Chen & Du, 2016 (**A, C–E** male **B** female), all from Yinggeling, Hainan Province **A** head and pronotum, dorsal view **B** head and pronotum, dorsal view **C** Aedeagus, lateral view **D** Large spines of aedeagal sac, ventral view **E** legs, dorsal view. Scale bars: 1 mm (**A–C, E**); 0.1 mm (**D**).

endemic species of *Neoperla*, including the two new species listed below—*N. lihuae*, *N. yanlii*, *N. obscurofulva*, *N. yunnana*, *N. hájeki*, and *N. gaoligongshana*—three of them are distributed in Baoshan City. Five species are widely distributed: *N. cavaleriei*, *N. diehli*, *N. hubleyi*, *N. limbatella*, and *N. lui*. *Neoperla binodosa* Wu, 1973 was transferred to the genus *Phanoperla* and is placed as a synonym of *P. pallipennis* Banks, 1938 by Mo et al. (2021c). Most species are distributed in western and southeastern Yunnan Province and central and northern Yunnan still needs to be surveyed (Fig. 7).

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RESEARCH ARTICLE

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Nothotytthonyx, a new genus of Malthininae (Coleoptera, Cantharidae) from mid-Cretaceous amber of northern Myanmar

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Abstract

A new fossil genus and species of Cantharidae, *Nothotytthonyx serratus* Li, Biffi, Kundrata & Cai **gen. et sp. nov.**, is reported from mid-Cretaceous Burmese amber. The new species is tentatively attributed to the extant subfamily Malthininae based on a combination of characters, including the symmetrical apical maxillary palpomeres, shortened elytra, pronotum with arched margins and well-defined borders, tibiae with apical spurs, and tarsal claws simple, although its well-developed gonostyli are atypical in Malthininae. The discovery of *Nothotytthonyx* also suggests a possible Gondwanan origin for Malthininae.

Keywords

Burmese amber, Cretaceous, fossil, paleontology, soft-bodied Elateroidea, soldier beetles, systematics

Introduction

Cantharidae is a diverse group among the soft-bodied Elateroidea, with over 5000 species distributed worldwide (Ramsdale 2010). Cantharid adults are highly active, and may feed on foliage-frequenting invertebrates, nectar or pollen (Crowson 1972;

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Ramsdale 2010). Both larvae and adults of cantharids have paired lateral glandular pores for chemical defense against predators, although the pores may sometimes be inconspicuous and hard to determine. The family appears to be closely related to the elaterid-lampyroid group. However, its accurate position remains unsettled, as several recent phylogenomic studies have produced inconsistent results (Zhang et al. 2018; McKenna et al. 2019; Douglas et al. 2021; Cai et al. 2022). Brancucci (1980) conducted a comprehensive study on the taxonomy of Cantharidae, and divided it into five subfamilies, namely Cantharinae, Chauliognathinae, Dysmorphocerinae, Silinae and Malthininae. The relationships among the subfamilies varied in different studies and were not well understood (e.g., Brancucci 1980; Kundrata et al. 2014; McKenna et al. 2015, 2019; Zhang et al. 2018; Hsiao et al. 2021; Cai et al. 2022).

Records of fossil cantharids are relatively abundant, especially in amber deposits. More than 80 species have been reported from Eocene Baltic amber (e.g., Fanti and Kupryjanowicz 2017; Fanti and Damgaard 2020; Fanti 2021). Additional cantharids have been described from Early Cretaceous Spanish amber (Peris and Fanti 2018), Late Cretaceous Agdzhakend amber (Kazantsev and Perkovsky 2019a), Eocene Rovno amber (Kazantsev and Perkovsky 2020), Eocene Sakhalinian amber (Kazantsev and Perkovsky 2019b), and Miocene Dominican amber (Fanti and Damgaard 2019; Fanti and Pankowski 2021). From the fossiliferous mid-Cretaceous Burmese amber, about 20 species have been described in nine genera (e.g., Hsiao et al. 2021; Yang et al. 2021). Most cantharids from Burmese amber were originally assigned to Cantharinae diagnosed by, for example, securiform apical maxillary palpomeres, unmodified pronotal margins and well-developed elytra concealing the wings and abdomen. However, the subfamilial placement of at least some of the genera (*Ornatomalthinus* Poinar & Fanti and *Sanaungulus* Fanti et al.) is controversial due to their conflicting diagnostic characters (Fanti 2018; Hsiao and Huang 2018; Hsiao et al. 2021). In the morphology-based phylogenetic analysis by Hsiao et al. (2021), such group of genera was retrieved forming the "Burmite Cantharinae" clade, as sister to Silinae, and their placement within Cantharinae was rejected. In the same work, *Archaeomalthodes* Hsiao et al., originally placed in Malthininae (Hsiao et al, 2017), was suggested as a member of Dysmorphocerinae (Hsiao et al. 2021). Here, we describe a new fossil cantharid from Burmese amber, and tentatively assign it to subfamily Malthininae.

Materials and methods

The Burmese amber specimen studied herein (Figs 1–5) originated from an amber mine near Noije Bum (26°20'N, 96°36'E), Hukawng Valley, Kachin State, northern Myanmar. Jewellery-grade Burmese amber specimens are commonly carried and sold legally in Ruili, Dehong Prefecture on the border between China and Myanmar. The specimen in this study was purchased in late 2016, and is permanently deposited in the Nanjing Institute of Geology and Palaeontology (**NIGP**), Chinese Academy of Sciences, Nanjing, China. The amber piece was trimmed with a small table saw, ground with emery paper of different grit sizes, and finally polished with polishing powder.

Photographs under incident light were taken with a Zeiss Discovery V20 stereo microscope. Widefield fluorescence images were captured with a Zeiss Axio Imager 2 light microscope combined with a fluorescence imaging system. Confocal images were obtained with a Zeiss LSM710 confocal laser scanning microscope, using the 488 nm (Argon) or 561 nm (DPSS 561-10) laser excitation lines (Fu et al. 2021). Images under incident light and widefield fluorescence were stacked in Helicon Focus 7.0.2 or Zerene Stacker 1.04. Confocal images were stacked with Helicon Focus 7.0.2 and Adobe Photoshop CC. Microtomographic data were obtained with a Zeiss Xradia 520 Versa 3D X-ray microscope at the micro-CT laboratory of NIGP and analyzed in VG-Studio MAX 3.0. Scanning parameters were as follows: isotropic voxel size, 6.1511 μm; power, 4 W; acceleration voltage, 50 kV; exposure time, 1.5 s; projections, 2401. Images were further processed in Adobe Photoshop CC to adjust brightness and contrast.

Data availability

The original confocal and micro-CT data are available in Zenodo repository (https://doi.org/10.5281/zenodo.6336149).

Systematic paleontology

Order Coleoptera Linnaeus, 1758
Superfamily Elateroidea Leach, 1815
Family Cantharidae Imhoff, 1856
Subfamily Malthininae Kiesenwetter, 1852

Genus *Nothotytthonyx* Li, Biffi, Kundrata & Cai, gen. nov.
http://zoobank.org/A56DECAD-2C71-4822-B48C-690DD67B4C3E

Type species. *Nothotytthonyx serratus* sp. nov.

Etymology. The generic name is derived from the Greek "*nothos*", false, and the generic name *Tytthonyx* LeConte. The name is masculine in gender.

Diagnosis. Antennae strongly serrate (Figs 3F, 4C). Mandibles with a prominent tooth on incisor edge (Fig. 5D). Apical maxillary palpomere symmetrical, fusiform (Fig. 4A). Gular sutures confluent (Figs 3A, 5B). Elytra shortened; surface somewhat punctate. Tibial spurs present (Fig. 4D). Gonostyli well developed (Fig. 4F).

***Nothotytthonyx serratus* Li, Biffi, Kundrata & Cai, sp. nov.**
http://zoobank.org/44E1AFDB-31BC-4B43-B8FA-D3F566934E3F
Figs 1–5

Material. ***Holotype***, NIGP179427, female.

Figure 1. General habitus of *Nothotytthonyx serratus* Li, Biffi, Kundrata & Cai sp. nov., holotype, NIGP179427, under incident light **A** dorsal view **B** ventral view. Scale bars: 1.5 mm.

Etymology. The specific name refers to its distinctly serrate antennae.

Locality and horizon. Amber mine located near Noije Bum Village (26°20'N, 96°36'E), Tanai Township, Myitkyina District, Kachin State, Myanmar; unnamed horizon, mid-Cretaceous, Upper Albian to Lower Cenomanian.

Diagnosis. As for the genus.

Description. Adult female. Body weakly sclerotized, elongate, about 5.3 mm long, 1.4 mm wide (widest across abdomen).

Head (Fig. 3A,F) fully exposed, prognathous, subquadrate, weakly narrowed posteriorly, including eyes almost as wide as pronotum; dorsal surface flat, without protuberance or depression. Compound eyes moderately large and weakly protruding, finely facetted, without interfacetal setae. Antennal insertions located anteriorly, dorsally exposed, separated by approximately the length of antennomere 1. Subantennal grooves absent. Antennae (Fig. 4B,C) with 11 antennomeres; antennomere 1 moderately broad; antennomeres 2 short; antennomere 3–10 distinctly serrate. Mandibles with

one prominent tooth on incisor edge (Fig. 5D). Apical maxillary and labial palpomeres elongate, symmetrical, fusiform, not unequally expanded, apex acute (Fig. 4A). Gular sutures confluent (Figs 3A, 5B).

Pronotal disc (Fig. 3G) transverse; anterior and posterior angles broadly rounded; lateral and posterior margins clearly bordered. Elytra (Fig. 3H) relatively short, covering only about half of posterior body; surface somewhat punctate. Procoxae (Fig. 5B) conical, well projecting, contiguous. Mesocoxae (Fig. 5B) conical, well projecting, narrowly separated. Metaventrite (Fig. 3C) large, with distinct discrimen and metakatepisternal suture. Metacoxae (Fig. 3C) transverse, almost contiguous.

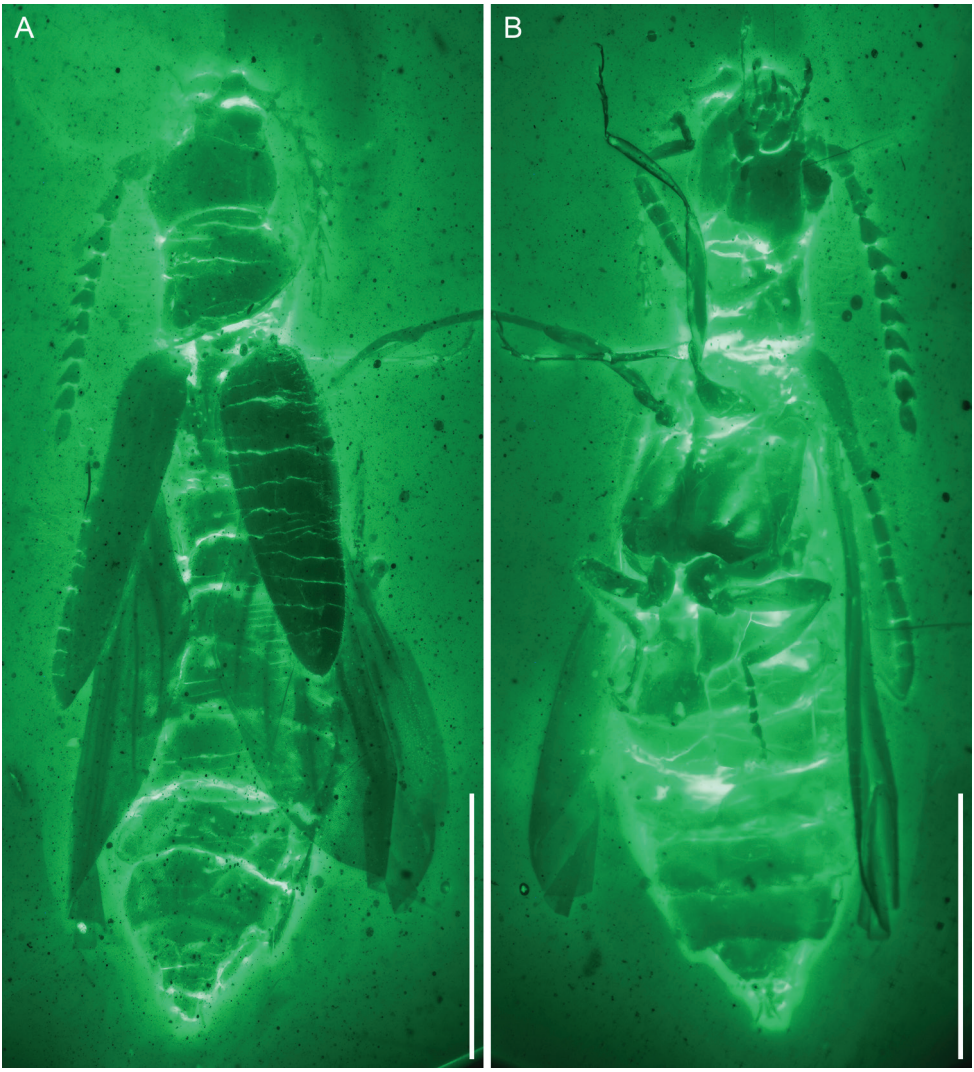

Figure 2. General habitus of *Nothotytthonyx serratus* Li, Biffi, Kundrata & Cai sp. nov., holotype, NIGP179427, under widefield fluorescence **A** dorsal view. **B** ventral view. Scale bars: 1.5 mm.

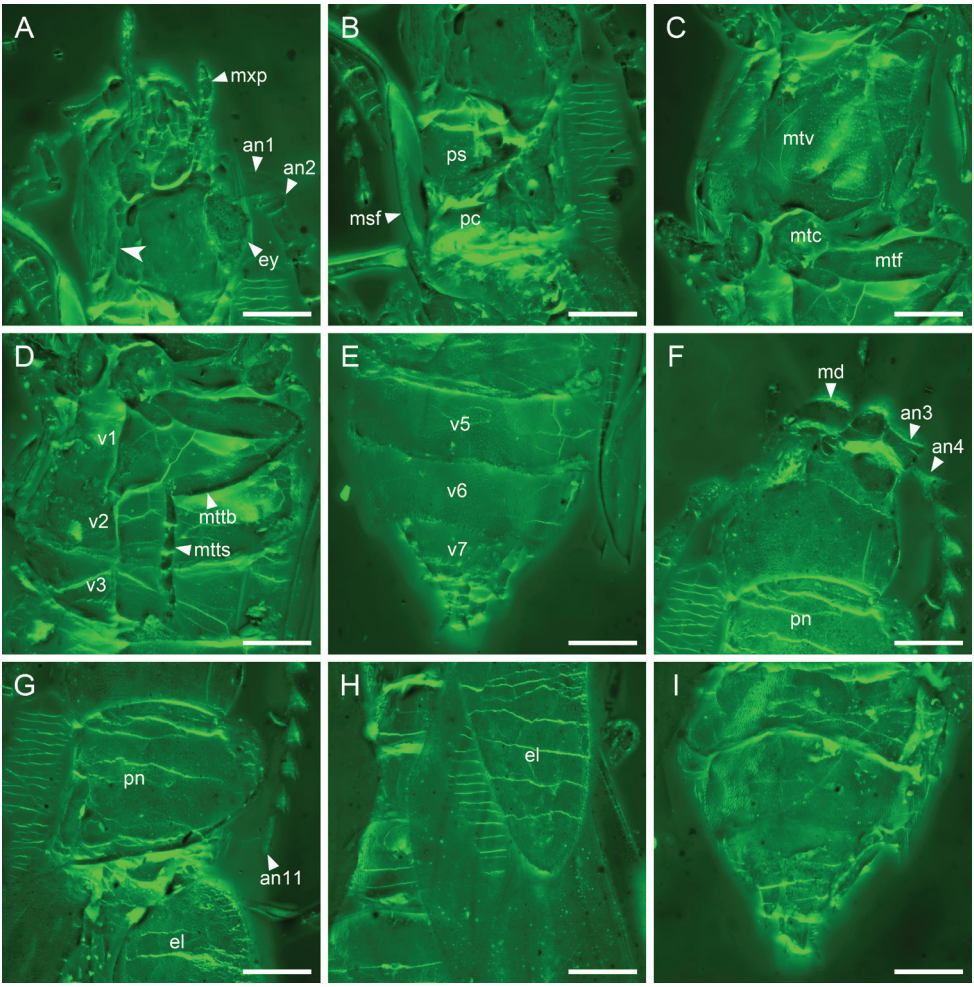

Figure 3. Details of *Nothotytthonyx serratus* Li, Biffi, Kundrata & Cai sp. nov., holotype, NIGP179427, under confocal microscopy **A** head, ventral view, showing the confluent gular suture (arrowhead) **B** prothorax, ventral view **C** metathorax, ventral view **D** abdominal base, ventral view **E** abdominal apex, ventral view **F** head, dorsal view **G** prothorax, dorsal view **H** elytral base, dorsal view **H** abdominal apex, dorsal view. Abbreviations: an1–11, antennomeres 1–11; el, elytron; ey, compound eye; md, mandible; msf, mesofemur; mtc, metacoxa; mttb, metatibia; mtts, metatarsus; mtv, metaventrite; mxp, maxillary palp; pc, procoxa; pn, pronotum; ps, prosternum; v1–7, ventrites 1–7. Scale bars: 300 μm.

Legs slender. Trochanters obliquely articulated to femoral bases. Tibiae with weak spurs (at least as seen on left mesotibia; Fig. 4D). Tarsal formula 5–5–5; tarsomere 4 ventrally bilobed (Figs 4D, 5E). Claws simple.

Abdomen with seven free ventrites. Gonostyli well developed (Fig. 4F).

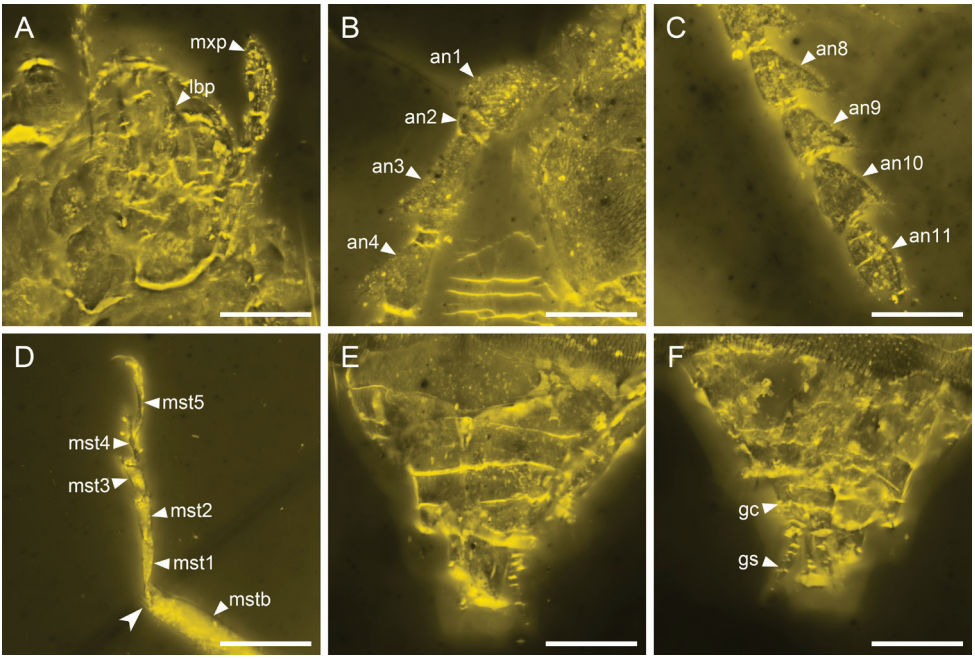

Figure 4. Details of *Nothotytthonyx serratus* Li, Biffi, Kundrata & Cai sp. nov., holotype, NIGP179427, under confocal microscopy **A** mouthparts, ventral view **B** antennal base, dorsal view **C** antennal apex **D** mid leg, showing the two weak tibial spurs (arrowhead) **E** abdominal apex, dorsal view **F** ovipositor, ventral view. Abbreviations: an1–11, antennomeres 1–11; gc, gonocoxite; gs, gonostylus; lbp, labial palp; mst1–5, mesotarsomeres 1–5; mstb, mesotibia; mxp, maxillary palp. Scale bars: 200 μm.

Discussion

Within soft-bodied elateroids, *Nothotytthonyx* is firmly placed in Cantharidae, primarily based on the fully exposed prognathous head (Fig. 3A,F), 11-segmented antennae (Fig. 1), and ventrally bilobed tarsomere 4 (Figs 4D, 5E).

The current classification of Cantharidae into five subfamilies is solely based on extant species (Brancucci 1980). However, there are no incontestable diagnostic characters for most subfamilies (except for Chauliognathinae). Many characters may have evolved independently in separate subfamilies, and some characters used for diagnosis may be absent in certain lineages within a subfamily, which hampers the precise systematic placement of some genera (e.g., *Tytthonyx*). In the case of fossils, this problem is aggravated by the impossibility of observation of important characters, especially the genitalia and wing venation, leading to the conflicting hypotheses of placement (e.g., Fanti 2018; Hsiao and Huang 2018; Hsiao et al. 2021). For instance, Malthininae and a few members of Dysmorphocerinae have radially symmetrical apical maxillary

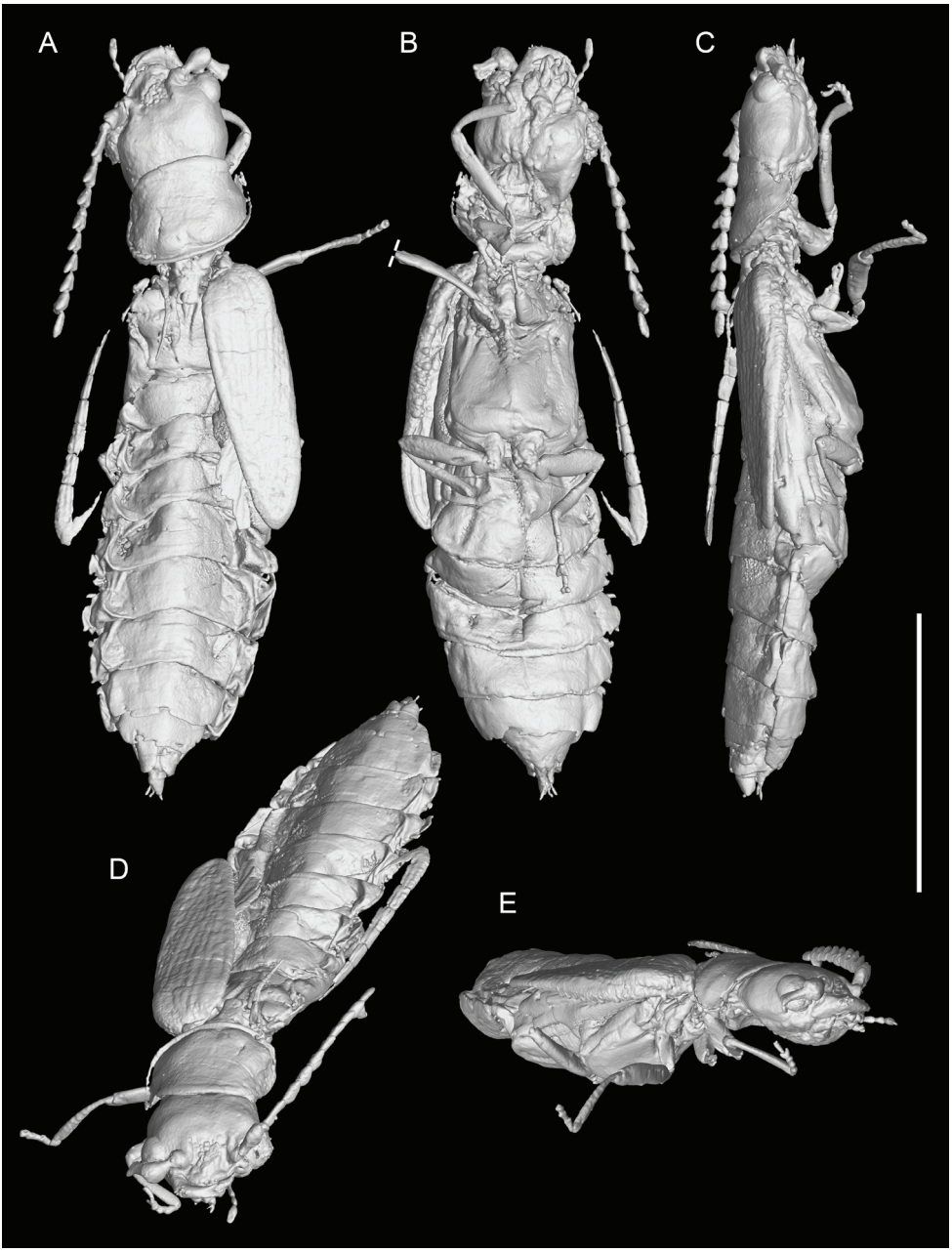

Figure 5. X-ray microtomographic reconstruction of *Nothotytthonyx serratus* Li, Biffi, Kundrata & Cai sp. nov., holotype, NIGP179427 **A** dorsal view **B** ventral view **C** lateral view **D** anterodorsal view **E** anterolateral view. Scale bar: 2 mm.

palpomeres, while in other subfamilies and most of Dysmorphocerinae the apical maxillary palpomeres are securiform, except for *Tytthonyx*, currently classified as *incertae sedis* in Silinae. Dysmorphocerinae, however, generally have a wide pronotum and

complete elytra. The elytra are reduced in most of Malthininae genera, although this feature is also present in species in most other subfamilies (e.g., Chauliognathinae: *Ichthyurus* Westwood, *Lobetus* Kiesenwetter; Cantharinae: some *Lycocerus* Gorham; Silinae: some *Polemius* LeConte, *Brachysilidius* Pic).

Nothotytthonyx is herein tentatively assigned to the subfamily Malthininae by a combination of characters, such as the radially symmetrical apical maxillary palpomeres, shortened elytra, pronotum with arched margins and well-defined borders, tibiae with apical spurs, and tarsal claws simple. However, the ovipositor with long gonostyli of *Nothotytthonyx* seems to be quite aberrant in Malthininae. No extant species of Malthininae (and Dysmorphocerinae and Silinae) has long and clearly defined styli. According to Brancucci (1980), the well-defined coxites and styli are the "primitive form", and they are typical of the subfamily Cantharinae. In Malthininae, the styli are indistinct; according to Brancucci, they are either extremely reduced or, most probably, solidly fused to the coxites, and correspond to the pubescent area of the coxites.

Within Malthininae, Malthinini have confluent or almost confluent gular sutures, while Malthodini and Malchinini have separated gular sutures (Brancucci 1980). Besides, there is a prominent tooth on the incisor edge of mandibles in Malthinini, while in Malthodini and Malchinini the mandibles are armed with a weak tooth, with a row of small teeth, or simple (without teeth) (Brancucci 1980). *Nothotytthonyx* differs from genera in the Malthodini and Malchinini in having confluent gular sutures and mandibles with a prominent tooth on the incisor edge. Yet, *Nothotytthonyx* is distinctive among genera in Malthinini for having strongly serrate antennae. Most genera in Malthinini have filiform or weakly serrate antennae, and *Paramalthinus* Brancucci has pectinate antennae (even though the antennae of *Paramalthinus* are pectinate, its antennomere bodies are rather elongate). *Nothotytthonyx* is different from other genera in Malthinini additionally in the combination of the moderately shortened elytra, clearly confluent gular sutures, presence of tibial spurs, and unelongated metacoxae (Brancucci 1980; Fanti and Castiglione 2017; Fanti and Vitali 2017).

It is notable that *Nothotytthonyx* is somewhat similar to *Tytthonyx*. This genus shares characters with both Malthininae (e.g., mandibles with retinaculum, radially symmetrical apical maxillary palpomeres, the shape of pronotum, reduced elytra and wing venation) and Silinae (e.g., the structures of terminal ventrites and tergites and the aedeagus). *Tytthonyx* has been kept in its own tribe Tytthonyxini as *incertae sedis* in Silinae (Brancucci 1980); however, in a recent morphology-based phylogenetic analysis, *Tytthonyx* was revealed as the sister group of Malthininae (Hsiao et al. 2021). *Nothotytthonyx* shares with *Tytthonyx* a similar habitus, symmetrical apical maxillary palpomeres, and shortened elytra. In some species of *Tytthonyx* (subgenus *Tytthonyx*), the antennae are also distinctly serrate. *Nothotytthonyx* nevertheless differs from *Tytthonyx* in the confluent gular sutures (separated in *Tytthonyx*) and the structure of abdomen (gonostyli absent in *Tytthonyx*; Brancucci 1980).

Malthininae today generally have a Holarctic (Laurasian) distribution, with only limited fauna known from Gondwanan parts of the World, whereas Dysmorphocerinae have a strictly Gondwanan distribution. Although *Archaeomalthodes* from Burmese amber was once classified in Malthininae (Hsiao et al. 2017), it was later revised as a

member of Dysmorphocerinae (Hsiao et al. 2021). Thus, as the first fossil of Malthininae from Burmese amber and also from the Mesozoic Era, *Nothotytthonyx* has important biogeographical implications. If we accept that the Burmese amber, which comes from the mines located on the West Burma Block, is of a Gondwanan origin (Poinar 2019), then our current discovery indicates that Malthininae were present in Gondwanan lands in the Mesozoic, and taking into consideration that they are not known from any northern-hemisphere Mesozoic deposits, they may have originated in the south, and only later dispersed to north where they greatly diversified and survived until now whereas they became rare in the south. However, this hypothesis will need to be tested in future.

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RESEARCH ARTICLE

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A contribution to the genus *Didrepanephorus* Wood-Mason, 1878 (Coleoptera, Scarabaeidae, Rutelinae)

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Abstract

The diagnostic characters of the genera *Didrepanephorus* Wood-Mason, 1878 and *Fruhstorferia* Kolbe, 1894 are clarified. The following nomenclatorial acts are proposed: *Didrepanephorus birmanicus* (Arrow, 1907), **comb. nov.**, *Didrepanephorus fukinukii* (Muramoto & Araya, 2000), **comb. nov.**, *Fruhstorferia baron* (Prokofiev, 2013), **comb. nov.**, and *Fruhstorferia anthracina* Ohaus, 1903, **comb. rev.** *Didrepanephorus tangzhaoyangi* Zhao & Liu, **sp. nov.** is described from Yunnan Province, China. A lectotype is designated for *Fruhstorferia birmanica* Arrow, 1907. *Didrepanephorus mizunumai* Nagai & Hirasawa, 1991 is reported from Myanmar for the first time.

Keywords

China, Didrepanephorina, lectotype, Myanmar, new combination, new record, new species, Rutelini, Scarabaeoidea

Introduction

The subtribe Didrepanephorina was established by Ohaus (1918) to accommodate a morphologically remarkable genus *Didrepanephorus* Wood-Mason, 1878. The type species of this genus, *D. bifalcifer* Wood-Mason, 1878, is a densely setose ruteline beetle with strong sexual dimorphism in the shape of mandibles (Wood-Mason 1878).

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The morphological affinities between *Didrepanephorus* and *Fruhstorferia* Kolbe, 1894 had resulted in a chaos of generic separations when different characters were referred: Arrow (1917) separated *Fruhstorferia* from *Didrepanephorus* mainly by the dorsal surface generally without dense setae. Ohaus (1934a) recognized *Didrepanephorus* species by the complete frontoclypeal suture and reassigned species of the two genera. Young (1999) took the orientation of mandibles into account, i.e., bent upward in *Didrepanephorus* but directed forward in *Fruhstorferia*. Most recently, Muramoto (2005) differentiated the two genera by the prosternal process and abbreviation of abdominal ventrites 1–4 in males. Besides, some authors questioned the separation of the two genera (Nagai and Hirasawa 1991; Qiu et al. 2021). The authors of the present paper had found reliable morphological characters to distinguish the two genera. Based on these characters, the delimitation of the two genera is herein clarified.

The Chinese *Didrepanephorus* species are still poorly known. Qiu et al. (2021) described a new species from Guizhou and recorded two species new to Chinese fauna. Their biology was also reported, which greatly improved the knowledge of this genus. During the taxonomic study of the Old World Rutelini, a new species similar to *D. ohbayashii* (Nagai, 2004) was received by the first author from Yunnan Province of China. Additionally, based on the examination of the type material of *F. birmanica* Arrow, 1907, some taxonomic problems are also solved herein.

Material and methods

Images of the external characters and male genitalia were taken using a Canon EOS 760D camera in conjunction with a Tamron 90 mm f/2.8 1:1 Macro Lens and a Laowa 25 mm f/2.8 2.5-5X Ultra Macro Lens, respectively. Zerene Stacker (version 1.04) was used for stacking. All images were modified and arranged in plates in Adobe Photoshop CS5.

Data of material in NHMUK are cited verbatim. Different labels are separated by a double slash (//). Specimens studied in this research are deposited in the following public and private collections:

CCPC Chang-Chin Chen's personal collection, Tianjing, China;
GGPC Guy Guerlach's personal collection, Orny, France;
LCPC Chao Li's personal collection, Beijing, China;
LZPC Ze-Chuan Li's personal collection, Tai'an, China;
MYNU Invertebrate Collection of Mianyang Normal University, Mianyang, China;
NHMUK The Natural History Museum, London, United Kingdom;
SCAU South China Agricultural University, Guangzhou, China;
SFPC Feng-Yi Sun's personal collection, Yong'an, China;
TZPC Zhao-Yang Tang's personal collection, Shenzhen, China;
ZMPC Ming-Zhi Zhao's personal collection, Zhuhai, China.

Taxonomy

Delimitation of the genera *Didrepanephorus* Wood-Mason, 1878 and *Fruhstorferia* Kolbe, 1894

The following specimens were studied for comparative purpose: *D. yunnanus wakaharai* (Nagai, 2004): 1♂ (ZMPC), Laos, Houaphanh Province, Mt. Phu Pane, 2060 m, 2017.IV; *D. takuyai* (Muramoto, 2003): 1♂, 1♀ (ZMPC), Vietnam, Dalat, Lamdong, 2016.V; *Didrepanephorus* specimens studied in Qiu et al. (2021); *F. anthracina* Ohaus, 1903: 1♂, (CCPC), Vietnam, Bac Giang, Son Dong, Thanh Son, Tay Yen Tu, 120 m, 2014.VI.2, N.-Y. Tsai leg.; *F. javana javana* Kolbe, 1894: 1♂, 1♀ (TZPC), Indonesia, West Java, 2016.VI; *F. nigromuliebris* Nagai, 1984: 1♂ (ZMPC), Sabah, Croker Range, 800 m, 2019.V; *Kibakoganea sexmaculata* (Kraatz, 1900): 3♂ (ZMPC), Vietnam, Yen Bai Province, Nghia Lo, 2017.VII; *K. akikoae satoi* Nagai, 2004: 1♂ (ZMPC), Laos, Houaphanh Province, Mt. Phu Pane, 2060 m, 2016.IV; *K. yoshitomii* Nagai, 2004: 1♂ (ZMPC), Laos, Houaphanh Province, Mt. Phu Pane, 2060 m, 2016. III; *Masumotokoganea kinabalensis* (Ohaus, 1932): 1♂ (CCPC), Malaysia, Sabah, Tambunan, 1600 m, 2014.V.7, light, Yu-Tang Wang leg.

The authors of the present paper tentatively delimitate the two genera based on the shape of the male mandible and the range of body length. Regarding the *Didrepanephorus* species, there is a prominent protrusion at the base of lower margin of male mandible, which is either sharp or blunt at apex, and the lower margin is concave or strongly concave before the protrusion. Such prominent protrusion is replaced by a weak lump in *Fruhstorferia*, with exception of *F. flavipennis* Nagai, 1984, in which the lump is acute at apex. But the lower margin is never concave before the protrusion in *Fruhstorferia*. Sometimes there is a basal protrusion also at upper margin of mandible in *Didrepanephorus* species, which is absent in all *Fruhstorferia* species. The mandible of *Didrepanephorus* bent upwards, but directed forward in *Fruhstorferia*. The body length of *Didrepanephorus* varies from 13.0–22.4 mm in males (mandibles excluding) and 13.5–23.2 mm in females (Nagai and Hirasawa 1991; Muramoto and Araya 2000; Muramoto 2003b, 2005, 2013; Qiu et al. 2021). In the genus *Fruhstorferia*, the range is 22.0–31.1 mm in males (mandibles excluding) and 23.0–30.0 mm in females (Nagai 1984, 1989; Ohaus 1903; Prokofiev 2013). The range of body length is almost not overlapped and the genus *Fruhstorferia* is generally longer. At this stage, authors are unable to provide diagnostic characters of females due to lack of material.

The following nomenclatorial acts can be proposed based on the above delimitation: *D. birmanicus* (Arrow, 1907), comb. nov., *D. fukinukii* (Muramoto & Araya, 2000), comb. nov., *F. baron* (Prokofiev, 2013), comb. nov. and *F. anthracina* Ohaus, 1903, comb. rev. Prokofiev (2013) transferred *F. anthracina* to the genus *Didrepanephorus* because of the strongly abbreviated abdominal ventrites 1–4 in male. In the same paper, Prokofiev described a new species, i.e., *D. baron* and assigned it to the genus *Didrepanephorus* for the same reason. The two species lack basal protrusion at the lower margin of male mandible and have body longer, therefore they should be placed in the

genus *Fruhstorferia*. The placement of *D. takuyai* (Muramoto, 2003) is still unclear: the male of this species has upright mandible without protrusion or lump at base of lower margin, and the body length of male can reach 23.5 mm (Muramoto 2003a). Consequently, a checklist of the two genera is provided (Table 1). Only type localities are cited to avoid probable misidentifications.

Morphological remarks. Minute and dense setae on dorsal surface can be traced in the species with glabrous appearance in *Didrepanephorus* and *Fruhstorferia*, as well as in the related genera *Kibakoganea* Nagai, 1984, *Masumotokoganea* Hirasawa, 1992 (the genera *Nagainokoganea* Hirasawa, 1992 and *Pukupuku* Muramoto, 2006 are not examined). This character sometimes has a different arrangement in closely allied species,

Table 1. Checklist of the genera *Didrepanephorus* and *Fruhstorferia* with type localities.

No.	Taxon name	Type locality (verbatim from original description)
1	*Didrepanephorus arnaudi* Muramoto, 2003	Bao Loc, 1400 m, Lam Dong Prov., Vietnam
2	*Didrepanephorus bifalcifer* Wood-Mason, 1878	Wakidgaon, a Village 30–35 miles S.E. of Sadia, in the valley of the Noa Dehing, India
3	*Didrepanephorus birmanicus* (Arrow, 1907), **comb. nov.**	Ruby Mines, Burma
4	*Didrepanephorus fukinukii* (Muramoto & Araya, 2000), **comb. nov.**	Fang, Chiang-Mai Prov., N. Thailand
5	*Didrepanephorus heterocolor* Qiu, Zhao & Xu, 2021	Loudousenlin, 679 m, 25°17'51"N, 108°04'28"E, Maolan Nature Reserve, Libo County, Guizhou, China
6	*Didrepanephorus lamdongensis* Muramoto, 2013	Bao Loc, Lam Dong, South Vietnam
7	*Didrepanephorus lao* Nagai, 2005	Mt. Phu Pan, 1700 m, Ban Saleui, Xam Neua, Houa Phan Prov., N.E. Laos
8	*Didrepanephorus mizunumai* Nagai & Hirasawa, 1991	Fang, Chiangmai Prov., North Thailand
9	*Didrepanephorus mucronatus* Arrow, 1921	Laos, Indo-China
10	*Didrepanephorus nishiyamai* Muramoto, 2006	Mts. Damingshan, Guangxi Prov., China
11	*Didrepanephorus ohbayashii* (Nagai, 2004) = *Didrepanephorus pilosus* Bouchard, 2007 (synonymized by Prokofiev 2014)	Ban Saleui, 1400 m, Xam Neua, Houa Phan Prov., N.E. Laos (*D. pilosus*: Mout Phouu-phien-kha-sieng, Dakchung District, Xekong, Laos)
12	*Didrepanephorus subvittatus* Benderitter, 1922	Chapa, Tonkin
13	*Didrepanephorus tangzhaoyangi* Zhao & Liu, **sp. nov.**	Mangyun Village, 780 m, Taiping Town, Yingjiang County, Dehong Prefecture, Yunnan Prov., China
14	*Didrepanephorus vietnamicus* Muramoto & Kobayashi, 2019	Mt. Axan, 1300 m, Tay Giang, Quang Nam, Vietnam
15	*Didrepanephorus yunnanus yunnanus* (Ohaus, 1911)	Yunnan, China
16	*Didrepanephorus yunnanus clermonti* (Benderitter, 1929)	Chapa, Tonkin
17	*Didrepanephorus yunnanus kachinensis* Muramoto, 2005	Eastern Kachin State, Myanmar
18	*Didrepanephorus yunnanus piaoacensis* (Nagai, 2004)	Mt. Pia Oac, Cao Bang Prov., N. Vietnam
19	*Didrepanephorus yunnanus wakaharai* (Nagai, 2004)	Mt. Phu Pan, 1750 m, Ban Saleui, Xam Neua, Houa Phan Prov., N.E. Laos
20	*Didrepanephorus zen* Muramoto, 2009	Pu Mat, Nghe An Prov., Vietnam
21	*Didrepanephorus takuyai* (Muramoto, 2003), **incertae sedis**	Mt. Braian, 45 km east of Bao Loc, Lam Dong Prov., Vietnam
22	*Fruhstorferia anthracina* Ohaus, 1903, **comb. rev.**	Mauson Berge, Tonkin
23	*Fruhstorferia baron* (Prokofiev, 2013), **comb. nov.**	about 72 km east of Dalat, 750–800 m, Khan Vinh County, KhanhHoa Prov. bordering Lamdong Prov., Dalat Plateau, Vietnam
24	*Fruhstorferia egregia* Pouillaude, 1915	Kon-Tum, Annam
25	*Fruhstorferia flavipennis* Nagai, 1984	Cameron Highlands, Pahang, Malaysia
26	*Fruhstorferia javana javana* Kolbe, 1894	West-Java
27	*Fruhstorferia javana castanea* Pouillaude, 1915	Monts Kawie, Java
28	*Fruhstorferia nigromuliebris* Nagai, 1984	Croker range, ca. 1400 m, near Keningau city, Sabah, Malaysia
29	*Fruhstorferia ohtanii* Nagai, 1989	Lampung, South Sumatra, Indonesia

e.g., *D. mizunumai* Nagai & Hirasawa, 1991 and *D. zen* Muramoto, 2009 (Muramoto 2009). It should be a synapomorphy shared by these genera. The complete frontoclypeal suture in *D. bifalcifer* (Ohaus 1934a) should be an autapomorphy, since its closest congener *D. mucronatus* Arrow, 1921 and other examined *Didrepanephorus* species have incomplete frontoclypeal suture (Qiu et al. 2021). And the prosternal process and medially abbreviated abdominal ventrites 1–4 in males (Muramoto 2005) are present in the species of both genera. It cannot be applied to distinguish the two genera.

***Didrepanephorus tangzhaoyangi* Zhao & Liu, sp. nov.**
http://zoobank.org/F7D27A21-A9C0-4141-A463-2471C3435350
Figs 1–7, 9, 10

Type locality. China, Yunnan Province, Dehong Prefecture, Yingjiang County, Taiping Town, Mangyun Village, 780 m.

Type material (28 specimens). ***Holotype.*** ♂ (SCAU), China: Yunnan Prov., Dehong Pref., Yingjiang County, Taiping Town, Mangyun, 780 m, 2021.VI.3, Shao-Fu Chen leg. // HOLOTYPE *Didrepanephorus tangzhaoyangi* sp. nov. des. Zhao Ming-Zhi & Wei-Xin Liu 2021 [red label].

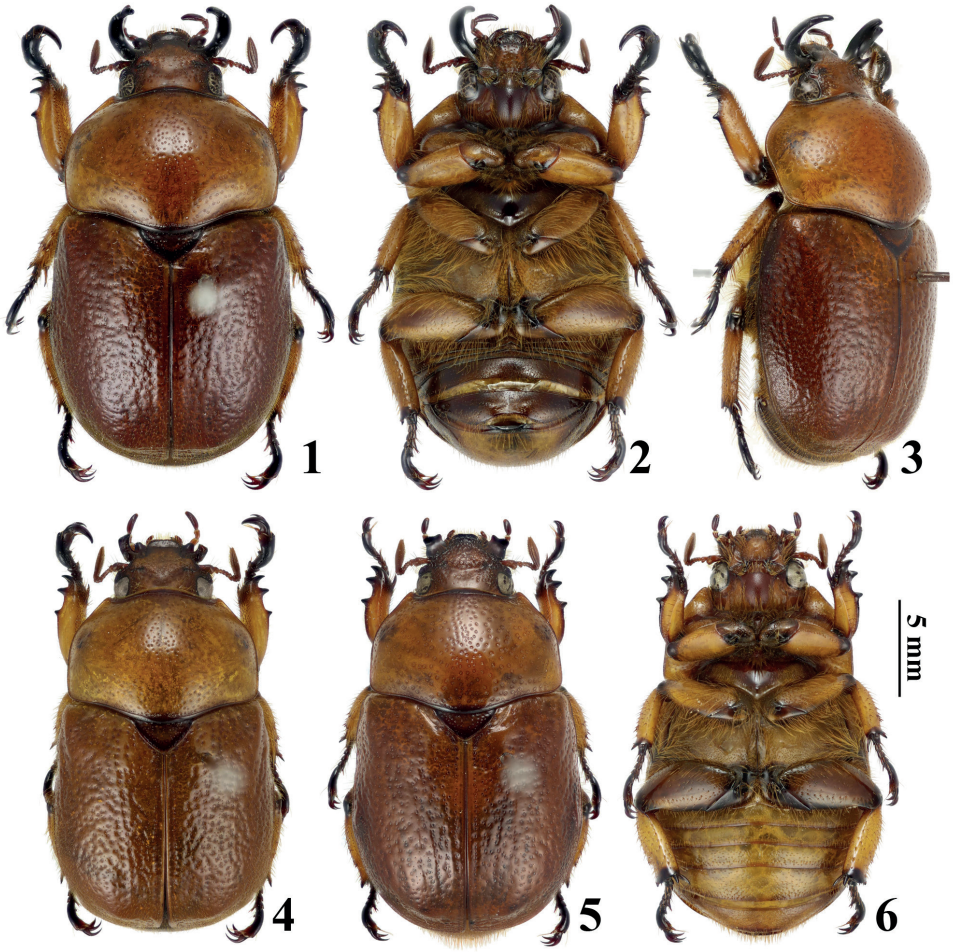
Paratypes (14♂ & 13♀). 3♂, 2♀ (ZMPC), 1♂ (LZPC), same data as holotype; 2♂, 3♀ (TZPC), 1♀ (SCAU), 1♀ (ZMPC), same as preceding but 2021.VI.22; 2♂ & 1♀ (TZPC), same as preceding but 2020.VI; 1♂, 1♀ (MYNU), same as preceding but 750 m, 2019.V, local collector leg.; 1♂ (LCPC), CHINA: Yunnan Prov., Yingjiang County, Mangyun Village, 2017.VI.10; 2♂, 4♀ (TZPC), 1♂ (SFPC), China: Yunnan Prov., Dehong Pref., Yingjiang County, Taiping Town, Mangyun, Husonghe River, 750 m, 2021.VI, Zhao-Wei Guo leg.; 1♂ (CCPC), China: Yunnan Prov., Ruili Botanical Garden, 2013.V.6, Xiao-Dong Yang leg. All paratypes were provided with an additional yellow label: PARATYPE *Didrepanephorus tangzhaoyangi* sp. nov. des. Zhao & Liu 2021.

Description of the holotype (Figs 1–3, 7, 9–10). ***General.*** Body broadly ovoid and strongly convex. All external setae yellowish brown.

Head. Dorsal surface yellowish brown, marginal portions darkened. Clypeus flat, trapezoidal, anterior margin nearly straight, anterior corner obtusely right-angled, side strongly convergent anteriad and weakly swollen in basal two fifth, then roundly curved, and almost subparallel in apical half; punctures large at disc but absent in middle, punctures small at marginal portions. Frontal-clypeal suture broadly interrupted medially, black at each side. Frons and vertex with scattered large punctures. Eyes canthus with roundly curved outer margin, not extends beyond outermost point of eye. Antenna reddish brown, length of antennal club distinctly shorter than antennomeres 2–7 combined. Dorsal surface of head with moderately dense, erect long setae, broadly glabrous medially. Labrum blackish brown, strongly exposed dorsally, with dense, erect long setae along margin, anterior margin feebly sinuate. Mandible blackish brown, bends upward, upper margin with a large, acute basal protrusion and a small, blunt proximal protrusion, lower margin with a large protrusion at base. Maxilla and maxillary palp

reddish brown, maxilla with dense and long setae. Mentum yellowish brown, apical fourth of mentum darkened and slightly swollen, anterior margin curved but strongly concave medially, surface with sparse short setae each emerging from a puncture.

Pronotum. Orange-brown, darkened at anterior and posterior margins. Strongly convex, ca. 1.46 × as wide as long, widest near middle. Anterior margin bisinuate; anterior marginal membrane complete. Sides feebly convergent posteriad in posterior half, roundly and broadly curved at middle, then strongly convergent anteriad in anterior half. Posterior margin broadly protruding in middle. All marginal lines complete. Anterior angle weakly protruding, posterior angle round. Surface with sparse large punctures, somewhat aggregate and smaller at disc. Each dorsal puncture accommodates a minute seta; lateral margin with a row of erect short setae.



Figures 1–6. Habitus of *Didrepanephorus tangzhaoyangi* Zhao, sp. nov. **1** holotype, dorsal view **2** holotype, ventral view **3** holotype, oblique lateral view **4** male paratype, dorsal view **5** female paratype, dorsal view **6** female paratype, ventral view.

Figures 7–10. Morphological details of *Didrepanephorus* species **7** head of holotype of *D. tangzhaoyangi* Zhao & Liu, sp. nov., oblique lateral view **8** head of *D. birmanicus* (Arrow, 1907) (Lectotype of *Fruhstorferia birmanica* Arrow, 1907),oblique lateral view, photo © Keita Matsumoto (NHMUK) **9–10** male genitalia of holotype of *D. tangzhaoyangi* **9** dorsal view **10** ventral view. Scale bar for genitalia only.

Scutellum. Brown, margin blackish brown. Semicircular in shape. Surface with sparse punctures, impunctate medially.

Elytra. Dark orange-brown. Convex, length of each elytron slightly longer than cross width of the two elytra. Surface uneven, humeral and apical umbones weakly prominent. Strial punctures large and deep, punctures on primary striae as large as punctures on secondary striae, 1st primary stria well defined by a longitudinal row of regular punctures, other striae unrecognizable; the whole surface with sparse small punctures, denser on lateral portions. Surface with moderately dense, semierect short setae, denser apically. Epipleura with a row of dense, short to moderately long setae.

Propygidium and pygidium. Brown, disc and apical portions of pygidium yellowish brown. Surfaces with moderately dense small punctures and erect, short to moderately long setae. Pygidium strongly convex and curved to ventrum, apex with a short row of erect long setae.

Ventral thoracic surface. Ventral prothoracic surface yellowish brown, dark brown around procoxal cavity; surface with moderately dense, erect long setae, each emerging from a small puncture; anterior margin with a row of dense and very long setae. Prosternal process gradually narrower toward apex, with very dense, erect long setae. Ventral mesothoracic surface dark brown, with scattered small punctures; a broad mid-

dle portion smooth and glabrous, with an oblique row of small punctures at each side; each puncture with a recumbent short seta. Ventral metathoracic surface yellowish brown, gradually darkened toward each side; with dense small punctures and very long setae, less setose medially.

Abdominal ventrites. Dark brown, ventrites 2–4 yellowish brown between anterior and posterior margin. Ventrites 1–4 strongly abbreviated; ventrite 6 strongly concave apically. Surface with the following arrangements of small punctures: moderately dense at medial portions of each ventrites, moderately dense and forming a row at each side near posterior margin of ventrites 1–5, sparse at each side of ventrites 1–5. Each puncture with a semierect short seta, which become moderately long to long at marginal portions and sides.

Fore legs. Yellowish brown; joints of trochanter, femur, and tibia, including protibial spur and teeth dark brown; protarsus and claws blackish brown. Protibia tridentate, apical and proximal teeth sharp at apices; third tooth shorter and blunter, more spaced from the two anterior teeth. Protarsus strongly thickened, the weakly protruding ventrolateral apex of protarsomere 4 with a small spiniform seta at each side, protarsomere 5 with a small and blunt internomedial protuberance. Protarsal claws strongly bent, unsplit at apices, inner one distinctly larger than the outer one. Empodium with one long seta. Protibial notch distinct. Dorsal surface of protibia with dense, erect short setae at inner half.

Middle and hind legs. Yellowish brown; joints of trochanters, femora, and tibiae (base) pale reddish brown; apex of tibial spurs, as well as tarsi and claws reddish brown. Mesotibia with two sharp teeth at apex, the upper one smaller. Metatibia with an apically subtruncate ramus at apex, the ridge with several small teeth. Base of the sharply protruding ventrolateral apices of tarsomeres 4 with a large spiniform seta at each side; tarsomeres 5 with a large and sharp internobasal protuberance. Outer mesotarsal claws widely and deeply split at apex and forming two branches, upper branches slightly thinner and sharper, that of hindlegs also longer than the lower one; inner tarsal claw simply sharp at apex. Empodium of mesotarsus with one long seta, of metatarsus with two long setae. Femora and inner surface of tibia with dense and very long setae, tibia with dense, semierect, and moderately long setae.

Male genitalia. As Figs 9, 10. Parameres strongly asymmetric, basally fused. Phallobase strongly curved in lateral view.

Male paratypes. Most specimens consistent in morphological features, small-sized male (Fig. 4) has distinctly shorter mandible with proximal tooth absent, pronotum narrower and less convex (1.41 × as wide as long).

Female paratypes (mainly based on individual of Figs 5, 6, with modification based on variability of paratype series). ***General.*** Body more elongated ovoid than male, coloration similar to male.

Head. Clypeus flat, subtrapezoidal (posterior margin ca. 3 × wider than anterior margin), anterior margin weakly sinuate and distinctly reflexed, anterior corner broadly rounded, side strongly convergent anteriad and weakly swollen in basal two fifth, then roundly curved, and strongly convergent anteriad to anterior corner; punctures

large and almost not spaced. Frontal-clypeal suture formed by a sinuate row of large and not spaced punctures. Frons and vertex with irregular large punctures in anterior half, punctures smaller at inner side of eye. Mandible reddish brown, short, anterior edge strongly reflected with two apically blunt teeth, outer edge weakly concave medially and convex basally. Anterior margin of mentum distinctly bilobed. Antennomeres 3–7 somewhat abbreviated.

Pronotum. Pronotum less convex than male, ca. 1.51 ×as wide as long, anterior margin strongly bisinuate; sides feebly convergent anteriad in posterior half, roundly and broadly curved at middle, then strongly convergent anteriad and feebly concave in anterior half; anterior angle distinctly protruding, posterior angle round.

Scutellum. Scutellum more triangular than male.

Elytra. Elytral surface less uneven compared to male, with irregular and vague longitudinal costae; lateral portion of elytron distinctly bulging behind midpoint; punctures sparser.

Pygidium. Pygidium not strongly convex, subtriangular, not bent to ventrum; setae denser than in male.

Abdominal ventrites. Abdominal ventrites light yellowish brown, slightly darkened at posterior margin of each ventrite; ventrites 2–4 not abbreviated, ventrite 6 not concave at apex; extensively bearing moderately dense punctures, ventrite 6 broadly rugopunctate medially.

Legs. Procoxae situated closer. Three teeth of protibia almost equal in size and shape, not very sharp at apices. Protarsus not thickened, base of the sharply protruding ventrolateral apices of protarsomere 4 with a large spiniform seta at each side, protarsomere 5 without internomedial protuberance. Protarsal claws less bent than in male, two claws almost equal in size; the inner protarsal claw widely and deeply split into two branches, the lower branch is a small dent at middle of inner protarsal claw. Empodium of protarsus with two long setae. Dorsal surface of protibia with sparser setae formed in rows. Metafemur thicker than in male. Protibia and mesotibia feebly curved inward.

Measurements. Body length from apex of clypeus to apex of elytron: 15.6–18.3 mm of male (holotype 17.1 mm) and 15.9–18.1 mm of female; greatest width: 9.2–10.6 mm of male (holotype 9.9 mm) and 8.9–10.0 mm of female.

Differential diagnosis. The new species is most similar to Laotian *D. ohbayashii* (Nagai, 2004), but the large-sized male of the new species has distinctly shorter mandibles. The large and acute basal protrusion is absent in upper margin of mandible in male of *D. ohbayashii*. The parameres of the two species are basally fused and strongly asymmetric. However, the parameres of *D. tangzhaoyangi* differ as follows: the left paramere without an incision at outer margin, apex of the left paramere distinctly narrower, the right paramere strongly curved outward proximally (orients apically in *D. ohbayashii*). The female of *D. ohbayashii* has more concave outer edge of mandible.

Etymology. The specific epithet is dedicated to Zhao-Yang Tang, who generously provided most of the type material of the new taxon.

Distribution. China (Yunnan: Dehong Prefecture).

***Didrepanephorus birmanicus* (Arrow, 1907), comb. nov.**
Figs 8, 11–15

Fruhstorferia birmanica Arrow, 1907: 354 [original description]; Arrow 1917: 49 [partim], fig. 15; Ohaus 1918: 43 [catalogued]; Ohaus 1934b: 121 [catalogued]; Machatschke 1972: 53 [catalogued]; Muramoto and Araya 2000: 12, figs 3–4 [syntype male figured]; Krajčík 2007: 70 [catalogued]; Krajčík 2012: 110 [catalogued, subgeneric placement unnoted].
Fruhstorferia (*Kibakoganea*) *birmanica* Arrow, 1907: Nagai 1984: 29 [catalogued].

Type locality. "Burma, Ruby Mines", in currently Mogok City of Mandalay, Myanmar.

Type material (1 specimen). ***Lectotype*** of *Fruhstorferia birmanica* Arrow, 1907 (hereby designated). ♂ (BMNH), "Birmah [R]uby M^es^ // Doherty // 64607 // Fry Coll. 1905-100. // *Fruhstorferia birmanica*, Arrow type ♂ A. a M., 1907. // Type // HOLOTYPE *Fruhstorferia birmanica* A. M. SOULA det 1994 // NHMUK014379787". It will be provided with an additional red label: LECTOTYPE *Fruhstorferia birmanica* Arrow, 1907 des. Zhao Ming-Zhi 2021.

Remarks. The taxon *Fruhstorferia birmanica* was originally described based on a pair of specimens from Ruby Mines, Burma (Arrow 1907). The lectotype has not yet been designated and the male illustrated by Muramoto and Araya (2000) has been erroneously fixed as holotype. According to Art. 74.7.1 (ICZN 1999), both specimens should be regarded as syntypes. The examination of both syntypes reveals that the female is conspecific with *D. mizunumai* Nagai & Hirasawa, 1991. Therefore, a lectotype designation is necessary.

The male genitalia of the lectotype (Figs 8, 11–15) is partly damaged, which greatly complicates the comparison to its related species. However, the similarity of this species to small-sized male of *D. yunnanus* (Ohaus, 1911) is still apparent in many external features, especially in the allied shape of terminal segment of maxillary palp, which is more expanded and compressed than other *Didrepanephorus* species. There is a strong concavity at the base of lower margin of mandible. The protrusion at lower margin is partly hidden under the labrum. These characters match the above definitions for *Didrepanephorus*. Thus, this species is transferred to the genus *Didrepanephorus* herein. Among the five subspecies of *D. yunnanus*, i.e., *D. y. yunnanus* (Ohaus, 1911), *D. y. clermonti* Benderitter, 1929, *D. y. piaoacensis* Nagai, 2004, *D. y. wakaharai* Nagai, 2004, and *D. y. kachinensis* Muramoto, 2005, recognized by Muramoto (2005), *D. y. kachinensis* appears to be most similar to *D. birmanicus* due to the generally reddish brown body in combination to the closest geographical distance. To fully understand the relation between the two species, examination of topotypical specimens of *D. birmanicus* with undamaged male genitalia is needed.

This species was partly misinterpreted and the name was previously applied to two different species (see below). This species is so far only known from the lectotype.

Distribution. Myanmar (Mandalay Region: Mogok).

Didrepanephorus fukinukii (Muramoto & Araya, 2000), comb. nov.

Fruhstorferia fukinukii Muramoto & Araya, 2000: 12, figs 1–2, 7 [original description]; Nagai 2004: 150, figs 21–22, 30 [additional record from Mt. Doi Suthep, near Chiang Mai]; Krajčík 2007: 71 [catalogued]; Krajčík 2012: 110 [catalogued, subgeneric placement unnoted].

Fruhstorferia birmanica Arrow, 1907: Nagai and Hirasawa 1991: 7, figs 19, 29–31 [recorded from Northwest Thailand]; Young 1999: 357, fig. 1b; Nagai 2004: 150, figs 19–20, 29 [recorded from Thailand, Fang].

Type locality. North Thailand, Chiang Mai Province, Fang.

Material examined (2 specimens). 1♂, 1♀ (GGPC), Thailand, Chiang Mai, Fang, 07.2015.

Remarks. This species is transferred to the genus *Didrepanephorus* here because of the distinct basal protrusion at the lower margin of mandible, as shown by Nagai and Hirasawa (1991).

Judging from the figures of habitus and male genitalia, the records of *F. birmanica* from Northwest Thailand (Nagai and Hirasawa 1991; Nagai 2004) are considered as *D. fukinukii* here. Thus, the record of *F. birmanica* in Thailand should be omitted. Arrow (1917, 1919) and Muramoto and Araya (2000) partly misinterpreted the taxon *F. birmanica* and applied the name to a species from Chin Hills. The species from Chin Hills appears to be very similar to *D. fukinukii* but having different male genitalia, which has strong incision at outer margin of left paramere.

Distribution. Thailand (Chiang Mai).

Didrepanephorus mizunumai Nagai & Hirasawa, 1991

Figs 16–18

Fruhstorferia birmanica Arrow, 1907: Arrow 1907: 354 [partim, female]; Arrow 1917: 49, fig. 16 [partim, female].

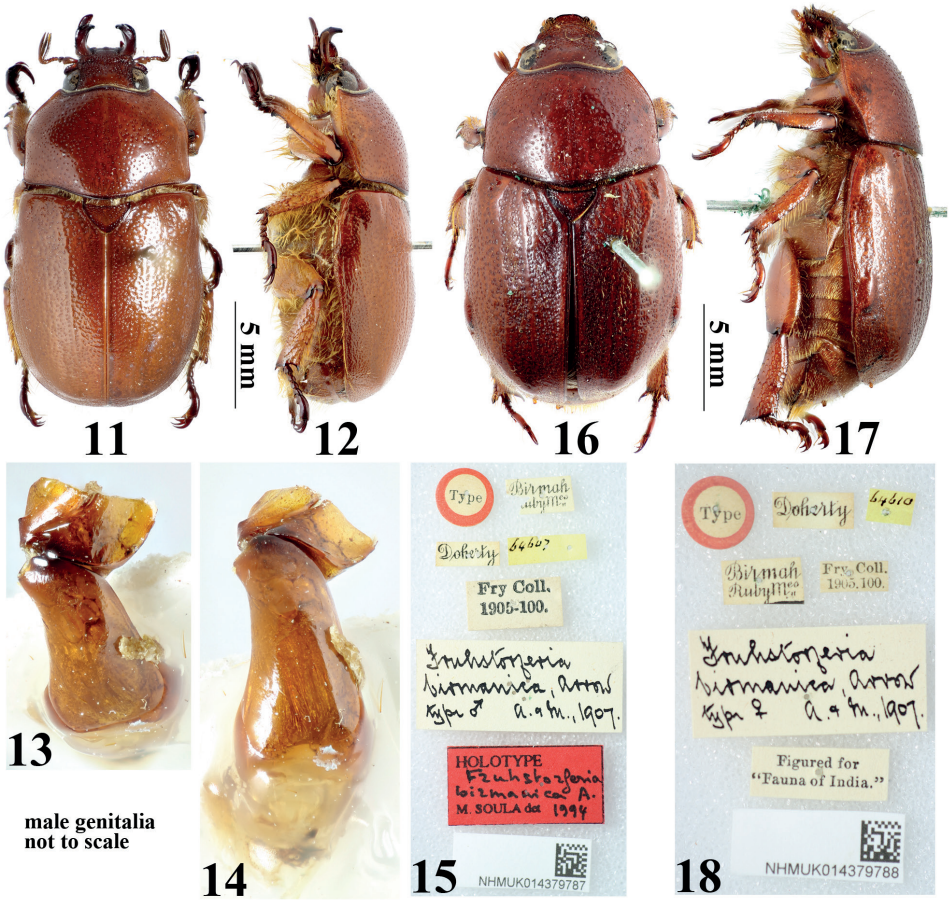
Didrepanephorus mizunumai Nagai & Hirasawa, 1991: 10, figs 2–5, 20, 32–34, 39–40 [original description]; Nagai 2005: 271, figs 4–6, 17; Muramoto 2009: 59, figs 4–6.

Fruhstorferia mizunumai (Nagai & Hirasawa, 1991): Jameson 1997: 170, figs 21–22 [new combination]; Nagai 2004: 150, figs 13–16, 27 [recorded from Houa Phan Prov., Laos]; Krajčík 2007: 71 [catalogued]; Krajčík 2012: 93 [catalogued, subgeneric placement unnoted].

Fruhstorferia yunnana Ohaus, 1911: Muramoto 1993: 7, figs 6, 10 [misidentification, recorded from Sapa, N. Vietnam].

Type locality. North Thailand, Chiang Mai Province, Fang.

Material examined (5 specimens). 1♀ (BMNH), "Birmah Ruby M^{es} // Doherty // 64610 // Fry Coll. 1905. 100. // *Fruhstorferia birmanica*, Arrow type ♀ A. a M.,



Figures 11–18. Type material of *Didrepanephorus species*. **11–15** male of *D. birmanicus* (Arrow, 1907) (Lectotype of *Fruhstorferia birmanica* Arrow, 1907) **16–18** female of *D. mizunumai* Nagai & Hirasawa, 1991 (paralectotype of *F. birmanica*), habitus in dorsal view **11, 16** habitus in dorsal view **12, 17** habitus in lateral view **13** aedeagus showing parameres in dorsal view **14** aedeagus in dorsal view **15, 18** attached labels. All photos © Keita Matsumoto (NHMUK).

1907. // Figured for "Fauna of India." // Type // NHMUK014379788", it will be provided with an additional red label: PARALECTOTYPE *Fruhstorferia birmanica* Arrow, 1907 des. Zhao Ming-Zhi 2021; 1♂, 1♀ (ZMPC), Thailand, Chiang Mai, Fang, 26.VI.2011; 1♂, 1♀ (ZMPC), same as preceding but 2015.V.

Remarks. The female of *D. mizunumai* is easily characterized by the three strongly elevated costae between humeral and apical umbone, as well as a bulge on lateral portions of elytron. The paralectotype of *F. birmanica* (Figs 16–18) well fits topotypical female of *D. mizunumai* from Fang. Therefore, the female paralectotype represents a new distributional record for Myanmar. Two similar species, i.e., Laotian *D. lao* Nagai, 2005 and Vietnamese *D. zen* Muramoto, 2009 have minor morphological differences, but both are more restricted in their known distribution ranges.

Distribution. Laos (Houaphanh); Myanmar (Mandalay) (new record); Thailand (Chiang Mai); Vietnam (Lao Cai).

Discussion

In this study, we propose a new delimitation for *Didrepanephorus* and *Fruhstorferia*, which temporarily solves those taxonomic conflicts at generic level. But the placement of *D. takuyai* (Muramoto, 2003) remains uncertain and this species requires further examination. Type material of five of the seven taxa of the genus *Didrepanephorus* described before 2000 had been re-examined and illustrated (Muramoto and Fujioka 2000; Muramoto 2005; Qiu et al. 2021; the present paper). Species described in this century were all well-illustrated. Hence there is a good taxonomic fundament at specific or infraspecific level. To date, the genus *Didrepanephorus* comprises 21 valid taxa distributed in the Indochina Peninsula, southern China, and the Himalaya. Two thirds of the valid taxa were described in this century and it is likely that new species will be discovered in the future. The Chin Hills species similar to *D. fukinukii* should be studied to ensure its status. The registered Chinese fauna of *Didrepanephorus* increased rapidly from two to six species within two years. New faunistic records can be expected due to the existence of other congeners known from the adjacent regions.

Moreover, no phylogenetic analysis was conducted for *Didrepanephorus* and related genera, i.e., *Fruhstorferia*, *Kibakoganea*, *Masumotokoganea*, *Nagainokoganea* and *Pukupuku*. In the morphology-based phylogenetic study (Jameson 1997), *D. mizunumai* and *K. sexmaculata* were used as representatives of the subtribe Fruhstorferiina Ohaus, 1918 and formed a clade together with the genera *Ceroplophana* Gestro, 1893, *Dicaulocephalus* Gestro, 1888 and *Peperonota* Westwood, 1847, which were traditionally recognized as members of the subtribe Parastasiina Burmeister, 1844 (Ohaus 1918, 1934b). It suggests that these three genera should be taken into consideration as well.

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Three new species of *Retusigaster* Dangerfield, Austin & Whitfield, 1999 (Hymenoptera, Braconidae, Cardiochilinae) with an illustrated key to the New World species

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Abstract

Retusigaster Dangerfield, Austin & Whitfield, 1999 is a genus of the subfamily Cardiochilinae Ashmead, 1900 and exhibits high species richness in the New World. Eight species of the genus were recorded before this work: five species from the Nearctic region, two species from the Neotropical region, and one species from the Palearctic region. In this article, three new species of New World *Retusigaster* are described based on morphological characters: *R. pulawskii* **sp. nov.**; *R. purshi* **sp. nov.**; *R. vanduzeei* **sp. nov.** In addition, potential food sources of the members of *R. arugosus* (Mao, 1949) and *R. purshi* **sp. nov.** are reported, and an illustrated key to the New World species of *Retusigaster* is provided. The number of species of *Retusigaster* in the New World is increased from seven to ten.

Keywords

Gossypium sp., parasitoid wasps, *Purshia mexicana*, taxonomy

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Introduction

Retusigaster Dangerfield, Austin & Whitfield, 1999 is a genus of Cardiochilinae Ashmead, 1900 (Ashmead 1900) with eight valid species (Yu et al. 2016). Seven species were recorded from the New World: *R. arugosus* (Mao, 1949), *R. albopilosus* Mercado, 2003, *R. brevitarsus* (Mao, 1949), *R. dignus* (Mao, 1949), *R. noguerai* Mercado, 2003, *R. pullus* (Mao, 1949) and *R. rubidus* (Mao, 1949). One species, *R. eremita* (Kokujev, 1904) was recorded from the Palearctic region. Genus-level phylogenetic analyses, based on morphological data, were conducted by Dangerfield et al. (1999) and Mercado and Wharton (2003) and validated the genus. In the phylogeny of Dangerfield et al. (1999), which included representatives of all the cardiochiline genera in the world, *Retusigaster* was resolved as a monophyletic group. In the phylogeny of Mercado and Wharton (2003), *Retusigaster* species groups, which were defined by the authors based on the degree of thickening of the apex of hind tibia were clustered with the members of *Toxoneuron* Say, 1836 (Say 1836) but made *Toxoneuron* paraphyletic. Regarding the result of their analysis, Mercado and Wharton (2003) described that "Nevertheless, *Retusigaster*, as defined by its type species *rubidus*, is readily identifiable and is accepted here as a monophyletic group regardless of the rank eventually accorded." In the current project, I follow the definition of Dangerfield et al. (1999) and describe three new species collected in the New World. Potential food sources of *R. arugosus* and *R. purshi* sp. nov. are reported, and an illustrated key to the New World species is included. In addition, the species groups defined by Mercado and Wharton (2003) with their diagnostic characters are re-evaluated and discussed, and the placement of *R. eremita* is discussed.

Materials and methods

Specimen information

The specimens for this work were borrowed from the California Academy of Sciences (**CAS**; San Francisco, CA, USA), Hymenoptera Institute (**HIC**; Redlands, California, USA), Museum of Comparative Zoology (**MCZ**; Cambridge, Massachusetts, USA), and Texas A&M University Insect Collection (**TAMU**; College Station, Texas, USA). Types of the new species will be deposited in CAS and the National Museum of Natural History (**NMNH**; the Smithsonian Institution, Washington D.C., USA).

Morphological analyses

Specimens were examined using a Leica MZ75 stereomicroscope. The morphological terminology follows Dangerfield et al. (1999) and Sharkey and Wharton (1997). The terms used in this work can be found as synonyms on the website of Hymenoptera Anatomy and Consortium (2022). Terms for surface sculpture are based on Harris (1979). The following acronyms are used for morphological terms: POL: distance between posterior ocelli, T2:

second metasomal tergum, and T3: third metasomal tergum. Using a Visionary Digital BK Plus imaging system (Dun, Inc.) with a Canon EOS 5DS DSLR, images were captured. Image stacking was performed via Zerene Stacker v.1.04 (Zerene Systems LLC.). Images were edited using Adobe Photoshop CS 6 and Photoshop CC 2022 v. 23.0 (Adobe Systems, Inc), and final image plates were produced using the same Adobe software. Body parts were measured using the same Adobe software mentioned. Numbers in parentheses in species descriptions indicate 0.01× the actual size of each body character. The unit of length is mm.

Results

Taxonomy

***Retusigaster* Dangerfield, Austin & Whitfield, 1999**

Type species. *Cardiochiles rubidus* Mao, 1949

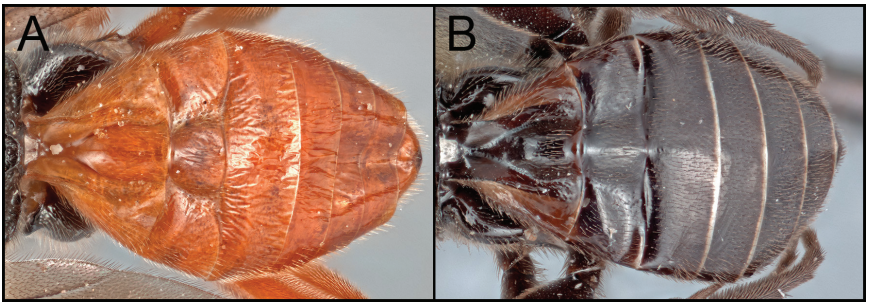
Diagnosis. Dangerfield et al. (1999) and Mercado and Wharton (2003) provided detailed diagnostic characters. *Retusigaster* can be easily distinguished from other cardiochiline genera by the combination of the following characters: eye seemingly bare (Figs 2C, 3C, 5C); clypeal tubercle absent (Figs 2C, 3C, 5C); mouthparts short (Figs 2C, 3C, 5C); scutellum apically with carinate margin (Key image 2); hind tibia without apical cuplike projection (Figs 2A, 3A, 5A); ovipositor and ovipositor sheath short (Figs 2A, 3A, 5A); hypopygium entirely sclerotized and ventro-apically blunt (Figs 2A, 3A, 5A).

Distribution. Nearctic region (Canada, USA, Mexico), Neotropical region (Jamaica and Mexico), Palearctic region (Kazakhstan, Mongolia, Turkey, Turkmenistan).

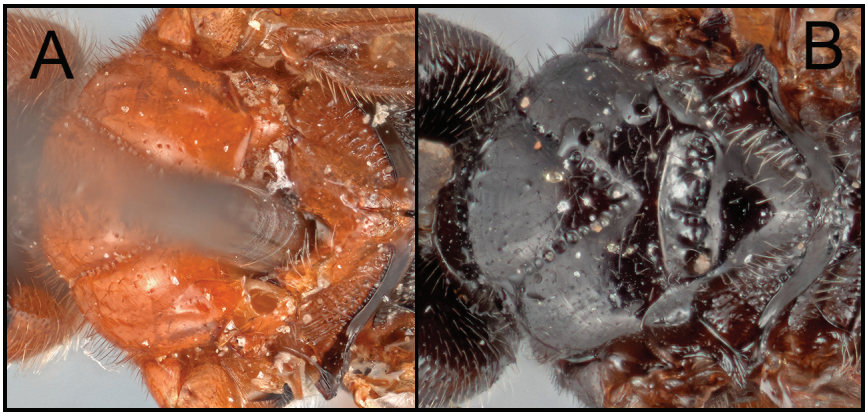
Biology. Potential food sources of two species of *Retusigaster* are found. A member of *R. arugosus* was collected on cotton (*Gossypium* sp.; Malvaceae) in Texas, and a specimen of *R. purshi* sp. nov. was collected on Mexican cliffrose (*Purshia mexicana* (D. Don) S. L. Welsh; Rosaceae) in Nevada.

Key to species of *Retusigaster* of the New World

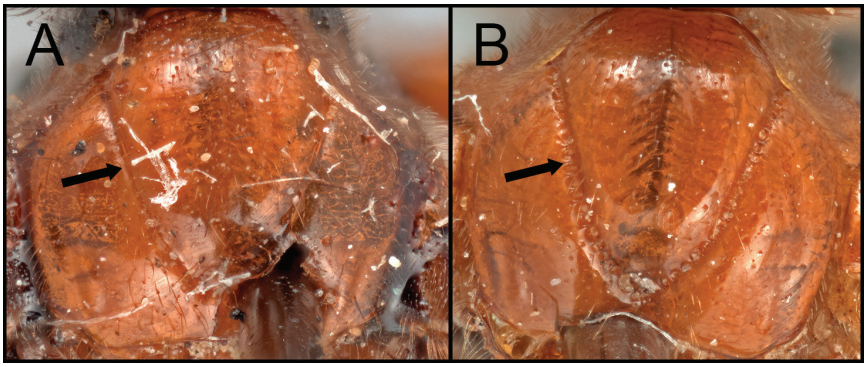
1 Metasoma mostly or entirely pale.....**2**
– Metasoma mostly or entirely dark.....**5**



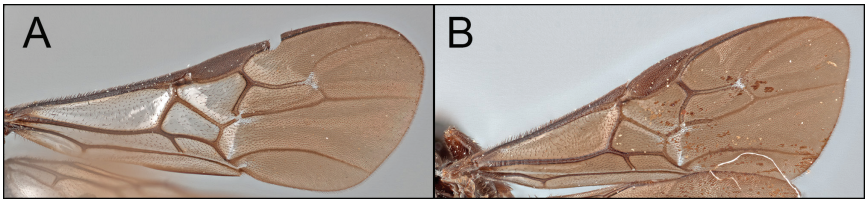
2 Mesoscutum mostly or entirely pale **3**
– Mesoscutum mostly or entirely dark **4**



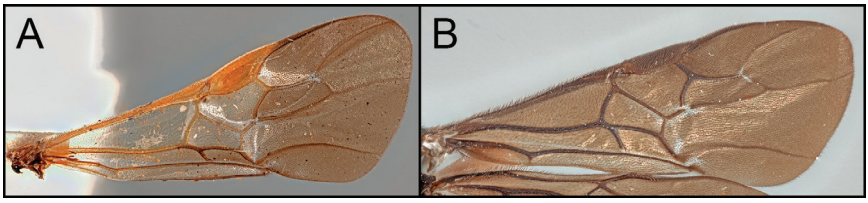
3 Notauli smooth ..... ***R. brevitarsus***
– Notauli crenulate ..... ***R. rubidus***



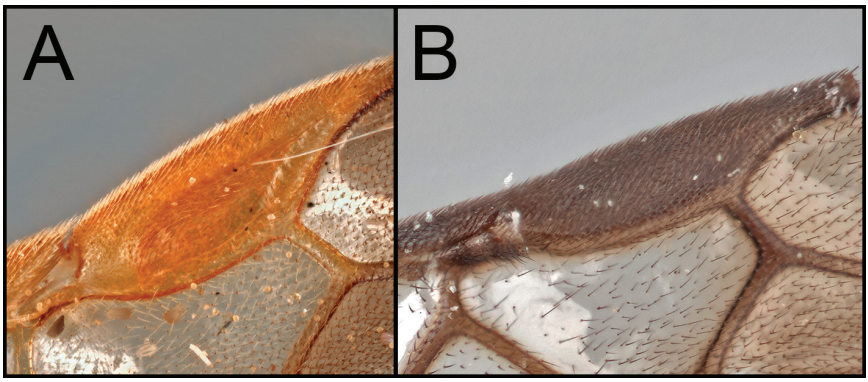
4 Fore wing apically infuscate ..... ***R. arugosus***
– Fore wing entirely infuscate ..... ***R. pullus***



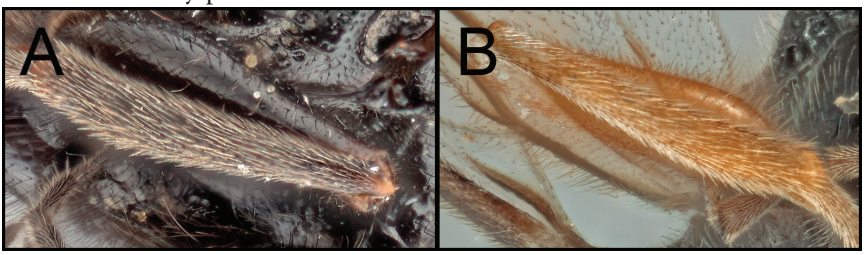
5 Fore wing apically infuscate **6**
– Fore wing entirely infuscate **9**



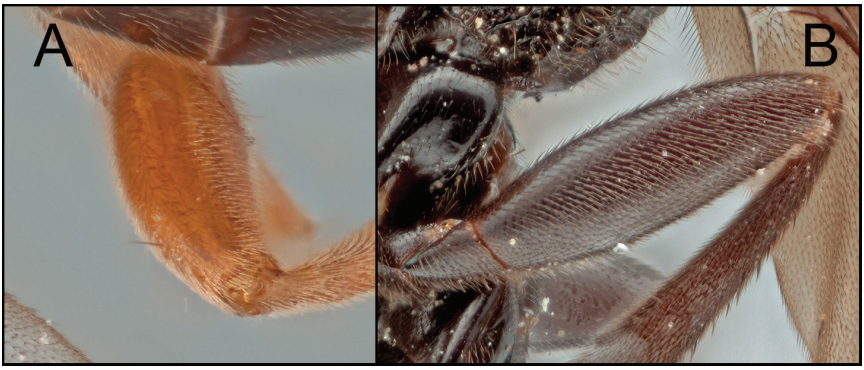
6 Stigma entirely pale.....***R. dignus***
– Stigma entirely dark.....7



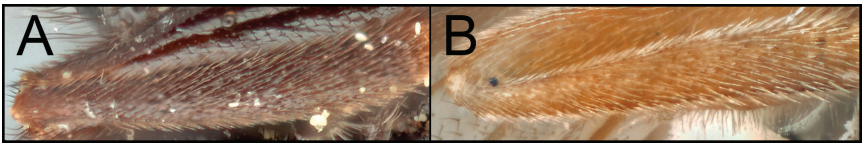
7 Fore tibia entirely dark.....***R. purshi* sp. nov.**
– Fore tibia entirely pale.....**8**



8 Metafemur entirely pale..... ***R. pulawskii* sp. nov.**
– Metafemur entirely dark ..... ***R. albopilosus***



9 Fore tibia entirely black.....***R. vanduzeei* sp. nov.**
– Fore tibia entirely pale..... ***R. noguerai***



Species descriptions

Retusigaster albopilosus Mercado, 2003

Material examined. ***Paratypes*** Mexico • 2 ♀; Xmatkuil, Mérida, Yucatán; 25–28.v.1996; Wharton & León; Malaise Trap. Deposited in TAMU.

Diagnosis. Members of *Retusigaster albopilosus* can be recognized by the combination of the following characters: body 3.5–5.5 mm; fore wing entirely infuscate with dark stigma; fore tibia pale; mid and hind femur entirely dark; T2 entirely dark.

Description. See Mercado and Wharton (2003).

Male. See Mercado and Wharton (2003).

Biology. Unknown.

Distribution. Neotropical region (Mexico).

Retusigaster arugosus (Mao, 1949)

Material examined. ***Non-type specimens*** USA: 1♀; Lexington, Massachusetts; 8.ix.1963; H. E. Evans. Deposited in MCZ. 1♀; only collected location was labelled (Chicago). Deposited in MCZ. 1♀; only collected month was labelled (July). Identified as *Cardiochiles abdominalis* Cresson by a previous examiner. Deposited in MCZ. 1♀; near Rio Frio, Garner State Park, Uvalde Co.; 21.vii.1986; 1400'; Wooley & Zolnerowich. Deposited in TAMU. 1♀; Brazos County, Texas; 25.vi.1937; J. E. Gillaspy. Deposited in TAMU.

Diagnosis. *Retusigaster arugosus* is nearly identical to *R. pullus*. The members of both species possess dark head and metasoma with pale metasoma. As Mao (1949) mentioned, *R. arugosus* is distinguished from *R. pullus* by having basally hyaline and apically infuscate wings (Key image 4A). Body ~ 5.5 mm.

Description. See Mao (1949).

Male. Unknown.

Biology (potential food source). Cotton (*Gossypium* sp.; Malvaceae; recorded on the label of one specimen collected in Brazos County, Texas).

Distribution. Nearctic region (Canada, USA).

Retusigaster brevitarsis (Mao, 1949)

Material examined. ***Non-type specimens*** USA: 1♀; Saugus, Los Angeles, California; 18.viii.1917; J. Bequaers. Deposited in MCZ. 1♀; Warren, San Diego, California; 13.viii.1917; J. Bequaers. Deposited in MCZ.

Diagnosis. Members of *Retusigaster brevitarsis* are most similar to *R. rubidus*. *Retusigaster brevitarsis* can be distinguished from other members of the genus by the following characters: body length (~ 7.0mm); notauli smooth (Key image 3A);

mesoscutum mostly orange pale; forewing entirely infuscate with dark (Key image 5B); metasoma mostly orange pale.

Description. See Mao (1949).

Male. Unknown.

Biology. Unknown.

Distribution. Nearctic region (USA).

Retusigaster dignus **(Mao, 1949)**

Fig. 1

Material examined. ***Non-type specimen*** USA: 1♀; Pearsall, Texas. 30.ix.1936. Deposited in TAMU.

Diagnosis. *Retusigaster dignus* can be distinguished from other members of *Retusigaster* by having longer body length (~ 7.5mm); fore wing apically infuscate with pale stigma (Key Image 5A); basal spur on hind tibia 0.67 × longer than length of basitarsus; T1 pale; T2 mostly pale, medially and submedially dark (Fig. 1).

Description. See Mao (1949).

Male. Unknown.

Biology. Unknown.

Distribution. Nearctic region (USA).

Figure 1. Dorsal habitus of *Retusigaster dignus*.

Retusigaster noguerai **Mercado, 2003**

Material examined. ***Paratype*** Mexico: 1♀; Estación de Biología Chamela, Jalisco, Mexico; 3–9.vii.1993; Wharton & Sharkey. ***Non-type specimen*** Mexico • 1♀; same as previous except for collecting date and collector. 8.vii.1994; I. Mercado. Deposited in TAMU.

Diagnosis. *Retusigaster noguerai* is similar to *R. vanduzeei* sp. nov. *R. noguerai* can be distinguished from other members of the genus by the combination of the following

characters: body 4.5–6.0 mm; fore wing entirely infuscate with dark stigma; fore femur and tarsus pale; metasoma mostly dark; T2 1.0–1.3 × longer than its posterior width.

Description. See Mercado and Wharton (2003).

Male. See Mercado and Wharton (2003).

Host. Unknown.

Distribution. Neotropical region (Mexico).

Retusigaster pulawskii **Kang, sp. nov.**
http://zoobank.org/B6B59B1C-6EFE-4793-BA8B-0D5DB4A67502
Fig. 2A–G

Material examined. ***Holotype*** Jamaica: ♀; Port Henderson, Catherine Parish; 16.xi.1986; W. J. Pulawski. Holotype will be deposited in CAS.

Diagnosis. *Retusigaster pulawskii* sp. nov. is most similar to *R. albopilosus*. The following characters can distinguish the new species from other species of *Retusigaster*: precoxal sulcus not reaching posterior margin of mesopleuron (Fig. 2G); fore tibia entirely pale (Fig. 2A); fore wing apically infuscate (Fig. 2E); transverse carina of propodeum reaching lateral margin (Figs 2D, 2F); stigma entirely dark (Fig. 2E); hind femur entirely pale (Fig. 2A); metasoma mostly dark (Fig. 2B); T1 laterally orange (Fig. 2D); Y-shaped suture of T1entirely smooth (Fig. 2D); T2 medially orange (Fig. 2D).

Description. Body ~ 4.69 mm. ***Head*****:** Antenna 37-segmented. Face width ~ 1.28 × longer than its height (73:57). Interantennal space with median carina. Width of anterior ocellus ~ 0.92 × longer than POL (11:12). Eye seemingly without interommatidial setae; median width of eye ~ 0.97 × longer than the median width of gena in lateral view (31:32). Gena extended ventroposteriorly into weak prominence. Clypeus ~ 2.25 × longer than its height (54:24); clypeal tubercles absent. Mandible bidentate. Maxillary palpus five-segmented. Labial palpus four-segmented. Galea short. Glossa short. Occipital carina absent. ***Mesosoma*****:** Notauli entirely crenulate, strongly crenulate posteriorly. Scutellar sulcus ~ 0.44 × longer than width (19:43), with three carinae. Postscutellar depression finely crenulate. Pronotum dorsally crenulate and posteriorly rugulose. Mesopleulon mostly smooth, posterior margin strongly crenulate; precoxal sulcus crenulate not reaching posterior margin; epicnemial carina absent; episternal scrobe present. Metapleuron anteriorly smooth and posteriorly rugulose. Propodeum strongly rugulose, ~ 0.36 × longer than its median width (36:100); propodeal areola heart-shaped, ~ 1.17 × longer than its maximum width (27:23); transverse carina reaching lateral margin. ***Legs*****:** Basal spur on fore tibia ~ 0.58 × longer than length of basitarsus (19:33). Basal spur on mid tibia ~ 0.63 × longer than length of basitarsus (30:48). Hind tibia without apical cup-like projection; basal spur on hind tibia ~ 0.64 × longer than length of basitarsus (47:74); claws pectinate. ***Wings*****:** Fore wing ~ 4.14 mm; second submarginal cell trapezoid, ~ 3.20 × longer than height (80:25); 1r absent; 3r absent; RS evenly curved; pterostigma ~ 2.89 × longer than wide medially (81:28).

Hind wing ~ 3.43 mm; 2r-m absent; 2–1A basally present. ***Metasoma*:** T1 ~ 1.32 × longer than its posterior width (66:50), anteriorly with lateral carina; Y-shaped suture of T1entirely smooth. T2 ~ 0.34 × longer than its posterior width (36:105), ~ 0.95 × longer than T3 (36:38). T3 ~ 0.36 × longer than its posterior width (38:106). Hypopygium without median longitudinal fold. Protruded ovipositor sheath ~ 0.27 × longer than length of hind basitarsus (20:74), apically with short setae. ***Color*:** Body mostly dark brown. Fore wing apically infuscate; stigma entirely dark. The following areas orange: fore tibia; all femora, basal mid and hind tibiae; medial and lateral T1; medial T2.

Etymology. Named in honor of Dr Wojciech Jerzy Pulawski, Curator of Entomology, Emeritus, at CAS, the person who collected the specimen from Jamaica.

Biology. Unknown.

Distribution. *Retusigaster pulawskii* sp. nov. is known from a single female specimen collected in Jamaica.

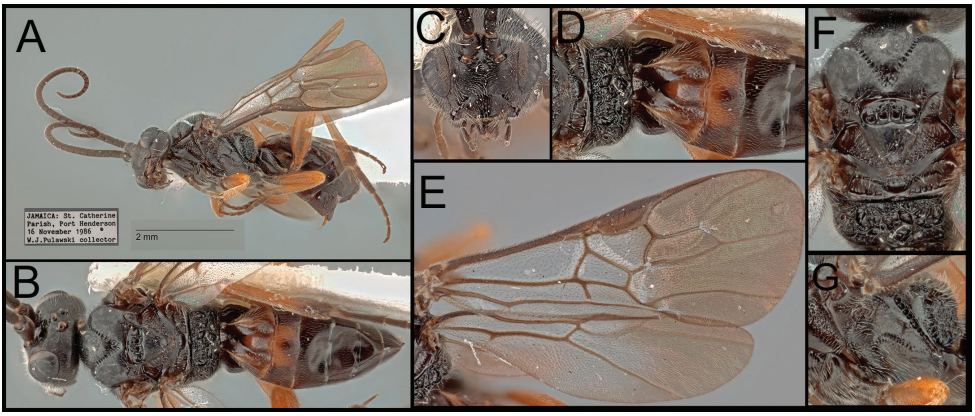


Figure 2. *Retusigaster pulawskii* sp. nov. **A** lateral habitus **B** dorsal habitus **C** anterior head **D** dorsal propodeum to T3 **E** wings **F** dorsal mesosoma **G** mesopleuron and metapleuron.

Retusigaster pullus (Mao, 1949)

Material examined. ***Non-type specimens*** USA • 1♀; three miles east of Presidio, Texas; 1–3.v.1963; H. E. Evans. Deposited in MCZ. 1♀; Randall County, Texas; Bushland; 26.vii.–7.viii.1983; T. J. Kring; Malaise trap. Deposited in TAMU.

Diagnosis. By having dark head and mesosoma with pale metasoma, members of *R. pullus* and *R. arugosus* can be distinguished from the other members of *Retusigaster*. The members of *R. pullus* are distinguished from the members of *R. arugosus* by having entirely infuscate wings (Key image 4B).

Description. See Mao (1949).

Male. Unknown.

Biology. Unknown.

Distribution. Nearctic region (USA).

Retusigaster purshi **Kang, sp. nov.**
http://zoobank.org/F46EE693-08F0-45D5-ABEF-0E30F533153B
Fig. 3A–E

Material examined. ***Holotype*** USA: ♀; 36°16.15'N, 115°33.29'W; Telephone Canyon, Clark County, Nevada, USA; 16.vi.1998; K. Keen & M. Andres; Collected on *Purshia Mexicana*. Holotype will be deposited in NMNH.

Diagnosis. *Retusigaster purshi* sp. nov. is most similar to *R. vanduzeei* sp. nov. The following characters can distinguish *R. purshi* sp. nov. from other species of *Retusigaster*: body ~ 7.0 mm, mostly black except for medial mandible (reddish brown) and ovipositor (Fig. 3A, C); precoxal sulcus crenulate reaching posterior margin (Fig. 3A); propodeal areola pentagonal (Fig. 3B); fore wing apically infuscate with dark stigma (Fig. 3A); fore tibia entirely dark; Y-shaped suture posteriorly crenulate (Fig. 3B).

Description. Body ~ 7.06 mm. ***Head*****:** Head entirely with long setae. Antenna 44-segmented. Face width ~ 1.56 × longer than its height (128:82). Width of anterior ocellus ~ 0.70 × longer than POL (16:23). Eye seemingly without interommatidial setae; median width of eye about ~ 0.90 × longer than the median width of gena in lateral view (47:52). Gena extended ventro-posteriorly into moderate prominence. Clypeus ~ 2.46 × longer than its height (96:39), with punctures; clypeal tubercles absent. Mandible bidentate. Maxillary palpus five-segmented. Labial palpus four-segmented. Galea short. Glossa short. Occipital carina absent. ***Mesosoma*****:** Notauli entirely evenly crenulate. Scutellar sulcus ~ 0.45 × longer than width (28:62), with seven carinae, posteriorly rugulose. Postscutellar depression dorsally rugulose and ventrally crenulate. Pronotum dorsally crenulate and posteriorly rugulose. Mesopleuron dorsally with punctures and ventrally crenulate and rugulose, posterior margin strongly crenulate; precoxal sulcus crenulate reaching posterior margin; epicnemial carina absent; episternal scrobe present. Metapleuron anteriorly smooth and posteriorly rugulose. Propodeum strongly rugulose, ~ 0.38 × longer than its median width (61:162); propodeal areola pentagonal, ~ 1.45 × longer than its maximum width (48:33); transverse carina reaching lateral margin. ***Legs*****:** Basal spur on mid tibia ~ 0.64 × longer than length of basitarsus (40:63). Hind tibia without apical cup-like projection; basal spur on hind tibia ~ 0.61 × longer than length of basitarsus (57:93); claws pectinate. ***Wings*****:** Fore wing ~ 6.59 mm; second submarginal cell trapezoid, ~ 3.02 × longer than height (124:41); 1r present as basal stump; 3r absent; RS evenly curved; pterostigma about 3.00 × longer than wide medially (105:35). Hind wing ~ 4.57 mm; 2r-m absent; 2–1A present reaching basal half. ***Metasoma*****:** T1 ~ 1.01 × longer than its posterior width (93:92), anteriorly with lateral carina; Y-shaped suture of T1 anteriorly smooth and posteriorly crenulate. T2 ~ 0.27 × longer than its posterior width (43:158), ~ 0.77 × longer than T3 (43:56). T3 ~ 0.34 × longer than its posterior width (56:164). Hypopygium without median longitudinal fold. Protruded ovipositor sheath ~ 0.29 × longer than length of hind basitarsus (27:93), apically with long setae. ***Color*****:** Body

mostly black. Wings basally hyaline and apically infuscate. Pterostigma entirely dark brown. Mandible apically black. Apical tarsomeres pale.

Etymology. Named in honor of Fredrick Traugott Pursh, a German American botanist. The genus of the potential food source was also named after him, *Purshia*.

Biology (potential food source). Mexican Cliffrose (*Purshia mexicana* (D. Don) S. L. Welsh; Rosaceae)

Distribution. *Retusigaster purshi* sp. nov. is known from one female specimen collected in Telephone Canyon, Clark County, Nevada, USA. (Fig. 4)

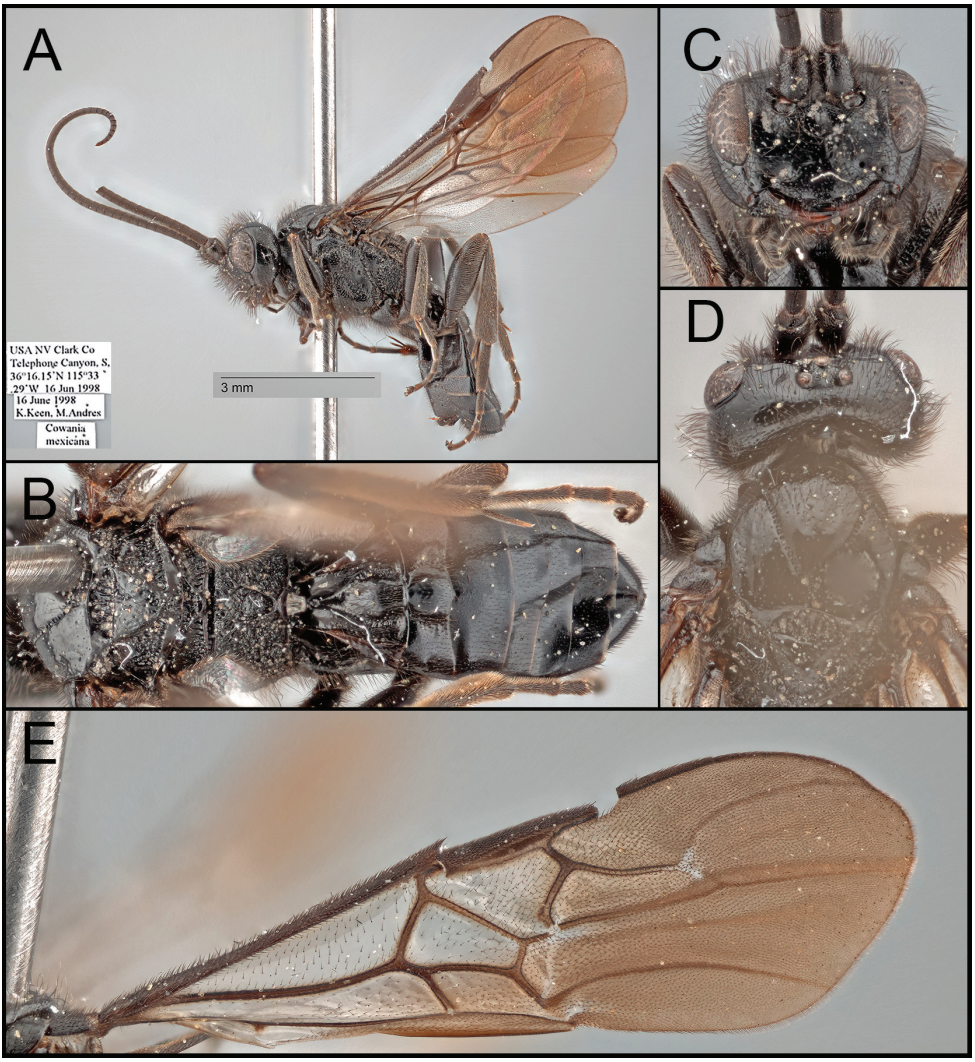


Figure 3. *Retusigaster purshi* sp. nov. **A** lateral habitus **B** dorsal habitus **C** anterior head **D** dorsal mesosoma **E** forewing.

Figure 4. Habitat near the type locality of *Retusigaster purshi* sp. nov. in Nevada, USA.

Retusigaster rubidus (Mao, 1949)

Material examined. ***Non-type specimens*** Mexico • 3♀; seven miles east of San Luis Potosí; 3.vii.1987; 6225'; R. Wharton. USA • 1♀; same as previous except for collecting date and collector. 8.vii.1994; I. Mercado. Deposited in TAMU.

Diagnosis. Members of *Retusigaster rubidus* are most similar to those of *R. brevitarsis*. *R. rubidus* can be distinguished from other members by the following characters: body ~ 7.5 mm. notauli crenulate (Key image 3B); mesoscutum mostly orange pale; fore wing with pale stigma (Key image 6A); metasoma mostly orange pale.

Description. See Mercado and Wharton (2003).

Male. Unknown.

Host. Unknown.

Distribution. Nearctic region (USA and Mexico).

Retusigaster vanduzeei Kang, sp. nov.

http://zoobank.org/6CF56EA2-C9D0-4CEA-B780-17D6D6613E66
Fig. 5A–H

Material examined. ***Holotype*** USA • ♀**;** Nixon, Washoe County, Nevada; 30.vi.1927; EP Van Duzee. Holotype will be deposited in CAS.

Diagnosis. *Retusigaster vanduzeei* sp. nov. is most similar to *R. noguerai* Mercado. Using the following characters, the members of *R. vanduzeei* sp. nov. can be distinguished from other members the genus: inner and outer orbits orange (Fig. 5A–E); fore

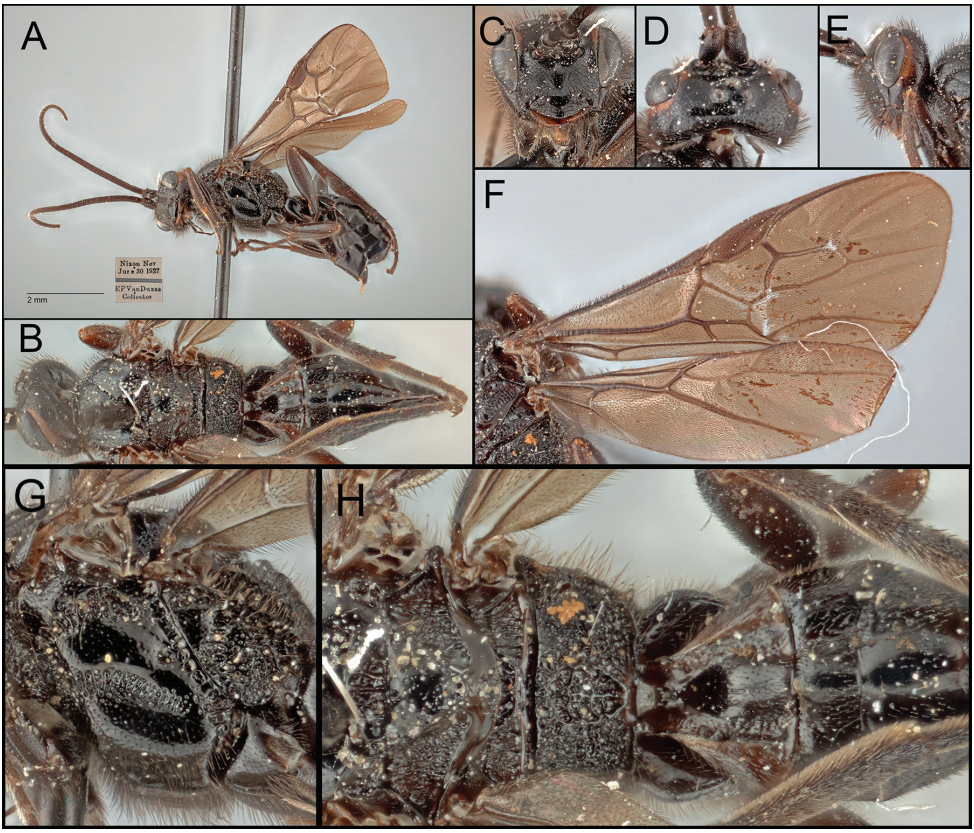


Figure 5. *Retusigaster vanduzeei* sp. nov. **A** lateral habitus **B** dorsal habitus **C** anterior head **D** dorsal head **E** lateral head **F** wings **G** mesopleuron and metapleuron **H** scutellum to T3.

wing entirely infuscate (Fig. 5F); precoxal sulcus crenulate nearly reaching posterior margin (Fig. 5G); propodeal areola oval (Fig. 5H); metasoma entirely dark (Fig. 5B); T1 antero-laterally crenulate and postero-laterally slightly rugulose; T2 ~ 0.27 × longer than its posterior width (Fig. 5B, H).

Description. Body ~ 6.32 mm. ***Head*:** Head entirely with long setae. Antenna 37-segmented. Face width ~ 1.50 × longer than its height (96:64). Width of anterior ocellus ~ 0.80 × longer than POL (16:20). Eyes seemingly without interommatidial setae; median width of eye about ~ 1.15 × longer than the median width of gena in lateral view (45:39). Gena extended ventro-posteriorly into moderate prominence. Clypeus ~ 2.67 × longer than its height (72:27), with punctures; clypeal tubercles absent. Mandible bidentate. Maxillary palpus five-segmented. Labial palpus four-segmented. Galea short. Glossa short. Occipital carina absent. ***Mesosoma*:** Notauli entirely evenly crenulate. Scutellar sulcus ~ 0.30 × longer than width (22:74), with six carinae; lateral margins forming cup-like pit posteriorly. Postscutellar depression entirely rugulose. Pronotum mostly rugulose. Mesopleuron dorsally and ventrally with punctures, posterior margin strongly crenulate;

precoxal sulcus crenulate nearly reaching posterior margin; epicnemial carina absent; episternal scrobe present. Metapleuron anteriorly smooth and posteriorly rugulose. Propodeum strongly rugulose, ~ 0.40 × longer than its median width (57:142); propodeal areola nearly oval, ~ 1.31 × longer than its maximum width (42:32); transverse carina absent. ***Legs*:** Basal spur on fore tibia ~ 0.58 × longer than length of basitarsus (29:50). Basal spur on mid tibia ~ 0.64 × longer than length of basitarsus (39:61). Hind tibia without apical cup-like projection; basal spur on hind tibia ~ 0.61 × longer than length of basitarsus (55:90); claws pectinate. ***Wings*:** Fore wing ~ 6.06 mm; second submarginal cell trapezoid, ~ 3.06 × longer than height (110:36); 1r absent; 3r absent; RS evenly curved; pterostigma about ~ 3.34 × longer than wide medially (117:35). Hind wing ~ 4.88 mm; 2r-m absent; 2–1A present reaching basal half. ***Metasoma*:** T1 ~ 1.13 × longer than its posterior width (79:70), antero-laterally crenulate and postero-laterally slightly rugulose. T2 ~ 0.27 × longer than its posterior width (37:136), ~ 0.55 × longer than T3 (37:67). Hypopygium without median longitudinal fold. Protruded ovipositor sheath ~ 0.46 × longer than length of hind basitarsus (41:90), apically setaceous. **Color:** Body mostly black. Wings entirely infuscate. Pterostigma entirely dark brown. Antenna dark brown. Inner and outer orbits orange. Mandible medially reddish brown. First laterotergite brown.

Etymology. Named in honor of Mr Edward P. Van Duzee, a former curator of CAS and fellow of Entomological Society of America (ESA), the person who collected the specimen.

Host. Unknown.

Distribution. *Retusigaster vanduzeei* sp. nov. is known from Nixon, Washoe County, Nevada, USA.

Discussion

Mercado and Wharton (2003) separated the two species groups, *R. arugosus* and *R. rubidus*, by the degree of expansion of the apex of hind tibia and the shape and location of the propodeal spiracles as mentioned in the introduction section. I examined and compared the diagnostic characters of all the species of *Retusigaster* designated by Mercado and Wharton (2003). In my examination, I did not see a distinct difference in the hind tibial character between the two groups. The shape of the propodeal spiracles (Fig. 6) was somewhat useful to identify the species groups rather than the location of the propodeal spiracle, but still it was not easy to confidently distinguish two species groups based on the shape. Accordingly, the new species are placed neither in *R. arugosus* nor in *R. rubidus* due to the difficulties separating the two species groups based on the suggested diagnostic characters by Mercado and Wharton (2003). Further research based on molecular data will clarify the relationships among species and species groups of *Retusigaster* and *Toxoneuron*.

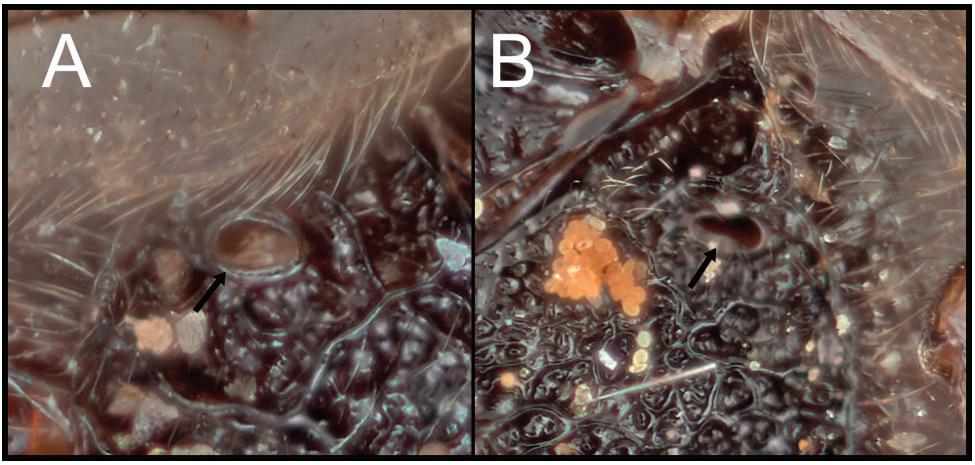


Figure 6. A propodeal spiracle of *R. arugosus* **B** propodeal spiracle of *R. vanduzeei* sp. nov.

Regarding the placement of *R. eremita*, Mercado and Wharton (2003) were unsure of the placement because the species is only a member of *Retusigaster* recorded from the Palearctic region. I was also inquisitive about its generic placement and reviewed the species descriptions by Telenga (1955) and Tobias (1995) to reconfirm the placement of the species. Telenga (1955) wrote that the members of *R. eremita* possess much thickened tips of hind tibiae and simple claws, which have not been recorded in other species of *Retusigaster*. Both of the characters suggest placement in *Pseudcardiochilus* Hedwig, 1957 among the Old World cardiochilines. According to the description by Tobias (1995), the members of *R. eremita* have simple claws but the apices of their hind tibia are not as expanded as those of *Pseudcardiochilus acutus* (Tobias & Alexeev, 1977). However, because I did not examine type specimens of *R. eremita*, I do not change the generic placement of the species. Erdoğan (2015) reported the first record of *R. eremita* from Turkey, but the species may not be *R. eremita* because of its extremely different body coloration.

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I am grateful to Mr Chris Grinter at CAS, Ms Crystal Maier and Mr Charles Farnum at MCZ, and Dr Karen Wright at TAMU for specimen loan. I would like to thank Dr Michael Sharkey for reviewing the manuscript and Dr van Achterberg for sharing his documents about *Pseudcardiochilus*. Among the people at LSU, I would like to acknowledge Drs Chris Carlton, Michael Stout, and Rodrigo Diaz for help and support, and Ms Victoria Bayless for her encouragement. Finally, I am grateful to the LSU Agricultural Center and LSU Entomology Department for financial and logistical support.

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RESEARCH ARTICLE

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A new species of *Petalacmis* firefly from Bolivia, with a key to species (Coleoptera, Lampyridae)

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Abstract

Petalacmis Olivier, 1908 is a poorly known genus of firefly endemic to South America and is currently the only member of the subfamily Lampyrinae, tribe Lampyrini known to occur on the continent. Here, we describe a new species, *Petalacmis triplehorni* **sp. nov.** from Bolivia and compare it to the two other described species in the genus. A key to *Petalacmis* species based on male traits, as well as illustrations of morphological features, are given in detail for the first time. We present unique, previously neglected traits of *Petalacmis* species and compare them to other Lampyrinae.

Keywords

Firefly, Lampyrini

Introduction

Petalacmis E. Olivier, 1908 is an interesting and unique genus of fireflies (Coleoptera, Lampyridae) with distinctive antennal morphology: males have only nine antennomeres, the ninth very elongate and paddle-shaped. *Petalacmis* is poorly represented even in large collections worldwide (LS and MB pers. obs.), and even basic aspects of its morphology are lacking due to the rarity of specimens available for dissection. In fact, this genus is only known from male specimens, a widespread phenomenon in

* Both authors equally contributed to the manuscript

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lampyrids (Silveira and Mermudes 2013, 2014; Ferreira et al. 2019, 2020; Bocakova et al. 2022) and in elateroids as a whole (e.g., Bocak et al. 2016; Biffi et al. 2021). Therefore, detailed studies on the diversity of *Petalacmi*s species are greatly needed in order to produce a more comprehensive understanding of the family Lampyridae, particularly in the tribe Lampyrini. Astonishingly, *Petalacmis* is the only known genus of its tribe known to occur in South America, where it remains more poorly known than its counterparts in both the Old World and North America.

Petalacmis was erected for its type species, *Petalacmis praeclarus* E. Olivier, 1908, with no subfamilial placement, by Olivier (1908). In a later work, Olivier (1910) placed the genus in the subfamily Photininae. In his 1959 work, Green moved *Petalacmis* to the superfamily Lampyrinae and the tribe Lampyrini. Green's placement of *Petalacmis* was followed in McDermott's subsequent taxonomic work on Lampyridae (McDermott 1964) and his 1966 catalog. Phylogenetic analyses consistently placed *Petalacmis* in the subfamily Lampyrinae, but its affinities remain unsteady. Phylogenetic analyses based on morphological data recovered *Petalacmis* close to the Neotropical Pleotomini Summers, 1875 (Jeng 2008), whereas molecular-based phylogenies found it closer to part of Lamprocerini Olivier, 1907 (Martin et al. 2019). The most recent comprehensive classification places *Petalacmis* in Lampyrini (Martin et al. 2019).

*Petalacmi*s currently consists of two species: *P. praeclarus* from Brazil, Bolivia, and Peru, and *Petalacmis wittmeri* Reichardt, 1963 known only from Brazil. A third species, *Petalacmis triplehorni* sp. nov. only known from Bolivia, is described here. We provide the first identification key to *Petalacmis* species based on male morphology and document the morphological features of this genus for the first time. A discussion of *Petalacmis* morphology and its comparison to other Lampyrinae is presented.

Materials and methods

Specimens were both studied and imaged under dissection microscope Leica M205 C. Digital images were obtained and stacked using the Leica Application Suite X. Specimens of *P. praeclarus* and *P. triplehorni* sp. nov. were measured under a Leica MZ16 microscope with a calibrated eyepiece graticule, and measurements were converted to millimeters (Table 1). A whole specimen, as well as the abdomen of a second were soaked in KOH 10% for 24 h before dissection to digest soft tissues. The classification scheme used in this study follows Martin et al. (2019), morphological terminology follows Silveira and Mermudes (2014), and wing venation nomenclature follows Lawrence et al. (2021). Specimens were deposited at the following institutions: Museo Nacional de Historia Natural, La Paz, Bolivia (**ANCB**; J. Tavel); Division of Plant Industry, Florida State Collection of Arthropods, Gainesville, Florida, United States of America (**FSCA**; P. Skelley); United States of America National Museum of Natural History, Washington, DC, USA (**USNM**; M. Branham), University of Georgia Collection of Arthropods, Athens, Georgia, USA (**UGCA**; J. McHugh); Ohio State University, C.A. Triplehorn Insect Collection, Columbus, Ohio, USA (**OSUC**; L. Musetti).

Table 1. Comparative measurements (average, range between parentheses) between the three known species of *Petalacmis.* Measurements were taken from the material examined (see above), except for those of *P. wittmeri*, which were taken from Reichardt (1963).

Dimensions (mm)	*P. praeclarus* (*n* = 8)	*P. wittmeri* (*n* = 1)	*P. triplehorni* (*n* = 15)
Total Length	9.01 (8.13–9.46)	6.8	5.34 (5.06–5.81)
Pronotal Length	2.04 (1.74–2.24)	1.5	0.99 (0.91–1.07)
Elytral Length	7.02 (6.39–7.3)	5.3	4.35 (4.15–4.73)

Results

Taxonomy

Lampyridae: Lampyrinae: Lampyrini

***Petalacmis triplehorni* Silveira & Branham, sp. nov.**
http://zoobank.org/2F8DCDAF-6A31-48BE-B757-74A91AFCDA37
Figs 1–4; Suppl. material 1: Fig. S1

Diagnosis. The three species of *Petalacmis* are easily diagnosable by size (Table 1), along with the morphology of antennae, elytra, and pygidium (see key below). *Petalacmis triplehorni* sp. nov. can be identified by the following combination of characters: antennomeres V and VII slightly longer and wider than adjacent antennomeres (Fig. 2H–I), elytron subparallel-sided (Fig. 3L), pygidium with sides divergent to basal third, then convergent apically with almost straight margins, posterior margin slightly bisinuose, lateral thirds subequal to or slightly longer than median third (Fig. 4A, C). Measurements are given in Table 1.

Description of male. Color pattern: overall brown, except for the dark brown pronotal disc, translucent parasagittal rounded spots on pronotal expansions, and translucent sterna VI–VIII (Fig. 1); pronotal expansions often light brown (Suppl. material 1: Fig. S1).

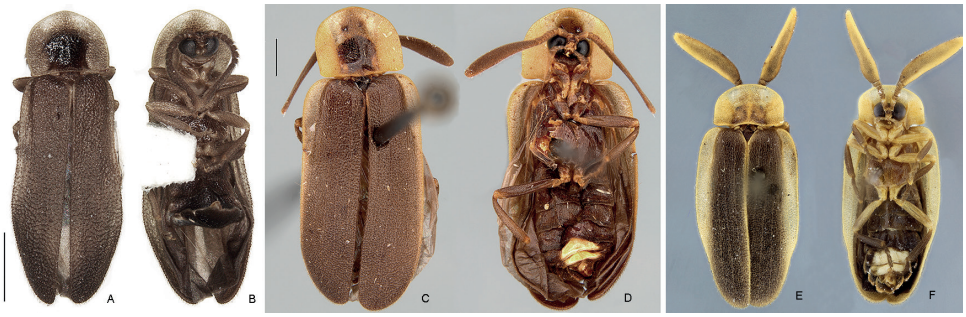

Figure 1. Habiti of *Petalacmis* species **A, B** *P. triplehorni* sp. nov., holotype (male, prior to dissection), habitus **A** dorsal **B** ventral **B, C** *P. praeclarus* (male, from Piracicaba, São Paulo) **B** dorsal **C** ventral **E, F** *P. wittmeri* holotype (male), habitus **E** dorsal **F** ventral. Scale bars: 1 mm (**A–D**).

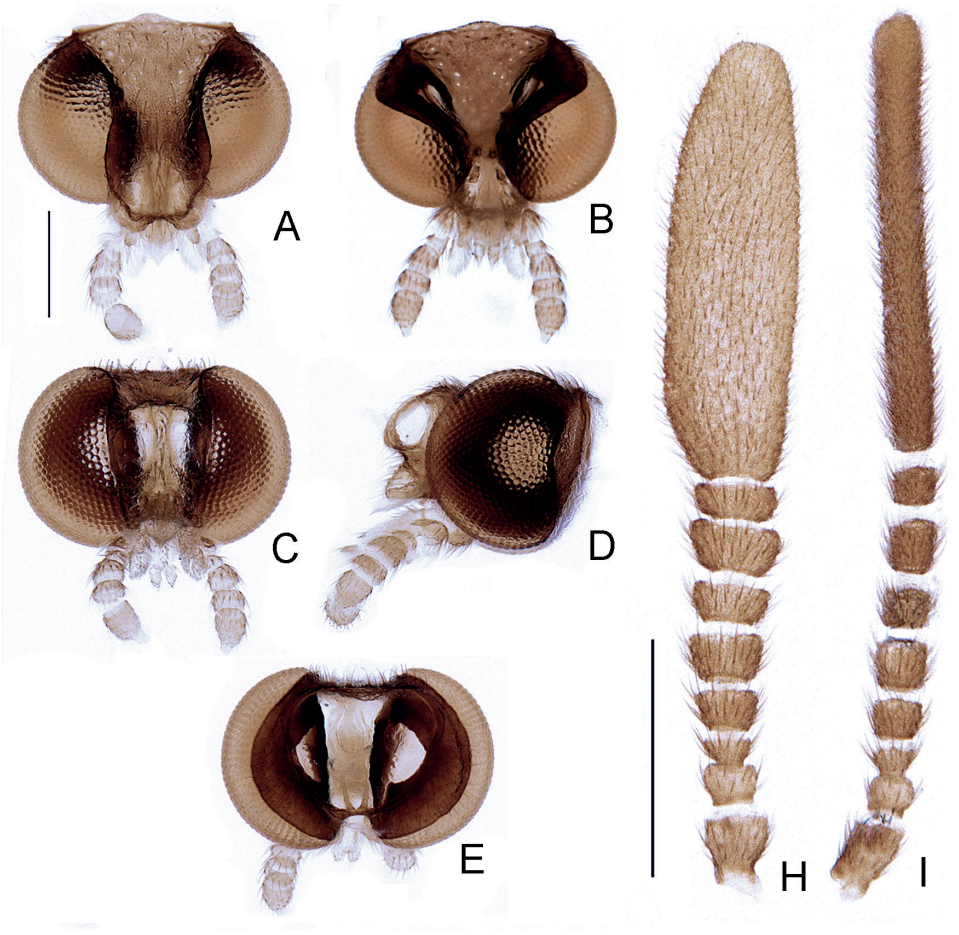

Figure 2. *Petalacmis triplehorni* sp. nov., male head **A–F** core head **A** dorsal **B** ventral/occipital **C** frontal **D** lateral **E** posterior **H, I** antenna **H** lateral **I** frontal. Scale bars: 250 µm (**A–E**); 500 µm (**H, I**).

***Head*:** head capsule about 1/3× wider than long, posterior margin almost straight, except for the dorsal margin of occiput, which is rounded (see dorsal view, Fig. 2A), slightly taller than long (Fig. 2D), vertex slightly depressed between the eyes (Fig. 2E). Frons slightly intumescent (Fig. 2D), antennal sockets elliptical, 2× taller than wide, obliquely disposed, as wide as 1/3 eye; antennifer process barely visible (Fig. 2C). Eye as wide as 1/3 head width in dorsal view (Fig. 2A), 2/5 in ventral view (Fig. 2B), dorsal margin emarginated inwards (Fig. 2A), frontal inner margin rounded, strongly convergent ventrally (Fig. 2B), almost occupying the whole head capsule in lateral view (Fig. 2D), indented posteriorly (Fig. 2B, D). Antenna with nine antennomeres (Fig. 2H, I); scape slightly longer than wide, basally constricted; pedicel basally constricted, slightly wider than long, 1/2 as long as scape; antennomeres III–VIII transverse, progressively compressed, with decumbent bristles, subequal in length, except for V and VII, which are slightly longer and wider than neighboring antennomeres, IX

petal-shaped, lateral margins asymmetrical (Fig. 2H); frontoclypeus strongly depressed between antennal sockets and labrum (Fig. 2C). Labrum (Fig. 2A–C) subcircular, slightly acuminate anteriorly, connate to frontoclypeus, slightly wider than antennal socket. Mandibles short (as long as labrum), slightly curved, apically obtuse, homogeneously bristled (Fig. 2A, D). Maxilla (Fig. 2B, C) with cardo well sclerotized, rectangular; stipes oblong, subtriangular in ventral view, internal margin slightly curved, posterior margins rounded, palp with 4 palpomeres; II–IV subcylindrical and transverse, II longer than I and as long as palpifer, I as long as III, III transverse; IV lanceolate, 3× longer than III, with apical margin covered with bristles. Labium (Fig. 2B) with mentum membranous and barely distinct, divided sagittally forming two plates, each plate elongate; submentum membranous and indistinct; palp with 2 distinct palpomeres, apical palpomere obconical. Gula coriaceous, as long as wide, paired tentorial pits conspicuous. Occiput subtriangular, maximum width slightly over 1/2 head width, anterior margin slightly sinuose (Fig. 2E).

***Thorax*:** pronotum with anterior margin slightly sinuose and acuminate anteriorly (Fig. 3A), lateral margins slightly rounded to subparallel, posterior angles somewhat acute but not pointed, posterior margin almost straight, slightly rounded by the disc; disc subquadrate (Fig. 3A), slightly depressed by posterior half (in lateral view, Fig. 3E), regularly punctured, punctures small and bristled, evenly spaced about 2× puncture size; without a distinct line of deeper marginal punctures; pronotal expansions well developed, anterior expansion convex in lateral view (Fig. 3C, E), maximal length almost as long as disc (Fig. 3A); posterior margin about as wide as distance between elytral humeri (Fig. 1A); lateral expansions bent upwards in posterior view (Fig. 3D). Hypomeron slightly over 2× longer than tall, with a well-delimited posterior angle (Fig. 3E). Prosternum smallest length about 10× as wide as its greatest length (Fig. 3B). Proendosternite apically acute, widely divergent, as long as core prosternum smallest length (Fig. 3D). Mesoscutellum very short (Fig. 3F), with posterior margin pointed, normally at a lower level than elytra (Fig. 1A). Elytron (Fig. 3L, M) subparallel-sided, almost 5× longer than wide, pubescent, secondary pubescence absent, with shallow irregular punctures, texturized, with evanescent 4 costae, marginal costa narrow, epipleuron reaching basal ¼. Hind wing well developed (Fig. 3N), posterior margin with anal embayment (sensu Lawrence et al. 2021), slightly less than 2× wider than long, r4 3× longer than r3, radial cell 3× wider than long, distant from anterior margin more than the caliper of RA, costal row of setae conspicuous (Fig. 3N); CuA1 cross vein evanescent, CuA3+4 cross vein absent; radial cell, r3 and r4 evanescent, veins posterior to MP progressively evanescent from apex to base.

Alinotum overall weakly sclerotized, slightly wider than long (Fig. 3G), lateral margins convergent posteriorly, posterior margin slightly emarginate; prescutum extending up to half metascutum length; without a distinct rounded area, scutum-prescutal plates distinct and extending ridges to half alinotum length; metascutellum glabrous, with lateral margins subparallel-sided, scutum-scutellar ridge strongly divergent posteriorly. Mesosternum weakly sclerotized, posterior margin medially rounded (Fig. 3H). Mesosternum-mesepisternum suture barely visible (Fig. 3H). Mesepisternum-mesepimeron

suture conspicuous (Fig. 3H). Mesepimeron-metasternum suture coriaceous (Fig. 3H, I). Metasternum strongly depressed by mesocoxae, without a distinct anterior medial keel, discrimen reaching basal 1/3 of metasternum length, lateral margins divergent posteriorly up to outermost part of metacoxa, then convergent posteriorly, posterior margin bisinuose (Fig. 3H–I). Metepisternum almost 3× longer than tall Fig. (3K). Profemur about as long as protibia; meso and metatibia of about the same length and slightly longer than protibia (Fig. 3O). All legs lacking tibial spurs, with tarsomeres progressively shorter up to IV, which is bilobated, lobes reaching ½ V length, V slightly shorter than I, and with simple, untoothed claws (Fig. 3O, P). Mesendosternum with 2 parasagittal projections slightly directed outwards, irregularly alate (Fig. 3I–K).

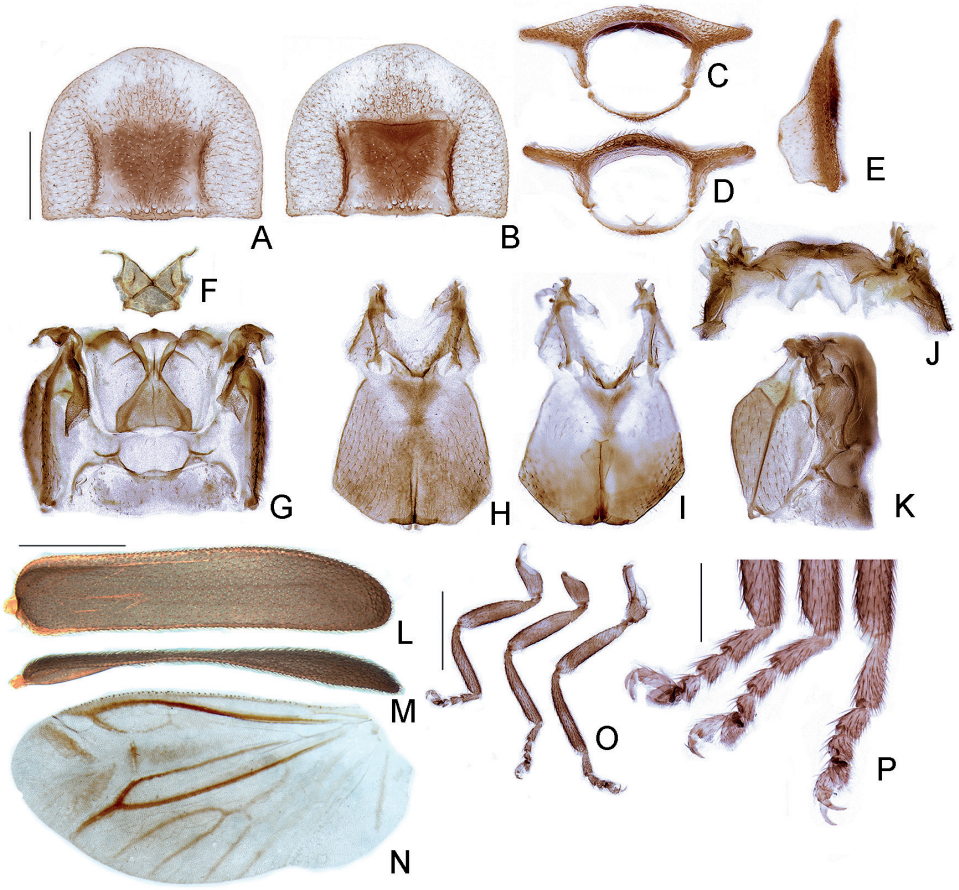

Figure 3. *Petalacmis triplehorni* sp. nov., male thorax. **A–E** prothorax: **A** dorsal **B** ventral **C** anterior **D** posterior **E** lateral. **F–K** pterothorax: **F** mesoscutellum, dorsal **G** alinotum, dorsal **H** pterothorax, ventral **I** pterothorax, dorsal (detail of meso and metaendosterna **J** alinotum, dorsal **K** pterothorax and abdominal tergum I, lateral **L–N** wings: **L** elytron, dorsal **M** elytron, lateral (outer view) **N** left wing, dorsal **O, P** legs: **O** left pro, meso and metaleg (left to right) **P** detail of left pro, meso and metaleg apices (left to right). Scale bars: 500 µm (**A–K**); 1 mm **L–N**; 750 µm (**O**); 250 µm (**P**).

Metendosternum spatulate, roughly rhomboid (about as long as wide, with 2 acute lateral laminae), anteriorly indented (Fig. 3I).

***Abdomen*:** tergum I with laterotergite membranous, roughly triangular, almost indistinct (Fig. 3K); spiracle elliptical, obliquely attached to thorax (Fig. 3G, K). Posterior corners of terga I–III almost right-angled, IV slightly projected, V–VII rounded and progressively projected and acute (Fig. 4A–C). Sterna II–IX visible (Figs 1B, 4C), V distinctly more sclerotized than neighboring sterna, VI and VII with well-developed, transverse light organs, almost as long and wide as sterna (Fig. 4B, C, Suppl. material 1: Fig. S1). Spiracles ventral, at mid-length (Fig. 4B, C). Sternum VIII with posterior margin slightly emarginate (Fig. 4B, C). Pygidium with anterior margin strongly emarginate, lateral margins almost straight and convergent posteriorly, posterior margin bisinuate, lateral thirds subequal to or slightly longer than median third (Fig. 4C). Syntergite membranous, as long as 4/5 sternum IX length, widely connate to sternum IX, without distinct sutures, posteriorly bristled, anterior margin slightly emarginate (Fig. 4D–F). Sternum IX symmetric, medially divided by a membranous line, anterior margin rounded, lateral margins strongly convergent anteriorly (Fig. 4D–F). Aedeagus overall well sclerotized (Fig. 4G–J). Phallus (Fig. 4G–I) with a well-sclerotized dorsal plate, ventral plate indistinct; dorsal plate basally connate to parameres, curved dorsally, apically truncate, deeply excavate ventrally (Fig. 4G), without apical lobes or arrow-shaped structures. Parameres ventrally projected basally, projection somewhat rounded; reaching the dorsal plate of phallus length, with typical lampyrine inner lobes but coriaceous; with an apical pointed projection, which is membranous.

Female and immature stages. Unknown.

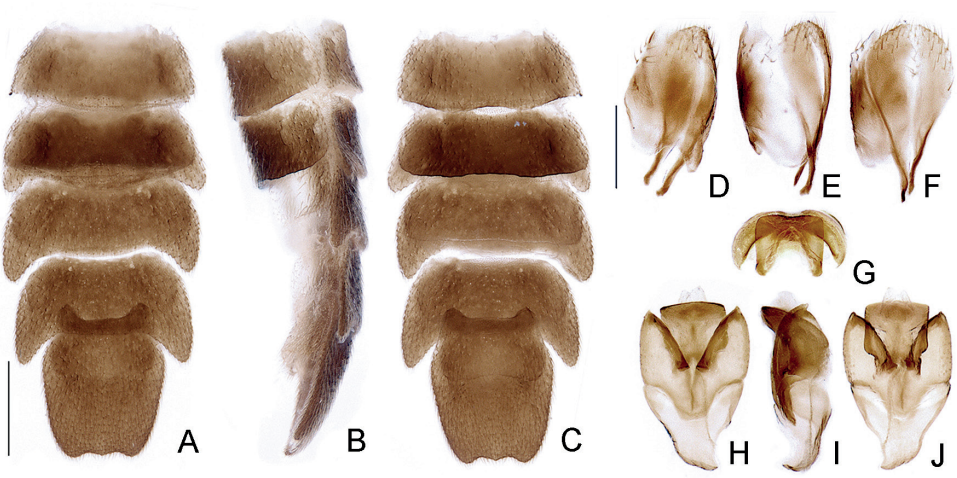

Figure 4. *Petalacmis triplehorni* sp. nov., male abdomen **A–C** core abdomen (segments IV–VIII) **A** dorsal **B** lateral **C** ventral **D–F** aedeagal sheath **D** dorsal **E** lateral **F** ventral **G–J** aedeagus (distal tips oriented toward top of the figure) **G** apical/posterior **H** dorsal **I** lateral, **J** ventral. Scale bars: 500 μm (**A–C**); 250 μm (**D–I**).

Etymology. This species is named for Dr Charles "Chuck" Triplehorn, Professor Emeritus of the Ohio State University, who collected the first specimens of *Petalacmis praeclarus* that one of us (MAB) first encountered as a graduate student while investigating the systematics of the family Lampyridae. Dr Triplehorn has been both a mentor and an inspiration to MAB. It is with great appreciation and respect for Dr Triplehorn that we name this species after him.

Material examined. ***Holotype***, male. Bolivia: Santa Cruz, Potrerillo del Guendá Reserve, 1322' elev., 17°40.262'S, 63°27.445'W, at light, J. McHugh lab exped. leg., 6–12-I-2005 (ANCB).

Paratypes (*n* = 14). Bolivia • Santa Cruz, Potrerillo del Guendá Reserve.; 1322' elev.; 17°40.262'S, 63°27.445'W; at light; J. McHugh lab exped. leg.; 6–12-I-2005 (1 ♂, USNM) • Santa Cruz, 3.7 km SSE of Buena Vista, Hotel Flora and Fauna; 405 m elev.; 5–15-XI-2001; 17°29.949'S, 63°33.152'W; M.C. Thomas & B.K. Dozier leg.; tropical transition forest (3 ♂, FSCA) • idem. (2 ♂, ANCB); Santa Cruz, 3.7 km SSE of Buena Vista, Hotel Flora and Fauna; 405 m elev.; 5–15-XI-2001, 17°29.949'S, 63°33.152'W; M.C. Thomas & B.K. Dozier leg.; tropical transition forest (1 ♂, OSUC) • Santa Cruz, 3.7 km SSE of Buena Vista, Hotel Flora and Fauna; 405 m elev.; 5–15-XI-2001; 17°29.949'S, 63°33.152'W; M.C. Thomas & B.K. Dozier leg.; tropical transition forest, blacklight trap (2 ♂, UGCA) • Santa Cruz, 3.7 km SSE of Buena Vista, Hotel Flora and Fauna; 430 m elev.; 2–13-III-2000; M.C. Thomas leg.; tropical transition forest (3 ♂, ANCB) • Santa Cruz, 3.7 km SSE of Buena Vista, Hotel Flora and Fauna; 430 m elev.; 14–19-X-2000; M.C. Thomas leg.; tropical transition forest (1 ♂, ANCB) • Santa Cruz, 40 km NW of Potrerillo del Guendá; 400 m elev.; Gino Nearns leg., 17-XII-2004 (1 male, USNM).

Key to the species of *Petalacmis*

1 Elytron subparallel-sided, slightly tapering distally (Fig. 1A–D) **2**

– Elytra elliptical, widest in middle (Fig. 1E, F) .... ***Petalacmis wittmeri*** **Reichardt**

2 (1). Antennomeres V and VII as wide as VI and VIII, apical antennomere nearly 2× longer than remaining antennomeres together (Fig. 5A); elytral outer expansion (also known as explanate margin) extending up to 2/3 of elytral length, yellowish (Fig. 3C, D); pygidium with sides rounded, posterior margin strongly bisinuose, slightly longer at median 1/3 .... ***Petalacmis praeclarus*** **E. Olivier**

– Antennomeres V and VII slightly longer and wider than neighbor antennomeres, apical antennomere as long as the remaining antennomeres together (Fig. 2H, I); elytral outer expansion feebly developed throughout, and of the same color as the rest of the elytron (brown) or slightly brighter (Figs 1A, B, 3L; Suppl. material 1: Fig. S1A); pygidium with sides almost straight, posterior margin slightly bisinuose, lateral thirds subequal to or slightly longer than median 1/3 (Fig. 4A–C) ..... ***Petalacmis triplehorni*** **sp. nov.**

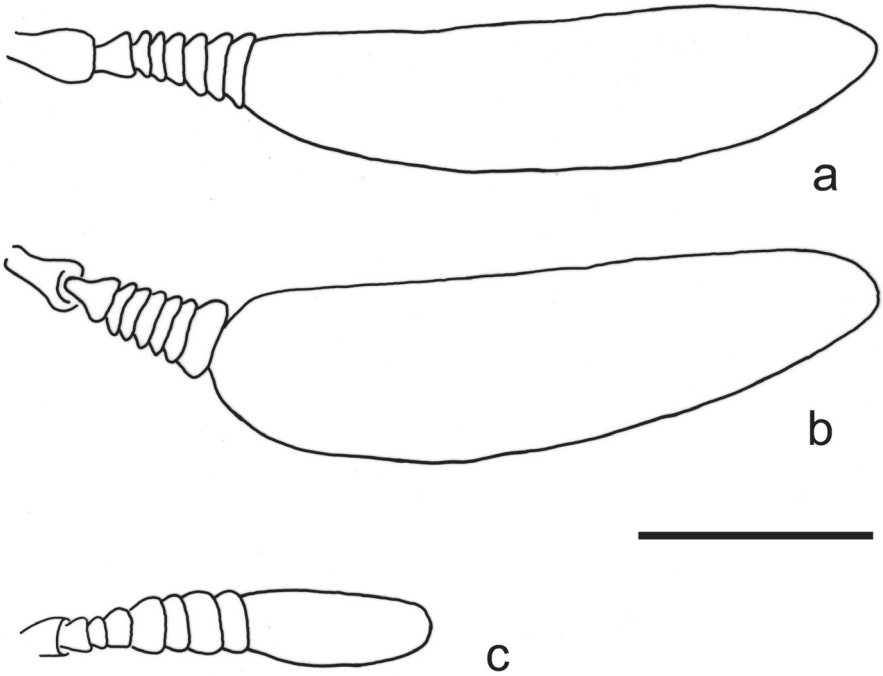

Figure 5. Comparison between the antennal morphologies **A** *Petalacmis praeclarus* **B** *P. wittmeri* **C** *P. triplehorni* sp. nov. Scale bar: 1.0 mm.

Petalacmis praeclarus Olivier, 1908

Material examined. Brazil: Minas Gerais, Lambari [spelled Lambary], XI.1924, J. Halik col. (1 male, USNM 3083) // Brazil Halik 1966 coll.; same data, XI.1924 (1 male, USNM 3084); same data, XI.1924 (1 male, USNM 3085); São Paulo, São Paulo, Santana [spelled St. Anna, Cap. S. Paulo], XII.1934, J. Halik col. (1 male, USNM 5047).] // Brazil Halik 1966 coll. collection; São Paulo, Cantareira, 23.VII.1933, J. Halik col. (1 male, USNM 2208) // Brazil Halik 1966 coll. collection; São Paulo, Botanical garden [spelled *horto flor.*], XII.1921, J. Halik col. (1 male, USNM 7190) // Brazil Halik 1966 coll. collection; São Paulo, Piracicaba, 6.X.1965, Blacklight, C. A. Triplehorn col. (2 males, M. Branham collection).

Discussion

Distribution of *Petalacmis* spp.

To date, all *Petalacmis* species are known from lowland localities across South America east of the Andes. *Petalacmis praeclarus* was described from "Brazil". It has since been

collected in Bolivia and Peru (Olivier 1908; Reichardt 1963; McDermott 1964, 1966; Lawrence et al. 2001) and the Atlantic Rainforest in Brazil (see Material examined above). Such a widespread distribution is uncommon in Neotropical fireflies, and the existence of overlooked or cryptic species should be considered in future comprehensive taxonomic reviews. In 1963, Reichardt described the second species, *P. wittmeri* which was collected Ananindeua, in Pará state, Brazil. *Petalacmis triplehorni* sp. nov. was collected near Buena Vista, Santa Cruz, Bolivia. Due to its small size and nocturnal habit, the genus is likely to have been overlooked, particularly in South America, where taxonomic expertise in fireflies was largely lacking until fairly recently.

Thoughts on the mating system of *Petalacmis* species

Due to the presence of large eyes and photic organs in the male, one might expect that both the male and female of these species are luminous and use luminous signals for pair-formation, as seen in several firefly subfamilies (Branham and Wenzel 2003; Branham 2010; Stanger-Hall et al. 2018). The fact that no females are currently known for any of the three species in this genus may suggest that females are sedentary, perhaps brachypterous or even apterous, as seen in other lampyrids (e.g., Faust 2017; Stanger-Hall et al. 2018). Alternatively, these species may be so uncommonly encountered that no females have been collected.

Morphology and systematics of *Petalacmis*

The affinities of *Petalacmis* have been investigated in two comprehensive phylogenies of Lampyridae. Based on morphological data, Jeng (2008) found Neotropical Pletomini Summers, 1875 (i.e., *Calyptocephalus* Gray, 1832, *Phaenolis* Gorham, 1880, *Ophoelis* Olivier, 1911, and *Roleta* McDermott, 1962) sister to *Petalacmis*. On the other hand, the molecular-based phylogeny by Martin et al (2019) found *Petalacmis* sister to *Lucio* Laporte, 1833 and *Lamprocera* Laporte, 1833, both in the Lamprocerini Olivier, 1907. Neither phylogenetic hypothesis found evidence of exclusive shared ancestry with the Lampyrini, where they are currently placed (Martin et al. 2019). However, the taxa which were more closely associated with *Petalacmis* by Jeng (2008) were not included in Martin et al. (2019); hence, the sister-lineage of *Petalacmis* remains unclear.

As our study was the first to thoroughly survey the anatomy of *Petalacmis*, we provide some comparisons to inform the ongoing debate on the phylogenetic affinities of this genus. We assume that our description of *P. triplehorni* sp. nov. includes traits that are likely to be shared with other species in the genus, or even traits common to all of them. In addition to the very distinctive "petal-like" antennal morphology, we observed previously obscured traits of *Petalacmis* that differ significantly from those of other lampyrine genera. For example, *Petalacmis* is unique among lampyrine genera in having (i) an intumescent and laterally keeled frons (Fig. 2A, D), (ii) mandibles short apically rounded (i.e., obtuse, not pointed) frons (Fig. 2A, C–D), and (iii) a dorsal plate of the phallus much shorter than the phallobase and strongly bent dorsally (in

ventral view), with sides parallel and straight in apical view, deeply grooved (in apical/posterior view), and apically truncate (Fig. 4H–J). Other genera of Lampyrini often have frons that are not intumescent (e.g., flat or depressed between antennal sockets), mandibles apically very acute (i.e., needle-like), and phalli at least slightly longer than phallobase, sinuose or almost straight (but never strongly bent dorsally), with sides sinuose, and apex variably acute, often with arrow-shaped apices (e.g., Green 1959; Geisthardt 1986; Kazantsev 2010; Constantin 2014). Interestingly, the intumescent frons seen in *Petalacmis* is known in at least some Pleotomini (e.g., *Roleta*; Jeng et al. 2006), and in the amydetine taxa *Magnoculus* and *Memoan* (Silveira and Mermudes 2013; Campello-Gonçalves et al. in press).

Another trait shared with all three amydetine genera (*Amydetes* Illiger, 1807, *Magnoculus* McDermott, 1964, *Memoan* Silveira & Mermudes, 2013; Campello-Gonçalves et al. in press), as well as many other glowing firefly taxa (*Phausis* LeConte, 1851, *Lamprohiza* Motschulsky, 1853) is the more sclerotized and slightly emarginated sternum V (Fig. 4C), which precedes the lanterns. Another feature of *P. triplehor*ni sp. nov. that catches the eye is the shape of abdominal sternum IX (Fig. 4F), which is medially divided by a membranous line—a typical trait of the Lampyrini (e.g., Kazantsev 2010) that is also commonly observed across Lamprocerini and Cratomorphini (e.g., Campos et al. 2018; Silveira et al. 2019; Lima et al. 2021), but seldom seen in Photinini (e.g., Silveira et al. 2022).

Concerning aedeagal morphology, lampyrine taxa very often have parameres with an elongate, membranous apex—a trait also commonly found across Lamprocerini and Cratomorphini (e.g., Campos et al. 2018; Silveira et al. 2019). The same membranous apex is found on the aedeagus of *P. triplehorni* sp. nov., but in a rudimentary form (Fig. 4). The typical inner lobe of parameres (as seen for example in *Lampyris* (e.g., Geisthardt 1986; Kazantsev 2010; Constantin 2014) is also present in *P. triplehorni* sp. nov., although distinctly thinner and less sclerotized.

Recently, it has become more common that taxonomic studies report detailed exo- and endoskeletal traits of the thorax, like the shape of meso and metatergal ridges, as well as those of the endosternites. Currently, no such information is available for any taxa of Lampyrini, which hampers any comparison. Nevertheless, we observed some interesting traits in *Petalacmis triplehorni* sp. nov. and compare it to known lampyrine taxa. For instance, the mesoscutellum of *P. triplehorni* sp. nov. is so reduced that it is almost triangular, despite the median pointed projection at the posterior margin (Fig. 3F). To our knowledge, no such rudimentary shape has been observed before in any other lampyrid. Moreover, no other Lampyrini is known to possess an extremely reduced and posteriorly pointed mesoscutellum. However, we observed a rather pointed mesoscutellum in the lamprocerine genus *Tenaspis* (e.g., *T. angularis*, *T. sinuosa*; LFLS pers. obs.).

The alinotum of *P. triplehorni* sp. nov. is clearly distinct, with a scutum–prescutal ridge that extends to less than half the length of the metanotum (Fig. 3G), otherwise reaching or almost so the posterior margin in most other lampyrids, where known (e.g., Silveira et al. 2019). Such a short scutum–prescutal ridge is only known in the distantly related Amydetinae (Silveira and Mermudes 2014; Campello-Gonçalves et al.

in press). The function of that modified alinotum in Lampyridae remains unknown, but it likely reflects changes in the flight muscles that attach to these ridges, and possibly associated with changes in flight pattern. The metascutelum of *P. triplehorni* sp. nov. has rather oblique anterior ridges (about 45° to the lateral ridges), otherwise almost transverse as found in most other lampyrids (e.g., Silveira et al. 2019). It is also noteworthy that *P. triplehorni* sp. nov. has a metaendosternum with anterior margin wide and emarginate (a trait so far only observed in Cratomorphini; Campos et al. 2018).

Petalacmis shares with Lampyrini, Pletomonini, and Lamprocerini, the ventral position of abdominal spiracles, as well as the reduced mandibles. However, this genus lacks key traits of all these three tribes. For example: both *Lucio* and *Lamprocera*, the taxa placed close to *Petalacmis* in Martin et al.'s (2019) phylogenetic analysis, have biflabellated antennae, elytra broadly expanded laterally and bent ventrally, and a transverse pygidium. In contrast, *Petalacmis* has a petal-shaped antenna, elytra feebly expanded and almost flat in lateral view (not bent ventrally), and a pygidium much longer than wide. *Petalacmis* also lacks the typical biflabellate antennae, and the bilobate sternum VIII, of the Neotropical Pleotomini. Yet, *Petalacmis* and the Neotropical Pleotomini share an intumescent frons, and an elongate pygidium. Lampyrini taxa usually have a transverse pygidium (elongate in *Petalacmis*), and their parameres have a well-developed apical membranous projection (e.g., Geisthardt 1986; Kazantsev 2010; Constantin 2014), which is at best rudimentary in *Petalacmis*. Therefore, the unique combination of characters seen in *Petalacmis* makes its taxonomic placement within the family Lampyridae challenging. A well-substantiated tribal placement of *Petalacmis* in Lampyrinae would benefit from its inclusion in future phylogenetic analyses with expanded taxon sampling across the Lampyridae.

Taken together, these observations highlight the potential value of traits typically neglected in lampyrid taxonomy, and invite future anatomical studies concerning the Lampyrinae, particularly the Lampyrini. We hope that our study fosters a future comprehensive review of this interesting firefly genus.

Acknowledgements

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Supplementary material 1

Figure S1

Authors: Luiz F. L. da Silveira, Marc A. Branham

Data type: Figure

Explanation note: *Petalacmis triplehorni* sp. nov. habitus of one of the paratypes (note lantern morphology and the brighter pronotal expansions) A dorsal B ventral.

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RESEARCH ARTICLE

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Okalia necopinata sp. nov. (Insecta, Coleoptera, Elmidae) from Gunung Mulu National Park in Sarawak (Malaysia)

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Abstract

Okalia necopinata **sp. nov.**, from Sarawak, northwest Borneo, Malaysia, is described and illustrated along with an identification key. The standard barcoding fragment of the mitochondrial gene coding for cytochrome c oxidase subunit I (COI) was used together with morphological characters to delimit the taxonomic boundaries of the two known species, which live in shallow streams flowing through dense primary forests in limestone areas in Pahang (West Malaysia) and Sarawak (East Malaysia). The majority of all examined *Okalia* are flightless. Morphological distinguishing characters are the length of the granulated fifth elytral interval, the elytral and pronotal punctation, the aedeagal morphology, and the distal portion of the ovipositor.

Keywords

Barcoding, Borneo, DNA, Dryopoidea, Macronychini, Oriental Region, riffle beetles, taxonomy

Introduction

The island of Borneo is known for its exceptionally diverse fauna, currently surviving mainly in regions still covered by primary forests. A faunistic survey on the diversity of Elmidae and Dryopidae in the Malaysian state of Sarawak (nortwest Borneo) was carried out by Ján Kodada and Dávid Selnekovič in 2018 and 2019.

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Some of the best-preserved biotopes are located in Gunung Mulu National Park, which has an area of 544 km^2 and a wide range of rainforest, soils, and types of running water.

Sampling in a small stream meandering through lowland forest yielded an interesting assemblage of riffle beetles, including, for instance, specimens of *Ancyronyx* Erichson (Kodada et al. 2020a, 2020b) and *Leptelmis* Sharp, and a new species of the macronychine genus *Okalia* Kodada & Čiampor, which is described below. Specimens of *Ancyronyx* preferred submerged wood, while *Leptelmis* inhabited submerged root bundles of *Phymatarum borneense* M. Hotta (Araceae), densely growing along the muddy banks. Contrarily, most of the *Okalia* were sampled from the sandy gravelly substrate, together with adults and larvae of several species of *Stenelmis* Dufour; however, a few *Okalia* specimens were also found on submerged wood.

So far, one species of *Okalia*, *O. globosa* Kodada & Čiampor, has been described. This species is known from the type locality in the Malaysian state of Pahang (Kodada and Čiampor 2003). Ten of the type specimens are wingless and only one is winged. The single (winged) female recorded from Sabah (Kodada and Čiampor 2003: 794) remains undescribed.

Material and methods

Specimens were immediately preserved in 96% ethanol, specifically for the use of DNA barcoding.

The material examined is deposited in the following collections:

CFDS Forest Department Sarawak, Kuching, Malaysia;
CKB Collection Kodada, Comenius University, Bratislava, Slovakia;
NMW Naturhistorisches Museum Wien, Austria.

Dried type specimens of *Okalia globosa* were relaxed in warm water with several drops of concentrated acetic acid and cleaned. Detached abdomina were exposed to lactic acid for 1–2 days and temporarily mounted in Berlese's fluid on a cavity slide covered with a cover glass.

Specimens were examined and measured using a Leica M205C stereomicroscope with fusion optics and diffuse lighting at magnifications up to 160×. Measurements were made with an eyepiece graticule (5 mm: 100) or a Leica MC190-HD camera attached to the microscope and LAS software. The specimens were photographed with a Zeiss AxioZoom.V–16 stereomicroscope using diffuse LED lighting and a Canon 5D Mark IV camera attached. Each stacked microphotograph was created by stacking 100–120 focal planes with the image-stacking software ZereneStacker (https://zerenesystems.com/cms/stacker). Dissected genitalia and pregenital segments were studied and drawn at magnifications up to 640× with a Leica DM 1000 microscope and a Leica drawing device. In several speci-

mens, one elytron was removed in order to confirm the absence of hind wings. The morphological terminology follows Kodada et al. (2016). For scanning electron microscopy specimens were dehydrated in graded ethanol series and air-dried in a desiccator, coated with gold, and examined with a TESCAN microscope.

The following morphological characters were measured:

BL body length without head, length of pronotum and elytra measured along midline;
EL elytral length, measured along suture from the level of the most anterior point to the most posterior tip in dorsal view;
EW maximum elytral width;
MW maximum pronotal width;
PL pronotal length along midline.

Nine specimens of *O. necopinata* and two exemplars of *O. globosa* stored in 96% ethanol were used for molecular analyses. A tissue sample contained either one leg with coxa and attached muscles or the entire (divided) adult specimen. DNA was isolated with the E.Z.N.A. Tissue DNA kit (OMEGA Bio-tek Inc., Norcross, GA, USA) or the DNeasy Blood and Tissue Kit (Qiagen, Hilden, Germany) according to the manufacturer's protocol. The fragment of the 5' end of the mitochondrial gene coding for cytochrome c oxidase subunit I (COI) was amplified with primers LCO1490 and HCO2198 (Folmer et al. 1994) or CLepFolF and CLepFolR (Hendrich et al. 2015). PCR reactions were conducted in a total volume of 25 µl and included 0.4 µl of DreamTaq DNA Polymerase (5 U/µl) (Thermo Scientific), 2.5 µl of 10× DreamTaq Green Buffer, 2.5 µl of $MgCl_2$ (25 mM), 2 µl of the dNTPs mix (2 mM), 1 µl of each primer (10 pmol/µl), ca 50 ng of template DNA, and 12.6 µl nuclease-free water. The PCR thermocycler program was as follows: 94 °C for 180 s, 35–40 cycles (depending on the concentration of the DNA extracts) of 94 °C for 40 s, 52 °C for 40 s, and 72 °C for 60 s, and 72 °C for 10 min. PCR products were viewed on the 1% TBE agarose gel and purified with the Exo-CIP Rapid PCR Cleanup Kit (New England Biolabs Inc., Ipswich, MA, USA) according to the manufacturer's protocol and sequenced from both sides in Macrogen Europe B.V. (Amsterdam, Netherlands). Raw nucleotide sequences were edited and aligned using the invertebrate mitochondrial genetic code and the Muscle codon algorithm in Geneious 6.1.8 (https://www.geneious.com). To infer phylogenetic relationships, we used two algorithms. Maximum-likelihood (ML) and neighbor-joining (NJ) trees were constructed using the K2P model and 1,000 bootstrap replicates in MEGA-X software (Kumar et al. 2018). Pairwise uncorrected *p*-distances were calculated in MEGA-X as well. Sequences are available in GenBank and BOLD databases. COI sequences of *Graphelmis anulata* Čiampor, *G. obesa* Čiampor, and *G. monticola* (Grouvelle) were retrieved from the GenBank database and were used as the outgroup (see Table 1 for accession numbers). Voucher IDs for sequenced specimens are provided in square brackets.

Table 1. Samples used in the molecular analyses.

Specimens, voucher IDs	Origin	GenBank no.	BOLD ID no.
Okalia necopinata JK097	Malaysia, Sarawak, Gunung Mulu	MT667271	BOLD: AEE6243
Okalia necopinata JK001	Malaysia, Sarawak, Gunung Mulu	MT667272	BOLD: AEE6243
Okalia necopinata JK201	Malaysia, Sarawak, Gunung Mulu	MT667273	BOLD: AEE6243
Okalia necopinata JK203	Malaysia, Sarawak, Gunung Mulu	MT667274	BOLD: AEE6243
Okalia necopinata JK205	Malaysia, Sarawak, Gunung Mulu	MT667275	BOLD: AEE6243
Okalia necopinata JK207	Malaysia, Sarawak, Gunung Mulu	MT667276	BOLD: AEE6243
Okalia necopinata JK206	Malaysia, Sarawak, Gunung Mulu	MT667277	BOLD: AEE6243
Okalia necopinata JK204	Malaysia, Sarawak, Gunung Mulu	MT667278	BOLD: AEE6243
Okalia necopinata JK202	Malaysia, Sarawak, Gunung Mulu	MT667279	BOLD: AEE6243
Okalia globosa FZ2651	Malaysia, Pahang	–	–
Okalia globosa FZ0001	Malaysia, Pahang	–	–
Outgroup			
Graphelmis anulata FZ510	Malaysia, Pahang	MK505424	BOLD: ADC0259
Graphelmis obesa FZ544	Malaysia, Sabah	MK505408	BOLD: ADB9823
Graphelmis monticola FZ530	Malaysia, Kelantan	MK505416	BOLD: ADB9822

Table 2. Pairwise genetic distances (*p*-distance) between two *Okalia* species and the genus *Graphelmis* (outgroup).

	O. necopinata JK097	*O. necopinata* JK001	*O. necopinata* JK201	*O. necopinata* JK203	*O. necopinata* JK205	*O. necopinata* JK207	*O. necopinata* JK206	*O. necopinata* JK204	*O. necopinata* JK202	*O. globosa* FZ2651	*O. globosa* FZ0001	*G. anulata* FZ510	*G. obesa* FZ544	*G. monticola* FZ530
O. necopinata JK097	–													
O. necopinata JK001	0.000													
O. necopinata JK201	0.000	0.000												
O. necopinata JK203	0.000	0.000	0.000											
O. necopinata JK205	0.000	0.000	0.000	0.000										
O. necopinata JK207	0.000	0.000	0.000	0.000	0.000									
O. necopinata JK206	0.000	0.000	0.000	0.000	0.000	0.000								
O. necopinata JK204	0.003	0.003	0.003	0.003	0.003	0.003	0.003							
O. necopinata JK202	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.005						
O. globosa FZ2651	0.024	0.024	0.024	0.024	0.024	0.024	0.024	0.028	0.023					
O. globosa FZ0001	0.028	0.028	0.028	0.028	0.028	0.028	0.028	0.031	0.026	0.003				
G. anulata FZ510	0.178	0.178	0.178	0.178	0.178	0.178	0.178	0.178	0.178	0.182	0.186			
G. obesa FZ544	0.166	0.166	0.166	0.166	0.166	0.166	0.166	0.166	0.164	0.164	0.168	0.141		
G. monticola FZ530	0.203	0.203	0.203	0.203	0.203	0.203	0.203	0.203	0.201	0.194	0.198	0.161	0.141	–

Results

Phylogenetic analyses

Altogether, nine sequences of *O. necopinata* were obtained and used together with two provided sequences of *O. globosa* (Table 1). The COI alignment was 633-bp long, unambiguous, and without indels. ML and NJ trees had identical topologies, with nodal supports as shown in Fig. 1. The interspecific divergence of the two species of *Okalia* varied from 2.3–3.1%, while the intraspecific distance ranged from 0.0–0.5% in *O. necopinata*, and it was 0.3% in *O. globosa* (Table 2). Both *Okalia* species are grouped with maximum statistical support.

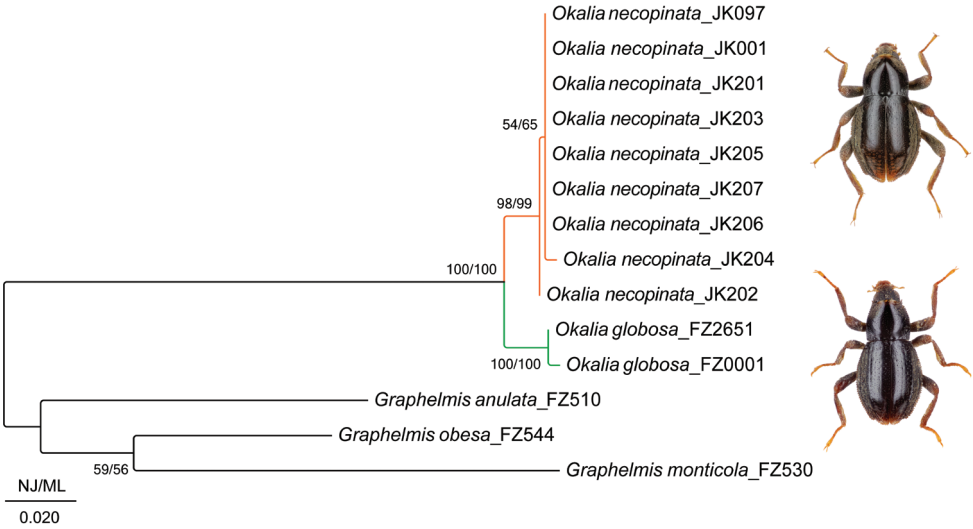

Figure 1. Phylogenetic tree based on the 633 bp fragments of the mitochondrial COI gene. Bootstrap values (1,000) for maximum-likelihood and neighbor-joining analyses were performed in MEGA-X. The scale bar denotes two substitutions per 100 nucleotide positions.

Okalia necopinata **sp. nov.**

http://zoobank.org/3ABC4391-3889-4914-ABF6-E735A2E2CB0A
Figs 2A, 3A–F, 4A, B, 5A, E, F, 6

Diagnosis (all specimens examined are wingless). Length: 1.44–1.63 mm, width: 0.78–0.88 mm. Body widely obovate and strongly convex dorsally. Surface scarcely finely punctate, smooth; dorsal plastron on head, anterolateral portion of pronotum, and elytra between lateral margin and fifth interval. Pronotal median groove absent, sublateral carinae very fine, indistinct; femora moderately expanded; fifth elytral interval granulate on posterior half, sixth near apex, seventh entirely; elytral striae obsolete; elytral apices obliquely truncate; lateral sides of pronotum and elytra serrate. Penis apically arrowhead-shaped (in ventral/dorsal view). Ovipositor: coxite long and narrow; posterolateral angle strongly produced laterad, acute. Female internal genital tract with bursa copulatrix enlarged, saccular, as long as ovipositor, with a pair of mesal longitudinal sclerites, a pair of admedian densely denticulate sclerites, and with numerous short spinules, especially laterally; spermatheca with two branches.

The new species differs from *Okalia globosa* in the larger size, longer elytral declivity, and especially in the granulation of the fifth elytral interval being confined to the posterior half. Furthermore, the elytral and pronotal punctation is less distinct than in *O. globosa*. The arrowhead-shaped apex of the aedeagus is more elongate, and the apex of the coxite of the ovipositor is more strongly produced laterad and more acute.

Furthermore, the single available female from Sabah differs in the more extensive granulation of the fifth elytral interval, and the irregular microscopic wrinkles of the elytral intervals. This winged female has also a narrower and longer pronotum with

lateral sides subparallel posteriorly, and the sublateral pronotal carinae are more prominent than in the new species.

Etymology. The epithet, a Latin adjective (*necopinata* = unexpected, unforeseen), refers to the unexpected discovery of this species in a small, very slowly flowing stream, a somewhat atypical habitat for riffle beetles.

Type locality. Very shallow, slowly flowing, meandering stream (Fig. 6), which is entirely shaded by the trees of a primary dipterocarp forest in the limestone area of Gunung Mulu National Park, ca 4°02'59.5"N, 114°49'24.3"E, 70 m a.s.l. (north-eastern Sarawak, Borneo, Malaysia). The stream is ca 1 m wide, with a few deeper pools, and contains large amounts of accumulated leaves; the bottom is sandy with fine gravel and wood debris; the muddy banks are densely covered with *Phymatarum borneense*. [Note. Unfortunately, Kodada et al. (2020a, 2020b) provided incorrect coordinates for this locality for *Ancyronyx pulcherrimus* Kodada, Jäch, Čiampor and *A. sarawacensis* Jäch].

Material examined. ***Holotype*** ♂ (CFDS): "Malaysia, Sarawak, Marudi distr., Gunung Mulu NP, 12.10.2018, (40) 4°02'59.5"N, 114°49'24.3"E, 70 m a.s.l., small stream in primary forest, Kodada & Selneković lgt.". ***Paratypes*** including sequenced voucher specimens (CFDS, CKB, NMW): 5 ♂♂, 10 ♀♀ and 7 specimens (sex not examined) with same collecting data as holotype.

Description of holotype. Habitus (Fig. 2A). Body form widely obovate, widest at elytral midlength, lacking shoulders (Fig. 3A); body 1.81× as long as wide (BL/EW); BL: 1.49 mm, EW: 0.82 mm. Plastron structures on clypeus, frons, area posteriad of eyes, an-

Figure 2. Habitus of *Okalia* species **A** *O. necopinata* sp. nov., wingless male, holotype, body length 1.49 mm **B** *O. globosa* Kodada & Čiampor, wingless male, paratype, body length 1.38 mm.

terolateral portion of pronotum, hypomera, lateral portions of prosternum, mesepisterna, metepisterna, lateral portion of metaventrite, epipleura, lateral portions of ventrites, elytra between margin and fifth interval, anterior face of metacoxae, femora and tibiae.

Head. Partly retractable, retracted portion reticulated, without plastron structures; head width 0.31 mm; interocular distance 1.4× as long as longitudinal diameter of eye. Labrum wider than long, anterior margin with row of shorter trichoid setae ventrally, anterolateral portion with row of longer setae, posterior portion microreticulate. Clypeus about as long as labrum, wider than long; frontoclypeal suture distinct, arcuate; surface finely punctate, punctures setigerous, setae adpressed. Frons with setigerous micropunctures and scattered pointed granules; granules half as wide as a facete diameter, separated by distances of about 1.5–3.0× a facete diameter. Eyes small, feebly protuberant in dorsal view, ellipsoidal in lateral view, longer than wide, with about 50 facets (Fig. 3B). Subantennal groove very shallow, confined to anteroventral portion of eye. Antenna short, reaching posterior margin of eye, eight-segmented, capitate; scape short; pedicel longer, enlarged distally, with a few trichoid setae; segment 3 shorter than pedicel; segments 4–7 short, wider than long; segment 8 nearly as long as combined length of five preceding segments, enlarged, with numerous setae.

Thorax. Pronotum slightly wider than long, widest near posterior fourth, PW: 0.54 mm, PL: 0.46 mm; disc strongly convex, sparsely, and finely punctate; punctures with moderately long semi-erect setae, distinctly smaller than facets, and separated by distances 1.5–3.0× of a facete diameter. Sublateral carinae indistinct, present on posterior fifth of pronotum; median groove absent; prebasal pits shallow; anterior margin translucent, moderately arcuate; anterior angles acute and strongly protruding; posterior angles with fine wrinkles; lateral margin serrate, more strongly along anterior than along posterior half. Plastron area nearly triangular, on each side of midline, widest anteriorly, reaching nearly midlength. Hypomeron broadest near middle, separated by a gap from prosternum anteriorly, postcoxal projection absent. Prosternum in front of coxae about as long as prosternal process, feebly deflected anteriad; prosternal process subtriangular, narrowed posteriad, with apex feebly rounded, nearly truncate, sides weakly and widely raised. Procoxae subglobular, separated near middle by distance of about 0.5× of head width (Fig. 3D); mesocoxae subglobular, more transverse than procoxae, intercoxal distance near middle twice as long as in procoxae; metacoxae about twice as wide as long, reaching elytra, separated by same distance as mesocoxae; pro- and mesocoxal cavities deep; paired mesoventral procoxal rest deep, strongly oblique. Mesothorax short, strongly sclerotized ventrally and dorsally; scutellum small, subtriangular; mesoventrite short, about twice as long as wide (Fig. 3E), medial groove deep and narrow; mesepisterna fused with metaventrite; mesepimeron short, strongly sclerotized; mesoventral process with lateral sides raised. Metaventrite ca 1.5× as long as mesoventrite, slightly depressed on disc; mesometaventral junction formed by distinct angulated suture; discrimen fine; transverse suture absent, its position marked by row of larger punctures; exposed portion of metepisternum long and very narrow; metaventral process wide, with lateral sides raised; surface of disc very finely punctate, punctures distinctly smaller than a facete diameter, widely separated. Elytra strongly convex dorsally, highest near

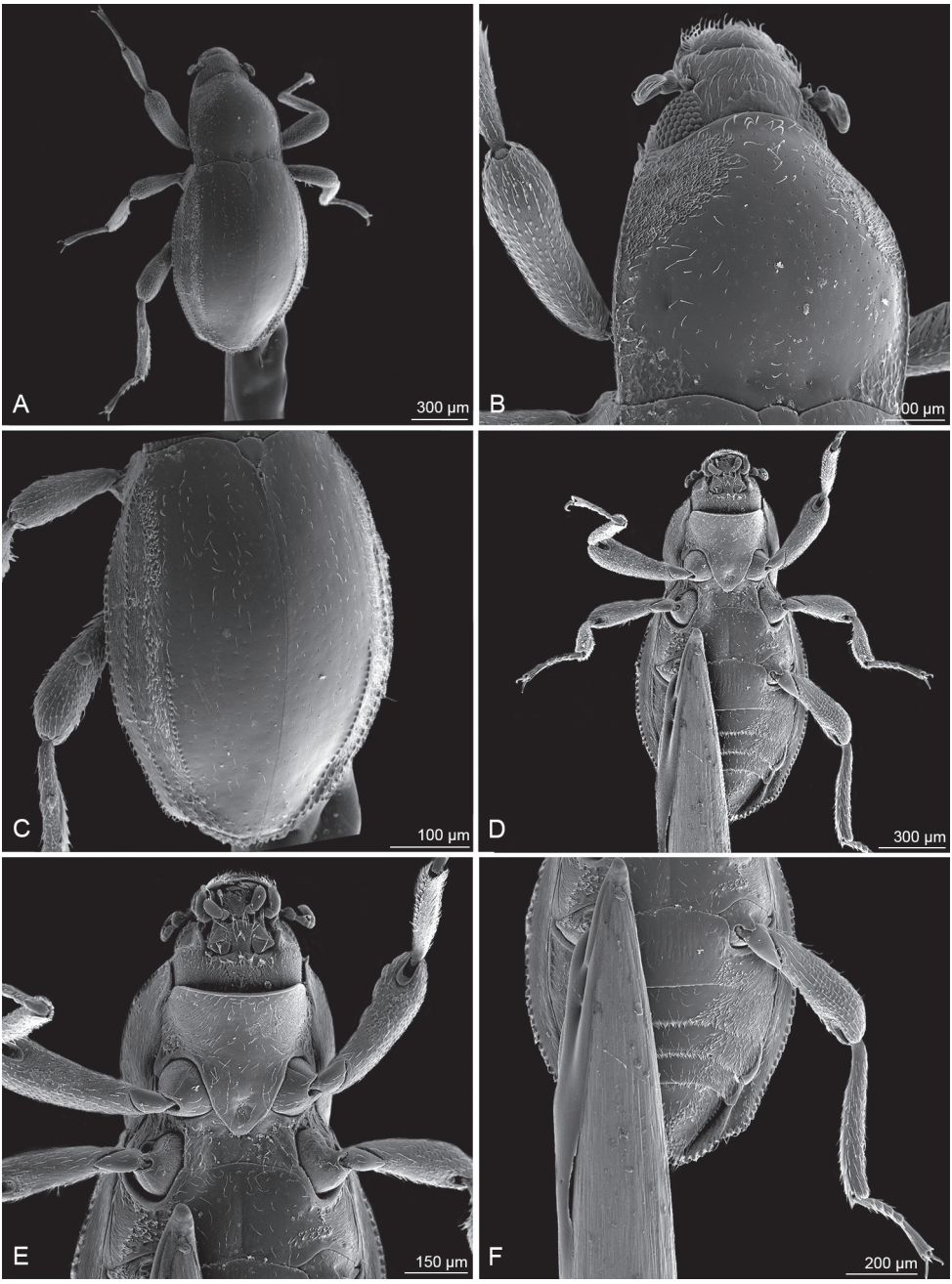

Figure 3. *Okalia necopinata* sp. nov., scanning electron micrographs **A** habitus, dorsal aspect **B** head and pronotum, dorsal aspect **C** elytra, dorsal aspect **D** habitus, ventral aspect **E** head and thorax, ventral aspect **F** abdomen, ventral aspect.

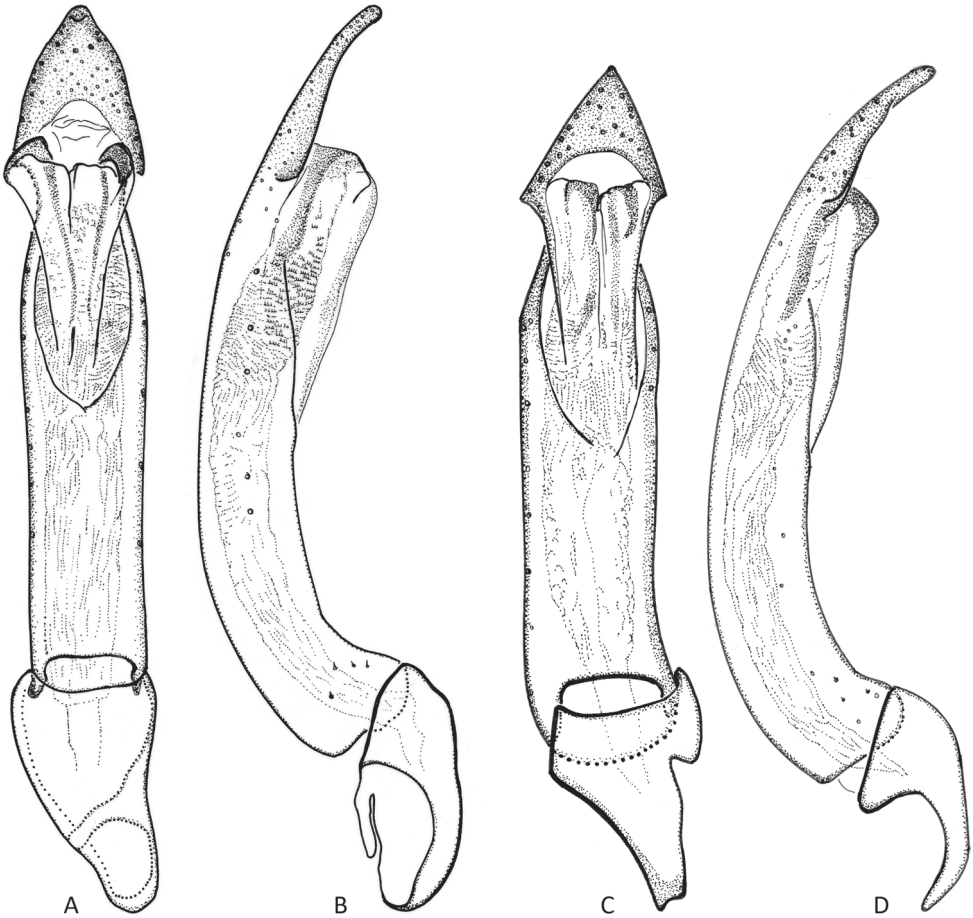

Figure 4. Aedeagi **A** *Okalia necopinata* sp. nov., holotype, dorsal aspect **B** same, lateral aspect **C** *O. globosa* Kodada & Čiampor, paratype, dorsal aspect **D** same, lateral aspect. Scale bar: 0.1 mm.

anterior third (lateral view), obovate; EL: 1.04 mm, EW: 0.82 mm; apices more or less obliquely truncate; lateral sides and apices serrate. Striae obsolete, their punctures very fine, slightly larger than punctures of intervals; surface with semi-erect, moderately long trichoid setae on striae and intervals, and with a few scattered longer and thinner setae on plastron area. Interval 5 with a dense row of granules along posterior half (Fig. 3C); sixth interval with a few scattered granules anteriorly, densely granulate near apex; seventh interval granulate along entire length; shoulders absent. Epipleura widest anteriorly, inflected and slightly narrowed at level of metacoxa, concealed by lateral projection of ventrites 3 and 4, effaced at truncate apical portion. Legs shorter than elytra and pronotum combined, surface granulate and setose. Femora nearly as long as pronotum, moderately expanded and feebly grooved distally; mesofemur shorter than pro- and metafemur; pro- and mesofemur with dense adpressed long setae in proximal

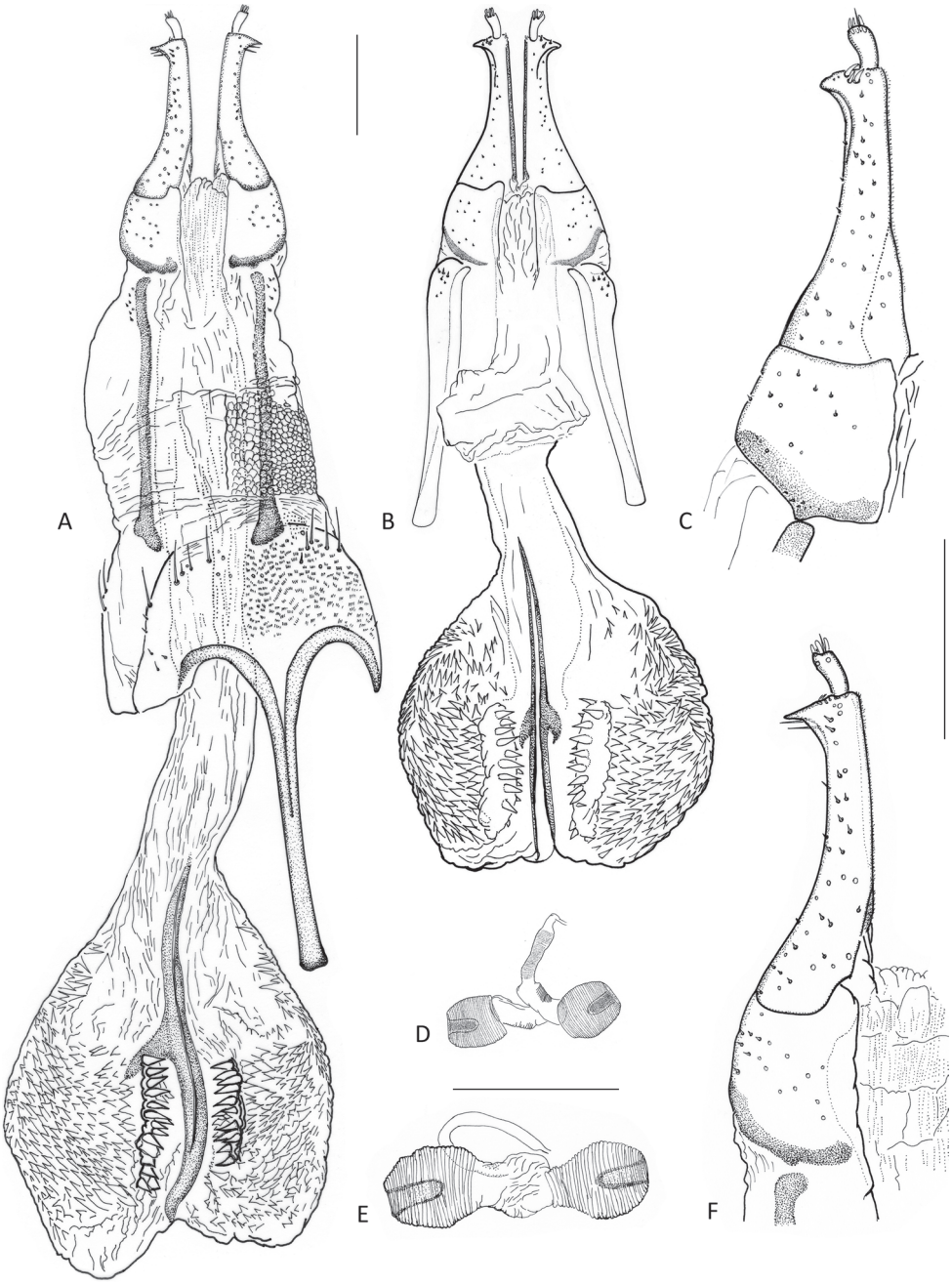

Figure 5. Female genitalia **A** *Okalia necopinata* sp. nov., ovipositor with bursa copulatrix and sternite VIII, paratype, ventral aspect **B** *O. globosa* Kodada & Čiampor, ovipositor with bursa copulatrix, paratype, ventral aspect **C** same, coxite and gonostylus, enlarged **D** *O. globosa*, spermatheca **E** *O. necopinata*, spermatheca **F** same, coxite and gonostylus, enlarged. Scale bar: 0.1 mm.

half on face adjacent to body. Tibiae subequal in length with femora, straight and simple. Tarsi five-segmented, shorter than tibia, reticulate; terminal tarsomere nearly as long as combined length of preceding segments; segments 1–4 with a few peg-like stout setae ventrally and with a few trichoid setae laterally and dorsally; terminal segment with trichoid setae only. Claws shorter than half of terminal segments, moderately curved, similar in form and inclination angle; empodium with two short setae.

Abdomen. Ventrites strongly sclerotized, moderately convex, separated by sutures; lateral margins of ventrites 1–2 evenly arched, in ventrites 3–4 projecting laterad (Fig. 3F), in ventrite 5 with fine denticles. Abdominal intercoxal process wide and short, ca 3.0× as wide as long; anterior portion with irregular fine longitudinal furrows; admedian carinae of ventrite 1 absent; ventrite 5 with numerous irregularly spaced granules, posterior margin narrowly truncate, with one pair of lateral clusters of stronger setae. Aedeagus (Fig. 4A, B) ca 0.70 mm long, bent and strongly sclerotized, tubular, without parameres, subapically abruptly constricted to form arrowhead-like apex (ventral/dorsal view); ventral sac present in posterior portion of aedeagus, lacking corona, bearing two longitudinal lateral sclerotizations; endophallus with numerous small spinules; phallobase short, its anterior portion strongly asymmetrical.

Female genitalia. Ovipositor (Fig. 5A), ca 0.53 mm long, as long as combined length of ventrites 3–5; vulva between base of coxites. Transverse baculum well sclerotized, longitudinal baculum ca 1.1× as long as coxite (measured from the apical margin of coxite to point where it is joining the transverse baculum). Coxite long and narrow, divided by transverse line ventrally, apicolateral angle strongly produced laterad, acute (Fig. 5F); distal portion ca. 1.8× as long as proximal portion; stylus short, curved, with apical sensilla. Female internal genital tract: vagina elongate, simple; bursa copulatrix enlarged, saccular, as long as ovipositor, with a pair of mesal longitudinal sclerites, a pair of admedian, densely denticulate sclerites, and numerous short spinules, especially laterally; spermatheca with two branches, like those of *O. globosa* (Fig. 5D, E).

Secondary sexual dimorphism. Females are on average slightly longer and broader than males. No other prominent secondary sexual characters were found.

Variability. The examined specimens vary moderately in punctation of pronotum and elytra as well as in size: BL ♂♂: 1.44–1.46 mm, ♀♀: 1.52–1.63 mm; EW ♂♂: 0.78–0.80 mm, ♀♀: 0.82–0.86 mm; PW ♂♂: 0.52–0.53 mm, ♀♀: 0.53–057 mm, PL ♂♂: 0.48–0.49 mm, ♀♀: 0.47–0.50 mm; EL ♂♂: 0.97–0.99 mm, ♀♀: 1.05–1.11 mm.

Distribution. The species is so far known only from the type locality in Sarawak.

Discussion

Borneo is an island with very high biodiversity; however, in the last 40 years, human activities have significantly impacted local biota (Ocampo-Peñuela et al. 2020). Nine

Figure 6. Stream in primary forest of Gunung Mulu National Park, Sarawak, type locality of *Okalia necopinata* sp. nov.

genera and 16 species of Macronychini have been recorded from Borneo so far. Three of these, *Homalosolus* Jäch & Kodada, *Loxostirus* Jäch & Kodada, and *Rhopalonychus* Jäch & Kodada, are currently regarded as endemic. The remaining genera, including *Okalia*, have larger distribution areas (Jäch et al. 2016). The ecology and larval stages of the Bornean species are largely unknown, and the only available fragmental information comes from original descriptions (e.g., Jäch and Boukal 1996; Jäch and Kodada 1996a, 1996b, 1997).

We found all genera of Elmidae recorded from Borneo, though deforestation, climate change, and environmental pollution are very adverse factors seriously affecting insects on the island. We collected many species in streams flowing through secondary forests covering most of Sarawak, although in rather a low abundance. The remaining primary forests are relatively small and fragmented. Still, in their streams, we have confirmed a very high diversity and population density of Elmidae and Dryopidae (e.g., Kodada et al. 2020a, 2020b).

Surprisingly, in the numerous lotic habitats examined, we found *Okalia* in only one calcareous stream. We do not know whether this is due to extinction or due to very specific habitat requirements. The wingless populations are likely much more sensitive to environmental changes and appear to become extinct faster. We assume that the species only survives in primary rainforests and may also occur in nearby Brunei, like *Ancyronyx pulcherrimus*.

Key to wingless specimens of *Okalia*

1 Elytral interval 5 with densely spaced granules along posterior half (Figs 2A, 3C); elytral and pronotal punctation very fine (Fig. 3B), punctures of elytral striae hardly larger than those of intervals; apex of aedeagus elongated arrowhead-like (Fig. 4A, B); coxite of ovipositor with apicolateral angle strongly produced laterad, acute (Fig. 5A, F); spermatheca as in Fig. 5E. Body length: ♂♂ 1.44–1.46 mm, ♀♀ 1.52–1.63 mm, maximum width: ♂♂ 0.78–0.80 mm, ♀♀ 0.82–0.86 mm. Known only from Sarawak (East Malaysia) .... ***O. necopinata* sp. nov.**

– Elytral interval 5 with densely spaced granules from anterior 0.1 to apex (Fig. 2B); elytral and pronotal punctation stronger, punctures of elytral striae larger than those of intervals; apex of aedeagus triangular arrowhead-like (Fig. 4C, D); coxite of ovipositor with apicolateral angle less acute (Fig. 5B, C); spermatheca as in Fig. 5D. Body length: ♂♂ 1.30–1.38 mm, ♀♀ 1.44–1.48 mm; maximum width: ♂♂ 0.72–0.75 mm, ♀♀ 0.74–0.76 mm. Known only from Pahang (West Malaysia)..... ***O. globosa* Kodada & Čiampor**

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A new species of beaded lacewings (Neuroptera, Berothidae) from mid-Cretaceous Myanmar amber

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Abstract

A new species of Berothidae, *Jersiberotha musivum* sp. nov., is described and illustrated from mid-Cretaceous (lowest Cenomanian) Myanmar amber. It is easily distinguished from other species of Berothidae by the configuration of the wing venation including: forewing with distinct areas of infuscation surrounding cross-veins and vein forks, all cross-veins simple prior to ScP-RA fusion, presence of two cross-veins ra-rp; absence of inner or outer graduate series of cross-veins; RP with three branches; and absence of ma-mp cross-veins and cua-cup cross-veins; while hind wing has cross-vein 1r-m absent. The previous diagnoses of *Iceloberotha* Grimaldi, 2000 and *Jersiberotha* Grimaldi, 2000 are quite unclear because some characters occur mosaically in both genera. In order to solve this problem and distinguish *J. musivum* from other species in the family, a new key to species of Berothidae from Myanmar amber has been provided and the diagnoses of *Iceloberotha* and *Jersiberotha* have been revised.

Keywords

fossil, lower Cenomanian, Mantispoidea, Neuropterida, taxonomy

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Introduction

The family Berothidae, commonly known as beaded lacewings, together with Mantispidae and Rhachiberothidae, belongs to the superfamily Mantispoidea, which represents one of the major lineages of the crown group of Neuroptera (Wang et al. 2016; Engel et al. 2018; Winterton et al. 2018). The extant Berothidae are distributed in all zoogeographical regions and currently comprise less than 130 described species of 28 genera worldwide (Oswald 2019). The genus *Jersiberotha* was firstly erected by Grimaldi from the New Jersey amber for sharing the wing characters: two adjacent ra-rp cross-veins in the forewing, only one ma- mp cross-vein (Grimaldi 2000). Engel and Grimaldi (2008) described two other species (*J. myanmarensis* and *J. tauberorum*) and a related genus *Iceloberotha* from Myanmar amber.

Molecular evidence suggested the Berothidae might have diverged during the Late Triassic (Wang et al. 2016). Winterton et al. (2018) and Vasilikopoulos et al. (2020) estimated the divergence between Beorthidae and Mantispidae was in the Early Jurassic, although the oldest definite fossil of Berothidae was reported from the Middle Jurassic (Makarkin et al. 2011). So far, there are about 27 genera and 41 species of fossil berothids described from the Middle Jurassic to late Eocene (Yang et al. 2019; Fuente et al. 2021). The amber from Myanmar is one of the most intensively studied objects amongst Cretaceous fossiliferous resins and contains a remarkably diverse flora and fauna (Grimaldi et al. 2002). It is remarkable that the palaeodiversity of Berothidae is extraordinarily rich from the mid-Cretaceous of Myanmar, being one of the major Neuropteran lineages in this deposit (Ross 2019), with 13 genera and 19 species described, based on the Myanmar amber specimens (Engel and Grimaldi 2008; Yuan et al. 2016; Huang et al. 2018; Makarkin 2018; Yang et al. 2019; Yang et al. 2020). These Myanmar amber berothids show diverse morphological characters and are probably the members, or as the stem-groups of different subfamilies (Huang et al. 2018).

Herein, a new species of *Jersiberotha* Grimaldi, 2000 is described, based on a well-preserved female specimen from the mid-Cretaceous (ca. 98.8 Ma) of Myanmar. In addition, a revised key to the species of Berothidae from Myanmar amber has been provided. The diagnoses of *Iceloberotha* and *Jersiberotha* also have been revised.

Materials and methods

This study is based on a single, female specimen preserved in a piece of clear, yellowish Myanmar amber, which was collected from an amber mine, located in the Hukawng Valley of Kachin Province, Myanmar (Chen et al. 2019). The age of Myanmar amber in this investigation is radiometrically dated at 98.79 ± 0.62 Ma, based on U-Pb zircon dating of the volcanoclastic matrix (Shi et al. 2012). However, it is important to highlight that the Zircon date only gives the age of the top bed and a minimum age for the amber, so the geologic age of Myanmar amber may be slightly older than the Zircon date.

The amber piece that contains the inclusions was cut and polished with different grain sizes of sandpaper and finally buffed with polishing powder. The specimen is housed in the Institute of Paleontology and Stratigraphy, School of Earth Sciences, Lanzhou University, Gansu Province, China. Examinations of the specimen were accomplished using a Leica S8APO stereomicroscope, equipped with a Leica DFC295 camera. Images were digitally stacked as photomicrographic composites of approximately 20 individual focal planes obtained using the software Helicon Focus 6 for better visualisation of the 3D structures. Drawings for the analysis were based on the specimen and photographs. Figures were prepared with CorelDraw X4 and Adobe Photoshop CS6.

General terminology of wing venation follows Kukalová-Peck and Lawrence (2004) as interpreted by Yang et al. (2012) and Yang et al. (2014). Terminology of the wing spaces and details of venation (e.g. spaces, veinlets) follows Oswald (1993) and the cross-veins designation follows Makarkin (2015). Terminology of genitalia follows Aspöck and Aspöck (2008). Cross-veins are designated after the longitudinal veins which they connect and are numbered in sequence from the base to the apex of the wing, for example, 1sc-r, first (proximal-most) cross-vein connecting Sc and R; 2m-icu, second cross-vein between M/MP and Cu/CuA.

Abbreviations are as follows: wing venation: ScA, subcosta anterior, ScP, subcosta posterior, RA, anterior radius, RP, posterior sector, RP1, proximal-most branch, MA and MP, anterior and posterior branches of media, CuA, anterior cubitus, CuP, posterior cubitus, AA1-AA3, first to third anterior anal vein; head and antennal structures: La, labrum, MP, maxillary palp, Pe, pedicel, Sp, scape; abdominal and genital structures: T: Tergite; S: sternite; phc: pseudohypocaudae; e: ectoproct; gcx, gonocoxites.

The identification key to the Berothidae species from Myanmar amber was modified from that provided by Yuan et al. (2016), based on the characters of the new species.

Systematic palaeontology

Order Neuroptera Linnaeus, 1758
Family Berothidae Handlirsch, 1906
Genus *Jersiberotha* Grimaldi, 2000

***Jersiberotha musivum* sp. nov.**
http://zoobank.org/76B6E201-6262-4FC0-ACAC-1FF50C04815C

Diagnosis. *Jersiberotha musivum* may be easily distinguished from the other four species of *Jersiberotha* by a combination of the following character states: in forewing, two cross-veins ra-rp are present; inner or outer graduate series of cross-veins are absent; RP has three branches; ma-mp cross-veins and cua-cup cross-veins are absent; and basal cross-vein 1r-m is absent from hind wing.

Etymology. The specific name is from the Latin "*musivum*" (meaning "mosaic"), in reference of the new species with some characters in wing venation occurring mosaically in both two similar genera, i.e. *Iceloberotha* and *Jersiberotha*.

Locality and horizon. Noije Bum Hill, Hukawng Valley, Kachin State, Myanmar; lower Cenomanian, mid-Cretaceous.

Material examined. ***Holotype*** LZUGSW20210219; deposited in the Institute of Paleontology and Stratigraphy, School of Earth Sciences, Lanzhou University, Gansu Province, China.

Description. Female (Fig. 1A). Body length ca. 1.50 mm as preserved. ***Head*:** oval in lateral view, length ca. 0.2 mm. Compound eyes prominent, ovoid, large, length ca. 0.14 mm. Vertex with sparse long setae. 3rd and 4th segments of maxillary palpus relatively short, approximately twice as long as wide; apical tarsomere elongated, very acute distally, approximately five times as long as wide. Labial palpus not fully visible. Antenna: length ca. 0.5 mm (Fig. 1B), scapus elongate, approximately three times as long as maximum width; pedicellus elongate, approximately two times longer than maximum width and slightly broader than flagellomeres; the following 21 flagellomeres, cylindrical, slightly longer than wide, with relatively long setae around; basal flagellomeres transverse, distal flagellomeres slightly elongate; apical flagellomere conical.

***Forewing*:** narrowly slender and oval shaped (Fig. 2A, B), length ca. 1.70 mm, width ca. 0.55 mm. Leading edge with short setae, trailing edge with long setae. Costal space narrow, slightly narrowed medially. All subcostal veinlets simple, basal and distal subcostal veinlets slightly curved. Humeral veinlet cross-vein-like. Subcostal space nearly as broad as costal space, proximal cross-vein (1scp-r) located proximad at origin of RP; ScP terminating at RA. ScP+RA entering margin before wing apex, shallowly forked distally with five short branches. RA space a little broader than subcostal space, with only two cross-veins present, the basal one proximad to middle of wing and the distal one proximad at fusion of ScP and RA. RA slightly thickened; RP originating from RA relatively distant from wing base, with two long branches originating between 2ra-rp and 3ra-rp and one short branch distad at 3ra-rp. RP1 with 2 branches, primary fork distad at 3ra-rp, one branch not forked, other with three pectinate distal branches; stem of RP, RP2 and RP3 shallowly forked. No cross-veins between branches of RP. M fused with R basally. One cross-vein between RP and M (2r-m) connecting stem of RP and MA. M basally approaching R; forked nearly at origin of RP. MA forked primarily distad at 3ra-rp, proximal branch with two pectinate distal branches, distal branch once forked distally; MP forked primarily between 2ra-rp and 3 ra-rp, proximal branch with two pectinate distal branches, distal branch once forked distally. No cross-veins between MA and MP. Two cross-veins between M and Cu: 1m-cu connecting M and Cu distad at origin of CuP; 2m-cu connecting MP and CuA. Cu divided into CuA and CuP rather far from wing base. CuA and CuP dichotomously branched. No intracubital cross-veins. One cross-vein (1cu-aa1) between Cu and AA1 connecting CuP, AA1 much proximad to their branching. AA1 once forked distally, AA2 thickened, pectinately branched, with two short branches. AA3 short, simple. Marginal setae long to very long and

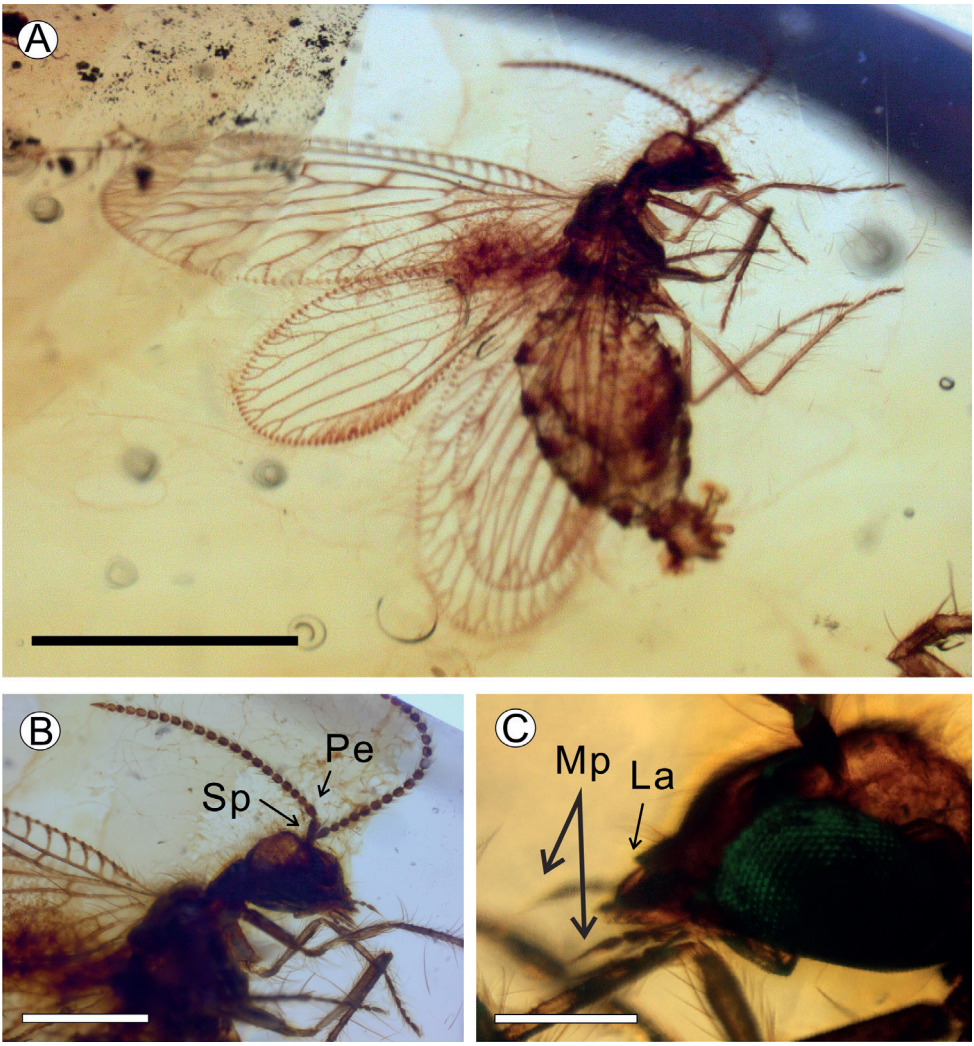

Figure 1. *Jersiberotha musivum* sp. nov. Holotype LZUGSW20210219 **A** photograph of holotype habitus (lateral left view) **B** photograph of head, pedicel (Pe) and scape (Sp) **C** photograph of antenna, maxillary palpus (Mp) and labrum (La). Scale bars: 1 mm (**A**); 200 μm (**B**); 100 μm (**C**).

arranged in bunches at end of veins and trichosors. Trichosors prominent along entire wing margin. Wing membrane hyaline, with following dark brown maculation; narrowly margined cross-vein 2ra-rp, 3ra-rp and 2r-m; widely margined cross-vein 2m-cu; spots at origin (inside) of RP, RP1, RP3 and at primary forks of RP1, MA, MP, CuA and CuP.

***Hind wing*:** narrowed proximally, broadened distally, length ca. 1.40 mm, width ca. 0.55 mm (Fig. 2C, D). Costal space strongly narrowed medially, slightly dilated proximally and strongly dilated distad at fusion of ScP and RA. Subcostal veinlets

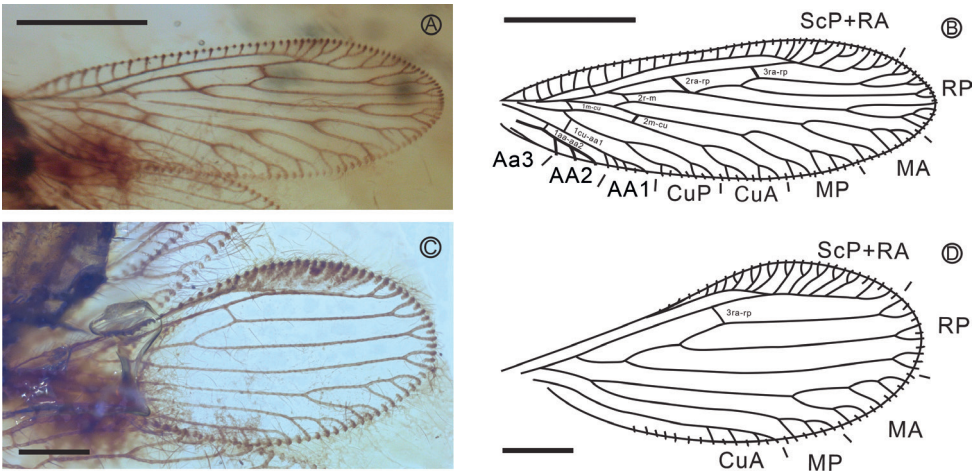

Figure 2. Wing venation of *Jersiberotha musivum* sp. nov., Holotype LZUGSW20210219 **A** photograph of forewing **B** line drawing of forewing **C** photograph of hind wing **D** line drawing of hind wing. Scale bars: 500 μm (**A, B**); 200 μm (**C, D**).

simple, closely spaced; distal subcostal veinlets strongly oblique, thickened. Subcostal space rather broad, basally appears narrowed; no cross-veins detected. ScP stout, nearly straight before terminating at RA, ScP + RA entering margin far before wing apex, veinlets are difficult to be accurately counted, but it appears there are six veinlets. RA space clearly wider than subcostal space, with one cross-vein proximad to fusion of ScP and RA, none distad. RP originating rather far from wing base, with two branches originated proximad to 3ra-rp, none distad. Stem of RP, RP1 and RP2 shallowly once forked. No cross-veins between branches of RA, RP and M; basal 1r-m absent. M basally fused with R; forked distad origin of RP. MA and MP nearly parallel for most of the length; MA dichotomously branched; MP pectinately branched, with two short simple branches, no intramedian cross-veins. Cross-veins between M, Cu (1m-cu) not discernible. CuA pectinately branched, with three short simple branches. CuP and AA1 not detected. Marginal setae very long, arranged in bunches at end of veins, especially along hind margin. Wing membrane hyaline, without maculation.

Abdomen oval, stout. All segments clearly visible except terminal-most, with broad membranous space between sternites and tergites (Fig. 3A). Tergite I not visible, Tergite II and sternite II shorter than tergites and sternites of abdominal segments III – VII, without specialised modifications. Tergite VIII well developed, dorsally broader than laterally, elongate and extending towards the sternite. Tergite IX not clearly identified, sternite VIII reduced. The genitalia structures of the new species are not well preserved, the pair of ectoprocts (e) are slightly shorter than the other pair of gonocoxites (gcx) and the unpaired club-shape process may be a part of inner genitalia (Fig. 3B, C). All tergites and sternites covered with dense, long fine setae.

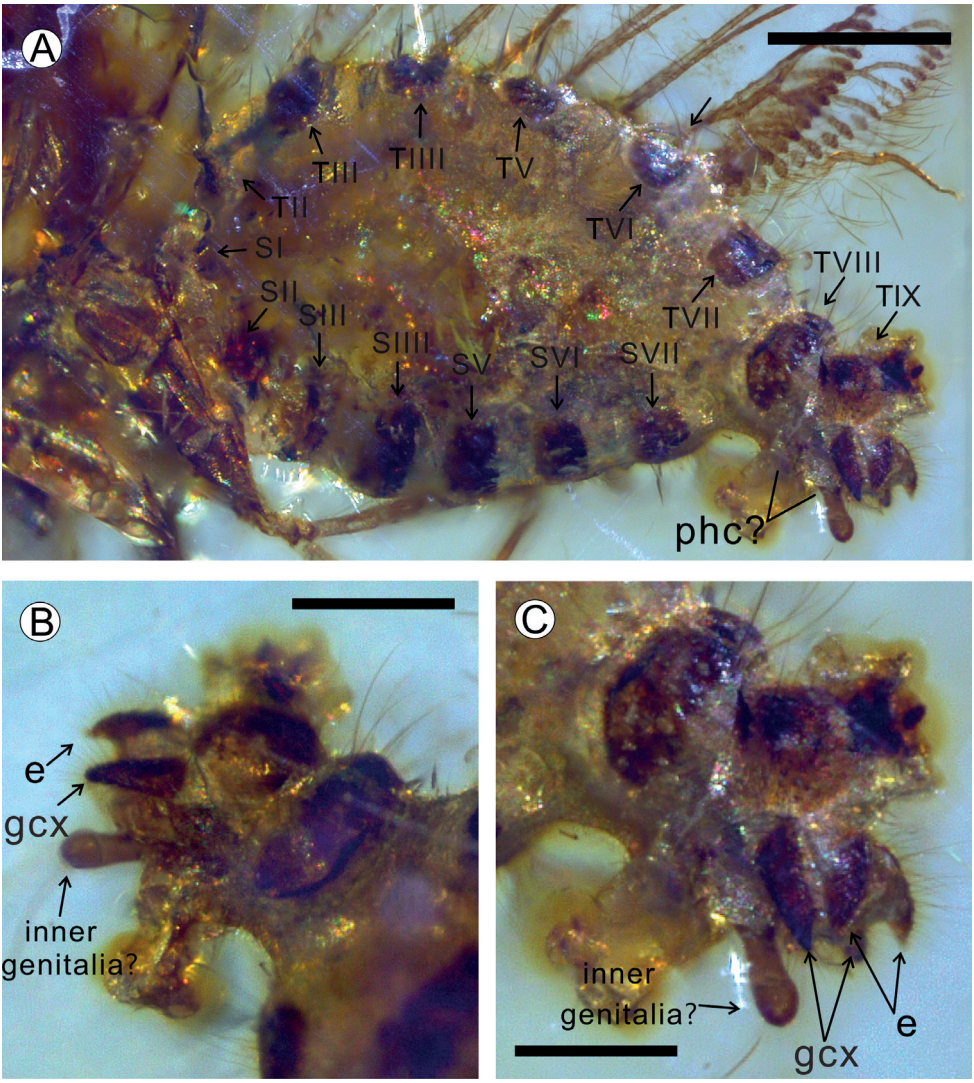

Figure 3. Abdomen and genital of *Jersiberotha musivum* sp. nov., Holotype LZUGSW20210219 **A** abdomen, lateral view **B** terminal segments, ventro-lateral view **C** terminal segments, lateral view. Scale bars: 200 µm (**A**); 100 µm (**B, C**).

Discussion

Key to species of Berothidae from Myanmar amber

1 Cross-veins ra-rp present in forewing; forewing typically with parse setae, rarely with dense setae.....**2**

– Cross-veins ra-rp absent in forewing; forewing very densely covered with elongate setae.....***Ethiroberotha elongata*** **Engel & Grimaldi, 2008**

2 Only one ra-rp cross-vein **3**
– More than one ra-rp cross-vein (at least two) **5**
3 Flagellum with 21-22 flagellomeres **4**
– Flagellum with more than 70 flagellomeres ..... ***Maculaberotha*, Yuan, 2016**
4 Vein RP with only one branch in forewing ..... ***Haploberotha persephone* Engel & Grimaldi, 2008**
– Vein RP with three branches in forewing ..... ***Haploberotha carsteni* Makarkin, 2018**
5 Distalmost ra-rp cross-vein present beyond Sc-R1 fusion in forewing **6**
– Distalmost ra-rp cross-vein present before Sc-R1 fusion in forewing **7**
6 Forewing with numerous setae on margins, sparse over wing surface; not obscuring wing venation; apical rp-rp and rp-m cross-veins absent. Body setae short and scattered ..... ***Telistoberotha libitina* Engel & Grimaldi, 2008**
– Forewing with dense setae on margins and over surface; apical rp-rp and rp-m present. Body setae dense and elongate ..... ***Dasyberotha eucharis* Engel & Grimaldi, 2008**
7 Forewing narrowly elongate, apex acute; costal space considerably broader basally than apically at ScP-RA fusion; scape short, as long as wide ..... ***Systenoberotha magillae* Engel & Grimaldi, 2008**
– Forewing ovoid, apex broadly round; costal space not broader basally than apically at ScP-RA fusion; scape 2-3 times as long as wide **8**
8 Humeral vein recurrent ..... ***Magniberotha recurrens* Yuan, 2016**
– Humeral vein simple, not recurrent **9**
9 Flagellum with more than 70 flagellomeres **10**
– Flagellum with 21-22 flagellomeres **15**
10 Forewing with 4-5 ra-rp cross-veins proximad to fusing point of ScP and RA **11**
– Forewing with 2-3 ra-rp cross-veins proximad to fusing point of ScP and RA **14**
11 Frons without a pair of short horns anteriad to antennal bases ..... ***Ansoberotha jiewenae* Yang, 2019**
– Frons with a pair of short horns anteriad to antennal bases **12**
12 Vein RP with eight branches ..... ***Cornoberotha monogona* Yang, 2020**
– Vein RP with less than eight branches **13**
13 Vein RP with five branches ..... ***Cornoberotha aspoeckae* Yang, 2020**
– Vein RP with six branches ..... ***Cornoberotha anomala* Yang, 2020**
14 Vein RP with six branches ..... ***Dolichoberotha bifurcate* Yang, 2020**
– Vein RP with four branches ..... ***Dolichoberotha burmana* Yang, 2020**
15 Forewing with distinct areas of infuscation surrounding cross-veins and vein forks, some or all cross-veins simple prior to ScP-RAfusion **16**
– Forewing lacking areas of infuscation; all c-sc cross-veins simple prior to ScP-RAfusion **18**

16 Forewing with one ma-mp cross-vein and one cua-cup cross-vein present ..... ***Jersiberotha myanmarensis*** **Engel & Grimaldi, 2008**
– Forewing with ma-mp cross-vein and cua-cup cross-vein absent **17**
17 Hind wing with basal cross-vein 1r-m present..... ..... ***Jersiberotha tauberorum*** **Engel & Grimaldi, 2008**
– Hind wing with basal cross-vein 1r-m absent..... ..... ***Jersiberotha musivum*** **sp. nov.**
18 Forewing with outer gradate series of cross-veins present..... .....***Iceloberotha kachinensis*** **Engel & Grimaldi, 2008**
– Forewing with outer gradate series of cross-veins absent..... .....***Iceloberotha simulatrix*** **Engel & Grimaldi, 2008**

The new species *Jersiberotha musivum* sp. nov. can be assigned to the family Berothidae, based on the forked veins in subcostal region and the scape three times as long as wide. A new identification key to the species of Berothidae from Myanmar amber has been presented and compared with the new species of other ones of this family. The venation of *Jersiberotha musivum* sp. nov. differs from that of *Protoberotha* Huang, 2018 and *Ethiroberotha* Engel & Grimaldi, 2008 in presence of cross-veins ra-rp in forewing, which is absent in both above-mentioned genera. The new species has more than one ra-rp cross-veins in forewing, differentiating it from the representatives of *Haploberotha* Engel & Grimaldi, 2008, which only has one ra-rp cross-vein.

The species of *Maculaberotha* Yuan, 2016 has RP with four branches in forewing and more than 70 flagellomeres, while the *J. musivum* sp. nov. possesses RP with three branches and flagellum with 21 flagellomeres. The distalmost ra-rp cross-vein before ScP-RA fusion in forewing differs that of *Telistoberotha* Engel & Grimaldi, 2008 and *Dasyberotha* Engel & Grimaldi, 2008, which have the cross-vein ra-rp beyond ScP-RA fusion.

Jersiberotha musivum sp. nov. also differs from that of *Systenoberotha* Engel & Grimaldi, 2008 in the scape three times as long as wide, in contrast to the scape being as long as wide in *Systenoberotha*, from *Magniberotha* Yuan, 2016 in humeral vein simple, not recurrent and RP with three branches in forewing, in contrast to the humeral vein being recurrent and RP with five branches in *Magniberotha*, as well as from that of *Ansoberotha* Yang, 2019, *Cornoberotha* Yang, 2020 and *Dolichoberotha* Yang, 2020 in flagellum with 21 flagellomeres, in contrast to the flagellum having more than 70 flagellomeres in all the three above-mentioned genera.

Amongst all known members of Berothidae, the venation of *Jersiberotha musivum* sp. nov. is more similar to that of *Iceloberotha* Engel & Grimaldi, 2008. *Jersiberotha* and *Iceloberotha* were initially distinguished, based on the obviously diagnostic characters of venation, i.e. speckless forewing in *Iceloberotha* vs. distinctly spotted forewing in *Jersiberotha*; absence of cross-vein ma-mp and cua-cup in *Iceloberotha* vs. presence of ma-mp and cua-cup in *Jersiberotha* (referring to the key to genera in Engel and Grimaldi 2008). Actually, these characters occurred mosaically in both genera, for example, the Myanmar species *J. tauberorum* Engel & Grimaldi, 2008 clearly loses the cross-veins ma-mp and cua-cup, while the

type species of *Iceloberotha* has an evident ma-mp cross-vein in the original drawings (Engel and Grimaldi 2008). The new species can be assigned to *Jersiberotha*, based on flagellum with 21 flagellomeres, forewing with distinct areas of infuscation surrounding cross-veins and vein forks, all cross-veins simple prior to ScP-RA fusion, presence of two cross-veins ra-rp, absence of inner or outer graduate series of cross-veins; RP with three branches.

The venation of the new species clearly differs from that of *Iceloberotha* Engel & Grimaldi, 2008 in forewing with distinct areas of infuscation surrounding cross-veins and vein forks, but the representatives of *Iceloberotha* lack areas of infuscation and all c-sc cross-veins are simple prior to ScP-RA fusion. *J. musivum* sp. nov. also differs from that of *J. myanmarensis* Engel & Grimaldi, 2008 and two New Jersey species (*J. luzzii* Grimaldi, 2000 and *J. similis* Grimaldi, 2000) in forewing with ma-mp cross-vein and cua-cup cross-vein absent, with the forewing with ma-mp cross-vein and cua-cup cross-vein being present in all three above-mentioned genera, as well as from *J. tauberorum* that has a 1r-m cross-vein on hind wing and cross-vein absent in the new species. Additionally, the absence of outer gradate series of cross-veins in the new species is similar to that of *I. simulatrix* Engel & Grimaldi, 2008 and *J. tauberorum* Engel & Grimaldi, 2008. The loss of the gradate series is not found in extant berothids (Makarkin 2018).

In summary, the above analysis indicates the fossil specimen here is most closely related to the genus *Jersiberotha* due to the observed combination of character states. The previous diagnoses of *Jersiberotha* and *Iceloberotha* are quite unclear because some characters occur mosaically in both genera. The diagnosis of *Jersiberotha* should be revised as flagellum with 21–22 flagellomeres, forewing with distinct areas of infuscation surrounding cross-veins and vein forks, some or all cross-veins simple prior to ScP-RA fusion, presence of more than one cross-veins ra-rp, absence of inner or outer graduate series of cross-veins; RP with no more than three branches and the diagnosis of *Iceloberotha* should be revised as flagellum with 21–22 flagellomeres, forewing without distinct areas of infuscation surrounding cross-veins and vein forks, all cross-veins simple prior to ScP-RA fusion, presence of more than one cross-veins ra-rp, RP with no more than three branches.

Conclusions

Jersiberotha musivum sp. nov. was described, based on a single, female from mid-Cretaceous Myanmar amber. The previous diagnosis between *Iceloberotha* and *Jersiberotha* was quite indistinct because some characters occurred mosaically in both genera. A new identification key to the Berothidae species from Myanmar amber was provided to distinguish the new species from others in the Berothidae and the revised diagnoses of *Iceloberotha* and *Jersiberotha* were also updated.

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The genus *Aridelus* Marshall (Hymenoptera, Braconidae, Euphorinae) from Japan, with description of a new species

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Abstract

Six Japanese species belonging to the genus *Aridelus* Marshall, 1898 (Hymenoptera, Braconidae) were recorded and photographed. Three species, *A. dubius* Belokobylskij, *A. egregius* Schmiedeknecht and *A. rufotestaceus* Tobias (= *Aridelus rufiventris* Luo & Chen **syn. nov.**), are new to Japan, and a new species, *A. rutilipoides* **sp. nov.** is described. An identification key to the Japanese species of *Aridelus* is also provided. In addition, new host records are provided, i.e., *A. flavicans* Chao reared from *Homoeocerus unipunctatus* and *Riptortus pedestris* (Alydidae) and *A. rufotestaceus* reared from *Glaucias subpunctatus* (Pentatomidae). The Alydidae is a newly recorded host family of *Aridelus*.

Keywords

Aridelus, host records, identification key, new species, stink bug parasitoids, taxonomy

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Introduction

The braconid subfamily Euphorinae is unique in attacking a wide range of host orders, including both larvae and adult insects (Stigenberg et al. 2015). Its adult morphology varies greatly, probably due to adaptive evolution, which enables it to utilize a variety of free-living host insects (Shaw 1985, 1988; Maeto 2018).

The genus *Aridelus* Marshall, 1887 has an aberrant morphology, that is, the entirely areolate mesosoma and the elongated tubular first metasomal tergite. Using a petiolated metasoma with a short ovipositor, females lay eggs into nymphs or adults of heteropteran stink bugs (Shaw 1985; Maeto and Kudo 1992; Shaw et al. 2001). They are hitherto known to be solitary koinobiont endoparasitoids of the families Acanthosomatidae, Pentatomidae, Plataspidae, and Scutelleridae (Shaw et al. 2001). Although more than 40 species of *Aridelus* are known worldwide (Yu et al. 2016), only two species, *A. elasmuchae* Maeto & Kudo, 1992 and *A. flavicans* Chao, 1974, have been recorded in Japan (Maeto and Kudo 1992; Konishi and Maeto 2000).

In our study of Japanese Euphorinae, we identified six species of *Aridelus*, that is, *A. dubius* Belokobylskij, 1981, *A. egregius* (Schmiedeknecht, 1907), *A. elasmuchae*, *A. flavicans*, *A. rufotestaceus* Tobias, 1986, and *A. rutilipoides* sp. nov. In this study, all Japanese species are photographed, a new species is described, and an identification key to the Japanese species is provided. In addition, new host records of *A. flavicans* and *A.rufotestaceus* are presented herein.

Materials and methods

The specimens examined were deposited in Kanagawa Prefectural Museum of Natural History, Odawara, Japan (**KPMNH**), Laboratory of Entomology, Faculty of Agriculture, Meijo University, Nagoya, Japan (**MUNJ**), Insect Museum, National Agriculture and Food Research Organization, Tsukuba, Japan (**NARO**), National Science Museum, Tokyo, Japan (**NSMT**), Osaka Museum of Natural History, Osaka, Japan (**OMNH**), Taiwan Agricultural Research Institute, Taichung, Taiwan (**TARI**), and Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia (**ZISP**). MsT. and LT. refer to a Malaise trap and a light trap, respectively. Besides six Japanese species, two females of *A. rutilipes* Papp, 1965 from Taiwan [2♀, Lixing Industry Road, Renai Township, Nantou Country, 8.X.2015, So Shimizu leg. (TARI)] were also examined.

Morphological observation was conducted using a stereoscopic microscope (SMZ800N, Nikon, Tokyo, Japan). The specimens were photographed using a digital microscope (VHX-1000, Keyence, Osaka, Japan) with a 10–130× lens. Multi-focus photographs were stacked in the software associated with the Keyence System. The figures were edited using Microsoft PowerPoint 2019.

The morphological terminology used is mostly based on van Achterberg (1988, 1993). OOL, OD, and POL refer to the ocellar-ocular line, the diameter of the posterior ocellus, and the postocellar line, respectively.

Taxonomic accounts

Genus *Aridelus* Marshall, 1887

Aridelus Marshall, 1887: 66; Papp 1965: 181; Shenefelt 1969: 11; Shaw 1985: 309; Chou 1987: 21; Chen and van Achterberg 1997: 11; Belokobylskij 2000: 362. Synonyms are presented in Shenefelt (1969) and Shaw (1985).

Type species (by monotypy). *Aridelus bucephalus* Marshall, 1887.

Diagnosis. ***Head*** transverse; antenna filiform or moniliform, with 18 segments, its terminal segment with an apical spine; maxillary palp with 6 segments; labial palp with 4 segments; occipital carina complete or absent mediodorsally for a long distance, rarely completely absent, ventrally joining hypostomal carina; frons punctate or smooth with a median carina extending to frontal ocellus; face wider than clypeus in female; lower clypeal margin usually indented medially, rarely rounded; malar suture usually absent; mandibles overlapping each other; mesonotum, mesopleuron, and propodeum mostly areolate; petiolar notch extending nearly to mesocoxal insertions; parastigma large; vein 1-SR of fore wing absent to rarely shortly present and thickened; vein 3-SR of fore wing absent to distinctly present; vein 1-R1 of fore wing short; end of vein SR1 of fore wing much closer to pterostigma than to apex of wing; vein r-m of fore wing present; veins SR and 2-M of hind wing present, darkly pigmented; first metasomal tergite about 3/4 times as long as remainder of metasoma and completely fused ventrally; third tergite nearly reaching end of metasoma, following segments hidden; second and third tergites ventrally overlapping, without lateral fold; ovipositor and its sheath shortly exposed.

Distribution. Cosmopolitan and the most diverse in tropical regions (Yu et al. 2016).

Bionomics. Endoparasitoids of nymphs and adults of Acanthosomatidae, Pentatomidae, Plataspidae, and Scutelleridae (Shaw et al. 2001), and of Alydidae (present study). Usually diurnal, but a few species were collected at night in light traps (e.g., *A. dubius* in the present study).

Key to the Japanese species of the genus *Aridelus* Marshall

1 Median carina of frons only weakly developed (Fig. 2B); occipital carina absent dorsally; inner margins of eyes not parallel, distinctly convergent ventrally (Fig. 2B); hind femur distinctly stout, 3.0× longer than wide (Fig. 2E); mesosoma black, head and metasoma except for first metasomal tergite black to dark brown (Fig. 2A); body length shorter, 2.7–3.7 mm [vein m-cu of fore wing postfurcal to interstitial (Fig. 2D)]..... ***A. egregius* (Schmiedeknecht)**

– Median carina of frons distinct (Figs 1B, 3B, 4B, 7B); occipital carina complete; inner margins of eyes almost parallel or weakly convergent (Figs 1B, 3B, 4B, 7B); hind femur comparatively slender, at least 4.0× longer than wide (Figs 1G, 7H); body colour variable, but not entirely black (Figs 1A, 3A, 4A, 5A, 7A); body length longer, 3.6–6.5 mm **2**

2 Head yellow, yellowish red, yellowish brown or reddish brown (Figs 3C, 4C, 5B, C); fore wing without distinct fuscous bands (Figs 3A, 4A, 5A) **3**

– Head black (Figs 1C, 7C); fore wing with two distinct fuscous bands (Figs 1F, 7G) **5**

3 First metasomal tergite pale yellow, distinctly contrast to blackish or dark brownish second and following tergites (Fig. 3A); fore wing fuscous in distal half (Fig. 3A); mesosoma entirely black (Fig. 3A) [head yellowish brown; vein m-cu of fore wing postfurcal, rarely interstitial; body length 3.6–5.0 mm].... ..... ***A. elasmuchae*** **Maeto & Kudo**

– First metasomal tergite yellowish red to reddish brown, not distinctly contrasting to second and following tergites (Figs 4F, 5A); fore wing hyaline or slightly infuscated medially (Fig. 4A, 5A); colour of mesosoma variable..... **4**

4 Vertex punctate and without transverse rugae (Fig. 4C); scutellum with median smooth area (Fig. 4E); mesosoma yellow to yellowish brown, not distinctly contrast to head and metasoma (Fig. 4A); penultimate segment of ♀ antenna 1.1–1.6× longer than wide (Fig. 4D) [vein m-cu of fore wing postfurcal to antefurcal; body length 4.1–5.3 mm] ..... ***A. flavicans*** **Chao**

– Vertex punctate, often transversely rugose (Fig. 5B, C); scutellum uniformly areolate, without median smooth area (cf. Fig. 7F); mesosoma reddish brown to black, usually distinctly contrasting to reddish head and metasoma (Figs 5D, E); penultimate segment of ♀ antenna 1.8–2.0× longer than wide [body length 4.5–5.7 mm]..... ***A. rufotestaceus*** **Tobias**

5 Penultimate segment of antenna 1.2–1.3 times as long as its width (Fig. 7E); antenna yellowish brown basally (Fig. 7D), darkened towards apex (Fig. 7E); face finely punctate laterally, transversely punctate-rugose medially; malar suture indistinct or absent; vein m-cu of fore wing distinctly antefurcal (Fig. 7G); apical hyaline area of fore wing comparatively large, almost reaching apex of marginal cell (Fig. 7G); hind femur slenderer, 4.6–5.2× longer than wide (Fig. 7H) [body length 5.8–6.5 mm]..... ***A. rutilipoides*** **sp. nov.**

– Penultimate segment of antenna 1.6–1.7× longer than wide (Fig. 1E); antennal segments entirely reddish brown (Fig. 1D, E); face fairly finely punctate; malar suture distinct; vein m-cu of fore wing slightly postfurcal to interstitial (Fig. 1F); apical hyaline area of fore wing comparatively small, not reaching apex of marginal cell (Fig. 1F); hind femur stouter, 4.1–4.3× longer than wide (Fig. 1G) [body length 5.1–6.1 mm] ..... ***A. dubius*** **Belokobylskij**

Aridelus dubius **Belokobylskij, 1981**

Fig. 1A–G

Aridelus dubius Belokobylskij, 1981: 44. [Type locality: Russia]

Material. Japan Honshû: 1♀, Niigata Pref., Myoukou City, Suginosawa, Sasagamine, 36-52N/138-4E, about 1200–1335 m alt., 18.IX.2013, S. Shimizu leg. (OMNH);

1♀, same data except 36-52-2N/138-4-42E, about 1300 m alt., 14.IX.2013, LT. (NARO); .1♀, Hiroshima Pref., Shôbara City, Saijô Town, Mts. Hiba, Tachieboshi Parking Lot, 30–31.VII.2019, LT., S. Shimizu leg (OMNH).

Description. Females (*N* = 3) (Fig. 1). Body length 5.1–6.1 mm.

Head (Fig. 1B, C, D, E). Width of head 2.0–2.2× median length and 1.0× width of mesonotum. Length of eye 1.1–1.3× length of temple in dorsal view. OOL / OD = 4.0–4.1. POL / OD = 1.7. Vertex and temple densely punctate. Occipital carina complete. Frons smooth and shiny, with a distinct median carina. Face 1.8× as wide as high; finely punctate. Intertentorial distance / tentorio-ocular distance = 0.4–0.5×. Clypeus finely punctate, slightly concave medially, without apical teeth. Length of malar space 0.4–0.5× eye height. Malar suture distinct. Antenna filiform with 18 segments; 3rd segment 3.8–4.0× longer than wide and 1.3× longer than 4th one; penultimate one 1.6–1.7× longer than wide.

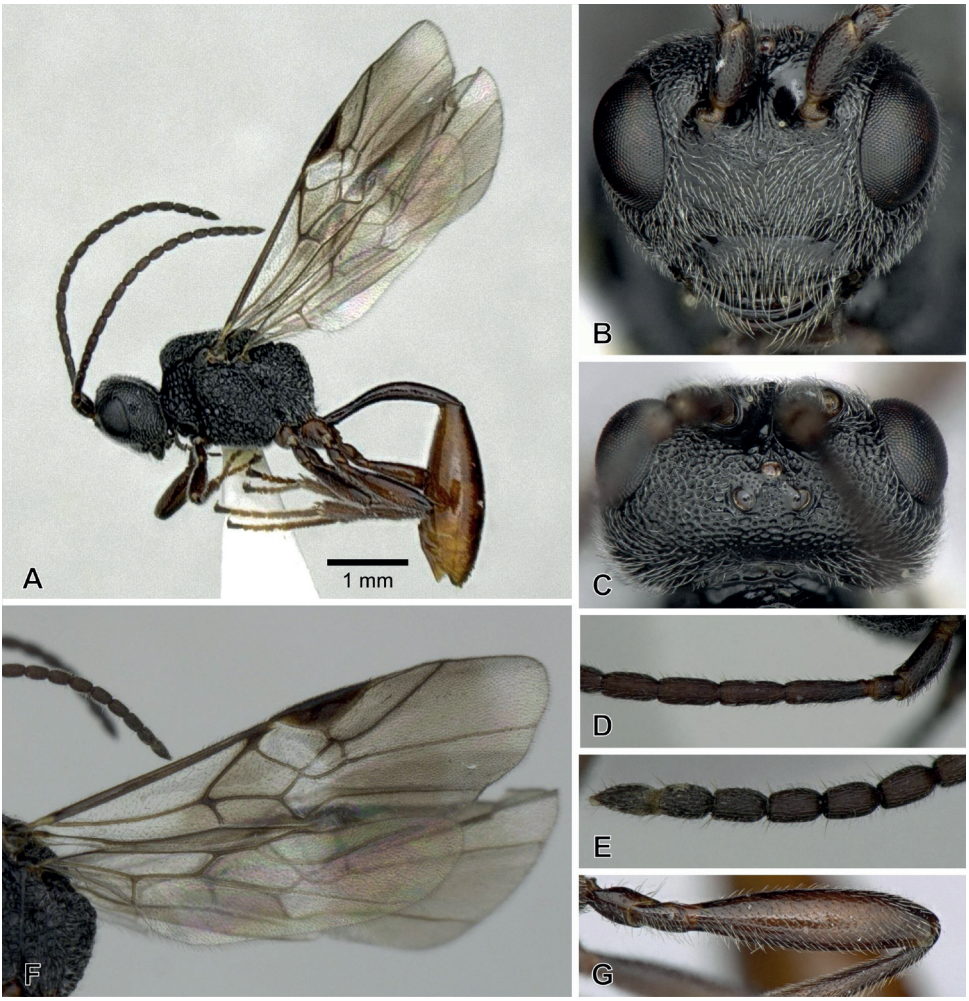

Figure 1. *Aridelus dubius* Belokobylskij, 1981, ♀ from Niigata Prefecture, Japan **A** habitus **B** head, frontal view **C** head, dorsal view **D** basal antennal segments **E** apical antennal segments **F** wings **G** hind femur.

Mesosoma. Mesosoma areolate, 1.3× as long as high. Scutellum without median smooth area.

Wings (Fig. 1F). Fore wing 4.4–4.7 mm in length, 1-R1 / length of pterostigma = 1.3–1.4, r / 3-SR = 2.3–3.5, m-cu slightly postfurcal. Hind wing with 1r-m / 2-SC+R = 0.7–0.9.

Legs (Fig. 1G). Hind leg: femur 4.1–4.3× longer than wide, length of femur: tibia: basitarsus = 1: 1.3: 0.6.

Metasoma. Metasoma smooth and polished. First metasomal tergite 6.0× longer than its apical width. Hypopygium truncated and excised apically. Ovipositor sheath hardly exserted beyond apex of metasoma.

Colour. Black. Palpi, antenna entirely, mandible, tegula, legs except for telotarsus and first metasomal tergite dark reddish brown; remainder of metasoma reddish brown, telotarsus and veins dark brown; pterostigma pale in basal 1/5 or faintly pale basally. Fore wing hyaline with two fuscous bands. Hind wing with a fuscous band in its apical third.

Distribution. Japan (Honshû: Niigata and Hiroshima Prefectures); Russian Far East (Belokobylskij 1981, 2000).

Hosts. Unknown.

Remarks. This species was described with only the male holotype available. The Japanese specimens mostly agree well with the original description (Belokobylskij 1981) and run in the key by Belokobylskij (2000) to *A. dubius*. The redescription of this species based on Japanese female specimens is represented here.

This species resembles *A. rutilipes* Papp described from Taiwan (Fig. 6) but differs in having the distinct malar suture (absent in *rutilipes*), the palpi dark reddish brown (light reddish brown in *rutilipes*), the apical hyaline area of the fore wing comparatively small, not reaching the apex of marginal cell (Fig. 1F) and the apico-posterior edge of the fore wing (in *rutilipes* comparatively large, almost reaching the apex of marginal cell and reaching the apico-posterior edge (Fig. 6A)), and the metasoma reddish brown to dark reddish brown (Fig. 1A) (dark brown in *rutilipes* (Fig. 6A)).

Aridelus egregius (Schmiedeknecht, 1907)

Fig. 2A–E

Helorimorpha egregia Schmiedeknecht, 1907: 523. [Type locality: Germany]
Aridelus egregia (Schmiedeknecht): Muesebeck 1936: 6; Shenefelt 1969: 12.
Aridelus nigricans Chao, 1974: 455. Syn. by Belokobylskij 2000: 366. [Type locality: China]
Aridelus destitutus Chou, 1987: 26. Syn. by Chen and van Achterberg 1997: 17. [Type locality: Taiwan]

Material. Japan Honshû: 1♀, Tôkyô Pref., Chiyoda Ward, Imperial Palace, Fukiagegyoen, Kajuen, 14–21.X.2009, MsT. (NSMT); 1♀, Fukui Pref., Tsuruga City, Marsh of

Nakaikemi, 19.IX–16.X. 2016, MsT., A. Noishiki leg. (OMNH). **Kyûshû:** 2♀♀, Ôita Pref., Mt. Sobo, 1600–1750 m alt., 27.IX.1979, K. Maetô leg. (NARO). **Korea** 1♂, Kyongsangpuk-do, Mt. Sudo, 1000 m alt., 13–14.VII.1971, K. Yamagishi leg. (MUNJ). **Taiwan** 2♂♂, Nantou Country, Renai Township, 2.V.2015, S. Fujie leg. (TARI).

Distribution. Japan (Honshû: Tôkyô and Fukui Prefectures; Kyûshû: Ôita Prefecture); Western Palaearctic region; China, Korea, Russian Far East, Taiwan (Yu et al. 2016; Lee at al. 2017). New to Japan.

Hosts. No host records are available in Japan, while Pentatomidae (*Aelia*, *Dolycoris*, *Eurydema*, *Holcostethus*, *Palomena*) (Dupuis 1952; Tobias 1986), Plataspidae (*Coptosoma*) (Capek and Davidova-Vilimova 1978), and Scutellaridae (*Eurygaster*) (Tobias 1986) are known host insects.

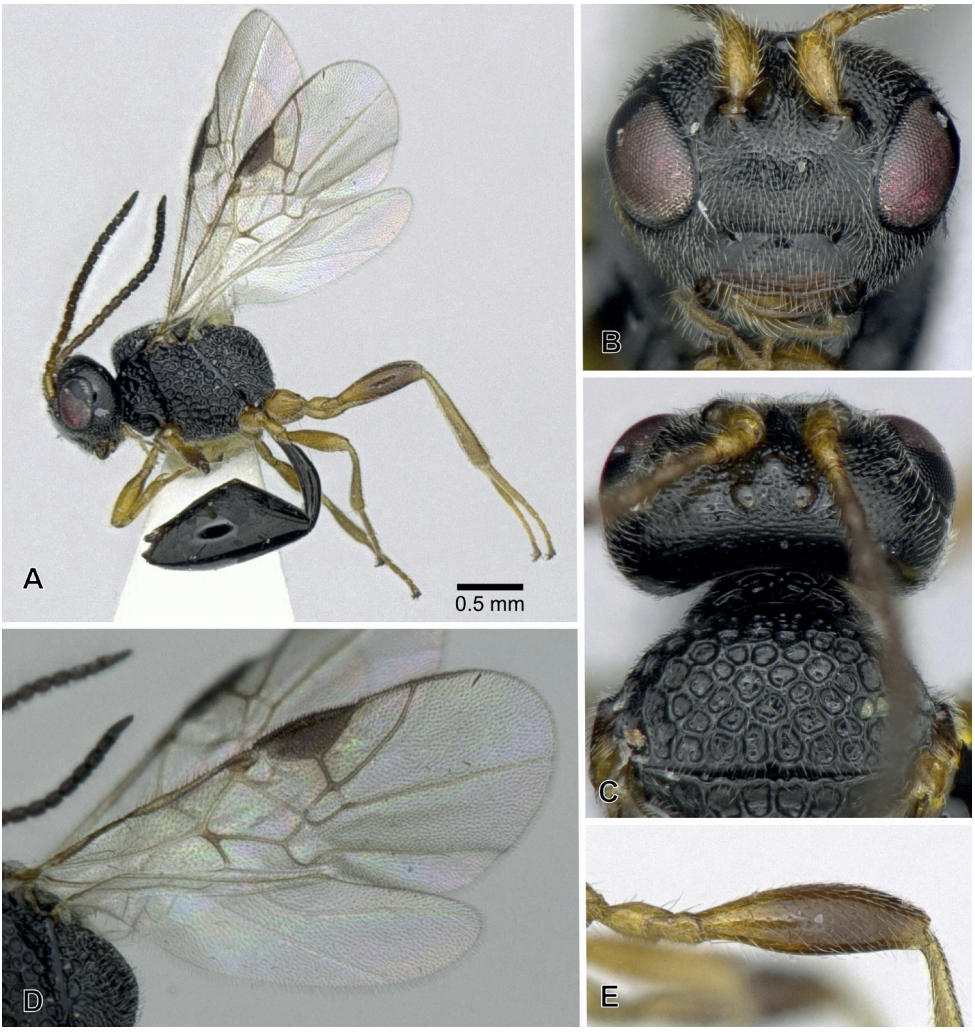

Figure 2. *Aridelus egregius* Schmiedeknecht, 1907, ♀ from Fukui Prefecture, Japan **A** habitus **B** head, frontal view **C** head and mesoscutum, dorsal view **D** wings **E** hind femur.

Aridelus elasmuchae **Maeto & Kudo, 1992**
Fig. 2A–C

Aridelus elasmuchae Maeto & Kudo, 1992: 78. [Type locality: Japan]

Material. Japan Hokkaidô: 1♀, ***holotype***, Nopporo, 15.VII.1986, S. Kudô leg. (NARO); 2♂♂, Sapporo City, Hitsujigaoka, 20–27.VI.2011, MsT., K. Konishi leg. (OMNH). 2♀♀ and 2♂♂, same data except 27.VI–4.VII.2011 (OMNH); 1♀, Kumaishi Town, Ken'ichi-gawa, Iwafuchi-zawa, 15–20.VI.1995, MsT., Y. Itô & T. Itô leg. (NARO). **Honshû:** 1♀, Aomori Pref., Mt. Iwaki, 28.IX.1983, M. Miyazaki leg. (NARO); 9♀♀ 7♂♂, Miyagi Pref., Minamisanriku Town, Hinokuchi, 5.VI–12.VII.2015, MsT., H. Yamazaki & S. Fujie leg. (OMNH); 2♂♂, same data except 28.IX–6.XI.2015 (OMNH); 1♀, Miyagi Pref., Minamisanriku Town, Mt. Tatsugane, 5.VIII.2016, S. Fujie leg. (OMNH); 1♂, Toyama Pref., Toyama City, Arimine, Jurodani, 1120 m alt., 7–14.VII.2009, MsT., M. Watanabe leg. (KPMNH); 1♀, Hyôgo Pref., Kami Town, Niiya, 20.VI–11.VII.2015, MsT., S. Fujie leg. (OMNH); 1♀, Hyôgo Pref., Kami Town, Niiya, 15.VI–14.VII.2013, MsT., S. Fujie & M. Itô leg. (OMNH). **Kyûshû:** 1♂, Kumamoto Pref., Izumi Vil., Mt. Hakuchô, 10.VII.1978, K. Ohara leg. (NARO).

Distribution. Japan (Hokkaidô; Honshû: Aomori, Miyagi, Tochigi, Toyama, Hyôgo and Tottori Prefectures; Shikoku: Ehime Prefecture; Kyûshû: Ôita Prefecture) (Maeto and Kudo 1992; Takahashi and Shiraishi 2018; Fujie and Katayama 2020; present study); Russian Far East (Yu et al. 2016).

Hosts. *Elasmucha putoni* Scott, 1874 (Acanthosomatidae) (Maeto and Kudo 1992).

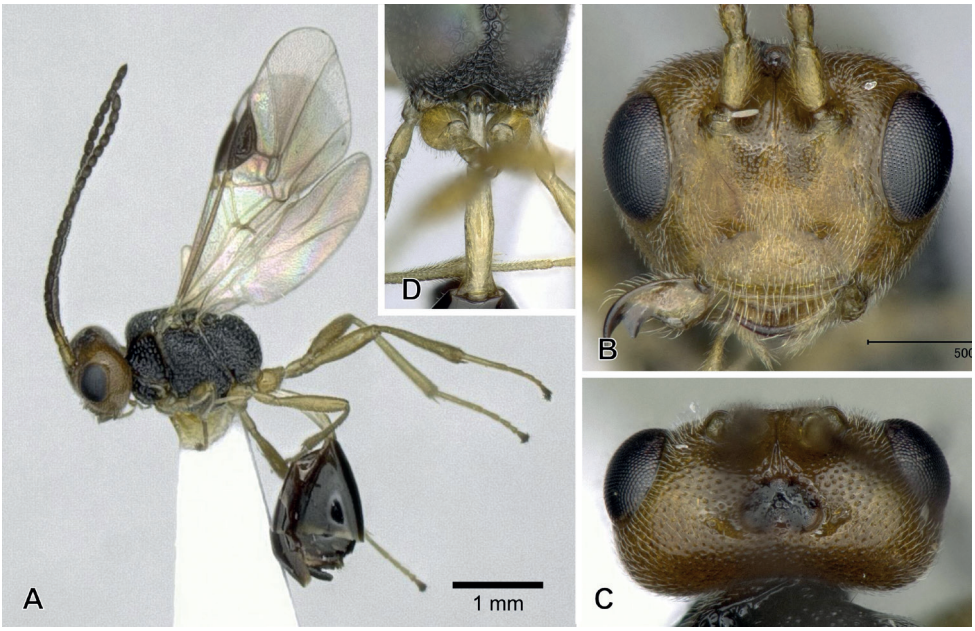

Figure 3. *Aridelus elasmuchae* Maeto & Kudo, 1992, ♀ from Hyôgo Prefecture, Japan **A** habitus **B** head, frontal view **C** head, dorsal view **D** first metasomal tergite, dorsal view.

Aridelus flavicans **Chao, 1974**
Fig. 4A–F

Aridelus flavicans Chao, 1974: 455; Chou 1987: 23; Luo and Chen 1994: 484; Chen and van Achterberg 1997: 16. [Type locality: China]
Aridelus guizhouensis Luo, 1985: 203. Syn. by Luo and Chen 1994. [Type locality: China]

Material. Japan Honshû: 1♀, Aomori Pref., Aomori City, Yokouchi-Yaegiku, 11.IX.1993, T. Ichita leg. (NARO); 1♂, Tôkyô Pref., Hachiôji City, Minamiôsawa, Tôkyô Metropolitan University, 10.VIII.2010, N. Kikuchi leg. (OMNH); 1♀, Kyôto Pref., Yawata City, Yawatahayashinomoto, collected as a host larva of *Homoeocerus unipunctatus* feeding on *Pueraria lobata* on 12.VII.2021, cocoon formed on 23.VII.2021, and emerged on 29.VII.2021, S. Fujie leg. (OMNH); 2♀♀, Nara Pref., Yamatokôriyama City, Yamadachô, Nara-gakuen, 8.VII.2017, R. Itô leg. (OMNH); 1♀, Nara Pref., Yamatokôriyama City, Yamadachô, 6.IX.2016, R. Itô leg. (OMNH); 3♀♀, Nara Pref., Yamatokôriyama City, Yamadachô, Yata-kyûryô, about 135 m alt., 8.IX.2018, R. Itô leg. (OMNH); 1♀, same data except 13.IX.2018 (OMNH); 1♀, Nara Pref., Uda City, Haibarahagihara, Torimiyama-kôen, about 585 m alt., 20.VIII.2018, R. Itô leg. (OMNH); 1♀, Ôsaka Pref., Takatsuki City, Settsukyô, 24.IX.2017, S. Fujie leg. (OMNH); 6♀♀ and 1♂, Ôsaka Pref., Habikino City, Shakudo, 3.VIII.2020, S. Fujie leg. (OMNH); 2♂♂, same data except 22.VIII.2020 (OMNH); 2♀♀, same data except 2.VIII.2021 (OMNH); 1♀, Hyôgo Pref., Kawanishi City, collected as a host adult of *Riptortus clavatus* feeding on *Phaseolus vulgaris* on 24.VIII.2011, cocoon formed on 13.IX.2011, and emerged on 27.IX.2011, I. Hikino leg. (NARO); 1♂, same locality, host, collector and date of cocoon formation, collected on 29.VIII.2011 and emerged on 27.IX.2011 (NARO); 1♂, same locality, host, collector and date of cocoon formation, collected on 31.VIII.2011 and emerged on 28.IX.2011 (NARO); 1♀, Hyôgo Pref., Kôbe City, Nada Ward, Nadamaruyama Park, 23.VI.2019, M. & S. Fujie leg. (OMNH); 1♀, Hyôgo Pref., Asago City, Tataragi, 185 m alt., 30.VII. 2016, T. Tokuhira leg. (KPMNH); 1♀, Tottori Pref., Inaba Prov., Ketaka, Tsuyutani, alt. 20 m, 8.VIII.1964, H. Aoki leg. (OMNH); 1♀, Hiroshima Pref., Tôjô Town, Taishaku, 9.VIII.1978, K. Maetô leg. (NARO). **Kyûshû:** 1♀, Fukuoka Pref., Mt. Tachibana, 22.IX.1979, K. Maetô leg. (NARO); 1♀, Ôita Pref., Mt. Sobo, 800–900 m alt., 22.VII.1978, K. Maetô leg. (NARO); 1♀, Ôita Pref., Yufuin Town, Shimoyunohira, 1.IX.1991, M. Hiratate leg. (NARO).

Distribution. Japan (Honshû: Aomori, Tôkyô, Nara, Ôsaka, Hyôgo, Tottori and Hiroshima Prefectures; Kyûshû: Fukuoka and Ôita Prefecture) (Konishi and Maeto 2000; present study); China, Russian Far East, Taiwan (Yu et al. 2016).

Hosts. *Homoeocerus unipunctatus* (Thunberg, 1783) (Alydidae) feeding on *Pueraria lobata* (Fabaceae) and *Riptortus pedestris* (Linnaeus, 1758) (Alydidae) on *Phaseolus vulgaris* (Fabaceae) (both new records). The family Alydidae is the first record of the host of the genus *Aridelus*.

Remarks. The female specimens examined agree well with the redescription by Chou (1987) and that in the key by Chen and van Achterberg (1997); they differ

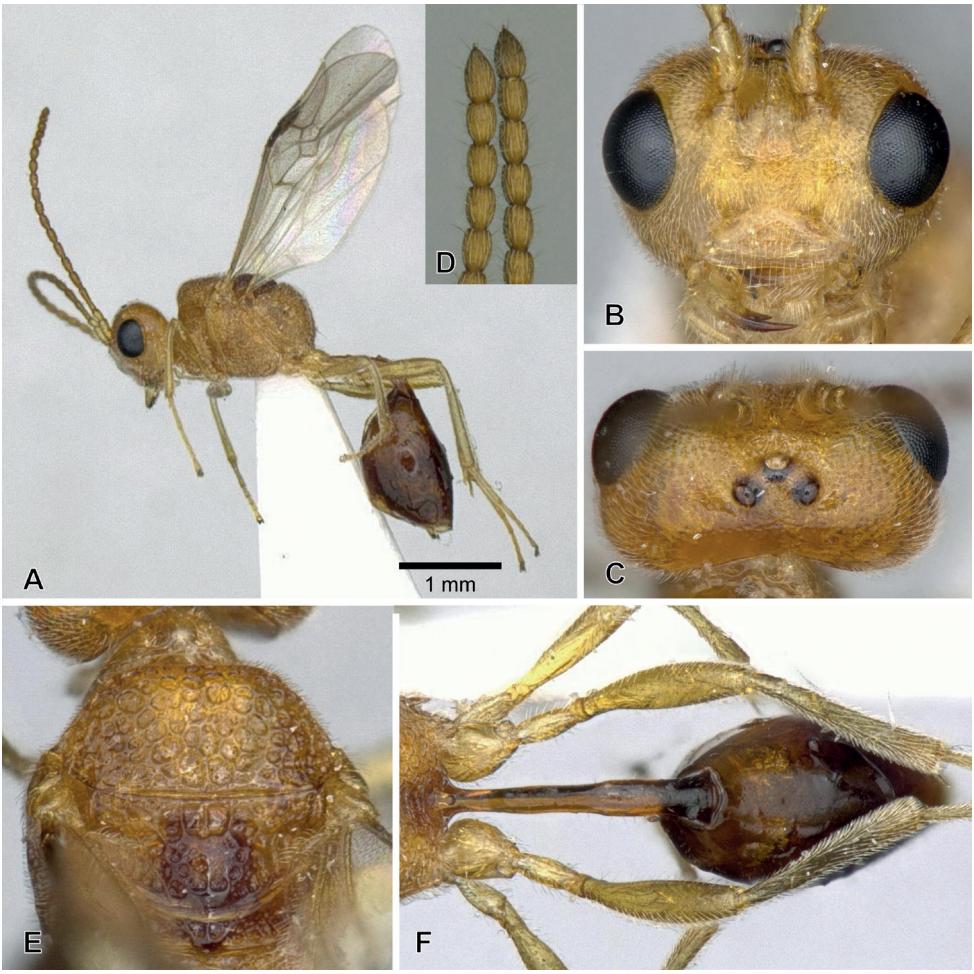

Figure 4. *Aridelus flavicans* Chao, 1974, ♀ from Tôkyô Prefecture (except for **D** from Ôsaka Prefecture), Japan **A** habitus **B** head, frontal view **C** head, dorsal view **D** apical part of antennae **E** mesoscutum and scutellum, dorsal view **F** metasoma, dorsal view.

slightly by having the body length 4.1–5.3 mm (4.2–5.1 mm in the previous redescriptions) and the penultimate antennal segment 1.1–1.6× longer than wide (1.2–1.6× in the redescriptions).

Aridelus rufotestaceus Tobias, 1986

Fig. 5A–I

Aridelus rufotestaceus Tobias, 1986: 229 (English translation: 399); Chen and van Achterberg 1997: 18; Shaw et al. 2001: 132. [Type locality: Russia]

Aridelus rufiventris Luo & Chen, 1994: 483; Chen and van Achterberg 1997:18. Syn. nov. [Type locality: China]

Material. **Russia** 1♀, ***holotype***, Lazarevskoe, Sochi, forest along rivulet, 14.IX.1981, V. Tobias leg. (ZISP). **Japan Honshû:** 1♂, Shizuoka Pref., Shizuoka City, Shimizu Ward, Muramatsu, collected as a host adult of *Glaucias subpunctatus* on 14.XII.2018, recognized a cocoon on 23.I.2019, and emerged on 8.II.2019, K. Itoyama & A. Tsunashima leg. (OMNH); 1♂, Toyama Pref., Toyama City, Arimine, Inonedani, 1120 m alt., 15–22.IX.2009, MsT., M. Watanabe et al. leg. (KPMNH); 1♀, Mie

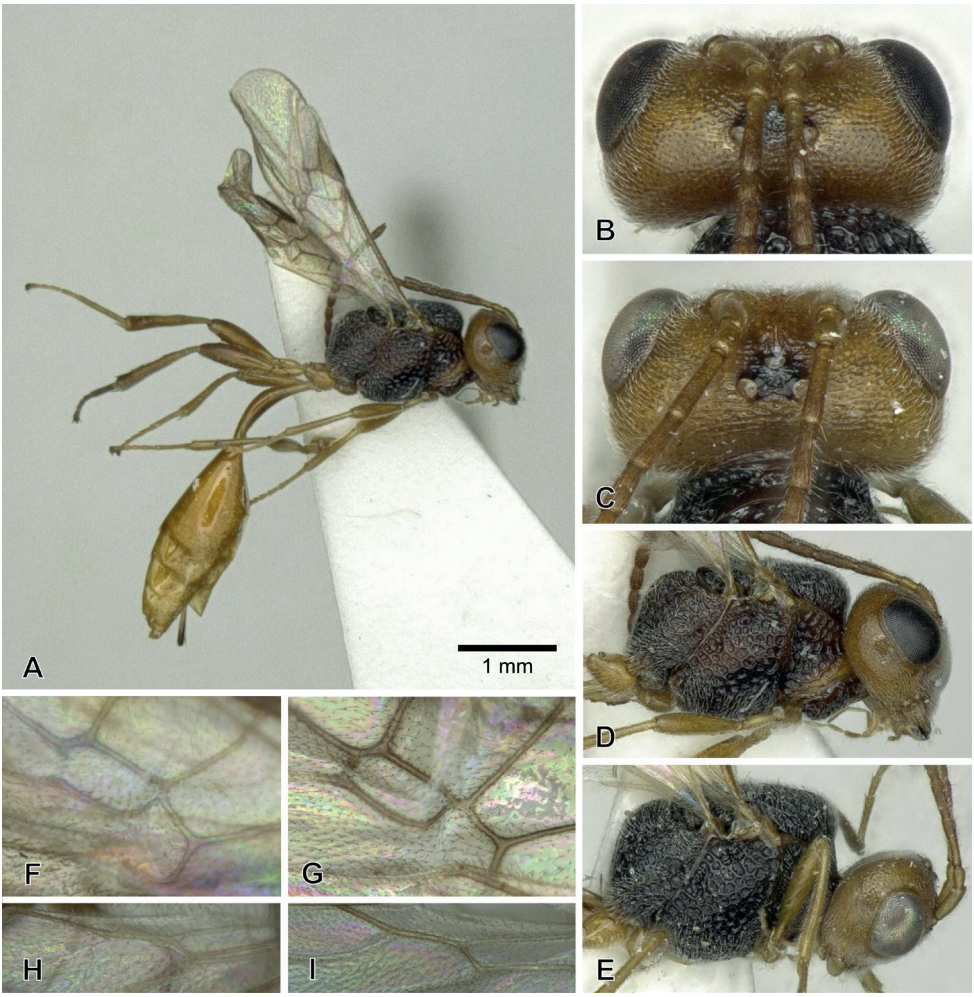

Figure 5. *Aridelus rufotestaceus* Tobias, 1986, ♀ from Yakushima Is. (A, B, D, F, H) and ♂ from Toyama Prefecture (C, E, G, I) **A** habitus **B, C** head, dorsal view **D, E** head and mesosoma, lateral view **F, G** second submarginal cell and vein m-cu of fore wing **H, I** vein 1r-m and 2-SC+R of hind wing.

Pref., Taiki Town, Nishiki, 9–21.X.2007, MsT., M. Nakaseko leg. (MUNJ); 1♂, Kyôto Pref., Yawata City, Morigaito, left bank of Kidu River, 17.VI.2018, S. Fujie leg. (OMNH); 1♀, Nara Pref., Uda City, Haibarahagihara, Torimiyama-kôen, about 585 m alt., 20.VIII.2018, R. Itô leg. (OMNH). **Hachijôjima Is.:** 2♂♂, Eigo, 2.VI.1964, Y, Hirashima & M. Shiga leg. (NARO). **Kyûshû:** 1♂, Kumamoto Pref., Izumi Vil., Gokanosô, 1.VIII.1981, H. Kurokawa leg. (OMNH). **Yakushima Is.:** 1♀, Kankake, 25.VIII–28.IX.2007, MsT., T. Yamauchi leg. (KPMNH); Mt. Aiko, 8–28.VI.2007, MsT., T. Yamauchi leg. (KPMNH); 1♀, same data except 29.VII–25.VIII.2007. (KPMNH); 1♀, same data except 28.IX–2.XI.2007. (KPMNH). **Korea** 1♂, Kyongsangpuk-do, Mt. Sudo, 700 m alt., 9–12.VII.1971, K. Yamagishi leg. (MUNJ).

Distribution. Japan (Honshû: Shizuoka, Toyama, Mie and Kyôto Prefecture; Hachijôjima Is.; Kyûshû: Kumamoto Prefecture; Yakushima Is.); China, Georgia, Korea, Italy, Russian Far East (Yu et al. 2016; Lee et al. 2017). New to Japan.

Hosts. *Glaucias subpunctatus* (Walker, 1867) (a new record) and *Nezara viridula* (Linnaeus, 1758) (Shaw et al. 2001) (both Pentatomidae).

Remarks. Chen and van Achterberg (1997) indicated the differences between *A. rufiventris* Luo & Chen and *A. rufotestaceus* Tobias from only one specimen of each taxon in the sculpture of the vertex, the condition of vein m-cu of the fore wing, the relative length of vein 1r-m of the hind wing, and the colour of the mesosoma, as shown in Suppl. material 1: Table S1. However, these characters could not separate the Japanese specimens into the two species (Suppl. material 1: Table S1). These are most likely intraspecific variations. Hence, *A. rufiventris* is considered a junior synonym of *A. rufotestaceus*.

Aridelus rutilipoides **sp. nov.**

http://zoobank.org/7A58CF41-B558-41CA-A5E6-DBDF8D66D1F2
Fig. 7A–I

Type material. ***Holotype***, ♀, "(JAPAN) Nagano Pref., Ueda City, Sugadaira-kougen, Tsukuba Univ., 36-31N/138-20E, about 1300 m alt., 13 IX 2013 (sweeping), Sou Shimizu leg." (OMNH). ***Paratypes*****:** 1♀, Hokkaidô Pref., Sapporo City, Teine Ward, Mt. Teine, 18.IX.2013, S. Fujie leg. (OMNH); 1♀, Tochigi Pref., Nikkô, 13.X.1986, M. Miyazaki leg. (NARO); 1♀, Nagano Pref., Shimashima-dani, 1300–1600 m alt., 26.VIII.1978, K. Maetô leg. (NARO); 1♀, Tokushima Pref., Ichiu Vil., Mt. Tsurugi, 15.X.1980, Y. Shôno leg. (NARO).

Etymology. Named after its similarity to *A. rutilipes* Papp. The Latin suffix –"oides" taken from Greek means similar but not the same.

Description. Female *holotype* (Fig. 7). Body length 6.5 mm.

Head (Fig. 7B, C, D, E). Width of head 2.0× median length and 1.1× width of mesonotum. Length of eye 1.2× length of temple in dorsal view. OOL / OD = 4.1. POL / OD = 1.7. Vertex and temple densely punctate. Occipital carina complete.

Frons smooth and shining, with a distinct median carina. Face 1.9× as wide as high; finely punctate laterally, transversely punctate-rugose medially. Intertentorial distance / tentorio-ocular distance = 1.7. Clypeus finely punctate, slightly concave medially, without apical teeth. Length of malar space 0.60× eye height. Malar suture indistinct. Antenna filiform with 18 segments; 3rd segment 3.5× longer than wide and 1.2× longer than 4th one; penultimate one 1.3× longer than wide.

Mesosoma (Fig. 7F). Mesosoma areolate, 1.3× as long as high. Scutellum without median smooth area.

Wings (Fig. 7G). Fore wing 5.0 mm in length, 1-R1 / length of pterostigma = 1.3, r / 3-SR = 2.4, m-cu distinctly antefurcal. Hind wing with 1r-m / 2-SC+R = 0.8.

Legs (Fig. 7H). Hind leg: femur 5.2× longer than wide, length of femur: tibia: basitarsus = 1: 1.3: 0.6.

Metasoma (Fig. 7I). Metasoma smooth and polished. First metasomal tergite 5.9× longer than its apical width. Hypopygium truncated and excised apically. Ovipositor sheath hardly exserted beyond apex of metasoma.

Colour. Black. Antenna basally, mandible medially, palpi, tegula, legs except for telotarsus, metasoma reddish brown; mandible basally and apically, veins, telotarsus dark brown, antenna gradually darkened towards apex; pterostigma pale in basal quarter. Fore wing hyaline with two fuscous band. Hind wing with a fuscous band in apical third.

Variation in females. Body length 5.8–6.5 mm. Length of eye 1.2–1.4× length of temple in dorsal view; OOL / OD = 3.5–4.1. POL / OD = 1.5–1.9. Face 1.7–1.9× as wide as high. Intertentorial distance / tentorio-ocular distance = 1.7–1.9. Length of malar space 0.5–0.6× eye height. Malar suture indistinct or absent. Third antennal segment 3.5–4.0× longer than wide and 1.2–1.4× longer than 4th one; penultimate one 1.2–1.3× longer than wide. Mesosoma length 1.3–1.4× height. Fore wing 4.8–5.2 mm

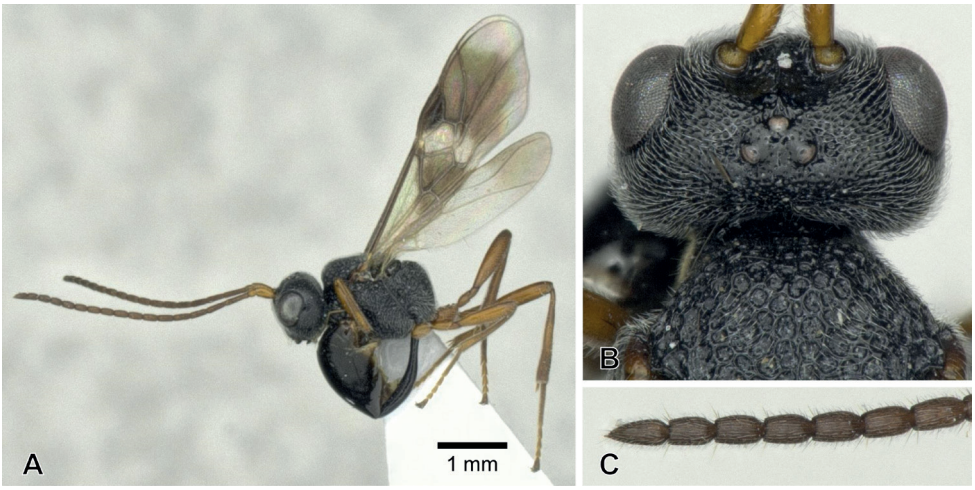

Figure 6. *Aridelus rutilipes* Papp, 1965, ♀ from Taiwan **A** habitus **B** head, dorsal view **C** apical antennal segments.

Figure 7. *Aridelus rutilipoides* sp. nov., ♀ holotype **A** habitus **B** head, frontal view **C** head, dorsal view **D** basal antennal segments **E** apical antennal segments **F** mesosoma, dorsal view **G** wings **H** hind femur **I** first metasomal tergite, dorsal view.

in length, 1-R1 / length of pterostigma = 1.2–1.5, r / 3-SR = 2.2–3.6. Hind wing with 1r-m / 2-SC+R = 0.8–1.0. Hind leg: femur 4.6–5.2× longer than wide, length of femur: tibia: basitarsus = 1: 1.3–1.4: 0.6. First metasomal tergite 5.9–6.3× longer than its apical width.

Male. Unknown.

Distribution. Japan (Hokkaidô; Honshû: Nagano Prefecture; Shikoku: Tokushima Prefecture).

Hosts. Unknown.

Remarks. This species closely resembles *A. rutilipes* Papp (Fig. 6) but differs in having the stouter penultimate antennal segment (in *rutilipoides*, 1.2–1.3× longer than wide (Fig. 7E), in *rutilipes* 1.8× (Fig. 6C)), the face finely punctate laterally, transversely punctate-rugose medially (finely punctate in *rutilipes*), the apical hyaline area of the fore wing not reaching the apico-posterior edge (Fig. 7G) (in *rutilipes*, reaching the apico-posterior edge (Fig. 6A)) and the metasoma reddish brown (Fig. 7A) (dark brown in *rutilipes* (Fig. 6A)). This species also resembles *A. dubius* Belokobylskij, but differs in having the antenna gradually darkened towards the apex (Fig. 7A) (in *dubius* uniformly reddish brown, not darkened towards the apex (Fig. 1A)), the penultimate antennal segment stouter (in *rutilipoides*, 1.2–1.3× longer than wide (Fig. 7E), in *dubius* 1.6–1.7× (Fig. 1E)), the face finely punctate laterally, transversely punctate-rugose medially (finely punctate in *dubius*), the malar suture indistinct or absent (distinct in *dubius*) the apical hyaline area of the fore wing comparatively large, almost reaching the apex of the marginal cell (Fig. 7G) (in *dubius* comparatively small, not reaching the apex of the marginal cell (Fig. 1F)), the vein m-cu of the fore wing antefurcal (Fig. 7G) (slightly postfurcal to interstitial in *dubius* (Fig. 1F)), and the hind femur slenderer, 4.6–5.2 times as long as wide (Fig. 7H) (4.1–4.3 times as long as wide in *dubius* (Fig. 1G)). This species is also similar to *A. ussuriensis* Belokobylskij, 1981 described from the Russian Far East, but differs in having the vertex densely punctate (vertex with distinct transverse striation in *ussuriensis*), the mesosoma black (mesosoma red except for the prothorax black in *ussuriensis*) and the metasoma entirely yellowish brown (metasoma black except for the red first metasomal tergite in *ussuriensis*).

Discussion

Among the six Japanese species, *A. egregius* and *A. rufotestaceus* are widely distributed in the Palaearctic region, but four other species (*A. dubius*, *A. elasmuchae*, *A. flavicans*, and *A. rutilipoides* sp. nov.) are virtually confined to East Asia (China, Japan, Korea, the Russian Far East and Taiwan). Two Japanese species, *A. rutilipoides* sp. nov. and *A. dubius*, have a comparatively larger body and the fore wing with two fuscous bands and belong to a species complex with *A. rutilipes* from continental China, Korea, and Taiwan, and *A. ussuriensis* from continental China, Korea, and the Russian Far East. A comprehensive study on the fauna and phylogeny of *Aridelus* in and around East Asia is required.

All previously known host families of *Aridelus* (Acanthosomatidae, Pentatomidae, Plataspidae, Scutelleridae) belong to the superfamily Pentatomoidea (Shaw et al. 2001), but our study has revealed that *Aridelus* can also use the superfamily Coreoidea (including Alydidae) as host insects. While the most widely distributed species,

A. egregius, is known to parasitize three host families, other Japanese species so far only one host family is known (Yu et al. 2016; present study). The host specificity of *Aridelus* species is an interesting problem that deserves further study.

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Yu DSK, van Achterberg C, Horstmann K (2016) Taxapad 2016, Ichneumonoidea 2015 Database on flash-drive. Nepean, Ontario, Canada. www.taxapad.com

Supplementary material 1

Table S1
Authors: Shunpei Fujie, Kaoru Maeto
Data type: xlsx file
Explanation note: Comparison of Chinese specimens of *Aridelus rufotestaceus* Tobias and *A. rufiventris* Luo & Chen with Japanese and Korean specimens of *A. rufotestaceus*.
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ZooKeys 1092: 123–146 (2022)
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RESEARCH ARTICLE

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Two new species of *Platensina* Enderlein (Diptera, Tephritidae, Tephritinae, Dithrycini) from India

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Abstract

Two new species of *Platensina* Enderlein, *P. rabbanii* David & Hancock, **sp. nov.**, and *P. flavistigma* David & Hancock, **sp. nov.**, are described from Meghalaya and southern India, respectively. *Platensina rabbanii* can be differentiated from *P. alboapicalis* Hering by the presence of a single hyaline indentation in cell r_1 and the apical hyaline band in cell r_{2+3} restricted to the apex; *P. flavistigma* differs from *P. quadrula* Hardy by the presence of a yellow/fulvous pterostigma and shape of the epandrium. DNA barcode sequences of *P. acrostacta* (Wiedemann), *P. flavistigma* and *P. platyptera* Hendel were obtained and reported. Post-abdominal descriptions and illustrations of *P. acrostacta*, *P. platyptera* and *P. zodiacalis* (Bezzi) are also provided along with keys to all 23 species and the 7 known from India.

Keywords

Identification key, *Ludwigia*, Meghalaya, Onagraceae, Platensinina, south India

Introduction

Platensina Enderlein is predominantly an Oriental and Australasian genus with 24 species recognized by Norrbom et al. (1999) [some generically misplaced] and 21 by Hancock (2012). They are medium-sized flies with broad, dark brown wings with hyaline indentations and spots. Host plants are not recorded except for *Platensina acrostacta* (Wiedemann), reared from stem galls of an undetermined *Ludwigia* species

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in southern India (Hardy 1973; Hancock 2012). Agarwal and Sueyoshi (2005) listed five species from India, while David and Ramani (2011) provided keys to four species from peninsular India and the Andaman and Nicobar Islands. Hancock (2012) recorded *P. platyptera* Hendel and *P. quadrula* Hardy from India, regarded records of *P. amplipennis* (Walker) from India as misidentifications of *P. platyptera* and provided a key to species of *Platensina*. In this paper two new species, one collected from Meghalaya and one from southern India, are described, along with descriptions of postabdominal structures of other species recorded from India except *P. tetrica* Hering and *P. fulvifacies* Hering, as specimens of these two taxa were not available for study. A key to species of *Platensina* recorded from India is provided, together with a revised key to all known species.

Material and methods

Specimens studied are deposited in the National Insect Museum, ICAR – National Bureau of Agricultural Insect Resources, Bengaluru, India (**NIM**).

Collections were done by sweep netting. Images of specimens were taken using a Leica DFC 420 camera mounted on a Leica M205A stereo zoom microscope; images of genitalia were taken using an 8 MP camera temporarily attached to a Leica DM 1000 compound research microscope; the images were stacked and combined to a single image using Combine ZP (Hadley 2011). Measurements of male and female genitalia were taken using Leica Automontage Software, LAS 3.4. Terminology adopted here follows White et al. (1999) and wing terminology by Cumming and Wood (2017).

One hind leg was removed from one specimen of each of three species and used for DNA extraction. The DNA extraction was performed using a DNeasy Blood and Tissue Kit (Qiagen India Pvt. Ltd.) following the manufacturers' instruction. For the molecular study, the standard DNA barcoding region of the mitochondrial COI gene was sequenced and the PCR was performed using the Universal COI primers (LCO1490/HCO2198) (David et al. 2020). The sequences were annotated using NCBI Blast tools and submitted to the NCBI GenBank Database where accession numbers were obtained (*Platensina flavistigma* – MT019893; *Platensina acrostacta* – MT019891; *Platensina platyptera* – MW448367).

The pairwise genetic distance between three species of *Platensina* viz., *P. acrostacta*, *P. platyptera* and *P. flavistigma* has been calculated using mitochondrial COI gene sequences. Analyses were conducted using the Maximum Composite Likelihood model (Tamura et al. 2004). This analysis involved 4 nucleotide sequences. Codon positions included were 1st+2nd+3rd. All positions with less than 95% site coverage were eliminated, i.e., fewer than 5% alignment gaps, missing data, and ambiguous bases were allowed at any position (partial deletion option). There were a total of 557 positions in the final dataset. Evolutionary analyses were conducted in MEGA11 (Tamura et al. 2021).

Results

Taxonomy

Platensina Enderlein, 1911

Platensina Enderlein, 1911: 454. Type species: *Platensina sumbana* Enderlein.
Tephrostola Bezzi, 1913: 153. Type species: *Trypeta acrostacta* Wiedemann.

Diagnosis. Medium-sized flies (4–5 mm long), with frons as wide as long, three frontal setae, two orbital setae, well developed ocellar setae. First flagellomere shorter than face, with short-pilose arista, face usually fulvous, black in males of a few species. Scutum grey pubescent with yellow-white reclinate setulae; scutellum flat with one or two pairs of setae, apical pair less than half length of basal setae or absent. Wing broad, often distinctly angled along posterior margin, dark brown with hyaline indentations and subhyaline spots. Abdomen predominantly black with fulvous lateral regions. Epandrium broad, without demarcation between epandrium and lateral surstylus, lateral surstylus broad, epandrium elongate-oval in posterior view; medial surstylus with well sclerotised prensisetae (lateral one broader than medial one), proctiger not higher than epandrium, glans of phallus stout, with single sclerotised acrophallus. Taeniae short (0.25 of eversible membrane); spicules on eversible membrane conical; aculeus dorsoventrally flattened, tip conical, with reduced preapical setae; spermathecae club-shaped, with numerous papillae.

Key to species of *Platensina* from India

1 Apex of wing hyaline from middle of cell r_{2+3} to cell cua (Fig. 6); posterior wing margin not distinctly angled near apex of cell cua..... .....***P. rabbanii*** **David & Hancock sp. nov.**

– Wing with a hyaline spot restricted to apex of cell r_{4+5} (e.g. Figs 16, 20, 21); posterior wing margin distinctly angled near apex of cell cua **2**

2 Wing with discal spots small and often indistinct or subhyaline; cell r_1 with 0–2 small hyaline indentations from costa in basal portion beyond stigma, often not crossing cell; cell cua with 3 small, isolated hyaline marginal spots and with or without additional small, isolated discal spots; holotype illustrated by Hering 1939a, fig. 14.....***P. tetrica*** **Hering, 1939**

– Wing with distinct hyaline discal spots; hyaline indentations in basal portion of cell r_1 with at least the basal one broad and crossing into cell r_{2+3}; cell cua with 2–3 hyaline marginal indentations, the basal pair usually elongate but often divided medially into 2 separate spots.....**3**

3 Wing (Figs 20, 21) with pterostigma entirely dark brown to black, 2 elongate marginal hyaline indentations in cell r_1, both crossing vein R_{2+3} into cell r_{2+3}, no marginal preapical hyaline spots in cell r_{2+3}, large hyaline spots near base

of cell r_{4+5} and near base and apex of cell dm, 1 marginal spot in cell m near apex of vein CuA, 2 indentations in cell cua and 1 or 2 spots along margin of anal lobe **4**

– Wing markings not as above (Figs 16, 31, 32, 42, 43); pterostigma usually with a subhyaline or fulvous basal patch or spot, marginal preapical hyaline spot in cell r_{2+3} usually present, and cell m usually with 2 or 3 hyaline marginal spots **5**

4 Face black in male, yellow in female; wing (Figs 20, 21) with basal spot in cell dm not distinctly larger than apical spot and not crossing or almost crossing cell; hyaline indentations in cell cua of approximately equal length, almost crossing cell but basal spot sometimes narrowly divided medially ..... ***P. acrostacta* (Wiedemann, 1824)**

– Face yellow in both sexes; wing with basal spot in cell dm distinctly larger than apical spot and crossing or almost crossing cell; basal hyaline indentation in cell cua much smaller than second indentation or broadly divided medially into 2 small spots; holotype illustrated by Hering 1941, fig. 4 ..... ***P. fulvifacies* Hering, 1941**

5 Wing (Fig. 16) with base and pterostigma largely fulvous to pale brown, contrasting with rest of wing; cell m without an isolated anterobasal hyaline spot ..... ***P. flavistigma* David & Hancock, sp. nov.**

– Wing (Figs 31, 32, 42, 43) with pattern variable but uniformly dark brown with hyaline spots and markings; cell m with an isolated anterobasal hyaline spot **6**

6 Scutellum with apical and basal setae ..... ***P. platyptera* Hendel, 1915**

– Scutellum with only basal setae ..... ***P. zodiacalis* (Bezzi, 1913)**

Key to all known species of *Platensina*

Modified from Hancock (2012).

1 Wing broad and almost circular beyond basal third, apex evenly rounded and entirely dark, without hyaline discal or marginal spots or indentations except for pair of small costal spots at bases of pterostigma and cell r_1 adjacent to apices of veins Sc and R_1, respectively; illustrated by Hardy 1974, fig. 129 [Philippines (Luzon)] ..... ***P. bezzii* Hardy, 1974**

– Wing often broad but distinctly longer than wide, apex at least slightly produced and with at least a hyaline apical spot in cell r_{4+5}; usually with hyaline discal and marginal spots or indentations **2**

2 Wing (Fig. 6) with hyaline apical band distinctly crossing veins R_{4+5} and M_1 into cells r_{2+3} and m_1 ..... **3**

– Wing (Figs 10, 16, 20, 21, 32, 43) with oval or quadrate hyaline apical spot confined to cell r_{4+5} **7**

3 Male wing without hyaline spots or indentations apart from small marginal indentation in cell r_1 at apex of vein R_1 and crescentic hyaline apex; female wing with crescentic hyaline apex plus hyaline marginal spots and indentations and subbasal hyaline spot in cell dm but no spot near base of cell r_{4+5}; illustrated by Wang 1998, fig. 253–4 [China (Yunnan)] .....***P. nigripennis* Wang, 1998**

– Male wing (where known) with one broad or 2 narrow marginal hyaline indentations in cell r_1 near apex of vein R_1 and often a spot near base of cell r_{4+5}; female wing (where known) with hyaline medial spot close to line of crossvein r-m and often a spot near base of cell r_{4+5} **4**

4 Wing of both sexes without hyaline spot near base of cell r_{4+5} and hyaline apex in cell m separate from the 2 hyaline marginal spots; hyaline marginal indentation in cell r_1 broad and rectangular in male, divided into elongate indentation and 2 small round spots in female; male illustrated by Hardy and Drew 1996, fig. 167 [Australia (Queensland)] .....***P. parvipuncta* Malloch, 1939**

– Wing of both sexes (where known) with hyaline spot near base of cell r_{4+5}; apex with hyaline band in cell m enclosing one or both marginal spots, leaving no more than a single separate marginal spot; hyaline indentation from costa in cell r_1 not as above.....**5**

5 Male unknown; female posterior to vein R_{4+5} with spots in cells r_{4+5} (1, at base), bm (1, near apex), dm (1, near middle), m (1 marginal near apex of vein CuA), cua (3, 2 basal and 1 near middle) and anal lobe (1); not illustrated [Taiwan] ..... ***P. apicalis* Hendel, 1915**

– Female unknown; male with 1 or 2 hyaline indentations in cell r_1 near apex of vein R_1 and 1 or no hyaline marginal spots in cell m near apex of vein CuA separate from the apical hyaline area, large hyaline spots at base of cell r_1 and at basal third of cell dm, and 2 elongate marginal indentations in cell cua [India and Burma] **6**

6 Wing in cell r_1 with 2 hyaline indentations near apex of vein R_1; cell m with one hyaline marginal spot in addition to apical hyaline area; cell cua with hyaline marginal indentations reaching or almost reaching vein CuA; illustrated by Hering 1938, fig. 50 [NE Burma].....***P. alboapicalis* Hering, 1938**

– Wing (Fig. 6) with cell r_1 with 1 hyaline indentation near apex of vein R_1 and cell m without a hyaline marginal spot in addition to apical hyaline area; cell cua with hyaline marginal indentations ending at or before middle of cell ....***P. rabbanii* David & Hancock, sp. nov.**

7 Wing with cell c and basal two-thirds of pterostigma hyaline; hyaline marginal spots (including 2 in cell m_1 and 3 in cell cua) present but pale discal spots absent; head with 1–2 pairs of frontal setae; illustrated by Hardy 1974, fig. 127 [Philippines (Luzon)] ..... ***P. amita* Hardy, 1974**

– Wing with cell c not entirely hyaline and pterostigma with at most a hyaline basal spot; both hyaline marginal and pale discal spots usually present; head with 3 pairs of frontal setae **8**

8 One pair of scutellar setae, apicals absent; illustrated by Bezzi 1913, fig. 65, Hardy 1973, pl. v, fig. 45, Hardy 1974, fig. 130, Wang 1998, fig. 256 and this paper, figs 42–43 [India and Sri Lanka to Philippines, Indonesia and northern Australia] ..... ***P. zodiacalis* (Bezzi, 1913)**

– Two pairs of scutellar setae, apicals present.....**9**

9 Wing cell r_{2+3} with 2 narrow marginal hyaline spots or indentations; marginal hyaline indentations in cell r_1 close to apex of vein R_1 normally reduced in cell r_{2+3} to isolated spots in yellowish field; illustrated by Hancock 2012, figs 3–4 [Indonesia to NE Australia and Solomon Islands]....***P. ampla* de Meijere, 1914**

– Wing cell r_{2+3} with 0–1 narrow marginal hyaline spots or indentations; marginal hyaline indentations in cell r_1 close to apex of vein R_1 present or reduced in cell r_{2+3} but not reduced to isolated spots in a yellowish field.....**10**

10 Wing with single large marginal hyaline indentation in cell r_1 close to apex of vein R_1 that extends across cell r_{2+3} and is aligned with posterior indentation in cell cua that crosses cell; cell m with single hyaline marginal spot placed close to apex of vein CuA; illustrated by Hardy 1974, fig. 128 [Philippines (Luzon)] ..... ***P. aptata* Hardy, 1974**

– Wing with 2 marginal hyaline indentations in cell r_1 close to apex of vein R_1, the distal one sometimes reduced and largely united with basal one, sometimes both reduced to small marginal spots or single indistinct pale area; cells m and cua not both with a single hyaline marginal spot or band.....**11**

11 Wing cell m with 3 hyaline marginal spots or indentations.....**12**

– Wing cell m with at most 2 hyaline marginal spots or indentations **13**

12 Wing cell dm with 3 rounded hyaline spots; cell m with 2 hyaline spots in anterobasal quarter; illustrated by Hardy and Drew 1996, fig. 168 [Australia (Queensland)]..... ***P. trimaculata* Hardy & Drew, 1996**

– Wing cell dm with 2 rounded hyaline spots; cell m with 1 hyaline spot in anterobasal quarter; illustrated by Wang 1998, fig. 251 [Japan (Ryukyu Is), Taiwan and China (Sichuan, Guangxi)] .....***P. assimilis* (Shiraki, 1968)**

13 Wing cell r_{4+5} with very small apical hyaline spot; illustrated by Hardy 1988, fig. 22 [Indonesia (Java, Sumba)] .....***P. sumbana* Enderlein, 1911**

– Wing cell r_{4+5} with large apical hyaline spot filling all or most of cell apex....**14**

14 Wing cell r_1 with 2 large and quadrate hyaline indentations, distal one broader than wide, plus subapical posterior spot not reaching costa; cell m with 2 elongate hyaline indentations, the anterior one much smaller and narrower than the posterior one; cell cua with 3 broad hyaline indentations, the basal pair crossing or almost crossing cell, plus basally with extension of large hyaline mark in anal lobe; male with distinct white or silvery parafacial stripes (females unknown) **15**

– Wing markings not as above, distal hyaline indentation in cell r_1 narrower than wide and/or one or both marks often reduced or absent, subapical spot in cell r_1, when present, small and marginal at costa or crossing cell, and marginal marks in cell m usually subequal in size; male without white or silvery parafacial stripes.....**16**

15 Wing (Figs 9, 10, 16) with dark markings anterior to vein R_{4+5} pale brown to yellow-brown in basal two-thirds and dark brown elsewhere; pterostigma with basal spot yellow; hyaline spot at base of cell r_{4+5} circular; head with parafacial stripes white [southern India (Karnataka, Tamil Nadu)] .... ***P. flavistigma*** **David & Hancock, sp. nov.**

– Wing with dark markings uniformly dark brown; pterostigma with basal spot hyaline; hyaline spot at base of cell r_{4+5} oval; head with parafacial stripes silvery; illustrated by Hardy 1973, fig. 149 [Thailand, Cambodia and Vietnam] ..... ***P. quadrula*** **Hardy, 1973**

16 Wing cell r_{2+3} without small and narrow marginal spot posterior to apex of vein R_{2+3} and pterostigma without hyaline basal spot; cell m with 1 small semicircular marginal hyaline spot near apex of vein CuA..... **17**

– Wing cell r_{2+3} with small and narrow marginal spot below apex of vein R_{2+3} and pterostigma often with hyaline basal spot; cell m usually with 2 small and often elongate marginal hyaline spots..... **18**

17 Face largely black in male, yellow in female; basal spot in cell dm not distinctly larger than apical spot and not crossing or almost crossing cell; hyaline indentations in cell cua of approximately equal length, almost crossing cell but basal spot sometimes narrowly divided medially; illustrated by Bezzi 1913, fig. 57, Hancock 2012, fig. 1 and this paper, figs 20–21 [India and Sri Lanka to southern China (Yunnan) and Cambodia]..... ***P. acrostacta*** **(Wiedemann, 1824)**

– Face yellow in both sexes; basal spot in cell dm distinctly larger than apical spot and crossing or almost crossing cell; basal hyaline indentation in cell cua much smaller than second indentation or broadly divided medially into 2 small spots; illustrated by Hering 1941, fig. 4 [India (Maharashtra, Rajasthan)]..... ***P. fulvifacies*** **Hering, 1941**

18 Wing with discal spots often subhyaline or indistinct and pale brown; cell r_1 often with 0–2 small hyaline indentations or spots in basal portion (especially in males) or with 2 indentations often largely fused; cell cua with 2 or 3 small and isolated hyaline marginal spots and with or without additional small and isolated discal spot **19**

– Wing with discal spots normally hyaline and distinct; cell r_1 with second hyaline indentation distinct and at most weakly joined to first; cell cua with 2–3 hyaline marginal indentations not all small and isolated, basal pair often almost crossing cell or medially divided into separate spots..... **20**

19 Wing cell r_1 with basal hyaline indentations often reduced to 0–2 small hyaline spots (especially in males, better developed in females); cell cua with 3 small and isolated hyaline marginal spots and with or without additional small and isolated discal spots; anal lobe with 2 distinct hyaline marginal spots; illustrated by Hardy 1973, pl. v, fig. 44 and Wang 1998, figs 252 & 255 [India (Tamil Nadu), Thailand and West Malaysia to China (Guangxi, Fujian) and Taiwan]..... ***P. tetrica*** **Hering, 1939**

– Wing cell r_1 with second hyaline indentation narrow and strap-like or fused with first indentation leaving only small dark costal spot between them; cell cua

with 2 small marginal spots; anal lobe with hyaline marginal spots vestigial or absent; illustrated by Bezzi 1913, fig. 64 and Hardy 1973, pl. v, fig. 42 [southern Burma to Vietnam and Indonesia (Sumba)] ..... ***P. euryptera*** **(Bezzi, 1913)**

20 Wing cell m with a small anterobasal hyaline spot and no marginal spots; cell cua with 2 undivided indentations almost crossing cell; cell r_{4+5} with basal spot large and ovate, much larger than the 2 distinct spots in cell dm; illustrated by Hardy 1973, pl. v, fig. 43 [Thailand, Cambodia and Vietnam] .... ***P. intacta*** **Hardy, 1973**

– Wing cell m with 2 small hyaline marginal spots; cell cua with 2 or 3 indentations, with at least the more distal of the 2 basal indentations divided medially and apical spot small or absent; cell r_{4+5} with basal spot small and circular, not much larger than the 2 distinct spots in cell dm.....**21**

21 Wing evenly rounded posteriorly, not distinctly angled basal of end of vein CuA and with numerous distinct discal spots, 1–2 in cell br, 3 in cell r_{4+5}, 1–2 in cell r_{4+5}, 2 in cell dm and 1 anterobasally in cell m; posterior marginal spot in cell m distinctly larger and broader than anterior marginal spot; illustrated by Wang 1998, fig. 259–260 [Japan (Ryukyu Is), China (Sichuan) and possibly Indonesia (West Papua)] ..... ***P. shirouzui*** **(Ito, 1984)**

– Wing distinctly angled posteriorly, broadest just basal of end of vein CuA and with only 3 distinct discal spots, 1 at base of cell r_{4+5} and 2 in cell dm; posterior marginal spot in cell m not distinctly larger and broader than anterior marginal spot.....**22**

22 Apical scutellar setae distinct, about half length of basals; anal lobe of wing with hyaline marginal spots vestigial or absent; posterior hyaline marginal spot in cell m narrow, elongate and perpendicular; illustrated by Hancock 2012, fig. 2 [southern Thailand to Indonesia (Java, Sulawesi)] ....***P. amplipennis*** **(Walker, 1860)**

– Apical scutellar setae weak, about quarter length of basals; anal lobe of wing with hyaline marginal spots round and distinct; posterior hyaline marginal spot in cell m often short and broad; illustrated by Hancock 2012, figs 5–6 and this paper, figs 31–32 [India to Japan (Ryukyu Is), Australia, Solomon Islands and Vanuatu] ..... ***P. platyptera*** **Hendel, 1915**

New species

Platensina rabbanii **David & Hancock, sp. nov.**
http://zoobank.org/FF51328D-55A7-49B0-934F-48D1D61EF92D

Type locality. India: Meghalaya, East Khasi Hills, Laitsopliah.

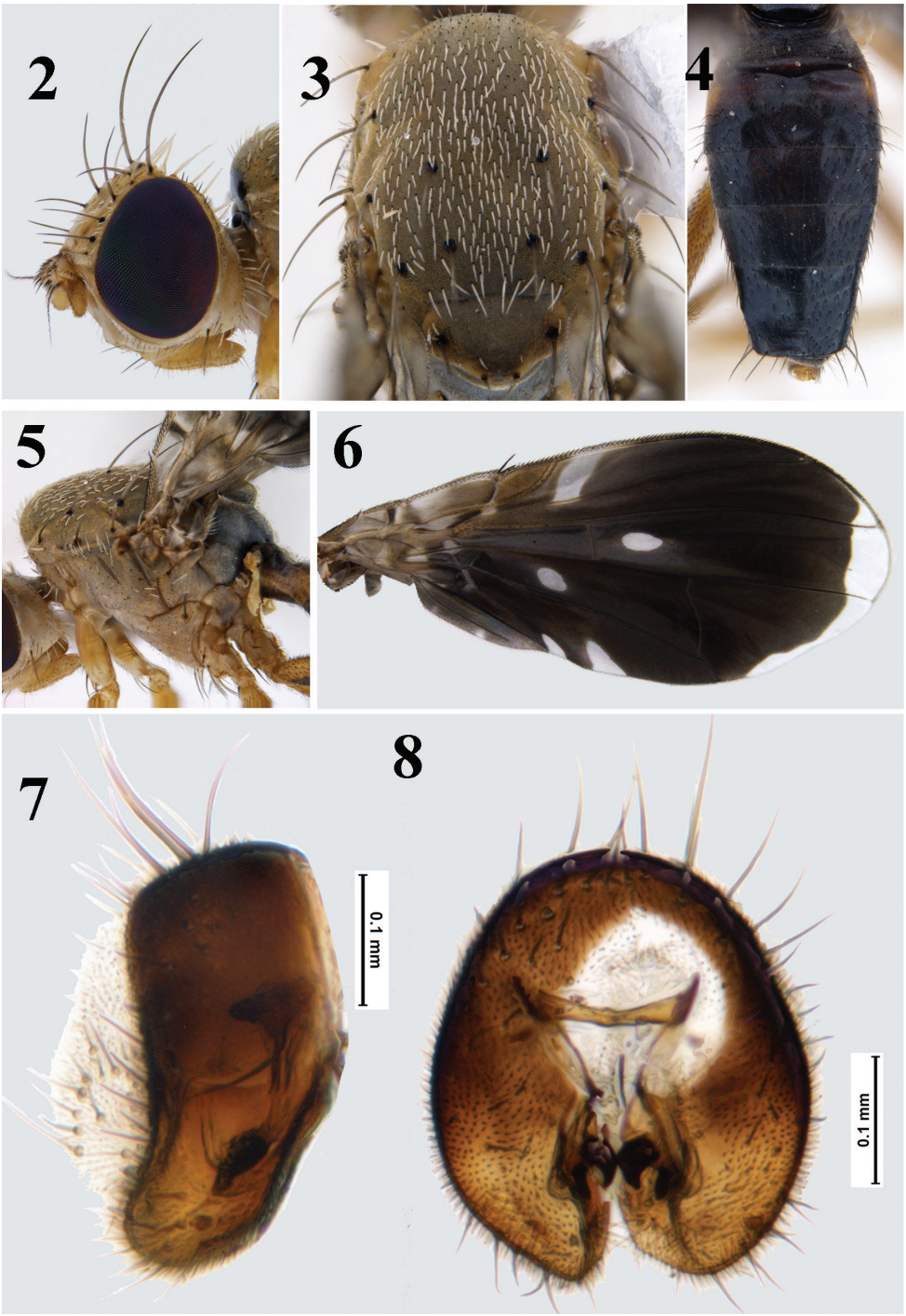
Type data. ***Holotype*** male, pinned. Original label: "INDIA: Meghalaya, East Khasi Hills, Laitsopliah, 17.iii.2021, Rabbani M. K." (NIM).

Diagnosis. This species is similar to *P. alboapicalis* Hering from Burma in the presence of an apical hyaline band extending from cell r_{2+3} to cell m_1 but can be differentiated by the presence of a single hyaline indentation in cell r_{2+3}, versus two

Figure 1. Habitus (lateral) of male of *Platensina rabbanii* David & Hancock, sp. nov.

hyaline indentations and spot in *P. alboapicalis*; the apical hyaline band restricted to the apical one-third of cell r_{2+3}, versus the whole of apex of cell r_{2+3} in *P. alboapicalis*; and the hyaline indentations in cell cua ending well before vein CuA, unlike in *P. alboapicalis* where they almost reach vein CuA.

Description. Male. Medium-sized fly (4.03 mm long) with broad, dark brown wing with hyaline apex.



Figures 2–8. *Platensina rabbanii* David & Hancock, sp. nov. **2** head (lateral view) **3** thorax (dorsal view); **4** abdomen (dorsal view) **5** thorax (lateral view) **6** wing **7** epandrium (lateral view) **8** epandrium (posterior view).

Head (Fig. 2): nearly as high as long; frons fulvous with three pairs of frontal setae and two pairs of orbital setae (posterior one white); ocellar triangle fuscous, with well developed ocellar setae; medial vertical seta black; lateral vertical seta, paravertical seta and postocellar seta lanceolate and white; postocular setae black interspersed with prominent, white lanceolate setae. Face fulvous without any markings. Scape and pedicel fulvous, first flagellomere less than half length of face, concolorous with frons, arista short pilose. Gena narrow, with prominent genal seta, subvibrissal setae present.

Thorax (Figs 3, 5): Scutum uniformly grey microtrichose, with creamy-white setulae. Chaetotaxy well developed: 1 postpronotal, 1 presutural supra-alar, 1 anterior notopleural, 1 posterior notopleural, 1 postsutural supra-alar, 1 dorsocentral placed in line with postsutural supra-alar, 1 postalar, 1 intra-alar, and 1 prescutellar acrostichal seta. Scutellum brown with two pairs of scutellar setae; apical one less than half length of basal one. Anepisternum grey, with single seta near phragma; anepimeron grey, with single seta, katepisternum fulvous, with single seta; anatergite dark brown; katatergite and meron fulvous. Legs predominantly fulvous without any black/dark markings except basal, brown longitudinal streaks present on ventral surface of mid and hind femora; forefemur with single row of 4 ventral setae.

Wing (Fig. 6) broad, with posterior margin evenly rounded, length 4.47 mm; length/width ratio-2.10, predominantly dark brown, with hyaline indentations and spots; cell bc hyaline, cell c predominantly moderate brown, with narrow basal and broader medial hyaline areas, pterostigma entirely moderate brown without any hyaline markings, cell r_1 with one trapezoidal basal hyaline indentation not extending beyond vein R_{2+3}, cell r_{4+5} with elongate subbasal hyaline spot, cell dm with large hyaline spot at basal third, cell cua with two short hyaline indentations not reaching vein CuA, and apical hyaline band extending from apex of cell r_{2+3} to cell m; anal lobe and alula dark brown.

Abdomen (Fig. 4): Entirely black with yellowish orange patches laterally on tergites 1–2.

Male genitalia (Figs 7, 8). Epandrium broad, lateral surstylus as broad as epandrium and connected at acute angle to epandrium (Fig. 7); apex of lateral surstylus blunt (in lateral view); proctiger short, smaller than epandrium; epandrium elongate oval in posterior view, medial surstylus with well developed prensisetae (lateral one broader than medial one).

Female. Unknown

Distribution. Meghalaya (Northeast India).

Habitat. Marshy grasslands.

Etymology. The species is named after the collector, Rabbani Mehaboob K. It is a noun in apposition.

Platensina flavistigma **David & Hancock, sp. nov.**
http://zoobank.org/7512FEB5-3888-4CFF-8229-80C146706273

Platensina quadrula: Hancock 2012: 315 (misidentification, India record).

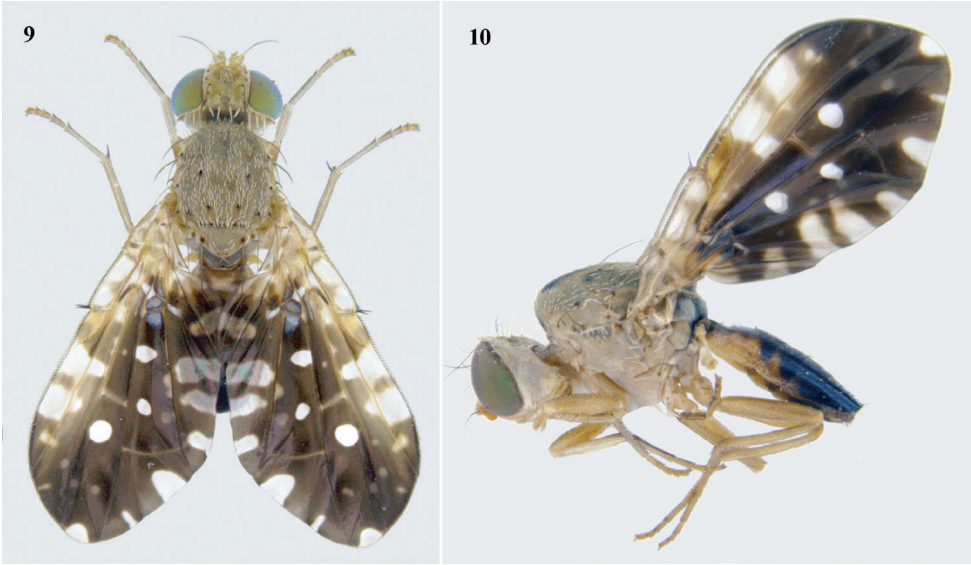
Type locality. India: Karnataka, Bangalore, Attur.

Type data. ***Holotype*** male, pinned. Original label: "INDIA: Karnataka, Bangalore, Attur, 05.ii.2020, Sachin K (NIM)". ***Paratypes*:** **India:** Periyakulam, 30.iii.2012, David, K. J. (1♂ NIM); India, Tamil Nadu, Thandikudi, C.R.S, 31.iii.2012, David, K. J. (1♂ NIM).

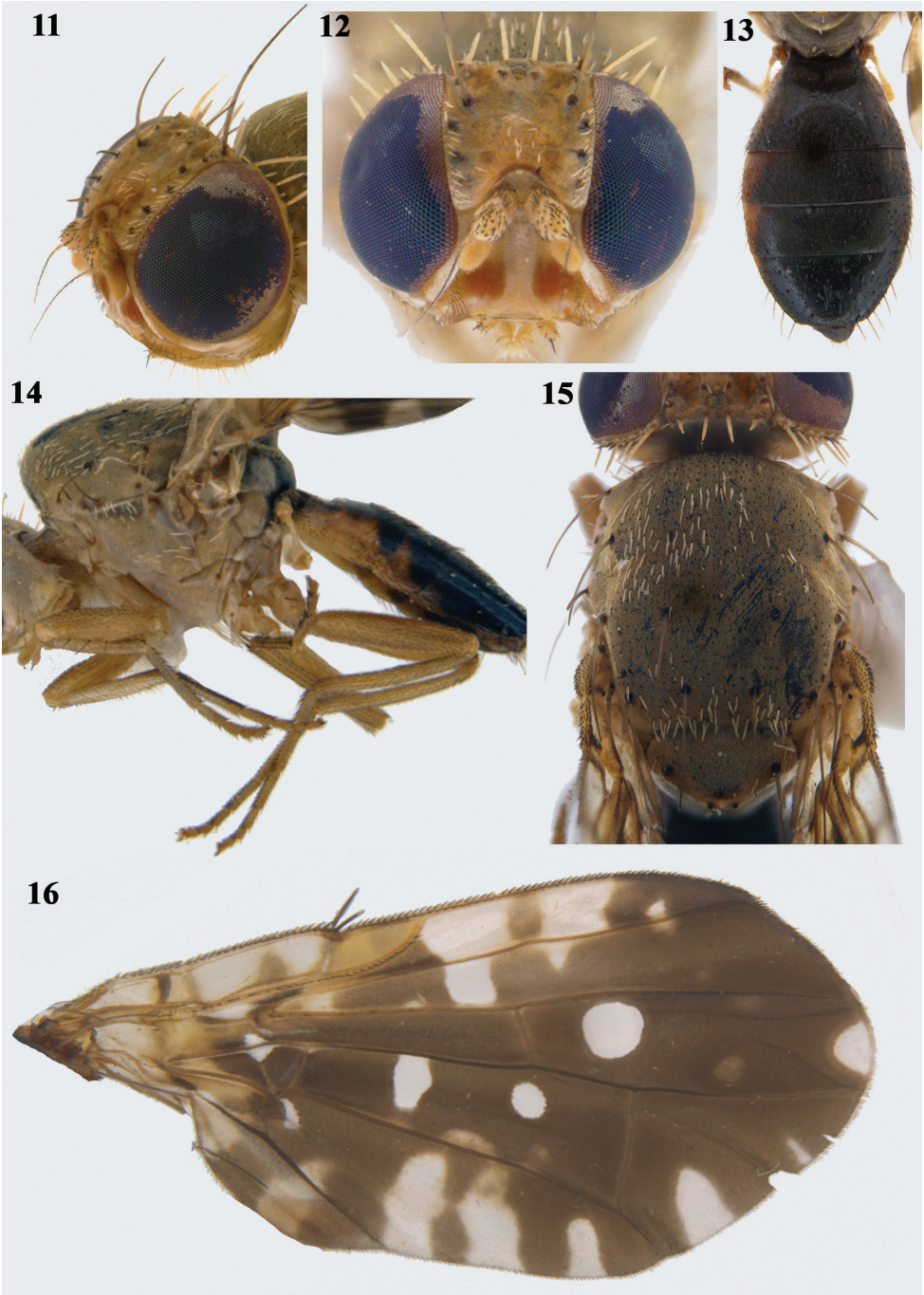
Diagnosis. This species is similar to *P. quadrula* Hardy from Thailand, Cambodia and Vietnam in the presence of two broad quadrate areas in wing cell r_1, an enlarged basal discal spot in cell r_{4+5} and large, broad hyaline indentations in cell cua. It can be differentiated by the lack of silvery facial spots and white rather than silvery parafacial stripes in males, as well as the angulate posterior wing margin, pterostigma predominantly fulvous/yellow and pale brown, and epandrium of uniform width throughout its length, whereas in *P. quadrula* the parafacial is silvery rather than white and facial silvery spots are present lateroventrally in males, the wing is evenly rounded posteriorly, the pterostigma is hyaline basally and dark brown apically, and the epandrium tapers apically. This species was mistakenly listed as *P. quadrula* from India by Hancock (2012).

Description. Male. Medium-sized fly (4.10–4.99 mm long) with broad, angulate wing with fulvous markings (Figs 9, 10).

Head (Figs 11, 12). as high as long; frons fulvous with three pairs of frontal setae and two pairs of orbital setae; ocellar triangle dark brown, with well-developed ocellar seta; medial vertical seta black; lateral vertical seta, paravertical seta and postocellar setae white; postocular setae black interspersed with prominent, white lanceolate setae. Face fulvous with broad orange-brown patches on ventral half of antennal groove. Scape and pedicel fulvous, first flagellomere shorter than face, concolorous with frons, arista short pilose. Parafacial alongside ventral half of face distinctly whitish. Gena narrow, with prominent genal seta, subvibrissal setae present.



Figures 9–10. Habitus of *Platensina flavistigma* David & Hancock, sp. nov. **9** dorsal view **10** lateral view.



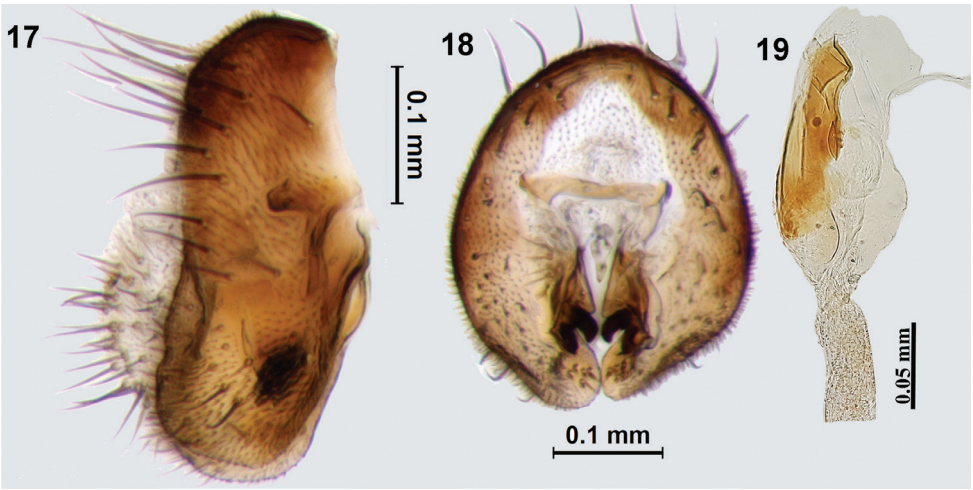
Figures 11–16. *Platensina flavistigma* David & Hancock, sp. nov. **11** head (profile view) **12** head (frontal view) **13** abdomen (dorsal view) **14** thorax (lateral view) and legs **15** scutum **16** wing.

Thorax (Figs 14, 15). Scutum uniformly grey microtrichose with creamy-white setulae. Chaetotaxy well developed: 1 postpronotal, 1 presutural supra-alar, 1 anterior notopleural, 1 posterior notopleural, 1 postsutural supra-alar, 1 dorsocentral placed in line with postsutural supra-alar, 1 postalar, 1 intra-alar, and 1 prescutellar acrostichal seta. Scutellum grey with two pairs of scutellar setae; apical one less than half length of basal one. Anepisternum grey, with single seta near phragma; anepimeron grey, with single seta, katepisternum fulvous, with single seta; anatergite dark brown; katatergite and meron fulvous. Legs predominantly fulvous without any black/dark markings; forefemur with single row of 4 ventral setae.

Wing (Fig. 16) broad, angulate, length 4.44–4.99 mm, length/width ratio, 1.92–2.05; predominantly dark brown with hyaline indentations and spots; cell bc hyaline, cell c predominantly hyaline with pale basal and medial infuscations, pterostigma fulvous basally, dark brown apically, cell r_1 with two broad quadrate indentations and small posterior subapical hyaline spot, the proximal quadrate indentation extended to vein R_{4+5}, cell r_{4+5} with large circular hyaline spot near base and large, semicircular hyaline apical spot, cell dm with two large hyaline spots, cell m with two marginal hyaline marks, subbasal one much larger than subapical one, cells r_{2+3} and r_{4+5} with indistinct and isolated pale brown subapical spots, cell cua with three large marginal hyaline indentations, basal two almost reaching vein CuA, and anal lobe with two broad subhyaline markings, proximal one crossing into cell cua.

Abdomen (Fig. 13). Entirely black with yellowish orange patches laterally on tergites 1–3.

Male genitalia. Epandrium broad, lateral surstylus as broad as epandrium (Fig. 17); apex of lateral surstylus blunt (in lateral view); proctiger short, smaller than



Figures 17–19. *Platensina flavistigma* David & Hancock, sp. nov. **17** epandrium (lateral view) **18** epandrium (posterior view) **19** glans of phallus.

epandrium; epandrium oval in posterior view (Fig. 18); medial surstylus shorter than lateral surstylus and with well developed prensisetae (lateral one broader than medial one). Phallus elongate (1.78 mm long), with sclerotised acrophallus (Fig. 19).

Female. Unknown

Etymology. The specific name is derived from two Latin words *flavus* (=yellow) and *stigma* (=ptersotigma).

Distribution. Karnataka and Tamil Nadu (southern India).

DNA Barcode. NCBI GenBank accession number – MT019893 (1♂, India: Karnataka, Bangalore, Attur, 17.v.2018, Prabhu, G.)

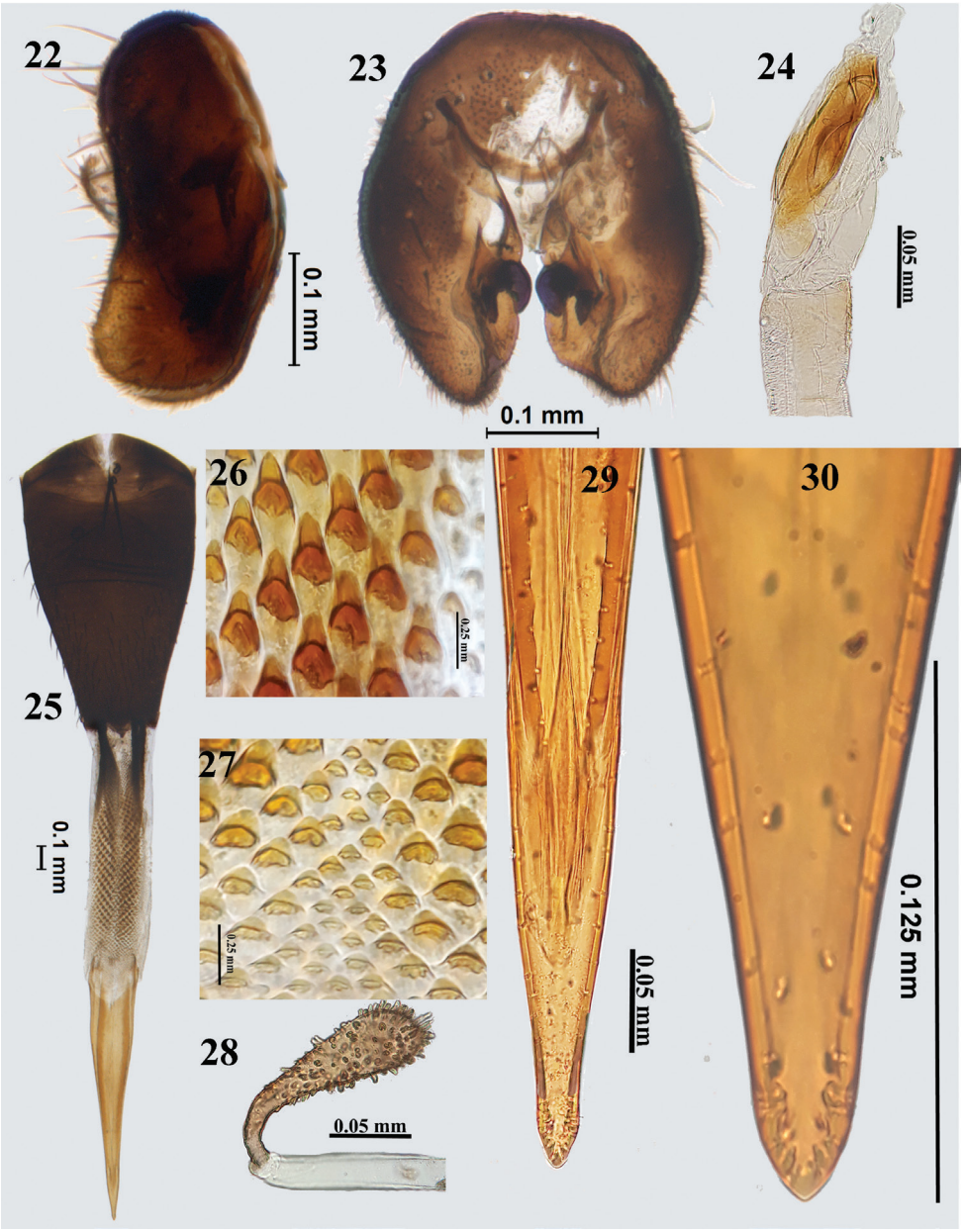
Taxonomic notes on other species of *Platensina* from India

Platensina acrostacta (Wiedemann)

Tephritis acrostacta Wiedemann, 1824: 54. Type locality: India-orientali [east India].
Ensina guttata Macquart, 1843: 387. Type locality Coromandel coast, Tamil Nadu, India.
Trypeta stellata Walker, 1849: 1030. Type locality North Bengal, India.
Trypeta voneda Walker, 1849: 1028. Type locality 'Bahia, Brazil' [*recte* Bengal, India].

Material examined. India: 1♂, Karnataka, Tumkur, Kunigal, 05.iv.2013, Prabhu G. "leg"; 1♂, Karnataka, Bengaluru, Hebbal, 28.xi.2014, Prabhu G. "leg"; 1♂, Karnataka, Bengaluru, Attur, 24.iii.2016, Prabhu G. "leg"; India. 1♀, Karnataka, Chikkaballapur, 12.iv.2016, Prabhu G. "leg"; 1♂,1♀ Karnataka, Bengaluru, Attur, 16.v.2017, Prabhu G. "leg"; 1♂,1♀, Karnataka, Bengaluru, Attur, 20.vi.2017, Prabhu G. "leg"; 1♀, Karnataka, Bengaluru, Attur, 04.vii.2017, Prabhu G. "leg"; 1♂, Karnataka, Bengaluru, Attur, 07.ii.2018, Prabhu G. "leg"; 1♀, Karnataka, Bengaluru, Attur, 21.iii.2018, Prabhu G. "leg"; 1♂,1♀, Karnataka, Bengaluru, Attur, 24.iv.2018, Prabhu G. "leg"; 1♂, Karnataka, Bengaluru, Hebbal, 03.v.2018, Prabhu G. "leg"; 1♂,1♀, Karnataka,

Figures 20–21. *Platensina acrostacta* (Wiedemann) **20** habitus (dorsal) **21** habitus (lateral).



Figures 22–30. *Platensina acrostacta* (Wiedemann) **22** epandrium (lateral) **23** epandrium (posterior) **24** glans of phallus **25** ovipositor **26** spicules on proximal end of eversible membrane **27** spicules on distal end of eversible membrane **28** spermatheca **29** aculeus **30** aculeus tip (100×).

Bengaluru, Attur, 17.v.2018, Prabhu G. "leg"; 2♀, Karnataka, Bengaluru, Attur, 24.v.2018, Prabhu G. "leg"; 1♂, Karnataka, Bengaluru, Attur, 14.vi.2018, Prabhu G. "leg"; 1♂, Karnataka, Bengaluru, Attur, 14.x.2019, Sachin K. "leg"; 1♂, Kerala,

Kasargod, C.P.C.R.I, 17.ii.2015, Prabhu, G."leg", 1♀,1♂, Tamil Nadu, Periyakulam, 30.iii.2012, David, K.J."leg", 1♂, Tamil Nadu, Thandikudi, C.R.S, 01.iv.2012, David, K.J. "leg"(NIM).

Diagnosis (Figs 20–30). A medium-sized species separated from the similar *P. fulvifacies* Hering largely by the black face in males; length of male (4.29–4.47 mm), of female (5.45–5.49 mm). This species was adequately described by Hardy (1973) except for detailed structures of male and female postabdomen. Epandrium broad, not demarcated from surstylus (profile view); proctiger smaller than epandrium. Epandrium and surstyli elongate oval in posterior view; prensisetae well developed. Phallus elongate (2.71 mm); glans with a sclerotised rod. Oviscape (1.21 mm) dark brown to black, dorsoventrally flattened; eversible membrane shorter than oviscape (0.96 mm) with conical spicules in the proximal region and triangular spicules towards distal end. Aculeus (1.01 mm) as long as eversible membrane and with triangulate apex. Spermatheca elongate oval with numerous papillae.

Distribution. This species is known from India (Karnataka, Tamil Nadu and Kerala) and Sri Lanka to Cambodia (Hancock 2012).

DNA Barcode. NCBI GenBank accession number – MT019891 (1♂, India: Karnataka, Bangalore, Attur, 29.v.2019, Sachin, K.).

Platensina fulvifacies Hering

Platensina fulvifacies Hering, 1941: 71. Type locality Lonaula, Maharashtra, India.

Diagnosis. This species is similar to *P. acrostacta* but can be differentiated primarily by the yellow face in males and larger basal spot in cell dm. Specimens were not available for study but photographs of both sexes have been examined: 2♂, 2♀, India: Rajasthan, Jodhpur District, 10 km SW Jodhpur, Machia Safari Pk, Malaise in dry wash 29.II–5.III.2008, 300 m, 26°18.60'N, 72°58.71'E (in California Academy of Sciences, San Francisco, California, USA).

Distribution. This endemic Indian species is known only from Maharashtra and Rajasthan.

Platensina platyptera Hendel

Platensina platyptera Hendel, 1915: 461. Type locality Taihorin, Taiwan.
Platensina malaita Curran, 1936: 29. Type locality Tai Lagoon, Malaita, Solomon Is.
Platensina dubia Malloch, 1939: 459. Type locality Gordonvale, Qld, Australia.
Platensina amplipennis: authors, *nec* Walker, 1860. Misidentifications.

Material examined. India: 1♀, Karnataka, Bengaluru, G.K.V.K, 02.ii.2012, David K.J. "leg"; 1♂, A&N Islands, Middle Andamans, Kadamtala, 09.iii.2012, David, K.J.

"leg"; 1♀, Karnataka, Mandya, Maddur, 09.i.2013, David, K.J. "leg"; 1♀, Karnataka, Uttara Kannada, Dandeli, 15.i.2015, Rajesh S. "leg"; 1♀, Meghalaya, Mawlynnong Road, 12.x.2019, David, K.J. "leg" (NIM).

Diagnosis (Figs 31, 32). This species was originally described by Hendel (1915) from Taiwan. It was recorded from India by Hancock (2012), based on photographs by the senior author. It is a medium-sized species with broad quadrate hyaline markings in cells c and r_1, round hyaline spots along the wing margin and in almost all the cells. It is similar to *P. zodiacalis* (Bezzi) but can be differentiated by the presence of apical scutellar setae.

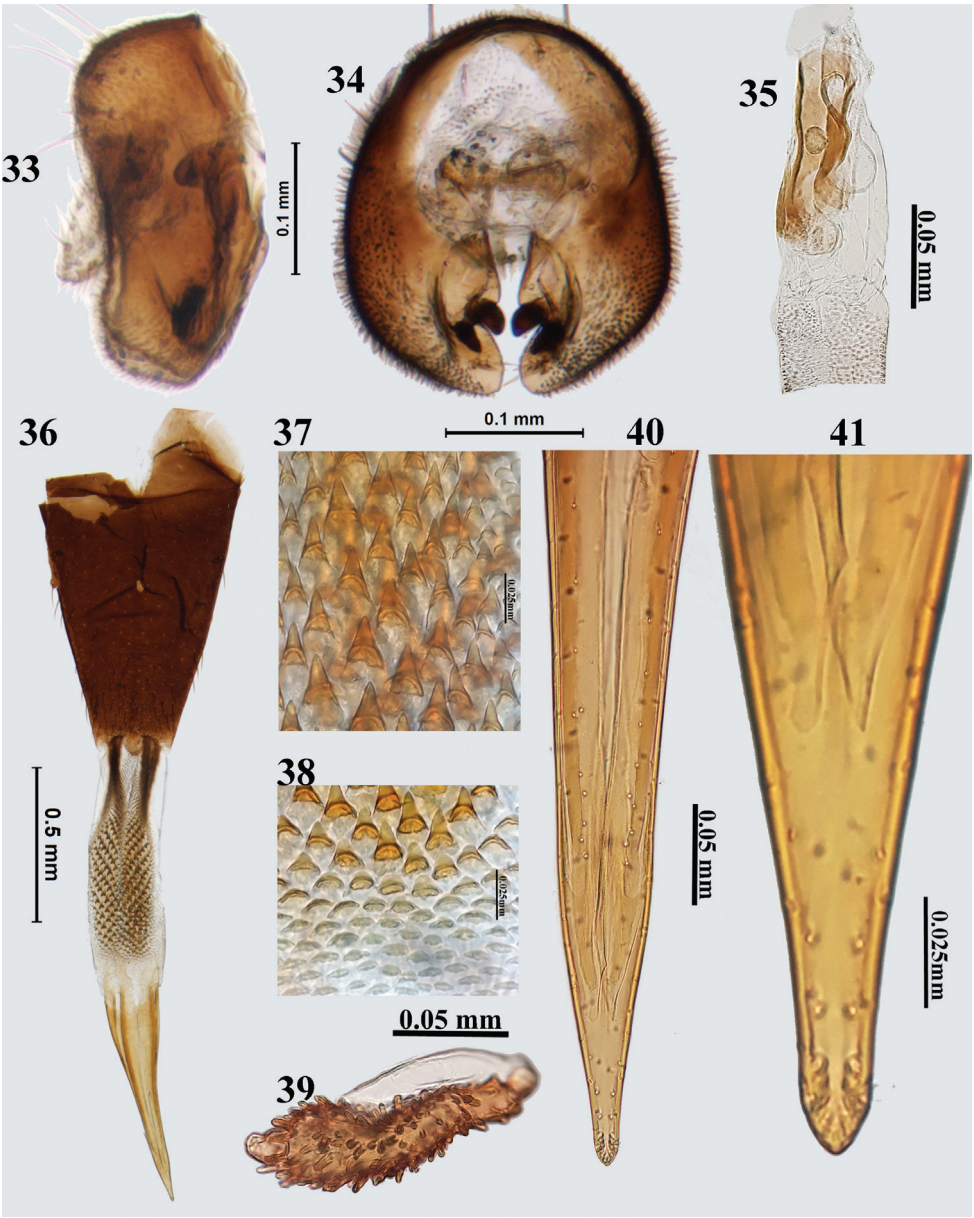
Male genitalia. Epandrium (Fig. 33) dark brown, heavily sclerotised, with no demarcation from lateral surstylus (in profile view); epandrium and surstyli oval in posterior view, with well developed prensisetae (Fig. 34). Phallus elongate (1.54 mm long including glans); glans stout, with broad sclerotised rod (Fig. 35).

Female genitalia. Oviscape 0.99 mm long, dark brown, conical, dorsoventrally flattened (Fig. 36); eversible membrane 0.83 mm long, shorter than oviscape, with conical spicules along entire length except for a few rows of flattened ones distally (Figs 37, 38); taeniae short, dark brown, 0.25 of length of eversible membrane. Aculeus shorter than eversible membrane, not dorsoventrally flattened, curved at its proximal end; apex of aculeus pointed and conical (Figs 40, 41). Spermatheca brown, club-shaped, with numerous papillae (Fig. 39).

Distribution. This species is widespread from India (Kerala, Karnataka, Meghalaya, Andaman and Nicobar Islands) to Japan and Australasia (Hancock 2012).

DNA Barcode. NCBI GenBank accession number – MW448367 (1♂, India: Kerala, Kannur, Aaralam, 13.i.2020, David, K. J.).

Figures 31–32. *Platensina platyptera* Hendel **31** habitus (dorsal) **32** habitus (lateral).



Figures 33–41. *Platensina platyptera* Hendel **33** epandrium (lateral) **34** epandrium (posterior view) **35** glans of phallus **36** ovipositor **37** spicules on proximal end of eversible membrane **38** spicules on distal end of eversible membrane **39** spermatheca **40** aculeus **41** aculeus tip (100×).

Platensina tetrica Hering

Platensina tetrica Hering, 1939a: 179. Type locality Trichinopolis, Tamil Nadu, India.
Platensina fukienica Hering, 1939b: 146. Type locality Fujian, China.

Diagnosis. This species was adequately described by Hering (1939a, b) and is characterised by the reduced and often indistinct hyaline markings. Indian specimens were not available for study but wings of both *P. tetrica* Hering and *P. fukienica* Hering, considered synonyms by Hancock (2012), were illustrated by Wang (1998).

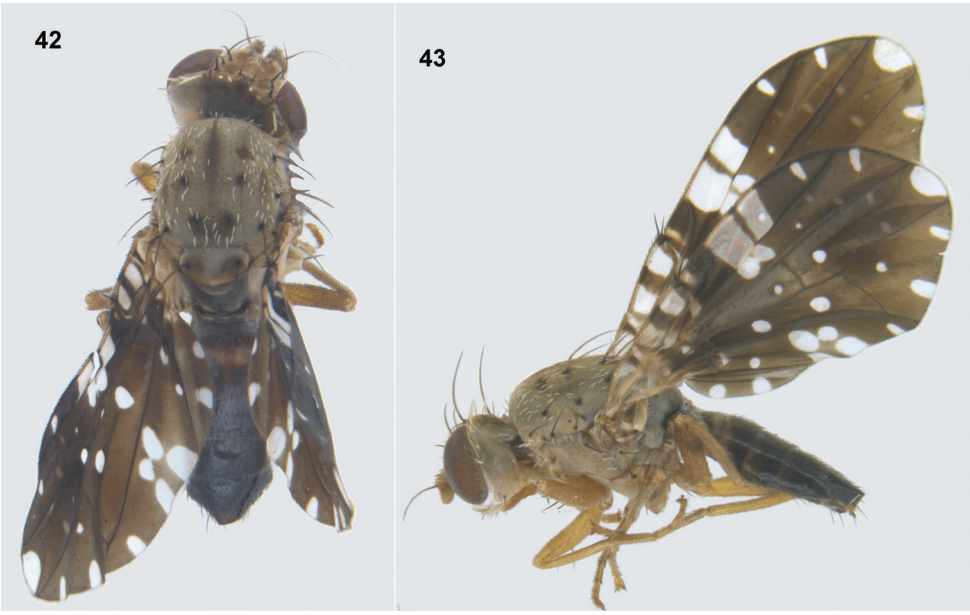
Distribution. This species is known in India only from the type locality in Tamil Nadu. Elsewhere, it is known from China, Taiwan, Vietnam and West Malaysia (Hancock 2012).

Platensina zodiacalis (Bezzi)

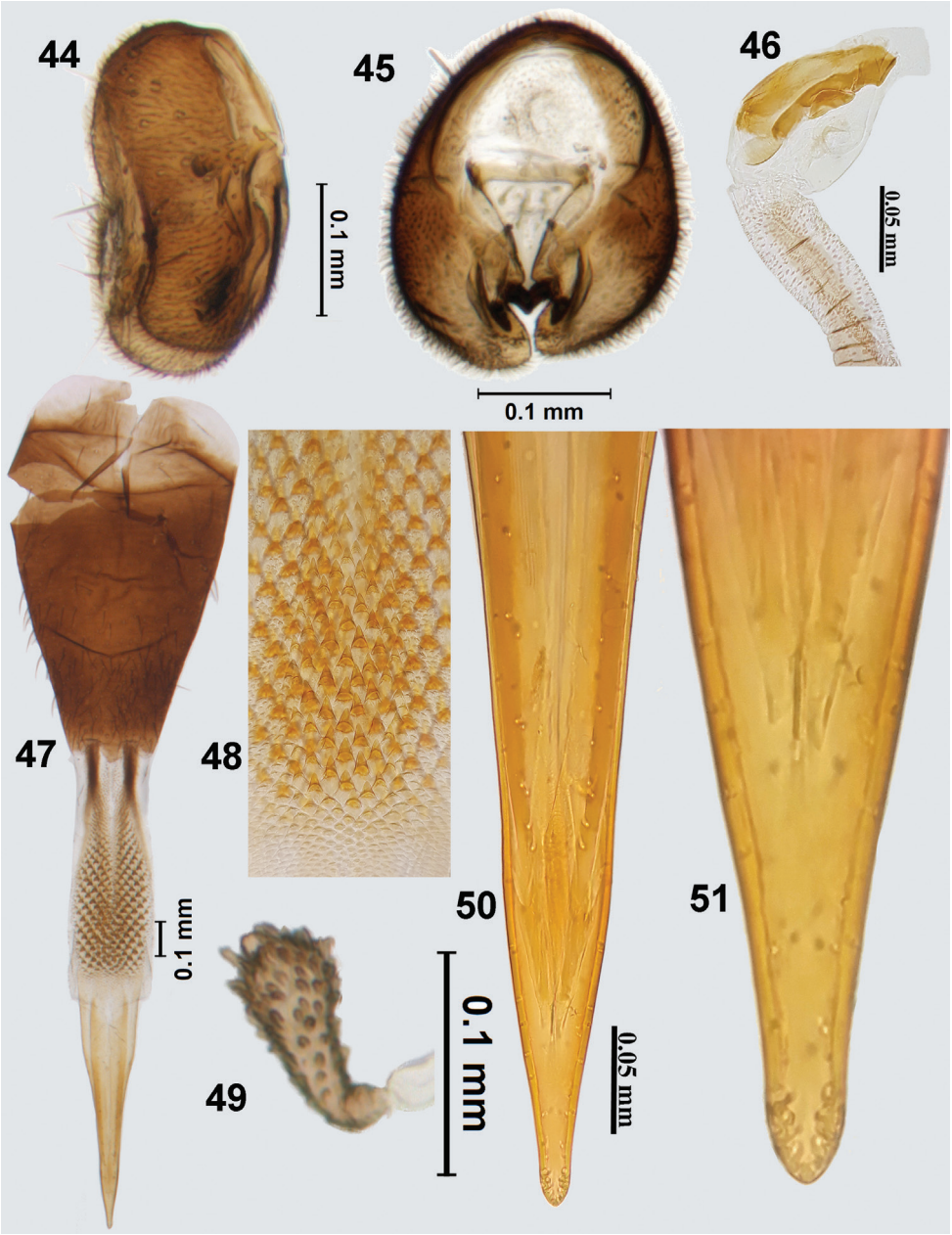
Tephritis zodiacalis Bezzi, 1913: 163. Type locality Calcutta [Kolkata], India.
Platensina zodiakalis: Hering 1956: 69. Lapsus calami.
Platensina zodiacalis: Hendel 1915: 461.

Material examined. India: 1♂, Karnataka, Madikeri, Chettalli, 05.xi.2012, David K.J. "leg"; 1♀, Assam, Dibrugarh, 07.xi.2014, Ramesh Kumar A. "leg"; 1♂, Karnataka, Kidu, CPCRI, 19.ii. 2015, David K.J. "leg"; 1♂, Karnataka, Chettalli, C.H.E.S, 03.ii.2021, David K.J. "leg"; 1♂, Assam, Barpeta, K.V.K, 09.iii.2021, Sachin K. "leg"; 1♂, Assam, Barpeta, K.V.K, 10.iii.2021, David. K.J. "leg"; 1♀, Assam, Chirang, K.V.K, 13.iii.2021, Sachin K. "leg"; 1♂, Assam, Golpara, 14.iii.2021, Rabbani M.K. "leg" (NIM).

Diagnosis. This species was adequately described by Bezzi (1913) except for the postabdominal structures. It is almost inseparable from *P. platyptera* except for the presence of only basal scutellar setae instead of both apical and basal setae as in *P. platyptera* (Figs 42, 43).



Figures 42–43. *Platensina zodiacalis* (Bezzi) **42** habitus (dorsal) **43** habitus (lateral).



Figures 44–51. *Platensina zodiacalis* (Bezzi) **44** epandrium (lateral) **45** epandrium (posterior view) **46** glans of phallus **47** ovipositor **48** spicules on eversible membrane **49** spermatheca **50** aculeus **51** aculeus tip (100×).

Male genitalia. Epandrium (Fig. 44) brown, sclerotised, with no demarcation from lateral surstylus (in profile view); epandrium and surstyli oval in posterior view, with well-developed prensisetae (Fig. 45). Phallus 1.39 mm long including glans; glans stout, with broad sclerotised rod (Fig. 46).

Female genitalia. Oviscape 0.92 mm long, dark brown, conical, dorsoventrally flattened (Fig. 47); eversible membrane 0.72 mm long, shorter than oviscape, with conical spicules along entire length except for a few rows of flattened ones distally (Fig. 48); taeniae short, dark brown, 0.25 length of eversible membrane. Aculeus shorter than eversible membrane, 0.63 mm long, dorsoventrally flattened; apex of aculeus rounded (Figs 50, 51). Spermatheca brown, club-shaped, with numerous papillae (Fig. 49).

Distribution. This species is widespread from India (Karnataka, Assam) and Sri Lanka to southern China and Australia (Hancock 2012).

Evolutionary divergence among the Indian species of *Platensina*

Table 1 shows the pair-wise evolutionary divergence/distance between four sequences available in NCBI database for three species namely *P. acrostacta*, *P. platyptera* and *P. flavistigma*. Evolutionary distance between *P. flavistigma* David & Hancock, sp. nov. and *P. acrostacta* is 0.0429 and between *P. flavistigma* and *P. platyptera* is 0.0759 which reveals that *P. flavistigma* is a distinct species in *Platensina* based on the available sequences. Among the species included in the analysis, evolutionary distance between *P. platyptera* and *P. acrostacta* was the highest (0.0837), which is evident in the morphological differences between these two species with respect to facial markings and wing pattern.

Table 1. Evolutionary divergence among the Indian species of *Platensina*.

Species name with accession numbers	*P. acrostacta* (MH748566)	*P. platyptera* (MW448367)	*P. flavistigma* (MT019893)	*P. acrostacta* (MT019891)
P. acrostacta (MH748566)				
P. platyptera (MW448367)	0.0837			
P. flavistigma (MT019893)	0.0429	0.0759		
P. acrostacta (MT019891)	0.0036	0.0882	0.0470	0.0000

Acknowledgements

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An update to the 2014 nomenclator of Valvatidae

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Abstract

This contribution is an update to the 2014 compilation of all supra- and (infra-) specific taxa of extant and fossil Valvatidae, a group of freshwater operculate snails near the base of Heterobranchia with a nearly worldwide distribution. This update includes corrections and many additions (two replacement taxon names, 21 mainly fossil taxa previously overlooked, and 37 invalid names) to the 2014 contribution and adds all newly described species (11) during the past eight years. The extensive reference list is directly linked, where possible, to the available electronic source of the cited papers.

Keywords

freshwater snails, Gastropoda, taxonomy, Valvatidae

Introduction

My compilation of all taxa of extant and fossil valvatid gastropods (Haszprunar 2014) has been positively received by the scientific community and was followed by similar taxonomic work on other important groups of freshwater gastropods such as Neubauer (2016) for Melanopsidae or Neiber and Glaubrecht (2019) for Paludomidae. My work inspired and facilitated several recent papers on the taxonomy of Valvatidae. In particular, Russian authors cleared up the status of many uncertain taxa and provided valuable data and high-quality images of type material (e.g., Sitnikova et al. 2015, 2017; Vinarski 2016; Sitnikova 2018; Shirokaya et al. 2019; Andreeva et al. 2021; Osipova et al. 2021).

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In contrast, the paleontological analysis of Valvatidae (and other taxa with similar shell morphologies) is still hampered by the unavailability of key literature. Many important and also quite recent taxonomic papers on fossil taxa have been written in non-Roman alphabets and often are not available as a digitized version. Thanks to the kindness of several colleagues, I could access some of the most important papers in particular by Russian or Chinese authorities, and the results of checking the original descriptions and their circumstances are compiled and reviewed herein.

Whereas there is constant progress in detecting and describing new valvatid species, concerning both fossil and extant taxa (Table 1), our understanding of species delimitation in Valvatidae generally is still limited. Also, a robust phylogeny of the family is still in its infancy, since only a few papers have provided molecular data on valvatids (e.g., Hauswald et al. 2008; Clewing et al. 2014; Saito et al. 2018; Falniowski et al. 2021). In particular, the seemingly well-known and widely distributed *Valvata piscinalis* (O.F. Müller, 1774) is likely to represent a species complex spread all over the Palaearctic and (by introduction) also the Nearctic region.

As a result, there have not been any recent proposals of new genera or further revisions to the supraspecific classification. Accordingly, this update is limited to the species level. The present update adds two extant and nine fossil species recently described, two replacement taxon names, another 21 mainly fossil taxa previously overlooked, and nearly 40 names based on confusions, misspellings, or invalid publications (Table 1). In addition, numerous data on type localities or type material or sequence information are provided.

Table 1. List of new names (alphabetically arranged) since publishing of the nomenclator (Haszprunar 2014).

(1) Newly described taxa:

Valvata (*Tropidina*) *armeniaca* Walther & Glöer, 2019

† *Valvata ducati* Esu & Girotti, 2015

† *Valvata jiaolaiensis* Yu, Salvador, Wang, Fang, Neubauer, Li, Zhang, Wan, 2021

Valvata (*Tropidina*) *kebapcii* Odabaşi, Glöer & Yildirim, 2015

† *Valvata koehleri* Harzhauser, Neubauer & Hosgör, 2018

Valvata kournasi Glöer & Hirschfelder, 2019

† *Provalvata maior* Cataldo, Lazo, Luci & Aguirre-Urreta, 2019

† *Valvata mathiasi* Esu & Girotti, 2018

† *Provalvata minor* Cataldo, Lazo, Luci & Aguirre-Urreta, 2019

† *Valvata pyramidula* Esu & Girotti, 2015

† *Valvata heidemariae willmanni* Neubauer, Harzhauser, Kroh, Georgopoulou & Mandic, 2014

(2) Previously overlooked taxa:

† *Valvata alta* K.A. Ali-Zade, 1932

† *Valvata andrussovi* A.A. Ali-Zade, 1967

† *Valvata* (*Cincinna*) *arnaudi* Repelin, 1902

† *Paludina avia* Eichwald, 1853

† *Valvata balchanica* A.A. Ali-Zade, 1967

Valvata piscinalis var. *cancellata* Baudon, 1884

Valvata bicarinata var. *connectans* Walker, 1906

† *Valvata cosinensis* Stache, 1889

† *Valvata egregia* Noulet, 1857

† *Valvata faujasii* Dumas, 1876

† *Valvata vanciana* var. *kubanica* Krestovnikov, 1931

† *Valvata* (*Valvata*) *platispira* Szőts, 1953

† *Valvata polita* A.A. Ali-Zade, 1973

† *Valvata* (*Cincinna*) *pontica* Pană, 1990

† *Valvata* (*Borysthenia*) *pronaticina* Lindholm, 1932

† *Valvata* (*Cincinna*) *rakovetzae* Popova & Starobogatov, 1970

† *Valvata* (*Cincinna*) *splendida* Szőts, 1953

† *Valvata tanaiticus* Sanco, 2007

† *Valvata turbinata* Stache, 1889

† *Valvata turbinoides* K.A. Ali-Zade, 1936

† *Valvata uralica* Popov, 1965

(3) Other names that are not valid or available:

"*Valvata baikalensis*" [*Valvata baicalensis*]

"*Valvata californiensis* Mss." [nomen nudum]

"*Cincinna* (*Sibirovalvata*) *chankensis* Prozorova, 1988" [*Cincinna* (*Sibirovalvata*) *hankensis*]

† "*Valvata unicarinifera chiknaformis*" [invalidly published]

† "*Valvata* (*Cincinna*) *circinata* (Greppin, 1855)" [*Paludina circinata* Greppin, 1855; non *Valvata circinata* Sandberger, 1871]

† "*Valvata piscinalis* var. *cistopolitana* G.I. Popov" [nomen nudum]

"*Valvata cupensis*" [*Valvata kupensis*]

† "*Valvata densistriata*" [*Valvata densestriata*]

"*Valvata bicarinata depressa* Walker" [*Valvata biarinata perdepressa* Walker, 1906]

"*Valvata euzonia* Ziegler" [trade name]

† "*Valvata* (*Cincinna*) *fuiensis*" [†*Valvata* (*Cincinna*) *fuxinensis* Yü, 1987]

"*V.* [i.e., *Valvata*] *impressa*" [*Valvata depressa*]

† "*Valvata* (*Cincinna*) *joncheryacensis* Wenz, 1923" [*Valvata joncheryensis* Wenz, 1930]

"*Valvata* (*Cincinna*) *aliena* var. *korotnewi* Ldh. 1909" [*Valvata korotnevi* Lindholm, 1909]

"*Valvata kurensis*" [*Valvata kupensis* Fuchs, 1870]

"*Valvata lanta*" [*Valvata lauta* Lindholm, 1909]

"*Valvata luguensis*" [nomen nudum]

† "*Valvata* (*Cincinna*) *mengyinensis* (Grabau)" [†*Bithynia mengyinensis* X *Valvata suturensis*]

"*Valvata montenegrinus* Glöer & Pešić, 2008" [*Valvata montenegrina*]

† "*Valvata nikosi*" [*Pyrgula nikosi* Esu & Girotti, 2015]

† "*Valvata cristata palustris* Kormos" [*Valvata cristata* X *Stagnicola palustris*]

† "*Valvata cristata pslustris*" [*Stagnicola palustris* (O.F. Müller, 1774)]

"*Costovalvata pulchra*" [nomen nudum]
"*Valvata pygrncea*" [*Valvata pygmaea*]
† "*Valvata* (*Cincinna*) *rakovetzae*" [† *Valvata* (*Cincinna*) *racovetzae* Popova & Starobogatov, 1970]
"*Valvata skniadica*" [†*Valvata* (*Aphanotylus*) *skhiadica*]
"*Valvata radiatula subnaticina*" [*Valvata subnaticina* Łomnicki, 1886]
"*Valvata cristata* monstr. *subscalaris*" [monstrosity]
"*Valvata theotokii*" [*Valvata theodokii*]
"*Liratina tongbinzhenensis*" [nomen nudum]
† "*Valvata turkmena*" [*Pyrgula turkmena* Ali-Zade, 1967]
"*Valvata piscinalis* (Müll.) var. *uistopolitana* Pop." [*Valvata cistopolitana*]
† "*Planorbis symmetricus* Ludwig, 1865" [*Planorbis symmetrus* Ludwig, 1865]
† "*Valvata unicarinifera unicarinifera*" [invalidly published]
"*Valvata vaciani* Nourn." [*Valvata vanciana* Tournouër, 1875]
"*Valvata venciana*" [*Valvata vanciana* Tournouër, 1875]
"*Cincinna* (*Cincinna*) *vinogradovkensis*" [*Valvata vinogradokaensis* (Gozhik, 2002)]

General remarks

As in the previous work (Haszprunar 2014) all taxa (species, subspecies, named varieties) are listed alphabetically in their original version (only the spelling may be corrected according to the actual ICZN rules) regardless of validity, current taxonomic status, and synonymy. It is followed by either the citation to the page in my 2014 publication or indicated as a name newly treated herein. I also add available data sources (type material, anatomy, molecular data), which may be useful for future species delineation.

Two Ph.D. theses are discussed, since they contain the description of new taxa of Valvatidae (and of several other families): Bingle-Davis (2012) (University of North Dakota, U.S.A.) and Siodiropoúlou (2003) (Aristotle University of Thessaloniki, Greece). Both theses do not satisfy the criteria for publication of the International Code of Zoological Nomenclature, Articles 8.1 and 8.6. Students and faculty advisors should ensure that Ph.D. theses do not include proposed new taxa, except as, e.g., "Species A" so that these manuscript names will not enter the taxonomic literature and databases.

A widely cited Chinese-language work, "Youlou 1978" is particularly problematic. Previous authors, myself included, did not realize that this name actually means "Editors" or "Editorial Board" in Chinese, and no individuals are identified as the authors of either this publication or specific sections of this publication. I was uncertain about the true authorship of the very many taxon names of fossil gastropods introduced in this work. Indeed, the authorship "Youluo" appeared in all cases in the online type catalogue of the Nanjing Institute as well as in the Zoological Record, and has been repeatedly cited by later authors. Meanwhile I was able to check the original paper and can confirm the term "Youluo" as the true (i.e., printed in this way) authority in all cases [checked by a native Chinese colleague]. Most important, the actual names of

any member of this group are not provided anywhere in this volume. However, ICZN Art. 14 clearly states that "A new name or nomenclatural act published after 1950 with anonymous authorship [Art. 50.1] is not thereby made available". Accordingly, all species names (more than 120 new taxa!) as well as higher taxa (e.g., family Bohaispiridae and many hydrobiid genera; see Kabat and Hershler 1993) being introduced in this work are not available from there, but may have become available later by other authorities, if they clearly refer to the reference with an image of specimens or a diagnosis of the species. Among the Valvatidae they are listed in alphabetic order below and the names are marked as fossil taxa by "†":

† *Valvata* (*Cincinna*) *applanata* Zhu X., 1995
† "*Liratina basicarinata*"
† "*Tropidina bellireticulata*"
† "*Liratina fahaniuensis*"
† "*Liratina hedobia*"
† "*Aphanotylus humeratus*"
† "*Valvata magniumbilicata*"
† "*Costovalvata minuta*"
† "*Valvata* (*Atropidina*) *pileiformis*"
† "*Liratina qikouensis*"
† "*Valvata* (*Cincinna*) *rehetaiensis*" → *Valvata rehetaiensis* Zhu G.-X., 1980
† "*Valvata ringentis*"
† "*Liratina tuozhuangensis*"
† "*Valvata zhouqingzhuangensis*"

Details on these names are outlined below under each name.

Update of species names

The page number for the taxon name in my previous work (Nomenclator of Valvatidae: Haszprunar 2014) is given in parentheses as (Nom: ##).

Valvata aliena C.A. Westerlund, 1877 (Nom: 16)

Remarks: Sitnikova et al. (2015: 3–4, fig. 1B) provided a photo of the lectotype and from specimens of several localities as well as an extensive and annotated citation record in the Russian literature. Andreeva et al. (2021: fig. 1A) added excellent photos from specimens of the Taz River basin (western Siberia).

Valvata alpestris Küster, 1853 (Nom: 16)

Type locality: "in kleinen Seeen an der Quelle des Giessbaches ohnweit des Faulhorns bei Grindelwald" (Küster 1853: 87). According to current maps this is probably the "Schwarzseeli" near the Faulhorn at Grindelwald, Switzerland.

Types are figured by Boeters and Falkner (1998, not 2002 as stated).

† ***Valvata alta*** K.A. Ali-Zade, 1932 (NEW)

Original source: K.A. Ali-Zade 1932: 21, pl. 2: figs 12–14 (not seen, but according to Ali-Zade 1936: 17).

Type locality: near Naftalan, Azerbaijan.

Type horizon: Akchagylian, Upper Pliocene or Lower Pleistocene.

Remarks: Junior homonym of *Valvata alta* Deshayes, 1867, replaced by *Valvata turbinoides* K.A. Ali-Zade, 1936 (p. 17, pl. 1: figs 28–30).

† ***Valvata* (*Cincinna*) *altaica*** Popova & Starobogatov (in Popova, Devyatkin & Starobogatov, 1970) [not 1981 as stated in Haszprunar 2014] (Nom: 17)

Original source: Popova et al. 1970: 25, pl. 1: fig 2, pl. 2: figs 13, 14.

Type locality: Chuya Basin, left bank of the Chuya River, not located in Irkutsk Region as indicated in Haszprunar (2014), but in the southeastern part of Altai Mountains, Russia.

Type material: Holotype deposited in the Zoological Institute, of the Russian Academy of Sciences, St. Petersburg (No. ZIN 1/533-1968).

Remarks: Unfortunately this fossil species was omitted from the recent review of taxa created by Starobogatov (Sitnikova et al. 2017).

Cincinna* (*Sibirovalvata*) *amurensis Moskvicheva, 1985 (in Starobogatov & Zatravkin, 1985) (Nom: 17)

Type material: Holotype deposited in the Zoological Institute of the Russian Academy of Sciences, St. Petersburg (No. ZIN 1/405-1973).

Remarks: Saito et al. (2018) provided molecular data from specimens from Vladimiro-Petrovka (near southwest border of Khanka Lake), Primorsky region, Russia.

†***Valvata andreaei*** Menzel, 1904 (Nom: 18)

Type horizon: Quaternary.

Type material: not designated as such, but a sample with more than 20 specimens collected 1903 from the type localities (Alfeld an der Leine and Wallensen, Niedersachsen, Germany) with the original label stating "Zwergform von *piscinalis*" is stored in the Geozentrum Hannover (originally from Geowissenschaftliche Sammlungen Berlin, BGR) under BGR-B-STGR-000032180 (Alfeld) and BGR-B-STGR-000032693 (Wallensen).

"***Valvata andrezowski***" (GNI, GBIF) (Nom: 18)

Remarks: I reported about a label with this name in the Academy of Natural Sciences of Drexel University (Philadelphia). According to Bram van der Bijl (pers. comm. email 06 Feb 2014) the collection of the Biodiversity Center Naturalis (Leiden, Netherlands) holds a sample with a similar label.

† ***Valvata andrussovi*** A.A. Ali-Zade, 1967 (NEW)

Original source: A.A. Ali-Zade 1967: 224–225, pl. 84: figs 5, 6.

Type locality: Maly Balkhan, northwest Turkmenistan.

Type horizon: Upper Akchagylian, Lower Pleistocene.

Type material: Dr Pavel Frolov (pers. comm. via Dr. Paval Kijashko, 22 Feb 2022) said that the fossil molluscs described by A.A. Ali-Zade in 1967 are all stored in the Museum of Earth Sciences of Moscow State University (MES MSU).

Remarks: not treated in the last 50 years.

† ***Amplovalvata suturalis anjipingensis*** Yü, 1980 (in Yü & Pan, 1980) (Nom: 18)

Original source: Yü and Pan 1980: 149, pl. 3: figs 1, 2.

† ***Amplovalvata antiqua*** Pan, 1980 (in Yü & Pan, 1980) (Nom: 19)

Original source: Yü and Pan 1980: 148, pl. 2: figs 21–24.

† ***Valvata* (*Cincinna*) *applanata*** Zhu X., 1995 (Nom: 20)

Original source: Zhu X. 1995: 79, pl. 22: 1–14, pl. 23: 9–12. Directly referred to Youluo 1978 (not available from there; see above).

Type locality: Qinghai Goulucuonan.

Type horizon: Cenozoic.

Type series: Nanjing Institute of Geology and Paleontology, Samples ## 118778-118786 and ## 118794-118797 (13 specimens).

Valvata arenifera Lea, 1834 (Nom: 20)

Remarks: The history of misidentifications and nomenclature of this trichopteran insect with figures of the original description and with further links was presented by Lee (2015).

Valvata* (*Tropidina*) *armeniaca Walther & Glöer, 2019 (NEW)

Original source: Walther and Glöer 2019: 1–5: fig. 2 (1–3 shell of holotype, 9 and 10 shell of paratype), fig. 3 (environment of type locality).

Type locality: Armenia, Armavir Province, bridge over river Kasakh, 1.6 km W of Vagharshapat, 40.1650°N, 44.2558°E, 870 m asl, 27 Aug. 2018, F. Walther leg.

Type material: Holotype: Shell height 1.5 mm, width 2.5 mm, from type locality (Zoological Museum Hamburg ZMH 59491); Paratypes: from type locality (ZMH 59492, 3 specimens in ethanol); from type locality (F. Walther 13603; 1 dry shell); Ararat Province, Jrahovit, ditch S of the cemetery, 40.0450°N, 44.4880°E, 850 m asl., 26 Aug. 2018, leg. F. Walther (FW 14008, 1 specimen in ethanol).

† ***Valvata* (*Cincinna*) *arnaudi*** Repelin, 1902 (NEW)

Original source: Repelin 1902: 90, pl. 5: figs 40–42.

Type locality: Simeyroles, Département Dordogne in Nouvelle-Aquitaine, south France.

Type horizon: Cenomanian, Lowest Upper Cretaceous.

Type material: described from the collection Matheron, Museum nationale d´Histoire naturelle (MNHN), Paris.

† ***Valvata* (*Cincinna*) *austrina*** Pan, 1977 (Nom: 20)

Type locality: YH 5054-8-1, Mimalong, Lufeng County, Yunnan Province, China.

Type horizon: Fluvial-lacustrine horizon in the Zhanghe Formation, Bajocian, Jurassic.

Type material: Holotype at Nanjing Institute of Geology and Paleontology #24250.

† ***Paludina avia*** Eichwald, 1851 (NEW)

Original source: Eichwald 1851: 136, pl. 10: fig. 28a–c; reprinted in Eichwald 1852: pl. 10: fig. 28a–c (atlas) and Eichwald 1853: 288 (text). Nosowska (2020: 455) recently outlined that the names of all illustrations of Eichwald (1852, 1853) had been made available in 1851 in a Russian version with valid descriptions and an identical atlas. Until this paper all authors did not realize that the 1851 publication was a book on its own due to the identical plate numbering (this book is nearly unknown in European libraries). The year 1859 on the cover of the atlas being digitized at the Biodiversity Heritage Library (see references) and cited by Janssen (1984) obviously concerns a later edition.

Type locality: near Kuncza (today Kuncha, region of Khmelnytskyi/ Chmelnyzkyj), Ukraine.

Type horizon: Neogene (details not provided).

Remarks: Frauenfeld (1864: 576) regarded this species as belonging to *Hydrobia*, but later it was considered to belong to *Amnicola*. Recently, however, it has been listed as "*Valvata avia* (Eichwald, 1853)" by Neubauer et al. (2014c: Supplement 1). "*Paludina* cf. *avia* Eichw." was found by Stiny (1924) in Tertiary layers at several locations near Feldbach in Styria (Austria).

Valvata baicalensis Gerstfeldt, 1859 (Nom: 21)

Remarks: Sitnikova (1991: 64–65, fig. 4) described and figured the egg capsules. Saito et al. (2018) provided molecular data from specimens from the type locality, Lake Baikal (Listvyanka), Russia. Sitnikova (2018: fig. 6A) illustrated the lectotype.

"***Valvata baikalensis***" mentioned in Bogachev (1961: 152) (NEW)

Remarks: misspelling of *Valvata baicalensis* Gerstfeldt, 1859.

† ***Valvata balchanica*** A.A. Ali-Zade, 1967 (NEW)

Original source: A.A. Ali-Zade 1967: 224, pl. 84: figs 1–4.

Type locality: Maly Balkhan, northwest Turkmenistan.

Type horizon: Akchagylian, Upper Pliocene to Lower Pleistocene.

Type material: Dr Pavel Frolov (pers. comm. via Dr. Paval Kijashko, 22 Feb 2022) stated that the fossil molluscs described by A.A. Ali-Zade in 1967 were all stored in the Museum of Earth Sciences of Moscow State University (MES MSU).

Remarks: not treated in the last 50 years.

† "***Liratina basicarinata***" mentioned in Youluo 1978 (Nom: 22)

Remarks: Not available from there (see above). I could not find a subsequent full reference on this species.

Valvata bathybia W. Dybowski, 1886 (Nom: 22)

Remarks: Type material unknown. Sitnikova (2018: fig. 2B) figured a topotype and further specimens from various localities from Lake Baikal.

† "***Tropidina ? bellireticulata***" mentioned in Youluo (1978) (Nom: 23)

Remarks: Not available from there (see above) or from Ye et al. (1996: 37; nomen nudum, no reference). I could not find a subsequent full reference on this species that would validate the name.

Valvata beltrani Contreras-Arquieta, 1993 (Nom: 23)

Remarks: Contreras-Balderas and Lozano-Vilano (1996) reported that this species, which lived in isolated springs in North Mexico, had become extinct at the time of discovery by the drying of the springs due to agricultural needs.

† ***Valvata beysehirensis*** Glöer & Girod, 2013 (Nom: 23)

Type material: Holotype deposited in Zoological Museum Hamburg (ZMH 79381). Paratypes: 3 shells in Museo Civico di Storia Naturale, Milano, Italy (MSNM Mo-36591), numerous shells in the collection of Alberto Girod (AGMal 3595), 3 shells in collection Glöer (Hettlingen, Germany).

† "***Valvata heidemariae bicarinata*** Willmann, 1981" (Nom: 24)

Type material: According to Neubauer et al. (2014b: 22) deposited in the Geological-Paleontological Institute, University of Kiel, no number indicated.

Remarks: As outlined, the name is a junior homonym of *Valvata bicarinata* Lea 1841. Accordingly, the species has been renamed as *Valvata heidemariae willmanni* Neubauer, Harzhauser, Kroh, Georgopoulou & Mandic, 2014.

Valvata* (*Cincinna*) *biwaensis Preston, 1916 (Nom: 25)

Remarks: Saito et al. (2018) provided molecular data from specimens from the type locality, Lake Biwa, Japan.

Valvata* (*Cincinna*) *brandti Westerlund, 1897 (Nom: 26)

Type material: Walther and Glöer (2019: 4) checked the taxonomy of the species and although they did not have contact to type material, they concluded that "The original description of *V. brandti* is based on two lots. One was collected by A. Brandt in Lake Sevan, while the other was found by L. Młokosiewicz near Lagodekhi in Georgia. Between both localities is a distance of more than 150 km. The Lagodekhi record belongs to *Caspicyclotus sieversi* .... (Cyclophoridae)…..The other lot, however, seems to belong to *Valvata piscinalis*, which is known to occur in Lake Sevan (e.g., Mashkova et al. 2018)".

Dr Pavel Kaijashko (pers. comm. 22 Feb 2022) provided the following additional valuable information: "Indeed, the original description of *V. brandti* is based on two lots … [mentioned by Walther and Glöer (2019)]. In 1912 W. Lindholm [Lindholm 1912] redefined the Lagodekhi finds and placed them to *Cyclotus sieversi*

(now *Caspicyclotus sieversi*). The other lot he attributed to the genus *Valvata*. There is a handwritten entry by W. Lindholm in the ZIN RAS catalogue about this. The specimens of *V. brandti* collected by A. Brandt are poorly preserved. Nevertheless, their conchological features (shell size, shape and sculpture of the whorls, diameter of the umbilicus) indicate belonging to *Valvata* (*Tropidina*), but not to *V. piscinalis*."

Valvata* (*Cincinna*) *aliena* var. *brevicula Kozhov, 1936 (Nom: 26)

Type material: Sitnikova et al. (2004) designated a lectotype, which was later illustrated by Sitnikova et al. (2015: fig. 1D). However, Vinarski and Kantor (2016: 274) reported that only syntypes but no lectotype could be found at the Zoological Institute, Academy of Sciences, St. Petersburg (ZIN). Thus, it remains unclear whether or not the designated lectotype has been lost.

Remarks: Clewing et al. (2014, supplementary material) provided molecular data (as RU05/1). Sitnikova et al. (2015: 13–15) provided photographs of specimens from several localities as well as an extensive and annotated citation record in particular of the Russian literature. Recently, Andreeva et al. (2021: fig. 3B) added excellent photographs from specimens of the Taz River basin (western Siberia).

"***Valvata californiensis*** Mss." [manuscript] mentioned in Schmeltz (1869, IV: 75) (NEW)

Remarks: A nomen nudum like many other similar cases in the catalogue of the Godeffroy Museum (Bieler and Petit 2012: 46; #5353). Interestingly, a specimen with this name and "from California" was offered ten years later for 30 Pfennig in the "Tausch-Catalog" of the Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft (1879, Vol. 11: 102).

Valvata piscinalis* var. *cancellata Baudon, 1884 (NEW)

Original source: Baudon 1884: 293, pl. 10: fig. 5.

Type locality: Département de l Oise, France.

† ***Valvata cangshanensis*** Pan, 1982 (Nom: 28)

Original source: Pan 1982: 430–431, pl. 1: figs 24–27.

† "***Valvata carinata*** Fuchs, 1870" (Nom: 28–29)

Remarks: As stated in Haszprunar (2014), a junior homonym of *Valvata carinata* Sowerby, 1834. Accordingly, the name has been meanwhile replaced by Neubauer et al. (2014a) by *Muellerpalia pseudovalvatoides* Neubauer, Harzhauser, Kroh, Georgopoulou & Mandic, 2014 (Hydrobiidae).

"***Cincinna* (*Sibirovalvata*) *chankensis*** Prozorova, 1988" (NEW)

mentioned in Prozorova 1992: 106–107 (fig. 8 legend).

Remarks: Misspelling of *Cincinna* (*Sibirovalvata*) *hankensis* Prozorova, 1988.

Cincinna chersonica Chernogorenko & Starobogatov, 1987 (Nom: 29)

Type material: Vinarski and Kantor (2016: 270) stated that the "holotype" in the Zoological Institute of the Russian Academy of Sciences, St. Petersburg (ZIN 1/41-1974) mentioned by Kantor et al. (2011: 66) is in fact a paratype and that the holotype is missing.

† "***Valvata unicarinifera chiknaformis***" (NEW)

mentioned in Bingle-Davis (2012: 104)

Horizon: Upper Cretaceous.

Locality: near the villages of Butera and Machhaghoda (Chhindwara District: Madhya Pradesh) ca. 160 km north of Nagpur (22.11 N, 79.14 E), eastern Dekkan Plateau, India.

Material: "Holotype": InS1199 (Appendix 2 (Nom: 137), fig. N; 6.8 mm × 7.6 mm), deposited at University of North Dakota, Grand Forks, North Dakota, USA.

Remarks: This subspecies name was mentioned in an unpublished PhD thesis (no ISBN or ISSN numbering) and thus is not formally described as required by ICZN Art. 8.1.3 and 8.6.

† "***Valvata* (*Cincinna*)**" ***circinata*** (Greppin, 1855) mentioned in Wenz (1928: 2427) (NEW / Nom. 30)

Original source: Greppin 1855: 29, 71, pl. 3: fig. 11a–c (as *Paludina circinata*)

Type locality: Limestone banks von Sornetan and Tramelan, Val de Délemont/ Bezirk Delsberg, Kanton Jura, Switzerland.

Type horizon: Lower to middle Miocene.

Remarks: Referred to Merian (1849: 34, mentioned there as *Paludina circinata*, a nomen nudum). ICZN Art. 50.1.1. states clearly that "If the identity of that other person is not explicit in the work itself, then the author is deemed to be the person who publishes the work", making Greppin the author of *Paludina circinata*. However, contrary to the classification by Wenz (1928: 2427) this taxon with an extended large whorl and a broad apertural lip is certainly not a valvatid, but much more likely a *Lithoglyphus*. It is also not identical to those specimens from a nearby locality, which are illustrated and described by Sandberger (1870–1875: 324, pl. 18: fig. 5a–c) as *Valvata circinata* (and also referred to Merian). Accordingly, both *Paludina circinata* Greppin, 1855 and *Valvata circinata* Sandberger, 1871 remain valid taxa.

† "***Valvata piscinalis* var. *cistopolitana*** G.I. Popov" (NEW)

cited as "*cistopolitana* nov.", a nomen nudum in Goretsky (1964: 55) and secondarily by Balabanov et al. (2010: 196).

Remarks: I could not find any trace of this name in the papers of G.I. Popov or in subsequent papers, accordingly a "taxon inquirendum", probably a nomen nudum, not available.

Valvata* (*Cincinna*) *confusa (Westerlund, 1879) (Nom: 31)

Remarks: Clewing et al. (2014: supplementary material) provided molecular data (as RU08/1). Saito et al. (2018) provided additional molecular data from specimens from Delga River, Khuvsgul, Mongolia. Andreeva et al. (2021: fig. 1B) added excellent photographs from specimens of the Taz River basin (western Siberia).

Valvata bicarinata* var. *connectans B. Walker, 1906 (NEW)

Original source: Walker 1906: 30 (not figured, described as unicarinate).

Type location: Lake Michigan, New Buffalo, Michigan, USA.

Type material: No. 24142 of coll. Walker (presumably now in University of Michigan Museum of Zoology). Alan Kabat (pers. comm. 30 Jan 2022) could not find it in the UMMZ database, but the sample may not yet be catalogued online.

Nerita contorta Müller, 1774 (Nom: 32)

Type material: Nekhaev et al. (2015) and Vinarski and Kantor (2016: 271) stated that they could not find type material in the Zoological Museum of Copenhagen, where Kantor et al. (2011: 66) had suggested it might exist.

† ***Valvata cosinensis*** Stache, 1889 (NEW)

Original source: Stache 1889: 117, pl. 2: fig. 26.

Type locality: In old coalmines, north of Cosina (today Hrpelje-Kozina) [5 km east of Trieste, Italy], Slovenia.

Type horizon: *Stomatopsis* horizon, Paleocene (see Jurkovšek et al. 2016: 358).

Remarks: Stache himself noted the high similarity with *Valvata pupoidea* Gould, 1961, currently considered as *Lyogyrus pupoideus* (Gould, 1841) (Amnicolidae).

"***Valvata cupensis***" mentioned in Bogachev (1961: 73) (NEW)

Remarks: misspelling of *Valvata kupensis* Fuchs, 1870.

† ***Aphanotylus dakangensis*** Pan, 1982 (Nom: 35)

Original source: Pan 1982: 432, pl. 2: figs 5–8.

† ***Valvata? dalaziensis*** Zhu G.-X., 1980 (Nom: 35)

Original source: Zhu 1980: 38, pl. 14: figs 24–26.

Type locality: Yanji, Jilin, Northeast [not northwest as stated in Haszprunar 2014] China.

Type horizon: Dalazi Formation, Lower Cretaceous.

† ***Valvata decollata*** Hislop, 1859 (Nom: 36)

Type horizon: Upper Cretaceous (not Tertiary as stated by Hislop).

Type material: Lectotype designated and figured by Hartman et al. (2008: fig. 18A–C), reprinted by Bingle-Davis (2012: 132), deposited under PIMG 1188 (Palaeo Invertebrate Mesozoic Gastropod) at the Natural History Museum of the United Kingdom (NHMUK), the original Latin description was translated to English.

† ***Amplovalvata deformis*** Pan, 1980 (in Yu & Pan, 1980) (Nom: 36)
Original source: Yu and Pan 1980: 149, pl. 2: figs 25, 26.

† ***Valvata*** (***Cincinna***) ***delaunayi*** Cossmann, 1907 (Nom: 36)
Type material: Museum national d´Histoire naturelle, Paris (MNHN F-J08320 (holotype) and F-J08321 (paratype).

Valvata (***Liratina***) ***baicalensis*** **var.** ***demersa*** Lindholm, 1909 (Nom: 37)
Remarks: Sitnikova (1991: 64, fig. 3) described and figured the egg capsules. Sitnikova (2018: fig. 6G) illustrated the lectotype and specimens from various localities in Lake Baikal (fig. 8A–F, H).

† "***Valvata densistriata***" mentioned in Henderson (1935: 296) (NEW)
Remarks: Misspelling of *Valvata densestriata* Pilsbry, 1934 (Nom: 37).

"***Valvata bicarinata depressa*** Walker" mentioned by Sterki (1907: 387) (NEW)
Remarks: Misspelling of *Valvata bicarinata perdepressa* Walker, 1906.

† ***Valvata*** (***Tropidina***) ***donghucensis*** Pan, 1977 (Nom: 38)
Type locality: YH 5033, Donghucun, Lufeng County, Yunnan, China.
Type horizon: Fengjiahe Formation, Jurassic (201.6 to 175.6 Mya).

† ***Valvata dromica*** Fontannes, 1881 (Nom. 39)
Remarks: Currently considered as *Pseudamnicola dromica* (Fontannes, 1881) (Hydrobiidae) (Neubauer et al. 2014c).

† ***Valvata ducati*** Esu & Girotti, 2015 (NEW)
Original source: Esu and Girotti 2015b: 151–152, figs 3–5. Previously mentioned and illustrated as "*Valvata* sp. nov." by Ciangherotti et al. (1997: 307, pl. 1: fig. 3).
Type locality: Stirone River section, between Laurano and San Nicomede, Emilia, northern Italy.
Type horizon: Lower Middle Pleistocene.
Type material: stored in Senckenberg Museum Frankfurt (Holotype SMF 345836, paratypes SMF 345837/2).

† ***Valvata egregia*** Noulet, 1857 (NEW)
Original source: Noulet 1857: 12 (no figure).
Type locality: Calcaire de Villeneuve-la-Comtal et du Mas-Saintes-Puelles (Département Aude), southwest France.
Type horizon: Upper Eocene.
Remarks: Currently considered as *Physotrema egregia* (Noulet, 1857), a terrestrial species of the architaenioglossan family Craspedopomatidae.

"***Valvata euzonia*** Ziegler" mentioned in Baudon (1884: 293) (NEW)

Remarks: one of the many unavailable names created by the Viennese shell dealer Franz Andreas Ziegler (see Rossmässler 1837: 32, legend to pl. 26: fig. 356, footnote; Schmidt 1846).

† ***Liratina fahaniuensis*** Zhu G.-X., 1980 [non Youluo 1978] (Nom: 41)

Original source: Zhu 1980: 39, pl. 19: fig. 4, referred to Youluo (1978).

Remarks: Not available from Youluo 1978 (see above), but Zhu (1980) fulfils all requirements of validation (description and figure).

Type locality: Xinmin, northeast China.

Type horizon: The lower part of the first section of the Eocene–Oligocene Shahejie Formation.

Cincinna falsifluviatilis Starobogatov in Anistratenko V.V. and Anistratenko O.Yu., 2001 (Nom: 41)

Original source: Anistratenko V.V. and Anistratenko O.Yu. 2001: 139–140, fig. 110 (as *Cincinna falsifluviatilis*; description by Starobogatov pro *Valvata fluviatilis* sensu Westerlund, 1886: 34 (actually, 134); non Colbeau, 1859) [see Sitnikova et al. (2017: 260)].

Type locality: The locality of the lectotype is unfortunately not provided by Vinarski and Kantor (2016: 268).

Type material: Lectotype in the Zoological Institute of the Russian Academy of Sciences, St. Petersburg (ZIN), #1 in the systematic catalogue under the name.

Remarks: Originally the name was erected to replace "*Valvata fluviatilis* sensu Westerlund, 1886". However, as outlined by Haszprunar (2014) a "sensu" name is not available, thus cannot be replaced. On the other hand, Vinarski and Kantor (2016: 268) recently found the original material of Westerlund mentioned by Anistratenko and Anistratenko (2001) and designated a lectotype. Accordingly, the requirements of ICZN Art. 16.4 are fulfilled to name this species.

† ***Valvata faujasii*** Dumas, 1876 (NEW)

Original source: Dumas 1876: 462, referred to: "Mém. De Faujas, etc. …., t. xiv, pl. 19: figs 13–17" (i.e., Faujas de Saint Fond 1809).

Type locality: coal mine near Saint-Paulet (de-Caisson), Départment du Gard, south France.

Type horizon: Paulétien, Upper Cretaceous.

Remarks: Faujas de Saint Fond (1809) did not provide a name. According to Repelin (1902: 89, as *V. faujasi*) the taxon is a junior synonym of *Valvata minuta* Draparnaud, 1805, currently considered as *Islamia minuta* (Draparnaud, 1805) (Hydrobiidae).

Valvata (***Tropidina***) ***fezi*** Altimira, 1960 (Nom: 42)

Remarks: Arconada and Ramos (2002) designated this hydrobiid species as the type species of their newly erected genus *Spathogyna* and provided SEM

photographs of the shell, protoconch, radula, and body surface as well as anatomical data.

Valvata frigida Westerlund, 1873 (Nom: 43)

Remarks: Andreeva et al. (2021: fig. 5B–D) added excellent photos from specimens of the Ratta river and Taz River basin (western Siberia).

† "***Valvata*** (***Cincinna***) ***fuiensis***" mentioned in Wan et al. (2013: 464) (NEW)

Remarks: Misspelling of *Valvata* (*Cincinna*) *fuxinensis*.

Valvata (***Cincinna***) ***gafurovi*** Izzatullaev, 1977 (Nom: 44)

Type material: Holotype and 1 paratype in the Zoological Institute of the Russian Academy of Sciences, St. Petersburg (ZIN), ##1, 2 in the systematic catalogue under the name. Nineteen further paratypes are listed by Vinarski and Kantor (2016: 271). Holotype figured by Shirokaya et al. (2019: fig. 13C).

Remarks: Sitnikova (1983) described in detail the reproductive system and placed the species in the subgenus *Pamirocincinna* Sitnikova & Starobogatov in Sitnikova, 1983. Shirokaya et al. (2019: 238) followed this replacement and provided a detailed bibliography of the species.

† "***Valvata antiqua*** **var.** ***gigas***" mentioned by Goretsky (1956a: 33) (Nom: 45)

Remarks: mentioned as "sp. nov.", but is a nomen nudum like several other species names in the same paper. Also mentioned some years later by Bogachev (1961: 85, 91, 93: *Valvata antiqua* - morpha *gigas*), again without any description or image.

"***Valvata*** (***Jekeliusiana***) ***oecsensis halavatsi*** Gozhik, 2002" (Nom: 49)

Type locality: in Ukraine.

Remarks: Neubauer et al. (2014b: 20) pointed out that the original name "*öcsensis*" (Soós, 1934: 189) was erroneously emended to "*oecsensis*". However, the correct emendation following ICZN rules is "*ocsensis*", since it is not derived from a German but a Hungarian expression (ICZN 32.5.2.1). Current status: *Valvata* (*Jekeliusiana*) *ocsensis halavatsi* Gozhik, 2002.

Cincinna (***Sibirovalvata***) ***hankensis*** Prozorova, 1988 (Nom: 49)

Original source: Prozorova 1988: 1936–1938, figs 1 (shell), 2 (spawn).

Type material: Holotype (ZIN 1/514-1986) and 6 paratypes (ZIN 2/514-1986) are deposited in the Zoological Institute of the Russian Academy of Sciences, St. Petersburg (ZIN).

† "***Liratina hedobia***" mentioned in Youluo 1978 (Nom: 50)

Remarks: Not available from there (see above) or from Ye et al. (1996: 48; misspelled as *Liratina* ? *helobia*; nomen nudum, no reference). I could not find a subsequent full reference on this species that would validate the name.

Valvata lewisi* var. *helicoidea Dall, 1905 (Nom: 50)

Remarks: Andreeva et al. (2021: 13, figs 1C, 2) confirmed the presence of this species in Siberia and added excellent photographs from specimens of the Taz River basin (western Siberia).

Valvata cristata hokkaidoensis Miyadi, 1935 (Nom: 52)

Remarks: Saito et al. (2018) provided molecular data from specimens from the type locality, Lake Toro, Hokkaido Prefecture, and from Doba River, Aomori Prefecture, Japan. These data suggest that this species name actually encompasses multiple species. A short live movie of this species by Akira Ooyagi is presented at www.youtube.com/watch?v=f6p3w4WWgG4.

† ***Valvata homalogyra*** Brusina, 1874 (Nom: 52)

Type material: According to Neubauer et al. (2016: 18, fig. 2A–C) "The syntype series includes 14 specimens [Croatian Natural History Museum in Zagreb] (NHMZ #1613 and NHMZ #1625.1–13) from Goručica SW Sinj (= Ruduša) described by Brusina (1874) but not illustrated due to bad preservation. Brusina (1897) subsequently illustrated only one specimen from Miočič. This misled Milan et al. (1974) to regard Miočič as the type locality and the specimen, which was available for the present study, as the "holotype" [fig. 2A–C]. Yet, surprisingly, the latter is apparently not even the specimen documented by Brusina (1897)".

Remarks: Brusina (1874: 90) himself regarded *Valvata homalogyra* as closely related to the extant *Valvata erythropomatia* Hauffen, 1856. As outlined (Haszprunar 2014: 39), the latter species became type of *Erythropomatiana* Radoman, 1978, a genus name currently considered as a junior synonym of *Hauffenia* Pollonera, 1898 (Hydrobiidae). Accordingly, it is also likely that *Valvata homalogyra* is in fact a hydrobiid.

† "***Aphanotylus humeratus***" mentioned in Youluo 1978 (Nom: 53)

Remarks: Not available from there (see above) or from Ye et al. (1996: 49; nomen nudum, no reference). I could not find a subsequent full reference on this species that would validate the name.

"***V.* [i.e., *Valvata*] *impressa***" (NEW) Mentioned by Bogachev (1961: 91) and as "*V. impressa* Pfeff." [Pfeffer?] by Goretsky (1964: 55) in the chapter Конхилиофауна кинельских отложений [Conchiliofauna of the Kinel-Lagerstätten] available at http://www.bibliotekar.ru/5-prareki-chetvertichnyi-period/7.htm

Remarks: I could not find any description of a "*Valvata impressa*". The malacologist Georg Pfeffer (1854–1931) did not describe any *Valvata* species. The name is likely a double misspelling of *Valvata depressa* Pfeiffer, 1821.

Valvata inconspicua C.B. Adams, 1851 (Nom. 55)

Remarks: currently considered as *Nanivitrea inconspicua* (C.B. Adams, 1851) (Cochliopidae) (Jaume and Abbott 1948).

† ***Borysthenia intermedia*** Konrashov, 2007 (Nom: 56)

Type material: Holotype deposited at Paleontological Institute, Russian Academy of Sciences (PIN) #5148/1.

† ***Borysthenia jalpuchense*** Gozhik, 2002 (Nom: 57)

Type locality: near Vinogradovka village, Odesa oblast, Bolhrads'kyi district, Ukraine.

Type horizon: Miocene, Middle Pontian.

Type material: Holotype (coll. Gozhik, #3162) figured by Osipova et al. (2021: fig. 3H).

Remarks: The species name should be *jalpuchensis*, since *Borysthenia* is feminine. Morphometric data of the shell compared with *Borysthenia menkeana* (Jelski, 1863) were provided by Osipova et al. (2021).

Valvata japonica Martens, 1877 (Nom: 57)

Type material: 1 syntype (of 2) from the Museum für Naturkunde, Berlin (ZSM # 38883 from the type locality, i.e., Hakone Lake) is figured by Vinarski (2016: 7, fig. 4E, F).

Remarks: Saito et al. (2018) provided molecular data of specimens from Doba River (Amori Prefecture) and Sagami-gawa River (Nagano Prefecture), Japan. These data suggest that this species name actually encompasses several biological species.

† ***Valvata jiaolaiensis*** Yu, Salvador, Wang, Fang, Neubauer, Li, Zhang & Wan, 2021 (NEW)

Original source: Yu et al. 2021: 5, fig. 3M–P.

Type locality. LK-1 borehole (36°15'55"N, 119°57'04"E), northern part of Jiaozhou City, Shandong Province, China.

Type horizon: Uppermost Cretaceous, Jiaozhou Formation; sample taken at a depth of 370.5 m.

Type material deposited in Nanjing Institute of Geology & Palaeontology: Holotype: NIGP #168642, paratype: NIGP #16864.

† ***Amplovalvata jingguensis*** Pan, 1977 (Nom: 57)

Original source: Pan 1977: 118, pl. 5: fig. 18.

Type locality: YHS492, Heping township, Jinggu County, Yunnan Province, China.

Type horizon: Bajocian/Bathonian fluvial-lacustrine horizon in the Hepingxiang Formation of China, Middle Jurassic (171.6–164.7 Mya).

Type material: Holotype deposited at Nanjing Institute of Geology & Paleontology NIGP #24247.

† "***Valvata* (*Cincinna*) *joncheryacensis*** Wenz, 1923" (NEW)

Mentioned in Le Renard and Pacaud (1995: 98) and in Worldwide Mollusc Species Data Base (WMSDB).

Remarks: Misspelling of †*Valvata joncheryensis* Wenz, 1930. Wenz (1923) only included pulmonate species.

† ***Aphanotylus jurassicus*** Pan, 1980 (in Yü & Pan, 1980) (Nom: 58)
Original source: Yü and Pan 1980: 150, pl. 3: figs 15, 16.

Cincinna kamchatica Prozorova & Starobogatov, 1998 (Nom. 58)
Type material: Holotype (ZIN 1/97-1911) and 21 paratypes (ZIN 2/97-911) in Zoological Institute of the Russian Academy of Sciences, St. Petersburg (ZIN).

† ***Valvata* (*Mesovalvata*) *karameilica*** Wei, 1984 (Nom: 58)
Original source: Wei in Xinjiang Dizhi Ju 1984, 84, pl. 49: figs 1, 2.
Type locality: Yandi's booth: Qitai Jubei Yingxun, Xinjang province, China.
Type horizon: Quishan Street, Upper Triassic.

Valvata* (*Tropidina*) *kebapcii Odabasi, Glöer & Yildirim, 2015 (NEW)
Original source: Odabaşi et al. 2015: 137, figs 2–4, 11 (shell), 5 (head), 6 (operculum).
Type locality: Turkey, northwestern Anatolia, Ayvacik town, Tuzla Stream, 39°31'30.8264"N, 26°17'9.57"E, 81 m altitude.
Type material: Holotype COMULM-G 0050 (also figured by Walther and Glöer 2019: fig. 2.7, 2.8 and by Glöer 2019: 210, fig. 264), 5 paratypes COMULM-G 0051, Limnology Museum of Çanakkale Onsekiz Mart University, Turkey (COMULM).

Cincinna kizakikoensis Fujita & Habe, 1991 (Nom: 59)
Remarks: Saito et al. (2018) provided molecular data of specimens from Lake Nakatsuna, Nagano Prefecture, Japan.

Valvata* (*Costovalvata*) *klemmi Schütt, 1962 (Nom: 59).
Type material: A paratype (FS/8894) is stored in the Biologiezentrum Linz (Austria) (Aescht 2003).

Valvata fluviatilis* var. *kliniensis Milachevich/Milaschewitsch, 1881 (Nom: 59)
Type locality: According to Vinarski and Kantor (2016: 267), the type locality "Moujevo" near Moscow is currently named "Muzhevo" and is at approx. 56°27´14"N, 36°50´54"E.
Type material: 56 syntypes in the Zoological Institute of the Russian Academy of Sciences, St. Petersburg (ZIN), #1 in systematic catalogue.

Cincinna* (*Sibirovalvata*) *klucharevae Starobogatov, 1985 (Nom: 60)
Type material: There are no type specimens in the collection of the Zoological Institute of the Russian Academy of Sciences (ZIN). The specimen with number ZIN 1/523-2014 is a topotype that is not included in the type series.

† ***Valvata koehleri*** Harzhauser, Neubauer & Hoşgör, 2018 (NEW)

Original source: Harzhauser et al. 2018: 362–364, fig. 4 (shell and protoconch SEM).

Type locality: Kömürlü (40°46'14.74"N, 42°18'21.05"E, WGS84), Oltu-Narman Basin, northeastern Turkey.

Type horizon: Marly silt and sand of the upper Susuz Formation; Upper Oligocene or Lower Miocene.

Type material: Holotype (NHMW 2018/0019/0015) and paratypes (NHMW 2018/0019/0016-0019), all from type locality and horizon, are deposited at the Naturhistorisches Museum Wien (NHMW).

Valvata* (*Cincinna*) *korotnevi Lindholm, 1909 (Nom: 60)

Remarks: Remarks: Sitnikova et al. (2015: 3–9, fig. 1C) provided photographs of the lectotype and of specimens from several localities as well as an extensive and annotated citation record of the Russian literature in particular. Recently, Andreeva et al. (2021: fig. 3A) added excellent photographs from specimens of the Taz River basin (western Siberia).

"***Valvata* (*Cincinna*) *aliena* var. *korotnewi*** Ldh. 1909" mentioned in Kozhov (1936: 17, 18). (NEW)

Remarks: Misspelling of *Valvata* (*Cincinna*) *korotnevi* Lindholm, 1909, correctly listed by Sitnikova et al. (2015: 11).

Valvata kournasi Glöer & Hirschfelder, 2019 (NEW)

Original source: Glöer and Hirschfelder 2019: 18–21, figs 40–42 (shell), fig. 43 (maps), figs 44–46 (type locality).

Type locality: Nómos Chaniá, outflow of Lake Kournas, 3 km southeast of Georgioúpoli, Crete, Greece.

Type material: Holotype (ZMH 140040: also figured by Glöer 2019: 211, fig. 265) and 1 paratype (ZMH 140041) are stored in the Zoological Museum of Hamburg, Germany (ZMH), remaining paratypes (9 + 1 juv.) in coll. Hirschfelder (Kelheim, Germany).

Remarks: The anatomy of this species is unknown because only subrecent (fossil or dead) shells have been found.

Megalovalvata kozhovi Sitnikova, 1983 (Nom: 60)

Remarks: Sitnikova (2018) illustrated the holotype (fig. 6H) and paratypes (fig. 10G–J) from various localities of Lake Baikal.

† ***Valvata vanciana* var. *kubanica*** Krestovnikov, 1931 (NEW)

Original source: Krestovnikov 1931: 20, pl. 2: figs 19–25. Redescribed and figured by Yakhimovich et al. (2000: 65, pl. 4: figs 7–10) as *Valvata kubanica* Krestovnikov, 1929

Type locality: Sediments of Estuary of Velykyi Kuyalnik River near Odessa, northwest Black Sea, Ukraine.

Type horizon: Pleistocene.

"***Valvata kurensis***" mentioned in Bogachev (1961: 73) (NEW)
Remarks: Misspelling of *Valvata kupensis* Fuchs, 1870.

Valvata* (*Pseudomegalovalvata*) *laethmophila Bekman & Starobogatov, 1975 (Nom: 61)
Remarks: Sitnikova (2018: fig. 2D) figured the holotype.

"***Valvata lanta***" mentioned in Bogachev (1961: 152) (NEW)
Remarks: Misspelling of *Valvata lauta* Lindholm, 1909.

† ***Valvata* (*Cincinna*) *andreana* var. *latior*** Menzel, 1904 (Nom: 62)
Type horizon: Quaternary.
Type material (more than 20 specimens without designation as types) is stored in the Geozentrum Hannover (originally from Geowissenschaftliche Sammlungen Berlin, BGR) starting with # BGR-B-ORIG-000181564 to # BGR-B-ORIG-000181888.

Valvata lietuvensis Chernogorenko & Starobogatov, 1987 (Nom: 64)
Type material: Holotype (ZIN 1/601-1986) and 10 paratypes (ZIN 2/601-1986 and ZIN 3/601-1986) in the Zoological Institute of the Russian Academy of Sciences, St. Petersburg (ZIN). The type series includes the holotype and 10 paratypes. Holotype figured by Sitnikova et al. (2017: 257, fig. 3A–C). Additional data by Vinarski and Kantor (2016: 264).

"***Valvata luguensis***" mentioned by Du et al. (2017: 871) (NEW)
Locality: Lake Lugu (alpine, 2690 m above sea level), with the middle of the lake forming the border between the Ninglang County of Yunnan Province and the Yanyuan County of Sichuan Province, China.
Remarks: Not described or figured by the authors or subsequently, thus a nomen nudum. According to Wiese et al. (2020: 1101) this species might be endemic to Lake Lugu. Clewing et al. (2014) have previously provided molecular data of this lineage as "*Valvata* sp. from Lake Lugu", resp. "clade CN07/1". According to their analysis the species belongs to the subgenus *Tropidina*.

† ***Amplovalvata magna*** Pan, 1980 (in Yu & Pan, 1980) (Nom: 65)
Original source: Yu and Pan 1980: 150, pl. 2: figs 5, 6.

† "***Valvata magniumbilicata***" mentioned in Youluo 1978 (Nom: 65)
Remarks: Not available from there (see above). I could not find a subsequent reference on this species that would validate the name.

† ***Provalvata maior*** Cataldo, Lazo, Luci & Aguirre-Urreta, 2019 (NEW)
Original source: Cataldo et al. 2019: 453–455, figs 6 (9–12), 7 (9–12).
Type locality: Quebrada del Gastrópodo, Mendoza Province, Argentina.

Type horizon: La Tosca Member, Huitrín Formation, facies D1, Barremian, Lower Cretaceous.

Type material: Holotype deposited in Museo de Ciencias Naturales y Antropológicas Juan Cornelio Moyano, Colección de Paleontología de Invertebrados, Mendoza, Argentina (MCNAM-PI) 24524.3; paratypes MCNAM-PI 24524.1, 24524.5, and 24524.6; Colección de Paleontología, Universidad de Buenos Aires, Ciudad Autónoma de Buenos Aires, Argentina (CPBA) 23706.1.

Remarks: Cataldo et al. (2019: 451) placed the species "not without hesitation" in Provalvatidae.

† ***Amplovalvata mansueta*** Pan, 1982 (Nom: 66)

Original source: Pan 1982: 431–432, pl. 2: figs 3, 4.

† ***Valvata mathiasi*** Esu & Girotti, 2018 (NEW)

Original source: Esu & Girotti, 2018: 49–54, figs 2, 3.

Type locality: Sambuca Lago Piccolo, Tavarnelle Val di Pesa, Tuscany, Italy.

Type horizon: Lower Pliocene.

Type material. Holotype Senckenberg Museum Frankfurt (SMF) 349126, from SLP3;

paratypes SMF 349127/3 and 349128/1, also Museo di Scienze della Terra of Sapienzia Universita (formerly Museo di Paleontologia), Roma, Italy, MPUR7-3959/50, 3960/80, 4153/20.

Remarks: the largest true *Valvata* known.

† "***Valvata* (*Cincinna*) *mengyinensis*** (Grabau)" mentioned in Kobayashi (1983: 57) (NEW)

Remarks: probably an error for *Bithynia mengyinensis* Grabau, 1923, which is shown in the same figure as *Valvata suturensis* by Grabau (1923: 161, fig. 7a–d (*Bithynia mengyinensis*), fig. 7e–g (*Valvata suturalis*)).

Valvata microscopica Nevill, 1889 (Nom: 68)

Type material: According to Ponder et al. (2014: 139) the holotype, originally deposited in Calcutta Museum, India, is apparently lost. Annandale and Kemp (1916: 347, text fig. 3) figured a "co-type" labelled as *Cyclostrema microscopica*, which was reproduced by Ponder et al. (2014: 140, fig. 27).

Remarks: Ponder et al. (2014: 139ff) tentatively treated this species as *Coliracemata? microscopica* (Nevill, 1877) (Truncatelloidea, Clenchiellidae).

Cincinna* (*Sibirovalvata*) *sibirica middendorffi Starobogatov & Zatravkin, 1985 (Nom: 69)

Remarks: Saito et al. (2018) provided molecular data from specimens from Nadezhdinsky District, Primorsky region, Russia.

† ***Valvata minima*** Hislop, 1859 (non Fuchs, 1877) (Nom: 69)

Type horizon: Upper Cretaceous (not Tertiary).

Type material: Lectotype designated and figured by Hartman et al. (2008: fig. 15A, B), reprinted by Bingle-Davis (2012: 132), deposited under PIMG 1251 (Palaeo Invertebrate Mesozoic Gastropod) at the Natural History Museum of the United Kingdom (NHMUK); the original Latin description was translated to English.

† "***Valvata minima*** Fuchs, 1877" (Nom: 69)

Remarks: As outlined this name is a junior homonym of *Valvata minima* Hislop, 1859. Accordingly, the name was replaced by *Pseudamnicola welterschultesi* Neubauer, Harzhauser, Kroh, Georgopoulou & Mandic, 2014 (Hydrobiidae: Pseudamniocolinae). Neubauer et al. (2014b: 19) did not agree with Wenz (1928: 2439), who considered synonymy of *Valvata minima* Fuchs, 1877 with *Valvata serbica* Brusina, 1902 (an available name).

† ***Provalvata minor*** Cataldo, Lazo, Luci & Aguirre-Urreta, 2019 (NEW)

= *Provalvata* sp. in Lazo et al. (2017: 32, fig. 5k, l).

Original source: Cataldo et al. 2019: 451–453, figs 6 (1–8), 7 (1–8).

Type locality: Quebrada del Gastrópodo, Mendoza Province, Argentina.

Type horizon: La Tosca Member, Huitrín Formation, facies D1, Barremian, Lower Cretaceous.

Type material: Holotype deposited in Museo de Ciencias Naturales y Antropológicas Juan Cornelio Moyano, Colección de Paleontología de Invertebrados, Mendoza, Argentina (MCNAM-PI) 24523.3, paratypes MCNAM-PI 24523.2, 24523.4 and 24523.5; Colección de Paleontología, Universidad de Buenos Aires, Ciudad Autónoma de Buenos Aires, Argentina (CPBA) 23704.1.

Remarks: Cataldo et al. (2019: 451) placed the species "not without hesitation" in Provalvatidae.

† "***Costovalvata minuta***" mentioned in Youluo, 1978 (Nom: 70)

Original source: Youluo 1978 (not available from there, see above).

Type locality: Qingjiang Basin, Jiangxi, China.

Type horizon: Linjang Formation, Eocene.

Type material: Nanjing Institute of Paleontology and Geology, sample # 93414.

Valvata minutissima Wattebled, 1884 (Nom: 70).

Type material: Ponder et al. (2014: fig. 2A–C) figured the holotype, which is stored in the Muséum national d´Histoire naturelle, Paris (MNHN-IM-2000-33594).

Remarks: Ponder et al. (2014: 126ff, figs 2, 4, 15, 33) confirmed synonymy with *Clenchiella papuensis* Benthem Jutting, 1963 and provided details on morphology, SEM photographs of the operculum (fig. 4E, F), radula (fig. 5C, D), anatomy (fig. 15), and COI sequences (fig. 33) of this species, which is now treated as *Clenchiella minutissima* (Wattebled, 1884) (Truncatelloidea, Clenchiellidae).

† ***Valvata montanaensis*** Meek, 1876 (Nom: 71)

Remarks: In a published abstract of a conference, Canoy Illies and Hartmann (2018) designated a lectotype (USNM-PAL 2177a) and proposed (but not named) a new genus with this species as type species. Also, the type horizon is specified as the upper part of the Judith River Formation in Upper Missouri, Montana (Coal Ridge Member, Rogers et al. 2016).

Valvata montenegrina Glöer & Pešić, 2008 (Nom: 71)

Remarks: The holotype of *V. montenegrina* is figured by Glöer (2019: 203, fig. 254). Barcoding sequences of the COI gene are deposited by Falniowski et al. (2021) in GenBank with the numbers MZ027632 and MZ027633.

"***Valvata montenegrinus*** Glöer & Pešić, 2008" in Glöer (2019: 203) (NEW)

Remarks: Misspelling of *Valvata montenegrina* Glöer & Pešić, 2008 (no reason given for gender change).

† ***Valvata multicarinata*** Hislop, 1859 (non Yen, 1946) (Nom: 73)

Type horizon: Upper Cretaceous (not Tertiary).

Type material: Lectotype designated and figured by Hartman et al. (2008: fig. 17A–D), reprinted by Bingle-Davis (2012: 132), stored under PIMG 1190 (Palaeo Invertebrate Mesozoic Gastropod) at the Natural History Museum of the United Kingdom (NHMUK); the original Latin description was translated to English.

Valvata nowshahrensis Glöer & Pešić, 2012 (Nom: 75)

Holotype also figured by Glöer (2019: 213, fig. 267).

† "***Valvata nikosi***" mentioned in Esu and Girotti (2015: 78) (NEW)

Remarks: Mismatch of *Pyrgula nikosi* Esu & Girotti, 2015 and *Valvata pyramidula* Esu & Girotti, 2015, both described in the same paper.

Cyclostoma obtusum Draparnaud, 1801 (Nom: 76)

Type material (10 syntypes, most of them juveniles or subadults) have been located by Vinarski and Kantor (2016: 269) in the Naturhistorisches Museum Wien (NHM), # 14704.

Remarks: Several Russian authors regard this species as valid, whereas most European authors consider this to be a synonym of *Valvata piscinalis* O.F. Müller, 1774.

† ***Valvata octonaria*** Brusina, 1902 (Nom: 76)

Remarks: The taxon was ranked as subspecies of *Valvata simplex* Fuchs, 1870 (non Gould 1847) by Wenz (1928: 2476). According to Neubauer et al. (2014b: 20) its generic affiliation is currently uncertain and needs revision; the current status is *Muellerpalia octonaria* (Brusina, 1902) (Hydrobiidae).

† "***Valvata oecsensis*** Soós, 1934" mentioned in Papp (1953: 109), Schlickum (1978: 246, pl. 18: fig. 1), Stojaspal (1990: 651, pl. 1: fig. 2), and Harzhauser and Binder (2004: 10, pl. 3: figs 9–11).] (NEW)

Remarks: Neubauer et al. (2014b: 20) pointed out that the original name "*öcsensis*" in the cited publications was erroneously emended to "*oecsensis*". However, the correct emendation following ICZN rules is "*ocsensis*", since it is not derived from a German word (ICZN 32.5.2.1). Current status: *Valvata ocsensis* Soós, 1934.

Valvata* (*Pseudomegalovalvata*) *olkhonica Bekman & Starobogatov, 1975 (Nom: 77)

Remarks: Sitnikova (2018: fig. 2C) figured the holotype.

Valvata lewisi* var. *ontariensis Baker, 1931 (Nom: 77)

Remarks: Recently, Hinchliffe et al. (2019) confirmed by DNA barcoding that, despite the open coiling of the shell, this taxon is genetically identical to and thus a junior synonym of *Valvata lewisi* Currier, 1868. The authors also provided good photographs of the shells of both taxa.

† "***Valvata oregonensis***" mentioned in Hanna (1922: 11) (Nom: 78)

Remarks: As already outlined by Henderson (1935: 190), this name has been introduced in express synonymy by Hanna (1922: 12: "This species was briefly described under two names [*V. whitei* and *V. calli*] in 1910 by Hannibal"). Since the two names previously published are both available, the name *Valvata oregonensis* is not valid.

"***Valvata cristata palustris*** Kormos" twice mentioned in Motuz 1975: 57), also listed in the Global Names Index GNI (Nom. 79)

Remarks: As assumed in Haszprunar (2014) this is a confusion between *Valvata cristata* Müller, 1774 and *Lymnaea palustris* Müller, 1774, both listed in Kormos (1912).

Valvata* (*Cincinna*) *pamirensis Starobogatov, 1972 (Nom: 79)

Type material: Type data were provided by Sitnikova et al. (2017: 259), who also figured the holotype (fig. 3G–I) (ZIN 1/241-1955) and paratype (ZIN 10/241-1955) from the type locality (# 10, fig. 3J–L) in the Zoological Institute of the Russian Academy of Sciences, St. Petersburg (ZIN).

† "***Valvata panagilae***" [sic! not *panagile*] mentioned in Siodiropoúlou (2003: 41–42) (Nom: 79)

Remarks: This and four other fossil species (*V. catariane*, *V. olgae*, *V. mariae*, *V. theocleti*) from Pliocene – Pleistocene sediments of the Ptolemaida Basin (west Macedonia, Greece) are all extensively described and figured by Siodiropoúlou (2003). However, this PhD thesis never has been formally published, and thus the names are not available. I have also failed to detect any secondary reference using the name with a diagnosis or figure, which would make any of these names available.

Valvata* (*Megalovalvata*) *lauta* var. *parvula Kozhov, 1936 (Nom: 79)

Remarks: Sitnikova (2018: fig. 6D) illustrated the lectotype.

† ***Cincinna penglaizhenensis*** Pan, 1982 (Nom: 81)

Original source: Pan 1982: 431, pl. 1: figs 22–23, pl. 2: figs 1, 2.

† "***Valvata* (*Atropidina*) *pileiformis***" mentioned in Youluo 1978 (Nom: 83)

Remarks: Not available from there (see above) or from Ye et al. (1996: 49; nomen nudum, no reference). I could not find a subsequent full reference on this species that would validate the name.

Valvata* (*Liratina*) *baicalensis* var. *piligera Lindholm, 1909 (Nom: 83)

Remarks: Sitnikova (1991: figs 1.1, 2.1–4,) figured spawn and embryos [as *Megalovalvata piligera piligera*]. Vinarski and Kantor (2016: 282) provided data on types, type locality with coordinates, distribution, and bionomics. Saito et al. (2018) added molecular data from specimens from Lake Baikal (Listvyanka), Oblast Irkutsk, Russia. Sitnikova (2018) illustrated the lectotype (fig. 6E) and specimens of morphs *nudicarinata* (fig. 6F) and *minor* (fig. 8D).

Nerita piscinalis O.F. Müller, 1774 (Nom: 83)

Type material: Vinarski and Kantor (2016: 268) stated that they could not find type material in the Zoological Museum of Copenhagen as assumed by Kantor et al. (2011: 70).

† ***Valvata* (*Valvata*) *platispira*** Szőts, 1953 (NEW)

Original source: Szőts, 1953: 33, 145, pl. 2: figs 13–15.

Type locality: "Hosszúharasztos" (Harasztos quarry), Gánt, District Fejér, Hungary.

Type horizon: Eocene.

† ***Valvata* (*Cincinna*) *polita*** A.A. Ali-Zade, 1973 (NEW)

Original Source: A.A. Ali-Zade 1973: 155–156, pl. 45: figs 1a, 1b.

Type locality: Bozdag (hill), Lower Absheron Peninsula of Azerbaijan.

Type horizon: Lower Akchagylian, uppermost Pliocene.

Type material: Dr Pavel Frolov (pers. comm. via Dr. Paval Kijashko, 22 Feb 2022) provided information that the fossil molluscs described by A.A. Ali-Zade in 1973 are all stored in the Museum of Earth Sciences of Moscow State University (MES MSU). The holotype has inventory number (MES MSU # 28/308).

Remarks: judged from the figures, which show a non-circular aperture, this taxon is not a valvatid and is in need of revision.

† ***Valvata* (*Cincinna*) *pontica*** Pană, 1990 (NEW)

Original source: Pană, 1990: 63, pl. 1: figs 3–10.

Type locality: Valley Croitorului, village Sibiciul de Jos, district Buzău, Romania.

Type horizon: Upper Miocene, lower Pontium.

Type material: Holotype No. 674, Collection Laboratoire de Paléontologie III g, Bucarest, Romania.

† ***Valvata simplex* var. *polycincta*** Lörenthey, 1906 (Nom: 85)

Remarks: The name was synonymized with *V. simplex octonaria* by Wenz (1928: 2476), a view shared by Neubauer et al. (2014b: 21). Since the parent species name is not available and has been replaced (see below under *Vatributarylvata simplex*), the current status is *Muellerpalia haszprunari octonaria* Neubauer, Harzhauser, Kroh, Georgopoulou & Mandic, 2014 (Hydrobiidae).

Valvata* (*Pseudovalvata*) *profundicola Bekman & Starobogatov, 1975 (Nom: 87)

Remarks: Sitnikova (2018: fig. 12F) figured the reticulate pattern of the shell by SEM and provided photographs (fig. 2A) and measurements of paratypes.

† ***Valvata* (*Borysthenia*) *pronaticina*** Lindholm, 1932 (NEW)

Original source: Lindholm 1932: 17, pl. 3: fig. 8a–h.

Type locality: East border of creek Betekei, a tributary of river Ischim near Selim-Dzhevar; district Petropavlovsk, province Akmolinsk (now Astana), North Kazachstan.

Type horizon: Lower Pliocene.

Type material: stored in the Central Scientific Research Geological Exploration Museum named after F.N. Chernyshev (CNIGR) # 412–419/3355 (see Malchevskoya 1985: 211). 21 syntypes are deposited in the Zoological Institute of the Russian Academy of Sciences, St. Petersburg (ZIN 1/359-1935).

† "***Valvata cristata pslustris***" [sic] mentioned in Ye et al. (1996: 166) (NEW)

Remarks: probably misspelled and confused with *Stagnicola palustris* (O.F. Müller, 1774).

"***Costovalvata pulchra***" mentioned in Ye et al. (1996: 47) (NEW)

Remarks: nomen nudum, not available.

Nerita pusilla Müller, 1774 (Nom: 88)

Original source: Müller 1774: 171 (# 357) referring to "Berl(in) Magaz(in) [Berlinisches Magazin: 4. B(and) p(agina) 268, t(abula) 8, f(igura) 26", published 1769].

Type material: Not mentioned by Nekhaev et al. (2015). Vinarski and Kantor (2016: 265) failed to find type material in the Zoological Museum of Copenhagen.

Remarks, The figures (25 and 26)) in the article "Berlinisches Magazin" (an author is not identified) certainly refers to a species of Valvatidae and not to a neritid.

"***Valvata pygrncea***" mentioned at many webpages, e.g., https://commons.wikimedia.org/wiki/File:The_Quarterly_journal_of_the_Geological_Society_of_London_(1867)_(14595069379).jpg (NEW)

Remarks: Misspelling of *Valvata pygmaea* C.B. Adams, 1849 because of erroneous text recognition.

† ***Valvata pyramidula*** Esu & Girotti, 2015 (NEW)

Original source: Esu and Girotti 2015a: 76–78, figs 29–32.

Type locality: S-SW of Neos Erineos, Greece (GPS w66 = 38°16'45.22"N, 21°59'46.33"E).

Type horizon: Upper Lower Pleistocene, grey-yellow silty clays of the Synania Formation.

Type material in Senckenberg Museum Frankfurt (holotype SMF 345727, paratypes SMF 345728/3).

† "***Liratina qikouensis***" mentioned in Youluo 1978 (Nom: 89)

Remarks: Not available from there (see above) or from Ye et al. (1996: 49; nomen nudum, no reference). I could not find a full reference on this species that would validate the name.

† ***Valvata* (*Cincinna*) *racovetzae*** Popova & Starobogatov (in Popova, Devyatkin & Starobogatov, 1970) (NEW)

Original source: Popova et al. 1970: 23 (pl. 1: fig. 3), 26.

Type locality: The Chuya Basin (or Chuya Steppe), southeastern part of the Altai Mountains, Russia.

Type horizon: Kyzylgir formation, Middle to Upper Pliocene.

Type material: Holotype deposited in the Zoological Institute of the Russian Academy of Sciences, St. Petersburg (ZIN 1/533-1968).

Remarks: Unfortunately this fossil species is not included in the review of freshwater gastropod taxa created by Starobogatov (Sitnikova et al. 2017).

† "***Valvata* (*Cincinna*) *rakovetzae***" mentioned in Popova et al. 1970: 26

Remarks: Probably a misspelling of † *Valvata* (*Cincinna*) *racovetzae*: (1) The figure legend at page 23 (first mention in the paper) states "*racovetzae*". (2) The same paper includes the description of *Anisus* (*Pseudocarinogyraulus*) *racovetzae* (Hygrophila: Planorbidae; pp. 43, 44) and *Odhneripisidium racovetzae* (Bivalvia: Pisidiidae; pp. 72, 74), showing the general preference of the authors for the latter spelling. (3) The second author, Bogachkin (1981: 33) listed a similar species as "*Valvata* cf. *racovetzae* Pop. Et Starob.". On the other hand, Dr Pavel Kijashko (pers. comm. 22 Feb 2022) stated that "I believe that the name "*rakovetzae*" is a priority. It is indicated in the original description and on the original identification label by the hand of Starobogatov it is written: "*V. rakovetzae*, holotype". Perhaps it is Starobogatov's typo (it cannot be clarified now), but it does not contradict ICZN." The matter may be decided by the Commission of Zoological Nomenclature.

† ***Valvata* (*Cineinna*) [sic!] *rehetaiensis*** Zhu G.-X., 1980 [non Youluo 1978] (Nom: 90)

Original source: Zhu 1980: 38, pl. 19: fig. 3, referred to Youluo (1978).

Remarks: Not available from Youluo 1978 (see above), but Zhu (1980) fulfils all requirements of validation (description and figure). The subgenus *Cincinna* is misspelled as *Cineinna.*

Type locality: Coastal region of Bohai, northeast China.

Type horizon: The lower part of the first section of the Eocene–Oligocene Shahejie Formation.

† "***Valvata ringentis***" mentioned in Youluo 1978 (Nom: 91)

Remarks: Not available from there (see above). I could not find a subsequent full reference on this species, which would validate the name. The name "*A.* [*Amnicola*] *ringentis* Youluo" mentioned in Qu et al. (2006: 361) refers to another (likewise not available) name and species (Youluo 1978: 49, pl. 6: figs 29, 30, pl. 7: figs 19, 20).

† ***Valvata robusta*** Martinson, 1882 (Nom: 91)

Original source: Martinson 1982: 70, pl. 16: figs 23, 24.

Type locality: Tsogt-Ovoo of Gobi desert, southeastern Mongolia.

Type horizon: Upper Cretaceous, Albian, Khukhtyk Formation.

Type material: Holotype No. 5577/4 deposited at Limnological Institute, Siberian Branch of the Russian Academy of Sciences. Paratypes: 10 in good condition, 8 in satisfactory condition.

† ***Valvata sayni*** Delafond & Deperet, 1893 (Nom: 93)

Remarks: Also listed as "*Valvata sibinensis* Neum. Var. *sayni* Font." by Jodot (1955: 601). As previously noted, Fontannes (1883: 440) only published a nomen nudum, which was later made available by Delafond and Depéret (1893: 47).

† ***Valvata serbica*** Brusina, 1902 (Nom. 94)

Remarks: As previously noted, Brusina's name is a junior synonym of *Valvata minima* Fuchs, 1877, the latter is a junior homonym of *Valvata minima* Hislop, 1859. Accordingly, the Brusina/Fuchs name has been replaced by Neubauer et al. (2014b: 19) as *Pseudamnicola welterschultesi* Neubauer, Harzhauser, Kroh, Georgopoulou & Mandic, 2014 (Hydrobiidae).

Valvata cristata* var. *sibirica Middendorff, 1851 (Nom: 95)

Type material: Vinarski and Kantor (2016: 277) explained that Bogatov and Zatravkin (1992: 33) did not designate a lectotype as assumed by Prozorova and Starobogatov (1998: 56) but only listed a syntype (collected in Barnaul). This syntype is kept in Zoological Institute of the Academy of Sciences, St. Peterburg (ZIN), as # 1 under the name. Glöer (2019: 213, fig. 268: 5–7) also figured syntypes from the Naturalhistoriska Museet Goteborg (GNHM 4677).

Remarks: Andreeva et al. (2021: fig. 5A) published excellent photographs of specimens of the Taz River basin (western Siberia).

† "***Valvata* (*Valvata*) *simplex*** Fuchs, 1870" (Nom: 95–96)

Remarks: As outlined in Haszprunar (2014: 95), the taxon is a junior homonym of *Valvata tricarinata* var. *simplex* Gould, 1841 and is in fact a hydrobiid. Accordingly, the name has been replaced by Neubauer et al. (2014b: 19–20) with *Muellerpalia haszprunari*

Neubauer, Harzhauser, Kroh, Georgopoulou & Mandic, 2014 (Hydrobiidae). The same authors also renamed *†Valvata octonaria* Brusina, 1902 (although only tentatively: "needs revision") as *Muellerpalia haszprunari octonaria* (Brusina, 1902).

"***Valvata skniadica***" mentioned in Ye et al. (1996: 166) (NEW)

Remarks: Misspelling of *Valvata* (*Aphanotylus*) *skhiadica* Bukowski, 1895.

Valvata* (*Cincinna*) *sorensis Dybowski, 1886 (Nom: 97)

Type material: According to Sitnikova et al. (2015: 10) type material may be stored in the Collection of the Benedict Dybowski Zoological Museum, Ivan Franko National University, Lviv (Ukraine).

Remarks: Clewing et al. (2014: supplementary material) provided molecular data (as RU02/2). Sitnikova et al. (2015: 10–19, figs. 4C, D) considered *Valvata* (*Cincinna*) *sorensis* var. *abbreviata* Lindholm, 1909 as a junior synonym, provided photographs of syntypes and from specimens of several localities as well as an extensive and annotated citation record in the Russian literature in particular. Andreeva et al. (2021: fig. 3C) added excellent photographs from specimens of the Taz River basin (western Siberia).

Valvata spirorbis Draparnaud, 1897 (Nom: 98)

Type material: According to Vinarski and Kantor (2016: 263) a single shell (syntype) is stored in the Naturhistorisches Museum Wien (NHM #14717).

† ***Valvata* (*Cincinna*) *splendida*** Szőts, 1953 (NEW)

Original source: Szőts, 1953: 33, 145–146, pl. 2: fig. 16.

Type locality: "Hosszúharasztos" (Harasztos quarry), Gánt, District Fejér, Hungary.

Type horizon: Upper Lutetian to lower Bartonian, Middle to upper Eocene.

† ***Valvata stevanovici*** Ilyina (in Stevanovich & Ilyina, 1982) (Iljina in Global Names Index GNI and Index of Organism Names ION) (Nom: 98)

Type material: Holotype stored in the Paleontological Institute, Russian Academy of Sciences (PIN 2220/587).

"***Valvata radiatula subnaticina***" (NEW) mentioned at GBIF, Catalogue of Life, World Register of Marine Species, and at Mineralienatlas https://www.mineralienatlas.de/lexikon/index.php/FossilData?fossil=Valvata%20radiatula%20subnaticina.

Remarks: The name is a mistake based on the description of *Valvata subnaticina* Łomnicki, 1886 (Nom: 100). There it is stated that fossils of forms similar to *Valvata radiatula* Sandberger, 1875 also occur at the type locality; the latter are clearly different from *V. subnaticina*, however.

"***Valvata cristata* monstr. *subscalaris***" mentioned in Baudon (1884: 294, pl. 9: fig. 19) (NEW)

Remarks: Obviously considered as a monstrosity, therefore not available.

† ***Liratina subtilostriata*** Pan, 1980 (in Yü & Pan, 1980) (Nom: 102)
Original source: Yü and Pan 1980: 148, pl. 2: figs 7–10.

† "***Planorbis symmetricus*** Ludwig, 1865" mentioned in Haszprunar (2014: 103) (NEW)
Remarks: Misspelling for *Planorbis symmetrus* Ludwig, 1865; the current name is *Valvata symmetra* (Ludwig, 1865).

† ***Valvata tanaiticus*** Sanko, 2007 (NEW)
Original source: Sanko 2007: 75–76, text fig. 52.
Type locality: Korotoyak section at the Upper Don river, District of Voronezh Oblast, Russia.
Type horizon: Deeper than Alexandrian Interglacial, Middle Pleistocene.

Valvata* (*Pseudomegalovalvata*) *tenagobia Bekman & Starobogatov, 1975 (Nom: 104)
Type material: According to Vinarski and Kantor (2016: 273) holotype and 15 paratypes in the Zoological Institute of the Russian Academy of Sciences, St. Petersburg (ZIN 1/122-1976 and ZIN 2/122-1976). The holotype is figured by Sitnikova (2018: fig. 2E).

"***Valvata theotokii***" mentioned in Haszprunar (2014: 105) and Glöer and Hirschfelder (2019: 10) (NEW)
Remarks: Misspelling of *Valvata theodokii* Locard, 1889.

"***Liratina tongbinzhenensis***" mentioned in Ye et al. (1996: 49, 50) (NEW)
Remarks: nomen nudum – not available.

† ***Valvata transbaicalensis*** Martinson, 1956 [non 1961] (Nom: 105)
Original source: Martinson 1956: 21, text fig. 16; pl. 2: fig. 14.
Type locality: Mordoy area, east Sibiria (Transbaikalia), Russia.
Type horizon: Lower Cretaceous (Valanginian – Hauterivian).

Cyclostoma tricarinata Say, 1817 (Nom: 105)
Remarks: Yurco and Keeney (2018) provided microsatellite data to enable analyses of population genetics of this widespread species.

† ***Valvata tuostaiensis*** Wei, 1984 (Nom: 107)
Original source: Wei in Xinjiang Dizhi Ju 1984, 84, pl. 49: figs 3, 4.
Type locality: Wuyiju Tostai, Xinjang Province, China.
Type horizon: Taxihe Formation, Miocene.

† "***Liratina tuozhuangensis***" [not *Valvata tuozhuangensis* as stated] mentioned in Youluo 1978 (Nom: 107)
Remarks: Not available from there (see above), nor from Meyerhoff et al. (1991: 102), Ye et al. (1996: 47, 160, 285), Ryo et al. (2000: 11), or Lin et al. (2005: 56): all

these citations are nomina nuda lacking descriptions, figures, or detailed reference. I could not find any full reference on this species that would validate the name.

† ***Valvata turbinata*** Stache, 1889 (NEW)

Original source: Stache 1889: 117, pl. 2: fig. 24.

Type locality: Caracaea-oogones, north of Cosina (today Hrpelje-Kozina), (5 km east of Trieste) Slovenia.

Type horizon: *Stomatopsis* horizon, Eocene.

Remarks: Because of the *Conus*-like shell, a very doubtful member of Valvatidae.

† ***Valvata turbinoides*** K.A. Ali-Zade, 1936 (NEW)

Original source: K.A. Ali-Zade 1936: 17, pl. 1: figs 28–30 (not seen, according to MolluscaBase (2022: see references).

Type locality: near Naftalan, west Azerbaijan.

Type horizon: Akchagylian, uppermost Pliocene and lower Pleistocene.

Remarks: Replacement name for *Valvata alta* K.A. Ali-Zade, 1932, a junior homonym of *Valvata alta* Deshayes, 1862 (now considered as *Bythinella alta* (Deshayes, 1862), Bythinellidae). Not treated in the last 50 years.

"***Valvata turkmena***" mentioned in A.A. Ali-Zade (1967: 225) (NEW)

Remarks: Probably a misattribution of *Pyrgula turkmena* A.A. Ali-Zade, 1967, described in the same volume.

"***Valvata piscinalis* (Müll.) var. *uistopolitana*** Pop[ov]" (NEW) mentioned in Petrova and Linkina (2014: 113) (NEW)

Remarks: A misspelling of *Valvata cistopolitana* (see above).

"***Valvata umbilicata*** Parreyss" is also mentioned in Baudon (1884: 293) (Nom: 108)

† ***Valvata unicarinifera*** Hislop, 1859 (Nom: 108)

Type horizon: Upper Cretaceous (not Tertiary as stated by Hislop).

Type material: Lectotype designated and figured by Hartman et al. (2008: fig. 16A, B), reprinted by Bingle-Davis (2012: 132), deposited under PIMG 1239 (Palaeo Invertebrate Mesozoic Gastropod) at the Natural History Museum of the United Kingdom (NHMUK); the original Latin description was translated to English.

† "***Valvata unicarinifera unicarinifera***" mentioned in Bingle-Davis (2012: 104) (NEW)

Locality: near Kalmeshwar (station InL0096b), west of Nagpur, Savner Subdivision of Nagpur district in the state of Maharashtra, India.

Horizon: Cretaceous.

Material: "Holotype": InS1159 (Appendix 2 (Nom: 137), fig. O; 1.5 mm × 1.7 mm) stored at University of North Dakota, Grand Forks, North Dakota, USA.

Remarks: Although freely available online, this PhD dissertation lacks ISBN or ISSN numbering, thus is not formally published. Moreover, in erecting a second subspecies of *Valvata unicarinifera* Hislop, 1859 by Bingle-Davis in the same work (see above for "*V. u. chiknaformis*"), the original taxon becomes the nominal subspecies and cannot be replaced. Thus, the specimens of Bingle-Davis are formally not named and remain to be described in accordance with the rules of ICZN.

Valvata simplex* var. *unicincta Lörenthey, 1906 (Nom: 109)

Remarks: As outlined above (see under *Valvata simplex*) the parent species name is not available and has been replaced by Neubauer et al. (2014b: 21). The current status of this taxon, which needs revision, is *Muellerpalia octonaria unicincta* (Lörenthey, 1906) (Hydrobiidae).

† ***Valvata uralica*** Popov, 1965 (NEW)

Original source: Popov 1965: 227, pl. 5: figs 25–29.

Type locality: Kama tributary of the Middle Volga, Russia.

Type horizon: Pleistocene, Sokol Suite of the Kinel Formation.

Type material: unknown.

Remarks: also mentioned by Danukalova and Morozova (2003: 80) and Matoshko et al. (2004: 21).

"***Valvata vaciani*** Nourn." mentioned in Yahimovich et al. (2000: 65) (NEW)

Remarks: misspelling of *Valvata vanciana* Tournouër, 1875.

"***Valvata venciana***" mentioned in Bogachev (1961: 74) (NEW)

Remarks: misspelling of *Valvata vanciana* Tournouër, 1875.

† ***Cincinna* (*Cincinna*) *vinogradovskaense*** [sic] Gozhik, 2002 (Nom: 110)

Type locality: near Vinogradovka village, Odesa oblast, Bolhrads'kyi district, Ukraine.

Type horizon: Miocene, Middle Pontian.

Type material: Holotype (coll. Gozhik, #3163) figured by Osipova et al. (2021: fig. 3D).

Remarks: The species name should be *vinog radovskaensis*, since both *Cincinna* and *Borysthenia* are feminine. "*Cincinna* (*Cincinna*) *vinogradovkensis*" mentioned in Haszprunar (2014: 110) is a misspelling. Currently considered a species of *Borysthenia* Lindholm, 1914.

Valvata* (*Microcincinna*) *vystitiensis Chernogorenko & Starobogatov, 1987 (Nom: 111)

Type material: Type data provided and holotype figured by Sitnikova et al. (2017: 257, fig. 3D–F).

† ***Valvata heidemariae willmanni*** Neubauer, Harzhauser, Kroh, Georgopoulou & Mandic, 2014 (NEW).

Original source: Neubauer et al. 2014b: 22

Type locality: Vokasia-Tal, Kos, Greece.

Type horizon: Lower Pleistocene, Middle Iraki-Formation.

Type material: According to Neubauer et al. (2014b: 22) deposited in the Geological-Paleontological Institute, University of Kiel, no number provided.

Remarks: Replacement name for *Valvata heidemariae bicarinata* Willmann, 1981, a junior homonym of *Valvata bicarinata* Lea 1841.

† ***Valvata windhauseni*** Parodiz, 1961 (Nom: 112)

Remarks: Parodiz (1969: 110) himself later assigned this species to the freshwater genus *Potamolithus* Pilsbry, 1896 (Truncatelloidea, Tateidae).

† ***Valvata yongkangensis*** Yü, 1980 (Nom: 112)

Original source: Yü and Pan 1980: 147–148, pl. 2: figs 3, 4.

Type horizon: Middle Jurassic.

† ***Valvata zhongjiangensis*** Pan, 1982 (Nom: 113)

Original source: Pan 1982: 430, pl. 1: figs 18–21.

† "***Valvata zhouqingzhuangensis***" mentioned in Youluo 1978 (Nom: 113)

Remarks: Not available from there (see above) or from Ye et al. (1996: 48; nomen nudum, no reference). I could not find any full reference on this species that would validate the name.

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The complete mitochondrial genomes of five Agrilinae (Coleoptera, Buprestidae) species and phylogenetic implications

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Abstract

Five complete mitochondrial genomes of five species from the subfamily Agrilinae were sequenced and annotated, including *Coraebus diminutus* Gebhardt, 1928 (15,499 bp), *Coraebus cloueti* Théry, 1893 (15,514 bp), *Meliboeus sinae* Obenberger, 1935 (16,108 bp), *Agrilus sichuanus* Jendek, 2011 (16,521 bp), and *Sambus femoralis* Kerremans, 1892 (15,367 bp). These mitogenomes ranged from 15,367 to 16,521 bp in length and encoded 37 typical mitochondrial genes: 13 protein-coding genes (13 PCGs), 2 ribosomal RNA genes (2 rRNAs), 22 transfer RNA genes (22 tRNAs), and a control region (CR). Most of PCGs had typical ATN start codons and terminated with TAR or an incomplete stop codon T–. Among these five mitogenomes, Leu2, Ile, Phe, Ser2, Gly, Met, and Val were the seven most frequently encoded amino acids. Interestingly, in *A. sichuanus*, a 774 bp insertion was present at *trnW* and *trnC* junction, which is unusual in Buprestidae. Additionally, phylogenetic analyses were performed based on three kinds of nucleotide matrixes (13 PCGs, 2 rRNAs, and 13 PCGs + 2 rRNAs) using Bayesian inference and maximum-likelihood methods. The results showed that the clade of Buprestidae was well separated from outgroups and all Agrilinae species formed to a single highly supported clade. The tribe Coraebini was polyphyletic, as the genus *Meliboeus* (Coraebini) clustered with the genus *Trachys* (Tracheini). The rRNA genes had important impact for the tree topology of Agrilinae. Compared to the tribes Tracheini and Agrilini, the tribe Coraebini is a younger group.

Keywords

Comparative analysis, mitogenome, phylogenetic analysis

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Introduction

The superfamily Buprestoidea, which contains the families Buprestidae and Schizopodidae, differs from other groups of the Elateriformia by their serrate antennae, hypognathous head, transverse suture of metaventrite present, and two connate basal abdominal ventrites (Bellamy and Volkovitsh 2016). The buprestid beetles are a large group containing six subfamilies, 521 genera, and more than 15,000 species widely distributed in the world (Bellamy 2008; Kubáň et al. 2016). The adults exhibit a broad range of host utilization in leaves, flowers, and stems, whereas larvae are mostly internal feeders on roots and stems, or feed on foliage of woody or herbaceous plants (Bellamy and Volkovitsh 2016). Only adults of the Australian *Xyroscelis crocata* were reported to feed on the sap of the host plant *Macrozamia communis* (Bellamy 1997).

Although taxonomists have made important contributions to the buprestid classification of subfamilies and tribes based on several morphological characteristics (Cobos 1980, 1986; Tôyama 1987; Hołyński 1988, 1993, 2009; Bellamy 2003), the problems of the overall classification in Buprestoidea remain unsettled.

In the past two decades, molecular systematic approaches have been used to resolve unsettled classification and phylogenetic relationships in Insecta (Short and Fikáček 2013; Cline et al. 2014; Robertson et al. 2015; Kundrata et al. 2017; Gimmel et al. 2019; Lee et al. 2020). As to Buprestidae, Bernhard et al. (2005) first used molecular phylogenetic methods based on three mitochondrial markers (*nad1*, *12S*, and *16S*) and confirmed that the *Agrilus viridis* complex, which is widely distributed across Eurasia, is monophyletic. Pentinsaari et al. (2014) and Pellegrino et al. (2017) used mitochondrial markers to evaluate the diversity of *A. viridis* complex, their results suggest that different feeding forms of *A. viridis* represent distinct species. Subsequently, Evans et al. (2015) performed the first large-scale phylogenetic trees combing nuclear and mitochondrial data from 141 species to understand the higher-level relationships in Buprestidae. In that study, the monophyly of the family Schizopodidae and subfamilies Agrilinae, Julodinae, and Galbellinae were strongly supported, while the interrelationships of Chrysochroinae and Buprestinae remained uncertain. Hansen et al. (2016) used molecular systematic methods based on nuclear and mitochondrial data (*coi* and *ak*) to investigate the relationships within *Chrysobothris femorata* species group, and their results showed that some morphological species were not well separated. Kelnarova et al. (2019) provided a molecular phylogeny of *Agrilus* species from the Northern Hemisphere and their results suggest that DNA barcoding is a powerful species identification to *Agrilus*.

During this time, the mitogenome emerged as a valuable source for higher-level phylogenetic analyses, evolutionary strategies, and genetic diversity analyses (Saccone et al. 1999; Krzywinski et al. 2011; Cameron 2014; Qin et al. 2015; Song et al. 2019; Wang et al. 2019). Several buprestid mitogenomes have been sequenced and reported, such as the mitogenome of *Chrysochroa fulgidissima* (Schönherr, 1817) by Hong et al. (2009); the mitogenome of *Agrilus planipennis* Fairmaire, 1888 by Duan et al. (2017), who also performed phylogenetic analyses based on 13 PCGs of 45 mitogenomes of coleopterans;

Table 1. Information on the mitogenomes of Buprestidae and two outgroups used in this study.

No.	Taxa	Accession no.	Genome size (bp)	A%	A+T%	AT skew	GC skew	References
1	*Coraebus diminutus*	OK189521	15,499	38.34	68.42	0.12	−0.25	This study
2	*Coraebus cloueti*	OK189520	15,514	38.53	69.27	0.11	−0.25	This study
3	*Meliboeus sinae*	OK189522	16,108	40.18	72.42	0.11	−0.22	This study
4	*Sambus femoralis*	OK349489	15,367	40.98	73.23	0.12	−0.18	This study
5	*Agrilus sichuanus*	OK189519	16,521	40.19	71.73	0.12	−0.21	This study
6	*Agrilus planipennis*	KT363854	15,942	40.25	71.90	0.12	−0.24	Duan et al. 2017
7	*Agrilus mali*	MN894890	16,204	40.34	74.46	0.08	−0.18	Sun et al. 2020
8	*Coraebus cavifrons*	MK913589	15,686	38.94	69.79	0.12	−0.18	Cao and Wang 2019b
9	*Trachys auricollis*	MH638286	16,429	38.94	71.05	0.10	−0.20	Xiao et al. 2019
10	*Trachys troglodytiformis*	KX087357	16,316	41.03	74.62	0.10	−0.19	Unpublished
11	*Trachys variolaris*	MN178497	16,771	39.92	72.11	0.11	−0.21	Cao and Wang 2019a
12	*Melanophila acuminata*	MW287594	15,853	38.74	75.66	0.02	−0.25	Peng et al. 2021
13	*Anthaxia chinensis*	MW929326	15,881	40.12	73.61	0.09	−0.29	Chen et al. 2021
14	*Chrysochroa fulgidissima*	EU826485	15,592	40.31	69.92	0.15	−0.24	Hong et al. 2009
15	*Acmaeodera* sp.	FJ613420	16,217	38.11	68.41	0.11	−0.25	Sheffield et al. 2009
16	*Heterocerus parallelus* (outgroup)	KX087297	15,845	41.90	74.03	0.13	−0.24	Unpublished
17	*Dryops ernesti* (outgroup)	KX035147	15,672	39.04	72.98	0.07	−0.23	Unpublished

the mitogenome of *Trachys variolaris* Saunders, 1873 by Cao and Wang (2019a); and the mitogenome of *Coraebus cavifrons* Descarpentries & Villiers, 1967 by Cao and Wang (2019b). More detailed information of buprestid mitogenomes is presented in Table 1.

Currently, the subfamily Agrilinae contains four tribes (Agrilini, Coraebini, Aphanisticini, and Tracheini); however, the phylogenetic placement of several genera of this subfamily remains unstable. The genera in the tribes Coraebini and Agrilini were revised by Kubáň et al. (2000). In that study, the genus *Sambus* in the tribe Coraebini was transferred to Agrilini based on the female behavior of ovipositing on rather smooth surfaces of living plants. Later, Kubáň (2016) placed the genera *Sambus*, *Parasambus*, and *Pseudagrilus* in *incertae sedis*. In order to solve these problems, we contribute mitogenomic data of five species of buprestids, *Coraebus diminutus* Gebhardt, 1928, *Coraebus cloueti* Théry, 1893, *Meliboeus sinae* Obenberger, 1935, *Agrilus sichuanus* Jendek, 2011, and *Sambus femoralis* Kerremans, 1892, and perform a molecular phylogenetic analysis in this study. The phylogenetic trees of 15 species from nine genera belonging to four subfamilies of Buprestidae were constructed based on the newly sequenced and previously reported mitogenomes (Table 1).

Material and methods

Sampling and DNA extraction

Specimens of five species were collected using an entomological net. Among them, *C. diminutus*, *C. cloueti*, *M. sinae*, and *A. sichuanus* were collected in the Dayaoshan Mountains in Guangxi Zhuang Autonomous Region, and *S. femoralis* was collected at

Yingjiang County in Yunnan Province, China. Specimens were immediately preserved in 95% ethanol in the field after collected and then stored at –24 °C in the laboratory. The specimens were identified based on morphological characteristics under a Leica M205 FA stereomicroscope. Total DNA was extracted from muscle tissues using the Ezup Column Animal Genomic DNA Purification Kit (Shanghai, China) following the manufacturer's instructions.

Sequencing, sequence assembly, annotation, and heterogeneity

DNA sequencing and de novo assembly of each mitogenome were performed by Beijing Aoweisen Gene Technology Co. Ltd (Beijing, China). 22 tRNA genes were identified using the MITOS webserver, with the parameters of the Invertebrate Mito genetic code (Bernt et al. 2013). Their secondary structures were plotted manually from the MITOS predictions using Adobe Illustrator. Every sequence of tRNA genes was manually checked separately. The PCGs were identified as open reading frames corresponding to the 13 PCGs. The rRNAs and control regions were identified by the boundaries of the tRNA genes. The tRNA secondary structures were identified using tRNAscan-SE (Lowe and Chan 2016). Mitogenome maps (Suppl. material 1: Fig. S1) were produced using Organellar Genome DRAW (OGDRAW) (Greiner et al. 2019). The Base composition and relative synonymous codon usage values were determined using MEGA 6.0 (Kumar 2016). Strand asymmetry was calculated using the formulae AT-skew = (A – T) / (A + T), and GC-skew = (G – C) / (G + C) (Perna and Kocher 1995). In the control region (CR), tandem repeat elements were detected by Tandem Repeats Finder (Benson 1999). The heterogeneous analysis of the 13 PCGs and two rRNAs datasets were performed using AliGROOVE 1.06 (Kück et al. 2014), and the nucleotide diversity (Pi) and the ratio of Ka/Ks of PCGS were calculated with DnaSP v. 5 (Librado and Rozas 2009).

Phylogenetic analyses

Phylogenetic trees for *A. sichuanus*, *C. diminutus*, *C. cloueti*, *M. sinae*, *S. femoralis*, and 10 other buprestid species belonging to four subfamilies were reconstructed by three separate datasets (13 PCGs, 2 rRNAs, and 13 PCGs + 2 rRNAs) using different best-fit models (Table 4). The mitogenomes of *Heterocerus parallelus* (Heteroceridae) and *Dryops ernesti* (Dryopidae) were used as outgroups, as they are phylogenetically distant from Buprestidae in the suborder Polyphaga (Xiao et al. 2019). The phylogenetic analyses were performed using PhyloSuite v. 1.2.2 (Zhang et al. 2020). Nucleotide sequences of the 13 PCGs and 2 rRNAs of all 17 mitogenomes were aligned using ClustalW (Thompson et al. 1994) and trimmed using trimAl v. 1.2 (Capella-Gutiérrez et al. 2009). The best-fit model for three datasets was determined by ModelFinder based on Bayesian information criterion. The maximum-likelihood (ML) and Bayesian inference (BI) methods were used to reconstruct the phylogenetic trees by IQ-tree v. 1.6.8 (Guindon et al. 2010) and MrBayes v. 3.2.6 program respectively (Ronquist et al.

2012). Bayesian analyses were run with two independent chains spanning 2,000,000 generations, four Markov chains, sampling at every 100 generations, and a burn-in period of 0.25 for each chain. The phylogenetic trees were edited and visualized by Figtree v. 1.4.3.

Results and discussion

Genome organization and base composition

The complete mitogenomes of the buprestids *A. sichuanus*, *C. diminutus*, *C. cloueti*, *M. sinae*, and *S. femoralis* have the following GenBank accession numbers attributed to them: OK189519, OK189521, OK189520, OK189522, OK349489. The mitogenomes of these five species contained the 37 typical mitochondrial genes (13 PCGs, 22 tRNAs, and 2 rRNAs) and a control region (CR) (Table 2). The composition and arrangement of the mitochondrial genes in these species (Table 2) were highly similar as those in most other buprestid species (Duan et al. 2017; Cao and Wang 2019a, 2019b; Xiao et al. 2019; Chen et al. 2021; Peng et al. 2021).

Four of the 13 PCGs (*nad1*, *nad4L*, *nad4*, and *nad5*), eight tRNAs (*trnQ*, *trnV*, *trnL1*, *trnP*, *trnH*, *trnF*, *trnY*, and *trnC*), and two rRNAS (*rrnL* and *rrnS*) are encoded on the N-strand, whereas the other 23 genes (9 PCGs and 14 tRNAs) are encoded on the J-strand. The mitogenome sequence of these five buprestid species ranged in size from 15,367 to 16,521 bp.

The mean A + T nucleotide contents of five complete mitogenomes were similar: 68.42% in *C. diminutus*, 69.27% in *C. cloueti*, 72.42% in *M. sinae*, 71.73% in *A. sichuanus*, and 73.23% in *S. femoralis*. The entire mitogenomes had a higher A + T contents of 68.42–73.23% (66.05–72.50% for PCGs, 70.95–74.03% for tRNA genes, 75.20–77.33% for rRNA genes, and 74.17–78.38% for the CR) than G + C contents, which is consistent with the typical base of buprestid mitogenomes. The overall AT skews in these five complete mitogenomes were 0.12, 0.11, 0.11, 0.12, and 0.12, respectively. These five species showed a positive TA skew, suggesting that a slight AT bias which are similar to those observed in other buprestid species (Duan et al. 2017; Cao and Wang 2019a, 2019b; Xiao et al. 2019; Chen et al. 2021; Peng et al. 2021).

Protein-coding regions, codon usage, and nucleotide diversity

The total lengths of PCGs in these five buprestid species ranged from 11,090 to 11,158 bp, accounting for 67.54–72.17% of the entire mitogenomes. Similar to the other buprestid mitogenomes, *nad5* and *atp8* were found to be the largest (1708–1723 bp) and smallest (156–159 bp) genes, respectively. The majority of PCGs strictly started with an ATN (ATA/ATT/ATC/ATG) start codon, except for the *nad1* starting with TTG. All PCGs strictly terminated with TAR (TAG/TAA) or an incomplete stop codon T–. Similar to most previously sequenced members of Buprestidae, the AT skew

Table 2. The five newly annotated Buprestidae mitogenomes. The order of these five species in the table is as follows: *Agrilus sichuanus*, *Coraebus diminutus*, *Coraebus cloueti*, *Meliboeus sinae*, and *Sambus femoralis*. – not determined.

Gene	Strand	Position From	To	Start codons	Stop condons	Anticodon	Intergenic nucleotides
trnI	J	1/1/1/1/1	65/63/63/64/65			GAT	-3/-3/-3/5-3
trnQ	N	63/61/61/70/63	131/129/129/138/131			AAG	-1/0/0/0/-1
trnM	J	131/129/129/138/131	199/196/196/205/196			CAA	0/0/0/0/0
nad2	J	200/197/197/206/197	1222/1219/1219/1231/1210	ATC/ATT/ATT/ATC/ATT	TAA/TAG/TAA/TAA/TAA		1/1/-2/0/-2
trnW	J	1224/1221/1218/1232/1209	1293/1286/1283/1303/1273			ACA	774/-8/-13/13/-8
trnC	N	2068/1279/1276/1296/1266	2130/1339/1336/1356/1326			GCA	0/2/2/0/0
trnY	N	2131/1342/1339/1357/1327	2195/1404/1401/1419/1387			GAA	9/1/1/1/1
cox1	J	2205/1406/1403/1421/1389	3735/2936/2933/2951/2919	–/–/–/–/–	TAA/TAA/TAA/TAA/TAA		0/0/0/0/0
trnL2	J	3736/2937/2934/2952/2920	3802/3003/3001/3016/2984			AAG	0/0/0/0/0
cox2	J	3803/3004/3002/3017/2985	4484/3670/3668/3698/3666	ATT/ATA/ATA/ATC/ATT	TAA/TAA/TAA/TAA/TAA		0/0/0/0/0
trnK	J	4485/3671/3669/3699/3667	4553/3740/3738/3768/3736			CAA	0/0/0/0/0
trnD	J	4554/3741/3739/3769/3737	4618/3803/3802/3830/3798			GAC	0/0/0/0/0
atp8	J	4619/3804/3803/3831/3799	4777/3962/3961/3989/3954	ATT/ATA/ATC/ATT/ATA	TAG/TAA/TAA/TAA/TAG		0/-7/-7/-7-7
atp6	J	4771/3956/3955/3983/3948	5445/4630/4629/4657/4622	ATG/ATG/ATG/ATG/ATG	TAA/TAA/TAA/TAA/TAA		-1/-1/-1/-1/-1
cox3	J	5445/4630/4629/4657/4622	6233/5416/5415/5443/5405	ATG/ATG/ATG/ATG/ATG	TAG/TAA/TAA/TAA/TAA		8/0/0/0/0
trnG	J	6242/5417/5416/5444/5406	6306/5477/5476/5509/5469			ACC	0/0/0/0/0
nad3	J	6307/5478/5477/5510/5470	6660/5831/5830/5863/5823	ATT/ATT/ATT/ATT/ATT	TAG/TAG/TAG/TAG/TAG		-2/-2/-2/-2/-2
trnA	J	6659/5830/5829/5862/5822	6721/5890/5889/5924/5884			AGC	0/-1/-1/-1/0
trnR	J	6722/5890/5889/5924/5885	6781/5952/5951/5988/5947			ACG	1/-1/-1/-1/1
trnN	J	6783/5952/5951/5988/5949	6849/6017/6016/6051/6013			GAA	0/0/0/0/0
trnS1	J	6850/6018/6017/6052/6014	6916/6075/6074/6117/6080			ACA	1/0/7/-1/0
trnE	J	6918/6076/6082/6117/6081	6982/6139/6143/6179/6143			AAC	-1/-4/-4/-1/-1
trnF	N	6982/6136/6140/6179/6143	7045/6198/6202/6240/6207			GAA	0/0/0/0/0
nad5	N	7046/6199/6203/6241/6208	8768/7915/7919/7960/7915	ATA/ATT/ATT/ATT/ATA	TAA/TAA/TAA/TAA/TAA		0/0/0/0/0
trnH	N	8769/7916/7920/7961/7916	8830/7977/7981/8026/7978			GAG	0/0/0/0/0
nad4	N	8831/7978/7982/8027/7979	10,166/9295/9299/9362/9308	ATG/ATG/ATG/ATG/ATG	TAA/TAA/TAA/TAA/TAA		-7/-7/-7/-7/-7
nad4L	N	10,160/9289/9293/9356/9302	10,444/9576/9580/9640/9589	ATG/ATG/ATG/ATG/ATA	TAA/TAA/TAA/TAA/TAA		4/3/3/2/1
trnT	J	10,449/9580/9584/9643/9591	10,511/9642/9646/9704/9654			AGA	-1/-1/-1/-1/-1
trnP	N	10,511/9642/9646/9704/9654	10,574/9704/9708/9769/9717			AGG	1/1/1/1/1
nad6	J	10,576/9706/9710/9771/9719	11,079/10,185/10,189/10,259/10,192	ATT/ATA/ATA/ATG/ATT	TAA/TAA/TAA/TAA/TAA		-1/-1/-1/-1/-1
cytb	J	11,079/10,185/10,189/10,259/10,192	12,224/11,327/11,331/11,401/11,334	ATG/ATG/ATG/ATG/ATG	TAA/TAG/TAG/TAG/TAG		8/-2/-2/-2/-2
trnS2	J	12,233/11,326/11,330/11,400/11,333	12,298/11,391/11,395/11,465/11,400			ACA	17/9/9/19/14
nad1	N	12,316/11,411/11,415/11,485/11,415	13,266/12,361/12,365/12,432/12,365	TTG/TTG/TTG/TTG/TTG	TAA/TAA/TAA/TAG/TAA		1/1/1/0/1
trnL1	N	13,268/12,363/12,367/12,433/12,367	13,334/12,427/12,431/12,495/12,434			AAG	0/0/0/0/0
rrnL	N	13,335/12,428/12,432/12,496/12,435	14,605/13,693/13,697/13,757/13,692				0/0/0/0/0
trnV	N	14,606/13,694/13,698/13,758/13,693	14,674/13,762/13,766/13,826/13,761			AAC	0/0/0/0/0
rrnS	N	14,675/13,763/13,767/13,827/13,762	15,379/14,480/14,483/14,531/14,457				0/0/0/0/0
A + T rich region		15,380/14,481/14,484/14,532/14,458	16,521/15,499/15,514/16,108/15,367				0/0/0/0/0

Table 3. Summarized mitogenomic characteristics of the five buprestid species in this study.

Species	PCGs			rRNAs			tRNA			CR		
	Size (bp)	A+T content	AT skew	Size (bp)	A+T content	AT skew	Size (bp)	A+T content	AT skew	Size (bp)	A+T content	AT skew
A. sichuanus	11,158	70.08	−0.15	1976	75.96	−0.13	1444	74.03	−0.0009	1142	74.17	0.06
C. diminutus	11,093	66.05	−0.14	1984	75.20	−0.11	1477	70.95	0.03	1019	77.72	0.02
C. cloueti	11,093	67.09	−0.15	1983	75.39	−0.11	1414	71.22	0.019	1031	78.27	0.02
M. sinae	11,135	70.70	−0.15	1967	77.33	−0.11	1435	72.13	0.007	1577	78.38	0.13
S. femoralis	11,090	72.50	−0.16	1954	75.69	−0.13	1430	73.85	0.03	910	75.82	0.18

Table 4. Best-fit models of three datasets used for phylogeny.

	ML method	BI method
13 PCGs	GTR+F+I+G4	GTR+F+I+G4
2 rRNAs	TVM+F+I+G4	GTR+F+I+G4
13 PCGs +2 rRNAs	GTR+F+I+G4	GTR+F+I+G4

(0.11–0.12) of these five PCGs (Table 3) were similar among the 15 buprestid species. Summaries of the numbers of amino acids in the annotated PCGs and relative synonymous codon usage are presented in Figs 1 and 2. Overall codon usage among the sequenced buprestid mitogenomes was found to be similar, with Leu2, Ile, Phe, Ser2, Gly, Met, and Val being the seven most frequently coded amino acids.

The nucleotide diversity (Pi) of the 13 PCGs among five species of Agrilinae is provided (Fig. 3), which ranged from 0.202 to 0.375. In these genes, *nad2* (Pi = 0.375) presented the highest variability, followed by *nad6* (Pi = 0.346), *nad4* (Pi = 0.300), and *nad5* (Pi = 0.290); *cox1* (Pi = 0.20) exhibited the lowest variability. The ratio of Ka/Ks (Fig. 4) for each gene of the 13 PCGs was calculated. The values of *nad4* and *nad4L* are distinctly higher than others, which suggests that the genes *nad4* and *nad4L* have a relatively higher evolutionary rate.

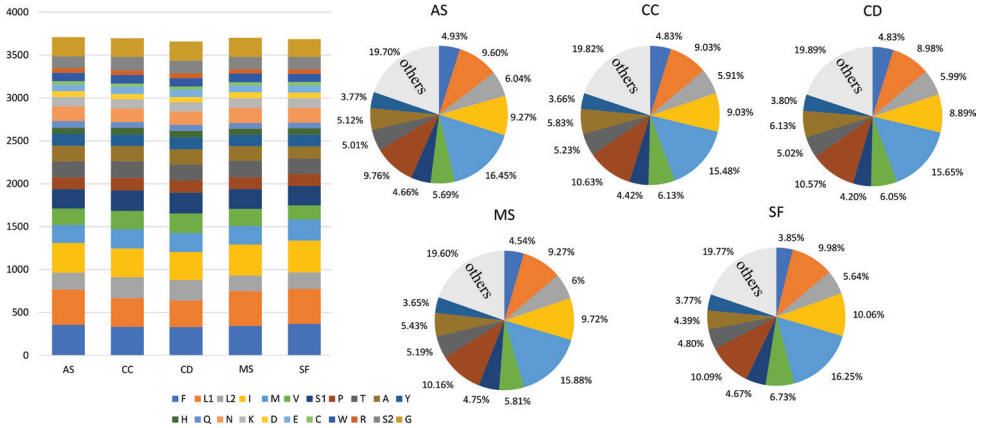

Figure 1. Numbers of different amino acids in the mitogenomes of the five buprestid species; the stop codon is not included. AS: *Agrilus sichuanus*, CC: *Coraebus cloueti*, CD: *Coraebus diminutus*, MS: *Meliboeus sinae*, and SF: *Sambus femoralis*.

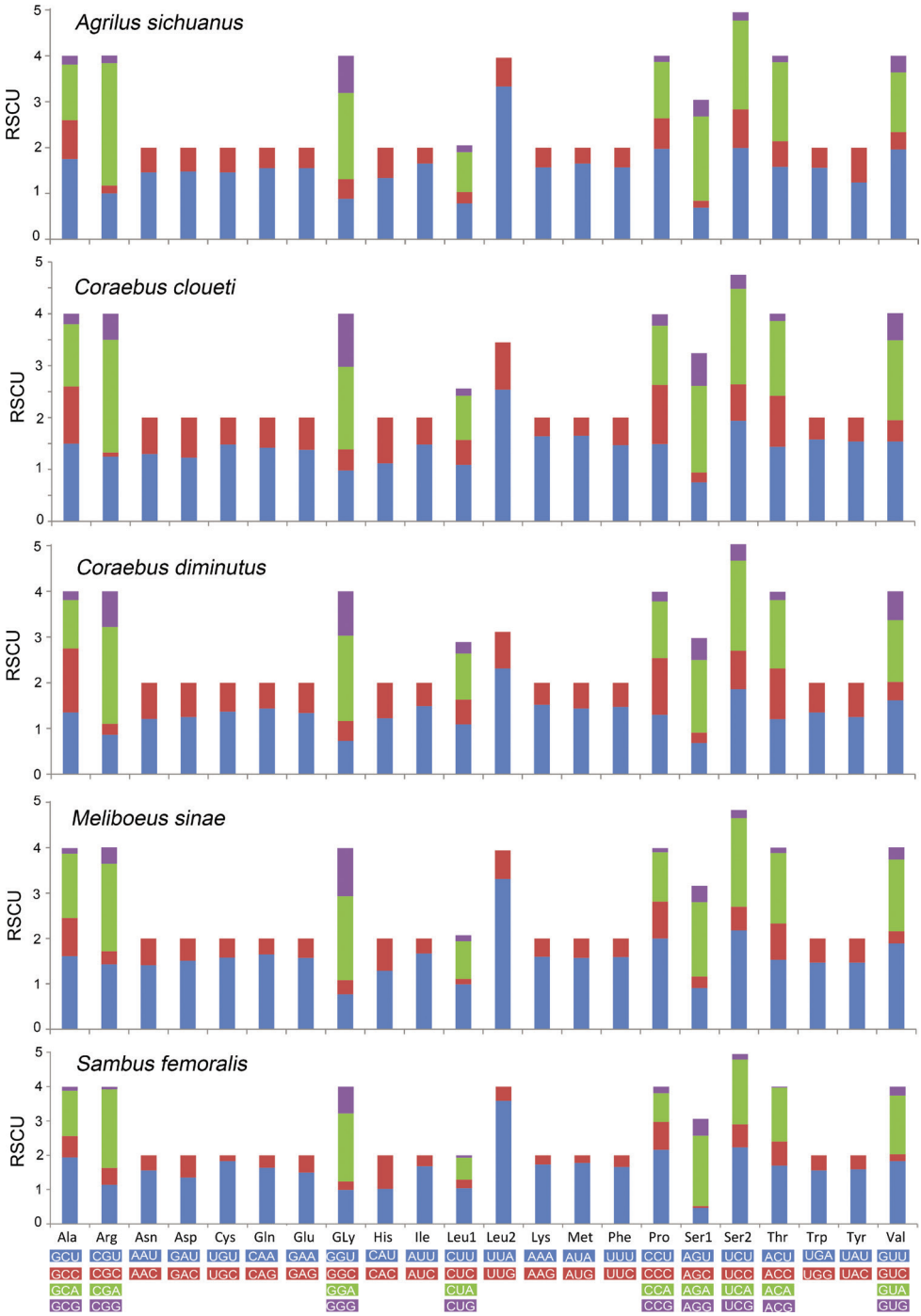

Figure 2. RSCU (relative synonymous codon usage) of the mitogenomes of the five buprestid species; the stop codons are not included.

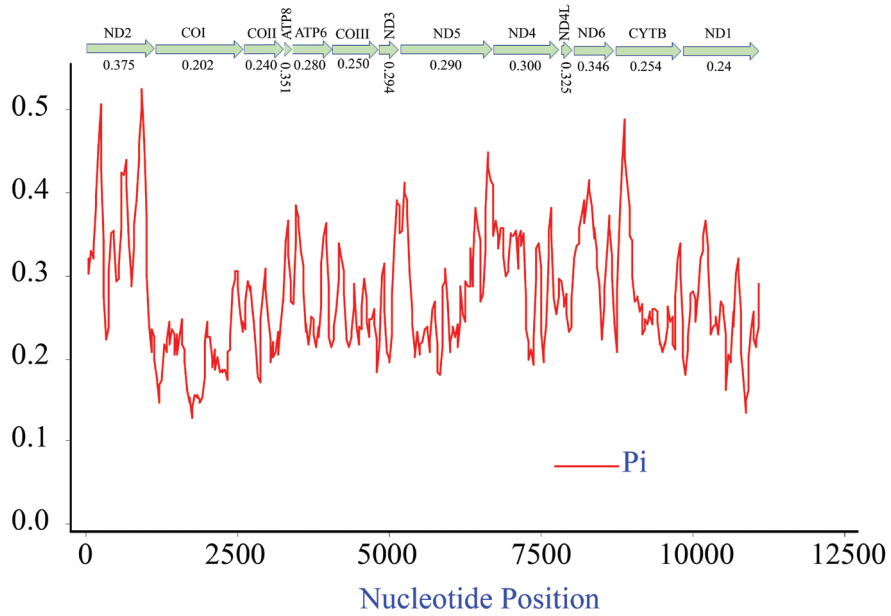

Figure 3. Nucleotide diversity (Pi) of 13 PCGs among five newly sequenced Agrilinae mitogenomes.

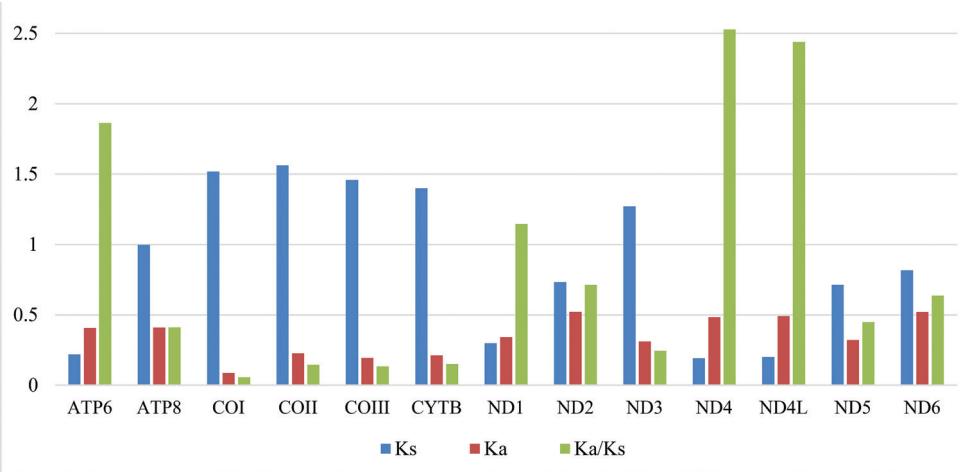

Figure 4. The ratio of Ka/Ks of 13 PCGs among the 15 reported Buprestidae mitogenomes.

tRNA, rRNA genes, and heterogeneity

The length of *rrnL* genes ranged from 1258 bp (*S. femoralis*) to 1271 bp (*A. sichuanus*), whereas *rrnS* ranged from 696 bp (*S. femoralis*) to 718 bp (*C. diminutus*). The A + T content of the rRNA genes ranged from 75.20% (*C. diminutus*) to 77.33% (*M. sinae*) (Table 3). Compared with those in other sequenced buprestid mitogenom-

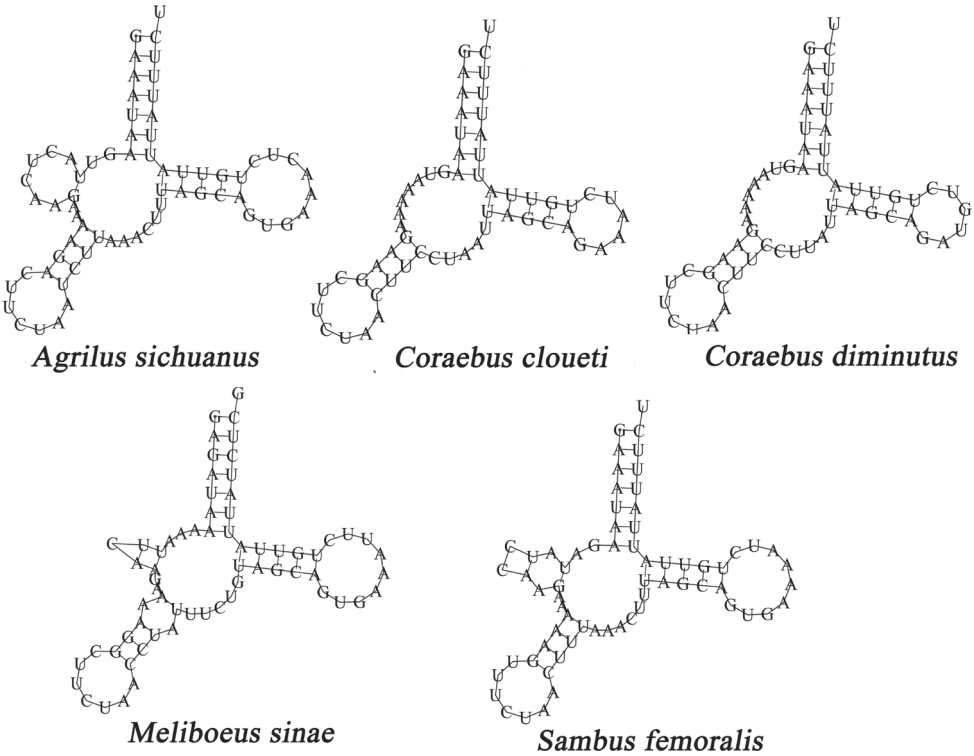

Figure 5. The predicted secondary structures of the tRNA-Ser in the mitogenomes of the five buprestid species.

es, the rRNA genes in these five newly sequenced buprestid mitogenomes are highly conserved (Hong et al. 2009; Duan et al. 2017; Cao and Wang 2019a, 2019b; Xiao et al. 2019; Sun et al. 2020; Chen et al. 2021; Peng et al. 2021). These rRNAs were located between the CR and *trnL1*, and separated by *trnV*. The total lengths of the 22 tRNA genes ranged from 1414 bp (*C. cloueti*) to 1444 bp (*C. diminutus*), whereas individual tRNA genes typically ranged in size from 58 to 70 bp, among which, eight tRNAs were encoded on the N-strand and the remaining 14 encoded on the J-strand. The secondary structures of tRNAs showed a standard clover-leaf structure (Suppl. material 1: Figs S2–S6), except for tRNA-Ser (Fig. 5) which lacks or has an unusual dihydrouridine arm, which forms a loop commonly found in other insects (Xiao et al. 2011; Park et al. 2012; Yu et al. 2016; Yan et al. 2017; Yu and Liang 2018; Li et al. 2019). In *A. sichuanus*, the longest intergenic nucleotide (774 bp) was located between *trnW* and *trnC*, which is an interesting and specific phenomenon in Buprestidae. The degree of heterogeneity of the 13 PCGs dataset was higher than that of the two rRNAs dataset (Suppl. material 1: Fig. S7). Additionally, the heterogeneity in sequence divergences was slightly stronger for *Coraebus* than for other buprestid genera (Suppl. material 1: Fig. S7).

Control region

The CR, also known as the A + T-rich region (Wolstenholme 1992), was the largest non-coding region and located between *trnI* and *rrnS*. The length of CR ranged from 910 bp (*S. femoralis*) to 1577 bp (*M. sinae*). The A + T content (74.17–78.38%) of the CR of these five species was found to be higher than that of the whole genome (68.42–73.23%), PCGs (66.05–72.50%), rRNAs (75.20–77.33%), and tRNAs (70.95–73.85%) (Table 3). Moreover, the compositional analysis revealed that the mitogenomes of the five buprestid species had a positive AT skew (0.02–0.18) in the CR. In these five species, only *C. cloueti* and *C. diminutus* had no tandem repeat element detected; however, those of *A. sichuanus* (20 and 40 bp), *M. sinae* (53 bp), and *S. femoralis* (265 bp) had different lengths.

Phylogenetic analyses

Both ML and BI trees using three datasets produced identical topologies (Figs 6–8), (Buprestinae + ((Chrysochroniae + Polycestinae) + Agrilinae)), in terms of subfamily-level relationship. The monophyly of Buprestidae is corroborated again, as all the buprestid species converged together as an independent clade, and two outgroup taxa obviously separated from the buprestid clade. The target species *C. diminutus*, *C. cloueti*, *Meliboeus sinae*, *Agrilus sichuanus*, and *Sambus femoralis*, as well as other species of Agrilinae, converged together as an independent clade. And the target species, *M. sinae*,

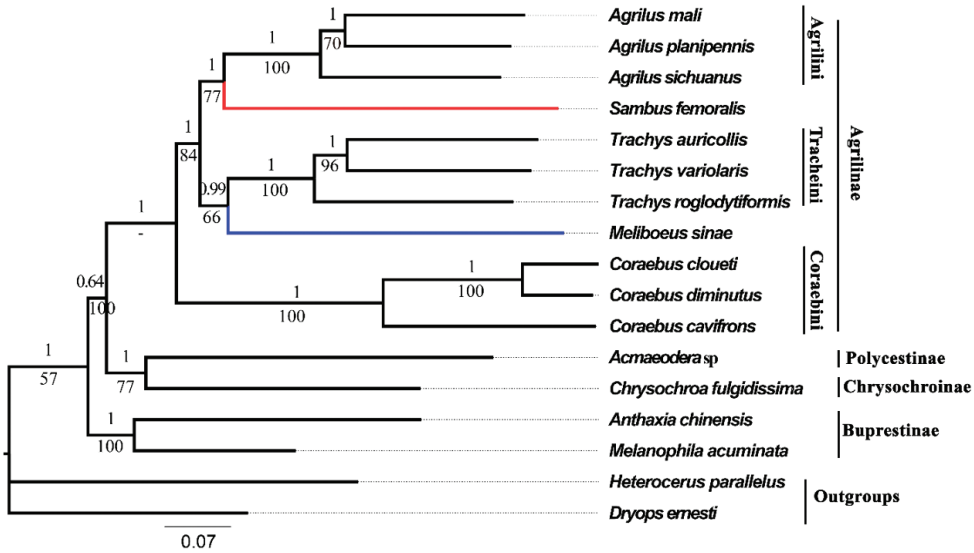

Figure 6. Phylogenetic relationships of 15 selected buprestid species using both BI and ML analyses based on 13 PCGs of mitogenomes. The numbers on the branches show posterior probability (BI tree), whereas the values under branches are bootstrap (ML tree).

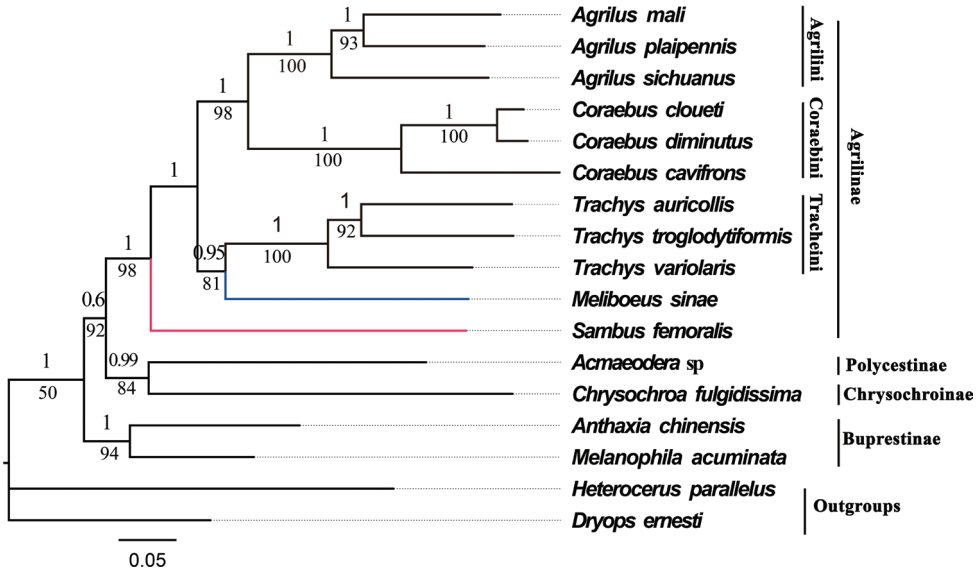

Figure 7. Phylogenetic relationships of 15 selected buprestid species using both BI and ML analyses based on 2 rRNAs of mitogenomes. The numbers on the branches show posterior probability (BI tree), whereas the values under branches are bootstrap (ML tree).

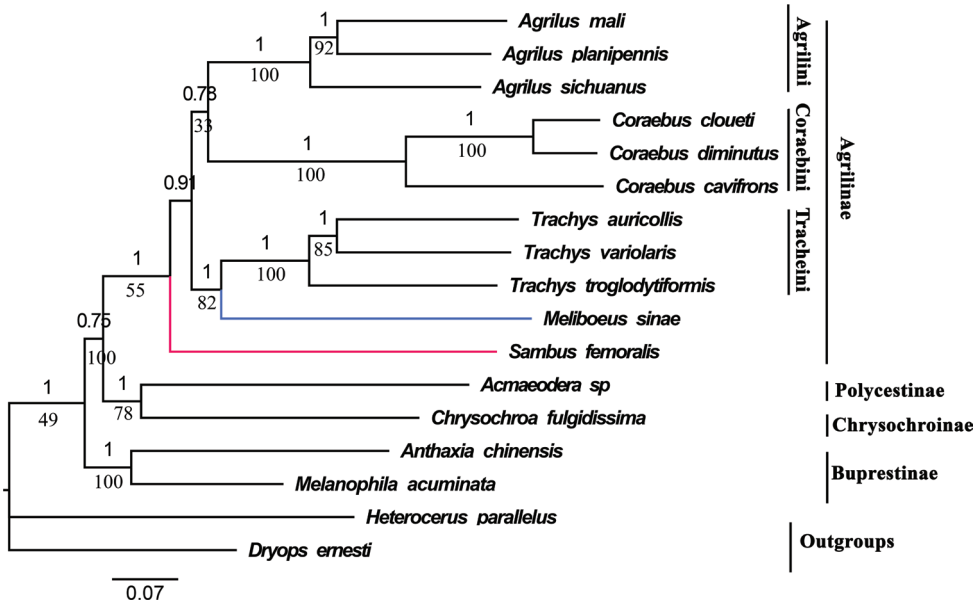

Figure 8. Phylogenetic relationships of 15 selected buprestid species using both BI and ML analyses based on 13 PCGs + 2 rRNAs of mitogenomes. The numbers on the branches show posterior probability (BI tree), whereas the values under branches are bootstrap (ML tree).

was most closely related to the genus *Trachys* with high value support (Figs 6–8) which is inconsistent with the previous studies (Kubáň et al. 2000; Evans et al. 2015). The relationship of Agrilinae clades obtained from 2 rRNAs and 13 PCGs + 2 rRNAs datasets are identical but with different topology from the 13 PCGs dataset. In the topology generated from the 13 PCGs dataset, *S. femoralis* and *Agrilus* were clustered into a single branch with high support value (Fig. 6, ML: 77, BI: 1) whereas, in the topology generated from the 2 rRNAs and 13 PCGs + 2 rRNAs datasets, *S. femoralis* split from base of the Agrilinae clades (Figs 7, 8). Based on these results the position of the genus *Sambus* in the tribe Agrilini was not suitable and suspect. The different tree topologies suggested that the rRNA genes were extremely valuable for the phylogenetic analysis of Agrilinae. Coraebini is the most diverse tribe in Agrilinae, and 10 subtribes are defined (Kubáň et al. 2000). The genus *Meliboeus* (Meliboeina) and *Coraebus* (Coraebina) in different clades suggested that the tribe Coraebini was polyphyletic, which is consistent with the previous study of Evans et al. (2015). The samples used in this study might be too limited for a comprehensive phylogeny of Buprestidae which still needs a deep study in the future.

Conclusions

In this study, five mitogenomes (15,367–16,521 bp) were newly sequenced and annotated, including representatives from the tribes Coraebini and Agrilini in subfamily Agriinae. The mitogenomes of the genera *Sambus* and *Meliboeus* are reported for the first time. These five sequences showed a positive AT skew, and the amino acids Leu, Ile, Phe, Ser2, Gly, Met, and Val were most frequently used. The secondary structures of tRNA-Ser are absent the D-arm, which is similar to other orders of Insecta. The rRNA genes are valuable for phylogenetic analyses of Agrilinae as they could affect the tree topologies. The results show that Coaebini is polyphyletic, and the genus *Sambus* belongs to neither Coaebini nor Agrilini. However, more mitogenome samplings are needed to resolve the phylogeny of the Buprestidae in the future to better understand the phylogenetics of jewel beetles.

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Supplementary material 1

Figures S1–S7

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Data type: Images (pdf file)

Explanation note: Figure S1. The mitogenome maps of *Agrilus sichuanus*, *Coraebus cloueti*, *Coraebus diminutus*, *Meliboeus sinae*, and *Sambus femoralis*. Figure S2. The secondary cloverleaf structure for the tRNAs of *Agrilus sichuanus*. Figure S3. The secondary cloverleaf structure for the tRNAs of *Coraebus cloueti*. Figure S4. The secondary cloverleaf structure for the tRNAs of *Coraebus diminutus*. Figure S5. The secondary cloverleaf structure for the tRNAs of *Meliboeus sinae*. Figure S6. The secondary cloverleaf structure for the tRNAs of *Sambus femoralis*. Figure S7. Heterogeneous sequence divergence within datasets 13 PCGs and 2 rRNAs of Buprestidae species.

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