

Revision of the genus *Cuvierina* Boas, 1886 based on integrative taxonomic data, including the description of a new species from the Pacific Ocean (Gastropoda, Thecosomata)

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Abstract

Shelled pteropods (Gastropoda, Thecosomata, Euthecosomata) are a group of holoplanktonic gastropods that occur predominantly in the surface layers of the world's oceans. Accurate species identifications are essential for tracking changes in species assemblages of planktonic gastropods, because different species are expected to have different sensitivities to ocean changes. The genus *Cuvierina* has a worldwide warm water distribution pattern between ~36°N and ~39°S. Based on an integrative taxonomic approach combining morphometric, genetic, and biogeographic information, the two subgenera of *Cuvierina*, *Cuvierina s. str.* and *Urceolarica*, are rejected. A new species is introduced: *Cuvierina tsudai* **sp. n.**, which has to date been considered the same species as *Cuvierina pacifica*. *Cuvierina tsudai* **sp. n.** is endemic to the Pacific Ocean and is characterised by a shell height of 7.2–8.0 mm, a moderately cylindrical shell shape, the absence of micro-ornamentation and a triangular aperture. *Cuvierina pacifica* is restricted to the centre of the oligotrophic southern Pacific gyre, has a shell height of 6.6–8.5 mm, a more cylindrical shell shape, no micro-ornamentation and a less triangular aperture than *C. tsudai* **sp. n.**

Keywords

Integrative taxonomy, DNA barcoding, geometric morphometrics, pteropods, biogeography

Introduction

Pteropods are holoplanktonic heterobranch gastropods classified in a superorder comprised of the orders Thecosomata and Gymnosomata, commonly referred to as “sea butterflies” and “sea angels”, respectively (Lalli and Gilmer 1989, Pierrot-Bults and Peijnenburg 2015). The order Thecosomata consists of Euthecosomata that have sinistrally coiled or straight, bilaterally symmetrical shells, and Pseudothecosomata that have either sinistrally coiled shells, an internal gelatinous pseudoconch, or are shell-less in the adult stage (Meisenheimer 1905, Tesch 1913). Pteropods play an important role in marine food webs (Jörger et al. 2010), and although most species occur in warm tropical and subtropical waters, the highest abundances have been observed for some (sub)polar cold water species (Bé and Gilmer 1977, Van der Spoel and Heyman 1983, Bednaršek et al. 2012, Burridge et al. 2016). Because of their thin-walled, aragonite shells, euthecosomes are exceptionally vulnerable to the effects of ocean acidification (e.g., Fabry et al. 2008, Bednaršek and Ohman 2015, Gattuso et al. 2015, Moya et al. 2016).

The genus *Cuvierina* is a remarkable group of shelled pteropods with relatively large (5.1–11.1 mm), straight, bottle-shaped shells (Janssen 2005). Ever since *Cuvierina* was described as a mollusc genus (as *Cuvieria* Rang, 1827, emended by Boas 1886), it has often been considered to consist of a single species, *C. columnella* (Rang, 1827), the type species of the genus by monotypy. The first taxonomic division within the genus came with the description of a second *Cuvierina* species, introduced as *Cuvieria urceolaris* (Mörch, 1850), but in later literature it was often interpreted as a form or subspecies of *C. columnella* (e.g., Tesch 1913, Van der Spoel 1967, Rampal 1975). A third form, *Cuvierina columnella* f. *atlantica*, was described by Van der Spoel (1970), and validated as a taxon of the species group by Bé et al. (1972). Bé and Gilmer (1977) interpreted the morphological differences between the three taxa as infraspecific variability. Contrarily, Rampal (2002) distinguished these taxa as independent species but introduced the taxon *C. spoeli* to replace the taxonomically invalid *Cuvierina columnella* f. *atlantica*. Because the holotype of *C. spoeli* was from the Indian Ocean, where *C. atlantica* is absent, it rather represented *C. columnella* and was rejected as a valid species by Janssen (2005). Two further extant species, *C. cancapae* and *C. pacifica*, were described by Janssen (2005).

According to the most recent taxonomic revision of *Cuvierina*, five extant species were assigned to two subgenera based on shell morphology and supposed lineages of fossil occurrences since the early Miocene (Janssen 2005, 2006). The subgenus *Cuvierina* s. str. consisted of *C. atlantica*, *C. columnella*, and *C. pacifica*, which are characterised by relatively slender, cylindrical shells, triangular rather than kidney-shaped apertures and the presence (*C. columnella*) or absence (*C. atlantica*, *C. pacifica*) of micro-ornamentation. Two geographical varieties were recognised within *C. pacifica*, one from the North Pacific and the other from the South Pacific, but were not formally introduced as new species. The subgenus *Urceolarica*, containing *C. cancapae* and *C. urceolaris*, is characterised by more inflated, bottle-shaped rather than

cylindrical shells, pronounced micro-ornamentation, and kidney-shaped rather than triangular apertures.

All extant *Cuvierina* species are restricted to the surface layers of tropical and subtropical waters from $\sim 45^{\circ}\text{N}$ to $\sim 40^{\circ}\text{S}$. In the Atlantic Ocean, *C. atlantica* occurs in the subtropical gyres and *C. cancapae* is found in tropical waters. In the Indian Ocean, *C. columnella* is found in the southern subtropical zone and *C. urceolaris* occurs in tropical waters and further south along Madagascar towards South Africa. *Cuvierina columnella* and *C. urceolaris* also occur in the Pacific Ocean along with *C. pacifica* (Janssen 2005, BurrIDGE et al. 2015).

BurrIDGE et al. (2015) examined the diversity, distribution, and evolution of *Cuvierina* taxa using integrative geometric morphometric, molecular, and biogeographic methods. They confirmed that the five species described for *Cuvierina* species have significantly different shell shapes and that *C. pacifica* consists of two disjunct morphometric groups, registered as *C. pacifica* N and *C. pacifica* S in their study. Three genetic lineages were distinguished based on mitochondrial Cytochrome Oxidase I DNA: the Atlantic lineage with *C. atlantica* and *C. cancapae*, the Indo-Pacific lineage with *C. columnella*, *C. urceolaris*, and *C. pacifica* N, and the South Pacific lineage with *C. pacifica* S. A new taxonomic description of *C. pacifica* N is required because the holotype of *C. pacifica* has the shell shape of *C. pacifica* S.

Based on the findings of Janssen (2005) and the integrative approach of BurrIDGE et al. (2015) the taxonomy of the genus *Cuvierina* is revised. The subgenera *Cuvierina* s. str. and *Urceolarica* are rejected, a new species, *C. tsudai*, is described from the Pacific Ocean, and the species description of *C. pacifica* is restricted to the South Pacific lineage. A taxonomic key is provided for the identification of *Cuvierina* species.

Methods

Two approaches were used to distinguish between *C. tsudai* and *C. pacifica* based on differences in shell shape. First, simple measurements of shell height and width, aperture diameters, and position of maximum shell width as applied to museum specimens by Janssen (2005) were used to distinguish between *C. tsudai* and *C. pacifica*. Second, geometric morphometric data of shell shapes in ventral and apertural orientations were used for 168 adult specimens of *Cuvierina* that were registered as *C. pacifica* N or *C. pacifica* S in BurrIDGE et al. (2015). The specimens corresponded to museum specimens as identified and measured by Janssen (2005, $N = 92$), additional museum specimens ($N = 24$), and recently collected fresh specimens ($N = 52$). Geometric morphometric methods consisted of digitising shell outlines using tpsDig and tpsUtil (Rohlf 2006) to contain 76 ventral and 37 apertural semi-landmarks per shell, after which a generalised least square Procrustes superimposition was applied (GLS, Kendall 1977 in Zelditch et al. 2004) to rotate, translate, and scale the semi-landmark coordinates. A subsequent thin-plate spline (TPS) analysis (e.g., Zelditch et al. 2004) provided centroid sizes, a size measure depending on surface area, and multiple relative

warp axes per specimen, containing information on shape. To describe the new species *C. tsudai* as well as to reject the validity of the *Cuvierina* subgenera, Cytochrome Oxidase I mitochondrial (COI) DNA and 28S ribosomal DNA sequence data from Burridge et al. (2015) were used.

Results and discussion

Distinction between *Cuvierina tsudai* and *C. pacifica*

Cuvierina tsudai and *C. pacifica* are similar in size but have different shell shapes, COI mtDNA and 28S rDNA. Because of their Pacific distributions and similarities in shell size, *C. tsudai* and *C. pacifica* have to date been considered the same species. Although Janssen (2005) demonstrated their presence as morphological varieties within *C. pacifica*, the congruence between morphometric and genetic differentiation supports the separation into two species (Figs 1A–J and 2, fig. 4 in Burridge et al. 2015). Shell heights of *C. tsudai* specimens are between 7.2 and 8.8 mm, showing a large overlap with *C. pacifica*, which measures between 6.6 and 8.5 mm (Janssen 2005). However, in terms of shell shape, *C. pacifica* and *C. tsudai* are significantly different (fig. 29 lower left in Janssen 2005, Burridge et al. 2015). The shell of *C. tsudai* is wider (more inflated) than the slender and more cylindrical *C. pacifica* (Fig. 2). *Cuvierina pacifica* has a larger height/width-ratio between 3.25 and 3.96 (mean 3.50) compared to *C. tsudai*, which has a ratio between 2.77 and 3.46 (mean 3.14). The position of maximum shell width is located at 34–45% (mean 40%) of the shell height from the septum upwards for *C. pacifica* and at 33–42% (mean 37%) for *C. tsudai* (Janssen 2005). The aperture of *C. tsudai* is wider, more triangular and more concave on the ventral side than in *C. pacifica*. The overall shape variation is larger for *C. tsudai* than for *C. pacifica* (Fig. 2). The average pairwise genetic distance of COI mtDNA (658bp fragment) between *C. tsudai* (N = 16) and *C. pacifica* (N = 43) is 4.5%. The genetic variation of COI within *C. tsudai* is 1.6% compared to 0.8% within *C. pacifica*. The 28S rDNA fragment (965bp) of *C. tsudai* differs at least at one position compared with other *Cuvierina* species, except for *C. columnella* (Burridge et al. 2015).

The larger genetic and shell shape variation for *C. tsudai* compared to *C. pacifica* coincides with a much larger Pacific distribution and lower ecological specificity of *C. tsudai*. *Cuvierina pacifica* is restricted to the centre of the oligotrophic southern Pacific gyre and occupies a more specialised ecological niche based on ecological niche modelling (ENM) than *C. tsudai* (Burridge et al. 2015). This study used presence-only data and six uncorrelated environmental parameters, of which ocean surface temperature and chlorophyll *a* concentration were the most important. The distribution of *C. tsudai* was mostly explained by maximum monthly sea surface temperatures (SST) and near-surface chlorophyll *a* concentrations (both 30.8%). The distribution of *C. pacifica* was best explained by low maximum monthly chlorophyll *a* concentrations (57.1%).

Description of *Cuvierina tsudai* sp. n.**Superfamily Cavolinioidea Gray, 1840****Family Cuvierinidae Gray, 1840****Genus *Cuvierina* Boas, 1886 (= replacement name for *Cuvieria* Rang, 1827 non Lesueur & Petit, 1807, pl. 30 (Coelenterata))****Type species.** *Cuvieria columnella* Rang, 1827, p. 323, pl. 45 figs 1–3, by monotypy.***Cuvierina tsudai* sp. n.**<http://zoobank.org/B33A28E9-BCDE-4F2B-9349-F3E18CCD87BE>*Cuvieria columnella* Rang, 1827: 323 (partim).*Cuvierina columnella*: Boas 1886: 132, 217, pl. 6 fig. 95g (*partim, non* Rang); Rampal 2002: 214 (*partim, non* Rang).*Cuvierina columnella* (Rang, 1827) forma *columnella* (Rang, 1827) – Van der Spoel 1967: 79 (*partim, non* Rang); Van der Spoel 1970: 120, fig. 19 (*partim, non* Rang).*Cuvierina* (*Cuvierina*) *pacifica* Janssen, 2005: 46 figs. 18–20 (*partim, northern Pacific specimens only, non* figs. 14–17 = *C. pacifica*).*Cuvierina pacifica* N (Janssen, 2005): BurrIDGE et al. 2015: 5, fig. 2.**Holotype.** RMNH.5004167, also see Fig. 1A and Table 1.**Type locality.** 8°47'N, 158°49'W.**Paratypes.** See Fig. 1B–I and Table 1 for all specimen information. Three specimens from the type locality (RMNH.5004168); three specimens from the Zoological Museum of the University of Copenhagen, Denmark (ZMUC, not registered) illustrated by Janssen (2005, figs. 18–20); five specimens from four locations (RMNH.5004169–72) studied by BurrIDGE et al. (2015, referred to as *C. pacifica* N therein). The latter five specimens have COI mtDNA and 28S rDNA sequences available at GenBank (see Table 1).**Additional material examined.** Specimens recorded as *C. pacifica* from the North Pacific Ocean in Janssen (2005: 49, 71), housed in the Muséum National d'Histoire Naturelle (MNHN, Paris, France) and ZMUC (Copenhagen, Denmark). Specimens from BurrIDGE et al. (2015), referred to as *C. pacifica* N in Table S1 therein, with photographs deposited at the Dryad repository (<http://dx.doi.org/10.5061/dryad.7n1q4>) and COI mtDNA (KP292730–72) and 28S rDNA sequences (KP292636–42) deposited at GenBank. These specimens are housed in Naturalis Biodiversity Center (Leiden, The Netherlands) and ZMUC (Copenhagen, Denmark). Registration numbers, if available, from Janssen (2005).**Diagnosis.** Shell moderately small, adult specimens 7.2–8.8 mm high, height/width-ratio 2.77–3.46 (mean 3.14), position of maximum shell width 33–42% (mean 37%) of shell height from septum upwards. Aperture triangular. No longitudinal micro-ornamentation.

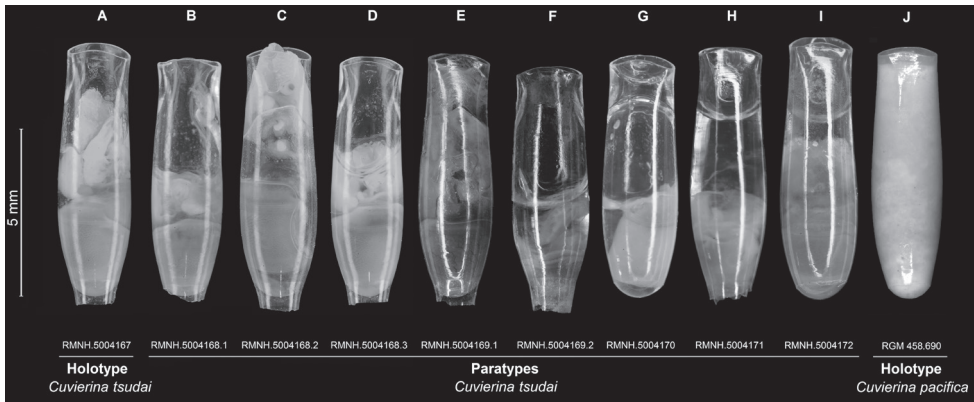


Figure 1. Holotype and paratypes of *C. tsudai* and holotype of *C. pacifica*. **A** Holotype (RMNH.5004167) and **B–I** paratypes (RMNH.5004168–72) of *C. tsudai* and **J** holotype of *C. pacifica* (RGM 458.690) photographed in a ventral view. Photographs of RMNH.5004169–72 from Burridge et al. (2015); RMNH.5004167–68 taken by R. van der Hulst and RGM 458.692 taken by E.F. de Vogel, this study. RMNH = Naturalis Biodiversity Center, mollusc collection and RGM = Naturalis Biodiversity Center, fossil planktonic mollusc collection, Leiden.

Description. The shell shape of *Cuvierina tsudai* differs from other *Cuvierina* species. Its shell height is smaller than in *C. columnella*, *C. cancanae*, and *C. atlantica*, but larger than in *C. urceolaris*, and of similar size compared to *C. pacifica*. The position of maximum shell width is distinctly higher than for *C. columnella* and *C. atlantica* and lower than for *C. pacifica*. It is more cylindrical in shape than the inflated (bottle-shaped) *C. urceolaris* but less cylindrical than *C. atlantica* and *C. pacifica*. It differs from *C. urceolaris* and *C. cancanae* by the absence of micro-ornamentation. It has a more triangular and wider aperture than *C. urceolaris* and *C. pacifica* (Fig. 3, Janssen 2005, Burridge et al. 2015).

Distribution. *Cuvierina tsudai* has a wide, exclusively Pacific distribution between 36°N and 39°S, in which it co-exists with *C. columnella*, *C. urceolaris*, and *C. pacifica*. It has been found most often in the North Pacific, but also occurs in the South Pacific. It has not been found thus far in the central, oligotrophic parts of the South Pacific subtropical gyre, the southeast Pacific, the coral triangle west of the Philippines or southwest of Papua New Guinea.

Etymology. Named after Atsushi Tsuda, professor in biological oceanography at the University of Tokyo, Japan, for sending us pteropod samples from the Pacific Ocean and in recognition of his services to the zooplankton research community.

Rejection of the subgenera in *Cuvierina*

Two subgenera of *Cuvierina* were described that supposedly evolved since the early Miocene (Aquitian, 23 million years ago): *Cuvierina s. str.*, with extant species *C.*

Table 1. Voucher and sampling information of type specimens of *C. tsudai* including the holotype of *C. pacifica*.

Museum voucher	Image voucher	Collection date	Latitude	Longitude	Cruise	Station	COI GenBank	28S GenBank	First studied
Holotype of <i>C. tsudai</i>									
RMNH.5004167	C_PNE_SEI201_21_01	2012-05-15	8°47'N	158°49'W	SE1201	21			This study
Paratypes of <i>C. tsudai</i>									
RMNH.5004168.1	C_PNE_SEI201_21_02	2012-05-15	8°47'N	158°49'W	SE1201	21			This study
RMNH.5004168.2	C_PNE_SEI201_21_03	2012-05-15	8°47'N	158°49'W	SE1201	21			This study
RMNH.5004168.3	C_PNE_SEI201_21_04	2012-05-15	8°47'N	158°49'W	SE1201	21			This study
RMNH.5004169.1	C_PNE_KH1110_08_01	2011-12-19	22°47'N	158°06'W	KH-11-10	8	KP292730	KP292636	Burridge et al. 2015
RMNH.5004169.2	C_PNE_KH1110_08_20	2011-12-19	22°47'N	158°06'W	KH-11-10	8	KP292748	KP292637	Burridge et al. 2015
RMNH.5004170	C_PNE_KM1109_02_02	2011-03-04	21°14'N	158°11'W	Kilo Moana 1109	2	KP292755	KP292639	Burridge et al. 2015
RMNH.5004171	C_PNE_KM1109_08_01	2011-03-06	21°20'N	158°22'W	Kilo Moana 1109	8	KP292759	KP292640	Burridge et al. 2015
RMNH.5004172	C_PNW_TMKT1020_05_01	2010-09-29	27°08'N	125°33'E	R/V Tansei-Maru KT-10-20	5	KP292766	KP292642	Burridge et al. 2015
ZMUC, not registered	figure 18	1933-08-21	33°45'N	137°30'W	DANA	4794			Janssen 2005
ZMUC, not registered	figure 19	1934-02-12	32°56'N	131°50'W	DANA	4807			Janssen 2005
ZMUC, not registered	figure 20	1929-05-25	20°04'N	125°59'E	DANA	3718 V			Janssen 2005
Holotype of <i>C. pacifica</i>									
RGM 458.692	figure 15	1986-04/05	18°39'S	172°12'W	Manihiki Plateau Expedition	U351a			Janssen 2005

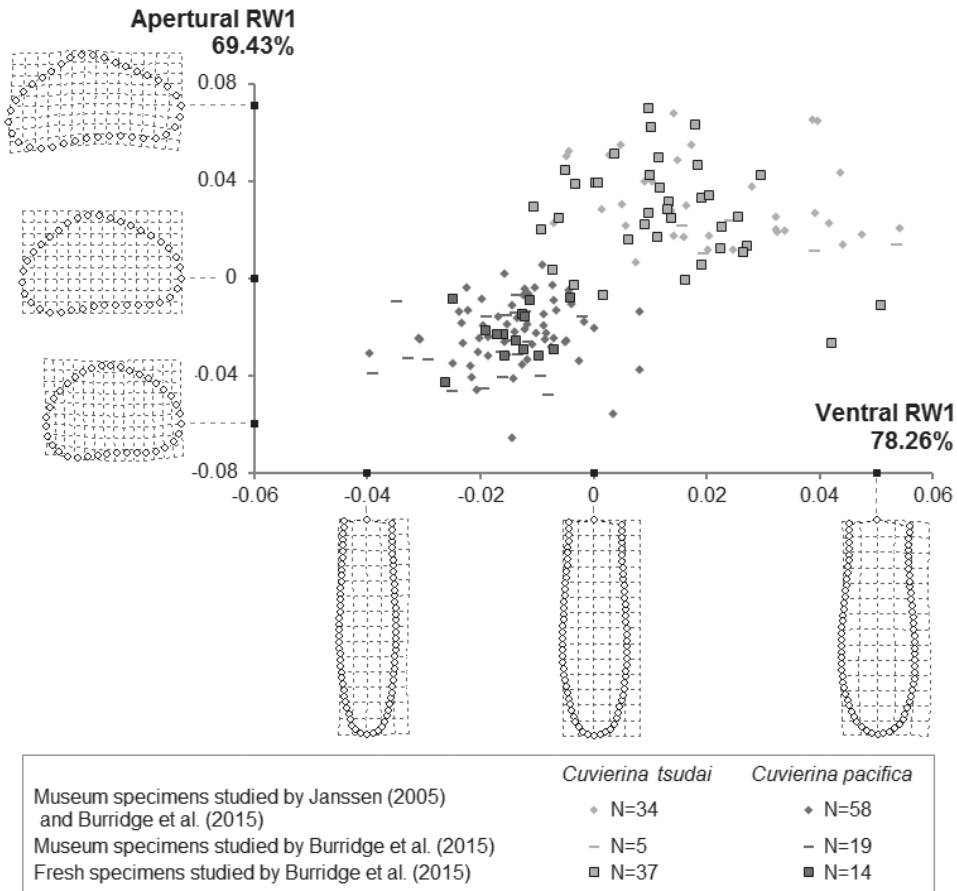


Figure 2. Shape variation in *C. tsudai* and *C. pacifica* by means of Relative Warp (RW) data. Ordination of RW data of *C. tsudai* and *C. pacifica* for the first ventral and apertural RWs (N = 167 excluding 1 specimen with only one orientation). On the X-axis, RW1 depicts 78.26% of the total ventral shape variation. On the Y-axis, 69.43% of the apertural shape variation is explained by its RW1. Shape variations depicted by ventral and apertural RW1 (with subsequent RWs = 0) are shown.

atlantica, *C. columnella*, and *C. pacifica*, and *Urceolarica* with extant species *C. cancapae* and *C. urceolaris* (see Janssen 2005, 2006). They were based on distinguishing shell characteristics in fossil species such as the position of maximum shell width, aperture shape and presence or absence of micro-ornamentation. However, the morphology and molecular phylogenetic information of recent species are in conflict with this separation. *Cuvierina columnella*, typically a *Cuvierina s. str.* species, has distinct micro-ornamentation, which was considered one of the distinguishing characters of the subgenus *Urceolarica*. It was shown that there are three divergent and well-supported lineages based on genetic data: the Atlantic (*C. atlantica* and *C. cancapae*), Indo-Pacific (*C. columnella*, *C. urceolaris* and *C. tsudai*), and South Pacific (*C. pacifica*) lineages (fig. 4 in Burridge et al. 2015). Hence, we reject the two subgenera within *Cuvierina*.



The following taxonomic key identifies adult *Cuvierina* pteropod species based on distinctive shell shape characteristics and shell sizes. Photographs of typical adult shells are shown in Fig. 3.

- | | | |
|---|---|----------------------|
| 1 | Micro-ornamentation present..... | 2 |
| – | Micro-ornamentation absent | 4 |
| 2 | Strongly inflated shell shape, shell height 5.1–6.7 mm..... | <i>C. urceolaris</i> |
| – | Moderately inflated or cylindrical shell shape, shell height 7.5–11.1 mm.... | 3 |
| 3 | Cylindrical shell shape, shell height 8.8–11.1 mm | <i>C. columnella</i> |
| – | Moderately inflated shell shape, shell height 7.5–9.3 mm | <i>C. cancapae</i> |
| 4 | Cylindrical shell shape and triangular aperture, shell height 6.7–10.5 mm.... | <i>C. atlantica</i> |
| – | Moderately inflated or cylindrical shell shape, triangular to kidney-shaped aperture, shell height 6.6–8.8 mm | 5 |
| 5 | Cylindrical shell shape and kidney-shaped aperture, shell height 6.6–8.5 mm.... | <i>C. pacifica</i> |
| – | Moderately inflated shell shape and triangular aperture, shell height 7.2–8.8 mm..... | <i>C. tsudai</i> |

Morphometric, genetic, and biogeographic information has led to the introduction of a new species of the warm water pteropod genus *Cuvierina* and the rejection of its

subgenera. We encourage a combined evidence approach of taxonomy to more accurately identify species boundaries and higher taxonomic relationships in planktonic gastropods. Accurate taxonomic identification is a prerequisite to assess to what extent species are affected by ocean changes and to potentially use them as bioindicators.

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References

- Bé AWH, MacClintock C, Currie DC (1972) Helical shell structure and growth of the pteropod *Cuvierina columnella* (Rang) (Mollusca, Gastropoda). *Biom mineralization Research Reports* 4: 47–79.
- Bé AWH, Gilmer RW (1977) A zoogeographic and taxonomic review of euthecosomatous Pteropoda. In: Ramsay ATS (Ed.) *Oceanic Micropaleontology* 1. Academic Press, London, 733–808.
- Bednaršek N, Možina J, Vogt M, O'Brien C, Tarling GA (2012) The global distribution of pteropods and their contribution to carbonate and carbon biomass in the modern ocean. *Earth System Science Data* 4: 167–186. doi: 10.5194/essd-4-167-2012
- Bednaršek N, Ohman MD (2015) Changes in pteropod distributions and shell dissolution across a frontal system in the California Current System. *Marine Ecology Progress Series* 523: 93–103. doi: 10.3354/meps11199
- Boas JEV (1886) *Spolia atlantica*. Bidrag til Pteropodernes. Morfologi og Systematik samt til Kundskaben om deres geografiske Udbredelse. Videnskabernes Selskab Skrifter 6. Naturvidenskabelig og matematisk Afdeling 4(1): 1–231.
- Burridge AK, Goetze E, Raes N, Huisman J, Peijnenburg KTCA (2015) Global biogeography and evolution of *Cuvierina* pteropods. *BMC Evolutionary Biology* 15: 39. doi: 10.1186/s12862-015-0310-8 [Additional data available at doi: 10.5061/dryad.7n1q4]
- Burridge AK, Goetze E, Wall-Palmer D, Le Double SL, Huisman J, Peijnenburg KTCA (2016) Diversity and abundance of pteropods and heteropods along a latitudinal gradient across the Atlantic Ocean. *Progress in Oceanography* 65: 414–432. doi: 10.1016/j.pocean.2016.08.003
- Fabry VJ, Seibel BA, Feely RA, Orr JC (2008) Impacts of ocean acidification on marine fauna and ecosystem processes. *ICES Journal of Marine Science* 65: 414–432. doi: 10.1093/icesjms/fsn048

- Gattuso J-P, Magnan A, Billé R, Cheung WWL, Howes EL, Joos F, Allemand D, Bopp L, Cooley SR, Eakin CM, Hoegh-Guldberg O, Kelly RP, Pörtner H-O, Rogers AD, Baxter JM, Laffoley D, Osborn D, Rankovic A, Rochette J, Sumaila UR, Treyer S, Turley C (2015) Contrasting futures for ocean and society from different anthropogenic CO₂ emissions scenarios. *Science* 349: aac4722 1–10.
- Gray JE (1840) Shells of molluscos animals. In: Synopsis of the contents of the British Museum, 42: 105–152.
- Janssen AW (2005) Development of Cuvierinidae (Mollusca, Euthecosomata, Cavolinioidea) during the Cainozoic: a non-cladistic approach with a re-interpretation of recent taxa. *Basteria* 69: 25–72.
- Janssen AW (2006) Notes on the systematics, morphology and biostratigraphy of fossil holoplanktonic Mollusca, 16. Some additional notes and amendments on Cuvierinidae and on classification of Thecosomata (Mollusca, Euthecosomata). *Basteria* 70(1–3): 67–70.
- Jörger KM, Stöger I, Kano Y, Fukuda H, Kneibelsberger T, Schrödl M (2010) On the origin of Acochlidia and other enigmatic euthyneuran gastropods, with implications for the systematics of Heterobranchia. *BMC Evolutionary Biology* 10: 323. doi: 10.1186/1471-2148-10-323
- Kendall D (1977) The diffusion of shape. *Advances in Applied Probability* 9: 428–430. doi: 10.1017/S0001867800028743
- Lalli CM, Gilmer RW (1989) Pelagic snails: the biology of holoplanktonic gastropod molluscs. Stanford University Press, Stanford, California, 380 pp.
- Lesueur CA, Petit N (1807) Voyage de découvertes aus terres Australes exécuté par ordre de S. M. l'Empereur et Roi. Langlois, Paris; atlas, part 1, 40 pls.
- Meisenheimer J (1905) Pteropoda. Wissenschaftliche Ergebnisse der deutschen Tiefsee-Expedition auf dem Dampfer 'Valdivia' 1898-1899, 9, 314 pp.
- Mörch OAL (1850) Catalogus conchyliorum quae reliquit C.P. Kierulf, md. dr. nunc publica auctione X Decembris MDCCCL Havniae Dividenda. Hafniae, Trieri, 33 pp. doi: 10.5962/bhl.title.39642
- Moya A, Howes EL, Lacoue-Labarthe T, Forêt S, Hanna B, Medina M, Munday PL, Ong J-S, Teyssié J-L, Torda G, Watson S-A, Miller DJ, Bijma J, Gattuso J-P (2016) Near-future pH conditions severely impact calcification, metabolism and the nervous system in the pteropod *Heliconoides inflatus*. *Global Change Biology*. doi: 10.1111/gcb.13350
- Pierrot-Bults AC, Peijnenburg KTCA (2015) Pteropods. In: Harff J, Meschede M, Petersen S, Thiede J (Eds) Encyclopedia of marine geosciences. Springer, 1–10. doi: 10.1007/978-94-007-6644-0_88-1
- Rampal J (1975) Les thécosomes (mollusques pélagiques). Systématique et évolution - écologie et biogéographie méditerranéennes. PhD thesis Université de Provence, U.E.R. Scientifiques (Aix-Marseille 1).
- Rampal J (2002) Biodiversité et biogéographie chez les Cavoliniidae (Mollusca, Gastropoda, Opisthobranchia, Euthecosomata). Régions faunistiques marines. *Zoosystema* 24(2): 209–258.
- Rang PCAL (1827) Description de deux genres nouveaux (*Cuvieria* et *Euribia*) appartenant à la classe des ptéropodes. *Annales des Sciences Naturelles* 12: 320–329. [pl. 45B dated 1826]

- Rohlf FJ (2006) Tps series. <http://life.bio.sunysb.edu/morph>
- Tesch JJ (1913) Mollusca, Pteropoda. In: Schulze FE (Ed.) Das Tierreich. Eine Zusammenstellung und Kennzeichnung der rezenten Tierformen, 36. Friedländer & Sohn, Berlin, 154 pp.
- Van der Spoel S (1967) Euthecosomata, a group with remarkable developmental stages (Gastropoda, Pteropoda), PhD thesis. University of Amsterdam, Noorduijn en Zoon, Gorinchem.
- Van der Spoel S (1970) Morphometric data on Cavoliniidae, with notes on a new form of *Cuvierina columnella* (Rang, 1827) (Gastropoda, Pteropoda). Basteria 34: 103–151.
- Van der Spoel S, Heyman RP (1983) A comparative atlas of zooplankton: biological patterns in the oceans. Springer, New York, 186 pp. doi: 10.1007/978-3-662-02366-2
- Zelditch ML, Swiderski DL, Sheets HD, Fink WL (2004) Geometric morphometrics for biologists. Elsevier Academic Press, San Diego and London, 437 pp.

A new species of *Aulacaspis* Cockerell, 1893 from China with a key to Chinese species (Hemiptera, Coccoidea, Diaspididae)

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Abstract

A new species of armored scale insect, *Aulacaspis zunyiensis* **sp. n.** is described and illustrated from collections on cycads in China. A key to the *Aulacaspis* species known from China is provided.

Keywords

Aulacaspis, China, Diaspididae, Hemiptera, new species

Introduction

The scale insects or Coccoidea are small, sap-sucking insects with at least 30 families and approximately 8000 species (Andersen et al. 2010; Hodgson and Peronti 2012), sister to Aphidoidea in the suborder Sternorrhyncha. Together with Psylloidea and Aleyrodoidea, they comprise the hemipterous suborder Sternorrhyncha (Kondo et al. 2008).

Diaspididae is the largest family of scale insects with over 2650 described species in around 400 genera as currently known (García et al. 2016). Conventionally, new species of armored scales are diagnosed based on extreme modification of the adult

females, with the complete loss of legs, reduction of the eyes and antennae, and modification in the terminal segments of abdomen (Andersen et al. 2010). Many armored scale insects are agricultural pests and invasive species (Miller et al. 2005). The higher classification within the family is inconsistent, but two of the major subfamilies are the Aspidiotinae and the Diaspidinae.

The genus *Aulacaspis* Cockerell, 1893 is a large group of Diaspididae that belongs to the subfamily Diaspidinae. The genus was originally established by Cockerell (1893) with *Aspidiotus rosae* Bouché, 1833 as the type species. Since the introduction of the generic name *Aulacaspis*, many additional species have been described (e.g., Chen 1983; Chou 1982; Tang 1986; Takagi 1961, 1967; 1970; 1988; 1998; 1999; 2009; 2010a; 2010b; 2012a; 2012b; 2013; 2014; 2015; Williams 1988; 2010; Rutherford 1915; Robinson 1917; Takahashi 1931). The genus currently comprises 120 species (García et al. 2016; Takagi. 2012b; 2013; 2015), which occur in almost all zoogeographical regions except Antarctica (Suh 2013) and most are found in the Oriental and Palaearctic regions (Suh 2013). The species of this genus are associated with diverse plants and mostly feed on woody angiosperms (Takagi 2015). Some species of *Aulacaspis*, such as *A. rosae* (Bouché) and *A. yasumatsui* Takagi, are considered to be serious pests of ornamental plants (Milek et al. 2008; Miller et al. 2005; Watson and Marler 2014). China is the largest distributional region according to records of *Aulacaspis*, with 55 species having been reported in this country.

Recently, a new species of *Aulacaspis* was discovered in China, and it is described and illustrated herein, bringing the number of species recorded in this genus to 121, of which 56 are recorded from China. A key to the Chinese species of *Aulacaspis* is provided.

Materials and methods

Infested plant samples were collected in the field. Permanent slide mounts of adult females from the samples were made according to Henderson (2011). The illustrations of the adult female are drawn from slide-mounted specimens, with the figure displaying the dorsal body surface on the left side and the ventral body surface on the right side. Enlargements of significant features are located around the body. The morphological terminology and measurements in the descriptions follows those of Miller and Davidson (2005). The abbreviations in the text refer to different pygidial lobes: L1 stands for the median lobes, L2 for the second pair of lobes, L3 for the third pair of lobes, and L4 for the fourth pair of lobes. All measurements are given in micrometres (µm). Measurements were made using the measurement tools NIT-Elements D.

The type series of the new species is deposited in the Insect Collection of Shanxi Agricultural University, Taigu, Shanxi Province, China.

Taxonomy

Aulacaspis Cockerell

Aulacaspis Cockerell, 1893: 180.

Type species. *Aspidiotus rosae* Bouché: by subsequent designation by Newstead, 1901: 168.

Generic diagnosis. Female scale. White, circular, exuviae located on front end.

Male scale. White, long and narrow, exuviae located on front end.

Adult female. Body shape varied, mushroom-shaped, fusiform or cuniform; derm membranous except for the margin of pygidium; prosoma swollen or wider than metathorax and abdomen, slightly squared in most species. *Cephalothorax.* Antennae each with a seta. Anterior spiracles each usually with a cluster of trilocular pores, posterior spiracles each with or without associated trilocular pores. Dorsal ducts present or absent on prosoma, scattered. *Pygidium.* Usually with three pairs of lobes (rarely with two or four pairs). Median lobes (L1) well-developed, much larger than lobules of lateral lobes, zygotic basally, without marginal setae between lobes. In general, L1 are divided into two types depending on feeding site: bark-type, where individuals occur on bark and L1 protrudes at the end of the pygidium; and leaf-type, on leaves and L1 is sunken into the end of pygidium. Second lobes (L2) much smaller than L1, bilobed, divided into inner lobule and outer lobule, outer lobule usually smaller than inner. Third lobes (L3) smaller than L2, bilobed, outer lobule smaller than inner. Fourth lobes (L4) present in some species and usually represented by serrations along the body margin. *Gland spines.* Marginal gland spines developed, present on lateral of abdominal segment II and III; usually single on abdominal segments V-VIII, but in some species there are two or more. Marginal gland spines becoming shorter to conical on anterior segments; in some species they are called gland tubercles. *Ducts.* Dorsum with double-barred ducts. Marginal macroducts of pygidium usually larger than dorsal macroducts. Dorsal macroducts forming submedial and submarginal rows on abdominal and pygidium, sometimes occurring in two sizes. Ventral microducts scattered. *Anal opening* situated at the center of the pygidium, small. Perivulvar disc pores in five groups.

Remarks. Members of this genus, like other members of the subfamily Diaspidinae, have a pygidium with macroducts of the two-barred type, the second pygidial lobe bilobulate, and fringed plates absent between the lobes, but *Aulacaspis* is distinguished from other genera, especially *Chionaspis* Signoret, 1868 by having a remarkably swollen prosoma. Moreover, *Aulacaspis* lacks lateral macroducts and gland spines on abdominal segment I and on the thorax, present in these locations on *Chionaspis*. Furthermore, *Pseudaulacaspis* MacGillivray, 1921 is similar in features of the body, but can be distinguished by the presence of a pair of setae between the L1, which are absent in *Aulacaspis*.

***Aulacaspis zunyiensis* sp. n.**

<http://zoobank.org/D255B8CB-9DCB-4902-BBD1-2B12486EF0CF>

Figures 1–9

Material examined. Holotype and 11 paratypes, adult female. China: Guizhou Province. Zunyi city, longitude 106.9122, latitude: 27.7087, on *Cycas revoluta* Thunb, 17.vii. 2015, leg. Weijiufeng and Niu Minmin.

Description. Female scale. Adult female cover convex, circular white; exuvia on front end. **Male scale.** Not recorded.

Adult female. Slide-mounted adult female 1150–1301 μm long (holotype 1246 μm long); widest part of body 901–950 μm wide (holotype 922 μm wide). Body outline fusiform, derm membranous except for pygidium. Usually widest at mesothorax, lateral abdominal and thoracic lobes well-developed; prosomatic tubercles slightly produced. *Cephalothorax.* Antennae each with one seta. Anterior spiracles each with 14–16 trilocular pores in a cluster, posterior spiracles without trilocular pores. *Pygidial lobes.* With three pairs of lobes; L1 well-developed, zygotic basally, much larger than lateral lobes; protruding from pygidial margin, with one deep notch and small serrations on outer margin and one obvious notch on apex. Without setae between median lobes; L2 bilobate, inner lobule rounded, much larger than outer lobule, outer lobule very small, smaller than L3, a pair of obvious paraphyses arising from the mesal margin of the L2 lobes. L3 bilobate, slightly smaller than L2. *Gland spines.* One present between L1 and L2, one present between L2 and L3, two present on abdominal segment VI, 3–5 on abdominal segment III, 4–5 on abdominal segment IV, 5–6 on abdominal segment V, 1–2 on abdominal segment II, 0–1 on abdominal segment I. Gland spines on segment I and II shorter than those on other segments. *Ventral gland tubercles* present on submargins of metathorax and abdominal segments I and II. *Ducts.* Marginal macroducts, of two-barred type, 12.8–16.3 μm long (holotype 16.0 μm long), absent between L1, one present between L1 and L2, two present between L2 and L3, two present on the abdominal segment V. Dorsal macroducts on pygidium and abdominal segments shorter than marginal macroducts; 8.5–10.2 μm long (9.6 μm long), of two-barred type, arranged segmentally in submedian and submarginal rows; submarginal dorsal macroducts present on abdominal segment II to V: 10–11 on segment II, 8–9 on segment III, 5–6 on segment IV, 4–7 on segment V; submedian dorsal macroducts present on segment II to V: 4–6 on segment II, 5–6 on segment III, 4–5 on segment IV, 3–6 on segment V. Lateral macroducts few, 5–7 in total, present between abdominal II and III, of which, 2–3 on segment II, 3–4 on segment III, smaller than dorsal ducts present on abdominal and pygidium. Ventral microducts scattered on pygidium, few. *Anal opening* small, in holotype posterior margin of anal opening is situated 155 μm from base of L1. Perivulvar pores in five groups, 13–16 in the median group, 30–35 in each of the anteriolateral and 29–30 in each of the posteriolateral groups.

Remarks. This species is very similar to *A. maesae* (Takagi, 1970) in body shape. But differs in having (character-states on *A. maesae* in brackets): (i) posterior spiracle

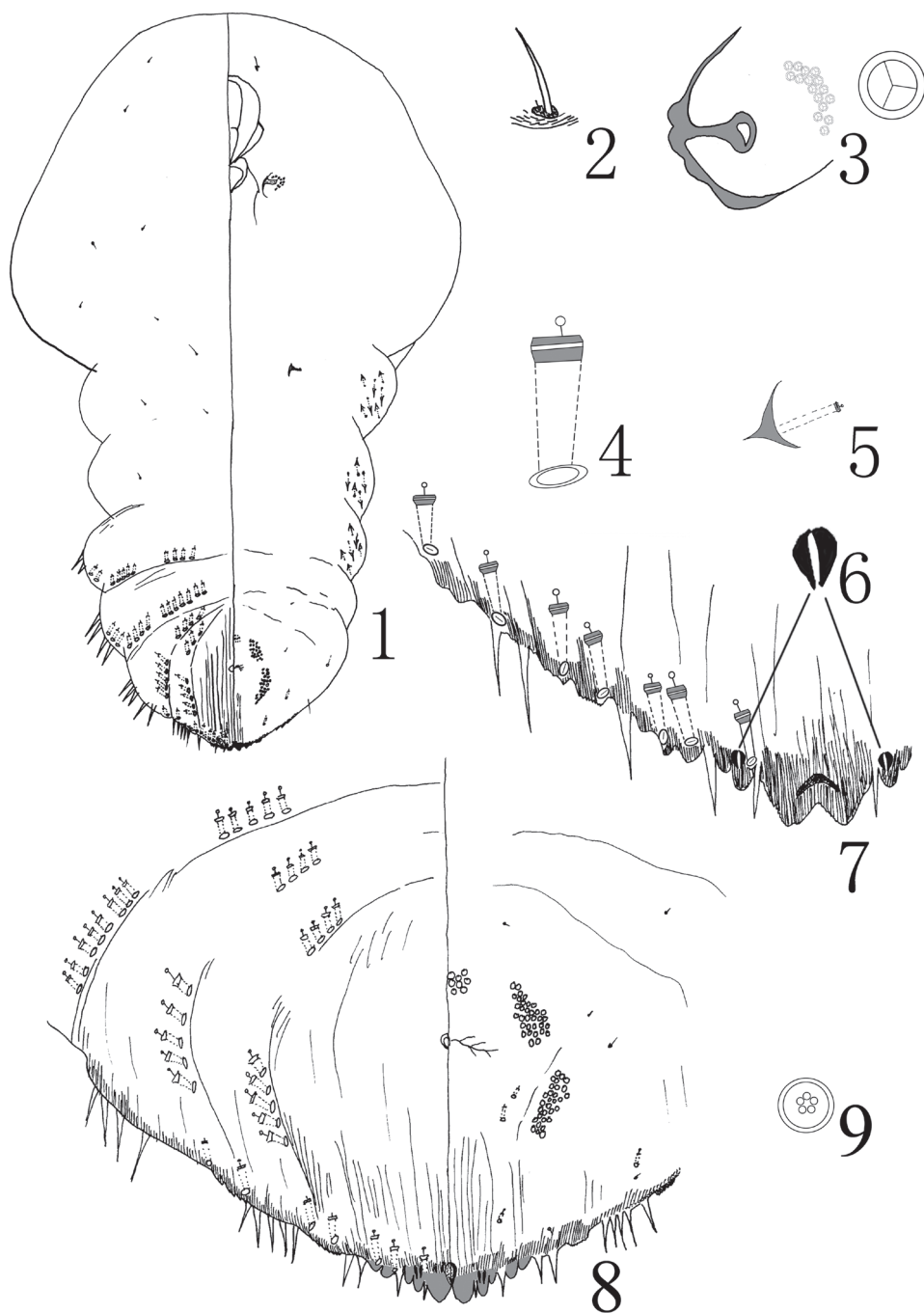


Figure 1–9. *Aulacaspis zunyiensis* Wei & Jing, sp. n., adult female; **1** habitus **2** antennae **3** anterior spiracle **4** detail of dorsal gland macroduct **5** gland tubercles **6** paraphyses **7** detail of end of pygidium **8** pygidium **9** quinquelocular pores.

without trilocular pores (posterior spiracle with trilocular pores); (ii) dorsal macroducts absent from submedial region of abdominal segment VI (present); (iii) dorsal macroducts absent from submedial region of abdominal segment II (present).

Host plant. *Cycas revoluta* Thunb.

Etymology. The specific epithet is named after Zunyi, the type locality.

Distribution. China (Guizhou).

Key to adult female *Aulacaspis* Cockerell from China

(The descriptions of three species, *A. aceris* Takahashi, *A. formosana* Takahashi, and *A. depressa* Zehntner are inadequate for inclusion in this key)

- 1 Trilocular pores absent near each posterior spiracle.....2
- Trilocular pores present near each posterior spiracle9
- 2 Dorsal microducts present on abdominal segment I, II, III....*A. vitis* (Green)
- Dorsal microducts present on abdominal segment I, II, III.....3
- 3 Dorsal macroducts present on submarginal and submedial area of abdominal segment II.....4
- Dorsal macroducts absent from submarginal and submedial area of abdominal segment II.....5
- 4 Dorsal macroducts present on submedial area of abdominal segment VI*A. yunnanensis* (Feng)
- Dorsal macroducts absent from submedial area of abdominal segment VI....*A. zunyiensis* sp. n.
- 5 Dorsal macroducts absent from submarginal and submedial area of abdominal segment II.....6
- Dorsal macroducts present on submarginal and submedial area of abdominal segment II.....*A. pudica* (Ferris)
- 6 With two or three dorsal macroducts present on submedial area of abdominal segment VI*A. fagraeae* (Green)
- With one or no dorsal macroducts present on submedial area of abdominal segment I.....7
- 7 Dorsal macroducts absent from submedial area of abdominal segment VI.....*A. oblonga* (Chen)
- Dorsal macroducts present on submedial area of abdominal segment VI8
- 8 With spur present on each of abdominal segment IV and V, submedial dorsal microducts present on abdominal II and III.....*A. calcarata* Takagi
- Without spur on abdominal segment IV and V, submedial dorsal microducts present on abdominal segment III, absent from abdominal II.....*A. schizosoma* (Takagi)
- 9 Dorsal macroducts present on submarginal area of abdominal segment VI.....10
- Dorsal macroducts absent from submarginal area of abdominal segment VI...11

- 10 Submedial dorsal macroducts present on abdominal segment II, forming double row; dorsal submarginal macroducts present on abdominal segment II ***A. difficilis* (Cockerell)**
- Submedial dorsal macroducts present on abdominal segment II, forming single row; dorsal submarginal macroducts absent from abdominal segment II ***A. altiplagae* Chen**
- 11 Submedial dorsal macroducts absent from abdominal segment II ***A. litzeae* (Green)**
- Submedial dorsal macroducts present on abdominal segment III **12**
- 12 Dorsal macroducts absent from abdominal segment II **13**
- Dorsal macroducts present on abdominal segment II **34**
- 13 Dorsal microducts present on submedial of abdominal segment I, II **14**
- Dorsal microducts absent from submedial of abdominal segment I and II **15**
- 14 With four pairs of lobes on pygidium ***A. madiunensis* (Zehntner)**
- With three pairs of lobes on pygidium ***A. ferrisi* Scott**
- 15 Both submedial and submarginal dorsal macroducts present on abdominal segment V and VI, forming double row **16**
- Both submedial and submarginal dorsal macroducts present on abdominal segment V and VI, forming single row **17**
- 16 With four pairs of lobes on pygidium; L1 protrude the end of pygidium ***A. wakayamaensis* (Kuwana)**
- With three pairs of lobes on pygidium; L1 sunken into the apex of the pygidium ***A. saigusai* Takagi**
- 17 Submedial dorsal macroducts forming double row on abdominal segment IV ... **18**
- Submedial dorsal macroducts forming single row on abdominal segment IV ... **21**
- 18 Prosomatic tubercles robust; only 1 dorsal macroduct on abdominal segment VI **19**
- Prosomatic tubercles not discernible; with more than 2 dorsal macroducts on abdominal segment VI **20**
- 19 Postsoma robust, with abdominal segment II strongly lobed out laterally; basal zygonia of L1 distinct ***A. yabunikkei* (Kuwana)**
- Postsoma slender, with the pygidium rather narrow; basal zygonia of L1 inconspicuous ***A. alisiana* (Takagi)**
- 20 Anterior spiracles with about 20 trilocular pores; with 3 pairs of lobes on pygidium ***A. sassafra* Chen, Wu & Su**
- Anterior spiracles with about 70 trilocular pores; with 4 pairs of lobes on pygidium ***A. tegalensis* (Zehntner)**
- 21 Submedial dorsal macroducts present on abdominal segment III, forming double row **22**
- Submedial dorsal macroducts present on abdominal segment III, forming single row **24**
- 22 Dorsal macroducts absent from abdominal VI ***A. robusta* Takahashi**
- Dorsal macroducts present on abdominal VI **23**

- 23 With more than three dorsal submedial macroducts on abdominal VI; anterior spiracles with 19 trilocular pores; the widest of body present on head
.....*A. amamiana* Takagi
- With only one dorsal submedial macroducts on abdominal VI; anterior spiracles With 10 trilocular pores; the widest of body present on prothorax.....
.....*A. ima* Scott
- 24 Gland spines present on abdominal segment II.....*A. nitida* Scott
- Gland spines absent from abdominal segment II.....25
- 25 Submedial dorsal macroducts absent from abdominal segment VI.....26
- Submedial dorsal macroducts present on abdominal segment VI.....28
- 26 Prosoma well swollen; with more than 11 gland spines on abdominal segment III.....*A. sirodamo* Takagi
- Prosoma not swollen; with less than ten gland spines on abdominal segment III.....27
- 27 Posterior spiracles with 4–5 trilocular pores; with slender paraphyses placed at base of L1*A. fuzhouensis* Tang
- Posterior spiracles with 2–3 trilocular pores; without slender paraphyses placed at base of L1.....*A. latissima* (Cockerell)
- 28 Prosomatic tubercles robust29
- Prosomatic tubercles not discernible30
- 29 With a pair of elongate scleroses on the base of L1; only 1 dorsal macroduct present on abdominal segment VI; anterior spiracles each with 4–5 trilocular pores.....*A. tubercularis* (Newstead)
- Without a pair of elongate scleroses on the base of L1 ; with 2–3 dorsal macroducts on abdominal segment VI; anterior spiracles each with 8–13 trilocular pores.....*A. rosae* (Bouché)
- 30 Without dorsal microducts on prosoma.....31
- With dorsal microducts on prosoma.....33
- 31 L1 almost parallel on inner basal margins, then strongly divergent to their apices; gland tubercles absent from segment I32
- L1 sunken into the apex of pygidium, forming a large notch at the apex of the pygidium; gland tubercles present on segment I....*A. actinodaphnes* Takagi
- 32 Only one submedial macroduct present on abdominal segment III; prosoma as broad as or slightly wider than postsoma.....*A. bedyotidis* (Green)
- With 2–8 submedial macroducts on abdominal segment III; prosoma swollen, distinctly wider than postsoma.....*A. ericacearum* Takagi
- 33 L1 sunken into the apex of pygidium, forming a large notch at the apex of the pygidium; anterior spiracles each with 16 trilocular pores; only one submedial macroducts on abdominal segment VI*A. yasumatsui* Takagi
- L1 almost parallel on inner basal margins, then strongly divergent to their apices; anterior spiracles each with 30–50 trilocular pores; with 2–4 submedial macroducts on abdominal segment VI*A. machili* (Takahashi)

34	Submedial dorsal macroducts present on abdominal segment I, forming a double row.....	35
–	Submedial dorsal macroducts present or absent on abdominal segment I; if present, forming single row.....	41
35	Submedial dorsal macroducts present on segment VI, forming double or triple row.....	<i>A. murrayae</i> (Takahashi)
–	Submedial dorsal macroducts present or absent on segment VI; if present, forming a single row	36
36	Submarginal dorsal macroducts present on abdominal segment II, forming a double row.....	37
–	Submarginal dorsal macroducts present on abdominal segment II, forming a single row	38
37	Both submedial and submarginal dorsal macroducts present on abdominal segment I	<i>A. actinidiae</i> Takagi
–	Both submedial and submarginal dorsal macroducts absent from abdominal segment I	<i>A. spinosa</i> (Maskell)
38	Submarginal dorsal macroducts present on abdominal segment I	<i>A. citri</i> Chen
–	Submarginal dorsal macroducts absent from abdominal segment I	39
39	Submarginal dorsal macroducts present on abdominal segment II and III, forming double row, gland tubercles present on segment I	<i>A. intermedius</i> (Chen, Wu & Su)
–	Submarginal dorsal macroducts present on abdominal segment II and III, forming single row, gland tubercles absent from segment I	40
40	L1 projecting beyond apex of pygidium; anterior spiracles each with 40–60 trilocular pores, posterior spiracles each with 20–30 trilocular pores	<i>A. projecta</i> Takagi
–	L1 sunken into the apex of pygidium; anterior spiracles each with less than 30 trilocular pores, posterior spiracles each with 2–7 trilocular pores	<i>A. crawii</i> (Cockerell)
41	Dorsal macroducts forming a double row on submedial area of abdominal segment I	42
–	Dorsal macroducts forming a single row on submedial area of abdominal segment I	46
42	Dorsal macroducts forming a double row on submedial area of abdominal segment IV	43
–	Dorsal macroducts forming a single row on submedial area of abdominal segment IV	44
43	Prosomatic tubercles robust; L1 parallel on inner basal margins, then strongly divergent to their apices	<i>A. rosarum</i> (Borchsenius)
–	Prosomatic tubercles not discernible; L1 sunken into the apex of pygidium, forming a large notch at the apex of the pygidium	<i>A. megaloba</i> Scott

44	L1 sunken into the apex of pygidium, forming a large notch at the apex of the pygidium	<i>A. litseae</i> Tang
–	L1 almost parallel on inner basal margins, then strongly divergent to their apices.....	45
45	Prosomatic tubercles robust; with 4–5 dorsal macroducts on submarginal area of abdominal segment V	<i>A. guangdongensis</i> Chen, Wu & Su
–	Prosomatic tubercles not discernible; with 1 dorsal macroduct on submarginal area of abdominal segment V	<i>A. longanae</i> Chen, Wu & Su
46	Dorsal macroducts forming a double row on submedial area of abdominal segment III	47
–	Dorsal macroducts forming a single row on submedial area of abdominal segment III	50
47	Dorsal macroducts present on abdominal segment I	48
–	Dorsal macroducts absent from abdominal segment I	49
48	Prosomatic tubercles robust; marginal macroducts between L1 and L2 longer than the length of L1; inner margin of L1 slightly serrate	<i>A. greeni</i> Takahashi
–	Prosomatic tubercles not discernible; marginal macroducts between L1 and L2 equal or shorter than the length of L1; inner margin of L1 not serrate.....	<i>A. phoebicola</i> Takahashi
49	Dorsal macroducts present on submedial area of abdominal segment II, forming double row; anterior spiracles with 30 trilocular pores.....	<i>A. acronymychiae</i> Takagi & Martin
–	Dorsal macroducts present on submedial area of abdominal segment II and IV, forming single row; anterior spiracles with 15 trilocular pores.....	<i>A. thoracica</i> (Robinson)
50	Dorsal macroducts present on submedial area of abdominal segment VI ..	51
–	Dorsal macroducts absent from submedial area of abdominal segment VI	<i>A. neospinosa</i> Tang
51	Both submedial and submarginal dorsal macroducts present on abdominal segment I	<i>A. divergens</i> (Takahashi)
–	Both submedial and submarginal dorsal macroducts absent from abdominal segment I	<i>A. maesae</i> Takagi

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References

- Andersen JC, Wu J, Gruwell ME, Morse GE, Santana S, Feliciano N, Gwiazdowski RA, Normark BB (2010) A phylogenetic analysis of armored scale insects, based up on nuclear, mitochondrial, and endosymbiont gene sequences. *Molecular Phylogenetics and Evolution* 57: 992–1003. doi: 10.1016/j.ympev.2010.05.002
- Bouché PF (1833) *Naturgeschichte der Schädlichen und Nützlichen Garteninsekten und die bewährtesten Mittel*. Nicolai Berlin, 176 pp. doi: 10.5962/bhl.title.9692
- Chen FG (1983) *The Chionaspidini (Diaspididae, Coccoidea, Homoptera) from China*. Science & Technology Publishing House. Sichuan Province, China, 175 pp.
- Chou I (1982) *Monograph of the Diaspididae of China*. Vol. 1. Shanxi Publ. House of Science & Technology, Shanxi, 195 pp.
- Cockerell TDA (1893) Museum notes, Coccidae. *Journal of the Institute of Jamaica* 1: 1–180.
- Feng JN, Wang PM, Li LM, Chou I (2004) Two new species of the Family Diaspididae (Homoptera: Diaspididae) from China. *Entomotaxonomia* 26(1): 19–22.
- García M, Denno B, Miller DR, Miller GL, Ben-Dov Y, Hardy NB (2016) ScaleNet: A Literature-based model of scale insect biology and systematics. <http://scalenet.info> [accessed: 2016]
- Henderson RC (2011) *Diaspididae (Insecta: Hemiptera: Coccoidea)*. Fauna of New Zealand 66. Manaaki Whenua Press, Lincoln, Canterbury, 275 pp.
- Hodgson CJ, Peronti LBG (2012) A revision of wax scale insects (Hemiptera: Sternorrhyncha: Coccoidea: Ceroplastinae) of the Afrotropical Region. *Zootaxa* 3372: 1–265.
- Kondo T, Gullan PJ, Williams DJ (2008) Coccidology. The study of scale insects (Hemiptera: Sternorrhyncha: Coccoidea). *Revista Corpoica – Ciencia y Tecnología Agropecuaria* 9(2): 55–61.
- Milek TM, Šimala M, Novak A (2008) Species of genus *Aulacaspis* Cockerell, 1836 (Hemiptera: Coccoidea: Diaspididae) in Croatia, with emphasis on *Aulacaspis yasumatsui* Takagi, 1977. *Entomology of Croatia* 12(1): 55–64.
- Miller DR, Davidson JA (2005) *Armored Scale Insect Pests of Trees and Shrubs (Hemiptera: Diaspididae)*. Cornell University Press, Ithaca, 456 pp.
- Newstead R (1901) *Monograph of the Coccidae of the British Isles*. Ray Society, London, 220 pp.
- Robinson E (1917) Coccidae of the Philippine Islands. *Philippine Journal of Science (Ser. D.)* 12: 1–47.
- Rutherford A (1915) Some new Ceylon Coccidae. *Journal of the Bombay Natural History Society* 24: 111–118.
- Suh SJ (2013) On the armored scales, genus *Aulacaspis* Cockerell (Hemiptera: Diaspididae) of Korea. *Insecta Mundi* 2095: 1–8.
- Takahashi R (1931) Descriptions of some new Formosan Coccidae. (Rhynchota). *Bulletin of Entomological Research* 22: 211–220. doi: 10.1017/S0007485300035173
- Takagi S (1961) A contribution to the knowledge of the Diaspidini of Japan (Homoptera: Coccoidea) Pt. III. *Insecta Matsumurana* 24: 69–103.
- Takagi S (1967) Examinations of the type slides of three Diaspididae described from Japan (Homoptera: Coccoidea). *Insecta Matsumurana* 30(1): 52–55.

- Takagi S (1970) Diaspididae of Taiwan based on material collected in connection with the Japan-US co-operative science programme, 1965 (Homoptera: Coccoidea) Part II. *Insecta Matsumurana* 33(1): 1–142.
- Takagi S (1988) A possible case of site-caused polymorphism in *Aulacaspis* (Homoptera: Coccoidea: Diaspididae). *Insecta Matsumurana* 39: 49–63.
- Takagi S, Williams DJ (1998) A new mangrove-infesting species of *Aulacaspis* occurring in South-east Asia, with a revision of *A. vitis* (Homoptera: Coccoidea: Diaspididae). *Insecta Matsumurana* 54: 51–76.
- Takagi S (1999) For a better understanding of *Aulacaspis*: the *calcarata* species group (Homoptera: Coccoidea: Diaspididae). *Insecta Matsumurana* 55: 133–180.
- Takagi S (2009) Notes on scale insects of *Aulacaspis* associated with mangroves and cycads (Sternorrhyncha: Coccoidea: Diaspididae). *Insecta Matsumurana* 55: 133–180.
- Takagi S, Martin JH (2010a) A new scale insect genus from Hongkong: another clue to the Rugaspidiotini-Problem (Sternorrhyncha: Coccoidea: Diaspididae). *Insecta Matsumurana* 66: 37–55.
- Takagi S (2010b) The tubercularis species group of *Aulacaspis* (Sternorrhyncha: Coccoidea: Diaspididae). *Insecta Matsumurana* 66: 57–144.
- Takagi S (2012a) Two new species of *Aulacaspis* from Japan, with notes on a strange organ and seasonal variation (Sternorrhyncha: Coccoidea: Diaspididae). *Insecta Matsumurana* 68: 117–132.
- Takagi S (2012b) Atypical species of *Aulacaspis* (Sternorrhyncha: Coccoidea: Diaspididae). *Insecta Matsumurana* 68: 17–115.
- Takagi S (2013) Some species of *Aulacaspis* related to Mangrove-associated Australian species (Sternorrhyncha: Coccoidea: Diaspididae). *Insecta Matsumurana* 69: 41–95.
- Takagi S (2014) The *yabunikkei* complex and some other species of *Aulacaspis* occurring on Lauraceae (Sternorrhyncha: Coccoidea: Diaspididae). *Insecta Matsumurana* 70: 89–151.
- Takagi S (2015) Notes on scale insects of the genus *Aulacaspis* occurring on grasses and herbs (Sternorrhyncha: Coccoidea: Diaspididae). *Insecta Matsumurana* 71: 121–177.
- Tang FT (1986) The scale insects of horticulture and forest of China. Volume III. Shanxi Agricultural University Press Taigu, Shanxi, 305 pp.
- Watson GW, Marler TE (2014) Does cycad *Aulacaspis* scale insect (*Aulacaspis yasumatsui*, Hemiptera: Diaspididae) play a direct role in causing soil phytotoxicity? *Communicative & Integrative Biology* March (2014): e27881.
- Williams DJ, Watson GW (1988) The Scale Insects of the Tropical South Pacific Region. Pt. 1. The Armoured Scales (Diaspididae). CAB International Wallingford, 290 pp.
- Williams DJ, Miller DR (2010) Scale insects (Hemiptera: Sternorrhyncha: Coccoidea) of the Krakatau Islands including species from adjacent Java. *Zootaxa* 2451: 43–52.
- Zhou CY, Zhao GD, Liu WA, Fu YS, Guo XS (2011) A new species of *Aulacaspis* Cockerell (Hemiptera: Diaspididae) from China. *Transactions of the American Entomological Society* 137(3+4): 373–377.

Immature stages of giants: morphology and growth characteristics of *Goliathus* Lamarck, 1801 larvae indicate a predatory way of life (Coleoptera, Scarabaeidae, Cetoniinae)

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Abstract

The third larval instar of *Goliathus goliatus* (Drury, 1770), *G. orientalis* Moser, 1909 and *G. albosignatus* Boheman, 1857 are described and illustrated for the first time and compared with the immature stages of other Cetoniinae. Larval development of *G. goliatus* is investigated under laboratory conditions, with particular emphasis on food requirements. These results support the obligatory requirement of proteins in the larval diet. The association between larval morphological traits (e. g., the shape of the mandibles and pretarsus, presence of well-developed stemmata) and larval biology is discussed. Based on observations and the data from captive breeds it is concluded that a possible shift from pure saprophagy to an obligatory predaceous way of larval life occurred within the larvae of this genus, which may explain why these beetles achieve such an enormous size.

Keywords

Afrotropical region, captive breeding, *Goliathus*, growth trajectories, immature stages, larval development, nutrition shift, rose chafers

Introduction

Goliath beetles (*Goliathus* Lamarck, 1801) are among the largest beetles in the world and undoubtedly the largest of the subfamily Cetoniinae. With their size exceeding 11 cm in the largest males, they have been the focus of entomologists' interest for centuries. Strangely enough, their systematics, ecological requirements, and developmental characteristics remain largely unknown and have been poorly investigated. Due to their colour polymorphism and suspected ability of hybridization (Wiebes 1968, Lachaume 1983, McMonigle 2006, Meier (undated)) a vast number of taxonomic names was introduced to cover the variability of the several species attributed to this genus (Marais and Holm 1992, Krajčák 1998). The genus is most commonly considered to encompass five species inhabiting tropical forests and savannas of tropical and subtropical Africa (Krajčák 1998, Sakai and Nagai 1998), but Mawdsley (2013) in concordance with Marais and Holm (1992) includes the closely related genera *Argyrophegges* Kraatz, 1895, and *Hegemus* White, 1845 as subgenera of *Goliathus*. Moreover Wiebes (1968) also included members of the genus *Fornasinius* Berlontoni, 1853 in the genus. Neither of these views is supported in this article. Information on the ecology of the genus is somewhat sparse, and available only for *G. albosignathus* Boheman, 1857 (Holm and Marais 1992). Males are generally larger than females, and use their cephalic horns as well as prolonged forelimbs in combat over feeding spots and females. At least some species are known to aggregate at 'sleeping' trees at dusk (Holm and Marais 1992). Nothing is known of the immature stages and development under natural conditions, however larvae of the closely related genus *Argyrophegges* are suspected to be associated with the burrows of hyrax species (Mammalia: Procaviidae) (Malec (undated)).

The availability of Goliath beetles to breeders has led to the publication of several breeding manuals, which contain very interesting information on the nutritional requirements of larvae (McMonigle 2006). It is generally believed that the genus is difficult to breed and that a protein-rich diet is necessary for its successful development. Some breeders even report *Goliathus* larvae to be predaceous (McMonigle 2001, 2006, 2012, Meier 2003, Meier and Campbell (undated)). This is in contrast to most other rose chafers, whose larvae are able to develop successfully on a substrate composed only of decaying plant matter; this is also true for some genera with very large beetles (e.g., *Mecynorhina* Hope, 1837, *Mecynorhinella* Marais & Holm, 1992) (Micó et al. 2008, Christiansen 2013). However, no experimental study has been carried out to confirm or disprove the assumptions made in these breeding manuals.

The immature stages of Goliathini have been described in several works (e.g. Sawada 1991, Donaldson 1992, Nogueira et al. 2004, Šípek et al. 2008, Perissinoto and Orozco 2013). Micó et al. (2008) provide a matrix of 38 larval characters for 12 species of this tribe including the larvae of *Goliathus orientalis* Moser, 1909 and *Fornasinius fornasinii* (Berlontoni, 1852), but without a proper description. Larvae of *Hypsologenia geotrupina* (Bilberg, 1817) described by Oberholzer (1959) thus remain the only known and fully described immature stages of the subtribe Goliathina. According to Nogueira et al. (2004), a knowledge of *Goliathus* immature stages is crucial for a bet-

ter understanding of Cetoniinae phylogeny, and we therefore decided to contribute towards this goal.

The aims of this study are: 1) to describe the third-instar larva of three goliath beetle species – namely *G. goliatus* (Drury, 1770), *G. orientalis* Moser, 1909 and *G. albosignatus* Boheman, 1857 and compare them with larvae of other known Goliathini; 2) to examine larval biology and development, with particular consideration of the importance of proteins in larval growth.

Materials and methods

Origin of material and morphological investigations

Larval material was obtained either by direct breeding of wild collected adults by the authors or donated by other scarab breeders for the purpose of this study: 2 last instar larvae of *G. albosignatus* Boheman, 1857 donated by O. Jahn (Czech Republic), having been reared from beetles imported from Tanzania in 2004; 12 last instar larvae of *G. goliatus* (Drury, 1770) reared from adults imported from Cameroon in December 2010; 6 last instar larvae of *G. orientalis* Moser, 1909 donated by O. Jahn (Czech Republic), having been reared from beetles imported from Tanzania in 2004.

The terminology for larval description follows Hayes (1929), Böving (1936) and Ritcher (1966). Antennomeres I–IV were abbreviated in the description with ‘an I’ – ‘an IV’. In order to provide the most accurate information on chaetotaxy, the hair-like setae of the cranium and other structures, were classified by their relative size into two groups: medium to long (80–300 µm) and minute or small (5–40 µm or less). Morphological observations and measurements were made using a Nikon SMZ 745 stereomicroscope and Olympus BX 40 dissecting microscopes, equipped with an Olympus Camedia 5060 digital camera. Photographs were taken using a Canon 70D digital camera, equipped with a Canon MP-E 65/2.8 macro lens with 5:1 optical magnification and a Canon EFs 60/2.8 macro lens for images of larger body parts. Partially focused images of each specimen were combined using Zerene photo stacker software (Zerene systems LLC, Richland, USA). All pictures were digitally enhanced using Adobe Photoshop CS4.

The specimens included in this study are deposited in the following collections:

- CUPC** Department of Zoology, Charles University, Prague, Czech Republic (Petr Šípek);
NMPC National Museum, Prague, Czech Republic (Martin Fikáček, Jiří Hájek).

Larval rearing and experimental design

For these experiments, larvae obtained by breeding two pairs of goliath beetles (*G. goliatus*) imported from Cameroon in January 2009 were used. They were kept together

in a breeding terrarium (90 × 45 × 55 cm) with a 30 cm deep mixture of soil and leaf litter. The substrate was checked once a week and the newly laid eggs were transferred individually to 500 ml plastic boxes for hatching. The larvae were kept in the same boxes during the entire first and second instar. Third instar larvae were transferred to 1000 ml plastic boxes. Larvae were raised in separate containers during the entire experiment to prevent cannibalism and to allow individual tracking of growth. The breeding substrate was composed of a mixture (1:1) of crushed beech (*Fagus sylvatica*) leaf litter and organic soil (common garden compost). Approximately half of the substrate was replaced with fresh substrate every weighing period. Boxes were kept in a climate chamber at an average temperature of 28°C with a 12:12 L/D cycle. Water was added to the substrate when necessary and the substrate was kept damp but not sopping. The eggs were monitored every other day to determine the date of hatching and newly hatched larvae were randomly divided among three diet regimes.

To examine the dependence of larval development on nutriment, larvae of *G. goliatus* were reared under three different dietary regimes: 1) on substrate with proteins added *ad libitum* ('fully nourished regime', 23 larvae); 2) reared on substrate, but proteins were supplied after a period of starvation ('partly nourished', 11 larvae); and 3) reared on substrate without the addition of proteins during the entire experiment ('undernourished regime', 11 larvae); see below. Some of the larvae were killed at the end of the experiment and used for the study of intestinal microorganisms (Zadrobílková et al. 2016).

The rearing conditions of the initial two instars were identical for all larvae in the experiment. In accordance with the breeding manual (McMoningle 2001, 2012; Meier 2003; Meier and Campbell (undated)) we started to feed all larvae on pellets of soft-moist dog food (FROLIC® Complete with Beef) from the onset of the second instar. These pellets were replaced every weighing session to prevent an excessive growth of mites and other unwanted organisms. In order to monitor the effect of nourishment on larval growth, one cohort of larvae was allowed to continue to feed on pellets ('fully nourished group') from the onset of the third instar whereas the other larvae were denied pellets. A part of the unfed larvae were allowed to resume feeding on pellets at a given point after a period of protein deprivation during the third instar (100–240 days after the onset of the third instar). These individuals are referred to as the 'partly nourished' larvae. The last cohort of larvae ('undernourished group') was raised without a supply of pellets during their entire final instar.

To monitor larval development, we weighed larvae every five days from hatching throughout their entire development using a KERN 450-3M digital scale with a precision to 0.001 g. This weighing interval was chosen in view of the optimal frequency of pellet replacement (McMoningle 2006, 2012; Meier 2003, Meier and Campbell (undated)), which minimizes larval stress and the proliferation of scavenger mites and moulds. For each instar, we determined development time (in days) and maximal mass (in milligrams). In order to compare growth under different feeding regimes in the third instar, we calculated the growth rate at the beginning of the instar and the growth rate just before and after the start of pellet supply to the partly nourished lar-

vae. Growth rate was calculated as a daily mass increment measured over a period of ten days in all aforementioned periods. The initial weight, first recorded at the beginning of the instar was not taken into account because the larvae moult with an empty gut which is refilled after ecdysis, thus growth rate computed with this initial weight would contain false growth caused by new gut content. The recording period before pellet supply was ten days immediately prior to protein addition, after pellet supply it was from the fifth to the fifteenth day after protein addition (pellet supply). The calculating period of growth rate for undernourished larvae was arbitrarily set as the 150th – 160th day after the beginning of the instar which corresponded roughly to the point when the feeding of the partly nourished larvae with proteins began.

Data analysis

To compare the development times and body mass under the food regimes of the first two instars and the final instar we used a one-way ANOVA and Student's t-test, respectively. As initial weight is expected to be correlated with growth rate, differences in growth rate were tested using an ANCOVA with the initial weight of the recording period as covariate. Normality of the data was verified using the Kolmogorov-Smirnov test, the Cochran test indicated that variances were homogeneous so no transformations were necessary. The significance level was set to 0.05. Statistical analyses were performed using the program STATISTICA, version 6.0 (StatSoft Inc. 2001).

Results

Larval morphology

Description of *Goliathus* third instar larvae

Figs 1–3

Live larvae straight, unbent, relatively slim, but C-shaped when killed using standard methods. Abdomen 9-segmented; abdominal segments IX and X fused dorsally, ventral border of the respective segments indicated by an incomplete groove. Abdomen relatively slim, segments I–VI proximally of the same size and thickness as thoracic segments II–III, segments VII and VIII usually slightly thickened, last abdominal segment usually much thinner than the preceding one. Length of larvae studied (third instars) 58–150 mm.

Head capsule (Fig. 1E, G, I): maximum width between 7.5 and 12.8 mm. Surface of cranium with rugose sculpture, dark brown to black, parts of antennae and anteclypeus yellowish-brown. Frontal sutures bisinuate, more or less warped. Epicranial insertions of antennal muscles distinct. Cranial chaetotaxy summarized in Table 1. Setae of cranium generally indistinct, often broken or worn. Anterior and exterior

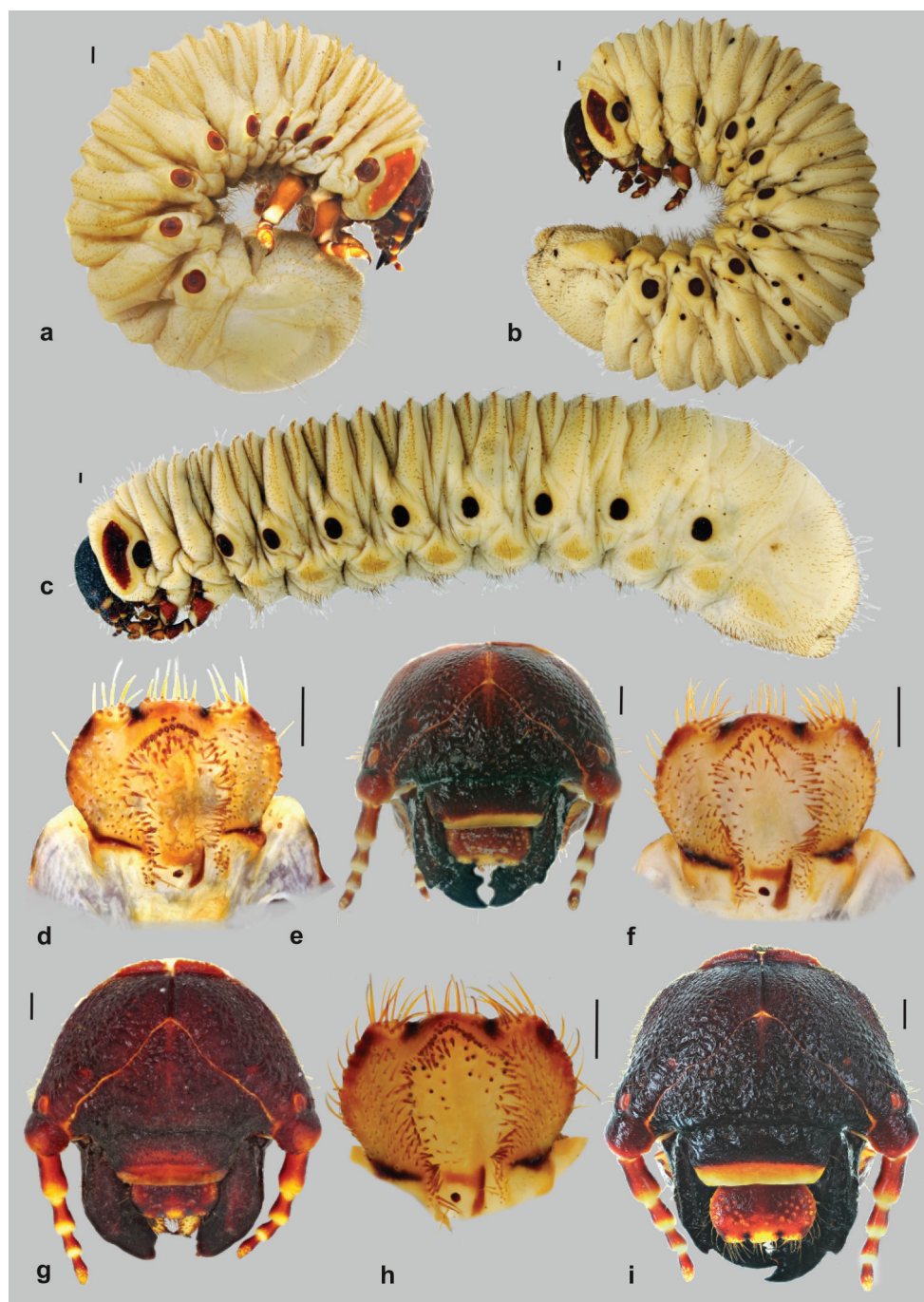


Figure 1. Immature stages of the genus *Goliathus*: **A–C** habitus (**A** *G. albosignatus* **B** *G. goliatus* **C** *G. orientalis*) **D, F, H** epipharynx (**D** *G. albosignatus* **F** *G. goliatus* **H** *G. orientalis*) **E, G, I** cranium (**E** *G. albosignatus* **G** *G. goliatus* **I** *G. orientalis*). Scale bars: 1 mm.

Table 1. Cranial chaetotaxy of *G. albosignatus*, *G. goliatus*, and *G. orientalis*.

Group of setae	epicranium				frons				clypeus		labrum				
	DES	PES	AES	EES	PFS	EFS	AFS	AAS	ACS	ECS	PLS	PMS	ELS	LLS	MLL
<i>G. albosignatus</i>															
long and medium setae	1	0	1	2–6	1	0	0	1	1	1	4–9	1–2	2	8–9	8–9
minute setae	6–8	6–7	2–7	11–17	5–7	1–4	6–7	(1)	0	0–1	0–4	0 (1)	0	0	0
<i>G. goliatus</i>															
long and medium setae	2	1	1	11–13	1	0	0	1	1	1	0	1	3–4	9–12	8
minute setae	3–7	7–10	(1)	8–15	0–3	1–2	1–5	1	0	0	2–4	1–3	0–1	0	0
<i>G. orientalis</i>															
long and medium setae	(1)3–4	1–2	1	7–15	1–2	0	0	1	1	1	(1)4–6	1+0-5	3–6	7–8	8
minute setae	3–9	0–3	0–1	7–17	0–3	0–2	0–3	0	0	0–1	0–2	0–2	0	0	0

Abbreviations: AAS = setae on anterior frontal angle; ACS = anterior clypeal setae; AES = anterior epicranial setae; AFS = anterior frontal setae; DES = dorsoepicranial setae; ECS = exterior clypeal setae; EES= exterior epicranial setae; EFS = exterior frontal setae; ELS = exterior labral setae; LLS = setae on lateral labral lobe; MLL = setae of medial labral lobe, PES = posterior epicranial setae; PFS = posterior frontal setae; PLS = posterior labral setae; PMS = paramedial labral setae. Numbers in brackets indicate a rarely occurring state. For explanation of length categories of setae see 'Materials and methods'.

frontal setae minute, almost invisible (unless observed with particular care). Clypeus subtrapezoidal, membranous anteclypeus taking up nearly 1/3 of entire clypeal area. Postclypeus strongly sclerotized with one anterior and one exterior clypeal seta (often with a minute seta nearby). Frontoclypeal suture distinct. Stemmata present, well developed with optical active layer.

Labrum: Symmetrical, anterior margin trilobed, with numerous setae and several pores. Clithra present. Dorsal labral surface with several setae organised in irregular rows and groups. Posterior row with approximately 2–6 minute or medium length setae, anterior row with one prominent paramedian and several smaller ones. Lateral margin of labrum with 2–3 prominent setae and another 1–2 medium length setae.

Antennae (Fig. 2A–C): tetramerous (an I–IV); relative length of antennomeres: an I > an II > an IV > an III. Ventral and apical projection of the penultimate antennomere III indistinct or entirely absent, the respective sensorium present, but tiny and indistinct. Ultimate antennomere (an IV) beside round apical sensory field with 10–30 dorsal and ventral sensory spots.

Epipharynx (Fig. 1D, F, H): Haptomerum: zygum strongly convex (haptomeral process absent), with arched or angulate row of approximately 14–18 stout setae. Another 8–12 stout setae scattered on the inner surface of zygum, typically longer than those arranged in row. Exterior surface of zygum with central group of approximately 8 sensilla (often organised in two paramedian subgroups) and a further two paramedian groups of 3–4 sensilla next to clithra. Proplegmata absent. Acroparia: external margin of medial labral lobe with 8–9 long setae. Lateral labral lobes with 5–6 long setae. Lateral

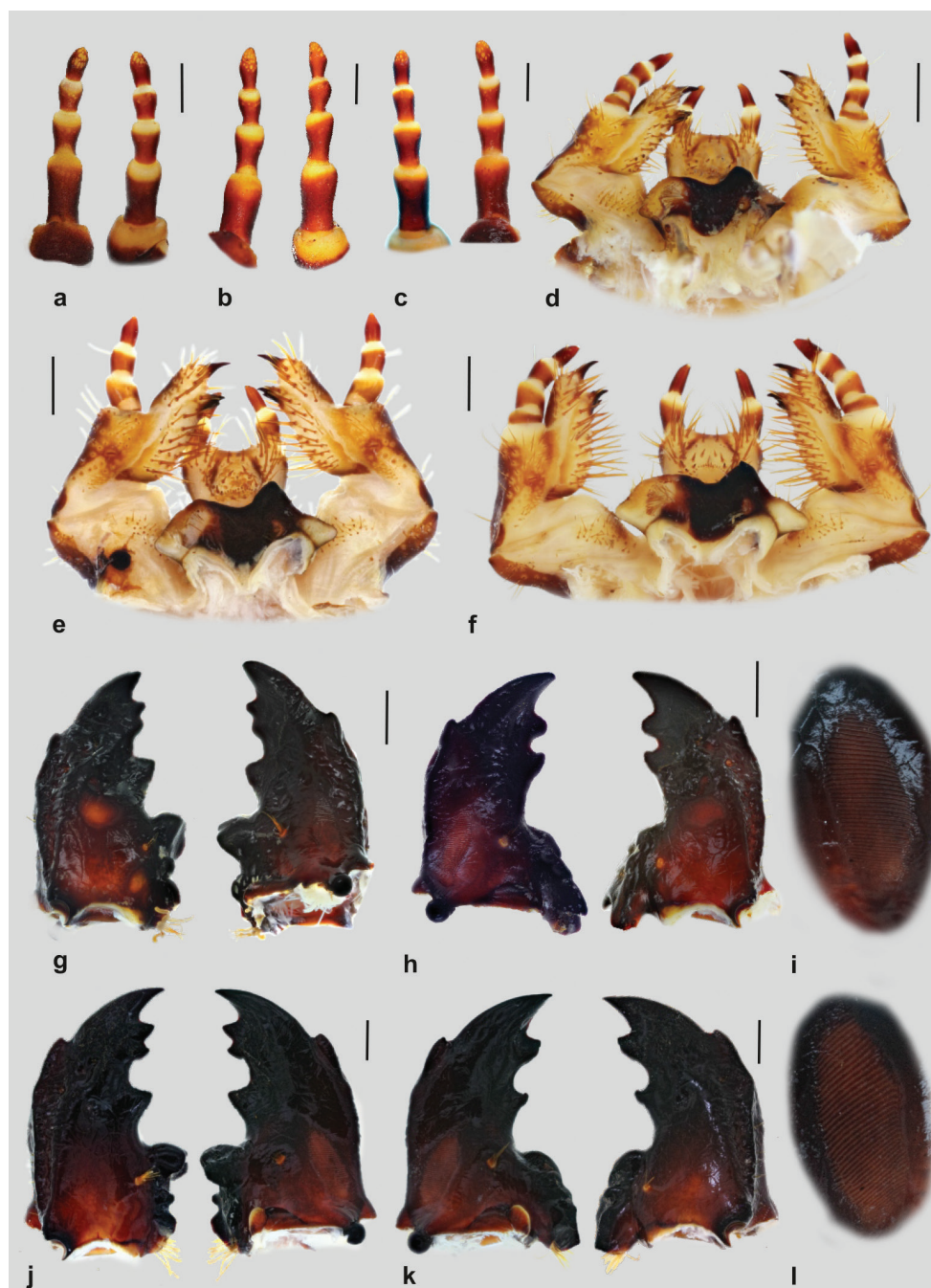


Figure 2. Immature stages of the genus *Goliathus*: **A–C** right antenna, dorsal and ventral aspect (**A** *G. albosignatus* **B** *G. goliatus* **C** *G. orientalis*) **D–F** maxillo-labial complex, dorsal aspect (**D** *G. albosignatus* **E** *G. goliatus* **F** *G. orientalis*) **G–I** *G. albosignatus*, mandibles (**G** left mandible, dorsal and ventral aspects **H** right mandible, dorsal and ventral aspects **I** stridulatory area **J–L** *G. goliatus*, mandibles (**J** left mandible, dorsal and ventral aspects **K** right mandible, dorsal and ventral aspects **L** stridulatory area. Scale bars: 1 mm.

margin of acanthoparia fairly sclerotized, straight or undulated. Acanthoparia with up to ten setae often originating from a tubercle. However, the presence and development of the tubercles as well as the number of setae present on acanthoparia may be variable even on opposite sides of the same epipharynx (possibly due to abrasion). Setae in the proximal third of acanthoparia small, hair-like, the remaining setae equal in size and similar to those of acroparia. Plegmata absent. Chaetoparia asymmetric, exhibiting 6–10 irregular longitudinal rows of setae. Central rows with stout, spine-like setae similar in shape to those of the setae of zygum. Setae in exterior rows of chaetoparia decreasing in size towards the margin of epipharynx. Right half of chaetoparia with around 70–106 setae, left with approximately 85–115. Dexiotorma straight, relatively narrow, right pternotorma absent. Laetotorma well developed, left pternotorma more or less well developed. Haptolachus: sense cone (left nesium) high, with 4 pores, sclerotized plate absent. Platesclerite large, in shape of reversed Greek letter “I”; longitudinal part heavily sclerotized, while transverse part (bordering with pedium) is less sclerotized. Posterior part of haptolachus with only 1–2 pore-like sensilla. Phoba and crepis absent.

Mandibles (Figs 2G–L; 3A, D): asymmetrical, narrow. Scissorial part about two times longer than molar part. Scrobis with a row of 4–6 setae; longitudinal furrow deep. Anterolateral portion of dorsal mandibular surface with two prominent setae (which may often be broken). Patches of 4–18 dorsomolar and ventromolar setae concealed in a single rim. Stridulatory area with 29–50 fine transversal ridges, interval between ridges subequal in entire area. Scissorial area with four and three prominent, sharply pointed teeth on left and right mandible, respectively. The second and third tooth on left mandible fused at base but with well separated apical blade. Exterior margin of both mandibles with prominent, sharply pointed exterior tooth situated approximately at base of its apical third.

Molar lobes of both mandibles with projections. Base of right mandibular calyx bilobed (in medial aspect), dorsal lobe about twice as large as ventral. Calyx of left mandible flattened with arcuate basal margin.

Maxilla (Figs 2D–F, 3B–C): dorsal surface of cardo and labacoparia with 8–14 and 20–44 setae, respectively. Stipes dorsal with approximately 35–45 setae, interior stipital setae more or less slender, hair-like; setae stouter and larger towards exterior stipital margin; exterior margin with 2–5 prominent very long and stout setae. Stridulatory area composed of 4–7 feebly sclerotized conical or semi-conical (almost truncate or even abraded in older specimens) stridulatory teeth (Fig. 3B); truncate process low and transverse. Ventral surface of stipes with apical group of approximately 5 hair-like setae. Galea and lacinia entirely fused forming mala, galeo-lacinal suture indistinct, entirely absent on ventral face. Galear portion of mala with single falcate uncus and 15–22 setae in longitudinal rows; setae around apex and on interior row very long and stout. Lacinal part of mala with 2 subequal unci (Fig. 3C), subtriangular and fused at base; larger uncus sometimes with lateral hump, apices of both unci pointing towards each other. Base of unci with 2–3 conspicuous conical setae, one usually very small, not exceeding one third of larger uncus; dorsomedial side of lacinia with ca. 30–40 very long hair-like setae.

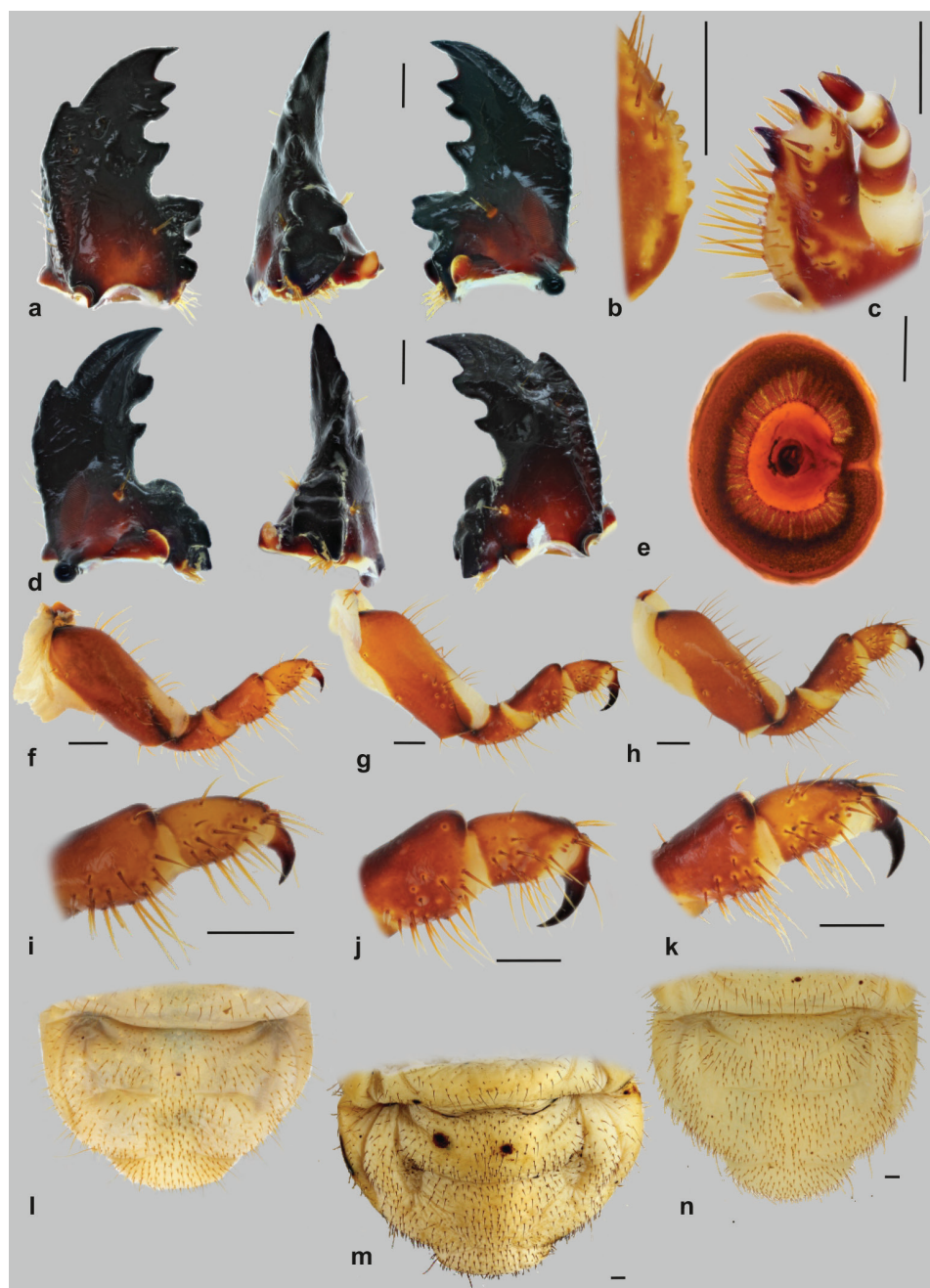


Figure 3. Immature stages of the genus *Goliathus*: **A** *G. orientalis*, left mandible, dorsal, medial and ventral aspect **B** *G. orientalis*, maxillar stridulatory teeth, lateral aspects **C** *G. orientalis*, detail of mala and unci, ventro-lateral aspect **D** *G. orientalis*, right mandible dorsal, medial and ventral aspect **E** *G. albosignatus*, thoracic spiracle **F–H** prothoracic leg (**F** *G. albosignatus* **G** *G. goliatus* **H** *G. orientalis*) **I–J** tibiotarsus and pre-tarsus (claw) (**I** *G. albosignatus* **J** *G. goliatus* **K** *G. orientalis*) **L–N** raster (**L** *G. albosignatus* **M** *G. goliatus* **N** *G. orientalis*). Scale bars: 1mm (when not otherwise specified), 0.1 mm (**A, B, C**); 0.5 mm (**D**)

Ventral surface of mala markedly sclerotized, apical part with 2 irregular longitudinal rows of 3–4 hair-like setae. Maxillary palps four-jointed, basal joint somewhat reduced on ventral side and retracted into palpifer, thus visible only as narrow sclerotized ring on dorsal face of maxilla, alternatively basal joint entirely retracted into palpifer; penultimate joint of maxillary palpus with 2 setae.

Hypopharyngeal sclerome (Fig. 2D–F). Asymmetric, hypopharyngeal process subtriangular, pointed. Row of approximately 30–35 tegumentary expansions (= phoba, *sensu* Böving 1936) present on left lateral lobe. Approximately 10–15 tegumentary expansions present on right central part of scleroma and below its right medio-posterior margin. Lateral lobes feebly to moderately sclerotized, both with approximately 12 hair-like setae.

Ligula (Fig. 2D–F). Anterior margin of ligula deeply concave. Dorsal surface with two paramedial oblique sclerotized bar-like areas and paramedial group of approximately 25–35 hair-like setae on each side; posterior and medial setae of this group shorter and stouter. Paramedial pair of prominent setae on anterior margin absent. Labial palpi dimerous.

Thorax (Fig. 1A–C). Prothorax with single dorsal lobe, meso- and metathorax with 3 well-developed lobes. Prothoracic sclerite large, well sclerotized, bordered with only few setae at its anterior margin. Chaetotaxy of thoracic sublobes rather sparse. Prothorax: dorsum with only few irregular setae, lacking the typical rows of setae found on dorsal and lateral parts of subsequent segments. Pleural part of meso- and metathoracic sublobes with 3–6 tenuous rows of rather short, hair-like setae, tergal part with 1–3 dense rows of short hair-like to spiny setae, interspersed with a few very long, hair-like setae on some lobes. Thoracic spiracle (Fig. 3E) approximately 2.5×1.6 mm, elliptic, heavily sclerotized; respiratory plate C-shaped, arms of lobes approximated, almost concealed. Respiratory plate with numerous tiny holes. All pairs of legs (Fig. 3F–K) subequal. Pretarsi with falcate, sharply pointed claw, bearing 2 basal setae (Fig. 3I–K).

Abdomen (Figs 1A–C, 3L–N): nine-segmented. Segment IX and X fused dorsally, ventral border of the respective segments indicated by a shallow ridge. Dorsa of abdominal segments I–VI with 3 sublobes, segments VII and VIII with 2 sublobes. Chaetotaxy of abdominal segments I–VII similar to those of meso- and metathorax. Abdominal spiracles slightly smaller than mesothoracic one, all spiracles subequal, however spiracles of posterior segments more circular. Dorsum of last abdominal segment sparsely, but evenly covered with short setae, with four tenuous rows of medium long or long hair-like setae.

Raster (Fig. 3L–N). Palidium absent (*G. goliatus*) or rudimental, composed of 2 more or less irregular rows of 4–8 shortened obtuse pali. Septula poorly developed or entirely absent. Tegilla fused, composed of numerous evenly distributed short setae, covering almost whole ventral surface of last abdominal segment. Chaetotaxy of ventral and dorsal anal lip similar to those of tegilla, composed of numerous short setae and with approximately 5–10 longer setae.

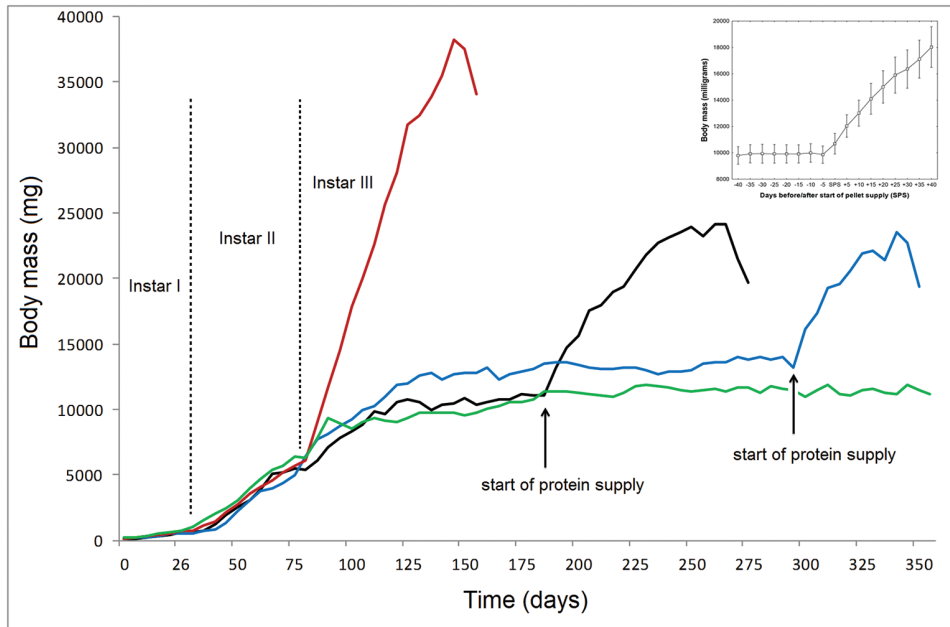


Figure 4. Individual growth trajectories of the fully nourished larva (red line), partly nourished larvae (black and blue lines) and undernourished larva (green line). Evidently, the absence of proteins in larval diet had profound consequences on development. In the third instar, the starved larvae were able to resume growth immediately after the addition of protein to their diet. The inset image shows mean growth of all eleven partly nourished larvae 40 days before and after pellet supply (SPS), irrespective of actual time of pellet supply. Means \pm standard errors are depicted.

Diagnostic characters of *G. albosignatus* Boheman, 1857

Figs 1A, D, E; 2A, D, G–I; 3 E, F, I, L

The morphology of third stage larva of *G. albosignatus* corresponds to the general morphology of *Goliathus* larvae with the following exceptions: Body length 60–70 mm. Cranial width 7.5–8 mm, cranium brown to dark brown. Antennae with 9–12 and 11–13 ventral sensory spots, respectively. Sensory spots elongate in shape and separated from each other only by a very thin portion of cuticle. The ventro-apical projection of penultimate antennal joint rudimental, the respective sensorium small. Epipharynx with 71–75 setae on right part and 85 on the left part of chaetoparia, respectively. Acanthoparia with 6–8 setae on distinctly swollen tubercles; however, the presence and development of these tubercles as well as the setae of the acanthoparia itself may be variable even in the same epipharynx, probably also due to wear. Mandibles: stridulatory area with 29–37 stridulatory ridges, right mandible with the second and third scissorial tooth nearly equal in size and shape. Brustia of calyx with 10–12 and 17–25 setae on right and left mandible, respectively. Pretarsus (claw) about half as long as tibiotarsus. Raster of abdomen with or without rudimental rows of 4–8 pali.

Diagnostic characters of *G. goliatus* (Drury, 1770)

Figs 1B, F, G; 2B, E, J–L; 3 G, J, M

The morphology of third stage larva of *G. goliatus* corresponds to the general morphology of *Goliathus* larvae with the following exceptions: Body length 114–150 mm, cranium width 10.2–14 mm. Antennae with 14–25 dorsal and 21–32 ventral sensory spots, respectively. Sensory spots rounded and separated from each other by a relatively thick portion of cuticle. Ventro-apical projection of penultimate antennal joint absent, the respective sensorium very small. Epipharynx with 90–106 setae on right part and 107–113 setae on left part of chaetoparia, respectively. Acanthoparia variable, with 6–10 setae on tubercles, however these structures may be abraded in older specimens. Mandibles: stridulatory area with 42–45 ridges, right mandible with third scissorial tooth distinctly smaller than second, third tooth of left mandible about the size of second. Calyx of right mandible bilobed, ventral lobe reaching only one third of the size of the dorsal one. Brustia of calyx with 26–30 and 43–50 setae on right and left mandible, respectively. Pretarsus (claw) almost as long as tibiotarsus. Raster of abdomen without rows of pali.

Diagnostic characters of *G. orientalis* Moser, 1909

Figs 1C, H, I; 2C, F; 3A–D, H, K, N

The morphology of third stage larva of *G. orientalis* corresponds to the general morphology of *Goliathus* larvae with the following exceptions: Body length of studied larvae: 83–95 mm, but it is likely that the larvae can reach a similar size to *G. goliatus* (i.e., 150 mm). Cranium width 10.8–12 mm. Antennae with 11–17 dorsal and 17–24 ventral sensory spots, respectively. Sensory spots slightly elliptical and not densely aggregated. Ventro-apical projection of penultimate antennal joint absent, the respective sensorium very small. Epipharynx with 87–103 setae on right part and 92–104 setae on left part of chaetoparia, respectively. Acanthoparia variable, with 6–8 setae on tubercles, however these structures may be abraded in older specimens. Mandibles: stridulatory area with 39–49 ridges, left and right mandible with third scissorial tooth distinctly smaller than second. Calyx of right mandible bilobed, ventral lobe reaching approximately one half of the size of the dorsal one. Brustia of calyx with 26–37 and 35–37 setae on right and left mandible, respectively. Pretarsus (claw) almost as long as tibiotarsus. Raster of abdomen with two rows of 2–6 pali.

Larval growth under different nutritional regimes

Breeding conditions during the first and second instar were identical for all larvae; therefore development times and maximal larval mass of these larval stages are pre-

sented as a whole irrespective of the experimental regime (Table 3). Uniformity of the development times and maximal body mass in the first two instars under all three experimental regimes was also confirmed by a one-way ANOVA ($p > 0.4$ for development times and body mass in both instars). Total development time of the fully nourished larvae was 193 ± 5 days. The larvae spent the longest period of time in the third instar, which lasted roughly twice as long as the previous two instars combined. Also, most of the growth took place in the final instar, as the larvae gained 80% of their final body mass during this time (Table 3).

Food manipulation had a considerable effect on survival and growth. None of the eleven starved larvae pupated, whilst 20 out of the 23 larvae (87%) reared under the fully nourished regime and four out of the eleven larvae (36%) reared under the partly nourished regime pupated; this difference was statistically significant (two-tailed Fisher's exact test: $p < 0.01$). On the other hand, all larvae died during the prepupal stage in the pupal cell.

In the third instar, there were clear differences in growth trajectories between the breeding regimes (Fig. 4). Whilst fully nourished larvae grew regularly till construction of the pupal cell, larvae reared under the other two regimes grew only for a short period after the onset of the third instar (although considerably slower than fully nourished larvae; $F_{1,42} = 99.1$, $p < 0.001$; see also Table 4). The larvae subsequently stopped growing and remained around the reached weight (9969 ± 435 mg; the values were not significantly different between the partly nourished and undernourished regimes: $t_{20} = 1.07$, $p = 0.42$). Nevertheless, after the addition of pellets to their diet, the partly nourished larvae were able to resume growth, although their final body mass ($t_{32} = 5.45$, $p < 0.001$; see also Table 3) and growth rate ($F_{1,31} = 20.9$, $p < 0.001$; see also Table 4) were significantly lower than those of the fully nourished larvae.

Discussion

Morphology

In the character matrix of 38 larval features published by Micó et al. (2008) no distinct character distinguishing *Goliathus* larvae from the other 41 cetoniinae taxa was identified (except for the evidently wrongly coded character 34/0 – abdominal segments IX and X not fused). Among the other characters shared with only a few other Goliathini or Cetoniinae larvae were the number of respiratory holes on the thoracic spiracle (state 30/2 – more than 60; shared with *Mecynorhina polyphemus* (Fabricius, 1781) and *Fornasinius fornasinii*) and the pretarsi with a sharply pointed claw bearing 2 basal setae (character state 32/0, shared with members of Valgini, Trichiini, Schizorhinini, Cremastochelini, *Fornasinius fornasinii* and *Dicronocephalus wallichi* Hope, 1831). Similar looking pretarsi have also been described for *Hypselogenia geotrupina* (Oberholzer 1959), *Agestrata orichalca* (Linnaeus, 1769) (Zhang 1984) and members of Taenioderini (Vendl et al. 2014). While the number of respiratory holes may be a size-dependent

character, the shape of the pretarsus deserves a more detailed investigation. A falcate claw with two setae at the base clearly represents an ancestral/plesiomorphic stage of pretarsal morphology in the entire plant feeding lineage of scarab beetles (Ritcher 1966, Sawada 1991) but its morphology varies considerably. There are species/groups with a highly developed claw (e.g., the apical part distal to the setae is longer than the proximal part, e.g., the Trichiini), or there are species with an extremely reduced apical portion of the claw (most Taenioderini) and all possible transitional stages occur. McMonigle (2006) argued that the claws of the genus *Goliathus* are retractable and compared them with the claws of *Mecynorhina* (*Mecynorhina*) *torquata* (Drury, 1782) and *Mecynorhina* (*Megalorrhina*) *harrisii* Westwood, 1847. He stated that only the (sub)genus *Megalorrhina* possess claws similar to *Goliathus*, although less developed. We were not able to confirm that the claws of *Goliathus* are “retractable”, but it is clear that the claws are capable to fold back against the tibiotarsus, which seems unusual among pleurostict scarabs. In general we may state that the development of the pretarsal claw in *Goliathus* is exceptional, in *G. goliatus* and *G. orientalis* the claw is even equal in length to the tibiotarsus.

Other distinct characters of *Goliathus* larvae include the extraordinarily coarse surface of the cranium and the extremely well developed stemmata (larval eyes). The most striking feature is the general habitus of living larvae which are straight (Fig. 1C), unbent and have a relatively slim appearance (e.g., the posterior part of the abdomen is more or less as thick as the other parts of the abdomen and thorax) compared with the size of the imago. The characteristic C-shaped form, which is common to most other scarab larvae (living, non-moving), is not present here (unless killed and preserved using standard methods (Figs 1A, B)). Several other larvae of Coryphocerina (Cetoniinae: Goliathini) also have a similar slim appearance, but tend to be C-shaped when in a resting position in substrate (personal observation). The extremely well-developed mandibular scissorial teeth of *Goliathus* larvae (the first tooth is falcate) are also rather extraordinary and exceptional among Cetoniinae (although with this character more caution needs to be exercised as these teeth are often abraded in older larvae). Similarly, the sharply pointed external tooth of the mandible may be another unique character, although there are species with a similar but more or less blunt tubercle: *Hypselogenia geotrupina*, *Ichneostoma pringlei* Perissinotto et al., 1999, *Rhomborhina polita* Waterhouse, 1875 (Oberholzer 1959, Sawada 1991, Perissinotto et al. 1999) and others.

Species-specific characters

Several species-specific characters have been identified in the immature stages of *G. albosignatus*, *G. goliatus*, and *G. orientalis*, most of them distinguishing *G. albosignatus* from the other two species (see Table 2), which may be due to the different size range of this species. Nevertheless a few characters distinguishing *G. goliatus* from *G. orientalis* have been identified which is quite surprising as these species are closely related and even hybridizing to the F1 generation in captivity (McMonigle 2006, Meier and

Table 2. Main diagnostic characters for larvae of *Goliathus* species.

Species/character	<i>G. albosignatus</i>	<i>G. goliatus</i>	<i>G. orientalis</i>
cranium width	7.5–8 mm	10.2–14 mm	10.8–12 mm
number of dorsal / ventral sensory spots on antennae	9–12 / 11–13	14–25 / 21–32	11–17 / 17–24
shape of sensory spots on antennae	elongate, separated only by a very thin portion of cuticle	rounded and separated by thick portion of cuticle	slightly elongated, separated by a relatively thick portion of cuticle
left chaetoparia of epipharynx	85	107–113	92–104
third scissorial tooth of right mandible	equal to the second tooth	distinctly smaller than the second tooth	distinctly smaller than the second tooth
third scissorial tooth of left mandible	equal to the second tooth	equal to the second tooth	distinctly smaller than the second tooth
calyx of right mandible	ventral lobe about half of the size of the dorsal lobe	ventral lobe about one third of the size of the dorsal lobe	ventral lobe about half of the size of the dorsal lobe
left brustia of calyx	14–23	45–50	35–37
relative length of tarsungulus (claw)	about one half of the length of tibiotarsus	subequal to tibiotarsus	subequal to tibiotarsus

Table 3. Summary of the instar-specific developmental characteristics. The values are given as mean \pm SE.

Instar	Feeding regime	Development time (days)	Maximal weight (mg)	N
1		35.5 \pm 0.88	655 \pm 19	45
2		55.1 \pm 1.8	5825 \pm 132	45
3	fully nourished	104.4 \pm 3.36	28712 \pm 860	23
	partly nourished	n/a	20412 \pm 1273	11
	undernourished	> 197 \pm 17	9638 \pm 551	11

Table 4. Growth rates (in mg/day) of the differentially fed larvae at the start of the final instar/ before and after protein addition to the starved larvae. The values are given as mean \pm SE.

Feeding regime	Start of instar	Before protein supply	After protein supply	N
fully nourished	372.3 \pm 26.8	n/a	n/a	23
partly nourished	69.4 \pm 8.6	- 0.35 \pm 7.7	232.5 \pm 27.3	11
undernourished	58.5 \pm 7.2	- 0.69 \pm 4.9	n/a	11

Campbell (undated)). The validity of these characters still needs to be confirmed, but they might be regarded as additional support for the current separation of the species-level classification of *G. goliatus* and *G. orientalis*.

Development and nutrition

Although there are no data available on larval biology and development of goliath beetles in the wild, thanks to the long-standing efforts of beetle breeders some interesting find-

ings about their developmental requirements in captivity are available. One of these is the presumed obligatory requirement of proteins in larval diet during its development (McMonigle 2001, 2006; Meier 2003; Meier and Campbell (undated)). Our results confirm this statement. The growth rate of larvae without added protein clearly slowed down immediately after the exclusion of protein pellets at the beginning of the third instar and from a certain point they were not able to achieve a higher body weight (the average weight after ecdysis was around 6 g, while the threshold weight when the larvae ceased their growth was around 10 g). This was in contrast to larvae which were fully nourished with proteins, most of which were able to construct a pupal cell. After the addition of protein pellets to their diet the larvae clearly responded by resuming growth and, interestingly, some of them even constructed a pupal cell, some of them after up to 200 days of starvation. However, all larvae in our experiment died in the pupal cell, possibly due to a high rearing temperature. It is not clear how long the larvae could live without a protein diet, but some of them were still alive 250 days after the beginning of the third instar, when the experiment was terminated and the larvae were inspected for intestinal microorganisms (see Materials and methods). Some of the breeding manuals state that from a certain point in time the larva does not consume the substrate and feeds purely on protein pellets (Wong 2008). Nevertheless, in our experiment the starved larvae produced an amount of faecal pellets comparable to the fully nourished larvae. It is possible that in adverse conditions, when the larva cannot find a suitable source of nutrients, it feeds solely on substrate and waits for more favourable conditions when prey becomes available.

Conclusions

It has been suggested that goliath beetle larvae are carnivorous and prey on the larvae of other rose chafers in the wild (McMonigle 2001, 2006, 2012; Meier 2003). Indeed, in captivity goliath beetle larvae readily consume the larvae of other common species (e.g., *Pachnoda*; Klátil and Vrána 2008, personal observation). It is also known that other rose chafer larvae (e.g., *Eudicella*, *Cheirolasia*, etc.) enhance their diet by feeding on rose chafer larvae of other species or are even cannibalistic (Klátil and Vrána 2008, Micó et al. 2008, personal observation), but this behaviour is only facultative and the larvae are able to finish their development normally without protein input (Christiansen 2013, personal observation). The possible dependence on live prey may also be reflected in their larval morphology. Mandibles with sharp scissorial teeth (Figs 2, 3), an additional pointed tooth on the lateral face of mandible, legs with conspicuously long and pointed claws (Fig. 3J–K), and well developed stemmata may possibly be linked to a predatory way of life. It is also possible that thanks to a protein rich diet goliath beetles develop considerably faster than comparably sized scarab beetles such as *Megasoma* or *Dynastes*, which thrive well on a “classical” substrate. The development of these species normally takes up to two or three years (Glaser 1976, Morón and Deloya 2001, Klátil and Vrána 2008). However, it can be considerably faster if fed with protein-rich pellets (McMonigle pers. comm.). In this experiment, the regularly fed

larvae developed in less than 200 days on average, although their maximal weight was considerably lower than the commonly reported weight (up to 100 g in large males and 50 g in females). The alleged association of the closely related *Argyrophegges* larvae and hyrax (Mammalia: Procaviidae) may indicate that other representatives of the subtribe Goliathina also have alternative larval feeding strategies which may be helpful in achieving their exceptionally large size.

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References

- Böving AG (1936) Description of the larva of *Plectris aliena* Chapin and explanation of new terms applied to the epipharynx and raster. Proceedings of the Entomological Society of Washington 38: 169–185.
- Christiansen P (2013) Larval growth rates and sexual differences of resource allocation in the cetoniine scarab *Mecynorhina polyphemus* Fabricius 1781 (Coleoptera: Scarabaeidae: Goliathini). Journal of Natural History 47: 1287–1307. doi: 10.1080/00222933.2012.763061
- Donaldson MIJ (1987) Descriptions of, and a key to larvae of some South African Cetoniinae (Coleoptera: Scarabaeidae). Entomologist's Monthly Magazine 123: 1–13.
- Glaser JD (1976) The biology of *Dynastes tityus* (Linn.) in Maryland (Coleoptera: Scarabaeidae). Coleopterists Bulletin 30: 133–138.
- Hayes WP (1929) Morphology, taxonomy and biology of larval Scarabaeoidea. Illinois Biological Monographs 12: 88–200.
- Holm E, Marias E (1992) The fruit chafers of Southern Africa. Ekogilde cc, Hartebeespoort, 326 pp.
- Klátil L, Vrána T (2008) Chov Zlatohlávků a Nosorožníků [Breeding of Flower and Rhinoceros beetles in captivity]. Robimaus – sdružení Magdaléna a Robert Javorských, Rudná u Prahy, 163 pp. [In Czech]
- Krajčák M (1998) Cetoniidae of the world. Catalogue – Part I. Typos Studio Most, Most, Czech Republic.
- Lachaux G (1983) Les Coleopteres du Monde 3, Goliathini 1. Sciences Nat., Compiègne, France, 67 pp.
- Malec P (undated) Goliathina genera. <http://www.flower-beetles.com/hegemus.html> [accessed 13 January 2016]

- Marais E, Holm E (1992) Type catalogue and bibliography of the Cetoniinae of sub-Saharan Africa (excluding Trichiini and Valgini) (Coleoptera: Scarabaeidae). Cimbebasia Memoir 8: 1–125.
- Mawdsley JR (2013) Taxonomy of the Goliath beetle *Goliathus orientalis* Moser, 1909 (Coleoptera: Scarabaeidae: Cetoniinae). Journal of Natural History 47: 1451–1461. doi: 10.1080/00222933.2012.763052
- McMonigle O (2001) Flower Beetles (p.278–291). In: Lai JT (Ed) For the Love of Rhinoceros and Stag Beetles, first edition. Morning Star Group, Taiwan, 346 pp.
- McMonigle O (2006) The complete guide to rearing flower and jewel scarabs. Elytra and Antenna, Brunswick Hills, Ohio, 44 pp.
- McMonigle O (2012) The Ultimate Guide to Breeding Beetles: Coleoptera Laboratory Culture Methods. Coachwhip Publications, Darke County, Ohio, 208 pp.
- Meier K (2003) Breeding the Goliath Beetle. Invertebrates-Magazine 2: 4–9.
- Meier K, Campbell C (undated), The breeding/rearing of *Goliathus*. http://www.naturalworlds.org/goliathus/manual/Goliathus_breeding_1.htm [accessed 13 January 2016]
- Micó E, Morón MA, Šípek P, Galante E (2008) Larval morphology enhances phylogenetic reconstruction in Cetoniidae (Coleoptera: Scarabaeoidea) and allows the interpretation of the evolution of larval feeding habits. Systematic Entomology 33: 128–144.
- Morón MA, Deloya C (2001) Observaciones sobre el ciclo de vida de *Megasoma elephas elephas* (Fabricius) (Coleoptera: Melolonthidae: Dynastinae). Folia Entomológica Mexicana 40: 233–244.
- Nogueira G, Morón MA, Fierros-López HE, Navarette-Heredia JL (2004) The immature stages of *Neoscelis dohrni* (Westwood) (Coleoptera: Scarabaeidae: Cetoniinae: Goliathini) with notes on the adult behavior. The Coleopterists Bulletin 58: 171–183. doi: 10.1649/604
- Oberholzer JJ (1959) A morphological study of some South African lamellicorn larvae. I–Descriptions of the third instar larvae. South African Journal of Agricultural Science 2: 41–74.
- Perissinotto R, Smith TJ, Stobbia P (1999) Description of adult and larva of *Ichnestoma pringlei* n. sp. (Coleoptera Scarabaeidae Cetoniinae), with notes on its biology and ecology. Tropical Zoology 12: 219–229. doi: 10.1080/03946975.1999.10539390
- Ritcher PO (1966) White Grubs and their Allies. A study of North American Scarabaeoid Larvae. Oregon State Monographs. Studies in Entomology 4. Oregon State University Press, Corvallis, 219 pp.
- Sakai K, Nagai S (1998) The Cetoniinae Beetles of the World. Muschi-Sha's Iconographic Series of Insects 3. Mushi-Sha, Tokyo, 422 pp.
- Sawada H (1991) Morphological and Phylogenetical Study on the Larvae of Pleurostict Lamellicornia in Japan. Tokyo University of Agriculture Press, Tokyo, 132 pp.
- Šípek P, Král D, Jahn O (2008) Description of the larvae of *Dicronocephalus wallichi bourgoini* (Coleoptera: Scarabaeidae: Cetoniinae) with observations on nesting behavior and life cycle of two *Dicronocephalus* species under laboratory conditions. Annales de la Société Entomologique de France 44: 409–417. doi: 10.1080/00379271.2008.10697577
- StatSoft Inc (2001) STATISTICA, version 6.0. <http://www.statsoft.com>
- Vendl T, Vondráček D, Kubáň V, Šípek P (2014) Immature stages of Taenioderini (Coleoptera: Scarabaeidae: Cetoniinae): a report of hidden diversity. Acta Entomologica Musei Nationalis Pragae 54: 571–604.

- Wiebes JT (1968) Catalogue of the Coleoptera Cetoniinae in the Leiden Museum. 1. *Goliathus* Lamarck, sensu lato. Zoologische Mededelingen 43: 19–40 + 2 plates.
- Wong J (2008) Journal of a Goliathus breeder. <http://insect-collection.com/invertebrate-caresheet/journal-of-a-goliathus-breeder/> [accessed 26 January 2016]
- Zadrobílková E, Smejkalová P, Walker G, Čepička I (2016) Morphological and molecular diversity of the neglected genus *Rhizomastix* Alexeieff, 1911 (Amoebozoa: Archamoebae) with description of five new species. The Journal of Eukaryotic Microbiology 63: 181–197 doi: 10.1111/jeu.12266
- Zhang ZL (1984) Coleoptera: Larvae of Scarabaeoidea. Economic Insect Fauna of China 28. Science Press, Beijing. 107pp + XXI plates.

Taxonomic revision of New Guinea diving beetles of the *Exocelina danae* group, with the description of ten new species (Coleoptera, Dytiscidae, Copelatinae)

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Abstract

Ten new species of *Exocelina* Broun, 1886 from New Guinea are described: *E. andakombensis* **sp. n.**, *E. garaina* **sp. n.**, *E. injiensis* **sp. n.**, *E. kabuwumensis* **sp. n.**, *E. marawaga* **sp. n.**, *E. posmani* **sp. n.**, *E. tekadu* **sp. n.**, *E. varivata* **sp. n.**, *E. wareaga* **sp. n.**, and *E. woitapensis* **sp. n.** All of them together with five already described species are united into the newly defined *E. danae*-group (with *E. miriae*-subgroup), a polyphyletic complex of related species with lateral setation on the median lobe. In the light of newly available material, all previously described species of the *E. rivulus*-group are considered to belong to a single species, *E. damantiensis* (Balke, 1998), which is now placed into the *E. danae*-group, and three new synonyms are therefore proposed: *E. madangensis* (Balke, 2001) **syn. n.**, *E. patepensis* (Balke, 1998) **syn. n.**, and *E. rivulus* (Balke, 1998) **syn. n.** *Exocelina tarmluensis* (Balke, 1998) **syn. n.** is a junior synonym of *E. danae* (Balke, 1998). Redescription of *E. atratus* (Balfour-Browne, 1939) is provided based on its type material. An identification key to all known species of the group is provided, and important diagnostic characters are illustrated. Data on the species distribution are given, showing that whilst most species are local endemics, *E. damantiensis* is extremely widely distributed.

Keywords

Exocelina danae-group, Copelatinae, Dytiscidae, new species, New Guinea

Introduction

This paper continues our previous studies on the New Guinea species of the genus *Exocelina* Broun, 1886 (Balke 1998, 1999, Shaverdo and Balke 2014, Shaverdo et al. 2005, 2012, 2013, 2014, 2016a, b, c). So far, the New Guinea representatives of this genus are organized into five species group: the *E. rivulus*-group with four species (Balke 1998), the *E. aipo(me)*-group with four species (Balke 1998; Balke et al. 2007), the *E. ullrichi*-group with three species (Balke 1998; Shaverdo and Balke 2014), the *E. broschii*-group with five species (Shaverdo et al. 2005, 2016a), and by far, the largest, with 51 species, the *E. ekari*-group (Balke et al. 2007, Shaverdo et al. 2012, 2014, 2016b). In the present study, we continue to build up a species group structure of the genus that can, in our opinion, provide an important tool for species identification in highly diverse genera. *Exocelina* is one of these, with 98 species described from New Guinea and 154 worldwide, including the results of this study. The *E. danae*-group is defined and proposed for five already described species, together with ten new species described herein. The *E. rivulus*-group was revised and abolished to avoid confusion, since all its representatives are recognized to belong to the same species, *E. damantiensis* (Balke 1998), with *E. rivulus* (Balke 1998) as a junior synonym. The present work also aims to provide an identification key to all treated species, as well as information about their distribution and habitats. All species data will be presented on the species-id.net portal automatically created by ZooKeys with the publication of this paper.

Material and methods

The present work is based on the material from the following collections:

BMNH	The Natural History Museum, London, UK
NARI	Papua New Guinea National Insect Collection, Port Moresby, PNG
NHMW	Naturhistorisches Museum Wien, Vienna, Austria
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany
ZSM	Zoologische Staatssammlung München, Munich, Germany

All methods follow those described in details in our previous articles (Shaverdo et al. 2012, 2014, 2016b). The following abbreviations were used: TL (total body length), TL-H (total body length without head), MW (maximum body width), and hw (handwritten).

Diagnosis of the *Exocelina danae*-group

The representatives of the *E. danae*-group share the following diagnostic characters:

- beetles small or medium-sized (TL-H 3.4–4.75 mm);

- habitus oblong-oval (broadest approximately at elytral midlength), with rounded pronotal and elytral sides, body outline continuous;
- pronotum short, trapezoidal, with posterior angles not drawn backwards;
- coloration brown to piceous, mainly uniform, sometimes with paler head and pronotum and darker elytra;
- microreticulation and punctation of dorsal surface very fine to strongly impressed, beetles shiny to matt dorsally;
- metacoxae and abdominal ventrites 1–5 (and 6 in males) with thin, almost longitudinal striae/strioles;
- pronotum and elytra without striae or strioles;
- pronotum with lateral bead;
- antennomeres not modified or modified: antennomere 2 distinctly enlarged in male and female;
- male protarsomeres 1–3 not expanded laterally;
- male protarsomere 4 cylindrical, narrow, with large or small anterolateral hook-like seta;
- male protarsomere 5 not modified: long and narrow, without expansion and concavity, ventrally with two rows of short setae or with anterior band and posterior row of relatively long setae;
- median lobe of aedeagus with continuous outline in ventral and lateral views;
- ventral sclerite of median lobe more or less deeply divided apically;
- distal part of median lobe with lateral setae;
- paramere with or without notch on dorsal side;
- paramere with subdistal setae dense, strong, long; proximal setae similar to subdistal but sparser and thinner, often weakly visible.

Based on analyses of the molecular data (Toussaint et al. 2014, supplementary figs 1–4), we state that the *E. danae*-group is a polyphyletic complex of the related species, most of which together with the *E. broschii*-group and *E. monae* (Balke, 1998) build a monophyletic cluster of morphologically diverse species with some general characters: presence of lateral pronotal bead and lateral setation of the median lobe, unmodified paramere, with distinct, dense subdistal setae and inconspicuous proximal setae, and antennomere 2 distinctly enlarged or equal to or larger than antennomere 3.

In the *E. danae*-group, the *Exocelina miriae*-subgroup is recognized based on the distinctly enlarged antennomere 2. This subgroup includes three species: *Exocelina miriae* (Balke, 1998), *Exocelina rufa* (Balke, 1998), and *Exocelina tekadu* Shaverdo & Balke, sp. n. In former species, antennomere 2 is enlarged in both males and females (less strongly). The females of two latter species are unknown, therefore, we can only assume the modification of the female antennomere 2 in them. This state is also recorded for *Exocelina ullrichi* (Balke, 1998), which also has an enlarged antennomere 2 in both sexes. This is an interesting fact, since, in the majority of *Exocelina* species in New Guinea, males have modified antennomeres, but females do not have such modifications.

Checklist and distribution of the species of the *Exocelina danae*-group

Abbreviations: IN – Indonesia, PNG – Papua New Guinea.

<i>Exocelina miriae</i> -subgroup		
1.	<i>Exocelina miriae</i> (Balke, 1998)	PNG: Eastern Highlands, Morobe
2.	<i>Exocelina rufa</i> (Balke, 1998)	PNG: Morobe
3.	<i>Exocelina tekadu</i> sp. n.	PNG: Morobe
Other species		
4.	<i>Exocelina andakombensis</i> sp. n.	PNG: Morobe, Gulf
5.	<i>Exocelina atrata</i> (Balfour-Browne, 1939)	PNG: Oro (Northern)
6.	<i>Exocelina damantiensis</i> (Balke, 1998)	IN: West Papua: Teluk Wondama; Papua: Paniai, Intan Jaya, Puncak Jaya, Puncak, Pegunungan Bintang. PNG: Sandaun, Western, Madang, Enga, Western Highlands, Simbu, Eastern Highlands, Morobe
7.	<i>Exocelina danae</i> (Balke, 1998)	IN: Papua: Pegunungan Bintang. PNG: Sandaun
8.	<i>Exocelina garaina</i> sp. n.	PNG: Morobe
9.	<i>Exocelina injiensis</i> sp. n.	PNG: Morobe
10.	<i>Exocelina kabwumensis</i> sp. n.	PNG: Morobe
11.	<i>Exocelina maruwaka</i> sp. n.	PNG: Eastern Highlands, Gulf
12.	<i>Exocelina posmani</i> sp. n.	PNG: Central
13.	<i>Exocelina varinata</i> sp. n.	PNG: National Capital District, Central
14.	<i>Exocelina wareaga</i> sp. n.	PNG: National Capital District, Central
15.	<i>Exocelina woitapensis</i> sp. n.	PNG: Central

Species descriptions

Exocelina miriae-subgroup

1. *Exocelina miriae* (Balke, 1998)

Figs 2, 3, 25

Copelatus (Papuadytes) miriae Balke, 1998: 333; Nilsson 2001: 77 (catalogue).

Papuadytes miriae (Balke, 1998): Nilsson and Fery 2006: 56 (comb. n.).

Exocelina miriae (Balke, 1998): Nilsson 2007: 34 (comb. n.); Toussaint et al. 2014: supplementary figs 1–4, tab. 2.

Type locality. Papua New Guinea: Morobe Province, Herzog Range, Wagau (Vagau), ca. 06°48'S; 146°48'E, ca. 1300 m a.s.l.

Type material studied. *Paratype*: 1 male “Stn. No. 137”, “NEW GUINEA: Morobe Dist., Herzog Mts., Vagau, C.4,000ft. 4-17.i.1965”, “M. E. Bacchus. B. M. 1965-120”, “Paratypus *Copelatus miriae* sp.n. Balke des. 1997” [red] (NHMW).

Additional material. Eastern Highlands: 16 males, 15 females “Papua New Guinea: Eastern Highlands, Aiyura, 1670m, 5.iv.2006, 06.21.131S 145.54.398E, Balke & Sagata (PNG 32)” (NHMW, ZSM). 1 male “Papua New Guinea: Eastern Highlands, Aiyura, ditch in forest, 1670 m, 20.v.2006, 06.21.131S 145.54.398E, John & Balke (PNG 69)”

(ZSM). 3 males, 1 female "Papua New Guinea: Eastern Highlands, Aiyura, creek, 1670 m, 20.v.2006, 06.21.131S 145.54.398E, John & Balke (PNG 70)" (ZSM). 12 males, 18 females "Papua New Guinea: Eastern Highlands, Onerunka, small creek, red soil /rock, 1700m, 21.v.2006, 06.20.936S 145.46.874E, John & Balke (PNG 71)" (NHMW, ZSM). 5 males, 5 females "Papua New Guinea: Eastern Highlands, Onerunka-Kainantu, 1799m, 14.i.2003, 06 20.561S 145 46.525E, K. Sagata (WB3)" (ZSM). 1 male, 4 females "Papua New Guinea: Eastern Highlands, Yoginofi-Kainantu, 1940m, 14.i.2003, 06 21.483S 145 45.281E, K. Sagata (WB4)" (ZSM). 1 male "390 DNA M Balke", "PNG: EHL, Onerunka-Kainantu, ii.2003, Sagata, DNA M Balke: MB 390" (ZSM). 2 males, 1 female "Papua New Guinea: Eastern Highlands, Abave, small creek, 1500 m, 21.v.2006, 06.17.35S 145.37.681E, John & Balke (PNG 72)" (ZSM). 251 males, 127 females "Papua New Guinea: Eastern Highlands, Kainantu, Yoginofi, 1900m, 9.v.1994, 06.21.799S 145.45.463E, Balke & Sagata (PNG 55)" (NHMW, ZSM). 1 male "385 DNA M Balke", "PNG: EHL, Kainantu, Yoginofi-Kainantu, ii.2003, Sagata, DNA M Balke: MB 385" (ZSM). 20 males, 14 females "Papua New Guinea: Eastern Highlands, Hogu, 1 km E Mt. Barola, 1900m, 9.v.1994, 06.17.556S 145.45.036E, Balke & Sagata (PNG 56)" (NHMW, ZSM). **Morobe:** 3 females "Stn. No. 139", "NEW GUINEA: Morobe Dist., Herzog Mts., Vagau, C.4,000ft. 4-17.i.1965", "M. E. Bacchus. B. M. 1965-120" (BMNH). 1 male, 3 females "Stn. No. 140A", "NEW GUINEA: Morobe Dist., Herzog Mts., Vagau, C.4,000ft. 4-17.i.1965", "M. E. Bacchus. B. M. 1965-120" (BMNH). 2 males, 1 female "Stn. No. 144", "NEW GUINEA: Morobe Dist., Herzog Mts., Vagau, C.4,000ft. 4-17.i.1965", "M. E. Bacchus. B. M. 1965-120" (BMNH). 1 female "Stn. No. 150", "NEW GUINEA: Morobe Dist., Herzog Mts., Vagau, C.4,000ft. 4-17.i.1965", "M. E. Bacchus. B. M. 1965-120" (BMNH). 42 males, 52 females "Papua New Guinea: Morobe, Wagau, Herzog Mts., 1150m, 19.xi.2006, 06.51.067S 146.48.068E, Balke & Kinibel (PNG 102)", one male with a green label "DNA M.Balke 1380" (NHMW, ZSM). 6 males, 8 females "Papua New Guinea: Morobe, Herzog Mts., 1000m, 20.xi.2006, nr. 06.51.067S 146.48.068E, Balke & Kinibel (PNG 104)" (ZSM). 2 males, 3 females "Papua New Guinea: Morobe, Menyamya, 4-5h towards [towards] Aseki, 1500-2000m, 15.XI.2006, nr 07.14.956S 146.05.687E, Balke & Kinibel, (PNG 100)" (ZSM). 101 males, 54 females "Papua New Guinea: Gulf [sic], Menyamya, Mt Inji 1700m, 14.xi.2006 nr 07.14.813S 146.01.330E Balke & Kinibel (PNG 96)", one male with a green label "DNA M.Balke 1374" (NHMW, ZSM). 1 female "PAPUA NEW GUINEA Wau, Morobe Prov. Mt. Missim, 1500 m Coldwater Crk. 3 Nov 1985 Col. By MP Kowalski" (ZSM).

Diagnosis. Beetle medium-sized (TL-H 3.9–4.5 mm); piceous, usually with brownish pronotal sides and head; shiny, with fine but evident punctation and microreticulation; pronotum with distinct lateral bead; male and female antennomere 2 distinctly enlarged, antennomeres 3–6 stout (Fig. 25); protarsomere 4 with large, strongly curved anterolateral hook-like setae; male protarsomere 5 ventrally with anterior band of ca. 60 and posterior row of 13 relatively long, thin setae (Fig. 2A); median lobe evenly curved, with slightly curved, elongate and broadly pointed apex in lateral view, evenly tapering, with rounded apex in ventral view, on both lateral sides with

numerous fine setae situated linearly usually on anterior half of distal part of median lobe; paramere without notch, slightly concave on dorsal side and with dense, strong setae on subdistal part and fine proximal setae (Fig. 2B–D).

Variability. Specimens from the Eastern Highlands have a shorter apex of the median lobe and more numerous lateral setae situated on almost the whole distal part of the median lobe (Fig. 3).

Distribution. Papua New Guinea: Morobe and Eastern Highlands Provinces (Fig. 40).

2. *Exocelina rufa* (Balke, 1998)

Figs 1, 24

Copelatus (*Papuadytes*) *rufus* Balke, 1998: 335; Nilsson 2001: 77 (catalogue).

Papuadytes rufus (Balke, 1998): Nilsson and Fery 2006: 56 (comb. n.).

Exocelina rufa (Balke, 1998): Nilsson 2007: 34 (comb. n.).

Type locality. Papua New Guinea: Morobe Province, Herzog Range, Wagau (Vagau), ca. 06°48'S; 146°48'E, ca. 1300 m a.s.l.

Type material studied. *Paratypes*: 2 males “Stn. No. 150.”, “NEW GUINEA: Morobe Dist., Herzog Mts., Vagau, C.4,000ft. 4-17.i.1965”, “M. E. Bacchus. B. M. 1965-120”, “Paratypus *Copelatus rufus* sp.n. Balke des. 1997” [red] (NHMW).

Diagnosis. Beetle small (TL-H 3.45–3.5 mm); reddish brown; matt, with dense, strong punctuation and strongly impressed microreticulation; pronotum with distinct lateral bead; male antennomere 2 distinctly enlarged, antennomeres 3–6 stout (Fig. 24); protarsomere 4 with large, strongly curved anterolateral hook-like setae; male protarsomere 5 ventrally with anterior band of 23 and posterior row of 5 relatively long, thin setae (Fig. 1A); median lobe evenly curved, with slightly curved, elongate and broadly pointed in lateral view, evenly tapering, with broadly rounded apex (slightly truncate on very tip) in ventral view, on both lateral sides with numerous fine setae situated linearly on almost whole distal part of median lobe; paramere without notch, slightly concave on dorsal side and with dense, strong setae on subdistal part and fine proximal setae (Fig. 1B–D).

Distribution. Papua New Guinea: Morobe Province. The species is known only from the type locality (Fig. 40).

3. *Exocelina tekadu* Shaverdo & Balke, sp. n.

<http://zoobank.org/E2F24500-5AB1-4AFE-B6BD-32CC3BCCC9F0>

Figs 4, 26

Type locality. Papua New Guinea: Morobe Province, Tekadu, ca. 07°38'19.4"S; 146°32'12.4"E, 400–500 m a.s.l.

Type material. *Holotype*: male “PAPUA N.G.: Morobe Prov., Lakekamu Bas., Tekadu 28.2.1998, 400–500 m leg. Riedel” (NHMW).

Diagnosis. Beetle medium-sized; brown, with reddish head and pronotum; shiny; male antennomeres modified: antennomere 2 distinctly enlarged, antennomeres 3–6 stout; protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta; median lobe with slightly curved, broad apex in lateral view and with concave apex in ventral view, on both lateral sides with small bunch of fine distal setae; paramere without notch on dorsal side. The species is similar to *E. miriae* and *E. rufa* in the presence of the enlarged male antennomere 2, but differs from them in the shape and setation of the median lobe, as well as in distinctly finer dorsal punctation and microreticulation; from *E. rufa* also in size and coloration.

Description. *Size and shape*: Beetle medium-sized (TL-H 3.95 mm, TL 4.5 mm, MW 2.2 mm), with oblong-oval habitus, broadest at elytral middle. *Coloration*: Head reddish brown, with small darker areas posterior to eyes; pronotum reddish brown, with small brown to dark brown area on disc; elytra dark brown, with narrow reddish sutural lines; head appendages yellowish red, legs reddish, distally darker, especially metathoracic legs (Fig. 26).

Surface sculpture: Head with rather dense punctation (spaces between punctures 1–2 times size of punctures), evidently finer and sparser anteriorly; diameter of punctures smaller than diameter of cells of microreticulation or equal for some punctures. Pronotum with much sparser and finer punctation than on head. Elytra with very sparse and fine punctation. Pronotum and elytra with weakly impressed microreticulation, dorsal surface shiny. Head with microreticulation stronger. Metaventricle and metacoxa distinctly microreticulate, metacoxal plates with longitudinal striae and transverse wrinkles. Abdominal ventrites with distinct microreticulation, striae, and very fine sparse punctation.

Structures: Pronotum with distinct lateral bead. Base of prosternum and neck of prosternal process with distinct ridge, slightly rounded anteriorly. Blade of prosternal process lanceolate, relatively narrow, slightly convex, with distinct lateral bead and few setae; neck and blade of prosternal process evenly jointed. Abdominal ventrite 6 slightly truncate.

Male: Antennomere 2 distinctly enlarged, antennomeres 3–6 stout (Fig. 26). Protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta. Protarsomere 5 ventrally with anterior band of more than 50 and posterior row of 7 rather long setae (Fig. 4A). Median lobe with slightly curved, broad apex in lateral view and with concave apex in ventral view, on both lateral sides with small number of fine setae situated in a bunch on distal part of median lobe close to apex. Paramere without notch, slightly concave on dorsal side and with dense setae on subdistal part; proximal setae inconspicuous (Fig. 4B–D). Abdominal ventrite 6 with 7–8 lateral striae on each side.

Female: unknown.

Distribution. Papua New Guinea: Morobe Province. The species is known only from the type locality (Fig. 40).

Etymology. The species is named after Tekadu Village. The name is a noun in the nominative singular standing in apposition.

Other species

The species described below do not have modified antennae.

4. *Exocelina andakombensis* Shaverdo & Balke, sp. n.

<http://zoobank.org/91325799-1256-468B-88EB-2E19175DAF80>

Figs 7, 29

Exocelina undescribed sp. MB1361: Toussaint et al. 2014: supplementary figs 1–4, tab. 2.

Type locality. Papua New Guinea: Gulf Province, Marawaka, Andakombe towards Morobe, 07°08.96'S; 145°45.48'E, 1000 m a.s.l.

Type material. *Holotype*: male “Papua New Guinea: Gulf, Marawaka, Andakombe towards Morobe, 1000m, 12.xi.2006, 07.08.958S 145.45.482E, Balke & Kinibel (PNG 91)” (ZSM). *Paratypes*: **Morobe**: 1 male, 4 females “Papua New Guinea: Morobe, Herzog Mts., Bundun, 700–800m, 2.iv.2006, 06.51.598S 146.37.07E, Balke & Sagata (PNG 27)”, the male additionally with a green label “DNA M.Balke 1314” (NHMW, ZSM). **Gulf**: 2 males, 1 female with the same label as the holotype (NHMW, ZSM). 1 male “Papua New Guinea: Gulf, Marawaka, Andakombe towards Morobe, 1500m, 12.xi.2006, 07.10.413S 145.49.555E, Balke & Kinibel (PNG 93)”, “DNA M.Balke 1361” [green] (ZSM). 2 males “Papua New Guinea: Gulf, Marawaka, Mala, 1400m, 11.xi.2006, 07.05.664S 145.44.467E, Balke & Kinibel (PNG 90)” (ZSM). 3 males, 1 female “Papua New Guinea: Gulf, Marawaka, nr Ande, 1000m, 10.xi.2006, 07.03.598S 145.44.375E, Balke & Kinibel (PNG 89)” (NHMW, ZSM).

Diagnosis. Beetle small; piceous, with brown head and pronotum; matt, with strong punctation and microreticulation; male antennae simple; protarsomere 4 with weakly curved anterolateral hook-like seta, equal to more laterally situated large seta; median lobe with slightly curved, rounded apex in lateral view and with slightly concave apex in ventral view, on both lateral sides with strong, relatively long setae situated broad-linearly on anterior half of distal part of median lobe; paramere without notch on dorsal side. The species is very similar to *E. injiensis* sp. n. but differs from it in small, equal to laterally situated large seta, weakly curved anterolateral hook-like seta of protarsomere 4 (large, thick, strongly curved anterolateral hook-like seta in *E. injiensis* sp. n.), shorter and less numerous ventral setae of protarsomere 5, and absence of fine lateral carina, bordering shorter distal setae, on the median lobe.

Description. *Size and shape*: Beetle small (TL-H 3.15–3.55 mm, TL 3.55–4.1 mm, MW 1.7–1.95 mm), with oblong-oval habitus, broadest at elytral middle. *Coloration*: Head reddish brown to dark brown, with small darker areas posterior to eyes; pronotum reddish brown to dark brown, paler laterally, sometimes piceous on disc; elytra piceous, dark brown laterally, with narrow reddish sutural lines; head append-

ages and legs proximally yellowish red, legs distally darker, reddish brown, especially metathoracic legs (Fig. 29). Teneral specimens paler.

Surface sculpture: Head with very dense punctation (spaces between most of punctures equal size of punctures), sparser anteriorly; diameter of most of punctures equal diameter of cells of microreticulation. Pronotum and elytra with sparser and slightly finer punctation than on head. Pronotum and elytra with strongly impressed microreticulation, dorsal surface matt. Head with microreticulation stronger. Metaventrite and metacoxa distinctly microreticulate, metacoxal plates with longitudinal striae and transverse wrinkles, abdominal ventrites with distinct microreticulation and striae. Metaventrite medially, metacoxal plates, and abdominal ventrites with sparse but distinct punctation.

Structures: Pronotum with distinct lateral bead. Base of prosternum and neck of prosternal process with distinct ridge, slightly rounded anteriorly. Blade of prosternal process lanceolate, relatively broad, slightly convex, and smooth, with distinct lateral bead and few lateral setae; neck and blade of prosternal process evenly jointed. Abdominal ventrite 6 slightly truncate.

Male: Antennae simple. Protarsomere 4 with small (equal to laterally situated large seta), weakly curved anterolateral hook-like seta; small setae around it reduced. Protarsomere 5 ventrally with anterior row of 8 and posterior row of 3 short setae (Fig. 7A). Median lobe with slightly curved, rounded apex in lateral view and with almost truncate apex in ventral view, on both lateral sides with strong, short setae situated almost linearly on a half of distal part of median lobe. Paramere without notch, slightly concave on dorsal side and with dense setae on subdistal part; proximal setae inconspicuous (Fig. 7B–D). Abdominal ventrite 6 with 6–9 lateral striae on each side.

Holotype: TL-H 3.25 mm, TL 3.6 mm, MW 1.75 mm.

Female: Without evident differences in external morphology from males, except for not modified pro- and mesotarsi and abdominal ventrite 6 without striae.

Distribution. Papua New Guinea: Gulf and Morobe Provinces (Fig. 40).

Etymology. The species is named after Andakombe Village. The name is an adjective in the nominative singular.

5. *Exocelina atrata* (Balfour-Browne, 1939)

Figs 22, 36

Copelatus atratus J. Balfour-Browne 1939: 66; Guignot 1956: 55 (catalogue); Guéorguiev 1968: 32 (catalogue); Guéorguiev and Rocchi 1993: 161 (catalogue).

Copelatus (Papuadytes) atratus J. Balfour-Browne, 1939: Balke 1998: 326 (notes, diagnosis); Nilsson 2001: 76 (catalogue).

Papuadytes atratus (J. Balfour-Browne, 1939): Nilsson and Fery 2006: 56 (comb. n.).

Exocelina atrata (J. Balfour-Browne, 1939): Nilsson 2007: 33 (comb. n.).

Type locality. Papua New Guinea: Oro (Northern) Province, Kokoda, approximately 08°53'S; 147°44'E, approximately 366 m a.s.l.

Type material. *Holotype*: male “Type” [round, with red bead], “Under stones: river side.”, “PAPUA:Kokoda. 1,200ft. viii.1933. L.E.Cheesman. B.M.1933-577.”, “*Copelatus atratus*, ♂ Type nov.sp.” [hw, blue ink, the word “type” with red ink], “Holotype” [red] (BMNH). *Paratypes*: 1 female “Type” [round, with red bead], “Under stones: river side.”, “PAPUA:Kokoda. 1,200ft. viii.1933. L.E.Cheesman. B.M.1933-577.”, “*Copelatus atratus*, ♀ Type nov.sp.” [hw, blue ink, the word “type” with red ink] (BMNH). 4 males, 1 female “Co-type” [round, with yellow bead], “Under stones: river side.”, “PAPUA:Kokoda. 1,200ft. viii.1933. L.E.Cheesman. B.M.1933-577.”, “*Copelatus atratus*, ♂ [or ♀] Cotype nov.sp.” [hw, blue ink, the word “Cotype” with red ink] (BMNH). 4 males “Co-type” [round, with yellow bead], “PAPUA:Kokoda. 1,200ft. vi-vii.1933. L.E.Cheesman. B.M.1933-427.”, “*Copelatus atratus*, B-B ♂ Co-type.” [hw, black ink] (BMNH).

Diagnosis. Beetle medium-sized, dark brown, with paler, reddish-brown, head and pronotal sides; dorsal surface with fine punctation and evident microreticulation, shiny; pronotum with distinct lateral bead; male antennomeres simple; male protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta; median lobe broad, with almost parallel sides and broadly rounded apex in ventral view and with slightly curved apex, some short distal setae in lateral view; paramere without notch on dorsal side.

Redescription. *Size and shape*: Beetle medium-sized (TL-H 4.20–4.25 mm, TL 4.75 mm, MW 2.25 mm), with rather oblong habitus, broadest at elytral middle. *Coloration*: Head dark brown, with reddish-brown clypeus and vertex; pronotum dark brown on disc and reddish-brown on sides; elytra uniformly dark brown; ventrally pale brown to brown, slightly darker on metacoxal plates; head appendages yellowish-brown to reddish-brown, legs darker distally (Fig. 36).

Surface sculpture: Head with dense and coarse punctation (spaces between punctures 1–2 times size of punctures); diameter of punctures smaller than diameter of cells of microreticulation. Pronotum with evident, dense punctation, finer, sparser than on head. Elytra with finer, sparser punctation than on pronotum, punctation fine but distinct. Pronotum and elytra with distinct microreticulation, dorsal surface shiny. Head with microreticulation slightly stronger. Metaventricle, metacoxa, and abdominal ventrites distinctly microreticulate, but with cells of microreticulation larger than on dorsal side. Metacoxal plates with longitudinal striae and transverse wrinkles; abdominal ventrites with striae. Ventrums with inconspicuous punctation, more evident on metacoxal plates and two last abdominal ventrites.

Structures: Pronotum with distinct lateral bead. Base of prosternum and neck of prosternal process with distinct ridge, smooth anteriorly, without anterolateral extensions. Blade of prosternal process lanceolate, relatively narrow, convex, with distinct bead and few setae laterally; neck and blade of prosternal process evenly jointed. Abdominal ventrite 6 truncate apically.

Male: Antenna simple. Protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta. Protarsomere 5 ventrally with dense anterior band of ca. 70 relatively long, thin setae and posterior row of 15 similar setae (Fig. 22A). Abdominal

ventrite 6 with 4–5 lateral striae on each side. Median lobe broad, with almost parallel sides and slightly concave apex in ventral view and with slightly curved apex, some short distal setae situated in small groups under very fine carinas in lateral view; ventral sclerite of medial lobe as long as median lobe or slightly longer (Fig. 22B–C). Paramere without notch, slightly concave on dorsal side, with thin, sparse, inconspicuous proximal setae and thicker, denser, and longer subdistal setae (Fig. 22D).

Female: Without evident differences in external morphology from males, except for not modified pro- and mesotarsi and abdominal ventrite 6 rounded apically, without striae.

Distribution. Papua New Guinea: Oro (Northern) Province. The species is known only from its type locality (Fig. 40).

6. *Exocelina damantiensis* (Balke, 1998)

Figs 9–16, 31

Copelatus (Papuadytes) damantiensis Balke 1998: 314; Nilsson 2001: 76 (catalogue).

Papuadytes damantiensis (Balke, 1998): Nilsson and Fery 2006: 56 (comb. n.).

Exocelina damantiensis (Balke, 1998): Nilsson 2007: 33 (comb. n.); Toussaint et al. 2014: Supplementary Figs 1–4, Tab. 2.

Copelatus (Papuadytes) inornatus Balke 1998: 316, not *Copelatus inornatus* Sharp, 1882; Nilsson 2001: 77 (catalogue); **syn. n.**

Copelatus (Papuadytes) madangensis Balke 2001: 362 (nom.n. for *Copelatus (Papuadytes) inornatus* Balke, 1998).

Exocelina madangensis (Balke, 2001): Nilsson 2007: 34 (comb. n.); Toussaint et al. 2014: Supplementary Figs 1–4, Tab. 2.

Copelatus (Papuadytes) patepensis Balke 1998: 317; Nilsson 2001: 77 (catalogue); **syn. n.**

Papuadytes patepensis (Balke, 1998): Nilsson and Fery 2006: 56 (comb. n.).

Exocelina patepensis (Balke, 1998): Nilsson 2007: 34 (comb. n.); Toussaint et al. 2014: supplementary figs 1–4, tab. 2.

Copelatus (Papuadytes) rivulus Balke 1998: 318; Nilsson 2001: 77 (catalogue); **syn. n.**

Papuadytes rivulus (Balke, 1998): Nilsson and Fery 2006: 56 (comb. n.).

Exocelina rivulus (Balke, 1998): Nilsson 2007: 34 (comb. n.).

Type locality. Papua New Guinea: Madang Province, Finisterre Range, Damanti, 05°53'26.5"S; 145°57'50.6"E.

Type material studied. *Exocelina damantiensis*. *Holotype*: male “Stn. No. 37”, “NEW GUINEA: Madang Dist., Finisterre Mts. Damanti 3,550 ft. 2-11.x.1964.”, “M.E. Bacchus. B.M. 1965-120”, “*Copelatus damantiensis* sp.n. Balke des. 1997” [red], “Holotypus” [red] (BMNH). Note: “Stn. 387” in the original description is obviously a type error. *Paratypes*: 2 males, 11 females “Stn. No. 37”, “NEW GUINEA: Madang Dist., Finisterre Mts. Damanti 3,550 ft. 2-11.x.1964.”, “M.E. Bacchus. B.M. 1965-120” (BMNH, NHMW). 16 males, 16 females “Stn. No. 38”, “NEW GUIN-

EA: Madang Dist., Finisterre Mts. Damanti 3,550 ft. 2-11.x.1964.”, “M.E. Bacchus. B.M. 1965-120” (BMNH, NHMW). 3 males, 7 females, 26 exs. “Stn. No. 39”, “NEW GUINEA: Madang Dist., Finisterre Mts. Damanti 3,550 ft. 2-11.x.1964.”, “M.E. Bacchus. B.M. 1965-120” (BMNH, NHMW). 2 males, 1 female, 14 exs. “Stn. No. 61”, “NEW GUINEA: Madang Dist., Finisterre Mts. Budemu c. 4000 ft. 15-24.x.1964.”, “M.E. Bacchus. B.M. 1965-120” (BMNH, NHMW). 1 male, 1 female, 5 exs. “Stn. No. 62”, “NEW GUINEA: Madang Dist., Finisterre Mts. Budemu c. 4000 ft. 15-24.x.1964.”, “M.E. Bacchus. B.M. 1965-120” (BMNH, NHMW). 2 males, 1 female, 13 exs. “Stn. No. 73”, “NEW GUINEA: Madang Dist., Finisterre Mts. Budemu c. 4000 ft. 15-24.x.1964.”, “M.E. Bacchus. B.M. 1965-120” (BMNH, NHMW). 3 males, 11 exs. “Stn. No. 74”, “NEW GUINEA: Madang Dist., Finisterre Mts. Budemu c. 4000 ft. 15-24.x.1964.”, “M.E. Bacchus. B.M. 1965-120” (BMNH, NHMW). 6 males, 8 females “Stn. No. 78”, “NEW GUINEA: Madang Dist., Finisterre Mts. Moro.C.5550ft. 30.x.-15.xi.1964.”, “M.E. Bacchus. B.M. 1965-120” (BMNH, NHMW). 4 males, 6 females, 18 exs. “Stn. No. 82”, “NEW GUINEA: Madang Dist., Finisterre Mts. Moro.C.5550ft. 30.x.-15.xi.1964.”, “M.E. Bacchus. B.M. 1965-120” (BMNH, NHMW). 2 males, 5 exs. “Stn. No. 83”, “NEW GUINEA: Madang Dist., Finisterre Mts. Moro.C.5550ft. 30.x.-15.xi.1964.”, “M.E. Bacchus. B.M. 1965-120” (BMNH, NHMW). 2 males, 3 exs. “Stn. No. 89”, “NEW GUINEA: Madang Dist., Finisterre Mts. Moro.C.5550ft. 30.x.-15.xi.1964.”, “M.E. Bacchus. B.M. 1965-120” (BMNH, NHMW). 5 males “Stn. No. 95”, “NEW GUINEA: Madang Dist., Nr. Sewe, c.5,300 ft. 15.xi.1964.”, “M.E. Bacchus. B.M. 1965-120” (BMNH, NHMW). All these specimens are with red paratype labels “Paratypus Copelatus damantiensis sp.n. Balke des. 1997” [red].

***Exocelina madangensis*.** *Paratypes*: 4 males, 3 females with the same label as the holotype, except for “Paratypus Copelatus inornatus sp.n. Balke des. 1997” [red] (NHMW).

***Exocelina patepensis*.** *Holotype*: male “Stn. No. 126”, “NEW GUINEA: Morobe Dist., Lae-Bulolo Rd., Patep Ck., 28.xii.1964.”, “M.E. Bacchus. B.M. 1965-120”, “Holotypus” [red], “Copelatus patepensis sp.n. Balke des. 1997” [red] (BMNH). *Paratypes*: 4 males, 1 female with the same label as the holotype, except for “Paratypus Copelatus patepensis sp.n. Balke des. 1997” [red] (NHMW).

***Exocelina rivulus*.** *Holotype*: male “IRIAN JAYA, 12.8.1992 Zentralmassiv, Borme, 140°25'E 04°24'S 900m, leg. M. Balke (8)”, “HOLOTYPUS” [red], “Copelatus rivulus Balke des. 1997” [red] (NHMW). *Paratypes*: 25 males, 15 females with the same label as the holotype (NHMW). 7 males, 5 females “IRIAN JAYA: Borme ca. 140°25'E 04°24'S 950m, 3.9.1993 leg. M. Balke (2)” (NHMW). 12 males, 5 females “IRIAN JAYA Zentralmassiv 140°25'E 04°24'S”, “16.8.1992 Borme, 1000m leg. Balke (15)” (NHMW). 3 males, 5 females “IRIAN JAYA, 4.9.1992 Diuremna - Nalca 139°49'E 04°24'S 1500m, leg. Balke (36)” (NHMW). 38 males, 31 females “IRIAN JAYA, 6.9.1992 Nalca 1700-1800m 139°49'E 04°24'S leg. Balke (38)” (NHMW). 3 males, 1 female “IRIAN JAYA, 7.9.1992 Kono, 1800m 139°47'E 04°21'S, leg. Balke (41)” (NHMW). 55 males, 47 females “IRIAN JAYA, 12.9.1992 Angguruk, 1400m

139°25'E 04°15'S, leg. Balke (48)" (NHMW). 5 males, 1 female "IRIAN JAYA: Angguruk, 8.10.1993 Angguruk, ca. 1350m", "ca. 139°25'E 04°15'S leg. M. Balke (32)" (NHMW). 1 male "IRIAN JAYA: Borme Tarmalu, 1500m 6.9.1993", "ca. 140°25'E 04°24'S, leg. M. Balke (4-6)" (NHMW). 53 males, 42 females "IRIAN JAYA: 11.9.1993 Bime – Calab Gebiet, Bime, 1400m", "leg. M. Balke (12) ca. 140°12'E 04°20'S" (NHMW). 57 males, 20 females "IRIAN JAYA: 22.9.1993 Bime – Calab Gebiet, Bime, 1400m", "ca. 140°12'E 04°20'S, leg. M. Balke (16)" (NHMW). These females are a mixture of two species: *E. damantiensis* and *E. aipomek* (Balke, 1998). 2 males, 3 females "IRIAN JAYA: 28.9.1993 Eme Gebiet Emdoman, 1150m", "ca. 139°55'E 04°14'S, leg. M. Balke (23)" (NHMW). 6 males, 5 females "IRIAN JAYA: 29.9.1993 Eme Gebiet Emdoman, 800m", "ca. 139°55'E 04°14'S, leg. M. Balke (24)" (NHMW). 2 males "IRIAN JAYA: 29.9.1993 Eme Gebiet Emdoman, 800-1000m", "leg. M. Balke (25) ca. 139°55'E 04°14'S" (NHMW). 23 males "IRIAN JAYA: 1.10.1993 Eme Gebiet Okloma, 1500m", "ca. 139°55'E 04°14'S, leg. M. Balke (28)" (NHMW). All these specimens are with red paratype labels "PARATYPUS *Copelatus rivulus* sp.n. M. Balke des. 1997" or "Paratypus *Copelatus rivulus* sp.n. Balke des. 1997" [red].

Additional material. Indonesia: West Papua Province: Teluk Wondama Regency: 3 males, 1 female "IRIAN JAYA: Wandammen Bay, Wondiwoi Mts. Wasior, 300-700 m, 14.I.2001 leg. A. RIEDEL" (NHMW, SMNS, ZSM). 3 females "IRIAN JAYA: Wandammen Bay, Wondiwoi Mts. Wasior, 250-600 m, 4.I.2001 leg. A. RIEDEL" (SMNS). 2 males "INDONESIA: West Papua: Wandammen Bay, Wasior, 4-5.I.2001 leg. A. Riedel 2°45.940'S 134°31.738'E" (ZSM). **Papua Province: Paniai Regency:** 2 males "IRIAN JAYA: Paniai Prov. road Nabire-Ilaga, km 140 4.9.1996, 450 m leg. M. Balke (96 # 13)" (NHMW). 1 male, 5 females "IRIAN JAYA: Paniai Prov. road Nabire-Ilaga, km 160 4.9.1996, 600 m leg. M. Balke (96 # 14)" (NHMW). 1 male "IRIAN JAYA: Paniai Prov. road Nabire-Ilaga, km 165 4.9.1996, 650 m leg. M. Balke (96 # 15)" (NHMW). All these specimens (locs. 13, 14, 15) are with red paratype labels "PARATYPUS *Copelatus rivulus* sp.n. M. Balke des. 1997" or "Paratypus *Copelatus rivulus* sp.n. Balke des. 1997" [red] but they are not considered as paratypes because they are not included into the type material of the original description. **Intan Jaya Regency:** 8 males, 13 female "IRIAN JAYA: Paniai Prov. Kemandoga, Homeyo, Sabisa 1700-1900m, 5.1.1996 leg. A. Riedel" (NHMW, ZSM). **Puncak Jaya Regency:** 1 male "Indonesia: Papua, Wano Land, red clay creek nr cave, 1100m, 3.ix.2014, nr -3.587955 137.5114945 (Pap024)", "M.Balke 6516" [green text] (ZSM). 12 males, 7 females "Indonesia: Papua, Wano Land, river grey sediment, 980m, 3.ix.2014, -3,587955 137,5114945 (Pap025)" (NHMW, ZSM). 8 males, 1 female "Indonesia: Papua, Wano Land, river ca 15m wide, 930m, 3.ix.2014, -3,587955 137,5114945 (Pap026)" (NHMW, ZSM). 6 males, 3 females "Indonesia: Papua, Wano Land, creek @ jungle helipad, 870m, 4.ix.2014, -3,584077 137,5042947 (Pap027)", two males with an additional labels "M.Balke 6525" and "M.Balke 6526" [green text] (NHMW, ZSM). **Puncak Regency:** 11 males, 4 females "Indonesia: Papua, Wano Land, below Puluk, 1100m, 2.ix.2014, nr -3.660272 137.5207436 (Pap021)", one of the males with

an additional label “M.Balke 6510” [green text] (NHMW, ZSM). **Pegunungan Bintang Regency:** 15 males, 15 females “IRIAN JAYA Zentralmassiv 140°25'E 04°24'S”, “Kali Takime, 1000m 15.8.1992 leg. Balke (14)” (NHMW). 6 males, 7 females “IRIAN JAYA Zentralmassiv 140°25'E 04°24'S”, “Kali Takime, 900m 18.8.1992 leg. Balke (16)” (NHMW). 19 males, 27 females “IRIAN JAYA Zentralmassiv 140°25'E 04°24'S”, “Kali Takime, 900m 18.8.1992 leg. Balke (17)” (NHMW). All these specimens (locs. 14, 16, 17) are with red paratype labels “PARATYPUS *Copelatus rivulus* sp.n. M. Balke des. 1997” or “Paratypus *Copelatus rivulus* sp.n. Balke des. 1997” [red] but they are not considered as paratypes because they are not included into the type material of the original description. 9 females “IRIAN JAYA: 11.9.1993 Bime – Calab Gebiet, Bime, 1400m”, “leg. M. Balke (12) ca. 140°12'E 04°20'S” (NHMW).

Papua New Guinea: Sandaun: 3 females “Papua New Guinea: Sandaun, Mianmin, Fak River, 775m, 14.xi.2003, 453 53.00S 141 36 39.40E, K. Sagata (WB17)”, one of them with an additional label “DNA M. Balke 678” [green text] (ZSM). 2 females “Papua New Guinea: Sandaun, Mianmin, Fak River, 775m, 15.xi.2003, 453 53.00S 141 36 39.40E, K. Sagata (WB22)” (ZSM). 1 male “Papua New Guinea: Sandaun, Sandaun, Fak River (WB24), 23.x.2003, K. Sagata, DNA M Balke: MB 685”, “DNA M. Balke 685” [green text] (ZSM). 2 males, 5 females “Papua New Guinea: Sandaun, Sandaun, Fak River, 775m, 15.x.2003, 4 53 53.00S #, K. Sagata (WB24)” (ZSM). 1 male “Papua New Guinea: Sandaun, Sandaun, Sek River (WB50), 21.x.2003, K. Sagata, DNA M Balke: MB 668”, “DNA M. Balke 668” [green text] (ZSM). 3 males, 3 females “Papua New Guinea: Sandaun, Sandaun, Sek River 775m, 13.x.2003, K. Sagata (WB50)” (NHMW, ZSM). 5 males, 1 female “Papua New Guinea: Sandaun, May River, 970m, 19.x.2003, 4 49.779S 141 38.174E, K. Sagata (WB43)”, one of the males with an additional label “DNA M. Balke 687” [green text] (NHMW, ZSM). 2 males, 5 females “Papua New Guinea: Sandaun, Wara Uk, - 900m, 14.xi.2003, Not taken, K. Sagata (WB16)”, “DNA M. Balke 676”, “DNA M. Balke 677” [green text] (ZSM). 1 male “Papua New Guinea: Sandaun, Sandaun, Faklows (WB87), 24.x.2003, K. Sagata, DNA M Balke: MB 656”, “DNA M. Balke 656” [green text] (ZSM). 1 male “Papua New Guinea: Sandaun, Sokamin4, 1200m, 19.x.2003, 4 50.845S 141 37.865E, K. Sagata (WB102)”, “DNA M. Balke 675” [green text] (ZSM). 2 males, 2 females “Papua New Guinea: Sandaun, MekilWX25, 1718m, 13.x.2003, 4 48.637S 141 38.994E, K. Sagata (WB109)”, one of the males with an additional label “DNA M. Balke 669” [green text] (ZSM). 2 males, 1 female “Papua New Guinea: Sandaun, Mianminold, 898m, 20.x.2003, 4 53.419S 141 37.028E, K. Sagata (WB66)”, one male additionally with “DNA M. Balke 674” [green text] (ZSM). 1 female “Papua New Guinea: Sandaun, Sandaun, Mianmin (WB75), 9.x.2003, K. Sagata, DNA M Balke: MB 667”, “DNA M. Balke 667” [green text] (ZSM). 11 males, 1 female “Papua New Guinea: Sandaun, Mianmin, 670m, 22.x.2008, 4.53.329S 141.35.263E, Ibalim (PNG 189)”, one of males with an additional green label “DNA M Balke 3718” (NHMW, ZSM). 69 males, 88 females “Papua New Guinea: Sandaun, Mianmin, 670m, 20.x.2008, 4.53.292S 141.34.118E, Ibalim (PNG 191) (NHMW, ZSM). 22 males, 28 females “Papua New Guinea: Sandaun,

Mianmin (river), 990m, 23.x.2008, 4.54.570S 141.35.490E, Ibalim (PNG 192)", one of males with an additional green label "DNA M Balke 3738" (NHMW, ZSM). 8 males, 8 females "Papua New Guinea: Sandaun, Mianmin (pool), 990m, 23.x.2008, 4.54.570S 141.35.490E, Ibalim (PNG 193) (NHMW, ZSM). 51 males, 85 females "Papua New Guinea: Sandaun, Mianmin (river), 1080m, 24.x.2008, 04.55.780S 141.38.185E, Ibalim (PNG 195), some of them with green labels "DNA M Balke" with numbers 3743, 3744, 3779, 3780, 3781, 3782 (NHMW, ZSM). 21 males, 4 females "Papua New Guinea: Sandaun, Mianmin (pool), 1080m, 24.x.2008, 04.55.780S 141.38.185E, Ibalim (PNG 196)", one of males with an additional green label "DNA M Balke 3748" (NHMW, ZSM). 82 males, 82 females "Papua New Guinea: Sandaun, Mianmin (pool), 700m, 21.x.2008, 04.52.858S 141.31.706E, Ibalim (PNG 197) (NHMW, ZSM). 27 males, 43 females "Papua New Guinea: Sandaun, Mianmin (pool), 700m, 21.x.2008, 04.52.858S 141.31.706E, Ibalim (PNG 198) (ZSM). 7 males, 15 females "Papua New Guinea: Sandaun, Mianmin area, >1000m, 23.xii.209, Ibalim & Pius (PNG232)" (ZSM). 9 males, 15 females "Papua New Guinea: Sandaun, Mianmin area, >1000m, 23.xii.2009, Ibalim & Pius (PNG240)" (NHMW, ZSM). 2 males, 2 females "Papua New Guinea: Sandaun, Mianmin area, >1000m, 26.xii.209, Ibalim & Pius (PNG233)" (ZSM). 1 male "Papua New Guinea: Sandaun, Mianmin area, >600m, 13.i.2010, Ibalim & Pius (PNG236)", "DNA M. Balke 4928" [green text] (ZSM). 8 males, 9 females "Papua New Guinea: Sandaun, Mianmin area, >600m, 13.i.2010, Ibalim & Pius (PNG236)" (NHMW, ZSM). 11 males, 7 females "Papua New Guinea: Sandaun, Mianmin area, >600m, 9.i.2010, Ibalim & Pius (PNG237)" (NHMW, ZSM). 7 males, 4 females "Papua New Guinea: Sandaun, Mianmin area, >600m, 6.i.2010, Ibalim & Pius (PNG239)" (NHMW, ZSM). 20 males, 12 females "Papua New Guinea: Sandaun, Mianmin area, >700m, 7.i.2010, Ibalim & Pius (PNG231)" (NHMW, ZSM). **Western Province:** 27 males, 17 females "Papua New Guinea: Western Province, Tabubil, 600m, 22.vi.2008, 05.15.673S 141.13.738E, Posman (PNG 181)" (NHMW, ZSM). **Madang:** 1 female "Stn. No. 30", "NEW GUINEA: Madang Dist., Finisterre Mts. Damanti 3,550 ft. 2-11.x.1964.", "M.E. Bacchus. B.M. 1965-120" (BMNH). 1 male, 9 females "Stn. No. 46", "NEW GUINEA: Madang Dist., Finisterre Mts. Damanti 3,550 ft. 2-11.x.1964.", "M.E. Bacchus. B.M. 1965-120" (BMNH). 2 males, 3 females, 15 exs. "Stn. No. 47", "NEW GUINEA: Madang Dist., Finisterre Mts. Damanti 3,550 ft. 2-11.x.1964.", "M.E. Bacchus. B.M. 1965-120". These beetles are with paratypes labels "Paratypus Copelatus damantiensis sp.n. Balke des. 1997" but they are not considered as paratypes because they are not included into the type material of the original description (BMNH, NHMW). 2 males, 2 females "Stn. No. 49", "NEW GUINEA: Madang Dist., Finisterre Mts. Damanti 3,550 ft. 2-11.x.1964.", "M.E. Bacchus. B.M. 1965-120" (BMNH). 2 females "Stn. No. 61", "NEW GUINEA: Madang Dist., Finisterre Mts. Budemu c. 4000 ft. 15-24.x.1964.", "M.E. Bacchus. B.M. 1965-120" (BMNH). 3 females "Stn. No. 82", "NEW GUINEA: Madang Dist., Finisterre Mts. Moro. C. 5550ft. 30.x.-15.xi.1964.", "M.E. Bacchus. B.M. 1965-120" (BMNH). 2 males, 1 female "Stn. No. 92", "NEW GUINEA: Madang Dist., Finisterre Mts. Moro.

C. 5550ft. 30.x.-15.xi.1964.”, “M.E. Bacchus. B.M. 1965-120” (BMNH). 20 males “Papua New Guinea: Madang, Akameku - Brahmin, Bismarck Range, 750m, 25.xi.2006, 05.49.892S 145.24.491E, Balke & Kinibel (PNG 113)” (NHMW, ZSM). 34 males “Papua New Guinea: Madang, Akameku - Brahmin, Bismarck Range, 750m, 25.xi.2006, nr 05.49.307S 145.24.389E, Balke & Kinibel (PNG 114)” (NARI, NHMW, ZSM). 1 male “PAPUA NEW GUINEA Madang Pr. Below Bundi, 500 m, 26IX2002, M Balke (PNG 23), “268 DNA M Balke” [green] (ZSM). 4 males, 11 females “PAPUA NEW GUINEA: Madang, below Bundi, 500 m, 26.IX.2002 Balke & Sagata (PNG023)” (NHMW, ZSM). 3 males “Papua New Guinea: Madang, Simbai area, 1200m, 10.iii.2007, 05.13.389S 144.37.285E, Kinibel (PNG 152) (ZSM). 2 males “Papua New Guinea: Madang, Simbai area, 1200m, 11.iii.2007, 05.13.333S 144.37.611E, Kinibel (PNG 153) (NHMW, ZSM). **Enga:** 8 males “Papua New Guinea: Enga, Wapanamanda, 1500m, 6.xii.2006, 05.38.105S 143.55.338E, Balke & Kinibel, (PNG 128)”, one of them with an additional green label “DNA M.Balke 1527” (NHMW, ZSM). **Western Highlands:** 7 males “Papua New Guinea: Western Highlands, Kurumul, 6 Km SW Kudjip, small stream, 1580 m, 13.vi.2006, 05.53.426S 144.36.600E, John (PNG 78)”, one of them with an additional green label “DNA M.Balke 1340” (NHMW, ZSM). 1 male “Papua New Guinea: Western Highlands, Lugup River, 1700m, 4.iii.2007, 05.17.237S 144.28.214E, Kinibel (PNG 143)” (ZSM). 7 males “Papua New Guinea: Western Highlands, Above Sendiap, 1400m, 5.iii.2007, 05.19.774S 144.28.307E, Kinibel (PNG 145)”, one of them with an additional green label “DNA M.Balke 3314” (NHNW, ZSM). 10 males “Papua New Guinea: Western Highlands, Jimi Valley, above Sendiap Station, 950m, 6.iii.2007, 05.20.587S 144.28.847E, Kinibel (PNG 147) (NHNW, ZSM). **Simbu:** 1 female “Ibisca Niugini, PNG 6-8.xi.2012 Mount Wilhelm 200m -5,739897251 145,3297424 MW0200 / P0786 Vial 09596” (ZSM). 8 females “Ibisca Niugini, PNG 3-5.xi.2012 Mount Wilhelm 700m”, “-5,731960773 145,2521667 FIT-MW700-R-5/8-d10 / Plot 18 / P1238 Vial 15969-CODYTI” (ZSM). 4 females “Ibisca Niugini, PNG 28-30.x.2012 Mount Wilhelm 700m”, “-5,731960773 145,2521667 FIT-MW700-S-7/8-d04 / Plot 15 / P1211 Vial 16189-CODYTI” (ZSM). 1 female “Ibisca Niugini, PNG 30.x.-1.xi.2012 Mount Wilhelm 700m”, “-5,731960773 145,2521667 FIT-MW700-M-3/8-d06 / Plot 13 / P1196 Vial 15980-CODYTI” (ZSM). 1 male “Ibisca Niugini, PNG 31.x.-2.xi.2012 Mount Wilhelm 700m”, “-5,731960773 145,2521667 FIT-MW700-D-4/8-d07 / Plot 4 / P1125 Vial 16045-CODYTI” (ZSM). 1 male “Ibisca Niugini, PNG 7-9.xi.2012 Mount Wilhelm 700m”, “-5,731960773 145,2521667 FIT-MW700-S-7/8-d14 / Plot 19 / P1248 Vial 15781-CODYTI” (ZSM). 2 males, 1 female “Ibisca Niugini, PNG 3-5.xi.2012 Mount Wilhelm 700m”, “-5,731960773 145,2521667 FIT-MW700-K-5/8-d10 / Plot 11 / P1182 Vial 16083-CODYTI” (NHMW, ZSM). 1 female “Ibisca Niugini, PNG 4-6.xi.2012 Mount Wilhelm 700m”, “-5,731960773 145,2521667 FIT-MW700-A-6/8-d11 / Plot 1 / P1103 Vial 07195-CODYTI” (ZSM). 1 female “Ibisca Niugini, PNG 3-5.xi.2012 Mount Wilhelm 700m”, “-5,731960773 145,2521667 FIT-MW700-Q-5/8-d10 / Plot 17 / P1230 Vial 16097-CODYTI” (ZSM). 1 female “Ibisca Niugini, PNG

29-31.x.2012 Mount Wilhelm 700m", "-5,731960773 145,2521667 FIT-MW700-J-3/8-d05 / Plot 10 / P1172 Vial 07200-CODYTI" (ZSM). 1 male "Ibisca Niugini, PNG 29-31.x.2012 Mount Wilhelm 700m", "-5,731960773 145,2521667 FIT-MW700-D-3/8-d05 / Plot 4 / P1124 Vial 07290-CODYTI" (ZSM). 1 female "Ibisca Niugini, PNG 29-30.x.2012 Mount Wilhelm 700m", "-5,731960773 145,2521667 FIT-MW700-E-3/8-d05 / Plot 5 / P1132 Vial 07294-CODYTI" (ZSM). 1 male, 8 females "Ibisca Niugini, PNG 27-29.x.2012 Mount Wilhelm 700m", "-5,731960773 145,2521667 FIT-MW700-F-2/8-d03 / Plot 6 / P1139 Vial 15944-CODYTI" (ZSM). 1 female "Ibisca Niugini, PNG 31.x.-2.xi.2012 Mount Wilhelm 700m -5,73213905 145,2568207", "FIT-MW700-C-4/8-d07 / Plot 3 / P1117 Vial 15664-CODYTI" (ZSM). 1 male, 10 females "Ibisca Niugini, PNG 27-29.x.2012 Mount Wilhelm 700m -5,731960773 145,2521667", "FIT-MW700-D-2/8-d03 / Plot 4 / P1123 Vial 15972-CODYTI" (ZSM). 2 females "Ibisca Niugini, PNG 27-29.x.2012 Mount Wilhelm 700m -5,731960773 145,2521667", "FIT-MW700-H-2/8-d03 / Plot 8 / P1155 Vial 15976-CODYTI" (ZSM). 3 females "Ibisca Niugini, PNG 28-30.x.2012 Mount Wilhelm 700m -5,731960773 145,2521667", "FIT-MW700-M-2/8-d04 / Plot 13 / P1195 Vial 16167-CODYTI" (ZSM). 3 females "Ibisca Niugini, PNG 26-28.x.2012 Mount Wilhelm 700m -5,731960773 145,2521667", "FIT-MW700-T-1/8-d02 / Plot 20 / P1250 Vial 16254-CODYTI" (ZSM). 1 male, 2 females "Ibisca Niugini, PNG 27-29.x.2012 Mount Wilhelm 700m -5,731960773 145,2521667", "FIT-MW700-E-2/8-d03 / Plot 5 / P1131 Vial 15937-CODYTI" (ZSM). 1 female "Ibisca Niugini, PNG 25-27.x.2012 Mount Wilhelm 700m -5,731960773 145,2521667", "FIT-MW700-D-1/8-d01 / Plot 4 / P1122 Vial 15947-CODYTI" (ZSM). 1 male, 1 female "Ibisca Niugini, PNG 3-5.xi.2012 Mount Wilhelm 700m -5,731960773 145,2521667 MW700 / P1222 Vial 16098" (ZSM). 1 female "Ibisca Niugini, PNG 3-5.xi.2012 Mount Wilhelm 700m -5,731960773 145,2521667 MW700 / P1254 Vial 16105" (ZSM). 1 male "Ibisca Niugini, PNG 5-7.xi.2012 Mount Wilhelm 700m -5,731960773 145,2521667 MW700 / P1247 Vial 16078" (ZSM). 1 male, 4 females "Ibisca Niugini, PNG 28-30.x.2012 Mount Wilhelm 700m -5,731960773 145,2521667 MW700 / P1243 Vial 16156" (ZSM). 1 male, 7 females "Ibisca Niugini, PNG 28-30.x.2012 Mount Wilhelm 700m -5,731960773 145,2521667 MW700 / P1235 Vial 16164" (ZSM). 6 females "Ibisca Niugini, PNG 26-28.x.2012 Mount Wilhelm 700m -5,731960773 145,2521667 MW700 / P1210 Vial 16172" (ZSM). 1 female "Ibisca Niugini, PNG 6-8.xi.2012 Mount Wilhelm 700m -5,731960773 145,2521667 MW700 / P1144 Vial 15649" (ZSM). 1 female "Ibisca Niugini, PNG 30.x.-1.xi.2012 Mount Wilhelm 700m -5,731960773 145,2521667 MW700 / P1220 Vial 15992" (ZSM). 1 female "Ibisca Niugini, PNG 26-28.x.2012 Mount Wilhelm 700m -5,731960773 145,2521667 MW700 / P1178 Vial 16181" (ZSM). 1 male "Ibisca Niugini, PNG 30.x.-1.xi.2012 Mount Wilhelm 700m -5,731960773 145,2521667 MW700 / P1244 Vial 16285" (ZSM). 5 females "Ibisca Niugini, PNG 28-30.x.2012 Mount Wilhelm 700m -5,731960773 145,2521667 MW700 / P1179 Vial 16186" (ZSM). 2 females "Ibisca Niugini, PNG 26-28.x.2012 Mount Wilhelm 700m -5,731960773

145,2521667 MW700 / P1226 Vial 16196" (ZSM). 1 male "Ibisca Niugini, PNG 1-3.xi.2012 Mount Wilhelm 700m -5,731960773 145,2521667 MW700 / P1237 Vial 16231" (ZSM). 2 females "Ibisca Niugini, PNG 1-3.xi.2012 Mount Wilhelm 700m -5,731960773 145,2521667 MW700 / P1213 Vial 16236" (ZSM). 6 females "Ibisca Niugini, PNG 26-28.x.2012 Mount Wilhelm 700m -5,731960773 145,2521667 MW700 / P1234 Vial 16270" (ZSM). 3 females "Ibisca Niugini, PNG 28-30.x.2012 Mount Wilhelm 700m -5,731960773 145,2521667 MW700 / P1227 Vial 16277" (ZSM). 1 male, 1 female "Ibisca Niugini, PNG 26-28.x.2012 Mount Wilhelm 700m", "-5,731960773 145,2521667 FIT-MW700-S-1/8-d02 / Plot 19 / P1242 Vial 16118-CODYTI" (ZSM). 1 female "Ibisca Niugini, PNG 3-5.xi.2012 Mount Wilhelm 700m", "-5,731960773 145,2521667 FIT-MW700-S-5/8-d10 / Plot 19 / P1246 Vial 16092-CODYTI" (ZSM). 1 female "Ibisca Niugini, PNG 27-29.x.2012 Mount Wilhelm 700m", "-5,731960773 145,2521667 FIT-MW700-I-2/8-d03 / Plot 9 / P1163 Vial 15933-CODYTI" (ZSM). 1 female "Ibisca Niugini, PNG 7-9.xi.2012 Mount Wilhelm 700m", "-5,731960773 145,2521667 FIT-MW700-P-7/8-d14 / Plot 16 / P1224 Vial 15796-CODYTI" (ZSM). 5 females "Ibisca Niugini, PNG 27-29.x.2012 Mount Wilhelm 700m", "-5,731960773 145,2521667 FIT-MW700-A-2/8-d03 / Plot 1 / P1099 Vial 15960-CODYTI" (ZSM). 1 female "Ibisca Niugini, PNG 9-11.xi.2012 Mount Wilhelm 700m", "-5,731960773 145,2521667 FIT-MW700-P-8/8-d16 / Plot 16 / P1225 Vial 16066-CODYTI" (ZSM). 1 female "Ibisca Niugini, PNG 31.x.-2.xi.2012 Mount Wilhelm 1200m", "-5,720873833 145,2694702", "FIT-MW1200-E-4/8-d07 / Plot 5 / P1523 Vial 17348" (ZSM). **Simbu/Eastern Highlands:** 3 males "Papua New Guinea: Crater Mountain, trek Haia - Wara Sera, 500m, 12IX2002, Balke & Sagata, (PNG 006)" (ZSM). 4 males "Papua New Guinea: Simbu/EHPr. Crater Mountain, Wara Sera Station, 800 m, 14IX2002, Balke & Sagata, (PNG 009)" (NHMW, ZSM). 10 males "Papua New Guinea: Crater Mountain, Wara Sera Station, 800 m, 14IX2002, Balke & Sagata (PNG 010)" (NHMW, ZSM). 1 female "Papua New Guinea: Simbu/EHPr. Crater Mountain, Sera - Herowana, Jau river, 1000 m, 15IX2002, Balke & Sagata (PNG 015)" (ZSM). 2 females "Papua New Guinea: Simbu/EHP, Crater Mountain, Sera - Herowana, Sima river, 1250 m, 15IX2002, Balke & Sagata (PNG 016)" (ZSM). 1 male "PNG Simbu / EHPr. Crater Mountain, Sera - Herowana, Wara Hulene, 1000 m, 16IX2002, Balke & Sagata (PNG 17)", "263 DNA M Balke" [green] (ZSM). 8 males, 5 female "Papua New Guinea: Simbu / EHPr. Crater Mountain, Sera - Herowana, Hulene river, 1000 m, 16IX2002, Balke & Sagata (PNG 017)" (NHMW, ZSM). **Eastern Highlands:** 1 female "Stn. No. 182", "NEW GUINEA: E. Highland Dist., Purosa Valley, nr. Okapa. 8.ii.1965.", "M.E. Bacchus. B.M. 1965-120" (BMNH). 1 female "Stn. No. 190", "NEW GUINEA: E. Highland Dist., Okapa, c. 5.000ft. 10-11.ii.1965.", "M.E. Bacchus. B.M. 1965-120" (BMNH). 11 males "Papua New Guinea: Eastern Highlands, Akameku - Brahmin, Bismarck Range, 700m, 24.xi.2006, 05.52.754S 145.23.209E, Balke & Kinibel (PNG 109)", one of them with an additional green label "DNA M.Balke 1519" (NHMW, ZSM). 20 males "Papua New Guinea: Eastern Highlands, Akameku - Brahmin, Bismarck Range,

800m, 24.xi.2006, 05.50.021S 145.24.664E, Balke & Kinibel (PNG 112)” (NARI, NHMW, ZSM). 2 males, 1 female “Papua New Guinea: Eastern Highlands, below Yonki, 850m, 4.iv.2006, 06.11.332S 146.03.052E, Balke & Sagata (PNG 31)”, one male additionally with “DNA M.Balke 1311” [green] (ZSM). **Morobe:** 5 females “Stn. No. 112”, “NEW GUINEA: Morobe Dist., Finisterre Mts. Hinggia, c. 2,500ft. 28.xi.1964.”, “M.E. Bacchus. B.M. 1965-120” (BMNH). 16 males, 25 females “Papua New Guinea: Morobe, Huon, 1 km E Yakop, 1400m, 14.v.2006, nr 06.10.961S 147.08.204E, Sagata (PNG 74)” (NHMW, ZSM). 74 males, 24 females “Papua New Guinea: Morobe, Huon, Dalasi, 3 km N Yakop, 1900m, 15.v.2006, 06.10.961S 147.08.204E, Sagata (PNG 75)”, “DNA M.Balke 1286” [green] (NHMW, ZSM). 1 male “PNG: Huon Peninsula, Morobe Prov., Yus conservation area, 1398m.”, “DNA M.Balke 541” [green text] (ZSM). 10 males, 4 female “Papua New Guinea: Morobe, Mindik, 1480m, 10.x.2009, 06.27.335S 147.25.233E, Inaho (03) (PNG 203) (NHMW, ZSM). 6 males “Papua New Guinea: Morobe, Mindik, 1490m, 11.x.2009, 06.27.315S 147.25.166E, Inaho (04) (PNG 204) (NHMW, ZSM). 1 male “PAPUA N.G.: Morobe Prov. Mindik, 1200 – 1500 m, 26.4.1998 leg. A. Riedel” (NHMW). 63 males, 38 females “PAPUA N.G.: Morobe Prov. E Pindiu, Kobau 24.4.1998, 1400 m leg. A. Riedel” (NHMW, ZSM). 3 males, 1 female “Papua New Guinea: Morobe, Penjengjeng, 1200m, 12.x.2009, 06.27.497S 147.29.219E, Inaho (05) (PNG205)”, one male additionally with “DNA M.Balke 3822” [green] (NHMW, ZSM). 3 males, 1 female “Papua New Guinea: Morobe, Pindiu, Sulemana, 850m, 15.x.2009, 06.25.169S 147.32.112E, Inaho (08) (PNG 208)” (NHMW, ZSM). 1 male “Papua New Guinea: Morobe, Sattelberg, Maro Creek, 670m, x.2009, ca 06.27.239S 147.42.531E, Inaho (10) (PNG210)”, “DNA M.Balke 3826” [green] (ZSM). 3 males, 1 female “Papua New Guinea: Morobe, Sattelberg, Zige River, ca 700m, x.2009, 6 29.233S 147 46.482E, Inaho (12a) (PNG212)” (NHMW, ZSM). 4 males, 3 females “Papua New Guinea: Morobe, Sattelberg, Siki River, ca 700m, 20.x.2009, 6 29.352S 147 46.544E, Inaho (12c) (PNG 214)” (NHMW, ZSM). 15 males, 6 females “Papua New Guinea: Morobe, Huon Pen., Kwapsanek, 850m, 31.iii.2006, 06.34.913S 147.00.526E, Balke & Sagata (PNG 25)”, one of males with an additional green label “DNA M.Balke 1315” (ZSM).

Females of doubtful identity. Indonesia: Papua Province: Pegunungan Bintang Regency: 3 females “IRIAN JAVA: Borme Tarmlu 1500m 6.9.1993”, “ca. 140°25'E 04°24'S leg. M. Balke (4-6)” (NHMW). 1 female “IRIAN JAVA: Borme Tarmlu 1500m 6.9.1993”, “ca. 140°25'E 04°24'S leg. M. Balke (4)” (NHMW). 2 females “IRIAN JAVA: Borme Tarmlu 1500m 6.9.1993”, “ca. 140°25'E 04°24'S leg. M. Balke (6)” (NHMW). These females are a mixture of four species: *E. damantiensis*, *E. ketembang* (Balke, 1998), *E. aipomek* (Balke, 1998), and *E. danae* (Balke, 1998). 1 male (no genitals), 27 females “IRIAN JAYA: 1.10.1993 Eme Gebiet Okloma, 1500m”, “ca. 139°55'E 04°14'S, leg. M. Balke (28)” (NHMW). These females are a mixture of three species: *E. damantiensis*, *E. ketembang*, and *E. aipomek*. 13 females “IRIAN JAYA: 22.9.1993 Bime – Calab Gebiet, Bime, 1400m”, “ca. 140°12'E 04°20'S, leg. M. Balke (16)” (NHMW). 2 females “IRIAN JAYA, 24.-26.9.1993 Eipomek [sic!]

Gebiet Eipomek [sic!] - Diruemna”, “ca. 140°01'E 04°27'S 1800-2600m, leg. M. Balke (21-22)” (NHMW). These females are a mixture of two species: *E. damantiensis* and *E. aipomek*. **Papua New Guinea: Madang:** 15 females “Papua New Guinea: Madang, Akameku - Brahmin, Bismarck Range, 750m, 25.xi.2006, 05.49.892S 145.24.491E, Balke & Kinibel (PNG 113)” (NHMW, ZSM). 25 females “Papua New Guinea: Madang, Akameku - Brahmin, Bismarck Range, 750m, 25.xi.2006, nr 05.49.307S 145.24.389E, Balke & Kinibel (PNG 114)” (NARI, NHMW, ZSM). These females are a mixture of two species: *E. broschii* (Balke, 1998) and *E. damantiensis*. 19 females “Papua New Guinea: Madang, Simbai area, 1200m, 10.iii.2007, 05.13.389S 144.37.285E, Kinibel (PNG 152)” (NHMW, ZSM). These females are a mixture of two species: *E. broschii* and *E. damantiensis*. 53 females “Papua New Guinea: Madang, Simbai area, 1200m, 11.iii.2007, 05.13.333S 144.37.611E, Kinibel (PNG 153)” (NARI, NHMW, ZSM). These females are a mixture of three species: *E. broschii*, *E. simbaiarea* Shaverdo & Balke, 2014, and *E. damantiensis*. **Enga:** 10 females “Papua New Guinea: Enga, Wapanamanda, 1500m, 6.xii.2006, 05.38.105S 143.55.338E, Balke & Kinibel, (PNG 128)” (ZSM). These females are a mixture of two species: *E. mondmillensis* Shaverdo, Sagata & Balke, 2016 and *E. damantiensis*. **Western Highlands:** 142 females “Papua New Guinea: Western Highlands, Kurumul, 6 Km SW Kudjip, small stream, 1580 m, 13.vi.2006, 05.53.426S 144.36.600E, John (PNG 78)” (NARI, NHMW, ZSM). These females are a mixture of three species: *E. mondmillensis*, *E. edeltraudae* (Shaverdo, Hendrich & Balke, 2012), and *E. damantiensis*. 34 females “Papua New Guinea: Western Highlands, Lugup River, 1700m, 4.iii.2007, 05.17.237S 144.28.214E, Kinibel (PNG 143)” (NHMW, ZSM). 9 females “Papua New Guinea: Western Highlands, Above Sendiap, 1400m, 5.iii.2007, 05.19.774S 144.28.307E, Kinibel (PNG 145)” (ZSM). 9 females “Papua New Guinea: Western Highlands, Jimi Valley, above Sendiap Station, 950m, 6.iii.2007, 05.20.587S 144.28.847E, Kinibel (PNG 147)” (ZSM). These females are a mixture of two species: *E. mondmillensis* and *E. damantiensis*. **Eastern Highlands:** 12 females “Papua New Guinea: Eastern Highlands, Akameku - Brahmin, Bismarck Range, 700m, 24.xi.2006, 05.52.754S 145.23.209E, Balke & Kinibel (PNG 109)” (ZSM). 24 females “Papua New Guinea: Eastern Highlands, Akameku - Brahmin, Bismarck Range, 800m, 24.xi.2006, 05.50.021S 145.24.664E, Balke & Kinibel (PNG 112)” (NARI, NHMW, ZSM). These females are a mixture of two species: *E. broschii* and *E. damantiensis*.

Diagnosis. Beetle medium-sized (TL-H 3.7–4.5 mm); uniformly brown to piceous or with paler head, pronotum or only its sides, with or without reddish sutural lines on elytra; shiny, with fine punctation and microreticulation; dorsal punctation on elytra often almost invisible; pronotum with distinct lateral bead; male antennae simple (Fig. 31); protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta; male protarsomere 5 ventrally with anterior band of more than 40 and posterior row of 8 relatively long, thin setae (Fig. 9A); median lobe broad, of characteristic shape in ventral view: broadened subdistally and narrowed apically, with slightly to distinctly concave apex, in lateral view, with curved, slightly elongate and broadly pointed apex, on both lateral sides with fine setae situated on distal part of median lobe under very fine carinas;

paramere without notch on dorsal side and dense, long subdistal setae and inconspicuous proximal setae (Fig. 9B–D). See also the original descriptions in Balke (1998). The species can be easily mixed up with some occurring species: the shiny species of the *E. broschii*-group, *E. broschii* and *E. mondmillensis*, or with *E. ketembang* and *E. aipomek*, from which can be reliably distinguished only by the shape of the median lobe.

Variability and notes on species delimitation. Herein, we synonymize with *E. damantiensis* three species, which were described and treated as representatives of the *E. rivulus*-group: *E. madangensis*, *E. patepensis*, and *E. rivulus* (Balke 1998). The main difference between these species was in the shape of the medial lobe, therefore, this character was carefully studied in all available populations and illustrated (in ventral and lateral views) for almost all of them (Figs 10–16). It has been found that the shape of the median lobe varies both within and among populations. It can be slightly (e.g., Figs 10B, D, 11A, C, F, 12D, E, F, 13C) or strongly (e.g., Figs 10A, 12A–C, H, 13A, B, D) broadened subdistally. Sometimes, the narrower shape might be due to the fact that specimens are teneral (e.g., Fig. 12D) or were treated for SEM (e.g., paratype of *E. madangensis*, Fig. 12E). The shape can be less and more narrowed apically, the narrower form being characteristic of eastern populations: Simbu, EHL, Madang, and Morobe, but is also found in specimens from Papua, Sandaun, and the Western Province. The less narrowed apically shape is characteristic of specimens from one population in Morobe (Yakop, Fig. 13C), and sometimes both shapes are found in the same population (Tabubil, Western Pr., Fig. 11E, F). The males of the type series of *E. patepensis* from the Lae–Bulolo region (Morobe) have a median lobe with a more elongate, almost truncate apex (Figs 13D, 16E), but a similar shape can be also observed in some specimens from the other Morobe populations or in some paratypes of *E. damantiensis* from the Finisterre Range, Madang. A less elongate apex of the median lobe is found in the population from the border region Simbu/EHL (Fig. 15G, H). In short, the shape of the median lobe is not a reliable character to support the earlier recognized species, or to split the present material into several new species or subspecies. The other characters, such as size, coloration, and dorsal punctuation, vary little between localities. The beetles are medium-sized, piceous or reddish brown (probably more teneral forms), often with a paler head and pronotal sides, sometimes with reddish sutural lines on the elytra, and are shiny dorsally, with the punctuation on the elytra fine, rather distinct or almost invisible. Protarsomere 4 always has a large, thick, strongly curved anterolateral hook-like seta; indication of the “small antero-lateral hook” for *E. madangensis* in Balke (1998) is probably a mistake.

Thus, the *E. rivulus*-group is apparently not a complex of several species, but instead a single, very successful polymorphic species *E. damantiensis*, with the largest geographical range of any New Guinea *Exocelina*: along the central mountain range from Wandammen Peninsula to Huon Peninsula. Of course, it is not out of the question that further material and study of other aspects (e.g., population genomics) might change this situation.

Distribution and habitats. Indonesia and PNG. It occurs in the central mountain chain and the mountains of Wandammen and Huon Peninsulas (Fig. 39). There, it is

one of the most common and numerous species from 450 m to 1900 m. Usually, it is a dominate species in the biotope and co-occurs with many species, some of which are mentioned under “Females of doubtful identity”.

7. *Exocelina danae* (Balke, 1998)

Figs 19, 32

Copelatus (*Papuadytes*) *danae* Balke, 1998: 328; Nilsson 2001: 76 (catalogue).

Papuadytes danae (Balke, 1998): Nilsson and Fery 2006: 56 (comb. n.).

Exocelina danae (Balke, 1998): Nilsson 2007: 33 (comb. n.).

Copelatus (*Papuadytes*) *tarmluensis* Balke, 1998: 338; Nilsson 2001: 77 (catalogue);

syn.n.

Papuadytes tarmluensis (Balke, 1998): Nilsson and Fery 2006: 56 (comb. n.).

Exocelina tarmluensis (Balke, 1998): Nilsson 2007: 34 (comb. n.).

Exocelina undescribed sp. MB0673: Toussaint et al. 2014: supplementary figs 1–4, tab. 2.

Type locality. Indonesia: Papua Province: Pegunungan Bintang Regency, Aipomek area, between Bime and Tanime, 04°27'S; 140°06'E, 1600 m a.s.l.

Type material studied. *Exocelina danae*: *Holotype*: male “IRIAN JAYA Aipomek area 140°06'E 04°27'S”, “21.8.1992, 1600m, Bime - Tanime leg. Balke (18)”, “HOLOTYPUS” [red], “*Copelatus danae* Balke des. 1997” [red] (NHMW). *Paratypes*: 5 males, 3 females with the same label as the holotype and additionally with red labels “*Paratypus Copelatus danae* Balke des. 1997” (NHMW). *Exocelina tarmluensis*: *Holotype*: male “IRIAN JAYA: Borma, Tarmlu, 1500m, 6.9.1993”, “ca. 140°25'E 04°24'S leg. Balke (4-6)”, “HOLOTYPUS” [red], “*Copelatus tarmluensis* Balke des. 1997” [red] (NHMW). *Paratypes*: 1 male with the same label as the holotype (NHMW). 1 male “IRIAN JAYA: Borma, Tarmlu, 1500m, 6.9.1993”, “ca. 140°25'E 04°24'S leg. Balke (5)” (NHMW). 2 males “IRIAN JAYA: Borma, Tarmlu, 1500m, 6.9.1993”, “ca. 140°25'E 04°24'S leg. Balke (4)” (NHMW). All paratypes are additionally with red labels “*Paratypus Copelatus tarmluensis* Balke des. 1997”.

Additional material. PNG: **Sandaun**: 1 male “Papua New Guinea: Sandaun, Sokamin4, 1200m, 19.x.2003, 4 50.845S 141 37.865E, K. Sagata (WB 102)” (ZSM). 1 male “DNA M. Balke 673”, “Papua New Guinea: Sandaun, Mianminold [sic!], 898m, 20.x.2003, 4 53.419S 141 37.028E, K. Sagata (WB66)” (ZSM).

Diagnosis. Beetle medium-sized (TL-H 3.4–4.1 mm); uniformly dark brown to piceous or with paler pronotal sides; shiny, with very fine punctuation and microreticulation; pronotum with distinct lateral bead; male antennae simple (Fig. 19D); protarsomere 4 with very small, weakly curved anterolateral “hook-like” (not modified into a hook) seta, smaller than more laterally situated large seta; male protarsomere 5 ventrally with anterior band of more than 40 and posterior row of 7 relatively long, thin

setae; median lobe evenly curved, with elongate and broadly pointed apex in lateral view, evenly tapering, with rounded apex in ventral view, on both lateral sides with fine setae situated linearly on anterior half of distal part of median lobe under fine carina; paramere with notch on dorsal side and very dense, strong setae on subdistal part and fine proximal setae (Figs 19A–C, E, F).

Our study of the types of *E. tarmluensis* revealed no significant difference of this species from *E. danae* in the external morphology and in the structure of its genitals. Only slight variability in the shape of the apex of the median lobe was noted (Figs 19A–C). Therefore, *E. tarmluensis* is recognized as a synonym of *E. danae*.

Distribution. Indonesia: Papua Province: Pegunungan Bintang Regency; PNG: Sandaun Province (Fig. 40).

8. *Exocelina garana* Shaverdo & Balke, sp. n.

<http://zoobank.org/E8822E47-3948-4B40-9032-169007EA9561>

Figs 21, 37

Exocelina undescribed sp. MB3876: Toussaint et al. 2014: supplementary figs 1–4, tab. 2.

Type locality. Papua New Guinea: Morobe Province, Garaina, 07°45'05.8"S; 147°08'57.0"E, 720 m a.s.l.

Type material. *Holotype*: male “Papua New Guinea: Garaina, 720m, vi.2008, 07.51.032S 147.07.007E Ibalim & Sosanika PNG216”, “DNA M.Balke 3876”, (ZSM). *Paratype*: 1 female with the same geographical label as the holotype (ZSM).

Diagnosis. Beetle medium-sized, dark brown to piceous; dorsal punctation and microreticulation fine; pronotum with lateral bead; male antennomeres simple; male protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta; median lobe slightly broadened and almost rounded distally, with apex weakly concave in ventral view and evenly curved in lateral view, with numerous fine laterodistal setae; paramere without notch on dorsal side; subdistal setae dense, proximal inconspicuous. This species is very similar to *E. damantiensis* but differs from it in the shape of the median lobe: almost rounded distally in ventral view and evenly tapering in lateral view; its apex not curved in lateral view, as well in less numerous subdistal setae of the paramere. These morphological characters and the fact that this species is phylogenetically quite isolated from *E. damantiensis* (Toussaint et al. 2014) support its delimitation.

Description. *Size and shape*: Beetle medium-sized (TL–H 4.25–4.5 mm, TL 4.75–5.0 mm, MW 2.2–2.35 mm), with oblong-oval habitus, broadest at elytral middle. *Coloration*: Male distinctly darker than female. Head reddish-brown to almost piceous; pronotum brown to piceous, with paler (reddish to dark brown) sides and darker (piceous) disc; elytron uniformly piceous or dark brown with reddish sutural line; head appendages yellowish-red, legs reddish-brown (Fig. 37).

Surface sculpture: Head with dense punctation (spaces between punctures 1–3 times size of punctures), evidently finer and sparser anteriorly; diameter of punctures smaller than diameter of cells of microreticulation. Pronotum with finer, sparser, and more evenly distributed punctation than on head. Elytra with very sparse and fine punctation, almost invisible. Pronotum and elytra with weakly impressed microreticulation, dorsal surface, thus, shiny. Head with microreticulation stronger. Metaventricle and metacoxa distinctly microreticulate, metacoxal plates with longitudinal striae and transverse wrinkles. Abdominal sternites with distinct microreticulation, striae, and fine sparse punctation, coarser and denser on two last abdominal sternites.

Structures: Pronotum with distinct lateral bead. Base of prosternum and neck of prosternal process with distinct ridge, smooth and not rounded anteriorly, without anterolateral extensions. Blade of prosternal process lanceolate, relatively narrow, convex, with distinct bead and few setae; neck and blade of prosternal process evenly jointed. Abdominal ventrite 6 slightly truncate apically.

Male: Antenna simple. Protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta. Protarsomere 5 ventrally with anterior band of ca. 50 and posterior row of 11 relatively long setae (Fig. 21B). Abdominal ventrite 6 with 4 lateral striae on each side. Median lobe slightly broadened and almost rounded distally, with apex weakly concave in ventral view and evenly tapering in lateral view; on both lateral sides with fine setae situated on distal part of median lobe (Fig. 21B–C). Paramere without notch on dorsal side and with dense setae on subdistal part; proximal setae more numerous but inconspicuous (Fig. 21D).

Holotype: TL-H 4.25 mm, TL 4.75 mm, MW 2.2 mm; dorsally piceous.

Female: Pro- and mesotarsi not modified; abdominal ventrite 6 without striae; dorsal coloration paler than in male: dark brown with reddish brown head, pronotal sides and sutural lines on elytra; dorsal punctation slightly stronger.

Distribution. Papua New Guinea: Morobe Province. This species is known only from the type locality area (Fig. 40).

Etymology. The species is named after Garaina Village. The name is a noun in the nominative singular standing in apposition.

9. *Exocelina injiensis* Shaverdo & Balke, sp. n.

<http://zoobank.org/96D815A9-1FE6-4B24-81B3-28FA6BCF38DB>

Figs 8, 30

Exocelina undescribed sp. MB1376: Toussaint et al. 2014: supplementary figs 1–4, tab. 2.

Type locality. Papua New Guinea: Morobe Province, Menyamya, Inji Mountain, 07°14.26'S; 146°01.40'E, 1500 m a.s.l.

Type material. *Holotype*: male “Papua New Guinea: Morobe, Menyamya, Mt Inji, deep well, 1500m, 14.xi.2006, 07.14.264S 146.01.400E, Balke & Kinibel (PNG 98)” (ZSM). *Paratypes*: 22 males, 29 females with the same label as the holotype, one male additionally with a green label “DNA M.Balke 1376” (NHMW, ZSM).

Diagnosis. Beetle small; piceous, with reddish brown to brown head and pronotum laterally; matt, with strong punctation and microreticulation; male antennae simple; male protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta; median lobe with slightly curved, rounded apex in lateral view and with almost truncate apex in ventral view, on both lateral sides with strong, short setae situated almost linearly on anterior half of distal part of median lobe under fine carina; paramere without notch on dorsal side. The species is very similar to *E. andakombensis* sp. n. but differs from it in presence of the lateral carina, bordering shorter distal setae, on the median lobe and the large, thick, strongly curved anterolateral hook-like seta of protarsomere 4, as well as longer and much numerous ventral setae of protarsomere 5, see also under diagnosis of *E. andakombensis* sp. n.

Description. *Size and shape*: Beetle small (TL-H 3.05–3.55 mm, TL 3.4–3.85 mm, MW 1.6–1.9 mm), with oblong-oval habitus, broadest at elytral middle. *Coloration*: Head reddish brown to dark brown, with small darker areas posterior to eyes; pronotum reddish brown to dark brown, paler laterally, often piceous on disc; elytra piceous, dark brown laterally, with narrow reddish sutural lines; head appendages and legs proximally yellowish red, legs distally darker, reddish brown, especially metathoracic legs (Fig. 30). Teneral specimens paler.

Surface sculpture: as in *E. andakombensis* sp. n.

Structures: Pronotum with distinct lateral bead. Base of prosternum and neck of prosternal process with distinct ridge, slightly rounded anteriorly. Blade of prosternal process lanceolate, relatively broad, slightly convex, and smooth, with distinct lateral bead and few lateral setae; neck and blade of prosternal process evenly jointed. Abdominal ventrite 6 slightly truncate.

Male: Antennae simple. Protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta. Protarsomere 5 ventrally with anterior band of 19 and posterior row of 8 relatively long setae (Fig. 8A). Median lobe with slightly curved, rounded apex in lateral view and with almost truncate apex in ventral view, on both lateral sides with strong, short setae situated almost linearly on a half of distal part of median lobe under fine carina (Fig. 8B–C). Paramere without notch, slightly concave on dorsal side and with dense setae on subdistal part; proximal setae inconspicuous (Fig. D). Abdominal ventrite 6 with 6–9 lateral striae on each side.

Holotype: TL-H 3.6 mm, TL 3.9 mm, MW 1.9 mm.

Female: Without evident differences in external morphology from males, except for not modified pro- and mesotarsi and abdominal ventrite 6 without striae.

Distribution. Papua New Guinea: Morobe Province. The species is known only from the type locality (Fig. 40).

Etymology. The species is named after Inji Mountain. The name is an adjective in the nominative singular.

10. *Exocelina kabwumensis* Shaverdo & Balke, sp. n.

<http://zoobank.org/CBA1FBC1-3873-4046-987D-F9D6F28CC0A1>

Figs 5, 27

Exocelina undescribed sp. MB1285: Toussaint et al. 2014: supplementary figs 1–4, tab. 2.

Type locality. Papua New Guinea: Morobe, Huon, Kabwum, 06°08.01'S; 147°11.34'E, 1600 m a.s.l.

Type material. *Holotype*: male “Papua New Guinea: Morobe, Huon, 1 km SE Kabwum, 1600m, 16./17.v.2006, 06.08.007S 147.11.337E, Sagata (PNG 76)”, “DNA M.Balke 1285” [green] (ZSM). *Paratypes*: 3 males, 3 females with the same labels as the holotype (NHMW, ZSM).

Diagnosis. Beetle small to medium-sized; piceous, with reddish brown to brown head and pronotum laterally; matt, with strong punctation and microreticulation; male antennae simple; protarsomere 4 with weakly curved anterolateral “hook-like” (not modified into a hook) seta, smaller than more laterally situated large seta; median lobe narrow, with almost parallel sides and askew truncate apex in ventral view, with slightly curved apex and very few fine distal setae in lateral view; paramere with small notch on dorsal side. The species is very similar to *E. andakombensis* sp. n., *E. injiensis* sp. n., and *E. woitapensis* sp. n., but differs from them in size, shape of the median lobe, and the presence of only few fine distal setae laterally on the median lobe.

Description. *Size and shape*: Beetle small to medium-sized (TL-H 3.5–3.8 mm, TL 3.75–4.15 mm, MW 1.85–2.05 mm), with oblong-oval habitus, broadest at elytral middle. *Coloration*: as in *E. andakombensis* sp. n. (Fig. 27).

Surface sculpture: As in *E. andakombensis* sp. n.

Structures: Pronotum with distinct lateral bead. Base of prosternum and neck of prosternal process with distinct ridge, slightly rounded anteriorly. Blade of prosternal process lanceolate, relatively broad, slightly convex, and smooth, with distinct lateral bead and few lateral setae; neck and blade of prosternal process evenly jointed. Abdominal ventrite 6 slightly truncate or broadly rounded.

Male: Antennae simple. Protarsomere 4 with very small, weakly curved anterolateral “hook-like” (not modified into a hook) seta, smaller than more laterally situated large seta. Protarsomere 5 ventrally with anterior band of 27 and posterior row of 6 relatively long, thin setae (Fig. 5A). Median lobe narrow, with almost parallel sides and askew truncate apex in ventral view, with slightly curved, relatively broad apex and very few fine distal setae in lateral view (Figs 5B–C). Paramere with small notch on dorsal side and with dense setae on subdistal part; proximal setae inconspicuous (Fig. 5D). Abdominal ventrite 6 with 8–10 lateral striae on each side.

Holotype: TL-H 3.65 mm, TL 4.0 mm, MW 2.0 mm.

Female: Without evident differences in external morphology from males, except for not modified pro- and mesotarsi and abdominal ventrite 6 without striae.

Distribution. Papua New Guinea: Morobe Province. The species is known only from the type locality (Fig. 40).

Etymology. The species is named after Kabwum Village. The name is an adjective in the nominative singular.

11. *Exocelina marawaka* Shaverdo & Balke, sp. n.

<http://zoobank.org/421FB9C2-1F26-4764-AE88-33CB5E9C9E84>

Figs 20, 35

Exocelina undescribed sp. MB1366: Toussaint et al. 2014: supplementary figs 1–4, tab. 2.

Type locality. Papua New Guinea: Eastern Highlands Province, Marawaka, Ande, 07°01.70'S; 145°49.81'E, 1700 m a.s.l.

Type material. *Holotype*: male “Papua New Guinea: Eastern Highlands, Marawaka, Ande, 1700m, 8.xi.2005, 07.01.697S 145.49.807E, Balke & Kinibel (PNG 86)” (ZSM). *Paratypes*: **Eastern Highlands**: 32 males, 17 females with the same label as the holotype, one male with a green label “DNA M.Balke 1366” (NHMW, ZSM). 8 males, 6 females “Papua New Guinea: Eastern Highlands, Marawaka, Ande, 1700–1800m, 9.xi.2006, 07.01.697S 145.49.807E, Balke & Kinibel (PNG 87)” (NHMW, ZSM). **Gulf**: 1 female “Papua New Guinea: Gulf, Marawaka, Andakombe towards Morobe, 2160m, 12.xi.200, 07.11.717S 145.51.177E, Balke & Kinibel (PNG 94)”, “DNA M.Balke 1370” [green] (ZSM).

Diagnosis. Beetle medium-sized, piceous, with paler sides of pronotum; dorsal surface with fine punctation and evident microreticulation, shiny; pronotum with distinct lateral bead; male antennomeres simple; protarsomere 4 with weakly curved anterolateral hook-like seta, smaller than more laterally situated large seta; median lobe evidently broadened in distal part, broadly pointed to apex in ventral view and with slightly curved, rounded apex in lateral view, on both lateral sides with numerous fine setae situated linearly on anterior half of distal part of median lobe under fine carina; paramere without notch on dorsal side. The species is similar to *E. posmani* sp. n. but differs from it mainly in the structure of the median lobe: apex longer and narrower in lateral view and pointed in ventral view, distal setae not arranged into one area but situated linearly along the lateral margin.

Description. *Size and shape*: Beetle medium-sized (TL-H 4.05–4.6 mm, TL 4.4–5.0 mm, MW 2.15–2.45 mm), with oblong-oval habitus, broadest at elytral middle. *Coloration*: Head uniformly dark brown to piceous; pronotum dark brown to piceous, paler on sides; elytra uniformly piceous; ventrally dark brown; head appendages and legs proximally yellowish red, legs distally darker, reddish brown (Fig. 35).

Surface sculpture: Head with relatively dense and coarse punctation (spaces between punctures 1–3 times size of punctures); diameter of punctures smaller than diameter of cells of microreticulation. Pronotum with finer, sparser, and more evenly distrib-

uted punctation than on head. Elytra with much finer, sparser punctation than on pronotum. Pronotum and elytra with distinct microreticulation, dorsal surface shiny. Head with microreticulation slightly stronger. Metaventrite, metacoxa, and abdominal ventrites distinctly microreticulate. Metacoxal plates with longitudinal striae and transverse wrinkles; abdominal ventrites with striae. Ventrum with inconspicuous punctation, more evident on metacoxal plates and two last abdominal ventrites.

Structures: Pronotum with distinct lateral bead. Base of prosternum and neck of prosternal process with distinct ridge, not rounded anteriorly, without anterolateral extensions. Blade of prosternal process lanceolate, relatively narrow, convex, with distinct bead and few setae laterally; neck and blade of prosternal process evenly jointed. Abdominal ventrite 6 broadly rounded or slightly truncate.

Male: Antenna simple. Protarsomere 4 with very small (smaller than more laterally situated large seta), weakly curved anterolateral hook-like seta. Protarsomere 5 ventrally with anterior band of 27 setae and posterior row of 5 short, relative thick setae (Fig. 20A). Abdominal ventrite 6 with 7–10 lateral striae on each side. Median lobe evidently broadened in distal part, broadly pointed to apex in ventral view and with slightly curved, rounded apex in lateral view, on both lateral sides with numerous fine setae situated linearly on anterior half of distal part of median lobe under fine carina (Fig. 20B–C). Paramere without notch, slightly concave on dorsal side, with thin, sparse, inconspicuous proximal setae and thicker, denser, and longer subdistal setae (Fig. 20D).

Holotype: TL-H 4.5 mm, TL 4.9 mm, MW 2.2 mm.

Female: Without evident differences in external morphology from males, except for not modified pro- and mesotarsi and abdominal ventrite 6 without striae.

Variability. Elytral punctation varies from inconspicuous to distinct.

Distribution. Papua New Guinea: Eastern Highlands and Gulf Provinces. The species is known only from the Marawaka area (Fig. 40).

Etymology. The species is named after the Marawaka area. The name is a noun in the nominative singular standing in apposition.

12. *Exocelina posmani* Shaverdo & Balke, sp. n.

<http://zoobank.org/F0F916E9-4088-43E0-B068-3D6DB744833F>

Figs 23, 38

Exocelina undescribed sp. MB3406: Toussaint et al. 2014: supplementary figs 1–4, tab. 2.

Type locality. Papua New Guinea: Central Province, Myola, 09°08.05'S; 147°42.24'E, 1760 m a.s.l.

Type material. *Holotype:* male “Papua New Guinea: Central, Myola, 1760m, i.2008, [09°] 08.052S 147 42.241E, Posman (PNG 176)” (ZSM). *Paratypes:* 2 males, 4 females with the same label as the holotype, one male with an additional green label “DNA M.Balke 3406” (NHMW, ZSM). 1 male, 1 female “Papua New Guinea:

Central, Woitape, 1700m, i.2008, [08°] 31.290S 147 13.684'E, Posman (PNG 166)" (ZSM). 2 males "Papua New Guinea: Central, Woitape, 1500m, i.2008, [08°] 33.178S 147 15.481E, Posman (PNG 167)" (NHMW, ZSM). 4 males, 2 females "Papua New Guinea: Central, Kokoda Trek, 1400m, i.2008, [09°] 14.339S 147 40.538E, Posman (PNG 171)" (NHMW, ZSM). 1 female "Papua New Guinea: Central, Kokoda Trek, 1400m, i.2008, [09°] 01.952S 147 44.455E, Posman (PNG 172)" (ZSM).

Diagnosis. Beetle medium-sized, piceous, with paler head and sides of pronotum; dorsal surface with fine punctation and evident microreticulation, shiny; pronotum with distinct lateral bead; male antennomeres simple; protarsomere 4 with weakly curved anterolateral hook-like seta, equal to more laterally situated large seta; median lobe only slightly broadened in distal part, with almost parallel sides and slightly concave apex in ventral view, with slightly curved, broad, rounded apex in lateral view, on both lateral sides with numerous fine setae situated not linearly but on large area of anterior half of distal part of median lobe under short fine carina; paramere without notch on dorsal side. The species is similar to *E. marawaka* sp. n. but differs from it in the structure of the median lobe: apex shorter and broader in lateral view and slightly concave in ventral view, distal setae arranged into one area, not situated linearly. This species was collected together with of *E. woitapensis* sp. n., which is smaller and matt, with stronger punctation and microreticulation of the dorsal surface.

Description. *Size and shape:* Beetle medium-sized (TL-H 3.65–4.4 mm, TL 4–4.5 mm, MW 1.95–2.2 mm), with oblong-oval habitus, broadest at elytral middle. *Coloration:* Head uniformly dark brown to piceous or reddish-brown to brown, dark brown behind eyes and on middle; pronotum dark brown to piceous, paler on sides; elytra uniformly dark brown to piceous, seldom with narrow reddish sutural lines; ventrally reddish-brown; head appendages and legs proximally yellowish red, legs distally darker, reddish brown (Fig. 38).

Surface sculpture: As in *E. marawaka* sp. n.

Structures: Pronotum with distinct lateral bead. Base of prosternum and neck of prosternal process with distinct ridge, not rounded anteriorly, without anterolateral extensions. Blade of prosternal process lanceolate, relatively narrow, convex, with distinct bead and few setae laterally; neck and blade of prosternal process evenly jointed. Abdominal ventrite 6 broadly rounded.

Male: Antenna simple. Protarsomere 4 with small (equal to more laterally situated large seta), weakly curved anterolateral hook-like seta. Protarsomere 5 ventrally with anterior band of 22 setae and posterior row of 5 short setae (Fig. 23A). Abdominal ventrite 6 with 4–7 lateral striae on each side. Median lobe only slightly broadened in distal part, with almost parallel sides and slightly concave apex in ventral view, with slightly curved, broad, rounded apex in lateral view, on both lateral sides with numerous fine setae situated not linearly but on large area of anterior half of distal part of median lobe under short, fine carina (Fig. 23B–C). Paramere without notch, slightly concave on dorsal side, with thin, sparse, inconspicuous proximal setae and thicker, denser, and longer subdistal setae (Fig. 23D).

Holotype: TL-H 3.9 mm, TL 4.35 mm, MW 2.15 mm.

Female: Without evident differences in external morphology from males, except for not modified pro- and mesotarsi and abdominal ventrite 6 without striae.

Variability. Elytral punctuation varies from inconspicuous to distinct.

Distribution. Papua New Guinea: Central Province (Fig. 40).

Etymology. The species is named for Aloysius Posman. The species name is a noun in the genitive case.

13. *Exocelina varirata* Shaverdo & Balke, sp. n.

<http://zoobank.org/610FF2E1-A763-4AF1-AABA-FEA533636427>

Figs 18, 34

Exocelina undescribed sp. MB3303: Toussaint et al. 2014: supplementary figs 1–4, tab. 2.

Type locality. Papua New Guinea: National Capital District Province, Varirata National Park, 09°26.13'S; 147°22.09'E, 600 m a.s.l.

Type material. *Holotype*: male “Papua New Guinea: National Capital District, Varirata NP, 600m, 16.xii.2007, 09.26.13S 147.22.09E, Balke & Sagata (PNG 159)”, “DNA M.Balke 3303” [green] (ZSM). *Paratype*: **Central**: 1 male “Papua New Guinea: Central, Myola, 1110m, i.2008, 09 12.630S 147 31.880E, Posman (PNG 177)”, “DNA M.Balke 3407” [green] (ZSM).

Diagnosis. Beetle medium-sized, dark brown, with reddish-brown pronotal sides; dorsal surface with strong punctuation and microreticulation, matt; pronotum with distinct lateral bead; male antennomeres simple; male protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta; median lobe slender, with slightly curved, short, broad apex and compact area of fine distal setae in lateral view, with slightly concave apex in ventral view; paramere with very shallow notch on dorsal side. The species is very similar to *E. wareaga* sp. n. but differs from it in shape of the median lobe: it is more slender, lateral margins apically and subapically not very thick and not bordered with a carina; also the fine distal setae on lateral sides of the median lobe are not situated linearly, but in compact areas.

Description. *Size and shape*: Beetle medium-sized (TL-H 4.25–4.35 mm, TL 4.5–4.85 mm, MW 2.25–2.45 mm), with oblong-oval habitus, broadest at elytral middle. *Coloration*: Head reddish brown to dark brown, paler on clypeus; pronotum dark brown on disc and reddish-brown on sides; elytra uniformly dark brown; ventrally dark brown; head appendages reddish-brown, legs darker distally (Fig. 34).

Surface sculpture: as in *E. wareaga* sp. n.

Structures: Pronotum with distinct lateral bead. Base of prosternum and neck of prosternal process with distinct ridge, smooth anteriorly, without anterolateral extensions. Blade of prosternal process lanceolate, relatively narrow, convex, with distinct bead and few setae laterally; neck and blade of prosternal process evenly jointed. Abdominal ventrite 6 broadly rounded.

Male: Antenna simple. Protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta. Protarsomere 5 ventrally with anterior band of more than 70 short setae and posterior row of 12 relatively long, thin setae (Fig. 18A). Abdominal ventrite 6 with 4–6 lateral striae on each side. Median lobe slender, with slightly curved, short, broad apex and compact area of fine distal setae in lateral view, with slightly concave apex in ventral view (Figs 18B–C). Paramere with very shallow notch on dorsal side, with thin, sparse, inconspicuous proximal setae and thicker, denser, and longer subdistal setae (Fig. 18D).

Holotype: TL-H 4.35 mm, TL 4.85 mm, MW 2.45 mm.

Female: Unknown.

Distribution. Papua New Guinea: National Capital District and Central Provinces (Fig. 40).

Etymology. The species is named after Varirata National Park. The name is a noun in the nominative singular standing in apposition.

14. *Exocelina wareaga* Shaverdo & Balke, sp. n.

<http://zoobank.org/BC69F25B-00F5-4C97-8854-BBFFB4B008DD>

Figs 17, 33

Exocelina undescribed sp. MB3404: Toussaint et al. 2014: supplementary figs 1–4, tab. 2.

Type locality. Papua New Guinea: Central Province, Moroka, Kailaki, 09°24.13'S; 147°33.52'E, 827 m a.s.l.

Type material. *Holotype*: male “Papua New Guinea Central, Moroka, Kailaki Wareaga, 760m, 27.x.2009 9.25.424S 147.31.068E Sagata (PNG227)” (ZSM). *Paratypes*: **Central**: 39 males, 46 females with the same label as the holotype (NHMW, ZSM). 7 males, 6 females “Papua New Guinea: Central, Moroka area, Kailaki, 827 m, 26.x.2009, 9.24.134S 147.33.521E, Sagata (PNG225)” (NHMW, ZSM). 10 males, 3 females “Papua New Guinea Central, 755m, 28.x.2009 S9 25 47 5 E147 32 59.1, Sagata (PNG229)” (NHMW, ZSM). 2 males, 2 females “Papua New Guinea: Central, Kokoda Trek, 980m, i.2008, 09 15.933S 147 36.590E, Posman (PNG 169)”, one male and female with green labels “DNA M.Balke 3410” and “DNA M.Balke 4118” correspondently (NHMW, ZSM). 4 males, 6 females “Papua New Guinea: Central, Kokoda Trek, 320m, i.2008 09 19.236S 147 31.791E, Posman (PNG 168)”, one male with a green label “DNA M.Balke 3404” (NHMW, ZSM). 3 males, 2 females “Papua New Guinea: Central, Kokoda Trek, 590m, i.2008, 09 14.339S 147 36.920E, Posman (PNG 170)” (NHMW, ZSM). **National Capital District**: 1 male “Papua New Guinea: National Capital District, Varirata NP, 600m, 16.xii.2007, 09.26.13S 147.22.09E, Balke & Sagata (PNG 159)” [specimen without head and pronotum] (ZSM).

Diagnosis. Beetle medium-sized, dark brown, with paler, reddish-brown, head and pronotum; dorsal surface with fine punctation and evident microreticulation, shiny;

pronotum with distinct lateral bead; male antennomeres simple; male protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta; median lobe robust, apicolaterally with thick margins bordered with dorsolateral carina, with slightly curved, broad apex in lateral view and with truncate apex in ventral view, on both lateral sides with numerous fine setae situated linearly on anterior half of distal part of median lobe; paramere with very shallow notch on dorsal side. The species is very similar to *E. varirata* sp. n. but differs from it in the shape of the median lobe: it is more robust, lateral margins apically and subapically thicker, bordered with a dorsolateral carina; also fine distal setae on lateral sides of the median lobe are situated linearly.

Description. *Size and shape:* Beetle medium-sized (TL-H 3.65–4.4 mm, TL 4.05–4.8 mm, MW 1.95–2.35 mm), with oblong-oval habitus, broadest at elytral middle. *Coloration:* Head reddish-brown, dark brown behind eyes; pronotum reddish-brown, dark brown on disc; elytra uniformly brown to dark brown; ventrally reddish-brown, slightly darker on metacoxal plates; head appendages red to reddish-brown, legs darker distally (Fig. 33). Teneral specimens paler, with yellowish-red head and pronotum and pale brown elytra.

Surface sculpture: Head with relatively dense and coarse punctation (spaces between punctures 1–3 times size of punctures); diameter of punctures smaller than diameter of cells of microreticulation. Pronotum with finer, sparser, and more evenly distributed punctation than on head. Elytra with finer, sparser punctation than on pronotum, punctation very fine but evident. Pronotum and elytra with distinct microreticulation, dorsal surface shiny. Head with microreticulation slightly stronger. Metaventrite, metacoxa, and abdominal ventrites distinctly microreticulate, but with cells of microreticulation larger than on dorsal side. Metacoxal plates with longitudinal striae and transverse wrinkles; abdominal ventrites with striae. Ventrums with inconspicuous punctation, more evident on metacoxal plates and two last abdominal ventrites.

Structures: Pronotum with distinct lateral bead. Base of prosternum and neck of prosternal process with distinct ridge, smooth anteriorly, without anterolateral extensions. Blade of prosternal process lanceolate, relatively narrow, convex, with distinct bead and few setae laterally; neck and blade of prosternal process evenly jointed. Abdominal ventrite 6 slightly truncate.

Male: Antenna simple. Protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta. Protarsomere 5 ventrally with anterior band of more than 70 short setae and posterior row of 13 relatively long, thin setae (Fig. 17A). Abdominal ventrite 6 with 3–5 lateral striae on each side. Median lobe robust, apicolaterally with thick margins bordered with dorsolateral carina, with slightly curved, broad apex in lateral view and with truncate apex in ventral view, on both lateral sides with numerous fine setae situated linearly on anterior half of distal part of median lobe (Fig. 17B–C). Paramere with very shallow notch on dorsal side, with thin, sparse, inconspicuous proximal setae and thicker, denser, and longer subdistal setae (Fig. 17D).

Holotype: TL-H 4.15 mm, TL 4.55 mm, MW 2.25 mm.

Female: Without evident differences in external morphology from males, except for not modified pro- and mesotarsi and abdominal ventrite 6 without striae.

Distribution. Papua New Guinea: Central and National Capital District Provinces (Fig. 40).

Etymology. The species is named after Wareaga village. The name is a noun in the nominative singular standing in apposition.

15. *Exocelina woitapensis* Shaverdo & Balke, sp. n.

<http://zoobank.org/B59DD2AA-1304-42DD-86A2-00DA8342BFCC>

Figs 6, 28

Exocelina undescribed sp. MB3399: Toussaint et al. 2014: supplementary figs 1–4, tab. 2.

Type locality. Papua New Guinea: Central Province, Woitape, 08°31.29'S; 147°13.68'E, 1700 m a.s.l.

Type material. *Holotype*: male “Papua New Guinea: Central, Woitape, 1700m, i.2008, 08 31.290S 147 13.684'E, Posman (PNG 166)” (ZSM). *Paratypes*: 2 males, 1 female with the same label as the holotype, the male additionally with a green label “DNA M.Balke 3399” (ZSM). 1 male, 3 females “Papua New Guinea: Central, Woitape, 1500m, i.2008, 08 33.178S 147 15.481E, Posman (PNG 167)”, one female additionally with a green label “DNA M.Balke 3402” (NHMW, ZSM). 1 male “Papua New Guinea: Central, Woitape, 1600m, i.2008, 08 31.581S 147 14.099E, Posman (PNG 165)” (ZSM). 1 female “Papua New Guinea: Central, Kokoda Trek, 590m, i.2008, 09 14.339S 147 36.920E, Posman (PNG 170)” (ZSM).

Diagnosis. Beetle medium-sized; piceous, with reddish brown head and pronotum, later often with darker disc; matt, with strong punctation and microreticulation; male antennae simple; male protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta; median lobe relatively broad, with slightly curved, rounded apex in lateral view and with askew truncate apex in ventral view, on both lateral sides with numerous strong setae situated broad-linearly on whole distal part of median lobe; paramere with small notch on dorsal side. The species is very similar to *E. kabwumensis* sp. n. but differs from it in the larger body size, broader median lobe, and the presence of numerous thick distal setae laterally on the median lobe. It is also similar to *E. andakombensis* sp. n. and *E. injiensis* sp. n. but differs from them in the larger body size, shape of the median lobe, and more numerous and more sparsely situated thick distal setae laterally on the median lobe. From *E. kabwumensis* and *E. andakombensis*, it also differs in the large, thick, strongly curved anterolateral hook-like seta of protarsomere 4. This species co-occurs with *E. posmani* sp. n., see under its diagnosis for their morphological differences.

Description. *Size and shape*: Beetle medium-sized (TL–H 3.6–4.0 mm, TL 4.0–4.35 mm, MW 2.0–2.15 mm), with oblong-oval habitus, broadest at elytral mid-

dle. **Coloration:** Head reddish brown to dark brown, with small darker areas posterior to eyes and sometimes brown V-like spot in vertex; pronotum reddish brown, with darker (to piceous) disc; elytra brown to piceous, with narrow reddish sutural lines; head appendages and legs proximally yellowish red, legs distally darker, reddish brown, especially metathoracic legs (Fig. 28). Teneral specimens paler.

Surface sculpture: As in *E. andakombensis* sp. n.

Structures: Pronotum with distinct lateral bead. Base of prosternum and neck of prosternal process with distinct ridge, slightly rounded anteriorly. Blade of prosternal process lanceolate, relatively broad, slightly convex, and smooth, with distinct lateral bead and few lateral setae; neck and blade of prosternal process evenly jointed. Abdominal ventrite 6 slightly truncate.

Male: Antennae simple. Protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta. Protarsomere 5 ventrally with anterior band of ca. 60 and posterior row of 16 relatively long, thin setae (Fig. 6A). Median lobe relatively broad, with slightly curved, elongate, rounded apex in lateral view and with askew truncate apex in ventral view, on both lateral sides with numerous strong setae situated broadly on whole distal part of median lobe (Fig. 6B–C). Paramere with small notch on dorsal side and dense setae on subdistal part; proximal setae inconspicuous (Fig. 6D). Abdominal ventrite 6 with 5–8 lateral striae on each side.

Holotype: TL-H 4 mm, TL 4.5 mm, MW 2.15 mm.

Female: Without evident differences in external morphology from males, except for not modified pro- and mesotarsi and abdominal ventrite 6 without striae.

Distribution. Papua New Guinea: Central Province (Fig. 40).

Etymology. The species is named after Woitape Village. The name is an adjective in the nominative singular.

Key to species of the *Exocelina danae*-group

The key is based mostly on male characters. In many cases females cannot be assigned to species due to the similarity of their external and internal structures (for female genitalia see figs 17a and 17b in Shaverdo et al. (2005)). Some species are rather similar on external morphology, therefore, in most cases the male genitalia need to be studied for reliable species identification. Numbers in parentheses refer to the arrangement of the species descriptions above.

- 1 Male and female antennomere 2 enlarged, evidently larger than other antennomeres (Figs 24–26)(*miriae*-subgroup) **2**
- Male and female antennomeres simple, not modified **4**
- 2 Beetle smaller, TL-H: 3.5 mm, reddish-brown, matt dorsally due to strong microreticulation and punctation (Fig. 24) (2) *rufa*

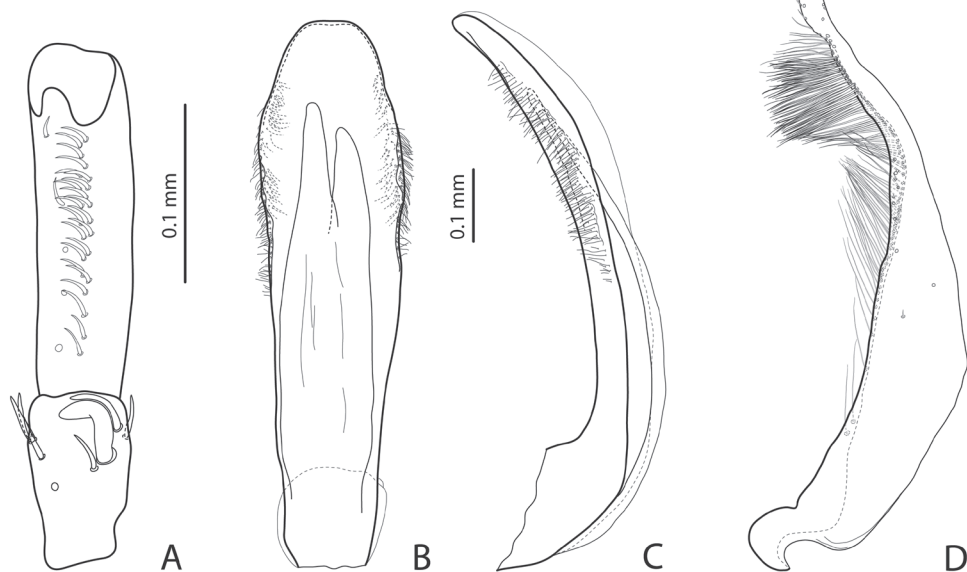
- Beetle larger, TL-H: 3.9–4.5 mm, with darker dorsal coloration, shiny, with evident microreticulation and weak punctation (Figs 25–26).....**3**
- 3 Median lobe with apex slightly curved, elongate in lateral view and rounded in ventral view; numerous fine setae situated linearly on distal part of median lobe along the lateral sides (Figs 2–3, figs 76, 82 in Balke (1998)) (1) *miriae*
- Median lobe with apex slightly curved, broad in lateral view and concave in ventral view, and with a small bunch of fine distal setae on both lateral sides (Fig. 4B–C) (3) *tekadu* **sp. n.**
- 4 Beetle matt dorsally due to strong microreticulation and punctation **5**
- Beetle shiny, with evident microreticulation and weak punctation..... **8**
- 5 Median lobe narrow, with slightly curved, broad apex and few fine distal setae in lateral view (Fig. 5B–C) (10) *kabwumensis* **sp. n.**
- Median lobe broader, with numerous thick setae in lateral view (Figs 6–8) ... **6**
- 6 Beetle larger, TL-H: 3.6–4.0 mm (Fig. 28). Median lobe with more numerous and more sparsely situated thick distal setae laterally; paramere with small dorsal notch (Fig. 6C–D) (15) *woitapensis* **sp. n.**
- Beetle smaller, TL-H: 3.05–3.55 mm (Figs 29–30). Median lobe with less numerous and more compactly situated thick distal setae laterally; paramere without notch, slightly concave dorsally (Figs 7C–D, 8C–D) **7**
- 7 Protarsomere 4 with weakly curved anterolateral hook-like seta, equal to more laterally situated large seta (Fig. 7A). Median lobe with apex broader in lateral view and slightly concave in ventral view; distal setae of median lobe situated on broader area, especially apically, carina absent (Fig. 7B–C) (4) *andakombensis* **sp. n.**
- Protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta (Fig. 8A). Median lobe with apex narrower in lateral view and truncate in ventral view; distal setae of median lobe situated linearly under fine carina (Fig. 8B–C) (9) *injiensis* **sp. n.**
- 8 Apex of median lobe more strongly curved in lateral view (Figs 9–18) **9**
- Apex of median lobe evenly curved in lateral view (Figs 19–23) **11**
- 9 Median lobe distinctly broadened subdistally and narrowed apically, lateral sides like strong, thick folds in ventral view (Figs 9–13) (6) *damantiensis*
- Median lobe with subparallel sides and broader apex, lateral folds inconspicuous (Figs 17B, 18B) **10**
- 10 Median lobe robust, with lateral margins apically and subapically thicker, bordered with dorsolateral carina, and with longer apex in lateral view; distal setae of median lobe situated linearly (Fig. 17B–C) (13) *wareaga* **sp. n.**
- Median lobe slender, with lateral margins thinner, without dorsolateral carina, and with shorter apex in lateral view; distal setae of median lobe situated on broader, compacter area (Fig. 18B–C) (14) *varirata* **sp. n.**

- 11 Beetle smaller, TL-H: 3.4–4.1 mm (Fig. 32). Median lobe smaller, thinner, and narrower (Fig. 19, figs 51, 69 in Balke (1998)); paramere with dorsal notch, its subdistal part larger, with stronger setation (Fig. 19F, fig. 38 in Balke (1998))..... (7) ***danae***
- Beetle larger, TL-H: 3.65–4.75 mm (Figs 35–38). Median lobe larger, thicker, and broader; paramere without notch, slightly concave dorsally, its subdistal part narrower, with weaker setation (Figs 20–23)..... **12**
- 12 Median lobe with broadly pointed apex in ventral view (Fig. 20B). Protarsomere 4 with weakly curved anterolateral hook-like seta, smaller than more laterally situated large seta (Fig. 20A)..... (11) ***marawaka* sp. n.**
- Median lobe with slightly concave apex in ventral view (Figs 21–23). Protarsomere 4 with large or small anterolateral hook-like seta..... **13**
- 13 Median lobe with more elongate, narrower apex in lateral view and lateral sides with numerous fine distal setae almost linearly situated (Fig. 21C) (8) ***garaina* sp. n.**
- Median lobe with more rounded, broader apex and lateral sides almost without setae or with fine distal setae situated on broader area, not linearly in lateral view (Figs 22C, 23C) **14**
- 14 Median lobe with less rounded apex in lateral view and only some fine distal setae (Fig. 22C). Protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta (Fig. 22A) (5) ***atrata***
- Median lobe with distinctly rounded apex in lateral view and with much more numerous fine distal setae (Fig. 23C). Protarsomere 4 with weakly curved anterolateral hook-like seta, equal to more laterally situated large seta (Fig. 23A) (12) ***posmani* sp. n.**

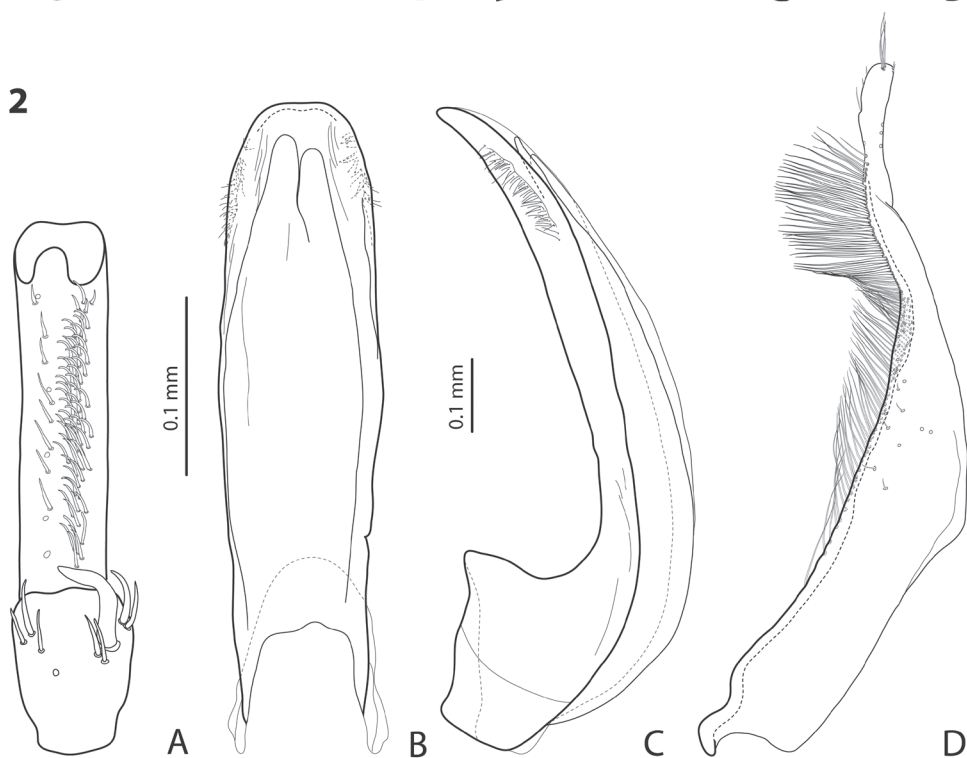
Habitats

All species treated here are associated with running water as almost all previously studied New Guinea *Exocelina* (Shaverdo et al. 2012). Figure 41 shows one of the habitats in the Marawaka area: a mid-montane forest stream with small bays and puddles at its edge, which yielded a large number of these beetles. The following nine species are known from this area: *E. marawaka* sp. n., *E. andakombensis* sp. n., *E. injiensis* sp. n., *E. miriae* (Balke, 1998), *E. hintelmannae* (Shaverdo, Sagata & Balke, 2005), *E. bismarckensis* Shaverdo & Balke, 2014, *E. kisli* Shaverdo & Balke, 2014, *E. craterensis* Shaverdo & Balke, 2014, and *E. kinibeli* Shaverdo & Balke, 2014. The most abundant of them are *E. miriae* and *E. hintelmannae* followed by *E. marawaka* sp. n., *E. andakombensis* sp. n., and *E. injiensis* sp. n.

1

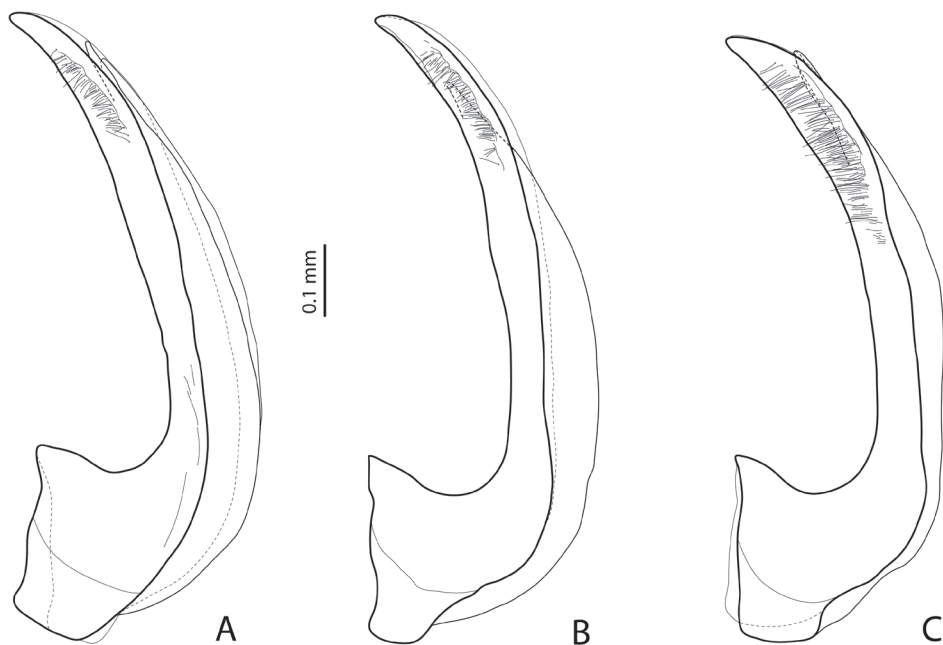


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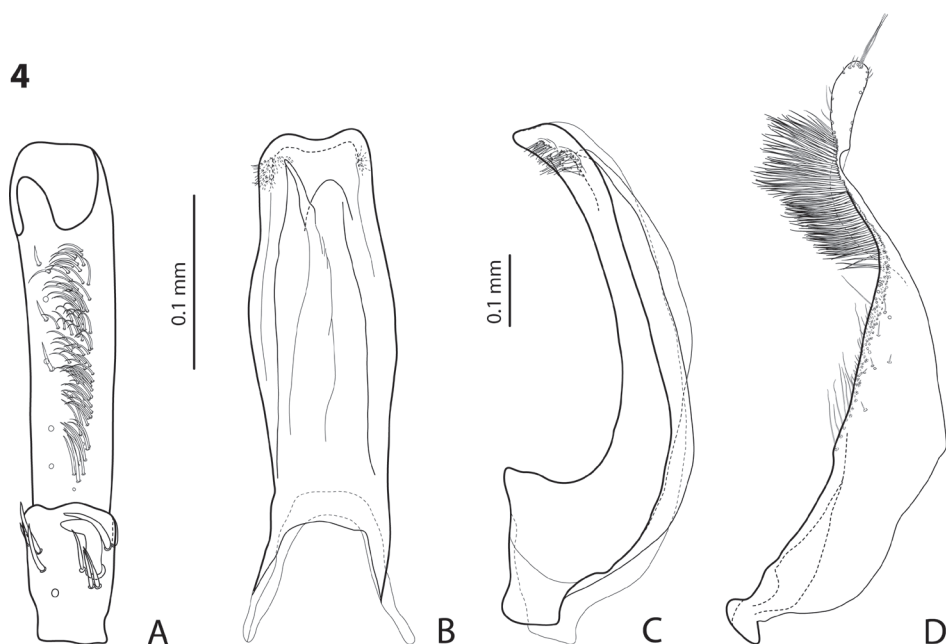


Figures 1–2. 1 *Exocelina rufa* (Balke, 1998) 2 *E. miriae* (Balke, 1998), Herzog Range, Wagau **A** male protarsomeres 4–5 in ventral view **B** median lobe in ventral view **C** median lobe in lateral view **D** paramere in external view.

3

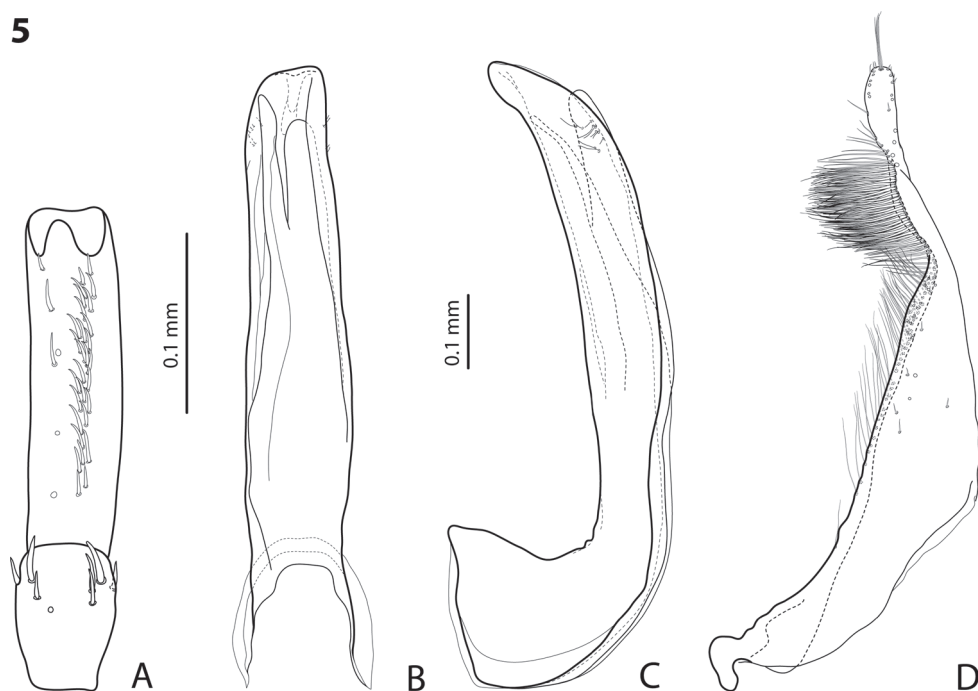


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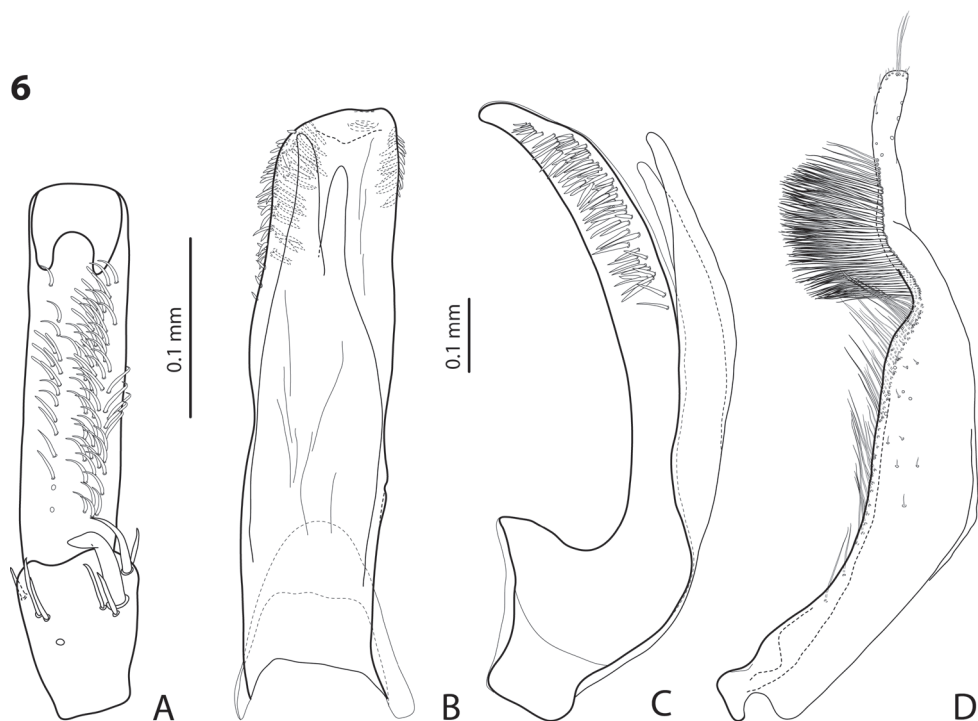


Figures 3–4. 3 *Exocelina miriae* (Balke, 1998), median lobe in lateral view **A** Herzog Range, Wagau **B** Morobe, Mount Inji, PNG96 **C** Eastern Highlands, Yeginofi, PNG55 4 *E. tekadu* sp. n. **A** male pro-tarsomeres 4–5 in ventral view **B** median lobe in ventral view **C** median lobe in lateral view **D** paramere in external view.

5

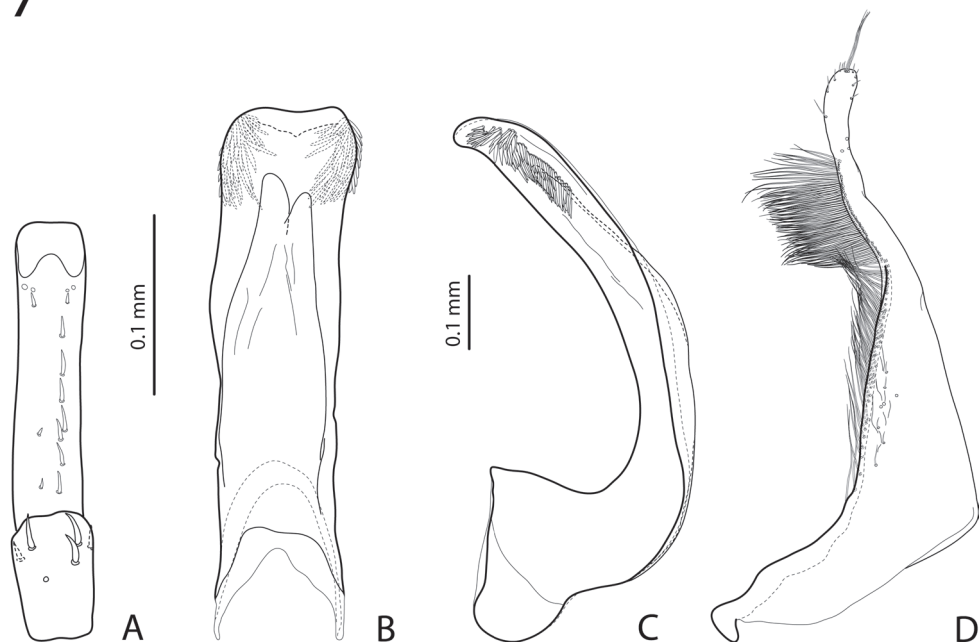


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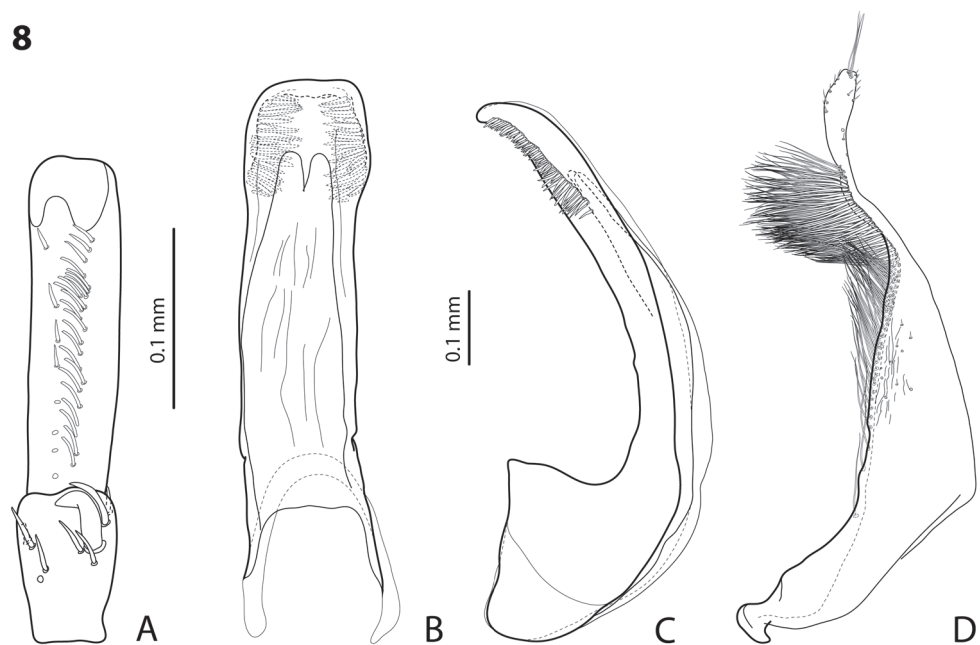


Figures 5–6. 5 *Exocelina kabwumensis* sp. n. 6 *E. woitapensis* sp. n. **A** male protarsomeres 4–5 in ventral view **B** median lobe in ventral view **C** median lobe in lateral view **D** paramere in external view.

7

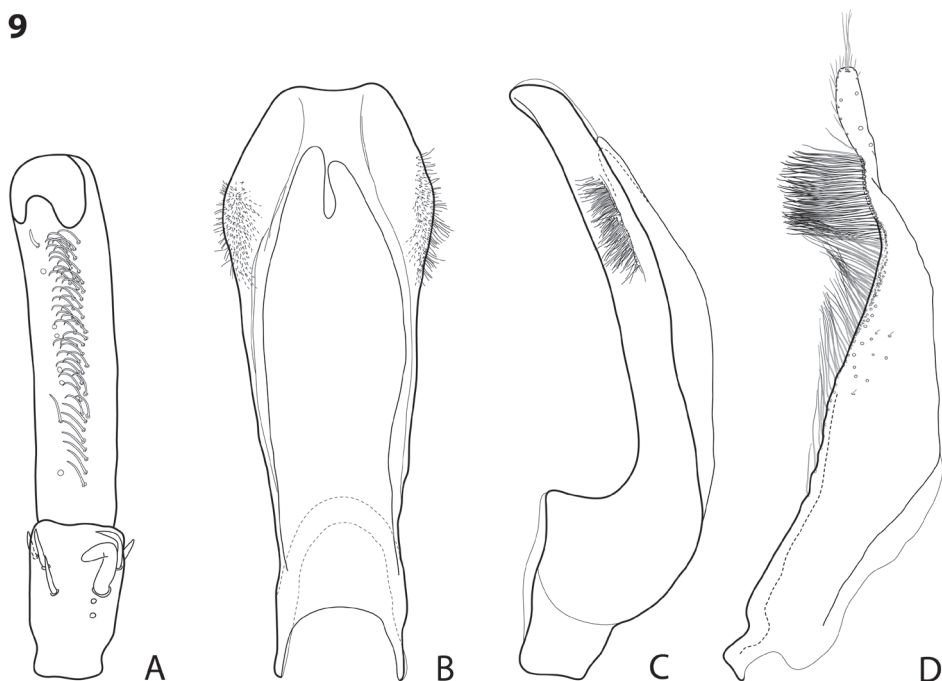


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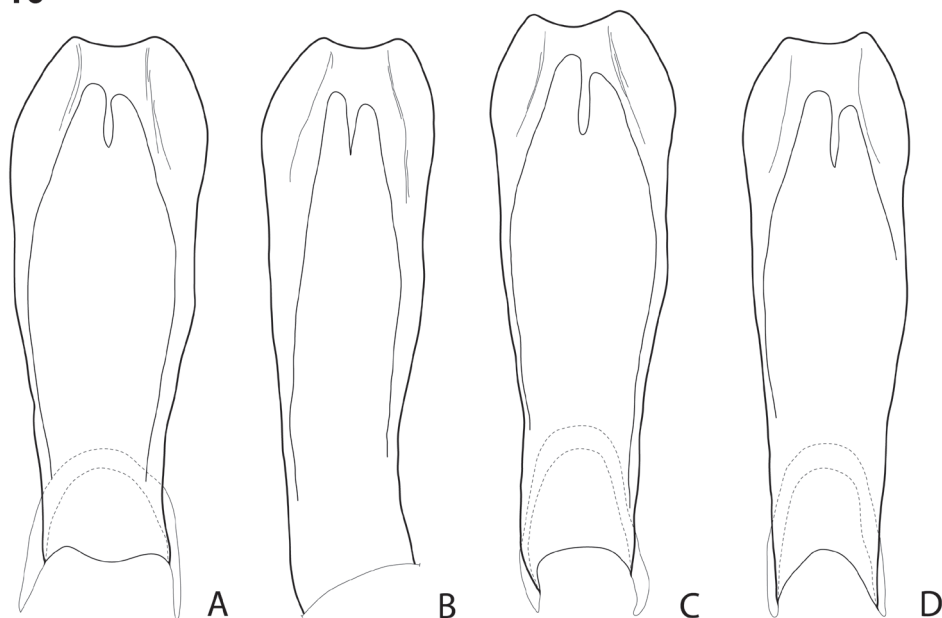


Figures 7–8. **7** *Exocelina andakombensis* sp. n. **8** *E. injiensis* sp. n. **A** male protarsomeres 4–5 in ventral view **B** median lobe in ventral view **C** median lobe in lateral view **D** paramere in external view.

9



10



Figures 9–10. 9 *Exocelina damantiensis* (Balke, 1998), paratype, Madang, Damanti **A** male protarsomeres 4–5 in ventral view **B** median lobe in ventral view **C** median lobe in lateral view **D** paramere in external view 10 *E. damantiensis*, median lobe in ventral view, setae are not shown **A** IN, West Papua, Wasior **B** IN, Papua, Nabire-Illaga, 96#13 **C, D** IN, Papua, Wano, Pap027 and Pap024.

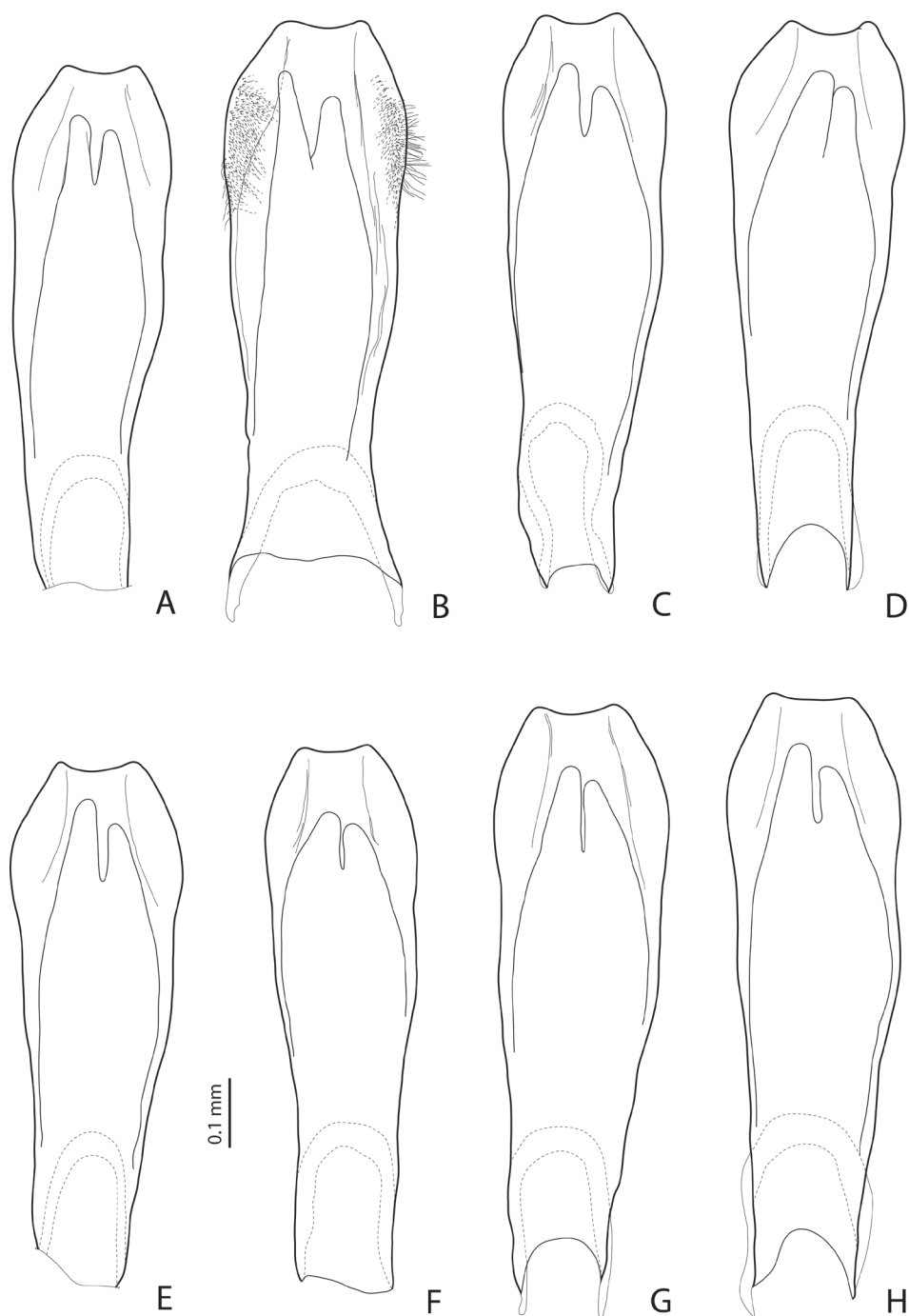


Figure 11. *Exocelina damantiensis* (Balke, 1998), median lobe in ventral view, setae are not shown **A** IN, Papua, Bime-Calab, 16, paratype of *E. rivulus* (Balke, 1998) **B** IN, Papua, Angguruk, 32, paratype of *E. rivulus* **C, D** PNG, Sandaun, Mianmin area, PNG236 and Wara-Uk, WB16 **E, F** PNG, Western Province, Tabubil, PNG181 **G** PNG, Enga, PNG128 **H** PNG, WHL, PNG147.

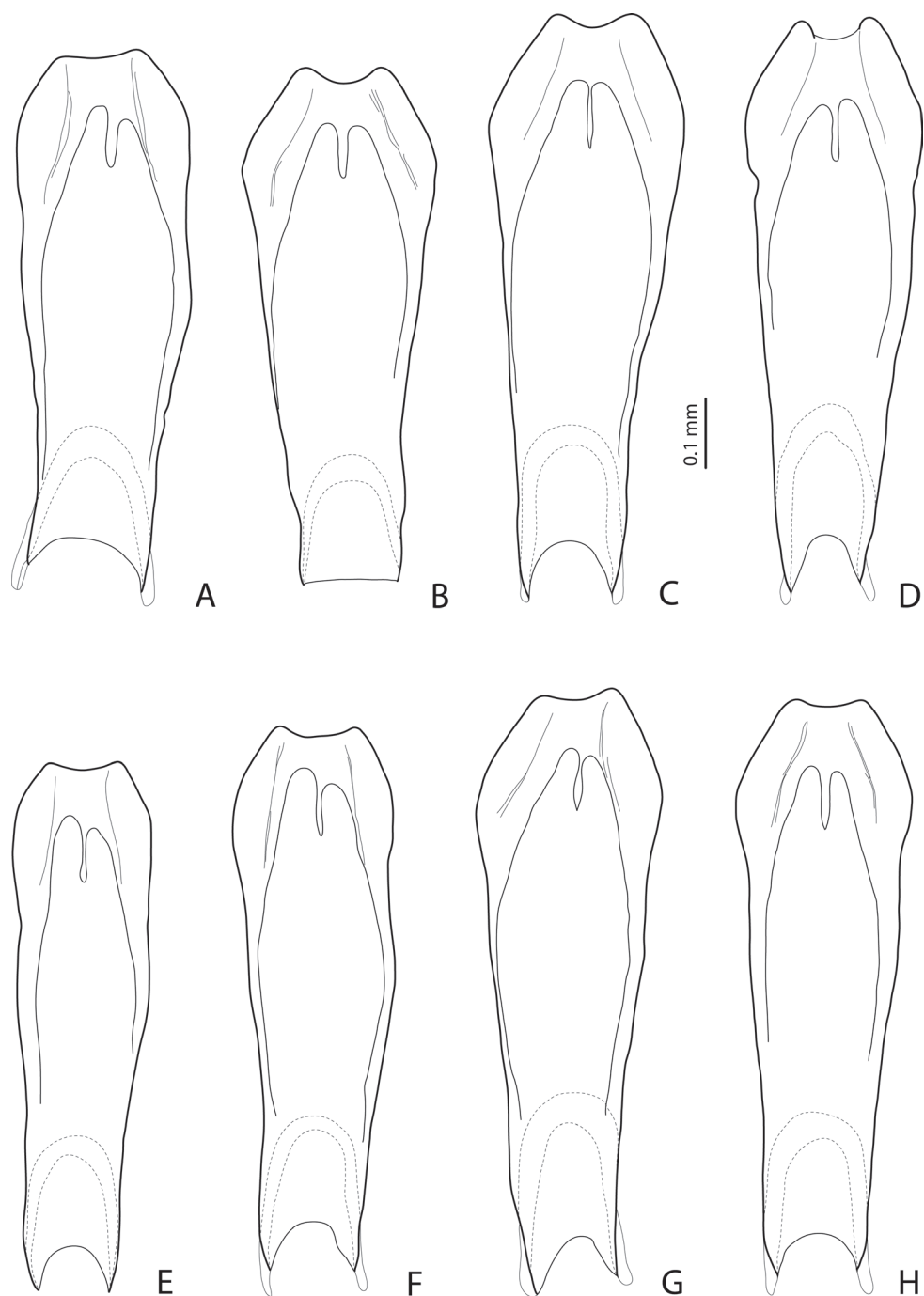
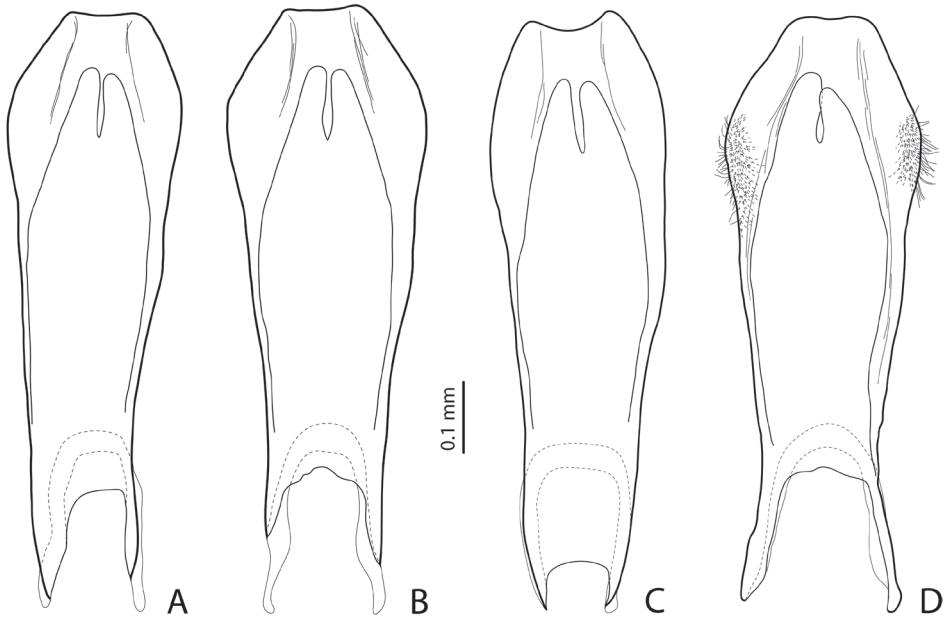
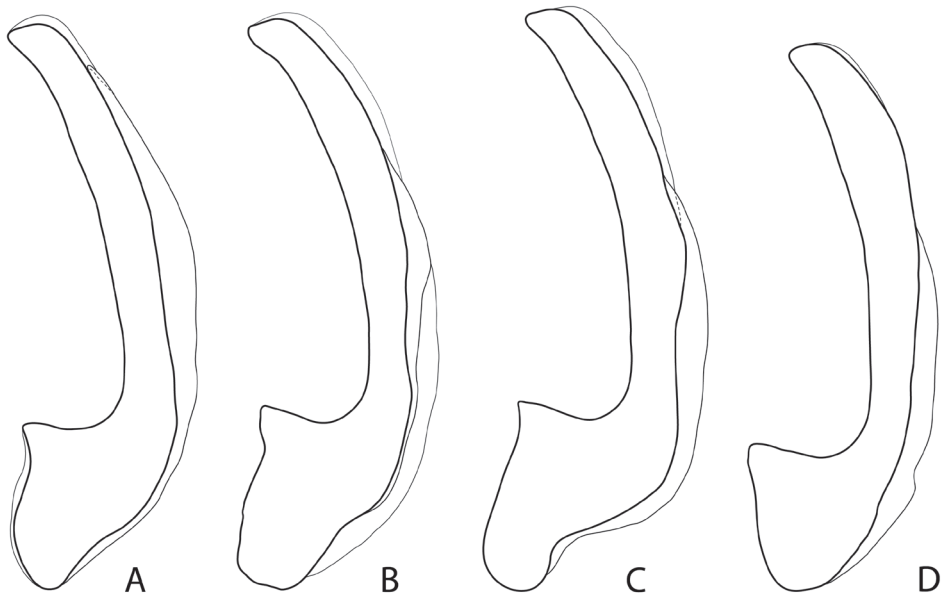


Figure 12. *Exocelina damantiensis* (Balke, 1998), PNG, median lobe in ventral view, setae are not shown **A** Simbu, Mount Wilhelm **B** Simbu/EHL, Wara Sera, PNG10 **C, D** Simbu/EHL, Hulene River, PNG17 **E** Madang, Brahman-Bundi, paratype of *E. madangensis* (Balke, 2001) **F** Madang, Akameku-Brahman, PNG114 **G, H** Madang, Damanti, paratypes of *E. damantiensis*.

13



14



Figures 13–14. *Exocelina damantiensis* (Balke, 1998), setae are not shown **13** median lobe in ventral view, PNG, Morobe **A**, **B** Kobau **C** Yakob, PNG74 **D** Lae-Bulolo, paratype of *E. patepensis* (Balke, 1998) **14** median lobe in lateral view, IN **A** West Papua, Wasior **B** Papua, Nabire-Illaga, 96#13 **C** Papua, Wano, Pap027 **D** Papua, Bime-Calab, 16, paratype of *E. rivulus* (Balke, 1998).

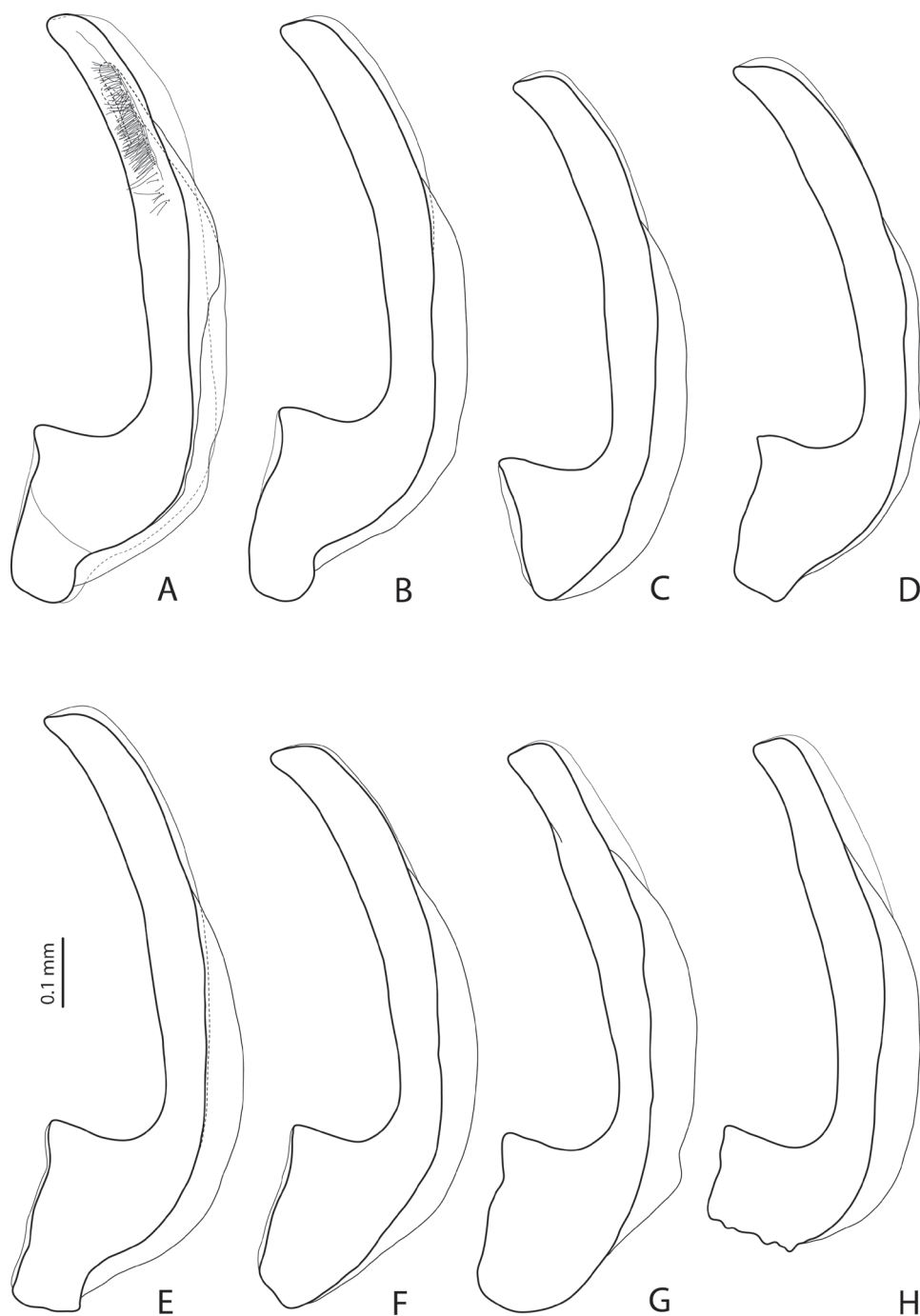


Figure 15. *Exocelina damantiensis* (Balke, 1998), median lobe in lateral view, setae are not shown **A** IN, Papua, Angguruk, 32, paratype of *E. rivulus* **B** PNG, Sandaun, Mianmin area, PNG236 **C, D** PNG, Western Province, Tabubil, PNG181 **E** PNG, Enga, PNG128 **F** PNG, WHL, PNG147 **G** PNG, Simbu/EHL, Hulene River, PNG17 **H** PNG, Simbu/EHL, Wara Sera, PNG10.

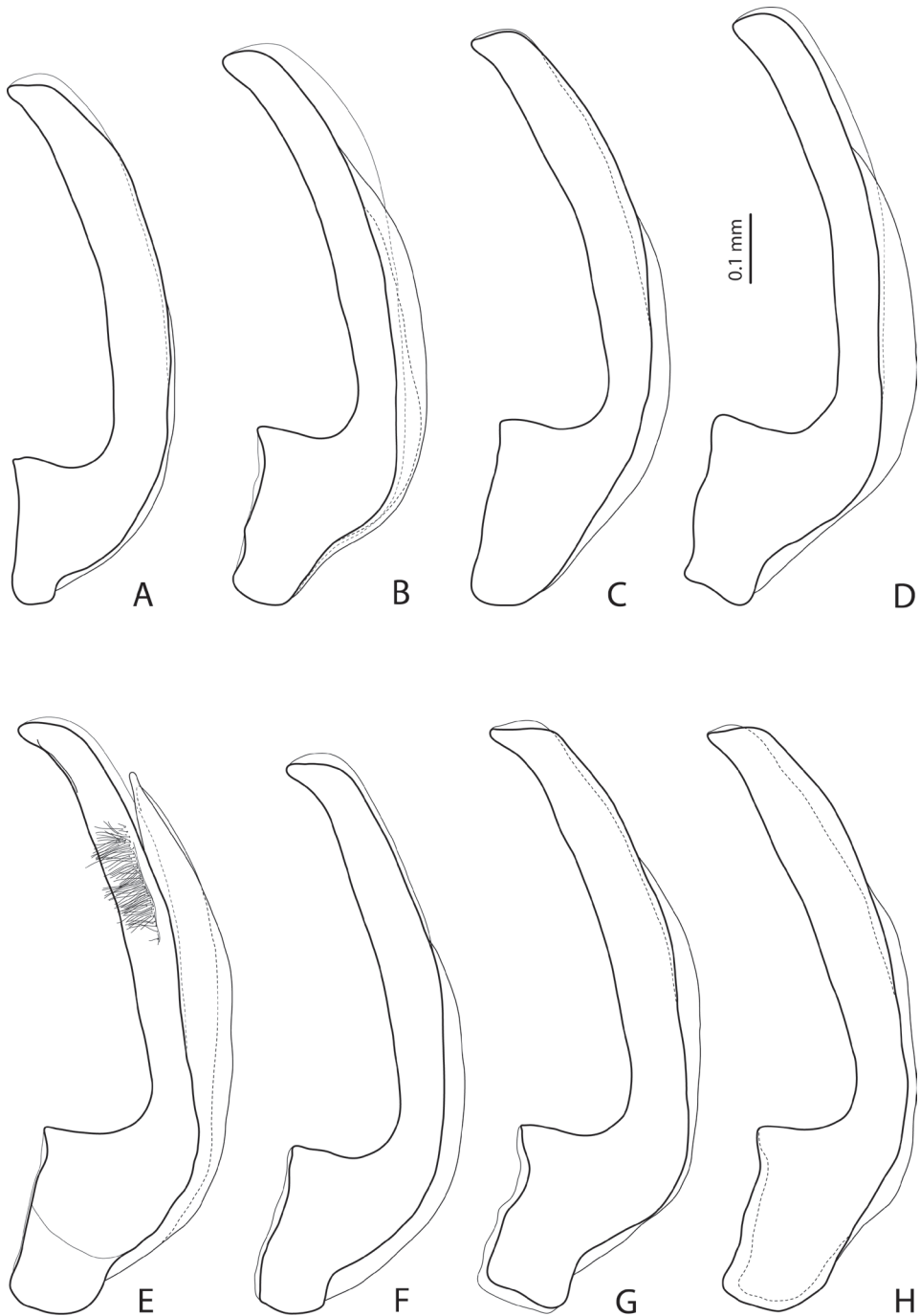
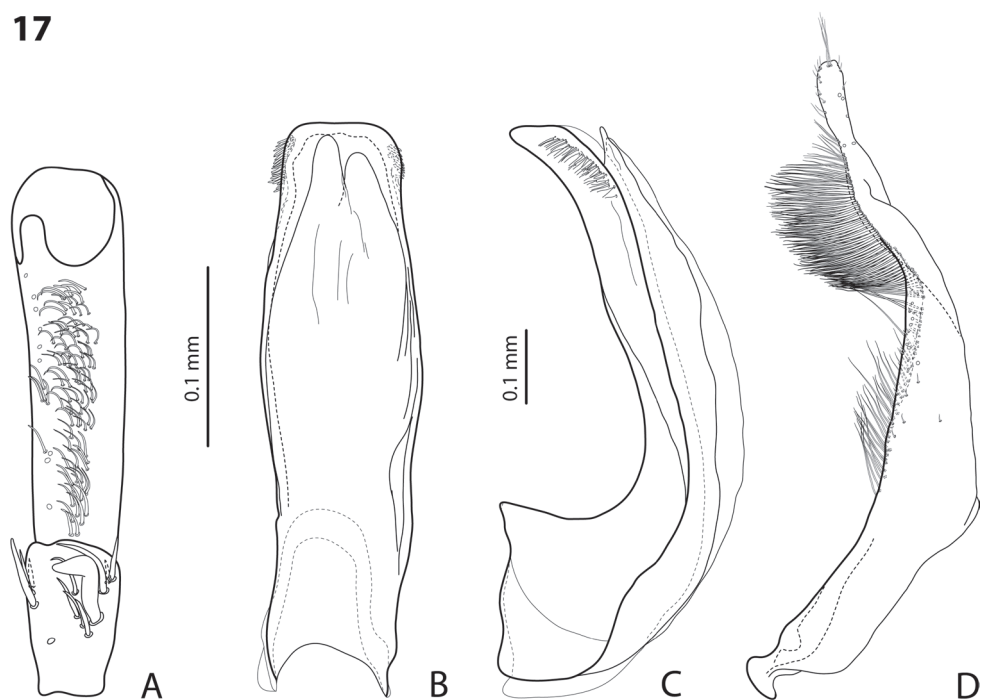
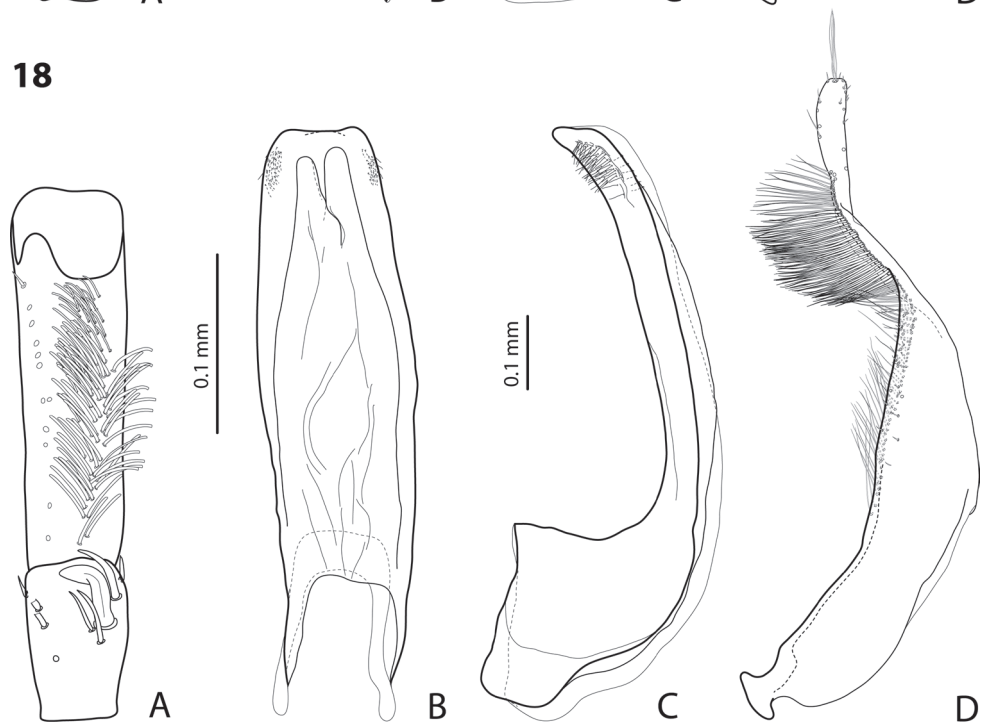


Figure 16. *Exocelina damantiensis* (Balke, 1998), PNG, median lobe in lateral view, setae are not shown **A** Madang, Brahman-Bundi, paratype of *E. madangensis* (Balke, 2001) **B** Madang, Akameku-Brahman, PNG114 **C** Madang, Damanti, paratype of *E. damantiensis* **D** Morobe, Yakob, PNG74 **E** Morobe, Lae-Bulolo, paratype of *E. patepensis* (Balke, 1998) **F** Morobe, Kwapsanek, PNG25 **G, H** Morobe, Kobau.

17



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Figures 17–18. 17 *Exocelina wareaga* sp. n. 18 *E. varirata* sp. n. **A** male protarsomeres 4–5 in ventral view **B** median lobe in ventral view **C** median lobe in lateral view **D** paramere in external view.

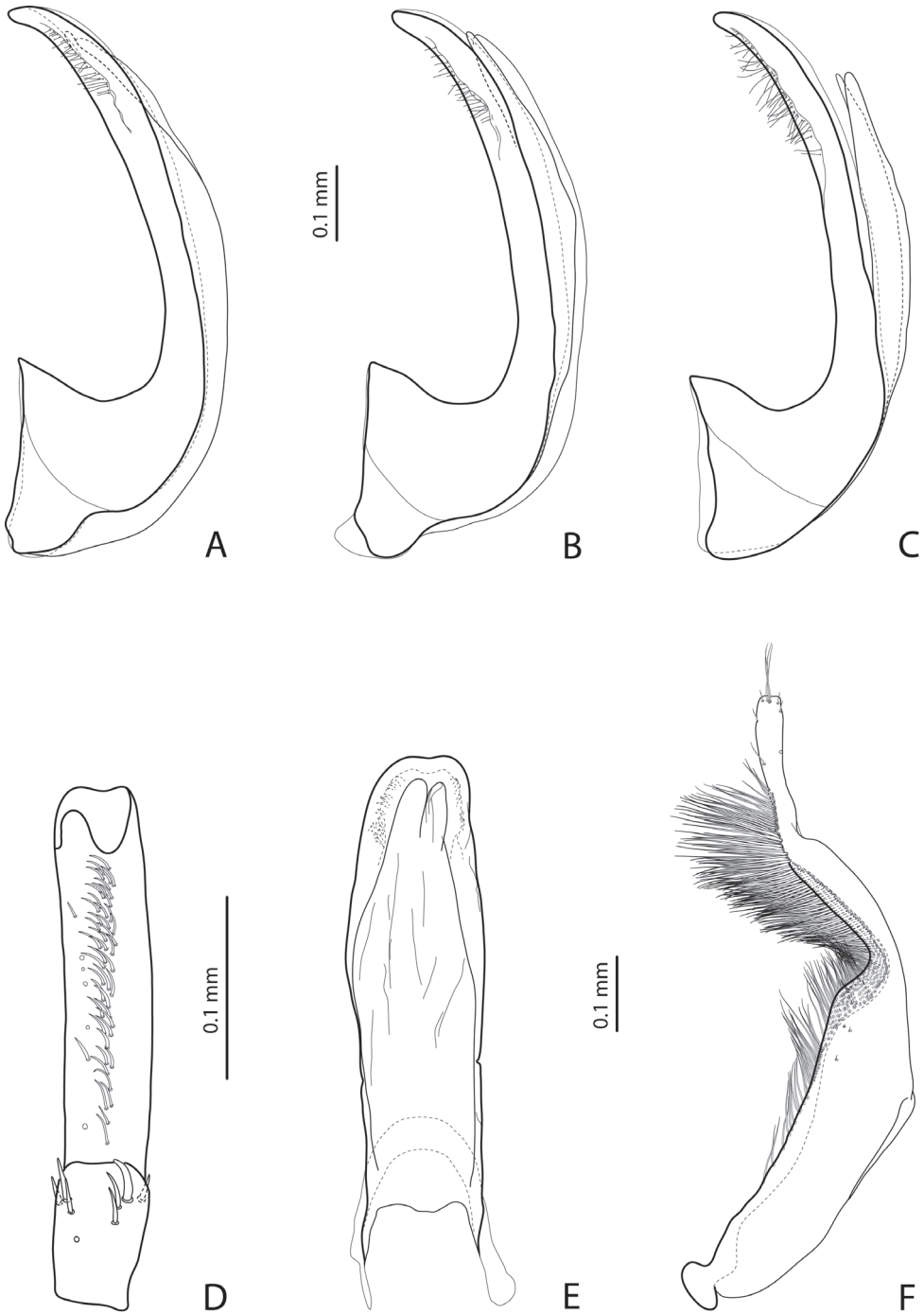
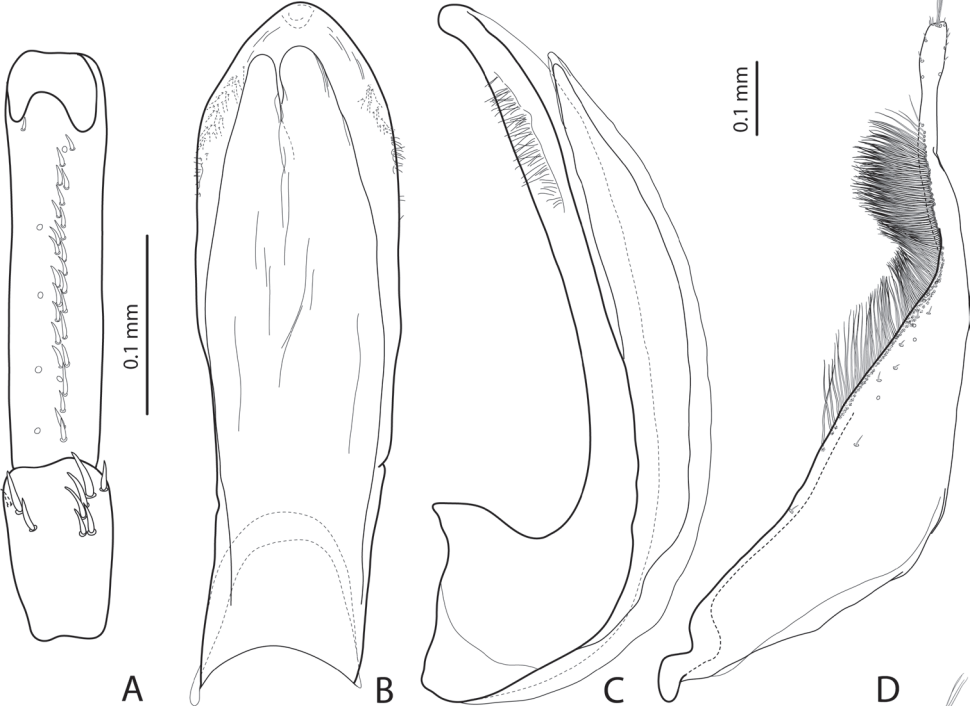
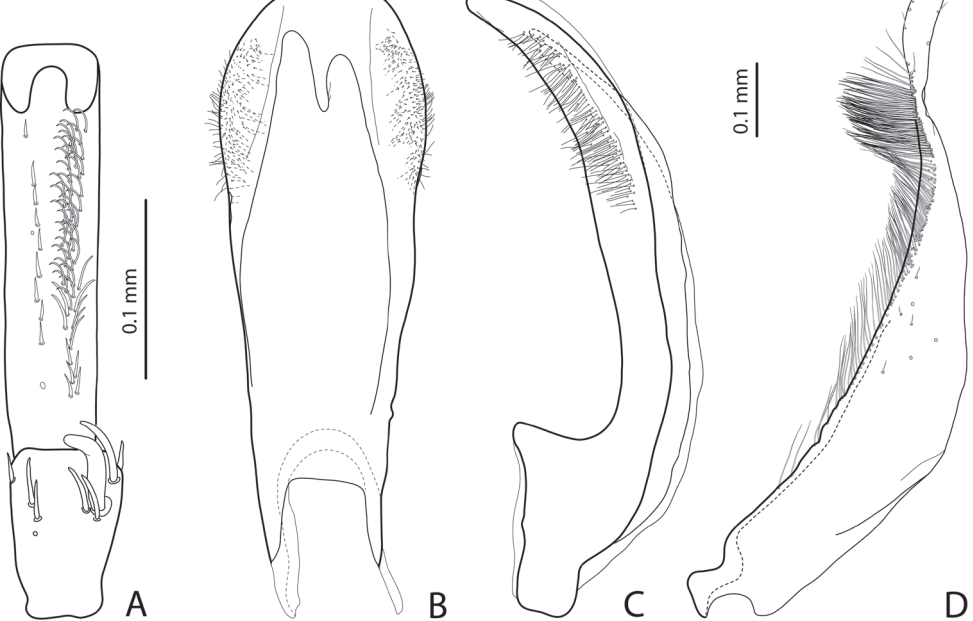


Figure 19. *Exocelina danae* (Balke, 1998) **A–C** median lobe in lateral view **A** paratype of *E. danae* **B** paratype of *E. tarmluensis* (Balke, 1998) **C–F** PNG, Sandaun, Sokamin4, WB102 **D** male protarsomeres 4–5 in ventral view **E** median lobe in ventral view **F** paramere in external view.

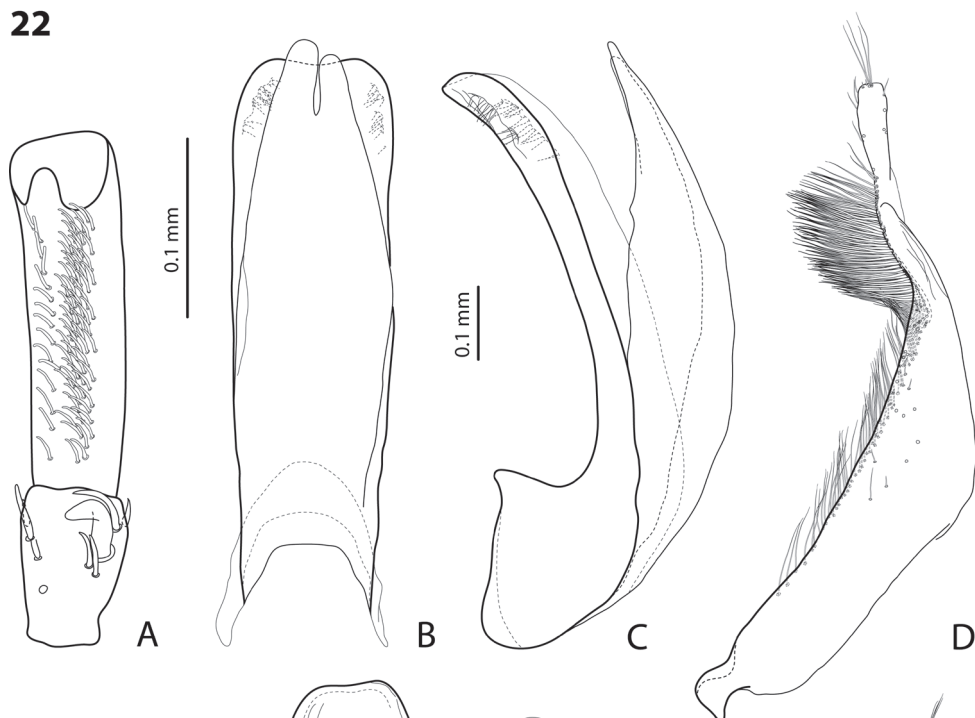
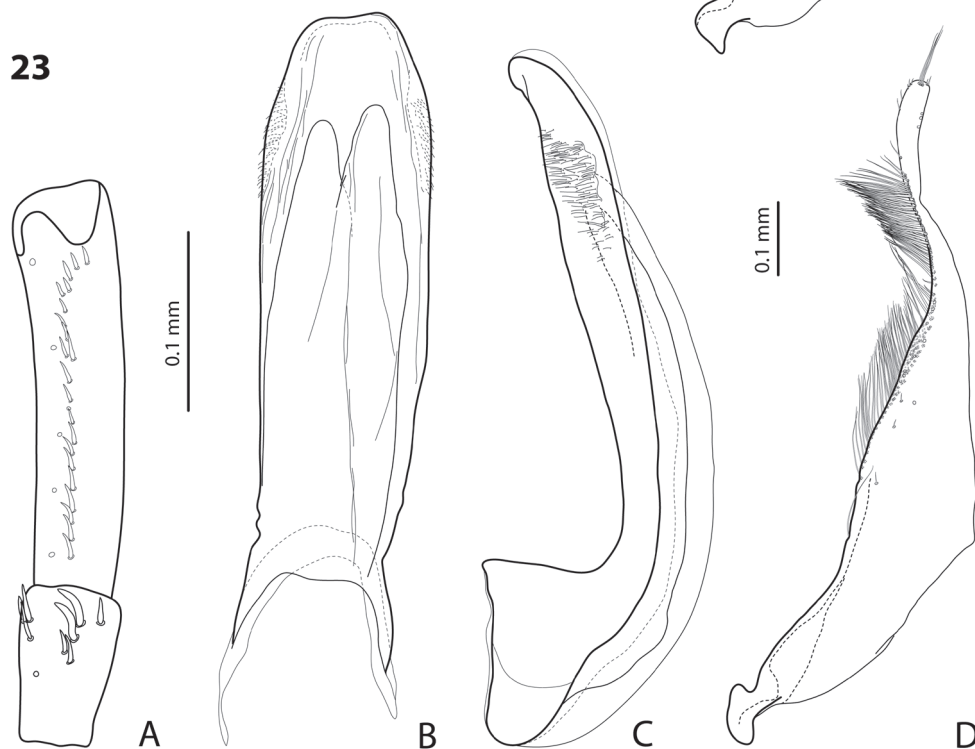
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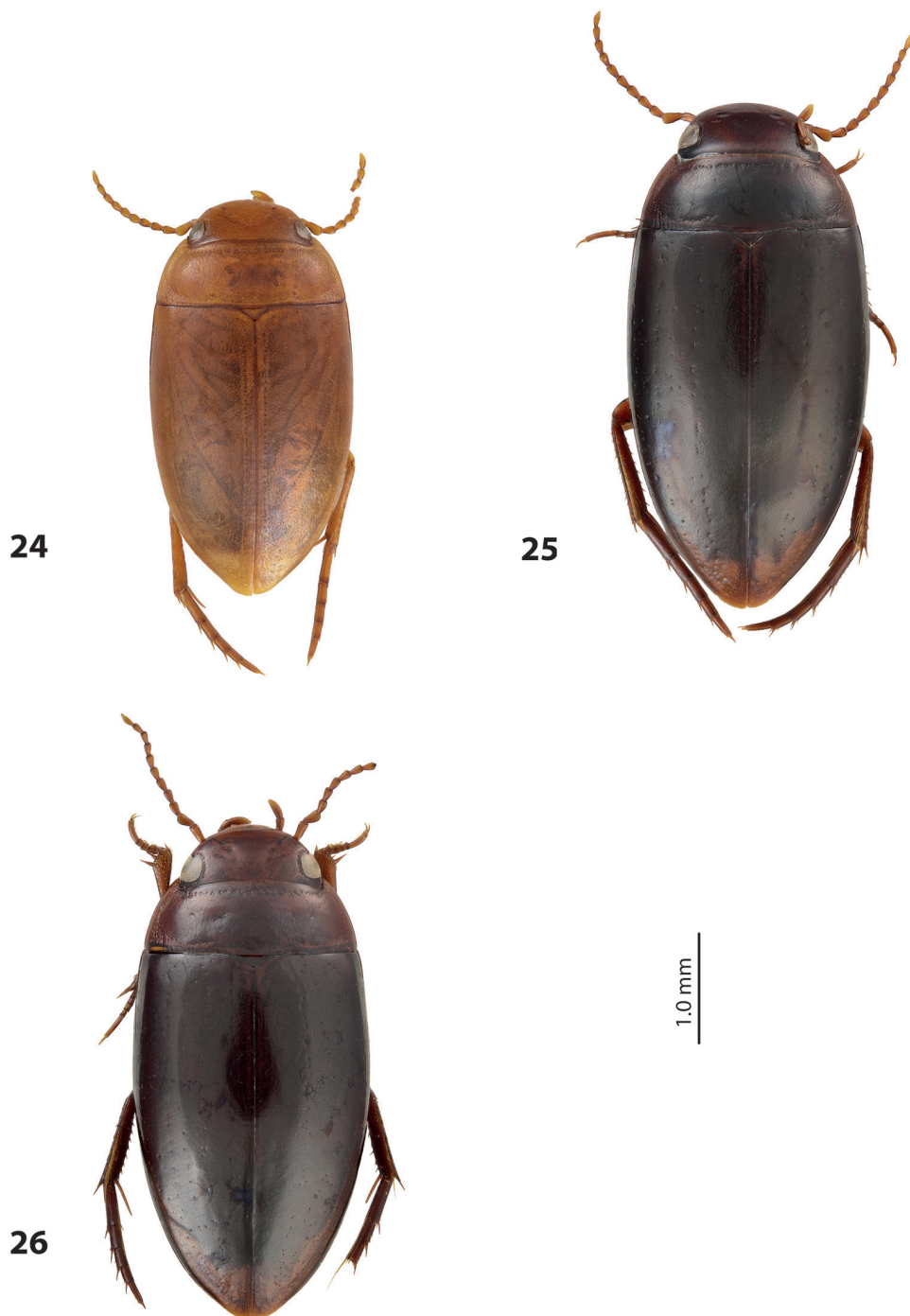
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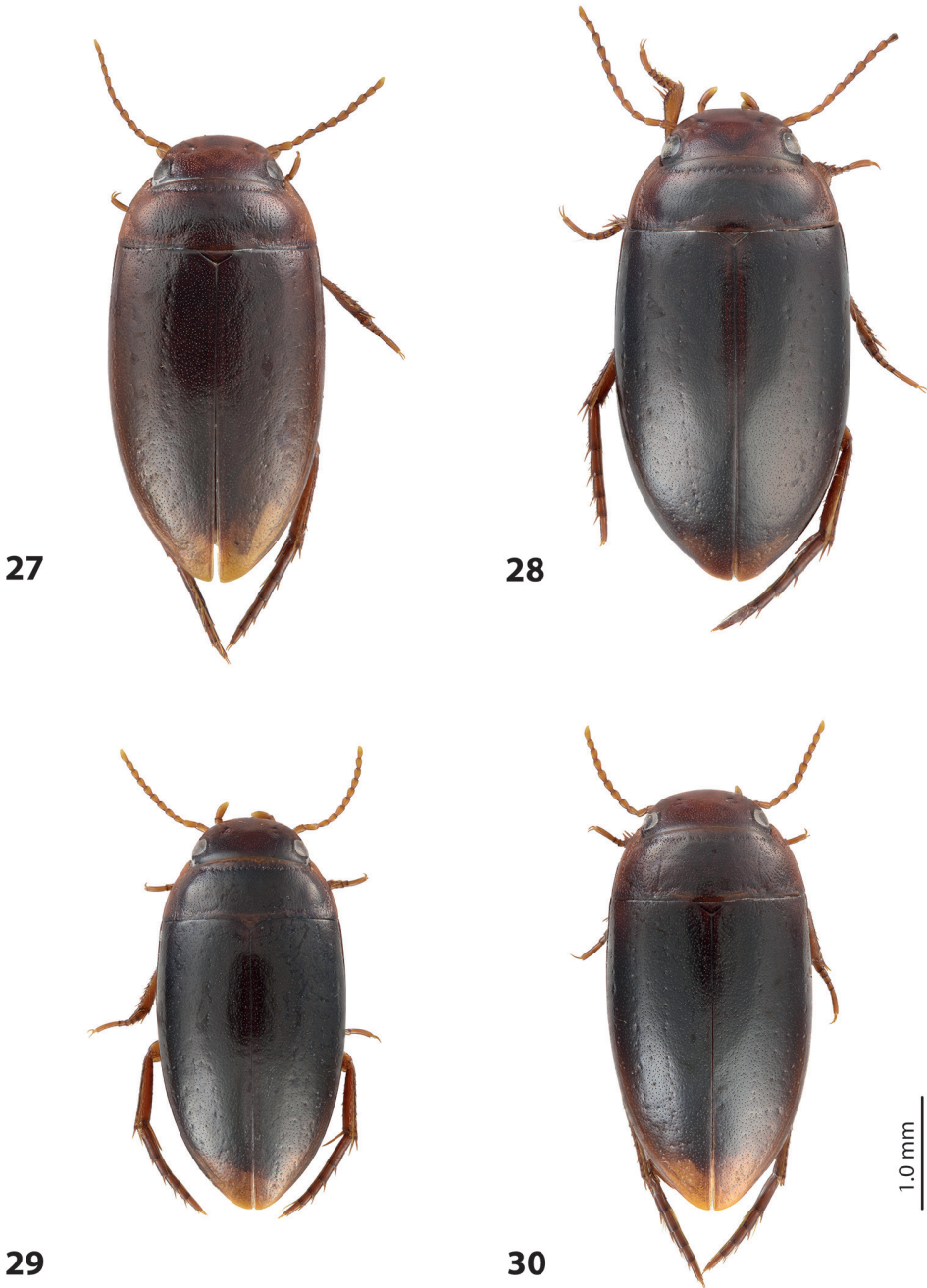
Figures 20–21. 20 *Exocelina marawaka* sp. n. 21 *E. garaina* sp. n. **A** male protarsomeres 4–5 in ventral view **B** median lobe in ventral view **C** median lobe in lateral view **D** paramere in external view.

22**23**

Figures 22–23. 22 *Exocelina atrata* (Balfour-Browne, 1939) 23 *E. posmani* sp. n. **A** male protarsomeres 4–5 in ventral view **B** median lobe in ventral view **C** median lobe in lateral view **D** paramere in external view.



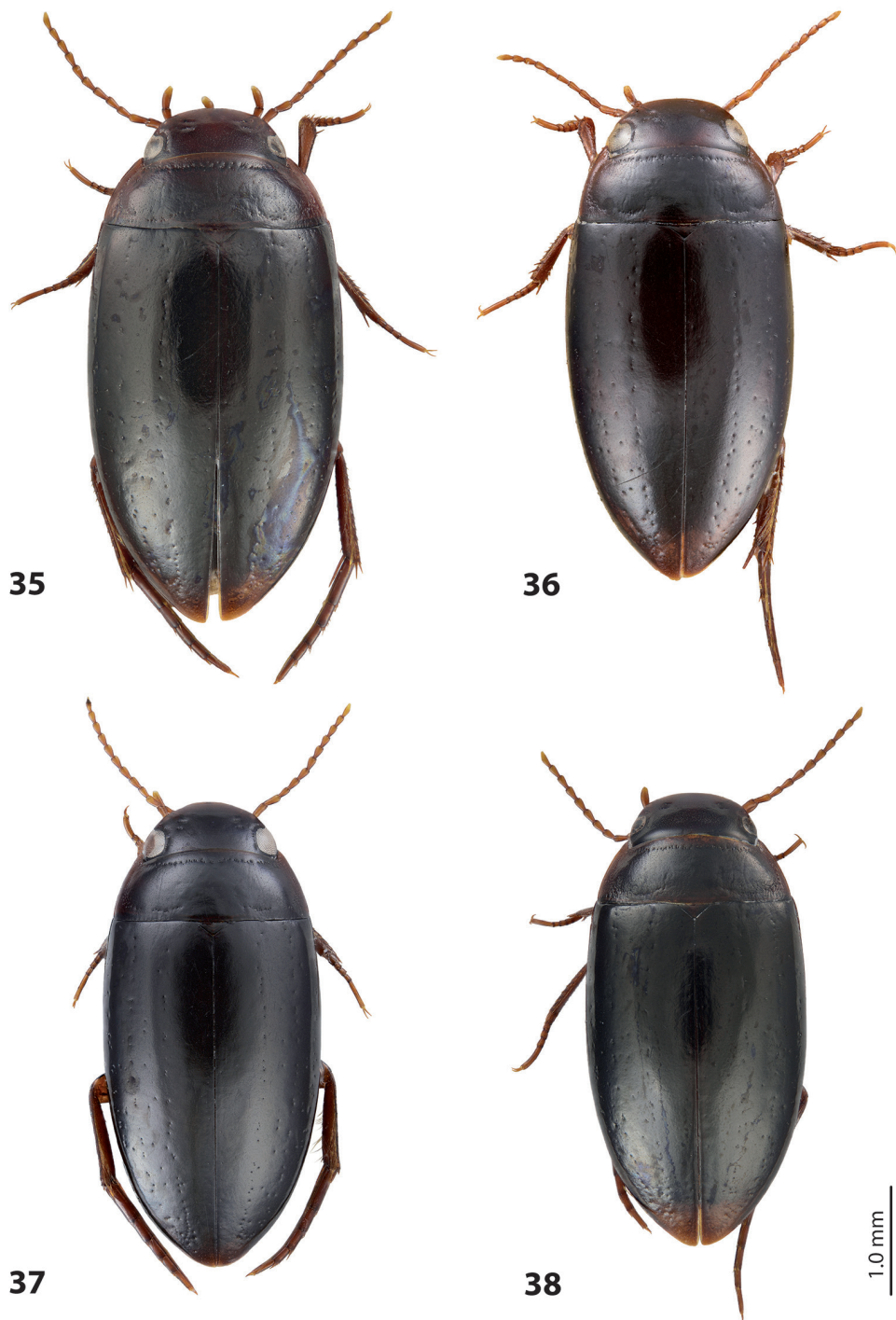
Figures 24–26. Habitus and coloration **24** *Exocelina rufa* (Balke, 1998) **25** *E. miriae* (Balke, 1998) **26** *E. tekadu* sp. n.



Figures 27–30. Habitus and coloration **27** *Exocelina kabwumensis* sp. n. **28** *E. woitapensis* sp. n. **29** *E. andakombensis* sp. n. **30** *E. injiensis* sp. n.



Figures 31–34. Habitus and coloration **31** *Exocelina damantiensis* (Balke, 1998) **32** *E. danae* (Balke, 1998) **33** *E. wareaga* sp. n. **34** *E. varirata* sp. n.



Figures 35–38. Habitus and coloration **35** *Exocelina marawaka* sp. n. **36** *E. atrata* (Balfour-Browne, 1939) **37** *E. garaina* sp. n. **38** *E. posmani* sp. n.

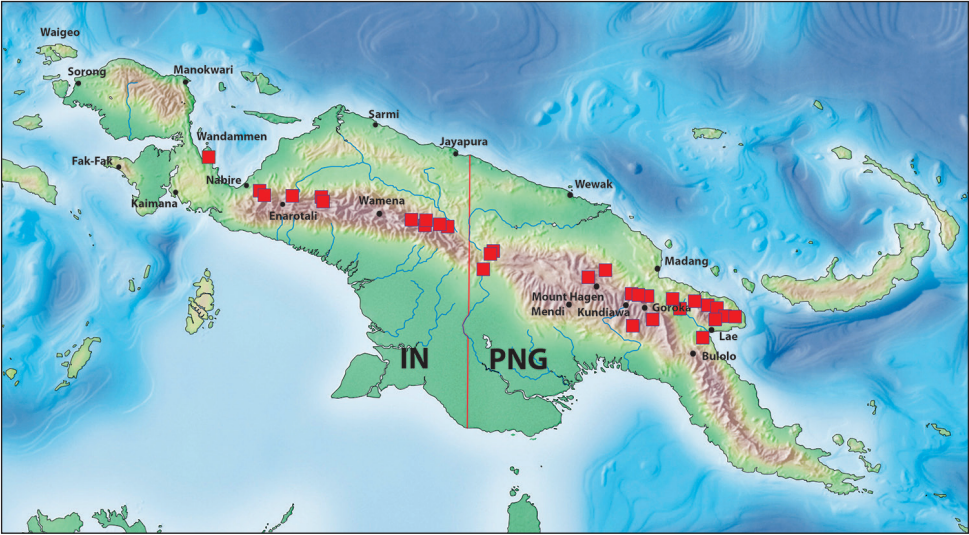


Figure 39. Map of New Guinea showing distribution of *Exocelina damantiensis* (Balke, 1998).



Figure 40. Map of Papua New Guinea showing distribution of species of the *Exocelina danae*-group.



Figure 41. Papua New Guinea, Marawaka area, mid-montane forest stream, with Andrew Kinibel; photo by M. Balke.

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References

- Balfour-Browne J (1939) On *Copelatus* Er. and *Leiopterus* Steph. (Coleoptera: Dytiscidae) with descriptions of new species. Transactions of the Royal entomological Society of London 88(2): 57–88. doi: 10.1111/j.1365-2311.1939.tb00250.x
- Balke M (1998) Revision of New Guinea *Copelatus* Erichson, 1832 (Insecta: Coleoptera: Dytiscidae): The running water species, Part I. Annalen des Naturhistorischen Museum Wien 100B: 301–341.
- Balke M (1999) Two new species of the genus *Copelatus* Erichson, 1832, subgenus *Papuadytes* Balke, 1998, from Papua New Guinea (Insecta: Coleoptera: Dytiscidae). Annalen des Naturhistorischen Museum Wien 101B: 273–276.
- Balke M (2001) Replacement names for three New Guinea species of *Copelatus*, subgenus *Papuadytes* Balke, 1998 (Coleoptera: Dytiscidae). Annalen des Naturhistorischen Museum Wien 103B: 361–362.
- Balke M, Pons J, Ribera I, Sagata K, Vogler AP (2007) Infrequent and unidirectional colonization of hyperdiverse *Papuadytes* diving beetles in New Caledonia and New Guinea. Molecular Phylogenetics and Evolution 42: 505–516. doi: 10.1016/j.ympev.2006.07.019
- Broun T (1886) Manual of the New Zealand Coleoptera. Parts III and IV. Government Printer, Wellington, 745–973.
- Guéorguiev VB (1968) Essai de classification des coléoptères Dytiscidae. I. Tribus Copelatini (Colymbetinae). Izvestiya na Zoologicheskaya Institut (s Muzei) Sofiya 28: 5–45.
- Guéorguiev VB, Rocchi S (1993) Contributo alla conoscenza dei Dytiscidae della Nuovo Guinea (Coleoptera). Frustula entomologica (1992), n.s. XV(XXVIII): 147–166.
- Guignot F (1956) Dytiscides récoltés par le Dr. L. Biro en nouvelle Guinée et dans l'île de Java (Coleoptera). Annales historico-naturales Musei nationalis hungarici (N.S.) VII: 51–60.
- Nilsson AN (2001) Dytiscidae. World catalogue of insects. Vol. 3. Apollo Books, Stenstrup, 1–395.
- Nilsson AN (2007) *Exocelina* Broun, 1886, is the valid name of *Papuadytes* Balke, 1998. Latissimus 23: 33–34.
- Nilsson AN, Fery H (2006) World Catalogue of Dytiscidae – corrections and additions, 3 (Coleoptera: Dytiscidae). Koleopterologische Rundschau 76: 55–74.
- Shaverdo HV, Balke M (2014) *Exocelina kinibeli* sp.n. from Papua New Guinea, a new species of the *E. ullrichi*-group (Coleoptera: Dytiscidae). Koleopterologische Rundschau 84: 31–40.
- Shaverdo HV, Sagata K, Balke M (2005) Five new species of the genus *Papuadytes* Balke, 1998 from New Guinea (Coleoptera: Dytiscidae). Aquatic Insects 27(4): 269–280. doi: 10.1080/01650420500290169
- Shaverdo HV, Surbakti S, Hendrich L, Balke M (2012) Introduction of the *Exocelina ekari*-group with descriptions of 22 new species from New Guinea (Coleoptera, Dytiscidae, Copelatinae). ZooKeys 250: 1–76. doi: 10.3897/zookeys.250.3715
- Shaverdo HV, Hendrich L, Balke M (2013) *Exocelina baliem* sp. n., the only known pond species of New Guinea *Exocelina* Broun, 1886 (Coleoptera, Dytiscidae, Copelatinae). ZooKeys 304: 83–99. doi: 10.3897/zookeys.304.4852

- Shaverdo H, Sagata K, Panjaitan R, Menufandu H, Balke M (2014) Description of 23 new species of the *Exocelina ekari*-group from New Guinea, with a key to all representatives of the group (Coleoptera, Dytiscidae, Copelatinae). ZooKeys 468: 1–83. doi: 10.3897/zookeys.468.8506
- Shaverdo H, Panjaitan R, Balke M (2016a) A new, widely distributed species of the *Exocelina ekari*-group from West Papua (Coleoptera, Dytiscidae, Copelatinae). ZooKeys 554: 69–85. doi: 10.3897/zookeys.554.6065
- Shaverdo H, Sagata K, Balke M (2016b) Description of two new species of the *Exocelina broschii*-group from Papua New Guinea, with revision and key to all representatives of this species group (Coleoptera, Dytiscidae, Copelatinae). ZooKeys 577: 125–148. doi: 10.3897/zookeys.577.7254
- Shaverdo H, Panjaitan R, Balke M (2016c) *Exocelina ransikiensis* sp. nov. from the Bird's Head of New Guinea (Coleoptera: Dytiscidae: Copelatinae). Acta Entomologica Musei Nationalis Pragae 56(1): 103–108.
- Toussaint EFA, Hall R, Monaghan MT, Sagata K, Ibalim S, Shaverdo HV, Vogler AP, Pons J, Balke M (2014) The towering orogeny of New Guinea as a trigger for arthropod megadiversity. Nature Communications 1: 1–10 + 10 supplements, 5: 4001. doi: 10.1038/ncomms5001

Jewelled spider flies of North America: a revision and phylogeny of *Eulonchus* Gerstaecker (Diptera, Acroceridae)

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Abstract

The spider fly genus *Eulonchus* Gerstaecker is found throughout the Nearctic Region. Six species are recognized and intraspecific morphological variation is documented in several species. A phylogeny of *Eulonchus* based on DNA sequence data of three molecular markers (COI, CAD, and 16S) is presented and relationships of species are discussed in the light of biogeography and host usage. All six species of *Eulonchus* are redescribed using natural language descriptions exported from a character matrix, and a key to species is presented. Lectotypes are designated for *E. sapphirinus* Osten Sacken, *E. smaragdinus* Gerstaecker, and *E. tristis* Loew.

Keywords

Antrodiaetidae, Euctenizidae, spider parasitoid, phylogeny, small-headed fly, tarantula, biodiversity, cybertaxonomy, Lucid

Introduction

Acroceridae are a small group of flies commonly known as spider flies or small-headed flies. The family comprises a morphologically heterogeneous assemblage of taxa, with approximately 550 species in 55 genera (Schlinger et al. 2013) distributed in all major

biogeographic regions. Acroceridae is divided into three subfamilies: Philopotinae, Panopinae and the polyphyletic Acrocerinae (Schiner 1868; Cole 1919; Schlinger 1981; Winterton et al. 2007; Gillung and Nihei 2016). Adults are remarkably diverse in morphology, sometimes with elongated mouthparts for nectar feeding or with a strongly arched thorax, while the larvae are specialised endoparasitoids of spiders. First instar acrocerid larvae are free-living planidia that either actively seek out a spider host or sit and wait for the host to pass by (Cole 1919; Schlinger 1987; Nielsen et al. 1999).

Panopinae (tarantula flies) represent some of the smallest and largest spider flies, with a body size ranging from 4.0 mm (*Corononcodes* Speiser) to 19.0 mm (*Exetasis* Walker). Winterton (2012) recently diagnosed the subfamily, which is characterised by the antennal flagellum cylindrical or paddle shaped (never stylate), lacking an arista, postpronotal lobes widely separated, wing venation relatively conserved with cells m_3 , d, bm and basal r_{4+5} normally present, tibial spines present (absent only in *Apsona* Westwood), and parasitism on Mygalomorphae. Only *Corononcodes* deviates significantly from this diagnosis, due to reduction in wing venation associated with the very small body size of most species. All species of Panopinae with known life histories are exclusive parasitoids of mygalomorph spiders and have been recorded from 5 families, including Antrodiaetidae, Ctenizidae, Dipluridae, Euctenizidae, Migidae, and Theraphosidae (Schlinger 1987; Winterton et al. 2007; Barneche et al. 2013). Panopinae contains ~135 species divided into 23 genera. The fauna of the Palaearctic, Oriental, and Afrotropical Regions contains seven genera, including *Corononcodes*, *Astomella* Latreille, *Astomelloides* Schlinger, *Physegasterella* Brunetti, *Psilodera* Gray, *Rhyzogaster* Aldrich, and *Stenopialea* Speiser. The panopine fauna of the Australasian Region was recently revised by Winterton (2012) to contain only four genera: *Apsona*, *Leucopsina* Westwood, *Mesophysa* Macquart and *Panops* Lamarck. The Neotropical Region is rich in genera, containing *Apelleia* Bellardi, *Archipialea* Schlinger, *Arrhynchus* Philippi, *Camposella* Cole, *Coquena* Schlinger, *Eulonchus* Gerstaecker, *Exetasis*, *Lasia* Wiedemann, *Lasioides* Collado, *Ocnaea* Erichson, *Pialea* Erichson, and *Pteropexus* Macquart, although the group is in need of revision, with several generic synonyms likely (Schlinger et al. 2013). *Pterodontia* Lamarck was considered by some authors as part of Panopinae, but was conclusively shown to be a derived member of Acrocerinae by Winterton et al. (2007) based on molecular data. The Nearctic Region is faunistically depauperate in panopine taxa, with only three genera: *Eulonchus*, *Lasia*, and *Ocnaea*.

Species of *Eulonchus*, *Lasia* and the Australasian genera *Apsona* and *Panops* are commonly called ‘jewelled spider flies’, while species of the New World genus *Ocnaea* are known as ‘hairy tarantula flies’. *Lasia* and *Ocnaea* are relatively diverse in the Neotropical Region but are represented in the Nearctic Region only by a few extralimital species. In contrast, *Eulonchus* is endemic to the Nearctic Region. Six species of *Eulonchus* are present, distributed from Canada to Mexico. *Eulonchus marialiciae* Brimley is known only from the eastern USA, while all other species are recorded from the western part of the continent, from Baja California, Mexico, north to British Columbia, Canada, and east to Utah and Arizona. The greatest number of species is known

from California, although there are records from Arizona, Idaho, Montana, Nevada, Oregon, Utah, and Washington. *Eulonchus marginatus* Osten Sacken, *E. sapphirinus* Osten Sacken, and *E. tristis* Loew are known from Northern California, the latter two species extending northwards to Oregon, Idaho, Washington and British Columbia. *Eulonchus halli* Schlinger and *E. smaragdinus* Gerstaecker are found in California south to Baja California, Mexico. Brunetti (1926) recorded a specimen of *Eulonchus* from Uruguay, but this record was subsequently dismissed as a likely misidentification of a species of *Lasia* (Schlinger 1960). Some species of *Eulonchus* were previously revised by Cole (1919) and Schlinger (1960), and a total of six species are described (as well as two subspecies of *E. smaragdinus*). Considerable sexual dimorphism and variation in pile density and cuticle colouration is evident in several species. Schlinger indicated at several times (1960, 1966, 1969) that there were a large number (>15) of undescribed species, and that the genus should be divided into species groups, but he only defined a single species group comprising *E. smaragdinus* and *E. halli*.

Eulonchus attack spiders in the families Euctenizidae and Antrodiaetidae (Coyle 1971; Vincent 1986; Schlinger 1987), although hosts are only known conclusively for *E. marialiciae*, *E. smaragdinus*, and *E. tristis*. Little is known of the biology of the parasitoid larvae, though one of us (C. Borkent) has observed that the newly hatched first instars are active in searching for a host. The larvae crawl in the manner of geometrid larvae, inching along and occasionally rearing up and wiggling their body side to side, presumably hoping to attach to a passing spider leg.

Several studies also demonstrate the importance of species of *Eulonchus* as pollinators of several plant families in montane areas of the Nearctic Region, including Boraginaceae, Geraniaceae, Themidaceae, and Iridaceae (Borkent and Schlinger 2008a, b). They have also been previously recorded visiting flowers of species in the Phrymaceae, Polemoniaceae, Primulaceae, and Ericaceae. Schlinger (1960) suggested that *E. halli* was a mutualist pollinator of *Cryptantha intermedia* Greene (Boraginaceae) as the flowering time of this plant appeared to coincide closely with the flight period of *E. halli*. Based on the behaviour observed by Borkent and Schlinger (2008a, b) this seems unlikely.

We revise the jewelled spider flies of North America (*Eulonchus*) and redescribe all valid species using cybertaxonomic methods of natural language description. A molecular phylogeny of the genus is presented along with a discussion of its evolution in a biogeographical context.

Materials and methods

Generic revision

Terminology for general morphology follows Cumming and Wood (2009), with wing venation as in Gillung and Winterton (2011) and Winterton (2012). Modifications of wing terminology as proposed by Saigusa (2006) were used, in which the dipteran vein

A_1 (as used in Cumming and Wood 2009) was homologized with CuP of Mecoptera. Consequently, the following wing venation terms are used here: CuA_1 (of Cumming and Wood) = M_4 , CuA_2 = CuA , and anal vein (A_1) = CuP.

Descriptions were constructed with Lucid Builder 3.5, using a matrix database of character states, which were then exported using the natural language function into a text document (for further editing) and accompanying XML. Specimen images were taken using a digital camera at different focal points and combined into a montage image using Helicon Focus software. Distribution maps were generated using ArcGIS 10.1 software (ESRI 2012). When GPS data were not available on the label, latitude and longitude were obtained by consulting online gazetteers and Google Earth™. Any plants listed as visited by *Eulonchus*, but without citation, are new records based on label data and collection records from this study.

Material examined

The specimens examined during the course of this study (Table 3) were principally part of the collection amassed by Dr. Evert Schlinger over more than 60 years. This collection now resides at the California Academy of Sciences (CAS). While most belonged to the Schlinger collection, a small minority of these specimens were loaned from other collections, but do not have that information clearly associated with them (either physically or in the incomplete specimen database). Therefore we cannot determine whether the specimen was loaned versus gifted; here we use a conservative approach and list only what is noted in the database or associated labels in the collection.

Annotations of collection label data are included where appropriate in brackets. The following collection codes are cited in the Material Examined: **CAS** – California Academy of Sciences, San Francisco, USA; **EMEC** – Essig Museum of Entomology, University of California Berkeley, California, USA; **MCZ** – Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; **OSUC** – Oregon State University, Oregon, Corvallis, USA; **DEI** – Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany; **TCAC** – Insect Collection of the Tulare County Agricultural Commissioner/Sealer, Tulare, California, USA; **TAIU** – Texas A&M University, Kingsville, Texas, USA; **UCDC** – Bohart Museum of Entomology, University of California Davis, California, USA; **USNM** – National Museum of Natural History, Washington D.C., USA; **ZMB** – Museum für Naturkunde, Berlin, Germany. Museum acronyms follow Evenhuis (2015).

Phylogenetic analysis

Five species of *Eulonchus* and two outgroup species (*Apsona muscaria* Westwood and *Lasia corvina* Erichson (given as *L. carbonanicus* in Winterton et al. 2007, a misspelling of *L. carbonarius* Philippi = *L. corvina* (Edwards 1930))) were included in the analyses.

Multiple DNA loci, as used previously in the phylogenetic study of spider fly evolution by Winterton et al. (2007), were included here. The dataset comprises sequences of two mitochondrial genes, 16S rDNA and cytochrome oxidase I (COI), as well as a single nuclear gene, the carbamoyl phosphate synthetase (CPSase) active site region of carbamoyl-phosphate synthetase-aspartate transcarbamoylase-dihydroorotase (CAD). Sequences from *A. muscaria*, *L. corvina*, *E. marialiciae*, *E. sapphirinus*, and *E. smaragdinus* were downloaded from Genbank, and new sequences for *E. marginatus*, *E. sapphirinus*, and *E. tristis* were added. DNA sequencing for these additional taxa was carried out following the protocol outlined by Winterton et al. (2007). Genbank accession and specimen voucher numbers are presented in Table 1. Sequences were aligned manually, with CAD and COI aligned with reference to translated amino acid sequences using Mesquite 2.75 (Maddison and Maddison 2014). Parsimony analyses were conducted using PAUP* 4.0b10 (Swofford 2003) using a branch and bound search protocol. Bootstrap support values were calculated from 200 heuristic search (TBR) pseudoreplicates of re-sampled data sets, each with 30 random additions (constant characters excluded).

Taxonomy

Eulonchus Gerstaecker, 1856

Figs 1–19

Eulonchus Gerstaecker, 1856: 359

References. Westwood 1876: 517 (generic checklist); Williston 1888: 40 (key), 1896: 71 (key), 1908: 185 (key); Bigot 1890: 315 (key); Coquillett 1910: 541 (type checklist); Cole 1919: 31 (description, key); Sabrosky 1948 (revision, key); Paramonov 1955: 20 (comments); Schlinger 1960 (revision), 1966: 112 (distribution), 1981: 583 (key), 1987 (host records); Coyle and Icenogle 1994 (host records); Poole 1996: 36 (checklist).

Type species. *Eulonchus smaragdinus* Gerstaecker, 1856 by monotypy.

Common name. North American jewelled spider flies.

Diagnosis. *Eulonchus* can be immediately identified from other Panopinae in the New World by the presence of elongate mouthparts, metallic colouration, and pilose eyes. The only other genus in the New World with metallic colouration is *Lasia*, which is distinguished from *Eulonchus* in the eyes being separated below the antennae, and in lacking the palpus and alula. *Eulonchus* is remarkably similar to the endemic New Zealand genus *Apsona* and is distinguished from it by the presence of tibial spines (lacking in *Apsona*), the wing medial veins reaching the wing margin (attenuated in *Apsona*) and the antennae placed in the middle of the frons (higher in *Apsona*).

Description. Body length: 7.2–12.8 mm; wing length: 5.2–12.6 mm. Body colouration metallic green, blue or purple, rarely non-metallic (likely due to poor preservation or collection methods). *Head* hemispherical, width slightly smaller

Table 1. Specimens used for sequencing in this study, with associated Genbank accession numbers. EIS = E.I. Schlinger Collection specimen numbers; NCSU = North Carolina State University collection specimen number.

	Collection #	Genbank Accession No.			Collection Data
		16S	COI	CAD	
<i>Apsona muscaria</i> Westwood	EIS 009956	AY140851	—	AF539866	New Zealand: Otrira Valley; January, 1999; LJ Boutin
<i>Lasia corvina</i> Erichson	EIS 010914	AY140856	DQ631969	AF539865	Chile: Nuble Prov.: Las Trancas; January, 2000; DK Yeates
<i>Eulonchus marginatus</i> Osten Sacken	EIS 020189	KU215393	KU215390	—	USA: California: Mendocino County: Angelo Coast Range Reserve; May, 2005; CJ Borkent
<i>Eulonchus marialiciae</i> Brimley	EIS 009955	AY140853	DQ631979	AF539887	USA: North Carolina: Great Smoky Mountains N.P.; June, 1999; D Dafoe
<i>Eulonchus sapphirinus</i> Osten Sacken	NCSU 99-07-21-48	AY140852	—	AF539877	USA: Washington: South Fork: Wenatchee N.F.; July, 2000; KC Holston
<i>Eulonchus sapphirinus</i> Osten Sacken	CSCA15L303-16V350	—	KU215391	—	USA: California: Calaveras County: Calaveras Big Trees State Park; June, 2010; AR Cline
<i>Eulonchus smaragdinus</i> Gerstaecker	NCSU 99-07-09-76	AY140854	—	AF539867	USA: California: San Diego County: San Diego; June 2000; SL Winterton
<i>Eulonchus smaragdinus</i> Gerstaecker	CSCA15L304-16V351	—	KU215392	—	USA: California: Alameda County: Pleasanton Ridge Regional Park; June, 2012; JM Ayala
<i>Eulonchus tristis</i> Loew	CSCA15L302-16V349	KU215394	—	—	USA: Oregon: Lane County: Trail Creek; July 2000; JK Moulton

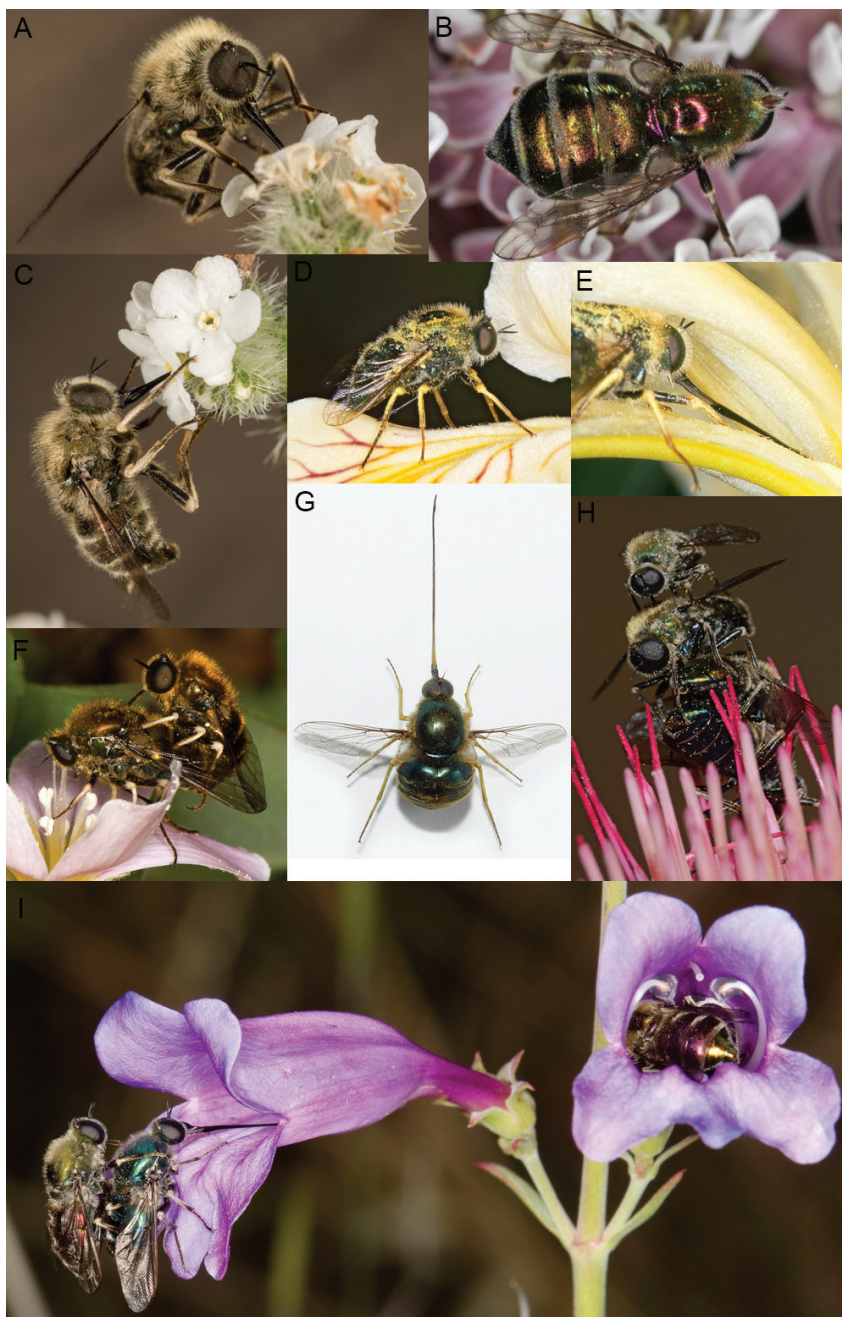


Figure 1. *Eulonchus* spp. on various flowers. **A, C** Male *E. tristis* Loew on *Cryptantha intermedia* **B** Male *E. marginatus* Osten Sacken trapped on flower of *Asclepias* sp **D, E** Male *E. tristis* approaching and feeding from *Iris bracteata* **F** Mated pair of *E. tristis* on *Oxalis oregana* **G** *E. smaragdinus* Gerstaecker **H** Three male *E. marginatus* attempting to mount a single female feeding on thistle **I** Mated pairs of *E. tristis* on *Penstemon heterophyllus*, with one pair resting at length inside the flower. Photo credits: A. Schusteff (**D, E, F, I**); A. Abela (**A, C**); G. McDonald (**B, H**); R. Waayers (**G**).

than thorax width; ocellar tubercle slightly to strongly raised, shape variable and either rounded, bifid or trifid, two or three ocelli present; postocular ridge and occiput rounded; eye densely pilose, setae relatively long (2x pedicel length), posterior margin of eye rounded (*i.e.* not emarginate); antenna located on middle of frons; eye contiguous above and below antennal base; palpus present; proboscis length greater than head length; antennal flagellum elongate, cylindrical to laterally compressed, slightly to strongly tapered apically; in western species male flagellum cylindrical, broader distally, female flagellum more tapered distally; flagellum apex with or without terminal setae; scapes separate (*i.e.* not fused medially). *Thorax* with postpronotal lobes not enlarged or contiguous medially; antenotum narrow; subcutellum barely visible beneath scutellum; legs not greatly elongated; tibial spines present apically; pulvilli present; wing hyaline, markings absent; costal vein circumambient around wing, costal margin straight along entire length, rounded apically; humeral crossvein present; vein R_1 not inflated distally; R_4 and R_5 present as forked petiolate veins; radial veins curved towards wing anterior margin; crossvein 2r-m present between M_1 and R_{4+5} , bisecting cell r_{4+5} ; R_4 with or without spur vein; veins M_1 , M_2 and M_3 present and reaching wing margin; discal cell closed completely; M_4 joining M_3 , cell m_3 petiolate; CuA fused to CuP before wing margin, cell CuA petiolate; wing microtrichia absent; anal lobe well developed; alula weakly developed; abdominal tergites smooth, rounded. *Abdomen* shape conical to turbinate. *Male genitalia* (Figs 17–19). Cerci smooth, densely pilose; dorsal surface of epandrium covered with dense, long pile, posterior margin of epandrium usually concave (straight in *E. marialiciae* and *E. smaragdinus*); gonocoxite variable in shape and size, with distal apex thinned; aedeagus broad at apex (slightly thinned in *E. halli*).

Included species. *Eulonchus halli* Schlinger, 1960: 418; *Eulonchus marginatus* Osten Sacken, 1877: 277; *Eulonchus marialiciae* Brimley, 1925: 77; *Eulonchus sapphirinus* Osten Sacken, 1877: 276; *Eulonchus smaragdinus* Gerstaecker, 1856: 360 (including *E. s. smaragdinus* Gerstaecker, 1856 and *E. s. pilosus* Schlinger, 1960); *Eulonchus tristis* Loew, 1872: 60.

Distribution (Fig. 20). *Eulonchus* is distributed throughout the Nearctic, with *E. marialiciae* found in the eastern state of North Carolina and the remaining species distributed throughout the USA west of the Rocky Mountains, northwards to Canada and south to Baja California, Mexico (Fig. 20). There is significant overlap in the distribution of species of *Eulonchus* with that of the host (or presumed host) spiders in the families Antrodiaetidae (*Aliatypus* sp., *Antrodiaetus riversi* Cambridge, *A. unicolor* Hentz) and Euctenizidae (*Aptostichus stanfordianus* Smith) (Fig. 21) (Schlinger 1987), with the range of *Eulonchus* being clearly inside the range of its hosts. Antrodiaetidae comprise two genera, *Aliatypus* Smith, and *Antrodiaetus* Ausserer, with a disjunct distribution in Japan and North America (Coyle 1971; Hendrixson and Bond 2006). Nearctic antrodiaetids inhabit three primary geographic regions: the deciduous forests of the eastern United States (USA), the forested ‘sky islands’ of the southwestern USA, and various habitats throughout the northwestern USA and adjacent portions of southwestern Canada (Hendrixson and Bond 2006). The euctenizid genus *Aptostichus*

Simon is a genus of trapdoor spiders found predominantly in southern California; *A. stanfordianus* is commonly called the Stanford Hills Trapdoor Spider, and is distributed throughout California (Bond 2012).

Conservation. Most species of *Eulonchus* are relatively widely distributed, and locally abundant, except the sole eastern North American species *E. marialiciae*. This species is known from only a few specimens, all found within a small contiguous area in the Great Smoky Mountains, with collections from Haywood, Jackson, Macon, Transylvania, and Swain counties in North Carolina. Even though the spider host and floral food source of *E. marialiciae* are distributed over much of western North Carolina, southwestern Virginia, and eastern Tennessee, the species is only found in five mountainous counties of western North Carolina, at elevations of 1250m or higher. Considering the apparent limited and very isolated distribution of this species, the conservation status of *E. marialiciae* should be further evaluated. Future studies should focus on identifying potential extralimital populations of this species outside of the presently known distribution, as well as understanding potential biotic (e.g. spider host and plant food source range and distribution) and abiotic (e.g. elevation, climate, vegetation and soil type) factors associated with the apparent limited distribution of this species.

Biology. Adult *Eulonchus* are locally abundant on flowers (Cole 1919; Schlinger 1960) and exhibit behaviours that show constancy to particular plant species (Borkent and Schlinger 2008a, b). Thus, North American jewelled spider flies may form a large and important component of the pollinator fauna for some plant species. *Eulonchus* visit species from more than 30 plant families (see Table 2), and in multiple habitats (Borkent and Schlinger 2008a, b). However, the ability of *Eulonchus* species to serve as pollinators needs to be further studied.

Coyle (1971) reported a large aggregation of *E. marialiciae* forming as he was excavating burrows of *Antrodiaetus unicolor* in North Carolina. A relatively large number of flies (~12 individuals) approached very quickly, hovering close to the ground where the burrows were being excavated, apparently attracted by some chemical released during the process. The author observed multiple adults hovering over and landing near closed burrow entrances. As mentioned above, one of us (C. Borkent) has observed that the newly hatched first instar acrocerid larvae actively search for their hosts, rearing up in search of a spider. Once successful they subsequently penetrate their cuticle and develop as an endoparasitoid (Schlinger 1987). Additionally, Coyle (1971) observed several instances in which the larva, after feeding on the spider in the bottom end of the burrow, climbed up the burrow wall, attached somewhere above the bottom end and completed development within the burrow.

Comments. Species of *Eulonchus* are very similar to species of *Lasia* and *Apsona*, and these three genera, as well as some species of *Panops*, are commonly known as jewelled spider flies due to their metallic body colouration. *Eulonchus* species are commonly called Emeralds or Sapphires, depending on the body colour. Winterton (2012) described the thoracic pile in the Australian genus *Panops* as being reflective, thus brighter when the individual was viewed anteriorly, a characteristic of many Old

Table 2. Specimen label and literature records of plants visited by *Eulonchus* species. The genus has also been recorded visiting flowers of Brassicaceae (*Cakile*), Fabaceae (*Lotus nevadensis*), Hydrophyllaceae (*Nama parryi*), Ranunculaceae (*Delphinium*, *Ranunculus*), and Saxifragaceae (*Lithophagma*).

Plant family	Plant visited	Eulonchus species visiting					
		<i>E. halli</i>	<i>E. marginatus</i>	<i>E. marialiciae</i>	<i>E. sapphirinus</i>	<i>E. smaragdinus</i>	<i>E. tristis</i>
Asteraceae	<i>Cirsium</i>		X			X	X
	<i>Cirsium cymosum</i>						X
	<i>Erigeron</i>				X		
	<i>Wyethia</i>						X
Boraginaceae	<i>Cryptantha intermedia</i>	X					
	<i>Eriodictyon californicum</i>		X			X	X
	<i>Hackelia bella</i>						X
	<i>Hackelia floribunda</i>				X		
	<i>Myosotis</i>				X		
	<i>Myosotis sylvatica</i>				X		
	<i>Phacelia</i>				X		
	<i>Phacelia heterophylla</i>					X	
Caprifoliaceae	<i>Linnaea borealis</i>				X		
Caryophyllaceae	<i>Stellaria crispa</i>				X		X
Convolvulaceae	<i>Convolvulus</i>				X	X	
Crassulaceae	<i>Dudleya cultrata</i>					X	
	<i>Azalea occidentalis</i>						X
	<i>Rhododendron</i>						X
	<i>Rhododendron occidentale</i>				X		
Ericaceae	<i>Vaccinium</i>						X
	<i>Vaccinium ovatum</i>				X		X
Gentianaceae	<i>Fraseria tubulosa</i>						X
Geraniaceae	<i>Geranium robertianum</i>				X		
Grossulariaceae	<i>Ribes cereum</i>						X
	<i>Ribes roezlii</i>						X
Iridaceae	<i>Iris douglasiana</i>		X		X		X
	<i>Iris hartwegii</i>				X		X

Plant family	Plant visited	Eulonchus species visiting				
		<i>E. halli</i>	<i>E. marginatus</i>	<i>E. marialiciae</i>	<i>E. sapphirinus</i>	<i>E. smaragdinus</i>
Iridaceae	<i>Iris macrosiphon</i>					X
	<i>Iris purdyi</i>					X
Lamiaceae	<i>Lepechinia calycina</i>		X			
	<i>Monardella</i>				X	
	<i>Monardella lanceolata</i>					X
	<i>Monardella odoratissima</i>					X
	<i>Sabia carduacea</i>				X	
Liliaceae	<i>Sabia clevelandi</i>					X
	<i>Clintonia uniflora</i>				X	X
Melanthiaceae	<i>Veratrum</i>				X	
	<i>Calyptridium umbellatum</i>				X	
Montiaceae	<i>Lewisia cotyledon</i>				X	
	<i>Montia</i>					
Onagraceae	<i>Clarkia</i>					X
	<i>Clarkia breweri</i>		X			
Orchidaceae	<i>Clarkia concinna</i>		X			X
	<i>Corallorhiza maculata</i>				X	
Oxalidaceae	<i>Oxalis organa</i>					X
	<i>Eschscholzia californica</i>					
Papaveraceae	<i>Mimulus aurantiacus</i>		X			X
	<i>Mimulus glutinosus</i>				X	
Phrymaceae	<i>Mimulus guttatus</i>					
	<i>Mimulus longiflorus</i>		X		X	
Plantaginaceae	<i>Penstemon</i>		X			X
	<i>Penstemon cardwelli</i>				X	
	<i>Penstemon heterophyllus</i>		X			X
	<i>Veronica americana</i>					X
Polemoniaceae	<i>Gilia capitata</i>					X
	<i>Gilia splendens</i>					X
	<i>Leptosiphon</i>					X

Plant family	Plant visited	Eulonchus species visiting				
		<i>E. halli</i>	<i>E. marginatus</i>	<i>E. marialiciae</i>	<i>E. sapphirinus</i>	<i>E. smaragdinus</i>
Polemoniaceae	<i>Leptostaphyon bicolor</i>					X
	<i>Linanthus</i>					
	<i>Linanthus androsaceus</i>					X
	<i>Microsteris gracilis</i>				X	
	<i>Navaretia capitatus</i>		X			
Polygonaceae	<i>Eriogonum</i>					
Primulaceae	<i>Trientalis borealis</i>				X	
Rhamnaceae	<i>Ceanothus cordulatus</i>					
	<i>Ceanothus integerrimus</i>				X	
	<i>Chamaebatia foliolosa</i>				X	
	<i>Fragaria vesca</i>				X	
	<i>Prunus emarginata</i>				X	
Rosaceae	<i>Rubus</i>			X		
	<i>Rubus canadensis</i>			X		
	<i>Rubus parviflorus</i>					
	<i>Rubus ursinus</i>				X	
	<i>Salix</i>					
Salicaceae	<i>Brodiaea</i>					X
Themidaceae	<i>Brodiaea bridgesii</i>					
	<i>Brodiaea congesta</i>		X			
	<i>Brodiaea elegans</i>		X			
	<i>Brodiaea lutea</i>					X
	<i>Brodiaea pulchella</i>					
Verbenaceae	<i>Dichelostemma multiflora</i>					
	<i>Triteleia ixioides</i>					
	<i>Verbena</i>		X			

World panopine species. This character is absent in *Eulonchus* and most New World panopine genera, with the thoracic pile being of similar brightness regardless of which angle it is viewed. Phylogenetic relationships among Panopinae genera are still poorly known. Based on DNA sequence data, Winterton et al. (2007) found *Eulonchus* to be placed between *Lasia* and more derived genera such as *Ocnaea*, *Archipialea*, and *Arrhynchus*.

Phylogenetic relationships (Fig. 22). The phylogeny performed in this study is based on DNA sequence data and includes five of the six species of *Eulonchus*. The parsimony analysis resulted in a single most parsimonious tree with length = 904, consistency index (CI) = 0.92, and retention index (RI) = 0.62. The eastern species *Eulonchus marialiciae* (Fig. 6) and the northwestern *E. sapphirinus* (Figs 8–9) were recovered as sister taxa in a clade that is sister to the remaining species of the genus. Even though the support for the branch was low (Fig. 22) we are confident in this relationship as *E. marialiciae* and *E. sapphirinus* share multiple characters, such as the ovate epandrium (which is thinner at the apex; Fig. 18C–D), the gonocoxite taller than wide (Fig. 19C–D), and the aedeagus broad at the apex and not heavily laterally sclerotized (Fig. 17C–D). These two species are typically bright metallic green or blue with yellow legs. This feature is shared with some individuals of the highly variable *E. smaragdinus* from southern California, USA and Baja California, Mexico. *Eulonchus smaragdinus* (Figs 10–11) was recovered as an intermediate species that subtends the clade comprising the more northern species, *E. tristis* and *E. marginatus*. *Eulonchus halli* was not included in the phylogenetic analysis due to lack of fresh material for DNA extraction. However, placement of the species in the *Eulonchus* tree was postulated based on morphology (see dashed lines on Fig. 20). We hypothesize that *E. halli* is more closely related to *E. smaragdinus* based on their bifid ocellar tubercles, epandrium somewhat rectangle shaped and wide at the apex, gonocoxite deeply emarginate along anterior margin, fenestrae lacking (Fig. 19A, E) and aedeagus thin at the apex (Fig. 17A, E). The sister-grouping was already suggested by Schlinger (1960). *Eulonchus tristis* (Figs 13–14) and *E. marginatus* (Figs 3–4) have dark brown coloured legs and a thorax and abdomen with dark metallic to brownish-black colouration. *Eulonchus tristis* is also a highly morphologically variable species with body colour ranging from metallic light blue (Fig. 14) to dark brown (Fig. 13). These two species share multiple genitalia characters such as a somewhat round epandrium, gonocoxite with anterior margin almost straight, with large fenestrae, and aedeagus heavily sclerotized laterally.

Key to species of *Eulonchus*

- 1 Femora and tibiae completely bright yellow.....2
- Femora completely dark brown, or light to dark brown with dark yellow or cream portion distally; tibiae completely dark brown, or brown with dark yellow to cream basally4

- 2 Flagellum laterally compressed, thicker than scape and pedicel, pendulous, and ~twice length of head; proboscis length rarely extending beyond midpoint of abdomen, typically extending to end of thorax (eastern North America)
..... ***E. marialiciae* Brimley**
- Flagellum not laterally compressed, basal portion ~equal to thickness of scape and pedicel, erect, and equal to length of head; proboscis extending beyond midpoint of abdomen, often longer than body (western North America)....**3**
- 3 Proboscis approximately equal to body length, straight; ocellar tubercle typically taller than wide and apex irregularly trifid; median ocellus often weakly developed..... ***E. sapphirinus* Osten Sacken**
- Proboscis distinctly longer than body length, curved at tip; ocellar tubercle wider than tall and apex weakly bifid; median ocellus clearly defined.....
..... ***E. smaragdinus* Gerstaecker**
- 4 Ocellar tubercle bifid in anterior view; flagellum as long as the head.....
..... ***E. halli* Schlinger**
- Ocellar tubercle trifid; flagellum half as long as the head.....**5**
- 5 Margin of calypter light yellow to light brown; femur and tibia light to dark brown with variable amounts of yellow or ivory patterning; pile on the abdomen yellow to light yellow (highly variable species); aedeagus in lateral view with a single rounded point dorsally just before opening of the aedeagus (Fig. 17F)..... ***E. tristis* Loew**
- Margin of calypter dark brown with brown bleeding into calypter membrane; femur completely dark brown, tibia usually dark brown, occasionally with cream yellow on dorsal surface basally (joint between femur and tibia always yellow); pile on abdomen white; aedeagus in lateral view with two rounded points prior to the opening of the aedeagus (Fig. 17B) ***E. marginatus* Osten Sacken**

***Eulonchus halli* Schlinger, 1960**

Figs 2, 16B, 17A, 18A, 19A

Eulonchus halli Schlinger, 1960: 418

References. Arnaud 1979: 203 (holotype depository); Schlinger 1981: 576 (figs); Poole 1996: 36 (checklist).

Common name. Hall's Sapphire.

Diagnosis. Proboscis curved and extending beyond abdomen apex (but shorter than wing length), ocellar tubercle bifurcate; calypter margin pale; legs dark brown-black; abdomen dark brown with reddish metallic hue; extensive white pile on thorax and as bands on abdomen.

Redescription. Body length: 9.8–12.0 mm, Wing length 8.0–10.6 mm. *Head.* Flagellum dark brown, scape and pedicel brown; male flagellum cylindrical, shorter than head height; clypeus elongate, extending beyond oral cavity, shape rounded

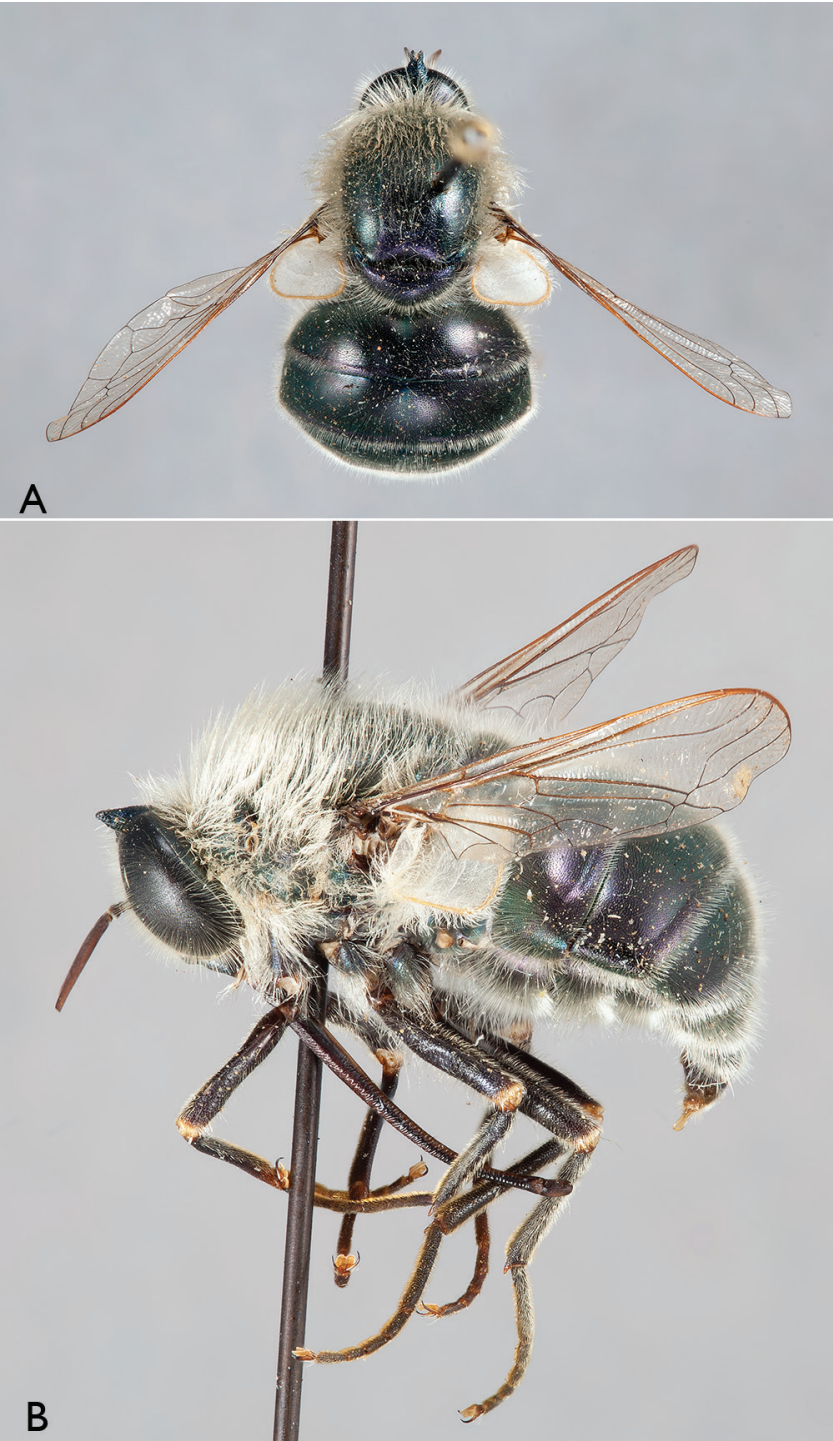


Figure 2. *Eulonchus halli* Schlinger, male (EIS 003122). **A** dorsal view **B** lateral view. Body length: 11.4 mm.

with raised ridge dorsally, surface glossy black-brown with sparse pubescence; labial palp brown, extending anteriorly beyond proboscis at point of attachment; margin of oral cavity (parafacial) finely pubescent, lacking pile; proboscis length extending to middle of abdomen; ocellar tubercle bifurcate, apices narrowly digitate and sub-parallel, tubercle height taller than width, median ocellus greatly reduced; occiput metallic blue or metallic purple, occipital pile densely white. *Thorax*. Metallic green, metallic blue or metallic purple in colour, setal pile white; coxae black with metallic blue sheen; femora dark brown, apices white; tibia brown; tarsi brown; calypter margin yellow or light brown, membrane translucent; haltere entirely dark brown. *Abdomen*. Metallic green, metallic blue violet or black with metallic green sheen, vestiture white, dominant setae erect, other pile posteriorly directed, marginal band of denser setae on T3–4. *Male genitalia* (Figs 17A, 18A, 19A). Epandrium rectangular, wide at the apex, with posterior margin concave; gonocoxite deeply emarginate along anterior margin, fenestrae lacking; aedeagus thinned at the apex, only slightly sclerotized.

Type material examined. **Holotype** male, CAS, “Riverside/ Cal. Mar 7, 34” [white]; “Timberlake/ Coll.” [white]; “*on Cryptanthal intermedia*” [white]; “HOLO-TYPE/ *Eulonchus halli* ♂ Schlinger” [orange]; “Genitalia 51-3-id/ Dissection No./ by E.I. Schlinger” [white]; “California Academy/ of Sciences/ Type No. 6392” [white]; “IMAGE” [green]; “CAS/ Dec-07” [green]; specimen condition: good, proboscis, right flagellum and right front leg broken off and glued to a paper triangle on pin with specimen. Body length: 10.2 mm, Wing length: 9.2 mm.

Other material examined. Listed in Table 3 (Suppl. material 1).

Distribution (Fig. 20). Nearctic: Southern California (USA) to Baja California (Mexico).

Ecology. Schlinger (1960) notes that this species has a relatively short adult flight period (*ca.* six weeks) during spring and has a feeding preference on *Cryptantha intermedia* flowers (Table 2).

Biology. The larval host for this species is unknown.

Comments. *Eulonchus halli* is a distinctive species that can be distinguished by the dark leg and body colouration, erect white thoracic and abdominal pile, raised bifurcate ocellar tubercle, and a curved proboscis that is shorter than the body length.

Eulonchus marginatus Osten Sacken, 1877

Figs 3–5, 16A, 17B, 18B, 19B

Eulonchus marginatus Osten Sacken, 1877: 277

References. Osten Sacken 1878: 99 (catalogue); Aldrich 1905: 221 (catalogue); Kertész 1909: 12 (catalogue); Cole 1919: 38 (key notes, figs), 1923: 46 (California); Sabrosky 1948: 388 (key); Cole 1969: 221 (notes); Poole 1996: 36 (checklist).

Common name. Sombre Sapphire or Emerald.

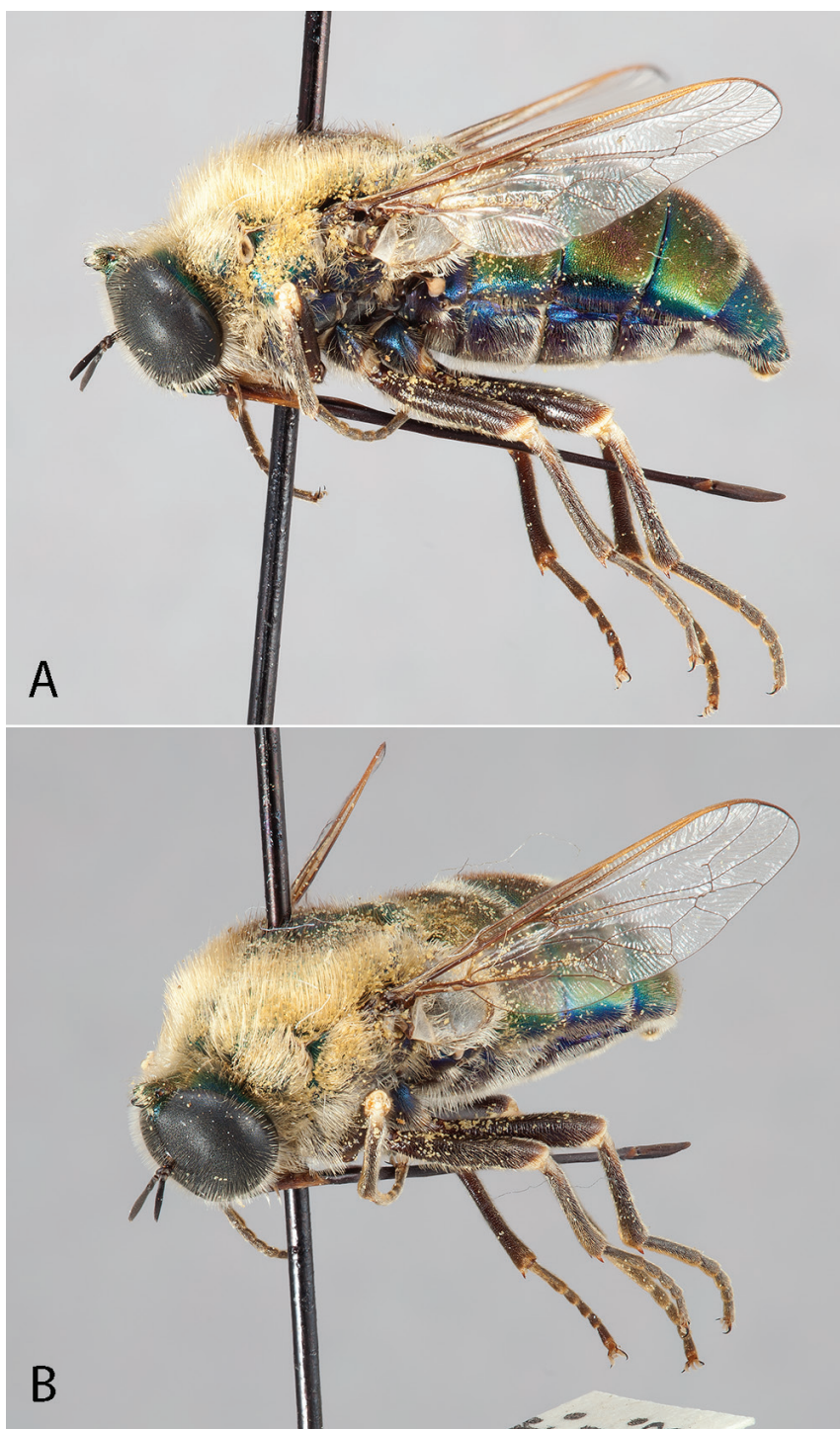


Figure 3. *Eulonchus marginatus* Osten Sacken, male (EIS 000290). **A** lateral view **B** oblique view. Body length: 12.2 mm.



Figure 4. *Eulonchus marginatus* Osten Sacken, female (EIS 000370). **A** lateral view **B** oblique view. Body length: 8.7 mm.



Figure 5. *Eulonchus marginatus* Osten Sacken, holotype, male, oblique view. Body length: 8.9 mm.

Diagnosis. Proboscis straight, approximately reaching apex of abdomen; ocellar tubercle trifurcate; legs dark brown (pale ‘knee’ joint); calypter margin black or brown.

Redescription. Body length: 7.2–11.4 mm, wing length: 5.2–9.5 mm. *Head.* Flagellum dark brown; scape and pedicel brown, male flagellum cylindrical, shorter than head height; clypeus elongate, extending beyond oral cavity, shape rounded with flat area dorsally, clypeus black-brown, glossy with sparse pubescence; labial palp brown, extending anteriorly beyond proboscis at point of attachment; margin of oral cavity (parafacial) pilose, admixed with short pubescence; ocellar tubercle trifurcate, processes narrow (anteromedial process taller), height taller than width; median ocellus greatly reduced or absent; occiput metallic green-blue, metallic blue or metallic purple, pile densely white or yellow. *Thorax.* Metallic green, blue or purple, setal pile erect, white or yellow; coxae black with metallic blue sheen; femora dark brown, apices white; tibiae brown (whitish basally on dorsal surface); tarsi brown; calypter margin light to dark brown, membrane translucent, with suffused brown marginally; haltere stem dark brown, knob lighter brown. *Abdomen.* Metallic olive green, green or blue-violet, vestiture white or yellow, dominant setae erect, pile posteriorly directed, marginal band

of laterally directed pile on T2–4. *Male genitalia*. Epandrium round, with posterior margin concave; gonocoxite with anterior margin almost straight, with large fenestrae; aedeagus heavily sclerotized laterally, with a secondary dorsal point just prior to the opening of the aedeagus.

Type material examined. **Holotype** male, MCZ, “Napa Col/ California.” [white]; “*O. Sacken/ West Dipt.*” [white]; “Type/ 1078” [red and white]; “*Eulonchus/ marginatus/ O.S.*” [white]; “Eug-Dec 2006/ MCZ Image/ Database” [white]; “MCZ-ENT/ 00001078” [white]; “HOLOTYPE ♂/ *Eulonchus marginatus/ Osten Sacken/ Det. C.J. Borkent 2015*” [red]; specimen condition: excellent, no parts missing. Body length: 8.9 mm, Wing length: 7.0 mm.

Other material examined. Listed in Table 3 (Suppl. material 1).

Distribution (Fig. 20). Nearctic: Northern California (USA).

Ecology. *Eulonchus marginatus* has been recorded visiting the flowers of 10 different plant families and 14 different species (Table 2).

Biology. Host unknown.

Comments. *Eulonchus marginatus* is closely related to *E. tristis*, sharing features such as extensive white thoracic pile and dark colouration on the legs. *Eulonchus marginatus* is easily distinguished from other species in the genus by the leg colour, trifurcate ocellar tubercle and dark margin of the calypter. This species displays considerable variation in body colour, ranging from metallic green, blue to purple.

Eulonchus marialiciae Brimley, 1925

Figs 6–7, 16E, 17C, 18C, 19C

Eulonchus marialiciae Brimley, 1925: 77

References. Brimley 1938: 335 (North Carolina); Sabrosky 1948: 388 (key ref.); Schlinger 1965: 404 (catalogue); Coyle 1971: 281 (host *Antrodiaetus unicolor*, distr.); Poole 1996: 36 (checklist); Adler et al. 1997: 190 (biology, abundance).

Common name. Mary-Alice’s Emerald.

Diagnosis. Antennal flagellum elongate, basally broad and flattened laterally; proboscis straight, relatively short (~half body length); ocellar tubercle trifurcate; legs yellow; calypter margin brown; body colour metallic green.

Redescription. Body length: 9.9–12.0 mm, Wing length: 9.1–10.2 mm. *Head*. Flagellum dark brown, male flagellum laterally compressed and variable in amount of distal tapering, longer than head height (pendulous in pinned specimen); scape and pedicel light brown to yellow; clypeus elongate, extending beyond oral cavity, rounded with raised ridge dorsally, surface black-brown, glossy with sparse pubescence; labial palp brown or yellow, length not extending beyond proboscis at point of attachment; margin of oral cavity (parafacial) glabrous or pilose, admixed with pubescence; proboscis straight, shorter than thorax or reaching middle of abdomen; ocellar tubercle trifurcate with processes relatively short and subequal (posterolat-

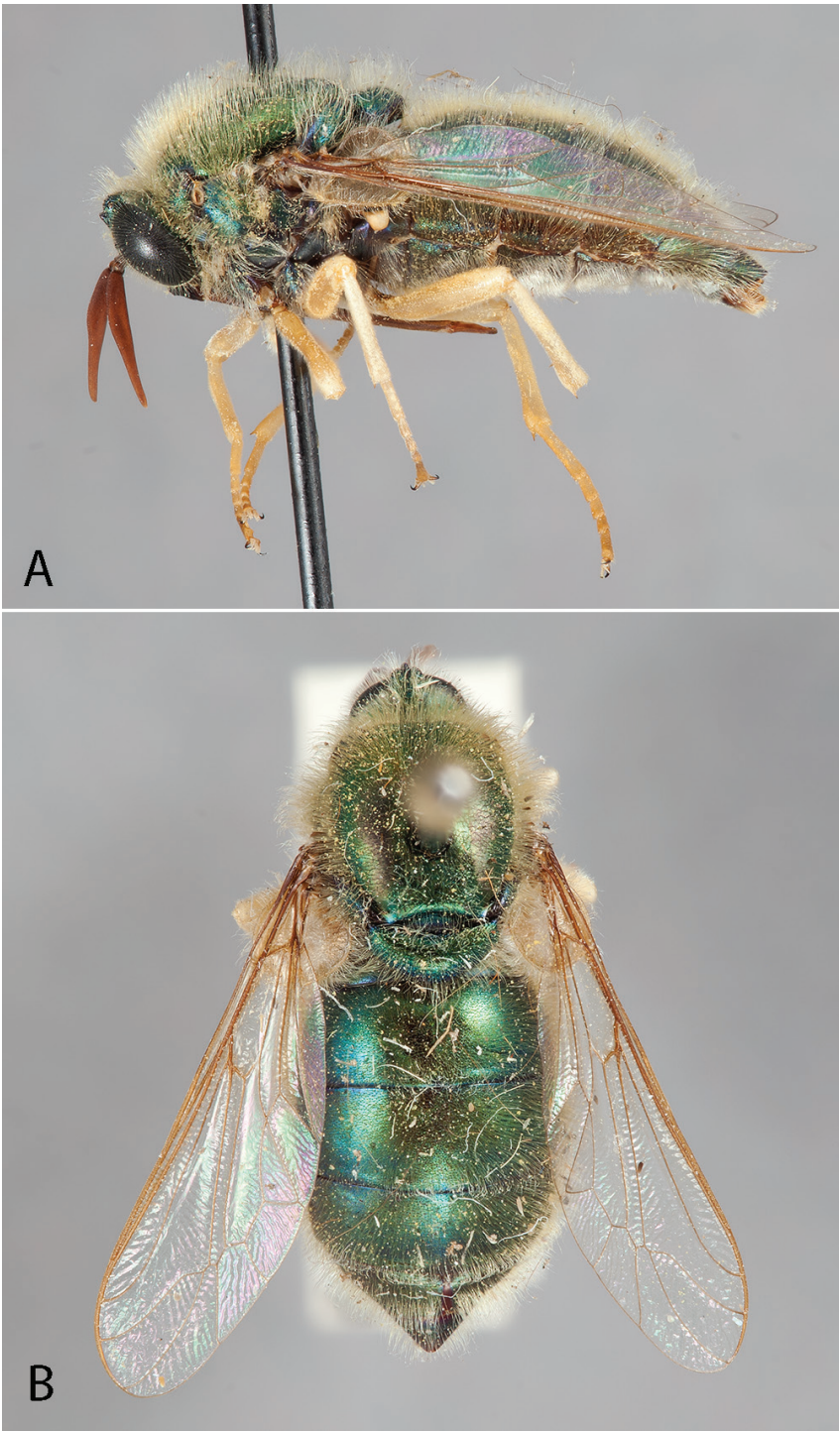


Figure 6. *Eulonchus marialiciae* Brimley, male (EIS 014839). **A** lateral view **B** dorsal view. Body length: 11.0 mm.



Figure 7. *Eulonchus marialiciae* Brimley, holotype, male. Body length: ~12.0 mm.

eral processes often rounded), tubercle height shorter than width; median ocellus present; occiput metallic green-blue or blue, pile densely white or yellow. *Thorax*. Metallic green, blue or purple, setal pile yellow; coxae black with metallic blue and/or green sheen; femora yellow; tibiae dark yellow; tarsi dark yellow; calypter margin brown, membrane translucent, with suffused brown marginally; haltere stem dark brown, knob lighter brown. *Abdomen*. Metallic green or blue-violet, vestiture yellow, dominant setae erect. *Male genitalia* (Figs 17C, 18C, 19C). Epandrium ovate, thinned at the apex, with posterior margin straight; gonocoxite taller than wide, with broad fenestrae; aedeagus broad at the apex, bilobate in posterior view, not heavily sclerotized laterally.

Type material examined. **Holotype** male, USNM, “Andrews Bald/ IVIT.5 700ft/ Swain Co N.C./ VI.26.23” [white]; “JC Crawford/ Coll” [white]; “Type No./ 55797/ U.S.N.M.” [red]; “*Eulonchus/ marialiciae/ TYPE Brimley*” [pink]; specimen condition: poor, all legs missing except left front and right mid leg, right wing missing, abdomen and a leg glued to a paper triangle on pin. Body length: ~12.0, (this is an approximation due to the disarticulation of the specimen), wing length: 10.2 mm.

Other material examined. Listed in Table 3 (Suppl. material 1).

Distribution (Fig. 20). Nearctic: North Carolina: Great Smoky Mountains: Macon, Swain and Hayward Counties (USA).

Ecology. Flowers visited: Rosaceae: *Rubus canadensis* L., *Rubus* sp. (Table 2).

Biology. Host: *Antrodiaetus unicolor* (Antrodiaetidae) (Schlinger 1987).

Comments. *Eulonchus marialiciae* is the only disjunct species in the genus, with a relatively small distribution in the Great Smoky Mountains of North Carolina (USA);

all other species are found in contiguous distributions in the far western part of the continent. This species is the sister species to the north-western *E. sapphirinus* and both have characteristic bright green metallic colouration, short proboscis, yellow legs and similarities in the male genitalia shape. *Eulonchus marialiciae* has the shortest proboscis of any species in the genus, as well as a much more elongated and laterally compressed flagellum.

***Eulonchus sapphirinus* Osten Sacken, 1877**

Figs 8–9, 16D, 17D, 18D, 19D

Eulonchus sapphirinus Osten Sacken, 1877: 276

References. Osten Sacken 1878: 99 (catalogue); Melander 1902: 181 (California); Aldrich 1905: 221 (catalogue); Kertész 1909: 12 (catalogue); Woodworth 1913: 152 (California); Cole 1919: 36 (key, notes, figs, California, Utah, Oregon), 1927: 422 (male genitalia); Cole and Lovett 1921: 238 (Oregon); Brunetti 1926: 582 (Washington); Essig 1926: 559 (notes, California and Oregon); Knowlton et al. 1939: 6 (Utah); Sabrosky 1948: 389 (key, notes); Schlinger 1965: 404 (catalogue); Cole 1969: 221 (notes); Poole 1996: 36 (checklist).

Common name. Northern Sapphire or Emerald.

Diagnosis. Antennal flagellum relatively short, cylindrical or tapered; proboscis straight, shorter than length of body; ocellar tubercle trifurcate; legs yellow; calypter margin pale; body colour metallic green, blue or purple.

Redescription. Body length: 8.3–11.9 mm, Wing length: 7.1–12.0 mm. *Head.* Flagellum red-brown or dark brown, male flagellum cylindrical, shorter than head height; scape and pedicel brown; clypeus elongate, extending beyond oral cavity, rounded with flat area dorsally, surface glossy, glabrous, black-brown; labial palp brown, length extending anteriorly beyond proboscis at point of attachment; margin of oral cavity (parafacial) pilose, proboscis length extending to middle of abdomen or equal to abdomen length; ocellar tubercle trifurcate, processes relatively short, subequal (posteromedial processes rounded), height equal to width; median ocellus present, greatly reduced or absent; occiput metallic green-blue, blue or purple, pile densely white or yellow. *Thorax.* Metallic green, blue or purple, setal pile white or yellow; coxae brown or black with metallic blue (and purple) sheen; femora yellow; tibiae dark yellow; tarsi dark yellow (distal tarsomeres often darker); calypter margin yellow to light brown, membrane transparent or translucent; haltere entirely light brown to yellow. *Abdomen.* Colour highly variable, metallic olive green, bright green or blue violet, vestiture white or yellow, dominant setae appressed or erect, pile posteriorly directed, marginal band of dense thicker setae on T3–4, or laterally directed pile on T2–4. *Male genitalia* (Figs 17D, 18D, 19D). Epandrium ovate, thinned at the apex, with posterior margin slightly concave; gonocoxite taller than wide, with

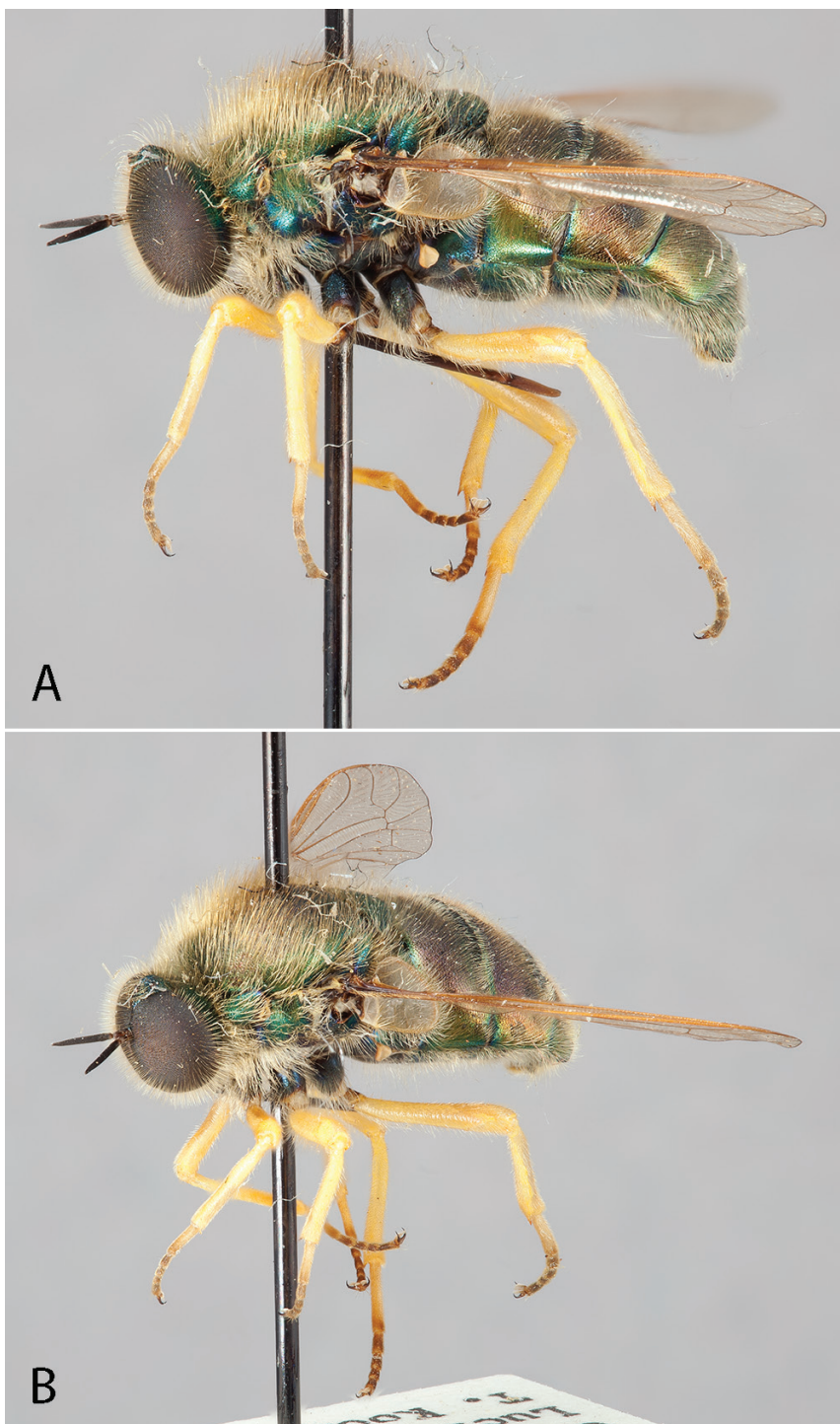


Figure 8. *Eulonchus sapphirinus* Osten Sacken, male (EIS 013101). **A** lateral view **B** oblique view. Body length: 10.2 mm.



Figure 9. *Eulonchus sapphirinus* Osten Sacken. Paralectotype male. Body length: 9.0 mm.

broad fenestrae; aedeagus broad at the apex, bilobate in posterior view, not heavily sclerotized laterally.

Type material examined. **Lectotype** male (designated here), MCZ, “Webber Lake, Cal/ July 23. O Sacken” [white]; “West. Dipt./ O. Sacken.” [white]; “TYPE/ 4/ 1076” [red and white]; “MC-ENT/ 00303277” [white]; “LECTOTYPE ♂/ *Eulonchus sapphirinus*/ Osten Sacken/ Des. C.J. Borkent 2015” [red]; specimen condition: excellent, no parts missing. Body length: 9.2 mm, wing length: 8.7 mm. **Paralectotype** female, MCZ, “Webber Lake, Cal./ July 23. O. Sack.” [white]; “O. Sacken./ West. Dipt.” [white]; “Type/ 5/ 1076” [red and white]; “MCZ-ENT/ 00303278” [white]; “PARALECTOTYPE ♀/ *Eulonchus sapphirinus*/ Osten Sacken/ Det. C.J. Borkent 2015” [yellow]; specimen condition: excellent, no parts missing. **Paralectotype** male, MCZ, “Webber Lake, Cal. July 26./ O. Sacken” [white]; “O. Sacken./ West. Dipt.” [white]; “Type/ 3/ 1076” [red and white]; “MCZ-ENT/ 00303276” [white]; “PARALECTOTYPE ♂/ *Eulonchus sapphirinus*/ Osten Sacken/ Det. C.J. Borkent 2015” [yellow]; specimen condition: very good, tarsi of both mid legs missing, genetic anomaly with only one antenna present. **Paralectotype** male, **paralectotype** female [mating pair on same pin], MCZ, “Webber Lake, Cal./ July 26 O. Sacken” [white]; “O. Sacken./ West. Dipt.” [white]; “Aug-Dec

2006/ MCZ Image/ Database” [white]; “*Eulonchus sapphirinus* O.S.” [white]; “MCZ-ENT/ 00001076” [white]; “PARALECTOTYPE ♂/ *Eulonchus sapphirinus* Osten Sacken/ Det. C.J. Borkent 2015” [yellow]; specimen condition: male, very good, tarsi of hind legs missing, left flagellum missing; female, excellent, no parts missing.

Other material examined. Listed in Table 3 (Suppl. material 1).

Distribution (Fig. 20). Nearctic: California, Idaho, Nevada, Oregon, Utah, Washington (USA); British Columbia (Canada).

Ecology. *Eulonchus sapphirinus* has been recorded visiting the flowers of 19 different plant families and 30 different species (Table 2). *Eulonchus sapphirinus* adults have been observed exhibiting strong fidelity to a single flowering plant species, suggesting their role as important pollinators (Borkent and Schlinger 2008a).

Biology. Host unknown.

Comments. *Eulonchus sapphirinus* is the sister species to the eastern *E. marialiciae* as both have characteristic bright green metallic colouration, short proboscis, yellow legs and similar shaped male genitalia. The shape of the antennal flagellum and colour of calypter separate the two species.

Eulonchus smaragdinus Gerstaecker, 1856

Figs 10–12, 16F, 17E, 18E, 19E

Eulonchus smaragdinus Gerstaecker, 1856: 360.

Eulonchus smaragdinus pilosus Schlinger, 1960: 418, **syn. n.**

References. Osten Sacken 1877: 276 (California, notes), 1878: 99 (catalogue); Melander 1902: 181 (California); Aldrich 1905: 221 (catalogue); Kertész 1909: 12 (catalogue); Verrall 1909a: 451 (fig wing); Cole 1919: 34 (key, notes, figs, California); Essig 1926: 559 (descr. note, California); Brunetti 1926: 583 (Uruguay [misidentification]); Sabrosky 1948: 388 (key ref., notes); Schlinger 1953: 220 (LT designation), 1960: 417 (description, distr., figs), 1965: 404 (catalogue), 1987: 320 (host *Aptostichus standfordianus*); Paramonov 1955: 20 (comparison with *Apsona muscaria*); Cole 1969: 221 (notes); Poole 1996: 36 (checklist).

Common name. Southern Emerald or Sapphire.

Diagnosis. Proboscis curved and longer than abdomen apex (as long or longer than wing length); ocellar tubercle nearly flat, weakly bifurcated; legs bright yellow; body colour metallic green, blue or purple; thorax covered in yellowish pile.

Redescription. Body length: 8.3–12.9 mm, Wing length: 6.9–12.6 mm. *Head.* Flagellum red-brown or dark brown, male flagellum cylindrical, shorter than head height; scape and pedicel brown; clypeus elongate, length equal to oral cavity; rounded with flat area dorsally, black-brown, surface glossy, glabrous; labial palp brown or yellow, extending anteriorly beyond proboscis at point of attachment; margin of oral cavity (parafacial) glabrous, admixed with pubescence; proboscis length extending beyond abdomen; ocellar tubercle bifurcate (processes short and rounded), tubercle height

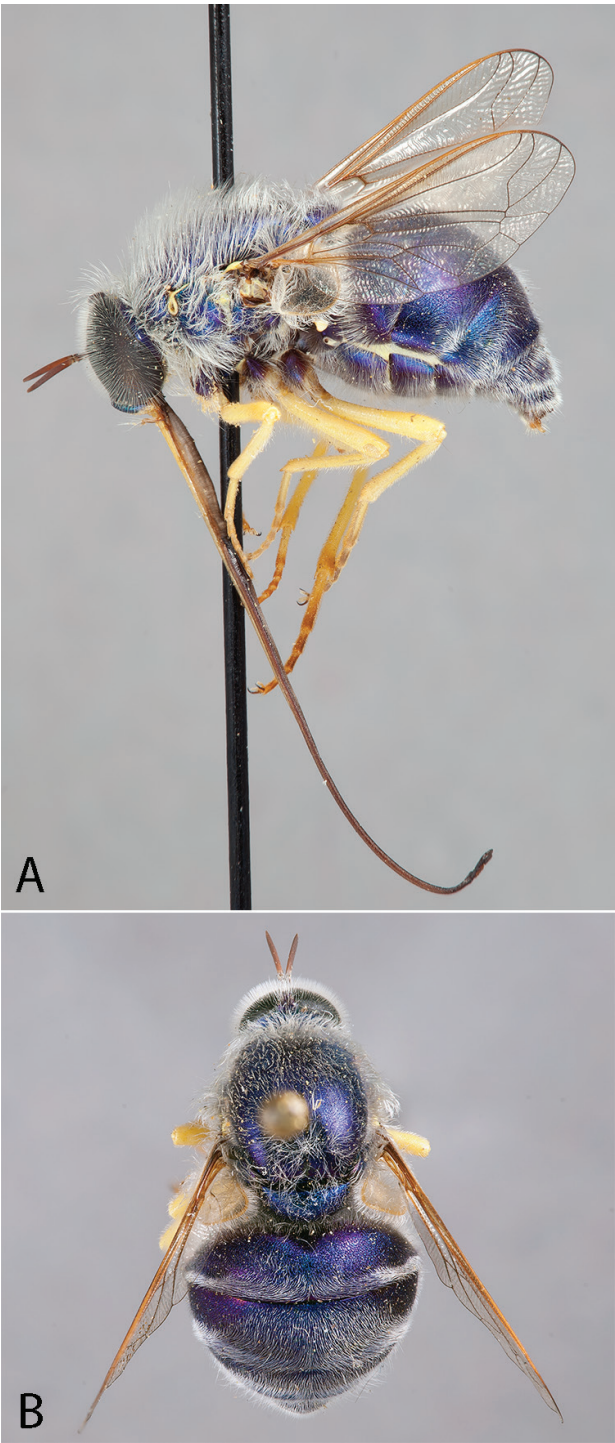


Figure 10. *Eulonchus smaragdinus* Gerstaecker, male (EIS 000465). **A** lateral view **B** dorsal view. Body length: 11.4 mm.

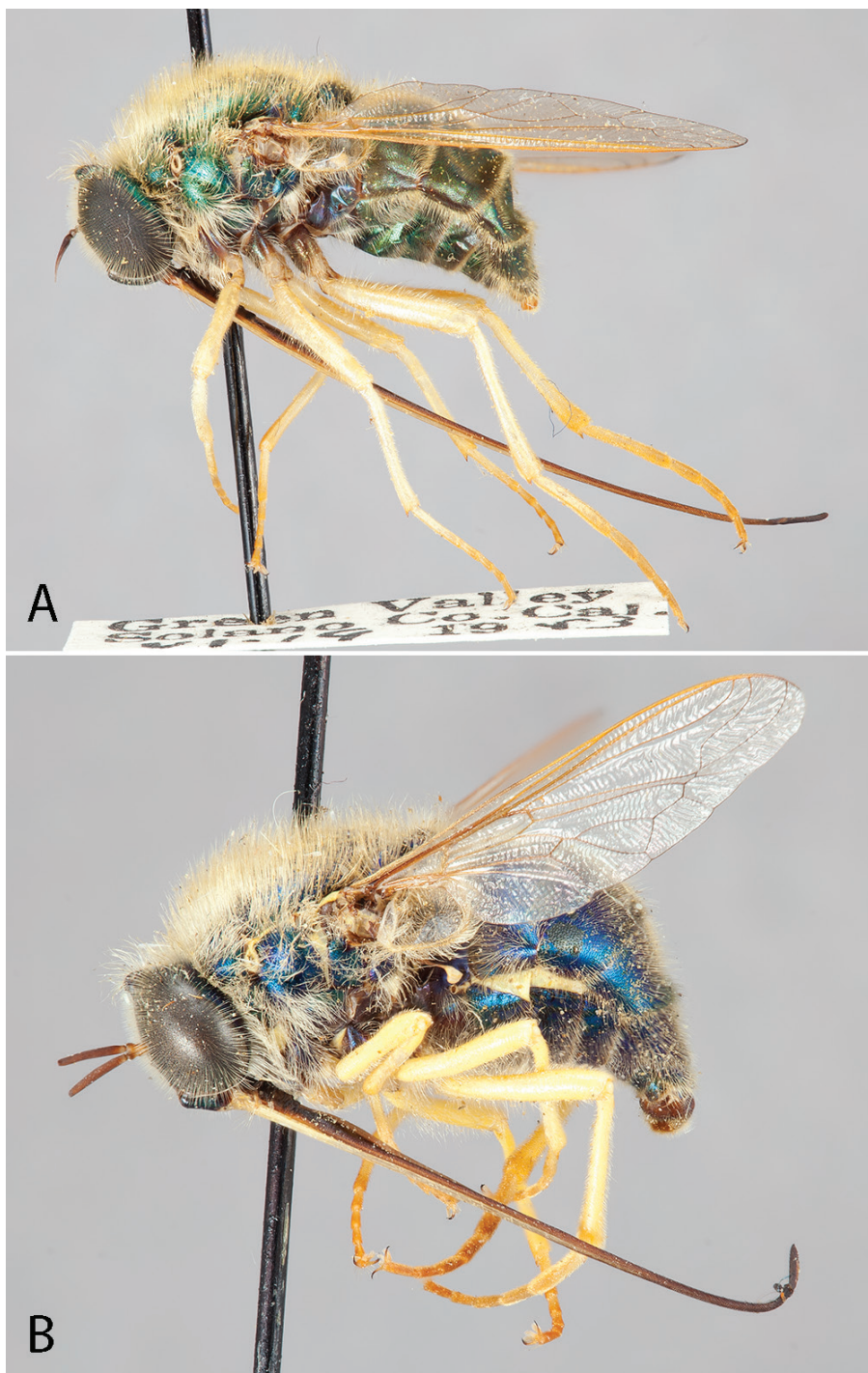


Figure 11. *Eulonchus smaragdinus* Gerstaecker. **A** Female (EIS 000191), lateral view. Body length: 11.1 mm
B Male (EIS 000027), lateral view. Body length: 10.1 mm.



Figure 12. *Eulonchus smaragdinus* Gerstaecker (*E.s. pilosus* Schlinger holotype), dorsal view. Body length: 11.9 mm.

shorter than width; median ocellus present or greatly reduced; occiput metallic green-blue or blue, pile densely white or yellow. *Thorax*. Metallic green, blue or purple, pile white or yellow; coxae brown or black with metallic blue (and green) sheen; femora yellow; tibiae dark yellow; tarsi dark yellow (distal tarsomeres often darker); calypter margin yellow or light brown; calypter membrane transparent; haltere entirely light brown to yellow. *Abdomen*. Metallic green or blue-violet, vestiture white or yellow, dominant setae appressed or erect, pile posteriorly directed, marginal band of laterally directed pile on T2–4. *Male genitalia* (Figs 17A, 18A, 19A). Epandrium rectangular, wide at the apex, with posterior margin slightly concave; gonocoxite deeply emarginate along anterior margin, fenestrae lacking; aedeagus thinned at the apex, only slightly sclerotized.

Type material examined. **Lectotype** male, ZMB, “*Californien* von Müller” [green]; “1251” [white]; “Type” [orange]; “*smaragdinus* Gerst.*” [green]; “*Californ. v. Müller*” [green]; “**LECTOTYPE** *Eulonchus smaragdinus* Gerst.” Designation of.

E.I. Schlinger-1952 [blue]; specimen condition: very good, tarsi of both mid legs missing. Body length: 10.0 mm, wing length: 8.6 mm. **Paralectotype** female, ZMB, “*Californien/ von Müller S.*” [green]; “Type” [orange]; “PARALECTOTYPE ♀/ *Eulonchus smaragdinus/ Gerstaecker/ Det. C.J. Borkent 2015*” [yellow]; specimen condition: fair, head crushed, antennae broken off, tarsi of left mid leg and hind right leg missing.

Eulonchus smaragdinus pilosus Schlinger, 1960: 418; **Holotype** male, USNM, “S Bernadino/ Co. CAL.” [white]; “Coquillet/ Collector” [white]; “Insect Book./ Pl. 18 fig 23” [white]; “HOLOTYPE/ *Eulonchus/ smaragdinus/ pilosus/ ♂ Schlinger*” [orange]; specimen condition: excellent, tarsi of left hind leg missing. Body length: 10.1 mm, Wing length: 9.0 mm.

Other material examined. Listed in Table 3 (Suppl. material 1).

Distribution (Fig. 20). Nearctic: northern California (USA) to Baja California (Mexico). Erroneous record of Uruguay, see discussion by Schlinger 1960.

Ecology. *Eulonchus smaragdinus* has been recorded visiting the flowers of 11 different plant families and 18 different species (Table 2, Borkent and Schlinger 2008b).

Biology. Host: *Aptostichus standfordianus* (Euctenizidae) (Schlinger 1987).

Comments. *Eulonchus smaragdinus* is highly variable in size and colour, and is superficially morphologically similar to *E. sapphirinus*, most notably in the bright yellow legs. However, it can be easily distinguished from the latter in having a proboscis that is curved (rather than straight) that extends beyond the abdomen, and is often longer than body. Male genital characters otherwise indicate a closer relationship to *E. halli*, as suggested by Schlinger (1960) (see Fig. 22). Schlinger (1960) erected the subspecies *E. s. pilosus* due to the lighter coloured pile of the individuals he collected. In our study we found that these lighter individuals were just one end of the colouration spectrum (golden pile changing progressively to white pile when moving north to south) of *E. smaragdinus*, and therefore do not recognize it as a distinct subspecies.

Eulonchus tristis Loew, 1872

Figs 13–15, 16C, 17F, 18F, 19F

Eulonchus tristis Loew, 1872: 60.

References. Osten Sacken 1877: 276 (California), 1878: 99 (catalogue); Melander 1902: 181 (California, Idaho, notes); Howard 1902: pl. 18, fig. 23 (habitus); Aldrich 1905: 221 (catalogue); Kertész 1909: 12 (catalogue); Woodworth 1913: 152 (California); Peterson 1916: 181, Figs 284a, 364a, 425a, 425b and 543 (head capsule, mouthparts); Cole 1919: 34, pl. 5, fig. 18 (habitus) (key, notes, Idaho, British Columbia, Oregon, California), 1927: 422, fig. 86 (male genitalia); Cole and Lovett 1921: 239 (Oregon); Essig 1926: 559 (descr. note, Idaho, Oregon, California); Brunetti 1926:

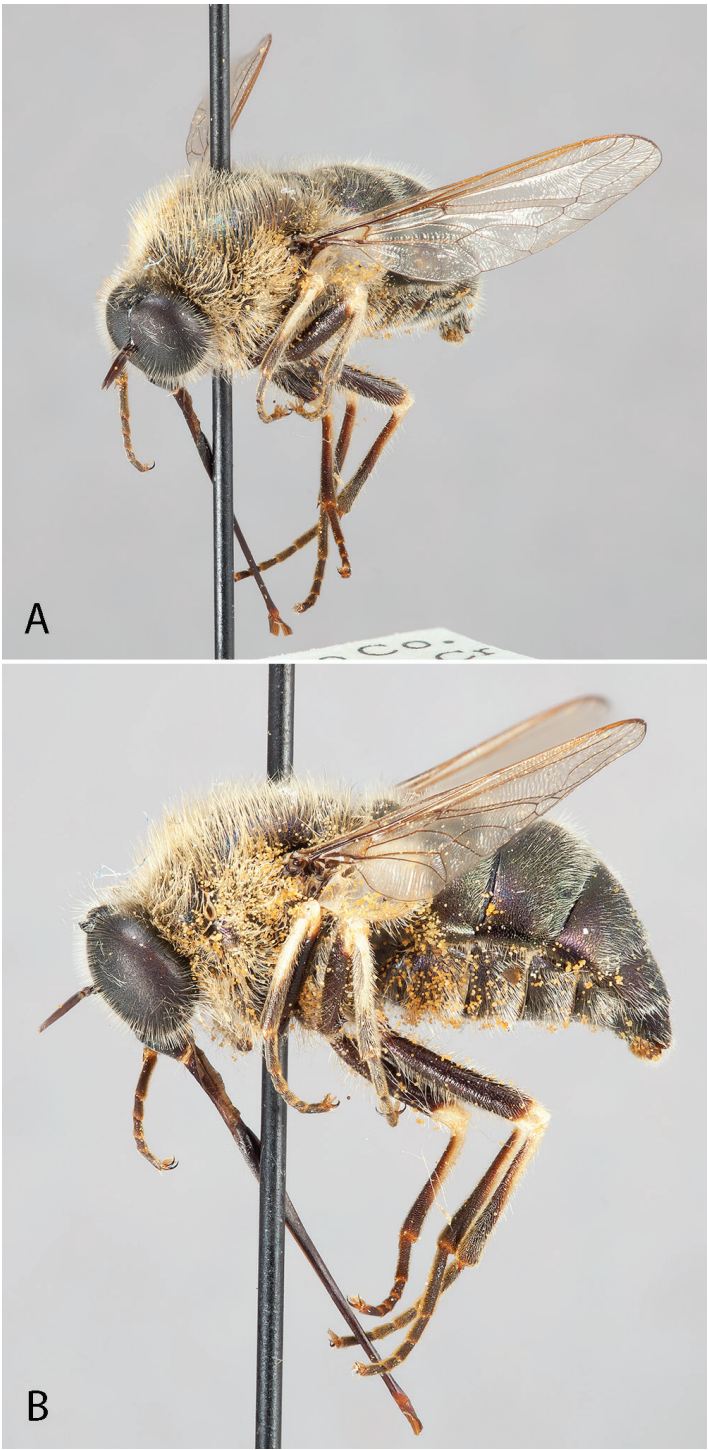


Figure 13. *Eulonchus tristis* Loew, male (EIS 008947). **A** oblique view **B** lateral view. Body length: 10.6 mm.

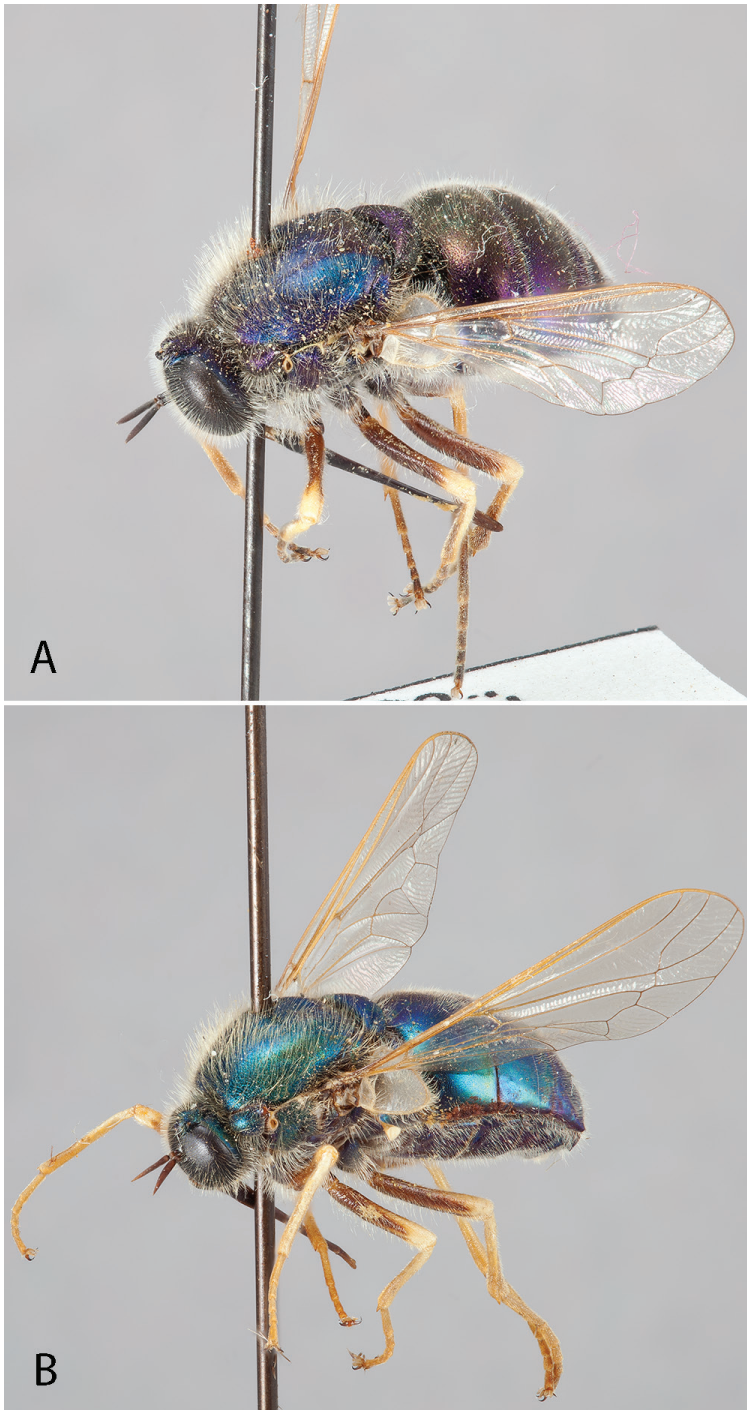


Figure 14. *Eulonchus tristis* Loew. **A** oblique view, male (EIS 009592), body length: 10.0 mm **B** oblique view, female (EIS 017865), body length: 10.8 mm.



Figure 15. *Eulonchus tristis* Loew, lectotype male, lateral view. Body length: 9.8 mm.

583 (Idaho); Sabrosky 1948: 390 (key ref., notes); Schlinger 1965: 404 (catalogue), 1969: 221, fig. 134 (notes), 1987: 320 (host); Poole 1996: 36 (checklist); Coyle and Icenogle 1994 (larval host).

Common name. Dusky Sapphire.

Diagnosis. Proboscis reaching apex of abdomen; ocellar tubercle trifurcate with three ocelli present (median smaller than laterals); legs mostly dark brown ('knee' pale), calypter margin dark and membrane white or light yellow.

Redescription. Body length: 7.9–12.8 mm, Wing length: 6.0–11.2 mm. *Head.* Flagellum dark brown, scape and pedicel brown, male flagellum cylindrical, shorter than head height; clypeus elongate, extending beyond oral cavity, rounded with flat area dorsally, black-brown, surface glossy, glabrous; labial palp brown, length extending anteriorly beyond proboscis at point of attachment; margin of oral cavity (parafacial) pilose admixed with pubescence (faint); proboscis length from middle of abdomen or extending beyond abdomen; ocellar tubercle trifurcate, processes subequal (narrowly digitate), height equal to or shorter than width; median ocellus present, greatly reduced or absent; occiput metallic green-blue, blue or purple, pile densely white or yellow. *Thorax.* Metallic green, blue or purple, setal pile white or yellow; coxae brown or black with metallic blue sheen; femora dark brown, apices

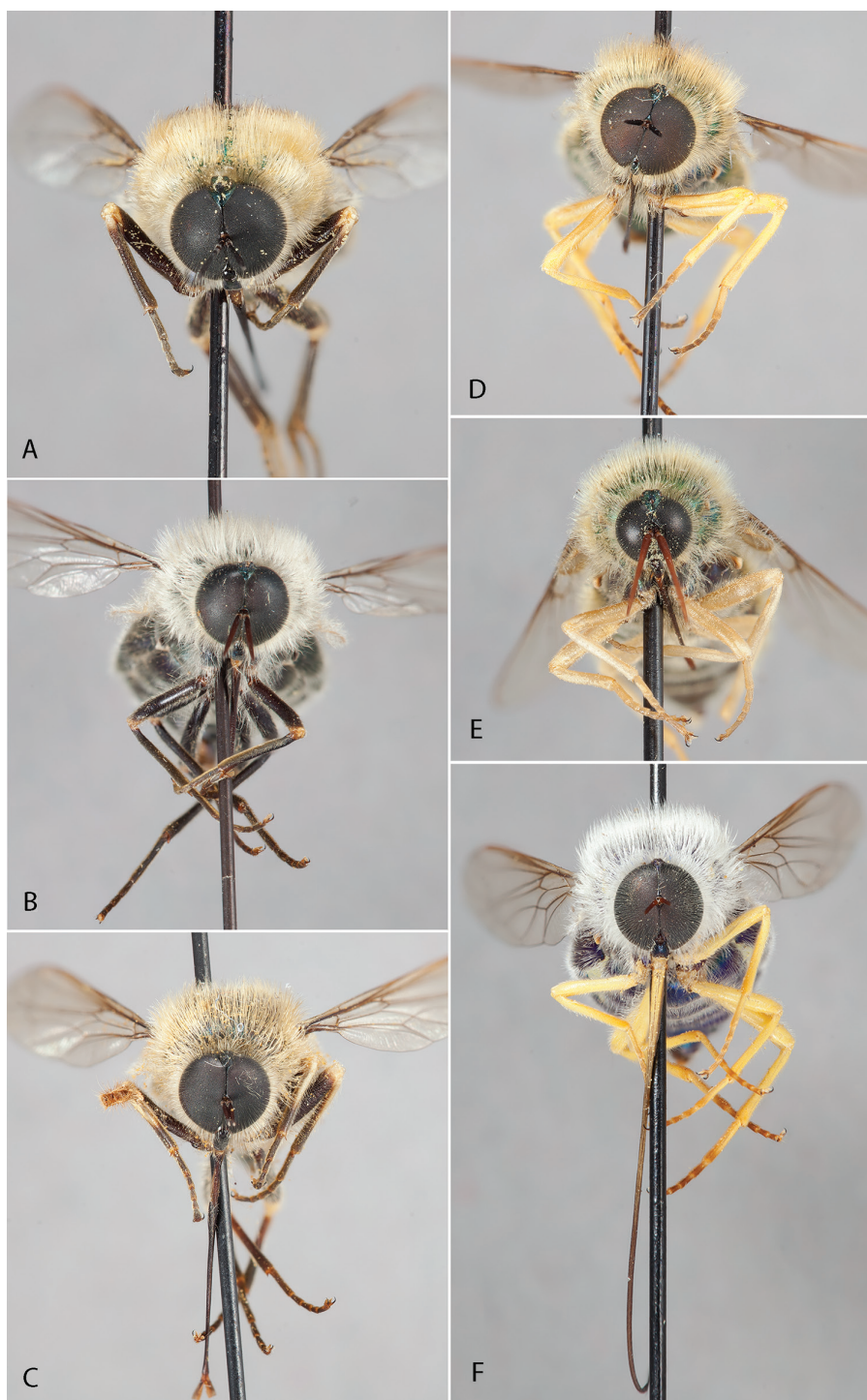


Figure 16. *Eulonchus* species, anterior view. **A** *E. marginatus* **B** *E. halli* **C** *E. tristis* **D** *E. sapphirinus* **E** *E. marialicae* **F** *E. smaragdinus*.



Figure 17. Gonocoxite and aedeagus, lateral view. **A** *E. halli* (EIS 004397) **B** *E. marginatus* (EIS 009172) **C** *E. marialiciae* (EIS 017824) **D** *E. sapphirinus* (EIS 017824) **E** *E. smaragdinus* **F** *E. tristis* (EIS 014098). Scale bar: 0.5 mm.

white; tibiae dark yellow or brown; tarsi dark yellow; calypter margin dark brown or light brown, membrane translucent; haltere entirely dark brown. *Abdomen*. Metallic olive green, bright green to blue-violet, vestiture white or yellow, dominant setae appressed or erect, pile posteriorly directed, marginal band of dense thicker setae on T3-4, or posteriorly directed, marginal band of laterally directed pile on T2-4. *Male genitalia*. Epandrium round, with posterior margin almost straight; gonocoxite as tall as wide, with anterior margin almost straight, with large fenestrae; aedeagus heavily sclerotized laterally.



Figure 18. Epandrium, lateral view. **A** *E. halli* (EIS 004397) **B** *E. marginatus* (EIS 009172) **C** *E. mari- aliciae* (EIS 017824) **D** *E. sapphirinus* (EIS 017824) **E** *E. smaragdinus* **F** *E. tristis* (EIS 014098). Scale bar: 0.5 mm.

Type material examined. **Lectotype** male (designated here), MCZ, “*S. Franciscol H. Edw*” [white]; “Loew” [white]; “Type/ 3/ 1077” [red and white]; “MCZ-ENT/ 00303280” [white]; “LECTOTYPE ♂/ *Eulonchus tristis*/ Loew/ Des. C.J. Borkent 2015” [red]; specimen condition: tarsi of right mid leg and left flagellum missing, membrane of both wings slightly damaged on posterior portion. Body length: 9.8 mm, wing length: 9.2 mm. **Paralectotype** female, MCZ, “*S. Franciscol H. Edw.*” [white]; “Loew” [white]; “Type/ 2/ 1077” [red and white]; “MCZ-ENT/ 00303279” [white]; “PARALECTOTYPE ♀/ *Eulonchus tristis*/ Loew/ Det. C.J. Borkent 2015” [yellow]; specimen condition: very good, tarsi of right hind leg missing. **Paralectotype female**, MCZ, “*S. Franciscol H. Edw*” [white]; “Loew” [white]; “Type/ 4/ 1077” [red and white]; “MCZ-ENT/ 00303281” [white]; “PARALEC- TOTYPE ♀/ *Eulonchus tristis*/ Loew/ Det. C.J. Borkent 2015” [yellow]; specimen condition: very good, left mid and hind legs missing. **Paralectotype male**, MCZ,

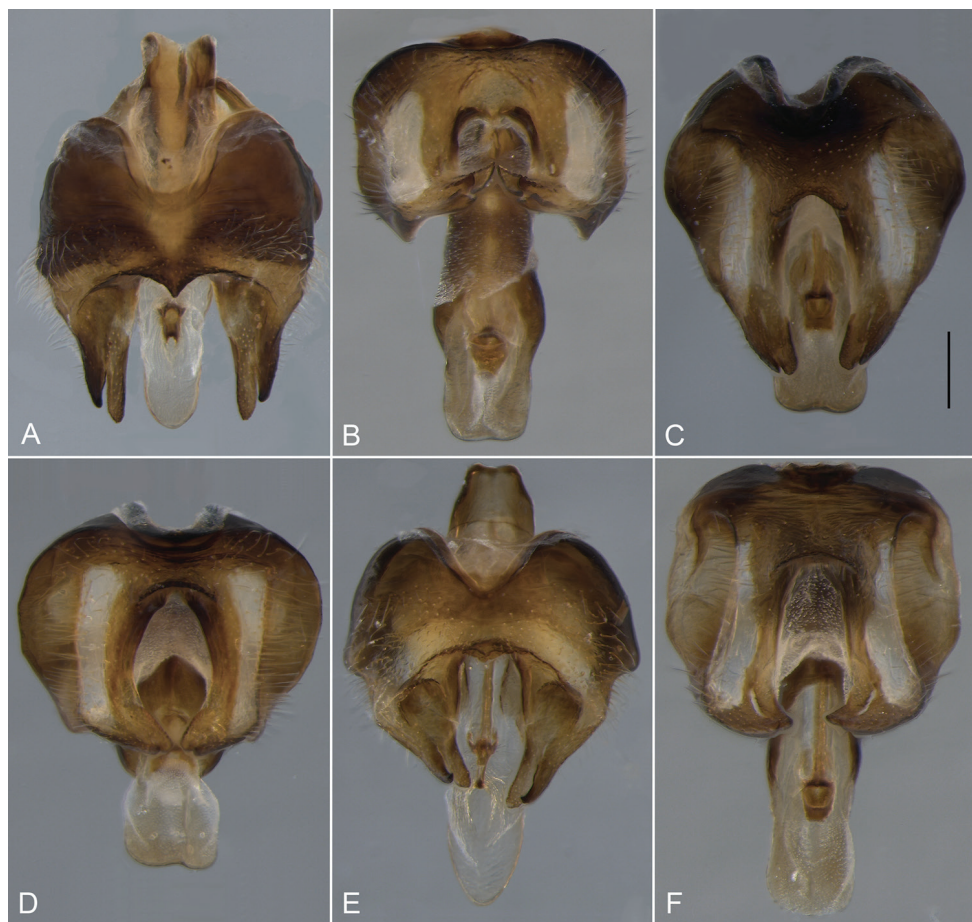


Figure 19. Gonocoxite, ventral view. **A** *E. halli* (EIS 004397) **B** *E. marginatus* (EIS 009172) **C** *E. marialiciae* (EIS 017824) **D** *E. sapphirinus* (EIS 017824) **E** *E. smaragdinus* **F** *E. tristis* (EIS 014098). Scale bar: 0.5 mm.

“*Californi* Edwards” [white]; “Loew” [white]; “*Eulonchus* *tristis* Lw./ Cant. X” [white]; “Type/ 1077” [red and white]; “MCZ-ENT/ 00001077” [red and white]; “Aug-Dec 2006/ MCZ Image/ Database” [white]; “PARALECTOTYPE ♂/ *Eulonchus tristis*/ Loew/ Det. C.J. Borkent 2015” [yellow]; specimen condition: very good, flagella missing.

Other material examined. Listed in Table 3 (Suppl. material 1).

Distribution (Fig. 20). Nearctic: Northern California, Oregon, Washington, Arizona.

Ecology. Pollen loads and diversity from individual *E. tristis* visiting flowers of *Brodiaea elegans* (Themidaceae) and *Iris douglasiana* (Iridaceae) in California has been studied, showing high levels of constancy to a single species (Borkent and Schlinger

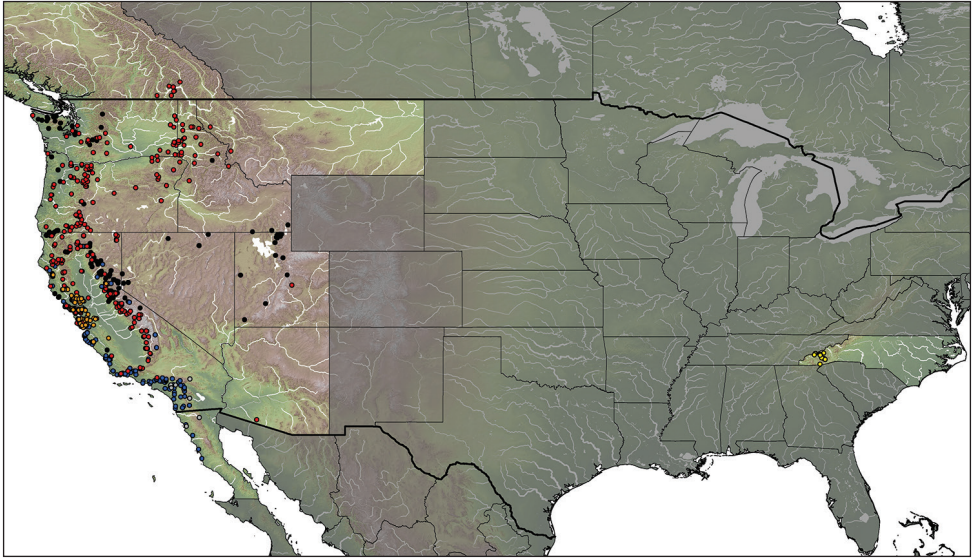


Figure 20. Distribution of *Eulonchus* species. Grey circles: *E. halli*; orange circles: *E. marginatus*; yellow circles: *E. marialiciae*; black circles: *E. sapphirinus*; blue circles: *E. smaragdinus*; red circles: *E. tristis*.

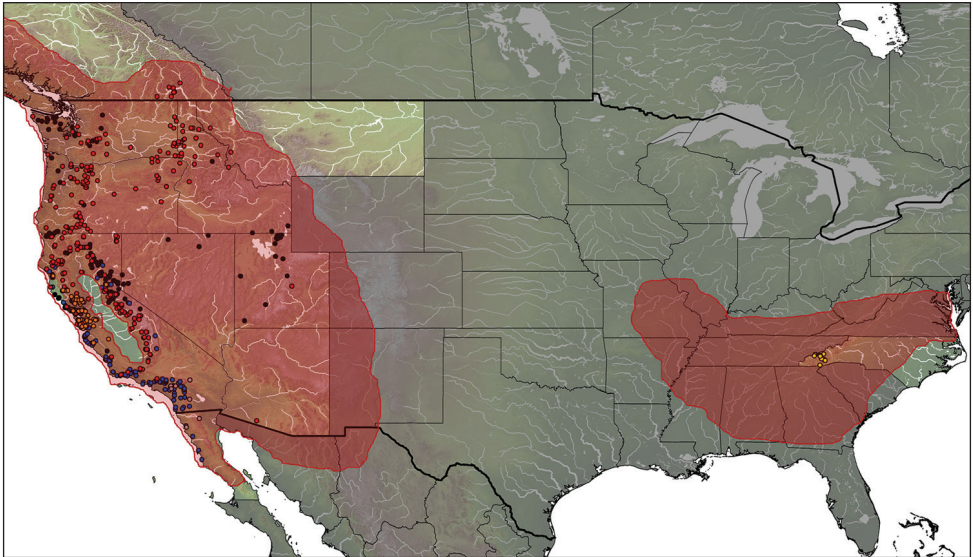


Figure 21. Distribution of species of *Eulonchus* and their hosts. Coloured circles: *Eulonchus* spp.; red shaded area: potential Antrodiaetidae spider fly host distribution inferred from Coyle 1971, Hendrixson and Bond 2006, and Bond 2012.

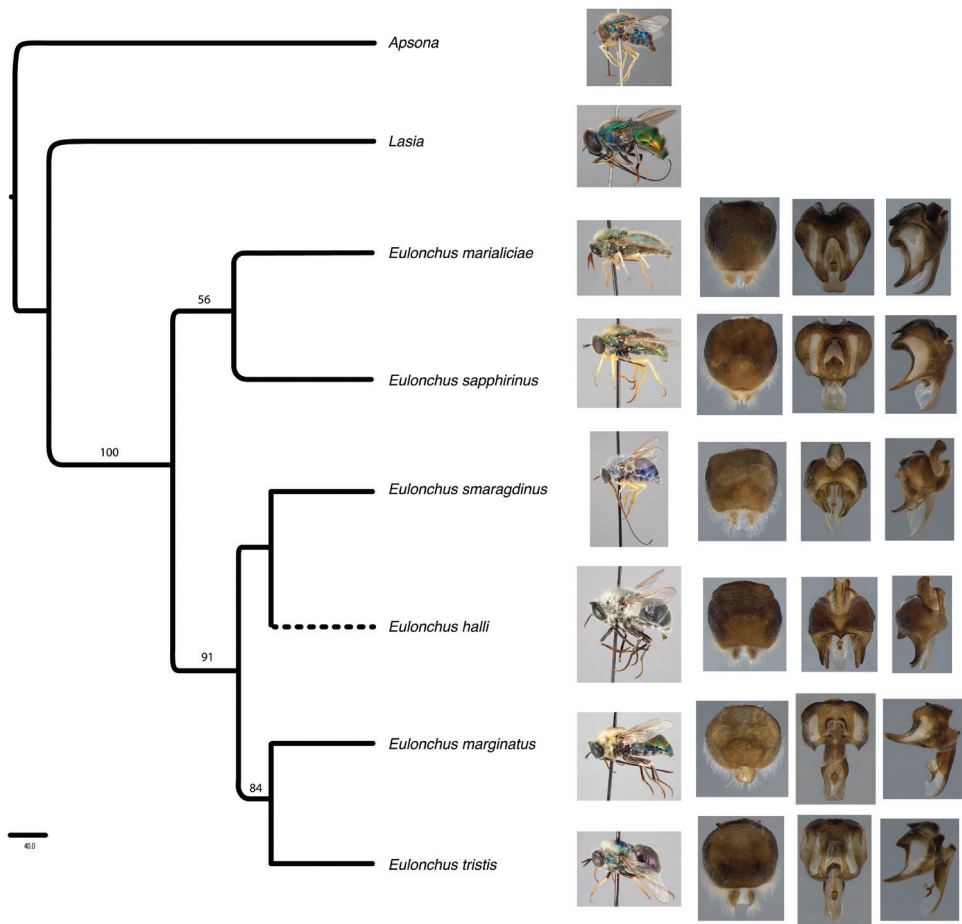


Figure 22. Phylogeny of *Eulonchus* based on DNA sequence data (16S, COI, CAD). Single tree resulting from branch and bound parsimony search. Bootstrap support values are shown above the branches.

2008b). *Eulonchus tristis* has been recorded visiting the flowers of 19 different plant families and 38 different species (Table 2).

Biology. Host: *Aliatypus* sp. (Antrodiaetidae) (Schlinger 1987).
Comments. *Eulonchus tristis* is most similar to *E. marginatus*, with which it shares the ocellar tubercle trifold and the flagellum half as long as the head. *Eulonchus tristis* can be easily distinguished from *E. marginatus* by its femur and tibia with yellow markings and the pile on abdomen yellow.

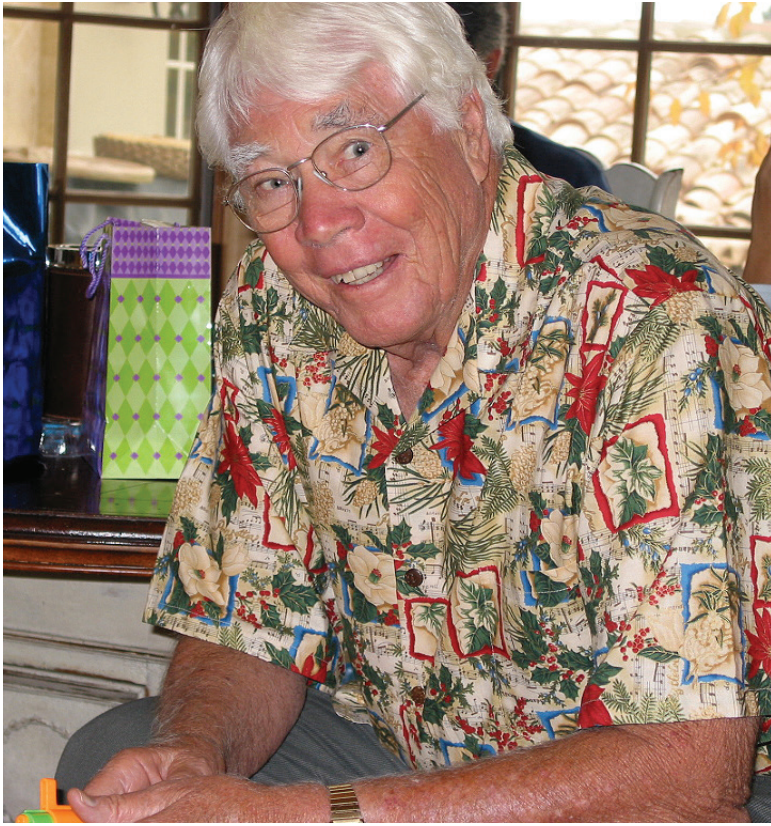


Figure 23. Evert I. Schlinger (1928–2014) was a world renowned expert on spider fly taxonomy and biology. This paper is dedicated to him and his legacy.

Acknowledgements

Thank you to Philip Perkins (MCZ), Charles Griswold and Michelle Trautwein (CAS), Torsten Dikow and Norman Woodley (USNM), Joachim Ziegler (ZMB), Peter Oboyski (EMEC), Lynn Kimsey (UCDC), and R. Dennis Haines (TCAC) for allowing access to specimens in their care. We also thank the numerous other collections who waited just a little bit longer for the return of acrocerid material that had been loaned out decades ago to E.I. Schlinger. Thank you also to Chris Grinter for access to the specimen database and Dr. Evert Schlinger and Dr. Chris Thompson for access to nomenclatural notes. Thanks to Scott Kinnee for his assistance with DNA sequencing, to Eliza Fraser for her help with location coordinates and data entry, and to Dr. Fred Hrusa for checking botanical nomenclature. This paper was much improved by comments from Dr. N. Woodley and an anonymous reviewer. We are also grateful to the photographers and users of bugguide.net who gave us permission to use the in situ pictures in Figure 1. This paper is dedicated to the late Professor Evert Schlinger (1928–2014, Fig. 23), a world expert on spider flies and dedicated dipterist, arachnologist,

and patron of insect systematics and biodiversity. Funding support was received by CJB from FQRNT postdoctoral grant (Quebec, Canada) and NSF-Calbug (to S. Gaimari). Funding to JPG was received from a doctoral scholarship from the Brazilian National Council for Scientific and Technological Development (CNPq 209447/2013-3) and a Jastro-Shields UC Davis Research Award (2014–2016). Funding support for SLW was provided by the National Science Foundation (NSF) (DEB-0614213, DEB-1144119) and the Australian Biological Resources Study (ABRS-209-48).

References

- Adler PH, Reitz SR, Watson CN (1997) Distribution and abundance of *Eulonchus marialiciae* (Diptera: Acroceridae). *Entomological News* 108: 190–192
- Aldrich JM (1905) A catalog of North American Diptera. Smithsonian miscellaneous collections 46, 680 pp
- Arnaud PH Jr (1979) A catalog of the types of Diptera in the collection of the California Academy of Sciences. *Myia* 1, 505 pp
- Barneche JA, Gillung JP, González A (2013) Description and host interactions of a new species of *Exetasis* Walker (Diptera: Acroceridae), with a key to species of the genus. *Zootaxa* 3664: 525–536. doi: 10.11646/zootaxa.3664.4.6
- Bigot JMF (1890) Dipteres nouveaux ou peu connus, 35^e partie, Cyrtidi. *Annales de la Société entomologique de France* 9: 313–320
- Bond JE (2012) Phylogenetic treatment and taxonomic revision of the trapdoor spider genus *Aptostichus* Simon (Araneae: Mygalomorphae: Euctenizidae). *ZooKeys* 252: 1–209. doi: 10.3897/zookeys.252.3588
- Borkent CJ, Schlinger EI (2008a) Flower-visiting and mating behaviour of *Eulonchus sapphirinus* (Diptera: Acroceridae). *The Canadian Entomologist* 140: 250–256. doi: 10.4039/n07-060
- Borkent CJ, Schlinger EI (2008b) Pollen loads and pollen diversity on bodies of *Eulonchus tristis* (Diptera: Acroceridae): implications for pollination and flower visitation. *The Canadian Entomologist* 140: 257–264. doi: 10.4039/n07-061
- Brimley CS (1925) New species of Diptera from North Carolina. *Entomological News* 36: 73–77.
- Brimley CS (1938) The Insects of North Carolina, being a list of the Insects of North Carolina and their close relatives. The North Carolina Department of Agriculture and Consumer Services, Division of Entomology, Raleigh, 560 pp
- Brunetti E (1926) New and little-known Cyrtidae (Diptera). *Journal of Natural History Series* 9 18: 561–606. doi: 10.1080/00222932608633552
- Cole FR (1919) The dipterous family Cyrtidae in North America. *Transactions of the American Entomological Society* 45: 1–79
- Cole FR (1923) Notes on the dipterous family Cyrtidae. *Psyche* 30: 46–48. doi: 10.1155/1-923/31254
- Cole FR (1927) A study of the terminal abdominal structures of male Diptera. *Proceedings of the California Academy of Sciences* 16: 397–499.

- Cole FR (1969) The Flies of Western North America. University of California Press, Berkeley and Los Angeles, 693 pp
- Cole FR, Lovett AL (1921) An annotated list of the Diptera (flies) of Oregon. Proceedings of the California Academy of Sciences 11: 197–344. doi: 10.5962/bhl.title.57901
- Coquillett DW (1910) The type-species of the North American genera of Diptera. Proceedings of the United States National Museum 37: 499–647. doi: 10.5479/si.00963801.37-1719.499
- Coyle FA (1971) Systematics and natural history of the mygalomorph spider genus *Antrodiaetus* and related genera (Araneae Antrodiaetidae). Bulletin of the Museum of Comparative Zoology 141: 269–402.
- Coyle FA, Icenogle WR (1994) Natural history of the Californian trapdoor spider genus *Aliatypus* (Araneae, Antrodiaetidae). Journal of Arachnology 22: 225–255.
- Cumming JM, Wood DM (2009) Adult Morphology and Terminology. In: Brown BV, Borkent A, Cumming JM, Wood DM, Woodley NE, Zumbado MA (Eds) Manual of Central American Diptera, Volume 1. NRC Research Press, Ottawa, 9–50.
- Edwards FW (1930) Bombyliidae, Nemestrinidae, Cyrtidae. Diptera of Patagonia and South Chile 5(2): 166–197.
- ESRI 2012. ArcGIS Desktop: Release 10.1. Environmental Systems Research Institute, Redlands, CA.
- Essig EO (1926) Insects of Western North America. Macmillan, New York, 1035 pp.
- Evenhuis NL (2015) Abbreviations for insect and spider collections of the world. <http://hbs.bishopmuseum.org/codens/codens-inst.html> [Accessed on 7 December 2015]
- Hendrixson BE, Bond JE (2006) Molecular phylogeny and biogeography of an ancient Holarctic lineage of mygalomorph spiders (Araneae: Antrodiaetidae: *Antrodiaetus*). Molecular Phylogenetics and Evolution 42: 738–55. doi: 10.1016/j.ympev.2006.09.010
- Gerstaecker A (1856) Beiträge zur Kenntniss der Henopier. Stettiner Entomologische Zeitung 17: 339–361.
- Gillung JP, Nihei SS (2016) Evolution of Philopotinae, with a revision and phylogeny of the New World spider fly genus *Philopota* Wiedemann (Diptera, Acroceridae). Zoological Journal of the Linnean Society 176: 707–780. doi: 10.1111/zoj.12360
- Gillung JP, Winterton SL (2011) New genera of philopotine spider flies (Diptera, Acroceridae) with a key to living and fossil genera. ZooKeys 127: 15–27. doi: 10.3897/zookeys.127.1824
- Howard LO (1902) The Insect Book. Doubleday, Page & Co., New York, 429 pp
- Kertész K (1909) Catalogus Dipteriorum hucusque descriptorum. Vol. 4, Oncodidae, Nemestrinidae, Mydidae, Apioceridae, Asilidae. Museum Nationale Hungaricum, Budapest, 349 pp.
- Knowlton GF, Harmston FC, Stains GS (1939) Insects of Utah: Diptera. Utah Agricultural Experiment Station Mimeograph Series, Technical, No. 200, Part 5, 22 pp.
- Loew H (1872) Diptera Americae septentrionalis indigena. Centuria decima. Berliner entomologische Zeitschrift 16: 49–124. doi: 10.1002/mmnd.18720160110
- Maddison WP, Maddison DR (2014) Mesquite: a modular system for evolutionary analysis. Version 3.0. <http://mesquiteproject.org>
- Melander AL (1902) Notes on the Acroceridae. Entomological News 13: 178–182.
- Nielsen BO, Funch P, Toft S (1999) Self-injection of a dipteran parasitoid into a spider. Naturwissenschaften 86: 530–532. doi: 10.1007/s001140050668

- Osten Sacken CR (1877) Western Diptera: Descriptions of new genera and species of Diptera from the region west of the Mississippi and especially from California. Bulletin of the United States Geological and Geographical Survey of the Territories 3: 189–354. doi: 10.5962/bhl.title.57939
- Osten Sacken CR (1878) Catalogue of the described Diptera of North America. Smithsonian miscellaneous Collections 16, 276 pp.
- Paramonov S (1955) New Zealand Cyrtidae (Diptera) and the problem of the Pacific island fauna. Pacific Science 9: 16–25.
- Peterson A (1916) Head-capsule and mouthparts of Diptera. Illinois Biological Monographs 3: 3–112.
- Poole RW (1996) Diptera, Lepidoptera, Siphonaptera. Nomina Insecta Nearctica. A checklist of the insects of North America. Vol. 3. Entomological Information Service, Rockville, 1143 pp.
- Sabrosky CW (1948) A further contribution to the classification of the North American spider parasites of the Acroceratidae (Diptera). The American Midland Naturalist Journal 39: 382–430. doi: 10.2307/2421592
- Saigusa T (2006) Homology of wing venation of Diptera. Unpublished handout distributed at the 6th International Congress of Dipterology, Fukuoka, Japan, 1–26.
- Schiner IR (1868) Diptera. In: Wüllerstorff-Urbair B von (Ed.) Reise der österreichischen Fregatte Novara um die Erde in den Jahren 1857, 1858, 1859 unter den Befehlen des Commodore B. von Wüllerstorff-Urbair. B. K. Gerold's Sohn, Wien, vi + 388. doi: 10.5962/bhl.title.7913
- Schlinger EI (1953) A lectotype designation in the genus *Eulonchus* (Diptera: Acroceridae). Pan-Pacific Entomologist 28: 220.
- Schlinger EI (1960) A review of the genus *Eulonchus* Gerstaecker. Part I. The species of the *smaragdinus* group (Diptera: Acroceridae). Annals of the Entomological Society of America 53: 416–422. doi: 10.1093/aesa/53.3.416
- Schlinger EI (1965) Acroceridae. A Catalog of the Diptera of America North of Mexico: 403–407.
- Schlinger EI (1966) Distributional patterns of selected western North American Insects. An analysis of the distribution of *Eulonchus* Gerstaecker (Diptera: Acroceridae). Bulletin of the Entomological Society of America 12: 112–113. doi: 10.1093/besa/12.2.112a
- Schlinger EI (1969) Acroceridae (Cyrtidae). In: Cole FR (Ed.) The flies of western North America. Univ. California Press, Berkeley & Los Angeles, 219–224.
- Schlinger EI (1981) Acroceridae. In: McAlpine JF, Peterson BV, Shewell GE, Teskey HJ, Vockeroth JR, Wood DEM (Eds) Manual of Nearctic Diptera. Vol. I. Research Branch, Agriculture Canada, Ottawa, Monograph 27: 575–584.
- Schlinger EI (1987) The biology of Acroceridae (Diptera): True endoparasitoids of spiders. In: Nentwig W (Ed.) Ecophysiology of Spiders. Springer-Verlag, Berlin, 319–327. doi: 10.1007/978-3-642-71552-5_24
- Schlinger EI, Gillung JP, Borkent CJ (2013) New spider flies from the Neotropical Region (Diptera, Acroceridae) with a key to New World genera. ZooKeys 270: 59–93. doi: 10.3897/zookeys.270.4476
- Swofford DL (2003) PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.

- Verrall GH (1909) Stratiomyidae and succeeding families of the Diptera Brachycera of Great Britain. In: Verrall GH (Ed.) British Flies, Vol. 5. Gurney & Jackson, London, 780 pp.
- Vincent LS (1986) Pathogens and parasitoids of the fossorial mygalomorph spider, *Atypoides riversi* O. P. Cambridge (Antrodiaetidae: Araneae) of various age and size classes. In: Eberhard WG, Lubin YD, Robinson BC (Eds.) Proceedings of the IX International Congress of Arachnology, Panama 1983. Smithsonian Institution Press, Washington, 291–294.
- Westwood JO (1876) Notae Dipterologicae, No. 3. Descriptions of new genera and species of the family Acroceridae. Transactions of the Royal Entomological Society of London 24: 507–518. doi: 10.1111/j.1365-2311.1876.tb01927.x
- Williston SW (1888) Synopsis of the families and genera of North American Diptera. Exclusive of the genera of the Nematocera and Muscidae, with bibliography and new species. JT Hathaway, New Haven, 84 pp.
- Williston SW (1896) Manual of North American Diptera, Second Edition. JT Hathaway, New Haven, 167 pp.
- Williston SW (1908) Manual of North American Diptera, Third Edition. JT Hathaway, New Haven, 495 pp.
- Winterton SL (2012) Review of Australasian spider flies (Diptera, Acroceridae) with a revision of *Panops* Lamarck. ZooKeys 172: 7–75. doi: 10.3897/zookeys.172.1889
- Winterton SL, Wiegmann BM, Schlinger EI (2007) Phylogeny and Bayesian divergence time estimations of small-headed flies (Diptera: Acroceridae) using multiple molecular markers. Molecular Phylogenetics and Evolution 43: 808–832. doi: 10.1016/j.ympev.2006.08.015
- Woodworth CW (1913) Guide to California insects. The Law Press, Berkeley, 380 pp. doi: 10.5962/bhl.title.49919

Supplementary material I

Table 3

Authors: Christopher J. Borkent, Jessica P. Gillung, Shaun L. Winterton

Data type: material examined

Explanation note: Non-type material examined (EIS # = Evert I. Schlinger collection database specimen accession number). See Materials and methods section for notes on depositories.

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Resurrection of *Anolis ustus* Cope, 1864 from synonymy with *Anolis sericeus* Hallowell, 1856 (Squamata, Dactyloidae)

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Abstract

In this study, based on a morphological analysis, the resurrection of the name *Anolis ustus* Cope 1864, is proposed for populations from the Yucatán Peninsula (Campeche, Yucatán, and Quintana Roo, Mexico, and Belize), formerly referred as *A. sericeus* Hallowell, 1856. *Anolis ustus* differs from *A. sericeus* by its mean snout-vent length and number of gorgetal scales in males, in tibia length and head width in females, and dorsal and ventral scales for both sexes. In addition, *A. ustus* has a small dewlap of similar size between males and females, whereas in *A. sericeus* males have a dewlap much larger than that of the females. These characteristics allow *A. ustus* to be identified within the *A. sericeus* complex. In this study, a description of the characteristics of the hemipenis is also provided, and its importance in the taxonomy of *Anolis* is discussed.

Keywords

Anolis, Atlantic versant, dewlap, hemipenes, Yucatan Peninsula

Introduction

The name *Anolis sericeus* has a relatively old and complex taxonomic history. *Anolis sericeus* was described by Hallowell (1856) on the basis of a specimen from “El Euceros, Jalapa, Veracruz” (because there is no known location by this name currently, we believe the actual location may be El Lencero, Xalapa, Veracruz). Unfortunately, the type specimen is now also lost (Barbour 1934; Stuart 1963). During the rest of the 19th and the first half of the 20th centuries, several other nominal species of *Anolis* were described from Mexico and Central America (*A. sallaei* Günther 1859, *A. longicauda* Hallowell 1861, *A. cumingii* Peters 1863, *A. ustus* Cope 1864, *A. heliactin* Cope 1864, *A. jacobii* Bocourt 1873, *A. kidderi* Ruthven 1933, and *A. ustus wellbornae* Ahl 1940), but all of these taxa were eventually placed in the synonymy of *A. sericeus* by Boulenger (1885), Barbour (1934), Smith and Taylor (1950), Stuart (1955), Duellman (1961), and Lee (1980). Thus, *A. sericeus* has been regarded until recently as a single species with a wide distribution extending from Tamaulipas and Oaxaca on the Atlantic and Pacific versants of Mexico, respectively, to the east (including the Isthmus of Tehuantepec and the Yucatan Peninsula) and south through Central America to Costa Rica (Lee 1980).

Köhler and Vesely (2010) recently proposed that *A. sericeus* is actually composed of three species: *A. sericeus*, distributed on the Atlantic versant from Tamaulipas, San Luis Potosí, and Hidalgo in Mexico south and east through the Yucatan Peninsula to Belize and Guatemala; *A. wellbornae*, from the Pacific versant of Nuclear Central America (Pacific versant of Guatemala to approximately Mazatenango, El Salvador, extreme southern Honduras, and northwestern Nicaragua); and *A. unilobatus*, which ranges on the Pacific versant from Oaxaca, Mexico south and east through Guatemala, Honduras, and Nicaragua to Costa Rica. Köhler and Vesely (2010) diagnosed *A. sericeus* by the presence of large bilobate hemipenes and dewlaps of similar size ($\leq 50 \text{ mm}^2$) in males and females.

Nonetheless, preliminary observations of substantial geographic variation in several morphological characters (e.g., dewlap size, hemipenial morphology, and numbers of dorsal and ventral scales) among populations of *A. sericeus sensu* Köhler and Vesely (2010) suggested that this taxon may be composed of more than one species. Herein, we performed a morphological analysis of 140 specimens from throughout the geographic distribution of *A. sericeus* to assess the existence of multiple species within this taxon.

Materials and methods

We examined specimens from most of the geographic distribution of *A. sericeus sensu* Köhler and Vesely (2010), including specimens from Tamaulipas, Hidalgo, Veracruz, Tabasco, Campeche, Yucatán, and Quintana Roo, Mexico, as well as the two syntypes

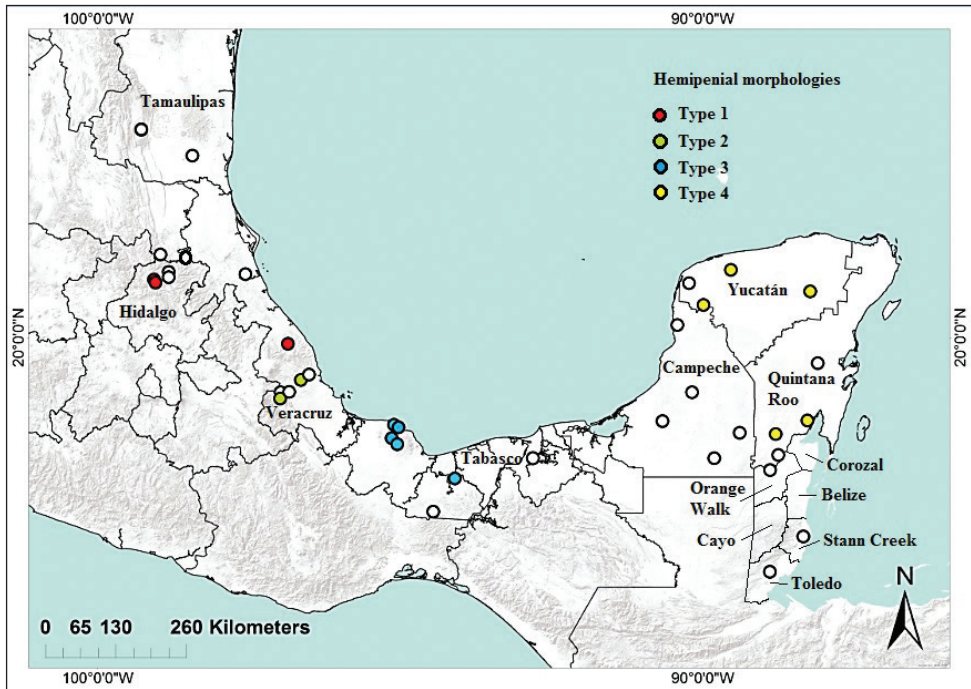


Figure 1. Localities of specimens examined in this study. Colored circles represent specimens with everted hemipenis (see text for details). Areas above 500 m shaded gray.

of *A. ustus* in the Natural History Museum of London (NHM 1946.8.5.60-61) and other specimens from Belize (Fig. 1). We performed fieldwork in the states of Hidalgo, Veracruz (north, center and south), and Quintana Roo, Mexico from April to November 2015. Only adult specimens (≥ 38 mm snout-vent lengths [SVL]) were collected. Specimens of *A. sericeus* were not found at the type-locality of El Lencero, Xalapa, Veracruz; however, we collected specimens of *A. sericeus* at Xotla, Veracruz, only 26 km from the type-locality. Collected specimens were fixed with 10% buffered formalin and preserved in 70% ethanol. Hemipenis were everted and hardened by immersion in formalin for 40 seconds.

The remaining examined specimens were borrowed from the following collections: ECOSUR, Chetumal, Quintana Roo (ECOCHH); Centro de Investigaciones Biológicas, Universidad Autónoma del Estado de Hidalgo (CIB); Museo de Zoología Alfonso L. Herrera, Facultad de Ciencias, Universidad Nacional Autónoma de México (MZFC); Instituto de Investigaciones Biológicas, Universidad Veracruzana (IIB-UV); Instituto Tecnológico de Ciudad Victoria, Tamaulipas (ITCV); Estación de Biología Tropical de Los Tuxtlas, Veracruz (CAR-EBTT); University of Kansas (KU); Carnegie Museum of Natural History (CMNH); and the The Natural History Museum, London (NHM).

Measurements were taken under a microscope trademark Leica (model MS-512X) with a digital caliper trademark Mitutoyo (model CD-8" CX) and recorded to the nearest

0.1 mm. Nomenclature of measured characters follows Köhler (2014). A total of 14 morphometric and 14 meristic characters was recorded in both males and females:

SVL	snout-vent length
TL	tail length
HL	head length
HW	head width
SL	snout length
LDIS	longitudinal diameter of the interparietal scale
TDIS	transverse diameter of the interparietal scale
NRL	naris-rostrum length
IL	internarial length
DA	dewlap area
AGL	axilla-groin length
FL	forearm length
ShL	shank length
LFT	length of the fourth toe
DLW	dilated lamellae width
NPS	number of postrostral scales
NIS	number of internasal scales
NSSSS	number of scales separating supraorbital semicircles
NLS	number of loreal scales
NSuperciliary	number of superciliary scales
NSupraoculars	number of supraocular scales
NSupralabials	number of supralabial scales
NInfralabials	number of infralabial scales
NPS	number of postmental scales
NLFT	number of subdigital lamellae of fourth toe (from the lamella situated at the level of the joint of phalanges III and IV to the beginning of the terminal lamellae
NTL	number of terminal lamellae
NDS	number of dorsal scales
NVS	number of ventral scales.

In addition, the number of gorgetal scales (NGS) in males was recorded. In this review variation in color pattern was not considered because of changes in pattern with preservation. Dewlap area was measured on field specimens only. The area was measured by tracing the outline of the extended dewlap onto a sheet of grid paper with 1 mm² squares, and counted the number of squares that were completely within the outline. Nomenclature for hemipenial structures follows Myers (1971) and Myers et al. (1993). In this study we adopted the unified concept of species proposed by de Queiroz (2007), which states that a species is a metapopulation lineage evolving independently of other lineages.

Analysis of data

Each examined character was tested for normality with a Komolgorov-Smirnov test using the statistics program STATISTICA v. 7 (StatSoft 2004). To assess whether populations of *A. sericeus* comprise multiple morphologically distinct groups we performed a Principal Component Analysis (PCA) of all of the measured characters for each sex; this analysis also was performed to identify characters highly correlated (< -0.50 or > 0.50) with the three main principal components. A Generalized Discriminant Analysis (GDA) was then used with the latter characters, also for each sex, using STATISTICA v. 7. This analysis evaluated whether groups observed in the PCA for both sexes are significantly different using the squared Mahalanobis distances, with an F test (Johnson 2000; Montanero-Fernandez 2015). Wilks' Lambda test was also used to identify the characteristics that allow discrimination between groups. In addition, when two or more discriminant functions were obtained, an ordination scatter plot was made. If only one function was obtained, a box plot was generated. These graphs were made with the program PAST v. 3.08 (Hammer 2015).

Results

In the PCA for males, the first three principal components explained 47.11% of the variation in the analyzed characters, of which 18 were highly correlated with these components (Table 1). The PC1 vs PC2 ordination plot (Fig. 2) identified three groups, composed of the specimens from: (i) Tamaulipas, Hidalgo, and northern and central Veracruz (i.e., the northern and central portions of the Atlantic versant, or AV1), (ii) southern Veracruz and western Tabasco (i.e., the southern portion of the Atlantic versant, or AV2), and (iii) Campeche, Yucatán, Quintana Roo, and Belize (i.e., the Yucatan Peninsula, or YP). In the PCA for females, the first three principal components explained 39.58% of the variation in the analyzed characters, of which 13 were highly correlated with these components (Table 1). The PC1 vs PC2 ordination plot identified two morphologically distinct groups, composed of the specimens from: (i) Tamaulipas, Hidalgo, Veracruz and western Tabasco (i.e., the Atlantic versant, or AV), and (ii) Campeche, Yucatán, Quintana Roo, and Belize (i.e., the Yucatan Peninsula, or YP), respectively (Fig. 3).

GDA for males showed that the first two functions explained 100% of the total variance; Wilks' lambda test indicated that SVL, SL, NGS, and DA are the characters that allow discrimination among groups (Table 2). In the ordination scatter plot from this analysis (Fig. 4), individuals of the AV1 and AV2 groups (see above) formed distinct groups that were close to each other, whereas individuals of the YP group formed a third group clearly separated from the other two. The three groups were significantly different from each other (AV1 vs AV2: $F = 9.99$, $p = < 0.0001$; AV1 vs. YP: $F = 24.79$, $p = < 0.0001$; AV2 vs. YP: $F = 17.86$, $p = < 0.0001$). The three specimens from near the type-locality of *A. sericeus* belonged to the AV1 group, whereas the male syntype of *A.*

Table 1. Statistics from the PCA for males and females. Correlation coefficients among characters for the first three principal components. * Characters that explained the highest percentage of variation for each component. Also shown here are the eigenvalue, explained variance, and accumulated explained variance for the first three components.

Characters	Males			Females		
	PC1	PC2	PC3	PC1	PC2	PC3
SVL	-0.85173*	-0.20534	0.07991	-0.85924*	-0.11391	0.06696
TL	-0.63747*	0.42139	0.14205	-0.08738	0.10816	-0.15747
HL	-0.75132*	-0.21300	0.02761	-0.51013*	-0.11974	-0.10871
HW	-0.89301*	-0.01137	0.08725	-0.85500*	0.11310	-0.03773
SL	-0.16205	-0.76203*	0.06875	-0.62754*	-0.47109	-0.06681
LDIS	0.02718	-0.38966	-0.41556	-0.18201	-0.09325	-0.00660
TDIS	-0.26775	-0.34381	-0.40685	0.03118	-0.37480	0.07133
NRL	-0.59741*	-0.35489	-0.15510	-0.37018	0.16997	-0.64634*
IL	-0.53550*	-0.21165	-0.22670	-0.17989	0.16189	-0.63214*
AGL	-0.61223*	-0.32925	0.15488	-0.79493*	-0.22509	0.24664
FL	-0.67579*	0.15599	-0.10419	-0.73863*	0.25637	0.21445
ShL	-0.79747*	0.35656	-0.10989	-0.61786*	0.51700	0.30123
NLFT	-0.40566	-0.09677	-0.16376	-0.39755	0.25495	0.36898
DLW	-0.49120	-0.06745	0.20022	-0.35303	0.03498	-0.11668
NPS	-0.55101*	0.07934	0.26717	-0.19525	0.52569*	-0.29213
NIS	-0.62932*	-0.00681	0.34277	-0.48324	0.12972	-0.56355
NSSSS	0.21946	0.18801	0.61755*	0.10245	0.22969	-0.07205
NLS	-0.24362	0.11200	0.66801*	-0.23420	0.34496	0.35073
NESupraoculars	-0.25903	0.03750	0.14125	-0.42631	0.27921	-0.05066
NSuperciliary	0.24871	-0.46196	0.08580	0.19944	-0.39344	-0.41732
NSupralabials	-0.3210	-0.44249	0.04213	-0.18859	-0.37790	0.42922
NInfralabials	-0.29243	-0.47001	-0.05932	-0.34863	-0.26685	0.06765
NPS	0.07640	0.10760	-0.04845	-0.09248	0.30053	-0.38155
NLFT	0.38912	0.35547	0.46492	0.20960	0.44236	0.20140
NTL	-0.26142	-0.22149	-0.09782	-0.05959	-0.07437	-0.47491
NDS	0.08872	-0.70684*	0.25048	-0.31800	-0.61508*	0.00925
NVS	-0.02688	-0.66557*	0.44827	-0.15787	-0.69712*	-0.15984
DA	-0.52824	0.76774*	-0.11198	-0.09344	-0.67078*	-0.02167
NGS	-0.47798	0.78351*	-0.11481	-	-	-
Eigenvalue	7.00	4.58	2.13	5.08	3.45	2.55
Explained variance (%)	24.05	15.80	7.35	18.15	12.30	9.11
Accumulated variance (%)	24.05	39.80	47.20	18.15	30.45	39.58

ustus belonged to the YP group. In the GDA for females, the first function with its own root of 5.26 explained 100% of the total variance, and according to Wilks’s lambda test, ShL, NDS, NVS, and DA are the characters that allow discrimination between

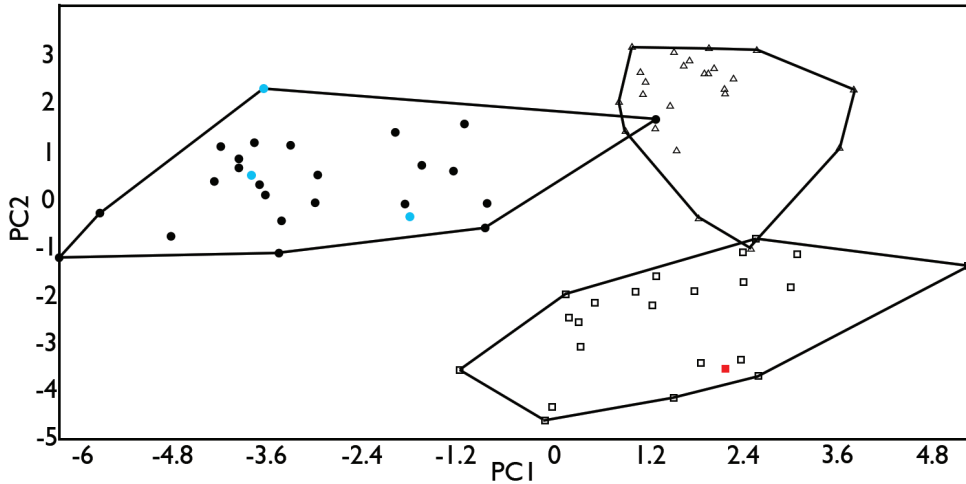


Figure 2. Ordination diagram of principal components 1 and 2 from the PCA of morphological data for males. Circles represent specimens from Tamaulipas, Hidalgo, and northern and central Veracruz; triangles represent specimens from southern Veracruz and western Tabasco; squares represent specimens from the Yucatan Peninsula. Blue circles represent specimens from near the type locality of *Anolis sericeus*. The red square indicates the syntype specimen of *A. ustus*.

Table 2. The Own Root and Explained Variance of canonical functions 1 and 2, and results from Wilks' Lambda tests from GDA of morphological data for males. Only statistically significant morphological variables according to Wilks's Lambda test are presented. * $p < 0.05$.

Character	Canonical function 1	Canonical function 2	Wilks' Lambda	F	p
SVL	-0.0656	-0.2333	0.8896	3.2877	0.0450*
TL	0.0314	-0.0151	0.9573	1.1809	0.3149
HL	0.0138	-0.4059	0.9462	1.5055	0.2312
HW	-0.0147	0.4540	0.9895	0.2802	0.7567
SL	-0.3391	-1.6851	0.7992	6.6572	0.0026*
NRL	-0.7577	0.6368	0.9740	0.7063	0.4980
IL	-0.3024	-1.7315	0.9075	2.6980	0.0765
AGL	-0.0966	0.0590	0.9862	0.3685	0.6934
FL	0.2231	-0.0495	0.9705	0.8054	0.4522
ShL	-0.1509	-0.2002	0.9862	0.3694	0.6928
NPS	-0.0724	-0.4489	0.9440	1.5692	0.2177
NIS	0.4141	-0.0372	0.9674	0.8914	0.4161
NSSSS	-0.1466	0.3262	0.9809	0.5159	0.5998
NLS	-0.1596	-0.3107	0.9710	0.7903	0.4589
NDS	-0.0333	-0.0710	0.9014	2.8966	0.0639
NVS	0.0386	0.0568	0.9606	1.0861	0.3449
NGS	-0.1724	-0.7870	0.8599	4.3144	0.0183*
DA	0.1726	0.0445	0.3439	50.5422	0.0000*
Own Root	17.0669	3.4759	—	—	—
Explained Variance (%)	0.8308	1.0000	—	—	—

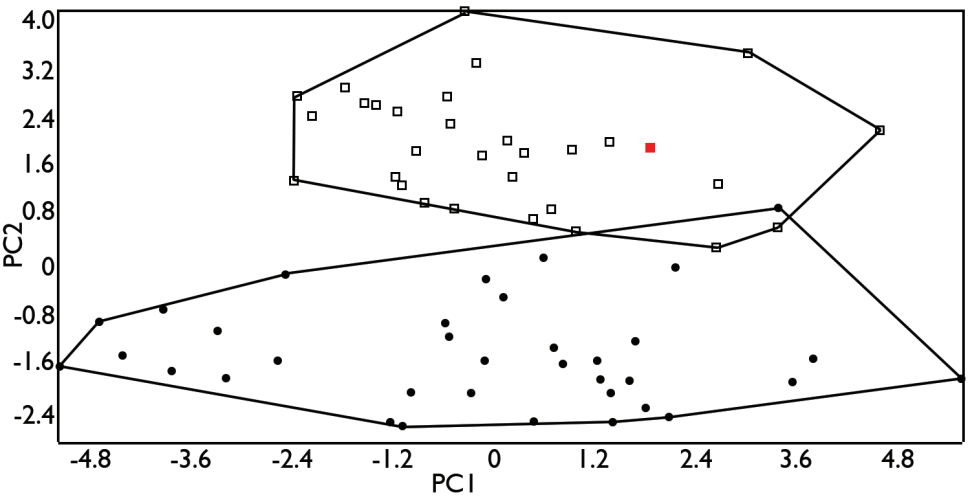


Figure 3. Ordination diagram of principal components 1 and 2 from the PCA of morphological data for females. Circles represent specimens from the Atlantic variant; squares represent specimens from the Yucatan Peninsula. The red square indicates the syntype of *Anolis ustus*.

Table 3. The Own Root and Explained Variance of canonical function 1 for female morphological data obtained with GDA. Only statistically significant morphological variables according to Wilks’s Lambda test are presented. * $p < 0.05$.

Character	Canonical Function 1	Wilk’s Lambda	F	p
SVL	-0.12862	0.959861	2.21631	0.142485
LCA	-0.07654	0.992848	0.38178	0.539296
WH	1.91975	0.818575	11.74666	0.001186*
LH	-0.74607	0.941677	3.28255	0.075687
LNR	-1.27415	0.972540	1.49646	0.226628
LEN	0.76652	0.970452	1.61375	0.209514
AGL	-0.00895	0.999859	0.00747	0.931467
FL	-0.01099	0.999978	0.00118	0.972746
ShL	0.84336	0.839738	10.11490	0.002458*
NPS	0.14725	0.985193	0.79654	0.376163
NDS	-0.06274	0.926137	4.22696	0.044726*
NVS	-0.09454	0.879576	7.25631	0.009440*
DA	-0.09182	0.737254	18.88838	0.000063*
Own Root	4.75	–	–	–
Accumulated Variance (%)	100	–	–	–

groups (Table 3). The AV and YP groups were significantly different ($F = 19.37$, $p < 0.0001$). In the box plot the two groups were nearly completely separated (Fig. 5). Descriptive statistics of the characters most important according to the Wilks’s Lambda test for males and females are given in Table 4.

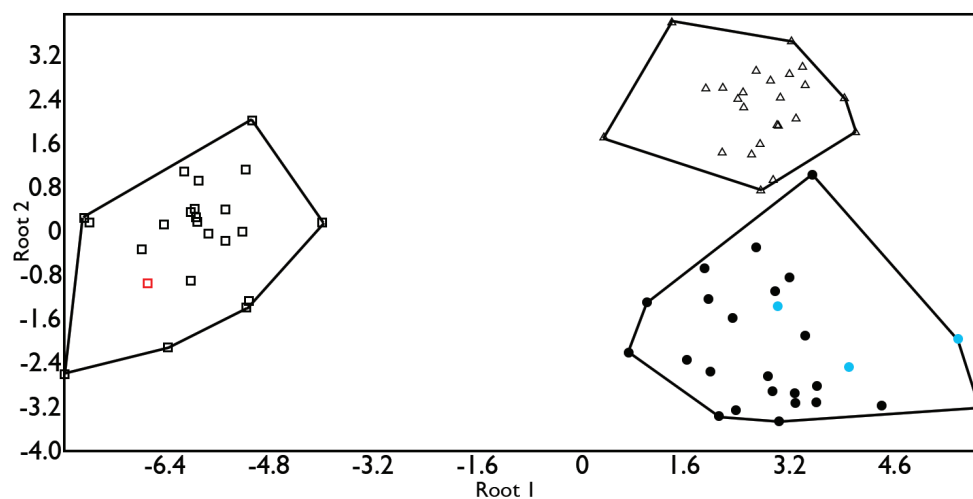


Figure 4. Ordination diagram from the GDA analysis of the morphological data for males. Circles represent specimens from Tamaulipas, Hidalgo, and northern and central Veracruz; triangles represent individuals from southern Veracruz and western Tabasco; squares represent individuals from the YP. Blue circles indicate specimens collected near the type locality of *Anolis sericeus*. The red square indicates the syntype of *A. ustus*.

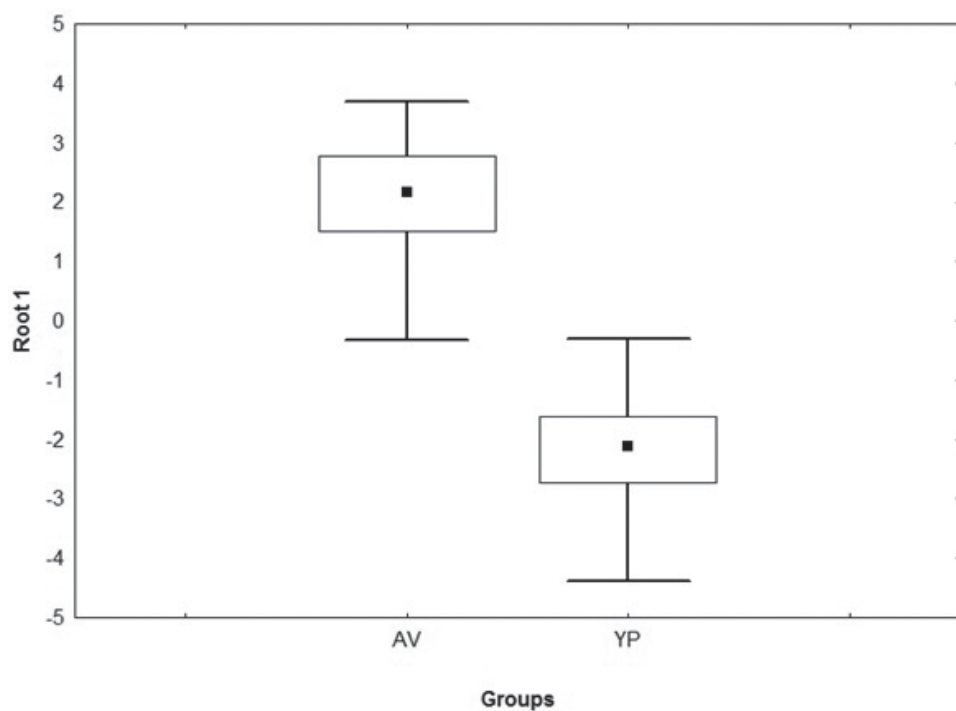


Figure 5. Box plot generated with the root 1 of GDA of morphological data for females. Rectangles: 25–75% from the data; squares: means. Boxplot stems represented 95% confidence interval.

Table 4. Mean \pm standard deviation and range for the most important morphological characters according to the GDA.

Character	Males			Females	
	AV1 (<i>n</i> = 26)	AV2 (<i>n</i> = 24)	YP (<i>n</i> = 23)	AV (<i>n</i> = 35)	YP (<i>n</i> = 32)
SVL	45.72 \pm 2.71 (38.52–49.94)	39.49 \pm 1.32 (36.5–42.38)	41.50 \pm 2.20 (37.36–44.59)	41.33 \pm 2.48 (38.21–53.01)	44.28 \pm 3.8 (35.07–48.93)
SL	5.3 \pm 0.39 (4.47–6.02)	4.56 \pm 0.29 (3.99–5.85)	5.7 \pm 0.44 (5.0–6.93)	5.14 \pm 0.46 (4.16–6.08)	5.56 \pm 0.50 (4.83.6.56)
ShL	10.79 \pm 0.95 (9.9–13.38)	9.52 \pm 0.57 (8.52–10.78)	8.47 \pm 0.49 (7.54–9.78)	10.0 \pm 1.0 (8.32–11.42)	8.7 \pm 0.6 (7.22–9.91)
NDS	48.92 \pm 6.55 (36–62)	43.59 \pm 6.09 (37–60)	57.5 \pm 7.60 (44–78)	47.5 \pm 7.62 (37–60)	56.7 \pm 5.66 (45–71)
NVS	42.15 \pm 6.14 (32–54)	38.59 \pm 5.24 (31–51)	47.7 \pm 4.55 (39–59)	39.4 \pm 6.11 (28–47)	48.3 \pm 6.72 (37–66)
DA	97.3 \pm 8.12 (85–120)	92.13 \pm 5.36 (83–110)	45 \pm 5.9 (31–58)	30.14 \pm 4.8 (31–40)	41.1 \pm 5.1 (32–50)
NGS	8.53 \pm 0.58 (8–9)	8.31 \pm 0.47 (8–9)	5.4 \pm 0.61 (4–6)	-	-

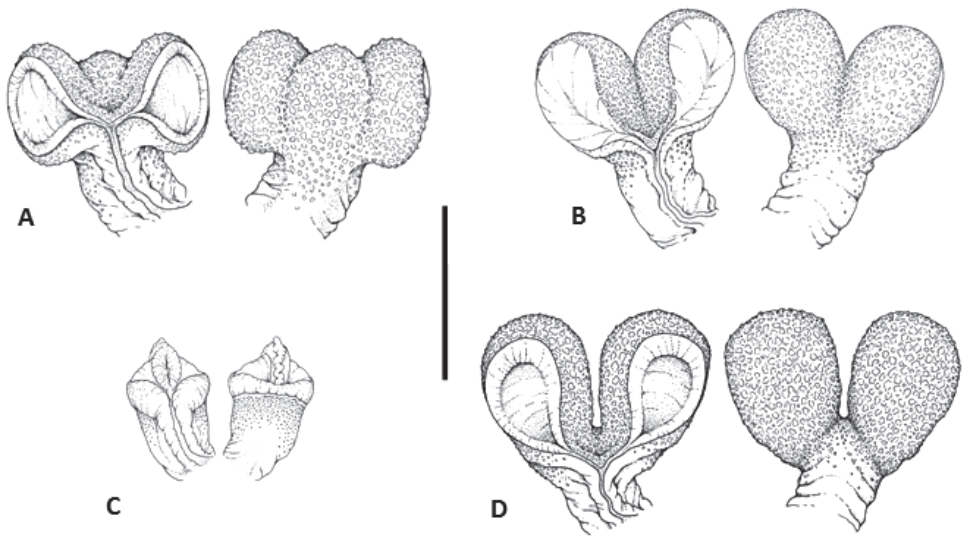


Figure 6. Hemipenial morphologies in sulcate and asulcate views. **A** North of Sierra de Chiconquiaco, Veracruz (AV; CIB 4945) **B** South of Sierra de Chiconquiaco, Veracruz (AV;MZFC 227) **C** Southern Veracruz (AV;CIB 4957) **D** Yucatan Peninsula (CIB 4982). Scale bar: 0.5 mm.

Hemipenial morphology

Forty out of 78 examined males had everted hemipenes (29 from the AV and 11 from the YP). Four different hemipenial morphologies were found. The geographic distribution of these morphologies is shown in Fig. 1. The first morphology was found in

males from north of the Sierra de Chiconquiaco, Veracruz ($n = 9$). The hemipenes are large, slightly bilobate with a small protuberance between the lobes; the surface is calyculate, especially in asulcate view. The lobes are well developed, about as wide as the trunk. The borders of the sulcus spermaticus are well developed (Fig. 6A). The second morphology was exhibited by males from south of the Sierra de Chiconquiaco, Veracruz ($n = 5$). The hemipenes are large, strongly bilobate with no protuberance between the lobes; the surface is conspicuously calyculate in asulcate view. The lobes are well developed, as wide as the trunk, which is relatively long. The borders of the sulcus spermaticus are barely engrossed (Fig. 6B). The third morphological class was exhibited by males from southeast Veracruz ($n = 15$). The hemipenes are small and unilobate, with a widened crest at the apex. The surface is calyculate, especially near the trunk in asulcate view. The borders of the sulcus spermaticus are well developed (Fig. 6C). The fourth morphology was found in males of the YP group ($n = 11$). The hemipenes are large, with well-developed lobes larger than the trunk; the surface is strongly calyculate in asulcate view. The borders of the sulcus spermaticus borders are conspicuously developed (Fig. 6D).

Discussion

Statistical analyses showed three morphologically different groups of males (AV1, AV2, and YP), although only two of females (AV and YP). However, we consider that the morphological evidence that separates the two groups of males from the AV is not enough to question their conspecificity, because they only differ in average SVL and SL from those of the group AV1 (Table 4). At this point, additional evidence supporting their status as distinct species (e.g., molecular data, ecology) is lacking.

The YP group was distinguishable from the AV groups in both males and females. The characters with the largest contributions to the separation of the AV and YP groups included SVL, SL, and NGE in males; HW and ShL in females, and DA, NDS, and NVS in both sexes. Of these characters, the one with the largest contribution to the separation of the AV and YP groups was dewlap size (DA). The differences in dewlap size between males and females of both groups were obvious (Fig. 7). In the AV populations, the dewlap is large in males ($> 85 \text{ mm}^2$, Fig. 7A) and small in females ($< 55 \text{ mm}^2$, Fig. 7B), whereas in the YP populations the males have a much smaller dewlap, only slightly larger than that of females ($< 55 \text{ mm}^2$ and $< 50 \text{ mm}^2$, respectively; Fig. 7C, D). The small size of the dewlap in YP males (and the lack of strong sexual dimorphism in this character) also distinguishes the YP populations from those of *A. wellbornae* and *A. unilobatus* (Köhler and Vesely 2010). The dewlap does not seem to differ in color between the AV and YP populations; however, the central blue spot is conspicuous in females from the YP (Fig. 7D) and diffuse or absent in females from the AV (Fig. 7B). Two other characters that had an important contribution to the separation of the AV and YP groups were NDS and NVS. In general, males and females of the YP group had more dorsal and ventral scales than those of the AV group (Table 4).

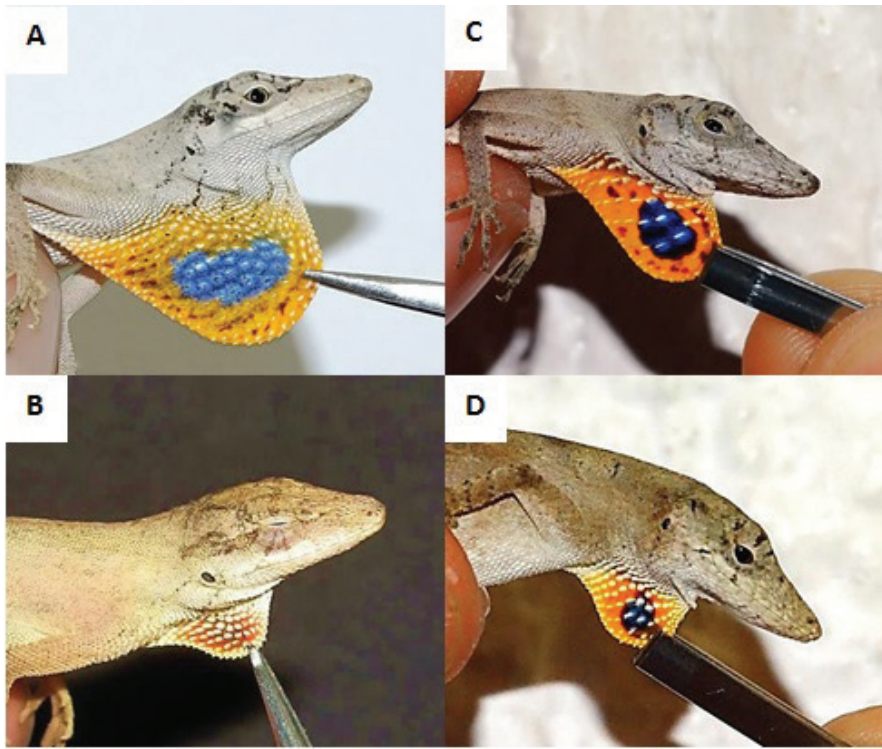


Figure 7. Dewlaps. **A** male from AV, photo by Ismael Reaño Hernández **B** female from AV, photo by Luis M. Badillo Saldaña **C** male from YP **D** female from YP.

The dewlap has been regarded as a taxonomically important character in *Anolis* by many authors (summarized in Losos 2009). Variation in dewlap size, shape, and color determines many intra- and interspecific interactions in *Anolis*. Thus, the dewlap is an important attribute in the defense of territory and sexual displays. Moreover, it is a primary source of recognition among species (Jenssen 1977; Fitch and Hillis 1984; Losos 2009). It has also been suggested that evolution of the dewlap has been driven by sexual selection (Fitch and Hillis 1984). Therefore, variation in dewlap size and color is likely important for the development of reproductive isolation barriers between populations of the AV and YP groups of *A. sericeus*. Lee (1980) compared the dewlap of 25 males and 25 females of *A. sericeus* from the YP with that of the male holotype of *A. kidderi* Ruthven 1933 and one female referred by Smith (1938) to this species (failing to find significant differences), but did not compare males or females of the AV and YP. Also, Köhler and Vesely (2010) stated that the dewlap of male *A. sericeus* is small ($< 50 \text{ mm}^2$) and similar in size to that of females in populations of both the AV and YP. However, we found this statement to be true only for the populations of the YP group.

Male *A. sericeus* from the AV and YP groups also differed in hemipenial morphology (Fig. 6). This finding is unsurprising, as it has been noted that hemipenes evolve much faster than other morphological characters in *Anolis* (Klaczko et al. 2015). Given these

recent findings, differentiation in hemipenial traits is likely to occur prior to speciation. We suspect many species will be polymorphic for these characters, and using them to delimit species should be done with care. Our own work on this species complex supports this suggestion, as we found at least two different hemipenial morphologies (unilobate and bilobate) within *A. sericeus*. Evidence for reproductive isolation between closely related populations with differentiated hemipenes in *Anolis* is currently lacking. For instance, Köhler et al. (2012) found that individuals of *Anolis polylepis*, *A. osa*, and putative hybrids between these two taxa were able to copulate and produce offspring even though they possessed differentiated hemipenes. Thus, hemipenes should be treated like any other potentially informative trait that is expected to be varying within species. In addition, recent molecular studies have shown that evolutionary lineages may not be at all concordant with the distributions of forms associated with hemipenes (e.g., Phillips et al. 2015; Gray unpublished).

Although differences in hemipenial morphology between populations may not warrant recognition of the differentiated populations as distinct species (see above), we argue that the other consistent morphological differences between the AV and YP groups of *A. sericeus* do warrant their recognition as distinct evolutionary lineages. Because the type locality of *A. sericeus* is in Veracruz (El Lencero, Xalapa), the lineage in Tamaulipas, Hidalgo, Querétaro, Veracruz, and Tabasco should retain this name, whereas the oldest available name for the lineage in Campeche, Yucatán, Quintana Roo, and Belize is *Anolis ustus* Cope 1856 (type locality = “Belize”). *Anolis kidderi* Ruthven 1933, described from “Quinta, Mérida, Yucatán” becomes a junior synonym of *A. ustus*.

The specimens from Tabasco (two males and two females) were placed within the AV group with the specimens from Veracruz, Hidalgo, and Tamaulipas in our analyses, and possessed the diagnostic characters of this group: the dewlap is large in males and small in females, and both males and females have low counts of NDS and NVS. In contrast, and despite the geographic proximity between their localities and those of the specimens from Tabasco, the specimens from Campeche (seven males and nine females) belonged into the YP group and possessed the diagnostic characters of this group: the dewlap is small in both males and females and the NDS and NVS counts are high. Recent field work in southern Campeche, between the coordinates 18°07'38.67"N, 91°36'43.91"W and 18°22'48.60"N, 91°11'54.32"W (WGS84) revealed an abrupt transition in form (LNG, unpublished). While every non-Yucatan population within the *A. sericeus* group exhibits strong sexual dimorphism in dewlap size between males and females, *A. ustus* stands out as the one lineage that is easily diagnosable morphologically. Additional studies are needed to determine the existence of a contact zone between the two groups, and the existence and extent of any gene flow between them.

There were no evident differences in behavior or microhabitat between the AV and YP groups of *A. sericeus*. Individuals of both groups were observed perching between 30 and 400 cm on grasses, branches, or thin trunks. Also, individuals of both groups were found in open areas bordering dense vegetation, pasture land, and crop fields. In our experience, lizards in the *A. sericeus* group tend to be quite variable in morphology,

habitat preference, and behavior. Lee (1980) found some evidence of local adaptation within populations and follow-up studies are needed to corroborate his findings. Given the extensive environmental variation found within the geographic range of the *A. sericeus* group, convergence in some morphological traits (despite divergent evolutionary history and distant geographic proximity) is likely, making species identification exceptionally difficult in this group. *Anolis ustus*, thanks to a small dewlap size in both sexes, appears to be the only lineage that is easily diagnosable within the complex.

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References

- Ahl E (1940) Über eine Sammlung von Reptilien aus El Salvador. Sitzungsberichte der Gesellschaft Naturforschender Freunde Berlin 1940: 245–248.
- Barbour T (1934) The anoles II. The mainland species from Mexico southward. Bulletin of the Museum of Comparative Zoology 77: 119–155.
- Boulenger GA (1885) Catalogue of the lizards in the British Museum (Natural History). Vol. II. Second edition. Trustees of the British Museum, London, 497 pp.
- Cope ED (1864) Contributions to the herpetology of tropical America. Proceedings of the Academy of Natural Sciences of Philadelphia 16: 166–181.

- de Queiroz K (2007) Species concepts and species delimitations. *Systematic Biology* 56: 879–886. doi: 10.1080/10635150701701083
- Duellman WE (1965) Amphibians and reptiles from the Yucatán Peninsula, Mexico. University of Kansas Publications Museum of Natural History 15: 577–614. doi: 10.5962/bhl.part.7291
- Fitch HS, Hillis DM (1984) The *Anolis* dewlap: interspecific variability and morphological associations with habitat. *Copeia* 1984: 315–323. doi: 10.2307/1445187
- Günther ACLG (1859) Description of a new species of *Anolis* from Central America. *Proceedings of the Zoological Society London* 27: 421–422.
- Hallowell E (1856) Notes on the reptiles in the collection of the Academy of Natural Sciences of Philadelphia. *Proceedings of the Academy of Natural Sciences of Philadelphia* 8: 221–238.
- Hallowell E (1861) Report upon the Reptilia of the North Pacific Exploring Expedition, under command of Capt. John Rogers, U. S. N. *Proceedings of the Academy of Natural Sciences of Philadelphia* 12: 480–510.
- Hammer O, Harper DAT, Ryan PD (2001) PAST: Paleontological Statistics software package for education and data analysis. *Palaeontological Electronica* 4: 1–9.
- Jennsen TA (1977) Evolution of anoline lizard display behavior. *American Zoology* 17: 203–215. doi: 10.1093/icb/17.1.203
- Johnson DE (2000) Métodos multivariados aplicados al análisis de datos. International Thomson Editores, México, 553 pp.
- Klaczko J, Ingram T, Losos JB (2015) Genitals evolve faster than other traits in *Anolis* lizards. *Journal of Zoology* 295: 44–48. doi: 10.1111/jzo.12178
- Köhler G (2014) Characters of external morphology used in *Anolis* taxonomy: Definition of terms, advice on usage, and illustrated examples. *Zootaxa* 3774: 201–257. doi: 10.11646/zootaxa.3774.3.1
- Köhler G, Vesely M (2010) A revision of the *Anolis sericeus* complex with the resurrection of *A. wellbornae* and the description of a new species (Squamata: Polychrotidae). *Herpetologica* 66: 207–228. doi: 10.1655/07-074R1.1
- Köhler J (2012) Divergent evolution of hemipenial morphology in two cryptic species of mainland anoles related to *Anolis polyblepis*. *Salamandra* 48: 1–11.
- Lee JC (1980) Variation and systematics of the *Anolis sericeus* complex (Sauria: Iguanidae). *Copeia* 1980: 310–320. doi: 10.2307/1444008
- Losos JB (2009) Lizards in an evolutionary tree: Ecology and adaptive radiation of anoles. University of California Press, 507 pp.
- Montanero-Fernández J (2015) Manual de métodos multivariantes. Universidad de Extremadura, España, 79 pp.
- Myers CW (1971) Central American lizards related to *Anolis pentaprin*: two new species from the Cordillera de Talamanc. *American Museum Novitates* 2471: 1–40.
- Myers CW, Williams EE, McDiarmid RW (1993) A new anoline lizard (*Phenacosaurus*) from the highlands of Cerro de la Neblina, southern Guatemala. *Museum American Novitates* 3070: 1–15.
- Peters WCH (1863) Über einige neue Arten der Saurier-Gattung *Anolis*. *Monatsberichte der Königlich Preußischen Akademie der Wissenschaften zu Berlin* 1863: 135–149.

- Ruthven AG (1933) Description of a new *Anolis* from Yucatán. Occasional Papers of the Museum of Zoology. University of Michigan 257: 1–2.
- Smith HM (1938) Notes on reptiles and amphibians from Yucatán and Campeche, Mexico. Occasional papers of the Museum of Zoology, University of Michigan 388: 1–22.
- StatSoft Inc. (2004) STATISTICA (data analysis software system), version 7. www.statsoft.com
- Stuart LC (1955) A brief review of the Guatemalan lizards of the genus *Anolis*. Miscellaneous Publications Museum of Zoology University of Michigan 91: 1–31.
- Stuart LC (1963) A checklist of the herpetofauna of Guatemala. Miscellaneous Publications Museum of Zoology University of Michigan 122: 1–150.

Appendix I

Examined specimens

***Anolis sericeus*.**– **MÉXICO:** **Tamaulipas:** Victoria: ITCV 0097; González: ITCV 0174. **Hidalgo:** San Felipe Orizatlán: CIB 2799-2800; Jacala: CIB 4944-4949; Molango: CIB-4950; Tepehuacán de Guerrero: CIB-4951; Pisaflores: CIB-4952. **Veracruz:** Tuxpan: IIB-UV 040-044, 047-048, 052, 055-057, 059; Ixhuatlán del Café: MZFC 227; Misantla: MZFC 124-128, 235; Huatusco: MZFC 29996-29997, 29991, 29983, 29988, 2993; Atoyac: MZFC 29994; Uxpanapa: MZFC 1931-1932, 476, 463; Xotla: CIB-4953-4955; San Andrés Tuxtla: MZFC 01789, 01790, 01797, 01811-01812, CIB- 4956-4979; Acayucan: MZFC 01792; Las Choapas: MZFC 0108, 01809. **Tabasco:** Emiliano Zapata: MZFC 241-244. ***Anolis ustus*.**– **Campeche:** Escárcega: MZFC 245-249, 251, 254; Calakmul: ECOCHH 628, 698, 1283, 1459, 1518, 1526, 1290; Isla Jaina: MZFC 0283. **Quintana Roo:** Othón P. Blanco: MZFC 8690, 01852; Tres Garantías: ECOCHH 2284; La Pantera: ECOCHH 0912; Chetumal: ECOCHH 1557, CIB-4980-4989; Felipe Carrillo Puerto: ECOCHH 1807, 1880; Ejido Caobas: ECOCHH 2578, 2590; Xpujil: ECOCHH 0976; La Unión: ECOCHH 144. **Yucatán:** Mérida: MZFC 258, 286-287, 293, 300, 305; Valladolid: MZFC 316; Celestún: ECOCHH 1675, 1679, 1725. **BELIZE:** “Belize” NHM-1946.8.5.60-61; Toledo: KU 299709; Stann Creek: KU 157228-157229.

New name for the soft coral *Alcyonium rubrum* Stokvis & van Ofwegen, 2006 (Alcyonacea, Alcyoniidae): *Alcyonium burmedju* nom. n.

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Keywords

Octocorallia, zoological nomenclature, homonymy, East Atlantic

Alcyonium rubrum Stokvis & van Ofwegen, 2006, an encrusting soft coral (Figure 1), was described from the Northeast Atlantic Ocean based on specimens collected during the Dutch CANCAP VII Expedition to the Cape Verde Archipelago (Stokvis and van Ofwegen 2006). This species was later reported from the Azores (Braga-Henriques et al. 2013).

A review on the taxonomic literature of octocorals by the first author revealed the existence of a species described from Scandinavia under the same name, *Alcyonium rubrum* Müller, 1776, which was also reported from Ireland (Hassall 1841). In such a case of primary homonymy, the International Code of Zoological Nomenclature Article 60, states that the junior homonym is invalid and needs to be replaced by a new name. We propose to replace *Alcyonium rubrum* Stokvis & van Ofwegen, 2006 by *Alcyonium burmedju* nom. n.

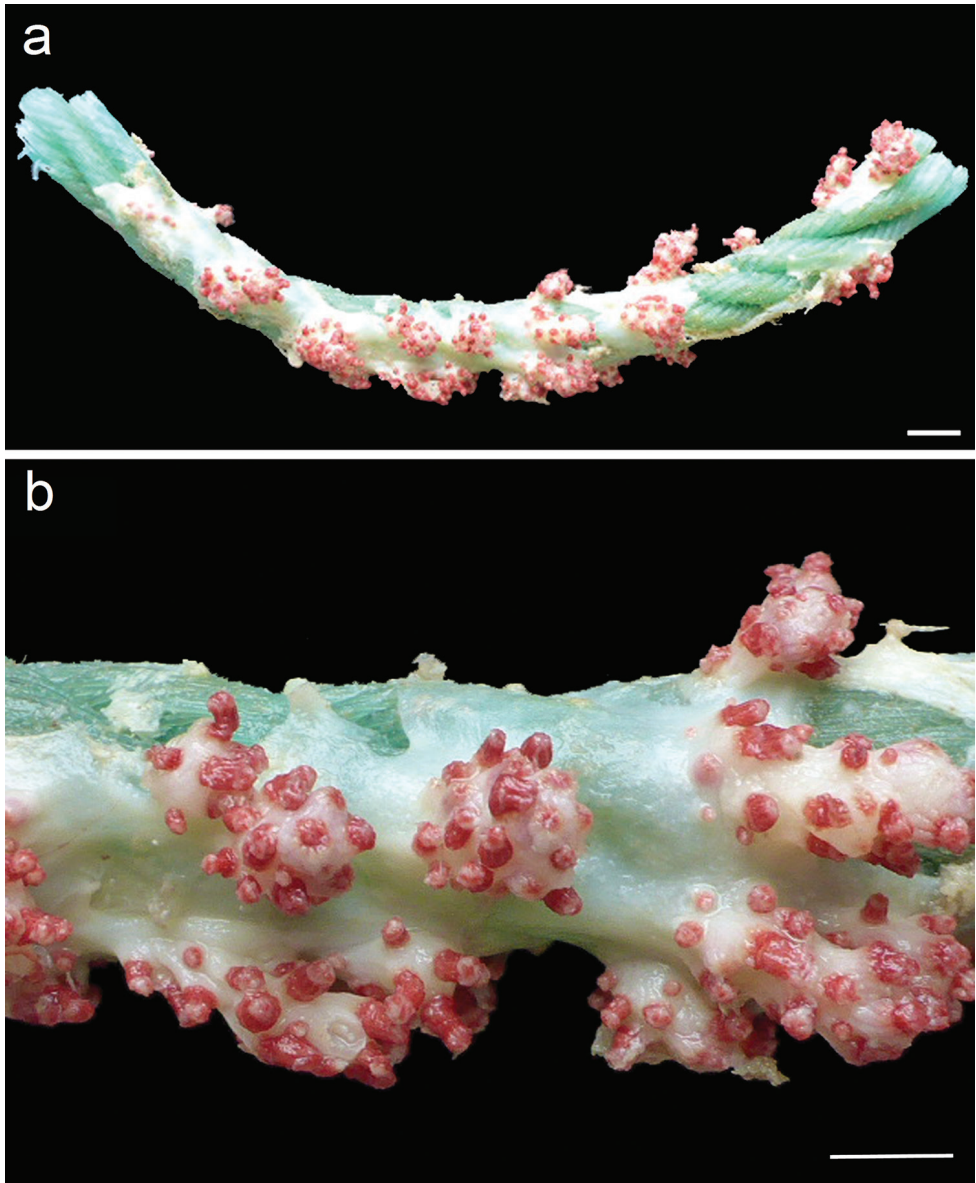


Figure 1. Holotype (RMNH Coel. 33879) of *Alcyonium rubrum* Stokvis & van Ofwegen, 2006, renamed *Alcyonium burmedju* nom. n. **a** Fishing rope serving as substrate for the encrusting soft coral (scale bar: 10 mm) **b** Detail of the colony. Scale bar: 5 mm.

Etymology. The epithet “burmedju” means red in the crioulo language spoken on Santiago Island in the Cape Verde Archipelago. The type locality is south of Raso islet, also localized in this island group (Stokvis and van Ofwegen 2006). Red is the predominant polyp colour of this species (Figure 1).

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References

- Braga-Henriques A, Porteiro FM, Ribeiro PA, de Matos V, Sampaio Í, Ocaña O, Santos RS (2013) Diversity, distribution and spatial structure of the cold-water coral fauna of the Azores (NE Atlantic). *Biogeosciences* 10: 4009–4036. doi: 10.5194/bg-10-4009-2013
- Hassall AH (1841) XXXIII – Supplement to a Catalogue of Irish Zoophytes. *Journal of Natural History* 7(44): 276–287. doi: 10.1080/03745484109442700
- ICZN (1999) International Code of Zoological Nomenclature (4th edn). International Trust for Zoological Nomenclature. London, 306 pp.
- Müller OF (1776) *Zoologiae Danicae prodromus, seu animalium Daniae et Norvegiae indigenarum characteres, nomina, et synonyma imprimis popularium*. Hallageriis, Havniae, 282 pp. doi: 10.5962/bhl.title.13268
- Stokvis FR, Van Ofwegen LP (2006) New and redescribed encrusting species of *Alcyonium* from the Atlantic Ocean (Octocorallia: Alcyonacea: Alcyoniidae). *Zoologische Mededelingen* 80(4): 165–183.

***Elthusa nierstraszi* nom. n., the replacement name for *Elthusa parva* (Nierstrasz, 1915), a junior secondary homonym of *Elthusa parva* (Richardson, 1910) (Isopoda, Cymothoidae)**

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Abstract

The recent transfer of *Elthusa parva* (Richardson, 1910) from *Ceratothoa* created a homonymy with *Elthusa parva* (Nierstrasz, 1915). *Elthusa parva* (Richardson, 1910) has priority and *Elthusa nierstraszi* **nom. n.** is proposed as the new replacement name for the junior secondary homonym *Elthusa parva* (Nierstrasz, 1915).

Keywords

Meinertia parva, *Livoneca parva*, junior homonym, new combination, marine fish parasite

Introduction

Hadfield et al. (2016) in redescribing poorly characterised species of *Ceratothoa* Dana, 1852 transferred the species *Ceratothoa parva* (Richardson, 1910) to *Elthusa* Schioedte & Meinert, 1884. In so doing *Elthusa parva* (Nierstrasz, 1915) was rendered a junior secondary homonym.

According to Articles 23.3.5, 52 and 60.3 of the International Code of Zoological Nomenclature (Anon 1999) *Elthusa parva* (Richardson, 1910) (originally in combination with *Meinertia* Stebbing, 1893) has priority and a new name *Elthusa nierstraszi* **nom. n.** is proposed for *Elthusa parva* (Nierstrasz, 1915) to remove the homonymy.

Abbreviations. RMNH – Rijksmuseum voor Natuurlijke Historie (Naturalis Biodiversity Center).

Taxonomic history

Meinertia parva Richardson, 1910: 21, fig. 20.

Codonophilus parvus: Nierstrasz 1931: 132.

Ceratothoa parva: Trilles 1994: 127.

Elthusa parva: Hadfield et al. 2016: 75, fig. 12.

Livoneca parva Nierstrasz, 1915: 98, pl. IV, figs. 18, 19; 1931: 143.

Elthusa parva: Bruce 1990: 287.

Lironeca parva: Trilles 1994: 182.

Suborder Cymothoida Wägele, 1989

Superfamily Cymothooidea Leach, 1814

Family Cymothoidae Leach, 1814

Genus *Elthusa* Schioedte & Meinert, 1884

Elthusa nierstraszi **nom. n.**

Livoneca parva Nierstrasz, 1915: 98–99, pl. IV, figs. 18, 19; 1931: 143.

Elthusa parva: Bruce 1990: 287; Sidabalok 2013: 56.

Lironeca parva: Trilles 1994: 182.

Holotype. Single ovigerous female (11 mm long; 5 mm wide), Kisser, Indonesia, coll. K. Schädler, 1898 (RMNH.CRUS.I.71).

Distribution. Kisser (= Kisar?) Island, Moluccas, Indonesia (Nierstrasz 1915).

Hosts. Unknown.

Etymology. The new name honours the original author Hugo Frederik Nierstrasz (1872–1937).

Remarks. *Elthusa nierstraszi* **nom. n.** replaces the name *Elthusa parva* (Nierstrasz, 1915), originally *Livoneca parva* Nierstrasz, 1915. *Elthusa nierstraszi* **nom. n.** has mesially directed, narrow anterolateral margins on pereonite 1; pereonite 7 not overlapping pleonite 1; pleonites all subequal in width and narrower than the pereon; and the posterior margin of the pleotelson forms a caudomedial point.

The cover date for Trilles' (1994) '*Prodromus*' was 1991, but the work was most likely completed prior to that of Bruce (1990) and Trilles was simply retaining *Livoneca parva* in its original combination (albeit using the alternative incorrect spelling *Lironeca*; see Anon 1996). Prior to Bruce (1990) the name *Livoneca* (also as *Lironeca*) was largely used in the sense of *Elthusa*, and there is no possibility that Nierstrasz's species would remain in or be returned to *Livoneca*, a strictly New World genus.

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References

- Anonymous (1996) Opinion 1849. *Livoneca* Leach, 1818 (Crustacea, Isopoda): the original spelling confirmed as correct, and the spelling *Lironeca* rejected. Bulletin of Zoological Nomenclature 53(3): 210–212.
- Anonymous (1999) International Code of Zoological Nomenclature. International Commission on Zoological Nomenclature, London, 306 pp.
- Bruce NL (1990) The genera *Catoessa*, *Elthusa*, *Ichthyoxenus*, *Idusa*, *Livoneca* and *Nortileca* n. gen. (Isopoda, Cymothoidae), crustacean parasites of marine fishes, with descriptions of eastern Australian species. Records of the Australian Museum 42: 247–300. doi: 10.3853/j.0067-1975.42.1990.118
- Hadfield KA, Bruce NL, Smit NJ (2016) Redescription of poorly known species of *Ceratothoa* Dana, 1852 (Crustacea, Isopoda, Cymothoidae), based on original type material. ZooKeys 592: 39–91. doi: 10.3897/zookeys.592.8098
- Leach WE (1814) Crustaceology. In: Brewster D (Ed.) The Edinburgh Encyclopaedia. Baldwin, London, 383–437.
- Leach WE (1818) Cymothoadées. In: Cuvier F (Ed.) Dictionnaire des Sciences Naturelles. Strasbourg et Levrault, Paris, 338–354.
- Nierstrasz HF (1915) Die Isopoden-Sammlung im Naturhistorischen Reichsmuseum zu Leiden – 1. Cymothoidae. Zoologische Mededelingen (Leiden) 1: 71–108.
- Nierstrasz HF (1931) Isopoda genuina. II. Flabellifera. In: Weber M, De Beaufort LF (Eds) Die Isopoden der Siboga-Expedition Siboga Expeditie (Uitkomsten op Zoologisch, Botanisch, Oceanographisch en Geologisch Gebied verzameld in de Oost-Indische 1899–1900 aan boord HM Siboga onder commando van Luitenant ter zee 1e kl GF Tydeman). EJ Brill, Leiden, 123–233.

- Richardson H (1910) Marine isopods collected in the Philippines by the U.S. Fisheries steamer *Albatross* in 1907–1908. Department of commerce and labor (USA), Bureau of fisheries document 736: 1–44.
- Schioedte JC, Meinert F (1884) Symbolæ ad monographium Cymothoarum crustaceorum isopodum familiæ. IV. Cymothoidæ Trib. II. Cymothoinæ. Trib. III: Lironecinæ. Naturhistorisk Tidsskrift, Kjøbenhavn 14: 221–454.
- Sidabalok CM (2013) List of marine isopods recorded from Indonesian waters. Marine Research in Indonesia 38(1): 49–66.
- Stebbing TRR (1893) A History of Crustacea. Recent Malacostraca. Kegan Paul, Trench, Trubner & Co. Ltd., London, 466 pp.
- Trilles J-P (1994) Les Cymothoidae (Crustacea, Isopoda) du Monde. Prodrome pour une faune. Studia Marina 21/22[for 1991]: 1–288.
- Wägele JW (1989) Evolution und phylogenetisches System der Isopoda. Stand der Forschung und neue Erkenntnisse. Zoologica (Stuttgart) 140: 1–262.