

**Research Article** 

# Redescription of the enigmatic myriapod *Hanseniella chilensis* (Hansen, 1903) (Symphyla, Scutigerellidae) based on scanning electron microscope images of Chilean specimens

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#### Abstract

Hanseniella chilensis is the only myriapod of the class Symphyla known from Chile. This garden centipede, or pseudocentipede, was described more than 120 years ago based on morphologically incomplete specimens collected in central Chile, a well-known biodiversity hotspot. In this study, we redescribe this species based on morphologically complete specimens collected near the type locality using scanning electron microscope images. Our study provides the description of diagnostic characters hitherto unknown in this species such as macrochaetae of the tergites and spinnerets of the cerci. We also include a new record from central Chile and discuss the presumed presence of this species in Argentina and Madagascar.

**Key words:** Biodiversity hotspot, biogeography, Chile, garden centipede, Myriapoda, pseudocentipede, SEM images, soil-dwelling arthropod, symphylans, taxonomy

# Introduction

Symphylans, also known as garden centipedes or pseudocentipedes, are soil-dwelling arthropods of the class Symphyla in the subphylum Myriapoda. Symphylans are among the least studied soil microarthropods in the world. Often, the identity and geographic distribution of these myriapods are uncertain because they are relatively small and so difficult to study that many researchers simply overlook them (Minelli and Golovatch 2001). Globally, these invertebrates are represented by around 250 species and two families, namely Scutigerellidae and Scolopendrellidae (Minelli 2011; Salazar-Moncada et al. 2015; Jin and Bu 2020; Jin et al. 2023). Symphyla inhabit moist soils on all continents except Antarctica (Minelli 2011). They are whitish and fragile-looking, typically measuring between 5 and 8 mm in length (Minelli and Golovatch 2001).

In the Neotropical region, symphylans are represented by 21 species distributed across six genera and two families (Scheller and Adis 1996). Of these 21 species, only 14 are endemic to this biogeographic region. The known number of Neotropical species is remarkably low considering the area and habitat heterogeneity of the region (Scheller and Adis 1996). These 14 species likely represent a tiny fraction of the true and still unknown diversity of Neotropical symphylans.

Chilean symphylans are among the least known in the Neotropical region (Vega-Román et al. 2012). In 1897, Attems reported the presence of *Scutig-erella immaculata* (Newport, 1845) on Navarino Island, a remote island on the southern tip of South America, Chile, between the Beagle Channel and the Drake Passage (Attems 1897). However, *S. immaculata* is endemic to the Holarctic region (northern hemisphere) and, therefore, Scheller (1992) suspects that Attems may have observed a similar, yet unidentified species on Navarino Island. Two years later, Silvestri (1899) also reported *S. immaculata* in central Chile, a well-known biodiversity hotspot. However, shortly afterwards, Hansen (1903) concluded that the specimens observed by Silvestri belonged to a new species he called *Scutigerella chilensis* Hansen, 1903. Finally, Bagnall (1913) transferred *S. chilensis* to the genus *Hanseniella*. Currently, *Hanseniella chilensis* (Hansen, 1903) is the only known symphylan species for Chile.

Later, Aubry and Masson (1953) allegedly recorded *H. chilensis* in Madagascar, which is more than 11,000 km from the type locality (central Chile) of this species. *Hanseniella chilensis* has not been observed again on that island, so its occurrence in Madagascar has yet to be confirmed. Subsequently, Juberthie-Jupeau (1962) documented the presence of *H. chilensis* in Argentina. This researcher noted that the specimens observed in Argentina were about twice as long as the specimens described in Chile.

To date, it is unknown whether the symphylans recorded in Madagascar and Argentina belonged to *H. chilensis* or to other similar yet undescribed species. Unfortunately, Hansen's original description of *H. chilensis* was based on individuals that lacked key morphological traits for identification and diagnosis of symphylans, such as most macrochaetae of the tergites and spinnerets of the cerci (Hansen 1903). Therefore, it is necessary to redescribe *H. chilensis* based on complete specimens and modern methods to improve the identification of this species and our knowledge of Neotropical symphylans.

In this study, we redescribe *H. chilensis* based on scanning electron microscope images of morphologically complete specimens collected in central Chile. Additionally, we report a new record in Chile and discuss the presumed presence of this species in Madagascar and Argentina.

#### Material and methods

Specimens of *H. chilensis* included in this study were collected between 2022 and 2023 in the rural locality of Lefuco, near Temuco city, La Araucanía region, central Chile. This reference is important because some of the specimens used by Hansen to describe *H. chilensis* came from the surroundings of this city (Hansen 1903). In the field, individuals were photographed alive with an Olympus Tough TG-6 digital camera, collected by hand and deposited in vials with 95% ethanol. The geographic location of each specimen was recorded using the coordinate format proposed by the world geodetic reference system

WGS84. The georeferenced data were plotted on a map constructed with QGIS v. 3.28.1 with ©MapTiler and ©OpenStreetMap data.

Once in the laboratory, specimens were deposited in Petri dishes with 95% ethanol or mounted on concave microscope slides filled with glycerol and examined under dissecting and light microscopes, respectively. Morphological features were measured using IMAGEJ v. 1.53u software (Schneider et al. 2012).

Specimens coded as APG-17-a and PG-71-L-a (field code, see results) were photographed under the scanning electron microscope (SEM). SEM specimens were mounted on stubs and then dehydrated using a Hitachi HCP-2 critical point dryer. Afterwards, specimens were coated with gold and palladium on a Leica EM ACE200 and photographed with a Zeiss EVO M10 SEM operating at 20 kV. The SEM photographs were processed in GIMP v. 2.10.32 software, and FIGUREJ plugin for IMAGEJ (Mutterer and Zinck 2013).

The investigated specimens were deposited at the Museo Nacional de Historia Natural de Chile (National Museum of Natural History of Chile, MNHN), Santiago, Chile.

#### Results

#### Taxonomy

Subphylum Myriapoda Latreille, 1797 Class Symphyla Ryder, 1880 Family Scutigerellidae Bagnall, 1913 Genus *Hanseniella* Bagnall, 1913

Hanseniella chilensis (Hansen, 1903) Figs 1–6

Scolopendrella immaculata Silvestri 1899: 370 (Not Newport, 1845).

Scutigerella chilensis Hansen, 1903: 27, 32, 46, 48, 51, plate 4, figs 4a–g; Silvestri 1905: 746; Porter 1912: 52; Domínguez 1992: 40; Vega-Román et al. 2012: 21, fig. 1.

Hanseniella (Hanseniella) chilensis Bagnall 1913: 198.

Hanseniella chilensis Ringuelet 1955: 110; ?Aubry and Masson 1953: 63; ?Juberthie-Jupeau 1962: 63, 75, fig. 5b; Scheller 1979: 607; 1992: 171; Soesbergen 2019: 34.

**Type locality.** Types not designated by Hansen (1903), but the author described species based on specimens collected from San Vicente, Biobío region and Temuco, La Araucanía region, central Chile.

**Material studied.** 2 males, **CHILE:** La Araucanía region, Malleco province, Estero Lefuco, under rotting wood chips, -38.5153, -71.7273, 15-I-2022, APG14 (field code); 1 male, same locality, leaf litter, -38.5135, -71.7263, 31-I-2022, APG17-a (field code); 1 male, 2 female, same locality, under a rotting log ca. 944 m a.s.l., -38.5132, -71.7275, 19-IX-2023, PG-71-L/PG-71-L-a (field code).

**Diagnosis.** Adults specimens of *Hanseniella chilensis* can be separated from related species by the following combination of characters: Central rod follow by a triangular sulcus with a distinct small anterior seta, and two posterior setae (Figs 1A, 2A); antennae usually with 29–37 (30–40 in Hansen (1903)



**Figure 1**. APG-17-a Male, dorsal view **A** head, first tergite and part of the second tergite (dfs-distinct frontal seta, ms-macroseta) **B** tergites 2-5 (am-anterolateral macrochaeta, hm-hind macrochaeta, pm-posterolateral macrochaeta) **C** tergites 11-13 **D** last tergite and cerci (hm-hind macrochaeta (abraded), hs-hind seta). Scale bars: 200.0  $\mu$ m (**A**-**C**); 100.0  $\mu$ m (**D**).

specimens) antennomeres; first tergite rudimentary with one row of 9-11 setae (Fig. 1A); dorsal cuticle scale-like and no pubescence or microsetae present (Fig. 2B), macrochaetae present on most tergites as in Table 1 (Fig. 1B–D); first podomere of first pair of legs bearing a posterolateral line of ca. 10 laminar needles; third podomere of  $12^{th}$  pair with one large dorsoposterior seta, 0.8 times the breadth of the podomere and fourth podomere bearing two distinct dorsoposterior larger setae, the largest being 1.2 times the breadth of the podomere [larger than in *Hanseniella capensis* (Hansen, 1903)].

**Description.** Length of body (measured dorsally) without cerci and antennae: female ca. 3.5–4.3 mm, males ca. 4.7–5.2 mm. *Head.* 1.4 times broader than



**Figure 2**. Details of some relevant structures of APG-17-a Male (**A**, **B**) and PG-71-L-a Female (**C**, **D**) **A** central rod and triangular sulcus from the top of the head (hs-hind seta, oe-ovoid end, ss-short seta, ts-triangular sulcus) **B** tergal surface of tergite 3 (cr-cuticular rim) **C** Tömösváry organ and proximal surface (km-knob with microseta, lp-linguiform protuberance) **D** apical zone of the last antennomere (sb-sensilla basiconica, so-sensory organ). Scale bars: 50.0 μm (**A**, **B**); 10.0 μm (**C**, **D**).

long, frontal margin slightly convex with 1+1 distinct setae, lateral margins convex with a sharp anterolateral angle, posterior margin concave with rounded posterolateral angles (Fig. 1A). Central rod well defined, posterior end slightly ovoid, followed by a triangular sulcus with a short seta near the anterior end, and 1+1 hind setae, both directed inwards and forwards (Figs 1A, 2A). Frontal and top of head sparsely covered with setae, 3+3 macrosetae near the antennal base and 1+1 anterolateral macrosetae, ca. 2.1 as long as common head setae (Fig. 1A). Tömösváry organ circular, proximal surface covered by linguiform protuberances and small knobs bearing microsetae (Fig. 2C). First maxillae

simple, with a single subtriangular palp, ca. 1.6-2.0 longer than wider, around the same length of the most proximal setae. Second maxillae distal margin with 3+3 papilla-bearing lobes, anterior part with several protuberances, each one supporting a single seta, anterolateral margin with 3+3 (some males with 4+4) two-forked organs with a small medial process subtruncated at the tip. Both maxillae bearing setae across the surface. Antennae. Long, ca. 0.4-0.5 times the body length, with 29-37 antennomeres. Surface covered by pubescence, 1st antennomere with only one distal whorl of setae, 2<sup>nd</sup>-10<sup>th</sup> antennomeres with two poorly defined whorls very close to each other, middle whorl composed by larger setae and the distal by shorter setae, a 3rd whorl begins around 8th-14th antennomere below middle whorl. Small tri-forked organ on the distal margin starting from 4-9th antennomere and on, appears to be four-forked on later antennomeres. Sensilla basiconica present on distal margin from 8-10th antennomere and on, increasing in number and more acuminated in shape towards distal antennomeres (Fig. 4A). Distal margin of antennomeres with granular surface. First antennomeres ca. 1.7-1.8 times broader than long (Figs 1A, 3A), 2-4 antennomeres ca. 2.7-2.8 times broader than long, middle antennomeres ca. 1.1-1.5 times broader than long, distal antennomeres elongated and ca. 0.8 times broader than long. Apical antennomere spherical, sensilla basiconica present, apex of the segment bearing a large sensory organ borne from a small protuberance, composed of a central stalk which yields 5 slightly longer spiniform processes with curved-inwards tips; two additional similar organs, a large and a smaller one, composed of 4 spiniform processes in total besides the central stalk, basal protuberance absent or remarkably reduced (Figs 2D, 4B). Tergites. Cuticle scale-like, surface smooth except for seta and macrochaeta (Figs 1B–D, 2B). Rows and number of setae as in Table 1. First tergite rudimentary, with one row of 9–11 setae, a pair longer than the rest (however it seems to be a variable character) (Fig. 1A). Anterior surface portion from the second tergite and on with a set of circular cuticular rims (Fig. 2B). Hind setae rather large, increasing gradually but considerable in length towards the posterior body portion, on last segments almost equal in length to macrochaetae (Fig. 1C). First, third, sixth, tenth, and fourteenth tergite semicircular, fourth, fifth, seventh, eleventh, and twelfth subtrapeziform, eighth and thirteen subrectangular, fifteenth subquadrate. Third, sixth, ninth, twelfth and fourteenth tergites longitudinally broader than preceding ones. Posterior margin as in Table 1. Tergal surface with poorly defined rows of setae as in Table 1 (Figs 1B, C, 2B). Second and third tergite bearing on each side one anterolateral macrochaeta directed slightly forwards, one posterolateral macrochaeta directed outwards and forwards, and a posterior macrochaeta borne from the hind margin also directed outwards and forwards (Fig. 1B). Fourth and fifth tergite bearing only one posterolateral and hind-borne macrochaetae on each side (Fig. 1B). Sixth with macrochaetae same as second and third tergite. Seventh and eighth with macrochaetae same as fourth and fifth tergite. Ninth macrochaetae same as sixth tergite. Tenth and eleventh macrochaetae same as seventh and eighth. Twelfth macrochaetae same as ninth. Thirteenth and fourteenth macrochaetae same as tenth and eleventh. Posterior margin of last tergite with two short hind setae between cerci and two macrochaetae pointed outwards near the cerci base, U-shaped incision absent (Fig. 1D). Ventral surface. Covered by microsetae (Fig. 3B), last segment surface with laminar needles borne at the posterior end

Tergite number	Number of setae on tergal surface and margins (ca.)	Number of rows (counting hind setae as so)	Anterolateral macrochaeta (per side)	Posterolateral macrochaeta (per side)	Hind macrochaeta pointing outwards and/or forwards (per side)	Posterior margin
2	33-38	3	1	1	1	Almost straight
3	41-55	3	1	1	1	Almost straight
4	42-52	3	0	1	1	Almost straight
5	37-47	3	0	1	1	Almost straight
6	61-82	5	1	1	1	Almost straight
7	56-65	3	0	1	1	Slightly concave
8	38-55	3	0	1	1	Slightly concave
9	67-82	5	1	1	1	Almost straight
10	57-65	3	0	1	1	Slightly concave
11	44-59	3	0	1	1	Slightly concave
12	66-84	5	1	1	1	Almost straight
13	54-65	3	0	1	1	Slightly concave
14	61-71	5	0	1	1	Slightly concave
15	33-46	2-3	0	0	1	Convex between cerci

Table 1. Chaetotaxy and posterior margin shape of the tergites, except the rudimentary first tergite.

of scale-like layers. Coxal sacs. Mostly heart-shaped, fully developed at the bases on legs 3-9, margins with short setae and around 8-13 larger setae (Fig. 3C). Male organs. Two very simple ventral contiguous semicircular plates held closely together and covered by pubescence. Legs. First pair of legs composed of 4 segments, from proximal to distal: First podomere short, bearing 3-4 setae, lateral cuticle scale-like, bearing a posterolateral line of ca. 10 laminar needles (similar to Fig. 3B). Second podomere 2.0 times longer than wider, dorsal and lateral cuticle scale-like (similar to Fig. 3B), one large distinct seta held proximolaterally and ca. 12 lateral setae, anteroventrally with 2 setae, largest seta held medioventrally and 0.8 times the breadth of the podomere, followed by a short spine held on a small bump, and two ventrodistal large setae, a line of several laminar needles near the laterodistal margin and most distal "scales" also bearing laminar needles (similar to Fig. 3B). Third podomere subequal in length and width, surface pubescent, bearing 3 dorsal setae and 4 lateral setae. First to third podomere distal margins glabrous and microgranulated, scale-like surface also glabrous. Fourth podomere 3.9 times longer than wider, surface pubescent, with ca. 11 dorsal, 6 lateral and ca. 9 ventral setae; dorsal and ventral setae increasing gradually in length towards the apex. Two claws, posterior more curve and around 3/5 the length of the anterior claw, frontal seta around 1/2 the length of the anterior claw (Figs 3A, 4C). 12th pair of legs composed of 5 segments: First podomere short, with ca. 12-13 ventral setae, surface scalelike, distal "scales" bearing laminar needles. Second podomere 1.7 times longer than wider, dorsal surface scale-like, 1-3 distodorsal setae, ca. 31 lateral setae, dorsolateral surface also scale-like, lateroventrally with "scales" bearing laminar needles (similar to Fig. 3B), and a short spine near the margin held on a small bump, ventral surface pubescent and bearing ca. 14 setae, 2 large distinct setae and one medial short spine. Third podomere subequal in length and



**Figure 3.** PG-71-L-a Female, ventral view **A** head and first pair of legs **B** ventral surface details proximal to left leg of pair 8 and its 2 first podomeres, podomere 4 and 5 of pair 7 partially show (Im-laminar needles, sc-scale-like cuticle, slm-"scales" with laminar needles) **C** coxal sac near leg pair 4 **D** last pair of legs and cerci (ap-apical seta, ls-large seta, os-outer seta). Scale bars: 100.0  $\mu$ m (**A**, **D**); 50.0  $\mu$ m (**B**); 20.0  $\mu$ m (**C**).

width, bearing ca. 13 dorsal setae and one large dorsoposterior seta, 0.8 times the breadth of the podomere (Fig. 3D), laterally with ca. 9 setae, posterior margin with a line of several needles and "scales" also with laminar needles. Fourth podomere 1.6 times longer than wider, surface pubescent, bearing several setae and two distinct dorsoposterior larger setae, the largest being 1.2 times the breadth of the podomere (Fig. 3D). First to fourth podomere distal margins glabrous and microgranulated, scale-like surface also glabrous. Fifth podomere 3.1 times longer than wider, surface pubescent with several setae. Dorsal setae of podomeres generally longer than the ventral ones (Fig. 3D). Two claws, both





curve, anterior claw basally thicker and slightly longer, frontal setae around 7/10 the length of anterior claw (Fig. 4D). *Styli*. Short and straight, densely covered by pubescence, bearing two distinct large setae on distal end, largest one around 1.8–2.2 times the length of the shorter one, last one difficult to see sometimes, held posterolaterally (Fig. 4E). *Sense calicles*. Pit margin covered by simple short setae and what appears to be bi- and tri-branched setae. Two distinct larger setae posteromedial to pit, 5.3 times the length of the short pit margin setae. Sensory seta inserted in the middle of the cavity, very long. *Cerci*. Surface covered by medium-size setae, which increase in length towards the apex, distal end without setae, apical seta 0.9 times the wider part of cerci, accompanied by a smaller outer seta around 0.25 times the length of the apical seta (Figs 1D, 3D).

**Distribution.** Africa: ?Madagascar: Banks of Betaly River, near Bezavona (see Remarks); South America: Argentina: Neuquén Province: Lago Curruhué (Currhue mendum Juberthie-Jupeau 1962); Lago Los Cántaros. Neuquén-Río Negro Provinces: Nahuel Huapi Reserve. Río Negro Province: Lago Frías; Puerto Blest. Chile: Biobío Region: San Vicente. Araucanía Region: Lefuco; Temuco; ?Villarrica (see Remarks). (Silvestri 1899; Hansen 1903; Aubry and Masson 1953; Juberthie-Jupeau 1962) (Fig. 5).



**Figure 5.** All known records of *Hanseniella chilensis* (Hansen, 1903). Diamond = uncertain records from the literature, Star = new record herein, Circle = literature records.

**Remarks.** Direction of macrochaetae can be variable due to specimen conservation and preparation on slides, but on live specimens in the field, the macrochaetae seem to point forwards in most, if not all, tergites (Fig. 6A–C); it is important to note that some setae and macrochaetae were abraded on the SEM specimens. An additional record of *H. chilensis* is reported in Madagascar by Aubry and Masson (1953), however, it is very likely that it is a morphologically similar species or accidentally introduced on the island; the authors likewise point out that the presence of this species on the island is strange (Fig. 5). Silvestri (1899) also mentions Villarrica as an additional record where he observed *H. chilensis* (at the time misidentified as *S. immaculata*), nevertheless, this locality is never mentioned again by Hansen (1903) nor Bagnall (1913) (Fig. 5).

**Affinities.** Investigation of complete specimens of *H. chilensis* collected in central Chile allowed us to conclude that this species shares important morphological similarities with only one other congeneric species. Particularly, we



Figure 6. A, B habitus of the species C general habitat where the species can be found.

noted that *H. chilensis* exhibits macrochaetae on all tergites (excluding the rudimentary first), a trait shared only with *H. capensis* (Hansen 1903; Soesbergen 2019). Although it can be easily distinguished from *H. capensis* by the shape of the claws of the last pair of legs, as in this last species, the claws are distinctively thicker basally (Hansen 1903). Also, the overall number of macrochaeta per tergite is higher in *H. chilensis* than in *H. capensis*.

Additionally, Soesbergen (2019) described in his appendix that *H. arborea* Scheller, 1979 possesses macrochaeta on all tergites; however, in the original description, Scheller (1979) explicitly describes that the species exhibit macrochaeta on tergites 2-4, 6, 7, 9, 10, 12, 13 and 14. This last author also mentions that the distribution of macroseta or "large setae" on the fourth and fifth podomeres of the last pair of legs is closely similar to *H. chilensis*, but we noted that they are remarkedly shorter in length.

Unfortunately, we were unable to compare *H. chilensis* with *H. hardyi* (Chamberlin, 1920), *H. neozelandica* (Chamberlin, 1920) and *H. paolettii* Scheller, 1993 because the number of macrochaetae present in their tergites remains unknown (Soesbergen 2019). Therefore, the morphological affinity between *H. chilensis* and these last three species remains mostly unresolved.

#### Discussion

Hanseniella chilensis is a symphylan species described by Hansen (1903) using damaged specimens collected in central Chile. Our study provides a detailed

redescription of this species based on morphological analysis via SEM images and microscopy observation of morphologically complete specimens. We collected our specimens in Lefuco, a rural locality near Temuco, the place of origin of some of the specimens used by Hansen to describe *H. chilensis* in 1903. One of the most important contributions of our study was to describe, for the first time, morphological traits that were previously unknown in this species, such as the macrochaetae of all tergites. These traits were not included in the original description of *H. chilensis* and remained unknown for more than 120 years. The lack of knowledge of these and other morphological traits has historically hindered the identification of this species.

After being described in Chile, *H. chilensis* was recorded in Madagascar (Aubry and Masson 1953) and in Argentina (Juberthie-Jupeau 1962). At present, it is not clear whether the symphylans recorded in Madagascar and Argentina really belong to *H. chilensis*. Prior to our study, some important diagnostic characters of this species were unknown, and therefore, there is a high chance that specimens identified outside Chile may have belonged to another species.

The latter scenario is plausible because Chile is surrounded by biogeographic barriers that limit species dispersal, including the Atacama Desert in the north, the Andes Mountains in the east, the Pacific Ocean in the west, and the Drake Passage to the south (Fernández et al. 2016). These barriers have kept Chilean biota isolated from the rest of the world for thousands of years and have favored the radiation of endemic animals, plants and microorganisms (e.g., Eisenberg and Redford Kent 1992; Lazo Araya 2015; Fernández et al. 2015, Rodriguez et al. 2018; Campello-Nunes et al. 2022; Parra-Gómez and Fernández 2022). These barriers surely represent insurmountable hurdles for animals such as symphylans. It is difficult to imagine them climbing mountains of more than 6,000 m altitude to cross from Chile to Argentina or swimming more than 11,000 km to reach Madagascar. At least not by their own means. Therefore, *H. chilensis* could be a species endemic to central Chile, a region recognized as a biodiversity hotspot.

Alternatively, *H. chilensis* could be a truly ubiquitous species, which has managed to establish viable populations in different countries. The means of dispersal of symphylans remains unknown, but we can assume that they could overcome biogeographic barriers by passive dispersal. Airborne dispersal is used by some arthropods, but symphylans are unlikely to use this method. They are soil-dwelling and apparently do not have morpho-physiological adaptations to balloon-like spiders or to resist desiccation and UV radiation for long periods of time. Phoretic dispersal seems more plausible since symphylans could overcome biogeographic barriers by being transported on the fur of mammals or feathers of migratory birds. They could also colonize islands by floating on objects such as driftwood. Accidental introduction might be another plausible means of passive dispersal. There is currently an active trade in raw materials and products of plant origin among Chile, Madagascar and Argentina (World Trade Organization 2024). Repeated introductions of *H. chilensis* could eventually favor the establishment of viable populations in exotic sites.

The ecology of *H. chilensis* is unknown, so we are unaware of the consequences that the introduction of this species into exotic ecosystems could have. For example, the symphylan *Scutigerella immaculata* has been accidentally introduced in several countries and now is considered an agricultural pest (Waterhouse 1968). Moreover, we ignore the geographic origin of this species. If we assume that *H. chilensis* is a ubiquitous species it could have radiated and been introduced in any of the countries where it has been reported. Perhaps the symphylans identified as *H. chilensis* in Chile (Hansen 1903), Madagascar (Aubry and Masson 1953) and Argentina (Juberthie-Jupeau 1962) are just ecophenotypes of the same species, which could explain why Argentine specimens are longer than those from Chile.

The information provided in our study could contribute to resolving the geographic range of *H. chilensis*, including its status as an endemic or ubiquitous species. We have redescribed *H. chilensis* in detail: we provided SEM images as well as drawings and descriptions of diagnostic characters that were previously unknown in this species. Therefore, it is now possible to investigate whether the putative specimens of *H. chilensis* from Madagascar and Argentina belong to the same species. The resolution of this long-standing question would not only improve our understanding of Symphyla diversity, but also provide indirect information on the dispersal strategies and dispersal ability of these arthropods.

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# **Additional information**

## **Conflict of interest**

The authors have declared that no competing interests exist.

#### **Ethical statement**

No ethical statement was reported.

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#### Author contributions

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#### **Data availability**

All of the data that support the findings of this study are available in the main text.

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**Research Article** 

# An updated synthesis of the Geophilomorpha (Chilopoda) of Asian Russia

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#### Abstract

A comprehensive overview of the state of knowledge on the Chilopoda Geophilomorpha of the Asian part of Russia is presented, based on the critical revision of all published morphological descriptions and all geographical records. Revised diagnoses for all the 38 nominal species so far reported from Asian Russia are given, with comments on their validity. Among them a total of 18 species are recorded only from this region and many of them from a single locality only. The species belong to Geophilidae s. I., (in the genera *Arctogeophilus, Geophilus, Pachymerium,* and *Strigamia*), Schendylidae (*Escaryus*), and Mecistocephalidae (*Agnostrup, Arrup,* and *Tygarrup*). At least two species have been introduced, namely *Geophilus flavus* and *Tygarrup javanicus*. The history of studies on the Geophilomorpha in the Asian part of Russia are also summarized.

**Key words:** Biodiversity, fauna, Geophilidae, Mecistocephalidae, Russian Far East, Schendylidae, Siberia

#### Introduction

The fauna of Chilopoda Geophilomorpha of large part of the Palearctic region, especially the Asian part of Russia, is still badly understood in comparison with other regions. While the species recorded from Europe, including the European part of Russia, have been recently reviewed (Bonato and Minelli 2014; Volkova 2016), available information and records on the Geophilomorpha living in the Asian part of Russia are still scattered in many and relatively old publications. Moreover, the overall knowledge of many species is largely incomplete, with brief descriptions hardly accessible or comparable.

The present paper aims to provide a comprehensive overview of the state of knowledge of Geophilomorpha from Asian Russia, in order to promote and facilitate further taxonomic and faunistic investigations.



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## Material and methods

We searched the entire taxonomic, faunistic, and ecological literature, to the best of our abilities, to retrieve all taxonomic descriptions, morphological data, and occurrence records of Geophilomorpha from the Asian part of Russia.

For the taxonomy and nomenclature, we referred to Bonato et al. (2014) and ChiloBase (Bonato et al. 2016). For each nominal species, we produced a diagnosis by translating and interpreting its original description, other published morphological information reliably referring to the species, all published illustrations, and taxonomic opinions. We also added diagnoses for the genera. However, for the diagnoses of families we refer to Bonato (2011).

We referred the occurrence records to modern administrative units (Fig. 1). The translation of names of Russian administrative divisions into English follows Kazantsev (2022). The Asian part of Russia is a huge region from the Ural Mountains in the west to the Pacific Ocean in the east (Gvozdetskiy and Mikhailov 1978). It spans an area of 13.1 million square kilometers and is often divided into three regions: Western Siberia, Eastern Siberia, and Far East. Western Siberia (approximately between the Urals and the Yenisei River) includes the following administrative units: Yamalo-Nenets and Khanty-Mansi autonomous okrugs; Sverdlovsk, Chelyabinsk, Kurgan, Tyumen, Omsk, Tomsk, Novosibirsk, and Kemerovo oblasts; Altai krai; republics of Altai and Khakassia. Eastern Siberia (approximately between the Yenisei River and the watersheds that run parallel to the coast of the Pacific Ocean) includes the following units: Krasnoyarsk and Zabaykalsky krais; Irkutsk oblast; republics of Tuva, Buryatia, and Sakha (Yakutia); the western parts of Khabarovsk krai, Magadan oblast, and Chukotka autonomous okrug. Russian Far East (river basins flowing into the Pacific Ocean, as well as Wrangel, Commander, Shantar Islands, the Kuril, and Sakhalin) includes the following units: Amur and Sakhalin oblasts, the eastern part of Magadan oblast; Jewish autonomous oblast; the eastern part of Chukotka autonomous okrug; Kamchatka, Maritime krais, and the eastern part of Khabarovsk krai.

Families, genera within families, and species within genera are listed alphabetically (see also Table 1). For each species, we report the type locality/ies, both as indicated in the original publications and with their modern names; the estimated coordinates of the type locality/ies (only for species described from Asian Russia); information on the type material, including the depository (only for species described from Asian Russia or adjacent territories); references to all sources of records for Asian Russia, and to other selected publications that are relevant for the taxonomy, morphology, and distribution of the species; the distribution within Asian Russia and outside; and finally, remarks on the taxonomic status and distribution.

An asterisk (\*) indicates nominal species whose taxonomic validity requires confirmation.

#### Abbreviations for depositories

- NHMD Natural History Museum of Denmark, Copenhagen;
- NHMW Natural History Museum Vienna (Austria);
- **ZISP** Zoological Institute of the Russian Academy of Sciences (Saint Petersburg, Russia);
- ZMH Zoological Museum in Hamburg (Germany);
- **ZMMU** Zoological Museum of the Moscow State University (Moscow, Russia).



Figure 1. Administrative units of Asian Russia. Western Siberia: Chel – Chelyabinsk oblast, Sver – Sverdlovsk oblast, Kha – Khanty-Mansi autonomous okrug, Yam – Yamalo-Nenets autonomous okrug, Kur – Kurgan oblast, Tyum – Tyumen oblast, Omsk – Omsk oblast, Tomsk – Tomsk oblast, Novos – Novosibirsk oblast, Altkr – Altai krai, RepAlt – Republic of Altai, Kem – Kemerovo oblast, Khak – Republic of Khakassia; Eastern Siberia: Tuva – Republic of Tuva, Krasn – Krasnoyarsk krai, Irkut – Irkutsk oblast, Buryat – Republic of Buryatia, Zabayk – Zabaykalsky krai, Sakha – Republic of Sakha (Yakutia); Far East: Amur – Amur oblast, Khabar – Khabarovsk krai, Magad – Magadan oblast, Chukot – Chukotka autonomous okrug, Kamch – Kamchatka krai, Jewish – Jewish autonomous oblast, Marit – Maritime krai, Sakh – Sakhalin oblast.

# Results

Family Geophilidae Leach, 1816

# Genus Arctogeophilus Attems, 1909

**Diagnosis.** Geophilids with head distinctly elongate; clypeal areas present, variously distinct; labral side-pieces almost touching medially; second maxillary coxosternite medially very short and poorly sclerotized, with statuminia, without anterior inner processes; second maxillary pretarsus claw-like; forcipular tergite distinctly narrower than subsequent tergite, with pleurites exposed dorsally; forcipular coxosternite relatively broad posteriorly, without anterior denticles, with chitin-lines short or absent, with coxopleural sutures subparallel in their anterior half; forcipular trochanteroprefemur distinctly elongate, with distal denticle; forcipular tarsungulum with basal denticle; trunk sternites without "carpophagus" structures; ventral pore-fields usually absent; metasternite of ultimate leg-bearing segment longer than wide; coxopleura usually with sparse pores; legs of the ultimate pair longer than the penultimate legs, often without pretarsus. See Table 2. **Table 1.** Nominal species of Geophilomorpha reported from Asian Russia: i – anthropochore introduction, \* – uncertain taxonomic validity, ! – known from Asian Russia only.

Nº	Species	European Russia	Western Siberia	Eastern Siberia	Far East			
Fam	ily Geophilidae Leach, 1816	1						
Geni	us Arctogeophilus Attems, 1909							
1	A. glacialis (Attems, 1909)				+			
2	A. macrocephalus Folkmanová & Dobroruka, 1960 *	+	+	+	+			
3	A. sachalinus Verhoeff, 1934 * !				+			
Genus Geophilus Leach, 1814								
4	G. bipartitus Takakuwa, 1937 !				+			
5	G. flavus (De Geer, 1778)	+	+i	+				
6	G. orientalis Sseliwanoff, 1881 * !				+			
7	G. proximus C.L. Koch, 1847	+	+					
8	G. rhomboideus Takakuwa, 1937				+			
9	G. sibiricus Stuxberg, 1876 * !			+				
10	G. sounkyoensis Takakuwa, 1937				+			
Geni	us Pachymerium C.L. Koch, 1847							
11	P. ferrugineum (C.L. Koch, 1835)	+	+		+			
12	P. pilosum (Meinert, 1870) * !			+	+			
Geni	us Strigamia Gray, 1843							
13	S. cf. acuminata (Leach, 1815)	+			+			
14	S. alokosternum (Attems, 1927)				+			
15	S. hirsutipes (Attems, 1927) *				+			
16	S. pusilla (Sseliwanoff, 1884)	+	+	+				
17	S. sacolinensis (Meinert, 1870) * !				+			
18	S. sibirica (Sseliwanoff, 1881) * !			+				
19	S. sulcata (Sseliwanoff, 1881) * !				+			
20	S. cf. transsilvanica (Verhoeff, 1928)		+		+			
Fam	ily Mecistocephalidae Bollman, 1893							
Geni	us Agnostrup Foddai, Bonato, Pereira & Minelli, 2003							
21	A. striganovae (Titova, 1975) !				+			
Geni	us Arrup Chamberlin, 1912							
22	A. dentatus (Takakuwa, 1934)				+			
23	A. mamaevi (Titova, 1975) !				+			
Geni	us <i>Tvaarrup</i> Chamberlin. 1914							
24	T. javanicus Attems, 1929		+i					
Fam	ily Schendylidae Cook, 1896							
Geni	us Escaryus Cook & Collins, 1891							
25	E. chadaevae Titova, 1973	+	+	+				
26	E. chichibuensis Shinohara. 1955 *				+			
27	E. dentatus Titova. 1973 * !				+			
28	E. hirsutus Titova 1973 * !				+			
29	E. japonicus Attems. 1927 *	+	+	+	+			
30	E. koreanus Takakuwa. 1937 *		+	+	+			
31	E. krivolutskiji Titova. 1973 * !				+			
32	E. molodovae Titova, 1973 * !				+			
33	E perelae Titova 1973 * I				+			
34	E polygonatus Titova 1973 * 1				+			
35	E retusidens Attems 1904	+	+		+			
36	E sachalinus Takakuwa 1935				+			
37	E sibiricus Cook 1899 l				+			
38	E. vitimicus Titova. 1973 * !			+	-			

 Table 2. Differences between species of the genus Arctogeophilus Attems, 1909 known from Asian Russia and adjacent territories.

Species	Characters					
Species	First maxillary lappets Denticles on forcipular intermediate article		Ventral pore-fields			
A. glacialis (Attems, 1909)	short	slightly shorter than other denticles	absent			
A. macrocephalus Folkmanová & Dobroruka, 1960	long	smaller than other denticles	on some anterior segments			
A. sachalinus Verhoeff, 1934	long	absent	on some anterior segments			
A. attemsi Folkmanová, 1956	long	absent	absent			

#### 1. Arctogeophilus glacialis (Attems, 1909)

Geophilus (Arctogeophilus) glacialis Attems 1909: 23. Arctogeophilus glacialis – Attems 1929: 297; Chamberlin 1946: 182. Cryophilus alaskanus Chamberlin 1919: 18 (synonymy by Chamberlin 1946: 182).

**Type localities.** RUSSIA: Chukotka autonomous okrug: "Nunamo" (Attems 1909; see Remarks), "Konyam Bay im Senjavin Sund" (Attems 1909) = Penkigney Bay, ca 64°49'N, 172°53'W; USA: Alaska: "Port Clarence" (Attems 1909), ca 65°15'N, 166°51'W.

**Type series.** *Syntypes*: 7 specimens, including 3 males and 4 females. Deposited in NHMW (Ilie et al. 2009).

**Diagnosis.** A species of *Arctogeophilus* with first maxillary lappets relatively short; denticles on all forcipular articles; denticles on the forcipular intermediate articles only slightly shorter than those on trochanteroprefemur and tarsungulum; 39 leg-bearing segments, possibly invariably; ventral pore-fields absent; pretarsus of ultimate legs absent.

**Distribution.** Far East: Chukotka autonomous okrug (Attems 1909). Outside Asian Russia: Alaska and Canada (e.g., Attems 1909; Chamberlin 1946; Langor and Langor 2022).

**Remarks.** The position of the locality "Nunamo" (indicated by Attems 1909) is uncertain: the original material was collected during the Vega expedition, and Nordenskiöld (1882: 565, 567) mentioned a tent-village "Nunamo" located in Chukotka, but he did not indicate the precise position of this place. Instead, Nordenskiöld (1882: 565) provided coordinates for "Konyam Bay" = Penkigney Bay.

#### 2. Arctogeophilus macrocephalus Folkmanová & Dobroruka, 1960 \*

Arctogeophilus macrocephalus Folkmanová & Dobroruka, 1960: 1815. Arctogeophilus sp. – Byzova and Chadaeva 1965: 333.

Arctogeophilus macrocephalus – Zalesskaja et al. 1982: 188; Ganin 1997: 105, 109, 112, 114, 129, 134, 141; Vorobiova 1999: 33; 2002: 63; Rybalov 2002: 83; Farzalieva 2008: 56; Volkova 2016: 671; Nefediev et al. 2017a: 8; 2017c: 221; 2018: 236; 2021: 37; Dyachkov and Tuf 2019: 25; Nefediev 2019: 24.

**Type locality.** RUSSIA: Republic of Tatarstan: Chistopolsky District: "Bliz s. Zmievo" (Folkmanová and Dobroruka 1960) = near Zmievo village, ca 55°23'N, 50°43'E. **Type series.** *Syntypes*: 20 specimens. Depository unknown. **Diagnosis.** A species of *Arctogeophilus* with first maxillary lappets relatively long; denticles on all forcipular articles, those on intermediate articles smaller than those on trochanteroprefemur and tarsungulum; 35–43 leg-bearing segments; ventral pore-fields on some anterior segments; pretarsus of ultimate legs absent.

**Distribution**. Western Siberia: Sverdlovsk, Chelyabinsk, Tomsk, and Kemerovo oblasts, Altai krai, republics of Altai and Khakassia (Byzova and Chadaeva 1965; Zalesskaja et al. 1982; Farzalieva 2008; Nefediev et al. 2017a, 2017c, 2018, 2021; Nefediev 2019). Eastern Siberia: Republic of Tuva and Krasnoyarsk krai (Zalesskaja et al. 1982; Vorobiova 1999; Rybalov 2002; Vorobiova et al. 2002). Far East: Jewish autonomous oblast, Amur oblast, Khabarovsk and Maritime krais, Chukotka autonomous okrug, and Sakhalin oblast (Sakhalin and Kunashir islands) (Zalesskaja et al. 1982; Ganin 1997). Outside Asian Russia: westwards to Transcarpathia (Zalesskaja et al. 1982; Volkova 2016) and Eastern Kazakhstan (Dyachkov and Tuf 2019).

**Remarks.** Zalesskaja et al. (1982: 189) suggested this species can be a junior synonym of *A. glacialis* (Attems, 1909), and this is still in doubt (Nefediev et al. 2017a). Because of this uncertainty, the actual taxonomic status of the populations of *Arctogeophilus* from the Far East remains to clarify.

The type locality for *A. macrocephalus* has been sometimes reported erroneously in previous publications (e.g., Bonato and Minelli 2014).

#### 3. Arctogeophilus sachalinus Verhoeff, 1934 \*

Arctogeophilus sachalinus Verhoeff 1934: 15.

Arctogeophilus sachalinus – Takakuwa 1940: 135; Molodova 1973: 67; Kurcheva 1977: 45; Zalesskaja et al. 1982: 188; Ganin 1997: 121, 124, 126, 128, 134.

**Type locality.** RUSSIA: Sakhalin oblast: "Insel Sachalin" (Verhoeff 1934) = Sakhalin Isl.

Type series. Holotype: male. Depository unknown.

**Diagnosis.** A species of *Arctogeophilus* with first maxillary lappets relatively long; forcipular denticles only on the trochanteroprefemur and tarsungulum, not on the intermediate articles; 39 leg-bearing segments, possibly invariably; ventral pore-fields on some anterior segments; pretarsus of ultimate legs absent.

**Distribution**. Far East: Sakhalin oblast (Sakhalin Isl.) (Verhoeff 1934; Takakuwa 1940; Molodova 1973; Kurcheva 1977; Ganin 1997), Maritime krai (Kurcheva 1977; Ganin 1997), and Chukotka autonomous okrug (Kurcheva 1977). Outside Asian Russia: no records.

**Remarks.** It has been suggested that *A. sachalinus* could be a junior synonym of *A. glacialis* (Attems, 1909) (Nefediev et al. 2017a). More generally, the actual taxonomic status of the populations of *Arctogeophilus* from the Far East remains to clarify.

#### Genus Geophilus Leach, 1814

**Diagnosis.** Geophilids with head usually only slightly elongate; clypeal areas usually not distinct; labral side-pieces distinctly separated by an intermediate

part; second maxillary coxosternite medially long and sclerotized, without both statuminia and anterior inner processes; second maxillary pretarsus claw-like or reduced; forcipular tergite approximately as broad as the subsequent tergite, covering most part of the pleurites; forcipular coxosternite usually wider than long, gradually narrowing posteriorly, without anterior denticles, with chitin-lines, with coxopleural sutures diverging anteriorly also in their anterior half; forcipular trochanteroprefemur only moderately elongate, usually without denticles; forcipular tarsungulum with at most a small basal denticle; trunk sternites often with "carpophagus" pits and often with ventral pore-fields, usually a transverse band on the posterior part of the sternite; metasternite of the ultimate leg-bearing segment usually wider than long; coxopleura with sparse ventral pores, most of them close to metasternite; pretarsus of ultimate leg pair claw-like or reduced. See Table 3.

Table 3. Differences between species of the genus Geophilus Leach, 1814 known from Asian Russia.

	Characters								
Species	Leg-bearing "Carpophagus" segments pits		Ventral pore-fields on the anterior metasternites	Coxal pores	Anal pores				
G. bipartitus Takakuwa, 1937	35-39	present	transverse diamond	all close to the margin of metasternite	present				
G. flavus (De Geer, 1778)	37-61	absent	transverse band	all close to the margin of metasternite	present				
G. orientalis Sseliwanoff, 1881	39	?	?	on the ventral and lateral sides of coxopleura	present				
G. proximus C.L. Koch, 1847	45-55	present	an entire posterior diamond	all close to the margin of metasternite	present				
G. rhomboideus Takakuwa, 1937	43-49	present	transverse diamond	most pores close to the margin of metasternite and one pore located separately	present				
G. sibiricus Stuxberg, 1876	57-59	?	?	on the ventral and lateral sides of coxopleura	absent				
G. sounkyoensis Takakuwa, 1937	55-57	present	transverse band and sparse pores	most pores close to the margin of metasternite and one pore located separately	present				

#### 4. Geophilus bipartitus Takakuwa, 1937

Geophilus bipartitus Takakuwa 1937b: 285. Geophilus bipartitus – Takakuwa 1937c: 80; 1940: 104; Molodova 1973: 67; Kurcheva 1977: 45.

**Type locality.** RUSSIA: Sakhalin oblast: Sakhalin Isl.: "Otako (Chikuka)" (see Remarks) (Takakuwa 1937c).

**Type series.** *Syntypes***:** unknown number of specimens, both sexes. Depository unknown.

**Diagnosis.** A species of *Geophilus* with head slightly longer than wide, 35–39 leg-bearing segments; "carpophagus" pits present, up to as wide as the metasternites; ventral pore-fields present, an entire posterior diamond on the anterior metasternites, absent on most of the posterior metasternites, two paired posterior groups on the penultimate metasternite; metasternite of ultimate leg-bearing segment wider than long; a few coxal pores on each coxopleuron, all close to the margin of metasternite; pretarsus of ultimate leg pair claw-like; anal pores present.

**Distribution.** Far East: Sakhalin oblast (Sakhalin and Kurile Islands) (Takakuwa 1937b; Molodova 1973; Kurcheva 1977). Outside Asian Russia: no records.

**Remarks.** The current identity and position of the locality "Otako (Chikuka)" (indicated by Takakuwa 1937c) is uncertain.

#### 5. Geophilus flavus (De Geer, 1778)

Geophilus longicornis Leach 1815: 386 (synonymy by Stuxberg 1871: 508). Arthronomalus longicornis – Gerstfeldt 1859: 275; Sseliwanoff 1884: 90. Necrophloeophagus longicornis – Brolemann 1930: 151.

Schizotaenia ornata Folkmanová & Dobroruka, 1960: 1816 (synonymy by Bonato and Minelli 2014: 41).

Geophilus flavus - Nefediev et al. 2017a: 9.

Type locality. Unknown, possibly in France (Bonato and Minelli 2014).

**Diagnosis.** A species of *Geophilus* with head ~ 1.2× as long as wide; antennal articles  $\leq$  2× as long as wide; second maxillary pretarsus claw-like, longer than surrounding setae; forcipular trochanteroprefemur ~ 1.5× as long as wide; forcipular trochanteroprefemur, femur, and tibia without denticles; tarsungulum bearing a small basal denticle; 37–61 leg-bearing segments; "carpophagus" pits absent; ventral pore-fields present, an entire transverse posterior band on the anterior metasternites, two paired posterior groups on the posterior metasternites; metasternite of ultimate leg-bearing segment wider than long; up to a dozen coxal pores on each coxopleuron, all close to the margin of metasternite; pretarsus of ultimate leg pair claw-like; anal pores present.

**Distribution.** Western Siberia: Tomsk oblast (Nefediev et al. 2017a). Eastern Siberia: Zabaykalsky krai (Gerstfeldt 1859, as *Arthronomalus longicornis*). Outside Asian Russia: Western Palaearctic (e.g., Bonato et al. 2005; Stoev 2007).

**Remarks.** The record from Western Siberia seems to be due to anthropochore introduction (Nefediev et al. 2017a), while the record from Eastern Siberia requires confirmation (see Discussion).

#### 6. Geophilus orientalis Sseliwanoff, 1881 \*

Geophilus orientalis Sseliwanoff 1881: 4.

Geophilus orientalis – Sseliwanoff 1884: 80; Attems 1903a: 45; 1903b: 235; 1929: 329.

**Type locality.** RUSSIA: Khabarovsk krai: "Nikolaevsk na Amure" (Sseliwanoff 1881) = Nikolayevsk-on-Amur city, 53°8'N, 140°42'E.

Type series. Holotype: male. Deposited in ZISP.

**Diagnosis.** A species of *Geophilus* with head slightly longer than wide; forcipular coxosternite with short and wide denticles; all forcipular articles with small denticles, except the tarsungulum; 39 leg-bearing segments; metasternite of ultimate leg-bearing segment longer than wide, only slightly narrowing backwards; numerous coxal pores, on the ventral and lateral sides of coxopleura; anal pores present. **Distribution.** Far East: Khabarovsk krai (Sseliwanoff 1881, 1884). Outside Asian Russia: no records.

**Remarks.** The species was originally described under the genus *Geophilus*, but its taxonomic position is considered uncertain since Attems (1929). The few morphological characters reported in the descriptions and keys by Sseliwanoff (1881, 1884) do not allow it to be assigned confidently to one of the known genera.

#### 7. Geophilus proximus C.L. Koch, 1847

Geophilus proximus – Sseliwanoff 1881: 6. 1884: 87; Titova 1969: 165; Zalesskaja et al. 1982: 188; Poryadina 1991: 14; Striganova and Poryadina 2005: 130; Farzalieva 2008: 58; Bukhkalo and Sergeeva 2012: 61; Bukhkalo et al. 2014: 73; Sergeeva 2013: 530; 2014: 72; Volkova 2016: 673; Nefediev et al. 2017a: 9; 2017b: 114; Dyachkov and Tuf 2019: 25; Nefediev 2019: 24; Bragina et al. 2020: 30.

Type locality. GERMANY: near Regensburg (Bonato and Minelli 2014).

**Diagnosis.** A species of *Geophilus* with head slightly longer than wide; antennal articles  $\leq \sim 1.5 \times$  as long as wide; second maxillary pretarsus claw-like, longer than surrounding setae; forcipular trochanteroprefemur slightly longer than wide; forcipular trochanteroprefemur, femur, and tibia without denticles; forcipular tarsungulum bearing a small basal denticle; 45-55 leg-bearing segments; "carpophagus" pits present, up to as wide as the metasternites; ventral pore-fields present, an entire posterior diamond on the anterior metasternites, absent on the posterior metasternites; metasternite of ultimate leg-bearing segment wider than long; up to a dozen coxal pores on each coxopleuron, all close to the margin of metasternite; pretarsus of ultimate leg pair claw-like; anal pores present.

**Distribution.** Western Siberia: "Western Siberia" (Sseliwanoff 1881); Sverdlovsk, Chelyabinsk, Tyumen, Omsk, Novosibirsk, Kemerovo, and Tomsk oblasts, Altai krai, Republic of Khakassia (Zalesskaja et al. 1982; Poryadina 1991; Striganova and Poryadina 2005; Farzalieva 2008; Bukhkalo and Sergeeva 2012; Sergeeva 2013, 2014; Bukhkalo et al. 2014; Nefediev et al. 2017a, 2017b, 2021; Nefediev 2019). Outside Asian Russia: Northern Europe (Bonato et al. 2005).

#### 8. Geophilus rhomboideus Takakuwa, 1937

Geophilus rhomboideus Takakuwa 1937b: 284. Geophilus rhomboideus – Takakuwa 1937c: 78; 1940: 101; Kurcheva 1977: 45.

**Type localities.** RUSSIA: Sakhalin oblast: "Sachalin (Tomaruoru (= Tomari city, 47°45'N, 142°3'E), Maoka (= Kholmsk city, 47°02'N, 142°02'E), Sirutori (= Ma-karov city, 48°37'N, 142°46'E))" (Takakuwa 1937c).

**Type series.** *Syntypes***:** unknown number of specimens, both sexes. Depository unknown.

**Diagnosis.** A species of *Geophilus* with head approximately as long as wide; second maxillary pretarsus claw-like and relatively long; forcipular trochanteroprefemur, femur, and tibia without denticles; forcipular tarsungulum bearing a small basal denticle; 43–49 leg-bearing segments; "carpophagus" pits present, up to as wide as the metasternites; ventral pore-fields present, an entire posterior diamond on the anterior metasternites; metasternite of ultimate leg-bearing segment wider than long; a few coxal pores on each coxopleuron, most of them close to the margin of metasternite and one pore located separately; pretarsus of ultimate leg pair claw-like; anal pores present.

**Distribution.** Far East: Sakhalin oblast (Sakhalin Isl.) (Takakuwa 1937b, 1937c; Kurcheva 1977). Outside Asian Russia: Japan (Takakuwa 1937c).

#### 9. Geophilus sibiricus Stuxberg, 1876 \*

Geophilus sibiricus Stuxberg 1876a: 31.

*Geophilus sibiricus* – Stuxberg 1876b: 315; Sseliwanoff 1884: 90; Attems 1903a: 45; 1903b: 235; 1929: 329.

**Type locality.** RUSSIA: Krasnoyarsk krai: "Krasnojarsk" (Stuxberg 1876b) = Krasnoyarsk city, 56°0'N, 92°53'E.

Type series. Syntypes: 3 females. Depository unknown.

**Diagnosis.** A species of *Geophilus* with head ~ 1.2× as long as wide; tarsungulum without basal denticle; 57–59 leg-bearing segments; more than a dozen coxal pores on each coxopleuron, both on the ventral and lateral sides; pretarsus of ultimate leg pair claw-like; anal pores absent.

**Distribution.** Eastern Siberia: Krasnoyarsk krai (Stuxberg 1876b). Outside Asian Russia: no records.

**Remarks.** The species was originally described under the genus *Geophilus*, but its taxonomic position was considered uncertain since Attems (1929). The few morphological characters reported in the descriptions by Stuxberg (1876a, 1876b) do not allow to confidently assign it to one of the known genera.

#### 10. Geophilus sounkyoensis Takakuwa, 1937

Geophilus sounkyoensis Takakuwa 1937b: 283.

Geophilus sounkyoensis – Takakuwa 1937c: 77; 1940: 99; Ghilarov and Perel 1973: 46; Kurcheva 1977: 45; Ganin 1997: 121, 124, 126, 128.

#### Type locality. JAPAN: Hokkaido: "Sounkyo" (Takakuwa 1937c).

**Type series.** *Syntypes***:** unknown number of specimens, both sexes. Depository unknown.

**Diagnosis.** A species of *Geophilus* with second maxillary pretarsus claw-like, longer than surrounding setae; forcipular trochanteroprefemur slightly longer than wide; forcipular trochanteroprefemur, femur and tibia without denticles; forcipular tarsungulum bearing a small basal denticle; 55–57 leg-bearing segments; "carpophagus" pits present, up to as wide as the metasternites; ventral pore-fields present, an entire posterior band and other sparse pores on the

anterior metasternites, absent on the posterior metasternites; metasternite of ultimate leg-bearing segment wider than long; a few coxal pores on each coxopleuron, most of them close to the margin of metasternite and one pore located separately; anal pores present.

**Distribution.** Far East: Maritime krai (Ghilarov and Perel 1973; Kurcheva 1977; Ganin 1997). Outside Asian Russia: Japan (Takakuwa 1937b, 1937c, 1940).

#### Genus Pachymerium C.L. Koch, 1847

**Diagnosis.** Geophilids with head distinctly elongate; clypeal areas distinct; labral side-pieces distinctly separated by an intermediate part; second maxillary coxosternite medially long and sclerotized, without both statuminia and anterior inner processes; second maxillary pretarsus claw-like; forcipular tergite distinct-ly narrower than subsequent tergite, with pleurites exposed dorsally; forcipular coxosternite relatively broad posteriorly, with coxopleural sutures subparallel in their anterior half; forcipular trochanteroprefemur distinctly elongate, with distal denticle; chitin-lines present but short; forcipular tarsungulum with basal denticle; trunk sternites without "carpophagus" structures; ventral pore-fields present at least on the anterior part of the trunk, two paired anterior groups and a posterior entire transverse band on each sternite; metasternite of ultimate leg-bearing segment approximately as long as wide or longer than wide; coxopleura with sparse pores; legs of the ultimate pair with claw-like pretarsus. See Table 4.

Table 4. Differences between species of the genus Pachymerium C.L. Koch, 1847 known from Asian Russia.

	Characters							
Species	Chitin-lines	Denticle on forcipular tarsungulum	Leg-bearing segments	Ultimate metasternite: lateral margins				
P. ferrugineum (C.L. Koch, 1835)	extending for most part of the length of the coxosternite	yes	41-69	distinctly converging posteriorly				
P. pilosum (Meinert, 1870)	very short	no	45-49	subparallel				

#### 11. Pachymerium ferrugineum (C.L. Koch, 1835)

Geophilus ferrugineus - Sseliwanoff 1884: 77.

Pachymerium ferrugineum – Titova 1969: 166; Zalesskaja et al. 1982: 187; Ganin 1997: 105, 112, 116, 146; Farzalieva 2008: 61; Sergeeva 2013: 530; Zuev 2016: 36; Zuev and Evsyukov 2016: 424; Bukhkalo et al. 2014: 73; Volkova 2016: 673; Dyachkov 2018a: 252; Nefediev et al. 2017a: 11; Dyachkov and Tuf 2019: 26; Dyachkov 2020: 79; 2022: 71; 2023: 1077; Dyachkov and Nedoev 2021: 42; Dyachkov et al. 2022: 73; 2023: 63; Dyachkov and Farzalieva 2023: 228.

Type locality. GERMANY: Arklee, near Regensburg (Bonato and Minelli 2014).

**Diagnosis.** A species of *Pachymerium* with two paired clypeal areas; forcipular coxosternite with chitin-lines, which extend for most part of the length of the coxosternite, but do not reach the anterior margin; both forcipular trochanteroprefemur and tarsungulum with relatively small denticles; 41–69 leg-bearing segments; ventral pore-fields present, also on the posterior part of the trunk,

where they are reduced to two paired posterior groups on each metasternite; ultimate metasternite trapezoidal, approximately as long as wide, distinctly tapering towards the posterior margin; all coxal pores sparse from the ventral to the dorsal sides of the coxopleura.

**Distribution.** Western Siberia: Chelyabinsk, Sverdlovsk, Tyumen, and Tomsk oblasts, Altai krai (Zalesskaja et al. 1982; Farzalieva 2008; Sergeeva 2013; Bukhkalo et al. 2014; Nefediev et al. 2017a). Far East: Amur oblast, Jewish autonomous oblast, and Maritime krai (Zalesskaja et al. 1982; Ganin 1997). Outside Asian Russia: Western Palaearctic.

#### 12. Pachymerium pilosum (Meinert, 1870) \*

Geophilus pilosus Meinert 1870: 86.

*Geophilus pilosus* – Stuxberg 1876a: 32; 1876b: 315; Sseliwanoff 1881: 3; 1884: 76; Daday 1889: 146; Attems 1929: 324.

Geophilus (Pachymerium) pilosus – Attems 1903a: 45; 1903b: 257. Pachymerium pilosum – Muralewicz 1926: 42; Bonato et al. 2016.

**Type locality.** RUSSIA: Sakhalin oblast: "Sartung, paa Oen Sacolin" (Meinert 1870) = "Sartung" (see Remarks), Sakhalin Isl.

Type series. Syntypes: 2 specimens, both sexes. Deposited in NHMD.

**Diagnosis.** A species of *Pachymerium* with forcipular coxosternite with very short chitin-lines; forcipular tarsungulum without denticle; 45–49 leg-bearing segments; ultimate metasternite narrow, with subparallel lateral edges; all coxal pores sparse from the ventral to the dorsal sides of the coxopleura.

**Distribution.** Eastern Siberia: Krasnoyarsk krai, Irkutsk oblast (Stuxberg 1876a, 1876b; Sseliwanoff 1881, 1884; Daday 1889). Far East: Sakhalin oblast (Sakhalin Isl.) (Meinert 1870). Outside Asian Russia: no records.

**Remarks.** Sseliwanoff (1884) reported specimens from "near Baikal", collected by G. Dybovskiy. According to the catalogue of Chilopoda of the ZMMU, these specimens were collected from the Kultuk (urban-type settlement in the Irkutsk oblast, 51°43'N, 103°40'E).

The assignment of this nominal species to the genus *Pachymerium* is only tentative (Bonato et al. 2016), and is suggested only by the following few characters described by Meinert (1870): head ~ 1.2× as long as wide, forcipular coxosternite very broad and with two anterior denticles, forcipules surpassing the anterior margin of the head, coxopleura elongate and with dense coxal pores not only on the ventral side but also on the lateral and dorsal ones, ultimate legs slightly longer than penultimate legs and bearing a claw.

The current identity and position of the locality "Sartung" (indicated by Meinert 1870) is uncertain.

#### Genus Strigamia Gray, 1843

**Diagnosis.** Geophilids with head slightly wider or as wide as long; clypeal areas absent; labrum without obviously distinct lateral parts; second maxillary coxosternite medially long and sclerotized, without both statuminia and anterior

inner processes; second maxillary pretarsus relatively small, claw-like; forcipular tergite approximately as wide as the subsequent tergite, covering pleurites almost completely; forcipular coxosternite distinctly shorter than wide, without both anterior denticles and chitin-lines, with coxopleural sutures distinctly diverging also in their anterior half; forcipular trochanteroprefemur relatively stout, without denticle; forcipular tarsungulum with a relatively large basal denticle; trunk sternites without "carpophagus" structures; ventral pore-fields present, at least two paired ovoid posterior fields on each metasternite; coxal pores only on the ventral side of coxopleura, denser near the metasternite; leg of the ultimate pair usually with claw-like pretarsus. See Table 5.

Table 5. Differences between species of the genus Strigamia Gray, 1843 known from Asian Russia.

	Characters								
Species	Head	Head Forcipular tarsungula			Anterior sternites	Number	Ultimate leg-bearing segment		
Species	Clypeal setae	Clypeal setae Surpassing the anterior margin of the head part		Size of basal denticle	Mid-longitudinal sclerotized stripe	bearing segments	Intercalary pleurites	Metasternite	
S. cf. acuminata (Leach, 1815)	three groups	no	variable	short	no	37-43	no	ca as long as wide	
S. alokosternum (Attems, 1927)	?	no	subparallel	large	yes	51-67	yes	distinctly wider than long	
S. hirsutipes (Attems, 1927)	?	no	gradually converging	short	?	39-53	yes	longer than wide	
S. pusilla (Sseliwanoff, 1884)	?	no	gradually converging	short	no	33–39	yes	as long as wide or longer than wide	
S. sacolinensis (Meinert, 1870)	?	yes	?	?	no	43-47	?	?	
S. sibirica (Sseliwanoff, 1881)	?	no	?	?	?	33-35	?	?	
S. sulcata (Sseliwanoff, 1881)	?	no	?	?	?	41-43	?	?	
S. cf. transsilvanica (Verhoeff, 1928)	entire band	no	gradually converging	large	no	43-57	no	ca as long as wide	

#### 13. Strigamia cf. acuminata (Leach, 1815)

- Scolioplanes acuminatus Sseliwanoff 1881: 15; 1884: 92; Verhoeff 1928: 278; Attems 1929: 222; Takakuwa 1933: 133; 1938: 241; 1940: 124; Shinohara 1972: 66; Kurcheva 1977: 46.
- *Strigamia acuminata* Ganin 1997: 105, 112, 116, 129, 134, 141; Barber 2009: 74; Bonato et al. 2012: 9; 2023: 11; Volkova 2016: 675.

**Type localities.** UNITED KINGDOM: "Roborough Down near Plymouth" and "Battersea fields" (Leach 1815).

**Diagnosis.** A species of *Strigamia* with clypeal setae arranged in an intermediate and two lateral groups; forcipular tarsungula not surpassing the anterior margin of the head; basal denticle of forcipular tarsungulum relatively short and with straight converging margins; 37–43 leg-bearing segments; metasternites of the anterior part of the trunk without a mid-longitudinal sclerotized stripe; ultimate leg-bearing segment with pleuropretergite entire, i.e., without distinct intercalary pleurites, and metasternite approximately as long as wide.

**Distribution.** Far East: Amur oblast and Khabarovsk krai (Ganin 1997), Sakhalin oblast (Kuril Islands) (Takakuwa 1933; Kurcheva 1977). Outside Asian Russia: Europe (Barber 2009; Bonato et al. 2012, 2023; Volkova 2016). **Remarks.** All records from Russian Far East need confirmation, as are the records from Japan and the Western part of North America, because of probable confusion with other species including *S. chionophila* Wood, 1862 (Bonato et al. 2012).

#### 14. Strigamia alokosternum (Attems, 1927)

Scolioplanes alokosternum Attems 1927: 294.

Scolioplanes alokosternum – Attems 1929: 223; Takakuwa 1938: 243; 1940: 128; Kurcheva 1977: 45.

Strigamia alokosternum – Murakami 1993: 105; Bonato et al. 2012: 9.

**Type localities.** JAPAN: "Yamanaka, Suruga" and "Bukenji" (Attems 1927).

**Type series.** *Syntypes*: 2 specimens, both sexes. Deposited in NHMW (Ilie et al. 2009).

**Diagnosis.** A species of *Strigamia* with forcipular tarsungula not surpassing the anterior margin of the head; basal denticle of forcipular tarsungulum relatively large; internal and external margins of forcipular tarsungulum subparallel in their intermediate part; 51–67 leg-bearing segments; metasternites of the anterior part of the trunk with a mid-longitudinal sclerotized stripe; ultimate leg-bearing segment with distinct intercalary pleurites, and metasternite distinctly wider than long.

**Distribution.** Far East: Sakhalin oblast (Sakhalin Isl.) (Kurcheva 1977). Outside Asian Russia: Korean Peninsula and Japan (Bonato et al. 2012).

#### 15. Strigamia hirsutipes (Attems, 1927) \*

Scolioplanes hirsutipes Attems 1927: 293.

Scolioplanes hirsutipes – Attems 1929: 222; Takakuwa 1938: 243; 1940: 127; Ghilarov and Perel 1973: 46; Kurcheva 1977: 45.

Strigamia hirsutipes - Ganin 1997: 124, 126, 128; Bonato et al. 2012: 15.

**Type localities.** JAPAN: "Kanagava", "Yamanaka (Suruga)", "Bukengi", and Negishi" (Attems 1927).

**Type series.** *Syntypes*: ca 42 specimens, both sexes. Deposited in NHMW (Ilie et al. 2009).

**Diagnosis.** A species of *Strigamia* with forcipular tarsungula not surpassing the anterior margin of the head; basal denticle of forcipular tarsungulum relatively short; internal and external margins of forcipular tarsungulum gradually converging through the entire length; 39–53 leg-bearing segments; ultimate leg-bearing segment with distinct intercalary pleurites and metasternite longer than wide.

**Distribution.** Far East: Maritime krai, Sakhalin oblast (Sakhalin Isl.) (Ghilarov and Perel 1973; Kurcheva 1977; Ganin 1997). Outside Asian Russia: Japan (Attems 1927; Bonato et al. 2012).

**Remarks.** The taxonomic distinction of this nominal species from *S. sacolinensis* is uncertain.

Records from South-Eastern Asia are doubtful (Bonato et al. 2012).

#### 16. Strigamia pusilla (Sseliwanoff, 1884)

Scolioplanes pusillus Sseliwanoff 1884: 92.

Scolioplanes pusillus - Attems 1929: 224.

Scolioplanes perkeo Verhoeff 1935: 19 (synonymy by Dobroruka 1955: 202).

Scolioplanes pseudopusillus Loksa 1962: 857 (synonymy by Zalesskaja et al. 1982: 190).

Strigamia pusillus – Zalesskaja et al. 1982: 189; Volkova 2016: 675.

Strigamia pusilla – Farzalieva 2008: 64; Bonato et al. 2012: 18; Tuf and Kupka 2015: 110; Poloczek et al. 2016: 117; Tuf and Tajovsky 2016: 47; Nefediev et al. 2017c: 223; 2018: 237; Nefediev 2019: 25; Dyachkov and Farzalieva 2023: 229.

**Type locality.** RUSSIA: Moscow oblast: "Zaraysk, Ryazanskoy Gubernii" (Sseliwanoff 1884) = Zaraysk city, 54°45'N, 38°53'E.

**Type series.** *Syntypes*: 11 specimens, including 4 males and 7 females. Deposited in ZISP.

**Diagnosis.** A species of *Strigamia* with forcipular tarsungula not surpassing the anterior margin of the head; basal denticle of forcipular tarsungulum relatively short, pointed, and with straight outlines; internal and external margins of forcipular tarsungulum gradually converging through the entire length; 33–39 leg-bearing segments; metasternites of the anterior part of the trunk without a mid-longitudinal sclerotized stripe; ultimate leg-bearing segment with distinct intercalary pleurites and metasternite as long as wide or longer than wide.

**Distribution.** Western Siberia: Sverdlovsk oblast (Zalesskaja et al. 1982; Farzalieva 2008), Altai krai (Nefediev et al. 2018; Nefediev 2019), and Republic of Altai (Nefediev et al. 2017c). Eastern Siberia: Republic of Sakha (Yakutia) (Nefediev 2019). Outside Asian Russia: westwards to Central Europe (Zalesskaja et al. 1982; Bonato et al. 2012; Tuf and Tajovsky 2016; Volkova 2016), and southwards to Northern Mongolia (Poloczek et al. 2016; Dyachkov and Farzalieva 2023).

#### 17. Strigamia sacolinensis (Meinert, 1870) \*

Scolioplanes sacolinensis Meinert 1870: 53.

Scolioplanes sacolinensis – Sseliwanoff 1881: 16; 1884: 93; Attems 1903a: 46; 1903b: 267; 1929: 224; Molodova 1973: 67; Kurcheva 1977: 46.

Strigamia sacolinensis – Ganin 1997: 134; Bonato et al. 2012: 18.

**Type locality.** RUSSIA: Sakhalin oblast: "Sartung paa Oen Sacalin" (Meinert 1870) = "Sartung" (see Remarks), Sakhalin Isl.

Type series. Holotype: female. Deposited in NHMD.

**Diagnosis.** A species of *Strigamia* with forcipular tarsungula surpassing the anterior margin of the head; 43–47 leg-bearing segments; metasternites of the anterior part of the trunk without a mid-longitudinal sclerotized stripe.

**Distribution.** Far East: Khabarovsk krai (Sseliwanoff 1881, 1884) and Sakhalin oblast (Sakhalin Isl.) (Meinert 1870; Molodova 1973; Kurcheva 1977; Ganin 1997). Outside Asian Russia: no records. **Remarks.** Bonato et al. (2012) suggested the putative projection of the forcipules in front of the anterior margin of the head can be due to some post-mortem displacement of the head with respect to the trunk. Based on the incomplete description provided by Meinert (1870), this nominal species could be a senior synonym of either *S. hirsutipes* or *S. japonica* (Verhoeff, 1935).

The current identity and position of the locality "Sartung" (indicated by Meinert 1870) is uncertain.

#### 18. Strigamia sibirica (Sseliwanoff, 1881) \*

Scolioplanes sibiricus Sseliwanoff 1881: 16.

Scolioplanes sibiricus – Sseliwanoff 1884: 94; Attems 1903a: 46; 1903b: 268; 1929: 224.

Linotaenia sibirica – Cook 1896: 866.

Strigamia sibirica – Bonato et al. 2012: 18.

**Type locality.** RUSSIA: Zabaykalsky krai: "Yablonoviy Khrebet" (Sseliwanoff 1881) = Yablonoviy Mt. Range, ca 52°2'N, 113°35'E.

**Type series.** *Syntypes***:** 4 specimens, including 1 male and 3 females. Deposited in ZISP.

**Diagnosis.** A species of *Strigamia* with forcipular tarsungula not surpassing the anterior margin of the head; 33–35 leg-bearing segments.

**Distribution.** Eastern Siberia: Zabaykalsky krai (Sseliwanoff 1881). Outside Asian Russia: no records.

**Remarks.** The distinction between this nominal species and *S. pusilla* is unclear (Bonato et al. 2012).

#### 19. Strigamia sulcata (Sseliwanoff, 1881) \*

Scolioplanes sulcatus Sseliwanoff 1881: 17.

Scolioplanes sulcatus – Sseliwanoff 1884: 95; Attems 1903a: 46; 1903b: 267; 1929: 224.

Linotaenia sulcata – Cook 1896: 866.

Strigamia sulcatus – Ganin 1997: 114, 141. Strigamia sulcata – Bonato et al. 2012: 19.

**Type locality.** RUSSIA: Khabarovsk krai: "Nikolaevsk-na-Amure" (Sseliwanoff 1881) = Nikolayevsk-on-Amur city, 53°8'N, 140°42'E.

**Type series.** *Syntypes***:** 3 specimens, including 2 males and 1 female. Deposited in ZISP.

**Diagnosis.** A species of *Strigamia* with forcipular tarsungula not surpassing the anterior margin of the head; 41–43 leg-bearing segments.

**Distribution.** Far East: Khabarovsk krai (Sseliwanoff 1881, 1884; Ganin 1997). Outside Asian Russia: no records.

**Remarks.** The distinction between this nominal species and many other congeneric species is unclear (Bonato et al. 2012).

#### 20. Strigamia cf. transsilvanica (Verhoeff, 1928)

Scolioplanes transsilvanicus Verhoeff 1928: 278.

Scolioplanes transsilvanicus – Takakuwa 1938: 240; 1940: 123; Kurcheva 1977: 45.

Strigamia transsilvanicus - Ganin 1997: 121, 126.

Strigamia transsilvanica – Bonato et al. 2012: 19; 2023: 17.

Strigamia cf. transsilvanica – Zuev and Evsyukov 2016: 425; Nefediev et al. 2018: 237; Dyachkov 2018b: 255; Dyachkov et al. 2022: 75; Dyachkov and Zuev 2023: 159.

**Type localities.** ROMANIA: "Hermannstadt" = Sibiu. Slovenia: "Gottschee" = Kocevje. Austria: "Ostalpen" = Eastern Alps; "Hermagor"; "Arlberg". Italy: "Schneelagern am Schlüsseljoch beim Brenner" = Colle della Chiave, near Brennero. Slovakia: "Tatra-Höhlenhain" = Tatranska Kotlina. Germany: "Titisee". Switzerland: "Pilatus Kulm" (Verhoeff 1928).

**Diagnosis.** A species of *Strigamia* with clypeal setae uniformly spaced in a continuous array, without recognizable gaps between intermediate and lateral groups of setae; forcipular tarsungula not surpassing the anterior margin of the head; basal denticle of forcipular tarsungulum relatively large and with distinctly curved outlines; internal and external margins of forcipular tarsungulum gradually converging through the entire length; 43–57 leg-bearing segments; metasternites of the anterior part of the trunk without a mid-longitudinal sclerotized stripe; ultimate leg-bearing segment with pleuropretergite entire, i.e., without distinct intercalary pleurites, and metasternite approximately as long as wide.

**Distribution.** Western Siberia: Altai krai (Nefediev et al. 2018). Far East: Maritime krai, Sakhalin oblast (Sakhalin Isl.) (Kurcheva 1977; Ganin 1997). Outside Asian Russia: westwards to Central Europe (Iorio 2005; Reip and Voigtländer 2009).

**Remarks.** *Strigamia transsilvanica* belongs to a species complex whose taxonomy is only partially resolved (Bonato et al. 2023).

Bonato et al. (2012) suggested that the records from Russian Far East are probably due to misidentification of a different species. Nefediev et al. (2018) suggested the presence of a possible undescribed species similar in morphology to *S. transsilvanica* from Western Siberia, so that also the presence of *S. transsilvanica* in Western Siberia is doubtful. Doubtful are also the records from European Russia and Caucasus (Zuev and Evsyukov 2016; Dyachkov et al. 2022; Dyachkov and Zuev 2023), Eastern Kazakhstan (Dyachkov 2018b), Japan, and Taiwan (Bonato et al. 2012).

#### Family Mecistocephalidae Bollman, 1893

#### Genus Agnostrup Foddai, Bonato, Pereira & Minelli, 2003

**Diagnosis.** Mecistocephalids with head moderately longer than wide; two clypeal plagulae, separated by a mid-longitudinal areolate stripe and extending to the lateral margins of the clypeus; cephalic pleurites without both spiculum and setae; first maxillary coxosternite medially divided by a sulcus, without

antero-lateral corners; second maxillary coxosternite medially undivided, with the grooves from the metameric pores reaching the posterior corners; second maxillary telopodites relatively small, not distinctly overreaching the first maxillary telopodites, without pretarsus; forcipular tergite distinctly wider than long, without a distinct mid-longitudinal sulcus; forcipular trochanteroprefemur with only a distal denticle, tarsungulum with a basal denticle; invariably 41 leg-bearing segments; sternites with non-furcate mid-longitudinal sulcus and without pore-fields; legs of the ultimate pair ending with a short spine. See Table 6.

Table 6. Differences between members of the family Mecistocephalidae Bollman, 1893 known from Asian Russia.

	Characters											
Species	Clypeal plagulae	First maxillary coxosternite: mid-longitudinal sulcus	Second maxillary telopodites surpassing first maxillary telopodites	Second maxillary pretarsus	Denticle on forcipular tarsingulum	Denticles on forcipular intermediate articles	Leg- bearing segments					
Agnostrup striganovae (Titova, 1975)	two, extending to lateral margins of clypeus	yes	no	no	yes	small bulges	41					
Arrup dentatus (Takakuwa, 1934)	two, not extending to lateral margins of clypeus	no	no	yes	yes	large on tibia	41					
Arrup mamaevi (Titova, 1975)	two, not extending to lateral margins of clypeus	no	no	no	yes	small bulges	41					
<i>Tygarrup javanicus</i> Attems, 1929	single, extending to lateral margins of clypeus	yes	yes	yes	no	tibia with denticle	45					

#### 21. Agnostrup striganovae (Titova, 1975)

Krateraspis striganovae Titova 1975: 40.

Krateraspis striganovae – Markelov and Mineeva 1981: 130; Ganin 1997: 124; 2011: 341.

Agnostrup striganovae - Foddai et al. 2003: 1254.

**Type locality.** RUSSIA: Maritime krai: "Sudzuhinsky Zapovednik, Tachingauz" (Titova 1975) = Lazovsky Nature Reserve, Tachingauz bay, ca 43°1'N, 134°8'E.

**Type series.** *Holotype*: male. Deposited in ZMMU (S. Golovatch and A. Schileyko, pers. comm., 13.II.2023 and XII.2023).

**Diagnosis.** An *Agnostrup* species with body length reaching  $\geq$  3 cm; clypeal plagulae with an irregular anterior margin and slightly smaller than the areolate part of the clypeus; many setae near the anterior margin of plagulae and on the center of the areolate part of the clypeus; forcipular trochanteroprefemur 1.3× as long as wide, both forcipular femur and tibia with small bulges.

**Distribution.** Far East: Maritime krai (Titova 1975; Markelov and Mineeva 1981; Ganin 1997). Outside Asian Russia: no records.

#### Genus Arrup Chamberlin, 1912

**Diagnosis.** Mecistocephalids with head moderately longer than wide; two clypeal plagulae, separated by a mid-longitudinal areolate stripe and not extending to the lateral margins of the clypeus; cephalic pleurites without both spiculum and setae; first maxillary coxosternite medially undivided, without

antero-lateral corners; second maxillary coxosternite medially undivided, with the grooves from the metameric pores reaching the posterior corners; second maxillary telopodites relatively small, not distinctly overreaching the first maxillary telopodites, usually without pretarsus; forcipular tergite distinctly wider than long, without a distinct mid-longitudinal sulcus; forcipular trochanteroprefemur with only a distal denticle, tarsungulum with a basal denticle; invariably 41 leg-bearing segments; sternites with non-furcate mid-longitudinal sulcus and without pore-fields; legs of the ultimate pair ending with a short spine. See Table 6.

#### 22. Arrup dentatus (Takakuwa, 1934)

Prolamnonyx dentatus Takakuwa 1934a: 707 (see Remarks).
Prolamnonyx dentatus – Takakuwa 1934b: 359; 1934c: 883.
Prolamnonyx dentatus – Shinohara 1972: 66; Titova 1975: 45; Ganin 1997: 134.
Arrup dentatus – Crabill 1964: 166; Foddai et al. 2003: 1261; Uliana et al. 2007: 13.

Type locality. JAPAN: Hokkaido: "Zyôzankei (bei Sapporo)" (Takakuwa 1934b).

**Type series.** Unknown number of specimens, possibly lost (Jonishi and Nakano 2022). Depositary unknown.

**Diagnosis.** An Arrup species with body reaching  $\ge 2$  cm; second maxillary pretarsi present (see Remarks); forcipular trochanteroprefemur with a large distal denticle, tibia with large denticle, tarsungulum with pointed basal denticle.

**Distribution.** Far East: Maritime krai, Sakhalin oblast (Sakhalin and Kuril Islands: Shikotan) (Titova 1975; Ganin 1997). Outside Asian Russia: Japan (Takakuwa 1934b; Shinohara 1972).

**Remarks.** The name *Prolamnonyx dentatus* was validly introduced by Takakuwa (1934a) in a key; specimens were later described in more detail by Takakuwa (1934b, 1934c). Uliana et al. (2007) described the presence of second maxillary pretarsi in this species, according to the original description and Titova (1975), it is absent in this species.

#### 23. Arrup mamaevi (Titova, 1975)

Prolamnonyx mamaevi Titova 1975: 44. Prolamnonyx holstii – Titova 1969: 165 (see Remarks). Prolamnonyx mamaevi – Ganin 1997: 121. Arrup mamaevi – Foddai et al. 2003: 1262.

**Type locality.** RUSSIA: Maritime krai: "Primorsky Kray, zapovednik Kedrovaya Pad", Kedrovaya Pad Nature Reserve, ca 43°05'N, 131°30'E, (Titova 1975).

**Type series.** *Holotype*: female. Deposited in ZMMU (S. Golovatch and A. Schileyko, pers. comm., 13.II.2023 and XII.2023).

**Diagnosis.** An *Arrup* species with body length reaching  $\geq$  3 cm; second maxillary pretarsi absent; forcipular trochanteroprefemur with a large distal denticle, both femur and tibia with small bulges, tarsungulum with pointed basal denticle.

# **Distribution.** Far East: Maritime krai (Titova 1975; Ganin 1997). Outside Asian Russia: no records.

**Remarks.** The holotype had been previously assigned to *Prolamnonyx holstii* (Pocock, 1895) by Titova (1969).

#### Genus Tygarrup Chamberlin, 1914

**Diagnosis.** Mecistocephalids with head distinctly longer than wide; clypeus with an entire plagula, without mid-longitudinal areolate stripe and extending to the lateral margins of the clypeus; cephalic pleurites without both spiculum and setae; first maxillary coxosternite medially divided by a sulcus, without antero-lateral corners; second maxillary coxosternite medially undivided, with the grooves from the metameric pores reaching the lateral margins; second maxillary telopodites distinctly overreaching the first maxillary telopodites, with claw-like pretarsus; forcipular tergite only slightly wider than long, without a distinct mid-longitudinal sulcus; forcipular trochanteroprefemur with only a distal denticle, tarsungulum without denticle; invariably 43 or 45 leg-bearing segments; sternites with non-furcate mid-longitudinal sulcus and sometimes with pore-fields; legs of the ultimate pair ending with a short spine. See Table 6.

#### 24. Tygarrup javanicus Attems, 1929

Tygarrup javanicus Attems 1929: 152.

*Tygarrup javanicus* – Bonato et al. 2004; Nefediev 2019: 24; Tuf et al. 2018: 560; Damasiewicz and Leśniewska 2020: 52; Gilgado et al. 2022: 92.

**Type localities.** INDONESIA: Java: "Buitenzorg", "Tjibodas" and "Tjompea" (Attems 1929).

**Diagnosis.** A *Tygarrup* species with body length  $\leq$  2 cm; no distinct dark patches along the body; second maxillary pretarsus with a long slender point; both forcipular trochanteroprefemur and tibia with denticles; invariably 45 leg-bearing segments; ventral pore-fields absent in females, present in males; metasternite of the ultimate leg-bearing segment slightly wider than long.

**Distribution.** Western Siberia: Altai krai (Nefediev 2019). Outside Asian Russia: Southeast Asia and introduced in Europe (e.g., Bonato et al. 2004; Tuf et al. 2018; Damasiewicz and Leśniewska 2020; Gilgado et al. 2022).

**Remarks.** The species is regarded as an anthropochore introduction in Asian Russia (Nefediev 2019).

#### Family Schendylidae Cook, 1896

#### Genus Escaryus Cook & Collins, 1891

**Diagnosis.** Schendylids with head slightly longer than wide; antennae gradually tapering; labrum with distinct denticles in the intermediate part; first maxillae with lappets; second maxillary pretarsi fringed by two rows of filaments;
forcipular tergite narrower than subsequent tergite; ventral pore-fields absent; coxal pores numerous and scattered; legs of the ultimate pair with two tarsal articles and claw-like pretarsus, swollen in adult males and slender in females; gonopods biarticulated in both sexes. See Table 7.

#### 25. Escaryus chadaevae Titova, 1973

Escaryus chadaevae Titova 1973: 105.

*Escaryus chadaevae* – Rybalov 2002: 83; Vorobiova et al. 2002: 62; Poloczek et al. 2016: 117; Volkova 2016: 675; Nefediev et al. 2017c: 221; Dyachkov and Farzalieva 2023: 229.

**Type localities.** RUSSIA: Kemerovo oblast: "Prokopyevsky i Novokuznetsky r-ny" (Titova 1973) = Prokopyevsky, ca 53°53'N, 86°43'E, and Novokuznetsky, ca 53°45'N, 87°07'E, districts.

**Type series.** *Holotype*: female. Paratypes: 10 specimens, including 5 males and 5 females. Deposited in ZMMU (S. Golovatch and A. Schileyko, pers. comm., 13.II.2023 and XII.2023).

Table 7. Differences between species of the genus Escaryus Cook & Collins, 1891 known from Asian Russia.

	Characters												
		Labrum	Firet	Dentic	les on fo	rcipular	articles		Ultimate leg-				
Species	Margin	Denticles	maxillae: pairs of lappets	Trochantero- prefemur	Femur	Tibia	Tarsungulum	Leg- bearing segments	bearing segment: metasternite: shape, length/ width	Anal pores			
E. chadaevae Titova, 1973	shallow	short and obtuse	1	small bulge	small bulge	large bulge	large denticle	33-35	trapezoid, < 1	absent			
E. chichibuensis Shinohara, 1955	shallow	short and obtuse	1	small bulge	small bulge	small bulge	no	35-39	trapezoid, ~ 1	present			
E. dentatus Titova, 1973	shallow	short and obtuse	1	large	small	small	large	37-39	trapezoid, > 1	present			
E. hirsutus Titova 1973	deep	long and obtuse	1	large bulge	large bulge	large bulge	large bulge	37-39	rectangular, 1.5	present			
E. japonicus Attems, 1927	shallow	long and obtuse	1	small	small bulge	small bulge	small bulge	43-55	rectangular, 2	present			
E. koreanus Takakuwa, 1937	shallow	long, middle denticles obtuse, lateral ones pointed	1	small	no	no	small bulge	43-55	rectangular, 2	present			
E. krivolutskiji Titova, 1973	deep	short and obtuse	1	large bulge	small bulge	large bulge	small bulge	45-49	trapezoid, ~ 1	present			
E. molodovae Titova, 1973	shallow	short and obtuse	1	small	small	small	large	35	trapezoid, ~ 1	present			
E. perelae Titova, 1973	shallow	short and obtuse	1	small	no	small	large	39-43	trapezoid, < 1	present			
E. polygonatus Titova, 1973	deep	short and obtuse	1	small bulge	small bulge	small bulge	no	39	trapezoid, 1.5	present			
E. retusidens Attems, 1904	deep	long and obtuse	1	small	small	small	small bulge	49-55	trapezoid, ~ 1	absent			
<i>E. sachalinus</i> Takakuwa, 1935	deep	short and obtuse	?	small	small	small	no	35-39	rectangular, 1.5	present			
E. sibiricus Cook, 1899	shallow	middle denticles obtuse, lateral ones long and pointed	2	small bulge	no	no	no	49-51	rectangular, 2	absent			
E. vitimicus Titova, 1973	shallow	long and obtuse	1	small bulge	small bulge	small bulge	small bulge	37	rectangular, 1.5	present			

**Diagnosis.** An *Escaryus* species with body length reaching  $\geq$  1.5 cm; clypeus without plagulae; labral arc relatively shallow, with denticles short and obtuse; first maxillae with one pair of lappets; forcipular trochanteroprefemur and femur with small bulges, tibia with a large bulge, tarsungulum with a large basal denticle; 33–35 leg-bearing segments; metasternite of the ultimate leg-bearing segment trapezoid, distinctly wider than long; coxal pores only on the ventral side of coxopleura; anal pores absent.

**Distribution.** Western Siberia: Kemerovo oblast, Republic of Altai (Titova 1973; Nefediev et al. 2017c). Eastern Siberia: Krasnoyarsk krai (Rybalov 2002; Vorobiova et al. 2002). Outside Asian Russia: European Russia (Republic of Bashkortostan) (Titova 1973; Volkova 2016), and Northern Mongolia (Poloczek et al. 2016; Dyachkov and Farzalieva 2023).

#### 26. Escaryus chichibuensis Shinohara, 1955 \*

Escaryus chichibuensis Shinohara 1955: 59. Escaryus chichibuensis – Titova 1973: 114; Kurcheva 1977: 45.

**Type localities.** JAPAN: Honshu: Saitama Prefecture: "Chichibu (Mt. Kumotori, Kasatori pass, Mt. Kobushi, Kabagoya-ato, Karisaka pass, Jumonji pass, Mt. Shiraiwa, Mt. Mae-Shiraiwa" (Shinohara 1955).

**Type series.** *Syntypes:* unknown number of specimens, both sexes. Depository unknown.

**Diagnosis.** An *Escaryus* species with body length reaching  $\ge 2$  cm; clypeus with small plagulae; labral arc relatively shallow, with denticles short and obtuse; first maxillae with one pair of lappets; forcipular trochanteroprefemur, femur, and tibia with small bulges, tarsungulum without bulge; 35-39 leg-bearing segments; metasternites with relatively sparse setae; metasternite of the ultimate leg-bearing segment trapezoid, approximately as long as wide; coxal pores on both ventral and lateral sides of coxopleura; anal pores present.

**Distribution.** Far East: Sakhalin oblast (Kuril Islands: Kunashir and Shikotan) (Titova 1973; Kurcheva 1977). Outside Asian Russia: Japan (Shinohara 1955).

#### 27. Escaryus dentatus Titova, 1973 \*

Escaryus dentatus Titova 1973: 99.

*Escaryus dentatus* – Kurcheva 1977: 45; Markelov and Mineeva 1981: 130; Ganin 1997: 121, 124, 126, 128; 2006: 501.

**Type localities.** RUSSIA: Maritime krai: "Suputinsky zapovednik" = Ussuriysky Nature Reserve, ca 43°40'N, 132°32'E, and "Kedrovaya Pad" (both Titova 1973) = Kedrovaya Pad Nature Reserve, ca 43°05'N, 131°30'E, (see Remarks).

**Type series.** *Holotype*: female. Paratypes: 11 specimens, including 6 males and 5 females. Deposited in ZMMU (S. Golovatch and A. Schileyko, pers. comm., 13.II.2023 and XII.2023).

**Diagnosis.** An *Escaryus* species with body length reaching  $\ge$  2 cm; clypeus without plagulae (polygonal structure poorly visible, but recognizable); labral

arc relatively shallow, with denticles short and obtuse; first maxillae with one pair of lappets; forcipular trochanteroprefemur and tarsungulum with large denticles, femur and tibia with small denticles; 37–39 leg-bearing segments; metasternites with relatively sparse setae; metasternite of the ultimate leg-bearing segment trapezoid, slightly longer than wide; coxal pores on both ventral and lateral sides of coxopleura; anal pores present.

**Distribution.** Far East: Maritime krai (Titova 1973; Kurcheva 1977; Ganin 1997, 2006). Outside Asian Russia: no records.

**Remarks.** Titova (1973) indicated that the type series was from two localities ("Suputinsky zapovednik" and "Kedrovaya Pad"), but she did not state explicitly which is the locality of the holotype.

#### 28. Escaryus hirsutus Titova 1973 \*

Escaryus hirsutus Titova 1973: 96. Escaryus hirsutus – Molodova 1973: 67; Kurcheva 1977: 45; Ganin 1997: 134.

**Type locality.** RUSSIA: Sakhalin oblast: "O-v Sakhalin, Yuzhno-Sakhalinsk, gora Chekhova" (Titova 1973) = Chekhova Mt., near Yuzhno-Sakhalinsk city, ca 47°00'N, 142°50'E.

**Type series.** Holotype: female. Paratypes: 10 specimens, including 5 males and 5 females. Deposited in ZMMU (S. Golovatch and A. Schileyko, pers. comm., 13.II.2023 and XII.2023).

**Diagnosis.** An *Escaryus* species with body length reaching  $\ge 2.5$  cm; clypeus with large plagulae; labral arc relatively deep, with denticles long and obtuse; first maxillae with one pair of lappets; all forcipular articles with large bulges; 37-39 leg-bearing segments; metasternites with relatively dense setae; metasternite of the ultimate leg-bearing segment almost rectangular, ~  $1.5 \times$  as long as wide; coxal pores on both ventral and lateral sides of coxopleura; anal pores present.

**Distribution.** Far East: Sakhalin oblast (Sakhalin Isl.) (Titova 1973; Molodova 1973; Kurcheva 1977; Ganin 1997). Outside Asian Russia: no records.

#### 29. Escaryus japonicus Attems, 1927 \*

Escaryus japonicus Attems 1927: 299.

Escaryus japonicus – Attems 1929: 96; Byzova and Chadaeva 1965: 333; Shinohara 1972: 66; Titova 1969: 165; 1972: 135; 1973: 113; Ghilarov and Perel 1973: 46; Molodova 1973: 67; Alekseeva 1974: 8; Kurcheva 1977: 45; Markelov and Mineeva 1981: 130; Ganin 1997: 105, 109, 112, 114, 121, 124, 126, 129, 134, 141; 2006: 501; Vorobiova 1999: 33; Farzalieva 2008: 67; Volkova 2016: 676; Dyachkov 2017: 454; Nefediev et al. 2017a: 11; 2017c: 222; Dyachkov and Tuf 2018: 296; Nefediev 2019: 25; Dyachkov and Farzalieva 2023: 229.

Type locality. JAPAN: Hokkaido: "Todohokhe" (Attems 1927).

**Type series.** *Syntypes***:** 2 specimens, including a male and a juvenile. Deposited in NHMW (Ilie et al. 2009).

**Diagnosis.** An *Escaryus* species with body length reaching  $\geq$  4.3 cm; clypeus with large plagulae; labral arc relatively shallow, with denticles long and obtuse; first maxillae with one pair of lappets; forcipular trochanteroprefemur with a small distal denticle, all other articles with very small bulges; 43–55 leg-bearing segments; metasternites with relatively sparse setae; metasternite of the ultimate leg-bearing segment rectangular, ~ 2× as long as wide; coxal pores of similar size, on both ventral and lateral sides of coxopleura; anal pores present.

**Distribution.** Western Siberia: Sverdlovsk, Chelyabinsk, Tomsk, and Kemerovo oblasts, republics of Altai and Khakassia (Byzova and Chadaeva 1965; Titova 1972, 1973; Farzalieva 2008; Dyachkov 2017; Nefediev et al. 2017a, 2017c; Nefediev 2019). Eastern Siberia: Republic of Buryatia and Krasnoyarsk krai (Alekseeva 1974; Titova 1973; Vorobiova 1999), Magadan oblast (Berman and Leirikh 2019). Far East: Amur oblast, Maritime and Khabarovsk krais, Sakhalin oblast (Sakhalin Isl.) (Titova 1973; Ghilarov and Perel 1973; Molodova 1973; Kurcheva 1977; Markelov and Mineeva 1981; Ganin 1997, 2006). Outside Asian Russia: European Russia (Titova 1973; Farzalieva 2008; Volkova 2016), eastern Kazakhstan (Dyachkov and Tuf 2018), Mongolia (Dyachkov and Farzalieva 2023), Northern China (Takakuwa and Takashima 1949), and Japan (Attems 1927).

**Remarks.** The record from the Krasnoyarsk krai by Vorobiova (1999) was questioned by Nefediev et al. (2017a).

#### 30. Escaryus koreanus Takakuwa, 1937 \*

Escaryus koreanus Takakuwa 1937a: 297.

*Escaryus koreanus* – Takakuwa 1940: 39; Titova 1972: 135; 1973: 112; Ghilarov and Perel 1973: 46; Kurcheva 1977: 45; Ganin 1997: 105, 109, 112, 114, 121, 124, 126, 128; 2006: 501; Rybalov 2002: 83; Vorobiova et al. 2002: 62; Nefediev et al. 2017a: 11; 2017c: 222; 2018: 238; Dyachkov 2017: 454; Dyachkov and Tuf 2018: 296; Nefediev 2019: 26.

Type locality. NORTH KOREA: "Husenzan" (Takakuwa 1937a).

**Type series**. *Syntypes*: unknown number of specimens, both sexes. Depository unknown.

**Diagnosis.** An *Escaryus* species with body length reaching  $\geq$  6.5 cm; clypeus with large plagulae; labral arc relatively shallow, with long denticles, the middle denticles obtuse, the lateral ones pointed; first maxillae with one pair of lappets; forcipular trochanteroprefemur with an small obtuse denticle, femur and tibia without denticles, tarsungulum with a small basal bulge; 43–55 leg-bearing segments; metasternites with relatively dense setae; metasternite of the ultimate leg-bearing segment rectangular, ~ 2× as long as wide; coxal pores of different size, on both ventral and lateral sides of coxopleura, including a pair of much larger pores on each coxopleuron; anal pores present.

**Distribution.** Western Siberia: Altai krai, republics of Altai and Khakassia, Kemerovo, Novosibirsk, and Tomsk oblasts (Titova 1972, 1973; Dyachkov 2017; Nefediev et al. 2017a, 2017c, 2018; Nefediev 2019). Eastern Siberia: Krasnoyarsk krai, Irkutskaya oblast (Rybalov 2002; Vorobiova et al. 2002; Nefediev 2019). Far East: Maritime and Khabarovsk krais, Amur Oblast (Titova 1972, 1973; Ghilarov and Perel 1973; Kurcheva 1977; Ganin 1997). Outside Asian Russia: Eastern Kazakhstan (Dyachkov and Tuf 2018), Japan, and North Korea (Takakuwa 1937a, 1940).

**Remarks.** Titova (1973: 113) suggested that *E. koreanus* can be a junior synonym of *E. sibiricus* Cook, 1899.

#### 31. Escaryus krivolutskiji Titova, 1973 \*

Escaryus krivolutskiji Titova 1973: 102.

*Escaryus krivolutskiji* – Kurcheva 1977: 45; Markelov and Mineeva 1981: 129; Ganin 1997: 121, 124, 126, 128.

**Type localities.** RUSSIA: Maritime krai: "Suputinsky zapovednik" = Ussuriysky Nature Reserve, ca 43°40'N, 132°32'E, and "Kangauz" = Anisimovka Village, ca 43°10'N, 132°47'E and "Kedrovaya Pad" = Kedrovaya Pad Nature Reserve, ca 43°05'N, 131°30'E, (all Titova 1973) (see Remarks).

**Type series.** *Holotype*: male. Paratypes: 10 specimens, including 5 males and 5 females. Deposited in ZMMU (S. Golovatch and A. Schileyko, pers. comm., 13.II.2023 and XII.2023).

**Diagnosis.** An *Escaryus* species with body length reaching  $\ge 2$  cm; clypeus without plagulae; labral arc relatively deep, with denticles short and obtuse; first maxillae with one pair of lappets; forcipular trochanteroprefemur and tibia with large bulges, femur and tarsungulum with small bulges; 45–49 leg-bearing segments; metasternite of the ultimate leg-bearing segment trapezoid, approximately as long as wide; coxal pores on both ventral and lateral sides of coxopleura, the pair of largest pores close to inner edge of coxopleura; anal pores present.

**Distribution.** Far East: Maritime krai (Titova 1973; Kurcheva 1977; Markelov and Mineeva 1981; Ganin 1997, 2006). Outside Asian Russia: no records.

**Remarks.** Titova (1973) indicated that the type series was from three localities ("Suputinsky zapovednik", "Kangauz", and "Kedrovaya Pad"), but she did not state explicitly which is the locality of the holotype.

#### 32. Escaryus molodovae Titova, 1973 \*

*Escaryus molodovae* Titova 1973: 95. *Escaryus molodovae* – Molodova 1973: 67; Kurcheva 1977: 45; Ganin 1997: 134.

**Type locality.** RUSSIA: Sakhalin oblast: "O-v Sakhalin, Yuzhno-Sakhalinsk, gora Chekhova" (Titova 1973) = Chekhova Mt., near Yuzhno-Sakhalinsk city, ca 47°0'N, 142°50'E.

**Type series.** *Holotype*: male. Paratypes: 8 specimens, including 5 males and 3 females. Deposited in ZMMU (S. Golovatch and A. Schileyko, pers. comm., 13.II.2023 and XII.2023).

**Diagnosis.** An *Escaryus* species with body length reaching  $\geq$  1.4 cm: clypeus with small plagulae; labral arc relatively shallow, with denticles short and obtuse; first maxillae with one pair of lappets; forcipular trochanteroprefemur,

femur and tibia with small denticles; forcipular tarsungulum with a large, pointed basal denticle; 35 leg-bearing segments; metasternites with relatively sparse setae; metasternite of the ultimate leg-bearing segment trapezoid, approximately as long as wide; coxal pores only on the ventral side of coxopleura; anal pores present.

**Distribution.** Far East: Sakhalin oblast (Sakhalin Isl.) (Titova 1973; Molodova 1973; Kurcheva 1977; Ganin 1997). Outside Asian Russia: no records.

#### 33. Escaryus perelae Titova, 1973 \*

Escaryus perelae Titova 1973: 101.

*Escaryus perelae* – Kurcheva 1977: 45; Markelov and Mineeva 1981: 129; Ganin 1997: 105, 109, 112, 121, 124, 126, 128; 2006: 501.

**Type localities.** RUSSIA: Maritime krai: "Suputinsky zapovednik" = Ussuriysky Nature Reserve, ca 43°40'N, 132°32'E, and "Rayon r. Sinancha" = near Cheremukhovaya River, inflow of Dzhigitovka River, ca 44°50'N, 136°07'E (both Titova 1973) (see Remarks).

**Type series.** *Holotype*: female. Paratypes: 6 specimens, including 2 males and 4 females. Deposited in ZMMU (S. Golovatch and A. Schileyko, pers. comm., 13.II.2023 and XII.2023).

**Diagnosis.** An *Escaryus* species with body length reaching  $\ge 2$  cm; clypeus with small plagulae; labral arc relatively shallow, with denticles short and obtuse; first maxillae with one pair of lappets; forcipular trochanteroprefemur and tibia with small denticles, femur without denticle, tarsungulum with a large basal denticle; 39–43 leg-bearing segments; metasternite of the ultimate leg-bearing segment trapezoid, distinctly wider than long; most of coxal pores on the ventral side of coxopleura, mostly close to metasternite; anal pores present.

**Distribution.** Far East: Amur oblast, Maritime and Khabarovsk krais (Titova 1973; Kurcheva 1977; Markelov and Mineeva 1981; Ganin 1997, 2006). Outside Asian Russia: no records.

**Remarks.** Titova (1973) indicated that the type series was from two localities ("Suputinsky zapovednik" and "Rayon r. Sinancha"), but she did not state explicitly which is the locality of the holotype.

#### 34. Escaryus polygonatus Titova, 1973 \*

Escaryus polygonatus Titova 1973: 98.

*Escaryus polygonatus* – Kurcheva 1977: 45; Markelov and Mineeva 1981: 130; Ganin 1997: 121, 124, 126, 128; 2006: 501.

**Type localities.** RUSSIA: Maritime krai: "Suputinsky zapovednik" = Ussuriysky Nature Reserve, ca 43°40'N, 132°32'E, and "Kedrovaya Pad" = Kedrovaya Pad Nature Reserve, ca 43°05'N, 131°30'E, (both Titova 1973).

**Type series.** *Holotype*: male. Paratypes: 17 specimens, including 9 males and 8 females. Deposited in ZMMU (S. Golovatch and A. Schileyko, pers. comm., 13.II.2023 and XII.2023).

**Diagnosis.** An *Escaryus* species with body length reaching  $\ge 2.8$  cm; clypeus with small plagulae; labral arc relatively deep, with denticles short and obtuse; first maxillae with one pair of lappets; forcipular trochanteroprefemur, femur, and tibia with small bulges; forcipular tarsungulum without denticle; 39 leg-bearing segments; metasternites with relatively sparse setae; metasternite of the ultimate leg-bearing segment trapezoid, ~ 1.5× as long as wide; coxal pores of different size, on both ventral and lateral sides of coxopleura; anal pores present.

**Distribution.** Far East: Maritime krai (Titova 1973; Kurcheva 1977; Markelov and Mineeva 1981; Ganin 1997). Outside Asian Russia: no records.

**Remarks.** Titova (1973) indicated that the type series was from two localities ("Suputinsky zapovednik" and "Kedrovaya Pad"), but she did not state explicitly which is the locality of the holotype.

#### 35. Escaryus retusidens Attems, 1904

Escaryus retusidens Attems 1904: 121.

*Escaryus retusidens* – Attems 1929: 96; Titova 1972: 135, 116; 1973: 110; Volkova 2016: 675; Zuev 2016: 33; Nefediev et al. 2017a: 11; 2017c: 222; 2018: 239; Dyachkov and Tuf 2018: 295; Nefediev 2019: 27; Dyachkov 2022: 25.

**Type locality.** KYRGYZSTAN: Issyk-Kul Region: "Przewalsk" (Attems 1904) = Karakol.

**Type series.** *Syntypes***:** 4 specimens, including 2 males and 2 females. Deposited in NHMW (Ilie et al. 2009).

**Diagnosis.** An *Escaryus* species with body length reaching  $\geq$  4 cm; clypeus with small plagulae; labral arc relatively deep, with denticles long and obtuse; first maxillae with one pair of lappets; forcipular trochanteroprefemur, femur, and tibia with small denticles, tarsungulum with a small bulge; 49–55 leg-bearing segments; metasternites with relatively sparse setae; metasternite of the ultimate leg-bearing segment trapezoid, approximately as long as wide; coxal pores on both ventral and lateral sides of coxopleura; anal pores absent.

**Distribution.** Western Siberia: Altai krai, Republic of Altai, and Kemerovo oblast (Nefediev et al. 2017a, 2017c, 2018; Nefediev 2019). Possibly Far East (Titova 1972, 1973; see Remarks). Outside Asian Russia: westwards to Moldova (Titova 1973; Volkova 2016; Zuev 2016; Zuev and Evsyukov 2016); southwards to Kazakhstan and Kyrgyzstan (Attems 1904; Titova 1972, 1973; Dyachkov and Tuf 2018; Dyachkov 2022).

**Remarks.** A total of 19 males and 26 females collected from Trans-Ili Alatau (Almaty Region of Kazakhstan) were indicated by Titova (1973: 110) as lecto-types, but this action is not valid, as the syntypes still exist (llie et al. 2009).

Titova (1972: 135; 1973: 116) wrote "... it is possible to distinguish territories from Cisamuria to Kuzbass and Altai, where 4 species are spread: *E. koreanus, E. japonicus, E. retusidens*, and *E. chadaevae*". However, she did not mention material from this area when she listed the studied material of *E. retusidens* (Titova 1973: 110): "Kazakhstan, Trans-Ili Alatau... Moreover, *E. retusidens* were studied from the Dzhungarian Alatau, the Greater Caucasus, Crimea, Moldova, Rostov, Voronezh and Voroshilovograd oblasts".

#### 36. Escaryus sachalinus Takakuwa, 1935

Escaryus sachalinus Takakuwa 1935: 48.

*Escaryus sachalinus* – Titova 1969: 165; 1972: 135; 1973: 94, 118; Shinohara 1972: 66; Kurcheva 1977: 45.

**Type localities.** RUSSIA: Sakhalin oblast: "Sachalin" = Sakhalin Isl. Japan: Hokkaido Isl.: "Sapporo" (both Takakuwa 1935).

Type series. Syntypes: 3 specimens. Depository unknown.

**Diagnosis.** An *Escaryus* species with body length reaching  $\ge$  3 cm; clypeus without plagulae; labral arc relatively deep, with denticles short and obtuse; first maxillae with lappets; all forcipular articles with small denticles, except tarsungulum; 35–39 leg-bearing segments; metasternite of the ultimate leg-bearing segment rectangular, ~ 1.5× as long as wide; numerous coxal pores on ventral side of coxopleuron; anal pores present.

**Distribution.** Far East: Sakhalin oblast (Sakhalin Isl.) (Titova 1973; Kurcheva 1977). Outside Asian Russia: Japan (Takakuwa 1935; Shinohara 1972) and northern China (Shinohara 1972).

#### 37. Escaryus sibiricus Cook, 1899

Escaryus sibiricus Cook 1899: 304.

*Escaryus sibiricus* – Attems 1904: 122; 1927: 301; 1929: 95; Titova 1972: 135; 1973: 94, 113; Ganin 1997: 141; Thofern et al. 2021: 30.

**Type locality.** RUSSIA: Maritime krai: "Vladivostock" (Cook 1899) = Vladivostok city, 43°7'N, 131°54'E.

**Type series.** *Syntypes***:** 12 specimens, both sexes, including 10 specimens deposited in ZMH (Thofern et al. 2021) and 2 specimens deposited in NHMW (Ilie et al. 2009).

**Diagnosis.** An *Escaryus* species with body length reaching 6.5 cm; labral arc relatively shallow, with middle denticles obtuse and lateral ones long and pointed; first maxillae with two pairs of lappets; forcipular trochanteroprefemur with a small distal bulge, other forcipular articles without denticles; 49–51 leg-bearing segments; metasternite of the ultimate leg-bearing segment rectangular,  $\sim 2 \times$  as long as wide; coxal pores of different size, on both ventral and lateral sides, including a pair of much larger ventral pores on each coxopleuron; anal pores absent.

**Distribution.** Far East: Maritime krai (Cook 1899; Attems 1904) and Amur oblast (Ganin 1997). Outside Asian Russia: no records.

**Remarks.** Titova (1969) reported this species from Western Siberia (Kemerovo oblast) but later (Titova 1973) she regarded the same record as *E. koreanus*, even though she also suggested that the latter species can be a junior synonym of *E. sibiricus*. The anal pores were indicated as absent by Cook (1899) and Attems (1904) but illustrated as present in specimens identified as *E. sibiricus* by Thofern et al. (2021), and they are known to be present in *E. koreanus*.

#### 38. Escaryus vitimicus Titova, 1973 \*

Escaryus vitimicus Titova 1973: 103. Escaryus vitimicus – Alekseeva 1974: 8.

**Type locality.** RUSSIA: Republic of Buryatia: "r. Vitim, Aniboli" (Titova 1973) = ? Anibud river, inflow of Vitim River, ca 53°39'N, 113°53'E.

**Type series.** *Holotype*: female. Paratypes: 3 specimens, including 1 male and 2 females. Deposited in ZMMU (S. Golovatch and A. Schileyko, pers. comm., 13.II.2023 and XII.2023).

**Diagnosis.** An *Escaryus* species with body length reaching  $\ge 2.7$  cm; clypeus with large plagulae; labral arc relatively shallow, with denticles long and obtuse; first maxillae with one pair of lappets; all forcipular articles with small bulges; 37 leg-bearing segments; metasternites with relatively sparse setae; metasternite of the ultimate leg-bearing segment rectangular, ~ 1.5× as long as wide; coxal pores on both ventral and lateral sides of coxopleura, the largest pores near the metasternite; anal pores present.

**Distribution.** Eastern Siberia: Republic of Buryatia (Titova 1973; Alekseeva 1974). Outside Asian Russia: no records.

#### Other records of uncertain species

During ecological studies (Ghilarov and Perel 1973; Molodova 1973; Kurcheva 1977; Markelov and Mineeva 1981; Ganin 1997) some specimens of Geophilomorpha were not identified at the species level. These records are listed below.

- Arctogeophilus sp. Ghilarov and Perel 1973: 46 (Maritime krai); Markelov and Mineeva 1981: 130 (Maritime krai).
- Geophilus sp. Molodova 1973: 67 (Sakhalin oblast: Sakhalin Isl.); Ganin 1997: 105, 109, 112, 114, 128, 141 (Amur oblast and Khabarovsk krai); Markelov and Mineeva 1981: 130 (Maritime krai).
- Pachymerium sp. Kurcheva 1977: 46 (Khabarovsk and Maritime krais).

Scolioplanes sp. – Ghilarov and Perel 1973: 46 (Maritime krai); Alekseeva 1974: 8 (Republic of Buryatia); Markelov and Mineeva 1981: 130 (Maritime krai).

Strigamia sp. - Markelov and Mineeva 1981: 130 (Maritime krai).

*Prolamnonyx* sp. – Kurcheva 1977: 46 (Maritime krai and Sakhalin oblast: Kuril Islands).

Escaryus sp. - Markelov and Mineeva 1981: 129 (Maritime krai).

## Discussion

#### History of studies

The first record of Geophilomorpha from Asian Russia was published by Gerstfeldt (1859), who recorded *Arthronomalus longicornis* Leach, 1815 (=Geophilus flavus (De Geer, 1778)) from the Zabaykalsky krai.

Other records of Geophilidae were provided by Meinert (1870), who described *Geophilus pilosus* from Sakhalin Isl., and by Stuxberg (1876a, 1876b),

who recorded the latter species in the Krasnoyarsk krai and also described G. sibiricus from this region. Around the same time Sseliwanoff (1881) described G. orientalis from the Khabarovsk krai, and recorded G. pilosus from the Krasnoyarsk krai and Irkutsk oblast, and G. proximus C.L. Koch, 1847 from Western Siberia. Attems (1909) described Arctogeophilus glacialis from three localities (two of them in the Chukotka Peninsula). Later, Verhoeff (1934) and Takakuwa (1937c) described A. sachalinus, Geophilus bipartitus and G. rhomboideus from Sakhalin Isl. Numerous faunistic and ecological studies (Byzova and Chadaeva 1965; Ghilarov and Perel 1973; Molodova 1973; Kurcheva 1977; Markelov and Mineeva 1981; Zalesskaja et al. 1982; Poryadina 1991; Striganova and Poryadina 2005; Ganin 1997, 2006; Vorobiova 1999; Vorobiova et al. 2002; Rybalov 2002; Farzalieva 2008; Sergeeva 2013; Bukhkalo and Sergeeva 2012; Bukhkalo et al. 2014; Nefediev et al. 2017a, 2017b, 2017c, 2018, 2021; Nefediev 2019) provided additional data for seven species of geophilids from Asian Russia: Arctogeophilus macrocephalus Folkmanová & Dobroruka, 1960, Geophilus bipartitus, G. flavus, G. proximus, G. rhomboideus, G. sounkyoensis Takakuwa, 1937, and Pachymerium ferrugineum (C.L. Koch, 1835).

The first record of *Strigamia* Gray, 1843 from Asian Russia was published by Meinert (1870), who described *Scolioplanes sacolinensis* from Sakhalin Isl. Later, Sseliwanoff (1881) described *S. sibiricus* from the Zabaykalsky krai and *S. sulcatus* from the Khabarovsk krai. A number of papers (Ghilarov and Perel 1973; Molodova 1973; Kurcheva 1977; Ganin 1997; Farzalieva 2008; Nefediev et al. 2017c, 2018; Nefediev 2019) provided other distribution data for seven *Strigamia* species from Asian Russia: *S. acuminata*, *S. alokosternum*, *S. hirsutipes*, *S. pusilla*, *S. sacolinensis*, *S. sulcata*, and *S. transsilvanica*.

The first record of the family Mecistocephalidae was published by Titova (1969), who reported a specimen from the Maritime krai, first as *Prolamnonyx holstii* (Pocock, 1895) and later (Titova 1975) as a new species, *Prolamnonyx mamaevi*. She also described *Krateraspis striganovae* from the Maritime krai and recorded *Prolamnonyx dentatus* from Far East. Markelov and Mineeva (1981) and Ganin (1997, 2011) published additional data for the species mentioned by Titova; Nefediev (2019) recorded an anthropochore introduction, *Tygarrup javanicus* Attems, 1929, in the Altai krai.

The first species of *Escaryus* Cook & Collins, 1891 (Schendylidae), *E. sibiricus*, was described by Cook (1899) from Vladivostok (Maritime krai). Later, Attems (1904) redescribed this species based on the type material, and Takakuwa (1935) described another species, *E. sachalinus*, from Sakhalin Isl. Eight other species of *Escaryus* were described by Titova (1973): *E. molodovae* and *E. hirsutus* from Sakhalin Isl.; *E. dentatus*, *E. krivolutskiji*, *E. perelae*, and *E. polygonatus* from the Maritime krai; *E. vitimicus* from the Republic of Buryatia; *E. chadaevae* from the Kemerovo oblast. Some ecological and faunistic papers (Titova 1972, 1973; Ghilarov and Perel 1973; Molodova 1973; Alekseeva 1974; Kurcheva 1977; Markelov and Mineeva 1981; Rybalov 2002; Ganin 1997, 2006; Vorobiova et al. 2002; Dyachkov 2017; Nefediev et al. 2017a, 2017c, 2018; Nefediev 2019) provided new data of *Escaryus* species, including four other species, namely *E. chichibuensis* Shinohara, 1955, *E. japonicus* Attems, 1927, *E. koreanus* Takakuwa, 1937, and *E. retusidens* Attems, 1904.

## State of knowledge

The published records of Geophilomorpha from Asian Russia refer to 38 nominal species, arranged in eight genera (Table 1). However, the taxonomic validity of  $\geq$  19 species is uncertain, including 14 species that are known from Asian Russia only (Table 1). The taxonomic status of most of these species has never been revised since they were originally described. Of all the species reported from Asian Russia, only nine are also known from European Russia, where, a total of 41 species from 17 genera have been reported so far (Volkova 2016; Zuev and Evsyukov 2016; Dyachkov and Bonato 2022).

The records of *Tygarrup javanicus* and *Geophilus flavus* from hothouses in Western Siberia by Nefediev et al. (2017a; Nefediev 2019) seems to be due to anthropochore introduction. However, the occurrence of *Geophilus flavus* outside hothouses in Asian Russia requires confirmation. Gerstfeldt (1859) identified a sole specimen from Eastern Siberia (Zabaykalsky krai) as *Arthronomalus longicornis* (= *Geophilus flavus*), but Sseliwanoff (1884: 90) questioned this identification. Moreover, the nominal species *Schizotaenia ornata* Folkmanová & Dobroruka, 1960 was mentioned by Zalesskaja et al. (1982) from Western Siberia, however without providing information on specimens or published sources. This nominal species was considered a junior synonym of *Geophilus proximus* by Zalesskaja et al. (1982), but was later synonymized under *G. flavus* by Bonato and Minelli (2014). Nefediev et al. (2017a) suggested that some previous records of *G. flavus* from the former USSR may be reported under the name *G. proximus*.

Other species require confirmation from Asian Russia. The records of *Strigamia acuminata* from Far East and *S. transsilvanica* from Western Siberia and Far East are dubious because of possible confusion with other species (Bonato et al. 2012, 2023). Moreover, Titova (1972, 1973) indicated the presence of *Escaryus retusidens* from the Russian Far East, but she did not mention material from that region when she listed the studied specimens. Nefediev et al. (2017a, 2017c, 2018) indicated this species from the Far East with reference to Titova (1972, 1973). It is worth noting that *E. retusidens* has never been recorded during ecological studies in Eastern Siberia (Alekseeva 1974; Vorobiova 1999; Vorobiova et al. 2002; Rybalov 2002) or the Far East (Kurcheva 1977; Ganin 1997, 2006, 2011).

Our synthesis of all published information on Geophilomorpha from Asian Russia shows that the knowledge of this fauna is very far from being satisfactory. We hope that this work may provide a background reference and will prompt further investigations.

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# **Additional information**

## **Conflict of interest**

The authors have declared that no competing interests exist.

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All authors have contributed equally.

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#### Data availability

All of the data that support the findings of this study are available in the main text.

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**Research Article** 

# Next step in *Monacha cantiana* (Montagu, 1803) phylogeography: northern French and Dutch populations (Eupulmonata, Stylommatophora, Hygromiidae)

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## Abstract

Features of shell and genitalia as well as nucleotide sequences of selected mitochondrial and nuclear genes of specimens of *Monacha cantiana* from ten northern French and two Dutch populations were compared with the same features of British and Italian populations. They were found to be very similar to populations previously identified as belonging to the CAN-1 lineage of *M. cantiana*. This confirms previous suggestions that *M. cantiana* was introduced to western Europe (England, France and the Netherlands) in historical times.

**Key words:** 16SrDNA, COI, genitalia, H3, ITS2, mitochondrial and nuclear genes, nucleotide sequences, population distribution, shell

## Introduction

*Monacha* Fitzinger, 1833 is a species-rich genus including numerous nominal species diversified mainly in the Anatolian and European parts of Turkey, in the southern parts of the Balkans and in Italy (Hausdorf 2000a, 2000b; Welter-Schultes 2012; Neiber and Hausdorf 2017). Only two species, *Monacha cantiana* (Montagu, 1803) and *M. cartusiana* (Müller, 1774), used to be reported from Western Europe. Two more were introduced not long ago, namely *M. ocellata* (Roth, 1839) and *M. samsunensis* (Pfeiffer, 1868), the latter until recently reported as *M. atacis* Gittenberger & de Winter, 1985 (Welter-Schultes 2012; Anderson et al. 2018; Pieńkowska et al. 2018a, 2022).

Monacha cantiana, commonly known as the Kentish snail, was described by Montagu (1803: 422) from Kent in Britain "where it is found chiefly upon the chalky soil". Type material consists of three syntypes, which were probably collected around Sandwich in Kent (51°16'26.46"N, 1°20'14.74"E) by William Boys, and are kept with the Montagu Collection in the Royal Albert Memorial Museum



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**Copyright:** © Joanna R. Pieńkowska et al. This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0). & Art Gallery, Exeter (Oliver et al. 2017). Montagu later added several localities in other counties of southern Britain to the original description (Montagu 1808: 145, pl. 23, fig. 1).

It has been suggested that this species was introduced to the British Isles in historical times (Kerney 1970, 1999; Evans 1972). Our previous research on several *M. cantiana* populations, using an integrative approach combining analysis of the shell structure and genital anatomy with that of nucleotide sequences of mitochondrial and nuclear gene fragments, revealed six lineages, namely CAN-1, CAN-2, CAN-3, CAN-4, CAN-5 and CAN-6 (Pieńkowska et al. 2018b, 2019a). CAN-1 (representing true M. cantiana) was found to occur in the Latium region of Italy and in Spain and Britain (Pieńkowska et al. 2018b; Čejka et al. 2020), in line with the suggestion that this lineage probably spread with the Roman conquests (Pieńkowska et al. 2018b). Populations of CAN-2 were found in regions of Italy (Emilia Romagna) north of Latium (Pieńkowska et al. 2018b) and somewhat surprisingly in Slovakia (Bratislava) (Čejka et al. 2022), while those of CAN-3 were reportedly widespread even further north in Italy (Friuli-Venezia Giulia) as far as Vienna in Austria (Pieńkowska et al. 2018b, 2019b) and Bratislava in Slovakia (Čejka et al. 2022). The lineage CAN-4, corresponding to Monacha cemenelea (Risso, 1826), was found in south-eastern France (Pieńkowska et al. 2018b; Čejka et al. 2020). CAN-5 and CAN-6 are reported from the Apuan Alps and represent one or two different species, the naming of which requires further studies on topotypical material (Pieńkowska et al. 2019a).

Monacha cantiana has been reported from France (Kerney et al. 1983; Falkner et al. 2002; Cucherat 2005; Lecaplain 2007; Gargominy et al. 2011; Welter-Schultes 2012; Bichain et al. 2019; Brulé and Bichain 2019; INPN 2019). Brulé and Bichain (2019) carefully analysed shell and genitalia features of *M. cantiana* specimens collected at two sites in north-eastern France near the towns of Cutry and Longwy. However since the CAN-1, CAN-2, CAN-3, and CAN-4 lineages of *M. cantiana* do not differ in shell or genital features, the phylogenetic relationships of populations from north-eastern France had to be clarified by genetic analysis. Although *M. cantiana* is known to occur in the Netherlands (Kerney et al. 1983; Gittenberger et al. 1984; Welter-Schultes 2012), it has never been confirmed genetically.

The aim of the present research was: 1) to study morphological (shell and genitalia) and molecular variation in specimens of *M. cantiana* collected in northern France and the Netherlands in order to clarify their relations to the British and Italian populations; 2) to test the hypothesis that the English, French and Dutch populations originated from the same introduced propagules.

## Materials and methods

## **Taxonomic samples**

Specimens from ten French and two Dutch populations of *Monacha cantiana* were considered for analysis of the variability of their molecular and morphological (shell and genitalia) features (Table 1, Fig. 1). Specimens from four new British and one new Italian population were used for comparative molecular analysis with other populations of *M. cantiana* s.l. (Table 1, Fig. 1). Sequences deposited in GenBank for *M. cantiana* s.l. from other populations (Manganelli



**Figure 1.** Map of localities of the populations of *Monacha cantiana* analysed. See Table 1 for details of populations 1–26, Brulé and Bichain (2019) for populations 27 and 28, and Pieńkowska et al. (2019a) for populations 29–32.

et al. 2005; Duda et al. 2011; Kruckenhauser et al. 2014; Cadahia et al. 2014; Pieńkowska et al. 2015, 2018b, 2019a, 2019b; Razkin et al. 2015; Neiber and Hausdorf 2017; Čejka et al. 2020, 2022) and three other *Monacha* species (*M. cartusiana*: Pieńkowska et al. 2015, 2022; Neiber and Hausdorf 2017; Caro et al. 2019; Čejka et al. 2020; *M. pantanellii* (De Stefani, 1879): Pieńkowska et al. 2020; *M. parumcincta* (Rossmässler, 1834): Pieńkowska et al. 2018b) were also selected for molecular analysis (Suppl. materials 1–4) and supplemented with several new sequences of mitochondrial (16SrDNA) and nuclear (ITS2 flanked with 5.8SrDNA and 28SrDNA) genes (Table 1). Sequences of *Trochulus hispidus* (Linnaeus, 1758) deposited in GenBank by Neiber et al. (2017), Neiber and Hausdorf (2017), Caro et al. (2019) and Proćków et al. (2021) were used as an outgroup to construct phylogenetic trees (Suppl. materials 1–4). The localities for reference populations of *M. cantiana* s.l. CAN-1 – CAN-6, *M. pantanellii*, *M. cartusiana*, and *M. parumcincta* were shown on maps published in our previous papers (Pieńkowska et al. 2018b: fig. 63, 2020: fig. 1).

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5.8SrDN/ 28Sr	new haplotype	ITS2 1	ITS2 2	ITS2 1	ITS2 1			ITS2 3		ITS2 4	ITS2 5	ITS2 6	ITS2 1	ITS2 7	ITS2 7	ITS2 1	ITS2 8	ITS2 1	ITS2 9	ITS2 1	ITS2 10	ITS2 11		ITS2 12	ITS2 13	ITS2 14	ITS2 1		ITS2 15	ITS2 16	ITS2 1	ITS2 17	ITS2 18	
e	GenBank ##	OR939858	OR939859	OR939860	OR939861	OR939862	OR939863	OR939864	OR939865	OR939866	OR939867	OR939868	OR939869	OR939870	OR939871	OR939872	OR939873	OR939874	OR939875	OR939876	OR939877	OR939878	OR939879	OR939880	OR939881	OR939882	OR939883	OR939884	OR939885	OR939886	OR939887	OR939888	OR939889	
Ξ	new haplotype	H3 1	H3 2	H3 1	H3 1	H3 3	H3 1	H3 1	H3 1	H3 1	H3 3	H3 1	H3 1	H3 4	H3 1	H3 1	H3 1	H3 3	H3 1	H3 1	H3 1	H3 1	H3 1	H3 1	H3 1	H3 1	H3 1	H3 1	H3 1	H3 3	H3 1	H3 1	H3 5	
6SrDNA	GenBank ##	OR918363	OR918364	OR918365	OR918366		OR918367	OR918368	OR918369		OR918370	OR918371	OR918372		OR918373	OR918374	OR918375	OR918376	OR918377	OR918378	OR918379		OR918380	OR918381	OR918382	OR918383			OR918384	OR918385	OR918386		OR918387	
Long 1	new haplotype	16S 1	16S 1	16S 1	16S 2		16S 3	16S 1	16S 3		16S 3	16S 4	16S 4		16S 4	16S 1	16S 3	16S 5	16S 5	16S 1	16S 3		16S 6	16S 6	16S 3	16S 3			16S 3	16S 7	16S 3		16S 8	
5	GenBank ##		OR918493		OR918494		OR918495	OR918496	OR918497	OR918498	OR918499	OR918500	OR918501	OR918502	OR918503	OR918504	OR918505		OR918506	OR918507	OR918508	OR918509		OR918510	OR918511	OR918512	OR918513	OR918514	OR918515	OR918516	OR918517	OR918518		
ö	new haplotype		COI 1		COI 1		COI 1	COI 1	COI 1	COI 1	COI 1	COI 2	COI 1	COI 3	COI 1	COI 1	COI 1		COI 1	COI 1	COI 1	COI 1		COI 1	COI 1	COI 1	COI 1	COI 1	COI 1	COI 1	COI 1	COI 4		100
	Designation of DNA voucher sps	Ard1	Ard2	Ard3	Ard4	Ard5	Ble1	Ble2	Ble4	Ble5	Lar1	Lar2	Lar3	Lar4	Lar5	Lic1	Lic2	Lic3	Lic4	Lic5	Bet1	Bet2	Bet3	Bet4	Bet5	Pie1	Pie2	Pie3	Pie4	Epa1	Epa2	Epa3	Epa4	L
	Clade	CAN-1					CAN-1				CAN-1					CAN-1					CAN-1					CAN-1				CAN-1				
	Current taxonomy	M. cantiana					M. cantiana				M. cantiana					M. cantiana					M. cantiana					M. cantiana				M. cantiana				
	collector / date / no. of specimens (collection)	M. Proćków	/ 20.06.2018	/ 5 (MNHW* E1813)	6		M. Proćków	/ 20.06.2018	/ 5 (MNHW F1810)	6	M. Proćków	/ 20.06.2018	/ 5 (ININHW F1814)	6		M. Proćków	/ 20.06.2018	/ 5 (ININHW F18.12)	(1.0.1)		M. Proćków	/ 23.06.2018	/ 5 (ININHW F.18.22)			M. Proćków	/ 23.06.2018	/ 5 (ININHW F1821)	(	M. Proćków	/ 19.06.2018	/ 5 (MINHW F.18.08)	(	
Localities	country and site	France, Pas-de-Calais,	Bonningues-lès-Ardres,	vegetation under shrubs, 42 m a e l			France, Pas-de-Calais,	Blecquenecques n.	Marquise, roadside, 26 m a e l		France, Pas-de-Calais,	Larré, vegetation along	stream, oo m a.s.i.			France, Pas-de-Calais,	Licques, vegetation along	road, ot fit a.s.t.			France, Seine-Maritime,	Béthencourt n.	under trees. 97 m a.s.l.			France, Seine-Maritime,	Pierrepont, forest edge,	140 m a.s.i.		France, Somme, Épagne-	Épagnette, roadside, 13	m a.s.i.		
	coordinates	50°47'56.7"N,	02°00'57.5"E				50°49'28.1"N,	01°44'01.9"E			50°40'56.7"N,	02°03'39.1"E				50°47'48.2"N,	01°56'34.4"E				49°54'23.6"N,	01°30'58.9"E				49°55'05.6"N,	01°31'38.1"E			50°04'05.1"N,	01°52'20.9"E			
	No.	-	5				2	<u> </u>			3	_				4	2				5	_				9	_			7	_			

	Figs						I SH/AN																											
ž	and RDA						SH/AN																											
A + ITS2 + rDNA	GenBank ##		OR917374	OR917375			OR917376	OR917377	OR917378	OR917379	OR917380	OR917381	OR917382		OR917383	OR917384											OR917385		OR917386	OR917387	OR917388	OR917389	OR917390	OR917391
5.8SrDN 28S	new haplotype		ITS2 19	ITS2 1			ITS2 20	ITS2 21	ITS2 22	ITS2 23	ITS2 17	ITS2 24	ITS2 1		ITS2 25	ITS2 26											ITS2 1		ITS2 1	ITS2 1	ITS2 27	ITS2 1	ITS2 1	ITS2 1
<u>8</u>	GenBank ##	OR939891	OR939892	OR939893	OR939894	OR939895	OR939896	OR939897	OR939898	OR939899	OR939900	OR939901	OR939902	OR939903	OR939904	OR939905	OR939906	OR939907	OR939908	OR939909	OR939910	OR939911	OR939912	OR939913	OR939914	OR939915	OR939916	OR939917	OR939918	OR939919	OR939920	OR939921	OR939922	OR939923
T	new haplotype	H3 2	H3 1	H3 1	H3 1	H3 2	H3 1	H3 2	H3 6	H3 1	H3 6	H3 3	H3 1	H3 7	H3 7	H3 1	H3 1	H3 8	H3 1	H3 1	H3 1	H3 1	H3 5	H3 1	H3 1	H3 1	H3 1	H3 9	H3 9	H3 9	H3 10	H3 1	H3 1	H3 1
6SrDNA	GenBank ##	OR918389	OR918390	OR918391	OR918392	OR918393	OR918394		OR918395		OR918396	OR918397	OR918398	OR918399	OR918400	OR918401	OR918402	OR918403	OR918404	OR918405	OR918406	OR918407	OR918408	OR918409	OR918410	OR918411	OR918412		OR918413	OR918414		OR918415	OR918416	OR918417
Long 1	new haplotype	16S 4	16S 10	16S 11	16S 12	16S 13	16S 14		16S 14		16S 15	16S 3	16S 16	16S 3	16S 17	16S 18	16S 19	16S 1	16S 3	16S 19	16S 3	16S 3	16S 3	16S 19	16S 3	16S 3	16S 1		16S 3	16S 3		16S 3	16S 3	16S 3
0	GenBank ##		OR918520	OR918521	OR918522	OR918523	OR918524	OR918525	OR918526	OR918527	OR918528	OR918529	OR918530			OR918531	OR918532	OR918533	OR918534	OR918535	OR918536		OR918537	OR918538	OR918539	OR918540		0R918541						
ō	new haplotype		COI 1	COI 1	COI 1	COI 1	COI 1	COI 1	COI 1	COI 1	COI 1	COI 1	COI 5			COI 1	COI 1	COI 1	COI 1	COI 1	COI 6		C017	COI 1	COI 1			COI 8						
	Designation of DNA voucher sps	Fro1	Fro2	Fro3	Fro4	Fro5	Esc1	Esc2	Esc3	Esc4	Esc5	Fou1	Fou2	Fou3	Fou4	Fou5	Vee1-1	Vee1-2	Vee1-3	Vee1-4	Vee1-5	Vee2-1	Vee2-2	Vee2-3	Vee2-4	Vee2-5	Hum1	Hum2	Ver1	Ver2	Ver3	Ver4	Upt1	Upt2
	Clade	CAN-1					CAN-1					CAN-1					CAN-1					CAN-1					CAN-1		CAN-1				CAN-1	<u> </u>
	Current taxonomy	M. cantiana					M. cantiana					M. cantiana					M. cantiana					M. cantiana					M. cantiana		M. cantiana				M. cantiana	
	collector / date / no. of specimens (collection)	M. Proćków	/ 19.06.2018	/ 5 (MNHW	1.10.20		M. Proćków	/ 19.06.2018	/ 5 (MNHW E18 06)	(00.01.1		M. Proćków	/ 19.06.2018	/ 5 (MNHW F18.05)	(0000		M. Proćków	/ 6.06.2019/	5 (MNHW)	140.01		M. Proćków	/ 7.06.2019/	MNHW) S			M. Proćków /	15.06.2022/ 2 (MNHW GB.22.04)	M. Proćków /	15.06.2022/	4 (MNHW GB 22 05)	(00.33.00)	M. Proćków /	15.06.2022/ 2 (MNHW GB.22.06)
Localities	country and site	France, Somme, Froise,	forest edge, 86 m a.s.l.				France, Oise, Escales-	Saint-Pierre, roadside, 164	m a.s.l.			France, Oise, Fouquenies,	vegetation along forest	road, 29 m a.s.l.			The Netherlands, Veere,	edge of forest, 15 m a.s.l.				The Netherlands, Veere 6,	vegetation near windmill,	81 m a.s.l.			United Kingdom, Hurn,	vegetation along road, 7 m a.s.l.	United Kingdom,	Vernhams Dean,	vegetation along shaded		United Kingdom, Upton,	vegetation along road, 120 m a.s.l.
	coordinates	50°16'54.7"N,	01°37'41.9"E				49°44'14.7"N,	01°47'53.9"E				49°27'38.2"N,	02°03'35.0"E				51°32'57.0"N"	03°39'27.9"E				51°32'57.1"N"	03°39'40.1"E				50°46'23.5"N,	01°50'06.3"W	51°17'43.7"N,	01°29'34.9"W			51°17'32.3"N,	01°29'10.9"W
	No.	80					7 6	5				10					1					12	_				13.		14.				15.	

		Localities				Docimention	Ö	ō	Long 1	16SrDNA	-	3	5.8SrDN 28SI	A + ITS2 + IDNA	Č	
No.	coordinates	country and site	collector / date / no. of specimens (collection)	Current taxonomy	Clade	Designation of DNA voucher sps	new haplotype	GenBank ##	new haplotype	GenBank ##	new haplotype	GenBank ##	new haplotype	GenBank ##	and RDA	Figs
16.	55°02'13.6"N,	United Kingdom,	M. Proćków /	M. cantiana	CAN-1	New1	COI 9	OR918542	16S 20	OR918418	H3 9	OR939924	ITS2 1	OR917392		
	01°42'51.0"W	Newcastle upon Tyne,	15.06.2022/			New2			16S 20	OR918419	H3 9	OR939925	ITS2 1	OR917393		
		vegetation near airport, ou m a s l	68 22 07)			New3	COI 10	OR918543	16S 20	OR918420	H3 9	OR939926	ITS2 1	OR917394		
			( )		1	New4	COI 9	OR918544	16S 20	OR918421	H3 1	OR939927	ITS2 1	OR917395		
					1	New5	COI 1	OR918545	16S 3	OR918422	H3 9	OR939928	ITS2 1	OR917396		
					1	New6	COI 9	OR918546	16S 20	OR918423	H3 1	OR939929	ITS2 1	OR917397		
17.	53°31'29"N,	United Kingdom, Barrow	R.A.D.	M. cantiana	CAN-1	8FG-1		MG208884	16S 1	OR918424		MG209031	ITS2 1	OR917398		
	01°27'54"W	near Barnsley	Cameron / 10.2011 / 5 (FGC* 40329)		1	8FG-2		MG208885	16S 1	OR918425		MG209032	ITS2 1	0R917399		
18.	53°25'04.2"N, 01°24'00.5"W	United Kingdom, Rotherham	R.A.D. Cameron / 07.2015 / 7 (DCBC*)	M. cantiana	CAN-1	Sit1-1		MG208893	16S 1	0R918426		MG209035	ITS2 28	OR917400		
19.	53°24'49.1"N, 01°24'36.6"W	United Kingdom, Sheffield	R.A.D. Cameron / 07.2015 / 6 (DCBC)	M. cantiana	CAN-1	Sit2-1		MG208899	16S 21	0R918427		MG209038	ITS21	OR917401		
20	42°28'41.05"N,	Italy, Latium, Gole del	A. Hallgass /	M. cantiana	CAN-1	4FG-1		MG208905	16S 24	OR918428		MG209039	ITS2 29	OR917402		
	13°05'09.46"E	Velino, near Sigillo (Posta, Rieti)	30.09.2012 / 8 (FGC 42960)			4FG-2		MG208910	16S 25	OR918429		MG209042	ITS2 29	OR917403		
21.	42°43'39.87"N, 13°16'01.44"E	Italy, Latium, Valle del Tronto (Accumoli, Rieti)	A. Hallgass / 30.09.2012 / 4 (FGC 42963)	M. cantiana	CAN-1	Tro1		MG208921	16S 26	OR918430		MG209043	ITS2 1	OR917404		
22.	42°07'53.39"N,	Italy, Latium, Valle del	A. Hallgass /	M. cantiana	CAN-1	Tur5-1		MG208923	16S 27	OR918431		MG209048	ITS2 29	OR917405		
	13°01'39.81"E	Turano, near Turania (Rieti)	04.11.2013/2 (FGC 42969)			Tur5-2		MG208924	16S 28	OR918432						
23.	43°44'26.18"N,	Italy, Tuscany, Sasso di	G. Manganelli /	M. cantiana	CAN-2	Sim-1	COI 11	OR918547	16S 22	OR918433	H3 1	OR939930				
	12°17'13.71"E	Simone, Rifugio Casa del Re (Sestino, Arezzo)	21.10.2017 / 4 (FGC 47484)			Sim-2	COI 11	OR918548	16S 23	OR918434	H3 1	OR939931				
24.	45°11'59.85"N,	Italy, Venetum, Sorgà	A. Hallgass /	M. cantiana	CAN-2	12FG-1		MG208925	16S 29	OR918435		MG209050	ITS2 30	OR917406		
	10°58'49.30"E	(Verona)	09.2012 / 6 (FGC 42964)			12FG-2		MG208928	16S 30	OR918436	H3 1	OR939932	ITS2 31	OR917407		
25.	48°15'25.50"N, 16°30'46.38"E	Austria, Breitenlee, abandoned railway station	M. Duda / 09.2015 / 3 (FGC 44020)	M. cantiana	CAN-3	Dud-2		MG208938	16S 31	OR918437		MG209056	ITS2 32	OR917408		
26.	43°46'11.79"N,	France, Alpes-Maritimes,	A. Hallgass /	M.	CAN-4	3FG-1		MG208939	16S 32	OR918438		MG209058	ITS2 33	OR917409		
	07°22'21.50"E	Vallée de Peillon, Sainte Thècle	24.10.2011/ 5 (FGC 40320)	cemenelea		3FG-2		MG208940	16S 32	OR918439		MG209059	ITS2 34	OR917410		
* Acr versit	onyms for collec tà di Siena, Italy; I	tions: DCBC – the collection MNHW – the Małgorzata Pro	of the Departme	ant of Cell Biok at the Museun	gy, Adan ס ר Natu	n Mickiewicz I ral History. Un	Jniversity, Pc iversity of Wr	land; FGC – 'ocław. Polari	the Folco G	iusti collectio	n at Dipartir	nento di Scie	nze Fisiche,	della Terra e	dell'Ambie	ente, Uni-

ZooKeys 1198: 55-86 (2024), DOI: 10.3897/zookeys.1198.119738

## **Material examined**

The material examined originated from the populations listed in Table 1 with the following data: geographic coordinates, country and region, short description of collection site, name of collector, date, number of specimens studied and the collection where the material is stored (in brackets). The origin of the material used for comparison has been described in previous publications (Pieńkowska et al. 2015: appendix 1; Pieńkowska et al. 2018b, 2019a, 2019b, 2020, 2022: table 1).

## Morphological study

Sixty-six specimens of the six lineages of *M. cantiana* s.l. (CAN-1, CAN-2, CAN-3, CAN-4, CAN-5, and CAN-6) (Pieńkowska et al. 2018b, 2019a) and five specimens suitable for morphological analysis of the French populations were considered for shell variability (Table 1). Twelve shell variables were measured to the nearest 0.1 mm using ADOBE PHOTOSHOP 7.0.1 on digital images of standard apertural and umbilical views taken with a Canon EF 100 mm 1:2.8 L IS USM macro lens mounted on a Canon F6 camera (see also Pieńkowska et al. 2018b: fig. 1):

aperture height,
aperture width,
last whorl final width,
last whorl medial width,
height of adapical sector of last whor
height of medial sector of last whorl,
penultimate whorl height,
penultimate whorl final width,
penultimate whorl medial width,
shell diameter,
shell height,
umbilicus diameter.

Sixty-four specimens of the six lineages of *M. cantiana* s.l. (CAN-1, CAN-2, CAN-3, CAN-4, CAN-5 and CAN-6) (Pieńkowska et al. 2018b, 2019a) and seven adult specimens of the French populations were analysed for anatomical variability (Table 1). Snail bodies were dissected under a light microscope (Wild M5A or Zeiss SteREO Lumar V12). Anatomical details were drawn using a Wild camera lucida. Abbreviations/acronyms are as follows (see also Pieńkowska et al. 2018b: fig. 2):

- BC bursa copulatrix,
- BW body wall,
- **DBC** duct of bursa copulatrix,
- DG digitiform glands,
- **E** epiphallus (from base of flagellum to beginning of penial sheath),
- F flagellum,
- **FO** free oviduct,
- GA genital atrium,
- GAR genital atrium retractor,

Р	penis,
PP	penial papilla,
SOD	spermoviduct,
V	vagina,
VA	vaginal appendix (also known as appendicula),
VAS	vaginal appendix sac,
VD	vas deferens.

Six anatomical variables (DBC, E, F, P, V, VA) were measured using a calliper under a light microscope (0.01 mm) (Pieńkowska et al. 2018b: fig. 2).

Detailed methods of multivariate ordination by Principal Component Analysis (PCA) and Redundancy Analysis (RDA), performed on the original shell and genitalia matrices as well as on the Z-matrices (shape-related matrices), are described in our previous papers (Pieńkowska et al. 2018b, 2019a).

We used 95% confidence interval ellipses to evaluate the uncertainty of the estimate of the population mean (centroid) of the data sample. The function *ordiellipse* with standard errors in the package *vegan* (Oksanen et al. 2022) was used. Convex hulls (function *ordihull* in *vegan*) were used to visually enclose the individuals forming each clade as a measure of data spread. All analyses were performed with RStudio (R version 4.2.1; R Core Team 2021).

#### Molecular study

Eighty-eight specimens representing 26 populations of the four lineages of *M. cantiana* s.l. (CAN-1, CAN-2, CAN-3, and CAN-4; Pieńkowska et al. 2018b, 2019a) were used for molecular analysis (Table 1). Molecular methods including DNA extraction, amplification and sequencing are described in our previous paper (Pieńkowska et al. 2018a).

Two mitochondrial and two nuclear gene fragments were analysed, namely cytochrome c oxidase subunit 1 (COI), 16S ribosomal DNA (16SrDNA), histone 3 (H3) and an internal transcribed spacer 2 of rDNA (ITS2) flanked by the 3'end of 5.8SrDNA and the 5'end of 28SrDNA, respectively. Sequences were edited by eye using BioEdit, v. 7.0.6 (Hall 1999; BioEdit 2017) and aligned using ClustalW, implemented in BioEdit (Thompson et al. 1994). Fragments of COI were amplified using two pairs of primers: F01/R04 (Dabert et al. 2010) or bcsmF1/ bcsmR1 (Proćków et al. 2013). Fragments of 16SrDNA were amplified using 16Scs1/16Scs2 primers (Chiba 1999). Sequences containing the 3'end of 5.8SrDNA, complete sequence of ITS2 and 5'end of 28SrDNA were amplified using two sets of primers: LSU1/LSU3 (Wade and Mordan 2000) and NEWS2/ ITS2-RIXO (Almeyda-Artigas et al. 2000). Products of the two PCR reactions were aligned and used to assemble single sequences. Fragments of H3 gene were amplified using the primers H3F and H3R (Colgan et al. 1998). The protein coding sequences were aligned according to the translated amino acid sequences. The ends of all sequences were trimmed. After trimming, the lengths of sequences were 615 bp for COI, 804-821 bp for 16SrDNA, 303 bp for H3, and 749-753 bp for ITS2 flanked by the 3'end of 5.8SrDNA and 5'end of 28SrDNA (including 45 bp 5.8SrDNA + 489–493 bp ITS2 + 215 bp 28SrDNA). The borders of ITS2 sequence were searched using ITS2-Database (http://its2.bioapps.biozentrum.uni-wuerzburg.de) (Eddy 1998; Koetschan et al. 2010). The sequences

were collapsed to haplotypes using the programme ALTER (Alignment Transformation EnviRonment) (Glez-Peña et al. 2010). The following alignments were made for phylogenetic inference: 591 bp long for COI, 292 or 809 positions long for 16SrDNA, and 775 positions long for ITS2 flanked by the 3'end of 5.8SrDNA and 5'end of 28SrDNA. Finally, the sequences of COI, 16SrDNA, ITS2, and H3 were concatenated. Three sets of concatenated sequences were created: 1) COI16S of 1444 positions in length (615 COI + 829 16SrDNA); 2) H3ITS2 of 1054 positions in length (279 H3 + 775 ITS2 with flanks); 3) CS of 2498 positions in length (615 COI + 829 16SrDNA + 279 H3 + 775 ITS2 with flanks).

Estimates of genetic distances between the COI sequences obtained in this study and other sequences from GenBank were conducted with MEGA7 using the Kimura two-parameter model (K2P) (Kimura 1980). All positions containing gaps and missing data were eliminated. There were a total of 591 positions in the final dataset. The analysis involved 53 nucleotide sequences.

To infer the phylogenetic relationships the following programmes were used: MEGA7 (Hasegawa et al. 1985; Nei and Kumar 2000; Kumar et al. 2016), IQ-Tree (http://iqtree.cibiv.univie.ac.at/) (Trifinopoulos et al. 2016), RAxML v1.0.0 (Stamatakis 2014) and MrBayes 3.2.6 (Ronquist et al. 2012). For phylogenetic inference Neighbour-Joining, Maximum-Likelihood and Bayesian Inference methods were used.

For each alignment file, best nucleotide substitution models were specified according to the Bayesian Information Criterion (BIC) (see captions to figures). Phylogenetic analyses performed with IQ-Tree, RAxML and MrBayes for three sets of concatenated sequences were done dividing the data set into 2 or 4 partitions: (1) COI, (2) 16SrDNA or (1) COI, (2) 16SrDNA, (3) H3, (4) 5.8SrDNA + ITS2 + 28SrDNA. Best substitution models were inferred according to the Bayesian Information Criterion (BIC) for each of the partitions by MODELFIND-ER (Kalyaanamoorthy et al. 2017) implemented in IQ-TREE. Bayesian analysis were conducted with four Monte Carlo Markov chains running for 1 million generations, sampling every 100 generations (the first 25% of trees were discarded as 'burn-in').

The robustness of the NJ and ML trees generated by MEGA7 were assessed by bootstrap analysis with 1000 replicates (Felsenstein 1985). ML trees built by RAxML were tested by bootstrap analysis with 100 replicates. ML trees obtained with IQ-Tree were constructed under 1000 ultrafast bootstrap replicates (Minh et al. 2013). Finally, BI trees were supported by posterior probability (PP) values. Bootstrap support values from NJ and ML analysis as well as posterior probability (PP) values obtained on 50% majority rule consensus Bayesian tree were mapped onto the ML tree obtained by MEGA7. All the resulting trees were rooted with *Trochulus hispidus* sequences obtained from GenBank.

## Results

#### Morphological study: shell

Shells of French specimens of *M. cantiana* (Fig. 2A–D) are globose-subglobose in shape, variable in size and usually whitish or pale yellowish in colour, with slightly descending, roundish to oval aperture, similar to those of the other populations of the lineage CAN-1 (Pieńkowska et al. 2018b: figs 8–11).



**Figure 2**. Shells of *Monacha cantiana* from France. Specimen Esc1 from Oise, Escales-Saint-Pierre (**A**), specimen Ble1 from Pas-de-Calais, Blecquenecques n. Marquise (**B**), specimen Pie1 from Seine-Maritime, Pierrepont (**C**) and specimen Bet1 from Seine-Maritime, Béthencourt n. Grandcourt (**D**).

RDA with French specimens and "lineage" constraint on the shape and size matrix (Fig. 3B, C) showed that RDA 1 (22.2%, P < 0.01) separated CAN-6 from CAN-4, with CAN-5 and the large group CAN-1, CAN-2, CAN-3, and FRA in intermediate position, as confirmed by 95% confidence interval ellipses (Fig. 3B). The convex hull measure of data spread showed considerable overlap of some clusters. In both cases, FRA specimens fell within CAN-1 variability (Fig. 3B). The preliminary classic PCA showed that size was the first major source of morphological variation, since PC1 (69%) was a positive combination of all variables (Fig. 3A). On the contrary, RDA 2 was not significant (p > 0.05) and accounted for little morphological variation (2.6%). PC2 (15%) mostly reflected a contrast between LWaH and PWH versus LWmH and UD.

RDA on the shape (Z) matrix (Fig. 3E, F) showed that RDA 1 (34%, P < 0.001) clearly separated CAN-5 and CAN-6 from the group CAN-1, CAN-2, CAN-3, CAN-4, and FRA, as confirmed by the 95% confidence interval ellipses (Fig. 3E) and



**Figure 3.** Analysis of French specimens with "lineage" constraint on the original matrix (**A**–**C**) and Z-matrix (shape-related) (**D**–**F**) of selected shell sections. Principal component analysis (PCA) (**A**, **D**) and redundancy analysis (RDA) with groups shown as ellipses representing 95% confidence intervals with standard errors (**B**, **E**) and as convex hull polygons (**C**, **F**).

the convex hulls (Fig. 3F). On the contrary, the RDA2 axis was not significant (P > 0.05), reflecting little morphological variation (5.3%). Shape-related PCA indicated that SH, LWaH and PWH vs LWmW, SD, LWfW, LWmH, and UD were the principal shape determinants on PC1, and AH and AW vs PWH, LWmH, and UD on PC2 (Fig. 3D).

## Morphological study: anatomy

French specimens of *M. cantiana* have distal genitalia (Figs 4–6) resembling the other populations assigned to CAN-1, which are in turn similar to those of the populations belonging to the CAN-2, CAN-3 and CAN-4 lineages (Pieńkowska et al. 2018b: figs 20–30).

RDA with French specimens and "lineage" constraint on the shape and size matrix (Fig. 7B, C) showed that RDA 1 (24.3%, P < 0.001) separated CAN-2 and CAN-6 from FRA and CAN-5, with CAN-1, CAN-3, CAN-4 in intermediate position, as confirmed by 95% confidence interval ellipses (Fig. 7B). The preliminary classic PCA showed that size was the first major source of morphological variation, since PC1 (48.3%) was a positive combination of all variables (Fig. 7A). On the other hand, RDA 2 (21.7%, P < 0.001) clearly separated the group CAN-1, CAN-2, CAN-3, CAN-4 and FRA from CAN-5 and CAN-6. PC2 (17.9%) reflected a contrast between P, VA and DBC vs F and V. Differences between clusters were confirmed visually by 95% confidence interval ellipses (Fig. 7B) and convex hulls (Fig. 7C).

RDA on the shape (Z) matrix (Figs 7E, F) showed that RDA 1 (33.7%, P < 0.001) separated the 95% confidence interval ellipses of CAN-5, CAN-6 and CAN-4 from the large group CAN-1, CAN-2, CAN-3, and FRA; RDA 2 (8%, P < 0.001) separated CAN-5 and the group CAN-1, CAN-2, CAN-3, FRA from CAN-6 and CAN-4 (Fig.7E). Convex hulls showed some overlaps, especially in the data spread of CAN-1 (Fig. 7F). Shape-related PCA indicated that P and E vs VA and F were the two principal shape determinants on PC1 and DBC and VA vs V and F on PC2 (Fig. 7D).

## Molecular study

Although sequences of all the genes analysed (COI, 16SrDNA, H3, and ITS2 with 5.8SrDNA and 28SrDNA) were not obtained from all 88 specimens (Table 1), as a result of molecular analysis, 272 new sequences were deposited in GenBank. These were 56 new sequences of COI: OR918493–OR918548, 77 of 16SrDNA (long): OR918363–OR918439, 75 of H3: OR939858–OR939932 and 64 of ITS2 (with flanking fragments of 5.8SrDNA and 28SrDNA): OR917347–OR917410 (Table 1). Eleven haplotypes of the COI gene were identified (COI 1 – COI 11), 32 of 16SrDNA (16S 1 – 16S 32), 10 of H3 (H3 1 – H3 10), and 34 of ITS2 with flanking sequences (ITS2 1 – ITS2 34) (Table 1). These haplotypes were used for phylogenetic analysis based on single gene sequences and concatenated mitochondrial and nuclear gene data sets of sequences.

The phylogenetic analysis of COI sequences obtained from the specimens and comparative sequences derived from GenBank is shown in Fig. 8. The results are consistent with previously published findings (Pieńkowska et al. 2018b, 2019a, 2019b, 2020, 2022), distinguishing six lineages (CAN-1 – CAN-6) in *M. cantiana* s.l. that clustered separately from COI sequences of other species including *M. parumcincta*, *M. pantanellii* and *M. cartusiana*. The new COI sequences (haplotypes 1–10) from France, the Netherlands and England clustered in the CAN-1 lineage. Only the COI 11 haplotype obtained from two specimens of the Italian population from Sasso di Simone (population no. 23 in Table 1) grouped with the CAN-2 lineage.



**Figure 4**. Distal genitalia of *Monacha cantiana* from France. Specimen Bet1 from Seine-Maritime, Béthencourt n. Grandcourt (**A–C**) and specimen Ble1 from Pas-de-Calais, Blecquenecques n. Marquise (**D–F**). Distal genitalia (**A**, **D**), transverse sections of medial epiphallus (**B**, **E**) and apical penial papilla (**C**, **F**).











Figure 7. Analysis of French specimens with "lineage" constraint on the original matrix (A–C) and Z-matrix (shape-related) (D–F) of selected genital sections. Principal component analysis (PCA) (A, D) and redundancy analysis (RDA) with groups shown as ellipses representing 95% confidence intervals with standard errors (B, E) and as convex hull polygons (C, F).

K2P genetic distances (Table 2) showed small genetic differentiation between COI sequences of particular CAN-1 populations (infra-populational distances ranged from 0.2% in Dutch populations to 1.1% in French populations). The K2P distances between these populations were also small (in the range 0.5–1.2%). The K2P distances between French, Dutch, English and Italian populations of CAN-1 and CAN-2 were also small (in the range 3.5–4.1%) while the distance separating the CAN-1 populations from the CAN-3 and CAN-4 populations was much larger (in the range 18.0–18.8%). In turn, the distance separating the CAN-3 and CAN-4 populations was 5.6–6.1%.



**Figure 8.** Maximum Likelihood (ML) tree of COI haplotypes of *Monacha cantiana*. New COI sequences of *M. cantiana* (Table 1) were compared with COI sequences of *M. cantiana* s.l., *M. parumcincta*, *M. pantanellii* and *M. cartusiana* obtained from GenBank (Suppl. material 1). Sequences were cut to 591 bp. HKY+G+I was the best nucleotide substitution model according to the Bayesian Information Criterion (BIC). The tree was rooted with *Trochulus hispidus* sequences obtained from GenBank (Suppl. material 1).

		1	2	3	4	5	6	7	8
M. cantiana CAN-1 of French populations	1	1.1							
M. cantiana CAN-1 of Dutch populations	2	0.7	0.2						
M. cantiana CAN-1 of English populations	3	0.9	0.5	0.7					
M. cantiana CAN-1 of Italian populations	4	1.2	0.8	0.9	0.6				
M. cantiana CAN-2 of Italian populations	5	4.1	3.7	3.8	3.5	2.4			
M. cantiana s.l. CAN-3 of Italian populations	6	18.7	18.6	18.6	18.5	18.3	1.0		
M. cantiana s.l. CAN-3 of Austrian populations	7	18.8	18.7	18.7	18.7	18.5	1.5	1.0	
M. cantiana s.l. CAN-4 (M. cemenelea) of French populations	8	18.3	18.2	18.1	18.0	18.6	5.6	6.1	0.9

Table 2. K2P genetic distances between COI sequences of the populations analysed.

Results similar to those of COI analysis were obtained for other single gene analyses (Suppl. materials 8, 9 for 16SrDNA, Suppl. material 10 for the ITS2 gene with flanking 5.8S and 28S gene fragments). Note that the newly obtained 16SrDNA sequences in Suppl. material 8 were trimmed to 292 positions in alignment length because GenBank lacks the reference long 16SrDNA sequences of the 809 positions used to construct the tree in Suppl. material 9. Analysis of newly obtained longer sequences (i.e. ITS2 flanked by 5.8SrDNA and 28SrDNA gene fragments) (ITS2 1 – ITS2 34 haplotypes) and the only comparable sequence of Neiber and Hausdorf (2017) showed that this gene did not differentiate the CAN-1, CAN-2 and CAN-3 lineages. Similar results were obtained previously using ITS2 gene sequences without flanking fragments of 5.8SrDNA and 28SrDNA (Pieńkowska et al. 2018b: fig. 64). Only in the case of sequences assigned to the CAN-4 lineage were they distinct from CAN-1, CAN-2 and CAN-3, as shown in Pieńkowska et al. (2018b: fig. 64).

The phylogenetic tree for concatenated sequences were similar in ML analyses obtained with different software. The tree for mitochondrial gene sequences (COI+16SrDNA) in Fig. 9 shows that the sequences obtained from specimens of the French, Dutch, and English populations (see also Suppl. material 5) grouped with the reference sequences for CAN-1. In a tree of concatenated nuclear genes (Fig. 10: H3+ITS2 with flanks), the sequences from the French populations grouped with CAN-1, CAN-2, and CAN-3 lineages, only sequences of the CAN-4 lineage being distinguished. However, note that the bootstrap and posterior probability values weakly supported the results of the concatenated H3+ITS2 gene sequences. The tree for the concatenated sequences of all the genes analysed in this paper (Fig. 11, see also Suppl. material 7) showed that concatenated sequences CS 1–CS 25 from northern French populations clustered together with CS 26–CS 34 and CS 35–CS 38 sequences obtained from English and Italian specimens, respectively. They all belonged to the CAN-1 lineage. The CAN-1, CAN-2, CAN-3, and CAN-4 lineages grouped separately.

## Discussion

At a first glance, the shells and genitalia of the French specimens do not differ from those of the other populations assigned to CAN-1, which in turn are similar to those of the populations of the CAN-2, CAN-3 and CAN-4 lineages (see Pieńkowska et al. 2018b). This was fully confirmed by RDA and PCA: the French specimens fell entirely in CAN-1 on the basis of shell characters (Fig. 3C, F), and almost entirely, based on anatomical characters (Fig. 7C, F).


**Figure 9.** Maximum Likelihood (ML) tree of concatenated COI and 16SrDNA haplotypes of *Monacha cantiana*. New COI and 16SrDNA sequences of *M. cantiana* (Table 1, Suppl. material 5) were compared with concatenated COI and 16SrDNA sequences of *M. cantiana* s.l. and *M. cartusiana* obtained from GenBank (Suppl. materials 1, 2, 5). Length of sequences was 1444 positions (615 of COI + 829 of 16SrDNA). The Bayesian Information Criterion (BIC) specified T92+G+I the best nucleotide substitution model in MEGA7, or HKY+F+G4 for COI and TIM2+F+G4 for 16SrDNA partition in IQ-Tree, RAxML and MrBayes. Numbers next to main branches indicate (left to right): bootstrap supports above 50% calculated by NJ-MEGA7 (Saitou and Nei 1987), ML-MEGA7 (Kumar et al. 2016), IQ-Tree (Trifinopoulos et al. 2016), RAxML (Stamatakis 2014), and posterior probabilities by BI (Ronquist et al. 2012). The tree was rooted with *Trochulus hispidus* concatenated sequences obtained from GenBank (Suppl. material 5).

The results of molecular analysis were consistent with those of morphological analysis (shell and genital structure). Both showed that the populations from northern France should be assigned to the CAN-1 lineage. In this sense, the molecular results complement the conclusions of Brulé and Bichain (2019). Consequently, their results corroborate the results of four previous papers on *M. cantiana* lineages and their phylogeography (Pieńkowska et al. 2018b, 2019a, 2019b, 2020).



**Figure 10.** Maximum Likelihood (ML) tree of concatenated H3 and ITS2 (flanked with 5.8S and 28SrDNA) haplotypes of *Monacha cantiana*. New H3 and ITS2 sequences of *M. cantiana* (Table 1) were compared with concatenated H3 and ITS2 sequences of *M. cantiana* s.l. obtained from GenBank (Suppl. materials 3, 4). Length of sequences was 1054 positions (279 of H3 + 775 of ITS2). The Bayesian Information Criterion (BIC) specified T92+G+I the best nucleotide substitution model in MEGA7, or K2P+I for H3 and K3P+I for ITS2 partition in IQ-Tree, RAxML, and MrBayes. Numbers next to main branches indicate (left to right): bootstrap supports above 50% calculated by NJ-MEGA7 (Saitou and Nei 1987), ML-ME-GA7 (Kumar et al. 2016), IQ-Tree (Trifinopoulos et al. 2016), RAxML (Stamatakis 2014) and posterior probabilities by BI (Ronquist et al. 2012). The tree was rooted with *Trochulus hispidus* concatenated sequences obtained from GenBank (Suppl. material 6).



**Figure 11.** Maximum Likelihood (ML) tree of concatenated COI, 16SrDNA, H3, and ITS2 (flanked with 5.8S and 28SrDNA) haplotypes of *Monacha cantiana*. COI, 16SrDNA, H3, and ITS2 sequences of *M. cantiana* were compared with sequences of *M. cantiana* s.l. and *M. cartusiana* obtained from GenBank (Suppl. materials 1–4, 7). Length of sequences was 2498 positions (615 of COI, 829 of 16SrDNA, 279 of H3, and 775 of ITS2). Bayesian Information Criterion (BIC) specified GTR+G+I the best nucleotide substitution model in MEGA7, or HKY+F+G4 for COI, TIM2+F+I for 16SrDNA, TIM3e+I+G4 for H3, and K3P+I+G4 for ITS2 partition in IQ-Tree, RAxML, and MrBayes. Numbers next to main branches indicate (left to right): bootstrap support above 50% calculated by NJ-MEGA7 (Saitou and Nei 1987), ML-MEGA7 (Kumar et al. 2016), IQ-Tree (Trifinopoulos et al. 2016), RAxML (Stamatakis 2014), and posterior probabilities by BI (Ronquist et al. 2012). The tree was rooted with *Trochulus hispidus* concatenated sequences obtained from GenBank (Suppl. material 7).

Prior suggestions that *M. cantiana* was introduced into England in historical times (Kerney 1970, 1999; Evans 1972; Pieńkowska et al. 2018b) appear to be correct. This allows us to speculate that the Roman conquests also spread *M. cantiana* in northern France (as well as in the area of modern-day Holland). The slightly greater genetic diversity of French populations compared to the English ones (expressed as slightly larger K2P distances) indicates that *M. cantiana* 

reached northern France earlier than England. Simultaneously, the occurrence of the CAN-2 and CAN-3 lineages in Italy implies that *M. cantiana* populations diversified for longer in this area. Nevertheless, further analysis of *M. cantiana*, especially specimens from northern Italy, is needed to determine the relationships between the CAN-1/CAN-2 and CAN-3/CAN-4 lineages. Until these results are available, we refrain from proposing any nomenclatural taxonomic framework for these lineages.

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# Additional information

# **Conflict of interest**

The authors have declared that no competing interests exist.

# **Ethical statement**

No ethical statement was reported.

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## **Author contributions**

Conceptualization: AL, FG and GM; Methodology, Formal analysis, Investigation, Data Curation on shell and genitalia: FG, DB and GM; Methodology, Formal analysis, Investigation, Data Curation on molecular data: AL, JRP, KS and MP; Writing - Original draft & Writing - Review and Editing: AL, FG and GM; Supervision: FG, AL and GM; Funding Acquisition: AL and GM.

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#### **Data availability**

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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# COI sequences from GenBank used for molecular analysis comparisons (haplotypes in bold)

Authors: Joanna R. Pieńkowska, Giuseppe Manganelli, Małgorzata Proćków, Debora Barbato, Katarzyna Sosnowska, Folco Giusti, Andrzej Lesicki

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# Supplementary material 2

# 16SrDNA sequences from GenBank used for molecular analysis comparisons (haplotypes in bold)

Authors: Joanna R. Pieńkowska, Giuseppe Manganelli, Małgorzata Proćków, Debora Barbato, Katarzyna Sosnowska, Folco Giusti, Andrzej Lesicki

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## Supplementary material 3

# H3 sequences from GenBank used for molecular analysis comparisons (haplotypes in bold)

Authors: Joanna R. Pieńkowska, Giuseppe Manganelli, Małgorzata Proćków, Debora Barbato, Katarzyna Sosnowska, Folco Giusti, Andrzej Lesicki

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# ITS2 sequences from GenBank used for molecular analysis comparisons (haplotypes in bold)

Authors: Joanna R. Pieńkowska, Giuseppe Manganelli, Małgorzata Proćków, Debora Barbato, Katarzyna Sosnowska, Folco Giusti, Andrzej Lesicki

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#### Supplementary material 5

# Concatenated sequences of COI+16SrDNA used in NJ/ML-MEGA7/IQ Tree/ RAxML/BI analysis (Fig. 9)

Authors: Joanna R. Pieńkowska, Giuseppe Manganelli, Małgorzata Proćków, Debora Barbato, Katarzyna Sosnowska, Folco Giusti, Andrzej Lesicki

Data type: docx

- Explanation note: COI sequences were 615 bp in length. Long 16SrDNA sequences were cut to 829 positions (the alignment of concatenated sequences COI and long 16SrD-NA was then 1444 positions in length).
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#### Supplementary material 6

## Concatenated sequences of H3 + [(5.8SrDNA)+ITS2+(28SrDNA)] used in NJ/ ML-MEGA7/IQ Tree/RAxML/BI analysis (Fig. 10)

Authors: Joanna R. Pieńkowska, Giuseppe Manganelli, Małgorzata Proćków, Debora Barbato, Katarzyna Sosnowska, Folco Giusti, Andrzej Lesicki

Data type: docx

Explanation note: H3 sequences were cut to 279 bp, 5.8SrDNA+ITS2+28SrDNA sequences were 775 positions in length (the alignment of concatenated sequences H3 + [(5.8SrDNA)+ITS2+(28SrDNA)] was therefore 1054 positions).

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# Concatenated sequences of COI + 16SrDNA long + H3 + [(5.8SrDNA)+ITS2+(28SrDNA)] used in NJ/ML-MEGA7/ML-IQ Tree/RAxML/ BI analysis (Fig. 11)

Authors: Joanna R. Pieńkowska, Giuseppe Manganelli, Małgorzata Proćków, Debora Barbato, Katarzyna Sosnowska, Folco Giusti, Andrzej Lesicki

Data type: docx

- Explanation note: The lengths of the particular sequences were COI 615 bp, 16SrDNA 829 bp, H3 279 bp, 5.8SrDNA+ITS2+28SrDNA 775 bp (the alignment of concatenated sequences COI + 16SrDNA long + H3 + [(5.8SrDNA)+ITS2+(28SrDNA)] was therefore 2498 positions).
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#### Supplementary material 8

#### Maximum Likelihood (ML) tree of 16SrDNA haplotypes of Monacha cantiana

Authors: Joanna R. Pieńkowska, Giuseppe Manganelli, Małgorzata Proćków, Debora Barbato, Katarzyna Sosnowska, Folco Giusti, Andrzej Lesicki

Data type: eps

- Explanation note: New 16SrDNA sequences of *M. cantiana* (Table 1) were compared with 16SrDNA sequences of *M. cantiana* s.l., *M. parumcincta*, *M. pantanellii* and *M. cartusiana* from GenBank (Suppl. material 2). Sequences were cut to 292 positions. GTR+G+I (Nei and Kumar 2000; Kumar et al. 2016) was the best nucleotide substitution model according to the Bayesian Information Criterion (BIC). Numbers next to branches indicate bootstrap support above 50% calculated by ML-MEGA7 (Kumar et al. 2016) on 1000 replicates (Felsenstein 1985). The tree was rooted with *Trochulus hispidus* sequences from GenBank (Suppl. material 2).
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#### Maximum Likelihood (ML) tree of 16SrDNA haplotypes of Monacha cantiana

Authors: Joanna R. Pieńkowska, Giuseppe Manganelli, Małgorzata Proćków, Debora Barbato, Katarzyna Sosnowska, Folco Giusti, Andrzej Lesicki

Data type: eps

- Explanation note: New 16SrDNA sequences of *M. cantiana* (Table 1) were compared with 16SrDNA sequences of *M. cantiana* s.l. and *M. cartusiana* from GenBank (Suppl. material 2). Sequences were cut to 809 positions. T92+G (Tamura 1992; Kumar et al. 2016) was the best nucleotide substitution model according to the Bayesian Information Criterion (BIC). Numbers next to branches indicate bootstrap support above 50% calculated by ML-MEGA7 (Kumar et al. 2016) on 1000 replicates (Felsenstein 1985). The tree was rooted with *Trochulus hispidus* sequences from GenBank (Suppl. material 2).
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Link: https://doi.org/10.3897/zookeys.1198.119738.suppl9

#### Supplementary material 10

# Maximum Likelihood (ML) tree of ITS2 (flanked with 5.8S and 28SrDNA) haplotypes of *Monacha cantiana*

Authors: Joanna R. Pieńkowska, Giuseppe Manganelli, Małgorzata Proćków, Debora Barbato, Katarzyna Sosnowska, Folco Giusti, Andrzej Lesicki

Data type: eps

- Explanation note: New ITS2 sequences of *M. cantiana* (Table 1) were compared with ITS2 sequences of *M. cantiana* s.l. and *M. cartusiana* from GenBank (Suppl. material 3). Sequences of specimens representing CAN-2 and CAN-3 lineages are shown. Sequences were cut to 775 positions. JC+G (Jukes and Cantor 1969; Kumar et al. 2016) was the best nucleotide substitution model according to the Bayesian Information Criterion (BIC). Numbers next to branches indicate bootstrap support above 50% calculated by ML-MEGA7 (Kumar et al. 2016) on 1000 replicates (Felsenstein 1985). The tree was rooted with *Trochulus hispidus* sequences from GenBank (Suppl. material 4).
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**Research Article** 

# The genus *Platypalpus* Macquart (Diptera, Hybotidae, Tachydromiinae) from Inner Mongolia, China, with the description of four new species

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#### Abstract

*Platypalpus* Macquart is reported in Inner Mongolia, China for the first time. Four new species are found: *P. flavipilosus* **sp. nov.**, *P. longus* **sp. nov.**, *P. shengi* **sp. nov.** and *P. shuimogouanus* **sp. nov.** This paper provides a description of the four species and a key to the genus in Inner Mongolia.

**Key words:** Dance flies, Identification key, Inner Mongolia, new species, *Platypalpus*, taxonomy



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# Introduction

*Platypalpus* Macquart, 1827 belongs to Tachydromiinae of Hybotidae. It is characterized by its raptorial mid leg and wing with an anal cell (Chvála 1975; Grootaert and Chvála 1992; Barták and Kubík 2015). The genus is cosmopolitan and found in all major zoogeographic regions, but over 75% of its 559 known species are from the Palearctic and Nearctic realms (Chvála and Wagner 1989; Grootaert 1992; Yang et al. 2007). Although most reports of the genus in the Palearctic region are from Europe, its presence in Asia is poorly documented (Barták and Shamshev 2015; Kanavalová et al. 2021). In China, 58 species have been reported, but none have been reported from Inner Mongolia, which borders Mongolia and Russia, despite the abundance of reports of the genus in these areas (Yang et al. 2007, 2018; Li et al. 2021).

Inner Mongolia is a long and narrow region located in the northern part of China, extending diagonally from northeast to southwest. The region is known for its low and uneven precipitation, strong winds, and significant seasonal variations, which nurture a diverse range of vegetation. Dongsheng District is situated in the southwestern part of Inner Mongolia and the eastern to central part of the Ordos Plateau. It has a temperate continental climate, which, coupled with its vast arid grassland, supports a unique ecosystem. Shuimogou is situated in the Helan Mountains of Inner Mongolia, a dry desert area in the middle temperate zone (Fig. 1). The region exhibits a clear vertical distribution



Figure 1. The habitat in Shuimogou.

pattern of climate, which is associated with various vegetation types, such as coniferous forests, broad-leaved forests, mixed coniferous and broad-leaved forests, scrub, grasslands, deserts, and meadows. This diverse vegetation is advantageous for the formation and maintenance of biodiversity.

In this research, the genus *Platypalpus* is newly reported from Inner Mongolia with four new species. A key to *Platypalpus* from Inner Mongolia is provided.

# **Material and methods**

The specimens used in this study were collected by sweep nets in Inner Mongolia in 2006 and 2010. All specimens are deposited in the Entomological Museum of China Agricultural University (CAU), Beijing. Morphological terminology follows Cumming and Wood (2009). The following abbreviations are used in the descriptions for the following bristles: **acr** – acrostichal bristles, **av** – anteroventral bristles; **dc** – dorsocentral bristles; **h** – humeral bristle; **npl** – notopleural bristles; **vt** – vertical bristles; presc – prescutellar bristles; **psa** – postalar bristles; **sc** – scutellar bristles.

## Taxonomy

#### Platypalpus Macquart, 1827

Type species. Musca cursitans Fabricius, 1775 (by designation of Westwood 1840).

**Diagnosis.** Small to middle-sized, body length 2.0–4.0 mm; eyes narrowly separated on face; proboscis significantly shorter than head height, palpus very small, rounded; 2 pairs of vts; first flagellomere short-conical or long-conical; distinctive humerus, no distinctive humeral bristle; 2–6 rows of acrostichal bristles separated with dc; dense acrostichal on mesonotum, acr multiseriate, mixed with dc; costa vein terminating at apex of  $M_{1+2}$ ; subcostal vein not reaching costal margin of wings;  $R_{4+5}$  and  $M_{1+2}$  parallel or distinctly convergent apically; anal vein weak or absent; 1<sup>st</sup> and 2<sup>nd</sup> basal cell short; anal cell significantly smaller than basal cell; no discal cell; fore femur slightly thickened; mid leg raptorial, significantly thickened, with 2 rows of short black spine-like ventral bristle; mid femur slightly curved, with 1 sparse row of black spine-like ventral bristles and 1 apical spur, apex of male abdomen rotating to right (Chvála 1975; Grootaert and Chvála 1992).

#### Key to species (males) of Platypalpus from Inner Mongolia

1	Thorax wholly black2
-	Thorax mostly dark yellow, somewhat blackish dorsally
2	First flagellomere, 1.9–2.0 times as long as wide; stylus, much longer than
	first flagellomere3
-	First flagellomere, 4.9 times as long as wide; stylus, 1/3 as long as first
	flagellomere
3	One pair of vt; mid femur with brown anterior spot at tip; tarsomeres with
	narrow blackish apical annulation
-	Two pairs of vt; mid femur without anterior spot at tip; tarsomeres without
	dark apical annulation P. shuimogouanus sp. nov.

#### Platypalpus flavipilosus sp. nov.

https://zoobank.org/8F176C04-4B67-4A62-A8D9-A8FADF7FB17C Figs 2, 6-9

**Diagnosis.** Thorax dark yellow, somewhat blackish dorsally. Antenna yellowish; first flagellomere oval, short, slightly wider than pedicel, 1.3 times longer than wide. Mid tibia with 1 short finger-like apical spur.

**Description. Male** (Fig. 2). Body length 2.6–2.7 mm, wing length 2.7–2.8 mm. *Head* black, with pale gray pollen. Eyes narrowly separated on face; frons distinctly wider than face. Hairs on head yellowish, bristles black or brownish yellow. Ocellar tubercle with 2 oc and 2 short posterior hairs. 2 pairs of vt. Antenna (Fig. 6) yellowish; first flagellomere oval, short, 1.3 times longer than wide, slightly wider than pedicel, with indistinct blackish pubescence; stylus blackish, 2.9–3.0 times longer than first flagellomere, with short blackish pubescence. Proboscis yellowish, 0.6–0.7 times as long as head height. Palpus oval, longer than wide, yellowish, with yellow hairs and bristles.



Figures 2–5. Habitus, lateral view 2 *P. flavipilosus* sp. nov., male (dissected) 3 *P. longus* sp. nov., male (dissected) 4 *P. shengi* sp. nov., male (dissected) 5 *P. shuimogouanus* sp. nov., male (dissected). Scale bars: 1 mm.

**Thorax** dark yellow with thin pale gray pollen, blackish dorsally, humerus dark yellow, postalar callus brownish yellow; sutures of mesopleuron somewhat blackish. Hairs and bristles on thorax yellow, bristles strong; mesonotum with dense hairs, acr and dc multiseriate and not separated; 1 h, 2 npl (anterior bristle short), 1 psa, 1 presc; two pairs of sc (lateral pair short, 1/3 as long as apical pair).

*Legs* yellow, but tarsomere V brown apically. Hairs on legs yellowish. Fore femur slightly thickened, 1.3–1.4 times wider than hind femur; mid femur distinctly thickened, 2.3–2.4 times wider than hind femur. Mid femur with 2 rows of short, black, spine-like, ventral bristles (few basal bristles brownish yellow, pv slightly longer than av), without row of outer pv. Mid tibia with 1 row of short black ventral bristles; apical spur short, finger-like (almost as long as tibia width). Wing hyaline, veins brownish;  $R_{4+5}$  and M nearly parallel, r–m and m–m contiguous. Squama yellow with pale hairs. Halter yellowish.

**Abdomen** partly dark yellow, with pale gray pollen, sternites I–VI and hypopygium dark brown. Hairs and bristles on abdomen yellowish except those on hypopygium blackish. Hypopygium (Figs 7–9): left epandrial lamella short



Figures 6–9. *Platypalpus flavipilosus* sp. nov., male 6 antenna 7 genitalia, dorsal view 8 right surstylus, lateral view 9 left epandrial lamella, lateral view. Scale bars: 0.2 mm.

and small, apically widely obtuse. Right epandrial lamella extremely wide and large; right surstylus (Fig. 8) short and small, pointed at tip. Left cercus (Fig. 7) strongly dilated at base, narrowed towards apex, pointed at tip; right cercus almost as long as left cercus, narrow at tip, slightly curved inwards.

**Female.** Body length 3.0-3.5 mm, wing length 2.9-3.0 mm. Similar to male, but abdomen dark brown except sternites I–IV or I–V dark yellow.

**Type material.** *Holotype*: male, CHINA, Inner Mongolia, Erdos, Dongsheng, 2006.VIII.7, Maoling Sheng (CAU). *Paratypes*: 1 male, 6 females, same data as holotype (CAU).

Etymology. The specific name refers to the yellow body hairs.

**Remarks.** The new species belongs to the *P. longicornis* group. It is somewhat similar to *P. baotianmanensis* Yang, An et Gao from Henan of China, but can be easily distinguished from the latter by the wholly blackish mesonotum and postnotum. In *P. baotianmanensis*, the mesonotum is yellow with a wide black middle spot, and the postnotum is brownish-yellow laterally (Grootaert and Shamshev 2006).

#### Platypalpus longus sp. nov.

https://zoobank.org/B850E0AF-7F4A-49C8-9A7E-E7EBA445382C Figs 3, 10-13

**Diagnosis.** One pair of vt. First flagellomere, 4.9 times longer than wide. Arista 1/3 as long as first flagellomere. Mid femur apically with 3–4 outer av. Mid tibia with short pointed, apical spur, almost as long as tibia width.

**Description. Male** (Fig. 3). Body length 2.4–3.0 mm, wing length 3.3–3.4 mm. *Head* black with pale gray pollen. Eyes narrowly separated on face; frons distinctly wider than face. Hairs on head yellowish, bristles brownish. Ocellar tubercle with 2 oc and 2 short hairs. 1pair of vt. Antenna (Fig. 10) blackish; first flagellomere very long, 4.9 times longer than wide, with short blackish pubescence; arista rather short, blackish, 1/3 as long as first flagellomere, with very short blackish pubescence. Proboscis dark brown, 0.7 times as long as head height; palpus yellowish, with yellow hairs and bristles, distinctly longer than wide, nearly acute at tip.

*Thorax* black with thin pale gray pollen; mesonotum mostly subshiny. Sternopleuron with shiny spot. Hairs and bristles on thorax yellow; mesonotum with somewhat dense hairs, 6 rows of acr, narrowly separated with dc; 1 h, 2 long npl, 1 psa, 1 presc; 2 pairs of short sc (apical pair short, 1/3 as long as apical pair).

**Legs** yellow, but tarsomeres V mostly dark brown with yellow base. Hairs and bristles on legs yellowish. Fore femur slightly thickened, 1.3 times wider than hind femur; mid femur distinctly thickened, 2.1–2.2 times wider than hind femur. Mid femur with 2 rows of short spine-like blackish ventral bristles (pv distinctly longer than av), 3–4 short spine-like outer av at tip, without row of outer pv. Mid tibia with row of black ventral bristles, apical spurt short, acute (nearly as long as tibia width).

**Wing** hyaline, veins brownish;  $R_{4+5}$  and M nearly parallel; crossveins r-m and m-m slightly or distinctly separated. Squama yellow with pale hairs. Halter yellowish.

**Abdomen** blackish with pale gray pollen. Hairs and bristles on abdomen yellowish. Hypopygium (Figs 11–13): left epandrial lamella (Fig. 13) rather narrow, apically widely obtuse. Right epandrial lamella wide; right surstylus (Fig. 12) rather long, finger-like. Left cercus (Fig. 11) slightly thickened at base, blunt and narrow at tip; right cercus slightly shorter, with shallow depression on outer edge of middle part, slightly widened at tip.

Female. Unknown.



Figures 10–13. *Platypalpus longus* sp. nov., male 10 antenna 11 genitalia, dorsal view 12 right surstylus, lateral view 13 left epandrial lamella, lateral view. Scale bars: 0.2 mm.

**Type material.** *Holotype*: male, CHINA, Inner Mongolia, Erdos, Dongsheng, 2006. VIII.7, Maoling Sheng (CAU). Paratypes: 5 males, same data as holotype (CAU). **Etymology.** The specific name refers to the long right surstylus.

**Remarks.** The new species belongs to *P. longicornis* group. It is somewhat similar to *P. longicornioides* Chvála, 1972 from Europe but can be distinguished from the latter by the 6 rows of irregular acr which are separated narrowly from the dc. In *P. longicornioides*, the acr bristles are biserial, and widely separated from the dc (Grootaert and Chvála 1992).

#### Platypalpus shengi sp. nov.

https://zoobank.org/36E931EB-7107-435C-B9EB-6D31B24D914C Figs 4, 14-17

**Diagnosis.** Mid femur with brown anterior spot at tip. All tarsomeres with blackish annulation at tip. Fore tibia distinctly thickened, with 3 spine-like dorsal bristles at middle and 2 rows of very long ventral hairs at apical 2/3.

Description. Male (Fig. 4). Body length 3.1 mm, wing length 3.5 mm.

*Head* black, with dense, pale gray pollen; clypeus pollinose. Eyes narrowly separated on face; frons slightly wider than face. Hairs and bristles on head yellowish. Ocellar tubercle with 2 oc and 2 short posterior hairs. 1 pair of vt. Antenna (Fig. 14) black, but first flagellomere blackish; first flagellomere short, subconical, with uniformly thin tip, 1.9 times longer than wide, with short brown pubescence; arista blackish, with short brown pubescence, 3.5 times longer than first flagellomere. Palpus dark yellow, short oval, with yellowish hairs and 2 short yellow bristles.

**Thorax** black, with distinct pale gray pollen; mesopleuron with shiny black anterior spot. Hairs and bristles on thorax yellowish; hairs on mesonotum short and sparse; 1 weak h, 2 short npl, acr biserial, 1 long psa, 1 long presc; 2 pairs of sc (lateral pair short).

Legs yellow, but tarsomeres with narrow, blackish, apical annulation; mid femur with brown anterior spot at apex. Hairs on legs mostly yellowish except tarsi with blackish hairs; bristles mostly black. Fore femur distinctly thickened, 1.4 times wider than hind femur; mid femur strongly thickened, 2.1 times wider than hind femur. Fore femur with 1 row of short yellowish av; mid femur with 2 rows of short, black, spine-like ventral bristles and 1 row of short outer yellow av and 1 row of long outer yellow pv; hind femur with 1 row of pale yellow av (apical av rather long). Fore tibia distinctly thickened, with 3 spine-like dorsal bristles at middle, 2 rows of very long ventral hairs at apical 2/3. Mid tibia with 1 row of black ventral bristles; apical spur long and acute, with 1 short terminal hair at tip.

**Wing** hyaline, veins brownish yellow; cell  $R_{4+5}$  distinctly widened, M distinctly curved,  $R_{4+5}$  and M distinctly convergent apically, r-m and m-m distinctly separated. Squama yellow with pale hairs. Halter yellow.

**Abdomen** subshiny brown, with pale gray pollen, but hypopygium blackish. Hairs and bristles on abdomen yellowish, but partly dark brown on hypopygium. Hypopygium (Figs 15–17): left epandrial lamella (Fig. 17) relatively narrow, longer than wide, apically slightly sharp. Right epandrial lamella relatively wide; right surstylus (Fig. 16) fused with right epandrial lamellas, basally short and wide, apically twisted and curved inwards, with row of long, marginal bristles. Right cercus (Fig. 17) almost as long as left cercus, weakly curved inwards apically, with weak bulge; left cercus apically widened and distinctly curved inward.

**Female.** Body length 3.0–3.5 mm, wing length 2.9–3.0 mm. Fore tibia slightly swollen, with 4 dorsal bristles.

**Type material.** *Holotype*: male, CHINA, Inner Mongolia, Erdos, Dongsheng, 2006. VIII.7, Maoling Sheng (CAU). *Paratype*: 4 females, same data as holotype (CAU).

**Etymology.** The specific name refers to the specimen collector, Professor Maoling Sheng.

**Remarks.** The new species belongs to the *P. pallidiventris-cursitans* group. It is similar to *P. beijingensis* Yang et Yu from Beijing, but may be separated from the latter by the mid femur with a brown anterior spot at the tip, the distinctly



**Figures 14–17**. *Platypalpus shengi* sp. nov., male **14** antenna **15** genitalia, dorsal view **16** apex of right surstylus **17** left epandrial lamella, lateral view. Scale bars: 0.2 mm.

thickened fore tibia with 3 spine-like dorsal bristles at middle and the 2 rows of long ventral hairs on the apical 2/3. In P. beijingensis, the mid femur is wholly brownish yellow, the fore tibia has no spine-like dorsal bristles and no long ventral hair (Yang and Yu 2005).

#### Platypalpus shuimogouanus sp. nov.

https://zoobank.org/AA797927-8E91-4A3D-AC9F-BD82A7603A8E Figs 5, 18-21

**Diagnosis.** Two pairs of vt. Mid femur with 1 row of 3 long blackish outer pv on apical half. Mid tibia with 1 short, pointed, acute apical spur. First flagellomere 2.1 times longer than wide.  $R_{4+5}$  and M little convergent apically; crossveins r-m and m-m very narrowly separated.

Description. Male (Fig. 5). Body length 2.7 mm, wing length 3.3 mm.

*Head* black with distinct pale gray pollen; clypeus shiny black. Eyes narrowly separated on frons and face. Hairs yellowish on head, bristles blackish. Ocellar tubercle with 2 oc and 2 very short posterior hairs. 2 pairs of vt, outer vt short and curved inward. Antenna (Fig. 18) black; first flagellomere moderately long, subtriangular, 2.1 times longer than wide, distinctly blackish pubescent; arista black very long, 2 times longer than first flagellomere, with short blackish pubescence. Proboscis nearly blackish, 0.9 times as long as head height, palpus longer than wide, lobate, obtuse apically, yellowish, with 4 brown bristles (2 apical bristles long).

**Thorax** black with thin pale grey pollen; mesonotum subshiny black with thin pollen; mesopleuron shiny black except postero-upper margin. Hairs on thorax yellowish, bristles yellow; mesonotum with dense hairs, acr and dc multiseriate and not separated; 1 h, 2 npl of subequal lengths, 1 psa, 1 presc; 2 pairs of sc (lateral pair short and weak, about 1/3 as long as apical pair).

*Legs* yellow, but mid tibia brown, all tarsi brown to dark brown except tarsomere 1 brownish yellow with brown tip. Hairs on legs yellowish, but hairs on tibia and tarsi partly blackish. Fore femur weakly thickened, 1.2 times wider than hind femur; mid femur distinctly thickened, 1.5 times wider than hind femur. Fore femur with 1 row of pv (about 1/2 as long as femur width); mid femur with 2 rows of short spine-like black bristles (pv slightly longer than av) and 1 row of 3 long blackish outer pv on apical half. Mid tibia with 1 row of short, black, ventral bristles; apical spur short, pointed, shorter than tibia width.

**Wing** hyaline, veins dark brown, R4+5 and M little convergent apically; 1<sup>st</sup> basal cell slightly shorter than 2<sup>nd</sup> basal cell, crossveins r-m and m-m very narrowly separated. Squama yellow with yellowish hairs. Halter yellowish.

**Abdomen** black, with pale gray pollen. Hairs and bristles on abdomen yellowish. Hypopygium (Figs 19–21): left epandrial lamella wide, with wide and blunt apex. Right epandrial lamella very wide and large; right surstylus (Fig. 20) nearly fused with right epandrial lamella, somewhat narrowed, distinctly curved inward, with distinctly apical incision bearing several short marginal hairs. Left cercus (Fig. 19) nearly finger-like, slightly broader at base; right cercus almost as long as left cercus, finger-like.

Female. Unknown.

**Type material.** *Holotype*: male, CHINA, Inner Mongolia, Helan Mountain back, 2010.VIII.4, Yan Li (CAU).

Etymology. The specific name refers to the type locality Shuimogou.

**Remarks.** The new species belongs to the *P. pallidiventris-cursitans* group. It is somewhat similar to *P. henanensis* Saigusa et Gao from Henan of China (Saigusa and Yang 2002), but maybe separated from the latter by the yellow antenna and mid femur with 1 row of 3 long blackish outer pv on the apical half. In P. henanensis, the antenna is black, and the mid femur has 1 row of outer pv along the whole length (Yang and Yu 2005).



Figures 18–21. *P. shuimogouanus* sp. nov., male 18 antenna, lateral view 19 genitalia, dorsal 20 right surstylus 21 left epandrial lamella. Scale bars: 0.2 mm.

## Discussion

This study reports the first occurrence of *Platypalpus* Macquart, 1827 in Inner Mongolia. Four new species from Dongsheng and Shuimogou of Inner Mongolia are described. As the survey is restricted to only a part of the region, more reports of *Platypalpus* in Inner Mongolia are expected.

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# Additional information

#### **Conflict of interest**

The authors have declared that no competing interests exist.

#### **Ethical statement**

No ethical statement was reported.

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# **Author contributions**

Investigation: NW. Supervision: KL. Writing – original draft: YW. Writing – review and editing: DY.

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#### **Data availability**

All of the data that support the findings of this study are available in the main text.

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**Research Article** 

# Five new epigean *Lagynochthonius* species (Pseudoscorpiones, Chthoniidae) from southern China

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#### Abstract

Five new Lagynochthonius species of the pseudoscorpion family Chthoniidae are described, based on morphological characters: Lagynochthonius duo **sp. nov.**, Lagynochthonius gibbus **sp. nov.**, Lagynochthonius hepingensis **sp. nov.**, Lagynochthonius houi **sp. nov.**, and Lagynochthonius sanhuaensis **sp. nov.** All specimens were collected from epigean habitats in southern China.

Key words: Morphology, new species, pseudoscorpion, taxonomy

## Introduction

The genus *Lagynochthonius* Beier, 1951, belonging to the family Chthoniidae Daday, 1889, subfamily Chthoniinae Daday, 1889, tribe Tyrannochthoniini Chamberlin, 1962, was erected by Beier (1951) as a subgenus of *Tyrannochthonius* Chamberlin, 1929, subsequently elevated to generic status by Chamberlin (1962). It can be recognized by the trichobothria *ib* and *isb* situated close together in a median or sub-basal position on the dorsum of the chelal hand; the trichobothrium *sb* situated midway between *st* and *b*; the coxal spines commonly long and present only on coxae II; the chelal hand distally constricted (or flask-shaped), base of movable finger with strongly sclerotized apodeme and the modified tooth (*td*) of the fixed chelal finger displaced onto the prolateral-retrolateral face (Chamberlin 1962; Harvey 1989; Muchmore 1991; Judson 2007; Edward and Harvey 2008). The movable finger of *Tyrannochthonius* is only slightly sclerotized, and the fixed chelal finger does not have modified tooth (*td*), which are the most important differences between these two genera (Chamberlin 1962; Harvey 1989; Muchmore 1991).



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**Copyright:** © Jianzhou Sun et al. This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0). Lagynochthonius pseudoscorpions usually live in litter layer or soil, under rocks and stones, in caves. At present, this chthoniid genus contains 79 species, of which 32 are distributed in China (Hou et al. 2023a; WPC 2024). Because the biodiversity of cave environments has received a high attention in recent years, most of the reported *Lagynochthonius* species from China are cave-dwelling (Li et al. 2019; Hou et al. 2022a, b, 2023a, b), and only seven species, *Lagynochthonius brachydigitatus* Zhang & Zhang, 2014, *L. harveyi* Zhang & Zhang, 2014, *L. leptopalpus* Hu & Zhang, 2012, *L. medog* Zhang & Zhang, 2014, *L. niger* Hu & Zhang, 2012, *L. sinensis* Beier, 1967 and *L. tonkinensis* Beier, 1951, are reported in epigean environments. In this study, five new species of *Lagynochthonius* are described, all of them collected from epigean habitats in southern China.

# Materials and methods

#### Specimen preparation and examination

The specimens examined for this study are preserved in 75% ethyl alcohol in a refrigerator at -20 °C and deposited in the Museum of Hebei University (MHBU) (Baoding, China). Photographs and measurements were taken using a Leica M205A stereomicroscope equipped with a Leica DFC550 camera. Drawings was made using the Inkscape software (v. 1.0.2.0). Detailed examination was conducted with an Olympus BX53 general optical microscope. All images were edited and formatted using Adobe Photoshop 2017.

## Terminology

Terminology and measurements follow Chamberlin (1931) with some small modifications to the terminology of trichobothria (Harvey 1992; Judson 2007) and chelicera (Judson 2007). The chela and legs are measured in lateral view and others are taken in dorsal view. All measurements are given in mm unless noted otherwise. Proportions and measurements of chelicerae, carapace and pedipalps correspond to length/breadth, and those of legs to length/depth.

The following abbreviations are used in the text: for the chelal trichobothria: **b** = basal; **sb** = sub-basal; **st** = subterminal; **t** = terminal; **ib** = interior basal; **isb** = interior sub-basal; **ist** = interior sub-terminal; **it** = interior terminal; **eb** = exterior basal; **esb** = exterior sub-basal; **est** = exterior sub-terminal; **et** = exterior terminal. For other abbreviations: **af**, apical sensilla of fixed chelal finger, **am**, apical sensilla of movable chelal finger; **dx**, duplex trichobothria; **p**<sub>1-2</sub>, proximal sensilla of movable chelal finger; sc, microsetae (chemosensory setae); **td**, modified tooth.

## Taxonomy

Family Chthoniidae Daday, 1889 Subfamily Chthoniinae Daday, 1889 Tribe Tyrannochthoniini Chamberlin, 1962

Genus Lagynochthonius Beier, 1951

Type species. Chthonius johni Redikorzev, 1922, by original designation.

#### Lagynochthonius duo sp. nov.

https://zoobank.org/C97FE3FA-C67E-47FF-B960-895E9F933AFE Figs 1-5 Chinese name: 双毛拉伪蝎

**Type material.** *Holotype*  $\Diamond$  (Ps.-MHBU-GX2022080201): CHINA, Guangxi, Guilin City, Longsheng Autonomous County, Longji Town, Anjiangping Area, under topsoil and in the leaf litter layer [25°42'15.15"N, 110°3'3.87"E], 419 m a.s.l., 2 August 2023, Kun Yu & Jianzhou Sun leg. *Paratypes*: 3  $\Diamond$  (Ps.-MHBU-GX2022080203–05) and 1  $\bigcirc$  (Ps.-MHBU-GX2022080202), all with the same data as the holotype.

**Etymology.** The specific name is derived from the Latin word *duo*, meaning dual, which refers to the presence of two setae on both tergites I and II. A noun in apposition.

**Diagnosis.** ( $\mathscr{J} \hightharpow$ ). Moderately sized epigean species; carapace with four eyes, anterior margin smooth and epistome triangular; tergites I and II each with two setae, III and IV each with four setae. Rallum with eight blades. Pedipalps slender, chela 6.17–7.27 ( $\mathscr{J}$ ), 5.06 ( $\mathfrak{Q}$ ) × as long as broad; femur 5.60–6.67 ( $\mathscr{J}$ ), 6.70 ( $\mathfrak{Q}$ ) × as long as broad; only fixed chelal finger with intercalary teeth and a modified accessory tooth (*td*) on prolateral-retrolateral face; chemosensory setae (*sc*) present on dorsum of chelal hand; sensilla present.

Description. Males (holotype and paratypes) (Figs 1A, 2A-F, 3, 4).

**Color** generally pale yellow, chelicerae, carapace, pedipalps and tergites slightly darker.

**Cephalothorax** (Figs 2D, 3A): carapace nearly subquadrate,  $0.95-0.97 \times as$  long as broad, weakly constricted basally; posterior region with squamous sculpturing laterally, other area smooth, without furrows; anterior margin smooth, without serrate; epistome small and triangular; four well-developed eyes; with 18 setae arranged s4s: 4: 2: 2, most setae heavy, long and gently curved, anterolateral setae much shorter than others; with two pairs of lyrifissures, first pair situated middle to the setae of ocular row, second pair situated lateral to the sole pair of setae of posterior row. Manducatory process with two acuminate distal setae, anterior seta less than 1/2 length of medial seta; apex of coxa I with a rounded anteromedial process; coxae II with 10 or 11 terminally indented coxal spines on each side, set as an oblique and arc row, central spines slightly longer than the others (Fig. 3D); intercoxal tubercle absent; Chaetotaxy of coxae: P 3, I 3, II 4, III 5, IV 5.

**Chelicera** (Figs 2C, 3B): almost as long as carapace,  $1.76-1.94 \times as$  long as broad; five setae and two lyrifissures (exterior condylar lyrifissure and exterior lyrifissure) present on hand, all setae acuminate, ventrobasal setae shorter than others; movable finger with one medial seta. Cheliceral palm has moderate wrinkle on both ventral and dorsal sides. Both fingers well provided with teeth, fixed finger with 11-17 teeth, distal one largest; movable finger with 13-18 retrorse contiguous small teeth; galea completely vestigial (Fig. 3B). Serrula exterior with 20 and serrula interior with 14 blades. Rallum with eight blades, the distal one longest and recumbent basally, with fine barbules and slightly set apart from the other blades, latter tightly grouped and with long pinnae, some of which are subdivided (Fig. 3C).

*Pedipalp* (Figs 2A, B, E, 3E, 4A, B): trochanter 1.78–1.89, femur 5.60–6.67, patella 2.30–2.56, chela 6.17–7.27, hand 2.83–3.27 × as long as broad; femur



Figure 1. Lagynochthonius duo sp. nov. A holotype male (dorsal view) B paratype female (dorsal view).

2.43-2.84 × as long as patella; movable chelal finger 1.11-1.27 × as long as hand and 0.55 × as long as chela. Setae generally long and acuminate. Chelal palm gradually constricted towards fingers, apodeme complex of movable chelal finger strongly sclerotized. Fixed chelal finger and hand with eight trichobothria, movable chelal finger with four trichobothria, ib and isb situated close together, submedially on dorsum of chelal hand; eb, esb and ist at base of fixed chelal finger; esb and eb at almost the same level and ist slightly distal to esb; it slightly distal to est, situated subdistally; et slightly near to tip of fixed chelal finger, close to chelal teeth; dx situated distal to et; sb slightly closer to st than to b; b and t situated subdistally, t situated at the same level as it and distal to b; est situated distal to b and close to *it* (Figs 2A, 4A). Fixed chelal finger with sensilla  $af_{1-2}$  close together, near tip; movable chelal finger with four sensilla:  $am_{1-2}$  near tip,  $p_2$  slightly distad of  $p_1$ , p, slightly distad of sb and very close to chelal teeth (Fig. 4A). Microsetae (chemosensory setae) present on dorsum of chelal hand (Figs 2B, 4B). Both chelal fingers with a row of teeth, spaced regularly along the margin, teeth smaller distally and proximally: fixed finger with 17 or 18 well-spaced, pointed teeth, plus three or four intercalary microdenticles, and a modified accessory tooth on prolateral-retrolateral face (td, slightly distal to dx); movable finger with six or seven well-spaced, pointed teeth, plus nine or ten vestigial, rounded, contiguous basal teeth.

**Opisthosoma**: generally typical, pleural membrane finely granulated. All tergites and sternites undivided; setae uniseriate and acuminate. Tergal chaeto-taxy I–XII: 2: 2: 4: 4: 4: 4–5: 5–7: 5–6: 4: T2T: 0. Sternal chaetotaxy IV–XII: 8–10: 10–12: 11–12: 10–11: 10–12: 10–12: 9: -: 2. Genital region: sternite II with 6–10 setae scattered on median area, genital opening slit-like, sternite III with 18–20 setae (Fig. 3F).



Figure 2. *Lagynochthonius duo* sp. nov., holotype male (A–F) paratype female (G): A left chela (lateral view) B left chela (dorsal view) C right chelicera (dorsal view) D carapace (dorsal view) E Left pedipalp (minus chela, dorsal view) F male genital area (ventral view) G female genital area (ventral view).



Figure 3. *Lagynochthonius duo* sp. nov., holotype male **A** carapace (dorsal view) **B** left chelicera (dorsal view), with details of teeth **C** rallum **D** coxal spines on coxae II (ventral view) **E** left pedipalp (minus chela, dorsal view).



**Figure 4.** *Lagynochthonius duo* sp. nov., holotype male **A** left chela (lateral view), with details of teeth and trichobothrial pattern **B** left chela (dorsal view) **C** Leg I (lateral view) **D** leg IV (lateral view). Abbreviations: for the chelal trichobothria:  $b = basal; sb = sub-basal; st = subterminal; t = terminal; ib = interior basal; isb = interior sub-basal; ist = interior sub-terminal; it = interior terminal; eb = exterior basal; esb = exterior sub-basal; est = exterior sub-terminal. For other abbreviations: af, apical sensilla of fixed chelal finger, am, apical sensilla of movable chelal finger; dx, duplex trichobothria; <math>p_{1-2^{t}}$  proximal sensilla of movable chelal finger; td, modified tooth.

**Legs** (Fig. 4C, D): fine granulation present on anterodorsal faces of trochanter IV, femur I; scale-like texture display on anterodorsal faces of femoropatella IV. Leg I: femur 1.71–1.94 × as long as patella; tarsus 1.88–2.13 × as long as tibia. Leg IV: femoropatella 2.65–2.81 × as long as deep; tibia 4.38–5.14 × as long as



Figure 5. Type locality of *Lagynochthonius duo* sp. nov. A stone step road B selected deciduous layers C beside the stream D areas where *L. duo* sp. nov. specimens were collected.

deep; with basal tactile setae on both tarsal segments: basitarsus  $2.50-3.20 \times$  as long as deep (TS = 0.35-0.53), telotarsus  $9.25-12.00 \times$  as long as deep and  $2.29-2.47 \times$  as long as basitarsus (TS = 0.23-0.33). Setae of leg I (trochanter to tibia) 3-5: 7-11: 6-7: 8-12, setae of leg IV (trochanter to basitarsus) 3: 3: 7-8: 8-9: 5-8. Arolium not divided, slightly shorter than the simple claws.

Adult female (paratype) (Figs 1B, 2G). Mostly same as males; tergal chaetotaxy I–XII: 2: 2: 4: 4: 6: 6: 7: 7: 4: T2T: 0; sternal chaetotaxy IV–XII: 9: 12: 12: 10: 10: 11: 9: -: 2. Genital region: sternite II with 10 setae scattered on median area, sternite III with a row of 10 setae.

**Dimensions** (length/breadth or, in the case of the legs, length/depth in mm; ratios in parentheses). Males: body length 1.24-1.44. Pedipalps: trochanter 0.16-0.17/0.09 (1.78-1.89), femur 0.56-0.60/0.09-0.10 (5.60-6.67), patella 0.21-0.24/0.09-0.10 (2.30-2.56), chela 0.74-0.80/0.11-0.12 (6.17-7.27), hand 0.34-0.37/0.11-0.12 (2.83-3.27), movable chelal finger length 0.41-0.44. Chelicera 0.29-0.33/0.16-0.17 (1.76-1.94), movable finger length 0.20-0.21. Carapace 0.34-0.36/0.35-0.38 (0.95-0.97). Leg I: trochanter 0.10-0.12/0.08 (1.25-1.50), femur 0.29-0.33/0.06 (4.83-5.50), patella 0.17/0.05-0.06 (2.83-3.40), tibia 0.15-0.17/0.04 (3.75-4.25), tarsus 0.32-0.35/0.04 (8.00-8.75). Leg IV: trochanter 0.15-0.17/0.10 (1.50-1.70), femoropatella 0.45-0.53/0.16-0.20 (2.65-2.81), tibia 0.33-0.36/0.06-0.08 (4.38-5.14), basitarsus 0.15-0.17/0.05-0.06 (2.50-3.20), telotarsus 0.36-0.39/0.03-0.04 (9.25-12.00).
**Females**: body length 1.57. Pedipalps: trochanter 0.17/0.11 (1.54), femur 0.67/0.10 (6.70), patella 0.26/0.11 (2.36), chela 0.91/0.18 (5.06), hand 0.44/0.18 (2.44), movable chelal finger length 0.49. Chelicera 0.37/0.21 (1.76), movable finger length 0.23. Carapace 0.38/0.43 (0.88). Leg I: trochanter 0.18/0.10 (1.80), femur 0.35/0.07 (5.00), patella 0.18/0.06 (3.00), tibia 0.18/0.06 (3.00), tarsus 0.39/0.04 (9.75). Leg IV: trochanter 0.19/0.11 (1.73), femoropatella 0.59/0.22 (2.68), tibia 0.38/0.08 (4.75), basitarsus 0.18/0.07 (2.57), telotarsus 0.42/0.04 (10.50).

**Remarks.** *Lagynochthonius duo* sp. nov. differs from all other epigean species of the genus *Lagynochthonius* from China except *L. medog* by the tergal chaetotaxy I–IV: 2: 2: 4: 4. It differs from *L. medog* in the presence of an epistome, which is absent in *L. medog*, and in the presence of only fixed chelal fingers with intercalary teeth in *L. duo* sp. nov., whereas both chelal fingers have intercalary teeth in *L. medog* (Beier 1951, 1967; Hu and Zhang 2012a, b; Zhang and Zhang 2014).

Distribution. China (Guangxi).

#### Lagynochthonius gibbus sp. nov.

https://zoobank.org/133928D2-D809-499F-A7B7-BD05D648727D Figs 6-9 Chinese name: 驼峰拉伪蝎

**Type material.** *Holotype* ♂ (Ps.-MHBU-GZ2022070301): CHINA, Guizhou Province, Tongren City, Jiangkou County, 500 m near Wanjiatun, under topsoil and in the leaf litter layer [27°43'32.5"N, 108°41'17.9"E], 509 m a.s.l., 3 July 2022, Yanmeng Hou, Lu Zhang, Nana Zhan, Jianzhou Sun & Long Lin leg. *Paratype:* 1 ♀ (Ps.-MHBU-GZ2022070302), all with the same data as the holotype, 2 ♂ (Ps.-MHBU-GZ2022062805–06) and 2 ♀ (Ps.-MHBU-GZ2022062803–04): Tongren City, Sinan County, Zhangjiazhai Town, 700 m near Zhangjiaping, under topsoil and in the leaf litter layer [27°56'39.16"N, 108°4'21.8"E], 731 m a.s.l., 28 June 20, Yanmeng Hou, Lu Zhang, Nana Zhan, Jianzhou Sun & Long Lin leg.

**Etymology.** The specific name is derived from the Latin word *gibbus*, meaning hump-shaped, which refers to the shape of epistome. A noun in apposition.

**Diagnosis.** ( $\mathscr{S} \hfill \circ$ ). Moderately sized epigean species; carapace with four eyes, anterior margin smooth and epistome hump-shaped; tergites I–IV each with four setae. Rallum with eight blades. Pedipalps slender, chela 6.64–7.00 ( $\mathscr{S}$ ), 5.12–5.69 ( $\mathfrak{P}$ ) × as long as broad; femur 5.78–7.00 ( $\mathscr{S}$ ), 5.64–6.33 ( $\mathfrak{P}$ ) × as long as broad; only fixed chelal finger with intercalary teeth and a modified accessory tooth (*td*) on prolateral-retrolateral face; chemosensory setae (*sc*) present on dorsum of chelal hand; sensilla present.

Description. Males (holotype and paratypes) (Figs 6A, 7A-F, 8, 9).

**Color** generally pale yellow, chelicerae, carapace, pedipalps and tergites slightly darker.

**Cephalothorax** (Figs 7D, 8A): carapace nearly subquadrate, 0.97–1.03 × as long as broad, weakly constricted basally; posterior region with squamous sculpturing laterally, other area smooth, without furrows; anterior margin smooth, without serrate; epistome small and hump-shaped; four eyes, anterior pair of eyes well-developed, posterior pair with flat lenses; with 18 setae arranged s4s: 4: 2: 2, most setae heavy, long and gently curved, anterolateral setae much



Figure 6. Lagynochthonius gibbus sp. nov. A holotype male (dorsal view) B paratype female (dorsal view).

shorter than others; with two pairs of lyrifissures, first pair situated middle to the setae of ocular row, second pair situated lateral to the sole pair of setae of posterior row. Manducatory process with two acuminate distal setae, anterior seta less than 1/2 length of medial seta; apex of coxa I with a rounded anteromedial process; coxae II with 9–12 terminally indented coxal spines on each side, set as an oblique and arc row, central spines slightly longer than the others (Fig. 8D); intercoxal tubercle absent; Chaetotaxy of coxae: P 3, I 3, II 4, III 5, IV 5.

**Chelicera** (Figs 7C, 8B): almost as long as carapace,  $1.71-2.00 \times as$  long as broad; five setae and two lyrifissures (exterior condylar lyrifissure and exterior lyrifissure) present on hand, all setae acuminate, ventrobasal setae shorter than others; movable finger with one medial seta. Cheliceral palm has moderate wrinkle on both ventral and dorsal sides. Both fingers well provided with teeth, fixed finger with 12–15 teeth, distal one largest; movable finger with 16–18 retrorse contiguous small teeth; galea completely vestigial (Fig. 8B). Serrula exterior with 17–20 and serrula interior with 14–20 blades. Rallum with eight blades, the distal one longest and recumbent basally, with fine barbules and slightly set apart from the other blades, latter tightly grouped and with long pinnae, some of which are subdivided (Fig. 8C).

**Pedipalp** (Figs 7A, B, E, 8E, 9A, B): trochanter 1.78–1.89, femur 5.78–7.00, patella 2.33–2.56, chela 6.64–7.00, hand 3.09–3.18 × as long as broad; femur 2.43–2.60 × as long as patella; movable chelal finger 1.15–1.20 × as long as hand and 0.53–0.55 × as long as chela. Setae generally long and acuminate. Chelal palm gradually constricted towards fingers, apodeme complex of movable chelal finger strongly sclerotized. Fixed chelal finger and hand with eight



Figure 7. *Lagynochthonius gibbus* sp. nov., holotype male (A–F) paratype female (G): A left chela (lateral view) B left chela (dorsal view) C right chelicera (dorsal view) D carapace (dorsal view) E left pedipalp (minus chela, dorsal view) F male genital area (ventral view) G female genital area (ventral view).

trichobothria, movable chelal finger with four trichobothria, *ib* and *isb* situated close together, submedially on dorsum of chelal hand; *eb*, *esb* and *ist* forming a straight oblique row at base of fixed chelal finger; *it* slightly distal to *est*, situated subdistally; *et* slightly near to tip of fixed chelal finger, close to chelal teeth; *dx* situated distal to *et*; *sb* slightly closer to *st* than to *b*; *b* and *t* situated subdistally, *t* situated at the same level as *it* and distal to *b*; *est* situated distal to *b* and close to *it* (Figs 7A, 9A). Fixed chelal finger with sensilla  $af_{1-2}$  close together, near tip; movable chelal finger with four sensilla:  $am_{1-2}$  near tip,  $p_2$  slightly distad of *sb*,  $p_1$  proximad of *sb* and very close to chelal teeth (Fig. 9A). Microsetae (chemosensory setae) present on dorsum of chelal hand (Figs 7B, 9B). Both chelal fingers with a row of teeth, spaced regularly along the margin, teeth smaller distally and proximally: fixed finger with 20 or 21 well-spaced, pointed teeth, plus three or four intercalary microdenticles, and a modified accessory tooth on prolateral-retrolateral face (*td*, slightly distal to *dx*); movable finger with 6–8 well-spaced, pointed teeth, plus 5–7 vestigial, rounded and contiguous basal teeth.

**Opisthosoma**: generally typical, pleural membrane finely granulated. All tergites and sternites undivided; setae uniseriate and acuminate. Tergal chaetotaxy I–XII: 4: 4: 4: 4: 5–6: 6–7: 6: 4: T2T: 0. Sternal chaetotaxy IV–XII: 10–12: 12–16: 10–13: 12–13: 12–13: 11–12: 9–10: -: 2. Genital region: sternite II with eight setae scattered on median area, genital opening slit-like, sternite III with 18–24 setae (Fig. 7F).

**Legs** (Fig. 9C, D): fine granulation present on anterodorsal faces of trochanter IV, femur I; scale-like texture display on anterodorsal faces of femoropatella IV. Leg I: femur 1.65–1.71 × as long as patella; tarsus  $2.06-2.20 \times$  as long as tibia. Leg IV: femoropatella  $2.50-3.06 \times$  as long as deep; tibia  $4.43-4.71 \times$  as long as deep; with basal tactile setae on both tarsal segments: basitarsus  $2.33-3.40 \times$  as long as deep (TS = 0.29-0.42), telotarsus  $9.00-12.00 \times$  as long as deep and  $2.12-2.57 \times$  as long as basitarsus (TS = 0.25-0.28). Setae of leg I (trochanter to tibia) 3-4: 7-11: 6-8: 8-9, setae of leg IV (trochanter to basitarsus) 3: 2-3: 4-7: 7-9: 6-10. Arolium not divided, slightly shorter than the simple claws.

Adult females (paratypes) (Figs 6B, 7G). Mostly same as males; tergal chaetotaxy I–XII: 4: 4: 4-5: 5-6: 6: 5-6: 6: 5-8: 4-5: T2T: 0; sternal chaetotaxy IV–XII: 10–13: 11–13: 11–13: 10–14: 10–13: 10–13: 9–10: -: 2. Genital region: sternite II with 10 setae scattered on median area, sternite III with a row of 10–12 setae.

**Dimensions** (length/breadth or, in the case of the legs, length/depth in mm; ratios in parentheses). Males: body length 1.23-1.39. Pedipalps: trochanter 0.16-0.17/0.09 (1.78-1.89), femur 0.52-0.56/0.08-0.09 (5.78-7.00), patella 0.20-0.23/0.08-0.09 (2.33-2.56), chela 0.73-0.77/0.11 (6.64-7.00), hand 0.34-0.35/0.11 (3.09-3.18), movable chelal finger length 0.39-0.42. Chelicera 0.29-0.30/0.15-0.17 (1.71-2.00), movable finger length 0.18-0.19. Carapace 0.33-0.35/0.34-0.35 (0.97-1.03). Leg I: trochanter 0.10-0.11/0.08-0.09 (1.11-1.38), femur 0.28-0.30/0.06 (4.67-5.00), patella 0.17-0.18/0.05 (3.40-3.60), tibia 0.15-0.16/0.04 (3.75-4.00), tarsus 0.33/0.03-0.04 (8.25-11.00). Leg IV: trochanter 0.10-0.17/0.10-0.11 (1.00-1.70), femoropatella 0.48-0.50/0.16-0.20 (2.50-3.06), tibia 0.31-0.33/0.07 (4.43-4.71), basitarsus 0.14-0.17/0.03-0.04 (2.33-3.40), telotarsus 0.36/0.03-0.04 (9.00-12.00).

**Females**: body length 1.64–1.82. Pedipalps: trochanter 0.16–0.19/0.09–0.11 (1.60–1.78), femur 0.57–0.64/0.09–0.11 (5.64–6.33), patella 0.23–



Figure 8. *Lagynochthonius gibbus* sp. nov., holotype male **A** carapace (dorsal view) **B** right chelicera (dorsal view), with details of teeth **C** rallum **D** coxal spines on coxae II (ventral view) **E** left pedipalp (minus chela, dorsal view).

0.26/0.08-0.12 (1.92-2.30), chela 0.79-0.91/0.15-0.17 (5.12-5.69), hand 0.38-0.43/0.15-0.17 (2.53-2.69), movable chelal finger length 0.42-0.48. Chelicera 0.34-0.38/0.19-0.22 (1.72-1.79), movable finger length 0.21-0.24. Carapace 0.35-0.40/0.39-0.44 (0.88-0.91). Leg I: trochanter 0.12-0.13/0.07-0.09 (1.33-1.71), femur 0.29-0.33/0.06-0.07 (4.71-5.50), patella 0.16-0.19/0.04-0.06 (2.67-4.75), tibia 0.15-0.18/0.04-0.05 (3.60-3.75), tarsus 0.34-0.37/0.04 (8.50-9.25). Leg IV: trochanter 0.16-0.17/0.10-0.14



**Figure 9.** *Lagynochthonius gibbus* sp. nov., holotype male **A** left chela (lateral view), with details of teeth and trichobothrial pattern **B** left chela (dorsal view) **C** leg I (lateral view) **D** leg IV (lateral view). Abbreviations: for the chelal trichobothria:  $b = basal; sb = sub-basal; st = subterminal; t = terminal; ib = interior basal; isb = interior sub-basal; ist = interior sub-terminal; it = interior terminal; eb = exterior basal; esb = exterior sub-basal; est = exterior sub-terminal. For other abbreviations: af, apical sensilla of fixed chelal finger, am, apical sensilla of movable chelal finger; dx, duplex trichobothria; <math>p_{1-2'}$  proximal sensilla of movable chelal finger; td, modified tooth.

(1.14–1.70), femoropatella 0.49–0.56/0.18–0.22 (2.52–2.72), tibia 0.33–0.37/0.06–0.08 (4.50–4.71), basitarsus 0.17–0.19/0.06 (2.83–3.17), telotarsus 0.36–0.43/0.03–0.04 (10.00–12.00).

**Remarks.** *Lagynochthonius gibbus* sp. nov. most closely resembles *L. duo* sp. nov. due to the presence of intercalary teeth only on the fixed chelal finger, the presence of eight blades on rallum, and similar size (chela length of males 0.73–0.80 mm, females 0.79–0.91 mm). However, the new species differs from *L. duo* sp. nov. in the shape of the epistome which is hump-shaped in *L. gibbus* sp. nov., but triangular in *L. duo* sp. nov., and in the number of setae on tergites I and II, with four setae on each in *L. gibbus* sp. nov. compared to two setae on each in *L. duo* sp. nov.

Distribution. China (Guizhou Province).

#### Lagynochthonius hepingensis sp. nov.

https://zoobank.org/513D6885-A8B7-4527-9985-F14D9216A01F Figs 10-13 Chinese name: 和平拉伪蝎

**Type material.** *Holotype*  $\stackrel{\circ}{\circ}$  (Ps.-MHBU-GZ2022080701): CHINA, Guizhou Province, Qianxinan Prefecture, Wangmu County, Dayi Town, Heping Village, Near Provincial Highway 209, under topsoil and in the leaf litter layer [25°23'54.8"N, 106°7'37.08"E], 1553 m a.s.l., 7 August 2022, Yanmeng Hou, Lu Zhang, Jianzhou Sun & Wenlong Fan leg. *Paratypes*: 5  $\stackrel{\circ}{\circ}$  (Ps.-MHBU-GZ2022080702–06) and 2  $\stackrel{\circ}{=}$  (Ps.-MHBU-GZ2022080707–08), all with the same data as the holotype.

**Etymology.** Named after the Heping Village, the type locality. A noun in apposition.

**Diagnosis.** ( $\mathscr{J} \hightharpow$ ). Moderately sized epigean species; carapace with four eyes, anterior margin smooth and epistome hump-shaped; tergites I–IV each with four setae. Rallum with seven blades. Pedipalps slender, chela 6.08–6.82 ( $\mathscr{J}$ ), 5.33–5.44 ( $\mathfrak{Q}$ ) × as long as broad; femur 6.25–7.00 ( $\mathscr{J}$ ), 6.20–6.30 ( $\mathfrak{Q}$ ) × as long as broad; both chelal fingers with intercalary teeth, fixed chelal finger with a modified accessory tooth (*td*) on prolateral-retrolateral face; chemosensory setae (*sc*) present on dorsum of chelal hand; sensilla present.

Description. Males (holotype and paratypes) (Figs 10A, 11A-F, 12, 13).

**Color** generally pale yellow, chelicerae, carapace, pedipalps and tergites slightly darker.

**Cephalothorax** (Figs 11D, 12A): carapace nearly subquadrate, 0.97–1.03 × as long as broad, strongly constricted basally; posterior region with squamous sculpturing laterally, other area smooth, without furrows; anterior margin smooth, without serrate; epistome small and hump-shaped; four well-developed eyes; with 18 setae arranged s4s: 4: 4: 2: 2, most setae heavy, long and gently curved, anterolateral setae much shorter than others; with two pairs of lyrifissures, first pair situated middle to the setae of ocular row, second pair situated lateral to the sole pair of setae of posterior row. Manducatory process with two acuminate distal setae, anterior seta less than 1/2 length of medial seta; apex of coxa I with a rounded anteromedial process; coxae II with 8–10 terminally indented coxal spines on each side, set as an oblique and arc row, central spines slightly longer than the others (Fig. 12D); intercoxal tubercle absent; Chaetotaxy of coxae: P 3, I 3, II 4, III 5, IV 5. Jianzhou Sun et al.: Five new epigean Lagynochthonius species from southern China



Figure 10. Lagynochthonius hepingensis sp. nov. A holotype male (dorsal view) B paratype female (dorsal view).

**Chelicera** (Figs 11C, 12B): almost as long as carapace,  $1.63-1.81 \times as long$  as broad; five setae and two lyrifissures (exterior condylar lyrifissure and exterior lyrifissure) present on hand, all setae acuminate, ventrobasal setae shorter than others; movable finger with one medial seta. Cheliceral palm has moderate wrinkle on both ventral and dorsal sides. Both fingers well provided with teeth, fixed finger with 9-12 teeth, distal one largest; movable finger with 12-15 retrorse contiguous small teeth; galea completely vestigial (Fig. 12B). Serrula exterior with 16-23 and serrula interior with 14-20 blades. Rallum with eight blades, the distal one longest and recumbent basally, with fine barbules and slightly set apart from the other blades, latter tightly grouped and with long pinnae, some of which are subdivided (Fig. 12C).

Pedipalp (Figs 11A, B, 11E, 12E, 13A, B): trochanter 1.50-1.78, femur 6.25-7.00, patella 2.11-2.88, chela 6.08-6.82, hand 2.83-3.10 × as long as broad; femur 2.43-2.84 × as long as patella; movable chelal finger 1.11-1.27 × as long as hand and 0.53-0.57 × as long as chela. Setae generally long and acuminate. Chelal palm gradually constricted towards fingers, apodeme complex of movable chelal finger strongly sclerotized. Fixed chelal finger and hand with eight trichobothria, movable chelal finger with four trichobothria, ib and isb situated close together, submedially on dorsum of chelal hand; eb, esb and ist at base of fixed chelal finger; esb and eb at almost the same level and ist slightly distal to esb; it slightly distal to est, situated subdistally; et slightly near to tip of fixed chelal finger, close to chelal teeth; dx situated distal to et; sb slightly closer to st than to b; b and t situated subdistally, t situated at the same level as it and distal to b; est situated distal to b and close to it (Figs 11A, 13A). Fixed chelal finger with sensilla  $af_{1-2}$  close together, near tip; movable chelal finger with four sensilla:  $am_{1-2}$  near tip,  $p_2$  slightly distad of sb,  $p_1$  proximad of sb and very close to chelal teeth (Fig. 13A). Microsetae (chemosensory setae) present on dorsum of chelal



Figure 11. Lagynochthonius hepingensis sp. nov., holotype male (A–F) paratype female (G): A left chela (lateral view) B left chela (dorsal view) C left chelicera (dorsal view) D carapace (dorsal view) E left pedipalp (minus chela, dorsal view) F male genital area (ventral view).



Figure 12. *Lagynochthonius hepingensis* sp. nov., holotype male **A** carapace (dorsal view) **B** right chelicera (dorsal view), with details of teeth **C** rallum **D** coxal spines on coxae II (ventral view) **E** left pedipalp (minus chela, dorsal view).

hand (Figs 11B, 13B). Both chelal fingers with a row of teeth, spaced regularly along the margin, teeth smaller distally and proximally: fixed finger with 16–20 well-spaced, pointed teeth, plus 5–7 intercalary microdenticles, and a modified accessory tooth on prolateral-retrolateral face (*td*, slightly distal to *dx*); movable finger with seven or eight well-spaced, pointed teeth, plus 2–5 intercalary microdenticles and six or seven vestigial, rounded and contiguous basal teeth.

**Opisthosoma**: generally typical, pleural membrane finely granulated. All tergites and sternites undivided; setae uniseriate and acuminate. Tergal chaetotaxy I-XII: 4: 4: 4: 4: 4-5: 5-6: 5-7: 5-6: 4: T2T: 0. Sternal chaetotaxy IV-XII: 8-12: 10-12: 10-13: 10-12: 11-12: 10-12: 9: -: 2. Genital region: sternite II with 10 setae scattered on median area, genital opening slit-like, sternite III with 16-18 setae (Fig. 11F).

**Legs** (Fig. 13C, D): fine granulation present on anterodorsal faces of trochanter IV, femur I; scale-like texture display on anterodorsal faces of femoropatella IV. Leg I: femur  $1.69-2.00 \times as$  long as patella; tarsus  $1.93-2.36 \times as$  long as tibia. Leg IV: femoropatella  $2.40-2.67 \times as$  long as deep; tibia  $4.00-4.71 \times as$  long as deep; with basal tactile setae on both tarsal segments: basitarsus  $2.50-2.80 \times as$  long as deep (TS = 0.33-0.43), telotarsus  $8.75-11.67 \times as$  long as deep and  $2.33-2.64 \times as$  long as basitarsus (TS = 0.24-0.30). Setae of leg I (trochanter to tibia) 3-4: 8-10: 6-7: 7-10, setae of leg IV (trochanter to basitarsus) 2-3: 3-4: 6-8: 7-9: 6-10. Arolium not divided, slightly shorter than the simple claws.

Adult females (paratypes) (Figs 10B, 11G). Mostly same as males; tergal chaetotaxy I–XII: 4: 4: 4-5: 5-6: 6: 6: 6-8: 6: 4: T2T: 0; sternal chaetotaxy IV–XII: 10-12: 12-13: 12-14: 11-12: 10-12: 8-11: 10: -: 2. Genital region: sternite II with 10 setae scattered on median area, sternite III with a row of 12 setae.

**Dimensions** (length/breadth or, in the case of the legs, length/depth in mm; ratios in parentheses). Males: body length 1.18-1.38. Pedipalps: trochanter 0.14-0.16/0.08-0.10 (1.50-1.78), femur 0.50-0.56/0.08-0.09 (6.25-7.00), patella 0.19-0.23/0.08-0.09 (2.11-2.88), chela 0.67-0.75/0.10-0.12 (6.08-6.82), hand 0.31-0.35/0.10-0.12 (2.83-3.10), movable chelal finger length 0.37-0.42. Chelicera 0.26-0.32/0.16-0.18 (1.63-1.81), movable finger length 0.15-0.18. Carapace 0.31-0.37/0.34-0.38 (0.89-1.09). Leg I: trochanter 0.10-0.12/0.07-0.10 (1.20-1.57), femur 0.26-0.30/0.05-0.06 (4.50-6.00), patella 0.15-0.16/0.05-0.06 (2.67-3.20), tibia 0.13-0.16/0.04 (3.25-4.00), tarsus 0.29-0.33/0.03-0.04 (7.25-11.00). Leg IV: trochanter 0.14-0.18/0.10-0.11 (1.36-1.63), femoropatella 0.44-0.50/0.17-0.20 (2.40-2.67), tibia 0.29-0.33/0.07-0.08 (4.00-4.71), basitarsus 0.13-0.15/0.05-0.06 (2.50-2.80), telotarsus 0.34-0.37/0.03-0.04 (8.75-11.67).

**Females**: body length 1.34-1.43. Pedipalps: trochanter 0.15-0.18/0.11-0.12 (1.25-1.64), femur 0.63-0.64/0.10 (6.20-6.30), patella 0.24-0.25/0.11-0.12 (2.08-2.18), chela 0.83-0.87/0.15-0.16 (5.33-5.44), hand 0.41-0.44/0.15-0.16 (2.73-7.75), movable chelal finger length 0.51-0.52. Chelicera 0.34-0.39/0.20 (1.70-1.95), movable finger length 0.21-0.23. Carapace 0.38-0.39/0.42 (0.90-0.93). Leg I: trochanter 0.11-0.13/0.09-0.10 (1.10-1.44), femur 0.32/0.06-0.07 (4.57-5.33), patella 0.16-0.17/0.06 (2.67-2.83), tibia 0.16-0.17/0.05 (3.2-3.4), tarsus 0.34-0.35/0.04-0.05 (6.80-8.75). Leg IV: trochanter 0.16-0.18/0.11-0.12 (1.45-1.50), femoropatella 0.54-0.55/0.18-0.21 (2.62-3.00), tibia 0.33-0.35/0.08-0.09 (3.89-4.12), basitarsus 0.16/0.06 (2.67), telotarsus 0.39/0.04 (9.75).



**Figure 13.** *Lagynochthonius hepingensis* sp. nov., holotype male **A** left chela (lateral view), with details of teeth and trichobothrial pattern **B** left chela (dorsal view) **C** leg I (lateral view) **D** leg IV (lateral view). Abbreviations: for the chelal trichobothria: *b* = basal; *sb* = sub-basal; *st* = subterminal; *t* = terminal; *ib* = interior basal; *isb* = interior sub-basal; *ist* = interior sub-terminal; *it* = interior terminal; *eb* = exterior basal; *esb* = exterior sub-basal; *est* = exterior sub-terminal; *et* = exterior terminal. For other abbreviations: *af*, apical sensilla of fixed chelal finger, *am*, apical sensilla of movable chelal finger; *dx*, duplex trichobothria;  $p_{1-2^{n}}$  proximal sensilla of movable chelal finger; *td*, modified tooth.

**Remarks.** Lagynochthonius hepingensis sp. nov. most closely resembles *L. tonkinensis* in the presence of intercalary teeth on both chelal fingers and the presence of four setae on both tergal chaetotaxy I–II. However, it differs by the

presence of a hump-shaped epistome and four well-developed eyes, whereas *L. tonkinensis* has a flat, rounded epistome and spot-like posterior pair of eyes (Beier 1951).

**Distribution.** China (Guizhou Province).

#### Lagynochthonius houi sp. nov.

https://zoobank.org/B0877E10-C978-48E8-8F96-6274F4E0BFD7 Figs 14-17 Chinese name: 侯氏拉伪蝎

**Type material.** *Holotype*  $\Diamond$  (Ps.-MHBU-GZ2022080901): CHINA, Guizhou Province, Qiannan Prefecture, Pintang County, Tangbian Town, Xindian Village, under topsoil and in the leaf litter layer [25°37'42.19"N, 106°43'55.15"E], 991 m a.s.l., 9 August 2022, Yanmeng Hou, Lu Zhang, Jianzhou Sun & Wenlong Fan leg. *Paratypes*: 2  $\Diamond$  (Ps.-MHBU-GZ2022080902–03) and 1  $\subsetneq$  (Ps.-MHBU-GZ2022080904), all with the same data as the holotype.

**Etymology.** This species is named for Yanmeng Hou, who participated in field work and collected some of the specimens. A noun in apposition.

**Diagnosis.** ( $\mathscr{J} \hfill \equiv}$ ). Moderately sized epigean species; carapace with four eyes, anterior margin smooth and epistome triangular; tergites I and II each with two setae, III and IV each with four setae. Rallum with eight blades. Pedipalps slender, chela 6.31–6.75 ( $\mathscr{J}$ ), 5.20 ( $\mathfrak{Q}$ ) × as long as broad; femur 5.90–6.78 ( $\mathscr{J}$ ), 6.25 ( $\mathfrak{Q}$ ) × as long as broad; chelal fingers without intercalary teeth, fixed chelal finger with a modified accessory tooth (*td*) on prolateral-retrolateral face; chemosensory setae (*sc*) present on dorsum of chelal hand; sensilla present.

Description. Males (holotype and paratypes) (Figs 14A, 15A-F, 16, 17).

**Color** generally pale yellow, chelicerae, carapace, pedipalps and tergites slightly darker.

**Cephalothorax** (Figs 15D, 16A): carapace nearly subquadrate,  $0.91-0.97 \times as$  long as broad, weakly constricted basally; posterior region with squamous sculpturing laterally, other aera smooth, without furrows; anterior margin smooth, without serrate; epistome small and triangular; four eyes, anterior pair of eyes well-developed, posterior pair with flat lenses; with 18 setae arranged s4s: 4: 2: 2, most setae heavy, long and gently curved, anterolateral setae much shorter than others; with two pairs of lyrifissures, first pair situated middle to the setae of ocular row, second pair situated lateral to the sole pair of setae of posterior row. Manducatory process with two acuminate distal setae, anterior seta less than 1/2 length of medial seta; apex of coxa I with a rounded anteromedial process; coxae II with 9–12 terminally indented coxal spines on each side, set as an oblique and arc row, central spines slightly longer than the others (Fig. 16D); intercoxal tubercle absent; Chaetotaxy of coxae: P 3, I 3, II 4, III 5, IV 5.

**Chelicera** (Figs 15C, 16B): almost as long as carapace,  $1.71-1.88 \times as$  long as broad; five setae and three lyrifissures (including an exterior condylar lyrifissure, an exterior lyrifissure and extra lyrifissure (near sub basal setae)) present on hand, all setae acuminate, ventrobasal setae shorter than others; movable finger with one medial seta. Cheliceral palm has moderate wrinkle on both ventral and dorsal sides. Both fingers well provided with teeth, fixed finger with 9-12 teeth, distal one largest; movable finger with 11-13 retrorse contiguous



Figure 14. Lagynochthonius houi sp. nov. A holotype male (dorsal view) B paratype female (dorsal view).

small teeth; galea completely vestigial (Fig. 16B). Serrula exterior with 17–22 and serrula interior with 11–14 blades. Rallum with eight blades, the distal one longest and recumbent basally, with fine barbules and slightly set apart from the other blades, latter tightly grouped and with long pinnae, some of which are subdivided (Fig. 16C).

Pedipalp (Figs 15A, B, E, 16E, 17A, B): trochanter 2.00-2.12, femur 5.90-6.78, patella 2.44-2.67, chela 6.31-6.75, hand 3.23-3.25 × as long as broad; femur 2.45-2.68 × as long as patella; movable chelal finger 0.95-1.05 × as long as hand and 0.49-0.51 × as long as chela. Setae generally long and acuminate. Chelal palm gradually constricted towards fingers, apodeme complex of movable chelal finger strongly sclerotized. Fixed chelal finger and hand with eight trichobothria, movable chelal finger with four trichobothria, ib and isb situated close together, submedially on dorsum of chelal hand; eb, esb and ist forming a straight oblique row at base of fixed chelal finger; it slightly distal to est, situated subdistally; et slightly near to tip of fixed chelal finger, very close to chelal teeth; dx situated distal to et; sb slightly closer to st than to b; b and t situated subdistally, t situated at the same level as it and distal to b; est situated distal to b (Figs 15A, 17A). Fixed chelal finger with sensilla  $af_{1-2}$  close together, near tip; movable chelal finger with four sensilla:  $am_{1-2}$  near tip,  $p_2$  slightly distad of sb,  $p_1$  distad of  $p_2$  and very close to chelal teeth (Fig. 17A). Microsetae (chemosensory setae) present on dorsum of chelal hand (Figs 15B, 17B). Both chelal fingers with a row of teeth, spaced regularly along the margin, teeth smaller distally and proximally: fixed finger with 15-19 well-spaced, pointed teeth, and a modified accessory tooth on prolateral-retrolateral face (td, slightly distal to dx); movable finger with seven well-spaced, pointed teeth, plus 10–12 vestigial, rounded and contiguous basal teeth.



Figure 15. Lagynochthonius houi sp. nov., holotype male (A-F) paratype female (G): A left chela (lateral view) B left chela (dorsal view) C left chelicera (dorsal view) D carapace (dorsal view) E left pedipalp (minus chela, dorsal view) F male genital area (ventral view) G female genital area (ventral view).



Figure 16. *Lagynochthonius houi* sp. nov., holotype male **A** carapace (dorsal view) **B** left chelicera (dorsal view), with details of teeth **C** rallum **D** coxal spines on coxae II (ventral view) **E** left pedipalp (minus chela, dorsal view).



Figure 17. Lagynochthonius houi sp. nov., holotype male **A** left chela (lateral view), with details of teeth and trichobothrial pattern **B** left chela (dorsal view) **C** leg I (lateral view) **D** leg IV (lateral view). Abbreviations: for the chelal trichobothria: *b* = basal; *sb* = sub-basal; *st* = subterminal; *t* = terminal; *ib* = interior basal; *isb* = interior sub-basal; *ist* = interior sub-terminal; *it* = interior terminal; *eb* = exterior basal; *esb* = exterior sub-basal; *est* = exterior sub-terminal; *et* = exterior terminal. For other abbreviations: *af*, apical sensilla of fixed chelal finger, *am*, apical sensilla of movable chelal finger; *dx*, duplex trichobothria;  $p_{1-2t}$  proximal sensilla of movable chelal finger; *td*, modified tooth.

**Opisthosoma**: generally typical, pleural membrane finely granulated. All tergites and sternites undivided; setae uniseriate and acuminate. Tergal chaetotaxy I–XII: 2: 2: 4: 4: 4: 4: 5-6: 5-8: 4: T2T: 0. Sternal chaetotaxy IV–XII: 10: 10-11: 8-10: 8-10: 9-10: 9-10: 9: -: 2. Genital region: sternite II with 8-9 setae scattered on median area, genital opening slit-like, sternite III with 16-18 setae (Fig. 15F).

**Legs** (Fig. 17C, D): fine granulation present on anterodorsal faces of trochanter IV, femur I, IV and patella IV. Leg III: Femur 1.94–2.21 × as long as patella; tarsus  $2.00-2.29 \times as$  long as tibia. Leg IV: Femoropatella  $2.67-3.29 \times as$  long as deep; tibia  $5.00-5.83 \times as$  long as deep; with basal tactile setae on both tarsal segments: Basitarsus  $2.67-3.60 \times as$  long as deep (TS = 0.31-0.39),

telotarsus  $10.50-13.00 \times as$  long as deep and  $2.47-2.50 \times as$  long as basitarsus (TS = 0.23-0.26). Setae of leg I (trochanter to tibia) 3-4: 9-10: 4-6: 6-8, setae of leg IV (trochanter to basitarsus) 2-3: 2-3: 4-6: 7-8: 5-7. Arolium not divided, slightly shorter than the simple claws.

Adult female (paratype) (Figs 14B, 15G). mostly same as males; tergal chaetotaxy I–XII: 2: 2: 4: 4: 5: 5: 6: 6: 4: T2T: 0; sternal chaetotaxy IV–XII: 8: 11: 10: 10: 10: 11: 9: -: 2. Genital region: sternite II with 10 setae scattered on median area, sternite III with a row of 10 setae.

**Dimensions** (length/breadth or, in the case of the legs, length/depth in mm; ratios in parentheses). Males: Body length 1.29-1.41. Pedipalps: trochanter 0.17-0.18/0.08-0.09 (2.00-2.12), femur 0.59-0.61/0.09-0.10 (5.90-6.78), patella 0.22-0.24/0.09-0.10 (2.30-2.67), chela 0.77-0.82/0.12-0.13 (6.31-6.75), hand 0.39-0.42/0.12-0.13 (3.23-3.25), movable chelal finger length 0.38-0.41. Chelicera 0.29-0.32/0.17 (1.71-1.88), movable finger length 0.17-0.19. Carapace 0.32-0.36/0.35-0.37 (0.91-0.97). Leg I: trochanter 0.11-0.12/0.07-0.09 (1.33-1.57), femur 0.31-0.35/0.07-0.09 (5.50-6.20), patella 0.14-0.17/0.04-0.05 (2.80-4.25), tibia 0.16-0.18/0.04 (4.00-4.50), tarsus 0.36-0.39/0.03-0.04 (9.75-12.67). Leg IV: trochanter 0.17-0.19/0.10-0.13 (1.31-1.72), femoropatella 0.54-0.56/0.17-0.21 (2.67-3.29), tibia 0.35-0.37/0.06-0.07 (5.00-5.83), basitarsus 0.16-0.18/0.05-0.06 (2.67-3.60), telotarsus 0.39-0.42/0.03-0.04 (10.50-13.00).

**Females**: body length 1.68. Pedipalps: trochanter 0.22/0.11 (2.00), femur 0.75/0.12 (6.25), patella 0.28/0.13(2.15), chela 1.04/0.20 (5.20), hand 0.55/0.12 (2.75), movable chelal finger length 0.50. Chelicera 0.41/0.24 (1.71), movable finger length 0.25. Carapace 0.40/0.47 (0.85). Leg I: trochanter 0.13/0.12 (1.08), femur 0.40/0.08 (5.00), patella 0.21/0.07 (3.00), tibia 0.21/0.06 (3.50), tarsus 0.46/0.05 (9.20). Leg IV: trochanter 0.21/0.14 (1.50), femoropatella 0.67/0.25 (2.68), tibia 0.43/0.08 (5.38), basitarsus 0.22/0.07 (3.14), telotarsus 0.51/0.05 (10.20).

**Remarks.** *Lagynochthonius houi* sp. nov. differs from all other epigean species of the genus *Lagynochthonius* from China except *L. duo* sp. nov. by the following combination of characters: the presence of a triangular epistome and the presence of two setae on tergite I and II (Beier 1951, 1967; Hu and Zhang 2012a, b; Zhang and Zhang 2014).

Lagynochthonius houi sp. nov. differs from *L*. duo sp. nov. in the length of the movable chelal finger which is  $0.95-1.05 \times as$  long as the hand in males and  $0.91 \times as$  long as the hand in female, whereas in *L*. duo sp. nov. it is  $1.11-1.27 \times as$  long as the hand in males and  $1.11 \times as$  long as hand in female. Additionally, *L*. houi sp. nov. lacks intercalary tooth on the chelal fingers, whereas the fixed chelal finger posesses intercalary teeth in *L*. duo sp. nov.

Distribution. China (Guizhou Province).

#### Lagynochthonius sanhuaensis sp. nov.

https://zoobank.org/0A34AF68-B0BD-4BBA-BB44-A98AB2F32872 Figs 18-21 Chinese name: 三花拉伪蝎

**Туре material.** *Holotype*  $\stackrel{\circ}{\phantom{}}$  (Ps.-MHBU-GZ2022070201): Сніла, Guizhou Province, Tongren City, Yinjiang County, 500 m near Sanhua Mountain, under topsoil and in the leaf litter layer [27°53'40.73"N, 108°32'46.16"E], 818 m a.s.l., 7 July 2022, Yanmeng Hou, Lu Zhang, Nana Zhan, Jianzhou Sun & Long Lin leg. *Paratypes*: 2  $\bigcirc$  (Ps.-MHBU-GZ2022070203 & GZ2022070205) and 2  $\bigcirc$  (Ps.-MHBU-GZ2022070204), all with the same data as the holotype.

**Etymology.** Named after the Sanhua Mountain, near the type locality. A noun in apposition.

**Diagnosis.** ( $\mathcal{S} \hightharpoind$ ). Moderately sized epigean species; carapace with four eyes, anterior margin smooth and epistome hump-shaped; tergites I–IV each with four setae. Rallum with seven blades. Pedipalps slender, chela 6.80–7.89 ( $\mathcal{S}$ ), 5.31–5.40 ( $\mathcal{Q}$ ) × as long as broad; femur 6.50–6.63 ( $\mathcal{S}$ ), 5.70–6.00 ( $\mathcal{Q}$ ) × as long as broad; chelal fingers without intercalary teeth, fixed chelal finger with a modified accessory tooth (*td*) on prolateral-retrolateral face; chemosensory setae (*sc*) present on dorsum of chelal hand; sensilla present.

Description. Males (holotype and paratypes) (Figs 18A, 19A-F, 20, 21).

**Color** generally pale yellow, chelicerae, carapace, pedipalps and tergites slightly darker.

**Cephalothorax** (Figs 19D, 20A): carapace nearly subquadrate,  $0.92-0.97 \times as$  long as broad, weakly constricted basally; posterior region with squamous sculpturing laterally, other area smooth, without furrows; anterior margin smooth, without serrate; epistome small and hump-shaped; four eyes, anterior pair of eyes well-developed, posterior pair with flat lenses; with 18 setae arranged s4s: 4: 4: 2: 2, most setae heavy, long and gently curved, anterolateral setae much shorter than others; with two pairs of lyrifissures, first pair situated middle to the setae of ocular row, second pair situated lateral to the sole pair of setae of posterior row. Manducatory process with two acuminate distal setae, anterior seta less than 1/2 length of medial seta; apex of coxa I with a rounded anteromedial process; coxae II with 9–11 terminally indented coxal spines on each side, set as an oblique and arc row, central spines slightly longer than the others (Fig. 20D); intercoxal tubercle absent; Chaetotaxy of coxae: P 3, I 3, II 4, III 5, IV 5.

**Chelicera** (Figs 19C, 20B): almost as long as carapace, 1.81–1.93 × as long as broad; five setae and three lyrifissures (including an exterior condylar lyrifissure, an exterior lyrifissure and extra lyrifissure (near sub basal setae)) present on hand, all setae acuminate, ventrobasal setae shorter than others; movable finger with one medial seta. Cheliceral palm has moderate wrinkle on both ventral and dorsal sides. Both fingers well provided with teeth, fixed finger with 14–18 teeth, distal one largest; movable finger with 16–18 retrorse contiguous small teeth; galea completely vestigial (Fig. 20B). Serrula exterior with 19–20 and serrula interior with 10–12 blades. Rallum with seven blades, the distal one longest and recumbent basally, with fine barbules and slightly set apart from the other blades, latter tightly grouped and with long pinnae, some of which are subdivided (Fig. 20C).

**Pedipalp** (Figs 19A, B, E, 20E, 21A, B): trochanter 1.88-2.14, femur 6.50-6.75, patella 2.22-2.50, chela 6.80-7.89, hand  $3.20-3.67 \times as$  long as broad; femur  $2.57-2.65 \times as$  long as patella; movable chelal finger  $1.15-1.19 \times as$  long as hand and  $0.53-0.56 \times as$  long as chela. Setae generally long and acuminate. Chelal palm gradually constricted towards fingers, apodeme complex of movable chelal finger strongly sclerotized. Fixed chelal finger and hand with eight trichobothria, movable chelal finger with four trichobothria, *ib* and *isb* situated close together, submedially on dorsum of chelal hand; *eb*, *esb* and *ist* at base of fixed chelal finger; *esb* and *eb* at almost the same level and *ist* slightly distal



Figure 18. Lagynochthonius sanhuaensis sp. nov. A holotype male (dorsal view) B paratype female (dorsal view).

to *esb*; *it* slightly distal to *est*, situated subdistally; *et* slightly near to tip of fixed chelal finger, very close to chelal teeth; *dx* situated distal to *et*; *sb* slightly closer to *st* than to *b*; *b* and *t* situated subdistally, *t* situated at the same level as *it* and distal to *b*; *est* situated distal to *b* and close to *it* (Figs 19A, 21A). Fixed chelal finger with sensilla  $af_{1-2}$  close together, near tip; movable chelal finger with four sensilla:  $am_{1-2}$  near tip,  $p_2$  slightly distad of *sb*,  $p_1$  proximad of *sb* and very close to chelal teeth (Fig. 21A). Microsetae (chemosensory setae) present on dorsum of chelal hand (Figs 19B, 21B). Both chelal fingers with a row of teeth, spaced regularly along the margin, teeth smaller distally and proximally: fixed finger with 18 or 19 well-spaced, pointed teeth, and a modified accessory tooth on prolateral-retrolateral face (*td*, slightly distal to *dx*); movable finger with six well-spaced, pointed teeth, plus 8–10 vestigial, rounded and contiguous basal teeth.

**Opisthosoma**: generally typical, pleural membrane finely granulated. All tergites and sternites undivided; setae uniseriate and acuminate. Tergal chaetotaxy I–XII: 4: 4: 4: 4: 4: 4-6: 4–6: 5–6: 6: 4: T2T: 0. Sternal chaetotaxy IV–XII: 10–12: 10–11: 11–13: 9–13: 10–12: 10–12: 9: -: 2. Genital region: sternite II with ten setae scattered on median area, genital opening slit-like, sternite III with 16–18 setae (Fig. 19F).

Legs (Fig. 21C, D): fine granulation present on anterodorsal faces of trochanter IV, femur I; scale-like texture display on anterodorsal faces of femoropatella IV. Leg I: femur 2.57–2.65 × as long as patella; tarsus  $2.07-2.28 \times as$  long as tibia. Leg IV: femoropatella  $2.67-3.00 \times as$  long as deep; tibia  $4.43-5.33 \times as$  long as deep; with basal tactile setae on both tarsal segments: basitarsus  $2.50-3.50 \times as$  long as deep (TS = 0.36-0.43), telotarsus  $8.75-11.67 \times as$  long as deep and  $2.33-2.36 \times as$  long as basitarsus (TS = 0.21-0.23). Setae of leg I (trochanter to tibia) 3-4: 7-8: 3-6: 6-9, setae of leg IV (trochanter to basitarsus) 2-3: 3-5: 5-6: 7-8: 5-7. Arolium not divided, slightly shorter than the simple claws.

Adult females (paratypes) (Figs 18B, 19G). Mostly same as males; tergal chaetotaxy I–XII: 4: 4: 4: 4: 4-6: 6: 5-6: 6: 4: T2T: 0; sternal chaetotaxy IV–XII:



Figure 19. Lagynochthonius sanhuaensis sp. nov., holotype male (A–F) paratype female (G): A left chela (lateral view) B left chela (dorsal view) C left chelicera (dorsal view) D carapace (dorsal view) E left pedipalp (minus chela, dorsal view) F male genital area (ventral view).



Figure 20. *Lagynochthonius sanhuaensis* sp. nov., holotype male **A** carapace (dorsal view) **B** left chelicera (dorsal view), with details of teeth **C** rallum **D** coxal spines on coxae II (ventral view) **E** left pedipalp (minus chela, dorsal view).

12–13: 13–15: 11–13: 11–12: 12: 11: 9–10: -: 2. Genital region: sternite II with ten setae scattered on median area, sternite III with a row of 10–12 setae. *Dimensions* (length/breadth or, in the case of the legs, length/depth in mm; ratios in parentheses). Males: body length 1.30–1.36. Pedipalps: trochanter 0.15/0.07–0.08 (1.88–2.14), femur 0.52–0.54/0.08 (6.50–6.63), patella 0.20–0.21/0.08–0.09



**Figure 21.** Lagynochthonius sanhuaensis sp. nov., holotype male **A** left chela (lateral view), with details of teeth and trichobothrial pattern **B** left chela (dorsal view) **C** leg I (lateral view) **D** leg IV (lateral view). Abbreviations: for the chelal trichobothria: b = basal; sb = sub-basal; st = subterminal; t = terminal; ib = interior basal; isb = interior sub-basal; ist = interior sub-terminal; it = interior terminal; eb = exterior basal; esb = exterior sub-basal; est = exterior sub-terminal; et = exterior terminal. For other abbreviations: af, apical sensilla of fixed chelal finger, am, apical sensilla of movable chelal finger; dx, duplex trichobothria;  $p_{1-2}$ , proximal sensilla of movable chelal finger; td, modified tooth.

(2.22-2.50), chela 0.68-0.73/0.09-0.10 (6.80-7.89), hand 0.32-0.34/0.09-0.10 (3.20-3.67), movable chelal finger length 0.38-0.41. Chelicera 0.29-0.30/0.15-0.16 (1.81-1.93), movable finger length 0.18-0.19. Carapace 0.32-0.36/0.35-0.37 (0.91-0.97). Leg I: trochanter 0.09-0.11/0.08-0.09 (1.00-1.22), femur 0.27-0.28/0.05 (5.40-5.60), patella 0.13-0.15/0.05-0.06 (2.33-3.00), tibia 0.14-0.15/0.04-0.05 (2.80-3.75), tarsus 0.30-0.32/0.03 (10.00-10.67). Leg IV: trochanter 0.13-0.16/0.10-0.11 (1.30-1.45), femoropatella 0.46-0.48/0.16-0.18 (2.67-3.00), tibia 0.31-0.32/0.06-0.07 (4.43-5.33), basitarsus 0.14-0.15/0.04-0.06 (2.50-3.50), telotarsus 0.33-0.35/0.03-0.04 (8.75-11.67).

**Females**: body length 1.61–1.71. Pedipalps: trochanter 0.15-0.19/0.08-0.09 (1.67–2.38), femur 0.57-0.60/0.10 (5.70-6.00), patella 0.25-0.26/0.11 (2.27-2.36), chela 0.81-0.85/0.15-0.16 (5.2), hand 0.39-0.41/0.15-0.16 (2.75), movable chelal finger length 0.43-0.45. Chelicera 0.34-0.37/0.19-0.21 (1.76-1.79), movable finger length 0.22-0.23. Carapace 0.35-0.36/0.34-0.37 (0.82-0.88). Leg I: trochanter 0.09-0.13/0.09 (1.33-1.44), femur 0.30-0.32/0.06-0.08 (3.75-5.33), patella 0.17-0.18/0.05-0.06 (2.83-3.60), tibia 0.16-0.17/0.04-0.05 (3.20-4.25), tarsus 0.34-0.35/0.04 (8.50-8.75). Leg IV: trochanter 0.15-0.19/0.10-0.12 (1.50-1.58), femoropatella 0.49-0.54/0.21 (2.33-2.57), tibia 0.35-0.36/0.07 (5.00-5.14), basitarsus 0.15-0.16/0.06-0.07 (2.29-2.50), telotarsus 0.36-0.38/0.03-0.04 (9.50-12.00).

**Remarks.** Lagynochthonius sanhuaensis sp. nov. most closely resembles *L. niger* in the absence of intercalary teeth and the presence of four setae on tergites I and II, but differs from it in several characters. First, the new species has a shorter (0.68-0.73 mm compared to 0.75-0.93 mm in *L. niger*) and thinner chela ( $6.80-7.89 \times as$  long as broad compared to  $5.17-6.25 \times as$  long as broad in *L. niger*) in males. Second, the shape of the epistome is hump-shaped in *L. sanhuaensis* sp. nov., whereas it is triangular in *L. niger*. Third, the rallum has seven blades in *L. sanhuaensis* sp. nov., whereas it has eight blades in *L. niger* (Hu and Zhang 2012a).

Distribution. China (Guizhou Province).

#### Key to the epigean species of Lagynochthonius from China

I Tergites I and II each with two setae	2
- Tergites I and II each with four setae	4
2 Epistome present	3
- Epistome absentL. medog Zhang & Zhang,	2014
3 Only fixed chelal finger with intercalary teeth <b>L. duo sp</b>	. nov.
- Both chelal fingers without intercalary teeth	. nov.
At least one finger of chela with intercalary teeth	5
- Both chelal fingers without intercalary teeth	8
5 Both chelal fingers with intercalary teeth	6
- Only fixed chelal finger with intercalary teeth	7
Carapace with a hump-shaped epistome; the four well-developed ey	es
L. hepingensis sp	. nov.
- Carapace with a flat, rounded epistome; posterior pair of eyes spot-l	ike
L. tonkinensis (Beier, 1	1951)
7 Carapace without epistome L. harveyi Zhang & Zhang,	2014
- Carapace with a hump-shaped epistome	. nov.
3 Epistome present	9
- Epistome absent	10
Epistome triangular; pedipalpal chela length 0.75–0.93 mm, 5.17–6	5.25 ×
as long as broad <b>L. niger Hu &amp; Zhang</b> ,	2012
- Epistome hump-shaped; pedipalpal chela length 0.68-0.73 mm, 6	5.80-
7.30 × as long as broad <b>L. sanhuaensis sp</b>	. nov.
10 Four well-developed eyes	11
- Anterior pair of eyes well-developed, posterior pair of eyes reduced to	o eye-
spot L. brachydigitatus Zhang & Zhang,	2014

Pedipalpal chela length 0.72 mm, 4.80 × as long as broad......
*L. sinensis* (Beier, 1967)
Pedipalpal chela length 0.95–1.00 mm, 5.56–6.33 × as long as broad......
*L. leptopalpus* Hu & Zhang, 2012

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# **Additional information**

## **Conflict of interest**

The authors have declared that no competing interests exist.

## **Ethical statement**

No ethical statement was reported.

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## **Data availability**

All of the data that support the findings of this study are available in the main text.

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**Review Article** 

# Revision of the leafhopper genus *Smyga* (Hemiptera, Cicadellidae, Typhlocybinae)

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#### Abstract

The leafhopper genus *Smyga* Dworakowska (Typhlocybinae, Empoascini) is reviewed and a new species, *S. brevipenis* Webb & Xu, **sp. nov.** from Brunei and Malaysia, is described based on specimens previously identified as "aberrant specimens" of *Smyga distincta* Dworakowska. Images of the types of *S. brevipenis* and *S. distincta* are given for the first time. A checklist and key to known species of *Smyga* are also provided.

Key words: Auchenorrhyncha, distribution, Homoptera, morphology, taxonomy

## Introduction

The typhlocybine leafhopper genus, *Smyga* Dworakowska, 1995, was described for five species from Brunei and Malaysia (Sarawak and Sabah) (Dworakowska 1995; Knight 2010). The genus is recognized by a brown spot on the fore margin of the head and sinuate transverse brown band on the pronotum (Figs 1, 9), a well-developed coronal suture extended onto the face (Fig. 2), and a hind wing with veins MP and CuA free distally. Although species are very similar externally, there are considerable differences in their male genitalia, particularly with respect to the aedeagus, so much so that Dworakowska (1995) tentatively regarded one species, *S. distincta*, as having an aberrant form with a remarkably short aedeagal shaft. However, the discovery of two new species from Papua New Guinea in Xu's (2019) PhD thesis, with similar aedeagus, suggests that the specimens described and illustrated by Dworakowska as an aberrant form represent a separate species. This new species is described and illustrated below and a checklist and key to the known species of the genus are presented.

## Materials and methods

Morphological terminology used in this work follows Xu et al. (2021). Studied specimens are deposited in the insect collection of the Natural History Museum, London, UK (NHM).



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## Taxonomy

#### Smyga Dworakowska, 1995

Smyga Dworakowska, 1995: 151.

Type species. Smyga distincta Dworakowska, 1995 by original designation.

**Description.** Body relatively robust. Pale yellow; head with a brown patch anteriorly (Figs 1, 9); face with anteclypeus brown distally (Fig. 2), sometimes with more extensive brown marking (*S. divergens*); pronotum with a brown transverse narrow band at midlength, pale yellow anterior to band and silvery posterior to band (Figs 1, 9); mesonotum with yellow to brown basal triangles (Figs 1, 9).

Head including eyes broader than pronotum in dorsal view, crown short and broad, round anteriorly, length along midline shorter than one-half width between eyes; coronal suture well developed, extended onto face, and terminating at level of antennal bases (Fig. 2). Ocelli distinct, well separated from eyes (Fig. 2). Face moderately broad; lateral frontal suture well developed, curved mesad above antennal pit and meeting coronal suture at midline ventromesad of ocelli; anteclypeus slightly convex, not expanded (Fig. 2). Pronotum large with sinuate transverse depression (Figs 1, 9). Forewing narrow, rounded apically; apical cells occupying almost one-third of total length; vein R2 and RM dissociated at bases, joined by cross-vein, both arising from r cell; vein ScP+RA is not detectable; vein MCu almost parallel with vein RM apically. Hindwing with MP+CuA confluent. Front femur seta AM1 stout, situated near ventral margin; intercalary row with one large basal seta and eight or nine smaller setae near tip of femur. Hind femur with macrosetal formula 2 + 1 + 1; tibia row AV with six or seven preapical macrosetae.

Male basal abdominal sternal apodemes (2S apodemes) well developed (Fig. 3). Male pygofer elongated, strongly narrowing caudad, posterior margin acute with few rigid microsetae distally, dorsal margin with macrosetae, long fine ventrolateral setae present, ventral appendage absent (Figs 4, 10). Anal tube process elongate, extended to ventral margin of genital capsule (Figs 4, 10). Subgenital plate broadest near base (Fig. 10) or subapically (Fig. 4), all categories of setae well differentiated; basal setae encompassing mid-length of plate; marginal setae well defined; macrosetae uniserate; feeble microsetae arranged in 2–4 irregular rows apically (Fig. 4). Connective with media sclerotization, anterior margin and posterior margin deeply emarginated (Fig. 7). Style short, sinuate, with tiny teeth and microsetae preapically (Fig. 11). Aedeagus shaft short, tubular, with basal apodeme long (Figs 5, 13) or laterally compressed with basal apodeme short (Figs 6, 12); gonopore apical on ventral surface (Fig. 12).

**Notes.** *Smyga* superficially resembles *Dapitana* Mahmood, 1967 in the features of the head and wings (coronal suture extended onto face and terminating at level of antennal bases (Fig. 2), forewing with vein R2 and RM dissociated at bases, joined by cross-vein, both arising from r cell and vein ScP+RA is not detectable). It differs from *Dapitana* in color pattern (see generic description) and in having the male pygofer with one or two dorsal macrosetae and long fine ventrolateral setae (Figs 4, 10) (pygofer without macrosetae and long fine setae in *Dapitana*). Both genera occur on both sides of Wallace's Line, separating the Oriental from Australian regions.

*Smyga* includes five previously known species, all from Borneo, described by Dworakowska (1995). In her treatment of the type species, *S. distincta*, Dworakowska also described and illustrated some "aberrant specimens" that she excluded from the type series because she considered the small, ventrally positioned aedeagal shaft to be "not functional." Here we recognize these specimens as a valid species: *S. brevipenis* sp. nov., as similar specimens of two new species have been seen in Xu's (2019) PhD thesis.

As most *Smyga* species are from similar localities in Borneo (see Checklist) and as males are needed for identification, the female paratypes of two species (*S. distincta* and *S. zonata*) must be regarded as of uncertain identity (see also comments under *S. distincta* and *S. zonata*). It is also of some interest that, compared to males, the number of known females is very low.

Distribution. Oriental Region (Brunei, Malaysia).

## Checklist to species of Smyga

- *S. brevipenis* Webb & Xu, sp. nov. (Brunei, Ulu Temburong; Sarawak, Gunong Mulu National Park)
- S. distincta Dworakowska, 1995: 153–155, figs 168–177 (Brunei, Ulu Temburong)
- S. exhibita Dworakowska, 1995: 155, figs 198-205 (Brunei, Ulu Temburong)
- S. niema Dworakowska, 1995: 155–156, figs 206–212 (Sabah)
- S. ziewa Dworakowska, 1995: 155, figs 188-192 (Brunei, Bukit Sulang)
- S. zonata Dworakowska, 1995: 155, figs 193–197 (Sarawak, Gunung Mulu National Park)

## Key to species Smyga Dworakowska (males)

1	Aedeagus with basal apodeme (dorsal apodeme) very lo	ng (Fig. 5)
		S. brevipenis
_	Aedeagus with basal apodeme very short (Fig. 13)	2
2	Aedeagus without processes (Figs 12, 13)	S. distincta
-	Aedeagus with processes	3
3	Aedeagus with processes near base of shaft	4
_	Aedeagus with processes at apex of shaft	5
4	Aedeagus with processes near base of shaft long	S. zonata
_	Aedeagus with processes near base of shaft short	S. ziewa
5	Aedeagus with short apical processes	S. exhibita
_	Aedeagus with long apical processes	S. niema

## Smyga brevipenis Webb & Xu, sp. nov.

https://zoobank.org/23A87192-5521-448F-B080-84EC4CCEC98D Figs 1-8

Smyga distincta Dworakowska, 1995: 153, figs 178-182, in part.

Material examined. *Holotype*. ♂, Brunei, Ulu Temburong; 300 m elev.; Feb-Mar. 1982; M.C. Day leg.; B.M. 1983-75 (NHM).

**Paratypes.** Brunei, 8 ♂♂, same data as holotype; 10 ♂♂, same data as holotype except Ulu Temburong ridge; (NHM). Malaysia, Sarawak, Gunung Mulu National Park: 5 ♂♂, Gunung Api, 900 m elev., site 25, April; montane forest, mv and act light trap; J.D. Holloway leg.; 2 ♂♂, nr Long Melinau, 50 m elev., site 17, May; low secondary forest, mv light on river-bank; J.D. Holloway; 7 ♂♂, W. Melinau Gorge leg., 250 m elev., site 23, April; limestone forest, canopy/understory, mv light; J.D. Holloway leg.; 1 ♂, W. Melinau Gorge leg., Kerankas, 150 m elev., Mar.–Apr. 1978; J.D. Holloway leg.; 2 ♂♂, camp 2.5, 30 Apr. 1978, V.F. Eastop. All paratypes from Sarawak were collected on the RGS Mulu Expedition, B.M. 1978-206 (NHM).

Description. Body length: 3.5–4.4 mm.

Color as in generic description (Fig. 1).

Male 2S apodemes not extending to end of segment V (Fig. 3). Anal-tube appendage hook-shaped at apex (Fig. 4). Male pygofer strongly emarginate dorsally in profile, and posteriorly extended into sharp point with spine-like setae; ventral appendage absent; bearing one long macroseta near dorsal margin (Fig. 4); dorsal bridge with a posterior lobe-like projection each side of midline, in dorsal view. Subgenital plate surpassing pygofer lobe, broadened medially in later view, all categories of setae represented (Fig. 4). Connective anterior margin with undeveloped median lobe, posterior margin notched medially (Fig. 7). Style sinuate (Figs 4, 8). Aedeagus without preatrium, basal apodeme well developed, plate-like; shaft with pair of lamellate lateral processes; gonopore subapical, ventrad (Figs 5, 6).

**Etymology.** The name is derived from the Latin words *brevis* (short) and *penis*, which refers to the very short aedeagal shaft.

Distribution. Brunei, Malaysia.

**Notes.** Specimens of *S. brevipenis* were considered aberrant specimens of *S. distincta* by Dworakowska (1995) and of uncertain status. However, based on the high degree of difference between these two species and the discovery of two similar new species from Papua New Guinea noted in Xu's (2019) PhD thesis, we describe the above specimens as a new species. All type specimens listed here (with some amendments) were identified by I. Dworakowska as the aberrant form of *S. distincta*. All are male and most have a Dworakowska genitalia dissection affixed to a card placed beneath the specimen. Three females (NHM) with identical data to the males could be the same species but, as three other species are also from these localities (see Checklist), their identity is uncertain. See also the concluding comments under the genus description. In Dworakowska's (1995) figure of the head and thorax there are some fine lines in the basal triangles of the mesonotum. These are seen in some specimens, but it is not clear if they are markings or perhaps caused by shrinkage of internal tissue during drying.

#### Smyga distincta Dworakowska

Figs 9-13

Smyga distincta Dworakowska, 1995: 153-155, figs 168-177.

**Notes.** The type series was originally stated as holotype male from Brunei, Ulu Temburong and one paratype male and two females from three different localities in Sarawak, Gunung Mulu National Park; however, the paratype male is in fact female. The identity of these three females must remain uncertain until



Figures 1–13. *Smyga* species 1–8 *S. brevipenis* 1 head and thorax, dorsal view (holotype) 2 face (holotype) 3–8 male genitalia after Dworakowska's (1995) figures of aberrant form of *S. distincta* 3 basal sternal apodemes 4 male genital capsule, left lateral view 5 aedeagus left lateral view 6 aedeagus, ventral view 7 connective 8 connective, style and sub-genital plate 9–13 *S. distincta* 9 habitus (holotype) 10–13 male genitalia, after Dworakowska (1995) 10 genital capsule 11 style 12 aedeagus ventral view 13 aedeagus, left lateral view.

females in the genus can be identified, particularly as other species are sympatric with *S. distincta* (see Checklist).

Aberrant specimens regarded as possibly this species in its original description are described above as a new species. Therefore, this species is known with certainty only from a single male, the holotype (NHM).

#### Smyga zonata Dworakowska

Smyga zonata Dworakowska, 1995: 155, figs 193-197.

**Notes.** The type series was originally stated to include a holotype male from Sarawak, Gunung Mulu National Park and one male and two female paratypes from Brunei, Ulu Temburong. The identity of these two females must remain uncertain until females in the genus can be identified, particularly as other species are sympatric with *S. zonata* (see Checklist). Therefore, this species is known with certainty only from two male specimens (NHM).

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## Additional information

#### **Conflict of interest**

The authors have declared that no competing interests exist.

#### **Ethical statement**

No ethical statement was reported.

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#### Data availability

All of the data that support the findings of this study are available in the main text.

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Research Article

# A taxonomic study of *Cheiloneurus* Westwood (Hymenoptera, Encyrtidae) from China

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#### Abstract

Fourteen species of *Cheiloneurus* from China are studied. *Cheiloneurus guangxiensis* Zu, **sp. nov.**, is described as new to science, and *C. boldyrevi* Trjapitzin & Agekyan, 1978, *C. bouceki* Anis & Hayat, 2002, *C. gonatopodis* Perkins, 1906, and *C. hadrodorys* Anis & Hayat, 2002 are newly recorded from China. A key to Chinese species based on females is also presented.

Key words: Chalcidoidea, Cheiloneurini, new species, parasitoids

## Introduction

The genus *Cheiloneurus*, established by Westwood (1833), with *C. elegans* Dalman as it type species, is very large and diverse (Noyes and Hayat 1984). It encompasses 151 recognized species worldwide (Noyes 2019). All *Cheiloneurus* species exhibit hyperparasitic behavior, targeting a broad spectrum of parasitoid wasps (Trjapitzin and Zuparko 2004). In China, nine *Cheiloneurus* species have been documented, primarily parasitizing Aphelinidae, Encyrtidae, and Dryinidae, engaging in hyperparasitism on various insects, including Hemiptera (e.g. Coccidae, Pseudococcidae) and Diptera (e.g. Drosophilidae) (Xu and Huang 2004; Li et al. 2020; Wang et al. 2023). *Cheiloneurus* is characterized by distinctive features, including the arrangement of setae in the basal cell of the fore wing, typically infuscate fore wings, the presence of an apical tuft of setae on the scutellum, and a hypopygium that does not reach the apex of the gaster (Noyes and Hayat 1984).

Various taxonomists, including Girault (1915) in Australia, Trjapitzin (1989) in the Palaearctic, Hayat and Veenakumari (2017) and Anis and Hayat (2002) in India, Trjapitzin and Triapitsyn (2008) in the New World, and Xu and He (2003) and Shi et al. (1994) in China, have contributed significantly to the taxonomy of the genus *Cheiloneurus*. In this study, we present a comprehensive taxonomic examination of nine known species, introduce one new species, and newly report four other *Cheiloneurus* species from China. The primary objective is to enhance the precision of identifying Chinese *Cheiloneurus* parasitoids. Additionally, we furnish a key for the female species of *Cheiloneurus* in China.



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# Materials and methods

Photographs of specimens in ethanol were taken using a Canon EOS 80D camera equipped with a Laowa 25 mm lens. A Motic SMZ-168 stereomicroscope was used to dissect specimens, which were mounted on slides according to Zhang et al. (2022) and Noyes (1982). Slide-mounted specimens were photographed with a digital camera attached to an Olympus BX51 running Olympus cellSens Standard v. 1.18. The pictures were synthesized through Helicon Focus v. 6 and processed using Photoshop 2020. Each characteristic part was measured using an Olympus CX21 equipped with a micrometer in the eyepiece. All materials were deposited in the insect collections of Tianjin Agricultural University (TJAU), China.

Morphological terminology and abbreviations were based on Noyes (2010). The subsequent list provides the employed abbreviations:

AOL	minimum distance between a lateral ocellus and median ocellus
F1-6	funicle segments 1-6
FV	minimum frontovertex width
FWL	fore wing length
HWL	hind wing length
HWW	hind wing width
MS	malar space
МТ	mid tibia
OCL	minimum distance between a lateral ocellus and occipital margin
OD	longest diameter of an ocellus
OL	ovipositor length
00L	minimum distance between a lateral ocellus and the corresponding
	eye margin
POL	minimum distance between lateral ocelli
SMV	submarginal vein
MV	marginal vein
PMV	postmarginal vein
SV	stigmal vein
BMNH	The Natural History Museum, London, UK
HAUZ	Department of Plant Protection, Henan Agricultural University, Zheng-
	zhou, China
LUNZ	Department of Entomology, Lincoln University, Canterbury, New Zea-
	land
USNM	United States National Museum of Natural History, Washington DC,
	USA
BPBM	Bernice Pauahi Bishop Museum, Honolulu, Hawaii
ZAUC	Institute of Applied Entomology, Zhejiang University, Hangzhou, Zheji-
	ang, China
ZAFU	Department of Plant Protection, School of Agriculture and Food Sci-
	ence, Zhejiang Agriculture & Forestry University, Huangzhou, Zhejiang,
	China
ZDANU	Department of Zoology, Aligarh Muslim Uiversity, Aligarh, India
NIES	National Institute of Agro-Environmental Sciences, Ibaraki, Japan
## Results

# Key to Chinese species of Cheiloneurus (females)

1	Scutellum without a tuft of bristles at apex2
-	Scutellum with a tuft of bristles at apex4
2	Fore wing hyaline C. lateocaudatus (Xu & He, 2003)
-	Fore wing infuscate
3	F4 yellowish white; linea calva closed posteriorly by several lines of setae 
-	F4 dark brown; linea calva open posteriorly C. exitiosus Perkins, 1906
4	Scape at least 4.75× as long as wide5
-	Scape not more than 4.5× as long as wide8
5	Fore wing hyaline towards base, at apex and along anterior margin distad of venation
-	Fore wing with basal cell almost completely hyaline, small area at apex of venation and area on opposite margin hyaline <b>7</b>
6	F5-F6 vellowish white: ovipositor not more than 1× as long as mid tibia
_	<b>C.</b> gonatopodis Perkins, 1906
	C houceki Anis & Havat 2002
7	Clava not more than 1.78x as long as wide slightly shorter than F4-F6
,	combined head not more than 0.80x as wide as long
	C. nankingensis Li & Xu. 2020
_	Clava at least 2.72× as long as wide, slightly longer than F3-F6 combined:
	head at least 0.90× as wide as long C. elegans (Dalman, 1820)
8	F6 black9
-	F6 entirely white or mixed with brown11
9	Fore wing hyaline towards base, at apex and along anterior margin distad of venation: frontovertex not more than $1/10$ width of head
	C. axillaris Havat, Alam & Agarwal, 1975
_	Fore wing with basal cell almost completely hyaline, small area at apex of
	venation and area on opposite margin hvaline: frontovertex at least 1/9
	width of head
10	width of head
10 _	width of head
10 -	width of head
10 - 11	width of head
10 - 11 -	<ul> <li>width of head</li></ul>
10 - 11 - 12	width of head       10         F4-F5 entirely whitish       10         F4-F5 whitish with a brown stripe on ventral margin       10         F1 entirely whitish       12         F1 yellowish-brown       13         Clava as long as F4-F6 combined; pedicel as long as F1       11
10 - 11 - 12	<ul> <li>width of head</li></ul>
10 - 11 - 12 -	<ul> <li>width of head</li></ul>
10 - 11 - 12 -	<ul> <li>width of head</li></ul>
10 - 11 - 12 - 13	<ul> <li>width of head</li></ul>
10 - 11 - 12 - 13 -	width of head

## **Cheiloneurus axillaris Hayat, Alam & Agarwal, 1975** Figs 1-3

*Cheiloneurus axillaris* Hayat et al. 1975: 47. Holotype ♀, BMNH, India, Maharashtra, not examined.

Cheiloneurus axillaris Anis and Hayat 2002: 171–172.

Cheiloneurus axillaris Xu and He 2003: 103–104, examined plates.

Material examined. CHINA – Yunnan • 2♀; Longchuan; 24°10'59"N, 97°47'32"E; 1336 m elev.; 27 Ari. 2013; Guo-Hao Zu, Xiang-Xiang Jin, Chao Zhang leg.; by yellow pan trapping; TJAU-YN-CHE-001 to 002.



Figures 1–9. 1–3 Cheiloneurus axillaris  $\bigcirc$  1 dorsal habitus 2 lateral habitus 3 ventral habitus 4–6 Cheiloneurus boldyrevi  $\bigcirc$  4 dorsal habitus 5 lateral habitus 6 ventral habitus 7–9 Cheiloneurus bouceki  $\bigcirc$  7 dorsal habitus 8 lateral habitus 9 ventral habitus.

**Diagnosis. Female**. Length, excluding ovipositor, 1.78–1.89 mm; head dark brown, gena with bluish-green metallic luster; antennal scape brown, with an apical white area; pedicel yellow; funicle yellowish brown; clava dark brown. Legs pale yellow to white.

Description. See Hayat et al. (1975).

**Host.** Coccidae: *Ceroplastes japonicus, Pulvinaria psidii*; Margarodidae: *Ic-erya* sp. (Hayat et al. 1975).

Distribution. China (Fujian, Yunnan), Bangladesh, India.

## Cheiloneurus boldyrevi Trjapitzin & Agekyan, 1978

Figs 4-6, 10-16

*Cheiloneurus boldyrevi* Trjapitzin and Agekyan, in Trjapitzin 1978: 309–310. Holotype ♀, ZISP, Russia, not examined.

*Cheiloneurus boldyrevi* Guerrieri and Viggiani 2005: 312–313. *Cheiloneurus boldyrevi* Japoshvili et al. 2016: 367.

**Material examined.** CHINA – Tianjin • 1♀; Xiqing, Tianjin Agricultural University; 39°5′21″N, 117°5′38″E; 13 m elev.; 12−30 Jun. 2023; Hai-Yang Wang, Xin-Yu Cao leg.; by Malaise trapping; TJAU-TJ-CHE-001.

**Description.** Length, excluding ovipositor, 2.88 mm. Head generally brown; gena with metallic-green luster; antennal scape orange, pedicel and F1–F2 brown, F3 brown with whitish spot in the upper corner of the fore margin, F4– F6 white, clava black, apex paler; basal half of pronotum dark brown and apical half orange, mesoscutum dark brown with metallic-green luster, axilla and scutellum orange, propodeum black, legs orange, fore coxa and basal half of femur, mid basal half of femur, hind coxa, base and apex of tibia whitish. Frontovertex 0.19× head width; eye height 2.06× malar space (Fig. 10); antennal scape 4.14× as long as wide; pedicel 2.22× as long as wide and longer than F1, funicle 6-segmented, F1–F3 and F5 longer than width, F4 subquadrate, F6 wider than long; clava 3-segmented, 2.26× as long as width, longer than F4–F6 combined (Fig. 11); fore wing 3.33× as long as wide; linea calva not interrupted and open posteriorly (Fig. 13); ovipositor (Fig. 15) 1.36× as long as mid tibia (Fig. 16), distinctly exserted.

**Host.** Dryinidae: *Neodryinus typhlocybae*; Syrphidae: *Paragus* sp., Syrphidae sp.; Flatidae: *Metcalfa pruinose* (Guerrieri and Viggiani 2005).

**Distribution.** China (Tianjin), Armenia, Bulgaria, France, Georgia, Greece, Iran, Italy, Moldova, Netherlands, Portugal, Russia, Spain, Tadzhikistan, Ukraine, Uzbekistan.

Comments. This is the first record from China.

#### Cheiloneurus bouceki Anis & Hayat, 2002 Figs 7-9, 17-22

*Cheiloneurus bouceki* Anis and Hayat 2002: 164–165. Holotype ♀, BMNH, India-Karnataka, not examined.



Figures 10-16. *Cheiloneurus boldyrevi*  $\bigcirc$  10 head 11 antenna 12 mesosoma 13 fore wing 14 hind wing 15 metasoma 16 legs. Scale bars: 100  $\mu$ m.

**Material examined.** CHINA – Guangxi • 26♀; Qinzhou, Beibu Culf University; 21°53′53″N, 108°36′56″E; 24 m elev.; 06−13 Oct. 2019; Wen-Quan Zhen leg.; by Malaise trapping; TJAU-GX-CHE-001 to 026.



Figures 17-22. *Cheiloneurus bouceki*  $\stackrel{\circ}{_{-}}$  17 head 18 antenna 19 mesosoma and metasoma 20 fore wing 21 hind wing 22 legs. Scale bars: 100 µm.

**Description. Female**. Length, excluding ovipositor, 1.78–1.89 mm. Body generally dark brown; gena with metallic-bluish green luster, frontovertex metallic-green luster, mandible with three acute teeth (Figs 5–7). Antenna mostly dark brown, an irregular white longitudinal strip in the middle of the scape. Mesosoma dark brown, mesoscutum, axilla, and scutellum with me-

tallic green luster; mesopleuron and propodeum with metallic blue luster. Leg mostly dark brown, basal 1/3 of mid femora, mid tibia, and all tarsi white; frontovertex  $0.08-0.12 \times$  head width; eye height  $1.17-1.33 \times$  malar space (Fig. 17); antennal scape  $5.05-5.80 \times$  as long as wide; pedicel  $2-2.19 \times$  as long as wide and longer than F1, funicle 6-segmented, F1-F5 longer than width, F6 subquadrate, funicle with linear sensilla on F2-F6; clava 3-segmented,  $2.31-2.43 \times$  as long as wide; linea calva not interrupted and open posteriorly (Fig. 20); ovipositor (Fig. 19)  $1.29 \times$  as long as mid tibia (Fig. 22), distinctly exserted.

Host. Unknown.Distribution. China (Guangxi), India.Comments. This is the first record from China.

*Cheiloneurus chinensis* Shi, Wang, Si & Wang, 1994 Figs 23-25, 32-38

*Cheiloneurus chinensis* Shi et al. 1994: 26. Holotype ♀, HAUZ, China, examined plates.

Material examined. CHINA – Henan • 3♀; Gongyi, Luzhuang; 34°37'1"N, 112°52'18"E; 213 m elev.; 15 Jun. 2016; Guo-Hao Zu, Nai-Zhi Li, Jian-Wei Zu leg.; by yellow pan trapping; TJAU-HN-CHE-001 to 003.

**Diagnosis. Female**. Length, excluding ovipositor, 2.4 mm; Antennal (Fig. 33) scape slightly expanded in middle, yellowish brown, ventral margin brown and with an apical one-third white; pedicel brown; F1–F2 brown, F3–F5 white and lower margin brown, F6 dark; clava dark; apical half of msoscutum darker than basal half (Fig. 34); legs (Fig. 38) yellowish brown, except for fore coxa, basal half of fore femora, basal two-thirds of mid femora, hind coxa and basal of tibia yellowish white.

Description. See Shi et al. (1994).

**Host.** Coccidae: *Ericerus pela, Eulecanium* sp.; Kermesidae: *Kermes quercus* (Xu and Huang 2004).

**Distribution.** China (Beijing, Liaoning, Henan, Hunan, Hainan, Shandong, Tianjin).

#### Cheiloneurus claviger Thomson, 1876

Figs 26-31, 39-51

Cheiloneurus claviger Thomson 1876: 160. Lectotype ♀, LUZN, Sweden, not examined.

*Cheiloneurus japonicus* Ashmead 1904: 156. Holotype ♀, USNM, Japan. Synonymized with *C. claviger* by Japoshvili et al. (2016: 367).

- *Chiloneurus graeffei* Ruschka 1923: 9–10. Holotype ♀, Austria. Synonymized with *C. claviger* by Claridge (1958: 156–161).
- Cheiloneurus claviger Shi 1994: 27–28; Xu and Huang 2003: 104–106, examined plates.



Figures 23–31. 23–25 Cheiloneurus chinensis  $\bigcirc$  23 dorsal habitus 24 lateral habitus 25 ventral habitus 26–31 Cheiloneurus claviger  $\bigcirc$  26 dorsal habitus (Oriental) 27 lateral habitus (Oriental) 28 ventral habitus (Oriental) 29 dorsal habitus (Palaearctic) 30 lateral habitus (Palaearctic) 31 ventral habitus (Palaearctic).

Material examined. CHINA – Liaoning • 1♀; Huludao, Jianchang, Bailong Mountain National Nature Reserve; 40°49'28"N, 119°50'14"E; 716 m elev.; 13 Jul. 2012; Guo-Hao Zu, Ye Chen, Chao Zhang leg.; by yellow pan trapping; TJAU-LN-CHE-001 – Hainan • 1♀; Lingshui Li Autonomous County Diaoluo Mountain; 18°39'35"N, 109°54'57"E; 1499 m elev.; 06 May 2016; Guo-Hao Zu leg.;



**Figures 32–38**. *Cheiloneurus chinensis* <sup>Ω</sup> **32** head **33** antenna **34** mesosoma **35** fore wing **36** hind wing **37** metasoma **38** legs. Scale bars: 100 μm.

by yellow pan trapping; TJAU-HN-CHE-001 – Beijing • 4; Huairou; 40°18'59"N, 116°37'55"E; 58 m elev.; 20–30 May 2012; Guo-Hao Zu leg.; by Malaise trapping; TJAU-BJ-CHE-001 to 004 – Shandong • 1; Qingdao, Cha Mountain National Nature Reserve; 26°52'18"N, 119°51'1"E; 560 m elev.; 13 Jul. 2012;



Figures 39-45. *Cheiloneurus claviger* (Palaearctic)  $\stackrel{\circ}{_{-}}$  39 head 40 antenna 41 mesosoma 42 fore wing 43 hind wing 44 metasoma 45 legs. Scale bars: 100 µm.

Guo-Hao Zu leg.; by sweep netting; TJAU-SD-CHE-001 – Henan • 3 $\bigcirc$ ; Gongyi, Luzhuang; 34°37'1"N, 112°52'18"E; 213 m elev.; 07 Mar. 2016; Guo-Hao Zu, Nai-Zhi Li, Jian-Wei Zu leg.; by yellow pan trapping; TJAU-HN-CHE-004 – Tianjin • 3 $\bigcirc$ ; Zhangjiawo, Tianjin Academic Agriculture Sciences; 39°6'14"N, 117°3'32"E;



Figures 46–51. Cheiloneurus claviger (Oriental)  $\bigcirc$  46 head 47 antenna 48 mesosoma and metasoma 49 fore wing 50 hind wing 51 legs. Scale bars: 100  $\mu$ m.

13 m elev.; 29 Oct.-02 Nov. 2021; Guo-Hao Zu, Peng-Hua Bai leg.; by Malaise trapping; TJAU-TJ-CHE-002 to 004.

**Diagnosis. Female**. Length, excluding ovipositor, 1.75–2.42 mm; Head (Fig. 46) brown, antenna dark brown (Fig. 47), except for F3–F5 almost completely

white; mandible with three acute teeth; fore wing (Fig. 49) with apical two-thirds dark brown, the basal one-third and the hind wing hyaline; F1-F3 longer than width, F4 subquadrate, F5-F6 2.50× as wide as long.

**Description.** See Xu and Huang (2004).

Host. Aphelinidae: Coccophagus aterrimus; Encyrtidae: Blastothrix hungarica, Blastothrix longipennis, Blastothrix scenographica, Blastothrix turanica, Metaphycus insidiosus, Microterys sp., Microterys cuprinus, Microterys intermedius, Microterys praedator, Microterys sylvius; Coccidae: Acanthopulvinaria orientalis, Ceroplastes ceriferus, Ceroplastes japonicus, Chloropulvinaria aurantia, Coccus hesperidum, Didesmococcus unifasciatus, Ericerus pela, Eulecanium ciliatum, Eulecanium corni, Eulecanium giganteum, Eulecanium kunoense, Eulecanium kuwanai, Eulecanium quercifex, Eulecanium rugulosum, Eulecanium tiliae, Filippia folicularis, Filippia viburni, Parthenolecanium corni, Parthenolecanium persicae, Parthenolecanium quercifex, Parthenolecanium rufulum, Physokermes fasciatus, Physokermes hemicryphus, Pulvinaria sp., Pulvinaria aurantia, Pulvinaria betulae, Pulvinaria idesiae, Pulvinaria populi, Pulvinaria vitis, Rhizopulvinaria sp., Rhodococcus spiraeae, Rhodococcus turanicus, Saissetia oleae, Sphaerolecanium prunastri, Stotzia maxima, Takahashia japonica; Eriococcidae: Eriococcus brachypodii, Greenisca brachypodii, Neoacanthococcus tamaricicola; Kermesidae: Kermes miyasakii, Kermes vermilio; Pseudococcidae: Maconellicoccus hirsutus, Nesticoccus sinensis, Nipaecoccus filamentosus, Phenacoccus aceris, Phenacoccus mespili, Planococcus citri (Noyes 2019).

**Distribution.** China (Liaoning, Hebei, Henan, Shaanxi, Zhejiang, Jiangxi, Hunan, Sichuan, Guangxi), Armenia, Austria, Azerbaijan, Bulgaria, Croatia, Czech Republic, Egypt, France, Georgia, Greece, Hungary, Iran, Israel, Italy, Japan, Kazakhstan, Moldova, Montenegro, Netherlands, Norway, Romania, Russia, Serbia, Slovakia, Spain, Sweden, Tadzhikistan, Turkey, Turkmenistan, Ukraine, England, Uzbekistan.

## Cheiloneurus elegans (Dalman, 1820)

Figs 52-57, 61-72

*Encyrtus elegans* Dalman 1820: 151–152. Syntypes, NHRM, Sweden, lost. *Cheiloneurus elegans* (Dalman); Westwood 1833: 343.

*Cheiloneurus elegantissmus* De Santis 1964: 343–345. Holotype ♀, MLP, Argentina, digital image examined, as subspecies of *C. elegans* (Dalman). Synonymized with *C. elegans* by Noyes (2023: 372–374).

**Material examined.** CHINA – Guangxi • 26 $\bigcirc$ ; Qinzhou, Beibu Culf University; 21°53′53″N, 108°36′56″E; 24 m elev.; 09–22 Jun. 2019; Wen-Quan Zhen leg.; by Malaise trapping; TJAU-GX-CHE-027 to 052 – Yunnan • 1 $\bigcirc$ ; Chuxiong Yi Autonomous Prefecture; 25°1′58″N, 101°32′45″E; 1773 m elev.; 15–31 Oct. 2020; Jia-Le Lv leg.; by Malaise trapping; TJAU-YN-CHE-003 – Tianjin • 20 $\bigcirc$ ; Xiqing, Tianjin Agricultural University; 39°5′21″N, 117°5′38″E; 13 m elev.; 14–31 Jul. 2021; Guo-Hao Zu, Ze-Ning Yang leg.; by Malaise trapping; TJAU-TJ-CHE-005 to 024.

**Description. Female**. Length, excluding ovipositor, 1.30–1.89 mm. Head (Figs 61, 67) yellowish brown to brown, mandible with three acute teeth. Antenna (Figs



Figures 52–60. *Cheiloneurus elegans* ♀ 52 dorsal habitus (Palaearctic) 53 lateral habitus (Palaearctic) 54 ventral habitus (Palaearctic) 55 dorsal habitus (Oriental) 56 lateral habitus (Oriental) 57 ventral habitus (Oriental) 58–60 *Cheiloneurus gonatopodis* ♀ 58 dorsal habitus 59 lateral habitus 60 ventral habitus.

62, 68) brown to yellow, apex of clava relatively shallow. Mesosoma (Figs 63, 69) yellowish brown, apical half of mesoscutum brown, scutellum yellowish white; fore wing (Figs 64, 70) with apical two-thirds dark brown, basal third and hind wing hyaline (Figs 65, 71); leg yellow (Figs 66, 72), fore coxa, basal half of mid femora, basal third of mid tibial, hind coxa, and basal third of hind tibia white; frontover-



Figures 61–66. Cheiloneurus elegans (Palaearctic)  $\stackrel{\circ}{_{\sim}}$  61 head 62 antenna 63 mesosoma and metasoma 64 fore wing 65 hind wing 66 legs. Scale bars: 100 µm.

tex  $0.26-0.33 \times$  head width; eye height  $1.67-2.38 \times$  malar space; antennal scape  $4.75-5 \times$  as long as wide; pedicel  $2.09-2.27 \times$  as long as wide and longer than F1, funicle 6-segmented, clava 3-segmented,  $2.72-2.96 \times$  as long as width, longer than F4-F6 combined; fore wing  $2.94-4.09 \times$  as long as wide; linea calva not interrupted and open posteriorly; ovipositor  $1.51-1.63 \times$  as long as mid tibia, slightly exserted.



Figures 67–72. *Cheiloneurus elegans* (Oriental)  $\bigcirc$  67 head 68 antenna 69 mesosoma and metasoma 70 fore wing 71 hind wing 72 legs. Scale bars: 100 µm.

**Variation.** There is significant variation in body color, size of F5–F6, and fore wings between specimens collected in the Palaearctic and in the Oriental realms. The specimens from the Palaearctic have a darker body, F5–F6 are longer than wide (Fig. 33), and the fore wing is  $4.09 \times as$  long as wide, while Ori-

ental specimens have a relatively lighter body color, F5-F6 are wider than long (Fig. 34), and the fore wing is 2.94× as long as wide.

**Host.** Encyrtidae: *Epidinocarsis lopezi*; Platygastridae: *Platygaster zosine*; Cecidomyiidae: *Mayetiola destructor*, *Phytophaga destructor*, Aclerdidae: *Aclerda subterranean*; Coccidae: *Anapulvinaria pistaciae*, *Eulecanium franconicum*, *Physokermes piceae*, *Pulvinaria vitis*, Kermesidae: Kermes sp.; Pseudococcidae: *Antonina purpurea*, *Phenacoccus hordei*, *Phenacoccus manihoti*, *Trionymus aberrans* (Noyes 2019).

**Distribution.** China (Tianjin, Guangxi, Yunnan), America, Argentina, Armenia, Austria, Azerbaijan, Bulgaria, Canada, Croatia, Denmark, England, Finland, France, Georgia, Germany, Hungary, India, Israel, Italy, Kazakhstan, Lithuania, North Macedonia, Mexico, Moldova, Mongolia, Netherlands, Nigeria, Romania, Russia, Saudi Arabia, Serbia, Spain, Sweden, Switzerland, Tadzhikistan, Transcaucasus, Turkey, Turkmenistan, Ukraine, Uzbekistan.

#### Cheiloneurus exitiosus (Perkins, 1906)

- *Echthrogonatopus exitiosus* Perkins, in Perkins et al. 1906: 256. Holotype ♀, BPBM, Australia, not examined.
- *Metapterencyrtus nigricornis* Hayat 1980: 644. Holotype ♀, ZDANU, India. Synonymized with *exitiosus* by Guerrieri and Viggiani (2005: 305–317).
- *Echthrogonatopus nigricornis* (Hayat); Hayat 1981: 20; Xu and He 2003: 527, examined plates.

Cheiloneurus exitiosus (Perkins); Guerrieri and Viggiani 2005: 305.

**Diagnosis.** Body dark brown, antennae dark, mesoscutum and axilla with metallic-green luster, scutellum without a tuft of bristles at apex, leg yellowish white, mid coxa dark basally.

**Description.** See Xu and He (2003).

**Host.** Bethylidae: *Goniozus* sp.; Dryinidae: *Dryinidae unspecified* sp., *Gonatopus* sp., *Haplogonatopus* sp., *Haplogonatopus vitiensis*, *Pseudogonatopus flavifemur*, *Pseudogonatopus hospes*, *Pseudogonatopus perkinsi*; Delphacidae: *Megamelus proserpina*, *Nilaparvata lugens*, *Sogata* sp., *Sogata furcifera*, *Sogatella furcifera*, Pyra-lidae: *Cnaphalocrocis medinalis*, *Marasmia exigua* (Guerrieri and Viggiani 2005).

**Distribution.** China (Fujian, Zhejiang, Jiangxi, Guangxi), American, Australia, Fiji, Guam, India, Malaysia, Philippines.

#### Cheiloneurus gonatopodis Perkins, 1906

Figs 58-60, 73-77

*Cheiloneurus gonatopodis* Perkins, in Perkins et al. 1906: 261. Lectotype ♀ designated by Noyes 1988: 63: Australia, Queensland, Childers (BPBM).

*Cheiloneurus gonatopodis* Perkins; Anis and Hayat 2002: 152; Guerrieri and Viggiani 2005: 310.

**Material examined.** CHINA – Hainan • 1 $\bigcirc$ ; Lingshui Li Autonomous County, Diaoluo Mountain; 18°39'35"N, 109°54'57"E; 1499 m elev.; 15 May 2016; Guo-Hao Zu leg.; by yellow pan trapping; TJAU-HN-CHE-005.



**Figures 73-77.** *Cheiloneurus gonatopodis* <sup>Ω</sup> **73** mesosoma **74** antenna **75** metasoma **76** fore wing **77** legs. Scale bars: 100 μm.

**Description. Female**. Length, excluding ovipositor, 1.16 mm. Head yellow, frontovertex brown. Antenna yellowish brown, scape yellow. Mesosoma yellowish brown, leg yellowish white, basal half of hind tibial white. Metasoma mostly yellow, but basally and apically brown, frontovertex 0.21× head width; eye height 1.62× malar space; antennal (Fig. 74) scape 6.38× as long as wide; pedicel 2.23× as long as wide and longer than F1–F2 combined, funicle 6-segmented, clava 3-segmented, 2.6× as long as width, shorter than F2–F6 combined; fore wing (Fig. 76) 2.96× as long as wide; linea calva not interrupted and

open posteriorly; mid tibial spur (Fig. 77) 0.31× as long as mid tibia and shorter than basitarsus, ovipositor (Fig. 75) as long as mid tibia, not exserted.

**Host.** Dryinidae: Echthrodelphax sp., Pseudogonatopoides mauritianus, Pseudogonatopus sp., Pseudogonatopus mauritianus, Richardsidryinus sp.; Delphacidae: Dicranotropis muiri, Nilaparvata myersi, Perkinsiella saccharicida (Guerrieri and Viggiani 2005).

**Distribution.** China (Hainan), Afrotropical, Australia, India, Madagascar, Mauritius, New Zealand.

Comments. This is the first record from China.

#### Cheiloneurus guangxiensis Zu, sp. nov.

https://zoobank.org/BDEFCF90-E941-4AC9-B6A6-EA4C172B2EA4 Figs 78-83

**Type material.** *Holotype*. ♀, [on slide]; CHINA – Guangxi, Qinzhou, Beibu Gulf University; 21°53′53″N, 108°36′56″E; 24 m elev.; 14–24 Dec. 2019; Wen-Quan Zhen leg.; by Malaise trapping; TJAU-GX-CHE-053. *Paratype*. 1♀; same date as holotype; TJAU-GX-CHE-054.

**Description. Female**. Holotype. Length, 1.51 mm (excluding ovipositor). Head with yellow to yellowish brown and metallic-green luster, basal half of antennal scape brown, apical half white, and dorsal margin brown; pedicel brown; F1 brown with dorsal margin white, F2–F4 lower margin brown and dorsal margin white, F5 lower margin slightly brown and dorsal margin white, F6 white and small part of lower margin brown; clava dark brown. Mesosoma yellow; leg white, nearly transparent, basal third of mid tibia and apical fifth of hind femora brown. Metasoma dark brown, with metallic-blue luster, but slightly yellowish brown in middle and lower part.

Head (Fig. 78) in frontal view, length equal to width, frontovertex 0.14× head width; ocelli forming an angle of 40°, OCL about 1.67× diameter of posterior ocellus, OOL about 0.10× the diameter of posterior ocellus; antennal torulus with its dorsal margin well above lower margin of eye; eye length about 1.77× as long as malar space. Antennal (Fig. 79) scape flattened and expanded, about 2.37× as long as width, pedicel about 2.26× as long as wide, funicle 6-segmented, F1 longer than width, F2–F3 subquadrate, F4–F6 wider than long, clava 3-segmented, 1.98× as long as wide, longer than F3–F6 combined, funicle with linear sensillae on F3–F6. Mandible with three acute teeth. Measurements ( $\mu$ m): HH, 460; HW, 460; FV, 63; OD, 30; POL, 23; OOL,3; OCL, 50; AOL, 43; EL, 270; MS, 153; length (and width): radicle, 45; scape, 225 (95); pedicel, 88 (39); F1, 38 (35); F2, 35 (35); F3, 38 (38); F4, 45 (48); F5, 48 (55); F6, 46 (63); clava, 206 (103).

Mesosoma (Fig. 80). Mesoscutum densely setose; mesoscutum and scutellum with finely reticulate sculpture, mesoscutum 0.60× as long as wide, scutellum 0.90× as long as wide and with a tuft of bristles at apex. Fore wing (Fig. 81) 2.70× as long as wide, apical half of submarginal vein strongly curved, marginal vein longer than width, and 4.91× as long as postmarginal vein, linea calva not interrupted and open posteriorly, hind wing (Fig. 82) 4.32× as long as width. Mid tibial spur (Fig. 83) 0.35× as long as mid tibia and longer than basitarsus. Measurements ( $\mu$ m): FWL, 960; FWW, 355; submarginal vein, 350; MV, 113; PMV, 23; SV, 45; HWL, 800; HWW,185; MT, 450; mid tibial spur, 163; mid basitarsus, 140.



Figures 78-83. *Cheiloneurus guangxiensis* sp. nov.  $\bigcirc$  holotype 78 head 79 antenna 80 mesosoma and metasoma 81 fore wing 82 hind wing 83 legs. Scale bars: 100 µm.

Metasoma (Fig. 80) slightly longer than mesosoma, ovipositor 1.51× as long as mid tibia, distinctly exserted. Measurements (μm): OL, 680. [MT, 450]. **Male.** Unknown. **Host.** Unknown. **Etymology.** The specific name refers to the province where the type locality is located.

**Diagnosis.** The new species is similar to *C. chinensis* Shi, Wang, Si & Wang, 1994 but differs from *C. chinensis* as follows: frontovertex 0.14× head width (0.20× in *chinensis*); scape flattened and expanded, about 2.37× as long as wide (scape 3× as long as wide in *chinensis*); F6 white and small part of the lower margin brown (F6 black in *chinensis*); clava longer than F3–F6 combined (nearly equal length F3–F6 combined in *chinensis*); legs off white nearly transparent, mid tibia basal one-third and hind femora apical one-fifth brown (legs brownish yellow except fore tibia; apical third of mid feroma, outer margin of hind feroma and tibia brown in *chinensis*).

## *Cheiloneurus hadrodorys* Anis & Hayat, 2002 Figs 84–86, 93–98

*Cheiloneurus hadrodorys* Anis and Hayat 2002: 138, 173–175. Holotype ♀, BMNH, Nepal.

**Material examined.** CHINA – Guangxi • 6 $\bigcirc$ ; Qinzhou, Beibu Culf University; 21°53'53"N, 108°36'56"E; 24 m elev.; 11–18 May 2019, 04–13 Jan. 2020; Wen-Quan Zhen leg.; by Malaise trapping; TJAU-GX-CHE-055 to 060 – Yunnan • 1 $\bigcirc$ ; Chuxiong Yi Autonomous Prefecture; 25°1'58"N, 101°32'45"E; 1773 m elev.; 01–15 Jun. 2022; Jia-Le Lv; by Malaise trapping; TJAU-YN-CHE-004.

Description. Female. Length, excluding ovipositor, 1.67–1.89 mm. Body generally brown; gena with metallic-green luster, frontovertex dark brown, mandible with three acute teeth. Antennal radicle brown, scape yellow, and inner margin brown, pedicel and F1-F3 with brown, F4 yellowish white, F5 brown, F6 and clava with dark brown. Pronotum mostly brown, but left and right margin with yellow; mesoscutum dark brown; axilla, scutellum and mesopleuron yellow, propodeum yellow, left and right margin dark brown with metallic-green luster. Leg yellowish white, except apical half of hind femora dark brown. Metasoma mostly brown to dark brown and basal quarter yellow; frontovertex (Fig. 93) 0.24-0.27× head width; eve height 2.13-2.5× malar space; antennal (Fig. 94) scape 5-5.48× as long as wide; pedicel 2.07× as long as wide and longer than F1, funicle 6-segmented, with F1-F6 widening gradually, clava 3-segmented, 2.25–2.25× as long as wide, longer than F4–F6 combined; fore wing (Fig. 96) 3.47-3.71× as long as wide; linea calva closed posteriorly by several lines of setae; mid tibial spur (Fig. 98) 0.36–0.38× as long as mid tibia and longer than basitarsus, ovipositor (Fig. 95) 1.86–2.07× as long as mid tibia, strongly exserted.

**Host.** Pseudococcidae: *Saccharicoccus sacchari* (Anis and Hayat 2002). **Distribution.** China (Yunnan, Guangxi), India, Nepal, Pakistan, Sri Lanka. **Comments.** This is the first record from China.

#### Cheiloneurus lateocaudatus (Xu & He, 2003)

*Echthrogonatopus lateocaudatus* Xu and He 2003: 527. Holotype ♀. ZAUC, China, examined plates.



Figures 84–92. 84–86 *Cheiloneurus hadrodorys* ♀ 84 dorsal habitus 85 lateral habitus 86 ventral habitus 87–89 *Cheiloneurus nankingensis* ♀ 87 dorsal habitus 88 lateral habitus 89 ventral habitus 90–92 *Cheiloneurus quercus* ♀ 90 dorsal habitus 91 lateral habitus 92 ventral habitus.

**Diagnosis.** Body dark, head with dark metallic-blue luster; antennal dark brown dark; scutellum without a tuft of bristles at apex; fore wing hyaline; leg yellowish white but base of mid coxa dark; F1 1.1× as long as wide; F2 and F5 subquadrate; F3–F4 and F6 wider than long; clava slightly shorter than F1–F6 combined.

Description. See Xu and He (2003).

**Host.** Dryinidae: *Haplogonatopus apicalis, Haplogonatopus oratorius* (Xu and He 2003).

**Distribution.** China (Anhui, Fujian, Guangdong, Guangxi, Guizhou, Hubei, Hunan, Jiangsu, Jiangxi, Shanghai, Sichun, Yunnan, Zhejiang).

#### Cheiloneurus nankingensis Li & Xu, 2020

Figs 87-89, 99-106

*Cheiloneurus nankingensis* Li and Xu 2020: 23. Holotype ♀, ZAFU, China; digital image examined.

**Material examined.** CHINA – Guangxi • 6♀; Qinzhou, Beibu Culf University; 21°53′53″N, 108°36′56″E; 24 m elev.; 02–17 Nov. 2019, 01–29 Dec. 2019; Wen-Quan Zhen leg.; by Malaise trapping; TJAU-GX-CHE-061 to 066 – Jiangxi • 6♀, 2♂; Jiujiang, De'an; 29°16′6″N, 115°22′38″E; 64 m elev.; 17–19 Aug. 2020, 06–07 Sep. 2020; Yan-Yan Qiao leg.; ex. *Aenasius arizonensis* on *Phenacoccus solenopsis*; TJAU-JX-CHE-001 to 008 – Jiangsu • 2♂; Nanjing, Nanjing Agricultural University; 32°01′10″N, 118°51′21″E; 18 m elev.; 01–31 Oct. 2019; Zhuo-Miao Li leg.; ex. *Aenasius arizonensis* on *Phenacoccus solenopsis*; TJAU-JS-CHE-001 to 002.

**Diagnosis. Female.** Length, excluding ovipositor, 1.54–1.75 mm; head (Fig. 99) dark brown, with purple sheen; antennal (Fig. 100) scape and pedicel yellowish brown; funicle and clava dark; fore and mid legs yellowish brown, except middle part of mid tibia brown; hind femur and tibia brown, except tibial base white.

**Description.** See Li et al. (2020).

**Host.** Encyrtidae: *Aenasius arizonensis*; Pseudococcidae: *Phenacoccus solenopsis* (Li et al. 2020).

Distribution. China (Jiangsu, Jiangxi, Guangxi).

**Comments.** This species is very similar to *C. compressicommis* (Ashmead, 1894). After comparing with the original description and the text description and figures by Noyes (2023), it was found that *C. nankingensis* is only slightly different from *C. compressicommis* in the color of the male forewing. For this reason, we examined the paratype specimens from Nanjing and the specimens collected from Jiangxi, and reconfirmed the above differences. Therefore, we maintain the same view as Noyes, and the species is still designated as *C. nankingensis* here.

#### Cheiloneurus quercus Mayr, 1876

Figs 90-92, 107-113

Cheiloneurus quercus Mayr 1876: 744, 746, Austria, not examined.
Cheiloneurus tenuicornis Ishii 1928: 147–148. Lectotype ♀, NIES, Japan. Synonymized with C. quercus by Trjapitzin (1989: 305).
Cheiloneurus quercus Japoshvili et al. 2016: 368.



Figures 93–98. *Cheiloneurus hadrodorys*  $\stackrel{\circ}{_{\sim}}$  93 head 94 antenna 95 mesosoma and metasoma 96 fore wing 97 hind wing 98 legs. Scale bars: 100 µm.

**Material examined.** CHINA – Henan  $\cdot 1^{\circ}$ ; Gongyi, Luzhuang;  $34^{\circ}37'1"N$ ,  $112^{\circ}52'18"E$ ; 213 m elev.; 07 May 2016; Guo-Hao Zu, Nai-Zhi Li, Jian-Wei Zu leg.; by yellow pan trapping; TJAU-HN-CHE-006 – Tianjin  $\cdot 1^{\circ}$ ; Jixian, Baxian Mountain National Nature Reserve;  $40^{\circ}11'58"N$ ,  $117^{\circ}33'52"E$ ; 1052 m elev.; 01 Oct. 2023; Ke-Long Jiao leg.; by sweep netting; TJAU-TJ-CHE-025.



Figures 99–104. Cheiloneurus nankingensis  $\bigcirc$  99 head 100 antenna 101 mesosoma and metasoma 102 fore wing 103 hind wing 104 legs. Scale bars: 100 µm.

**Diagnosis. Female**. Length, excluding ovipositor, 1.71–2.0 mm; antennal scape brown, apex white, dorsal margin of pedicel brown, ventral margin of pedicel and all funiculars white, clava dark; mandible with one tooth and a broadly truncate upper tooth; legs pale; all femora apically light brown; basal half of all tibia light brown; metasoma forming a long triangle, slightly shorter and narrower than mesosoma; ovipositor slightly exserted.



Figures 105, 106. Cheiloneurus nankingensis  $\ensuremath{ ? \ \ }$  105 antenna 106 fore wing. Scale bars: 100  $\mu m.$ 

Description. See Ma (2004).

**Host.** Coccidae: *Eulecanium* sp., *Pulvinaria vitis*, Kermesidae: Kermes miyasakii, Kermes nakagawae, Kermes quercus, Kermococcus sp., Kermococcus miyasakii, Kermococcus nakagawae, Pseudococcidae: Coccura ussuriensis, Phenacoccus polyphagus (Noyes 2019).

**Distribution.** China (Liaoning, Tianjin, Henan, Shaanxi, Shandong), Austria, Czech Republic, Hungary, Italy, Japan, Russia, Turkey.

#### Cheiloneurus sinensis Özdikmen, 2011

*Cheiloneurus phenacocci* Shi, in Shi et al. 1994: 25. Holotype ♀, HAUZ, China; not examined.

Cheiloneurus sinensis Ozdikmen 2011: 801.

**Diagnosis. Female**. Antennal scape light brown, basal half of pedicel dark and apical half white; funicle white; clava white; mesosoma brown; axilla yellowish brown, mid tibial spur as long as basitarsus.

Description. See Shi et al. (1994).

Host. Pseudococcidae: Phenacoccus flaxinus (Shi et al. 1994).

Distribution. China (Henan, Shaanxi).



Figures 107–113. Cheiloneurus quercus  $\hfill 2$  107 head 108 antenna 109 mesosoma 110 fore wing 111 hind wing 112 metasoma 113 legs. Scale bars: 100  $\mu m.$ 

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## Additional information

## **Conflict of interest**

The authors have declared that no competing interests exist.

## **Ethical statement**

No ethical statement was reported.

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## **Author contributions**

Investigation: XC, WL. Software: CX. Writing – original draft: HW, WC. Writing – review and editing: GZ.

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## **Data availability**

All of the data that support the findings of this study are available in the main text.

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**Research Article** 

# Clavigeritae (Coleoptera, Staphylinidae, Pselaphinae) of the Arabian Peninsula with the description of a new species of *Corynotopsis* Jeannel, 1951 from Oman

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#### Abstract

*Corynotopsis omanicus* **sp. nov.** of the myrmecophilous supertribe Clavigeritae is described from Oman. The type series was collected at night and the ant host species remains unknown. *Corynotopsis scotti* Jeannel, 1951 is newly recorded for Yemen, and *Commatocerus concinnus* Besuchet & Cuccodoro, 2011 for Oman. *Lasius* Fabricius, 1804 and *Lepisiota* Santschi, 1926 are, for the first time, determined as hosts of the latter species. The problematic taxonomic status of *Corynotopsis scotti* is discussed. A distribution map of all Clavigeritae known from the Arabian Peninsula is provided.

Key words: Articerodes, Commatocerus, new country records, rove beetles, taxonomy



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## Introduction

The obligate myrmecophilous supertribe Clavigeritae is very poorly represented on the Arabian Peninsula. To date only three genera with three species have been recorded from this vast area. *Articerodes syriacus* Saulcy, 1865 is a widespread species, known from Greece, Iran, Iraq, Israel, Lebanon, Tadzhikistan, Turkey, Uzbekistan, Yemen (Socotra I.) and Ethiopia (Schülke and Smetana 2015). *Commatocerus concinnus* Besuchet & Cuccodoro, 2011 was described from Ras Al Khaimah (United Arab Emirates), and *Corynotopsis scotti* Jeannel, 1951 originally described from Ethiopia, and later recorded from Saudi Arabia (Besuchet 1999), is here recorded from Yemen.

The aim of this paper is to provide a synopsis of Clavigeritae of the Arabian Peninsula with the description of a new species, *Corynotopsis omanicus* sp. nov., as well as to provide new records and the host ant association for *Commatocerus concinnus*.

## Material and methods

Specimens prepared for the morphological study were examined with a Leica S8APO stereoscopic microscope with diffuse lighting at magnifications up to 128×. Habitus images were taken with a Canon EOS 6D in combination with

a Canon MP-E65  $1-5\times$  macro lens; final images were composed from partial photographs using Helicon Focus 7.0. and post-processed in Adobe Photoshop 2020.

The aedeagi were studied using a Zeiss transmitted-light microscope at magnifications up to ×500. They were dissected and preserved in Euparal on plastic label pinned together with the specimen. All drawings were made using a drawing tube.

The head length was measured from the occipital constriction to the anterior margin of the frontal rostrum; head width was measured across the eyes; elytral length was measured along the suture; width means maximum width of pronotum, elytra, etc. The body length is a combined length of the head, pronotum, elytra, and abdomen. The length of basal and apical parts of the median lobe were measured in dorsal view.

The terminology applied here follows Chandler (2001), except we use 'ventrite' instead of 'sternite' when discussing ventral thoracic structures. Paired structures are treated as singular. The description is for males; the differences for females are treated in the sexual dimorphism section.

Label data are cited verbatim, with slashes (/) separating lines of text. The comments of the authors are in square brackets. All labels of the studied material are printed. All type specimens were provided with the following red printed label: HOLOTYPE or PARATYPE, *Corynotopsis omanicus* sp. nov., P. Hlaváč det., 2023.

Specimens studied herein are deposited at the following institutes and collections:

- MHNG Muséum d'histoire naturelle, Geneva, Switzerland
- MMBC Moravian Museum, Brno, Czech Republic
- **NMPC** National Museum (Natural History), Prague, Czech Republic
- **PCJP** private collection of Jan Pelikán, Hradec Králové, Czech Republic.
- **PCJV** private collection of Jaroslav Větrovec, Hradec Králové, Czech Republic.
- **PCPH** private collection of Peter Hlaváč, Prague, Czech Republic.
- **PCTK** private collection of Tomáš Kopecký, Hradec Králové, Czech Republic.

## Taxonomy

#### Corynotopsis omanicus sp. nov.

https://zoobank.org/661F1795-811C-4B6B-8535-1E33032B6D12 Figs 1A, 2A, B

**Type material.** *Holotype*, 3: **OMAN**: one label "OMAN, DHOFAR PR. / 18 km NW of Sadah / near Lagga Shalyon / 422 m / 17°11'10.046"N, 54°56'34.295"E / Větrovec J. leg. 20.9.2022" [white, printed] (NMPC). *Paratypes* (8 33, 2 9 9): 2 33: same data as for holotype. (PCJV, PCPH). 1 3: one label "OMAN – DHOFAR PR. / E of Aytin, Wadi Hinnah / wadi - Baobab Forest 300 m / 17°3'12.964"N, 54°36'32.143"E / Větrovec J. leg. 21.9.2022" [white, printed] (PCJV). 1 9: one label "Oman, 21.9.2022, Dhofar / Govern. E of Aytin, Wadi / Hinnah, wadi - Baobab Forest / 17.0536011°N, 54.6089286°E, / Lgt. T. Kopecký, 300 m" [white, printed] (PCTK). 5 33, 1 9: two labels "S Oman, Dhofar Gov. / Sadah,

18 km NW / 20.9.2022 / lgt. Jan Pelikan" [white, printed], "near Lagga Shalyon / 17°11'10.046"N, 54°56'34.295"E wadi / at UV light" [white, printed] (PCJP, PCPH, NMPC, MMBC).

**Diagnosis.** Head lacking frontal and vertexal foveae; clypeus massive, well-visible on sides as well as in front of rostrum; eyes prominent; disc of venter part of head smooth, sides with rugose surface, posterior tentorial pits separated; antennae hexamerous; antennomere 3 and 4 subequal; terminal antennomere longest, cylindrical, about five times as long as 5 and three times as long as wide; pronotum lacking antebasal median foveae, with weakly-defined lateral fovea; lacking sulci; elytra lacking basal foveae, with short discal and sutural striae; lateral posterior margin with weak, short trichome; abdomen with basal basin of composite tergite transverse, almost entire but with two small protrusions forming two, small lateral lodges; first visible sternite (III) about half as long as second (IV), sternites (IV–VII) with median impression; legs stout; mesofemur with basal bifurcate thorn; mesotibia with predistal spine; aedeagus about 2.20 times as long as wide; dorsal circular diaphragm well-defined.

**Description.** Body (Fig. 1A) length 2.20–2.30 mm, maximum width of elytra about 0.80–0.85 mm; reddish-brown, elytra slightly lighter, head and pronotum with rugose structure, elytra shiny with sparse short setae, abdomen shiny, glabrous.

Head elongate, about 1.20–1.25 times as long as wide; lacking frontal and vertexal foveae; frontal lateral margins parallel, rostrum narrow, expanded anteriad; clypeus massive, well-visible on sides as well as in front of rostrum; eyes prominent; temples slightly longer than length of eyes and slightly convergent posteriad. Disc of venter part of head smooth, sides with rugose surface, with separated posterior tentorial pits; well-separated gular plate shagreened.

Antenna hexamerous, about 0.5 mm long, slightly longer than head; scape minuscule, completely hidden in antennal cavity; antennomere 2 larger than scape and antennomere 3, slightly expanded distad, partly hidden in antennal cavity; antennomere 3 and 4 subequal, about as long as 2; 5 about as long as wide, 1.5 times as long as 4, strongly expanded distad; terminal antennomere longest, cylindrical, about five times as long as 5 and about three times as long as wide.

Pronotum 1.08–1.13 times as wide as long, about as long as head, widest before midlength, strongly convergent anteriad, slightly convergent posteriad; posterior margin triangular; lacking antebasal median foveae, with weakly-defined lateral fovea; lacking sulci.

Elytra 1.40–1.45 times as wide as long, 1.50–1.60 times as long as pronotum; lacking basal foveae, with short discal and sutural striae, almost reaching anterior third of elytral length; lateral posterior margin with weak, short trichome, sutural posterior margin with one long setae.

Mesoventrite shorter than metaventrite; mesocoxae narrowly separated by confluent posterior mesoventral and anterior metaventral process, isthmus about 0.25 diameter of mesocoxa, mesoventrite with median carina; metaventral disc with short setae, lacking trichome-like macrosetae, elevated, with medium, short, acute spine, in posterior third with large impression; posterior metaventral process wide, with slightly concave margin.



Figure 1. Dorsal habitus A Corynotopsis omanicus sp. nov., holotype male B Corynotopsis scotti, male C Corynotopsis sp., female. Scale bars: 1.0 mm.



Figure 2. Aedeagus of Corynotopsis omanicus sp. nov., holotype male A dorsal view B lateral view. Scale bar: 0.2 mm.

Abdomen long, 1.50–1.60 times as long as and 1.08–1.12 times as wide as elytra; basal basin of composite tergite transverse, almost entire but with two small protrusions forming two, small lateral lodges, basal basin long, in middle its posterior margin reaching half of length of composite tergite length; with lateral trichome born at foot of edge of paratergite I and directed mesad; with three, almost confluent paratergites, paratergite I and II with weakly-defined trichome on upper edge. First visible sternite (III) about half as long as second (IV), third and fourth (V–VI) about as long as first (III), fifth (VII) longer than fourth VI, sternites (IV–VII) with median impression.

Legs stout, all tibiae distally expanded; all femora and tibiae with interlocking ridges; mesofemur with basal thorn; mesotibia with predistal spine.

Aedeagus (Fig. 2A, B) about 0.53 mm long, about 2.20 times as long as wide, basal capsule about 1.25 times as long as apical lobe; maximum width in distal third; apex of aedeagus sharply pointed, with pair of long setae; dorsal circular diaphragm well-defined.

Sexual dimorphism. Females with all legs simple, lacking thorn or spines.

**Natural history.** All specimens were collected at a UV light placed in a semidry habitat on the edge of a sandy wadi with *Acacia*, and in an open area with a small stream in the Baobab Forest (Fig. 5A, B); one specimen was beaten from branches of bushes at night. The host ant is unknown.

**Etymology.** Locotypic, referring to the country of its type locality, Oman. **Distribution.** Oman (Dhofar Province).

**Remarks.** *Corynotopsis omanicus* sp. nov. is very similar in external morphology to its congener *C. scotti* from which it can be distinguished only by: the different proportion of antennomeres 3 and 4; antennomere 3 and 4 subequal in length (antennomere 3 about 1.3 times longer than 4 in C. scotti); and by the different structure of the aedeagus with the distal projection of the median lobe triangular and wide at the base in ventral view, evenly narrowing to the apex (highly variable but much narrower at base and converging somewhat unevenly to apex in *C. scotti*).

#### Corynotopsis scotti Jeannel, 1951

Figs 1B, 3A, B, 4A-C

Corynotopsis scotti Jeannel, 1951: 229, fig. 2 (habitus). Type locality: Ethiopia, Province of Harrar, Dire Dawa [Diré-Daoua], 9°36'3.15"N, 41°51'0.51"E, 2300 m. Corynotopsis scotti Jeannel: Jeannel 1959: 695 (in key), 704 (distribution), fig. 257 (habitus); Coulon 1982: 67 (redescription), figs 5–6 (aedeagus).

Material examined. 1 ♂, YEMEN: two labels "S Yemen, 27–28.III.2007 / 20 km W Lawdar / 13°53'N 45°48'E / ca 1100 m, David Král Igt." [white, printed], "*CO-RYNOTOPSIS / scotti* JEANNEL / P. Hlaváč det., 2023" [white, printed] (NMPC). 2 ♂, 1 ♀: one label "YEMEN, 1101 m, 20 km / W Lawdar, 26–27.III.2007 / N13°53' E45°48' / P. Kabátek Igt." [white, printed] (MHNG, PCPH). 1 ♂: one label "YEMEN: Al Lahima / (6105) in Malaise trap / 24.VII-17.IX.2001 / leg. A. van Harten" [white, printed] (MHNG). 1 ♂: one label "W YEMEN, Wadi Surdud / (Sari') W San'a; N15°15' / E43°30', 627 m, 2.XI.2005 / leg. P. Kabátek Igt." [white, printed] (MHNG). 1 ♀: one label "YEMEN: 12 km NW of / (5986) Manakátekhah / in Malaise trap / 03.VII-21.VIII.2001 / leg. A. van Harten" [white, printed] (MHNG);

**Remarks.** *Corynotopsis scotti* was described by Jeannel (1951) based on a single male from Ethiopia (Prov. de Harrar: Diré-Daoua [Dire Dawa], 2300 m). Later, the holotype was studied, the species was redescribed and the illustration of the aedeagus was provided by Coulon (1982). Besuchet (1999) provided a record of one female from Saudi Arabia. The species is also mentioned from Yemen in the last edition of the Palaearctic Coleoptera (Schülke and Smetana 2015), but the source of this record is unknown to us. New record for Yemen.

Species of the genus *Corynotopsis* are very similar concerning the external morphology. The only external difference between *C. scotti* and *C. omanicus* is a slightly different proportion of antennomeres 3 and 4 (see remarks for *C. omanicus*). All specimens from Yemen, assigned here to *C. scotti*, have quite different shapes of the distal part of the medial lobe of the aedeagus in ventral view (Figs 3A, 4A–C). The main differences are in the length and shape of the distal projection of the median lobe and its size relative to the pair of distal setae. To solve the question of whether this is just intraspecific variability or a complex of more closely related species, more material will be needed.

Host ant. Unknown.

Distribution. Ethiopia, Saudi Arabia, Yemen.

#### Corynotopsis sp.

Fig. 1C

**Material studied.** 1 ♀: **YEMEN**: one label "YEMEN, 1101 m, 20 km / W Lawdar, 26-27.III.2007 / N13°53' E45°48' / Р. Kabátek Igt." [white, printed] (MHNG).

**Remarks.** This single female certainly represents a new, undescribed species. It is readily separated from all other females of *Corynotopsis* by: 1) the larger body, length 2.43 mm, maximal width 0.94 mm; 2) the pronotum slightly longer than wide; 3) the pair of paratergal trichomes, fine, formed by one to two macrosetae; and mainly; and 4) by having the sharp, pointed projection on the



Figure 3. Aedeagus of Corynotopsis scotti A dorsal view B lateral view. Scale bar: 0.2 mm.

end of the abdomen. Due to the absence of a male and taking into account the complicated taxonomic situation in *C. scotti* (see Remarks for that species), we decided not to formally describe this species.

#### Articerodes syriacus Saulcy, 1865

- Articerus syriacus Saulcy, 1865: 25. Type locality: Saïda [Sidón], en Syrie; types: HT, probably ♂.
- Articerus ponticus Sharp, 1878: 62. Type locality: Mésopotamie; types: unknown, synonymy in Raffray 1890: 167.
- *Commatocerus bucharicus* Reitter, 1900: 50. Type locality: Transcaspien, Buchara, Karatak; types: more ST, synonymy in Winkler 1925: 470.
- *Commatocerus* sbg. *Articerus subnitidus* Pic, 1903: 145. Type locality: Crete; types: more ST, synonymy in Besuchet 1999: 63 (as *C. subnitidius* [sic]).

Articerus spriacus Saulcy: King 1869: 57. [error]

**Host ant.** *Lasius* (*Lasius*) *niger* (Linnaeus, 1758); *Lepisiota capensis* Mayr, 1862; *L. canescens* Emery, 1897 and *L. spinisquama* (Kuznetsov-Ugamsky, 1929).

**Distribution.** Greece (Crete), Turkey, Lebanon, Syria, Israel, Iraq, Iran, Yemen (Socotra I..), Ethiopia, Tajikistan, Uzbekistan.

**Remarks.** The genus *Articerodes* Raffray 1890, comprising 11 species, is distributed in a large area from the Republic of South Africa, through the Democratic Republic of Congo, Ethiopia, Middle East, Central Asia, southern India,



Figure 4. Variability of aedeagus of Corynotopsis scotti, dorsal view. Scale bar: 0.2 mm.

Indochina, and north to Japan. Such a large distribution is relatively unusual for genera of Clavigeritae and it is possible that not all species will remain in the genus. The type species of the genus, *Articerodes syriacus* Saulcy, 1865, is also unusually widespread. We tried to find all localities from where the species was recorded and they are listed here. The only locality listed in the last edition of the Palaearctic catalogue (Schülke and Smetana 2015) which remains unknown to us is Iran.

**Literature records. ETHIOPIA**, Mekallé in Enderta and Harrar; **GREECE**, Crete (type locality of *C. subnitidus*); **IRAQ**, as Mesopotamia, but more precise information on the locality is unknown (type locality of *C. ponticus*); **ISRAEL**, St.-Jeand'Acre [Akko]; **LEBANON**, Sidón (type locality *C. syriacus*); **UZBEKISTAN**, Buchara, Karakat (type locality of *C. bucharicus*); **YEMEN**, island Socotra, Al Haghier Mts., wadi Madar, 1180–1230 m 12°33.2'N, 54°00.4'E.

**New records. TURKEY**, 1 ♀: one label "N36°50' E028°42' / T Umg. Mugla / Köycegiz; Auenwald / 29.4.2001 / Meybohm/Brachat" (PCPH). 1 ♂: one label "Türkei / Südküste / zw. Antalya u. Alanya / 22.5–3.6.1983 / leg. V u. C. Brachat" (PCPH). **TADJIKISTAN**, 1 ex, one label "Mts. Karategthin [Rasht Valley], Baldshuan, 924 m" (PCPH).

#### Commatocerus concinnus Besuchet & Cuccodoro, 2011

*Commatocerus concinnus* Besuchet & Cuccodoro, 2011: 165, plate 14 (habitus), figs 22–24 (aedeagus); type locality: United Arab Emirates, Ras al Khaimah, Wadi Shawkah, 25°6'15.30"N, 56°2'47.55"E.


Figure 5. Type locality of Corynotopsis omanicus sp. nov.

**Material examined.** 1  $\Diamond$ , 1  $\bigcirc$ , **OMAN**: two labels "Oman, 28–29.3.2019, Ad / Dakhilyiah Gov., near Subayb / 23°14'7.966"N, 57°8'57.977966"E, / wadi, 1442 m, Lgt. T. Kopecký" [white, printed], "*COMMATOCERUS* / *concinnus* BES & Cucc. / P. Hlaváč det., 2023" [white, printed] (PCTK, PCPH). New record for Oman.

**Natural history.** The two specimens were collected from two different ant nests under stones. One with an unknown species of *Lasius* Fabricius, 1804 and the other with *Lepisiota* (cf.) *spinisquama* (Kuznetsov-Ugamsky, 1929), M. Sharaf det., 2023, collected in the evening on an open, dry area in the mountains (Fig. 6A).

**Remarks.** Commatocerus concinnus was described based on one male from United Arab Emirates, Ras al Khaimah, Wadi Shawkah, 25°6'15.30"N, 56°2'47.55"E, collected by a water-trap. The species is readily separated from its congeners by having the terminal antennomeres cylindrical, instead of distally expanded.



**Figure 6. A** Oman, Ad Dakhilyiah Gov., near Subayb wadi, locality with the occurrence of *Commatocerus concinnus* **B** distribution map of all Clavigeritae species known from the Arabian Peninsula.

The generic name *Commatocerus* has been subjected to much instability. It was established by Raffray (1882: 1) for *Commatocerus elegantulus* Raffray. In the same year, Reitter (1882) synonymized it with the genus *Fustiger* LeConte, 1866 under the name *Comatocerus* [sic] (Reitter 1882: 200). Jeannel (1949:

37) redescribed the genus and resurrected its generic status. He also pointed out that the American and Old World species of the genus *Fustiger* cannot be congeneric and should be placed in separate genera. Later, Jeannel (1954: 152) discussed the status of similar genera *Commatocerus*, *Fustigerinus* Wasmann, 1912 and its actual synonym *Neocommatocerus* Jeannel, 1949. Célis (1975: 441) confirmed the generic status of *Commatocerus*. Besuchet (1977: 261) again synonymized it with *Fustiger* and provided a key to species of India. When describing *Commatocerus concinnus* (Besuchet and Cuccodoro 2011: 164), the authors discussed and supported the validity of the genus and they apparently overlooked the synonymy of Besuchet from 1977.

**Species included.** *Commatocerus concinnus* Besuchet & Cuccodoro, 2011, *C. elegantulus* Raffray, 1882, *C. leleupi* Jeannel, 1953 and *C. turkmenicus* Kryzhanovski, 1957.

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# **Additional information**

#### **Conflict of interest**

The authors have declared that no competing interests exist.

# **Ethical statement**

No ethical statement was reported.

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# **Author contributions**

All authors have contributed equally.

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# Data availability

All of the data that support the findings of this study are available in the main text.

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**Research Article** 

# A new chemosymbiotic bivalve species of the genus *Acharax* Dall, 1908 (Bivalvia, Solemyida, Solemyidae) from the Haima cold seep of the South China Sea

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#### Abstract

Solemyidae is an ancient group of protobranch bivalves that typically inhabit unusual environments, such as deep-sea chemosynthetic environments, and are symbiotic with chemoautotrophic and gill-hosted bacteria. In May 2018, a living solemyid bivalve was collected using a remotely operated vehicle at a depth of 1,390 m from the Haima cold seep in the northwestern slope of the South China Sea. Through a comprehensive taxonomic approach combining morphological observations and molecular phylogeny reconstruction of concatenated mitochondrial COI,16S rRNA and 18S rRNA gene sequences, a new species, *Acharax haimaensis* **sp. nov.** is identified and described. The discovery of this new species contributes to the diversity of known solemyids in deepsea chemosynthetic environments.

Key words: Acharax haimaensis sp. nov., Bathyal, deep-sea, taxonomy

#### Introduction

Solemyidae is a group of ancestral protobranch bivalves (Pojeta 1988) with a worldwide marine distribution across various depths ranging from 0 to 6,000 m (Conway et al. 1992; Fujiwara et al. 2003). This family consists of over 30 valid living species that are classified into two reciprocally monophyletic genera: *Acharax* Dall, 1908 and *Solemya s.l.* Gray 1840. These genera are distinguished by their unique thickened frill of radially pleated periostracum, which extends beyond the calcified shell margins. The main difference between these genera lies in the position of the ligament; it is external in *Acharax* and internal in *Solemya s.l.* (Taylor et al. 2008; Kamenev 2009; Oliver et al. 2011; Sharma et al. 2013). Solemyid bivalves predominantly inhabit chemosynthesis-based ecosystems (Conway et al. 1992; Walton 2015; Bailey 2021) and rely on intracellular chemosynthetic symbionts for nutrition (Fisher and Childress 1986; Rodrigues et al. 2010; Fukasawa et al. 2017).



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The classification of Solemyidae based on external features is problematic (Kamenev 2009; Oliver et al. 2011; Bailey 2021) due to the lack of distinguishing characteristics such as shell sculpture and hinge teeth. These bivalves are uniformly covered by a distinctive, thick, shiny periostracum (Taylor et al. 2008). Furthermore, there has been limited research on the morphology and molecular aspects of solemyid bivalves. As a result, the taxonomy and systematic status of Solemyidae have remained problematic. Recently, Sato et al. (2013) described and depicted the shell microstructures of five solemyid species from Japan by scanning electron microscopy.

In this study, we diagnose and describe a new *Acharax* species from the Haima cold seep, China. Additionally, we conducted an analysis of interspecific genetic distances within the family Solemyidae based on the mitochondrial cytochrome c oxidase subunit I (COI) gene. Furthermore, we examined the phylogenetic relationships within the order Solemyida using COI,16S rRNA and 18S rRNAgene sequences.

# Materials and methods

The specimen was collected from the Haima cold seep in the northwestern slope of the South China Sea at a depth of 1,390 m using a remotely operated vehicle (ROV) in 2018 (Fig. 1). On board, the specimen was photographed with a Canon EOS-1D digital single lens reflex camera. Then, the specimen was fixed in 95% ethanol and deposited in the Marine Biological Museum of the Chinese Academy of Sciences (**MBMCAS**) in the Institute of Oceanology, Chinese Academy of Sciences, Qingdao. Measurements were taken point-to-point with digital calipers, recorded to the nearest 0.1 mm.

Total genomic DNA was extracted from the muscle tissues using TIANamp Marine Animals DNA Kit (TIANGEN, China) following the manufacturer's instructions. Then the genomic DNA was used for Illumina sequencing and Oxford Nanopore sequencing (Shanghai BIOZERON Co. Ltd). After assembly and annotation, we successfully obtained the complete mitochondrial genome of the new Acharax specimen (GenBank accession number: ON023263).



Figure 1. Sampling site of Acharax haimaensis sp. nov.

The Kimura's 2-parameter (K2P) genetic distances between COI sequences of solemyid species were estimated by MEGA 6.06 (Tamura et al. 2013). The phylogenetic relationships within Solemyida were conducted using COI, 16S rRNA and 18S rRNA gene sequences from 17 in-group species (Suppl. material 1). The nucleotide sequences of each gene were aligned in batches using MAFFT (Katoh et al. 2019), and ambiguously aligned regions were deleted using Gblocks 0.91b (Gblocks parameters: minimum length of a block = 5; allowed gap positions = with half) (Talavera and Castresana 2007). Subsequently, the sequences were concatenated into a single alignment used to generate nexus files in PhyloSuite 1.2.2 (Zhang et al. 2020). A maximum-likelihood analysis was performed with the GTR+I+G substitution model in IQ-TREE (Nguyen et al. 2015), and branch support was evaluated with ultrafast bootstrap (UFB) with 1,000 replicates. The phylogenetic tree and node labels were graphically edited with iTOL (Letunic and Bork 2007).

#### Results

#### **Systematics**

Order Solemyoida Dall, 1889 Superfamily Solemyoidea Gray, 1840 Family Solemyidae Gray, 1840

Genus Acharax Dall, 1908

Type species. Solemya johnsoni Dall, 1891; Recent, North Pacific.

#### Acharax haimaensis sp. nov.

https://zoobank.org/2356CE0D-13A0-4AA7-A322-D5ACD518F028 Fig. 2

**Material examined.** *Holotype*: Complete, Haima cold seep cruise, HOV *Shen Hai Yong Shi* 71, 1390 m, coll. crew of R/V *Tan Suo Yi Hao*, 17 May 2018, MBM287872.

**Description.** *Shell:* the shell is elongate, rectangular, equivalve, and robust. Shell length 103.32 mm, width 48.68 mm, height 45.20 mm. The length/width ratio and length/height ratio are 2.12 and 2.29, respectively. The beak is positioned at approximately the posterior quarter of the shell. The anterior margin is broadly rounded and compressed medially, while the posterior margin is tightly rounded. The ventral margin is straight and shallowly concave towards the posterior. The periostracum extends well beyond the calcified shell margin, folding inwards, and reddish brown but gradually paler towards the prodissoconch. The shell has radial ridges with strong, flattened summits. The ridges are more crowded anteriorly and posteriorly, and vary in both width and colour. There are four closely spaced ridges over the posterior area, and the median area is almost smooth, with two or three low ribs. The anterior region with eight or nine deeply cut ribs. Hinge teeth are absent, and the ligament is mainly external. The posterior siphon aperture is lined by two rings of papillae. The foot is



Figure 2. Holotype of Acharax haimaensis sp. nov.

large, with a broadly oval sole, and its margin interdigitates between large and small blunt papillae.

Adductor muscle scar and pallial scars: the anterior adductor-muscle scar has a D-shaped, irregularly and posteriorly oriented straight face. There is a loop of muscle scar that extends from the hinge plane, reaching halfway along the valve and connecting ventrally to adductor scar. The posterior adductor scar is ovoid, with irregular contours, and exhibits faint radial sculpture. It is separated by a line that extends from the scar to the beak along a subtle depression. The foot is flattened at anterior end when open. The flattened face is longitudinally bifurcated, displaying horizontal lamellae, and is fringed with approximately 32 short, adzeshaped ridges. These ridges interlock when the foot is closed, and each ridge is topped with a small, rounded papilla. The mantle is fused along the ventral margin and covers large gills that extend about three-fifths of the total length of the body.

**Etymology.** Named after the type locality, the Haima cold seep in the northwestern slope of the South China Sea.

**Distribution.** Currently, *Acharax haimaensis* sp. nov. is known only from the type locality, in the northwestern slope of the South China Sea, at a depth of 1,390 m.

**Remarks.** The genus *Acharax* has a worldwide distribution in cold seep habitats with sulfide present (Sibuet and Olu 1998) at depths ranging from approximately 400 m to 6,000 m (Neulinger et al. 2006). *Acharax* has approximately nine extant species (WoRMs 2024) and more than 20 fossil seep species (Amano and Ando 2011; Saether et al. 2016; Isaji and Kato 2017; Hansen et al. 2020). *Acharax clarificata* Dell, 1995 closely resembles to our specimen, but the new species differs from *A. clarificata* in the shape of the shell. Our specimen has an elongate, nearly rectangular shell with parallel dorsal and ventral margins, whereas *A. clarificata* has a shallowly concave ventral margin and is particularly more deeply concave towards the posterior end. The genus *Acharax* exhibits distinct morphological differences from *Solemya*, including a prominent large external ligament located on a narrow nymph and larger size (Walton 2015). However, due to the striking similarities in gross morphology with *Solemya*, there is a possibility that *Acharax* species have been misclassified as *Solemya* in the past (Sibuet and Olu 1998). Even within the genus *Acharax*, certain species share morphological similarities, but molecular data suggests the presence of cryptic speciation (Neulinger et al. 2006). Therefore, gene-sequence analysis can provide valuable information for the classification of solemyid bivalves.

**Molecular support.** The genetic divergence between *Acharax haimaensis* sp. nov. and the solemyid species analyzed ranged from 21.4% (*A. johnsoni*) to 28.2% (*Solemya pusilla*) (Table 1). It is evident that the lowest genetic distance was observed between the two *Acharax* species. The phylogenetic tree of the family Solemyidae, reconstructed using maximum likelihood based on mitochondrial COI,16S rRNA and 18S rRNA sequence data, is shown in Fig. 3. Both *Acharax* and *Solemya* formed monophyletic clades with strong support values (≥95%).

The placement of the new species, *Acharax haimaensis* sp. nov., within the genus *Acharax* is supported by both the morphological and molecular phylogenetic analyses. Its discovery at the Haima cold seep contributes to the known diversity of solemyids in chemosynthesis-based ecosystems. The Protobranchia represent an intriguing group of Bivalvia in terms of their early evolution, unique anatomy, larval development, and ecological diversification. However, there are still controversies surrounding the origin and evolutionary process of Protobranchia, particularly the phylogenetic relationships among higher taxa. Currently, research into the morphological taxonomy and molecular systematics of the Protobranchia is relatively limited. More comprehensive taxon collections in the future will be necessary to lead us closer to the goal of reconstructing the evolutionary history of protobranch bivalves.





Species	1	2	3	4	5	6	7	8	9
Acharax haimaensis	-								
Acharax johnsoni	21.4	_							
Solemya elarraichensis	27.8	28.0	-						
Solemya flava	25.8	29.5	18.4	-					
Solemya pervernicosa	23.4	22.6	26.4	24.5	_				
Solemya pusilla	28.2	25.0	17.3	20.4	27.7	-			
Solemya tagiri	25.1	22.7	19.8	19.6	25.1	18.8	_		
Solemya velesiana	25.6	24.0	17.7	19.6	24.6	12.2	15.2	_	
Solemya velum	27.5	29.6	16.4	17.8	29.1	18.7	16.5	15.6	-

**Table 1.** Kimura's 2-parameter pair-wise genetic distances (in percentage) between species of Solemyidae using COI gene sequences.

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# **Additional information**

#### **Conflict of interest**

The authors have declared that no competing interests exist.

#### **Ethical statement**

No ethical statement was reported.

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#### **Author contributions**

Mei Yang, Baoquan Li, Zhibin Gan, Dong Dong and Xinzheng Li designed the study. Xinzheng Li collected the specimen. Mei Yang, Baoquan Li and Xinzheng Li examined the specimens, performed morphological comparisons, and conducted the molecular analysis. Zhibin Gan and Dong Dong was involved in contributions to the conception of the work and took the photos of the specimen. All authors prepared the manuscript, read, and approved the final version.

#### **Data availability**

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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# **Supplementary material 1**

#### The mitochondrial gene sequences used in this study

Authors: Mei Yang, Baoquan Li, Zhibin Gan, Dong Dong, Xinzheng Li Data type: docx

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Research Article

# A review of Nearctic *Lathrobium* (Coleoptera, Staphylinidae), with revision and descriptions of new flightless species from the mountains of the southeastern U.S.

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#### Abstract

Species of the genus Lathrobium Gravenhorst (Coleoptera: Staphylinidae: Paederinae) from North America north of Mexico are reviewed and 41 species are recognized. Morphology and mitochondrial COI sequence data were used to guide species designations in three flightless lineages endemic to the southern Appalachian Mountains, a biologically diverse region known for cryptic diversity. Using a combination of phylogeny, algorithm-based species delimitation analyses, and genitalic morphology, five new cryptic species are described and possible biogeographic scenarios for their speciation hypothesized: L. balsamense Haberski & Caterino, sp. nov., L. camplyacra Haberski & Caterino, sp. nov., L. islae Haberski & Caterino, sp. nov., L. lividum Haberski & Caterino, sp. nov., L. smokiense Haberski & Caterino, sp. nov. Five additional species are described: L. absconditum Haberski & Caterino, sp. nov., L. hardeni Haberski & Caterino, sp. nov., L. lapidum Haberski & Caterino, sp. nov., L. solum Haberski & Caterino, sp. nov., and L. thompsonorum Haberski & Caterino, sp. nov. Two species are transferred from Lathrobium to Pseudolathra Casey: Pseudolathra parcum (LeConte, 1880), comb. nov. and Pseudolathra texana (Casey, 1905), comb. nov. Twenty-six names are reduced to synonymy. Lectotypes are designated for 47 species. Larvae are described where known, and characters of possible diagnostic value are summarized. Species diagnoses, distributions, illustrations of male and female genitalia, and a key to Lathrobium species known from the Nearctic region (including several introduced species) are provided.

**Key words:** Appalachian Mountains, cryptic species, larvae, molecular phylogeny, morphology, Paederinae, sky-islands, species delimitation

#### Introduction

The Holarctic genus *Lathrobium* Gravenhorst, 1802 is the most speciose genus of Paederinae with over 650 species (Assing 2019). The Nearctic fauna is relatively species poor and incompletely known, with 64 described species and no new descriptions in more than 100 years (Notman 1921). A revision was attempted by Casey (1905), but it caused more confusion than clarity because he created copious synonyms. Although the generic limits have since been clarified (Blackwelder 1939; Assing and Schülke 2012; Żyła et al. 2020;



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Staniec and Bordoni 2022), identification of species remains nearly impossible without referring to the type specimens, because external morphology is highly conserved, and the only comprehensive key is outdated and based on dubious characters (Casey 1905). Regional keys exist for northeastern North America (Downie and Arnett 1995) and Indiana (Blatchley 1910), but both are derived from Casey (1905) and share its shortcomings.

Much of *Lathrobium* diversity can be attributed to flightless, short-range endemics that are restricted to cryophilic microhabitats such as mountains, caves, and deep soil layers. They are numerous in mountain ranges where complex topography produces clusters of allopatric endemics, such as 48 species endemic to the Himalayas and 29 endemic to the Apennine Mountains of Italy (Assing, 2012; Bordoni, 2018). Among these, species that are depigmented, microphthalmous, and generally subterranean are placed in the subgenera *Abletobium* Casey (Nearctic) and *Glyptomerus* Müller (Palearctic). Both subgenera lack clear synapomorphies beyond their gestalt, which is convergent among hypogean taxa, and their boundaries are unclear. Leaf litter and soil layers in the southeastern United States are just now being fully explored and have already revealed new flightless *Lathrobium* diversity, including new species of *Abletobium* and high elevation endemics in the southern Appalachian Mountains. They present an opportunity to reexamine the relationship between *Abletobium* and *Glyptomerus*, and to explore patterns of montane diversification.

Recent phylogeographic studies of southern Appalachian arthropods have repeatedly uncovered cryptic diversity among seemingly widespread flightless species (Gusarov 2002; Miller and Wheeler 2005; Carlton 2008; Ferro and Carlton 2010; Caterino and Vásquez-Vélez 2017; Caterino and Langton-Myers 2019; Caterino 2022; Caterino and Recuero 2024; Caterino and Harden 2024). A cursory examination of Appalachian *Lathrobium* genitalia suggested there might be cryptic diversity among three lineages endemic to southern Appalachian "sky-islands." Two of these lineages are endemic to a rare bryophyte mat microhabitat in the endangered red spruce-Fraser fir (*Picea rubens* and *Abies fraseri*) forests, a habitat they share with the federally protected spruce-fir moss spider, *Microhexura montivaga* Crosby & Bishop, 1925. Properly delimiting species boundaries and distributions could therefore have implications for conservation and provide additional motivation to protect these sensitive habitats.

To address current taxonomic deficiencies and document new diversity, we review the Nearctic species of *Lathrobium*, with emphasis on the flightless species of the southern Appalachian Mountains. We use an integrative approach that combines morphology, molecular phylogeny, and algorithmic species delimitation to guide species designations and test the hypothesis of cryptic speciation in three high elevation Appalachian lineages. We also describe five new microphthalmous species from lower elevations and the larvae of five species. Larval morphology is compared with that of other known larvae to ascertain characters of possible diagnostic value.

#### Materials and methods

We follow the generic concepts of Assing and Schülke (2012), which treat *Lathrobium* in a restricted sense and recognize *Lobrathium* Mulsant and Rey, *Pseudolathra* Casey, and *Tetartopeus* Czwalina as distinct genera. Species are

described under a phylogenetic species concept, in which species are "the smallest aggregation of populations or lineages diagnosable by a unique combination of character states" (Wheeler and Meier 2000). We have avoided the use of subspecies as the biological requirements for such designation (e.g., the ability of populations to interbreed) are undefined, and instead treat consistent lineages exhibiting morphological or molecular variation as full species.

An initial morphological investigation revealed three lineages that might contain cryptic diversity, *Lathrobium carolinae* (Casey, 1905), and the yet undescribed lineages "*Lathrobium smokiense*," and "*Lathrobium islae*". They belong to the subgenera *Apteralium*, *Abletobium*, and *Lathrobium* s. str., respectively. Each lineage contains two allopatric morphotypes that are indistinguishable externally but differ in genitalic morphology. We use morphology, phylogenetic inference, Assemble Species by Automatic Partitioning (ASAP), and Multi-rate Poisson tree processes (mPTP) to guide species delimitation in these lineages. ASAP and mPTP are complementary species discovery methods. ASAP uses pairwise distances to partition samples into putative species (Puillandre et al. 2021), but unlike previous "barcode gap" methods, ASAP tests and ranks multiple partition thresholds. mPTP is a single-locus, tree-based coalescence method that uses a maximum-likelihood criterion to delimit species based on branch lengths (Kapli et al. 2017).

A revision of *Lathrobium* was begun by L. Watrous (formerly of the Field Museum, Chicago, Illinois, USA) but never published. He dissected all of the type specimens and first hypothesized the synonymies recognized herein.

#### **Molecular methods**

A larger-scale molecular phylogeny of Nearctic *Lathrobium* was conducted in tandem with this study and will be published separately. It includes a more detailed explanation of the DNA extraction and amplification processes used. Briefly, whole genome DNA was non-destructively extracted from freshly collected specimens and from museum specimens fixed in 100% ethanol using the GeneJET Genomic DNA Purification Kit (Thermo Fisher Scientific Inc., Waltham, MA, USA). The abdomen was separated from the thorax and both halves were digested with lysis buffer and proteinase K. Following extraction, cleared specimens were dissected, point mounted, and assigned unique Clemson University Arthropod Collection (**CUAC**) numbers.

We amplified and sequenced a 658bp fragment of the mitochondrial gene cytochrome oxidase I (COI) using standard primers (HCO1490+LCO2198; Folmer et al. 1994) and following the amplification profile of Chatzimanolis et al. (2010). Sanger sequencing was performed by Psomagen (Rockville, MD) and all fragments were sequenced in both directions.

Pairwise alignment of reads was performed in GENEIOUS v. 8.1.8. Primer sequences were trimmed, and alignments were visually inspected for quality. Next, we used the EXPASY webtool (Artimo et al. 2012) to find a read frame free of stop codons. Multiple sequence alignment was then performed with MAFFT (Katoh et al. 2019) using the Muscle algorithm and default settings.

We performed a maximum-likelihood analysis with IQ-TREE (Minh et al. 2020) on 50 *Lathrobium* sequences. Our samples included all three cryptic lineages and five other flightless species. We chose *Tetartopeus tetricum* Casey,

1905, *Medon icarus* Caterino, 2023, and *Astenus* sp. as outgroups. Sequence data were initially partitioned by codon position and then we allowed candidate partitions to be merged during model estimation to avoid over-parameterization of the model. The best-fitting model was selected automatically with free rate heterogeneity (+R). We performed 1000 ultrafast bootstrap analyses to determine branch support values.

For ASAP analysis, we chose Kimura 2-parameter (K2P) distances and report results for the best partitioning schemes. We used the maximum likelihood tree as the input tree for mPTP analysis.

#### Morphology

Adult terminology follows Watrous (1980), and larval terminology follows Staniec and Bordoni (2022). Adults were examined with a Leica M80 stereomicroscope, or equivalent, and measurements were taken with a Leica M80 eyepiece micrometer. Larvae were suspended in a drop of hand sanitizer on a recessed slide and examined with a Zeiss Axioscope. Most specimens were cleared in conjunction with DNA extraction. After tissue digestion, abdominal segment VIII and the genitalia were removed. Additional specimens were dissected by relaxing in boiling water, removing the genitalia, and clearing them in 85% lactic acid warmed to 110 °C for 20 min (Blahnik et al. 2007).

Digital illustrations were created by importing hand sketches and photographs into Affinity Designer (Serif Europe Ltd, Nottingham, UK). Multiple specimens were sometimes referenced to create a single illustration that displayed all characters. Dashed lines are used to indicate structures that are obscured from view, such as the female subgenital plate and spines of the internal sac of the aedeagus. Distribution data were compiled from specimen label data and the literature. New state or province records are in bold.

We examined material from the following institutions:

- CMNH Carnegie Museum of Natural History
- **CNC** Canadian National Collection
- CUAC Clemson University Arthropod Collection
- GSNP Great Smoky Mountains National Park Collection
- LSAM Louisiana State Arthropod Museum
- **MCZC** Museum of Comparative Zoology
- NBC Nicolas Bédard Private Collection
- **UAM** University of Alaska Museum
- **UNHC** University of New Hampshire
- **USNM** United States National Museum

Holotypes were deposited in the **FMNH**, Chicago, Illinois, USA. Paratypes and additional specimens were vouchered in the **CUAC**, Great Smoky Mountains National Park, Gatlinburg, Tennessee (**GSNP**), and Virginia Museum of Natural History, Martinsville, Virginia (**VMNH**).

We did not examine material from five species because the types were inaccessible at the time, and we could not find authoritatively identified specimens in available collections. We could not locate Casey's specimens of *Lathrobium subgracile* Casey, 1905 in the USNM collection. The holotype of *Lathrobium puncticolle* Kirby, 1837 is at the Natural History Museum, London, United Kingdom, and we did not attempt to borrow it. Time and access constraints during the COVID-19 pandemic prevented us from examining the types *Lathrobium insanum* Blatchley, 1910 in the Purdue Entomological Research Collection and *Lathrobium lintneri* Notman, 1921 and *Lathrobium tenebrosum* Notman, 1921, reportedly in the Staten Island Institute of Arts and Sciences collection. These species were excluded from the key. Similarly, we were unable to illustrate some characters for *Lathrobium crurale* (Casey, 1905) and *Lathrobium lineatocolle* Scriba, 1859 due to a lack of authorita-tively identified specimens.

External morphology is highly conserved, but species are easily identified by their sexual characters, especially the aedeagus and male abdominal sternite VIII. Comparing the terminalia to illustrations is essential for accurate identifications, so dissection is strongly encouraged. The few somatic characters of diagnostic value include the relative dimensions of the head, pronotum, and elytra, the shape of the antennomeres, the shape of the gular sutures (Fig. 1), and the size of the eyes.

Measurements were taken from uncleared adults and cleared larvae. References to color were based on uncleared specimens. Head length was measured at midline from the anterior margin of the frons to the anterior edge of the neck constriction. Pronotal length was measured along the midline. Elytral length was measured from the anterior angle, or "shoulder", to the apex. Head and pronotum widths were measured at their widest points, and elytra width was measured



across both elytra at the widest point. An estimate of total body length is given, but forebody length (**FL**), a surrogate unaffected by the expansion or contraction of intersegmental membranes, was calculated by adding head, pronotum, and elytra length. Eye width was measured in lateral view from the anterior-most to posterior-most point of the eye. Larval body length was measured from the anterior margin of the nasale to the posterior edge of the last abdominal segment (excluding the urogomphi). The relative lengths of larval antennomeres and palpomeres are presented as ratios, beginning with the basal article.

The side of the aedeagus with the median foramen is arbitrarily designated as "ventral" for convenience, although it is positioned laterally in life. The median lobe is divided into a lightly sclerotized basal portion and an elongate and well-sclerotized ventral process, although shape and degree of sclerotization varies. The female sternite VIII occurs in two shapes, conical with sides convex their entire length or oblong with sides concave in the apical 1/3. The female tergite IX (= paraprocts) can be either divided its entire length (Fig. 2A) or continuous in the basal portion. If undivided, the apices can be longer (Fig. 2B) or shorter (Fig. 2C) than the basal portion.



Figure 2. Genitalia morphology **A** female paraprocts divided **B** female paraprocts undivided **C** female terminalia, ventral **D** aedeagus, ventral **E** aedeagus, lateral. Abbreviations: al – apical lobe of paraproct, bp – basal portion of paraproct, co – coxite, dp – dorsal plate, mf – median foreman, ml – median lobe, pa – paraprocts, pt – proctiger, sgp – subgenital plate, sp – spine of the internal sac, va – valvifer, vp – ventral process.

Several characters used in previous keys are not reliable for diagnosis. Elytra length varies in some wing-dimorphic species, being longer than the pronotum in winged individuals and subequal in non-winged individuals. Elytra length does not vary in micropterous species with elytra shorter than the pronotum. Elytra color is likewise variable, with some individuals possessing bicolored elytra (black anteriorly and reddish posteriorly) but others with elytra entirely black.

#### Results

#### **Phylogenetics**

Our final COI alignment contained 221 parsimony-informative sites, 398 constant sites, 39 singleton sites, and 0.14% missing data. Automatic model estimation selected a two-partition scheme fitting the TN+F+I substitution model to the first and second codon positions and the TPM3+F+G4 model to the third codon position. The maximum-likelihood consensus tree was fully resolved, except for a polytomy among the outgroups *Astenus* and *Tetartopeus*, and had good branch support within *Lathrobium* (Fig. 3). Relationships among species at deeper levels are specious due to the globally sparse taxon sampling.

The two morphotypes of L. carolinae resolved as reciprocally monophyletic with a deep divergence and 100% bootstrap support. The first clade (Fig. 3: L. carolinae) includes the more widespread morphotype which spans 250 km from Brasstown Bald, Georgia, to the French Broad River basin (Asheville depression), although most are west of the Little Tennessee River (with the disjunct exception of one individual form Wilkins Creek, north of Asheville). It is characterized by an aedeagus with a ventral process that is not projected ventrad and two structures on the internal sac visible when invaginated (Fig. 4D, E). The female terminalia are more robust and lack a subgenital plate (Fig. 4A). The second clade (Fig. 3: L. camplyacra) is restricted to the Plott Balsam, Great Balsam, and Cowee Mountains. Aedeagi in this morphotype have a ventral process that projects beyond the median foramen in lateral view (Fig. 5F) and one structure visible on the internal sac. The female terminalia are more elongate, with noticeably shorter coxites and a small, lightly sclerotized subgenital plate (Fig. 5B). Examination of 130 specimens found no intermediate forms and a single specimen of morphotype 2 out of range. Within-clade K2P distances were close to zero, and between clade distances were up to 7% (Fig. 6A). The highest-ranking ASAP scheme included three partitions, two corresponding to the two morphotypes and a third partition for a single low-quality read of morphotype 1. mPTP supported two putative species. The type locality of L. carolinae is on the border of the two ranges, but the aedeagus of the lectotype matches that of morphotype 1, so we designate morphotype 2 as a new species, Lathrobium camplyacra sp. nov., described below.

The "L. islae" lineage occupies high-elevation (>1500 m) spruce-fir forests north of the French Broad River basin. A clade containing morphotype 1 (Fig. 3: L. islae) was paraphyletic with respect to morphotype 2 (Fig. 3: L. lividum). Intraspecific K2P distances ranged from 0 to 3% distance (Fig. 6B), and mPTP suggested the existence of a single species. The highest-ranking ASAP scheme included seven partitions, five containing only morphotype 1 and two containing only morphotype 2. Each morphotype has distinct genitalic morphology. The major spine of the



**Figure 3.** COI maximum-likelihood majority-rule consensus tree of flightless *Lathrobium*. Abbreviations: (bc) Big Cataloochee Mtn; (bt) Big Tom; (cd) Clingmans Dome; (ck) Celo Knob; (cr) Copper Ridge Bald; (cw) Cowee Bald; (gf) Grandfather Mtn; (hg) Horse Cove Gap; (hk) Huckleberry Knob; (ic) Indian Camp Creek; (jg) Jones Gap; (kp) Mt. Kephart; (lb) Little Bald; (lc) Mt. LeConte; (II) Mt. Lyn Lowry; (mr) Mt. Rogers; (pg) Pisgah National Forest; (rb) Richland Balsam Mtn; (rh) Roan High Knob; (rk) Riley Knob; (su) Sugarloaf Mtn; (tx) Toxaway Mtn; (ty) Teyahalee Bald.

internal sac of the aedeagus is long, sinuate, and club-tipped in morphotype 1 (Fig. 7E), but short, curved, and projecting above the median lobe in morphotype 2 (Fig. 8E). They also differ in the shape of the ventral process (straight vs apically projecting) and width of the gonocoxites. Examination of 54 specimens found no further morphological variation or intermediate forms. We designate morphotype 1 as *Lathrobium islae* sp. nov. and morphotype 2 as *Lathrobium lividum* sp. nov.

The "L. smokiense" lineage inhabits high elevation spruce-fir forests south of the French Broad River basin. The morphotypes are geographically coherent, with morphotype 1 (Fig. 3: L. smokiense) restricted to the Great Smoky Mountains and morphotype 2 (Fig. 3: L. balsamense) to the Plott Balsam and Great Balsam Mountains. They can be distinguished only by their aedeagi. Morphotype 1 has a distinctive median lobe that is fully sclerotized and tube-like, with a small dorsal plate (operculum) positioned at the apex like a cap on the tube (Fig. 9E, F). The aedeagus of morphotype 2 is more typical of the genus, with a distinct ventral process and dorsal plate positioned dorsally (Fig. 10D, E). No distinguishing characters were found for females. Each morphotype was resolved as polyphyletic, intermingled in two clades (Fig. 3). The first clade contained a sequence of morphotype 1 from Clingmans Dome (cd) and three sequences of morphotype 2 from Richland Balsam (rb), two geographic extremes of the lineage's range. The remaining sequences resolved in a mixed clade spread across the



**Figure 4**. *Lathrobium carolinae* **A** female terminalia **B** female sternite VIII **C** male sternite VIII **D** aedeagus in ventral view **E** aedeagus in lateral view. Scale bars: 1 mm.





Smokies and Plott Balsams. Intraspecific K2P distances were low (Fig. 6C) and in several cases sequences from divergent morphotypes were identical. mPTP suggested one species, and the highest-ranking ASAP scheme included three partitions, one for the Clingmans Dome sequence (cd), one containing the



**Figure 6.** Species by Automatic Partitioning (ASAP) histograms of K2P distances for **A** *Lathrobium carolinae* + *L. camplyacra* **B** *Lathrobium islae* + *L. lividum*, and **C** *Lathrobium smokiense* + *L. balsamense*. Y-axis is the number of sequence pairs (Nbr), and x-axis is K2P distance between paired sequences (Dist. Dt). Arrows indicate the "barcode gap" between intra- and interspecific variation.



Figure 7. Lathrobium islae A habitus B female terminalia C female sternite VIII D male sternite VIII E aedeagus in ventral view F aedeagus in lateral view. Scale bars: 1 mm.

three sequences from Richland Balsam (rb), and a mixed partition containing the remainder. Nonetheless, given the consistency of clear morphological differences in geographically disparate ranges, we designate morphotype 1 as *Lathrobium smokiense* sp. nov. and morphotype 2 as *Lathrobium balsamense* sp. nov. based primarily on morphology.



**Figure 8**. *Lathrobium lividum* **A** female terminalia **B** female sternite VIII **C** male sternite VIII **D** aedeagus in ventral view **E** aedeagus in lateral view. Scale bars: 1 mm.



Figure 9. Lathrobium smokiense A habitus B female terminalia C female sternite VIII D male sternite VIII E aedeagus in ventral view F aedeagus in lateral view. Scale bars: 1 mm.



Figure 10. *Lathrobium balsamense* **A** female terminalia **B** female sternite VIII **C** male sternite VIII **D** aedeagus in ventral view **E** aedeagus in lateral view. Scale bars: 1 mm.

#### Taxonomy

Subfamily Paederinae Fleming, 1821 Tribe Lathrobiini Laporte, 1835 Subtribe Lathrobiina Laporte, 1835 Genus *Lathrobium* Gravenhorst, 1802 Subgenus *Abletobium* Casey, 1905: 70.

Lathrobium (Abletobium) absconditum Haberski & Caterino, sp. nov. https://zoobank.org/F524D9C1-23EC-4511-9883-61137650F36E

**Type material.** *Holotype*  $3^{\circ}$  (FMNH): "USA: VA: Bath Co., 38.0744°N, 79.6836°W, Dry Run Gorge, X.28.2018, C. Harden, oak-hickory woods; limestone gorge." / "CLEMSON ENT [QR CODE] CUAC000185176". *Paratypes* (3, CUAC, FMNH, VMNH): same data as holotype (CUAC000185174, CUAC000185175, CUAC000185177).

**Other material.** Virginia: same data as holotype, CUAC000187891 (1 larva, CUAC); Highland Co.: Owl Cave, 2070', Water Sinks (38.2205, -79.6046), C. Harden, 31 May–2 Aug 2019 (CUAC); Highland Co.: Water Sinks, 2080' (38.2211, -79.6042), C. Harden, 4 May–31 May 2019 (VMNH).

**Diagnosis.** This species is larger than most microphthalmous *Lathrobium* known from Virginia and West Virginia. Males can be distinguished from most species by the lack of setal combs on sternite VIII and females by the presence of gonocoxite lobes. *Lathrobium solum* is of similar size and also lacks the transverse combs on sternite VIII. However, *Lathrobium solum* has transverse antennomeres V–VII, and more widely separated gular sutures. Aedeagi differ in the shape of their major spines, and *L. solum* has a characteristically shaped ventral process that reaches the dorsal plate in lateral view. The female of *L. solum* is unknown, so no distinctions can be made.

**Description.** Habitus (Fig. 11A). Large species, total body length ~ 9 mm long, FL 3.4–4.0 mm long. Coloration: body and appendages pale reddish.

Head slightly wider than long, widest at posterior; posterior angles rounded. Epicranium coarsely punctate with punctures less dense in median dorsal portion; interstices with strong transversely reticulate microsculpture throughout; head setose throughout, with long macrosetae projecting at posterior corners of head, corners of eyes, laterally posterior to eyes, and above mandible insertions; gular sutures (sulci) narrowing posteriorly until nearly touching; neck 1/2 as wide as head. Eyes reduced to small white membranes without ommatidia, occupying 1/9 length of head. Antennae moniliform, as long as head and pronotum combined; scape as long as antennomeres II and III combined; antennomeres II–IX obconic, longer than wide but become progressively wider; apical antennomere longer, subacute.

Pronotum longer than wide, narrower than head and elytra; widest at anterior angles and tapering slightly posteriorly; all angles round, posterior angles less so; punctation is dense, punctures spaced one diameter apart, impunctate at midline with a faint line visible on posterior two thirds; interstices shiny with no microsculpture. Elytra distinctly shorter than pronotum, as wide as head, approximately as long as wide; posterior margin sinuate; punctures small and shallow with indistinct edges, irregularly spaced, most one diameter apart; setae angled to posterior; interstices with finely punctate microsculp-





ture. Hindwings vestigial. Posterior margin of abdominal tergite VII without palisade fringe.

♂: Larger, forebody 3.8–4.0 mm. Posterior margin of sternite VIII with broad but shallow emargination, patch of dense setae medially (Fig. 11D). Aedeagus 1.5 mm long; ventral process long, narrow, and asymmetrical (Fig. 11E, F); dor-



**Figure 12**. *Lathrobium absconditum* second instar larva **A** habitus **B** nasale **C** mandible **D** maxilla **E** antenna. Scale bars: 1 mm (**A**, **C**); 500 µm (**B**, **D**, **E**).

sal plate short and broad; internal sac with five spines, major spine long with two narrow asymmetrical processes.

 $\bigcirc$ : Smaller, forebody 3.4 mm. Sternite VIII oblong, apex notched with micropubescence (Fig. 11C); paraprocts undivided anteriorly, apices longer than

basal portion; proctiger conical; sternum IX with coxites and valvifers fused (Fig. 11B), base produced into distinct setose lobes; subgenital plate absent.

**Second instar larva:** Body elongate, ~ 7 mm long; lightly sclerotized (Fig. 12A), head more sclerotized; head and thoracic tergites light brown, legs and body white, translucent.

Head ovate, tapered posteriad (in dorsal view), dorsoventrally flattened, 1.3× as long as wide, with dorsal setae as in Fig. 12A; head 3.6× wider than neck; dorsal ecdysial lines bifurcate 2/5 distance between neck and nasale margin; stemmata absent; anterior margin of nasale (Fig. 12B) as in *L. hardeni*, but median tooth triangular with edge serrated; Apotome of gula not reaching tentorial pits.

Antennae (Fig. 12E) length ratios: 1.0:3.8:2.9:1.7; antennomere I triangular; antennomere II with two pores; antennomere III with three elongate macrosetae, three solenidia, one pore; antennomere IV club-shaped with apical solenidia; sensory appendage 0.8× as long as antennomere IV.

Mandibles (Fig. 12C) long, falciform, serrate along apical 1/3 of inner margin, with a single seta near base on outer ventral edge. Maxilla (Fig. 12D) with cardo triangular; stipes elongate, 1.7× longer than cardo; mala digitiform, tapering toward apex, 0.9× as long as palpomere I, with apical sensory appendages and two pores; palpifer with one seta. Maxilla and labium as in *L. hardeni*, except maxillary palpomere length ratios: 1.0:1.4:2.7; ligula separated from prementum by a distinctly sclerotized transverse strip; palpomere I 1.2× as long as II; palpomere II bent near apex.

Dorsal sclerites of thorax with ecdysial lines along midline; prothorax narrow, 1.1× as long as wide, narrowed anteriorly, chaetotaxy as in Fig. 12A; thoracic tergite II longer than tergite III; abdominal sclerites lightly sclerotized, with two small pleural sclerites per segment on each side; basal segment of urogomphus 4× as long as terminal segment, with seven prominent lateral setae; terminal segment of urogomphus slender, with one short and one long apical seta.

**Etymology.** The specific name is Latin (singular, neuter), meaning hidden or concealed, in reference to the species' endogean habitat.

**Distribution and ecology.** *Lathrobium absconditum* is known from Highlands County and Bath County, Virginia (Fig. 13). Two specimens were collected near the mouth of Owl Cave, but none were found inside the cave. All specimens were collected with buried pipe traps, which suggests they are hypogean. Adults collected Mar–Oct. Larvae collected in Oct. Males and females have yet to be collected together.

Remarks. Larvae were associated with adults by DNA barcoding.

Lathrobium (Abletobium) balsamense Haberski & Caterino, sp. nov. https://zoobank.org/5694CA73-B2C9-48EE-849E-2BD354476BA9

Typematerial. *Holotype* (FMNH): "USA:NC:HaywoodCo.,35.3632°N,82.9885°W, Richland Balsam Mountain, 6180', IX.11.2019, Sifted Litter, M. Caterino." / Caterino DNA voucher, Ext. MSC-4413, Morphosp RB.B.320" / "CLEMSON ENT [QR CODE] CUAC000003949". *Paratypes* (4, CUAC, FMNH): 2: same locality as type, 35.3627°N, 82.9885°W, IX.11.2019 (CUAC000003627, CUAC000177150); same locality as type, 35.3630°N, 82.9890°W, 6200ft, v.08.2018 (CUAC000177151); same locality as type, 35.3676, -82.9902, 6398', v.8.2018 (CUAC000048512).



**Figure 13.** Distribution of *Lathrobium absconditum* (triangle), L. *balsamense* (square), *L. hardeni* (star), *L. smokiense* (circle).

Other material. North Carolina: Jackson Co.: Balsam Mountain Preserve, Nantahala National Forest, (35.3751, -83.0981), S. Myers, 15 Jun 2015 (CUAC); Haywood Co.: Mt. Lyn Lowry, 6205' (35.4640, -83.1100), M.S. Caterino, 22 Sep 2020 (2, CUAC); Haywood Co.: Mt. Lyn Lowry, 6192-6203' (35.4640, -83.1101), M.S. Caterino, 15 Apr 2021 (9, CUAC); Haywood Co.: Mt. Lyn Lowry, 6200' (35.4638, -83.1108), M.S. Caterino, 22 Apr 2020 (3, CUAC); Haywood Co.: Richland Balsam, 6398', Blue Ridge Parkway (35.3676, -82.9902), M.S. Caterino, 8 May 2018 (USNM); Haywood Co.: Richland Balsam, 6069-6397', Blue Ridge Parkway, A. Smetana, 25 May 1986 (CNC); Haywood Co.: Waterrock Knob, 6275', Blue Ridge Parkway (35.4643, -83.1374), M.S. Caterino, 29 May 2018 (4, CUAC); Haywood Co.: Waterrock Overlook, 5800', Blue Ridge Parkway, J.M. & B.A. Campbell, 1 Sep 1967 (4, CNC); Haywood Co.: Browning Knob, 6003–6200', Blue Ridge Parkway, A. Smetana, 28 May 1986 (CNC); Haywood Co.: Browning Knob, 6140', Blue Ridge Parkway (35.4630, -83.1310), 22 Sep 2020, M.S. Caterino (7, CUAC); Haywood Co.: Browning Knob, 6200-6220', Blue Ridge Parkway (35.4633, -83.1315), 22 Sep 2020 M.S. Caterino, A. Haberski (5, CUAC).

**Diagnosis.** This species can be distinguished from its close relative, *L. smokiense*, only by their aedeagi. In *L. smokiense*, the entire aedeagus is well sclerotized, whereas the aedeagus of *L. balsamense* is more typical for the genus with a distinct ventral process (Fig. 9E, F vs Fig. 10D, E). Females can only be identified by geography, association with males, or DNA.

One other microphthalmous species, *L. shermani* Fall, 1917, occurs above 1000 m elevation in the southern Appalachians, although their ranges do not overlap. Adults are similar in size and appearance but are distinguished by the sexual characters. Males of *L. balsamense* lack a conspicuous comb of thick black setae on sternite VIII and has no spines on the internal sac of the aedeagus. In females, the gonocoxites lack the pubescence of *L. shermani* in the lower half.

**Description.** Habitus (Fig. 9A). Small species, total body length ~ 6 mm long, FL 2.6-2.8 mm long. Coloration: body reddish becoming lighter towards posterior segments of abdomen; legs, palpomeres, and antennae a paler reddish yellow.

Head subquadrate, posterior angles rounded; epicranium coarsely punctate with punctures less dense in median dorsal and anterior regions; interstices with strong transversely reticulate microsculpture throughout; head setose throughout, with long macrosetae projecting at posterior corners of head, corners of eyes, laterally posterior to eyes, and above mandible insertions; gular sutures straight and widely separated, 1/8 width of head but narrowing slightly posteriorly; neck 1/2 as wide as head. Eyes reduced to small white membranes without ommatidia, occupying 1/9 length of head. Antennae moniliform, as long as head and pronotum combined; scape as long as antennomeres II and III combined; antennomeres II–IV obconic and elongate, gradually widening so that antennomeres V–IX are as wide as long; apical antennomere longer, subacute.

Pronotum longer than wide, narrower than head and elytra; widest at anterior angles and tapering slightly posteriorly; anterior angles round, posterior angles less so; punctures small, spaced 1–2× their diameter apart, impunctate at mid-line; interstices shiny with no microsculpture. Elytra shorter than pronotum, as wide as head, approximately as long as wide; posterior margin slightly sinuate; punctures large and shallow with indistinct edges, irregularly spaced, most approximately one diameter apart; setae angled to posterior; interstices with finely punctate microsculpture. Hindwings vestigial, 0.2 mm long, 1/4 length of elytra. Posterior margin of abdominal tergite VII without palisade fringe.

♂: Posterior margin of sternite VIII with a shallow U-shaped notch (Fig. 10C). Aedeagus 1.1 mm long (Fig. 10E, F), ventral process long, broad, and symmetrical, tapering to a blunt tip; dorsal plate long and situated dorsally; internal sac without spines.

 $\bigcirc$ : Sternite VIII conical (Fig. 9B); paraprocts undivided anteriorly, apices as long as basal portion; proctiger conical; sternum IX with coxites and valvifers fused, basal half glabrous (Fig. 9B); subgenital plate absent.

**Etymology.** This species is named for the Plott Balsam and Great Balsam Mountains.

**Distribution and ecology.** *Lathrobium balsamense* inhabits spruce-fir forests above 1500 m in the Great Balsam Mountains and Plott Balsam Mountains (Fig. 13) but is absent from the Great Smoky Mountains where the closely related *L. smokiense* occurs. It does not occur in spruce-fir forests north of the French Broad River basin, where its microhabitat is inhabited by *L. lividum* and *L. islae.* It can be collected from leaf litter but is most common beneath bryophyte mats on boulders. Collected May–Sep.

#### Lathrobium (Abletobium) hardeni Haberski & Caterino, sp. nov. https://zoobank.org/07EEDC41-8050-4B49-B07A-539459101D12

Type material. *Holotype* ♂ (FMNH): "USA: WEST VIRGINIA, Pocahontas Co., Monongahela Nat. For. Cranberry Backcountry, past glades, 38.2101, -80.2871, 11-June-2019, C.W. Harden, under large rock nr. steep stream. Spruce/ Northern hardwoods." / "Caterino DNA voucher, Ext. MSC-7071" / "CLEMSON ENT [QR CODE] CUAC000169036". *Paratypes* (4, FMNH, CUAC, VMNH): 3: "USA: WEST VIRGINIA, Pocahontas Co. Monongahela Nat. For. Kennison Mtn Tr., W of Cranberry Glades, 1224m, 38.18002, -80.27846, 10-June-2019, C.W. Harden, Under rock during rain" (also 2 larvae from this collecting event). 1: "USA: WEST VIRGINIA, Pocahontas Co. Monongahela Nat. For. Kennison Mtn Tr., 38.19114N, 80.28524W, 1181m elev. 11.June–3.August.2019, C.W. Harden & L.M. Thompson, Buried jar trap, northern hardwood forest, sandstone boulders present. Rich dark rocky soil. KEN-04" (also 2 larvae from this collecting event).

**Other material.** West Virginia: Pocahontas Co.: Dogway Rd., 4019', Cranberry Wildlife Management Area (38.1903, -80.2893), C. Harden, 02 Sep 2018 (5, CUAC, VMNH); Pocahontas Co.: Monongahela Nat. For. Cranberry Backcountry (38.1800, -80.2785), C. Harden, 10 Jun 2019, CUAC000187895, CUAC000187896 (3 larvae, CUAC); Pocahontas Co.: Kennison Mountain Trail, Cranberry Wildlife Management Area (38.1900, -80.2780), C. Harden, 11 Sep 2017 (CUAC); Pocahontas Co.: Kennison Mountain Trail, 4388', Kennison Mountain (38.1979, -80.2915), C. Harden, 19 Sep 2018 (CUAC). Pocahontas Co.: Kennison Mountain (38.1979, -80.2915), C. Harden, 19 Sep 2018 (CUAC). Pocahontas Co.: Kennison Mountain Trail, W. of Cranberry Glades, 4015', Kennison Mountain (38.18002, -80.27846), C. Harden, 06 Oct 2019 (CUAC); Pocahontas Co.: Monongahela Nat. For. Kennison Mtn Tr. (38.19114, -80.28524), C. Harden, 11 Jun–3 Aug 2019, CUAC000187894 (1 larva, CUAC); Pocahontas Co.: Monongahela Nat. For. Kennison Mtn Tr. (38.1903, -80.2893), C. Harden, 2 Sep 2018, CUAC000187897, CUAC000187898 (5 larvae, CUAC).

**Diagnosis.** Three other species of microphthalmous *Lathrobium* are known from West Virginia and Virginia, *L. absconditum*, *L. lapidum*, and *L. shermani*. The extents of their ranges are unknown and might overlap. Adults of *L. hardeni* can be distinguished from those of *L. absconditum* by its smaller body size, transverse combs of thick setae on male sternite VIII, and the presence of a ventral process in the female genitalia, which is unique among the microphthalmous *Lathrobium* of North America. Males of *L. shermani* are approximately the same size but have a single row of thick black setae on sternite VIII. Males of *L. lapidum* are most similar in appearance but are larger and have quadrate elytral margins. The aedeagus of *L. lapidum* has a characteristic ventral process that reaches the dorsal plate in lateral view, and asymmetrical spines on the internal sac.

**Description.** Habitus (Fig. 14A). Small species, total body length  $\sim$  6 mm long, FL 3.1–3.3 mm long. Coloration: body pale reddish becoming lighter towards posterior segments of abdomen; legs, palpomeres, and antennae paler reddish yellow.

Similar in appearance to *L. absconditum*, except head subquadrate; gular sutures straight, separated by 1/15 width of head and narrowing slightly posteriorly. Eyes reduced to small white membranes without ommatidia, occupying 1/8 lateral width of head. Pronotum with sides parallel, just perceptibly nar-





rowed posteriorly; punctation spaced less than one diameter apart, impunctate at midline. Posterior margins of elytra less sinuate; punctures larger.

♂: Posterior margin of sternite VIII with broad but shallow emargination and three transverse combs of thick black setae to either side of midline (Fig. 14D).

Aedeagus 1.2 mm long; ventral process long, curved ventrally, narrowing to a rounded point with small apical tooth (Fig. 14E, F); dorsal plate long and broad, distal end narrowing to an abrupt point curved away from ventral process with small apical tooth; internal sac with four more-or-less symmetrical spines.

 $\bigcirc$ : Sternite VIII oblong, apex notched, with micropubescence (Fig. 14C); paraprocts undivided anteriorly, apices shorter than basal portion; proctiger conical; sternum IX with valvifers and coxites fused, finely setose (Fig. 14B); subgenital plate square, distal end with round projection.

*First instar larva*: Body elongate, 4 mm long; lightly sclerotized (Fig. 15A), head more sclerotized; head light brown, legs and body white, translucent.

Head ovate, tapered posteriad (in dorsal view), dorsoventrally flattened, 1.2× as long as wide, dorsal setae as in Fig. 15A; head 3.2× longer than neck; dorsal ecdysial lines bifurcate halfway between neck and nasale margin; stemmata absent; anterior margin of nasale (Fig. 15B) with nine blunt teeth pointing anteriorly, one short median tooth with edge emarginated, a pair of paramedian teeth, and three pairs of lateral teeth; innermost lateral teeth are small and indistinct; paramedian and lateral teeth armed with nodular setae, and a pair of nodular setae separate median and paramedian teeth; Apotome of gula just reaching tentorial pits.

Antennae (Fig. 15E) length ratios: 1.0:2.4:2.7:1.6; antennomere I triangular; antennomere II with two pores; antennomere three with three elongate macrosetae, three solenidia, one pore; antennomere IV parallel sided with apical solenidia; sensory appendage 0.8× as long as antennomere IV.

Mandibles (Fig. 15C) long, falciform, serrate along basal 1/3 of inner margin, with a single seta near base on outer ventral edge. Maxilla (Fig. 15D) with cardo triangular; stipes elongate, 1.3× longer than cardo; mala digitiform, tapering toward apex, 0.9× as long as palpomere I, with apical sensory appendages and two pores; palpifer with one seta. Maxillary palpomere length ratios: 1.0:1.1:2.5; palpomere II with two setae; palpomere III with one basal sensory appendage and numerous small apical appendages. Labium with prementum subquadrate, basal portion strongly sclerotized; ligula with elongate membranous apex, 3× as long as wide, densely fimbriate, separated from prementum by a lightly sclerotized transverse strip; palpomere I 1.3× as long as II; palpomere II bearing short sensilla at apex.

Dorsal sclerites of thorax with ecdysial lines along midline of body; prothorax as long as wide, as long as tergite II and III combined, narrowed anteriorly, with chaetotaxy as in Fig. 15A; thoracic tergite II wider than III, but with similar chaetotaxy; abdominal sclerites lightly sclerotized, with two small pleural sclerites per segment on each side; basal segment of urogomphus 3× as long as terminal segment, with seven prominent lateral setae; terminal segment of urogomphus slender, with one short and one long apical setae.

**Second instar larva:** Second instar (Fig. 16A) resembles first, except as follows. Body larger, ~ 7 mm long. Head 1.4× as long as wide, dorsal ecdysial lines bifurcate 1/3 distance between nasale margin and neck; median tooth of nasale projecting, trifurcate (Fig. 16B). Antenna (Fig. 16D) length ratios: 1.0:2.4:2.7:1.6; antennomere IV club shaped. Maxillary palpomere length ratios: 1.0:1.2:2.8 (Fig. 16C). Labial palpomere I 1.6× longer than II and distinctly curved; palpomere II bent near apex. Thoracic tergite II narrower than III; urogomphi slender.


**Figure 15**. *Lathrobium hardeni* first instar larva **A** habitus **B** nasale **C** mandible **D** maxilla **E** antenna. Scale bars: 1 mm (**A**); 250 μm (**B**, **C**); 500 μm (**D**, **E**).

**Etymology.** Named in honor of the collector Curt Harden. Curt designed the buried pipe trap that has been instrumental in collecting microphthalmous *Lathrobium* and was the first to collect several of the species described here.

**Distribution and ecology.** *Lathrobium hardeni* is known from two locations in the Monongahela National Forest, West Virginia (Fig. 13). Specimens have been collected in buried pipe traps and from underneath embedded rocks, which suggest this species is hypogean. Adults collected May–Sep. Larvae collected Aug–Sep in the same trap as adults.



Figure 16. *Lathrobium hardeni* second instar larva **A** habitus **B** nasale **C** mandible **D** maxilla **E** antenna. Scale bars: 1 mm (**A**); 250 μm (**B**); 500 μm (**C**, **D**, **E**).

# *Lathrobium (Abletobium) lapidum* Haberski & Caterino, sp. nov. https://zoobank.org/351364B1-0580-44E7-B8C7-AF4F09A92E52

**Type material.** *Holotype* ♂ (FMNH): "USA: VA: Dickenson Co., 37.2724°N, 82.2956°W, Breaks Interstate Park, Camp Branch Trail, VI.09.2022, C. Harden, under large rock in sandy soil nr rock face, mesic stream hollow." / "Caterino DNA voucher, Ext. MSC-11164"/ "CLEMSON ENT [QR CODE] CUAC000169038".



Figure 17. Lathrobium lapidum A habitus B female terminalia C female sternite VIII D male sternite VIII E aedeagus in ventral view F aedeagus in lateral view. Scale bars: 1 mm.

*Paratypes* (1, VMNH): "USA: VA: Scott Co., 36.8584°N, 82.4477°W, Jefferson NF, N of Dungannon, VI.09.2022, C. Harden, On rock face under root/soil mat on base of boulder." / "Caterino DNA voucher, Ext. MSC-11165" / "CLEMSON ENT [QR CODE] CUAC000169039".

**Diagnosis.** This species' range might overlap with *L. absconditum, L. shermani,* and *L. hardeni.* Compared to these, it has a more rounded head, square elytral margins, and glabrous bases of the gonocoxites. It can be further distinguished from *L. absconditum* by its smaller size and transverse black setae on male sternite VIII. Males of *L. shermani* are approximately the same size but have a single setal comb on sternite VIII. *Lathrobium hardeni* is most similar and distinguishing the two requires comparison of genitalia. Males of *L. hardeni* have more-or-less symmetrical spines on the internal sac of the aedeagus, and females have a subgenital plate.

**Description.** Habitus (Fig. 17A). Large species, total body length ~ 8 mm long, FL 3.5 mm long. Coloration: body and appendages pale reddish.

Similar to *L. hardeni*, except posterior angles of head more strongly rounded. Eyes smaller, reduced to small white membranes occupying 1/9 lateral width of head.

Pronotum with punctures spaced one diameter apart, no line visible down midline. Posterior margin of elytra quadrate; punctures small and shallow, relatively sparse, irregularly spaced 2× their diameters apart.

♂: Posterior margin of sternite VIII with a broad, shallow, V-shaped emargination and three transverse combs of irregularly spaced thick black setae either side of midline (Fig. 17D). Aedeagus 1.3 mm long; ventral process long, reaching dorsal plate in lateral view, apex curved, asymmetrical (Fig. 17E, F); dorsal plate short and oval, distal end with a curved spine; internal sac with four spines, one bulbous and covered with short spikes.

 $\bigcirc$ : Sternite VIII oblong, apex notched with micropubescence (Fig. 17C); paraprocts undivided anteriorly, apices longer than basal portion; proctiger conical; sternum IX with valvifers and coxites fused, setose in apical 2/3 with a dense patch of thick setae at base (Fig. 17B); subgenital plate absent.

**Etymology.** The specific name is from Latin, meaning stone, because both specimens were found on or under rocks.

**Distribution and ecology.** *Lathrobium lapidum* is known from two specimens collected in Jefferson National Forest, Virginia (Fig. 18). One was collected under an embedded rock, and the other beneath a root and soil mat on top of a boulder. Collected in June.

#### Lathrobium (Abletobium) pallescens (Casey, 1905)

Abletobium pallescens Casey, 1905: 79. Lathrobium (Abletobium) pallescens: Bernhauer and Schubert 1912: 265.

**Type material.** *Lectotype*, *Abletobium pallescens* Casey herein designated (USNM): "MASS / CASEY bequest 1925 / [red] TYPE USNM 38106 / [handwritten] *Abletobium pallescens* Jul / Lectotype *Abletobium pallescens* Casey Desg. Haberski & Caterino."

Other material. Canada, Ontario: Carleton Co.: Fitzroy Provincial Park, 02 May 1979, A. & Z. Smetana, (1 CNC); Grey Co.: Ingli's Falls, 24 Jun 1985, B. Sinclair



**Figure 18.** Distribution of *Lathrobium lapidum* (star), *L. shermani* (triangle), *L. solum* (square), *L. thompsonorum* (circle)

(1 CNC). Quebec: Haut Saint François: Johnville, 01 Nov 1987, C. Levesque (1 CNC); same locality, 03 Jul 1988 (1 CNC); same locality, 30 Oct 1988 (1 CNC).

**Diagnosis.** This species can be distinguished from all other *Abletobium* by the presence of eyes with ommatidia.

**Description.** Body length 6 mm; Body coloration pale red. Eyes small, ~ 30 ommatidia. Head wider than pronotum; gular sutures parallel, widely separate throughout; antennomeres V–VII 1.8× longer than wide. Elytra slightly shorter than pronotum. Females with paraprocts undivided, apices longer than basal portion; sternite VIII conical with small apical notch. Median lobe of aedeagus fully sclerotized and tube-like (Fig. 19).

Distribution. Canada: ON, QC. USA: MA.

**Remarks.** This species had not been previously recorded in Canada because CNC specimens had been misidentified as *L. shermani*. We corrected these identifications.

## Lathrobium (Abletobium) shermani Fall, 1917

Lathrobium shermani Fall, 1917: 164.

**Type material. Holotype** ♂ (MCZ): "[Handwritten] Grandfather Mt Early Sep 1915 N.C. 4000 to 5000 ft. / ♂ / FSherman Collector / H. C. FALL COLLECTION / TYPE [handwritten] *shermani* / [red] M. C. Z. Type 24086."



Figures 19, 20. *Lathrobium* terminalia **A** female terminalia **B** male sternite VIII **C** aedeagus in ventral view **D** aedeagus in lateral view. **19** *L*. *pallescens* **20** *L*. *shermani*. Scale bars: 1 mm.

**Other material.** USA: Virginia: Patrick Co.: Stuart (36.7004, -80.2622), 12 Aug-10 Nov 2022, K. Ivanov, J. Means, L. Hightower (5 CUAC and VMNH).

**Diagnosis.** Lathrobium shermani is similar in appearance to *L. hardeni*, *L. lapidum*, and *L. thompsonorum*, all of which have combs of black setae on male sternite VIII. However, those species all have multiple combs, and the combs are continuous across the midline. They also differ in the shape and spines of the aedeagus. Females of *L. shermani* can be distinguished from *L. hardeni* by the lack of a subgenital plate, and from *L. thompsonorum* and *L. lapidum* by the pubescent gonocoxites.

**Description.** We present descriptions and illustrations of the male and female genitalia, which were missing from the original description.

Body length 6 mm; body coloration pale red. Head wider than pronotum; eyes reduced to small white membranes without ommatidia; gular sutures parallel and widely separate; antennomeres V–VII 1.8× longer than wide. Elytra shorter than pronotum.

♂: Type specimen differs from specimens collected in Virginia in the number of thick black setae on sternite VIII: type has ~ 8 per comb whereas Virginia specimens have five. Aedeagus large, 1.4 mm long; ventral process long, broad, and bent ventrally in lateral view (Fig. 20D, E); lightly sclerotized median lobe protrudes beyond ventral process in lateral view; dorsal plate short and diamond-shaped; internal sac with four spines, major spine wide and 1/2 as long as ventral process, other three spines shorter than dorsal plate.

 $\bigcirc$ : Sternite VIII with a shallow, curved notch at apex (Fig. 20B); paraprocts undivided anteriorly, apices approximately equal in length with basal portion; proctiger conical; sternum IX with valvifers and coxites fused, setose with fine pubescence on lower 2/3 (Fig. 20C); subgenital plate absent.

Distribution. USA: NC, VA.

**Remarks.** *Lathrobium shermani* was previously known from only the holotype. Recently, additional specimens were collected in buried pipe traps in Stuart County, Virginia (Fig. 18). Fall (1917) did not state the method used to collect the holotype, but several attempts by the authors to recollect it at the type locality via litter sifting failed. In their checklist of Canadian beetles, Bousquet et al. (2013) listed *L. shermani* as occurring in Ontario, but this was due to a misidentification of *L. pallecens. Lathrobium shermani* is restricted to the southeastern USA.

*Lathrobium* (*Abletobium*) *smokiense* Haberski & Caterino, sp. nov. https://zoobank.org/63F86704-4FC0-4F62-85C9-94A7201D1F04

**Type material.** *Holotype* ♂ (FMNH): "USA: TN: Sevier Co., 35.6308°N, 83.3904°W, Mt. Kephart, V.6.2018, M. Caterino, Sifted Litter." / Caterino DNA voucher, Extraction MSC-6218., Extraction Date: XXX/ "CLEMSON ENT [QR CODE] CUAC000169009". *Paratypes* (21, FMNH, CUAC, GSNP): 2: same data as holo-type (CUAC000169008, CUAC000169010); 8: same locality as type, 35.6311°N, 83.3895°W, VI.5.2018 (CUAC000079121, CUAC000169007, CUAC000169011); 6: same locality as type, 35.6311°N, 83.3895°W, IX.14.2021 (CUAC000156757, CUAC000177157, CUAC000177158, CUAC000177159, CUAC000177160, CUAC000177161); 5: same locality as type, 35.6308°N, 83.3904°W, 6190ft, vi.05.2018 (CUAC000177152, CUAC000177153, CUAC000177154, CUAC000177156).

**Other material.** North Carolina: Haywood, Co.: Balsam Mountain Trail, 5167', Great Smoky Mountains National Park (35.6425, -83.2007), M.S. Caterino, 6 May 2020 (2, CUAC, GSNP); Haywood Co.: Big Cataloochee Mountain, 5725', Great Smoky Mountains National Park (35.6425, -83.2007), M.S. Caterino, C. Harden, 14 Jul 2020 (3: CUAC, GSNP); Haywood Co.: Big Cataloochee Mountain, 6107', Great Smoky Mountains National Park (35.6727, -83.1762), M.S. Caterino, 5 Nov 2020 (CUAC); Swain Co.: Clingmans Dome, 6364', Great Smoky Mountains

National Park (35.5613, -83.5006), M.S. Caterino, 5 Jun 2018 (CUAC); Swain Co.: Mills Overlook, Great Smoky Mountains National Park (35.6079, -83.4380), C. Harden, 29 Sep 2020 (CUAC); Haywood Co.: Mount Sterling Trail, 5586', Great Smoky Mountains National Park (35.6675, -83.1805), M.S. Caterino, 14 Jul 2020 (CUAC). Tennessee: Sevier Co.: Newfound Gap Rd., 4575', Great Smoky Mountains National Park (35.6237, -83.4163), M.S. Caterino, F. Etzler, 12 Mar 2020 (2, CUAC); Sevier Co.: Mount LeConte, 6467', Great Smoky Mountains National Park (35.6529, -83.4378), M.S. Caterino, 25 Jun 2019 (CUAC); Sevier Co.: Mount LeConte, 6467', Great Smoky Mountains National Park (35.6529, -83.4378), M.S. Caterino, 25 Jun 2019 (CUAC); Sevier Co.: Mount LeConte, 6571', Great Smoky Mountains National Park (35.6542, -83.4363), M.S. Caterino, 25 Jun 2019 (2, CUAC); Sevier Co.: Indian Gap, 5500', Great Smoky Mountains National Park, H. & A. Howden, 26 Apr 1956 (CNC).

**Diagnosis.** This species can be distinguished from its close relative, *L. bal-samense*, only by their aedeagi. In *L. smokiense*, the entire aedeagus is well sclerotized, whereas those of *L. balsamense* are more typical for the genus with distinct ventral processes (Fig. 9E, F vs Fig. 10D, E). Females can only be identified by geography, association with males, or DNA.

*Lathrobium smokiense* can be distinguished from *L. shermani* by the same characters given for *L. balsamense*.

**Description.** External morphology is identical to *L. balsamense* but differs in the aedeagus. Aedeagus (Fig. 9E, F) with median lobe entirely sclerotized, sides meeting at a seam on dorsal side to produce a tube; dorsal plate small and distal; internal sac without spines.

**Etymology.** The specific name refers to the Great Smoky Mountains where the species was first collected and is most abundant.

**Distribution and ecology.** *Lathrobium smokiense* inhabits spruce-fir forests above 1500 m in the Great Smoky Mountains (Fig. 13). It is not found north of the French Broad River basin (Asheville depression), where its microhabitat is inhabited by *L. lividum* and *L. islae*. It can be collected from leaf litter but is most often beneath bryophyte mats on boulders. One specimen was collected from wildcat dung. Collected May–Sep.

## Lathrobium (Abletobium) solum Haberski & Caterino, sp. nov.

https://zoobank.org/981FEB2B-311A-41A0-BAE6-85B55B380793

**Type material.** *Holotype* ♂ (FMNH): "USA: VIRGINIA: Botetourt Co., Jefferson NF, 0.25mi NW Blackhorse Gap parking, 37.42796N, 79.7558W, 2425ft., 24.May–19.July-2019, C.W Harden, Buried pipe trap baited with cheese, in gravelly soil, deciduous wooded rocky gully. BHG-02" / "CLEMSON ENT [QR CODE] CUAC000185155". *Paratypes* (6, VMNH, CUAC, FMNH): 6: same data as holotype (CUAC000185154, CUAC000177139, CUAC000177140, CUAC000177141, CUAC000177142, CUAC000177143).

**Diagnosis.** Can be distinguished from all other microphthalmous *Lathrobium*, except *L. absconditum*, by its large size and unadorned male sternite VIII. It differs from *L. absconditum* in its transverse middle antennomeres and widely separate gular sutures but is most easily recognized by the aedeagus. *Lathrobium solum* has a distinct stirrup-shaped major spine in the internal sac, and the ventral process reaches the dorsal plate in lateral view, unlike in *L. absconditum* (Fig. 21C).



Figure 21. *Lathrobium solum* **A** habitus **B** male sternite VIII **C** aedeagus in ventral view **D** aedeagus in lateral view. Scale bars: 1 mm.

**Description.** Habitus (Fig. 21A). Large species, total body length  $\sim$  9 mm long, FL 3.5 mm long. Coloration: body and appendages pale reddish, distal segments of antennae lighter.

Similar to *L. hardeni*, except gular sutures straight and widely separated, 1/8 width of head but narrowing slightly posteriorly. Eyes reduced to small white membranes without ommatidia, occupying 1/10 lateral width of head. Antennomeres II–IV elongate, gradually widening so that antennomeres V–IX are as long as wide. Pronotum without a visible line at midline; interstices shiny with no microsculpture. Posterior margin more sinuate.

♂: Posterior margin of sternite VIII with a broad, shallow emargination (Fig. 21B). Aedeagus 1.5 mm long; ventral process long, reaches dorsal plate, apex produced in an asymmetrical trunk (Fig. 21C, D); dorsal plate short and diamond-shaped; internal sac with five more-or-less symmetrical spines, two largest spines connected by a thin stirrup.

 $\bigcirc$ : Female unknown.

**Etymology.** The specific name is a play on words. In Latin *solum* can mean soil but also "lonely." This species is hypogean, and the males are alone until a female is found.

**Distribution and ecology.** *Lathrobium solum* is known only from the type locality in Botetourt County, Virginia (Fig. 18), where it was collected from a rocky gully in deciduous forest. All specimens were collected with buried pipe traps, suggesting they are hypogean. Collected May–July.

# *Lathrobium* (*Abletobium*) *thompsonorum* Haberski & Caterino, sp. nov. https://zoobank.org/E7FCB1CA-BEB0-4AD4-AC24-5722F61A29C6

Type material. *Holotype* ♂ (FMNH): "USA: KY: Monroe Co., 36.6579°N, 85.6259°W, Hestand, Thompson Ln., C.W.Harden, 28.v-3.ix.2022, Buried pipe trap, house-03" / "CLEMSON ENT [QR CODE] CUAC000185201". *Paratypes* (12, CUAC, CNCI, and FMNH): 1: same data as holotype (CUAC000177144); 1: same locality as type, 25.ii-8.v.2021 (CUAC000169037, DNA Extract MSC-7054); 5: same locality as type, 22.xii.2022–19.iv.2023; 5: same locality as type, 19.iv–17.vi.2023.

**Other material.** Kentucky: same data as holotype, CUAC000187892 (1 larva, CUAC).

**Diagnosis.** *Lathrobium thompsonorum* is the only microphthalmous *Lathrobium* known from west of the Appalachian Plateaus. Males can be distinguished by the unique, twisted ventral process of the aedeagus (Fig. 22E, F). Females have valvifers and coxites fully divided, which is unique among microphthalmous species in the Nearctic.

**Description.** Habitus (Fig. 22A). Mid-size species, total body length ~ 7.5 mm long, FL 3.0 mm long. Coloration: body and appendages pale reddish.

Similar to *L. hardeni*, except posterior angles of head more strongly rounded; gular sutures straight, separated by 1/10 width of head but narrowing slightly posteriorly. Eyes reduced to small white membranes without ommatidia, occupying 1/7 lateral width of head. Antennomeres II–IX obconic and longer than wide, V–VII twice as long as wide; apical antennomere longer, subacute. Pronotum with punctures spaced one diameter apart. Posterior margin of elytra more sinuate.

♂: Posterior margin of sternite VIII with rounded emargination, wider than deep; armed with two transverse combs of ~ 20, and one comb of 10 thick black setae (Fig. 22D). Aedeagus 1.4 mm long; ventral process long, asymmetrical, distal end twisted in lateral view (Fig. 22E, F); dorsal plate broad, distal end narrowing to curved point; internal sac with three spines, major spine longer than dorsal plate, 2× length of minor spines.

 $\bigcirc$ : Sternite VIII oblong (Fig. 22C); paraprocts undivided anteriorly, apices longer than basal portion; proctiger conical; sternum IX with coxites and valvifers





fully divided, equal in length (Fig. 22B), coxite narrower and setose, valvifer sinuate and glabrous; subgenital plate absent.

*First instar larva*: Body elongate, ~ 5 mm long; lightly sclerotized (Fig. 23A), head more sclerotized; head light brown, legs and body white, translucent.



**Figure 23**. *Lathrobium thompsonorum* first instar larva **A** habitus **B** nasale **C** mandible **D** maxilla **E** antenna. Scale bars: 1 mm (**A**); 250 μm (**B**); 500 μm (**C**, **D**, **E**).

Head ovate, strongly tapered posteriad (in dorsal view), dorsoventrally flattened, 1.3× as long as wide, dorsal setae as in Fig. 23A; head 3.6× wider than neck; dorsal ecdysial lines bifurcate 2/5 distance between neck and nasale margin; stemmata absent; anterior margin of nasale (Fig. 23B) as in *L. hardeni*, but median triangular tooth with edge serrated; Apotome of gula reaching tentoral pits.

Antennal (Fig. 23E) length ratios: 1.0:3.1:3.1:2; antennomere I triangular; antennomere II with two pores; antennomere III with three elongate macrosetae, three solenidia, one pore; antennomere IV club-shaped with apical solenidia; sensory appendage 0.8× as long as antennomere IV.

Mandibles (Fig. 23C) long, falciform, serrate along middle 1/3 of inner margin, with a single seta near base on outer ventral edge. Maxilla (Fig. 23D) with cardo triangular; stipes elongate, 1.6× longer than cardo; mala digitiform, tapering toward apex, 1.1× as long as palpomere I, with apical sensory appendages and two pores; palpifer with one seta. Maxilla as in *L. hardeni*, but palpomere length ratios: 1.0:1.2:2.5. Labium with prementum quadrate, basal 2/3 strongly sclerotized; ligula with elongate membranous apex, 4× as long as wide, densely fimbriate, separated from prementum by a lightly sclerotized transverse strip; palpomere I 1.4× as long as II; palpomere II bearing short sensilla at apex.

Dorsal sclerites of thorax with ecdysial lines along midline of body; prothorax narrow, 1.2× as long as wide, narrowed anteriorly, chaetotaxy as in Fig. 23A; thoracic tergite II subquadrate; tergite III wider than long; abdominal sclerites lightly sclerotized, with two small pleural sclerites per segment on each side; basal segment of urogomphus 3× as long as terminal segment, with seven prominent lateral setae; terminal segment of urogomphus slender, with one short and one long apical setae.

**Etymology.** Named in honor of the Thompson family, who own the property where this species was discovered and graciously allowed it to be collected.

**Distribution and ecology.** *Lathrobium thompsonorum* is known only from the type locality in Monroe County, Kentucky (Fig. 18). All specimens were collected with buried pipe traps, suggesting they are hypogean. Adult and larvae were collected in May, found in the same traps.

## Subgenus Apteralium Casey, 1905: 70.

## Lathrobium (Apteralium) brevipenne LeConte, 1863

Lathrobium brevipenne LeConte, 1863: 44. Apteralium brevipenne: Casey 1905: 78.

**Type material.** *Lectotype, Lathrobium brevipenne* LeConte, herein designated (MCZ): "[handwritten] *L. brevipenne* Lec. / III. / [red] Type 6447 / Lectotype *Lathrobium brevipenne* LeConte Desg. Haberski & Caterino."

**Other material.** USA: Arkansas: Logan Co.: 1 km E Lookout, Mt. Magazine, 23 May 1986, J. M. Campbell, oak-hickory leaf litter (11, CNC); Logan Co.: Brown Springs, Mt. Magazine, 23 May 1986, J. M. Campbell, leaf litter edge of stream (1, CNC); Logan Co.: Lookout, Mt. Magazine, 26 May 1986, J. M. Campbell, deciduous leaf litter (15 CNC); same locality, 14 Nov 2021, A. Haberski, P. Wooden (1 CUAC); Logan Co.: Cameron Bluffs, Mt. Magazine, 27 May 1986, J. M. Campbell, leaf litter at base of cliff (4 CNC); Logan Co.: Cove Lake Campground, 27 May 1986, J. M. Campbell (2 CNC); Stone Co.: Blanchard Springs St. Park, 18 May 1973, J. M. Campbell (1, CNC): same locality, 13 Nov 2021, A. Haberski, P. Wooden, litter on rocky outcrop (1, CUAC); Stone Co.: Sylamore Creek near

Gunner Pool Recreation Area, 21 May 2017, C. Harden, litter in dry run (1 CUAC); Franklin Co.: FSR 1510, near Ozark Highland Trail, 21 May 1986, J. M. Campbell (6 CNC); Franklin Co.: Ozark Highlands Trail, 22 May 2017, C. Harden, active at night (1 CUAC); Franklin Co.: Gray Springs, Ozark National Forest, 19 May 1986, J. M. Campbell, leaf litter edge of stream (2 CNC); Pulaski Co.: Pinnacle Mountain State Park, 11 May 1986, J. M. Campbell, flood debris on bank (1 CNC); Washington Co.: Lake Wedington area, 19 May 2017, C. Harden, litter in woods above lake (1 CUAC); Cross Co.: Village Creek State Park, 13 Nov 2021, A. Haberski, P. Wooden (1 CUAC). Illinois: Union Co.: Pine Hills Field Station, 15 May 1967, J. M. Campbell (2 CNC); same locality, 19 May 1967 (1 CNC); St. Clair Co.: 01 Aug 1967, G. W. Bock (1 CNC). Indiana: 'In.' (1 USNM). Iowa: 'Ia.' (5 USNM). Missouri: Boone Co.: Columbia, 02 May 2011 (1 CNC); Oregon Co.: Surprise Sinkhole Cave, 8.5 mi NE Alton, 26 Dec 1979, J. E. Gardener (1 CNC); St. Louis Co.: Clayton, 21 June 1983, B. F. & J. L. Carr (3 CNC).

**Diagnosis.** Both *L. camplyacra* and *L. carolinae* share a similar gestalt with *L. brevipenne*, but they are endemic to the southern Appalachian Mountains, so their ranges do not overlap. *Lathrobium brevipenne* can be distinguished from either species by genitalia. Its aedeagus is highly variable but is never fully sclerotized as in *L. camplyacra* and *L. carolinae*. Female genitalia of *L. brevipenne* are also variable, but all have larger and more sclerotized subgenital plates.

**Description.** Large species, body length 9 mm; body coloration dark red, appendages lighter. Eyes small; elytra shorter than pronotum. Females with paraprocts undivided, apices shorter than basal portion; sternite VIII strongly oblong. *Lathrobium brevipenne* which has several allopatric populations with distinct genitalic morphotypes and is likely a species complex (Figs 24–26). All morphotypes have a subgenital plate.

Distribution. USA: AR, IL, IN, IA, MO (Casey 1905).

## Lathrobium (Apteralium) camplyacra Haberski & Caterino, sp. nov. https://zoobank.org/74B8FA6C-392A-4D7E-985D-D370B075D6C5

Type material. *Holotype* ♂ (FMNH): "USA: NC: McDowell Co., 35.2784°N, 82.8008°W, Horse Cove Gap Trail, vii.23.2015, S. Myers, sifted litter." / "Caterino DNA voucher, Ext. MSC-7059" / "CLEMSON ENT [QR CODE] CUAC000168998". *Paratype* (11, CUAC, FMNH): 8: same data as holotype (CUAC000168999, CUAC000177162, CUAC000177163, CUAC000177164, CUAC000177165, CUAC000177166, CUAC000177167, CUAC000177168). 3: same locality as type, 35.2782°N, 82.8018°W.

**Other material.** North Carolina: Jackson Co.: Balsam Mountain Preserve, S. Myers, 15 Jun–7 Jul 2015 (20, CUAC, FMNH, CNC); Transylvania Co.: Courthouse Falls Trail, 3385' Nantahala National Forest (35.2716, -82.8964), S. Myers, 23 Jul 2015 (CUAC); Jackson Co.: Cowee Bald, 4926', Nantahala National Forest (35.3270, -83.3361), M.S. Caterino, 9 Jul 2019 (2, CUAC); Jackson Co.: Cowee Bald, 4931', Nantahala National Forest (35.3270, -83.3359), M.S. Caterino, 15 Sep 2020 (CUAC); Jackson Co.: Dark Ridge, 3467', Nantahala National Forest (35.3980, -83.1088), S. Myers, 19 Jun 2015 (CUAC); Jackson Co.:



Figures 24–26. *Lathrobium* terminalia **A** female terminalia **B** male sternite VIII **C** aedeagus in ventral view **D** aedeagus in lateral view. **24** *L*. *brevipenne* morphotype 1 **25** *L*. *brevipenne* morphotype 2 **26** *L*. *brevipenne* morphotype 3. Scale bars: 1 mm.

Sugarloaf Mountain, 4576', Nantahala National Forest (35.3699, -83.1212), S. Myers, 15 Jun 2015 (CUAC); Transylvania Co.: Toxaway Mountain, 4746', Nantahala National Forest (35.1321, -82.9842), M.S. Caterino, 13 Oct 2020 (CUAC); Jackson Co.: 6 km S Cashiers, 3198' Nantahala National Forest (35.085, -83.1015), A. Smetana, 20 Jun 1986(3, CNC); Jackson Co.: Whiteside Mountains, 4494–4921', Nantahala National Forest (35.0817, -83.13846), A. Smetana, 21 May 1986 (5, CNC). South Carolina: Oconee Co.: East Fork Chattooga River, Sumter National Forest (34.9843, -83.0981), S. Myers, 4 May 2015 (2, CUAC); Oconee Co.: Indian Camp Creek, Sumter National Forest (34.9899, -83.0724), S. Myers, 4 May 2015 (5, CUAC). Tennessee: Sevier Co.: Newfound, 5000', Great Smoky Mountains National Park (35.6127, -83.4246), A. Smetana, 09 Jun 1982 (CNC).

**Diagnosis.** This species can be distinguished from the closely related *L. carolinae* only by the genitalia. Aedeagi are similar, but those of *L. camplyacra* have bent ventral processes. The terminalia of female *L. camplyacra* have partially sclerotized subgenital plates and are longer and narrower than those of *L. carolinae*, with relatively shorter coxites. No intermediate forms are known.

Both *L. camplyacra* and *L. carolinae* share a similar gestalt with *L. brevipenne*. The latter is endemic to the Interior Highlands of the south-central Unit-

ed States. *Lathrobium brevipenne* can be distinguished from either species by genitalia. Its aedeagus is highly variable in shape but is never fully sclerotized (Figs 24–26). The females of *L. brevipenne* have larger, more sclerotized subgenital plates.

**Description.** External morphology (Fig. 5A) identical to *L. carolinae*. It differs only in the sexual characters.

♂: Aedeagus (Fig. 5E, F) with median lobe well sclerotized; ventral process strongly curved, distal tip lying beyond median foreman in lateral view; dorsal plate long; internal sac with three patches of rugose flagella, visible as one structure when invaginated.

 $\bigcirc$ : Apical lobes of paraproct shorter than continuous basal portion in dorsal view; proctiger conical; sternum IX with coxites and valvifers fully divided, coxites less than ½ length of valvifers (Fig. 5B); subgenital plate a lightly sclerotized chevron.

**Etymology.** The specific name is from the Greek *camplyo*- meaning bent, and *acra* meaning tip, in reference to the bent ventral process of the aedeagus.

**Distribution and ecology.** *Lathrobium camplyacra* inhabits mid-elevation (600–1600 m) hardwood forests in the Great Balsam, Plott Balsam, and Cowee Mountains of the southern Appalachians (Fig. 27). This area is bordered by the Cullasaja River and Little Tennessee River to the west, the Maggie Valley to the north, and the French Broad River Valley to the east. A single specimen from the CNC collection was reportedly collected from Newfound Gap in the Great Smoky Mountains, which is well outside of this range and needs to be verified.



Figure 27. Distribution of L. camplyacra (star), Lathrobium carolinae (circle).

#### Lathrobium (Apteralium) carolinae (Casey, 1905)

Apteralium carolinae Casey, 1905: 78. Lathrobium (Apteralium) carolinae: Bernhauer and Schubert 1912: 257.

**Type material.** *Lectotype*, *Apteralium carolinae* Casey, herein designated (USNM): "♂ / Highlands NC, Jun 6 88 / CASEY bequest 1925 / [red] *carolinae* – 2, TYPE USNM 38105 / Lectotype *Apteralium carolinae* Casey Desg. Haberski & Caterino."

Other material. USA: Georgia: Rabun Co.: Satoloh, 13 Jun 1957, R. M. Mason (3, CNC); Rabun Co.: Rabun Bald, 11 May 2021, M. Caterino (1, CUAC); Dillard Co.: 15 Apr 1948, F. Rapp (1, CNC); Union Co.: Brasstown Bald, 02 Jul 2020, M. Caterino (1, CUAC); same locality, 17 Sep 2020 (1, CUAC); Union Co.: Little Bald Mountain, 02 July 2020, M. Caterino (2, CUAC). North Carolina: same data as holotype (1, USNM); Macon Co.: Hwy 64 near Dry Falls NW Highlands, 16 May 1986, A. Smetana (1, CNC): Macon Co.: near Cliffside Lake Campground NW highlands 16 May 1986, A. Smetana (3, CNC); Macon Co.: Van Hook Glade, 4 mi W Highlands, 30 Aug 1967, J. M. & B. A. Campbell (1, CNC); Macon Co.: Copper Ridge Bald, 09 Jul 2019, M. Caterino (2, CUAC); Macon Co.: Forest Service Rd 77, 10 Jul 2020, A. Deczynski (1, CUAC); Macon Co.: Hickory Branch Trail, 26 Jul 2015, M. Caterino, S. Langton-Myers, hardwood litter (5, CUAC); Macon Co.: Hickory Gap, 16 Jul 2015, M. Caterino, S. Langton-Myers (1, CUAC); Macon Co.: Jones Gap, 16 July 2015, M. Caterino, S. Langton-Myers, litter around bracket fungus (8, CUAC); same data, except 22 July 2015, hardwood litter against logs (4, CUAC); Macon Co.: Wayah Bald Rd, 18 Apr 2020, C. Harden, under rock by seep (1, CUAC); Clay Co.: Chunky Gal Trail, 01 Sep 2020, M. Caterino, S. Langton-Myers (1, CUAC); Clay Co.: Riley Knob, 11 May 2020, M. Caterino (1, CUAC); Clay Co.: Shooting Creek Bald, 11 May 2020, M. Caterino (1, CUAC); Caly Co.: Tusquitee Bald, 06 Jul 2021, M. Caterino (1, CUAC); Cherokee Co.: London Bald Trail, 26 Jul 2015, M. Caterino, S. Langton-Myers, hardwood litter (4, CUAC); Graham Co.: Cherohala Skyway, 27 Sep 2020, C. Harden (1, CUAC); Graham Co.: Huckleberry Knob, 04 May 2020, M. Caterino (1, CUAC); same data, except 13 Oct 2020 (2, CUAC); Joyce Kilmer Memorial Forest, 24 Jun 2015, M. Caterino, S. Langton-Myers (8, CUAC); same data, except 20 Jul 2015 (7, CUAC); Graham Co.: Teyahalee Bald, 09 Jul 2019, M. Caterino (1, CUAC); Haywood Co.: Balsam Mountain Trail, 05 Sep 2020, M. Caterino (1, CUAC); Haywood Co.: Pisgah National Forest, 14 July 2020, A. Deczynski (1, CUAC); Swain Co.: Miller Cove Trail, 20 July 2015, M. Caterino, S. Langton-Myers (1, CUAC); Swain Co.: Smokemont Campground, 10 km N Cherokee, 09 Jun 1982, A. Davies (9, CNC); Swain Co.: Lakeshore Trail, Great Smoky Mountains National Park, 18 July 2003, A. Tishechkin (2, LSAM); Transylvania Co.: Twentymile Trail near Twentymile Creek, 19 Oct 2007, I. M. Sokolov, litter on rock explosion (1, LSAM). Tennessee: Blount Co.: Cades Cove, Great Smoky Mountains National Park, Jun 1954, H. Howden (1, CNC); Blount Co.: Greenbrier Cove, Great Smoky Mountains National Park, 27 Jun 2001, C. Carlton, A. Tishechkin, V. Moseley (1, LSAM); Monroe Co.: Indian Boundary Camp, 28 May 2020, C. Harden (1, CUAC).

**Diagnosis.** This species can be distinguished from *L. camplyacra* only by the genitalia. Aedeagi are similar but the ventral processes of *L. carolinae* are straight, not bent as those of *L. camplyacra*. The terminalia of female *L. carolinae* 



**Figure 28**. *Lathrobium carolinae* second instar larva **A** habitus **B** head in lateral view **C** nasale **D** mandible **E** maxilla **F** antenna. Scale bars: 1 mm (**A**, **B**); 100 μm (**C**); 250 μm (**D**, **E**, **F**).

lack subgenital plates and are shorter and wider than those of *L. camplyacra*. No intermediate forms are known.

*Lathrobium carolinae* can be distinguished from *L. brevipenne* by the same characters given for *L. camplyacra*.

**Description.** The original description lacked a description of the genitalia. We present descriptions and illustrations of the male and female genitalia, as well as the first description of the mature larva.

♂: Aedeagus 1.7 mm long (Fig. 4D, E), median lobe well sclerotized; ventral process relatively straight, distal tip not bending beyond median foreman in lateral view; dorsal plate long; internal sac with three patches of rugose flagella, visible as two structures when invaginated.

 $\bigcirc$ : Paraprocts undivided anteriorly, apices shorter than basal portion; proctiger conical; sternum IX with coxites and valvifers fully divided, coxites <sup>3</sup>/<sub>4</sub> length of valvifers (Fig. 4A); subgenital plate absent.

**Second instar larva:** Larvae were associated with adults by DNA barcoding. Body elongate, ~ 5 mm long; well sclerotized (Fig. 28A); head, thoracic, and abdominal tergites brown, appendages light yellow, intersegmental membrane white, translucent.

Head ovate, widest at stemmata and slightly tapered posteriad (in dorsal view), dorsoventrally flattened, 1.3× as long as wide; dorsal setae as in Fig. 28A; head 2.9× as wide as neck; dorsal ecdysial lines bifurcate 3/8 distance between neck and nasale margin; six stemmata present, arranged as in Fig. 28B; anterior margin of nasale (Fig. 28C) with nine blunt teeth pointing anteriorly, one round median tooth with edge serrated, a pair of paramedian teeth, and three pairs of lateral teeth; innermost lateral teeth are small and indistinct; paramedian and lateral teeth armed with nodular setae, and a pair of nodular setae separate median and paramedian teeth; Apotome of gula reaching tentoral pits.

Antennae (Fig. 28F) length ratios: 1.0:2.7:2.8:1.5; antennomere I triangular; antennomere II with two pores; antennomere III with three elongate macrosetae, three solenidia, one pore, and a curved sensory appendage 2/3 as long as terminal antennomere; antennomere IV club-shaped with apical solenidia; sensory appendage 0.6× as long as antennomere IV.

Mandibles (Fig. 28D) long, falciform, serrate along middle 1/3 of inner margin, with a single seta near base on outer ventral edge. Maxilla (Fig. 28D) with cardo triangular; stipes elongate, 1.3× longer than cardo; mala digitiform, tapering toward apex, 0.7× as long as palpomere I, with apical sensory appendages and two pores; palpifer with one seta. Maxillary palpomere length ratios: 1.0:1.2:2.2; palpomere II with two setae; palpomere III with one basal sensory appendage and numerous small apical appendages. Labium with prementum trapezoidal, basal <sup>3</sup>/<sub>4</sub> strongly sclerotized; ligula with elongate membranous apex, 3× as long as wide, densely fimbriate, separated from prementum by a distinctly sclerotized transverse strip; palpomere I 1.8× as long as II; palpomere II bent near apex and bearing short sensilla at apex.

Dorsal sclerites of thorax with ecdysial lines along midline of body (Fig. 28A); prothorax narrow, 1.3× as long as wide, widest posteriorly and narrowing anteriorly, chaetotaxy as in Fig. 28A; thoracic tergites II and III subequal in width and length; abdominal sclerites well sclerotized, with two small pleural sclerites per segment on each side; urogomphi broken off of only known specimen.

**Distribution and ecology.** *Lathrobium carolinae* inhabits mid-elevation (600–1600 m) hardwood forests in the Appalachian Mountains, from Georgia to the French Broad River basin in North Carolina (Fig. 28), except in those ranges occupied by *L. camplyacra* as described above. Collected Feb–Oct.

## Subgenus Lathrobioma Casey, 1905: 72.

#### Lathrobium (Lathrobioma) divisum LeConte, 1880

Lathrobium divisum LeConte, 1880: 176. Lathrobium franciscanum Casey, 1905: 84. New synonym.

**Type material.** *Lectotype*, *Lathrobium divisum* LeConte, herein designated (MCZ): "Vanc. / [handwritten] L. divisum Lec. / COLLECTION / TYPE [handwritten] *divisum* / [red] Type 6453 / Lectotype *Lathrobium divisum* LeConte Desg. Haberski & Caterino." *Lectotype*, *Lathrobium franciscanum* Casey, herein designated (USNM): "LosGatos CAL/ CASEY bequest 1925 / [handwritten] *Los Gatos is in Santa Clara Co. not far from Sta. Cruz California* / [red] TYPE USNM 38114 / Lectotype *Lathrobium franciscanum* Casey Desg. Haberski & Caterino."

**Other material.** USA: California: Santa Clara Co.: Los Gatos (1, USNM); Mendocino Co.: Gualala (1, USNM); Illinois (1, MCZ).

**Diagnosis.** This species can be distinguished from other *Lathrobioma* by its large size. Additionally, males are the only *Lathrobioma* to lack an emargination on sternite VIII and have an asymmetrical aedeagus. Females have paraprocts subequal in length to the basal portion of tergite IX, while other species have paraprocts that are short or fully divided.

**Description.** Large species, body length 7–8 mm. Body coloration red, elytra bicolored, appendages lighter yellow. Gular sutures arcuate; antennomeres V– VII as long as wide. Elytra as long as pronotum. Females with paraprocts undivided, apices as long as basal portion; sternite VIII weakly oblong. Male sternite VIII without emargination, thick black setae at apex; genitalia as in Fig. 29.

Distribution. Canada: BC. USA: CA, IL, OR, WA (Newton 2022).

**Remarks.** Lathrobium franciscanum is reduced to synonymy with Lathrobium divisum because the distinguishing characters given by Casey (1905) were insufficiently distinctive. Lathrobium franciscanum was described from one female and one male, which were differentiated from *L. divisum* based on subtle morphological differences in somatic characters. Its body was supposedly "more slender," punctures "somewhat sparser," head "not so large," and prothorax "slightly narrower" than the head as opposed to "much narrower" in *L. divisum* (Casey 1905). These differences are difficult to see and fall within the range of intraspecific variation in longer series of other Lathrobium. We examined the genitalia of both species and found no differences in the shape of their aedeagi.

Casey (1905) placed *L. divisum* in *Lathrobium* s. str., but after examining the types, we transfer it to *Lathrobioma* based on the following synapomorphies: metatarsi compact, tarsomeres I–IV subequal in length, each ~ 1/3 as long as fifth tarsomere; maxillary palpomere III more than 0.4× as wide as long; and male sternite VIII with bristles positioned apically. The final character is presented here for the first time.

#### Lathrobium (Lathrobioma) nanulum (Casey, 1905)

Lathrobioma nanula Casey, 1905: 100. Lathrobium (Lathrobioma) nanulum: Bernhauer and Schubert 1912: 264.



Figures 29–34. *Lathrobium* terminalia **A** female terminalia **B** male sternite VIII **C** aedeagus in ventral view **D** Aedeagus in lateral view. **29** *L*. *divisum* **30** *L*. *nanulum* **31** *L*. *othioides* **32** *L*. *scolopaceum* **33** *L*. *tenue* **34** *L*. *amplipenne*. Scale bars: 1 mm.

**Type material.** *Lectotype*, *Lathrobioma nanula* Casey, herein designated (USNM): "MASS / CASEY bequest 1925 / [red] TYPE USNM 38139 / [handwritten] *nanula* / Lectotype *Lathrobioma nanula* Casey Desg. Haberski & Caterino."

**Other material.** Same data as lectotype (1, USNM).

**Diagnosis.** Lathrobium nanulum can be distinguished from other Lathrobioma by unique genitalic characters. The ventral process of the aedeagus is narrow instead of broad. Female sternum IX with valvifers and coxites fully divided instead of fused.

**Description.** Small species, body length 5 mm; body and appendages dark red coloration. Gular sutures arcuate; antennomeres V–VII wider than long; maxillary palpomere III more than 0.4× as wide as long. Elytra 1.2× longer than pronotum. Females with paraprocts undivided, apices shorter than basal portion; sternite VIII oblong. Dorsal plate and ventral process of aedeagus with large apical teeth (Fig. 30).

Distribution. USA: MA.

**Remarks.** Blackwelder (1939), in his revision of the paederine genera, placed *L. nanulum* in the subgenus *Deratopeus*, now a synonym of the genus *Tetartopeus*, without providing any explanation. We transfer it back to *Lathrobioma*, because it lacks any of the defining characters of *Tetartopeus*, such as a narrow neck, but does share the subgeneric synapomorphies of *Lathrobioma* listed above for *L. divisum*.

#### Lathrobium (Lathrobioma) othioides LeConte, 1880

Lathrobium othioides LeConte, 1880: 175.

Lathrobioma othioides: Casey 1905: 101.

Lathrobium (Lathrobioma) inops Casey, 1885: 135; Bernhauer and Schubert 1912: 264 [in error].

**Type material.** *Lectotype*, *Lathrobium othioides* LeConte, herein designated (MCZ): "Mas. /  $\Im$  / [handwritten] *L. othioides* Lec. / [red] Type 6448 / Lectotype *Lathrobium othioides* LeConte Desg. Haberski & Caterino."

**Other material.** Canada: Lake Superior (2, USNM). USA: Iowa: 'Ia.' (1, USNM). Massachusetts: 'Mass.' (5, MCZ); Norfolk Co.: Brookline, 21 Mar 1899 (1, MCZ); same locality, 17 Apr 1899, C. A. Frost (1, CUAC); same data, except 09 Apr 1899 (1, MCZ); 'Mass' (1, USNM). New Jersey: 'N.J.?' (2, USNM).

**Diagnosis.** Males have distinctive aedeagi with the apex of the ventral process divided into two projecting horns, absent in all other *Lathrobioma*. Females can be difficult to distinguish from *L. tenue*, but their gonocoxites are generally more robust and convex in the basal half.

**Description.** Body length 6 mm; body coloration dark red, appendages lighter red. Gular sutures arcuate; maxillary palpomere III > 0.4× as wide as long; antennomeres V–VII as wide as long. Elytra as long as pronotum. Females with paraprocts undivided, apices shorter than basal portion; sternite VIII weakly oblong. Aedeagus with characteristic projections of ventral process (Fig. 31).

**Distribution.** Canada: ON, NB, QC (Bousquet et al. 2013). USA: IA, **NJ**, MA, RI. **Remarks.** Bernhauer and Schubert (1912) listed *L. inops* as a synonym of *L. othioides*, but after comparing the types, we determined this was incorrect. The

aedeagus of *L. othioides* is quite distinctive and that of the *L. inops* lectotype did not match it. Instead, it was indistinguishable from that of *L. scolopaceum*, with which we synonymize *L. inops* below.

#### Lathrobium (Lathrobioma) scolopaceum (Casey, 1905)

Lathrobioma scolopacea Casey, 1905: 103. Lathrobium (Lathrobioma) scolopaceum: Bernhauer and Schubert 1912: 267. Lathrobioma dakotana Casey, 1905: 100. New synonym. Lathrobium (Lathrobioma) dakotanum: Bernhauer and Schubert 1912: 258. Lathrobioma virginica Casey, 1905: 99. New synonym. Lathrobium (Lathrobioma) virginicum: Bernhauer and Schubert 1912: 269. Lathrobioma inops Casey, 1885; Casey 1905: 103. New synonym. Lathrobium (Lathrobioma) inops: Blackwelder 1939, 108.

**Type material.** *Lectotype*, *Lathrobioma scolopacea* Casey, herein designated (USNM): "B MASS / CASEY bequest 1925 / [red] TYPE USNM 38143 / [handwritten] *scolopacea* / Lectotype *Lathrobioma scolopacea* Casey Desg. Haberski & Caterino." *Lectotype*, *Lathrobioma dakotana* Casey, herein designated (USNM): "[handwritten] Bismarck Dak / CASEY bequest 1925 / [red] TYPE USNM 38136 / [handwritten] *Lathrobioma dakotana* / Lectotype *Lathrobioma dakotana* Casey Desg. Haberski & Caterino." *Lectotype*, *Lathrobioma dakotana* / Lectotype *Lathrobioma dakotana* Casey Desg. Haberski & Caterino." *Lectotype*, *Lathrobioma virginica* Casey, herein designated (USNM): "Grafton WV / CASEY bequest 1925 / [red] TYPE USNM 38139 / Lectotype *Lathrobioma virginica* Casey Desg. Haberski & Caterino." *Lectotype*, *Lathrobioma inops* Casey, herein designated (USNM): "L.Sup /  $\mathcal{A}$  / CASEY bequest 1925 / [red] TYPE USNM 38144 / Lectotype *Lathrobioma inops* Casey Desg. Haberski & Caterino."

**Other material.** Canada: Ontario: 'L. Sup' (1, USNM). USA: Massachusetts: 'Mass' (2, USNM); Middlesex Co.: Framingham, 1944, C. A. Frost (1, MCZ). Maine: Knox Co.: Isle-au-haut, Aug 1905 (1, MCZ). New Hampshire: Grafton Co.: Downes Brook, Potash Mountain, 05 Jun 2021, A. Haberski (2, CUAC); Grafton Co.: Mount Lafayette, 04 Jun 2012, A. Haberski (1, CUAC); Strafford Co.: Spruce Hole Conservation Area, D. S. Chandler (1, UNHC); Grafton Co.: Hubbard Brook Experimental Forest, D. S. Chandler (1, UNH).

**Diagnosis.** Females of *L*. *scolopaceum* are readily distinguished from all other *Lathrobioma* by their divided paraprocts. Males can be distinguished by their uniquely shaped aedeagus, which has a ventrally projected apex of the ventral process.

**Description.** Body length 6 mm; coloration reddish, appendages lighter. Gular sutures arcuate; maxillary palpomere III > 0.4× as wide as long; antennomeres V–VII as long as wide. Elytra at least as long as pronotum, sometimes longer and wider. Females with paraprocts divided; sternite VIII weakly oblong. Characteristic aedeagus as in Fig. 32.

**Distribution.** Canada: ON, NB, NS, QC (Bousquet et al. 2013). USA: IA, MA, ME, NH, ND, RI, VA, **WV** (Newton 2022).

**Remarks.** We reduce *Lathrobium dakotanum*, *Lathrobium virginicum*, and *Lathrobium inops* to synonymy with *Lathrobium scolopaceum* because the distinguishing characters given by Casey (1905) were inaccurate. *Lathrobium dakotanum* 

and *L. virginicum* were each described from a single female and differentiated from *L. scolopaceum* based on their elytra being at least equal in length to the pronotum, as opposed to "much shorter" (Casey 1905). We measured the specimens in Casey's collection and found that the elytra of *L. scolopaceum* were 1.1× longer the pronotum, approximately the same as that of *L. dakotanum* and *L. virginicum*.

*Lathrobium virginicum* was further differentiated by having a head as wide as its elytra, as opposed to narrower in *L. scolopaceum*, *L. dakotanum*, and *L. inops*. Upon measuring, we found all four species have a head wider than their pronotum.

*Lathrobium inops* was distinguished as being larger and more slender than *L. scolopaceum* (Casey, 1905), but this was not the case.

The genitalia are identical in all four species.

## Lathrobium (Lathrobioma) tenue LeConte, 1863

Lathrobium tenue LeConte, 1863: 44. Lathrobioma tenuis Casey, 1905: 101. Lathrobioma hespera Casey, 1905: 100. New synonym. Lathrobium (Lathrobioma) hesperum: Bernhauer and Schubert 1912: 261 Lathrobium anigrolinea Casey, 1905: 102. New synonym. Lathrobium (Lathrobioma) nigrolinea: Bernhauer and Schubert 1912: 264. Lathrobium (Lathrobioma) nigrolineum: Blackwelder 1939: 108. Lathrobioma oregona Casey, 1905: 102. New synonym. Lathrobium (Lathrobioma) oregonum Bernhauer and Schubert 1912: 264. Lathrobium (Lathrobioma) oregonum Bernhauer and Schubert 1912: 264. Lathrobium (Lathrobioma) oregonum Bernhauer and Schubert 1912: 264. Lathrobium (Lathrobioma) shoshonicum Bernhauer and Schubert 1912: 267.

**Type material.** *Lectotype*, *Lathrobioma tenuis* Casey, herein designated (MCZ): Pink Disc / "[handwritten] *L. tenue* Lec. / [red] Type 6452 / Lectotype *Lathrobium tenue* LeConte Desg. Haberski & Caterino." *Lectotype*, *Lathrobioma hespera* Casey, herein designated (USNM): "Br.C/ CASEY bequest 1925 / [red] TYPE USNM 38140 / Lectotype *Lathrobioma hespera* Casey Desg. Haberski & Caterino." *Lectotype*, *Lathrobioma nigrolinea* Casey, herein designated (USNM): "Winnipeg Man./ CASEY bequest 1925 / [handwritten] *nigrolinea* / [red] TYPE USNM 38141 / Lectotype *Lathrobioma nigrolinea* Casey Desg. Haberski & Caterino." *Lectotype*, *Lathrobioma oregona* Casey, herein designated (USNM): "Port Oreg/ CASEY bequest 1925 / [handwritten] *oregona* / [red] TYPE USNM 38142 / Lectotype *Lathrobioma oregona* Casey Desg. Haberski & Caterino." *Lectotype*, *Lathrobioma shoshonica* Casey, herein designated (USNM): "Or. / O / CASEY bequest 1925 / [handwritten] *shoshonica* / [red] TYPE USNM 38138 / Lectotype Lathrobioma shoshonica Casey Desg. Haberski & Caterino."

**Other material.** Canada: Ontario (3, MCZ). USA: Colorado: Alamosa (1, MCZ). Connecticut: New Haven (1, USNM). Michigan: 'Mic.' (1, MCZ). Oregon: 'Oreg' (1, USNM). Rhode Island: 'R.I.' (7, USNM). Virginia: Highland Co.: Water Sinks, Lucas Tract, 04 May 2019, C. Harden, gravel stream bank (1, CUAC). West Virginia: Pocahontas Co.: Cranberry Wilderness, Monongahela National Forest, 11 Jun 2019, C. Harden, under rock near stream in spruce/hardwoods (1, CUAC).

**Diagnosis.** Males of *L. tenue* have a broadly rounded and symmetrical ventral process of the aedeagus that is unique among *Lathrobioma* spp. Females

are difficult to differentiate from *L. othioides*, but their gonocoxites are narrower and concave in the basal half.

**Description.** Body length 6 mm; coloration dark, appendages yellow or light red. Gular sutures arcuate; maxillary palpomere III > 0.4× as wide as long; antennomeres V–VII as long as wide. Elytra at least as long as pronotum, sometimes longer and wider. Females with paraprocts undivided, apices shorter than basal portion; sternite VIII weakly oblong. Ventral process of aedeagus broadly rounded (Fig. 33).

Distribution. Canada: BC, MB, ON, QC, SK (Bousquet et a. 2013). USA: CO, CT, ID, MA, MI, NY, OR, RI, VA, WA, WV (Newton 2022).

**Remarks.** We reduce *Lathrobium hesperum*, *Lathrobium oregonum*, *Lathrobium nigrolinea*, and *Lathrobium shoshonicum* to synonymy with *Lathrobium tenue* due to insufficient morphological differences between species. *Lathrobium shoshonicum* and *L. hesperum* were described as having elytra longer than their pronota, in contrast to *L. tenue* which supposedly had elytra shorter than their pronota. However, upon measuring the type specimen and those in Casey's collection, we found *L. tenue* also has elytra longer than its pronotum.

Lathrobium oregonum and L. nigrolinea were differentiated primarily on the shape of the emargination of male sternite VIII. In these species, the setae at the tips of the emargination are inflexed, rather than diverging as in L. tenue. This difference was based on a single male of each species and could represent normal variation, regional difference, or coincidence.

We examined the genitalia of all five species and found no differences.

## Subgenus Lathrobium s. str.

Litolathra Casey, 1905: 71. Lathrobium (Litolathra): Bernhauer and Schubert 1912: 40.

#### Lathrobium (Lathrobium) amplipenne Casey, 1905

Lathrobium amplipenne Casey, 1905: 81.

**Type material.** *Lectotype*, *Lathrobium amplipenne* Casey, herein designated (USNM): "N. Y. / CASEY bequest 1925 / [red] TYPE USNM 38107 / [handwritten] *Lathrobium amplipenne* / Lectotype *Lathrobium amplipenne* Casey Desg. Haberski & Caterino."

**Other material.** Illinois: Union Co., 1 mi E Wolf Lake, 8.V.1976, A. Smetana (2, CNC); 2 mi NE Reynoldsville, 9.V.1976, A. Smetana (1, CNC). Indiana: Tippecanoe Co., 27.X.1956, N.M. Downie (1, CNC). Louisiana: Concordia Pa. [Park?], 5 mi W Ferriday, 1.V.1976, A. Smetana (1, CNC). Missouri: St. Louis Co., 9.V.1920, G.W. Bock (1, CNC). New York: Tompkins Co.: Ithaca Valley, (9, USNM). Pennsylvania: 'Penn.'. F. C. Bowditch (1, MCZ). South Carolina: Charleston Co.: Ravenel, 05 May 2001, J. C. Ciegler, UV light (2, CUAC); Dorchester Co.: Bluff Trail, McAlheny Nature Preserve, Reevesville, 11 May 2013, J. C. Ciegler (1, CUAC); Marion Co.: Woodbury, 10 Sep 2011, J. C. Ciegler (1, CUAC).

**Diagnosis.** The habitus of this species closely resembles that of *L. armatum*, *L. geminum*, *L. praelongum*, and *L. pedale*. Males differ from those species in

their unique sternite VIII, which has three small emarginations at the apex and two longitudinal patches of dense setae (Fig. 34B). Females are difficult to tell apart from *L. armatum* and *L. praelongum*. Their paraprocts are slightly shorter than those of *L. armatum*, and longer than those of *L. amplipenne*, relative to the basal portion of tergite IX. Females can be easily distinguished from *L. geminum*, which has gonocoxites shorter than paraprocts, and *L. pedale*, which has valvifers and coxites divided.

**Description.** Large species, body length 10 mm; body coloration dark, appendages lighter red, elytra bicolored. Gular sutures converging, nearly touching posteriorly; antennomeres V–VII longer than wide. Elytra 1.3× as long as pronotum. Females with paraprocts undivided, apices shorter than basal portion; sternite VIII conical with shallow notch at tip. Male sternite VIII with three emarginations (Fig. 34B). Genitalia as in Fig. 34. The length of the ventral process of the aedeagus can vary.

Distribution. Canada: ON, NB, QC (Bousquet et al. 2013). USA; IL, IN, LA, MI, MO, NY, PA, SC.

#### Lathrobium (Lathrobium) armatum Say, 1830

Lathrobium armatum Say, 1830: 40. Lathrobium deceptivum Casey, 1905: 83. New synonym. Lathrobium nigrolucens Casey, 1905: 83. New synonym. Lathrobium procerum Casey, 1905: Bernhauer and Schubert 1912: 255. Lathrobium subaequale Casey, 1905: 82. New synonym.

**Type material.** Holotype not examined. It was presumably lost with much of Say's collection (Mawdsley, 1993). *Lectotype* Lathrobium deceptivum Casey, herein designated (USNM): "N.Y. / CASEY bequest 1925 / [red] TYPE USNM 38108 / [handwritten] deceptivum / Lectotype Lathrobium deceptivum Casey Desg. Haberski & Caterino." *Lectotype* Lathrobium subaequale Casey, herein designated (USNM): "N.J. / CASEY bequest 1925 / [red] TYPE USNM 38110 / [handwritten] subaequale / Lectotype Lathrobium subaequale Casey Desg. Haberski & Caterino." *Lectotype* Lathrobium subaequale Casey Desg. Haberski & Caterino." *Lectotype* Lathrobium subaequale Casey Desg. Haberski & Caterino." *Lectotype* Lathrobium procerum Casey, herein designated (USNM): "III. / CASEY bequest 1925 / [red] TYPE USNM 38110 / [handwritten] procerum / Lectotype Lathrobioma procerum Casey Desg. Haberski & Caterino." *Lectotype* Lathrobium attin designated (USNM): "III. / CASEY bequest 1925 / [red] TYPE USNM 38110 / [handwritten] procerum / Lectotype Lathrobioma procerum Casey Desg. Haberski & Caterino." *Lectotype* Lathrobium attin designated (USNM): "III. / CASEY bequest 1925 / [red] TYPE USNM 38110 / [handwritten] procerum / Lectotype Lathrobioma procerum Casey Desg. Haberski & Caterino." *Lectotype* Lathrobioma nigrolucens Casey Desg. Haberski & Caterino."

**Other material.** Canada: Ontario (1, USNM). Quebec: MRC des Deux-Montagnes, Parc National d'Oka, 06 May 2023, R. Vigneault, handpicked near a beach (1, NBC). USA: Illinois (6, USNM). Indiana: Allen Co.: New Haven, 15 Jun 1986, N. M. Downie (1, UNHC). Massachusetts: 'Mass.' (1, MCZ). Michigan: 'Mi.' (2, MCZ). Missouri: 'Mo.' (1, MCZ). New Hampshire: Strafford Co.: Spruce Hole Conservation Area, 3 mi SW Durham, 09 Jun 1982, D. S. Chandler, bog margin in oak, beech, huckleberry litter (17, UNCH); same data, except 16 Apr 1982, marsh (1, UNHC); same data, except 22 Apr 1982, near bog edge (2, UNHC); same data, except 30 Aug 1982, along pond (5, UNHC); Hillsborough Co.: Antrim, 11 Jun 1932, C. A. Frost (1, UNHC); Rockingham Co.: Hampton, 15 Mar 2003, S. A. Shaw (1, UNHC); Rockingham Co.: Hampton, 10 Jun 2011 (1, UNHC); Grafton Co.: Rumney, 22 Apr 1926, P. J. Darlington (1, MCZ). New York (7, USNM); North Carolina (1, MCZ). Vermont: Burlington Co., Apr 1953, D. S. Chandler (1, UNHC).

**Diagnosis.** *Lathrobium armatum* is similar in external appearance to *L. amplipenne* and *L. pedale* and are especially difficult to distinguish form *L. praelongum*. The female terminalia of *L. armatum* are shorter with a more convex inner margin, and its paraprocts are longer relative to the basal portion of tergite IX than in the aforementioned species. Males are easily identified by their aedeagus, which has a unique rear-facing hook projecting form the apex of the dorsal plate.

**Description.** Large species, body length 10 mm; body coloration dark, appendages red, elytra sometimes bicolored. Gular sutures converging, nearly touching posteriorly; antennomeres V–VII as wide as long. Elytra 1.3× longer than pronotum. Females with paraprocts undivided, apical lobes shorter than basal portion,  $\sim 0.9 \times$  as long; sternite VIII conical. Male sternite VIII either with a small round emargination or no emargination. Dorsal plate of aedeagus with large, rear-facing hook (Fig. 35).

Distribution. Canada: ON, NB, QC (Bousquet et al. 2013). USA: DC, IL, IN, MA, MI, MO, NH, NJ, NY, NC, SC, VT.

**Remarks.** We reduce *Lathrobium deceptivum*, *Lathrobium nigrolucens*, and *Lathrobium subaequale* to synonymy with *Lathrobium armatum* based on a lack of distinguishing morphological characters. Casey recognized that the herein synonymized species were difficult to discriminate and that they might not be full species. He differentiated them based on a combination of elytra length and color. *Lathrobium subequale* was described as having bicolored elytra, in contrast to the solid black elytra of *L. armatum*. However, this character is variable and specimens of *L. armatum* in LeConte's collection have lightly bicolored elytra. *Lathrobium deceptivum* and *L. nigrolucens* were distinguished from *L. armatum* based on the length of elytra relative to pronotum, but many species are dimorphic for this character. *Lathrobium deceptivum* was described from two males, *L. subaequale* from a single female, and *L. nigrolucens* from a short series of both. Genitalia of all of the above species were indistinguishable.

## Lathrobium (Lathrobium) confusum LeConte, 1880

Lathrobium confusum LeConte, 1880: 176. Litolathra confusa (LeConte, 1880): Casey 1905: 96. Litolathra amputans Casey, 1905: 95. New synonym. Lathrobium (Litolathra) amputans: Bernhauer and Schubert 1912: 255. Litolathra convictor Casey, 1905: 95. New synonym. Lathrobium (Litolathra) convictor: Bernhauer and Schubert 1912: 257. Litolathra inornata Casey, 1905: 96. New synonym. Lathrobium (Litolathra) inornatum: Bernhauer and Schubert 1912: 261. Litolathra suspecta Casey, 1905: 97. New synonym. Lathrobium (Litolathra) suspectum: Bernhauer and Schubert 1912: 268.

**Type material.** *Lectotype*, *Lathrobium confusum* LeConte, herein designated (MCZ): White disc / "[handwritten] L. confusum Lec. / [handwritten] 8117 / [red]

Type 6456 / Lectotype Lathrobium confusum LeConte Desg. Haberski & Caterino." Lectotype, Litolathra amputans Casey, herein designated (USNM): "Ia. / CASEY bequest 1925 / [red] TYPE USNM 38132 / [handwritten] amputans / Lectotype Litolathra amputans Casey Desg. Haberski & Caterino." Lectotype, Litolathra convictor Casey, herein designated (USNM): "City ham / CASEY bequest 1925 / [red] TYPE USNM 38130 / [handwritten] convictor / Lectotype Litolathra convictor Casey Desg. Haberski & Caterino." Lectotype Litolathra convictor Casey Desg. Haberski & Caterino." Lectotype, Litolathra inornata Casey, herein designated (USNM): "Wshngtn D.C. / CASEY bequest 1925 / [red] TYPE USNM 38133 / [handwritten] inornata / Lectotype Litolathra inornata Casey Desg. Haberski & Caterino." Lectotype Litolathra inornata Casey Desg. Haberski & Caterino." Lectotype Litolathra inornata Casey Desg. Haberski & Caterino." Lectotype Litolathra isey, herein designated (USNM): "N.Y. /  $\casey$  Desg. Haberski & Caterino." Lectotype Litolathra Sey, herein designated (USNM): "N.Y. /  $\casey$  Desg. Haberski & Caterino." Lectotype Litolathra Sey, herein designated (USNM): "N.Y. /  $\casey$  Desg. Haberski & Caterino." Lectotype Litolathra Sey, herein designated (USNM): "N.Y. /  $\casey$  Desg. Haberski & Caterino." Lectotype Litolathra Sey, herein designated (USNM): "N.Y. /  $\casey$  Desg. Haberski & Caterino." Lectotype Litolathra Sey, herein designated (USNM): "N.Y. /  $\casey$  Desg. Haberski & Caterino."

Other material. USA: Connecticut: New Haven Co.: New Haven (5, USNM). Massachusetts: 'Mass' (4, USNM). New Hampshire: Strafford Co.: Cooper Cedar Woods 1mi SE New Durham, 15 Aug 1982, D. S. Chandler, cedar swamp litter (1, UNHC); Strafford Co.: Foss Farm Rd water tower, 22 Oct 1982, W. J. Morse (1, UNHC); same data, except 30 Aug 1982 (3, UNHC); Strafford Co.: Spruce Hole Conservation Area 3 mi SW Durham, 09 Jun 1982, D. S. Chandler, litter on bog edge (12, UNHC); Strafford Co.: 1 mi SW Durham, 30 Oct 1982, W. J. Morse (4, UNHC). New Jersey: Mercer Co.: Princeton, 07 Jun 2021, A. Deczynski (1, CUAC). New York: 'N. Y.' (4, USNM); 'skill NY' [=Catskills] (1, USNM); Yates Co.: Dundee (1, USNM). North Carolina: Henderson Co.: Bearwallow Mountain, 10 Aug 2021, M. Caterino, A. Haberski, flood debris (1, CUAC); Jackson Co.: 6 km S Cashiers, 20 Jun 1986, A. Smetana (1, CNC). South Carolina: Pickens Co.: Clemson, 07 May 1940 (1, CUAC). Virginia: Shenandoah Co.: George Washing National Forest, Crooked Run Rd, Rte 720, 17 Mar 2019, C. harden, litter/duff along stream in laurel hardwoods (1, CUAC); Shenandoah Co.: George Washing National Forest, Dead Deer Creek near Signal Knob, 01 May-31 May 2015, C. Harden, flood debris (1, CUAC); Shenandoah Co.: George Washing National Forest, Rte 678 2 mi S jct w/619, 03 Jul 2018, C. Harden (1, CUAC); Shenandoah Co.: Passage Creek near Elizabeth Furnace Recreational Area, 20 Mar 2017, C. Harden, flood debris (1, CUAC); Highland Co.: Locust Springs, George Washing National Forest, 28 Jul 2017, C. Harden (3, CUAC); Smyth Co.: Mount Rogers, 15 Jun 2019, C. Harden (1, CUAC); Smyth Co.: Whitetop Mountain, 16 Jun 2019, C. Harden, litter along stream (1, CUAC); Powhatan Co.: Powhatan State Park, 02 Apr 2017, C. Harden, wetlands, nr vernal pool (1, CUAC); Washington D. C.: 'D. C.' (1, USNM). West Virginia: Pocahontas Co.: Cranberry Wilderness, Monongahela National Forest, 11 Jun 2019, C. Harden, under rock nr steep stream in spruce/hardwoods (1, CUAC); Pocahontas Co.: Gaudineer Knob Scenic Area, 29 Jun 2017, C. Harden (2, CUAC); Pocahontas Co.: Kennison Mountain FS Rd 232, 20 May 2018, C. Harden, litter nr rushing ephemeral rivulet (1, CUAC); Pocahontas Co.: Pocahontas Trail near Cranberry Mountain Lodge, 10 Sep 2017, C. Harden (1, CUAC).

**Diagnosis.** Lathrobium confusum superficially resembles Lathrobioma, although it is not closely related. It differs from all Lathrobioma by having long antennomeres, and males lack the thick black setae on sternite VIII that are characteristic of the subgenus. Lathrobium confusum is more closely related to L. rhodeanum, with which is shares characteristically long antennomeres and paraprocts. The two can be distinguished by the hind tarsomeres which are shorter and more compact in *L. confusum*.

**Description.** Body length 6 mm; coloration dark, appendages light yellow. Gular sutures arcuate (Fig. 1C); antennomeres V–VII longer than wide. Elytra approximately as long as pronotum. Male sternite VIII with shallow notch and no thick setae; Female with paraprocts undivided, apices 2.6× longer than basal portion, sternite VIII conical; genitalia as in Fig. 36.

Distribution. Canada: ON, NB, QC (Bousquet et al. 2013). USA: CT, DC, IA, MA, NH, NJ, NY, NC, SC, VA, WV.

**Remarks.** We reduce *Lathrobium amputans*, *Lathrobium convictor*, *Lathrobium inornatum*, and *Lathrobium suspectum* to synonymy with *Lathrobium confusum*, because the characters given by Casey (1905) were either inaccurate or insufficiently distinctive. *Lathrobium amputans* was described as having elytra shorter than wide in females, and those of *L. confusum* were said to be subequal. Upon measuring the types, we found the elytra to be subequal in length and width in both species. *Lathrobium convictor* was described as having elytra equal in length to the pronotum, and those of *L. confusum* were described as shorter than the pronotum, but we found the elytra of both species were  $1.1-1.2 \times longer$  than the pronotum.

Lathrobium inornatum was described as having the emargination of sternite VIII smaller, shallower, and more broadly rounded compared to that of *L. confusum*, but we found no differences in width or depth. The difference in shape was modest and the emargination of *L. amputans* was actually less round than that of *L. confusum*.

Lathrobium suspectum and L. confusum were differentiated based on obscure minutia such as form "moderately stout" vs "rather stouter", pronotal punctures "fine and moderately sparse" vs "moderately coarse and sparse," but these differences were not observed in the types (Casey 1905). The length of the antennae relative to the head and pronotum combined were supposedly shorter in L. suspectum, but this too proved incorrect when measured.

We examined the genitalia of the above species and found no differences in aedeagi or female terminalia.

## Lathrobium (Lathrobium) crurale (Casey, 1905)

*Litolathra cruralis* Casey, 1905: 94. *Lathrobium (Litolathra) crurale*: Bernhauer and Schubert 1912: 258.

**Type material.** *Lectotype Litolathra cruralis* Casey, herein designated (USNM): "N. J. /  $\Im$  / CASEY bequest 1925 / [red] TYPE USNM 38129 / Lectotype *Litolathra cruralis* Casey Desg. Haberski & Caterino."

**Other material.** USA: Iowa: 'Ia.' (1, USNM). New Jersey: same data as lectotype (1, USNM). Ohio: Ross Co. (1, USNM).

**Diagnosis.** This species closely resembles *L. fauveli*. The antennomeres IV and V are 2× as long as wide in *L. crurale* and 1.6× times as long in *L. fauveli*. Males of *L. crurale* can also be distinguished by the deeper emargination on sternite VIII which is ~  $\frac{1}{4}$  the depth of the sternite, as opposed to 1/10 as deep in *L. fauveli*. The female sternite VIII is more conical in *L. fauveli* than *L. crurale*.



Figures 35–40. *Lathrobium* terminalia **A** female terminalia **B** male sternite VIII **C** aedeagus in ventral view **D** aedeagus in lateral view. **35** *L*. *armatum* **36** *L*. *confusum* **37** *L*. *crurale* **38** *L*. *fauveli* **39** *L*. *fulvipenne* **40** *L*. *geminum*. Scale bars: 1 mm.

**Description.** Body length 7 mm; body coloration red, appendages light yellow. Gular sutures parallel, widely separate; antennomeres V–VIII 2× as long as wide. Elytra as long as pronotum. Females with paraprocts undivided, apices

longer than basal portion; sternite VIII oblong. Male genitalia as in Fig. 37. We were unable to dissect the genitalia of Casey's female specimens. **Distribution.** USA: IA, NJ, OH.

#### Lathrobium (Lathrobium) fauveli Duvivier, 1883

Lathrobium fauveli Duvivier, 1883: 161. Lathrobium simplex LeConte, 1880: 176 (preoccupied). Lathrobium gravidulum Casey, 1905: 90. New synonym. Lathrobium innocens Casey, 1905: 89. New synonym. Lathrobium neglectum Casey, 1905: 89. New synonym.

Type material. Lectotype, Lathrobium fauveli Duvivier, herein designated (MCZ): Faded disc / "3" / [handwritten] L. simplex Lec. / [red] Type 6451 / Lectotype Lathrobium simplex LeConte Desg. Haberski & Caterino." Lectotype, Lathrobium gravidulum Casey, herein designated (USNM): "Mass / 3" / CASEY bequest 1925 / [red] TYPE USNM 38124 / [handwritten] gravidulum / Lectotype Lathrobium gravidulum Casey Desg. Haberski & Caterino." Lectotype, Lathrobium innocens Casey, herein designated (USNM): "Marq / 3" / CASEY bequest 1925 / [red] TYPE USNM 38126 / [handwritten] innocens / Lectotype Lathrobium innocens Casey Desg. Haberski & Caterino." Lectotype Lathrobium innosey, herein designated (USNM): "RI / CASEY bequest 1925 / [red] TYPE USNM 38125 / [handwritten] neglectum / Lectotype Lathrobium neglectum Casey Desg. Haberski & Caterino."

**Other material.** Canada: Nova Scotia: Queens Co.: Kejimkujik National Park, 09 May 1999, J. C. Ciegler (1, CUAC). Quebec: MRC de Portneuf: Pont-Rouge, 22 Apr 2023, N. Bédard, sifted from dead leaves in a sandpit (1, NBC). USA: Connecticut: New Haven Co. New Haven (6, USNM). Massachusetts: 'Mass.' (1, MCZ); 'Mass.' (4, USNM). Michigan: Marquette Co.: Marquette (1, USNM). New Hampshire: Grafton Co.: Downes Brook, Potash Mountain, 05 Jun 2021, A. Haberski, along creek edge (1, CUAC); Coos Co.: Mount Washington 2700' elev. (1, UNHC); Strafford Co.: Spruce Hole Conservation Area, D. S. Chandler (1, UNHC); Grafton Co.: Hubbard Brook Experimental Forest, D. S. Chandler (1, UNHC). Rhode Island: 'R. I.' (1, USNM).

**Diagnosis.** This species closely resembles *L*. *crurale* and can be distinguished from that species by the characters discussed in the diagnosis of *L*. *crurale*.

**Description.** Body length 8 mm; body coloration dark red, appendages lighter red. Gular sutures parallel, widely separate; antennomeres V–VIII longer than wide. Elytra as long as pronotum. Females with paraprocts undivided, apices longer than basal portion; sternite VIII conical. Ventral process of aedeagus with distinctive apical tooth (Fig. 38).

**Distribution.** Canada: AB, BC, MB, NB, NF, NS, ON, PE, QC, SK (Bousquet et al. 2013). USA: CT, MA, ME, MI, NH, RI, WI (Casey 1905; Newton 2022).

**Remarks.** We reduce *Lathrobium gravidulum*, *Lathrobium innocens*, and *Lathrobium neglectum* to synonymy with *Lathrobium fauveli*, based on the absence of clear distinguishing characters. *Lathrobium neglectum* and *L. innocens* were distinguished from *L. fauveli* based on larger emarginations in male sterni-

te VIII. However, we found no difference in size among species. *Lathrobium gravidulum* was distinguished based on subtle differences in punctation and the coloration of appendages, but neither are consistent. Examination of the genitalia found no differences in either aedeagi or female terminalia.

#### Lathrobium (Lathrobium) fulvipenne (Gravenhorst, 1806)

Lathrobium alpestre Heer, 1839: 239. Lathrobium atriceps Stephens, 1833: 267. Lathrobium castaneipenne Kolenati, 1846: 22. Lathrobium letzneri Gerhardt, 1869: 257. Lathrobium muelleri Bernhauer, 1899: 435. Lathrobium punctulatum Mannerheim, 1830: 37. Staphylinus fulvipenne Gravenhorst, 1806: 104. Staphylinus fulvipennis Gravenhorst, 1806: 104.

#### Type material. Types not examined.

**Diagnosis.** Males have a distinctive, asymmetrical aedeagus that differs from all other Nearctic species (Fig. 39C). Females can be distinguished by the shape of their valvifers (Fig. 39A).

**Description.** Body length 8 mm; body coloration dark, appendages and mouthparts light red, elytra bicolored with narrow black base, or monochromatic black. Gular sutures parallel; antennomeres V–VII longer than wide. Wing dimorphic, elytra as long or slightly longer than pronotum. Females tergite IX with paraprocts undivided, apical lobes shorter than basal portion in dorsal view; sternite VIII oblong, valvifers and coxites divided (Fig. 39A). Male sternite VIII without patches of dark setae, apical emargination shallow and round (Fig. 39 B). Ventral process of aedeagus asymmetrical in ventral view (Fig. 39C; Assing and Schülke 2012).

Distribution. Canada: AB, BC, NB, NF, QC (Bousquet et al. 2013).

**Remarks.** Native to the Palearctic and adventive in North America. Common in unforested habitats (Assing and Schülke 2012).

#### Lathrobium (Lathrobium) geminum Kraatz, 1857

Lathrobium bicolor Heer, 1839: 240 (junior homonym). Lathrobium boreale Thomson, 1860: 198. Lathrobium boreale Hochhuth, 1851: 41. Lathrobium difficile Coiffait, 1953: 104. Lathrobium fallaciosum Coiffait, 1953: 104. Lathrobium obscuriceps Motschulsky, 1860: 564. Lathrobium rufescens Motschulsky, 1860: 563. Lathrobium volgense Hochhuth, 1851: 42.

Type material. Types not examined.

**Diagnosis.** In North America, this species is most similar to *L. amplipenne*. Males can be distinguished from *L. amplipenne*, and all other Nearctic species,

by their distinctive aedeagus (Fig. 40D), and females can be distinguished by their short gonocoxites, which are only  $\sim \frac{1}{2}$  as long as their paraprocts, rather than subequal as in *L. amplipenne*.

**Description.** Large species, body length 8–11 mm; body coloration dark, appendages light brown, elytra bicolored with broad black base, rarely solid black. Gular converging, antennomeres V–VII 1.2× as long as wide. Wing dimorphic, elytra approximately as long as pronotum. Females tergite IX with paraprocts undivided, apical lobes shorter than basal portion in dorsal view; sternite VIII with truncate apex; valvifers and coxites fused (Fig. 40A). Male sternite VIII with two longitudinal patches of dark setae in posterior third, apex indistinct-ly emarginated. Ventral process of aedeagus distinctively shaped with apical tooth (Fig. 40D) (Assing and Schülke 2012).

Distribution. Canada: BC (Pentinsaari et al. 2019).

**Remarks.** Native to the Palearctic and adventive in North America. Common in moist, open habitats (Assing and Schülke 2012). Canadian specimens collected in wetland adjacent to lake (Pentinsaari et al. 2019).

# Lathrobium (Lathrobium) islae Haberski & Caterino, sp. nov. https://zoobank.org/F12B5DD3-06F5-4F5B-AE25-1BF7B7B593B0

Type material. Holotype ♂ (FMNH): "USA: NC: Caldwell Co., 36.1117°N, 81.8068°W, Grandfather Mountain, Calloway Peak X.6.2020, M. Caterino, F. Etzler, A. Haberski, sifted litter." / "Caterino DNA voucher, Ext. MSC-6239" / "CLEM-SON ENT [QR CODE] CUAC000169030". Paratypes (36, CUAC, FMNH, VMNH): 10: same locality as type, 36.1118°N, 81.8105°W, x.06.2020 (CUAC000112914, CUAC000112915, CUAC000177130, CUAC000177131, CUAC000177132, CUAC000177133, CUAC000177134, CUAC000177135, CUAC000177136, CUAC000177137); 3: same locality as type, 36.0978°N, 81.8293°W, 5370ft., iv.21.2022 (CUAC000177093, CUAC000177094, CUAC000177095); 1: same locality as type, 36.1118°N, 81.8112°W, x.06.2020 (CUAC000177109); 20: same locality as type, 36.1117°N, 81.8088°W, x.06.2020 (CUAC000177110, CUAC000177111, CUAC000177112, CUAC000177113, CUAC000177114, CUAC000177115, CUAC000177116, CUAC000177117, CUAC000177118, CUAC000177119, CUAC000177120, CUAC000177121, CUAC000177122, CUAC000177123, CUAC000177124, CUAC000177125, CUAC000177126, CUAC000177127, CUAC000177128, CUAC000177129); 1: same locality as type, 36.1104°N, 81.8046°W, v.17.2021 (CUAC000177138); 1: same locality as type, 36.1116°N, 81.8117°W, V.17.2021 (CUAC000135036).

**Other material.** North Carolina: Mitchell Co.: Grassy Ridge Bald, 6135', (36.0985, -82.1791), M.S. Caterino, 08 Jun 2020 (CUAC); Mitchell Co.: Roan High Bluff, 6225–6251', (36.0931, -82.1453), M.S. Caterino, 15 Aug 2018 (3, CUAC); Mitchell Co.: Roan High Knob, 5756–6286', (36.1045, -82.1224), M.S. Caterino, 08 Jun 2020 (3, CUAC). Virginia: Smyth Co.: Mt. Rogers, 5699', Jefferson National Forest (36.6602, -81.5447), M.S. Caterino & P. Marek, 03 Jul 2018 (7, CUAC); Smyth Co.: Mt. Rogers, 5699', Jefferson National Forest (36.6602, -81.5447), M.S. Caterino & P. Marek, 03 Jul 2018 (7, CUAC); Smyth Co.: Mt. Rogers, 5699', Jefferson National Forest (36.6602, -81.5447), M.S. Caterino & P. Marek, 03 Jul 2018, CUAC000187893, CUAC000187899 (15 larvae, CUAC); Smyth Co.: Mt. Rogers, 5666–5680', Jefferson National Forest (36.6605, -81.5447), M.S. Caterino & F. Etzler, A. Haber-

ski, 27 Oct 2020 (27, CUAC); Smyth Co.: Mt. Rogers, 5686', Jefferson National Forest (36.6612, -81.5456), M.S. Caterino, 27 Oct 2020 (3, CUAC); Smyth Co.: Mt. Rogers, Jefferson National Forest (36.657, -81.555), C.W. Harden, 15 Apr 2019 (CUAC); Smyth Co.: Whitetop Mountain, 5503', Jefferson National Forest (36.6391, -81.6064), M.S. Caterino & P. Marek, 03 Jul 2018 (CUAC); Smyth Co.: Whitetop Mountain, 5436', Jefferson National Forest (36.6379, -81.6053), M.S. Caterino, 27 Oct 2020 (CUAC); Smyth Co.: Whitetop Mountain, Jefferson National Forest (36.629, -81.6053), C.W. Harden, 15 Apr 2019 (CUAC); Grayson Co.: Wilburn Ridge, 5450', Jefferson National Forest (36.6525, -81.5167), M.S. Caterino & P. Marek, 03 Jul 2018 (2, CUAC).

**Diagnosis.** This species can be distinguished from the closely related *L. liv-idum* only by its genitalia. The spines of the internal sac of their aedeagi differ conspicuously (Fig. 7E, F vs Fig. 8D, E). Differences in female genitalia are more subtle, but the gonocoxites of *L. islae* are narrower at their base. No intermediate forms are known.

Four other species of Nearctic *Lathrobium* have short elytra and functional eyes, but none are likely to be mistaken for *L. islae* or *L. lividum*. *Lathrobium brevipenne*, *L. carolinae*, and *L. camplyacra* are twice as large, lighter in color, and have an overall different gestalt. *Lathrobium pallescens* has a pale red body color and its eyes are much smaller, 1/8 the lateral length of the head with ~ 30 ommatidia.

**Description.** Habitus (Fig. 7A). Small species, total body length  $\sim 4.5$  mm long, FL 2.5–3.0 mm long. Coloration: body black; legs, palpomeres, and antennae dark red.

Head subquadrate, as wide as long, widest posteriorly and narrower anterior to eyes; posterior angles slightly rounded; epicranium coarsely punctate, punctures less dense in median dorsal and anterior regions; interstices with strong transversely reticulate microsculpture throughout; head setose throughout, with long macrosetae projecting at posterior corners of head, corners of the eyes, laterally posterior to the eyes, and above the mandible insertions; gular sutures arcuate, widely separate, 1/16 width of head apart at their most proximal point; neck ½ as wide as head. Eyes large and well developed with ~ 95 ommatidia, occupying ¼ lateral length of the head. Antennae moniliform, as long as head and pronotum combined; scape as long as antennomeres II and III combined; antennomeres II–IV elongate, gradually widening so that antennomeres V–IX are as wide as long; apical antennomere longer, subacute.

Pronotum longer than wide, as wide or slightly wider than head; sides parallel; angles rounded; punctures large, spaced one diameter apart, impunctate at midline with a visible line; interstices shiny with a finely punctate microsculpture. Elytra shorter but slightly wider than pronotum, as wide as head, as long as wide; anterior angles somewhat squared, posterior margins sinuate; scutellum round; punctures small, irregularly spaced, most 1–2× their diameter apart; interstices with finely punctate microsculpture. Hindwings vestigial, 0.2 mm long, 1/5 length of elytra. Posterior margin of abdominal tergite VII without palisade fringe.

 $\Diamond$ : Sternite VII flattened medially with shallow notch on the posterior margin; posterior margin of sternite VIII with a deep U-shaped notch (Fig. 7D). Aedeagus 1.7 mm long (Fig. 7E, F), ventral process short, not extending much beyond the median foramen posteriorly, lightly sclerotized portion of the median lobe

protruding beyond it in lateral view; dorsal plate asymmetrical; internal sac with a single large spine with a characteristic club tip in ventral view.

 $\bigcirc$ : Sternite VIII slightly oblong with a triangular patch of dense setae at the tip (Fig. 7C); paraprocts divided anteriorly; proctiger conical. sternum IX with valvifers and coxites fused, valvifers narrow at base (Fig. 7B); subgenital plate absent.

*First instar larva*: Body elongate, ~ 3 mm long; well sclerotized (Fig. 41A); head, thoracic, and abdominal tergites brown, appendages light yellow, intersegmental membrane white, translucent.

Head ovate, widest at stemmata and slightly tapered posteriad (in dorsal view), dorsoventrally flattened, 1.1× as long as wide, dorsal setae as in Fig. 41A; head 2.5× wider than neck, dorsal ecdysial lines bifurcate 1/2 distance between neck and nasale margin; six stemmata present, arranged as in Fig. 41B; anterior margin of nasale (Fig. 41C) with nine blunt teeth pointing anteriorly, one quadrate median tooth with tetradentate anterior edge, a pair of paramedian teeth, and three pairs of lateral teeth; the innermost lateral teeth are small and indistinct; paramedian and lateral teeth armed with nodular setae, and a pair of nodular setae separate median and paramedian teeth; Apotome of gula not reaching tentoral pits.

Antennae (Fig. 41F) length ratio: 1.0:2:3.1:1.6; antennomere I triangular; antennomere II with two pores; antennomere III with three elongate macrosetae, three solenidia, one pore; antennomere IV club-shaped with apical solenidia; sensory appendage 0.9× as long as antennomere IV.

Mandibles (Fig. 41D) long, falciform, serrate along inner margin, with a single seta near the base on the outer ventral edge. Maxilla (Fig. 41D) with cardo triangular, widening from base to apex; stipes quadrate, 1.3× longer than cardo; mala digitiform, tapering toward apex, 0.9× as long as palpomere I, with apical sensory appendages and two pores; palpifer with one seta. Maxillary palpomere length ratios: 1.0:1.2:2.8; palpomere II with two setae; palpomere III with one basal sensory appendage and numerous small apical appendages. Labium with prementum subquadrate, basal portion strongly sclerotized; ligula with elongate membranous apex, twice as long as wide, densely fimbriate, separated from prementum by a distinctly sclerotized transverse strip; palpomere I 1.6× as long as II; palpomere II bearing short sensilla at apex.

Dorsal sclerites of thorax with ecdysial lines along midline of body; prothorax subquadrate, narrowing slightly anteriorly, chaetotaxy as in Fig. 41A; thoracic tergite II and III subequal; abdominal sclerites well sclerotized, with two small pleural sclerites per segment on each side; basal segment of urogomphus 2.6× as long as terminal segment, with seven prominent lateral setae; terminal segment of urogomphus slender, with one short and one long apical seta.

**Second instar larva:** Second instar (Fig. 42A) resembles first, except as follows. Body larger, ~ 6 mm long. Head subquadrate; dorsal ecdysial lines of the head bifurcate 2/5 distance between nasale margin and neck; median tooth of nasale triangular with serrated edges and a blunt tip (Fig. 42C). Apotome of gula reaching tentoral pits. Antenna (Fig. 42F) length ratios: 1.0:3.5:2.8:1.5; antennomere IV club-shaped with apex 2× as wide as base. Mandible interior margin smooth (Fig. 42D). Maxilla palpomere length ratios: 1.0:1.5:3.3; Labial palpomere I 1.5× II (Fig. 42E); palpomere I distinctly curved; palpomere II bent near apex. Prothorax round. Urogomphi broken off of only known specimen.






**Figure 42**. *Lathrobium islae* second instar larva **A** habitus **B** head in lateral view **C** nasale **D** mandible **E** maxilla **F** antenna. Scale bars: 1 mm (**A**, **B**); 250 μm (**C**); 500 μm (**D**, **E**, **F**).



Figure 43. Distribution of Lathrobium islae (circle), L. lividum (star).

**Etymology.** Named in honor of Isla Haberski, daughter of the first author, who was born during the preparation of this manuscript.

**Distribution and ecology.** *Lathrobium islae* inhabits spruce-fir forests above 1500 m in the Grayson Highlands, Roan Highlands, and on Grandfather Mountain (Fig. 43). It can be collected from leaf litter but is most common on boulders beneath bryophyte mats. It has not been found in spruce-fir forests south of the French Broad River basin, where its microhabitat is inhabited by *L. smokiense* and *L. balsamense*. Adults collected Jul–Sep. Larvae collected Mar–Jul.

**Remarks.** *Lathrobium islae* was not monophyletic in our COI phylogeny and ASAP identified five genetic partitions. Given this degree of genetic variation, populations outside the type locality might also differ in minor ways morphologically, perhaps in characters not yet evaluated. Larvae were associated with adults by DNA barcoding.

## Lathrobium (Lathrobium) leconteanum Scheerpeltz, 1933

Lathrobium leconteanum Scheerpeltz, 1933: 1274. Lathrobium concolor LeConte, 1880: 175 (junior homonym).

**Type material.** *Lectotype*, *Lathrobium leconteanum* Scheerpeltz, herein designated (MCZ): Faded disc / "♂ ♀ / [handwritten] *L. concolor* Lec. / [red] Type 6450 / Lectotype *Lathrobium concolor* LeConte Desg. Haberski & Caterino."

**Other material.** USA: Indiana: 'Ind.' (1, USNM). New Hampshire: Coos Co.: Mount Washington (1, UNHC); Grafton Co.: Hubbard Brook Experimental Forest, D. S. Chandler (1, UNHC).

**Diagnosis.** This species is similar in appearance to *L. washingtoni* but differs in having elongate antennomeres. Males are otherwise difficult to tell apart, even in the primary and secondary sexual characters. *Lathrobium leconteanum* has four spines on the internal sac of the aedeagus whereas *L. washingtoni* has two. Females are more easily differentiated because *L. leconteanum* has an undivided tergite IX and *L. washingtoni* has tergite IX fully divided.

**Description.** Body length 7 mm; body coloration dark red, appendages lighter. Gular sutures parallel, widely separate; antennomeres V–VII longer than wide. Elytra 1.2× longer than pronotum. Females with paraprocts undivided, apices 1.3× as long as basal portion; sternite VIII conical with small apical notch. Genitalia as in Fig. 44.

Distribution. Canada: ON, NF (Bousquet et al. 2013). USA: IN, NH.

#### Lathrobium (Lathrobium) lineatocolle Scriba, 1859

## Type material. Types not examined.

**Diagnosis.** This species is most similar to *L. fulvipenne* but can be distinguished by the ventral process of the aedeagus, which lacks an apical tooth and is nearly symmetrical in ventral view (Fig. 45C).

**Description.** Body length 8 mm; body coloration dark, appendages light brown, elytra usually bicolored with narrow black base. Gular sutures parallel; antennomeres V–VII longer than wide. Elytra as long as pronotum or slightly shorter. Female tergite IX with apical lobes of paraprocts longer than continuous anterior portion in dorsal view; sternite VIII with truncate apex. Ventral process of the aedeagus strongly deflexed, distal tip lying beyond median foreman in lateral view (Fig. 45C).

Distribution. Canada: ON (Pentinsaari et al. 2019).

**Remarks.** Native to the Palearctic and adventive in North American. Found in forest and riparian habitats (Pentinsaari et al. 2019).

# Lathrobium (Lathrobium) lividum Haberski & Caterino, sp. nov.

https://zoobank.org/53298BFA-CDA9-49A4-9584-C2D01C39C768

Type material. *Holotype* ♂ (FMNH): "USA: NC: Yancey Co., 35.7643°N, 82.2629°W, Mt. Mitchell SP, Mt. Mitchell, 6556', ix.07.2021, M. Caterino & E. Recuero, sifted litter." / "Caterino DNA voucher, Ext. MSC-7880, Morphosp. MM.B.318" / "CLEM-SON ENT [QR CODE] CUAC000135757". *Paratypes* (40): 5 (CUAC): same locality as type, 35.7643°N, 82.2633°W, X.06.2020 (CUAC000169022, CUAC000169023, CUAC000177098, CUAC000177099, CUAC000177100); 9 (CUAC): same locality as type, 35.7643°N, 82.2633°W, 6589ft, ix.07.2021 (CUAC000169022, CUAC000169023, CUAC000177169, CUAC000177170, CUAC000177171, CUAC000177172, CUAC000177173, CUAC000177174, CUAC000177175); 1 (CUAC): same locality as type, 35.7644°N, 82.2641°W, V.15.2018 (CUAC00079253);



Figures 44–49. *Lathrobium* terminalia A female terminalia B male sternite VIII C aedeagus in ventral view D aedeagus in lateral view. 44 *L. leconteanum* 45 *L. lineatocolle* 46 *L. pedale* 47 *L. praelongum* 48 *L. rhodeanum* 49 *L. simile.* Scale bars: 1 mm.

5 (MCZ): "Black Mts. N. C., Mt. Mitchell 5000–6711 ft, IX.05.1930, Darlington."; 2 (CUAC): "USA: NC: Yancey Co., 35.7798°N, 82.2599°W, Mount Mitchell State Park, Big Tom, 6586', v.15.2018, M. Caterino, sifted litter." (CUAC000048570); 10 (CUAC) same locality, 35.7795°N, 82.2596°W, 6554', ix.07.2021, M. Caterino (CUAC000157555, CUAC000157567, CUAC000157568, CUAC000172501,

CUAC000172506, CUAC000172509, CUAC000172511, CUAC000172505, CUAC000172513, CUAC000172514); 2 (CUAC) "USA: NC: Yancey Co., 35.8525°N, 82.2468°W, Pisgah National Forest, Celo Knob, 6284', vi.15.2020, M. Caterino, sifted litter" (CUAC000004036, CUAC000169024); 4: "USA: NC: Yancey Co., 35.8524°N, 82.2485°W, Pisgah National Forest, Celo Knob, 6300', x.19.2021, M. Caterino, E. Recuero & A. Haberski, sifted litter" (CUAC000177101, CUAC000177102, CUAC000177103, CUAC000177104); 4: "USA: NC: Yancey Co., 35.8527°N, 82.2487°W, Pisgah National Forest, Celo Knob, 6294', x.19.2021, M. Caterino, E. Recuero & A. Haberski, sifted litter" (CUAC000177105, CUAC000177106, CUAC000177107, CUAC000177108); 3: "USA: NC: Yancey Co., 35.8522°N, 82.2485°W, Pisgah National Forest, Celo Knob, 6300', vi.15.2020, M. Caterino & F. Etzler, sifted litter" (CUAC000177145, CUAC000177146, CUAC000177147); 2: "USA: NC: Yancey Co., 35.8523°N, 82.2486°W, Pisgah National Forest, Celo Knob, 6300', vi.15.2020, M. Caterino & F. Etzler, sifted litter" (CUAC000177148, CUAC000177149); 2 (CUAC) "USA: NC: Yancey Co., 35.8525°N, 82.2468°W, Pisgah National Forest, Celo Knob, 6284', vi.15.2020, M. Caterino, sifted litter" (CUAC000004036, CUAC000169024); 2 (CUAC) "USA: NC: Yancey Co., 35.7782°N, 82.2610°W, Mount Mitchell State Park, Mt. Craig, 6550' v.15.2018, M. Caterino, sifted litter" (CUAC00003088, CUAC000169028).

**Other material. North Carolina:** Buncombe Co.: Base of Mt. Mitchell, 5413', Blue Ridge Parkway, A. Smetana, 03 Jun 1986 (5, CNC); Yancey Co.: Mt. Mitchell, 6561–6679', Mount Mitchell State Park, A. Smetana, 04 Jun 1986 (6, CNC); Buncombe Co.: Craggy Dome, 5696–5845' 13 Sep 2022 (4, CUAC).

**Diagnosis.** This species can be distinguished from the closely related *L. islae* only by its genitalia. The spines of the internal sac of their aedeagi differ conspicuously (Fig. 8D, E vs Fig. 7E, F), but differences in female genitalia are more subtle. The gonocoxites of *L. islae* are narrowed at the base, but not in *L. lividum*. No intermediate forms are known.

**Description.** External morphology is identical to that of *L. islae*. It differs only in genitalia.

♂: Aedeagus (Fig. 8D, E) with ventral process longer, nearly reaching the end of the median lobe; dorsal plate small and blade-like; the internal sac with a single large, curved spine that projects above the median lobe.

 $\bigcirc$ : Gonocoxite width subequal from base to apex (Fig. 8A).

**Etymology.** The specific name is Latin, meaning bruised, in reference to its dark coloration.

**Distribution and ecology.** *Lathrobium lividum* might have the smallest range of any Nearctic *Lathrobium*. It is endemic to spruce-fir forests above 1500 m elevation in the Black Mountains and Craggy Mountains of North Carolina (Fig. 43). Collected Jul–Sep.

## Lathrobium (Lathrobium) pedale LeConte, 1863

Lathrobium pedale LeConte, 1863: 43.

**Type material.** *Lectotype*, *Lathrobium pedale* LeConte, herein designated (MCZ): "La. / ♂ / [handwritten] L. pedale Lec. / [red] Type 6454 / Lectotype *Lathrobium pedale* LeConte Desg. Haberski & Caterino."

**Other material.** USA: North Carolina: Swain Co.: Hazel Creek, Great Smoky Mountains National Park, 18 Jul 2003, S. L. Staines, C. Ware (1, LSAM). South Carolina: Colleton Co.: Canadys, 30 Jul 1993, J. C. Ciegler (1, CUAC); Kershaw Co.: Wateree Floodlands Memorial Forest, 13 Apr, 2021, C. Harden, pine stump/ flood debris (1, CUAC). Virginia: Botetourt Co.: Solitude Swamp, 28 Jun 2018, C. Harden, deep oak litter on swamp margin (1, CUAC).

**Diagnosis.** This species closely resembles *L. amplipenne, L. armatum*, and *L. praelongum* in external morphology, but differs in the primary and secondary sexual characters. Males of *L. pedale* have a large emargination on sternite VIII, where the aforementioned species have small emarginations or none at all. They also lack a dorsal plate of the aedeagus. Females differ from the three aforementioned species by having valvifers and coxites fully divided.

**Description.** Large species, body length 9 mm; body coloration dark red, appendages lighter red or yellow. Gular sutures converging, nearly touching posteriorly; antennomeres V–VII as wide as long. Elytra as long as pronotum. Females with paraprocts undivided, apices shorter than basal portion; sternite VIII weakly oblong. Genitalia as in Fig. 46.

Distribution. USA: LA, NC, SC, VA.

## Lathrobium (Lathrobium) praelongum Casey, 1905

Lathrobium praelongum Casey, 1905: 82.

**Type material.** *Lectotype*, *Lathrobium praelongum* Casey, herein designated (USNM): "Coll J B: / CASEY bequest 1925 / [handwritten] *praelongum* / [red] TYPE USNM 38113 / Lectotype *Lathrobium praelongum* Casey Desg. Haberski & Caterino."

**Other material.** USA: Maryland: Allegany Co.: Little Orleans, 05 Jun 2021, A. Deczynski (1, CUAC). North Carolina: Swain Co.: Hazel Creek Great Smoky Mountains National Park, 18 Jul 2003, S. L. Staines, C. Ware (2, LSAM). Virginia: Highland Co.: Bullpasture River, 02 Jun 2019, C. Harden, streamside gravel/ cobble/sand (1, CUAC); Shenandoah Co.: Passage Creek near Buzzard Rock, 18 Apr 2016, C. Harden, under stones, wet sandy soil (1, CUAC); Shenandoah Co.: Elizabeth Furnace Recreational Area, Rte 619 Mudhole Gap trail, 09 Jan 2016, C. Harden (1, CUAC); Shenandoah Co.: George Washing National Forest, Signal Knob trailhead, 25 Oct 2017, C. Harden, moist ditch in floodplain (1, CUAC); Appomattox Co.: Holiday Lake State Park, 15 Jun 2017, C. Harden (1, CUAC); Bath Co.: Whites Cave, 15 Oct 2020, C. Harden (1, CUAC).

**Diagnosis.** This species closely resembles *L. amplipenne*, *L. armatum*, and *L. pedale* in external morphology. Males are readily distinguished by the uniquely shaped ventral process of the aedeagus that is twice as long as the median lobe. Females are more challenging, but they have shorter paraprocts than the aforementioned species, and denser pubescence on their gonocoxites.

**Description.** Large species, body length 9 mm; body coloration dark, appendages paler red, elytra bicolored. Gular sutures converging, nearly touching posteriorly; antennomeres V–VII as wide as long. Elytra at least as long as pronotum. Females with paraprocts undivided, apices shorter than basal portion,  $\sim 0.7 \times$  as long; sternite VIII weakly oblong. Characteristic aedeagus (Fig. 47).

Distribution. USA: IL, MD, NJ, NC, VA.

#### Lathrobium (Lathrobium) rhodeanum (Casey, 1905)

Litolathra rhodeana Casey, 1905: 94. Lathrobium (Litolathra) rhodeanum: Bernhauer and Schubert 1912: 266. Litolathra semirubida Casey, 1905: 94. New synonym. Lathrobium (Litolathra) semirubidum: Bernhauer and Schubert 1912: 267.

**Type material.** *Lectotype*, *Litolathra rhodeana* Casey, herein designated (USNM): "R. I. /  $\bigcirc$  / CASEY bequest 1925 / [red] TYPE USNM 38127 / [handwritten] *rhodeana* / Lectotype *Litolathra rhodeana* Casey Desg. Haberski & Caterino." *Lectotype Litolathra semirubida* Casey, herein designated (USNM): "R.I. / CASEY bequest 1925 / [red] TYPE USNM 38128 / [handwritten] *semirubida* / Lectotype *Litolathra semirubida* Casey Desg. Haberski & Caterino."

**Other material.** USA: Massachusetts: 'Mass' (1, USNM). New York: 'N. Y.' (1, USNM). Rhode Island: 'R. I.' (2, USNM). South Carolina: Hampton Co.: Bluff Lake, Webb Wildlife Management Area, 29 Apr 2017, J. C. Ciegler, UV light (1, CUAC). Virginia: Sussex Co.: Chub Sandhill Natural Area Preserve, 24 Sep 2017, C. Harden, litter from dark moist woods near pool (2, CUAC); Botetourt Co.: Solitude Swamp, 28 Jun 2018, C. Harden, deep oak litter on swamp margin, exposed mounds (5, CUAC).

**Diagnosis.** This species closely resembles *L. confusum*. They differ in the lengths of the hind tarsomeres which are longer in *L. rhodeanum* than in *L. confusum*. Females are otherwise difficult to tell apart, but males are easily identified by the elongate spine in the internal sac of the aedeagus, which is unique.

**Description.** Body length 7 mm. Body coloration red throughout. Females with paraprocts undivided, apices 2.7× longer than basal portion, sternite VIII oblong. Elytra longer and wider than pronotum. Antennomeres V–VII 2× as long as wide. Aedeagus with characteristic elongate structures of the internal sac (Fig. 48).

Distribution. Canada: QC (Newton 2022). USA: MA, NY, RI, SC, VA.

**Remarks.** We reduce *Lathrobium semirubidum* to synonymy with *Lathrobium rhodeanum*. *Lathrobium semirubidum* was described from a single specimen that subtly differs from *L. rhodeanum* in body coloration, punctation, and head width, but these differences do not exceed the intraspecific variation observed in longer series of other *Lathrobium*. The lectotypes of both species were collected from the same location, on the same day, and their aedeagi are indistinguishable.

#### Lathrobium (Lathrobium) simile LeConte, 1863

Lathrobium simile LeConte, 1863: 43.

**Type material.** *Lectotype*, *Lathrobium simile* LeConte, herein designated (MCZ): Pink disc / "♂ / [handwritten] L. simile Lec. / [red] Type 6449 / Lectotype *Lathrobium simile* Leconte Desg. Haberski & Caterino."

**Other material.** Canada: Manitoba: Aweme (4, USNM). USA: Massachusetts: 'Mass' (4, USNM). New Hampshire: Strafford Co.: Spruce Hole Conservation Area, D. S. Chandler (1, UNHC); Grafton Co.: Hubbard Brook Experimental Forest, D. S. Chandler (1, UNH). New Jersey: 'N. J.?' (1, USNM). New York: 'N. Y.' (3,

USNM). Pennsylvania: Philadelphia, July 1928 (1, CNC). Rhode Island: 'R. I.' (6, USNM). Vermont: White River Junction, 29.V.1979, E.J. Kiteley (4, CNC).

**Diagnosis.** This species can be difficult to distinguish from *L. sparsellum*. *Lathrobium simile* has elongate antennomeres, whereas *L. sparsellum* has subquadrate antennomeres. Additionally, *L. simile* has a marginally thicker neck. Males can be further distinguished by the emargination on sternite VIII. The emargination of *L. simile* is wider than deep and there is a patch of thick black setae below. The emargination of *L. sparsellum* is deeper than wide and there are no thick black setae. Females are easily distinguished by the shape of the proctiger, which is conical in *L. simile* but pointed in *L. sparsellum*, a unique characteristic of that species.

**Description.** Body length 8 mm; body coloration red, appendages light yellow. Gular sutures parallel, widely separate; antennomeres V–VII longer than wide. Elytra as long as pronotum. Females with paraprocts divided; sternite VIII oblong. Male sternite VIII with wide, shallow emargination and two vertical rows of thick black setae (Fig. 49B). Genitalia as in Fig. 49.

Distribution. Canada: MB, NB, NS, ON, QC (Bousquet et al. 2013). USA: CT, DC, IN, MA, ME, NH, NJ, NY, PA, RI, VT (Newton 2022).

## Lathrobium (Lathrobium) sparsellum Casey, 1905

Lathrobium sparsellum Casey, 1905: 87. Lathrobium obtusum Casey, 1905: 86. New synonym. Lathrobium postremum Casey, 1905: 88. New synonym. Lathrobium rigidum Casey, 1905: 88. New synonym.

**Type material.** *Lectotype*, *Lathrobium sparsellum* Casey, herein designated (USNM): "Winnipg. Man. / CASEY bequest 1925 / [red] TYPE USNM 38120 / [handwritten] *sparsellum* / Lectotype *Lathrobium sparsellum* Casey Desg. Haberski & Caterino." *Lectotype*, *Lathrobium obtusum* Casey, herein designated (USNM): "Mass/ CASEY bequest 1925 / [red] TYPE USNM 38119 / Lectotype *Lathrobium obtusum* Casey Desg. Haberski & Caterino." *Lectotype*, *Lathrobium obtusum* Casey, herein designated (USNM): "Mass/ CASEY bequest 1925 / [red] TYPE USNM 38119 / Lectotype *Lathrobium obtusum* Casey, herein designated (USNM): "R.I. / CASEY bequest 1925 / [red] TYPE USNM 38123 / [handwritten] *postremum* / Lectotype *Lathrobium rigidum* Casey, herein designated (USNM): "R.I. / CASEY bequest 1925 / [red] TYPE USNM 38123 / [handwritten] *postremum* / Lectotype *Lathrobium rigidum* Casey, herein designated (USNM): "R.I. / CASEY bequest 1925 / [red] TYPE USNM 38122 / [handwritten] *rigidum* / Lectotype *Lathrobium rigidum* Casey. Haberski & Caterino."

**Other material.** Canada: 'Can' (1, USNM). Quebec: MRC des Deux-Montagnes: Parc National d'Oka, 06 May 2023, R. Vigneault, handpicked near beach (1, NBC); same data, except white tulle interception trap in composting site (1, NBC). USA; Connecticut: New Haven Co.: New Haven (1, USNM). Massachusetts: 'Mass' (2, USNM). New Hampshire: Strafford Co.: Spruce Hole Conservation Area, D. S. Chandler (1, UNHC); Rhode Island: 'R. I.' (4, USNM).

**Diagnosis.** This species closely resembles *L. simile* but can be differentiated as described under the diagnosis for *L. simile*.

**Description.** Body length 8 mm; body coloration dark, appendages lighter red. Gular sutures parallel, widely separate; antennomeres V–VII as long as wide. Elytra as long as pronotum. Females with paraprocts divided; proctiger

narrow; sternite VIII weakly oblong. Male sternite VIII with narrow, deep emargination. Genitalia as in Fig. 50.

**Distribution.** Canada: AB, MB, NB, NF, NS, ON, QC (Bousquet et al. 2013). USA: **CT**, MA, ME, NH, NY, RI, VT (Newton 2022).

**Remarks.** We reduce *Lathrobium obtusum*, *Lathrobium postremum*, and *Lathrobium rigidum* to synonymy with *Lathrobium sparsellum* based on the inaccuracies of the original descriptions and the inability to find alternative distinguishing characters. *Lathrobium postremum* and *L. rigidum* were differentiated from *L. sparsellum* based on their elytra being shorter than the pronotum, as opposed to subequal as in *L. sparsellum*. However, we measured Casey's specimens and found the elytra to be subequal or slightly longer than the pronotum in all three species.

Lathrobium obtusum was distinguished from *L. sparsellum* primarily based on the gular sutures being "moderately separated and feebly converging" as opposed to "widely separated, almost straight" in *L. sparsellum* (Casey 1905). However, we could not see a difference in suture shape, and sutures in both species were approximately equidistant. We examined the genitalia of all four species and found no morphological differences in males or females.

# Lathrobium (Lathrobium) spissicorne Casey, 1905

Lathrobium spissicorne Casey, 1905: 83.

**Type material.** *Lectotype Lathrobium spissicorne* Casey, herein designated (USNM): "Mass / CASEY bequest 1925 / [red] TYPE USNM 38111 / [handwritten] *spissicorne* / Lectotype *Lathrobium spissicorne* Casey Desg. Haberski & Caterino."

**Other material.** USA: Massachusetts: 'Mass' (1, USNM); 'Mass' (1, MCZ). Michigan: Wayne Co.: Detroit, Oct (1, USNM).

**Diagnosis.** *Lathrobium spissicorne* can be distinguished from all other Nearctic *Lathrobium* by unique primary and secondary sexual characters. The male sternite VIII has a scalloped emargination, and the dorsal plate of the aedeagus bends over the top of the ventral process. In females, the inner margin of the gonocoxites is broad and distinctively arched.

**Description.** Body length 7 mm; body coloration dark red throughout. Gular sutures parallel, widely separate; antennomeres V–VII as wide as long. Elytra longer than pronotum. Female sternite VIII weakly oblong. Genitalia as in Fig. 51.

Distribution. Canada: NB, ON, QC, PE (Bousquet et al. 2013). USA: MA, MI.

#### Lathrobium (Lathrobium) washingtoni Casey, 1905

Lathrobium washingtoni Casey, 1905: 87. Lathrobium illini Casey, 1905: 86. New synonym. Lathrobium longiventre Casey, 1905: 85. New synonym. Lathrobium picescens Casey, 1905: 85. New synonym. Lathrobium vancouveri Casey, 1905: 86. New synonym.

**Type material.** *Lectotype*, *Lathrobium washingtoni* Casey, herein designated (USNM): "N. H. / ♂ / [red] TYPE USNM 38121 / CASEY bequest 1925 / [hand-



Figures 50–53. *Lathrobium* terminalia **A** female terminalia **B** male sternite VIII **C** aedeagus in ventral view **D** aedeagus in lateral view. **50** *L*. *sparsellum* **51** *L*. *spissicorne* **52** *L*. *washingtoni* **53** *L*. *debile*. Scale bars: 1 mm.

written] washingtoni / Lectotype Lathrobium washingtoni Casey Desg. Haberski & Caterino." Lectotype, Lathrobium illini Casey, herein designated (USNM): "Illinois / CASEY bequest 1925 / [handwritten] illini / [red] TYPE USNM 38118 / Lectotype Lathrobium illini Casey Desg. Haberski & Caterino." Lectotype, Lathrobium longiventre Casey, herein designated (USNM): "Bayfld / CASEY bequest 1925 / [handwritten] longiventre / [red] TYPE USNM 38115 / Lectotype Lathrobium longiventre Casey Desg. Haberski & Caterino." Lectotype, Lathrobium longiventre Casey Desg. Haberski & Caterino." Lectotype, Lathrobium picescens Casey, herein designated (USNM): "N.H. / CASEY bequest 1925 / [handwritten] picescens / [red] TYPE USNM 38116 / Lectotype Lathrobium picescens Casey Desg. Haberski & Caterino." Lectotype Lathrobium vancouveri Casey, herein designated (USNM): "Br.C / CASEY bequest 1925 / [handwritten] vancouveri / [red] TYPE USNM 38117 / Lectotype Lathrobium vancouveri Casey Desg. Haberski & Caterino."

**Other material.** Canada: British Columbia: Terrace, Hippisley (1, MCZ). Newfoundland: 'N'f'land' 19–24 Jul 1907 (1, MCZ). USA: Alaska: Fairbanks North Star Borough: Nome Creek, 11 Jun 2018, R. Nowicki (1, UAM). Minnesota: 'Min.' (2, USNM). New Hampshire: 'N. H.' (1, USNM); Coos Co.: Mount Washington (1, MCZ); Grafton Co.: Woodstock, White Mountains (1, USNM). Wisconsin, Bayfield Co. Bayfield (1, USNM).

**Diagnosis.** This species is similar in appearance to *L*. *leconteanum* and can be differentiated as discussed in the diagnosis of *L*. *leconteanum*.

**Description.** Body length 6–7 mm; body coloration dark red, appendages lighter red. Gular sutures, widely separate, converging slightly posteriorly; antennomeres V–VIII as wide as long. Elytra as long as pronotum. Females with paraprocts divided; sternite VIII strongly oblong, tip 1/3 width of base. Genitalia as in Fig. 52.

**Distribution.** Canada: AB, BC, MB, NB, NF, NS, NT, ON, QC, SK (Bousquet et al. 2013). USA: AK, ID, IL, **MN**, MT, NH, WI (Newton 2022).

**Remarks.** We reduce *Lathrobium illini*, *Lathrobium longiventre*, *Lathrobium picescens*, and *Lathrobium vancouveri* to synonymy with *Lathrobium washingtoni*, because the original diagnoses were based on a single inaccurate character. All four of the herein synonymized species were distinguished from *L. washingtoni* by having the middle joints of the antennae not longer than wide, as opposed to "elongate" (Casey 1905). We measured the fifth antennomeres of each species and found the ratio of length to width varied within and between species from 1.1 to  $1.4 \times$  as long as wide, making this character useless for diagnosis. We examined the genitalia and found no differences among species in males or females.

## Subgenus Lathrolepta Casey, 1905: 72.

## Lathrobium (Lathrolepta) debile LeConte, 1880

Lathrobium debile LeConte, 1880: 176. Lathrolepta debilis Casey, 1905: 104. Lathrobium (Lathrolepta) debilie: Bernhauer and Schubert 1912: 258.

**Type material.** *Lectotype*, *Lathrobium debile* LeConte, herein designated (MCZ): "Mic. / [handwritten] 463 / [handwritten] L. debile Lec. / Lectotype *Lathrobium debile* LeConte Desg. Haberski & Caterino." **Other material.** Canada: Ontario: 'Ont. Can.' (1, USN). USA: Indiana: 'In.' (1, USNM). Massachusetts: 'Mass,' Jul 1903, J. Blanchard (1, MCZ); 'Mass' (5, USNM). Michigan: 'Mic.' (1, USNM). New Hampshire: Grafton Co.: Downes Brook, Potash Mountain, 05 Jun 2021, A. Haberski (1, CUAC); Belknap Co.: Lower Gilmanton, 23 Apr 1982, D. S. Chandler (6, UNHC); Chesire Co.: Rhodo-dendron State Park, 22 Apr 1982, D. S. Chandler, sifted rotten spruce & fir logs (4, UNHC); Hillsborough Co.: Miller State Park, 22 Apr 1982, D. S. Chandler, and SW Durham, 02 Jul 1987, litter near bog (2, UNHC). New York: 'N. Y.' (1, USNM).

**Diagnosis.** Lathrobium debile differs from all other described species of Nearctic Lathrobium in its small size and diverging gular sutures. However, it resembles members of the *sibiricum* group, which may have undescribed diversity in Alaska and Northwest Territories. Species in the *sibiricum* group lack a dorsal plate on the aedeagus and have a sclerotized ring-like structure on the membranous endophallus. Lathrobium debile has a dorsal plate and lacks the ring-like structure.

**Description.** Extremely small species, body length 3.5–4 mm; coloration reddish, appendages lighter. Gular sutures divergent (Fig. 1D). Antennae short, antennomeres as long as wide. Female sternite VIII oblong. Genitalia as in Fig. 53.

**Distribution.** Canada: ON, NB, QC (Bousquet et al. 2013). USA: IA, **IN**, MA, MI, NH, NY (Newton 2022).

#### Genus Pseudolathra Casey

Pseudolathra parcum (LeConte, 1880), comb. nov.

Lathrobium parcum LeConte, 1880: 92.

**Type material.** *Holotype* (MCZ): "Capron 15.4. Fla / 741 / [handwritten] *L. parcum* Lec. / [red] Type 6458."

**Remarks.** This species is transferred to *Pseudolathra* based on the protibia not being expanded with protibial combs in lateral view (Żyła et al. 2020).

# Pseudolathra texana (Casey, 1905), comb. nov.

Lathrobiopsis texana Casey, 1905: 98. Lathrobium (Lathrobiopsis) texanum: Bernhauer and Schubert 1912: 269.

**Type material.** *Lectotype*, *Lathrobiopsis texana* Casey, herein designated (USNM): "Tex. / CASEY bequest 1925 / [red] TYPE USNM 38120 / [handwritten] *Lathrobiopsis texanum Csy* / Lectotype *Lathrobiopsis texana* Casey Desg. Haberski & Caterino."

**Remarks.** This species is transferred to *Pseudolathra* based on the protibia not being expanded with protibial combs (Żyła et al. 2020) and the presence of a carina on the elytral epipleuron (Assing and Schülke 2012). Its habitus is overall inconsistent with North American *Lathrobium*. The head is square with the posterior angles projecting; the pronotum is quadrate rather than long; and the elytral punctures are arranged in regular rows.

# Checklist of the Nearctic species of Lathrobium north of Mexico

#### Subgenus Abletobium Casey

- 1. Lathrobium absconditum Haberski & Caterino, sp. nov.
- 2. Lathrobium balsamense Haberski & Caterino, sp. nov.
- 3. Lathrobium hardeni Haberski & Caterino, sp. nov.
- 4. Lathrobium lapidum Haberski & Caterino, sp. nov.
- 5. Lathrobium pallescens (Casey, 1905)
- 6. Lathrobium shermani Fall, 1917
- 7. Lathrobium smokiense Haberski & Caterino, sp. nov.
- 8. Lathrobium solum Haberski & Caterino, sp. nov.
- 9. Lathrobium thompsonorum Haberski & Caterino, sp. nov.

## Subgenus Apteralium Casey

- 10. Lathrobium brevipenne LeConte, 1863
- 11. Lathrobium camplyacra Haberski & Caterino, sp. nov.
- 12. Lathrobium carolinae (Casey, 1905)

#### Subgenus Lathrobioma Casey

- 13. Lathrobium divisum LeConte, 1880
- 14. Lathrobium nanulum (Casey, 1905)
- 15. Lathrobium othioides LeConte, 1880
- 16. Lathrobium scolopaceum (Casey, 1905)
- 17. Lathrobium tenue LeConte, 1863

# Subgenus Lathrobium s. str.

- 18. Lathrobium amplipenne Casey, 1905
- 19. Lathrobium armatum Say, 1830
- 20. Lathrobium confusum LeConte, 1880
- 21. Lathrobium crurale (Casey, 1905)
- 22. Lathrobium fauveli Duvivier, 1883
- 23. Lathrobium fulvipenne (Gravenhorst, 1806)
- 24. Lathrobium geminum Kraatz, 1857
- 25. Lathrobium insanum Blatchley, 19108.
- 26. Lathrobium islae Haberski & Caterino, sp. nov.
- 27. Lathrobium leconteanum Scheerpeltz, 1933
- 28. Lathrobium lineatocolle Scriba, 1859
- 29. Lathrobium lintneri Notman, 1921
- 30. Lathrobium lividum Haberski & Caterino, sp. nov.
- 31. Lathrobium pedale LeConte, 1863
- 32. Lathrobium praelongum Casey, 1905
- 33. Lathrobium puncticolle Kirby, 1837
- 34. Lathrobium rhodeanum (Casey, 1905)
- 35. Lathrobium simile LeConte, 1863
- 36. Lathrobium sparsellum Casey, 1905

- 37. Lathrobium spissicorne Casey, 1905
- 38. Lathrobium subgracile (Casey, 1905)
- 39. Lathrobium tenebrosum Notman, 1919
- 40. Lathrobium washingtoni Casey, 1905

#### Subgenus Lathrolepta Casey

41. Lathrobium debile LeConte, 1880

The MCZ contains labelled holotypes for two additional species from California, "Lathrobium atrapubes Watrous, 1983" and "Lathrobium subcarinatum Watrous, 1983". The CNC contains an un-named holotype of an undescribed species near Lathrobium sibiricum Fauvel, 1875 from Arctic Alaska. These have not yet been properly described, though we have confirmed that they are members of Lathrobium and morphologically distinct from other species.

## Key to North American Lathrobium north of Mexico

- 4 Aedeagus tubular (Fig. 9E, F).....Lathrobium smokiense
- Aedeagus not tubular (Fig. 10D, E).....Lathrobium balsamense
- Male sternite VIII without thick black setae (Fig. 21B); aedeagus with dorsal plate 1/3 length of ventral process, ventral process weakly asymmetrical in ventral view (Fig. 21C, D).....Lathrobium solum
- Smaller species, body length < 9 mm. Male sternite VIII with transverse combs of thick black setae (Figs 14D, 20B). Female gonocoxites without lobe-like projections (Figs 20B, 22A)</li>

7	Male sternite VIII with two combs of 5–8 thick black setae to either side of
	midline (Fig. 20B). Female gonocoxites with fine pubescence (Fig. 20A);
	subgenital plate absent Lathrobium shermani
-	Male sternite VIII with three combs of thick black setae (Fig. 14D). Female
	with either valvifers and coxites divided, or with subgenital plate8
8	Male sternite VIII with V-shaped emargination (Fig. 22D). Female sternite
	VIII without apical notch; sternum IX with valvifers and coxites divided
	(Fig. 22B); no subgenital plate; apical lobes of paraproct longer than con-
	tinuous basal portion in dorsal view Lathrobium thompsonorum
_	Male sternite VIII without emargination (Fig. 14D). Female sternite VIII
	with apical notch; sternite IX with valvifers and coxites fused; subgenital
	plate present (Fig. 14B); apical lobes of paraproct shorter than continuous
	basal portion in dorsal view Lathrobium hardeni
9	Elvtra distinctly shorter than pronotum 10
_	Elytra longer than or equal to pronotum 15
10	Eves small ~ 30 ommatidia Body nale Head wider than elytra
10	Lycs small, 50 ommatiala. Dody pale. Head wider than clyfra
_	Eves larger Body black or reddish Head width subegual to elytra 11
11	Small species body length < 5 mm; coloration black Gular sutures ar-
	Small species, body length $< 5$ min, coloration black. Gual sutures all outto (Fig. 1C). Postrioted to enruge fir forests $> 1500$ m elevation in the
	cuate (Fig. 1C). Restricted to spruce-in folests > 1500 in elevation in the
_	Southern Appalacitians
_	Larger species, body length > 6 mm, coloration redusit. Gular sutures
	straight (Fig. TA). Restricted to hardwood forest < 1500 m elevation in the
10	Southern Apparachians of the interior Highlands
IZ	Spine of internal sac of aedeagus long with ball-shaped tip (Fig. 7F). Fe-
	male gonocoxites narrow at base (Fig. 7B)Lathrobium islae
-	Spine of internal sac of aedeagus short, with curved spine projecting
	above ventral process (Fig. 8E). Female gonocoxites not narrowed at base
4.0	(Fig. 8A)Lathrobium lividum
13	Male sternite VIII with two projecting lobes (Fig. 24B); aedeagus variable
	(Figs 24–26C, D). Female sternite VIII oblong. Endemic to the Interior
	Highlands of the United States Lathrobium brevipenne
-	Male sternite VIII without projections (Fig. 5D); aedeagus with median
	lobe fully sclerotized. Female sternite VIII conical (Fig. 5C). Endemic to
	the Southern Appalachian Mountains14
14	Aedeagus with ventral process straight in lateral view (Fig. 4e). Female
	subgenital plate absent (Fig. 4A) Lathrobium carolinae
-	Aedeagus with ventral process curved, tip ending below median foreman
	in lateral view (Fig. 5F). Female with subgenital plate present as small,
	lightly sclerotized chevron (Fig. 5B)Lathrobium camplyacra
15	Metatarsi compact, tarsomeres I-IV subequal in length. Small species,
	body length $\leq$ 6 mm (except <i>L. divisum</i> ) <b>16</b>
-	Metatarsi elongate, tarsomere II longer than III or IV. Body length $\geq$ 6mm
16	Very small species, body length < 4 mm. Gular sutures divergent (Fig. 1D)
	Lathrobium debile
-	Body length > 4mm. Gular sutures arcuate or parallel (Fig. 1A, C)17

17	Antennomeres V and VI longer than wide. Male sternite VIII without thick
	black setae (Fig. 36B) Lathrobium confusum
_	Antennomeres V and VI not longer than wide. Male sternite VIII with apical
	thick black setae (Figs 29-33B)18

- Aedeagus wide and scoop-shaped in ventral view (Figs 30C, 31–33C). Female with valvifers and coxites fused (Fig. 31A) ......20
  Ventral process of aedeagus with apex downturned in lateral view with
- Ventral process of aedeagus broadly rounded or with horn-like projections (Figs 31C, 33C). Female with paraprocts continuous (Fig. 2B)......21
- 21 Ventral process of aedeagus with two horn-like projections (Fig. 31C). Females with median edge of gonocoxites broad and sinuate (Fig. 31A) ...... Lathrobium othioides
- Ventral process of aedeagus broadly rounded (Fig. 33C). Females with median edge of gonocoxites narrow and concave (Fig. 33A).....
- 22 Gular sutures converging, often nearly touching posteriorly (Fig. 1B). Large
- - out (Fig. 1A). Smaller species, body length ≤ 8 mm. Elytra rarely bicolored... **26**

26	Dorsal plate of aedeagus with large, back-curving hook-like projection
	(Fig. 35D). Female sternite VIII conical; interior edge of gonocoxites con-
	vex (Fig. 35A)Lathrobium armatum
-	Aedeagus with apex of ventral process narrow and as long as median
	lobe (Fig. 47C). Female sternite VIII oblong; interior edge of gonocoxites
~ 7	concave (Fig. 47A) Lathrobium praelongum
27	Antennomeres V and VI as long as wide
_	Antennomeres V and VI more than 1.5× longer than wide29
28	Male sternite VIII with deep emargination, 1/3 depth of sternite (Fig. 52B).
	Aedeagus with dorsal plate relatively short (Fig. 52D). Female with parap-
	rocts divided (Fig. 2A)Lathrobium washingtoni
-	Male sternite VIII with shallow emargination, 1/8 depth of sternite (Fig.
	51B). Aedeagus with dorsal plate longer (Fig. 51D). Female with parap-
	rocts continuous (Fig. 2B)
29	Male sternite VIII with a shallow emargination, < 1/8 depth of sternite (Figs
	38B, 48B). Female with valvifers and gonocoxites divided (Fig. 38A)30
_	Male sternite VIII with a deep emargination, > 1/5 depth of sternite (Figs 3/B,
~~	50B). Female with valvifers and gonocoxites fused (where known)
30	Ventral process of aedeagus more-or-less straight, tip level with foreman
	in lateral view, excluding apical projection (Figs 38D, 48D). Female tergite
	IX with apical lobes of paraprocts longer than continuous anterior portion
	In dorsal view (Fig. 2B)
-	ventral process of aedeagus angled ventrally, tip ending below median
	foreman in lateral view (Figs 39D, 45D). Female tergite IX with apical lobes
	of paraprocts longer than continuous anterior portion in dorsal view (Fig.
21	ZD)
51	valvifers and covites subequal in length (Fig. 480): remain sterning vin obiolog,
	roct more than twice as long as basal portion <b><i>L</i> attrobium rhodeanum</b>
_	Male sternite VIII as long as wide (Fig. 38B). Female sternite VIII conical:
	covites shorter than valvifers (Fig. 38A): anical lobes of paraproct 1.5x
	longer than basal portion
32	Ventral process of aedeagus considerably asymmetrical in ventral view
02	(Fig. 39C) Female sclerite VIII oblong
_	Ventral process of aedeagus symmetrical in ventral view (Fig. 45C) Fe-
	male sclerite VIII conical with truncate apex Lathrobium lineatocolle
33	Female with paraprocts undivided (Fig. 2B. C). Male sternite VIII without
	thick black setae, emargination 1/5 depth of sternite (Fig. 37B)
	Lathrobium crurale
_	Female with paraprocts divided (Fig. 2A). Male sternite VIII with thick
	black setae along medial line (Figs 44B, 49B), or emargination ½ depth of
	sternite (Fig. 50B)
34	Male sternite VIII without thick black setae, emargination deeper than
	wide, <sup>1</sup> / <sub>2</sub> depth of sternite (Fig. 50B). Female with gonocoxites narrow and
	glabrous at base (Fig. 50A); proctiger pointed Lathrobium sparsellum
_	Male sternite VIII with thick black setae medially, emargination < 1/2 depth
	of sternite (Fig. 44B, 49B). Female gonocoxites wide at base (Fig. 50A), or
	with fine pubescence (Fig. 44A); proctiger conical

35 Ventral process of aedeagus with apex divided (Fig. 44). Female gonocoxites with pubescent lobes (Fig. 44A); proctiger narrow .....

.....Lathrobium leconteanum

# Discussion

After the taxonomic changes made in this paper, there are 41 valid species of Nearctic *Lathrobium*, and three as yet undescribed species. Forty-four species is assuredly an underestimate of the true diversity. The subterranean fauna is poorly documented and a relatively modest effort by a few collectors discovered five of the new species described here. Buried pipe traps are an efficient and inexpensive method for collecting hypogean beetles, but their use has so far been limited, and a wider deployment is likely to reveal more undescribed species. We have already seen morphologically distinct specimens from Illinois and North Carolina, but further material is needed to warrant their descriptions.

We used a combined morphological and molecular approach to test the hypothesis of cryptic speciation among three flightless lineages of Appalachian *Lathrobium*. They have accumulated genotypic and phenotypic variations at different rates making it difficult to delimit species based on a single character system. We obtained incongruent results in the *L. smokiense–balsamense* and *L. islae–lividum* lineages. In the case of *L. islae–lividum*, only mPTP failed to split the lineage into at least two putative species, and the paraphyly in our tree was consistent with some scenarios of recent speciation (Bush and Butlin 2004).

The results for *L. smokiense–balsamense* were more ambiguous, but we felt the morphological differences justified species designation. Our molecular methods were based on a single mitochondrial locus, COI. Gene-tree/ species-tree discordance is therefore a potential source of error in our phylogenetic and mPTP analyses (e.g., Maddison 1997). Furthermore, uniparental inheritance and smaller effective population size in mtDNA can cause mito-nuclear discordance in biogeographic signals, so interpreting COI alone might present an incomplete picture of *Lathrobium* evolution (Toews and Brelsford 2012). Morphology avoids these complications because it is influenced by multiple genes. Our morphological dataset had the additional advantage of a larger sample size with a broader geographic scope. However, we recognize that there might be one or more additional cryptic species that we cannot adequately defend with the current data.

The Lathrobium smokiense-balsamense and L. islae-lividum lineages are endemic to isolated sky-islands of red spruce-Fraser fir forest on peaks above 1700 m elevation. Linear distance between islands did not correlate with genetic distance. The highest pairwise genetic distances all occurred between neighboring localities, Grandfather Mountain and Roan High Knob (33 km), Clingmans Dome and Mount Kephart (8 km), and Mt. Lyn Lowry and Richland Balsam Mountain (25 km). The lack of isolation by distance effects and lack of strong population structure are consistent with a hypothesis of range expansion in the recent past (Crespi et al. 2003), possibly when spruce-fir forest was more contiguous ~ 10,000 ya (Delcourt and Delcourt 1998).

Polyphyly of *L. smokiensis* and *L. balsamensis* may indicate speciation was more recent than in *L. islae–lividum*, or it may be indicative of recent secondary contact. Linear distances between spruce-fir islands south of the French Broad River basin are shorter than to the north. Forest patches may therefore have come into contact more often or stayed connected longer.

The southern Appalachian red spruce-Fraser fir forest is among the most endangered forest types in the United States (Noss and Scott 1995; Wear and Greis 2002), and the above-mentioned species are endemic to a rare bryophyte mat microhabitat within it. They share this microhabitat with the spruce-fir moss spider, *Microhexura montivaga*, which was added to the Federal List of Endangered and Threatened Wildlife and Plants by the USFWS in 1994 due to low abundance and significant threats to its remaining habitat (Fridell 1995). A conservation assessment of *Lathrobium* populations is unlikely, but they may benefit from the habitat protection already afforded to *M. montivaga*.

The deep divergence in the *L. carolinae–camplyacra* lineage implies ancient vicariance, and the lack of genetic diversity within the two species suggests a recent population bottleneck. Unlike spruce-fir species, *L. carolinae* and *L. camplyacra* might have experienced a recent range contraction. The expansion of spruce-fir into lower elevations during the last glacial maximum might have pushed northern hardwoods into small refugia, causing a bottleneck.

River basins appear to be the primary barriers to gene flow in the region. The French Broad River basin is a well-documented barrier implicated in numerous taxa (Crespi et al. 2003; Thomas and Hedin 2008; Caterino and Langton-Myers 2019), and none of the flightless *Lathrobium* have been able to disperse across it. The Little Tennessee River basin, which largely separates *L. camplyacra* and *L. carolinae*, acts as an impediment to gene flow but not an absolute physical barrier. *Lathrobium carolinae* occurs east of the basin along the Great Smoky Mountains, but apparently there has not been enough time, or insufficient isolation, to observe genetic variation in COI between populations east and west of the river, at least as sampled. A similar pattern has been observed in *Dasycerus* staphylinids (Caterino and Harden 2024) and *Sabacon* harvestmen (Hedin and McCormack 2017). Hedin and McCormack (2017) hypothesized that reduced gene flow across the river basin combined with competitive exclusion or low hybrid fitness maintains lineage boundaries.

# Subgeneric placement of microphthalmous Lathrobium

The depigmented, microphthalmous, and flightless *Abletobium* bears a strong resemblance to the Palearctic subgenus *Glyptomerus*, as noted by Casey (1905) and Fall (1917). These characters are common in hypogean and troglobitic taxa across Arthropoda, so it is unclear how the two are related or if they are synonyms. The addition of seven new Nearctic *Abletobium* allowed us to reassess characters that may be phylogenetically relevant to this question.

Three characters, in addition to the general habitus, have been proposed as synapomorphies for *Glyptomerus* (Coiffait 1982): 1) dorsal plate and ventral process of the aedeagus without teeth, except sometimes at the apex; 2) median lobe of the aedeagus always divided in two at the apex; and 3) male sternite VIII with transverse combs of thick black setae. However, these characters are variable within, or not exclusive to *Glyptomerus* (Bordoni 2020, 2018, 2012).

Among Nearctic *Lathrobium* the first character is not exclusive to the "glyptomeroid" habitus, and in fact applies to most species. The second character does not occur in any Nearctic glyptomeroids. Only the third character, combs of black setae, is exclusive to glyptomeroids, but is present in only half the species (*L. lapidum*, *L. thompsonorum*, *L. hardeni*, and *L. shermani*).

Casey (1905) erected *Abletobium* as a monospecific genus for *L. pallescens* and distinguished it from *Glyptomerus* based on a single character: *Abletobium* had eyes that were small, with distinct ommatidia, whereas *Glyptomerus* had eyes reduced to white scars. It also lacks characters two and three listed above. Fall (1917) added *L. shermani* to the subgenus, which does not have eyes but does have combs of black setae on sternite VIII. He noted its resemblance to *Glyptomerus* but determined *Abletobium* was a better fit. To further cloud the matter, several Palearctic *Glyptomerus* (e.g., *Lathrobium zoiai* Briganti, 1980) have setal combs and eyes resembling *L. pallescens*. The lack of stemmata in Nearctic larvae might distinguish the two subgenera, but too few larvae have been described to be certain. We placed new species in *Abletobium* until the matter can be further tested.

Our COI phylogeny did not include any representatives of *Glyptomerus* and was inadequate to evaluate subgeneric boundaries. DNA is the most promising avenue for unraveling relationships among morphologically convergent taxa. A more complete phylogeny is needed.

# Larval morphology

Thirteen diagnostic characters were found by Staniec and Bordoni (2022) to distinguish mature (2<sup>nd</sup> instar) larvae of *Lathrobium* from the well-known larvae of closely related genera: 1) nasale with median tooth; 2) head at least 3× as wide as neck; 3) apotome at most reaching tentorial pits; 4) antennal sensory appendage > ½ length of antennomere IV; 5) mandibular seta L1 residual; 6) stipes quadrate in outline with four setae (one tiny), cuticular process near mala and microstructure near trichobothrium; 7) mala > ½ length of maxillary palpomere I; 8) hypopharynx with microtrichia in central area forming inverted triangle in outline; 9) prementum extended anteriorly; 10) labial palpomere II more or less bent inside; 11) both halves of sternum of thoracic segment I almost touch each other along middle line; 12) prosternum strongly developed, divided into two sternites by narrow, membranous area of width at most 1/10 that of sternite; 13) article I of urogomphi at least 1.5× as long as abdominal segment X (pygopod).

The Nearctic larvae we described conform to all of these characters, except number 2. *Lathrobium islae* and *L. carolinae* had necks slightly wider than 1/3 the width of the head, though within rounding error. Character 13 could not be judged in *L. carolinae* or *L. islae* because the urogomphi were broken off.

Paederines have only two larval instars, but distinguishing between them is difficult without a side-by-side comparison. We were able to compare  $1^{st}$  and  $2^{nd}$  instars for *L. islae* and *L. hardeni* and found the following differences: body length increased ~ 2× and 1.75× respectively; antennae, maxilla, and labial palpomeres became more elongate; stipes of *L. hardeni* changed from quadrate to elongate; median tooth of the nasale became larger and more sagittate; antennomere IV became club-shaped; and labial palpomere II acquired its characteristic inward bend. These characters might make it easier to age larvae.

Second instar larvae have now been described for 14 species of Lathrobium: Lathrobium alzonai Capra & Binaghi, 1938, Lathrobium brunnipes (Fabricius, 1792), Lathrobium cavicola (H. Müller, 1856), Lathrobium freyi Koch, 1938, Lathrobium elongatum (Linnaeus, 1767), Lathrobium fulvipenne (Gravenhorst, 1806), Lathrobium geminum Kraatz, 1857, Lathrobium lineatocolle Scriba, 1859, L. absconditum, L. carolinae, L. hardeni, L. islae, and L. thompsonorum. This is a small fraction of worldwide Lathrobium, so it difficult to know the extent of intraspecific and interspecific variability. Nevertheless, Staniec and Bordoni (2022) summarized 25 variable characters that might be useful for species diagnosis. We here review those characters variable in Nearctic larvae: 1) body length (5-7 mm); 2) presence or absence of stemmata; 3) head shape (triangular, U-shaped, or quadrate); 4) width ratio of neck and head (2.5:1-3.6:1); 5) shape of the median tooth of the nasale (round, emarginate, trifurcate); 6) apotome reaching or not reaching tentorial pits; 7) length ratio of antennomeres; 8) inner margin of mandibles serrate or smooth; 9) mandibles serrate in apical, middle, or basal 1/3; 10) shape of stipes (1.5× to 2.8× as long as wide); 11) length ratio of maxillary palpomeres; 12) strip separating ligula from prementum strongly or poorly sclerotized; 13) abdominal sclerites poorly or strongly sclerotized. Characters 2, 8, 9, and 13 are new, although 8 was noted by previous authors (Staniec et al. 2014), bringing the total number of potentially informative characters to 29. Characters 2, 3, 4, and 13 differentiate eyed species, L. carolinae and L. islae, from eyeless Abletobium larvae.

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# **Additional information**

# **Conflict of interest**

The authors have declared that no competing interests exist.

# **Ethical statement**

No ethical statement was reported.

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## **Data availability**

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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# **Supplementary material 1**

#### COI sequence data from Appalachian Lathrobium and outgroups

Authors: Adam Haberski, Michael S. Caterino Data type: txt

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Link: https://doi.org/10.3897/zookeys.1198.118355.suppl1



**Research Article** 

# A new troglomorphic species of *Larca* (Pseudoscorpiones, Larcidae) from Colorado

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#### Abstract

A new species of *Larca* is described from dry habitats in a cave in central Colorado. Like other cave-dwelling species of *Larca*, the new species *Larca boulderica* **sp. nov.**, shows relatively modest morphological adaptations, such as pale colouration and slightly elongated appendages, compared with their epigean counterparts. This species is the sixth cave-dwelling species of *Larca* described from North America and, like other cave-dwelling *Larca* in North America and Europe, tends to be distributed in more southerly regions.

Key words: morphology, Nearctic, new species, pseudoscorpion, taxonomy, troglomorphic



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# Introduction

The pseudoscorpion family Larcidae consists of only 15 species found throughout Europe and North America. Although the family was traditionally divided into two genera with *Larca* Chamberlin, 1930 distinguished from *Archeolarca* Hoff & Clawson, 1952 only in the number of trichobothria on the movable chelal finger (*Larca* with 2 or 3 trichobothria and *Archeolarca* with 4 trichobothria), these genera were regarded as synonyms by Harvey and Wynne (2014). The European fauna consists of *L. bosselaersi* Henderickx & Vets, 2002, *L. fortunata* Zaragoza, 2005, *L. hispanica* Beier, 1939, *L. italica* Gardini, 1983, *L. lata* (Hansen, 1884) and *L. lucentina* Zaragoza, 2005, and the North American fauna consists of *L. aalbui* (Muchmore, 1984), *L. cavicola* (Muchmore, 1981), *L. chamberlini* Benedict & Malcolm, 1978, *L. granulata* (Banks, 1891), *L. guadalupensis* (Muchmore, 1981), *L. laceyi* Muchmore, 1981, *L. notha* Hoff, 1961, *L. rotunda* (Hoff & Clawson, 1952) and *L. welbourni* (Muchmore, 1981).

*Larca* was originally treated as a member of the family Garypidae by Chamberlin (1930) until both it and *Archeolarca* Hoff & Clawson, 1952 were transferred to their own family by Harvey (1992). A recent phylogenomic study found that Larcidae are sister to Garypinidae, and that they belong to their own superfamily, Garypinoidea, which in turn is sister to a larger clade of Cheiridioidea + Sternophoroidea + Cheliferoidea (Benavides et al. 2019). A multi-gene analysis of larcids and garypinids found that *Larca* nested within Garypinidae (Harvey 2023).

Among some recently collected cave-dwelling pseudoscorpions from Colorado were specimens of Larcidae that differed in several ways from other species of *Larca*. That species is described here.

# Materials and methods

The specimens examined for this study are lodged in the Denver Museum of Nature & Science, Colorado (DMNS) and the Western Australian Museum, Perth (WAM). They were studied using temporary slide mounts prepared by immersion of the specimens in lactic acid at room temperature for several hours, and mounting them on microscope slides with a 10 mm coverslip supported by small sections of 0.25 mm diameter nylon fishing line. After the study, the specimens were rinsed in water and returned to 75% ethanol with the dissected portions placed in 12 × 3 mm glass genitalia microvials (BioQuip Products, Inc.). The specimens were examined with a Leica MZ16 A dissecting microscope and an Olympus BH2 compound microscope, and illustrated with the aid of a drawing tube attached to the compound microscope. Measurements were taken at the highest possible magnification using an ocular graticule.

Terminology and mensuration mostly follow Chamberlin (1931), with the exception of the nomenclature of the pedipalps, legs and some minor modifications to the terminology of the trichobothria (Harvey 1992), chelicera (Judson 2007) and faces of the appendages (Harvey et al. 2012).

# Ecology

The type locality, Mallory Cave, is at the eastern edge of the Rocky Mountains in the foothills of Boulder County, Colorado (Fig. 1). The cave is on Dinosaur Mountain to the west of City of Boulder on City of Boulder Open Space and Mountain Parks land. Mallory Cave formed in the Fountain Formation which is a sandstone conglomerate that was deposited approximately 280 Ma during the Pennsylvanian Period (Evanoff and Hirschfeld 2016).

Mallory Cave consists of one large room 25 m wide by 7 m deep with a single walk-in entrance that faces east. The temperature inside is 55 °F (13 °C). The cave is gated to protect a maternity colony of Townsend's big-eared bats (*Corynorhinus townsendii* Cooper, 1837). There were less than 10 bats roosting in Mallory Cave in 2008 and 2009. Over 60 Townsend's big-eared bats were documented roosting in the cave in 2023 (B. Stoner, personal communication, 20 March 2024). The cave was gated in 2011 which limited human disturbances to the bats and helped the bat colony increase in size. The *Larca* specimens were collected in the fall of 2008 and 2009 after the bats left the cave for the winter and no guano was observed.

The Larca specimens were found among the remnants of packrat nests and under rocks in arid and dusty areas in the dark zone of the cave. They were clustered in groups of 4–10 individuals. Mallory Cave is dry in the southern section where the Larca specimens were collected. The western and northern sections of the cave have ceiling drips, wet seeping walls, and a moist floor further inside.

Packrats that use Mallory Cave are bushy-tailed woodrats (*Neotoma cinerea*) which is the only packrat species known from Boulder County (Armstrong et al.



Figure 1. The foothills of Boulder where Mallory Cave is located.

2011). The packrat nest remnants were 3–5 cm deep and 30 cm in diameter consisting of scattered debris from abandoned nests. The nest remnants were visually searched for invertebrates. They contained leaves, sticks, pine cones, grasses and fresh packrat scat. Tweezers were used to move the nesting materials around while looking for invertebrates. There are no large packrat middens in the cave. No packrats were observed, and no lice or fleas were seen in the packrat nest remnants.

There are a few smaller caves located near Mallory Cave that were not searched for invertebrates, including Harmon Cave and Bear Cave, which could harbour populations of *L. boulderica* sp. nov. Deep cracks in the local rock formations, plus nearby boulder talus fields and packrat nests, may also provide habitat for *L. boulderica*.

Other invertebrates living in Mallory Cave include springtails, harvestmen, spiders, flies, beetles, centipedes and mites. No fleas or lice, which can be associated with rodents, were observed in the cave. Mice (*Peromyscus* sp.) may enter Mallory Cave, though no evidence of mice, including mouse scat or nests, was seen. Guano from Townsend's big-eared bats provide organic nutrient input for the invertebrates inhabiting the cave.

# Biogeography

With the description of *Larca boulderica*, the North American larcid fauna now comprises 10 species. Four are rather widely distributed in epigean habitats: *L. granulata* occurs across a wide variety of habitats from the mid-west to New Hampshire (Muchmore 1981; World Pseudoscorpiones Catalog 2023); *L. ro-tunda* from New Mexico, Oregon, Utah and Wyoming (e.g., Hoff and Clawson 1952; Muchmore 1981), *L. notha* in Colorado, Oregon and southern Canada (e.g., Hoff 1961; Benedict and Malcolm 1978; Muchmore 1981), and *L. chamberlini* in Oregon, California and Mexico (e.g., Benedict and Malcolm 1978; Villegas-Guzmán and Pérez 2005) (Fig. 2). The other six species appear to be obligate cave-dwelling forms with morphological modifications that are indicative of troglomorphic traits. The pedipalps and legs are slightly longer and

thinner than their epigean counterparts, they are paler, and the eyes are reduced in size. They appear to represent short-range endemic species with highly restricted distributions: *L. aalbui* from Mitchell Caverns, California (Muchmore 1984), *L. cavicola* from Grand Canyon National Park and Parashant National Monument, Arizona (Muchmore 1981; Harvey and Wynne 2014), *L. guadalupensis* from Guadalupe Mountains National Park, Texas (Muchmore 1981), *L. laceyi* from Music Hall Cave, California (Muchmore 1981) and *L. welbourni* from Wupatki National Monument, Arizona (Muchmore 1981) (Fig. 3). There is a single record of *L. chamberlini* from a cave in Calaveras County, California but Muchmore (1981) surmised that it was only accidentally found in the cave.

Whereas the epigean species generally occur across a wide range of habitats in North America (Fig. 2), the subterranean species occur in more southerly regions in Arizona (*L. cavicola* and *L. welbourni*), California (*L. aalbui* and *L. laceyi*), Colorado (*L. boulderica*) and Texas (*L. guadalupensis*) (Fig. 3).

A similar pattern occurs in Europe where the widespread species *L. lata* occurs sporadically throughout northern and central Europe (e.g., Lohmander 1939; Ressl and Beier 1958; Beier 1963; Dumitresco and Orghidan 1964; Ressl 1965; Beier 1970; Andersson et al. 1987; Gärdenfors and Wilander 1992; Drogla and Lippold 1994; Judson and Legg 1996; Ranius and Wilander 2000; Nilsson et al. 2001; Ranius 2001; Tooren 2001; Jansson and Hultengren 2002; Ranius 2002; Ranius and Douwes 2002; Drogla and Lippold 2004; Stol 2005; Petrov and Šťáhlavský 2007; Christophoryová et al. 2011a; Šťáhlavský 2011; Novák 2013) (Fig. 4), and the other five species are each found in one or a few caves in the Mediterranean region: *L. bosselaersi* from Milatos Cave, Crete (Henderickx and Vets 2002), *L. hispanica* in eastern Spain (Beier 1939; Estany 1980), *L. italica* from Grotta San Angelo, Italy (Gardini 1983), *L. fortunata* from Cueva del Solin, Spain (Zaragoza 2005) and *L. lucentina* from Sima del Poste, Spain (Zaragoza 2005) (Fig. 5). A cave-dwelling population of *Larca* has also been recorded from southern France (Leclerc 1979) but its identity has not been ascertained (Judson and Legg 1996).

The biogeographic patterns in North America and Europe (Figs 2-5) are extremely similar, with the epigean species usually occupying northerly habitats, and the hypogean taxa restricted to southern caves. The preponderance of cave-dwelling Larca species at more southerly latitudes in North America (Fig. 3) and Europe (Fig. 5) may be the result of caves becoming refuges for invertebrates where species can adapt to live in isolated subterranean habitats while the surface climate, temperature, and habitat conditions are changing over the millennia. Caves provide relatively stable temperatures and humidities compared to above-ground areas. The Pleistocene Effects Model postulates that wetter conditions during glacial periods of the Pleistocene provide connections between caves with the drier interglacial periods isolating populations and leading to genetic divergence (Barr 1968; Barr and Holsinger 1985; Derkarabetian et al. 2010). Studies of the harvestman Sclerobunus steinmanni Derkarabetian & Hedin, 2014 from Mallory Cave determined that S. steinmanni diverged from its ancestor in the late Miocene (7.2-13.4 Ma) (Derkarabetian et al. 2010). Given that the Mallory Cave harvestmen evolved to inhabit caves for at least 7 million years, it seems possible that L. boulderica began adapting to the cave environment in the order of a million years ago or more.

As noted by Judson and Legg (1996), species of *Larca* are xerophilic and prefer dry, dusty habitats, including tree hollows, dry caves, mammal and bird



Figures 2, 3. Distribution of *Larca* in North America: 2 epigean species 3 cave-dwelling species.

nests (Ranius et al. 2010; Turienzo et al. 2010; Christophoryová et al. 2011b; Ranius et al. 2011; Machač et al. 2018). The packrat nest remnants and the rocks where *L. boulderica* were collected were dry and dusty habitats with no moisture. The nests were on the cave floor and on a small ledge approximately 1.5 m above the floor level. There is moisture from drips and seeps further back in Mallory Cave from where the *Larca* specimens were collected. No pseudoscorpions were found in the moist parts of the cave.

## Morphological variation

Detailed examination of the eight specimens of *L. boulderica* has revealed significant intra-population variations in characters that are often cited as of inter-specific value in larcid taxonomy. Cheliceral seta *sbs* was found to be



Figures 4, 5. Distribution of *Larca* in Europe: 4 epigean species 5 cave-dwelling species.

absent in most specimens leading to the presence of only four setae on the cheliceral hand. However, in two specimens, a male and a female, a fifth seta is present on one of the chelicerae. All of the species previously attributed to *Archeolarca (L. aalbui, L. cavicola, L. guadalupensis, L. rotunda* and *L. welbourni* from North America) as well as *L. chamberlini* and *L. laceyi* from North America and *L. bosselaersi* from Crete have four setae (Hoff and Clawson 1952; Benedict and Malcolm 1978; Muchmore 1981, 1984; Henderickx and Vets 2002; Harvey and Wynne 2014), and all other species, *L. granulata* and *L. notha* from North America and *L. fortunata, L. hispanica, L. italica, L. lata* and *L. lucentina* from Europe, usually have the full complement of five setae (Hoff 1961; Muchmore 1981; Gardini 1983; Zaragoza 2005). Zaragoza (2005) reported that specimens of *L. bosselaersi* have four or five setae on the same specimen, and among a large series of *L. hispanica* most specimens have five setae on both chelicerae;

several have five setae on one chelicera and 6 on the other, and two adults had 6 setae on both chelicerae, leading him to caution against relying on cheliceral setal number to characterise species of *Larca*. The variation noted in the specimens of *L. boulderica* lends further support to that advice.

Another variable feature is the number of carapaceal setae. The holotype male of *L. boulderica* had 25 setae (arranged 6: 8: 7: 4) whereas the other male had 41 setae (10: 17: 8: 6). The four measured females had the following arrangements 6: 10: 7: 3 (= 26), 5: 13: 7: 3 (= 28), 4: 15: 7: 4 (= 30) and 6: 10: 7: 4 (= 24). Zaragoza (2005) reported similar variation in specimens of *L. lucentina* with most having four setae on the posterior margin of the carapace, but others having three, two or even one seta. Once again, caution must be taken when using this feature to characterise species of *Larca*.

# Taxonomy

Family Larcidae Harvey, 1992

# Genus Larca Chamberlin, 1930

Larca Chamberlin, 1930: 616. Archeolarca Hoff & Clawson, 1952: 2–3.

**Type species.** *Larca: Garypus latus* Hansen, 1884, by original designation. *Archeolarca: Archeolarca rotunda* Hoff & Clawson, 1952, by original designation.

# Key to Larca species of North America

1	Movable chelal finger with 4 trichobothria (Figs 14, 15)2
-	Movable chelal finger with 2 or 3 trichobothria7
2	Trichobothrium ist situated midway between ib and isb3
_	Trichobothrium <i>ist</i> situated much closer to <i>ib</i> than to <i>isb</i> (Figs 14, 15)4
3	Chelal hand rounded in outline (dorsal view); trichobothrium st separated
	by less than one areolar diameter from <i>t L. cavicola</i> (Muchmore, 1981)
-	Chelal hand less rounded in outline (dorsal view); trichobothrium st sepa-
	rated by at least one areolar diameter from t
	L. guadalupensis (Muchmore, 1981)
4	Chelal hand rounded in outline (dorsal view)5
-	Chelal hand less rounded in outline (dorsal view) (Figs 12, 13)6
5	Pedipalps larger, e.g., femur 0.90−0.995 (♂), 1.20−1.31 (♀) mm in length
	L. welbourni (Muchmore, 1981)
-	Pedipalps smaller, e.g., femur 0.795−0.83 (♂), 0.86−0.91 (♀) mm in length
	<i>L. rotunda</i> (Hoff & Clawson, 1952)
6	Trichobothrium st situated less than one areolar diameter from t; pedipalpal
	segments slender, e.g., femur $5.3-5.9 \times 1000$ km broad, patella $3.9-4.35$
	× longer than broad L. aalbui (Muchmore, 1984)
-	Trichobothrium st situated more than one areolar diameter from t (Figs 14,
	15); pedipalpal segments less slender, e.g., femur 4.57−4.59 (♂), 4.07−4.71
	(♀) × longer than broad, patella 3.09–3.22 (♂), 3.21–3.32 (♀) × longer than
	broad (Figs 12, 13) L. boulderica sp. nov.

- 8 Cheliceral hand with 5 setae, sbs present ........ L. granulata (Banks, 1891)
- Cheliceral hand with 4 setae, *sbs* absent......9
- 9 Anterior margin of carapace with 6 setae; larger species (e.g., pedipalpal femur greater than 0.85 mm in length).....*L. laceyi* Muchmore, 1981
- Anterior margin of carapace with 8 setae; smaller species (e.g., pedipalpal femur less than 0.80 mm in length) ... L. chamberlini Benedict & Malcolm, 1978

#### Larca boulderica sp. nov.

https://zoobank.org/771E4C1C-56BD-4977-99BD-6DE45C97160A Figs 6-21

**Material examined. Types:** U.S.A.: **Colorado:** Boulder County: *holotype* male, Mallory Cave, 39°58.45'N, 105°17.37'W, 7000 ft (2140 m) a.s.l., 29 November 2008, under rock, dark zone of cave, D. Steinmann (DMNS). *Paratypes:* 4 females, collected with holotype (DMNS); 1 male, collected with holotype (WAM T162363); 1 female, same data as holotype except 12 November 2009 (DMNS); 1 female, same data as holotype except 12 November 2009 (WAM T162059).

**Diagnosis.** *Larca boulderica* most closely resembles *L. aalbui*, *L. rotunda* and *L. welbourni* as all have four trichobothria on the movable chelal finger (Figs 14, 15) and trichobothrium *ist* is closer to *ib* than to *isb* (Figs 14, 15). The only other species with four trichobothria, *L. cavicola* and *L. guadalupensis*, have trichobothrium *ist* situated midway between *ib* and *isb. Larca rotunda* and *L. welbourni* have a rounded chelal hand, whereas *L. aalbui* and *L. boulderica* have a thinner hand (Figs 12, 13). *Larca boulderica* differs from *L. aalbui* by the positions of trichobothria *st* and *t* (separated by at least one areolar diameter in *L. boulderica* but by less than one areolar diameter in *L. aalbui*), and the less slender pedipalpal segments [e.g., 4.57–4.59 (♂), 4.07–4.71 (♀) × and patella 3.09–3.22 (♂), 3.21–3.32 (♀) × longer than broad in *L. boulderica* (Figs 12, 13); femur 5.3–5.9 × and patella 3.9–4.35 × longer than broad in *L. aalbui*].

**Description (adults).** *Colour*: most body parts pale yellow-brown, genital region of female and legs slightly paler (Figs 6–9).

Setae and cuticle: setae long, usually curved, distally acuminate; most cuticular surfaces granulate.

**Chelicera:** with 4 (rarely 5) setae on hand, with *sbs* usually absent, and 1 subdistal seta on movable finger; all setae acuminate; seta *bs* slightly shorter than others; with 2 dorsal lyrifissures and 1 ventral lyrifissure; galea of  $\Im$  short with terminal bifurcation (Fig. 16), of  $\heartsuit$  long and slender with 3 terminal to subterminal rami (Fig. 17); rallum of 4 blades, the most distal blade with several serrations on leading edge, other blades smooth; serrula exterior with 16 ( $\Im$ ), 18 ( $\heartsuit$ ) blades; lamina exterior present.

**Pedipalps:** Pedipalp (Figs 12, 13): most surfaces of trochanter, femur, patella and chelal hand lightly and granulate, chelal fingers smooth; trochanter, femur, patella and chelal hand with prominent, curved, slightly denticulate setae arranged sparsely; patella with 3 small sub-basal lyrifissures; trochanter 1.85 (♂),



Figure 6. Larca boulderica sp. nov., in situ in Mallory Cave.

1.79 ( $\mathbb{Q}$ ), femur 4.57–4.59 ( $\mathbb{C}$ ), 4.07–4.71 ( $\mathbb{Q}$ ), patella 3.09–3.22 ( $\mathbb{C}$ ), 3.21–3.32 ( $\mathbb{Q}$ ), chela (with pedicel) 4.36–5.00 ( $\mathbb{C}$ ), 3.83–4.03 ( $\mathbb{Q}$ ), chela (without pedicel) 4.09–4.78 ( $\mathbb{C}$ ), 3.60–3.81 ( $\mathbb{Q}$ ), hand (with pedicel) 2.09–2.33 ( $\mathbb{C}$ ), 1.83–1.87 ( $\mathbb{Q}$ ) × longer than broad, movable finger (with pedicel) 0.96–1.05 ( $\mathbb{C}$ ), 0.97–1.03 ( $\mathbb{Q}$ ) × longer than hand. Fixed chelal finger with 8 trichobothria, movable chelal finger with 4 trichobothria (Figs 14, 15): *eb*, *esb*, *ib* and *ist* situated subbasally, *est*, *isb* and *it* submedially, *et* subdistally, *est* slightly distal to *it*, *ib* opposite *esb*, and *ist* distal to *esb*; *b* and *sb* situated subbasally, and *st* and *t* situated submedially, with *st* situated very close to *t*, separated by slightly more than 1 areolar diameter; patch of microsetae not present on retrolateral margin of fixed chelal finger near *et*. Venom apparatus present in both chelal fingers, venom ducts not visible. Chelal teeth rounded, very low; fixed finger with 30 ( $\mathbb{C}$ ), 30 ( $\mathbb{Q}$ ) teeth; movable finger with 29 ( $\mathbb{C}$ ), 28 ( $\mathbb{Q}$ ) teeth; accessory teeth absent.

**Cephalothorax:** carapace (Figs 9, 10): 0.73-0.75 ( $\mathcal{C}$ ), 0.79-0.83 ( $\mathcal{Q}$ ) × longer than broad; anterior margin straight; with 2 pairs of rounded corneate eyes, tapetum present; with 25–41 ( $\mathcal{C}$ ), 24–30 ( $\mathcal{Q}$ ) setae, arranged with 6–8 ( $\mathcal{C}$ ), 4–6 ( $\mathcal{Q}$ ) near anterior margin, 8–17 ( $\mathcal{C}$ ), 10–15 ( $\mathcal{Q}$ ) in prozone, 7–8 ( $\mathcal{C}$ ), 7 ( $\mathcal{Q}$ ) in metazone and 4–6 ( $\mathcal{C}$ ), 3–4 ( $\mathcal{Q}$ ) near posterior margin; with 1 deep, broad median furrow. Coxal region: manducatory process rounded with 1 distal seta, 1 small sub-oral seta, and 12 ( $\mathcal{C}$ ), 9 ( $\mathcal{Q}$ ) additional setae; median maxillary lyrifissure rounded. Coxae I to IV becoming progressively wider. Chaetotaxy of coxae I–IV:  $\mathcal{C}$ , 8: 8: 12;  $\mathcal{Q}$ , 8: 8: 7: 11.

**Legs:** femora I and II longer than patellae; junction between femora and patellae III and IV very angulate; femora III and IV much smaller than patellae III and IV; femur + patella of leg IV 5.21 (3), 4.81 (2) × longer than broad (Fig. 18); metatarsi and tarsi not fused; tarsus IV without tactile seta; subterminal tarsal setae arcuate and acuminate; claws simple; arolium much longer than claws, not divided.

**Abdomen:** tergites II–VIII and sternites IV–VIII of male and female with medial suture line fully dividing each sclerite. Tergal chaetotaxy: 3, 7: 8: 8: 11: 11: 11: 11: 10: 6: 6 (arranged T4T): 6: 2; Q, 4: 6: 10: 11: 12: 11: 12: 11: 10: 8 (arranged T6T): 4: 2; tergites I–X uniseriate. Sternal chaetotaxy: 3, 22: (0) 7 [3 + 3] (0): (0) 21 (0): 8: 9: 8: 8: 6: 6: 4: 2; <math>Q, 13: (0) 12 (0): (0) 7 (0): 8: 7: 8: 9: 7: 6: 4: 2; sternites IV–X uniseriate; 3 and Q sternite II with all setae situated near posterior margin



Figures 7–9. *Larca boulderica* sp. nov., paratype female (DMNS): 7 body, dorsal 8 body, ventral 9 cephalothorax, dorsal. Scale bars: 0.5 mm.

(Figs 19, 20); most setae of male sternite III clustered near posterior margin (Fig. 19). Spiracles with helix. Anal plates (tergite XII and sternite XII) situated between tergite XI and sternite XI, and surrounded by desclerotized region of tergite XI and sternite XI; sternite XI with 26 ( $\Im$ ), 22 ( $\Im$ ) small lyrifissures. Pleural membrane finely wrinkled-plicate; without any setae.

**Genitalia:** male: very similar to that described for *L. laceyi* Muchmore, 1981 by Muchmore (1981). Female with 1 pair of lateral cribriform plates and 2 median cribriform plates, one of which is larger than the other (Fig. 21); spermathecae absent.

**Dimensions (mm):** Male: holotype, with 1 other male in parentheses (when measured): Body length (excluding chelicerae) 2.37 (2.25). Pedipalp: trochanter 0.370/0.200, femur 0.895/0.195 (0.845/0.185), patella 0.725/0.225 (0.650/0.210), chela (with pedicel) 1.200/0.275 (1.225/0.245), chela (without pedicel) length 1.200 (1.170), chelal hand (without pedicel) length 0.575 (0.570), movable finger length 0.550 (0.600). Carapace 0.640/0.850 (0.580/0.800), anterior eye diameter 0.055, posterior eye diameter 0.050. Leg IV: femur + patella 0.730/0.140, tibia 0.530/0.100, metatarsus 0.265/0.065, tarsus 0.250/0.055.

Female: paratype, with 3 other females in parentheses (when measured): Body length (excluding chelicerae) 2.51 (2.51-2.74). Pedipalp: trochanter 0.375/0.210, femur 0.895/0.205 (0.895-0.990/0.205-0.220), patella 0.755/0.235 (0.765-0.795/0.230-0.240), chela (with pedicel) 1.205/0.315 (1.190-1.255/0.295-0.325), chela (without pedicel) length 1.135 (1.125-1.255), chelal hand (without pedicel) length 0.575 (0.550-0.595), movable finger length 0.565 (0.565-0.575). Carapace 0.640/0.815 (0.645-0.655/0.805-0.815), anterior eye diameter 0.065, posterior eye diameter 0.060. Leg IV: femur + patella 0.745/0.155, tibia 0.530/0.095, metatarsus 0.270/0.065, tarsus 0.250/0.055.


Figures 10–18. *Larca boulderica* sp. nov., holotype male and paratype female (DMNS): 10 carapace, dorsal, male 11 left pair of eyes, dorsal, male 12 right pedipalp, dorsal, male 13 right pedipalp, dorsal, male 14 left chela, retrolateral, male 15 left chela, retrolateral, female 16 left galea, dorsal, male 17 left galea, ventral, female 18 left leg IV, retrolateral, male. Scale bars: 0.5 mm (12, 13); 0.25 mm (10, 14, 15, 18); 0.1 mm (11); 0.05 mm (16, 17).



Figures 19–21. *Larca boulderica* sp. nov., holotype male and paratype female (DMNS): 19 genital sternites, ventral, male 20 genital sternites, ventral, female 21 genitalia, ventral, female. Scale bars: 0.2 mm.

**Etymology.** The species epithet is a noun taken from the type locality of Boulder County, Colorado. Mallory Cave is situated on City of Boulder, Open Space and Mountain Parks property.

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## **Additional information**

## **Conflict of interest**

The authors have declared that no competing interests exist.

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### **Author contributions**

Conceptualization: MSH, DBS. Writing - original draft: MSH. Writing - review and editing: DBS.

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### Data availability

All of the data that support the findings of this study are available in the main text.

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Checklist

# Checklist of land snail species of Gua Rumbang, Sarawak, Malaysian Borneo (Mollusca, Gastropoda), with a description of a new species, *Diplommatina rumbangensis* sp. nov.

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### Abstract

The current study presents an annotated checklist of the land snail species in the vicinity of the limestone hill of Gua (= cave) Rumbang, an outcrop located at the district of Padawan, Sarawak, Malaysian Borneo. The sampling was conducted at the surrounding areas and near the cave's entrance. A total of 62 species, involving 19 families and 38 genera, were recorded. Comparison with previous surveys made in the Bau limestone hills revealed similarities with respect to the species-rich families Diplommatinidae and Cyclophoridae, and the genera *Kaliella* and *Diplommatina*, highlighting the regional consistency of the land snail diversity of the Bau-Padawan-Serian cluster. Possibly because of its smaller size, Gua Rumbang is home to two endemic species, while there are eight endemic species in the Bau limestone karsts. This suggests a potential for a significant species diversity within the areas of the limestone ranges that remain to be explored. Nonetheless, the occurrence of endemic species in Gua Rumbang highlights the need to conserve certain areas within the Padawan limestone range since hitherto no protected areas have been proposed in this region. In this checklist, a new species for science is also described, namely, *Diplommatina rumbangensis* **sp. nov.** 

Key words: Endemism, habitat types, limestone outcrop, species abundance, species diversity

## Introduction

Borneo's karst areas are renowned for their diverse and abundant biodiversity, including species that are endemic to specific sites or regions (Vermeulen and Whitten 1999). The species abundance is mainly caused by the multitude of different ecological niches which typically occur in karst areas, ranging from sundrenched, bare rock faces to damp, and dark caves (Clements et al. 2006). These ecosystems are characterised by high calcium carbonate deposits and serve as habitat for numerous calcium-dependent organisms, including land snails.

Gua (= Cave) Rumbang (1°16.77'N, 110°15.69'E) is located to the north of Gunung Temugan, a limestone outcrop in the Padawan district. Gua Rumbang

is part of a long belt of limestone ranges in the south of Kuching division called the 'Bau-Padawan-Serian' cluster (see Fig. 1) between the town of Bau in the west, and the Serian district in the east (Liew et al. 2021). This cave has been explored and documented for the first time by Spencer St. John in the 1800s (John 1862). Five species of land snails were described from Gua Rumbang in 1894–1895, namely *Georissa everetti* E. A. Smith, 1895, *Kaliella rumbangensis* (E. A. Smith, 1895), *Ditropopsis everetti* (E. A. Smith, 1895), *Plectostoma pumilio* (E. A. Smith, 1894a), and *Plectostoma austeni* (E. A. Smith, 1894a). Since then, this limestone hill was not further inventoried. Therefore, this study presents the first checklist of the malacofauna of Gua Rumbang after almost 130 years.

Recently, Marzuki et al. (2021) documented the land snail fauna in the south of Bau district, in the western part of the Kuching limestone ranges. The study listed 122 land snail species including 46 species that are endemic to these ranges. According to Vermeulen (1993, 1994) limestone ranges are areas of endemism, with species occurring restricted to the ranges or parts of them. Despite collecting efforts have focused on the more accessible hills of the ranges, it is probable that some species are endemic to only limited parts of the ranges (Foon et al. 2017; Phung et al. 2018; Foon and Marzuki 2023; Lee et al. 2024). Hence, land snails are a suitable indicator group for limestone biodiversity studies (Vermeulen 2003; Vermeulen and Junau 2007; Liew et al. 2014; Marzuki et al. 2021; Vermeulen and Liew 2022).



**Figure 1.** Map showing the location of Gua Rumbang (yellow) on top of an overlay of limestone outcrops in the districts of Kuching, Bau, Siburan, Padawan, Serian, and Tebedu extracted from Liew et al. (2021). The green locations are the hills surveyed by Marzuki et al. (2021). The map highlights individual limestone outcrops with red, whereas grey areas around the limestone outcrops are background to emphasise outcrops that are too small to discern on the map.

In this study, we incorporate the endemic species of these limestone ranges based on literature data, information from the collections at the Zoological Museum of Universiti Malaysia Sarawak (UNIMAS), and the combined knowledge of the authors. Next, we present an annotated checklist of land snail species that were found during our survey. Finally, we describe a new species of land snail of the family Diplommatinidae, namely, *Diplommatina rumbangensis* sp. nov.

## Materials and methods

## Land snail sampling and processing

Two separate field surveys were conducted at the surrounding areas near the Gua Rumbang's entrance (1°16.77'N, 110°15.69'E) on 2 September 2022 and 28 June 2023. Two 20 × 20 m plots were established, and the same plots were sampled for both field surveys. Four persons spent an hour for each plot, totalling 16 person-hours. All living snails and empty shells were collected during the search. This includes sifting through leaf litter, scanning the surface of limestone rocks, wood logs, and the surrounding karst vegetation. The microhabitats where the land snails were found were characterized with respect to their leaf litter, limestone, and vegetation (see Table 1). Leaf litter is the surface litter of the outermost layer of the ground. Limestone rocks refers to the vertical and horizontal wall surfaces, pockets, and cervices. Vegetation refers to the leaf surface, tree trunks and vines. Approximately five litres of soil collected from the area were dried before micro snails and shells were extracted by floatation and left to dry. Living specimens were stored in sample vials containing 70% ethanol. Empty shells were cleaned and dried prior to storage in the museum collection. Specimens were identified by their shell morphology using the literature of Bornean land snails (Vermeulen 1991, 1993, 1994, 1996; Khalik et al. 2019; Marzuki et al. 2021; Vermeulen and Liew 2022). The material was deposited at the Zoological Museum UNIMAS (ZMU), with duplicate specimens deposited in the private collection of the third author (ME).

## Imaging and scanning electron microscopy

A representative shell of each species was selected for imaging. A set of stacked images were taken using a Nikon DSLR with CaptureOne 15.0.0 software. Then, the composite images were generated in Helicon 8.2.0 software. The images were edited using Adobe Photoshop 24.1 and GIMP 2.10.34 software. Scanning electron microscopy was used to obtain detailed images of *Diplommatina rumbangensis* sp. nov. To this end shells of the new species were coated with platinum.

## Land snails diversity and endemism

The species diversity observed at Gua Rumbang was compared with land snail diversity data from elsewhere in Sarawak, including Bau (Marzuki et al. 2021), and limestone hills outside of western Sarawak namely Bukit (= Hill) Sarang (Vermeulen and Junau 2007), Niah National Park (NP), and Gunung

			Habitat types		
Family / Species	Number of individuals	Relative abundance (%)	Leaf litter	Vegetation	Limestone
Alycaeidae				_	
Pincerna globosa	59	2	_	59	_
Stomacosmethis hosei	492	16.7	3	_	489
Ariophantidae					
Rahula raricostulata	21	0.7	21	_	_
Macrochlamvs sanctiiohni	1	0.03	1	_	_
Macrochlamvs infans	2	0.07	1	1	_
Vitrinula alutinosa	2	0.07	_	2	_
Camaenidae					
Amphidromus angulatus	1	0.03	_	1	_
Amphidromus epidemiae	2	0.07	_	2	_
Chronidae					
Kaliella busauensis	28	0.95	_	28	-
Kaliella barrakporensis	73	2.5	_	73	_
Kaliella calculosa	4	0.1	_	4	_
Kaliella microconus	67	2.3	_	67	_
Kaliella rumbangensis	585	19.9	_	552	33
Kaliella scandens	3	0.1	_	3	_
Exrhysota brookei	1	0.03	_	_	1
Cyclophoridae					
Cyclophorus perdix borneensis	2	0.07	2	_	_
Craspedotropis borneensis	176	6	173	_	3
Japonia barbata	1	0.03	1	_	_
Japonia borneensis	3	0.1	3	_	_
Japonia mundyana	1	0.03	_	1	_
Opisthoporus biciliatus	2	0.07	1	_	1
Diapheridae					
Platycochlium sarawakense	270	9.2	270	_	_
Diplommatinidae					
Diplommatina baritensis	111	3.8	111	_	_
Diplommatina concinna	2	0.07	2	_	_
Diplommatina maduana maduana	6	0.2	6	_	_
Diplommatina adversa	5	0.2	5	_	_
Plectostoma austeni	34	1.2	_	_	34
Plectostoma anisopterum	120	4.1	_	_	120
Plectostoma pumilio	670	22.6	_	_	670
Opisthostoma brachyacrum lambii	44	1.5	44	_	_
Opisthostoma tridens	6	0.2	-	_	6
Dyakiidae	1	1		I	
Dyakia subdebilis	4	0.1	_	3	1
Rhinocochlis nasuta	2	0.07	-	2	_
Helicarionidae	1	1		1	1
Helicarion dyakanum	2	0.07	_	2	_
Hydrocenidae	1				1
Georissa everetti	17	0.6	_	_	17
Punctidae	<u> </u>	1	1	1	1
Paralaoma sarawakensis	96	3.3	96	_	_
Valloniidae				1	1
Pupisoma dioscoricola	33	1.1	_	33	_
Total	2.948		740	833	1.375
	· · ·				,

### Table 1. List of living snails collected in Gua Rumbang and their habitat types.

(= Mountain) Mulu National Park (NP) (Vermeulen 2003). These localities are isolated and far from the limestone ranges of western Sarawak, since Niah NP and Gunung Mulu NP are in the east, while Bukit Sarang is located in central Sarawak. We evaluated species diversity by considering two factors: (1) species richness, i.e. the total number of species per locality, and (2) the number of unique species, i.e. the number of species that occur only in one of the surveyed limestone hills. These species are for the time being considered unique, even if some of them may turn up in other limestone hills that are yet-to-be surveyed (Foon et al. 2017). Representative land snails sampled during the surveys are shown in Figs 4–24. The following abbreviations are used in the text:

SH	Shell height
SW	Shell width
ME	Marzuki Effendi
NP	National Park
UNIMAS	Universiti Malaysia Sarawak
ZMU	Zoological Museum UNIMAS

## **Results and discussion**

## Land snail diversity and endemism

A total of 5,221 individuals were obtained from surveys done at Gua Rumbang comprising 62 species of land snails belonging to 38 genera and 19 families (see Suppl. material 1). The family of Diplommatinidae was the most species-rich family, with 11 species. This was followed by Cyclophoridae with ten species. The most diverse genera were *Diplommatina* and *Kaliella* with six species each.

Our study targeted the land snails of Gua Rumbang in Padawan, which is a hill in the central part of the Bau-Padawan-Serian limestone range of western Sarawak. The malacofauna of the Padawan limestone ranges remains largely to be explored. When comparing with the malacofauna survey conducted by Marzuki et al. (2021) in Bau, the species compositions are similar in terms of the most diverse families (i.e., Diplommatinidae and Cyclophoridae) and genera (i.e., *Kaliella* and *Diplommatina*). Marzuki et al. (2021) recorded eight endemic land snail species, whereas this study found two endemic species in Gua Rumbang (Table 2). This probably reflects the smaller sampling area at Gua Rumbang compared to the more extensive sampling area covering eight limestone hills in the Bau limestone range. Among these eight limestone hills, Gunung Kapor had the highest number of species (n = 11) that did not overlap with the other limestone hills. Of these 11 species, only two species are endemic to Gunung Kapor.

When compared with other limestone karsts in Sarawak beyond the Bau-Padawan-Serian cluster, Gua Rumbang possesses the lowest species richness and number of endemic species (Table 2). Both Niah NP and Gunung Mulu NP have a higher species richness and more endemic species than Gua Rumbang. Also, this may be explained by the larger areas of both these national parks compared to Gua Rumbang. In contrast, Bukit Sarang is

Limestone hill	Area (km²)	Species richness	Endemic species	Reference
Niah National Park	9	108	38	Vermeulen 2003
Gunung Mulu National Park	80	97	33	Vermeulen 2003
Bukit Sarang	0.3	83	26	Vermeulen and Junau 2007
Bau limestone ranges				
Gunung Kapor	0.08	91	2	Marzuki et al. 2021
Gunung Batu	0.06	83	3	
Gunung Doya	0.09	78	1	
Gunung Lobang Angin	0.07	50	2	
Padang Pan	0.02	25	0	
Bukit Sekunyit	0.07	17	0	
Gunung Sebayat	0.03	14	0	
Gunung Stulang	0.06	12	0	
Gua Rumbang	0.04	62	2	Current study

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<b>Table 2</b> List of limestone hills with the number	of snecies richness and i	endemic snecies in Sarawak
Table 2. List of inflestone fills with the number	or species nonness and	

home to a large number of endemic species despite its relatively small area (0.3 km<sup>2</sup>). The high endemism of land snails in Bukit Sarang may be due to its geographic isolation from nearby limestone ranges, such as Ulu Kakus, which is 60 km away.

Based on these comparisons, two species are endemic to Gua Rumbang, but when considered together with the Bau-Padawan-Serian cluster, the number increases to 50 endemic species. No fewer than 80 species from the Bau-Padawan-Serian cluster can be found beyond the southwestern Sarawak limestone clusters. There are also 37 species from Gua Rumbang that have a wider distribution beyond the borders of Sarawak. However, these comparisons should be interpreted with some reservation since each study used different sampling methods, so that their degrees of coverage and completeness may differ. Consequently, the assessments and explanations regarding species richness and endemism are only preliminary and could change if a standardized sampling regime is applied (sensu Clements et al. 2008; Liew et al. 2008; Foon et al. 2017).

The presence of species that are endemic to only a small part of the range complicates effective biodiversity conservation of the Bau-Padawan-Serian limestone ranges. Based on Marzuki et al. (2021), four out of eight surveyed limestone hills in Bau had endemic species (Table 2). This could indicate a high species diversity for the unexplored parts of the Bau-Padawan-Serian limestone range. Hence, it may be necessary to conserve several parts of the ranges to safeguard a representative selection of the limestone biodiversity. Gua Rumbang is a part of Gunung Temugan, with an approximate size of 6.3656 km<sup>2</sup> (Liew et al. 2021) and no protected areas have been proposed in this vicinity. The selection of the Bau-Padawan-Serian limestone ranges. In this context, land snails are a suitable indicator group for such studies, as their abundance and species composition can reflect the impact of habitat fragmentation and disturbance (Nekola 2012; Douglas et al. 2013; Dhiman et al. 2020; Lee et al. 2024).

## **Systematics**

Class Gastropoda Cuvier, 1795, Subclass Caenogastropoda Cox, 1960 Family Diplommatinidae L. Pfeiffer, 1856 Genus Diplommatina Benson, 1849

Diplommatina rumbangensis sp. nov. https://zoobank.org/C34336B3-6421-49FD-84AC-154E8A1C4691 Figs 2A-F, 8E

**Type material examined.** *Holotype*. MALAYSIA • (SH = 5.25 mm, SW = 2.52 mm); Sarawak, Gua Rumbang, near Kampung Semadang, along Sarawak Kanan River, ~ 11 miles Southwest Padawan, Kuching Division; 1°16.77'N, 110°15.69'E; 2 Sep. 2022; N.S. Nasir and M. E. Marzuki leg.; MZU.MOL.22.132. *Paratypes*. MALAYSIA • 4 ex. (SH = 5.1 mm, SW = 2.7 mm; SH = 5.06 mm, SW = 2.5 mm; SH = 5.37 mm, SW = 2.58 mm; SH = 5.01 mm, SW = 2.65 mm); same data as holotype; MZU.MOL.22.491, ME 14983, ME 15021. Both holotype and paratypes were deposited in Zoological Museum UNIMAS (ZMU) and additional paratypes in the private collection of the third author.

Description. Shell dextral, fusiform to moderately conical, reddish orange, shining and translucent, with the penultimate whorl widest, convex, well rounded. Suture impressed. Protoconch with 11/2 whorls, punctate with small pits, without radial and spiral lines. Constriction nearly level with the edge between the parietal and columellar side of the peristome, with two parietales, two upper longitudinal palatales which are not covered by the peristome on the outer surface of the shell, one transversal palatalis and one columellaris. The columellaris positioned at the start of the constriction together with the longitudinal palatales. Tuba approximately <sup>3</sup>/<sub>4</sub> whorl. Sculpture: Radial ribs on the top whorls only, widely spaced, inconspicuous, but halfway the whorl with an almost tubular projection, in adults sometimes abraded to a semi-circular scar. Spiral striation inconspicuous, on top whorls only. Aperture: Hardly tilted regarding the coiling axis; columellaris distinct, directed downwards. Peristome double, expanding; palatal side hardly sinuous, without edge; basal side with an edge; basal edge hardly sinuous, rounded; inner peristome somewhat expanding beyond the outer, with a palatal lip, free and erect on the columellar side, expanding on the parietal side. Umbilicus: Open, narrow. Dimensions: Height 5.01-5.37 mm; width 2.5-2.7 mm; number of whorls 6<sup>3</sup>/<sub>4</sub>-7; height and width aperture 1.91-2.05 mm; 2.05-2.09 mm.

**Differential diagnosis.** *Diplommatina rumbangensis* sp. nov. has two distinct upper longitudinal palatales at the shell constriction that are not covered by the peristome on the outer surface of the shell (Fig. 3). This differs from *Diplommatina spinosa* Godwin-Austen, 1889 which has one longitudinal palatalis only. Additionally, *D. spinosa* exhibits a tubular projection that extends to the penultimate whorl, whereas in *D. rumbangensis* sp. nov., this projection only reaches halfway through the ultimate whorl. *Diplommatina spinosa* is distributed in the Kuching and Serian divisions. It also differs from *Diplommatina bicoronata bicoronata* von Martens, 1884 which is endemic to Kalimantan, Indonesia by having two or three longitudinal palatales with two of them



**Figure 2.** Scanning Electron Microscope images of *Diplommatina rumbangensis* sp. nov. **A–F** Paratypes (ME 14471). **A** apertural view **B** side view **C** apical view **D** enlargement of apical view showing the apex with radial ribs **E** umbilical view **F** top whorls view showing the tubular projection and semi-circular scars.



**Figure 3.** Sketch of *Diplommatina spinosa* and *Diplommatina bicoronata bicoronata* extracted from Vermeulen (1993), and *Diplommatina rumbangensis* sp. nov. showing the position of the longitudinal palatalis (red), the transversal palatalis (blue), and the constriction area (grey).

covered by the peristome. *Diplommatina bicoronata bicoronata* also has radial ribs near the suture of the whorls which is absent in *D. rumbangensis* sp. nov. This latter species can be distinguished from *Diplommatina aurisdiaboli* Vermeulen, 1993 by the absence of palatal lip expanding up the suture of the previous whorl.

**Etymology.** The epithet *rumbangensis* refers to the type locality Gua Rumbang. **Geographic distribution and habitat.** *Diplommatina rumbangensis* sp. nov. is known from the type locality only. The living animals were not observed.

**Remarks.** The spine or tubular projection of the shells of *Diplommatina rumbangensis* sp. nov. are mostly broken, leaving semi-circular scars.

## Checklist

Class Gastropoda Cuvier, 1795, Subclass Caenogastropoda Cox, 1960 Family Alycaeidae W. T. Blanford, 1864

Chamalycaeus specus (Godwin-Austen, 1889) Fig. 4A

Type locality. "In limestone caves at Jambusan, Borneo".

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Apr. 2016–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14470, ME 14982, ME 15020, MZU.MOL.16.116.

**Distribution.** Widespread in Borneo. Endemic to Borneo (Marzuki et al. 2021; Vermeulen and Liew 2022).

**Remarks.** Among leaf-litter and plant debris at the base of limestone cliffs. Only empty shells were found.

### Pincerna globosa (H. Adams, 1871)

Figs 4B, 19A

Type locality. "Busan, near Sarawak, Borneo".

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Apr. 2016–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14468, ME 15018, MZU.MOL.16.109, MZU.MOL.22.135, MZU.MOL.23.139.

**Distribution.** Scattered localities between Bau and Serian-Padawan limestone hills in western Sarawak to Niah, further to the north. Also found in Sabah and West Kalimantan. Endemic to Borneo (Marzuki et al. 2021; Vermeulen and Liew 2022).

**Remarks.** Living snails were observed foraging on leaf surface of trees at the base of limestone cliffs.



**Figure 4. A** *Chamalycaeus specus* (Godwin-Austen, 1889) ME 14470 **B** *Pincerna globosa* (H. Adams, 1871) ME 14468 **C** *Stomacosmethis hosei* (Godwin-Austen, 1889) ME 14469 **D** *Solenomphala scalaris* (Heude, 1882) ME 14512.

#### Stomacosmethis hosei (Godwin-Austen, 1889)

Figs 4C, 19B

### Type locality. "Busan Hills, Borneo".

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Apr. 2016–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14469, ME 14981, ME 15019, MZU.MOL.16.108, MZU.MOL.22.136

**Distribution.** Scattered localities between Bau and Serian-Padawan limestone hills in western Sarawak. Endemic to western Sarawak (Marzuki et al. 2021).

**Remarks.** Living snails found on wet limestone surfaces covered with mosses. Empty shells were found among leaf litter at the base of limestone hills.

### Family Assimineidae H. Adams & A. Adams, 1856

Solenomphala scalaris (Heude, 1882)

Fig. 4D

**Type locality.** "Ad parietes humidos in civitate Chang-hai sat copiosa" [= Shang-hai, China].

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Sep. 2022; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14512.

**Distribution.** Widely distributed in Borneo. Also found in China and Peninsular Malaysia (Marzuki et al. 2021; Vermeulen and Liew 2022).

**Remarks.** Only empty shells were found. An introduced species. Records show that it occurs in the damp areas around human settlements (Chan 1997).

### Family Cyclophoridae Gray, 1847

Craspedotropis borneensis (Godwin-Austen, 1889) Figs 5A, 19C

Type locality. "Busan Hills, Borneo" [= Jambusan Hills, Sarawak].

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Sep. 2022–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14980, ME 15016. MZU.MOL.22.137, MZU.MOL.23.141.

**Distribution.** Scattered localities between Bau and Serian-Padawan limestone hills in western Sarawak. Endemic to western Sarawak.

**Remarks.** Living snails were found foraging on limestone surfaces and among leaf-litter and topsoil at the base of limestone cliffs. Living individuals of this species are always covered by dirt, which makes it difficult to be spotted.

### Cyclophorus perdix borneensis (Metcalfe, 1852)

Fig. 5B

### Type locality. "Borneo".

Material examined. MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Sep. 2022–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14461, ME 15010, MZU.MOL.22.184.

**Distribution.** Widely distributed in Borneo and Sarawak but rare in Sabah (Marzuki et al. 2021; Vermeulen and Liew 2022). Also found in West Malaysia (Stoliczka 1872; Morgan 1885).

**Remarks.** Among leaf-litter and plant debris at the base of limestone cliffs. Only empty shells were found.

## *Ditropopsis everetti* (E. A. Smith, 1895) Fig. 5C

Type locality. "Rumbang, Sarawak" [= Rumbang Hills, Padawan, Sarawak].

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Sep. 2022–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14467, ME 15017.



Figure 5. A Craspedotropis borneensis (Godwin-Austen, 1889) MZU.MOL.22.137 B Cyclophorus perdix borneensis (Metcalfe, 1852) MZU.MOL.22.184 C Ditropopsis everetti (E. A Smith, 1895) ME 14467.

**Distribution.** Scattered localities between Bau and Serian-Padawan limestone hills in western Sarawak. Endemic to western Sarawak (Marzuki et al. 2021).

**Remarks.** Among leaf-litter and plant debris at the base of limestone cliffs. Only empty shells were found.

Japonia barbata (L. Pfeiffer, 1855) Fig. 6A

Type locality. "Borneo, Sarawak".

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Sep. 2022–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14464, ME 15012, MZU.MOL.22.149.

**Distribution.** Scattered localities between Bau and Serian-Padawan limestone hills in western Sarawak to Mukah, also in central Sarawak. Endemic to Sarawak (Marzuki et al. 2021).

**Remarks.** Among leaf-litter and plant debris at the base of limestone cliffs. Only empty shells were found.

## Japonia bauensis Marzuki, Liew & Mohd-Azlan, 2021

Fig. 6B

Type locality. "Bau and Serian-Padawan limestone hill clusters."

Material examined. MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Sep. 2022–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14465, ME 15013, MZU.MOL.22.156.

**Distribution.** Scattered localities between Bau and Serian-Padawan limestone hills in Sarawak. Endemic to Sarawak (Marzuki et al. 2021).

**Remarks.** Among leaf-litter and plant debris at the base of limestone cliffs. Only empty shells were found.

Japonia borneensis (E. A. Smith, 1893)

Figs 6C, 19D

**Type locality.** "Westliches Borneo bei Bengkajang" [= Western Borneo near Bengkayang].

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Apr. 2016–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; MZU.MOL.23.138, MZU.MOL.22.155, MZU.MOL.16.110.

Distribution. Widely distributed in Borneo (Vermeulen and Liew 2022).

**Remarks.** Living snails were found foraging in leaf-litter and plant debris at the base of limestone cliffs.

### Japonia mundyana (Godwin-Austen, 1889)

Fig. 6D

Type locality. "Busan Hills, Borneo" [= Jambusan Hills, Bau, Sarawak].

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Sep. 2022–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 15014, MZU.MOL.22.133.



Figure 6. A Japonia barbata (L. Pfeiffer, 1855) MZU.MOL.22.149 B Japonia bauensis Marzuki, Liew & Mohd-Azlan, 2021 ME 0014465 C Japonia borneensis (E. A. Smith, 1893) MZU.MOL.22.155 D Japonia mundyana (Godwin-Austen, 1889) MZU.MOL.22.133.

**Distribution.** Scattered localities between Bau and Serian-Padawan limestone hills in western Sarawak. Endemic to western Sarawak (Marzuki et al. 2021). **Remarks.** Living snail was observed foraging on leaf surface of plants at the base of limestone cliffs.

*Leptopoma sericatum* (L. Pfeiffer, 1851) Fig. 7A

Type locality. "Borneo".

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 15015, MZU.MOL.23.135.

**Distribution.** Widely distributed in Borneo (Marzuki et al. 2021; Vermeulen and Liew 2022).

**Remarks.** Among leaf-litter and plant debris at the base of limestone cliffs. Only empty shells were found.

**Opisthoporus biciliatus (Mousson, 1849)** Figs 7B, 20A

Type locality. "Java" [= Borneo (Metcalfe 1852].

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Sep. 2022–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14463, ME 14979, ME 15011, MZU.MOL.22.152.

**Distribution.** Scattered localities between Bau and Serian-Padawan limestone hills in western Sarawak to Mukah, also in central Sarawak. Endemic to Sarawak (Marzuki et al. 2021).

**Remarks.** Among leaf-litter and plant debris at the base of limestone cliffs. Only empty shells were found.



Figure 7. A Leptopoma sericatum (L. Pfeiffer, 1851) MZU. MOL.23.135 B Opisthoporus biciliatus (Mousson, 1849) ME 14463 C Pterocyclos tenuilabiatus (Metcalfe, 1852) MZU.MOL.22.129.

### Pterocyclos tenuilabiatus (Metcalfe, 1852)

Fig. 7C

### Type locality. "Borneo".

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Sep. 2022; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14462, ME 14978, MZU.MOL.22.129.

**Distribution.** Widely distributed in Borneo. Endemic to Borneo (Marzuki et al. 2021; Vermeulen and Liew 2022).

**Remarks.** Among leaf-litter and plant debris at the base of limestone cliffs. Only empty shells were found.

### Family Diplommatinidae L. Pfeiffer, 1856

*Diplommatina adversa* (H. Adams & A. Adams, 1851) Figs 8A, 20B

### Type locality. "Singapore".

Material examined. MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Sep. 2022–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14476, MZU.MOL.22.140, MZU.MOL.23.140.

**Distribution.** Scattered localities between Bau and Serian-Padawan limestone hills in western Sarawak. In Sabah found in Ulu Segama only (Marzuki et al. 2021; Vermeulen and Liew 2022). Also found in West Malaysia and Singapore (Laidlaw 1949).

**Remarks.** Living snails were found foraging in leaf-litter and plant debris at the base of limestone cliffs.

### Diplommatina baritensis E. A Smith, 1893

Figs 8B, 20C

### Type locality. "Barit Mountain, N.W. Borneo".

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Sep. 2022–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14472, ME 14984, ME 15022, MZU.MOL.22.169, MZU. MOL.23.137.

**Distribution.** Scattered localities between Padawan limestone hills at western Sarawak and Mulu limestone hills in northern Sarawak (Smith 1895; Vermeulen 1993).

**Remarks.** Living snails were found foraging in leaf-litter and plant debris at the base of limestone cliffs.

### Diplommatina concinna H. Adams, 1872

Fig. 8C

### Type locality. "Borneo".

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Sep. 2022; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14473, MZU.MOL.22.83.

**Distribution.** Scattered localities between Bau and Serian-Padawan limestone hills in western Sarawak to Niah, in northern Sarawak. Also found in Bunguran, Indonesia (Marzuki et al. 2021) and Singapore (Chan 2020).

**Remarks.** Living snails were found foraging in leaf-litter and plant debris at the base of limestone cliffs.

### Diplommatina maduana maduana Laidlaw, 1949 Fig. 8D

### Type locality. "Gua Madu, Kelantan".

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Sep. 2022–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14474, ME 15023, MZU.MOL.22.190.

**Distribution.** Scattered localities between Bau and Serian-Padawan limestone hills in western Sarawak to Mulu hills in northern Sarawak (Marzuki et al. 2021). Also found in West Malaysia (Laidlaw 1949).

**Remarks.** Living snails were found foraging in leaf-litter and plant debris at the base of limestone cliffs.

## Diplommatina subglaber subisensis (Vermeulen, 1993)

Fig. 8F

Type locality. "Sarawak 4th Div.: G. Subis (Batu Niah)".

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Sep. 2022; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14475.

**Distribution.** Scattered localities between Padawan limestone hills in western Sarawak and Niah limestone hills in northern Sarawak (Vermeulen 1993, 1996).

**Remarks.** Among leaf-litter and plant debris at the base of limestone cliffs. Only empty shells were found.

### Opisthostoma brachyacrum lambii (Vermeulen, 1991)

Fig. 9A

**Type locality.** "Sarawak 1<sup>st</sup> Div.: W of Kpg. Lobang Batu 12.5 km S of Tebakang". **Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N,

110°15.69'E; 2 Sep. 2022–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14480, ME 15027, MZU.MOL.22.211.

**Distribution.** Scattered localities between Bau and Serian-Padawan limestone hills in western Sarawak. Also found in Sabah. Endemic to Borneo (Marzuki et al. 2021).

**Remarks.** Living snails were found foraging in leaf-litter and plant debris at the base of limestone cliffs.

## Opisthostoma tridens Vermeulen, 1991

Fig. 9B

Type locality. "Sarawak 1st Div.: Kpg. Beratok along road Kuching-Serian".



**Figure 8.** A Diplommatina adversa (H. Adams & A. Adams, 1851) ME 14476 **B** Diplommatina baritensis E. A. Smith, 1893 ME 14472 **C** Diplommatina concinna H. Adams, 1872 ME 14473 **D** Diplommatina maduana maduana Laidlaw, 1949 ME 14474 **E** Diplommatina rumbangensis sp. nov. holotype MZU.MOL.22.132 **F** Diplommatina subglaber subisensis (Vermeulen, 1993) ME 14475.

Material examined. MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Sep. 2022–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14481, ME 15028, MZU.MOL.22.443.

**Distribution.** Scattered localities between Bau and Serian-Padawan limestone hills in western Sarawak. Endemic to western Sarawak region (Marzuki et al. 2021).

**Remarks.** Living snails found on wet vertical limestone surfaces covered with mosses.

## Plectostoma anisopterum (Vermeulen, 1994)

Figs 9C, 20D

Type locality. "G. Saak 1 mile W. of Begu, 24 miles S. of Kuching".

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Apr. 2016–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14479, ME 14987, ME 15026, MZU.MOL.16.112, MZU. MOL.22.134, MZU.MOL.23.142.

**Distribution.** Scattered localities in Serian-Padawan limestone hills in western Sarawak. Endemic to western Sarawak (Vermeulen 1994).

**Remarks.** Living snails found on wet vertical limestone surfaces covered with mosses. It can also be found among boulders.

### Plectostoma austeni (E. A. Smith, 1894a)

Figs 9D, 21B

### Type locality. "Rumbang, Sarawak".

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Apr. 2016–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14478, ME 14986, ME 15025, MZU.MOL.22.144, MZU. MOL.16.113.

**Distribution.** Scattered localities between Bau and Serian-Padawan limestone hills in western Sarawak. Endemic to western Sarawak region (Marzuki et al. 2021).

**Remarks.** Living snails found on wet vertical limestone surfaces and was observed foraging inside the rock crevices and cave walls, avoiding direct exposure to light.

### Plectostoma pumilio (E. A Smith, 1894a)

Figs 9E, 21A

### Type locality. "Rumbang, Sarawak".

Material examined. MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Apr. 2016–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14477, ME 14985, ME 15024, MZU. MOL.16.114.

**Distribution.** Scattered localities in Serian-Padawan limestone hills in western Sarawak. Endemic to western Sarawak region (Vermeulen 1994).

**Remarks.** Living snails found on wet vertical limestone surfaces covered with mosses.



**Figure 9. A** *Opisthostoma brachyacrum lambii* Vermeulen, 1991 ME 14480 **B** *Opisthostoma tridens* Vermeulen, 1991 ME 14481 **C** *Plectostoma anisopterum* (Vermeulen, 1994) ME 14479 **D** *Plectostoma austeni* (E. A. Smith, 1894a) ME 14478 Gua Rumbang **E** *Plectostoma pumilio* (E. A. Smith, 1894a) ME 14477.

### Subclass Heterobranchia Burmeister, 1837 Family Achatinidae Swainson, 1840

## Allopeas clavulinum (Potiez & Michaud, 1838) Fig. 10A

Type locality. "L'ile Bourbon" [= La Réunion].

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Sep. 2022–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14485, ME 14990, ME 15035, MZU.MOL.22.159.

**Distribution.** Widely distributed in Borneo. Circumtropical (Marzuki et al. 2021; Vermeulen and Liew 2022).

**Remarks.** Among leaf-litter and plant debris at the base of limestone cliffs. Only empty shells were found.

## Allopeas gracile (T. Hutton, 1834)

Fig. 10B

### Type locality. "Mirzapoor, India".

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Sep. 2022–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14486, ME 14991, ME 15036, MZU.MOL.22.161.

**Distribution.** Widely distributed in Borneo. Circumtropical (Marzuki et al. 2021; Vermeulen and Liew 2022).

**Remarks.** Among leaf-litter and plant debris at the base of limestone cliffs. Only empty shells were found.

### Opeas hannense (Rang, 1831)

Fig. 10C

Type locality. "Village of Hann, Cap Vert peninsula, Dakar, Senegal".

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Sep. 2022–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14484, ME 14989, ME 15034, MZU.MOL.22.158.

**Distribution.** Scattered localities between Bau and Serian-Padawan limestone hills in western Sarawak. Also found in Sabah. Distributed from Central America to Africa and Pacific (Marzuki et al. 2021; Vermeulen and Liew 2022).

**Remarks.** Among leaf-litter and plant debris at the base of limestone cliffs. Only empty shells were found.

## Paropeas achatinaceum (L. Pfeiffer, 1846)

Fig. 10D

### Type locality. "Java".

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Apr. 2016–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14487, ME 14992, ME 15037, MZU.MOL.16.147, MZU. MOL.22.160.



**Figure 10. A** *Allopeas clavulinum* (Potiez & Michaud, 1838) ME 14485 **B** *Allopeas gracile* (T. Hutton, 1834) ME 14486 **C** *Opeas hannense* (Rang, 1831) ME 14484 **D** *Paropeas achatinaceum* (L. Pfeiffer, 1846) ME 14487.

**Distribution.** Widely distributed in Borneo. Distributed from South to East Asia, South-east Asia, and Pacific Islands (Marzuki et al. 2021; Vermeulen and Liew 2022).

**Remarks.** Among leaf-litter and plant debris at the base of limestone cliffs. Only empty shells were found.

### Family Achatinellidae Gulick, 1873

### Elasmias sundanum (Möllendorff, 1897)

Fig. 11A

## Type locality. "Java".

**Material examined**. MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Sep. 2022–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14514, ME 15058, MZU.MOL.23.149.

**Distribution.** Scattered localities between Bau and Serian-Padawan limestone hills in western Sarawak to Niah at further northern Sarawak (Marzuki et al. 2021). Also found in Sumatra and Java (van Benthem-Jutting 1952).

**Remarks.** Among leaf-litter and plant debris at the base of limestone cliffs. Only empty shells were found.

### Family Ariophantidae Godwin-Austen, 1883

*Rahula raricostulata* (E. A. Smith, 1893) Figs 11B, 21C

### Type locality. "Busau or Busan, Sarawak".

Material examined. MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Sep. 2022–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14495, ME 15043, MZU.MOL.22.139.

**Distribution.** Scattered localities between Bau and Serian-Padawan limestone hills in western Sarawak. Endemic to western Sarawak (Marzuki et al. 2021).

**Remarks.** Living snails were observed foraging on leaf surface of trees at the base of limestone cliffs.

## Macrochlamys sanctijohni (Godwin-Austen, 1891)

Fig. 11C

Type locality. "Busan Hills".

Material examined. MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Sep. 2022–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14500, ME 14998, ME 15048, MZU. MOL.22.451.

**Distribution.** Scattered localities between Bau and Serian-Padawan limestone hills in western Sarawak to Niah in northern Sarawak (Marzuki et al. 2021). Also found in Palawan, Philippines (Smith 1895).

**Remarks.** Among leaf-litter and plant debris at the base of limestone cliffs. Only empty shells were found.

### Macrochlamys infans (Reeve, 1854)

Figs 11D, 21D

### Type locality. "Borneo".

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Apr. 2016–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14501, ME 15061, MZU.MOL.16.118, MZU.MOL.22.449, MZU.MOL.23.144.

**Distribution.** Widely distributed in Borneo. Distributed from Sumatra to Philippines (Vermeulen and Liew 2022).

**Remarks.** Empty shells were found among leaf-litter and plant debris at the base of limestone cliffs while living snails were found foraging on leaf surfaces.

#### Vitrinula glutinosa (Metcalfe, 1852)

Figs 11E, 22A

### Type locality. "Borneo".

Material examined. MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Sep. 2022–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14502, ME 15049, MZU.MOL.22.130, MZU. MOL.23.146.

**Distribution.** Scattered localities between Bau and Serian-Padawan limestone hills in western Sarawak to Mulu at northern Sarawak. Endemic to Borneo (Marzuki et al. 2021).

**Remarks.** Empty shells were found among leaf-litter and plant debris at the base of limestone cliffs while living snails were found foraging on leaf surfaces. Individuals of this species show variability in the height of the spire and in the colour (pale to dark brown) (Marzuki et al. 2021).

## Microcystina arabii Marzuki, Liew & Mohd-Azlan, 2021

Fig. 12A

**Type locality.** "Malaysia, Sarawak, Kuching, Division, Bukit Sokwang (Site 2), northern site of Gunung Doya, limestone hill along Skio road, 2.05 miles E Bau".

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Sep. 2022–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14505, MZU.MOL.23.152.

**Distribution.** Scattered localities between Bau and Serian-Padawan limestone hills in western Sarawak. Endemic to western Sarawak (Marzuki et al. 2021).

**Remarks.** Among leaf-litter and plant debris at the base of limestone cliffs. Only empty shells were found.

### *Microcystina kilat* Marzuki, Liew & Mohd-Azlan, 2021 Fig. 12B

**Type locality.** "Malaysia, Sarawak, Kuching Division, Lobang Angin (Site 2), limestone outcrop near Sungai Sarawak Kanan, 1.75 miles W Bau".



Figure 11. A Elasmias sundanum (Möllendorff, 1897) ME 15058 B Rahula raricostulata (E. A. Smith, 1893) MZU. MOL.22.139 C Macrochlamys sanctijohni (Godwin-Austen, 1891) ME 14500 D Semi adult Macrochlamys infans (Reeve, 1854) ME 14501 E Vitrinula glutinosa (Metcalfe, 1852) ME 14502.

Material examined. MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 15050, MZU.MOL.23.151.

**Distribution.** Scattered localities between Bau and Serian-Padawan limestone hills in western Sarawak. Endemic to western Sarawak (Marzuki et al. 2021).

**Remarks.** Among leaf-litter and plant debris at the base of limestone cliffs. Only empty shells were found.

## Microcystina paripari Marzuki, Liew & Mohd-Azlan, 2021

Fig. 12C

**Type locality.** "Malaysia, Sarawak, Kuching Division, Fairy Cave (Site 2), south part of Gunung Kapor, 4 miles SW Bau".

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Sep. 2022–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14503, ME 15000, ME 15052, MZU.MOL.22.132.

**Distribution.** Scattered localities between Bau and Serian-Padawan limestone hills in western Sarawak. Endemic to western Sarawak (Marzuki et al. 2021).

**Remarks.** Among leaf-litter and plant debris at the base of limestone cliffs. Only empty shells were found.

## *Microcystina physotrochus* Vermeulen, Liew & Schilthuizen, 2015 Fig. 12D

**Type locality.** "Malaysia, Sabah, Sandakan Province, Kinabatangan Valley, Batu Keruak 2, near Sukau".

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 15060.

**Distribution.** Scattered localities between Bau and Serian-Padawan limestone hills in western Sarawak to Niah in northern Sarawak. Also found in Sabah. Endemic to Borneo (Marzuki et al. 2021; Vermeulen and Liew 2022).

**Remarks.** Among leaf-litter and plant debris at the base of limestone cliffs. Only empty shells were found.

### Microcystina vitreiformis (Möllendorff, 1897)

Fig. 12E

Type locality. "Java".

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Apr. 2016–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 15051, MZU.MOL.16.117.

**Distribution.** Scattered localities between Bau and Serian-Padawan limestone hills in western Sarawak to Niah in northern Sarawak. Also found in Java and its adjacent islands, Indonesia (Nurinsiyah, 2021).

Remarks. Only empty shells were found.



Figure 12. A Microcystina arabii Marzuki, Liew & Mohd-Azlan, 2021 ME 14505 B Microcystina kilat Marzuki, Liew & Mohd-Azlan, 2021 ME 15050 C Microcystina paripari Marzuki, Liew & Mohd-Azlan, 2021 ME 15052 D Microcystina physotrochus Vermeulen, Liew & Schilthuizen, 2015 ME 15060 E Microcystina vitreiformis (Möllendorff, 1897) MZU.MOL.16.117.

### Family Camaenidae Pilsbry, 1895

### Amphidromus angulatus Fulton, 1896

Fig. 13A

Type locality. "Sarawak".

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Sep. 2022; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; MZU.MOL.22.147.

**Distribution.** Scattered localities between Bau and Serian-Padawan limestone hills in western Sarawak, to Niah, further northern Sarawak. Also found in West Kalimantan (Marzuki et al. 2021).

**Remarks.** Living snails were observed foraging on leaf surface of trees at the base of limestone cliffs.

### Amphidromus epidemiae Wang, 2021

Fig. 13B

Type locality. "Sarawak, Kuching Division, Bau".

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Sep. 2022–28 Jun. 2023; ME 14507, ME 15004, ME 15054, MZU. MOL.22.183.

**Distribution.** Scattered localities between Bau and Serian-Padawan limestone hills in western Sarawak. Endemic to western Sarawak.

**Remarks.** Among leaf-litter and plant debris at the base of limestone cliffs. Only empty shells were found.

### Ganesella acris (Benson, 1859)

Fig. 13C

Type locality. "Teria Ghát montium Khasiæ" [= Khasi Hills, Teria Ghat, India].

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Apr. 2016–2 Sep. 2022; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14508, MZU.MOL.22.150, MZU.MOL.16.146.

**Distribution.** Widely distributed with scattered localities in Borneo. Distributed from Sumatra to Java Indonesia, and South to Southeast Asian mainland (Marzuki et al. 2021; Vermeulen and Liew 2022).

**Remarks.** Among leaf-litter and plant debris at the base of limestone cliffs. Only empty shells were found.

### Family Charopidae Hutton, 1884

Philalanka kusana (Aldrich, 1889)

Fig. 13D

Type locality. "Kusan and Penggiron districts in South-eastern Borneo".

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Apr. 2016–2 Sep. 2022; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14509, MZU.MOL.16.111.



**Figure 13. A** *Amphidromus angulatus* Fulton, 1896 MZU.MOL.22.147 **B** *Amphidromus epidemiae* Wang, 2021 ME 14507 **C** *Ganesella acris* (Benson, 1859) MZU.MOL.22.150 **D** *Philalanka kusana* (Aldrich, 1889) MZU.MOL.16.111 **E** *Sundacharopa argos* Vermeulen & Liew, 2022 ME 14511.

**Distribution.** Widely distributed in Borneo. Distributed from West Malaysia to Papua (Marzuki et al. 2021; Vermeulen and Liew 2022).

**Remarks.** Among leaf-litter and plant debris at the base of limestone cliffs. Only empty shells were found.

Sundacharopa argos Vermeulen & Liew, 2022 Fig. 13E

Type locality. "Malaysia, Sabah, upper Padas River valley, Long Pa Sia".

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Sep. 2022; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14511.

**Distribution.** Widely distributed in Borneo. Endemic to Borneo (Vermeulen and Liew 2022).

**Remarks.** Among leaf-litter and plant debris at the base of limestone cliffs. Only empty shells were found.

### Family Chronidae Thiele, 1931

### Kaliella barrakporensis (Reeve, 1852)

Figs 14A, 22B

Type locality. "Barrakpore Indiae (Bacon)" [= Barrackpore, West Bengal, India].

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Sep. 2022–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14489, ME 14994, ME 15039, MZU.MOL.22.148, MZU. MOL.23.143.

**Distribution.** Widely distributed in Borneo. Distributed from Africa and South Asia mainland to Indo-Australian archipelago and Europe (Marzuki et al. 2021; Vermeulen and Liew 2022).

**Remarks.** Living snails were observed foraging on leaf surface of trees at the base of limestone cliffs.

*Kaliella busauensis* (E. A. Smith, 1895) Figs 14B, 22C

Type locality. "Busau, Sarawak".

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Apr. 2016–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14488, ME 14993, ME 15038, MZU.MOL.16.115, MZU. MOL.22.144.

**Distribution.** Scattered localities between Bau and Serian-Padawan limestone hills in western Sarawak. Endemic to western Sarawak.

**Remarks.** Living snails were observed foraging on leaf surface of trees at the base of limestone cliffs. Vermeulen and Liew (2022) mentioned that this species is synonymous with *K. barrakporensis*. In contrast, Marzuki et al. (2021) listed it as separate species. *Kaliella busauensis* has a higher, dark brown shell with a cancellated shell surface caused by prominent spiral grooves and oblique radial riblets.
## Kaliella calculosa (Gould, 1852)

Fig. 14C

Type locality. "Tahiti" [= Tahiti Island, French Polynesia].

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Sep. 2022; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14493, ME 14506, MZU.MOL.22.450.

**Distribution.** Widely distributed in Borneo. Distributed from India to Australia and Pacific (Marzuki et al. 2021; Vermeulen and Liew 2022).

**Remarks.** Living snails were observed foraging on leaf surface of trees at the base of limestone cliffs.



Figure 14. A Kaliella barrakporensis (Reeve, 1852) ME 14489 B Kaliella busauensis (E. A. Smith, 1895) ME 14488 C Kaliella calculosa (Gould, 1852) ME 14493 D Kaliella microconus (Mousson, 1865) ME 14490.

#### Kaliella microconus (Mousson, 1865)

Fig. 14D

Type locality. "Lomma-Lomma (Viti)" [= Loma Loma, Fiji].

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Sep. 2022–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14490, ME 14995, ME 15040, MZU.MOL.22.168.

**Distribution.** Widely distributed in Borneo. Distributed from South-east Asia to Australia and the Pacific Islands (Marzuki et al. 2021; Vermeulen and Whitten 1998).

**Remarks.** Living snails were observed foraging on leaf surface of trees at the base of limestone cliffs.

Kaliella rumbangensis (E. A. Smith, 1895)

Figs 15A, 22D

Type locality. "Rumbang, Sarawak and Mount Rabong".

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Sep. 2022–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14491, ME 14504, ME 14996, ME 15041, MZU.MOL.22.163, MZU.MOL.22.145.

**Distribution.** Padawan limestone hills in western Sarawak only. Endemic to western Sarawak (Smith, 1895).

**Remarks.** Living snails were observed foraging on leaf surface of trees at the base of limestone cliffs. Vermeulen and Liew (2022) listed this as synonymous with *K. barrakporensis. Kaliella rumbangensis* differs from *K. barrakporensis* by its smaller size and by the inconspicuous (or even absent) peripheral keel on the last whorl.

#### Kaliella scandens (Cox, 1872)

Fig. 15B

Type locality. "Port Macquarie, east coast of Australia".

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Sep. 2022–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14492, ME 14997, ME 15042, MZU.MOL.22.444.

**Distribution.** Widely distributed in Borneo. Distributed from South-east Asia to Australia and the Pacific Islands (Marzuki et al. 2021; Vermeulen et al. 2015).

**Remarks.** Living snails were observed foraging on leaf surface of trees at the base of limestone cliffs.

Exrhysota brookei (A. Adams & Reeve, 1850)

Figs 15C, 23

Type locality. "Mountains of Borneo".

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Sep. 2022; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; MZU.MOL.22.151.

**Distribution.** Widespread in Borneo. Endemic to Borneo (Marzuki et al. 2021). **Remarks.** Living snails were found foraging in limestone crevices and in leaf litter. This is the largest native land snail species in Borneo.



Figure 15. A Kaliella rumbangensis (E. A. Smith, 1895) ME 14491 B Kaliella scandens (Cox, 1872) ME 14492 C Exrhysota brookei (A. Adams & Reeve, 1850) MZU.MOL.22.151.

## Family Diapheridae Panha & Naggs, 2010

*Platycochlium sarawakense* Laidlaw, 1950 Figs 16A, 24A

Type locality. "Gunong Kapor, Bau District, Sarawak".

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Sep. 2022; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14483, ME 14988, ME 15033, MZU.MOL.22.153.

**Distribution.** Scattered localities between Bau and Serian-Padawan limestone hills in western Sarawak. Endemic to western Sarawak (Marzuki et al. 2021).

**Remarks.** Living snails found foraging among leaf-litter and plant debris at the base of limestone cliffs.

#### Family Dyakiidae Gude & B. B. Woodward, 1921

# Dyakia subdebilis E. A. Smith, 1895

Figs 16B, 24B

## Type locality. "Sarawak".

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Sep. 2022–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14496, ME 15044, MZU.MOL.22.141, MZU.MOL.23.136.

**Distribution.** Scattered localities between Bau and Serian-Padawan limestone hills in western Sarawak. Endemic to western Sarawak (Marzuki et al. 2021).

**Remarks.** Living snails were found foraging on leaf surface of trees at the base of limestone cliffs and on limestone surfaces covered with mosses and lichens.

#### Rhinocochlis nasuta (Metcalfe, 1852)

Fig. 16C

### Type locality. "Borneo".

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Sep. 2022–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14497, ME 15002, ME 15045, MZU.MOL.22.146.

**Distribution.** Widely distributed in Borneo. Endemic to Borneo (Marzuki et al. 2021).

**Remarks.** Living snails were observed foraging on leaf surface of trees at the base of limestone cliffs.

#### Family Geotrochidae Schileyko, 2002

# Geotrochus conicoides (Metcalfe, 1852)

Fig. 16D

### Type locality. "Borneo".

Material examined. MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 15057, MZU.MOL.23.150

**Distribution.** Widely distributed in Borneo. Widespread. Also found in Sumatra, Indonesia and Palawan, Philippines (Marzuki et al. 2021; Vermeulen and Liew 2022).

**Remarks.** Among leaf-litter and plant debris at the base of limestone cliffs. Only empty shells were found.

### Family Helicarionidae Bourguignat, 1877

Helicarion dyakanum (Godwin-Austen, 1891) Figs 17A, 24C

Type locality. "Busan Hills, Borneo" [= Jambusan Hills, Bau, Sarawak].



Figure 16. A Platycochlium sarawakense Laidlaw, 1950 ME 14483 B Dyakia subdebilis E. A. Smith, 1895 ME 14496 C Rhinocochlis nasuta (Metcalfe, 1852) ME 14493 D Juvenile Geotrochus conicoides (Metcalfe, 1852) ME 15057.

**Material examined**. MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Sep. 2022–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14499, ME 15001.

**Distribution.** Widely distributed in Sarawak. In Sabah on Mount Trusmadi only. Endemic to Borneo (Marzuki et al. 2021; Vermeulen and Liew 2022).

**Remarks.** Living snails were observed foraging on leaf surface of trees at the base of limestone cliffs.

## Family Punctidae Morse, 1864

Paralaoma sarawakensis Marzuki, Liew & Mohd-Azlan, 2021 Figs 17B, 24D

**Type locality.** "Limestone hill along Skio road, 2.05 miles E Bau, Northern site of Gua Doya, Bukit Sokwang (Site 3), Kuching Division, Sarawak, Malaysia".

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Sep. 2022–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14510, ME 15055, MZU.MOL.22.448.

**Distribution.** Scattered localities between Bau and Serian-Padawan limestone hills in western Sarawak. Also found in Baram, in northern Sarawak. Endemic to Sarawak (Marzuki et al. 2021).

**Remarks.** Living snails were found foraging among leaf-litter and plant debris at the base of limestone cliffs.

### Family Pupinidae L. Pfeiffer, 1853

## Pupina evansi Godwin-Austen, 1889

Fig. 17C

**Type locality.** "From deposit in Cave A, Borneo" [= Tupak Cave, Jambusan Hills, see Cranbrook 2013)].

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Sep. 2022–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 15029.

**Distribution.** Scattered localities in Serian-Padawan limestone hills in western Sarawak (Marzuki et al. 2021). Also found in Sirhassen, Natuna Island (Smith 1894b).

**Remarks.** Among leaf-litter and plant debris at the base of limestone cliffs. Only empty shells were found.

#### Family Trochomorphidae Möllendorff, 1890

Videna nepiadelphos Vermeulen & Liew, 2022 Fig. 17D

Type locality. "Danum valley Conservation Area, Tawau Prov., Sabah".

Material examined. MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Sep. 2022–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14513, ME 15056, MZU.MOL.22.447.

**Distribution.** Widely distributed in Borneo. Widespread. Also found in Panaitan island, Indonesia (Vermeulen and Liew 2022)

**Remarks.** Only empty shells were found among leaf-litter and plant debris at the base of limestone cliffs.

# Family Valloniidae Morse, 1864

Pupisoma dioscoricola (C. B. Adams, 1845)

Fig. 17E

Type locality. "Jamaica".

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Sep. 2022–28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14498, ME 15003, ME 15046, MZU.MOL.22.445.

**Distribution.** Widely distributed in Borneo. Widespread. Distributed in Africa, Asia, Australia, and America (Marzuki et al. 2021).

**Remarks.** Living snails were observed foraging on leaf surface of trees at the base of limestone cliffs.



**Figure 17. A** *Helicarion dyakanum* (Godwin-Austen, 1891) ME 14499 **B** *Paralaoma sarawakensis* Marzuki, Liew & Mohd-Azlan, 2021 ME 14510 **C** *Pupina evansi* Godwin-Austen, 1889 ME 15029 **D** *Videna nepiadelphos* Vermeulen & Liew, 2022 ME 14513 **E** *Pupisoma dioscoricola* (C. B. Adams, 1845) ME 14498.

# Subclass Neritimorpha Golikov & Starobogatov, 1975 Family Hydrocenidae Troschel, 1857

*Georissa everetti* E. A. Smith, 1895 Fig. 18A

Type locality. "Rumbang, W. Sarawak".

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 2 Sep. 2022; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 14482, MZU.MOL.22.157.

**Distribution.** Scattered localities between Bau and Serian-Padawan limestone hills in western Sarawak to Niah in northern Sarawak. Also found in Sabah, Sepulut valley. Widespread. Endemic to Borneo (Khalik et al. 2019; Marzuki et al. 2021).

**Remarks.** Living snails were observed foraging on wet limestone wall surfaces covered with mosses.

# Georissa hungerfordi Godwin-Austen, 1889

Fig. 18B

# Type locality. "Borneo".

**Material examined.** MALAYSIA • Sarawak, Padawan, Gua Rumbang; 1°16.77'N, 110°15.69'E; 28 Jun. 2023; N.S. Nasir, M.E Marzuki, J.Y. Lee, and M.Z Khalik leg.; ME 15032.

**Distribution.** Scattered localities between Bau and Serian-Padawan limestone hills in western Sarawak. Endemic to western Sarawak (Khalik et al. 2019; Marzuki et al. 2021).

**Remarks.** Living snails were observed foraging on wet limestone wall surfaces covered with mosses.



Figure 18. A Georissa everetti E. A. Smith, 1895 ME 14482 B Georissa hungerfordi Godwin-Austen, 1889 ME 15032.



**Figure 19.** Living snails from Gua Rumbang. **A** *Pincerna globosa* (H. Adams, 1871) MZU.MOL.22.135 **B** *Stomacosmethis hosei* (Godwin-Austen, 1889) MZU.MOL.22.136 **C** *Craspedotropis borneensis* (Godwin-Austen, 1889) MZU.MOL.23.141 **D** *Japonia borneensis* (E. A. Smith, 1893) MZU. MOL.23.138. Images not to scale.



**Figure 20**. Living snails from Gua Rumbang. **A** *Opisthoporus biciliatus* (Mousson, 1849) ME 14979 **B** *Diplommatina adversa* (H. Adams & A. Adams, 1851) MZU. MOL.23.140 **C** *Diplommatina baritensis* E. A. Smith, 1893 MZU. MOL.23.137 **D** *Plectostoma anisopterum* ME 14479 (Vermeulen, 1994). All images not to scale.



**Figure 21**. Living snails from Gua Rumbang. **A** *Plectostoma pumilio* (E. A. Smith, 1894a) ME 14477 **B** *Plectostoma austeni* (E. A. Smith, 1894a) ME 14477 **C** *Rahula raricostulata* (E. A. Smith, 1893) MZU.MOL.22.139 **D** Semi adult *Macrochlamys infans* (Reeve, 1854) MZU.MOL.23.144. Images not to scale.



**Figure 22**. Living snails from Gua Rumbang. **A** Juvenile *Vitrinula glutinosa* (Metcalfe, 1852) MZU.MOL.23.146 **B** *Kaliella barrakporensis* (Reeve, 1852) MZU.MOL.23.143 **C** *Kaliella busauensis* (E. A. Smith, 1895) MZU.MOL.22.144 **D** *Kaliella rumbangensis* (E. A. Smith, 1895) MZU.MOL.22.163. Images not to scale.



Figure 23. Living snail from Gua Rumbang. Exrhysota brookei (A. Adams & Reeve, 1850) MZU.MOL.22.151.



**Figure 24.** Living snails from Gua Rumbang. **A** *Platycochlium sarawakense* Laidlaw, 1950 MZU.MOL.22.153 **B** *Dyakia subdebilis* E. A. Smith, 1895 MZU.MOL.23.136 **C** *Helicarion dyakanum* (Godwin-Austen, 1891) ME 14499 **D** *Paralaoma sarawakensis* Marzuki, Liew & Mohd-Azlan, 2021 ME 14510. All imaged not to scale.

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# **Additional information**

# **Conflict of interest**

The authors have declared that no competing interests exist.

# **Ethical statement**

No ethical statement was reported.

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## **Author contributions**

Conceptualization, M.Z.K., J.J.V., N.S.N., L.J.Y., and J.M.A; Fieldwork, N.S.N., L.J.Y., M.E.M., and M.Z.K.; Laboratory work, N.S.N., L.J.Y., M.E.M., and M.Z.K.; Analysis, N.S.N.; Data curation, all authors.; Writing the manuscript N.S.N., L.J.Y., M.E.M., J.J.V., J.M.A, and M.Z.K.; Supervision, M.Z.K.; Funding acquisition, M.Z.K.

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## Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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# **Supplementary material 1**

## List of land snails and their microhabitat preferences of Gua Rumbang

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Data type: xlsx

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