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Revision of the birch-associated genus *Massalongia* (Diptera, Cecidomyiidae), with description of a new species from Japan and a taxonomic key to worldwide species

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Abstract

Betula (Betulaceae), or birch, is a Holarctic genus of trees and shrubs whose species have ornamental, industrial, and medical importance. Gall midges of the genus *Massalongia* (Diptera: Cecidomyiidae: Cecidomyiidi) are exclusively associated with birches in the Palearctic region. In 2018, an undescribed *Massalongia* species was discovered forming leaf galls on the midveins of *B. grossa* on Mount Tara, Saga Prefecture, Kyushu, Japan. In this study the species is described as *M. nakamuratetsui* Elsayed & Tokuda, **sp. nov.**, and a DNA barcode provided for it. The other known species of Massalongia are redescribed because the original descriptions are outdated and insufficient. A lectotype is designated for *M. bachmaieri*. In addition, the monotypic genus *Apagodiplosis*, containing *A. papyriferae* associated with *B. papyrifera* in the Nearctic region, is synonymized here under *Massalongia*, resulting in *M. papyriferae* **comb. nov.**, rendering *Massalongia* a Holarctic genus with six species. Comparing the sequence data of *M. nakamuratetsui* with all sequences available in The Barcode of Life Data (BOLD) system supports the occurrence of

Massalongia in the Nearctic region and suggest that more species could be discovered there. *Massalongia* species form leaf or bud galls, and their mature larvae drop to the ground in autumn and overwinter in characteristic waterproof bottle-like cocoons, which is possibly a protective adaptation for pupation in wet and snowy lands. A taxonomic key to all *Massalongia* species is provided.

Keywords
Betula, Betulaceae, Cecidomyiidi, cocoon, DNA barcode, gall midges

Introduction

Betula L. (Betulaceae), or birch, is a genus of trees and shrubs broadly distributed in the northern hemisphere, from the sub-tropics to the arctic. *Betula* species are valued by gardeners and landscapers and are commonly planted in urban areas, roadsides, and parks (Shaw et al. 2014). They constitute the most important sources of hardwood in northern Europe and are also used as fuel and the production of tool handles, barrels, toys and musical instruments (Praciak 2013). Some *Betula* species were used in traditional medicine in different regions of the world (Huh et al. 2011; Al-Snafi 2015; Rastogi et al. 2015). Moreover, some birches are used for the production of tea and beer (Svanberg et al. 2012; Praciak 2013). Thus, investigations on insect fauna associated with birches are important for identifying potential pest species.

At least 17 species of phytophagous gall midges (Diptera: Cecidomyiidae: Cecidomyiinae) are known to occur on *Betula* worldwide, including seven species of *Semudobia* Kieffer, 1913a (Lasiopteridi: unplaced to tribe), four species of *Massalongia* Kieffer, 1897 (Cecidomyiidi: unplaced to tribe), two species each of *Anisostephus* Rübsaamen, 1917 (Cecidomyiidi: Cecidomyiini) and *Dasineura* Rondani, 1840 (Lasiopteridi: Dasineurini), and one species each of *Resseliella* Seitner, 1906 and *Apagodiplosis* Gagné, 1973 (Cecidomyiidi: unplaced to tribe) (Gagné and Jaschhof 2017). In Japan, three gall midge species are known to occur on *Betula*. Namely, *Semudobia betulae* (Winnertz, 1853), *S. tarda* Roskam, 1977, and *S. skuhravae* Roskam, 1977 (Roskam 1977).

Two of us, K. Ohta and S. Yoshida, discovered leaf galls on *B. grossa* Siebold & Zucc. induced by a gall midge species on Mount Tara, Saga Prefecture, Kyushu, Japan (Fig. 1) during the course of our field investigations. Morphological examinations indicated that the gall midge is an undescribed species of the Palearctic genus *Massalongia*. In this study we review *Massalongia* and describe the Japanese species as new to science. In addition, we synonymize the Nearctic genus *Apagodiplosis* under *Massalongia* because no differences were found between the two genera.

Materials and methods

Collecting and rearing. Leaves with galls on main leaf veins on *B. grossa* (Fig. 1) were collected from Nakayama camp site (elevation 550 m a.s.l.), Mount Tara, Saga Prefecture, Japan (32°59'8"N, 130°5'40"E) in late August and late September 2018. Galls were dissected under a stereoscopic microscope and larvae were preserved in 75% ethanol for morphological examinations and 99.5% ethanol for molecular analysis.

Mature larvae inside their cocoons (Figs 2, 3) were collected from leaf litter under the galled tree in the same location as the earlier leaf collection. Some cocoons were cut open to retrieve larvae and preserve them in 75% ethanol. Remaining cocoons were transferred to plastic cups containing a mixture of peat moss and sand following Elsayed et al. (2018a). The cups were half buried in the soil and maintained until the beginning of March 2019 in a research farm of Faculty of Agriculture, Saga University, Saga Prefecture (elevation 5.5 m a.s.l.). After the cups were brought back to the laboratory, gall midge adults emerged in late March 2019. Adults were preserved in 75% ethanol and pupal exuviae were preserved in 99.5% ethanol.

Morphological examination and terminology. Gall midge specimens of the newly described species and *M. bachmaieri* Möhn, 1958 were mounted on microscope slides in Canada balsam following the technique outlined in Gagné (1994), except for the clearing step for the larval and adult specimens following Elsayed et al. (2018b). The slide–mounted specimens were examined under a bright–field and phase–contrast microscope (CX43, Olympus, Tokyo) and line illustrations were made with a mechanical pencil with the aid of a drawing tube. These illustrations were scanned and inked using Apple Pencil 2 and the application Procreate (version 5.0.3) on iPad Pro 2018 (Apple Inc., California). Photomicrographs were taken with a digital camera (DP22, Olympus, Tokyo) attached to a semi-motorized fluorescence microscope (BX53, Olympus, Tokyo).

Morphological terminology mainly follows Kirk-Spriggs and Sinclair (2017) for adults. Larval and pupal terminology follow Gagné (1994). All types of the newly described species are deposited in the collection of Entomological Laboratory, Faculty of Agriculture, Kyushu University, Japan (ELKU).

The ethanol-preserved adults, pupal exuviae and larvae of *M. bachmaieri* were borrowed from the collection of Staatliches Museum für Naturkunde, Stuttgart (SMNS) The holotype and paratypes of *M. betulifolia* Harris, 1974 adults were borrowed from the Natural History Museum in London, United Kingdom (BMNH). The ethanol-preserved larvae of *M. rubra* (Kieffer, 1890) were obtained from the collection of Marcela Skuhravá and mounted on slides following the technique mentioned above.

DNA extraction, sequencing, and alignment. The total DNA was extracted from the whole body of three second instars and one third instar of the Japanese species using the NucleoSpin Tissue kit (Macherey Nagel, Germany) following the manufacturer's protocol. Fragment of the mitochondrial cytochrome oxidase subunit I (COI) gene was amplified using a TaKaRa Ex Taq (Takara Bio Inc., Shiga, Japan) and following set of primers: J–1718 (5'–GGA GGA TTT GGA AAT TGA TTA GTT CC–3') (Simon et al. 1994) and COIA (5'–CCC GGT AAA ATT AAA ATA TAA ACT TC–3') (Funk et al. 1995). The PCR products were purified using ExoSAP-IT reagent (Affymetrix Inc., USB products, Ohio, USA). The sequencing reaction was performed using the BigDye Terminator Cycle Sequencing Reaction Kit (Applied Biosystems, Foster City, CA, USA). Ethanol precipitation was used for post-reaction cleanup, and an ABI 3130 sequencer (Applied Biosystems) was

Figures 1–3. *Massalongia nakamuratetsui* sp. nov. **1** leaf galls (red arrows) on *B. grossa* **2** overwintering larva in cocoon on leaf litter **3** bottle-shaped cocoon.

used for sequence determination. The obtained sequences were aligned using the software MEGA (ver. 6.0) (Tamura et al. 2013), and were deposited in the DNA Data Bank of Japan (DDBJ), European Molecular Biology Laboratory (EMBL), and GenBank (http://www.ncbi.nlm.nih.gov/genbank).

Results

Taxonomy

Genus *Massalongia* Kieffer, 1897

Massalongia Kieffer, 1897: 12. Type species, *Hormomyia rubra* Kieffer by original designation.
Apagodiplosis Gagné, 1973: 862. Type species, *Oligotrophus papyriferae* Gagné, comb. nov.

Diagnosis. *Massalongia* differs from other genera of the supertribe Cecidomyiidi in the following combination of characters: antennal flagellomeres are cylindrical in both sexes; male flagellomeres possess three sets of short-looped circumfila that appear interconnected at least in some flagellomeres of each specimen; the reduced abdominal setation; the unmodified female tergite VIII; the presence of dorsal pigmentation on the protrusible part of ovipositor; the massive gonocoxites and mediobasal lobes; the habit of mature larvae to pupate in the soil inside hyaline bottle-shaped cocoons. The following diagnosis lists the attributes shared by known species and can serve as a checklist for future species descriptions.

Description. *Adults. Head.* Eye bridge 5–6 facets long; facets rounded. Occiput without dorsal protuberance (Fig. 4). Mouthparts (Fig. 5): labrum with short setae and no microtrichia; hypopharynx microtrichose; labellum ellipsoid, with stout setae laterally; palpus 3-segmented, consecutively longer, microtrichose, with scattered setae and no scales. Antenna (Figs 6–9): scape conical, pedicel rounded; flagellomeres cylindrical in both sexes, successive flagellomeres diminishing gradually in length; flagellomeres I–II connate. Female flagellomeres with 2 sets of interconnected circumfila. Male flagellomeres with 3 sets of short-looped circumfila, some flagellomeres with interconnected circumfila.

Thorax (Figs 10, 11). Wing hyaline; Rs present but rudimentary; R_{4+5} curved toward apex, joining C posteriad of wing apex; C not broken after the conjunction with R_{4+5}. Acromere: claws untoothed, bent beyond midlength; empodia longer than claws. Scutum with 4 rows of numerous setae. Anepimeron with setae. Anepisternum and katepisternum bare.

Female abdomen (Figs 12–15). Tergites I–VII entire, rectangular, without scales, with anterior pair of trichoid sensilla; tergites I–VI with 1 row of posterior setae; tergite VII with 1–2 rows of posterior setae; tergite VIII unpigmented, differentiated from remainder of tergum only by anterior pair of trichoid sensilla, without scales and setae. Sternites II–VI with scattered setae near midlength, 1 posterior row of setae; sternites III–VII with anteromedial pair of trichoid sensilla; sternite VIII unpigmented, without anterior pair of trichoid sensilla, with scattered setae posteriorly. Ovipositor: protrusible portion with stiff dorsal sclerite, scattered setae ventrally and few setae dorsally; cerci separate, bilaterally flattened, with 2 slightly thickened sensory setae at apex; hypoproct with 2 apical setae.

Male abdomen. Tergites I–VII as in female; tergite VIII short, sclerotized only anteriorly, with anterior pair of trichoid sensilla located on the sclerotized part. Sternites II–VI as in female; sternite VII with anteromedial pair of trichoid sensilla, scattered setae near midlength and 1–2 posterior rows of setae; sternite VIII short, with pair of trichoid sensilla placed anterolaterally and 2–3 posterior rows of setae. Terminalia (Figs 16–18): Gonostylus covered mostly with microtrichia and setae dorsally and ventrally, with comb-like denticles; gonocoxite robust, massive, with enlarged mediobasal lobes and microtichose; hypoproct elongate, constricted after midlength, without setae dorsally, with setae posteroventrally.

Pupa (Figs 19–20). Exuviae not pigmented except antennal horns and prothoracic spiracles. Two asetose and 2 setose cephalic papillae present. Prothoracic spiracle long, slightly curved. Abdominal spiracles present on segments II–VI. Abdominal segments I–VII each with 6 dorsal papillae. Dorsal and lateral parts of abdominal segments covered evenly with pointed spinules, diminishing gradually in length and width, except on posterior third.

Mature larva. Spatula bilobed (Fig. 22) or absent (Fig. 39). Ventral papillar pattern basic for Cecidomyiidi (Gagné 1989). One asetose anal papilla present on each side of anal opening; other 2 asetose papillae situated posterolaterally, each on separate plaque (Fig. 23). Six dorsal papillae present on thoracic segments and abdominal segments I–VII; 2 setose dorsal papillae present on abdominal segment VIII.

Remarks. Comparisons with other possibly related genera revealed that the Nearctic genus *Apagodiplosis* Gagné, which contains a single species, *A. papyriferae* (Gagné), fits the definition of *Massalongia* (Gagné, 1973). No differences were found between the two genera (Gagné 1967, 1973). Thus, we synonymize *Apagodiplosis* under *Massalongia* and *M. papyriferae* (Gagné) is a new combination.

Taxonomic key to species of *Massalongia*

1 Gonostylus with pointed denticles (e.g. Fig. 33) **2**
– Gonostylus with blunt denticles (e.g. Fig. 16) **3**
2 Aedeagus cylindrical; male hypoproct entire or slightly notched and as long as cerci (Figs 33, 35) .... ***M. bachmaieri* Möhn, 1958**
– Aedeagus narrowed at midlength; male hypoproct notched, longer than cerci (based on Fedotova 1991) .... ***M. altaica* Fedotova, 1990**
3 Male hypoproct entire; larva without spatula and with 4 corniform terminal papillae .... ***M. betulifolia* Harris, 1974**
– Male hypoproct bilobed; larva with bilobed spatula and 4 setose and 4 corniform terminal papillae **4**
4 Aedeagus enlarged apically and longer than hypoproct (Fig. 52) .... ***M. rubra* (Kieffer, 1890)**
– Aedeagus cylindrical and shorter than hypoproct **5**
5 Gonostylus curved distally; ovipositor has dorsal pigmentation on distal 2 thirds of protrusible portion; anterior lobes of larval spatula curved medially .... ***M. papyriferae* (Gagné, 1967)**
– Gonostylus not curved distally (Fig. 16); ovipositor has dorsal pigmentation along protrusible portion (Figs 14, 15); anterior lobes of larval spatula directed anteriorly (Fig. 22) .... ***M. nakamuratetsui* Elsayed & Tokuda, sp. nov.**

Massalongia nakamuratetsui **Elsayed & Tokuda, sp. nov.**

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Description. *Head* (Figs 4–9). Eyes separated on vertex by diameter of 0.0–1.25 facets. Frons with 3–9 setae (n = 9). Mouthparts: labrum with 8–10 setae (n = 9); hypopharynx with thick microtrichia on edges; labellum microtrichose, with 4–5 setae (n = 5); palpal segments consecutively longer. Antenna: scape and pedicel microtrichose and with few ventral setae on basal half; flagellomeres III–XII usually with few microtrichia concentrated on base of node; male flagellomere XII sometimes pointed apically.

Thorax (Figs 10, 11). Wing 2.6–2.9 mm long in males (n = 6), 3.1–3.3 mm long in females (n = 3). Anepimeral setae 11–17 (n = 9).

Female abdomen (Figs 12–15). Tergites I–VII with few lateral setae. Ovipositor: stiff dorsal sclerite present along protrusible portion, posteriorly wider than anteriorly; protrusible portion ca. 1.3 as long as tergite VII; cerci elongated, with scattered setae lateroapically; hypoproct short.

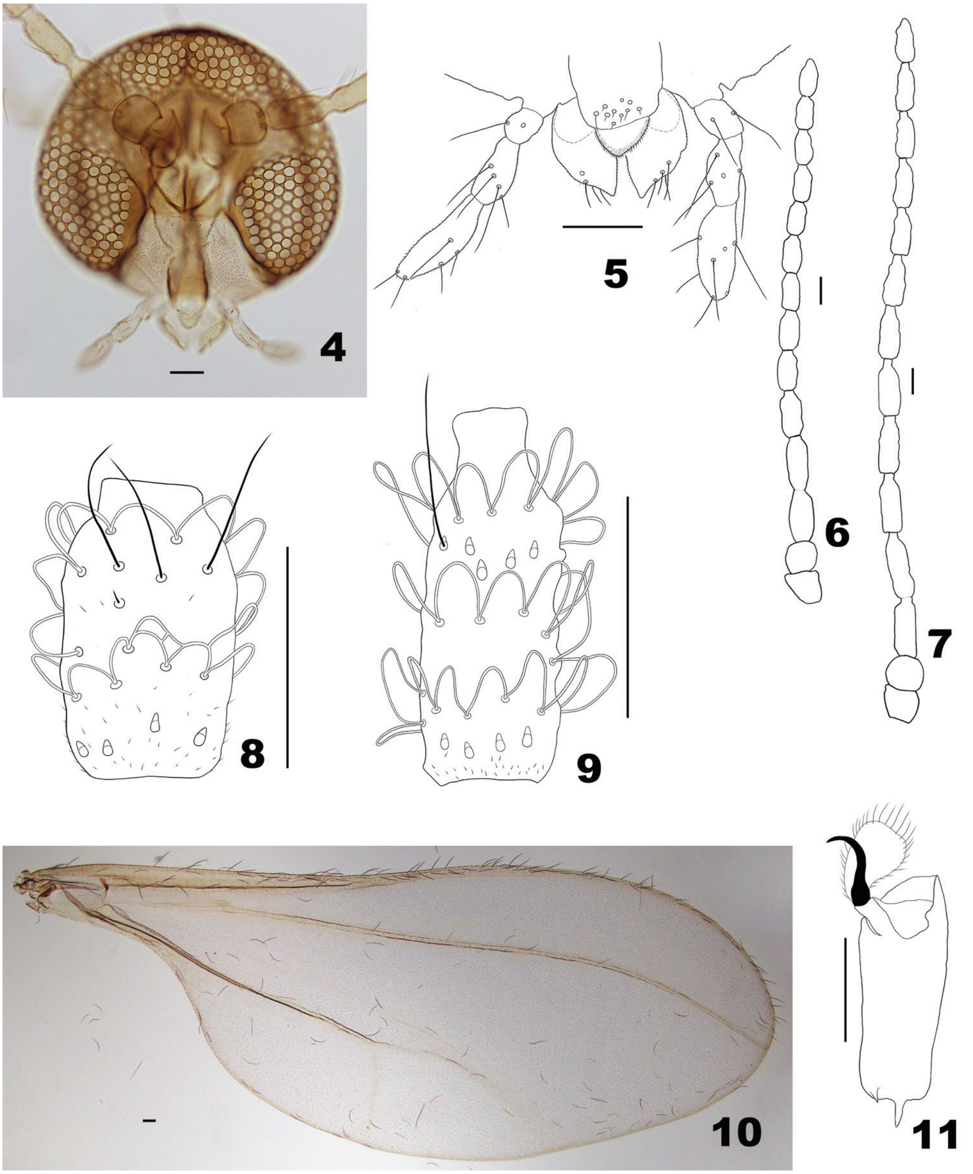
Male abdomen. Tergite VIII without posterior row of setae. Terminalia (Figs 16–18): gonostylus with blunt denticles, ventrally with cluster of short setae near base; cerci with tapered and setose apex, basal part of cerci without setae; hypoproct bilobed, narrowed after midlength; aedeagus shorter than cerci and hypoproct, cylindrical in dorsoventral view, wide basally in lateral view.

Pupa (Figs 19–21). Antennal horns with short, acute, apical protuberances; 2 setose and 2 asetose lower facial papillae present; 1 asetose and 2 setose lateral facial papillae present on each side. Prothoracic spiracle, about 270 μm long, with trachea extending to tip. Abdominal terga I–VII each with 4 setose and 2 asetose dorsal papillae; terga VIII with 4 setose dorsal papillae. Abdominal terga II–VIII with 3–4 median rows of slightly wider and longer spinules than surrounding ones.

Mature larva (Figs 22–24). In life, orange. Spatula short and bilobed. Dorsal papillae without setae on thoracic segments, with setae on abdominal segments. Two asetose pleural papillae on thoracic segments; 2 setose and 1 asetose pleural papillae on abdominal segments. Terminal segment with 8 papillae: 4 corniform and 4 setose.

Etymology. The species is named in honor of the late Japanese physician Dr. Tetsu Nakamura in recognition to his lifelong dedication to supporting poor people and his significant contributions to the development of Afghanistan. Dr. T. Nakamura was fatally shot by extremists on 4 December 2019 in Afghanistan, exactly on the date when we prepared the first draft of this paper and were considering what to name the species. In this way, we wish to immortalize his contributions to humanity.

Type material. *Holotype*. 1♂ (ELKU): Reared from larvae in bottle-like cocoons collected under *B. grossa* by A. K. Elsayed on 15.xii.2018 from Mount Tara, Saga Prefecture, Japan on 15.xii.2018, emerged on 15.iii.2019. ***Paratypes***. All reared from larvae in bottle-like cocoons collected under *B. grossa* by A. K. Elsayed at the type locality, as follows. 3 larvae: obtained from cocoons on 15.xii.2018; 1 pupal exuviae: emerged on 23.iii.2019; 2♂, 1♀, 2 pupal exuviae: emerged on 27.iii.2019; 2♂, 2♀: emerged on 30.iii.2019; 1♂: emerged on 4.iv.2019.

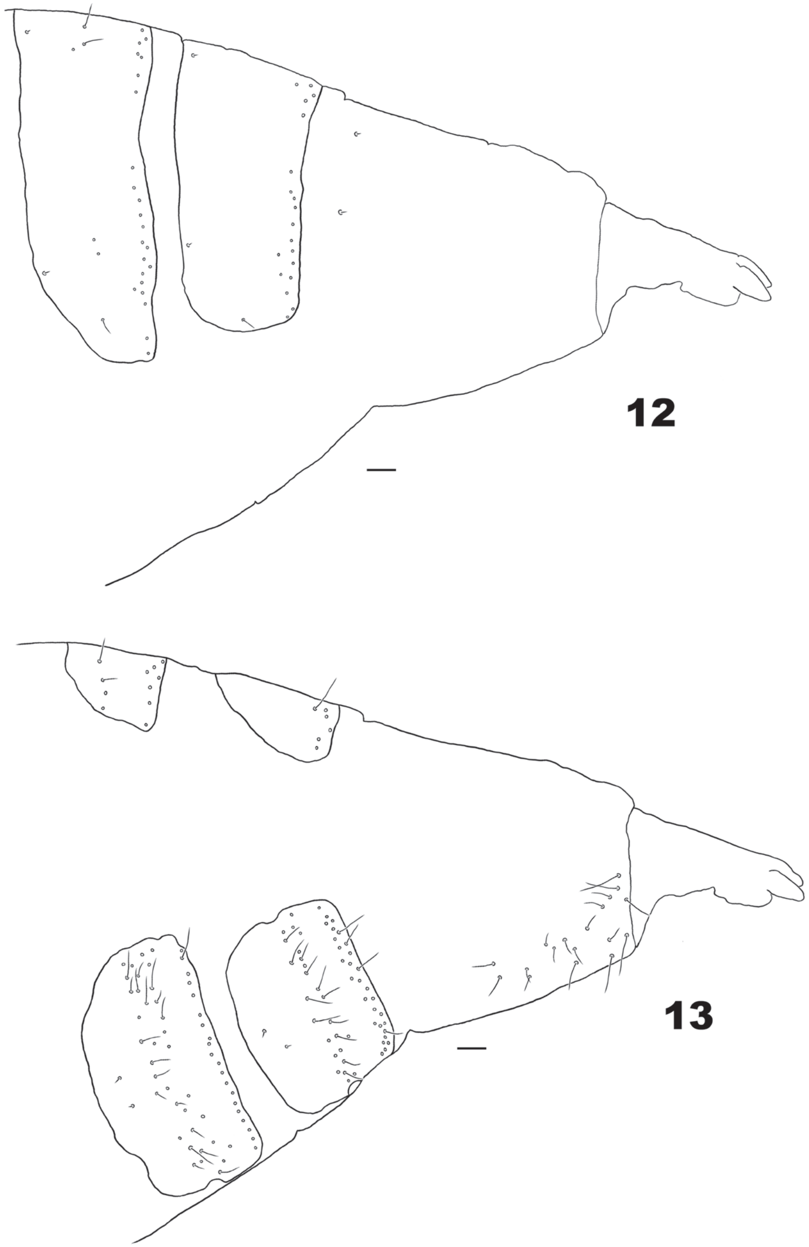


Figures 4–11. *Massalongia nakamuratetsui* sp. nov. **4** head **5** ventral view of mouthparts **6** female antenna **7** male antenna **8** dorsal view of female flagellomere V. **9** dorsal view of male flagellomere V. **10** wing **11** tarsomere V and acromere. Scale bars: 50 µm.

DNA accession numbers. LC557490–LC557493.

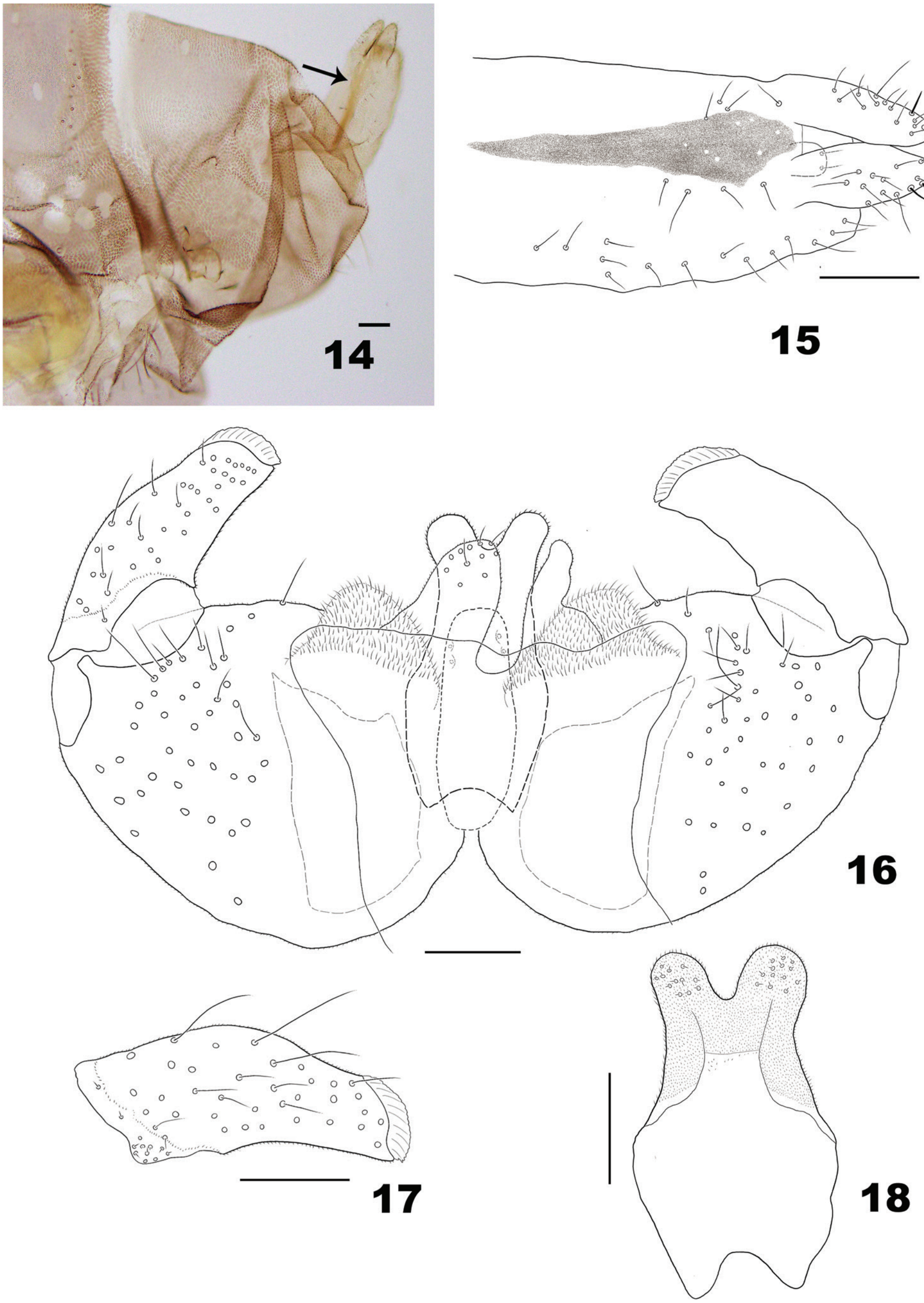
Distribution. Japan: Kyushu Island, Saga Prefecture.

Gall and life history. *Massalongia nakamuratetsui* forms galls on the midveins of *B. grossa* (Fig. 1). One leaf can bear several galls and some galls become fused with larvae occupying separate chambers. Galls are 1.52–3.10 mm in diameter and 6.46–

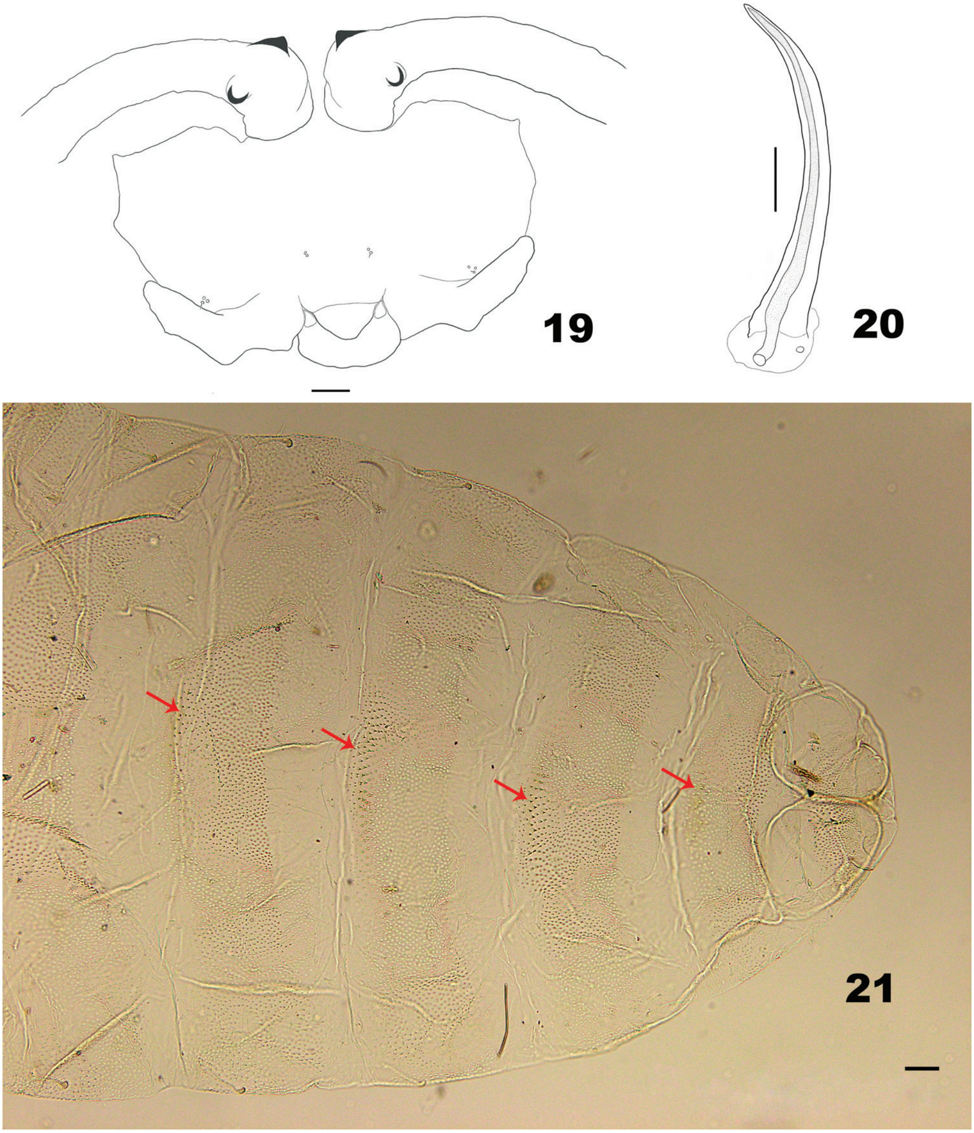


Figures 12–13. Terminal part of female abdomen of *Massalongia nakamuratetsui* sp. nov. **12** dorso-lateral view **13** ventro-lateral view. Scale bars: 50 μm.

18.03 mm long. Galls collected at the end of August contained white first instars. Larvae develop to second and mature larvae by the end of September. In late October, the mature larvae leave the galls to overwinter in the ground, where they spin hyaline, bottle-shaped cocoons on leaf litter (Figs 2, 3). The cocoon of *M. nakamuratetsui* is



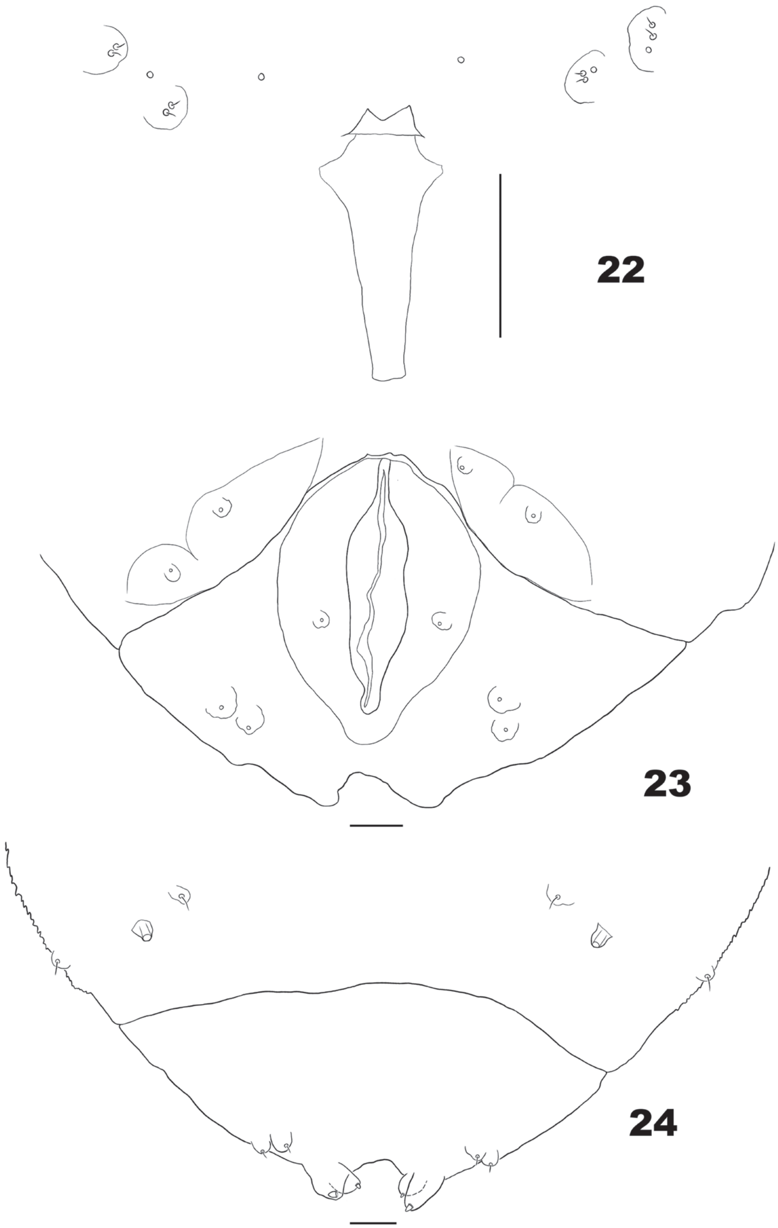
Figures 14–18. *Massalongia nakamuratetsui* sp. nov. **14** terminal part of female abdomen (arrow indicate the dorsal sclerite on the protrusible portion) **15** protrusible portion of ovipositor **16** male terminalia **17** ventral view of gonostylus **18** ventral view of male hypoproct. Scale bars: 50 µm.



Figures 19–21. Pupa of *Massalongia nakamuratetsui* sp. nov. **19** ventral view of head **20** prothoracic spiracle **21** dorsal view of terminal part of abdomen (arrows indicate dorsal spines). Scale bars: 50 µm.

waterproof and does not allow water to reach the overwintering larva (Suppl. material 1: Video S1). Adults emerge between the end of March and the beginning of April.

Remarks. *Massalongia nakamuratetsui* is most similar to *M. papyriferae*, sharing a bilobed sternal spatula, four setose and four coniform larval terminal papillae, gonostyli ending with blunt denticles and bilobed male hypoproct (Gagné 1967, 1973). They can be separated as follows: anterior lobes of spatula are directed anteriorly in *M. nakamuratetsui*, but curved toward each other in *M. papyriferae*; gonostylus is less



Figures 22–24. Larva of *Massalongia nakamuratetsui* sp. nov. **22** spatula **23** ventral view of terminal abdominal segments **24** dorsal view of terminal abdominal segments. Scale bars: 50 µm.

curved distally in *M. nakamuratetsui* compared to *M. papyriferae*; ovipositor has dorsal pigmentation along the protrusible portion in *M. nakamuratetsui*, but only on the distal two thirds in *M. papyriferae*.

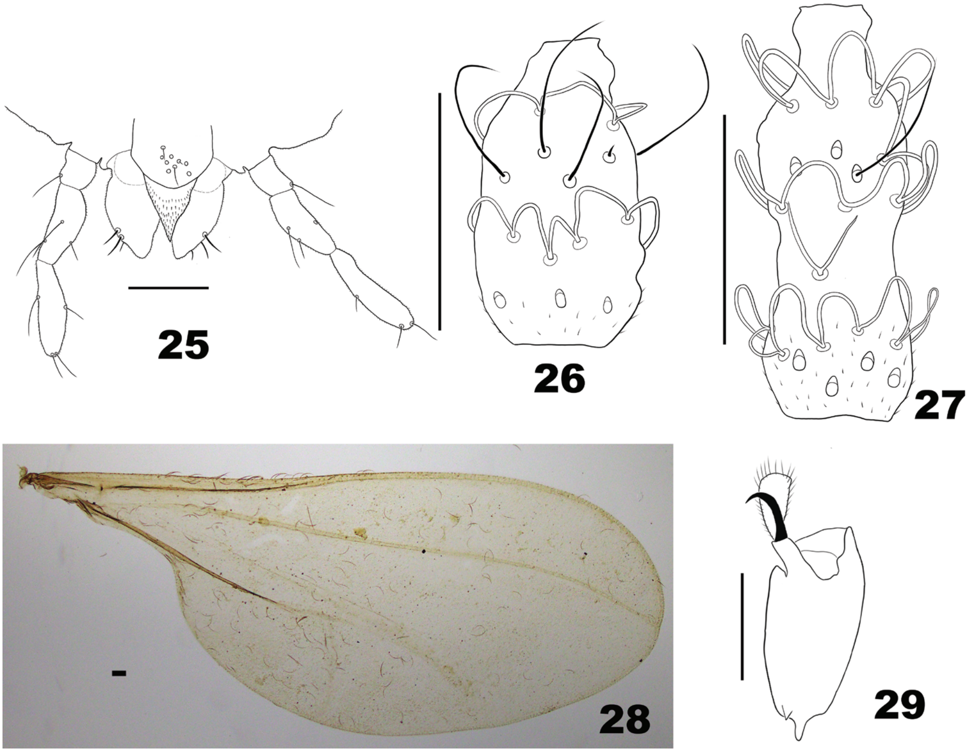
Massalongia bachmaieri Möhn, 1958

Description. *Head* (Figs 25–27). Eyes separated on vertex by diameter of 0.0–1.5 facets. Frons with 3–9 setae (n = 6). Mouthparts: labrum with 8–17 short setae (n = 9), hypopharynx pointed, mostly microtrichose; labellum with 4–5 stout setae (n = 5) laterally. Antenna: scape and pedicel with few ventral setae.

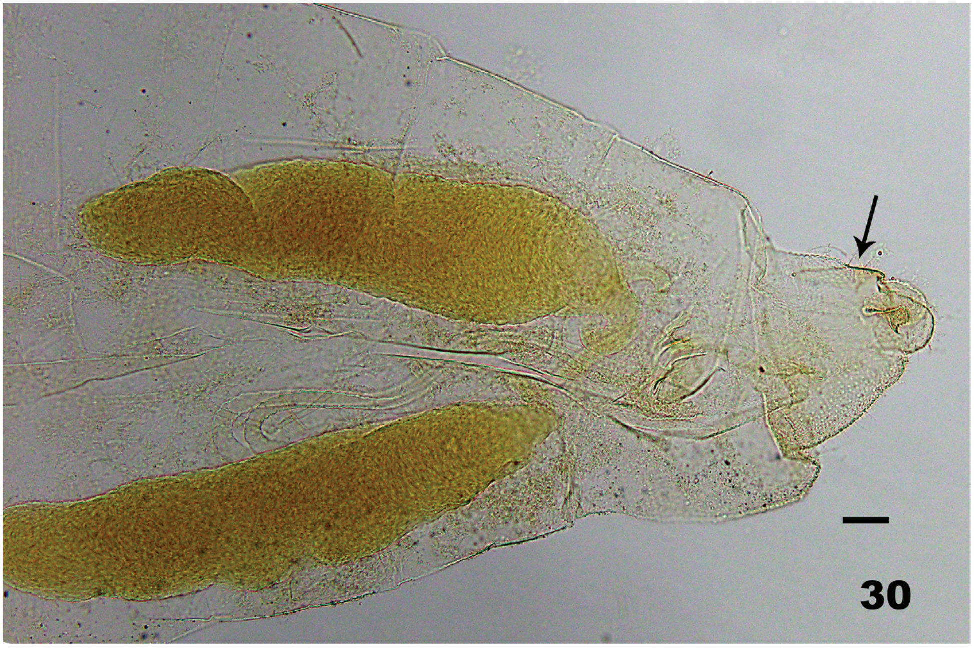
Thorax (Figs 28, 29). Wing 2.10–2.25 mm long in males (n = 4), 2.10–2.30 mm long in females (n = 4). Anepimeral setae 3–6 (n = 6).

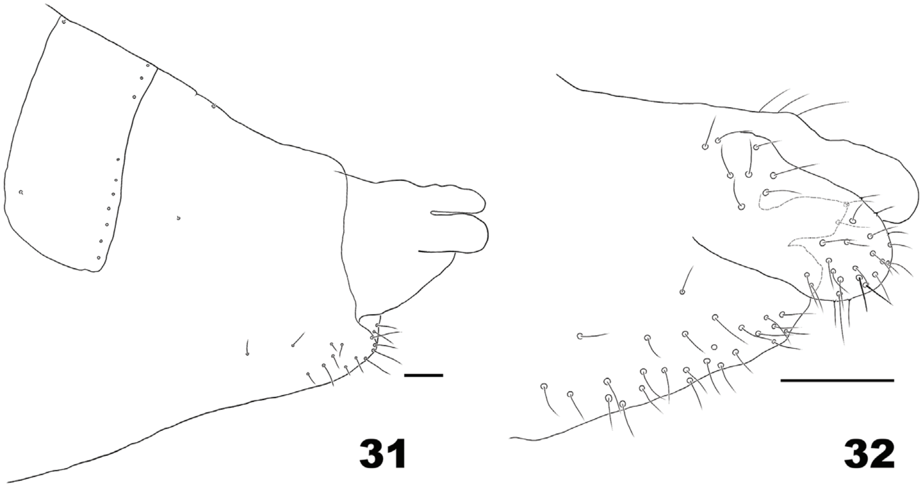
Female abdomen (Figs 30–32). Ovipositor: protrusible portion ca. 1.2 as long as tergite VII, with dorsal sclerite on posterior 2 thirds; cerci elongate-ovoid, with dorsal setae on base, and scattered setae apically.

Male abdomen. Tergite VIII with posterior row of setae. Terminalia (Figs 33–35): gonostylus with pointed denticles; cerci base with setae; cerci with setae on apical margin; hypoproct entire, slightly notched, narrowed after basal third; aedeagus shorter than cerci and hypoproct, cylindrical in dorsoventral view, wide basally in lateral view.



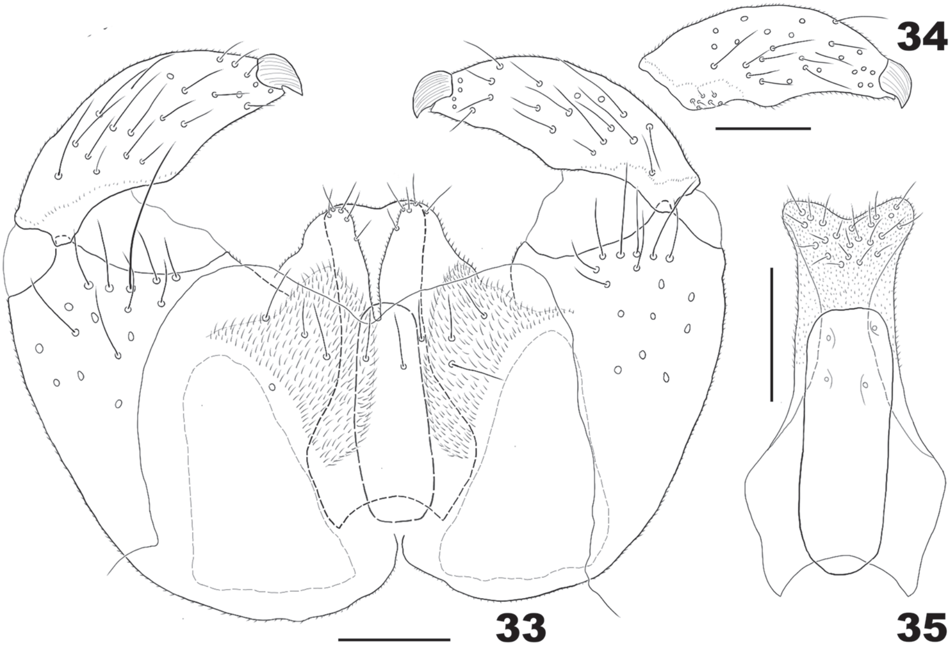
Figures 25–29. *Massalongia bachmaieri*. **25** ventral view of mouthparts **26** ventral view of female flagellomere V. **27** ventral view of male flagellomere III **28** wing **29** tarsomere V and acromere. Scale bars: 50 µm.





Figures 30–32. *Massalongia bachmaieri.* **30–31** terminal part of female abdomen (arrow in Fig. 31 indicate the dorsal sclerite on the protrusible portion) **32** protrusible portion of ovipositor. Scale bars: 50 µm.

Pupa (Figs 36–38). Head and thorax of exuviae slightly pigmented; abdomen not pigmented. Antennal horns with short, acute, apical protuberances. Two setose lower facial papillae present; 1 asetose and 1 setose lateral facial papillae present on each side. Prothoracic spiracle long, ca. 210 µm, with trachea extending to just before tip. Abdominal segment VIII with 2 setose dorsal papillae. Abdominal terga II–VIII with 2–3 median rows of wider and longer spinules than surrounding ones.



Figures 33–35. *Massalongia bachmaieri*. **33** male terminalia **34** ventral view of gonostylus **35** ventral view of male hypoproct and aedeagus. Scale bars: 50 µm.

Mature larva (Figs 39–41). Orange to red (Bachimaier 1965). Spatula absent. Terminal segment with 6 papillae: 2 tiny corniform and 4 setose papillae.

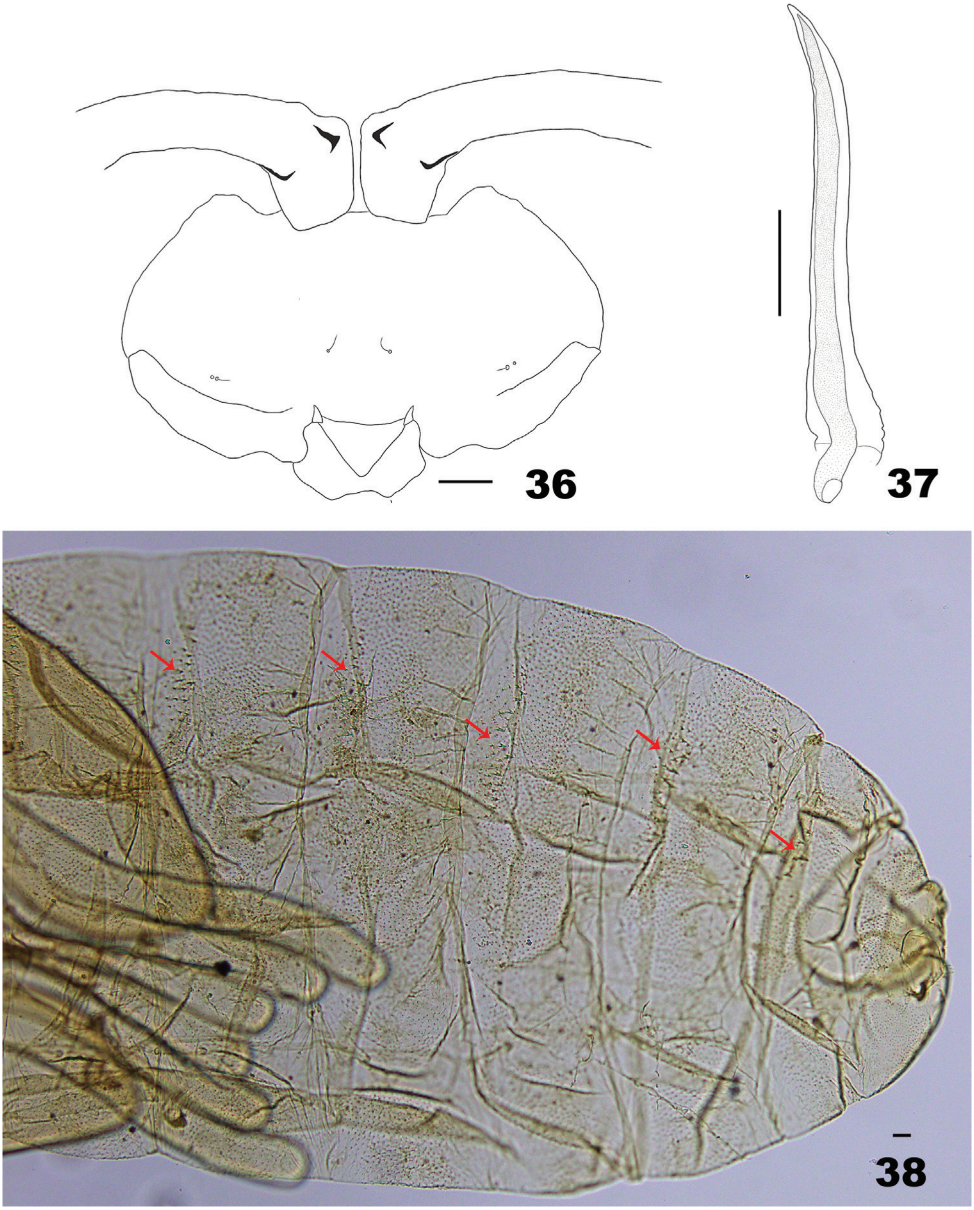
Material examined. *Lectotype*. 1♂ (SMNS): obtained from Möhn collection Nr. 1205. *Paralectotypes*. 8 larvae collected on 10.iv.1954 from leaf galls on *B. nana*, Bernrieder Filz; 3♂, 4♀, 2 pupal exuviae in Möhn collection Nr. 1205.

Distribution. Europe: Germany and Russia (Gagné and Jaschhof 2017).

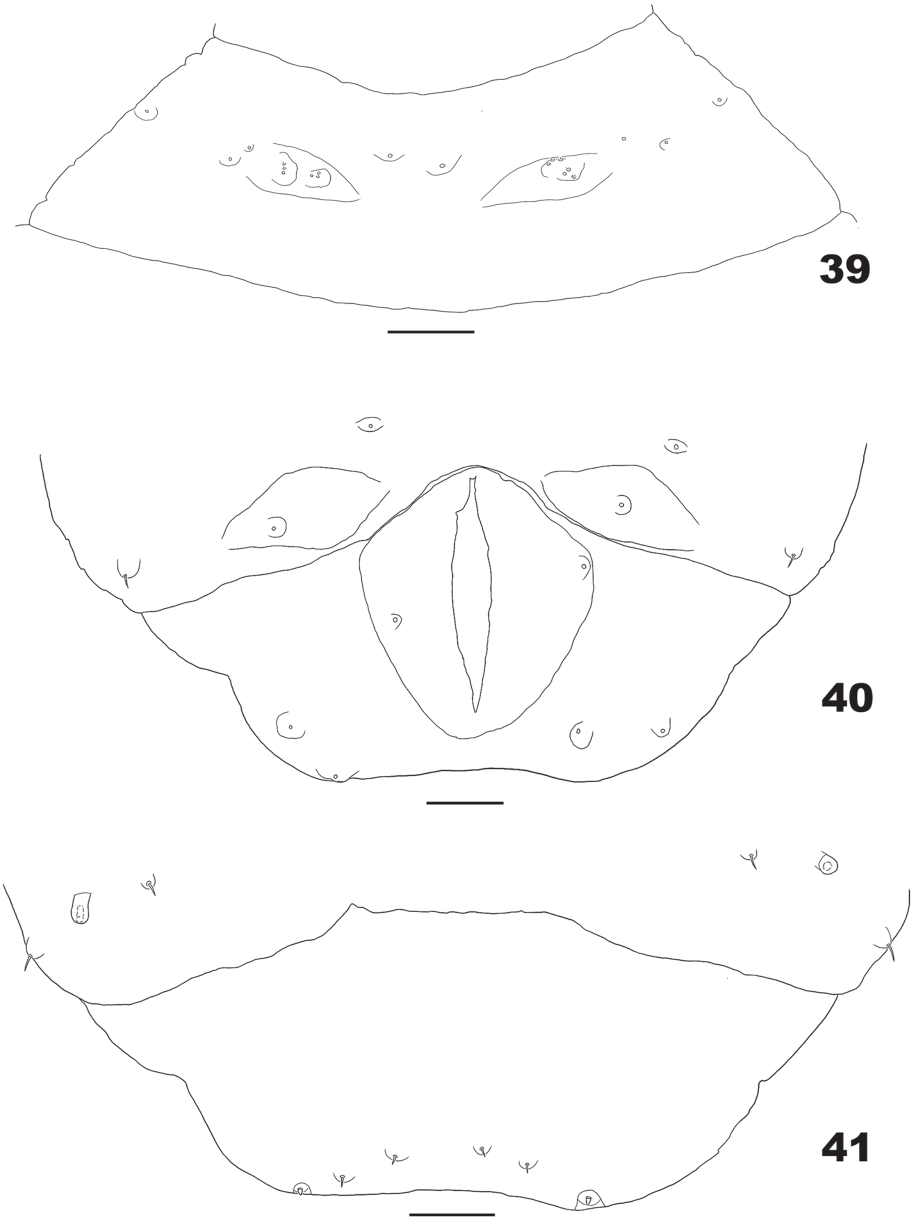
Gall and life history. *Massalongia bachmaieri* induces parenchymal leaf galls on *B. nana* (Fig. 42). Mature larvae leave the galls and drop to the ground in mid to late October. They overwinter in cocoons that are spun on the fallen leaves. This species has one generation a year (Möhn 1958; Bachimaier 1965).

Remarks. Möhn (1958) designated a male specimen as a holotype of *M. bachmaieri* and two males and a female as paratypes. When we requested the types for this study, we found that all specimens deposited in SMNS were preserved in alcohol. Möhn probably prepared his illustrations of the species from temporary slide mounts and then put the specimens back in alcohol with the others. Because it was not possible to determine Möhn's holotype and paratypes among these ethanol-preserved specimens, we designated a lectotype and paralectotypes from the permeant slide-mounted specimens we prepared.

Adults of *M. bachmaieri* are morphologically most similar to *M. altaica*. See more under *M. altaica* below.



Figures 36–38. Pupa of *Massalongia bachmaieri*. **36** ventral view of head **37** prothoracic spiracle **38** dorsal view of terminal part of abdomen (arrows indicate dorsal spines). Scale bars: 50 µm.



Figures 39–41. Larva of *Massalongia bachmaieri*. **39** ventral view of prothoracic segment **40** ventral view of terminal abdominal segments **41** dorsal view of terminal abdominal segments. Scale bars: 50 µm.

Figure 42. Ethanol-preserved leaf gall of *Massalongia bachmaieri* on *B. nana*.

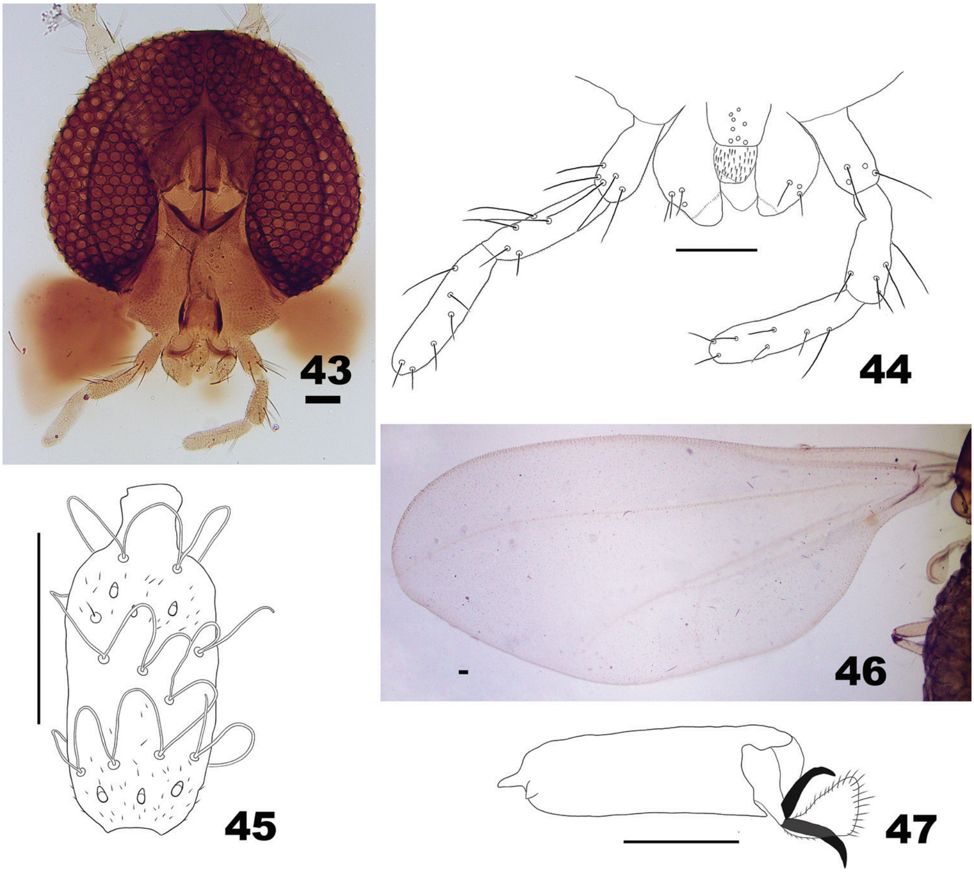
Massalongia betulifolia Harris, 1974

Description. *Head* (Figs 43–45). Eyes separated on vertex by diameter of 0.5–1.25 facets. Frons with 7–12 setae (n = 5). Mouthparts: labrum with 6–11 short setae (n = 5), hypopharynx pointed, covered with thick microtrichia; labellum with 5–8 stout setae (n = 4) laterally. Antenna: scape and pedicel with few ventral setae on basal third of segment.

Thorax (Figs 46, 47). Wing 2.8–3.0 mm long in males (n = 2), 3.1–3.2 mm in females (n = 2). Anepimeral setae 6–10 (n = 6).

Female abdomen (Figs 48, 49). Tergites I–VI bare posteromedially; tergite VII with entire posterior row of setae. Ovipositor: protrusible portion with, ca. 2 times as long as tergite VII, with dorsal sclerite almost along dorsal portion; cerci setose.

Male abdomen. Tergites I–VII as in female; tergite VIII with few setae posteriorly. Terminalia (Figs 50, 51): gonostylus with blunt denticles; cerci base with few setae; cerci with setae apically; hypoproct entire, narrowed at midlength; aedeagus shorter than cerci and hypoproct, cylindrical in dorsoventral view, wide basally in lateral view.



Figures 43–47. *Massalongia betulifolia*. **43** head **44** ventral view of mouthparts (hypopharynx is folded). **45** dorsal view of male flagellomere VIII **46** wing **47** tarsomere V and acromere. Scale bars: 50 µm.

Mature larva. Spatula absent. Terminal segment with short conical papillae (Harris 1974).

Pupa. Exuviae generally unpigmented. Antennal horns short (Askew and Ruse 1974).

Materials examined. *Holotype* (BMNH): 1♂, emerged on vi.1971, reared by J. Ruse from larva forming lamina and midrib blister galls on *Betula pendula* leaves, collected on x.1970 from Lindow Common, Cheshire, England. ***Paratypes***: 4♂, 2♀, data same as for holotype.

Distribution. Europe: England and Norway (Gagné and Jaschhof 2017).

Gall and life history. *Massalongia betulifolia* forms blister-like leaf galls on *B. pendula* and *B. pubescens*. Galls are formed usually between or on veins and are 2.5–3.0 mm wide and 5.0–6.0 mm long. Mature larvae drop to the ground to overwinter in cocoons. Adults emerge probably in May and June, and the galls can be found on the trees between June to October (Harris 1974; Askew and Ruse 1974).

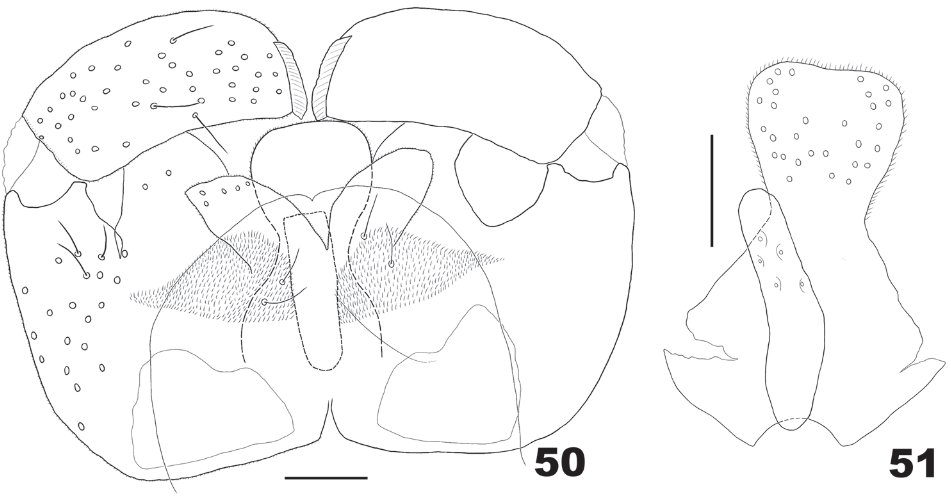
Remarks. See Remarks under *M. bachmaieri* and *M. nakamuratetsui*.

Figures 48–49. *Massalongia betulifolia.* **48** terminal part of female abdomen (arrow indicate the dorsal sclerite on the protrusible portion) **49** protrusible portion of ovipositor. Scale bars: 50 µm.

Massalongia rubra (Kieffer, 1890)

Hormomyia rubra Kieffer, 1890: 199.
Oligotrophus ruber Kieffer, 1895: lxxi.

Description. *Female abdomen*. Ovipositor: protrusible portion long; cerci elongated; hypoproct short (Kieffer 1913b).



Figures 50–51. *Massalongia betulifolia*. **50** male terminalia **51** ventral view of male hypoproct and aedeagus. Scale bars: 50 µm.

Male abdomen. Terminalia: gonostyli with blunt denticles; cerci with rounded tips, shorter than hypoproct; hypoproct notched; aedeagus longer than hypoproct, with enlarged tip (Fig. 52) (Kieffer 1913b).

Mature larva (Figs 53, 54). Spatula bilobed. Dorsal papillae on thoracic segments with tiny setae. Terminal segment with 4 corniform papillae, outer 2 longer than inner ones, and 2 setose papillae.

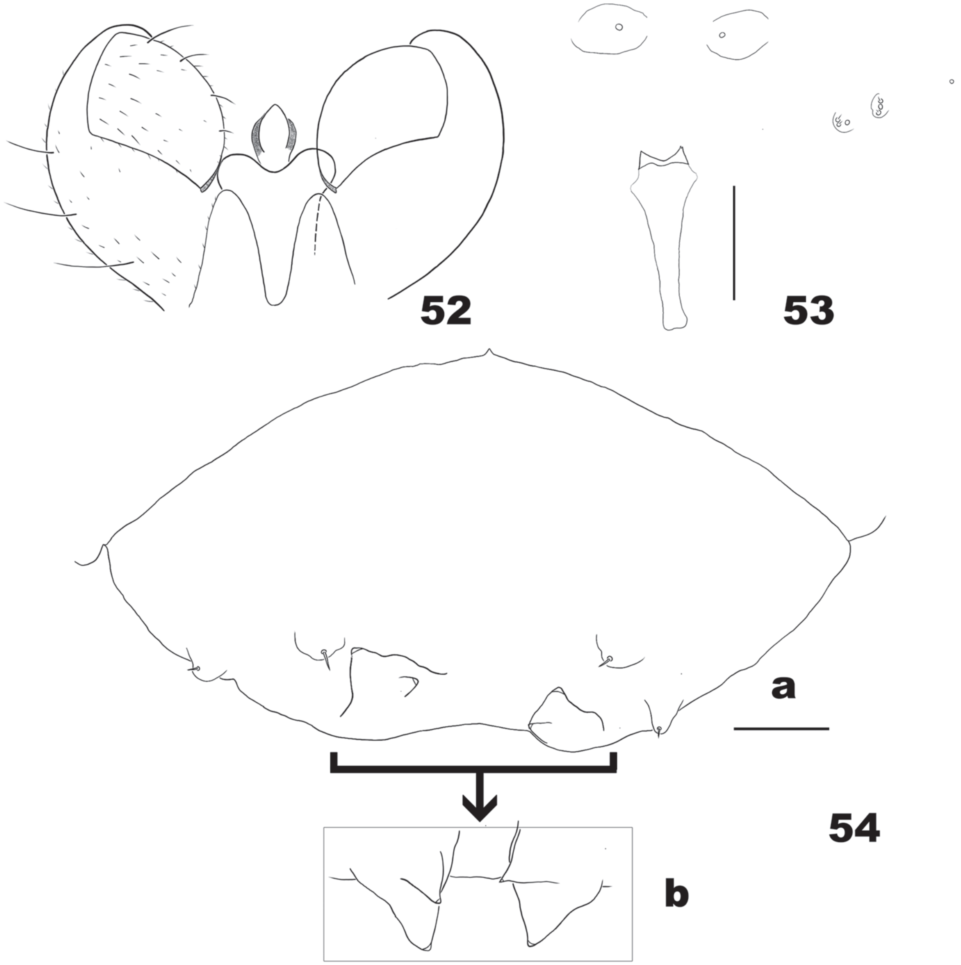
Pupa. Unknown.

Material examined. 3 larvae: collected in August 1964 from *Betula* sp. Pěčín Village, Rychnov nad Kněžnou Region, Hradec Králové, Czech Republic, M. Skuhravá leg.

Distribution. Widespread in Europe and west Asia (Gagné and Jaschhof 2017).

Gall and life history. *Massalongia rubra* induces barely noticeable midrib leaf galls on *Betula pubescens* Ehrh. and other *Betula* spp. (Gagné and Jaschhof 2017; Kieffer 1913b). The females lay eggs on young leaves in May, and most mature larvae leave the galls to overwinter in the ground in October, but some hibernate in the galls (Skuhravá and Skuhravý 1973).

Remarks. The larval specimens we described here were collected from similar galls to those described by Kieffer (1913b) for *M. rubra* and the larval morphology fits Kieffer's description and illustrations, thus we believe they indeed belong to *M. rubra*. Types of *M. rubra*, like most of Kieffer's types, are considered lost (Gagné and Jaschhof 2017). We considered using one larva for designating a neotype for the species, but because no adults were reared from these larvae, we cannot be completely certain about their identity and decided to refrain from doing so. Kieffer (1913b) provided an illustration of male terminalia showing that the species is distinctive from the other known species of *Massalongia* by its long and apically enlarged aedeagus (Fig. 52). Because this illustration is important for separating species and it was drawn from the type speci-



Figures 52–54. *Massalongia rubra*. **52** male terminalia (after Kieffer 1913b) **53** spatula **54** dorsal view of larval terminal abdominal segments (**a** the inner four terminal papillae are folded on the segment **b** the inner four terminal papillae are unfolded in another specimen). Scale bars: 50 µm.

men, future designation of a neotype for the species must rely on reared adults that will enable to compare characters of the male terminalia.

Massalongia papyriferae (Gagné, 1967), comb. nov.

Oligotrophus papyriferae Gagné, 1967: 132.
Apagodiplosis papyriferae Gagné, 1973: 862.

Description. (Based on Gagné 1967, 1973). *Head*. Frons with 2–5 setae. Male flagellomere XII tapered distally.

Thorax. Anepimeron with 7–17 setae.

Female abdomen. Tergites I–VI bare posteromedially; tergite VII with entire posterior row of setae. Ovipositor: protrusible portion with pencil-shaped dorsal sclerite on posterior 2 thirds.

Male abdomen. Terminalia: gonostyli with blunt denticles; cerci rounded; hypoproct bilobed; aedeagus shorter than cerci and hypoproct.

Pupa. Antennal horns short; 2 setose lower facial papillae present; cephalic setae short. Abdominal terga covered with uniformly tiny spinules.

Larva. Spatula short, bilobed, with anterior lobes slightly curved toward each other. Terminal segment with 4 corniform papillae and 4 setose terminal papillae.

Distribution. North America: Canada (Quebec) and USA (Washington, Oregon and Michigan) (Gagné and Jaschhof 2017).

Gall and life history. *Massalongia papyriferae* forms bud galls on the paper birch, *B. papyrifera*. The mature larva drops to the leaf litter to overwinter in a bottle-shaped cocoon. Adults emerge in spring (Gagné 1967).

Remarks. See under *M. nakamuratetsui*.

Massalongia altaica Fedotova, 1990

Description. (Based on Fedotova 1991). *Head*. Female flagellomere XII variable in shape, rounded to oblong with apical constriction; male flagellomere XII slightly tapered distally.

Thorax. Wing length 2.7 times width.

Female abdomen. Ovipositor: cerci rounded, microtrichose, without setae.

Male abdomen. Terminalia: gonostylus with pointed denticles; cerci triangular; hypoproct bilobed, longer than cerci; aedeagus widened apically and basally, shorter than hypoproct.

Pupa. Unknown.

Larva. Unknown.

Distribution. Kazakhstan: Central Altaï, Koksuïskiï Mountain Range, Lymin Belok Mt., 60 km NE of Leninogorsk (Fedotova 1991).

Gall and life history. *Massalongia altaica* form barely visible swellings, 5–7 mm long, on the leaves of *Betula nana* var. *rotundifolia* (Spach) Regel. (*B. rotundifolia* in the original description). The mature larva leaves the gall through an opening on the lower side of the leaf and overwinters in the ground (Fedotova 1991).

Remarks. *Massalongia altaica* was described from adult specimens reared from larvae that emerged from leaf galls on *B. rotundifolia*, which is currently known as a variety of *B. nana*, the same host plant of *M. bachmaieri* (The Plant List 2013). The illustration of *M. altaica* galls provided in its original description (Fedotova 1991) is quite similar to the galls of *M. bachmaieri* (Fig. 43). Morphologically, the adults of *M. altaica* are closest to *M. bachmaieri* and differ from them only in the shape of the aedeagus and male hypoproct and the relative length of cerci to male hypoproct, but these differences are based on the original description of *M. altaica* (Fedotova 1991). Because the type specimens of *M. altaica* were not available to us, we could not verify the differences between *M. altaica* and *M. bachmaieri*. A future examination of *M. altaica* types and its immature stages may result in synonymizing it under *M. bachmaieri*.

Discussion

Massalongia has been considered so far a Palearctic genus (Gagné and Jaschhof 2017), but in the present study we synonymized the Nearctic *Apagodiplosis* under *Massalongia*, thus the distribution of *Massalongia* corresponds now to that of its Holarctic host plant, *Betula* (Shaw et al. 2014). Comparing the sequence data of *M. nakamuratetsui* with all sequences available in The Barcode of Life Data (BOLD) system revealed several sequences with interspecific similarity of up to 96.85% (Ratnasingham and Hebert 2007), all from Canada (Hebert et al. 2016). The profile of one of these cecidomyiids (sequence ID: CNPKE263–14) included a photo of a female specimen that resembles *Massalongia* and the interspecific similarity was 95.3%. This strongly supports *Massalongia* as a Holarctic genus and suggests that more *Massalongia* species can be discovered in the Nearctic region.

Larvae of many gall midge species that drop to the ground are known to spin cocoons in which they overwinter and eventually pupate (Gagné 1989). Bakhshi and Grover (1976) studied cocoons of various gall midge taxa and concluded that the cocoon shape is specific to genus. The bottle-shaped cocoon of *Massalongia* has never been reported from other gall midge taxa and thus it appears to be a unique characteristic of the genus. Cocoons of many insects that overwinter in the soil provide mechanical protection against unfavorable surrounding conditions (Danks 2004). Because the cocoon of *M. nakamuratetsui* is waterproof, the bottle-like cocoons of *Massalongia* possibly represent a protective adaptation for pupation in wet and snowy lands. Further research on these cocoons is necessary in order to understand the nature of its texture and other roles of its bottle-like shape.

Acknowledgements

We are grateful to Raymond J. Gagné (Systematic Entomology Laboratory, USDA, Washington, DC, USA) for bringing *Apagodiplosis* to our attention to be synonymized, and for his valuable comments on the manuscript. We are thankful to Hans Roskam (Mathematics and Natural Sciences Institute of Biology, Leiden University, Netherlands) and Robin Adair (Australis Biological Pty Ltd, Bittern, Australia) for commenting on an early draft of the manuscript. We thank Duncan Sivell (Natural History Museum of London, UK) for arranging the loan of type specimens of *M. betulifolia*, and Daniel Whitmore and Hans-Peter Tschorsnig (Staatliches Museum für Naturkunde, Stuttgart, Germany) for arranging the loan of type specimens of *M. bachmaieri*. Ayman K. Elsayed is JSPS International Research Fellow (Graduate School of Science, The University of Tokyo, Japan).

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Supplementary material 1

Video S1

Authors: Ayman Khamis Elsayed, Marcela Skuhravá, Kazuki Ohta, Satoshi Yoshida, Makoto Tokuda

Data type: multimedia

Link: https://doi.org/10.3897/zookeys.958.54300.suppl1

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RESEARCH ARTICLE

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Two new species of *Ancystrocerus* Raffray from the Oriental region (Coleoptera, Staphylinidae, Pselaphinae)

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Abstract

Two new species of the genus *Ancystrocerus* Raffray, *A. lueliangi* **sp. nov.** (China: Yunnan) and *A. philippinus* **sp. nov.** (Philippines: Mindanao), are described, illustrated, and distinguished from related congeners.

Keywords

ant-loving beetle, biodiversity, China, Philippines, taxonomy

Introduction

The genus *Ancystrocerus* Raffray of the pselaphine tribe Tmesiphorini currently comprises ten species distributed in Indonesia (4 species), Singapore (3 species), Malaysia (2 species, 1 shared with Singapore), India (1 species), and China (1 species) (see Yin et al. 2015 for a historical review, and references therein; Newton 2020). Members of *Ancystrocerus* differ from those of all other Oriental genera of the tribe by the elongate habitus and appendages, notably long and slender maxillary palpi, and often modified antennomeres 9 and 10 in the male. The only recently described species, *A. chinensis* Yin, Wang & Li from Hainan Island, southern China, represents the northernmost record of the genus (Yin et al. 2015). The biology of the genus is largely unknown, three species (*A. rugicollis* Raffray, *A. punctatus* Raffray, *A. longicornis* Raffray) were collected by sifting, one (*A. pallidus* Raffray) was taken under bark of a rotten tree (Raffray 1895), and *A. chinensis* was found in decomposing logs inhabited by termites (Yin et al. 2015).

In the present paper, two new species occurring in China (Yunnan) and the Philippines (Mindanao) are described, one of which was sifted from a leaf litter sample in a broad-leaved forest.

Materials and methods

The type material of the new species described in this paper is deposited in the Insect Collection of Shanghai Normal University, Shanghai, China (**SNUC**). The text of the specimen label is quoted verbatim in quotation marks (‘’).

Male genital parts (tergite and sternite VIII, and aedeagus) were dissected, and are preserved in Euparal on a plastic slide pinned beneath the specimen. The habitus images were taken using a Canon 5D Mark III camera in conjunction with a Canon MP-E 65 mm f/2.8 1–5× Macro Lens, and a Canon MT-24EX Macro Twin Lite Flash was used as the light source. Images of the external characters were taken using a Leica DMC5400 color CMOS camera in conjunction with a Leica M205 C stereomicroscope. Images of the aedeagi were produced using a Canon G9 camera mounted to an Olympus CX31 microscope under transmitted light. Zerene Stacker (version 1.04) was used for image stacking. Line drawings were made using Adobe Illustrator CC 2018. All images were optimized and grouped into plates using Adobe Photoshop CC 2018.

The abdominal tergites and sternites are numbered following Chandler (2001) in Arabic (starting from the first visible segment) and Roman (reflecting true morphological position) numerals, e.g., tergite 1 (IV), or sternite 1 (III).

Taxonomy

Ancystrocerus lueliangi sp. nov.

http://zoobank.org/916A4D1B-B395-4318-BAEB-F73205C4C10A

Fig. 1

Type material. ***Holotype*: China:** ♂, ‘China: Yunnan, Yingjiang Co. (盈江县), Tongbiguan N. R. (铜壁关自然保护区), 24.6136444N, 97.5851155E, 1255 m, 28.viii.2019, Liang Lü leg.’ (SNUC).

Diagnosis. Male. Length 2.4 mm (combined length of head, pronotum, elytra and abdomen). Head and pronotum roughly punctate. Antennomeres 4 and 5 subequal in length, 9 and 10 expanded laterally, apex of antennomeres 9 and base of antennomeres 10 obliquely constricted, each with one bunch of bristles. Pronotum with small, conical discal spine. Tergites 1 and 2 (IV and V) with median carina extending through entire tergal length. Aedeagus relatively more slender, median lobe symmetrical in dorso-ventral view; endophallus with single long sclerite and two pairs of short sclerites; parameres each elongate and with two long apical setae.

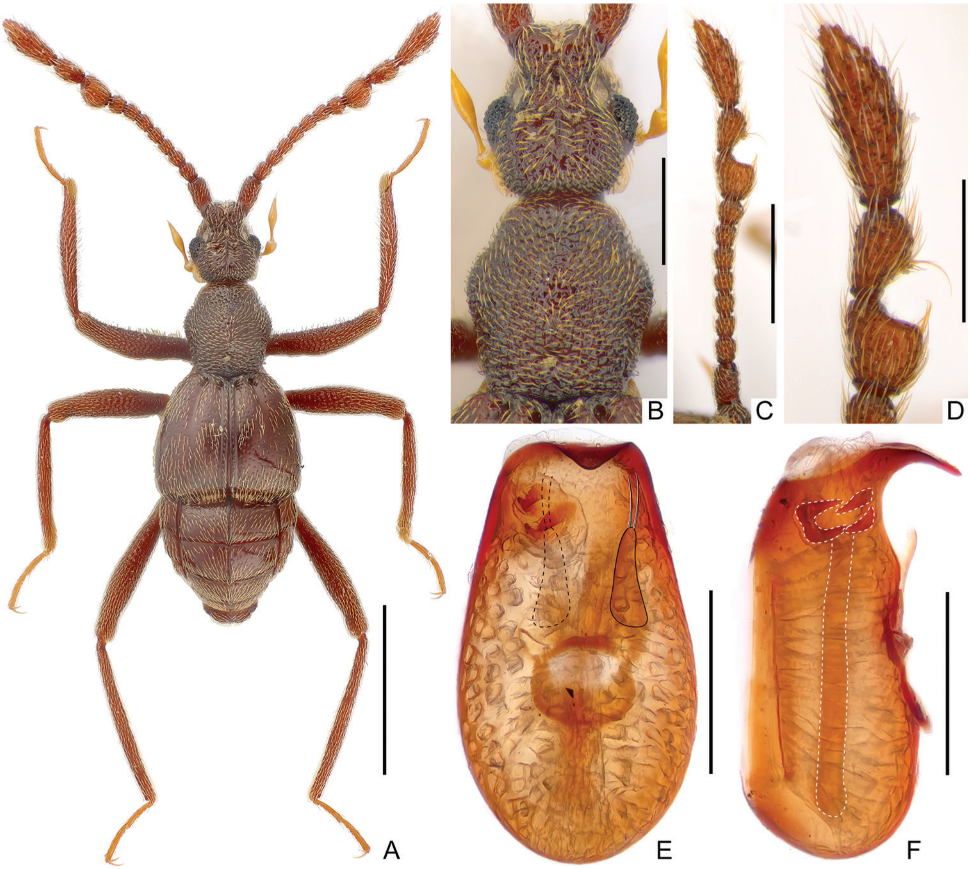

Figure 1. *Ancystrocerus lueliangi* sp. nov., male **A** habitus **B** head dorsum and pronotum **C** right antenna **D** antennal club of right antenna **E, F** aedeagus in ventral (**E**) and lateral (**F**) view. Scale bars: 1.0 mm (**A**); 0.3 mm (**B, D**); 0.5 mm (**C**); 0.2 mm (**E, F**).

Description. Male (Fig. 1A). ***Length*** 2.4 mm. ***Head*** (Fig. 1B) slightly longer than wide, length from anterior margin of clypeus to posterior margin of vertex (excluding occipital construction) 0.51 mm, width across eyes 0.43 mm; dorsal surface roughly punctate; postocular margins with dense tufted hairs; eyes prominent, each composed of about 35 facets. ***Antennae*** (Fig. 1C) elongate, with clubs (Fig. 1D) formed by apical three antennomeres; scapes large, antennomeres 2 smaller than scapes, antennomeres 3–8 each subquadrate, 8 slightly transverse and larger than each of antennomeres 2–7, antennomeres 9–10 modified, antennomeres 11 largest, elongate, widest at middle. ***Pronotum*** (Fig. 1B) slightly longer than wide, length along midline 0.56 mm, maximum width 0.52 mm, roughly punctate, disc with small, acute denticle at middle. ***Elytra*** much wider than long, length along suture 0.66 mm, maximum width 0.87 mm; shallow and broad discal striae extending posteriorly to past half of elytral length. ***Legs*** simple, elongate. ***Abdomen*** wider than long, length along midline 0.66 mm, maximum width 0.87 mm. ***Tergite*** 1 (IV) approximately as long as tergite 2 (V), both tergites with entire and distinct median carina. Length of aedeagus (Fig. 1E, F) 0.47 mm, elongate, well sclerotized; median lobe curved ventrally at apex in lateral view; endophallus composed of one elongate sclerite at middle and two short and strongly sclerotized sclerites at apex; parameres elongate and flattened, each with two long setae at apex.

Female. Unknown.

Comparative notes. Males of the new species can be readily separated from *A. chinensis* and all other congeners by the roughly punctate head and pronotum, and the different shape of antennomeres 9–10 and structure of the aedeagus. *Ancystrocerus chinensis* from Hainan has finely punctate head and pronotum, the antennomeres 9 and 10 more elongate, and aedeagus much more robust and with a large projection at the apex of the median lobe.

Distribution. China: Yunnan.

Biology. The single male was sifted from a leaf litter sample in a shady broad-leaved forest.

Etymology. The new species is named after Liang Lü, collector of the holotype.

***Ancystrocerus philippinus* sp. nov.**

http://zoobank.org/D6BC17D4-ACC9-4F59-B545-C4A7D2F63C37
Fig. 2

Type material. ***Holotype*: Philippines**: ♂, 'Philippines: Alamada, North Corabato, Mindanao, i.2019, local collector' (SNUC).

Diagnosis. Male. Length 2.6 mm (combined length of head, pronotum, elytra and abdomen). Head and pronotum finely punctate. Antennomeres 4 longer than 5, antennomeres 9 expanded and projected laterally, 10 hardly so, lateral margin of antennomeres 9 and 10 with one bunch of bristles. Pronotum with small, conical discal spine. Tergite 1 (IV) with median carina extending through entire tergal length, tergite 2 lacking such carina. Aedeagus relatively stout, median lobe symmetrical in dorso-ventral view; endophallus with several short and two elongate sclerites; parameres each elongate and with two long apical setae.

Description. Male (Fig. 2A). ***Length*** 2.6 mm. ***Head*** (Fig. 2B) as long as wide, length from anterior margin of clypeus to posterior margin of vertex (excluding occipital construction) 0.46 mm, width across eyes 0.46 mm; dorsal surface finely punctate; postocular margins with rather dense tufts of hairs; eyes prominent, each composed of about 55 facets. ***Antennae*** (Fig. 2C) elongate, with clubs (Fig. 2D) formed by apical three antennomeres; scapes large, antennomeres 2 smaller than scapes, antennomeres 3–8 each subquadrate, 8 as long as wide and larger than each of antennomers 2–7, antennomeres 9–10 modified, antennomeres 11 largest, elongate, widest at 1/3. ***Pronotum*** (Fig. 2B) slightly longer than wide, length along midline 0.58 mm, maximum width 0.49 mm, finely punctate, disc with small, acute spine at middle. ***Elytra*** much wider than long, length along suture 0.74 mm, maximum width 0.94 mm; shallow broad discal striae extending posteriorly to less than half elytral length. Legs sim-

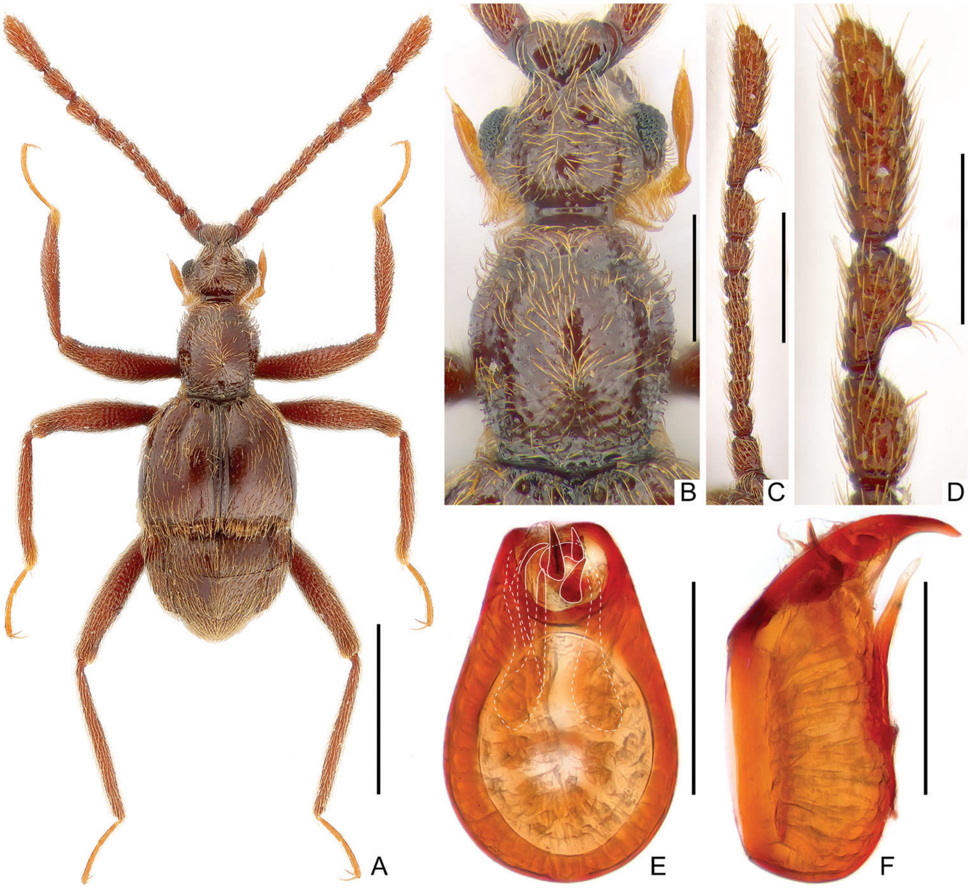

Figure 2. *Ancystrocerus philippinus* sp. nov., male **A** habitus **B** head dorsum and pronotum **C** right antenna **D** antennal club of right antenna **E, F** aedeagus in dorsal (**E**) and lateral (**F**) view. Scale bars: 1.0 mm (**A**); 0.3 mm (**B, D**); 0.5 mm (**C**); 0.2 mm (**E, F**).

ple, elongate. ***Abdomen*** wider than long, length along midline 0.78 mm, maximum width 0.87 mm. ***Tergite*** 1 (IV) approximately as long as tergite 2 (V), tergite 1 with entire and distinct median carina, which is absent on tergite 2. Length of aedeagus (Fig. 2E, F) 0.35 mm, relatively stout, well sclerotized; median lobe curved ventrally at apex in lateral view; endophallus composed of three thick and short sclerites at apex and two elongate ones on the left; parameres elongate and flattened, each with two long setae at apex.

Female. Unknown.

Comparative notes. Males of the new species can be readily separated from all congeners by the presence of very dense hairs along the postocular margins, the unique shape of antennomeres 9 and 10, and the structure of the aedeagal endophallus. The elongate antennomeres 9 and 10 of *A. philippinus* are somewhat similar to those of *A. chinensis*, however, the antennomeres 9 are much less expanded in the new species and the aedeagus is totally different in form and structure. *Ancystrocerus philippinus* further differs by tergite 1 with a complete median carina, which in *A. chinensis* is short and extending posteriorly only to less than half of tergal length.

The antennomeres 10 of *A. irregularis* Raffray, *A. sumatrensis* Raffray, *A. rugicollis* Raffray, and *A. punctatus* Raffray all bear one bunch of bristles on the lateral surface. In addition to the form of the aedeagal median lobe, the unique structure of the endophallus, and the different proportions of antennomeres 9–11, *A. philippinus* can be readily separated from the former three species by the presence of a thin bunch of bristles also on antennomeres 9, and from *A. punctatus* by the smooth mesal margin of antennomeres 10 (strongly protuberant in *A. punctatus*).

Distribution. Philippines: Mindanao.

Biology. Unknown.

Etymology. The specific epithet refers to the Philippines, where the type locality of the new species is located.

Acknowledgments

My friend Liang Lü (Hebei Normal University, Hebei, China) collected the single male of *A. lueliangi* and kindly donated the specimen to SNUC. Rostislav Bekchiev (National Museum of Natural History, Sofia, Bulgaria) provided valuable unpublished notes on *Ancystrocerus* types which helped me to compare the new species with the known ones. Comments from Peter Hlaváč (Czech University of Life Sciences Prague, Czech) and Christopher Carlton (Louisiana State Arthropod Museum, USA) improved the paper. The present study was supported by the National Natural Science Foundation of China (No. 31872965), and the 'Phosphorus' Science Foundation, Shanghai Municipal Science and Technology Commission, China (19QA1406600).

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Catalogue of the type material of Scarabaeoidea (Coleoptera) deposited in the Research Institute of Evolutionary Biology, Tokyo, Japan

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Abstract

A detailed catalogue of the type material of the Scarabaeoidea housed in the Research Institute of Evolutionary Biology, Tokyo, Japan is listed. The catalogue includes the data of the type material of four families and 111 species.

Keywords

Allotype, Geotrupidae, holotype, Lucanidae, neotype, paratype, Scarabaeidae, Trogidae

Introduction

In this report we present a catalogue of the type material of Scarabaeoidea housed in the Research Institute of Evolutionary Biology, Tokyo, Japan (RIEB). The beginning of the RIEB collection dates back to 1950, when the first natural objects were deposited at the Research Institute of Thremmatology of the Tokyo University of Agriculture (RIT) established that year. RIT was transformed into an incorporated foundation in 1974 and renamed Research Institute of Evolutionary Biology (Yamamoto 2000). The Lepidoptera collection in the RIEB was listed in detail by Aoki et al. (2005, 2008) and Yamaguchi et al. (2006, 2008, 2009, 2011, 2017), but the Coleoptera collection has never been catalogued. This creates a problem because well-organized museum collections and published type specimen catalogues are very important to facilitate taxonomic and systematic investigations of animals.

The majority of the types of Scarabaeidae deposited in the RIEB originate from the collection of Mr Yoshikazu Miyake (1926–2003), a well-known Japanese amateur specialist on Scarabaeidae, who was also the author of those taxa. A part of types of Miyake's species is also housed in the National Museum of Nature and Science, Tokyo (NMNS) and the Nagaoka Municipal Science Museum, Niigata (NMSM). Unfortunately, some of his types are missing.

In addition, other researchers that contributed to the Scarabaeoidea type collection in RIEB are: Dirk Ahrens, Aleš Bezděk, Toshiyuki Ichikawa, Takeshi Itoh (Takeshi Matsumoto), Kimio Masumoto, Sizumu Nomura, Teruo Ochi, and Kaoru Wada.

Materials and methods

The scientific names of higher taxa in this catalogue follow Scholtz and Grebennikov (2016). The structure of each entry is as follows:

- original combination of the taxon name;
- original combination and spelling of the taxon name, followed by the author, year of description, and pagination;
- type material, number of specimens (including sex, if known), and exact label data. A double slash '//' indicates separate labels and single slash '/' indicates lines within each label. The words in Japanese or Chinese were transcribed into Roman alphabet. Paratypes with discrepancies between collection data on the label and data quoted in the original description are indicated by '[[ ]]';
- remarks on types condition (given only for holotypes and neotypes);
- current taxonomic status;
- remarks, if any.

The majority of holotypes and neotypes were photographed with a Nikon D7200 camera using a Nikon AF-S DX Micro NIKKOR 40 mm f/2.8 G lens, and some types were photographed with a KEYENCE VHX-1000 Digital Microscope.

Catalogue

Family Geotrupidae
Subfamily Geotrupinae
Genus *Sinogeotrupes*

Sinogeotrupes taiwanus Miyake & Yamaya

Sinogeotrupes taiwanus Miyake & Yamaya, 1995: 32–34.

Note. The following paratypes are deposited in RIEB (ex coll. Y. Miyake):

Paratypes. 3 exs.: 1 ex. 'Wusha / –VI–1941 / R. Boloudo // Paratype / Sinogeotrupes taiwanus / Y. MIYAKE et YAMAYA, 1995'. 1 ex. 'Wu sha / Formosa / 21. Viii. 1941 / Col. Bumua Tin // Geotrupes / subshiatelluo FAIRMAIR / DET. Y. MIYAKE // Paratype / Sinogeotrupes taiwanus / Y. MIYAKE et YAMAYA, 1995'. 1 ex. '台湾= taiwan 台中= taichû / 関刀山= guandaoshan / 1993. V. 31 // Paratype / Sinogeotrupes taiwanus / Y. MIYAKE et YAMAYA, 1995'.

Current status. *Phelotrupes* (*Sinogeotrupes*) *taiwanus* (Miyake and Yamaya, 1995), see Nikolajev et al. (2016).

Remark. In addition to the paratypes mentioned above, the following specimens labeled as paratypes are not designated in the original description: 3 exs. 'Tattaka / Formosa / 10. Vi. 1965 / T. Shirozu // Paratype / Sinogeotrupes taiwanus / Y. MIYAKE et YAMAYA, 1995'. 1 ex. '(FORMOSA) / Mt Rata / Vi–Vii–1972 / L. F, Hang // Paratype / Sinogeotrupes taiwanus / Y. MIYAKE et YAMAYA, 1995'. 1 ex. '(FORMOSA) / Mt Rata / –Vii–1972 / L. F, Hang // Paratype / Sinogeotrupes taiwanus / Y. MIYAKE et YAMAYA, 1995'. 2 exs. '[Taiwan] / 台中= taichû 関刀山= guandaoshan / 3–VI–1993 // Paratype / Sinogeotrupes taiwanus / Y. MIYAKE et YAMAYA, 1995'. 1 ♂ '[Taiwan] / 台中= taichû 関刀山= guandaoshan / 3–VI–1993 // Paratype / Sinogeotrupes taiwanus / Y. MIYAKE et YAMAYA, 1995'. 3 exs. 'Paratype / Sinogeotrupes taiwanus / Y. MIYAKE et YAMAYA, 1995'.

Family Lucanidae
Subfamily Lucaninae
Genus *Aegus*

Aegus laevicollis nakanei Ichikawa & Imanishi

Aegus laevicollis nakanei Ichikawa & Imanishi, 1976: 9.

Note. The following paratype is deposited in RIEB (ex coll. Y. Kusui):

Paratype. 1 ex.: [[1 ♀ 'Mt. Yonahadake, / Kunigami-son, / Is. Okinawa-Hontō, / 28. VI. 1972 (the date given in the original description is 16–17. VI. 1970), / HEIKICHI IRIE leg., // KUSUI // Paratype']].

Current status. *Aegus nakanei nakanei* Ichikawa and Imanishi, 1976, see Huang and Chen (2017).

Family Scarabaeidae
Subfamily Aphodiinae
Genus *Aphodius*

Aphodius (*Agoliinus*) *tanakai* Masumoto

Aphodius (*Agoliinus*) *tanakai* Masumoto, 1981: 73–74.

Note. The following paratype is deposited in RIEB (ex coll. K. Masumoto):

Paratype. 1 ex.: 'Nikko / Date: 23 V 1981 / K. MASUMOTO leg. // Paratype / Aphodius (Agr) / tanakai MASUMOTO'.

Current status. *Agoliinus tanakai* (Masumoto, 1981), see Dellacasa et al. (2016).

Aphodius (*Phaeaphodius*) *himalorectus* Ahrens & Stebnicka

Aphodius (*Phaeaphodius*) *himalorectus* Ahrens & Stebnicka, 1997: 12–13.

Note. The following paratypes are deposited in RIEB (ex coll. D. Ahrens):

Paratypes. 2 exs.: 'Phalante 20. 3. / unt. Nebelwaldstufe / 2100–2300 m // PARATYPUS / *Aphodius* (*Phaeaphodius*) *himalorectus* sp. n. / det. D. AHRENS 1994'.

Current status. *Phaeaphodius himalorectus* (Ahrens and Stebnicka, 1997), see Dellacasa et al. (2016).

Aphodius (*Sinodiapterna*) *zeni* Ochi

Aphodius (*Sinodiapterna*) *zeni* Ochi, 1991: 53–55.

Note. The following paratype is deposited in RIEB (ex coll. T. Ochi):

Paratype. 1 ex.: 'SUNGKAN / C. TAIWAN / 29–V. 1987 / K. LAH // PARATYPE / Aphodius (Sinodiapterna) / zeni / OCHI 1991'.

Current status. *Sinodiapterna zeni* (Ochi, 1991), see Dellacasa et al. (2016).

Genus *Rhyparus*

Rhyparus kitanoi Miyake
Figure 1A

Rhyparus kitanoi Miyake, 1982: 65–67.

Note. The holotype and following specimen are deposited in RIEB (ex coll. Y. Miyake):

Holotype (♂). 'C, Sata 〘KYUSHU〙 Japan / 25, VI 1971 / T. Kitano leg. // PARATYPE // Holotype: / Rhyparus / kitanoi / Y. MIYAKE, 1992'. (Fig. 1A)

Type condition. The right and left protarsus and the right antenna of the holotype are missing.

Current status. *Rhyparus kitanoi kitanoi* Miyake, 1982, see Ochi (2001).

Remark. In addition to the holotype mentioned above, the following specimen labeled as paratype is not designated in the original description: 1 ex.: 'Sesonoura / Is. Shimokoshiki / Kagoshima-pref. / 18. VI. 1982 / S. Imasaka leg. // Paratype: Rhyparus / kitanoi / Y. MIYAKE, 1992'.

Subfamily Scarabaeinae
Genus *Caccobius*

Caccobius bawangensis Ochi, Kon & Kikuta

Caccobius bawangensis Ochi, Kon & Kikuta, 1997: 262–264.

Note. The following paratype is deposited in RIEB (ex coll. T. Ochi):

Paratype. 1 ex.: 'Mt. Bawang / Sarawak S. / VIII. 1991 / M. Kon Coll. // PARATYPE / Caccobius / bawangensis OCHI, KON and KIKUTA'.

Current status. Valid species.

Genus *Copris*

Copris (*Microcopris*) *mindorensis* Ochi

Copris (*Microcopris*) *mindorensis* Ochi, 1992: 13.

Note. The following paratype is deposited in RIEB (ex coll. T. Ochi):

Paratype. 1 ex.: 'MT. HALKON / IS. MINDRO / 28–XII. 1988 / D. MOHAGAN // PARATYPE / Copris / (Microcopris) / mindorensis / OCHI, 1992.

Current status. Valid species.

Genus *Onthophagus*

Onthophagus setchan Masumoto

Onthophagus setchan Masumoto, 1984: 80–81.

Note. The following paratype is deposited in RIEB (ex coll. K. Masumoto):

Paratype. 1 ex.: 'FENGCHIFU / FORMOSA / 7–VII. 74. / T. OCHI // PARATYPE / Onthophagus / setchan / MASUMOTO (1984)'.

Current status. Valid species.

Onthophagus (*Parascatonomus*) *acuticollis sakishimanus* Nomura

Onthophagus (*Parascatonomus*) *acuticollis sakishimanus* Nomura, 1976a: 29.

Note. The following paratypes are deposited in RIEB (ex coll. S. Nomura):

Paratypes. 6 exs.: 3 ♂ 'Kanpira / Iriomote Is. / Yaeyama Iss. / 12. VII. 1975 / R. YANO leg. // ♂ // Onthophagus (P.) / acuticollis / sakishimanus / NOMURA (1976)'. 3 ♀ 'Kanpira / Iriomote Is. / Yaeyama Iss. / 12. VII. 1975 / R. YANO leg. // ♀ // Onthophagus (P.) / acuticollis / sakishimanus / NOMURA (1976)'.

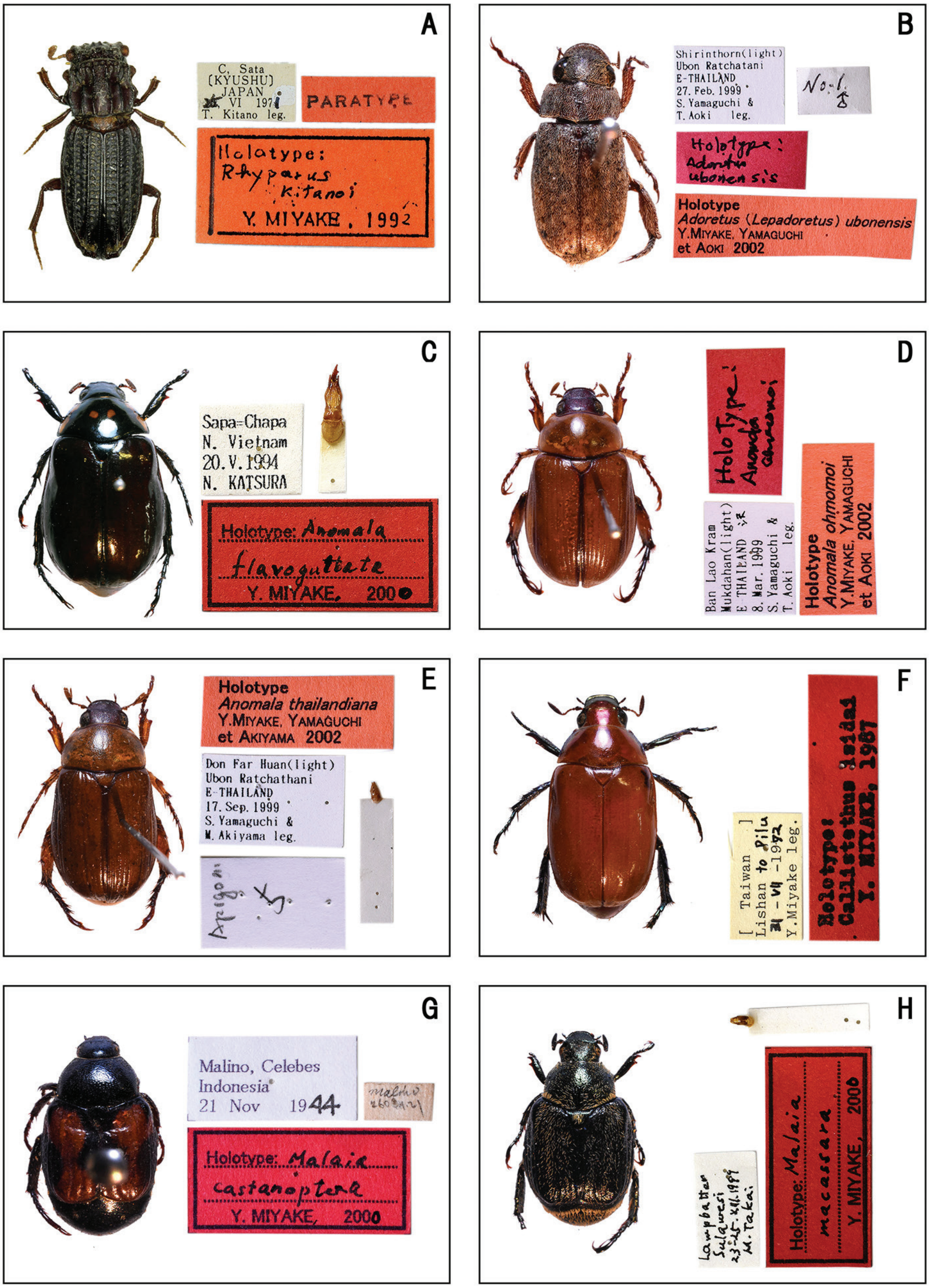

Figure 1. Habitus of holotype specimens. **A** *Rhyparus kitanoi* (Miyake) **B** *Adoretus* (*Lepadoretus*) *ubonensis* (Miyake, Yamaguchi et Aoki) **C** *Anomala flavoguttata* Miyake **D** *Anomala ohmomoi* Miyake, Yamaguchi et Aoki **E** *Anomala thailandiana* Miyake, Yamaguchi et Akiyama **F** *Callistethus isidai* Miyake **G** *Malaia castanoptera* Miyake **H** *Malaia macassara* Miyake.

Current status. *Parascatonomus* (*Necramator*) *acuticollis sakishimanus* (Nomura, 1976), see Ochi and Kon (2017).

***Onthophagus* (*Parascatonomus*) *murasakianus* Nomura**

Onthophagus (*Parascatonomus*) *murasakianus* Nomura, 1976a: 30.

Note. The following paratype is deposited in RIEB (ex coll. S. Nomura):

Paratype. 1 ex.: 'Kanpira, / Iriomote Is. / Yaeyama Iss. / 12. VII 1975 / R. YANO leg. // PARATYPE / Onthophagus (P.) / murasakianus / NOMURA (1976)'.

Current status. *Parascatonomus* (*Necramator*) *murasakianus* (Nomura, 1976), see Ochi and Kon (2017).

***Onthophagus* (*Parascatonomus*) *takedai* Ochi & Araya**

Onthophagus (*Parascatonomus*) *takedai* Ochi & Araya, 1992: 99–100.

Note. The following paratype is deposited in RIEB (ex coll. T. Ochi):

Paratype. 1 ex.: 'QUESON. N. P / IS. LUZON / 10–VIII. 1981 / K. SUGINO // PARATYPE / Onthophagus / (Parascatonomus) / takedai / OCHI et ARAYA, 1992'.

Current status. *Parascatonomus* (*Granulidorsum*) *takedai* (Ochi et Araya, 1992), see Ochi and Kon (2017).

***Onthophagus* (*Proagoderus*) *watanabei* Ochi & Kon**

Onthophagus (*Proagoderus*) *watanabei* Ochi & Kon, 2002: 306–311.

Note. The following paratype is deposited in RIEB (ex coll. T. Ochi):

Paratype. 1 ex.: 'SEPIROK / N. BORNEO / 4–VII. 1985 / M. KON // PARATYPE / Onthophagus / (Proagoderus) / watanabei / OCHI and KON. 2002'.

Current status. *Proagoderus watanabei* (Ochi et Kon, 2002), see Philips (2016).

***Onthophagus* (*Strandius*) *hiurai* Ochi**

Onthophagus (*Strandius*) *hiurai* Ochi, 1984: 63–65.

Note. The following paratype is deposited in RIEB (ex coll. T. Ochi):

Paratype. 1 ex.: 'PILU / Taiwan / 21, VIII, 1979 / K. Sugino leg. // PARATYPE / Onthophagus (St) / hiurai / OCHI (1984)'.

Current status. *Onthophagus* (*Phanaeomorphus*) *potanini hiurai* Ochi, 1984, see Ziani and Bezděk (2016).

Subfamily Rutelinae

Genus *Adoretus*

Adoretus (_Lepadoretus_) _ubonensis_ Miyake, Yamaguchi & Aoki
Figure 1B

Adoretus (*Lepadoretus*) *ubonensis* Miyake, Yamaguchi, Aoki & Akiyama, 2002: 62–63.

Note. The holotype is deposited in RIEB (ex coll. Y. Miyake):

Holotype (♂). 'Shirinthorn (light) / Ubon Ratchatani / E–THAILAND / 27. Feb. 1999 / S. Yamaguchi and / T. Aoki leg. // No. 1 / ♂ // Holotype: / Adoretus / ubonensis // Holotype / *Adoretus* (*Lepadoretus*) *ubonensis* / Y. MIYAKE, YAMAGUCHI / et AOKI 2002'. (Fig. 1B)

Type condition. The left mesotarsus and the left metaleg of the holotype are missing.

Current status. Junior subjective synonym of *Adoretus compressus* (Weber, 1801), see Kobayashi (2018).

Genus *Anomala*

***Anomala flavoguttata* Miyake**
Figure 1C

Anomala flavoguttata Miyake, 2000: 108–109.

Note. The holotype is deposited in RIEB (ex coll. Y. Miyake):

Holotype (♂). 'Sapa=Chapa / N. Vietnam / 20. V. 1994 / N. KATSURA // Holotype: Anomala / flavoguttata / Y. MIYAKE, 2000'. (Fig. 1C)

Type condition. The aedeagus of the holotype is pinned separately.

Current status. Valid species.

***Anomala ohmomoi* Miyake, Yamaguchi & Aoki**
Figure 1D

Anomala ohmomoi Miyake, Yamaguchi, Aoki & Akiyama, 2002: 58–60.

Note. The holotype and the following paratypes are deposited in RIEB (ex coll. Y. Miyake):

Holotype (♂). 'Ban Lao Kram / Mukdahan (light) / E–THAILAND沢= sawa / 8. Mar. 1999 / S. Yamaguchi and / T. Aoki leg. // Holo Type: / Anomala / ohmomoi // Holotype / *Anomala ohmomoi* / Y. MIYAKE, YAMAGUCHI / et AOKI 2002'. (Fig. 1D)

Paratypes. 4 exs.: 'Ban Lao Kram / Mukdahan (light) / E–THAILAND沢= sawa / 8. Mar. 1999 / S. Yamaguchi and / T. Aoki leg. // Paratype / Anomala ohmomoi / Y. MIYAKE, YAMAGUCHI / et AOKI 2002'.

Current status. Valid species.

Anomala thailandiana Miyake, Yamaguchi & Akiyama

Figure 1E

Anomala thailandiana Miyake, Yamaguchi, Aoki & Akiyama, 2002: 60–61.

Note. The holotype is deposited in RIEB (ex coll. Y. Miyake):

Holotype (♂). 'Don Far Huan (light) / Ubon Ratchathani / E–THAILAND / 17. Sep. 1999 / S. Yamaguchi and / M. Akiyama leg. [white label, front] // Apigoni / 5 [white label, back] // Holotype / Anomala thailandiana / Y. MIYAKE, YAMAGUCHI / et AKIYAMA 2002'. (Fig. 1E)

Type condition. The aedeagus of the holotype is pinned separately.

Current status. Valid species.

Genus *Callistethus*

Callistethus isidai Miyake

Figure 1F

Callistethus isidai Miyake, 1987: 5–6.

Note. The holotype and the following paratype are deposited in RIEB (ex coll. Y. Miyake):

Holotype (♂). '[Taiwan] / Lishan to Pilu / 31–VII–1972 / Y. Miyake leg. // Holotype: / Callistethus isidai / Y. MYAKE, 1987'. (Fig. 1F)

Paratype. 1 ex.: '[Taiwan] / Lishan to Pilu / 31–VII–1972 / Y. Miyake leg. // Paratype / Callistethus isidia / Y. MIYAKE, 1987'.

Type condition. The right and left metatarsi of the holotype are missing.

Current status. *Callistethus plagiicollis isidai* Miyake, 1987, see Zorn and Bezděk (2016).

Remark. The habitus photograph in the original description does not agree with the holotype. This is also the case with some other species described by Miyake. Apparently, he did not intend to provide the photographs of the holotypes. Also, as noted below, we were unable to trace some specimens illustrated in the original descriptions.

Genus *Kibakoganea*

Kibakoganea ohtanii Miyake & Muramoto

Kibakoganea ohtanii Miyake & Muramoto, 1992: 22–24.

Note. The following paratypes are deposited in RIEB (ex coll. Y. Miyake):

Paratypes. 2 exs.: [[1 ♂, 1 ♀ ‘Tam Dao / N. VIETNAM / 28–30, IV, 1991 (the date given in the original description is 28–30. III. 1991) / M. Fujioka and / R. Muramoto – leg. // PARATYPE / Kibakoganea / ohtanii / Y. MIYAKE et / MURAMOTO, 1992.’]].

Current status. Junior subjective synonym of *Kibakoganea sexmaculata* (Kraatz, 1900), see Miyake (2003).

Genus *Malaia*

Malaia castanoptera Miyake
Figure 1G

Malaia castanoptera Miyake, 2000: 112.

Note. The holotype is deposited in RIEB (ex coll. Y. Miyake):

Holotype (♂). ‘Malino, Celebes / Indonesia / 21 Nov 1944 // malino / 2603.11.21 // Holotype: Malaia / castanoptera / Y. MIYAKE, 2000’. (Fig. 1G)

Paratypes. 7 exs.: 1 ♂, 3 ♀ ‘Malino, Celebes / Indonesia / 21 Nov 1944 // malino / 2603.11.21 // Paratype: Malaia / castanoptera / Y. MIYAKE, 2000’. 2 exs. ‘Malino, Celebes / Indonesia / 21 Nov 1944 // malino / 2603.11.21 // Paratype: Malaia / castanoptera / Y. MIYAKE, 2000’. 1 ex. ‘malino / 2603.11.21 // Paratype: Malaia / castanoptera / Y. MIYAKE, 2000’.

Current status. Valid species.

Remark. The habitus photo in the original description belongs to the female paratype with the label ‘Malino, Celebes / Indonesia / 21 Nov 1944 // malino / 2603.11.21’.

Malaia cyanea Miyake

Malaia cyanea Miyake, 1996: 38–39.

Note. The following paratypes are deposited is RIEB (ex coll. Y. Miyake):

Paratypes. 2 exs.: 1 ♂ ‘32 km from / Palopo / Surawesi / 10. VI. 1982 // Paratype: / Malaia cyanea / Y. MIYAKE, 1996’. 1 ♀ ‘Punchak–Lombanan / Mamasa, / S. SULAWESI / 1991. AUG. 10. / N. Kashiwai–leg. // Paratype: / Malaia cyanea / Y. MIYAKE, 1996’.

Current status. Valid species.

Malaia macassara Miyake

Figure 1H

Malaia macassara Miyake, 2000: 109–110.

Note. The holotype and the following paratype are deposited in RIEB (ex coll. Y. Miyake):

Holotype (♂). 'Lampbatter / Sulawesi / 23–25. VIII. 1999 / M. Takai // Holotype: Malaia / macassara / Y. MIYAKE, 2000'. (Fig. 1H)

Paratype. 1ex.: 1 ♂ 'Lampbatter / Sulawesi / 23–25. XII. 1999 / M. Takai leg. // Paratype: Malaia / macassara / Y. MIYAKE, 2000'.

Type condition. The left protarsus and metatarsus of the holotype are missing.

Current status. Valid species.

Malaia rufofemorata Miyake

Malaia rufofemorata Miyake, 1996: 40–41.

Note. The following paratypes are deposited in RIEB (ex coll. Y. Miyake):

Paratypes. 4 exs.: 1 ♂, 1 ♀ 'Puncak, Palopo / VI–VII, 1989 / Central SULAWESI // Paratype: Malaia / rufofemorata / Y. MIYAKE, 1996'. 2 ♂ 'Palu Palolo / VIII. 1990 / Central SULAWESI // Paratype: Malaia / rufofemorata / Y. MIYAKE, 1996'.

Current status. Valid species.

Remark. In addition to the paratypes mentioned above, the following specimens labeled as paratypes are not designated in the original description: 2 ♂, 1 ♀ 'Palolo, Palu / 01–10/XI. 1990 / native coll. / CELEBES // Paratype: Malaia / rufofemorata / Y. MIYAKE, 1996'.

Malaia sulawesi Miyake

Malaia sulawesi Miyake, 1996: 41–42.

Note. The following paratypes are deposited in RIEB (ex coll. Y. Miyake):

Paratypes. 58 exs.: 1 ♂ 'Mt. Pedamaran / Tana Toraja / 1985. III–17 / South SULAWESI / Soma, K. leg. // Paratype: / Malaia / sulawesi / Y. MIYAKE, 1996'. 1 ex. 'Puncak Palopo / 1989. III. 31 / Centr. CELEBES // Paratype: / Malaia / sulawesi / Y. MIYAKE, 1996'. 3 exs. 'Palu Pulu / C. Sulawesi / II. 1989 // Paratype: / Malaia / sulawesi / Y. MIYAKE, 1996'. [[44 exs. 'Mt. Pedamaran / S. Sulawesi (real data is C. Sulawesi) / 20. X. 1983 (real date is 20. V. 1983) / K. Soma leg. // Paratype: / Malaia / sulawesi / Y. MIYAKE, 1996']]. [[9 exs. 'Mt. Pedamaran / Tana Toraja / 1983. X–20 (real date is 1983. V–20) / South SULAWESI (real data is Central SULAWESI) / Soma, K. leg. // Paratype: / Malaia / sulawesi / Y. MIYAKE, 1996']].

Current status. Valid species.

Malaia taoi Miyake

Malaia taoi Miyake, 1996: 39–40.

Note. The following paratypes are deposited in RIEB (ex coll. Y. Miyake):

Paratypes. 4 exs.: 1 ♂ '37 km from / Palopo C.- / Sulawesi / 9. IV. 1982 // Paratype: / Malaia / taoi / Y. MIYAKE, 1996'. 1 ♀ '32 km from / Palopo / Surawesi / 10. VI. 1982 // 37 km from / Palopo C.- / Sulawesi / 10. VI. 1982 // Paratype: / Malaia / taoi / Y. MIYAKE, 1996'. 1 ♂ '37 km from / Palopo C.- / Sulawesi / 11. IV. 1982 // Paratype: / Malaia / taoi / Y. MIYAKE, 1996'. 1 ♀ '32 km from / Palopo / Surawesi / 13. VI. 1982 // 37 km from / Palopo C.- / Sulawesi / 13. VI. 1982 // Paratype: / Malaia / taoi / Y. MIYAKE, 1996'.

Current status. Valid species.

Malaia tondanoensis Miyake

Malaia tondanoensis Miyake, 1996: 42–43.

Note. The following paratype is deposited in RIEB (ex coll. Y. Miyake):

Paratype. 4exs.: 'Tondano / N. Sulawesi / 10–IV–1989 / Y. Miyake leg. // Paratype: / Malaia / tondanoensis / Y. MIYAKE, 1996'.

[[1 ex. 'Tangkoko N. / N. Sulawesi / 10–III–1989 (the date given in the original description is 10–IV–1989) / Y. Miyake leg. // Paratype: / Malaia / tondanoensis / Y. MIYAKE, 1996']]. [[2 exs. 'Tondano / N. Sulawesi / 9–IV–1989 (the date given in the original description is 10–IV–1989) / Y. Miyake leg. // Paratype: / Malaia / tondanoensis / Y. MIYAKE, 1996']].

Current status. Valid species.

Malaia toraja Miyake
Figure 2A

Malaia toraja Miyake, 2000: 110–111.

Note. The holotype and following paratypes are deposited in RIEB (ex coll. Y. Miyake):

Holotype (♂). 'Mt. Pedamaran / Tana Traja / 20–X. 1983 / K. SOHMA lgd. / South SULAWESI // Holotype: Malaia / toraja / Y. MIYAKE, 2000'. (Fig. 2A)

Paratypes. 27 exs.: 1 ♂ 'Mt. Pedamaran / Tana Traja / 20–X. 1983 / K. SOHMA lgd. // Paratype: Malaia / toraja / Y. MIYAKE, 2000'. 9 exs. 'Mt. Pedamaran / Tana Traja / 20–X. 1983 / K. SOHMA lgd. // Paratype: Malaia / toraja / Y. MIYAKE, 2000'. 2 exs. 'Mt. Pedamaran / S. Sulawesi / 20. X. 1983 / K. Soma leg. // Paratype: Malaia / toraja / Y. MIYAKE, 2000'.8 exs. 'Puncak, Palopo / VI–VII, 1989 / Central SULAWESI // Paratype: Malaia / toraja / Y. MIYAKE, 2000'. 2 exs. 'Central

SULAWESI / Puncak, Palopo / VI–VII, 1989 // Paratype: Malaia / toraja / Y. MIYAKE, 2000'. 1 ♂ 'Puncak Palopo / 1989. / Centr. CELEBES // SI [yellow label] // Paratype: Malaia / toraja / Y. MIYAKE, 2000'. 4 exs. 'Puncak Palopo / 1989. / Centr. CELEBES // SI [yellow label] // Paratype: Malaia / toraja / Y. MIYAKE, 2000'.

Current status. Valid species.

Remark. The habitus photo in the original description belongs to the female paratype with the label 'Mt. Pedamaran / Tana Toraja / S. Sulawesi / 7, VIII, 1988 / K. Soma leg.'.

In addition to the paratypes listed above, the following specimens labeled as the paratypes are not designated in the original description: 1 ♀ 'Mt. Pedamaran / Tana Toraja / S. Sulawesi / 7, VIII, 1988 / K. Soma leg. // SI [yellow label] // Paratype: Malaia / toraja / Y. MIYAKE, 2000'. 1 ex. '(Pulu Pulu) / C. Sulawesi / INDONESIA / Dec. 1988 // [yellow label] // Paratype: Malaia / toraja / Y. MIYAKE, 2000'. 2 exs. 'Puncak, Palopo / Centr. CELEBES / 1989. I / INDONESIA // [yellow label] // Paratype: Malaia / toraja / Y. MIYAKE, 2000'. 1 ex. 'Puncak Palopo / 1989. III. 31 / Centr. CELEBES // Paratype: Malaia / toraja / Y. MIYAKE, 2000'. 3 exs. 'Palu, Palolo / VII 1989 / Central SULAWESI // Paratype: Malaia / toraja / Y. MIYAKE, 2000'.

Genus *Mimela*

Mimela kitanoi Miyake

Figure 2B

Mimela kitanoi Miyake, 1987: 7–8.

Note. The holotype is deposited in RIEB (ex coll. K. Wada):

Holotype (♀). 'Larashan / Hsinchu Hs. / VI. 1975, / Fang leg // Holotype: / Mimela kitanoi / Y. MIYAKE, 1987 // Kaoru WADA / Collection 2001'. (Fig. 2B)

Current status. Junior subjective synonym of *Mimela flavocincta* Lin, 1966, see Zorn and Bezděk (2016).

Mimela marginipennis Miyake

Figure 2C

Mimela marginipennis Miyake, 1994: 151.

Note. The holotype is deposited in RIEB (ex coll. Y. Miyake):

Holotype (♂). '[Borneo] / Crocker Range / 1800–1400m alt. / nr. Keningau C. / X. 1988. M. ITOI leg. // Holotype: / Mimela / marginipennis / Y. MIYAKE, 1994'. (Fig. 2C)

Type condition. The aedeagus of the holotype is pinned separately, and the left mesotarsus is missing.

Current status. Junior subjective synonym of *Mimela margarita* Arrow, 1910, see Wada (2001).

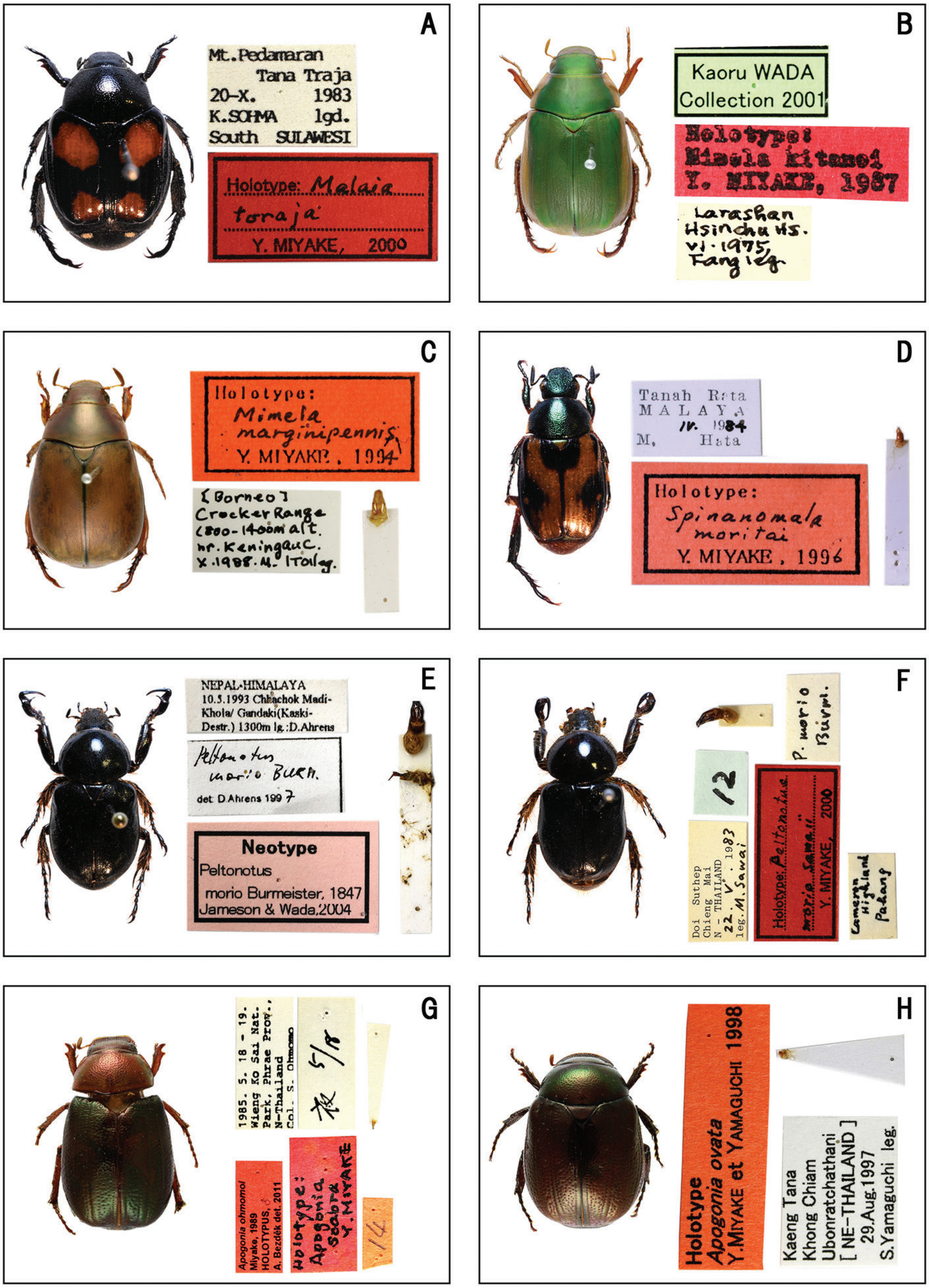

Figure 2. Habitus of holotype and neotype specimens. **A** *Malaia toraja* Miyake **B** *Mimela kitanoi* Miyake **C** *Mimela marginipennis* Miyake **D** *Spinanomala moritai* Miyake **E** *Peltonotus morio* Burmeister **F** *Peltonotus morio sawaii* Miyake **G** *Apogonia ohmomoi* Miyake **H** *Apogonia ovata* Miyake et Yamaguchi.

Mimela sawaii Miyake

Mimela sawaii Miyake, 1994: 149–150.

Note. The following paratype is deposited in RIEB (ex coll. Y. Miyake):

Paratype. 1 ex.: 1 ♂ 'Crocker Range / (1000–1400 m) / Nr. Keningau C. / N. Borneo, – / 15–V–1989 // [blue label] // Paratype: / Mimela / sawaii / Y. MIYAKE, 1994'.

Current status. Junior subjective synonym of *Mimela pallidicauda* Arrow, 1910, see Wada (2001).

Mimela suspecta Miyake

Mimela suspecta Miyake, 1994: 150.

Note. The following paratypes are deposited in RIEB (ex coll. Y. Miyake):

Paratype. 2ex.: 1 ♂ 'Mt. Trus Madi / (SW Slopa 1200m alt.) / Sabah, MALAYSIA / 14–IV–1993 / Minoru SAWAI leg. // Paratype: / Mimela / suspecta / Y. MIYAKE, 1994'. [[1 ex. 'Mt. Trus Madi / (SW Slopa 1200m alt.) / Sabah, MALAYSIA / 18–IV–1993 (the date given in the original description is 4–IV–1993) / Minoru SAWAI leg. // [yellow label] // Paratype: / Mimela / suspecta / Y. MIYAKE, 1994']].

Current status. Valid species.

Remark. In addition to the paratypes mentioned above, the following specimen labeled as paratype is not designated in the original description: 1 ♂ 'Trus Madi Mts. / near Keningau / Saba MALAYSIA / 1993. iv. 17–30. // F //Paratype: / Mimela / suspecta / Y. MIYAKE, 1994'.

Genus *Popillia*

Popillia iwasei Miyake

Popillia iwasei Miyake, 1996: 43–44.

Note. The following paratypes are deposited in RIEB (ex coll. Y. Miyake):

Paratypes. 6 exs.: 2 ♀ 'Puncak, Palopo / Centr. CELEBES / 1989. I / INDONESIA // Paratype: / Popillia / iwasei / Y. MIYAKE, 1996'. 2 ♀ 'Puncak Palopo / C. Sulawesi / 1. 1989 // Paratype: / Popillia / iwasei / Y. MIYAKE, 1996'. 1 ♀ 'Puncak Palopo / C. Sulawesi / 1989. V / INDONESIA // SI [yellow label] // Paratype: / Popillia / iwasei / Y. MIYAKE, 1996'. [[1 ♂ 'Palolo (the locality given in the original description is Palopo) / II. 1991 (the date given in the original description and Telnov and Zorn (2019) are I. 1989) // Paratype: / Popillia / iwasei / Y. MIYAKE, 1996']].

Current status. Valid species.

Genus *Spilopopillia*

Spilopopillia rugosa Miyake

Spilopopillia rugosa Miyake, 1989a: 180–181.

Note. The following paratypes are deposited in RIEB (ex coll. Y. Miyake):

Paratypes. 18 exs.: [[1 ex. '[Malaya] / Fraser's Hill / 29–III–1977 (the date given in the original description is 28. III. 1977) / Y. Miyake leg. // Paratype: / Spilopopillia / rugosa / Y. MIYAKE, 1989']]. [[1 ex. '[Malaya] / Freaser's Hill (the locality given in the original description is Fraser's Hill) / 30–III–1977 (the date given in the original description is 28. III. 1977) / Y. Miyake leg. // Paratype: / Spilopopillia / rugosa / Y. MIYAKE, 1989']]. 6 exs. '[Malaya] / Tanah Rata / 30–III–1974 / Y, Miyake leg // Paratype: / Spilopopillia / rugosa / Y. MIYAKE, 1989'. 9 exs. 'TANARATA / MALAYA / 30 III 1974 / Y. Miyake leg. // Paratype: / Spilopopillia / rugosa / Y. MIYAKE, 1989'. [[1 ex. 'Gentig / Hiland (the locality given in the original description is Genting Highland) MALAYA / 5. IV. 1974 (the date given in the original description is 5. IV. 1975) / Y Miyake leg. // Paratype: / Spilopopillia / rugosa / Y. MIYAKE, 1989']].

Current status. Valid species.

Remark. In addition to the paratypes mentioned above, the following specimens labeled as paratypes are not designated in the original description: 8 exs. 'Tanah Rata / MALAYA / 1. III. 1977 / Y. Miyake // Paratype: / Spilopopillia / rugosa / Y. MIYAKE, 1989'. 5 exs. 'TANARATA / MALAYA / 28, 29, 30 III 1974 / Y. Miyake leg. // Paratype: / Spilopopillia / rugosa / Y. MIYAKE, 1989'. 1 ex. '84. IV // Paratype: / Spilopopillia / rugosa / Y. MIYAKE, 1989'. 2 exs. 'Paratype: / Spilopopillia / rugosa / Y. MIYAKE, 1989'.

Genus *Spinanomala*

Spinanomala moritai Miyake

Figure 2D

Spinanomala moritai Miyake, 1996: 38.

Note. The holotype and following paratypes are deposited in RIEB (ex coll. Y. Miyake):

Holotype (♂). 'Tanah Rata / MALAYA / IV. 1984 / M. Hata // Holotype: / Spinanomala / moritai / Y. MIYAKE, 1996'. (Fig. 2D)

Paratypes. 11 exs.: 1 ex. 'Tanah Rata / MALAYA / I–II. 1973 / MORITA, Kozo // Paratype: Spinanomala / moritai / Y. MIYAKE, 1996'. 2 ♂, 3 ♀ 'Tanah Rata / MALAYA / 1. III. 1977 / Y. Miyake // Paratype: Spinanomala / moritai / Y. MIYAKE, 1996'. 3 ♂, 2 ♀ 'Tanah Rata / MALAYA / IV. 1984 / M. Hata // Paratype: Spinanomala / moritai / Y. MIYAKE, 1996'.

Type condition. The aedeagus of the holotype is pinned separately and the right metaleg is missing.

Current status. Valid species.

Remark. The collecting data of the specimen labelled as the holotype do not match the original description. There are two male paratypes ('Tanah Rata / MALAYA / 1. III. 1977 / Y. Miyake // Paratype: Spinanomala / moritai / Y. MIYAKE, 1996') that match the holotype data.

In addition to the paratypes mentioned above, the following specimen labeled as the paratype is not designated in the original description: 1 ex. 'フレーザーヒル= furêzâhiru / MALAYA / 4 – 6. IV. 1977 / M. Hata // Paratype: Spinanomala / moritai / Y. MIYAKE, 1996'.

Subfamily Dynastinae

Genus *Papuana*

Papuana timorensis Miyake & Yamaya

Papuana timorensis Miyake & Yamaya, 1999: 103–104.

Note. The following paratype is deposited in RIEB (ex coll. Y. Miyake):

Paratype. 1 ex.: 1 ♂ 'Timor Is. / Indonesia / V. 1993 / Native Coll. // Timor / Is. [aedeagus mount] // Paratype: / Papuana / timorensis YAMAYA / Y. MIYAKE, 1999'.

Current status. Valid species.

Genus *Peltonotus*

Peltonotus morio Burmeister

Figure 2E

Peltonotus morio Burmeister, 1847: 75.

Note. The neotype is deposited in RIEB (ex coll. K. Wada):

Neotype (♂). 'NEPAL・HIMALAYA / 10. 5. 1993 Chhachok Madi– / Khola/ Gandaki (Kaski– / Destr.) 1300m lg: D. Ahrens //Peltonotus / morio Burn. / det: D. Ahrens 1997 // Neotype / Peltonotus / morio Burmeister, 1847 / Jameson and Wada, 2004'. (Fig. 2E)

Type condition. The aedeagus of the neotype is pinned separately.

Current status. Valid species.

Remark. The neotype was designated by Jameson and Wada (2004).

Peltonotus morio sawaii Miyake

Figure 2F

Peltonotus morio sawaii Miyake, 2000: 112–113.

Note. The holotype and the following paratypes are deposited in RIEB (ex coll. Y. Miyake):

Holotype (♂). 'Doi Suthep / Chieng Mai / N–THAILAND/ 22. V. 1983 / leg. M. Sawai // 12 // P. morio / Burmi. [white label, front] // Cameron / Highland / Pahang [white label, back] // Holotype: Peltonotus / morio sawaii / Y. MIYAKE, 2000'. (Fig. 2F)

Paratypes. 4 exs.: 2 ♂, 1 ♀ 'Doi Suthep / Chieng Mai / N–THAILAND / 22. V. 1983 / leg. M. Sawai // Paratype: Peltonotus / morio sawaii / Y. MIYAKE, 2000 // P. morio /Burmeister'. 1 ♀ 'Doi Suthep / Chieng Mai / N–THAILAND / 22. V. 1983 / leg. M. Sawai // Paratype: Peltonotus / morio sawaii / Y. MIYAKE, 2000'.

Type condition. The aedeagus of the holotype is pinned separately.

Current status. Junior subjective synonym of *Peltonotus morio* Burmeister, 1847, see Krell and Bezděk (2016).

Peltonotus podocrassus Jameson & Wada

Peltonotus podocrassus Jameson & Wada, 2004: 34–37.

Note. The following paratypes are deposited in RIEB (ex coll. Y. Miyake):

Paratypes. 7 exs.: 2 exs. '[Malaya] / Tanah Rata / 30–III–1976 / Y. Miyake leg. // Paratype: Peltonotus peninsularis / Y. MIYAKE, 2000 // Paratype / Peltonotus podocrassus / Jameson and Wada, 2004'. 1 ♂ '39 miles from / Tapah, Malaya / 30–III–1976 / Y. Miyake leg. // Paratype: Peltonotus peninsularis / Y. MIYAKE, 2000 // Paratype / Peltonotus podocrassus / Jameson and Wada, 2004'. 1 ♂ 'TANARATA / MALAYA / 30. III. 1976 / Y. Miyake leg. // Paratype: Peltonotus peninsularis / Y. MIYAKE, 2000 // Paratype / Peltonotus podocrassus / Jameson and Wada, 2004'. 1 ♂ 'V. R〔C. H.〕Malaya / 21. III. 1978 // 46 // Paratype: Peltonotus peninsularis / Y. MIYAKE, 2000 // Paratype / Peltonotus podocrassus / Jameson and Wada, 2004'. 1 ex. [Malaya] / Tanah Rata / 1–IV–1984 / Y. Miyake leg. // Paratype: Peltonotus peninsularis / Y. MIYAKE, 2000 // Paratype / Peltonotus podocrassus / Jameson and Wada, 2004'. 1 ex. 'TANARATA / MALAYA / 1. IV. 1984 / Y. Miyake // Paratype: Peltonotus peninsularis / Y. MIYAKE, 2000 // Paratype / Peltonotus podocrassus / Jameson and Wada, 2004'.

Current status. Valid species.

Peltonotus sakaii Miyake & Yamaya

Peltonotus sakaii Miyake & Yamaya, 1994: 39–40, 42.

Note. The following paratype is deposited in RIEB (ex coll. Y. Miyake):

Paratype. 1 ex.: 'Mt. Serapi / SARAWAKU / 1991/III. // 20 // Paratype: / Peltonotus sakaii / Y. MIYAKE et YAMAYA, 1994 // Peltonotus / similis Arrow, 1931 / det. Kaoru Wada, 2004'.

Current status. Junior subjective synonym of *Peltonotus similis* Arrow, 1931, see Krajcik (2012).

Remark. In addition to the paratypes mentioned above, the following specimens labeled as paratypes are not designated in the original description: 1 ♂ 'Mt. Serapi / Kuching, Sarawak / IX. 1990 / BORNEO // Paratype: / Peltonotus sakaii / Y. MIYAKE et YAMAYA, 1994 // Peltonotus / similis Arrow, 1931 / det. Kaoru Wada, 2004'. 1 ex. 'Lembah Anai / W. Sumatra / VI. 1990 / INDONESIA // [yellow label] // Paratype: / Peltonotus sakaii / Y. MIYAKE et YAMAYA, 1994 // Peltonotus / similis Arrow, 1931 / det. Kaoru Wada, 2004'. 1 ♂ 'Kimanis Road / Near Keningau / N. Borneo / 3–V–1994 // Paratype: / Peltonotus sakaii / Y. MIYAKE et YAMAYA, 1994 // Peltonotus / similis Arrow, 1931 / det. Kaoru Wada, 2004'. 2 exs. 'Kimanis Road / Near Keningau / N. Borneo / 3–V–1994 // Paratype: / Peltonotus sakaii / Y. MIYAKE et YAMAYA, 1994 // Peltonotus / similis Arrow, 1931 / det. Kaoru Wada, 2004'.

Peltonotus sulawesiensis **Wada**

Peltonotus sulawesiensis Wada, 1990: 1–2.

Note. The following paratypes are deposited in RIEB (ex coll. Y. Miyake):

Paratypes. 4 exs.: 'Tondano N. Celebes / INDONESIA / V 1988 / leg. N. Nisikawa // PARATYPE / Peltonotus sulawesiensis / Kaoru WADA, 1990'.

Current status. Junior subjective synonym of *Neohyphus celebesus* Heller, 1896, see Kuijten (1994).

Subfamily Melolonthinae

Genus *Amiserica*

Amiserica rufidula **Nomura**

Amiserica rufidula Nomura, 1974: 84.

Note. The following paratypes are deposited in RIEB (ex coll. S. Nomura):

Paratypes. 2 exs.: 1 ♂ 'Li-shan / Taiwan / 29. VII. 1974 / Y. Miyake // ♂ // PARATYPE / Amiserica / rufidula / NOMURA (1974)'. 1 ♂ 'Li-shan / Taiwan / 1. VIII. 1974 / Y. Miyake // ♂ // PARATYPE / Amiserica / rufidula / NOMURA (1974)'.

Current status. Valid species.

Genus *Apogonia*

Apogonia fujiokai **Miyake & Yamaya**

Apogonia fujiokai Miyake & Yamaya, 1997: 6–7.

Note. The following paratype is deposited in RIEB (ex coll. Y. Miyake):

Paratype. 1 ex.: 'Flores Is. / Indonesia / May. 1995 // Y // Paratype: / Apogonia fujiokai / Y. MIYAKE et YAMAYA, 1997'.

Current status. Valid species.

Apogonia fusciventris Miyake & Yamaya

Apogonia fusciventris Miyake & Yamaya, 1997: 5–6.

Note. The following paratype is deposited in RIEB (ex coll. Y. Miyake):

Paratype. 1 ex.: 'Vangvieng / P. Vietiane / LAO. P. D. R. / 25–26. MAY. 1994. / K. Miura–leg. // Y // Paratype: Apogonia / fuscoventris / Y. MIYAKE et YAMAYA, 1997'.

Current status. Junior subjective synonym of of *Apogonia striatipennis* Frey, 1971, see Kobayashi (2010).

Remark. The species name on the paratype label is '*fuscoventris*', which is invalid. Probably, the name was confused with *fusciventris* by Y. Miyake.

Apogonia hongkongica Miyake

Apogonia hongkongica Miyake, 1989b: 38–39.

Note. The following paratypes are deposited in RIEB (ex coll. Y. Miyake):

Paratypes. 11 exs.: 1 ♂ 'Hong Kong / China / C. K. Yu / 1974. V. [white label, front] // Native Collector / legt. [white label, back] // Paratype: / Apogonia / hongkongica / Y. MIYAKE, 1989'. 1 ♂ 'Hong Kong / China / V. 1974 / C. K. Yu [white label, front] // Legt. / Native / Collector [white label, back] // Paratype: / Apogonia / hongkongica / Y. MIYAKE, 1989'. 1 ♂ 'Hong Kong / China / V. 1974 / C. K. Yu [white label, front] // Native Collector [white label, back] // Paratype: / Apogonia / hongkongica / Y. MIYAKE, 1989'. 1 ♀ '♀ // Hong Kong / China / V. 1974 / C. K. Yu [white label, front] // Legt. / Native / Collector // Paratype: / Apogonia / hongkongica / Y. MIYAKE, 1989'. 1 ♀ '♀ // Hong Kong / China / V. 1974 / C. K. Yu [white label, front] // Native / Collector / legt. // Paratype: / Apogonia / hongkongica / Y. MIYAKE, 1989'. 1 ♀ 'Hong Kong / 1974 / From C. K. Yu ♀ // Paratype: / Apogonia / hongkongica / Y. MIYAKE, 1989'. 1 ex. 'Hong Kong / China / V. 1974 / C. K. Yu [white label, front] // Legt. / native / Collector [white label, back] // Paratype: / Apogonia / hongkongica / Y. MIYAKE, 1989'. 2 exs. 'Hang Kong / China / V. 1974 / C. K. Yu Col [white label, front] // Native / Collector / legt. // Paratype: / Apogonia / hongkongica / Y. MIYAKE, 1989'. 2 exs. 'Hong Kong / V. 1974 / From C. K. Yu // Paratype: / Apogonia / hongkongica / Y. MIYAKE, 1989'.

Current status. Valid species.

Remark. In addition to the paratypes mentioned above, the following specimens labeled as paratypes are not designated in the original description: 1ex. 'Hong Kong / 1975 / From. C. K-Yu // Paratype: Apogonia / hongkongica / Y. MIYAKE, 1989'.

1 ♀ 'Hong Kong / ♀ 1975 [white label, front] // from / C. K. Yu [white label, back] // Paratype: / Apogonia / hongkongica / Y. MIYAKE, 1989'.

Apogonia inconstans Kobayashi & Bezděk

Apogonia inconstans Kobayashi & Bezděk, 2011: 64–65.

Note. The following paratypes are deposited in RIEB (ex coll. A. Bezděk):

Paratypes. 4 exs.: 1 ♂ '1985. 5. 18–19. / Wieng Ko Sai Nat. / Park, Phrae Prov., / N-Thailand / Col. S. Ohmomo [white label, front] // 5/18 夜= yoru [white label, back] // PARATYPE / *Apogonia* / *inconstans* / Kobayashi et Bezděk, 2011'. 1 ex. '1985. 5. 18–19. / Wieng Ko Sai Nat. / Park, Phrae Prov., / N-Thailand / Col. S. Ohmomo [white label, front] // 5/18 夜= yoru [white label, back] // PARATYPE / *Apogonia* / *inconstans* / Kobayashi et Bezděk, 2011'. 1 ex. '1985. 5. 18–19. / Wieng Ko Sai Nat. / Park, Phrae Prov., / N-Thailand / Col. S. Ohmomo [white label, front] // 夜= yoru 5/18 [white label, back] // PARATYPE / *Apogonia* / *inconstans* / Kobayashi et Bezděk, 2011'. 1 ex. '1985. 5. 18–19. / Wieng Ko Sai Nat. / Park, Phrae Prov., / N-Thailand / Col. S. Ohmomo [white label, front] // night [white label, back] // PARATYPE / *Apogonia* / *inconstans* / Kobayashi et Bezděk, 2011'.

Current status. Valid species.

Apogonia ohmomoi Miyake

Figure 2G

Apogonia ohmomoi Miyake, 1989: 177–178.

Note. The holotype is deposited in RIEB (ex coll. Y. Miyake):

Holotype (♂). '1985. 5. 18–19. / Wieng Ko Sai Nat. / Park, Phrae Prov., / N–Thailand / Col. S. Ohmomo [white label, front] // 夜= yoru 5/18 [white label, back] // 14 // Holotype: / Apogonia / scabra / Y. MIYAKE // *Apogonia ohmomoi* / Miyake, 1989 / HOLOTYPUS, ♂ / A. Bezděk det. 2011'. (Fig. 2G)

Type condition. The aedeagus of the holotype is pinned separately, and the right antenna, right and left protarsus, right mesoclaw, left mesotarsus, right metatarsus and mesonotum are missing.

Current status. Valid species.

Remark. The label '*Apogonia scabra*' was apparently accidentally put by Miyake.

Apogonia ovata Miyake & Yamaguchi

Figure 2H

Apogonia ovata Miyake & Yamaguchi, 1998: 25–27.

Note. The holotype is deposited in RIEB (ex coll. Y. Miyake):

Holotype (♂). 'Kaeng Tana / Khong Chiam / Ubonratchathani / [NE-THAILAND] / 29. Aug. 1997 / S. Yamaguchi leg. // Holotype / *Apogonia ovata* / Y. MIYAKE et YAMAGUCHI 1998'. (Fig. 2H)

Type condition. The aedeagus of the holotype is pinned separately.

Current status. Senior synonym of *Apogonia miyakei* Bezděk, 2004, see Bezděk (2004).

Apogonia terminalis Miyake, Yamaguchi & Akiyama

Figure 3A

Apogonia terminalis Miyake, Yamaguchi & Akiyama, 2002: 56–58.

Note. The holotype and following paratypes are deposited in RIEB (ex coll. Y. Miyake):

Holotype (♂). 'Don Far Huan (light) / Ubon Ratchathani / E-THAILAND / 17. Sep. 1999 / S. Yamaguchi & / M. Akiyama leg. // Holotype / *Apogonia terminalis* / Y. MIYAKE, YAMAGUCHI / et AKIYAMA 2002'. (Fig. 3A)

Paratypes. 4exs.: 1 ♂ 'Ban Lao Kram / Mukdahan (light) / NE-THAILAND / 5. Sep. 1999 / S. Yamaguchi & / M. Akiyama leg. // Paratype / *Apogonia terminalis* / Y. MIYAKE, YAMAGUCHI / et AKIYAMA 2002'. 3 ♀ 'Don Far Huan (light) / Ubon Ratchathani / E-TAILAND / 17. Sep. 1999 / S. Yamaguchi & / M. Akiyama leg. // ♀ // Paratype / *Apogonia terminalis* / Y. MIYAKE, YAMAGUCHI / et AKIYAMA 2002'.

Type condition. The aedeagus of the holotype is pinned separately, and the left proclaw, right and left mesotarsus, right metaclaw and left metatarsus are missing.

Current status. Valid species.

Apogonia unidentata Miyake, Yamaguchi & Akiyama

Figure 3B

Apogonia unidentata Miyake, Yamaguchi & Akiyama, 2002: 55–56.

Note. The holotype and following paratypes are deposited in RIEB (ex coll. Miyake):

Holotype (♂). 'Ban Lao Kram / Mukdahan (light) / NE-THAILAND / 5. Sep. 1999 / S. Yamaguchi & / M. Akiyama leg. // Holotype / Apogonia / unidentata // Holotype / *Apogonia unidentata* / Y. MIYAKE, YAMAGUCHI / et AKIYAMA 2002'. (Fig. 3B)

Paratypes. 6 exs.: 4exs. 'Ban Lao Kram / Mukudahan (light) / NE-THAILAND / 5. Sep. 1999 / S. Yamaguchi & / M. Akiyama leg. // Paratype / *Apogonia unidentata* / Y. MIYAKE, YAMAGUCHI / et AKIYAMA 2002'. 1 ex. 'Ban Lao Kram / Mukudahan (light) / NE-THAILAND / 5. Sep. 1999 / S. Yamaguchi & / M. Akiyama leg. // 63 // Paratype / *Apogonia unidentata* / Y. MIYAKE, YAMAGUCHI / et AKIYAMA 2002'. 1 ex. 'Ban Lao Kram / Mukudahan (light) / NE-THAILAND / 14. Sep. 1999 / S.

Yamaguchi & / M. Akiyama leg. / シミレア= shimirea // Paratype / *Apogonia unidentata* / Y. MIYAKE, YAMAGUCHI / et AKIYAMA 2002'.

Type condition. The aedeagus of the holotype is pinned separately, and the right protarsus and right and left metatarsi are missing.

Current status. Valid species.

Genus *Dichelomorpha*

Dichelomorpha sublineata Miyake

Figure 3C

Dichelomorpha sublineata Miyake, 1994: 140–141.

Note. The holotype and following paratypes are deposited in RIEB (ex coll. Y. Miyake):

Holotype (♂). 'Is. Tioman, east of / Malay Pennisular March. 1993, nat, col // 1 [aedeagus mount] // Holotype: / Dichelomorpha / sublineata / Y. MIYAKE, 1994'. (Fig. 3C)

Paratypes. 34 exs.: 10 ♂ 'Is. Tioman, east of / Malay Pennisular / March. 1993. nat, col // Paratype: / Dichelomorpha / sublineata / Y. MIYAKE, 1994'. 14 exs. 'Is. Tioman, east of / Malay Pennisular / March. 1993. nat, col // Paratype: / Dichelomorpha / sublineata / Y. MIYAKE, 1994'. 1 ♂ 'Is. Tioman, east of / Malay Pennisular / March. 1993. nat, col // 11 // Paratype: / Dichelomorpha / sublineata / Y. MIYAKE, 1994'. 1 ex. 'Is. Tioman, east of / Malay Pennisular / March. 1993. nat, col // 4 // Paratype: / Dichelomorpha / sublineata / Y. MIYAKE, 1994'. [[8 exs. 'Tioman Is. / E. of Malaya / III–1933 (the date given in the original description is III–1993), W. // Paratype: / Dichelomorpha / sublineata / Y. MIYAKE, 1994']].

Type condition. The aedeagus of the holotype is pinned separately. The right mesotarsus is missing.

Current status. Valid species.

Remark. Miyake (1994) did not provide a photograph of the holotype. Apparently he provided a photograph of a paratype, but we could not trace that specimen.

Genus *Holomelia*

Holomelia gigantea Miyake

Figure 3D

Holomelia gigantea Miyake, 1996: 35–36.

Note. The holotype and following paratypes are deposited in RIEB (ex coll. Y. Miyake).

Holotype (♂). '19 miles from / Tapah, Malaya / 1–II–1974 / Y. Miyake leg [white label, front] // Wu TET KONG / legt. [white label, back] // 29・5 // 家= ie [aedeagus mount] // Holotype: / Holomelia / gigantea / Y. MIYAKE, 1996'. (Fig. 3D)

Paratypes. 2 exs.: 1 ♂ ‘Cameron H. / MALAYA / Jan–Feb 1974 / Y. Miyake leg. // 30.5 // Paratype: / Holomelia gigantea / Y. MIYAKE, 1996 // 19 miles from / Tapah, Malaya / 1–II–1974 [white label, front] // Wu Tet Kong legt. [white label, back]’. 1 ex. ‘19 miles from / Tapah, Malaya / 1–II–1974 [white label, front] // Wu Tet Kong legt. [white label, back] // Paratype: / Holomelia gigantea / Y. MIYAKE, 1996’.

Type condition. The aedeagus of the holotype is pinned separately.

Current status. Valid species.

Remark. Miyake (1996) did not provide a photograph of the holotype. Apparently he provided a photograph of a paratype, but we could not trace that specimen.

Genus *Holotrichia*

Holotrichia loochooana umebayashii Miyake
Figure 3E

Holotrichia loochooana umebayashii Miyake, 1986a: 1–2.

Note. The holotype is deposited in RIEB (ex coll. Y. Miyake):

Holotype (♂). 〔‘Loo-Choo〕 Okinoerabuzima / 21. IV. 1957. / K. Umebayashi // 7 [white label, mounted on a part of tarsus] // HOLOTYPE / Holotrichia / loochooana / umebayashii / Y. MIYAKE, 1986’. (Fig. 3E)

Type condition. The aedeagus of the holotype is pinned separately. The left protarsus and the right and left metatarsus are missing.

Current status. Junior subjective synonym of *Nigrotrichia loochooana okinawana* (Nomura, 1964), see Matsumoto (2016).

Remark. The collecting date in the original description is 1.V.1957, which disagrees with the label data.

Holotrichia yamayai Miyake & Yamaguchi
Figure 3F

Holotrichia yamayai Miyake & Yamaguchi, 1998: 27–28.

Note. The holotype and following paratype are deposited in RIEB (ex coll. Y. Miyake):

Holotype (♂). ‘North Thailand / Chiangmai-Saraphee / 15th, June, 1996 / Native collector // Holotype / *Holotricchia yamayai* / Y. MIYAKE et YAMAGUCHI 1998’. (Fig. 3F)

Paratype. 1 ex.: 1 ♀ ‘Kaeng Tana / Khong Chiam / Ubonratohathani / [NE-THAILAND] / 27. Aug. 1997 / S. Yamaguchi leg. // Paratype / Holotrichia yamayai / Y. MIYAKE et YAMAGUCHI 1998’.

Type condition. The aedeagus of the holotype is pinned separately.

Current status. Valid species.

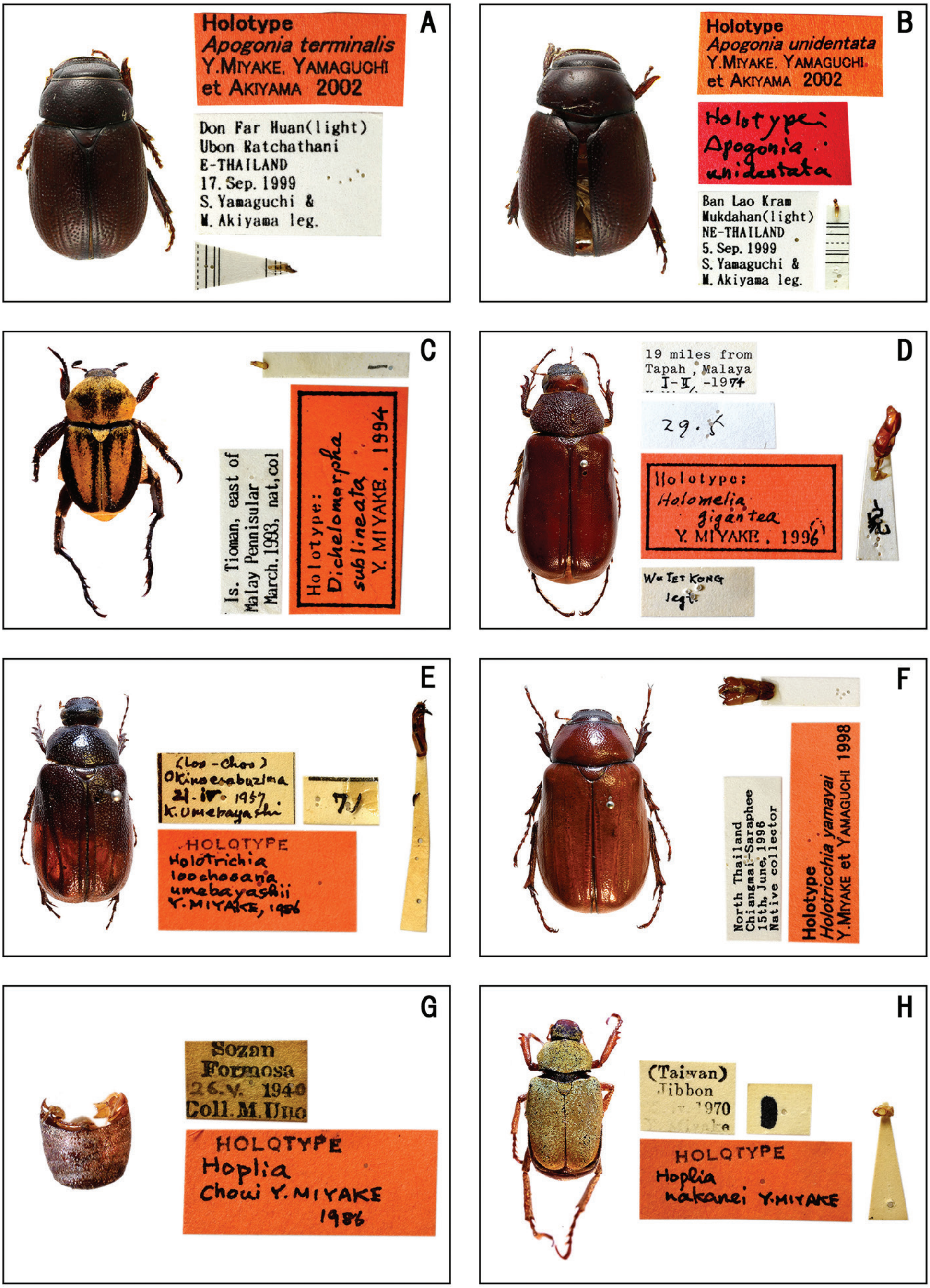

Figure 3. Habitus of holotype specimens. **A** *Apogonia terminalis* Miyake, Yamagushi et Akiyama **B** *Apogonia unidentata* Miyake, Yamaguchi et Akiyama **C** *Dichelomorpha sublineata* Miyake **D** *Holomelia gigantea* Miyake **E** *Holotrichia loochooana umebayashii* Miyake **F** *Holotrichia yamayai* Miyake et Yamaguchi **G** *Hoplia choui* Miyake **H** *Hoplia nakanei* Miyake.

Genus *Hoplia*

Hoplia choui Miyake
Figure 3G

Hoplia choui Miyake, 1986b: 203–204.

Note. The holotype is deposited in RIEB (ex coll. Y. Miyake):

Holotype (♂). ‘Sozan / Formosa / 26. V. 1940 / Coll. M. Uno // HOLOTYPE / Hoplia / Choui Y. MIYAKE / 1986’. (Fig. 3G)

Type condition. Abdomen only.

Current status. Valid species.

Remark. Most part of the holotype specimen was destroyed by *Anthrenus verbasci*.

Hoplia nakanei Miyake
Figure 3H

Hoplia nakanei Miyake, 1986b: 207.

Note. The holotype and following paratypes are deposited in RIEB (ex coll. Y. Miyake): **Holotype (♂).** ‘(Taiwan) / Jibbon / 2. iv. 1970 / Y. Miyake // 1 // HOLOTYPE / Hoplia / nakanei Y. MIYAKE’. (Fig. 3H)

Paratypes. 29 exs.: 4 exs. ‘[Taiwan] / 六亀= liugui. 石山= shi shan / 9–VI–1976 / Y. Miyake leg. // Paratype / Hoplia / nakanei / Y. Miyake, 1986’. 5 exs. ‘[Taiwan] / Liukuei 石山= shi shan / 9–VI–1976 / Y. Miyake leg. // Paratype / Hoplia / nakanei / Y. Miyake, 1986’. 1 ex. ‘[Taiwan] / 六亀= liugui. 石山= shi shan / 9–VI–1976 / 陳文竜= chen wenzhao leg. // Paratype / Hoplia nakanei / Y. Miyake, 1986’. 4 exs. ‘[Taiwan] / Baibara / –V–1963 / T. Shirozu leg. // Paratype / Hoplia / nakanei / Y. Miyake, 1986’. 1 ex. ‘[Taiwan] / Baibara / –V–1963 / Shirozu leg. // Paratype / Hoplia / nakanei / Y. Miyake, 1986’. 1 ex. ‘[Taiwan] / Baibara / –V–1963 / T. Shirozu // Paratype: Hoplia / nakanei Y. Miyake, 1986’. 1 ♂ ‘六亀= liugui. 石山= shi shan / alt. 2000 m / 9. VI. 1976 // Paratype: / Hoplia / nakanei / Y. MIYAKE, 1986’. 1 ex. ‘FENCHIFO / FORMOSA / 24. V. 1975 / K. MATSUDA // Paratype: / Hoplia nakanei / Y. MIYAKE, 1986’. 1 ex. ‘Swakang / Taiwan / 15. VI. 1970 / Fukuda // Paratype: / Hoplia nakanei / 1986. Y. MIYAKE’. 1 ex. ‘NANSHANCHI / TAIWAN / 1. IV. 1970 / H. NOMURA // PARATYPE / Hoplia / nakanei / Y. MIYAKE, 1986’. [[4 exs. ‘[Taiwan] / Baibara / V. 1965 (the date given in the original description is V. 1963) / T. Shirozu // Paratype / Hoplia nakanei / Y. Miyake’]]. [[2 exs. ‘[Taiwan] / Baibara / V. 1965 (the date given in the original description is V. 1963) / T. Shirozu // Paratype / Hoplia nakanei / Y. Miyake, 1986’]]. [[1 ♂ ‘[Taiwan] / Baibara / V. 1965 (the date given in the original description is V. 1963) / Col. T. Shirozu // Paratype / Hoplia nakanei / Y. Miyake, 1986’]]. [[1 ex. ‘[Taiwan

] / Baibara / V. 1965 (the date given in the original description is V. 1963) / Col. T. Shirozu // Paratype / Hoplia nakanei / Y. Miyake, 1986']]. [[1 ex. '[Taiwan] / Baibara / V. 1965 (the date given in the original description is V. 1963) / Col. T. Shirozu // Paratype / Hoplia nakanei / 1986. Y. Miyake']].

Type condition. The aedeagus of the holotype is pinned separately.

Current status. Valid species.

Remark. The label data the holotype do not match the original description. There is one male paratype ('六亀= liugui. 石山= shi shan / alt. 2000 m / 9. VI. 1976 // Paratype: / Hoplia / nakanei / Y. MIYAKE, 1986') that agrees with the data of the holotype. Probably the type labels were mixed up and this specimen should be considered the holotype.

In addition to the paratypes listed above, the following specimens labeled as paratypes are not designated in the original description: 1 ex. '[Taiwan] / Liukuei / –V–1963 / T. Shirozu col. // Paratype / Hoplia / nakanei / Y. Miyake, 1986'. 1 ex. 'APR II. 1971 / 榮華= ronghua / B-S. CHANG // PARATYPE / Hoplia / nakanei / Y. MIYAKE, 1986'. 1 ex. 'Paratype / Hoplia nakanei / Y. MIYAKE, 1986'.

Hoplia nengkaoshana Miyake

Hoplia nengkaoshana Miyake, 1986b: 211.

Note. The allotype and following paratypes are deposited in RIEB (ex coll. Y. Miyake):

Allotype (♀). 'Allotype // mt. Noko (2650 m) / V. 20–VI. 2, 1966 // 1 // PARATYPE / Hoplia / nengkaoshana / Y. MIYAKE, 1986'.

Paratypes. 3ex.: 1 ♂ 'mt. Nōhō / C-Formosa / V–20 ~ Vi–21 1966 // PARATYPE / Hoplia / nengkaoshana / Y. MIYAKE, 1986'. 1 ♂ 'MT. HÔFAN / FORMOSA / 5–V. 73 / T. OCHI // 1 // PARATYPE / Hoplia / nengkaoshana / Y. MIYAKE, 1986 // Hoplia / inornata / H. Kobayashi, 1990 / Det. H. Kobayashi, 2015'. 1 ex. 'JUL. 16. 1966 / 合欢山= hehuan shan / B. S. Chang // PARATYPE / nengkaoshana / Y. MIYAKE, 1986 // Hoplia / inornata / H. Kobayashi, 1990 / Det. H. Kobayashi, 2015'.

Current status. Valid species.

Remark. In addition to the paratypes mentioned above, the following specimens labeled as paratypes are not designated in the original description: 1 ex. '台中= tai chung 和平郷= heping xiang 早等村= zaodeng cun / 横貫公路= hengguan gonglu. 梨山站 = lishan zhan / 海拔= kaibatsu 1679–2196 m. / 13–16. V. 1958. 陶家駒= tao jiayu // PARATYPE / Hoplia / nengkaoshana / Y. MIYAKE, 1986'. 1 ex. 'AUG 13. 1970 / 新坡 = xinpo / B-S. CHANG // PARATYPE / Hoplia / nengkaoshana / Y. MIYAKE, 1986'.

Hoplia simillima Miyake
Figure 4A

Hoplia simillima Miyake, 1986b: 206–207.

Note. The holotype and following paratypes are deposited in RIEB (ex coll. Y. Miyake):

Holotype (♂). '[Taiwan] / Liukuei 石山= shi shan / 9–VI–1979 / Y. Miyake leg. // HOLOTYPE / Hoplia / simillima / Y. MIYAKE, 1986'. (Fig. 4A)

Paratypes. 5 exs.: 3 exs. '(FORMOSA) / Baibara / –V–1969 // Paratype / Hoplia / simillima / 1989, Y. Miyake'. 2 exs. '(FORMOSA) / Baibara / –V–1969 / T. Shirozu // Paratype / Hoplia / simillima / 1989, Y. Miyake'.

Current status. Valid species.

Remark. In addition to the paratypes mentioned above, the following specimens labeled as paratypes are not designated in the original description: 1 ex. '[Taiwan] / Liukuei 石山= shi shan / 9–VI–1979 / Y. Miyake leg. // Paratype / Hoplia / simillima / 1989, Y. Miyake'. 1 ♂ '石= ishi // [Taiwan] / 六亀= liugui 石山= shi shan / 9–VI–1976 / Y. Miyake leg. // Paratype / Hoplia / simillima / 1989, Y. Miyake'. 1 ex. '(FORMOSA) / Mt. Ali / 14 V 1968 / Y. HAYASHI // Paratype'.

Hoplia taiwana Miyake

Figure 4B

Hoplia taiwana Miyake, 1986b: 204.

Note. The holotype and following paratypes are deposited in RIEB (ex coll. Y. Miyake):

Holotype (♂). 'HOLOTYPE / Hoplia / Taiwana Y. MIYAKE / 1986'. (Fig. 4B)

Paratypes. 9 exs.: 1 ex. 'NANSHANCHI / TAIWAN / 3. IV. 1970 / H. NOMURA // PARATYPE / Hoplia taiwana / Y. MIYAKE, 1986'. 1 ex. 'NANSHANCHI / TAIWAN / 4. IV. 1970 / H. NOMURA // PARATYPE / Hoplia taiwana / Y. MIYAKE, 1986'. 1 ex. 'NANSHANCHI / TAIWAN / 5. IV. 1970 / Y. KIYOYAMA // PARATYPE / Hoplia taiwana / Y. MIYAKE, 1986'. 1 ex. 'SUNGKANG / FORMOSA / 29. VI. 1971 / Y. MAEDA // PARATYPE / Hoplia taiwana / Y. MIYAKE, 1986'. 1 ex. 'NANSHANCHI / TAIWAN / 31. III. 1981 / Y. YAMAMOTO // Paratype / Hoplia / taiwana / Y. MIYAKE, 1986'. 1 ex. 'NANSHANCHI / TAIWAN / 1. IV. 1981 / F. KIMURA // Paratype / Hoplia / taiwana Y. MIYAKE / (1968)'. 1 ex. 'NANSHANCHI / TAIWAN / 2. IV. 1981 / F. KIMURA // Paratype / Hoplia / taiwana Y. MIYAKE'. 1 ex. 'NANSHANCHI / TAIWAN / 2. IV. 1981 / F. KIMURA // Paratype / Hoplia taiwana / 1986 Y. MIYAKE'. 1 ex. 'NANSHANCHI / TAIWAN / 3. IV. 1981 / Y. YAMAMOTO // PARATYPE / Hoplia taiwana / Y. MIYAKE, 1986'.

Current status. Valid species.

Remark. The locality label data of the holotype are missing but the specimen agrees with the original description.

In addition to the paratypes mentioned above, the following specimens labeled as paratypes were not designated in the original description: 3 exs. '[Taiwan] / Liukuei 石山= shi shan / 9–VI–1976 / Y. Miyake leg. // PARATYPE / Hoplia / taiwana / Y. MIYAKE, 1986'. 1 ex. '[Taiwan] / 六亀= liugui 石山= shi shan / 9–VI–1976 / Y. Miyake leg. // PARATYPE

/ Hoplia / taiwana / Y. MIYAKE, 1986'. 2 exs. 'Mt. YUSHAN / TAIWAN / 8. VI. 1980 / M. YAMAMOTO // Paratype / Hoplia / taiwana Y. MIYAKE'. 4 exs. 'TAIWAN / 陽明山= mt. yangmingshan / 20. IV. 1956 / COL. K. S. LIN // Paratype / Hoplia / taiwana / Y. MIYAKE, 1986'. 1 ex. 'LUSHAN / FORMOSA / 13–IV. 74 / S. TAKEDA // PARATYPE / Hoplia / taiwana / Y. MIYAKE, 1986'. 1 ex. '榮華= ronghua / APR. 7. 1971 / BS, CHANG // PARATYPE / Hoplia taiwana / Y. MIYAKE, 1986'. 1 ex. '[Taiwana] / Baibara / –V–1965 / T. Shirozu leg. // Paratype: Hoplia / taiwana Y. MIYAKE. 1986'.

Genus *Maladera*

Maladera hiranoi Miyake

Figure 4C

Maladera hiranoi Miyake, 1986b: 3–5.

Note. The holotype is deposited in RIEB (ex coll. Y. Miyake):

Holotype (♂). '三京= mikyô / 21/VII–82 // HOLOTYPE / Maladera / hiranoi MIYAKE / (1986) // Maladera / impressthorax / hiranoi Y. MIYAKE / DET. Y. MIYAKE, 199 // ムナクボビロウドコガネ= munakubobirôdokogane / *Maladera* (*japonica*–G) / *impressithorax* / Nomura, 1973 / Det. H. Hirasawa 2012'. (Fig. 4C)

Current status. Junior subjective synonym of *Maladera okinoerabuana* Kobayashi, 1978, see Ahrens and Bezděk (2016).

Remark. The date on the collecting data label of the holotype is 21.VII.1982, but the collecting date quoted in the original description is 22.VII.1982. Probably, Miyake made a typographical error when writing the description.

Maladera kobayashii Nomura

Maladera kobayashii Nomura, 1974: 106–107.

Note. The following paratypes are deposited in RIEB (ex coll. S. Nomura):

Paratypes. 2 exs.: 1 ♂ 'Li-shan / Taiwan / 29. VII. 1974 / Y. Miyake // ♂ // PARATYPE / Maladera (s. str) / kobayashii / NOMURA (1974)'. 1 ♀ 'Li-shan / Taiwan / 29. VII. 1974 / Y. Miyake // ♀ // PARATYPE / Maladera / kobayashii / NOMURA (1974)'.

Current status. Valid species.

Maladera kusuii Miyake

Figure 4D

Maladera kusuii Miyake, 1986b: 2–3.

Note. The holotype is deposited in RIEB (ex coll. Y. Miyake):

Holotype (♂). ‘三宅= miyake / コガネムシ上科標準図鑑= koganemushijyôka-hyôjyunzukan / ビロウドコガネ族= birôdokoganezoku / 図鑑使用標本= zukanshiyôhyôhon / 執筆担当= shippitsutantô：平沢 伴明= hirasawa tomoaki / 学研教育出版= gakkenkyôikushuppan (2012) // GAKIYA / Iheya-jima / Aug. 11 1977 / leg. Y Kusui // イヘヤビロウドコガネ= iheyabirôdokogane / Maladera (japonica–G) / kusuii / Y. Miyake, 1986 / Det. H. Hirasawa 2012 // Holotype: / Maladera kusuii / Y. MIYAKE, 1986’.

Type condition. The aedeagus of the holotype is pinned separately. The right and left protarsi, the left mesotarsus, and the right and left metatarsi are missing, but some of the missing parts are pinned separately.

Current status. Valid species.

Maladera lishana Miyake

Maladera lishana Miyake, 1989b: 37–38.

Note. The following paratype is deposited in RIEB (ex coll. Y. Miyake):
Paratype. 1 ex.: 1 ♀ ‘Lishan / Taiwan / 28. VII. 1973 / Y. Miyake // Paratype: / Maladera / lishana / Y. MIYAKE, 1989’.

Current status. Valid species.

Maladera nanshanchiana Nomura

Maladera nanshanchiana Nomura, 1974: 111–112.

Note. The following paratypes are deposited in RIEB (ex coll. S. Nomura):

Paratypes. 2 exs.: 1 ex. ‘Puli 24 // PARATYPE / Maladera / nanshanchiana / NOMURA (1974)’. 1 ♀ ‘Puli 24 // ♀ // PARATYPE / Maladera / nanshanchiana / NOMURA (1974) // ナンザンケイビロウドコガネ= nanzenkeibirodokogane / *Maladera* (*Cephaloserica*) / *nanshanchiana* / Nomura, 1974 / Det. H. Hirasawa 2012’.

Current status. Valid species.

Maladera secreta horaiana Nomura

Maladera secreta horaiana Nomura, 1974: 112.

Note. The following paratype is deposited in RIEB (ex coll. S. Nomura):

Paratype. 1 ex.: 1 ♂ ‘Lishan / C. Taiwan / 29. vii. 1973 / Y. Miyake // 三宅= miyake // PARATYPE / Maladera / secreta / horaiana / NOMURA (1974)’.

Current status. Valid species.

Genus *Melanomaladera*

Melanomaladera yunnana Miyake & Yamaya

Melanomaladera yunnana Miyake & Yamaya, 2001: 38–39.

Note. The following paratypes are deposited in RIEB (ex coll. Y. Miyake):

Paratypes. 2 exs.: 1 ♂ 'China, N W Yunnan / Degen City env. / 3300 m alt. / 29. Jun. 1998 / A. Gorodinsky leg. // 13 // Paratype: / Melanoserica / yunnana'. 1 ♀ 'China, N W Yunnan / Degen City env. / 3300 m alt. / 29. Jun. 1998 / A. Gorodinsky leg. // 13 // Paratype: / Melanoserica / yunnana'.

Current status. *Archeohomaloplia yunnana* (Miyake et Yamaya, 2001), see Ahrens and Bezděk (2016).

Remark. The genus name on the paratype labels is '*Melanoserica*', which is invalid. Probably, it was confused with '*Melanomaladera*' by Y. Miyake.

Genus *Microserica*

Microserica (*Parvulomaladera*) *annapurnae* Ahrens

Microserica (*Parvulomaladera*) *annapurnae* Ahrens, 1995: 46–48.

Note. The following paratype is deposited in RIEB (ex coll. D. Ahrens):

Paratype. 1 ex.: 'NEPAL–HIMALAYA / Annapurna–Mts. / leg. Ahrens 1993 // Pisang bis / Manang, 30. 5. / 3000–3300 m // PARATYPEUS / *Parvulomaladera* / *annapumae sp. n.* / det. D. AHRENS 1994'.

Current status. *Oxyserica pygidialis annapurnae* (Ahrens, 1995), see Ahrens and Bezděk (2016).

Microserica nitidipyga Nomura

Microserica nitidipyga Nomura, 1974: 99.

Note. The following paratype is deposited in RIEB (ex coll. S. Nomura):

Paratype. 1 ex.: 'Lu-SHAN / FORMOSA / 27. IV. 1973 / K. MATSUDA // 三宅= miyake // Paratype / Microserica / nitidipyga / NOMURA (1974) // Microserica / nitidipyga NOM. / DET. Y. MIYAKE, 1994'.

Current status. Valid species.

Genus *Nematophylla*

Nematophylla sugiharai Miyake

Figure 4E

Nematophylla sugiharai Miyake, 2000: 106–108.

Note. The holotype is deposited in RIEB (ex coll. Y. Miyake):

Holotype (♂). 'Kiau Gap / Mt. Kinabalu / Sabah, Borneo / 1. IV. 2000 / H. SUGIHARAI leg. // Holotype: Nematophylla / sugiharai / Y. MIYAKE 2000'. (Fig. 4E)

Current status. Junior subjective synonym of *Nematophylla carinicollis* Arrow, 1938, see Krajcik (2012).

Genus *Nipponoserica*

Nipponoserica pubiventris Nomura

Nipponoserica pubiventris Nomura, 1976b: 189–190.

Note. The following paratype is deposited in RIEB (ex coll. S. Nomura):

Paratype. 1 ex.: 'Takashinohama, / Osaka Pref. / 3. VI. 1974 / Coll. Mitsuo Goto // at light // PARATYPE / Nipponoserica / pubiventris / NOMURA (1976)'.

Current status. Valid species.

Genus *Paramaladera*

Paramaladera makiharai Nomura

Paramaladera makiharai Nomura, 1974: 101–102.

Note. The following paratypes are deposited in RIEB (ex coll. S. Nomura):

Paratypes. 4 exs.: 4 ♂ 'Li-shan / Taiwan / 29. VII. 1974 / Y. Miyake // ♂ // Paratype / Paramaladera / makiharai / NOMURA (1974)'.

Current status. Valid species.

Genus *Pseudohoplia*

Pseudohoplia shibatai Miyake

Pseudohoplia shibatai Miyake, 1986b: 201.

Note. The following paratypes are deposited in RIEB (ex coll. Y. Miyake):

Paratypes. 2 exs.: 1 ♂ '(FORMOSA)/ Mt. Ali / 15 V 1968 / Y. HAYASHI // Paratype // Hoplia / shibatai shibatai / Y. Miyake, 1986 / Det. H. Kobayashi, 2015'. 1 ex. '(FORMOSA)/ Mt. Ali / 15 V 1968 / Y. HAYASHI // Paratype // Hoplia / shibatai shibatai / Y. Miyake, 1986 / Det. H. Kobayashi, 2015'.

Current status. *Hoplia shibatai shibatai* (Miyake, 1986), see Kobayashi (2017).

Remark. In addition to the paratypes mentioned above, the following specimens labeled as paratypes are not designated in the original description: 1 ex. 'Mt. Arishan / Formosa / 1. V. 1973 / K. MATSUDA // Paratype // Paratype / Pseudohoplia / shibatai / Y. Miyake, 1986 // 贈台湾農試= zou-taiwan-noushi'. 1 ♂ 'Houanchi- / Sundchuankang / Nantou Hsien / Taiwan / 25. VI. 1976 / H. Makihara leg. // Paratype // Paratype / Pseudohoplia / shibatai / Y. Miyake, 1986'. 1 ex. 'Mt. Arishan / Formosa / 1. V. 1973 / K. MATSUDA // Paratype / Pseudohoplia / shibatai / Y. Miyake, 1986'. 1 ex. 'MT. ARI / FORMOSA / 1. V. 1973 / K. MATSUDA // Paratype // Paratype / Pseudohoplia / shibatai / Y. Miyake, 1986'.

Pseudohoplia shibatai makiharai **Miyake**

Figure 4F

Pseudohoplia shibatai makiharai Miyake, 1986b: 202.

Note. The holotype is deposited in RIEB (ex coll. Y. Miyake):

Holotype (♂). 'Mt. Lalashan / Taoyuan Hsien / Taiwan / 21–24. V. 1980 / H. Makihara // HOLOTYPE / Pseudohoplia / shibatai makiharai / Y. MIYAKE, 1886'. (Fig. 4F)

Type condition. The aedeagus of the holotype is pinned separately. The right antenna is missing.

Current status. *Hoplia shibatai makiharai* (Miyake, 1986), see Kobayashi (2017).

Pseudohoplia shibatai matsudai **Miyake**

Figure 4G

Pseudohoplia shibatai matsudai Miyake, 1986b: 202.

Note. The holotype is deposited in RIEB (ex coll. Y. Miyake):

Holotype (♂). 'Mt. Nōko / C-Formosa / v–20〜vi–21' 66 // HOLOTYPE / Pseudohoplia / shibatai matsudai / Y. MIYAKE, 1986'. (Fig. 4G)

Type condition. The aedeagus of the holotype is pinned separately.

Current status. Junior subjective synonym of *Hoplia shibatai shibatai* (Miyake, 1986), see Kobayashi (2017).

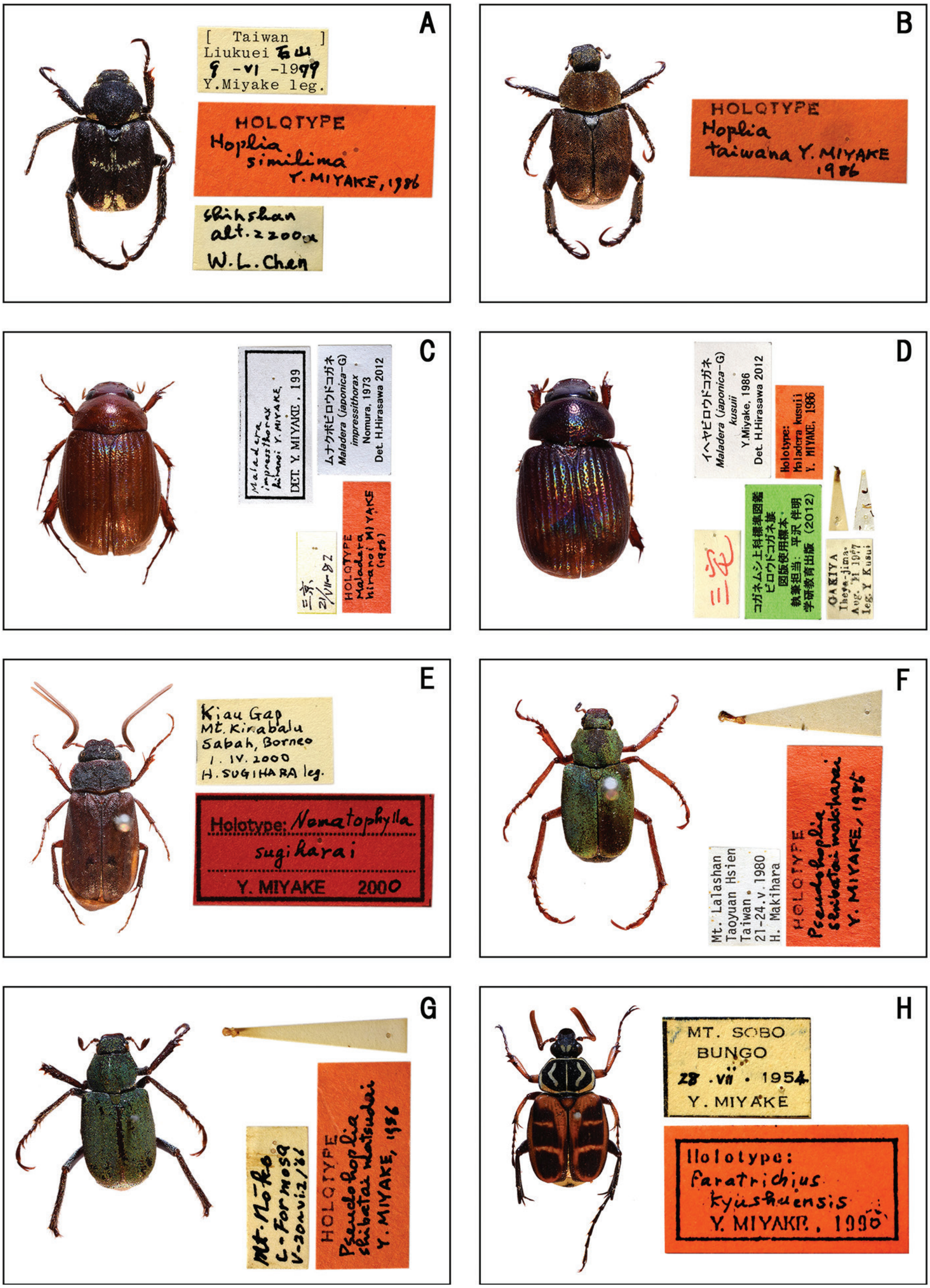

Figure 4. Habitus of holotype specimens. **A** *Hoplia simillima* Miyake **B** *Hoplia taiwana* Miyake **C** *Maladera hiranoi* Miyake **D** *Maladera kusuii* Miyake **E** *Nematophylla sugiharai* Miyake **F** *Pseudohoplia shibatai makiharai* Miyake **G** *Pseudohoplia shibatai matsudai* Miyake **H** *Paratrichius kyushuensis* Miyake.

Genus *Pseudomaladera*

Pseudomaladera nitidifrons Nomura

Pseudomaladera nitidifrons Nomura, 1974: 96.

Note. The following paratypes are deposited in RIEB (ex coll. S. Nomura):

Paratypes. 2 exs.: 1 ♂ 'FUNCHIHO / FORMOSA / 1. VIII. 1973 / H. OHASHI // ♂ // 三宅= miyake // Paratype / Pseudomaladera / nitidifrons / NOMURA, 1974'. 1 ♂ 'MEIFENG / FORMOSA / 1. VIII. 1973 / T. OCHI // ♂ // Paratype / Pseudomaladera / nitidifrons / NOMURA, 1974'.

Current status. Valid species.

Genus *Sinoserica*

Sinoserica maculipennis Miyake & Yamaya

Sinoserica maculipennis Miyake & Yamaya, 2001: 40–41.

Note. The following paratypes are deposited in RIEB (ex coll. Y. Miyake):

Paratypes. 2 exs.: 'China, Yunnan / Boshan C. env. / 2100 m alt. / 10. VII. 1998 / A. Gorodinski // 12 // Paratype / Sinoserica / maculipennis'.

Current status. *Trioserica maculipennis* (Miyake et Yamaya, 2001), see Ahrens and Bezděk (2016).

Genus *Serica*

Serica fusifemorata Nomura

Serica fusifemorata Nomura, 1974: 91.

Note. The following paratypes are deposited in RIEB (ex coll. S. Nomura):

Paratypes. 11 exs.: 1 ♀ 'Lishan / C. Taiwan / 29. vii. 1973 / Y. Miyake // ♀ // 三宅= miyake // Paratype / Serica / fusifemorata / NOMURA (1974)'. 2 ♀ 'Li-shan / C. Taiwan / 26. VII. 1974 / Y. Miyake // ♀ // Paratype / Serica / fusifemorata / S. NOMURA (1974)'. 2 ♂ 'Li-shan / C. Taiwan / 29. VII. 1974 / Y. Miyake // ♂ // Paratype / Serica / fusifemorata / S. NOMURA (1974)'. 2 ♀ 'Li-shan / C. Taiwan / 29. VII. 1974 / Y. Miyake // ♀ // Paratype / Serica / fusifemorata / S. NOMURA (1974)'. 1 ♂ 'Li-shan / C. Taiwan / 1. VIII. 1974 / Y. Miyake // ♂ // Paratype / Serica / fusifemorata / S. NOMURA (1974)'. 2 ♀ 'Li-shan / C. Taiwan / 1. VIII. 1974 / Y. Miyake // ♀ // Paratype / Serica / fusifemorata / S. NOMURA (1974)'. 1 ♀ '27 // ♀ // Paratype / Serica / fusifemorata / S. NOMURA (1974)'.

Current status. Valid species.

Serica gansuensis Miyake & Yamaya

Serica gansuensis Miyake & Yamaya, 2001: 35–36.

Note. The following paratype is deposited in RIEB (ex coll. Y. Miyake):

Paratype. 1 ex.: 'China, Gangu / Mts. Minshan / nr. Wudn. 2100 / 1. VI. 1997 / A. Gorodinski // 4 // Paratype: / Serica / gansuensis'.

Current status. Valid species.

Genus *Sericania*

Sericania miyakei Nomura

Sericania miyakei Nomura, 1960: 60.

Note. The following paratype is deposited in RIEB (ex coll. S. Nomura):

Paratype. 1 ex.: 'Paratype // TASHIRO / CHIKUGO / 4. V. 1952 / Y. MIYAKE // Sericania / miyakei / NOMURA (1960)'.

Current status. Valid species.

Genus *Sophrops*

Sophrops takatoshii Itoh

Sophrops takatoshii Itoh, 1990: 9–10.

Note. The following paratypes are deposited in RIEB (ex coll. T. Itoh):

Paratypes. 3 exs.: '1989–4–17 / 平良植物園= hirara-syokubutsuen /(宮古島)= miyako-jima / leg. T. Ueno // Paratype / Sophrops / takatoshii / T. Itoh'.

Current status. Valid species.

Genus *Taiwanoserica*

Taiwanoserica elongata Nomura

Taiwanoserica elongata Nomura, 1974: 86.

Note. The following paratype is deposited in RIEB (ex coll. S. Nomura):

Paratypes. 1 ex.: 1 ♂ 'MT. ARI / FORMOSA / 30. VII. 1973 / H. OHASHI // ♂ // 三宅= miyake // Paratype / Taiwanoserica / elongata / NOMURA (1974)'.

Current status. *Serica* (*Taiwanoserica*) *elongata* (Nomura, 1974), see Ahrens and Bezděk (2016).

Taiwanoserica lishana Nomura

Taiwanoserica lishana Nomura, 1974: 87.

Note. The following paratypes are deposited in RIEB (ex coll. S. Nomura):

Paratypes. 22 exs.: 2 ♂ 'Lishan / C. Taiwan / 30. vii. 1970 / Y. Miyake // ♂ // PARATYPE / Taiwanoserica / lishana / S. Nomura (1974)'. 6 ♂ 'Lishan / C-Taiwan / 29. vii. 1973 / Y. Miyake // ♂ // PARATYPE / Taiwanoserica / lishana / S. Nomura (1974)'. 4 ♀ 'Lishan / C-Taiwan / 29. vii. 1973 / Y. Miyake // ♀ // PARATYPE / Taiwanoserica / lishana / S. Nomura (1974)'. 4 ♂ 'Li-shan / Taiwan / 29. VII. 1974 / Y. Miyake // ♂ // PARATYPE / Taiwanoserica / lishana / S. Nomura (1974)'. 1 ♀ 'Li-shan / Taiwan / 29. VII. 1974 / Y. Miyake // ♀ // PARATYPE / Taiwanoserica / lishana / S. Nomura (1974)'. 4 ♂ 'Li-shan / Taiwan / 1. VII. 1974 // Y. Miyake // ♂ // PARATYPE / Taiwanoserica / lishana / S. Nomura (1974)'. 1 ♀ 'Li-shan / Taiwan / 1. VII. 1974 // Y. Miyake // ♀ // PARATYPE / Taiwanoserica / lishana / S. Nomura (1974)'.

Current status. *Serica* (*Taiwanoserica*) *lishana* (Nomura, 1974), see Ahrens and Bezděk (2016).

Genus *Trichomaladera*

Trichomaladera elongata Nomura

Trichomaladera elongata Nomura, 1974: 93–94.

Note. The following paratype is deposited in RIEB (ex coll. S. Nomura):

Paratype. 1 ex.: 1 ♂ 'Paratype / Trichomaladera / elongata / NOMURA (1974)'.

Current status. Valid species.

Remark. The collecting data label of the paratype is missing.

Genus *Trichoserica*

Trichoserica elongata nitididorsis Nomura

Trichoserica elongata nitididorsis Nomura, 1971: 70–71.

Note. The following paratype is deposited in RIEB (ex coll. S. Nomura):

Paratype. 1 ex.: 'Mt. Hiko / [KYUSHU] / 27. 7. 1960 / TAKEISHI // Paratype / Trichoserica / elongata / nitididorsis / Nomura'.

Current status. *Serica nitididorsis* (Nomura, 1971), see Ahrens and Bezděk (2016).

Trichoserica incurvata Nomura

Trichoserica incurvata Nomura, 1971: 67–68.

Note. The following paratypes are deposited in RIEB (ex coll. S. Nomura):

Paratypes. 8 exs.: 1 ex. 'Aomori-pref / 17–vii–1956 / S. Kimotog // Paratype / Trichoserica / incurvata / Nomura (1971) // Aomori / 17. VII. 1956 / S. Kimoto'. 1 ♂ '17. VII. 1956 / S. Kimoto // Paratype / Trichoserica / incurvata / Nomura (1971)'. 2 exs. 'Aomori-pref / 19–vii–1956 / S. Kimotog // Paratype / Trichoserica / incurvata / Nomura (1971) // Kimoto S. / 19. VII. 1956'. 1 ex. 'Aomori-pref / 19–vii–1956 / S. Kimotog // Paratype / Trichoserica / incurvata / Nomura (1971) // 19. VII. 1956 / S. Kimoto'. 2 exs. 'Sensuidani 1200 m / Okutama Tokyo / 21–VII–1968 / Coll. H. Yuasa // Paratype / Trichoserica / incurvata / Nomura (1971)'. 1 ex. 'Okutama / 21. VII. 1968 / YUASA // Paratype / Trichoserica / incurvata / Nomura (1971)'.

Current status. *Serica incurvata* (Nomura, 1971), see Ahrens and Bezděk (2016).

Trichoserica nitidiceps Nomura

Trichoserica nitidiceps Nomura, 1971: 69–70.

Note. The following paratype is deposited in RIEB (ex coll. S. Nomura):

Paratype. 1 ex.: 1 ♂ '(Kyushu) / Mt. Sobo / 23. V. 1952 / Y. Miyake //Paratype / Trichoserica / nitidiceps / NOMURA'.

Current status. Junior subjective synonym of *Serica inexspectata* (Kontkanen, 1956), see Ahrens and Bezděk (2016).

Remark. In addition to the paratype mentioned above, the following specimen labeled as paratype is not designated in the original description: 1 ex. 'Mt. Kuju / Bungo / 28. vii. 1961 / Y. Miyake // Paratype / Trichoserica / nitidiceps / NOMURA (1971)'.

Trichoserica opacifrons Nomura

Trichoserica opacifrons Nomura, 1971: 68–69.

Note. The following paratypes are deposited in RIEB (ex coll. S. Nomura):

Paratypes. 3 exs.: 1 ♂ 'Mt. Hiko / Buzen / 1. VIII. 1953 / Y. Miyake // Paratype / Trichoserica / opacifrons / NOMURA'. 1 ex. 'mt. Kujū / Hokkeein / 27. VII. 1961 / Y. Miyake Coll // Paratype / Trichoserica / opacifrons / NOMURA'. 1 ♂ '[Kyushu] / Yakushima / 21. Vi. 1954 / Col. K. Matsuda // Paratype / Trichoserica / opacifrons / NOMURA // Ophthalmoserica/ matsudai / sp.n. / DET. Y. MIYAKE'.

Current status. Senior objective synonym of *Serica planifrons* Nomura, 1972, see Ahrens and Bezděk (2016). Nomura (1972) proposed *Serica planifrons* as a replacement name for *Serica opacifrons* (Nomura, 1971), a junior secondary homonym of *Serica opacifrons* Fairmaire, 1891.

Subfamily Cetoniinae
Genus *Anomalocera*

Anomalocera paotao Masumoto & Sakai

Anomalocera paotao Masumoto & Sakai, 1987a: 51–54.

Note. The following paratypes are deposited in RIEB (ex coll. Masumoto):

Paratypes. 2 exs.: 1 ex. 'Lishan / Taiwan / 28. VII. 1974 / Y. Miyake // Paratype / Anomalocera / paotao MAS. et SAK.'. 1 ex. 'Lishan / C, -Taiwan / 29 vii. 1973 / Y. Miyake // Paratype / Anomalocera / paotao MAS. et Sak.'.

Current status. *Diphyllomorpha paotao* (Masumoto et Sakai, 1987), see Bezděk (2016).

Genus *Rhomborhina*

Rhomborhina kurosawai Masumoto & Sakai

Rhomborhina kurosawai Masumoto & Sakai, 1987b: 104–105, 107.

Note. The following paratypes are deposited in RIEB (ex coll. Masumoto):

Paratypes. 3 exs.: 2 ♂ 'FORMOSA / tattaka / 9, VIII 1971 / H. OHARA // Paratype / Rhomborrhina / kurosawai / MASUMOTO et K. SAKAI'. [[1 ♂ 'Tsuifeng / C. Tsiwan / 26. vii. 1970 (the date given in the original description is 27.vii.1970) // Y. Miyake // Paratype / Rhomborrhina / kurosawai / MASUMOTO et K. SAKAI']].

Current status. Valid species.

Genus *Thaumastopeus*

Thaumastopeus chicheryi tenuigenius Miyake & Yamaya

Thaumastopeus chicheryi tenuigenius Miyake & Yamaya, 1995: 38.

Note. The following paratype is deposited in RIEB (ex coll. Y. Miyake):

Paratype. 1 ex.: 1 ♂ 'N. Keningau / N. Borneo / 30. V. 1994 // Paratype: Thaumastopeus / chicheryi tenuigenius / Y. MIYAKE et YAMAYA, 1995'.

Current status. Valid species.

Genus *Paratrichius*

Paratrichius hatai Miyake

Paratrichius hatai Miyake, 1989: 41–42.

Note. The following paratypes are deposited in RIEB (ex coll. Y. Miyake):

Paratypes. 4 exs.: [['Tanah Rata / MALAYA / 7. IV. 1972 (the date given in the original description is 7.IV.1978) / M. Hata // Paratype: / Paratrichius / hatai / Y. MIYAKE, 1989']].

Current status. Valid species.

Paratrichius kyushuensis **Miyake**

Figure 4H

Paratrichius kyushuensis Miyake, 1990: 30–32.

Note. The holotype and following paratypes are deposited in RIEB (ex coll. Y. Miyake):

Holotype (♂). 'MT. SOBO / BUNGO / 28. vii. 1954 / Y. MIYAKE // Holotype: / Paratrichius / kyushuensis / Y. MIYAKE, 1990'. (Fig. 4H)

Paratypes. 5 exs.: 1 ex. '(Kyushu) / Mt. Sobo / 24. VII. 1950 / Y. Miyake // Paratype: Paratrichius / kyushuensis / Y. MIYAKE, 1990'. 1 ♂ '(Kyushu) / Mt. Sobo / 24. VII. 1952 / Y. Miyake // Paratype: Paratrichius / kyushuensis / Y. MIYAKE, 1990'. 1 ex. '(Kyushu) / Mt. Ichi Fu Sa / 28 VII 1952 / Col. S. Kimoto // Paratype: Paratrichius / kyushuensis / Y. MIYAKE, 1990'. 1 ex. 1 ♂ '(Kyushu) / Mt. Sobo / 24. VII. 1953 / K. MATSUDA // Paratype: Paratrichius / kyushuensis / Y. MIYAKE, 1990'.

Type condition. The left metatarsus of the holotype is missing.

Current status. Valid species.

Remark. The date on the label of the holotype is 28.VII.1954 while that in the original description is 28.VII.1952.

In addition to the paratypes mentioned above, the following specimen labeled as paratype is not designated in the original description.: 1 ex. '⑦ // Paratype: Paratrichius / kyushuensis / Y. MIYAKE, 1990'.

Genus *Tibiotrichius*

Tibiotrichius vietnamensis **Miyake**

Figure 5A

Tibiotrichius vietnamensis Miyake, 1996: 44.

Note. The holotype is deposited in RIEB (ex coll. Y. Miyake):

Holotype (♂). 'M. ITO leg / Sapa=Chapa / N. Vietnam / 23–V–1995 // サパ= sapa [aedeagus mount] // Holotype: Tibiotrichius / vietnamensis Y. MIYAKE, 1996'. (Fig. 5A)

Type condition. The aedeagus of the holotype is pinned separately.

Current status. Valid species.

Subfamily Valginae
Genus *Charitovalgus*

Charitovalgus banzai **Sawada**
Figure 5B

Charitovalgus banzai Sawada, 1941: 8–9.

Note. The neotype is deposited in RIEB (ex coll. Y. Miyake):

Neotype (♂). 'Hourng Shoei ken / near Liukuei, / Kao Hsung Hsien / VII. 1972 W. Chen leg // Holotype: Neotype / Charitovalgus / banzai SAWADA / Y. MIYAKE, 1993'. (Fig. 5B)

Type condition. The right and left metatarsi of the neotype are missing.

Current status. Valid species.

Remark. The neotype was designated by Miyake (1993).

Genus *Dasyvalgus*

Dasyvalgus annamensis **Miyake**
Figure 5C

Dasyvalgus annamensis Miyake, 1993a: 21–22.

Note. The holotype and following paratype are deposited in RIEB (ex coll. Y. Miyake):

Holotype (♂). '4. 4 / 203 // Iluon Ma Thuot / Annam M. ITO // Holotype: Dasyvalgus / Annamensis / Y. MIYAKE, 1993'. (Fig. 5C)

Paratype. 1 ex.: 1 ♂ 'Iluon Ma Thuot / Annam M. ITO // Paratype: Dasyvalgus / annamensis / Y. MIYAKE, 1993'.

Current status. Valid species.

Remark. The locality on the collecting data label of the holotype is 'Iluon Ma Thuot', but the locality given in the original description is 'Ban Me Thuot'. However, the habitus of the holotype and the figure in the original description match. Probably, Miyake made a typographical error when writing the description.

Dasyvalgus castaneodorsalis **Miyake**
Figure 5D

Dasyvalgus castaneodorsalis Miyake, 1993a: 24–25.

Note. The holotype and following paratypes are deposited in RIEB (ex coll. Y. Miyake):

Holotype (♂). '〔Thailand〕 Pupin–Doi Phui / 19–IV–1985 / M. TAO leg. // Holotype: Dasyvalgus / casraneodorsalis / Y. MIYAKE, 1993'. (Fig. 5D)

Paratypes. 6 exs.: 2 ♂ ‘[Thailand] Pupin-Doi-Phui / 19–IV–1985 / M. TAO leg. // Paratype: Dasyvalgus / castaneodorsalis / Y. MIYAKE, 1993’. 1 ♂ ‘[Thailand] Pupin-Doi-Phui / 21–IV–1985 / M. TAO leg. // Paratype: Dasyvalgus / castaneodorsalis / Y. MIYAKE, 1993’. 2 ♂ ‘[Thailand] Pupin / 21–IV–1985 / M. TAO // Paratype: Dasyvalgus / castaneodorsalis / Y. MIYAKE, 1993’. 1 ♂ ‘[Thailand] Doi Suthep / 10–V–1985 / M. TAO leg. // Paratype: Dasyvalgus / castaneodorsalis / Y. MIYAKE, 1993’.

Type condition. The aedeagus of the holotype is pinned separately.

Current status. Valid species.

Dasyvalgus decamaculatus Miyake

Figure 5E

Dasyvalgus decamaculatus Miyake, 1993a: 22–23.

Note. The holotype and following paratypes are deposited in RIEB (ex coll. Y. Miyake):

Holotype (♂). ‘Iluon Ma Thuot / Annam M. ITO // Holotype: / Dasyvalgus / decamaculatus / Y. MIYAKE, 1993’. (Fig. 5E)

Paratypes. 2 exs.: 1 ex. ‘Near Chang Mai / N. Thailand / 7–V–1994 / K. KUME leg. // Paraype: Dasyvalgus / decamaculatus / Y. MIYAKE, 1993’. 1 ex. ‘Paratype: Dasyvalgus / decamaculatus / Y. MIYAKE, 1993’.

Type condition. The right and left metatarsus are missing.

Current status. Valid species.

Remark. The locality on the collecting data label of the holotype is ‘Iluon Ma Thuot’, but the locality given in the original description is ‘Ban Me Thuot’. However, the habitus of the holotype and the figure in the original description match. Probably, Miyake caused a typographical error when writing the description.

Dasyvalgus flavicauda Miyake, Yamaguchi et Aoki

Figure 5F

Dasyvalgus flavicauda Miyake, Yamaguchi, Aoki et Akiyama, 2002: 65–66.

Note. The holotype and following paratype are deposited in RIEB (ex coll. Y. Miyake):

Holotype (♂). ‘Ban Lao Kram / Mukdahan / E-THAILAND / 17. Feb. 1999 / S. Yamaguchi and / T. Aoki leg. // Holotype: / Dasyvalgus / flavicauda // Holotype / Dasyvalgus flavicauda / Y. MIYAKE, YAMAGUCHI / et AOKI 2002’. (Fig. 5F)

Paratype. 1 ex.: 1 ♂ ‘Phu Huai Sing / Mukdahan / E–THAILAND / 19. Feb. 1999 / S. Yamaguchi and / T. Aoki leg. // Paratype / Dasyvalgus flavicauda / Y. MIYAKE, YAMAGUCHI / et AOKI 2002’.

Current status. Valid species.

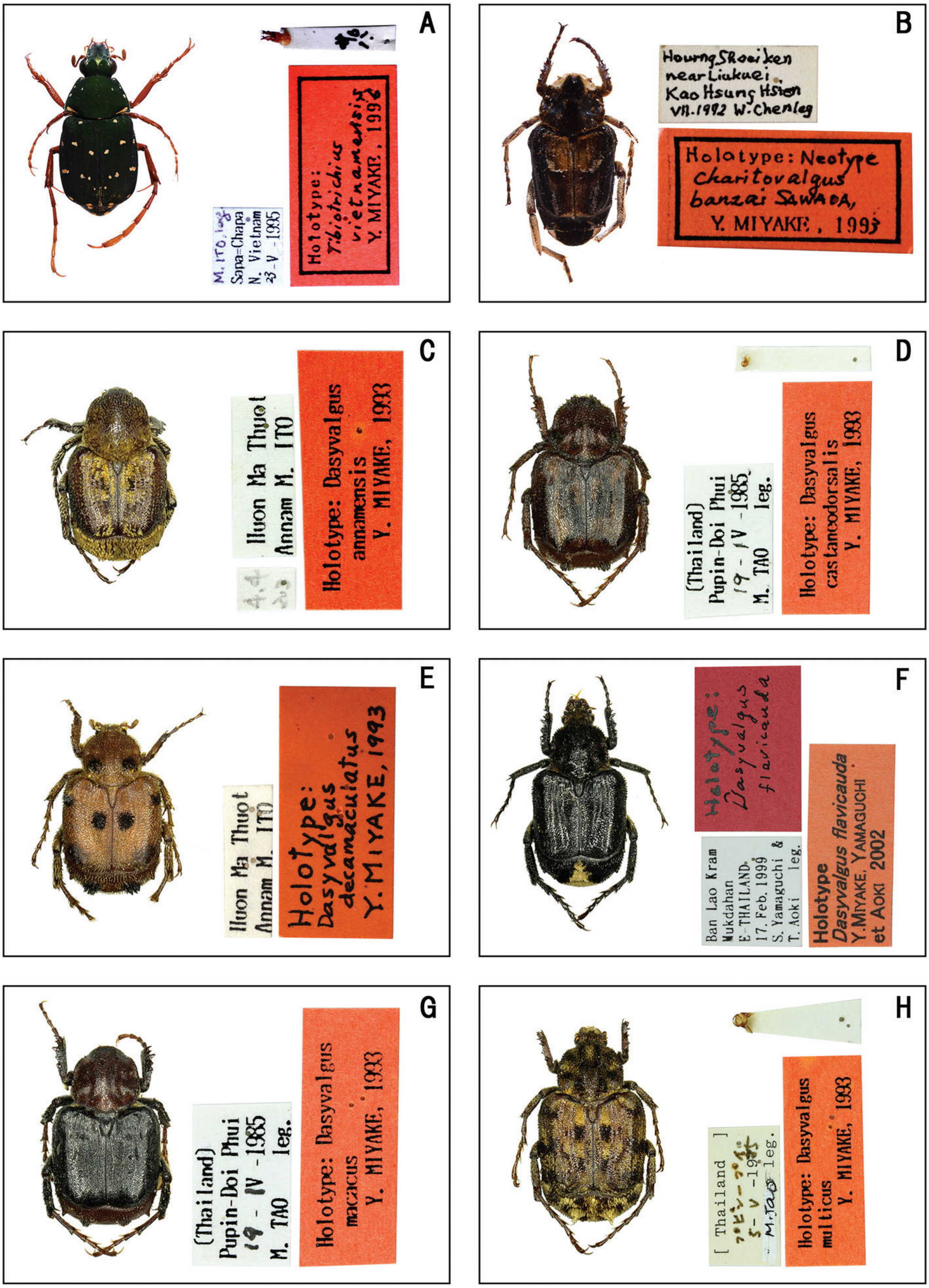

Figure 5. Habitus of holotype specimens. **A** *Tibiotrichius vietnamensis* Miyake **B** *Charitovalgus banzai* Sawada **C** *Dasyvalgus annamensis* Miyake **D** *Dasyvalgus castaneodorsalis* Miyake **E** *Dasyvalgus decamaculatus* Miyake **F** *Dasyvalgus flavicauda* Miyake **G** *Dasyvalgus macacus* Miyake **H** *Dasyvalgus multicus* Miyake.

Dasyvalgus macacus Miyake

Figure 5G

Dasyvalgus macacus Miyake, 1993a: 24.

Note. The holotype and following paratypes are deposited in RIEB (ex coll. Y. Miyake):

Holotype (♂). ‘〔Thailand〕Pupin–Doi Phui / 19–IV–1985 / M. TAO leg. // Holotype: Dasyvalgus / macacus / Y. MIYSKE, 1993’. (Fig. 5G)

Paratypes. 4 exs.: 1 ♂ ‘〔Thailand〕 Pupin-Doi Phui / 1–V–1985 / M. TAO leg. // Paratype: Dasyvalgus / macacus / Y. MIYAKE, 1993’. 1 ♂ ‘〔Thailand〕 Pupin-Doi Phui / 5–V–1985 / M. TAO leg. // Paratype: Dasyvalgus / macacus / Y. MIYAKE, 1993’. 1 ♂ ‘〔Thailand〕 Pupin-Doi Phui / 12–V–1985 / M. TAO leg. // Paratype: Dasyvalgus / macacus / Y. MIYAKE, 1993’. 1 ♂ ‘〔Thailand〕 Pupin-Doi Phui / 21–V–1985 / M. TAO leg. // Paratype: Dasyvalgus / macacus / Y. MIYAKE, 1993’.

Current status. Valid species.

Remark. The habitus photograph in the original description does not refer to the holotype.

Dasyvalgus makiharai Miyake

Dasyvalgus makiharai Miyake, 1985: 11–12.

Note. The following paratypes are deposited in RIEB (ex coll. Y. Miyake):

Paratype. 1 ex.: ‘MEIFENG / FORMOSA / 3–VII. 74 / T, OCHI // Paratype: / Dasyvalgus / makiharai Y. MIYAKE / (1985)’.

Current status. Valid species.

Remark. In addition to the paratype mentioned above, the following specimens labeled as paratype are not designated in the original description: 1 ex. ‘松崗= song-gang / 27～29. VII 1968 / K. YAMAMOTO // Paratype: Dasyvalgus / makiharai / Y. MIYAKE, 1985’. 1 ♂ ‘SUNG KANG / FORMOSA / 30–VI, 74 / T. OCHI // Paratype: / Dasyvalgus / makiharai Y. MIYAKE / (1985)’.

Dasyvalgus minahasanus Miyake

Dasyvalgus minahasanus Miyake, 1989b: 42–43.

Note. The following paratypes are deposited in RIEB (ex coll. Y. Miyake):

Paratypes. 78 exs.: 75 exs. ‘Tondano / N. Sulawesi / 10–IV–1989 / Y. Miyake leg. // Paratype: / Dasyvalgus / minahasanus / Y. MIYAKE, 1989’. 3 exs. ‘Tondano / N. Sulawesi / 9–IV–1989 / Y. Miyake leg. // Paratype: / Dasyvalgus / minahasanus / Y. MIYAKE, 1989’.

Current status. Valid species.

Remark. In addition to the paratypes mentioned above, the following specimen labeled as paratypes is not designated in the original description: 1 ex. 'Tondano / N. Sulawesi / 11–IV–1989 / Y. Miyake leg. // Paratype: / Dasyvalgus / minahasanus / Y. MIYAKE, 1989'.

Dasyvalgus multicus Miyake

Figure 5H

Dasyvalgus multicus Miyake, 1993a: 25–26.

Note. The holotype is deposited in RIEB (ex coll. Y. Miyake):

Holotype (♂). '[Thailand] / プピン-プイ= pupin-pui / 5–V–1985 / M. Tao leg. // Holotype: Dasyvalgus / multicus / Y. MIYAKE, 1993'. (Fig. 5H)

Type condition. The aedeagus of the holotype is pinned separately. The right and left protarsus are missing.

Current status. Valid species.

Dasyvalgus nudis Miyake

Figure 6A

Dasyvalgus nudis Miyake, 1994: 153.

Note. The holotype and following paratypes are deposited in RIEB (ex coll. Y. Miyake):

Holotype (♂). 'Cao Bang / N. Vietnam / 9–11. VI, 1993 / M. ITO leg // Holotype: Dasyvalgus / nudis / Y. MIYAKE, 1994'. (Fig. 6A)

Paratypes. 9 exs.: 3 ♂ 'Cao Bang / N. Vietnam / 8–10 VI, 1993 / M. ITO leg. // Paratype: / Dasyvalgus / nudis / Y. MIYAKE, 1994'. 3 ♂ 'Cao Bang / N. Vietnam / 10. VI, 1993 / M. ITO leg. // Paratype: / Dasyvalgus / nudis / Y. MIYAKE, 1994'. [[2 ♂ 'Cao Bang / N. Vietnam / 9–11. VI, 1993 (real date is 8–10. VI. 1993) / M. ITO leg. // Paratype: / Dasyvalgus / nudis / Y. MIYAKE, 1994']]. [[1 ex. 'Cao Bang / N. Vietnam / 11. VI, 1993 (real date is 8–10. VI. 1993) / M. ITO leg. // Paratype: / Dasyvalgus / nudis / Y. MIYAKE, 1994']].

Type condition. The aedeagus of the holotype is pinned separately. The right antenna is missing.

Current status. Valid species.

Remark. The date on the collecting data label of the holotype is 9–11,VI,1993, but the collecting date quoted in the original description is 8–10,VI,1993. However, the habitus of the holotype and the figure in the original description match. Probably, Miyake caused a typographical error when writing the description.

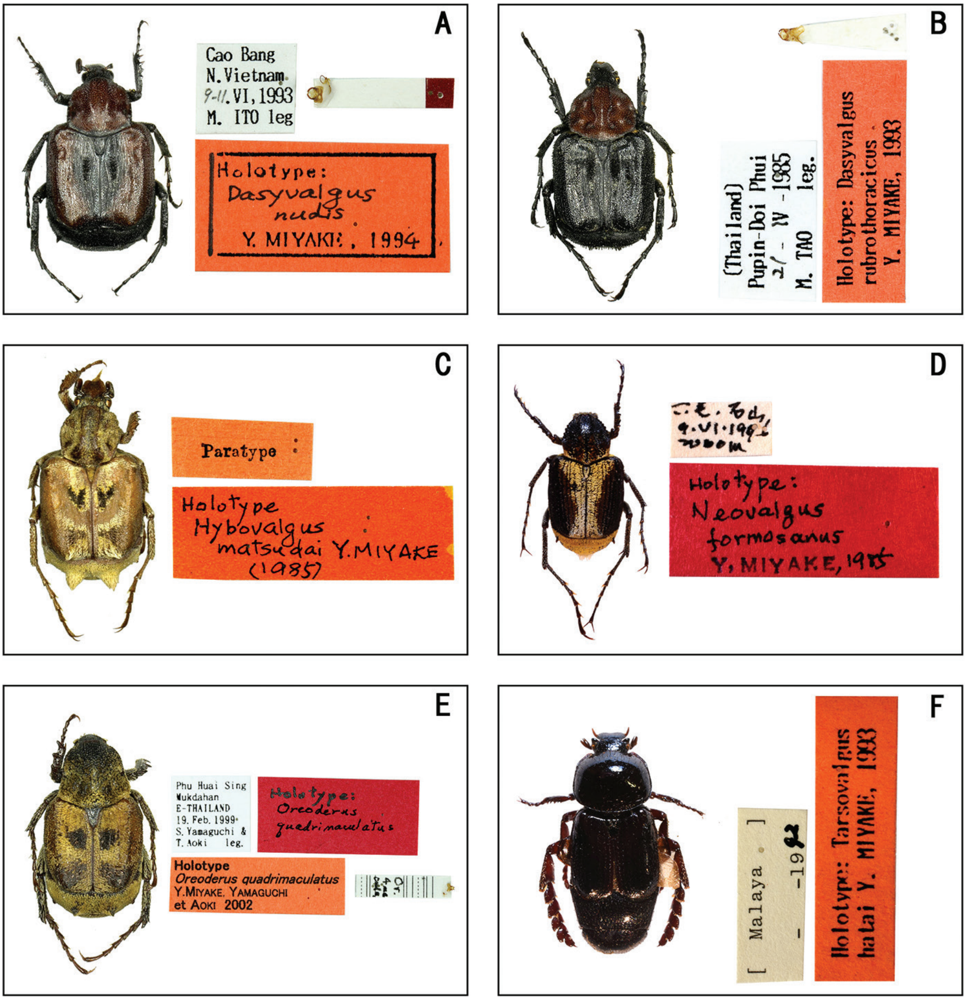

Figure 6. Habitus of holotype specimens. **A** *Dasyvalgus nudis* Miyake **B** *Dasyvalgus rubrothoracicus* Miyake **C** *Hybovalgus matsudai* Miyake **D** *Neovalgus formosanus* Miyake **E** *Oreoderus quadrimaculatus* Miyake **F** *Tarsovalgus hatai* Miyake.

Dasyvalgus rubrothoracicus Miyake

Figure 6B

Dasyvalgus rubrothoracicus Miyake, 1993a: 23–24.

Note. The holotype and following paratypes are deposited in RIEB (ex coll. Y. Miyake):

Holotype (♂). 〘Thailand〙 Pupin–Doi Phui / 21–IV–1985 / M. TAO leg. // Holotype: Dasyvalgus / rubrothoracicus / Y. MIYAKE, 1993’. (Fig. 6B)

Paratypes. 11 exs.: 1 ex. ‘Doi Sutehp / Thailand / 28–IV–1985 / M Tao leg. // TDvA // Paratype: Dasyvalgus / rubrothoracicus / Y. MIYAKE, 1993’. 1 ♂ 〘Thailand〙 Pupin-Doi-Phui / 1–V–1985 / M. TAO leg. // Paratype: Dasyvalgus / rubrothoracicus

/ Y. MIYAKE, 1993’. 1 ♂ 〔‘Thailand〕 Pupin-Doi-Phui / 1–V–1985 / M. TAO leg. // TDvA // Paratype: Dasyvalgus / rubrothoracicus / Y. MIYAKE, 1993’. 1 ♂ 〔‘Thailand〕 Pupin-Doi-Phui / 5–V–1985 / M. TAO leg. // TDvA // TDvA // Paratype: Dasyvalgus / rubrothoracicus / Y. MIYAKE, 1993’. 1 ♂ 〔‘Thailand〕 Pupin-Doi-Phui / 11–V–1985 / M. TAO leg. // Paratype: Dasyvalgus / rubrothoracicus / Y. MIYAKE, 1993’. [[1 ♂ 〔‘Thailand〕 Pupin-Doi-Phui / 17–V–1985 (the date given in the original description is 17–IV–1985) / M. TAO leg. // Paratype: Dasyvalgus / rubrothoracicus / Y. MIYAKE, 1993’]]. [[1 ♂ 〔‘Thailand〕 Pupin-Doi-Phui / 21–V–1985 (the date given in the original description is 21–IV–1985) / M. TAO leg. // TDvA // Paratype: Dasyvalgus / rubrothoracicus / Y. MIYAKE, 1993’]]. [[1 ♂ 〔‘Thailand〕 Pupin-Doi-Phui / 21–V–1985 (the date given in the original description is 21–IV–1985) / M. TAO leg. // TDvA // Paratype: Dasyvalgus / rubrothoracicus / Y. MIYAKE, 1993’]]. [[1 ♂〔‘Thailand〕 Pupin-Doi-Phui / 23–V–1985 (the date given in the original description is 23–IV–1985) / M. TAO leg. // Paratype: Dasyvalgus / rubrothoracicus / Y. MIYAKE, 1993’]]. [[2 ♂ 〔‘Thailand〕 Pupin-Doi-Phui / 28–V–1985 (the date given in the original description is 28–IV–1985) / M. TAO leg. // TDvA // Paratype: Dasyvalgus / rubrothoracicus / Y. MIYAKE, 1993’]].

Type condition. The aedeagus of the holotype is pinned separately.

Current status. Valid species.

Remark. The date on the collecting data label of the holotype is 21–IV–1985, but the collecting date quoted in the original description is 5–V–1985. However, the habitus of the holotype and the figure in the original description match. Probably, Miyake caused a typographical error when writing the description.

Dasyvalgus similis **Miyake**

Dasyvalgus similis Miyake, 1985: 8–9.

Note. The following paratypes are deposited in RIEB (ex coll. Y. Miyake):

Paratypes. 3 exs.: 1 ♂ ‘蓬来= hôrai / 20, 21 VIII 1968 / H. MAKIHARA // Paratype’. 1 ♂ ‘FUNCHIIFO / FORMOSA / 1. VI. 1970 / Y. KIYOYAMA // Paratype // Paratype / Dasyvalgus / similis, Y. MIYAKE / 1985’. 1 ♂ ‘FUNCHIIFO / FORMOSA / 1. VI. 1970 / Y. KIYOYAMA // Paratype’.

Current status. Senior objective synonym of *Dasyvalgus taiwanus* Miyake, 1991. Miyake in Miyake et al. (1991) proposed *Dasyvalgus taiwanus* as a replacement name for *Dasyvalgus similis* Miyake, 1985, a junior primary homonym of *Dasyvalgus similis* Moser, 1908.

Remark. In addition to the paratypes mentioned above, the following specimens labeled as paratypes are not designated in the original description: 1 ex. ‘LIUKUEI / FORMOSA / 3. X. 1970 / Y. KIYOYAMA // 16 // Paratype // Paratype / Dasyvalgus / similis Y. MIYAKE, 1985’. 1 ex. ‘NANSHANCHI / FORMOSA / 27. VI. 1971 / Y. MAEDA // Paratype // Paratype / Dasyvalgus / similis Y. MIYAKE, 1985’. 1 ex. ‘紅水坑= hongshuikeng / Liukuei / 11. V. 1978 / Chen. W. // Paratype’. 1 ♂ ‘紅水坑= hongshuikeng / Liukuei / 11. V. 1978 / Chen. W. // Paratype’. 1 ex. ‘紅水坑= hongshuikeng / Liukuei / 11. V. 1978 / W. Chen // Paratype // Paratype / Dasyvalgus / similis Y. MIYAKE, 1985'. 1 ex. 'Paratype'.

***Dasyvalgus wadai* Miyake**

Dasyvalgus wadai Miyake, 1985: 9–10.

Note. The following paratype is deposited in RIEB (ex coll. Y. Miyake):

Paratype. 1 ex.: 1 ♂ 'Paratype / Dasyvalgus / wadai Y. MIYAKE, 1985'.

Current status. Valid species.

Remark. This paratype has no collecting data label.

Genus *Hybovalgus*

***Hybovalgus matsudai* Miyake**

Figure 6C

Hybovalgus matsudai Miyake, 1985: 6.

Note. The holotype is deposited in RIEB (ex coll. Y. Miyake):

Holotype (♂). 'Paratype // Holotype / Hybovalgus / matsudai Y. MIYAKE / (1985)'.

Type condition. The right protarsus is missing.

Current status. Valid species.

Remark. There is no data label attached to the holotype, but the habitus of the holotype matches the figure in the original description. If confidence is placed in the pinned holotype label and the habitus, the above holotype specimen is the true holotype.

Genus *Neovalgus*

***Neovalgus formosanus* Miyake**

Figure 6D

Neovalgus formosanus Miyake, 1985: 3.

Note. The holotype and following paratypes are deposited in RIEB (ex coll. Y. Miyake):

Holotype (♂). '六亀= liugui. 石山= shi shan / 9. VI. 1976 / 2000m // Holotype: / Neovalgus / formosanus / Y, MIYAKE, 1985'. (Fig. 6D)

Paratypes. 2 exs.: 1 ex. '[Taiwan] / Baibara, mt. Puli / –V–1965 // Paratype: Neovalgus / formosanus Y. MIYAKE, 1985'. 1 ex. '[Taiwan] / Liukuei / 16–V–1978 // PARATYPE / Neovalgus / formosanus / Y. MIYAKE, 1985'.

Current status. Valid species.

Remark. The date on the collecting label of the holotype is 9.VI.1976, but the collecting date quoted in the original description is 16.V.1978. However, the habitus of the holotype matches the figure in the original description. Probably, Miyake caused a typographical error when writing the description.

In addition to the paratypes mentioned above, the following specimens labeled as paratypes are not designated in the original description: 3 exs. '[Taiwan] / Baibara, mt. Puli / –V–1965 // PARATYPE / Neovalgus / formosanus / Y. MIYAKE, 1985'. 1 ex. 'Formosa / Wushe / V. 1965 / T. Shiroz / Paratype: Neovalgus / formosanus / Y. MIYAKE, 1985'. 1 ex. '六 亀= liugui, 石山= shi shan / 2000 m / 9–VI–1976 / Paratype / Neovalgus / formosanus / Y. MIYAKE, 1985'. 1 ex. 'Paratype: / Neovalgus / formosanus / Y. MIYAKE, 1985'.

Genus *Oreoderus*

Oreoderus quadrimaculatus Miyake, Yamaguchi et Aoki

Figure 6E

Oreoderus quadrimaculatus Miyake, Yamaguchi, Aoki et Akiyama, 2002: 64–65.

Note. The holotype is deposited in RIEB (ex coll. Y. Miyake):

Holotype (♂). 'Phu Huai Sing / Mukdahan / E-THAILAND / 19. Feb. 1999 / S. Yamahuchi and T. Aoki leg. // Holotype: / Oreoderus / quadrumaculatus // Or. 4ml / Coll. // Holotype / Oreoderus quadrimaculatus / Y. MIYAKE, YAMAGUCHI / et AOKI 2002'. (Fig. 6E)

Type condition. The aedeagus of the holotype is pinned separately. The right protarsus is missing.

Current status. Valid species.

Genus *Tarsovalgus*

Tarsovalgus hatai Miyake

Figure 6F

Tarsovalgus hatai Miyake, 1993b: 32–33.

Note. The holotype and following paratype are deposited in RIEB (ex coll. Y. Miyake):

Holotype (♂). '[Malaya] / – –1992 // Holotype: Tarsovalgus / hatai Y. MIYAKE, 1993'. (Fig. 6F)

Paratype. 1 ex.: '[Malaya] / – –1992 // Paratype: / Tarsovalgus / hatai / Y. MIYAKE, 1993'.

Current status. Valid species.

Family Trogidae
Genus *Trox*

Trox kyotensis Ochi & Kawahara

Trox kyotensis Ochi & Kawahara, 2000: 53–56.

Note. The following paratype is deposited in RIEB (ex coll. T. Ochi):

Paratype. 1 ex.: 'YAMAZAKI- / CHO, KYOTO. / 5–IV, 1999 / M. KAWAHARA // PARATYPE / Trox / kyotensis / OCHI and KAWAHARA / 2000'.

Current status. *Trox* (*Niditrox*) *kyotensis* Ochi et Kawahara, 2000, see Kalz (2019).

Trox sabulosus fujiokai Ochi

Trox sabulosus fujiokai Ochi, 2000: 43–44.

Note. The following paratype is deposited in RIEB (ex coll. T. Ochi):

Paratype. 1 ex.: 'Yukyuzan-Park, Nagaoka / Niigata Pref., Japan / 28. V. 1997 / Y and M. Kawahara leg // PARATYPE / Trox / Sabulosus / Subsp. fujiokai / OCHI, 2000'.

Current status. Valid species.

Trox setifer horiguchii Ochi & Kawahara

Trox setifer horiguchii Ochi & Kawahara, 2002: 54–55.

Note. The following paratype is deposited in RIEB (ex coll. T. Ochi):

Paratype. 1 ex.: 1♂ 'MEBORO-DAM / KAMIAGATA. T. / IS. TSUSHIMA / NAGASAKI. J. P / 25–V. 2002 / Y and M. KAWAHARA // 対県= tsu-ken上県町= kamiagata-chô / 目保呂ダム= meborodamu / 25. V. 2002 / Y and M. Kawahara // ♂ // PARATYPE / Trox / setifer / subsp. horiguchii / OCHI and KAWAHARA / 2002'.

Current status. *Trox horiguchii* Ochi and Kawahara, 2002, see Pittino (2006).

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Trioza turouguei sp. nov. (Hemiptera, Psylloidea, Triozidae), a new psyllid species from Taiwan inducing pea-shaped stem galls on *Cinnamomum osmophloeum* (Lauraceae), with notes on its galling biology

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Abstract

Trioza turouguei **sp. nov.**, a new species of jumping plant lice (Hemiptera, Triozidae) from Taiwan, is described and illustrated based on adults and immatures. The latter induce pea-shaped galls on the stems of *Cinnamomum osmophloeum* Kaneh. (Lauraceae). The gall phenology of the new species is described. A list of species of Triozidae associated with *Cinnamomum* in the Old World is provided. The following nomenclatorial acts are proposed: *Trioza inflata* Li, 1992 = *Trioza xiangicamphorae* Li, 1992, **syn. nov.**; *Siphonaleyrodes formosanus* Takahashi, 1932, **stat. rev**., is removed from synonymy with *Trioza cinnamomi* (Boselli, 1931).

Keywords

Asia, jumping plant lice, Oriental region, phenology, *Siphonaleyrodes*, Sternorrhyncha, taxonomy

Introduction

Jumping plant lice or psyllids (Hemiptera, Sternorrhyncha, Psylloidea) are phloem-feeding insects that are highly host specific, especially during the immature stages (Hodkinson 1974). The superfamily is comprised of approximately 4,000 species in more than 200 genera worldwide (Li 2011; Burckhardt and Ouvrard 2012; Ouvrard 2020). Closely related psyllid species tend to develop on closely related plant species (Burckhardt and Basset 2000; Percy et al. 2004; Ouvrard et al. 2015; Burckhardt and Queiroz 2020). As other phytophagous insects, many psyllids are gall inducers, particularly those of the families Triozidae, Phacopteronidae, and Calophyidae (Burckhardt 2005; Malenovský et al. 2007; Yang and Raman 2007). Psyllid galls are characterized by a very specific morphology, formation site, and restriction to a single or a few related plant species (Hodkinson 1984; Burckhardt 2005).

The first studies on the psyllid fauna of Taiwan are from foreign researchers made during the first half of the 20th century (Kuwayama 1908, 1910, 1931; Enderlein 1914). Half a century later, Yang (1984) published the first comprehensive monograph, which was subsequently supplemented and expanded (Fang and Yang 1986; Yang et al. 1986; Lauterer et al. 1988; Fang 1990; Yang et al. 2004, 2009, 2013; Liao et al. 2016; Liao and Yang 2018; Cho et al. 2020). According to these studies, more than half of the Taiwanese psyllid species are gall inducers and several of these are associated with the Lauraceae (Yang et al. 2006), a family of Magnoliids, an early branch in the angiosperm tree. Hollis and Martin (1997) compiled a list of the known psyllids associated with Lauraceae and recorded ten species developing on the lauraceous genus *Cinnamomum* in the Oriental realm.

Cinnamomum osmophloeum Kaneh. is a tree species endemic to Taiwan, growing at low elevations around the island. The tree species has some economic potential for its essential oils in the leaves (Chang et al. 2001), which are similar to those found in the bark of Indonesian cassia (*Cinnamomum burmanni* (Nees & T. Nees) Blume) with antibacterial, carminative, and anti-fungal properties. On the stems of *C. osmophloeum*, pea-shaped closed galls were found, in the field as well as on herbarium specimens in Taiwan, which are induced by an undescribed psyllid species. According to Hodkinson (1984, 2009), stem galls induced by psyllids are relatively rare compared to the much more common leaf galls. For this reason, also little is known about the phenology of stem galls.

Here, we formally name the species on *C. osmophloeum* as *Trioza turouguei* sp. nov., describe its adults and immatures, discuss its relationships to other psyllids developing on *Cinnamomum*, and provide information on the life cycle and gall phenology.

Materials and methods

Psyllids were collected by sweeping and directly searching on *Cinnamomum osmophloeum*. The material is dry mounted or preserved in 70% and 99% ethanol. Some specimens were cleared in 15% potassium hydroxide and examined in orange oil or glycerol or permanently mounted in Canada balsam on a slide. Information on galls was taken in the field and from herbarium specimens.

Specimens from following institutions were examined: Entomological Museum, China Agricultural University, Beijing, China (**CAUB**); National Chung Hsing University, Taichung, Taiwan (**NCHU**); Naturhistorisches Museum, Basel, Switzerland (**NHMB**); National Museum of Natural Science, Taichung, Taiwan (**NMNS**); Herbarium of School of Forestry and Resource Conservation, National Taiwan University, Taipei, Taiwan (**NTUF**); Herbarium of National Taiwan University, Taipei, Taiwan (**TAI**); Herbarium of Taiwan Forest Research Institute, Taipei, Taiwan (**TAIF**).

Photographs of most morphological characters were taken with a compound microscope (Leica DM 750) equipped with a digital camera (Canon EOS 600D). Images of the forewings of adults were taken with a stereomicroscope (Leica MZ 125) equipped with a digital camera (Olympus EP-1). The photographs were montaged using focus stacking software (Helicon Focus, Helicon Soft). The morphological terminology follows White and Hodkinson (1982), Ossiannilsson (1992), Hollis (2004) and Yang et al. (2013).

The life cycle and gall phenology were observed at the Huisun Experimental Forest Station (24°05'24"N, 121°02'03"E; 660–370 m a.s.l.) from January to December 1996. We selected eight trees of *C. osmophloeum* to record the phenology of the plants and the galls induced by *T. turouguei* sp. nov. The terminology of gall development follows Lalonde and Shorthouse (1984) and Rohfritsch (1992). The stage of immatures inside the gall was checked by dissection of the gall.

Taxonomy

Trioza turouguei sp. nov.

http://zoobank.org/A5C30F1F-9539-40E2-A2E0-5ECDEEBECC01
Figs 1–5

Type material. *Holotype*: Taiwan • ♂; Taichung City, Shalien Lane; 24°11'20"N, 120°55'06"E; 20 Dec. 2018; Y. C. Liao leg.; *Cinnamomum osmophloeum*; NCHU, dry mounted. ***Paratypes*:** Taiwan • 15 ♂, 17 ♀, 13 immatures; same data as for holotype • 1 ♀; same data as for holotype but 31 Jan. 2018 • 13 ♂, 23 ♀, 4 immatures, 1 skin; Taichung City, Upper Kukuan; 27 Jan. 2006; G. S. Tung leg.; *Cinnamomum osmophloeum* • 1 ♂, 1 ♀, 6 immatures; Nantou Co., Hui-Sun Forest Station; 24°05'24"N, 121°02'03"E; 17 Jan. 1996; G. S. Tung and M. M. Yang leg.; *Cinnamomum osmophloeum* • 6 immatures; same locality as for preceding; 24 Dec. 1996; G. S. Tung leg.; *Cinnamomum osmophloeum*. Paratypes in NCHU, NHMB, NMNS, dry and slide mounted or stored in ethanol.

Other material examined (not included in type series). Galls on herbarium specimens of *Cinnamomum osmophloeum*, Taiwan: • Nantou Co., Meiyuunshan; 8 Oct. 1935; TAI 049104 • Nantou Co., Shuishe; 1 Mar. 1918; TAIF 107581 • Taichung City, Tungmaoshan; 5 Apr. 1984; TAI 194343 • Taichung City, Pahsienshang; 6 Dec. 1985; TAIF 123377, 123581, 123582 • same locality as for preceding; 6 Nov. 1985; TAIF 123670, 123671 • Taichung City, Chiabautai; 9 Sep. 1962; NTUF 001769, 001771, 001775 • same locality as for preceding; 10 Sep. 1962; NTUF 001773 • Taichung City, Kukuan, 14 Mar. 1971; NTUF 001776.

Diagnosis. Forewing vein M < 2.0 times vein M_{1+2}, cell cu_1 value > 2.0, cell m_1 value > 1.8. Genal processes massive, blunt apically. Male paramere, in profile, with

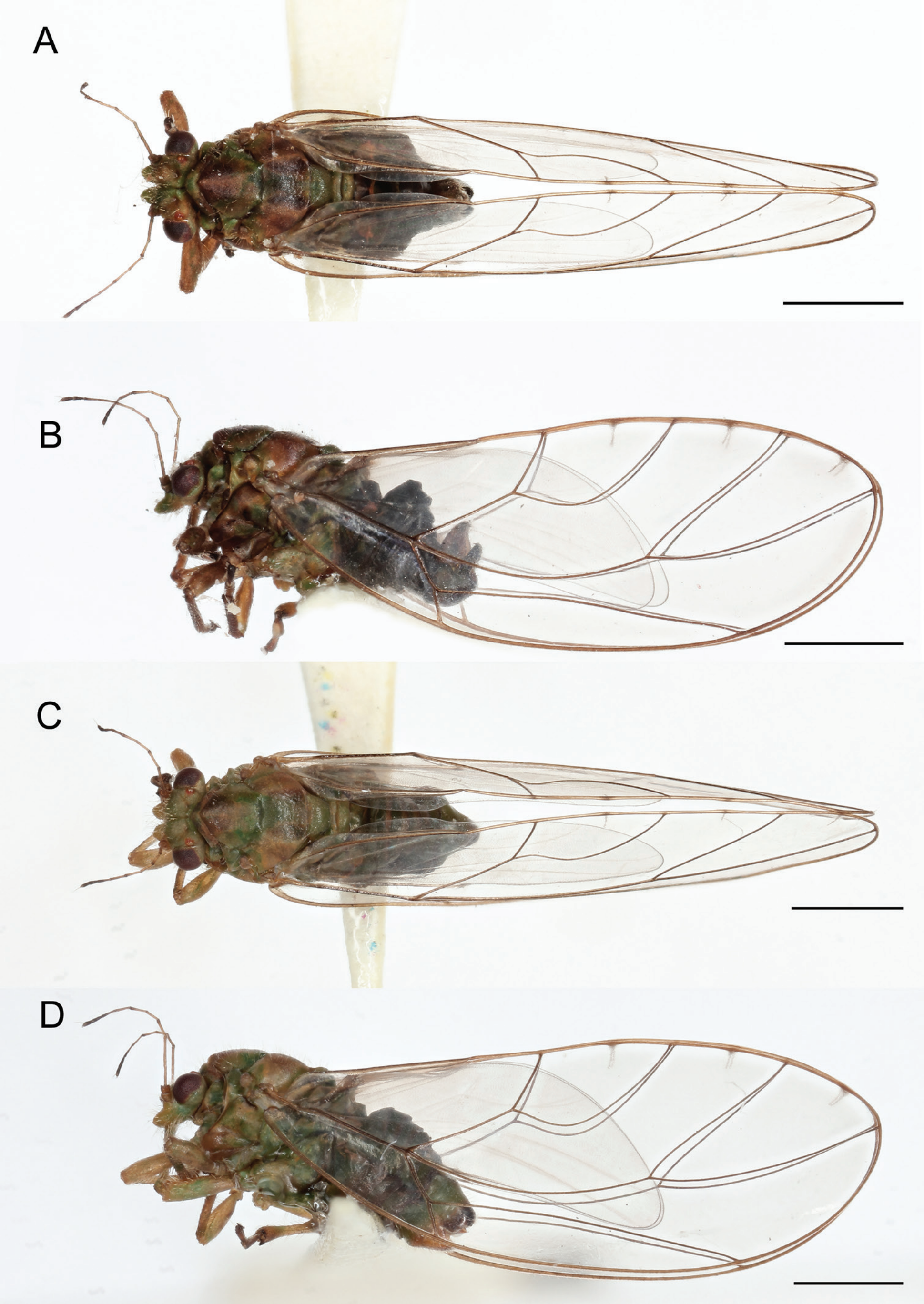

Figure 1. Adults of *Trioza turouguei* sp. nov. **A** male, dorsal view **B** male, lateral view **C** female, dorsal view **D** female, lateral view. Scale bars: 1 mm.

almost straight anterior margin; apex pointed. Distal segment of aedeagus shorter than paramere, apical third inflated, spoon-shaped. Female proctiger truncate apically.

Description. ***Adults*** (Figs 1, 5A, B). Coloration. Body color greenish brown (Fig. 1). Newly emerged individuals light green. Antennae yellow with apices of segments 4, 6, and 8 dark brown, and entire segments 9 and 10 black. Compound eyes dark brown. Ocelli orange. Legs brown. Forewing and hindwing transparent.

Structure. Body large, length from anterior head margin to tip of folded forewing 5.4–6.8 mm; covered in long fine setae. Head (Fig. 2A) nearly as wide as thorax, inclined in a 45° angle from longitudinal body axis. Vertex 1.8–2.0 times as wide as long, moderately concave at posterior margin. Genal processes prominent, 0.8–1.0 times as long as vertex along mid-line, divergent, conical, blunt at apex, pubescent. Antenna (Fig. 2B) slender, 10-segmented, 1.5–1.8 times as long as head width, relative length of flagellar segments as 1.0: 0.4: 0.3: 0.4: 0.3: 0.3: 0.2: 0.2, with a single rhinarium on each of segments 4, 6, 8 and 9; longer, pointed terminal seta 1.1 times and shorter, truncate terminal seta 0.2 times as long as segment 10. Thorax weakly arched dorsally. Pronotum deflexed from mesothorax in a 45° angle. Legs slender. Meracanthus well developed, horn-shaped, acute at apex (Fig. 2C); metatibia 0.9–1.2 times as long as head width, slightly inflated basally with four or five small spines, with 1+2 or rarely 1+3 apical spurs. Forewing (Fig. 2D) 5.4–6.4 times as long as head width, 2.5–2.7 times as long as wide, widest slightly distal to the middle; wing apex subacute, lying in cell m_1 near apex of vein M_{1+2}; vein R+M+Cu strictly trifurcating into veins R, M and Cu; vein Rs moderately long, irregularly, concavely curved to fore margin of wing; vein M weakly curved with very long diverging branches; cell m_1 large; vein Cu_{1a} strongly curved in the basal third; cell cu_1 smaller than cell m_1; line connecting apices of veins Rs and Cu_{1a} distal of bifurcation of vein M; surface spinules absent except for base of cell cu_2; radular spinules present along wing margin in the middle of cells m_1, m_2 and cu_1. Hindwing 0.7 times as long and 0.5 times as wide as forewing; costal margin with five or six setae proximal to costal break, setae distal to costal break clearly divided into two groups. Abdominal tergites glabrous except for a lateral row on either side of tergite 2 in male and tergite 3 in female.

Male terminalia (Fig. 3A–C). Proctiger tubular, in profile broadly convex posteriorly, covered in long setae except for basal third laterally (Fig. 3A). Subgenital plate subglobular, with long setae laterally and ventrally; dorsal margin angular in basal third. Paramere (Fig. 3B) about as long as proctiger; in profile lamellar, irregularly narrowing to apex which is acute and weakly directed anteriad; outer face glabrous except for margins and apex; inner face beset with long setae mostly along fore and hind margins as well as basally. Distal segment of aedeagus (Fig. 3C) shorter than paramere, apical third inflated, spoon-shaped; sclerotized end tube of ductus ejaculatorius short, sinuous. Female terminalia (Fig. 3D) cuneate, short. Proctiger with straight dorsal margin and blunt apex, as long as subgenital plate; with a transverse row of long setae in the middle and long setae apically; circumanal ring one third as long as proctiger,

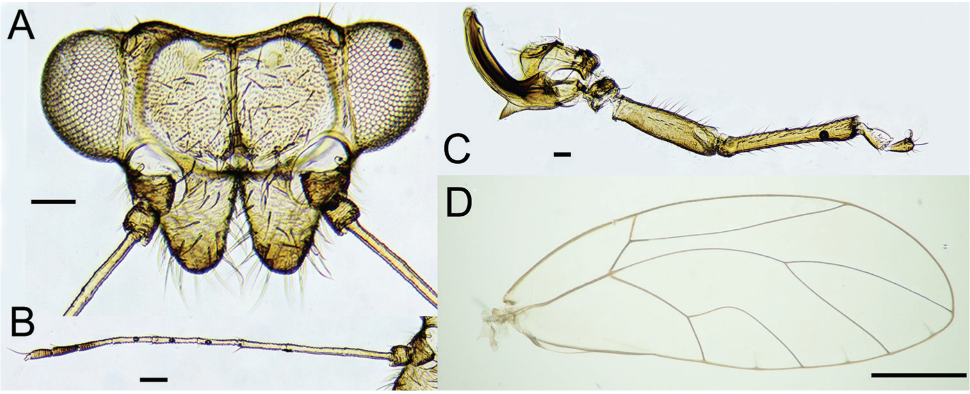

Figure 2. *Trioza turouguei* sp. nov. **A** head **B** antenna **C** hind leg **D** forewing. Scale bars: 0.1 mm (**A, B, C**); 1 mm (**D**).

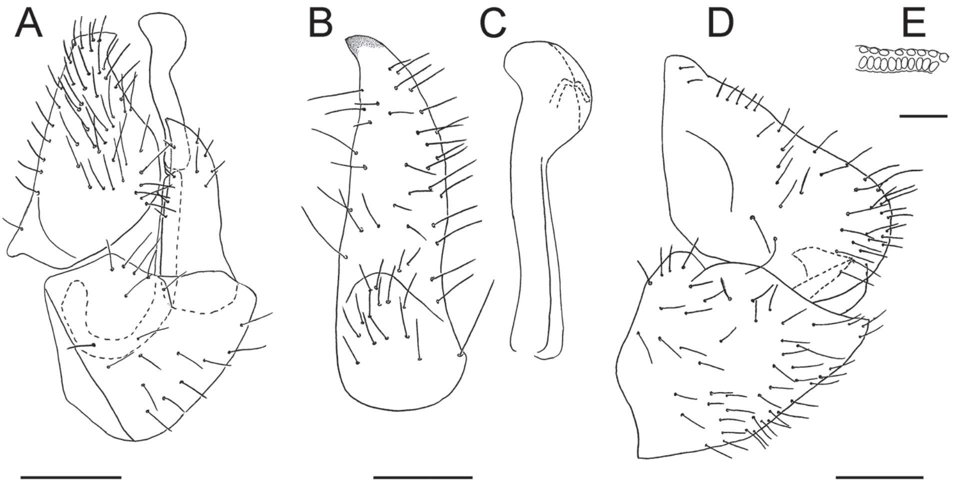

Figure 3. Terminalia of *Trioza turouguei* sp. nov. in lateral view **A** male terminalia **B** paramere, inner surface **C** distal portion of aedeagus **D** female terminalia **E** detail of female circumanal ring. Scale bars: 0.2 mm (**A, D, E**); 0.1 mm (**B, C**).

consisting of two unequal rows of pores (Fig. 3E). Subgenital plate, in profile, irregularly triangular, acute at apex; beset in long hairs laterally and ventrally. Dorsal valvulae cuneate, ventral valvulae straight lacking teeth.

Measurements (range, mean ± SD) in mm (5 males, 5 females). Body length (including forewing) ♂ 5.38–6.38, 6.04 ± 0.33; ♀ 6.00–6.81, 6.60 ± 0.27. Head width ♂ 0.83–0.95, 0.89 ± 0.05; ♀ 0.85–0.98, 0.93 ± 0.04. Vertex length ♂ 0.25–0.30, 0.28 ± 0.02; ♀ 0.28–0.30, 0.30 ± 0.01. Genal cone length ♂ 0.23–0.25, 0.25 ± 0.01; ♀ 0.28–0.30, 0.28 ± 0.01. Antenna length ♂ 1.23–1.58, 1.43 ± 0.11; ♀ 1.38–1.55, 1.46 ± 0.07. Metatibia length ♂ 0.88–0.95, 0.93 ± 0.03; ♀ 0.88–0.98, 0.92 ± 0.03. Forewing length ♂ 4.44–5.31, 5.02 ± 0.31; ♀ 5.25–5.88, 5.63 ± 0.19.

Fifth instar immatures (Figs 4A, 5D). Coloration. General color pale green. Body (Fig. 4A) form oval, 1.4–1.5 times as long as wide; sclerotized dorsally, membranous ventrally. Dorsal body surface covered in short normal setae or subacute sectasetae; margin of head (Fig. 4B), forewing (Fig. 4C) and hindwing pads (Fig. 4D), as well as caudal plate (Fig. 4E) with long, very slender, subacute sectasetae which are relatively densely spaced (distance between setae 0.5–1.0 times their length). Antenna (Fig. 4G) weakly curved; 8-segmented; scape and pedicel much thicker than flagellum; relative length of flagellar segments as 1.0: 0.6: 0.3: 0.3: 0.4: 2.3; with a single subapical rhinarium on each of segments 4 and 6, and two on segment 8. Legs moderately long, femur about as long as tibiotarsus; tarsus with two well-developed claws, tarsal arolium (Fig. 4F) longer than claws, triangular, with unguitractor but lacking pedicel. Forewing pad 3.0–3.8 times long as broad, 3.0–3.4 times as long as antenna; humeral lobe relatively short, reaching about basal third of eye, angular. Caudal plate broadly rounded caudally, 0.6–0.7 times as long as wide. Circumanal ring (Fig. 4H) relatively small, transverse, narrowly oval, 0.2–0.3 times as wide as caudal plate; in ventral position close to hind of caudal plate; outer ring composed of 2–5 rows of pores.

Measurements (range, mean ± SD) in mm (5 immatures). Body length 2.63–2.83, 2.76 ± 0.08. Head width 0.85–0.93, 0.88 ± 0.03. Antenna length 0.43–0.48, 0.45 ± 0.02. Metatibiotarsus length 0.60–0.68, 0.65 ± 0.03. Forewing pad length 1.35–1.45, 1.41 ± 0.04. Caudal plate length 0.85–1.00, 0.97 ± 0.07. Caudal plate width 1.45–1.55, 1.52 ± 0.04. Circumanal ring width 0.38–0.44, 0.41 ± 0.02.

Etymology. Named after the Chinese common name of the host plant, 土肉桂, transliterated as “turouguei“; to be treated as a noun in the nominative singular standing in apposition.

Distribution. Taiwan.

Host plant and its phenology. *Cinnamomum osmophloeum* Kaneh. (Lauraceae). Leaf and flower buds of *C. osmophloeum* appear in late April. Young leaves grow from late May to late June and flowers bloom from early June to August. Fruits ripen from September to November.

Biology. *Trioza turouguei* sp. nov. is univoltine and induces pea-shaped galls (Fig. 5C, D) on the stems of new shoots of *C. osmophloeum*. The galls are unilocular with a single immature in each chamber. The annual life cycle of the gall is synchronized with the host phenology and passes through the following four stages of development as defined by Rohfritsch (1992). (1) Initiation: this stage is very short lasting from late April to the early May. After the first instar inserts its stylets into the phloem and injects saliva, the area on which it sits, either a flower, or leaf petiole, or a tender stem, transforms into a tiny pit and the surrounding area starts swelling. (2) Growth and differentiation: from late May to November, the gall forms and completely covers the immature. The second instar appears in late May and lasts until September. The third and fourth instars can be found in October and November, respectively. (3) Maturation: in December, the gall enters the maturation stage, and the immatures attain the final (fifth) instar. The gall reaches its maximum size with a diameter/length of 5.0/7.8 mm. (4) Dehiscence: during January and March, the gall dehisces by mechani-

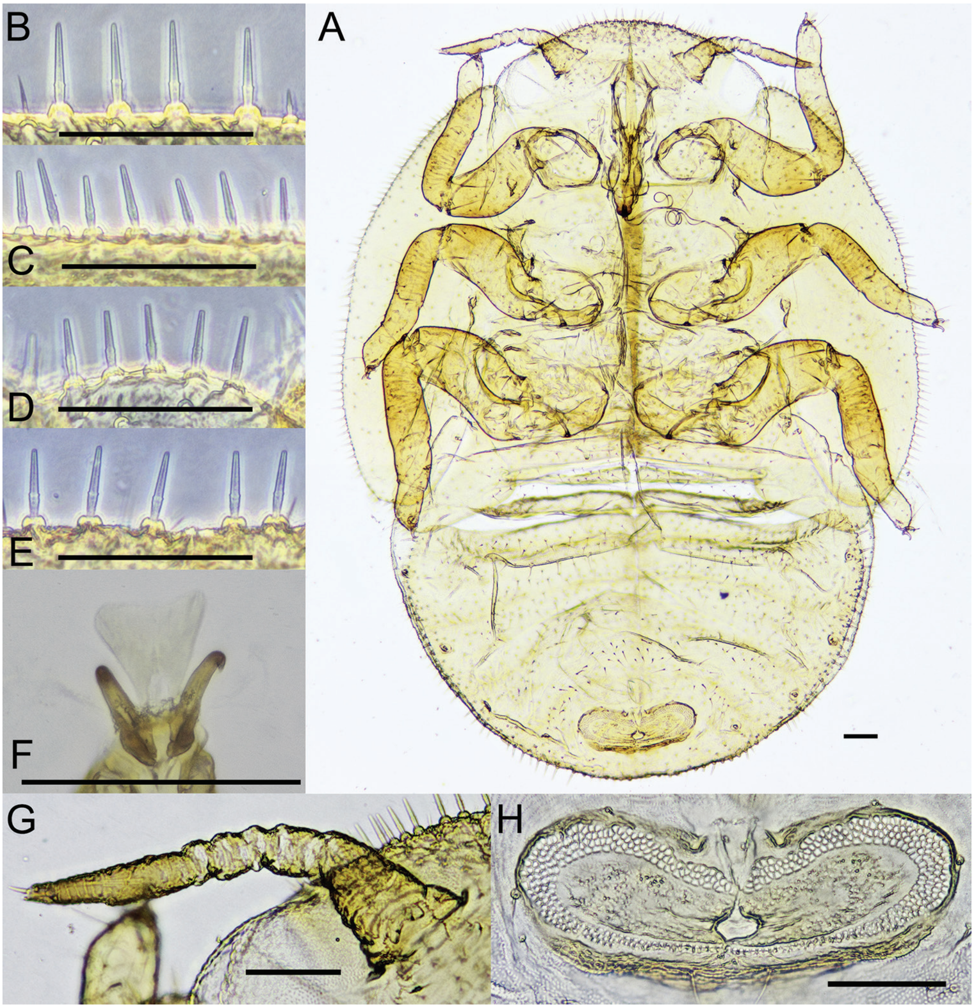

Figure 4. Fifth instar immature of *Trioza turouguei* sp. nov. **A** habitus **B** marginal sectasetae of head **C** marginal sectasetae of forewing pad **D** marginal sectasetae of hindwing pad **E** marginal sectasetae of caudal plate **F** tarsal arolium **G** antenna **H** circumanal ring. Scale bars: 0.1 mm.

cal force in the gall tissue. The final instar immatures crawl out of the gall where the adults emerge. Soon after, the adults start mating.

Affinities. Hollis and Martin (1997) listed ten named triozid species from the Old World and one undescribed *Trioza* species from the New World associated with *Cinnamomum* spp. An updated list of the Old World species is provided in Table 1, taking into account taxonomical changes of the last 20 years including some proposed here. Despite a certain morphological resemblance among the Old World species, it is questionable if the group is monophyletic. The species share (mostly) following characters: genal processes developed, more than half vertex length; antennal segment 3 very long

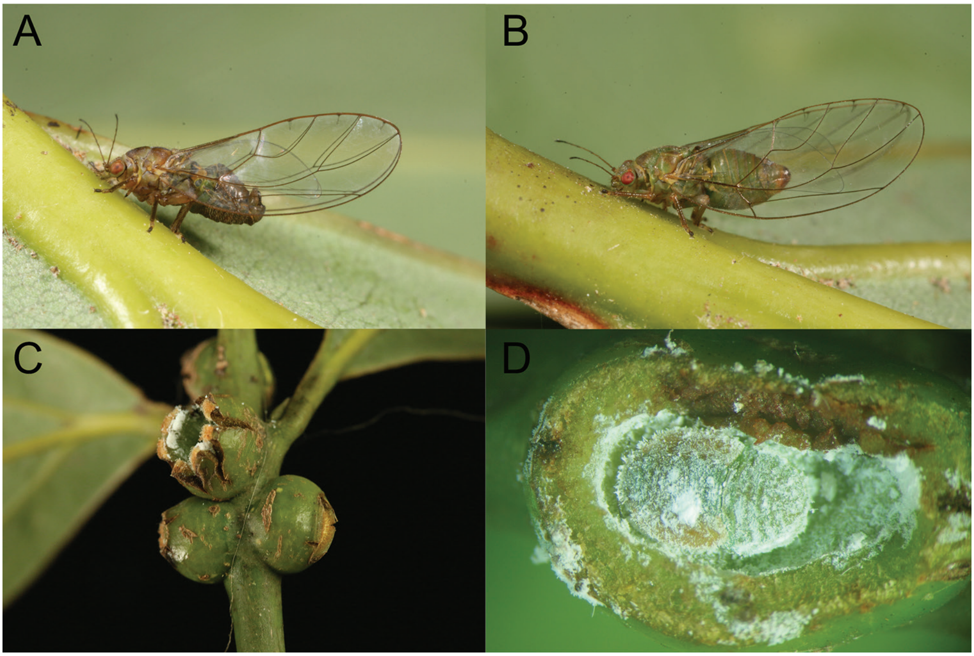

Figure 5. *Trioza turouguei* sp. nov. on its host plant, *Cinnamomum osmophloeum* Kanehira **A** male **B** female **C** pea-like galls on stem **D** fifth instar immature in a gall.

(not in *T. hangzhouica* (Li, 1994)); terminal antennal setae strongly unequal in length; forewing transparent, with short concave or sometimes sinuous vein Rs; hindwing over half as long as forewing; metatibia with a group of basal spines and 1+2 small apical spurs (1+3 in *T. exoterica* Yang, 1984 and *T. nigricamphorae* Li, 1993).

Li (2005, 2011) erected two ill-defined, probably polyphyletic genera *Triozopsis* (type species *Trioza nigricamphorae*) and *Metatriozidus* (type species *Metatriozidus ileicisuga* Li, 2011) in which he also placed species associated with *Cinnamomum*. Here we adopt the broad concept of *Trioza* Foerster by Hollis (1984) and consider *Metatriozidus* and *Triozopsis* as subjective synonyms following Yang et al. (2013).

Based on the examination of relevant types (CAUB) we propose here following new synonymy: *Trioza inflata* Li, 1992, = *Trioza xiangicamphorae* Li, 1992, syn. nov.

Mound and Halsey (1978) transferred *Siphonaleyrodes formosanus* Takahashi, 1932 from whiteflies to psyllids and synonymised it with *Trioza cinnamomi* (Boselli, 1931). According to the original description, the immatures of *S. formosanus* are relatively slender and possess several rows of marginal sectasetae (Takahashi 1932). Immatures of *T. cinnamomi* on the other hand are broader and possess only a single row of marginal sectasetae (Miyatake 1969; NHMB data). Based on this evidence, we conclude that the two taxa are not conspecific and remove the former from synonymy with *Siphonaleyrodes formosanus*, stat. rev. The species is currently only known from immatures which makes it difficult to place this genus within the current classification of Triozidae

Table 1. Old World Triozidae associated with *Cinnamomum* (Lauraceae). Plant names marked with asterisk are confirmed hosts as defined by Burckhardt et al. (2014).

Psylloid species	Host species	Gall type	Distribution	Reference
Siphonaleyrodes formosanus Takahashi, 1932, stat. rev.	**Cinnamomum reticulatum* Hayata	pit galls	Taiwan	Takahashi (1932)
Trioza camphorae Sasaki, 1910	**Cinnamomum camphora* (L.) J. Presl	pit galls	India ?, Japan, Taiwan, China	Li (2011), Yang et al. (2013), Burckhardt et al. (2018)
Trioza camphoricola Li, 1993	*Cinnamomum camphora* (L.) J. Presl	?	China	Li (2011)
Trioza cinnamomi (Boselli, 1931)	**Cinnamomum doederleinii* Engl., **C. loureiroi* Nees, **C. tenuifolium* (Makino) Sugim., **C. yabunikkei* H. Ohba, *Neolitsea aciculata* (Blume) Koidz.	pit galls	Japan, Korea (the record from Taiwan is erroneous as *T. cinnamomi* was described from Japan and not Taiwan)	Hodkinson (1983, 1986), Cho et al. (2017)
Trioza exoterica Yang, 1984; = *Trioza parthenoxyli* Yang & Li, in Li & Yang, 1985	*Cinnamomum porrectum* (Roxb.) Kosterm., **Cryptocarya chinensis* (Hance) Hemsl. (Lauraceae)	leaf curling gall	China, Taiwan	Li (2011)
Trioza guipicircularis (Li, 2011) = *Trioza circularis* Li, 1993 nec Froggatt, 1901; primary homonym	*Cinnamomum austrosinense* H. T. Chang	closed gall (not pit gall as recorded in Hollis and Martin 1997)	China	Li (2011)
Trioza hangzhouica (Li, 1994)	*Cinnamomum tenuifolium* (Makino) Sugim.	unknown	China	Li (2011)
Trioza inflata Li, 1992, = *Trioza xiangicamphorae* Li, 1992, syn. nov.	*Cinnamomum iners* Reinw. ex Blume, *C. verum* J. Presl	?	China	Li (2011)
Trioza macularicamphorae Li, 1992	*Cinnamomum iners* Reinw. ex Blume	?	China	Li (2011)
Trioza magnicamphorae Li, 1993	*Cinnamomum camphora* (L.) J.Presl	?	China	Li (2011)
Trioza monri Burckhardt, 2018 = *Trioza laqueus minor* Kandasamy, 1986	*Cinnamomum* sp.	?	India	Burckhardt et al. (2018)
Trioza nigricamphorae Li, 1993	*Cinnamomum camphora* (L.) J.Presl	?	China	Li (2011)
Trioza turouguei sp. nov.	**Cinnamomum osmophloeum* Kaneh.	mung-pea like stem gall	Taiwan	this paper
Trioza pseudocinnamomi Li, 1993	*Cinnamomum burmanni* (Nees & T. Nees) Blume	?	China	Li (2011)

(Burckhardt and Ouvrard 2012, Percy et al. 2018). The type material of *S. formosanus* is apparently lost (M. M. Yang, pers. obs.).

Trioza turouguei sp. nov. differs from the other species associated with *Cinnamomum* as indicated in the following keys. In particular, it is diagnosed by details of the male and female terminalia and the multilayered circumanal ring in the immature.

Keys to the Old World Triozidae associated with *Cinnamomum*

Adults

(Adults of *Siphonaleyrodes formosanus* are unknown)

1 Metatibia with 1+3 apical spurs **2**
– Metatibia with mostly 1+2 apical spurs **3**
2 Genal processes shorter than vertex along midline. Vein Rs of forewing short, concavely curved towards fore margin .... ***Trioza exoterica* Yang**
– Genal processes longer than vertex along midline. Vein Rs of forewing long, sinuous .... ***Trioza nigricamphorae* Li**
3 Forewing vein M > 2.0 times vein M$_{1+2}$ **4**
– Forewing vein M < 2.0 times vein M$_{1+2}$ **5**
4 Genal processes about as long as vertex along midline. Vein Cu of forewing longer than Cu$_{1b}$. China .... ***Trioza hangzhouica* (Li)**
– Genal processes distinctly shorter than vertex along midline. Vein Cu of forewing shorter than Cu$_{1b}$. India .... ***Trioza monri* Burckhardt**
5 Forewing with cell cu$_1$ value > 2.0 .... **6**
– Forewing with cell cu$_1$ value < 1.9 .... **9**
6 Genal processes slender, subacute apically. Forewing with cell m$_1$ value < 1.8 ... **7**
– Genal processes massive, blunt apically. Forewing with cell m$_1$ value > 1.8 .... **8**
7 Forewing widest in apical third; apex subacute ... ***Trioza cinnamomi* (Boselli)**
– Forewing widest in the middle; apex narrowly rounded .... ***Trioza macularicamphorae* Li**
8 Paramere, in profile, with basal lobe anteriorly; apex blunt. Female proctiger with digitiform apical process .... ***Trioza magnicamphorae* Li**
– Paramere, in profile, with almost straight anterior margin; apex pointed. Female proctiger truncate apically .... ***Trioza turouguei* sp. nov.**
9 Genal processes around two thirds of vertex length measured along midline .... ***Trioza camphoricola* Li**
– Genal processes as long as or longer than vertex along midline **10**
10 Male proctiger short, weakly produced posteriorly, without very long conspicuous setae along hind margin. Paramere, in profile, distinctly narrowed in apical third **11**
– Male proctiger long, strongly produced posteriorly, with long conspicuous setae along hind margin. Paramere, in profile, not strongly narrowed in apical third. **12**
11 Forewing narrowly rounded apically; vein Rs of forewing relatively long, almost straight, slightly turned towards fore margin apically .... ***Trioza camphorae* Sasaki**
– Forewing pointed apically; vein Rs short, concavely curved towards fore margin .... ***Trioza inflata* Li**

12 Forewing 2.3 times as long as broad. Paramere, in profile, lamellar, truncate apically .... ***Trioza guipicircularis* Li**
– Forewing 2.9 times as long as broad. Paramere, in profile, lanceolate, subacute apically .... ***Trioza pseudocinnamomi* Li**

Immatures

(Immatures of *Trioza camphoricola*, *T. guipicircularis*, *T. hangzhouica*, *T. inflata*, *T. macularicamphorae*, *T. magnicamphorae*, *T. monri*, *T. nigricamphorae* and *T. pseudocinnamomi* are unknown)

1 Body relatively slender, > 1.6 times as long as wide **2**
– Body relatively broad, < 1.5 times as long as wide **3**
2 Body margin with several rows of sectasetae... .... ***Siphonaleyrodes formosanus* Takahashi**
– Body margin with a single row of sectasetae............... ***Trioza exoterica* Yang**
3 Outer circumanal ring consisting of 2–5 rows of pores .... ***Trioza turouguei* sp. nov.**
– Outer circumanal ring consisting of a single row of pores **4**
4 Dorsal outline subcircular, 1.1 times as long as wide. Tarsal arolium circular... .... ***Trioza camphorae* Sasaki**
– Dorsal outline broadly oval, 1.2 times as long as wide. Tarsal arolium triangular .... ***Trioza cinnamomi* (Boselli)**

Discussion and conclusions

Hollis and Martin (1997) showed that sap sucking insects colonized Lauraceae more successfully than chewing insects by an order of magnitude of percentage of number of species associated with this family. The reason may be the phytochemicals in the leaves deterring chewing insects more efficiently than sucking insects. Among psyllid host plant families, Lauraceae is ranked 7th in terms of number of associated psyllid genera (Ouvrard et al. 2015). More than two thirds of the psyllid species associated with Lauraceae belong to the Triozidae and of these almost two thirds induce galls or other deformations on their hosts (Hollis and Martin 1997). The Old World triozids developing on *Cinnamomum* (Table 1) fit this pattern. Of the 14 species, five with confirmed hosts (hosts marked with asterisk in Table 1) induce galls. Of the remainder, the association with *Cinnamomum* of seven species is likely but that of two (*Trioza exoterica*, *T. hangzhouica*) is questionable. The former develops on *Cryptocarya chinensis* (host confirmed by the presence of immatures) and *Cinnamomum porrectum* may be just casual plant (Burckhardt et al. 2014). The same is true for *T. hangzhouica*. Among the five species with confirmed hosts, all are monophagous except for *T. cinnamomi* which is narrowly oligophagous.

Trioza turouguei sp. nov. is characterized by the induction of pea-shaped galls on stems of its host. Stem galls induced by psyllids are much rarer than those on leaves (Hodkinson 1984, Burckhardt 2005, Yang et al. 2006, Yang and Raman 2007). Examples are *Pachypsylloides* species (Liviidae) on *Calligonum* species (Polygonaceae), two *Pachypsylla* species (Aphalaridae) on *Celtis* species (Cannabaceae), *Egeirotrioza bifurcata* (Mathur 1975) and *Egeirotrioza populi* (Horváth 1915) (Triozidae) on *Populus* species (Salicaceae) or *Calophya rubra* (Blanchard 1852) (Calophyidae) on *Schinus polygama* (Anacardiaceae) (Yang and Mitter 1994, Burckhardt and Basset 2000, Hodkinson 2009).

Cinnamomum osmophloeum, the host of *Trioza turouguei* sp. nov., has a scattered distribution in Taiwan growing in broad-leaved forests. Its conservation status is "Vulnerable" in the International Union for Conservation of Nature (IUCN) Red List (Pan 1998). This plant species is not hard to find at low to medium mountain areas in Taiwan, but the majority of trees are planted and only a few grow naturally. The unintentional introduction of *Cinnamomum burmannii* into Taiwan may endanger the natural population of *C. osmophloeum* (Tseng et al. 2008). Contrary to its host, adults, and galls of *Trioza turouguei* were found only in central Taiwan. Adults of *Trioza turouguei* are quite big and the galls are conspicuous on a plant species of medicinal interest. It is, therefore, surprising that the species has not been described before. One reason for this may be the very short period of adult emergence (1–2 weeks). Another reason is certainly that psyllid diversity in general, and that of the tropics in particular, is still insufficiently known.

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CHECKLIST

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Annotated checklist of freshwater molluscs from the largest freshwater lake in Southeast Asia

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Abstract

The Tonle Sap Lake in Cambodia is a crucial freshwater biodiversity hotspot and supports one of the world's largest inland fisheries. Within the Tonle Sap basin, freshwater molluscs provide vital ecosystem services and are among the fauna targetted for commercial harvesting. Despite their importance, freshwater molluscs of the Tonle Sap basin remain poorly studied. The historical literature was reviewed and at least 153 species of freshwater molluscs have been previously recorded from throughout Cambodia, including 33 from the Tonle Sap basin. Surveys of the Tonle Sap Lake and surrounding watershed were also conducted and found 31 species, 15 bivalves (five families) and 16 gastropods (eight families), in the Tonle Sap basin, including three new records for Cambodia (*Scaphula minuta*, *Novaculina siamensis*, *Wattebledia siamensis*), the presence of globally invasive *Pomacea maculata* and potential pest species like *Limnoperna fortunei*. This study represents the most comprehensive documentation of freshwater molluscs of the Tonle Sap basin, and voucher specimens deposited at the Inland Fisheries Research and Development Institute, Cambodia, represent the first known reference collection of freshwater molluscs in the country. In order to combat the combined anthropogenic pressures, including invasive species, climate change and dams along the Mekong River, a multi-pronged approach is urgently required to study the biodiversity, ecology, ecosystem functioning of freshwater molluscs and other aquatic fauna in the Tonle Sap basin.

Keywords
alien species, bivalves, Cambodia, diversity, economic species, Lower Mekong basin, snails, Tonle Sap Lake

Introduction

"Clams, cockles, snails, et cetera can be obtained just by cupping one's hands into the Fresh Water Lake" (Zhou in Uk and Uk 2016).

Being the largest natural lake in Southeast Asia, the Tonle Sap Lake is a crucial freshwater habitat for various animals, including fish and birds (Campbell et al. 2006), but besides the above mentioned brief account by the Chinese diplomat, Zhou Daguan, in the 13th century (Uk and Uk 2016), little else is known about the freshwater molluscs of the lake. Although poorly studied, freshwater molluscs in the Tonle Sap basin, as with the fauna in the surrounding Indo-Burmese region, occupy a range of habitats and perform vital ecological roles, interacting with other fauna (Köhler et al. 2012). For its size, Cambodia is the most speciose country in East and Southeast Asia for unionid bivalves; although the data on bivalves in the country requires updating (Zieritz et al. 2018). The most comprehensive checklist of freshwater molluscs for Cambodia was based on material collected almost half a century ago from the main stem of the Mekong River, and did not include the Tonle Sap ecosystem (Brandt and Temcharoen 1971). Recent surveys and ecological studies in the fresh waters of Cambodia have targeted various taxa, and when molluscs were included, all were, at most, identified only to genera (Vongsombath et al. 2009; Ohtaka et al. 2011; Sor et al. 2017).

In addition, there has been interest in economically-important molluscs, including freshwater apple snails (Ampullariidae) and Asian clams (Cyrenidae) (Ngor et al. 2014, 2016, 2018d). The composition of ampullariids in the Tonle Sap Lake appears to vary seasonally, probably owing to the vastly different climatic and hydrological conditions (Ngor et al. 2018a, d). There is also growing concern about the economic and ecological impacts of invasive apple snails, *Pomacea* species, which were not established in Cambodia two decades ago (Cowie 1995), but are now spreading rapidly, including in the Tonle Sap Lake (Ngor et al. 2014; Khay et al. 2018; Ngor PB, pers. obs.). The threat of invasive species, in addition to climate change, flow modification within the Mekong River basin, overharvesting, pollution, and land use change, would most probably impact the ecosystem and biodiversity of the Tonle Sap Lake (Arias et al. 2014, 2019; McCann et al. 2016; Ngor et al. 2018a, b, d; Uk et al. 2018).

Furthermore, most of the recent studies did not include voucher specimens nor photographs of species that could be used by local stakeholders and research scientists. The lack of proper reference material may lead to incorrect identification of species, allowing non-native species to establish and spread unnoticed (e.g., Ng et al. 2015, 2018).

It is therefore imperative to document the biodiversity of freshwater molluscs of Tonle Sap as a foundation for further evolutionary and ecological research, and to make available the necessary information to the government, local residents, and other stakeholders to allow for more effective management of threatened, economic- and medically-important freshwater molluscs in this unique freshwater habitat. In this study, we aimed to conduct 1) a review of historical literature on freshwater molluscs of Cambodia; and 2) surveys of Tonle Sap Lake and the surrounding watershed to provide an updated checklist of species diversity for the freshwater molluscs in the largest lake in Southeast Asia, which is also one of the world's most productive lakes.

Materials and methods

Historical information

Historical data on freshwater mollusc records from Cambodia were gathered from relevant literature based on a search of the Global Biodiversity Information Facility (GBIF.org 2019), the IUCN Red List (IUCN 2018), MolluscaBase (2019), MUSSEL Project (Graf and Cummings 2019), Google and Web of Science using keywords (Cambodia, Cambodge, freshwater, fluviatiles, mollusc, mollusk, mollusques, clam, bivalve, snail, gastropod) or applying relevant filters. Major references included Mabille and Le Mesle (1866), Crosse and Fischer (1876), Morlet (1889), Fischer and Dautzenberg (1904), Brandt and Temcharoen (1971), and Brandt (1974). Only original descriptions and key references, including first record in Cambodia, if applicable, Brandt (1974), and major revisionary work, are listed in the annotated species checklist. Historical records from the Tonle Sap basin were noted based on specific mentions of 'Tonle Sap Lake' or 'grand lac', and localities within the provinces around the Lake, i.e., Kampong Chhnang, Pursat, Battambang, Banteay Meanchey, Siem Reap and Kampong Thom.

Sampling

We conducted surveys in and around the Tonle Sap Lake and its major tributaries over two one-week periods in May and December 2019, respectively. Samples were taken from 44 locations from the study area, covering major landing sites (Chhnouk Tru in Kampong Chhnang Province, Kampong Loung in Pursat Province, Chong Khneas in Siem Reap Province and Boeung Chhmar Ramsar wetlands in Kampong Thom Province), major Tonle Sap tributaries (Pursat, Sangkae, Mongkol Borei, Serei Saophoan, Sreng, Chi Kraeng, Staung, Sen, and Chinit Rivers), rain-fed and flooded zones along national road No. 5 and 6 around the Tonle Sap Lake (Fig. 1, Table 1). Specimens were collected by hand and with long-handled nets. Some specimens were also purchased from local markets.

Species identification

All the specimens were identified to genus or species level based on shell characteristics by referring to the historical literature with original species descriptions, Brandt (1974), Morton and Dinesen (2010), Jeratthitikul et al. (2019a, b) and Muanta et al. (2019). The annotated species checklist is based on freshly collected specimens in this study only, and is organised according to higher classification (class, subclass or equivalent, order, superfamily), family, and species, in alphabetical order. Higher classifications follow Lydeard and Cummings (2019), and valid names mainly follow MolluscaBase (2019) and Graf and Cummings (2019).

Voucher specimens are deposited in the following institutions:

CIFI	Inland Fisheries Research and Development Institute, Cambodia;
MUMNH	Mahidol University Museum of Natural History, Thailand;
ZRC	Zoological Reference Collection of the Lee Kong Chian Natural History Museum, National University of Singapore.

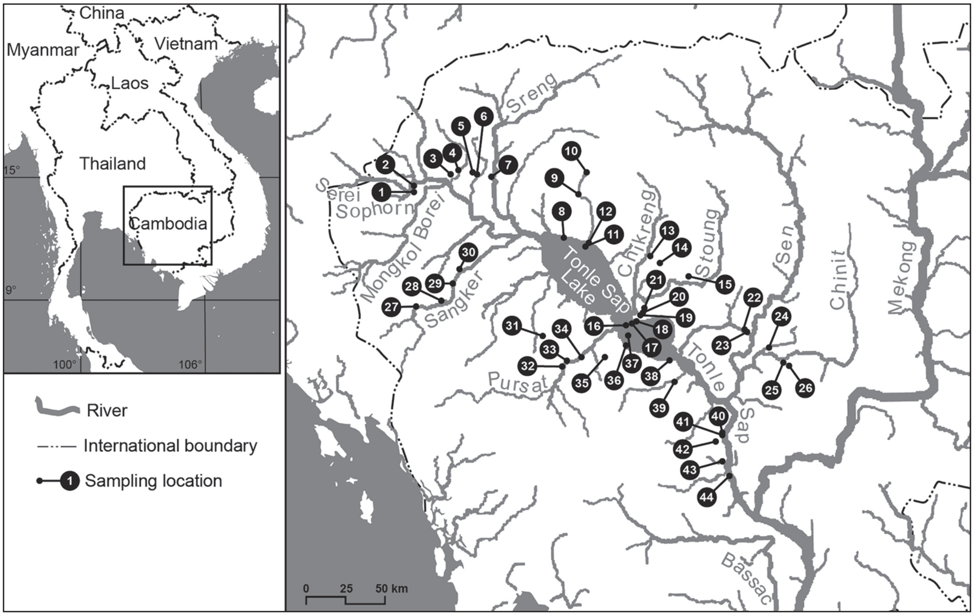

Figure 1. Map of sampling localities of freshwater molluscs within the Tonle Sap basin, Cambodia. The numbers indicate collection sites that correspond to Table 1. Inset shows location of the focal area within the Indochinese region.

Table 1. Sampling localities of freshwater molluscs collected from the Tonle Sap basin in 2019.

No.	Locality code and locality details	Coordinates
1	C078-Serei Saophoan River, Serei Saophoan city, Banteay Meanchey Province	13°35'08.9"N, 102°58'41.2"E
2	C073-Serei Saophoan River, Preah Ponlea, Serei Saophoan District, Banteay Meanchey Province	13°34'33.1"N, 102°58'58.5"E
3	C017-Paoy Samraong, Preah Netr Preah, Preah Netr Preah District, Banteay Meanchey Province	13°35'01.8"N, 103°09'24.8"E
4	C075-River in Chob Vari, Preah Netr Preah District, Banteay Meanchey Province	13°37'24.0"N, 103°11'50.0"E
5	C080-Lotus pond in Phnum Lieb, Preah Netr Preah District, Banteay Meanchey Province	13°36'31.8"N, 103°18'02.3"E
6	C079-River in Phnum Lieb, Preah Netr Preah District, Banteay Meanchey Province	13°36'16.9"N, 103°19'02.0"E
7	C074-Sreng River in Kralanh City, Kralanh District, Siem Reap Province	13°35'29.8"N, 103°24'15.8"E
8	C018-Tonle Sap Lake open area near Chong Khneas, Chong Khneas, Siem Reap Province	12°30'20.1"N, 103°50'06.2"E
9	C085-Siem Reap River, Leang Dai, Angkor Thom District, Siem Reap Province	13°29'24.3"N, 103°55'14.4"E
10	C081-Stream near Banteay Srei District, Siem Reap Province	13°35'44.0"N, 103°57'43.3"E
11	C020-Tonle Sap Lake open area near Kampong Phluk, Prasat Bakong District, Siem Reap Province	13°11'16.2"N, 103°57'25.4"E
12	C021-Tonle Sap Lake open area near Kampong Phluk, Prasat Bakong District, Siem Reap Province	13°11'40.6"N, 103°57'50.5"E
13	C082-Chi Kraeng River in Kampong Kdei, Chi Kraeng District, Siem Reap Province	13°07'55.3"N, 104°20'16.8"E
14	C023-Ponds in Thnol Keng, Kampong Kdei, Chi Kraeng District, Siem Reap Province	13°05'25.4"N, 104°23'32.5"E
15	C024-Paddy fields near Trach, Kampong Chen Cheung, Stoung District, Kampong Thom Province	12°58'43.7"N, 104°33'52.3"E
16	C009-Tonle Sap Lake open area in Kampong Thom Province	12°42'42.5"N, 104°11'58.2"E
17	C008-Tonle Sap Lake open area near Pean Bang, Stoung District, Kampong Thom Province	12°43'36.9"N, 104°14'11.6"E
18	C007-River flows from Boeng Tonle Chhma to Tonle Sap Lake, Stoung District, Kampong Thom Province	12°44'15.4"N, 104°15'30.9"E
19	C004-Don Sdeung, Peam Bang, Staung District, Kampong Thom Province	12°46'25.4"N, 104°17'02.9"E
20	C005-Don Sdeung, Boeung Chhmar Fish Sanctuary, Staung District, Kampong Thom Province	12°47'25.1"N, 104°17'55.7"E
21	C006-Provincial Fisheries Office, Boeung Chhmar Fish Sanctuary, Staung District, Kampong Thom Province	12°48'48.6"N, 104°18'11.6"E
22	C087-Sen River in Balang, Damrei Choan Khla, Stung Sen District, Kampong Thom Province	12°41'48.5"N, 104°53'58.8"E
23	C025-Sen River in Kampong Samraung, Srayav, Stung Sen District, Kampong Thom Province	12°40'58.3"N, 104°54'33.1"E
24	C090-Tang Krasang River in Santuk District, Kampong Thom Province	12°34'04.4"N, 105°03'02.3"E
25	C092-Chinit River in Kampong Thma, Santuk District, Kampong Thom Province	12°29'45.7"N, 105°07'18.4"E
26	C088-Canal from Makara Dam, Ballangk, Baray District, Kampong Thom Province	12°29'13.8"N, 105°08'47.0"E
27	C068-Recreational area, Sangkae River in Traeng, Rotanak Mondol, Battambang Province	12°49'51.4"N, 102°55'44.3"E
28	C071-Sangkae River in Chaeng Mean Chey, Banan District, Battambang Province	12°52'03.5"N, 103°06'03.8"E
29	C070-Sangkae River in Chheu Teal, Banan District, Battambang Province	12°58'54.7"N, 103°08'36.2"E
30	C014-Sangkae River in Wat Ta Meum, Oudambang Muoy, Sangkae District, Battambang Province	13°04'04.7"N, 103°12'17.2"E
31	C067-River in Ou Ta Paong, Bakan District, Pursat Province	12°39'34.8"N, 103°40'26.2"E
32	C013-Pursat River near Damnak Ampel Irrigation Dam, Damnak Ampel, Lolork Sor, Sampaov Meas District, Pursat Province	12°29'19.3"N, 103°48'29.7"E
33	C012-Pursat River in Wat Loung, Lolork Sor, Sampaov Meas District, Pursat Province	12°30'20.1"N, 103°50'07.8"E
34	C064-Pursat River in Sorya, Krong Pursat, Pursat Province	12°31'00.3"N, 103°54'54.7"E
35	C066-Thliem Ma-Orm River in Boeng Kantuot, Krakor District, Pursat Province	12°31'37.3"N, 104°03'13.8"E
36	C011-Tonle Sap Lake open area in Krakor District, Pursat Province	12°35'42.1"N, 104°12'13.1"E
37	C010-Tonle Sap Lake open area in Krakor District, Pursat Province	12°38'20.2"N, 104°12'12.1"E
38	C003-Kampong Chhnok Tru landing point, Chhnok Tru, Boribo District, Kampong Chhnang Province	12°30'36.5"N, 104°27'18.2"E
39	C063-Tributary of Tonle Sap Lake in Phumi Phsar, Kampong Chhnang Province	12°22'50.7"N, 104°29'0.2"E
40	C002-Tonle Sap River in Kampong Prasat, Saeb, Kampong Tralach District, Kampong Chhnang Province	12°04'23.6"N, 104°46'23.8"E
41	C097-Tonle Sap River in Kaoh Thkov, Chol Kiri District, Kampong Chhnang Province	12°03'31.7"N, 104°46'22.4"E
42	C001-Boeung Po, Sorvong, Tacheise, Kampong Tralach District, Kampong Chhnang Province	12°01'28.3"N, 104°43'54.1"E
43	C094-Tonle Sap River in Samretthi Chey, Kampong Tralach district, Kampong Chhnang Province	11°53'55.2"N, 104°46'01.6"E
44	C093-Tonle Sap River in Kaoh Chen, Popnhea Lueu district, Kandal Province	11°49'01.6"N, 104°48'40.5"E

Results

Historical records for Cambodia

Almost 300 species of freshwater molluscs have previously been recorded from Cambodia to date, but only 153 are currently considered to be valid species and among these, 33 species were recorded from the Tonle Sap basin (Table 2, Suppl. material 1: Table S1), including records mentioning Battambang Province and Kampong Svay in Kampong Thom Province (as 'Campong/Kompong-Soai' in Suppl. material 1: Table S1). Two species are noted to have uncertain or doubtful presence in Cambodia. The first, *Scaphula pinna* Benson, 1856, is present in the southern Mekong delta in Vietnam, and is thus presumed to be extant in Cambodia as well (Madhyastha 2012; but see species account for *Scaphula minuta* in the next section). Secondly, *Paludina fulva* Benson, 1863, described from Cambodia, was synonymised with *Idiopoma dissimilis* (OF Müller, 1774) by Brandt (1974), who recognised the species as being distributed from India to northern Thailand, and hence regarded the record from Cambodia to be doubtful. Among the historical records with known taxonomic issues are three species that are not recognised as valid in MolluscaBase (2019), i.e., *Filopaludina danieli* (Morlet, 1889), *Filopaludina obscurata* (Deshayes & Jullien, 1876) and *Mekongia paviei* (Morlet, 1889), and one species, although with an accepted name, i.e., *Mekongia turbinata* (Deshayes & Jullien, 1876), has been highlighted as requiring taxonomic revision (Köhler and Rintelen 2011).

A third of the previously recorded species are medically-important Pomatiopsidae and Stenothyridae, which are intermediate hosts of zoonotic parasites like *Schistosoma mekongi* Voge, Bruckner & Bruce, 1978, and are distributed in the Mekong River (Davis 1979; Attwood et al. 2004). One hundred and six species have had their conservation status assessed by the IUCN (2018), and among them, 66 species are Least Concern, 32 species are Data Deficient, and eight species of Pomatiopsidae have been assessed as Vulnerable or Near-Threatened (Suppl. material 1: Table S1).

Preliminary survey of Tonle Sap Lake and its watershed

At least 15 species of bivalves from five families, and 16 species of gastropods from eight families (Table 2) were collected from around Tonle Sap Lake and the surrounding habitats, including tributaries, paddy fields, and ponds.

Table 2. Summary of freshwater molluscs recorded in historical records of Cambodia, historical records that specify the Tonle Sap basin, and collected from the Tonle Sap basin in 2019. Higher classification follows Lydeard and Cummings (2019).

Higher classification	Order	Superfamily	Family	Number of species		
				Historical records of Cambodia	Historical records mentioning Tonle Sap basin	Present study of Tonle Sap basin
Bivalvia						
Pteriomorphia	Arcida	Arcoidea	Arcidae	1	–	1
	Mytilida	Mytiloidea	Mytilidae	2	2	2
Heterodonta	Adapedonta	Solenoidea	Pharidae	–	–	1
	Venerida	Cyrenoidea	Cyrenidae	14	6	> 1
Palaeoheterodonta	Unionida	Unioidea	Unionidae	40	13	10
Gastropoda						
Caenogastropoda	Architaenioglossa	Ampullarioidea	Ampullariidae	7	4	4
		Viviparoidea	Viviparidae	19	3	4
	Littorinimorpha	Truncatelloidea	Bithyniidae	4	1	2
			Iravadiidae	1	–	–
			Pomatiopsidae	46	–	–
			Stenothyridae	6	–	–
	Neogastropoda	Buccinoidea	Nassariidae	7	2	2
	(Cohort) Sorbeoconcha	Cerithioidea	Pachychilidae	2	1	1
			Thiaridae	2	1	1
Heterobranchia						
Hygrophila		Lymnaeoidea	Bulinidae	1	–	1
			Lymnaeidae	1	–	1
Total				153	33	31

Annotated checklist of freshwater molluscs recorded from Tonle Sap basin

Class Bivalvia Linnaeus, 1758
Subclass Pteriomorphia Beurlen, 1944
Order Arcida Stoliczka, 1871
Superfamily Arcoidea Lamarck, 1809
Family Arcidae Lamarck, 1809

***Scaphula minuta* Ghosh, 1922**
Fig. 2A

Scaphula minuta Ghosh, 1922: 1143–1144. Type locality: "Tale Sap or inland Sea of Singgora on the east coast of peninsular Siam".

Material examined. CIFI.MOL.044, ZRC.MOL.015755.

Distribution and habitat. Pursat River in Pursat Province, and Sreng River in Siem Reap Province (locality no. 7 and 32). Found attached to rocks in slow-moving waters.

Remarks. *Scaphula minuta* was first described from Songkhla Lake in southern Thailand (Ghosh 1929) and only recently reported to be distributed in southern Vietnam (Bogan and Do 2014). In addition, Bogan and Do (2014) mentioned that past records of '*Scaphula pinna*' in Thailand (i.e., Brandt 1974) should be referred to as *Scaphula minuta*. Based on Bogan and Do (2014), the species previously identified as *Scaphula pinna* and cited as being uncertain in Cambodia (Madhyastha 2012) was probably *Scaphula minuta*. However, the distinction between these two species is pending systematic revision, and our records represent the first confirmation of *Scaphula minuta* in Cambodia.

Order Mytilida Férussac, 1822
Superfamily Mytiloidea Rafinesque, 1815
Family Mytilidae Rafinesque, 1815

***Limnoperna fortunei* (Dunker, 1856)**
Fig. 2B

Volsella fortunei Dunker, 1856: 361, 362. Type locality: "Mare Chinense".
Limnoperna siamensis: Brandt 1974: 256.
Limnoperna fortunei: Morton and Dinesen 2010: 57–72.

Material examined. ZRC.MOL.015660, ZRC.MOL.015661, ZRC.MOL.015664, ZRC.MOL.015665, ZRC.MOL.015666.

Distribution and habitat. Tonle Sap River at Kampong Chhnang Province, and Tonle Sap Lake at Kampong Chhnang and Siem Reap Provinces (locality no. 8, 12, 37, 38 and 40). Occur in colonies attached by byssus threads to hard surfaces like man-made structures (e.g., boats, jetties, wooden pillars of homes), on unionid bivalves, and occasionally the shells of large freshwater gastropods.

Remarks. *Limnoperna fortunei* is native to East Asia, and although previously thought to be naturally distributed in the countries south of China (e.g., Brandt 1974), has recently been proposed to be introduced to tropical Indochina, including Cambodia (Morton and Dinesen 2010). However, its occurrence in Cambodia has been noted since the latter half of the 1800s (Suppl. material 1: Table S1, also see Morton and Dinesen (2010)). The species is known to be sympatric with *Sinomytilus harmandi* in Cambodia (Morton and Dinesen 2010), and in fact, we found that both species are syntopic, as most colonies of *Limnoperna fortunei* included individuals of *Sinomytilus harmandi*.

Sinomytilus harmandi (Rochebrune, 1882)

Fig. 2C

Dreissena harmandi Rochebrune, 1882: 102. Type locality: "Lac de Rhom-Penh, Mekong".

Sinomytilus harmandi: Brandt 1974: 307, pl. 26, fig. 69; Morton and Dinesen 2010: 57–72.

Material examined. ZRC.MOL.015657, ZRC.MOL.015658, ZRC.MOL.015659, ZRC.MOL.015667, ZRC.MOL.015668.

Distribution and habitat. Similar to that of *Limnoperna fortunei*.

Remarks. *Sinomytilus harmandi* appears to be limited in range to the Lower Mekong River basin, and it may have previously been mistaken for *Limnoperna fortunei*, resulting in a lack of historical records (Morton and Dinesen 2010). Our finding that *Sinomytilus harmandi* often co-occurs with *Limnoperna fortunei*, but in much lower densities, may further account for the former being overlooked in the literature. *Sinomytilus harmandi* may be distinguished from *Limnoperna fortunei* by the presence of an interior shell septum.

Subclass Heterodonta Meumayr, 1884
Order Adapedonta Cossmann & Peyrot, 1909
Superfamily Solenoidea Lamarck, 1809
Family Pharidae H. Adams & A. Adams, 1856

Novaculina siamensis Morlet, 1889

Fig. 3A

Novaculina siamensis Morlet, 1889: 198, pl. 9, fig. 4. Type locality: "Marais de Chantakam Siam".

Material examined. MUMNH.PHA.001, MUMNH.PHA.002

Distribution and habitat. Tonle Sap River in Kampong Chhnang Province (locality no. 41 and 43); tough clay bottom substrate, in which it makes cylindrical holes.

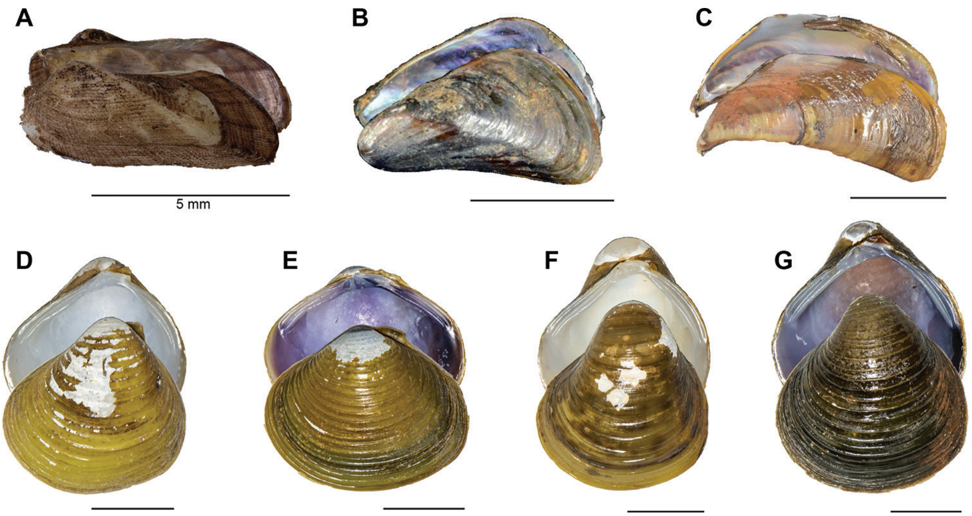

Figure 2. Freshwater bivalves of the Tonle Sap basin, Cambodia (Arcidae, Mytilidae, Cyrenidae) **A** *Scaphula minuta* **B** *Limnoperna fortunei* **C** *Sinomytilus harmandi* **D–G** *Corbicula* spp. Scale bars: 10 mm, unless stated otherwise. Photographs by TH Ng (**A–C**) and K Macharoenboon (**D–G**).

Remarks. The discovery of *Novaculina siamensis* in Tonle Sap River is a new record for Cambodia and fills in the distribution gap of the genus in Indochina. This species was first described from "Chantakam, Siam" [Prachantakham District, Prachinburi Province, Thailand], but the type series is thought to be lost (Bolotov et al. 2018). The type locality is probably a tributary of Bang Pakong River, in eastern Thailand. Brandt (1974) reported an additional population from Pasak River in Thailand. Sayenko et al. (2017) reported another abundant population from the Mekong Delta in Vietnam. The Tonle Sap River population is smaller, with more prominent umbo and lower posteriorly than the Thai population. All the collected shells were found empty, inside their cylindrical holes, under the shallow water near the riverbank. Only one living animal was obtained.

Order Venerida Gray, 1854
Superfamily Cyrenoidea Gray, 1840
Family Cyrenidae Gray, 1840

Corbicula spp.

Fig. 2D–G

Material examined. CIFI.MOL.029, CIFI.MOL.030, CIFI.MOL.031, CIFI.MOL.032, MUMNH.COR.0194, MUMNH.COR.0195, MUMNH.COR.0196, MUMNH.COR.0197, MUMNH.COR.0198, MUMNH.COR.0199, MUMNH.COR.0200, MUMNH.COR.0201, MUMNH.COR.0202, MUMNH.COR.0203, MUMNH.COR.0204, MUMNH.COR.0205, MUMNH.COR.0206, MUMNH.COR.0207,

MUMNH.COR.0208, MUMNH.COR.0209, MUMNH.COR.0210, MUMNH.COR.0211, MUMNH.COR.0212, ZRC.MOL.015634, ZRC.MOL.015635, ZRC.MOL.015636, ZRC.MOL.015637, ZRC.MOL.015638.

Distribution and habitat. Tonle Sap River and Lake, and most tributaries (locality no. 3, 6, 7, 8, 11, 12, 16, 18, 19, 20, 21, 22, 23, 24, 27, 32, 38, 39 and 40). Buried just below surface of soft, muddy substrate of the water bodies.

Remarks. Approximately 17 different species of *Corbicula* have previously been recorded from Cambodia (Suppl. material 1: Table S1), but there has been no known attempt to verify if all are valid records. In neighbouring Thailand, 21 nominal *Corbicula* species were all found to belong to only *Corbicula fluminea* (OF Müller, 1774), a single species (Kijviriya et al. 1991). Based on morphological examination of the fresh material from the Tonle Sap basin, it is possible that there may be more than one *Corbicula* species present. However, further investigation including molecular analysis will be required to confirm the species identities (Bieler and Mikkelsen 2019).

Corbicula species are the only bivalves that are commercially harvested from the Lake to be sold locally and exported abroad for human consumption and as animal feed (Fig. 4A, C). More than 6000 tonnes of *Corbicula* clams were recorded from five commercial landing sites in Kampong Chhnang Province, within the Tonle Sap basin, over the period of one year (Ngor et al. 2018d).

Subclass Palaeoheterodonta Newell, 1965
Order Unionida Gray, 1854
Superfamily Unionoidea Rafinesque, 1820
Family Unionidae Rafinesque, 1820

Bineurus mouhotii (Lea, 1863)
Fig. 3B

Monocondylaea mouhotii Lea, 1863: 190. Type locality: "Laos Mountains, Cambodia, Siam".
Pseudodon mouhoti: Brandt 1974: 265–266, pl. 19, fig. 25
Bineurus mouhotii: Pfeiffer et al. 2019: 116.

Material examined. MUMNH.UNI.2637, MUMNH.UNI.2646, MUMNH.UNI.2659 MUMNH.UNI.2670.

Distribution and habitat. Phumi Phsar River, Kampong Chnnang Province and Sangkae River, Battambang Province (locality no. 27 and 39); in sandy substrate of streams.

Remarks. *Bineurus mouhotii* is widespread along the Mekong basin in Thailand, Laos and Vietnam, and probably in northern Myanmar and Yunnan (Brandt 1974). The shell shape of present specimens was very inequilateral with concave ventral margin, which is a common form of the mountain race. The ventral margin of specimens collected from the downstream section is usually less concave, and nearly straight or even slightly curved (Brandt 1974). The combination of *Bineurus mouhotii* is a recent revision, and first appeared in Bolotov et al. (2017). The validity of the genus *Bineurus* was latter confirmed by phylogenomic analysis (Pfeiffer et al. 2019). However, the complete systematic revision of this taxon (and other related species previously included in the genus *Pseudodon* sensu Brandt, 1974) has yet to be investigated.

Contradens contradens **(Lea, 1838)**

Fig. 3C

Unio contradens Lea, 1838: 75, pl. 18, fig. 58. Type locality: Java.
Uniandra contradens tumidula: Brandt 1974: 290–291, pl. 24, figs 51, 52.
Uniandra contradens rustica: Brandt 1974: 291–292, pl. 24, fig. 53.
Uniandra contradens fischeriana: Brandt 1974: 292, pl. 24, fig. 55.

Material examined. CIFI.MOL.017, CIFI.MOL.018, MUMNH.UNI.2621, MUMNH.UNI.2629, MUMNH.UNI.2633, MUMNH.UNI.2648, MUMNH.UNI.2651, ZRC.MOL.015639.

Distribution and habitat. Tonle Sap Lake at Kampong Chhnang and Siem Reap Provinces, and Chhnok Tru landing point (locality no. 8, 11, 18, 36, 37, and 39); in soft muddy substrate.

Remarks. Not sold for food, collected as by-catch of *Corbicula* and *Mekongia* harvests, and were often observed to be discarded along with other large unionids. *Contradens contradens* was recently noted for its high varation in shell morphology dued to phenotypic plasticity (Jeratthitikul et al. 2019b). The species recognised here may represent one of *Contradens contradens* varations or could be recognised as a distinct species, e.g., *Unio dautzenbergi* Morlet, 1889. Further molecular studies are necessary to confirm the taxonomic status. The present collected specimens are strongly sculptured with irregularly concentric wrinkles throughout the shell, similar to some populations from Chao Praya basin, Thailand.

Ensidens ingallsianus **(Lea, 1852)**

Fig. 3D

Unio ingallsianus Lea, 1852: 282, pl. 24, fig. 41. Type locality: "Siam".
Ensidens ingallsianus ingallsianus: Brandt 1974: 288, pl. 24, fig. 47.
Ensidens ingallsianus: Muanta et al. 2019: 224–231.

Material examined. CIFI.MOL.019, CIFI.MOL.020, CIFI.MOL.021, CIFI.MOL.022, MUMNH.UNI.2617, MUMNH.UNI.2626, MUMNH.UNI.2634, MUMNH.UNI.2642, MUMNH.UNI.2644, MUMNH.UNI.2649, MUMNH.UNI.2655, MUMNH.UNI.2657, MUMNH.UNI.2666, MUMNH.UNI.2668,

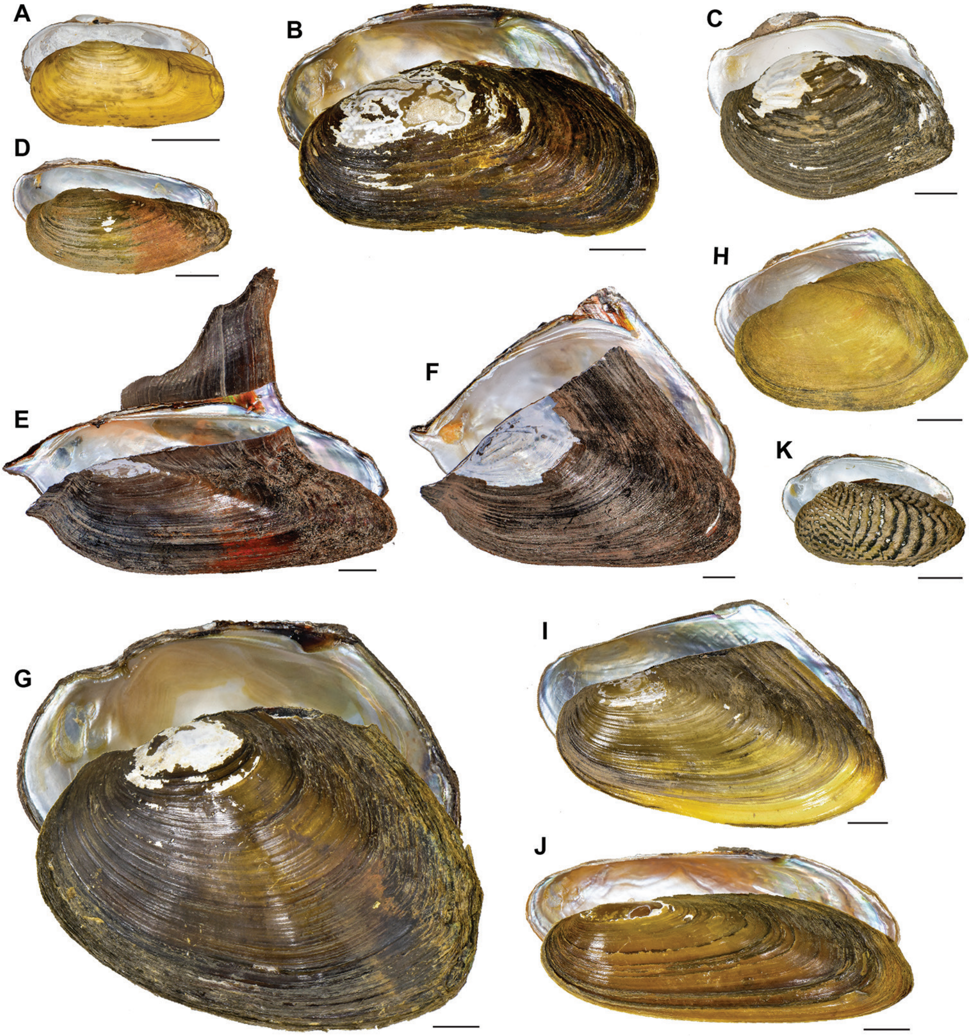

Figure 3. Freshwater bivalves of the Tonle Sap basin, Cambodia (Pharidae and Unionidae) **A** *Novaculina siamensis* **B** *Bineurus mouhotii* **C** *Contradens contradens* **D** *Ensidens ingallsianus* **E** *Hyriopsis bialata* **F** *Hyriopsis delaportei* **G** *Monodontina cambodjensis* **H** *Physunio micropterus* **I** *Pilsbryoconcha linguaeformis* **J** *Pilsbryoconcha lemeslei* and **K** *Scabies mandarinus*. Scale bars: 10 mm, unless stated otherwise. Photographs by K Macharoenboon.

MUMNH.UNI.2672, MUMNH.UNI.2673, ZRC.MOL.015640, ZRC.MOL.015641, ZRC.MOL.015642, ZRC.MOL.015643.

Distribution and habitat. Tonle Sap Lake at Kampong Chhnang, Siem Reap and Kampong Thom Provinces, Sen River in Kampong Thom Province, Sangkae River in Battambang Province, Chi Kraeng River and Kralanh River in Siem Reap Province, Tonle Sap River in Kandal Province (locality no. 3, 7, 8, 12, 13, 21, 23, 24, 30, 36, 40 and 44); in soft muddy substrate.

Remarks. Not sold for food, collected as by-catch of *Corbicula* and *Mekongia* harvests, and were often observed to be discarded along with other large unionids. The species previously identified as *Ensidens ingallsianus* has recently been revealed as a complex of two species (Muanta et al. 2019), one clade that is restricted to the Chao Praya River basin in Thailand, and another clade from the Tonle Sap and Bang Prakong River basins (Muanta et al. 2019). These two clades could be separated by using the position of the umbo, which is more anterior than in the Tonle Sap clade. As far as we know, there is no other available name for the species from the Tonle Sap basin. Therefore, the name *Ensidens ingallsianus* is herein used until the systematic revision of this species complex is completed.

Hyriopsis bialata (Simpson, 1900)
Fig. 3E

Unio delphinus Gruner, 1841: 276, pl. 9, fig. 1a–c. (non Spengler, 1793) Type locality: “sungi flumine, Malaccae”.
Hyriopsis bialatus Simpson, 1900: 579. (new replacement name for *Unio delphinus*).
Hyriopsis (*Hyriopsis*) *bialatus*: Brandt 1974: 272–273, pl.21, fig. 36.

Material examined. CIFI.MOL.007, CIFI.MOL.008, CIFI.MOL.009, MUMNH.UNI.2618, MUMNH.UNI.2622, MUMNH.UNI.2627, MUMNH.UNI.2630, MUMNH.UNI.2635, MUMNH.UNI.2650, MUMNH.UNI.2652, MUMNH.UNI.2658, MUMNH.UNI.2662, ZRC.MOL.015644.

Distribution and habitat. Tonle Sap River in Kampong Chhnang Province and Tonle Sap Lake at Kampong Chhnang and Siem Reap Provinces, Sen River in Kampong Thom Province, Sangkae River, Battambang Province (locality no. 8, 11, 16, 23, 27, 36, 37, 38 and 40); in soft muddy substrate.

Remarks. Not sold for food, collected as by-catch of *Corbicula* and *Mekongia* harvests, and were often observed to be discarded along with other large unionids. At some parts of the Tonle Sap Lake, shells of *Hyriopsis bialata* were often covered in mats of *Limnoperna fortunei* and *Sinomytilus harmandi*. *Hyriopsis bialata* is widespread in Indochina, from Thailand to Peninsular Malaysia, and along the middle Mekong basin to the Mekong Delta in southern Vietnam (Brandt 1974). Recent molecular analyses have revealed cryptic divergence in *Hyriopsis bialata* based on specimens from peninsular Malaysia and the Chao Phraya and Mekong basins (Zieritz et al. 2016). Pending systematic revision of this species complex, the name *Hyriopsis bialata* is herein used for the species in Cambodia.

Hyriopsis delaportei (Crosse & Fischer, 1876)
Fig. 3F

Unio (*Arconaia*) *delaportei* Crosse & Fischer, 1876: 327–329, pl. 10, fig. 1, pl. 11, fig. 5. Type locality: “Cambodge, dans la province de Compong-Soai”.

Hyriopsis (*Hyriopsis*) *delaportei*: Brandt 1974: 273–274, pl. 21, fig. 37.

Material examined. CIFI.MOL.025, CIFI.MOL.026, MUMNH.UNI.2623, MUMNH.UNI.2628, MUMNH.UNI.2631, MUMNH.UNI.2653, ZRC.MOL.015645.

Distribution and habitat. Tonle Sap Lake at Kampong Chhnang, Kampong Thom, Pursat and Siem Reap Provinces (locality no. 11, 16, 37 and 38); in soft muddy substrate.

Remarks. Not sold for food, collected as by-catch of *Corbicula* and *Mekongia* harvests, and were often observed to be discarded along with other large unionids. Shells of *Hyriopsis delaportei* were also found to be covered in mats of *Limnoperna fortunei* and *Sinomytilus harmandi*. *Hyriopsis delaportei* was originally described from "Compong Soai; Cambodia" (Morlet 1889). It is abundant in the Tonle Sap Lake and its tributaries. The distribution range outside the country is in Vietnam in the Mekong River delta at An Giang, close to the border with Cambodia (Bogan and Do 2014), and in Thailand at the Satung River, Srakaeo and Kaek River, Pitsanulok, although the latter record remains uncertain (Brandt 1974).

Monodontina cambodjensis **(Petit de la Saussaye, 1865)**

Fig. 3G

Monocondylaea cambodjensis Petit de la Saussaye, 1865: 16, pl. 4, fig. 4. Type locality: "Battabbang, Cambodge".
Pseudodon cambodjensis cambodjensis: Brandt 1974: 269, pl. 19, fig. 28.
Monodontina cambodjensis: Bolotov et al. 2017: 11573.

Material examined. CIFI.MOL.023, CIFI.MOL.024, MUMNH.UNI.2637, MUMNH.UNI.2646, MUMNH.UNI.2659, MUMNH.UNI.2670, ZRC.MOL.015652, ZRC.MOL.015653, ZRC.MOL.015654.

Distribution and habitat. Tonle Sap River in Kampong Chhnang Province, Pursat River in Pursat Province and Sen River in Kampong Thom Province, Chi Kraeng River in Siem Reap Province (locality no. 3, 13, 23 and 33); in soft muddy or sandy substrate.

Remarks. Not sold for food, collected as by-catch of *Corbicula* and *Mekongia* harvests, and were often observed to be discarded along with other large unionids. *Monodontina cambodjensis* has been recorded from Thailand and Cambodia, in several tributaries of the Mekong River (Brandt 1974). Bolotov et al. (2017) resurrected the genus *Monodontina* Conrad, 1853 and used it as a generic name for *Monodontina vondembuschiana* (Lea, 1840) and *Monodontina cambodjensis*. This taxonomic opinion was based solely on molecular evidence, without any morphological revision. *Monodontina cambodjensis* is distinguishable from its similar congener, *Monodontina vondembuschiana*, by its high posterior wing and the rounded triangular shape.

***Physunio micropterus* (Morelet, 1866)**

Fig. 3H

Unio micropterus Morelet, 1866: 63, 64. Type locality: "in torrentibus montanis Cambodiae".

Physunio micropterus: Brandt 1974: 296–297, pl. 25, fig. 60.

Material examined. CIFI.MOL.013, CIFI.MOL.014, CIFI.MOL.015, MUMNH.UNI.2639, MUMNH.UNI.2641, MUMNH.UNI.2656, MUMNH.UNI.2661, MUMNH.UNI.2665, MUMNH.UNI.2667, MUMNH.UNI.2671, ZRC.MOL.015646, ZRC.MOL.015647, ZRC.MOL.015648.

Distribution and habitat. Pursat River in Pursat Province, Sangkae River in Battambang Province, Sen River in Kampong Thom Province, Chi Kraeng River and Sreng River in Siem Reap Province (locality no. 7, 13, 22, 23, 27, 30, 32 and 39); in sandy substrate.

Remarks. The distribution of *Physunio micropterus* is restricted to the Tonle Sap basin. There are some reports outside its endemic range, such as in the Ping and Prachinburi rivers in Thailand, but these distributions need to be confirmed (Brandt 1974). Some specimens have been collected from Sai Khao river in Chanthaburi, Thailand (E Jeratthittikul, unpublished data), which flows into Cambodia, and finally drains into the Tonle Sap Lake.

***Pilsbryoconcha linguaeformis* (Morelet, 1875)**

Fig. 3I

Anodonta linguaeformis Morelet, 1875: 329, pl. 14, fig. 5. Type locality: "au Cambodje, probablement dans les marécages voisins de Battambang".

Pilsbryoconcha linguaeformis: Simpson 1900: 587.

Pilsbryoconcha exilis linguaeformis: Brandt 1974: 265.

Material examined. MUMNH.UNI.2616, MUMNH.UNI.2619, MUMNH.UNI.2624, MUMNH.UNI.2625, MUMNH.UNI.2636, MUMNH.UNI.2645 ZRC.MOL.015649, ZRC.MOL.015650, ZRC.MOL.015651.

Distribution and habitat. Pond in Kampong Chhnang Province, Tonle Sap Lake in Kampong Chhnang and Kampong Thom Provinces, Banteay Meanchey Province, Sen River in Kampong Thom Province (locality no. 3, 20, 36, 38, 40, and 42); in soft muddy substrate and swampy grounds.

Remarks. Not sold for food, collected as by-catch of *Corbicula* and *Mekongia* harvests, and were often observed to be discarded along with other large unionids. Distribution range of this species seems to be limited to the Tonle Sap basin. Brandt (1974) treated "*linguaeformis*" as a subspecies of *Pilsbryoconcha exilis* (Lea, 1838). Some authors included "*linguaeformis*" as a junior synonym of *Pilsbryoconcha carinifera* (Conrad, 1837) (e.g., Haas 1969). However, it differs from *Pilsbryoconcha exilis* and *Pilsbryoconcha carinifera* by the greater height of the posterior end.

Pilsbryoconcha lemeslei **(Morelet, 1875)**

Fig. 3J

Anodonta lemeslei Morelet, 1875: 328, pl. 14, fig. 1. Type locality: "Cambodge".
Pilsbryoconcha lemeslei: Brandt 1974: 263, pl. 18, fig. 22.

Material examined. MUMNH.UNI.2669

Distribution and habitat. Tributary of Tonle Sap Lake near Preah Tis Bridge in Chi Kraeng District, Siem Reap Province (locality no. 13); in soft muddy substrate of still water.

Remarks. This species is rare and known only from few places in Thailand, Laos, Cambodia and Vietnam (Brandt 1974; Do et al. 2018). It differs from other *Pilsbryoconcha* species by having a narrower and elongated shell, and more rounded posterior end.

Scabies mandarinus **(Morelet, 1864)**

Fig. 3K

Unio mandarinus Morelet, 1864: 159. Type locality: "Cochinchina".
Scabies crispata: Brandt 1974: 281–282, pl. 20, fig. 33.
Scabies mandarinus: Pfeiffer et al. 2018: 403–413.

Material examined. CIFI.MOL.001, CIFI.MOL.002, CIFI.MOL.003, CIFI.MOL.004, CIFI.MOL.004, CIFI.MOL.005, CIFI.MOL.006, MUMNH.UNI.2620, MUMNH.UNI.2632, MUMNH.UNI.2638, MUMNH.UNI.2640, MUMNH.UNI.2643, MUMNH.UNI.2647, MUMNH.UNI.2654, MUMNH.UNI.2663, MUMNH.UNI.2664, MUMNH.UNI.2672, ZRC.MOL.015655, ZRC.MOL.015656.

Distribution and habitat. Tonle Sap Lake open area in Banteay Meanchey and Siem Reap Provinces, Tonle Sap River in Siem Reap Province and Chhnok Tru landing point, Sangkae River in Battambang Province, Pursat River in Pursat Province, Tang Krasang River in Kampong Thom Province, Sreng River in Siem Reap Province (locality no. 2, 3, 7, 8, 12, 24, 27, 30, 32, 36 and 38); in soft muddy and sandy substrate.

Remarks. *Scabies mandarinus* was described by Morelet in 1864, based on specimens collected from "Cochinchina". This name was previously placed as a junior synonym under *Scabies scobinatus* (Lea, 1856) and *Scabies crispata* (Gould, 1843) (e.g., Haas 1969; Brandt 1974). Based on molecular phylogeny data, Pfeiffer et al. (2018) revealed a distinct clade of Parreysiinae from Mekong delta and eastern gulf of Thailand and resurrected the name *Scabies mandarinus* for this clade. Jeratthitikul et al. (2019a) later included *Scabies* populations from the Tonle Sap basin into this species, based on molecular data and shell morphology.

Class Gastropoda Cuvier, 1795

Subclass Caenogastropoda Cox, 1960
Order Architaenioglossa Haller, 1890
Superfamily Ampullarioidea Gray, 1824
Family Ampullariidae Gray, 1824

Pila gracilis (Lea, 1856)
Fig. 5A

Ampullaria gracilis Lea, 1856: 110. Type locality: "Siam".
Pila gracilis: Brandt 1974: 51–52, pl. 6, fig. 84.

Material examined. ZRC.MOL.015669, ZRC.MOL.015670, ZRC.MOL.015690, ZRC.MOL.015673, ZRC.MOL.015677.

Distribution and habitat. Tonle Sap River, Tonle Sap Lake open areas, and small ponds and paddy fields in the provinces surrounding the Lake (locality no. 4, 7, 9, 10, 24 and 28).

Remarks. The first record of this species from Cambodia was from the Kampong Svay District in Kampong Thom Province (Crosse and Fischer 1876), which is slightly to the north of the Tonle Sap basin. This species is widely distributed in southern Thailand to central Malay peninsula, very rare in eastern Thailand, and also known from southern Vietnam (Brandt 1974; Ng et al. in press). *Pila gracilis* seemed to be rare in the eastern Thai provinces that border Cambodia (Ng et al. in press) but appears to be common in the Tonle Sap basin. Although *Pila gracilis* was not previously recorded as being harvested from the Tonle Sap Lake (Ngor et al. 2016, 2018d), we recorded *Pila gracilis* being sold together with *Pila pesmei* (Morlet, 1889) and *Pila virescens* (Deshayes, 1824) at one landing site in Kampong Chhnang Province, and collected *Pila gracilis* and *Pila virescens* from within the Lake.

Pila pesmei (Morlet, 1889)
Fig. 5B

Ampullaria pesmei Morlet, 1899: 185, pl. 8, fig. 2. Type locality: "Phnom-Penh (Cambodge)".
Pila pesmei: Brandt 1974: 51, pl. 5, figs 70, 71.

Material examined. ZRC.MOL.015671.

Distribution and habitat. Tonle Sap open area (locality no. 38).

Remarks. Although *Pila pesmei* is widely distributed in Eastern and Northeastern Thailand (Ng et al. in press), the species does not appear to be as widespread as *Pila gracilis* in the Tonle Sap basin, especially during the dry season when our surveys were conducted. It is also uncertain if the species is still extant at its type locality of Phnom Penh.

Pila pesmei is harvested in abundance from the Tonle Sap Lake in the rainy season, with more than 380 tonnes recorded at five commercial landing sites in Kampong Chhnang Province within one year (as *Pila ampullacea* (Linneaus, 1758) in Ngor et al. 2016, 2018d). *Pila pesmei* may be confused with *Pila gracilis* owing to morphological similarity among some populations (Ng et al. in press), and further extensive examination of both species in Cambodia would be necessary to resolve the true distribution of both species in the country. The *Pila pesmei* morph from Tonle Sap Lake have relatively flat spires, compared to those in Thailand (Ng et al. in press), and appear to also be found in Southern Vietnam (as *Pila erythrochila* (Dautzenberg & Fischer, 1905) in Ng et al. 2019).

Pila virescens (Deshayes, 1824)

Fig. 5C

Ampullaria virescens Deshayes, 1824: un-numbered plate. Type locality: unknown.
Pila polita: Brandt 1974: 49, pl. 3, fig. 57.

Material examined. CIFI.MOL.010, ZRC.MOL.015681, ZRC.MOL.015682, ZRC.MOL.015683, ZRC.MOL.015684, ZRC.MOL.015685, ZRC.MOL.015686, ZRC.MOL.015687, ZRC.MOL.015688, ZRC.MOL.015689.

Distribution and habitat. Tonle Sap River and Lake, paddy fields and irrigation ponds in Kampong Chhnang, Banteay Meanchey and Siem Reap Provinces (locality no. 3, 13, 14, 18, 35, 38 and 42).

Remarks. *Pila virescens* is the largest among the native ampullariids, and commonly harvested for food (Fig. 4D), and is often sold in markets and roadside stalls. An annual harvest of more than 1500 tonnes of the species was recorded from five commercial landing points in Kampong Chhnang Province (Ngor et al. 2018d).

Pomacea maculata Perry, 1810

Fig. 5D

Pomacea maculata Perry, 1810: unnumbered plate and text. Type locality: Paraná, Argentina (see discussion in Hayes et al. 2012).

Material examined. CIFI.MOL.037, ZRC.MOL.015691, ZRC.MOL.015695, ZRC.MOL.015692, ZRC.MOL.015693, ZRC.MOL.015694.

Distribution and habitat. Tonle Sap River and Lake, and paddy fields in Banteay Meanchey and Kampong Thom Provinces (locality no. 1, 2, 5, 7, 15, 22, 38, 40, and 44).

Remarks. Unlike *Pila* species, *Pomacea maculata* is not native to Southeast Asia. *Pomacea maculata* (as *Pomacea insularum* d'Orbigny, 1835 in Hayes 2008), and another species, *Pomacea canaliculata* (Lamarck, 1822), have both been introduced to Asia from South America (Hayes et al. 2012; Joshi et al. 2017). Molecular methods are the most accurate way to distinguish between them (Rama Rao et al. 2018), and DNA

Figure 4. Freshwater mollusc fisheries at the Tonle Sap Lake, Cambodia. Small-scale harvesting of freshwater molluscs **A** *Corbicula* spp. and **B** *Mekongia rattei*, at open areas of the Lake. Freshwater molluscs **C** *Corbicula* spp. and **D** *Pila* spp., being sorted and packed at main landing sites around the Lake. Photographs by A Pholyotha (**A, B**), TH Ng (**C**), PB Ngor (**D**).

barcodes of two individuals from the Tonle Sap basin were a match to *Pomacea maculata* (GenBank Accession No. MT372328, MT372329). Because of the morphological similarity between the two species, some records of *Pomacea canaliculata* in Southeast Asia, including in Cambodia, may instead have been of *Pomacea maculata* (see Cowie and Hayes 2012). *Pomacea* species were first recorded in Cambodia only in the mid-1990s (compared to early 1980s in neighbouring Thailand), and even then, had only been collected from three localities (Cowie 1995). From then onwards, *Pomacea* spp. may have spread because these snails were mistaken for native ampullariids and were translocated to paddy fields in attempts to breed them for food – unfortunately, *Pomacea* spp. became pests that destroyed the crops instead (Khay et al. 2018). At present, *Pomacea maculata* appears to be widespread in the Tonle Sap basin.

Superfamily Viviparoidea Gray, 1847
Family Viviparidae Gray, 1847

Filopaludina martensi cambodjensis **(Mabille & Le Mesle, 1866)**
Fig. 5E

Paludina cambodjensis Mabille & Le Mesle, 1866: 135, pl. 7, fig. 4. Type locality: “Moth-Kasa, dans les marais”.

Filopaludina (*Siamopaludina*) *martensi cambodjensis*: Brandt 1974: 28, pl. 2, fig. 24.

Material examined. CIFI.MOL.033, CIFI.MOL.041, ZRC.MOL.015715, ZRC.MOL.015716, ZRC.MOL.015717, ZRC.MOL.015718, ZRC.MOL.015719, ZRC.MOL.015720, ZRC.MOL.015721, ZRC.MOL.015722, ZRC.MOL.015723, ZRC.MOL.015724, ZRC.MOL.015725, ZRC.MOL.015726, ZRC.MOL.015727, ZRC.MOL.015728, ZRC.MOL.015729, ZRC.MOL.015730, ZRC.MOL.015731, ZRC.MOL.015732, ZRC.MOL.015733.

Distribution and habitat. Tonle Sap River and Lake, and surrounding watershed including rivers, irrigation ponds and paddy fields (locality no. 1, 2, 3, 5, 8, 9, 10, 11, 12, 13, 16, 17, 19, 20, 21, 22, 24, 32, 37, 38, 40, 42 and 44).

Remarks. *Filopaludina martensi cambodjensis* is said to be lacking in spiral ridges compared to *Filopaludina martensi martensi* (Frauenfeld, 1865) (see Brandt 1974), but our specimens showed some variation, with some displaying ridges. The validity of the various *Filopaludina martensi* subspecies have not been investigated in detail to date. The species is sold in local markets, but did not appear to be harvested in as large quantities as *Mekongia rattei* (Crosse & Fischer, 1876), and its annual harvest at five main landing points in Kampong Chhnang Province has previously been recorded to be 68 tonnes, only ca. 1/5th of the *Mekongia swainsoni* (Lea, 1856) that were obtained (Ngor et al. 2016).

Idiopoma umbilicata (Lea, 1856)

Fig. 5F

Paludina umbilicata Lea, 1856: 109. Type locality: "Takrong River, Siam".
Idiopoma umbilicata: Brandt 1974: 34–35, pl. 2, fig. 35.

Material examined. ZRC.MOL.015734, ZRC.MOL.015735, ZRC.MOL.015736, ZRC.MOL.015737, ZRC.MOL.015738, ZRC.MOL.015739, ZRC.MOL.015740, ZRC.MOL.015741, ZRC.MOL.015742.

Distribution and habitat. Tonle Sap Lake and tributaries at Kampong Chhnang, Battambang, Siem Reap and Kampong Thom Provinces, irrigation ponds and paddy fields at Banteay Meanchey and Siem Reap Provinces (locality no. 7, 13, 24, 29 and 39).

Remarks. *Idiopoma umbilicata* is often found together with *Filopaludina martensi cambodjensis* and can be differentiated from the latter species by its smaller size and shouldered shells. It does not appear to be harvested for food.

Mekongia rattei (Crosse & Fischer, 1876)

Fig. 5G

Paludina rattei Crocsse & Fischer, 1876: 317. Type locality: "Stung Chinit, Cambodia".

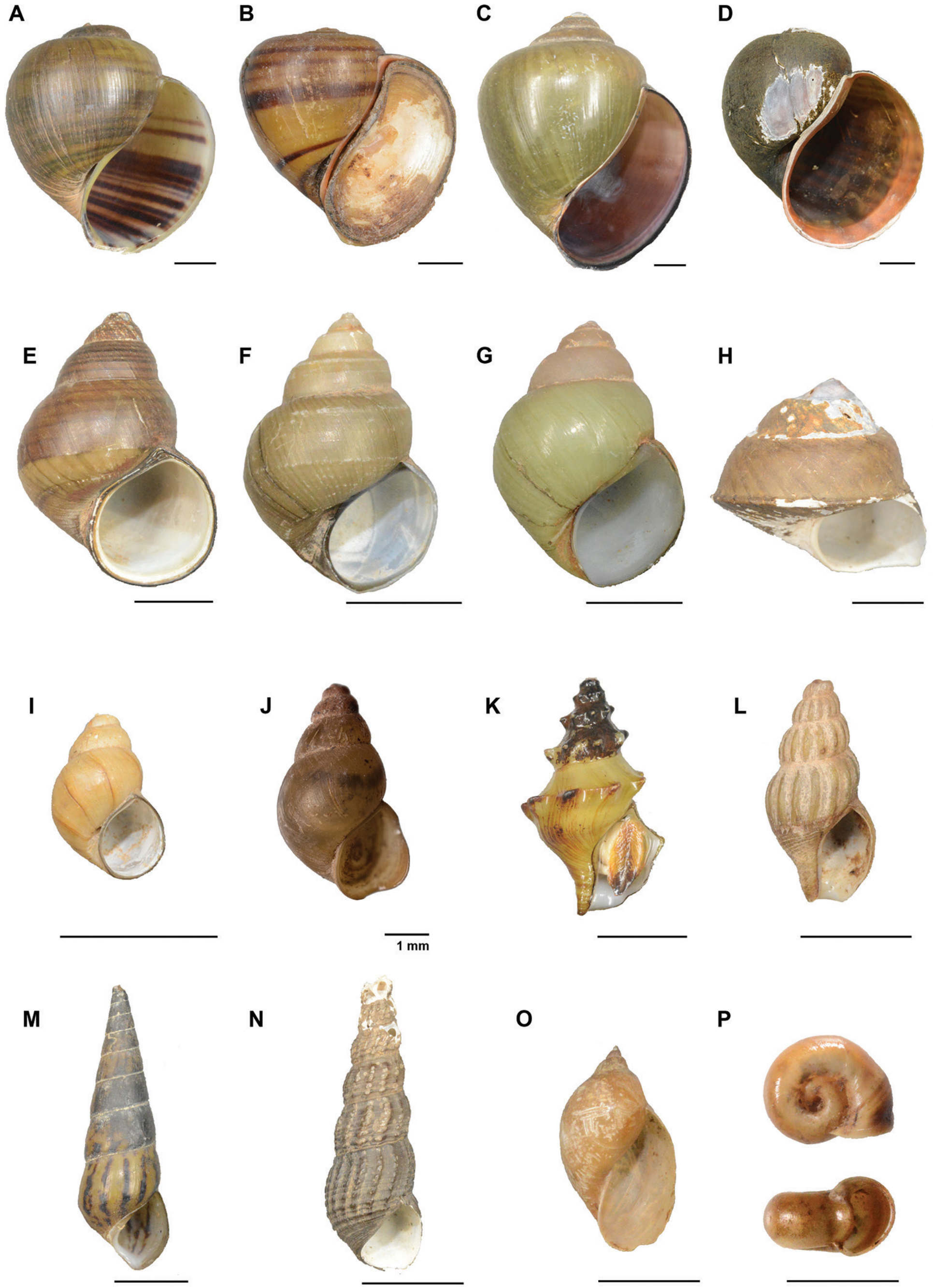

Figure 5. Freshwater gastropods of the Tonle Sap basin, Cambodia **A** *Pila gracilis* **B** *Pila pesmei* **C** *Pila virescens* **D** *Pomacea maculata* **E** *Filopaludina martensi cambodjensis* **F** *Idiopoma umbilicata* **G** *Mekongia rattei* **H** *Trochotaia trochoides* **I** *Bithynia siamensis goniomphalus* **J** *Wattebledia siamensis* **K** *Anentome cambojiensis* **L** *Anentome helena* **M** *Sulcospira housei* **N** *Melanoides tuberculata* **O** *Indoplanorbis exustus* and **P** *Radix rubiginosa*. Scale bars: 10 mm, unless stated otherwise. Photographs by TH Ng.

Mekongia rattei: Brandt 1974: 44–45, pl. 3, figs 51, 52.

Material examined. CIFI.MOL.042, MUMNH.VIV.001, MUMNH.VIV.002, MUMNH.VIV.003, ZRC.MOL.015744, ZRC.MOL.015745, ZRC.MOL.015743.

Distribution and habitat. Tonle Sap Lake; Chi Kraeng River and Sreng River in Siem Reap Province; Phumi Phsar River in Kampong Chhnang Province (locality no. 7, 8, 11, 13, 16, 20, 24, 27, 36, 37 and 39).

Remarks. *Mekongia rattei* is sold in local markets surrounding the Lake. This species along with *Corbicula* spp. are commercially harvested from the Lake to be sold locally and exported abroad for human consumption and as animal feed in local poultry farms (Fig. 4B). Another record of *Mekongia* from the Tonle Sap basin and surrounding drainages is *Mekongia swainsoni* (see Brandt 1974; Ngor et al. 2018d). *Mekongia rattei* differs from *Mekongia swainsoni* by its larger size and conic shape of spire.

Trochotaia trochoides (Martens, 1860)

Fig. 5H

Paludina trochoides Martens, 1860: 12. Type locality: "Siam".
Trochotaia trochoides: Brandt 1974: 32–33, pl. 2, figs 32, 33.

Material examined. CIFI.MOL.034, ZRC.MOL.015746.

Distribution and habitat. Paddy fields at Banteay Meanchey Province (locality no. 7).

Remarks. We found only a few dry shells in the northwestern province of Banteay Meanchey, close to the Thai border. The species was also occasionally encountered for sale at local markets.

Order Littorinimorpha Golikov & Starobogatov, 1975
Superfamily Truncatelloidea Gray, 1840
Family Bithyniidae Gray, 1857

Bithynia siamensis goniomphalus (Morelet, 1866)

Fig. 5I

Paludina goniomphalos Morelet, 1866: 167. Type locality: "Cochinchina".
Bithynia (*Digoniostoma*) *siamensis goniomphalus*: Brandt 1974: 60, pl. 4, fig. 68.

Material examined. CIFI.MOL.040, ZRC.MOL.015696, ZRC.MOL.015697, ZRC.MOL.015698, ZRC.MOL.015699, ZRC.MOL.015700, ZRC.MOL.015701.

Distribution and habitat. Found at the edges of Tonle Sap River and Lake, ponds and in paddy fields at Kampong Chhnang, Banteay Meanchey, and Siem Reap Provinces (locality no. 3, 4, 8, 11, 16, 40, 42, 43, and 44).

Remarks. *Bithynia siamensis goniomphalus* is of medical importance because it is an intermediate host of the zoonotic parasite, *Opisthorchis viverrini* (Poirier, 1886)

(TROPMED Medical Group 1986). The role of *Bithynia siamensis goniomphalus* in the transmission of this parasite in Cambodia has not been investigated in detail, although the parasite has been recorded in freshwater fishes at the border of the Kandal-Takeo Provinces in the south (Touch et al. 2009), and cases of human infections are well-studied throughout the country (Sithithaworn et al. 2012).

Wattebledia siamensis **Möllendorff, 1902**

Fig. 5J

Wattebledia siamensis Möllendorff, 1902: 160. Type locality: "Siam".
Wattebledia siamensis: Brandt 1974: 64–65, pl. 5, figs 78, 79.

Material examined. ZRC.MOL.016325

Distribution and habitat. Found among floating vegetation along the banks of the Tonle Sap River (locality no. 44).

Remarks. This is the first record of the species in Cambodia, and the species is known throughout Thailand (Brandt 1974). It could probably be more widespread along with the larger congeneric species, *Wattebledia crosseana* (Wattebled, 1886), which has previously been recorded from Cambodia (Brandt 1974).

Order Neogastropoda Wenz, 1938
Superfamily Buccinoidea Rafinesque, 1815
Family Nassariidae Iredale, 1916 (1835)

Anentome cambojiensis **(Reeve, 1861)**

Fig. 5K

Melania cambojiensis Reeve, 1861: *Melania* species 468, pl. 59. Type locality: "Cambojia".
Clea (*Anentome*) *cambojiensis*: Brandt 1974: 202.

Material examined. CIFI.MOL.039, ZRC.MOL.015708, ZRC.MOL.015709, ZRC.MOL.015710, ZRC.MOL.015711, ZRC.MOL.015712, ZRC.MOL.015713, ZRC.MOL.015714.

Distribution and habitat. Tonle Sap Lake; on muddy substrate (locality no. 8, 11, 12, 17 and 37).

Remarks. The type specimen of *Anentome cambojiensis* was collected by Henri Mouhot (Reeve 1861) and appears to be endemic to the Tonle Sap basin. Its range may extend to eastern Thailand in Rayong (Morlet 1889), although later surveys have not recorded this species beyond Cambodia (Brandt 1974) and we did not find it in tributaries around the Lake. Brandt (1974) also did not find the species after surveying 'the banks of Tonle Sap carefully', but we found it to be common and widespread throughout the Lake. Locals know the species to be carnivorous or a scavenger, and we found it around dead branches that are stuck into the mud to attract shrimp.

Anentome helena **(von dem Busch in Philippi, 1847)**

Fig. 5L

Melania helena von dem Busch in Philippi, 1847: 170, pl. 4, fig. 4. Type locality: Java.
Clea (*Anentome*) *helena*: Brandt 1974: 201–202, pl. 15, figs 64, 65.

Material examined. CIFI.MOL.035, ZRC.MOL.015702, ZRC.MOL.015703, ZRC.MOL.015704, ZRC.MOL.015705, ZRC.MOL.015706, ZRC.MOL.015707.

Distribution and habitat. Tonle Sap River, Lake and surrounding tributaries, irrigation ponds and canals (locality no. 2, 7, 8, 10, 11, 13, 16, 17, 21, 22, 24, 25, 26, 34, 38, 40, 41, 42, and 44).

Remarks. The species recognised as *Anentome helena* in Indo-China may in fact be a complex of three species (Strong et al. 2017), however further studies need to be conducted to determine which clade the Cambodian ones belong to. Pending systematic revision of this taxon, the name *Anentome helena* is herein used for the species in Cambodia. *Anentome helena* may be found in similar habitats as *Anentome cambojiensis* in the Lake but does not occur in as high numbers as the latter species. Beyond the Lake, it was commonly found in tributaries and other water bodies.

Cohort Sorbeoconcha Ponder & Lindberg, 1997

Superfamily Cerithioidea J. Fleming, 1822

Family Pachychilidae Fischer & Crosse, 1892

Sulcospira housei **(Lea, 1856)**

Fig. 5M

Melania housei Lea, 1856: 144–145. Type locality: “Korat, Takrong River, Siam”.
Adamietta housei: Brandt 1974: 171–172, pl. 12, fig. 24.

Material examined. CIFI.MOL.043, ZRC.MOL.015748, ZRC.MOL.015749.

Distribution and habitat. Tonle Sap River, Sangkae River in Battambang Province, canal in Kampong Thom Province (locality no. 1, 2, 26, 38, 41, 43 and 44).

Remarks. *Sulcospira housei* is widespread in neighbouring Thailand (Brandt 1974) and based on our study and past records (Crosse and Fischer 1876; Morlet 1889), appears to be widely distributed in Cambodia also, from around the Tonle Sap basin to the south in Kampot Province.

Family Thiaridae Gill, 1871 (1823)

Melanoides tuberculata **(OF Müller, 1774)**

Fig. 5N

Nerita tuberculata OF Müller, 1774: 191. Type locality: “In littore Coromandel”.
Melanoides tuberculata: Brandt 1974: 164–166, pl. 12, figs 9–12.

Material examined. CIFI.MOL.036, ZRC.MOL.015747, ZRC.MOL.015750, ZRC.MOL.015751, ZRC.MOL.01572.

Distribution and habitat. Tonle Sap Lake and Thliem Ma-Orm River in Pursat Province (locality no. 11, 12, 20, 27 and 35).

Remarks. *Melanoides tuberculata* has a global distribution but was not found to be common in the Tonle Sap basin during our surveys.

Subclass Heterobranchia Burmeister, 1837
Superorder Hygrophila Férussac, 1822
Family Bulinidae P. Fischer & Crosse, 1880

Indoplanorbis exustus (Deshayes, 1833)
Fig. 5O

Planorbis exustus Deshayes, 1833: 417, pl. 1, figs 11–13. Type locality: "Lieux man~cagieux de la cote de Malabar".
Indoplanorbis exustus: Brandt 1974: 234–235, pl. 16, fig. 99.

Material examined. ZRC.MOL.016324.

Distribution and habitat. Dry shells found at a lotus pond in Banteay Meanchey Province (locality no. 5).

Remarks. *Indoplanorbis exustus* has been recorded from Cambodia since the 1800s (Mabille and Le Mesle 1866; Crosse and Fischer 1876; Brandt and Temcharoen 1971), and although it was only collected from one locality during our surveys, the species is known to occur in paddy fields or shallow, ephemeral ponds across its distribution in Asia (Liu et al. 2010). The cosmopolitan species is an intermediate host of several zoonotic parasites (Liu et al. 2010).

Family Lymnaeidae Rafinesque, 1815

Radix rubiginosa (Michelin, 1831)
Fig. 5P

Lymnoeus rubiginosus Michelin, 1831: Moll. no. 22, pl. 22. Type locality: "Indes Orientales" (from Brandt 1974).
Lymnaea (*Radix*) *auricularia rubiginosa*: Brandt 1974: 229–230, pl. 16, fig. 95.

Material examined. ZRC.MOL.015753, ZRC.MOL.015754.

Distribution and habitat. At the edges of irrigation ponds and swampy grounds in Banteay Meanchey Province (locality no. 3).

Remarks. *Radix rubiginosa* is a cosmopolitan species, widely distributed from Indo-China to Sundaland (Hubendick 1951; Brandt 1974) and is known to be a host of numerous zoonotic parasites (Brandt 1974; TROPMED Medical Group 1986). However, we only encountered the species at one locality.

Discussion

Many of the 19th to early 20th century descriptions and records of freshwater molluscs from Cambodia were collected by expeditions, sponsored or led by the French, including those by the renowned traveller Henri Mouhot and the diplomat Auguste Pavie, and also by missionaries based in the country (e.g., Reeve 1861; Morelet 1865; Morlet 1889; Breure et al. 2018). The Tonle Sap Lake and surrounding watershed (e.g., Battambang) were specified as the collection locality or habitat of 33 species (Suppl. material 1: Table S1), with 20 of those species being collected from the Tonle Sap basin in our study. The family with the greatest number of species in the historical records for Cambodia, i.e., Pomatiopsidae, were previously recorded from the Mekong River only, which was not surveyed in this study. The absence of the specimens or figures in the literature prevents us from verifying the past records to check for misidentifications or taxonomic confusion, and some, for instance the *Corbicula* species, may be the same taxa that we collected. In any case, the outcome of our limited surveys recording 31 species of freshwater molluscs, including three new records for Cambodia (*Scaphula minuta*, *Novaculina siamensis*, and *Wattebledia siamensis*), appears to be the most comprehensive documentation for the Tonle Sap basin to date. In addition, the voucher specimens that we have deposited in the collection at IFReDI of the Fisheries Administration of Cambodia, represents the first known reference collection of freshwater molluscs in the country.

Our surveys have revealed that there remains much to be done in resolving the taxonomy and systematics of freshwater molluscs in Cambodia. In addition to the four species of Viviparidae that were highlighted in the Results as requiring taxonomic revision, many other taxa have not been collected or studied closely since the species were described, including the Cyrenidae, Nassariidae, and the speciose Pomatiopsidae (Suppl. material 1: Table S1). The Ampullariidae are also in need of taxonomic resolution as some records dating back to the 19th century, e.g., *Ampullaria borneensis* Philippi, 1852 and *Ampullaria malabarica* Philippi, 1852, that have been synonymised with species not recognised as being distributed in Cambodia, i.e., *Pila scutata* (Mousson, 1848) and *Pila virens* (Lamarck, 1822), respectively (Cowie 2015).

Aside from the taxonomic confusion, the Ampullariidae of Tonle Sap Lake are extremely unique in terms of the high volume of production for *Pila* species being harvested from Tonle Sap Lake, compared to elsewhere in Southeast Asia, where the native ampullariids appear to be declining whilst invasive confamilial *Pomacea* species are increasing (Marwoto and Isnaningsih 2011; Ng et al. 2019, in press). *Pila virescens* is also a popular food item in neighbouring Thailand, but has extremely low genetic diversity across different populations, characteristic of species that have experienced anthropogenic translocations (Ng et al. in press). It is therefore important to conduct further research on the genetic diversity and ecology of *Pila* species within the Tonle Sap basin, especially as *Pomacea* species are to be increasing in number and spreading rapidly throughout Cambodia (Khay et al. 2018). In addition, the building of hydropower dams (i.e., reservoirs) and the change in flow of the Mekong appear to be creating new habitats that are rapidly being colonised by *Pomacea* spp. (Ngor PB, pers. obs.).

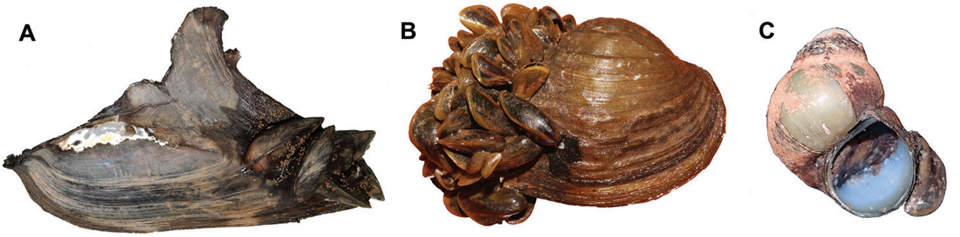

Figure 6. Mytilid colonies from Tonle Sap Lake, Cambodia growing on the shells of other freshwater molluscs **A** *Hyriopsis bialata* **B** *Contradens contradens* **C** *Mekongia rattei*. Photographs by A Pholyotha (**A, B**) and TH Ng (**C**).

Although the mytilid mussels are assumed to be native to Cambodia, *Limnoperna fortunei* in particular, has the potential to be classified as a pest species. The mixed species colonies of *Limnoperna fortunei*, and to a lesser extent, *Sinomytilus harmandi*, have byssus threads that form dense mats, not only on hard man-made surfaces, but also on the shells of unionid mussels and gastropods (Fig. 6). Aggregations of *Limnoperna fortunei* and similarly byssate *Dreissena polymorpha* on unionids have been recorded to prevent the biological functions of the attached hosts, for e.g. *Hyriopsis bialat*a, *Hyriopsis delaportei*, and *Contradens contradens*, causing difficulties to open their valves for feeding and respiration (Karatayev et al. 2007). We observed that many unionids at edges of the Tonle Sap Lake that were particularly stagnant and covered in cyanobacteria, to be infested with the mats of mytilids (e.g., at locality no. 8, 11, and 12), especially during the dry season.

Indeed, the comtemporary Mekong River system is now at a critical point in time, facing challenges of regional development, particularly the increasing numbers of hydropower dams, which alter the timing, magnitude and frequencies of seasonal flow of the tropical flood-pulse system. Such flow alterations have been demonstrated to dampen the seasonal flood pulses (Cochrane et al. 2014) and reduce the hydro-periods as well as the open water area of the Tonle Sap Lake (Lin and Qi 2017), which supports one of the world's largest inland fisheries (Ngor et al. 2018c). Aquatic fauna, such as freshwater fishes and molluscs, are among those that will be adversely impacted by the changes owing to the likely effects on their dispersal ability, reproductive success and rearing conditions (Ziv et al. 2012; Winemillers et al. 2016; Sabo et al. 2017; Ngor et al. 2018a, d). Combined with other anthropogenic effects in the Tonle Sap basin such as floodplain infrastructure development (Arias et al. 2019), overfishing (Ngor et al. 2018c; McCann et al. 2016), invasive species (e.g., *Pomacea* spp.), land cover change (e.g., habitat degradation) and climate change (Arias et al. 2014; Ngor et al. 2018b; Daly 2019), the future of these resources is in a precarious condition.

Our checklist is the first step toward more extensive research on freshwater molluscs in the Tonle Sap basin. It is imperative that more surveys of freshwater molluscs be conducted across different wet and dry seasons to allow for a better representation of the fauna to be captured, along with baseline data of the populations and ecology of the species to be documented. The presence of globally-invasive species like *Pomacea maculata*, and the prevalence of pest species like *Limnoperna fortunei*, which have the potential to replace and negatively impact the ecosystem and native species of the Tonle Sap basin is another major concern. In order to combat the combined pressures of invasive species, land cover change, climate change, dams along the main stem and tributaries of the Mekong River, among many other anthropogenic threats (Ngor et al. 2018b; Uk et al. 2018; Daly 2019), a multi-pronged approach is urgently required to study the biodiversity, ecology, ecosystem functioning of freshwater molluscs and other aquatic fauna in the Tonle Sap basin.

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Supplementary material 1

Table S1. Historical records of freshwater molluscs from Cambodia

Authors: Ting Hui Ng, Ekgachai Jeratthitikul, Chirasak Sutcharit, Samol Chhuoy, Kakada Pin, Arthit Pholyotha, Warut Siriwut, Ruttapon Srisonchai, Zeb S Hogan, Peng Bun Ngor

Data type: records

Explanation note: Historical records of freshwater molluscs from Cambodia based on literature review.

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Designation of a neotype for *Mazama americana* (Artiodactyla, Cervidae) reveals a cryptic new complex of brocket deer species

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Abstract

Mazama americana (red brocket deer) is the genus-type species (first species described for this genus) and the basis for the identity of other *Mazama* species. *Mazama americana* is one of the most abundant and widely distributed deer species in the neotropical forest. However, recent studies suggest that this taxon belongs to a species complex. Our goal was to collect an animal at the type locality (topotype) in French Guiana with the aim of characterizing the morphological (biometric, craniometric), cytogenetic (Giemsa, C-banding, G-banding and NOR) and molecular (mitochondrial DNA) features. The comparisons showed that the collected specimen was very similar morphologically to specimens from other South American populations, but it was cytogenetically and molecularly very different from any of the cytotypes already described for this species, corroborating the existence of a complex of cryptic species. The data suggest that the *M. americana* topotype is a different species from all the cytotypes already described in the literature and which occupy the southern region of the Amazon River. The characterization and designation of the *M. americana* neotype is the first step toward a taxonomic reorganization of the genus *Mazama*, with the potential identification of new species.

Keywords
biodiversity, chromosomes, cytogenetics, French Guiana, mitochondrial DNA, morphology, red brocket deer, topotype

Introduction

The genus *Mazama* Rafinesque, 1817 (Mammalia, Artiodactyla, Cervidae) has 10 species widely distributed throughout the neotropical region (Merino and Rossi 2010). However, there are controversies about the number of species and subspecies that compose the genus. Early taxonomic revisions suggested the existence of 17 species and 11 subspecies (Allen 1915), four species and 10 subspecies (Cabrera 1960), and six species and seven subspecies (Czernay 1987). However, it is suggested that morphology is not an useful tool for discrimination among species, because there is a high degree of homoplasy and morphological convergence (Grooves and Grubb 1987; Duarte et al. 2008; Merino and Rossi 2010; Gonzalez et al. 2016).

Several cytogenetically studied species have shown an extensive intraspecific polymorphism (Taylor et al. 1969; Jorge and Benirschke 1977; Neitzel 1987; Duarte and Jorge 1996; Duarte and Merino 1997; Abril and Duarte 2008; Abril et al. 2010; Valeri et al. 2018). This polymorphism would suggest a rapid speciation process driven by chromosomal rearrangements, with a diploid number of chromosomes ranging between 42 and 52, considered within six geographically established cytotypes (Duarte et al. 2008; Abril et al. 2010). As a result of this chromosomal variation, reproductive isolation has occurred in animals due to sterility problems caused by chromosomal meiosis pairing between different chromosomal lineages (Aquino et al. 2013; Cursino et al. 2014; Salviano et al. 2017). The populations in south-central South America are reproductively isolated from the Amazonian populations, being different species (Cursino et al. 2014; Salviano et al. 2017), that until now have not been described or nominated.

These results have been corroborated by mitochondrial DNA variation, which clearly demonstrates the differences between some populations of *M. americana* Erxleben, 1777 (Duarte et al. 2008, Abril et al. 2010), underlying the importance of research to characterize these taxa. Previous cytogenetic research has identified various *M. americana* cytotypes as potentially valid unamed species, and it is necessary to evaluate karyotypically previously designated names for *Mazama*. Therefore, animals should be sampled in all location types for each of the names currently positioned in the synonym of *M. americana* (Varela et al. 2010).

These taxonomic uncertainties resulted in the species being categorized by the International Union for Conservation of Nature as “deficient data”, since the identity of the current taxon had no value as an evolutionary unit (Duarte and Vogliotti 2016).

The species was described in 1777 by JCP Erxleben, a German naturalist, who is considered to be one of the founders of modern veterinary medicine. He did not collect any specimens; however, he used a series of reports by other authors as a basis for their description, mentioning the following characteristics: "*M. rufo-fufeus, ore nigro, gula alba, auriculae longitudine quatuor pollicum, oculi magni nigri, nares magnae, oris regio nigra, crura poftica longiora anticis, cauda brevis, pili breues mollesque, capitis collique fupra fufci, colli fubtus albi, corporis crurumque rufofufci, vngulae nigrae, timidiffimus, celerrimus, agilis, natat per fluuios, caro bona*". Cayenne, in French Guiana, was considered by Erxleben as the type locality for *M. americana*.

The absence of the species holotype for a more complete morphological and genetic analysis calls for the need to describe a current topotype of the species and to propose a neotype based on it. Thus, in this work we propose a neotype for the species, as well as its morphological and genetic characterization, based on a male specimen collected in French Guiana, near the type locality of the species. In addition, we performed comparisons with the known populations of this species already studied (Duarte et al. 2008; Abril et al 2010). The comparisons demonstrate that none of them belong to the same taxon described by the type location *M. americana*, a revision of the taxonomy of this red brocket complex being required.

Material and methods

Obtaining the animal and samples

An adult male specimen of *M. americana* (Fig. 1) was collected in the city of Régina, French Guiana, 70 km from Cayenne (type locality) on 14/02/2015 by a local hunter. In French Guiana, this species is not protected by law, and can be collected without permit, the requirement being to capture outside protected areas. After collection of the individual, skin biopsies were collected and frozen in liquid nitrogen (Duarte et al. 1999) Muscle and liver samples were taken, as well as the specimen's biometric data. The material analyzed in this study is deposited in the Museum of the Deer Research and Conservation Center (NUPECCE) – at São Paulo State University (UNESP), Jaboticabal campus, Brazil, recorded under catalog number NPC079. In accordance with the "Loi pour la reconquête de la Biodiversité" (2017) and, in compliance with Access and Benefits Sharing (above-mentioned law, titre V, article 37), a tissue sample is also kept in the collection JAGUARS, belonging to Kwata NGO, Cayenne, French Guiana, under the reference M3426_JAG.

Biometry

Eighteen body measurements were taken using a digital caliper (0.05 mm precision) and a measuring tape. Based on these measurements, a statistical analysis of the quantitative data was performed, along with those of 41 *M. americana* individuals (adult males and females) and four individuals of different species used as an external group from the NUPECCE database through cluster analysis using the Paleontological Statistics, PAST 3.20 program (Hammer et al. 2001).

Figure 1. Lateral view of the adult male *Mazama americana* collected in French Guiana and proposed as neotype.

Analysis of the external morphology of the specimen was performed based on criteria used by Rossi (2000), using the photos taken immediately after collection and the entire taxidermized skin. In addition, the chromogenetic fields of the head and body were analyzed according to the nomenclature used by Hershkovitz (1982).

Cranial morphology

Thirty-six cranial measurements were recorded using a digital caliper (0.01 mm accuracy), based on the criteria proposed by Von Den Driesch (1976). A cluster analysis using the PAST program (Hammer et al. 2001) was performed based on quantitative cranial measurements of the specimen collected and of 15 animals (male and female adults) belonging to various *M. americana* cytotypes: one *M. bororo* Duarte, 1996, two *M. gouazoubira* Fisher, 1814 and one *M. nemorivaga* Cuvier, 1817, which are stored in the NUPECCE museum (UNESP/Jaboticabal).

Cytogenetic analysis

Metaphase chromosome slides were prepared from tissue culture (Duarte and Jorge 2003), generated through biopsy according to Verma and Babu (1995). Chromosomal preparations were subjected to conventional Giemsa staining, G-banding using trypsin digestion (Seabright 1971), C-banding by barium hydroxide solution (Sumner 1972) and Ag-RON silver nitrate staining (Howell and Black 1980). The chromosomes were classified as metacentric, submetacentric or acrocentric according to their arm relationships (Levan et al. 1964) and organized into groups according to their relative lengths (CR): Group A (large two-armed chromosomes with CR > 6%); Group C (small two-armed chromosomes with CR < 6%); Group D (large acrocentric chromosomes with CR > 5%); Group E (small acrocentric chromosomes with CR < 5%); and Group B (microcromosomes or extranumerary chromosomes with CR < 1.5%). B chromosomes were not considered in the diploid and fundamental number calculation due to the variability between metaphases of the same individual (Abril et al. 2010). Karyotypes were carried out based on the G-bands, which were used to make the schematic representation of the G-band patterns of the neotype. The cytogenetic data of the neotype were compared with the cytogenetic patterns of the *M. americana* cytotypes. We proposed the chromosomal evolution of the neotype from the hypothetical ancestor suggested by Abril et al. (2010).

DNA extraction, amplification and sequencing

DNA was extracted from a muscle sample following the protocol of Sambrook et al. (1989). The sample was subjected to the PCR technique (Mullis et al. 1986), where two mitochondrial DNA fragments were amplified: cytochrome b (*Cyt-b*,1140 pb; Kocher et al. 1989; Duarte et al. 2008) and a control region (*D-Loop*, 690 bp; Vilà et al. 1999). DNA amplification used a final volume of 20 µl, containing 12 µl of H_2O, 0.5 mM of dNTP, 1X of reaction buffer, 1.5 mM of $MgCl_2$, 0.25 mM of each primer, 0.1 U of Taq polymerase and 3µl of DNA (15 ng/µl). The PCR protocol was 5 min at 94 °C, 35 cycles at 94 °C for 1 min, 54 °C and a final extension of 10 min at 72 °C. PCR products were submitted to 2% agarose gel electrophoresis for amplicon identification. The purification of the amplified samples followed the Dorado–Pérez (2012) protocol. Purified samples were sequenced on an automated Applied Biosystems 3730XL sequencer.

Molecular data analysis

The sense and antisense strands of all amplified fragments of two mitochondrial genes were sequenced. The two complementary strands were aligned, thus obtaining the consensus sequence from the Clustal W program (Higgins et al. 1992) included in Bioedit (Hall 1999). The sequences obtained were organized into a matrix along with all sequences of the *M. americana* species currently published in the GenBank System world databases (Suppl. material 1: Table S1). The best molecular evolution model was selected for the data set of each gene fragment using the jModelTest v. 0.1.1 (Posada and Crandall 1998), following the corrected Akaike information criterion, AICc (Akaike 1973). Sequences for the mitochondrial *Cyt-b* gene were obtained by concatenating data from the two fragments using internal primers L14724 and H15149 for the 3' end and FAR-L and FAR-H for the 5'end, obtaining a 1140-bp fragment.

The phylogenetic relationships between the different *M. americana* populations and the neotype were studied by Bayesian inference analysis (Huelsenbeck and Ronquist 2001), using the program MrBayes on XSEDE 3.2.6 (Ronquist and Huelsenbeck 2003), through the online program CIPRES Science Gateway (Miller et al. 2010).

Bayesian inference analyses were performed using 50,000,000 generations over four chains with two replications, adopting a 25% burn-in discard. To estimate the posterior probability, the Markov Chain Monte Carlo method was used. All trees were edited in the FigTree v. 1.4.0 program (Rambaut 2009). *Rangifer tarandus* Linnaeus, 1758, *Ozotoceros bezoarticus* Linnaeus, 1758 and *Mazama gouazoubira* were used as an external group.

Results

Morphology

The collected animal is presented in Figure 1 and the skull in Figure 2. The biometric and cranial measures are shown in the Suppl. material 2: Tables S2, Suppl. material 3: Tables S3.

Amended description of *Mazama americana* Erxleben, 1777 (Mammalia, Cervidae): Deer with predominant red coat, resembling reddish-brown brick color, gray in the face and neck region. The most intense color tone in the dorsal region. The side region the same tone as the back, slightly paler. The abdominal region the same color as the flanks, slightly brownish. Red tail in the dorsal region the same color as the back, and white in the ventral region. Whitish inguinal, buccal, gular and inner region of the ears. Black-colored posterior limbs in the caudal region, brown in the cranial region, external proximal region the same color as the lateral body region, white internal proximal region, brown external distal region, slightly reddish in the most distal portion, internal distal region also slightly brown, and the most distal portion slightly reddish. The lower and upper orbital bands slightly lighter than the rest of the face. Relatively deep lacrimal fossa. The outer ear surface lightly covered with brown hair. Smooth, varying hair lengths according to the body region, shorter and thinner hair covering the muzzle, the outer and inner surface of the ear (the latter partially hairless), the chin and the distal region of the anterior and posterior limbs. Somewhat longer hairs on the hips and tail. Strip of anteverted hair on dorsal midline of neck with more pigmented, blackened terminal band. Presence of a tuft of hair on the back of the head immediately preceding the horns. Relatively large and thick horns, dorso-caudal inclination, slightly curved and parallel to each other. Horns covered with soft tissue.

Recording location: Régina, French Guiana

Collection point coordinates: 4°19'52"N, 52°07'22"W

Specimen deposited in: Museum of Deer Research and Conservation Center (NUPECCE)–FCAV – São Paulo State University (UNESP) – Jaboticabal Campus.

Classification number: NPC079 (full skull, post skull, and taxidermized skin)

Tissue sample deposited in: JAGUARS collection, Kwata NGO, Cayenne, French Guiana, reference M3426_JAG

DNA sequence deposit numbers: MN726911 (*Cyt-b*), MN726914 (*D-Loop*)

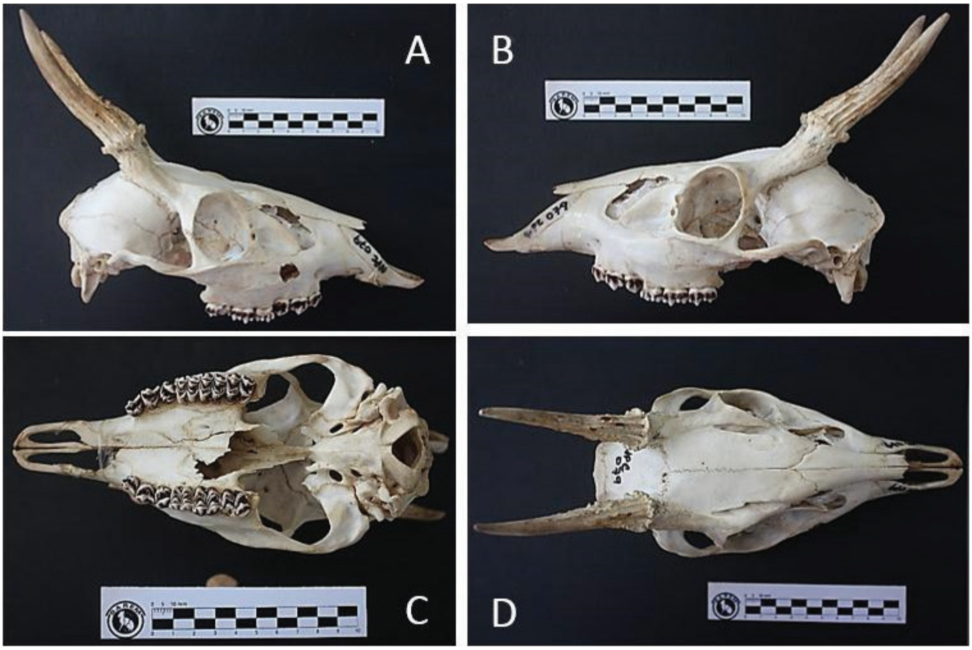

Figure 2. Right lateral (**A**), left lateral (**B**), ventral (**C**) and dorsal (**D**) views of the skull of the *M. americana* neotype. Scale illustrates measurement in centimeters.

Karyotype: 2n = 45 + 3Bs, FN = 51, sexual system XY_1Y_2

Synonymy: Given the cytogenetic and molecular results obtained to date, there is a high probability that several names currently synonymized with *M. americana* are valid names. Therefore, only names given to animals from French Guiana will be considered synonyms of *M. americana*, which are: *Cervus rufus* Cuvier, 1817 and *Mazama pita* Rafinesque, 1817.

The results of the cluster analysis made with body measurements did not reveal morphometric differences between the distinct geographic groups of *M. americana*. The distance tree (Fig. 3) shows substantial overlap between different geographic groups. Specimens from different localities in Brazil are widely scattered across tree branches, despite known to be cytogenetically different. Some specimens of *M. americana* are superimposed on the *M. bororo* sample, showing the morphological proximity between *M. americana* and this already well-established taxon (Duarte and Jorge 2003; Vogliotti and Duarte 2009). The morphological distance tree based on cranial measurements of the individuals shows the same result, with non-differentiation between the red brocket deer specimens and cytotypes (Fig. 4).

Cytogenetics

The collected animal presented a cytogenetic constitution with diploid number (2n) of 45 chromosomes and 51 chromosomal arms (fundamental number, FN). The bio-

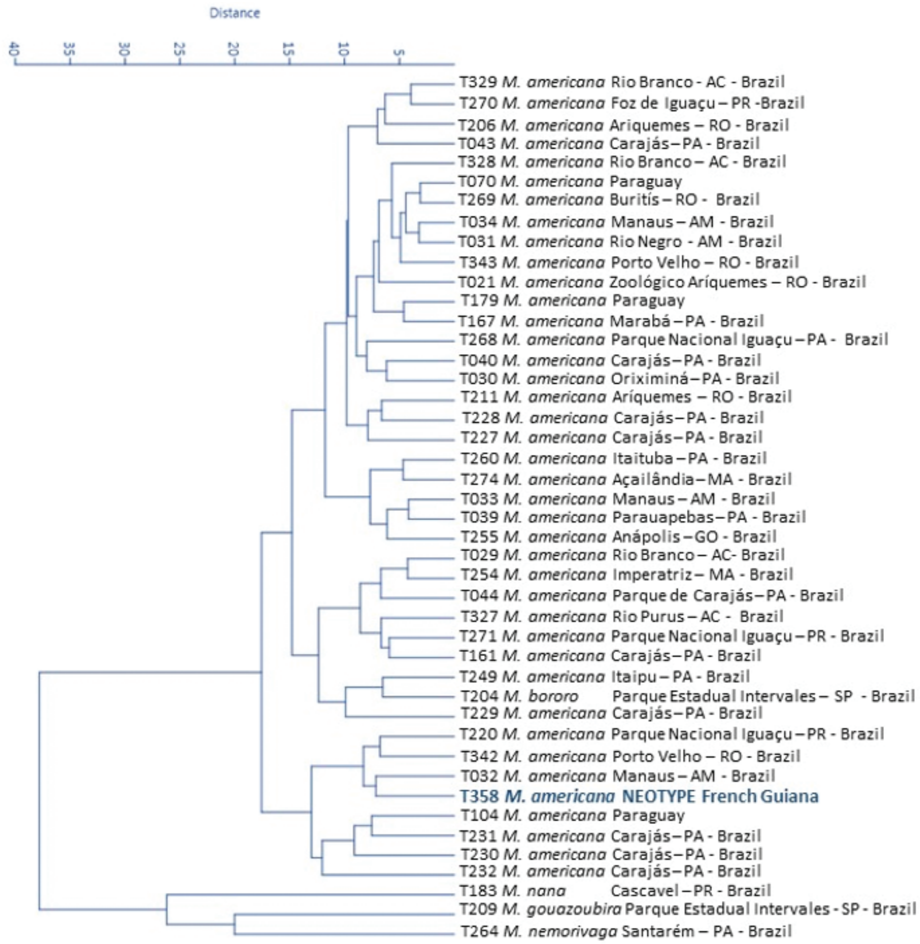

Figure 3. Distance tree (cluster analysis) made with biometric measurements of 39 *Mazama americana* specimens of various origins compared to the neotype and other *Mazama* species (*M. nemorivaga*, *M. gouazoubira*, *M. nana* and *M. bororo*).

metric analysis classified the pairs 1 and 2 belonging to Group A; 3, 4 and 5 to Group D; and 6 to 21 to Group E. The three chromosomes classified as supernumerary or B, were acrocentric and showed no numerical variation between the metaphases analyzed. The sexual system was XY_1Y_2, due to an X-autosomal fusion (Fig. 5).

Under AgNOR staining, the telomeric regions of one of the chromosomes of pair 3 and two chromosomes of pair 6 were marked. The C-band (Fig. 6) showed constitutive heterochromatin blocks in the pericentromeric region of all autosomal chromosomes, a strong interstitial heterochromatic band on the long arms of chromosomes 1 and 2, and weak bands on chromosomes 3, 4, 5, 6 and Y_2. The X chromosome showed a large heterochromatic block in the interstitial region, near the centromere of the long arm, as well as a small and weak heterochromatic band in the terminal region of this arm. The chromosome Y_1 is fully euchromatic and chromosomes B are heterochromatic.

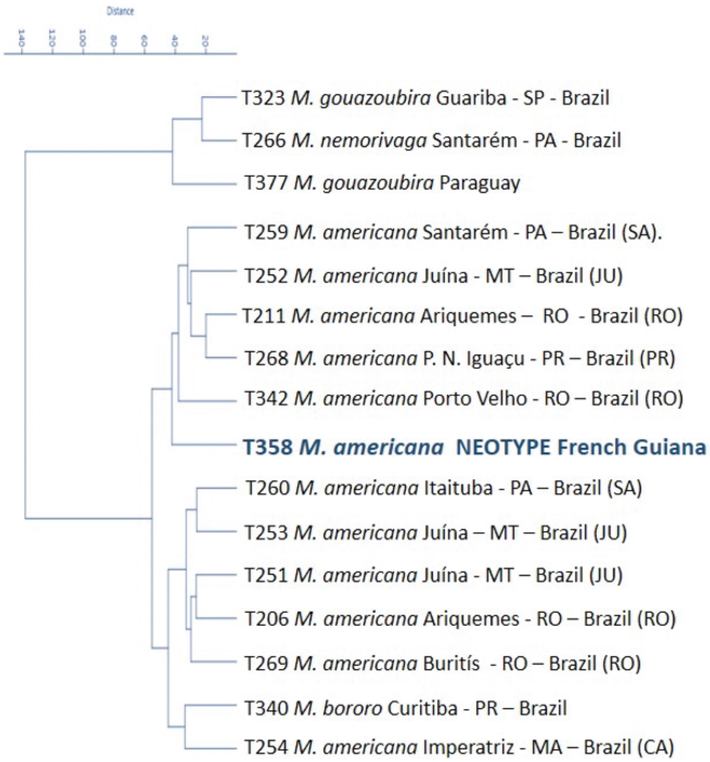

Figure 4. Distance tree (cluster analysis) made with cranial measurements of different *M. americana* cytotypes, in parenthesis, found in Brazil (SA-Santarém, JU-Juína, RO-Rondônia, PR-Paraná, CA-Carajás) compared to *M. americana* neotype and other *Mazama* species (*M. gouazoubira*, *M. nemorivaga* and *M. bororo*).

The schematic representation of the G-banding of the *M. americana* neotype is shown in Figure 7 and may be used in the future as a standard for describing new species based on the karyotype. The joint analysis of bands C and G allowed identification of the region of the homologous X chromosome to an acrocentric chromosome in Group E, thus confirming the autosomal X fusion responsible for the formation of the multiple sexual system.

Molecular genetics

The tree generated by the analysis of the mitochondrial *Cyt-b* gene (Suppl. material 4: Figure S1) shows several *M. americana* clades, two of them with well-supported posterior probability values. These clusters have no clear geographical correlation. The first clade (posterior probability = 1) grouped animals from Paraná (southern Brazil), from Pará (northern Brazil), and Rondônia (northwestern Brazil). Another well-supported clade (posterior probability = 0.99) included the neotype with animals from Acre, Amazonas, Paraguay and Pará.

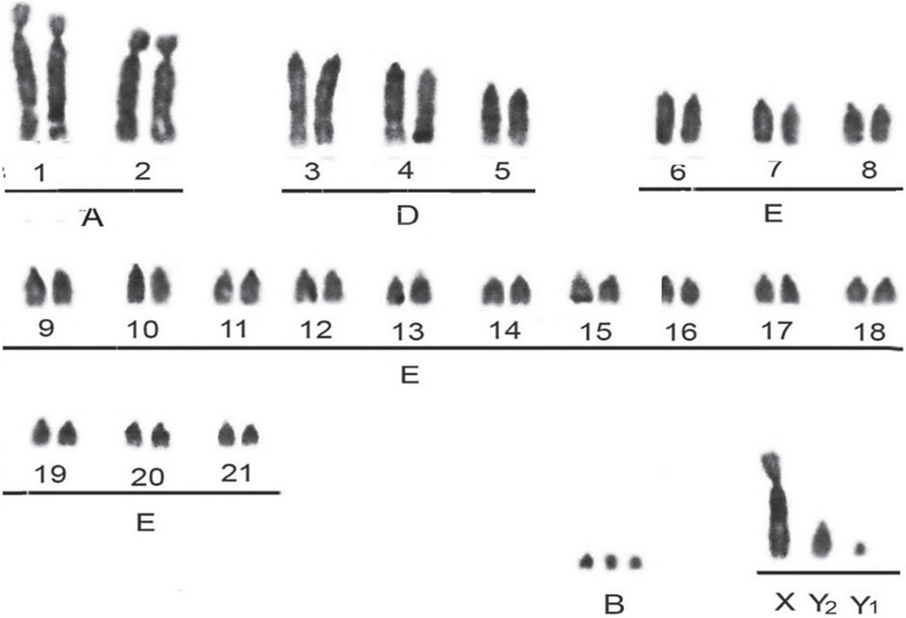

Figure 5. Basic karyotype belonging to the *Mazama americana* neotype (2n = 45 FN = 51 + 3Bs) under conventional Giemsa staining.

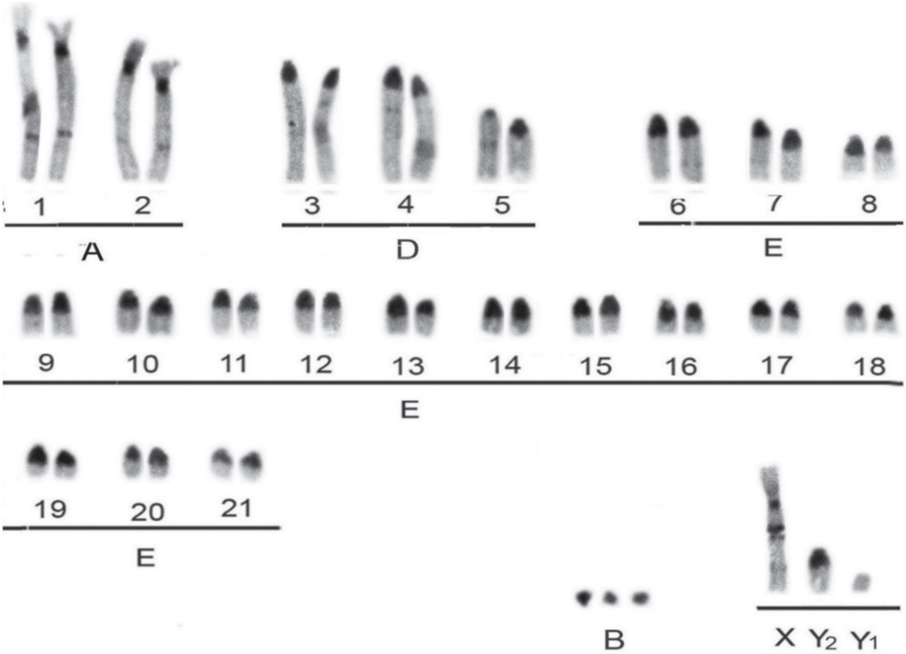

Figure 6. Basic karyotype belonging to the *M. americana* neotype (2n = 45, FN = 51 + 3Bs) under C-band.

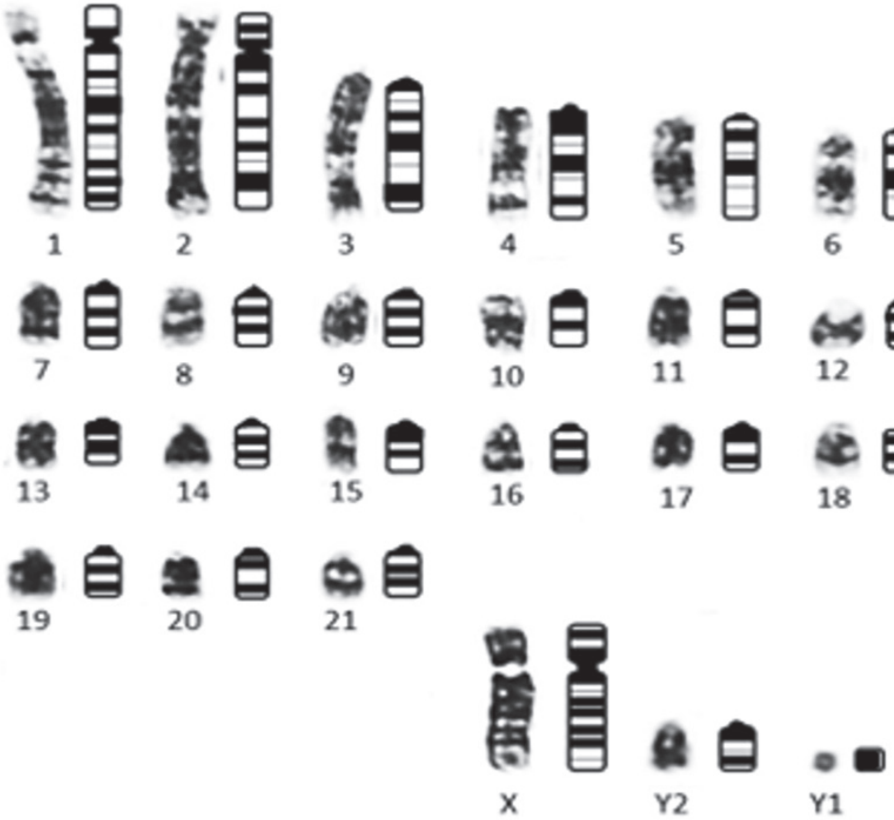

Figure 7. Basic karyotype belonging to the *M. americana* neotype (2n = 45 FN = 51 +3 Bs) under G-band and its schematic representation to facilitate future comparisons.

It is important to highlight that the species *M. bororo* and *M. nana* Hensel, 1872, taxonomically well-recognized and occurring in the south and southeast of Brazil, were grouped with *M. americana* from Rondônia and Juína. The distance between *M. nana* and *M. bororo* is smaller than the distance between several *M. americana* strains.

The analysis of the control region of the mitochondrial DNA *D-Loop* (Suppl. material 5: Figure S2) showed two clades: one composed of the samples of Paraná and Carajás cytotypes, together with the neotype, and another composed of the individuals from Rondônia, Juína and Jari and the *M. bororo* species. Both clades are clearly separated by a posterior probability support (posterior probability = 1).

The concatenated tree of the genes *Cyt-b* and *D-Loop* (Fig. 8) follows the results obtained in the *D-Loop* analysis, with two groups, separated by high posterior probability values (1.0): one composed of animals from Paraná, Carajás and the neotype, and another clade composed of individuals from the *M. bororo* species and Rondônia, Juína and Santarém cytotypes of *M. americana*.

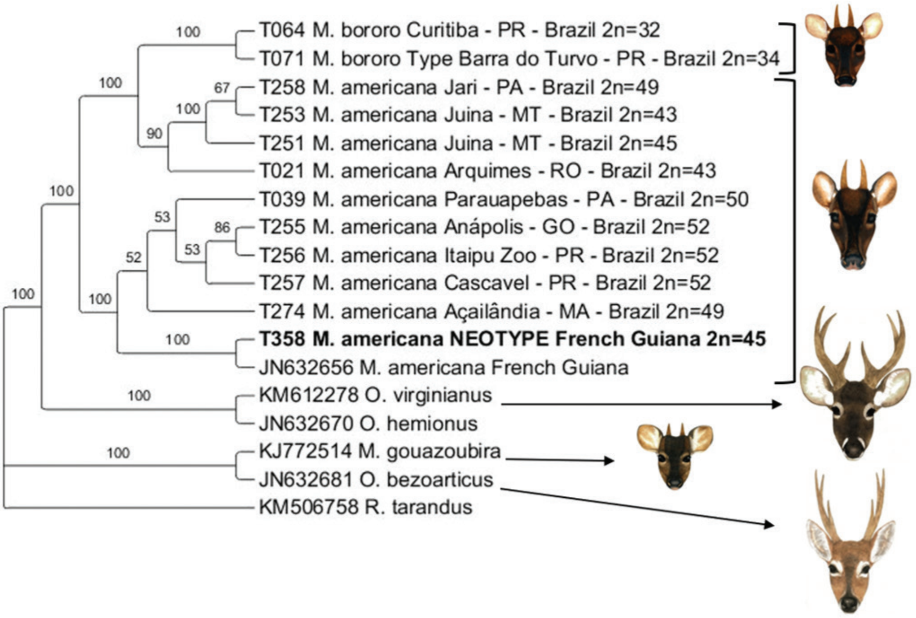

Figure 8. Phylogenetic tree from Bayesian inference of the fragments of the concatenated *D-Loop* and *Cyt-b* regions. The values represent the posterior probability of the analysis.

Discussion

Neotype designation

Mazama americana Erxleben, 1777 is the name given to a species commonly recognized for its wide distribution in the Neotropics. However, Erxleben's description was based solely on morphology, currently considered insufficient to discriminate species of the genus *Mazama* (Duarte et al. 2008; Abril et al. 2010), due to the morphological convergence within the genus as well as the recent divergence through chromosomal changes (Gonzalez and Duarte, in press). The holotype of the species is unknown, as is any specimen of the type series, precluding any current comparison. The taxonomic complexity of the species, indicative of the existence of a complex of several cryptic species, is a *prima facie* case and can only be solved by designating a neotype (International Code of Zoological Nomenclature 1999, art. 75.3.1).

Erxleben's (1777) original description of *M. americana* is very brief and does not include the many characteristics currently used to diagnose species of the genus *Mazama*, as he did not see any specimens but based his description on a series of reports by other authors, such as Des Marchais, 1725, who described the "*Biche de Guinee*", as well as on a drawing of a juvenile made by Seba in 1730 called "*Cervula surinamensis*", which simply illustrates a red deer. Linnaeus is known to have acquired specimens of Seba, but he never mentioned *Cervula surinamensis*, whose whereabouts were unknown, so it is suggested that there was no specimen that served as the basis for Erxleben's description.

Thus, the absence of any specimen of the type series, the lack of critical information in the original description, as well as the large taxonomic uncertainties in this species complex (Abril et al. 2010; Cursino et al. 2014; Salviano et al. 2017), indicate that their identity can only be clarified by designating a neotype.

Morphology

The genus *Mazama* is characterized by rapid diversification and morphological parallelism (Duarte et al. 2008; Gutiérrez et al. 2017), thus generating species complexes, such as in the case of *M. americana*, which present major challenges for today's science (Abril et al. 2010; Cursino et al. 2014).

The individuals belonging to the different cytotypes of *M. americana* found in Brazil (Abril et al. 2010) and the neotype analyzed herein could not be separated in the analyses made by morphological characteristics, as already observed by Rossi (2000) and Duarte et al. (2008), suggesting great morphological similarity between the different species of the *M. americana* complex.

In the tree of morphological distances, generated from the cranial measurements of the different *M. americana* cytotypes, we found two clades, where individuals belonging to the same cytotype are positioned in both clades, thus showing there is variation in individual cranial morphometric characteristics, which do not appear to have any geographical relation. Similarly, Rossi (2000) reported the difficulty in detecting any pattern of similarity between *M. americana* samples according to cranial morphological characteristics.

The results obtained with our morphological and morphometric analyses reveal that there is morphological parallelism between *M. americana* variants, suggesting the existence of closely related characteristics, even in phylogenetically distant groups, due probably to recent diversification from their last common ancestor (Duarte et al. 2008).

Cytogenetics

The chromosomal polymorphism found in red brocket deer is surprising and shows high levels of intra- and interspecific chromosome variation (Duarte et al. 2008; Abril et al. 2010). Thus, the neotype according to its karyotypic pattern does not fit into any of the red brocket deer cytotypes studied in Brazil (Abril et al. 2010), thus recognizing that these variants should be considered as different species according to cytogenetic evidence, since differences of more than two chromosomal pairs generate an efficient postzygotic reproductive barrier (Cursino et al. 2014; Salviano et al. 2017).

In the neotype chromosomes, the constitutive heterochromatin blocks are evident in chromosomes of Group A, weak in Group D and almost imperceptible in the first pair of Group E. According to Neitzel (1987), in chromosomes formed from tandem fusions the interstitial C bands shrink in size over time until they are so weak that they may disappear completely.

As previously reported by Sarria-Perea (2004), cytogenetic analysis of *M. americana* cytotypes reveal an intense process of chromosomal evolution. The chromosomal reorganization is mainly due to fusions between Group D and E chromosomes to form new chromosomes and a consequent decrease in diploid number (Abril et al. 2010). According to their diploid number, it is possible to observe the approximation of the neotype to the group of individuals from Rondônia (2n = 42/43; NF = 46) and Juína (2n = 44/45; NF = 48), which have lower numbers of chromosomes. However, the chromosomal changes that occurred in the formation of Rondônia and Juína cytotypes are not the same as those involved in the karyotype formation of the *M. americana* neotype (Fig. 9), clearly showing the isolation of populations, which is also geographically confirmed, with the Amazon River in their midst acting as the major geographical barrier.

Through the use of chromosomal banding techniques, important results were generated for the karyotype study of *M. americana*. Based on their comparison, it was observed that there is a chromosomal difference between the six *M. americana* cytotypes and the neotype due to pericentric inversions, tandem fusions and centric fusions, as previously reported by Sarria-Perea (2004) and Abril et al. (2010). Based on the hypothetical ancestor of *M. americana* and the chromosomal evolution among the cytotypes proposed by Abril et al. (2010), the rearrangements involved in the karyotype formation of the neotype were two pericentric inversions, two tandem fusions and two centric fusions, thus showing greater evolutionary proximity of the neotype to the *M. americana* strain, with a higher number of chromosomes (Paraná, Santarém, Jari and Carajás; Fig. 9).

The large chromosomal variation found in *M. americana* can be explained by the theory of chromosomal fragility proposed for *Mazama* (Duarte and Jorge 1996; Vargas-Munar et al. 2010; Tomazella et al. 2017), which would induce the occurrence of breakages and chromosomal exchanges. These chromosomal rearrangements could have led to the formation of new species in a relatively short time after geographical isolation, given that chromosomal changes can promote incipient divergence and lead ultimately to species diversification (Potter et al. 2017).

Consequently, it is clear that the proposed neotype does not belong to the same species as the known *M. americana* cytotypes (Duarte et al. 2008; Abril et al. 2010), since the number of chromosomal pairs involved in these differences certainly generate an insurmountable postzygotic reproductive barrier due to sterility of the hybrid, as evidenced by Salviano et al. (2011) and Cursino et al. (2014) in the same specific complex. Thus, cytogenetics is the more important characteristic for the reclassification of the individuals of the group at the species level. With *M. americana* of Cayenne as the first description (Erxleben 1777), it is now necessary to redescribe and name all other species that are different from this neotype.

Molecular phylogeny

The result of the concatenated analysis of the two *mtDNA* fragments (*Cyt-b* and *D-Loop*), broadly followed the results obtained from the analysis of the separate genes, showing at least two evolutionary units for *M. americana*, yielding results very similar to previous studies (Carnelossi 2008; Duarte et al. 2008; Abril et al. 2010), but comple-

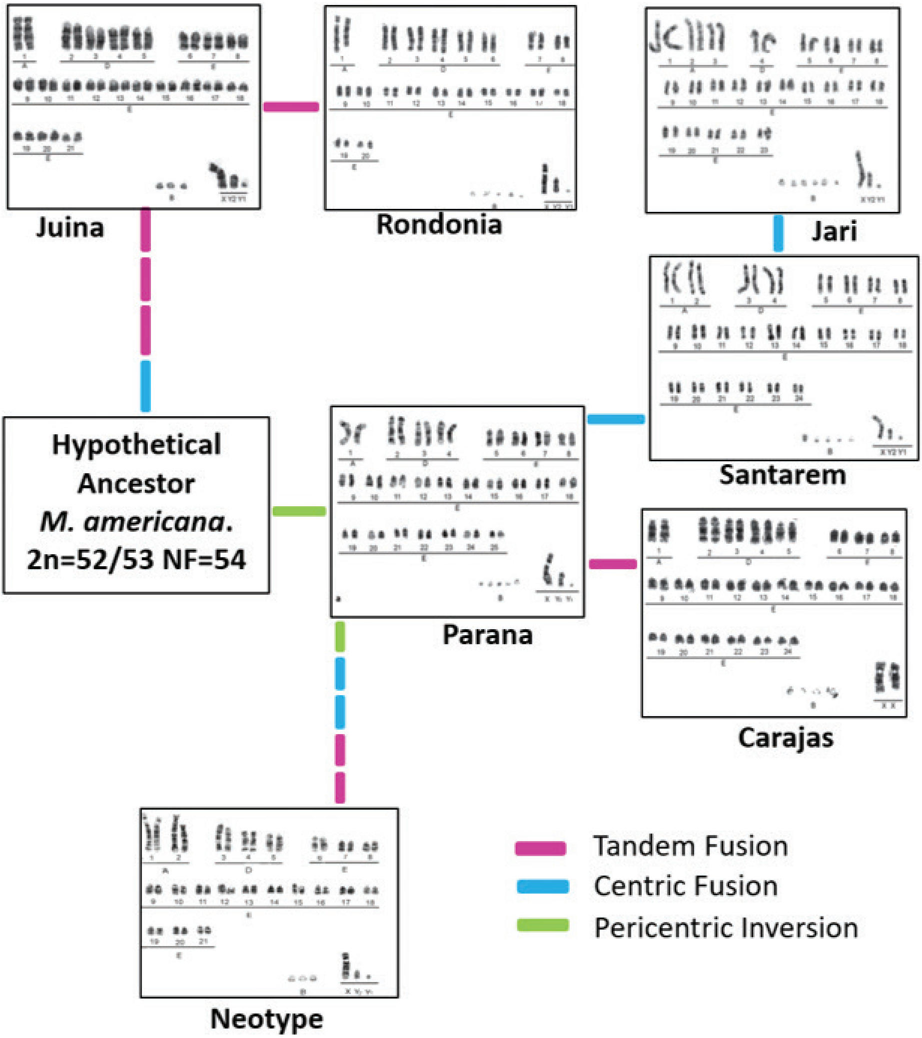

Figure 9. Chromosomal evolution showing the relationships of the six cytotypes compared to the *M. americana* neotype. Juine: 2n = 44/45; Rondônia: 2n = 42/43; Santarém: 2n = 50/51; Jari: 2n = 48/49; Paraná: 2n = 52/53; Carajás: 2n = 50/51; Neotype: 2n = 45 (Adapted from Abril et al. 2010).

mented now by information of the neotype. However, these analyses make clear the numerous gaps in taxonomic and evolutionary knowledge of the *M. americana* complex.

The specimen of *M. americana* analyzed in this study complies with all the conditions required by the International Code of Zoological Nomenclature (1999) in force to be considered as neotype. The proposal of a *M. americana* neotype based on the detailed description of a current topotype opens great possibilities for describing new species within the genus *Mazama*. At this time, since there is a *M. americana* pattern (neotype), it is possible to define where the current cytotypes will be positioned. It is necessary that the entire nomenclature assigned to *Mazama* be reviewed from a cytogenetic point of view. For this, it would be necessary to access the chromosomal pattern for each of the available names. This can only be achieved if current topotypes are collected to define their karyotypes and position them taxonomically. In addition, molecular analysis from type series in museums could be used to help clarify the taxonomy (Gutiérrez et al. 2017)

It should be reiterated that it remains a formidable challenge to resolve the relationships between recently separated species, as in, for instance, the case of *M. americana*. However, this study has been able to confirm the existence of different species within the *M. americana* complex, as previously proposed by Duarte et al. (2008), Carnelossi (2008), Abril et al. (2010), Cursino et al. (2014) and Salviano et al. (2017), since until now the neotype does not match with any known cytotype.

This is the first reference available in the literature regarding the establishment of a neotype for *M. americana*, which is the starting point for the description of new species and possible change in the nomenclature of the genus *Mazama*.

Acknowledgments

We thank Coaraci who collected the animal for this study. Fundação de amparo à Pesquisa do Estado de São Paulo (FAPESP) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) provided financial support. We also thank João Airton Boer for his support for the laboratory work at the NUPECCE/UNESP. We thank Natália Aranha de Azevedo for the drawings of the animal heads used in the molecular tree.

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Supplementary material 1

Table S1. Samples used in this study for genetic analysis

Authors: Analorena Cifuentes-Rincón, Jorge Alfonso Morales-Donoso, Eluzai Dinai Pinto Sandoval, Iara Maluf Tomazella, Aline Meira Bonfim Mantellatto, Benoit de Thoisy, José Maurício Barbanti Duarte

Data type: molecular data

Explanation note: Nupecce's identification, species, gene accessed, accession number in genbank, origin (locality) and source (when collected).

Link: https://doi.org/10.3897/zookeys.958.50300.suppl1

Supplementary material 2

Table S2. Biometric data of the *M. americana* neotype

Authors: Analorena Cifuentes-Rincón, Jorge Alfonso Morales-Donoso, Eluzai Dinai Pinto Sandoval, Iara Maluf Tomazella, Aline Meira Bonfim Mantellatto, Benoit de Thoisy, José Maurício Barbanti Duarte

Data type: species data

Explanation note: Measured in cm and mass in kg.

Link: https://doi.org/10.3897/zookeys.958.50300.suppl2

Supplementary material 3

Table S3. Cranial measurements of *M. americana* neotype represented in millimeters

Authors: Analorena Cifuentes-Rincón, Jorge Alfonso Morales-Donoso, Eluzai Dinai Pinto Sandoval, Iara Maluf Tomazella, Aline Meira Bonfim Mantellatto, Benoit de Thoisy, José Maurício Barbanti Duarte

Data type: species data

Link: https://doi.org/10.3897/zookeys.958.50300.suppl3

Supplementary material 4

Figure S1. Phylogenetic tree of the Cyt-b gene

Authors: Analorena Cifuentes-Rincón, Jorge Alfonso Morales-Donoso, Eluzai Dinai Pinto Sandoval, Iara Maluf Tomazella, Aline Meira Bonfim Mantellatto, Benoit de Thoisy, José Maurício Barbanti Duarte

Data type: phylogenetic tree

Explanation note: Bayesian Inference (BI) Analysis. The values represent the posterior probability of the analysis. External group: *R. tarandus*, *M. gouazoubira* and *O. bezoarticus*.

Link: https://doi.org/10.3897/zookeys.958.50300.suppl4

Supplementary material 5

Figure S2. Phylogenetic tree of the *D-loop* gene

Authors: Analorena Cifuentes-Rincón, Jorge Alfonso Morales-Donoso, Eluzai Dinai Pinto Sandoval, Iara Maluf Tomazella, Aline Meira Bonfim Mantellatto, Benoit de Thoisy, José Maurício Barbanti Duarte

Data type: phylogenetic tree

Explanation note: Bayesian inference (BI) Analysis. The values represent the posterior probability of BI. External group: *O. bezoarticus*, *R. tarandus*, *M. gouazoubira*.

Link: https://doi.org/10.3897/zookeys.958.50300.suppl5