# Description of immature stages of Rhinusa species (Coleoptera, Curculionidae, Mecinini) with a focus on diagnostic morphological characters at the species and genus levels 

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#### Abstract

The mature larvae of the following fourteen Rhinusa species are described and illustrated: Rhinusa antirrhini (Paykull, 1800), R. asellus (Gravenhorst, 1807), R. collina (Gyllenhal, 1813), R. eversmanni (Rosenschoeld, 1838), R. florum (Rubsaamen, 1895), R. herbarum (H. Brisout de Barneville, 1862), R. incana (Kirsch, 1881), R. linariae (Panzer, 1796), R. melas (Boheman, 1838), R. neta (Germar, 1821), R. pilosa (Gyllenhal, 1838), R. rara Toševski \& Caldara, 2015, R. tetra (Fabricius, 1792), and R. vestita (Germar, 1821). The pupae of thirteen of them (except $R$. incana) were also described. The comparison of larval morphological characters and plant preferences provides evidence supporting the existence of different species groups previously established according to a phylogenetic analysis based on adult morphological characters. The following diagnostic attributes distinguishing the genus Rhinusa are highlighted. For the larvae: (1) pronotal shield indistinct; (2) thoracic prodorsal fold small or even vestigial; (3) abdominal postdorsal folds (especially of segments III-VII) high or even in the form of conical protuberances; (4) cuticle of abdominal segments densely covered with asperities; (5) cuticle without dark spots or dark pigmentation; (6) head suboval, rarely round; (7) labrum usually with 2 als; (8) des, short or absent, rarely elongated; and (9) $f_{1-3}$ usually absent or minute. For the pupae: (1) body stout; (2) head protuberances always present; (3) pronotal protuberances (if present), separated at bases of the pronotum, always wider than higher; (4) abdominal protuberance usually present, wide or round; (5) femora usually with a single fes; and (6) urogomphi short or vestigial. Keys to the larvae and pupae described here are provided. All the characters used for identification are illustrated by photographs or drawings. Biological and distribution data, including new information, are provided for all the species studied.


Key words: Biology, mature larva, Mecinini, morphology, pupa, taxonomy

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## Introduction

The weevil genus Rhinusa Stephens, 1829, is a member of the tribe Mecinini (Curculionidae, Curculioninae) and is currently composed of 52 valid species with a Palearctic distribution (Reitter 1908; Caldara 2001; Caldara et al. 2010; Alonso-Zarazaga et al. 2023). Whereas two groups - the R. tetra group and the R. bipustulata group - live on Verbascum L. and Scrophularia L. in the plant family Scrophulariaceae (Caldara 2014), the other groups live on species of Plantaginaceae as presently circumscribed (APG 2016), which belong to the genera Antirrhinum L., Chaenorhinum (D.C.) Rchb, Kickxia Dumort., Linaria Miller, and Misopates Raf., all being either monophagous or oligophagous because living on one or several plant species of the same genus (Hernández-Vera et al. 2010; Caldara 2014; Caldara and Toševski 2019; Toševski et al. 2023). The larvae develop inside the ovaries, stems, or roots of their host plants and sometimes induce galls (Hoffmann 1958; Caldara 2001). Interestingly, several of them are inquilines in galls produced by other species of the same genus (Hoffmann 1958; Arzanov 2000; Caldara 2001, 2003, 2005, 2007; Korotyaev et al. 2005). The genus contains several species that have been the subject of detailed ecological studies (Smith 1959; Groppe 1992; Jordan 1994; Gassmann and Paetel 1998; Toševski and Gassmann 2004), because of their value as potential biological control agents of several species of toadflax (Linaria), which were introduced into North America and became invasive (Saner et al. 1995; Vujnovic and Wein 1997).

To date, larvae of approximately 45 Mecinini species have been described (Gardner 1934; van Emden 1938; Scherf 1964; Anderson 1973; Lee and Morimoto 1988; May 1994; Gosik 2010; Jiang and Zhang 2015; Ścibior and Łętowski 2018; Skuhrovec et al. 2018; Gosik et al. 2020; Skuhrovec et al. 2022), while descriptions of pupae are known for 33 Mecinini species (Scherf 1964; Anderson 1973; Gosik 2010; Jiang and Zhang 2015; Skuhrovec et al. 2018; Gosik et al. 2020; Skuhrovec et al. 2022). Unfortunately, the use of some of these descriptions for comparison is somewhat problematic due to missing data on the chaetotaxy and/or the absence of drawings with enough detail.

The taxonomic classification of species within Rhinusa and of the whole tribe Mecinini has proven difficult, and it is still the subject of extensive studies (Caldara 2008; Caldara and Fogato 2013; Caldara et al. 2013; Gosik et al. 2020). The previous arrangement of Rhinusa into four species groups as well as its treatment as a subgenus of Gymnetron, as proposed by Reitter (1908) based on few adult morphological characters, were generally accepted (Hustache 1931; Hoffmann 1958; Smreczyński 1976; Lohse and Tischler 1983). However, a more recent taxonomic treatment based on a comprehensive morphological study suggests that Rhinusa is monophyletic and sister group of Gymnetron Schoenherr, 1825 (Caldara 2001; Caldara et al. 2010). The immature stages are a source of additional characters that may help solve taxonomic problems at species, genus and tribal level for this important group of weevils.

Therefore, the aims of the present study are to describe the 14 Rhinusa species in complete detail (with larvae and pupae) for the first time, to identify characters that are diagnostic at the genus and species levels, and finally, to compare the characters of the immature stages of this genus with those of other genera of Mecinini.

## Materials and methods

## Insect collection

Mature larvae (those of the last, third, instar, L3) and pupae of each of the studied species were obtained by collecting them from the host plants on which the adults were observed or by rearing them from the galls or seed capsules of those same host plants. Some larvae were preserved for rearing pupae and these were in turn used to obtain adults in order to be sure about the identity of the species. These specimens were then preserved in 2 ml screw-cap microtubes (Sarstedt, Germany) that were half-filled with $96 \%$ ethanol and kept at $4-6^{\circ} \mathrm{C}$. RC and IT were responsible for classifying the insect and plant taxa, respectively. For the morphological descriptions, some of the larval and pupal material was employed. These specimens have been added to the collection of Maria Curie-Skłodowska University's Department of Zoology and Nature Protection in Lublin, Poland. The Results section includes information about the numbers of specimens obtained and their dates and localities of collection.

The larvae and pupae of the majority of the studied species (R. collina (Gyllenhal, 1813), R. eversmanni (Rosenschoeld, 1838), R. florum (Rubsaamen, 1895), R. herbarum (H. Brisout de Barneville, 1862), R. incana (Kirsch, 1881), R. linariae (Panzer, 1796), R. melas (Boheman, 1838), R. pilosa (Gyllenhal, 1838), R. rara Toševski \& Caldara, 2015, and R. vestita (Germar, 1821)) are described and illustrated for the first time. Detailed redescriptions are provided for those of R. asellus (Gravenhorst, 1807), R. antirrhini (Paykull, 1800), R. neta (Germar, 1821), and $R$. tetra (Fabricius, 1792), updating and enlarging the information given in previous papers (van Emden 1938; Scherf 1964; Anderson 1973; Ścibior and teq towski 2018).

## Morphological descriptions

The preparation of the slide-mounted material basically followed May (1994). The larvae chosen for microscopic examination were first dissected (the head, mouthparts, and body were separated), then cleared in $10 \%$ potassium hydroxide $(\mathrm{KOH})$, rinsed in distilled water, and mounted on permanent microscope slides in Faure-Berlese fluid ( 50 g of gum arabic and 45 g of chloral hydrate dissolved in 80 g of distilled water and $60 \mathrm{~cm}^{3}$ of glycerol; Hille Ris Lambers 1950). All of the mentioned specimens were preserved in $95 \%$ ethanol and examined using calibrated oculars and an optical stereomicroscope (Olympus SZ 60 and Nikon Eclipse 80i). Using Corel Photo-Paint X7 and Corel Draw X7, drawings and outlines were created using a drawing tube (MNR-1) mounted on a stereomicroscope (Ampliwal). The larval instars' body length (BL), body width (BW) at the third abdominal segment, and head capsule width (HW) were all measured (see Gosik et al. 2016, or Skuhrovec and Bogusch 2016). Pupae were measured for body length (BL), body width (BW) at the level of the midlegs, rostrum length (RL), and pronotum width (PW) (see Gosik and Skuhrovec 2011). Marvaldi $(1997,1999,2003)$ and Oberprieler et al. $(2014)$ were followed for terminology on chaetotaxy and body parts, and Zacharuk (1985) for terms concerning the antennae.

## Results

Rhinusa Stephens, 1829

Description of mature larva (L3). Measurements (in mm). Body length: 2.00 (R. florum) - 9.00 ( $R$. asellus). The widest point of the body (metathorax) measures up to 2.35 ( $R$. vestita). Head width: 0.46 ( $R$. florum) - 1.05 ( $R$. vestita).

General. Body elongate, slender, curved, and usually rounded in cross section. All thoracic segments almost equal in size, or pronotum smaller than the next segments. Meso- and metathorax each divided dorsally into two folds, the prodorsum distinctly smaller than postdorsum or even vestigial. The pedal fold of thoracic segments very distinct, usually conical, and prominent. Abdominal segments I-VI of similar size, next segments tapering towards the posterior body end. Abdominal segments I-VII each divided dorsally into two transverse folds: prodorsum slightly smaller than postdorsum; postdorsum usually higher than prodorsum or in the form of conical protuberances; seldom both folds equally raised. Segments VIII and IX dorsally undivided. Epipleural fold of segments I-VIII conical. Laterosternal and eusternal folds of segments I-VIII conical, usually weakly distinct. Thoracic and abdominal cuticle densely covered with fine, unicoloured cuticular asperities. Abdominal segment $X$ divided into four folds of equal size; almost completely hidden by the previous segment. Anus situated ventrally.

Thoracic spiracles often unicameral, but sometimes bicameral (R. antirrhini, $R$. florum, and $R$. melas), abdominal spiracles always unicameral; thoracic spiracles placed laterally on prothorax, close to mesothorax; abdominal spiracles placed antero-laterally or antero-medially on segments I-VIII.

Colouration. Head capsule light yellow to dark brown, medial parts of epicranium usually less sclerotised. All thoracic and abdominal segments whitish or light yellow. Pronotal sclerite indistinct, not more pigmented than the rest of the segment (only in $R$. eversmanni and $R$. neta slightly more pigmented than the rest of the segment).

Vestiture. Setae on body thin, yellowish, different in length (very short or medium), transparent or brownish.

Head capsule. Head suboval or slightly narrowed bilaterally, endocarinal line present, reaching from $1 / 2$ to $4 / 5$ of the length of frons. Frontal sutures usually very wide, hardly or weakly distinct. Frons covered with knobby asperities ( $R$. collina, $R$. eversmanni, $R$. incana, and $R$. neta) or smooth. Usually only one single pair of anterior stemmata present, in the form of small black spots (st) close to the end of the frontal suture, two pairs of stemmata present in $R$. asellus, $R$. collina, $R$. incana, and $R$. linariae. Des ${ }_{1}$ usually short or absent; des ${ }_{2}$ usually elongated, located on the lateral part of the epicranium; long des ${ }_{3}$ located anteriorly on the epicranium on the border of the frontal suture; des ${ }_{4}$ minute or absent; and $d e s_{5}$ long, located anterolaterally. $F s_{1-3}$ minute or absent, located medially; $f s_{4}$ long, located anteriorly; and long $f s_{5}$ located anterolaterally, close to the antenna. Les, and les 2 medium to short; single ves short or absent. One to five minute postepicranial setae (pes).

Antennae placed distally of the frontal suture, on the inside. Membranous and distinctly convex basal article bearing one conical sensorium plus some smaller sensilla: ampullacea, basiconica, or styloconica.

Clypeus trapezoidal, usually with two cls short to relatively elongated; sometimes basal part much more sclerotised than the apical parts; anterior border more or less curved towards the inside.

Mouth parts. Labrum usually distinct from clypeus by clypeo-labral suture (in R. pilosa, R. rara, and $R$. linariae clypeus and labrum fused) with three piliform Irs (only in $R$. linariae single $I r s$ ), usually $/ r s_{1}$ and $/ r s_{2}$ elongated, located medially, and Irs $_{3}$ short, located laterally; anterior border of labrum bi-sinuate or slightly rounded. Epipharynx mostly with two (rarely three) relatively elongated, finger-like als (almost identical in length); two or three piliform ams varying in size; without or with up to two short, finger-like mes; labral rods (Ir) usually prominent, elongated, kidney-shaped, or rounded, almost indistinct. Mandibles apically bifid, cutting edge with additional protuberance or smooth; two medium-sized piliform mds, both located close to the lateral border. Maxillolabial complex: maxilla usually more sclerotised than labium, stipes with one stps, two pfs, and one mbs; stps and both $\mathrm{pfs}_{1-2}$ short to elongated; mala with four to six finger-like $d m s$ variable in length; from two up to four piliform vms, medium to short in length. Maxillary palpi two-segmented; basal palpomere usually distinctly wider than distal one; length ratio of the basal and distal palpomeres usually almost 1:1; basal palpomere with short mpxs and two sensilla, distal palpomere with a group of two to six apical sensilla in the terminal receptive area. Prementum close to oval-shaped, with one medium prms (only R. herbarum with two prms); ligula with round or sinuate margin and one to three ligs; premental sclerite sclerotised in cup or ring form, sometimes incomplete, only in $R$. linariae indistinguishable, posterior extension absent or elongated; anterior median extension absent. Labial palpi one-segmented (in R. linariae labial palpi vestigial and almost invisible); each palp with a single pore, and a group of one to four apical sensilla (ampullacea) in the terminal receptive area; the surface of the labium smooth. Postmentum with two or three pms; membranous area smooth or partially covered with sharp or knobby asperities.

Thorax. Prothorax with four to 12 prns; two ps; and usually a short, single eus. Mesothorax with a single minute prs or without; three to four pds (variable in length) (only in R. linariae one pds and in R. pilosa two pds); one medium as (only $R$. rara without); three medium to minute ss; one medium eps; one or two medium ps; and a single minute eus (sometimes absent). Chaetotaxy of metathorax almost identical to that of mesothorax. Each pedal area of thoracic segments with three to six pda.

Abdomen. Segments I-VIII usually with one minute prs (sometimes absent on segment VIII, only R. bipustulata with two prs) and one to four pds; usually one minute and one medium ss; one to three eps; one $p s$; one minute Ists; and usually two minute eus. Abdominal segment IX without or with up to three minute $d s$; without or with up to two minute $p s$; and without or with up to two minute sts. Abdominal segment X mostly without seta.

Description of pupa. Measurements (in mm). Body length: 1.86 (R. florum) 6.50 ( $R$. vestita). Body width: 1.66-3.50. Thorax width: 1.00-2.00.

Body. Integument white, sometimes with some parts dark and sclerotised; setae sometimes placed on pigmented spots, more or less stout, curved. Head with a pair of protuberances (h-pr) above eyes. Rostrum moderately elongated, in males usually as long as in females or only slightly shorter than in females, reaching mesocoxae (only in $R$. asellus rostrum very elongated, distinctly variable in both sexes, much longer in females). Pronotum trapezoidal. Pronotal
protuberances ( $\mathrm{p}-\mathrm{pr}$ ) separated at bases, wider than tall (conical in $R$. asellus), sometimes vestigial ( $R$. linariae) or even absent ( $R$. herbarum, $R$. pilosa, and $R$. rara). Meso- and metanotum similar in size. Abdominal segments I-VI almost identical in size; segment VII semicircular; segment VIII narrow, small; segment IX reduced. Abdominal protuberance (a-pr) on abdominal segment VIII usually visible, flattened or rounded, sometimes vestigial ( $R$. linariae) or even absent (R. collina, R. eversmanni, R. pilosa, and R. rara). Urogomphi (ur) short, often ending in sclerotised, sharp apexes, sometimes vestigial or completely absent.

Chaetotaxy well developed, setae short to elongated, transparent or brownish. Head without or with one os, without or with one sos; rostrum without or with one pas, without or with up to two rs, without or with one es. Pronotum with one to three as, without or with up to four Is, two to four pls; without or with one ds. Dorsal parts of meso- and metathorax with two or three setae placed medially. Apex of femora usually with a single long fes, with two fes in $R$. asellus, R. tetra and $R$. bipustulata. Abdominal segments I-VII with two or up to six setae dorsally (segment VIII usually with fewer setae); one or two setae laterally, and two or up to five setae ventrally. Abdominal segment IX with two or up to four setae ventrally.

## Descriptions of the species

Species are arranged according to the species groups proposed by Caldara et al. (2010) on the basis of a morphological study of the adults. For each group, a combination of the diagnostic characters is here listed, whereas a key to all the groups is reported by Caldara and Toševski (2019).

## Rhinusa tetra group

Adult diagnosis. Protibiae and metatibiae with a premucro, which is more pronounced in female; uncus of protibiae with base placed towards middle of apex and almost as long as width of tibiae in female, protibiae in male distinctly arcuate in apical quarter, profemora very globose, ventrites 3-5 in male along midline with hairlike scales dense and ruffled.

## 1) Rhinusa asellus (Gravenhorst, 1807)

Material examined. 16 mature larvae; 4 § pupae and 1 ¢ pupa. Serbia, Pirot, 700 m a.s.I., ex Verbascum thapsus L., 06.03.2017, leg., det. I. Toševski.

Description of mature larva (Figs 1A, B, 2A-E, 3A-C). Measurements (in mm). Body length: 5.72-9.00 (avg. 7.55). The widest place in the body (meso- and metathorax) measures up to 2.40. Head width: 0.80-1.00 (avg. 0.85).

General. Body elongate, moderately slender, curved, rounded in cross section (Fig. 1A). Prothorax small, pronotal shield not pigmented. Mesothorax slightly smaller than metathorax; each divided dorsally into two folds (prodorsal fold smaller than postdorsal fold). Pedal folds of thoracic segments isolated, conical, prominent. Abdominal segments I-III of similar size, next segments tapering towards posterior body end. Abdominal segments I-VII each divided dorsally into two folds; postdorsal folds distinctly higher than prodorsal. Segments VIII and IX dorsally undivided. Epipleural folds of segments I-VII slightly conical.


Figure 1. Rhinusa asellus (Gravenhorst, 1807) mature larva A habitus B head, frontal view.

Laterosternal and eusternal folds of segments I-VII conical, weakly isolated. Abdominal segment $X$ divided into four folds of equal size. Anus situated ventrally.

All spiracles unicameral; thoracic spiracles placed laterally close to mesothorax; abdominal spiracles (Fig. 1A) placed mediolaterally on segments I-VIII.

Colouration. Yellow to brownish head, medial parts of epicranium less sclerotised (Fig. 1B). All thoracic and abdominal segments white (Fig. 1A). Cuticle covered with fine asperities.

Vestiture. Setae on body thin, yellowish, different in length (very short or medium).

Head capsule (Figs 1B, 2A). Head rather wide, endocarinal line present, reaching to $1 / 2$ of the length of frons. Frontal sutures on head wide, unclear. Two pairs of stemmata (st): first in the form of a prominent pigmented spot with a convex cornea, close to the end of the frontal suture, second pair small, placed laterally, above the anterior stemma. Des, short, located in the central part of epicranium; long des $_{2}$ placed mediolaterally; long des $_{3}$ located anteriorly on epicranium close to the border with the frontal suture; des $_{4}$ short; long des ${ }_{5}$ located anterolaterally above stemma (Fig. 2A). Fs ${ }_{1}$ absent; $f s_{2}$ short; $f s_{3}$ absent; $\mathrm{fs}_{4}$ long, located anteriorly; and long $f s_{5}$ located anterolaterally, close to antenna (Fig. 2A). Les , and $_{1}$ les ${ }_{2}$ medium, and one short ves. Epicranial area with four pes.

Antennae placed distally of the frontal suture, on the inside; membranous and distinctly convex basal article bearing one conical sensorium, relatively short, plus four sensilla differing in type: two basiconica and two styloconica (Fig. 2B).

Clypeus (Fig. 2C) ~ $3 \times$ as wide as long with two medium cls, localised posterolaterally, with one sensillum between them; basal part distinctly sclerotised; anterior border straight.

Mouth parts. Labrum (Fig. 2C) trapezoidal, $\sim 2.2 \times$ as wide as long, with three piliform Irs, different in length; $\operatorname{Ir} s_{1}$ elongated, located medially, $\operatorname{Ir} \boldsymbol{s}_{2}$ elongated, located posteromedially, and $/ \mathrm{rs}_{3}$ short, located anterolaterally; anterior border bi-sinuate. Epipharynx (Fig. 2C) with three medium finger-like als, almost identical in length; two medium piliform ams; and single medium finger-like mes; labral rods (Ir) distinct, kidney shaped. Mandibles (Fig. 2D) bifid, cutting edge


Figure 2. Rhinusa asellus (Gravenhorst, 1807) mature larva, head and mouth parts $\mathbf{A}$ head $\mathbf{B}$ antenna $\mathbf{C}$ clypeus and labrum (left side), epipharynx (right side) D left mandible E maxillolabial complex (schemes). Abbreviations: at-antenna, lr-labral rods, st-sensillum styloconicum, sb-sensillum basiconicum, Se-sensorium, st-stemmata, setae: als-anterolateral, ams-anteromedial, cls-clypeal, des-dorsal epicranial, dms-dorsal malar, fs-frontal epicranial, les-lateral epicranial, ligs-ligular, Irs-labral, mbs-malar basiventral, mds-mandibular dorsal, mes-medial, mpxs-maxillary palp, pes-postepicranial, pfs-palpiferal, pms-postmental, prms-premental, stps-stipital, ves-ventral, vms-ventral malar.
with additional protuberance; two medium piliform mds, both located in shallow pits, close to lateral border. Maxillolabial complex: maxilla (Fig. 2E) stipes with one stps, two pfs and one very short mbs and one sensillum, stps and both $\mathrm{pfs}_{1-2}$ relatively long; mala with six finger-like $d m s$ variable in length; four piliform vms, medium to short in length. Maxillary palpi two-segmented; basal palpomere distinctly wider than distal one; length ratio of basal and distal palpomeres almost 1:1; basal palpomere with short mpxs and one sensillum, distal palpomere with a group of four apical sensilla in terminal receptive area. Prementum (Fig. 2E) oval-shaped, with one long prms; ligula with round margin and three short ligs; premental sclerite broad, sclerotised, cup-shaped, posterior extension medium in length, with thick apex. Labial palpi one-segmented; palpi with a single pore, and a group of four apical sensilla (ampullacea) on terminal receptive area; surface of labium smooth. Postmentum (Fig. 2E) with three $p m s$, medium $p m s_{1}$ located posterolaterally, elongated $p m s_{2}$ located mediolaterally, and medium $\mathrm{pms}_{3}$ located anterolaterally; posterior part of membranous area covered with knobby asperities.

Thorax. Prothorax (Fig. 3A) with nine medium prns, dorsal sclerite weakly visible; two medium ps; and single short eus. Mesothorax (Fig. 3A) with one


Figure 3. Rhinusa asellus (Gravenhorst, 1807) mature larva, habitus $\mathbf{A}$ lateral view of thoracic segments $\mathbf{B}$ lateral view of abdominal segment I C lateral view of abdominal segments VII-X (schemes). Abbreviations: Th. 1-3-number of thoracic segments, Abd. 1-10-number of abdominal seg, setae: as-alar, ds-dorsal, eps-epipleural, eus-eusternal, Ists-laterosternal, pda-pedal, pds-postdorsal, prns-pronotal, prs-prodorsal, ss-spiracular, ps-pleural, sts-sternal.
short prs, one short and two medium pds; one medium as; three minute and one medium ss; one medium eps; one medium $p s$; and single short eus. Chaetotaxy of metathorax (Fig. 3A) almost identical to that of mesothorax. Each pedal area of thoracic segments with three long and two short pda.

Abdomen. Segments I-VII (Fig. 3B, C) with one very short prs; two short and one medium $p d s$; one minute and one medium $s s$; one medium eps; one medium ps; one short Ists; and two short eus. Segment VIII (Fig. 3B, C) with two medium and one short pds; one medium ss; one medium eps; one medium ps; and two short eus. Abdominal segment IX (Fig. 3C) with one minute ps and one minute sts.

Description of pupa (Figs 4A-C, 5A-C). Measurements (in mm). Body length: 4.50-6.00; body width: 2.75-3.15; thorax width: 1.75-2.90; rostrum length: up to $1.60 \delta^{7}$ and 2.60 .

Body. Integument brownish; moderately stout, curved. Elongated head protuberances present ( $\mathrm{h}-\mathrm{pr}$ ) on head above eyes. Rostrum very elongate, in male almost $4 \times$ as long as wide and reaching metacoxae; in female $7 \times$ as long as wide and protruding past metacoxae. Pronotum trapezoidal, $1.5 \times$ as wide as long. Pronotal protuberances ( $\mathrm{p}-\mathrm{pr}$ ) well developed, conical, sclerotised, fused at base. Mesonotum slightly smaller than metanotum. Abdominal segments I-VI almost identical in size; segment VII semicircular; segment VIII narrow; segment IX reduced. Abdominal segment VIII dorsally with rounded, prominent, sclerotised abdominal protuberance (a-pr). Urogomphi (ur) vestigial, in the form of very short sclerotised, sharp protuberances. (Fig. 5C).

Chaetotaxy. Well developed, setae medium to elongated, transparent. Head with one very short sos, one medium os, and one medium-sized pas. Rostrum with two rs and one minute es (Fig. 5A). Pronotum with two as, one ds, two ls, and four pls almost equal in length; ds located in shallow pits. Dorsal parts of meso- and metathorax with three setae of various lengths, placed medially. Apex of femora with two long fes (Fig. 5A-C). Procoxae with a single seta (cs). Abdominal segments I-VII with six setae dorsally, variable in length: first minute, placed anteromedially; second and fourth minute; third and fifth medium, placed close to posterior margin of the segment; six, medium, placed below stigma (on segments VI and VII all setae medium). Abdominal segment VIII


Figure 4. Rhinusa asellus (Gravenhorst, 1807) pupa habitus A ventral view B lateral view C dorsal view.


Figure 5. Rhinusa asellus (Gravenhorst, 1807) pupa habitus A ventral view B dorsal view C lateral view (schemes). Abbreviations: a-pr-abdominal protuberances, h - pr -head protuberances, p - pr -pronotal protuberances, ur-urogomphi, setae: as-apical, cs-coxal, d-dorsal, ds-discal, es-epistomal, fes-femoral, l, Is-lateral, os-orbital, pas-postantennal, pls-posterolateral, rs-rostral, sos-supraorbital, $v$-ventral.
with four elongated setae dorsally. Each lateral part of abdominal segments IVII with a single medium seta. Ventral parts of abdominal segments I-VIII with four setae, median pair longer than other ventral setae. Abdominal segment IX with four medium-sized setae ventrally (Fig. 5A-C).

Remarks and comparative notes. This species is widely distributed in central and southern Europe, in the states of the Caucasus, and in western and central Turkey (Alonso-Zarazaga et al. 2023). Recently, it was reported as introduced into the USA (DiGirolomo et al. 2019). It is clearly related to $R$. tetra, from which the adult differs by the longer rostrum, especially in the female, the elongated shape of the elytra, and the male genitalia (Caldara 2014).

Biological notes. Larval hosts of $R$. asellus are restricted to species of Verbascum (V. nigrum L., V. phlomoides L., V. pulverulentum Vill., V. sinuatum L., V. thapsoides Schw., V. thapsus, and V. virgatum Stokes; Caldara 2014). The biology of this species was carefully studied by Gumovsky (2007). Adults can be found feeding on the shoots and leaves of the host plant beginning in May. Oviposition sites are typically concentrated in the top portion of the host plant. The female drills a hole in the host-plant tissues with her very long rostrum, and then she lays eggs there. Eggs develop in $\sim 7$ days. After hatching, the larva bores into the stem and feeds on plant tissues, often leading to swelling of the stem. Mature larvae form a pupal cell just beneath the outer layer of plant tissue within the stem. Larval and pupal development take on average 20 and 10 days, respectively. Sometimes $R$. asellus lives on the same host plant as $R$. tetra, although they occupy different niches.
2) Rhinusa tetra (Fabricius, 1792)

Material examined. 21 mature larvae; 5 万人 and 2 q pupae. Italy, Lombardia, Linarolo (Pavia), ex Verbascum thapsus, 25.08.2015; 19 mature larvae; 7 premature; 3 o and 4 q pupae, Italy, Alto Adige, Castelrotto (Bolzano), ex Verbascum blattaria L., 10.08. 2017, all leg., det. R. Caldara.

Description of mature larva (Figs 6A, B, 7A-E, 8A-C). Measurements (in mm ). Body length: 3.25-6.50 (avg. 5.90). The widest place in the body (mesoand metathorax) measures up to 2.25 . Head width: $0.85-0.90$ (avg. 0.87).

General. Body elongate, slender, curved, rounded in cross section (Fig. 6A). Prothorax smaller than mesothorax. Metathorax as wide as mesothorax; each divided dorsally into two folds (prodorsal fold much smaller than postdorsal fold). Pedal folds of thoracic segments prominent, conical, well isolated. Abdominal segments I-V of similar size, next segments tapering towards posterior body end. Abdominal segments I-VI each divided dorsally into two folds almost identical in size. Segments VII-IX dorsally undivided. Epipleural folds of segments I-VIII conical, well developed. Laterosternal and eusternal folds of segments I-VIII conical, well isolated. Abdominal segment $X$ divided into four folds of equal size. Anus situated ventrally, almost completely hidden in segment IX.

Thoracic and abdominal spiracles unicameral; thoracic spiracles (Fig. 6A) placed laterally close to mesothorax; abdominal spiracles (Fig. 6A) placed medially on segments I-VIII.

Colouration. Light yellow to brownish head (Fig. 6B). All thoracic and abdominal segments whitish (Fig. 6A). Cuticle densely covered with fine asperities.


Figure 6. Rhinusa tetra (Fabricius, 1792) mature larva $\mathbf{A}$ habitus $\mathbf{B}$ head, frontal view.

Vestiture. Setae on body thin, hair-like, different in length (minute to medium).
Head capsule (Figs 6B, 7A). Head wide, endocarinal line present, reaching to
$1 / 2$ of the length of frons. Frontal sutures on head wide, indistinct. A single pair of stemmata in the form of small black spots (st) placed laterally, close to the end of the frontal suture. Des ${ }_{1}$ very short, located in middle part of epicranium; very long $\mathrm{des}_{2}$ located anteriorly; very long $\mathrm{des}_{3}$ placed almost on the border of the frontal suture; very short des ${ }_{4}$, located laterally; and long des ${ }_{5}$ placed anterolaterally above stemma (Fig. 7A). $F s_{1}$ and $f s_{2}$ minute, located posterolaterally; $f s_{3}$ absent; $\mathrm{fS}_{4}$ medium, located anteriorly; and long $\mathrm{fs}_{5}$ located anterolaterally, close to antenna (Fig. 7A). Les ${ }_{1}$ and $l e s_{2}$ medium; single short ves. Epicranial area with four pes.

Antennae placed distally of the frontal suture, on the inside; membranous and distinctly convex basal article bearing one conical, moderately elongate sensorium, plus two sensilla basiconica (Fig. 7B).

Clypeus (Fig. 7C) trapezoidal, $\sim 2.5 \times$ as wide as long with two relatively long cls, localised posterolaterally, with one sensillum between them; anterior border almost straight.

Mouth parts. Labrum (Fig. 7C) ~ $2.2 \times$ as wide as long, with three piliform Irs, various long; Irs ${ }_{1}$ elongated, located posteromedially, on small protuberance, $\operatorname{Irs}{ }_{2}$ medium, located lateromedially, and $\operatorname{Irs}{ }_{3}$ short, located laterally; anterior border almost straight. Epipharynx (Fig. 7C) with two elongated finger-like als identical in length, three piliform ams variable in length, and two short, finger-like mes; labral rods (Ir) distinct, kidney-shaped. Mandibles (Fig. 7D) bifid, cutting edge straight; two medium piliform and short $m d s$, both located close to lateral border. MaxilIolabial complex: maxilla brownish sclerotised (Fig. 7E) stipes with one stps, two $p f s$ and one short $m b s$, stps and both $p f s_{1-2}$ elongated; mala with six finger-like $d m s$ variable in length; four medium piliform vms. Maxillary palpi two-segmented; basal palpomere distinctly wider than distal one; both palpomeres equal in length; basal palpomere with short mpxs and two sensilla, distal palpomere with a group of six apical sensilla in terminal receptive area. Prementum (Fig. 7E) close to oval-shaped, with a single elongated prms; ligula with rounded margin and two, short ligs; premental sclerite broad, sclerotised, cup-shaped, posterior


Figure 7. Rhinusa tetra (Fabricius, 1792) mature larva, head and mouth parts $\mathbf{A}$ head $\mathbf{B}$ antenna $\mathbf{C}$ clypeus and labrum (left side), epipharynx (right side) D left mandible E maxillolabial complex (schemes). Abbreviations: at-antenna, lr-labral rods, sb-sensillum basiconicum, Se-sensorium, st-stemmata, setae: als-anterolateral, ams-anteromedial, cls-clypeal, des-dorsal epicranial, dms-dorsal malar, fs-frontal epicranial, les-lateral epicranial, ligs-ligular, Irs-labral, mbs-malar basiventral, mds-mandibular dorsal, mes-medial, mpxs-maxillary palp, pes-postepicranial, pfs-palpiferal, pms-postmental, prms-premental, stps-stipital, ves-ventral, vms-ventral malar.


Figure 8. Rhinusa tetra (Fabricius, 1792) mature larva, habitus $\mathbf{A}$ lateral view of thoracic segments $\mathbf{B}$ lateral view of abdominal segment I C lateral view of abdominal segments VII-X (schemes). Abbreviations: Th. 1-3-number of thoracic segments, Abd. 1-10-number of abdominal seg, setae: as-alar, ds-dorsal, eps-epipleural, eus-eusternal, Ists-laterosternal, pda-pedal, pds-postdorsal, prns-pronotal, prs-prodorsal, ss-spiracular, ps-pleural, sts-sternal.
extension short with thick apex. Labial palpi one-segmented; palpi with a single pore, and four apical sensilla in terminal receptive area; surface of labium smooth. Postmentum (Fig. 7E) with three pms, medium pms, located posteromedially, long $p m s_{2}$ located mediolaterally, and elongated $p m s_{3}$ located anterolaterally; membranous area partially covered with knobby asperities.

Thorax. Prothorax (Fig. 8A) with eight elongated and single medium prns; two elongated $p s$; and single short eus. Mesothorax (Fig. 8A) with a single short prs; two medium and one short pds (ordered: medium, medium, short); one short as; two medium and one short ss; one medium eps; one medium $p s$; and single minute eus. Chaetotaxy of metathorax (Fig. 8A) almost identical to that of mesothorax. Each pedal area of thoracic segments with five elongated and one short pda.

Abdomen. Segments I-VIII (Fig. 8B, C) with one very short prs (segment VIII without prs), three pds of various length; one medium and one long ss; single elongated eps; one medium ps; one short Ists; and two minute eus. Abdominal segment IX (Fig. 8C) with one short and two minute ds; two minute ps; and two minute sts.

Description of pupa (Figs 9A-C, 10A-C). Measurements (in mm). Body length: 3.75-5.25; body width: 2.40-2.75; thorax width: 1.05-1.75; rostrum length: up to 0.70 § ${ }^{\top}$ and


Figure 9. Rhinusa tetra (Fabricius, 1792) pupa habitus $\mathbf{A}$ ventral view $\mathbf{B}$ lateral view $\mathbf{C}$ dorsal view.

Body. Integument white, with some parts dark sclerotised; moderately elongated. Elongated head protuberances (h-pr) present on head above eyes. Rostrum moderately elongated, on both sexes almost $2.8 \times$ as long as wide and protruding mesocoxae. Pronotum trapezoidal $2 \times$ as wide as long. Pronotal protuberances ( $p-\mathrm{pr}$ ) flattened, sclerotised, separated at bases. Mesonotum slightly narrower than metanotum. Abdominal segments I-VI almost identical in size, VII semicircular, segment VIII narrow, segment IX reduced. Abdominal segment VIII dorsally with rounded, well developed abdominal protuberance (a-pr). Urogomphi (ur) very short, ending with sclerotised, sharp apexes (Fig. 9A-C).

Chaetotaxy. Well developed, setae medium to short. Head with one medium sos and one medium os. Rostrum with a single rs (Fig. 10A). Pronotum with two as, two Is, single ds, and four pls, all equal in length. Dorsal parts of meso- and metathorax with three setae of various length, placed medially. Apex of femora with two long fes (Fig. 10A-C). Abdominal segments I-VII dorsally with five setae dorsally, variable in length: first, second and fourth minute, third and fifth medium; first seta placed posteromedially, second to fourth placed close to posterior margin of the segment, fifth placed below stigma. Segment VII with four elongated setae dorsally, segment VIII with three elongated setae dorsally. Each lateral part of abdominal segments I-VIII with a single short seta. Ventral parts of abdominal segments I-VIII with four setae (first distinctly longer than other setae). Abdominal segment IX with three short setae ventrally (Fig. 10A-C).

Remarks and comparative notes. This species is one of the most common and widespread of the genus Rhinusa. It has been reported in all of Europe, Siberia, North Africa, the Middle East, central Asia, and northern India. It was accidentally introduced in North America, where it is currently distributed in several states of the USA and Canada (O'Brien and Wibmer 1982; DiGirolomo et al. 2019). Although it was proposed as a potential candidate for the biological control of invasive common mullein, Verbascum thapsus, it was not used in North America in this regard. In the southern part of its area of distribution, it can be confused with other species of the group, such as $R$. verbasci (Rosenschoeld, 1838), R. moroderi (Reitter, 1906), and R. weilli Caldara, 2014, from which it can be separated only by the shape of the female rostrum, most easily


Figure 10. Rhinusa tetra (Fabricius, 1792) pupa habitus $\mathbf{A}$ ventral view $\mathbf{B}$ dorsal view $\mathbf{C}$ lateral view (schemes). Abbreviations: $\mathrm{a}-\mathrm{pr}-\mathrm{abdominal}$ protuberances, $\mathrm{h}-\mathrm{pr}$-head protuberances, $\mathrm{p}-\mathrm{pr}$-pronotal protuberances, ur-urogomphi, setae: as-apical, $d$-dorsal, ds-discal, fes-femoral, I, /s-lateral, os-orbital, pls-posterolateral, sos-supraorbital, rs-rostral, v-ventral.
if observed in lateral view (Caldara 2014). It is well known that adults of $R$. tetra are highly variable in size ( $2.0-4.5 \mathrm{~mm}$ ), even among specimens collected from the same plant. Additionally, the rostrum length of the female distinctly varies among populations living on different plants, probably related to oviposition
inside seed capsules of different sizes and thicknesses, as suggested to occur in R. dieckmanni (Behne, 1988) (Toševski et al. 2023).

Biological notes. This species was reported to feed on several species of Verbascum. Caldara et al. (2012) verified the following plant associations: Verbascum blattaria, V. boerhavii L., V. creticum (L.) Cav., V. Iychnitis L., V. nigrum, V. phlomoides, V. phoeniceum L., V. pulverulentum, V. speciosum Schrader, V. thapsiforme Schrader, and V. thapsus. Adults were also collected on Scrophularia auriculata L., S. canina L., and S. Iaevigata Vahl.

Marquess (2000) provides very detailed information on the biology of this species. Adults feed on the dorsal surfaces of leaves and on the seed capsules of the host plant. Once a plant flowers, mating occurs on the entire inflorescence. The female usually oviposits 1-3 eggs per seed capsule. Egg hatching occurs 7-11 days after deposition. Larvae feed on seeds within capsules and consume the majority of them. Pupation occurs within the seed capsule, and the emergence of the adults occurs $\sim 25$ days later. Adults exit the seed capsule by chewing through the hardened pericarp.

## Rhinusa antirrhini group

Adult diagnosis. Rostrum in dorsal view from base to antennal insertion with a trapezoidal outline, with dorsal part narrower than ventral part, in male with distinctly visible scrobe; rostrum in lateral view with dorsal margin abruptly narrowed in apical part; first elytral interstria apically covered with dense vestiture.

## 3) Rhinusa antirrhini (Paykull, 1800)

Material examined. 29 mature larvae; 28 § and 26 q pupae. Serbia, Zemun, ex Linaria vulgaris Mill., 15.08.2017, leg., det. I. Toševski.

Description of mature larva (Figs 11A, B, 12A-E, 13A-C). Measurements (in mm ). Body length: 3.00-4.25 (avg. 3.60). The widest place in the body (mesoand metathorax) measures up to 1.25 . Head width: 0.55-0.60 (avg. 0.56).

General. Body elongate, slender, distinctly curved, rounded in cross section (Fig. 11A). All thoracic segments almost equal in size. Meso- and metathorax each divided dorsally into two folds (prodorsal fold distinctly smaller than postdorsal fold). Pedal folds of thoracic segments isolated, conical, prominent. Abdominal segments I-VI of similar size, next segments tapering towards posterior body end. Abdominal segments I-VII each divided dorsally into two folds: prodorsal fold slightly smaller than postdorsal; both folds equally in high. Segments VIII and IX dorsally undivided. Epipleural folds of segments I-VIII conical. Laterosternal and eusternal folds of segments I-VIII conical, weakly isolated. Abdominal segment $X$ (almost completely hidden in previous segment) divided into four folds of equal size. Anus situated ventrally.

Thoracic spiracles bicameral, abdominal unicameral; thoracic spiracles (Fig. 11A) placed laterally close to mesothorax; abdominal spiracles (Fig. 11A) placed antero-laterally on segments I-VIII.

Colouration. All thoracic and abdominal segments whitish (Fig. 11A). Cuticle densely covered with fine asperities. Dark yellow to dark brown head, medial parts of epicranium less sclerotised (Fig. 11B).


Figure 11. Rhinusa antirrhini (Paykull, 1800) mature larva A habitus B head, frontal view.

Vestiture. Setae on body thin, yellowish, different in length (very short or medium).

Head capsule (Figs 11B, 12A). Head slightly narrowed bilaterally, endocarinal line present, reaching to the $2 / 3$ of the length of frons. Frontal sutures on head very wide, indistinct. Single pair of stemmata in the form of small black spots (st) close to the end of the frontal suture. Des ${ }_{1}$ absent; des $_{2}$ short, located in lateral part of epicranium; long des $_{3}$ located anteriorly on epicranium on border of the frontal suture; des $_{4}$ minute; and des $_{5}$ long, located anterolaterally above stemma (Fig. 12A). Fs absent; $f s_{2}$ short, located medially; $f s_{3}$ absent; $f s_{4}$ long, located anteriorly; and long $\mathrm{fs}_{5}$ located anterolaterally, close to antenna (Fig. 12A). Les, short and medium les ${ }_{2}$; two short ves. Epicranial area with three pes.

Antennae placed distally of the frontal suture, on the inside; membranous and distinctly convex basal article bearing one conical sensorium, plus four sensilla ampullacea and single sensillum basiconicum (Fig. 12B).

Clypeus (Fig. 12C) trapezoidal, $\sim 3.2 \times$ as wide as long with two short cls, localised posterolaterally, with one sensillum between them; except the posterior part, whole clypeus darkly sclerotised; anterior border slightly curved towards the inside.

Mouth parts. Labrum (Fig. 12C) ~ $2.2 \times$ as wide as long, with three piliform Irs, various long; $/ r s_{1}$ and $/ r s_{2}$ elongated, located medially, and $/ r s_{3}$ short, located laterally; anterior border bi-sinuate. Epipharynx (Fig. 12C) with two relatively elongated finger-like als, almost identical in length; three ams various in size; and single short finger-like mes; labral rods (Ir) distinct, rounded. Mandibles (Fig. 12D) bifid, cutting edge with additional protuberance; two medium piliform mds , both located close to lateral border. Maxillolabial complex: maxilla more sclerotised than labium (Fig. 12E) stipes with one stps, two pfs and one short mbs , $s t p s$, and both $p \mathrm{fs}_{1-2}$ medium; mala with five finger-like dms variable in length; four piliform vms, medium to short in length. Maxillary palpi two-segmented; basal palpomere distinctly wider than distal one; length ratio of basal and distal palpomeres almost 1:1; basal palpomere with short mpxs and two sensilla, distal palpomere with a group of two or three apical sensilla in terminal receptive area. Prementum (Fig. 12E) close to oval-shaped, with one medium


Figure 12. Rhinusa antirrhini (Paykull, 1800) mature larva, head and mouth parts $\mathbf{A}$ head $\mathbf{B}$ antenna $\mathbf{C}$ clypeus and labrum (left side), epipharynx (right side) D left mandible E maxillolabial complex (schemes). Abbreviations: at-antenna, Ir-labral rods, sa-sensillum ampullaceum, sb-sensillum basiconicum, Se-sensorium, st-stemmata, setae: als-anterolateral, ams-anteromedial, cls-clypeal, des-dorsal epicranial, dms-dorsal malar, fs-frontal epicranial, les-lateral epicranial, ligs-ligular, Irs-labral, mbs-malar basiventral, mds-mandibular dorsal, mes-medial, mpxs-maxillary palp, pes-postepicranial, pfs-palpiferal, pms-postmental, prms-premental, stps-stipital, ves-ventral, vms-ventral malar.


Figure 13. Rhinusa antirrhini (Paykull, 1800) mature larva, habitus $\mathbf{A}$ lateral view of thoracic segments $\mathbf{B}$ lateral view of abdominal segment I C lateral view of abdominal segments VII-X (schemes). Abbreviations: Th. 1-3-number of thoracic segments, Abd. 1-10-number of abdominal seg, setae: as-alar, ds-dorsal, eps-epipleural, eus-eusternal, Ists-laterosternal, pda-pedal, pds-postdorsal, prns-pronotal, prs-prodorsal, ss-spiracular, ps-pleural, sts-sternal.
prms; ligula with round margin and two short ligs; premental sclerite vestigial, only lateral parts dark sclerotised. Labial palpi one-segmented; each palp with a single pore, and a group of one or two apical sensilla (ampullacea) on terminal receptive area; surface of labium smooth. Postmentum (Fig. 12E) with three $p m s$, elongated $p m s_{1}$ located medially, long $p m s_{2}$ located laterally, and medium $p m s_{3}$ located antero-laterally; membranous area smooth.

Thorax. Prothorax (Fig. 13A) with ten relatively long prns; two medium ps; and single short eus. Mesothorax (Fig. 13A) without prs; one minute and two medium pds; one medium as; three medium ss; one medium eps; one medium ps; and single minute eus. Chaetotaxy of metathorax (Fig. 13A) almost identical to that of mesothorax. Each pedal area of thoracic segments with three medium and three minute pda.

Abdomen. Segments I-VIII (Fig. 13B, C) with one minute prs (segment VIII without); one minute and two medium pds; one minute and one medium ss; two medium eps; one minute $p s$; one minute $I s t s$; and two minute eus. Abdominal segment IX (Fig. 13C) with two minute ds; two minute ps; and two minute sts.

Description of pupa (Figs 14A-C, 15A-C). Measurements (in mm). Body length: 2.35-3.30 (avg. 2.75); body width: 1.45-1.85 (avg. 1.60); thorax width: 0.90-1.20 (avg. 1.05); rostrum length: up to 0.60 § and 0.75 q.

Body. Integument white, with some parts dark sclerotised; moderately stout, curved (Fig. 14A-C). All pronotal setae placed on pigmented spots. Head with


Figure 14. Rhinusa antirrhini (Paykull, 1800) pupa habitus A ventral view B lateral view C dorsal view.
a pair of distinct head protuberances (h-pr) above eyes. Rostrum rather short, in male usually only slightly shorter than in female: almost $3 \times$ as long as wide, reaching mesocoxae. Pronotum trapezoidal $2 \times$ as wide as long. Pronotal protuberances ( $p-p r$ ) conical, flattened, sclerotised, separated at bases. Mesonotum and metanotum similar in size. Abdominal segments I-VI almost identical in size; segment VII semicircular; segment VIII narrow; segment IX reduced. Abdominal segment VIII dorsally with rounded, prominent, sclerotised abdominal protuberance (a-pr). Urogomphi (ur) short, ending with sclerotised, sharp apexes (Fig. 15A-C).

Chaetotaxy. Well developed, setae short to elongated, transparent. Head with one short os (Fig. 15A). Pronotum with two as, four Is, and three pls almost equally in length. Dorsal parts of meso- and metathorax with three setae of various length, placed medially. Apex of femora with a single long fes (Fig. 15A-C). Abdominal segments I-VII with five setae dorsally, variable in length: first and third minute, second, fourth and fifth medium; first to fourth placed close to posterior margin of the segment, fifth placed below stigma (on segments VI and VII all setae medium). Abdominal segment VIII with four elongated setae dorsally. Each lateral part of abdominal segments I-VII with two medium setae. Ventral parts of abdominal segments I-VIII with four medium-sized setae. Abdominal segment IX with two medium setae ventrally (Fig. 15A-C).

Remarks and comparative notes. This species is reported from all of Europe, although it is probable that, especially in the Balkans, it is confused with several cryptic species still to be described on the basis of molecular studies (Hernández-Vera et al. 2010; IT, pers. obs.). Rhinusa antirrhini lives on Linaria spp. other than L. vulgaris. This weevil was accidentally imported into North America at the beginning of the twentieth century, where it became important in applied entomology when proposed for the biological control of the invasive plant species L. vulgaris (see Hernández-Vera et al. 2010 and DiGirolomo et al. 2019 for references). The adult is sometimes confused with R. dieckmanni, as recently shown by Toševski et al. (2023).

Biological notes. This univoltine weevil feeds on L. vulgaris and L. angustissima (Loisel.) Borbás, in the capsules of which larvae and pupae can be found. Adults emerge at the end of May, visiting flowers to start consuming pollen, and


Figure 15. Rhinusa antirrhini (Paykull, 1800) pupa habitus A ventral view B dorsal view C lateral view (schemes). Abbreviations: a-pr-abdominal protuberances, h - pr -head protuberances, $\mathrm{p}-\mathrm{pr}$-pronotal protuberances, ur-urogomphi, setae: as-apical, $d$-dorsal, fes-femoral, I, Is-lateral, os-orbital, pls-posterolateral, v-ventral.
shortly after that, copulation begins. After mating, the females start laying eggs in well-developed floral ovaries, usually in their upper parts. When oviposition occurs, the outside of the seed capsule has a long, cone-shaped protrusion immediately above the oviposition site. This drives the formation of a semigall in that area. The early instar larvae feed primarily on hypertrophied seeds, while older and later instars consume abortive seeds. Most often, a single seed capsule contains one $R$. antirrhini larva, while at high densities, two larvae per capsule are commonly found. Development to adult takes ~ 30-50 days, depending on the environmental temperature. Newly emerged adults feed on young shoots of their host plant, expressing irregular aestivation periods until mid-autumn, when adults intensify feeding just before entering hibernation. Adults overwinter at the soil surface, sheltered below or between dry plant remains (IT, pers. obs.).

## 4) Rhinusa florum (Rubsaamen, 1895)

Material examined. 19 mature larvae; 20 万 and $6 \uparrow$ pupae. Serbia, Vinci, ex Linaria genistifolia (L.) Miller, 05.06.2017, leg., det. I. Toševski.

Description of mature larva (Figs 16A, B, 17A-E, 18A-C). Measurements (in mm ). Body length: 2.00-3.50 (avg. 3.00). The widest place in the body (mesoand metathorax) measures up to 1.20 . Head width: $0.46-0.54$ (avg. 0.52).

General. Body elongate, slightly curved, oblate dorsoventrally in cross section (Fig. 16A). Prothorax prominent, pronotal shield not pigmented; mesoand metathorax equal in size, smaller than prothorax. Meso- and metathorax each divided dorsally into two folds (prodorsal fold distinctly smaller than postdorsal fold). Pedal folds of thoracic segments isolated, conical, prominent. Abdominal segments I-VI of similar size, next segments tapering towards posterior body end. Abdominal segments I-VII each divided dorsally into two almost equal in size folds; postdorsal folds only slightly higher than prodorsal folds. Segments VIII and IX dorsally undivided. Epipleural folds of segments I-VIII conical. Laterosternal and eusternal folds of segments IVIII conical, weakly isolated. Abdominal segment $X$ divided into four folds of equal size. Anus situated ventrally, almost completely covered with the ninth abdominal segment.

Thoracic spiracles bicameral, abdominal unicameral; thoracic spiracles (Fig. 16A) placed laterally close to mesothorax; abdominal spiracles (Fig. 16A) placed mediolaterally on segments I-VIII.

Colouration. Cuticle covered with fine asperities. Brown head, medial parts of epicranium less sclerotised (Fig. 16B). All thoracic and abdominal segments whitish (Fig. 16A).

Vestiture. Setae on body thin, yellowish, different in length (very short or medium).

Head capsule (Figs 16B, 17A). Head suboval, endocarinal line present, reaching to the $3 / 4$ of the length of frons. Frontal sutures on head distinct, very wide. Single pair of stemmata in the form of small black spots (st) close to the end of the frontal suture. Des, short, located in middle part of epicranium; long des ${ }_{2}$; long des $_{3}$ located anteriorly on epicranium close to the border with the frontal suture; des $_{4}$ absent; and des $_{5}$ long, located anterolaterally above stemma


Figure 16. Rhinusa florum (Rubsaamen, 1895) mature larva $\mathbf{A}$ habitus $\mathbf{B}$ head, frontal view.
(Fig. 17A). $F s_{1}$ and $f s_{2}$ short, located medially; $f s_{3}$ absent; long $f s_{4}$ located anteriorly; and long $\mathrm{fs}_{5}$ located anterolaterally, close to antenna (Fig. 17A). Les ${ }_{1}$ and $l e s_{2}$ medium; single medium ves. Epicranial area with five pes.

Antennae placed distally of the frontal suture, on the inside; membranous and distinctly convex basal article bearing one conical, slightly elongate sensorium, plus three sensilla basiconica (Fig. 17B).

Clypeus (Fig. 17C) trapezoidal, $\sim 3.6 \times$ as wide as long with two relatively long cls, localised posterolaterally, with one sensillum between them; basal part distinctly sclerotised; anterior border curved towards the inside.

Mouth parts. Labrum (Fig. 17C) $\sim 3 \times$ as wide as long, with three piliform Irs, variously long; $I r s_{1}$ and $I r s_{2}$ elongated, located medially, $I r s_{3}$ short, located anterolaterally; anterior border bi-sinuate. Epipharynx (Fig. 17C) with two relatively elongated finger-like als, almost identical in length; two piliform ams various in size; and single short finger-like mes; labral rods (Ir) close to kidney-shaped. Mandibles (Fig. 17D) bifid, cutting edge straight; two medium piliform mds, both located in shallow pits, close to lateral border. Maxillolabial complex: maxilla dark sclerotised (Fig. 17E), stipes with one stps, two pfs, and one very short mbs and one sensillum, stps and both $p f s_{1-2}$ relatively long; mala with five finger-like $d m s$ variable in length (first and second much longer than others); five piliform vms, medium to short in length. Maxillary palpi two-segmented; basal palpomere distinctly wider than distal one; length ratio of basal and distal palpomeres almost 1:1; basal palpomere with short mpxs and two sensilla, distal palpomere with a group of six apical sensilla in terminal receptive area. Prementum (Fig. 17E) ovalshaped, with one long prms; ligula with round margin and three short ligs; premental sclerite vestigial, only basal part highly sclerotised. Labial palpi one-segmented; palpi with a single pore, and a group of five apical sensilla (ampullacea) on terminal receptive area; surface of labium smooth. Postmentum (Fig. 17E) with three $p m s$, elongated $p m s_{1}$ located medially, medium $p m s_{2}$ located laterally, and relatively short $p m s_{3}$ located antero-laterally; membranous area smooth.


Figure 17. Rhinusa florum (Rubsaamen, 1895) mature larva, head and mouth parts $\mathbf{A}$ head $\mathbf{B}$ antenna $\mathbf{C}$ clypeus and labrum (left side), epipharynx (right side) D left mandible E maxillolabial complex (schemes). Abbreviations: at-antenna, lr -labral rods, sb-sensillum basiconicum, Se -sensorium, st-stemmata, setae: als-anterolateral, ams-anteromedial, cls-clypeal, des-dorsal epicranial, dms-dorsal malar, fs-frontal epicranial, les-lateral epicranial, ligs-ligular, lrs-labral, mbs-malar basiventral, mds-mandibular dorsal, mes-medial, mpxs-maxillary palp, pes-postepicranial, pfs-palpiferal, pms-postmental, prms-premental, stps-stipital, ves-ventral, vms-ventral malar.

Thorax. Prothorax (Fig. 18A) with 12 medium prns, dorsal sclerite weakly visible; two medium ps; and single short eus. Mesothorax (Fig. 18A) with one minute prs, two minute and one medium pds (ordered: minute, medium, minute); one medium as; three medium ss; one medium eps; one medium $p s$; and single minute eus. Chaetotaxy of metathorax (Fig. 18A) almost identical to that of mesothorax. Each pedal area of thoracic segments with four medium and one minute $p d a$.

Abdomen. Segments I-VIII (Fig. 18B, C) with one minute prs (segment VIII without); one minute and one medium pds; one minute and one medium ss; two medium eps; one medium ps; one medium Ists; and two short eus. Abdominal segment IX (Fig. 18C) with one minute and medium ds; one medium ps; and two medium sts.

Description of pupa (Figs 19A-C, 20A-C). Measurements (in mm). Body length: 1.86-2.93 (avg. 2.60); body width: 1.66-1.86 (avg. 1.80); thorax width: 1.00-1.16 (avg. 1.06); rostrum length: up to 0.66 万 and 0.73 q.

Body. Integument white, with some parts dark sclerotised; moderately stout, curved. All setae placed on dark brown spots. Head protuberances (h-pr) present on head above eyes. Rostrum rather short, in male usually only slightly shorter than in female almost $2.3 \times$ as long as wide, reaching mesocoxae. Pronotum trapezoidal $2.4 \times$ as wide as long. Pronotal protuberances ( $p-p r$ ) conical, sclerotised, separated at bases. Meso- and metanotum similar in size. Abdominal segments I-VI almost identical in size; segment VII semicircular; segment VIII

Abd. 3


Figure 18. Rhinusa florum (Rubsaamen, 1895) mature larva, habitus A lateral view of thoracic segments $\mathbf{B}$ lateral view of abdominal segment I C lateral view of abdominal segments VII-X (schemes). Abbreviations: Th. 1-3-number of thoracic segments, Abd. 1-10-number of abdominal seg, setae: as-alar, ds-dorsal, eps-epipleural, eus-eusternal, Ists-laterosternal, pda-pedal, pds-postdorsal, prns-pronotal, prs-prodorsal, ss-spiracular, ps-pleural, sts-sternal.


Figure 19. Rhinusa florum (Rubsaamen, 1895) pupa habitus A ventral view B lateral view C dorsal view.
narrow; segment IX reduced. Abdominal segment VIII dorsally with rounded, prominent, sclerotised abdominal protuberance (a-pr). Urogomphi (ur) medium, ending with sclerotised, sharp apexes (Fig. 19A-C).

Chaetotaxy. Well developed, setae medium to elongated, transparent. Head with one medium os. Rostrum with a single rs (Fig. 20A). Pronotum with two as, one ds, two ls, and four pls variable in length. Dorsal parts of meso- and metathorax with three setae of various length, placed medially. Apex of femora with a single long fes (Fig. 20A-C). Abdominal segments I-VII with six setae dorsally, variable in length: first minute, placed anteromedially; second and fourth minute; third and fifth medium, placed close to posterior margin of the segment; sixth medium, placed below stigma (on segments VI and VII all setae from second to sixth medium). Abdominal segment VIII with four elongated setae dorsally. Each lateral part of abdominal segments I-VII with two medium setae. Ventral parts of abdominal segments I-VIII with four medium setae. Abdominal segment IX with four medium setae ventrally (Fig. 20A-C).

Remarks and comparative notes. This species is distributed in Central Europe, the Balkans, the Caucasus, and the Middle East (Alonso-Zarazaga et al. 2023). It is clearly distinguishable from $R$. antirrhini and the other species of this group by the shape of its rostrum, which in lateral view is almost straight and gradually narrowed from base to apex and not abruptly tapered at the antennal insertion.

Biological notes. Rhinusa florum is a univoltine weevil that inhabits lowlands, hilly slopes, and mountain meadows at elevations up to 2000 m. The host plants are Linaria genistifolia and L. dalmatica (L.) Mill. Adults emerge in early June following the occurrence of flowering. Copulation occurs shortly thereafter, with the egg-laying period lasting from mid-June until the end of July. Oviposition occurs on the widest part of the developing ovary. During oviposition, females secrete a fluid that fixes the egg to the ovule. Females lay one egg per ovary. Egg deposition triggers a strong proliferative tissue reaction manifested as a solid, conical gall formation that grows inside the flower lumen. The galled tissue is the only resource for larval development. Pupation takes place inside the gall, and adults emerge after approximately two weeks. The adults overwinter in soil and litter close to the host plants (IT, pers. obs.).


Figure 20. Rhinusa florum (Rubsaamen, 1895) pupa habitus A ventral view B dorsal view C lateral view (schemes). Abbreviations: $\mathrm{a}-\mathrm{pr}$-abdominal protuberances, $\mathrm{h}-\mathrm{pr}$-head protuberances, $\mathrm{p}-\mathrm{pr}$-pronotal protuberances, ur-urogomphi, setae: as-apical, $d$-dorsal, ds-discal, fes-femoral, I, Is-lateral, os-orbital, pls-posterolateral, rs-rostral, v-ventral.

## Rhinusa linariae group

Adult diagnosis. Rostrum strongly curved in lateral view; outer margin of tibiae distinctly curved outwards near apex; uncus of metatibiae well developed in both sexes.

## 5) Rhinusa linariae (Panzer, 1796)

Material examined. 7 mature larvae; $7 \delta^{\lambda}$ and $12 q$ pupae. Serbia, Didič, ex Linaria vulgaris galls, 05.07.2017, leg., det. I. Toševski.

Description of mature larva (Figs 21A, B, 22A-E, 23A-C). Measurements (in mm ). Body length: 2.33-4.30 (avg. 3.66). The widest place in the body (mesoand metathorax) measures up to 1.16. Head width: 0.46-0.53 (avg. 0.50).

General. Body elongate, slender, strongly curved, rounded in cross section (Fig. 21A). All thoracic segments almost equal in size. Pronotal shield not pigmented. Meso- and metathorax each divided dorsally into two folds (prodorsal fold small, postdorsal prominent). Pedal folds of thoracic segments prominent, conical, and well isolated. Abdominal segments I-IV of similar size, as large as metathorax. Segments $\mathrm{V}-\mathrm{IX}$ tapering towards posterior body end. Abdominal segments I-VI each divided dorsally into two variously sized folds: prodorsal small, postdorsal folds distinctly larger and much higher than prodorsal folds. Segments VII-IX dorsally undivided. Epipleural folds of segments I-VIII conical. Laterosternal and eusternal folds of segments I-VIII weakly isolated. Abdominal segment $X$ divided into four folds of equal size. Anus situated ventrally, hidden inside ninth segment.

Thoracic and abdominal spiracles unicameral; thoracic spiracles (Figs 21A, 23A) placed laterally close to mesothorax; abdominal spiracles (Figs 21A, 23B, C) placed antero-laterally on segments I-VIII.

Colouration. Light yellow head (Fig. 21B). All thoracic and abdominal segments white (Fig. 21A). Cuticle covered with fine asperities.

Vestiture. Setae on body thin, transparent, different in length (very short or medium).

Head capsule (Figs 21B, 22A). Head suboval, endocarinal line present, reaching to $2 / 3$ length of frons. Frontal sutures on head indistinct, very wide. Two pairs of stemmata in the form of small dark spots (st) placed mediolaterally. Des, short, located medially; des $_{2}$ long; long des $_{3}$ located anteriorly on border of the frontal suture; des $_{4}$ absent; and des $_{5}$ long, located anterolaterally (Fig. 22A).


Figure 21. Rhinusa linariae (Panzer, 1796) mature larva A habitus B head, frontal view.


Figure 22. Rhinusa linariae (Panzer, 1796) mature larva, head and mouth parts $\mathbf{A}$ head $\mathbf{B}$ antenna $\mathbf{C}$ clypeus and labrum (left side), epipharynx (right side) D left mandible E maxillolabial complex (schemes). Abbreviations: at-antenna, lr -labral rods, sa-sensillum ampullaceum, sb-sensillum basiconicum, Se-sensorium, st-stemmata, setae: als-anterolateral, ams-anteromedial, cls-clypeal, des-dorsal epicranial, dms-dorsal malar, fs-frontal epicranial, les-lateral epicranial, ligs-ligular, Irs-labral, mbs-malar basiventral, $m d s$-mandibular dorsal, mpxs-maxillary palp, pes-postepicranial, pfs-palpiferal, pms-postmental, prms-premental,, stps-stipital, ves-ventral, vms-ventral malar.
$F s_{1}$ and $f s_{2}$ minute, located medially; $f s_{3}$ absent; $f s_{4}$ long, located anteriorly; and long $f s_{5}$ located anterolaterally, close to antenna (Fig. 22A). Les ${ }_{1}$ and $l e s_{2}$ medium. Epicranial area with four pes.

Antennae placed distally of the frontal suture, on the inside; membranous and distinctly convex basal article bearing one conical elongate sensorium, plus three sensilla: two basiconica and single ampullacea (Fig. 22B).

Clypeus and labrum (Fig. 22C) completely fused, trapezoidal, $3 \times$ as wide as long, with a single short cls, localised posterolaterally; one sensillum posteromedially and single medium piliform Irs, located medially; anterior border sinuate. Epipharynx (Fig. 22C) with two finger-like als and single piliform ams, all relatively elongated; labral rods (Ir) rounded, placed close to the anterior border.

Mouth parts. Mandibles (Fig. 22D) bifid, cutting edge with small protuberance; two piliform various in size mds, both located, close to lateral border. Maxillolabial complex: maxilla dark sclerotised (Fig. 22E), stipes with one stps, two pfs, and one minute mbs , stps, and both $p f s_{1-2}$ relatively short; mala with four finger-like dms variable in length; three piliform vms, medium to short in length. Maxillary palpi two-segmented; basal palpomere distinctly wider than distal one; length ratio of basal and distal palpomeres almost 1:1; basal palpomere with short mpxs and single sensillum, distal palpomere with a group of five apical sensilla in terminal receptive area. Prementum (Fig. 22E) ovalshaped, with one medium prms; ligula with round margin and single medium ligs; premental sclerite undefined, weakly sclerotised, without posterior extension. Labial palpi one-segmented, vestigial, visible only under great magnification (40x). Each terminal receptive area with a single apical sensilla. Postmentum (Fig. 22E) with only two $p m s$ : $p m s_{1}$ absent medium $p m s_{2}$ located mediolaterally, and relatively short $\mathrm{pms}_{3}$ located anterolaterally; membranous area covered with knobby processes.

Thorax. Prothorax (Fig. 23A) with eigth medium prns, dorsal sclerite weakly visible; two medium ps; and single short eus. Mesothorax (Fig. 23A) with one medium pds; one medium as; two medium and single minute ss; and one short ps. Chaetotaxy of metathorax (Fig. 23A) almost identical to that of mesothorax. Each pedal area of thoracic segments with five various in size pda.

Abdomen. Segments I-VIII (Fig. 23B, C) with one medium pds; one medium ss; one short ps; one short Ists; and one short eus. Abdominal segment IX (Fig. 23C) with one medium ds and two short ps.

Description of pupa (Figs 24A-C, 25A-C). Measurements (in mm). Body length: 1.66-2.66 (avg. 2.10); body width: 1.40-1.93 (avg. 1.60); thorax width: 0.90-1.18 (avg. 1.05); rostrum length: up to 0.66 on both $q$ and ${ }^{1}$.

Body. Integument white, moderately stout slightly curved. Head elongated protuberances (h-pr) present on head above eyes, weakly sclerotised. Rostrum moderately elongated, curved, in male usually only slightly shorter than in female almost $3 \times$ as long as wide, reaching mesocoxae. Pronotum trapezoidal 3 $\times$ as wide as long. Pronotal protuberances ( $p-p r$ ) conical, flattened, indistinct. Meso- and metanotum similar in size. Abdominal segments I-III almost identical in size; segments IV-VII tapering gradually, segment VIII narrow; segment IX reduced. Abdominal segment VIII dorsally with very small, rounded, weakly sclerotised abdominal protuberance (a-pr). Urogomphi (ur) very short, ending with sclerotised, sharp apexes (Fig. 24A-C).


Figure 23. Rhinusa linariae (Panzer, 1796) mature larva, habitus $\mathbf{A}$ lateral view of thoracic segments $\mathbf{B}$ lateral view of abdominal segment I C lateral view of abdominal segments VII-X (schemes). Abbreviations: Th. 1-3-number of thoracic segments, Abd. 1-10-number of abdominal seg, setae: as-alar, ds-dorsal, eus-eusternal, Ists-laterosternal, pda-pedal, pds-postdorsal, prns-pronotal, ss-spiracular, ps-pleural.


Figure 24. Rhinusa linariae (Panzer, 1796) pupa habitus $\mathbf{A}$ ventral view $\mathbf{B}$ lateral view $\mathbf{C}$ dorsal view.

Chaetotaxy. Well developed, setae variable in length, transparent. Head with one short os and short pas. Rostrum with a single short rs (Fig. 25A). Pronotum with two as, two Is, and three elongated, equal-in-length pls. Dorsal parts of meso- and metathorax with a single medium-length seta, placed medially.


Figure 25. Rhinusa linariae (Panzer, 1796) pupa habitus $\mathbf{A}$ ventral view $\mathbf{B}$ dorsal view $\mathbf{C}$ lateral view (schemes). Abbreviations: $\mathrm{a}-\mathrm{pr}$-abdominal protuberances, h - pr -head protuberances, p - pr -pronotal protuberances, ur-urogomphi, setae: as-apical, $d$-dorsal, fes-femoral, $l$, ls-lateral, os-orbital, pas-postantennal, pls-posterolateral, rs-rostral, $v$-ventral.

Apex of femora with a single long fes (Fig. 25A-C). Abdominal segments I-VII with two, equal-in-length setae dorsally: first placed posteromedially, second posterolaterally. Abdominal segment VIII with a single elongated seta medially. Each lateral part of abdominal segments I-VII with a single short seta. Ventral parts of abdominal segments I-VIII with two short setae. Abdominal segment IX with two short setae ventrally (Fig. 25A-C).

Remarks and comparative notes. This species is widely distributed in all of Europe, Turkey, Kazakhstan, and western Siberia (Alonso-Zarazaga et al. 2023). It was introduced in North America, where it was approved for release for biological control of invasive toadflaxes (Linaria spp.) in Canada in 1995 and 1996 (Sing et al. 2016). Afterwards, a population was established at sites in British Columbia and Colorado (Sing et al. 2016; DiGirolomo et al. 2019). In Europe, the adults of this species are distinguishable from all the other species of Rhinusa by the shape of the rostrum, which is strongly curved in lateral view, and the shape of the tibiae, with the uncus of the metatibiae of the same length in both sexes and with the outer margin distinctly curved outwards apically (Caldara and Toševski 2019).

Biological notes. Rhinusa linariae is a univoltine root galling weevil. Gall induction and larval development are mainly recorded on Linaria vulgaris and rarely on L. genistifolia in Southeastern Europe. Adults emerge in early spring, feed, and copulate on top of the young toadflax shoots. During oviposition, females glue eggs onto toadflax roots or, rarely, below root crowns with oviposition fluid. Eggs are laid singly or in small groups. Shortly after, oviposition triggers cell proliferation, which entwists the egg, forming a round gall. Larvae feed on galled root tissue through three instars. Pupation occurs in galls, while new adults emerge in mid- to late summer or rarely stay inside galls during winter, overwintering in soil or in plant litter close to their host plant. Twenty-five years ago, $R$. linariae was introduced as a biological control agent for invasive toadflaxes in Canada and the USA, where it was recently confirmed as established only in British Columbia. However, the current populations are still too small to have a significant biological impact (Sing et al. 2016; DiGirolomo et al. 2019).

## Rhinusa pilosa group

Adult diagnosis. Dorsal vestiture composed of very long seta-like scales, 20$40 \times$ longer than wide; rostrum in lateral view strongly curved; eyes strongly convex; uncus of metatibiae well developed in both sexes; body of spermatheca globose at apex.

## 6) Rhinusa pilosa (Gyllenhal, 1838)

Material examined. 4 mature larvae; 3 § and 5 p pupae. Serbia, Zemun, ex Linaria vulgaris galls, 01.06.2018, leg., det. I. Toševski.

Description of mature larva (Figs 26A, B, 27A-E, 28A-C). Measurements (in mm ). Body length: 4.00-5.75 (avg. 4.25). The widest place in the body (mesoand metathorax) measures up to 1.50. Head width: 0.60-0.68 (avg. 0.65).

General. Body elongate, slightly curved, rounded in cross section (Fig. 26A). Prothorax slightly smaller than mesothorax, pronotal shield not pigmented. Meso- and metathorax equal in size; each divided dorsally into two folds


Figure 26. Rhinusa pilosa (Gyllenhal, 1838) mature larva A habitus B head, frontal view.
(prodorsal fold distinctly smaller than postdorsal fold); postdorsal fold of metathorax conical. Pedal folds of thoracic segments isolated, prominent. Abdominal segments I-VI of similar size, next segments tapering towards posterior body end. Abdominal segments I-VII each divided dorsally into two folds of almost identical size; postdorsal folds of segments I-VI higher than prodorsal folds. Segments VIII and IX dorsally undivided. Epipleural folds of segments I-VIII conical. Laterosternal and eusternal folds of segments I-VIII weakly isolated. Abdominal segment $X$ divided into four folds of equal size. Anus situated ventrally, almost completely covered with the ninth abdominal segment.

All spiracles unicameral; thoracic spiracles (Fig. 26A) placed laterally close to mesothorax; abdominal spiracles (Fig. 26A) placed anteromedially on segments I-VIII.

Colouration. Light yellow to dark yellow head, medial parts of epicranium less sclerotised (Fig. 26B). All thoracic and abdominal segments whitish (Fig. 26A). Cuticle covered with asperities.

Vestiture. Setae on body thin, transparent, different in length (very short or medium).

Head capsule (Figs 26B, 27A). Head wide, endocarinal line present, reaching to $2 / 3$ length of frons. Frontal sutures on head indistinct, very wide. Single pair of stemmata in the form of small black spots (st) close to the end of the frontal suture. Des, short, located in middle part of epicranium; medium des $_{2}$; long des ${ }_{3}$ located anteriorly on epicranium close to the border with the frontal suture; $\mathrm{des}_{4}$ minute; and des $_{5}$ long, located anterolaterally above stemma (Fig. 27A). Fs, and $f s_{2}$ absent; $f s_{3}$ minute; $f s_{4}$ medium, located anteriorly; and long $f s_{5}$ located anterolaterally, close to antenna (Fig. 27A). Les ${ }_{1}$ and les ${ }_{2}$ medium; single short ves. Epicranial area with a single pes.

Antennae placed distally of the frontal suture, on the inside; membranous and distinctly convex basal article bearing one conical relatively short sensorium, plus three sensilla basiconica (Fig. 27B).

Clypeus and labrum (Fig. 27C) completely fused, trapezoidal, $3 \times$ as wide as long, with two short c/s, localised posteriorly three medium piliform Irs, located


Figure 27. Rhinusa pilosa (Gyllenhal, 1838) mature larva, head and mouth parts A head B antenna C clypeus and labrum (left side), epipharynx (right side) D left mandible E maxillolabial complex (schemes). Abbreviations: at-antenna, Ir-labral rods, sb-sensillum basiconicum, Se-sensorium, st-stemmata, setae: als-anterolateral, ams-anteromedial, cls-clypeal, des-dorsal epicranial, dms-dorsal malar, fs-frontal epicranial, les-lateral epicranial, ligs-ligular, Irs-labral, mbs-malar basiventral, mds-mandibular dorsal, mpxs-maxillary palp, pes-postepicranial, pfs-palpiferal, pms-postmental, prms-premental, stps-stipital, ves-ventral, vms-ventral malar.
anteromedially. Epipharynx (Fig. 27C) with two finger-like elongated als; and two piliform ams, variable in length; labral rods (Ir) indistinct, close to ovalshape; anterior border almost straight.

Mouth parts. Mandibles (Fig. 27D) bifid, cutting edge with blunt additional teeth; two short piliform mds, close to lateral border. Maxillolabial complex: maxilla more sclerotised than labium (Fig. 27E) stipes with one stps, two pfs and one very short $m b s$ and one sensillum, stps and both $p f s_{1-2}$ relatively short; mala with four finger-like dms variable in length; four piliform vms, medium to short in length. Maxillary palpi two-segmented; basal palpomere distinctly wider than distal one; length ratio of basal and distal palpomeres almost 1:2; basal palpomere with short mpxs and two sensilla, distal palpomere with a group of five apical sensilla in terminal receptive area. Prementum (Fig. 27E) oval-shaped, with one short prms; ligula with round margin and two minute ligs; premental sclerite vestigial, only lateral parts highly sclerotised, posterior extension absent. Labial palpi one-segmented; palpi very small, with a single pore, and a group of three or four apical sensilla (ampullacea) on terminal receptive area; surface of labium smooth. Postmentum (Fig. 27E) with three pms, short $p m s_{1}$ located posteromedially, medium $\mathrm{pms}_{2}$ located mediolaterally, and short $p m s_{3}$ located anterolaterally; membranous area smooth.

Thorax. Prothorax (Fig. 28A) with seven elongated to medium prns; two medium ps; and single short eus. Mesothorax (Fig. 28A) without prs; with two medium pds; one medium as; three ss (two medium and one short); one me-


A


B

0.2 mm

Figure 28. Rhinusa pilosa (Gyllenhal, 1838) mature larva, habitus $\mathbf{A}$ lateral view of thoracic segments $\mathbf{B}$ lateral view of abdominal segment I C lateral view of abdominal segments VII-X (schemes). Abbreviations: Th. 1-3-number of thoracic segments, Abd. 1-10-number of abdominal seg, setae: as-alar, ds-dorsal, eps-epipleural, eus-eusternal, Ists-laterosternal, pda-pedal, pds-postdorsal, prns-pronotal, ss-spiracular, ps-pleural, sts-sternal.
dium eps; one medium ps; and single minute eus. Chaetotaxy of metathorax (Fig. 28A) almost identical to that of mesothorax. Each pedal area of thoracic segments with five pda of various length.

Abdomen. Segments I-VIII (Fig. 28B, C) without prs; with two medium pds; one minute and one medium ss; one medium eps; one medium $p s$; one short Ists; and two minute eus. Abdominal segment IX (Fig. 28C) with two minute ds; one minute $p s$; and two minute sts.

Description of pupa (Figs 29A-C, 30A-C). Measurements (in mm). Body length: 2.86-3.75 (avg. 3.25); body width: 1.90-2.25 (avg. 2.00); thorax width:


Body. Integument white, with some parts dark sclerotised; moderately elongated, curved. Head protuberances ( $\mathrm{h}-\mathrm{pr}$ ) elongated. Rostrum rather stout, on both sexes almost $2.3 \times$ as long as wide, extended only to procoxae. Pronotum trapezoidal $3 \times$ as wide as long. Pronotal protuberances ( $\mathrm{p}-\mathrm{pr}$ ) absent. Mesoand metanotum similar in size. Abdominal segments I-VI almost identical in size; segment VII semicircular; segment VIII narrow; segment IX reduced. Abdominal protuberances (a-pr) absent. Urogomphi (ur) medium-sized, ending with sclerotised, sharp apexes (Fig. 29A-C).

Chaetotaxy. Well developed, setae minute to elongated. Minute and medium setae transparent, elongated setae basally brown, apically transparent. Head with one minute os (Fig. 30A). Rostrum with a single minute pas. Pronotum with three as, single l , and two pls; all pronotal setae almost equally in length, prominent, basally brownish, apically transparent. Dorsal parts of meso- and metathorax with two identical in length setae, placed medially. Setae of mesothorax as long as those on pronotum. Apex of femora with a single long fes (Fig. 30A-C). Abdominal segments I-VI with three setae: first and second minute placed anteromedially, third medium placed below stigma. Abdominal segments VII with three elongated setae dorsally and segment VIII with two elongated setae dorsally. Each lateral part of abdominal segments I-VII with a single medium seta. Ventral parts of abdominal segments I-VIII with two minute setae. Abdominal segment IX with two minute setae ventrally (Fig. 30A-C).


Figure 29. Rhinusa pilosa (Gyllenhal, 1838) pupa habitus A ventral view B lateral view C dorsal view.


Figure 30. Rhinusa pilosa (Gyllenhal, 1838) pupa habitus A ventral view B dorsal view C lateral view (schemes). Abbreviations: h-pr-head protuberances, ur-urogomphi, setae: as-apical, d-dorsal, fes-femoral, I, Is-lateral, os-orbital, paspostantennal, pls-posterolateral, $v$-ventral.

Remarks and comparative notes. This species is distributed in northern and central Europe and in the Balkans (Alonso-Zarazaga et al. 2023). It is distinguishable from other species of the $R$. pilosa group by the rostrum being markedly bent at the level of antennal insertion in both sexes. It is a unique species in the group in being distributed northwards in the western Palaearctic, associated only with L. vulgaris as a host plant. All three species of this group differ from the other species of Rhinusa by the very long, hair-like scales of the dorsal vestiture.

Biological notes. Rhinusa pilosa is a shoot-galling weevil associated with $L$. vulgaris for larval development. Adults become active in early spring, and their appearance after winter hibernation coincides with the intensive shoot growth of their host plant. Females oviposit in the upper part of the young, growing shoots of $L$. vulgaris. Females oviposit three to six eggs, but the number of ovipositions has been observed to exceed 17 per shoot. Oviposition provokes the induction of a globose or elyptical gall on the apical part of the stem. Larvae feed and complete development within the induced galls. Pupation is also completed within the gall. Eclosed adults intensively feed on gall tissue, after which they leave the gall and enter into summer aestivation within the soil litter or soil cracks. In late autumn, adults are briefly active, feeding on young L. vulgaris shoots before entering diapause, sheltering close to the host plant. The biology of $R$. pilosa is described in detail by Gassmann et al. (2014).

## 7) Rhinusa rara Toševski \& Caldara, 2015

Material examined. 2 mature larvae, $26.04 .2014 ; 1$ and 3 ? pupae, 10.05.2014; 8 mature larvae; $2 \delta^{1}$ and 2 p pupae, 12.05.2014, ex Linaria dalmatica, Serbia, Staničenje, Pirot, leg., det. I. Toševski.

Description of mature larva (Figs 31A, B, 32A-E, 33A-C). Measurements (in mm ). Body length: $3.00-4.25$ (avg. 3.60). The widest place in the body (mesoand metathorax) measures up to 1.25 . Head width: $0.55-0.60$ (avg. 0.56).

General. Body elongate, slender, distinctly curved, rounded in cross section (Fig. 31A). All thoracic segments almost equal in size. Meso- and metathorax each divided dorsally into two folds (prodorsal fold distinctly smaller than postdorsal fold). Pedal folds of thoracic segments isolated, conical, prominent. Abdominal segments I-VI of similar size, next segments tapering towards posterior body end. Abdominal segments I-VII each divided dorsally into two folds: prodorsal fold slightly smaller than postdorsal, which form conical, prominent protuberances apically. Segments VIII and IX dorsally undivided. Epipleural folds of segments I-VIII conical. Laterosternal and eusternal folds of segments I-VIII conical, weakly isolated. Abdominal segment X (almost completely hidden in previous segment) divided into four folds of equal size. Anus situated ventrally.

All spiracles unicameral; thoracic spiracles (Fig. 31A) placed laterally close to mesothorax; abdominal spiracles (Fig. 31A) placed medio-laterally on segments I-VIII.

Colouration. Light yellow to yellow head, medial parts of epicranium less sclerotised (Fig. 31B). All thoracic and abdominal segments white (Fig. 31A). Cuticle covered with asperities.

Vestiture. Setae on body thin, yellowish, different in length (very short or medium).


Figure 31. Rhinusa rara Toševski \& Caldara, 2015 mature larva A habitus B head, frontal view.

Head capsule (Figs 31B, 32A). Head wide, endocarinal line present, reaching to $2 / 3$ length of frons. Frontal sutures on head very wide, indistinct. Single pair of stemmata in the form of small black spots (st) laterally to the end of the frontal suture. Des, short; des $_{2}$ short, located in lateral part of epicranium; long $\mathrm{des}_{3}$ located anteriorly on epicranium on border of the frontal suture; $\mathrm{des}_{4}$ absent; and des $_{5}$ long, located anterolaterally above stemma (Fig. 32A). Fs ${ }_{1}$ and $f s_{2}$ absent; $f s_{3}$ minute, located medially; $f s_{4}$ long, located anteriorly; and long $f s_{5}$ located anterolaterally, close to antenna (Fig. 32A). $L e s_{1}$ and $l e s_{2}$ medium. Epicranial area with a single pes.

Antennae placed distally of the frontal suture, on the inside; membranous and distinctly convex basal article bearing one conical elongate sensorium, plus five sensilla styloconica (Fig. 32B).

Clypeus and labrum (Fig. 32C) completely fused, trapezoidal, $2.7 \times$ as wide as long, with two minute cls, localised posterolaterally; three piliform Irs, various long; $I r s_{1}$ and $I r s_{2}$ medium, located anteromedially, and $/ r s_{3}$ short, located laterally; anterior border almost straight. Epipharynx (Fig. 32C) with two finger-like als, variable in length and two ams variable in length; labral rods (lr) indistinct, rounded; anterior border sinuate.

Mouth parts. Mandibles (Fig. 32D) bifid, cutting edge with additional protuberance; two medium piliform mds, both located close to lateral border. Maxillolabial complex: maxilla more sclerotised than labium (Fig. 32E) stipes with one stps, two pfs and one very short mbs, stps and both $p f s_{1-2}$ relatively short; mala with four piliform dms variable in length; two short piliform vms. Maxillary palpi two-segmented; basal palpomere distinctly wider and slightly longer than distal one; basal palpomere with short mpxs and single sensillum, distal palpomere with a group of four or five apical sensilla in terminal receptive area. Prementum (Fig. 32E) close to oval-shaped, with one short prms; ligula with slightly sinuate margin and three minute ligs; premental sclerite sclerotised U-shaped. Labial palpi one-segmented; each palp with a single pore, and a group of three or four apical sensilla (ampullacea) on terminal receptive area; surface of labium smooth. Postmentum (Fig. 32E) with only two pms, medium


Figure 32. Rhinusa rara Toševski \& Caldara, 2015 mature larva, head and mouth parts $\mathbf{A}$ head $\mathbf{B}$ antenna $\mathbf{C}$ clypeus and labrum (left side), epipharynx (right side) D left mandible E maxillolabial complex (schemes). Abbreviations: at-antenna, lr -labral rods, st-sensillum styloconicum, Se-sensorium, st-stemmata, setae: als-anterolateral, ams-anteromedial, cls-clypeal, des-dorsal epicranial, dms-dorsal malar, fs-frontal epicranial, les-lateral epicranial, ligs-ligular, lrs-labral, mbs-malar basiventral, mds-mandibular dorsal, mpxs-maxillary palp, pes-postepicranial, pfs-palpiferal, pms-postmental, prms-premental, stps-stipital, vms-ventral malar.


Figure 33. Rhinusa rara Toševski, Caldara, 2015 mature larva, habitus A lateral view of thoracic segments $\mathbf{B}$ lateral view of abdominal segment I C lateral view of abdominal segments VII-X (schemes). Abbreviations: Th. 1-3-number of thoracic segments, Abd. 1-10-number of abdominal seg, setae: ds-dorsal, eps-epipleural, pda-pedal, pds-postdorsal, prns-pronotal, prs-prodorsal, ss-spiracular, ps-pleural, sts-sternal.
pms, located medially and short $p m s_{2}$ located laterally, $p m s_{3}$ absent; membranous area smooth.

Thorax. Only pronotal and single pedal setae elongated, rest of thoracic minute, feebly visible. Prothorax (Fig. 33A) with four prns and two ps. Mesothorax (Fig. 33A) with one prs, three pds; three ss; one eps and one ps. Chaetotaxy of metathorax (Fig. 33A) almost identical to that of mesothorax. Each pedal area of thoracic segments with three minute and one elongated $p d a$.

Abdomen. All abdominal setae minute, feebly visible. Segments I-VIII (Fig. 33B, C) with one prs; three pds; one ss; one eps; one ps and one lsts. Abdominal segment IX (Fig. 33C) with a single ds, single ps, and single sts.

Description of pupa (Figs 34A-C, 35A-C). Measurements (in mm). Body length: 3.35-3.85 (avg. 3.75); body width: 1.60-2.10 (avg. 1.75); thorax width: 1.05-1.30 (avg. 1.20); rostrum length: up to 1.50 for both sexes.

Body. Integument white, moderately elongated, curved. Head protuberances (h-pr) above eyes present. Rostrum rather short, in male usually only slightly shorter than in female almost $2.5 \times$ as long as wide, reaching mesocoxae. Pronotum trapezoidal $2 \times$ as wide as long. Pronotal protuberances ( $\mathrm{p}-\mathrm{pr}$ ) absent. Meso- and metanotum similar in size. Abdominal segments I-VI almost identical in size; segment VII semicircular; segment VIII narrow; segment IX reduced. Urogomphi (ur) short, ending with sclerotised, sharp apexes (Fig. 34A-C).

Chaetotaxy. Well developed, setae short to elongated, short setae transparent, elongated brown. Head and rostrum without seta (Fig. 35A). Pronotum


Figure 34. Rhinusa rara Toševski \& Caldara, 2015 pupa habitus $\mathbf{A}$ ventral view $\mathbf{B}$ lateral view $\mathbf{C}$ dorsal view.
with three as, and three pls almost equally in length. Dorsal parts of meso- and metathorax with two setae of similar length, placed medially. Apex of femora with a single long fes (Fig. 35A-C). Abdominal segments I-VI with four short setae dorsally, all placed close to posterior margin. Abdominal segment VII with three elongated setae dorsally. Abdominal segment VIII with two elongated setae dorsally. Each lateral part of abdominal segments I-VII with a single short seta. Ventral parts of abdominal segments I-VIII with two short setae. Abdominal segment IX with two short setae ventrally (Fig. 35A-C).

Remarks and comparative notes. This species is very restricted in its distribution and scarce. It is known only from calcareous regions in Serbia (Sićevo Gorge between the towns of Niš and Pirot), Hungary (Balaton), southern Slovakia (Šturovo), southern Czechia (Znojmo), Austria (Wien) and southern Russia (Toševski et al. 2015). It differs from the other European species of the R. pilosa group in its evenly curved rostrum in lateral view in both sexes (vs. abruptly narrowed and bent along the dorsal margin), almost flat pronotum and elytra (vs. moderately convex), and integument of adults covered with recumbent hair-like scales (vs. suberect hair-like scales).

Biological notes. The biology of $R$. rara is similar to that of $R$. pilosa. The adults become active in the field very early, often in mid-February. The adults are hidden inside the rosette of the host plant, L. genistifolia or L. dalmatica. The females oviposit at the base of young, growing shoots. Induced galls are usually large, partly hidden below the soil surface. Usually, ~ 10 eggs are laid per shoot, but some shoots can be used for 20 or more ovipositions. The biology of $R$. rara is described in detail by Toševski et al. (2015).

## Rhinusa herbarum group

Adult diagnosis. Rostrum in lateral view straight; elytra rectangular and only slightly wider than pronotum; third tarsomere weakly bilobed and slightly wider than second tarsomere; femora unarmed; body of penis short and in lateral view with sides distinctly widening in apical part.


Figure 35. Rhinusa rara Toševski \& Caldara, 2015 pupa habitus $\mathbf{A}$ ventral view $\mathbf{B}$ dorsal view $\mathbf{C}$ lateral view (schemes). Abbreviations: h -pr-head protuberances, ur-urogomphi, setae: as-apical, $d$-dorsal, fes-femoral, $l$-lateral, $p l s$-posterolateral, $v$-ventral.

## 8) Rhinusa herbarum (H. Brisout de Barneville, 1862)

Material examined. 20 mature larvae; $6 \sigma^{\star}$ and $6 q$ pupae. Serbia, Sredrievo, ex Kickxia elatine (L.) Dumort., 15.08.2017, leg., det. I. Toševski.

Description of mature larva (Figs 36A, B, 37A-E, 38A-C). Measurements (in mm ). Body length: 2.50-4.00 (avg. 3.40). The widest place in the body (mesoand metathorax) measures up to 1.50 . Head width: 0.50-0.55 (avg. 0.55).

General. Body elongate, slender, strongly curved, rounded in cross section (Fig. 36A). All thoracic segments equal in size. Meso- and metathorax each divided dorsally into two folds (prodorsal fold vestigial, postdorsal fold prominent). Pedal folds of thoracic segments well isolated. Abdominal segments I-V of similar size, next segments tapering towards posterior body end. Abdominal segments I-VII each divided dorsally into two folds almost identical in size. Segments VIII and IX dorsally undivided. Epipleural folds of segments I-VIII conical well developed. Laterosternal and eusternal folds of segments I-VIII conical, well isolated. Abdominal segment $X$ divided into four folds of equal size. Anus situated ventrally, almost completely hidden in the ninth segment.

Thoracic and abdominal spiracles unicameral; thoracic spiracles (Fig. 36A) placed laterally close to mesothorax; abdominal spiracles (Fig. 36A) placed medially on segments I-VIII.

Colouration. Almost white to light yellow head (Fig. 36B). All thoracic and abdominal segments whitish (Fig. 36A). Cuticle covered with asperities.

Vestiture. Setae on body thin, transparent, different in length (minute to medium).

Head capsule (Figs 36B, 37A). Head suboval, endocarinal line present, reaching to $2 / 3$ length of frons. Frontal sutures on head indistinct, very wide. Single pair of stemmata in the form of small black spots (st) placed laterally, close to the end of the frontal suture. Des $\boldsymbol{p}_{1}$ short, located in middle part of epicranium; long $\mathrm{des}_{2}$ located anteriorly; long $\mathrm{des}_{3}$ placed almost on the border of the frontal suture; minute des $_{4}$, located laterally; and long $\mathrm{des}_{5}$ placed anterolaterally above stemma (Fig. 37A). Fs ${ }_{1}$ absent; $f s_{2}$ short, located posterolaterally; $f s_{3}$ absent; $f s_{4}$


Figure 36. Rhinusa herbarum (H. Brisout de Barneville, 1862) mature larva A habitus B head, frontal view.


Figure 37. Rhinusa herbarum (H. Brisout de Barneville, 1862) mature larva, head and mouth parts A head B antenna $\mathbf{C}$ clypeus and labrum (left side), epipharynx (right side) D left mandible $\mathbf{E}$ maxillolabial complex (schemes). Abbreviations: at-antenna, Ir-labral rods, sb-sensillum basiconicum, Se-sensorium, st-stemmata, setae: als-anterolateral, ams-anteromedial, cls-clypeal, des-dorsal epicranial, dms-dorsal malar, fs-frontal epicranial, les-lateral epicranial, ligs-ligular, Irs-labral, mbs-malar basiventral, mds-mandibular dorsal, mpxs-maxillary palp, pes-postepicranial, pfs-palpiferal, pms-postmental, prms-premental, stps-stipital, ves-ventral, vms-ventral malar.
long, located anteriorly; and long $f s_{5}$ located anterolaterally, close to antenna (Fig. 37A). Les ${ }_{1}$ and les ${ }_{2}$ medium; two short ves. Epicranial area with five pes.

Antennae placed distally of the frontal suture, on the inside; membranous and distinctly convex basal article bearing one conical elongate sensorium, plus three sensilla basiconica (Fig. 37B).

Clypeus (Fig. 37C) trapezoidal, $\sim 2.5 \times$ as wide as long with two short cls, localised posterolaterally, with one sensillum between them; anterior part distinctly less sclerotised than the basal part and slightly rounded towards the inside.

Mouth parts. Labrum (Fig. 37C) ~ $2.2 \times$ as wide as long, with three piliform Irs, various long; $I r s_{1}$ and $I r s_{2}$ elongated, located medially on small protuberances, and $/ \mathrm{Ir}_{3}$ medium, located anterolaterally; anterior border bi-sinuate. Epipharynx (Fig. 37C) with two elongated finger-like als, identical in length and three piliform ams variable in length; labral rods (lr) distinct, rounded. Mandibles (Fig. 37D) bifid, cutting edge straight; two medium piliform and short mds, both located close to lateral border. Maxillolabial complex: maxilla brownish sclerotised (Fig. 37E), stipes with one stps, two pfs and one mbs, stps and both $p f s_{1-2}$ elongated; mala with five finger-like $d m s$ variable in length; four medium piliform vms. Maxillary palpi two-segmented; basal palpomere distinctly wider than distal one, with short mpxs and two sensilla, distal palpomere with a group of two apical sensilla in terminal receptive area. Prementum (Fig. 37E) close to oval-shaped, with two prms variable in length; ligula with slightly sinuate margin and two short ligs; premental sclerite broad, sclerotised, cup-shaped, posterior extension medium, with thick apex. Labial palpi one-segmented; palpi with a single pore, and single, apical sensilla in terminal receptive area; surface of labium smooth. Postmentum (Fig. 37E) with three pms, short pms ${ }_{1}$ located posteromedially, long $\mathrm{pms}_{2}$ located mediolaterally, and short $\mathrm{pms}_{3}$ located anterolaterally; membranous area partially covered with knobby asperities.

Thorax. Prothorax (Fig. 38A) with nine medium to short prns; two medium ps; and single short eus. Mesothorax (Fig. 38A) with a single minute prs; three medium pds; one medium as; three minute ss; one medium eps; one medium $p s$; and single minute eus. Chaetotaxy of metathorax (Fig. 38A) almost identical to that of mesothorax. Each pedal area of thoracic segments with four short to minute pda.

Abdomen. Segments I-VIII (Fig. 38B, C) without prs; with four pds of various length; one minute and one medium ss; single, medium eps; one medium ps; one minute Ists; and two minute eus. Abdominal segment IX (Fig. 38C) with one medium and one minute $d s$; one minute $p s$; and two minute sts.

Description of pupa (Figs 39A-C, 40A-C). Measurements (in mm). Body length: 2.25-3.10; body width: 1.50-1.80; thorax width: 0.70-1.05; rostrum length: up to 0.70 § and 1.20 \&

Body. Integument white moderately elongated. Head and pronotum without protuberances. Rostrum rather short, reaching to mesocoxae; in both sexes $2.2 \times$ as long as wide. Clubs covered with knobby protuberances. Pronotum trapezoidal, $2 \times$ as wide as long. Meso- and metanotum similar in size. Abdominal segments I-IV almost identical in size; segments VI and VI tapering gradually, VII semicircular; segment VIII narrow; segment IX reduced. Abdominal segments VII and VIII each with semicircular, weakly sclerotised abdominal protuberances ( $\mathrm{a}-\mathrm{pr}_{1,2}$ ). Urogomphi absent (Fig. 39A-C).

Chaetotaxy. Well-developed setae, elongated to short, transparent. Head with a single short sos, single short os. Rostrum with a single short rs (Fig. 40A).

0.2 mm

Figure 38. Rhinusa herbarum (H. Brisout de Barneville, 1862) mature larva, habitus A lateral view of thoracic segments B lateral view of abdominal segment I C lateral view of abdominal segments VII-X (schemes). Abbreviations: Th. 1-3number of thoracic segments, Abd. 1-10-number of abdominal seg, setae: as-alar, ds-dorsal, eps-epipleural, eus-eusternal, Ists-laterosternal, pda-pedal, pds-postdorsal, prns-pronotal, prs-prodorsal, ss-spiracular, ps-pleural, sts-sternal.


Figure 39. Rhinusa herbarum (H. Brisout de Barneville, 1862) pupa habitus A ventral view B lateral view C dorsal view.

Pronotum with three as, single $l s$, single ds and three pls; all pronotal setae elongated, equal in length. Dorsal parts of meso- and metathorax with two medium setae, placed medially (Fig. 40A-C). Abdominal segments I-VIII dorsally with three short setae dorsally, placed close to posterior margin of the segments. Each lateral part of abdominal segments I-VIII with a single short seta.


Figure 40. Rhinusa herbarum (H. Brisout de Barneville, 1862) pupa habitus A ventral view B dorsal view C lateral view (schemes). Abbreviations: a-pr-abdominal protuberances, $\mathrm{h}-\mathrm{pr}$-head protuberances, setae: as-apical, $d$-dorsal, ds-discal, I, Is-lateral, os-orbital, pls-posterolateral, rs-rostral, sos- supraorbital, v-ventral.

Ventral parts of abdominal segments I-VIII with two short setae. Abdominal segment IX with two short setae ventrally (Fig. 40A-C).

Remarks and comparative notes. This species is distributed in Central and Southern Europe and in North Africa (Alonso-Zarazaga et al. 2023). The shape of the rostrum in adults is similar in lateral view to that of some species of the R. antirrhini group but not in dorsal view, where the basal half in cross section is normally rectangular and not trapezoidal, and the scrobes are only slightly visible (Caldara and Toševski 2019).

Biological notes. The host plants are Kickxia elatine and K. spuria (L.) Dumort. The females oviposit in the seed capsules of the host plant during the summer, following the phenology of plant flowering. Larvae complete their development and pupate inside seed capsules. The new adults emerge in late summer (Caldara and Toševski 2019).

## Rhinusa neta group

Adult diagnosis. Femora with a sharp tooth, which is more robust on metafemora; both body and apophysis of penis markedly long, taken together corresponding to length of whole abdomen; endophallus lacking inside body of penis and beginning from its base, with a long straight flagellum.

## 9) Rhinusa collina (Gyllenhal, 1813)

Material examined. 8 mature larvae; 3 万 and $3 q$ pupae. Serbia, Knjaževac, ex Linaria vulgaris inside $R$. linariae galls, 05.07.2017, leg., det. I. Toševski.

Description of mature larva (Figs 41A, B, 42A-E, 43A-C). Measurements (in mm ). Body length: 2.60-3.00 (avg. 2.75). The widest place in the body (mesoand metathorax) measures up to 0.90 . Head width: $0.55-0.65$ (avg. 0.60 ).

General. Body elongate, slender, distinctly curved, rounded in cross section (Fig. 41A). Prothorax prominent, pronotal shield not pigmented. Meso- and


Figure 41. Rhinusa collina (Gyllenhal, 1813) mature larva A habitus B head, frontal view.
metathorax equal in size, smaller than prothorax; each divided dorsally into two folds (prodorsal fold distinctly smaller than postdorsal fold). Pedal folds of thoracic segments isolated, conical, prominent. Abdominal segments I-VI of similar size, next segments tapering towards posterior body end. Abdominal segments I-VII each divided dorsally into two various in size folds; postdorsal folds much higher than prodorsal folds. Segments VIII and IX dorsally undivided. Epipleural folds of segments I-VII conical. Laterosternal and eusternal folds of segments IVIII conical, weakly isolated. Abdominal segment $X$ divided into four folds of equal size. Anus situated ventrally, almost completely hidden in previous segment.

Thoracic and all abdominal spiracles unicameral; thoracic spiracles (Fig. 41A) placed ventrolaterally; abdominal spiracles (Fig. 41A) placed anteromedially on segments I-VIII.

Colouration. Dark yellow to light brown head, medial parts of epicranium less sclerotised (Fig. 41B). Frons and ventrolateral parts of the head covered with knobby asperities. All thoracic and abdominal segments whitish. Cuticle covered with fine asperities (Fig. 41A).

Vestiture. Setae on body thin, yellowish, different in length (minute to medium).
Head capsule (Figs 41B, 42A). Head suboval, endocarinal line present, reaching to $3 / 4$ length of frons. Frontal sutures on head distinct, very wide. Two pairs of stemmata various in size in the form of small black spots (st); first medium size located close to end of frontal suture, second small placed mediolaterally. Des ${ }_{1}$ long, located in middle part of epicranium; long des ${ }_{2}$; long des ${ }_{3}$ located anteriorly on epicranium close to the border with the frontal suture; des ${ }_{4}$ very short; and $_{\text {es }}^{5} 5$ elongated, located anterolaterally above stemma (Fig. 42A). Fs ${ }_{1}$ and $f s_{2}$ absent; $f s_{3}$ minute, located medially; $f s_{4}$ long, located anteriorly; and long $f s_{5}$ located anterolaterally, close to antenna (Fig. 42A). Les ${ }_{1}$ and $l e s_{2}$ medium; and two minute ves. Epicranial area with two pes.

Antennae placed distally of the frontal suture, on the inside; membranous and distinctly convex basal article bearing one conical elongate sensorium, plus three sensilla basiconica and single ampullacea (Fig. 42B).

Clypeus (Fig. 42C) trapezoidal, $\sim 2.7 \times$ as wide as long with two cls: cls, relatively long, $\mathrm{cls}_{2}$ medium, both localised posterolaterally, with one sensillum between them; basal part distinctly more sclerotised than the apical part; anterior border slightly curved towards the inside.

Mouth parts. Labrum (Fig. 42C) $\sim 2 \times$ as wide as long, with three piliform Irs, various length; $I r s_{1}$ elongated, located posteromedially, $\operatorname{Irs}{ }_{2}$ elongated, located medially, and $/ \mathrm{rs}_{3}$ short, located anterolaterally; anterior border bi-sinuate. Epipharynx (Fig. 42C) with two elongated finger-like als, almost identical in length; two piliform ams equally in length; and single finger-like mes; labral rods (Ir) distinct, close to kidney shape. Mandibles (Fig. 42D) bifid, cutting edge with a single, blunt protuberance; two medium piliform and single minute mds, all located close to lateral border. Maxillolabial complex: maxilla dark sclerotised (Fig. 42E), stipes with one stps, two pfs and one mbs and one sensillum, stps and both $\mathrm{pfs}_{1-2}$ relatively long; mala with five finger-like $d m s$ variable in length (divided into two groups); four piliform vms, medium to short in length. Maxillary palpi two-segmented; basal palpomere distinctly wider than distal one; length ratio of basal and distal palpomeres almost 1:1; basal palpomere with short mpxs and two sensilla, distal palpomere with a group of three or four apical sensilla in terminal receptive area. Prementum (Fig. 42E) oval-shaped, with


Figure 42. Rhinusa collina (Gyllenhal, 1813) mature larva, head and mouth parts $\mathbf{A}$ head $\mathbf{B}$ antenna $\mathbf{C}$ clypeus and labrum (left side), epipharynx (right side) D left mandible E maxillolabial complex (schemes). Abbreviations: at-antenna, Ir-labral rods, sa-sensillum ampullaceum, sb-sensillum basiconicum, Se-sensorium, st-stemmata, setae: als-anterolateral, ams-anteromedial, cls-clypeal, des-dorsal epicranial, dms-dorsal malar, fs-frontal epicranial, les-lateral epicranial, ligs-ligular, Irs-labral, mbs-malar basiventral, mds-mandibular dorsal, mes-medial, mpxs-maxillary palp, pes-postepicranial, pfs-palpiferal, pms-postmental, prms-premental, stps-stipital, ves-ventral, vms-ventral malar.
one long prms; ligula with slightly sinuate margin and two short ligs; premental sclerite broad, sclerotised, U-shaped. Labial palpi one-segmented; palpi with a single pore, and a group of two or three apical sensilla (ampullacea) on terminal receptive area; surface of labium smooth. Postmentum (Fig. 42E) with three $p m s$, elongated $p m s_{1}$ located posteromedially, elongated $p m s_{2}$ located laterally, and medium $\mathrm{pms}_{3}$ located anterolaterally; lateral parts of membranous area covered with distinct knobby asperities.

Thorax. Prothorax (Fig. 43A) with five medium prns: three placed apically, next two above stigma; two medium ps; and single short eus. Mesothorax (Fig. 43A) with one minute prs, two short and one medium pds (ordered: short, medium, short); one medium as; three ss (two medium and one minute); one medium eps; two medium ps; and single minute eus. Chaetotaxy of metathorax (Fig. 43A) almost identical to that of mesothorax. Each pedal area of thoracic segments with three medium and two minute $p d a$.

Abdomen. Segments I-VIII (Fig. 43B, C) with one minute prs (segment VIII without); two minute and one medium pds; one minute and one medium ss; one medium eps; one short ps; one minute Ists; and two minute eus. Abdominal segment IX (Fig. 43C) with two minute ds; one minute ps; and two minute sts.


Figure 43. Rhinusa collina (Gyllenhal, 1813) mature larva, habitus $\mathbf{A}$ lateral view of thoracic segments $\mathbf{B}$ lateral view of abdominal segment I C lateral view of abdominal segments VII-X (schemes). Abbreviations: Th. 1-3-number of thoracic segments, Abd. 1-10-number of abdominal seg, setae: as-alar, ds-dorsal, eps-epipleural, eus-eusternal, Ists-laterosternal, pda-pedal, pds-postdorsal, prns-pronotal, prs-prodorsal, ss-spiracular, ps-pleural, sts-sternal.


Figure 44. Rhinusa collina (Gyllenhal, 1813) pupa habitus A ventral view B lateral view C dorsal view.
Description of pupa (Figs 44A-C, 45A-C). Measurements (in mm). Body length: 2.70-2.90 (avg. 2.75); body width: 1.75-1.80 (avg. 1.75); thorax width: $1.10-1.25$ (avg. 1.15); rostrum length: up to 0.60 कर and 0.85 q.

Body. Integument white, with some parts dark sclerotised; moderately stout, curved. Head with small head protuberances (h-pr) above eyes. Rostrum elongated, on both sexes almost $4 \times$ as long as wide, distinctly protruding to mesocoxae. Pronotum trapezoidal $2.4 \times$ as wide as long. Pronotal protuberances ( $\mathrm{p}-\mathrm{pr}$ ) indistinct, flattened, sclerotised, separated at bases. Meso- and metanotum similar in size. Abdominal segments I-VI almost identical in size; segment VII semicircular; segment VIII narrow; segment IX reduced. Abdominal segment VIII dorsally with rounded, prominent, sclerotised abdominal protuberance (a-pr). Urogomphi (ur) medium, ending with sclerotised, sharp apexes (Fig. 44A-C).

Chaetotaxy. Well developed, setae medium to elongated, transparent. Head with one medium os and one elongated sos. Rostrum with a single pas (Fig. 45A). Pronotum with three as, one $d s$, two $/ s$, and two pls variable in length. Dorsal parts of meso- and metathorax with three setae of various length, placed medially. Apex of femora with a single long fes (Fig. 45A-C). Abdominal segments I-VI with four setae dorsally, variable in length: first and third minute, second and fourth medium, placed close to posterior margin of the segment. Abdominal segments VII and VIII with three elongated setae dorsally. Each lateral part of abdominal segments I-VII with a single short seta. Ventral parts of abdominal segments I-VIII with three medium setae. Abdominal segment IX with two short setae ventrally (Fig. 45A-C).

Remarks and comparative notes. This species is widely distributed in Europe (Alonso-Zarazaga et al. 2023). In adults, the shape of the rostrum, together with the moderately elongated body, are useful characters that easily distinguish this species from the others in the group.

Biological notes. Rhinusa collina is an inquiline weevil whose development is closely linked to root galls on L. vulgaris and L. genistifolia caused by R. linariae. The females oviposit eggs exclusively on well-developed galls that are not occupied by $R$. linariae larvae. For this reason, the competition of these inquiline weevils with gall inducers has never been observed (IT, pers. obs.).


Figure 45. Rhinusa collina (Gyllenhal, 1813) pupa habitus A ventral view B dorsal view C lateral view (schemes). Abbreviations: a-pr-abdominal protuberances, p -pr-pronotal protuberances, ur-urogomphi, setae: as-apical, $d$-dorsal, ds-discal, fes-femoral, I, Is-lateral, os-orbital, pas-postantennal, pls-posterolateral, sos- supraorbital, v-ventral.
10) Rhinusa eversmanni (Rosenschoeld, 1838)

Material examined. 9 mature larvae; $4 \delta$ and 2 q pupae. Serbia, Didići, ex Linaria vulgaris, 05.07.2017, leg., det. I. Toševski.

Description of mature larva (Figs 46A, B, 47A-E, 48A-C). Measurements (in mm ). Body length: 2.70-4.10 (avg. 3.10). The widest place in the body (mesoand metathorax) measures up to 1.30. Head width: 0.60-065 (avg. 0.62).

General. Body elongate, slender, strongly curved, rounded in cross section (Fig. 46A). All thoracic segments equal in size. Meso- and metathorax each divided dorsally into two folds (prodorsal fold vestigial, postdorsal fold prominent). Pedal folds of thoracic segments isolated, conical. Abdominal segments I-III of similar size, next segments tapering towards posterior body end. Abdominal segments I-VII each divided dorsally into two folds: postdorsal folds much higher than prodorsal folds. Segments VIII and IX dorsally undivided. Epipleural folds of segments I-VIII conical. Laterosternal and eusternal folds of segments I-VIII conical, well isolated. Abdominal segment $X$ divided into four folds of equal size. Anus situated ventrally.

Thoracic and abdominal spiracles unicameral; thoracic spiracles (Fig. 46A) placed laterally close to mesothorax; abdominal spiracles (Fig. 46A) placed medially on segments I-VIII.

Colouration. Dark brown to brown head, medial parts of epicranium less sclerotised (Fig. 46B). Prodorsal sclerite brownish. All thoracic and abdominal segments whitish (Fig. 46A). Cuticle densely covered with cuticular asperities. All setae of thorax and abdomen placed on dark brown spots.

Vestiture. Setae on body thin, brown, different in length (minute to long).
Head capsule (Figs 46B, 47A). Head suboval, endocarinal line present, reaching to the $3 / 4$ of the length of frons. Frontal sutures on head distinct, very wide. Frons covered with knobby, dark asperities. Single pair of stemmata in the form of small black spots (st) placed laterally, close to the end of the frontal suture. Des, long, located in middle part of epicranium; long des ${ }_{2}$ located anteriorly; long $\mathrm{des}_{3}$ placed almost on the border of the frontal suture; minute des $_{4}$, located


Figure 46. Rhinusa eversmanni (Rosenschoeld, 1838) mature larva A habitus B head, frontal view.
laterally; and elongated des $_{5}$ placed anterolaterally above stemma (Fig. 47A). $F s_{1}$ short, located posterolaterally; $f s_{2}$ and $f s_{3}$ absent; $f s_{4}$ long, located anteriorly; and long $\mathrm{fs}_{5}$ located anterolaterally, close to antenna (Fig. 47A). Les ${ }_{1}$ and les ${ }_{2}$ medium; two short ves. Epicranial area with four pes.

Antennae placed distally of the frontal suture, on the inside; membranous and distinctly convex basal article bearing one conical, moderately elongate sensorium, plus a single sensillum ampullaceum and two sensilla basiconica (Fig. 47B).

Clypeus (Fig. 47C) trapezoidal, $\sim 2.7 \times$ as wide as long with two short cls, localised posterolaterally, with one sensillum between them; posterior part distinctly less sclerotised than the basal part; anterior border straight.

Mouth parts. Labrum (Fig. 47C) ~ $2.4 \times$ as wide as long, with three piliform Irs, various long; $I r s_{1}$ and $/ r s_{2}$ elongated, located medially, $I r s_{3}$ medium, located anterolaterally; anterior border bi-sinuate. Epipharynx (Fig. 47C) with three elongated fin-ger-like als, almost identical in length; two piliform ams variable in length; single finger-like mes; labral rods (Ir) distinct, kidney shaped. Mandibles (Fig. 47D) bifid, cutting edge with additional, blunt tooth; two medium piliform and short mds, both located close to lateral border. Maxillolabial complex: maxilla brownish sclerotised (Fig. 47E), stipes with one stps, two pfs and one short mbs and one sensillum, stps and both $p f s_{1-2}$ elongated; mala with five finger-like $d m s$ variable in length; four piliform vms, medium to short in length. Maxillary palpi two-segmented; basal palpomere wider and longer than distal one; basal palpomere with short $m p x s$ and single sensillum, distal palpomere with a group of two or three apical sensilla in terminal receptive area. Prementum (Fig. 47E) close to oval-shaped, with one long prms; ligula with slightly sinuate margin and two short ligs; premental sclerite well sclerotised, U-shaped. Labial palpi one-segmented; palpi with a single pore, and a pair of apical sensilla (ampullacea) on terminal receptive area; surface of labium smooth. Postmentum (Fig. 47E) with three $p m s$, medium $p m s_{1}$ located posteromedially, long $p m s_{2}$ located mediolaterally, and medium $p m s_{3}$ located anterolaterally; membranous area partially covered with knobby asperities.

Thorax. Prothorax (Fig. 48A) with 12 elongated to short prns, ten of them placed on dorsal sclerite; two medium ps; and single short eus. Mesothorax (Fig. 48A) without prs; with two elongated and two short pds (ordered: short, long, short, long); one long as; two long and single minute ss; one long eps; two long ps; and single minute eus. Chaetotaxy of metathorax (Fig. 48A) almost identical to that of mesothorax. Each pedal area of thoracic segments with four relatively long and one minute pda.

Abdomen. Segments I-VIII (Fig. 48B, C) with one minute prs (segments VII and VIII without); four pds of various length; one minute and one long ss; three long eps; one long ps; one medium Ists; and two short eus. Abdominal segment IX (Fig. 48C) with two minute and one medium ds; one medium and one minute $p s$; and two minute sts.

Description of pupa (Figs 49A-C, 50A-C). Measurements (in mm). Body length: 2.36-2.76; body width: 1.73-2.00; thorax width: 1.03-1.20; rostrum length: up to 0.86 and 1.23 q.

Body. Integument white, stout. Head elongated protuberances present on head above eyes (h-pr). Rostrum elongated, reaching over mesocoxae (almost $4.2 \times$ as wide as long on both male and female). Pronotum trapezoidal $2.5 \times$ as wide as long. Pronotal setae placed on dark brown spots. Pronotal protuberances (p-pr) conical, flattened, sclerotised, separated at bases. Meso- and metanotum similar


Figure 47. Rhinusa eversmanni (Rosenschoeld, 1838) mature larva, head and mouth parts $\mathbf{A}$ head $\mathbf{B}$ antenna $\mathbf{C}$ clypeus and labrum (left side), epipharynx (right side) D left mandible E maxillolabial complex (schemes). Abbreviations: at-antenna, Ir-labral rods, sa-sensillum ampullaceum, sb-sensillum basiconicum, Se-sensorium, st-stemmata, setae: alsanterolateral, ams-anteromedial, c/s-clypeal, des-dorsal epicranial, dms-dorsal malar, fs-frontal epicranial, les-lateral epicranial, ligs-ligular, Irs-labral, mbs-malar basiventral, mds-mandibular dorsal, mes-medial, mpxs-maxillary palp, pes-postepicranial, pfs-palpiferal, pms-postmental, prms-premental, stps-stipital, ves-ventral, vms-ventral malar.

0.2 mm

Figure 48. Rhinusa eversmanni (Rosenschoeld, 1838) mature larva, habitus A lateral view of thoracic segments B lateral view of abdominal segment I C lateral view of abdominal segments VII-X (schemes). Abbreviations: Th. 1-3-number of thoracic segments, Abd. 1-10-number of abdominal seg, setae: as-alar, ds-dorsal, eps-epipleural, eus-eusternal, Ists-laterosternal, pda-pedal, pds-postdorsal, prns-pronotal, prs-prodorsal, ss-spiracular, ps-pleural, sts-sternal.


Figure 49. Rhinusa eversmanni (Rosenschoeld, 1838) pupa habitus A ventral view B lateral view C dorsal view.
in size. Abdominal segments I-IV almost identical in size; segments V and VI tapering gradually, VII semicircular; segment VIII narrow; segment IX reduced. Urogomphi (ur) short, ending with sclerotised, sharp apexes (Fig. 49A-C).

Chaetotaxy. Well developed, setae elongated to short, transparent. Head with one medium sos and one medium os. Rostrum with a single rs (Fig. 50A).


Figure 50. Rhinusa eversmanni (Rosenschoeld, 1838) pupa habitus A ventral view B lateral view C dorsal view (schemes). Abbreviations: a-pr-abdominal protuberances, p-pr-pronotal protuberances, ur-urogomphi, setae: as-apical, d-dorsal, ds-discal, fes-femoral, l, /s-lateral, os-orbital, pas-postantennal, pls-posterolateral, rs-rostral, sos- supraorbital, v-ventral.

Pronotum with three as, three $l s$, and three $p l s$ all elongated, equal in length. Dorsal parts of meso- and metathorax with three setae of various length, placed medially. Apex of femora with a single long fes (Fig. 50A-C). Abdominal segments I-VII dorsally with four setae dorsally, variable in length: first and third minute, second, short, and fourth medium; setae first to third placed close to posterior margin of the segment, fourth placed below stigma (on segment VII
all setae medium). Abdominal segments VII and VIII with four elongated setae dorsally. Each lateral part of abdominal segments I-VIII with one short seta. Ventral parts of abdominal segments I-VIII with three short setae. Abdominal segment IX with four short setae ventrally (Fig. 50A-C).

Remarks and comparative notes. This is an uncommon species with a wide and fragmentary distribution: France, Italy, Germany, Czech Republic, Ukraine, Russia, Kazakhstan, Uzbekistan, and Tajikistan (Alonso-Zarazaga et al. 2023). At the adult stage, it is easily distinguishable from the other species of the group by the shape and length of the rostrum, especially in the female, which has a longer antennal club than all the other species of the genus.

Biological notes. The stem galls caused by R. pilosa on L. vulgaris and by $R$. rara on L. genistifolia or L. dalmatica are niches for the development of $R$. eversmanni, which is another inquiline weevil. The females oviposit their eggs on fully developed galls, and hatched larvae bore holes towards the central portion of the gall, where larvae of the gall inducer are positioned. Larvae of $R$. eversmanni are very aggressive, killing all resident larvae inside galls, while competition between them inside galls is pronounced and cannibalism is commonly observed. Over 20 adults of $R$. eversmanni can develop in the larger gall induced by R. pilosa or R. rara (Toševski et al. 2015).
11) Rhinusa incana (Kirsch, 1881)

Material examined. 5 mature larvae. Italia, Sicilia, San Cono, ex Linaria multicaulis (L.) Mill., 06.05.2017, leg. C. Baviera, det. R. Caldara.

Description of mature larva (Figs 51A, B, 52A-E, 53A-C). Measurements (in mm ). Body length: 2.25-3.00 (avg. 2.50). The widest place in the body (mesoand metathorax) measures up to 1.50. Head width: 0.60-070 (avg. 0.65).

General. Body elongate, slender, slightly curved, rounded in cross section (Fig. 51A). All thoracic segments equal in size. Meso- and metathorax each divided dorsally into two folds (prodorsal fold smaller than postdorsal fold). Pedal folds of thoracic segments isolated, conical. Abdominal segments I-V of similar size, next segments tapering towards posterior body end. Abdominal segments I-VII each divided dorsally into two folds: postdorsal folds much higher than prodorsal folds. Segments VIII and IX dorsally undivided. Epipleural folds of segments I-VIII conical. Laterosternal and eusternal folds of segments I-VIII conical, well isolated. Abdominal segment $X$ divided into four folds of equal size. Anus situated ventrally, hidden in ninth segment.

Thoracic and abdominal spiracles unicameral; thoracic spiracles (Fig. 51A) placed laterally close to mesothorax; abdominal spiracles (Fig. 51A) placed medially on segments I-VIII.

Colouration. Yellow to brown head, medial parts of epicranium less sclerotised (Fig. 51B). All thoracic and abdominal segments whitish, covered with fine asperities (Fig. 51A).

Vestiture. Setae on body thin, transparent, different in length (minute to long).
Head capsule (Figs 51B, 52A). Head slightly narrowed bilaterally, endocarinal line present, reaching to $3 / 4$ length of frons. Frontal sutures on head partially indistinct, very wide. Frons covered with knobby, dark asperities. Two pairs of stemmata in the form of small black spots (st) placed laterally. Des ${ }_{1}$ very short,


Figure 51. Rhinusa incana (Kirsch, 1881) mature larva A habitus B head, frontal view.
located in middle part of epicranium; medium des $_{2}$ located anteriorly; long des ${ }_{3}$ placed almost on the border of the frontal suture; minute des ${ }_{4}$, located laterally; and elongated $\operatorname{des}_{5}$ placed close to stemma (Fig. 52A). Fs $s_{1}$ minute, located posterolaterally; $f s_{2}$ and $f s_{3}$ minute; $f s_{4}$ medium, located anteriorly; and long $f s_{5}$ located anterolaterally, close to antenna (Fig. 52A). Les $_{1}$ and $l e s_{2}$ medium; two short ves. Epicranial area with three pes.

Antennae placed distally of the frontal suture, on the inside; membranous and distinctly convex basal article bearing one conical elongate sensorium, plus two sensilla basiconica (Fig. 52B).

Clypeus (Fig. 52C) trapezoidal, $\sim 2.7 \times$ as wide as long with two medium cls, localised posterolaterally, with one sensillum between them; anterior border straight.

Mouth parts. Labrum (Fig. 52C) ~ $2.4 \times$ as wide as long, with three piliform Irs, various long; $\operatorname{lr}$ 1 $_{1}$ elongated, placed posteromedially, $\operatorname{Irs_{2}}$ elongated, located anteromedially, Irs $3_{3}$ medium, located anterolaterally; anterior border bi-sinuate. Epipharynx (Fig. 52C) with two elongated finger-like als, almost identical in length, two piliform ams variable in length and two finger-like mes variable in length; labral rods (Ir) distinct, elongated. Mandibles (Fig. 52D) bifid, with two medium piliform mds, both located close to lateral border. Maxillolabial complex: maxilla brownish sclerotised (Fig. 52E) stipes with one stps, two pfs and one relatively long $m b s$ and one sensillum, stps and both $p f s_{1-2}$ elongated; mala with five finger-like $d m s$ variable in length, placed in two groups (three + two); four piliform, vms, medium to short in length. Maxillary palpi two-segmented; basal palpomere slightly wider than distal one; basal palpomere with short $m p x s$ and single sensillum, terminal receptive area of distal palpomere with a group of five or six apical sensilla; basal and distal palpomeres almost of the same length. Prementum (Fig. 52E) close to cup-shaped, with one long prms; ligula with distinctly sinuate margin and two ligs variable in length; premental sclerite well sclerotised, U-shaped. Labial palpi one-segmented; palpi with single pore; terminal receptive area with four or five apical sensilla (ampullacea); surface of labium smooth. Postmentum (Fig. 52E) with three pms, elongated $p m s_{1}$ located posteromedially, long $p m s_{2}$ located mediolaterally, and medium $p m s_{3}$ located anterolaterally; membranous area smooth.


Figure 52. Rhinusa incana (Kirsch, 1881) mature larva, head and mouth parts $\mathbf{A}$ head $\mathbf{B}$ antenna $\mathbf{C}$ clypeus and labrum (left side), epipharynx (right side) D left mandible E maxillolabial complex (schemes). Abbreviations: at-antenna, Irlabral rods, sb-sensillum basiconicum, Se-sensorium, st-stemmata, setae: als-anterolateral, ams-anteromedial, cls-clypeal, des-dorsal epicranial, dms-dorsal malar, fs-frontal epicranial, les-lateral epicranial, ligs-ligular, lrs-labral, mbs-malar basiventral, mds-mandibular dorsal, mes-medial, mpxs-maxillary palp, pes-postepicranial, pfs-palpiferal, pms-postmental, prms-premental, stps-stipital, ves-ventral, vms-ventral malar.

Thorax. Prothorax (Fig. 53A) with eight prns (four relatively long and four short); two elongated ps; and single short eus. Mesothorax (Fig. 53A) with minute prs, single short and two medium pds; one minute as; three minute ss; two long eps; single long ps; and single minute eus. Chaetotaxy of metathorax (Fig. 53A) almost identical to that of mesothorax. Each pedal area of thoracic segments with six relatively long pda.

Abdomen. Segments I-VIII (Fig. 53B, C) with one minute prs (segment VIII without); four medium pds; one minute and one medium $s s$; three medium eps; one medium ps; one medium Ists; and two minute eus. Abdominal segment IX (Fig. 53C) with two short and one minute ds; one medium and one minute $p s$; and two minute sts.

Remarks and comparative notes. This species is distributed in the Iberian Peninsula, in southern Italy and Sicily, and in the western part of North Africa (Alonso-Zarazaga et al. 2023). It is very closely related to $R$. neta, from which it can be separated at adult stage by a few but constant characters (shape of the female rostrum, antennae inserted slightly more towards the base of the rostrum in both sexes, and scales of the dorsal vestiture slightly thinner).

Biological notes. This species was collected in Sicily inside the seed capsules of Linaria multicaulis subsp. aetnensis Giardina and Zizza, L. multicaulis subsp. humilis (Guss.) De Leon. (Baviera and Caldara 2020) and L. striata (Lam.) DC. (Goggi 2004). In Algeria, its development occurs inside the seed capsules of L. baborensis Batt. and L. heterophylla Desf. ( de Peyerimhoff 1911).


Figure 53. Rhinusa incana (Kirsch, 1881) mature larva, habitus $\mathbf{A}$ lateral view of thoracic segments $\mathbf{B}$ lateral view of abdominal segment I C lateral view of abdominal segments VII-X (schemes). Abbreviations: Th. 1-3-number of thoracic segments, Abd. 1-10-number of abdominal seg, setae: as-alar, ds-dorsal, eps-epipleural, eus-eusternal, Ists-laterosternal, pda-pedal, pds-postdorsal, prns-pronotal, prs-prodorsal, ss-spiracular, ps-pleural, sts-sternal.

## 12) Rhinusa neta (Germar, 1821)

Material examined. 21 mature larvae; $7 \widehat{\jmath}$ and $12 \&$ pupae. Serbia, Zemun, ex Linaria vulgaris, 15.08.2017, leg., det. I. Toševski.

Redescription of mature larva (Figs 54A, B, 55A-E, 56A-C). Measurements (in mm). Body length: 4.60-7.00 (avg. 5.20). The widest place in the body (mesoand metathorax) measures up to 1.50. Head width: 0.62-0.75 (avg. 0.70).

General. Body elongate, moderately slender, curved, rounded in cross section (Fig. 54A). All thoracic segments equal in size. Meso- and metathorax each divided dorsally into two folds (prodorsal fold distinctly smaller than postdorsal fold). Pedal folds of thoracic segments isolated, conical, and prominent. Abdominal segments I-III of similar size, next segments tapering towards posterior body end. Abdominal segments I-VII each divided dorsally into two almost equal in size folds; postdorsal folds only slightly higher than prodorsal folds. Segments VIII and IX dorsally undivided. Epipleural folds of segments I-VIII conical. Laterosternal and eusternal folds of segments I-VIII conical, weakly isolated. Abdominal segment $X$ divided into four folds of equal size, lateral folds each with a single minute seta. Anus situated ventrally, almost completely covered by ninth segment.

Thoracic and abdominal spiracles unicameral; thoracic spiracles (Fig. 54A) placed laterally close to mesothorax; abdominal spiracles (Fig. 54A) placed medially on segments I-VIII.

Colouration. Dark yellow to brown head, medial parts of epicranium less sclerotised (Fig. 54B). All thoracic and abdominal segments whitish, premental shield only slightly darker than the rest of prodorsum (Fig. 54A). Cuticle covered with asperities.

Vestiture. Setae on body thin, yellowish, different in length (very short or medium).

Head capsule (Figs 54B, 55A). Head suboval, endocarinal line present, reaching more than the $2 / 3$ of the length of frons. Frontal sutures on head partially indistinct, wide. Frons covered with knobby, dark asperities. Single pair of stem-


Figure 54. Rhinusa neta (Germar, 1821) mature larva $\mathbf{A}$ habitus $\mathbf{B}$ head, frontal view.


Figure 55. Rhinusa neta (Germar, 1821) mature larva, head and mouth parts $\mathbf{A}$ head $\mathbf{B}$ antenna $\mathbf{C}$ clypeus and labrum (left side), epipharynx (right side) D left mandible E maxillolabial complex (schemes). Abbreviations: at-antenna, Ir-labral rods, sa-sensillum ampullaceum, sb-sensillum basiconicum, Se -sensorium, st-stemmata, setae: als-anterolateral, ams-anteromedial, cls-clypeal, des-dorsal epicranial, dms-dorsal malar, fs-frontal epicranial, les-lateral epicranial, ligs-ligular, Irs-labral, mes-medial, mbs-malar basiventral, mds-mandibular dorsal, mpxs-maxillary palp, pes-postepicranial, pfs-palpiferal, pms-postmental, prms-premental, stps-stipital, ves-ventral, vms-ventral malar.
mata in the form of small black spots (st) placed laterally, close to the end of the frontal suture. Des ${ }_{1}$ short, located in middle part of epicranium; long des ${ }_{2}$; long $\mathrm{des}_{3}$ located anteriorly, almost on the border of the frontal suture; minute des ${ }_{4}$ located laterally; and long des $_{5}$ placed anterolaterally above stemma (Fig. 55A). $F s_{1}$ short, located posterolaterally; $f s_{2}$ and $f s_{3}$ absent; $f s_{4}$ medium, located anteriorly; and long $\mathrm{fs}_{5}$ located anterolaterally, close to antenna (Fig. 55A). Les ${ }_{1}$ and les 2 medium; two short ves. Epicranial area with three pes.

Antennae placed distally of the frontal suture, on the inside; membranous and distinctly convex basal article bearing one conical elongate sensorium, plus a single sensillum basiconicum and single sensillum ampullaceum (Fig. 55B).

Clypeus (Fig. 55C) trapezoidal, $\sim 3.5 \times$ as wide as long with two medium cls, localised posterolaterally, with one sensillum between them; basolateral parts distinctly more sclerotised than the middle part; anterior border slightly curved towards the inside.

Mouth parts. Labrum (Fig. 55C) ~ $2.5 \times$ as wide as long, with three piliform Irs, variable in length; $/ r s_{1}$ and $/ r s_{2}$ elongated, located medially, $I r s_{3}$ short, located anterolaterally; anterior border bi-sinuate. Epipharynx (Fig. 55C) with three relatively elongated finger-like als, identical in length, three piliform ams variable in length and single short finger-like mes; labral rods (lr) elongated, close to kidney shaped. Mandibles (Fig. 55D) bifid, cutting edge smooth; two medium piliform and short mds, both located close to lateral border. Maxillolabial complex: maxilla brownish sclerotised (Fig. 55E), stipes with one stps, two pfs and one very short $m b s$ and one sensillum, stps and both $p \mathrm{sf}_{1-2}$ relatively long; mala with six finger-like $d m s$ variable in length; four piliform vms, medium to short in length. Maxillary palpi two-segmented; basal palpomere distinctly wider and slightly longer than distal one; basal palpomere with short mpxs and two sensilla, distal palpomere with a group of four apical sensilla in terminal receptive area. Prementum (Fig. 55E) close to oval-shaped, with one long prms; ligula with slightly sinuate margin and two medium ligs; premental sclerite weakly sclerotised, only lateral parts well visible. Labial palpi one-segmented; each palp with a single pore, and a group of three apical sensilla basiconica on terminal receptive area; surface of labium smooth. Postmentum (Fig. 55E) with three pms, medium $p m s_{1}$ located anteromedially, long $p m s_{2}$ located laterally, and medium $p m s_{3}$ located anterolaterally; membranous area covered with knobby asperities.

Thorax. Prothorax (Fig. 56A) with eight medium to short prns; two medium ps; and single short eus. Mesothorax (Fig. 56A) with one minute prs, two medium and one minute pds (ordered: minute, medium, medium); one medium as; two medium and single minute ss; one medium eps; two medium $p s$; and single minute eus. Chaetotaxy of metathorax (Fig. 56A) almost identical to that of mesothorax. Each pedal area of thoracic segments with four relatively long and one minute $p d a$.

Abdomen. Segments I-VIII (Fig. 56B, C) with one minute prs (segment VIII without); four pds of various length; one minute and one medium ss; three medium eps; one medium ps; one medium Ists; and two short eus. Abdominal segment IX (Fig. 56C) with one minute and one medium ds; one medium and one minute $p s$; and two minute sts.

Description of pupa (Figs 57A-C, 58A-C). Measurements (in mm). Body length: 2.70-4.20 (avg. 3.25); body width: 1.53-2.26 (avg. 2.10); thorax width: 1.00-1.53 (avg. 1.40); rostrum length: up to 0.73 万 and 0.83 q.


Figure 56. Rhinusa neta (Germar, 1821) mature larva, habitus $\mathbf{A}$ lateral view of thoracic segments $\mathbf{B}$ lateral view of abdominal segment I C lateral view of abdominal segments VII-X (schemes). Abbreviations: Th. 1-3-number of thoracic segments, Abd. 1-10-number of abdominal seg, setae: as-alar, ds-dorsal, eps-epipleural, eus-eusternal, Ists-laterosternal, pda-pedal, pds-postdorsal, prns-pronotal, prs-prodorsal, ss-spiracular, ps-pleural, sts-sternal.


Figure 57. Rhinusa neta (Germar, 1821) pupa habitus A ventral view B lateral view C dorsal view.

Body. Integument white, with some parts dark sclerotised; moderately stout, curved. All setae placed on dark brown spots. Head elongated protuberances present ( $\mathrm{h}-\mathrm{pr}$ ) on head above eyes. Rostrum elongated, on both sexes almost $4 \times$ as long as wide, reaching over mesocoxae. Pronotum trapezoidal $2.2 \times$ as wide as long. Pronotal protuberances ( $p-p r$ ) conical, flattened, sclerotised, separated at bases. Meso- and metanotum similar in size. Abdominal segments I-


Figure 58. Rhinusa neta (Germar, 1821) pupa habitus A ventral view B dorsal view $\mathbf{C}$ lateral view (schemes). Abbreviations: a-pr-abdominal protuberances, h - pr-head protuberances, p - pr -pronotal protuberances, ur-urogomphi, setae: as-apical, $d$-dorsal, ds-discal, fes-femoral, I, Is-lateral, os-orbital, pls-posterolateral, rs-rostral, sos-supraorbital, v-ventral.

IV almost identical in size; segments V and VI tapering gradually, VII semicircuIar; segment VIII narrow; segment IX reduced. Abdominal segment VIII dorsally with flattened, weakly sclerotised abdominal protuberance (a-pr). Urogomphi (ur) short, ending with sclerotised, sharp apexes (Fig. 57A-C).

Chaetotaxy. Well developed, setae medium to elongated, transparent. Head with one medium sos and one medium os. Rostrum with two rs (Fig. 58A). Pronotum with three as, single $/ s$, and three pls all equal in length. Dorsal parts of meso- and metathorax with three setae of various length, placed medially. Apex of femora with a single long fes (Fig. 58A-C). Abdominal segments I-VII dorsally with five setae, variable in length: first and third minute, second, fourth, and fifth medium; setae first to fourth placed close to posterior margin of the segment, fifth placed below stigma (on segments VI and VII all setae medium in size). Abdominal segment VIII dorsally with four elongated setae dorsally. Each lateral part of abdominal segments I-VIII with two short setae. Ventral parts of abdominal segments I-VIII with three medium setae. Abdominal segment IX with three short setae ventrally (Fig. 58A-C).

Remarks and comparative notes. This species is very common and has a wide distribution (western, central, and southern Europe, Caucasus, Iran, central Asia; Alonso-Zarazaga et al. 2023). It was accidentally introduced in North America (Buchanan 1937) but subsequently used as a biological control agent against the dalmatian toadflax (Linaria dalmatica) and yellow toadflax (Linaria vulgaris) (Sing et al. 2016). There are no noteworthy morphological differences between various populations living on different species of Linaria. The shape of the rostrum is the most useful character, which allows easy separation at adult stage of $R$. neta from the other species of the genus with short elytra, except for the western Mediterranean $R$. incana, from which it can be distinguished only by the shape of the female rostrum, the antennal insertion being located slightly more towards the apex of the rostrum in both sexes, and the scales of the dorsal vestiture being slightly stouter.

The descriptions of the larva and pupa of $R$. neta given by Ścibior and Łętowski (2018) are generally similar to ours, with some differences probably due to the nomenclature used by these authors. In our opinion, some setae were incorrectly identified in the larva, e.g., as ${ }_{1}$ instead of $/ s_{1}$. There are also some discrepancies in the interpretation of pupal characters, such as a lack of $r s_{2}$ or sos instead of os and four abdominal dorsal setae instead of five.

Biological notes. This is an oligophagous species whose larvae develop on different toadflaxes (Linaria spp.). The females oviposit eggs from mid-June to the end of September in an already developed seed capsule. The larvae are typical seed feeders. Larval development was recorded on many Linaria species: L. vulgaris, L. genistifolia, L. dalmatica, L. grandiflora Desf., L. angustissima, L. arvensis (L.) Desf., L. corifolia Desf., L. peloponnesiaca Boiss. and Heldr., L. repens (L.) Mill., L. rubioides Vis. \& Pancic, L. spartea (L.) Chaz., L. supina (L.) Chaz., and L. vulgaris. Oviposition of eggs and larval feeding do not cause swelling of seeds, but larvae may consume a large proportion of seeds within a capsule, decreasing the seed output but not killing the host plant (Sing et al. 2016).

## Rhinusa vestita group

Adult diagnosis. Rostrum short and stout in both sexes; elytra subquadrate, distinctly flattened on disc; penis with short endophallus beginning just in front of basal third of its body.

## 13) Rhinusa vestita (Germar, 1821)

Material examined. 21 mature and 7 premature larvae; 7 § and 11 \& pupae. France, Alpes-Maritimes, La Turbie, ex Antirrhinum majus L., 01.06.2014, leg., det. R. Caldara.

Description of mature larva (Figs 59A, B, 60A-E, 61A-C). Measurements (in mm ). Body length: 6.50-8.25 (avg. 7.50). The widest place in the body (mesoand metathorax) measures up to 2.50 . Head width: 0.90-1.05 (avg. 1.00).

General. Body elongate, moderately slender, slightly curved, rounded in cross section (Fig. 59A). Prothorax relatively small, pronotal shield not pigmented; meso- and metathorax equal in size, distinctly wider than prothorax. Mesoand metathorax each divided dorsally into two folds (prodorsal fold vestigial, postdorsal fold prominent). Pedal folds of thoracic segments isolated, conical. Abdominal segments I-III of similar size, as large as metathorax; segment IV the widest; next segments tapering towards posterior body end. Abdominal segments I-VII each divided dorsally into two folds various in size; postdorsal folds larger than prodorsal folds. Segments VIII and IX dorsally undivided. Epipleural folds of segments I-VII conical. Laterosternal and eusternal folds of segments I-VIII conical, well isolated. Abdominal segment $X$ divided into four folds of equal size. Anus situated ventrally, almost completely hidden in previous segment.

All spiracles unicameral, thoracic spiracles (Fig. 59A) placed ventrolaterally; abdominal spiracles (Fig. 59A) placed anteromedially on segments I-VIII.

Colouration. Dark yellow to light brown head, medial parts of epicranium less sclerotised (Fig. 59B). All thoracic and abdominal segments white (Fig. 59A). Cuticle densely covered with cuticular asperities.

Vestiture. Setae on body well developed, yellowish, different in length (minute to medium).

Head capsule (Figs 59B, 60A). Head wide, endocarinal line present, reaching to the $3 / 4$ of the length of frons. Frontal sutures on head distinct, very wide. Single pair of stemmata in the form of small black spots (st) close to the end


Figure 59. Rhinusa vestita (Germar, 1821) mature larva A habitus B head, frontal view.
of the frontal suture. Des $\boldsymbol{1}_{1}$ short, located in middle part of epicranium; long des ${ }_{2}$; long des $_{3}$ located anteriorly on epicranium, close to border with frontal suture; des $_{4}$ short; des $_{5}$ elongated, located anterolaterally above stemma (Fig. 60A). $F s_{1}, f s_{2}$ and $f s_{3}$ minute, located along frontal suture; $f s_{4}$ long, located anteriorly; and long $f s_{5}$ located anterolaterally, close to antenna (Fig. 60A). Les ${ }_{1}$ and $l e s_{2}$ medium; two minute ves. Epicranial area with two pes.

Antennae placed distally of the frontal suture, on the inside; membranous and distinctly convex basal article bearing one conical, medium in length sensorium, plus four sensilla ampullacea (Fig. 60B).

Clypeus (Fig. 60C) trapezoidal, $\sim 2.7 \times$ as wide as long with two cls: $\mathrm{cls}_{1}$ relatively long, $\mathrm{cls}_{2}$ medium, both localised posterolaterally, with one sensillum between them; basal part distinctly more sclerotised than the apical part; anterior border slightly curved towards the inside.

Mouth parts. Labrum (Fig. 60C) $\sim 2 \times$ as wide as long, with three piliform Irs, various long; Irs ${ }_{1}$ elongated, located posteromedially, $\operatorname{lrS_{2}}$ elongated, located medially, and $/ \mathrm{rs}_{3}$ short, located anterolaterally; anterior border bisinuate. Epipharynx (Fig. 60C) with two elongated finger-like als, almost identical in length and three piliform ams equally in length; labral rods (Ir) distinct, elongated, converging posteriorly. Mandibles (Fig. 60D) bifid, cutting edge with a single, blunt protuberance; two medium piliform and single minute mds, all located close to lateral border. Maxillolabial complex: maxilla dark sclerotised (Fig. 60E) stipes with one stps, two pfs and one short $m b s$ and one sensillum, stps and both $p f s_{1-2}$ elongated; mala with six finger-like dms variable in length; four piliform vms, medium to short in length. Maxillary palpi two-segmented; basal palpomere distinctly wider than distal one; length ratio of basal and distal palpomeres almost 1:1; basal palpomere with short mpxs and two sensilla, distal palpomere with a group of three or four apical sensilla in terminal receptive area. Prementum (Fig. 60E) cup-shaped, with one medium prms; ligula with sinuate margin and two medium ligs; premental sclerite broad, highly sclerotised, Y-shaped, posterior extension with elongated apex. Labial palpi one-segmented; palpi with two pores, and a group of three or four apical sensilla (ampullacea) on terminal receptive area; surface of labium smooth. Postmentum (Fig. 60E) with three $p m s$, medium $p m s_{1}$ located posteromedially, elongated $p m s_{2}$ located laterally, and medium $\mathrm{pms}_{3}$ located anterolaterally; membranous area smooth.

Thorax. Prothorax (Fig. 61A) with five elongated and two medium prns: five placed apically, next two laterally; two elongated $p s$; and single short eus. Mesothorax (Fig. 61A) with one short and two medium pds (ordered: short, medium, medium); one medium as; three medium ss; one elongated eps; one elongated ps; and single minute eus. Chaetotaxy of metathorax (Fig. 61A) almost identical to that of mesothorax. Each pedal area of thoracic segments with two elongated, three medium and one minute pda.

Abdomen. Segments I-VIII (Fig. 61B, C) with one minute prs; one medium and two elongated pds; one minute and one elongated ss; two elongated eps; one medium ps; one medium Ists; and two minute eus. Abdominal segment IX (Fig. 61C) with two medium and single minute $d s$; one medium and one minute $p s$; and single minute sts.

Description of pupa (Figs 62A-C, 63A-C). Measurements (in mm). Body length: 4.75-6.50 (avg. 5.25); body width: 2.75-3.50 (avg. 3.15); thorax width: 1.60-2.00 (avg. 1.90); rostrum length: up to 1.25 § and $q$.


Figure 60. Rhinusa vestita (Germar, 1821) mature larva, head and mouth parts $\mathbf{A}$ head $\mathbf{B}$ antenna $\mathbf{C}$ clypeus and labrum (left side), epipharynx (right side) $\mathbf{D}$ left mandible $\mathbf{E}$ maxillolabial complex (schemes). Abbreviations: at-antenna, lr -labral rods, sb-sensillum basiconicum, Se-sensorium, st-stemmata, setae: als-anterolateral, ams-anteromedial, cls-clypeal, des-dorsal epicranial, dms-dorsal malar, fs-frontal epicranial, les-lateral epicranial, ligs-ligular, Irs-labral, mbs-malar basiventral, mds-mandibular dorsal, mpxs-maxillary palp, pes-postepicranial, pfs-palpiferal, pms-postmental, prms-premental, stps-stipital, ves-ventral, vms-ventral malar.


Figure 61. Rhinusa vestita (Germar, 1821) mature larva, habitus A lateral view of thoracic segments B lateral view of abdominal segment I C lateral view of abdominal segments VII-X (schemes). Abbreviations: Th. 1-3-number of thoracic segments, Abd. 1-10-number of abdominal seg, setae: as-alar, ds-dorsal, eps-epipleural, eus-eusternal, Ists-laterosternal, pda-pedal, pds-postdorsal, prns-pronotal, prs-prodorsal, ss-spiracular, ps-pleural, sts-sternal.


Figure 62. Rhinusa vestita (Germar, 1821) pupa habitus A ventral view B lateral view C dorsal view.

Body. Integument white or light yellow, moderately elongated, slightly curved. Head with a pair of small head protuberances (h-pr) above eyes. Rostrum moderately stout, almost $2.5 \times$ as long as wide, reaching mesocoxae, on both sexes. Pronotum trapezoidal $2.0 \times$ as wide as long. Pronotum with a pair of conical, scle-


Figure 63. Rhinusa vestita (Germar, 1821) pupa habitus A ventral view B dorsal view C lateral view (schemes). Abbreviations: p -pr-pronotal protuberances, ur-urogomphi, setae: as-apical, $d$-dorsal, ds-discal, fes-femoral, $I, l s$-lateral, os-orbital, pls-posterolateral, $v$-ventral.
rotised, protuberances ( $\mathrm{p}-\mathrm{pr}$ ) separated at bases. Meso- and metanotum similar in size. Abdominal segments I-VI almost identical in size; segment VII semicircular; segment VIII narrow with broad protuberances (a-pr); segment IX reduced. Urogomphi (ur) small, ending with sclerotised, sharp apexes (Fig. 62A-C).

Chaetotaxy. Well developed, setae medium to elongated, transparent. Head with one small os (Fig. 63A). Pronotum with two as, one ds, two Is, and four pls all medium in length. Dorsal parts of meso- and metathorax with two equal in length setae, placed medially. Apex of femora with a single elongated fes (Fig. 63A-C). Abdominal segments I-V with six setae dorsally, variable in length: first, second and fifth minute, third, fourth, and sixth medium, first placed anteromedially, the rest placed close to posterior margin of the segment. Abdominal segment VI with six setae dorsally, variable in length: first minute, second to sixth elongated, first placed anteromedially, second to sixth placed close to posterior margin of the segment. Abdominal segment VII with four elongated setae dorsally. Each lateral part of abdominal segments I-VII with two medium setae. Ventral parts of abdominal segments I-VIII with four setae (median pair robust, second to fourth short). Abdominal segment IX with two short setae ventrally (Fig. 63A-C).

Remarks and comparative notes. This species is known from Spain, Portugal, southern France, Switzerland, and northwestern and central Italy (Alon-so-Zarazaga et al. 2023). At the adult stage, due to the medium-large size and the broad subquadrate shape of the elytra, which are almost flattened on the disc, this species is similar to $R$. depressa (Rottenberg, 1872) and R. fuentei (Pic, 1906). From the former, with which it is also closely related phylogenetically, it can be mainly distinguished by the shape and the greater length of the rostrum and of the penis; from the latter, which belongs to the $R$. antirrhini group, it distinctly differs in the shape of the rostrum and obviously in the characters that easily distinguish the $R$. vestita group from the $R$. antirrhini group (femora strongly toothed, shape of the penis; Caldara et al. 2010).

Biological notes. The female usually oviposits 1-3 eggs per seed capsule. Egg hatching occurs 7-11 days after deposition. Larvae feed on seeds within capsules of Antirrhinum majus and A. Iatifolium Mill., consuming the majority of them. Pupation occurs within the seed capsule, and the emergence of the adults occurs $\sim 20$ days later. Adults exit the seed capsule by chewing through the hardened pericarp (IT and RC, pers. obs.).

## Rhinusa melas group

Adult diagnosis. Rostrum poorly sexually dimorphic and short in both sexes; elytra short; body of penis abruptly narrowing toward apex ending in a narrow acute point; flagellum distinctly sclerotised, sinuous in its apical section; spermatheca with distinct emargination at passage point between nodus and body.

## 14) Rhinusa melas (Boheman, 1838)

Material examined. 11 mature and 5 premature larvae; 8 万 and 6 q pupae. Serbia, Mokra Gora, ex Chaenorhinum minus (L.) Lange, 10.08.2017, leg., det. I. Toševski.


Figure 64. Rhinusa melas (Boheman, 1838) mature larva A habitus B head, frontal view.

Description of mature larva (Figs 64A, B, 65A-E, 66A-C). Measurements (in mm ). Body length: 2.50-3.66 (avg. 2.83). The widest place in the body (mesoand metathorax) measures up to 1.16. Head width: $0.43-0.50$ (avg. 0.46 ).

General. Body elongate, slender, moderately curved, rounded in cross section (Fig. 64A). All thoracic segments equal in size. Meso- and metathorax each divided dorsally into two folds (prodorsal fold very small, postdorsal fold prominent). Pedal folds of thoracic segments conical. Abdominal segments I-V of similar size, next segments tapering towards posterior body end. Abdominal segments I-VII each divided dorsally into two folds almost identical in size. Segments VIII and IX dorsally undivided. Epipleural folds of segments I-VIII conical. Laterosternal and eusternal folds of segments I-VIII conical, poorly isolated. Abdominal segment $X$ divided into four folds of equal size. Anus situated ventrally, almost completely hidden in segment IX.

Thoracic spiracle bicameral, all abdominal spiracles unicameral; thoracic spiracle (Fig. 64A) placed laterally close to mesothorax; abdominal spiracles (Fig. 64A) placed medially on segments I-VIII.

Colouration. Light to dark yellow head (Fig. 64B). All thoracic and abdominal segments whitish (Fig. 64A). Cuticle covered with asperities.

Vestiture. Setae on body thin, transparent, different in length (minute to medium).

Head capsule (Figs 64B, 65A). Head suboval, endocarinal line present, reaching to $1 / 2$ of the length of frons. Frontal sutures on head indistinct, very wide. Single pair of stemmata in the form of small dark spots (st) placed laterally, close to the end of the frontal suture. Des, short, located in middle part of epicranium; long des ${ }_{2}$ located anteriorly; long des $_{3}$ placed almost on the border of the frontal suture; very short des ${ }_{4}$ located laterally; very long des ${ }_{5}$ placed anterolaterally above stemma (Fig. 65A). Fs minute, placed posteriorly; $f s_{2}$ minute, located posterolaterally; $f s_{3}$ absent; $f s_{4}$ medium; and long $f f_{5}$ located anterolaterally, close to antenna (Fig. 65A). Les, medium and les ${ }_{2}$ short; two short ves. Epicranial area with three pes.


Figure 65. Rhinusa melas (Boheman, 1838) mature larva, head and mouth parts $\mathbf{A}$ head $\mathbf{B}$ antenna $\mathbf{C}$ clypeus and labrum (left side), epipharynx (right side) D left mandible E maxillolabial complex (schemes). Abbreviations: at-antenna, Ir-labral rods, sa-sensillum ampullaceum, Se-sensorium, st-stemmata, setae: als-anterolateral, ams-anteromedial, cls-clypeal, des-dorsal epicranial, dms-dorsal malar, fs-frontal epicranial, les-lateral epicranial, ligs-ligular, lrs-labral, mbs-malar basiventral, mds-mandibular dorsal, mes-medial, mpxs-maxillary palp, pes-postepicranial, pfs-palpiferal, pms-postmental, prms-premental, stps-stipital, ves-ventral, vms-ventral malar.

Antennae placed distally of the frontal suture, on the inside; membranous and distinctly convex basal article bearing one conical elongate sensorium, plus two sensilla ampullacea (Fig. 65B).

Clypeus (Fig. 65C) trapezoidal, $\sim 2.5 \times$ as wide as long with two medium c/s, localised posterolaterally, with one sensillum between them; anterior part distinctly less sclerotised than the basal part; anterior border slightly rounded towards the inside.

Mouth parts. Labrum (Fig. 65C) ~ $2.2 \times$ as wide as long, with three piliform Irs, various long; Irs , and $/ r s_{2}$ elongated, located medially, and $/ r s_{3}$ medium, located anterolaterally; anterior border bi-sinuate. Epipharynx (Fig. 65C) with two elongated finger-like als, identical in length; two piliform ams variable in length, and single finger-like mes; labral rods (Ir) distinct, kidney-shaped. Mandibles (Fig. 65D) bifid, cutting edge with small additional teeth; two medium piliform and short $m d s$, both located close to lateral border. Maxillolabial complex: maxilla brownish sclerotised (Fig. 65E) stipes with one stps, two pfs and one very short mbs, stps and both $p f s_{1-2}$ elongated; mala with six finger-like dms variable in length; four medium piliform vms. Maxillary palpi two-segmented; basal palpomere distinctly wider than distal one; basal palpomere with short mpxs and two sensilla, distal palpomere with a group of four apical sensilla in terminal receptive area. Prementum (Fig. 65E) close to cup-shaped, with a single, medium prms; ligula with slightly sinuate margin and two short ligs; premental sclerite broad, sclerotised, posterior extension with elongated apex. Labial palpi one-segmented; palpi with a single pore, and four or five apical sensilla in terminal receptive area; surface of labium smooth. Postmentum (Fig. 65E) with three $p m s$, medium $p m s_{1}$ located posteromedially, long $p m s_{2}$ located mediolaterally, and medium $\mathrm{pms}_{3}$ located anterolaterally; membranous area partially covered with knobby asperities.

Thorax. Prothorax (Fig. 66A) with seven elongated and two medium prns; two medium ps; and single short eus. Mesothorax (Fig. 66A) with a single minute prs; three pds (ordered: minute, medium and medium); one medium as; two medium and one minute $s s$; one medium eps; one medium $p s$; and single minute eus. Chaetotaxy of metathorax (Fig. 66A) almost identical to that of mesothorax. Each pedal area of thoracic segments with four medium and single minute pda.

Abdomen. Segments I-VIII (Fig. 66B, C) with a single minute prs; three pds of various length; one minute and one medium $s s$; one medium and one minute eps; one medium $p s$; one medium Ists; and two minute eus. Abdominal segment IX (Fig. 66C) with two medium and one minute ds; one medium and one minute $p s$; and two minute sts.

Description of pupa (Figs 67A-C, 68A-C). Measurements (in mm). Body length: 2.30-2.90; body width: 0.80-1.75; thorax width: 0.90-1.05; rostrum length: up to 0.75 and + .

Body. Integument white; moderately elongated. Head and pronotum with protuberances. Rostrum rather short, reaching to mesocoxae; on both sexes almost $2.2 \times$ longer than wider. Pronotum trapezoidal $2 \times$ as wide as long. Mesoand metanotum similar in size. Abdominal segments I-IV almost identical in size; segments V and VI tapering gradually, VII semicircular; segment VIII narrow; segment IX reduced. Abdominal segment VIII with, semicircular, weakly sclerotised abdominal protuberance (a-pr). Urogomphi vestigial, weakly sclerotised (Fig. 67A-C).


Figure 66. Rhinusa melas (Boheman, 1838) mature larva, habitus A lateral view of thoracic segments $\mathbf{B}$ lateral view of abdominal segment I C lateral view of abdominal segments VII-X (schemes). Abbreviations: Th. 1-3-number of thoracic segments, Abd. 1-10-number of abdominal seg, setae: as-alar, ds-dorsal, eps-epipleural, eus-eusternal, Ists-laterosternal, pda-pedal, pds-postdorsal, prns-pronotal, prs-prodorsal, ss-spiracular, ps-pleural, sts-sternal.


Figure 67. Rhinusa melas (Boheman, 1838) pupa habitus A ventral view B lateral view C dorsal view.

Chaetotaxy. Well-developed setae, elongated to short, dark brown. Head with a single short os. Rostrum without seta (Fig. 68A). Pronotum with a single as, single $d s$, four $/ s$, and three pls; all pronotal setae elongated, equal in length. Dorsal parts of meso- and metathorax with two elongated setae, placed medially (Fig. 68A-C). Abdominal segments I-VIII dorsally with three medium (on segments VII and VIII elongated) setae dorsally, placed close to posterior margin of the segments. Each lateral part of abdominal segments I-VIII with one short seta. Ventral parts of abdominal segments I-VIII with three short


Figure 68. Rhinusa melas (Boheman, 1838) pupa habitus A ventral view B lateral view C dorsal view (schemes). Abbreviations: $\mathrm{a}-\mathrm{pr}$-abdominal protuberances, $\mathrm{h}-\mathrm{pr}$-head protuberances, p - pr -pronotal protuberances, ur-urogomphi, setae: as-apical, $d$-dorsal, ds-discal, fes-femoral, I, Is-lateral, os-orbital, pls-posterolateral, v-ventral.
setae, of which medial are robust, almost thorn-like. Abdominal segment IX without seta ventrally (Fig. 68A-C).

Remarks and comparative notes. This species is widely distributed, although uncommon, in southern, western, and central Europe (Alonso-Zarazaga et al. 2023). The apparent presence only in southern Spain and in the Pyrenees of adults of a form with a reddish elytral integument together with specimens with black elytra is unusual, although not unique in the genus Rhinusa. In fact, the same occurs in $R$. bipustulata (Rossi, 1792) and $R$. tetra, which live on Scrophularia and Verbascum and are unrelated to $R$. melas. It will surely be very interesting to confirm this distributional pattern through a molecular study.

Biological notes. The host plant of $R$. melas is Chaenorhinum minus. Larvae develop in the seed capsules, where they pupate (Hoffmann 1958; Smreczyński 1976). Adults were also collected on Linaria vulgaris, L. repens and L. spartea, but most likely as occasional visitors.

## Key to mature larvae of selected Rhinusa species

The following key is for the larvae of 14 Rhinusa species treated in this paper plus one species (R. bipustulata) in a previously published paper (Gosik 2010).

1 Pronotal spiracle bicameral (Figs 13A, 18A, 66A)2

- Pronotal spiracle unicameral (Figs 3A, 8A, 23A, 28A, 33A, 38A, 43A, 48A,53A, 56A, 61A) 42 Endocarinal line reaching $1 / 2$ of length of frons (Fig. 65A). Postmentumpartially covered with knobby asperities (Fig. 65E). Premental scleritebroad, well sclerotised, its posterior extension elongated (Fig. 65E). Malawith 6 dms (Fig. 65E)
R. melas
- Endocarinal line reaching < $2 / 3$ of the length of the frons (Figs 12A, 17A). Postmentum smooth (Figs 12E, 17E). Premental sclerite weakly sclerotised, its posterior extension vestigial (Figs 12E, 17E). Mala with 5 dms (Figs 12E, 17E) .3

3 Des, present, $\operatorname{des}_{4}$ absent (Fig. 17A). Antenna with 3 sensilla basiconica (Fig. 17B). Cls very long (Fig. 17C). Ligula with 3 ligs (Fig. 17E). Mala with 5 vms (Fig. 17E). Pronotum with 12 prns (Fig. 18A). Abdominal segments I-VIII with 2 pds (Fig. 18B, C)
R. florum

- Des, absent, des ${ }_{4}$ present (Fig. 12A). Antenna with 1 sensillum basiconicum and 4 sensilla ampullacea (Fig. 12B). Cls very short (Fig. 12C). Ligula with 2 ligs (Fig. 12E). Mala with 4 vms (Fig. 12E). Pronotum with 10 prns (Fig. 13A). Abdominal segments I-VIII with 3 pds (Fig. 12B, C).
R. antirrhini

4 Frons covered with knobby protuberances (Figs 42A, 47A, 52A, 55A)...... 5

- Frons smooth (Figs 2A, 7A, 22A, 27A, 32A, 37A, 60A).............................. 8

5 Pronotum with 5 prns (Fig. 43A). Abdominal segments I-VIII with 3 pds and single eps (Fig. 43B, C)
R. collina

- Pronotum with 7 or more prns (Figs 48A, 53A, 56A). Abdominal segments I-VIII with 4 pds and 3 eps (Figs 48B, C, 53B, C, 56B, C)
- Postmentum partially covered with knobby asperities (Figs 47E, 55E). $\mathrm{Fs}_{2}$ and $f s_{3}$ absent (Figs 47A, 55A) .7

7 Des, short (Fig. 55A). Epipharynx with 3 ams (Fig. 55C). Mala with 6 dms (Fig. 55E). Premental sclerite without sclerotisation (Fig. 55E). Pronotum with 7 prns (Fig. 56A). Meso- and metathoracic segments with 3 pds (Fig. 56A). Abdominal segment IX with 2 ds (Fig. 56B, C)
R. neta

- Des, elongate (Fig. 47A). Epipharynx with 2 ams (Fig. 47C). Mala with 5 $d m s$ (Fig. 47E). Premental sclerite highly sclerotised (Fig. 47E). Pronotum with 12 prns (Fig. 48A). Meso- and metathoracic segments with 4 pds (Fig. 48A). Abdominal segment IX with 3 ds (Fig. 47B, C).... R. eversmanni
8 Posterior extension of premental sclerite very elongated (Fig. 60E). Frons with 5 fs (Fig. 60A)
R. vestita
- Posterior extension of premental sclerite very short, vestigial or even absent (Figs 2E, 7E, 22E, 27E, 32E, 37E). Frons with 3 or 4 fs (Figs 2A, 7A, 22A, 27A, 32A, 37A)

9
9 Clypeus and labrum fused, anterior margin almost straight (Figs 22C, 27C, 32C). Premental sclerite weakly sclerotised, posterior extension absent (Figs 22E, 27E, 32E). Mala wit 4 dms (Figs 22E, 27E, 32E). Postdorsal folds of abdominal segments I-VI distinct, conical, much higher than prodorsal folds (Figs 23B, 28B, 33B) 10

- Clypeus and labrum separated, anterior margin of labrum round or sinuate (Figs 2C, 7C, 37C). Premental sclerite well sclerotised, posterior extension present (Figs 2E, 7E, 37E). Mala with 5-6 dms (Figs 2E, 7E, 37E). Postdorsal folds of abdominal segments I-VI as high as prodorsal folds dorsally (or only slightly higher) (Figs 3B, 8B, 38B) 12
10 Labial palpi well developed and protruding past the outline of the prementum (Fig. 32E). Ligula with 3 ligs (Fig. 32E). Pronotum with 4 prns (Fig. 33A). Each pedal area with 1 elongated and 3 minute setae (Fig. 33A). Meso-, metathorax and abdominal segments I-VIII with 1 prs (Fig. 33AC). All abdominal setae minute, weakly visible (Fig. 33B, C). Abdominal segments I-VIII with 3 pds (Fig. 33B, C).
R. rara
- Labial palpi small or vestigial, not protruding past the outline of the prementum (Figs 22E, 27E). Ligula with 2 ligs (Figs 22E, 27E). Pronotum with more than 7 prns (Figs 23A, 28A). Each pedal area with 5 setae of various lengths (Figs 23A, 28A). Meso-, metathorax and abdominal segments IVIII without prs (Figs 23A-C, 28A-C). All abdominal setae well visible, variable in length (Figs 23B, C, 28B, C). Abdominal segments I-VIII with 1 or 2 pds (Figs 23B, C, 28B, C)
11 Labial palpi vestigial, almost invisible (Fig. 22E). Ligula with 1 ligs (Fig. 22E). Postmentum partially covered with knobby asperities (Fig. 22E). Clypeus with 1 cls (Fig. 22C). Ams and als almost identical in size (Fig. 22C). Sensorium elongated (Fig. 22B). Thoracic and abdominal segments without eps (Fig. 23A-C). Meso- and metathorax with 1 pds (Fig. 23A). Abdominal segments I-VIII with 1 ss and 1 eus (Fig. 23B, C)
R. linariae
- Labial palpi small, but still visible (Fig. 27E). Ligula with 2 ligs (Fig. 27E). Postmentum smooth (Fig. 27E). Clypeus with 2 cls (Fig. 27C). Als fin-ger-like and distinctly larger than small and piliform ams (Fig. 27C). Sensorium rather stout (Fig. 27B). Thoracic and abdominal segments with 1 eps (Fig. 28A-C). Meso- and metathorax with 2 pds (Fig. 28A). Abdominal segments I-VIII with 2 ss and 2 eus (Fig. 28B, C).
R. pilosa

12 Prementum with 2 prms (Fig. 37E). Epipharynx without mes (Fig. 37C). Labral rods round (Fig. 37C). Endocarinal line reaching to $2 / 3$ of the frons (Fig. 37A). Pronotum with 12 prns (Fig. 38A). Abdominal segments I-VIII without prs and with 4 pds (Fig. 38B, C)
$R$. herbarum

- Prementum with 1 prms (Figs 2E, 7E). Epipharynx with 1 or 2 mes (Figs 2C, 7C). Labral rods elongated or kidney-shaped (Figs 2C, 7C). Endocarinal line reaching to $1 / 2$ of frons (Figs 2A, 7A). Pronotum with 6-9 prns (Figs 3A, 8A). Abdominal segments I-VIII with 1-2 prs and with $1-3$ pds (Figs 3B, C, 8B, C)
13 Epipharynx with 2 als (Fig. 7C). Postmentum partially covered with knobbly asperities (Fig. 7E).
R. tetra
- Epipharynx with 3 als (Fig. 2C). Postmentum smooth (Fig. 2E)............... 14

14 Head with 2 pairs of stemmata (Fig. 2A). Antenna with 2 sensilla basiconica and 2 styloconica (Fig. 2B). Posterior extension of premental sclerite moderately elongated (Fig. 2E). Ligula with 3 ligs (Fig. 2E). Abdominal segment IX without ds (Fig. 3C)
R. asellus

- Head with single pair of stemmata. Antenna with 7 sensilla styloconica. Posterior extension of premental sclerite short. Ligula with 2 ligs. Abdominal segment IX with 1 ds
R. bipustulata


## Key to pupae of selected Rhinusa species

The following key is for the pupae described in this paper for 13 Rhinusa species plus the pupa of one species (R. bipustulata), described in a previously published paper (Gosik 2010).

1 Pronotal and abdominal protuberances absent (Figs 30A-C, 35A-C) ..... 2

- Pronotal and/or abdominal protuberances present (Figs 5A-C, 10A-C, 15AC, 20A-C, 25A-C, 40A-C, 45A-C, 50A-C, 58A-C, 63A-C, 68A-C) 3

2 Head and rostrum without seta (Fig. 35A, C). Pronotum with 3 pls and without Is (Fig. 35A-C). Abdominal segments I-VI with 4 setae dorsally (Fig. 35B)
R. rara

- Head with 1 os and rostrum with 1 pas (Fig. 30A, C). Pronotum with 2 pls and 1 ls (Fig. 30A-C). Abdominal segments I-VI with 3 setae dorsally (Fig. 30B).
R. pilosa

3 All femora with 2 setae (Figs 5A-C, 10A-C)............................................... 4

- All femora with 1 seta (Figs 15A-C, 20A-C, 25A-C, 40A-C, 45A-C, 50AC, 58A-C, 63A-C, 68A-C)6

4 Rostrum with 2 pas. Abdominal segments I-VII with 5 setae ventrally .

- Rostrum without or with 1 pas (Figs 5A,C, 10A,C). Abdominal segments I-VII with 4 setae ventrally (Figs 5A, 10A).
5 P-pr elongated, sharply ended (Fig. 5A, C). Rostrum up to 1.60 mm 万 and 2.60 mm . . Rostrum with 1 pas, 2 rs, and 1 es (Fig. 5A, C). Pronotum with 2 as and 4 pls (Fig. 5A-C). Procoxae with 1 seta (Fig. 5A) ..........R. asellus
- $\quad$-pr short, flattened (Fig. 10A, C). Rostrum up to $0.70 \mathrm{~mm}{ }^{\top}$ and $q$. Rostrum without pas and es, with 1 rs (Fig. 10A, C). Pronotum with 1 as and 3 pls (Fig. 10A-C). Procoxae without seta (Fig. 10A).
R. tetra

6 Each of abdominal segments I-VII with 3 or more setae dorsally (Figs 15B, 20B, 40B, 45B, 50B, 58B, 63B, 68B).

- Each of abdominal segments I-VII with 2 setae dorsally (Fig. 25B)............ R. linariae

7 A-pr well developed, prominent, protruding past the outline of the body (Figs 15A-C, 20A-C, 40A-C)
.8

- A-pr vestigial (almost invisible) or absent (Figs 45A-C, 50A-C, 58A-C, 63A-C, 68A-C) 10
8 P-pr well developed, prominent (Figs 15A-C, 20A-C). Clubs smooth (Figs 15A-C, 20A-C). .9
- P-pr vestigial (almost invisible; Fig. 40A-C). Clubs covered with knobby protuberances (Fig. 40A-C)
R. herbarum

9 Pronotum with 2 as, without $d s, 4 \mathrm{ls}$, and 3 pls (Fig. 15A-C). Rostrum without seta (Fig. 15A, C)
R. antirrhini

- Pronotum with 2 as, 1 ds, 2 ls, and 4 pls (Fig. 20A-C). Rostrum with 1 rs (Fig. 20A, C)
R. florum

10 Medial abdominal ventral seta much longer (or robust, spike-like) than the remaining ventral setae (Figs 63A, 68A)
.11

- All abdominal ventral setae similar in size (Figs 45A, 50A, 58A) ............. 12

11 Pronotum with 2 as, 1 ds , 2 ls , and 4 pls (Fig. 63A-C). Abdominal ventral setae robust, spike-like (Fig. 63A). Abdominal segments I-VII with 6 setae dorsally (Fig. 63B)
R. vestita

- Pronotum with 1 as, 1 ds, 4 ls, and 3 pls (Fig. 68A-C). Abdominal ventral setae elongated, hair-like (Fig. 68A). Abdominal segments I-VII with 3 setae dorsally (Fig. 68B)
R. melas

12 Abdominal segments I-VII with 4 setae dorsally (Figs 45B, 50B)........... 13

- Abdominal segments I-VII with 5 setae dorsally (Fig. 58A) ............ R. neta

13 Rostrum with 1 pas, without rs (Fig. 45A, C). Pronotum with 3 as, $1 \mathrm{ds}, 2$ ls, and 2 pls (Fig. 45A-C)
R. collina

- Rostrum with 1 rs, without pas (Fig. 50A, C). Pronotum with 3 as, without ds, 3 ls , and 3 pls (Fig. 50A-C)
R. eversmanni


## Discussion

## Comparison of the immature stages of Rhinusa

The most characteristic and commonly shared attributes among Rhinusa larvae are as follows: (1) pronotal shield is indistinct and not pigmented (only in $R$. eversmanni pigmented slightly more than the rest of the segment); (2) thoracic prodorsal folds are always much smaller than postdorsal folds or even vestigial; (3) abdominal postdorsal folds (especially of segments III-VII) higher than prodorsal folds or even in the form of conical protuberances; (4) cuticle covered with fine, sharp asperities; (5) cuticle without dark spots or dark pigmentation; (6) head slightly narrowed bilaterally, seldom rounded; (7) labrum with 2 als (except in $R$. asellus, $R$. bipustulata and $R$. neta, which have 3 als); (8) des ${ }_{1}$ short or absent, rarely elongated; and (9) $f s_{1-2}$ usually absent or minute. Other larval characters, such as the colour of the head, or some chaetotaxy as the counts of setae on the head (pes and ves) and mouth parts (lrs, mes, and
ams) and finally the counts of thoracic and abdominal setae, show significant interspecific variability in Rhinusa larvae.

The identification of attributes diagnostic of genus Rhinusa seems to be much easier for the pupal than for the larval stage. All described pupae present large interspecific variability both in chaetotaxy and body shape. Among all pupal characters, the most commonly shared are (1) head protuberances always present; (2) head and rostrum with very limited numbers of setae (except in $R$. asellus and $R$. bipustulata); (3) pronotal protuberances (if present) separated at the base of the pronotum, flattened (only in $R$. asellus conical); (4) abdominal protuberance on abdominal segment VIII usually visible; (5) femora usually with a single fes; and (6) urogomphi short or vestigial. The other characters (mainly chaetotaxy) are highly variable between species.

Based on adult morphological characters and host plants, Caldara et al. (2010) proposed the division of Rhinusa into several groups of species. Except for $R$. rara, all currently studied species were investigated in the species group study by Caldara et al. (2010): namely, the R. bipustulata group (here with only the nominotypic species); the $R$. tetra group with two species ( $R$. tetra, $R$. asellus); the $R$. antirrhini group with two species ( $R$. antirrhini, R. florum); the $R$. linariae group with the nominotypic species; the $R$. herbarum group with the nominotypic species; the $R$. neta group with four species ( $R$. neta, $R$. collina, $R$. eversmanni, R. incana); the $R$. vestita group with the nominotypic species; and finally the $R$. melas group with the nominotypic species. Our study confirms that some specific morphological characters are uniquely characteristic of each species group according to Caldara et al. (2010) and, in particular, shows again that all species considered can be identified by examining larvae and pupae based on at least one character state. However, it is worth stressing that immatures of species that belong to a particular group have some important similarities with each other. Unique morphological characters of larvae or pupae are listed here for groups with more than one described representative:
R. tetra group: larvae (epicranial line reaching $1 / 2$ of the frons (Figs 2A, 6A); premental sclerite well sclerotised, Y -shaped (Figs 2E, 6E); posterior extension of premental sclerite present (Figs 2E, 6E); labral rods kidney-shaped (Figs 2C, 6C)) and pupae (abdominal protuberances rounded (Figs 5A-C, 10A-C); urogomphi very short (Figs 5A-C, 10A-C); each femora with two fes (Figs 5A, C, 10A, C))
$\boldsymbol{R}$. antirrhini group: larvae (epicranial line reaching $3 / 4$ of the frons (Figs 12A, 17A); premental sclerite vestigial (Figs 12E, 17E); posterior extension of premental sclerite absent (Figs 12E, 17E); thoracic spiracles bicameral (Figs 13A, 18A); abdominal segments I-VII with two eps (Figs 13B, 18B)) and pupae (urogomphi relatively well developed (Figs 15A-C, 20A-C))
R. neta group: larvae (epicranial line reaching $4 / 5$ of the frons (Figs 42A, 47A, 52A, 55A); frons densely covered with cuticular processes (Figs 42A, 47A, 52A, 55A); premental sclerite U-shaped, posterior extension of premental sclerite absent (Figs 42E, 47E, 52E, 55E); labium usually covered with asperities (Figs 42E, 47E, 52E, 55E); labral rods kidney-shaped (Figs 42C, 47C, 52C, 55C)) and pupae (abdominal ventrites with three setae each (Figs 45A, 50A, 58A); abdominal protuberances vestigial or absent (Figs 45A-C, 50A-C, 58A-C))

Based on the following morphological similarities, $R$. rara is an undeniable member of the R. pilosa group: larvae (head wide (Figs 27A, 32A); epicranial line reaching $1 / 2$ of the frons (Figs 27A, 32A); premental sclerite vestigial, posterior extension of premental sclerite absent (Figs 27E, 32E); clypeus and labrum fused (Figs 27C, 32C); labral rods rounded (Figs 27C, 32C); abdominal postdorsal folds in the form of conical protuberances (Figs 28B, 33B)) and pupae (pronotal and abdominal protuberances absent (Figs 30A-C, 35A-C)).

It was very challenging to identify traits distinguishing a particular species group because the remaining species groups were represented by only one species. However, it is worth stressing that immatures of species representing these species groups differ significantly from those of other species groups. As a result, the findings of the investigation regarding immature stages strongly support the taxonomic division that Caldara et al. (2010) proposed.

## Comparison of the immature stages of Rhinusa and Gymnetron

The taxonomic positions of the genera Gymnetron and Rhinusa within Mecinini are still the subject of extensive study and discussion. With regard to the characters of the immature stages, despite the predominant similarities between the two genera, there are obvious visible differences in body structures.

Specifically, in the larval stage, the most visible differences between Gymnetron and Rhinusa are as follows: (1) cuticle smooth or covered with knobby, darkly pigmented spots (vs. cuticle covered with sharp asperities, unicoloured); (2) abd. segment $X$ exserted, well visible, setae present (vs. abd. segment $X$ completely hidden inside the IX segment, seta mostly absent); (3) pronotal shield usually well separated, darkly pigmented (vs. pronotal sclerite usually absent); (4) thoracic prodorsal folds usually with 2 prs (vs. thoracic prodorsal folds usually with 1 prs); (5) epipharynx mostly with 3 als (vs. epipharynx mostly with 2 als); and (7) premental sclerite usually incomplete, at most in the form of a tiny ring, posterior extension always absent (vs. premental sclerite at least in the form of an incomplete ring, usually well developed with elongated posterior extension (indistinguishable only in $R$. linariae)).

In the pupal stage, Gymnetron differs from Rhinusa by the following: (1) lack of head protuberances (vs. head protuberances always present); (2) pronotal protuberances well developed, always higher than wide, spoon-like (vs. pronotal protuberances always wider than higher, flattened) (elongated, conical only in $R$. asellus); (3) femora usually with 2 fes (vs. femora mostly with a single fes); and (4) urogomphi always present, relatively elongated (vs. urogomphi variable in shape: elongated, vestigial or absent).

The structure of the cuticle (in the larval stage) being smooth or covered with knobby, darkly pigmented spots and the presence of head protuberances (in the pupal stage) can be considered apomorphies for the genus Rhinusa.

However, the differentiation between Gymnetron and Rhinusa might be difficult due to some very characteristic features shared by species of the two genera: frontal suture sometimes very wide, but indistinct (e.g., Fig. 1B); labrum and clypeus fused; four anal folds, anus placed ventrally; count of setae greatly reduced; and postmentum covered with asperities. Unfortunately, other features useful in species recognition (e.g., length of endocarina, shape of labral rods) are highly interspecific variable for Gymnetron or Rhinusa species.

## Conclusions

As expected based on the appearance and lifestyles of the adults, the larvae and pupae of Gymnetron and Rhinusa are more closely similar to those of Me cinus than to those of Miarus and Cleopomiarus. However, it is noteworthy that the morphological differences in the immature stages between Gymnetron + Rhinusa and Mecinus, e.g., des, usually short, minute or absent (vs. des ${ }_{1}$ always elongated), fes ${ }_{2}$ always present (vs. fes ${ }_{2}$ usually absent), and mes usually lacking or single (vs. almost two mes), are surely more consistent than the very few distinctive characters in the adults. On this basis, we think that a phylogenetic approach for the Mecinini based on the morphological characters of the immature stages will be able to further clarify the complex systematics of these genera, and this is our intended next step.

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## Additional information

Conflict of interest
The authors have declared that no competing interests exist.

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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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# First mitogenomic characterization of Macromotettixoides (Orthoptera, Tetrigidae), with the descriptions of two new species 

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#### Abstract

Classification of species is commonly based on morphological, molecular, and distribution depending on the taxa. Macromotettixoides Zheng, Wei \& Jiang, 2005 and Formosatettix Tinkham, 1937 are both wingless types of Tetrigidae with extremely similar morphological characteristics, and in the current taxonomic system they are placed in two different subfamilies, Metrodorinae and Tetriginae, respectively. It is difficult to clearly identify the species of these two genera by morphological characteristics, and molecular data is often needed to assist identification. Here, the complete mitogenomes of two new species were sequenced and assembled, with that of Macromotettixoides orthomargina. Molecular data of species of Formosatettix were used to test the monophyly of Macromotettixoides and to re-assess the generic characters, and also to test whether Macromotettixoides belongs to the Asian Metrodorinae or Tetriginae. Furthermore, mitochondrial characteristics were analyzed and the phylogeny of the Tetrigidae reconstructed based on mitochondrial proteincoding genes (PCGs). The results indicated that the two new species were clustered with Macromotettixoides rather than Formosatettix, and the anterior margin of the fastigium and pronotum of the two new species usually had the humeral angle different from that of Formosatettix. Therefore, after integrating morphological and molecular data, the two new species were placed in the genus Macromotettixoides, $M$. maoershanensis $\mathbf{s p}$. nov. and $M$. brachycorna sp. nov. Finally, a phylogenetic reconstruction supported Macromotettixoides being assigned to Tetriginae rather than Metrodorinae, in contrast to the previous classification of this genus.


Key words: China, Formosatettix, Metrodorinae, mitochondrial genome, phylogeny, taxonomy, Tetriginae

## Introduction

Tetrigidae is a family of Orthopteran insects in the superfamily Tetrigoidea. The pygmy grasshoppers are an ancient group of Orthoptera with a relatively uniform body structure (Holst 1986; Zhao et al. 2016). However, the
polymorphism within species, including different wing morphs and color variation, poses several challenges to classification. In order to effectively identify species, it is therefore necessary to combine as many different types of data as possible.

Mitogenomes are stable in structure and composition; they have maternal inheritance and less recombination (Simon et al. 2006; Cameron 2014). Mitochondrial genomes have been widely used to study species lineages, biological evolution, and species classification. The mitochondrial genomes of insects are generally between $15 \mathrm{k}-20 \mathrm{k}$ bp in size, containing 22 tRNAs, 13 protein-coding genes (the ND series, the CO series, the ATP series, and Cytb, two rRNAs, and a control region (or A+T rich region)) (Clary and Wolstenholme 1985; Cheng et al. 2000). The transposition of trnD and trnK is common in Caelifera (Boore 1999).

To date, among the Tetrigidae, only 35 species have their mitochondrial genomes published in GenBank. Additionally, many Tetrigidae have known COI sequences, but these are not adequate for deep phylogeny, only for species identification (Fang et al. 2010; Kasalo et al. 2023). More mitochondrial genomes should be sequenced in the future to help researchers further investigate the evolutionary history of the Tetrigidae.

Macromotettixoides Zheng, Wei \& Jiang, 2005 (Zheng et al. 2005) is a genus of the subfamily Metrodorinae, for which a total of 24 species have been recorded as endemic to China. Macromotettixoides is very similar to Formosatettix Tinkham, 1937 (subfamily Tetriginae). The differences between the two genera occur in the vertex and the pronotum. In Formosatettix, the fastigium of the vertex in dorsal view surpasses the anterior margin of the eyes; the anterior margin of the fastigium is generally arched or angularly projecting, sometimes straight; the pronotum is usually without a humeral angle, with the posterior angles of the lateral lobes turned downwards, and the apex of the posterior angles obtuse and rounded. In Macromotettixoides, the fastigium of the vertex in dorsal view does not surpass the anterior margin of the eyes; the pronotum is with humeral angles; the posterior angles of the lateral lobes are usually turned outwards, and the apex of the posterior angles is truncated or sometimes slightly obtuse and rounded. In reality, the classification and identification of the two genera is relatively difficult, and sometimes molecular methods are needed for determination.

In this study, we collected two new species in Guangxi from China and discovered that they shared traits with both genera Macromotettixoides and Formosatettix. The two new species are similar to Formosatettix in that the anterior margin of the fastigium is angularly projecting and the posterior angles of pronotum turned downwards, and the apex of the posterior angles obtuse and rounded, while the pronotum is with humeral angles are similar to Macromotettixoides. Therefore, based solely on their morphology, it was difficult to classify them to any genus. The purposes of this study were to sequence the complete mitochondrial genomes of two new species and Macromotettixoides orthomargina Wei \& Deng, 2023, to examine their phylogenetic positions and relationships within the genus Macromotettixoides and Formosatettix, and to describe and illustrate the two new species from China.

## Materials and methods

## Taxon sampling

Specimens of M. orthomargina, M. maoershanensis sp. nov., and M. brachycorna sp. nov. were selected as representatives of the genus Macromotettixoides. (1) M. orthomargina, $n=3$, collected at Lingshan, Mianning County, Sichuan Province, China; 23 June 2020; (2) M. brachycorna sp. nov., $n=3$, collected at Jiuwanshan National Nature Reserve, Huanjiang Country, Guangxi, China; $25^{\circ} 11^{\prime} 41^{\prime \prime} \mathrm{N}$, 108³8'51'E; 29 July 2022; (3) M. maoershanensis sp. nov., $n=14$, collected at Maoershan National Nature Reserve, Xing'an County, Guangxi, China; $25^{\circ} 51^{\prime} 35^{\prime \prime} \mathrm{N}$, $110^{\circ} 29^{\prime} 34^{\prime \prime} \mathrm{E} ; 12$ July 2021. The specimens were preserved in $100 \%$ anhydrous ethanol (Xilong Scientific, Sichuan, MA, China) and stored in the refrigerator at $-20{ }^{\circ} \mathrm{C}$ in the Key Laboratory of Ecology of Rare and Endangered Species and Environmental Protection, Ministry of Education of Guangxi Normal University (MEGNU). All photographs were taken using the Keyence VHX-5000 (Keyence Corporation, Osaka, Japan) and edited in Adobe Photoshop 23.0.0.

To clarify the taxonomic status of $M$. maoershanensis sp. nov. and M. brachycorna sp. nov., we combined the mitochondrial genome data assembled in the laboratory and the complete mitochondrial genome data of Tetrigidae from GenBank, representing one family, five subfamilies, 23 genera, and 36 species in total (Table 1). Mirhipipteryx andensis Günther, 1969 in Tridactyloidea (NC_028065) was selected as the outgroup. A phylogenetic tree of the Tetrigidae was constructed based on Bayesian inference (BI) and maximum likelihood (ML) methods.

## Sequencing, assembly, and annotation

All muscle tissues of each sample were extracted using a TIANamp Genomic DNA Kit (Tiangen Biotech, Beijing, China), and the extracted samples were sent to Berry Genomics (Beijing, China) for genomic sequencing using Next Generation Sequencing (NGS). The remaining specimens were deposited as voucher specimens at the Guangxi Normal University. Separate 350-bp insert libraries were created from the whole genome DNA and sequenced using the Illumina HiSeq $X$ Ten sequencing platform. A total of 5 Gb of 150-bp pairedend (PE) reads were generated in total for each sample. The mitogenome sequences were assembled using NOVOPlasty 4.2.1 and annotated using the MITOS Web Server (http://mitos2.bioinf.uni-leipzig.de/index.py, accessed on 17 March 2023; Donath et al. 2019). The annotated mitogenome sequences were checked in CLC Genomics Workbench 12.0.0, MEGA 11.0.1, and Geneious Prime 11.0.15. The maps of the mitogenomes were generated using the Proksee website (https://proksee.ca, accessed on 19 December 2023, Grant et al. 2023). The secondary structures of the RNA encoding genes predicted in MITOS were visualized manually using Adobe Photoshop 23.0.0. All sequences generated from this study were deposited in GenBank (for accession numbers see Table 1).

The base compositions, G-C- and A-T-skews, and codon usages were calculated in PhyloSuite v. 1.2.3. The formulas used to calculate the skews of the composition were $(\mathrm{A}-\mathrm{T}) /(\mathrm{A}+\mathrm{T})$ for the $\mathrm{A}-\mathrm{T}$-skew and $(\mathrm{G}-\mathrm{C}) /(\mathrm{G}+\mathrm{C})$ for the $\mathrm{G}-\mathrm{C}$-skew.

Table 1. Accession numbers and references of the mitogenomes of Tetrigidae included in this study.

| Subfamily | Species | Accession number | Reference |
| :---: | :---: | :---: | :---: |
| Tripetalocerinae | Tripetaloceroides tonkinensis | MW770353 | Zhang et al. 2021 |
| Batrachideinae | Saussurella borneensis | MZ169555 | Deng et al. 2021 |
| Metrodorinae | Bolivaritettix lativertex | MN083173 | Chang et al. 2020 |
|  | Bolivaritettix sikkinensis | MN083174 | Yang 2017 |
|  | Bolivaritettix yuanbaoshanensis | KY123121 | Yang 2017 |
|  | Mazarredia convexa | MN938924 | Li et al. 2020c |
| Criotettigini | Criotettix japonicus | MT162542 | Li et al. 2021a |
| Scelimeninae | Falconius longicornis | MT162543 | Li et al. 2021a |
|  | Paragavialidium hainanense | NC_071831 |  |
|  | Paragavialidium sichuanese | MT162549 | Li et al. 2021a |
|  | Scelimena melli | MW722938 | Li et al. 2021b |
|  | Zhengitettix curvispinus | MT162544 | Li et al. 2021a |
| Thoradontini | Eucriotettix oculatus | MN083176 | Chang et al. 2020 |
|  | Loxilobus prominenoculus | MT162545 | Li et al. 2021a |
|  | Thoradonta nodulosa | MT162547 | Li et al. 2021a |
|  | Thoradonta obtusilobata | KY798414 | Lin et al. 2017 |
|  | Thoradonta yunnana | OP805341 |  |
| Tetriginae | Alulatettix yunnanensis | NC_018542 | Xiao et al. 2012a |
|  | Coptotettix longjiangensis | KY798413 | Lin et al. 2017 |
|  | Coptotettix longtanensis | OK540319 |  |
|  | Ergatettix serrifemora | MN938923 | Chang et al. 2020 |
|  | Ergatettix dorsifera | NC_046540 | Chang et al. 2020 |
|  | Euparatettix bimaculatus | NC_046541 | Chang et al. 2020 |
|  | Euparatettix variabilis | NC_046542 | Chang et al. 2020 |
|  | Formosatettix qinlingensis | KY798412 | Lin et al. 2017 |
|  | Macromotettixoides brachycorna sp. nov. | OR003899 | This study |
|  | Macromotettixoides maoershanensis sp. nov. | OR030790 | This study |
|  | Macromotettixoides orthomargina | OR030789 | This study |
|  | Systolederus anhuiensis | OP113951 |  |
|  | Systolederus bashanensis | NC_063118 | Li et al. 2021 |
|  | Systolederus hainanensis | NC_063117 | Li et al. 2021 |
|  | Systolederus nigropennis | MN938922 | Li et al. 2020b |
|  | Systolederus spicupennis | MH791445 |  |
|  | Tetrix japonica | NC_018543 | Xiao et al. 2012b |
|  | Tetrix ruyuanensis | NC_046412 | Chang et al. 2020 |
| Outgroup | Mirhipipteryx andensis | NC_028065 | Song et al. 2015 |

## Phylogenetic analyses

To systematically understand the phylogenetic relationships of $M$. orthomargina and the two new species, the mitochondrial genomes of the three species obtained in the laboratory and the mitogenomes of 36 species taken from GenBank were used to construct a phylogeny of the Tetrigidae, and Mirhipipteryx andensis of the Tridactyloidea was selected as the outgroup. The analysis was performed using PhyloSuite 1.2.3. Redundant sequences were removed, and protein-coding genes in the mitochondrial genome were extracted and aligned
in batches with MAFFT (Katoh and Standley 2013). The aligned sequences were concatenated. ModelFinder (Kalyaanamoorthy et al. 2017) was used to select the best-fit model using AICc and BICc standards. The best-fitting model was used for the phylogenetic analyses of the mitochondrial PCGs (Table 2).

Bayesian inference phylogenies were obtained using MrBayes v. 3.2.7a (Ronquist et al. 2012) under the GTR+F+I+G4 model. The analysis was run for 4000006 generations, two parallel runs, sampling every 100 generations, and the first $25 \%$ generations were discarded as burn in, whereas the remaining samples were used to summarize Bayesian posterior probabilities (PP). Support for each branch was derived from the posterior probabilities (PP) observed on the majority-rule consensus.

The maximum likelihood phylogenies were inferred using IQ-TREE v. 2.2.0 (Nguyen et al. 2015) under the Edge-linked partition model with 5000 ultrafast bootstrap replicates (Minh et al. 2013). The resulting phylogenetic tree was further edited on the iTOL website (https://itol.embl.de/itol.cgi, accessed on 20 March 2023; Letunic and Bork 2021).

Table 2. Best-fitting models used for phylogenetic analyses of the mitochondrial PCGs dataset.

| Information Criterion for model selection | Best model | Partition names |
| :---: | :---: | :---: |
| AICc | GTR+F+R4 | cox3_mafft, nad4L_mafft, nad4_mafft |
|  | TIM $+\mathrm{F}+\mathrm{I}+\mathrm{I}+\mathrm{R} 5$ | nad1_mafft |
|  | GTR+F+I+I+R5 | cox1_mafft, nad5_mafft |
|  | TIM2+F+I+I+R4 | cox2_mafft |
|  | TIM3+F+R5 | atp6_mafft, nad2_mafft |
|  | TIM2+F+R4 | cytb_mafft, nad3_mafft |
|  | TIM3+F+I+I+R4 | nad6_mafft |
|  | TN+F+l+l+R3 | atp8_mafft |
| BIC | GTR+F+I+G4 | atp6_mafft, cox2_mafft, cytb_mafft, cox1_mafft, cox3_mafft, nad1_mafft, nad4L_mafft, nad4_mafft, nad2_mafft, nad3_mafft, nad5_mafft, nad6_mafft, atp8_mafft |

## Results

## Characteristics of newly sequenced mitogenomes

In this study, the mitochondrial genomes of M. orthomargina, M. brachycorna sp. nov., and $M$. maoershanensis sp. nov. were all circular molecules, with total lengths of $16,995 \mathrm{bp}, 18,034 \mathrm{bp}$, and $16,999 \mathrm{bp}$, respectively (Fig. 1). The structures of the three newly sequenced Macromotettixoides species mitogenomes were the same as those of the mitochondrial genomes of other metazoan animals (Bernt et al. 2013), with 13 protein-coding genes, 22 tRNAs, 2 rRNAs and control regions rich in A+T bases. Among the 13 protein-coding genes, nad1, nad4, nad4L, and nad5 were located on the N strand, while the other genes (nad2, nad3, nad6, cox1, cox2, cytb, atp6, and atp8) were located on the J strand. In all mitochondrial genes, 14 genes were located on the minority strand, and 23 genes were located on the majority strand.

The gene arrangements of the newly sequenced mitochondrial genomes were similar to those of other species of Tetrigidae (Lin 2014). The base composition was A+T-biased, and the proportions of A+T content were $73.1 \%$ (M. orthomar-


Figure 1. Circular map of the mitogenomes A M. orthomargina B M. maoershanensis sp . nov. C M. brachycorna sp. nov.
gina), $71.4 \%$ (M. brachycorna sp. nov.), and $73.7 \%$ ( $M$. maoershanensis sp. nov.). The AT-skews were 0.1997 ( $M$. orthomargina), 0.158 ( $M$. brachycorna sp. nov.), and 0.1967 (M. maoershanensis sp. nov.), and the GC-skews were -0.2937 (M. orthomargina), -0.274 ( $M$. brachycorna sp. nov.) and -0.2966 ( $M$. maoershanensis sp. nov.) (Table 3). The relative synonymous codon usage (RSCU) values of the mitogenome were summarized (Fig. 2). The codon distribution analysis showed that the two codons UUA (Leu2) and UCA (Ser2) were the most frequently used in $M$. maoershanensis sp . nov. and $M$. brachycorna sp. nov. The codons of UUA (Leu2) and UCU (Ser2) in M. orthomargina were the most frequently used. The frequency of the codons ending with $A / U$ was much higher than with $G / C$, suggesting that the AU composition at the third position of codons had a positive influence on the nucleotide AT (or AU) bias of the PCGs in Macromotettixoides.

As in most pygmy grasshoppers, ATN was the initiation codon of M. orthomargina, M. brachycorna sp. nov., and M. maoershanensis sp. nov., with ATG being the most frequently used (Table 4). The initiation codons of ND2, ND3, and ND6 in M. brachycorna sp. nov. were different from those of the other two species. ND2, ND3, and ND6 in M. brachycorna sp. nov. initiated from ATA, ATC, and ATG respectively, whereas ND2, ND3, and ND6 in M. maoershanensis sp. nov. and $M$. orthomargina initiated from ATT, ATA, and ATA, respectively. The termination codon was the typical TAN, in which TAA was used most frequently, followed by TAG. The termination codon of ND4 was TAA (M. brachycorna sp. nov.) and TAG (M. maoershanensis sp. nov. and M. orthomargina).

Table 3. Nucleotide composition of the mitogenomes of Macromotettixoides.

| Regions | A\% | G\% | AT\% | AT-skew | GC-skew |
| :--- | :---: | :---: | :---: | :---: | :---: |
| Full genome | $41.4 / 44.1 / 43.9$ | $10.4 / 9.2 / 9.5$ | $71.4 / 73.7 / 73.2$ | $0.158 / 0.198 / 0.200$ | $-0.274 /-0.296 /-0.293$ |
| PCGs | $31.0 / 31.9 / 31.2$ | $14.1 / 13.2 / 13.6$ | $69.4 / 72.3 / 71.2$ | $-0.108 /-0.117 /-0.124$ | $-0.079 /-0.046 /-0.051$ |
| $1^{\text {st }}$ codon position | $34.0 / 34.8 / 34.3$ | $18.5 / 17.9 / 18.1$ | $67.1 / 69.0 / 68.9$ | $0.013 / 0.008 /-0.004$ | $0.128 / 0.152 / 0.163$ |
| $2^{\text {nd }}$ codon position | $20.3 / 20.3 / 20.4$ | $14.8 / 14.7 / 14.7$ | $65.6 / 65.9 / 66.2$ | $-0.382 /-0.384 /-0.384$ | $-0.140 /-0.135 /-0.130$ |
| $3^{\text {rd }}$ codon position | $38.6 / 40.5 / 38.9$ | $9.0 / 7.1 / 8.1$ | $75.4 / 81.7 / 78.6$ | $0.023 /-0.009 /-0.01$ | $-0.270 /-0.217 /-0.240$ |
| rRNAs | $40.8 / 41.8 / 41.6$ | $12.7 / 12.2 / 12.5$ | $74.2 / 75.0 / 74.0$ | $0.100 / 0.115 / 0.124$ | $-0.017 /-0.026 /-0.038$ |
| tRNAs | $28.8 / 27.3 / 27.6$ | $16.1 / 15.9 / 16.4$ | $75.2 / 76.9 / 76.1$ | $-0.234 /-0.290 /-0.274$ | $0.296 / 0.374 / 0.372$ |
| CR | $36.2 / 46.3 / 48.1$ | $13.1 / 9.6 / 8.0$ | $69.4 / 79.2 / 80.0$ | $0.040 / 0.170 / 0.203$ | $-0.140 /-0.077 /-0.200$ |

Note: Data are given as M. brachycorna sp. nov./ M. maoershanensis sp. nov./ M. orthomarginis. CR, control region.

Table 4. Initiation and termination codons of PCGs of the newly sequenced complete mitogenomes.

| PCGs | Initiation codons |  |  | Termination codons |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
|  | M. maoershanensis | $\boldsymbol{M} . \boldsymbol{b r a c h y c o r n a}$ | $\boldsymbol{M}$. orthomargina | $\boldsymbol{M}$. maoershanensis | $\boldsymbol{M}$. brachycorna | $\boldsymbol{M}$. orthomargina |
| ATP6 | ATG | ATG | ATG | TAA | TAA | TAA |
| ATP8 | ATG | ATG | ATG | TAA | TAA | TAA |
| COX1 | ATC | ATC | ATC | TAA | TAA | TAA |
| COX2 | ATG | ATG | ATG | TAA | TAA | TAA |
| COX3 | ATG | ATG | ATG | T | T | T |
| CYTB | ATG | ATG | ATG | TAA | TAA | TAA |
| NAD1 | ATT | ATT | ATA | TAA | TAA | TAA |
| NAD2 | ATT | ATA | ATT | TAA | TAA | TAA |
| NAD3 | ATA | ATC | ATA | TAG | TAG | TAG |
| NAD4 | ATG | ATG | ATG | TAG | TAA | TAG |
| NAD4L | ATT | ATT | ATT | TAA | TAA | TAA |
| NAD5 | ATG | ATG | ATG | T | TA | T |
| NAD6 | ATA | ATG | ATA | TAA | TAA | TAA |

Comparing the AT content of the mitochondrial genomes' PCGs, rRNAs, tRNAs, and the control regions of Tetrigidae (Suppl. material 1: table S1), there was not significantly difference in the lengths of PCGs and 16S rRNA within the same genus, such as Macromotettixoides, Systolederus Bolívar, 1887, and Thoradonta Hancock, 1909. The lengths of tRNAs and 12S rRNA varied in the different genera. The difference in the total length of the mitochondrial genes among different species is mainly due to the difference in the control region length, and there were also differences in the AT content among different genes within the same genus. The PCGs of Bolivaritettix is shorter compared to other species, due to its lack of nad4. The overall AT content of Scelimena and Tripetaloceroides was relatively low, while the AT content of Systolederus was relatively high.

Comparison of the codons of PCGs in Tetrigids (Suppl. material 1: tables S2, S3) showed that most species mainly started with ATN, with a small number using TTG, GTG, ACA, AAA, etc. as the starting codons. Among them, the cox1 of many species started with ACA and AAA. The starting codons of the same genus were not exactly the same, such as these genera Macromotettixoides and Paragavialidium Zheng, 1994, Systolederus, and Thoradonta. The termination codons of PCGs were typical TAG or TAA, with cox1, cox3, and nad5 mainly ter-


Figure 2. Relative synonymous codon usage (RSCU) of the mitochondrial genomes of three species in Macromotettixoides.
minate with incomplete codons, T or TA. There were certain differences in the termination codons among species of the same genus. Some studies proposed that the incomplete T -termination codons can form complete termination codons through polyadenylation during mRNA processing (Weng et al. 2022).

There was little difference in the lengths of all tRNAs in the newly sequenced mitochondrial genomes of $M$. orthomargina and $M$. maoershanensis sp. nov. All secondary structures of the tRNAs of the three species could be folded into a typical clover structure (Fig. 3), except for trnS1 of M. orthomargina and M. brachycorna sp. nov. The trnS1 of $M$. orthomargina and $M$. brachycorna sp. nov. lacked the DHU arm. The types and number of tRNA mismatches differed between $M$. orthomargina and $M$. maoershanensis sp. nov. The mismatch of A-A occurred in trnW and $t r n$; A-G occurred in $\operatorname{trnG}$ and $t r n F$; A-C occurred in $\operatorname{trnG}$ and $t r n S 2$; and $\mathrm{C}-\mathrm{U}$ only occurred in $\operatorname{trnM}$ (Table 5). The mismatch of U-U existed in trnE, trnF, trnR, and trnY. The G-U mismatch occurred most frequently, but it did not appear in $t r n I$, $t r n W$, $t r n R$, trnE, or $\operatorname{trn} T$, and there were six G-U mismatches (Table 6).

## Phylogeny

This study supported the non-monophyly of Metrodorinae and Scelimeninae (Figs 4, 5), and this was highly supported by the BI analysis (PP > 0.90). Howev-



(N M. orthomarginis
(N) M. maoershanensis sp. nov.
(N M. brachycorna sp. nov.
-N lacking in the taxon

Figure 3. Secondary structure for the tRNAs of three species in Macromotettixoides.
er, there was only one species' datum for Tripetalocerinae and Batrachideinae, and thus their monophyly could not be determined. The monophyly of most species in the same genus as Bolivaritettix Günther, 1939, Paragavialidium, Thoradonta, Coptotettix Bolívar, 1887, Euparatettix Hancock, 1904, and Tetrix Latreille, 1802 was supported in the BI tree, the same as in Wang et al. (2021).

In this study (Figs 4, 5), the phylogenetic reconstruction suggested that the two new species were clustered into a monophyletic group with $M$. orthomargina rather than with F. qinlingensis ( $\mathrm{PP}=1.00$ ). Although the two new species were very similar to Formosatettix in the posterior angles of the lateral lobes being turned downwards and the apex of the posterior angles being obtuse and rounded, they were not classified in the genus Formosatettix but rather in Macromotettixoides. Therefore, we named the two new species as M. maoershanensis sp. nov. and M. brachycorna sp. nov. In the phylogenetic analysis, Macromotettixoides was found to be


Figure 4. BI tree resulting from the analysis of 13 PCGs of mitochondrial genomes in the Tetrigidae.

Table 5. Total numbers of different types of base mismatches in tRNAs of the three newly sequenced mitogenomes.

| Species | A-A | A-G | A-C | G-U | C-U | U-U |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
| M. orthomargina | $1(\operatorname{trn} W)$ | $1(\operatorname{trn} G)$ | $1(\operatorname{trn} S 2)$ | 34 |  | $2(\operatorname{trn} Y, \operatorname{trn} E)$ |
| M. brachycorna sp. nov. | $2(\operatorname{trn} W, \operatorname{trn} G)$ | $1(\operatorname{trn} F)$ | $2(\operatorname{trn} G)$ | 35 | $1(\operatorname{trn} M)$ | $4(\operatorname{trn} Y, \operatorname{trn} R, \operatorname{trn} E, \operatorname{trn} F)$ |
| M. maoershanensis sp. nov. | $2(\operatorname{trn} W, \operatorname{trn} G)$ |  |  | 35 |  | $2(\operatorname{trn} Y, \operatorname{trn} E)$ |

Table 6. Distribution of G-U base mismatches in tRNAs of M. orthomargina, M. brachycorna sp. nov., and M. maoershanensis sp. nov.

| Transfer RNA | M. orthomargina | M. brachycorna | M. maoershanensis | Transfer RNA | M. orthomargina | M. brachycorna | M. maoershanensis |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| trnl | 0 | 0 | 0 | trnR | 0 | 0 | 0 |
| trnQ | 5 | 4 | 4 | trnN | 1 | 1 | 0 |
| trnM | 0 | 1 | 0 | trnS1 | 0 | 0 | 2 |
| trnW | 0 | 0 | 0 | trnE | 0 | 0 | 0 |
| trnC | 3 | 3 | 3 | trnF | 5 | 3 | 5 |
| $t r n Y$ | 3 | 3 | 2 | trnH | 3 | 3 | 5 |
| $t r n L 2$ | 1 | 1 | 0 | $\operatorname{trnT}$ | 0 | 0 | 0 |
| $t r n D$ | 1 | 1 | 1 | trnP | 5 | 4 | 6 |
| trnK | 0 | 1 | 0 | trnS2 | 0 | 1 | 0 |
| $t r n G$ | 1 | 1 | 1 | trnL1 | 3 | 3 | 2 |
| trnA | 1 | 2 | 1 | $t r n \mathrm{~V}$ | 2 | 3 | 3 |



Figure 5. ML tree resulting from the analysis of 13 PCGs of mitochondrial genomes in the Tetrigidae.
a sister group to Systolederus, and the clades of Macromotettixoides and Systolederus were clustered with the traditional Tetriginae. This agreed with the findings of Devriese and Husemann (2023) who proposed that the species of Teredorus in Indo-Malaysia be placed in Systolederus, and Systolederus should be placed in Tetriginae based on morphology and distribution. We also support the temporary classification of Systolederus within the subfamily Tetriginae, but this subfamily is polyphyletic and in need of revision. Therefore, the phylogenetic trees indicated that Macromotettixoides (lateral lobes of pronotum produced forward; end of posterior angles truncated) is a genus of Tetriginae rather than Metrodorinae.

Previous studies on the classification of Metrodorinae or Tetriginae were based on the morphology of the posterior angles of lateral lobes of pronotum (turned downwards, rounded, or produced forward, truncated), but some investigations suggested that distinguishing between Metrodorinae and Tetriginae based on the shape of the lateral lobes of the pronotum was unreliable (Adžić et al. 2020; Devriese and Husemann 2023). Therefore, it is necessary to use several morphological features, alongside molecular evidence, to correctly distinguish the subfamilies in Tetrigidae.

## Taxonomy

Macromotettixoides maoershanensis sp. nov.
https://zoobank.org/EB83298E-FE9B-4536-9D58-60177DF22802
Figs 6, 7

Materials examined. Holotype: CHINA $\varphi$; Guangxi, Guilin, Xing'an Country, Gaozhai; $25^{\circ} 51^{\prime} 35$ "N, $110^{\circ} 29^{\prime} 34$ "E; alt. $652.7 \mathrm{~m} ; 12$. VII.2021; Wei'an Deng, Chaomei Huang leg. Paratypes: China 5q, 1 ${ }^{\text {¹; }}$; Guangxi, Guilin, Xing’an Country, Gaozhai; $25^{\circ} 51^{\prime} 35$ "N, $110^{\circ} 29^{\prime} 34$ "E; alt. 652.7 m; 20.VII.2022, Jieling Luo, Chaomei Huang leg. 6? ${ }^{\circ}{ }^{\top}$; Guangxi prov., Guilin, Longsheng Country, Hongtan; $25^{\circ} 36^{\prime} 34^{\prime \prime} \mathrm{N}$, $109^{\circ} 57^{\prime} 55^{\prime \prime}$ E; alt. 818 m; 04-9.VII.2022; Jieling Luo, Chaomei Huang leg.

Diagnosis. New species is generally similar to M. orthomargina (Figs 8, 9) from which it differs in the width of vertex between eyes $2.0 \times$ the width of a compound eye (the width of vertex between eyes $3.0 \times$ the width of a compound eye in M. orthomargina); upper margin of pronotum wide arch-like in lateral view (upper margin of pronotum wavy in lateral view in M. orthomargina); the lower margin of hind pronotal process curved (the lower margin of hind pronotal process is straight in $M$. orthomargina); lower outer carina of hind femora smooth and without projection (posteromedian of lower outer carina of hind femora with two or three projections in M. orthomargina); lower margin of hind femora serrated (lower margin of hind femora big sawtooth in $M$. orthomargina). It is also similar to $M$. undulatifemura Deng et al. (2012) but differs from the latter by median carina of pronotum slightly arc in profile (median carina of pronotum undulated in profile in $M$. undulatifemura); apex of hind pronotal process rounded (apex of hind pronotal process slightly concave in M. undulatifemura); lower margin of hind femora serrated (lower margin of hind femora with five or six teeth and undulated in $M$. undulatifemura).

Description. Female. short and small size. Body length 7-8 mm, pronotum length 6-7 mm, hind femur length 4-5 mm.

Head. Head and eyes not exserted above pronotal surface (Fig. 6B). Compound eyes nearly rounded; in dorsal view, width of vertex between eyes $2 \times$ width of a compound eye; anterior margin of fastigium nearly straight, surpassing anterior margin of eye; median carina visible anteriorly; vertex uneven with paired fossulae (Fig. 6C). In lateral view, frontal ridge and vertex forming fillet; frontal costa concave between eyes, protruded anteriorly, and wide arc between antennal grooves (Fig. 6D). In frontal view, lateral ocelli are located on both sides of frontal costa, frontal costa bifurcated above lateral ocelli, the bifurcation of the frontal costa in the middle of the compound eye height; longitudinal furrow divergent between antennae, width of longitudinal furrow of frontal ridge 1.3× antennal groove diameter (Fig. 6E). Antennae short, filiform, antennal grooves inserted below inferior margins of compound eyes, 15 -segmented, the $10^{\text {th }}$ and $11^{\text {th }}$ segments are the longest, $\sim 2.0-3.0 \times$ longer than its width. Eyes globose, lateral (paired) ocelli located in lowest third of compound eye height.

Thorax. Pronotum not smooth and has irregular tuberculate (Fig. 6A). In dorsal view, median carina of pronotum obvious, anterior margin of pronotum nearly truncate and not reaching the posterior margin of the compound eye; humeral angle obtuse angle, interhumeral carina visible; hind pronotal process narrow and short, surpassing knee of hind femur and almost reaching apex of hind femur and its apex rounded; In profile (Fig. 6B), median carina of pronotum


Figure 6. Macromotettixoides maoershanensis sp. nov., holotype female A body, dorsal view $\mathbf{B}$ the same, lateral view $\mathbf{C}$ head and anterior part of pronotum, dorsal view $\mathbf{D}$ the same, lateral view $\mathbf{E}$ head, frontal view.
slightly arch-like; lower margin of hind process curved, external lateral carinae of metazona also slightly curved, width of infrascapular area is $0.8-0.9 \mathrm{~mm}$. Posterior angles of lateral lobes turned downwards, apex of posterior angles obtuse rounded, posterior margins of lateral lobes of pronotum only with ventral sinus and tegminal (upper) sinus absent. Tegmina and hind wings invisible.

Legs. Upper margin of fore and middle femora finely serrated, with carinated, ventral margins undulated (Fig. 7A, B). Hind femora robust and short, $2 \times$ as


Figure 7. Macromotettixoides maoershanensis sp. nov., holotype female A left fore femur, lateral view Bleft mid femur, lateral view $\mathbf{C}$ left hind femur, lateral view $\mathbf{D}$ left hind tibia, lateral view $\mathbf{E}$ left posterior tarsus, lateral view $\mathbf{F}$ subgenital plate of female, lateral view $\mathbf{G}$ subgenital plate of female, ventral view. male, paratype $\mathbf{H}$ body in dorsal view I body in lateral view.
long as wide; with carinated, dorsal margin, and ventral margin finely serrated (Fig. 7C); antegenicular denticles and genicular denticles acute. Outer side and inner side of hind tibia with 5-7 spines (Fig. 7D). First segment of posterior tarsi is $1.5 \times$ as long as the third, pulvilli of first segment of posterior tarsi as long as the second, apices of first and second acute, apices of third right angle (Fig. 7E).


Figure 8. M. orthomargina, female A body, dorsal view B the same, lateral view $\mathbf{C}$ head and anterior part of pronotum, dorsal view $\mathbf{D}$ the same, lateral view $\mathbf{E}$ head, frontal view.

Abdomen. Ovipositor narrow and short; upper and lower valvulae with slender saw-like teeth; length of upper valvulae $2.0 \times$ its width. Length of subgenital plate $2.5 \times$ its width, middle of posterior margin of subgenital plate slightly triangular and projecting (Fig. 7F, G).

Coloration. Body dark brown. Hind tibia yellowish brown, with two light rings in the middle.

Male. Similar to female, but smaller and narrower (Fig. 7H, I). Body length 6-8 mm, pronotum length 5-6 mm, hind femur length 4 mm . Width of vertex between eyes $2 \times$ width of compound eye. Subgenital plate short conical.

Etymology. The new species was named after the type locality, Maoershan, Guangxi, China.

Distribution. China: Guangxi.


Figure 9. M. orthomargina, female $\mathbf{A}$ left fore femur, lateral view $\mathbf{B}$ left mid femur, lateral view $\mathbf{C}$ left hind femur, lateral view D left hind tibia, lateral view $\mathbf{E}$ left posterior tarsus, lateral view $\mathbf{F}$ subgenital plate of female, lateral view $\mathbf{G}$ subgenital plate of female, ventral view. male, paratype.

Macromotettixoides brachycorna sp. nov.
https://zoobank.org/E88A7215-0F52-49E5-B63B-E26F7518BADA
Figs 10, 11

Material examined. Holotype: CHINA $\odot$; Guangxi Province, Hechi, Huanjiang, Yangmei'ao; $25^{\circ} 11^{\prime} 41^{\prime \prime} \mathrm{N}, 108^{\circ} 38^{\prime} 51^{\prime \prime} \mathrm{E}$; alt. 1169.13 m ; 03.IX.2021; Chaomei Huang leg. Paratypes: CHINA $1 \delta^{\top} 1$; Guangxi, Hechi, Huanjiang, Yangmei'ao; $25^{\circ} 11^{\prime} 41^{\prime \prime} \mathrm{N}$, $108^{\circ} 38^{\prime} 51^{\prime \prime} \mathrm{E}$; alt. $1169.13 \mathrm{~m} ; 29$. VII.2022; Chaomei Huang and Jieling Luo leg.

Diagnosis. The new species is similar to Macromotettixoides maoershanensis sp . nov. from which it differs in width of vertex between eyes $1.3 \times$ width of a compound eye (width of vertex between eyes $2.0 \times$ width of a compound eye in M. maoershanensis); anterior margin of fastigium not surpassing anterior
margin of eye (anterior margin of fastigium surpassing anterior margin of eye in $M$. maoershanensis); median carina of pronotum slightly elevated and undulated in profile (median carina of pronotum slightly arc-like in profile in $M$. maoershanensis); ventral margin of middle femora slightly undulate (ventral margin of middle femora distinctly undulate in $M$. maoershanensis). It is also similar to Macromotettixoides tuberculata Mao, Li \& Han, 2020 but differs from the latter by width of vertex between eyes $1.3 \times$ width of compound eye (width of vertex between eyes $1.7 \times$ width of compound eye in $M$. tuberculata); antennal grooves inserted far below inferior margin of compound eyes (antennal grooves inserted between inferior margin of compound eyes); hind pronotal process narrowly rounded (hind pronotal process broad in $M$. tuberculata); lower margin of hind process bend upwards at $1 / 4$ and then tilt straight up, lateral carinae of metazona curved (lower margin of hind process and lateral carinae of metazona slightly straight in $M$. tuberculata),

Description. Female. Body size small. Body length 8 mm , pronotum length 6-7 mm, hind femur length 4 mm .

Head. Head and eyes exserted above pronotal surface (Fig. 10B). Face and vertex rough, covered with small granules, not fossulae; medial carina erected in anterior half, but absent in posterior half; vertex $1.3 \times$ as wide as a compound eye, not surpassing anterior margin of eyes; anterior margin arc and depressed, curved inward and level with the top of the eyes (Fig. 10C). In lateral view, frontal ridge and vertex forming a rounded-angle shape; eyes oval and not protruding with vertex; frontal costa rounded between antennal grooves (Fig. 10D). In frontal view, frontal costa bifurcated above lateral ocelli, the bifurcation of the frontal costa in the middle of the compound eye height; antennae short, filiform, antennal grooves inserted far below inferior margin of compound eyes, 13 -segmented, the $7^{\text {th }}$ and $8^{\text {th }}$ segments are the longest, $\sim 3-3.5 \times$ longer than its width, antennal grooves $1.5 \times$ as wide as diameter of scapus; lateral ocelli placed at lower one third of inner margin of eyes (Fig. 10E).

Thorax. The dorsal surface of the pronotum is coarse dorsum with dense granules, anterior margin of pronotum straight; median carina entire and wavy in profile; lateral carinae of prozona slightly parallel; humeral angle obtuse; hind pronotal process narrow and its apex rounded, reaching pregenicular knee (Fig. 10A); lower margin of hind process bends upwards at $1 / 4$ and then tilt straight up, lateral carinae of metazona curved, width of the area between the two is 0.9 mm (Fig. 10B). Posterior angles of lateral lobes slightly produced outwards, end of posterior angles truncate, posterior margins of lateral lobes of pronotum only with ventral sinus. Tegmina and hind wings invisible.

Legs. Fore femora and middle femora with slightly undulated ventral margins (Fig. 10F, G). Hind femora robust and short, $2.3 \times$ as long as wide, with carinated and margins finely serrated (Fig. 11A); antegenicular denticles and genicular denticles acute; outer side of hind tibia with 5-7 spines, inner side with five or six spines (Fig. 11B); length of first segment of posterior tarsi slightly longer than third, three pulvilli of first segment of posterior tarsi are increased in turn, three apices acute (Fig. 11C).

Abdomen. Ovipositor narrow and long (Fig. 11D, E), length of upper valvulae $3 \times$ its width, upper and lower valvulae with slender saw-like teeth; length of subgenital plate $3.3 \times$ its width, middle of posterior margin of subgenital plate triangular projecting.


Figure 10. Macromotettixoides brachycorna sp. nov., holotype female $\mathbf{A}$ body, dorsal view $\mathbf{B}$ the same, lateral view $\mathbf{C}$ head and anterior part of pronotum, dorsal view $\mathbf{D}$ head, lateral view $\mathbf{E}$ head and anterior part of pronotum, frontal view $\mathbf{F}$ left fore femur, lateral view $\mathbf{G}$ left mid femur, lateral view.

Coloration. Body dark brown or brown; antennae tawny; hind femur yellowish brown in the middle and dark brown around the sides; hind tibia yellowish brown, with two light rings in the middle.


Figure 11. Macromotettixoides brachycorna sp. nov., holotype female $\mathbf{A}$ left hind femur, lateral view $\mathbf{B}$ left hind tibia, lateral view $\mathbf{C}$ left posterior tarsus, lateral view $\mathbf{D}$ subgenital plate of female, lateral view $\mathbf{E}$ subgenital plate of female, ventral view. male, paratype $\mathbf{F}$ body in dorsal view $\mathbf{G}$ body in lateral view.

Male. Similar to female, but smaller and narrower (Fig. 11F, G). Body length 6 mm , pronotum length 5 mm , hind femur length 4 mm . Width of vertex between eyes $1.5 \times$ width of compound eye. Subgenital plate short, cone-shaped, apex bifurcated.

Etymology. The specific epithet is derived from brachycorna, meaning the antennae are shorter and the number of segments is less.

Distribution. China: Guangxi.

## Discussion

Unfortunately, we do not have access to the species of the South American Tetriginae and Metrodorinae, which makes it impossible to evaluate whether Systolederus + Macromotettixoides truly belong to the subfamily Metrodorinae. As a result, we cannot provide any conclusive evidence to support their classification within this subfamily. Therefore, further research is needed to clarify their taxonomic status and evolutionary relationships with other Southern American species. But the problematics of the Metrodorinae definition in Asia, especially when differentiated from very diverse Tetriginae, it is often seen that some species of Metrodornae are moved to Tetriginae (Tumbrinck 2019; Subedi 2022). The main reason for this problem is the use of a single character to distinguish between Metrodornae and Tetriginae (the posterior angles of lateral lobes of pronotum produced forward, truncated, or turned downwards, rounded). Typical Metrodorinae are mainly characterized by having the median ocellus and the antenna placed below the eyes, a relatively small divergence of the rami of the frontal costa not forming wide scutellum, and a similar length of the first and third segments of the hind tarsus (Pavón-Gonzalo et al. 2012). Many species of Metrodorinae also share the posterior angles of the lateral lobes of the pronotum produced outwards, often becoming acutely spinose. These characters taken together can separate the subfamily from the other eight subfamilies of Tetrigidae, but single characteristic is not enough to separate itself from the other eight subfamilies (Skejo et al. 2018; Tumbrinck 2019).

Macromotettixoides is an apterous genus, but the non-flying Tetrigidae in the Oriental regions have multiple origins. For example, the genus Hainantettix Deng, 2020 (Zhang et al. 2020) and the genus Epitettix Hancock, 1907 in the subfamily Cladonotinae, as well as the genus Formosatettix in the subfamily Tetriginae, are all wingless Tetrigidae that are morphologically similar to Macromotettixoides, sometimes making taxonomic identification difficult. At the same time, Macromotettixoides is also similar to some brachypronotal and brachypterous Tetriginae such as the genera of Alulatettix Liang, 1993 and Skejotettix Subedi, 2022. The main differences between them are summarized in Table 7.

Since the genus Macromotettixoides was erected in 2005, a total of 22 species has been described, another six species transferred to this genus (Zheng et al. 2006, 2009; Zheng and Shi 2009; Deng 2011; Deng et al. 2012, 2014, 2020; Zheng 2013a, 2013b; Zha et al. 2017; Han et al. 2020; Li et al. 2020a; Peng et al. 2021; Fan et al. 2023; Wei and Deng 2023; this study), and two species were moved to Hainantettix (Subedi 2022). As a result, 26 species of this genus are now known in the world.

Although the phylogenetic tree in this study supports the genus Macromotettixoides being assigned to Tetriginae rather than Metrodorinae, it is limited by the available data and cannot fully confirm its taxonomic placement and monophyletic. Therefore, more comprehensive molecular and morphological data are needed to further investigate the evolutionary relationships and taxonomic status of Macromotettixoides.

Table 7. Morphological comparison of Macromotettixoides, Epitettix, Hainantettix, Formosatettix, Alulatettix, and Skejotettix.

| Characteristics | Macromotettixoides | Epitettix | Hainantettix | Formosatettix | Alulatettix | Skejotettix |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Wing type | apterous | apterous | apterous | apterous | brachypterous | brachypterous |
| Head | not exserted above the pronotum | not exserted above the pronotum | not exserted above the pronotum | not exserted above the pronotum | not exserted above the pronotum | not exserted above the pronotum |
| Fastigium of vertex in dorsal view | not surpassing the anterior margin of eyes | distinctly surpassing the anterior margin of eyes | not surpassing the anterior margin of eyes | distinctly surpassing the anterior margin of eyes | not surpassing the anterior margin of eyes | not surpassing the anterior margin of eyes |
| Fastigium of vertex | vertex not narrowed toward the front | vertex not narrowed toward the front | vertex very strongly narrowed toward the front drawing the eyes together | vertex not narrowed toward the front | vertex not narrowed toward the front | vertex not narrowed toward the front |
| Width of longitudinal furrow of frontal ridge | narrower than antennal groove diameter | 1.3-3.0x antennal groove diameter | 1.6-1.8x antennal groove diameter | narrower than antennal groove diameter | narrower than antennal groove diameter | narrower than antennal groove diameter |
| Tegminal sinus | absent | absent | absent | absent | present | present |
| Posterior angles of lateral lobes | produced outwards and with truncated apex | produced outwards and with truncated apex | produced outwards and with truncated apex | turned downwards and with rounded apex | turned downwards and with rounded apex | turned downwards and with rounded apex |

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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, J.-L.L. and W.-A.D. R.-J.Z.; methodology, J.-L.L. and W.-A.D..; software, J.-L.L.; validation, all authors; formal analysis, J.-L.L. and W.-A.D.; investigation, J.-L.L.; resources, W.-A.D. and R.-J.Z.; writing-original draft preparation, J.-L.L.; writingreview and editing, W.-A.D.; visualization, J.-L.L.; supervision, W.-A.D.; project administration, W.-A.D.; funding acquisition, W.-A.D.

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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

Mitochondrial genome comparison of 37 species in Tetrigidae, the initiation and termination codons of PCGs of mitogenomes in Tetrigidae

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# One new species of Stegocephalus Krøyer, 1842 (Amphipoda, Stegocephalidae) described from a seamount of the Caroline Plate, NW Pacific 

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#### Abstract

A new species of the subfamily Stegocephalinae, Stegocephalus carolus sp. nov., is described from a seamount in the Caroline Plate. Two related species, S. cascadiensis (Moore, 1992) and S. Iongicornis (Gurjanova, 1962), were previously reported in the North Pacific. Important morphological characters which differentiate $S$. carolus sp. nov. from S. cascadiensis are found in antenna 1, the mouthparts, pereopod 7 and the length of rami of uropods 2 and 3 . The new species differs from S. longicornis by characters of antenna 1, the mouthparts and the shape of epimeral plate 3. Additionally, the morphological differences between the new species and the remaining seven species of Stegocephalus are also presented.


Key words: Deep sea, morphology, new species, Stegocephalinae, taxonomy

## Introduction

The family Stegocephalidae Dana, 1852 was revised by Berge and Vader (2001), and divided into five subfamilies: Andaniexinae Berge \& Vader, 2001, Andaniopsinae Berge \& Vader, 2001, Bathystegocephalinae Berge \& Vader, 2001, Parandaniinae Berge \& Vader, 2001 and Stegocephalinae Dana, 1852. Of these, Stegocephalinae is the largest, comprising 14 genera with 49 species (Horton et al. 2023), characterized by the presence of gaping and geniculate outer plate of maxilla 2, the flagellum of antenna 1 composed of not more than 10 articles and a telson that is longer than broad (Berge and Vader 2001). As the type genus of the Stegocephalinae, Stegocephalus Krøyer, 1842 can be distinguished from the other 13 genera by having the flagellum article 1 of antenna 1 not longer than the peduncle, the flagellum of antenna 2 with more than 10 articles and the palp of the maxilla 1 two-articulate (Barnard and Karaman 1991; Berge and Vader 2001). There are nine valid species of Stegocephalus, which are found in the Arctic, Southern Ocean (Antarctica), Atlantic, southern Mediterranean Sea and North Pacific (Berge and Vader 2001).

During a biodiversity survey of seamounts on the Caroline Plate in the northwest Pacific in 2019, conducted by the Chinese research vessel KEXUE, several individuals referable to Stegocephalus were collected. These specimens exhibit some distinctive characteristics differentiating them from the other nine described Stegocephalus species, and they are described as a new species herein.

## Materials and methods

The present material was collected by ROV FAXIAN, during expeditions to seamounts (Fig. 1) on the Caroline Plate by the Institute of Oceanology, Chinese Academy of Sciences (IOCAS) during June and July 2019. The material was sorted on board and fixed in $96 \%$ ethanol, then transferred to $75 \%$ ethanol in the laboratory. The specimens are deposited in the Marine Biological Museum, Chinese Academy of Sciences, Qingdao, China. The specimens were examined and dissected with a dissecting microscope (ZEISS Discovery V20). Line drawings were completed using the software Adobe Photoshop CS6 with a graphics tablet. Length measurement was made along the outline of the animal, beginning from the rostrum to the posterior margin of the telson; total length of the specimens ranged from 3.4 to 8.9 mm . Additionally, COI (PP188368), 16S rDNA (PP187329) and 18S rDNA (PP187328) sequences of Stegocephalus carolus sp. nov. were obtained from its mitochondrial genome by homologous alignment.


Figure 1. A map showing the location of the sampling site (red triangle) in the NW Pacific.

Systematics<br>Order Amphipoda Latreille, 1816<br>Suborder Amphilochidea Boeck, 1871<br>Superfamily Stegocephaloidea Dana, 1852<br>Family Stegocephalidae Dana, 1852<br>Subfamily Stegocephalinae Dana, 1852

Genus Stegocephalus Krøyer, 1842

Diagnosis. Body smooth. Antenna 2 with peduncular article 4 shorter or longer than article 5. Epistomal plate absent. Mandible incisor lateral, toothed; left lacinia mobilis powerful, toothed, distally produced. Maxilla 1 palp well developed, 1- or 2-articulated. Outer plate of maxilla 2 gaping and geniculate, with setae distally with hooks (absent in S. ampulla). Palp of maxilliped 4-articulated, article 2 unproduced or inner margin produced distally. Pereopods 1-2 simple. Pereopod 6 basis conspicuously expanded. Uropod 3 biramous, outer ramus l-articulate, peduncle shorter than rami. Telson elongate, cleft (amended after Barnard and Karaman 1991; Berge and Vader 2001).

## Stegocephalus carolus sp. nov.

https://zoobank.org/35CA4012-7AB1-4E86-BBC4-51A5B05F6EB2
Figs 2-4

Material examined. Holotype. MBM 286610, $q$ ( 8.9 mm , with 6 big yolks), dissected, unnamed seamount on Caroline Plate, NW Pacific, M5173, $10^{\circ} 03^{\prime} \mathrm{N}$, $140^{\circ} 10^{\prime} E$, depth 1221 m, 30 May 2019. Paratypes: MBM 287879, 2 § ( 6.0 and 7.0 mm ), not dissected, unnamed seamount on Caroline Plate, NW Pacific, M5117, $10^{\circ} 04^{\prime} \mathrm{N}, 140^{\circ} 12^{\prime} \mathrm{E}$, depth $870-944 \mathrm{~m}, 28$ May 2019; MBM 287878, $2^{\top}{ }^{\top}$ ( 7.6 and 3.4 mm ), not dissected, unnamed seamount on Caroline Plate, NW Pacific, M5362, $10^{\circ} 04^{\prime} \mathrm{N}, 140^{\circ} 11^{\prime} \mathrm{E}$, depth 813-1182 m, 2 June 2019.

Description. First pereon segment longer than the rest; pleonite 1-3 dorsally smooth; epimeral plate 1 with posteroventral corner broadly rounded; epimeral plate 2 with posteroventral corner subacute; epimeral plate 3 without minute serration at posteroventral corner, posteroventral corner strongly produced, triangular. Head partially covered by pereonite 1 and coxa 1; much deeper than long. Rostrum absent. Eyes not apparent in ethanol-fixed material. Antenna 1 with callynophore well developed; peduncle about twice as long as first primary flagellar article; article 1 slightly longer than articles 1-2 combined; primary flagellum 7-articulate, article 1 longest; accessory flagellum 1-articulate, beyond article 1 of primary flagellum, bearing long setae apically. Antenna 2 slightly longer than antenna 1, peduncle (articles 3-5) slightly shorter than flagellum, article 4 longer than article 5 , not setose; flagellum 12 articles, article 1 longer than rest of articles.

Mouthparts. Epistomal plate absent. Upper lip broader than long, bilobate, slightly asymmetrical. Lower lip with the narrow lobes bearing row of simple setae. Right Mandible incisor with 9 teeth; incisor of left mandible with 7 teeth, left lacinia mobilis with 9 teeth. Maxilla 1 palp 2-articulate, rectangular, apex not reaching above the


Figure 2. Stegocephalus carolus $s p$. nov., MBM 286610, holotype, $\&(8.9 \mathrm{~mm})$ : G1 R, right gnathopod 1; G2 R, right gnathopod 2.
apex of outer plate, apically bearing 4 plumose setae; outer plate with 9 setal-teeth arranged in a pseudocrown; inner plate with a well-developed shoulder, setae pappose. Maxilla 2 gaping and geniculate; outer plate with about 10 apical setae bearing distal hooks; inner plate with marginal and submarginal setae pappose. Maxilliped with inner plate subrectangular, not exceeding base of palp article 2 , distal margin slightly concave, setose, medial setae-row present; outer plate only with inner margin bearing about 7 small robust setae; palp 4-articulate, article 2 distinctly shorter than article 1, inner margin produced distally, dactylus short, about 1/5 length of article 3 .

Gills present on coxae 2-7. Oostegites present on 2-5.
Pereopods. Gnathopod 1 simple; coxa triangular, tapering, anterior margin convex; basis with anterior margin sinuous, both margins heavily setose; ischium not elongate, posterior margin bearing long setae, anterior margin with several short robust setae; carpus subequal in length to propodus, expanded distally, anterior margin bearing group of long setae distally, posterior margin setose; propodus tapering anterior margin bearing row of 6 robust setae about $2 / 3$ length of propodus and two short robust setae subdistally, posterior surface rows of pectinate setae and rows of plumose setae; dactylus nearly straight, tapering, about $1 / 3$ length of propodus. Gnathopod 2 simple; coxa much longer than broad, subrectangular, ventral margin slightly curved; basis much more slender than gnathopod 1, both margins setose; ischium slightly shorter than merus, subrectangular; carpus slender, not expanded distally, shorter than propodus, distal and posterior margin setose; propodus slender, setae on posterior surface similar to that of gnathopod 1; dactylus tapering, curved. Pereopod 3 coxa similar to that of gnathopod 2; basis linear, anterior margin bearing dense short robust setae, posterior margin bearing several long setae; ischium short; merus longer than carpus, anterodistally drawn out, with one long robust seta, posterior margin bearing several setae; carpus subequal in length to propodus, posterior margin with few setae; propodus with only posterior margin bearing few small setae; dactylus tapering, slightly curved. Pereopod 4 similar to pereopod 3, but coxa large, posteroventral lobe broadly rounded, posterior margin excavate. Pereopod 5 slightly longer than pereopod 4; coxa bilobate, posterior lobe deeper; basis linear, both margins setose; merus to dactylus of similar appearance to pereopod 4, but merus subequal in length to carpus, and propodus much slender, distinctly longer than carpus. Pereopod 6 longer than pereopod 5; coxa unilobate; basis expanded posteriorly, rounded below, anterior margin and anterior dorsal surface with several robust setae, posterior margin serrated with small setae; distal 5 articles of similar appearance to pereopod 5 . Pereopod 7 shorter than pereopod 6, but longer than pereopod 5; basis expanded posteriorly, distinctly larger than that of pereopod 6, posterior margin serrated with small setae, beyond end of ischium; merus longer than carpus, margins setose; carpus shorter than propodus, anterior margin with three groups setae; propodus shorter than that of pereopod 6, anterior margin with small setae; dactylus slightly curved, tapering.

Uropods and telson. Uropod 1 peduncle 1.4 times longer than rami, outer margin densely setose, inner margin with only 2 robust setae; rami lanceolate, subequal in length, both rami with inner and outer margins setose. Uropod 2 shorter than uropod 1, peduncle subequal in length to rami, both margins setose; rami subequal in length, both rami with inner and outer margins setose. Uropod 3 shortest, peduncle distinctly shorter than rami, not setose; outer ramus 1-articulate, shorter than inner ramus, both rami with inner and outer margins setose. Telson longer than broad, without setae, cleft about 0.8 of total length, distally acute.


Figure 3. Stegocephalus carolus sp. nov., MBM 286610, holotype, $\odot(8.9 \mathrm{~mm})$ : H, head; A1, antenna 1; A2, antenna 2; UL, upper lip; LL, lower lip; Md L, left mandible; Md R, right mandible; Mx1, maxilla 1; Mx2, maxilla 2; Mxp, maxilliped.


Figure 4. Stegocephalus carolus sp. nov., MBM 286610, holotype, $+(8.9 \mathrm{~mm})$ : P3 R, right pereopod 3 ; P4 R, right pereopod 4; P5 R, right pereopod 5; P6 R, right pereopod 6; P7 R, right pereopod 7; U1 R, right uropod 1; U2 L, left uropod 2; U3 L , left uropod 3 ; T , telson.

Etymology. The new species is named after its type locality, the Caroline Plate

Distribution. Presently known only from a seamount of the Caroline Plate, at a depth of 813-1221 m.

Remarks. According to the revision of the family Stegocephalidae Dana, 1852 by Berge and Vader (2001), Stegocephalus carolus sp. nov. belongs to the subfamily Stegocephalinae Dana, 1852. The new species shares distinctive characteristics with other species in the genus Stegocephalus Krøyer, 1842, including a two-articulate palp of maxilla 1, a produced palp article 2 of the maxilliped, a conspicuously expanded basis of pereopod 6, a 1-articulate outer ramus of uropod 3, and a cleft telson. Two Stegocephalus species, S. cascadiensis (Moore, 1992) and S. Iongicornis (Gurjanova, 1962), have been previously reported in the North Pacific (Moore 1992; Berge and Vader 2001).

Stegocephalus cascadiensis (Moore, 1992) was originally reported from the Cascadia Abyssal Plain at a depth of 2740-2818 m (Moore 1992). Stegocephalus carolus sp . nov. differs from $S$. cascadiensis by the peduncle of antenna 1 longer than the first flagellar article, and the accessory flagellum extending beyond the distal margin of the first flagellar article. Additionally, the apical setae on the outer plate of maxilla 2 are hooked in the new species, whereas, they are unhooked in $S$. cascadiensis. In S. carolus sp. nov., the first palp article of the maxilliped is subequal in length to the second article, whereas in $S$. cascadiensis, the first palp article is much longer than the second. The inner plate of the maxilliped is subrectangular with a concave distal margin in $S$. carolus $s p$. nov., whereas it is subtriangular in $S$. cascadiensis. The second palp article of the maxilliped in S. carolus sp. nov. has a produced inner margin, and the posterior margin of pereopod 7 is slightly serrate instead of smooth. Furthermore, the rami of uropod 2 are subequal in $S$. carolus sp . nov., whereas the inner ramus is longer than the outer ramus in $S$. cascadiensis. Lastly, the outer ramus of uropod 3 in $S$. carolus sp . nov. is shorter than the inner ramus, while in S. cascadiensis, it is longer than the inner ramus (Moore 1992, fig. 7).

Stegocephalus longicornis (Gurjanova, 1962) was originally reported from the Bering Sea at a depth of over 2440 m . The new species differs from S. Iongicornis by: the shorter antenna 1, the 7-articulated primary flagellum and the 1-articulated accessory flagellum, while the primary flagellum is 11-articulate and the accessory flagellum is 3-articulate in S. longicornis; the distal margin of the inner plate of the maxilliped is concave rather than convex, and the inner margin of palp article 2 is produced, versus not produced in S. longicornis; and the posteroventral corner of epimeral plate 3 is strongly produced and triangular, while epimeral plate 3 is only produced in a small triangular angle in S. Iongicornis (Gurjanova 1962, fig. 130).

The remaining species of Stegocephalus are found in the Arctic, North Atlantic, or the Southern Ocean (Berge and Vader 2001). Stegocephalus carolus sp. nov. can be easily distinguished from S. abyssicola (Oldevig, 1959) by its strongly projected posteroventral corner of the third epimeral plate (Oldevig 1959). It is also different from S. ampulla (Phipps, 1774), S. inflatus Krøyer, 1842, S. rostrata KH Barnard, 1932, and S. similis Sars, 1891 by the absence of a rostrum (Barnard 1932; Steele 1967; Berge and Vader 2001). Especially, it differs from $S$. inflatus by the pale of maxillae 1 being 2 -articulated, while it is 1-articulated in S. inflatus (Steele 1967, fig. 1B); epimeral plates 2 and 3 have the posteroventral corner broadly rounded, while epimeral plates 2 and 3 are
produced into a sharp tooth in S. inflatus (Steele 1967, fig. 1A). Additionally, the new species can be distinguished from S. kergueleni (Schellenberg, 1926) and S. nipoma (J.L. Barnard, 1961) by the presence of a toothed left lacinia mobilis, the posterior margin of gnathopod 1 is not densely setose; and the subacute posteroventral of epimeral 2 is not broadly rounded (Schellenberg 1926; Barnard 1961). Lastly, it also differs from $S$. similis by the shape of the third epimeral plate, which is neither serrated nor notched (Oldevig 1959).

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The authors have declared that no competing interests exist.

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No ethical statement was reported.

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## Author contributions

Funding acquisition: ZS, YW. Methodology: YW, XR. Project administration: ZS. Supervision: ZS, XR. Writing - original draft: YW.

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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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# On Ypsolopha micromoths (Lepidoptera, Ypsolophidae) associated with Adesmia shrubs (Fabaceae) in the arid western slope of the central Andes 

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#### Abstract

Ypsolopha Latreille, 1796 (Lepidoptera, Ypsolophidae) is a genus comprised mostly of Holarctic micromoth species with a fairly broad range of larval hosts (e.g. Aceraceae, Rosaceae, and Fagaceae). The only previous record of herbivory on a representative of the South American genus Adesmia DC. (Fabaceae) was based on the discovery of Ypsolopha moltenii Vargas, 2018 larvae feeding on Adesmia verrucosa Meyen in the Andes of northern Chile. Further surveys revealed Adesmia atacamensis Phil. as another host for $Y$. moltenii, and Adesmia spinosissima Meyen as the single host of Ypsolopha sp. The genetic distance between DNA barcodes of the two micromoth species was $7.9-8.1 \%$ (K2P). These results suggest narrow host ranges for Adesmia-feeding Ypsolopha and highlight the need to further explore the taxonomic diversity of these micromoths in other South American environments.


Key words: Arid environments, DNA barcoding, oligophagy, phytophagous larvae, South America

## Introduction

The widespread and highly diverse micromoth genus Ypsolopha Latreille, 1796 (Lepidoptera, Yponomeutoidea, Ypsolophidae) includes more than 160 described species, most of which occur in the Nearctic and Palearctic regions (Jin et al. 2013; Ponomarenko 2020; Sachkov and Zolotuhin 2020; Corley and Ferreira 2021). Only eight Neotropical species have been recorded so far, but recent discoveries suggest that this apparent low diversity could be due to a lack of sampling effort and taxonomic studies (Vargas 2018, 2021). Larvae of Ypsolopha generally build a loose silk web on their host plants while feeding, and a dense silk cocoon with a narrow apical opening for pupation. Although the host plants are only partially known, the available records suggest that species are oligophagous or polyphagous (Dugdale et al. 1998; Anikin et al. 2006; Jin et al. 2013; Sohn et al. 2013; Akulov et al. 2018).

The South American plant genus Adesmia DC. (Fabaceae) includes nearly 230 species classified in two subgenera, Adesmia and Acanthadesmia, and 45 series (Burkart 1967). Despite the remarkable species richness, this genus remained unknown as a host for Ypsolopha until the recent discovery of larvae of Ypsolopha moltenii Vargas, 2018 feeding on the shrub Adesmia verrucosa Meyen, a member of the subgenus Adesmia, on the arid western slope of the Andes of northern Chile (Vargas 2018). Subsequent surveys in this mountainous area revealed larvae of the congeneric Ypsolopha chicoi Vargas, 2021 associated with the shrub Muehlenbeckia fruticulosa (Walp.) Standl. (Polygonaceae) (Vargas 2021), but no additional field observations of Adesmia-feeding Ypsolopha micromoths have been documented.

The distribution ranges of some members of the two subgenera of Adesmia overlap in northern Chile (Ulibarri 1986; Macaya-Berti and Teillier 2022), such as in the surroundings of the type locality of $Y$. moltenii, where $A$. verrucosa co-occurs with Adesmia atacamensis Phil. (subgenus Adesmia) and Adesmia spinosissima Meyen (subgenus Acanthadesmia), indicating the possibility of a wider host range for this micromoth (Figs 1-4). The aim of this study was to explore the interaction between Ypsolopha micromoths and Adesmia shrubs native to this arid, high-elevation area.


Figures 1-4. Shrubs of the South American genus Adesmia DC. (Fabaceae) co-occurring in the Andes of northern Chile 1 typical landscape near Socoroma Village at about 3400 m elevation 2 Adesmia verrucosa Meyen 3 Adesmia atacamensis Phil. 4 Adesmia spinosissima Meyen.

## Material and methods

Surveys were performed near Murmuntani ( $18^{\circ} 20^{\prime} 43^{\prime \prime} \mathrm{S}$, $69^{\circ} 33^{\prime} 06^{\prime \prime} \mathrm{W}$ ), Socoroma ( $18^{\circ} 16^{\prime} 42^{\prime \prime} \mathrm{S}, 69^{\circ} 34^{\prime} 15^{\prime \prime} \mathrm{W}$ ), Putre ( $18^{\circ} 13^{\prime} 01^{\prime \prime} \mathrm{S}, 69^{\circ} 33^{\prime} 39^{\prime \prime} \mathrm{W}$ ) and Zapahuira ( $18^{\circ} 19^{\prime} 22^{\prime \prime} \mathrm{S}, 69^{\circ} 35^{\prime} 18{ }^{\prime \prime} \mathrm{W}$ ), at about 3400-3700 m elevation on the western slope of the Andes of the Parinacota Province of northern Chile between April 2018 and April 2022. This area has a tropical xeric climate, with seasonal rains concentrated mainly in summer (Luebert and Pliscoff 2006). Larvae of Ypsolopha were searched for on at least 50 plants of the following native species of Fabaceae: A. atacamensis, A. spinosissima, Dalea pennellii (J.F. Macbr.) J.F. Macbr. var. chilensis Barneby, Lupinus oreophilus Phil., and Senna birostris (Dombey ex Vogel) H.S. Irwin \& Barneby var. arequipensis (Meyen ex Vogel) H.S. Irwin \& Barneby. The collected larvae were brought to the laboratory in plastic vials with parts of the respective host plants and reared to obtain adults. In order to provide taxonomic identifications, the abdomens of adults were removed for dissection of the genitalia using standard procedures. In addition, larvae of the only two species of Ypsolopha previously recorded in the study area, Y. chicoi and Y. moltenii, were collected from their hosts for comparison; some were placed in ethanol $95 \%$ and kept at $-20^{\circ} \mathrm{C}$ to be used for DNA extraction, while the others were reared to obtain adults. Vouchers and slides containing genitalia are deposited in the "Colección Entomológica de la Universidad de Tarapacá" (IDEA), Arica, Chile.

Genomic DNA was extracted from adult legs or larvae using the QIAamp Fast DNA Tissue Kit (Qiagen). The primers LCO1490 and HCO2198 (Folmer et al. 1994) were used for PCR amplification and sequencing of the barcode region (Hebert et al. 2003) with a program of 5 min at $94^{\circ} \mathrm{C}, 35$ cycles of 30 s at $94^{\circ} \mathrm{C}, 30 \mathrm{~s}$ at $47^{\circ} \mathrm{C}, 1 \mathrm{~min}$ at $72^{\circ} \mathrm{C}$, and a final elongation step of 10 min at $72^{\circ} \mathrm{C}$. DNA purification, amplification, and sequencing were performed at Macrogen Inc. (Seoul, South Korea). MEGA v. 11 (Tamura et al. 2021) was used for sequence alignment with the ClustalW method, to assess the genetic distance using the Kimura 2-Parameter (K2P) method and to build a neighbor-joining tree with 1,000 bootstrap replicates.

## Results

The surveys revealed larvae of Ypsolopha on A. atacamensis and A. spinosissima but not on D. p. chilensis, L. oreophilus, or S. b. arequipensis. Two females and two males of $Y$. moltenii were reared from the larvae collected on $A$. atacamensis, and two males of Ypsolopha sp. from the larvae collected on A. spinosissima (Figs 5, 6). In addition, adults of Y. chicoi and Y. moltenii were obtained by rearing the larvae collected on $M$. fruticulosa and $A$. verrucosa, respectively.

DNA barcodes were obtained from two females (BOLD Process IDs NCMIC005-23, NCMIC006-23) and two larvae (NCMIC008-23, NCMIC009-23) of $Y$. moltenii from A. atacamensis and A. verrucosa, respectively; one male (NC-MIC007-23) of Ypsolopha sp.; and three larvae (NCMIC010-23, NCMIC011-23, NCMIC012-23) of $Y$. chicoi. Genetic divergence (K2P) between individuals of Y. moltenii collected on different plants was $0-0.3 \%$. In contrast, genetic divergence of $Y$. moltenii was 7.9-8.1\% from Ypsolopha sp. and 9.2-9.5\% from Y. chicoi, while Ypsolopha sp. and Y. chicoi diverged by 5.9-6.1\% (Fig. 7).


Figures 5, 6. Micromoths of the genus Ypsolopha Latreille, 1796 (Lepidoptera, Ypsolophidae) from the Andes of northern Chile, representing new host records of the South American genus Adesmia DC. (Fabaceae) 5 male of Ypsolopha moltenii Vargas, 2018 reared from larvae collected on Adesmia atacamensis Phil., dorsal view, abdomen removed 6 male of Ypsolopha sp. reared from larvae collected on Adesmia spinosissima Meyen, dorsal view, abdomen removed. Scale bar: 5 mm .

0.01

Figure 7. Neighbor-joining tree of DNA barcodes of the genus Ypsolopha Latreille, 1796 (Lepidoptera, Ypsolophidae) from the Andes of northern Chile. Stars and squares indicate specimens of Ypsolopha moltenii Vargas, 2018 collected on Adesmia atacamensis Meyen and Adesmia verrucosa Meyen (Fabaceae), respectively. Numbers near branches indicate bootstrap support (1,000 replicates).

## Material examined

Ypsolopha chicoi Vargas, 2021
Chile • 1 ふ̄; Parinacota, Socoroma; [adult emerged] May 2022; H.A. Vargas leg.; ex-larva; Muehlenbeckia fruticulosa; [larva collected] April 2022; [genitalia slide] HAV1687•2 2 + $q$; same data as for preceding; [genitalia slides] HAV1685, HAV1686; all in IDEA.

Ypsolopha moltenii Vargas, 2018
CHILE - 1 §; Parinacota, Putre; [adult emerged] May 2022; H.A. Vargas leg.; ex-larva; Adesmia verrucosa; [larva collected] April 2022; [genitalia slide] HAV1668
-1 ㅇ; same data as for preceding; [genitalia slide] HAV1669•2 2 q; Zapahuira; [adult emerged] October 2021; H.A. Vargas leg.; ex-larva; Adesmia atacamensis; [larva collected] September 2021; [genitalia slides] HAV1670, HAV1684; [BOLD
 ing; [adult emerged] May 2018; ex-larva Adesmia atacamensis; [larva collected] April 2018; [genitalia slides] HAV1179, HAV1671; all in IDEA.

## Ypsolopha sp.

Chile • 2 §入̃; Parinacota, Murmuntani; [adult emerged] May 2021; H.A. Vargas leg.; ex-larva; Adesmia spinosissima; [larva collected] April 2021; [genitalia slides] HAV1469, HAV1672; [BOLD Process ID] NCMIC007-23; all in IDEA.

## Discussion

Detailed knowledge of host ranges is essential to understand abundance and distribution patterns and to plan the conservation of phytophagous lepidopterans (Kozlov 2002; Bassett et al. 2022; Clarke 2022; Vargas 2023). Although the micromoth fauna of the arid, high-elevation area of the western slope of the Andes of northern Chile remains little known, recent surveys have revealed that plants native to this mountain region harbor previously overlooked species whose taxonomic descriptions have become available (e.g. Vargas 2018, 2021). However, some important aspects of the natural history of many recently discovered micromoths, such as their host ranges, remain only partially documented. Thus, surveys for larvae on native plants help to explore the host ranges of the little-known species and to detect unknown ones.

The low genetic divergence between $Y$. moltenii individuals collected on A. atacamensis or $A$. verrucosa is similar to conspecific distances previously recorded for Ypsolopha micromoths (Ponomarenko 2020), providing further support for the morphological identification. The only host previously recorded for Y. moltenii was $A$. verrucosa (Vargas 2018). However, the surveys revealed that this micromoth also uses $A$. atacamensis as a host, while its larvae were not found on other Fabaceae native to the study area, including the congeneric A. spinosissima. Since A. atacamensis and A. verrucosa belong to the same series (Bracteatae) of the subgenus Adesmia (Burkart 1967), these data suggest the host range of $Y$. moltenii is restricted to closely related plant species. These results rule out monophagy, suggesting instead oligophagy for $Y$. moltenii.

Ypsolopha sp. differs from Y. moltenii in morphology and host plant. The genetic divergence between Ypsolopha sp. and Y. moltenii is also greater than those reported between morphologically similar congeneric species (Corley et al. 2019; Ponomarenko 2020; Corley and Ferreira 2021). Thus, morphology, host plant use, and DNA barcodes confirm that Ypsolopha sp. represents a second species of this micromoth genus associated with a member of Adesmia. However, as only two males were reared from the larvae collected on A. spinosissima in this study, further surveys for larvae on this shrub are needed to obtain females before the formal taxonomic treatment of this micromoth. Although the results suggest that this species is not associated with members the subgenus Adesmia, its larvae should be searched for on additional species of the subgenus Acanthadesmia to assess its host range.

The results of the present study suggest narrow host ranges for Adesmia-feeding Ypsolopha and highlight the need to explore further the taxonomic diversity of these micromoths in other areas inhabited by these plants. Burkart (1967) recognized two main areas of high species richness for Adesmia, the Argentine-Chilean part of the Andes Range and the semiarid area of Argentina east of the Andes. Surveys for larvae in these areas could reveal additional Ypsolopha species associated with this highly diverse South American plant genus.

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## Additional information

## Conflict of interest

The author has declared that no competing interests exist.

## Ethical statement

No ethical statement was reported.

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## Author contributions

The author solely contributed to this work.

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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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# A new species of the genus Soriculus (Soricidae, Eulipotyphla, Mammalia) from Medog in the eastern Himalaya 

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#### Abstract

Himalayan shrews of the genus Soriculus (Soricidae, Eulipotyphla), currently represented by four nominal species, are endemic to the Himalayas and the Gaoligong Mountains. In April 2022 and April 2023, a total of 10 specimens of Soriculus were collected from Beibeng and Damu, Medog County, Tibet, China. The morphology of the specimens was compared with the four recognised species of the genus Soriculus. Additionally, two mitochondrial (Cyt b and 12S) and three nuclear (APOB, BRCAI and RAG2) genes were sequenced to test the phylogenetic relationships of these specimens with the other species. Our results indicate that these specimens represent a distinct species, Soriculus beibengensis sp. nov., which is formally described here. The new species is distinguished from the other Soriculus species by the combination of darker pelages, smaller size, the relatively stubby nasal and the widened posterior processes of incisors. Phylogenetic analyses revealed the new species is sister to $S$. minor. The $p$-distance of $C y t b$ gene between $S$. beibengensis sp. nov. and other nominal Soriculus species ranges from $9.1-16.3 \%$. This new species has a known distribution at an elevation of $1,500-2,125 \mathrm{~m}$ in Medog County, Tibet, China. The discovery of this new species from Medog County has important implications for interpreting small mammal biogeographic patterns in the eastern Himalaya and the mountain chains of south-west China.


Key words: Phylogeny, small mammals, taxonomy

## Introduction

The genus Soriculus Blyth, 1854 (Mammalia, Eulipotyphla, Soricidae) is an endemic genus in the Himalayas and Gaoligong Mountains and which is mainly distributed in countries and regions across the eastern Himalayas (Bhutan, Sikkim of India, Nepal, and Yunnan and Tibet of PR China) (Hutterer 2005; Motokawa et al. 2008; Li et al. 2024). The small size and preference to inhabit remote forested mountainous areas make it challenging to collect specimens, limiting further studies.

[^1]For a long time, Episoriculus Ellerman and Morrison-Scott, 1966 and Chodsigoa Kastchenko, 1907 were considered subgenera or junior synonyms of the genus Soriculus (Ellerman and Morrison-Scott 1951; Hoffmann 1986; Corbet 1992). However, Repenning (1967) distinguished them into three separate genera, based on the mandibular and dental characteristics, which have since become widely recognised (Hutterer 2005). The first described species of the genus Soriculus was Soriculus nigrescens (Gray, 1842) from the specimens collected in West Bengal, India. For many decades, the genus was known to include only this species and two subspecies (S. n. nigrescens and S. n. minor Dobson, 1890) (Burgin and He 2018). Jiang et al. (2023) revealed deep divergence within the genus Soriculus and proposed S. n. minor should recover the full species status and might represent a new genus. Recently, Chen et al. (2023) systematically reviewed the taxonomy of the genus and described two new species Soriculus nivatus (Chen \& Jiang, 2023) and Soriculus medogensis (Chen \& Jiang, 2023) from the eastern Himalayas and elevated S. n. minor as a distinct species (S. minor). Meanwhile, Chen et al. (2023) reported another putative species (referring to Soriculus sp. 3 in their study) in Medog. However, because only one specimen was collected, this specimen was not described systematically.

Medog is located in the eastern Himalayas with complex climate and geographic structure, making a biodiversity rich region. Due to the remoteness of Medog and the limited field surveys in the area, the biodiversity has remained poorly known and underestimated. Multiple new taxa have been recently described from the area, including mammals, for example, one new genus and species of mole (Chen et al. 2021), three new mountain voles (Liu et al. 2022) and two new shrews (Chen et al. 2023). In April 2023, we conducted further field surveys in Medog and collected another 9 specimens of the putative species mentioned by Chen et al. (2023). Based on morphological and molecular phylogenetic analyses from multiple mitochondrial and nuclear loci, we confirmed that these specimens represent a distinct species of the genus Soriculus, which we describe herein as Soriculus beibengensis sp. nov.

## Materials and methods

A total of 10 Soriculus specimens of S. beibengensis sp. nov. were collected from Medog, Tibet, China in April 2022 (Chen et al. 2023) and April 2023 (Fig. 1). Animals were handled, based on the animal care and use guidelines of the American Society of Mammologists (Sikes and the Animal Care and Use Committee of the American Society of Mammalogists 2016) and following the guidelines and regulations approved by the internal review board of the Kunming Institute of Zoology (KIZ), and with the permission of local government authorities. All specimens were deposited at the Kunming Natural History Museum of Zoology, Kunming Institute of Zoology (KIZ), Chinese Academy of Sciences, Kunming, China.

Five external measurements: weight (W), ear length (EL), head and body length (HBL), hind foot length (HL) and tail length (TL) were measured in the field and were reported to the nearest 0.1 g (for weight) or 0.5 mm (for different length categories). Eighteen craniodental metrics were measured using a digital caliper graduated to 0.01 mm following Chen et al. (2023). These metrics included


Figure 1. Map showing the collection sites of $S$. beibengensis sp. nov. in Beibeng, Medog, Tibet, China.
(Table 1): basal length (BL), cranial breadth (CB), cranial height (CH), condyle-incisive length (CIL), distance between infra-orbital foramina (DIF), height of articular condyle (HAC), height of coronoid process (HCP), height of coronoid valley (HCV), interorbital breadth (IOB), lower tooth-row length (LTR), maxillary breadth (MB), mandibular length (ML), maximum width across the upper second molars $\left(\mathbf{M}^{2} \mathbf{M}^{2}\right)$, distance from the front of upper fourth premolar to the end of upper third molar ( $\mathbf{P}^{4} \mathbf{M}^{3}$ ), palato-incisive length (PIL), postpalatal depth (PPD), foramen magnum breadth (BMF) and upper tooth-row length (UTL). All craniodental measurements were taken by the single researcher (ZZC).

Comparative morphological data of another 62 Soriculus specimens including S. nigrescens (11), S. nivatus (23), S. medogensis (7) and S. minor (21) were obtained from Chen et al. (2023). Principal component analysis (PCA) was employed to evaluate the morphological variation amongst populations of Soriculus. The PCA was implemented in SPSS 19.0 (SPSS Inc., USA) and all craniodental measurements were first $\log _{10}$-transformed. The morphological measurements of $S$. beibengensis sp. nov. was compared with other Soriculus species. The terminologies for morphological descriptions followed Motokawa and Lin (2005) and Chen et al. (2023).

The total genomic DNA of five $S$. beibengensis sp. nov. specimens was extracted from muscle or liver using a DNA extraction kit (Qiagen DNeasy Blood and Tissue Kit, Germany). Two mitochondrial genes (complete cytochrome b, Cyt b and segment of $12 S$ rRNA, 12S) and segments of three nuclear genes (apolipoprotein B, APOB; breast cancer 1, BRCA1; and recombination activating protein 2, RAG2) were amplified using primers and PCR conditions similar to Chen et al. (2023).

Table 1. Summary statistics (mean, standard deviation, ranges and number of samples) of external and skull measurements (in millimetres) of Soriculus specimens used in the study; character abbreviations are detailed in the "Material and methods".

|  | S. beibengensis sp. nov. | S. minor | S. nigrescens | S. medogensis | S. nivatus |
| :---: | :---: | :---: | :---: | :---: | :---: |
| W | $11.7 \pm 1.4$ | $8.9 \pm 1.2$ | $17.6 \pm 2.5$ | $13.3 \pm 0.7$ | $11.7 \pm 1.7$ |
|  | 8.8-13.2; 10 | 7.7-12.1; 21 | 12.9-20.7; 11 | 12-14.1; 7 | 9.6-15.3; 23 |
| HBL | $77.2 \pm 4.1$ | $71 \pm 3.9$ | $88.6 \pm 3.4$ | $84.7 \pm 0.8$ | $82.6 \pm 4.1$ |
|  | 70-81; 10 | 62-77; 20 | 83-93; 11 | 83-85; 7 | 70-90; 23 |
| TL | $40.6 \pm 1.8$ | $36.7 \pm 4.1$ | $45.8 \pm 3.2$ | $50.7 \pm 3.6$ | $51.6 \pm 2.7$ |
|  | 38-44; 10 | 31.5-43; 21 | 42-52; 11 | 43-54; 7 | 46-58; 23 |
| HF | $12.6 \pm 1.1$ | $12.3 \pm 0.6$ | $15.4 \pm 0.9$ | $14.9 \pm 0.7$ | $15.3 \pm 1$ |
|  | 11-14; 10 | 11-13.5; 21 | 14-17; 11 | 14-16; 7 | 13-17; 23 |
| EL | $8.1 \pm 1.4$ | $7.9 \pm 1.1$ | $8.7 \pm 0.9$ | $10.3 \pm 1$ | $9.3 \pm 1.2$ |
|  | 6-10; 10 | 6-10; 6 | 8-11; 11 | 9-12; 7 | 7-12; 23 |
| CIL | $20.8 \pm 0.3$ | $19.6 \pm 0.4$ | $23.4 \pm 0.5$ | $23.7 \pm 0.7$ | $23.4 \pm 0.3$ |
|  | 20.4-21.3; 10 | 19.2-20.2; 7 | 22.5-24.2; 9 | 22.7-24.5; 4 | 22.8-24.1; 22 |
| PIL | $9.3 \pm 0.2$ | $8.9 \pm 0.2$ | $10.7 \pm 0.2$ | $11.1 \pm 0.2$ | $10.7 \pm 0.2$ |
|  | 9-9.5; 10 | 8.6-9.3; 6 | 10.4-11.1; 10 | 10.8-11.5; 5 | 10.4-11.1; 22 |
| BL | $18.4 \pm 0.3$ | $17.4 \pm 0.3$ | $20.8 \pm 0.5$ | $21 \pm 0.7$ | $20.7 \pm 0.3$ |
|  | 17.9-19; 10 | 17-17.9; 7 | 19.9-21.4; 9 | 20.1-21.7; 4 | 20.1-21.3; 22 |
| UTL | $9 \pm 0.2$ | $8.5 \pm 0.2$ | $10.2 \pm 0.2$ | $10.8 \pm 0.2$ | $10.3 \pm 0.2$ |
|  | 8.8-9.2; 10 | 8.3-8.9; 7 | 9.9-10.6; 9 | 10.6-11; 5 | 10-10.7; 22 |
| $\mathrm{P}^{4} \mathrm{M}^{3}$ | $5.5 \pm 0.1$ | $5.3 \pm 0.1$ | $6.3 \pm 0.1$ | $6.4 \pm 0.1$ | $6.1 \pm 0.1$ |
|  | 5.3-5.6; 10 | 5.2-5.4; 7 | 6.2-6.5; 10 | 6.3-6.5; 5 | 6-6.3; 22 |
| IOB | $4.8 \pm 0.1$ | $4.8 \pm 0.1$ | $5.6 \pm 0.5$ | $5.4 \pm 0.1$ | $5.4 \pm 0.1$ |
|  | 4.6-5; 10 | 4.7-5; 7 | 5.3-6.9; 11 | 5.3-5.5; 5 | 5.2-5.6; 22 |
| DIF | $3.9 \pm 0.1$ | $3.7 \pm 0.1$ | $4.3 \pm 0.1$ | $3.9 \pm 0.1$ | $3.7 \pm 0.1$ |
|  | 3.7-4; 10 | 3.6-3.9; 7 | 4.2-4.5; 11 | 3.8-4; 5 | 3.6-3.9; 22 |
| CB | $10.7 \pm 0.2$ | $10.4 \pm 0.3$ | $11.7 \pm 0.2$ | $11.8 \pm 0.3$ | $11.4 \pm 0.2$ |
|  | 10.2-11; 10 | 9.8-10.7; 7 | 11.5-11.9; 10 | 11.3-12.1; 4 | 11.2-11.7; 22 |
| CH | $6.3 \pm 0.2$ | $6.2 \pm 0.2$ | $6.8 \pm 0.1$ | $7 \pm 0.2$ | $7 \pm 0.1$ |
|  | 6-6.5; 10 | 5.9-6.6; 7 | 6.7-7; 10 | 6.8-7.2; 4 | 6.8-7.5; 22 |
| MB | $6.2 \pm 0.2$ | $6 \pm 0.1$ | $7.1 \pm 0.2$ | $6.9 \pm 0.1$ | $6.6 \pm 0.1$ |
|  | 5.7-6.5; 10 | 5.8-6.1; 7 | 6.9-7.4; 11 | 6.8-7; 5 | 6.3-6.8; 22 |
| $M^{2} M^{2}$ | $5.9 \pm 0.2$ | $5.7 \pm 0.1$ | $7 \pm 0.1$ | $6.8 \pm 0.2$ | $6.3 \pm 0.1$ |
|  | 5.6-6.1; 10 | 5.6-5.8; 7 | 6.9-7.1; 11 | 6.7-7.2; 5 | 6-6.6; 22 |
| PPD | $3.9 \pm 0.1$ | $3.9 \pm 0.1$ | $4.5 \pm 0.1$ | $4.6 \pm 0.1$ | $4.3 \pm 0.1$ |
|  | 3.8-4; 10 | 3.8-4; 6 | 4.3-4.7; 11 | 4.5-4.7; 5 | 4.2-4.5; 22 |
| BMF | $3.6 \pm 0.1$ | $3.4 \pm 0.2$ | $3.7 \pm 0.1$ | $3.5 \pm 0.2$ | $3.5 \pm 0.1$ |
|  | 3.5-3.8; 10 | 3.1-3.6; 7 | 3.5-3.9; 10 | 3.2-3.8; 4 | 3.2-3.7; 22 |
| ML | $11.6 \pm 0.2$ | $10.8 \pm 0.2$ | $12.8 \pm 0.4$ | $13.6 \pm 0.3$ | $13.2 \pm 0.3$ |
|  | 11.3-11.9; 9 | 10.5-11; 7 | 12.3-13.4; 11 | 13.3-14.1; 5 | 12.5-13.7; 22 |
| LTR | $8.3 \pm 0.2$ | $7.8 \pm 0.2$ | $9.1 \pm 0.3$ | $9.8 \pm 0.1$ | $9.5 \pm 0.2$ |
|  | 8-8.5; 9 | 7.7-8.1; 7 | 8.7-9.6; 11 | 9.7-10; 5 | 8.9-9.7; 22 |
| HCP | $4.9 \pm 0.2$ | $4.7 \pm 0.2$ | $5.9 \pm 0.2$ | $6.7 \pm 0.1$ | $5.6 \pm 0.3$ |
|  | 4.5-5.1; 10 | 4.5-4.9; 7 | 5.7-6.1; 11 | 6.6-6.9; 5 | 4.6-6; 22 |
| HCV | $3.1 \pm 0.1$ | $2.9 \pm 0.1$ | $3.7 \pm 0.1$ | $3.8 \pm 0.1$ | $3.2 \pm 0.1$ |
|  | 3-3.2; 10 | 2.7-3.1; 7 | 3.5-3.8; 11 | 3.7-3.9; 5 | 3.1-3.5; 22 |
| HAC | $3.8 \pm 0.2$ | $3.6 \pm 0.1$ | $4.5 \pm 0.2$ | $4.6 \pm 0.1$ | $4.3 \pm 0.1$ |
|  | 3.7-4.1; 10 | 3.4-3.8; 7 | 4.2-4.8; 11 | 4.5-4.8; 5 | 4-4.5; 22 |

The PCR products were sequenced in both directions using the BigDye Terminator Cycle Sequencing kit v. 3.1 (ThermoFisher Scientific, USA) on an ABI 3730xI sequencer. The DNA sequences were assembled using SeqMan (DNASTAR, Lasergene v.7.1). In addition, corresponding sequences of other Soriculus species were downloaded from the GenBank database. Corresponding sequences of several Soricidae genera were retrieved from the GenBank and used as outgroups. All sequences used in the study were aligned using MUSCLE (Edgar 2004), then checked manually. The uncorrected p-distance of Cyt $b$ gene between the species pairs were calculated in MEGA-X (Kumar et al. 2018).

Three concatenated datasets were used for the phylogenetic analyses: (1) mitochondrial genes (mtDNA, Cyt b+12S, 1963 bp ), (2) nuclear genes (nDNA, APOB + $R A G 2+B R C A 1,1974 \mathrm{bp}$ ) and (3) the mitochondrial and nuclear genes (mtDNA + nDNA, Cyt b $+12 S+A P O B+R A G 2+B R C A 1,3937 \mathrm{bp})$. Maximum-Likelihood (ML) and Bayesian Inference (BI) methods were used to reconstruct phylogenetic relationships. The ML phylogenies were inferred using IQ-TREE (Nguyen et al. 2015), with 10000 ultrafast bootstraps to estimate branch support. The BI phylogenies were inferred using MrBayes 3.2.6 (Ronquist et al. 2012) with two parallel runs and $10,000,000$ generations, in which the initial $25 \%$ of sampled data were discarded as the burn-in. Before the phylogenetic inferences, the best-fit partitioning scheme and evolutionary models were selected using PartitionFinder v.2.1.1 (Lanfear et al. 2017) with greedy algorithm and BIC criterion (Suppl. material 1). The above analysis were performed in PhyloSuite (Zhang et al. 2020). The posterior probabilities (PP) $\geq 0.95$ and ultrafast bootstrap value (UFBoot) $\geq 95$ were considered as strong support (Huelsenbeck and Rannala 2004; Minh et al. 2013).

We estimated divergence time using BEAST v.2.6.7 (Bouckaert et al. 2014) on the concatenated nuclear gene dataset for which also the best partition schemes and evolutionary models were estimated using PartitionFinder v.2.1.1 (Lanfear et al. 2017) with greedy algorithm and BIC criterion (Suppl. material 1). Divergence dates were calibrated, based on three secondary calibrations following Chen et al. (2023): (1) the split between Crocidurinae and Soricinae is estimated at about 36 Ma ( $95 \%$ confidence interval [CI] = 28.6-44.0 Ma; Springer et al. (2018)). We established the prior using log-normal distribution with offset: 0 , mean: 36 , standard deviation: 0.135 , which will specify a distribution centred at about 35.7 Ma and the $95 \% \mathrm{Cl}$ was $28.6-44.5 \mathrm{Ma}$. (2) The oldest Blarinellini was from the Early Middle Miocene (Harris 1998, Rzebik-Kowalska 1998) and the oldest Blarinini was in the Barstovian (Repenning 1967) at approximately $13.6-16.3 \mathrm{Ma}$. We established the prior for the divergence of Blarinellini-Blarinini using log-normal distribution with an offset of 15 Ma , mean of 0 and standard deviation of 0.98 , which will specify a distribution centred at about 16.0 Ma and the $95 \% \mathrm{Cl}$ was $15.2-20.0 \mathrm{Ma}$. (3) The oldest fossil of Nectogalini was in the Late Miocene (MN10, 9.7-11.5 Ma; Fejfar and Sabol (2005)). We established the prior for the divergence of Nectogalini-Notiosoricini using log-normal distribution with an offset of 9.7 Ma , mean of 0 and standard deviation of 0.95 , which will specify a distribution centred at about 10.7 Ma and the $95 \% \mathrm{Cl}$ was $9.91-14.5 \mathrm{Ma}$. The analyses were implemented with 100 million generations, sampled every 10,000 generations. Each analysis used a random starting tree, a log-normal relaxed clock model and a birth-death tree prior. Finally, the convergence of the parameters was assessed using Tracer 1.7 (Rambaut et al. 2018) and the tree was annotated using FigTree v.1.4.4.

## Results

## Morphological analyses

A summary of the external and cranial measurements of the five species under the genus Soriculus is given in Table 1. The $S$. beibengensis sp. nov. showed the highest morphometric similarity to $S$. minor, but is much smaller than S. medogensis, S. nigrescens and S. nivatus. The PCA, based on 55 intact skulls, produced two principal components with eigenvalues exceeding 1.0, which explained $88.17 \%$ of the variation (Table 2). The first principal component (PC1) explained $66.62 \%$ of the total variation and was strongly positively correlated with most of the variables (UTL, PIL, CIL, ML, LTR, BL, $\mathrm{CH}, \mathrm{P}^{4} \mathrm{M}^{3}, \mathrm{PPD}, \mathrm{HAC}, \mathrm{CB}, \mathrm{HCP}, I O B, \mathrm{M}^{2} \mathrm{M}^{2}, \mathrm{MB}$, DIF, BMF and HCV), indicating that it represented the overall skull size. The second principal component (PC2) explained $21.55 \%$ of the total variation and was strongly positively correlated with $\mathrm{M}^{2} \mathrm{M}^{2}, \mathrm{MB}$, DIF, BMF and HCV (loading > 0.668 ), indicating that it represented the skull width. The plot of PC1 and PC2 (Fig. 2) showed that S. beibengensis sp. nov. is well-separated from other species, but positioned closer to $S$. minor. The two species plot on the negative axis of PC1, indicating the smaller skull in the genus. S. beibengensis sp. nov. is located in the upper right corner of $S$. minor, indicating it had a larger and wider skull compared to $S$. minor.

Table 2. Craniodental variation in Soriculus, based on principal component analysis (PCA). Character abbreviations are detailed in the "Material and methods".

| Character | PC1 | PC2 |
| :--- | :---: | :---: |
| UTL | 0.973 | 0.168 |
| PIL | 0.972 | 0.166 |
| CIL | 0.960 | 0.178 |
| ML | 0.955 | 0.056 |
| LTR | 0.952 | 0.002 |
| BL | 0.950 | 0.202 |
| CH | 0.935 | -0.022 |
| P4M ${ }^{4}$ | 0.916 | 0.356 |
| PPD | 0.869 | 0.409 |
| HAC | 0.839 | 0.452 |
| CB | 0.839 | 0.458 |
| HCP | 0.826 | 0.398 |
| IOB | 0.743 | 0.371 |
| M $^{2}$ M $^{2}$ | 0.695 | 0.681 |
| MB | 0.674 | 0.670 |
| DIF | 0.100 | 0.932 |
| BMF | -0.096 | 0.717 |
| HCV | 0.625 | 0.668 |
| Eigenvalue | 13.727 | 6.862 |
| Variance explained | 66.620 | 21.550 |



Figure 2. Results of principal component analysis (PCA) of Soriculus, based on the $18 \log _{10}$-transformed craniodental measurements.

## Phylogenetic relationship

In total, we obtained 3937 bp long sequences for five specimens of $S$. beibengensis, including 1140 bp Cyt b, 823 bp 12S, 507 bp APOB, 693bp RAG2 and 774 bp BRCA1. All new sequences have been deposited in the GenBank (Accession Numbers: PP213259-PP213263 and PP226949-PP226968, Suppl. material 2). The topologies of ML and BI trees of the three datasets were highly similar and only the BI gene trees are shown (Fig. 3). The phylogenetic trees generated from the datasets of nDNA and mtDNA + nDNA strongly supported the monophyly of Soriculus and clustered into two major clades: the first clade was composed of $S$. minor and $S$. beibengensis sp. nov. (Clade I) and the second clade was composed of S. medogensis, S. nigrescens and S. nivatus (Clade II) (PP = 1.00, UFboot $\geq 94$ ). In contrast, the tree, based on concatenated mitochondrial genes, showed a closer phylogenetic relationship between Clade I and Chimarrogale himalyica, Nectogale elegans and Neomys fodiens, but this result was not significantly supported ( $\mathrm{PP}=0.79$, UFboot $=62$ ). A sister relationship of $S$. beibengensis and $S$. minor was strongly supported in all gene trees ( $\mathrm{PP}=1.00$, UFboot $=100$ ). The $p$-distance of the Cyt $b$ gene between the S. beibengensis sp. nov. and other species ranged from $9.1 \%$ (with S. minor) to $15.9 \%$ (with S. medogensis) (Table 3). The results of divergence time estimates (Fig. 4) showed that $S$. beibengensis sp . nov. and $S$. minor diverged at the early Pleistocene (ca. 2.06 Ma, $95 \% \mathrm{Cl}=1.05-3.40 \mathrm{Ma}$ ).



## S．nivatus

## S．medogensis

S．nigrescens

## S．minor

S．beibengensis sp．nov．

## Outgroups

$\frac{\text { The median ages }}{\text { Posterior probabilities }}$
Figure 4．The divergence time of Soriculus species inferred from a time－calibrated phylogeny，based on the nuclear genes in BEAST v．2．6．7．The node numbers represent the median ages of the divergence times（upper）and posterior probabil－ ities（below）．The branch lengths represent divergence time，node bars indicate the $95 \% \mathrm{Cl}$ for each clade age and red bars indicate the calibration points．

Table 3．The p－distance between Soriculus species，based on the Cyt $b$ gene．

|  | S．beibengensis sp．nov． | S．minor | S．nigrescens | S．medogensis |
| :--- | :---: | :---: | :---: | :---: |
| S．beibengensis sp．nov． |  |  |  |  |
| S．minor | 0.091 |  |  |  |
| S．nigrescens | 0.154 | 0.163 |  |  |
| S．medogensis | 0.159 | 0.156 | 0.113 |  |
| S．nivatus | 0.151 | 0.153 | 0.118 | 0.105 |

## Taxonomic account

## Soriculus beibengensis sp．nov．

https：／／zoobank．org／516798F9－7726－47D0－9C81－F73436F24D96
Suggested common name．Beibeng large－clawed shrew，背崩大爪鼩鲭．

Type material. Holotype. KIZ042755, adult female, collected on 08 April 2023 by Mingjin Pu, at Beibeng Town, Medog County, southeast Tibet, China ( $29.219^{\circ} \mathrm{N}, 95.189^{\circ} \mathrm{E}, 1610 \mathrm{~m}$ a.s.I.). Dried skin, cleaned skull and muscle tissue are deposited in KIZ.

Paratypes. Five specimens KIZ042756 (adult female), KIZ042757 (adult female), KIZ042758 (adult female), KIZ042759 (adult female), KIZ042760 (adult female). Collected from the type locality at Medog in April 2023 at elevations from 1500 m to 2125 m . All specimens are deposited in KIZ.

Specimens examination. Four specimens KIZO42761 (adult female), KIZ042762 (adult male), KIZ042763 (adult female), KIZ042764 (adult female).

Etymology. The specific Latin name beibengensis named for Beibeng, the type locality, with the Latin adjectival suffix -ensis means "belonging to".

Diagnosis. The new species is assigned to the genus Soriculus, based on the typically enlarged forefeet and claws (Fig. 5). Dark grey to black pelage; nearly similar ventral and dorsal pelage colour, similar to S. minor (Fig. 5); size (CIL: $20.8 \pm$ $0.3 \mathrm{~mm}, 20.4-21.3 \mathrm{~mm}$ vs. $19.6 \pm 0.4 \mathrm{~mm}, 19.2-20.2 \mathrm{~mm} ; \mathrm{ML}: 11.6 \pm 0.2 \mathrm{~mm}$, $11.3-11.9 \mathrm{~mm}$ vs. $10.8 \pm 0.2 \mathrm{~mm}, 10.5-11.0 \mathrm{~mm}$ ) larger than S . minor, but much smaller than S. nivatus, S. nigrescens and S. medogensis. The tail ( $40.6 \pm 1.8 \mathrm{~mm}$ ) is longer than $S$. minor ( $36.7 \pm 4.1 \mathrm{~mm}$ ), but shorter than $S$. nivatus ( $51.6 \pm 2.7 \mathrm{~mm}$ ), S. nigrescens ( $45.8 \pm 3.2 \mathrm{~mm}$ ) and $S$. medogensis ( $50.7 \pm 3.6 \mathrm{~mm}$ ). The TL/HBL $(53 \%)$ is close to that of $S$. minor ( $52 \%$ ) and $S$. nigrescens ( $52 \%$ ), but smaller than S. nivatus (63\%) and S. medogensis (60\%). The nasal and rostrum are not clearly transitioned and seem to be stubby. The posterior process of the incisors widens, forming a narrow funnel-shaped channel between the processes. The basioccipital and basisphenoid are fused and narrowed, like a spade (Fig. 6).

Description. Amongst five species of the genus Soriculus, S. beibengensis sp. nov. is the second smallest species. Its size is larger than $S$. minor, but smaller than S. nivatus, S. nigrescens and S. medogensis (Table 1). External morphology is similar to $S$. minor, with the dorsal pelage being dark grey to black and ventral pelage slightly paler. Tail is ambiguously bicoloured, dark above and pale below (Fig. 5). The tail is short ( $\mathrm{TL}=40.6 \pm 1.8 \mathrm{~mm}, 38-44 \mathrm{~mm}$ ), averages $53 \%$ of the head and body length and 8 of 10 specimens examined have a tail length more than 40 mm . The foreclaws are enlarged, similar to other Soriculus species. The back of hands and feet are covered by light brown to black hairs.

The skull is distinctly smaller than S. nivatus, S. nigrescens and S. medogensis, but larger than $S$. minor. Braincase is low and relatively flattened and the posterior of the skull is rounded. The sagittal and lambdoidal crest are well-developed and clear, the latter is especially prominent. The nasal and rostrum are not clearly transitioned and are stubby. The posterior process of incisor is widened, forming a narrowed funnel-shaped channel between the processes of adjacent teeth. The basioccipital and basisphenoid are fused and narrowed markedly in the middle region, forming a spade-like structure (Fig. 6).

The coronoid process is high and straight, with a concave anterior surface and a spatulate tip. The condyloid process has a single slender point and is angled upward at roughly 45 degrees, with the tip sitting below the coronoid process (Fig. 6). The angular process is long, straight and very thin, the tip slightly expands and bends upwards. The condyloid process is double-faceted, having two projections. The dental formula of the $S$. beibengensis sp . nov.is the same as the genus is: $\operatorname{l} 3 / 2, \mathrm{C} 1 / 0, \mathrm{P} 2 / 1, \mathrm{M} 3 / 3(\times 2)=30$. The apex of the first upper


Figure 5. Dorsal and ventral view of the skin of A S. beibengensis sp. nov. (KIZ042755) B S. minor (KIZO20545).
incisor is straight downwards, the tip of the first upper incisor is slightly pigmented with orange. There are four upper unicuspids $\left(\mathrm{U}^{1}-\mathrm{U}^{4}\right)$; $\mathrm{U}^{1}$ is the highest, followed by $\mathrm{U}^{2}, \mathrm{U}^{3}$ and $\mathrm{U}^{4}$ is the smallest. $\mathrm{M}^{1}$ and $\mathrm{M}^{2}$ are similar in size, while $M^{3}$ is reduced. The lower incisor $\left(I_{1}\right)$ is long, with only a low cusp and the tips are pigmented with orange. The lower unicuspid $\left(U_{1}\right)$ and $P_{4}$ are crowded. $M_{1}$ is larger than $M_{2} ; M_{3}$ is the smallest.

Comparison. Amongst species of the genus Soriculus, S. beibengensis sp. nov. is morphologically similar to its sister species, the $S$. minor. Both of them have a darker pelage and smaller size than other species. However, the new species can be distinguished from $S$. minor by multiple features. $S$. beibengensis sp. nov. is larger than S. minor for most of the external and craniomandibular measurements (Table 1). Especially, the skull of $S$. beibengensis sp. nov. is significantly longer than that of the S. minor, the measurements of CIL (20.421.3 mm vs. $19.2-20.2 \mathrm{~mm}$ ) and ML ( $11.3-11.9 \mathrm{~mm}$ vs. $10.5-11.0 \mathrm{~mm}$ ) between the two species do not overlap. The nasal and rostrum of $S$. beibengensis sp. nov. are not clearly transitioned and seem to be stubby, while S. minor, as well as the other species, has a clear transition of the nasal and rostrum (Fig. 6). The posterior process of incisors in S. beibengensis sp. nov. are widened, forming a narrowed funnel-shaped channel between the processes, whereas they are not widened in S. minor (Fig. 6).


Figure 6. Dorsal, ventral and lateral views of the skull and mandibles of A S. beibengensis sp. nov. (KIZ042755) B S. minor (KIZO20545).

Soriculus beibengensis sp. nov. can be easily distinguished from S. nigrescens, $S$. nivatus and $S$. medogensis by its smaller size, the darker pelage colour and almost no pigmentation of the teeth (Fig. 5). Compared to S. nivatus, the measurements of CIL, PIL, BL, UTL, $\mathrm{P}^{4} \mathrm{M}^{3}, ~ I O B, C B, C H, P P D, M L$ and LTR of $S$. beibengensis sp . nov. are smaller, with no overlap and the teeth of $S$. nivatus
are slender, appear to be the most delicate in the genus. Amongst $S$. beibengensis sp. nov., S. nigrescens and S. medogensis, the ranges of most of their external and craniodental measurements do not overlap (Table 1). The teeth of $S$. beibengensis $s p$. nov. are significantly smaller, but the teeth of $S$. medogensis are robust, with the broadest ramus region and the highest coronoid process in the genus. Compared to S. nivatus (TL/HBL = 63\%) and S. medogensis (TL/ $\mathrm{HBL}=60 \%$ ), the tail of $S$. beibengensis sp. nov. (TL/HBL $=53 \%$ ) is shorter and the tail length of $S$. nivatus more than 46 mm , the tail length of $S$. medogensis usually more than 50 mm ( 6 of 7 (species measurements?)), while $S$. beibengensis sp . nov. less than 44 mm . The size arrangement of the unicuspids of $S$. beibengensis sp . nov. is similar to S . minor, $\mathrm{U}^{1}$ is the highest, followed by $\mathrm{U}^{2}, \mathrm{U}^{3}$ and $U^{4}$ is the smallest, while other species usually have the largest $U^{2}$, followed by $\mathrm{U}^{1}, \mathrm{U}^{3}$ and $\mathrm{U}^{4}$.

Distribution and habits. Soriculus beibengensis sp. nov. is known only from the type locality in Beibeng and Damu Town, Medog, Tibet, China at elevations from 1501 to 2123 m a.s.l. They were mainly distributed in mixed forest dominated by oak and a few individuals were distributed in conifer-broadleaf mixed forest.

## Discussion

The genus Soriculus is one of the least-studied small mammals. Owing to the limited studies, several species were not described until recently and it was considered a monotypic genus for a long time (Motokawa 2003; Burgin and He 2018). With a series of recent surveys conducted by Chinese scientists in the Himalayan Region, the diversity of the Soriculus has gradually been discovered with four species recognised (Chen et al. 2023). Herein, we described the fifth species, S. beibengensis sp. nov, collected in Medog, Tibet, China. In the genus Soriculus, $S$. beibengensis sp . nov. is morphologically similar to $S$. minor, both having darker pelage and smaller body size, but the former has a significantly larger body and skull size than the latter. Moreover, the phylogenetic tree showed that the sequences of the $S$. beibengensis sp . nov. clustered as a single clade, sister to $S$. minor and the $p$-distance between the two clades is up to $9.1 \%$. According to the diagnostic and monophyletic species concept (Mayden 1997; Gutiérrez and Garbino 2018), we recognise S. beibengensis sp. nov. as a distinct species under the genus Soriculus.

As research has progressed, the evolutionary relationships amongst species of the genus Soriculus have become clearer. The genus is mainly split into two clades, representing two different evolutionary processes. The fossil evidence of Nectogalini shows that different taxa in this family migrated southwards from the late Miocene to the early Pleistocene (He et al. 2010). Therefore, Soriculus also likely migrated southwards under the influence of global cooling and desiccation and settled in the Gaoligong Mountains and Himalayas in southwest China. Our results showed that both clades of Soriculus have extant species distributed in Medog, indicating that the genus Soriculus entered Medog at least twice and adopted Medog as a key refuge. However, the current evidence is not sufficient to determine the specific dispersal history of the genus Soriculus. Deeper biological and geological surveys will become the key for analysing the evolutionary history of the genus.

## Key to the species of Soriculus

1 Small; CIL < $22.0 \mathrm{~mm}, \mathrm{ML}<12.0 \mathrm{~mm}$....................................................... 2

- Large; CIL > $22.0 \mathrm{~mm}, \mathrm{ML}>12.0 \mathrm{~mm}$..................................................... 3
$2 \mathrm{CIL}<20.3 \mathrm{~mm}, \mathrm{ML}<11.2 \mathrm{~mm}$......................................................S. minor
- $\quad \mathrm{CIL}>20.3 \mathrm{~mm}, \mathrm{ML}>11.2 \mathrm{~mm}$.............................. S. beibengensis sp. nov.

3 Mandible well developed, the ramus region broader and coronoid process is high, HCP > 6.6 mm . $\qquad$ S. medogensis

- Mandible less developed, the ramus region is narrow and coronoid process is short, HCP < 6.1 mm $\qquad$ .4
4 Maxillary region narrower, teeth are slender, $\mathrm{M}^{2} \mathrm{M}^{2}<6.6 \mathrm{~mm}$..... S. nivatus
- Maxillary region broader, teeth are robust, $\mathrm{M}^{2} \mathrm{M}^{2}>6.8 \mathrm{~mm}$. S. nigrescens


## 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

Data curation: HW. Investigation: QL, XL, CP, JL, KL, MP. Writing - original draft: XP. Writing - review and editing: XJ, ZC, LK.

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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

## The best-fit partitioning schemes and evolutionary models estimated using PartitionFinder

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Data type: xlsx
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Link: https://doi.org/10.3897/zookeys.1195.115699.suppl1

## Supplementary material 2

## Samples, sampling localities and DNA sequences used for molecular analyses

Authors: Xiaoxin Pei, Zhongzheng Chen, Quan Li, Xueyou Li, Changzhe Pu, Kang Luo, Jing Luo, Mingjin Pu, Hongjiao Wang, Laxman Khanal, Xuelong Jiang
Data type: xlsx
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Link: https://doi.org/10.3897/zookeys.1195.115699.suppl2

# Contributions of a small collection of terrestrial microsnails (Pupilloidea, Hypselostomatidae) from Myanmar with description of three new species 

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#### Abstract

Land snails were collected for the project 'Conserving Myanmar's Karst Biodiversity' from the limestone karsts in Mon, Kayin, and Shan states and in the regions of Tanintharyi and Mandalay between 2015 and 2017, through cooperation with Fauna and Flora International (FFI) and the Forestry Department of Myanmar. Here, we report on a portion of the collection, and list 17 species from seven genera of the Hypselostomatidae microsnails. Three new species from two genera are described as Bensonella taiyaiorum Tongkerd \& Panha, sp. nov., B. lophiodera Tongkerd \& Panha, sp. nov., and Gyliotrachela aunglini Tongkerd \& Panha, sp. nov. All new species are known only from the type locality in Shan State (Bensonella) and Kayin State (Gyliotrachela). A new combination of Acinolaemus dayanum and three newly recorded species, namely A. cryptidentatus, $B$. anguloobtusa and $G$. hungerfordiana are discussed. The low morphological variability of the widely distributed $G$. hungerfordiana is discussed, and two species are proposed for formal synonymisation. Constituting the first records for Myanmar, five species of Bensonella and two species of Acinolaemus were collected.


Key words: Conservation, endemism, FFI, limestone, systematics

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## Introduction

The Indo-Burma Region is globally recognised as a biodiversity hotspot that supports many species unique to Southeast Asia, and at the same time, it is one of the most threatened due to its high population density (Mittermeier et al. 2004; Tordoff et al. 2012; CEPF 2020). The limestone habitats are home to uniquely adapted plants and animals that have evolved in the special micro-habitat conditions existing there. Various families of land snails are associated with limestone habitats; one of these, Hypselostomatidae Zilch, 1959, possesses a trumpet shell shape and contains the world's smallest land snails. Although some researchers consider this group a subfamily and others a distinct family (Schileyko 1998; Bouchet and Rocroi 2005; MolluscaBase 2023), we regard it as

Hypselostomatidae because it lacks a broad-scale phylogeny and wish to maintain consistency with recent revisions (i.e., Páll-Gergely et al. 2015, 2020a, 2022).

Members of the family Hypselostomatidae are generally known as 'microsnails', possessing shells smaller than 5 mm (Panha and Burch 2005). They are widely distributed in Southeast Asia, southern China, Australia, and the Philippines, where they inhabit limestone-rich areas (Páll-Gergely et al. 2015, 2022). Studies of Burmese microsnails dates back to the mid-19 th to early $20^{\text {th }}$ century, during the British rule in Burma (1824-1948; now Myanmar) by the European naturalists (i.e., Gude 1914 and references therein). No new information records of new species were published in the following hundred years, until recently, when exploration of the hypselostomatid microsnails resumed. Prior to this study, only eleven hypselostomatid microsnails belonging to six genera were known from Myanmar. Among the five genera, Clostophis Benson, 1860 and Angustopila Jochum et al., 2014 have been systematically revised recently and are well-documented for Myanmar (Gude 1914; Páll-Gergely et al. 2020a, 2023; Gojšina et al. 2022; Páll-Gergely and Hunyadi 2022). Meanwhile the other genera, Anauchen Pilsbry, 1917, Bensonella Pilsbry \& Vanatta, 1900, Gyliotrachela le Tomlin, 1930 and Hypselostoma Benson, 1856 have received little attention, with only a few reports (Gojšina et al. 2022; Páll-Gergely 2023a; Páll-Gergely and White 2023).

With the invitation from Fauna and Flora International (FFI) and the Forestry Department of Myanmar, we joined the ongoing 'Conserving Myanmar’s Karst Biodiversity' project to survey the land snails from the limestone karsts in the areas of Mon, Kayin, and Shan states and Tanintharyi and Mandalay regions between 2015 and 2017. The surveys have led to several systematic revisions and descriptions of new taxa, including the following: new genera and species of the limacoid and helicoid snails (see Páll-Gergely et al. 2020c; Pholyotha et al. 2020, 2022a, b; Sutcharit et al. 2020b), the carnivorous snails (see Páll-Gergely et al. 2020b; Sutcharit et al. 2020a; Man et al. 2022), the door snails (see Man et al. 2023), and the Cyclophoroidea (see Páll-Gergely et al. 2021; Tongkerd et al. 2023). These revisionary works, including the discovery of new taxa, have vastly improved the documented knowledge of land snails while confirming the high biodiversity within the limestone habitats of the lowland areas in the Salween River Basin as well as in the upland areas of the Shan Plateau of Myanmar. In sync with these studies, we specifically address the hypselostomatid microsnails, a large but overlooked fraction of Myanmar land snails. This present work aims to record and investigate all species of hypselostomatid microsnails known from Myanmar based on the literature and recent collections from our ongoing project with Fauna and Flora International.

## Material and methods

Microsnail samples were collected by hand while searching limestone walls and leaf litter (Fig. 1) in all accessible localities. Due to armed conflict in the country, specimen sampling and access was only allowed with special government permissions under an MOU (Memorandum of Understanding Agreement) between the Forest Department of the Ministry of Natural Resources and Environmental Conservation and Forestry, Myanmar and Fauna \& Flora International, acknowledged by Letter No. 0092. Thus, only a small number of limestone sites in the Salween River Basin and Shan Hills could be explored between 2015


Figure 1. Approximate collecting localities of the hypselostomatid species from Myanmar examined in this study.
and 2017. The Salween karsts are located on the east slope of the Tenasserim Range, mainly in Mon and Kayin states and in the Tanintharyi Region. These regions have a typical tropical monsoon climate, with heavier rainfall usually occurring from May to November (Wang and Myint 2016). The Shan Hills, often called 'Plateau Limestone', are located in the east, mainly in the Shan and Kayah states and in the Mandalay Region. The area is bisected by the deep trench of the Salween River (Dreybrodt and Steiner 2015). The Shan Plateau has a mean elevation of approximately 1100 m and experiences a monsoon season between the end of May and October.

Shells were first soaked in a petri dish with water and detergent and then manually brushed of mud or dirt using fine painting brushes. The shells were air-dried, examined, and imaged by scanning electron microscopy (SEM; JEOL, JSM-6610 LV), and a Leica M205C microscope with a fusion optics stereo microscope and the Leica Application Suite Image System. Shell whorls were counted to the nearest quarter whorl. Shell measurements were taken from digital images by Cell'D Imaging Software (Olympus).

The systematic relationships of the genera classified in the Hypselostomatidae are largely unclear. Several criteria are used to classify the representatives
of this group. The nomenclature of apertural dentitions mostly follows Pilsbry (1948) and, regarding the palatal tubercle, Pilsbry (1918). To maintain consistency, the traditional genus-level identification of Pilsbry (1916-1918) has been used for Hypselostoma Benson, 1856 and Gyliotrachela le Tomlin, 1930. Meanwhile, Angustopila Jochum et al., 2014, Bensonella Pilsbry \& Vanatta, 1900, and Clostophis Benson, 1860 have recently been re-defined, and several species have been systematically revised (Panha and Burch 2000; Páll-Gergely et al. 2022, 2023; Páll-Gergely and White 2023). The term 'cervical crest' refers to an additional swelling on the shell behind the aperture, as seen in lateral and umbilical views (Fig. 2A).

## Institutional abbreviations

| CUMZ | Chulalongkorn University Museum of Zoology (Bangkok, Thailand); |
| :--- | :--- |
| HA | Collection András Hunyadi (Budapest, Hungary); |
| HNHM | Hungarian Natural History Museum (Budapest, Hungary); |
| IZCAS TM | National Zoological Museum of China, Institute of Zoology, Chi- |
|  | nese Academy of Sciences (Beijing, China); |
| MNHN | Muséum National d'Histoire Naturelle (Paris, France); |
| NHM | The Natural History Museum (London, UK); |
| NHMUK | When citing registered specimens; |
| SMF | Senckenberg Forschungsinstitut und Naturmuseum (Frankfurt am |
|  | Main, Germany); |
| UMZC | University Museum of Zoology (Cambridge, United Kingdom). |

## Systematics

Superfamily Pupilloidea Turton, 1831
Family Hypselostomatidae Zilch, 1959

Genus Acinolaemus Thompson \& Upatham, 1997

Acinolaemus Thompson \& Upatham, 1997: 223, 224. Panha and Burch 2005: 39.

Type species. Acinolaemus ptychochilus Thompson \& Upatham, 1997, by original designation.

Remarks. The general shell characteristics of this genus, such as shell form, with or without tuba, and ascending to descending aperture, are similar to the other Southeast Asian hypselostomatid genera.

This genus has similar shell form, protoconch sculpture, tuba shape, and aperture opened (ascending or descending), making it congruent with those of other Southeast Asian hypselostomatid genera. Since only the shell morphology has been published so far, the systematic relationship with its confamilials remains unknown and needs further study. In the meantime, Acinolaemus can be distinguished from other genera in having a small size (height 1-2 mm), enlarged and conspicuous angular lamella, prominent posterior corner bal-loon-shaped by angular lamella and upper palatal plica. Moreover, the two species known from Myanmar are characterised by a teleoconch sculpture with a pattern of rectangular, malleated pitting, crossed by spiral and radial ridges.

Currently, ten nominal species of the genus are known to occur in Thailand and the Mekong Delta and in limestone areas of Cambodia and Vietnam (Changlom et al. 2019; MolluscaBase 2023). The two species reported here represent the first records of the genus Acinolaemus in Myanmar.

Acinolaemus dayanum (Stoliczka, 1871), comb. nov.
Figs 2A, 13A
Hypselostoma dayanum Stoliczka, 1871: 172, 173, pl. 7, fig. 2. Type locality: Damotha, prope Moulmein [Kayon Hill, Dhammasa Village, Mawlamyine District, Mon State]. Hanley and Theobald 1876: 59, pl. 147, fig. 10. Pfeiffer 1876: 488. Pfeiffer 1880: 344
Boysidia (?) dayana. Pilsbry 1917: 205, 206, pl. 34, figs 5, 6.
Pupa (Hypselostoma) dayana. Nevill 1878: 193.
Pupa (Hypselostoma) dayanum. Gude 1914: 300, 301.
Material examined. Dhammasa Cave ( 8 m ), Mawlamyine centre NEE ca 26 km , Mon State, Myanmar ( $16.506715^{\circ} \mathrm{N}, 97.810763^{\circ} \mathrm{E}$ ), leg. Otani, J.U., Okubo, K. and Hunyadi, A. 11 October 2018: HA Collection ( 11 shells; Figs 2A, 13A).

Description. Shell turban shaped, low spire, ~ 3-4 whorls and whitish in colour. Shell height 1.2-1.3 mm and shell width $1.3-1.4 \mathrm{~mm}$. Apex blunt; protoconch with fine spiral striae. Teleoconch sculptured with regularly spaced radial ribs, paralleled with strongly wrinkled and malleated pits; suture well impressed and deep. Last whorl shouldered and flattened below periphery. Peristome thickened and weakly expanded; constriction and cervical crest very weak; lip whitish. Aperture subquadrate with eight dentitions marking peristome. Parietal lamella large and long, deeper inside aperture with tall ridge; infraparietal lamella small with long and low rise. Angular lamella smaller and weaker than parietal lamella, long, low rise with slope somewhat bent. Palatal tubercle strongly developed with triangular shape. Upper-, inter-, and lower- palatal plicae small, connecting peristome, and continuous with thin and straight ridges deeper inside aperture. Basal plica small, tubercle-like. Columellar lamella strong, continuing deep inside aperture with undulated ridge. Umbilicus widely perforate, $\sim 1 / 3$ of shell width, rounded and deep.

Distribution. Currently, this species is known only from the type locality, a limestone outcrop in Mon State, Myanmar.

Differential diagnosis. Acinolaemus dayanum differs from all known Bensonella species in Myanmar and Thailand by its unique, turban shaped shell and teleoconch surface sculptured with malleated wrinkles and pits. In contrast, the four species from Myanmar and three species from Thailand, namely B. tamphathai (Panha \& Burch, 2000), B. nabhitabhatai (Panha \& Burch, 2002) and B. pangmapaensis (Panha \& Burch, 2002) possess a conical shell and a teleoconch surface generally with conspicuous irregular growth lines and fine spiral striae (Panha and Burch 2000, 2002b).

Compared to the Acinolaemus species from Thailand, A. dayanum differs by having pitted sculpture on the shell surface, weaker spiral and radial striae, a larger parietal than angular lamella, and a shouldered last whorl. Acinolaemus ptychochilus Thompson \& Upatham, 1997 differs from A. dayanum by its


Figure 2. A Acinolaemus dayanum, topotype specimen HA Collection from Mawlamyine Township, Mon State B Acinolaemus cryptidentatus, specimen CUMZ 14413 from Taunggyi District, Shan State. The white arrow indicates constriction, the yellow arrow indicates a cervical crest. Abbreviations: $\mathbf{a}$ : angular lamella, $\mathbf{b}$ : basal plica, $\mathbf{c}$ : columellar lamella, ip: infraparietal lamella, itpl: interpalatal plica, Ipl: lower palatal plica, p: parietal lamella, pt: palatal tubercle, upl: upper palatal plica.
rounded last whorl, strong tubercles on the peristomal lip, and the presence of supra- and subcolumellar lamellae. Acinolaemus colpodon Thompson \& Upatham, 1997 also has a rounded last whorl, possesses a hooked columellar lamella, and lacks an interpalatal plica, a basal plica and an infraparietal lamella. In addition, A. sphinctinion Thompson \& Upatham, 1997 has a shouldered
last whorl with blunt periphery, a short, weakly ascending tuba, and lacks the angular lamella, the parietal fold, the basal plica and the interpalatal plica (Thompson and Upatham 1997; Panha and Burch 2005).

Additionally, A. dayanum has a similar shell form and sculpture to the two Acinolaemus species recently described from northern Thailand. It differs from A. cryptidentatus Changlom et al., 2019, which has 4-5 whorls, strong spiral striae, and discontinuous infraparietal and angular lamellae. It is also distinct from A. mueangonensis Changlom et al., 2019 [corrected original spelling], which has 4-5 whorls, brownish shell colour, and a more prominent subcolumellar than columellar lamella.

Remarks. The holotype (single shell mentioned in the original description) could not be located in the NHM collection, but we were able to examine recently collected topotypic shells. Originally, this species was classified in Hypselostoma and later reclassified into the genus Boysidia Ancey, 1881 (i.e., Stoliczka 1871; Pilsbry 1917). Based on the small size, the whitish shell and the strong teleoconch sculpture, we transfer H. dayanum into the genus Acinolaemus. In contrast, the genus Bensonella is characterised by a brownish shell with nearly smooth or finely, spirally striated shell (Páll-Gergely and White 2023), whereas Hypselostoma (at least the type species and the morphologically similar and geographically close species; see Gojšina et al. 2022 and Preece et al. 2022) and Boysidia are much larger, and have brownish, finely sculptured shells. Furthermore, Hypselostoma is defined on the basis of a detached body whorl and a concrescent angular and parietal lamellae, characters which do not appear in A. dayanum.

Acinolaemus cryptidentatus Changlom, Chan-ard \& Dumrongrojwattana, 2019 Figs 2B, 13B

Acinolaemus cryptidentatus Changlom et al., 2019: 158, 159, fig. 2a-f. Type locality: Tham Wua (Wua Cave), Mueang District, Mae Hong Son Province [Thailand].

Material examined. Monastery, Ywangan Township, Taunggyi District, Shan State, Myanmar (locality code SH12; 21¹3'43.3"N, 96³3'19.2"E): CUMZ 14413 (1 shell; Figs 2B, 13B).

Remarks. This species was recently described from a limestone outcrop in northern Thailand that is ~ 200 km southeast of Taunggyi District, Shan State, Myanmar. This single specimen from Shan State slightly differs from the type specimen in having weak radial ridges and many weak interpalatal lamellae; whereas the type specimen possesses strong radial ridges and is without interpalatal lamellae. Further surveys should employ specialised sampling techniques (i.e., multiple series of sieves) that yield more specimens, which will clarify the identity of these tiny shells.

Acinolaemus cryptidentatus differs from A. ptychochilus and A. mueangonensis in having a shouldered last whorl and weak upper and lower palatal lamellae. In comparison, A. ptychochilus possesses a rounded last whorl, strong upper and lower palatal lamellae, and a strong infraparietal lamella. Meanwhile A. mueangonensis has a less-shouldered last whorl and lacks interpalatal lamellae (Thompson and Upatham 1997; Changlom et al. 2019).

## Genus Anauchen Pilsbry, 1917

Anauchen Pilsbry, 1917: 174, 188. Panha and Burch 2005: 47.

Type species. Boysidia gereti Bavay \& Dautzenberg, 1904 (junior synonym of Hypselostoma rochebruni Mabille, 1887; see Páll-Gergely 2023b).

## Anauchen eotvosi Páll-Gergely, 2023

Fig. 13C

Anauchen eotvosi Páll-Gergely, 2023a: 452-454, fig. 1. Type locality: Shan-Siam Boundary.

Distribution. This species was described based on specimens collected by Colonel Woodthorpe in 1894 or in 1895 from the 'Shan-Siam Boundary'. Since the exact locality is unknown, it remains questionable that this species was originally collected from the area of present-day Laos or Myanmar.

## Genus Angustopila Jochum, Slapnik \& Páll-Gergely, 2014

Angustopila Jochum, Slapnik \& Páll-Gergely, 2014 in Jochum et al. 2014: 26. Páll-Gergely et al. 2023: 17-24.

Type species. Systenostoma tamlod Panha \& Burch, 2002, by original designation (Panha and Burch 2002a).

Remarks. The genus was recently introduced to include the tiniest known land snails (Páll-Gergely et al. 2022). Species of this genus are characterised by tiny, colourless shells (typically less than 1.2 mm ), 0-5 apertural barriers, and typically 10-20 spiral striae on the body whorl. Currently, the genus comprises more than 50 species that are mainly distributed in mainland Indochina (Laos, Myanmar, Thailand and Vietnam), with a few species recorded from southern China and a single species from India (Páll-Gergely et al. 2023). From Myanmar, two species are now recorded.

## Angustopila occidentalis Páll-Gergely \& Hunyadi, 2023

Figs 3, 13D

Angustopila occidentalis Páll-Gergely \& Hunyadi in Páll-Gergely et al. 2023: 118122, figs 70-72. Type locality: Shan State, ca 6 km east from Hsihseng centre.

Material examined. Parpant area, Taunggyi City, Shan State, Myanmar (locality code: Sh8) $20^{\circ} 15^{\prime} 3.7^{\prime \prime N}$, $97^{\circ} 14^{\prime} 23.9^{\prime \prime E} ; 1159 \mathrm{~m}$ a.s.I.: CUMZ 14389 ( 1 shell; Fig. 3A, B), CUMZ 14390 (7 shells; Fig. 3C, D).

Distribution. This species is known from several localities in Shan State, Myanmar (Páll-Gergely et al. 2023).


Figure 3. Angustopila occidentalis, specimen CUMZ 14389 from Taunggyi City, Shan State A, B specimen with four whorls and pronounced sculpture C, D specimen CUMZ 14390 with five whorls and weak or eroded sculpture.

Remarks. Angustopila occidentalis is uniquely recognised by a minute conical shell and whorls that are slightly shouldered and rounded on the periphery. The protoconch is uniquely radially striated (Fig. 3A, B), while all congeners known so far lack radial striation at this early developmental stage. Apertural dentition with one large parietal lamella.

In Myanmar, this species is widely distributed. The individuals examined herein were also collected from the limestone wall inside Parpant Cave, Shan State. These specimens agree well with the type specimen of this species (Fig. 13D) in having a medium-sized, low conical shell, one strong parietal lamella and lacking a palatal tooth.

## Angustopila elevata (Thompson \& Upatham, 1997)

Fig. 13E

Systenostoma elevata Thompson \& Upatham, 1997: 232, 233, figs 39-43. Type locality. Thailand, Chiang Mae Province [Chiang Mai Province], Doi Chiang Dao, 7 km west of Chiang Dao.

Angustopila elevata. Jochum et al. 2014: 27. Páll-Gergely et al. 2015: 33, fig. 11. Páll-Gergely et al. 2023: 27-32, figs 12, 13.
Angustopila subelevata Páll-Gergely et al., 2015: 39, fig. 4. Type locality: Jiaole Cun, Bama Xian, Hechi Shi, Guangxi, China. Páll-Gergely et al. 2017: 332, figs $1 b, 2 a-g, 7 e, f$.

Distribution. This species is known from several localities in Shan State (Páll-Gergely et al. 2023).

Remarks. Although this species was described from northern Thailand in Chiang Mai Province, subsequent revision by Páll-Gergely et al. (2023) has expanded its distribution to several localities in southern China, Laos, Myanmar, Vietnam and several additional localities in Thailand. It is considered one of the most widely distributed species, with a range spanning several hundred kilometres (Páll-Gergely et al. 2023).

The unique shell of this species is slightly concave-conical, bears a subquadrate aperture, lacking apertural dentitions, and shows a weakly elevated parietal wall.

## Genus Bensonella Pilsbry \& Vanatta, 1900

Bifidaria (Bensonella) Pilsbry \& Vanatta, 1900: 591. Boysidia (Bensonella). Pilsbry 1917: 198.
Boysidia (Paraboysidia) Pilsbry, 1917: 174, 201.

Type species. Pupa plicidens Benson, 1849, by original designation.
Remarks. The generic status and diagnostic morphological characters of the type species were recently revised (Páll-Gergely and White 2023). The type species was believed to possess 'hooked' teeth, i.e., apertural barriers forming hooks that point outside of the aperture (Pilsbry 1917). Later, when specimens without hooked apertural barriers were found in collections, normal and hooked teeth were hypothesised as intraspecific variability (Budha and Backeljau 2017). Páll-Gergely and White (2023) showed that the 'real' Bensonella plicidens was a species with normal (not hooked) barriers, while the Himalayan species with hooked teeth was an undescribed species (Bensonella hooki Páll-Gergely, 2023). Since the 'hooked' and 'not hooked' species are very similar in other shell characters, this trait could not be used as a diagnostic character for recognising Bensonella. Rather, this genus is diagnosed by a brownish shell with the last whorl attached to the penultimate whorl, and the presence of separate angular and parietal lamellae.

Since the type species of Bensonella and Paraboysidia (Boysidia paviei Bavay \& Dautzenberg, 1912) are very similar, the latter has been treated as a junior synonym of the former (Gittenberger et al. 2021; Páll-Gergely and White 2023).

## Bensonella salwiniana (Theobald, 1871)

Figs 4, 5, 6A, 13F

Pupa salwiniana Theobald, 1871: 400. Type locality: Shan States. Hanley and Theobald 1874: 40, pl. 100, fig. 9. Sowerby 1877: Pupa pl. 16, fig. 150. Pfeiffer 1877: 403.

Pupa (Scopelophila) salwiniana. Nevill 1877: 23.
Pupa (Pupilla) salwiniana. Pfeiffer 1880: 355.
Pupa salwinieana [sic]. Godwin-Austen 1888: 244.
Boysidia salwiniana. Gude 1914: 295, 296. Pilsbry 1917: 206-208, pl. 33, fig. 11.

Material examined. Burma [Myanmar]: NHMUK 1912.4.16.66 (2 shells; Fig. 4A) ex. Beddome collection. Shan State: SMF 227428/2 (2 shells). Monastery, Ywangan Township, Taunggyi District, Shan State, Myanmar (locality code SH1; $21^{\circ} 13^{\prime} 43.3^{\prime \prime} \mathrm{N}, 96^{\circ} 33^{\prime} 19.2^{\prime \prime}$ ) : CUMZ 14375 ( 1 shell; Fig. 4E); CUMZ 14391 (2 shells); CUMZ 14392 (11 shells; measured); CUMZ 14393 (2 shells; Figs 4F, 6A, 13F). Dragon Rock, Pindaya Township, Taunggyi District, Shan State, Myanmar (locality code SH5; 2055'31.5"N, $96^{\circ} 39^{\prime} 01.2^{\prime \prime} \mathrm{E}$ ): CUMZ 14376 (1 shell; Fig. 4D); CUMZ 14394 (4 shells). Blue Diamond Co., Ltd., Pyigyidagun Township, Mandalay Region, Myanmar (locality code MD1; $21^{\circ} 54^{\prime} 12.4^{\prime \prime} \mathrm{N}, 96^{\circ} 04^{\prime} 38.8^{\prime E} \mathrm{E}$ ): CUMZ 14377 (1 shell; Fig. 4B, C); CUMZ 14395 (1 shell). Aik Kham Cave, Taunggyi District, Shan State, Myanmar (locality code SH10; 20º49'07.0"N, 97¹3'42.0"E): CUMZ 14396 (22 shells). Montawa Cave, Taunggyi District, Shan State, Myanmar (locality code SH11; 20³5'15.8"N, $97^{\circ} 01^{\prime} 03.1^{\prime \prime} \mathrm{E}$ ): CUMZ 14397 ( 85 specimens in ethanol; Fig. 5).

Description. Shell ovate-conical, high spire, yellowish brown, with 6-6½ convex whorls. Shell height $5.6-6.3 \mathrm{~mm}$ and shell width $3.3-3.7 \mathrm{~mm}$. Apex blunt; protoconch $\sim 11 / 2$ whorls, sculptured with radial wrinkles. Teleoconch with smooth, irregular growth lines; suture well impressed and deep. Last whorl large and rounded. Peristome thickened and broadly expanded; lip whitish. Aperture rounded-subquadrate with six or seven dentitions. Parietal lamella large, long, strong, broadly blunt, and located slightly deeper inside aperture; infraparietal lamella very small and sometimes absent. Angular lamella blunt and reaching peristomal lip. Palatal tubercle inconspicuous. Upper palatal plica long, contacting peristome and sometimes elevated in middle; lower palatal plica strong and large. Basal plica weak to strong nodule shape. Columellar lamella strong and large, tubercle-like. Umbilicus very narrowly perforate, rounded and deep.

Genital system. Atrium short and slightly enlarged. Penis very long, thin tube and slightly enlarged at both ends; penial appendix short. Penial retractor muscle large and inserted between penis and epiphallus junction. Epiphallus slender tube, almost same length as penis, and $\sim 2 / 3$ of its length enlarged with similar diameter to free oviduct. Vas deferens very thin tube, connected between epiphallus and free oviduct, and held in position with thin connective tissue near epiphallus-vas deferens junction to atrium.

Vagina slender tube, short and $\sim 1 / 3$ of penis length. Gametolytic organ strongly developed; gametolytic duct slender tube, almost same length as vagina+free oviduct; gametolytic sac enlarged and bulbous. Free oviduct larger in diameter than vagina, and approximately same length as vagina.

Animal. Preserved specimen with blackish to greyish reticulated skin, and mantle collar well-developed and whitish. Pneumostome wide and situated in the bay of angular lamella and upper palatal plicae. Foot short, holopodal, unipartite, and sole of foot blackish to greyish in colour. Living snails possess blackish tentacles: upper tentacles short and stout, and lower tentacles very short.

Radula. Teeth arranged in nearly straight row with formula 15-(6, 5)-1-(5, $6)-11+$. Central tooth unicuspid, with long triangular shape and pointed tip.


Figure 4. Bensonella salwiniana A specimen NHMUK 1912.4.16.66 from Burma B, C specimen CUMZ 14377 from Pyigyidagun Township, Mandalay Region D specimen CUMZ 14376 from Taunggyi District, Shan State E specimen CUMZ 14375 from Taunggyi District, Shan State F specimen CUMZ 14393 from Taunggyi District, Shan State. Abbreviations: a: angular lamella, b: basal plica, c: columellar lamella, ip: infraparietal lamella, Ipl: lower palatal plica, p: parietal lamella, upl: upper palatal plica.

Lateral teeth bicuspid, inner and outer cusps clearly separated at base, situated next to each other, and nearly aligned in transverse row. Inner and outer cusps long and triangular, and outer cusp comparatively smaller than inner cusp. Marginal teeth starting at approximately tooth number 5 or 6, inner and outer cusps


Figure 5. Bensonella salwiniana, specimen CUMZ 14397 from Taunggyi District, Shan State A genitalia and a small inset of penial appendix $\mathbf{B}$ preserved specimen with mantle edge, body and foot $\mathbf{C}$ snail showing colour in life $\mathbf{D}$ radula morphology: blue highlighting indicates central teeth and numbers indicate tooth order from lateral to marginal end. Abbreviations: at: atrium, e: epiphallus, fo: free oviduct, gd: gametolytic duct, gs: gametolytic sac, mc: mantle collar; p: penis, pa: penial appendix, pn: pneumostome; pr: penial retractor muscle, v: vagina, vd: vas deferens.
of marginals joined at base. Innermost marginals bicuspid, similar to lateral teeth; outermost teeth multicuspid, cusps small with almost same size and shape, and situated on same base.

Distribution. This species is known from several localities in northern Myanmar: Bhamo [Bhamo District, Kachin State]; Pingoung [Pingku Hills, Muse District, Shan State]; Shan Hills (Gude 1914; Pilsbry 1917). In this study, several specimens were also collected from Shan State and the Mandalay Region.

Differential diagnosis. Bensonella salwiniana differs from Bensonella species reported from Thailand and Laos in having a much larger (height $4-6 \mathrm{~mm}$ ) and ovate conical shell, 6-7 whorls, inconspicuous palatal tubercle, and generally with six apertural dentitions. In contrast, B. nabhitabhatai, B. tamphathai and B. pangmapaensis tend to have smaller shells (height 2-4 mm), 4-5 whorls, a strong palatal tubercle, and generally bears 8-10 apertural dentitions (Panha and Burch 2000, 2002b).

For further comparison, the three species from Laos, namely $B$. wangviangensis (Panha \& Tongkerd, 2003), B. paralella (Inkhavilay \& Panha, 2016), and B. anguloobtusa (Inkhavilay \& Panha, 2016) possess a smaller shell (height $1-3 \mathrm{~mm}$ ), a strongly developed palatal tubercle and generally bears 3-4 whorls (Panha and Burch 2002b, 2005; Panha et al. 2003; Inkhavilay et al. 2016).

Although this species is very similar to B. gittenbergeri (Maassen, 2008) from Luang Namtha Province, Laos, in shell shape and size, it differs by having a lower palatal plica not extended to an expanded lip, a very narrow umbilicus, and an unextended palato-basal wall on the anterior side. In contrast, B. gittenbergeri possesses a long lower palatal plica that extends to an expanded lip, has a wider umbilicus, and its palato-basal wall is extended anteriorly (Maassen 2008; Inkhavilay et al. 2016).

Bensonella salwiniana clearly differs from the two newly described species, B. lophiodera sp. nov. and B. taiyaiorum sp. nov., in having a larger shell (height $5-6 \mathrm{~mm}$ ), and a broadly expanded peristome without cervical crest and lacking supra- and subcolumellar lamellae. Moreover, the latter two species possess smaller shells (height ~ 3 mm ), a slightly expanded lip, and a conspicuous cervical crest. In addition, B. taiyaiorum sp. nov. has two upper palatal plicae, palatal tubercle strongly developed, supra-, subcolumellar lamellae and u-shaped plica present on the parietal wall, and a cervical crest far from the apertural lip. In contrast, B. lophiodera sp. nov. possesses a weakly expanded lip, subcolumellar lamella present and cervical crest close to apertural lip.

Remarks. The species was described based on specimens received from F. Fedden (1839-1887). The specimens lacked a precise type locality, and only 'Shan States' was stated in the original description. Although the type specimen could not be located, several recently collected and historical specimens were examined. This species possesses strongly developed parietal and angular lamellae, and lacks a tuba, which are the diagnostic characters of Bensonella.

The examined individuals either possess or lack an infraparietal lamella.

## Bensonella anguloobtusa (Inkhavilay \& Panha, 2016)

Figs 6B, 7A, 13G
Paraboysidia anguloobtusus Inkhavilay \& Panha in Inkhavilay et al. 2016: 215217, figs 2d-f, 4b. Type locality: Kao Rao Cave, Vieng Phouka District, Luang Namtha Province, Laos. Inkhavilay et al. 2019: 61, fig. 26 f.

Material examined. Monastery, Ywangan Township, Taunggyi District, Shan State, Myanmar (locality code SH2; 21¹3'43.3"N, 96³3'19.2"E): CUMZ 14398 ( 1 shell; Fig. 7A); CUMZ 14399 ( 87 shells); CUMZ 14400 (12 shells; Fig. 13G; measured); CUMZ 14401 (1 shell; Fig. 6B).

Description. Shell concave-conical, spire high, yellowish brownish in colour, and $4 \frac{1}{2}-5$ convex whorls. Shell height $1.7-2.1 \mathrm{~mm}$ and shell width $1.5-$ 1.7 mm . Apex blunt; protoconch $\sim 11 / 2$ whorls with wrinkled roundish pits and spiral ridges. Teleoconch with wrinkles, irregular growth lines, and very fine, dense, inconspicuous spiral striae; suture well impressed and deep. Last whorl convex, very slightly shouldered. Aperture subrectangular with eight or nine apertural barriers. Peristome thickened and little expanded, cervical crest absent;


Figure 6. A Bensonella salwiniana, specimen CUMZ 14393 from Taunggyi District, Shan State B Bensonella anguloobtusa, specimen CUMZ 14401 from Taunggyi District, Shan State. Abbreviations: a: angular lamella, c: columellar lamella, itpl: interpalatal plica, Ipl: lower palatal plica, p: parietal lamella, pt: palatal tubercle, sbc: subcolumellar lamella, upl: upper palatal plica.
lip pale yellowish to brown. Parietal lamella strongly developed, robust, broadly blunt and starting deeper inside aperture than angular lamella; infraparietal lamella very small and sometimes absent. Angular lamella strong and low, as well as long and sinuous upon reaching peristome, increasing in height deeper inside aperture. Palatal tubercle strongly developed with triangular shape. Upper palatal plica long and very thin; interpalatal plicae and lower palatal plicae


Figure 7. A Bensonella anguloobtusa, specimen CUMZ 14398 from Taunggyi District, Shan State B Bensonella taiyaiorum sp. nov., holotype CUMZ 14380 from Taunggyi District, Shan State C Bensonella lophiodera sp. nov., holotype CUMZ 14378 from Taunggyi District, Shan State. Abbreviation: ip: infraparietal lamella.
approximately same size, large and long, tubercle-like. Columellar lamella large, strong, and horizontal; subcolumellar lamella bears small, robust fold. Umbilicus perforate, $\sim 1 / 4$ of shell width, rounded and deep.

Distribution. This species is currently known from the type locality in Luang Namtha Province, Laos. In the recent survey, individuals were collected from the limestone outcrops in Shan State, Myanmar.

Remarks. This is the first record of the species in Myanmar. The new specimens were collected $\sim 480 \mathrm{~km}$ away from the type locality. Therefore, more of these snails can be expected to be found in the northeastern part of Myanmar and the northern part of Thailand. The specimens from Shan State all agree well with the type specimen in both shell form and apertural dentition. However, only a very small infraparietal lamella is present in some individuals.

## Bensonella taiyaiorum Tongkerd \& Panha, sp. nov.

https://zoobank.org/E83B1A5F-A724-4BBF-9A7D-BB1604ECEFEF
Figs 7B, 8, 13H

Type locality. Dragon Rock, Pindaya Township, Taunggyi District, Shan State, Myanmar (locality code SH6; 2055'31.5"N, 96º39'01.2"E; 1300 m a.s.I.).

Type material. Holotype CUMZ 14380 (height 2.8 mm , width 2.1 mm ; Fig. 7B). Paratypes CUMZ 14381 (41 shells); CUMZ 14402 (12 shells; measured); CUMZ 14403 (3 shells; Figs 8, 13H), NHMUK 20230591 (3 shells), SMF 373019 (3 shells) all from the type locality.

Diagnosis. Shell elongate-conical and yellowish brown in colour. Cervical crest situated far from peristome. Aperture with several hookless barriers (i.e., parietal, infraparietal, angular, columellar, supra- and sub-columellae, basal, and upper, inter and lower palatals), and interpalatal and lower palatal plicae forming u-shaped plica.

Etymology. The specific name taiyaiorum is in recognition of the 'Tai Yai' or 'Shan', the largest ethnic group in Shan State, which is the type locality of this species.

Description. Shell conical, yellowish brown to reddish brown and with $51 / 4-6$ widely convex whorls. Shell height $2.5-2.9 \mathrm{~mm}$ and shell width $2.0-2.2 \mathrm{~mm}$. Apex blunt; protoconch $\sim 1 \not 1 / 2$ whorls with wrinkles and very weak spiral ridges. Teleoconch with strong and irregular growth lines, sometimes white growth lines are conspicuous; suture impressed and deep. Last whorl large and rounded. Peristome thickened and slightly expanded; constriction weak; lip reddish brown. Cervical crest sharp and situated far from peristome. Aperture subrectangular and with many apertural dentitions. Parietal lamella strongly developed and consisting of two parts separated by an incision: outer part large, strong, with rectangular shape and reaching peristome; inner part blunt. Infraparietal lamella small and blunt. Angular lamella lower than parietal lamella: outer part short and reaching peristome; inner part more strongly elevated. Palatal tubercle strongly developed with triangular shape; two upper palatal plicae with strong folding; inter- and lower palatal large, equal in size and connected to form u-shaped plica. Basal plica small, low and tubercle-like. Columellar lamella large, strong and distinct in its horizontal alignment; one small supracolumellar lamella and one small subcolumellar lamella present. Umbilicus narrowly perforate, $\sim 1 / 5$ of shell width, rounded and deep.

Distribution. This new species is known only from the type locality in Shan State. The snails live on limestone walls and can be found under leaf litter within rock crevices.

Differential diagnosis. The new species can be distinguished from Bensonella reported from Thailand and Laos in having inter- and lower- palatal pli-


Figure 8. Bensonella taiyaiorum sp. nov., from Taunggyi District, Shan State A-C paratypes CUMZ 14403. The white arrow indicates constriction. The yellow arrow indicates a cervical crest. Abbreviations: a: angular lamella, b: basal plica, c: columellar lamella, ip: infraparietal lamella, itpl: interpalatal plica, Ipl: lower palatal plica, p: parietal lamella, pt: palatal tubercle, sbc: subcolumellar lamella, spc: supracolumellar lamella, sppl: suprapalatal lamella, upl: upper palatal plica.
cae connected, forming a u-shaped plica, and with prominent cervical crest. In contrast, the three species from Thailand differ by: B. nabhitabhatai has one upper palatal plica and no supracolumellar and infraparietal lamellae; B. tamphathai possesses fine spiral striae on the teleoconch, one upper palatal plica, and bears no supracolumellar lamellae; B. pangmapaensis has fine spiral striae on the teleoconch, and hooked palatal and basal plicae (Panha and Burch 2000, 2002b, 2005; Panha et al. 2003; Inkhavilay et al. 2016).

For further comparison, the three species from Laos can be distinguished by: B. paralella has one upper palatal plica, and no interpalatal plicae, supra- and subcolumellar lamellae; B. anguloobtusa has one upper palatal plica and no basal and supracolumellar lamellae; $B$. wangviangensis has a unique shape, smaller shell size (height 1-2 mm), four whorls, shouldered last whorl, and bears no basal plicae and columellar lamellae (Panha et al. 2003; Inkhavilay et al. 2016).

Remarks. The two new species, $B$. taiyaiorum sp. nov. and B. lophiodera sp. nov., are the first Bensonella species to be described from Myanmar. The strongly developed and separated parietal and angular lamellae, and lack of a tuba are the main characters underscoring the assignment of these species to Bensonella.

Though the spiral striae on the protoconch are obscured under the light microscope, they are very faint but detectable under the SEM microscope. Of all the type series examined, no hooked-shaped dentitions were observed, while the u-shaped plicae are present in all specimens. A constriction on the palatal wall near the aperture and the cervical crest is possibly an important trait in response to resistance to desiccation.

## Bensonella lophiodera Tongkerd \& Panha, sp. nov.

https://zoobank.org/068CD744-43A6-407A-9876-71B249D66C72
Figs 7C, 9, 13I

Type locality. Myinmati Cave, Kalaw Township, Taunggyi District, Shan State, Myanmar (locality code SH4; 20³5'24.6"N, $96^{\circ} 36^{\prime} 42.1^{\prime \prime} \mathrm{E} ; 1312 \mathrm{~m}$ a.s.I.).

Type material. Holotype CUMZ 14378 (height 3.1 mm , width 1.8 mm ; Fig. 7C). Paratypes CUMZ 14379 (16 shells); CUMZ 14404 (12 shells; measured); CUMZ 14405 (3 shells; Figs 9, 13I), NHMUK 20230592 (3 shells), SMF 373020 ( 3 shells) all from the type locality.

Diagnosis. Shell ovate-conical, high spired and pale yellowish brown colour. Cervical crest situated far from peristome. Lip not expanded. Aperture usually with seven barriers (parietal, infraparietal, angular, columellar, basal, and upper and lower palatals). Palatal tubercle is lacking.

Etymology. The specific name lophiodera is a compound of the Greek words lophia meaning crest and dere meaning neck or throat. It refers to the prominent cervical crest on the palatal wall of the last whorl.

Description. Shell ovate-conical, pale yellowish brown in colour, high spire and 5½-6 convex whorls. Shell height 2.7-3.2 mm and shell width 1.9-2.1 mm. Apex blunt; protoconch consisting of $\sim 11 / 2$ whorls with wrinkles and weak spiral ridges. Teleoconch with somewhat strong and irregular growth lines; suture well impressed and deep. Last whorl large and rounded. Peristome slightly thickened and little expanded; constriction very weak; lip yellowish brown. Cervical crest sharp and situated close to peristome. Aperture subrectangular with seven or eight apertural barriers. Parietal lamella large, strongly developed, blunt, u-shaped from side view; infraparietal lamella small and knob shaped. Angular lamella weaker than parietal: outer part very low, weak and reaching peristome; inner part strong and tall. Palatal tubercle inconspicuous. Upper palatal plica small and low; lower palatal plica strong and tall, blunt. Basal plica small tubercle-like. Columellar lamella large and strong; sometimes an additional tiny subcolumellar lamella is present. Umbilicus narrowly perforate, $\sim 1 / 5$ of shell width, rounded and deep.


Figure 9. Bensonella lophiodera sp. nov., from Taunggyi District, Shan State A-C paratypes CUMZ 14405. The white arrow indicates constriction. The yellow arrow indicates a cervical crest. Abbreviations: $\mathbf{a}$ : angular lamella, $\mathbf{b}$ : basal plica, c: columellar lamella, ip: infraparietal lamella, Ipl: lower palatal plica, p: parietal lamella, sbc: subcolumellar lamella, upl: upper palatal plica.

Distribution. This species is currently known only from the type locality in Shan State. The living snails are found on limestone walls and under leaf litter in rock crevices.

Differential diagnosis. This new species is similar to $B$. salwiniana in shell shape, number of apertural dentitions, and bears no palatal tubercle. However,
B. lophiodera sp. nov. differs by having a strong cervical crest, and a very thin, fragile and unexpanded lip, while $B$. salwiniana shows no cervical crest, and has a thickened and expanded lip.

The new species is distinguishable from Bensonella reported from Thailand and Laos in having a weak palatal tubercle, a cervical crest, slightly expanded lip, no interpalatal plica, and apertural barriers are generally weak. Regarding the three species from Thailand, B. nabhitabhatai has one upper palatal plica, and lacks the basal plica and the infraparietal lamella; B. tamphathai possesses two interpalatal plicae, and its shell is sculptured with spiral striae; B. pangmapaensis has fine spiral striae and hooked palatal and basal plicae (Panha and Burch 2000, 2002b, 2005; Panha et al. 2003; Inkhavilay et al. 2016).

There are three Bensonella species known from Laos. Among them, B. paralella has an expanded lip and strongly prominent apertural dentitions; B. anguloobtusa has strong and sinuous apertural dentitions, and is sculptured with weak spiral striae; $B$. wangviangensis has a unique shell shape with small shell size (height 1-2 mm), a nearly closed sinulus, a shouldered last whorl, and lacks a basal plica and columellar lamella (Panha and Burch 2000, 2002b, 2005; Panha et al. 2003; Inkhavilay et al. 2016).

In addition, $B$. lophiodera sp. nov. differs from $B$. taiyaiorum sp . nov. in having eight apertural barriers, an inconspicuous palatal tubercle, one upper palatal plica, and lacking a supracolumellar lamella and interpalatal plica. In contrast, B. taiyaiorum sp. nov. possesses an expanded lip, has a strong palatal tubercle, two upper palatal plicae, and the inter- and lower- palatal plicae are connected and form a U-shaped plica.

Remarks. The spiral striae on the protoconch are very faintly detectable under the SEM microscope. Among all the type series examined, no hookedshaped dentitions were observed, while the apertural dentitions show minor variability in different degrees of thickness and sharpness. A clear constriction at the palatal wall near the aperture and a sharp cervical crest are present in all specimens.

## Genus Clostophis Benson, 1860

Clostophis Benson, 1860: 95. Páll-Gergely et al. 2022: 419.
Montapiculus Panha \& Burch, 2002c: 148.

Type species. Clostophis sankeyi Benson, 1860, by monotypy.
Remarks. The genus was recently revised, and several new species have been introduced or transferred to this genus by Páll-Gergely et al. (2020a) and Páll-Gergely and Hunyadi (2022). The currently known 19 species of Clostophis are recognised and distributed from western Myanmar and Peninsular Malaysia to Thailand, Laos, northern Vietnam and southern China. The genus is characterised by tiny ( $1-2 \mathrm{~mm}$ ) shells, colourless or whitish (but never brown) shells, mostly (but not always) detached last part of body whorl forming a free tube, shell surface with dense spiral striation, and possessing none or several apertural dentitions.

## Clostophis sankeyi Benson, 1860

Fig. 13J

Clostophis sankeyi Benson, 1860: 95, 96. Type locality: Farm Caves, prope [near] Moulmein.
Clostophis sankeyi. Páll-Gergely et al. 2020: 352, fig. 3a. Páll-Gergely and Hunyadi 2022: 419, figs 1, 2. Preece et al. 2022: 156, fig. 70e.

Distribution. Known from the type locality 'Farm Caves' (= Dhammathat Cave, Mawlamyine, Mon State) and several localities from Mon State (Páll-Gergely and Hunyadi 2022). No specimen identified as this species was collected.

## Clostophis thinbowguensis Páll-Gergely \& Hunyadi, 2022

Fig. 13K

Clostophis thinbowguensis Páll-Gergely \& Hunyadi, 2022: 427, fig. 9. Type locality. Phayahran Camp, Thin Bow Gu Cave, Tanintharyi Region, Myanmar.

Distribution. Known only from the type locality in Tanintharyi Region, Myanmar.

## Genus Gyliotrachela le Tomlin, 1930

Gyliotrachela le Tomlin, 1930: 24 [replacement name for Gyliauchen Pilsbry, 1917, non Nicoll 1915: Platyhelminthes, Trematodes]. Panha and Burch 2005: 63.

Type species. Hypselostoma hungerfordianum von Möllendorff, 1891, by typification of the replaced name.

Remarks. This is a widely distributed and specious genus in Southeast Asia, currently comprising ~ 40 nominal species (MolluscaBase 2023).

## Gyliotrachela bensonianum (Blanford, 1863)

Fig. 13L

Hypselostoma bensonianum Blanford, 1863: 326, 327. Type locality. Mya Leit Doung, Ava.
Hypselostoma bensonianum. Hanley and Theobald 1870: 4, pl. 8, fig. 2. Pfeiffer 1876: 488. Gude 1914: 299, 300.
Pupa (Hypselostoma) bensoni. Nevill 1878: 193.
Gyliauchen bensonianus. Pilsbry 1917: 211, pl. 37, figs 11, 12.
Gyliotrachela bensonianum. Gojšina et al. 2022: 138, figs 4a, 5a, b.

Distribution. This species seems to be endemic to central Myanmar and is currently known only from the type locality, Mya Leit Doung, Ava [Myaleit mountains, Mandalay Region] (Gude 1914; Pilsbry 1917; Gojšina et al. 2022).

## Gyliotrachela hungerfordiana (von Möllendorff, 1891)

Fig. 10, 13M

Hypselostoma hungerfordianum von Möllendorff, 1891: 337, 338, pl. 30, fig. 7, 7a. Type locality: Bukit Pondong [Gunung Pondok, Padang Rengas, Perak, Malaysia]. Sykes 1902: 61.
Gyliauchen hungerfordianus. Pilsbry 1917: 212, pl. 36, figs 1-4.
Gyliotrachela hungerfordiana. Laidlaw 1933: 214. van Benthem Jutting 1949: 60. van Benthem Jutting 1950: 26. Zilch 1959: 164, fig. 563. van Benthem Jutting 1960: 14. Berry 1961: 101. Berry 1966: 12. Zilch 1984: 166, pl. 2, fig. 19. Davison 1995: 239. Schileyko 1998: 141, fig. 162. Schilthuizen et al. 1999: 283. Foon et al. 2017: 79, fig. 30b.

Gyliotrachela khaochongensis Panha, 1998: 53-56, fig. 2. Type locality: Khaochong Wildlife Sanctuary, Trang Province, Thailand. Panha and Burch 2005: 70, 71, fig. 61. syn. nov.
Gyliotrachela phoca Tongkerd \& Panha in Tongkerd et al. 2013: 71-75, figs 5-7. Type locality: Bat cave near Klong Chak Waterfall, Lanta Yai Island, Lanta Islands National Park, Krabi Province, Thailand. syn. nov.

Material examined. Khaochong Wildlife Sanctuary, Trang Province, Thailand: Paratype CUMZ [CUIZM] Ver 011 (Fig. 10B). Bukit Pondok, Perak, Malaysia: NHMUK collection (2 shells: Figs 10A, 13M). Buddha Cave, Lenya city, Tanintharyi Region, Myanmar (locality code TN1; 11¹3'46.2"N, 99¹0'34.3"E): CUMZ 14382 (1 shell; Fig. 10C); CUMZ 14406 (61 shells); CUMZ 14407 (12 shells; measured).

Description. Shell concave-conical, pale yellowish to brown in colour, moderate spire and $4-4 \frac{1}{2}$ widely convex whorls. Shell height $1.6-1.9 \mathrm{~mm}$ and shell width (including tuba) $2.5-2.9 \mathrm{~mm}$. Apex blunt; protoconch $\sim 13 / 4$ whorls with wrinkled roundish pits. Teleoconch generally with very fine irregular growth lines and wrinkles; suture shallow. Last whorl angular with a prominent central keel with grooves above and below the keel. Tuba long and ~ 8-10 degrees angled upward compared to the shell axis. Peristome widely expanded; lip whitish to yellowish. Aperture roundly rectangular; aperture with many barriers. Parietal lamella large, strong, blunt, and located slightly deep inside aperture. Two small and weak infraparietal lamellae present. Angular lamella small, short, and reaching peristome. Upper palatal plica of approximately same size as angular lamella; very small suprapalatal plicae sometimes present. Lower palatal lamella tall and strong; very low and weak interpalatal plicae and infrapalatal plicae generally present. Columellar lamella strong and distinct; very low and weak supracolumellar and subcolumellar lamellae present. All dentitions generally covered with very fine spines on surface. Umbilicus widely perforate, ~ $1 / 3$ of shell width, rounded, deep, and surrounded by blunt periumbilical keel.

Distribution. This species has a wide distribution from southern Myanmar to southern Thailand and Peninsular Malaysia. Originally it was described from Perak and then subsequently reported from several localities in Peninsular Malaysia: Perlis, Pahang, Kelantan, Kedah, and Selangor states (von Möllendorff 1891; van Benthem Jutting 1949, 1950, 1960; Foon et al. 2017). This species was also reported in southern Thailand: Trang, Suratthani, Krabi, Patthalung, Songkla, and Satul provinces (Panha 1998; Panha and Burch 2005; Tongkerd


Figure 10. Gyliotrachela hungerfordiana A topotype specimen NHMUK collection from Perak, Malaysia B paratype CUIZM, Ver 011 of G. khaochongensis, from Trang Province, Thailand C specimen CUMZ 14382 from Tanintharyi Region, Myanmar. Abbreviations: a: angular lamella, c: columellar lamella, ip: infraparietal lamella, itpl: interpalatal plica, ifpl: infrapalatal plica, Ipl: lower palatal plica, p: parietal lamella, sbc: subcolumellar lamella, spc: supracolumellar lamella, sppl: suprapalatal lamella, upl: upper palatal plica.
et al. 2013). In Myanmar, this species recorded is known only from an isolated limestone karst in the Tanintharyi Region.

Differential diagnosis. Gyliotrachela hungerfordiana differs from all other known Gyliotrachela species from Myanmar in having a thin shell, long and slender tuba, tall spire, and strong and curved keel on periphery. In contrast,
G. bensonianum has a conical spire, short tuba, curved keel on last whorl, and apertural dentition without supra- and inter- palatal plicae or supra- and subcolumellar lamellae; G. tianxingqiaoensis and G. muangon possess angular last whorl, short tuba nearly adnate to last whorl, and with many small accessory plicae and lamellae (Gojšina et al. 2022).

Remarks. Gyliotrachela khaochongensis and G. phoca were described from southern Thailand; the type specimens look identical to the type and topotypic specimens of $G$. hungerfordiana in shell form, shell sculpture and apertural dentitions (Panha 1998; Tongkerd et al. 2013), with no significant differences. Therefore, they are considered here as junior synonyms of $G$. hungerfordiana.

## Gyliotrachela tianxingqiaoensis (Luo, Chen \& Zhang, 2000)

Fig. 13N

Boysidia (Bensonella) tianxingqiaoensis Luo et al., 2000: 147, figs 1-4. Type locality. Tianxingqiao Town, Zhenning Bouyeizu Miaozu Zizhixian, Guizhou Province, China.
Gyliotrachela tianxingqiaoensis. Gojšina et al. 2022: 132-138, figs 1, 4b, 5c, d.

Distribution. This species was originally described in Guizhou Province, China and subsequently reported from 'Ava' [Mandalay Region, Myanmar] based on the historical A.E. Salisbury collection (Luo et al. 2000; Gojšina et al. 2022).

## Gyliotrachela muangon Panha \& Burch, 2004

Figs 11, 130

Gyliotrachela muangon Panha \& Burch in Panha et al. 2004: 67, 68, fig. 7. Type locality. Muangon Cave, San Kam Pang District, Chiangmai Province, Thailand. Panha and Burch 2005: 76, 77, fig. 66. Gojšina et al. 2022: 138, fig. 6.

Material examined. Yum Cave, Kalaw City, Shan State, Myanmar (locality code KW1; $20^{\circ} 37^{\prime} 18.1^{\prime \prime} \mathrm{N}, 96^{\circ} 29^{\prime} 8.3^{\prime \prime} \mathrm{E} ; 854 \mathrm{~m}$ a.s.I.): CUMZ 14385 ( 1 shell; Fig. 11A, B); CUMZ 14408 (6 shells); CUMZ 14409 (12 shells; measured); CUMZ 14410 (2 shells; Figs 11C, 130).

Description. Shell broadly ovate-conical, reddish brown in colour, moderate spire, and $43 / 4-5$ widely convex whorls. Shell height $1.8-2.0 \mathrm{~mm}$ and shell width (including tuba) 2.5-2.9 mm. Appex blunt; protoconch $13 / 4$ whorls, wrinkled with roundish pits. Teleoconch with wrinkles and irregular growth lines crossed by conspicuous spiral ridges throughout; suture well impressed and deep. Last whorl widely angular, tuba short and $\sim 10-12$ degrees angled upward. Peristome widely expanded; lip reddish brown. Aperture roundly triangular and many aperture dentitions. Parietal lamella large, tall, strong, blunt and slightly deep inside aperture. One or two minute infraparietal lamellae may be present. Angular lamella strong and reaching peristome. Upper palatal plica strong; sometimes very small suprapalatal plicae present. Lower palatal plica tall and strong; one or two small interpalatal plicae and infrapalatal plicae usually present. Columellar lamella very strong, distinct and horizontal; very low


Figure 11. Gyliotrachela muangon from Kalaw City, Shan State A, B specimen CUMZ 14385 from Kalaw City, Shan State, (A) shell and (B) protoconch C specimen CUMZ 14410 from Kalaw City, Shan State. Abbreviations: a: angular lamella, c: columellar lamella, ip: infraparietal lamella, itpl: interpalatal plica, ifpl: infrapalatal plica, IpI: lower palatal plica, p: parietal lamella, sbc: subcolumellar lamella, spc: supracolumellar lamella, sppl: suprapalatal lamella, upl: upper palatal plica.
and weak supracolumellar and subcolumellar lamellae present. All dentitions generally with very fine spines on surface. Umbilicus perforate, $\sim 1 / 4$ of shell width, rounded, deep, and surrounded by blunt periumbilical keel.

Distribution. This species was originally described from Chiangmai Province, northern Thailand (Panha et al. 2004). Later, a few specimens were collected from Hsi Hseng Township, Taunggyi District, Shan State (Gojšina et al. 2022).

Recently, several specimens were collected from Kalaw Township, Taunggyi District, Shan State.

Differential diagnosis. Gyliotrachela muangon can be distinguished from G. tianxingqiaoensis from China and Myanmar, and G. plesiolopa Inkhavilay \& Panha, 2016 from Laos by having weak spiral striae, five strong major lamellae and plicae (parietal, angular, columellar, and upper and lower palatals). In contrast, G. tianxingqiaoensis lacks spiral striation on the teleoconch, has a more elevated aperture, a narrower umbilicus and has more numerous teeth in the aperture; G. plesiolopa has a more expanded peristome, and a slightly weaker peripheral keel, which is also less upturned and flatter on the lower side (Inkhavilay et al. 2016; Gojšina et al. 2022).

The three species from Thailand (G. saraburiensis Panha \& Burch in Burch et al. 2003, G. muangon and G. cultura Tanmuangpak \& Dumrongrojwattana, 2022) are very similar to G. muangon in the turbinate shell form, the short and slightly descending tuba, the weakly angulated last whorl, the spiral striae on the teleoconch, and by having five major apertural dentitions. The significant distinction among them is mainly the number of accessory plicae and lamellae. Specifically, G. muangon possesses two infraparietals, two interpalatal and two infrapalatals, while G. saraburiensis has three infraparietals, three interpalatals and five infrapalatals, and G. cultura exhibits one infraparietal, one interpalatal and two infrapalatals (Burch et al. 2003; Panha et al. 2004; Panha and Burch 2005; Tanmuangpak and Dumrongrojwattana 2022).

Remarks. The examined specimens from Myanmar show minor variability in terms of apertural dentition from the type specimen from Thailand. Two interpalatal plicae are observed in the Myanmar specimens, while the type specimen has only one interpalatal plica.

## Gyliotrachela aunglini Tongkerd \& Panha, sp. nov.

https://zoobank.org/76E8570A-172A-4E2C-BB8A-7A1D898CD149
Figs 12, 13P

Type locality. Kaw Gon Cave, Hpa-An, Kayin State, Myanmar (locality code PA5; $16^{\circ} 499^{\prime 2} 22^{\prime \prime} \mathrm{N}, 97^{\circ} 35^{\prime} 08.9^{\prime \prime} \mathrm{E}$ ).

Type material. Holotype CUMZ 14383 (height 1.8 mm , width 1.6 mm ; Fig. 12A, B). Paratypes CUMZ 14384 (2 shells); CUMZ 14411 (16 shells; measured); CUMZ 14412 (2 shell; Figs 12C, D, 13P), NHMUK 20230593 (2 shells), SMF 373021 (2 shells) all from the type locality.

Diagnosis. Shell ovate-conical with shouldered and flat-sided last whorl, aperture not detached from penultimate whorl; shell surface irregularly wrinkled, colour pale reddish brown; aperture roundly triangular, with five or six apertural dentitions (angular, parietal, upper palatal, lower palatal and columellar).

Etymology. The specific name aunglini is named after Mr. Aung Lin, the FFI coordinator, who took care of the survey team and arranged the limestone survey trip in Myanmar between 2015 and 2016.

Description. Shell broadly ovate-conical, pale reddish brown in colour, moderate spire, and $4 \frac{1}{2}-5$ widely convex whorls. Shell height $1.6-1.8 \mathrm{~mm}$ and shell width $1.6-1.8 \mathrm{~mm}$. Apex blunt; protoconch with $1 \frac{3}{4}$ whorls, wrinkled, with roundish pits and weak spiral ridges. Teleoconch with narrowly spaced radial


Figure 12. Gyliotrachela aunglini sp. nov. from Hpa-An, Kayin State A, B holotype CUMZ 14383, (A) shell and (B) protoconch C, D paratypes CUMZ 14412 from the type locality. Abbreviations: a: angular lamella, c: columellar lamella, IpI: lower palatal plica, p: parietal lamella, upl: upper palatal plica.
growth lines, parallel with very strong, irregular wrinkles; suture well impressed. Last whorl bluntly shouldered and flat-sided with shallow groove below shoulder. Tuba absent; peristome adnate and widely expanded; lip whitish to yellowish. Aperture roundly triangular and with five dentitions. Parietal lamella large, strong, blunt and located somewhat deeper inside aperture than angular lamella. Angular lamella strong and reaching peristome. Upper palatal plica strong, tall and approximately same size as parietal lamella; lower palatal plica


Figure 13. Synoptic view of representatives of hypselostomatid snails recorded from Myanmar A Acinolaemus dayanum, specimen HA Collection B Acinolaemus cryptidentatus, specimen CUMZ 14413 C Anauchen eotvosi, holotype NHMUK 1903.7.1.1227.1 (after Páll-Gergely 2023a: fig. 1c) D Angustopila occidentalis, holotype HNHM 103483 (after Páll-Gergely et al. 2023: fig. 70a) E Angustopila elevata, specimen HNHM 103484 (after Páll-Gergely et al. 2023: fig. 13a) F Bensonella salwiniana, specimen CUMZ 14393 G Bensonella anguloobtusa, specimen CUMZ 14400 H Bensonella taiyaiorum sp. nov., paratype CUMZ 14403 I Bensonella lophiodera sp. nov., paratype CUMZ 14405 J Clostophis sankeyi, holotype UMZC I. 103320 (after Preece et al. 2022: fig. 70e) K Clostophis thinbowguensis, holotype MNHN-IM-2000-38057 (after Páll-Gergely et al. 2022: fig. 9c) L Gyliotrachela bensonianum, syntype NHMUK 20191141 (after Gojšina et al. 2022: fig. 4a) M Gyliotrachela hungerfordiana, specimen NHMUK collection from Perak, Malaysia N Gyliotrachela tianxingqiaoensis, holotype IZCAS TM 025075 (after Gojšina et al. 2022: fig. 3a) O Gyliotrachela muangon, specimen CUMZ 14410 P Gyliotrachela aunglini sp. nov., paratype CUMZ 14412 Q Hypselostoma tubiferum, specimen NHMUK 1888.12.4.17-22 ex. Theobald collection from Tonduong, Burma.
strong and lower than upper palatal plica. Columellar lamella strong, distinct and pointing slightly upwards. Umbilicus widely perforate, $\sim 1 / 3$ of shell width, rounded, shallow, and surrounded by curved periumbilical keel.

Distribution. This new species is currently known only from the type locality in Kayin State. This snail lives on the limestone walls and under leaf litter.

Differential diagnosis. Gyliotrachela aunglini sp. nov. differs from G. bensonianum and $G$. tianxingqiaoensis from Myanmar in having high spire, peristome adnate to preceding whorl, shouldered last whorl, with very weak spiral striae on protoconch, and only five apertural dentitions (parietal, angular, upper- and lower- palatal, and columellar). In contrast, the other two species possess a depressed spire, a short and slightly ascending tuba, and an angular last whorl. Additionally, G. bensonianum has a spirally striated teleoconch, and it has a basal plica and infraparietal lamella; G. tianxingqiaoensis possesses numerous small accessory plicae and lamellae (Gojšina et al. 2022).

This new species can be distinguished from G. saraburiensis, G. muangon, and G. cultura (all known from Thailand) by having no tuba (i.e., peristome adnate to preceding whorl), possessing a shouldered last whorl, strong wrinkles on the shell surface and bearing only five to six major dentitions. In contrast, the three species from Thailand tend to have a short and slightly ascending tuba, an angular to weakly angular last whorl, spiral striae on the teleoconch, and numerous accessory plicae and lamellae inside the aperture (Burch et al. 2003; Panha et al. 2004; Panha and Burch 2005; Tanmuangpak and Dumrongrojwattana 2022).

Several Gyliotrachela species from southern Thailand are similar to the new species by having very short tuba, and few apertural dentitions. Gyliotrachela aunglini sp. nov. differs from G. transitans (von Möllendorff, 1894) in the short and slightly descending tuba, the angular last whorl, and the apertural dentition with supracolumellar lamella and a basal plica; G. tarutao (Panha \& Burch, 2002) has an elevated spire, an angular last whorl, a very short tuba, and the apertural dentition is characterised by a subcolumellar lamella, an infraparietal plica and a basal plica (von Möllendorff 1894; Panha and Burch 2002b, 2005). The new species differs from G. adela Thompson \& Upatham, 1997 in the depressed spire, the short and descending tuba, with prominent spiral striae on the teleoconch, and apertural dentition with a basal plica (Thompson and Upatham 1997).

Further comparison can be made with species from Peninsular Malaysia that have a very short tuba and few apertural dentitions. Gyliotrachela aunglini sp. nov. differs from G. emergens van Benthem Jutting, 1950 and G. modesta van Benthem Jutting, 1950 in having an elevated spire, short and slightly descending tuba and an angular or weakly angular last whorl. In addition, the apertural dentition of the former species includes a basal plica, and supra- and sub- columellar lamellae, while the latter species has a supracolumellar lamella and a weak infrapalatal plica. Additionally, this new species differs from G. troglodytes van Benthem Jutting, 1950 in the depressed spire, the very short and descending tuba, the angular last whorl, the apertural dentition with infraparietal and weak angular lamellae, and the strongly wrinkled shell surface (van Benthem Jutting 1950).

Remarks. The material examined here shows minor variability in terms of shell size, but the key morphological characters, shell sculpture and apertural dentition, are reliable.

## Genus Hypselostoma Benson, 1856

Tanystoma Benson, 1856a: 130 [non de Motschulsky 1845: Coleoptera, Carabidae]. Hypselostoma Benson, 1856b: 342 [new replacement name]. Panha and Burch 2005: 87.

Type species. Tanystoma tubiferum Benson, 1856a, by monotypy. Remarks. So far, only one species has been reported from Myanmar.

Hypselostoma tubiferum (Benson, 1856)
Fig. 13Q

Tanystoma tubiferum Benson, 1856a: 130. Type locality: Thyet-Mio [Thayet District, Magway Division].
Hypselostoma tubiferum. Pfeiffer 1859: 325. Pfeiffer 1860: 130, pl. 36, figs 1-4. Blanford 1863: 326. Hanley and Theobald 1870: 4, pl. 8, fig. 3. Stoliczka 1871: 173, pl. 7, fig. 1. Pfeiffer 1876: 488. Gude 1914: 298, 299. Pilsbry 1917: 178, 179, pl. 31, figs 1-5. Gojšina et al. 2022: 138, fig. 7. Preece et al. 2022: 155, 156, fig. 70d.
Pupa (Hypselostoma) tubifera. Nevill 1878: 193.

Distribution. So far, new specimens have yet to be collected, and only the historical museum collection was available for study. This species is known only from certain localities in central Myanmar: Thyet Mio [Thayet District, Magway Division]; Mya Leit Doung [Myaleit mountains, Mandalay Region]; Tsagyen Hills [Sagaing Hills, Sagaing Region]; Pegu and Henzada [Bago Region and Hinthada District, Ayeyarwady Region] (Gude 1914; Pilsbry 1917; Gojšina et al. 2022).

## Discussion

This inventory updates previous work and provides a comprehensive record of the hypselostomatid snail fauna of Myanmar. Before the $20^{\text {th }}$ century, the record was compiled by Gude (1914), including five species belonging to the genera Boysidia and Hypselostoma. Currently, 17 species are known to occur in Myanmar. Among these, seven species, namely Anauchen eotvosi, Angustopila elevata, Clostophis sankeyi, Clostophis thinbowguensis, Gyliotrachela bensonianum, Gyliotrachela tianxingqiaoensis, and Hypselostoma tubiferum are listed herein based solely on records in the literature (i.e., Gude 1914; Gojšina et al. 2022; Páll-Gergely and Hunyadi 2022; Páll-Gergely 2023a; Páll-Gergely et al. 2023). The synoptic views of the type or authenticated specimens of those species are provided for baseline comparison and identification. Additionally, three new species have been described, a new combination (Acinolaemus dayanum) was proposed, and three species are redescribed. Finally, three species (Acinolaemus cryptidentatus, Bensonella anguloobtusa, G. hungerfordiana) are newly recorded for Myanmar.

Gyliotrachela, a genus which exhibits a wide range of morphological variability among the Hypselostomatidae, is represented by five species. The redescription of the type species, G. hungerfordiana, described initially from Peninsula Malaysia, together with ' $G$. khaochongensis' and 'G. phoca' from southern Thailand, are for-
mally synonymised. Based on the recent collection from Myanmar, G. hungerfordiana and G. muangon appear to have relatively wide ranges of distribution; specimens of the former were collected 750 km from the type locality in Thailand, and specimens of the latter were found 250-350 km from the type locality. However, Burmese samples of both species exhibited some morphological variation, especially in terms of their 'additional' or 'supplementary' apertural dentition (i.e., tiny plicae between main plicae), although this does not appear useful in distinguishing species. The apparently low morphological variability of these widely distributed species may reflect that their broad distributions are due to recent dispersion events, or it may show convergence of the diagnostic value of shell traits. Additional new material and genetic data could help to address this question.

Bensonella (now united with Paraboysidia) and Acinolaemus have now been reported for the first time in Myanmar, and are represented by five and two nominal species, respectively. One of the little-known species, $A$. dayanum originally described from limestone hills in the Salween River Basin, has a shell that is morphologically unique and somewhat intermediate in that it demonstrates certain shell characters of other species. For instance, it shares a large angular lamella and wide umbilicus with Acinolaemus, and shares a cervical crest on the palatal wall behind the lip and three lamellae on the parietal wall with Bensonel$l a$; at the same time, the malleated pits of its shell sculpture seem to be a unique character, only shared with the probably closely related Acinolaemus cryptidentatus. However, the relationship between Acinolaemus and Bensonella could not be interpreted here, since a molecular phylogeny of some hypselostomatid taxa indicated that shell morphology, especially aperture dentition, can only be used with caution as diagnostic characters. Instead, shell sculpture is more taxonomically significant (Tongkerd et al. 2004). However, this study has attempted to present such differentiation as a baseline regarding shell morphology for future studies, especially concerning the phylogenetic interpretation of these genera.

Myanmar has the largest total karst area among the Indochinese countries and contains extensive limestone areas, i.e., Shan Plateau and Andaman coastal area (Day and Urich 2000; Gunn 2004; Clements et al. 2006). However, only a handful of studies concerning Myanmar's hypselostomatid snails have been published, and their known diversity is low compared to nearby countries. Therefore, extensive surveys covering a range of limestone habitats across different elevations, latitudes and karstic regions could be expected to uncover more cryptic taxa. Most hypselostomatids are smaller than 5 mm and prefer specific microhabitats such as limestone walls, caves, and litter. Therefore, we suggest using focused collecting techniques and procedures such as soil sampling from various habitat types and sieving via graduated sieves (Nekola and Coles 2010; Neubert and Bouchet 2015; Páll-Gergely et al. 2023).

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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

PT, NL, RC, AP, PP, TS, WS, RS, CS, and SP collected and prepared specimens in the field. PT, NL, CS, and SP provided financial and intellectual support. PT and CS prepared specimens and wrote the manuscript. SP and CS conceived, designed, supervised the study, prepared figures, and approved and edited the final manuscript. BPG reviewed, advised, and approved the final manuscript.

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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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# Two new ant species of the genus Leptogenys (Hymenoptera, Formicidae) from Hainan, China, with a key to the known Chinese species 

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[^3]
#### Abstract

Two new species of ponerine ants from Hainan Province, China, Leptogenys hainanensis sp. nov. and L. zhoui sp. nov., are delineated and depicted based on the worker caste. Leptogenys hainanensis sp. nov. belongs to the L. leleji species group, with mandibles elongate, slender and curved, lacking a distinct masticatory margin. On the other hand, L. zhoui sp. nov. belongs to the L. crassicornis species group, distinguished by its square head, smooth body, mandibles with a dentate masticatory margin, and short antennae. A key to workers for the known species of Leptogenys in China are provided and a map is provided for the newly described species.


Key words: L. crassicornis species group, L. leleji species group, Ponerinae, southern China, taxonomy

## Introduction

The genus Leptogenys Roger, 1861, encompasses more than 316 valid species and 14 valid subspecies (Bolton 2023). Twenty-four species of the genus Leptogenys are recorded in China. Predominately tropical and subtropical, there are some species that could be argued that extended into temperate, more seasonal regions (Guénard et al. 2017). Nests of New World Leptogenys may vary from 20 to 30 workers, rarely surpassing 50 . Small nest sizes are also reported for more than 15 species of this genus in the Oriental Tropics by Ito and Ohkawara (2000) with the outstanding exception of some SE Asian Leptogenys with army ant habits, which have colonies numbering in the thousands, and are generalists, taking diverse prey (Witte and Maschwitz 2002). These ants are known for their preference for small colonies and some have specialized predation on isopods (Schmidt and Shattuck 2014) or earwigs (SteghausKovac and Maschwitz 1993) for Oriental species, and termite predation for the African nitida group (Bolton 1975). In Cambodia and Thailand, L. cyanicatena

Arimoto \& Yamane specialize on a broad range of millipedes, and workers link together in chains to retrieve the larger millipedes.

The features of Leptogenys leleji Zryanin, including the shape of its cranio-mandibular system and petiole, bear resemblance to those of the representatives of the $L$. conradti species group (CASENT0907340) from Africa, the L. turneri species group (L. Iongensis CASENT0217531) from Australia (Zryanin 2016), and certain species of the L. unistimulosa species group (CASENT0178818) from the New World (Lattke 2011). On the other hand, the L. crassicornis species group (CASENT0281924) is distinguished by its square-shaped head, smooth body, mandibles with a dentate masticatory margin, and short antennae (Xu 2000).

Significant contributions to the understanding of Leptogenys on a global scale have been made through species listings, revisionary efforts, and the diagnostic and synoptic description of the genus by various researchers, including Lattke (2011), Sarnat and Economo (2012), Zhou et al. (2012), Bharti and Wachkoo (2013), Rakotonirina and Fisher (2014), Schmidt and Shattuck (2014), Xu and He (2015), Zryanin (2016), Sharaf et al. (2017), Arimoto (2017a, 2017b), Arimoto and Yamane (2018), López-Muñoz et al. (2018), Wachkoo et al. (2018), Ramage et al. (2019), Fernández and Guerrero (2019), and Subedi et al. (2022). Considerable effort is still required to unravel the regional diversity of Leptogenys species. A contemporary revision of Asian Leptogenys is notably absent.

In China, the first record of four Leptogenys species were documented by Wheeler (1930), followed by subsequent reports of Chinese species by Tang et al. (1995) (five species), Wu and Wang (1995) (three species), Xu (1996) (seven species), Xu (2000) (13 species), Zhou (2001) (seven species from Guangxi), Xu (2002) ( 11 species from Yunnan), Wang et al. (2009) (two species from Hubei), and Terayama $(1990,2009)$ (four species from Taiwan). Guénard and Dunn (2012) listed 20 species in China, while Xu and He (2015) revised the Oriental species and recorded 24 species in China.

The present study contributes to this body of work by describing Leptogenys hainanensis sp. nov. and L. zhoui sp. nov. from Hainan Province, China, accompanied by high-resolution images and measurements of important morphological characters. A key to all known Chinese species and a map of the distribution data of the two new species is provided.

## Materials and methods

The ant specimens were obtained using sample-plot and search-collecting methods (e.g., Xu 2002). Subsequently, the specimens were meticulously examined using an SDPTOP-SZM stereomicroscope. High-quality multifocus montage images were captured using a Keyence VHX-6000 ultra-depth microscopic three-dimensional microscope. The map was constructed using the software package ArcGIS v. 10.8. To compare the worker morphology of the two new species, reference was made to the original descriptions of related species (Emery 1887, 1895; Forel 1900, 1915; Zryanin 2016). sculptural, and hair terminology follow Harris (1979) and Wilson (1955). Images of L. crassicornis species group (CASENT0281924) were sourced from AntWeb (2023).

Standard measurements and indices were employed as defined in Bolton (1975) and Lattke (2011), with the addition of ML and ED, as outlined below. Furthermore, alitrunk length is substituted by WL (Weber's Length) in accordance with the methodology proposed by Xu and He (2015). Addition of HLL, HLA, CML, PrL, and PrH (Arimoto 2017a). All measurements are reported in millimeters.

HL Head length: straight-line length of head in perfect full-face view, measured from the mid-point of the anterior clypeal margin to the midpoint of the posterior margin. In species where one or both of these margins are concave, the measurement is taken from the mid-point of a transverse line that spans the apices of the projecting portions.
HLL Head lateral margin length: in full-face view, the head length measured from the mandible base to the nuchal carina.

HLA Anterior head length: in full-face view, the head length measured from the mandible base to the anterior edge of the eye.
HW Head width: maximum width of head in full-face view, excluding the eyes.
ML Mandible length: straight-line length of mandible measured from apex to the lateral base.
CML Clypeal median lobe length: in full-face view, the straight-line length measured from the anterior margin of the clypeus to the anterior margin of the torulus.
CI Cephalic Index $=\mathrm{HW} \times 100 / \mathrm{HL}$.
SL Scape length: straight-line length of the antennal scape, excluding the basal constriction or neck.
SI Scape index $=$ SL $\times 100 / \mathrm{HW}$.
ED Eye diameter: maximum diameter of eye.
PrL Pronotum length: in profile, the diagonal length of the pronotum, measured from the anterior margin of the pronotum excluding the collar to the posterior extremity of the pronotum.
PrH Pronotum height: in profile, the maximum height of the pronotum, measured from the posterior base of the lateral margin of the pronotum to the highest point of the pronotum.
PrW pronotum width: maximum width of pronotum measured in dorsal view.
WL Weber's length (= alitrunk length): diagonal length of the mesosoma in lateral view, measured from the point at which the pronotum meets the cervical shield to the posterior basal angle of the metapleuron.
TL Total length: total outstretched length of the individual, from the mandibular apex to the gastral apex.
PL Petiole length: length of petiole measured in lateral view from the anterior process to the posteriormost point of the tergite, where it surrounds the gastral articulation.
PH Petiole height: height of petiole measured in lateral view from the apex of the ventral (subpetiolar) process vertically to a line intersecting the dorsal most point of the node.
DPW Dorsal petiole width: maximum width of petiole in dorsal view.
LPI Lateral petiole index $=\mathrm{PH} \times 100 / \mathrm{PL}$.
PDPI Dorsal petiole index $=\mathrm{DPW} \times 100 /$ PL.

## Taxonomic account

## Leptogenys hainanensis sp. nov

https://zoobank.org/39DED636-393B-4EA7-B0E7-ABD4220B94A3
Figs 1A-D, 2

Type material. Holotype: worker, CHINA: Hainan Province, Qiongzhong County, Yinggeling Nature Reserve, Yinggezui sub-station, $19.048333^{\circ} \mathrm{N}, 109.559167^{\circ} \mathrm{E}$, $750 \mathrm{~m}, 28 . \mathrm{VII} .2022$, Chao Chen leg. The holotype specimen is deposited in Kunming Natural History Museum of Zoology, Kunming Institute of Zoology, Chinese Academy of Sciences (KIZCAS), Kunming, Yunnan Province, China, Reg. No. KIZ20220009 (unique specimen identifiers). Paratype: 1 worker, CHINA: Hainan Province, Ledong County, Jianfengling, 18.727222N, 108.898611E, 950 m, 9.IV.2016, Zhi-Lin Chen leg. The paratype specimen is deposited in the Insect Collection, Guangxi Normal University (GXNU), Guilin, Guangxi Zhuang Autonomous Region, China, Reg. No. G160246 (unique specimen identifiers).

Description. Holotype worker (Fig. 1A-D): HL 2.34, HLL 1.47, HLA 0.33, HW 2.42, ML 1.87, CML 0.45, CI 103, SL 2.54, SI 105, ED 0.48, PrL 1.44, PrH 1.06, PrW 1.58, WL 4.23, TL 13.1, PL 1.22, PH 1.54, DPW 1.05, LPI 126, PDPI 86.

In full-face view, head presents a roughly trapezoidal shape, with anterior widening, length slightly longer than its width. Posterior margin straight and carinate, posterior corners narrowly rounded, lateral margins display a subtle convexity. Mandibles elongate and slender, with a masticatory margin, forming into the inner margin without a distinct angle; lamellae extension at masticatory margin and inner mandible; large gap formed between clypeus and mandible when fully closed (Fig. 1C). Clypeus triangularly produced, with blunt apex; anterior clypeal margin fringed with narrow translucent lamella; median longitudinal carina of clypeus sharp. Antennae composed of 12 segments, with scape extending beyond posterior corner of head by $2 / 5$ of its length (SI 105). Basal flagellar (third antennal) segment elongate, markedly longer than neighboring antennal segments (lengths of segments 2, 3, 4: $0.36 \mathrm{~mm}, 0.64 \mathrm{~mm}, 0.43 \mathrm{~mm}$ ). Eyes moderately large, occupying $\sim 1 / 3$ of lateral cephalic margin, position in close proximity to base of mandibles (HLA 0.33).

In lateral view, promesonotum presents a moderately convex form and a slight elevation compared to propodeum. Promesonotal suture is discernible but not deeply marked. Prosternal process blunt round. Metanotal groove narrow and deeply impressed. Dorsum of propodeum displays a gentle convexity and slopes posteriorly, with a length $\sim 2 \times$ that of the declivity. Propodeum armed with triangular tooth at level of spiracle; propodeal declivity with carina uniting apices of these teeth; area anteriad to carina concave in cross-section, with mostly smooth and shiny surface; area posteriad to carina depressed as broad transverse sulcus. Petiolar node robust and approximately trapezoidal in shape, displaying a slight posterior inclination. Its anterior and dorsal margins exhibit a mild convexity, with anterodorsal corner broadly rounded and posterior margin straight. An acute spine extends posterodorsally from posterodorsal corner. Subpetiolar process shaped as sub-rectangular tubercle with gentle posterior slope. Gaster roughly cylindrical, with distinct constriction between two basal segments and extruding sting. Prora shaped as sharp, ventrally directed, lobe at anteroventral angle of first gastral segment.


Figure 1. Leptogenys hainanensis sp. nov. worker $\mathbf{A}$ body in lateral view $\mathbf{B}$ body in dorsal view $\mathbf{C}$ head in full-face view D petiole in dorsal view.


Figure 2. Distribution of the two new species of Leptogenys in Hainan, China. The gradients of the map indicate the topography.

In dorsal view, mesosoma exhibits a slight constriction at mesopleuron, with pronotum being marginally wider than propodeum. Sides of pronotum feature moderate convexity. Promesonotal suture and deeply notched metanotal groove present. Sides of mesopleuron appear almost straight, while those of propodeum display a mild convexity. Petiolar node roughly trapezoidal, widening posteriorly, with slightly convex sides and posterior margin that extends into triangular process with bifid apex.

Mandibles finely longitudinally striated with smooth and shiny interspaces, while clypeus and dorsum of the head exhibit dense longitudinal striae, vertex displaying dense transverse striae. Mesosomal dorsum densely longitudinally striated, with striation transitioning to reticulate pattern on mesonotum and posterior part of propodeum. Mesopleura and metapleura relatively smooth, with few oblique striations on lower part of metapleura. Petiole coarsely reticulate, with short, small prominences at interface. Gastral have many distinct hairs bearing punctures. Abundant suberect to subdecumbent short hairs and depressed pubescence adorn dorsal aspect of body, appressed pubescence present on cephalic dorsum, antennae, and legs. Scapes and tibiae exhibit dense depressed


Figure 3. Leptogenys leleji worker (from AntWeb 2023, photographer: V.A. Zryanin) A body in lateral view B mesosoma and petiole in dorsal view $\mathbf{C}$ head in full-face view.
pubescence. Body displays black coloration, with mandibles, apical antennal segments, and legs exhibiting reddish brown hue, and eyes appearing grey.

Paratype worker: HL 2.11, HLL 1.35, HLA 0.29, HW 2.17, ML 1.92, CML 0.39, CI 102, SL 2.40, SI 111, ED 0.48, PrL 1.51, PrH 1.01, PrW 1.62, WL 4.08, TL 12.6, PL 1.26, PH 1.46, DPW 1.03, LPI 116, PDPI $82(n=1)$. Resembling the holotype worker, the specimen exhibits relatively coarser striation on the mesosomal dorsum and obliquely coarse striation on the metapleura. Additionally, the legs display a brownish black hue.

Queen and male. Unknown.
Comparative notes. In addition to being similar to Leptogenys leleji Zryanin, 2016, this new species is significantly different from other Chinese and Oriental species. The common characteristics with L. leleji (Fig. 3A-C) are as follows: the cephalic capsule is wider than long; the anterior clypeal margin is fringed with a narrow translucent lamella; the mandibles are linear, a large gap is formed between clypeus and mandible when fully closed; the basal flagellar (third antennal)
segment is elongate; the dorsum of the body with standing hairs; the propodeum with lateral teeth, and posterior apex of petiole in profile is drawn out into a tooth (Zryanin 2016). In the new species (Fig. 1A-D), with the head in full-face view, the posterior margin is straight and carinate, and the posterior corners are narrowly rounded, while the lateral margins display a subtle convexity; the distance between the ventral eye margin and the anterior clypeal margin is shorter (HLA 0.33 ); dorsum of the head exhibits dense longitudinal striae; the eyes' greatest diameter is greater than the maximal width of the scape; the posterior process of the petiolar node is relatively longer and bifid at the apex, with an abundance of short, small prominences on the reticulation interface. Conversely, in L. leleji, the head in full-face view is markedly wider anteriorly than posteriorly, the lateral and posterior margins form a continuous convexity, the occipital carina is distinct; the distance between the ventral eye margin and the anterior clypeal margin is moderate (HLA 0.41); dorsum of the head with sparse longitudinal striae; eyes' greatest diameter is greater than the maximal width of the scape; the posterior process of the petiolar node is relatively shorter and not bifid at the apex, and lacks the short, small prominences on the reticulation interface.

Etymology. The species name hainanensis is a Latin feminine singular adjective in the nominative case and refers to Hainan Province, where the first specimen of this species was collected. The name is unchangeable.

## Leptogenys zhoui sp. nov.

https://zoobank.org/C5B46D93-7930-4CA0-A1A9-05F3FA8A5EA2
Figs 2, 4A-D

Type material. Holotype: worker, CHINA: Hainan Province, Baisha County, Nanmeiling forest park, Yaqiong sub-station, $19.144167^{\circ} \mathrm{N}, 109.349167^{\circ} \mathrm{E}, 700 \mathrm{~m}$, 2.VIII.2022, Chao Chen leg. The holotype specimen is deposited in Kunming Natural History Museum of Zoology, Kunming Institute of Zoology, Chinese Academy of Sciences (KIZCAS), Kunming, Yunnan Province, China, Reg. No. KIZ20220196 (unique specimen identifiers). Paratypes: 2 workers, data the same as holotype. One paratype worker is deposited in GXNU. No. KIZ20220197 (unique specimen identifiers); 1 paratype worker is deposited in the Insect Collection, Southwest Forestry University (SWFU), Kunming, Yunnan Province, China. No. KIZ20220198 (unique specimen identifiers)

Description. Holotype worker (Fig. 4): HL 0.91, HLL 0.75, HLA 0.17, HW 0.81, ML 0.49, CML 0.12, CI 89, SL 0.68, SI 84, ED 0.10, PrL 0.69, PrH 0.49, PrW 0.61, WL 1.53, TL 4.4, PL 0.26, PH 0.46, DPW 0.35, LPI 174, PDPI 135.

Head in full-face view slightly wider anteriorly than posteriorly with straight posterior margins and narrowly rounded posterior corners. Lateral margins exhibit a subtle convexity. Mandibles display parallel inner and outer margins, with masticatory margin adorned with three or four teeth. Anterior portion of clypeus concave medially, while dentate protrusions emerge on both sides. Short frontal ridge extends slightly beyond upper end of eyes, and well-developed frontal lobes cover antennal sockets. 12-segmented antennae boast thickened funiculus towards the end, with scape reaching just to posterior head corner. Eyes, of medium size, have maximum diameter $\sim 2 / 3$ that of scape and located at $1 / 5$ in front of lateral cephalic margin (HLL 0.75 , HLA 0.17).


Figure 4. Leptogenys zhoui sp. nov. worker $\mathbf{A}$ body in lateral view $\mathbf{B}$ body in dorsal view $\mathbf{C}$ head in full-face view $\mathbf{D}$ mandibles in full-face view.

In lateral view, promesonotum slightly raised, with distinct promesonotal suture and metanotal groove absent. Promesonotum pleural suture and me-so-metathoracic pleural suture evident, terminating at metathoracic spiracle. Dorsum of propodeum appears nearly straight, maintaining same horizontal plane as promesonotum, with slightly convex declivity. Length of dorsum of propodeum is $\sim 1.5 \times$ that of declivity, with curved transition from slope at back. Petiolar node carries a roughly trapezoidal shape, with weakly convex anterior margin and straight posterior margin, with convex dorsal margins. Well-developed subpetiolar process features a rounded anterior corner. Gaster adopts an approximately cylindrical form, with sting extruding.

In dorsal view, promesonotal suture distinct, while metanotal groove absent. Pronotum anteriorly a round shape, lateral margins convex. Mesonotum trapezoidal, wider in front and narrowing towards back. Propodeum square, with slightly convex lateral margins. Petiolar node dorsum semicircular, with round front and transverse posterior margin, $\sim 1.8 \times$ wider than its length (PL 0.26, PH 0.46).

Mandibles exhibit sparse pits along inner edge, while both sides of clypeus display longitudinal striae. Funiculus appears densely punctate, while remainder of body smooth and shiny. Erect or suberect hairs abundant abaxially on body, with only funiculus adorned with dense decumbent pubescence. Body reddish brown.

Paratype worker: HL 0.89-0.90, HLL 0.74-0.75, HLA 0.17, HW 0.81-0.83, ML 0.47-0.50, CML 0.11-0.12, CI 91, SL 0.67-0.68, SI 82, ED 0.10, PrL 0.62, PrH 0.46-0.47, PrW 0.60-0.61, WL 1.42-1.48, TL 4.1-4.2, PL 0.26, PH 0.43-0.45, DPW 0.34-0.37, LPI 165-172, PDPI 131-140 ( $n=2$ ). Similar to holotype worker.

Queen and male. Unknown.
Comparative notes. The new species is compared against species within the $L$. crassicornis species group, characterized by a square head, a smooth appearance, mandibles with a dentate masticatory margin, and short antennae. The new species exhibits the closest resemblance to Leptogenys crassicornis Emery, 1895 (Fig. 5A-C). In full-face view of the new species, sparse pits adorn the inner edge of the mandibles, while the middle part of the anterior clypeus displays a concave feature and forms dentate protrusions on both sides. The eyes are of moderate size, with a maximum diameter of ~ $2 / 3$ of the maximum diameter of the scape. In lateral view, the petiolar node is moderately thick and $\sim 1 / 2$ the height (PL $0.26, \mathrm{PH} 0.46$ ), while the dorsum of the propodeum appears nearly straight and aligns with the promesonotum in the same horizontal plane. Furthermore, the body, abaxially, exhibits a profusion of erect or suberect hairs. Conversely, in L. crassicornis, 'the inner edge of the mandible lacks pits or has only one or two pits in full-face view. The anterior aspect of the clypeus is rounded, and the eyes are smaller, with a maximum diameter of $\sim 1 / 2$ of the maximum diameter of the scape. In lateral view, the petiolar node appears thick and $\sim 4 / 5$ of the height (PL 0.33, PH 0.41 ), while the dorsum of the promesonotum is higher than the propodeum. Additionally, the body, abaxially, bears sparse erect or suberect hairs and decumbent pubescence.

The new species bears resemblance to Leptogenys myops (Emery, 1887) (Fig. 6A-C). In the new species, body size is relatively large (TL > 4 mm ); in full-face view, the anterior clypeal margin is fringed with two or three peg-like


Figure 5. Leptogenys crassicornis worker (from AntWeb 2023, CASENT0281924, photographer: Shannon Hartman) A body in lateral view $\mathbf{B}$ body in dorsal view $\mathbf{C}$ head in full-face view.
setae medially; the antennal scape reaches just to the posterior head corner; the eyes are relatively large (ED 0.1 mm ); the dorsum of the propodeum appears nearly straight and aligns with the promesonotum in the same horizontal plane. Furthermore, the body, abaxially, exhibits a profusion of erect or suberect hairs. Conversely, in $L$. myops, the body size is relatively small ( $\mathrm{TL}<4 \mathrm{~mm}$ ); in full-face view, the anterior clypeal margin is not fringed medially; the antennal scape does not reach the posterior head corner; the eyes are relatively small (ED 0.07 mm ); the metanotal groove divides the dorsal outline of the mesosoma into two distinct convexities in lateral view; body, abaxially, bears sparse erect or suberect hairs and decumbent pubescence.

Etymology. The newly discovered species is named in honor of Professor Shanyi Zhou of Guangxi Normal University, in commemoration of his exceptional contributions to the field of ant taxonomy in China. The name zhoui was created by adding the singular Latin genitive case suffix -it to the last name of a male person. The name is unchangeable.


Figure 6. Leptogenys myops worker (from AntWeb 2023, CASENT0281925, photographer: Shannon Hartman) A body in lateral view $\mathbf{B}$ body in dorsal view $\mathbf{C}$ head in full-face view.

## Key to species of Leptogenys found in China based on the worker caste

1 Masticatory margin of mandible with > 2 teeth and denticles in addition to the apical one2

- Masticatory margin of mandible usually edentate, at most with 1 tooth in addition to the apical one 8
2 Head quadrate or roughly trapezoidal in full-face view approx. as broad as long. Petiolar node longitudinally compressed and squamiform in lateral view, acute at summit, without distinct dorsal margin, the node above anterior and posterior articulations $\geq 2 \times$ as broad as long in dorsal view . 3
- Head rectangular in full-face view, distinctly longer than broad. Petiolar node longitudinally thickened or elongate, or roughly triangular, or cubical in lateral view, dorsal margin long or narrowly convex, always distinct, the node above anterior and posterior articulations $\leq 1.5 \times$ as broad as long in dorsal view

3 Medial side of eyes on dorsum of head longitudinally striate, anteromedian clypeal margin broadly angulate. Antennal segments IV-VI approx. as broad as long. Subpetiolar process broad and triangular. Body color reddish brown (Myanmar, India, China, Thailand)
L. birmana Forel

- Medial side of eyes on dorsum of head smooth and shiny, anteromedian clypeal margin bidentate. Antennal segments IV-VI longer than broad. Subpetiolar process narrow and cuneiform. Body color brownish black (India, Sri Lanka, Vietnam, China)
L. processionalis (Jerdon)

4 Petiolar node erectly triangular in lateral view, dorsal and anterior margins form a single arch, the two margins not separated by a distinct blunt angle (Vietnam, China)
L. davydovi Karavaiev

- Petiolar node subquadrate in lateral view, dorsal and anterior margins not forming a single arch, the 2 margins separated by a distinct blunt angle. 5
5 Petiolar node thickly trapezoidal in lateral view, dorsal margin as long as or longer than anterior margin. Body color brownish yellow (Myanmar, China)
L. crassicornis Emery
- Petiolar node thinly trapezoidal in lateral view, dorsal margin distinctly shorter than anterior margin. Body color reddish brown to black. .6

6 Mandible < 5 teeth, dorsum of the propodeum appears nearly straight and aligns with the promesonotum in the same horizontal plane
L. zhoui sp. nov.

- Mandible $\geq 5$ teeth, the dorsum of the promesonotum is higher than the propodeum .7

7 Body size is relatively large (TL 6.4 mm ). Subpetiolar process semicircular, rounded at apex. Body color reddish brown (China: Guangxi)
L. strena Zhou

- Body size is relatively small (TL 5.2 mm ). Subpetiolar process triangular, angled at apex. Body color black (India, Myanmar; China: Yunnan)
L. Iucidula Emery

8 Head dorsum striate throughout.................................................................. 9

- Head dorsum punctate throughout or mostly smooth and shiny, at most punctate or rugose anterior to eyes.11

9 Head slightly wider than long in full-face view. Petiolar node posterodorsal corner prominent with elongated triangular denticle ... L. hainanensis sp. nov.

- Head longer than wide in full-face view. Petiolar node posterodorsal corner broadly rounded without triangular denticle 10
10 Clypeus with distinct longitudinal central carina. Sides of pronotum smooth, finely rugulose or finely reticulate; sides of mesothorax, metathorax and propodeum irregularly rugose (India, Sri Lanka, Myanmar, China, Thailand, Philippines, Malaysia, Singapore, Indonesia, New Guinea, Solomon Islands
L. diminuta (Smith)
- Clypeus without longitudinal central carina. Mesosoma and petiolar node regularly longitudinally striate (India, Myanmar, Thailand, Vietnam, China, Malaysia, Indonesia, New Guinea)
L. kitteli (Mayr)
11 Head dorsum punctate throughout ..... 12
- Head dorsum mostly smooth and shiny, at most punctate or rugose ante- rior to eyes ..... 20
12 First gastral segment mostly punctate ..... 13
- First gastral segment smooth and shiny ..... 16

13 Head roughly rectangular in full-face view, not widening anteriorly, posterior margin roundly convex. Anterior apex of clypeus strongly convex (China)
L. hezhouensis Zhou

- Head roughly trapezoidal in full-face view, distinctly widening anteriorly, posterior margin nearly straight. Anterior apex of clypeus truncate or nearly truncate
14 Antennae relatively shorter, only one fourth of length of scape surpassing posterior head corner, segments 3 and 4 approx. equal. Anterior margin of petiolar node in lateral view straight and vertical (China).
L. yandii Xu \& He
- Antennae relatively longer, $1 / 3$ to $1 / 2$ of length of scape surpassing posterior head corner, segment 3 distinctly longer than segment 4. Anterior margin of petiolar node weakly convex and slope, anterodorsal corner broadly rounded
15 Eyes larger and occupying $1 / 3$ of head side. Antennae shorter, $1 / 3$ of scape length surpassing posterior head corner. Head dorsum finely densely punctate. Dorsa of mesosoma, petiole, and first gastral segment sparsely punctate with interspaces relatively shiny; sides of mesosoma and petiolar node longitudinally rugose, posterior $2 / 3$ of side of first gastral segment smooth and shiny, second gastral segment smooth and shiny. Total length 5-6 mm (India, Philippines, China)
L. punctiventris (Mayr)
- Eyes smaller and occupying 1/4 of head side. Antennae longer, near 1/2 of scape length surpassing posterior head corner. Head, mesosoma, petiole, and first gastral segment densely punctate with interspaces coarsely reticulate rugose and dull, second gastral segment sparsely punctate. Total length 9-10 mm (Myanmar, India, China)
L. binghamii Forel

16 Clypeus truncate at apex (China)
L. huapingensis Zhou

- Clypeus convex at apex, not truncate 17
17 Dorsal faces of head, mesosoma and petiolar node densely punctate and opaque18
- Dorsal face of head loosely punctate with interspaces relatively shiny, dorsal faces of mesosoma and petiolar node smooth and shiny 19
18 Inner margin of mandible roundly convex, basal corner bluntly angled. Pronotum densely punctate with sides longitudinally striate. Anterodorsal corner of petiolar node broadly rounded in lateral view. Body color black. Robust species with total length $7.1-7.8 \mathrm{~mm}$ (China) ....... L. zhuangzii Xu
- Inner margin of mandible nearly straight, basal corner rounded without clear angle. Pronotum finely rugulose with sides smooth and shiny. Anterodorsal corner of petiolar node narrowly rounded in lateral view. Body color blackish brown. Slender species with total length $4.5-5.0 \mathrm{~mm}$ (China)
L. laozii Xu

19 Petiolar node higher than long in lateral view, with anterodorsal corner narrowly rounded. Mesopleuron and metapleuron mostly smooth and shiny. Body color black to blackish brown. Total length 4.5-5.2 mm (China).......
L. mengzii Xu

- Petiolar node as high as long in lateral view, with anterodorsal corner broadly rounded. Mesopleuron and metapleuron mostly densely rugose and opaque. Body color reddish brown. Total length 5.6-6.4 mm (China).
L. rufida Zhou et al.

20 Petiolar node strongly elongate in lateral view, $\sim 1.5 \times$ as long as high (China)
L. pangui Xu

- Petiolar node moderately to weakly elongate in lateral view, $<1.2 \times$ as long as high......................................................................................................... 21
21 Petiolar node moderately elongate, as long as high or distinctly longer than high in lateral view .............................................................................. 22
- Petiolar node weakly elongate, distinctly higher than long in lateral view, $1.3-1.4 \times$ as high as long............................................................................ 25
22 Clypeus truncated at apex. Lager species with total length 8-11 mm..... 23
- Clypeus convex at apex. Smaller species with total length 4.5-7 mm ..... 24

23 Clypeus anterior clypeal lobes divided into 2 teeth. dorsal faces between eyes and antennal sockets smooth and shiny, without longitudinal rugae. Petiolar node relatively broader in dorsal view, $1.3 \times$ as long as broad, (India, Sri Lanka, Philippines, China .L. chinensis (Mayr)

- Clypeus anterior clypeal lobes round, dorsal faces between eyes and antennal sockets longitudinal rugose and opaque. Petiolar node relatively narrower in dorsal view, $2 \times$ as long as broad (Indonesia, Vietnam, Thailand, China)
L. kraepelini Forel

24 Petiolar node distinctly longer than high in lateral view.(PL 0.63, PH 0.51 CASENT0281935) Sides of mesothorax, metathorax, and propodeum mostly smooth and shiny. Body color black. Relatively larger species with total length 5.9-6.3 mm (Vietnam, Myanmar, India, Sri Lanka, Bangladesh, Thailand, Philippines, Singapore, Indonesia, China)....... L. peuqueti (André)

- Petiolar node as high as long in lateral view. Sides of mesothorax, metathorax, and propodeum mostly irregularly rugose and opaque. Body color black, gaster blackish brown. Relatively smaller species with total length 4.5 mm (Japan, China)
L. confucii Forel

25 In full-face view, greatest width of eye roughly equal to or less than the greatest width of antennal scape. Petiolar node relatively longer in lateral view, $1.3 \times$ as high as long, dorsal margin distinctly longer than anterior margin (China)
L. laeviterga Zhou et al.

- In full-face view, greatest width of eye markedly greater than the maximum width of antennal scape. Petiolar node relatively higher in lateral view, $\sim 1.4 \times$ as high as long, dorsal margin as long as anterior margin (China)
L. sunzii Xu \& He


## Discussion

During our specimen collection in Hainan Tropical Rainforest National Park, we found five species of the genus Leptogenys: L. diminuta (Smith), L. kitteli (Mayr), L. peuqueti (André), and the two new species. When identifying to which species group $L$. hainanensis belongs, we found that the species $L$. amazonica Borgmeier (CASENT0178836), L. bohlsi Emery (CASENT0173510), L. gatu Lattke (CASENT0178814), L. paraensis Lattke (CASENT0178816), and L. pubiceps Emery (CASENT0248759) in the New World $L$. unistimulosa group differed from $L$. hainanensis by having peg-like setae on the clypeal apex and large hypostomal lobes. The species L. crustosa Santschi (CASENTO281916) in the Ethiopian L. conradti group differed from $L$. hainanensis by the clypeus having a rounded prominent median lobe, but lacking a fringing lamella. The species L. longensis Forel (CASENT0217531) in
the Australian L. turneri group differed from L. hainanensis by the clypeus being dentate, whereas $L$. hainanensis has no denticles. However, the characters of the new species described above are the same as those of the species $L$. leleji Zryanin found in Vietnam, so we propose that the two species, L. hainanensis and L. leleji, be established in a new species group, the L. leleji group. The Leptogenys leleji group is formally diagnosed as follows: cephalic capsule wider than long; anterior clypeal margin fringed with narrow translucent lamella; mandibles linear, a large gap formed between clypeus and mandible when fully closed; basal flagellar (third antennal) segment elongate; dorsum of body with standing hairs; propodeum with lateral teeth, posterior apex of petiole in profile drawn out into a tooth. A formal diagnosis for this species group awaits further revisions of Asian Leptogenys.

In the island ecosystem of China's Hainan Province, a plethora of hitherto undiscovered species awaits exploration. A comprehensive future survey promises to augment the existing inventory of ant species in China. An unpublished study employing both sample-plot and search-collecting methods has revealed a total of 72 ant species in Hainan, including the two new species- described here. Regrettably, due to constraints in collection methods, the number of specimens retrieved for the two new species was limited. Both species, L. hainanensis and $L$. zhoui, were collected while foraging along streams in tropical rainforests at elevations of less than 1,000 meters. The individuals of our recent taxonomic discoveries were procured during foraging excursions, precluding the identification of their nests. Subsequent iterative surveys should yield more specimens, thus substantiating the status of these species.

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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

Habitat photos of two new species
Authors: Chao Chen, Zhilin Chen, Zhenghui Xu, Qishan Fu, Liwen Fu Data type: pdf
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Link: https://doi.org/10.3897/zookeys.1195.115889.suppl1

## Supplementary material 2

## Specific geographical coordinates of the two new species

Authors: Chao Chen, Zhilin Chen, Zhenghui Xu, Qishan Fu, Liwen Fu
Data type: csv
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Link: https://doi.org/10.3897/zookeys.1195.115889.suppl2

# A new monotypic genus of cobweb spiders from the Russian Far East (Araneae, Theridiidae) 

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#### Abstract

A new theridiid spider, Knoflachia kurilensis gen. et sp. nov., is described from the Kuril Islands (Kunashir). The new genus belongs to the 'Anelosimus clade (clade 24)' of Agnarsson (2004). A pair of raised, fused setal sockets on the cheliceral promargin adjacent to the fang base was found to be another synapomorphy of all the 'distal theridiids' (the 'elongated central claw clade (clade 33)': argyrodins, 'Anelosimus clade' and theridiins). Knoflachia kurilensis sp. nov. demonstrates a male polymorphism similar to some Anelosimus Simon, 1891 species (e.g., A. studiosus (Hentz, 1850)).


Key words: Anelosimus clade, Aranei, distal theridiids, Kunashir Island, Kuril Islands, new species

## Introduction

Theridiidae, or cobweb spiders, is the fourth largest family of the order. Currently, the family includes 2542 recent species placed in 124 genera. Among spe-cies-rich families with over 1000 species, it has the highest species/genus ratio 20.5 (WSC 2023). Worldwide Theridiidae genera were considered in three publications: Levi and Levi (1962), Agnarsson (2004) and Vanuytven (2021). Theridiidae of Far East Asia are relatively well studied due to revisions and surveys of Chinese, Japanese and Korean theridiids (Zhu 1998; Yoshida 2009; Kim 2021).

Over 30 years ago, the first author collected in Kunashir Island (Kuril Islands) a large series, over 200 specimens, of brightly-coloured theridiids, which he failed to identify to genus level. Recent attempts involving SEM microscopy allow us to recognize that the species is related to Anelosimus Simon, 189, a large genus with 75 named species (WSC 2023). The genus has chiefly a Pantropical distribution with 12 species occurring in Asia, from Indonesia northward to Korea and Japan (Zhang et al. 2011: fig. 19). The specimens from Kunashir have the habitus, colouration, pattern and copulatory organs different from Anelosimus species occurring in Asia. Comparison of somatic characters and conformation of copulatory organs between species from Kunashir Island with genotype, $A$. eximius (Keyserling, 1884) known from the Neotropics led us to
the conclusion that the new species should be placed in a separate new genus. The goal of this paper is to provide detailed descriptions of the species and genus and to trace the position of the new genus among Theridiidae lineages.

## Material and methods

SEM images were taken on a Tescan Vega2 and a Tescan Vega3 scanning electron microscope in the Palaeontological Institute (Moscow), operated in high vacuum mode at accelerating voltages of $10-20 \mathrm{kV}$, using SE and BSE detectors. Specimens were gradually dehydrated in $100 \%$ ethanol, dried, and sput-ter-coated with gold-palladium. Light microscopy photographs were obtained using an Olympus Camedia E-520 camera attached to an Olympus SZX16 stereomicroscope in the Zoological Museum of the University of Turku. Digital images of different focal planes were stacked with Helicon Focus 8.1.1. All measurements are given in millimeters. The holotype will be deposited in the Zoological Museum of the Moscow State University (ZMMU) and paratypes will be shared between the ZMMU and the Zoological Institute (ZISP) in St. Petersburg. Abbreviations of leg segments: Fe - femur, Mt - metatarsus, Pa - patella, Ta - tarsus, Ti - tibia.

## Taxonomy

Class Arachnida Cuvier, 1812
Order Araneae Clerck, 1757
Family Theridiidae Sundevall, 1833

## Knoflachia gen. nov.

https://zoobank.org/B5704C12-015F-4408-A670-CE9CB44CA6CB

Etymology. Named after Barbara Knoflach (Innsbruck, Austria), an outstanding expert in theridiid taxonomy. Gender is feminine.

Type species. Knoflachia kurilensis sp. nov.
Diagnosis (comparison of the generotype). The new genus is most similar to Anelosimus Simon, 1891 in both copulatory organ characters (cymbial mesial margin with an incision; conductor with a groove for a distal portion of the spiral embolus) and somatic characters (male leg I extremely elongated, femur longer than carapace). It differs from the latter by: 1) carapace uniformly orange, abdomen uniformly black (vs carapace pale coloured with dark medial strip, abdomen with characteristic leaf-shaped pattern); 2) carapace cuticle rugose (vs smooth); 3) fovea transversal (vs rounded); 4) pars cephalica mildly sloping (vs not elevated, flat); 5) eye area not projected (vs projected); 6) male prosomal stridulatory ridges (PSR) separated into two patches (vs continuous); 7) female PSR absent (vs weak); 8) sternum equilateral triangle (vs elongated orthogonal); 9) labium fused with sternum (vs separated by distinct seam); 10) bristles of the tarsus IV comb flattened and straight (vs conical and hooked); 11) tarsus IV central claw subequal to laterals in length, thickness and shape (vs elongated, thin and S-shaped); 12) tarsal organ clearly proximal: 0.33-035 (vs slightly distal: $0.55-0.60$ to slightly proximal: 0.45 ); 13) abdominal stridulatory pick row (SPR) setal bases strongly elongated, keeled in male, and dome-
like in female (vs moderately elongated and rounded in both sexes); 14) male palpal tibia spoon-like, extremely enlarged, covers more than a half of the bulb (vs cyathiform, usual for theridiids); 15) male palpal tibia with only 2 retrolateral trichobothria (vs 2 retrolateral and 1 prolateral trichobothria); 16) cymbial mesial margin incision fold-like (vs semicircular notch); 17) the tegular apophysis ( Ta ) is a curved spine (vs not pointed); 18) conductor semimembraneous, its groove forming a sheath for a distal portion of the embolus (vs not membranous, its grove for embolus more shallow); 19) tip of embolus unmodified (vs. modified); 20) epigynal plate smooth (vs ridged); 20) copulatory openings located in two foveae separated by a septum (vs. foveae and septum absent); 21) each fovea with a spiral ridge (epigynal plate with transverse ridges); 22) copulatory ducts (Cd) coiled (vs. not coiled); and 23) receptacles dumbbell-shaped located inside loops of copulatory ducts (vs. oval, not surrounded by copulatory ducts).

Description. Small (1.8-2.85) brightly coloured (orange and black) with unmodified carapace and abdomen in both sexes (Fig. 1A-F) and modified leg I in male (Figs 1D, F, 2A, B).

Carapace - rounded, almost as wide as long, moderately high, pars cephalica slightly elevated, clypeus vertical; fovea shallow, transversal (Figs 2C, 3A, C, D); 8 medium-sized eyes, AME same as others (ca $1 / 3$ of clypeus height), lateral eyes adjacent, eye area not projected (Figs 2C, 3A, C); carapace pars stridens consist of two separated patches of regular parallel fine ridges in male (Fig. 4, B) indistinct under light microscope (Fig. 2C) and completely absent in female (Fig. 4C,); carapace cuticle rugose, setal bases elevated (Fig. 3C, D).

Sternum - almost equilateral triangle (Figs 1E, 3B); sternal cuticle rugose, setal bases elevated (Fig. 3E).

Labium - sub-rectangular, completely fused to sternum (Fig. 3B, E).
Chelicera - unmodified, without humps; promargin in both sexes with 3 teeth (2 basal fused) and pair of raised, fused setal sockets adjacent to fang base (Fig. 3E, F); cheliceral cuticle rugose, setal bases elevated (Fig. 3F).

Legs - Leg formula 1243 in males and 1423 in females, leg I of male extremely long and stout, Fe I can be almost 1.5 times longer than carapace length (Figs 1A-D, 2A) in large specimens; distal part of femur 1.5 times wider than proximal; metatarsus and tibia I in large specimens with 2 ventral rows of tubercles, surmounted by robust blunt suberect macrosetae (Figs 2A, B, 5A); bristles of tarsus IV theridiid comb flattened and straight, not hook-like (Fig. 5B, C); tarsus IV central claw subequal to laterals by length, thickness and shape in both sexes, and not distinguished from claws of other leg pairs (Fig. 6A-C); metatarsal trichobothria 1-1-1-0, bothria dome-like (Fig. 5F), usual for theridiids (Eskov and Marusik in prep.); tarsal organ clearly proximal (0.33-0.35), its opening large, more than setal sockets (Fig. 5D, E); leg cuticle imbricate (Fig. 5E).

Female palp - full-segmented; palpal tibia with 2 trichobothria; palpal claw simple, non-semipalmate, strongly dentated (Fig. 6D).

Abdomen - more or less globular; pedicel area with suprapedicillate dorsal (11 o'clock) proprioceptor setae (Figs 4F, 7A); stridulatory pick row (SPR) lateral of pedicel, regular, not curved, consist of few (<7) setae (Fig. 4D, F); SPR setal bases strongly elongated and keeled, tetragonal in profile, with setae vertically protruded from its middle portion in male (Fig. 4D, E), and rounded, domelike in female (Fig. 4F); epiandrous gland spigots arranged in a pair of distinct depressions (sockets), 3 spigots per socket (Fig. 5D); wide tracheal spiracle
near spinnerets, not straight, with pair of lobes (SI, Fig. 7C); colulus absent, but median pair of colular setae persists (Fig. 7C); ALS piriform field small, less than 20 spigots (Fig. 8A, B, E); PLS posterior AG spigot enlarged and flattened, subquadrate in profile (Fig. 8A, C); PMS with 3 spigots ( $1 \mathrm{mAP}+2 \mathrm{AC}$ ) in male (Fig. $8 \mathrm{E}, \mathrm{F}$ ) and 4 spigots ( $1 \mathrm{mAP}+2 \mathrm{AC}+1 \mathrm{CY}$ ) in female (Fig. 8A, E); abdominal cuticle fingerprint (Fig. 7A), booklung cuticle smooth.

Male palp - patella short, almost as wide as long, 2.4 times shorter than tibia; tibia spoon-like, extremely enlarged, ca $2 / 3$ of cymbial length, covers more than half of proximal part of bulb (Figs 9A, 10A), with 2 retrolateral trichobothria (Fig. 10D) and with several setae on its inner surface (probably artifact) (Fig. 11A) and; cymbium 1.9 times longer than wide, with round proximal part and finger like tip slightly bent retrolaterally; cymbial mesial margin distally with small bulge (Sb) (when observed with light microscope: Fig. 9A-C), which is dissected longitudinally by fold-like excavation (when observed with SEM: Figs 10B, C, 11D); cymbial ectal margin distally with groove-like cymbial hood (Ch) (Fig. 11D). Bulb as long as wide, with relatively small tegulum (Te), tegular apophysis (Ta) appears as simple curved, weakly sclerotized spine (Figs 9A, 10A, B, 11B, D); elongated hyaline conductor (Co) with groove serving as sheath for distal portion embolus (Fig. 10B, C); embolus filamentous coiled forming loop ca. $400^{\circ}$, (Fig. 11B); radix (Ra) and median apophysis (Ma) (we are not sure about homology) in unexpanded palp completely hidden by enlarged retroventral part of tibia (Figs 10A, 11C); median apophysis (?) with 2 arms: large spine like posterior ( Mp ) and small prolateral ( Pm ).

Epigyne - as seen by light microscope (Fig. 9D, E): epigynal plate about as long as wide, weakly sclerotized, with pair of round membranous parts (Rm) separated by thin septum; endogyne with long coiled weakly sclerotized copulatory ducts (Cd) and dumbbell-shaped receptacles (Re) standing perpendicular to epigynal plate behind Rm. As seen by SEM (Fig. 7A, B): epigyne with kind of foveae, well delimited by latero-posterior rim (Lp) and septum (Sp). Rim and septum forming guide groove ( Gg ) for embolus, anteriorly from septum Gg shallower, Gg forms 2 coils (about $720^{\circ}$ ) and terminates in copulatory opening (Oc).

Composition and distribution. Only the type species, $K$. kurilensis sp. nov., known only from the type locality (South Kurile islands, Kunashir Island: Fig. 12). The future records of this genus are surely anticipated in other Far East regions such as Hokkaido.

## Knoflachia kurilensis sp. nov.

https://zoobank.org/0272E07A-7614-436B-8FFA-EFFDFF521EB4
Figs 1-12
Etymology. Named after the type locality, Kuril Islands.
 (ZMMU \& ZISP) with label "[KU-123] KUNASHIR Isl., CW part, S shore of Lagunnoye Lake, $44^{\circ} 03^{\prime} 05^{\prime \prime} \mathrm{N}, 145^{\circ} 45^{\prime} \mathrm{E}$, sweeping along road, mostly alder bushes, 24.09.1997 Yu. M. Marusik".

Diagnosis. Same as for the genus. Well differs from other Theridiidae occurring in East Asia by colouration (Fig. 1), epigyne with septum (Fig. 9D) and male palp with strongly enlarged tibia covering half of the bulb (Fig. 9A-C).


Figure 1. General appearance of Knoflachia kurilensis sp. nov. A, B female C, F male A, F dorsal B-D lateral E ventral C, D showing the size difference of males. Scale bars: $0.5 \mathrm{~mm}(\mathbf{A}-\mathbf{D}, \mathbf{F}) ; 0.2 \mathrm{~mm}(\mathbf{E})$.


Figure 2. Somatic characters of Knoflachia kurilensis sp. nov. A part of male tibial, showing modified ventral seta B whole male leg I C male prosoma, dorsal $\mathbf{D}$ posterior part of the female abdomen, ventral, cellular setae indistinct. Scale bars: 0.2 mm .


Figure 3. Prosoma of Knoflachia kurilensis sp. nov. A male carapace and legs, lateral view B female sternum C female carapace, dorsal view $\mathbf{D}$ lateral margin of male carapace $\mathbf{E}$ female labium $\mathbf{F}$ cheliceral promargin of female (note fused setal socket adjacent to fang base).

Description. Male (holotype). Total length 2.4. Carapace 1.38 long, 1.08 wide; abdomen 1.45 long, 1.35 wide. Prosoma, including legs orange-reddish, legs I as dark as carapace, sternum, mouthparts, and legs II-IV lighter. Abdomen uniformly dark dorsally, venter with lighter booklung covers and area near petiolus. Palp and leg lengths as per Table 1.

Table 1. Palp and leg lengths of the male holotype.

| $\sigma^{\pi}$ | Fe | Pa | Ti | Mt | Ta | Total |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
| Palp | 0.5 | 0.17 | 0.3 | - | 0.43 | 1.4 |
| I | 1.75 | 0.65 | 1.38 | 1.13 | 0.6 | 5.51 |
| II | 1.25 | 0.55 | 0.85 | 0.88 | 0.48 | 4.01 |
| III | 0.8 | 0.33 | 0.48 | 0.58 | 0.4 | 2.59 |
| IV | 0.95 | 0.38 | 0.55 | 0.75 | 0.48 | 3.11 |



Figure 4. Prosoma-abdomen stridulatory mechanism in Knoflachia kurilensis sp. nov. A posterior margin of male carapace, prosomal stridulatory ridges B the same, enlarged C posterior margin of female carapace (note absence of PSR) D male abdominal stridulatory pick row $\mathbf{E}$ the same, enlarged $\mathbf{F}$ female abdominal stridulatory pick row (note dome-like setal bases of SPR, the same as surrounding setal bases). Abbreviations: PSR - prosomal (carapace) stridulatory ridges; SPR - stridulatory pick row.


Figure 5. Knoflachia kurilensis sp. nov.: leg setae, tarsal organ and trichobothria $\mathbf{A}$ ventral macrosetae of male metatarsus I B tarsus IV comb of female $\mathbf{C}$ same, enlarged $\mathbf{D}$ tarsal organ of female leg II $\mathbf{E}$ same, enlarged $\mathbf{F}$ trichobothrial bases of male palpal tibia.

Palp - see genus description.
Small male. Total length 2.13. Carapace 1.0 long, leg I 4.26 (1.38. 0.5, 1.0, $0.88,0.5)$. Pattern as in holotype.

Variations. Total length varies from 1.9 to 2.5. At least one male has leg colouration like in females.


Figure 6. Knoflachia kurilensis sp. nov.: tarsal claws A tarsus IV of male B tarsus IV of female C tarsus II of female D female palpal claw.


Figure 7. Abdomen of Knoflachia kurilensis sp. nov.: female (A-C) and male (D) A epigastric region of female $\mathbf{B}$ epigyne C colular setae (arrow) and tracheal spiracle D socketed epiandrous spigots. Scale bars: 0.1 mm if not otherwise indicated. Abbreviations: $B L$ - booklung covers; $G g$ - guiding groove; $L p$ - latero-posterior rim of epigyne; Oc - copulatory opening; Se - septum; $S I$ - lobe of spiracle opening.


Figure 8. Spinnerets of Knoflachia kurilensis sp. nov. A female spinnerets B female ALS C female PLS and PMS D female PMS E male spinnerets F male PLS and PMS (note absence of CY). Abbreviations: AC - aciniform gland spigot(s); AG - aggregate gland spigot(s); ALS - anterior lateral spinneret; $C Y$ - cylindrical gland spigot(s); mAP - minor ampullate gland spigot(s); MAP - major ampullate gland spigot(s); Nu - nubbin; PI - piriform gland spigot(s); PLS - posterior lateral spinneret; $P M S$ - posterior median spinneret.

Female (allotype). Total length 2.75. Carapace 1.08 long, 1.0 wide. Carapace, sternum, mouth parts as in male. Legs I-II with dark tibiae, metatarsi and tarsi, legs III-IV with dark metatarsi and tarsi. Palps with dark tibiae and tarsi. Palp and leg lengths as per Table 2.

Table 2. Palp and leg lengths for female allotype.

| + | Fe | Pa | Ti | Mt | Ta | Total |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
| Palp | 0.39 | 0.16 | 0.21 | - | 0.34 | 1.1 |
| I | 1.24 | 0.41 | 0.87 | 0.8 | 0.46 | 3.78 |
| II | 0.99 | 0.41 | 0.57 | 0.57 | 0.39 | 2.93 |
| III | 0.66 | 0.27 | 0.39 | 0.43 | 0.34 | 2.09 |
| IV | 1.0 | 0.37 | 0.6 | 0.64 | 0.4 | 3.01 |



Figure 9. Male palp (A-G) and epigyne ( $\mathbf{D}-\mathbf{E}$ ) of Knoflachia kurilensis sp. nov. A-C ventral, prolateral and dorsal $\mathbf{D}$ intact, ventral E macerated, dorsal. Scale bars: 0.2 mm . Abbreviations: Cd - copulatory duct; Co - conductor; Em - embolus; $R e$ - receptacle; $R m$ - round part of epigyne; $S b$ - cymbial small bulge; $S e$ - septum; $T a$ - tegular apophysis.

Variations - Total length varies from 2.25 to 2.85 , colour of abdomen in alcohol from almost black to grey.

Natural history. All specimens were collected in one day by sweeping bushes. The great number of specimens collected in a few hours most likely indi-


Figure 10. Male palp of Knoflachia kurilensis sp. nov. A left palp, ventral view B left palp, ventro-mesial view $\mathbf{C}$ the same, enlarged (note grooved conductor, forming a sheath for a distal portion of embolus, and fold-like excavation on cymbial mesial margin) D tibia of right palp, dorso-ectal view. Scale bars: 0.1 mm . Abbreviations: $\mathbf{C o}$ - conductor; Em - embolus; $S b$ - cymbial small bulge; $T a$ - tegular apophysis; $T e$ - tegulum.
cates that they may form colonies, like Anelosimus. Some specimens look like penultimate. The presence of only one subadult specimen indicates that the species is monovoltine.

Distribution. Known from the single locality in Kunashir Island (Fig. 12).
Male polymorphism. Males vary in size and relative length of the first leg (cf. Fig. 1C and 1D). Larger males have a relatively longer femur I (femur I/carapace length ratio ca. 1.45 in large male and 1.33 in small). Larger males have a distinct tibial and metatarsal macrosetae on legs I and II (setae standing on tegumental stump-like outgrowth Figs 2A, B, 5A). Size polymorphism is known in several groups of Theridiidae (e.g., Parasteatoda tepidariorum (C.L. Koch, 1841), Steatoda triangulosa (Walckenaer, 1802) [Nentwig et al. 2023]). Large-size polymorphism was documented in Enoplognatha monstrabilis Marusik \& Logunov, 2002 (see Marusik and Logunov 2002), a species with similarly modified setae on leg I and occurring in Siberia. The carapace of the largest male is 1.7 times longer than in the smallest one. The same type of modified setae is documented in the New World Anelosimus studiosus (Hentz, 1850) (see Agnarsson 2004) and in the East Mediterranean Enoplognatha parathoracica Levy \& Amitai, 1981 and E. quadripunctata Simon, 1884 (see Huseynov and Marusik 2008).


Figure 11. Left male palp with removed tibia of Knoflachia kurilensis sp. nov. A separated tibia, inner surface B bulb and cymbium, ventral C same, proximal portion D same, distal portion (note ectal cymbial hood and mesial cymbial excavation). Scale bar: 0.1 mm if not otherwise indicated. Abbreviations: Ch - cymbial hood; Co - conductor; Em - embolus; $M a$ - median apophysis; $M p$ - posterior part of $M a$; $P m$ - prolateral part of $M a$; $R a$ - radix; $S b$ - cymbial small bulge; $T a-$ tegular apophysis; $T e$ - tegulum.


Figure 12. Collecting locality of Knoflachia kurilensis sp. nov. A Kunashir Island B Kurile islands Collecting locality.

## Discussion

The following characters of Knoflachia gen. nov. should be discussed in more detail, in comparison with other theridiid genera. In the naming (and the numbering) of the theridiid clades we are following Agnarsson's (2004: fig. 105) cladogram.
(1) Prosoma-abdomen stridulatory mechanism. "Typically, pairs of elevated setal bases, here called stridulatory picks (SP; the term plectrum refers to such stridulatory parts in general) bordering [as a row, SPR] the pedicel on the abdomen interact with ridges on the posterior margin of the carapace (pars stridens)" (Agnarsson 2004: char. 128). This mechanism is characteristic of theridiid spiders, and the presence of SPR was stated as a synapomorphy of the theridiids minus hadrotarsines ('SPR clade, clade 50'). "Although commonly present in both sexes, both the picks [...] and the ridges [...], are usually much reduced in the female, and the stridulatory role in male courtship shown for a number of species [...] can thus be presumed to be universal" (Agnarsson 2004: p. 474). The sexual dimorphism of this character in Knoflachia gen. nov. is extremely strong: SPR setal bases sharply differ in male (longitudinal and strongly keeled: Fig. 4D, E) and in female (dome-shaped, as well as other setal bases: Fig. 4F), while a ridged prosomal pars stridens is present in the male (Fig. 4A, B) and completely absent in the female (Fig. 4C). As regards the male prosomal stridulatory ridges (PSR), the two characters with two modalities may be distinguished here: (1) pars stridens separated into two patches, or continuous (Agnarsson 2004, char. 129); (2) ridges clear and deep, or fine, sometimes irregular (Agnarsson 2004, char. 128). Accordingly, every theridiid genus may be nested by its pars stridens parameters into the four-cell matrix: (A) clear-ridged / continuous; (B) clear-ridged / two-patches-separate; (C) fine-ridged / continuous; (D) fine-ridged / two-patches-separate, as follows: (A) clear-ridged / continuous: Crustulina Menge, 1868, Helvibis Keyserling, 1884, Pholcomma Thorell, 1869, Robertus Pickard-Cambridge, 1879, Tidarren Chamberlin \& Ivie, 1934 (see Agnarsson 2004: figs 42G, 49F, 60F, 66G, 87B, respectively). (B) clear-ridged / two-patches-separate: Argyrodes Simon, 1864, Coleosoma O. Pickard-Cambridge, 1882, Enoplognatha Pavesi, 1880, Neospintharus Exline, 1950, Rhomphaea L. Koch, 1872, Steatoda Sundevall, 1833 (see Agnarsson 2004: figs 32A, 41F. 44H, 57A, 64E, 71F, respectively). (C) fine-ridged / continuous: Anelosimus Simon, 1891, Chrysso O. Pickard-Cambridge, 1882, Carniella Thaler \& Steinberger, 1988, Episinus Walckenaer, 1809, Nesticodes Archer, 1950, Selkirkiella Berland, 1924, Theridion Walckenaer, 1805 (see Agnarsson 2004: figs 21D, 40F, 36G, 47B, 58D, 67G, 75D, respectively). (D) fine-ridged / two-patches-separate: Knoflachia gen. nov. (Fig. 4A, B) only, as it is known. Besides, tetragonal in profile SPR setal bases vertically protruded from its medial portion setae seem to be unique in Knoflachia gen. nov. (Fig. 4D, E) (i.e., neither ectally nor mesially directed: Agnarsson 2004, chars 153, 156, 157).
(2) Size of tarsal organ: "The typical araneoid tarsal organ (all legs and palpi) is about the size of a macrosetal or trichobothrial socket, with the opening clearly smaller than the width of adjacent setae [...] Some theridiids (clade 46) have enlarged tarsal organs in which the circumference is equal to
or larger than adjacent setal sockets, and the opening is as large or larger than those of setal or trichobothrial sockets" (Agnarsson 2004: char. 198). The tarsal organ opening of Knoflachia gen. nov. is clearly larger than those of the setal sockets (Fig. 5E), and it belongs to the 'enlarged TO clade (clade 46)', uniting all the non-hadrotarsin and non-latrodectin theridiids.
(3) Tarsus IV central claw vs. laterals. "The middle tarsal claw of all argyrodines is notably long in both sexes [...]. In most male theridiids the central claw is relatively longer than in females and here the central claw longer than laterals is a synapomorphy for clade 33" (Agnarsson 2004: char. 199). This character (i.e., notably elongated and S-shaped middle claw of the tarsus IV), provided the name to the 'elongated central claw clade (clade 33)', united all the 'distal theridiids': argyrodins (e.g., Argyrodes), 'Anelosimus clade' (e.g., Anelosimus) and Theridiinae (e.g., Theridion) (see Agnarsson 2004: figs 32H, 21C and 76C, respectively). Surprisingly, the middle tarsal claws in Knoflachia gen. nov. are unmodified: subequal to laterals in both sexes and on all leg pairs (Fig. 6A-C). However, it seems rather a reversal, unique for the 'distal theridiids' (the clade, supported, e.g., synapomorphy (4) - see below).
(4) Setal sockets on cheliceral promargin. A pair of raised, fused setal sockets on the cheliceral promargin adjacent to the fang base (Fig. 3E, F) seems an important character, overlooked (or at least underestimated) by earlier workers. Such fused sockets are present in all the 'distal theridiids': Argyrodinae (e.g., Argyrodes), 'Anelosimus clade' (e.g., Anelosimus) and Theridiinae (e.g., Theridion) (see Agnarsson 2004: figs 33G, 22E and 80C, respectively), and absent in all the 'basal theridiids': Hadrotarsinae (Dipoena Thorell, 1869 and Euryopis Menge, 1868), Latrodectinae (Latrodectus Walckenaer, 1805 and Steatoda) and Spintharinae (Spintharus Hentz, 1850 and Thwaitesia O. Pickard-Cambridge, 1881) (see Agnarsson 2004: figs 5B, 8E, 55E, 72E, 70E and 84D, respectively). As regards Pholcommatinae, with its intermediate position in Agnarsson's (2004: fig. 105) cladogram, it incorporates the genera with fused setal sockets (e.g., Cerocida Simon, 1894), as well as with unfused ones (e.g., Enoplognatha) (see Agnarsson 2004: figs 37D and 45B, respectively). So, the fused setal sockets on the promargin (as in Knoflachia gen. nov.) are an unambiguous synapomorphy of the 'distal theridiids', and autapomorphies of several pholcommatin genera. On the one hand, it is important support of the 'elongated central claw clade (clade 33)' by Agnarsson (2004: 462). On the other hand, it may be an additional argument on the heterogenity of Pholcommatinae ("The composition of this subfamily is uncertain": Agnarsson 2004: p. 468). For instance, the well-supported clade uniting Carniella, Theonoe, Robertus and Pholcomma (Knoflach 1996; Agnarsson 2004: 463) is sharply distinguished by a trichobothrial base morphology not only from all the rest of the pholcommatins, but from all the theridiids (Eskov and Marusik in prep.).
(5) Colulus and colular setae. "The colulus is generally considered homologous to the cribellum [...]. It has been lost frequently in araneoids. Here the loss of a colulus is synapomorphic for Anelosimus plus theridiines (clade 25, termed the lost colulus clade)" (Agnarsson 2004: char. 172), and later: "The colulus usually bears some setae, including a distinctive median pair of long setae [...]. Even when the colulus is absent this pair of setae often
persists [...]. These setae are lost distally in the lost colulus clade, a theridiine synapomorphy" (Agnarsson 2004: char. 174). In Knoflachia gen. nov. the colulus is lost, but a median pair of colular setae persists (Fig. 7C), as well as in, for example, Anelosimus (see Agnarsson 2004: fig. 16E). So, it belongs to the 'lost colulus clade (clade 25)' of the 'distal theridiids', but not to its terminal branch, the 'lost colular setae clade (clade 15)', that is, Theridiinae. Besides the absence of any trace of a colulus, this clade is unambiguously defined by a reduction of the trichobothria number on the male palpal tibia to one and the epiandrous gland spigots spread over the epiandral plate (Agnarsson 2004: p. 470), and Knoflachia gen. nov. also lacks all of the listed synapomorphies (see below).
(6) Male palpal tibia trichobothria. "The number and distribution of trichobothria on the male palpi seem quite informative phylogenetically [...]. Synotaxus and theridioids primitively have two retrolateral and one prolateral trichobothria [...] Reduction to a single retrolateral trichobothria [...] (or uniquely in Carniella [...] to none) occurred at least five times in theridiids, but although homoplasious [...], in most instances the reduction is informative [...]. The same applies to reduction in prolateral trichobothria" (Agnarsson 2004: char. 18). In the 'distal theridiids' the abovementioned plesiomorphous condition ' $2 \mathrm{rl}+1 \mathrm{pl}$ ' is conserved in the Argyrodinae (clade 32) and in the 'Anelosimus clade (clade 24)' (see Agnarsson 2004: figs 31G, 24C, respectively). A single retrolateral trichobothria in Theridiinae (clade 15) (e.g., Theridula Emerton, 1882, Thymoites Keyserling, 1884 and Tidarren Chamberlin \& Ivie, 1934 - see Agnarsson 2004: figs 81A, 85B, 86B, respectively) is an unambiguous synapomorphy of this clade (Agnarsson 2004: 470). Knoflachia gen. nov. possesses two retrolateral and no prolateral trichobothria (Fig. 10D), and this combination seems unique among the 'distal theridiids'. On the one hand, it is plesiomorphous relative to theridiins (clade 15), with their single retrolateral trichobothria. On the other hand, it is relatively apomorphous 'Anelosimus clade (clade 24)', where a prolateral trichobothria persists.
(7) Epiandrous spigots. "In many orbicularians the epiandrous gland spigots are arranged in irregular transverse rows along the male genital plate [...]. In, others [...], and many basal theridiids, however, the spigots are tightly arranged in two patches, usually in clear depressed sockets [...]. Here, [....] socketed epiandrous spigots are interpreted as synapomorphic for theridiids, with three reversals. A reversal to spigots in rows defines latrodectines [...]; it is autapomorphic in Ariamnes [...] and is a synapomorphy for Theridiinae" (Agnarsson 2004: char. 169). As regards the epiandrous spigot pair number, Agnarsson (2004: char. 170) recognized the trend of their reduction, from the plesiomorphic condition ( $>10$ spigots) to the apomorphic condition (<8 spigots). The final point of this trend is the reduction of the spigot number to $2-3$. It is quite usual among the 'spigots in rows' theridiids: Latrodectus, Ariamnes, Thymoites, Chrysso, some Ameridion Wunderlich, 1995 and Thwaitesia (see Agnarsson 2004: figs 55F, 34G, 85E, 40A, Figs 14F, 83F, respectively), but very rare among 'socketed spigots' theridiids: Faiditus, some Anelosimus (see Agnarsson 2004: figs 48G, 28G) and Glebych Eskov \& Marusik, 2021 (see Eskov and Marusik 2021: fig. 4F, G). So, the 'socketed spigots' of Knoflachia gen. nov. (Fig. 7D) is a
plesiomorphic condition for the 'distal theridiids'. On the other hand, the reduction of the spigot number up to 3 is an autapomorphy of this genus.
(8) Labium-sternum connection. "A distinct seam is sometimes present between the sternum and the labium. Although much used in keys and taxonomy [...], the presence or absence of a seam is extremely homoplasious within theridiids [...] and thus of limited usefulness at higher systematic levels. Here a fused connection is, for example, an ambiguous synapomorphy of Theridiinae [...] but is certainly not characteristic of the clade" (Agnarsson 2004: char. 135). However, the fused labium-sternum connection in Knoflachia gen. nov. (Figs 1E, 3B, E) is an informative autapomorphy, distinguishing it from such probable relatives as Anelosimus and Selkirkiella (Agnarsson 2004: figs 27C, 68A, respectively).
(9) Leg I of male. The extremely elongated male leg I in Anelosimus (see Vanuytven 2021: figs B.16, B.18) is provided with a unique thickened ventral macrosetae on metatarsus I (Agnarsson 2004: char. 188, fig. 26F). The same features found in Knoflachia gen. nov. (Figs 2A, B, 5A) may be interpreted as a synapomorphy of these genera in limits of the 'Anelosimus clade (clade 24)'.
(10) Cymbial mesial margin. "Many Anelosimus have a distinct incision on the cymbial mesial margin [...] and on this cladogram the feature is a synapomorphy of clade 22 [Anelosimus exclusive of $A$. vittatus and $A$. pulchellus]" (Agnarsson 2004: char. 25). The cymbial mesial margin of Knoflachia gen. nov. is modified too, but its incision is fold-like (Figs 10B, C, 11D), unlike the Anelosimus notch (see Agnarsson 2004: figs 17D, 20A).
(11) Tarsus IV ventral setal comb. "Tarsal comb bristle morphology varies greatly [...] Various theridiids have simple straight bristles [...], while in others the serrations form curved hooks" (Agnarsson 2004: char. 195). The straight and flattened, with clear 'theridiid grooves', comb bristles of Knoflachia gen. nov. (Fig. 5B, C) clearly differ from the hooked and conical bristles of Anelosimus species (see Agnarsson 2004: figs 19E, 23E) and are similar rather to those of Parasteatoda wau (Levi, Lubin \& Robinson, 1982) (see Agnarsson 2004: fig. 12F, as Achaearanea w.).
(12) Cuticle. "Theridiid taxonomic work often refers to carapace (and/or sternum) 'rugosity'. However, 'rugosity' differs between taxa [...]. Although autapomorphic here, these conditions will probably be generic synapomorphies. Steatoda and Crustulina, synapomorphically, have rugosity caused by the elevation of setal bases [...]. Most theridiid carapaces are relatively smooth" (Agnarsson 2004: char. 123); "As on the carapace, the setal bases of the sternum of Steatoda and Crustulina are elevated" (Agnarsson 2004: char. 139). Knoflachia gen. nov. possess, undoubtedly convergently, the carapace/sternum 'rugosity', caused by the elevation of setal bases (Fig. 3B-E), of the same type as mentioned above for Steatoda and Crustulina (see Agnarsson 2004: fig. 71D-F), whereas all members of the 'Anelosimus clade (clade 24)' possess a smooth cuticle (see Agnarsson 2004: figs 19F, 21B).
(13) Tarsal organ position. A few theridiids clearly have a proximal tarsal organ, for example, 0.3 in Glebych (Eskov \& Marusik, 2021: fig. 4D). The majority of theridiids have clearly distal TO (>0.6); in Anelosimus TO position varying from 'slightly distal ( $0.55-0.60$ ) on tarsi I and II' to "slightly proximal (0.45) on IV' (Agnarsson et al. 2015: 39).

So, clearly a proximal TO in Knoflachia gen. nov. (0.33-035) (Fig. 5D) is a remarkable character of this genus.

## Conclusions

The position of Knoflachia gen. nov. in Agnarsson's (2004: fig. 105) cladogram of the family can be clarified as follows:

The presence of a prosoma-abdomen stridulatory mechanism (1) and a large opening of the tarsal organ (2) places Knoflachia gen. nov. in the 'SPR clade (clade 50)' and the 'enlarged TO clade (clade 46)', respectively, uniting all non-hadrotarsin and non-latrodectin theridiids.

Despite the unmodified tarsal claws (3), Knoflachia gen. nov. should be nested in the 'elongated central claw clade (clade 33)', uniting all 'distal theridiids', due to the presence of a pair of fused setal sockets on the cheliceral promargin (4), a newly found synapomorphy of this clade.

The position of Knoflachia gen. nov. within the 'distal theridiids' is determined by its colular characters: colulus is lost, but a median pair of colular setae persists (5). So, it belongs to the 'lost colulus clade (clade 25)', uniting all the non-argyrodin 'distal theridiids', but does not belong to its terminal branch, the 'lost colular setae clade (clade 15)', i.e., Theridiinae.

The non-inclusion of Knoflachia gen. nov. to the 'lost colular setae clade (clade 15)' is supported by the lack of all theridiin synapomorphies: its colular setae persists (5), the number of male palpal tibia trichobothria is not reduced to a single one (6), and its epiandrous spigots are still socketed, not spread over the epiandral plate (7).

In summary, Knoflachia gen. nov. belongs neither to Argyrodine (i.e., the basal clade of 'distal theridiids'), nor to Theridiinae (i.e., the terminal clade of 'distal theridiids'). It should nest within the remaining 'distal theridiid' group, that is, 'Anelosimus clade (clade 24)', which was not attributed by Agnarsson (2004: p. 470) to conventional subfamilies due to its probable paraphyly.

Within the 'Anelosimus clade', Knoflachia gen. nov. possess several autapomorphies: reduction of the male palpal trichobothria up to 2 retrolateral, vs. 2 retrolateral and 1 prolateral (6), reduction of the epiandrous spigots to 3 per socket (7), and the labium fused to the sternum (8). It seems most close to the genus Anelosimus by the male leg I modification (9) and the cymbial mesial margin incision (10); however, it is distinguished by numerous characters, for example, prosomal stridulatory ridges separated into two patches in the male and completely lacking in the female (1), straight and flattened bristles of the tarsus IV comb (11), etc.

Besides, the rugose carapace cuticle (12) and the clearly proximal tarsal organ (13) of Knoflachia gen. nov. seem unique among the 'distal theridiids'.

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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: KE and YM. Material collection: YM. Making digital illustrations and map: YM. SEM images: KE. Arrangement of the illustrations into the plates: YM. Writing - original draft: $K Y, Y M$.

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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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# Two new species of Orchestina Simon, 1882 (Araneae, Oonopidae) from Cangshan Mountain, Yunnan, China 

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#### Abstract

Two new species of Orchestina, 0 . dapojing Tong \& Yang, sp. nov. ( ( $\uparrow$ ) and 0 . hyperofrontata Tong \& Yang, sp. nov. (§) are described from Yunnan, China. Descriptions, diagnoses and photographs of habitus and copulatory organs are provided.


Key words: Asia, goblin spiders, morphology, Orchestininae, taxonomy

## Introduction

Orchestina Simon, 1882 is a species-rich genus of oonopid spider that currently contains 164 extant species (WSC 2024). It has an almost global distribution and occurs in the Northern Hemisphere in the region south of $45^{\circ} \mathrm{N}$ (Marusik et al. 2018). Currently, 19 species of this genus are known to occur in China (Tong and Li 2011; Liu et al. 2016, 2019; Wang et al. 2021; Lin et al. 2024; Song et al. 2024). Only two species, O. manicata Simon, 1893 and O. striata Simon, 1909, are known in adjacent Vietnam (WSC 2024).

Although the genus Orchestina was well known among arachnologists, there are no global revisions for this genus up to now. The most recent regional revisions on the genus include a description of 18 new species of the Afrotropical region (Henrard and Jocqué 2012) and 85 new species and six known species from the Americas (Izquierdo and Ramírez 2017). Phylogenetic relationships of the species were explored for African species, and two species groups (each with two subgroups) were recognized (Henrard and Jocqué 2012). Species groupings for East Asian or Chinese species have yet to be recognized.

While studying oonopid spiders collected from Cangshan Mountain, Yunnan Province, two new species of the genus Orchestina were recognized. It is the first time that this genus has been found in Yunnan. The present paper aims to provide detailed descriptions and illustrations of the two new species, O. dapojing Tong \& Yang, sp. nov. and 0 . hyperofrontata Tong \& Yang, sp. nov.

[^4]
## Material and methods

All the specimens used in this study were collected by pitfall trapping and later examined using a Leica M205C stereomicroscope. Details of body parts and measurements were studied under an Olympus BX51 compound microscope. Photos were made with a Canon EOS 750D zoom digital camera (18 megapixels) mounted on the Olympus compound microscope. Endogyne were cleared in lactic acid. All measurements in the text are expressed in millimeters. Terminology and taxonomic descriptions follow Henrard and Jocqué (2012) and Tong and Li (2011). All materials studied are deposited at Shenyang Normal University (SYNU) in Shenyang, China.

The following abbreviations are used in the text and figures: ALE = anterior lateral eyes; AUS = anterior uterine sclerite; Ex = dorsolateral extension; PLE = posterior lateral eyes; PME = posterior median eyes.

## Taxonomy

Family Oonopidae Simon, 1890

## Genus Orchestina Simon, 1882

Type species. Schoenobates pavesii Simon, 1873.
Remark. Orchestina is considered a senior synonym of Ferchestina Saaristo \& Marusik, 2004 (type F. storozhenkoi Saaristo \& Marusik, 2004) by Platnick et al. (2012: 37).

## Orchestina dapojing Tong \& Yang, sp. nov.

https://zoobank.org/B0FF2F6A-2D30-41B5-A664-902C7BD87328
Figs 1-3

Type material. Holotype đ (SYNU-764): China, Yunnan Prov., Dali Bai Autonomous Pref., Dali City, Cangshan Mt., Dapojing, pitfall trapping in forest, $25^{\circ} 34^{\prime} 17^{\prime \prime} \mathrm{N}, 100^{\circ} 08^{\prime} 15^{\prime \prime} \mathrm{E}, 2600 \mathrm{~m}, \mathrm{Z}$. Yang leg., 25/1/2010; Paratypes 1 q (SYNU-765), same data as holotype; 1 § (SYNU-766), Cangshan Mt., Jishejing, pitfall trapping in forest, $25^{\circ} 40^{\prime} 29^{\prime \prime} \mathrm{N}, 100^{\circ} 06^{\prime} 36^{\prime \prime} \mathrm{E}, 2600 \mathrm{~m}$, Z. Yang leg., 15/11/2008.

Diagnosis. The new species is similar to O. apiculata Liu, Xiao \& Xu, 2016 in the shape of the bulb and the long psembolus, but can be distinguished by the palpal tibia narrower than the bulb (Fig. 2A) vs. distinctly wider than the bulb in O. apiculata (Liu et al. 2016: fig. 2A, B), triangular labium (Fig. 2D) vs. sub-circular (Liu et al. 2016: figs 1E, 3H), and the tubular anterior uterine sclerite (AUS) (Fig. 3G, H) vs. broad and column-shaped (Liu et al. 2016: fig. 2C, D).

Description. Male (holotype). Body: habitus as in Fig. 1A, C, E; body length 1.33. Carapace (Fig. 1B): 0.74 long, 0.56 wide; yellow, oval in dorsal view, with net-shaped pattern, pars cephalica slightly elevated in lateral view, with rounded posterolateral corners. Eyes (Fig. 1B, F): well developed, nearly equal-sized; posterior eye row recurved from above. Clypeus (Fig. 1B, F): margin unmodified, curved downwards in front view, sloping forward in lateral view, high, ALE


Figure 1. Orchestina dapojing sp. nov., male holotype A, C, E habitus (dorsal, ventral and lateral views) B, D, F prosoma (dorsal, ventral and anterior views). Scale bars: $0.4 \mathrm{~mm}(\mathbf{A}-\mathbf{F})$.
separated from edge of carapace by their diameter or more. Sternum (Fig. 1D): with marginal band and median dark brown patches; setae sparse, needle-like, evenly scattered. Mouthparts (Figs 1D, F, 2D): chelicerae straight, anterior face unmodified; labium triangular, anterior margin not indented at middle, lateral margins slightly sclerotized, labium pattern darkly spotted but medially delimiting 2 pale, adjacent, oval areas; endites unmodified. Abdomen (Fig. 1A, C, E): 0.59 long; with gray net-like pattern; pedicel tube short, unmodified. Palp (Fig. 2A-C): tibia enlarged, length/width ratio $=1.41$, more than 2 times as wide


Figure 2. Orchestina dapojing sp. nov., male holotype A-C left palp (prolateral, dorsal and retrolateral views) D endites and labium, ventral view. Scale bars: $0.2 \mathrm{~mm}(\mathbf{A}-\mathbf{D})$.
as femur; bulb pear-shaped, strongly enlarged, about 1.5 times as wide as tibia; psembolus nearly as long as bulb, whip-like, bent inwards.

Female (SYNU-765): Same as male except as noted. Body: habitus as in Fig. 3A, C, E; body length 1.63. Carapace (Fig. 3B): 0.74 long, 0.57 wide. Abdomen: 0.89 long. Epigaster: without special external features. Endogyne (Fig. 3G, H): with medial tubular sclerite (AUS) extending anteriorly, then flipped posteriorly, ending near epigastric furrow; dorsolateral extension (Ex) interrupted anteriorly.


Figure 3. Orchestina dapojing sp. nov., female paratype A, C, E habitus (dorsal, ventral and lateral views) B, D, F prosoma (dorsal, ventral and anterior views) $\mathbf{G}$ endogyne, dorsal view $\mathbf{H}$ endogyne, lateral view. Abbreviations: AUS = anterior uterine sclerite; $\mathrm{Ex}=$ dorsolateral extension. Scale bars: $0.4 \mathrm{~mm}(\mathbf{A}-\mathbf{F}) ; 0.1 \mathrm{~mm}(\mathbf{G}, \mathbf{H})$.

Affinities. The new species is similar to 0 . apiculata and 0 . clavigera Henrard \& Jocqué, 2012 (from Kenya). Based on the long, whip-like psembolus, the tubular anterior uterine sclerite (AUS), and the weakly sclerotized endites, the new species should be classified in the macrofoliata-subgroup of the macrofo-liata-group of Henrard and Jocqué (2012).

Etymology. The specific name is a noun in apposition taken from the type locality.

Distribution. Known only from the type locality, Yunnan Province, China.

## Orchestina hyperofrontata Tong \& Yang, sp. nov.

https://zoobank.org/C9704B06-8A4A-4647-9EF2-ED532C9D2271
Figs 4, 5

Type material. Holotype đo (SYNU-762): China, Yunnan Prov., Dali Bai Autonomous Pref., Dali City, Cangshan Mt., Jishejing, pitfall trapping in forest, $25^{\circ} 40^{\prime} 29 " N, 100^{\circ} 06^{\prime} 36 " E, 2600 \mathrm{~m}, \mathrm{Z}$. Yang leg., 15/11/2008; Paratype: 1 ठ (SYNU-763), Cangshan Mt., post-fire forest in 1999, pitfall trapping, $25^{\circ} 38^{\prime} 30^{\prime \prime} \mathrm{N}$, $100^{\circ} 08^{\prime} 04^{\prime \prime} \mathrm{E}, \mathrm{S}$. Huang \& Y. Zhang leg., 25/4/2009.

Diagnosis. The new species can be distinguished from all other congeneric species by the strongly elevated clypeus (Fig. 4A, B, E, F) and the prong on the distal part of the chelicerae (Fig. 5F), vs. lacking in congeners.

Description. Male (holotype). Body: habitus as in Fig. 4A, C, E; body length 1.31. Carapace (Fig. 4B, E): 0.74 long, 0.61 wide; yellow, oval in dorsal view; pars cephalica strongly sloped in lateral view, with rounded posterolateral corners. Eyes (Fig. 4B): well developed, nearly equal-sized; posterior eye row straight from above; ALE far away from PME. Clypeus (Fig. 4B, E, F): strongly elevated, curved downwards in front view, sloping forward in lateral view, dor-so-apically with hum elevating beyond eyes and provided with dense group of pores. Sternum (Fig. 4D): with brown patches, anteriorly with a thin median sclerotized bar connected to the labium base (Y-shaped pattern in Fig. 5D). Mouthparts (Figs 4D, 5D-H): chelicerae basally with small conical boss and distally with well-developed prong partially covering base of fang; labium rounded, lateral and basal margins sclerotized, anterior margin not indented at middle; endites unsclerotized, without serrula. Abdomen (Fig. 4A, C, E): 0.57 long; with gray net-shaped pattern; pedicel tube short, unmodified. Palp (Fig. 5A-C): tibia enlarged, length/width ratio $=1.65$, about 2 times as wide as femur; bulb globose, about 1.5 times as wide as palpal tibia, seminal duct slightly curved and partly visible through cuticle; psembolus about as long as 1/2 bulb, gradually narrowed.

Female. Unknown.
Affinities. The new species 0 . hyperofrontata sp . nov. is similar to 0 . utahana Chamberlin \& Ivie, 1935 and O. obscura Chamberlin \& Ivie, 1942 from the Nearctic in the general shape of the male palp and the presence of prongs on cheliceral promargin (Fig. 5A-C, F; Izquierdo and Ramírez 2017: figs 5B, 15A-C, G-I). Meanwhile, the new species is also similar to 0 . kasuku Henrard \& Jocqué, 2012 (from West Africa) in the eye pattern (ALE and PLE not touching


Figure 4. Orchestina hyperofrontata sp. nov., male holotype A, C, Ehabitus (dorsal, ventral and lateral views) B, D, F prosoma (dorsal, ventral and anterior views), arrows show strongly elevated clypeus. Scale bars: $0.4 \mathrm{~mm}(\mathbf{A}-\mathbf{F})$.

PME), the endites without serrula, and the shape of the bulb (Figs 4B, 5A-D; Henrard and Jocqué 2012: figs 378-416). It is reasonable to place the new species 0 . hyperofrontata sp . nov. in the macrofoliata-subgroup of the macrofo-liata-group of Henrard and Jocqué (2012).

Etymology. The specific name is derived from the Greek, hypero, meaning beyond, combined with frons, referring to the strongly elevated clypeus.

Distribution. Known only from the type locality, Yunnan Province, China.


Figure 5. Orchestina hyperofrontata sp. nov., male holotype A-C left palp (prolateral, dorsal and retrolateral views) D endites and labium, ventral view, black arrow shows the Y-shaped sclerotized pattern E, F chelicerae, anterior view, black arrow shows the prong G, H chelicerae, lateral view, white arrow shows small boss. Scale bars: $0.1 \mathrm{~mm}(\mathbf{A}-\mathbf{H})$.

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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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# Caribbean Amphipoda (Crustacea) of Panama. Part II: parvorder Hadziidira 

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#### Abstract

Amphipods in the parvorder Hadziidira are typically associated with algae, sponges, or coral rubble. Members of the parvorder have a gnathopod 2 that is stouter than gnathopod 1, a pair of dorsal robust setae on urosomite 2, and a basofacial robust seta on the uropod 1 peduncle. Within the parvorder, six families are documented from Bocas del Toro, Panama, represented by 26 species. This research documents range extensions for all 26 species and an identification key to the species of Caribbean Hadziidira of Panama is provided.

\section*{Resumen}

Los anfípodos del parvorden Hadziidira suelen estar asociados con algas, esponjas o escombros de coral. Los miembros del parvorden tienen un gnatópodo 2 que es más robusto que el gnatópodo 1 , un par de setas dorsales robustas en el urosomita 2 y una seta basofacial robusta en el pedúnculo del urópodo 1. Dentro del parvorden se documentan seis familias de Bocas del Toro, Panamá, representadas por 26 especies. Esta investigación documenta extensiones de rango para las 26 especies y se proporciona una clave de identificación para las especies de Hadziidira caribeña de Panamá.


Key words: Bocas del Toro, Hadziidae, Hornellidae, identification key, Maeridae, Megaluropidae, Melitidae, Pontogeneiidae

## Introduction

Parvorder Hadziidira S. Karaman, 1943 is comprised of 1159 species around the world (Lowry and Myers 2013). Members of the parvorder have a gnathopod 2 that is stouter than gnathopod 1, a pair of dorsal robust setae on urosomite 2, and a basofacial robust seta on the uropod 1 peduncle (Lowry and Myers 2013). The parvorder contains 14 families of amphipods: Crangoweckeliidae Lowry \& Myers, 2012 (three spp.), Eriopisidae Lowry \& Myers, 2013 (87 spp.), Gammaroporeiidae Bousfield, 1979 (one sp.), Hadziidae S. Karaman, 1943 (93 spp.), Maeridae Krapp-Schickel, 2008 (421 spp.), Melitidae Bousfield, 1973 (184 spp.), Metacrangonyctidae Boutin \& Messouli, 1988 (20 spp.), Nuuanuidae Lowry \& Myers, 2013 (25 spp.), Calliopiidae Sars, 1893 (105 spp.), Cheirocratidae d'Udekem d'Acoz, 2010 (19 spp.), Hornelliidae d'Udekem d'Acoz, 2010 (13 spp.),

Megaluropidae Thomas \& Barnard, 1986b (16 spp.), Pontogeneiidae Stebbing, 1906 (171 spp.), and Magnovidae Alves, Lowry \& Johnson, 2020 (one sp.). Just more than 200 species in the parvorder have been reported from the Caribbean Sea, representing ten families, but none of the species have been previously reported from Caribbean Panama (LeCroy et al. 2009; Martín et al. 2013).

Within the parvorder Hadziidira, 26 species of amphipods were collected from Bocas del Toro, Panama, with representatives from families Hadziidae, Hornellidae, Maeridae, Megaluropidae, Melitidae, and Pontogeneiidae. All species are diagnosed herein. An identification key is provided to distinguish between the Hadziidira species known from the Caribbean waters of Panama.

## Materials and methods

Various substrates were collected by hand and placed into buckets or plastic bags from various sites around Bocas del Toro, Panama at depths of 0.2-12 m. Coral rubble was elutriated with freshwater to remove amphipods and other samples were sorted through by hand. Live amphipods were sorted to morphospecies, placed in clove oil for imaging, and preserved in $99.5 \%$ EtOH for later examination. Preserved specimens were transferred to glycerol, measured from the tip of the rostrum to the base of the telson, and dissected under a stereomicroscope. Specimens were illustrated using a Meiji MT5900L phase contrast microscope with an Olympus U-DA drawing tube attached or an Olympus BH2 differential interference contrast microscope with an Olympus BH2-DA drawing tube attached. Illustrations were digitally inked following Coleman (2003) in Adobe Illustrator 2020 using a Wacom ${ }^{\circledR}$ Intuos Pro Pen Tablet. Specimens are deposited in the Smithsonian Institution, U.S. National Museum of Natural History (USNM) and the Gulf Coast Research Laboratory Museum (GCRL).

## Results

Parvorder Hadziidira S. Karaman, 1943
Superfamily Hadzoidea S. Karaman, 1943
Family Hadziidae S. Karaman, 1943

## Genus Dulzura J.L. Barnard, 1969

Diagnosis. Antenna 1 accessory flagellum 2-articulate; lower lip lacking inner lobes; gnathopod 1 smaller than gnathopod 2; coxa 4 not excavate posteriorly; pleonites 1-3 smooth; uropod 3 inner ramus minute, outer ramus greatly elongated, 2-articulate, article 2 short; telson deeply cleft.

## Dulzura schoenerae (Fox, 1973)

Figs 1, 27A

Eriopisa schoenerae Fox, 1973: 153-159, figs 5-8.
Protohadzia schoenerae: Zimmerman and Barnard 1977: 571-579, figs 1-5; Thomas 1993: 45, figs 48, 58; LeCroy 2000: 69, fig. 101.


Figure 1. Dulzura schoenerae, female, 2.8 mm , epimeron 3, coxa 6, telson, uropod 3, gnathopod 2 medial. Scale bars: 0.5 mm .

Material examined. PANAMA • 2.8-5 mm • 1 ; Bocas del Toro, Hospital Bight; $9.304483^{\circ} \mathrm{N}, 82.131617^{\circ} \mathrm{W}$; depth 1.5 m , surface of dead coral; 7 Aug 2005; S.E. LeCroy leg.; GCRL 6627•2 §, 1 ㅇ; Bocas del Toro, Isla Solarte; $9.244333^{\circ} \mathrm{N}, 82.250733^{\circ} \mathrm{W}$; depth 0.5 m , Halimeda and Thalassia; 9 Aug 2005; S.E. LeCroy leg.; GCRL 6628 • 5 ; Bocas del Toro, Isla Solarte; $9.290110^{\circ} \mathrm{N}$, $82.189732^{\circ}$ W; depth $1-5 \mathrm{~m}$, among coral rubble; 8 Aug 2021; K.N. White leg.; USNM 1703494.

Diagnosis. Male gnathopod 2 propodus palm with acute apical protrusion, much larger than female gnathopod 2 ; epimeron 3 with simple small posteroventral tooth; telson apically acute with apical spines.

Distribution. USA: Florida from Biscayne Bay to the Dry Tortugas (Thomas 1993); Bahama Islands: Bimini (Fox 1973); Puerto Rico: La Parguera (Zimmerman and Barnard 1977); Cuba: Caleta de San Lázaro (Ortiz et al. 2001); Mexico: Puerto Morelos National Park (Winfield et al. 2023); Panama: Bocas del Toro (present study).

Ecology and remarks. These amphipods are associated with coral rubble, algae, and seagrass near coral reefs at depths of 1-5 m. Panamanian specimens agree closely with previous descriptions of the species and are easily distinguishable based on the uropod 3, gnathopod 2 , and epimeron 3, even in smaller specimens.

Family Maeridae Krapp-Schickel, 2008

## Genus Ceradocus Costa, 1853

Diagnosis. Eyes oval. Maxilla 2 inner plate with dense facial setae. Coxa 1 produced anteroventrally. Pereopod 7 basis weakly expanded, posterior margin serrate. Urosomite segments usually serrate. Uropod 3 rami foliaceous, apically truncate, extending beyond tips of uropods 1 and 2 . Telson deeply cleft.

## Ceradocus sheardi Shoemaker, 1948

Figs 2, 27B

Ceradocus sheardi Shoemaker, 1948: 7-9, fig. 2; Thomas 1993: 43, figs 51, 56; LeCroy 2000: 73, fig. 124.

Material examined. PANAMA • 5-10 mm • 1 ; Bocas del Toro, Swan Cay; $9.4536^{\circ} \mathrm{N}, 82.300033^{\circ} \mathrm{W}$; depth 2 m , coral rubble; 24 June 2023; K.N. White leg.; USNM $1703495 \cdot 1 \widehat{J}^{\top}$; Bocas del Toro, Cayo Zapatilla $1 ; 9.269967^{\circ} \mathrm{N}, 82.0587^{\circ} \mathrm{W}$; depth 10-11 m, coral rubble; 28 June 2023; K.N. White leg.; USNM 1703496.

Diagnosis. Antenna 1 accessory flagellum 7- or 8-articulate. Gnathopod 2 not sexually dimorphic, right and left sides similar; propodus enlarged, palm


Figure 2. Ceradocus sheardi, male, 5.2 mm , gnathopod 2 medial, gnathopod 2 palm with setae removed, telson, epimeron and urosome uropod 3 , maxilla 2 , mandibular palp. Scale bars: 0.5 mm .
convex, defined by notch. Pereopod 7 basis without posterodistal lobe. Pleosome and urosome dorsally serrate. Epimera 1-3 posterior margins serrate. Telson approximately as long as wide with strong apical spines.

Distribution. USA: South Florida from Biscayne Bay to the Dry Tortugas (Thomas 1993); Puerto Rico (LeCroy 2000); Cuba (Shoemaker 1948; Varela et al. 2003); Mexico: Yucatan (Shoemaker 1948; Thomas 1993); Belize (Thomas 1993); Panama: Bocas del Toro (present study).

Ecology and remarks. These amphipods are common among coral rubble and under rocks at depths of 1-52 m. Panamanian specimens agree closely with previous descriptions of the species and are easily distinguishable based on the uropod 3 , gnathopod 2 , and heavily serrate epimeron and urosome.

## Ceradocus shoemakeri Fox, 1973

Figs 3, 27C

Ceradocus shoemakeri Fox, 1973: 147-152, figs 1-4; LeCroy 2000: 73, fig. 121.

Material examined. PANAMA•2.2-7 mm • 1 ; Bocas del Toro, Hospital Point; $9.3336^{\circ} \mathrm{N}, 82.218833^{\circ}$ W; depth $15-\mathrm{m}$, coral rubble and Halimeda; 6 Aug 2005;


Figure 3. Ceradocus shoemakeri, male, 2.2 mm , gnathopod 2 weak side lateral, weak gnathopod 2 propodus palm enlarged with setae removed, gnathopod 2 strong side lateral, strong gnathopod 2 propodus palm enlarged with setae removed, epimeron and urosome. Scale bars: 0.5 mm .
S. DeGrave leg.; GCRL 6629•1 1 ; Bocas del Toro, San Cristobal; $9.284977^{\circ} \mathrm{N}$, $82.294533^{\circ}$ W; depth 1-3 m, Halimeda; 21 June 2023; K.N. White leg.; USNM $1703497 \cdot 1 \delta^{\lambda}, 2$ ¢ ; Cayo Zapatilla $1 ; 9.269967^{\circ} \mathrm{N}, 82.0587^{\circ} \mathrm{W}$; depth $10-11 \mathrm{~m}$, coral rubble; 28 June 2023; K.N. White leg.; USNM 1703498.

Diagnosis. Antenna 1 accessory flagellum 4- or 5-articulate. Gnathopod 2 sexually dimorphic, right and left sides dissimilar; enlarged side palm oblique with two subquadrate and one triangular projection. Pereopod 7 basis with small posterodistal lobe. Pleosome and urosome dorsally smooth. Epimera 1-3 posterior margins serrate. Telson approximately as long as wide with subapical setae.

Distribution. U.S.A.: South Florida from Biscayne Bay to the Dry Tortugas; Apalachee Bay, Perdido Key, Florida (LeCroy 2000); Bahama Islands: Bimini (Fox 1973); Panama: Bocas del Toro (present study).

Ecology and remarks. These amphipods are associated with coral rubble, algae, and sponges at depths of 0.5-15 m. Panamanian specimens have a dorsally smooth pleosome and urosome; Fox (1973) mentioned that occasionally there is a mid-dorsal posterior tooth on pleonites 4 and/or 5 .

## Genus Elasmopus Costa, 1853

Diagnosis. Antenna 1 elongate, at least $1 / 3$ of body length; accessory flagellum 2- or 3- articulate. Mandibular palp article 3 falcate, anterior margin with pectinate setae. Uropod 1 peduncle with basofacial spine; uropod 3 rami subequal in length.

## Elasmopus balkomanus Thomas \& Barnard, 1988

Figs 4, 27D

Elasmopus balkomanus Thomas \& Barnard, 1988: 838-842, figs 1-3; LeCroy 2000: 86, fig. 133.

Material examined. PANAMA •1.6-8 mm • 1 ; Bocas del Toro, Crawl Cay; $9.2475^{\circ} \mathrm{N}, 82.1290^{\circ} \mathrm{W}$; depth 5 m , among coral rubble; 12 Aug 2021; K.N. White leg.; USNM $1703499 \cdot 1{ }^{\text {® }}$; Bocas del Toro, Crawl Cay; $9.245967^{\circ} \mathrm{N}, 82.136867^{\circ} \mathrm{W}$; depth 1-4 m, among sand; 25 June 2023; K.N. White leg.; USNM 1703500.

Diagnosis. Gnathopod 1 male propodus subovate, palm oblique, female propodus slender, ventral margin straight. Gnathopod 2 male propodus palm densely setose with crenulate longitudinal ridge on medial surface, female propodus with 2 spines at palmar angle. Pereopod 5 basis posterior margin concave. Pereopod 7 basis posterior margin without long setae, articles 4 and 5 of male unexpanded, slender. Epimeron 3 posteroventral margin with small tooth. Telson inner lobes shorter than outer lobes, apically acute.

Distribution. U.S.A.: South Florida, Looe Key (Thomas and Barnard 1988; Thomas 1993), Biscayne Bay (LeCroy 2000); Panama: Bocas del Toro (present study).

Ecology and remarks. These amphipods are associated with algal turf and coral rubble at depths of 1-5 m. Panamanian specimens have a less setose gnathopod 2 propodus and less concave pereopod 5 basis than described by Thomas and Barnard (1988). The gnathopod 2 propodus is also less inflated than


Figure 4. Elasmopus balkomanus, male 1.6 mm , pereopod 5 , telson, gnathopod 2 medial, epimeron 3 posterovental corner; female, 3.7 mm , gnathopod 1 lateral. Scale bars: 0.5 mm .
previously described. This suggests variation in these characters with size as the Panamanian specimens were smaller than those described by Thomas and Barnard (1988). Other characters agree with previous descriptions of this species.

Elasmopus elieri Ortiz, Lalana \& Varela, 2004
Figs 5, 27E

Elasmopus elieri Ortiz, Lalana \& Varela, 2004: 36-39, figs 1, 2.

Material examined. PANAMA•3.5-6 mm • 9 ठ, 9 ; Bocas del Toro, Lime Point; $9.4149^{\circ} \mathrm{N}, 82.33225^{\circ} \mathrm{W}$; depth $0.2-0.5 \mathrm{~m}$, among red algae and coral rubble; 5 Aug 2005; S. DeGrave leg.; GCRL 6630.

Diagnosis. Gnathopod 1 propodus subrectangular, palm oblique. Gnathopod 2 male propodus elongate, palm concave, with large distal triangular tooth, medial surface with two subtriangular processes; female propodus elongate, narrow, palm oblique with two spines at palmar angle. Pereopod 5 basis posterior margin evenly convex. Pereopod 7 basis posterior margin without long setae. Epimeron 3 posteroventral margin with small tooth. Telson inner lobes subequal in length with outer lobes, apically rounded.


Figure 5. Elasmopus elieri, male, 4.2 mm , epimeron 3, telson, gnathopods 1 and 2 medial, manidibular palp, uropod 3. Scale bars: 0.5 mm

Distribution. Cuba: Cayo Diego Pérez (Ortiz et al. 2004); Panama: Bocas del Toro (present study).

Ecology and remarks. These amphipods are associated with algae, and coral rubble at depths of 0-3 m. Panamanian specimens closely resemble specimens described by Ortiz et al. (2004) and can be readily distinguished from other species based on the unique shape of the gnathopod 2 propodus in males.

## Elasmopus levis (Smith, 1873)

Figs 6, 27F

Maera levis Smith, 1873: 559.
Elasmopus laevis: LeCroy 2000: 87, fig. 137.

Material examined. PANAMA • 5-10 mm • 1 万; Bocas del Toro, Playa Bluff; $9.3905^{\circ} \mathrm{N}, 82.23725^{\circ} \mathrm{W}$; depth 0 m , among algae; 5 Aug 2005; T.A. Haney leg.; GCRL 6631 • 1 ¢; Bocas del Toro, Hospital Point; $9.3336^{\circ} \mathrm{N}, 82.218883^{\circ} \mathrm{W}$; depth 15 m, among coral rubble; 6 Aug 2005; S. DeGrave leg.; GCRL 6632 • 2 ㅇ, 2 万, $^{\lambda}, 3$ juvenile; Pigeon Key Reef; depth 0.5-1 m, among Halimeda; 9 Aug 2005; T.A. Haney leg.; GCRL 6633•1 ${ }^{\lambda}$; Bocas del Toro, STRI Point; $9.34872^{\circ}$ N,


Figure 6. Elasmopus levis, male, 4.2 mm , gnathopod 1 lateral, gnathopod 2 medial, epimeron 3, telson. Scale bars: 0.5 mm .
$82.26258^{\circ} \mathrm{W}$; depth 12 m , among coral rubble; 6 Aug 2021, K.N. White leg.; USNM $1703501 \cdot 1$ q, 1 ठ $^{\lambda}$; Bocas del Toro, Drago; $9.418056^{\circ} \mathrm{N}, 82.3375^{\circ} \mathrm{W}$; depth 2-3 m, among coral rubble, 9 Aug 2021; K.N. White leg.; USNM $1703502 \cdot$ 2 ; Bocas del Toro, Cayo Zapatilla $1 ; 9.269967^{\circ} \mathrm{N}, 82.0587^{\circ} \mathrm{W}$; depth $10-11 \mathrm{~m}$, among coral rubble; 28 June 2023; K.N. White leg.; USNM 1703503.

Diagnosis. Gnathopod 1 propodus subrectangular, palm transverse. Gnathopod 2 male propodus with deep medial depression, lined with groups of long setae along ventral margin, with one small medial tooth, female propodus with two spines at palmar angle slightly longer than spines on palmar margin. Pereopod 5 basis posterior margin evenly convex. Pereopod 7 basis posterior margin without long setae, articles 4 and 5 of male expanded, articles 5 and 6 with long posterior setae. Epimeron 3 posteroventral margin with small tooth, sometimes with serrated edge. Telson inner lobes longer than outer lobes, apically subacute.

Distribution. U.S.A.: Cape Cod, Massachusetts (Bousfield 1973) to South Florida (LeCroy 2000); Mexico: Yucatan (McKinney 1977); Panama: Bocas del Toro (present study).

Ecology and remarks. These amphipods are associated with seagrass, algae, and coral rubble at depths of 0-11 m. Panamanian specimens show variation in the level of acuteness of the telson apices and the posterior margin of epimeron 3. Gulf of Mexico and western Atlantic specimens are described as
having acute telson lobes (subacute in Panamanian specimens) and all Panamanian specimens show the posteroventral tooth on epimeron 3, whereas this species is sometimes described as having an entire epimeron 3.

## Elasmopus longipropodus Senna \& Souza-Filho, 2011

Figs 7, 27G
Elasmopus rapax (non Elasmopus rapax Costa, 1851): Soares et al. 1987/89:
244, pl. 3, figs 1-12; Wakabara et al. 1991: 73.
Elasmopus aff. rapax: Souza-Filho and Senna 2009: 67.
Elasmopus longipropodus Senna \& Souza-Filho, 2011: 59-66, figs 1-6.

Material examined. PANAMA $\cdot 2.5-7 \mathrm{~mm} \cdot 3$ 万, 3 ; Bocas del Toro, Swan Cay; $9.453333^{\circ} \mathrm{N}, 82.298333^{\circ} \mathrm{W}$; depth $2-3 \mathrm{~m}$, among algae; 4 Aug 2005; S . DeGrave leg.; GCRL $6634 \cdot 2$ ठ, 5 ¢, 2 juvenile; Bocas del Toro, Hospital Point; $9.3336^{\circ} \mathrm{N}, 82.218883^{\circ} \mathrm{W}$; depth 15 m , among coral rubble; 6 Aug 2005; S. DeGrave leg.; GCRL $6635 \cdot 2$ d, 7 ㅇ, 2 juvenile; Bocas del Toro, Isla Solarte channel; $9.294574^{\circ} \mathrm{N}, 82.173114^{\circ} \mathrm{W}$; depth 2 m , among Halimeda, 8 Aug 2021; K.N. White leg.; USNM $1703504 \cdot 1$ Q, $3 \delta^{\text {º }}$; Bocas del Toro, San Cristobal; $9.2625^{\circ} \mathrm{N}$,


Figure 7. Elasmopus longipropodus, female, 2.5 mm , epimeron 3, pereopod 5, gnathopod 1 lateral; male, 4.5 mm , telson, gnathopod 2 lateral, uropod 3 . Scale bars: 0.5 mm .
$82.235^{\circ} \mathrm{W}$; depth 15 m , among coral rubble, 10 Aug 2021; K.N. White leg.; USNM $1703505 \cdot 1$ đ, 2 \&, 1 juvenile; Bocas del Toro, Crawl Cay; $9.2376^{\circ} \mathrm{N}, 82.1438^{\circ} \mathrm{W}$; depth 1.5-3 m, among Halimeda, 11 Aug 2021; K.N. White leg.; USNM1703506 - $1 \widehat{J}^{\lambda}, 2$ O ; Bocas del Toro, Hospital Point; $9.331967^{\circ}$ N, $82.214817^{\circ}$ W; depth 1-3 m, among Halimeda, 22 Jun 2023; K.N. White leg.; USNM1703507• 4 §, 1 ; Bocas del Toro, Swan Cay; $9.4536^{\circ} \mathrm{N}, 82.300033^{\circ} \mathrm{W}$; depth $1-4 \mathrm{~m}$, among red algae, 24 Jun 2023; K.N. White leg.; USNM 1703508 • 1 §, 1 juvenile, Bocas del Toro, Crawl Cay; $9.245967^{\circ} \mathrm{N}, 82.136867^{\circ} \mathrm{W}$; depth $1-4 \mathrm{~m}$, among green algae; 25 June 2023; K.N. White leg.; USNM 1703509 • 2 §; Bocas del Toro, Crawl Cay; $9.24756^{\circ} \mathrm{N}, 82.12901^{\circ} \mathrm{W}$; depth 5-8 m, among coral rubble, 26 Jun 2023; K.N. White leg.; USNM 1703510 • 1 §, 8 Q, 1 juvenile; Bocas del Toro, Hospital Point; $9.333383^{\circ} \mathrm{N}, 82.218467^{\circ} \mathrm{W}$; depth 11 m , among coral rubble, 26 Jun 2023; K.N. White leg.; USNM 1703511.

Diagnosis. Gnathopod 1 propodus subovate, palm oblique. Gnathopod 2 propodus elongate, male palm shorter than posterior margin with two large, rounded processes and one large subacute process at palmar angle. Pereopod 7 basis posterior margin with long setae, articles 4 and 5 of male unexpanded. Epimeron 3 posterior margin serrate. Uropod 3 rami subequal or slightly unequal in length. Telson inner lobes longer than outer lobes, apically rounded.

Distribution. Brazil: from Rio Grande do Norte State to Rio de Janeiro State (Senna and Souza-Filho, 2011); Panama: Bocas del Toro (present study).

Ecology and remarks. These amphipods are associated with algae, sponges, and coral rubble at depths of 1.5-15 m. Panamanian specimens agree closely with the description provided by Senna and Souza-Filho (2011) and can be readily distinguished from other species by the shape of the gnathopod 2 propodus.

## Elasmopus pocillimanus (Bate, 1862)

Figs 8, 28A

Maera pocillimanus Bate, 1862: 191, pl. 34, fig. 7.
Elasmopus pocillimanus: Della Valle 1893: 733, pl. 1, fig. 4, pl. 22, figs 23-25; LeCroy 2000: 89, fig. 138.

Material examined. PANAMA • 4-8 mm • 1 ; Bocas del Toro, Isla Solarte; $9.2475^{\circ} \mathrm{N}, 82.1290^{\circ} \mathrm{W}$; depth $1-4 \mathrm{~m}$, among coral rubble; 8 Aug 2021; K.N. White
 depth 2-4 m, among coral rubble; 9 Aug 2021; K.N. White leg.; USNM 1703513 - 1 \&; Bocas del Toro, Hospital Point; $9.331967^{\circ} \mathrm{N}, 82.214817^{\circ} \mathrm{W}$; depth $1-3 \mathrm{~m}$, among coral rubble, 22 Jun 2023; K.N. White leg.; USNM $1703514 \cdot 1$ §; Bocas del Toro, Swan Cay; $9.4536^{\circ} \mathrm{N}, 82.300033^{\circ} \mathrm{W}$; depth $1-4 \mathrm{~m}$, among coral rubble, 24 Jun 2023; K.N. White leg.; USNM 1703515.

Diagnosis. Gnathopod 1 propodus subrectangular, palm transverse. Gnathopod 2 male propodus with deep medial depression, lined with groups of long setae along ventral margin, with one small medial tooth, female propodus with two spines at palmar angle slightly longer than spines on palmar margin. Pereopod 5, basis posterior margin evenly convex. Pereopod 7 basis posteroventral margin with long setae, articles 4 and 5 of male expanded, articles 5 and


Figure 8. Elasmopus pocillimanus, female, 5.0 mm , telson; male, 6.1 mm , pereopod 7, gnathopod 1 lateral, setae removed from propodus, gnathopod 1 propodus medial enlarged, epimeron 3 (two variations), gnathopod 2 medial. Scale bars: 0.5 mm .

6 with long posterior setae. Epimeron 3 posteroventral margin entire, sometimes with small tooth or weakly crenulate. Telson inner lobes longer than outer lobes, apically rounded.

Distribution. Cosmopolitan distribution in warm temperate and tropical waters (McKinney 1977; Karaman 1982; Thomas 1993) most likely refers to multiple species. U.S.A.: New England through Gulf of Mexico and Caribbean (LeCroy 2000); Panama: Bocas del Toro (present study).

Ecology and remarks. These amphipods are associated with algae and coral rubble at depths of $0-30 \mathrm{~m}$. Panamanian specimens show variation in the amount of crenulation of epimeron 3 posterior margin, but consistently have rounded apices on the telson. Other characters align well with previous descriptions of $E$. pocillimanus. See LeCroy (2000) for a discussion of the status of the species.

Elasmopus thomasi Ortiz \& Lalana, 1994
Figs 9, 28B

Elasmopus thomasi Ortiz \& Lalana, 1994: 297-301, figs 4-6.

Material examined. PANAMA • 2-5 mm • 2 q, 4 juvenile.; Bocas del Toro, Swan Cay; $9.453333^{\circ} \mathrm{N}, 82.298333^{\circ} \mathrm{W}$; depth 3 m, among algae; 4 Aug 2005;
T.A. Haney leg.; GCRL 6636•1 §; Bocas del Toro tah2005.001; Aug 2005; T.A. Haney leg.; GCRL 6638-2 ${ }^{\wedge}, 3$; Bocas del Toro, Mangrove Inn; depth 1-1.5 m, among Halimeda; 3 Aug 2005; M. Faust leg.; GCRL 6637•1 〕, 1 q; Bocas del Toro, San Cristobal; $9.284977^{\circ} \mathrm{N}, 82.294533^{\circ} \mathrm{W}$; depth $1-3 \mathrm{~m}$, among sponges; 21 Jun 2023; K.N. White leg.; USNM 1703516-4 4 , 1 §; Bocas del Toro, Hospital Point; $9.331967^{\circ} \mathrm{N}, 82.214817^{\circ} \mathrm{W}$; depth $1-3 \mathrm{~m}$, among sand and coral rubble; 22 Jun 2023; K.N. White leg.; USNM 1703517.

Diagnosis. Gnathopod 1 propodus subovate, palm oblique. Gnathopod 2 propodus subovate, male palm with three processes and two notches; dactylus resting in notch at palmar angle. Pereopod 5 basis posterior margin evenly convex. Pereopod 7 basis posterior margin without long setae, articles 4 and 5 of male unexpanded. Epimeron 3 posterior margin serrate. Uropod 3 inner ramus shorter than outer ramus. Telson inner lobes longer than outer lobes, apically rounded.

Distribution. Cuba: North coast (Ortiz and Lalana 1994); Panama: Bocas del Toro (present study).

Ecology and remarks. These amphipods are associated with algae and coral rubble at depths of 0-3 m. Panamanian specimens closely resemble specimens described from Cuba and can be readily distinguished by the shape of gnathopod 2 propodus and the rounded apices of the telson.


Figure 9. Elasmopus thomasi, male, 3.0 mm , pereopod 5, uropod 3, telson, gnathopod 2 medial, epimeron 3. Scale bars: 0.5 mm .

Genus Meximaera J.L. Barnard, 1969

Diagnosis. Antenna 1 accessory flagellum 4-articulate. Mandibular palp article 2 longer than articles 1 or 3, article 3 slender, linear. Lower lip inner lobes present. Maxilla 1 and 2 inner plates lacking or with scarce medial setae. Gnathopods 1 and 2 small, subchelate. Epimeral plates smooth. Uropod 3 rami subequal in length, outer ramus minutely bi-articulate. Telson cleft, lobes apically excavated.

## Meximaera diffidentia J.L. Barnard, 1969

Figs 10, 28C

Meximaera diffidentia Barnard, 1969b: 209-210, figs 21-22; Krapp-Schickel and Vader 2009: 2082-2085, fig. 10.
Maera caroliniana: Bynum and Fox 1977: 11-14, figs 6, 7; LeCroy 2000: 99, fig. 143.

Material examined. PANAMA•4-6 mm•1 ${ }^{\lambda}$; Bocas del Toro, STRI Point; among coral rubble; 7 Aug 2005; S. DeGrave leg.; GCRL 6639•1 $\uparrow$; Bocas del Toro, Pandora; $9.327769^{\circ} \mathrm{N}, 82.222207^{\circ} \mathrm{W}$; depth 10 m , among coral rubble, 10 Aug 2021; K.N. White leg.; USNM 1703518.


Figure 10. Meximaera diffidentia, male, 2.5 mm , telson; female, 3.9 mm , pereopod 7 , uropods 2 and 3 , mandibular palp, gnathopod 1 medial, gnathopod 2 propodus with setae removed. Scale bars: 0.5 mm .

Diagnosis. Eyes oval. Gnathopod 1 carpus subequal to propodus. Gnathopod 2 propodus palm oblique without U-shaped excavation. Pereopods with simple dactyls; pereopod 7 basis slimmer than long, without posterodistal lobe. Uropod 3 rami three times length of peduncle, distally truncated, outer ramus with minute second article. Telson cleft, with one long and one short apical spine.

Distribution. U.S.A.: North Carolina (Bynum and Fox 1977), Apalachee Bay to South Florida (LeCroy 2000), West Florida (Krapp-Schickel and Vader 2009); Pacific California (Barnard 1969b); Panama: Bocas del Toro (present study).

Ecology and remarks. These amphipods are associated with sand and coral rubble at depths of 0-12 m. Panamanian specimens agree closely with the description provided by Barnard (1969b), particularly in the ornamentation and spination of the male gnathopod 2 propodus. The spines on the telson are spaced slightly differently in Panamanian specimens, but still show the same pattern.

## Genus Quadrimaera Krapp-Schickel \& Ruffo, 2000

Diagnosis. Mandibular palp article 1 not lengthened or tooth-like; article 3 narrow. Gnathopod 1 carpus with dorso-distal excavation. Gnathopod 2 propodus palmar corner at a right angle; dactylus outer margin bare or with one seta. Pereopod dactyli bifid; pereopod 7 basis with posterodistal lobe.

## Quadrimaera ceres (Ruffo, Krapp \& Gable, 2000)

Figs 11, 28D

Maera ceres Ruffo, Krapp \& Gable, 2000: 11-13, figs 4-6.

Material examined. PANAMA • 2-3 mm • 3 万, 5 ; Bocas del Toro, Drago; 9.418056 N, $82.3375^{\circ}$ W; depth 3 m , among coral rubble; 9 Aug 2021; K.N. White leg.; USNM 1703519.

Diagnosis. Antenna 1 accessory flagellum 7-articulate. Gnathopod 1 coxa anteroventrally rounded; carpus with dorsal depression and two short and four long facial setal rows. Gnathopod 2 propodus palmar margin with shallow U-shaped excavation between two subquadrate projections, palm defined by large projection; dactylus medially expanded, smooth. Telson inner corner acutely produced, each lobe with one medium and three long apical spines.

Distribution. Bermuda: St. George's Parish (Ruffo et al. 2000); Panama: Bocas del Toro (present study).

Ecology and remarks. These amphipods are associated with algae and coral rubble at depths of 0-3 m . Panamanian specimens closely resemble previously described specimens and can readily identified based on the gnathopod 2 propodus palm ornamentation.

Quadrimaera cristianae Krapp-Schickel \& Ruffo, 2000
Figs 12, 28E


Figure 11. Quadrimaera ceres, male, 3.4 mm , pereopod 7 , gnathopod 1 propodus and carpus medial, gnathopod 2 medial, telson, coxa 1. Scale bars: 0.5 mm .


Figure 12. Quadrimaera cristianae, male, 4.9 mm , gnathopod 1 propodus, carpus, dactylus medial, telson, gnathopod 2 lateral, coxa 1. Scale bars: 0.5 mm .

Material examined. PANAMA - 2-3.5 mm • 1 q; Bocas del Toro, Playa Bluff; $9.3905^{\circ} \mathrm{N}, 82.23725^{\circ} \mathrm{W}$; depth 0 m , among algae; 5 Aug 2005; T.A. Haney leg.; GCRL $6640 \cdot 1$ ¢ ; Bocas del Toro, Hospital Point; $9.3336^{\circ} \mathrm{N}, 82.218883^{\circ} \mathrm{W}$; depth 15 m, among coral rubble; 6 Aug 2005; S. DeGrave leg.; GCRL $6641 \cdot 3$ 亿, 5 , 1 juvenile; Bocas del Toro, Hospital Point; depth 2-3 m, in sponge Aplysinia cauliformis; 15 June 2009; K.N. White leg.; GCRL 6642•1 ${ }^{\text {T; }}$; Bocas del Toro, Hospital Point; $9.331967^{\circ} \mathrm{N}, 82.214817^{\circ} \mathrm{W}$; depth $1-3 \mathrm{~m}$, among Halimeda; 22 June 2023; K.N. White leg.; USNM $1703520 \cdot 2$ §̃, 2 ; Bocas del Toro, Crawl Cay; $9.245967^{\circ} \mathrm{N}, 82.136867^{\circ} \mathrm{W}$; depth $1-4 \mathrm{~m}$, among Halimeda and coral rubble; 25 June 2023; K.N. White leg.; USNM 1703521.

Diagnosis. Antenna 1 accessory flagellum 6-articulate. Gnathopod 1 coxa anteroventrally rounded; carpus with slight dorsal depression and two short and four long facial setal rows. Gnathopod 2 propodus palmar margin with three U-shaped excavations increasing in size distally, two subtriangular projections, and one subrectangular projection, palm defined by large projection; dactylus medially expanded. Telson lobes inner corner acutely produced, each with four apical spines and one medio-distal plumose seta.

Distribution. Turks and Caicos, Fort George Cay; Netherlands Antilles: Curaçao; Lesser Antilles: Bonaire and St. Martin; Venezuela: Margarita Island; Cayman Islands: Grand Cayman Island; Mexico: Yucatán; Brazil: Ceará State; Pernambuco State, Bahia State; Rio Grande do Norte State (Krapp-Schickel and Ruffo 2000); Panama: Bocas del Toro (present study).

Ecology and remarks. These amphipods are associated with algae and coral rubble at depths of 0-15 m. Panamanian specimens closely resemble previously described specimens, with the main difference being fewer plumose setae on the telson. This species can be readily identified by the gnathopod 2 propodus palm ornamentation.

## Quadrimaera miranda (Ruffo, Krapp-Schickel \& Gable, 2000)

Figs 13, 28F

Maera miranda Ruffo, Krapp \& Gable, 2000: 15-19, figs 7, 8; LeCroy 2000: 101, fig. 148.
Quadrimaera miranda: Krapp-Schickel and Ruffo 2000: 195-196.
Maera quadrimana (non Dana 1853): Ledoyer 1986) 190-191, fig. 11.

Material examined. PANAMA•4-7 mm • 1 §, 3 ; Bocas del Toro, Swan Cay; $9.453333^{\circ} \mathrm{N}, 82.298333^{\circ} \mathrm{W}$; depth $2-3 \mathrm{~m}$; among coral rubble; 4 Aug 2005; S. DeGrave leg.; GCRL 6643•1 ठ, 1 ㅇ; Bocas del Toro, Hospital Bight; $9.304483^{\circ} \mathrm{N}$, $82.172317^{\circ}$ W; depth 0.5 m , among coral rubble; 7 Aug 2005; T.A. Haney leg.; GCRL $6644 \cdot 2$; Bocas del Toro, 100 m west of STRI dock; depth 14 m, light trap; 8 Aug 2005; T.A. Haney leg.; GCRL $6645 \cdot 1$ ¢; Bocas del Toro, STRI mangroves; $9.353333^{\circ} \mathrm{N}, 82.2578^{\circ} \mathrm{W}$; depth 1 m , among Ecteinascidia turbinata ascidians, 11 Aug 2021; K.N. White leg.; USNM 1703522 •1 §; Bocas del Toro, Crawl Cay; $9.245967^{\circ}$ N, $82.136867^{\circ}$ W; depth $1-4$ m, among Halimeda, 25 June 2023; K.N. White leg.; USNM 1703523•3 $\uparrow$; Bocas del Toro, Hospital Point; $9.333383^{\circ} \mathrm{N}, 82.218467^{\circ} \mathrm{W}$; depth 0 m , buoy scraping, 26 June 2023; K.N. White leg.; USNM $1703524 \cdot 1 \delta^{\lambda}, 3$ ; Bocas del Toro, STRI dock; $9.351183^{\circ} \mathrm{N}$,


Figure 13. Quadrimaera miranda, male, 3.3 mm , pereopod 7, gnathopod 1 propodus, carpus, dactylus medial, telson; male, 2.8 mm , gnathopod 2 lateral, coxa 1 . Scale bars: 0.5 mm .
$82.257033^{\circ}$ W; depth 0-1 m, dock scraping, 27 June 2023; K.N. White leg.; USNM 1703525.

Diagnosis. Antenna 1 accessory flagellum 6-articulate. Gnathopod 1 coxa anteroventrally rounded; carpus with minute dorsal depression and two short and three long facial setal rows. Gnathopod 2 propodus palmar margin with subrectangular projection followed by a small U-shaped excavation and one short, truncate process, palm defined by small projection; dactylus medially expanded with median point. Telson lobes apically truncate, each with five long apical spines.

Distribution. Bermuda: St. George's Parish, Sandy's Parish (Ruffo et al. 2000); U.S.A.: Pigeon Key, FL; Turks and Caicos, Twin Cay; Netherlands Antilles: Bonaire; Lesser Antilles: St. Martin; Venezuela: Tobago Island, Los Roques Island; Brazil: Rio de Janeiro, Ilha de Fortaleza; Mexico: Yucatán (Krapp-Schickel and Ruffo 2000), Laguna de Terminos (Ledoyer 1986); Panama: Bocas del Toro (present study).

Ecology and remarks. These amphipods are associated with algae, sponges, ascidians, and coral rubble at depths of 0-15 m. Panamanian specimens closely resemble previously described specimens of this species and can be readily distinguished from other species based on the gnathopod 2 palm ornamentation and broadened dactylus.

## Quadrimaera quadrimana (Dana, 1852)

Figs 14, 28G

Gammarus quadrimanus Dana, 1852: 955-956, pl. 65, fig. 9.
Maera quadrimana: Schellenberg 1938: 45-48, figs 21, 22; LeCroy 2000: 101, fig. 147; Ruffo et al. 2000: 6-11, figs 1, 2.

Material examined. PANAMA • 2-3.5 mm • 7 §, 2 q, 10 juvenile; Bocas del Toro, Drago; $9.418056^{\circ} \mathrm{N}, 82.3375^{\circ} \mathrm{W}$; depth 2-4 m, among coral rubble; 9 Aug 2021; K.N. White leg.; USNM $1703526 \cdot 1$ juvenile; Bocas del Toro, Swan Cay; $9.4536^{\circ}$ N, $82.300033^{\circ}$ W; depth 1-4 m, among coral rubble; 24 Jun 2023; K.N. White leg.; USNM $1703527 \cdot 1$ ¢ ; Bocas del Toro, Crawl Cay; $9.245967^{\circ} \mathrm{N}, 82.136867^{\circ} \mathrm{W}$; depth 1-4 m, among Halimeda; 25 June 2023; K.N. White leg.; USNM 1703528.

Diagnosis. Antenna 1 accessory flagellum 6-articulate. Gnathopod 1 coxa anteroventrally rounded; carpus with distinct dorsal depression and two short and three long facial setal rows. Gnathopod 2 propodus palmar margin with three U-shaped excavations, increasing in size distally, two small subtriangular projections, and one large truncate projection, palm defined by large projection; dactylus smooth, not expanded. Telson lobes apically truncate, inner margins acute, each with four or five medium-to-long apical spines.


Figure 14. Quadrimaera quadrimana, male, 3.8 mm , gnathopod 1 propodus, carpus, dactylus medial, gnathopod 2 lateral, coxa 1, telson. Scale bars: 0.5 mm .

Distribution. Fiji Islands (Dana 1853); Red Sea (Ruffo 1969); Madagascar (Ledoyer 1972, 1982); Great

Barrier Reef, Australia (Berents 1983); Gilbert Islands (Schellenberg 1938); Micronesia (J.L. Barnard 1965); Hawaiian Islands (J.L. Barnard 1970, 1971); Bermuda: St. George's Parish, Devonshire Parish (Ruffo et al. 2000); U.S.A.: Florida (Nelson 1995; Thomas 1993; LeCroy 2000); Mexico: Yucatán (McKinney 1977); Brazil (Wakabara et al. 1991; Wakabara and Serejo 1998); Panama: Bocas del Toro (present study).

Ecology and remarks. These amphipods are associated with algae and coral rubble at depths of $0-10 \mathrm{~m}$. Panamanian specimens closely resemble the description of specimens from Bermuda, with the gnathopod 2 propodus palmar margin showing a slightly more truncate projection than illustrated by Ruffo et al. (2000).

## Quadrimaera sarae Krapp-Schickel \& Ruffo, 2000

Figs 15, 29A

Quadrimaera sarae Krapp-Schickel \& Ruffo, 2000: 206-213, figs 8-10.

Material examined. PANAMA•4-5 mm • 2 §, 2 ; Bocas del Toro, Swan Cay; $9.453333^{\circ} \mathrm{N}, 82.298333^{\circ} \mathrm{W}$; depth $2-3 \mathrm{~m}$; among coral rubble; 4 Aug 2005; S.


Figure 15. Quadrimaera sarae, male, 4.2 mm , gnathopod 1 propodus, carpus, dactylus medial, pereopod 3 dactylus, pereopod 5 dactylus, gnathopod 2 medial, coxa 1, telson. Scale bars: 0.5 mm .

DeGrave leg.; GCRL 6646•1 ${ }^{\text {万 }}$; Bocas del Toro, Drago; 9.418056 N, $82.3375^{\circ} \mathrm{W}$; depth 3 m, among coral rubble; 9 Aug 2021; K.N. White leg.; USNM 1703529.

Diagnosis. Antenna 1 accessory flagellum 7-articulate. Gnathopod 1 coxa anteroventrally produced; carpus elongate with slight dorsal depression and two short and three long facial setal rows. Gnathopod 2 propodus palmar margin with U-shaped excavation surrounded by one subquadrate and one quadrate projection, palm defined by small projection; dactylus medially expanded. Pereopods 3 and 4 dactyli simple; pereopods 5-7 dactyli bifid. Telson, lobes apically excavated, each with four long apical spines.

Distribution. Turks and Caicos, Fort George Cay; Mexico: Yucatán; Venezuela: Tobago Island (Krapp-Schickel and Ruffo 2000); Panama: Bocas del Toro (present study).

Ecology and remarks. These amphipods are associated with coral rubble at depths of 0.3-3 m. Panamanian specimens closely resemble previously described specimens, including the characteristic gnathopod 2 propodus palm, simple pereopods 3 and 4 dactyli, and bifid pereopods 5-7 dactyli, which are unique to this species. The excavation on the gnathopod 2 propodus is larger in our 4.2 mm male than shown in the holotype ( 4.7 mm male) and there are more than three spines on the pereopods 3 and 4 bases in Panamanian specimens, but given the striking similarity in every other character, we are considering this as a regional variation.

## Quadrimaera yemanjae Alves, Neves \& Johnson, 2018

Figs 16, 29B

Quadrimaera yemanjae Alves, Neves \& Johnson, 2018: 569-575, figs 2-7.

Material examined. PANAMA • $2-4.5 \mathrm{~mm} \cdot 10{ }^{\lambda}, 4$; Bocas del Toro, Swan Cay; $9.453333^{\circ} \mathrm{N}, 82.298333^{\circ} \mathrm{W}$; depth 2-3 m, among coral rubble; 4 Aug 2005; S. DeGrave leg.; GCRL 6647•1 1 , 9 juvenile; Bocas del Toro, TAH 001, Aug 2005; T.A. Haney leg.; GCRL 6648•1 ${ }^{\text {§ }}$, Bocas del Toro, Drago; $9.418056^{\circ} \mathrm{N}, 82.3375^{\circ} \mathrm{W}$; depth 2-4 m, among coral rubble; 9 Aug 2021; K.N. White leg.; USNM 1703530 - 2 q; Bocas del Toro, Crawl Cay; $9.245967^{\circ} \mathrm{N}, 82.136867^{\circ} \mathrm{W}$; depth $1-4 \mathrm{~m}$, among coral rubble; 25 June 2023; K.N. White leg.; USNM 1703531.

Diagnosis. Antenna 1 accessory flagellum 6-articulate, distal article minute. Gnathopod 1 coxa anteroventrally rounded; carpus with deep dorsal depression and two short and three long facial setal rows. Gnathopod 2 propodus palmar margin with two small U-shaped excavations separated by a subacute process, followed distally by a large truncate process and one large U-shaped excavation, palm defined by large projection; dactylus medially smooth, slightly expanded. Telson lobes apically truncate, inner margins acute, each with four long apical spines.

Distribution. Brazil: Rio Grande do Norte State (Alves et al. 2018); Panama: Bocas del Toro (present study).

Ecology and remarks. These amphipods are associated with Halimeda and coral rubble at depths of 0-4 m. Panamanian specimens closely resemble specimens described from Brazil ( 4.5 mm ), with slightly less acute projections on the palm of gnathopod 2 propodus. This can most likely be attributed to the smaller size of the Panamanian specimens ( 3.8 mm ).


Figure 16. Quadrimaera yemanjae, male, 3.8 mm , gnathopod 1 propodus, carpus, dactylus medial, gnathopod 2 lateral, coxa 1, maxilla 2, telson. Scale bars: 0.5 mm .

## Family Melitidae Bousfield, 1973

## Genus Dulichiella Stout, 1912

Diagnosis. Male gnathopod 2 large, asymmetrical, propodus with distolateral crown of spines; female gnathopod 2 equal in size. Pereopods 5-7 dactyli each with accessory spine. Pleosome and urosome with dorsolateral spines. Uropod 3 inner ramus minute; outer ramus 2-articulate. Telson, deeply cleft, tapering to an acute point.

## Dulichiella anisochir (Krøyer, 1845)

Figs 17, 29C

Melita anisochir Krøyer, 1845: 317, pl. II, fig. 1a-p; Dana 1852: 968, pl. 66, fig. $8 \mathrm{a}-\mathrm{d}$.
Dulichiella anisochir: Lowry and Springthorpe 2007: 10-12, figs 3-6.

Material examined. PANAMA - 4-6 mm • 4 §, 2 q, 4.0 mm ; Bocas del Toro, Crawl Cay; $9.2475^{\circ} \mathrm{N}, 82.1290^{\circ} \mathrm{W}$; depth 5 m , among coral rubble; 12 Aug 2021; K.N. White leg.; USNM 1703532.


Figure 17. Dulichiella anisochir, male, 4.4 mm , head, coxa 1, gnathopod 2 lateral, epimeron and urosome, pereopods 6 and 7, dactylus enlarged. Scale bars: 0.5 mm .

Diagnosis. Gnathopod 1 coxa anteroventral corner produced, rounded, anterior margin concave. Gnathopod 2 propodus distolateral crown with three rounded spines; dactylus apically blunt, overlapping corner of propodus. Pereopods 6 and 7 carpus and propodus without bunches of long slender setae. Epimeron 1 posteroventral corner acute; epimeron 3 posterodistal margin serrate.

Distribution. Brazil: Rio de Janeiro to Lagoa dos Patos (Krøyer 1845; Lowry and Springthorpe 2007); Panama: Bocas del Toro (present study).

Ecology and remarks. These amphipods are associated with soft bottoms and coral rubble at depths of 0-30 m. Panamanian specimens closely resemble previously described specimens, with the exception of a less serrate distal margin on epimeron 3 . This difference can most likely be attributed to the size difference of our specimens ( 4.4 mm ) and the lectotype ( 10.7 mm ) described by Lowry and Springthorpe (2007).

## Dulichiella lecroyae Lowry \& Springthorpe, 2007

Figs 18, 29D

Melita fresnelli Kunkel 1910: 31-34, fig. 11; Pearse 1912: 371.
Dulichiella sp. A: LeCroy 2000: 78, fig. 126.
Dulichiella lecroyae Lowry \& Springthorpe, 2007: 34-38, figs 25-28.

Material examined．PANAMA•5－10 mm • 1 §， 1 ；Bocas del Toro，Swan Cay； $9.453333^{\circ} \mathrm{N}, 82.298333^{\circ} \mathrm{W}$ ；depth $2-3 \mathrm{~m}$ ，in orange sponge； 4 Aug 2005；S． DeGrave leg．；GCRL 6649 － 4 đ， 1 ค，Bocas del Toro，Crawl Cay； $9.250467^{\circ} \mathrm{N}$ ， $82.131617^{\circ}$ W；depth 10 m，in sponge； 7 Aug 2005；S．DeGrave leg．；GCRL 6650 － 1 \＆；Bocas del Toro，Punta Caracol；depth 1 m，in Lissodendoryx columbien－ sis sponge， 9 June 2009；K．Hultgren leg．；GCRL 6651 • 5 万， 4 P；Bocas del Toro，STRI Point； $9.34872^{\circ} \mathrm{N}, 82.26258^{\circ} \mathrm{W}$ ；depth 12 m ，among coral rubble， 6 Aug 2021；K．N．White leg．；USNM 1703533• 1 §， 3 ；Bocas del Toro，Juan Point； $9.3015^{\circ} \mathrm{N}, 82.29404^{\circ} \mathrm{W}$ ；depth 10 m ，among coral rubble， 7 Aug 2021； K．N．White leg．；USNM $1703534 \cdot 12$ §， 5 ㅇ；Drago； $9.418056^{\circ} \mathrm{N}, 82.3375^{\circ} \mathrm{W}$ ； depth 2－3 m，among coral rubble， 9 Aug 2021；K．N．White leg．；USNM 1703535 － 1 ¢ ；Bocas del Toro，San Cristobal； $9.2625^{\circ} \mathrm{N}, 82.235^{\circ} \mathrm{W}$ ；depth 15 m ，among coral rubble， 10 Aug 2021；K．N．White leg．；USNM 1703536 － 1 §；Bocas del Toro，Pandora； $9.327769^{\circ} \mathrm{N}, 82,222207^{\circ} \mathrm{W}$ ；depth 10 m ，among coral rubble， 10 Aug 2021；K．N．White leg．；USNM 1703537 • 1 万人；Bocas del Toro，Crawl Cay； $9.2376^{\circ} \mathrm{N}, 82.1438^{\circ} \mathrm{W}$ ；depth $1.5-3 \mathrm{~m}$ ，among coral rubble， 11 Aug 2021；K．N． White leg．；USNM 1703538.

Diagnosis．Gnathopod 1 coxa anteroventral corner not produced，anterior margin straight．Gnathopod 2 propodus distolateral crown with four rounded or subacute spines；dactylus apically hooked，fitting into posterodistal corner


Figure 18．Dulichiella lecroyae，male， 3.6 mm ，pereopods 6 and 7 ，epimeron and urosome，gnathopod 2 lateral，head， coxa 1．Scale bars： 0.5 mm ．
of propodus. Pereopods 6 and 7 carpus and propodus without bunches of long slender setae. Epimeron 1 posteroventral corner subquadrate; epimeron 3 posterodistal margin smooth.

Distribution. U.S.A.: Gulf of Mexico, South Florida, Cedar Keys, Dry Tortugas, South Carolina, Georgia (LeCroy 2000; Lowry and Springthorpe 2007); Bermuda: Flatts Village, Castle Harbor, Harrington Sound (Kunkel 1910); Panama: Bocas del Toro (present study).

Ecology and remarks. These amphipods are associated with sponges and coral rubble at depths of 0-12 m. Panamanian specimens closely resemble previously described specimens, with slight variation in the anteroventral margin of the head. Panamanian specimens show a minutely bifid notch rather than a single acute point.

## Genus Melita Leach, 1814

Diagnosis. Male gnathopod 2 large, symmetrical; female gnathopod 2 smaller than in male. Pereopods 5-7, dactyli without accessory spines. Pleosome without serrations. Uropod 3 inner ramus minute; outer ramus 1 -articulate. Telson deeply cleft, sides straight or convex, tapering to a point, with apical spines.

## Melita planaterga Kunkel, 1910

Figs 19, 29E

Melita planaterga Kunkel, 1910: 34-37, fig. 12; LeCroy 2000: 115, fig. 149.

Material examined. PANAMA•4-9 mm•7 §, 5 ; Bocas del Toro, Swan Cay; $9.453333^{\circ} \mathrm{N}, 82.298333^{\circ} \mathrm{W}$; depth 2-3 m, among algae; 4 Aug 2005; S. DeGrave leg.; GCRL 6652•1 1 ; Bocas del Toro, San Cristobal; $9.284977^{\circ} \mathrm{N}, 82.294533^{\circ} \mathrm{W}$; depth 1-3 m, among Dictyota; 21 June 2023; K.N. White leg.; USNM 1703539 • $6 \delta^{\lambda}, 5$; Bocas del Toro, Drago; $9.413433^{\circ} \mathrm{N}, 82.33335^{\circ} \mathrm{W}$; depth $1-3 \mathrm{~m}$, among Halimeda, red algae and coral rubble; 23 June 2023; K.N. White leg.; USNM $1703540 \cdot 1 \delta^{\lambda}, 1$ \& Bocas del Toro, Swan Cay; $9.4536^{\circ} \mathrm{N}, 82.300033^{\circ} \mathrm{W}$; depth 2 m, among coral rubble; 24 June 2023; K.N. White leg.; USNM 1703541.

Diagnosis. Male antennae without bottle-brush setae. Male gnathopod 2 propodus ovate, palm densely setose, setae shorter than propodus length; female gnathopod 2 smaller and less setose than in male. Female coxa 6 with lateral ridge at base of hook, anteroventral angle flattened or notched. Urosome segment 1 posterodorsal margin with single median process; urosome segment 2 posterior margin smooth, each side with single dorsolateral spine. Telson lobes apically subacute with long terminal spines.

Distribution. U.S.A.: Gulf of Mexico, Florida Keys (Lazo-Wasem and Gable 1987; LeCroy 2000); Bermuda: Flatts Village (Kunkel 1910); Mexico: Terminos Lagoon, Bay of Campeche, Mexico (Ledoyer 1986); Panama: Bocas del Toro (present study).

Ecology and remarks. These amphipods are associated with algae and coral rubble at depths of 0-3 m. Panamanian specimens closely resemble previously described specimens. Females can be identified easily by the structure


Figure 19. Melita planaterga, male, 5.1 mm , uropod 3 , telson, gnathopod 2 medial, some setae removed from carpus, epimeron and urosome; female, 4.6 mm , coxa 6 lateral, coxa 6 medial hook. Scale bars: 0.5 mm .
of coxa 6 and males have a heavily setose gnathopod 2 propodus. The dark pigmentation is also characteristic of this species. Panamanian specimens ranged from having dark pigment bands as described by Kunkel (1910) to being almost completely dark blue (more so than in Fig. 29E).

Superfamily Calliopioidea Sars, 1895
Family Hornelliidae d'Udekem d'Acoz, 2010
Genus Hornellia Walker, 1904

Diagnosis. Head, without rostrum. Antenna 1 accessory flagellum present. Gnathopods 1 and 2 subequal and similar. Pereopods 5-7 long and slender. Pleosome and urosome with postero-dorsal teeth. Uropod 3 biramous, rami subequal in length. Telson long and deeply cleft.

## Hornellia tequestae Thomas \& J.L. Barnard, 1986

Figs 20, 29F

Hornellia (Metaceradocus) tequestae Thomas \& J.L. Barnard, 1986a: 478-483, figs 1-3; LeCroy 2007: 591.

Material examined. PANAMA • 2-3 mm 1 d; Bocas del Toro, Crawl Cay; $9.237675^{\circ} \mathrm{N}, 82.143833^{\circ} \mathrm{W}$; depth $2-3 \mathrm{~m}$, among Halimeda; 11 Aug 2021; K.N. White leg.; USNM $1703542 \cdot 1 \delta^{\lambda}, 2 q$, Bocas del Toro, Hospital Point; $9.331967^{\circ} \mathrm{N}$, $82.214817^{\circ}$ W; depth 1-3 m, coral rubble; 22 June 2023; K.N. White leg.; USNM $1703543 \cdot 2$ §, 2 ¢; Bocas del Toro, Crawl Cay; $9.245967^{\circ} \mathrm{N}, 82.136867^{\circ} \mathrm{W}$; depth 1-4 m, coral rubble; 25 June 2023; K.N. White leg.; USNM $1703544 \cdot 2$, 4 ; Bocas del Toro, Crawl Cay; $9.250217^{\circ} \mathrm{N}, 82.131767^{\circ} \mathrm{W}$; depth $5-13 \mathrm{~m}$, coral rubble; 29 June 2023; K.N. White leg.; USNM 1703545.

Diagnosis. Antenna 1 accessory flagellum 4-articulate. Gnathopod 1 carpus posterior margin densely setose. Gnathopod 2 not sexually dimorphic, propodus elongate, palm oblique, smooth. Pereopods 5-7 bases posterior margins strongly serrate; pereopod 7 basis without posterodistal lobe. Epimera 1-3 posterior margins smooth, each with well-developed posteroventral tooth. Telson $1.4 \times$ longer than broad, nearly cleft to base, lobes apically acute with two setae.

Distribution. U.S.A.: Southeastern Gulf of Mexico (LeCroy 2007), Florida Keys (Thomas and Barnard 1986a); Panama: Bocas del Toro (present study).

Ecology and remarks. These amphipods are associated with algae and coral rubble at depths of $0-45 \mathrm{~m}$. Panamanian specimens closely resemble previously described specimens and are readily identified by the distinctly serrate posterodorsal margins of the pleosome and urosome, large posteroventral tooth on each epimeron, and the shape of the telson.


Figure 20. Hornellia tequestae, male, 1.8 mm , epimeron and urosome; female, 2.2 mm , telson, gnathopods 1 and 2 medial. Scale bars: 0.5 mm .

Family Megaluropidae Thomas \& J.L. Barnard, 1986

## Genus Gibberosus Thomas \& J.L. Barnard, 1986

Diagnosis. Head rostrum short; ocular lobe with acute cusp. Antenna 1 accessory flagellum 2-articulate. Gnathopod 2 merus with large distal lobe. Uropod 1 peduncle with interramal tooth. Telson with long spines.

Gibberosus devaneyi Thomas \& J.L. Barnard, 1986
Figs 21, 30A

Gibberosus devaneyi Thomas \& J.L. Barnard, 1986b: 469-475, figs 11, 13-15.

Material examined. PANAMA•2-3 mm • 6 §, 56 ; Bocas del Toro, Cayo Solarte;; $9.3336^{\circ} \mathrm{N}$, $82.218883^{\circ} \mathrm{W}$; depth $0.1-1 \mathrm{~m}$, in sand; 7 Aug 2005; S.E. LeCroy leg.; GCRL $6653 \cdot 1$ §; Bocas del Toro, Drago; $9.413433^{\circ} \mathrm{N}, 82.33335^{\circ} \mathrm{W}$; depth $1-3 \mathrm{~m}$, among Halimeda, red algae and coral rubble; 23 June 2023; K.N. White leg.; USNM $1703546 \cdot 1 \delta^{\lambda}, 5$ 中; Bocas del Toro, Crawl Cay; 9.250217º N, 82.131767º W; depth 5-13 m, coral rubble; 29 June 2023; K.N. White leg.; USNM 1703547.

Diagnosis. Head ocular lobe with subacute cusp. Pleosome segment 3 and urosome segment 2 with dorsal serrations, other segments smooth, lacking




Figure 21. Gibberosus devaneyi, female, 3.7 mm , pereopod 7, telson, epimeron and urosome, head, uropod 1; male, 3.0 mm , gnathopod 2 , setae removed, uropod 3 . Scale bars: 0.5 mm .
dorsal spines. Epimeron 3 smooth. Uropod 3 rami continually lined with spines. Telson lobes with several dorsal and two apical spines.

Distribution. U.S.A.: La Jolla, California; Peru: Chincha Island (Thomas and Barnard 1986b); Panama: Bocas del Toro (present study).

Ecology and remarks. These amphipods are found in sand at depths of 0-18 m. Panamanian specimens closely resemble specimens described from the eastern Pacific with slight variation in the following characters: subacute anterior head margin (acute in Pacific material) and slightly more serrate posterodorsal margin on pleon segment 3 . All other characters match well, specifically the smooth posterior margin of epimeron 3 and the continually spinose margins of uropod 3 rami.

## Gibberosus myersi (McKinney, 1980)

Figs 22, 30B

Megaluropus longimerus: Barnard 1962: 103, figs 17o-q (non Megaluropus longimerus Schellenberg, 1925).
Megaluropus sp.: Camp et al. 1977: 17-18.
Megaluropus myersi McKinney, 1980: 93-98, figs 5-7.
Gibberosus myersi: Thomas and Barnard 1986b: 464-469, figs 6, 12; LeCroy 2007: 590

Gibberosus sp. A: Rakocinski et al. 1993: 102.
Gibberosus cf. myersi: Rakocinski et al. 1996: 350.

Material examined. PANAMA • $2-5 \mathrm{~mm} \cdot 2$; Bocas del Toro, Crawl Cay; $9.237675^{\circ} \mathrm{N}, 82.143833^{\circ} \mathrm{W}$; depth $2-3 \mathrm{~m}$, in sand; 11 Aug 2021; K.N. White leg.; USNM $1703548 \cdot 1$ §, 3 q, Bocas del Toro, Drago; $9.413433^{\circ} \mathrm{N}, 82.33335^{\circ} \mathrm{W}$; depth 1-3 m, in sand; 23 June 2023; K.N. White leg.; USNM 1703549 • 1 〕, 8 ; ; Bocas del Toro, Drago; $9.417183^{\circ} \mathrm{N}, 82.324783^{\circ} \mathrm{W}$; depth $0-1 \mathrm{~m}$ in sand; 27 June 2023; K.N. White leg.; USNM 1703550.

Diagnosis. Head ocular lobe with acute cusp. Pleosome segment 3 and urosome segments 1 and 2, with dorsal serrations; urosome segment 2 , with one or two dorsal spines. Epimeron 3 serrate. Uropod 3 peduncle with facial spines; rami with sparse marginal spines. Telson each lobe with one dorsal and two apical spines.

Distribution. U.S.A.: South Carolina to the Florida Keys; southwestern Gulf of Mexico, Tampa Bay, Perdido Key, British Columbia to La Jolla, California (Thomas and Barnard 1986b; Rakocinski et al. 1993, 1996; LeCroy 2007); Peru: Afuera; Costa Rica: Puerto Culebra; Brazil: Ilha Sao Sebastiao (Thomas and Barnard 1986b); Panama: Culebra Island (Thomas and Barnard 1986b), Bocas del Toro (present study).

Ecology and remarks. These amphipods are found in sand at depths of 0-29 m. Panamanian specimens closely resemble previously described specimens. See Thomas and Barnard (1986b) for a discussion of the variation in this species. Caribbean Panamanian specimens most closely resemble specimens from Brazil, Peru, Costa Rica, and Queen Charlotte, and Coronados based on having a smooth dorsal margin on pleonites 2 and 5 , a thin posterior most facial spine on peduncle of uropod 1 , and epimeron 2 without facial spines.


Figure 22. Gibberosus myersi, female, 2.1 mm , head, uropods 1 and 3, telson, epimeron and urosome, gnathopod 2 lateral. Scale bars: 0.5 mm .

## Genus Resupinus Thomas \& J.L. Barnard, 1986

Diagnosis. Head rostrum long; ocular lobe rounded. Antenna 1 accessory flagellum 1-articulate. Gnathopod 2 merus without distal lobe. Uropod 1 peduncle without interramal tooth. Telson with small spines (if present).

## Resupinus spinicaudatus Thomas \& J.L. Barnard, 1986

Figs 23, 30C

Resupinus spinicaudatus Thomas \& J.L. Barnard, 1986b: 445-454, figs 1-5.

Material examined. PANAMA • 2-2.5 mm • 2 §, 6 ; Bocas del Toro, Drago; $9.413433^{\circ} \mathrm{N}, 82.33335^{\circ} \mathrm{W}$; depth $0-1 \mathrm{~m}$, in sand; 23 June 2023; K.N. White leg.; USNM 1703551.

Diagnosis. Head eye not filling entire ocular lobe. Pleosome segments 2 and 3 with dorsal serrations. Urosome segments dorsally smooth. Epimera 1-3 with sparse facial setae; epimeron 3 posterior margin with sparse, shallow serrations. Telson covered with dorsal prickle spines.

Distribution. Belize: Sitee Point (Thomas and Barnard 1986b); Panama: Bocas del Toro (present study).


Figure 23. Resupinus spinicaudatus, male, 2.4 mm , epimeron and urosome, head, uropod 1, telson, gnathopod 2 lateral. Scale bars: 0.5 mm .

Ecology and remarks. These amphipods are found in sand at depths of 0.75-1.2 m. Panamanian specimens closely resemble previously described specimens and can be easily identified based on having smooth pleonites 4 and 5 , sparsely serrate epimeron 3 , and dorsally spinose telson.

Family Pontogeneiidae Stebbing, 1906

## Genus Eusiroides Stebbing, 1888

Diagnosis. Antenna 1 accessory flagellum 1-articulate. Rostrum short. Gnathopods 1 and 2 propodus palmar margins lined with stout peg-like spines. Epimeron 3 posterior margin serrate. Uropod 2 rami subequal with length of uropods 1 and 3.

## Eusiroides yucatanensis McKinney, 1980

Figs 24, 30D

Eusiroides yucatanensis McKinney, 1980: 89-93, figs 3, 4; Diaz and Martin 2000: 767.

Material examined. PANAMA•5-7 mm•1 〕, 1 q, 2 juvenile; Bocas del Toro, Crawl Cay; $9.2376^{\circ} \mathrm{N}, 82.1438^{\circ} \mathrm{W}$; depth $1.5-3 \mathrm{~m}$, among coral rubble, 11 Aug 2021; K.N. White leg.; USNM 1703552.


Figure 24. Eusiroides yucatanensis, male, 6.9 mm , telson, gnathopod 2 propodus medial, gnathopod 2 propodus medial enlarged, setae removed, epimeron 3, uropod 3. Scale bars: 0.5 mm .

Diagnosis. Pereopods 5-7 basis crenulate; propodus with spine formula 2, 2, 2, 2, and two locking spines. Epimera 1 and 2 smooth, posteroventral corner with acute point; epimeron 3 posterior margin with three serrations. Uropod 3 peduncle $1 / 2$ as long as rami. Telson subtriangular, longer than wide, apices of lobes subacute.

Distribution. Mexico: Yucatan (McKinney 1980); Venezuela: Puerto Viejo (Diaz and Martin 2000); Panama: Bocas del Toro (present study).

Ecology and remarks. These amphipods are associated with algae and coral rubble at depths of 0-3 m. Panamanian specimens closely resemble previously described specimens and can be easily identified based on the smooth epimera 1 and 2, epimeron 3 having three distinct serrations, and the length of uropod 3 peduncle.

## Genus Nasageneia Barnard \& Karaman, 1987

Diagnosis. Antenna 1 without accessory flagellum. Rostrum reaching ~ 1/2 length of first article of antenna 1 peduncle. Gnathopods 1 and 2 propodus relatively small, palmar margin lined with slender spines. Epimeron 3 posterior margin serrate. Telson subrectangular, slightly longer than wide, apices of lobes rounded or subtruncate.

## Nasageneia bacescui Ortiz \& Lalana, 1994

Figs 25, 30E

Nasageneia bacescui Ortiz \& Lalana, 1994: 285-291, figs 1-5; LeCroy 2007: 512 , fig. 451.

Material examined. PANAMA • 2.5-5 mm • 1 ठ Bocas del Toro, Drago; $9.413433^{\circ} \mathrm{N}, 82.33335^{\circ} \mathrm{W}$; depth $1-3 \mathrm{~m}$, among red algae; 23 June 2023; K.N. White leg.; USNM $1703553 \cdot 1 \delta^{\lambda}, 2$ ¢ Bocas del Toro, Swan Cay; $9.4536^{\circ} \mathrm{N}$, $82.300033^{\circ} \mathrm{W}$; depth 2 m , among red algae and coral rubble; 24 June 2023; K.N. White leg.; USNM 1703554.

Diagnosis. Rostrum narrow, curved, distally acute. Gnathopods 1 and 2 propodus palm each with four spines and several setae. Epimeron 3 posterior margin regularly serrate. Uropod 3 inner ramus slightly shorter than outer ramus Telson cleft $1 / 2$ of length, lobes not narrowing distally, apically rounded.

Distribution. U.S.A.: Tampa Bay to the Florida Keys (Ortiz and Lalana 1996); Cuba: Gulf of Batabano (Ortiz and Lalana 1994), Cayo Mendoza (Ortiz and Lalana 1996); Columbia: south of Cartagena (Ortiz and Lemaitre 1994); Panama: Bocas del Toro (present study).

Ecology and remarks. These amphipods are associated with algae and coral rubble at depths of 0-4 m. Panamanian specimens closely resemble previously described specimens. This species can be distinguished from the closely


Figure 25. Nasageneia bacescui, female, 3.1 mm , head, telson, epimeron 3 , uropod 3 ; male, 1.9 mm , gnathopods 1 and 2 medial. Scale bars: 0.5 mm .
related Tethygeneia longleyi based on the narrow, distally acute rostrum, regularly serrate epimeron 3, and wide telson lobes. See LeCroy (2007) for discussion of these species.

## Genus Tethygeneia J.L. Barnard, 1972

Diagnosis. Rostrum reaching ~ 3/4 length of first article of antenna 1 peduncle, linguiform. Gnathopods 1 and 2 propodus relatively small, palmar margin lined with slender spines. Epimeron 3 posterior margin smooth or weakly serrate. Telson subrectangular, slightly longer than wide, apices of lobes rounded or subtruncate.

## Tethygeneia longleyi (Shoemaker, 1933)

Figs 26, 30F

Pontogeneia longleyi Shoemaker, 1933: 253-254, figs 6, 7.
Tethygeneia longleyi: LeCroy 2007: 513, fig. 452.

Material examined. PANAMA•3-5 mm • 1 ; Bocas del Toro, Mangrove Inn; depth 1 m, among Caulerpa; 3 Aug 2005; M. Faust leg.; GCRL 6654•2 §ె, 1 ㅇ; Bocas del Toro, Drago; $9.418056^{\circ} \mathrm{N}, 82.3375^{\circ} \mathrm{W}$; depth $2-3 \mathrm{~m}$, among coral rubble, 9 Aug 2021; K.N. White leg.; USNM 1703555•3 〕, 7 q, 1 juvenile; Bocas


Figure 26. Tethygeneia longleyi, male, 2.1 mm , head, telson, epimeron 3, gnathopods 1 and 2 medial, uropod 3 . Scale bars: 0.5 mm .


Figure 27. Photographs of live specimens A Dulzura schoenerae B Ceraocus sheardi C Ceradocus shoemakeri D Elasmopus balkomanus E Elasmopus elieri (ethanol preserved specimen) F Elasmopus levis $\mathbf{G}$ Elasmopus longipropodus. Scale bars: 1.0 mm .


Figure 28. Photographs of live specimens unless noted A Elasmopus pocillimanus B Elasmopus thomasi C Meximaera diffidentia D Quadrimaera ceres (ethanol preserved specimen) E Quadrimaera cristianae F Quadrimaera miranda G Quadrimaera quadrimana. Scale bars: 1.0 mm .


Figure 29. Photographs of live specimens unless noted A Quadrimaera sarae B Quadrimaera yemanjae C Dulichiella anisochir (ethanol preserved specimen) D Dulichiella lecroyae E Melita planaterga F Hornellia tequestae. Scale bars: 1.0 mm .


Figure 30. Photographs of live specimens unless noted A Gibberosus devaneyi B Gibberosus myersi C Resupinus spinicaudatus (ethanol preserved specimen) D Eusiroides yucatanensis E Nasageneia bacescui F Tethygeneia longleyi. Scale bars: 1.0 mm .
del Toro, Drago; $9.413433^{\circ}$ N, $82.33335^{\circ}$ W; depth 1-3 m; among Halimeda and Dictyota, 23 June 2023; K.N. White leg.; USNM 1703556•2 §', Bocas del Toro, Swan Cay; $9.4536^{\circ} \mathrm{N}, 82.300033^{\circ} \mathrm{W}$; depth 2 m ; among red algae, 24 June 2023; K.N. White leg.; USNM $1703557 \cdot 2$ § 1 \& 1 , 3 juvenile; Bocas del Toro, Cayo Zapatilla 2; depth 0 m, buoy scraping; 29 June 2023; L. Hughes leg.; USNM 1703558.

Diagnosis. Rostrum wide, curved, distally rounded. Gnathopods 1 and 2 propodus palm each with one to three spines and several setae. Epimeron 3 posterior margin smooth or slightly serrate. Uropod 3 inner ramus subequal in length to outer ramus Telson cleft 3/4 of length, lobes narrowing distally, apically rounded.

Distribution. U.S.A.: Hutchinson Island to the Dry Tortugas, Florida (Shoemaker 1933; Camp et al. 1977; LeCroy 2007); Cuba: Archipélago Sabana-Camagüey (Ortiz and Lalana 1996); Venezuela: Maiguetia and Porlamar (Ruffo 1950); Brazil: Sao Paulo and Paraná (Wakabara and Serejo 1998); Panama: Bocas del Toro (present study).

Ecology and remarks. These amphipods are associated with algae and sand at depths of $0-11 \mathrm{~m}$. Panamanian specimens closely resemble previously described specimens in all aspects, and have the rounded telson apices as described by Shoemaker (1933) rather than the more subtruncate apices described by LeCroy (2007).

## Identification Key to the Caribbean Hadziidira of Panama

1 Gnathopod 2 simple; pereopod 7 elongate, distal articles extremely slender; uropod 3 rami broadly paddle-shaped (Fig. 21).

- Gnathopod 2 subchelate; pereopod 7 not elongate, or if elongate, distal articles not unusually slender; uropod 3 rami not broadly paddle-shaped (Fig. 10)
2 Head rostrum short, ocular lobe with cusp; antenna 1 accessory flagellum 2-articulate; gnathopod 2 merus with large distal lobe; uropod 1 peduncle with interramal tooth (Fig. 21)
- Head rostrum long, ocular lobe rounded; antenna 1 accessory flagellum 1-articulate; gnathopod 2 merus without distal lobe; uropod 1 peduncle without interramal tooth (Fig. 23).

Resupinus spinicaudatus
3 Head ocular lobe with subacute cusp; only pleosome segment 3 and urosome segment 2 with dorsal serrations; epimeron 3 smooth; uropod 3 rami continually lined with spines (Fig. 21)

Gibberosus devaneyi

- Head ocular lobe with acute cusp; pleosome segment 3 and urosome segments 1 and 2 with dorsal serrations; epimeron 3 serrate; uropod 3 rami with sparse marginal spines (Fig. 22)

Gibberosus myersi
4 Gnathopod 2 similar in size to gnathopod 1, not strongly sexually dimorphic; uropod 1 peduncle without basofacial spine(s), outer ramus distinctly shorter than inner ramus

- Gnathopod 2 larger than gnathopod 1, strongly sexually dimorphic; uropod 1 peduncle with basofacial spine(s), outer ramus subequal to or shorter than inner ramus
5 Antenna 1 accessory flagellum present (may be 1-articulate); telson lobes relatively narrow, apices acute or subacute (Fig. 24)
.. 6
- Antenna 1 lacking accessory flagellum; telson lobes relatively wide, apices rounded or subquadrate (Fig. 25)
.7

6 Antenna 1 accessory flagellum 1-articulate; gnathopods 1 and 2 propodus palmar margin lined with peg-like robust setae; epimeron 3 posterior margin serrate, posteroventral corner not produced; telson distinctly longer than wide, apices of lobes subacute (Fig. 24)

Eusiroides yucatanensis

- Antenna 1 accessory flagellum 5-articulate; gnathopods 1 and 2 propodus palmar margin lined with slender setae; epimeron 3 posterior margin smooth, posteroventral corner produced; telson slightly longer than wide, apices of lobes bifid and acute (Fig. 20)

Hornellia tequestae
7 Rostrum narrow, distally acute; epimeron 3 regularly serrate; telson cleft ~1/2 of length, lobes not narrowing distally; uropod 3 inner ramus slightly shorter than outer ramus (Fig. 25)

Nasageneia bacescui

- Rostrum wide, distally rounded; epimeron 3 smooth or with small serration; telson cleft $3 / 4$ of length, lobes narrowing distally; uropod 3 inner ramus subequal to outer ramus (Fig. 26)

Tethygeneia Iongleyi
8 Uropod 3 inner ramus minute (Fig. 1) .. 9

- Uropod 3 rami subequal or slightly unequal in length (Figs 5, 7) ................ 12

9 Gnathopod 2 of male, sides similar; posterodorsal margins of pleon segments 1-3 without serrations or teeth (Fig. 19) 10

- Gnathopod 2 of male, sides dissimilar, significantly different in size, larger side chelate; posterodorsal margins of pleon segments 1-3 with serrations or teeth (Fig. 17) 11
10 Coxa 6 of female anterior lobe with lateral ridge at base of hook; uropod 3 outer ramus 1-articulate (Fig. 19)

Melita planaterga

- Coxa 6 of female unmodified; uropod 3 outer ramus 2-articulate (Fig. 1)......

Dulzura schoenerae
11 Gnathopod 2 distolateral crown with four rounded or subacute spines, $4^{\text {th }}$ spine well developed, dactylus apically hooked, fitting into posterodistal corner; pereopods 6 and 7 carpus and propodus with bunches of long slender setae; epimeron 1 posteroventral corner subquadrate; epimeron 3 posterodistal margin smooth (Fig. 18)

Dulichiella lecroyae

- Gnathopod 2 propodus distolateral crown with three rounded indistinct spines, dactylus apically blunt, overlapping posterodistal corner; pereopods 6 and 7 carpus and propodus without bunches of long slender setae; epimeron 1 posteroventral corner acute; epimeron 3 posterodistal margin serrate (Fig. 17)

Dulichiella anisochir
12 Antenna 1 accessory flagellum 2- or 3-articulate; mandible, palp stout, article 3 falcate, with comb row of very short marginal setae; uropod 3 outer ramus < $3 \times$ longer than wide (Fig. 5)13

- Antenna 1 accessory flagellum at least 4-articulate; mandible, palp slender, article 3 linear, without comb row of short marginal setae; uropod 3 outer ramus $>3 \times$ longer than wide (Fig. 10) 18
13 Pereopod 7 basis posterior margin with long setae (Fig. 8)........................ 14
- Pereopod 7 basis posterior margin without long setae............................... 15

14 Male gnathopod 2 propodus elongate, palm with three teeth; epimeron 3, posteroventral margin serrate (Fig. 7)
.Elasmopus longipropodus

- Male gnathopod 2 propodus subovate, palm with large excavation; epimeron 3, posteroventral margin with single acute tooth (Fig. 8)

Elasmopus pocillimanus
15 Gnathopod 2 propodus palm with few setae; telson inner lobes apically rounded (Fig. 5)

- Gnathopod 2 propodus palm densely setose; telson inner lobes apically acute (Fig. 4) 17
16 Male gnathopod 2 propodus palm concave with one triangular process; epimeron 3 posteroventral margin with small tooth; telson inner lobes subequal in length with outer lobes (Fig. 5)

Elasmopus elieri

- Male gnathopod 2 propodus palm with 3 processes and 2 notches; epimeron 3 posterior margin serrate; telson inner lobes longer than outer lobes (Fig. 9)

Elasmopus thomasi
17 Pereopod 5 basis posterior margin concave; telson inner lobes shorter than outer lobes (Fig. 4)

Elasmopus balkomanus

- Pereopod 5 basis posterior margin evenly convex; telson inner lobes subequal to outer lobes (Fig. 6)

Elasmopus levis
18 Mandible palp article 1 with small distal tooth; maxilla 2 inner plate with dense oblique row of facial setae; uropod 3 rami broad, foliaceous, tips subacute (Fig. 2) 19

- Mandible palp article 1 without small distal tooth (Fig. 10); maxilla 2 inner plate without dense oblique row of facial setae (Fig. 16); uropod 3 rami slender, tips subtruncate (Fig. 10)
19 Male gnathopod 2 left and right sides dissimilar; pleon segments $1-3$ posterodorsal margins without strong teeth or serrations; urosome segments 1 and 2 posterodorsal margins each with single tooth (Fig. 3)

Ceradocus shoemakeri

- Male gnathopod 2 left and right sides similar; pleon segments 1-3, posterodorsal margins with many strong teeth or serrations; urosome segments 1 and 2 posterodorsal margins with many strong teeth (Fig. 2) ........ Ceradocus sheardi
20 Eyes oval; gnathopod 1 carpus subequal to propodus, without dorsal excavation; gnathopod 2 propodus palm oblique; pereopods with simple dactyli; pereopod 7 basis slimmer than long, without posterodistal lobe (Fig. 10)

Meximaera diffidentia

- Eyes round; gnathopod 1 carpus longer than propodus, with dorso-distal excavation; gnathopod 2 propodus palm with right angle; pereopods with bifid dactyli; pereopod 7 basis as slim as long, with posterodistal lobe (Fig. 11).... 21
21 Male gnathopod 2 propodus palm with deep excavations, palmar angle defined by elongate process below deep U-shaped notch (Fig. 14) 22
- Male gnathopod 2 propodus palm with shallow excavations, palmar angle defined by short process below shallow V-shaped notch (Fig. 15) ............ 24
22 Gnathopod 2 dactyl inner margin smooth in males and females; telson lobes apically truncate (Fig. 14) ............................................................................... 23
- Gnathopod 2 dactyl inner margin inflated in males and females; telson inner lobes inner corner acutely produced (Fig. 12)...........Quadrimaera cristianae
23 Gnathopod 1 propodus palm with short-to-medium setae; gnathopod 2 propodus palm with two large U-shaped excavations; telson with lateral plumose setae (Fig. 14)

Quadrimaera quadrimana

- Gnathopod 1 propodus palm with long setae; gnathopod 2 propodus palm with one large and two small excavations; telson without lateral setae (Fig. 16)

Quadrimaera yemanjae

24 Gnathopod 2 propodus palm transverse with central U-shaped concavity and subquadrate/quadrate processes, dactylus strong, medially expanded (Fig. 15)

Quadrimaera sarae

- Gnathopod 2 propodus palm transverse with smaller, deeper concavity and broad processes; dactylus not strong (Fig. 11)25

25 Gnathopod 2 dactylus inner margin inflated with median point (Fig. 13).......
Quadrimaera miranda

- Gnathopod 2 dactylus inner margin inflated without median point (Fig. 11).

Quadrimaera ceres

## Discussion

The results of this study represent range extensions for 26 species of hadziidirid amphipods to include Caribbean waters of Panama. Several species have a distribution pattern spanning the eastern Pacific and western Caribbean (Elasmopus pocillimanus, Meximaera diffidentia, Quadrimaera quadrimana, Gibberosus devaneyi, and Gibberosus myersi). Without examining material from every collection, it is impossible to be sure the species in the literature were identified correctly or if the specimens may represent a different species. Assuming proper identification, these distribution patterns may suggest that the species were established more than 3 mya, before the isthmus of Panama closed.

Several hadzidiiran species demonstrate variation in key characters or are identified based on males only. Several Elasmopus species are differentiated based on epimeron 3 serration patterns and the apices of telson lobes, both of which can vary among individual specimens. As discussed by LeCroy (2007) Tethygeneia and Pontogeneia show variation in epimeron 3 serration, which is a key character for identification of these species. Our identification key allows identification despite variation of both males and females of the Caribbean Hadziidira of Panama.

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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: KNW. Data curation: KNW. Formal analysis: SJS, KNW. Funding acquisition: KNW. Investigation: SJS, KNW. Project administration: KNW. Supervision: KNW. Writing - original draft: KNW. Writing - review and editing: SJS, KNW.

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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

## Locality table

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# Nomenclatural history of Megalonyx Jefferson, 1799 (Mammalia, Xenarthra, Pilosa, Megalonychidae) 

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#### Abstract

Both authorship and spelling of the extinct giant sloth genus Megalonyx and its type species, M. jeffersonii (Mammalia, Xenarthra, Pilosa, Megalonychidae), have been inconsistent. The genus-group name has been cited with two different authorships and three dates, and it has been spelled with two different suffixes. The species-group name has been cited with four different authors and dates, and it has been spelled with two different endings. Megalonyx Jefferson, 1799 is the first valid use of the genus-group name; the correct original spelling has the -onyx suffix. The type species of Megalonyx is Megatherium jeffersonii Desmarest, 1822; the correct original spelling has an -ii ending. A vernacular word, megalonyx, refers to species classified in the genus Megalonyx Jefferson, 1799.


Key words: Ground sloth, Pleistocene, Quaternary, Thomas Jefferson, Virginia, West Virginia

## Introduction

Megalonyx Jefferson, 1799 (Mammalia, Xenarthra, Pilosa, Megalonychidae) was the first genus-group name erected for an extinct vertebrate animal from the United States. This giant ground sloth, which was widespread across North America and now known from more than 180 localities (Semken et al. 2022), is emblematic of the large-mammal fauna of the Pleistocene Epoch of the Quaternary Period. Megalonyx ranks among the best known and most widely recognized extinct mammals; it appears in hundreds of scientific, historical, and popular publications, and appears in film and electronic media.

The first publications on Megalonyx (Jefferson 1799; Wistar 1799) were among the earliest contributions devoted to the scientific discipline that by the early 1820s would come to be known as "paleontology" (e.g., Simpson 1942; Boyd 1958; Bedini 1985; Rudwick 1997; Rowland 2009; Thomson 2011a, 2011b; De luliis 2018). The papers were published long before formal rules of zoological nomenclature were enacted, and standards for nomenclatural acts at the time were weak. These matters have led to misinterpretation or inconsistency about the authorship and correct spelling of Megalonyx, and about the authorship and correct spelling of its type species, M. jeffersonii. Inconsistency or dispute about these important nomenclatural matters have been a part of the scientific literature, and less formal media sources, from 1799 to the present.

The purpose of this paper is to review the nomenclatural history and authorship of Megalonyx and its type species by a review of pertinent early literature. This will serve to eliminate future inconsistency and confusion about the nomenclature of this animal.

## Discovery and early descriptions

Jefferson (1799), Cuvier (1804a), Leidy (1855), Simpson (1942), Bedini (1985), Stein (1993), Rudwick (1997), Rowland (2009), and Thomson (2011a, 2011b), among others, provided accounts of the discovery of the earliest-known skeletal remains of Megalonyx. The bones were collected in 1796 by saltpeter workers from unconsolidated Quaternary sediment in a cave in what was then Greenbriar County, Virginia, USA. The cave was said to belong to Frederic Cromer (Jefferson 1799: 246). Bones were removed from the cave and dispersed among various people as curiosities. From this assortment of skeletal remains, Colonel John Stuart of Virginia sent three bones to Thomas Jefferson, of MonticelIo, Virginia, in May 1796 (Rowland 2009: 236). Additional bones were supplied to Jefferson later, including by a Mr Hopkins of New York. Jefferson penned a paper on the remains, which in total comprised bones of the left manus, a radius and ulna, and the distal condyles of a femur (Boyd 1958; Rowland 2009; Thomson 2011a). The paper was delivered orally to the American Philosophical Society on 10 March 1797 and published, after emendation, in 1799

Jefferson's (1799) paper describing the skeletal remains included the erection of a genus-group name, Megalonyx, to receive them. Accompanying this paper, in the same volume, was a much more detailed analysis and interpretation of the remains, including illustrations, by Caspar Wistar (1799; Fig. 1), who recognized the resemblance of the remains to those of extant sloths. In or before 1804, Georges Cuvier received plaster casts, prepared by Charles Willson Peale, of the described bones, plus some additional remains putatively from the same cave as those reported by Jefferson (1799) and Wistar (1799). Those casts and fossils formed the nucleus for an extensive redescription and interpretation of Megalonyx (Cuvier 1804a, reprinted 1812a). Cuvier (1804a, 1812a) confirmed the conclusion of Jefferson (1799) and Wistar (1799) that Megalonyx was a sloth based on his comparison with Megatherium (Cuvier 1804b, 1812b; see also Bru 1804, 1812).

Some details about the occurrence of remains documented by Jefferson (1799), Wistar (1799), and Cuvier (1804a) were corrected by later authors. Grady (1997) provided cogent evidence that the Megalonyx remains described by Jefferson (1799) and Wistar (1799) originated from what is now called Haynes Cave, and which, after political reorganization, is currently located in Monroe County, West Virginia. The owner of the cave in 1796, identified as "Frederick Cromer," is an apparent misspelling of Frederick Gromer (Grady 1997). Leidy (1855) reported that the tooth (molar) that Cuvier (1804a: fig. 14) illustrated was collected from White Cave, Tennessee, not Frederick Gromer's cave, as originally reported.

Other early papers that addressed the nomenclature or anatomy of Megalonyx include Desmarest (1822), Harlan (1825), Leidy (1855), Orton (1891a), Claypole (1891), and Safford (1892). Many of the early papers citing Megalonyx were reviewed by Spamer et al. (1995: 213-216, 308). Desmarest (1822) erected a new species, Megatherium jeffersonii Desmarest, 1822 based on the remains


Figure 1. Megalonyx jeffersonii (Desmarest, 1822), bones of the holotype, left manus (see Daeschler in Thomson 2011a), reproduced from Wistar (1799: pl. 2, with modification), deposited in the Academy of Natural Sciences of Drexel University, Philadelphia, Pennsylvania (ANSP 12507); Quaternary (Pleistocene), probably from Haynes Cave, Monroe County, West Virginia (fide Grady 1997), USA. Wistar's numbers refer to: 1, 5 , metacarpals; 2, 3, phalanges; 4, unguals (claw cores). In the articulated digit at top of figure, the second phalanx (middle bone in the figure) is illustrated upside-down. For scale: the longest ungual, upper right, juxtaposed with other bones of the digit, is 17 cm long.
described by Jefferson (1799) and Wistar (1799). Harlan (1825) recombined this species as Megalonyx jeffersonii (Desmarest, 1822). Leidy (1855) published the first rather comprehensive description of the Megalonyx skeleton, incorporating new morphological information from post-1796 discoveries. Orton (1891a, 1891b) and Claypole (1891) described a partial skeleton from Millersburg, Ohio, that was mounted in 1896 (see McDonald et al. 2015; Babcock et al. 2023), providing an interpretation of the complete skeletal morphology and dimensions of the animal (Fig. 2). Safford (1892) provided a description of the pelvis of $M$. jeffersonii (see also Hovey 1891).

## Genus-group authorship and spelling

As first published, Megalonyx Jefferson, 1799 meets all the requirements for the availability of a new name published after 1757 and before 1931 (International Code of Zoological Nomenclature, Articles 8, 10-12, 21, 50; International


Figure 2. Megalonyx jeffersonii (Desmarest, 1822), reconstructed skeleton described by Orton (1891a, 1891b), Claypole (1891), and McDonald et al. (2015), from unconsolidated Quaternary sediment, Millersburg, Ohio, USA; mounted in 1896 by Ward's Natural Science Establishment for public display in the Orton Geological Museum of The Ohio State University (OSU 15758; see Babcock et al. 2023). The skull is a cast of a specimen illustrated by Leidy (1855: pls I-III, V), with three teeth inserted from the Millersburg megalonyx. As mounted, the skeleton stands 2.1 m tall.

Commission on Zoological Nomenclature 2000). This nomenclatural act has priority over all subsequent uses of Megalonyx in print (Article 23 of the Code; International Commission on Zoological Nomenclature 2000). The original description includes these components:

1. The nomenclatural act was published using ink on paper (Jefferson 1799: 248).
2. The name was stated to be new (Jefferson 1799: 248).
3. The scientific name, Megalonyx, with an uppercase " $M$," was accompanied by an etymology, "Great-Claw" (Jefferson 1799: 248). The Linnaean name derives from Greek roots, megalo-, great or large, and -onyx, claw or fingernail.
4. The scientific name was accompanied by a brief diagnosis; the genus being identified by the "distinguished size of that member," in reference to the "Great-Claw" (Jefferson 1799: 248).
5. The diagnosis was accompanied by a list and description of skeletal elements (Jefferson 1799: 247-251), plus a table of measurements of the available skeletal material (Jefferson 1799: 248-249).
6. The description was accompanied by a differential comparison with an extant mammal, the African lion (Jefferson 1799: 248-251). Jefferson's (1799) comparison reflected initial misinterpretation about the affinity of Megalonyx, an interpretation that was corrected in a postscript to the paper (Jefferson 1799: 259-260) with reference to Megatherium Cuvier, 1796.
7. The geographic and stratigraphic occurrence of the described skeletal elements was identified (Jefferson 1799: 246-247).

Jefferson (1799: 248, 250) introduced two names for the skeletal remains that he described, "Megalonyx" (p. 248), a properly formed, but not italicized, Linnaean name; and "megalonyx" (p. 250) a vernacular equivalent of Megalonyx. Ambiguity about the affinity of the animal's remains (Jefferson 1799: 259-260) is reflected in use of the vernacular term megalonyx, which, with a lowercase " $m$ " and as originally used, is different in form from the Linnaean name. Desmarest (1822: 366) recognized this distinction, indicating its equivalent in French, "Mégathère de Jefferson" (translated as "Jefferson's megatherium"), as a vernacular name, and separately proposing Megatherium jeffersonii as a Linnaean name. Such a distinction was common in early paleontological publications. Both Wistar (1799: 531) and Cuvier (1804a, 1812a), for example, used "megatherium" as a vernacular term for the ground sloth genus Megatherium Cuvier (1796). One of the bestknown examples of similar Linnaean and vernacular names is Mastodon Cuvier, 1817 as a genus-group name, and mastodon as a vernacular name, for the extinct proboscidean mammal now recognized as Mammut Blumenbach, 1799. Similarly, Buckland \& Conybeare (in Buckland 1824:391) applied both a Linnaean genus-group name, Megalosaurus, and a vernacular name, megalosaurus, for the first validly named animal that decades later would be called a dinosaur.

Authors (e.g., Boyd 1958; Rudwick 1997, 2005; Rowland 2009; herein, Fig. 2) commonly have used "megalonyx," or a variant, with a lowercase " $m$ " as a vernacular term for the genus Megalonyx. Cuvier (1804a) used the spelling "mégalonix," in French, but in other articles, which are also in French, he (Cuvier 1804b, 1812a, 1812b) used the spelling "megalonix." Desmarest (1822), writing in French, spelled the vernacular name as "mégalonyx." Both Wistar (1799) and Rudwick (1985) used the spelling "megalonix," in English, for the vernacular term.

Italicizing Latin names was not standard before 1931 (e.g., see Hovey 1891), and in some publication formats, non-italicized names have continued to be used even more recently (as in "Megalonyx"; e.g., Cohen 1995: 63). That Jefferson intended Megalonyx to be used as a Linnaean name, however, is evinced in a letter of his, which was reproduced by Faujas-Saint-Fond (1804: 316). In the letter, the name begins with a capital " $M$ " and is italicized. However, it is spelled with an -onix ending (see discussion below).

Megalonyx Jefferson, 1799 was named without designation of a type species or any included species at the time of first publication. As indicated below, Harlan (1825) is deemed to have subsequently designated Megatherium jeffersonii Desmarest, 1822 as the type species of Megalonyx. Specifying a type species, or even specifying any species included in a genus, was not always done prior to 1961. One salient example of this involves the dinosaur

Megalosaurus Buckland \& Conybeare in Buckland, 1824. Buckland and Conybeare (in Buckland 1824: 391) announced the genus as new, without naming or including any species in it. The type species, Megalosaurus bucklandii Mantell, 1827 was named and designated subsequently by a different author (Mantell 1827: 67-71; see Benson et al. 2008; Howlett et al. 2017).

In a paper that accompanied Jefferson (1799) in the same volume, Wistar (1799) first illustrated, and described in detail, the skeletal materials that Jefferson named as Megalonyx (Fig. 1). Wistar's (1799) analysis lent support for interpretation of Megalonyx as a sloth, a view more firmly advocated by Cuvier (1804a, 1812a).

As published, Megalonyx Jefferson, 1799, with an -onyx suffix is the correct original spelling of the genus-group name (see Article 32 of the Code; International Commission on Zoological Nomenclature 2000). This ending is correctly formed from the Greek root -onyx. Some early publications cited this genus with an -onix suffix (as Megalonix; e.g., Wistar 1799; Faujas-Saint-Fond 1804; Cuvier 1804a, 1804b, 1812a, 1812b). According to Article 33.3 of the Code (International Commission on Zoological Nomenclature 2000), this is an incorrect subsequent spelling.

Megalonyx was recognized as a valid genus-group name, with authorship and date stemming from Jefferson (1799) by all $19^{\text {th }}$ and $20^{\text {th }}$ century authors (e.g., Wistar 1799; Faujas-Saint-Fond 1804; Cuvier 1804a, 1812a; Desmarest 1822; Harlan 1825, 1831; Leidy 1855; Cope 1871, 1889; Orton 1891a, 1891b; Claypole 1891; Stock 1925; Osborn 1929, 1935; but see Lyon 1938, discussed below) until the work of Simpson (1942: 162, table), who argued that authorship of Megalonyx is "disputed," that its attribution to Jefferson "is certainly erroneous," and that Harlan (1825) "may have been the first to use the name in a valid Linnaean form ..." Harlan (1825: 201-203), in a compilation of extant and extinct mammals from North America known to the time, however, attributed the Linnaean name Megalonix (corrected to Megalonyx in an erratum) to Jefferson rather than stating that the name was being newly introduced. Some authors have implicitly accepted Simpson's (1942) argument and consequently cited Harlan (1825) for authorship of Megalonyx (e.g., Hirschfeld and Webb 1968; Hoganson and McDonald 2007; Holte 2012; Semken et al. 2022), whereas others have not (e.g., McDonald 1977; Ward and Allmon 2019). Regardless, Jefferson's (1799) original use of Megalonyx meets the requirements for an available nomenclatural act in all respects (Articles 8, 10-12, 21, 50 of the Code; International Commission on Zoological Nomenclature 2000), which invalidates Simpson's (1942) suggestion of an alternative authorship and date.

Lyon (1938: 15) attributed the genus Megalonyx to Jefferson, but cited 1797, the year the paper was read orally before the American Philosophical Society, as the date of publication. According to Articles 8 and 21 of the Code (International Commission on Zoological Nomenclature 2000), the name became available upon publication in the Society's Transactions in 1799, not 1797, when the paper was read.

## Species-group authorship and spelling

Desmarest (1822: 366) first published a species-group name for the skeletal remains that Jefferson (1799) described as Megalonyx. Desmarest (1822) placed Megalonyx in synonymy with Megatherium Cuvier, 1796 and erected the species Megatherium jeffersonii Desmarest, 1822. The skeletal elements of the individual
reported by Jefferson (1799) and Wistar (1799) comprise the holotype, by monotypy. The described fossils, which were originally deposited by Jefferson with the American Philosophical Society in 1797, were transferred to the Academy of Natural Sciences of Philadelphia in 1849 (Stein 1993), and they are now deposited in the Academy of Natural Sciences of Drexel University, Philadelphia, Pennsylvania, USA (ANSP 12507, bones of the left manus including metacarpals two, three, and five; the ungual of the first digit; the medial phalanx of the second digit; the proximal and ungual phalanges of the third digit, and the medial and ungual phalanges of the fourth digit, Fig. 1; ANSP 12508, left radius and ulna; see Spamer et al. 1995: 398). Some of the remains illustrated later by Cuvier (1804a, 1812a) also may have derived from this same individual animal, but this has not been unambiguously demonstrated (see discussion of a tooth, Leidy 1855: 4). Multiple Megalonyx individuals are known to occur at a few localities (Mercer 1897; Fields 2010; Holte 2011; Semken et al. 2022), including a cave site that possibly served as a maternity den (Holte 2012), so it is conceivable that Haynes Cave has yielded parts of multiple sloth skeletons. In the $19^{\text {th }}$ century, plaster casts of two unguals (claw cores) from the holotype were made widely available for sale by Ward's Natural Science Establishment, Rochester, New York (Ward 1870, 1891).

Harlan (1825: 26) resurrected the use of Megalonyx as a valid genus, which was monospecific at the time of his paper, and recombined the species as Megalonyx jeffersonii (Desmarest, 1822). As a result, Megatherium jeffersonii Desmarest, 1822 is the type species of Megalonyx, by subsequent designation (Harlan 1825) and monotypy.

With few exceptions, most authors have cited Desmarest (1822) as the first use of the binomen Megatherium jeffersonii. However, Leidy (1855) incorrectly cited Harlan (without a date, but presumably Harlan 1825; see Leidy 1855: 57) as the author of the species, recombined as Megalonyx jeffersonii, and this erroneous attribution was followed by Marsh (1874), Orton (1891a, 1891b), and Claypole (1891). Cope (1889: 660) mistakenly attributed authorship of Megalonyx jeffersonii to Cuvier (without a date, but presumably Cuvier 1804a). Hirschfeld and Webb (1968: 216) incorrectly cited Wistar (without a date, but undoubtedly Wistar 1799) as the author of Megalonyx jeffersonii.

The original spelling of the species-group name, Megalonyx jeffersonii (Desmarest, 1822) is with an -ii ending. However, some authors have spelled the species name with one -i as the ending (as M. jeffersoni; e.g., Orton 1891b; Slosson 1927; Lillegraven 1966; Hirschfeld and Webb 1968; Bedini 1985; Saarinen and Karme 2017). According to Articles 32, 33.3, and 33.4 of the Code (International Commission on Zoological Nomenclature 2000), M. jeffersonii is the correct original spelling, and substitution of -i for -ii constitutes an incorrect subsequent spelling.

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## Additional information

## Conflict of interest

The author has declared that no competing interests exist.

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Writing - original draft: LEB.

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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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# Three new species and one new record of Deimatidae (Echinodermata, Holothuroidea, Synallactida) discovered in the South China Sea and the Mariana fore-arc area using integrative taxonomic methods 

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#### Abstract

Deep-sea holothurian specimens were collected during five scientific expeditions (2018-2023) using the submersible vehicle 'Shenhaiyongshi'. Our examination of specimens of Deimatidae from the South China Sea and the Mariana fore-arc area revealed three new species, which were described as Oneirophanta idsseica sp. nov., Oneirophanta brunneannulata sp. nov., and Oneirophanta lucerna sp. nov. These species were distinguished from each other and from congeners by the arrangement, and number of ventrolateral tube feet and ossicle types. We also reported Oneirophanta mutabilis mutabilis Théel, 1879 for the first time from the Mariana fore-arc area, and we recorded Deima validum validum for the second time from the South China Sea. The taxonomy of these new species and new records is discussed, and a phylogenetic analysis based on a concatenated dataset of 16 S and COI genes was conducted. Additionally, the in-ter- and intraspecific genetic divergences we calculated among deimatid species. The results support the assignment of these new species to the genus Oneirophanta and their separation from congeners. A description of the main morphological characters of Oneirophanta species is also provided. The data were collected from geographically diverse areas and suggest that species of Deimatidae were abundant in the Pacific Ocean and occupied a wide range of depths.


Key words: COI, deep-sea, morphology, Oneirophanta, phylogeny, sea cucumber, SEM, taxonomy

## Introduction

Echinoderms are abundant in Chinese seas, and the South China Sea has more species than the Yellow Sea and the East China Sea (Liao and Xiao 2012). The South China Sea covers $\sim 3.5$ million $\mathrm{km}^{2}$, and it is studded with 200 islands and islets. It is in the center of the Indo-Western Pacific Biogeographic Province, and it is one of the most biodiverse seas in the world. The maximum recorded depth for echinoderms was 5377 m, with considerable habitat and species diversity (Morton and Blackmore 2001; Teh et al. 2019). Deep-sea exploration in

China began with the Jiaolong manned submersible in 2010, which has been used widely to uncover the deep-sea biodiversity in China seas and the Mariana Trench (Li 2017). Taxonomic research has revealed many new species and new geographical records of animal species in the deep waters of the South China Sea (Li et al. 2019).

Holothurians are the dominant epibenthic invertebrate taxon in many areas of the deep sea, and they account for $90 \%$ of that ecosystem's biomass (Hendler et al. 1995). However, our present knowledge of deep-sea holothurians is still limited due to the difficulty in collecting and depositing good specimens. Even the specimens collected by the submersible carefully and carried from the seabed to the sea surface in seawater-filled containers have arrived aboard the ship in very poor condition (Pawson 1982a). The epidermis and dermis of the whole holothurians begin to slough off, and the entire external body wall is often completely autotomized. The body wall contains a high proportion of water, even the most carefully preserved specimens will shrink greatly, and the shrinkage rate is frequently greater than $90 \%$ (Billett 1991). When preserved in absolute ethanol, the holothurians shrink, so all the external characters are easily distorted, which undoubtedly impacts their morphological identification negatively after collection. In recent years, few studies on the order Elasipodida have been conducted in the South China Sea (Li et al. 2018; Xiao et al. 2018, 2023), and studies on other taxa in the South China Sea have also been reported rarely. More morphological information and molecular data should be obtained for a comprehensive taxonomic evaluation of deep-sea holothurians in the South China Sea (Li et al. 2019).

The family Deimatidae formerly belonged in the order Elasipodida Théel, 1882, but was later transferred to the order Aspidochirotida by Smirnov (2012). Miller et al. (2017) subdivided paraphyletic ordo Aspidochirotida into three separate orders and placed family Deimatidae to the order Synallactida Miller, Kerr, Paulay, Reich, Wilson, Carvajal \& Rouse, 2017. The order Synallactida includes the families Deimatidae Théel, 1882, Stichopodidae Haeckel, 1896, and Synallactidae Ludwig, 1894. Deimatidae is the smallest family in the order, and it contains 13 accepted species within three genera (Oneirophanta Théel, 1879, Orphnurgus Théel, 1879, and Deima Théel, 1879) (WoRMS 2023). Only two of the recognized species in the family Deimatidae, Orphnurgus protectus (Sluiter 1901b) and Deima validum Théel, 1879, have been recorded from the South China Sea (Liao 1997). The genus Oneirophanta was established with Oneirophanta mutabilis Théel, 1879 as the type species (Théel 1879). Currently, there are only three species of Oneirophanta, and none of them have been found in China. Eleven deimatid specimens were collected from the South China Sea and the Mariana fore-arc area from 2018 to 2023. Morphological observations of these specimens suggested that they represented three new species and one new record from the Mariana fore-arc area, and they all belonged to the genus Oneirophanta.

In addition, we present a morphological description of Deima validum validum Théel, 1879, which was recorded for the second time in the South China Sea; the present specimens show some variations compared with specimens that were recorded previously. Our study provides comprehensive a description of morphological characters, an assessment of intraspecific divergence between the new species and all other known species, and more molecular details that may be useful for further studies of the phylogeny and diversity of the family Deimatidae.

## Materials and methods

## Sampling and preservation

Specimens were collected from the South China Sea and the Mariana forearc area (Fig. 1) using the manned submersible vehicle 'Shenhaiyongshi' from 2018 to 2023, at depths of 1340-3806 m. Samples were frozen or preserved in absolute ethanol, and then stored at the Institute of Deep-sea Sciences and Engineering (IDSSE), Chinese Academy of Sciences (CAS), Sanya, China.

## Morphological observations

The specimens of each species were identified using a variety of original descriptions and literature (Théel 1879; Koehler and Vaney 1905; Hansen 1967, 1975; Pawson 2002). External morphological features were examined under a dissecting stereomicroscope (OLYMPUS SZX7), and identification was based on in situ images or pictures photographed in our lab using a Canon EOS 6DII camera. To prepare the deposits, small pieces of body tissue (dorsal and ventral body wall, tentacles, papillae, and tube feet) were digested in a $15 \%$ sodium hypochlorite solution. The deposits were then washed three times in distilled water and dried in absolute ethanol before examination with a scanning electron microscope (Phenom ProX).

## DNA extraction, PCR amplification, and DNA sequencing

Total genomic DNA was extracted from small pieces of $20-30 \mathrm{mg}$ holothurian muscle tissue using a TIANamp Marine Animals DNA Kit (TianGen, Beijing),


Figure 1. Sampling sites for examined species of Deimatidae in the South China Sea and the Mariana fore-arc area.
according to the manufacturer's instructions. Mitochondrial cytochrome c oxidase I (COI) and 16S rRNA were generated for various specimens using the primers and methods outlined in Miller et al. (2017). The PCR amplification program was as follows: initial denaturation at $98^{\circ} \mathrm{C}$ for 3 min , followed by 40 cycles at $98^{\circ} \mathrm{C}$ for $10 \mathrm{~s}, 52^{\circ} \mathrm{C}$ for $10 \mathrm{~s}, 72^{\circ} \mathrm{C}$ for 10 s , and a final extension at $72^{\circ} \mathrm{C}$ for 5 min . Total reaction volume was $50 \mu \mathrm{~L}$ : $25 \mu \mathrm{~L}$ Premix Taq with 1.25 U Taq, 0.4 mM of each dNTP, $4 \mathrm{mMMg} 2+$ (Ex Taq version, Takara, Dalian, China), $0.5 \mu \mathrm{M}$ each of the primers and $\sim 100 \mathrm{ng}$ template DNA. The sequence chromatograms were then checked using CHROMAS 2.23 (Technelysium Pty Ltd.). The forward and reverse sequences were assembled using CONTIG EXPRESS, which is a component of Vector NTI Suite 6.0 (Life Technologies, Carlsbad, California).

## Phylogenetic analyses

Two partial sequences (COI and 16S) were obtained from specimens and were deposited in GenBank (Table 1), and some relevant sequences (from all available deimatid species) that were downloaded from BOLD (https://www. boldsystems.org/) and NCBI (https://www.ncbi.nlm.nih.gov/) databases were used for phylogenetic analyses. Apostichopus californicus and A. parvimensis in the family Stichopodidae (order Synallactida) were used to root the tree.

Sequence alignments were generated using MAFFT7 (Katoh and Standley 2013) with default parameters. Gblocks (Talavera and Castresana 2007) were used to remove batches of fragments from two alignments that were aligned ambiguously. The best partitioning scheme and evolutionary models for two pre-defined partitions were selected using PartitionFinder2 (Lanfear et al.

Table 1. List of GenBank accession numbers for all specimens used in this study.

| Species | GenBank accession number |  | Reference |
| :---: | :---: | :---: | :---: |
|  | 16S | COI |  |
| Deimatidae |  |  |  |
| Orphnurgus glaber | KX856746 | KX874361 | Miller et al. 2017 |
| Deima validum | KX856744 | KX874364 | Miller et al. 2017 |
| Deima validum validum SY155-HS01 | N/A | OR413734 | this study |
| Deima validum validum SY84-HS02 | OR658899 | OR413743 | this study |
| Oneirophanta setigera | KX856745 | KX874363 | Miller et al. 2017 |
| Oneirophanta stet. CCZ_100 | N/A | ON400706 | Bribiesca-Contreras et al. 2022 |
| Oneirophanta cf. mutabilis | ON406619 | ON400724 | Bribiesca-Contreras et al. 2022 |
| Oneirophanta idsseica sp nov. SY86-HS01 | OR658900 | OR413744 | this study |
| Oneirophanta idsseica sp. nov. SY84-HS01 | OR658898 | OR413742 | this study |
| Oneirophanta idsseica sp. nov. SY283-HS01 | OR658902 | OR413737 | this study |
| Oneirophanta brunneannulata sp. nov. SY157-HS01 | OR658901 | OR413733 | this study |
| Oneirophanta mutabilis SY310-HS01 | OR658897 | OR413735 | this study |
| Oneirophanta lucerna sp. nov. SY529-HS02 | OR658906 | OR413738 | this study |
| Oneirophanta lucerna sp. nov. SY530-HS01 | OR658903 | OR413739 | this study |
| Oneirophanta lucerna sp. nov. SY530-HS02 | OR658904 | OR413740 | this study |
| Oneirophanta lucerna sp. nov. SY530-HS03 | OR658905 | OR413741 | this study |
| Outgroups |  |  |  |
| Apostichopus californicus | DQ777096 | HM542319 | Miller et al. 2017 |
| Apostichopus parvimensis | KX856750 | KX874373 | Miller et al. 2017 |

2017), with all algorithms and AICc criteria. Maximum likelihood phylogenies (ML) were inferred using the Shimodaira-Hasegawa-like approximation likeli-hood-ratio test (Gascuel 2010) and IQ-TREE (Lam-Tung et al. 2015) models with 20,000 ultrafast bootstraps (Minh et al. 2013). Bayesian Inference phylogenies (BI) were inferred using MrBayes 3.2.6 (Ronquist et al. 2012) under the partition model (two parallel runs, 5,000,000 generations). The initial $25 \%$ of sampled data were discarded as burn-in, and the remaining trees were summarized in a $50 \%$ majority rule consensus tree. The results were visualized using FigTree v. 1.4.4. The Kimura two-parameter (K2P) genetic distances of COI among deimatid species were calculated using model MEGA X (Kumar et al. 2018).

## Results

## Taxonomy

Order Synallactida Miller, Kerr, Paulay, Reich, Wilson, Carvajal \& Rouse, 2017 Family Deimatidae Théel, 1882
Genus Oneirophanta Théel, 1879

Oneirophanta idsseica sp. nov.
https://zoobank.org/50ADB642-A7E7-476A-AE6C-B45C2803F272
Figs 2, 3

Oneirophanta stet. CCZ_100, Bribiesca-Contreras et al. 2022: 64-65, fig. 40.
Type material. Holotype. IDSSE-2018-0612-HS01, collected from the Xisha Trough of the South China Sea, station SY86-HSO1 ( $18^{\circ} 16.11^{\prime} \mathrm{N}, 113^{\circ} 25.32^{\prime} \mathrm{E}$ ), depth 2985 m, 12 Jun. 2018, preserved in absolute alcohol. Paratypes. Two specimens. IDSSE-2018-0531-HS01, collected from the Xisha Trough of the South China Sea, station SY84-HSO1 ( $18^{\circ} 2.70^{\prime} \mathrm{N}, 114^{\circ} 3.51^{\prime} \mathrm{E}$ ), depth 3156 m , 31 May 2018, preserved at $-80^{\circ} \mathrm{C}$. IDSSE-2020-0917-HSO1, collected from the northern slope of the South China Sea, station SY283-HSO1 ( $17^{\circ} 23.20^{\prime} \mathrm{N}$, $115^{\circ} 32.32^{\prime} \mathrm{E}$ ), depth $3806 \mathrm{~m}, 17 \mathrm{Sep}$. 2020, preserved in absolute alcohol.

Type locality. In the Xisha Trough, which is located in the northern slope of the South China Sea, depth 2985 m.

Diagnosis. Body elongated and cylindrical, color yellowish-white. Tentacles 15 . Ventrolateral tube feet up to $40-50$ pairs, in alternating two or three rows. Dorsal papillae 18-20 on each side, in single rows. Ventrolateral papillae 9-12 on each side, in single rows. Midventral tube feet two and rudimentary. Dorsal deposits irregular perforated plates and varying types of crosses. Perforated plates and crosses with open ramifications ventrally. Papillae deposits slender and sturdy rods with spatulated ends, and crosses with open ramifications. Spatulated rods and irregular deposits in tube feet. Sturdy spatulated rods in tentacles.

Description of holotype. External morphology. Body elongated and cylindrical, ventrum flattened. 29 cm long and 9 cm wide before fixation (Fig. 2A, B). Color in vivo yellowish-white, tentacles, papillae, and tube feet often darker (Fig. 2C, D). Mouth anteroventral, anus posteroventral. Tentacle discs with rounded knobs at the edges, and the tentacles partially retracted into the mouth, making the number of tentacles difficult to calculate. Ventrolateral tube


Figure 2. Oneirophanta idsseica sp. nov. (Holotype: IDSSE-2018-0612-HS01) A in situ image B holotype in live C dorsal view D ventrolateral view. Scale bars: 5 cm .
feet 40 pairs, arranged in alternating two or three rows on each ventrolateral ambulacrum. Midventral tube feet two and rudimentary, scattered along the mid-ventral ambulacrum, one positioned in the front third of the body, the other is positioned in the back third of the body, the anus surrounded by few small tube feet. Dorsal papillae roughly 18-20 on each body side, evenly distributed, measuring $4-10 \mathrm{~cm}$ in length, and placed in single rows along the dorsal radii. Ventrolateral papillae $\sim 9-12$ on each side, generally shorter than dorsal papillae, measuring $2.5-7 \mathrm{~cm}$ in length, arranged in single rows along the ventrolateral radii. All papillae slender and tapering from base to end.

Ossicle morphology. Dorsal deposits contain (1) perforated plates with open ramifications (Fig. 3A3, A9, A10), $0.3-0.8 \mathrm{~mm}$ in diameter, bearing $0-5$ processes on the surface, central holes smaller towards the edge. (2) crosses two types, the first with dichotomously ramified ends, one side bearing 2-5 processes and the other side smooth and without spines (Fig. 3A5-A8); the second irregular, with arms slender than the first type and numerous bifurcated spines throughout the length (Fig. 3A1, A2). (3) spatulated rods with enlarged ends (Fig. 3A4). Papillae deposits contain (1) extremely slender or sturdy spatulated rods, $0.8-1.6 \mathrm{~mm}$ long (Fig. 3B1, B7-B10); (2) spatulated crosses with 2-3 processes on the surface (Fig. 3B2, B5, B6); (3) crosses with open ramifications resembling dorsal deposits (Fig. 3B3, B4). Deposits in tentacles only spatulated rods (Fig. 3C), more robust than spatulated rods in papillae. Tube


Figure 3. SEM images of different tissues from Oneirophanta idsseica sp. nov. (Holotype: IDSSE-2018-0612-HS01) A1A10 dorsal body wall B1-B10 papillae C tentacles D1-D4 tube feet E1-E5 ventral body wall. Scale bars: $50 \mu \mathrm{~m}$ (A1, A2, A7, B3, B4, D3, D4, E4); $100 \mu \mathrm{~m}$ (A3-A6, A8, A10, B2, B5, B6, E3, E5); $300 \mu \mathrm{~m}$ (A9, B1, B7-B10, C, D1, D2, E1, E2).
feet deposits mainly robust spatulated rods (Fig. 3D1, D2), 0.6-0.8 mm long, and irregular deposits, possibly in the developmental stage of perforated plates (Fig. 3D3, D4). Deposits in the ventrum same as dorsal (Fig. 3E1-E5), except for large spatulated rods with enlarged ends (Fig. 3A4).

Etymology. Consists of IDSSE and the Latin suffix icus (belonging to), to honor IDSSE's contributions and efforts to the field of deep-sea exploration.

Distribution. A seamount in APEI 4, Clarion Clipperton Zone; Xisha Trough, the northern slope of the South China Sea, at depths of 2985-3806 m.

Remarks. Oneirophanta idsseica sp. nov. is characterized by the arrangement of ventrolateral tube feet in two or three rows that number up to 40-50 pairs with distinctive cross-types in dorsal deposits. O. idsseica sp. nov. is distinct from Oneirophanta setigera (Ludwig 1893) due to the presence of small, perforated plates and crosses with open ramifications that are usually bifurcated. 0 . idsseica sp. nov. differs from Oneirophanta conservata Koehler \& Vaney, 1905 and Oneirophanta mutabilis Théel, 1879 by the arrangement and high number of ventrolateral tube feet, and the absence of large, perforated plates on dorsum.

The phylogenetic trees showed that 0 . idsseica sp . nov., together with an unnamed species (Oneirophanta stet. CCZ_100, see below), formed a sister group that included Oneirophanta cf. mutabilis and O. mutabilis. From a morphological point of view, 0 . idsseica sp . nov. mostly resembled 0 . stet. CCZ_100 with ventrolateral tube feet arranged in two or three rows, two rudimentary midventral tube feet, spatulated crosses and small, irregular perforated plates on dorsum, and crosses with open ramifications in different stages of development on the ventrum. From a molecular point of view, the COI pairwise distance between 0 . idsseica sp. nov. and 0 . stet. CCZ_100 was $0.6 \%$ (Suppl. material 1). Compared with the description of 0 . stet. CCZ_100, our study provides more details of ossicle morphology of tentacles, tube feet, and papillae.

## Oneirophanta brunneannulata sp. nov.

https://zoobank.org/97066926-74E7-4525-A25D-0F047F525BCC
Figs 4, 5

Type material. Holotype. IDSSE-2018-0612-HS01, collected from the continental slope of the South China Sea, station SY157-HSO1 ( $18^{\circ} 51.18^{\prime} \mathrm{N}, 114^{\circ} 24^{\prime} \mathrm{E}$ ), depth 1340 m, 1 Jul. 2019, preserved in $-80^{\circ} \mathrm{C}$

Type locality. On the continental slope of the South China Sea, depth 1340 m.
Diagnosis. Body elongated, color reddish brown, with darker tentacles and tube feet. Mouth and anus ventral. Tentacle 20. Ventrolateral tube feet $\sim 37$ pairs, each tube foot end with a brown ring, arranged in alternating three rows, bilateral symmetry. Dorsal papillae 23-26 on each body side, arranged in single rows. Ventrolateral papillae 9-11 on each body side. Midventral tube feet two and rudimentary. Deposits perforated plates, rods of varying shapes and few spatulated crosses.

Description of holotype. External morphology. Body elongated, dorsum convex, ventrum flattened. 20 cm long, and 5 cm wide before fixation (Fig. 4A, B). Skin reddish brown, with darker coloration on tentacles and tube feet, a brown ring at the end of each tube foot. Tentacle 20, never with ramified processes, circum-oral papillae absent. Ventrolateral tube feet $\sim 37$ pairs, placed in alternating three rows, bilateral symmetry. Midventral tube feet two and rudimentary, one placed on half the body, the other placed on a rear quarter of the body, and several small tube feet surrounding anus. Dorsal papillae 23-26 on each body side, arranged in single rows along dorsal radii, measuring 5-6 cm.


Figure 4. Oneirophanta brunneannulata sp. nov. (Holotype: IDSSE-2018-0612-HS01) A dorsal view B ventral view. Scale bar: 6 cm .

Ventrolateral papillae 9-11 on each side, arranged in single rows, comparatively shorter than dorsal papillae, measuring $2.3-4.6 \mathrm{~cm}$.

Ossicle morphology. Dorsal deposits only robust perforated plates present (Fig. 5A1-A3), $0.6-1.1 \mathrm{~mm}$ in diameter, with central holes tapering from the center to the end, some perforated plates with irregular central apophysis (Fig. 5A1). Papillae contain (1) robust spatulated rods (Fig. 5B1-B3), 0.8-1 mm in length and partially connected at the ends (Fig. 5B1); (2) spatulated crosses (Fig. 5B4); (3) Perforated plates with 2-4 large central holes, rather slender than dorsal, measuring an average 0.9 mm in diameter (Fig. 5B5, B6). Tentacle deposits slender and sturdy rods with open ramifications (Fig. 5C), $0.4-0.6 \mathrm{~mm}$ in length. Tube feet with varying types of rods: (1) slender rods with open ramifications, 0.5-0.7 mm long (Fig. 5D1); (2) smooth spindle-shaped rods without spines, 0.7 mm in length (Fig. 5D2); (3) sturdy spatulated rods (Fig. 5D1, D3, D4), with rudimentary or enlarged ends, $0.5-0.9 \mathrm{~mm}$ in length. Numerous amorphous shaped, irregular broken deposits on ventrum (Fig. 5E1, E2).


Figure 5. SEM images of Oneirophanta brunneannulata sp. nov. (Holotype: IDSSE-2018-0612-HSO1) A1-A3 dorsal body wall B1-B6 papillae C tentacles D1-D4 tube feet E1-E2 ventral body wall. Scale bars: $300 \mu \mathrm{~m}$.

Etymology. The specific epithet brunneannulata in Latin means brown rings. It is here used as a noun in apposition and refers to the distinctive brown rings around the tube feet.

Distribution. Only in the type locality.
Remarks. Oneirophanta brunneannulata sp. nov. differs from other species in the genus in possessing brown rings at the end of tube feet that are arranged in three rows along ventrolateral radii. 0 . brunneannulata sp . nov. is relatively similar to 0 . mutabilis in possession of plates and spatulated rods, but there are differences: (1) different diameters of perforated plates, 0.6-1.1 mm in 0 . brunneannulata sp. nov., but 2-3 mm in 0 . mutabilis, and some perforated plates in O. brunneannulata sp. nov. possess a central apophysis. (2) different types of
deposits in tube feet, $O$. brunneannulata sp . nov. has various forms of spatulated rods and a few spindle-shaped rods, but lacks perforated plates, and there are perforated plates in addition to sturdy and spatulated rods in 0 . mutabilis. 0 . brunneannulata sp . nov. differs from 0 . setigera in having perforated plates on the dorsum and the ventrum, lacked spatulated crosses, and had a large number of tube feet that were arranged in three rows. Larger central perforations on perforated plates were in papillae, and the presence of spatulated rods and papillae were arranged in single rows along the dorsal radius (double rows along dorsal radius in 0 . conservata) distinguished $O$. brunneannulata sp . nov. from O. conservata (Table 2).

## Oneirophanta lucerna sp. nov.

https://zoobank.org/DF0BA6C4-E07A-467A-9983-603B303CDA6E Figs 6, 7

Type material. Holotype. IDSSE-2023-0208-HSO2, northern slope of the South China Sea, station SY530-HS02 ( $16^{\circ} 28.60^{\prime} \mathrm{N}, 110^{\circ} 18^{\prime} \mathrm{E}$ ), depth 1389 m, 8 Feb. 2023, preserved in absolute alcohol. Paratypes. Three specimens. IDSSE-2023-0204-HS02, northern slope of the South China Sea, station SY529-HSO2 ( $16^{\circ} 28.20^{\prime} \mathrm{N}, 110^{\circ} 43^{\prime} \mathrm{E}$ ), depth 1393 m, 4 Feb. 2023, preserved in absolute alcohol. IDSSE-2023-0208-HS01, northern slope of the South China Sea, station SY530-HSO1 ( $16^{\circ} 28.30^{\prime} \mathrm{N}, 110^{\circ} 43^{\prime} \mathrm{E}$ ), depth 1389 m, 8 Feb. 2023, preserved in absolute alcohol. IDSSE-2023-0208-HSO3, northern slope of the South China Sea, station SY530-HSO3 ( $16^{\circ} 28.18^{\prime} \mathrm{N}, 110^{\circ} 43^{\prime} \mathrm{E}$ ), depth 1392 m, 8 Feb. 2023, preserved in absolute alcohol.

Type locality. Northern slope of the South China Sea, depth 1389 m.
Diagnosis. Body elongated, skin smooth, color orange in vivo. Mouth anteroventral, anus posteroventral. Tentacle 19 or 20. Ventrolateral tube feet 11-14 on each body side, arranged in single rows. Midventral tube feet two and rudimentary. Dorsal papillae 15-27 on each side, placed in single rows along dorsal radius. Ventrolateral papillae 7-10 on each side, arranged in single rows. Dorsal deposits spatulated crosses, spatulated rods, and widely scattered spinous rods with branched spines. Papillae deposits with spinous rods and spatulated rods. Spatulated crosses with the arms twice divided and two types of spinous rods are in ventrum. Spinous rods and sturdy spatulated rods with open ramifications in tentacles and tube feet.

Description of holotype. External morphology. Body elongated, dorsum inflated, ventrum flattened, slightly narrowed anteriorly (Fig. 6). Length in vivo 22 cm (Fig. 6B), in ethanol 20 cm . Maximum body width 6 cm in vivo, 5.7 cm in ethanol. Color in vivo orange (Fig. 6C), tentacle and tips of papillae and tube feet more pigmented than the body skin. Tentacle 20. Circum-oral papillae absent. Mouth anteroventral, anus posteroventral terminal. Ventrolateral tube feet 14 pairs, placed in single rows on ventrolateral ambulacrum, partly projecting horizontally from the body (Fig. 6D). Midventral radius naked. Midventral tube feet two and rudimentary, with one placed on half the body, while the other placed on a rear quarter of the body, and several smaller tube feet close to anus. Left dorsal papillae 27, right dorsal papillae 21, measuring 1.5-5.2 cm, arranged in regular single rows along dorsal radii (Fig. 6C). Ventrolateral papillae 9-10 on each side, measuring 2.2-3.2 cm, placed in single rows along the ventrolateral radii.
Table 2. Main morphological characters in species of Oneirophanta Théel, 1879.

| Characteristics | O. idsseica sp. nov. | O. brunneannulata sp. nov. | O. lucerna sp. nov. | O. conservata | O. setigera | O. mutabilis mutabilis | O. mutabilis affinis |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Tentacle number | 15 | 20 | 19 or 20 | Only eight founded | 15-20 | 18-20 | 18-20 |
| Ventrolateral tube feet number and arrangement | 40-50 pairs, in alternating two or three rows | ~ 37 pairs, in alternating three rows | 11-14 on each side, in single rows | 33-34 on each side, in two rows | 16-30 on each side, in alter-nating double rows | 8-28 (36), in alternating double rows | 15-20 (44), - |
| Dorsal papillae number and arrangement | 18-20 on each side, in single rows | 23-26 on each body side, in single rows | 15-27 on each body side, in regular single rows | 30, in double rows | 12-32, in irregular double rows | 4-19, in single rows | $5-35$, in single or double rows |
| Ventrolateral papillae number and arrangement | 9-12 on each side, in single rows | $9-11$, in single rows | 7-10, in single rows | 13, in two rows | 9-17, - | 4-17, - | 5-11, - |
| Midventral tube feet number and arrangement | Two and rudimentary, one positioned in the front third of the body, the other positioned in the back third of the body | Two, rudimentary, one placed on half the body, the other placed on a rear quarter of the body | Two and rudimentary, one placed on half the body, the other on a rear quarter of the body | 12, placed through-out the entire length of this radius, sometimes in pairs | $0-6$, in front of the anus | 0-4, pre-anal | $3-9$, usually one pair placed pre-anal |
| Dorsal Deposit | Perforated plates with open ramifications and crosses with dichotomously ramified ends or irregular, and spatulated rods | Perforated plates, 0.6-1.1 mm in diameter, some with irregular central apophysis | Spatulated crosses, spinous rods with branched spines, spatulated rods up to 1 mm | Perforated plates, some in the developmental stage, rods with slightly thorny surfaces, pointed or bifid ends occasionally | Spatulated crosses, $1.1-3 \mathrm{~mm}$ | Perforated plates, 2-3 mm in diameter, bearing several small, vertical spines, with a rather slender mesh-work | Robust and rather small, vertical spines, often irregularly shaped due to elongation of the primary rod |
| Ventral | Perforated plates and crosses with open ramifications | Numerous irregular broken deposits, amorphous shaped | Spinous rods and spatulated crosses with arms twice divided | - | Spatulated crosses, $0.2-2.3 \mathrm{~mm}$ | Vary more, less welldeveloped, and less irregular than dorsal ones | - |
| Papillae | Slender or sturdy rods, crosses with open ramifications, some bearing 2-3 processes | Perforated plates with 2-4 large central holes, robust spatulated rods and few spatulated crosses | Spinous rods and spatulated rods |  | Spatulated rods | Perforated plates only | Perforated plates, small, sturdy and spatulated rods |
| Tube feet | Mainly robust spatulated rods and irregular deposits | Smooth spindle-shaped rods, slender rods with dichotomously ramified ends, sturdy spatulated rods with rudimentary or enlarged ends | Spinous rods of two types, one irregularly shaped, the other with few regularly distributed spines, sturdy spatulated rods with |  | - | Perforated plates | Sturdy and spatulated rods |
| Tentacle | Sturdy spatulated rods | Slender and sturdy rods with open ramifications | perforated extremities that occasionally bifurcated |  | - | Irregularly placed and stout rods, somewhat branched | Clusters of rod-shaped spicules |
| Data source | Bribiesca-Contreras et al. 2022; this study | This study | This study | Koehler and Vaney 1905; Hansen 1975 | Ludwig 1893; <br> Hansen1975 | Théel 1879; Hansen 1975 | Théel 1879; Hansen 1975 |

'-'means data not available.


Figure 6. Oneirophanta lucerna sp. nov. (Holotype IDSSE-2023-0208-HSO2) A, B in situ images C dorsal view D ventral view. Scale bars: 5 cm.

Ossicle morphology. Dorsal deposits contain spatulated crosses, spinous rods and spatulated rods. Spinous rods with irregular spines, $0.1-0.2 \mathrm{~mm}$ in length (Fig. 7A1, A2); spatulated crosses with arms 0.2-0.8 mm in length (Fig. 7A3); spatulated rods up to 1 mm (Fig. 7A4). Papillae with spinous rods 0.20.3 mm in length (Fig. 7B1, B2), and spatulated rods $0.4-0.9 \mathrm{~mm}$ in length, some with an extra branch from central part (Fig. 7B3), some bifurcated at the end (Fig. 7B4). Ventral body wall spatulated crosses with the arms twice divided (Fig. 7C1, C2) and the spinous rods of two types, one with more complex and irregularly placed spines (Fig. 7C3), the other with fewer and more regularly arranged spines (Fig. 7C4), up to 0.4 mm long. Tentacles and tube feet with similar ossicle types, spinous rods of two types, a few regularly distributed spines, $0.3-0.35 \mathrm{~mm}$ in length (Fig. 7D1, E1), irregularly shaped (Fig. 7D5, E2), and somewhat sturdy spatulated rods with perforated extremities that occasionally bifurcated (Fig. 7D2-D4, E3, E4), 0.2-0.7 mm in length.

Etymology. The species was named after the Latin word lucerna to commemorate the traditional Chinese Lantern Festival, which was relatively close to the time these specimens were collected.

Distribution. Northern slope of the South China Sea, depths of 1389-1393 m.
Remarks. The new species conformed to the genus Oneirophanta characterized by uncontracted the tentacles, the absence of oral papillae and tentacle discs without ramified processes. Oneirophanta lucerna sp. nov. differed from other species of Oneirophanta in possessing highly variable shaped spinous rods and ventrolateral tube feet that are only arranged in single rows, whereas,


Figure 7. SEM images of Oneirophanta lucerna sp. nov. (Holotype IDSSE-2023-0208-HS02) A1-A4 dorsal body wall B1B4 papillae C1-C4 ventral body wall D1-D5 tube feet E1-E5 tentacles Scale bars: $50 \mu \mathrm{~m}$ (A1-A2, B1-B2, C2); $100 \mu \mathrm{~m}$ (C3, D1-E5); $200 \mu \mathrm{~m}$ (A3, A4; B3-C1).
in other species (Table 2), they are arranged in two or three rows along ventrolateral ambulacrum: 0 . conservata, 0 . setigera, and 0 . mutabilis in double rows, O. idsseica sp. nov. in alternating two or three rows, and 0 . brunneannulata sp . nov. in three rows. The three accepted species of Oneirophanta and the other
two new species in this study all have perforated plates that are absent in Oneirophanta lucerna sp. nov. This is the first record of a species in the genus Oneirophanta with mainly irregular spinous rods.

## Oneirophanta mutabilis mutabilis Théel, 1879

Figs 8, 9

Oneirophanta mutabilis Théel, 1879: 6-7, figs 4-6; Théel 1882: 62-68, pls XXI: 2, XXII, XXXI: 1-3, XXXVI: 1, 2, 8-11, XXXVII: 4, 13, XXXVIII: 11-12, XL: 1-3, XLI: 1, 2, 4, XLII: 9, XLIII: 1, 6, XLV, XLVI: 6, 7; R. Perrier 1902: 374-380, pl. XVIII: 10-15; Grieg 1921: pl. II: 1, 2; Hérouard 1923: 39-40, pls IV: 10, V: 3, 4; Agatep 1967: 63-65, pl. X: 1-7.
Oneirophanta mutabilis mutabilis Théel: Hansen 1967: 485-488, figs 3, 4; Hansen 1975: 24-32, figs 2-5.
Oneirophanta alternata R. Perrier, 1900: 117-118; R. Perrier 1902: 380-386, pls XIV: 3, 4, XVIII: 16-22.
Oneirophanta alternata var. talismani R. Perrier, 1902: 386-388, fig. 6.

Material examined. One specimen. IDSSE-2020-1203-HS01, in the Mariana fore-arc area, western Pacific Ocean, station SY310-HSO1 ( $11^{\circ} 41.42^{\prime} \mathrm{N}$, $140^{\circ} 58.56^{\prime} \mathrm{E}$ ), depth $3394 \mathrm{~m}, 3$ Dec. 2020, preserved in absolute alcohol.


Figure 8. Oneirophanta mutabilis mutabilis Théel, 1879 (IDSSE-2020-1203-HS01) A dorsal view B ventral view. Scale bar: 3 cm.
cription. External morphology. Body cylindrical, nearly equal in width throughout the whole length and tapering anteriorly. 15 cm long and 4.5 cm wide after fixation with $95 \%$ alcohol for several days (Fig. 8A, B). Skin white, calcified and brittle. Tentacles 20, unretractile, $0.6-1.6 \mathrm{~cm}$ in length, with 7-9 marginal digits. Mouth and anus ventral. Ventrolateral ambulacra with 16 tube feet on each side, arranged in two irregular rows. Dorsal papillae 6 pairs, the maximum length up to 10 cm , placed in single rows along dorsal radii. Ventrolateral papillae 13 on each side, the maximum length up to 6 cm . Midventral tube feet not found due to damage to the mid-abdomen of the specimen, and only approximately six small tube feet observed near the anus.


Figure 9. SEM images of Oneirophanta mutabilis mutabilis Théel, 1879 (IDSSE-20201203-HS01). A1, A2 dorsal body wall B1, B2 dorsal papillae C1-C3 ventral body wall D1-D5 tube feet E1-E5 tentacle. Scale bars: $300 \mu \mathrm{~m}$ (A1-C3); $100 \mu \mathrm{~m}$ (D1-E1, E3-E5); $50 \mu \mathrm{~m}$ (E2).

Ossicle morphology. The body wall and papillae with perforated plates (Fig. 9A1-C3), 0.9-1.5 mm in diameter. The entire periphery of fully developed plates usually surrounded by closed holes, with large central holes (especially in ventrum) and small peripheral holes. Some plates bearing 8-14 small, vertical spines (Fig. 9B1, C3), but no formation of a secondary layer of meshwork. Tube feet with rods up to 0.8 mm long (Fig. 9D1, D2, D4) and incompletely developed plates with open ramifications (Fig. 9D3, D5). The irregular rods in tentacles with variable bending angles (Fig. 9E1-E5).

Distribution. Cosmopolitan, depth 2515-6000 m (Hansen 1975, 1967; Thandar 1984).

Remarks. Oneirophanta mutabilis was first described west of the Crozet Islands (H.M.S. Challenger station 146: $46^{\circ} 46^{\prime} \mathrm{S}, 45^{\circ} 31^{\prime} \mathrm{E}$ ) at depths of 2514 m (Théel 1879). It was divided into two subspecies, Oneirophanta mutabilis mutabilis Théel, 1879 and Oneirophanta mutabilis affinis Ludwig, 1893, based on differences in tentacle shape, the type of deposit, and the number of dorsal papillae (Hansen 1967). There are four main distinctions between them (see Table 2): (1) 0 . $m$. affinis was restricted to a relatively small area in the eastern Pacific where it replaced the otherwise cosmopolitan 0 . m. mutabilis. (2) tentacles with marginal digits were found in all specimens examined of $0 . \mathrm{m}$. mutabilis, but tentacle discs of $O$. m . affinis were smooth or had incised edges, and they lacked marginal digits. (3) the perforated plates of 0 . $m$. affinis were almost completely devoid of vertical spines, whereas those of 0 . m. mutabilis had vertical spines. (4) numerous rods of 0 . m. affinis were usually present in the tentacle discs, which was an additional difference from 0 . m. mutabilis. The morphological characteristics of our specimens were in accordance with the description of $O$. m. mutabilis (Hansen 1975). This was the first record of $O$. m. mutabilis from the Mariana fore-arc area.

## Genus Deima Théel, 1879

## Deima validum validum Théel, 1879

Figs 10, 11
Deima validum Théel, 1879: 5, figs 36-38; Théel 1882: 68-70, pls 18, 19, 31 : 4-9, 36: 4, 37: 8, 43: 7, 44: 13, 46: 5; Sluiter 1901a: 60.
Deima validum validum: Hansen 1967: 488-490, fig. 5; Hansen 1975: 17-23, fig. 1, pls 11 (fig. 1), 13, (figs 1, 2); Bohn 2006: 9, fig. 4; Fernández-Rodríguez et al. 2019: 298, fig. 6.
Deima fastosum Théel, 1879: 5-6, figs 1-3; Théel 1882: 71-73, pls 20, 21: 1, 31 : 10-13, 35: 7-10, 36: 7. 37: 3, 43: 2-3, 5, 46:8.
Deima blakei Théel, 1886b: 1-2, figs 1, 2; Koehler and Vaney 1905: 55-57, pl. 11: 13-15; Hérouard 1923: 40-41, pls. 5: 7, 6: 5; Deichmann 1930: 115-116, pls 10: 7-11, 11: 1-3; Deichmann 1940: 198-199.
Deima atlanticum Hérouard, 1898: 88-89, figs 1, 2.
Deima mosaicum Ohshima, 1915: 233-234.

Material examined. Two specimens. IDSSE-2019-0630-HSO1, collected from the northern slope of the South China Sea, station SY155-HSO1(170 $3^{\prime} \mathrm{N}, 114^{\circ} 13^{\prime} \mathrm{E}$ ), depth 3451 m, 30 Jun. 2019, preserved in absolute alcohol. IDSSE-2018-0531-

HS02, collected from the Xisha Trough of the South China Sea, station SY84HSO2 ( $18^{\circ} 2^{\prime} \mathrm{N}, 114^{\circ} 5^{\prime} \mathrm{E}$ ), depth $3404 \mathrm{~m}, 31$ May 2018 , preserved at $-80^{\circ} \mathrm{C}$.

Description. External morphology. Body ovate, dorsal vaulted, ventral flattened. $9-10 \mathrm{~cm}$ long and average 5.5 cm wide in vivo. Skin rigid, body wall brittle and easily broken. Color orange in vivo (Fig. 10A, B). Tentacles retracted into the mouth, resulting in uncountable quantities (Fig. 10C, D). 12 pairs of ventrolateral tube feet contractible based on morphology of different stages, single-rowed. Five pairs of rigid and conical dorsal papillae placed in two rows. Ventrolateral papillae three pairs, half the length of the body. Pre-anal tube feet absent.

Ossicle morphology. Basal layer and several additional layers amount in the center of the perforated plates on the body wall and dorsal papillae, in diameter $0.6-1.8 \mathrm{~mm}$ (Fig. 11A1-B3, D1, D2), with regular holes and a large, reticulated knob, $\sim 0.2 \mathrm{~mm}$ high. The tube feet with some types of developmental stages towards perforated plates (Fig. 11C1, C3) and perforated plates with one layer (Fig. 11C2), rods bearing spines (Fig. 11C4).


Figure 10. Deima validum validum (IDSSE-2018-0531-HSO2 and IDSSE-2019-0630-HS01) A in situ image (IDSSE-2018-0531-HSO2) B in vivo image (IDSSE-2018-0531-HSO2) C dorsal view (IDSSE-2019-0630-HS01) D ventral view (IDSSE-2019-0630-HS01). Scale bars: 5 cm .


$$
\mathrm{C} 3
$$



Figure 11. SEM images of Deima validum validum (IDSSE-2019-0630-HS01). A1-A3 dorsal body wall B1-B3 papillae C1-C4 tube feet D1-D2 ventral body wall. Scale bars: $300 \mu \mathrm{~m}$ (A1-B3); $50 \mu \mathrm{~m}$ (D1, D2)

Distribution. This subspecies probably has a cosmopolitan distribution, except for the Arctic and Southern Ocean, at depths of 724-5426 m (Théel 1882, 1886b; Sluiter 1901a; Hérouard 1902, 1923; Koehler and Vaney 1905; Ohshima 1915; Grieg 1921; Deichmann 1940; Hansen 1975; Sibuet 1977; O'Loughlin 1998; Bohn 2006).

Remarks. Deima validum was first described by Théel (1879) in the preliminary report of the exploring voyage of H. M. S. Challenger under Sir C. Wyville Thomson., with a detailed description of another novel species, Deima fastosum. Four new species were reported subsequently by different taxonomists: D. atlanticum Hérouard, 1898; D. blakei Théel, 1886; D. mosaicum Ohshima, 1915 and D. pacificum Ludwig, 1894. The family Deimatidae underwent a thorough revision by Hansen (1975), who regarded D. fastosum, D. atlanticum, D. blakei, D. mosaicum and $D$. pacificum as junior synonyms of $D$. validum. Hansen (1967) separated the species into two subspecies, cosmopolitan Deima validum validum and the eastern Pacific Ocean Deima validum pacificum Ludwig, 1894, based on differences in the number of dorsal papillae and the type of deposit in which they were found.

The two specimens examined here are consistent with the diagnosis of subspecies D. v. validum as described in detail by Hansen (1975). Perforated plates were like those of $D$. fastosum, with a large, reticulated, conical knob, which hardly ever approached in other known specimens that were used to investigate $D$. v. validum. This unique feature represents an extreme case of plate variation, where the spinous appearance of the skin is due to these very high and often vertically rising knobs on the plates. Hansen (1975) hypothesized that additional mesh structures on perforated plates varied with depth into two types: one-layered plates were characteristic of bathyal specimens, and many-layered plates were typical of abyssal specimens. However, it also exhibited a transitional type of plate in the abyssal Tasman Sea specimens and the bathyal Japanese specimens (perforated plates that were completely or almost completely devoid of additional meshwork), which prevented a clear distinction between a bathyal and an abyssal type of deposit.

Only in the Bay of Bengal (depth 1224-3365 m) did the development of additional layers of meshwork increase progressively with depth. In this research, high-knobbed plates were present in the abyssal South China Sea specimens (depth > 3000 m), but they were absent from the South China Sea specimens first reported (depth 1100 m ) by Liao (1997). This was the second time that Deima validum has been recorded in the South China Sea. The proposition that the development of additional meshwork on perforated plates increased with depths needs to be investigated on more specimens at different depths in the South China Sea.

## Genetic distance and phylogenetic analyses

The inter- and intraspecific genetic divergences of the COI gene were calculated to calculate the genetic distances in Deimatidae (Suppl. material 1). For the COI alignment, the interspecific distances in Oneirophanta ranged from 8.2-15.3\%, the intraspecific distances in Oneirophanta were in the range of $0-0.6 \%$, and the range of genetic distances among three genera was 15.1-21.9\%.

In total, 11 COI sequences and 10 T S sequences were deposited into GenBank (Table 1). To check the intrageneric relationships of species in Deimatidae, a Bayesian phylogenetic tree and a Maximum likelihood (ML) tree were
reconstructed using concatenated $16 \mathrm{~S}-\mathrm{CO}$ sequences of length 1191 bp . The result of the phylogenetic analyses showed quite similar topologies in BI and ML trees (Fig. 12), except for one area of the BI tree, where Oneirophanta setigera formed an independent clade within Oneirophanta (BI 0.99).

The phylogenetic relationships of Deimatidae clustered into three portions and were consistent with the traditional classification system (Fig. 12). Portion 1: Deima validum was clustered with Deima validum validum (ML 99\%, BI 1), which formed a monophyletic sister group (ML 89\%, BI 1) with Oneirophanta. Portion 2: The three new species and the new record fell into Oneirophanta, which was divided into three clades. Clade 1: 0 . setigera was shown to be distinct from the other congeners in the BI tree ( BI 0.99 ). But in the ML tree, O. setigera clustered with 0 . brunneannulata sp . nov., 0 . cf. mutabilis, O. mutabilis and O. idsseica sp. nov. with low support (ML 46\%). Clade 2: O. idsseica sp. nov. clustered with O. cf. mutabilis and O. mutabilis (ML 49\%, BI 0.79), followed by 0 . brunneannulata sp. nov. (ML 90\%, BI 1). Clade 3: O. lucerna sp. nov. clustered with all other congeners in the ML tree (ML 69\%). But in the BI tree, it was a sister taxon to species in clade 2, which then clustered with 0 . setigera. Portion 3: Orphnurgus glaber formed a separate clade with full node support (ML 100\%, BI 1), and it was the only species in Orphnurgus.

## Discussion

## Species delineation and generic assignment

Both the morphology and molecular phylogenetic analyses supported the assignment of the three new species to the genus Oneirophanta. The external morphological characteristics in Oneirophanta species were quite similar to those in Orphnurgus, but Oneirophanta never has tentacle discs with ramified processes, and they usually have rounded knobs on the margin. The three new species described in this study conformed to this feature.

Oneirophanta brunneannulata sp. nov., Oneirophanta idsseica sp. nov. and Oneirophanta lucerna sp. nov. can be separated from other congeners by ossicle types, the arrangement and the number of dorsal papillae and tube feet. The separations were confirmed by the p-distance analyses, which showed that the uncorrected p-distance for the COI among 0 . brunneannulata sp. nov. and other congeners was $8.2-13.1 \%$; among 0 . idsseica sp . nov. and other congeners was $8.2-14.1 \%$, and among 0 . lucerna sp. nov. and other congeners was 12.1-14.8\%. These divergences were much higher than the known intraspecific variation in Oneirophanta. spp. ( $0-0.6 \%$ ) (Suppl. material 1) and, thus, this warranted separation of $O$. brunneannulata sp . nov., $O$. idsseica sp . nov., and 0 . lucerna sp. nov. from other congeners.

The phylogenetic trees (Fig. 12) showed that O. idsseica sp. nov. clustered together with Oneirophanta stet. CCZ_100 from Clarion-Clipperton Zone, which was deposited in the Natural History Museum, London (voucher number: CCZ_100). Generally, taxonomic units with sequence differences of $<2 \%$ are likely to be the same species, and differences > $5 \%$ were confidently used to separate different species (Ward et al. 2008). Because the COI p-distance between the two species was $0.6 \%$ (Suppl. material 1), the divergences fell within the range of general intraspecific variation; both morphological characters and molecular data suggested that O. idsseica sp. nov. and O. stet. CCZ_100 are the same species.


Figure 12. Maximum likelihood (ML) and Bayesian inference (BI) trees based on concatenated $16 \mathrm{~S}-\mathrm{COI}$ sequences showing phylogenetic relationships among deimatid species. The new sequences provided in this study are in bold A ML tree, with bootstrap replications labeled B BI tree, with posterior probability labeled.

## Geographic distribution of deimatid species

There are a total of three genera and 16 species in the family Deimatidae, which include the three species that we described here. To date, 11 species of Deimatidae have been discovered in the deep water of the Pacific Ocean. Deima only includes one species: Deima validum, which occurs worldwide at depths of 724-5426 m. Nine species of Orphnurgus are accepted, with five species recorded from the Pacific: Orphnurgus dorisae Pawson, 2002 from the southern Pacific

Ocean (New Zealand), Orphnurgus glaber Walsh, 1891 from the central and western Pacific Ocean, Orphnurgus protectus (Sluiter 1901) and Orphnurgus bacillus Cherbonnier \& Féral, 1981 from the western Pacific Ocean (Celebes Strait and Philippines), and Orphnurgus vitreus (Fisher 1907) from the North Pacific Ocean (off Hawaiian Islands). On a vertical scale, all species in this genus inhabited the water from relatively shallow depths to the bathyal zone (depth 174-1301 m). Among the six species, which included the three new species of Oneirophanta, Oneirophanta mutabilis, the type species of the genus, is a cosmopolitan species (Hansen 1975). O. conservata was the only species recorded from the Indian Ocean (Koehler and Vaney 1905). All the other species were found mainly in the Pacific Ocean: O. setigera from the southern and eastern Pacific (Kermadec Trench and Gulf of Panama), O. mutabilis mutabilis is a cosmopolitan species with multiple records in the Pacific Ocean (Hansen 1975), and O. mutabilis affinis is restricted to a relatively small area in the eastern Pacific Ocean. The three new species were from the western Pacific Ocean (South China Sea). In addition, 0 . conservata has the shallowest record of the genus (depth 1315 m ), and $0 . \mathrm{mu}-$ tabilis has the deepest record (depth 6000 m ). Oneirophanta was distinguished from the other two genera by its inhabitance in the bathyal-abyssal zone.

Based on their distribution, deimatid holothurians are abundant in the Pa cific Ocean and inhabit a wide range of depths (174-6000 m). Future expeditions to the Pacific zone may discover even more species, and more research is needed to evaluate the species diversity and geographic distribution of these deep-sea holothurians.

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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

Yunlu Xiao conceived and designed this project, performed morphological examination and description, conducted molecular analyses, and wrote or reviewed drafts of the paper. Haibin Zhang conceived and designed this project, reviewed and edited drafts of the paper and approved the final draft.

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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

## Estimates of p-distances of the COI gene among deimatid species and studied sequences

Authors: Yunlu Xiao, Haibin Zhang
Data type: docx
Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.
Link: https://doi.org/10.3897/zookeys.1195.115913.suppl1

# A review of the semipunctata species group within the genus Lilioceris Reitter, 1913 (Coleoptera, Chrysomelidae) 

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[^5]
#### Abstract

A new species group of Lilioceris Reitter, 1913 is proposed and reviewed, the semipunctata group. It includes eleven species: L. atrilateralis Kimoto \& Takizawa, 1973, L. consentanea (Lacordaire, 1845), L. dentifemoralis Long, 1988, L. discrepens (Baly, 1879), L. jianfenglingensis Long, 1988, L. latissima (Pic, 1932), L. lianzhouensis Long, 2000a, L. rondoni Kimoto \& Gressitt, 1979, L. rufometallica (Pic, 1923), L. semipunctata (Fabricius, 1801), and L. yuae Long, 2000b. Lilioceris discrepens and L. rondoni were new records from China. Two synonyms are proposed: Lilioceris xinglongensis Long, 1988, syn. nov. of L. consentanea (Lacordaire, 1845), and Crioceris rufimembris Pic, 1921, syn. nov. of L. semipunctata. An identification key, descriptions, habitus photographs, geographic distributions, host plants and habitats (if available), are provided for these species.


Key words: Criocerinae, key, new record, new synonym

## Introduction

Lilioceris Reitter, 1913 has a high number of species in Criocerinae Latreille, 1804, which to date contains approximately 150 species worldwide, and at least 70 species in Asia (Monrós 1960; Heinze and Pinsdorf 1962; Gressitt 1965; Warchałowski 2011; Bezděk and Schmitt 2017). The genus is widely distributed in tropical and subtropical parts of the world, with the highest species diversity found in the Oriental Region. There are many taxonomic works focusing on regional species of the genus (e.g., Jacoby 1904, 1908; Gressitt and Kimoto 1961; Heinze and Pinsdorf 1962, 1963, 1964; Kimoto and Gressitt 1979; Tishechkin et al. 2011; Warchałowski 2011; Xu et al. 2021), but still many similar species are difficult to identify based on existing keys, and more revisionary work on species group is needed.

At present, three species groups in Lilioceris have been recognized and reviewed: the L. impressa group (Tishechkin et al. 2011), the L. neptis group (Xu et al. 2021), and the L. sinica group (Xu and Liang 2022). Here, we established the fourth, the semipunctata group, including eleven species. Some species have long been confused and misused, and the characteristics listed by different researchers are different. For example, Kimoto and Gressitt (1979) listed simple
characteristics of $L$. discrepens and L. latissima in a key, and provided illustrations for the sternum and episternum. However, we examined and compared the types (Figs 9,10 ) and found that their identifications were wrong. Therefore, these species need to be revised.

In this article, we compare types and re-identify syntypes, establish a new species group, propose two synonyms, and provide a key to aid identification.

## Materials and methods

Specimens from several museums and collections were examined. The collections cited in this article are indicated by the following abbreviations:

BSM Bishop Museum, Honolulu, Hawaii, USA;
IZCAS National Zoological Museum, Institute of Zoology, Chinese Academy of Sciences, Beijing, China;
MBSU Museum of Biology, Sun Yat-Sen University, Guangzhou, China;
MHU Museum of Hebei University, Baoding, China;
MNHN Museum National d'Histoire Naturelle, Paris, France;
NHML Natural History Museum, London, UK;
ZMUK Zoological Museum of Kiel University, Kiel, Germany;
SEHU Hokkaido University, Sapporo, Japan.

Except as noted, all specimens examined are deposited in IZCAS.
Dry specimens were soaked in hot water for $1-2 \mathrm{~h}$ to soften the body. The abdomen was opened at its latero-apical margin and genitalia were pulled out using forceps. Genitalia were soaked in warm $10 \% \mathrm{KOH}$ for 1 h , and dyed in Chlorazol Black E. The basal orifice of the median lobe was injected with $100 \%$ ethanol with a mi-cro-injector until the internal sac was fully everted. The median lobe with its everted internal sac was photographed using a large depth-of-field 3D digital microscope (Keyence VHX-1000C), and finally edited in Photoshop ${ }^{\circledR}$. A microvial with genitalia was pinned to the specimen from which the genitalia were removed for storage.

Body length (BL) was measured from the anterior margin of the labrum to the apex of the elytra; body width (BW) was measured along the greatest elytral width. Other methods of specimen observation and preparation follow previous publications (Tishechkin et al. 2011; Li et al. 2013). Morphological terminology follows Chou et al. (1993), Tishechkin et al. (2011) and Schmitt and Uhl (2015).

## Results

## The Lilioceris semipunctata species group of Lilioceris Reitter, 1913

Diagnosis. Species of this group share the following characters: 1) body almost brownish red, some with metallic luster, some of the lateral metasternum or base of abdominal sternites dark; 2) antennae more or less flattened; 3) pronotum without distinct transverse impression; 4) scutellum densely pubescent; 5) elytral punctures diminishing posteriorly and absent at $1 / 2,1 / 3$, or $1 / 4$ of apex; 6) apical portion of mesosternal process narrow, obliquely pointed, not horizontally connected with metasternum; 7) medium to large size, body length more than 7.5 mm .

Host plants. The known host plants of this species group are Smilax spp. (Smilacaceae), except for L. consentanea, whose host plant is Cycas revoluta Thunb. (Cycadaceae).

Remarks. This group is distinctly different from the impressa group in having elytral punctures absent at $\sim 1 / 3-1 / 4$ of apex; scutellum densely pubescent (in the impressa group, the elytral punctures distinct at apex; scutellum nearly glabrous). It is different from the neptis group in having apical portion of the mesosternal process narrow, obliquely pointed, and not horizontally connected with metasternum (in the neptis group, the apical portion of mesosternal process is strongly widened and convex, horizontally connected with the metasternum). It is different from the sinica group in having elytral punctures absent at 1/3-1/4 of apex; antennomeres 5-10 flat (in the sinica group, the elytral punctures distinct at apex; antennomers 5-10 cylindrical).

## Key to species of the Lilioceris semipunctata species group

1 Femora of mid- and hind legs with a ventral tooth (Fig. 28C)

.L. dentifemoralis

- Femora of mid- and hind legs without tooth (Figs 27C, 29-36C)............... 2

2 Anterior angles of pronotum more protruding, rounded (Fig. 37B)
L. consentanea

- Anterior angles of pronotum less protruding, angulate (Figs 38-46B) ..... 3

3 Metasternum glabrous (Fig. 41C) ..............................................L. Iatissima

- Metasternum pubescent (Figs 37-40C, 42-46C) ...................................... 4

4 Lateral transverse impressions on abdominal sternites 1-4 distinct, glabrous and large, area outside the transverse impression pubescent (Figs 29, 30A, 32A, 34A) .5

- Lateral transverse impressions on abdominal sternites 1-4 indistinct or absent, sternites laterally entirely pubsecent (Figs 33A, 35, 36A)8

5 Antennomeres 5-10~1.0-1.2x as long as wide (Figs 29, 30D, 34D) ...... 6

- Antennomeres 5-10 ~ 1.8× as long as wide (Fig. 32D)...... L. lianzhouensis

6 Body length > 10.0 mm ; pronotal disc with four or five rows of dense punctures (Fig. 39B)
L. discrepens

- Body length < 10.0 mm; pronotal disc with two rows of sparse punctures (Figs 40B, 44B) 7
7 Body with strong cupreous metallic luster; punctures of elytra diminishing posteriorly, absent on apical 1/4 (Fig. 34B)
L. rufometallica
- Body brown, at most with weak blue metallic luster; punctures of elytra diminishing posteriorly, absent on apical 1/2-1/3 (Fig. 30B).....L. jianfenglingensis
8 Vertex strongly raised (Fig. 43A).
L. rondoni
- Vertex slightly raised or flat (Figs 45, 46A) .9

9 Antennae, head, pronotum, leg and lateral metasternum with weak blue metallic luster (Figs 25, 26); lateroposterior corner of metasternum with a short oblique strip of pubescence (Fig. 46C) L. yuae

- Body without metallic luster, base of abdominal sternites dark (Figs 21, 22), lateral metasternum nearly black; metepisternum with a long narrow strip of pubescence (Fig. 45C)
10 Femora unicolor, brownish red L. semipunctata
- Femora bicolor, black with middle brownish red in ventral
L. atrilateralis


## Taxonomic account

Lilioceris atrilateralis Kimoto \& Takizawa, 1973
Figs 1, 2

Lilioceris atrilateralis Kimoto \& Takizawa, 1973: 171 (Nepal).

Type material examined. Holotype of Lilioceris atrilateralis (SEHU, photo), Nepal, T. Kumata / Balaju Kathmandy, 1968.IV. 16 / 5 / Lilioceris atrilateralis Kimoto \& Takizawa, 1973 / Holotype / Holotype, appended label by ÔHARA, INAPI, KANBE AUZUKI and HIRONACA, 2007 / 0000001233 Sys. Ent, Hokkaido Univ. Japan [SEHU].

Remarks. This species is very similar to L. semipunctata according to the original description and photographs of the holotype, but differs by the black femora with its middle brownish red in ventral view; sides of the abdomen are black. In L. semipunctata, the femora are brownish red; sides of the abdomen are brownish red. For this species, we have not collected sufficient specimens; therefore, the species is only listed and not treated in detail.

Distribution (Fig. 68). Nepal (Kimoto and Takizawa 1973).


Figures 1, 2. Habitus of Lilioceris atrilateralis, holotype, Nepal (Kathmandy). Photographed by Takuya Takemoto (SEHU). Scale bar: 5.0 mm .

## Lilioceris consentanea（Lacordaire，1845）

Figs 3－6，27A－D，37A－C，56A－D，58A－C，67，69A，B

Crioceris consentanea Lacordaire，1845： 561 （Vietnam）．
Lilioceris consentanea：Kimoto and Gressitt 1979： 222.
Lilioceris xinglongensis Long，1988： 232 （China：Hainan，holotype，male），syn．nov．

Type material examined．Syntype of Lilioceris consentanea（NHML，photo）， Type／Coll E．Chev．t／Crioceris consentanea Lac．Cochinchine ex mus Guerini， Type 20 ／Crioceris consentanea Lac．Type／BMNH（E）1344910／37；holotype of Lilioceris xinglongensis（MBSU），Holotype，Lilioceris xinglongensis Long，\＆， Jianguo Long det．／Hainan，Xinglong，1980．IX．29－X．3．Shiyang Xia coll．／ 603 ／En－207209 SYS．

Other material examined．Total 152 specimens．China：Hainan： $12 q 16 \widehat{\delta}^{\top}$ ， Xinglong Farm／1974．IV，host plant：Cycas revoluta；14 $27{ }^{2}$ §，Diaoluo Shan Forestry Bureau， $18.66590^{\circ} \mathrm{N}, 109.93044^{\circ} \mathrm{E} / 85 \mathrm{~m}, 2007 . \mathrm{XII} .10$ ，Zhu XY and Yang GY coll．，Inst．of Zoology，CAS； 1 q，Lingshui，Diaoluo Shan， 920 m， 2007．V．3，Li Xian／IOZ（E）1880967；1 ${ }^{\text {²，Lingshui，Diaoluo Shan，} 920 \text { m，2007．V．3，}}$ Li Xian／IOZ（E）1880965；1 §̄，Lingshui，Diaoluo Shan， 920 m，2007．V．3， Li Xian／IOZ（E）1880968；19，Lingshui，Diaoluo Shan， 920 m，2007．V．3， Li Xian／IOZ（E）1880969；1q，Lingshui，Diaoluo Shan， 920 m，2007．V．3，Li Xian／IOZ（E）1880970；1才，Lingshui，Diaoluo Shan， 920 m，2007．V．3，Li Xian／IOZ（E）1880971；1 ${ }^{\text {T，}}$ Lingshui，Diaoluo Shan， 920 m，2007．V．3，Li Xian／IOZ（E）1880972；1才，Lingshui，Diaoluo Shan， 920 m，2007．V．3，Li Xian ／IOZ（E）18809732；1 ${ }^{\text {T，}}$ Lingshui，Diaoluo Shan， 920 m，2007．V．3，Li Xian ／IOZ（E）1880974；1才，Lingshui，Diaoluo Shan， 920 m，2007．V．3，Li Xian／ IOZ（E）1880975；1 ${ }^{\text {T，}}$ Lingshui，Diaoluo Shan， 920 m，2007．V．3，Li Xian／ IOZ（E）1880976；1 ${ }^{\text {²，}}$ ，Lingshui，Diaoluo Shan， 920 m，2007．V．3，Li Xian／ IOZ（E）1880977；1才，Lingshui，Diaoluo Shan， 920 m，2007．V．3，Li Xian／ IOZ（E）1880978；1q，Lingshui，Diaoluo Shan， 920 m，2007．V．3，Li Xian／ IOZ（E）1880979；1q，Lingshui，Diaoluo Shan， 920 m，2007．V．3，Li Xian／ IOZ（E）1880980；1q，Lingshui，Diaoluo Shan， 920 m，2007．V．3，Li Xian／ IOZ（E）1880981；1ठ，Lingshui，Diaoluo Shan， 920 m，2007．V．3，Li Xian／ IOZ（E）1880982；1q，Lingshui，Diaoluo Shan， 920 m，2007．V．3，Li Xian／ IOZ（E）1880983；1 ${ }^{\text {T，Lingshui，Diaoluo Shan，} 920 \text { m，2007．V．3，Li Xian／}}$ IOZ（E）1880984；1 ${ }^{\text {万，}}$ ，Lingshui，Diaoluo Shan， 920 m，2007．V．3，Li Xian／ IOZ（E）1881004；2§，Lingshui，Diaoluo Shan， 921 m，2007．V．3，Liu Y．and Shi Hongliang coll．，Inst．of Zoology，CAS；2 ${ }^{\text {T，}}$ ，Lingshui，Diaoluo Shan， 921 m， 2007．V．3，Liu Y．and Shi Hongliang coll．，Inst．of Zoology，CAS； 2 ㅇ，Lingshui， Diaoluo Shan， 921 m，2007．V．3，Liu Y．and Shi Hongliang coll．，Inst．of Zoology， CAS； 15 q $_{26}{ }^{\wedge}$ ，Lingshui，Mt．Xin－an，on vegetation， $18.72510^{\circ} \mathrm{N}, 109.86861^{\circ} \mathrm{E} /$ 921 m，2007．03．25，Day，Shi H．L．，Yuan F．coll．，Institute of Zoology，Chinese Acad． Sciences； $49^{\circ}{ }^{\wedge}$ ，Lingshui，Diaoluo Shan，Xin－an，on vegetation， $18.72510^{\circ} \mathrm{N}$ ， $109.86861^{\circ} \mathrm{E} / 921 \mathrm{~m}, 2007 . \mathrm{III} .25$ ，Hongliang Shi and Feng Yuan coll．；3q5 ${ }^{\text {T，}}$ Lingshui，Diaoluo Shan， $18.72467^{\circ}$ N， $109.86804^{\circ}$ E， 920 m，Rui Chen and Ye Liu coll．；Yunnan：1q，Xishuangbanna，Menglun， 600 m／1994．IV．24，Huanli Xu coll． ／Lilioceris consentanea，det．Liang H．B．； 1 q，Xishuangbanna，Menghun， 750 m ／1958．VI．5，Xuwu Meng coll．；1 ${ }^{\imath}$ ，Xishuangbanna，Xiaomengyang， $850 \mathrm{~m} /$
1957.X.13, Lingchao Zang coll.; 1才, Menghai, 1060 m, 1980.V. 1 / Lilioceris consentanea, det. Peiyu Yu; 1才, Xishuangbanna, Menghai, 1200-1600 m, 1958. VII.25, Fuji Pu coll. / Lilioceris consentanea, det. Peiyu Yu; $1{ }^{\AA}$, Xishuangbanna, Xiaomengyang, 850 m / 1957.X.26, Lingchao Zang coll; LAOs: 1 specimen (NHML), Luang Prabang. Sept. 1917. R.V. de Salvaza. / Crioceris consentanea Lac. / 1344970, BMNH(E).

Diagnosis. Anterior angles of pronotum rounded, pronotal disc with two rows of fine punctures. Humeral groove of elytra indistinct, punctures sparse and diminishing posteriorly, absent on apical $1 / 3$. Femora of mid- and hind legs without tooth. Lateral metasternum with a wide strip of pubescence.

Redescription. $\mathrm{BL}=8.5-9.2 \mathrm{~mm}, \mathrm{BW}=3.5-4.0 \mathrm{~mm}$. Body mostly brownish red, antennae, legs, mesoepisternum, mesoepimeron, and lateral metaepisternum black; in some specimens, ventral surface black.

Head (Figs 3, 5, 37A). Vertex flat, with a shallow groove in the middle, sparsely punctate and pubescent laterally; frontoclypeal area triangular, lateral disc with punctures and setae; labrum transverse, with sparse setae; antennae nearly $1 / 3$ length of body, antennomeres 1-4 nearly globular, antennomere 2 shortest, antennomeres 5-10 slightly longer than wide.

Pronotum (Figs 3, 5, 37B). Anterior angles distinctly rounded, not protruding, posterior angles slightly protruding; sides strongly constricted in the middle; disc slightly raised; middle of disc with two rows fine punctures. Scutellum triangular and pubescent.

Elytra (Figs 3, 5, 27B). Humeri protruding, humeral groove and basal impression indistinct; strial punctures sparse and large in the base, diminishing posteriorly, absent on apical $1 / 3$; intervals smooth; epipleura raised, with a row of fine punctures.

Mesosternum pubescent. Lateral metasternum with a long strip of pubescence, extending from the posterior to anterior margin. Metepisternum densely pubescent (Fig. 37C).

Abdominal sternite (Fig. 27A). Densely pubescent, lateral transverse impressions absent.

Leg (Fig. 27C). Femora with dense pubescence on the dorsal surface, with sparse pubescence on the ventral surface, without tooth.

Male genitalia (Fig. 56A-D). Ostium occupying 1/4 length of median lobe (Fig. 56A); apex hooked (Fig. 56B); tegmen Y-shaped, basal piece of tegmen oval and broad, lateral lobes distinctly sclerotized and combined with second connecting membrane; internal sac membranous, with distinct dorsal and ventral sclerites, posterior part of dorsal sclerite in dorsal view parallel, ventral sclerite strongly extended and tubular (= flagellum), median sclerite very small (Fig. 56C, D).

Female reproductive organs (Fig. 58A-C). Tergites 8 and 9, sternites 8 and 9 sclerotized, posterior areas of tergite 8, sternite 8, and apodemes with pubescence, spiculum gastrale Y-shaped and strong; ovipositor with sparse pubescence, distal part of ovipositor cylindrical, short and with a protuberance; spermatheca simple and curved.

Distribution (Fig. 67). China (Yunnan, Hainan, Fujian (Bezděk and Schmitt 2017)); Laos; Vietnam (Warchałowski 2011).

Host plant and habitat (Fig. 69A, B). This species fed on Cycas revoluta Thunb. according to observation of HBL in Diaoluo Shan (Hainan). Diaoluo is one of the


Figures 3-6. Habitus of Lilioceris spp. 3, 4 L. xinglongensis, holotype, China (Hainan) 5, 6 L . consentanea, specimen from China (Yunnan). Photographed by Yuan Xu. Scale bars: 5.0 mm .
most well-preserved areas of tropical rainforest in China, located in the southeast of Hainan. The area has an oceanic tropical monsoon climate with abundant rainfall. The habitat of this species is open, composed of tall trees, woody vines, and weeds. It also occurred on $C$. revoluta planted in the garden.

Remarks. This species can be easily recognized by its anterior angles of the pronotum being particularly rounded (Fig. 37B), and its male genitalia with three sclerites that are not clearly separated. The male genitalia are similar to that of L. yuae Long, 2000b, but differ by the dorsal sclerite being cruciform in dorsal view (Fig. 56C). In L. yuae, the dorsal sclerite is cuneiform in dorsal view (Fig. 55C).

The body color of this species is variable. The abdomen and legs of the specimens from Hainan are brownish red, while the specimens from Yunnan are completely black. We have compared the genitalia of specimens from Hainan and Yunnan and found no differences. We compared the type of Lilioceris xinglongensis Long, 1988 (Figs 3, 4) with that of L. consentanea, and found no significant differences; the two species are therefore treated as conspecific.

## Lilioceris dentifemoralis Long, 1988

Figs 7, 8, 28A-D, 38A-C, 47A-D, 57A-C, 68

Lilioceris dentifemoralis Long, 1988: 231 (China: Hainan).

Type material examined. Holotype of Lilioceris dentifemoralis (MBSU, photo), Hainan, Jianfengling, Tianchi, 1981.7.6, Junxiong Zhang coll. / holotype, Lilioceris dentifemoralis Long ${ }^{1}$, Jianguo Long det. / 603 / En-207215 SYS; allotype of Lilioceris dentifemoralis (MBSU, photo), Hainan, Jianfengling, 1964.V.3-5, Hui Ren coll. / Allotype, Lilioceris dentifemoralis Long + , Jianguo Long det. / En-207214 SYS.

Other material examined. Total 6 specimens. CHINA: 1q, Hainan, Jianfengling, 1981.8.13 / Maobin Gu collector / Lilioceris dentifemoralis det. Liang H.B., 2020; 1 t, Hainan, Jianfengling, 1964.V. 10 / Tailu Chen collector/ Lilioceris dentifemoralis det. Peiyu Yu/ Lilioceris dentifemoralis, compared with type, det. Liang H.B., 2004.3; Vietnam: 1 q, Tonkin, Cho Ganh, L Duport / Lilioceris dentifemoralis, det. Liang H.B.; 1 Q $2 \widehat{ }$, Tonkin.

Diagnosis. Anterior angles of pronotum slightly protruding, pronotal disc with two or three irregular rows fine punctures. Humeral groove of elytra distinct, punctures of elytra diminishing posteriorly, absent on apical 1/4. Femora of mid- and hind legs with tooth. Lateral metasternum with a wide strip of pubescence.

Redescription. $\mathrm{BL}=7.0-8.0 \mathrm{~mm}, \mathrm{BW}=3.5-4.0 \mathrm{~mm}$. Body brownish red.
Head (Figs 7, 38A). Vertex flat, with a shallow groove in the middle, sparse punctate and pubescent laterally; frontoclypeal area triangular, lateral disc with sparse punctures and setae; labrum transverse, with sparse setae; antennae nearly $1 / 2$ of body length, antennomeres $1-4$ nearly globular, antennomere 2 shortest, antennomeres $5-10$ nearly $1.5 \times$ as long as wide, antennomere 11 slender.

Pronotum (Figs 7, 38B). Anterior angles slightly protruding, posterior angles not protruding; sides constricted in the middle; disc slightly raised; middle of disc with two or three irregular rows fine punctures.

Elytra (Figs 7, 28B). Humeri protruding, humeral groove and basal impression distinct; strial punctures large in the base, diminishing posteriorly, absent on apical 1/4; intervals smooth; epipleura raised, with a sparse row of fine punctures.

Mesosternum pubescent. Lateral metasternum with an arcuate strip of pubescence, extending from anterior margin to lateroposterior corner. Metepisternum densely pubescent (Fig. 38C).

Abdominal sternite (Fig. 28A). Lateral transverse impressions big and distinct on sternites $1-3$, other areas of sternites $1-3$ and all of sternites 4 and 5 densely pubescent.


Figures 7-10. Habitus of Lilioceris spp. 7, 8 L. dentifemoralis, holotype, China (Hainan), photographed by Yuan Xu 9, 10 L. discrepens, syntype, Laos, photographed by Hongbin Liang. Scale bars: 5.0 mm .

Leg (Fig. 28C). Femora with dense pubescence on the dorsal surface, nearly smooth on the ventral surface, femora of hind legs with a distinct tooth, and middle legs with a weak tooth.

Male genitalia (Fig. 47A-D). Ostium occupying 1/5 length of median lobe (Fig. 47A); apex round (Fig. 47B); tegmen Y-shaped, basal piece of tegmen tri-
angular and narrow, lateral lobes slightly sclerotized and combined with second connecting membrane; internal sac membranous, with distinct dorsal, median, and ventral sclerites, posterior part of dorsal sclerite in dorsal view slightly widen, ventral sclerite short and flat, median sclerite distinct (Fig. 47C, D).

Female reproductive organs (Fig. 57A-C). Tergites 8 and 9, sternites 8 and 9 sclerotized, posterior areas of tergite 8, sternite 8, and apodemes with pubescence, spiculum gastrale $Y$-shaped and long; ovipositor with dense pubescence, distal part of ovipositor cylindrical, short, and with a protuberance; spermatheca simple and hooked.

Distribution (Fig. 68). China (Hainan); Vietnam.
Host plant and habitat. Host plant is unknown. We visited Jianfengling of Hainan where all Chinese specimens were collected, located in a subtropical area. The habitat is mixed primeval forest, orchards, and farmland with high temperatures, plentiful precipitation, and plenty of sunlight. The type locality, Tianchi, refers to a lake area surrounded by shrubs and tall trees.

Remarks. Lilioceris dentifemoralis can be distinguished from other species in this group by the femora of mid- and hind legs with a tooth (Fig. 32C). This species seems to be very rare: we tried several times to collect this species in Hainan but failed.

## Lilioceris discrepens (Baly, 1879)

Figs 9, 10, 29A-D, 39A-C, 51A-D, 65A-C, 67, 70A, B

Crioceris discrepens Baly, 1879: 316 (Siam, Laos).
Lilioceris discrepens: Kimoto and Gressitt 1979: 220.

Type material examined. Syntype of Lilioceris discrepens (NHML, photo), Type / Type / Baly Coll. / Crioceris discrepens Baly, Siam / Crioceris discrepens Baly, Type / BMNH(E)1344920.

Other material examined. Total 29 specimens. China: Yunnan: 1 ${ }^{\top}$, Gongshan, Dulongjiang, Maku, 2021.5.31 / 27.68936 ${ }^{\circ}$ N, $98.30804^{\circ} \mathrm{E}, 1691$ m, Liang H.B., Xu Y., Zhang N. coll.; 1q, Jinping, Jinzhuzhai, 2012. 5.14, Yang XD coll.; 1q1 ${ }^{\lambda}$, Xinping, Ailao Shan, 2021.5.16 / N24.306612, E101. 351084, 1732 m, Zhang N. coll; $1{ }^{\top}$, Ruili, Bangdazhai, N. Y. Tsa coll.; 1 q, Gongshan, Dulongjiang, Qinlandang, beach. $27.67854^{\circ} \mathrm{N}, 98.28731^{\circ} \mathrm{E}, 1970 \mathrm{~m}, 2006.8 .31$ day, Liu Ye collector California Academy and IOZ. Chinese. Acad. Sci., L. discrepens, det. Liang H.B. 2019; 1 Q , Xishuangbanna, Mengla, Longlin Xincun, $21.52914^{\circ} \mathrm{N}$, $101.49415^{\circ}$ E, 1066 m / Hongbin Liang and Yuan Xu coll.; 1 q, Malipo, Lao Shan Yaowanggu, 2021.4.19 / 23.00919N, 104.82562${ }^{\circ} \mathrm{E}, 1050 \mathrm{~m}$, Hongbin Liang, Yuan Xu and Neng Zhang coll.; 1q, Xishuangbanna, Menghai, Bulang Shan, 2011.4.28, Hongbin Liang and Kaiqin Li coll.; 2 \& , Xishuangbanna, Mengla, 620-650 m, 1958.XI.16, Yiran Zhang coll.; 1q, Jinping, Changpotou, 1000 m, 1956.V.22, Keren Huang coll.; 2q, Xishuangbanna, Mengla, 620-650 m, 1959. VII.7, Facai Zhang coll.; 1q, Xishuangbanna, Menga, 1050-1080 m, 1958.V.17, Fuji Pu coll.; 1q, Jinping, Changpotou, 1200 m, 1956.V.23, Keren Huang coll.; 1 $\uparrow$, Xishuangbanna, Menglun botanic garden, 1988.XI.20; 1 ${ }^{\lambda}$, Xishuangbanna, Mengla, 620-650 m, 1959.VI.2, Yiran Zhang coll.; 1 ${ }^{\text {T, Xishuangbanna, Men- }}$ gla, 620-650 m, 1959.V.29, Suofu Li coll.; 1 ${ }^{\text {§ }}$, Ruili, Bangdazhai, 2014.IX.4,

NY Tsa coll.; 1q, Xishuangbanna, Mengla, Longlin New village, $21.52914^{\circ} \mathrm{N}$, $101.49415^{\circ}$ E, 1066 m, 2020.VI. 6, Hongbin Liang and Yuan Xu coll.; ${ }^{1}{ }^{1}$, Gongshan, Dulongjiang, Maku village, $27.68979^{\circ} \mathrm{N}, 98.30513^{\circ} \mathrm{E}, 1733 \mathrm{~m}, 2021 . \mathrm{V} .31$, Hongbin Liang and Yuan Xu coll.; 1q, Jinping, Jinzhuzhai, 2012.V.14, Xiaodong Yang coll.; 1q, Malipo, Lao Shan Yaowanggu, $23.00919^{\circ} \mathrm{N}, 104.82562^{\circ} \mathrm{E}$, 1050 m, 2021.IV.19, Hongbin Liang and Yuan Xu coll.; 1q1 ${ }^{\lambda}$, Xinping, Dacunzi, $24.306612^{\circ} \mathrm{N}, 101.351084^{\circ} \mathrm{E} 1731 \mathrm{~m}, 2021 . \mathrm{V} .16$, Neng Zhang coll.; Guangxi: 1 ${ }^{\top}$, Guangxi, Longzhou, Daqing Shan, 360 m, 1963.IV.23, Chunguang Wang coll.; Vietnam: $1 才$, Museum Paris, Tonkin N., Reg Dha-Giang (H Riviere Claire) Siebens Olivier 1916.

Diagnosis. Anterior angles of pronotum protruding, pronotal disc with four or five irregular rows of fine punctures. Humeral groove of elytra distinct, punctures of elytra sparse and diminishing posteriorly, absent on apical 1/3. Femora of mid- and hind legs without tooth. Lateral metasternum with a long strip of pubescence.

Redescription. $\mathrm{BL}=9.5-14.5 \mathrm{~mm}, \mathrm{BW}=4.4-4.7 \mathrm{~mm}$. Body brownish red.
Head (Figs 9, 39A). Vertex flat, with a deep groove in the middle, sparsely punctate and pubescent laterally; frontoclypeal area triangular, lateral disc with sparse punctures and pubescence; labrum transverse, with sparse pubescence; antennae nearly $1 / 2$ of body length, antennomeres $1-4$ nearly globular, antennomere 2 shortest, antennomeres $5-10$ nearly $1.1 \times$ as long as wide, antennomere 11 slender.

Pronotum (Figs 9, 39B). Anterior angles protruding, posterior angles not protruding; sides slightly constricted in the middle; disc flat; middle of disc with four or five irregular rows of fine punctures. Scutellum triangular and pubescent.

Elytra (Figs 9, 29B). Humeri protruding, humeral groove and basal impression distinct; elytra without completely punctate striae, punctures sparse and large in the base, diminishing posteriorly, absent on apical $1 / 3$; intervals smooth; epipleura raised, with a sparse row of fine punctures.

Mesosternum pubescent. Lateral metasternum with a long and arcuate strip of pubescence, metepisternum densely pubescent. Metepisternum densely pubescent (Fig. 39C).

Abdominal sternite (Fig. 29A). Lateral transverse impressions big and distinct on sternites 1-4, other areas of sternites 1-4 densely pubescent.

Leg (Fig. 29C). Femora with dense pubescence on the dorsal surface, with sparse pubescence on the ventral surface, without tooth.

Male genitalia (Fig. 51A-D). Ostium occupying 1/4 length of median lobe (Fig. 51A); apex sharp (Fig. 51B); tegmen Y-shaped, basal piece of tegmen triangular and broad, lateral lobes sclerotized and combined with second connecting membrane; internal sac membranous, with distinct dorsal and ventral sclerites, posterior part of dorsal sclerite in dorsal view parallel, ventral sclerite elongated and curly (= flagellum), median sclerite small (Fig. 51C, D).

Female reproductive organs (Fig. 65A-C). Tergites 8 and 9, sternites 8 and 9 sclerotized, posterior areas of tergite 8, sternite 8, and apodemes with pubescence, spiculum gastrale $Y$-shaped and long; ovipositor with dense pubescence, distal part of ovipositor cylindrical, long and with a protuberance; spermatheca simple and hooked.

Distribution (Fig. 67). China (Yunnan, Guangxi); Laos; Thailand; Vietnam. New record from China

Host plant and habitat (Fig. 70A, B). This species is fed on Smilax sp. according to our observations in Yunnan. One locality of this species in Maku village (Yunnan, Gongshan, Dulongjiang) is situated at the subtropics. The habitat is primeval forest, which is characterized by both high temperatures and humidity, plentiful precipitation, but without much sunlight. The forests are composed of tall trees, woody vines, and weeds.

Remarks. The body size of this species is very large for the genus. It is similar to L. latissima, but differs by the pronotal disc with four or five irregular rows of fine punctures, and the lateral metasternum with a long arcuate strip of pubescence (in L. latissima, the pronotal disc has two rows of fine punctures, and the lateral metasternum is smooth).

Lilioceris discrepens was described by Baly (1879) from Laos, subsequently listed with simple characteristics in a key by Kimoto and Gressitt (1979: 220) and an illustration of the sternum and episternum (Kimoto and Gressitt 1979: 224, fig. 14j), but we examined the types (Figs 9, 10) and found that the identification was wrong. The lateral metasternum has a long strip of pubescence, rather than the sparse pubescence as illustrated by Kimoto and Gressitt (1979).

## Lilioceris jianfenglingensis Long, 1988

Figs 11, 12, 30A-D, 40A-C, 54A-D, 61A-C, 68
Lilioceris jianfenglingensis Long, 1988: 231 (China: Hainan).
Type material examined. Holotype of Lilioceris jianfenglingensis (MBSU), Hainan, Jianfengling, Heiling, 1984.VII.26, Jianguo Long coll. / holotype, Lilioceris jianfenglingensis Long ${ }^{3}$, Jianguo Long det. / 603 / En-207213 SYS; allotype of Lilioceris jianfenglingensis (MBSU), Hainan, Jianfengling, Zhufeng, 1412.5 m, 1982.2.27, Yongcheng Long coll. / Allotype, Lilioceris jianfenglingensis Long ㅇ, Jianguo Long det. / En-207212 SYS; paratype of Lilioceris jianfenglingensis (MBSU), Hainan, Jianfengling, Fifth Area, (14)55, 1991.VII.7, Jiadong Chen coll. / En-207211 SYS / Lilioceris semipunctata ? (F. 1801), det. Liang H.B. 2004; 1 ${ }^{\text {T }}$, Hainan, Jianfengling, Fifth Area, 1982.2.22, Yongcheng Long coll. / Lilioceris jianfenglingensis Long, Jianguo Long det. © / En-207210 SYS.

Other material examined. Total 38 specimens. CHINA: Yunnan: 2 ${ }^{\widehat{1}}$, Xishuangbanna, Menga,1050-1080 m, 1958.V.13, Shuyong Wang coll.; 13, Xishuangbanna, Damenglong, 1050-1080 m, 1958.IV.24, Yiran Zhang coll.; 1 $\widehat{\text { h }}$ Xishuangbanna, Menghun, 1200-1400 m, 1958.IV.12, Chunpei Hong coll.; 1 ${ }^{\widehat{\prime}}$, Xishuangbanna, Mengsong, 1600 m, 1958.IV.24, Fuji Pu coll.; 1 ${ }^{\lambda}$, Xishuangbanna, Mengsong, 1600 m, 1958.IV.24, Fuji Pu coll.; 1ठ, Xishuangbanna, Mengzhe, $1200 \mathrm{~m}, 1958 . \mathrm{VI} .14$, Shuyong Wang coll.; 1 1 h, Xishuangbanna, Mengsong, 1600 m, 1959.IV.24, Chunpei Hong coll.; 1 ${ }^{\lambda}$, Xishuangbanna, Menghun, 12001400 m, 1959.IV.24, Chunpei Hong coll.; 1 §̊, Xishuangbanna, Menghun, 1200$1400 \mathrm{~m}, 1958 . \mathrm{V} .10$, Leyi Zheng coll.; $1 \delta^{\text {in }}$, Xishuangbanna, Mengsong, 1600 m , 1959.VII.26.; 1 ${ }^{\text {d }}$, Xishuangbanna, Mengsong, $1600 \mathrm{~m}, 1958 . I V .22$, Shuyong Wang coll.; 1 ${ }^{\text {§ }}$, Xishuangbanna, Menghai, $1200-1600 \mathrm{~m}, 1957$. VIII.10, Lingchao Zang coll.; 1 ${ }^{\text {², }}$, Xishuangbanna, Menga,1050-1080 m, 1958.V.17, Fuji Pu coll.; $1{ }^{\lambda}$, Xishuangbanna, Xiaomengyang, $850 \mathrm{~m}, 1958 . \mathrm{VIIII} .31 ;{ }^{\hat{\lambda}}$, Xishuangbanna, Mengsong, 1600 m, 1958.IV.27, Xuwu Meng coll.; 1 §̂, Xishuangbanna,

Menga,1050-1080 m, 1958.VI.1, Fuji Pu coll.; 1 ${ }^{\lambda}$, Xishuangbanna, Damenglong, 650 m, 1958.IV.8, Fuji Pu coll.; 1 ${ }^{\lambda}$, Xishuangbanna, Menghun, 1200-1400 m, 1958.V.10, Chunpei Hong coll.; 1 ${ }^{\text {§, }}$, Xishuangbanna, Menga,1050-1080 m, 1958.VIII.4, Fuji Pu coll.; 1q, Xishuangbanna, Menghun, 1200 m, 1958.V.28, Yiran Zhang coll.; 1 q, Xishuangbanna, Menga, 100 m, 1958.V.23, Fuji Pu coll.; 1ㅇ, Xishuangbanna, Menga, 1050-1080 m, 1958.X.19, Zhizi Chen coll.; 1ㅇ, Xishuangbanna, Mengla, 620-700 m, 1959.V.29, Yiran Zhang coll.; 1 中, Xishuangbanna, Menga,1050 m, 1958.V.17, Fuji Pu coll.; 1q, Xishuangbanna, Menga, 1050-1080 m, 1958.VIII.4, Shuyong Wang coll.; 1q, Xishuangbanna, Mengyang, 620 m, 1981.IV.12, Fasheng Li coll.; 1q, Xishuangbanna, Menga, 1050 m, 1958.V.23, Fuji Pu coll.; 1q, Xishuangbanna, Menghai, 1200 m, 1957.IV.24, Yiran Zhang coll.; 1q, Xishuangbanna, Menga, 1050-1080 m, 1958.V.17, Shuyong Wang coll.; 1 , Xishuangbanna, Mengsong, 1600 m, 1958.IV.24, Fuji Pu coll.; 1ㅇ, Xishuangbanna, Menga, 1050-1080 m, 1958.VIII.4, Shuyong Wang coll.; 1ㅇ, Xishuangbanna, Menghun, 1200 m, 1958.V.10, Yiran Zhang coll.; 1 ㅇ, Xishuangbanna, Mengsong, 1600 m, 1958.VIII.18, Fuji Pu coll.; 1q, Xishuangbanna, Menga, 1050-1080 m, 1958.VIII.22, Shuyong Wang coll.; 1 1 , Xishuangbanna, Mengzhe, 1700 m, 1958.VI.23, Zhizi Chen coll.; 1q, Xishuangbanna, Menga, 1050-1080 m, 1958.V.25, Shuyong Wang coll.; 1q, Xishuangbanna, Menga, 1050-1080 m, 1958.VIII.18, Fuji Pu coll.

Diagnosis. Antennomeres 5-10 as long as wide, flattened. Anterior angles of pronotum protruding, pronotal disc with two rows of fine punctures. Humeral groove of elytra indistinct, punctures sparse and diminishing posteriorly, absent on apical $1 / 3$. Lateral metasternum with a short strip of pubescence.

Redescription. $\mathrm{BL}=7.5-9.5 \mathrm{~mm}, \mathrm{BW}=3.5-4.0 \mathrm{~mm}$. Body brownish red.
Head (Figs 11, 40A). Vertex flat, with a very shallow groove in the middle, sparsely punctate and pubescent laterally; frontoclypeal area triangular, lateral disc with sparse punctures and pubescent; labrum transverse, with sparse pubescent; antennae nearly $1 / 2$ of body length, antennomeres 1-4 nearly globular, antennomere 2 shortest, antennomeres 5-10 as long as wide, antennomere 11 slender.

Pronotum (Figs 11, 40B). Anterior angles protruding, posterior angles not protruding; sides distinctly constricted in the middle; disc flat; middle of disc with two rows fine punctures. Scutellum triangular and pubescent.

Elytra (Figs 11, 30B). Humeri protruding, humeral groove and basal impression shallow; elytra without completely punctate striae, punctures sparse, diminishing posteriorly, absent on apical $1 / 3$; intervals smooth; epipleura raised, with a row of fine punctures.

Mesosternum pubescent. Lateral metasternum with oblique strip of pubescence. Metepisternum densely pubescent (Fig. 40C).

Abdominal sternite (Fig. 30A). Lateral transverse impressions big and distinct on sternites 1-4, other areas of sternites 1-4 densely pubescent.

Leg (Fig. 30D). Femora with dense pubescence on the dorsal surface, with sparse pubescence on the ventral surface, without tooth.

Male genitalia (Fig. 54A-D). Ostium occupying 1/2 length of median lobe (Fig. 54A); apex sharp (Fig. 54B); tegmen Y-shaped, basal piece of tegmen oval and narrow, lateral lobes slightly sclerotized and combined with second connecting membrane; internal sac membranous, with distinct ventral sclerites, dorsal sclerite nearly membranous, ventral sclerite greatly long and tubular (= flagellum), median sclerite small (Fig. 54C, D).


Figures 11-14. Habitus of Lilioceris spp. 11, 12 L. jianfenglingensis, holotype, China (Hainan), photographed by Yuan Xu 13, 14 L. latissima, syntype, Vietnam (Tonkin), photographed by Christophe Rivier (MNHN). Scale bars: 5.0 mm .

Female reproductive organs (Fig. 61A-C). Tergites 8 and 9, sternites 8 and 9 sclerotized, posterior areas of tergite 8, sternite 8, and apodemes with pubescence, spiculum gastrale Y -shaped and long; ovipositor with dense pubescence, distal part of ovipositor cylindrical, long and with a protuberance; spermatheca simple and hooked.

Distribution (Fig. 68). China (Hainan, Yunnan).
Host plant and habitat. Unknown.

Remarks. The species is most similar to $L$. yuae, but differs by the antenna being brownish red, without a metallic luster, and the antennomeres 7-10 as long as wide (Fig. 30D); the lateral transverse impressions are larger on the abdominal sternites 1-4 (Fig. 30A); the ventral sclerite is long and thin (Fig. 54C, D). (in L. yuae, the antenna is brownish red with a blue metallic luster, antennomeres 7-10 are distinctly longer than wide (Fig. 36D); lateral transverse impressions are very small on all sternites (Fig. 36A); and the ventral sclerite is shorter and thicker (Fig. 55C, D)).

## Lilioceris latissima (Pic, 1932)

Figs 13, 14, 31A-D, 41A-C, 53A-D, 60A-C, 67

Crioceris latissimus Pic, 1932: 10 (Vietnam: Tonkin). Lilioceris latissima: Kimoto and Gressitt 1979: 227.

Type material examined. Syntype of Lilioceris latissimus (MNHN, photo), Crioceris latissimi Pic / Type / Museum Paris, Coll. M. Pic / Type / Syntype / Syntype, Lilioceris latissimi (Pic, 1932) / MNHN, Paris EC15768.

Other material examined. Total 96 specimens. China: Yunnan: 19, Xishuangbanna, Mengla, 620-650 m, 1959.V.29, Suofu Li coll.; 1 ¢ $1{ }^{\lambda}$, Xishuangbanna, Menglun, 650 m, 1959.VIII.3, Fuji Pu coll.; 1 \&, Xishuangbanna, Damenglong, 650 m, 1958.VIII.8, Yiran Zhang coll.; 1ㅇ, Xishuangbanna, Mengla, 620-650 m, 1959.VI.8, Facai Zhang coll.; 1q, Lancang, 1200 m, 1957.VII.30, Lingchao Zang coll.; 1 ㅇ, Xishuangbanna, Mengla, 700 m, 1959.V.19, Fuji Pu coll.; 1 ㅇ, Xishuangbanna, Mengzhe, 870 m, 1958.VII.9, Shuyong Wang coll.; 1q, Xishuangbanna, Jinghong, 650 m, 1959.VI.8, Xuezhong Zhang coll.; 1 1 , Xishuangbanna, Mengzhe, 870 m, 1958.VII.11, Fuji Pu coll.; 1q, Xishuangbanna, Mengla, 620-650 m, 1959. VI.6, Yiran Zhang coll.; 1 ? , Xishuangbanna, Mengla, 620-650 m, 1959.VII.8, Suofu Li coll.; 1 q, Xishuangbanna, Xiaomengyang, 850 m, 1958.IX.1, Xuwu Meng coll.; 1 , Xishuangbanna, Mengzhe, 620-650 m, 1959.V.9, Facai Zhang coll.; 1 \& , Xishuangbanna, Mengla, 620-650 m, 1959.VI.30, Facai Zhang coll.; 2 q, Xishuangbanna, Menghun, 1200-1400 m, 1958.VI.13, Yiran Zhang coll.; 1q, Xishuangbanna, Xiaomenghun, 650-750 m, 1958.VI.13, Xuwu Meng coll.; 1q, Xishuangbanna, Menglun, 650 m, 1959.VIII.27, Fuji Pu coll.; 1q, Xishuangbanna, Mengla, 620650 m, 1959.VII.13, Suofu Li coll.; 1q, Xishuangbanna, Menghai, Nannuo Shan, 1100-1500 m, 1957.IV.27, Fuji Pu coll.; 1q, Jinping, Mengla, 500 m, 1956.IV.20, Keren Huang coll.; 1 , Xishuangbanna, Mengla, 620-650 m, 1959.VII.8, Facai Zhang coll.; 2오, Xishuangbanna, Menglun, 650 m, 1959.VII.24, Facai Zhang coll.; 1 \&, Xishuangbanna, Menghun, 750 m, 1958.VI.5, Xuwu Meng coll.; $1+$, Xishuangbanna, Menghai, 1400 m, 1980.III.10, Zhiming Li coll.; 1 q, Xishuangbanna, Menglun, 650 m, 1958.IX.29, Shuyong Wang coll.; 1 $\uparrow$, Xishuangbanna, Mengla, 620650 m, 1959.VII.8, Facai Zhang coll.; 1 t, Xishuangbanna, Mengla, 620-650 m, 1959.V.29, Suofu Li coll.; 1q, Jinghong, 1984.IV.20; 1 q, Ruili, Ruili Botanical garden, N 24.07230, E 97.81944 / 2012.X.27, 1152 m, Huang Xinle Leg. Inst. of Zoology, CAS; 1 § , Cheli [= Jinghong], 580 m, 1957.III.10, Fuji Pu coll.; 2 ${ }^{\text {§ }}$, Xishuangbanna, Mengla, 620-650 m, 1959.VI.8, Suofu Li coll.; 1 ${ }^{\lambda}$, Xishuangbanna, Menglun, 650 m, 1959.VII.24, Yiran Zhang coll.; 1 ${ }^{\text {¹, }}$, Xishuangbanna, Xiaomengyang, 850 m, 1958.IX.13, Yiran Zhang coll.; 1ठ, Xishuangbanna, Menglun, 650 m, 1959.VII.31,

 uangbanna, Mengla, 620-650 m, 1959.VII.13, Suofu Li coll.; 2 ${ }^{\text {® }}$, Xishuangbanna, Xiaomengyang, $850 \mathrm{~m}, 1958 . \mathrm{IX} .1$, Xuwu Meng coll.; 1 ${ }^{\imath 1}$, Xishuangbanna, Mengla, 620-650 m, 1959.V.19, Fuji Pu coll.; 1 ${ }^{\text {T, }}$, Xishuangbanna, Mengla, 620-650 m, 1959.V.19, Facai Zhang coll.; 1d, Xishuangbanna, Menghun,1200-1400 m, 1958. VI.13, Yiran Zhang coll.; $1^{\text {ºn }}$, Xishuangbanna, Mengla, 620-650 m, 1959.VI.5, Fuji Pu coll.; 1 ${ }^{\text {T, }}$, Xishuangbanna, Menglun, 650 m, 1959.VII.24, Yiran Zhang coll.; 1 ${ }^{\text {T, }}$ Xishuangbanna, Xiaomengyang, 850 m, 1957.IX.6, Lingchao Zang coll.; 1 §, Xishuangbanna, Mengla, 700 m , 1959.V.19, Fuji Pu coll.; 1d, Xishuangbanna, Mengla, 700 m, 1959.V.8, Fuji Pu coll.; 1 ${ }^{\text {², }}$, Xishuangbanna, Menglun, 650 m, 1959.VII.27, Fuji Pu coll.; 1 亿̂, Xishuangbanna, Menglun, 650 m, 1959.VII.30, Fuji Pu coll.; 1 ̂, Xishuangbanna, Menglun, 620-650 m, 1959.VII.8, Fuji Pu coll.; 1 ${ }^{\text {T, }}$, Xishuangbanna, Mengzhe, $1200 \mathrm{~m}, 1958 . I X .14$, Shuyong Wang coll.; 1 ${ }^{\boldsymbol{\lambda}}$, Xishuangbanna, Mengla, 620-650 m, 1959.V.14, Facai Zhang coll.; 1 ${ }^{\text {T, }}$, Xishuangbanna, Damenglong, 650 m, 1958.VIII.8, Yiran Zhang coll.; 1 ${ }^{\text {¹, }}$, Xishuangbanna, Menglun, $650 \mathrm{~m}, 1959$. VIII.3, Suofu Li coll.; 1才, Xishuangbanna, Menglun, 650 m, 1959.VIII.25, Suofu Li coll.; 1 ${ }^{\text {h }}$, Xishuangbanna, Menglun, 650 m, 1959.VIII.3, Facai Zhang coll.; 1 ${ }^{\text {T, }}$, Xishuangbanna, Menglun, $650 \mathrm{~m}, 1958.1 \mathrm{X} .29$, Shuyong Wang coll.; 1 ${ }^{1}$, Damenglong, 700 m , 1957.IV.12, Shuyong Wang coll.; 1 ${ }^{\text {T}}$, Jinping, Mengla, 500 m , Keren Huang coll.; 1 ${ }^{\text {h}}$, Xishuangbanna, Menglun, 650 m, 1959.VIII.3, Fuji Pu coll.; 1 ${ }^{\text {T, }}$, Xishuangbanna, Menglun, 650 m, 1959.VII. 27 , Fuji Pu coll.; ${ }^{\text {º }}$, Xishuangbanna, Xiaomengyang, 850 m, 1958.X.20, Fuji Pu coll.; 1 ${ }^{\text {º }}$, Xishuangbanna, Damenglong, $650 \mathrm{~m}, 1958$. IV.9, Fuji Pu coll.; 13̂, Xishuangbanna, Xiaomengyang, 850 m, 1958.IX.6, Yiran Zhang coll.; 1 ${ }^{\text {T, }}$, Xishuangbanna, Mengzhe, 1200 m , 1958.IX.14, Shuyong Wang
 Jinghong, 1984.IV.19; 19, Xishuangbanna, Mengyang, Baihua Shan, $22.17720^{\circ} \mathrm{N}$, $100.92428^{\circ} \mathrm{E}, 876 \mathrm{~m}, 2020 . \mathrm{VI} .3$, Hongbin Liang and Yuan Xu coll.; 1q1 ${ }^{\text {® }}$, Xishuangbanna, Mengyang, Baihua Shan, $22.17720^{\circ} \mathrm{N}, 100.92428^{\circ} \mathrm{E}, 876 \mathrm{~m}, 2021 . \mathrm{IV} .3$, Hongbin Liang, Yuan Xu and Neng Zhang coll.; $2 \neq 3{ }^{\text {h}}$, Jinping, Mengla, Wengdang village, 2011.IV.17, Hongbin Liang and Kaiqin Li coll.; 1 it, Tengchong, Datang,
 Tonkin, Hoa Binh, 1939.V.II, leg. A de Cooman; 2§, Tonkin, Hoa Binh, 1940.V.III, leg.
 Paris, Cochinchine, Amiral Vicnes, 1898; 1?, Tonkin, Hoa Binh, 1939.V.II, leg. A
 Tonkin, Hoa Binh, leg. A de Cooman.

Diagnosis. Anterior angles of pronotum protruding, pronotal disc with two rows of fine punctures. Humeral groove of elytra indistinct, punctures sparse and diminishing posteriorly, absent on apical $1 / 3$. Metasternum smooth.

Redescription. $\mathrm{BL}=7.7-8.9 \mathrm{~mm}, \mathrm{BW}=3.0-4.0 \mathrm{~mm}$. Body brownish red.
Head (Figs 13, 41A). Vertex flat, with a shallow groove in the middle, sparsely punctate and pubescent laterally; frontoclypeal area triangular, lateral disc with sparse punctures and pubescent; labrum transverse, with sparse pubescent; antennomeres 5-10 almost as long as wide, flattened.

Pronotum (Figs 13, 41B). Anterior angles protruding, posterior angles slightly protruding; sides slightly constricted in the middle; disc flat; middle of disc with three or four rows of fine and shallow punctures. Scutellum triangular and pubescent.

Elytra (Figs 13, 31B). Humeri protruding, humeral groove and basal impression shallow; elytra without completely punctate striae, punctures sparse, diminishing posteriorly, absent on apical $1 / 3$; intervals without punctures; epipleura raised, with a row of fine punctures.

Mesosternum pubescent. Metasternum smooth. Metepisternum densely pubescent (Fig. 41C).

Abdominal sternite (Fig. 31A). Lateral transverse impressions distinct on sternites 1-4, other areas of sternites 1-4 densely pubescent.

Leg (Fig. 31C). Femora with dense pubescence on the dorsal surface, with sparse pubescence on the ventral surface, without tooth.

Male genitalia (Figs 53A-D). Ostium occupying $1 / 3$ length of median lobe (Fig. 53A); apex hooked (Fig. 53B); tegmen $Y$-shaped, basal piece of tegmen triangular and broad, lateral lobes slightly sclerotized and combined with second connecting membrane; internal sac membranous, with distinct dorsal and ventral sclerites, posterior part of dorsal sclerite in dorsal view round, long and tubular (= flagellum), median sclerite small.

Female reproductive organs (Fig. 60A-C). Tergites 8 and 9, sternites 8 and 9 sclerotized, posterior areas of tergite 8, sternite 8, and apodemes with pubescence, spiculum gastrale $Y$-shaped and long; ovipositor with dense pubescence, distal part of ovipositor cylindrical, long and with a protuberance; spermatheca convoluted.

Distribution (Fig. 67). China (Yunnan; Guangxi); Vietnam. New record from China.

Host plant and habitat. This species is fed on Smilax corbularia Kunth according to our observation in Yunnan. One locality of this species in Baihua Shan (Yunnan, Xishuangbanna, Jinghong) is situated at subtropics. This habitat is mixed primeval forest and farmland, with high temperatures, plentiful precipitation, and plenty of sunlight.

Remarks. Lilioceris latissima can be distinguished from other species in this group by the smooth metasternum (Fig. 41C) and middle of pronotal disc with three or four rows of fine punctures (Fig. 41B).

This species was described by Pic (1932) from Tonkin, Vietnam. Subsequently, Kimoto and Gressitt listed simple characteristics in a key (1979: 220) and provided an illustration for the sternum and episternum (1979: 224, fig. 141). We examined the types (Figs 13,14) and found that their identification was wrong: the lateroposterior corner of the metasternum of the type is glabrous, rather than densely pubescent as illustrated by Kimoto and Gressitt (1979). Furthermore, the distributions in Thailand and Laos listed by Kimoto and Gressitt need confirmation, and we therefore exclude them in this study.

## Lilioceris lianzhouensis Long, 2000a

Figs $15,16,32 A-D, 42 A-C, 52 A-D, 59 A-C, 68$

Lilioceris lianzhouensis Long, 2000a: 262 (China: Guangzhou).

Type material examined. Holotype of Lilioceris lianzhouensis (MBSU), Lilioceris lianzhouensis, Holotype, Jianguo Long det., 1999 / Guangdong, Lianzhou County, Dadong Shan, 1992.9.8, Yingwen Xie coll. / EN-207217 SYS; allotype

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Figures 15-18. Habitus of Lilioceris spp. 15, 16 L. lianzhouensis, holotype, China (Guangdong), photographed by Yuan Xu 17, 18 L. rondoni, holotype, Laos (Sithandone), photographed by Jeremy Frank (BSM). Scale bars: 5.0 mm .
of Lilioceris lianzhouensis (MBSU), Lilioceris lianzhouensis, Allotype, Jianguo Long det. / Guangdong, Lianxian, Dadong Shan, 1996.8.26, Weicai Xie coll. / EN-207216 SYS.

Other material examined. Total 18 specimens. China: Hunan: 1才, Yizhang, Mangshan Park, near Nanling, 24.95127$N$, $112.98377^{\circ} \mathrm{E} / 1339$ m, 2008.7.19, Ganyan Yang coll., Institute of Zoology; 1q, Mangshan, 2021.VI.27, Yong Wang
coll.; Yunnan: 1 ${ }^{\text {², }}$, Yuanyang, Shangxincheng, 2022.IV.22, Neng Zhang coll.; 1q, Lvchun, Huanglian Shan, 2018.V.23, Kaiqin Li coll.; Guangxi: 2 1 ${ }^{\lambda}$, Nanning, Daming Shan Nature Reserve, 2011.5.20-23, Kaiqin Li coll.; 1 ${ }^{\lambda}$, Nanning, Daming Shan Daxiagu, on vegetation, $23.49960^{\circ} \mathrm{N}, 108.42891^{\circ} \mathrm{E} / 1111 \mathrm{~m}$, 2011.5.27, Kaiqin Li coll., Institute of Zoology, CAS; $1{ }^{1}$, Nanning, Daming Shan Nature Reserve, Tianping / 1230 m, 2011.V.29, Kaiqin Li coll., Inst. of Zoology, CAS; 1 \& Longsheng, Huaping, Anjiangping, 2006.VIII.3, Meiying Lin coll.; Guangdong: 1 , Dinghu Shan, 1979.IV.16-20, Shaokun Du and Jinying Liang coll.; 1q, Shikengkong, 1300 m, 1995.VII.22, W. Lu coll.; 1 q, Shenzhen, Dapeng peninsula, N22.82931, 114.52472 / 5m, 2018.VII.19, Hongbin Liang and Yuan Xu coll.; Hainan: $1^{\top}$, Baisha, Hongkan Reservior, $19.08121^{\circ} \mathrm{N}, 109.49839^{\circ} \mathrm{E} /$ 525 m, 2009.11.24, Hongbin Liang coll., Institute of Zoology; $1^{\wedge}$, Qiongzhong, Wuzhi Shan, 800 m, 1980.IV.5, Fuji Pu coll.; 2 ¹ ${ }^{\wedge}$, Baisha, Gaofeng village, $19.04059^{\circ} \mathrm{N}, 109.31583^{\circ} \mathrm{E}$, $886 \mathrm{~m}, 2020.7 .28$, Yuan Xu coll.

Diagnosis. Anterior angles of pronotum protruding, pronotal disc with two or three irregular rows of fine punctures. Humeral groove of elytra shallow, punctures of elytra diminishing posteriorly, absent on apical 1/3. Femora of legs without tooth. Lateral metasternum with a long and arcuate strip of pubescence.

Redescription. $\mathrm{BL}=8.7-11.2 \mathrm{~mm}, \mathrm{BW}=3.0-4.5 \mathrm{~mm}$. Body brownish red, head, antenna, legs and lateral metasternum with a blue metallic luster.

Head (Figs 15, 42A). Vertex flat, with a shallow groove in the middle, sparse punctate and pubescent laterally; frontoclypeal area triangular, lateral disc with sparse punctures and pubescent; labrum transverse, with sparse pubescent; antennae nearly $1 / 2$ of body length, antennomeres 1-4 nearly globular, antennomere 2 shortest, antennomeres $5-10$ nearly $1.5 \times$ as long as wide, antennomere 11 slender.

Pronotum (Figs 15, 42B). Anterior angles slightly protruding, posterior angles not protruding; sides constricted in the middle; disc slightly raised; middle of disc with two or four irregular rows of fine punctures.

Elytra (Figs 15, 32B). Humeri protruding, humeral groove and basal impression distinct; elytra without completely punctate striae, punctures large in the base, diminishing posteriorly, absent on apical 1/4; intervals smooth; epipleura raised, with a sparse row of fine punctures.

Mesosternum pubescent. Lateral metasternum with a long and arcuate strip of pubescence, extending from anterior margin to lateroposterior corner, metepisternum densely pubescent (Fig. 42A).

Abdominal sternite (Fig. 32A). Lateral transverse impressions big and distinct on sternites 1-4, other areas of sternite densely pubescent.

Leg (Fig. 32C). Femora with dense pubescence on the dorsal surface, nearly smooth on the ventral surface, without tooth.

Male genitalia (Fig. 52A-D). Ostium occupying 1/3 length of median lobe (Fig. 52A); apex crooked (Fig. 52B); tegmen Y-shaped, basal piece of tegmen triangular and broad, lateral lobes slightly sclerotized and combined with second connecting membrane; internal sac membranous, with distinct dorsal, median and ventral sclerites, dorsal sclerite wedge-shaped in dorsal view, ventral sclerite short and tubular (= flagellum), median sclerite small (Fig. 52C, D).

Female reproductive organs (Fig. 59A-C). Tergites 8 and 9 and sternites 8 and 9 sclerotized, posterior areas of tergite 8 , sternite 8 , and apodemes with
pubescence, spiculum gastrale Y-shaped and long; ovipositor with dense pubescence, distal part of ovipositor cylindrical, long and with a protuberance; spermatheca simple and curved.

Distribution (Fig. 68). China (Hunan, Yunnan, Guangxi, Guangdong, Hainan).
Host plant and habitat. Host plant is unknown. One collecting place, Hongkan Reservoir in Baisha, Hainan, is located in a subtropical area. The habitat is a lake area surrounded by primeval forests with high temperature and humidity.

Remarks. The species is similar to L. jianfenglingensis, but differs by the antennomeres $5-10$ nearly $1.8 \times$ as long as wide, and brownish red with a blue metallic luster (Fig. 32D); the disc of the pronotum with two or four irregular rows of fine punctures (Fig. 42A); and the dorsal sclerite of the male genitalia is strongly sclerotized (Fig. 52C, D). In L. jianfenglingensis, antennomeres 5-10 are almost as long as wide, and brownish red (Fig. 30D); the disc of the pronotum has two rows of fine punctures (Fig. 40B); and the ventral sclerite of male genitalia is weakly sclerotized (Fig. 54C, D).

Lilioceris rondoni Kimoto \& Gressitt, 1979
Figs 17, 18, 33A-D, 43A-C, 48A-D, 63A-C, 67, 71A, B

Lilioceris rondoni Kimoto \& Gressitt, 1979: 229 (Laos: Sithandone).

Type material examined. Holotype of Lilioceris rondoni (BSM, photo), Holo / Native Collector, Bishop / Laos, lle de Khong, 17.V. 1965 / Lilioceris rondoni Kimoto \& Gressitt / Lilioceris rondoni n. sp. Det. Kimoto, 19, Holo / Paratype. [in original description, collector of holotype is J. A. Rondon].

Other material examined. Total 137 specimens. CHINA: Yunnan: 19 , Xishuangbanna, Menghun, 1200-1400 m / 1958.V.17, Chunpei Hong coll.; 19, Xishuangbanna, Xiaomengyang, $850 \mathrm{~m} / 1958 . I V .15$, Chunpei Hong coll.; 1 i, Xishuangbanna, Menghun, $1200 \mathrm{~m} / 1958 . \mathrm{VI} .6$, Chunpei Hong coll.; 2ㅇ, Xishuangbanna, Menghun, 1200-1400 m / 1958.X.28, Shuyong Wang coll.; 1 1 , Xishuangbanna, Menghun, $1200 \mathrm{~m} /$ 1958.V.11, Yiran Zhang coll.; 1 1 , Xishuangbanna, Menghun, 1200-1400 m / 1958.V.12, Chunpei Hong coll.; 1ㅇ, Xishuangbanna, Menga, 1050-1080 m / 1958.VIII.16, Fuji Pu coll.; 1q, Xishuangbanna, Menga, 1050$1080 \mathrm{~m} /$ 1958.V.20, Fuji Pu coll.; 19, Xishuangbanna, Menghun, 650-750 m / 1958.VI.13, Xuwu Meng coll.; 19, Xishuangbanna, Menghun, 1200-1400 m / 1958.V.21, Yiran Zhang coll.; 1 1 , Xishuangbanna, Xiaomengyang, 850 m, 1957.V.17, Fuji Pu coll.; 1 1 , Xishuangbanna, Menghun, 1200-1400 m/1958.VI.1, Shuyong Wang coll.; 1 \& , Xishuangbanna, Jingdong, $1170 \mathrm{~m} / 1956 . \mathrm{VII} .4 ; 1$ 우, Xishuangbanna, Mengsong, $1600 \mathrm{~m} / 1958 . \mathrm{V}$.21, Chunpei Hong coll.; 1 ¢, Xishuangbanna, Damenglong, $650 \mathrm{~m} / 1958$. VIII.8, Yiran Zhang coll.; 1 ㅇ, Xishuangbanna, Xiaomengyang, 850 m, 1958.IX.1, Leyi Zheng coll.; 1 q, Xishuangbanna, Menghai, 1200-1600 m, 1957.VIII.10, Lingchao Zang coll.; 1 ¢, Lancang, 1200 m, 1957. VII.29, Lingchao Zang coll.; 1 ¢, Xishuangbanna, Mengla, $620-650 \mathrm{~m} / 1958 . \mathrm{V} .29$, Facai Zhang coll.; 1 ¢ , Xishuangbanna, Mengla, 620-650 m / 1959.VI.10, Fuji Pu coll.; 1 우, Xishuangbanna, Damenglong, 650 m / 1958.V.5, Yiran Zhang coll.; 2우, Xishuangbanna, Mengla, 1000 m / 1958.V.23, Fuji Pu coll.; 1 P, Xishuangbanna, Menga, 1050-1080 m / 1958.V.23, Shuyong Wang coll.; 1q, Xishuangbanna, Menga, 1050-1080 m / 1958.VIII.12, Fuji Pu coll.; 1q, Xishuangbanna, Menga,

1050-1080 m / 1958.VIII.22, Shuyong Wang coll.; 1우, Xishuangbanna, Mengla, 620-650 m / 1959.V.16, Fuji Pu coll.; 1q, Xishuangbanna, Menga, 1050$1080 \mathrm{~m} / 1958$. VIII.19, Fuji Pu coll.; 1q, Xishuangbanna, Menga, 1050-1080 m / 1958.X.19, Zhizi Chen coll.; 19, Xishuangbanna, Menga, 1050-1080 m / 1958. VIII.12, Fuji Pu coll.; 2q, Xishuangbanna, Mengla, 620-650 m / 1959.V.19, Facai Zhang coll.; 1 오, Xishuangbanna, Mengla, $1050-1080 \mathrm{~m} / 1959$. VIII. 5 , Fuji Pu coll.; 1우, Xishuangbanna, Mengla, 1050-1080 m / 1958.V.11, Shuyong Wang coll.; 19, Xishuangbanna, Mengzhe, 1200 m / 1958.VII.28, Shuyong Wang coll.; 1 ${ }^{\text {P }}$, Xishuangbanna, Mengla, $620-650 \mathrm{~m} / 1959 . \mathrm{V} .5$, Suofu Li coll.; 1 \& , Xishuangbanna, Mengla, 620-650 m / 1959.V.19, Facai Zhang coll.; 1우, Xishuangbanna, Damenglong, $650 \mathrm{~m} / 1958$. VIII.4, Leyi Zheng coll.; 1 ${ }^{\lambda}$, Tengchong, Qushi, Longkou, Shrubs, N25.28580, E. 98.59128 / 1478 m, 2006.6.6, Liang HB and Hu P, California Academy and IOZ, Chinese Acad. Sci; 1 ${ }^{1}$, Xishuangbanna, Menghun, $600 \mathrm{~m} /$ 1958.VI.12, Chunpei Hong coll.; 1 ${ }^{\lambda}$, Xishuangbanna, Jinghong, $650 \mathrm{~m} /$ 1958.XI.15, Fuji Pu coll.; 18, Xishuangbanna, Mengla, $620-650 \mathrm{~m} / 1958 . X I .15$, Fuji Pu coll.; 1 ${ }^{\text {on, }}$, Xishuangbanna, Xiaomengyang, $850 \mathrm{~m} /$ 1957.VIII.10, Shuyong Wang coll.; 1 1 , Xishuangbanna, Xiaomengyang, $850 \mathrm{~m} / 1957 . X .13$, Lingchao Zang coll.; ${ }^{1}{ }^{\lambda}$, Xishuangbanna, Xiaomengyang, $1200-1600 \mathrm{~m} / 1957$. VIII.10, Lingchao Zang coll.; $1^{\hat{1}}$, Lancang, $1200 \mathrm{~m}, 1957 . \mathrm{VIII} .6$, Lingchao Zang coll.; 1 º, Lancang, $1200 \mathrm{~m}, 1957$. VIII. 8 , Shuyong Wang coll.; 1 ${ }^{\lambda 1}$, Xishuangbanna, Mengla, 1050-1080 m / 1958.VIII.16, Fuji Pu coll.; 1 ${ }^{\text {T, }}$, Xishuangbanna, Mengla, 1050$1080 \mathrm{~m} / 1958$. VIII.12, Shuyong Wang coll.; 1 º, Xishuangbanna, Menga, 1050$1080 \mathrm{~m} /$ 1958.VIII.5, Fuji Pu coll.; 1 1 , Xishuangbanna, Menga, 1050-1080 m / 1958.V.23, Shuyong Wang coll.; $1 \delta^{1}$, Xishuangbanna, Menghun, 1200-1400 m / 1958.X.28, Shuyong Wang coll.; 18', Xishuangbanna, Menga, 1050-1080 m / 1958.V.23; 1 §§, Xishuangbanna, Mengzhe, $1200 \mathrm{~m} / 1958$. VIII. 29, Fuji Pu coll.; 1 ${ }^{\text {T }}$, Xishuangbanna, Mengzhe, $1200 \mathrm{~m} / 1958$. VIII. 28 , Fuji Pu coll.; ${ }^{\text {h }}$, Puer, 1400 m , 1955.IV.4; 1 ${ }^{\text {ºn }}$, Xishuangbanna, Mengla, $620-650 \mathrm{~m} / 1959 . \mathrm{V}$.29, Suofu Li coll.; 13², Xishuangbanna, Menghun, 1200-1400 m / 1958.VI.1, Shuyong Wang coll.;
 uangbanna, Menghun, $650 \mathrm{~m} / 1958 . \mathrm{VI} .13$, Leyi Zheng coll.; 1 ${ }^{\text {§ }}$, Xishuangbanna, Mengla, 620-650 m / 1959.V.21, Facai Zhang coll.; 1 $\widehat{\text { h, Xishuangbanna, Men- }}$ gla, $620-650 \mathrm{~m} / 1959 . \mathrm{VI} .8$, Suofu Li coll.; 1̊, Jingdong, $1200 \mathrm{~m}, 1957 . \mathrm{III} .18$;
 1958.VI.23, Shuyong Wang coll.; $1^{\text {² }}$, Xishuangbanna, Mengsong, $1600 \mathrm{~m} / 1958$. IV.26, Shuyong Wang coll.; 1 ${ }^{\text {® }}$, Xishuangbanna, Xiaomengyang, $850 \mathrm{~m} / 1957$. VI.23, Lingchao Zang coll.; 1 ${ }^{\text {T, }}$, Xishuangbanna, Mengla, Paozhuqin, $21.81349^{\circ} \mathrm{N}$, $101.38157^{\circ} \mathrm{E}, 935 \mathrm{~m}, 2020 . \mathrm{VI} .5$, Hongbin Liang and Yuan Xu coll.; 25${ }^{2} 32{ }^{\text {® }}$, Xishuangbanna, Mengla, Longlin New Village, $21.52914^{\circ} \mathrm{N}, 101.49415^{\circ} \mathrm{E}, 1066 \mathrm{~m}$, 2020.VI.5-6, Hongbin Liang and Yuan Xu coll.; 18, Eshan, Ayi Power Station, $24.09573^{\circ} \mathrm{N}, 102.54589^{\circ} \mathrm{E}, 1444 \mathrm{~m}, 2022 . \mathrm{VIII} 2$, Neng Zhang coll.; 1 우 ${ }^{\text {ºd }}$, Xishuangbanna, Menghai, Menga, Nanlanghe village, $22.21595^{\circ} \mathrm{N}, 100.30576^{\circ} \mathrm{E}$, 1020 m, 2020.VI.1, Hongbin Liang and Yuan Xu coll.; 1 ${ }^{1}$, Simao, Xiniuping, 2021. VII.17, Pingzhou Zhu coll.; Sichuan: 1? , Emei Shan, Xixiangchi, 1957.VIII.17, Keren Huang coll.; 1 ¢, Emei Shan, Jiulaodong, 1957.VII.26, Keren Huang coll.

Diagnosis. Anterior angles of pronotum protruding, pronotal disc with four or five irregular rows of fine punctures. Humeral groove of elytra distinct, punctures of elytra sparse and diminishing posteriorly, absent on apical 1/3. Femora of legs without tooth. Lateral metasternum with a long strip of pubescence.

Redescription. $\mathrm{BL}=6.3-7.2 \mathrm{~mm}, \mathrm{BW}=2.5-3.5 \mathrm{~mm}$. Body brownish red.
Head (Figs 17, 43A). Vertex strongly convex, with a shallow groove in the middle, sparse punctate and pubescent laterally; frontoclypeal area triangular, lateral disc with sparse punctures and pubescent; labrum transverse, with sparse pubescent; antennae nearly $1 / 2$ of body length, antennomeres 1-4 nearly globular, antennomere 2 shortest, antennomeres $5-10$ nearly $1.1 \times$ as long as wide, antennomere 11 slender.

Pronotum (Figs 17, 43B). Anterior angles protruding, posterior angles not protruding; sides slightly constricted in the middle; disc flat; middle of disc with four or five rows of fine punctures. Scutellum triangular and pubescent.

Elytra (Figs 17, 33B). Humeri protruding, humeral groove and basal impression distinct; elytra without completely punctate striae, punctures sparse and large in the base, diminishing posteriorly, absent on apical 1/3; intervals smooth; epipleura raised, with a row of fine punctures.

Mesosternum pubescent. Lateral metasternum with a long and arcuate strip of pubescence, metepisternum densely pubescent (Fig. 43C).

Abdominal sternite (Fig. 33A). Lateral transverse impressions small and indistinct on sternites 1-4, other areas of sternites 1-4 densely pubescent.

Leg (Fig. 33C). Femora with dense pubescence on the dorsal surface, with sparse pubescence on the ventral surface, without tooth.

Male genitalia (Fig. 48A-D). Ostium occupying 1/4 length of median lobe (Fig. 48A); apex hooked (Fig. 48B); tegmen Y-shaped, basal piece of tegmen triangular and broad, lateral lobes slightly sclerotized and combined with second connecting membrane; internal sac membranous, with distinct dorsal, median and ventral sclerites, posterior part of dorsal sclerite in dorsal view slightly widen, ventral sclerite short and flaky, median sclerite slightly sclerotized (Fig. 48C, D).

Female reproductive organs (Fig. 63A-C). Tergites 8 and 9, sternites 8 and 9 sclerotized, posterior areas of tergite 8, sternite 8, and apodemes with pubescence, spiculum gastrale $Y$-shaped and long; ovipositor with dense pubescence, distal part of ovipositor cylindrical, long and with a protuberance; spermatheca simple and hooked.

Distribution (Fig. 67). China (Sichuan, Yunnan); Laos (Warchałowski 2011); Thailand, new record from China.

Host plant and habitat (Fig. 71A, B). The host plant of this species is Smilax bracteata Presl according to our observation in Xishuangbanna. It shares the same habitat with L. latissima in Baihua Shan of Xishuangbanna, Yunnan.

Remarks. This species is most similar to L. semipunctata, but differed by the strongly convex vertex (Fig. 43A); the disc of pronotum has three or four rows of fine punctures (Fig. 43B); the posterior part of the dorsal sclerite is slightly widened in dorsal view, quadrate at the apex (Fig. 48C). In L. semipunctata, the vertex is slightly convex (Fig. 44A); the disc of the pronotum has two rows of fine punctures (Fig. 44B); and the posterior part of the dorsal sclerite is parallel in dorsal view, rounded at apex (Fig. 50C).

This species has obvious sexual dimorphism: the middle of the abdominal sternites have a dense pubescence in the male, but the middle of these abdominal sternites are smooth in the female.

## Lilioceris rufometallica（Pic，1923）

Figs 20，21，34A－D，44A－C，49A－D，64A－C，68，72A，B

Crioceris rufometallica Pic，1923： 10 （Vietnam：Tonkin） Lilioceris rufometallica：Kimoto and Gressitt 1961： 56.

Type material examined．Syntype of Lilioceris rufometallica（MNHN，photo）， Hoa－Binh，Tonkin／Type／$\uparrow$／Crioceris rufometallica，Pic／Museum Paris， 1958，M．Pic coll．／Type／Syntype／Syntype，Lilioceris rufometallica（Pic，1923） ／MNHN，Paris EC17305．

Other material examined．Total 75 specimens．China：Yunnan： $1 q 1$ §，Xi－ shuangbanna，Mengsong， $1600 \mathrm{~m} / 1958 . I V .26$ ，Shuyong Wang coll．； 1 Q，Xish－ uangbanna，Menghun，1200－1400 m／1958．V．12，Chunpei Hong coll．；1q，Xish－ uangbanna，Mengzhe， 1200 m／1998．VIII．29，Fuji Pu coll．； 1 ¢，Xishuangbanna， Xiaomengyang， 850 m，1957．X． 22 ／Lingchao Zang coll．； 1 ¢，Xishuangbanna， Menga，1050－1080 m／1958．VIII．4，Shuyong Wong coll．；1q，Xishuangbanna， Menga，1050－1080 m／1958．VIII．11，Shuyong Wong coll．；1 ${ }^{1}$ ，Xishuangbanna， Damenglong， 650 m，1958．V．5，Yiran Zhang coll．；2才，Xishuangbanna，Menga， 1050－1080 m／1958．VIII．16，Fuji Pu coll．；1 ${ }^{\lambda}$ ，Xishuangbanna，Menga，1050－ 1080 m／1958．VI．6，Shuyong Wong coll．； 1 §，Yongping to Baoshan，1955．V．5，
 Xishuangbanna，Menghai，2011．IV．26，Kaiqin Li and Hongbin Liang coll．；1 ${ }^{\text {T，Xi－}}$ shuangbanna，Menghai，Nanlanghe， $22.21595^{\circ} \mathrm{N}, 100.30576^{\circ} \mathrm{E}, 1020 \mathrm{~m}, 2020$. VI．1，Hongbin Liang and Yuan Xu coll．；3q1 ${ }^{\lambda}$ ，Xishuangbanna，Menghai，Man－ guo Laozhai， $21.77355^{\circ}$ N， $100.33148^{\circ}$ E， 1404 m，2021．IV．8，Hongbin Liang and Yuan Xu coll．；2q3才，Lufeng，Haitian village， $24.99330^{\circ} \mathrm{N}, 102.16692^{\circ} \mathrm{E}, 1914$ m，2022．VII．31，Neng Zhang coll．；1q，Gongshan，Dulongjiang，Maku village， $27.68979^{\circ} \mathrm{N}, 98.30513^{\circ} \mathrm{E}, 1733 \mathrm{~m}, 2020 . I X .26$ ，Neng Zhang coll．； $2 q$ ，Yuanyang， Shangxincheng，2022．IV．22，Neng Zhang coll．； 2 中，Lufeng，Haitian village， $24.99330^{\circ}$ N， $102.16692^{\circ}$ E， 1914 m，2021．IV．16，Hongbin Liang and Neng Zhang coll．； $5^{\text {º }}$ ，Kunming，Jindian， $25.087582^{\circ}$ N， $102.777105^{\circ} \mathrm{E}, 1954 \mathrm{~m}, 2022 . \mathrm{VII} .6$ ， Neng Zhang coll．； $3 \uparrow 6^{\top}{ }^{\top}$ ，Kunming，Jindian， $25.087582^{\circ} \mathrm{N}, 102.777105^{\circ} \mathrm{E}, 1954$ m，2020．VI．14，Hongbin Liang and Yuan Xu coll．；1q，Simao，Xiniuping， 2021. VII．28，Pingzhou Zhu coll．；1q，Wenshan，Gulinqin，Houcao village，2017．X．25， Beixiao Zheng coll．；Guangxi：1q，Longzhou，Daqing Shan， 360 m／ 1963. IV．25，Chunguang Wang coll．；1q，Longzhou，Daqing Shan， 360 m／1963．IV．20， Shuyong Wang coll．； 1 ㅇ，Napo，Nongxin， 1000 m，1998．IV．12，Chunsheng Wu coll．；1 1 ，Fangcheng，Tongzhong， 550 m，2000．VI．5，Jian Yao coll．； $1{ }^{1}$ ，Napo， Nongxin， 1000 m，1998．IV．12，Haisheng Zhou coll．；Hainan：1q，Jianfengling， 1982．IV． 27 ／Maobin Gu coll．；1q，Diaoluo Shan， 1000 m／1980．IV．23，Shuyong Wang coll．； 1 ㅇ，Jianfengling，1964．V．10，Sikong Liu coll．；1q1 ${ }^{\lambda}$ ，Diaoluo Shan， 1965．V．1，Sikong Liu coll．；1q，Jianfengling，1983．IV． 19 ／Maobin Gu coll．；1q， Ledong，Jianfengling，Near Jianfengling Peak， $18.70971^{\circ} \mathrm{N}, 108.888764^{\circ} \mathrm{E} 8 /$ 955m，2007．V．6，Liang HB collector，Institute of Zoology； 1 q，Baisha，Yinggeling， Nankai，Daoyin village to Zafu Village，2009．XI．22，Meiying Lin coll．； 1 q，Ledong，
 Shi HL coll．，Institute of Zoology；${ }^{1}{ }^{\top}$ ，Wanning，1964．IV．18，Sikong Liu coll．； 1 ㅇ， Baisha，Gaofeng village， $19.04059^{\circ} \mathrm{N}, 109.31583^{\circ} \mathrm{E}$ ， $886 \mathrm{~m}, 2020 . \mathrm{VII} .28$ ，Yuan

Xu coll.; 1q, Limu Shan, 2021.III.10, Yuchen Zhao coll.; Vietnam: 5q, Museum Paris, Tonkin N., Reg Dha Giang, Riviere Claire, Siebens Olivier, 1916; 1才, Museum Paris, Tonkin N., Reg Dha Giang, Riviere Claire, Siebens Olivier, 1916; 1中, Museum Paris, Mes du H Song-Chai, Rabier 258-95; 1q, Tonkin; $1 \not \subset 1{ }^{\AA}$, Tonkin, Hoa Binh, leg. A.de Cooman; (MNHN): Riviere Claire, Haut Tonkin Madon / Crioceris rufometallica Pic.

Diagnosis. Anterior angles of pronotum protruding, pronotal disc with four or five irregular rows of fine punctures. Humeral groove of elytra distinct, punctures of elytra sparse and diminishing posteriorly, absent on apical 1/3. Mesoand meta-femora without tooth. Lateral metasternum with a long strip of pubescence.

Redescription. $\mathrm{BL}=7.0-8.5 \mathrm{~mm}, \mathrm{BW}=3.0-3.8 \mathrm{~mm}$. Body brownish red.
Head (Figs 19, 44A). Vertex flatted, with a deep groove in the middle, sparse punctate and pubescent laterally; frontoclypeal area triangular, lateral disc with sparse punctures and pubescent; labrum transverse, with sparse pubescent; antennae nearly $1 / 2$ of body length, antennomeres 1-4 nearly globular, antennomere 2 shortest, antennomeres $5 \mathbf{- 1 0}$ almost as long as wide, antennomere 11 slender.

Pronotum (Figs 19, 44B). Anterior angles protruding, posterior angles not protruding; sides slightly constricted in the middle; disc flatted; middle of disc with 3-5 rows of fine punctures. Scutellum triangular and pubescent.

Elytra (Figs 19, 34B). Humeri protruding, humeral groove and basal impression distinct; punctures dense and large in the base, diminishing posteriorly, absent on apical $1 / 4$; intervals without punctures; epipleura raised, with a sparse row of fine punctures.

Mesosternum pubescent. Lateral metasternum with a long and arcuate strip of pubescence, metepisternum densely pubescent. Metepisternum densely pubescent (Fig. 44C).

Abdominal sternite (Fig. 34A). Lateral transverse impressions big and distinct on sternites 1-4, other areas of sternites 1-4 densely pubescent.

Leg (Fig. 34C). Femora with dense pubescence on the dorsal surface, with sparse pubescence on the ventral surface, without tooth.

Male genitalia (Fig. 49A-D). Ostium occupying 1/4 length of median lobe (Fig. 49A); apex hooked (Fig. 49B); tegmen Y-shaped, basal piece of tegmen triangular and broad, lateral lobes slightly sclerotized and combined with second connecting membrane; internal sac membranous, with distinct dorsal, median and ventral sclerites, posterior part of dorsal sclerite strongly widen in dorsal view, ventral sclerite extended and curly, median sclerite small (Fig. 49C, D).

Female reproductive organs (Fig. 64A-C). Tergites 8 and 9, sternites 8 and 9 sclerotized, posterior areas of tergite 8, sternite 8, and apodemes with pubescence, spiculum gastrale $Y$-shaped and long; ovipositor with dense pubescence, distal part of ovipositor cylindrical, long and with a protuberance; spermatheca simple and hooked.

Distribution (Fig. 68). China (Sichuan, Yunnan, Guangxi, Hainan); Vietnam.
Host plant and habitat (Fig. 72A, B). The host plant of this species is Smilax perfoliata Lour. according to our observation in Yunnan. It lives at altitudes of 500-2000 m. One locality of this species in Menghai (Yunnan, Xishuangbanna) is situated at the subtropics. The habitat is tea plantation, adjacent to primeval forests with high temperature and humidity, and plenty of sunlight.


Figures 19-22. Habitus of Lilioceris spp. 19, 20 L. rufometallica, syntype, Vietnam (Tonkin), photographed by Christophe Rivier (MNHN) 21, 22 L. semipunctata, lectotype, Sumatra, photographed by Michael Kuhlmann (ZMUK). Scale bars: 5.0 mm .

Remarks. This species is special in this group due to its strong cupreous metallic luster, the pronotal disc having 3-5 rows of fine punctures, and lateral metasternum with a long and arcuate strip of pubescence.

## Lilioceris semipunctata (Fabricius, 1801)

Figs 21, 22, 35A-D, 45A-C, 50A-D, 62A-C, 67, 73A, B

Lema semipunctata Fabricius, 1801: 472 (Sumatra).
Lilioceris semipunctata: Kimoto and Gressitt 1961: 58.
Lema dehaanii Guerin-Meneville, 1844: 261 (Java). Synonymized by Kimoto and Gressitt 1979: 231.
Crioceris rufimembris Pic, 1921: 2 (China: Yunnan, syntype, male), syn. nov.

Type material examined. Lectotype (here selected) of Lilioceris semipunctata (ZMUC, photo), L. semipunctata, Sumatra, Daldorff / TYPE / zmuc 00031030 [other two syntypes: zmuc 00031032 and zmuc 00031031 are identical to Lilioceris latissima]. Syntype of Lilioceris rufimembris (MNHN, photo): Yunnan / rufimembris, Pic / type / Museum Paris, Coll. M. Pic / Type / Syntype / Syntype, Lilioceris rufımembris (Pic, 1921) / MNHN, Paris, EC15769.

Other material examined. Total 451 specimens. China: Yunnan: 2 ? , Xiaomengyang, 1000 m / 1957.V.6, Dahua Liu coll.; 1 ㅇ, Xishuangbanna, Mengla, 620-650 m / 1959.VII.9, Yiran Zhang coll.; 1q, Yiwu toMenglun, 650 m / 1964. IV.14, Baolin Zhang coll.; 1q, Xishuangbanna, Menghai 1200-1600 m / 1958. VII.25, Shuyong Wang coll.; 1q, Xishuangbanna, Jinghong, 900-710 m / 1958. IV.29, Yiran Zhang coll.; 1 \&, Xishuangbanna, Damenglong, 650 m / 1958.VII.11; 1q, Xishuangbanna, Menga, 1050-1080 m / 1958.VIII.19, Fuji Pu coll.; 2q, Xishuangbanna, $750 \mathrm{~m} / 1958 . \mathrm{V} .31$, Chunpei Hong coll., Lilioceris semipunctata, det. Peiyu Yu; 2q, Xishuangbanna, Menga, 1050-1080 m / 1958.IV.30, Shuyong Wang coll.; 1q, Xishuangbanna, Menga, 1050-1080 m / 1958.IV.30, Fuji Pu coll.; 1q, Xishuangbanna, Xiaomengyang, $850 \mathrm{~m} / 1958$. VIII.31; 1q, Xishuangbanna, Mengla, 620-650 m / 1959.V.8, Fuji Pu coll.; 1 $\uparrow$, Xishuangbanna, Damenglong, $650 \mathrm{~m} ; 1$ ㅇ, Xishuangbanna, Menga, 1050-1080 m / 1958.VIII.10, Shuyong Wang coll.; 1q, Xishuangbanna, Damenglong, 650 m; 1q, Xishuangbanna, Menga, 1050-1080 m / 1958.V.6, Fuji Pu coll.; 1 q, Xishuangbanna, Mengzhe, 1890 m / 1958.VII.7, Fuji Pu coll.; 1 1 , Xiaomengyang, $850 \mathrm{~m} / 1957$. VI.21, Shuyong Wang coll.; 1q, Xishuangbanna, Mengla, 620-650 m / 1959.VII.9, Yiran Zhang coll.; 1q, Xishuangbanna, Xiaomengyang, 850 m / 1958.VII.20, Yiran Zhang coll.; 1q, Xishuangbanna, Mengla, 620-650 m / 1959.VII.10, Yiran Zhang coll.; 1q, Xishuangbanna, Mengla, 620-650 m / 1959.VI.6, Fuji Pu coll.; 1 Q, Xishuangbanna, Mengla, 620-650 m / 1959.V.19, Facai Zhang coll.; 1q, Xishuangbanna, Mengzhe, 620-650 m / 1959.V.8, Fuji Pu coll.; 1q, Xishuangbanna, Mengzhe, 850 m / 1958.VII.3, Fuji Pu coll.; 1 q, Xishuangbanna, Mengzhe, 850 m / 1958.VII.4, Shuyong Wang coll.; 2中, Xishuangbanna, Mengzhe, 1200 m / 1958.VI.14, Shuyong Wang coll.; 1 q, Xishuangbanna, Mengzhe, 875 m / 1958.VII.4, Zhizi Chen coll.; 1 , Xishuangbanna, Mengla, 620-650 m / 1959.V.16, Facai Zhang coll.; 1q, Xishuangbanna, Xiaomengyang, 850 m / 1957.VI.9, Shuyong Wang coll.; 1q, Xishuangbanna, Xiaomengyang, 850 m / 1957.VI.25, Shuyong Wang coll.; 2q, Xishuangbanna, Mengzhe, $870 \mathrm{~m} /$ 1958.IX.3, Shuyong Wang coll.; 1q, Xishuangbanna, Mengzhe, 1200 m / 1958.VI.14, Shuyong Wang coll.; 1q, Xishuangbanna, Mengzhe, 875 m / 1958.VII.1, Fuji Pu coll.; 1 ㅇ, Xishuangbanna, Mengla, 620-650 m / 1959.V.12, Facai Zhang coll.; 1q, Xishuangbanna, Mengla, 620-650 m / 1959.V.22, Fuji Pu coll.; 1 , Xishuangbanna, Mengla, 620-650 m / 1959.VI.29, Facai Zhang coll.; 1q, Xishuangbanna, Mengsong, 1600 m / 1958.
VII.25, Leyi Zheng coll.; 19, Xishuangbanna, Mengsong, $1600 \mathrm{~m} / 1958 . \mathrm{IX} .24$, Leyi Zheng coll.; 1 ¹, Xishuangbanna, Mengzhe, $870 \mathrm{~m} / 1958$. VII.11, Fuji Pu coll.; 1 ? Menghai, $1060 \mathrm{~m}, 1980.5 .1$, Zuyun Guo coll.; 1 \& , Xishuangbanna, Menghun, $750 \mathrm{~m}, 1958.5 .30$; 1 ㅇ, Xishuangbanna, Menghun, $750-950 \mathrm{~m}, 1958 . \mathrm{VI} .3$; 1ㅇ, Xishuangbanna, Menga, $800 \mathrm{~m} / 1958$. VI.1, Shuyong Wang coll.; 1 \& , Xishuangbanna, Xiaomengyang, $850 \mathrm{~m} / 1957 . I X .3$, Shuyong Wang coll.; 1 ㅇ, Xishuangbanna, Damenglong, 650 m, 1958.IV.21, Xuwu Meng; 1 ¢ , Ruili, Nongdao, Wudian, $23.98207^{\circ} \mathrm{N}, 97.61129^{\circ} \mathrm{E} / 2012 . X I .4,990 \mathrm{~m}$, Xinlei Huang leg. Inst. of Zoology, CAS.; 1ㅇ, Nabanhe Reserve, 2008.VIII.6, $727 \mathrm{~m} / 22.16713^{\circ} \mathrm{N}$, $100.65887^{\circ} \mathrm{E}$, Jingxin Liu coll.; 1q, Fugong, Shangpa Town, $26.86203^{\circ} \mathrm{N}$, $98.87142^{\circ} \mathrm{E} / 1177 \mathrm{~m}, 2005.8 .22$, Liang HB and Zhang JF coll.; 1 ¹, Xishuangbanna, Mengla, 620-650 m / 1959.V.12, Facai Zhang coll.; 1q, Xishuangbanna, Mengla, 1050-1080 m / 1958.VIII.15, Fuji Pu coll.; 1 ¢ , Xishuangbanna, Mengla, 1050-1080 m / 1958.VIII.20, Fuji Pu coll.; 1 ¢ , Xishuangbanna, Mengla, 1050$1080 \mathrm{~m} / 1958$. VIII.16, Shuyong Wang coll.; 1 t, Xishuangbanna, Xiaomengyang, $850 \mathrm{~m} / 1957$. VI. 18, Shuyong Wang coll.; 1 1 , X, Xishuangbanna, Xiaomengyang, $850 \mathrm{~m} / 1957$. VII.17, Shuyong Wang coll.; 1 1, Xishuangbanna, Xiaomengyang, $850 \mathrm{~m} / 1957$. VII.12, Shuyong Wang coll.; 1 1 , Xishuangbanna, Xiaomengyang, $850 \mathrm{~m} / 1957$. VII. 9 , Shuyong Wang coll.; 1 ㅇ, Xishuangbanna, Xiaomengyang, $850 \mathrm{~m} / 1957 . \mathrm{VI} .27$, Lingchao Zang coll.; 1 ? , Xishuangbanna, Menglun, $650 \mathrm{~m} /$ 1964.IV.14, Baolin Zhang coll.; 1 1 , Xishuangbanna, Ganlanba, 540 m, 1957. IV.17, Fuji Pu coll.; 1\&, Baoshan to Yongping, 1955.V.28, Tianrong Huang coll.; 1오, Wenshan / 1958.VIII.2; 1오, Xishuangbanna, Menghun, 1200-1400 m, 1958.X.28, Shuyong Wang coll.; 2q, Xishuangbanna, Menghun, 750 m, 1958. VI.1, Shuyong Wang coll.; 3? , Xishuangbanna, Menghun, $750 \mathrm{~m} / 1958 . \mathrm{VI} .5$, Chunpei Hong coll.; 1 if, Xishuangbanna, Menga, $800 \mathrm{~m} / 1958.1 \mathrm{X} .3$, Shuyong Wang coll.; 1 Q, Xishuangbanna, Menga, $1050-1080 \mathrm{~m} / 1958$. VIII. 16 , Shuyong Wang coll.; 1 q, Xishuangbanna, Mengla, $620-650 \mathrm{~m} / 1958$. VII.9, Fuji Pu coll.; 1 ¢, Xishuangbanna, Mengla, 620-650 m / 1958.V.30, Facai Zhang coll.; 1¢ , Xishuangbanna, Damenglong, $650 \mathrm{~m} / 1958 . I V .7 ; 1$ 1q, Xishuangbanna, Mengla, 620-650 m / 1959.V.31, Suofu Li coll.; 1 ¢ , Xishuangbanna, Mengla, 620-650 m / 1959.V.8, Fuji Pu coll. / host plant: Smilax sp.; 1̊, Ruili, 1979.IX.2, Mengqiao, Leyi Zheng coll. / $1400 \mathrm{~m} /$ Lilioceris semipunctata, det. Liang H.B.; 1 1 , Tengchong, Jietou, Wujia Jidi, 1929.IV.2, 1530 m, Xiaohong Ou coll.; 1q, Xishuangbanna, Damenglong, $650 \mathrm{~m} / 1958 . \mathrm{VI} .9$, Shuyong Wang coll.; 19, Xishuangbanna, Mengsong, $1600 \mathrm{~m} / 1958 . \mathrm{IV} .23$, Yiran Zhang coll.; 19 , Xishuangbanna, Mengsong, $1600 \mathrm{~m} / 1958 . \mathrm{IV} .28$, Fuji Pu coll.; 1 우, Xishuangbanna, Kongming Shan, $2600 \mathrm{~m} / 1957 . I X .23$, Lingchao Zang coll.; 2 2 , Lancang, $1000 \mathrm{~m} / 1957 . \mathrm{VIII} .26$, Shuyong Wang coll.; 1 1 , Lancang, $1100 \mathrm{~m} / 1957$. VIII. 8 , Lingchao Zang coll.; 1 오, Xishuangbanna, Menga, 1050-1080 m / 1958.VI.1, Fuji Pu coll.; 1 오, Lancang, $1100 \mathrm{~m} / 1957$. VIII.2, Lingchao Zang coll.; 1 ㅇ, Shuangjiang, 1953.VI; 1 우, 22 km northeast of Jingdong, 1957.V.9, Menchalsky [in Chinese]coll.; 1q, Xishuangbanna, Menghun, $650 \mathrm{~m} / 1958 . \mathrm{VI} .15$, Xuwu Meng coll.; 19, Xishuangbanna, Menga, $1000 \mathrm{~m} / 1958$. V. 16, Fuji Pu coll.; 1 P, Xishuangbanna, Mengla, 620-650 m / 1959.V.23, Fuji Pu coll.; 1 ㅇ, Tengchong, Qingshui, Rehai, on vegetation, $24.94861^{\circ} \mathrm{N}, 98.45181^{\circ} \mathrm{E} / 1470 \mathrm{~m}, 2006.6 .1$, Liang HB and Hu P coll., California Academy and IOZ, Chinese Acad. Sci.; 1 ${ }^{\lambda}$, Xishuangbanna, Mengzhe, $870 \mathrm{~m} /$ 1958.IX.2, Shuyong Wang coll.; 1才, Xishuangbanna, Mengzhe, $870 \mathrm{~m} / 1958$. IX.2, Fuji Pu coll.; $1{ }^{\widehat{ } \text {, }, \text { Ruili, Ruili Botanical garden, } 24.07230^{\circ} \mathrm{N}, 97.81944^{\circ} \mathrm{E} / \mathrm{I}}$
 $97.61129^{\circ} \mathrm{E}$ / 2012.XI, 990 m, Xinlei Huang coll. / Lilioceris latissima, det. Liang H.B. 2022; 1 $\widehat{1}$, Xishuangbanna, Menga, $1050-1080 \mathrm{~m} / 1958$. VIII.16, Shuyong Wang coll.; ${ }^{2}$, Xishuangbanna, Menga, $1050-1080 \mathrm{~m} / 1958 . \mathrm{VIIII}$ 10, Shuyong Wang coll.; 1 ${ }^{\text {ºn }}$, Xishuangbanna, Menga, $1050-1080 \mathrm{~m} /$ 1958.VIII.16, Fuji Pu coll.; 13, Xishuangbanna, Menghun, $1200 \mathrm{~m} / 1958 . \mathrm{VI} .28$, Shuyong Wang coll.; 1 ${ }^{\text {® }}$, Xishuangbanna, Mengzhe, $870 \mathrm{~m} / 1958 . I X .2$, Fuji Pu coll.; 1 ${ }^{\lambda}$, Xishuangbanna, Mengzhe, 870 m / 1958.IX.9, Fuji Pu coll.; 13, Xishuangbanna, Mengzhe, 870 m / 1958.VII.4, Shuyong Wang coll.; 1 1 , Xishuangbanna, Mengzhe, $1200 \mathrm{~m} /$
 na, Menghun, $1200 \mathrm{~m} /$ 1958.V.23, Xuwu Meng coll.; 3§, Xishuangbanna, Mengzhe, $1200 \mathrm{~m} / 1958 . \mathrm{VI} .14$, Shuyong Wang coll.; 2§̉, Xishuangbanna, Mengla, 620-650 m / 1959.VII.9, Fuji Pu coll.; 1 ${ }^{\text {º, }}$, Xishuangbanna, Mengla, 620-650 m / 1959.V.23, Suofu Li coll.; 1ठ̂, Xishuangbanna, Mengsong, $1600 \mathrm{~m} / 1958 . I V .24$,
 Xishuangbanna, Mengla, 620-650 m / 1959.V.11, Fuji Pu coll.; 1 ${ }^{\text {§, }}$, Xishuangbanna, Mengla, 620-650 m / 1959.V.16, Fuji Pu coll.; 1̊̂, Simao to Puwen, 950$1200 \mathrm{~m} / 1957 . \mathrm{V} .11$, Guangji Hong and Zhiran Meng coll.; 1 $\widehat{3}$, Xishuangbanna, Mengzhe, 620-650 m / 1959.VII.9, Facai Zhang coll.; 1³, Shuangjiang, 1953.VI;
 na, Menghun, $1200 \mathrm{~m} / 1958 . \mathrm{VI} .28$, Shuyong Wang coll.; 1 , Xishuangbanna, Menghun, $750 \mathrm{~m} / 1958 . \mathrm{VI} .2$; 1 1 , Xishuangbanna, Mengla, $620-650 \mathrm{~m} /$ 1959.V.11, Facai Zhang coll.; 1才, Xiaomengyang, $850 \mathrm{~m} / 1957 . I X .13$, Shuyong
 banna, Mengla, 620-650 m / 1959.V.16, Fuji Pu coll.; 1 1 , Xiaomengyang, 850 m
 Yiran Zhang coll.; ${ }^{10}$, Xishuangbanna, Mengla, $620-650 \mathrm{~m} / 1959 . V .7$, Facai Zhang coll.; 2§̂, Xiaomengyang, $850 \mathrm{~m} / 1957$. VII.11-12, Lingchao Zang coll.;
 mengyang, $850 \mathrm{~m} / 1957 . \mathrm{V} .7$, Bonfirov [in Chinese] coll.; 1 ${ }^{\text {T, }}$, Cheli [= Jinghong], Shihuiyao, 750 m , 1957.IV.27, Bonfirov [in Chinese] coll.; 1 ${ }^{\text {§t, }}$, Gaoligong Shan, $1200 \mathrm{~m} / 1958$. VIII.22, Fulong Li coll.; 1 ${ }^{\text {T, }}$, Xishuangbanna, Menglun, $650 \mathrm{~m} /$ 1964.V.10, Baolin Zhang coll.; 1 1 ², Xishuangbanna, Mengla, $620-650 \mathrm{~m} / 1959$. VI.6, Fuji Pu coll.; 1đ̂̉, Xishuangbanna, Menga, 1050-1080 m / 1958.VIII.15, Fuji Pu coll.; $1^{\lambda}$, Puwen, 1957.III. 27, Mengqiaciji coll.; 1 ${ }^{\lambda}$, Xishuangbanna, Menga, 1050-1080 m / 1958.V.23, Shuyong Wang coll.; 1 1 万, Xishuangbanna, Menglun,
 banna, Mengla, 620-650 m / 1959.V.23, Fuji Pu coll.; 10', Xishuangbanna, Damenglong, $650 \mathrm{~m} / 1958 . \mathrm{IV} .18$, Chunpei Hong coll.; 1 §', Xishuangbanna, Mengla, 1050-1080 m / 1958.V.20, Fuji Pu coll.; $1^{\text {h}}$, Xishuangbanna, Mengla, 1050$1080 \mathrm{~m} / 1958$. VIII.18, Fuji Pu coll.; 1 ${ }^{\text {², Xishuangbanna, Menglun, } 650 \mathrm{~m} / 1959 .}$ VIII.30, Yiran Zhang coll.; 1 $\widehat{3}$, Xiaomengyang, $850 \mathrm{~m} / 1957 . I X .12$, Shuyong
 Mengla, 620-650 m / 1959.V.8, Fuji Pu coll.; 1 ${ }^{\text {¹, }}$, Xishuangbanna, Mengla, 620$650 \mathrm{~m} / 1959$. VII. 9 , Yiran Zhang coll.; 23, Xishuangbanna, Mengla, 620-650 m / 1959.VI.6-9, Fuji Pu coll.; 1 ${ }^{\text {® }}$, Xishuangbanna, Menghun, $1200-1400 \mathrm{~m} / 1958$. VI.3, Shuyong Wang coll.; ${ }^{\lambda}{ }^{\lambda}$, Xishuangbanna, Menghun, $1300 \mathrm{~m} / 1958 . \mathrm{VI.7}$, Leyi Zheng coll.; 1 ${ }^{\text {h }}$, Xishuangbanna, Menghun, $750 \mathrm{~m} / 1958 . \mathrm{VI} .7$; 1 ${ }^{\text {h }}$, Xishuangbanna, Menghun, $1200 \mathrm{~m} / 1958 . \mathrm{V} .23$, Xuwu Meng coll.; ${ }^{\text {h }}$, Xishuangbanna,

Menghun， $750 \mathrm{~m} / 1958 . \mathrm{VI} .2$ ，Xuwu Meng coll．；1 1 ，Xishuangbanna，Menghun， $1200 \mathrm{~m} /$ 1958．V．22，Xuwu Meng coll．；1 1 ，Xishuangbanna，Mengla， $620-650 \mathrm{~m}$ ／1959．V．23，Facai Zhang coll．；1 ${ }^{\text {º }}$ ，Xishuangbanna，Menghun， $1200 \mathrm{~m} / 1958$. VI．3； $1 \delta^{\lambda}$ ，Xishuangbanna，Menghun， $750 \mathrm{~m} / 1958 . \mathrm{VII}^{2}$ ； $1 \mathrm{~h}^{\hat{}}$ ，Xishuangbanna， Mengzhe， $870 \mathrm{~m} / 1958$. VII． 10 ，Shuyong Wang coll．； 1 h，Xishuangbanna，Menga， $1800 \mathrm{~m} / 1958$. VI．2，Fuji Pu coll．；2 ${ }^{3}$ ，Xishuangbanna，Mengla， $620-650 \mathrm{~m} /$ 1959．V．23，Yiran Zhang coll．； 1 d＇$^{\lambda}$ ，Xishuangbanna，Mengla， $620-650 \mathrm{~m} / 1959 . \mathrm{V} .9$ ， Facai Zhang coll．；1 ${ }^{\text {T，Xishuangbanna，Mengla，620－650 m／1959．VI．6，Fuji Pu }}$ coll．；1才，Xishuangbanna，Mengla，620－650 m／1959．V．4，Yiran Zhang coll．；1 ${ }^{\text {T，}}$ Xishuangbanna，Menglun， $650 \mathrm{~m} / 1959$. VIII． 25 ，Facai Zhang coll．；1 ${ }^{\text {T，Xishuang－}}$ banna，Mengla，620－650 m／1959．V．4，Facai Zhang coll．；1 ${ }^{\text {º }}$ ，Xishuangbanna， Mengla，620－650 m／1959．V．19，Facai Zhang coll．；1 ${ }^{\lambda}$ ，Xishuangbanna，Men－ glun， $650 \mathrm{~m} / 1964 . I V .29$ ，Baolin Zhang coll．； $1{ }^{\text {T，}}$ ，Cheli［ $=$ Jinghong］， $620 \mathrm{~m}, 1957$. IV．17，Lingchao Zang coll．；${ }^{1}$ h，Baoshan to Yongping，1955．V．28，Tianrong Huang
 1957．VII．26，Shuyong Wang coll．；13＇，Lincang， $1100 \mathrm{~m} / 1957$. VIII．8，Lingchao Zang coll．；1 ㅇ，Xishuangbanna，Mengla，620－650 m／1958．V．30，Facai Zhang coll．；1q，Xishuangbanna，Mengla，620－650 m／1958．V．23，Facai Zhang coll．； 1？，Xishuangbanna，Mengla，620－650 m／1958．V．22，Fuji Pu coll．； 1 Q，Mengla／ 1982．IV．20，Shengqiao Jiang coll．；19，1984．V．9，Menglun／Lilioceris impressa （Fabricius）；1ㅇ，Xishuangbanna，Mengla， $620-650 \mathrm{~m} / 1958 . V I .6$, Fuji Pu coll．； 1ㅇ，Xishuangbanna，Mengzhe， $890 \mathrm{~m} / 1958$. VII．3，Fuji Pu coll．； 1 ㅇ，Xishuang－ banna，Mengzhe， $890 \mathrm{~m} / 1958 . I X .5$ ，Shuyong Wang coll．； 1 ¢ ，Xishuangbanna， Mengla，620－650 m／1959．V．23，Fuji Pu coll．； 1 ¢ ，Xishuangbanna，Mengzhe， $890 \mathrm{~m} / 1958$. VII． 8 ，Shuyong Wang coll．；1q，Xishuangbanna，Mengla，620－ $650 \mathrm{~m} / 1959 . \mathrm{VI} .2$ ，Fuji Pu coll．／Lilioceris semipunctata，det．Yuan Xu，2021；1 ㅇ， Xishuangbanna，Mengsong， $1600 \mathrm{~m} / 1958 . I V .23$, Yiran Zhang coll．；19，Jing－ hong，1979．X．30，Damenglong，Zuopei Lin coll．／Lilioceris latissima，det．Liang H．B．2020； 1 우，Xishuangbanna，Mengla，620－650 m／1959．VI．5，Yiran Zhang coll．； 1 ¢ ，Xishuangbanna，Mengla，620－650 m／1959．V．20，Fuji Pu coll．； 1 ㅇ，Xi－ shuangbanna，Mengla，620－650 m／1959．V．23，Fuji Pu coll．；1 ${ }^{\text {® }}$ ，Xishuangban－ na，Mengla，620－650 m／1959．V．23，Fuji Pu coll．；1ठ̂，Xishuangbanna，Xiao－ mengyang，1957．VI．15，Shuyong Wang coll．；1ठ，Xishuangbanna，Mengzhe， $1200 \mathrm{~m} / 1958 . \mathrm{VI} .14$, Shuyong Wang coll．；1 ${ }^{\text {T，}}$ ，Xishuangbanna，1958．VII． 8 ／ Mengzhe，Mengman， 870 m ，Fuji Pu coll．； $1{ }^{1}$ ，Xishuangbanna，Mengzhe， 870 m ／1958．IX．7，Shuyong Wang coll．；1đ̂，Xishuangbanna，Menga，1050－1080 m／ 1958．VIII．4，Fuji Pu coll．；18，Xishuangbanna，Xiaomengyang， 850 m，1957．VI．13， Shuyong Wang coll．； 1 ㅇ，Xishuangbanna，Mengla，620－650 m／1959．V．16，Fuji Pu coll．；19，Lancang， $1000 \mathrm{~m} / 1957$. VII．26，Lingchao Zang coll．；19，Xishuang－ banna，Menga，1050－1080 m／1958．VIII．16，Shuyong Wang coll．；1 1 ，Xishuang－ banna，Menga，1050－1080 m／1958．V．10；1 ¢，Xishuangbanna，Menglun， 650 m ／1964．IV．14，Baolin Zhang coll．；19，Xishuangbanna，Menga，1050－1080 m／ 1958．V．18，Fuji Pu coll．；19，Xishuangbanna，Menga，1050－1080 m／1958．V．18， Fuji Pu coll．； 1 P，Xishuangbanna，Xiaomengyang， 1100 m，1957．V．6，Dahua Liu coll．；1 ${ }^{\lambda}$ ，Xishuangbanna，Mengzhe， $800 \mathrm{~m} / 1958$. VII． 3 ，Fuji Pu coll．；1 ${ }^{\text {h }}$ ，Xish－ uangbanna，Menghun， $750 \mathrm{~m} / 1958 . \mathrm{VI} .2$ ； $1{ }^{\text {万人 }}$ ，Ruili，Ruili Botanical garden，
 uangbanna，2020．VI．30，Ying Yan coll．；1q，Xishuangbanna，Guomen Shan， 2019．V．11，Kaiqin Li coll．； 1 우즤，Xishuangbanna，Menghai，Menghun， 2011.

IV．26，Hongbin Liang and Kaiqin Li coll．； 8 中 $5^{\lambda}$ ，Xishuangbanna，Menghai，Man－ nong Xinzhai， $21.78233^{\circ} \mathrm{N}, 100.50706^{\circ} \mathrm{E}, 1582 \mathrm{~m}, 2021 . I V .3-8$ ，Hongbin Liang， Yuan Xu and Neng Zhang coll．； $1 \delta^{\lambda}$ ，Xishuangbanna，Guanlei，Nanlahe， $21.5796^{\circ} \mathrm{N}$ ， $101.1879^{\circ} \mathrm{E}, 465 \mathrm{~m}, 2021 . \mathrm{XI} .30$ ，Yong Wang coll．； 2 q $4{ }^{\wedge}$ ，Xishuangbanna，Meng－ la，Longlin New village，2020．VI．5－6， $21.52914^{\circ} \mathrm{N}, 101.49415^{\circ} \mathrm{E}, 1066 \mathrm{~m}$ ，Hong－ bin Liang and Yuan Xu coll．； $3 q 3$ § ${ }^{\lambda}$ ，Xishuangbanna，Xiaomengyang，Baihua Shan， $22.17720^{\circ} \mathrm{N}, 100.92428^{\circ} \mathrm{E}, 876 \mathrm{~m}, 2021 . I V .3$ ，Hongbin Liang and Yuan Xu coll．； $3 q 5{ }^{\circ}$ ，Xishuangbanna，Menghai，Nanlanghe， $22.17720^{\circ} \mathrm{N}, 100.92428^{\circ} \mathrm{E}$ ， 876 m，2020．IV．9，Hongbin Liang and Yuan Xu coll．； 1 1 $1{ }^{\lambda}$ ，Baoshan，Baihualing， N25．30499，98．80008， 1622 m，2020．IX．29，Yuan Xu coll．； 1 ㅇ，Baoshan，Baihual－ ing，N25．30499，98．80008， 1622 m，2019．X．2，Hongbin Liang and Yuan Xu coll．； 1q，Cangyuan，Banhong，2011．V．3，Kaiqin Li coll．；1q，Eshan，Ayi Power Station， $24.09573^{\circ}$ N， $102.54589^{\circ}$ E， 1444 m，2022．VII．2，Neng Zhang coll．；1q，Hekou， Huayudong， $22.67222^{\circ} \mathrm{N}, 103.93769^{\circ} \mathrm{E}, 97 \mathrm{~m}, 2021 . I V .22$ ，Hongbin Liang and Yuan Xu coll．； 3 q，Jianshui，Yunlongshan， $23.77582^{\circ} \mathrm{N}, 102.82258^{\circ} \mathrm{E}, 1645 \mathrm{~m}$ ， 2021．IV．23，Hongbin Liang and Yuan Xu coll．； 1 q，Lvchun，Huanglian Shan， 2018．5．23，Kaiqin Li coll．； $3 q 3{ }^{\text {T，}}$ ，Xishuangbanna，Menghai，Nanlanghe， $22.17720^{\circ}$ N， $100.92428^{\circ}$ E， 876 m，2020．VI．1，Hongbin Liang and Yuan Xu coll．； $16 \not$ 8 $^{\wedge}$ ，Xishuangbanna，Mengla，Longlin New village，2020．III．30， $21.52914^{\circ} \mathrm{N}$ ， $101.49415^{\circ} \mathrm{E}, 1066 \mathrm{~m}$ ，Hongbin Liang and Yuan Xu coll．；1 ${ }^{\lambda}$ ，Xishuangbanna， Menghai，Mengsong，Sanmai， $21.99943^{\circ} \mathrm{N}, 100.61022^{\circ} \mathrm{E}, 1028 \mathrm{~m}, 2020 . \mathrm{VI} .2$, Hongbin Liang and Yuan Xu coll．； 2 q，Ruili，Nongdao，2019．X．10，Yuan Xu coll．； 1 ${ }^{\lambda}$ ，Yingjiang，Nabang，2012．IX．29，Hongbin Liang coll．； 6 ใ $3 \delta^{\lambda}$ ，Eshan，Ayi Power Station， $24.09573^{\circ} \mathrm{N}, 102.54589^{\circ} \mathrm{E}, 1444 \mathrm{~m}, 2021$ ．IV．23，Hongbin Liang and Neng Zhang coll．； 1 \＆$, ~ Z h e n y u a n, ~ E n l e, ~ N a j i u, ~ 23.977826 º n, ~ 101.031797 º ~ E, ~ 1359 ~ m, ~$ 2022．VII．8，Yuan Xu and Neng Zhang coll．；2q，Zhenyuan，Sanzhangtian， 2022．V．28，Neng Zhang coll．；Guangxi：1 ${ }^{\text {¹，}}$ ，Yangshuo，Baisha／1963．VII．23， Shuyong Wang coll．； $2 q$ ，Baishou，1952．6．23； $1 q$ ，Baishou，1952．7．2；1 $q$ ，Fangc－ heng，Fulong， 240 m，1998．IV．20，Gexia Qiao coll．； 1 ？，Longlin／1984．V．21，Shu－ fang Wang coll．； 1 q，Yangshuo，Baisha／1963．VII．23，Shuyong Wang coll．； 1 q， Longzhou，Daqing Shan， 360 m，1963．VII．23，Shuyong Wang coll．； 1 q，Longzhou， Daqing Shan， 360 m，1963．IV．18，Shuyong Wang coll．； 1 q，Longzhou，Daqing Shan， 360 m，1963．IV．27，Shuyong Wang coll．；1q，Longzhou，Daqing Shan， 360 m，1963．IV．27，Shuyong Wang coll．；1q，Wuming，Daming Shan，1963．V．21， Sikong Liu coll．；1 ${ }^{\text {²，}}$ ，Longzhou，Daqing Shan， 360 m，1963．IV．25，Shuyong Wang coll．；1〕，Wuming，Daming Shan，1963．V．24，Jikun Yang coll．；1ð，Longlin／ 1980. IX．9，Lin Dong coll．；Tibet： 1 q，Mêdog，Bangxin， $29.48488^{\circ}$ N， $95.43508^{\circ} \mathrm{E}, 1418$ m，2020．IX．13， 1 q，Mêdog，Baibung Tea Farm， $29.26310^{\circ} \mathrm{N}, 95.20983^{\circ} \mathrm{E}, 1047 \mathrm{~m}$ ， 2020．IX．7，Hongbin Liang coll．；1 q，Mêdog，Baibung Tea Farm， $29.26310^{\circ}$ N， $95.20983^{\circ} \mathrm{E}$ ， $1047 \mathrm{~m}, 2021 . \mathrm{VI} .16$ ，Hongbin Liang and Neng Zhang coll．；9q7 ${ }^{\text {T，}}$ Mêdog，Baibung，Gelin， $29.23370^{\circ} \mathrm{N}, 95.17707^{\circ} \mathrm{E}, 1408 \mathrm{~m}, 2020 . \mathrm{VI} .11-15$ ，Hong－ bin Liang，Yuan Xu and Neng Zhang coll．；1q，Mêdog，Dexing，Wenlang， $29.36709^{\circ} \mathrm{N}, 95.34012^{\circ} \mathrm{E}, 1251 \mathrm{~m}, 2020.1 \mathrm{X} .4$ ，Hongbin Liang coll．； $5 中 50^{\top}$ ，Mêdog， Baibung，Gelin， $29.23370^{\circ}$ N， $95.17707^{\circ} \mathrm{E}, 1408 \mathrm{~m}, 2022$. VII．17－20，Hongbin Li－ ang，Yuan Xu and Neng Zhang coll．； 1 ¢ ，Mêdog，Lagong Tea Farm， $29.31879^{\circ} \mathrm{N}$ ，
 1912；1 ¢，Xishui，Linjiang， 300 m／IOZ and Guizhou Univ．Joint Expedition， 2000. VI．1，Song QZ coll．；1q，Libo，Maolan， 450 m，1998．X．27，Xinke Yang coll．；1 ${ }^{\text {T，}}$ Libo，Maolan， 450 m，1998．X．27，Xingke Yang coll．；3§，Maolan，1998．V，

Qiongzhang Song coll. / semipunctata; 1 đ, Libo, Maolan, 450 m, 1998.X.26, Wenzhu Li coll.; 1 ${ }^{\text {§ }}$, Wangmo, 1982. VI; 1 ${ }^{\text {T, }}$, Fanjing Shan, Huguo temple, 1350 m, 2001.VIII.03, Qiongzhang Song coll.; 1q, Libo, 500-700 m / 1998.V.24-30 / Lilioceris semipunctata, Det. Peiyu Yu; 1§̃, Libo, Xiaoqikong, 700 m, 1998.V.30, Runzhi Zhang coll.; 1 $\widehat{ }$, Libo, Yonggui, 700 m, 1998.V.29, Runzhi Zhang coll.; Hainan: 1 q, Baisha, Yinggeling, Nankai, Daoyin to Zafu village, 2009.XI.22, Meiying Lin coll.; 1 q, Changjiang, Bawang street, light trap, 19.11104, 109.08168 / 145 m, 2007.5.12, Hongbin Liang and Fuqiang Chen coll.; 1q, Xinglong / 1963. III.12, Baolin Zhang coll.; 1 q, Tongzha, 340 m / 1960.VII.31, Changqing Li coll.; 1q, Tongzha, 340 m / 1960.VII.31, Xuezhong Zhang coll.; 2q, Tongzha, 340 m / 1960.VII.4, Suofu Li coll.; 1q, 1934.10.27; 2才, Bawangling, Dongliu, 19.054112, 109.19445 / 635 m, 2007.5.11, Hongbin Liang coll.; $1{ }^{\lambda}$, Nada / 1954.IV.27, Keren Huang coll.; 1 ${ }^{\lambda}$, Tongzha, $340 \mathrm{~m} / 1960 . \mathrm{VI} .29$, Xuezhong Zhang coll.; 2 ${ }^{\text {§ }}$, Tongzha, 340 m / 1960.VIII.4-5, Suofu Li coll.; 1 ${ }^{\text {®̃, }}$ Tongzha, $340 \mathrm{~m} / 1960 . \mathrm{VII} .31$, Suofu Li coll.; 2 ${ }^{\lambda}$, Bawangling, 2019.IV.19, Run Zhou coll.; 1 q1 ${ }^{\lambda}$, Baisha, Gaofeng village, $19.04059^{\circ} \mathrm{N}, 109.31583^{\circ} \mathrm{E}, 886 \mathrm{~m}, 2020 . \mathrm{VII} .28$, Yuan Xu coll.; 2 q, Baisha, Fangza village, ${19.07599^{\circ}}^{\mathrm{N}}, 109.52348^{\circ} \mathrm{E}, 438 \mathrm{~m}, 2020 . \mathrm{VII} .29$, Yuan Xu coll.; 1 ใ $1 \delta^{\lambda}$, Nanfaling, $18.87220^{\circ} \mathrm{N}, 109.29446^{\circ} \mathrm{E}, 537 \mathrm{~m}, 2020 . \mathrm{VII} .26$, Yuan Xu coll.;
Fujian: 1q, Tongmuguan / 1979.VIII.4, Fusheng Huang coll. / Lilioceris semipunctata, det. Peiyu Yu / Lilioceris rufimembris, det. Liang H.B.; Vietnam: 1q, Tonkin, Hoa Binh, leg. A. de Cooman, 1939.VII; 2 ? , Tonkin, Hoa Binh, leg. A. de Cooman, 1940.VIII; 1 ¢ , Tonkin, Hoa Binh, L. Ouport; $1^{\lambda}$, Tonkin, Hoa Binh, leg. A. de Cooman, 1940.VIII; 2§, Tonkin, Hoa Binh, leg. A. de Cooman / Lilioceris rufimembris, det. Liang H.B; 2§, Tonkin.

Diagnosis. Anterior angles of pronotum protruding, pronotal disc with 2-5 irregular rows of fine punctures. Humeral groove of elytra distinct, punctures of elytra sparse and diminishing posteriorly, absent on apical $1 / 3$. Femora of legs without tooth. Lateral metasternum with a long strip of pubescence.

Redescription. BL = 7.5-9.0 mm, BW = 3.0-3.8 mm. Body brownish red.
Head (Figs 21, 45A). Vertex slightly convex, with a shallow groove in the middle, sparse punctate and pubescent laterally; frontoclypeal area triangular, lateral disc with sparse punctures and pubescent; labrum transverse, with sparse pubescent; antennae nearly $1 / 2$ of body length, antennomeres $1-4$ nearly globular, antennomere 2 shortest, antennomeres $5-10$ nearly $1.1 \times$ as long as wide, antennomere 11 slender.

Pronotum (Figs 21, 45B). Anterior angles protruding, posterior angles not protruding; sides slightly constricted in the middle; disc slightly raised; middle of disc with 2-5 rows of fine punctures. Scutellum triangular and pubescent.

Elytra (Figs 21, 35B). Humeri protruding, humeral groove and basal impression distinct; elytra without completely punctate striae, punctures sparse and large in the base, diminishing posteriorly, absent on apical $1 / 3$; intervals smooth; epipleura raised, with a sparse row of fine punctures.

Mesosternum pubescent. Lateral metasternum with a long and straight strip of pubescence, metepisternum densely pubescent (Fig. 45C).

Abdominal sternite (Fig. 35A). Lateral transverse impressions small and indistinct on sternites $1-4$, other areas of sternites $1-4$ and all of sternite 5 densely pubescent.

Leg (Fig. 35C). Femora with dense pubescence on the dorsal surface, with sparse pubescence on the ventral surface, without tooth.

Male genitalia (Fig. 50A-D). Ostium occupying 1/4 length of median lobe (Fig. 50A); apex hooked (Fig. 50B); tegmen Y-shaped, basal piece of tegmen triangular and broad, lateral lobes slightly sclerotized and combined with second connecting membrane; internal sac membranous, with distinct dorsal, median and ventral sclerites, posterior part of dorsal sclerite paralleled in dorsal view, ventral sclerite short and flaky, median sclerite distinctly sclerotized (Fig. 50C, D).

Female reproductive organs (Fig. 62A-C). Tergites 8 and 9, sternites 8 and 9 sclerotized, posterior areas of tergite 8, sternite 8, and apodemes with pubescence, spiculum gastrale Y -shaped and long; ovipositor with dense pubescence, distal part of ovipositor cylindrical, long and with a protuberance; spermatheca simple and hooked.

Distribution (Fig. 67). China (Fujian, Guangxi, Guizhou, Hainan Tibet, Yunnan); Indonesia (Java, Sumatra); Nepal; India (Kimoto and Takizawa 1973; Bezděk and Schmitt 2017).

Host plant and habitat (Fig. 73A, B). Host plant of this species is Smilax bracteata Presl. and Lilioceris semipunctata shares the same habitat as L. latissima according to our observations in Baihua Shan of Xishuangbanna, Yunnan.

Remark. Fabricius (1801: 472) described Lilioceris semipunctata based on specimens from Sumatra. We examined three syntype photographs of $L$. semipunctata. They obviously belong to two different species: the specimen with the identification label and locality is here designated as lectotype (Figs 21, 22). The other two specimens (TYPE / zmuc 00031032; TYPE / zmuc 00031031) with no label and no locality are here excluded from the type series. These two specimens with a glabrous metasternum are clearly different from the lectotype, but identical to Lilioceris latissima.

Lacordaire (1845: 559) redescribed Lema semipunctata based the specimens from Java, and indicated that Lema dehaanii (Guérin-Méneville, 1844) was completely similar to $L$. semipunctata, and moved it to the genus Crioceris. Then Kimoto and Gressitt (1979: 230) synonymized L. dehaanii with L. semipunctata, and subsequent researchers followed this treatment.

We also examined a syntype of Lilioceris rufimembris (Pic, 1921) in NHHN, and no significant morphological differences were found from the lectotype of $L$. semipunctata, except for two rows fine punctures on pronotum (Fig. 23), which are absent in the lectotype of $L$. semipunctata (Fig. 21). In IZCAS, there are more than 150 specimens from Yunnan that perfectly match these two types of punctures on the pronotum. We compared all these specimens and found that there were no significant morphological differences including male genitalia. Therefore, we conclude that $L$. semipunctata and $L$. rufimembris are conspecific, and that the pronotal punctures in $L$. semipunctata can be variable.

## Lilioceris yuae Long, 2000b

Figs $25,26,36 A-D, 46 A-C, 55 A-D, 66 A-C, 68,74 A-D$

Lilioceris yuae Long, 2000b: 416 (China: Hainan).

Type material examined. Holotype of Lilioceris yuae (MBSU), Holotype: ㅇ, Lilioceris yuae sp. nov., Jianguo Long det., 1999.9.30 / Hainan, Qiong Shan, Dongzhai Gang, 1985.VI.4, Shigui Jiang coll. En-207218 SYS.

Other material examined. Total 52 specimens. China: Guangxi: 18¢ 16 §, Fangchenggang, Jinhuacha Nature Reserve, 2021.III.24-29, Pingzhou Zhu coll.; 1ใ, Nanning, Daming Shan, 2019.VIII.20, Meiying Lin coll.; 1 ${ }^{\text {², }}$, Fangchenggang, Shangsi, Shiwan Dashan, 2023.6.1, Yuan Xu and Neng Zhang coll.; Guangdong: $2 q$, Dinghu Shan, 1980.VI.4-10, Yinshu Xie coll.; $2 q 4{ }^{\text {® }}$, Zhanjiang, Dalang village, 2016.IV.26-27, Hongbin Liang coll.; Hainan: 1 , Jianfengling, 1982.VIII. 5 / Chengfeng Liang coll. / Lilioceris yuae, det. Liang H.B.; $1{ }^{\top} 1$ Q, Qinglan / 1965.II.8, Enkong Liu coll.; 1q, Danzhou, SC Tropical Agr. Univ., beating, $19.50664^{\circ} \mathrm{N}, 109.47883^{\circ} \mathrm{E}$ / 150 m, 2007.V.16, Hongbin Liang coll.; 1q, Ledong, Jianfengling, Chahekou, 206 m, 2009. XII.4, $18.74552^{\circ}$ N, $108.99068^{\circ}$ E, Meiying Lin coll.; 1q, Jianfengling, E108.8716, N18.7170, 1412 m, 2019.4.14-16, Haitian Song coll.; 2 ${ }^{\top}$, Baisha, Gaofeng village, $19.04059^{\circ} \mathrm{N}, 109.31583^{\circ} \mathrm{E}, 886 \mathrm{~m}, 2020 . \mathrm{VII} .28$, Yuan Xu coll.

Diagnosis. Anterior angles of pronotum slightly protruding, pronotal disc with two rows of fine punctures. Humeral groove of elytra indistinct, punctures diminishing posteriorly, absent on apical 1/3. Lateral metasternum with sparse pubescence.

Redescription. $\mathrm{BL}=7.5-7.8 \mathrm{~mm}, \mathrm{BW}=3.5-3.8 \mathrm{~mm}$. Body brownish red, head, antenna, legs and lateral metasternum with a weak blue metallic luster.

Head (Figs 25, 46A). Vertex flat, with a very deep groove in the middle, sparsely punctate and pubescent laterally; frontoclypeal area triangular, lateral disc with sparse punctures and pubescent; labrum transverse, with sparse pubescent; antennae nearly $1 / 2$ of body length, antennomeres 1-4 nearly globular, antennomere 2 shortest, antennomeres 5-10 length almost equal, flatten, antennomere 11 slender.

Pronotum (Figs 25, 46B). Anterior angles protruding, posterior angles slightly protruding; sides distinctly constricted in the middle; disc flat; middle of disc with two rows of fine and shallow punctures. Scutellum triangular and pubescent.

Elytra (Figs 25, 36B). Humeri protruding, humeral groove and basal impression shallow; elytra without completely punctate striae, punctures sparse, diminishing posteriorly, absent on apical 1/3; intervals smooth; epipleura raised, with a row of fine punctures.

Mesosternum pubescent. Lateral metasternum with a short and oblique strip of pubescence. Metepisternum densely pubescent (Fig. 46C).

Abdominal sternite (Fig. 36A). Lateral transverse impressions big and distinct on sternites 1-4, other areas of sternites 1-4 densely pubescent. Middle of first abdominal sternite with a row of distinctly long pubescence in male, and first abdominal sternite without long pubescence in female.

Leg (Fig. 36C). Femora with dense pubescence on the dorsal surface, with sparse pubescence on the ventral surface, without tooth.

Male genitalia (Fig. 55A-D). Ostium occupying 1/4 length of median lobe (Fig. 55A); apex slightly hooked (Fig. 55B); tegmen Y-shaped, basal piece of tegmen oval and narrow, lateral lobes slightly sclerotized and combined with second connecting membrane; internal sac membranous, with distinct dorsal and ventral sclerites, posterior part of dorsal sclerite in dorsal view parallel, ventral sclerite extended and tubular (= flagellum), median sclerite very small (Fig. 55C, D).

Female reproductive organs (Fig. 66A-C). Tergites 8 and 9, sternites 8 and 9 sclerotized, posterior areas of tergite 8, sternite 8, and apodemes with pubescence, spiculum gastrale $Y$-shaped and long; ovipositor with dense pubescence, distal part of ovipositor cylindrical, long and with a protuberance; spermatheca simple and curved.


Figures 23-26. Habitus of Lilioceris spp. 23, 24 L. rufimembris, syntype, China (Yunnan), photographed by Christophe Rivier (MNHN) 25, 26 L. yuae, holotype, China (Hainan), photographed by Yuan Xu. Scale bars: 5.0 mm .


Figures 27-31. Abdominal sternites, elytra, leg, and antennae of Lilioceris spp. 27 L. consentanea, đ̂, China (Hainan) 28 L . dentifemoralis, $\widehat{\sigma}^{\lambda}$, China (Hainan) 29 L . discrepens, ${ }^{\lambda}$, China (Yunnan) 30 L . jianfenglingensis, ${ }^{\lambda}$, China (Yunnan) 31 L. latissima, ${ }^{\lambda}$, China (Hainan) A abdominal sternites B elytra C leg D antennae.


Figures 32-36. Abdominal sternites, elytra, leg, and antennae of Lilioceris spp. 32 L. lianzhouensis, ${ }^{3}$, China (Hainan) 33 L. rondoni, ${ }^{\circ}$, China (Yunnan) 34 L. rufometallica, $\uparrow$, China (Hainan) 35 L. semipunctata, ${ }^{\lambda}$, China (Yunnan) 36 L. yuae, ㅇ, China (Hainan) A abdominal sternites B elytra C leg D antennae.


Figures 37-46. Head, pronotum, abdominal sternites of Lilioceris spp. 37 L . consentanea, $\widehat{\jmath}$, China (Hainan) 38 L. dentifemoralis, ${ }^{\lambda}$, China (Hainan) 39 L. discrepens, ${ }^{\lambda}$, China (Yunnan) 40 L. jianfenglingensis, ${ }^{\lambda}$, China (Hainan) 41 L . latissima, $\uparrow$, China (Yunnan) 42 L . lianzhouensis, $\uparrow$, China (Yunnan) 43 L . rondoni, ${ }_{\mathrm{o}}$, China (Hainan) 44 L . rufometallica, $\odot$, China (Yunnan) 45 L. semipunctata, $\odot$, China (Yunnan) 46 L. yuae, $\odot$, China (Hainan) A head B pronotum C abdominal sternite.

Distribution (Fig. 68). China (Guangxi, Guangdong, Hainan).
Host plant and habitat (Fig. 74A-D). This species feeds on Smilax lanceifolia Roxb. according to our observation in Hainan. One locality of this species, near a road of Gaofeng village (Hainan, Baisha), is situated at the subtropics. The habitat is secondary forests, which is characterized by high temperature and humidity, plentiful precipitation, and much sunlight. The forests are open and composed of tall trees, woody vines, and many weeds.


Figures 47-50. Male genitalia of Lilioceris spp. 47 L . dentifemoralis, China (Hainan) 48 L . rondoni, China (Yunnan) 49 L. rufometallica, China (Yunnan) $\mathbf{5 0}$ L. semipunctata, China (Yunnan) A aedeagus, lateral view $\mathbf{B}$ aedeagus, dorsal view C sclerites in internal sac, lateral view D dorsal sclerite, dorsal view. Scale bars: 0.2 mm .


Figures 51-56. Male genitalia of Lilioceris spp. 51 L. discrepens, China (Hainan) 52 L. lianzhouensis, China (Yunnan) 53 L. latissima, China (Yunnan) 54 L. jianfenglingensis, China (Yunnan) 55 L. yuae, China (Hainan) 56 L. consentanea, China (Yunnan) A aedeagus, lateral view B aedeagus, dorsal view $\mathbf{C}$ sclerites in internal sac, lateral view $\mathbf{D}$ dorsal sclerite, dorsal view. Scale bars: 0.2 mm .

Remarks. Lilioceris yuae is very similar to L. cyanicollis but differs by the body color and pubescence on the metasternum; the body of $L$. yuae is brownish red, and only the head, antenna, leg, and lateral metasternum have a very weak blue metallic luster; lateroposterior corner of metepisternum with sparse pubescence. In L. cyanicollis, the elytra and abdomen are brownish red, pronotum is brownish red or blue, and the other areas are blue with a distinctly blue metallic luster; and the metepisternum is glabrous. However, the male genitalia and the female reproductive organs of these two species are very similar. We temporarily treat $L$. yuae as distinct species, as more material is needed to conclusively elucidate their relationship.


Figures 57-66. Female reproductive organs of Lilioceris spp. 57 L. dentifemoralis, China (Hainan) 58 L. consentanea, China (Hainan) 59 L. lianzhouensis, China (Yunnan: Wuding) 60 L. latissima, Japan (Tokyo) 61 L. jianfenglingensis, China (Yunnan) 62 L. semipunctata, China (Yunnan: Wuding) 63 L. rondoni, China (Yunnan) 64 L. rufometallica, China (Yunnan) 65 L. discrepens, China (Yunnan) 66 L. yuae, China (Hainan) A dorsal view B ventral view C spermatheca. Scale bars: 0.5 mm .


Figure 67. Distribution map of Lilioceris spp. (all marked location information is derived from the labels of available specimens).


Figure 68. Distribution map of Lilioceris spp. (all marked location information is derived from the labels of available specimens).


Figure 69. Lilioceris consentanea in China (Hainan: Yinggeling), 1 April 2010, photographed by Meiying Lin A adult B larva.


Figure 70. Lilioceris discrepens in China (Yunnan: Gongshan), 31 May 2021, photographed by HB Liang A host plant B habitat.


Figure 71. Lilioceris rondoni in China (Yunnan: Mengla), 2020.6.6, photographed by Y Xu A adult B host plant.


Figure 72. Lilioceris rufometallica in China (Yunnan: Gongshan), 31 May 2021, photographed by Y Xu and HB Liang A adult $\mathbf{B}$ host plant. (Lilioceris rufometallica lives together with L. discrepens at this site).


Figure 73. Lilioceris semipunctata in China (Yunnan: Jianshui), 22 April 2021, photographed by Y Xu. A adult B host plant.


Figure 74. Lilioceris yuae in China (Guangxi: Fangchenggang), 24 March 2021, photographed by Pingzhou Zhu A adult B eggs $\mathbf{C}$ host plant $\mathbf{D}$ habitat.

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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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