

Nineteen new species of *Desmopachria* Babington, 1841 (Coleoptera, Adephaga, Dytiscidae, Hydroporinae, Hyphdrini) with notes on the taxonomy of the genus

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Abstract

Nineteen new species of *Desmopachria* Babington, 1841 are described from multiple species groups. Two new species groups are erected, the *Desmopachria apicodente* species group and the *Desmopachria bifurcata* species group. *Desmopachria divergens* **sp. nov.** (Venezuela), *Desmopachria lineata* **sp. nov.** (Venezuela), *Desmopachria surinamensis* **sp. nov.** (Suriname), and *Desmopachria tenua* **sp. nov.** (Guyana) are described in *Desmopachria* but are not assigned to a species group. *Desmopachria apicodente* **sp. nov.** (Guyana, Venezuela), *Desmopachria lateralis* **sp. nov.** (Venezuela), and *Desmopachria tumida* **sp. nov.** (Venezuela) are described in the new *Desmopachria apicodente* species group and are the only members of the group. *Desmopachria bifurcata* **sp. nov.** (Peru), and *Desmopachria lata* **sp. nov.** (Brazil) are described in the new *Desmopachria bifurcata* group. Other members of the *Desmopachria bifurcata* group are *Desmopachria bifasciata* Zimmermann, *Desmopachria bolivari* Miller, *Desmopachria ovalis* Sharp, and *Desmopachria varians* (each previously “ungrouped”). *Desmopachria pseudocavia* **sp. nov.** (Venezuela) is described in the *Desmopachria convexa-signata* species group. *Desmopachria wolfei* **sp. nov.** (Venezuela) is described in the *Desmopachria nitida* species group. *Desmopachria angulata* **sp. nov.** (Guyana, Suriname), *Desmopachria emarginata* **sp. nov.** (Guyana, Suriname, Venezuela), *Desmopachria imparis* **sp. nov.** (Guyana), *Desmopachria impunctata* **sp. nov.** (Suriname, Venezuela), and *Desmopachria truncata* **sp. nov.** (Guyana, Suriname) are described in the *Desmopachria portmanni-aldessa* species group. *Desmopachria bisulcata* **sp. nov.** (Suriname), and *Desmopachria irregulara* **sp. nov.** (Venezuela) are described in the *Desmopachria portmanni-portmanni* species group. *Desmopachria robusta* **sp. nov.** (Venezuela) is described in the *Desmopachria striola* species group. A key to the species groups is included. Male genitalia are figured for all new species and dorsal habitus images are provided for most new species.

Keywords

Diving water beetles, male genitalia, South America, taxonomy

Introduction

The hyperdiverse diving beetle (Dytiscidae) genus *Desmopachria* Babington includes approximately 133 species prior to this paper (Nilsson and Hájek 2019). Within *Desmopachria*, there are a number of groups that are relatively well defined by distinctive synapomorphies, many of which were previously regarded as subgenera (Guignot 1949; Young 1980). Later these groups were relegated to species-group status because of concerns about monophyly of several of them (Miller 2001). A rather large number of new species in these various groups have been described in the past few years (Miller 1999, 2001, 2005; Braga and Ferreira Jr 2011, 2014; Gustafson and Miller 2012; Makhan 2012, 2015; Megna and Sanchez-Fernandez 2014; Miller and Wolfe 2018). Given the regular description of new species, it can be expected that species discovery may continue apace for some time. Species appear to be abundant and narrowly endemic, and as increased collecting occurs in new areas, especially in under-collected areas of South America, new species can be expected to be found. Fortunately, it seems that species in the genus often have very distinctive male genitalia and other features that make their delimitation and diagnoses possible.

Even though several of the subgroups in *Desmopachria* (whether subgenera or species groups) have rather distinctive synapomorphies and are likely monophyletic, there are many species that are not currently well-placed into them, which is partly what led to the obliteration of the subgenera and the recognition of an “ungrouped” collection of species (Miller 2001). Some species in this collection may belong to one of the subgroups, but descriptions do not provide enough information for their placement and specimens (primary types) have not been examined. In other cases, modern authors have described species, but did not place them in groups nor adequately describe them such that they can be placed into groups (specifically Makhan 2012, 2015).

The objective of this paper is to describe 19 new species of *Desmopachria*. Some of these belong to existing groups, some are placed in newly proposed groups, and others are not clearly placed into any of these groups yet are clearly in *Desmopachria*, so are left ungrouped. Following recent previous treatments of *Desmopachria* (Miller 1999, 2001, 2005; Braga and Ferreira Jr 2010, 2011, 2014, 2018; Gustafson and Miller 2012; Megna and Sanchez-Fernandez 2014; Miller and Wolfe 2018), keys to species are not provided; instead, specimens should be keyed to species groups, then dissected and male genitalia and other diagnostic features compared with published illustrations and diagnoses of species. New records are also provided for some known species, and some comments are provided regarding several of the groups.

Materials and methods

Methods closely follow recent work on the group by Miller and Wolfe (2018, 2019) and Miller (2020). Measurements were made with an ocular scale on a Zeiss Discovery V8 dissecting microscope. The diagnostic range of measurements of structures was emphasized, so the largest and smallest specimens were preferentially measured to the extent possible. In the case of available series of specimens ten or fewer, all intact specimens were measured. Specimens not intact were not measured. Measurements in the text are abbreviated as follows, while the ratios TL/GW and HW/EW were also calculated.

TL	total length
GW	greatest width across elytra
PW	greatest width of pronotum
HW	greatest width of head
EW	distance between eyes

Illustrations were made using a drawing tube on a Zeiss Discovery V8 dissecting scope. Sketches were first done in pencil then scanned, placed into an Adobe Illustrator artboard, and inked digitally using vector lines.

Specimens of *Desmopachria* were examined from the following collections:

CSBD	Center for Biological Diversity, University of Guyana.
KBMC	Kelly B. Miller Collection, Museum of Southwestern Biology, University of New Mexico, Albuquerque, NM, USA.
SEMC	University of Kansas Natural History Museum, University of Kansas, Lawrence, Kansas, USA (A.E.Z. Short).
MIZA	Museo del Instituto de Zoología Agrícola Francisco Fernández Yépez, Universidad Central de Venezuela, Maracay, Venezuela (L. Joly).
MSBA	Museum of Southwestern Biology Division of Arthropods, University of New Mexico, Albuquerque, NM, USA (K.B. Miller).
NZCS	National Zoological Collection of Suriname, Paramaribo, Suriname (P. Ouboter).
USNM	United States National Collection of Insects, Smithsonian Institution, Washington, DC, USA (C. Micheli).

Key to the species groups of *Desmopachria*

- 1 Anterior metatibial spine serrate.....*Desmopachria vicina* group
- Anterior metatibial spine not serrate2
- 2 Pronotum with an incised stria on each side of base*Desmopachria dispersa* group
- Pronotum without basal striae.....3

- 3 Prosternal process sexually dimorphic, male process apically strongly bifid, area between rami forming a deep pit, female process not as in male ***Desmopachria portmanni* group**
- Prosternal process not sexually dimorphic, not forked in either sex 4
- 4 Elytron with a distinct sutural stria (e.g., Fig. 72) ***Desmopachria striola* group**
- Elytron without a distinct sutural stria 5
- 5 Anterior clypeal margin sexually dimorphic, in males strongly modified, thin, translucent, strongly up-turned, anteriorly beaded in female, but not as strongly modified as in male ***Desmopachria ubangoides* group**
- Anterior clypeal margin not sexually dimorphic, anteriorly beaded in both sexes 6
- 6 Male lateral lobes deeply bifid, apex divided into two elongate rami (e.g., Fig. 50) ***Desmopachria nitida* group**
- Male lateral lobes not deeply bifid 7
- 7 Male lateral lobes with anteapical, articulable process (e.g., Fig. 45) ***Desmopachria convexa* group**
- Male lateral lobes without anteapical, articulable process 8
- 8 Male median and lateral lobes very strongly robust and heavily sclerotized ***Desmopachria glabricula* group**
- Male median and lateral lobes not strongly robust and sclerotized 9
- 9 Male median lobe short and broad, much shorter than lateral lobes (e.g., Figs 29, 32, 35, 36, 39, 41), male lateral lobes elongate, dorsoventrally flattened and laterally broad, medially distinctly bent dorsad, apical portion flattened and straight (e.g., Figs 30, 33, 37, 42) ***Desmopachria bifurcita* group**
- Male median and lateral lobes not as described above 10
- 10 Male lateral lobe apically with a distinct spur or tooth (e.g., Figs 17, 22, 27) ***Desmopachria apicodente* group**
- Male lateral lobe apically without distinct spur or tooth **ungrouped *Desmopachria***

Ungrouped *Desmopachria*

Many *Desmopachria* species do not have the distinctive synapomorphies of the various species groups recognized by Miller (2001) and in this work (see key above), or originally treated as subgenera (Young 1980). Most of these species were originally placed in *Desmopachria* (*Desmopachria*) Babington, but that subgenus does not exhibit a clear synapomorphy, instead it is a collection of species that do not have features present in other subgroups of *Desmopachria*. The following new species also do not fit into any of the defined species groups and are placed among the ungrouped *Desmopachria*.

***Desmopachria divergens* sp. nov.**

<http://zoobank.org/BEF901E2-265C-4401-8121-57E66ED970DF>

Figures 1, 2, 76

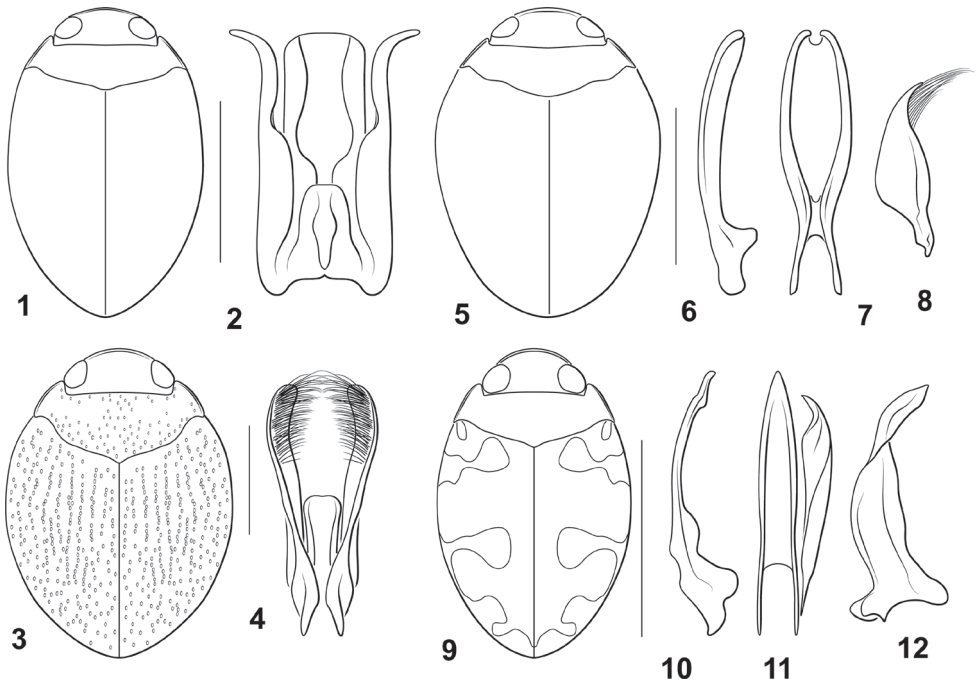
Type locality. Venezuela, Amazonas State, Comunidad Caño Gato on Rio Sipapo, 4°58.838'N 67°44.341'W.

Diagnosis. This species is characterized by dorsal iridescence and the shape of the male genitalia. The male median lobe in ventral aspect is extremely broad and apically very broadly truncate combined with lateral lobes with the apices strongly curved laterad and divergent (Fig. 2). This species is dorsally iridescent but lacks the bifurcate prosternal process of the *Desmopachria portmanni* species group. This makes it somewhat similar to specimens in the *Desmopachria ubangoides* species group, but *Desmopachria divergens* lacks the sexually dimorphic anterior clypeal margins of that group (males with the margin flattened and upturned, females beaded, but not as strongly modified (Miller 2001; Young 1980).

Description. Measurements. TL = 1.8–2.0 mm, GW = 1.1–1.2 mm, PW = 0.9–1.0 mm, HW = 0.6–0.7 mm, EW = 0.3–0.4 mm, TL/GW = 1.6–1.7, HW/EW = 2.1–2.2. Body elongate oval, laterally broadly curved, lateral margins somewhat discontinuous between pronotum and elytron, body broadest across elytra at midlength of body (Fig. 1).

Coloration. Dorsal surface of head and pronotum evenly yellow-orange. Elytron evenly orange-brown, distinctly iridescent. Ventral surfaces orange, slightly darker medially on metathorax, medially slightly iridescent.

Sculpture and structure. Head moderately broad, anteriorly rounded with anterior clypeal margin with narrow, continuous bead; surface of head shiny, finely and sparsely punctate; eyes large (HW/EW = 2.1–2.2); antennae short, scape and pedicel relatively large and rounded, flagellomere III long and slender, apically expanded, antennomeres IV–X short and broad, lobed at anterodorsal angle, antennomere XI elongate, apically pointed. Pronotum moderately short, lateral margins short, distinctly curved with continuous narrow bead, similar width throughout; surface shiny, very finely, evenly punctate. Elytron moderately broad, laterally broadly curved; surface shiny, more coarsely and evenly punctate than pronotum, punctuation distinctive and prominent, densely and evenly punctate. Prosternum extremely short, longitudinally compressed, medially slightly carinate; prosternal process slender anteriorly, with distinctive, small medial tubercle, apically short and broad, medially flattened, apically broadly rounded. Metaventrite broad and evenly smoothly convex medially, surface shiny, finely, sparsely, and evenly punctate; metaventrite wings extremely slender. Metacoxa with medial portion short, < 1/3 length of metaventrite medially, metacoxal lines slightly divergent anteriorly; lateral portion of metacoxa extremely large, anteriorly strongly expanded; surface shiny, finely, sparsely, and evenly punctate. Metatrochanter large, subequal to length of ventral margin of metafemur;



Figures 1–12. *Desmopachria* species. (1, 2) *Desmopachria divergens* 1 habitus 2 male genitalia, ventral aspect. (3, 4) *Desmopachria lineata* 1 habitus 2 male genitalia ventral aspect (5–8) *Desmopachria surinamensis* 5 habitus 6–8 male genitalia 6 median lobe, right lateral aspect 7 median lobe, ventral aspect 8 right lateral lobe, right lateral aspect (9–12) *Desmopachria tenua* 9 habitus 10 median lobe, right lateral aspect 11 median lobe and right lateral lobe, ventral aspect; 12 right lateral lobe, right lateral aspect. Scale bars: 1.0 mm for habitus drawings.

legs otherwise not noticeably modified. Abdomen with surfaces shiny and smooth, very finely and sparsely punctate.

Male genitalia. Male median lobe in ventral aspect very broad, lateral margins linear to very broad, truncate apex (Fig. 2). Lateral lobe in ventral aspect slender, medially constricted on medial margin, apically slender, strongly curved laterad, apex narrowly rounded (Fig. 2).

Sexual dimorphism. No obvious sexual dimorphic features were discovered.

Variation. No characteristic variation was examined among the specimens examined.

Etymology. This species is named *divergens*, Latin for divergent, for the apically distinctly divergent lateral lobes (Fig. 2).

Distribution. Specimens are only known from the type locality, Caño Gato, Amazonas, Venezuela (Fig. 76).

Type material. Holotype in MIZA, male labeled, “VENEZUELA: Amazonas State 4°58.838'N, 67°44.241'W, 95m Comunidad Caño Gato, on Rio Sipapo; 16.i.2009; leg. Short, Miller, Camacho, Joly, & García VZ09-0116-01Z: along stream/ SM0843057 KUNHM-ENT [barcode label]/ HOLOTYPE *Desmopachria*

divergens Miller, 2021 [red label with black line border].” Paratypes, 19 in MIZA, MSBA, and SEMC labeled same as holotype except different barcode labels (Table 1) and each with “/...PARATYPE *Desmopachria divergens* Miller, 2021 [blue label with black line border.”

***Desmopachria lineata* sp. nov.**

<http://zoobank.org/4B826E7E-1D9E-49C4-BEA3-42D3BA92962E>

Figures 3, 4, 76

Type locality. Venezuela, Amazonas State, near Iboruwa, “Tobogancito,” 5°48.414'N, 67°26.313'W.

Diagnosis. This species is distinct in having coarse punctation on the pronotum and elytron with many punctures on the elytron arranged in distinctive longitudinal linear series, often confluent such that linear grooves are formed (Fig. 3). The male genitalia are distinctive with the median lobe shorter than half the length of the lateral lobes, broad and apically truncate and the lateral lobes elongate, apically somewhat expanded and with a dense series of elongate setae on the apicomedial surface (Fig. 4). Specimens are rather large for *Desmopachria* (TL = 2.6–2.8 mm). This species is similar to members of the *Desmopachria portmanni* group, especially *Desmopachria grammoticta* Braga & Ferreira-Jr., which also has linear series of elytral punctures. However, *Desmopachria lineata* does not have the characteristic sexually dimorphic prosternal process of the *Desmopachria portmanni* species-group (including *Desmopachria grammoticta*). The prosternal process in males of *Desmopachria lineata* is not bifurcate with a medial pit, instead it is similar to the process in females. This is an unusual species in that it appears phonetically similar to members of the *Desmopachria portmanni* group, but it lacks the bifid male prosternal process. It is certainly possible that the character states and relationships among these taxa is more complicated than currently understood. It seems clear that investigation of the utility and diversity of these and other characters among this group of *Desmopachria* should be investigated in the future.

Description. Measurements. TL = 2.6–2.8 mm, GW = 1.9–2.0 mm, PW = 1.4–1.5 mm, HW = 1.0 mm, EW = 0.5–0.6 mm, TL/GW = 1.4, HW/EW = 1.8. Body large for genus, very broad, rounded, laterally broadly curved, lateral margins slightly continuous between pronotum and elytron, body broadest across elytra anterior at ca. midlength of body (Fig. 3).

Coloration. Dorsal surface of head, pronotum and elytron red brown, moderately uniform in color throughout. Head appendages, pro- and mesothoracic legs and ventral surfaces of head and prothorax orange; other ventral surfaces red.

Sculpture and structure. Head broad, anteriorly produced in rounded lobe; anterior margin of clypeus curved, flattened, margined with conspicuous, continuous flattened bead; surface of head shiny, finely but distinctly punctate over entire surface; eyes moderately large (HW/EW = 1.8); antennae short, scape and pedicel relatively large and rounded, flagellomere III long and slender, apically expanded,

[illegible]

antennomeres IV–X short and broad, lobed at anterodorsal angle, antennomere XI elongate, apically pointed. Pronotum very short, lateral margins short, broadly curved, more so anteriorly, with continuous narrow bead; surface shiny, coarsely punctate medially and along most of anterior margin, less punctate lateromedially, punctures irregular, some confluent. Elytron moderately broad, laterally broadly curved; surface shiny, more coarsely punctate than pronotum, punctuation distinctive and prominent, irregular, many punctures confluent forming distinctive longitudinal lines and grooves. Prosternum extremely short, longitudinally compressed, medially slightly carinate; prosternal process slender anteriorly, with distinctive, low medial tubercle, apical portion broad basally with broad basal U-shaped region and concave slender apical process emerging from between branches of U, apically narrowly rounded. Metaventricle broad and evenly convex medially, surface shiny, coarsely punctate, punctures forming longitudinal, linear series; metaventricle wings extremely slender. Metacoxa with medial portion short, $< 1/3$ length of metaventricle medially, metacoxal lines slightly divergent anteriorly; lateral portion of metacoxa extremely large, anteriorly strongly expanded; surface shiny, evenly and coarsely punctate. Metatrochanter large, subequal to length of ventral margin of metafemur; legs otherwise not noticeably modified. Abdomen with surfaces shiny and smooth, most of surface coarsely punctate.

Male genitalia. Male median lobe in dorsal aspect short and broad, $< 1/2$ length of lateral lobe, apex slightly broadened, apically truncate with rounded lateral margins, medially very finely emarginate, (Fig. 4). Lateral lobe in dorsal aspect slender, elongate, evenly expanded apically and broadly curved medially, apicomedial surface with dense, long setae (Fig. 4).

Sexual dimorphism. No obvious sexual dimorphic features were discovered.

Variation. There is some degree of variation in the punctuation on the pronotum, elytron and ventral surfaces from specimen to specimen with some with punctures coarser, more confluent, with more strongly marked linear series. But in all cases, some degree of coarse linear series is present on the elytra and punctuation is coarse overall compared with most other species in the genus.

Etymology. This species is named *lineata*, Latin for lined, for the distinctive linear series of punctures on the disc of the elytron (Fig. 3).

Distribution. This species is known from Amazonas and Bolívar States, Venezuela, and (Fig. 76).

Type material. Holotype in MIZA, male labeled, “VENEZUELA: Amazonas State 5°48.414'N, 67°26.313'W, 80m nr. Iboruwa: “Tobogancito” 13.ii.2009; leg. K.B. Miller VZ09-0113-02E; leaf-choked detrital pools in forest/ SEMC0858759 KUN-HM-ENT/ HOLOTYPE *Desmopachria lineata* Miller, 2021 [red label with black line border].” Paratypes, 2 in SEMC labeled, “VENEZUELA: Bolívar State 4°28.782'N, 61°34.904'W, 853m 1 km E. Pauji, trib. Of Rio Pauji 16.vii.2010; leg Short, Tellez, Arias along stream; VZ10-0716-01A/...” with barcode labels SEMC0906695 and SEMC0906722.

***Desmopachria surinamensis* sp. nov.**

<http://zoobank.org/1ECD49A5-390B-45B8-AA8E-1B1771B3DD23>

Figures 6–8, 76

Type locality. Suriname, Sipaliwini District, Raleighvallen Nature Reserve, Voltzberg Trail, 4°40.910'N, 56°11.138'W.

Diagnosis. This species is similar to members of the *Desmopachria apicodente* group in having a longitudinal tumidity laterally on the elytron, being extremely broad (TL/GW = 1.3–1.4) and having a very distinctive, flattened bead along the anterior clypeal margin. However, *Desmopachria surinamensis* lacks the apical tooth on the lateral lobe characteristic of the *Desmopachria apicodente* group (see below). The male genitalia are distinctive. The median lobe in ventral aspect is elongate, broad, and comprised of long, slender, evenly curved lateral margins with a thin region in between (Fig. 7). The apices of the lateral struts are narrowly rounded and proximate with a small emargination in-between (Fig. 7).

Description. Measurements. TL = 1.9–2.0 mm, GW = 1.4–1.5 mm, PW = 1.0–1.1 mm, HW = 0.6–0.7 mm, EW = 0.4–0.5 mm, TL/GW = 1.3–1.4, HW/EW = 1.8–1.9. Body very broad, rounded, laterally broadly curved, lateral margins continuous between pronotum and elytron, body broadest across elytra near midlength of body (Fig. 6).

Coloration. Dorsal surface of head and pronotum orange. Elytron red, slightly paler anterolaterally. Head appendages, pro- and mesothoracic legs and ventral surfaces of head and prothorax orange, other ventral surfaces red.

Sculpture and structure. Head broad, anteriorly produced, flattened, anterior margin of clypeus curved, margined with conspicuous, continuous flattened narrow bead; surface of head shiny, finely and sparsely punctate; eyes large (HW/EW = 1.8–1.9); antennae short, scape and pedicel relatively large and rounded, flagellomere III long and slender, apically expanded, antennomeres IV–X short and broad, lobed at anterodorsal angle, antennomere XI elongate, apically pointed. Pronotum very short, lateral margins short, slightly curved with continuous narrow bead, of even width throughout length; surface shiny, nearly impunctate medially, punctate around margins, punctation somewhat variable, with few larger punctures. Elytron moderately broad, laterally broadly curved; surface shiny, somewhat more coarsely and evenly punctate than pronotum, punctation fine, some punctures anteromedially on elytron forming moderately distinct longitudinal linear series; laterally with distinctive longitudinal rounded ridge extending posteriorly from humeral angle ~ 1/3 length of elytron. Prosternum extremely short, longitudinally compressed, medially slightly carinate; prosternal process slender anteriorly, with distinctive, small medial tubercle, apically short and broad, medially flattened, apically acutely pointed. Metaventricle broad and evenly smoothly convex medially, surface shiny, impunctate; metaventricle wings extremely slender. Metacoxa with medial portion short, ~ 1/3 length of metaventricle medially, metacoxal lines slightly divergent anteriorly; lateral

portion of metacoxa extremely large, anteriorly strongly expanded; surface shiny, impunctate. Metatrochanter large, subequal to length of ventral margin of metafemur; legs otherwise not noticeably modified. Abdomen with surfaces shiny and smooth, very finely and sparsely punctate.

Male genitalia. Male median lobe comprised of slender lateral margins between which is a membranous region, in lateral aspect entire median lobe broad, shallowly curved to rounded apex (Fig. 6); in ventral aspect, narrow basally, broad medially and apically, lateral margins converging, nearly touching apically, but separated by narrow, curved emargination (Fig. 7). Lateral lobe in lateral aspect short, broad, apically attenuated, and curved dorsad, with dense series of long, course setae along ventral margin to apex (Fig. 8).

Sexual dimorphism. No clear sexual dimorphic features were discovered.

Variation. No significant variation was examined among the specimens examined.

Etymology. This species is named *surinamensis* after the country of collection of the type series.

Distribution. This species is known only from Sipaliwini District, Suriname (Fig. 76).

Type material. Holotype in NZCS, male labeled, “SURINAME: Sipaliwini District 04°40.910'N, 56°11.138'W, 78 m/ Raleighfallen [sic] Nature Reserve Voltzberg trail; margin of stream leg. C. Maier, V. Kadosoe 30.vii.2012; SR12-0730-01A/ SEMC1114775 KUNHM-ENT [barcode label]/ HOLOTYPE *Desmopachria surinamensis* Miller, 2021 [red label with black line border].” Paratypes, 7, in SEMC and MSBA labeled same as holotype except with different SEMC barcode numbers (Table 1) and each with “/... PARATYPE *Desmopachria surinamensis* Miller, 2021 [blue label with black line border].”

***Desmopachria tenua* sp. nov.**

<http://zoobank.org/EE94A378-D23A-420A-AE21-5C5D23E38846>

Figures 9–12, 76

Type locality. Guyana, Region IX, Parabara, trail to mines, 2°05.095'N 59°14.174"W.

Diagnosis. This species has a distinctive dorsal maculate color pattern (Fig. 9). Also, the male median lobe in lateral aspect is extremely slender (Fig. 10). The lateral lobes are moderately broad and twisted with the apical portion leaf-like (Figs 11, 12). The species does not fit into any of the recognized groups of *Desmopachria*, and it is not especially similar to any others in the “ungrouped” species.

Description. Measurements. TL = 1.5 mm, GW = 1.0 mm, PW = 0.7 mm, HW = 0.5 mm, EW = 0.2 mm, TL/GW = 1.6, HW/EW = 2.1. Body oval, laterally broadly curved, lateral margins slightly discontinuous between pronotum and elytron, body broadest across elytra at ~ midlength of body (Fig. 9).

Coloration (Fig. 9). Dorsal surface of head and pronotum pale orange; elytron orange-brown with pale orange maculae at humeral angle, anterobasally, subbasally near humeral angle, medially, along mediolateral margin, subapically along margin and at apex. Head appendages, pro- and mesothoracic legs and ventral surfaces of prothorax pale orange, maculae relatively well defined and variously confluent (Fig. 9); other ventral surfaces orange-brown.

Sculpture and structure. Head broad, anteriorly produced, rounded; anterior margin of clypeus curved, flattened, margined with conspicuous, continuous narrow bead; surface of head shiny, very finely and sparsely punctate; eyes large (HW/EW = 2.1); antennae short, scape and pedicel relatively large and rounded, flagellomere III long and slender, apically expanded, antennomeres IV-X short and broad, lobed at anterodorsal angle, antennomere XI elongate, apically pointed. Pronotum short, lateral margins short, slightly curved with continuous narrow bead, slightly wider medially; surface shiny, finely, indistinctly punctate. Elytron moderately broad, laterally broadly curved; surface shiny, finely punctate throughout. Prosternum extremely short, longitudinally compressed, medially slightly carinate; prosternal process slender anteriorly, with distinctive, small medial tubercle, apically short and moderately broad, medially concave, apically pointed. Metaventrite broad and evenly smoothly convex medially, surface shiny, very finely punctate; metaventrite wings extremely slender. Metacoxa with medial portion short, < 1/3 length of metaventrite medially, metacoxal lines slightly divergent anteriorly; lateral portion of metacoxa extremely large, anteriorly strongly expanded; surface shiny, extremely finely punctate. Metatrochanter large, subequal to length of ventral margin of metafemur; legs otherwise not noticeably modified. Abdomen with surfaces shiny and smooth, very finely and sparsely punctate.

Male genitalia. Male median lobe in lateral aspect long, extremely slender, and slightly curved, slightly expanded subapically on dorsal surface, apex narrowly pointed (Fig. 10); in ventral aspect slender, lateral margins evenly, broadly curved to pointed apex (Fig. 11). Lateral lobe in lateral aspect broad, apically twisted, apex leaflike and curved dorsad, apex pointed (Figs 11, 12).

Sexual dimorphism and variation. Two specimens were examined, a male and one other. They are not noticeably different. It is not clear if the second specimen is a male or female.

Etymology. This species is named *tenua*, Latin for slender, for the very thin male median lobe in lateral aspect.

Distribution. This species is only known from the type locality in Guyana (Fig. 76).

Type material. Holotype in CSBD, male labeled, “GUYANA: Region IX 2°05.095'N, 59°14.174'W, 250m Parabara, Trail to mines detrital pools in forest leg. Short, Isaacs, Salisbury 2.xi.2013; GY13-1102-01A/ SEMC1271250 KUNHM-ENT [barcode label]/ HOLOTYPE *Desmopachria tenua* Miller, 2021 [red label with black line border].” Paratypes, 1 in SEMC labeled same as holotype except “.../ SEMC1271268 KINHM-ENT [barcode label]...” and “/...PARATYPE *Desmopachria tenua* Miller, 2021 [blue label with black line border].”

Checklist of ungrouped *Desmopachria* species

Desmopachria amrishi Makhan, 2012 – Suriname

Desmopachria andreae Megna & Sánchez-Fernández, 2014 – Cuba

Desmopachria attenuata Régimbart, 1895 – Brazil (Braga and Ferreira-Jr. 2014)

Desmopachria balfourbrownei Young, 1990 – Brazil (Braga and Ferreira-Jr. 2014)

Desmopachria barackobamai Makhan, 2015 – French Guiana. Although described as being near *Desmopachria geijskesi*, this species appears more likely to be in the *Desmopachria ubangoides* species-group given the shape of the genitalia and the seemingly prominent male anterior clypeal margin in the illustrations provided (Makhan 2015: fig. 2). The description is inadequate to make a more definitive assessment, so the species is left ungrouped in *Desmopachria* (Miller 2001).

Desmopachria divergens sp. nov. – Venezuela

Desmopachria geijskesi Young, 1990 – Suriname

Desmopachria hyllobates Young, 1993 – Brazil

Desmopachria nigrocapitata Braga and Ferreira-Jr., 2010 – Brazil

Desmopachria lineata sp. nov. – Venezuela

Desmopachria paradoxa Zimmermann, 1923 – Brazil

Desmopachria rex Gustafson & Miller, 2012 – Venezuela

Desmopachria rishwani Makhan, 2012 – Suriname

Desmopachria soesilae Makhan, 2012 – Suriname

Desmopachria striga Young, 1990 – Peru

Desmopachria subfasciata Young, 1990 – Bolivia

Desmopachria surinamensis sp. nov. – Suriname

Desmopachria tambopatensis Miller, 2005 – Peru

Desmopachria taniae Miller, 1999 – Bolivia

Desmopachria tenua sp. nov. – Guyana

Desmopachria apicodente species group

Diagnosis. The *Desmopachria apicodente* group (a hereby newly identified group within *Desmopachria*) is characterized by the lateral lobe with a distinctive apical socketed spur or “tooth” that is directed apicomediaally (Figs 17, 22, 27). Some species have a distinct lateral carina on the elytron dorsad to the epipleural carina (e.g., Figs 19, 24).

Comments. Another species, *Desmopachria surinamensis* sp. nov., (see above) has a distinctive longitudinal lateral rounded tumidity, but this species lacks the apical tooth on the lateral lobe (Fig. 8). It is not known how widespread the longitudinal elytral tumidity character is in *Desmopachria*, but it is possible that further examination of this feature will be important for grouping of certain species in the genus. It should also be noted that the species, *Desmopachria duodentata* Braga & Ferreira-Jr. (in the *Desmopachria portmanni-portmanni* subgroup) also has two similar spurs apically on the lateral lobe.

Desmopachria apicodente sp. nov.

<http://zoobank.org/55AFEE8C-DD1B-4E19-9B34-FB6DABA69C92>

Figures 13–17, 77

Type locality. Venezuela, Apure State, between Orinoco and Cinaruco Rivers, 6°30.900'N, 67°32.604'W.

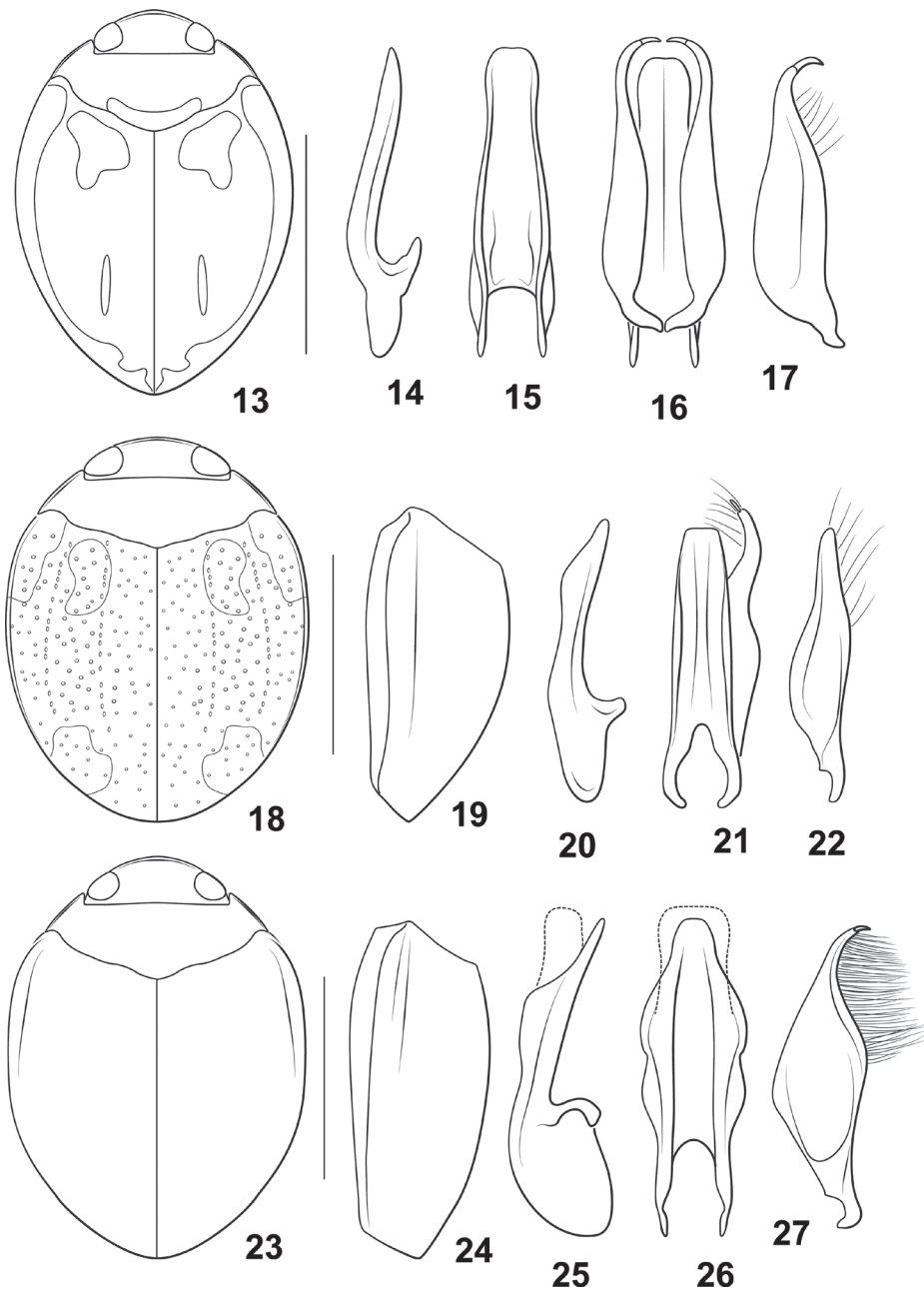
Diagnosis. Specimens are moderately large for a *Desmopachria* species (TL = 1.7–1.8 mm). The dorsal color pattern is distinctive with a large dark brown region on the elytron medially near the suture and with a large, diffuse pale macula apicomediaally and along the lateral margins to the apex (Fig. 13). The male genitalia are distinctive with the male median lobe straight and apically sharply pointed in lateral aspect (Fig. 14) and broad and apically broadly truncate in ventral aspect (Figs 15, 16). The lateral lobe is moderately broad with the apices sharply curved mediad with a distinct, small, elongate apical tooth (Figs 16, 17). *Desmopachria amyae* Miller, from Bolivia, has very similar genitalia including the apical tooth on the lateral lobe (Miller 2001: fig. 2), but that species has a different color pattern, an elytral sutural stria, and lateral furrows on the elytron (Miller 2001) which are missing in *Desmopachria apicodente*. *Desmopachria lateralis*, also from Venezuela, also has a minute apical tooth on the lateral lobe, but a different dorsal color pattern, a distinct carina along the lateral margin of the elytron, and the male median lobe is differently shaped, with a distinctive subapical expansion on the ventral margin medially (Fig. 20).

Description. Measurements. TL = 1.7–1.8 mm, GW = 1.2–1.3 mm, PW = 1.0–1.1 mm, HW = 0.7–0.8 mm, EW = 0.4–0.5 mm, TL/GW = 1.3–1.4, HW/EW = 1.8–1.9. Body broad, laterally broadly rounded, lateral margins continuous between pronotum and elytron; dorsoventrally rounded.

Coloration. Head pale orange. Pronotum pale orange with dark area along posterior margin. Elytron dark red-brown broadly along suture, becoming pale red medially, with pale, poorly demarked maculae anteromedially, laterally along border, apically, and often in small line medially (Fig. 13). Ventral surfaces yellow to orange.

Sculpture and structure. Head broad, short; anterior margin of clypeus finely margined with continuous narrow bead; surface of head shiny, punctation extremely fine and sparse; eyes large (HW/EW = 1.8–1.9); antennae short, scape and pedicel relatively large and rounded, flagellomere III long and slender, apically expanded, antennomeres IV–X short and broad, antennomere XI elongate, apically pointed. Pronotum short, lateral margins short, curved with continuous narrow bead; surface shiny, punctation very fine, of the same size and evenly distributed, posterior margin slightly sinuate. Elytron broad, laterally broadly curved; surface shiny, punctation small, some punctures arranged into indistinct series, especially anteromedially. Prosternum extremely short, longitudinally compressed, medially flattened; prosternal process short, broad, flattened, apically pointed. Metaventrite broad and evenly smoothly convex medially, surface shiny, impunctate; metaventrite wings extremely slender. Metacoxa with medial portion short, < 1/3 length of metaventrite medially, metacoxal lines slightly sinuate, divergent anteriorly; lateral portion of metacoxa extremely large, anteriorly strongly expanded; surface shiny, impunctate. Metatrochanter very large, longer than length of ventral margin of metafemur; legs otherwise not noticeably modified. Abdomen with surfaces shiny and smooth, surface impunctate.

Male genitalia. Male median lobe in lateral aspect moderately broad, elongate, straight, and of even width to sharply pointed apex, apically slightly curved ventrad (Fig. 14; in ventral aspect elongate and broad, subapically slightly constricted, apex broadly subtruncate (Fig. 15). Lateral lobe elongate, moderately broad throughout



Figures 13–27. *Desmopachria apicodente*-group species. (13–17) *Desmopachria apicodente* **13** habitus **14** male median lobe, right lateral aspect **15** male median lobe, ventral aspect **16** male median lobe and lateral lobes, ventral aspect **17** right lateral lobe, right lateral aspect (18–22) *Desmopachria lateralis* **18** habitus **19** left elytron, left lateral aspect **20** male median lobe, right lateral aspect **21** male median lobe and right lateral lobe, ventral aspect **22** right lateral lobe, right lateral aspect (23–27) *Desmopachria tumida* **23** habitus **24** left elytron, left lateral aspect **25** male median lobe, right lateral aspect **26** male median lobe, ventral aspect **27** right lateral lobe, right lateral aspect. Scale bars: 1.0 mm for habitus drawings.

most of length, apex strongly curved mediad with small but distinctive elongate “tooth” at apex (Figs 16, 17).

Sexual dimorphism. No obvious external sexual dimorphism was observed.

Variation. Specimens vary considerably in the extent of the fasciate pattern on the elytron and intensity of coloration, some of which is related to teneral condition. Some specimens barely have pale regions visible that are weakly delimited, others have a distinctive pattern on the dorsal surface.

Etymology. This species is named *apicodente*, from Latin, *apico*, for apical, and *dente*, for tooth, for the apical tooth on the male lateral lobe.

Distribution. This species is known only from Apure, Bolivar and Amazonas States, Venezuela and Region IX, Guyana (Fig. 77).

Type material. Holotype in MIZA, male labeled, “VENEZUELA: Apure State 6°30.900'N, 67°32.604'W; 68m Btw Orinoco and Cinaruco Rivers 17.i.2009; Short, Miller, Camacho VZ09-0117-01X; morichal/ SMEC085232 KUNHM-ENT [barcode label]/ HOLOTYPE *Desmopachria apicodente* Miller, 2021 [red label with black line border].” Paratypes, 400, all with different barcode labels (Table 1) and “.../ PARATYPE *Desmopachria apicodente* Miller, 2021 [blue label with black line border]”; 20 in MIZA, MSBA and SEMC labeled same as holotype; 31 in SEMC labeled, “VENEZUELA: Bolívar State 6°13'4.6"N, 67°14'26.4"W, 60m ca. 25 km E El Burro 12.i.2009; leg. Short et al. rocky morichal; VZ09-0113-01X/...”; 10 in SEMC labeled, “VENEZUELA: Amazonas State 5°20.514'N; 67°45.315'W, 87m S. Comunidad Porvenir 15.i.2009; leg. Miller & Short VZ09-0115-03B: small streamlet/...”; 50 in CSBD and SEMC labeled, “GUYANA: Region IX 2°48.531'N, 59°51.900'W, 170m Kusad Mts., Mokoro Creek pool in rock, with detritus leg. A. Short; 27.x.2013 GY13-1027-03E/...”; 29 in SEMC labeled, “GUYANA: Region IX 2°47.417'N, 59°53.986'W, 113m Kusad Mts., Taraara Wao Creek margin & isolated side pools leg. Short, Isaacs, Salisbury 28.x.2013; GY13-1028-01A/...”; 9 in SEMC labeled, “GUYANA: Region IX 2°48.588'N, 59°51.931'W, 194m Kusad Mts., basecamp area leg. A. Short; 23.x.2013; pool in creek bed; GY13-1023-02A/...”; 7 in SEMC labeled, “GUYANA: Region IX 2°48.531'N, 59°51.900'W, 170m Kusad Mts., Mokoro Creek pool in rock, with detritus leg. A. Short; 27.x.2013 GY13-1027-03E/...”; 12 in SEMC labeled same, except, “...main seepage area leg. Short, Isaacs, Salisbury 27.x.2013; GY13-1027-03B/...”; 1 in SEMC labeled, “GUYANA: Region IX 2°48.531'N, 59°51.900'W, 170m Kusad Mts., large seepage nr. Basecamp; on wet rocks leg. A. Short & W. Washington GY13-1024-03C/...”

***Desmopachria lateralis* sp. nov.**

<http://zoobank.org/C6485BE5-4B33-45C6-94E2-F16B26364EA9>

Figures 18–22, 77

Type locality. Venezuela, Amazonas State, Comunidad Caño Gato, on Rio Sipapo, 4°58.838'N, 67°44.341'W.

Diagnosis. This species is particularly distinctive because of the lateral carina extending along the lateral margin of the elytron from the humeral angle almost the entire length of the elytron. Specimens are moderately large for *Desmopachria* species (TL = 1.7–1.8 mm). The dorsal color pattern is distinctive in many specimens with most of the elytron brown with a broad region longitudinally along the suture dark brown (Figs 18, 19). The male genitalia are distinctive with the median lobe in lateral aspect elongate, sublinear along the dorsal margin and medially expanded along the ventral margin and apically narrowly rounded (Fig. 20). In ventral aspect the median lobe is broad with the lateral margins slightly convergent to the broadly truncate apex (Fig. 21). The lateral lobe is moderately broad basally and narrowed apically to a narrowly rounded apex, apically with a small, elongate apical tooth (Fig. 22). See under *Desmopachria apicodente* for additional diagnostic differences between that species, *Desmopachria amyae*, and *Desmopachria lateralis*.

Description. Measurements. TL = 1.7–1.8 mm, GW = 1.3–1.4 mm, PW = 1.0–1.1 mm, HW = 0.6–0.7 mm, EW = 0.3–0.4 mm, TL/GW = 1.3–1.4, HW/EW = 1.9–2.0. Body very broad, rounded, laterally broadly rounded, lateral margins slightly discontinuous between pronotum and elytron; dorsoventrally somewhat compressed.

Coloration. Head pale orange. Pronotum pale orange with narrow dark area medially along posterior margin. Elytron dark orange, with broad dark brown band longitudinally along suture, also with small diffuse, pale macula at apex, and paler diffuse areas anteromedially (Fig. 18). Ventral surfaces yellow to orange.

Sculpture and structure. Head broad, short; anterior margin of clypeus finely margined with continuous narrow bead, bead slightly more expanded medially; surface of head shiny, punctures extremely fine, nearly impunctate; eyes large (HW/EW = 1.9–2.0); antennae short, scape and pedicel relatively large and rounded, flagellomere III long and slender, apically expanded, antennomeres IV–X short and broad, antennomere XI elongate, apically pointed. Pronotum short, lateral margins short, curved with continuous narrow bead; surface shiny, punctuation very fine over most of surface, larger and denser posteromedially. Elytron broad, laterally broadly curved; surface shiny, punctuation variable, some punctures arranged into indistinct series, especially anteromedially (Fig. 18); lateral margin, dorsad of epipleural carina, with distinct, longitudinal carina extending from humeral angle most of length of elytron (Fig. 19). Prosternum extremely short, longitudinally compressed, medially flattened; prosternal process short, broad, flattened, apically pointed. Metaventrite broad and evenly smoothly convex medially, surface shiny, impunctate; metaventrite wings extremely slender. Metacoxa with medial portion short, < 1/3 length of metaventrite medially, metacoxal lines slightly sinuate, divergent anteriorly; lateral portion of metacoxa extremely large, anteriorly strongly expanded; surface shiny, impunctate, slightly rugulose. Metatrochanter very large, longer than length of ventral margin of metafemur; legs otherwise not noticeably modified. Abdomen with surfaces shiny and smooth, surface impunctate.

Male genitalia. Male median lobe in lateral aspect moderately broad, elongate, straight, with submedial expansion on ventral surface, apex narrowly rounded (Fig. 20); in ventral aspect elongate and broad, apex broadly subtruncate, slightly emarginate

(Fig. 21). Lateral lobe elongate, moderately broad medially, apically narrowed to apex, apex sharply curved mediad with small but distinctive elongate “tooth” at apex (Fig. 22).

Sexual dimorphism. No obvious external sexual dimorphism was observed.

Variation. Specimens vary in the extent of the color pattern on the elytron and intensity of coloration, some of which is related to teneral condition. Some specimens have pale regions barely visible and they are weakly delimited, others have a distinctive pattern on the dorsal surface.

Etymology. This species is named *lateralis*, from the Latin for the lateral carina on the elytron.

Distribution. This species is known only from Amazonas State, Venezuela (Fig. 77).

Type material. Holotype in MIZA, male labeled, “VENEZUELA: Amazonas State 4°58.838'N, 67°44.341'W; 95m Comunidad Caño Gato, on Rio Sipapo; 16.i.2009; leg. Short, Miller, Camacho, Joly, & García VZ09-0116-01X; along stream/ SM0843192 KUNHM-ENT [barcode label]/ HOLOTYPE *Desmopachria lateralis* Miller, 2021 [red label with black line border].” Paratypes, 1 in SEMC labeled same as holotype except with “.../ SM0843335 KUNHM-ENT [barcode label];” 14 in MSBA, MIZA, and SEMC labeled, “VENEZUELA: Amazonas State 5°20.514'N; 67°45.315'W, 87m S. Comunidad Porvenir 15.i.2009; leg. Miller & Short VZ09-0115-03B; small stream-let...”; 10 in USNM and MSBA labeled, “BRAZIL: Para:Rio Zingu Camp (52°22'W. 3°39'S) Altamira (ca 60km S.) 11 Oct 2986 P.Spangler & R.Crombie/...” Each paratype with different barcode labels (Table 1) and all paratypes with “...PARATYPE *Desmopachria lateralis* Miller, 2021 [blue label with black line border].”

***Desmopachria tumida* sp. nov.**

<http://zoobank.org/984AAC32-D689-4CD8-BD12-382AFEF9DB5E>

Figures 23–27, 77

Type locality. Venezuela, Bolivar State, Gran Sabana, Pauji, Esmeraldes, 4°28.233'N, 17°35.559'W.

Diagnosis. This species is characterized by the distinctive lateral longitudinal tumidity on the elytron (Figs 23, 24). The humeral angle in dorsal aspect is subsinuate because of lateral expansion of the tumidity. The male genitalia are distinct with the median lobe broad with the lateral margins medially bisinuate and apically narrowed to an apically rounded apex (Fig. 25) and in lateral aspect with the base large and rounded and the apical portion with the dorsal margin linear and with a broad expansion on the ventral margin with the apex slender and apically narrowly rounded (Fig. 26). The lateral lobe is broad medially and apically tapered to a pointed apex with a distinct apical socketed “tooth” (Fig. 27). This tooth is shared with two other species, *Desmopachria apicodente* sp. nov. and *Desmopachria lateralis* sp. nov., together making up the *Desmopachria apicodente* species-group (see Diagnosis under *Desmopachria apicodente* for discussion of differences). *Desmopachria lateralis* also has a prominent lateral longitudinal elytral tumidity, but that species has differently shaped male genitalia (Figs 20–22).

Description. Measurements. TL = 2.0 mm, GW = 1.5 mm, PW = 1.1 mm, HW = 0.7 mm, EW = 0.4 mm, TL/GW = 1.4, HW/EW = 1.8. Body very broad, laterally broadly rounded, lateral margins nearly continuously curved between pronotum and elytron (Fig. 23).

Coloration. Head and pronotum evenly orange. Elytron brown, laterally and apically somewhat paler brown-orange. Ventral surfaces and appendages orange to orange-brown.

Sculpture and structure. Head broad, short; anterior margin of clypeus distinctly margined with continuous flattened bead, broader and flatter medially; surface of head shiny, punctation extremely fine and sparse; eyes large (HW/EW = 1.8); antennae short, scape and pedicel relatively large and rounded, flagellomere III long and slender, apically expanded, antennomeres IV–X short and broad, antennomere XI elongate, apically pointed. Pronotum short, lateral margins short, gently curved with continuous narrow marginal bead; surface shiny, punctation very fine, of the same size and evenly distributed except more coarsely punctate posteromedially. Elytron broad, laterally broadly curved, lateral margin distinctly sinuate at humeral angle, with distinct lateral tumidity extending posteriorly from humeral angle (Figs 23, 24); surface shiny, punctation of two sizes, minute and small, evenly punctate. Prosternum extremely short, longitudinally compressed, medially flattened; prosternal process broad, flattened, concave with broad lateral bead, apically pointed. Metaventrite broad and evenly smoothly convex medially, surface shiny, impunctate; metaventrite wings extremely slender. Metacoxa with medial portion short, < 1/3 length of metaventrite medially, metacoxal lines slightly sinuate, divergent anteriorly; lateral portion of metacoxa extremely large, anteriorly strongly expanded; surface shiny, extremely minutely punctate. Metatrochanter very large, longer than length of ventral margin of metafemur; legs otherwise not noticeably modified. Abdomen with surfaces shiny and smooth, surface impunctate.

Male genitalia. Male median lobe in lateral aspect with large, broad, rounded base, apical portion with dorsal margin linear, ventral margin with large expansion medially, apically narrowed and slender to narrowly rounded apex (Fig. 25); in ventral aspect broad, long, lateral margins distinctly sinuate medially, apically narrowed to broadly rounded apex (Fig. 26). Lateral lobe large, broad medially, narrow basally and apically strongly and evenly narrowed to pointed apex, dorsal margin with long dense series of long setae (Fig. 27).

Sexual dimorphism and variation. Only a single male specimen was examined.

Etymology. This species is named *tumida*, Latin for swollen, for the laterally tumid, or swollen, elytral margins (Figs 23, 24).

Distribution. This species is known only from one site in the Gran Sabana of Bolívar State, Venezuela (Fig. 77).

Type material. Holotype in MIZA, male labeled, “VENEZUELA: Bolívar State 4°28.233'N, 61°35.559'W, 867 m Gran Sabana, Pauji: Esmeraldas 16.vii.2010;leg. Short, Tellez, Arias detrital pools by forested stream VZ10-0716-02A/ SEMC0908227 KUNHM-ENT [barcode label]/ HOLOTYPE *Desmopachria tumida* Miller, 2021 [red label with black line border].” This species is only known from the holotype.

Checklist of *Desmopachria apicodente* species group

Desmopachria apicodente sp. nov. – Guyana, Venezuela

Desmopachria lateralis sp. nov. – Venezuela

Desmopachria tumida sp. nov. – Venezuela

***Desmopachria bifurcata* species group**

Diagnosis. The *Desmopachria bifurcata* group (a newly identified group within *Desmopachria*) is characterized by the median lobe very short and stout and the lateral lobes long, broad, flattened, and medially bent dorsad (e.g., Figs 29, 30). Some species have the basal portion of the lateral lobe broad, and others smaller, but the apical half in these species in lateral aspect is linear and slender to the apex (e.g., Fig. 30).

Comments. This new species group, derived from two new species and several species previously not placed in a defined species group in the genus, is diagnosed by similar male genitalia (see above). The group does not have many other similarities. Some are dorsally maculate, others are not. They are of somewhat variable shape. More investigation will be needed to determine the naturalness of this grouping. In addition, other species of *Desmopachria* also have similar genitalia. *Desmopachria chei* Miller has diagnostically similar genitalia (Miller 1999: fig. 1) but has a subsutural stria, so is placed in the *Desmopachria striola* species group (Miller 1999). *Desmopachria mendozana* (Steinheil) also has similar genitalia (Young 1980: figs 2, 3) but has the anterior metatibial spur serrate, so is placed in the *Desmopachria vicina* species group (Miller 2001; Young 1980).

***Desmopachria bifurcata* sp. nov.**

<http://zoobank.org/B3351A38-F6E8-41FB-BCAA-DC78CB00A8F8>

Figures 28–30, 78

Type locality. Peru, Junín, Sani Beni. The type locality is ambiguous. According to Otto (2017) this collection locality by P. Woytkowski may refer to a misspelling of “Sani Benu” which is at approximately 11.253917°S, 74.565565°W (see below).

Diagnosis. Males of this species have the male genitalia very distinctive with the median lobe very short and strongly bifurcate (Fig. 29). The lateral lobes in dorsal aspect are broad, parallel-sided, and apically subtruncate (Fig. 29). In lateral aspect, they are slender and abruptly bent medially (Fig. 30). Specimens are very broad in dorsal aspect and dark reddish-brown dorsally. A number of species of *Desmopachria* have the median lobe short with long, medially bent lateral lobes like *Desmopachria bifurcata*, including *Desmopachria bifasciata* Zimmermann, *Desmopachria bolivari* Miller, *Desmopachria chei* Miller, *Desmopachria lata* sp. nov., *Desmopachria varians* Wehncke, and *Desmopachria ovalis* Sharp. Among these, *Desmopachria bifurcata* is the only one with a bifid median lobe (Fig. 29). These species may together form another spe-

cies group within *Desmopachria*, but more thorough examination of specimens will be needed to determine this.

Description. Measurements. TL = 1.8–1.9 mm, GW = 1.3 mm, PW = 1.0 mm, HW = 0.6 mm, EW = 0.3 mm, TL/GW = 1.4, HW/EW = 2.1–2.4. Body very broad, rounded, laterally broadly curved, lateral margins continuous between pronotum and elytron, body broadest across elytra anterior midlength of body (Fig. 28).

Coloration (Fig. 28). Dorsal surface of head dark red, paler red along anterior margin. Pronotum evenly red. Elytron red, vaguely darker along anterior and sutural margins. Head appendages, legs, and ventral surfaces red to dark red.

Sculpture and structure. Head broad, anteriorly produced in rounded lobe; anterior margin of clypeus curved, flattened, margined with conspicuous, continuous flattened narrow bead; surface of head shiny, finely and sparsely punctate; eyes large (Fig. 28, HW/EW = 2.1–2.4); antennae short, scape and pedicel relatively large and rounded, flagellomere III long and slender, apically expanded, antennomeres IV–X short and broad, lobed at anterodorsal angle, antennomere XI elongate, apically pointed. Pronotum very short, lateral margins short, slightly curved with continuous narrow bead, slightly wider medially; surface shiny, impunctate medially, punctate around margins, punctuation variable, fine to course. Elytron moderately broad, laterally broadly curved; surface shiny, more coarsely and evenly punctate than pronotum, punctuation distinctive and prominent. Prosternum extremely short, longitudinally compressed, medially slightly carinate; prosternal process slender anteriorly, with distinctive, small medial tubercle, apically short and broad, medially slightly carinate, concave, apically acutely pointed. Metaventrite broad and evenly smoothly convex medially, surface shiny, moderately and irregularly punctate; metaventrite wings extremely slender. Metacoxa with medial portion short, < 1/3 length of metaventrite medially, metacoxal lines slightly divergent anteriorly; lateral portion of metacoxa extremely large, anteriorly strongly expanded; surface shiny, evenly punctate, punctures evenly distributed. Metatrochanter large, subequal to length of ventral margin of metafemur; legs otherwise not noticeably modified. Abdomen with surfaces shiny and smooth, very finely and sparsely punctate.

Male genitalia. Male median lobe in lateral aspect extremely short, apically distinctly bifid, each branch apicolaterally pointed, (Fig. 29). Lateral lobe in ventral aspect evenly broad throughout length, lateral margins parallel, apically broadly rounded (Fig. 30) in lateral aspect slender throughout length, abruptly curved medially (Fig. 31).

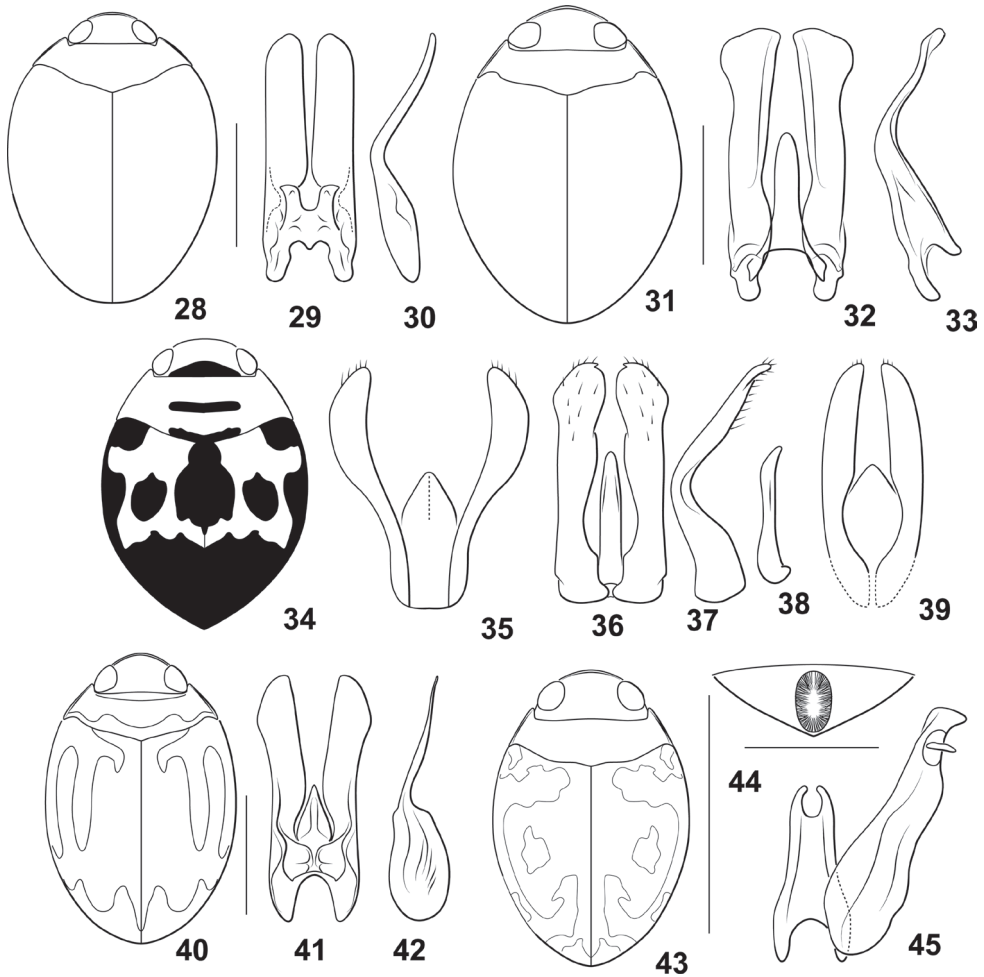
Sexual dimorphism. No obvious sexual dimorphic features were discovered.

Variation. No characteristic variation was examined among the specimens examined.

Etymology. This species is named *bifurcata*, Latin for the short, bifurcate male median lobe.

Distribution. The exact locality of collection of this species is somewhat ambiguous. The locality Sani Beni is probably “Sani Benu” at coordinates 11.253917°S, 74.565565°W, as with Eucnemidae Eschscholtz specimens collected by the same collector as documented by Otto (2017) (Fig. 78).

Type material. Holotype in SEMC, male labeled, “PERU Dept. Juni Sani Beni 1 Aug. 1935 [“1 Aug.” handwritten] P. Wyotkowski co/ HOLOTYPE *Desmopachria*



Figures 28–45. *Desmopachria* species. (28–30) *Desmopachria bifurcata* 28 habitus 29 male median and lateral lobes, dorsal aspect 30 male lateral lobe, right lateral aspect (31–33) *Desmopachria lata* 31 habitus 32 male genitalia, ventral aspect 33 right lateral lobe, right lateral aspect. (34, 35) *Desmopachria bifasciata* 34 habitus 35 male genitalia, ventral aspect (36–38) *Desmopachria bolivari* 36 male genitalia, dorsal aspect 37 right lateral lobe, right lateral aspect 38 median lobe, right lateral aspect 39 *Desmopachria ovalis*, male genitalia, dorsal aspect (40–42) *Desmopachria varians* 40 habitus 41 male genitalia, ventral aspect 42 right lateral lobe, right lateral aspect (43–45) *Desmopachria pseudocavia* 43 habitus 44 abdominal sternite VI, ventral aspect 45 male median lobe and right lateral lobe, ventral aspect. Scale bars: 1.0 mm for habitus drawings; 0.25 mm (44).

bifurcata Miller, 2021 [red label with black line border].” Paratypes, 5 in SEMC and MSBA labeled same as holotype except with dates, 10 Aug 1935, 11 Aug 1935, 19 Aug 1935, 20 Aug 1935, and 6 Nov 1935 and “/...PARATYPE *Desmopachria bifurcata* Miller, 2021 [blue label with black line border].”

***Desmopachria lata* sp. nov.**

<http://zoobank.org/3D15426D-6C1A-461D-A567-B0A1F59E31D7>

Figures 31–33, 78

Type locality. Brazil, Pará State, Cachimbo.

Diagnosis. Males of this species have the median lobe short and simple (Fig. 32). The lateral lobes are broad, long, and apically broadly expanded and truncate in dorsal aspect (Fig. 32) and medially abruptly bent and apically sinuate with a narrowly rounded apex (Fig. 33). The genitalia are similar to *Desmopachria bolivari* Miller, but that species has the apices of the lateral lobes broadened and with a distinctive medially directed tooth or hook, among other more subtle genitalic shape differences (Miller 1999: fig. 4).

Description. Measurements. TL = 2.3 mm, GW = 1.5–1.6 mm, PW = 1.2–1.3 mm, HW = 0.8 mm, EW = 0.4 mm, TL/GW = 1.4–1.5, HW/EW = 2.1–2.2. Body very broad, rounded, laterally broadly curved, lateral margins continuous between pronotum and elytron, body broadest across elytra near midlength of body (Fig. 31).

Coloration (Fig. 31). Dorsal surface of head, pronotum and elytron dark red-brown, slightly but distinctly paler laterally on pronotum. Head appendages, pro- and mesothoracic legs, and prothoracic ventral surfaces red-orange, other ventral surfaces and metathoracic legs dark red-brown.

Sculpture and structure. Head broad, anterior margin flattened, margined with distinctive narrow bead; surface of head shiny, finely and sparsely punctate; eyes large (Fig. 31, HW/EW = 2.1–2.2); antennae short, scape and pedicel relatively large and rounded, flagellomere III long and slender, apically expanded, antennomeres IV–X short and broad, lobed at anterodorsal angle, antennomere XI elongate, apically pointed. Pronotum very short, lateral margins short, slightly curved with continuous narrow bead, slightly wider medially; surface shiny, impunctate medially, finely punctate around margins. Elytron very broad, laterally broadly curved; surface shiny, more coarsely and evenly punctate than pronotum, punctation distinctive and prominent, moderately fine. Prosternum extremely short, longitudinally compressed, medially slightly carinate; prosternal process slender anteriorly, with distinctive, small medial tubercle, apically short and moderately broad, medially evenly convex, apically broadly pointed. Metaventricle broad and evenly smoothly convex medially, surface shiny, impunctate; metaventricle wings extremely slender. Metacoxa with medial portion short, < 1/3 length of metaventricle medially, metacoxal lines indistinct, slightly divergent anteriorly; lateral portion of metacoxa extremely large, anteriorly strongly expanded; surface shiny, evenly, finely punctate. Metatrochanter large, subequal to length of ventral margin of metafemur; legs otherwise not noticeably modified. Abdomen with surfaces shiny and smooth, very finely and sparsely punctate.

Male genitalia. Male median lobe in lateral aspect short, slightly curved, apically simple; in ventral aspect short, slender, parallel-sided to narrowly rounded apex (Fig. 32). Lateral lobe in ventral aspect evenly broad throughout much of length, apex broadly expanded laterally, apex broad, somewhat obliquely truncate (Fig. 32); in lateral aspect slender throughout length, abruptly curved medially, apex abruptly slightly expanded and apically narrowly rounded (Fig. 33).

Sexual dimorphism. No obvious sexual dimorphic features were discovered.

Variation. There is some variation in the dorsal coloration with some specimens paler than others, but otherwise, little variation exists.

Etymology. This species is named *lata*, Latin for broad, for the broad body in this species.

Distribution. This species is known only from the type locality, Brazil, Pará State, Cachimbo (Fig. 78).

Type material. Holotype in USNM, male labeled, “Cachimbo, Para, Brasil, X.1959 M.Alvarenga/ USNMENT01190957 [barcode label]/ HOLOTYPE *Desmopachria lata* Miller, 2021 [red label with black line border].” Paratypes, 21 in USNM and MSBA labeled same as holotype except with different barcode labels (Table 1) and each with “/...PARATYPE *Desmopachria lata* Miller, 2021 [blue label with black line border.”

Checklist of *Desmopachria bifurcata* species group

Desmopachria bifasciata Zimmermann, 1921 – Brazil (Figs 34, 35)

Desmopachria bifurcata sp. nov. – Peru

Desmopachria bolivari Miller, 1999 – Bolivia (Figs 36–38)

Desmopachria lata sp. nov. – Brazil

Desmopachria ovalis Sharp, 1882 – Brazil (Fig. 39)

Desmopachria varians Wehncke, 1877 – Brazil (Figs 40–42) (Braga and Ferreira-Jr. 2018)

Desmopachria convexa species group

Diagnosis. This group of *Desmopachria* has an articlable process subapically on the lateral lobe (Fig. 45; Miller 2001; Young 1980, 1981).

Comments. Miller (2020) recognized two subgroups based on the size and placement of the articlable process on the lateral lobe and geography. Those with a smaller subapical articlable appendage on the lateral lobe not extending beyond the truncate apex are in the *Desmopachria convexa-signata* subgroup, and those with a larger subapical articlable appendage that is leaf-like and extends well beyond the elongate, slender oblique apex of the lateral lobe are in the *Desmopachria convexa-convexa* subgroup (Miller 2020). *Desmopachria convexa-convexa* species are found in North and Central America and the Caribbean, and *Desmopachria convexa-signata* species are found in South America.

Desmopachria pseudocavia sp. nov.

<http://zoobank.org/E41416AC-93FD-4951-A2BD-4F063DBCD9F3>

Figures 43–45, 78

Type locality. Venezuela, Bolivar State, Rio Caripito, near Rio Orinoco, 6.58694°N 67.02912°W.

Diagnosis. This species belongs to the *Desmopachria convexa-signata* subgroup based on the small articable, subapical process on the lateral lobe (Fig. 45). Specimens are similar to those of *Desmopachria cavia* Braga & Ferreira Jr. in size, shape, general features, and the presence of a setose depression medially on abdominal sternite VI. However, *Desmopachria pseudocavia* has a distinctly different dorsal color pattern (Fig. 43; Braga and Ferreira-Jr. 2010: fig. 3A) and similar, but differently shaped **male genitalia**. In *Desmopachria pseudocavia* the male median lobe terminates in two short rami which are apically rounded and evenly and strongly curved mediad (Fig. 45). In *Desmopachria cavia* these rami are more linear and are apically more distinctly pointed (Braga and Ferreira-Jr. 2010: figs 3D, E). Also, although both species are extremely small diving beetles, *Desmopachria pseudocavia* (TL = 1.1–1.2 mm) are even smaller than *Desmopachria cavia* (TL = 1.3–1.5 mm, Braga and Ferreira-Jr. 2010).

Description. Measurements. TL = 1.1–1.2 mm, GW = 0.8 mm, PW = 0.6 mm, HW = 0.4–0.5 mm, EW = 0.2 mm, TL/GW = 1.4–1.5, HW/EW = 2.3–2.4. Body broad, ovoid, laterally broadly curved, lateral margins continuous between pronotum and elytron, body broadest across elytra at midlength of body (Fig. 43).

Coloration. Dorsal surface of head and pronotum yellow. Elytron brown with diffuse, complex maculae, margins of maculae indistinct (Fig. 43). Head appendages, legs, and ventral surfaces yellow.

Sculpture and structure. Head broad, anteriorly rounded, anterior margin of clypeus curved, flattened, margined with conspicuous, continuous flattened narrow bead; surface of head shiny, very finely and sparsely punctate; eyes very large (Fig. 43, HW/EW = 2.3–2.4); antennae short, scape and pedicel relatively large and rounded, flagellomere III long and slender, apically expanded, antennomeres IV–X short and broad, lobed at anterodorsal angle, antennomere XI elongate, apically pointed. Pronotum short, lateral margins short, curved with continuous narrow bead of even width throughout; surface shiny, impunctate to very finely and sparsely punctate. Elytron broad, laterally broadly curved; surface shiny, very finely and sparsely punctate. Prosternum extremely short, longitudinally compressed, medially slightly carinate; prosternal process slender anteriorly, with distinctive, small, sharp medial tubercle, apically short and broad, medially slightly carinate, concave, apically acutely pointed. Metaventricle broad and evenly smoothly convex medially, surface shiny, impunctate; metaventricle wings extremely slender. Metacoxa with medial portion short, < 1/3 length of metaventricle medially, metacoxal lines divergent anteriorly; lateral portion of metacoxa extremely large, anteriorly strongly expanded; surface shiny, impunctate. Metatrochanter large, subequal to length of ventral margin of metafemur; legs otherwise not noticeably modified. Abdomen with surfaces shiny and smooth, very finely and sparsely punctate; abdominal sternite VI with medial longitudinally oval depression with field of setae around margins (Fig. 44).

Male genitalia. Male median lobe in lateral aspect short, slightly curved ventrad; in ventral aspect broad basally, narrowed apically, apex formed as lateral, curved rami with medial rounded emargination (Fig. 45). Lateral lobe in ventral aspect robust, subapically concave on lateral margin, apex truncate, with distinct small subapical articable process (Fig. 45).

Sexual dimorphism. No obvious sexually dimorphic features were discovered.

Variation. There is substantial variation in the extent and distinctiveness of the dorsal coloration on the elytra (Fig. 43), though the basic pattern seems to be conserved. The humeral and anteromedial maculae and the apical maculae are nearly always present and distinctive. The medial longitudinal macula and lateral maculae are range from nearly absent to vague or indistinct to distinctive.

Etymology. This species is named *pseudocavia*, Latin for resembling *cavia*, for the similarities of this species to *Desmopachria cavia* Braga & Ferreira Jr.

Distribution. This species is known from Venezuela from the states of Amazonas, Anzoátegui, Apure, Bolívar, and Monagas (Fig. 78).

Type material. Holotype in MIZA, male labeled, “VENEZUELA: Amazonas State 4°58.838'N, 67°44.341'W; 95m Comunidad Caño Gato, on Rio Sipapo; 16.i.2009; leg. Short, Miller, Camacho, Joly, and García VZ09-0116-01X: along stream/ SM0842899 KUNHM-ENT [barcode label]/ HOLOTYPE *Desmopachria pseudocavia* Miller, 2021 [red label with black line border].” Paratypes, 94 specimens, each with paratype label, “.../ PARATYPE *Desmopachria pseudocavia* Miller, 2021 [blue label with black line border]” and different barcode labels (Table 1); 69 in in MIZA, MSBA and SEMC labeled same as holotype; 3 in SEMC labeled, “VENEZUELA: Amazonas State 4°58.845'N, 67°44.345'W; 100m Comunidad Caño Gato on Rio Sipapo; sandy stream; 7.i.2006 AS-06-016; leg. A.E.Z. Short/...”; 4 in SEMC labeled, “VENEZUELA: Amazonas State 4°55.849'N, 67°44.645'W, 87m Stream along Río Sipapo 16.i.2009; leg. Short, Garcia, Camacho, Miller, & Joly VZ09-0116-02X: stream habitats/...”; 3 in SEMC labeled, “VENEZUELA: Anzoátegui State 9°05.808'N, 64°19.445'W, 236 m River along highway, N. El Tigre 3.ii.2010; leg. A. Short; vegetated backwaters; VZ10-0203-03B/...”; 2 in SEMC labeled, “VENEZUELA: Apure State 7°37.298'N, 69°3.679'W, 83m side road ca. 10 km E. Mantecal leg. Short, Garcia, & Camacho 18.i.2009; marshy area and pool by road; VZ09-0118-02X/...”; 2 in SEMC labeled, “VENEZUELA: Apure State 7°38.660'N, 69°18.004'W, 90m between “La Ye” & Bruzual 19.i.2009; Short, Camacho, & García; VZ09-0118-03X: lagoon/...”; 3 in SEMC labeled, “VENEZUELA: Bolívar State 6.558694°N; 67.02912°W Río Caripito, nr. Río Orinoco, 12.i.2009; leg. Short & Miller VZ09-0112-02A: river margin/...” 7 in SEMC labeled, “VENEZUELA: Monagas State 9°36.591'N, 63°8.295'W, 45 m S. of Maturin; vegetated river/ morichal margin; 2.ii.2010; leg. Short & Garcia; VZ10-0202-01B/...”.

Desmopachria convexa species group

Desmopachria convexa-convexa species group

Desmopachria aspera Young, 1981 – Florida, USA

Desmopachria cenchramis Young, 1981 – Florida, USA

Desmopachria challeti Miller, 2001 – Colombia

Desmopachria circularis Sharp, 1882 – Guatemala

Desmopachria convexa – Aubé, 1838 – Eastern USA

Desmopachria defloccata Young, 1981 – Mexico
Desmopachria glabella Young, 1981 – Cuba
Desmopachria grana – LeConte, 1855 – Eastern USA
Desmopachria isthmia Young, 1981 – Panama
Desmopachria laesslei Young, 1981 – Jamaica
Desmopachria lewisi Young, 1981 – Jamaica
Desmopachria majuscula Young, 1990 – Guatemala
Desmopachria mortimer Miller, 2021 – Costa Rica
Desmopachria tarda Spangler, 1973 – Cuba

***Desmopachria convexa-signata* species group**

Desmopachria cavia Braga & Ferreira Jr., 2010 – Brazil
Desmopachria manco Miller, 2021 – Guyana
Desmopachria manus Braga & Ferreira Jr., 2010 – Brazil
Desmopachria pilosa Miller, 2005 – Peru
Desmopachria pseudocavia sp. nov. – Venezuela
Desmopachria signata Zimmermann, 1921 – Brazil
Desmopachria signatoides Miller, 2001 – Bolivia
Desmopachria varzeana Braga & Ferreira Jr., 2010 – Brazil

***Desmopachria nitida* species group**

Diagnosis. This species group is characterized by bifid lateral lobes (e.g., Fig. 50). In some species, the median lobe is relatively simply, apically narrowly bifid with the apices sharply pointed. In others, it is extremely complex, apically modified, with various branches and structures. This group includes some of the most complex, convoluted male genitalia in Dytiscidae (Miller and Wolfe 2018).

Comments. This species-group was originally in *Desmopachria* sensu stricto (Young 1980), with only one species. Additional species were added by Young (1986; 1989; 1990a), Miller (1999; 2005), and Braga and Ferreira-Jr. (2014). Other previously described species were moved into the group by Miller (2001). Miller and Wolfe (2018) described the species including new ones and reviewed the taxonomy of the group, including concerns about the species-group placement of newly described species by Makhan (2012, 2015).

***Desmopachria wolfei* sp. nov.**

<http://zoobank.org/854B6B76-1805-4601-8192-8772F6371F9E>

Figures 46–50, 79

Type locality. Venezuela, Bolivar State, Rio Aponwao at Highway 10, 5°50'49.2"N, 62°28'2.4"W.

Diagnosis. This species belongs to the *Desmopachria nitida* group sensu Miller (2001) because of presence of deeply bifid male lateral lobes (Fig. 50). Within the group, the species has a bilaterally symmetrical, but extremely complicated male median lobe that is very unique in shape, medially distinctly constricted, apically broadly truncate, and with an apicomedial emargination, among other shape characteristics (Figs 47–50). Dorsal coloration is simple with the head and pronotum orange and elytron brown.

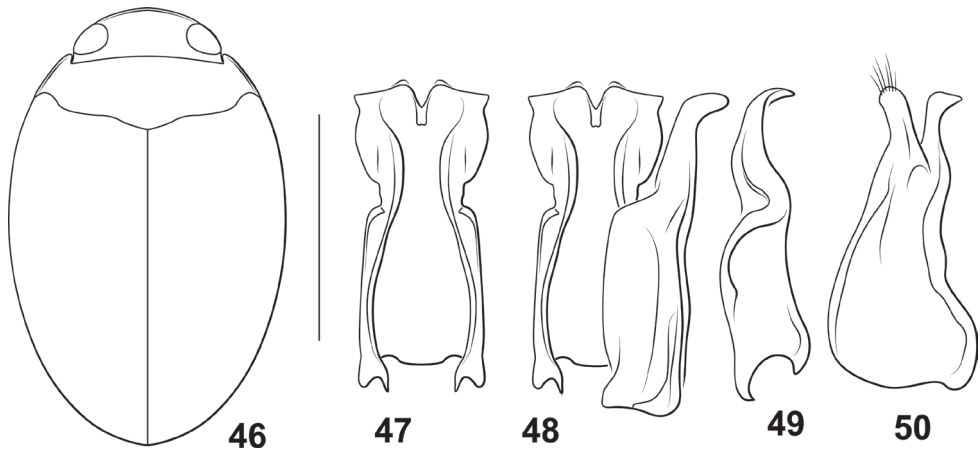
Description. Measurements. TL = 1.8–1.9 mm, GW = 1.2–1.3 mm, PW = 0.9–1.0 mm, HW = 0.6–0.7 mm, EW = 0.3 mm, TL/GW = 1.4–1.5, HW/EW = 1.9–2.0. Body broad, elongate oval, laterally broadly curved, lateral margins continuous between pronotum and elytron, body broadest across elytra at midlength of body (Fig. 46).

Coloration (Fig. 46). Dorsal surface of head and pronotum evenly pale orange. Elytron dark orange, darker than surface of pronotum. Head appendages, legs and ventral surfaces orange to dark orange or orange-red.

Sculpture and structure. Head broad; anterior margin of clypeus evenly curved, flattened, margined with conspicuous, continuous narrow bead; surface of head shiny, finely and sparsely punctate; eyes large (HW/EW = 1.9–2.0); antennae short, scape and pedicel relatively large and rounded, flagellomere III long and slender, apically expanded, antennomeres IV–X short and broad, lobed at anterodorsal angle, antennomere XI elongate, apically pointed. Pronotum short, lateral margins short, sublinear with continuous narrow bead, slightly wider medially; surface shiny, impunctate medially, punctation denser along anterior and posterior margins, punctation fine. Elytron moderately broad, laterally broadly curved; surface shiny, more coarsely and evenly punctate than pronotum, punctation distinctive and prominent. Prosternum extremely short, longitudinally compressed, medially slightly carinate; prosternal process slender anteriorly, with distinctive, small medial tubercle, apical blade short and broad, basally transversely carinate, medially concave, apically broadly pointed. Metaventrite broad and evenly smoothly convex medially, surface shiny, very finely and sparsely; metaventrite wings extremely slender. Metacoxa with medial portion short, $< 1/3$ length of metaventrite medially, metacoxal lines divergent anteriorly; lateral portion of metacoxa extremely large, anteriorly strongly expanded; surface shiny, very finely and sparsely punctate. Metatrochanter large, subequal to length of ventral margin of metafemur; legs otherwise not noticeably modified. Abdomen with surfaces shiny and smooth, very finely and sparsely punctate.

Male genitalia. Male genitalia complex; median lobe elongate in lateral aspect, broad basally, medially constricted, broadly sinuate, apex strongly curved dorsal, apically pointed (Fig. 47); median lobe in ventral aspect very broad, lateral margins subparallel in basal half, with distinct constriction medially due to distinct lateral emarginations, apical half with lateral margins curved to apicolateral angle, apex very broadly truncate with distinct medial emargination (Figs 48, 49). Lateral lobe in broad basally, apically conspicuously bifurcate, dorsal branch apically broadly rounded, ventral branch apically truncate with dorsal corner acutely pointed dorsad (Fig. 50).

Sexual dimorphism. No obvious sexual dimorphic features were discovered.



Figures 46–50. *Desmopachria wolfei*. **46** habitus **47** male median lobe, right lateral aspect **48** male median lobe, ventral aspect **49** male median lobe and right lateral lobe, ventral aspect **50** right lateral lobe, right lateral aspect. Scale bar: 1.0 mm.

Variation. Some specimens are variously paler or darker in coloration than others.

Etymology. This distinctive species is named *wolfei* for G.W. Wolfe, gifted coleopterist, exemplary water beetle biologist, exceptionally fine husband and father, and the author's dear friend for many years.

Distribution. This species is known only from Bolivar State, Venezuela (Fig. 79).

Type material. Holotype in MIZA, male labeled, “VENEZUELA: Bolivar State 5°50'49.2"N, 62°28'2.4"W, 1340 m Rio Aponwao @ Hwy 10 31.vii.2008; leg. A.Short, M. García AS-08-060a; small vegetated pool/ SM0827530 KUNHM-ENT [barcode label] / HOLOTYPE *Desmopachria wolfei* Miller, 2021 [red label with black line border].” Paratypes, 23; 9 in MIZA and SEMC labeled same as holotype except with “... PARATYPE *Desmopachria wolfei* Miller, 2021 [blue label with black line border]” and different barcode labels (see Table 1); 14 in SEMC labeled, “VENEZUELA: Bolivar State 4°49.944'N, 61°3.813'W, 890m ca. 25 km S. San Francisco 3.viii.2008; A.Short & M. García AS-08-069; large marsh/...”

Checklist of species in the *Desmopachria nitida* species group

Desmopachria annae Miller, 2005 – Bolivia

Desmopachria anauine Braga & Ferreira-Jr., 2018 – Brazil

Desmopachria aschnae Makhan, 2012 – Suriname. This species is hereby placed into the *Desmopachria nitida* species group based on published figures of bifid lateral lobes (Makhan 2012: fig. 4).

Desmopachria balionota Miller, 2005 – Peru, Brazil (Braga and Ferreira-Jr. 2010, 2014).

Desmopachria curseenae Miller & Wolfe, 2018 – Suriname

Desmopachria darlingtoni Young, 1989 – Jamaica, Cuba, Haiti, Colombia

Desmopachria delongi Miller & Wolfe, 2018 – Suriname

- Desmopachria draco* Miller, 1999 – Bolivia, Brazil (Braga and Ferreira-Jr. 2010)
Desmopachria gingerae Miller & Wolfe, 2018 – Venezuela
Desmopachria granoides Young, 1986 – Brazil (Braga and Ferreira-Jr. 2014), Bolivia, Suriname, Venezuela, Trinidad
Desmopachria gyrationi Miller & Wolfe, 2018 – Guyana
Desmopachria hardyae Miller & Wolfe, 2018 – Guyana
Desmopachria kemptonae Miller & Wolfe, 2018 – Venezuela
Desmopachria leptophallica Braga & Ferreira-Jr., 2014 – Brazil
Desmopachria liosomata Young, 1986 – Brazil
Desmopachria lloydi Miller & Wolfe, 2018 – Bolivia
Desmopachria margarita Young, 1990 – Panama, Brazil? (Braga and Ferreira-Jr. 2014).
Desmopachria nitida Babington, 1841 – Brazil
Desmopachria nitidoides Young, 1990 – Paraguay
Desmopachria phacoides Guignot, 1950 – Paraguay, Bolivia
Desmopachria psarammo Miller, 1999 – Bolivia
Desmopachria rhea Miller, 1999 – Bolivia
Desmopachria singhae Miller & Wolfe, 2018 – Venezuela
Desmopachria subnotata Zimmermann, 1921 – Brazil (Braga and Ferreira-Jr. 2010).
Desmopachria subtilis Sharp, 1882 – Brazil
Desmopachria vohrae Miller & Wolfe, 2018 – Venezuela
Desmopachria wolfei sp. nov. – Venezuela
Desmopachria zelota Young, 1990 – Brazil

Desmopachria portmanni species group

Diagnosis. The *Desmopachria portmanni* group is well characterized morphologically by males with a bifid prosternal process with a deep medial pit (Miller 2001; Young 1980; 1995). Some are dorsally distinctly iridescent (the *Desmopachria portmanni-aldessa* subgroup), but others are not (the *Desmopachria portmanni-portmanni* subgroup). Other species in *Desmopachria* are iridescent but lack the forked, pitted process and are not included in the *Desmopachria portmanni* group (see Miller 2001) including *Desmopachria divergens* sp. nov. (described above). There are also additional species that have similar genitalia (simple, elongate median lobe, elongate lateral lobes with dense medial series of setae (such as *Desmopachria lineata* sp. nov., described above, Fig. 4) but do not have a bifid prosternal process. Careful phylogenetic work needs to be conducted to determine the relationships among these various taxa.

Comments. Young (1980) placed those taxa with a forked prosternal process and a deep medial pit into two groups, those with distinct dorsal iridescence (the subgenus *Desmopachria (Pachiridis)* Young) and those without dorsal iridescence (the subgenus *Desmopachria (Portmannia)* Young). Given the exceptional uniqueness of the forked prosternal feature, Miller (2001) found it a compelling synapomorphy for these species and lumped them together into one group, the *Desmopachria portmanni* species group. Another group, the *Desmopachria ubangoides* species group sensu Miller (2001) (= *Desmopachria (Hintonia)* Young) exhibits dorsal iridescence, like some species in the *Desmopachria port-*

manni group. These species seem rather different in other ways since they lack the forked prosternal process and have male genitalia that are not consistent with the relatively simple structures present in the *Desmopachria portmanni* group. Their genitalia are relatively more complex and differently shaped. Also, the anterior clypeal margin is sexually dimorphic. In males it is strongly modified, flattened, and upturned, whereas in females it is beaded, but not so conspicuously modified. For this reason, they are still regarded here as a separate species group (the *Desmopachria ubangoides* species group). Prior to this paper 23 species were assigned to the *Desmopachria portmanni* group (Nilsson 2016).

Within the *Desmopachria portmanni* group (*Desmopachria* (*Portmannia*) Young), Young (1980) recognized two subgroups based on coloration and punctuation, but when later revising the subgenus (Young 1995) he mentioned the two groups but did not assign specimens to them and seemed to have abandoned a more formal recognition of them. However, there seems to be some utility in recognizing two groups, those that are iridescent versus those that are not, but which are often dorsally maculate. The two subgroups are here recognized as the *Desmopachria portmanni-aldessa* subgroup and the *Desmopachria portmanni-portmanni* subgroup (see below).

Young (1995) found members of the *Desmopachria portmanni* group (as *Desmopachria* (*Portmannia*) Young to be found mainly in higher elevations rather than lowland tropics. This may be true in North and Central American species but does not appear to be entirely consistent with northern South American species.

Although somewhat larger than many other *Desmopachria*, these are still tiny diving beetles occurring in a variety of habitats, but especially in tropical forest pools and streams. It should be noted that no specific adaptive significance is known for either the uniquely forked and deeply pitted male prosternal process nor the dorsal iridescence of specimens of both sexes of many species. Young (1995) thought the forked prosternal process might be a “...small suction organ during copulation, or is a device for pheromone retention,” but these hypotheses have not been critically examined, and each seem dubious.

As with *Desmopachria* in general (Braga and Ferreira-Jr. 2010, 2011, 2014; Gustafson and Miller 2012; Miller 1999, 2001, 2005), writing a key to species in this group is extremely difficult. It is much easier to simply compare diagnostic features of the male genitalia with illustrations to make species determinations. Other characters, such as degree and type of punctuation amount of iridescence, and size are somewhat variable between species are useful as diagnostic features. For this reason, illustrations are emphasized here rather than a dichotomous key. Diagnostic descriptions of punctuation should also be examined for identifications.

Desmopachria portmanni-aldessa subgroup

Diagnosis. Within the *Desmopachria portmanni* species-group, these species have the dorsal surface iridescent. In some species the amount of iridescence is more limited but is distinct at least medially on the elytron using standard microscopy lighting.

Comments. These are species of northern South America. They are difficult to identify and need additional work to clarify species limits. It seems likely that there are numerous

additional species given the narrow geographic ranges of the known species and the ambiguity of some species limits. Specifically species including and near *Desmopachria aurea* Young need some examination. These are species with male median lobes that are short with varying degrees of lateral margin curvature and apical truncation.

***Desmopachria angulata* sp. nov.**

<http://zoobank.org/29C963D1-E292-41B1-91E1-B0076283904>

Figures 51–53, 79

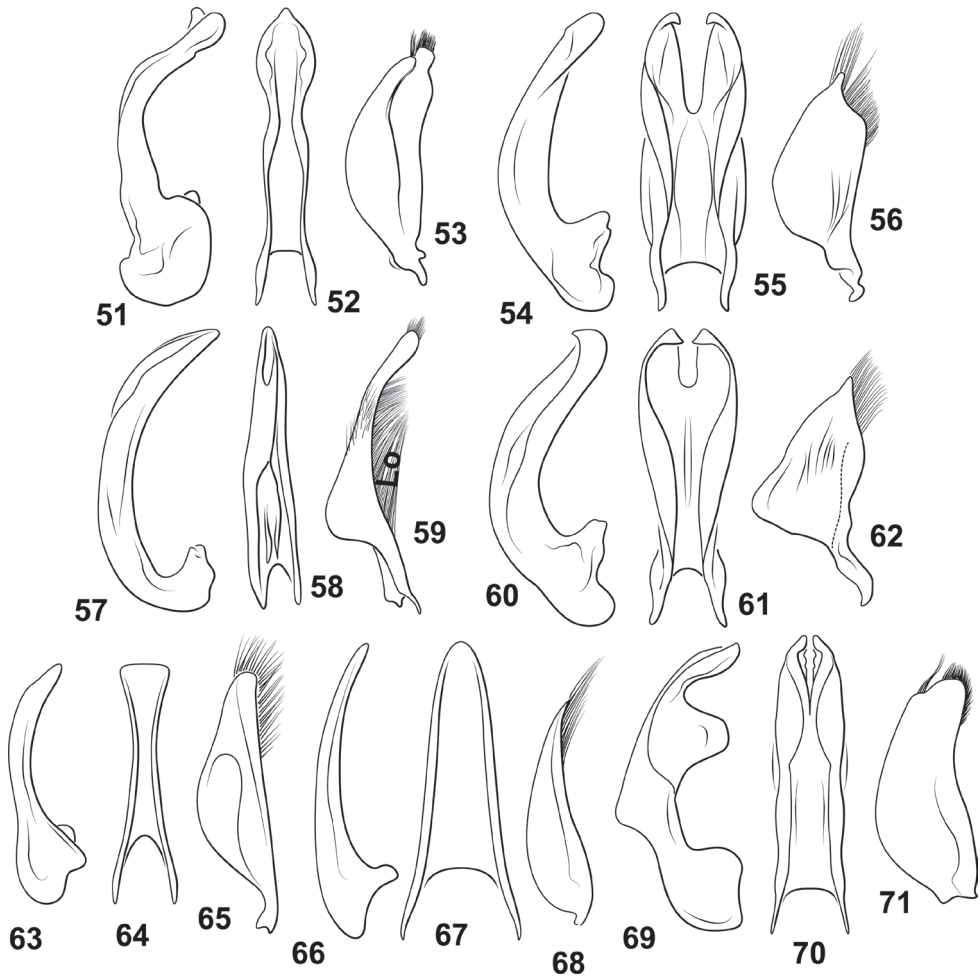
Type locality. Suriname, Sipaliwini District, Camp 2 on Sipaliwini River, large forest stream, 2°10.937'N 56°47.235°W.

Diagnosis. This species is dorsally iridescent. The punctation on the pronotum is very fine and sparse. The punctation on the elytron is dual, with some large and some small and interspersed among the larger ones. The male genitalia are distinctive with the median lobe elongate, slender and distinctly angulate medially with the apex rounded and with a distinct subapical lobe on the ventral margin (Fig. 51). The lateral lobe is broad medially with the apex lobate and narrowly rounded with a small, dense series of setae (Fig. 53).

Description. Measurements. TL = 2.0–2.2 mm, GW = 1.5–1.6 mm, PW = 1.1–1.2 mm, HW = 0.4–0.5 mm, EW = 0.4 mm, TL/GW = 1.4–1.5, HW/EW = 1.8–2.0. Body very broad, laterally rounded, lateral margins slightly discontinuous between pronotum and elytron; dorsoventrally compressed.

Coloration. Head and pronotum evenly orange, slightly iridescent. Elytron evenly brownish orange, iridescent. Ventral surface of head, prosternum, head appendages, and pro- and mesolegs yellow, other ventral surfaces and metalegs darker orange, lateral portion of metacoxa iridescent.

Sculpture and structure. Head broad, short; anterior margin of clypeus finely margined with continuous flattened narrow bead; surface of head shiny, punctation extremely fine, evenly distributed; eyes large (HW/EW = 1.8–2.0); antennae short, scape and pedicel relatively large and rounded, flagellomere III long and slender, apically expanded, antennomeres IV–X short and broad, antennomere XI elongate, apically pointed. Pronotum short, lateral margins short, broadly curved with continuous narrow bead; surface shiny, punctation fine, slightly irregular in size, few larger punctures; posterior margin sinuate. Elytron broad, laterally broadly curved; surface shiny, conspicuously punctate, punctures dual with fine and large interspersed. Prosternum extremely short, longitudinally compressed, medially slightly carinate; prosternal process in male very slender anteriorly, with low, indistinct medial tubercle, bifid apically with deep medial pit, in female slender anteriorly, with distinctive, small medial tubercle, apically short and broad, medially slightly carinate, apically acutely pointed. Metaventricle broad and evenly smoothly convex medially, surface shiny, impunctate; metaventricle wings extremely slender. Metacoxa with medial portion short, < 1/3 length of metaventricle medially, metacoxal lines sinuate, strongly divergent



Figures 51–71. *Desmopachria* species. (51–53) *Desmopachria angulata* 51 median lobe, right lateral aspect 52 median lobe, ventral aspect 53 right lateral lobe, right lateral aspect (54–56) *Desmopachria emarginata* 54 median lobe, right lateral aspect 55 median lobe, ventral aspect 56 right lateral lobe, right lateral aspect (57–59) *Desmopachria imparis* 57 median lobe, right lateral aspect 58 median lobe, ventral aspect 59 right lateral lobe, right lateral aspect (60–62) *Desmopachria impunctata* 60 median lobe, right lateral aspect 61 median lobe, ventral aspect 62 right lateral lobe, right lateral aspect (63–65) *Desmopachria truncata* 63 median lobe, right lateral aspect 64 median lobe, ventral aspect 65 right lateral lobe, right lateral aspect (66–68) *Desmopachria bisulcata* 66 median lobe, right lateral aspect 67 median lobe, ventral aspect 68 right lateral lobe, right lateral aspect (69–71) *Desmopachria irregulara* 69 median lobe, right lateral aspect 70 median lobe, ventral aspect 71 right lateral lobe, right lateral aspect.

anteriorly; lateral portion of metacoxa extremely large, anteriorly strongly expanded; surface shiny, impunctate. Metatrochanter very large, subequal to length of ventral margin of metafemur; legs otherwise not noticeably modified. Abdomen with surfaces shiny and smooth, very finely and sparsely punctate.

Male genitalia. Male median lobe in lateral aspect with basal portion broad and rounded, apically long and slender, medially conspicuously bent, with distinctive subapical lobe on ventral surface (Fig. 51); in ventral aspect elongate, slender, lateral margins sinuate, subapically broadly and roundly expanded, apex broadly pointed (Fig. 52). Lateral lobe broad, ventrally broadly rounded, apically lobate with subapical lobe on lateral surface, apices of lobes with dense fringe of setae (Fig. 53).

Sexual dimorphism. Male pro- and mesotarsomeres I-III slightly more broadly expanded and with ventral adhesive setae. Male and female prosternal processes different as in all *Desmopachria portmanni* group species.

Variation. Some specimens have the dorsal punctation more or less dense than described above. Also, coloration varies in intensity, though the head and pronotum are always paler than the elytra.

Etymology. This species is named *angulata*, Latin for angled, for the strongly angulate male median lobe in lateral aspect (Fig. 51).

Distribution. This species is known from Region 6, Guyana and Sipaliwini District, Suriname (Fig. 79).

Type material. Holotype in NZCS, male labeled, “SURINAME: Sipaliwini District 2°10.973'N, 56°47.235'W, 210m Camp 2, on Sipaliwini River; Short & Kadosoe; large forest stream 28–29.viii.2010; SR10-0828-02A 2010 CI-RAP Survey/SEMC0913662 KUNHM-ENT [barcode label]/ HOLOTYPE *Desmopachria angulata* Miller, 2021 [red label with black line border].” Paratypes, 144 total in NZCS and SEMC (from Suriname), CSBD and SEMC (from Guyana), and MSBA (various), each with different barcode labels (Table 1) and “...PARATYPE *Desmopachria angulata* Miller, 2021 [blue label with black line border]; 17 labeled same as holotype; 7 labeled, “GUYANA: Region 6 4°09.241'N, 58°10.627'W, 109 m Upper Berbice, Basecamp 1 puddles along road leg. Short, Salisbury, La Cruz 24.ix.2014; GY14-0924-02A/...”; 1 labeled same, except, “...4°09.143'N, 58°11.207'W, 105 m...margins of creek...22.iv.2014; GY1-0921-03H/...”; 1 labeled same, except, “...4°09.289'N, 58°11.717'W, 96 m...side pools of creek...21.iv.2014; GY1-0921-01B/...”; 1 labeled same, except, “...4°09.126'N, 58°12.274'W, 73 m...3km W. of Basecamp 1; pooled up creek.....[no date]; GY1-0923-01A/...”; 2 labeled, “GUYANA: Region 6 4°09.136'N, 58°11.365'W, 106 m Upper Berbice, ca 1.1km W of Basecamp 1; stream detrital pools leg. Short, Salisbury, La Cruz 23.ix.2014; GY14-0923-02A/...”; 4 labeled, “GUYANA: Region 6 4°09.143'N, 58°11.207'W, 105 m Upper Berbice, c. 1km W of Basecamp 1; small sandy stream leg. Short, Salisbury, La Cruz 21.ix.2014; GY14-0921-03A/...”; 2 labeled same, except, “...side pools of creek...22.ix.2014; GY14-0921-03G/...”; 11 labeled, “SURINAME: Sipaliwini District 2°21.776'N, 56°41.861'W, 237 m Camp 3, Wehepai leg. Short & Kadosoe; pooled up detrital creek 3.ix.2010; SR10-0903-01A 2010 CI-RAP Survey/...”; 1 labeled same, except, “...sandy forest creek 4-6.ix.2010; SR10-0904-01A/...”; 4 labeled, “SURINAME: Sipaliwini District 2°10.973'N, 56°47.235'W, 210 m Camp 2, on Silpaliwini [sic] River; Short & Kadosoe; small detrital stream 28.viii.2010; SR10-0828-03A 2010 CI-RAP Survey/...”; 6 labeled same, except, “...Sipaliwini...inselberg...29-30.viii.2010;

SR10-0829-01A...”; 7 labeled same, except, “...sandy forest creek w/detritus; SR10-0831-01B 31.viii.2010...”; 5 labeled same, except, “...forest creek 31.viii.2010; SR10-0831-01A...”; 9 labeled, “SURINAME: Sipaliwini District N 2.47700°N, 55.62941° W, 275 m Camp 1, Upper Palumeu leg. A Short; Flight Intercept Trap 10-16.iii.2012; SR12-0310-TN1 2012 CI-RAP Survey/...”; 1 labeled same, except, “... Upper Palumeu River...large detrital pools 10-12.iii.2012; SR12-0310-01A...”; 58 labeled, “SURINAME: Sipaliwini District 2°10.521'N, 56°7.244'W, 228 m on Kutari River; leg. Short & Kadosoe; forested swamp 19.viii.2010; SR10-0819-01A Camp 1; 2010 CI-RAP Survey/...”; 1 labeled same, except, “...forest stream...SR10-0819-02A...”; 5 labeled, “SURINAME S2005-13 03May2005. Palumeu off Tapanahoni R. just upstream fr S2005-10 N03.36951 W055.43654 Wolfe-Hiwat-class.”

***Desmopachria emarginata* sp. nov.**

<http://zoobank.org/C3F3E5FA-79B6-4F74-9A03-0C32E955606B>

Figures 54–56, 80

Type locality. Suriname, Sipaliwini District, Tafelberg Summit, near Augustus Creek Camp, pond on trail into Arrowhead Basin, 3°55.600'N, 56°11.300'W.

Diagnosis. This species includes some of the largest specimens in the group (TL = 2.0–2.2 mm). The elytra are more distinctly punctate than most species with distinctive dual punctation. Also, the elytra are very noticeably iridescent in most specimens, but a series from Raleighfallen Nature Preserve, Sipaliwini District, Suriname (NZCS) are less conspicuously iridescent. These specimens are similar in size, punctation and male genitalia, however. The male genitalia are most similar to *Desmopachria impunctata*, but the apical emargination in the median lobe is relatively deeper and in lateral aspect the apex is not distinctly hooked ventrad (Figs 54, 55 vs. Figs 60, 61). Also, *Desmopachria emarginata* are larger (TL = 2.0–2.2 mm) than *Desmopachria impunctata* (TL = 1.8–1.9 mm).

Description. Measurements. TL = 2.0–2.2 mm, GW = 1.4–1.5 mm, PW = 1.1–1.2 mm, HW = 0.7–0.8 mm, EW = 0.4–0.5 mm, TL/GW = 1.4–1.5, HW/EW = 1.8–1.9. Body very broadly oval, laterally broadly curved, lateral margins nearly continuous between pronotum and elytron.

Coloration. Head orange. Pronotum pale orange, in a majority of specimens paler in color than head or elytron. Elytron evenly brownish orange, strongly iridescent. Ventral surface of head, prosternum, head appendages, and pro- and mesolegs pale orange, other ventral surfaces and metalegs orange.

Sculpture and structure. Head broad, short; anterior margin of clypeus broadly curved, flattened, finely margined with conspicuous, continuous narrow bead, particularly evident medially; surface of head shiny, extremely finely and sparsely punctate; eyes large (HW/EW = 1.8–1.9); antennae short, scape and pedicel relatively large and rounded, flagellomere III long and slender, apically expanded, antennomeres IV–X short and broad, antennomere XI elongate, apically pointed. Pronotum short, lateral margins

short, slightly curved with continuous marginal bead; surface shiny, impunctate medially, but laterally and posteriorly with fine punctation. Elytron broad, laterally broadly curved and rounded; surface shiny, prominently punctate, punctures dual, some larger, some smaller, interspersed. Prosternum extremely short, longitudinally compressed, medially carinate; prosternal process in male very slender anteriorly, with low, indistinct medial tubercle, bifid apically with deep medial pit, in female slender anteriorly, with distinctive, small medial tubercle, apically short and broad, medially slightly carinate, apically acutely pointed. Metaventricle broad and evenly smoothly convex medially, surface shiny, impunctate or with few extremely minute punctures laterally; metaventricle wings extremely slender. Metacoxa with medial portion short, $\sim 1/3$ length of metaventricle medially, metacoxal lines slightly sinuate, divergent anteriorly; lateral portion of metacoxa extremely large, anteriorly strongly expanded; surface shiny, impunctate or with few extremely fine punctures. Metatrochanter very large, subequal to length of ventral margin of metafemur; legs otherwise not noticeably modified. Abdomen with surfaces shiny and smooth, impunctate, some specimens with few very fine punctures.

Male genitalia. Male median bilaterally symmetrical, in lateral aspect elongate, evenly broad, evenly and broadly curved on both dorsal and ventral margins, apex linear and apically broadly rounded (Fig. 54); in ventral aspect broad basally, apically broad, lateral margins irregularly sublinear, apex broad, medially deeply emarginate, emargination $\sim 2/5$ length, apical branches each apex with small process extending medially (Fig. 55). Lateral lobe very broad medially, ventral margin broadly rounded, apex narrowed to small lobe, with series of long setae apically and along apicodorsal margins (Fig. 56).

Sexual dimorphism. Male pro- and mesotarsomeres I-III slightly more broadly expanded and with ventral adhesive setae. Male and female prosternal processes different as in all *Desmopachria portmanni* group species.

Variation. Specimens vary in intensity of coloration and degree of difference between head, pronotum and elytron, but not strongly so.

Etymology. This species is named *emarginata*, Latin for the apical emargination in the male median lobe.

Distribution. This species is known from localities in Guyana, Suriname, and Venezuela (Fig. 80).

Type material. Holotype in NZCS, male labeled, "SURINAME: Sipaliwini District 3°55.600'N, 56°11.300'W, 600m CSNR: Tafelberg Summit, nr Augustus Creek Camp, pond on trail into Arrowhead basin leg. Short & Bloom; 16.viii.2013 SR13-0816-02A/ SEMC0930719 KUNHM-ENT [barcode label]/ HOLOTYPE *Desmopachria emarginata* Miller, 2021 [red label with black line border]." Paratypes, 153 specimens in CSBD, MIZA, MSBA NCZS, and SEMC each with paratype label, ".../ PARATYPE *Desmopachria emarginata* Miller, 2021 [blue label with black line border]" and different barcode labels (Table 1); 43 labeled same as holotype; 2 in SEMC labeled, "GUYANA: Region IX 2°09.557'N, 59°17.569'W, 268m along road to Parabara forest pools near Mushai Wao leg. Short, Isaacs, Salisbury 1.xi.2013; GY13-1101-02A/..."; 3 in SEMC labeled, "GUYANA: Region IX 2°47.417'N, 59°53.986'W, 113m Kusad Mts., Taraara Wao creek margin & isolated side pools

leg. Short, Isaacs, Salisbury 28.x.2013; GY13-1028-01A/...”; 2 in SEMC labeled, “GUYANA: Region IX 2°06.311'N, 59°14.072'W, 267m Parabara, N. side of river small detrital pool in forest leg. A.E.Z. Short; 2.xi.2013 GY13-1103-01A/...”; 3 in SEMC labeled, “GUYANA: Region 6 4°45.301'N, 58°00.404'W, 49 m Upper Berbice Basecamp 2 shallow detrital pool in forest draining into creek; leg. Short, Salisbury, La Cruz; 26.ix.2014 GY14-0926-01A/...”; 9 in SEMC labeled, “GUYANA: Region XIII [sic] 4.988650°N, 59.57890°W, 427 m Chenapau Village, trail between airstrip & town; large pool with lots of detritus; leg. A. Short 14.iii.2014; GY14-0314-03A/...”; 33 in CSBD and SEMC labeled, “GUYANA: Region XIII [sic] 5°10.514'N, 59°28.970'W, 440 m Kaieteur Nat'l Park, trail by guest house; small forest stream leg. A. Short; 15.iii.2014 GY14-0315-03A/...”; 7 in SEMC labeled, “GUYANA: Region XIII [sic] 4.98650°N, 59.57890°W, 427 m Chenapau village, between airstrip & town, small pools along trail leg. Short & Baca; 10.iii.2014 GY14-0310-01A/...”; 4 in SEMC labeled, “SURINAME: Sipaliwini District 3°47.479'N, 56°08.968'W, 320m CSNR: near Kappel airstrip forested stream & stream pools leg. Short & Bloom; 24.viii.2013 SR13-0824-03A/...”; 15 in NZCS and SEMC labeled, “SURINAME: Sipaliwini District 3°53.942'N, 56°10.849'W, 733m CSNR: Tafelberg Summit, nr. Caiman Crk Camp; dipnetting by stream margins: leg. Bloom 20.viii.2013, SR13-0820-02A/...”; 1 in SEMC labeled, “SURINAME: Sipaliwini District 2°10.973'N, 56°47.235'W, 210 m Camp 2, on Silpaliwini [sic] River; Short & Kadosoe; small detrital stream 28.viii.2010; SR10-0828-03A 2010 CI-RAP Survey/...”; 20 in NZCS labeled, “SURINAME: Sipaliwini District 3°55.600'N, 56°11.300'W, 600m CSNR: Tafelberg Summit, nr Augustus Creek Camp, pond on trail into Arrowhead basin leg. Short & Bloom; 16.viii.2013 SR13-0816-02A/...”; 7 in SEMC labeled, “SURINAME: Sipaliwini District 04°40.910'N, 56°11.138'W, 78 m Raleighfallen Nature Reserve Voltzberg trail; Margin of stream leg. C. Maier, V. Kadosoe 30.vii.2012; SR12-0730-01A/...”; 3 in MIZA and SEMC labeled, “VENEZUELA: Bolívar State 4°28.233'N, 61°35.559'W, 867 m Gran Sabana, Pauji: Esmeraldas 16.vii.2010; leg. Short, Tellez, Arias detrital pools by forested stream VZ10-0716-02A/...”; 1 in SEMC labeled, “VENEZUELA: Bolívar State 5°50'49.2"N, 61°28'2.4"W, 1340 m Rio Aponwao @ Hwy 10 31.vii.2008; leg. A.Short, M. García AS-08-060a; small vegetated pool/...”.

***Desmopachria imparis* sp. nov.**

<http://zoobank.org/27F2D74C-8D9B-4ACF-98C2-5C13309BE0F5>

Figures 57–59, 79

Type locality. Guyana, Region IX, Parabara, trail to mines, 2°05.095'N, 59°14.174'W.

Diagnosis. This species is unique because of the asymmetrical shape of the male median lobe. In ventral aspect the median lobe is distinctly asymmetrical, though not strongly so (Fig. 58). However, this is the only known species of the *Desmopachria*

portmanni group with an asymmetrical male median lobe. Punctuation on the elytron is dual with some small punctures interspersed among numerous larger punctures. The elytral surface is otherwise shiny with some opalescent iridescence evident. Externally, among northern South American species this one is similar to *Desmopachria lineata* sp. nov., but that species has distinctive linear series of punctures on the elytra and a differently shaped male median lobe (Figs 3, 4).

Description. Measurements. TL = 2.1–2.2 mm, GW = 1.5–1.6 mm, PW = 1.1–1.2 mm, HW = 0.7–0.8 mm, EW = 0.4 mm, TL/GW = 1.4, HW/EW = 1.8–1.9. Body broadly oval, laterally broadly curved, lateral margins approximately continuous between pronotum and elytron.

Coloration. Head and pronotum evenly yellow. Elytron evenly brownish orange, iridescent, especially apically. Ventral surface of head, prosternum, head appendages, and pro- and mesolegs yellow, other ventral surfaces and metalegs darker orange.

Sculpture and structure. Head broad, short; anterior margin of clypeus broadly curved, flattened, margined with conspicuous, continuous flattened narrow bead; surface of head shiny, extremely finely and sparsely punctate; eyes large (HW/EW = 1.8–1.9); antennae short, scape and pedicel relatively large and rounded, flagellomere III long and slender, apically expanded, antennomeres IV–X short and broad, antennomere XI elongate, apically pointed. Pronotum short, lateral margins short, slightly curved with continuous narrow bead; surface shiny, extremely finely and sparsely punctate, posterior margin sinuate. Elytron broad, laterally broadly curved and rounded; surface shiny, punctate, punctures dual, mostly larger, interspersed with smaller ones. Prosternum extremely short, longitudinally compressed, medially carinate; prosternal process in male very slender anteriorly, with low, indistinct medial tubercle, bifid apically with deep medial pit, in female slender anteriorly, with distinctive, small medial tubercle, apically short and broad, medially slightly carinate, apically acutely pointed. Metaventrite broad and evenly smoothly convex medially, surface shiny, impunctate medially, shallowly and minutely punctate laterally and posteromedially; metaventrite wings extremely slender. Metacoxa with medial portion short, < 1/3 length of metaventrite medially, metacoxal lines slightly sinuate, divergent anteriorly; lateral portion of metacoxa extremely large, anteriorly strongly expanded; surface irrorate, somewhat opalescent. Metatrochanter very large, subequal to length of ventral margin of metafemur; legs otherwise not noticeably modified. Abdomen with surfaces shiny and smooth, somewhat opalescent, very finely and sparsely punctate.

Male genitalia. Male median lobe slightly but distinctly asymmetrical; in lateral aspect long, evenly broad, evenly and broadly curved on both dorsal and ventral margins, apex narrowly rounded (Fig. 57); in ventral aspect asymmetry evident, moderately broad basally, apically narrowed to narrowly rounded apex, lateral margins irregularly sublinear on each side, but different in shape on each side, medial groove directed primarily to right of central line (Fig. 58). Lateral lobe broad basally, abruptly narrowed and slender for most of apical length, apex slightly broadened and broadly rounded, with dense long series of setae along dorsal margin medially and with field of short setae mediolaterally, apex with series of short setae (Fig. 59).

Sexual dimorphism. Male pro- and mesotarsomeres I–III slightly more broadly expanded and with ventral adhesive setae. Male and female prosternal processes different as in all *Desmopachria portmanni* group species.

Variation. No significant variation was discovered among the few specimens examined.

Etymology. This species is named *imparis*, Latin for uneven, referring to the asymmetrical male median lobe.

Distribution. This species is known from one locality in Region IX, Guyana (Fig. 79).

Type material. Holotype in CSBD, male labeled, “GUYANA: Region IX 2°05.095'N, 59°14.174'W, 250m Parabara, Trail to mines detrital pools in forest leg. Short, Isaacs, Salisbury 2.xi.2013; GY13-1102-01A/ SEMC1271236 KUNHM-ENT [barcode label]/ HOLOTYPE *Desmopachria imparis* Miller, 2021 [red label with black line border].” Paratypes, 3 in SEMC (1 male, 2 females) labeled same as holotype except with different specimen barcode labels [SEMC1271235, SEMC1271237, SEMC1271238] and each with “...PARATYPE *Desmopachria imparis* Miller, 2021 [blue label with black line border].”

***Desmopachria impunctata* sp. nov.**

<http://zoobank.org/8248D6E7-C6F1-43F0-B298-704E02A9F4D4>

Figures 60–62, 79

Type locality. Suriname, Sipaliwini District, Raleighfallen Nature Reserve, Voltzberg Trail, 04°40.910'N, 56°11.138'W.

Diagnosis. This species includes medium-sized *Desmopachria* specimens in this group (TL = 1.8–1.9 mm). The elytra are more finely and indistinctly punctate than many species and punctures are of only a single, fine size. Also, the elytra are only slightly iridescent. The male genitalia are most similar to *Desmopachria emarginata* (Figs 54–56), but the apical emargination in the median lobe in *Desmopachria impunctata* is relatively shallower and in lateral aspect the apex is distinctly hooked ventrad (Figs 60, 61). Also, specimens of *Desmopachria impunctata* are smaller (TL = 1.8–1.9 mm) than *Desmopachria emarginata* (TL = 2.0–2.2 mm).

Description. Measurements. TL = 1.8–1.9 mm, GW = 1.2–1.3 mm, PW = 1.0–1.1 mm, HW = 0.6–0.7 mm, EW = 0.4–0.5 mm, TL/GW = 1.5–1.6, HW/EW = 1.7–1.8. Body very broadly oval, laterally broadly curved, lateral margins slightly discontinuous between pronotum and elytron.

Coloration. Head orange to orange yellow. Pronotum evenly yellow, in most specimens paler in color than head or elytron. Elytron evenly brownish orange, iridescent, especially laterally and apically. Ventral surface of head, prosternum, head appendages, and pro- and mesolegs yellow, other ventral surfaces and metalegs orange.

Sculpture and structure. Head broad, short; anterior margin of clypeus broadly curved, flattened, finely margined with conspicuous, continuous narrow bead; surface of head shiny, extremely finely and sparsely punctate; eyes moderately large (HW/EW = 1.7–1.8); antennae short, scape and pedicel relatively large and rounded, flagel-

lomere III long and slender, apically expanded, antennomeres IV-X short and broad, antennomere XI elongate, apically pointed. Pronotum short, lateral margins short, slightly curved with continuous marginal bead; surface shiny, extremely finely and sparsely punctate, posterior margin sinuate. Elytron broad, laterally broadly curved and rounded; surface shiny, extremely minutely punctate, punctures of even size, somewhat denser along elytral suture. Prosternum extremely short, longitudinally compressed, medially carinate; prosternal process in male very slender anteriorly, with low, indistinct medial tubercle, bifid apically with deep medial pit, in female slender anteriorly, with distinctive, small medial tubercle, apically short and broad, medially slightly carinate, apically acutely pointed. Metaventrite broad and evenly smoothly convex medially, surface shiny, impunctate medially, shallowly and minutely punctate laterally and posteromedially; metaventrite wings extremely slender. Metacoxa with medial portion short, $< 1/2$ length of metaventrite medially, metacoxal lines slightly sinuate, divergent anteriorly; lateral portion of metacoxa extremely large, anteriorly strongly expanded; surface shiny, very finely punctate. Metatrochanter very large, subequal to length of ventral margin of metafemur; legs otherwise not noticeably modified. Abdomen with surfaces shiny and smooth, very finely and sparsely punctate.

Male genitalia. Male median bilaterally symmetrical, in lateral aspect elongate, evenly broad, evenly and broadly curved on both dorsal and ventral margins, apex slightly curved ventrad, pointed (Fig. 60); in ventral aspect moderately broad basally, apically expanded, lateral margins broadly rounded, apex broad, medially moderately deeply emarginate, apical branches each apically broadly triangular (Fig. 61). Lateral lobe very broad medially, irregularly and broadly narrowed to pointed apex, with series of long setae along apicodorsal margin (Fig. 62).

Sexual dimorphism. Male pro- and mesotarsomeres I-III slightly more broadly expanded and with ventral adhesive setae. Male and female prosternal processes different as in all *Desmopachria portmanni* group species.

Variation. There is variation in intensity and degree of coloration across specimens. Some specimens are more evenly colored, some have greater disparity between the pale color of the pronotum and the head and elytron. Other specific variation was not detected.

Etymology. This species is named *impunctata*, Latin for not punctate, for the relatively less punctate dorsal surface than in many species in the group.

Distribution. This species is known from localities in Sipaliwini District, Suriname and Bolívar State, Venezuela (Fig. 79).

Type material. Holotype in NZCS, male labeled, "SURINAME: Sipaliwini District 04°40.910'N, 56°11.138'W, 78 m Raleighfallen [sic] Nature Reserve Voltzberg trail; detrital pools along stream; leg. A. Short, C. McIntosh 30.vii.2012; SR12-0730-01B/ SEMC1113574 KUNHM-ENT [barcode label]/ HOLOTYPE *Desmopachria impunctata* Miller, 2021 [red label with black line border]." Paratypes, 232 specimens in MIZA, MSBA NCZS, and SEMC each with paratype label, ".../ PARATYPE *Desmopachria impunctata* Miller, 2021 [blue label with black line border]" and different barcode labels (Table 1); 23 labeled same as holotype; 24 in NZCS

and SEMC labeled, “SURINAME: Sipaliwini District 3°53.942'N, 56°10.849'W, 733m CSNR: Tafelberg Summit, nr Caiman Creek Camp, pools in forest; leg. Short & Bloom 19.viii.2013; SR13-0819-05B/...”; 15 in SEMC labeled, “SURINAME: Sipaliwini District 3°53.942'N, 56°10.849'W, 733m CSNR: Tafelberg Summit, nr Caiman Creek Camp, forest detrital pools; leg. Short & Bloom 19.viii.2013; SR13-0819-05C/...”; 11 in SEMC labeled, “SURINAME: Sipaliwini District 3°53.942'N, 56°10.849'W, 733m CSNR: Tafelberg Summit, nr Caiman Creek Camp, small streams with lots of plants & leaf litter; leg. Short & Bloom 18.viii.2013; SR13-0818-03A/...”; 1 in SEMC labeled, “SURINAME: Sipaliwini District 3°53.359'N, 56°10.052'W, 879m CSNR: Tafelberg Summit, near South Rim, pool in rock leg. Short & Bloom; 20.viii.2013 SR13-0820-01C/...”; 5 in SEMC labeled, “SURINAME: Sipaliwini District 04°40.910'N, 56°11.138'W, 78 m Raleighfallen [sic] Nature Reserve Voltzberg trail; margin of stream leg. C. Maier, V. Kadosoe 30.vii.2012; sr12-0730-01A/...”; 69 in NZCA and SEMC labeled, “SURINAME: Sipaliwini District 3°53.942'N, 56°10.849'W, 733m CSNR: Tafelberg Summit, nr. Caiman Crk. Camp; dipnetting by stream margins; leg. Bloom 20.viii.2013, SR13-0820-02A/...”; 3 in SEMC labeled, “SURINAME: Sipaliwini District 3°53.942'N, 56°10.849'W, 733m CSNR: Tafelberg Summit, near Caiman Creek Camp, forest detrital pools; leg. Short & Bloom 19.viii.2013; SR13-0819-05C/...”; 69 in SEMC labeled, “SURINAME: Sipaliwini District 3°53.942'N, 56°10.849'W, 733m CSNR: Tafelberg Summit, nr Caiman Creek Camp, pools in forest; leg. Short & Bloom 19.viii.2013; SR13-0819-05B/...”; 3 in SEMC labeled, “SURINAME: Sipaliwini District 3°53.942'N, 56°10.849'W, 733m CSNR: Tafelberg Summit, near Caiman Creek Camp, pooled up detrital forest stream leg. Short & Bloom; 19.viii.2013 SR13-0819-05A/...”; 4 in SEMC labeled, “SURINAME: Sipaliwini District 3°55.600'N, 56°11.300'W, 600m CSNR: Tafelberg Summit, nr Augustus Creek Camp, pond on trail into Arrowhead basin leg. Short & Bloom; 16.viii.2013 SR13-0816-02A/...”; 1 in SEMC labeled, “SURINAME: Sipaliwini District 3°55.600'N, 56°11.300'W, 600m CSNR: Tafelberg Summit, nr Augustus Creek Camp, pools & creeks on trail into Arrowhead basin; leg. Short & Bloom 17.viii.2013; SR13-0817-01A/...”; 3 in SEMC labeled, “SURINAME: Sipaliwini District 3°53.942'N, 56°10.849'W, 733m CSNR: Tafelberg Summit, near Caiman Creek Camp, stream margins: legs. Short & Bloom 18.viii.2013; SR13-0818-01A/...”; 1 in MIZA labeled, “VENEZUELA: Bolívar State 6°35.617'N, 66°49.238'W, 80m Los Pijiguaos: outcrop/morichal 12.i.2009; leg Miller & Short VZ09-0112-01C: detrital [sic] pools/...”

***Desmopachria truncata* sp. nov.**

<http://zoobank.org/E50C2B82-C005-4A50-8044-5842D61074C1>

Figures 63–65, 81

Type locality. Suriname, Sipaliwini District, Camp 4, Kasikasima, stream on trail to METS camp, 200m, 2.97731°N 55.38500°W.

Diagnosis. This species is characterized by the male median lobe slender, apically distinctly expanded with the apex broadly truncate and the lateral lobe longer than the median lobe (Figs 64, 65). The dorsal punctation on the head, pronotum and elytra is very fine and sparse. The elytra are iridescent. The genitalia are somewhat similar to *Desmopachria mutata* Sharp, but that species has the median lobe very slender, not as broadly expanded apically, and apically rounded, not truncate (Young 1995: fig. 2). That species also occurs in Mexico, not northern South America (Young 1995). *Desmopachria truncata* is otherwise not similar to other species in the *Desmopachria portmanni-aldessa* subgroup.

Description. Measurements. TL = 2.0–2.1 mm, GW = 1.3–1.4 mm, PW = 1.0–1.1 mm, HW = 0.6–0.7 mm, EW = 0.3–0.4 mm, TL/GW = 1.4–1.5, HW/EW = 1.8–2.2. Body very broad, laterally rounded, lateral margins continuous between pronotum and elytron; dorsoventrally compressed.

Coloration. Head and pronotum evenly dark orange, head slightly iridescent dorsally. Elytron evenly dark orange, iridescent, especially apically. Ventral surface of head, prosternum, head appendages, and pro- and mesolegs yellow, other ventral surfaces and metalegs darker orange, lateral portion of metacoxa and abdominal ventrites somewhat iridescent.

Sculpture and structure. Head broad, short; anterior margin of clypeus finely margined with continuous flattened narrow bead; surface of head shiny, punctation extremely fine, sparse but evenly distributed; eyes moderately large (HW/EW = 1.8–2.2); antennae short, scape and pedicel relatively large and rounded, flagellomere III long and slender, apically expanded, antennomeres IV–X short and broad, antennomere XI elongate, apically pointed. Pronotum short, lateral margins short, broadly curved with continuous narrow bead; surface shiny, punctation very fine, irregular, sparse; posterior margin sinuate. Elytron broad, laterally broadly curved; surface shiny, punctate, punctures dual, fine and large interspersed, without linear series. Prosternum extremely short, longitudinally compressed, medially slightly carinate; prosternal process in male very slender anteriorly, with low, indistinct medial tubercle, bifid apically with deep medial pit, in female slender anteriorly, with distinctive, small medial tubercle, apically short and broad, medially slightly carinate, apically acutely pointed. Metaventrite broad and evenly smoothly convex medially, surface shiny, impunctate; metaventrite wings extremely slender. Metacoxa with medial portion short, < 1/3 length of metaventrite medially, metacoxal lines sinuate, divergent anteriorly; lateral portion of metacoxa extremely large, anteriorly strongly expanded; surface shiny, impunctate. Metatrochanter very large, subequal to length of ventral margin of metafemur; legs otherwise not noticeably modified. Abdomen with surfaces shiny and smooth, very finely and sparsely punctate.

Male genitalia. Male median lobe in lateral aspect elongate, evenly curved, apically narrowly rounded (Fig. 63; in ventral aspect elongate, evenly constricted medially, expanded apically to abruptly broadly truncate apex (Fig. 64). Lateral lobe extending distinctly beyond apex of median lobe, moderately broad, apically rounded with dense margin of long setae apically and along apicodorsal margin (Fig. 65).

Sexual dimorphism. Male pro- and mesotarsomeres I–III slightly more broadly expanded and with ventral adhesive setae. Male and female prosternal processes different as in all *Desmopachria portmanni* group species.

Variation. The single specimen from “Upper Palumeu” has the male median lobe slightly longer and more slender with the lateral lobes apically a little more rounded. This does not seem to represent a significant difference however, and the specimen is from the same general area as the holotype. The series from Guyana similarly has some shape variation in the lateral and median lobes, but again, it does not seem to suggest species-level differences. However, additional specimens could help clarify the limits in these populations. A couple specimens are paler tan in color, but this could be because they are teneral.

Etymology. This species is named *truncata*, Latin for the characteristic apically truncate male median lobe in this species.

Distribution. This species is known from Sipaliwini District, Suriname and Region VIII, Guyana (Fig. 81).

Type material. Holotype in NZCS, male labeled, “SURINAME: Sipaliwini District 2.97731°N, 55.38500°W 200 m Camp 4 (low, Kasikasima; sandy stream on trail to METS camp 20.iii.2012; SR12-0320-02A leg. A. Short; 2012 CI-RAP Survey/ SEMC1087011 KUNHM-ENT [barcode label]/ HOLOTYPE *Desmopachria truncata* Miller, 2021 [red label with black line border].” Paratypes, 17; 14 in NZCS and SEMC labeled same as holotype except each with different barcode labels (Table 1); 1 in SEMC labeled, “SURINAME: Sipaliwini District N 2.47700', W 55.62941', 275 m Camp 1, Upper Palumeu leg. A. Short; Flight Intercept Trap 10-16.iii.2012; SR12-0310-TN1 2012 CI-RAP Survey/ SEMC1089093 KUNHM-ENT; 2 in CBDG and SEMC labeled, “GUYANA: Region XIII [sic] 5°10.514'N, 59°28.970'W, 440 m Kaiteur Nat'l Park, trail by guest house; small forest stream leg. A. Short; 15.iii.2014 GY14-0315-03A/ SEMC1328988 KUNHM-ENT [barcode label]” and “...SEMC1328993 KUNHM-ENT].” All paratypes also with “...PARATYPE *Desmopachria truncata* Miller, 2021 [blue label with black line border].”

***Desmopachria portmanni-aldessa* subgroup – iridescent *Desmopachria* with a forked male prosternal process (= *Desmopachria (Pachiridis)* Young, 1980)**

Desmopachria aldessa Young, 1980 – Brazil (Braga and Ferreira-Jr. 2014), Trinidad

Desmopachria anastomosa sp. nov. – Guyana

Desmopachria angulata sp. nov. – Guyana, Suriname

Desmopachria aurea Young, 1980 – Brazil (Braga and Ferreira-Jr. 2014), Suriname

Desmopachria emarginata sp. nov. – Suriname

Desmopachria imparis sp. nov. – Guyana

Desmopachria impunctata sp. nov. – Suriname

Desmopachria iridis Young, 1980 – Brazil

Desmopachria novacula Young, 1980 – Suriname

Desmopachria truncata sp. nov. – Guyana, Suriname.

The *Desmopachria portmanni*-*portmanni* subgroup

Diagnosis. Within the *Desmopachria portmanni* species-group, these species have the dorsal surface not iridescent.

Comments. These species tend to be either dorsally distinctly maculate or evenly darkly colored, but all without iridescence, but males have a distinctive bifid prosternal process with a medial pit as with all *Desmopachria portmanni*-species.

Desmopachria bisulcata sp. nov.

<http://zoobank.org/2F6FFF06-FD08-423A-97E4-890185DAB3DA>

Figures 66–68, 81

Type locality. Suriname, Sipaliwini District, Camp 3, Werehpai, SE Kwamala, 2°22.259'N 56°41.227'W, 229m.

Diagnosis. This species has a relatively simple median lobe that is slender, elongate, and curved in lateral aspect, and broad basally and apically evenly narrowed to a narrowly rounded apex in ventral aspect (Figs 66, 67). The lateral lobe is small and slender in lateral aspect, and much shorter than the median lobe (Fig. 68). The dorsal sculpture is shiny and with dual punctation in most specimens. No specimens of *Desmopachria bisulcata* display iridescence. In some specimens of both males and females the dorsum is matte, with a microreticulation that obscures the punctation. Other species with similar male median lobe shapes are *Desmopachria iridis* and *Desmopachria anastomosis*, but specimens of each of these are dorsally iridescent, whereas those of *Desmopachria bisulcata* are not.

Description. Measurements. TL = 2.0–2.1 mm, GW = 1.4–1.5 mm, PW = 1.0–1.1 mm, HW = 0.7–0.8 mm, EW = 0.4–0.5 mm, TL/GW = 1.4, HW/EW = 1.9–2.0. Body very broad, laterally rounded, lateral margins continuous between pronotum and elytron; dorsoventrally compressed.

Coloration. Head and pronotum evenly orange-red, same **coloration**. Elytron evenly brownish orange, not iridescent. Ventral surfaces evenly orange-red.

Sculpture and structure. Head broad, short; anterior margin of clypeus finely margined with continuous flattened narrow bead; surface of head shiny, but matte; eyes large (HW/EW = 1.9–2.0); antennae short, scape and pedicel relatively large and rounded, flagellomere III long and slender, apically expanded, antennomeres IV–X short and broad, antennomere XI elongate, apically pointed. Pronotum short, lateral margins short, broadly curved with continuous narrow bead; surface matte to shiny, but punctation very fine, of the same size and evenly distributed, posterior margin sinuate. Elytron broad, laterally broadly curved; surface matte or, less commonly, shiny; punctation very fine, of the same size and evenly distributed across most of elytron, when punctate, dual with a few minute, interspersed punctures laterally. Prosternum extremely short, longitudinally compressed, medially slightly carinate; prosternal process in male very slender anteriorly, with low, indistinct medial tubercle, bifid apically with deep medial pit, in female slender anteriorly, with distinctive, small medial tu-

bercle, apically short and broad, medially slightly carinate, apically acutely pointed. Metaventrite broad and evenly smoothly convex medially, surface matte, finely and irregularly punctate laterally; metaventrite wings extremely slender. Metacoxa with medial portion short, $< 1/3$ length of metaventrite medially, metacoxal lines sinuate, divergent anteriorly; lateral portion of metacoxa extremely large, anteriorly strongly expanded; surface matte, finely, evenly punctate, not iridescent. Metatrochanter very large, subequal to length of ventral margin of metafemur; legs otherwise not noticeably modified. Abdomen with surfaces shiny and smooth, very finely and sparsely punctate.

Male genitalia. Male median lobe in lateral aspect slender, evenly curved on both ventral and dorsal margins to narrowly pointed apex (Fig. 66); in ventral aspect very broad basally, evenly narrowed to broadly rounded apex (Fig. 67). Lateral lobe small, slender, apically slender, and slightly hooked dorsally with dense margin of long setae (Fig. 68).

Sexual dimorphism. Male pro- and mesotarsomeres I–III slightly more broadly expanded and with ventral adhesive setae. Male and female prosternal processes different as in all *Desmopachria portmanni* group species. Males tend to be both shinier and more punctate than females with are matte and not punctate in the few specimens examined.

Variation. Some specimens are matte between punctures on elytra. This does not seem correlated with sex, males and females may both be either shiny or matte. Extent of punctuation seems somewhat variable among the sexes.

Etymology. This species is named *bisulcata*, Latin for the male forked prosternal process.

Distribution. This species is known from one locality in Sipaliwini District, Suriname (Fig. 81).

Type material. Holotype in NZCS, male labeled, “SURINAME: Sipaliwini District 02°22.259'N, 56°41.227'W, 229m Camp 3; Werehpai, SE Kwamala detrital pools in dense forest 3–5.ix.2010; leg. Short & Kadosoe CI-rap Survey; SR10-0903-02A/ SEMC0912211 KUNHM-ENT [barcode label]/ HOLOTYPE *Desmopachria bisulcata* Miller, 2021 [red label with black line border].” Paratypes, 15 in NZCS, MSBA, and SEMC labeled same as holotype except with different specimen barcode labels (Table 1) and each with “...PARATYPE *Desmopachria bisulcata* Miller, 2021 [blue label with black line border].”

***Desmopachria irregulara* sp. nov.**

<http://zoobank.org/58E77BB3-EC2F-4F6A-85E7-E0FCBEF2E331>

Figures 69–71, 81

Type locality. Venezuela, Zulia State, Perija National Park, Tukuko, Río Manantial, 9°50.490'N, 72°49.310'W.

Diagnosis. This species is distinctive for the non-iridescent dorsal and ventral surfaces and the characteristic male median and lateral lobes. The median lobe has an extremely large lobe on the dorsal surface of the median lobe medially (Fig. 69). The lateral lobe is broad throughout with a short, dense series of setae along the apical and sub-

apical dorsal margins and a cluster of elongate setae subapically on the ventral margin (Fig. 71). The elytral punctation is large with few minute punctures interspersed. The pronotal punctation is extremely fine except posteromedially where it is large and dense.

Description. Measurements. TL = 2.1–2.2 mm, GW = 1.4–1.5 mm, PW = 1.1–1.2 mm, HW = 0.7–0.8 mm, EW = 0.4 mm, TL/GW = 1.4–1.5, HW/EW = 1.8–1.9. Body very broad, laterally rounded, lateral margins continuous between pronotum and elytron; dorsoventrally compressed.

Coloration. Head and pronotum evenly orange-red. Elytron evenly orange-red, similar to pronotum and head, not iridescent. Metaventriles, metacoxae and abdominal ventrites orange-red, other surfaces orange.

Sculpture and structure. Head broad, short; anterior margin of clypeus finely margined with continuous flattened narrow bead; surface of head shiny, impunctate medially, finely punctate posteriorly; eyes large (HW/EW = 1.8–1.9); antennae short, scape and pedicel relatively large and rounded, flagellomere III long and slender, apically expanded, antennomeres IV–X short and broad, antennomere XI elongate, apically pointed. Pronotum short, lateral margins short, shallowly curved with continuous narrow bead; surface shiny, punctation very fine and sparse over most of surface, punctation large and dense posteromedially, posterior margin sinuate. Elytron broad, laterally broadly curved; surface shiny, punctation dual, mostly large, relatively dense, with fewer fine punctures interspersed. Prosternum extremely short, longitudinally compressed, medially slightly carinate; prosternal process in male very slender anteriorly, with low, indistinct medial tubercle, bifid apically with deep medial pit, in female slender anteriorly, with distinctive, small medial tubercle, apically short and broad, medially slightly carinate, apically acutely pointed. Metaventrile broad and evenly smoothly convex medially, surface shiny, impunctate; metaventrile wings extremely slender. Metacoxa with medial portion short, < 1/3 length of metaventrile medially, metacoxal lines sinuate, divergent anteriorly; lateral portion of metacoxa extremely large, anteriorly strongly expanded; surface shiny, very finely punctate, not iridescent. Metatrochanter very large, subequal to length of ventral margin of metafemur; male metafemur curved ventrally with conspicuous series of short setae long entire margin. Abdomen with surfaces shiny and smooth, finely punctate.

Male genitalia. Male median lobe in lateral aspect irregular, ventral margin abruptly expanded submedially, evenly convexly curved in apical 2/5, ventral margin with large, apically subtruncate lobe medially, apex slight broadened, apex subtruncate (Fig. 69); in ventral aspect slender, lateral margins shallowly sinuate, apex deeply bifid, lateral rami apically broad, directed slightly mesad (Fig. 70). Lateral lobe very broad throughout length, slightly curved dorsad, apex broadly rounded, subapically on ventral surface with small cluster of elongate setae, apex and subapically on dorsal margin with dense series of short setae (Fig. 71).

Sexual dimorphism. Only males were examined, but male pro- and mesotarsomeres I–III appear to be slightly more broadly expanded and with ventral adhesive setae, and male prosternal process is different as in all *Desmopachria portmanni* group species.

Variation. There is little variation between the two male specimens examined.

Etymology. This species is named *irregulara*, Latin for irregular, for the unusual shape of the male median lobe.

Distribution. This species is known from one locality in Zulia State, Venezuela (Fig. 81).

Type material. Holotype in MIZA, male labeled, “VENEZUELA: Zulia State 9°50.490'N, 72°49.310'W, Perija, Nat. Park: Tukuko: Río Manatíal 29.i.2009; Short, García, Camacho VZ09-0129-01B: detrital pool/ SM0845453 KUNHM-ENT [barcode label]/ HOLOTYPE *Desmopachria irregulara* Miller, 2021 [red label with black line border].” Paratypes, 1 in SEMC labeled same as holotype except with “... SM08454561... [barcode label]” and with “...PARATYPE *Desmopachria irregulara* Miller, 2021 [blue label with black line border].”

Checklist of *Desmopachria portmanni-portmanni* subgroup – includes the non-iridescent *Desmopachria* with forked male prosternal process (= *Desmopachria* (Portmannia) Young, 1980)

Desmopachria basicollis Guignot, 1950 – Costa Rica

Desmopachria bisulcata sp. nov. – Suriname

Desmopachria bryanstoni Clark, 1862 – Mexico, Panama, Guatemala
= *Desmopachria polita* Sharp, 1882

Desmopachria carranca Braga & Ferreira-Jr., 2018 – Brazil

Desmopachria decorosa Young, 1995 – Mexico

Desmopachria dicrophalica Braga & Ferreira-Jr., 2014 – Brazil

Desmopachria dispar Sharp, 1882 – Mexico

Desmopachria disticta Braga & Ferreira-Jr., 2014 – Brazil

Desmopachria duodentata Braga & Ferreira-Jr., 2011 – Brazil

Desmopachria goias Young, 1995 – Brazil

Desmopachria grammosticta Braga & Ferreira-Jr., 2014 – Brazil

Desmopachria grandinigra Braga & Ferreira-Jr., 2014 – Brazil

Desmopachria irregulara sp. nov. – Venezuela

Desmopachria itamontensis Braga & Ferreira-Jr., 2014 – Brazil

Desmopachria laevis Sharp, 1882 – Brazil (Braga and Ferreira-Jr. 2014)

Desmopachria mutata Sharp, 1882 – Brazil

nomen novum for *Desmopachria bryanstoni* Sharp, 1882

Desmopachria niger Zimmermann, 1923 – Brazil (São Paulo)

Desmopachria nigricoxa Braga & Ferreira-Jr., 2018 – Brazil

Desmopachria nigrisphaera Braga & Ferreira-Jr., 2018 – Brazil

Desmopachria nitidissima Zimmermann, 1928 – Brazil

Desmopachria pittieri Young 1995 – Costa Rica

Desmopachria portmanni Clark, 1862 – USA and N Mexico

Desmopachria sobrina Young, 1995 – Panama

Desmopachria specula Sharp, 1887 – Panama (probably not part of *Desmopachria portmanni* species group according to Young (1995)).

Desmopachria ukuki Braga & Ferreira-Jr., 2014 – Brazil

Desmopachria undulatosterna Braga & Ferreira-Jr., 2011 – Brazil

Desmopachria variegata Sharp, 1882 – Mexico, El Salvador, Honduras

Desmopachria youngi Miller, 1999 – Bolivia

Desmopachria zetha Young, 1995 – Mexico

Desmopachria striola species group

Diagnosis. This species group is characterized by the elytron with a sutural stria (Miller 2001; Miller and Wolfe 2019; Young 1980, 1990b).

Comments. Miller and Wolfe (2019) described new species and discussed the likelihood that the group is not monophyletic since the sutural stria is not a particularly reliable synapomorphy in Dytiscidae and some of the species in this group are not similar in other ways. Within the group are several species, though, that have similar genitalia with the median lobe “shouldered” medially in ventral aspect and the lateral lobe characteristically angled in lateral aspect. The following new species appears to belong to this subgroup of the *Desmopachria striola* species group.

Desmopachria robusta sp. nov.

<http://zoobank.org/AA30C940-1C89-42EB-98AD-4484BC305A57>

Figures 72–75, 81

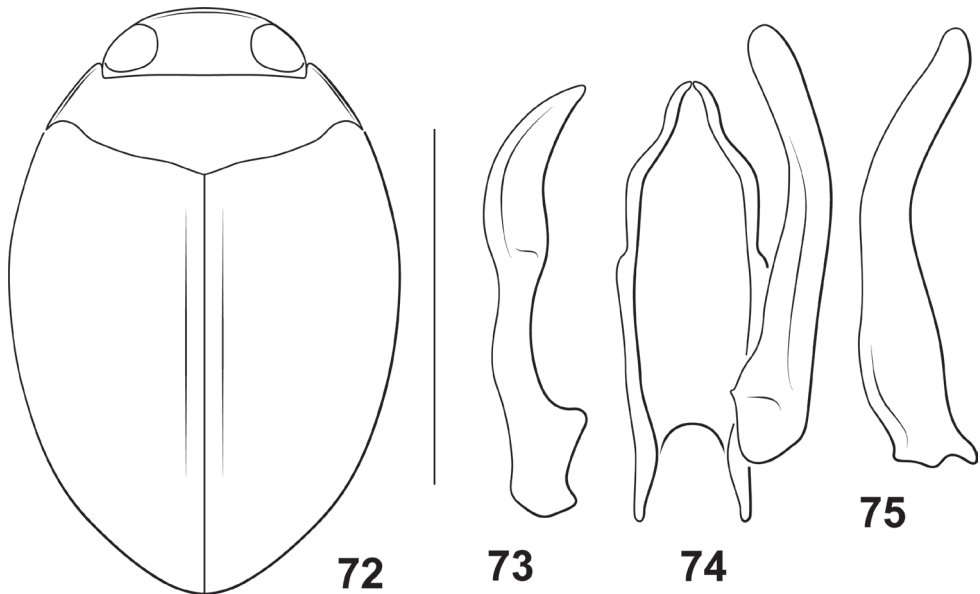
Type locality. Venezuela, Zulia State, Perija National Park, Tukuko, Rio Manantial, 9°50.490'N, 72°49.310'W.

Diagnosis. This species is similar to other species in the *Desmopachria striola* species group with “shouldered” median lobes (Miller and Wolfe 2019), but the male median lobe in this species is considerably broader than in other species (Fig. 74).

Description. Measurements. TL = 1.7 mm, GW = 1.1 mm, PW = 0.8 mm, HW = 0.6 mm, EW = 0.3 mm, TL/GW = 1.5, HW/EW = 2.2. Body very broad, broadly rounded, laterally broadly curved, lateral margins continuous between pronotum and elytron, body broadest across elytra at midlength of body (Fig. 72).

Coloration. Dorsal surface of head and pronotum evenly yellow. Elytron pale orange-brown, narrowly darker along anterior and sutural margins. Head appendages, legs, and ventral surfaces orange-yellow.

Sculpture and structure. Head broad, anteriorly curved; anterior margin of clypeus curved, flattened, margined with conspicuous, continuous narrow bead; surface of head shiny, finely and sparsely punctate; eyes large (Fig. 72, HW/EW = 2.2); antennae short, scape and pedicel relatively large and rounded, flagellomere III long and slender, apically expanded, antennomeres IV–X short and broad, lobed at anterodorsal angle, antennomere XI elongate, apically pointed. Pronotum very short, lateral margins short, slightly curved with continuous narrow bead, slightly wider medially; surface shiny, impunctate medially, very finely and indistinctly punctate around margins.

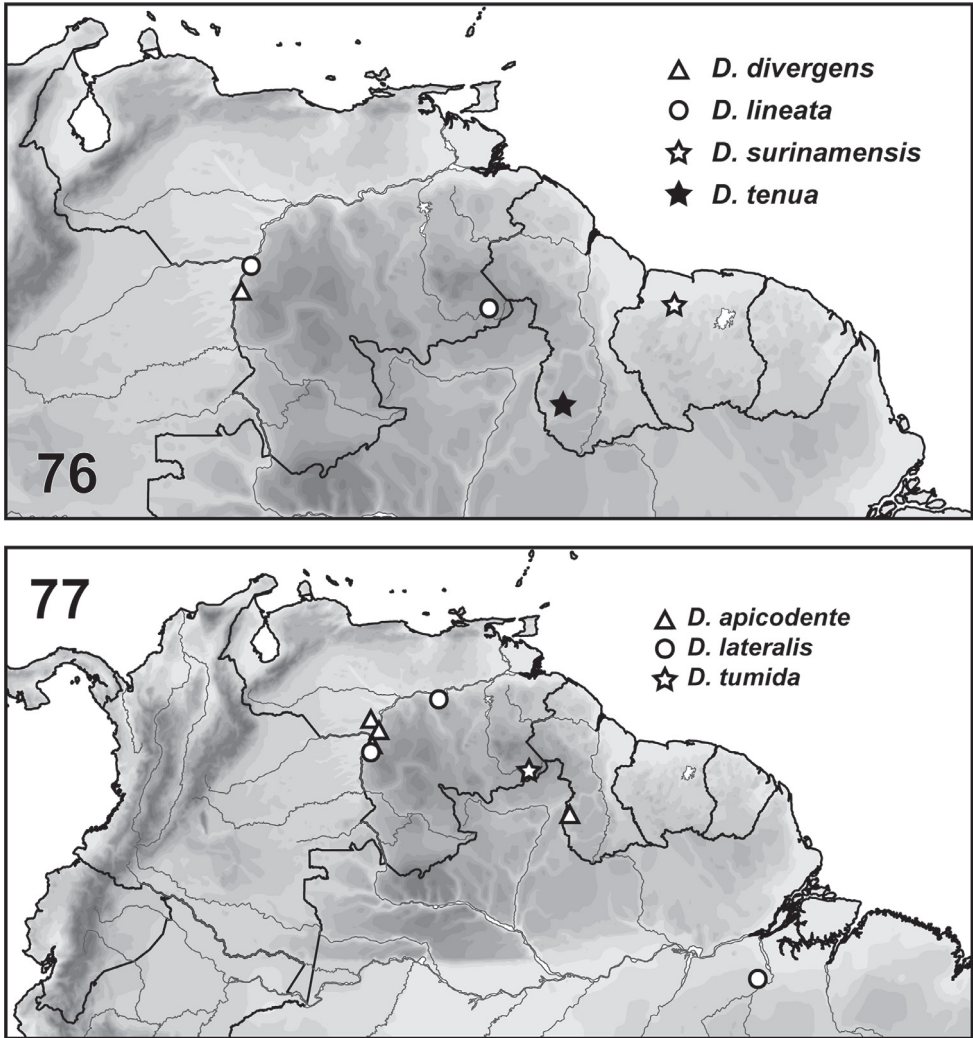


Figures 72–75. *Desmopachria robusta*. **72** habitus **73** lateral lobe, right lateral aspect **74** median lobe and right lateral lobe, ventral aspect **75** right lateral lobe, right lateral aspect. Scale bar: 1.0 mm.

Elytron moderately broad, laterally broadly curved; surface shiny, extremely finely punctate across surface; with distinctive subsutural stria, or groove, extending most of length of elytron (Fig. 72). Prosternum extremely short, longitudinally compressed, medially slightly carinate; prosternal process slender anteriorly, with distinctive, small medial tubercle, apical blade short and broad, medially concave, apically broadly pointed. Metaventrite broad and evenly smoothly convex medially, surface shiny, impunctate; metaventrite wings extremely slender. Metacoxa with medial portion short, $< 1/3$ length of metaventrite medially, metacoxal lines divergent anteriorly, sinuate; lateral portion of metacoxa extremely large, anteriorly strongly expanded; surface shiny, impunctate. Metatrochanter large, subequal to length of ventral margin of metafemur; legs otherwise not noticeably modified. Abdomen with surfaces shiny and smooth, impunctate.

Male genitalia. Male median lobe elongated in lateral aspect, robust, apical half broad, broadly and evenly curved dorsad to narrowly rounded apex (Fig. 73); in ventral aspect very broad, robust, lateral margins subparallel basally, with two distinct “shoulders” one medially, and one more distinct subapically, apically distinctly narrowed with medial rounded apex (Fig. 74). Lateral lobe in lateral aspect moderately throughout length, distinctly bent dorsad, apex slightly curved ventrad, rounded (Fig. 75); in ventral aspect evenly broad throughout length, medially distinctly bent mediad (Fig. 74).

Sexual dimorphism and variation. Only a male specimen was examined.



Figures 76, 77. *Desmopachria* species distributions. **76** ungrouped *Desmopachria* species **77** *Desmopachria apicodente* species group.

Etymology. This species is named *robusta*, Latin for strong or robust, for the conspicuously broader male median lobe than that of other similar species in the genus.

Distribution. This species is known from Zulia State, Venezuela (Fig. 81).

Habitat. The type specimen was collected from a “detrital pool.”

Type material. Holotype in MIZA, male labeled, “VENEZUELA: Zulia State 9°50.490'N, 72°49.310'W, Perija Nat. Park: Tukuko: Rio Manantial 29.i.2009; Short, García, Camacho VZ09-0129-01B: detrital [sic] pool/ SM0844647 KUNHM-ENT [barcode label]/ HOLOTYPE *Desmopachria robusta* Miller, 2021 [red label with black line border].”

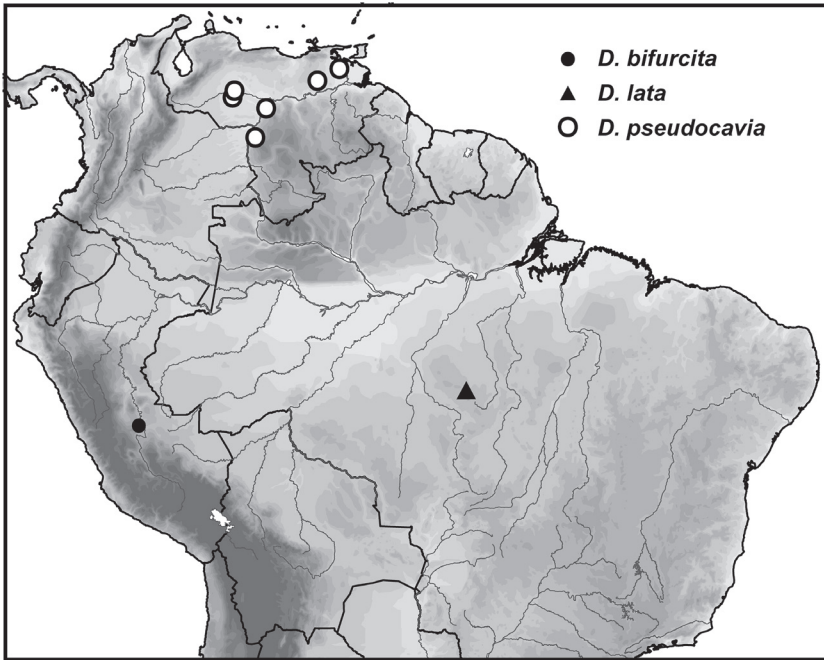


Figure 78. *Desmopachria* species distributions. *Desmopachria bifurcata* species group and *Desmopachria convexa* species group.

Checklist of *Desmopachria striola* species group

Desmopachria amya Miller, 2001 – Bolivia, Brazil (Braga and Ferreira-Jr. 2014)

Desmopachria atropos Miller & Wolfe, 2019 – Venezuela

Desmopachria chei Miller, 1999 – Bolivia

Desmopachria chlotho Miller & Wolfe, 2019 – Suriname

Desmopachria ferrugata Régimbart, 1895 – Brazil

Desmopachria fossulata Zimmermann, 1928 – Brazil (Braga and Ferreira-Jr. 2014)

Desmopachria grouvellei Régimbart, 1895 – Mexico, Argentina, Paraguay?

Desmopachria lachesis Miller & Wolfe, 2019 – Guyana, Suriname, Venezuela

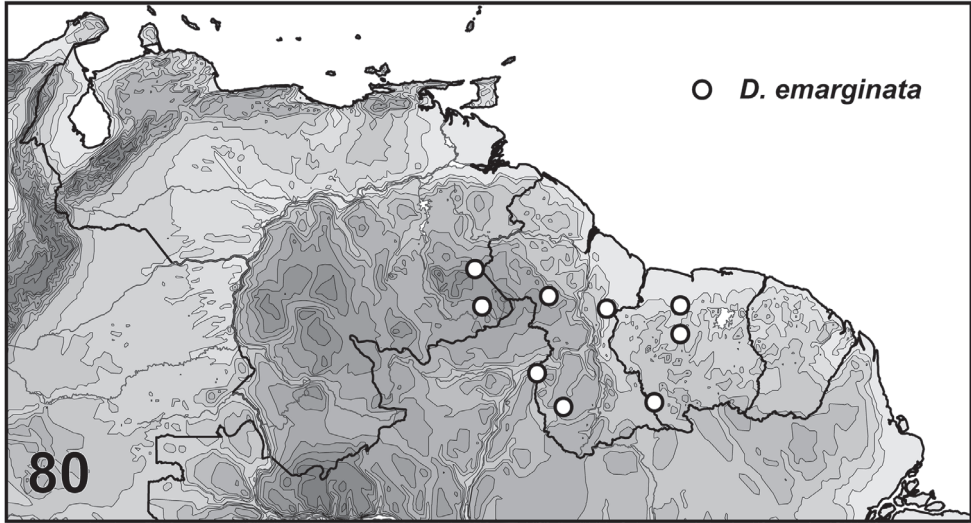
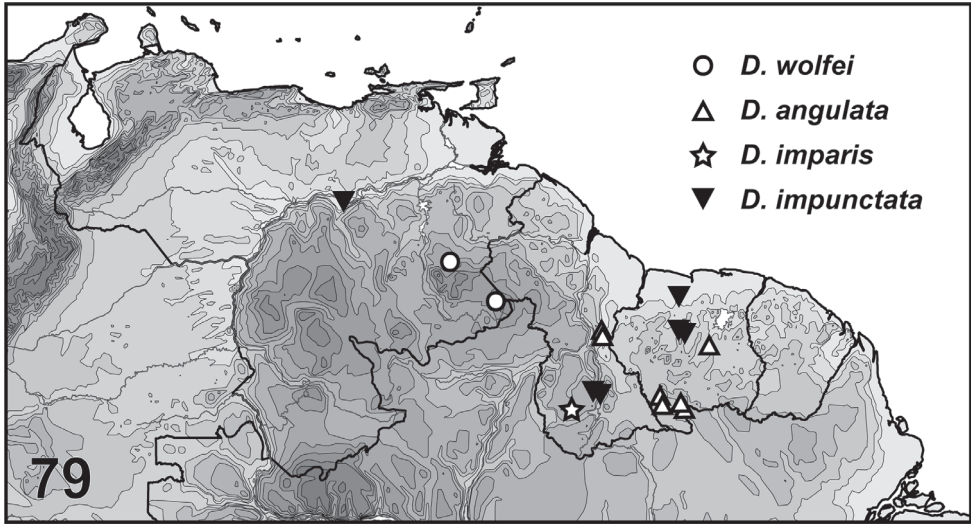
Desmopachria robusta sp. nov. – Venezuela

Desmopachria ruginosa Young, 1990 – Brazil

Desmopachria striola Sharp, 1887 – Argentina, Bolivia, Brazil (Braga and Ferreira-Jr. 2010), Colombia, Costa Rica, Ecuador, Guatemala, Panama, Peru, Suriname, Trinidad, USA (Florida), Venezuela.

Desmopachria vicina species group

Diagnosis. This group is characterized by the anterior metatibial spine serrate (Miller 2001) (historically the subgenus *D. (Nectoserrula)* Guignot, 1949 (Guignot 1949; Young 1980)).



Figures 79, 80. *Desmopachria* species distributions. **79** *Desmopachria nitida* species group and *Desmopachria portmanni-aldessa* species group **80** *Desmopachria portmanni-aldessa* species group.

Comments. No new species have been discovered in this group for over 100 years.

Checklist of *Desmopachria vicina* species group

Desmopachria concolor Sharp, 1882 – Uruguay

Desmopachria mendozana (Steinheil, 1869) – Argentina.

Desmopachria punctatissima Zimmermann, 1923 – Argentina

Desmopachria vicina Sharp, 1887 – Mexico

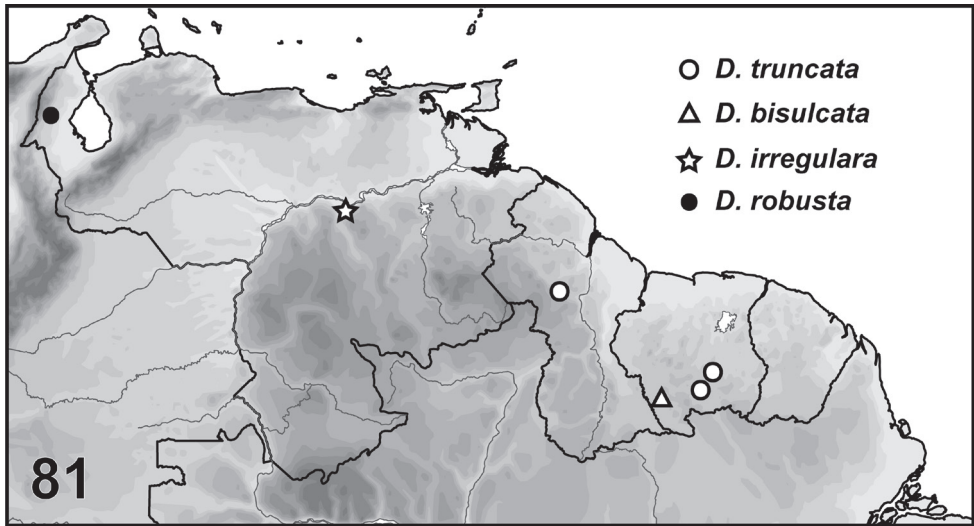


Figure 81. *Desmopachria* species distributions, *Desmopachria portmanni-aldessa* species group, *Desmopachria portmanni-portmanni* species group, and *Desmopachria striola* species group.

Desmopachria ubangoides species group

Diagnosis. These are iridescent *Desmopachria* without a forked male prosternum and with the anterior clypeal margin dimorphic, more developed in male (= *Desmopachria* (*Hintonia*) Young, 1980 (Guignot 1949; Young 1980)

Comments. A new species in this group, *D. yanomami* Braga & Ferreria Jr., 2018, was described recently.

Checklist of *Desmopachria ubangoides* species group

Desmopachria ubangoides Young, 1980 – Brazil, Ecuador

Desmopachria siolii Young, 1980 – Brazil

Desmopachria minuta Young, 1980 – Brazil

Desmopachria yanomami Braga & Ferreira Jr., 2018 – Brazil, Venezuela (new record, Venezuela, Amazonas State, Comunidad Caño Gato on Rio Sipapo, 4°58.838'N, 67°44.341'W, MIZA, SEMC, MSBA).

Desmopachria glabricula species group

Diagnosis. These are iridescent *Desmopachria* without a forked male prosternum and with the anterior clypeal margin dimorphic and more developed in males (= *Desmopachria* (*Hintonia*) Young, 1980 (Guignot 1949; Young 1980)

Comments. New species have been described recently in this group (Braga and Ferreira-Jr. 2014; Miller 1999, 2001).

Checklist of *Desmopachria glabricula* species group

- Desmopachria aphronoscelus* Miller, 1999 – Bolivia
Desmopachria flavida Young, 1981 – Mexico.
Desmopachria glabricula Sharp, 1882 – Guatemala.
Desmopachria leechi Young, 1981 – USA, Florida.
Desmopachria stethothrix Braga & Ferreira Jr., 2014 – Brazil.
Desmopachria strigata Young, 1981 – Brazil.
Desmopachria volatidisca Miller, 2001 – Bolivia.
Desmopachria volvata Young, 1981 – Panama.
Desmopachria zimmermani Young, 1981 – Mexico.

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Description of two new species of the genus *Spinirta* Jin & Zhang, 2020 (Araneae, Corinnidae) from southern China

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Abstract

Two new species of *Spinirta* Jin & Zhang, 2020 (Araneae: Corinnidae) from Jiangxi Province, China are described here: *S. sanxiandian* **sp. nov.** (♂♀) and *S. sishuishan* **sp. nov.** (♂). Detailed descriptions and photographs of the new species are provided.

Keywords

Corinnid, distribution, Jiangxi Province, taxonomy

Introduction

The total number of species in the family Corinnidae Karsch, 1880 has increased greatly in the past ten years (Haddad 2013; Raven 2015; Candiani and Bonaldo 2017; Jin and Zhang 2020; WSC 2022). Now, it comprises about 824 species from 73 genera. Only nine genera with 33 species were recorded from China (WSC 2022). More than half of them are known from a single sex: eight of these were described from females and nine from males (WSC 2022). Only one corinnid species from the genus *Spinirta* Jin & Zhang, 2020 is known from Jiangxi Province.

Spinirta Jin & Zhang, 2020 was erected by Jin and Zhang (2020) based on ten species. Meanwhile, one *Allomedmassa* species, *A. qiaoliaoensis* Lu & Chen, 2019 (Lu

et al. 2019) was transferred to the genus *Spinirta* by Jin and Zhang (2020). These species were collected from Sichuan, Chongqing, Guizhou, Hunan, Hubei, Zhejiang, and Anhui provinces and have a wide distribution in southern China. Recently, the first record of a species of *Spinirta* was reported from Wuyi Mountain in Jiangxi Province (Fan et al. 2022). However, there are still many unknown species because of the lack of systematic research and attention, especially in the southern provinces of China.

Spinirta spiders inhabit a wide range of habitats varying from tree canopies to the ground or leaf litter layers of the southern provinces of China (Jin and Zhang 2020; author's pers. obs.). When we studied corinnid spiders from Jiangxi Province, we found two new species belonging to *Spinirta* and describe them herein. Furthermore, the records of corinnid species in Jiangxi Province have been updated in this work.

Material and methods

Specimens were examined using a Jiangnan SZ 6100 stereomicroscope with a Zoom Microscope System. Both male palps and female copulatory organs were detached and examined in 80% ethanol, using an Olympus CX43 compound microscope with a KUY NICE CCD camera. All specimens treated in this work are deposited in the Animal Specimen Museum, Life Science of College, Jinggangshan University (ASM-JGSU). Measurements were taken with the AxioVision software (SE64 ver. 4.8.3) and are given in millimetres. Terminology of the male and female copulatory organs follows Jin and Zhang (2020).

Leg measurements are given as total length (femur, patella, tibia, metatarsus, tarsus). The abbreviations used in the text and figures are:

ALE	anterior lateral eye;
AME	anterior median eye;
At	atrium;
CD	copulatory duct;
CO	copulatory opening;
CS	cone-shaped spines;
d	dorsal;
E	embolus;
EA	embolic apophysis;
FD	fertilization duct;
GA	glandular appendage;
MOA	median ocular area;
p	prolateral;
PLE	posterior lateral eye;
PME	posterior median eye;
PTA	prolateral tibial apophysis;
r	retrolateral;

RTA	retrolateral tibial apophysis;
Sp	spermatheca;
St	subtegulum;
v	ventral;
VTA	ventral tibial apophysis.

Taxonomy

Family Corinnidae Karsch, 1880

Genus *Spinirta* Jin & Zhang, 2020

Type species. *Spinirta jinyunshanensis* Jin & Zhang, 2020. Type locality: Chongqing.

The genus includes 11 species, all of which are distributed in southern and southwest of China (WSC 2022). Currently, most of them are known only from females (three species) or males (four species) (WSC 2022). Most of China's nine species are recorded from southwestern China (Jin and Zhang 2020). Only one *Spinirta* species, *S. wuyishanensis* Zhou, 2022 was recorded from Jiangxi Province in southeast China. It is worth mentioning that the female remains unknown.

Spinirta sanxiandian Liu, sp. nov.

<https://zoobank.org/6CEBCD02-A0B5-452B-A1AD-E0F681296427>

(三仙殿刺突蛛)

Figs 1–5, 8

Material examined. Holotype: 1 ♂, **CHINA:** Jiangxi Province, Ji'an City, Qingyuan District, Donggu Town, Dawu Mountain, 26°40'48.69"N, 115°25'7.79"E, 1031 m, 25.X.2020, K. Liu et al. leg. (Cor-04). **Paratype:** 2 ♀, 13.XI.2021, K. Liu et al. leg., other data same as holotype (Cor-03 and Cor-05).

Etymology. The specific name is derived from the type locality, Sanxiandian Temple in Dawu Mountain; noun in apposition.

Diagnosis. The male of this new species is similar to that of *Spinirta sparsula* Jin & Zhang, 2020 (cf. Fig. 2 vs. Jin and Zhang 2020: fig. 12B–F, 13A–D) in having the fork-like tegular apex, but can be distinguished from it by the sperm duct (*SD*) with a curved posterior part (vs. straight in *S. sparsula*) and the ear-shaped retrolateral tibial apophysis (*RTA*) without protruded base (vs. digitiform with a kidney shaped protruded base in *S. sparsula*). It also resembles *S. sishuishan* sp. nov. in having a thumb-like ventral tibial apophysis (*VTA*), a thick horn-like prolateral tibial apophysis (*PTA*) and a curved sperm duct (*SD*), but can be separated from it by the ear-shaped retrolateral tibial apophysis (*RTA*) (vs. shield-shaped in *S. sishuishan* sp. nov.), the anterior part of the tegulum with a broad lateral apophysis (vs. absent in

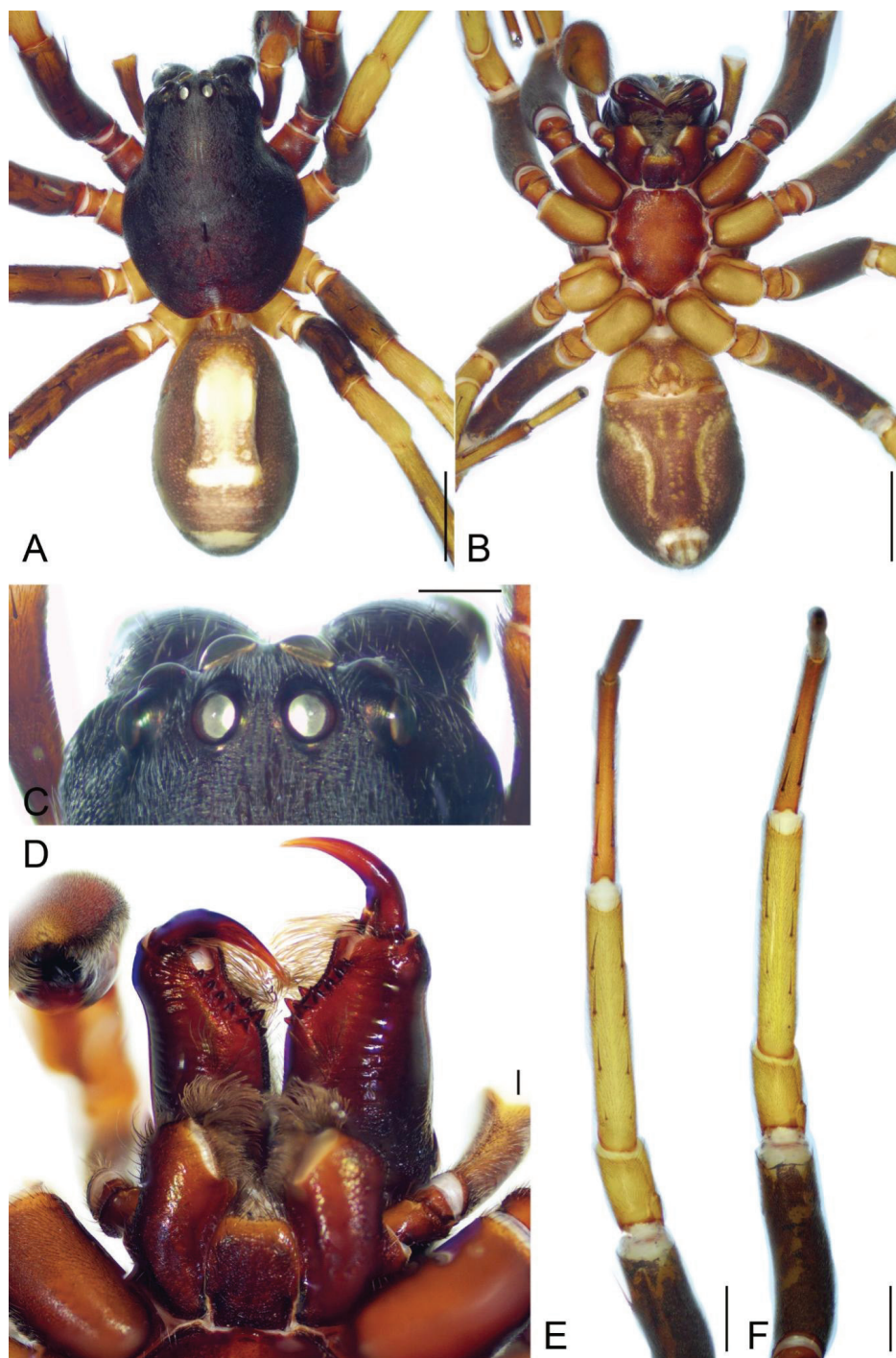


Figure 1. *Spinirta sanxiandian* Liu sp. nov., male holotype **A** habitus, dorsal view **B** same, ventral view **C** eyes, dorsal view **D** chelicerae, endites and labium, ventral view **E** leg I, ventral view **F** leg II, ventral view. Scale bars: 2 mm (**A**, **B**); 0.5 mm (**C**); 0.2 mm (**D**); 1 mm (**E**, **F**).

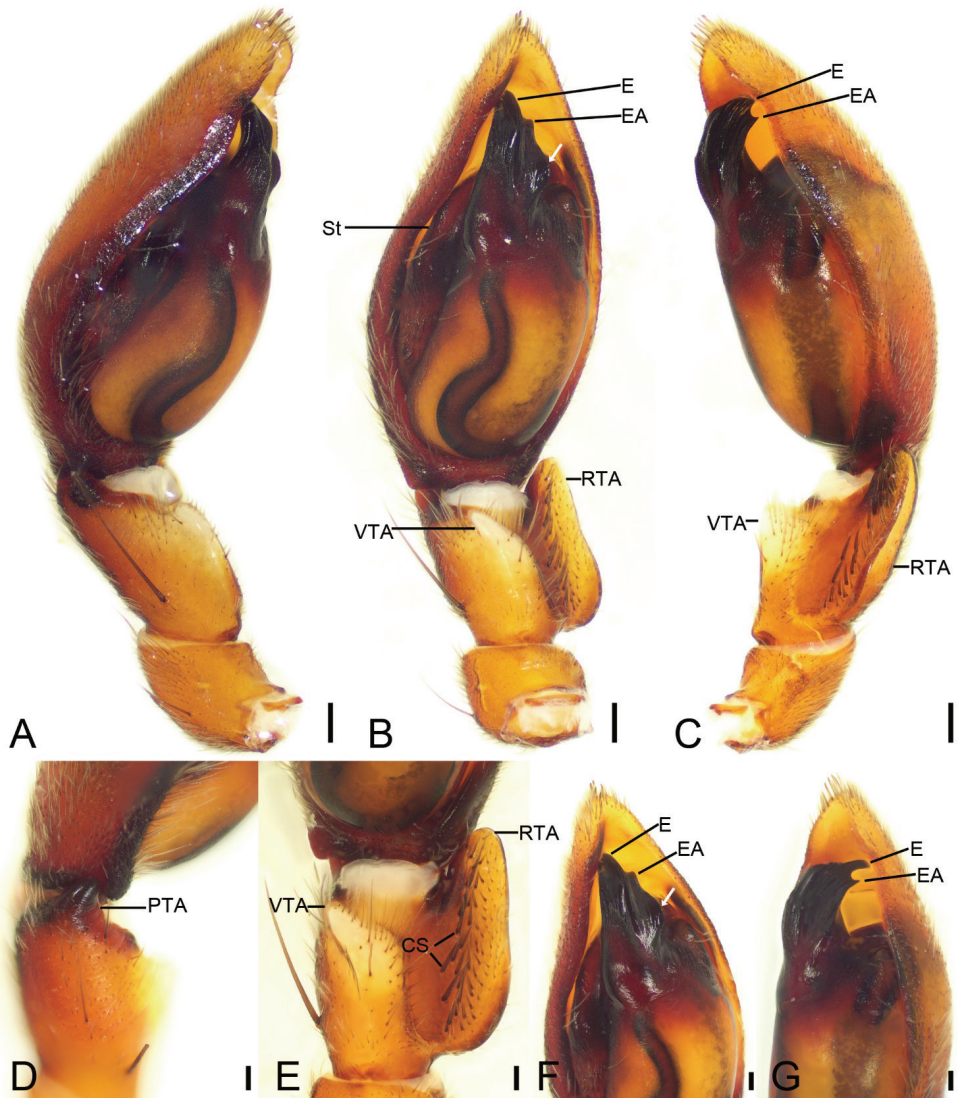


Figure 2. *Spinirta sanxiandian* Liu sp. nov., palp of male holotype **A** prolateral view **B** ventral view, white arrow shows the lateral apophysis located on anterolateral tegulum **C** retrolateral view **D** detail of PTA, dorso-prolateral view **E** detail of RTA, ventral view **F** detail of tegulum, white arrow shows the lateral apophysis located on anterolateral tegulum, ventral view **G** same, retrolateral view. Abbreviations: CS – cone-shaped spines, E – embolus, EA – embolic apophysis, PTA – prolateral tibial apophysis, RTA – retrolateral tibial apophysis, St – subtegulum, VTA – ventral tibial apophysis. Scale bars: 0.2 mm (**A–C**); 0.1 (**D–G**).

S. sishuishan sp. nov.) and the sharp embolic apophysis in retrolateral view (vs. relatively blunt in *S. sishuishan* sp. nov.) (cf. Fig. 2 vs. Fig. 7). The female of the new species resembles *S. qizimeiensis* Jin & Zhang, 2020 in having inflated and fused copulatory ducts (CD) (cf. Figs 4B, D, 5B vs. Jin and Zhang 2020: fig. 22E, F). It can also be

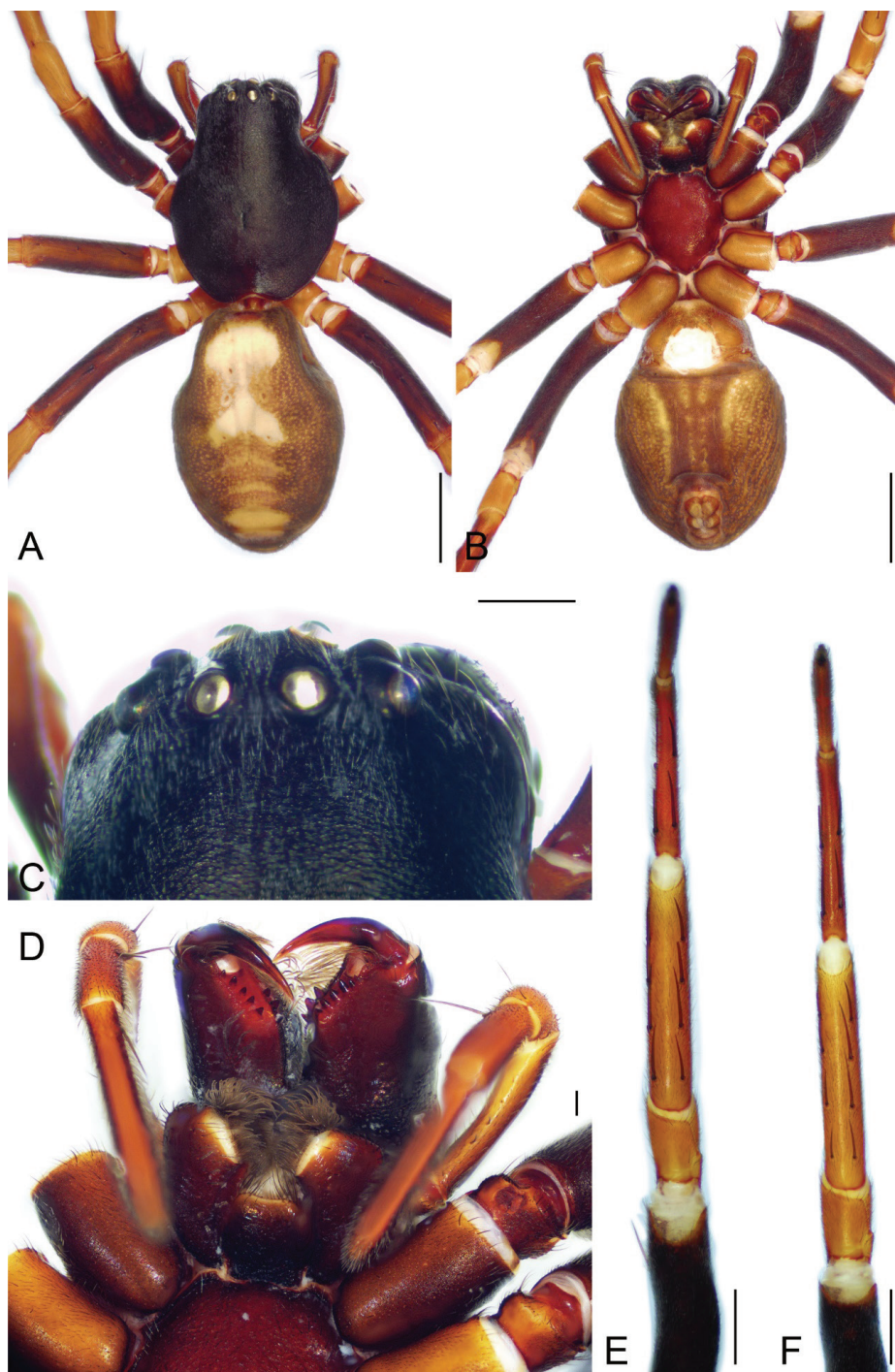


Figure 3. *Spinirta sanxiandian* Liu sp. nov., female paratype **A** habitus, dorsal view **B** same, ventral view **C** eyes, dorsal view **D** chelicerae, endites and labium, ventral view **E** leg I, ventral view **F** leg II, ventral view. Scale bars: 2 mm (**A**, **B**); 0.5 mm (**C**); 0.2 mm (**D**); 1 mm (**E**, **F**).

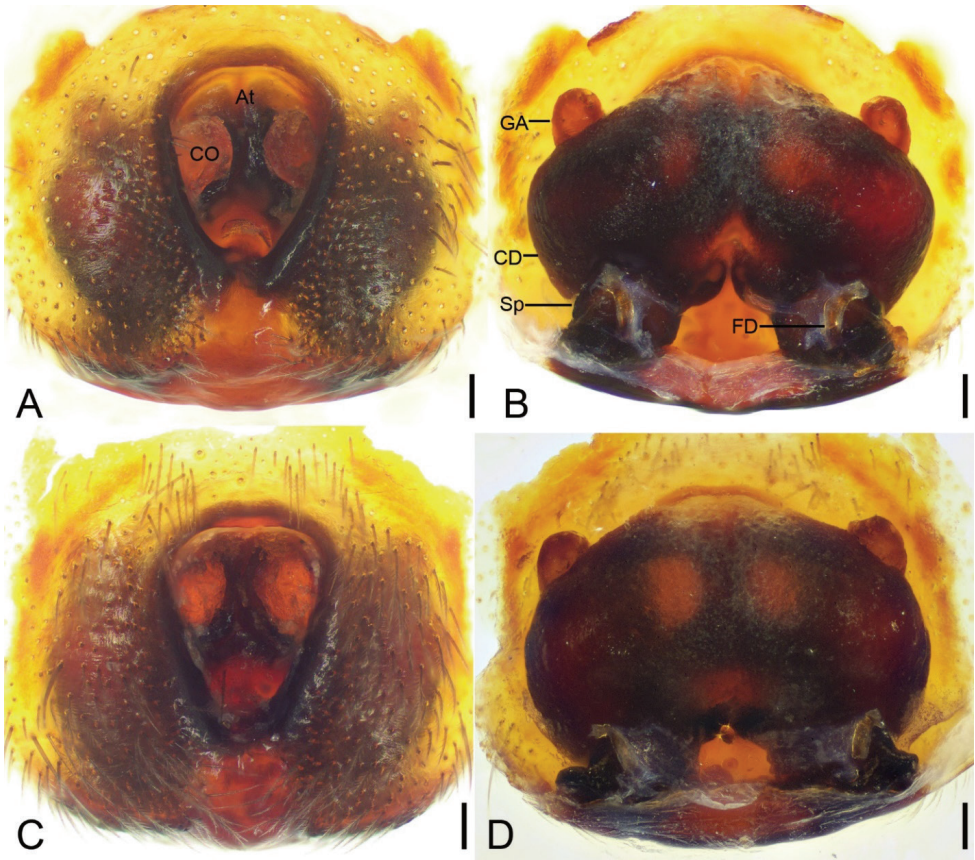


Figure 4. *Spinirta sanxiandian* Liu sp. nov., epigyne of female paratypes **A, C** ventral view **B, D** dorsal view. Abbreviations: At – atrium, CD – copulatory duct, CO – copulatory opening, FD – fertilization duct, GA – glandular appendage, Sp – spermatheca. Scale bars: 0.1 mm.

distinguished by the epigynal width/length ratio 0.88 (vs. 1.10 in *S. qizimeiensis*), the shield copulatory openings (CO) (vs. round in *S. qizimeiensis*), and the copulatory ducts (CD) extending from the anteromedial to the posterolateral part of the epigyne (vs. from anteromedial to postero-medial part of epigyne in *S. qizimeiensis*).

Description. Male. Habitus as in Fig. 1A, B. Total length 10.87. Carapace: 5.32 long, 4.16 wide. Carapace covered with abundant short hairs. Eye sizes and inter-distances (Fig. 1C): AME 0.32, ALE 0.31, PME 0.2, PLE 0.27, AME-AME 0.15, AME-ALE 0.07, PME-PME 0.3, PME-PL 0.36, AME-PME 0.25, AME-PL 0.47, ALE-ALE 0.87, PLE-PL 1.45, ALE-PL 0.2. MOA 0.74 long, front width 0.77, back width 0.72. Chelicera with three promarginal and five retromarginal teeth (Fig. 1D). Abdomen: 5.02 long, 3.31 wide. Leg measurements: I 15.48 (4.31, 1.97, 3.7, 3.52, 1.98); II 14.67 (4.25, 1.82, 3.38, 3.36, 1.86); III 12.45 (3.35, 1.62, 2.76, 3.05, 1.67); IV 16.73 (4.52, 1.83, 3.8, 4.83, 1.75); spination (Fig. 1E, F): I Fe: d2, p1; Ti:

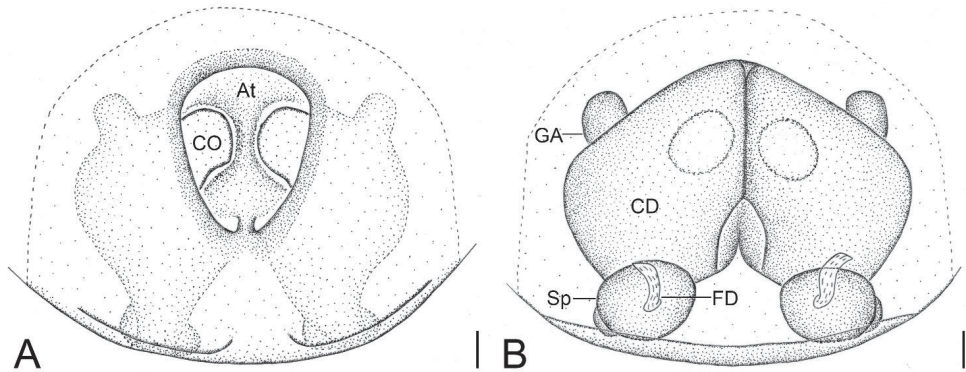


Figure 5. *Spinirta sanxiandian* Liu sp. nov., epigyne of female paratype **A** ventral view **B** dorsal view. Abbreviations: At – atrium, CD – copulatory duct, CO – copulatory opening, FD – fertilization duct, GA – glandular appendage, Sp – spermatheca. Scale bars: 0.1 mm.

v8; Mt: v4; II Fe: d2, p1; Ti: v8; Mt: v4; III Fe: d3, p1, r1; Ti: p2, r2, v4; Mt: d2, p3, r2, v5; IV: Fe: d3, p1, r1; Ti: p2, r2, v4; Mt: d2, p3, r2, v5.

Colouration (Fig. 1). Carapace and chelicerae dark brown. Endites and labium reddish brown. Sternum red-brown. Legs: femora I–IV, tibiae and metatarsi IV dark brown to yellow, with dark brown pattern; patellae I–IV, tibiae I–III, metatarsi I–III and tarsi I–III yellow. Palps brown. Abdomen: dorsum brown, medially with a broad, longitudinal, light marking including one broad and three nearly touching transversal dark brown stripes; venter with a pair of sloping yellow stripes submedially and a pair of yellow beaded spots. Spinnerets yellow-brown.

Palp as in Fig. 2. Tibia with distinct retrolateral groove, ventral apophysis (VTA) thumb-like in ventral view. Retrolateral tibial apophysis (RTA) ear-shaped, nearly as long as tibial length, ventral surface with two lines of short cone-shaped spines (CS). Prolateral tibial apophysis (PTA) thick horn-like, strongly sclerotized, nearly as long as 1/3 of tibia. Tegulum with strongly sclerotized apex. Subtegulum (St) with many wrinkles on posterior surface. Sperm duct (SD) S-shaped in posterior part. Embolus (E) short, with thick base, forming a C-shape with short spine-like embolic apophysis (EA), nearly 3× longer than embolic apophysis.

Female. Habitus as in Fig. 3A, B. As in male, except as noted. Total length 10.71. Carapace: 4.84 long, 3.89 wide. Eye sizes and interdistances (Fig. 3C): AME 0.28, ALE 0.26, PME 0.19, PLE 0.24, AME-AME 0.16, AME-ALE 0.08, PME-PME 0.27, PME-PLE 0.31, AME-PME 0.26, AME-PLE 0.4, ALE-ALE 0.83, PLE-PLE 1.3, ALE-PLE 0.18. MOA 0.72 long, front width 0.66, back width 0.66. Abdomen: 5.55 long, 3.85 wide. Leg measurements: I 13.57 (3.96, 1.75, 3.19, 3.01, 1.66); II 12.5 (3.36, 1.7, 2.92, 2.92, 1.6); III 11.2 (3.09, 1.5, 2.54, 2.69, 1.38); IV 14.77 (3.92, 1.7, 3.48, 4.11, 1.56); spination (Fig. 3E, F): I Fe: d3, p1; Ti: v8; Mt: v4; II Fe: d3, p1; Ti: v8; Mt: v4; III Fe: d4, p1; Ti: p2, r2, v4; Mt: p2, r2, v5; IV: Fe: d4, r1; Ti: p2, r2, v4; Mt: p3, r2, v5.

Colouration (Fig. 3). Abdomen dark brown, medially with a broad pale mark including a broad and a thin pale chevron markings and three transversal yellow stripes.

Epigyne as in Figs 4A, B, 5. Atrium (*At*) large, shield, covers equal or less than half of epigynal plate, anteromedially located. Copulatory openings (*CO*) very large, oval, located at anterolateral atrium. Copulatory ducts (*CD*) very broad, anteriorly touching, posteriorly slightly separated. Glandular appendages (*GA*) short, located at dorsal part of copulatory ducts, extending beyond medial part of copulatory ducts, directed anteriorly. Spermathecae (*Sp*) relatively broad, separated by 1/2 width of copulatory ducts. Fertilisation ducts (*FD*) directed anteriorly, shorter than spermathecal width.

Variability. The female specimens of this new species occur exactly in the same sites explored by the authors. They are identified as the same species based on appearance and epigyne. Variability was observed in the epigyne (Fig. 4), which may either have a shield/oval atrium, club-shaped or cap-like glandular appendages, and/or the anterior part of copulatory ducts closely touching or fused. The epigynal variability observed across the distribution of *Spinirta sanxiandian* sp. nov. may be the result of the influence of their development factors.

Distribution. Known only from the type locality, Jiangxi Province, China (Fig. 8).

***Spinirta sishuishan* Liu, sp. nov.**

<https://zoobank.org/F06E9311-8FE0-4858-B870-22E9F59F3262>

(汜水山刺突蛛)

Figs 6–8

Material examined. Holotype: 1 ♂, **CHINA:** Jiangxi Province, Ganzhou City, Chongyi County, Sishui Mountain, near parking lot, 25°27'11.73"N, 113°55'30.04"E, 965 m, 2.X.2020, K. Liu et al. leg. (Cor-02).

Etymology. The specific name, derived from the type locality, is a noun in apposition.

Diagnosis. The male of this new species can be distinguished from *S. sanxiandian* sp. nov. by the shield retrolateral tibial apophysis (*RTA*) (vs. ear-shaped), the anterior part of the tegulum lacking lateral apophysis (vs. present in *S. sanxiandian* sp. nov.) and the relatively blunt embolic apophysis (*EA*) in retrolateral view (vs. sharp in *S. sanxiandian* sp. nov.) (cf. Fig. 7 vs. Fig. 2).

Description. Male. Habitus as in Fig. 6A, B. Total length 10.45. Carapace: 5.6 long, 4.21 wide. Carapace covered with abundant short hairs. Eye sizes and interdistances (Fig. 6C): AME 0.35, ALE 0.24, PME 0.3, PLE 0.29, AME-AME 0.2, AME-ALE 0.08, PME-PME 0.27, PME-PLE 0.23, AME-PME 0.2, AME-PLE 0.41, ALE-ALE 0.96, PLE-PLE 1.43, ALE-PLE 0.07. MOA 0.76 long, front width 0.8, back width 0.85. Chelicera (Fig. 6D) with three promarginal and six retromarginal teeth. Abdomen: 4.79 long, 3.14 wide. Leg measurements: I 15.93 (4.62, 1.44, 4.18, 3.64, 2.05); II 15.78 (4.41, 1.9, 3.75, 3.73, 1.99); III 13.51 (3.75, 1.58, 3.15, 3.29, 1.74); IV 18.24 (4.84, 1.83, 4.29, 5.37, 1.91); spination (Fig. 6E, F): I Fe: d3, p1; Ti: v7;

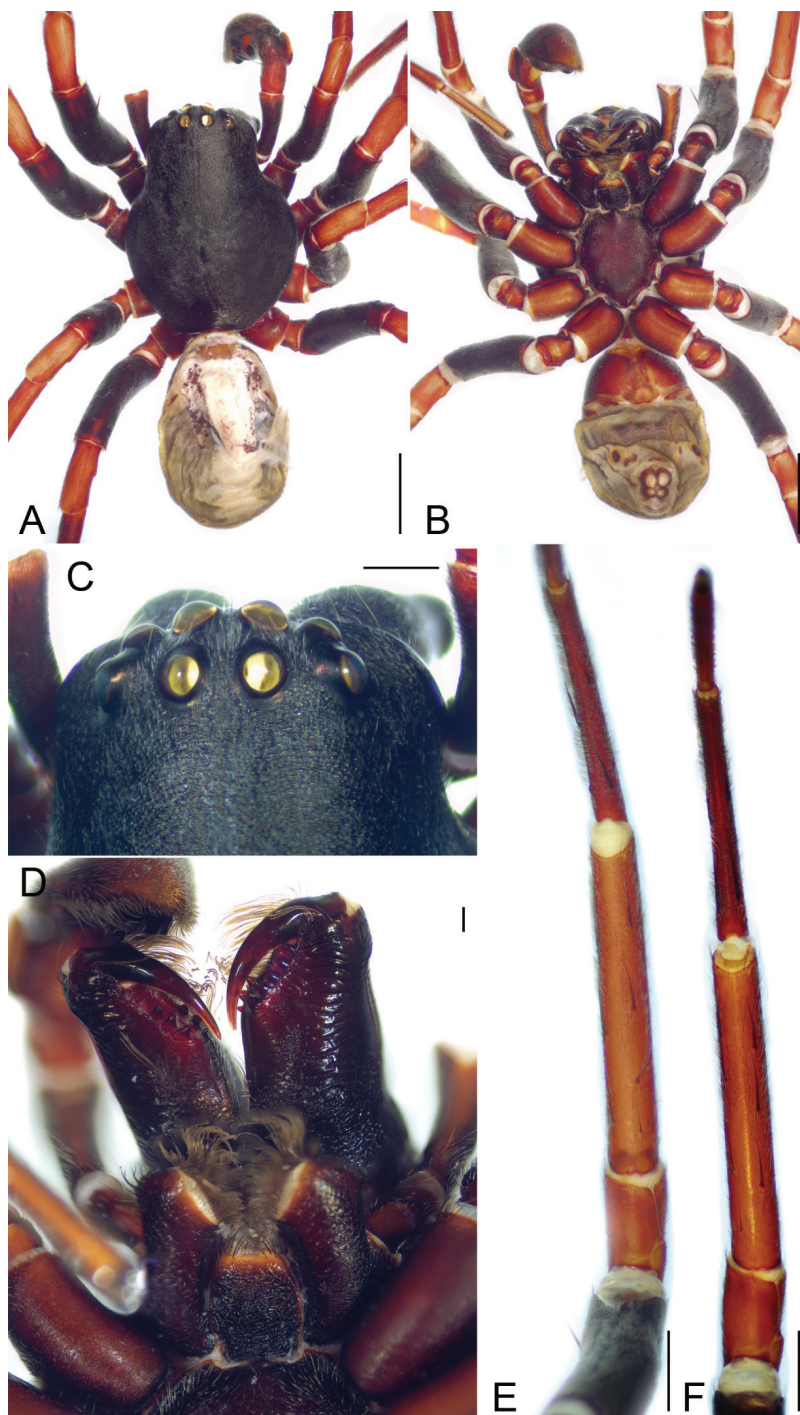


Figure 6. *Spinirta sishuishan* Liu sp. nov., male holotype **A** habitus, dorsal view **B** same, ventral view **C** eyes, dorsal view **D** chelicerae, endites and labium, ventral view **E** leg I, ventral view **F** leg II, ventral view. Scale bars: 2 mm (**A**, **B**); 0.5 mm (**C**); 0.2 mm (**D**); 1 mm (**E**, **F**).

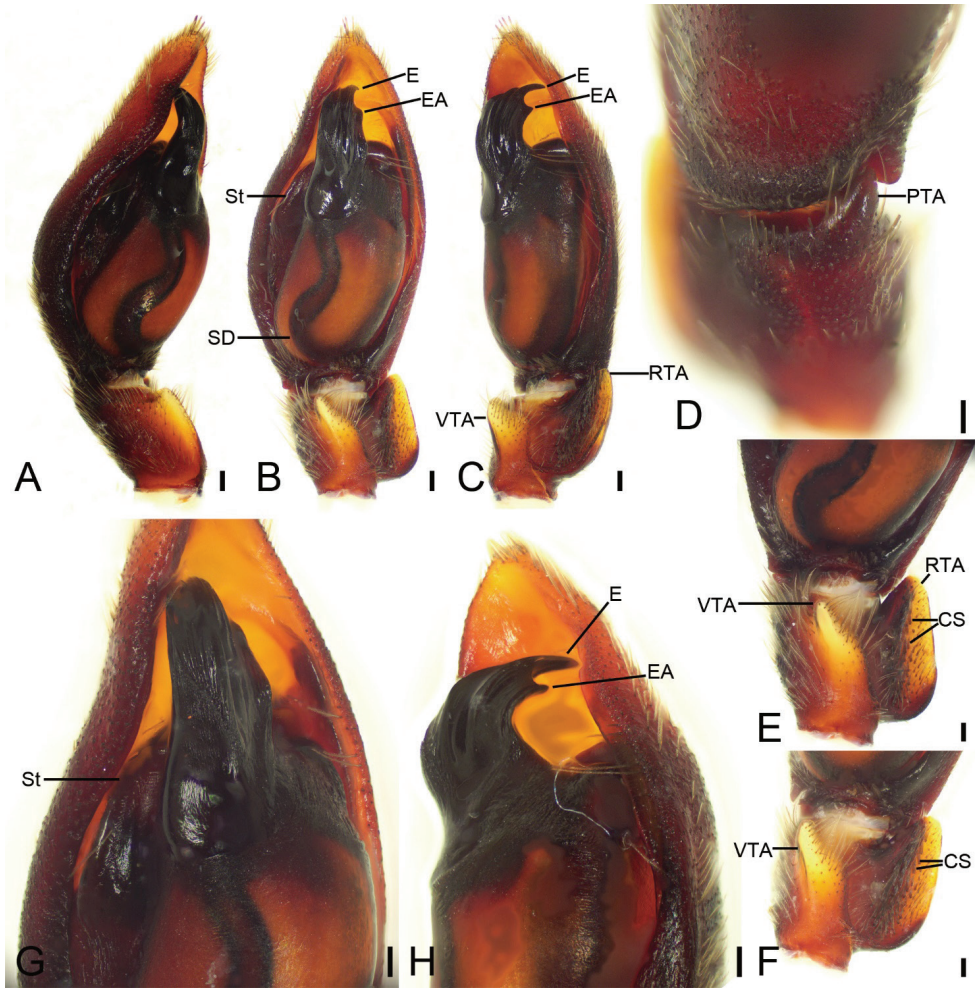


Figure 7. *Spinirta sishuishan* Liu sp. nov., palp of male holotype **A** prolateral view **B** ventral view **C** retro-ventral view **D** dorsal view **E** detail of VTA and RTA, ventral view **F** same, ventral view, slightly retro-lateral **G** detail of tegulum, ventral view **H** same, retro-ventral view. Abbreviations: CS – cone-shaped spines, E – embolus, EA – embolic apophysis, PTA – prolateral tibial apophysis, RTA – retrolateral tibial apophysis, St – subtegulum, VTA – ventral tibial apophysis. Scale bars: 0.1 mm.

Mt: v4; II Fe: d1, p1; Ti: r3, v7; Mt: r2, v4; III Fe: d3, r1; Ti: p4, r2, v4; Mt: p4, r1, v5; IV: Fe: d3, r1; Ti: p3, r2, v2; Mt: p2, r2, v2.

Colouration (Fig. 6). Carapace and chelicerae dark brown. Endites and labium red-brown to dark brown. Sternum dark brown. Legs: femora I-IV dark brown, tibia and metatarsus IV red to dark brown; patellae I-IV, tibiae and metatarsi I-III and tarsi I-IV red. Abdomen dark brown, medially with a pale serrulate marking. Spinnerets yellow-brown.

Palp as in Fig. 7. Tibia with distinct retrolateral groove, ventral apophysis (VTA) thumb-like in ventral view. Retrolateral tibial apophysis (RTA) shield in retrolateral



Figure 8. Records of *Spinirta sanxiandian* sp. nov. (circle) and *S. sisbushan* sp. nov. (triangle) from Jiangxi Province, China.

view, nearly as long as tibial length, ventral surface with four lines of short cone-shaped spines (*CS*). Prolateral tibial apophysis (*PTA*) thick horn-like, strongly sclerotised, nearly as long as $1/3$ of tibia. Tegulum with strongly sclerotized apex. Subtegulum (*St*) with many wrinkles on posterolateral tegulum. Sperm duct (*SD*) S-shaped in posterior part. Embolus (*E*) spine-like, with thick base, forming a C-shape with short blunt embolic apophysis (*EA*), nearly $4\times$ longer than embolic apophysis.

Female. Unknown.

Distribution. Known only from the type locality, Jiangxi Province, China (Fig. 8).

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A synopsis of the numbers of testicular follicles and ovarioles in true bugs (Heteroptera, Hemiptera) – sixty-five years of progress after J. Pendergrast's review

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Abstract

The structure of testes and ovaries can be described in its simplest form by the number of follicles and ovarioles they contain. Sixty-five years after the last review of the internal reproductive systems in true bugs (Heteroptera), the data accumulated today on the number of testicular follicles and ovarioles in their gonads are summarized. In addition, data on the number and type (mesadenia/ectadenia) of accessory glands are given. The hemipteran suborder Heteroptera constitutes one of the most diverse groups of non-homometabolous ('Hemimetabola') insects, comprising more than 40,000 described species worldwide and approximately 100 families, classified into seven infraorders. Data are available for all infraorders; however, more than 90% of studied species belong to the largest and most evolutionarily derived infraorders Cimicomorpha and Pentatomomorpha. In true bugs, in general, the number of follicles varies from one to nine (in a testis), and the number of ovarioles varies from two to 24 (in an ovary). Seven follicles per testis and seven ovarioles per ovary prevail being found in approximately 43.5% (307 species) and 24.4% (367 species) of studied species, respectively. Such a structure of testes and ovaries is considered an ancestral character state in the Heteroptera. In the evolution of this group, the number of follicles and ovarioles both increased and decreased, but the trend towards a decrease clearly prevailed.

Keywords

Accessory glands, ectadenia, evolution, mesadenia, ovarioles, phylogeny, testicular follicles, true bugs

Introduction

The hemipteran suborder Heteroptera (or true bugs) displays remarkable morphological variation and comprises more than 40,000 described species worldwide in ~ 100 families classified into seven infraorders including Enicocephalomorpha, Dipsocoromorpha, Nepomorpha, Gerromorpha, Leptopodomorpha, Cimicomorpha, and Pentatomomorpha. The majority of true bug species are herbivorous but some are predators and blood-suckers (Štys and Kerzhner 1975; Henry 2009; Schuh and Weirauch 2020).

The internal anatomy of the true bug males and females has been investigated for nearly two centuries. The first report on this topic appeared in the thirties of the 19th century (Dufour 1833). Substantial comparative research on the internal anatomy of true bugs had accumulated by the 1960s mostly as a consequence of publications by J. Carayon, D. Leston, S. Miyamoto, T.E. Woodward, and J.G. Pendergrast (see Pendergrast 1957 and Miyamoto 1957 for references). Pendergrast (1957) published the first and, up to the present time, the only review of data available by that time on the internal reproductive organs of true bugs. Overall, Pendergrast summarized the literature (~ 90 titles) and his own data on ~ 50 families of Heteroptera and also shortly commented on the value of different parts of the male and female reproductive organs as characters in the taxonomy and classification of the Heteroptera. Despite the fact that Pendergrast singled out some organs as potentially promising for these purposes (in particular, testes in terms of the number of follicles they contain), he concluded that there is still very little data to make any generalizations. A huge contribution was made by Miyamoto (1957), who summarized the literature and own data on the structure of the ovaries in almost 300 representatives of ~ 40 families (some of them no longer families and other subfamilies recently erected to the separate families). Since the Pendergrast's overview and Miyamoto's list, ~ 120 original articles concerning the internal reproductive organs of Heteroptera have been published. In most cases, studies concern single species, and comparative data across multiple species of a group are few (e.g., Kumar 1967: Aradidae; Leston 1961a; Leston and Gibbs 1968; Malipatil 1978: Lygaeidae; Akingbohunge 1983: Miridae; Grozeva and Kuznetsova 1992: Aradidae, Piesmatidae, Berytidae, Lygaeidae, Pyrrhocoridae). Much valuable information on true bugs can be found in special monographic works devoted to the reproductive systems of insects in general (Matsuda 1976; Büning 1994a, b; Chapman et al. 2013; Klowden 2013).

Although there is considerable diversity in detail, the internal parts of the male and female reproductive systems are organized similarly in different insects. In males of true bugs, it is formed by a pair of testes consisting of a variable number of testicular follicles, two different ducts, a median ejaculatory duct, and accessory glands. Accessory glands may be ectodermal or mesodermal in origin being known as ectadenia or

mesadenia, respectively. Ectadenia open into the ejaculatory duct, whereas mesadenia open into the vasa deferentia or the distal end of the ejaculatory duct. In some species, both ectadenia and mesadenia are present, while other species have no accessory glands at all (Pendergrast 1957; Suppl. material 1). In females, the reproductive system is formed by a pair of ovaries consisting of a variable number of ovarioles, two lateral oviducts, a median common oviduct, and a spermatheca. The ovarioles are known to be of the meroistic telotrophic type (Chapman et al. 2013). In some species, accessory glands may also be present.

During the years that have passed since the aforementioned overviews, the number of species and higher taxa of true bugs studied in relation to testes and ovaries has almost tripled, and it seems appropriate to publish an updated list. In this review article, all the data available today, including new data on 140 species obtained by the authors, are summarized in two tables. Suppl. material 1 includes all species studied to date in terms of the number of follicles and ovarioles. In some cases, additional information, e.g., on the number and type of accessory glands (ectadenia or mesadenia) in the male reproductive system, is also provided. Table 1 summarizes data presented in Suppl. material 1 and shows the variability of the number of follicles and ovarioles at different taxonomic levels, together with the modal values for each of the higher taxa explored. On Fig. 1, the internal reproductive organs of a male and a female of *Arocatus longiceps* Stål, 1872 (Lydaeidae) is given. In Figs 2 and 3, character states of testicular follicle and ovariole numbers, respectively, are mapped onto the phylogenetic tree of Heteroptera families taken from Weirauch et al. (2019). In the final section of the review, the diversity of the analyzed characteristics and main tendencies of their evolution in true bugs are discussed. We hope that our review will be of importance for future work on the diversity of reproductive morphology within the Hemiptera, and that the data may provide additional information for understanding relationships between the higher taxa of true bugs.

Materials and methods

The current review article is part of a long-term research project dedicated to the study of true bugs, including the morphology of their reproductive system, cytogenetics, and evolution. The data we have obtained over years on the structure of testes and ovaries of true bugs in terms of the number of testicular follicles and ovarioles constitute at the present time a significant part of all such data currently available for the Heteroptera in general (Suppl. material 1). The material was collected during the expeditions of the authors (1986–2021) or provided by colleagues, mainly by D. Gapon, L. Hill, and H. Gunther. Material comes from different regions of Palaearctic (Europe: predominantly southern Europe and the Balkans, Central Asia, Caucasus) and some parts of the Old Tropics (Vietnam, Indonesia, Himalayas, India, Thailand, Tasmania). Species identification was made by authors or collectors (in case of donated material). Voucher samples are deposited in the insect collections of the National Museum of Natural

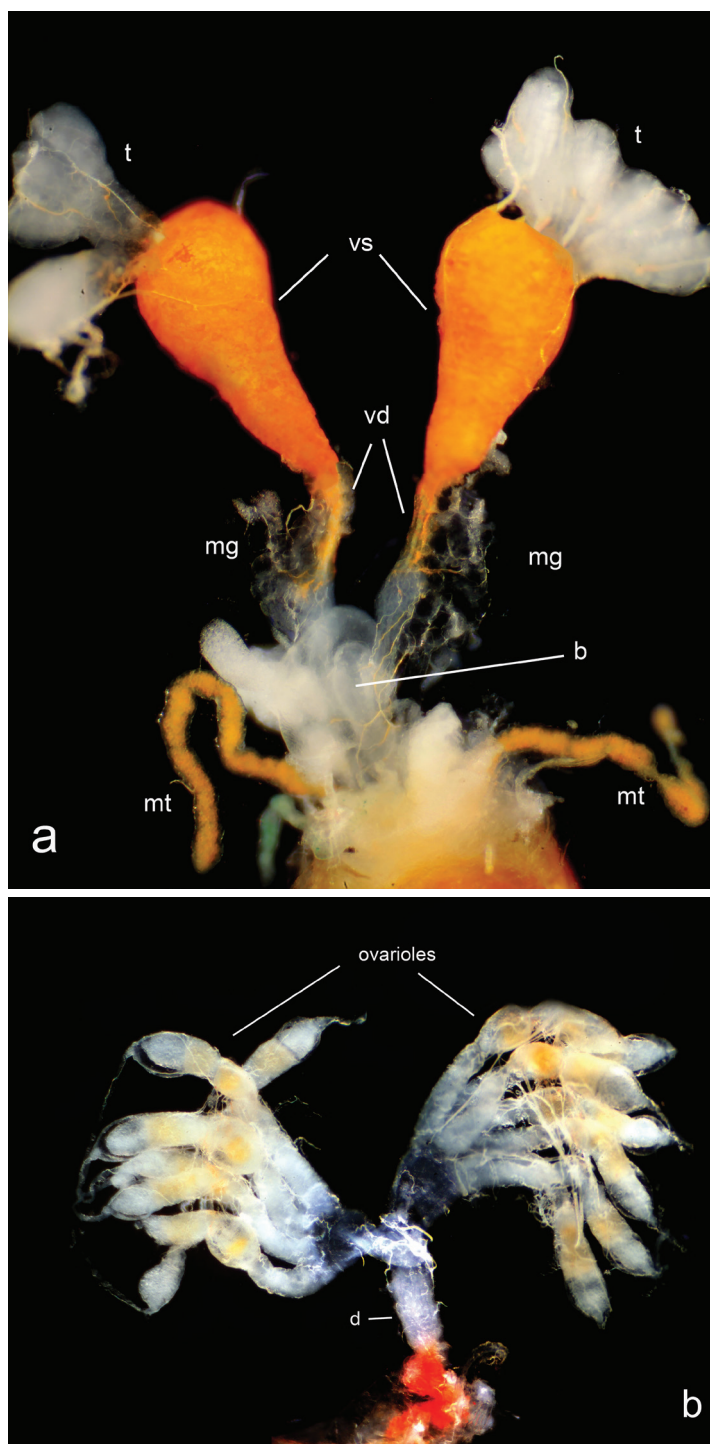


Figure 1. **a** Male (seven follicles) and **b** female (seven ovarioles) reproductive systems of *Arocatus longiceps* Stål, 1872 (Lygaeidae). Abbreviations: t – testis, vd – vas deferens, vs – vesicula seminalis, mg – mesadenia, b – bulbus, mt – malpighian tubule, d – ductus (spermatheca and accessory glands were not visible in females).

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Our original data cover 140 species belonging to 30 families, six infraorders, and represent 13.8% of all data on the structure of the testes and ovaries of true bugs accumulated to date and presented in Suppl. material 1. Some of these data have been published previously, the other part is presented here for the first time. Our study was carried out on specimens fixed in Carnoy fixative (3:1 96% ethanol and glacial acetic acid) that allowed both morphological and chromosomal analyses of the same individual. Material fixed in Duboscq Brasil (alcoholic Bouin's) and ethanol (95%) was also used. The gonads were dissected out of the abdomen in a drop of 45% acetic acid on a microscope slide. The testicular follicles of the male and the ovarioles of the female were carefully separated from each other and counted under a stereomicroscope. Other parts of the reproductive system have also been studied, most notably, the accessory glands in males.

Classification used in this work follows Schuh and Weirauch (2020) except for Mironectidae which are treated as a separate family due to distinct cytogenetic features (Grozeva et al. 2008) and following Nieser (2002). All taxa are listed alphabetically.

Numbers of testicular follicles and ovarioles were treated as unordered states of two hidden characters and optimized on the Bayesian total-evidence tree of Heteroptera published by Weirauch et al. (2019) with all terminals of the original topology collapsed to family level. The phylogenetic reconstruction of Weirauch et al. (2019) was chosen for character mapping as the most recent analysis of the entire Heteroptera employing comprehensive coverage of true bug families. The data recorded in this publication comes from all available literature (Dufour 1833; Gross 1901; Marshall and Severin 1903; Bowen 1922a, b; Kerkis 1926; Ludwig 1926; Poisson 1927; Sarel-Whitfield 1929; Wille 1929; Hagan 1931; Payne 1934; Baumgartner and Witherspoon 1937; Kirkpatrick 1937; Larsen 1938; Slack 1938; Schneider 1940; Kullenberg 1947; Carayon 1949, 1950, 1951, 1954, 1955, 1972; Woodward 1949, 1950, 1977; Bonhag and Wick 1953; Davis 1955, 1956, 1966, 1970; Pendergrast 1956, 1957; Miyamoto 1957, 1959; Scudder 1957; Barth 1958; Usinger and Matsuda 1959; Drake and Davis 1960; Schrader 1960a; Leston 1961a, b; Kumar 1962, 1964, 1965, 1967, 1969; Slater and Miyamoto 1963; Bhargava 1967; Leston and Gibbs 1968; Brunt 1971; Kauffman 1971; Huebner and Anderson 1972; Louis and Kumar 1973; Wightman 1973; Jansson and Scudder 1974; Malipatil 1978; Lung and Goeden 1982; Akingbohunge 1983; Heming-van Battum and Heming 1986, 1989; Gonçalves et al. 1987; Ma and Ramaswamy 1987; Postle and Woodward 1988; Grozeva and Kuznetsova 1989, 1992; Socha et al. 1988; Papáček and Gelbič 1989; Biliński et al. 1990; Jawale and Ranade 1990; Gelbič et al. 1991; Hunt and Stebbing 1992; Papáček and Soldán 1992, 2008; Lent et al. 1994; Grozeva 1995, 2003, 2007; Grozeva and Nokkala 1996, 2001; Simiczjew et al. 1996, 1998; Lalitha et al. 1997; Papáček et al. 1997; Štys et al. 1998; Simiczjew 1999; Adams 2001; Couturier et al. 2002; Lis 2003; Kuznetsova et al. 2004, 2007; Lemos et al. 2005a, b, 2010; Santos et al. 2005; Grozeva et al. 2006, 2007, 2008, 2009, 2013; Jahnke et al. 2006; Kugler

et al. 2006; Freitas et al. 2007a, b, 2008, 2010, 2012; Mróz 2007, 2012; Ogorzałek 2007; Pires et al. 2007; Grozeva and Simov 2008; Esquivel 2009; Marchini et al. 2009; Ogorzałek and Trochimczuk 2009; Souza et al. 2009; Chiang 2010, 2013; Van Doesburg et al. 2010; Horton and Lewis 2011; Mróz and Wojciechowski 2011; Souza et al. 2011, 2014; Uceli et al. 2011; Chiang et al. 2012; Kaur and Patial 2012, 2016; Soto et al. 2012; Gomes et al. 2013; Özyurt et al. 2013a, b, 2014a, b, 2015; Pluot-Sigwalt and Chérot 2013; Jyoti et al. 2015; Pereira et al. 2015; Cremonez et al. 2017, 2019; Elelimy et al. 2017a, b; Novais et al. 2017; Candan et al. 2018; Mahmood et al. 2018; Grodowitz et al. 2019, 2020; Khandelwal et al. 2019; Koçakoğlu et al. 2019; Xia 2019; Araújo et al. 2020a, b, 2021; Munhoz et al. 2020, 2021; Vélez et al. 2020; Gapon 2021; Oliveira et al. 2021; Bugaj-Nawrocka et al. 2022; Koutsogeorgiou et al. 2022; Samanta et al. 2022), and original observations (see Suppl. material 1).

The coding strategy aimed at reflecting diversity in numbers of follicles per testis (hereafter p.t.) and ovarioles per ovary (hereafter p.o.) observed within a given family. Therefore, states were coded as polymorphic in cases of large variability of follicle and ovariole numbers within a given family. This was the case for large and comparatively well studied families lacking widely accepted phylogenetic resolution e.g., Aradidae, Miridae, or Pentatomidae. However, in groups with a robust backbone phylogeny in place, e.g., Reduviidae (Weirauch 2008; Weirauch and Munro 2009; Hwang and Weirauch 2012), there was no doubt that the testis follicle number of seven is not only most common across the family, but may be treated as ancestral, and was coded as such. Within Veliidae, *Halovelia septentrionalis* Esaki, 1924 remains the only veliid species having two ovarioles p.o. Phylogeny of Gerromorpha by Damgaard (2008) rendered Haloveliinae as a sister group to Microveliinae which in turn forms a sister group to Gerridae. All veliid taxa including the second studied haloveliine species have four ovarioles p.o. and therefore we consider this number as an ancestral state for all veliids. History of both characters was traced using Mesquite 3.6.1 (Maddison and Maddison 2018) with the parsimony ancestral state reconstruction method (Figs 2, 3).

Results and discussion

In this work, we have compiled ~ 1200 records of the numbers of testicular follicles and ovarioles in 1008 true bug species from across 63 families and seven infraorders, including Enicocephalomorpha (one family, two species), Dipsocoromorpha (three families, twelve species), Nepomorpha (eleven families, 50 species), Gerromorpha (five families, 50 species), Leptopodomorpha (two families, five species), Cimicomorpha (12 families, 474 species), and Pentatomomorpha (29 families, 437 species). Below we will comment on the available data for each infraorder, with emphasis on those families in which such data are more or less representative. Data on male accessory glands, their numbers, and origins (mesadenia/ectadenia), although provided in Suppl. material 1, are not specifically discussed since they are still very few.

Infraorder	Family	Subfamily (Tribe)	The number of species with a certain number of follicles per testis										The number of species with a certain number of ovarioles per ovary									
			1	2	3	4	5	6	7	8	9	2	3	4	5	6	7	8	17	24		
Pentatomomorpha	Berytidae	3 subfamilies	6	5													1	6				
Pentatomomorpha	Berytidae	Berytinae	2	5														2				
Pentatomomorpha	Berytidae	Gampsocorinae	2														1	1				
Pentatomomorpha	Berytidae	Metacanthinae	2															3				
Pentatomomorpha	Blissidae	Blissinae			1		6	5									5	4				
Pentatomomorpha	Coreidae	2 subfamilies				1	16										17					
Pentatomomorpha	Coreidae	Coreinae					16										16					
Pentatomomorpha	Coreidae	Pseudophloeinae				1											1					
Pentatomomorpha	Cydnidae	7 subfamilies					4								1	1	1	12				
Pentatomomorpha	Cydnidae	Cephalosteinae													1							
Pentatomomorpha	Cydnidae	Cydninae					2										1	6				
Pentatomomorpha	Cydnidae	Parastrachiinae																1				
Pentatomomorpha	Cydnidae	Sehirinae					2										4					
Pentatomomorpha	Cydnidae	Thyreocorinae															1					
Pentatomomorpha	Cymidae														1		3					
Pentatomomorpha	Cymidae	Cyminae									2					1	2					
Pentatomomorpha	Cymidae	Ontiscinae															1					
Pentatomomorpha	Dinidoridae									1							2					
Pentatomomorpha	Dinidoridae	Dinidorinae								1								1				
Pentatomomorpha	Dinidoridae	Megymeninae																1				
Pentatomomorpha	Geocoridae				5			1									3					
Pentatomomorpha	Geocoridae	Geocorinae			5												2					
Pentatomomorpha	Geocoridae	Henestarinae						1									1					
Pentatomomorpha	Heterogasteridae							4									2					
Pentatomomorpha	Langidae	Physopeltinae						1									2					
Pentatomomorpha	Lygaeidae		1					12									14					
Pentatomomorpha	Lygaeidae	Ischnorhynchinae						1									1					
Pentatomomorpha	Lygaeidae	Lygaeinae						6									6					
Pentatomomorpha	Lygaeidae	Orsillinae	1					5									6					
Pentatomomorpha	Malcidae	Chaulipinae															1					
Pentatomomorpha	Ninidae						1										1					
Pentatomomorpha	Oxycarenidae	Oxycareninae	7															4				

Infraorder	Family	Subfamily (Tribe)	The number of species with a certain number of follicles per testis										The number of species with a certain number of ovarioles per ovary													
			1	2	3	4	5	6	7	8	9	2	3	4	5	6	7	8	17	24						
			2										1										4			
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Infraorder	Family	Subfamily (Tribe)	The number of species with a certain number of follicles per testis										The number of species with a certain number of ovarioles per ovary									
			1	2	3	4	5	6	7	8	9	2	3	4	5	6	7	8	17	24		
Pentatomomorpha	Rhyparochromidae	6 tribes	2	2	4	3	3	6										33				
Pentatomomorpha	Rhyparochromidae	Rhyparochrominae (Antilocorini)																2				
Pentatomomorpha	Rhyparochromidae	Rhyparochrominae (Drymini)	2															5				
Pentatomomorpha	Rhyparochromidae	Rhyparochrominae (Lethaeini)																5				
Pentatomomorpha	Rhyparochromidae	Rhyparochrominae (Myodochini)		4		3		1										12				
Pentatomomorpha	Rhyparochromidae	Rhyparochrominae (Rhyparochromini)						4										5				
Pentatomomorpha	Rhyparochromidae	Rhyparochrominae (Udeocorini)						1														
Pentatomomorpha	Scutelleridae							6										6				
Pentatomomorpha	Scutelleridae	Odontotarsinae						1										2				
Pentatomomorpha	Scutelleridae	Pachycorinae						1														
Pentatomomorpha	Scutelleridae	Scutellerinae						4										4				
Pentatomomorpha	Stenocephalidae							1										1				
Pentatomomorpha	Termitaphididae						1		1													
Pentatomomorpha	Tessaratomidae	Natalicolinae						1										1				
Pentatomomorpha	Urostylididae																4					
	Total		43	141	77	25	42	43	294	12	1	5	11	36	50	28	367	12	4	1		

CIMICOMORPHA

With more than 20,000 species placed in 17 families, this highly diverse infraorder is the largest within Heteroptera (Weirauch and Schuh 2011). Members of the Cimicomorpha show a wide range of adaptations to different terrestrial habitats, highly diverse life histories and prey capture strategies, including predation and blood feeding in the Reduviidae, mostly plant feeding in the Miroidea, traumatic insemination in the Cimicoidea and Miridae, and ectoparasitism in the Cimicidae and Polyctenidae. Some cimicomorphans (Cimicidae, Triatominae in Reduviidae, and Polyctenidae) are of medical importance and hematophagous at all stages (Kerzhner 1981; Schuh and Štys 1991; Schuh and Slater 1995; Schuh 1995; Tataric et al. 2006; Schuh et al. 2009; Weirauch and Schuh 2011; Schuh and Weirauch 2020). Data on the number of follicles and/or ovarioles are currently available for 12 families and missing for Plokiophilidae, Velocipedidae, Pachynomidae, Curaliidae, and Medocostidae.

Anthocoridae (minute pirate bugs)

The family comprises more than 500 species with seven tribes (Péricart 1972; Schuh and Štys 1991; Péricart 1996; Jung et al. 2010; Schuh and Weirauch 2020). Data are available for the number of follicles in 29 species of 12 genera from all currently recognized tribes, although ~ 40% of studied species belong to the most species-rich tribe Anthocorini. In all but six species and in all but two (the Xylocorini and Almeidini) tribes, males have two follicles p.t. The exceptions are two of the eleven studied species of the genus *Anthocoris* Fallén, 1814 (Anthocorini) having four (*A. nemorum* (Linnaeus, 1761)) and even 5–7 (*A. bakeri* Poppius, 1913) follicles p.t. Four species, *Scoloposcelis obscurella* (Zetterstedt, 1838) (Scolopini), *Australmeida derricki* (Gross, 1954), the single studied member of Almeidini, and the two studied species (subgenera *Proxylocoris* and *Arrostelus*) of the genus *Xylocoris* Dufour, 1931 in the monotypic tribe Xylocorini, have seven follicles p.t. The females of six studied species (in six genera of the Anthocorini, Almeidini, Cardistethini, Oriini, and Xylocorini) have seven ovarioles p.o.

Cimicidae (bed bugs)

The family consists of ~ 110 species and 24 genera in six recognized subfamilies (Schuh and Štys 1991; Weirauch et al. 2019). The three studied species, all belonging to the genus *Cimex* Linnaeus, 1758 (Cimicinae), have seven follicles p.t. and seven ovarioles p.o.

Joppeicidae (joppeicid bugs)

The family contains only one species, *Joppeicus paradoxus* Putton, 1881. This relict family of non-specialized general predators feeding on small insects, has an obscure history of phylogenetic placement although sometimes regarded as related to the family Tingidae (Davis and Usinger 1970; Štys 1971). Thus, any information on this spe-

cies is of considerable interest. Males of *J. paradoxus* have two follicles p.t., whereas females (according to different authors) have five or six ovarioles p.o. Five ovarioles are rarely observed in the Cimicomorpha (Davis and Usinger 1970) and its finding in Joppeicidae matches with *Cantacader* Amyot & Serville, 1843 species from the tingid subfamily Cantacaderinae and with *Corythucha marmorata* (Uhler, 1878) from the other tingid subfamily Tinginae.

Lasiochilidae (lasiochilid bugs)

A small family of predaceous true bugs with general appearance like that of Anthocoridae and Lyctocoridae and formerly classified as a subfamily within the family Anthocoridae (Schuh and Štys 1991; Schuh and Slater 1995). In two species of the genera *Lasiochilus* Reuter, 1871 and *Plochiocorella* Poppius, 1909, males have two follicles p.t. The females of *Lasiochilus* sp. have seven ovarioles p.o.

Lyctocoridae (lyctocorid bugs)

A monotypic group of predominantly predaceous true bugs formerly classified, like the Lasiochilidae, as a subfamily within the family Anthocoridae (Schuh and Slater 1995). *Lyctocoris* (*Lyctocoris*) *campestris* (Fabricius, 1794) has two follicles p.t. and seven ovarioles p.o., and the same structure of the ovaries was found in *L. beneficus* (Hiura, 1957).

Miridae (plant bugs)

The variation of testis follicle number has been used as a potentially important character for the higher-level taxonomy and phylogeny of plant bugs by several authors including Leston (1961a, b), Akingbohunge (1983), Grozeva and Simov (2008). In total, data on 259 species, less than 3% of the entire plant bug diversity, are currently available. Eight subfamilies and 39 tribes are generally recognized within Miridae (Cassis and Schuh 2012), and data on testis follicle numbers for many of these taxa are clearly insufficient due to sampling bias. Specifically, data on Psallopinae, Austromirini of Orthotylinae, Auricillocorini of Phylinae, three of six Deraeocorinae tribes, and four of six Mirinae tribes are lacking. Only a handful of species have been studied in the subfamilies Isometopinae (one) and Cylapinae (two), the deraeocorine tribe Hyaliadini (two), the phylina tribe Hallodapini (two), orthotyline tribes Coridromiini (one), and Nichomachini (one). However, available data for better studied taxa show a stable pattern of testis follicle numbers at the tribal and sometimes also subfamily levels. The modal numbers are briefly outlined below for each sufficiently studied subfamily.

Bryocorinae

In Dicyphini, a sister clade to the remaining bryocorines (Konstantinov et al. 2018), the presence of a single follicle p.t. was documented for all 21 examined species from four gen-

era. The same appears to be true for the monotypic tribe Felisacini (two species examined). In two Dicyphini species, *Tupiocoris rhododendri* (Dolling, 1972) and *Dicyphus* (*Brachyceroea*) *annulatus* (Wolff, 1804), two follicles p.t. were found. The modal number of one was observed in the small tribe Bryocorini although Akingbohunge (1983) documented two and two or three (“2-3”) follicles for *Monalocoris filicis* (Linnaeus, 1758) and *M. americanus* Wagner & Slater, 1952, respectively. Seven examined species of Monaloniini and the only examined Eccritotarsini species *Stenopterocoris laticeps* China, 1944 have either one or three follicles p.t. Females of the permanently parthenogenetic species *Campyloneura virgula* (Herrich-Schaeffer, 1835) (Eccritotarsini) were found to have seven ovarioles p.o.

Orthotylinae

Forty-three examined species of the largest tribe Orthotylini have two follicles p.t. Only *Cyrthorhinus caricis* (Fallén, 1807) is an exception displaying testes with a single follicle each (Leston 1961a). In contrast, the tribe Halticini (eight species examined) shows no uniform pattern with a follicle number ranging from one to three.

Phylinae

Almost all species (28) of the large and diverse tribe Phylini have remarkably stable follicle number of three. Alternative structural variants found in several species, viz., *Oncotylus viridiflavus* (Goeze, 1778) (four-five), *Platyscytus decempunctatus* (Carvalho, 1945) (four to six), and *Phylus melanocephalus* (Linnaeus, 1767) (two or three in different testes of the only studied male) may be treated as isolated cases of specialization (Akingbohunge 1983). The modal number for the tribe Pilophorini is also three, found in *Lasiolabops obscurus* Poppius, 1914 and three species from the genus *Pilophorus* Hahn, 1926 (the fourth studied *Pilophorus* species, *P. cinnamopterus* (Kirschbaum, 1856) has two follicles p.t.). The same pattern applies for the tribes Cremnorrhini (with one exception of *Orectoderus obliquus* Uhler, 1876) and Nasocorini. The tribes Hallodapini and Semiini remain insufficiently studied, but also follow the pattern of three, as evidenced by the currently available data.

Deraeocorinae

Data on this subfamily are scarce and most examined deraeocorine species (17 of 19) belong to the tribe Deraeocorini. The testis follicle number ranges from one (*Zacheila* Odhiambo, 1961, *Fingulus* Distant, 1904, and *Fingulus libbyi* Akingbohunge, 1981) to eight (most examined species of the subgenus *Deraeocoris* Kirschbaum, 1856) and no apparent pattern for this tribe could be established at this point.

Mirinae

Being the best studied plant bug tribe (73 species examined), Mirini unequivocally have seven testis follicles (in 66 species). The exceptions are very few and include

Garganus fusiformis (Say, 1832) (two), *Capsodes gothicus* (Linnaeus, 1758) (six), *Neurocolpus jessiae* Knight, 1934 (eight), and *Poecilocapsus lineatus* (Fabricius, 1798) (eight). Noteworthy, in three species (*Adelphocoris lineolatus* (Goeze, 1778), *Leptopterna dolabrata* (Linnaeus, 1758), *Stenotus binotatus* (Fabricius, 1794)) testis follicle number varies from seven to eight in different specimens or even in a single specimen of the same species. Stenodemini, the second well examined tribe (18 species), which forms a sister clade to all other tribes of the family (Schwartz 2008), also have the modal number of seven (in seven species). However, the tribe demonstrates exceptionally high diversity of testis follicle numbers, ranging from one (*Mimoceps insignis* Uhler, 1890) to eight (*Leptopterna* spp.). Various authors documented contrastingly different numbers (3–7) for different species of the genus *Stenodema* Laporte, 1832.

Data on the number of ovarioles are available for a total of 48 species and 17 genera from the subfamilies Bryocorinae, Cylapinae, Deraeocorinae, Mirinae, Orthotylinae, Isometopinae, and Phylinae. Most species have seven ovarioles p.o. (found in 38 species, 24 genera, all subfamilies). Other numbers, including eight (in seven species, five genera), four (in one species), three (in one species), or 5–7 (in one species), occur sporadically in different subfamilies that have a modal number of seven.

Nabidae (damselflags)

A relatively small family of predaceous true bugs with more than 30 genera and ca. 400 species distributed in two subfamilies, Prostematinae (two tribes, each with only two genera) and Nabinae (four tribes) (Schuh and Štys 1991; Kerzhner 1996; Henry 2009). In Prostematinae, the four studied species representing the tribes Prostematini and Phorticini have seven follicles p.t. In the Nabinae, all ten species studied in the tribe Nabini (genera *Nabis* Latreille, 1802 and *Himacerus* Wolff, 1811) also have seven testis follicles. Available data suggest a remarkably stable follicle number of seven in these subfamilies. The only exception presently known in both Nabinae and Nabidae is *Arachnocoris trinitatis* Bergroth, 1916 (tribe Arachnocorini) which has three follicles p.t. but seven ovarioles p.o. All other studied species (16) from both subfamilies share the same pattern of seven ovarioles.

Polycetenidae (bat bugs)

The family currently comprises 32 species belonging to five genera and two subfamilies, Polyceteninae and Hesperocteninae (Schuh and Weirauch 2020; Szentiványi et al. 2022). The females of the only studied species, *Hesperoctenes fumarius* (Westwood, 1874), have ovaries with two ovarioles each.

Reduviidae (assassin bugs)

With approximately 7000 species, 900 genera, and 25 subfamilies, Reduviidae are the second largest family of true bugs (Henry 2009; Hwang and Weirauch 2012; Weirauch

et al. 2014). Data on the number of follicles and/or ovarioles are available for 111 species, 72 genera and 18 subfamilies. In most species, testes are composed of seven follicles each with a few exceptions. Particularly, three of the 16 studied Emesinae species differ from that pattern. The number of follicles in *Nesidiolestes roberti* Wygodzinsky, 1966 (Emesinae, Ploiariolini) is described as “fewer than 7”; however, a figure in the original paper (Wygodzinsky 1966: fig. 11J) shows a testis with three follicles. Males of *Saicella usingeri* Wygodzinsky, 1966 (Ploiariolini) and *Bobba villiersi* Wygodzinsky, 1966 (Metapterini) were reported to have two and five follicles p.t., respectively. Within Harpactorinae (28 species studied), unusual testis follicle numbers were reported for *Polididus armatissimus* Stål, 1859 with nine follicles p.t., *Nagusta* sp. (eight), and *Repipta taurus* (Fabricius, 1803) for which two follicles p.t. were tentatively given. In *P. armatissimus*, the structure of the testis was shown to be complex: the follicles form two groups, one consisting of seven long and wide follicles and the other consisting of two smaller follicles (Gapon et al. 2021).

The testis comprising seven follicles are suggested to be an ancestral trait for the Reduviidae (Gapon et al. 2021). This testis structure has been described for *Lisarda vandenplasi* Schouteden, 1931 (Salyavatinae), eight species of the subfamily Reduviinae, 19 species of the Harpactorinae as well as for *Phymata* sp. from the Phymatinae complex, a sister group to the remaining “higher” reduviids. The number of ovarioles p.o. is seven in most species; however, some species have six (one species), three (two species), or eight (five species) ovarioles p.o. The available data suggest, thus, a high level of family stability in terms of both traits.

Thaumastocoridae (palm bugs)

The family comprises more than 30 species and six genera in two subfamilies, the Thaumastocorinae (21 species) and the Xylastodorinae (10 species) including nine recent and one described from the Dominican amber (Cassis et al. 1999; Schuh and Weirauch 2020). Data are available for four species and three genera of both subfamilies. Two species studied in the genus *Thaumastocoris* Kirkaldy, 1908 are similar in the number of follicles (two p.t.), but differ in the number of ovarioles p.o., which is three in *T. australicus* Kirkaldy, 1908 and two in *T. peregrinus* Carpintero & Dellapé, 2006. In Xylastodorinae, two species studied in the genera *Discocoris* Kormilev, 1955 and *Proxylastodoris* Heiss & Popov, 2002 are similar in having three ovarioles p.o.

Tingidae (lace bugs)

This family of herbivorous true bugs comprises ~ 2600 described species in more than 318 genera that are classified into the large subfamily Tinginae (~ 2500 species in 300 genera) and two smaller subfamilies, Cantacaderinae and Vianadinae (Golub et al. 2022). Data on follicle and/or ovariole numbers are available for a total of 25 species (12 genera) belonging to the Tinginae (21 species), Cantacaderinae (three), and Vianadinae (one). Within the Cantacaderinae, *Cantacader quadricornis* (Lepeletier &

Serville, 1828) and *C. quinquecostatus* (Fieber, 1844) were shown to have one and two follicles p.t., respectively. In the last of these species, females have ovaries with five ovarioles each, and the same structure of the ovaries is characteristic of *C. lethierryi* Scott, 1874. All studied species of the Tinginae (21 in ten genera) share consistent testis composition, with two follicles p.t. Fourteen species (ten genera) studied in terms of the ovaries have seven ovarioles; however, *Corythucha marmorata* (Uhler, 1878) has five ovarioles p.o. The only studied species from the subfamily Vianaidinae, *Anommatocoris coleopteratus* (Kormilev, 1955), has testes with a “bilobed follicle” each (Drake and Davis 1960). We are inclined to assume that this species actually has two follicles p.t.

Concluding remarks

In studied Cimicomorpha species, males may have 1–9 follicles p.t., and females may have 2–8 ovarioles p.o. Available data for the taxa where there are more data show a stable pattern of the number of follicles at different taxonomic levels. For example, seven follicles p.t. is the modal state in the families Reduviidae and Nabidae, in the tribes Mirini and Stenodemini (Miridae), and in the genus *Cimex* (Cimicidae); two follicles p.t. is the modal state in the family Anthocoridae, the subfamily Orthotylinae (Miridae) and the subfamily Tinginae (Tingidae); one follicle p.t. is the modal state in the tribe Dicyphini (Miridae). Data are scarcer on the ovariole numbers; however, in general, a pattern of seven ovarioles p.o. clearly predominates.

DIPSOCOROMORPHA

The small infraorder Dipsocoromorpha or minute litter bugs comprises ~ 430 species from 70 genera that are classified into six morphologically distinct families (Knyshov et al. 2021). Data on the number of follicles and/or ovarioles are currently available for the families Dipsocoridae, Ceratocombidae, and Schizopteridae.

Ceratocombidae (litter bugs)

This small cosmopolitan family, historically treated as a subfamily of the Dipsocoridae and raised to family level by Štys (1970), comprises eight genera and ~ 50 species in two subfamilies (Slater 1982; Štys 1995b; Henry 2009). In Ceratocombinae, *Ceratocombus* (*Ceratocombus*) *coleopratus* (Zetterstedt, 1819) displays seven follicles p.t., and *C. (Xylonnannus)* sp. has six ovarioles p.o.

Dipsocoridae (jumping ground bugs)

This cosmopolitan family was recently redefined to contain three genera and ca.30 species with many more awaiting descriptions (Schuh and Weirauch 2020). Data on testis and/or ovary structure are available for seven species representing all three genera. In each species studied in genera *Cryptostemma* Herrich-Schaeffer, 1835 (two species),

Alpagut Kıyak, 1995 (one), and *Pachycoleus* Fieber, 1860 (one), males have three follicles p.t. Females have five ovarioles p.o. in three studied *Cryptostemma* species while three ovarioles p.o. in *Pachycoleus pusillimus* (J. Sahlberg, 1870).

Schizopteridae (jumping soil bugs)

This family, which is the largest family of the infraorder, comprises approximately 355 species, 56 genera, and two subfamilies (Wygodzinsky 1955; Weirauch et al. 2018). Data are available for three representatives of the subfamily Hypselosomatinae. Males of *Hypselosoma hickmani* Wygodzinsky, 1959 and *Pateena polymitarior* Hill, 1980 have one follicle p.t., and females of *Hypselosoma* sp. have four ovarioles p.o.

Concluding remarks

In general, data are available for 12 species (seven genera), which is only 2.8% of the global diversity of the infraorder. Males of Dipsocoromorpha may have seven, three or one follicle p.t., the number three being characteristic of Dipsocoridae and the number one for Schizopteridae. Females may have four, five or six ovarioles p.o. It is worth noting the stability of the number of ovarioles in the genus *Cryptostemma* (three p.o.).

ENICOCEPHALOMORPHA

Unique-headed bugs comprise only two small families, Aenictopecheidae (~ 20 described species, 11 genera and four subfamilies) and Enicocephalidae (~ 300 described species, 47 genera and five subfamilies) (Štys 1995a, 2002). Enicocephalomorpha have a checkered history of phylogenetic placement and were considered as a sister group to Dipsocoromorpha (Popov 1971), a sister group to all other Heteroptera (Štys and Kerzhner 1975; Wheeler et al. 1993; Xie et al. 2008), or rendered within a clade uniting Dipsocoromorpha and Gerromorpha (Johnson et al. 2018; Weirauch et al. 2019). Data on the structure of testes for aenictopecheids and enicocephalids are lacking. However, Štys and Baňář (2008) provided a drawing of the fusiform testis in the male of *Xenicocephalus josifovi* Štys & Baňář, 2008 (Enicocephalidae, Enicocephalinae). Although the authors did not study the number of follicles, they described a testis as voluminous, suggesting that it consists of more than a single follicle. In two species of the Enicocephalidae, *Hoplitocoris lewisi* Distant 1903 and *Stenopirates japonicus* (Esaki, 1935) (Enicocephalinae), females have five ovarioles p.o.

GERROMORPHA

This infraorder of predatory, semiaquatic bugs, most of which live on the surface of the water or amongst floating plants, comprises more than 2100 species in 160 genera, eight families and five superfamilies (Polhemus and Polhemus 2008; Damgaard 2012). Data on the number of follicles and/or ovarioles are currently available for five families (not available for three very small families Hermatobatidae, Macroveliidae, and Paraphrynoveliidae).

Gerridae (water striders)

The family comprises at least 750 species and 71 genera in eight subfamilies and represents the second largest group of the infraorder in numbers of genera and species after the Veliidae (Schuh and Weirauch 2020). Data are available for the subfamilies Gerrinae (eight species, three genera), Halobatinae (six species, four genera), Hermatobatinae (one species), Ptilomerinae (one species), Rhagadotarsinae (two species, two genera), and Rheumatobatinae (one species). The number of follicles p.t. is two in all species of the Gerrinae, while males of *Rheumatobates crassifemur crassifemur* Esaki, 1926 (Rheumatobatinae) have one follicle p.t. Available data on the number of ovarioles demonstrate a highly stable pattern of four for all taxa (15 species, ten genera, five subfamilies without Rheumatobatinae for which there is no information).

Hebridae (velvet water bugs)

The family comprises 220 species and eight genera in two subfamilies (Andersen 1982; Schuh and Weirauch 2020). Data are available for the subfamily Hebrinae only, in which both studied species, *Hebrus* (*Hebrusella*) *ruficeps* Thomson, 1871 and *H. (Hebrus) pusillus* (Fallén, 1807), have two follicles p.t. These species and additionally *H. (Hebrus) nipponicus* Horváth, 1929 have five ovarioles p.o.

Hydrometridae (water measurers)

The family comprises at least 126 species and seven genera in three subfamilies (Andersen 1982). According to Pendergrast (1956), males of *Hydrometra stagnorum* (Linnaeus, 1758) (Hydrometrinae) have long and fusiform testes, each with supposedly one follicle. Females have seven ovarioles p.o. in each of the four studied species of the genus *Hydrometra* Latreille, 1797.

Mesoveliidae (pond treaders)

The family comprises ~ 50 species and 12 genera in two subfamilies and is considered a sister group to all other families of the infraorder (Schuh and Weirauch 2020). In the subfamily Mesoveliinae, *Mesovelia furcata* Mulsant & Rey, 1852 has one follicle p.t. and seven ovarioles p.o. Two more species of this genus were reported to have the same structure of the ovaries.

Veliidae (riffle bugs)

The family comprises more than 970 species and 60 genera in six subfamilies and thus represents the largest family of the infraorder (Andersen 1982). Data are available for the subfamilies Haloveliinae (two species, two genera), Microveliinae (eight species, three genera), Rhagoveliinae (two species, two genera), and Veliinae (two species, two

genera). All four riffle bug species studied in relation to the structure of the testes, two in the genus *Rhagovelia* Mayr, 1865 (Rhagoveliinae) and two others in the genus *Velia* Latreille, 1804 (Veliinae), have one follicle p.t. The number of ovarioles is also stable and equal to four in all studied species of the Microveliinae and in *Strongylovelia formosa* Esaki, 1924 from the Haloveliinae, although another species of this subfamily, *Halovelia septentrionalis* Esaki, 1924, has two ovarioles p.o.

Concluding remarks

In 43 studied species (in 21 genera) of the infraorder Gerromorpha, males may have one or two follicles p.t., and females may have two, four, five, or seven ovarioles p.o. Available data for the taxa in which more data is available demonstrate a stable pattern of the follicle number (e.g., two in Gerridae and one in Veliidae) or of the ovariole number (e.g., four in Gerridae and Veliidae, and seven in Hydrometridae).

LEPTOPODOMORPHA

The infraorder (shore bugs) comprises ca. 380 species in 42 genera and four extant families, including two larger Saldidae and Leptopodidae, both of worldwide distribution, and two rare and highly endemic families, the Omaniidae with four species in two genera, and monotypic Aepophilidae (Schuh and Polhemus 1980; Schuh et al. 1987; Schuh and Slater 1995; Polhemus and Polhemus 2012; Larivière and Laroche 2019).

Aepophilidae (marine bugs)

This enigmatic taxon encompasses a single species, *Aepophilus bonnairei* Signoret, 1879 that has seven follicles p.t. in males.

Saldidae (shore bugs)

The family comprises ~ 335 species in 29 genera. Two studied species of the genus *Saldula* Van Duzee, 1914, *S. arenicola* (Scholtz, 1847) and *S. saltatoria* (Linnaeus, 1758), have seven follicles p.t., whereas *Halosalda lateralis* (Fallén, 1807) has four follicles p.t. Seven ovarioles p.o. were found in *Macrosaldula scotica* (Curtis, 1833) and *Saldula arenicola* (Scholtz, 1847).

Concluding remarks

In five studied species of Leptopodomorpha (four genera, two families), males have seven or four follicles p.t. in four and one species, respectively. Note that the first number occurs in both explored families, and the same number of ovarioles p.o. is found in females of two studied species in two genera of shore bugs.

NEPOMORPHA

The infraorder Nepomorpha or water bugs is one of the most specialized groups of heteropterans, with most of its species spending the entire life cycle within the water. It comprises more than 2300 species arranged in 140 genera and 13 families (Polhemus and Polhemus 2008; Ribeiro et al. 2018; Ye et al. 2019). Data on the number of follicles and/or ovarioles are currently available for all but two (Diaprepocoridae and Potamocoridae) families.

Aphelocheiridae (benthic water bugs)

The family comprises at least 78 species in the only genus *Aphelocheirus* Westwood, 1833 (Polhemus and Polhemus 2008). In *A. aestivalis* (Fabricius, 1794), males have four follicles p.t. and five ovarioles p.o., and the same structure of the ovaries was found in three more species of the genus.

Belostomatidae (giant water bugs)

The family comprises ca. 160 species and 11 genera in three subfamilies (Perez-Goodwyn 2006). Presently, data on testis and/or ovary structure are available for eight species in four genera of the subfamily Belostomatinae (*Belostoma* Latreille 1807, *Diplonychus* Laporte, 1833, *Appasus* Amyot & Serville, 1843, and *Adebus* Stål, 1862), and three species of the subfamily Lethocerinae (genus *Lethocerus* Mayr, 1853). All five studied *Belostoma* species have five follicles p.t., whereas the only studied *Diplonychus* species, *D. rusticus* (Fabricius, 1781), has seven follicles p.t. In *Lethocerus indicus* (Lepeletier & Serville, 1825), testes consist of five follicles each, and in *L. patruelis* (Stål, 1854), the number of follicles p.t. is questionable (five or four). Females of the four studied species in the genera *Belostoma* (one species), *Diplonychus* (one), *Adebus* (one), and *Lethocerus* (one) have five ovarioles p.o.

Corixidae (water boatmen)

The family comprises 607 species and 35 genera in four subfamilies (Polhemus and Polhemus 2008; Schuh and Weirauch 2020). Data on testis and/or ovary structure are available for seven species of the subfamily Corixinae and the only representative of the subfamily Cymatinae, *Cymatia coleoptrata* (Fabricius, 1777). All studied Corixinae species from the genera *Sigara* Fabricius, 1775 (two species), *Cenocorixa* Hungerford, 1948 (one) and *Corixa* Geoffroy, 1762 (one) have seven follicles p.t., whereas male *C. coleoptrata* has five follicles p.t. The ovaries in all studied species (eight species, five genera, both subfamilies) consist of seven ovarioles each.

Gelastocoridae (toad bugs)

The family comprises at least 111 species and three genera from two subfamilies and belong to the secondarily terrestrial superfamily Ochteroidea (Hebsgaard et al. 2004).

Data are available for four species. Two species in the genus *Gelastocoris* Kirkaldy, 1897 (Gelastocorinae) have two follicles p.t., and the same testis structure is typical for *Nerthra terrestris* (Kevan, 1948) from the subfamily Nerthrinae. Females of *Nerthra macrothorax* (Montrouzier, 1855) have five ovarioles p.o.

Helotrephidae (backswimmers)

The family comprises more than 170 species (Papáček and Zettel 2005) and is considered as a sister group to the Pleidae (Chen et al. 2005). *Helotrephes formosanus* Esaki & Miyamoto, 1943, the only explored species of the family, has four ovarioles p.o., that is the same number that have females in the Pleidae (see below).

Micronectidae (pygmy boatmen)

The family comprises 150 species and five genera in two subfamilies (Polhemus and Polhemus 2008; Schuh and Weirauch 2020). Data are available for three species of *Micronecta* Kirkaldy, 1897 (Micronectinae), in which males were reported to have two follicles p.t.

Naucoridae (creeping water bugs)

The family comprises ~ 420 species and 43 genera in six subfamilies (Sites 2022). All three species studied in the genera *Limnocoris* Stål, 1860 (Limnocorinae), *Pelocoris* Stål, 1876, and *Ilyocoris* Stål, 1861 (Naucorinae) have seven follicles p.t. Various authors reported different numbers of ovarioles (seven or five) p.o. for *Ilyocoris cimicoides* (Linnaeus, 1758).

Nepidae (water scorpions)

The family comprises 268 species and 15 genera from two subfamilies (Polhemus and Polhemus 2008; Schuh and Weirauch 2020). Data on the follicle number are available for three species in two genera, *Ranatra* Fabricius, 1790 (Ranatrinae) and *Nepa* Linnaeus, 1758 (Nepinae). *Nepa cinerea* Linnaeus, 1758 have five follicles p.t., whereas males of *R. fusca* Palisot de Beauvois, 1820 and *R. linearis* (Linnaeus, 1758) have six and five follicles p.t., respectively. Among seven species with known structure of ovaries, all four *Ranatra* spp. share five ovarioles p.o., whereas two species of the genus *Laccotrephes* Stål, 1866 (Nepinae), *L. japonensis* Scott, 1874 and *L. maculatus* (Fabricius, 1775), have five and four ovarioles p.o., respectively.

Notonectidae (backswimmers)

The family comprises ~ 400 species and 11 genera in two subfamilies, Notonectinae and Anisopinae (Polhemus and Polhemus 2008; Schuh and Weirauch 2020). Data are available for four species only. In Notonectinae, *Notonecta glauca* Linnaeus, 1758 and

N. maculata Fabricius, 1794 have seven follicles p.t., whereas *Martarega bentoi* Truxal, 1949, the only studied species in the Anisopinae, has two follicles p.t. Ovaries (examined in three species of *Notonecta* Linnaeus, 1758) consist of seven ovarioles each.

Ochteridae (velvety shore bugs)

The family comprises at least 68 species and belongs to the lineage of the aquatic Nepomorpha, which returned to a terrestrial way of life. Most authors consider Ochteridae as a sister group to the Gelastocoridae (e.g., Hebsgaard et al. 2004; Hua et al. 2009). The only examined species of the family, *Ochterus marginatus marginatus* (Latreille, 1804), shares two follicles p.t. with studied gelastocorids (see above), but has seven ovarioles p.o.

Pleidae (pygmy backswimmers)

The family comprises ~ 40 species in three genera (Polhemus and Polhemus 2008; Schuh and Weirauch 2020). Males of *Plea minutissima* Leach, 1817 have four follicles p.t., and females have four ovarioles p.o. The same structure of the ovaries is characteristic of *Paraplea indistinguenda* (Matsumura, 1905) and *P. japonica* (Horváth, 1904).

Concluding remarks

In studied Nepomorpha species, males may have testes with different numbers of follicles (two to seven, except three), and females have ovaries with different numbers of ovarioles (four, five or seven). The numbers seven, five and two are most common, being found in 32%, 29% and 26% of studied species, respectively. In females, ovaries with five and seven ovarioles occur in 52% and 45% of studied species, respectively. Available data for relatively more fully studied taxa show a stable pattern of the follicle number at the generic level, e.g., five in *Belostoma* and two in *Micronecta* Kirkaldy, 1897, as well as at the subfamily level (seven in Corixinae), and it seems also at the family level (two in Gelastocoridae and Micronectidae). The ovariole numbers appear to show a stable pattern in some families (seven in Corixidae and Notonectidae, five in Aphelocheiridae, and four in Pleidae). However, only 50 species (in 25 genera) have been studied in the infraorder in general, i.e., ~ 2% of the global diversity of the group, which is, of course, too small to draw any conclusions.

PENTATOMOMORPHA

With nearly 15 000 extant species, this worldwide distributed group is the second largest infraorder of true bugs, with 40 currently recognized families arranged in six superfamilies viz., Aradoidea, Idiostoloidea, Coreoidea, Lygaeoidea, Pyrrhocoroidea, and Pentatomoidea (Weirauch et al. 2019; Schuh and Weirauch 2020). The majority

of pentatomorphan insects are terrestrial and phytophagous, but some of them are predaceous (Schuh and Slater 1995; Weirauch and Schuh 2011; Liu et al. 2019). Data on the number of follicles and/or ovarioles are currently available for 433 species (2.4%), 274 genera and 28 families (70%) in all superfamilies except Idiostoloidea, a small and poorly studied group containing six species only.

ARADOIDEA

Aradidae (flat bugs)

The family comprises approximately 1900 species, more than 230 genera, and eight subfamilies (Heiss 2001). Data on the number of follicles and/or ovarioles are available for 41 species, 17 genera and six subfamilies (unavailable for Isoderminae and Chinamyersiinae).

Prosypniestinae. In two studied species of the genus *Prosypniestus* Bergroth, 1894, males have six follicles p.t. and females have six ovarioles p.o.

Carventinae. Data are available for the genera *Carventus* Stål, 1865 (two species), *Euricoris* Kormilev, 1957 (two species), and *Paracarventus* Kormilev, 1964 (one species). Both testes and ovaries have the same range of numbers, three, four, or five, in each case the numbers of follicles and ovarioles coinciding in the same species.

Calisiinae. In *Calisius hackeri* Kormilev, 1958, males have two follicles p.t. and females have six ovarioles p.o.

Aneurinae. Data are available for the genera *Aneurus* Curtis, 1825 (six species) and *Paraneurus* Jacobs 1986 (one species). Both genera are characterized by a stable pattern of five follicles p.t. and five ovarioles p.o., with the only exception of *A. (Aneurus) laevis* (Fabricius, 1775) having six follicles p.t. For *Aneurus (Aneurodes) avenius* (Dufour, 1833) four and five ovarioles are reported by different authors.

COREOIDEA

Coreidae (leaf-footed bugs)

The family comprises more than 2570 extant species described in four subfamilies and 37 tribes (Coreoidea SF Team 2019). Data are available for the subfamilies Coreinae and Pseudophloeinae. The first is distinguished by the high stability of the structure of the testes and ovaries having seven follicles p.t. in all 16 studied species in 14 genera and the same number of ovarioles p.o. in all 16 studied species in nine genera. In the second subfamily, *Coriomeris hirticornis* (Fabricius, 1794) also has seven ovarioles p.o., although *Ceraleptus lividus* Stein, 1858 has six follicles p.t.

Rhopalidae (scentless plant bugs)

The family comprises more than 200 species in 30 genera and two subfamilies, the Rhopalinae and the Serinethinae (Schuh and Weirauch 2020). Data are available for 11 species and seven genera of both subfamilies. A testis may consist of four, five, or seven follicles, but the number of seven prevails (found in seven species, six genera, both subfamilies).

Stenocephalidae (spurgebugs)

In the sole genus of the family, *Dicranocephalus* Hope, 1831, one species has seven follicles p.t. and seven ovarioles p.o. (*D. agilis* (Scopoli, 1763)), whereas another species (*D. albipes* (Fabricius, 1781)) has five follicles p.t.

LYGAEOIDEA

Artheneidae

This group contains slightly more than 20 species arranged in seven genera and three subfamilies, with most species belonging to Artheneinae, while Dilompinae and Nothochrominae remain monotypic (Henry 1997a; Schuh and Weirauch 2020). The reproductive system was studied in seven species belonging to three genera or one-third of the described diversity of Artheneinae. A uniform pattern of two follicles p.t. and seven ovarioles p.o. was revealed in all cases.

Berytidae (stilt bugs)

This worldwide family comprises ~ 37 genera and 174 species in three subfamilies (Henry 1997b, c; Henry et al. 2015). Data are available for ~ 19% and 8% of genera and species, respectively, belonging to all subfamilies, Berytinae (seven species, three genera), Gampsocorinae (three species, one genus), and Metacanthinae (four species, three genera). There is one follicle p.t. in the two latter subfamilies and two, but sometimes one, in the Berytinae. The number of ovarioles is seven p.o. in all but one species studied. These species represent all three subfamilies and the only exception is *Gampsocoris viridiventris* (Matsumura, 1907) (Gampsocorinae), which has six ovarioles p.o. although another species of the same genus, *G. culicinus* Seidenstücker, 1948, has seven.

Blissidae

This family of strongly flattened and sap sucking lygeoids has a worldwide distribution and currently contains more than 400 species belonging to ca. 50 genera (Schuh and Weirauch 2020). No suprageneric classification was ever proposed for this group,

and the reproductive system was studied in 14 species from six genera. Of these, the most frequent number of follicles p.t. equals six, documented in all studied *Blissus* Burmeister, 1835 spp., *Macropes raja* Distant, 1909 and *Iphicrates spinicaput* (Scott, 1874). However, seven follicles p.t. were also frequently observed across some studied taxa, e.g., *Ischnodemus* spp., *Macropes obnubilus* (Distant, 1883), *Iphicrates spathus* Slater, 1961, and *Heinsius explicatus* Distant, 1901, and four follicles were documented for *Cavelerius saccharivorus* (Okajima, 1922). The number of ovarioles is either seven or six and appears to correspond to the number of follicles in males of a given species. *Cavelerius saccharivorus* (Okajima, 1922) forms the only exception, having six ovarioles but four follicles.

Cymidae

This group contains at least 64 species in ten genera classified into two subfamilies, Cyminae and Ontiscinae (Schuh and Weirauch 2020). Despite easy accessibility for specimen collecting, data on the male reproductive system are scarce. Two species of the genus *Ontiscus* Stål, 1874 were studied so far and possess both seven follicles p.t. Seven ovarioles p.o. were documented for three species from both subfamilies, and five ovarioles p.o. were registered in *Cymus aurescens* Distant, 1883.

Geocoridae (big-eyed bugs)

This family comprises 27 genera and ~ 280 species in five subfamilies (Henry et al. 2015). In the genus *Geocoris* Fallén, 1814 (Geocorinae), males have four follicles p.t. (five species) and females have seven ovarioles p.o. (two species). Males of *Henestaris halophilus* (Burmeister, 1835) (Henestarinae) have seven follicles p.t. and females have seven ovarioles p.o.

Heterogastridae

This small family currently consists of 23 genera and at least 105 species (Schuh and Weirauch 2020), four of which were studied in regard to the structure of the testes and ovaries. All three studied species of the genus *Heterogaster* Schilling, 1829 and *Platyplax salviae* (Schilling, 1829) have seven follicles p.t., and females of two studied *Heterogaster* spp. have seven ovarioles p.o.

Lygaeidae (seed bugs)

The family comprises 107 genera and more than 970 species in three subfamilies (Henry et al. 2015). Data are available for 16 species and six genera of the subfamilies Ischnorhynchinae (two species, two genera), Lygaeinae (nine species, five genera), and Orsillinae (seven species, three genera). Except for *Paranysius fraterculus* (Burmeister, 1835) (Orsillinae) having two follicles p.t., the number of follicles and ovarioles in seed bugs equals seven (p.t. and p.o., respectively).

Malcidae

The family comprises more than 40 described species and three genera in two subfamilies (Schuh and Weirauch 2020). In the only studied species, *Chauliops fallax* Scott, 1874 (Chaulipinae), females have five ovarioles p.o.

Ninidae

Five genera and 14 species are recognized in this small pantropical group (Schuh and Weirauch 2020). Among the two species studied, males of *Ninomimus flavipes* (Matsumura, 1913) have five follicles p.t., and the females of *Ninus insignis* Stål, 1860 have five ovarioles p.o.

Oxycarenidae

This worldwide distributed family contains slightly less than 150 species from 27 genera not arranged into subfamilies or tribes (Schuh and Weirauch 2020). All studied species have two follicles p.t. (eight species from six genera) and seven ovarioles p.o. (four species from four genera).

Pachygronthidae

With more than 80 species arranged in 14 genera, this predominantly tropical and subtropical taxon clusters into two subfamilies, Pachygrontinae and Teracriinae (Slater 1955). Available data on the morphology of the reproductive system are scarce, with four (two species) and seven (one species) follicles p.t. documented for Teracriinae. Female reproductive system has only been studied in four *Pachygrontha* spp. (Pachygronthinae) resulting in seven ovarioles p.o. in each case.

Piesmatidae

This small but nonetheless worldwide distributed group contains less than 50 species arranged in six genera and two morphologically and ecologically distinct subfamilies, Piesmatinae and Psamminae (Henry 1997a; Schuh and Weirauch 2020). While the reproductive system of Psamminae has never been studied, all six species from two genera of the subfamily Piesmatinae were shown to have two follicles p.t. The ovaries have been studied in only one species, *Parapiesma quadratum* (Fieber, 1844), that has been observed to have four or six ovarioles p.o.

Rhyparochromidae (dirt-colored seed bugs)

The family comprises more than 2000 species in two subfamilies, Plinthisinae and Rhyparochrominae, the latter with 14 tribes (Henry 1997a). Data are available for 40

species and 29 genera of the Rhyparochrominae (six tribes). The number of ovarioles p.o. is seven in all studied species, whereas the number of follicles p.t. is either two (in Anthillocorini and Drymini), three or five (in different genera of Myodochini), or seven (in the single species of Myodochini, and in all studied species of Udeocorini and Rhyparochromini), seven clearly prevailing in the family.

PENTATOMOIDEA

Acanthosomatidae

The family comprises more than 50 genera and more than 280 species in three subfamilies (Schuh and Slater 1995; Henry 2009; Schuh and Weirauch 2020). Data on the testis and ovary structure are available for 15 species within five genera of the subfamily Acanthosomatinae. The number of follicles may be seven (three species, three genera), four (one species) or six (one species), and both last numbers occur in the genus *Rhopalimorpha* Dallas, 1851 (*Rh. lineolaris* Pendergrast, 1950 and *Rh. obscura* Dallas, 1851, respectively). The number of ovarioles is seven in the majority (seven) of species. The genus *Elasmucha* Stål, 1864 is of interest showing seven ovarioles in *E. graminea* (Distant, 1883) while unusually high numbers, 17 and even 24, in five other species.

Cydnidae (burrowing bugs)

The family comprises more than 1180 species in ca. 145 genera worldwide, arranged in nine subfamilies (Henry 2009). Data are available for the subfamilies Cephalosteinae, Cydninae, Parastrachiinae, Sehirinae, and Thyreocorinae. In all species studied in the subfamilies Cydninae (two species, two genera) and Sehirinae (two species, two genera), testes consist each of seven follicles. Fourteen species (13 genera, five subfamilies) were studied with respect to the ovaries, and twelve of them have seven ovarioles p.o.; however, *Stibaropus* sp. (Cephalosteinae) and *Chilocoris confusus* Horváth, 1919 (Cydninae) have four and five ovarioles p.o., respectively.

Dinidoridae

The family comprises ~ 100 species in 16 genera and two subfamilies (see Lis et al. 2012 for references). The testis and ovary of *Coridius janus* (Fabricius, 1775) (Dinidorinae) consist of seven follicles and seven ovarioles, respectively, and the same structure of the ovaries is found in *Megynemum gracilicorne* Dallas, 1851 (Megyneminae).

Pentatomidae (stink bugs)

This third largest true bug family comprises almost 5 000 species in ca. 940 genera distributed in nine subfamilies including Asopinae, Cyrtocorinae, Discocephali-

nae, Edessinae, Pentatominae, Phyllocephalinae, Podopinae, Serbaninae, and Stiro-tarsinae (Rider 2006; Rider et al. 2018; Schuh and Weirauch 2020). Data on the testes and ovaries are available for all subfamilies, except Cyrtocorinae, Serbaninae, and Stiro-tarsinae. In total, the testis structure was studied in males of 88 species of 63 genera and five subfamilies (there is no data for Phyllocephalinae), and the structure of ovaries is studied in females of 57 species in 41 genera (Pentatominae, Asopinae, Podopinae, and Phyllocephalinae). The number of follicles varies from three to eight, but seven follicles appear to be the most frequent state being found in each subfamily and in most studied species and genera. The observed numbers of ovarioles were three, four, six, or seven and, like in the case of the number of follicles, seven ovarioles p.o. is the most common pattern found in more than two thirds of species and genera studied in this regard (43 species, 36 genera, all four subfamilies). Other numbers were observed in 14 species only. Nine of these species belong to the genera *Eysarcoris* Hahn, 1834 and *Eurydema* Laporte de Castelnau, 1833 (Pentatominae, Eysarcorini, and Strachiini respectively), for which the characteristic number is six. For some species, different authors reported different numbers for the same species, for example, six and seven for *Eysarcoris ventralis* (Westwood, 1837) and *Nezara viridula* (Linnaeus, 1758). In *Bagrada* (*Bagrada*) *hilaris* (Burmeister, 1835), different numbers of ovarioles were observed in different ovaries of the same specimen.

Pentatomids are remarkable in that their testes may possess a so-called “harlequin” lobe, in which meiosis is aberrant leading to the production of spermatids carrying numerically unbalanced chromosome complement with an abnormal and highly variable chromosome number (Schrader 1960a). Speculation on the evolutionary aspects of the harlequin lobe can be found in Schrader (1960b). To date, this specific follicle has been found mostly in the subfamilies Discocephalinae, Edessinae, and Pentatominae (Rebagliati et al. 2005).

Plataspidae

The family comprises ~ 530 species in 56 genera (Jessop 1983). The only species studied with respect to the testes, *Coptosoma* sp., has seven follicles p.t., and five species studied with respect to the ovaries have seven (three species, two genera) and six (two species, two genera) ovarioles p.o.

Scutelleridae (jewel bugs)

The family comprises ~ 80 genera and 500 described species worldwide (Tsai et al. 2011). Data are available for 11 species in nine genera of the subfamilies Odontotarsinae (three species, two genera), Pachycorinae (one species), and Scutellerinae (seven species, six genera). All species have seven follicles p.t. (six species studied) and seven ovarioles p.o. (six species studied).

Tessaratomidae

The family comprises three subfamilies, 49 genera and ~ 235 species worldwide (Rolston et al. 1993). The only studied species, *Cyclogastridea nigromarginalis* Reuter, 1884 (Natalicolinae), has seven follicles p.t. and seven ovarioles p.o.

Urostylididae

The family comprises four genera and ca. 80 species (Rider et al. 2018). No data on the male reproductive system are available at the moment. In three species of the genus *Urostylis* Westwood, 1837 and in *Urochela luteovaria* Distant, 1881, females have seven ovarioles p.o.

PYRROCOROIDEA

Largidae (bordered plant bugs)

The family comprises ~ 200 species in two subfamilies worldwide. In the subfamily Physopeltinae, *Physopelta gutta* (Burmeister, 1834) has seven follicles p.t. and seven ovarioles p.o.

Pyrrhocoridae (cotton stainers)

The family comprises more than 300 species worldwide in at least 30 genera and two subfamilies. Data are available for 11 species in four genera of the subfamily Pyrrhocorinae; all examined species have seven follicles p.t. and seven ovarioles p.o. The only exception is *Dysdercus* (*Paradysdercus*) *koenigii* (Fabricius, 1775) with a variable number of 5–7 follicles p.t.

Concluding remarks

In Pentatomomorpha species studied, males may have 3–8 follicles p.t., and females 3–7 ovarioles p.o., except the genus *Elasmucha* (Acanthosomatidae) in which a unique diversity (7–24 ovarioles p.o.) has been reported for the five studied species. The number seven is characteristic for some higher taxa studied in relation to the structure of the testes and ovaries (among the better studied families, these are Coreidae, Cydnidae, Lygaeidae, and Pentatomidae). The exception is the family Aradidae for which this number seems to not be characteristic of either the ovaries or the testes, with seven being only reported for the ovaries of *Aradus* (*Aradus*) *pictus* Baerensprung, 1859. In some families (e.g., Artheneidae, Oxycarenidae, Berytidae), the number seven is typical for the ovaries but not for the testes, which consist either of two follicles (in the first two families) or of one follicle (in the third family).

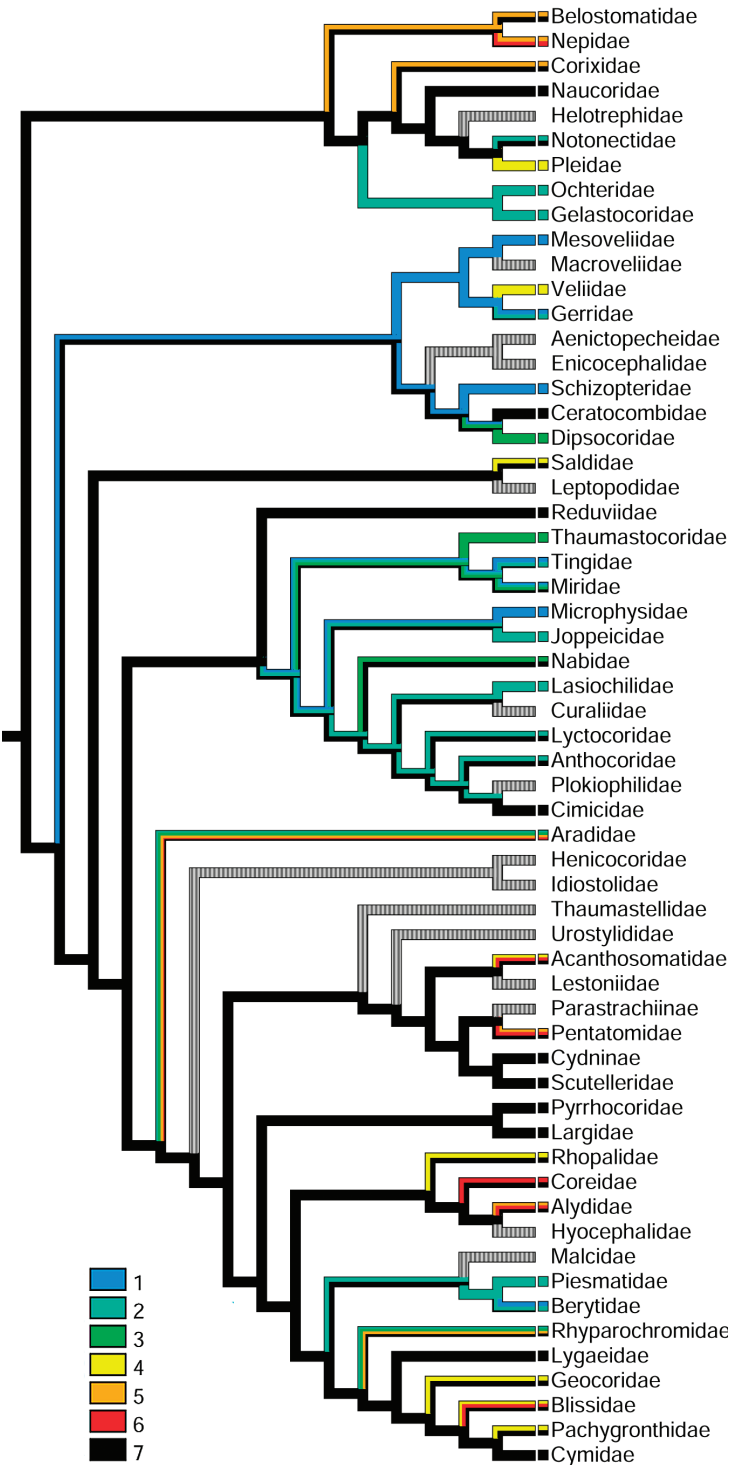


Figure 2. Testicular follicle numbers mapped on the true bug phylogeny after Weirauch et al. (2019).

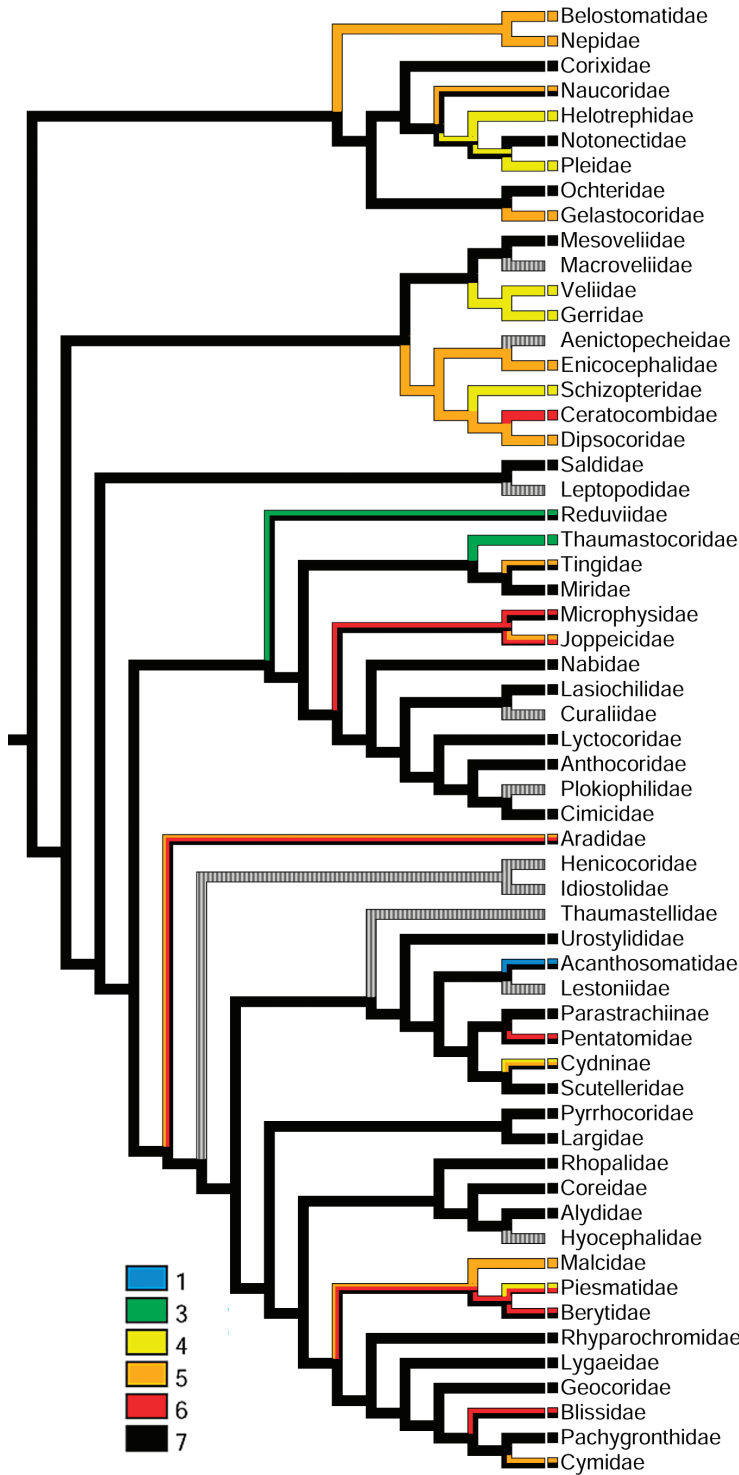


Figure 3. Oviole numbers mapped on the true bug phylogeny after Weirauch et al. (2019).

Conclusions

In this study, we analyzed the number of follicles in testes of 705 species (420 genera, 58 families) and the number of ovarioles in ovaries of 504 species (334 genera, 61 families) across all seven major lineages of the suborder Heteroptera (Figs 2, 3, Suppl. material 1). Our comprehensive review showed that the gonads in true bugs are paired organs, and the testis and the ovary may consist of a variable number of follicles and ovarioles ranging from one to nine and from one to eight (while occasionally even to 24 in some Acanthosomatidae) respectively. Approximately 40% of species have seven follicles p.t. and ~ 68% of species have seven ovarioles p.o. Numbers exceeding this modal value are rare; the exception is eight follicles in the genus *Deraeocoris* Kirschbaum, 1855 (Miridae), in which almost half of the studied species have this number. Lower numbers, on the other hand, are quite common; moreover, sometimes they characterize taxa of high rank. In the families Miridae, Pentatomidae, and Reduviidae, for which there is relatively much data, a variety of numbers is observed. It is most pronounced in the Miridae in which data on testes and ovaries are available for 220 and 48 species, respectively. Although the number of ovarioles in most mirid species is seven, the number of follicles varies widely, from one to eight (except five), the number seven and lower numbers (1–3) occurring with almost equal frequency. Some other families, e.g., Anthoridae, Aradidae, Belostomatidae, Berytidae, Gerridae, Oxycarenidae, and Tingidae, usually have low numbers of follicles. Noteworthy is also the family Aradidae, in which ovarioles vary in number, with numbers below the modal predominating. However, there is still very little data for all these families.

Ancestral reconstruction of testes suggests seven follicles p.t. as an ancestral state for true bugs (Fig. 2). This number was also recovered for the common ancestors of Pentatomomorpha and all its superfamilies except Aradoidea, Cimicomorpha, Leptopodomorpha, and Nepomorpha. This is consistent with the fact that seven follicles p.t. were documented in the majority of studied species across Heteroptera (Suppl. material 1; Akingbohunge 1983). However, the common ancestor of Gerromorpha appears to have a testis with one follicle, while the parsimony reconstruction for Enicocephalomorpha and Dipsocoromorpha indicates equal probability of one or seven follicles as an ancestral state. This variation in ancestral traits is noteworthy, given the ongoing debates on the backbone phylogeny of the Heteroptera, implying Enicocephalomorpha (Wheeler et al. 1993; Xie et al. 2008), Enicocephalomorpha + Dipsocoromorpha (Wang et al. 2016), or these two infraorders + Gerromorpha (Johnson et al. 2018) as a sister group to the remaining infraorders, or Panheteroptera. In all studied species of Peloridiidae (Coleorrhyncha), which is usually considered as a sister group to Heteroptera both on morphological (Schlee 1969; Grimaldi and Engel 2005), molecular (Xie et al. 2008; Cryan and Urban 2012), and cytogenetic (Kuznetsova et al. 2015) grounds, testes also consist of a single follicle (Grozova et al. 2014).

Reconstruction of an ancestral state for ovaries (Fig. 3) indicates a similar, but more straightforward, result, giving seven ovarioles p.o. for the entire clade, Pentatomomorpha (and all recognized superfamilies except Aradoidea), Cimicomorpha (and all included superfamilies except Microphysoidea and Reduvioidea), Leptopodomorpha, Gerromor-

pha, and Nepomorpha. The infraorders Enicocephalomorpha and Dipsocorimorpha form an exception, with five ovarioles p.o. recovered for each of them as an ancestral state.

Summing up, the number of seven appears to be an ancestral state for both testes and ovaries of true bugs. It is still retained in many lineages but may increase or decrease in separate groups. The trend towards decreasing the number of follicles and ovarioles undoubtedly prevailed in the evolution of the suborder Heteroptera in general.

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Supplementary material I

An updated list of testicular follicles' and ovarioles' numbers in Heteroptera

Authors: Snezana Grozeva, Desislava Stoianova, Fedor Konstantinov, Nikolay Simov, Valentina G. Kuznetsova

Data type: Morphological data

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New records of Curculionoidea from Newfoundland and Labrador, with the first records of *Orthochaetes setiger* ([Beck]) (Curculionidae, Curculioninae, Styphlini) for North America

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Abstract

Thirty species of Curculionoidea (28 Curculionidae and one each of Brentidae and Nemomychidae) are reported as new records from the Canadian province of Newfoundland and Labrador, most of them from the island of Newfoundland. As well, 13 species of Curculionidae and one of Brentidae previously recorded from Newfoundland are newly reported from Labrador, and one Curculionidae previously recorded from Labrador is newly reported from Newfoundland. The Palearctic species, *Orthochaetes setiger* ([Beck]), is herein reported as a new Canadian and North American record, with specimens documented from Newfoundland and British Columbia. Additions to the primary key for North American weevils are provided to help identify this genus among the North American fauna. Of the species of Curculionoidea previously recorded from the province in published literature, there is uncertain evidence for the occurrence of 14 species in the province as a whole or in the Labrador portion. Seven species are hereby removed from the faunal list for the province. One of those, *Trachodes hispidus* (Linnaeus), is also removed from the Canadian faunal list. The 134 species of Curculionoidea recorded from NL are listed and a brief synopsis of the fauna provided.

Keywords

Adventive species, distribution, faunistics, identification key, species list, weevil

Introduction

The Curculionidae comprise the largest beetle family in Canada with 839 recorded species (Bousquet et al. 2013; Webster et al. 2016; de Tonnancour et al. 2017; Pentinsaari et al. 2019; Franklin et al. 2021; Thurston et al. 2022). Together the Curculionidae and the related families Anthribidae (22 spp. in Canada), Attelabidae (14), Brachyceridae (18), Brentidae (48), Nemonychidae (8), and Dryophthoridae (27) constitute the superfamily Curculionoidea, commonly known as weevils. Of the 976 species of Curculionoidea in Canada, 111 species (11.4% of the Canadian fauna) have been reported in the province of Newfoundland and Labrador (NL), including 105 species on the island of Newfoundland (NF) and 18 species in Labrador (LB) (Bousquet et al. 2013). Thus, NL is relatively depauperate, and this is attributed to the entire province being glaciated during the Wisconsinan glaciation, that LB is further north and therefore not conducive to high biodiversity, and that NF is separated from the mainland by more than 162 km of ocean. The province's fauna has also not been particularly well sampled, especially that portion in LB; thus, it is unsurprising that many new records of weevils have been discovered in the province subsequent to publication of the 2013 Canadian beetle checklist (Bousquet et al. 2013). Herein we report on 45 species newly documented from either NF, LB, or the province as a whole. One of these species, *Orthochaetes setiger* ([Beck]), is newly recorded from North America, including Canada, with records from NF and British Columbia.

Materials and methods

New records are based on specimens in the six institutional collections with the largest known holdings of NL specimens. Some species identities were verified with DNA barcode data in the Barcode of Life Datasystems (BOLD) database (boldsystems.org), and the 'Sample ID' numbers for barcoded specimens are included under "Specimens examined" for relevant species. More than 6400 specimens were examined and their identity verified, and these represent more than 4000 collection events. A collection event is a unique combination of locality and date where one or more specimens were collected, labelled, and deposited in a public repository. Provincial species records based only on reports in catalogues, e.g., Bousquet et al. (2013), with no accompanying label information and repository of specimens, were given special consideration. For species present in the Maritime provinces of Canada, and for which NL provides suitable host species and climate, the records were retained for now as there seems to be a high likelihood they are valid. Other species were removed from the provincial list. The Curculionoidea classification system used herein follows that of Alonso-Zarazaga et al. (2017). World Flora Online (www.worldfloraonline.org) was used to confirm spellings and authorities for plant species.

Specimen repositories and institutional acronyms

- AAFC** Agriculture and Agri-Food Canada collection, St. John's, Newfoundland and Labrador, Canada;
- CBG** Centre for Biodiversity Genomics, University of Guelph, Guelph, Ontario, Canada;
- CFS** Canadian Forest Service, Atlantic Forestry Centre, Corner Brook, Newfoundland and Labrador, Canada;
- CMNC** Canadian Museum of Nature, Gatineau, Quebec, Canada;
- CNC** Canadian National Collection of Insects, Arachnids and Nematodes, Agriculture and Agri-Food Canada, Ottawa, Ontario, Canada;
- DLC** David Langor Collection of NL Insects, Canadian Forest Service, Edmonton, Alberta, Canada [Note: This collection consists of all the insect material from the former Memorial University of Newfoundland (MUN) Collection. The MUN collection was shipped to David Langor for safe keeping when the last curator (David Larson) retired in 2005 as the institution no longer wished to retain the collection. It is hoped that the collection will be returned to NL in the near future, but a new home has not yet been secured.];
- NFRC** Canadian Forest Service, Northern Forestry Centre, Edmonton, Alberta, Canada;
- RBCM** Royal British Columbia Museum, 675 Belleville St., Victoria, British Columbia, V8W 9W2, Canada.

Results

BRENTIDAE

Apioninae: Apionini

Betulapion simile walshii (J.B. Smith, 1884)

This Holarctic species is represented across the Palearctic as the nominotypical subspecies, and in Canada and the USA by *B. simile walshii*. In Canada, it has been reported from British Columbia to NF (Bousquet et al. 2013). Throughout its range the species feeds on catkins of various *Betula* spp. (Betulaceae), primarily *B. papyrifera* Marsh. in North America. Here we report the species for the first time from LB based on five teneral adult specimens.

Specimens examined: LABRADOR: Happy Valley, 10 August 1978, *Betula papyrifera*, coll. J. Peter Hall (3, DLC, Accession Nos 17-21970 to 17-21972; 2, NFRC, Accession Nos NFRC-2022-07480, NFRC-2022-07481; determined by RSA).

Perapion curtirostre (Germar, 1817)

This small Palearctic weevil was first recorded from the Maritime provinces of Canada by Majka et al. (2007a) where it is widely distributed. In Nova Scotia it has been associated with *Rumex acetosella* L. and *R. crispus* L. (Polygonaceae). This is a new provincial record for NL where the species is widespread on the island of NF.

Specimens examined (determined by RSA except where noted): NEWFOUNDLAND: Bunyan's Cove, 48.3960°N, 54.0129°W, 3 m, 14 August 2008, sweep of flowers, David Langor (3, DLC, Accession Nos 12-19, 17-17621, 17-17622); Cape Anguille, 47.899°N, 59.411°W, 18 m, 22 June 2010, sweep of marsh vegetation, David Langor (2, DLC, Accession Nos 12-24, 17-17623); Chamberlains, 15 October 2001, S. Garland (1, CMN, DLC Accession No. 12-18; 1, NFRC, Accession No. NFRC-2022-07474); Champney's West, 48.379°N, 53.298°W, 15 August 2014, sweep of vegetation on coastal barrens, David & Matthew Langor (1, DLC, Accession No. 17-17625); Clarendville, 48.173°N, 53.964°W, 22 July 2022, sweep of vegetation, D. Langor (DLC, 2, Accession Nos 17-22051, 17-22062; determined by DWL); Logy Bay, 47.6306°N, 52.6874°W, 29 July 2014, sweep of grass, Mardon Erbland (1, iNaturalist, [inaturalist.org/observations/819784](https://www.inaturalist.org/observations/819784)); Paddy's Pond, 26 Sept. 2002 (2, DLC, Accession Nos 12-17, 17-17624; latter with determination confirmed using DNA Barcode – BOLD: CCDB-28535-D06); Pasadena Beach, 49.022°N, 57.608°W, 21 m, 25 June 2010, sweep of vegetation, David Langor (1, DLC, Accession No. 12-23); Searston, 47.8299°N, 59.3064°W, 10 August 2022, sweep of vegetation on disturbed roadside and in field, D. Langor (1, DLC, Accession No. 17-22048; determined by DWL); St. Anthony, 51.365°N, 55.5918°W, 17 August 2022, sweep of vegetation on disturbed open areas, D. Langor (4, DLC, Accession Nos 17-22044 to 17-22047; determined by DWL); St. David's, 48.205°N, 58.866°W, 10 July, 2008, sweep of fallow field, coll. Goulet, Boudreault and Badiss (2, DLC, Accession Nos 12-20, 17-17618; 1, CMN, DLC Accession No. 17-17619); St. John's, 47.598°N, 52.713°W, 18 to 22 June 2006, sweep of shrubs and forbs, David Langor (3, NFRC, Accession Nos 2022-07475 to 2022-07477); St. John's, Botanic Garden, 23 August to 4 Sept. 1999, D. Larson (2, DLC, Accession Nos 12-09, 17-17596; latter determination confirmed using DNA Barcode - BOLD: CCDB-28535-D07); St. John's, Bowering Park, 47.5273°N, 52.5717°W, 2 August 2022, sweep of vegetation, D. Langor (1, DLC, Accession No. 17-22049; determined by DWL); Ibid., 47.528°N, 52.749°W, 20 August 2022 (1, DLC, Accession No. 17-22050; determined by DWL); St. John's, Mount Scio, 12 Oct. 2002 (1, DLC, Accession No. 12-13); St. John's, Newfoundland Drive, 47.6010°N, 52.7117°W, 83 m, 20 June 2009, sweep, D. Langor (1, CMN, DLC Accession No. 12-16; 4, DLC, Accession Nos 12-15, 17-17615 to 17-17617; determinations of three specimens confirmed using DNA Barcode - BOLD: CCDB-28535-D08 [12-15], CCDB-28535-D09 [17-17615] and CCDB-28535-D10 [17-17616]); St. John's, Oxen Pond Botanic Garden, Sept. 2000 (1, DLC, Accession No. 17-17611; 1, NFRC, Accession No. NFRC-2022-07473); Ibid., Oct. 2000, S. Lilly (1, DLC, Accession No. 12-11); Stephenville Crossing, 48.513°N, 58.454°W, 3 m, 22 June 2010, sweep of vegetation on coastal sand dunes, David Langor (1, DLC, Accession No. 12-22); York Harbour, 49.0555°N, 58.3687°W, 2 m, 28 June 2010, sweep shoreline vegetation, David Langor (2, DLC, Accession Nos 12-21, 17-17620).

CURCULIONIDAE

Ceutorhynchinae: Ceutorhynchini

Ceutorhynchus americanus Buchanan, 1937

This Nearctic species is newly recorded from NL based on one specimen collected in NF. It is otherwise widely distributed in Canada from Yukon Territory and British Columbia to Nova Scotia (Bousquet et al. 2013). Buchanan (1937) gives a list of plants, all Brassicaceae, on which adults have been collected. These are as follows: radish, horse-radish, *Lepidium* sp., cultivated mustard, mustard, and Chinese cabbage. Adults have also been reared from *Lepidium virginicum* L. (Buchanan 1937).

Specimens examined: NEWFOUNDLAND: Gros Morne National Park, Shallow Bay Beach, 14 July 2005, Sand Dune Ecosystem Study, Pitfall Trap 6, semi-stable vegetation on coastal sand dunes, Shelley Pardy (1, NFRC, Accession No. NFRC-2022-07175; determined by RSA).

Ceutorhynchus omissus Fall, 1917

This Nearctic species is newly recorded from NL with a single specimen from NF. It is distributed in Canada from Alberta to Nova Scotia (Bousquet et al. 2013). Host plants are in Brassicaceae.

Specimens examined: NEWFOUNDLAND: St. John's, 14 July 1949, W.J. Brown (1, CNC, Accession No. 04-1841; determined by PB).

Ceutorhynchus oregonensis Dietz, 1896

This Nearctic species is newly recorded from NL based on a specimen from northern NF. In Canada, it is widely distributed from Yukon Territory and British Columbia to Nova Scotia (Bousquet et al. 2013), with the Maritime province records only recently reported by Majka et al. (2007b). Anderson (1997) mentions that a number of adults of this species were collected from *Rorippa islandica* (Oeder) Borbás (Cruciferae) in Utah.

Specimens examined: NEWFOUNDLAND: St. Anthony, 51.37°N, 58.60°W, 10 July 2008, sweep sample #8, Goulet, Boudreault and Badiss (1, NFRC, Accession No. NFRC-2022-07183; determined by RSA).

Ceutorhynchinae: Cnemogonini

Cnemogonus lecontei Dietz, 1896

This Nearctic species is newly recorded from NL based on material from LB. In Canada, it is reported from Yukon Territory and British Columbia to New Brunswick. The species may be associated with plants in the family Onagraceae (Korotyaev and Anderson 2002).

Specimens examined: LABRADOR: Goose Bay, 2 August 1982, M. Colbo (1, NFRC, Accession No. NFRC-2022-07198; determined by PB; determination confirmed by DNA barcode – BOLD: CCDB-28535-H02); Goose Bay vicinity, 53.2889°N, 60.3810°W, 5 August 2008, sweep of roadside flowers, G.R. Pohl and D.W. Langor (1, NFRC, Accession No. NFRC-2022-07182; determined by PB; determination confirmed by DNA barcode – BOLD: CCDB-28535-H01).

Ceutorhynchinae: Phytobiini

***Pelenomus fuliginosus* (Dietz, 1896)**

This Nearctic species is newly recorded from NL based on material from LB. In Canada, it has been reported from British Columbia to New Brunswick (Bousquet et al. 2013). Species of *Pelenomus* are generally associated with *Polygonum* (Polygonaceae).

Specimens examined: LABRADOR: Mealy Mountains, 53.67°N, 58.87°W, July 2002, Anions, Sutton and Quicke (1, DLC, Accession No. 12-221; 2, NFRC, Accession Nos NFRC-2022-07199 to 2022-07200; determined by PB).

***Rhinoncus bruchoides* (Herbst, 1784)**

This Palearctic species is distributed throughout Europe and Asia (Alonso-Zarazaga et al. 2017). In Canada, this adventive species is newly documented from NL based on a series of three BugGuide photos (#225470 to #225472) of a specimen from NF. The earliest records from North America are from 1979 in Delaware and Maryland (Hoebeke and Whitehead 1980). In Canada, it is known from Ontario, Quebec, New Brunswick, and Nova Scotia (Bousquet et al. 2013; Webster et al. 2016). Hosts include species of *Polygonum*, *Oenanthe* (Apiaceae), and *Chaerophyllum* (Apiaceae) (Hoebeke and Whitehead 1980).

Specimens examined: NEWFOUNDLAND: Logy Bay, 47.6305°N, 52.6876°W, 15 September 2008, Mardon Erbland (1, photo posted on BugGuide, see <https://bugguide.net/node/view/225470/bgpage>; determined by RSA).

***Rhinoncus pericarpus* (Linnaeus, 1758)**

Formerly known by the name *Rhinoncus castor* (Fabricius, 1792), this Palearctic species is distributed throughout Europe and Asia (Alonso-Zarazaga et al. 2017) and is adventive in North America according to Bousquet et al. (2013), although Alonso-Zarazaga et al. (2017) do not record it as such. In Canada, it was previously known from NF but is herein newly recorded from LB. It is widely distributed in North America, and in Canada it is recorded from British Columbia to NF (Bousquet et al. 2013). Recorded hosts of this species are sheep's sorrel (*Rumex acetosella*), alfalfa (*Medicago sativa* L.; Fabaceae), and water dropworts (*Oenanthe* spp.) (Hoebeke and Whitehead 1980). The specimens previously determined as *R. pericarpus* and reported as such in Bousquet et al. (2013) were later determined to be *R. leucostigma* (Marsham, 1802).

Specimens examined: LABRADOR: Goose Bay, 5 July 1980, R. Morris (2, AAFC; determined by DWL); Goose Bay, vicinity of Mud Lake, 53.30570°N, 60.26812°W, 15 m, 29 July 2008, weedy shore of Churchill River, G.R. Pohl and D.W. Langor (1, NFRC, Accession No. NFRC-2022-07205; determined by PB as *R. castor*; Happy Valley, “Maxwells”, 53.29513°N, 60.30249°W, 15 m, MV light on building near Churchill River, at dusk, G.R. Pohl and D.W. Langor (1, NFRC, Accession No. NFRC-2022-07207; determined by PB).

Ceutorhynchinae: Scleropterini

***Prorutidosoma decipiens* (LeConte, 1876)**

This Nearctic species is newly recorded from NL based on material from both NF and LB. In Canada, it is widely distributed from Yukon Territory and British Columbia to Prince Edward Island (Bousquet et al. 2013). Adults have been associated with *Populus* (Salicaceae) (Anderson 1997).

Specimens examined: NEWFOUNDLAND: Burnt Cape, 51.573°N, 55.754°W, 10–24 July 2003, pitfall trap in cow parsnip patch, Site 1-3, A.M. Hynes (1, DLC, Accession No. 12-222; 1, NFRC, Accession No. NFRC-2022-07206; determined by RSA); Burnt Cape, 51.573°N, 55.756°W, July to August 2003, pitfall trap in crowberry patch, Site 1-1, A.M. Hynes (2, DLC, Accession Nos 17-17943; 1, NFRC, Accession No. NFRC-2022-07203; determined by DWL); same except Site 2-1 (1, NFRC, Accession No. NFRC-2022-07204; determined by DWL). LABRADOR: Mealy Mountains, 53°38'N, 58°52'W, July 2002, Anions, Sutton and Quicke (2, DLC, Accession Nos 12-224, 17-17945; 1, NFRC, Accession No. NFRC-2022-07205; determined by PB; determinations confirmed by DNA barcodes – BOLD: CCDB-28534-C07, -C08, -C09, respectively).

Cossoninae: Rhyncolini

***Rhyncolus brunneus* Mannerheim, 1843**

This Nearctic species was previously known from NF but herein is recorded from LB for the first time. In Canada, it is distributed from Yukon Territory and British Columbia to Prince Edward Island (Bousquet et al. 2013). Adults are found under the bark of dead Pinaceae (Anderson 1997).

Specimens examined: LABRADOR: Ossak Camp, 53.4233°N, 65.0129°W, 1 August 2004, pitfall trap, S. Pardy and R. Perry (1, DLC, Accession No. 12-234; determined by DWL).

***Rhyncolus macrops* Buchanan, 1946**

This Nearctic species is recorded from NL for the first time based on a specimen from NF. It was previously reported in Canada from British Columbia to Prince Edward Is-

land (Bousquet et al. 2013). It feeds in the phloem of various conifers, especially *Abies* and *Pinus* (Pinaceae) (Buchanan 1946).

Specimens examined: NEWFOUNDLAND: Notre Dame Provincial Park, 49.116°N, 55.079°W, 30 July 2011, pitfall trap, conifer forest, L. Pollett (1, NFRC, Accession No. NFRC-2022-07227; determined by RSA).

Curculioninae: Acalyptini

Acalyptus carpini (Fabricius, 1792)

This species is known in Canada from Yukon Territory and British Columbia to Nova Scotia (Bousquet et al. 2013). Here we record this species for the first time from the province based on material from LB. Adults are associated with species of *Salix* (Salicaceae), the larvae developing in the catkins (Anderson 1997).

Specimens examined: LABRADOR: Goose River, 7 km north of Goose Bay, 53.39229°N, 60.42094°W, 20 m asl, 30 July 2008, sweep of *Salix* on sand flats, D. Langor and G. Pohl (2, DLC, Accession Nos 12-50, 17-17693; 3, NFRC, Accession Nos NFRC-2022-07120 to 2022-07122 determined by DWL).

Curculioninae: Anthonomini

Anthonomus (*Anthonomus*) *lecontei* Burke, 1975

This Nearctic species is reported for the first time from NL with a single specimen from NF. It is widely distributed in Canada from British Columbia to Prince Edward Island (Bousquet et al. 2013). Burke (1968) described pupae of *A. lecontei* (as *Anthonomus scutellatus* Gyllenhal) from flower heads of *Aster* sp. (Asteraceae), probably *Aster divaricatus* (Nutt.) Kuntze, from Silver Springs, Maryland. Ahmad and Burke (1972) described the larva of the species from the same plant at the same locality.

Specimens examined: NEWFOUNDLAND: Portugal Cove, 47.6206°N, 52.8365°W, 15 m asl, 20 July 2006, sweep of vegetation, D. Langor (1, NFRC, Accession No. NFRC-2022-07126; determined by RSA and confirmed using DNA barcode – BOLD: CCDB-28535-E04).

Anthonomus (*Paranthonomus*) *rubidus* LeConte, 1876

This Nearctic species is newly recorded from the province based on material from NF. It is recorded from British Columbia, Ontario, and Quebec in Canada (Bousquet et al. 2013). Adults have been recorded from various Betulaceae, Fagaceae, Juglandaceae and Rosaceae (Clark 1987).

Specimens examined: NEWFOUNDLAND: South Branch, 17 July 1982, A. Raske (2, NFRC, Accession Nos NFRC-2022-07128 and 2022-07129; determined by RSA).

***Anthonomus (Tachypterellus) quadrigibbus* Say, 1832**

This Nearctic species is newly recorded from the province based on specimens from NF. In Canada, it is recorded from British Columbia to Nova Scotia (Bousquet et al. 2013). This species develops in fruits of various Rosaceae (Burke and Anderson 1989). In NF, specimens were collected from the fruit of pin cherry, *Prunus pensylvanica* L.f.

Specimens examined: NEWFOUNDLAND: St. John's, Bowering Park, 47.525°N, 52.749°W, 30 June 2012, sweep sample, D. Langor and G. Pohl (1, NFRC, Accession No. NFRC-2022-07127; determined by RSA); Ibid. 47.5273°N, 52.7517°W, 2 August 2022, D. Langor [4, DLC, Accession Nos 17-22008 to 17-22011; 1, NFRC, Accession No. NFRC-2022-07482; determined by DWL]; Ibid. 47.528°N, 52.749, 20 July 2019, D. Langor (1, NFRC, Accession No. NFRC-2022-07483); Ibid. site 2, 47.5278°N, 52.7480, 17 August 2022, pin cherry fruit, D. Langor (4, DLC, Accession Nos 17-22012 to 17-22015; 1, NFRC, Accession No. NFRC-2022-07483; determined by DWL); St. John's, Waterford Valley High School, 47.531°N, 52.753°W, 20 July 2019, sweep sample, D. Langor (1, NFRC, Accession No. NFRC-2022-07484; determined by DWL).

Curculioninae: Ellescini***Dorytomus laticollis* LeConte, 1876**

The first NL record of this Nearctic species is herein reported from LB. This species is distributed from British Columbia to Nova Scotia (Bousquet et al. 2013) and feeds on trembling aspen, *Populus tremuloides* Michx. (O'Brien 1970).

Specimens examined: LABRADOR: 35 km west of Goose Bay, 53.2687°N, 60.8626°W, 50 m asl, 2 July 2009, attracted to MV light, mixed forest, D. Langor and D. Macaulay (1, NFRC, Accession No. NFRC-2022-07143; determined by RSA and confirmed by DNA barcode – BOLD: CCDB-28535-E06).

***Dorytomus parvicollis* Casey, 1892**

This Nearctic species is herein reported for the first time from NL based on a single specimen from LB. In Canada, the species is recorded from British Columbia to Nova Scotia (Bousquet et al. 2013). Trembling aspen is the only known host of this species (O'Brien 1970).

Specimens examined: NEWFOUNDLAND: Glover's Harbour, 1 August 1968, FIS 68-1-0772(01), *Populus tremuloides* (1, NFRC, Accession No. NFRC-2022-07144; determined by RSA; DNA barcode was inconclusive – BOLD: CCDB-28535-E06).

***Dorytomus rufulus* (Mannerheim, 1853)**

This Nearctic species is reported for the first time from NL based on a single specimen from LB. The species is distributed in Canada from Yukon Territory and British

Columbia to Nova Scotia (Bousquet et al. 2013). Willows (*Salix* spp.) are the hosts of this species (O'Brien 1970).

Specimens examined: LABRADOR: Goose Bay, 24–26 Sept. 1981, M. Colbo (1, NFRC, Accession No. NFRC-2022-07142; determined by RSA and confirmed by DNA barcode – BOLD: CCDB-28535-E07).

***Dorytomus vagenotatus* Casey, 1892**

Although previously reported from NF (Bousquet et al. 2013), this Nearctic species is herein reported for the first time from LB. It is recorded in Canada from Yukon Territory and British Columbia to NF (Bousquet et al. 2013). The known hosts of this species are *Populus tremuloides* and *Populus grandidentata* Michx. (bigtooth aspen) (O'Brien 1970).

Specimens examined: LABRADOR: Goose Bay, shore of Churchill River, 53.29683°N, 60.28221°W, 10 m asl, 29 July 2008, sandy river shore, G. Pohl and D. Langor (1, DLC, Accession No. NFRC-2022-07146; determined by DWL and confirmed by DNA barcode – BOLD: CCDB-28535-E09); Happy Valley, Maxwell's Restaurant, 53.29513°N, 60.30249°W, 15 m asl, 29 July 2008, collected at MV light at dusk, G. Pohl and D. Langor (1, NFRC, Accession No. NFRC-2022-07147; determined by RSA and confirmed by DNA barcode – BOLD: CCDB-28535-E08).

Curculioninae: Mecinini

***Mecinus pascuorum* (Gyllenhal, 1813)**

This Palearctic weevil is native to the Palearctic where it is widely distributed, and it has been introduced to Africa, North America, and Australia (Alonso-Zarazaga et al. 2017). In Canada, it has been recorded from British Columbia and from Ontario to Nova Scotia. Here we record it from NL for the first time based on one specimen collected in western NF. This species feeds on *Plantago lanceolata* L. (Plantaginaceae) (Anderson et al. 2018).

Specimens examined: NEWFOUNDLAND: South of Frenchman's Cove on Route 450, 49.0499°N, 58.1552°W, 8 August 2022, sweep of vegetation along disturbed roadside, D. Langor (1, NFRC, Accession No. NFRC-2022-07486; determined by RSA).

Curculioninae: Rhamphini

***Orchestes pallicornis* Say, 1832**

This Nearctic species is recorded from British Columbia to NF (Bousquet et al. 2013). Although originally recorded from NF by O'Brien and Wibmer (1982), Anderson (1989) asserted that he had not seen specimens substantiating this record, nor have we

seen specimens or verified locality records of this species from NF. We hereby report the first record of this species from LB, which also represents the first published locality record for the entire province. Larvae feed on Rosaceae, including *Crataegus*, *Prunus*, *Pyrus* and likely *Amelanchier* (Anderson 1989).

Specimens examined: LABRADOR: Goose Bay, military base, 53.29833°N, 60.43562°W, 15 m, 28 July 2008, weedy Salix/grass clearing, Greg Pohl & David Langor (1, NFRC, Accession No. NFRC-2022-07160; determined by RSA).

Curculioninae: Styphlini

Orthochaetes setiger ([Beck], 1817)

This Palearctic species is native to Europe (Alonso-Zarazaga et al. 2017) and is herein reported for the first time as adventive in Canada based on specimens from NF (Fig. 1) and British Columbia. These are also the first records of the species from North America. In Britain, larvae are known to mine the leaves of many species in the families Amaryllidaceae, Asteraceae, Boraginaceae, Lamiaceae, Plantaginaceae, and Primulaceae (Pitkin et al. 2019). In the northern part of its European range, the species reproduces parthenogenetically (Ellis 2019). In Europe, adults have been located throughout the year under moss on old coniferous stumps, among rotten detritus in forest undergrowth, and in ant nests, e.g., *Lasius*, *Formica* (Formicidae) (González 1967). Adults are 2.3 - 2.9 mm long.



Figure 1. Dorsal habitus photo for *Orthochaetes setiger* ([Beck]). Body length is 2.5 mm. [photo credit: Udo Schmidt; for further details see Acknowledgements].

There are no other members of the Palearctic tribe Styphlini in North America. Adults of *O. setiger* will key out to couplet 26 (as Cyclominae) in the key to Nearctic subfamilies of Curculionidae for the USA and Canada (Anderson 2002). The genus *Orthochaetes* can be separated from Cyclominae by the combination of less well-developed postocular lobes, the lack of a metaepisternal suture, a proportionally longer elytra as compared to the length of the pronotum and the presence of erect, spatulate seta-like scales on the elytral intervals. In the key to Nearctic genera of Curculioninae, *Orthochaetes* will key to couplet 9 (as *Pachytychius*) but it lacks a tooth on the hind femur (present in *Pachytychius*).

Specimens examined (all determined by RSA): BRITISH COLUMBIA: Metchosin, summit of Camas Hill, 48°23'57"N, 123°35'44"W, 14 Dec. 1999 – 3 Jan. 2000, D. Blades, L. Rosenblood, C. Reznechenko, CH99 – 16P (1, RBCM, Accession No. ENT017-007401). NEWFOUNDLAND: St. John's, 4 Oct. 1995 (1, DLC, Accession No. 12-670); St. John's, Botanic Garden, 23 Aug. – 4 Sep. 1999, D. Larson (1, CMN).

Curculioninae: Tychiini

Tychius picirostris (Fabricius, 1787)

This Palearctic species is native to Europe and western Asia and is adventive in North America (Alonso-Zarazaga et al. 2017). In Canada, it has been reported from British Columbia to NF (Bousquet et al. 2013). Herein we provide the first report from LB. In North America and Europe, Fabaceae host plants are *Trifolium repens* L. (white clover) and *T. hybridum* L. (alsike clover) (Anderson and Howden 1994).

Specimens examined: LABRADOR: Goose Bay, air base, 53.301°N, 60.423°W, 46 m asl, 30 June 2009, sweep of shrubs and forbs, D. Langor (2, DLC; Accession Nos 17-17887, 17-17888; 1, NFRC, Accession No. NFRC-2022-07167; determined by DWL); Goose Bay, military base, 53.29833°N, 60.43562°W, 28 July 2008, 15 m asl, sweep of weeds, *Salix* and grasses, G. Pohl and D. Langor (6, DLC, Accession Nos 17-17879 to 17-17883, 12-160; 2, NFRC, Accession Nos NFRC-2022-07165 and 2022-07166; determined by RSA); Happy Valley, Maxwell's Restaurant, 53.29513°N, 60.30249°W, 15 m asl, 29 July 2008, MV light, G. Pohl and D. Langor (1, DLC, Accession No. 12-153; determined by DWL).

Tychius stephensi Schönherr, 1836

This Palearctic species is native to Europe and western Asia and is adventive in North America (Alonso-Zarazaga et al. 2017). In Canada, we report it from NL for the first time based on material from NF. In Canada, it is recorded from British Columbia to Prince Edward Island (Bousquet et al. 2013). In North America this species is found on *Trifolium pratense* L. (red clover); larvae feed on the developing seeds (Anderson and Howden 1994).

Specimens examined: NEWFOUNDLAND: Corner Brook, mid July 2004, pine, Erika Burke (4, DLC, Accession Nos 12-158, 17-17891 to 17-17893; determined by DWL); Corner Brook, 48°57.355'N, 57°54.681'W, 12 July 2008, fallow field, sweep sample #11, Goulet, Boudreault & Badiss (4, DLC, Accession Nos 17-17920 to 17-17922,

12-169; determined by DWL and confirmed by DNA barcode – BOLD: CCDB-28535-F11 [AN: 12-169]) Curling Brook, 48.9593°N, 57.9916°W, 11 m asl, 29 June 2010, sweep of cow parsnip flowers, David Langor (1, NFRC, Accession No. NFRC-2022-07171; determined by DWL); Deer Lake, 49°11.711'N, 57°54.681'W, 12 July 2008, fallow field, sweep sample #5, Goulet, Boudreault & Badiiss (12, DLC, Accession Nos 17-17902 to 17-17910, 17-17912, 12-164; 1, NFRC, Accession No. NFRC-2022-07174; determined by DWL); Gros Morne National Park, Stanleyville, 49.468°N, 57.773°W, 10 m asl, 6 July 2006, on beach near cliffs, D. Langor (6, DLC, Accession Nos 17-17896 to 17-17900, 12-162; determined by DWL); Lomond, 49.4619°N, 57.7610°W, 3 m asl, 6 July 2006, sweep sample, D. Langor (2, DLC, Accession Nos 17-17894, 17-17895; 1, NFRC, Accession No. NFRC-2022-07172; determined by DWL); Paddy's Pond, 7 Oct. 1995 (1, DLC, Accession No. 12-156; determined by DWL); Portugal Cove, 47.6206°N, 52.8365°W, 15 m asl, 20 July 2006, sweep sample, D. Langor (1, DLC, Accession No. 12-168; determined by DWL and confirmed by DNA barcode – BOLD: CCDB-28535-F12); St. John's, 47.598°N, 52.713°W, 18-22 July 2006, sweep of shrubs and forbs, D. Langor (1, DLC, Accession No. 17-17891; 2, NFRC, Accession Nos NFRC-2022-07169, 2022-07170; determined by DWL); St. John's, Long Pond, 4 July 2000, N. O'Dea (2, DLC, Accession Nos 17-17890, 12-157; determined by DWL); St. John's, Newfoundland Drive, 47.6010°N, 52.712°W, 83 m asl, 2 July 2010, sweep of vegetation, D. Langor (1, DLC, Accession No. 12-166; determined by DWL and confirmed by DNA barcode – BOLD: CCDB-28535-G03); St. John's, Quidi Vidi Lake outlet, 47.5841°N, 52.6799°W, 15 m asl, 20 June 2009, sweep of vegetation, D. Langor (1, NFRC, Accession No. NFRC-2022-07173; determined by DWL); Stephenville Crossing, 48.513°N, 58.454°W, 3 m asl, 22 June 2010, sweep of vegetation on coastal sand dunes, D. Langor (2, DLC, Accession Nos 17-17910, 12-167; determined by DWL and confirmed by DNA barcodes – BOLD: CCDB-28535-G01 and CCDB-28535-G02, respectively).

Dryophthorinae: Rhynchophorini

***Sitophilus zeamais* Motschulsky, 1855**

This cosmopolitan species is adventive in North America and has been recorded from Manitoba to Quebec (Bousquet et al. 2013).

Specimens examined: NEWFOUNDLAND: St. John's, 4 November 1985, Ray Morris (1, CNC, Accession No. CNC COLEO 00116857; determined by DNA barcoding – CNC774-11).

Entiminae: Phyllobiini

***Phyllobius oblongus* (Linnaeus, 1758)**

This Palearctic species, commonly called the European snout weevil, is native to Europe and western Asia, and is adventive in North America (Alonso-Zarazaga et al.

2017). We report it herein for the first time from NL, based on specimens from NF. It has been recorded in Canada from British Columbia in the west and from Ontario to Prince Edward Island in the east (Bousquet et al. 2013). Adults feed on the leaves of a wide variety of shade and fruit trees in the families Betulaceae (*Betula*), Rosaceae (*Malus*, *Prunus*, *Pyrus*), Salicaceae (*Populus*, *Salix*), Sapindaceae (*Acer*), and Ulmaceae (*Ulmus*), and larvae feed on the roots of various plants (Bright and Bouchard 2008, and references therein).

Specimens examined (all determined by DWL): NEWFOUNDLAND: Corner Brook, near Prince Edward Park, 48.967°N, 57.889°W, 2 m asl, 29 June 2010, sweep of vegetation, D. Langor (1, DLC, Accession No. 12-485); Marble Mountain, 48.9492°N, 57.8302°W, 12 m asl, 19 June 2010, UV light in mixed forest, D. Langor & D. Macaulay (1, NFRC, Accession No. NFRC-2022-07288); Pasadena, 49.0121°N, 57.6106°W, 2 m asl, 25 June 2011, gravel and sand on river bank, D. Langor & G. Pohl (1, DLC, Accession Nos 17-18297; 1, NFRC, Accession No. NFRC-2022-07289).

Entiminae: Polydrusini

Pachyrhinus elegans (Couper, 1865)

This Nearctic species is distributed in Canada from British Columbia to Nova Scotia (Bousquet et al. 2013). We report it for the first time from the province of NL based on specimens from NF. This species occurs mainly on eastern white pine, *Pinus strobus* L., which occurs in NF, and occasionally feeds on other pine species elsewhere in Canada (Bright and Bouchard 2008).

Specimens examined (all determined by DWL): NEWFOUNDLAND: Pasadena, east of on TCH, 49.0706°N, 57.5592°W, 5 August 2022, sweep of vegetation, D. Langor (2, DLC, Accession Nos 17-22080 and 17-22081); Upper Ferry, near bridge, 47.8496°N, 59.2477°W, 10 August 2022, sweep of vegetation at roadside, D. Langor (1, NFRC, Accession No. NFRC-2022-07487).

Polydrusus cervinus (Linnaeus, 1758)

This Palearctic species is native to Europe and western Siberia and is adventive in North America (Alonso-Zarazaga et al. 2017). Here we record it for the first time from NL based on specimens from NF. In Canada, the species is recorded from Ontario, Nova Scotia, and Prince Edward Island (Bousquet et al. 2013). Adults feed on the leaves of *Acer*, *Alnus*, *Betula*, *Corylus*, *Malus*, *Prunus*, *Populus*, *Quercus*, and *Salix*; the hosts of larvae are not fully documented but include roots of orchard grass, *Dactylis glomerata* L. (Bright and Bouchard 2008, and references therein).

Specimens examined: NEWFOUNDLAND: Tompkins (trail near), 47.781°N, 59.231°W, 20 m asl, 23 June 2010, sweep sample, D. Langor (3, DLC, Accession Nos 17-18326, 17-18327, 12-492; 2, NFRC, Accession Nos NFRC-2022-07297 and 2022-07298; determined by DWL).

Polydrusus formosus (Mayer, 1779)

This Palearctic species is native to Europe and is adventive in North America (Alonso-Zarazaga et al. 2017). Herein we record the species for the first time from NL based on specimens from NF where it is very widespread and often abundant. It is recorded in Canada from British Columbia in the west and Ontario to Prince Edward Island in the east (Bousquet et al. 2013). Adults of this species have been collected in canola fields and on wild radish in pea fields (Pinski et al. 2005). Much information about this species is published under the name *Polydrusus sericeus* (Schaller), now a junior synonym.

Specimens examined (determined by DWL unless otherwise noted): NEWFOUNDLAND: Blow Me Down, 49.061°N, 58.232°W, 6 July 2012, sweep of plants around river trailhead, J. Heron (2, DLC, Accession Nos 17-18319, 17-18320); Blue Pond Park, 48.783°N, 58.087°W, 212 m asl, 25 June 2010, sweep of vegetation along lake shore, D. Langor (3, DLC, Accession Nos 17-18313 to 17-18315; 2, NFRC, Accession Nos NFRC-2022-07292 and 2022-07295); Cheeseman Provincial Park, 47.628°N, 59.273°W, 8 July 2012, D. Langor and G. Pohl (1, DLC, Accession No. 17-18322; determination confirmed by DNA barcode – BOLD: CCDB-28536-D03); Cormack, 49.2679°N, 57.4408°W, 12 August 2022, sweep of vegetation along disturbed roadside, D. Langor (1, DLC, Accession No. 17-21990); Corner Brook, 48.975°N, 57.9°W, 10 July 2008, sweep of fallow field, Goulet, Boudreault, and Badiss (3, DLC, Accession Nos 17-18310, 17-18311, 12-490); Corner Brook, 49.9453°N, 57.9168°W, 13 July 2006, sweep sample, D. Langor (8, DLC, Accession Nos 17-18303 to 17-18309, 12-488; 1, NFRC, Accession No. NFRC-2022-07291); Corner Brook, 24 July 2002, sweep of maples, R. Feng (1, DLC, Accession No. 17-18317; 1, NFRC, Accession No. NFRC-2022-07293); Corner Brook, 24 July 2002, sweep of white birch, R. Feng (1, DLC, Accession No. 17-18316); Gander, near Silent Witness Memorial, 48.9177°N, 54.5688°W, 4 August 2022, sweep of vegetation in disturbed lot, D. Langor (3, DLC, Accession Nos 17-21996 to 17-21998); George's Lake, 48.780°N, 58.101°W, 134 m asl, 9 July 2012, brook margin, D. Langor and G. Pohl (1, DLC, Accession No. 17-18321; determination confirmed by DNA barcode – BOLD: CCDB-28536-D04); Grand Falls, Sanger Park, 48.9258°N, 55.6407°W, 5 August 2022, sweep of vegetation along forest trail (semi-natural), D. Langor (2, DLC, Accession Nos 17-21999 and 17-22000); Gros Morne National Park, James Callaghan Trail, 49.5686°N, 57.8302°W, 39 m, 16 July 2013, forest, malaise trap, Anderson (1, CBG, determination by DNA barcode – BOLD: BIOUG09982-H03); Ibid. 27 August 2013, R. Reid (1, CBG, determination by DNA barcode – BOLD: BIOUG10587-A01); Marble Mountain near Humber River, 48.952°N, 57.836°W, 24 m asl, 24 June 2010, at MV light, D. Langor (1, DLC, Accession No. 12-489); Port aux Basques, 47.5841°N, 59.1406°W, 9 August 2022, sweep of vegetation in field and forest edge, D. Langor (3, DLC, Accession Nos 17-21985 to 17-21987); Port Saunders, Route 430, 50.6496°N, 57.2795, 6 August 2022, sweep of vegetation in disturbed open area, D. Langor (1, DLC, Accession No. 17-21983); Rocky Harbour, 49.5848°N, 57.9066°W, 6 August 2022, sweep of vegetation on disturbed land, D. Langor (3,

DLC, Accession Nos 17-22001 to 17-22003); Searston, 47.8299°N, 59.3064°W, 10 August 2022, sweep of vegetation on disturbed roadside and field, D. Langor (1, DLC Accession No. 17-21984); Steady Brook, 48.9487°N, 57.8304°W, 20 m asl, 13 August 2008, sweep sample and pond edge, D. Langor (4, DLC, Accession Nos 17-18299, 17-18300, 17-18302, 12-487; 1, NFRC, Accession No. NFRC-2022-07290; determined by RSA); Terra Nova National Park, visitors center, 48.5796°N, 53.9471, 4 August 2022, sweep at vegetation at forest edge, D. Langor (3, DLC, Accession Nos 17-22004 to 17-22006); Upper Harbour near Deer Lake, 49.193°N, 57.434°W, 9 July 2012, sweep of shoreline vegetation, D. Langor and G. Pohl (1, NFRC, Accession No. NFRC-2022-07294); Wreckhouse, 47.7091°N, 59.3073°W, 9 August 2022, sweep of vegetation on disturbed roadside and in natural meadow, D. Langor (1, DLC, Accession No. 17-21988); York Harbour, 49.056°N, 58.369°W, 10 m asl, 6 July 2012, D. Langor (2, DLC, Accession Nos 17-18323 and 17-18324; determination confirmed by DNA barcodes – BOLD: CCDB-28536-D02, CCDB-28536-D01, respectively).

Entiminae: Sitonini

Sitona cylindricollis Fåhraeus, 1840

The natural range of this Palearctic species is Europe, western Asia, and North Africa (Alonso-Zarazaga et al. 2017). Commonly known as the sweet-clover weevil, it was first found in North America (Hemmingford, QC) in 1924 (Bright and Bouchard 2008). It is now found throughout the USA, and in Canada it is recorded from Yukon Territory and British Columbia to Prince Edward Island (Bright 1994; Bousquet et al. 2013). Here we report it for the first time from NL based on material from NF. The main host of this weevil is sweet clover (*Melilotus* spp.), but it can also be occasionally found on *Medicago sativa*, *Trifolium hybridum* and *Medicago lupulina* L. (black medick) (Bright 1994).

Specimens examined: NEWFOUNDLAND: Corner Brook, 48.975°N, 57.9°W, 10 July 2008, fallow field, sweep sample #11, Goulet, Boudreault & Badiss (2, DLC, Accession Nos 17-18416 and 12-611; 1, NFRC, Accession No. NFRC-2022-07250; determined by DWL); St. John's, 29 September 1980 (1, DLC, Accession No. 17-17580; determined by RSA); St. John's, 15 August 1997, P. Dixon (2, AAFC; determined by DWL); St. John's, 12 July 1999, J. Coombs (1, AAFC; determined by DWL); Ibid., 20 August 1999 (1, AAFC; determined by DWL).

Lixinae: Cleonini

Stephanocleonus plumbeus LeConte, 1876

This Nearctic species was reported from NF by Anderson (1987) and is now recorded from LB for the first time. In Canada, it is distributed from Alberta to NF (Anderson 1987; Bousquet et al. 2013). There is no recorded information about natural history.

Specimens examined: LABRADOR: Happy Valley – Goose Bay, 6 June 2005, S. Pardy-Moores (1, DLC, Accession No. 12-666; determined by DWL and confirmed by DNA barcode – BOLD: CCDB-28536-E09).

Mesoptiliinae: Magdalidini

***Magdalis alutacea* LeConte, 1878**

This Nearctic species is reported for the first time from the province based on specimens from both NF and LB. It is recorded in Canada from Yukon Territory and British Columbia to New Brunswick (Bousquet et al. 2013). This weevil has been reared from *Picea engelmanni* Parry ex Engelm. (Pinaceae) in Colorado (Anderson 1997).

Specimens examined (all determined by RSA): NEWFOUNDLAND: Gander, 30 June 1949, W. J. Brown (1, CNC). LABRADOR: Goose Bay, 10 August 1948, W. E. Beckel (1, CNC).

***Magdalis gentilis* LeConte, 1876**

This Nearctic species is reported from the province for the first time based on specimens from NF. In Canada, it is recorded from Yukon Territory and British Columbia to Nova Scotia (Bousquet et al. 2013). Adults have been reported from various species of *Pinus* and *Picea* (Pinaceae) (Anderson 1997).

Specimens examined: NEWFOUNDLAND: Birchy Lake (south side), 28 June 1972, *Pinus strobus*, FIS 72-1-0098 (1, CFS; determined by RSA).

Molytinae: Hylobiini

***Hylobius warreni* Wood, 1957**

This species was originally reported from NF in 1991 (McNamara 1991a) but was removed from the 2013 checklist (Bousquet et al. 2013) as verified specimens had not been seen. However, this Nearctic species is hereby reinstated as present in both NF and LB. It is recorded in Canada from British Columbia to Nova Scotia (Bousquet et al. 2013). The species is associated with conifers, primarily *Pinus* and *Picea* (Cerezke 1994).

Specimens examined (determined by DWL except where noted): NEWFOUNDLAND: Bonavista, 26 August 1960, FIS 60-1740(01), ex. Scots pine (1, CFS); Butterpot Provincial Park, 47.381°N, 53.044°W, 4 August 2012, forest, pitfall trap #2, A. Pretty (1, NFRC, Accession No. NFRC-2022-07363); Cormack, 12 June 1979, Lot 2, Larson and Swales (1, DLC, Accession No. 12-686); Gales Brook, 22 June 1977 (1, DLC, Accession No. 12-675); Gander, July 1979 (3, DLC, Accession Nos 12-681, 17-20374, 17-20375); Grand Falls (near), 48.974°N, 55.569°W, 44 m asl, 1-10 July 2012, pitfall trap in mixed wood forest, D. Langor and G. Pohl (1, NFRC, Accession No. NFRC-2022-07361; determined by RSA); Gros Morne National Park, Bakers Brook, July-August

2000, pitfall trap in tuckamoor, N. Chalk (1, DLC, Accession No. 12-692; identity confirmed by DNA Barcode – BOLD: CCDB-28536-F02); Lockston Path Provincial Park, 48.430°N, 53.361°W, 26 August 2011, pitfall trap in conifer forest, P. Perry (1, DLC, Accession No. 17-20379); Notre Dame Provincial Park, 49.116°N, 55.079°W, 13 September 2011, pitfall trap in conifer forest, L. Pollett (1, DLC, Accession No. 17-20377); Ibid., 2 July 2011 (1, NFRC, Accession No. NFRC-2022-07362); Portugal Cove, Indian Meal Line, 26 June 1981, D. Larson (1, DLC, Accession No. 12-690); Portugal Cove, Indian Meal Line, 27 May 1979, D. Larson (1, DLC, Accession No. 12-689); Terra Nova National Park, Wings Brook, 17 July 1982 (1, DLC, Accession No. 12-694). LABRADOR: Churchill River, 53.176°N, 60.948°W, 1 July 2009, shoreline of river, D. Langor and S. Pardy-Moores (1, DLC, Accession No. 12-691); Mealy Mountains, 15 July 2005, SWP PF6PF2 (1, NFRC, Accession No. NFRC-2022-07359); Middle Brook, 53.3785°N, 63.1429°W, 4-18 July 2005, pitfall trap in boreal forest, S. Pardy (1, DLC, Accession No. 12-698); Muskrat Falls, 53.2606°N, 60.7844°W, 5-19 July 2005, pitfall trap in boreal forest, S. Pardy (1, NFRC, Accession No. NFRC-2022-07360); Ibid, 17 June – 5 July 2005 (1, DLC, Accession No. 17-20376); St. Lewis, 52.3961°N, 55.7057°W, 5-22 July 2004, pitfall trap in coastal barrens, S. Pardy (1, DLC, Accession No. 12-699).

Molytinae: Lepyrini

***Lepyrus palustris* (Scopoli, 1763)**

This Holarctic species is native to Europe, throughout Siberia and in northern North America (Alonso-Zarazaga et al. 2017). It was recorded from LB by McNamara (1991a); however, we have not seen the locality data or specimens on which this record is based. Subsequently, two specimens were collected from Shuldham Island. Here we report it for the first time from NF and provide a hitherto unpublished record from LB. In Canada, it is recorded from Northwest Territories and British Columbia to LB (Bousquet et al. 2013). Hoffmann (1954) notes that larvae of *L. palustris* in Europe feed on the primary roots of *Rumex obtusifolius* L. (Polygonaceae) even though adults are found frequently on various species of Salicaceae.

Specimens examined (all determined by RSA): NEWFOUNDLAND: Burnt Cape, 51.571°N, 55.756°W, 10-24 July 2003, pitfall trap in crowberry lawn, Site 1-1, A.M. Hynes (1, NFRC, Accession No. 12-702; 3, NFRC, Accession Nos NFRC-2022-07366 to 2022-07368); Ibid, *Dryas* rock garden, Site 1-4 (1, DLC, 17-20387). LABRADOR: Shuldham Island, 28-29 July 2006, Michael Burzynski (1, DLC, Accession No. 17-20388; 1, NFRC, Accession No. NFRC-2022-07369).

Molytinae: Pissodini

***Pissodes rotundatus* LeConte, 1876**

This Nearctic species has a transcontinental distribution and was previously recorded from NF (Bousquet et al. 2013). Herein we report it for the first time from LB, and its

presence there is unsurprising. It was previously recorded in Canada from Yukon Territory and British Columbia to NF (Bousquet et al. 2013). Larvae breed in the phloem and cambium of the boles of recently dead or weakened *Picea* and *Pinus* (Hopkins 1911).

Specimens examined: LABRADOR: Churchill Road, 14 July 1976, FIS 76-1-0564, ex. *Picea mariana*, W. Sutton (1, CFS; determined by DWL).

Pissodes striatulus (Fabricius, 1775)

This transcontinental Nearctic species is already known from NF where it is widely distributed, but herein we report it for the first time from LB. In Canada, it is distributed from British Columbia to NF (Bousquet et al. 2013). Larvae breed in the phloem and cambium of *Abies* (Pinaceae) (Hopkins 1911).

Specimens examined: LABRADOR: 0.25 mi N of Goose River Bridge, 13 July 1977, FIS 77-1-0490-02, ex *Abies balsamea*, K.E. Pardy (1, CFS; determined by DWL); km 34 of Grand Lake Road near Goose Bay, 24 July 1986, K.E. Pardy (1, NFRC, Accession No. NFRC-2022-07387; determined by DWL and confirmed by DNA barcode – BOLD: CCDB-28536-G04); Minipi Lake, 1 July 1965, FIS 65-0324-01, ex *Abies balsamea* (1, CFS; determined by DWL); Muskrat Is., 15 km W. Goose Bay, 5 August 1984, ex. *Abies balsamea*, A.G. Raske (3, CFS; determined by DWL; two specimens confirmed by DNA barcodes – BOLD: CCDB-28536-G01, -G02).

Scolytinae: Dryocoetini

Dryocoetes affaber (Mannerheim, 1852)

This Nearctic species is known from NF but herein we report it for the first time from LB. In Canada, it is recorded from Yukon Territory and British Columbia to NF (Bousquet et al. 2013). It breeds in the phloem of various conifers, mainly *Picea* and *Pinus* but also *Larix* (Pinaceae) and *Abies* (Bright 1976).

Specimens examined (all determined by DWL): LABRADOR: Cartwright Highway, 52.9187°N, 60.2360°W, 5 August 2008, on log deck (5, DLC, Accession Nos 17-20468 to 17-20472; 2, NFRC, Accession Nos NFRC-2022-07408 and NFRC-2022-07409; determination confirmed by DNA barcode – BOLD: CCDB-28537-A09 [A.N. 17-20470], CCDB-28537-A10 [A.N. 17-20471]); Cartwright Highway, 53.0742°N, 60.5082°W, 5 August 2008, ex spruce logs under bark (7, DLC, Accession Nos 17-20473 to 17-20479; 1, NFRC, Accession No. NFRC-2022-07410; determination confirmed by DNA barcode – BOLD: CCDB-28537-A11 [A.N. 17-20478]); ca. 35 km W Goose Bay, 53.2687°N, 60.8626°W, 50 m asl, 2 July 2009, MV light in mixed forest, D. Langor and D. Macaulay (1, DLC, Accession No. 17-20485), Labrador City ski hill, 18 July 1981, Lot 1, M. Colbo and D. Larson (2, DLC, Accession Nos 12-1685 and 17-20465); Muskrat Falls, 53.254°N, 60.777°W, 114 m asl, 30 June 2009, MV light, D. Langor and D. Macaulay (4, DLC, Accession Nos 17-20481 to 17-20484).

Scolytinae: Hylastini

Scierus annectans LeConte, 1876

This Nearctic species was previously recorded from NF and is here reported from LB for the first time. The species is recorded in Canada from Northwest Territories and British Columbia to NF by Bousquet et al. (2013). It breeds in the phloem of *Picea*, *Abies lasiocarpa* (Hook.) Nutt. and *Pinus contorta* Dougl. ex Loudon (Bright 1976).

Specimens examined: LABRADOR: Cartwright Highway, 53.0742°N, 60.5082°W, 5 August 2008, ex spruce logs under bark, G. Pohl and D. Langor (1, DLC, Accession No. 12-1731; determined by DWL).

Scolytinae: Hylurgini

Dendroctonus rufipennis (Kirby, 1837)

This Nearctic species, commonly known as the spruce beetle, has a very wide distribution in North America. It is found throughout NF where it has caused outbreaks in white spruce stands, particularly along the Humber Valley (D. Langor, unpublished data). Herein we report it for the first time from LB. Larvae breed in the phloem and cambium of *Picea* spp. (Bright 1976).

Specimens examined (all determined by DWL): LABRADOR: Cartwright Highway, 52.9187°N, 60.2360°W, 5 August 2008, on log deck, G. Pohl and D. Langor (2, DLC, Accession Nos 12-1748 and 17-20668); Charlottetown, 52.772°N, 56.115°W, 24 m asl, 26 June 2009, MV light in spruce forest, D. Langor (1, NFRC, Accession No. NFRC-2022-07423); Churchill River, 53.176°N, 60.948°W, 1 July 2009, shore of river, D. Langor and S. Pardy-Moores (1, DLC, Accession No. 12-1755).

Scolytinae: Ipini

Ips borealis Swaine, 1911

This Nearctic species has been recorded from NF but here we report it for the first time from LB. In Canada, it is recorded from Yukon Territory and British Columbia to NF (Bousquet et al. 2013). It breeds in the phloem of *Picea* spp. (Bright 1976).

Specimens examined: LABRADOR: Labrador City ski hill, 18 July 1981, M. Colbo and D. Larson (5, DLC, Accession Nos 17-20717 to 17-20721; 1, NFRC, Accession No. NFRC-2022-13362; determined by DWL and all DLC specimens but 17-20718 confirmed by DNA barcodes – BOLD: CCDB-28537-B10, -B12, -C01, -C02).

Ips pini (Say, 1826)

This Nearctic species is one of the most common and widely distributed *Ips* in North America, and in Canada it was previously recorded from Yukon Territory and British

Columbia to NF (Bousquet et al. 2013). Here we report it for the first time from LB. Larvae feed in the phloem and cambium of the boles and large branches of weakened or recently dead *Pinus* (rarely *Picea*) (Bright 1976). Only jack pine, *Pinus banksiana* Lamb., occurs in LB so undoubtedly this is the host.

Specimens examined: LABRADOR: Cartwright Highway, 52.9187°N, 60.2360°W, 5 August 2008, ex log deck, G. Pohl and D. Langor (4, DLC, Accession Nos 17-20752 to 17-20755; 3, NFRC, Accession Nos NFRC-2022-13367 to 2022-13369; determined by DWL and all DLC specimens except for 17-20754 confirmed by DNA barcodes – BOLD: CCDB-28537-C03, -C04, -C06).

Scolytinae: Phloeotribini

Phloeotribus piceae Swaine, 1911

This Nearctic species is recorded for the first time from NL based on a single specimen from NF. In Canada, it has been recorded from Yukon Territory and British Columbia to Nova Scotia (Bousquet et al. 2013). Larvae breed in the phloem of *Picea* spp. (Bright 1976).

Specimens examined: NEWFOUNDLAND: Corner Brook, near Loggers School Road, 28 June to 13 July 1994, ex pitfall trap in 60 year-old fir-*Dryopteris* forest (1, NFRC, Accession No. NFRC-2022-13382; determined by DWL).

NEMONYCHIDAE

Cimberidinae: Cimberidini

Cimberis pilosa (LeConte, 1876)

This is the first record of this family and Nearctic species from NL, based on material from NF. Adults have been collected on *Pinus banksiana*, *P. palustris* Mill., *P. taeda* L., and *P. virginiana* Mill., and larvae on *P. virginiana* (Kuschel 1989).

Specimens examined: NEWFOUNDLAND: 1.5 km E of Long Harbour on Route 1, 28 June 1973, FIS 73-1-0268(03), *Abies balsamea* (1, CFS, determined by DWL).

Notes on other species

ATTELABIDAE

Temnocerus cyanellus (LeConte, 1876) [Rhynchitinae]

Blatchley and Leng (1916) report this Nearctic species from NF but give no specific collection localities nor a source of the record. Additionally, Hamilton (1971) gives no NL localities for this species, nor have we seen specimens or verified records from NL. This species is widely distributed in Canada, from Northwest Territories to

Nova Scotia, and the plant species with which it is associated – *Betula*, *Quercus* and *Salix* (Bright, 1993) – occur in NL. Nonetheless, we consider the record from NF as questionable.

CURCULIONIDAE

***Ceutorhynchus querceti* (Gyllenhal, 1813)** [Ceutorhynchinae]

This Nearctic species is recorded from NF (as *C. pusio* Mannerheim) by O'Brien and Wibmer (1982), and this record was reiterated by McNamara (1991a) and Bousquet et al. (2013). Dietz (1896) did not record it from NL. To date we have not seen verified locality records or specimens of this species from NL, although we believe the species is likely on the island of NF.

***Dietzella zimmermanni* (Gyllenhal, 1837)** [Ceutorhynchinae]

This Nearctic species is recorded from NF by O'Brien and Wibmer (1982), a record reiterated by McNamara (1991a) and Bousquet et al. (2013); however, we have seen no specimens or verified locality records. Dietz (1896) did not record this species from NL. The species is currently recorded from British Columbia to New Brunswick (Bousquet et al. 2013) so it is possible that it occurs in NF. However, we consider the record as questionable.

***Phytobius leucogaster* (Marshall, 1892)** [Ceutorhynchinae]

This Holarctic species is recorded from NF by O'Brien and Wibmer (1982), a record also reported by McNamara (1991a) and Bousquet et al. (2013), but we have seen no specimens or verified locality records. It was not reported from NL by Dietz (1896). The species is recorded from Yukon Territory and from British Columbia to Quebec. Given the lack of verified records of this species east of Quebec, we opt to remove it from the species list for NL.

***Isochnus sequensi* (Stierlin, 1894)** [Curculioninae]

This Palearctic species was first recorded in North America under the name *Isochnus populicola* (Silfverberg), a junior synonym of *I. sequensi*. Anderson (1989) and McNamara (1991a) did not record this species from NF, but Sweeney et al. (2012) and Bousquet et al. (2013) did record it from the province. There do not appear to be any published locality records for NL. This weevil is widely distributed across the island of NF.

Specimens examined: NEWFOUNDLAND (determinations by RSA): Bay D'Espoir, 14 July 1985, Lloyd Hollet [1, DLC, Accession No. 17-24845]; Blue Pond Park, 48.783°N, 58.087°W, 212 m, sweep of lakeshore vegetation, 25 June 2010, David Langor [2 DLC, Accession Nos 12-117 and 17-17848]; Cape St. George, 48.934°N,

59.263°W, coastal tundra, 11 July 2008, Goulet, Boudreault & Badiss [6, DLC, Accession Nos 17-17841 to 17-17846]; Cormack, 12 June 1979, Larson & Swales [8, DLC, Accession Nos 12-95, 17-17769 to 17-17776]; Corner Brook, mid July 2004, poplar, E. Burke [2, DLC, Accession Nos 12-104 and 17-17761]; Corner Brook, 48.975°N, 57.9°W, 10 July 2008, fallow field, sweep sample #11, Goulet, Boudreault & Badiss [2, DLC, Accession Nos 12-113 and 17-17816]; Corner Brook, 17 Sept. 2002, willow, H. Crummey [1, DLC, Accession No. 17-17840]; Deer Lake, 49.2°N, 57.46°W, 12 July 2008, fallow field, sweep sample #5, Goulet, Boudreault & Badiss [5, DLC, Accession Nos 12-116, 17-17819 to 17-178222]; Deer Lake shoreline, near Pynn's Brook, 49.0917°N, 57.5460, 25 June 2011, detritus, David Langor & Greg Pohl [1, DLC, Accession No. 17-17847]; Granddaddy's Brook, NE of Millville, 16 June 1979, Larson & Swales [1, DLC, Accession No. 12-100]; Gros Morne National Park, near Sally's Cove, 20 June 1979, near stream, Larson & Swales [8, DLC, Accession Nos 12-96, 17-17762 to 17-17768]; junction of TCH and Codroy River, 11 June 1979, small stream, Larson & Swales [2, DLC, Accession Nos 12-98 and 17-17808]; junction of Hwy. 430 & Upper Humber River, 12 June 1979, Larson & Swales [1, DLC, Accession No. 12-105]; Lomond, 49.4619°N, 57.7610°W, 3 m, 6 July 2006, sweep sample, D. Langor [7, DLC, Accession Nos 12-108, 17-17802 to 17-17807; 2, NFRC, Accession Nos NFRC-2022-07149 and 2022-07150]; Noel Paul River, 48.561°N, 58.491°W, 50 m, 22 June 2010, vegetation, sweep, David Langor [2, DLC, Accession Nos 12-120 and 17-17827; 1, NFRC, Accession No. NFRC-2022-07148]; Pasadena, 23 July 1984, D. Langor [1, DLC, Accession No. 12-101]; Ibid. 10 August 1982 [4, DLC, 12-94, 17-17755 to 17-17757]; Ibid., 23 July 1984 [2, DLC, Accession Nos 17-17797 and 17-17798]; Pasadena, 5 July 1993, malaise trap, L. Perry [1, DLC, Accession No. 17-24846]; Pasadena Beach, 49.022°N, 57.608°W, 31 m, 25 June 2010, vegetation, sweep, D. Langor [7, DLC, Accession Nos 12-121, 17-17828, 17-17829, 17-17831, 17-17832, 17-17834; 2, NFRC, Accession Nos NFRC-2022-07151 and 2022-07152]; Port Saunders, 50.65°N, 57.26°W, 16 July 2008, fallow field, sweep sample #10, Goulet, Boudreault & Badiss [3, DLC, Accession Nos 12-111, 17-17811, 17-17812]; Portugal Cove, Nov. 2000, ex. willow, David Larson [2, DLC, Accession No. 17-17760; 1, NFRC, Accession No. NFRC-2022-07153]; Pynn's Brook, 13 June 1979, Larson & Swales [3, DLC, Accession Nos 12-99, 17-17809, 17-17810]; Sandy Lake, 49.2874°N, 56.8743, 317 m, 11 August 2008, shoreline and vegetation, sweep, D. Langor [1, DLC, Accession No. 12-107]; Sandy Lake, 49.288°N, 56.871°W, 100 m, 20 June 2010, *Salix*, sweep, David Langor [1, DLC, Accession No. 12-122]; South Branch, 47.92°N, 59.03°W, 10 July 2008, fallow field, sweep sample #1, Goulet, Boudreault & Badiss [4, DLC, Accession Nos 12-112, 17-17813 to 17-17815]; St. Andrew's, 47.793°N, 59.232°W, 17 June 2004, sweep of field, Henri Goulet [3, DLC, Accession Nos 12-110, 17-17758, 17-17759]; St. Andrew's, 47.79°N, 59.235°W, 15 m, 18 July 2008, fallow field, sweep sample #12, Goulet, Boudreault & Badiss [2, DLC, Accession Nos 12-119 and 17-17823]; St. David's, 48.2°N, 58.6°W, 10 July 2008, fallow field, sweep sample #2, Goulet, Boudreault & Badiss [3, DLC, Accession Nos 12-115, 17-17817, 17-17818]; St. John's, 12 Sept. 1996 [1, DLC, Accession No. 12-97];

St. John's, Newfoundland Drive, 47.6010°N, 52.712°W, 83 m, 2 July 2010, vegetation, sweep, D. Langor [3, DLC, Accession Nos 12-119, 17-17824, 17-17825]; Ibid., 20 June 2009 [4, DLC, Accession Nos 12-123, 17-17836 to 17-17838]; St. John's, Oxen Pond Botanic Park, 23 Aug. to 4 Sept. 1999, David Larson [18, DLC, Accession Nos 12-102, 17-17780 to 17-17796]; St. John's, Quidi Vidi Lake outlet, 47.5841°N, 52.6799°W, 15 m, 20 June 2009, sweep, D. Langor [1, DLC, Accession No. 12-114].

***Tachyerges salicis* (Linnaeus, 1758)** [Curculioninae]

Although O'Brien and Wibmer (1982) recorded this Holarctic species from NF, Anderson (1989) was unable to substantiate the record. To date, we have not seen specimens or verified locality records of this species from the province. However, the species has a transcontinental distribution and occurs from British Columbia to Nova Scotia (Bousquet et al. 2013), so it possibly occurs in NF.

***Phyxelis rigidus* (Say, 1832)** [Entiminae]

McNamara (1991a) first reported this Nearctic species from NL; however, neither Bright and Bouchard (2008) or Anderson (2018) could confirm the record, but it is possible that the species occurs in the province based on its wide distribution in Canada. Still no specimens or verified locality records of this species from NL are known so its presence there cannot be verified and we opt to remove it from the species list for the province.

***Magdalis hispoides* LeConte, 1876** [Mesoptilinae]

This Nearctic species was recorded from NF by O'Brien and Wibmer (1982) but we have found no specimens or verified locality records of this species from the province. The species is common and has a wide distribution, from British Columbia to New Brunswick in Canada (Bousquet et al. 2013), therefore it possibly occurs in NL.

***Conotrachelus nenuphar* (Herbst, 1797)** [Molytinae]

This Nearctic species was recorded from NF by O'Brien and Wibmer (1982) but we have not seen specimens or verified locality records. The species is recorded from British Columbia to Prince Edward Island (Bousquet et al. 2013), so it possibly occurs in NL.

***Hylobius pinicola* (Couper, 1864)** [Molytinae]

This Nearctic species is widespread in NF and was also recorded from LB by Bousquet et al. (2013); however, we have not seen specimens or verified locality records from LB. Nonetheless it is highly likely the species occurs there as it is widely distributed in Canada and its hosts occur in LB.

***Lepyrus nordenskiöldi alternans* Casey, 1895** [Molytinae]

This Nearctic subspecies was reported from only LB by Van Dyke (1928), a record also reported by McNamara (1991a) and Bousquet et al. (2013); however, we have not seen specimens or verified locality records from LB. The two other subspecies in Canada are reported from Yukon to Saskatchewan (Bousquet et al. 2013). It seems unlikely the species (and subspecies) is present in LB so we remove it from the species list for NL.

***Pachylobius picivorus* (Germar, 1824)** [Molytinae]

This Nearctic species was reported from LB by O'Brien and Wibmer (1982), but we have not seen specimens or verified locality records. The only other records from Canada are from Ontario, but the species is widespread in the USA. It seems unlikely that the record from LB is valid, so we hereby remove it from the species list for NL.

***Trachodes hispidus* (Linnaeus, 1758)** [Molytinae]

This Palearctic species was recorded from NF by O'Brien and Wibmer (1982), and this is the only North American jurisdiction from which this species is recorded. We have not seen specimens or verified records from NL, but there is a specimen from the French island of St. Pierre, near the south coast of NF, collected in 1951 (CNC). It is possible that this specimen was the source of the putative record for NF. As the NF record cannot be confirmed, and may simply represent a mistaken attribution of St. Pierre as a part of NF, we opt to remove this species from the list for NL and Canada. However, the species is clearly recorded from North America, although it is uncertain whether it is still established in St. Pierre.

***Pityophthorus cascoensis* Blackman, 1928** [Scolytinae]

This Nearctic species was not recorded from NL by Bright (1981) but was recorded from "Newfoundland" by Wood (1982). We have not seen specimens or verified locality records from NL. The species is also recorded in Canada from Alberta, Northwest Territories and Ontario (Bousquet et al. 2013). Since there is a Newfoundland, New Jersey it is possible the record is from there rather than from NL. We opt to remove this species from the checklist for NL.

***Pityophthorus puberulus* (LeConte, 1868)** [Scolytinae]

This Nearctic species was not recorded from NL by Bright (1981) or Wood (1982) but was recorded from NF by McNamara (1991b). We have not seen specimens or verified locality records from NL. The species is recorded from Ontario to Nova Scotia so its presence in NF is possible. Hence, we consider the presence of this species in NF to be questionable.

***Dendroctonus punctatus* LeConte, 1868** [Scolytinae]

This Nearctic species was recorded from NF by McNamara (1991b), but we have seen no specimens or verified locality records. In Canada, it is distributed from British Columbia to New Brunswick (Bousquet et al. 2013), so its presence in NL is highly likely, especially given its hosts (mainly *Picea* spp. and occasionally *Pinus* and *Larix*; Bright 1976) are widespread in the province.

***Dendroctonus simplex* LeConte, 1868** [Scolytinae]

This Nearctic species is widespread in NF where it sometimes causes outbreaks in *Larix laricina* (Du Roi) K. Koch (Pinaceae) (Langor and Raske 1989). It was reported from LB by McNamara (1991b), but we have not seen specimens or verified locality records from there. Nonetheless, most likely it occurs in LB as its host is abundant there.

***Dendroctonus valens* LeConte, 1857** [Scolytinae]

Bright (1976) recorded this Nearctic species from NF; however, we have seen no specimens or verified locality records from there. One specimen in the CNC, where Bright worked, is from Newfoundland, New Jersey, and this may have been mistakenly recorded by him as from NL. Thus, we remove this species from the list for NL; however, because of its wide distribution in Canada (Bousquet et al. 2013) and the presence of its hosts (mainly *Pinus*; Bright 1976) in NF, it is possible it occurs there.

***Ips perturbatus* (Eichhoff, 1869)** [Scolytinae]

This Nearctic species was recorded from LB by McNamara (1991b), but we have not seen specimens or verified records. The species has a wide distribution and its host (*Picea*; Bright 1976) occurs in LB so it seems likely the species is there and in NF as well.

***Pityokteines sparsus* (LeConte, 1868)** [Scolytinae]

This Nearctic species was reported from NF and LB by McNamara (1991b), but we have not seen specimens or verified records from LB. Nonetheless, given its wide distribution in Canada (Bousquet et al. 2013) and presence of its host (*Abies*; Bright 1976) in LB, we expect it occurs there.

***Scolytus piceae* (Swaine, 1910)** [Scolytinae]

This Nearctic species was reported from NF and LB by McNamara (1991b), but we have not seen specimens or verified records from LB. Nonetheless, given its wide distribution in Canada (Bousquet et al. 2013) and presence of its hosts (mainly *Picea*; Bright 1976) in LB, we expect it occurs there.

Synopsis

With the addition of 30 species and removal of seven unsubstantiated species records from the province's fauna, currently 134 curculionoid species are recorded from NL as a whole, 126 from NF and 36 from LB (Table 1). We could not locate specimens for nine species previously reported by Bousquet et al. (2013) for either NF or LB; however, we opted to retain these records for now because their presence in the Maritime provinces and the availability of suitable host species and climate in NL suggests that these records could be valid, with specimens residing in collections other than those examined for this study.

Even with the additional provincial records reported herein, the curculionoid fauna of NL is depauperate compared to adjacent areas of the mainland of Canada. For example, while NL has almost seven times the area of Nova Scotia, it has only half the number of weevil species of its smaller neighbour. Considering only native species, the NL fauna is even more depauperate as only 89 indigenous species, 14 of them with Holarctic distributions, have been documented.

Clearly the province has a high richness of non-native weevils as 45 species (33.6%) of the total NL fauna is comprised of inadvertently introduced species, all from the Palearctic. Only three non-native species are documented from LB (8.3% of the fauna) while all 45 non-native species occur in NF (33.6% of the island fauna). Although other provinces may have more non-native species overall, in terms of proportion of the jurisdictional fauna represented by non-native species, the island of NF is the most 'Europeanized' part of the country (Bousquet et al. 2013). Notably, 23 non-native species are Entiminae, representing 85% of the species richness of this subfamily in NF. Larvae of most of the members of this subfamily are free-living in the soil and feed on roots or root nodules of plants (Bright and Bouchard 2008). As 17 of the non-native Entiminae species were already widespread in NF by 1949 (Table 1), and most had widespread distributions, it is highly likely many of these were brought to the island in ballast soil in fishing ships from western Europe (especially southwestern England), which was subsequently deposited on shore (Lindroth 1957). This is seemingly a common means of introduction of many soil dwelling insects and other invertebrates and plants to the island of NF (Lindroth 1957). As for other methods of introduction of non-native weevils, folivorous species may have been imported on plants, species of *Sitophilus* on grains/cereals and Scolytinae and Cossoninae on wood, wood products or dunnage. Some species were likely directly introduced to NL from the Palearctic and others likely spread with human assistance from established populations elsewhere in North America. There were undoubtedly multiple introduction events for some species.

It is now virtually impossible to ascertain exactly when and where currently established non-native species were first introduced to NL. By 1951, when the Fennoscandinavian expeditions to NL were complete, 23 of the 59 curculionoid species documented from the province were non-native (all recorded from NF and none from

LB); 16 of those non-native species (including some flightless species) were widely distributed (Table 1) suggesting they had already been present on the island for a long time. From 1961–2010, 3–5 new non-native species were documented from NF per decade, but no new species have been documented from the province since 2010 (Table 1). For the 28 non-native species for which a site of first detection is available (i.e., they were not already widely distributed by the date of first detection), 17 were first documented from St. John's and vicinity (Table 1). This is not surprising as St. John's has served as a major port for centuries, and this city was previously suggested as a likely major site of entry for many non-native insects (Langor et al. 2008, 2014). As well, St. John's likely received much more collecting activity than other parts of the province. Two non-native weevil species were first detected in Port aux Basques, the main ferry port for mainland travel, and two from Corner Brook, the province's largest city on the west coast (Table 1).

Non-native curculionoids in NF are also conspicuous by their relative abundance. According to data from the 1737 specimens in our database that were collected in NL by the conclusion of the Fennoscandinavian expedition in 1951, only two of which were from LB, more than 76% were non-native, representing 25 species. The 415 specimens of native species represented 34 species. Five of the eight most commonly collected species were non-native, and the three most widely and frequently collected species were the non-native *Otiorhynchus ovatus* (70 collection events), *O. rugifrons* (33) and *O. sulcatus* (103). By 2022, the date of the most recent record in our database, the dominance of non-native species was even more pronounced as 18 of the 22 most frequently and widely collected weevil species were non-native (Fig. 2; last two columns). During extensive sampling across NF between 2003–2022, sweep net samples were dominated by non-native *Tychius* spp., *Isochnus sequensi*, *Glocianus punctiger*, *Rhinoncus* spp., *Sitona lepidus* and *Polydrusus cervinus*, and pitfall traps collected large numbers of *Tournotaris bimaculata* and several species of non-native Entiminae (D. Langor, unpublished data).

With few exceptions, native species of Curculionoidea in NL (especially in NF) are much more uncommonly collected than non-native species. A majority of the 88 native species in the province have only been rarely collected; 34 native species are known from only one or two collection events, and a further 13 are known from 3–5 collection events (Table 1). Fourteen native species have not been collected within the last 50 years (Table 1). These facts give rise to important questions. Does the low incidence of collection of native species reflect low abundance or collection biases? If the abundance is truly low, is this attributable to the high diversity and abundance of non-native species? Unfortunately, our data set is unable to directly address these questions as it represents largely *ad hoc* sampling by many people using a variety of collection methods over more than 75 years. Undoubtedly, other curculionoid species are present in NL and will eventually be documented as sampling continues, especially in western NF and northern LB.

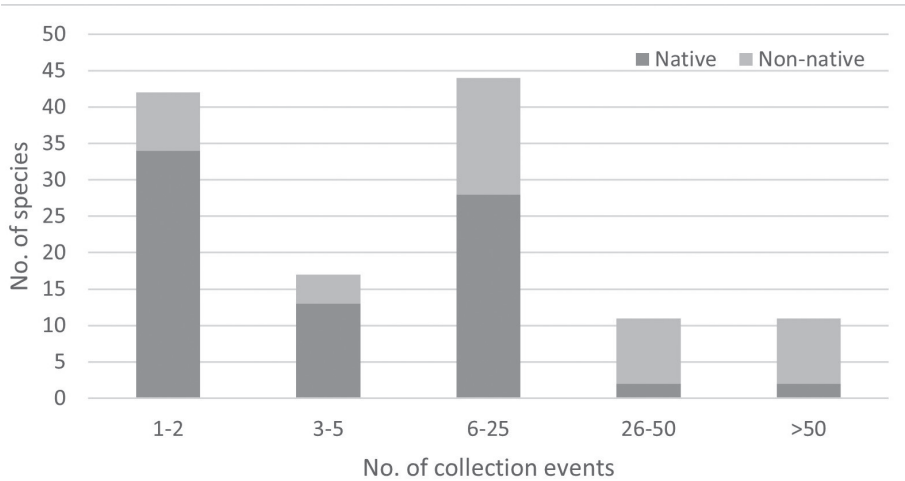


Figure 2. The number of native and non-native species of Curculionoidea in the province of Newfoundland and Labrador, partitioned by the number of collection events for each species. A collection event is a unique combination of locality and date where at least one specimen was collected, labelled, and deposited in a public repository. The dataset was compiled using more than 6400 observed and validated specimen records collected between 1942 and 2022.

Table 1. List of the species of Curculionoidea from the province of Newfoundland and Labrador. Species preceded by an asterisk (*) were documented from the province by the Fennoscandinavian expeditions of 1949 and 1951. A collection event is a unique combination of locality and date where one or more specimens were collected, labelled, and deposited in a public repository. The dataset was compiled using more than 5130 observed and validated specimen records and was the source of information to identify the year and locality of earliest detection for non-native species.

Taxon ¹	Distribution ²	No. collection events ³	Year of earliest [most recent] NL records, and site of first provincial record for non-native species only ⁴
Nemonychidae			
Cimberidinae			
Cimberidini			
<i>Cimberis pilosa</i> (LeConte, 1876)	ON QC NB NF ^{NPR}	1	1973 [1973]
Anthribidae			
Anthribinae			
Tropiderini			
<i>*Gonotropis dorsalis</i> (Thunberg, 1796) ^H	YT NT AB SK MB QC NB NF	2	1949 [1984]
Attelabidae			
Rhynchitinae			
Auletini			
<i>*Auletobius cassandrae</i> (LeConte, 1876)	SK ON QC NB NS PE NF	5	1949 [2010]
Rhynchitini			
<i>Tennocerus cyanellus</i> (LeConte, 1876)	NT AB SK MB ON QC NB NS NF [?]	0	NA
Brentidae			
Apioninae			
Apionini			

Taxon ¹	Distribution ²	No. collection events ³	Year of earliest [most recent] NL records, and site of first provincial record for non-native species only ⁴
<i>*Betulapion simile walshii</i> (J.B. Smith, 1884)	BC AB SK MB ON QC NB NS LB NF	9//1	1949/1978 [1975/2008]
<i>Perapion curtirostre</i> (Germar, 1817) ¹	QC NB NS NF ^{NPR}	18	1999, St. John's, [2014]
Curculionidae			
Brachycerinae			
Eirrhiniini			
<i>*Notaris aethiops</i> (Fabricius, 1792) ^H	YK NT BC AB SK MB ON QC NB NS LB NF	38//6	1949/2004 [2011/2009]
<i>*Notaris puncticolis</i> (LeConte, 1876)	NT BC AB SK MB ON QC NB NS PE NF	2	1951 [1951]
<i>*Tournotaris bimaculata</i> (Fabricius, 1787) ^H	YK NT BC AB SK MB ON QC NB NS NF	10	1949 [2003]
Curculioninae			
Acalyptini			
<i>Acalyptus carpini</i> (Fabricius, 1792)	YT NT BC AB SK MB ON QC NB NS LB ^{NPR}	1	2008 [2008]
Anthonomini			
<i>*Anthonomus (Anthonomus) corvulus</i> LeConte, 1876	BC AB SK MB ON QC NB NS PE NF	5	1949 [2010]
<i>Anthonomus (Anthonomus) lecontei</i> Burke, 1975	BC AB SK MB ON QC NB NS PE NF ^{NPR}	1	2006 [2006]
<i>Anthonomus (Anthonomus) signatus</i> Say, 1832	BC AB SK MB ON QC NB NS PE NF	1	1977 [2010]
<i>Anthonomus (Paranthonomus) rubidus</i> LeConte, 1876	BC ON QC NF ^{NPR}	2	1982 [1982]
<i>Anthonomus (Tachypterellus) quadrigibbus</i> Say, 1832	BC AB SK MB ON QC NB NS NF ^{NPR}	15	2012 [2012]
Ellescini			
<i>Dorytomus laticollis</i> LeConte, 1876	BC AB SK MB ON QC NB NS LB ^{NPR}	1	2009 [2009]
<i>Dorytomus parvicollis</i> Casey, 1892	BC AB SK MB ON QC NB NS NF ^{NPR}	1	1968 [1968]
<i>Dorytomus rufulus</i> (Mannerheim, 1853) ^H	YT NT BC AB SK ON QC NS LB ^{NPR}	1	1981 [1981]
<i>*Dorytomus vagenotatus</i> Casey, 1892	YT NT BC AB SK ON QC NB LB NF	2//2	1949/2008 [1966/2008]
<i>*Ellescus ephippiatus</i> (Say, 1832)	YT BC AB SK ON QC NB NF	1	1949 [1949]
Meciniini			
<i>Mecinus pascuorum</i> (Gyllenhal, 1813) ¹	BC ON QC NS PE NF ^{NPR}	1	2022, Frenchmans Cove, [2022]
<i>Rhinusa antirrhini</i> (Paykull, 1800) ¹	BC AB SK MB ON QC NB NS PE NF	24	1953, Topsail [2006]
Rhamphini			
<i>Isochnus rufipes</i> (LeConte, 1876)	BC AB SK MB ON QC NB NS NF	1	1979 [1979]
<i>Isochnus sequensi</i> (Stierlin, 1894) ¹	ON QC NB NS PE NF	34	1979, 6 sites in W. NF, [2012]
<i>Orchestes pallicornis</i> Say, 1832	BC AB MB ON QC NB NS LB NF ²	0//1	NA/2008 [NA/2008]
<i>*Orchestes testaceus</i> (O.F. Müller, 1776) ^H	BC AB SK MB ON QC NB NS NF	20	1949 [2010]
<i>Tachyerges niger</i> (Horn, 1873)	YT NT BC AB SK MB ON QC NB PE LB	2	2008 [2009]
<i>Tachyerges salicis</i> (Linnaeus, 1758) ^H	NT BC AB SK MB ON QC NB NS NF ²	0	NA
Styphlini			
<i>Orthochaetes setiger</i> ([Beck, 1817]) ¹	BC NF ^{NCR}	2	1995, St. John's, [1999]
Tychiini			
<i>Tychius picirostris</i> (Fabricius, 1787) ¹	BC AB SK MB ON QC NB NS PE LB NF	24//3	1965, St. John's, [2010/2009]

Taxon ¹	Distribution ²	No. collection events ³	Year of earliest [most recent] NL records, and site of first provincial record for non-native species only ⁴
<i>Tychius stephensi</i> Schönherr, 1836 ¹	BC AB SK ON QC NB NS PE NF ^{NPR}	13	1995, Paddy's Pond, [2010]
Ceutorhynchinae			
Ceutorhynchini			
<i>Amalus scortillum</i> (Herbst, 1795) ¹	BC AB SK MB ON QC NB NS NF	1	1965, St. John's, [1965]
<i>Ceutorhynchus americanus</i> Buchanan, 1937	YT NT BC AB SK MB ON QC NB NS NF ^{NPR}	1	2005 [2005]
* <i>Ceutorhynchus hamiltoni</i> Dietz, 1896	QC NB NS PE NF	16	1949 [2010]
* <i>Ceutorhynchus omissus</i> Fall, 1917	AB SK MB ON QC NB NS NF ^{NPR}	1	1949 [1949]
<i>Ceutorhynchus oregonensis</i> Dietz, 1896	YT BC AB MB ON QC NS NF ^{NPR}	1	2008 [2008]
<i>Ceutorhynchus querceti</i> (Gyllenhal, 1813) ^H	NT BC AB MB QC NB NS PE NF [?]	0	NA
* <i>Ceutorhynchus semirufus</i> LeConte, 1876	AB ON QC NB NF	2	1951 [1977]
* <i>Ceutorhynchus typhae</i> (Herbst, 1795) ¹	ON QC NB NS NF	10	1949, Harmon Field, [1977]
* <i>Glocianus punctiger</i> (C.R. Sahlberg, 1835) ¹	YT BC AB SK MB ON QC NB NS PE NF	27	1949, widespread, [2008]
Cnemogonini			
* <i>Auleutes epilobii</i> (Paykull, 1800) ^H	YT NT BC AB SK MB ON QC NB NS PE NF	17	1949 [2008]
<i>Cnemogonus lecontei</i> Dietz, 1896	YT NT BC AB MB ON QC NB LB ^{NPR}	2	1982 [2008]
<i>Dietzella zimmermanni</i> (Gyllenhal, 1837)	BC SK ON QC NB NF [?]	0	NA
* <i>Perigaster liturata</i> (Dietz, 1896)	YT ON QC NB NS PE NF	2	1949 [1973]
Phytobiini			
<i>Pelenomus fuliginosus</i> (Dietz, 1896)	BC AB ON QC NB LB ^{NPR}	2	2002 [2002]
<i>Rhinoncus bruchoides</i> (Herbst, 1784) ¹	QC NS NF ^{NPR}	1	2008, Logy Bay, [2008]
* <i>Rhinoncus leucostigma</i> (Marshall, 1802) ¹	BC ON QC NB NS PE NF	16	1949, St. John's, [2001]
* <i>Rhinoncus pericarpus</i> (Linnaeus, 1758) ¹	BC ON QC NB NS PE LB NF	28//3	1949/1980, widespread, [2005/2008]
Scleroterini			
<i>Prorutidosoma decipiens</i> (LeConte, 1876)	YT BC AB SK MB ON QC PE LB NF ^{NPR}	3//1	2003/2002 [2003/2002]
Cossoninae			
Cossonini			
* <i>Cossonus americanus</i> Buchanan, 1936	SK QC NB NS NF	5	1949 [1995]
Pentarthriini			
<i>Euophryum confine</i> (Broun, 1880) ¹	NF	9	1978, St. John's, [2002]
<i>Pentarthrum huttoni</i> Wollaston, 1854 ¹	QC BF	6	1978, St. John's, [1994]
Rhyncolini			
* <i>Carphonotus testaceus</i> Casey, 1892	BC AB SK ON QC NB NS PE NF	7	1949 [1992]
* <i>Rhyncolus brunneus</i> Mannerheim, 1843	YT NT BC AB SK MB ON QC NB NS PE LB NF	23//1	1949 [2011]
<i>Rhyncolus macrops</i> Buchanan 1946	BC ON QC NB NS NF ^{NPR}	1	2011 [2011]
Cryptorhynchinae			
Cryptorhynchini			
<i>Cryptorhynchus lapathi</i> (Linnaeus, 1758) ^H	BC AB SK MB ON QC NB NS PE NF	23	1958 [2002]
Cyclominae			
Listroderini			
* <i>Listronotus humilis</i> (Gyllenhal, 1834)	BC QC NB NF	8	1949 [1964]
Dryophthorinae			
Rhynchophorini			

Taxon ¹	Distribution ²	No. collection events ³	Year of earliest [most recent] NL records, and site of first provincial record for non-native species only ⁴
<i>Sitophilus granarius</i> (Linnaeus, 1758) ¹	BC AB SK MB ON QC NB NS PE NF	9	1974, St. John's [1995]
<i>Sitophilus oryzae</i> (Linnaeus, 1763) ¹	BC AB SK ON QC NB NS PE NF	9	1966, Port aux Basques, [2000]
<i>Sitophilus zeamais</i> Motschulsky, 1855 ¹	MB ON QC NF ^{NPR}	1	1985, St. John's, [1985]
Entiminae			
Brachyderini			
<i>*Strophosoma melanogrammum</i> (Forster, 1771) ¹	BC ON QC NS PE NF	86	1949, widespread, [2012]
Cneorhinini			
<i>*Philopodon plagiatum</i> (Schaller, 1783) ¹	ON QC NB NS PE NF	23	1949, Port aux Basques, [2010]
Geonemini			
<i>*Barynotus obscurus</i> (Fabricius, 1775) ¹	BC QC NB NS PE NF	27	1949, widespread, [2004]
<i>*Barynotus schoenherri</i> (Zetterstedt, 1838) ¹	QC NB NS PE NF	49	1949, widespread, [2012]
Hormorini			
<i>*Hormorus undulatus</i> (Uhler, 1856)	AB MB ON QC NB NS PE NF	2	1949 [2013]
Otiorynchini			
<i>*Otiorynchus desertus</i> Rosenhauer, 1847 ¹	NF	3	1949, Cape Broyle, [1997]
<i>*Otiorynchus ligneus</i> (Olivier, 1807) ¹	QC NB NS PE NF	11	1949, widespread, [1989]
<i>*Otiorynchus ovatus</i> (Linnaeus, 1758) ¹	YT NT BC AB SK MB ON QC NB NS PE LB NF	145//6	1949, widespread, [2003/2008]
<i>Otiorynchus porcatus</i> (Herbst, 1795) ¹	ON QC NC NF	8	1965, St. John's, [1992]
<i>*Otiorynchus rugifrons</i> (Gyllenhal, 1813) ¹	QC NB NS NF	58	1949, widespread, [2011]
<i>*Otiorynchus singularis</i> (Linnaeus, 1767) ¹	BC ON QC NB NS PE NF	72	1944, St. John's, [2012]
<i>*Otiorynchus sulcatus</i> (Fabricius, 1775) ¹	BC AB SK MB ON QC NB NS PE NF	240	1949, widespread, [2011]
Peritelini			
<i>Nemocestes horni</i> Van Dyke, 1936	BC SK ON QC NB NS NF	4	1966 [1983]
Phyllobiini			
<i>Phyllobius oblongus</i> (Linnaeus, 1758) ¹	BC ON QC NB NS PE NF ^{NPR}	3	2010, Corner Brook, [2011]
Polydrusini			
<i>Pachyrhinus elegans</i> (Couper, 1865)	BC AB SK AB QC NB NS NF ^{NPR}	2	2022, western NL, [2022]
<i>Polydrusus cervinus</i> (Linnaeus, 1758) ¹	QC NS PE NF ^{NPR}	1	2010, Tompkins, [2010]
<i>Polydrusus formosus</i> (Mayer, 1779) ¹	BC ON QC NB NS PE NF ^{NPR}	12	2002, Corner Brook, [2013]
Sciaphilini			
<i>*Barypeithes pellucidus</i> (Boheman, 1834) ¹	BC MB ON QC NB NS PE NF	56	1949, widespread, [2010]
<i>*Brachysomus echinatus</i> (Bonsdorff, 1785) ¹	QC NF	2	1949, widespread, [1949]
<i>*Sciaphilus asperatus</i> (Bonsdorff, 1785) ¹	BC AB MB ON QC NB NS PE NF	69	1949, widespread, [2011]
Sitonini			
<i>Sitona cylindricollis</i> (Fahraeus, 1840) ¹	YT NT BC AB SK MB ON QC NB NS PE NF ^{NPR}	5	1980, St. John's, [2008]
<i>Sitona hispidulus</i> (Fabricius, 1777) ¹	NT BC AB SK ON QC NB NS PE NF	5	1979, St. John's, [1986]
<i>*Sitona lepidus</i> Gyllenhal, 1834 ¹	BC AB SK MB ON QC NB NS PE NF	86	1949, widespread, [2008]
<i>Sitona lineellus</i> (Bonsdorff, 1785) ^{H1}	YT NT BC AB SK MB ON QC NB NS PE LB NF	11//1	1980/? [2008/?]
Trachyphlocini			
<i>*Romualdus bifoveolatus</i> ([Beck], 1817) ¹	BC MB ON QC NB NS PE NF	29	1949, widespread, [2008]
Tropiphorini			
<i>*Tropiphorus elevatus</i> (Herbst, 1795) ¹	NF	2	1951, Millertown, [1951]
<i>Tropiphorus terricola</i> (Newman, 1838) ¹	QC NB NS PE NF	7	1965, St. John's, [2000]
Hyperinae			
Hyperini			
<i>*Brachyptera zoilus</i> (Scopoli, 1763) ¹	BC ON QC NB NS PE NF	45	1949, widespread, [2000]

Taxon ¹	Distribution ²	No. collection events ³	Year of earliest [most recent] NL records, and site of first provincial record for non-native species only ⁴
<i>*Hypera nigrirostris</i> (Fabricius, 1775) ¹	BC ON QC NB NS PE NF	69	1949, widespread, [2014]
Lixinae			
Cleonini			
<i>*Stephanocleonus plumbeus</i> LeConte, 1876	AB SK MB QC LB NF	4/1	1949/2005 [1993/2005]
Mesoptilinae			
Magdalidini			
<i>*Magdalis alutacea</i> LeConte, 1878	YT NY BC AB SK QC MB LB NF ^{NPR}	1/1	1949/1948 [1949/1948]
<i>Magdalis gentilis</i> LeConte, 1876	BC NF ^{NPR}	1	1972 [1972]
<i>Magdalis hispidus</i> LeConte, 1876	YT BC AB ON QC NB NF [?]	0	NA
Molytinae			
Conotrachelini			
<i>Conotrachelus nenuphar</i> (Herbst, 1797)	BC AB SK MB ON QC NB NS PE NF [?]	0	NA
Hylobiini			
<i>*Hylobius congener</i> Dalla Torre, Schenk. & Marsh., 1932	YT NT BC AB SK MB ON QC NB NS PE LB NF	58/18	1949/1942 [2012/2005]
<i>*Hylobius pinicola</i> (Couper, 1864)	BC AB SK MB ON QC NB NS LB [?] NF	56/0	1949/NA [2011/NA]
<i>Hylobius warreni</i> Wood, 1957	BC AB SK MB ON QC NB NS LB NF ^{NPR}	15/6	1960/2004 [2012/2009]
Lepyritini			
<i>Lepyrus labradorensis</i> Blair, 1933	NT QC LB	2	1954 [1954]
<i>Lepyrus palustris</i> (Scopoli, 1763) ^H	NT BC AB SK MB ON QC NB LB NF	1/1	2003/2006 [2003/2006]
Molytini			
<i>Sthereus ptinoides</i> (Germar, 1824) ^H	BC NB NS NF	8	1965 [1999]
Pissodini			
<i>*Pissodes affinis</i> Randall, 1838	NT BC AB SK MB ON QC NB NS NF	3	1945 [1945]
<i>*Pissodes fiskei</i> Hopkins, 1911	YT BC AB SK MB ON QC NB NS PE NF	2	1953 [1998]
<i>*Pissodes nemorensis</i> Germar, 1824	MB ON QC NB NS PE NF	17	1942 [1989]
<i>Pissodes rotundatus</i> LeConte, 1876	YT NT BC AB SK MB ON QC NB NS LB NF	5/1	1943/1976 [1989/1976]
<i>*Pissodes similis</i> Hopkins, 1911	BC AB ON QC NB NS NF	19	1943 [2011]
<i>Pissodes striatulus</i> (Fabricius, 1775)	BC AB SK MB ON QC NB NS PE LB NF	18/5	1963/1965 [1988/1986]
Scolytinae			
Corthylini			
<i>Pityophthorus dentifrons</i> Blackman, 1922	AB ON QC NB NS PE NF	1	1970 [1970]
<i>Pityophthorus intextus</i> Swaine, 1917	YT BC AB SK MB ON QC NB NS NF	6	1970 [1982]
<i>*Pityophthorus nitidus</i> Swaine, 1917	YT NT BC AB ON QC NB NS NF	6	1949 [1988]
<i>Pityophthorus opaculus</i> LeConte, 1878	YT NT BC AB SK MB ON QC NB NS NF	1	1970 [1970]
<i>Pityophthorus puberulus</i> (LeConte, 1868)	ON QC NB NS NF [?]	0	NA
Cryphalini			
<i>*Cryphalus ruficollis ruficollis</i> Hopkins, 1915	YT BC AB MB ON QC NB NS NF	7	1979 [1988]
<i>Trypophloeus striatulus</i> (Mannerheim, 1853)	YT AB MB QC NS NF	1	?
Crypturgini			
<i>*Crypturgus borealis</i> Swaine, 1917	NT BC AB SK MB ON QC NB NS PE NF	4	1949 [1984]
<i>*Crypturgus pusillus</i> (Gyllenhal, 1813) ¹	SK ON QC NB NS PE NF	13	1949, Lomond, [1989]

Taxon ¹	Distribution ²	No. collection events ³	Year of earliest [most recent] NL records, and site of first provincial record for non-native species only ⁴
Dryocoetini			
<i>*Dryocoetes affaber</i> (Mannerheim, 1852)	YT NT BC AB SK MB ON QC NB NS PE LB NF	10//4	1949/1981 [1990/2009]
<i>*Dryocoetes autographus</i> (Ratzeburg, 1837) ^H	YT NT BC AB SK MB ON QC NB NS PE LB NF	44//5	1949/1982 [2011/2009]
<i>Dryocoetes betulae</i> Hopkins, 1894	BC AB ON QC NB NS NF	15	1970 [2012]
Hylastini			
<i>*Scierus annectans</i> LeConte, 1876	NT BC AB ON QC NB NS PE LB NF	3/1	1949/2008 [1984/2008]
Hylurgini			
<i>Dendroctonus punctatus</i> LeConte, 1868	YT NT NU BC AB ON QC NB NF [?]	0	NA
<i>*Dendroctonus rufipennis</i> (Kirby, 1837)	YT NT NU BC AB SK MB ON QC NB NS PE LB NF	19//3	1949/2008 [2010/2009]
<i>Dendroctonus simplex</i> LeConte, 1868	YT NU BC AB SK MB ON QC NB NS PE LB [?] NF	16/0	1970 [1989]
<i>Xylechinus americanus</i> Blackman, 1922	ON QC NB NS NL	1	2017 [2017]
Ipini			
<i>Ips borealis</i> Swaine, 1911	YT NT BC AB SK MB ON QC NB NS PE LB NF	10//1	1970/1981 [1988/1981]
<i>Ips perturbatus</i> (Eichhoff, 1869)	YT NT BC AB SK MB ON QC NB LB [?]	0	NA
<i>Ips pini</i> (Say, 1826)	YT NT BC AB SK MB ON QC NB NS PE LB NF	6//1	1970/2008 [1984/2008]
<i>*Orthotomicus caelatus</i> (Eichhoff, 1868)	YT NT BC AB SK MB ON QC NB NS PE NF	3	1949 [1982]
<i>Pityogenes hopkinsi</i> Swaine, 1915	SK MB ON QC NB NS NF	4	1970 [1987]
<i>Pityokteines sparsus</i> (LeConte, 1868)	AB SK MB ON QC NB NS PE LB [?] NF	10//0	1970/NA [1989/NA]
Phloeotribini			
<i>Phloeotribus piceae</i> Swaine, 1911	YT NT BC AB MB ON QC NB NS NF ^{NPR}	1	1994 [1994]
Polygraphini			
<i>*Polygraphus rufipennis</i> (Kirby, 1837)	YT NT BC AB SK MB ON QC NB NS PE LB NF	58//6	1949/1981 [2012/2009]
Scolytini			
<i>*Scolytus piceae</i> (Swaine, 1910)	YT NT BC AB SK MB ON QC NB NS LB [?] NF	5//0	1949/NA [1982/NA]
Xyleborini			
Xyloterini			
<i>*Trypodendron lineatum</i> (Olivier, 1795) ^H	YT BC AB SK MB ON QC NB NS PE NF	24	1949 [2011]

¹ * denotes species documented from NL by 1951 (completion of the Fennoscandinavian expeditions); Superscript definitions: H, species with a Holarctic distribution; I, denotes non-native species. ² Jurisdictional acronyms: AB – Alberta, BC – British Columbia, LB – Labrador, MB – Manitoba, NB – New Brunswick, NF – Newfoundland, NS – Nova Scotia, NT – Northwest Territories, NU – Nunavut, O – Ontario, PE – Prince Edward Island, QC – Quebec, SK – Saskatchewan, YT – Yukon. Jurisdictions indicated in bold font denote new records reported herein. Superscript definitions: NPR – new provincial record for NL, NCR – new Canadian record, ? – record for NL or LB that could not be yet verified by the existence of published locality records or observation of a specimen by the authors. ³ For entries containing two numbers separated by “/”, the first refers to NF and the second to LB. ⁴ Species that have not been captured in NL in the last 50 years are indicated in bold font.

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Nomenclature of the veins of the fore wings of male scale insects (Hemiptera, Coccoomorpha)

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Abstract

The venation of the fore wings of male scale insects is strongly reduced and the nomenclature used for each vein is inconsistent among taxonomists. This paper reviews the different nomenclatural systems in the wing venation of male scale insects that have been suggested previously and puts forward a new system based mainly on newly found wing venation in males of *Qinococcus podocarpus* Wu, 2022 (Hemiptera: Coccoomorpha: Qinococcidae).

Keywords

Coccoids, forewing, new nomenclature system, Qinococcidae, *Qinococcus podocarpus*, wing veins

Introduction

Comparative morphology of wing venation plays an important role in insect classification and phylogeny (Yang et al. 2012; Perrard et al. 2016). However, in the Coccoomorpha, the nomenclature for the wing veins varies in interpretation among taxonomists, impeding phylogenetic research within the infraorder. Based on a review of the different nomenclatural systems proposed previously and a newly found wing venation pattern in males of *Qinococcus podocarpus* Wu, 2022 (Hemiptera: Coccoomorpha: Qinococcidae), a new nomenclature system for the wing venation of scale insects is suggested.

Review of the nomenclature used for the veins of the fore wings of male scale insects

The scale insects belong to the infraorder Coccoomorpha (Fallen, 1814), suborder Sternorrhyncha, order Hemiptera. They are sexually dimorphic, the adult female being wingless whilst the adult male (of winged species) has two pairs of wings; the fore wings are reasonably well developed, folding flat over the abdomen when at rest and overlapping each other, whereas the hind wings are reduced to hamulohalteres (Hodgson and Foldi 2006; Hodgson 2020).

The fore wings of male scale insects are normally large and quite broad with a narrow base and a broadly rounded apex (e.g., *Orthezia urticae* (Linnaeus, 1758) and *Asiacornococcus kaki* (Kuwana in Kuwana and Muramatsu 1931)) (Hodgson and Foldi 2006) but are wider at the base and narrower at the apex in some species (e.g., *Drosicha* sp.). They are membranous throughout except for (usually) a longitudinal sclerotized (leather-like) thickening running parallel to and just posterior to the anterior margin called the Costal thickening (**Ct**). Compared with psyllids and aphids, the remaining wing venation in male scale insects is much more reduced, usually with two well-developed veins (or vein complexes, each composed of two veins) and some transparent but obvious lines (weakly developed veins or folds). The two main veins are the Anterior Vein (**AV**) just posterior to the Costal thickening (**Ct**), and the Posterior Vein (**PV**), which runs diagonally from near the base of the Anterior Vein (**AV**) obliquely to the margin of the Posterior Vein (**PV**); both the **AV** and the **PV** normally join at an acute angle in the basal area. Moreover, each wing also has either a long fold or a small alar lobe on its proximal hind margin, providing a structure for connecting with hooked haltere setae on the hind wing (hamulohalteres) (Hodgson 2020). The venation in the superfamily Orthezioidea (= Archaeococcoidea) is more complex than that in the superfamily Coccoidea (= Neococcoidea) (Giliomee 1961, 1967a; Hodgson and Foldi 2006).

Some workers have tried to analyze, interpret, and name the wing veins and lines, but the results have been variable and currently there is no standardized system for wing venation nomenclature. Patch (1909), after studying the homologies of the wing veins of aphids, psyllids, aleurodids, and coccoids, considered that the fore wings of *Dactylopius* sp. (Dactylopiidae) and *Planococcus citri* (Risso, 1813) (Pseudococcidae) were composed of a short sclerotized Subcosta (**Sc**), and well-developed Radial sector (**Rs**) and Media (**M**) in accordance with the Comstock-Needham system (Comstock and Needham 1898).

Morrison (1928) considered that the venation of the fore wing of Margarodidae *sensu lato* was composed of the costal complex, the basal diagonal vein, and an apical diagonal vein, which is poorly developed, short, and occasionally present. He also believed that: 1) the costal complex contained two veins, the Subcosta (**Sc**) and Radius (**R**); 2) the basal diagonal vein, considered by Patch to be the Media (**M**) of the Comstock-Needham system, should be the Cubitus (**Cu**); and 3) that the apical diagonal vein was the Radial sector (**Rs**).

Ghauri (1962) considered the two wing veins of the Diaspididae to be the Radius (**R**) and Media (**M**). This was also the case for the wing veins of the Pseudococcidae (Giliomee 1961; Afifi 1968), the Coccidae (Giliomee 1967b) and the Eriococcidae (Afifi 1968).

Afifi (1968) considered that the wing veins of Pseudococcidae and Eriococcidae were comprised of the Radius (**R**) and Media (**M**) only.

Beardsley (1968) considered that the wing venation of *Matsucoccus bisetosus* Morrison, 1939 (Matsucoccidae) was composed of a Subcostal thickening (**Sct**), a Radius (**R**), a Media (**M**), and the Anal fold (**Af**) (Fig. 1).

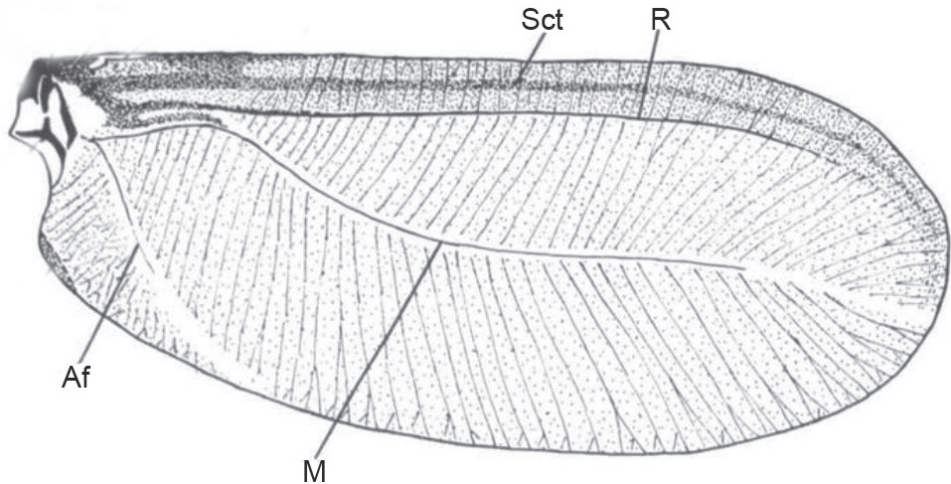


Figure 1. The fore wing of *Matsucoccus bisetosus* (after Beardsley 1968). Abbreviations: Af, Anal fold; M, Media; R, Radius; Sct, Subcostal thickening.

Koteja (1986) considered that, on the fore wing of *Orthezia urticae* (Ortheziidae), the Anterior Vein (**AV**) was the Subcostal ridge (**Scr**), the Posterior Vein (**PV**) was the Cubitus (**Cu**), and the two obvious lines between the AV and the PV were the Radial sector (**Rs**) and Medial sector (**Ms**), respectively, whilst the obvious line posterior to the PV was the Anal fold (**Af**) (Fig. 2).

Lambdin (2001) considered that the wing venation in the more “advanced” scale insects such as *Pseudococcus* (Pseudococcidae), was composed of a Radius (**R**) and a Media (**M**), whilst the venation in wings of the more “primitive” scale insects, such as *Drosicha* sp. (Monophlebidae), consisted of a costal complex (**Costa + Subcosta**), a Radius (**R**) and a Media (**M**), whereas the white line between AV and PV was termed the Radial sector (**Rs**), and the pale line posterior to the PV was the Cutino-anal vein (**Cu-a**) (Fig. 3).

Hodgson and Foldi (2006) followed Beardsley (1968), namely identifying the fore wing of *Drosicha* to be a Media and a Subcostal thickening, the Radius.

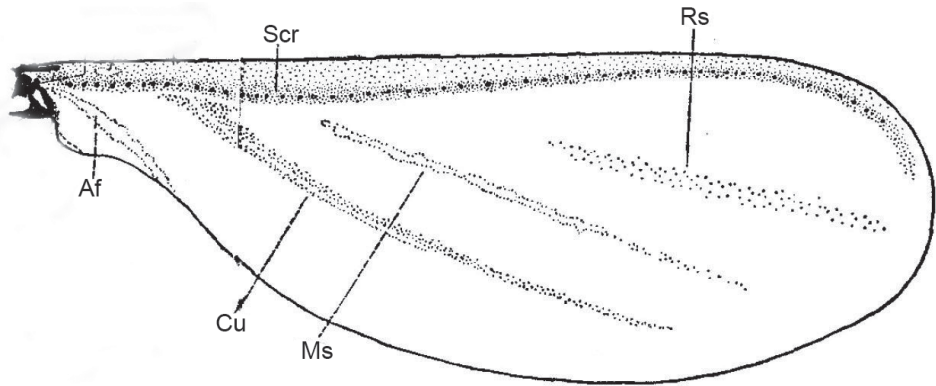


Figure 2. The fore wing of *Orthezia urticae* (after Koteja 1986). Abbreviations: Af, Anal fold; Cu, Cubitus; Ms, Medial sector; Rs, Radial sector; Scr, Subcostal ridge.

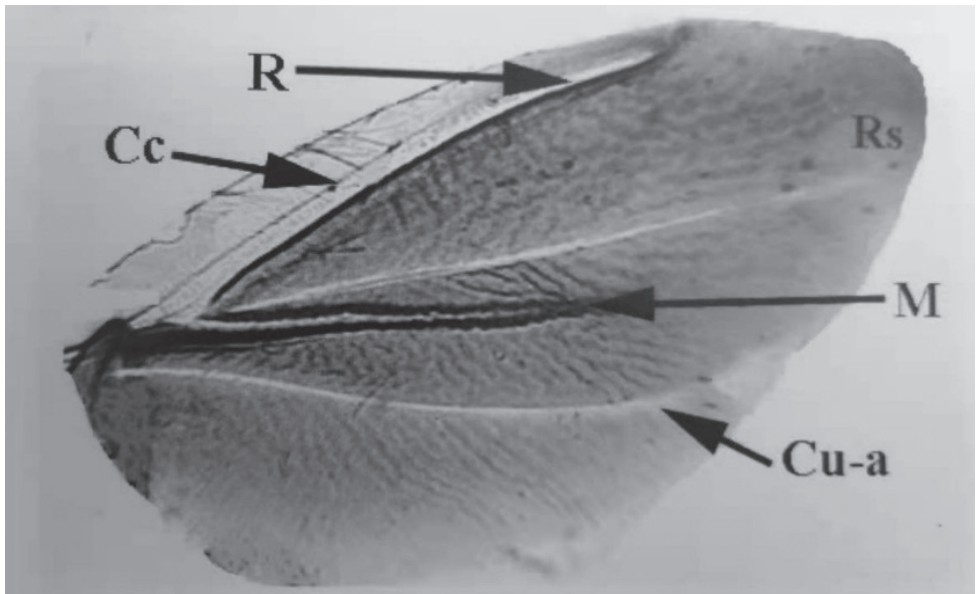


Figure 3. The fore wing of *Drosicha* sp. (after Lambdin 2001). Abbreviations: Cc, Costal complex (Costa + Subcosta); Cu-a, Cutino-anal vein; M, Media; R, Radius; Rs, Radial sector.

Shcherbakov (2007) considered that the venation of *Orthezia urticae* (Ortheziidae) consisted of the Sc+R (= Costal complex of Morrison (1928)), a Cubitus Anterior (**CuA**), a Radial sector (**Rs**) (= apical diagonal vein of Morrison (1928)), whilst the pale line between the AV and the PV was the Media (**M**) and the pale line posterior to the PV was the Cubitus Posterior (**CuP**) (= Anal fold of Beardsley (1968)). Shcherbakov also considered that the anal lobe or pocket was the fused Postcubitus and anal first vein (**Pcu+1A**), and the Sc+R and the CuA were composed of two folds, each with a convex and a concave part (Fig. 4).

Koteja (2008) explained the wing venation of the extinct species *Weitschatus vysniauskasi* Koteja, 2008 (Weitschatidae) as follows: the Subcostal ridge (**Scr**) runs along costal margin from the wing base toward the wing apex; the Cubital ridge (**Cur**) originates from the Scr at $\sim 1/5$ wing length and runs obliquely to the posterior wing margin, and the Radial sector (**Rs**) (= anterior diagonal vein of Morrison (1928)) is a slightly sclerotized oblique patch posterior to the Scr. He also described and illustrated an anterior flexing patch (**afx**) between Scr and Cur, a posterior flexing patch (**pfx**) posterior to the Cur, and a pterostigma (**ptst**) at the apex of the Scr (Fig. 5).

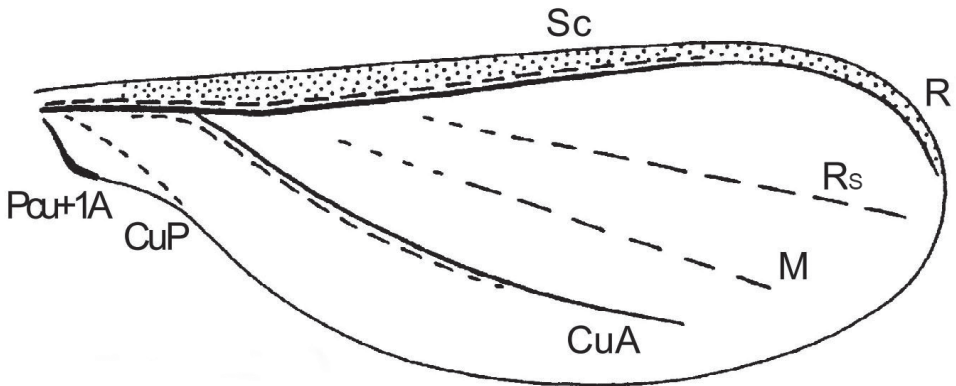


Figure 4. The fore wing of *Orthezia urticae* (after Shcherbakov 2007). Abbreviations: CuA, Cubitus Anterior; CuP, Cubitus Posterior; M, Media; Pcu+1A, fused Postcubitus and anal first vein; R, Radius; Rs, Radial sector; Sc, Subcosta.

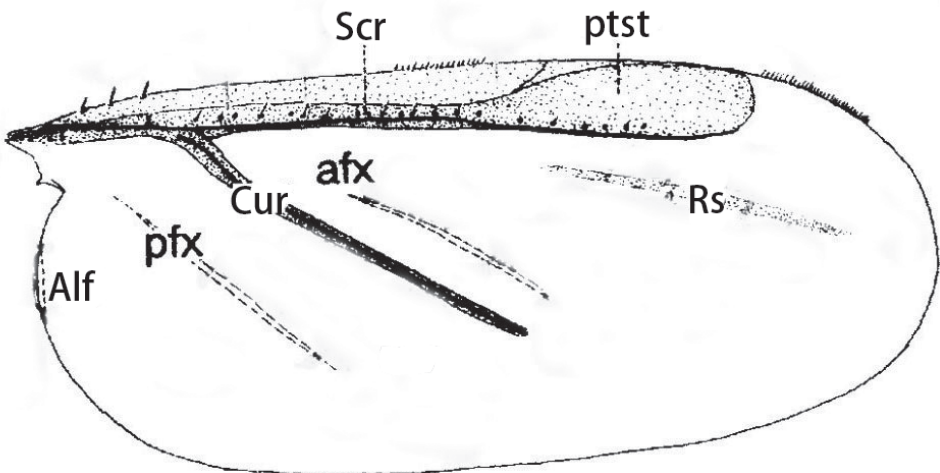


Figure 5. The fore wing of *Weitschatus vysniauskasi* (after Koteja 2008). Abbreviations: Alf, Alar fold; afx, anterior flexing patch; Cur, Cubital ridge; pfx, posterior flexing patch; ptst, pterostigma; Rs, Radial sector; Scr, Subcostal ridge.

Franielczyk-Pietryra et al. (2018) explained the wing venation of *Orthezia urticae* (Ortheziidae) as Sc+R and CuA with the two obvious lines between those two which were identified as rs (putative Rs) and ms (putative Ms), respectively (Fig. 6).

In 2021, Wu et al. (2022) collected *Qinococcus podocarpus* Wu (Qinococcidae), a new species in which the venation of the fore wing of the adult male is more complex than in previously described Coccoomorpha. The fore wing of this species has a pterostigma, an obvious forked line between the AV and the PV (= **R** and **CuA** in Fig. 7), and two obvious lines posterior to the PV (Fig. 7). The venation of the fore wings of *Q. podocarpus* is very similar to that of *Mindarus* (Hemiptera: Aphidomorpha) (see fig. 8 of Montagano and Favret 2016, here as Fig. 8), differing mainly in that, in the former species, the veins of the Rs and M are much reduced and both an Anal fold (Af) and Alar fold of the anal lobe (Alf) are present.

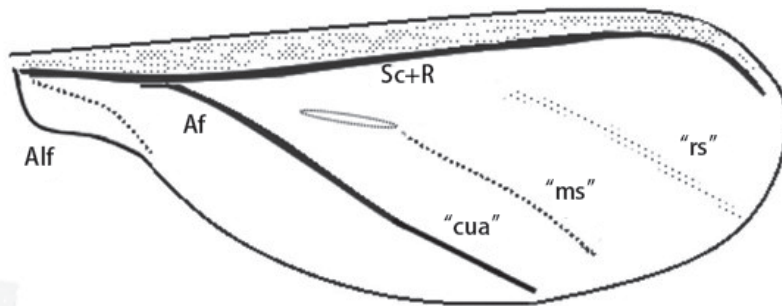


Figure 6. The fore wing of *Orthezia urticae* (after Franielczyk-Pietryra et al. 2018). Abbreviations: Af, Anal fold; Alf, alar fold of anal lobe; cua in quotes, putative cubitus anterior; ms in quotes, putative media sector; rs in quotes, putative radius sector; Sc+R, fused Subcosta and Radius.

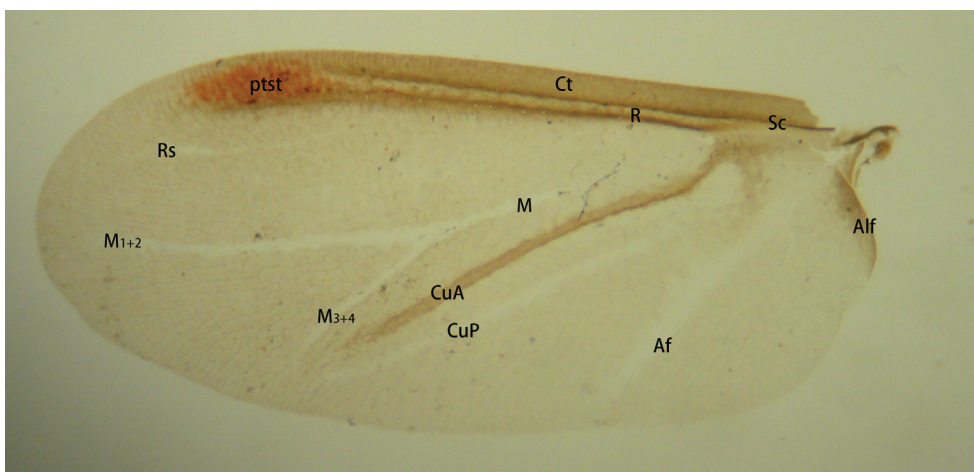


Figure 7. The fore wing of *Qinococcus podocarpus* Wu. Abbreviations: Af, Anal fold; Alf, alar fold; Ct, Costal thickening; CuA, Cubitus Anterior; CuP, Cubitus Posterior; M, Media; M₁₊₂, fusion of the first and second branch of media; M₃₊₄, fusion of the third and fourth branch of media; ptst, pterostigma; R, Radius; Rs, Radius sector; Sc, Subcosta.

The names of the fore wing veins of scale insects

The veins of insects are composed of nerves, tracheae, and a cavity for the haemolymph (Dudley 2000) and the nomenclature used to describe them is based on their positions and relationships on each wing. However, in practice, it is impossible to name each vein based on these structures, especially for fossil examples. To understand the evolution of a target group (e.g., Coccoomorpha), it is important to compare the venation of this group with that of its sister group (in this case, Aphidomorpha) and other closely related groups.

The infraorder Coccoomorpha (scale insects) belongs to the suborder Sternorrhyncha which includes three other infraorders: Psyllomorpha (jumping plant-lice), Aleyrodomorpha (whiteflies), and Aphidomorpha (aphids). For the choice of names for the veins of scale insects, references to those given to the veins of aphids and the jumping plant-lice are obviously very helpful.

The Sternorrhyncha belong to the Paraneoptera within the Hemiptera. The wing venation characters of the Paraneoptera, proposed by Grimaldi and Engel (2005), are “CuA and M basally fused to the R in a common stem, and both distally emerging again from this stem, either together or separately; a cross-vein CuA-CuP present or absent, but when present, its proximal part is concave and its distal part is convex (in some taxa, the distal part can be “captured” by the CuA, so that the CuA-CuP seems to continue from the distal part of the CuA); anal area generally rather reduced, especially in forewing with two anal veins or less; CuP simple and concave; CuA convex and with two distal branches or less; M more concave than surrounding veins R and CuA, at least in its distal part, with four branches or less”. Based on this hypothesis, we have analyzed each vein on *Q. podocarpus* and have provided names

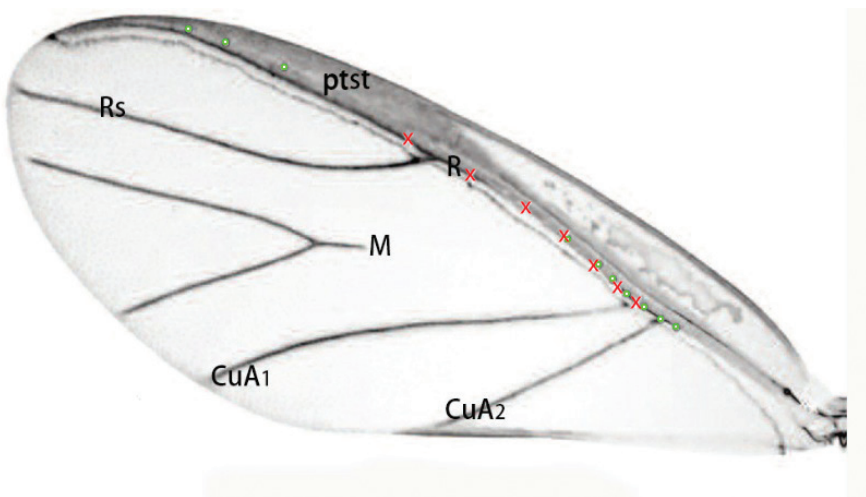


Figure 8. Fore wing of *Mindarus* (after Montagano and Favret 2016). Abbreviations: CuA₁, the first branch of cubitus anterior; CuA₂, the second branch of cubitus posterior; M, media; R, radius; Rs, radius sector. X-markers in red indicate campaniform sensilla located dorsally, O-markers in green are ventrally located sensilla.

for each of the veins, resulting in a new nomenclature system for the scale insects (Fig. 7) which follows.

1. Unlike in the Aphidomorpha and Psyllomorpha, the anterior margin of the fore wing in the Coccoomorpha is usually less developed, with no distinct cavity; the Coccoomorpha also lack tracheae, and usually have a sclerotized part posterior to the margin, so there is no costal vein present (Franielczyk-Pietryra et al. 2018); Lambdin (2001) named this structure the Costal complex. Comparing the fore wing of some jumping plant-lice (such as *Pachypsyllodes citreus* Loginova) with the anterior sclerotized part in the Coccoomorpha, we consider that the best name for this structure in the Coccoomorpha is the Costal thickening (**Ct**).

2. The anterior vein in the Coccoomorpha runs along the costal margin from the wing base toward the wing apex, and this was named the Subcostal ridge (**Scr**) by Koteja (1986, 2008). However, Shcherbakov (2007) considered this vein to be a merged vein in *Orthezia urticae* and named it as Sc + R (the fused Subcosta and Radius) and this was confirmed by Franielczyk-Pietryra et al. (2018). In *Matsucoccus* and *Q. podocarpus*, there are two distinct, separate veins present, and these were given the names Subcostal thickening (**Sct**) and Radius respectively by Beardsley (1968) and Hodgson and Foldi (2006). Franielczyk-Pietryra and Wegierek (2017, 2019) and Franielczyk-Pietryra et al. (2018) considered that the Sc was absent in all Sternorrhyncha but present in the Coccoomorpha. However, Hong (1999) considered some aphids such as *Paroviparosiphum opimum* Zhang to have a free Sc. Comparing the venation on Coccoomorpha with that of aphids, we consider the best name for (i) the anterior vein is Sc, and (ii) that, for the root stem of the posterior vein is R+M+CuA, with the top part as R, although the root stem of the posterior vein is weak in *Q. podocarpus*.

3. In the Coccoomorpha, the posterior vein originates from the R+M+CuA at about 1/5 along the wing length and runs obliquely to the posterior wing margin; this is termed the basal diagonal vein by Morrison (1928), M by Lambdin (2001) and Hodgson and Foldi (2006), Cu by Koteja (1986), CuA by Shcherbakov (2007) and Franielczyk-Pietryra et al. (2018), and Cubital ridge (**Cur**) by Koteja (2008). Here we consider it to be the CuA.

4. The vein that Morrison (1928) called the anterior diagonal vein is a slightly sclerotized oblique patch (e.g., in *Orthezia urticae* and *Xylococcus castanopsis* Wu & Huang, 2017) or a short obvious line (e.g., in *Kuwania bipora* Borchsenius, 1960 and *Q. podocarpus*) posterior to the radius (**R**). This vein is named the Radial sector (**Rs**) by Koteja (1986, 2008), Shcherbakov (2007), and Franielczyk-Pietryra et al. (2018). Here we believe it is best to call this vein the Rs.

5. The obvious patch or light line between R and CuA is usually unbranched and is named Ms by Koteja (1986), Rs by Lambdin (2001), and M by Beardsley (1968), Shcherbakov (2007) and Franielczyk-Pietryra et al. (2018); also, the anterior flexing patch (**afx**) by Koteja (2008). Here we consider it to be the Media (**M**).

In *Q. podocarpus*, this pale line is branched, and we refer to the two branches as M1+2 and M3+4, when the pairs are present. Although Koteja (2008) considered this vein to be a_{fx}, we think this is an error because this vein has no flexing function.

6. In previous descriptions of wing venation in the Coccomorpha, there is at most one obvious line posterior to the CuA: this line has a flexing function when the wing is folded flat over the abdomen, so here we consider it to be the Anal fold (**Af**), although it was named Cubito-anal vein (**Cu-a**) by Lambdin (2001); Cubitus posterior (**CuP**) by Shcherbakov (2007), and the posterior flexing patch (**pfx**) by Koteja (2008). This fold is possibly homologous to the claval fold in Psyllomorpha.

The fore wing of *Q. podocarpus* has two obvious lines posterior to the Cubitus Anterior (**CuA**), with the posterior line having a flexing function. Here we consider the name Anal fold (**Af**) to refer to the posterior line, and the anterior line to be the Cubitus Posterior (**CuP**) in agreement with Grimaldi and Engel (2005). Comparing the male scale insect venation with that of aphids, this anterior line should be the CuA₂. If so, the CuA is more correctly referred to as the CuA₁.

7. Shcherbakov (2007) considered that there is a Pcu+1A vein on the anal lobe fold, but this was not confirmed by Franielczyk-Pietryra et al. (2018). Here we agree with the latter authors and consider that there is no Pcu+1A on the anal lobe fold of *Q. podocarpus*.

In Fig. 9, the wing veins and folds of *Matsucoccus bisetosus* in Monophlebidae, *Drosicha* sp. in Monophlebidae, *Orthezia urticae* in Ortheziidae, *Weitschatus vysienskasi* in Weitschatidae, *Phenacoccus fraxinus* Tang, 1977 in Pseudococcidae, *Eulecanium tiliae* (Linnaeus, 1758) in Coccidae, *Asiacornococcus kaki* in Eriococcidae, and Diaspididae sp., are labeled based on our interpretation of the wing venation of male scale insects.

The different nomenclature used for the veins of the fore wing of adult male Coccomorpha are summarized in Table 1.

Table 1. Fore wing vein nomenclature for male scale insects. Abbreviations: a_{fx}: anterior flexing patch; Af: Anal fold; C: Costa; Cc: Costal complex (Costa + Subcosta); Ct: Costal thickening; Cu: Cubitus; Cur: Cubital ridge; CuA: Cubitus Anterior; Cu-a: Cubito-anal vein; CuP: Cubitus Posterior; M: Media; Ms: Medial sector; Pcu+1A: fused Postcubitus and anal first vein; p_{fx}: posterior flexing patch; R: Radius; Rs: Radial sector; Sc: Subcosta; Scr: Subcostal ridge; Sct: Subcostal thickening.

Author	Genus	veins and/or lines								
This study	<i>Qinococcus</i>	Ct	Sc	R	Rs	M ₁₊₂	M ₃₊₄	CuA	CuP	Af
Koteja (2008)	<i>Weitschatus</i>	–	Scr		Rs	a _{fx}		Cur	–	p _{fx}
Franielczyk-Pietryra et al. (2018)	<i>Orthezia</i>	–	Sc+R		Rs	'm'		CuA	–	Af
Shcherbakov (2007)	<i>Orthezia</i>	–	Sc+R		Rs	M		CuA	–	CuP
Koteja (1986)	<i>Orthezia</i>	–	Scr		Rs	Ms		Cu	–	Af
Lambdin (2001)	<i>Drosicha</i>		Cc	R	–	Rs		M	–	Cu-a
Beardsley (1968)	<i>Matsucoccus</i>	–	Sct	R	–		M		–	Af

Note: some authors use capital letters and others use small caps or a combination of capital letters and small caps for the abbreviation of wing veins and folds; however, these are written in the above Table according to the abbreviations given in this section to avoid confusion.

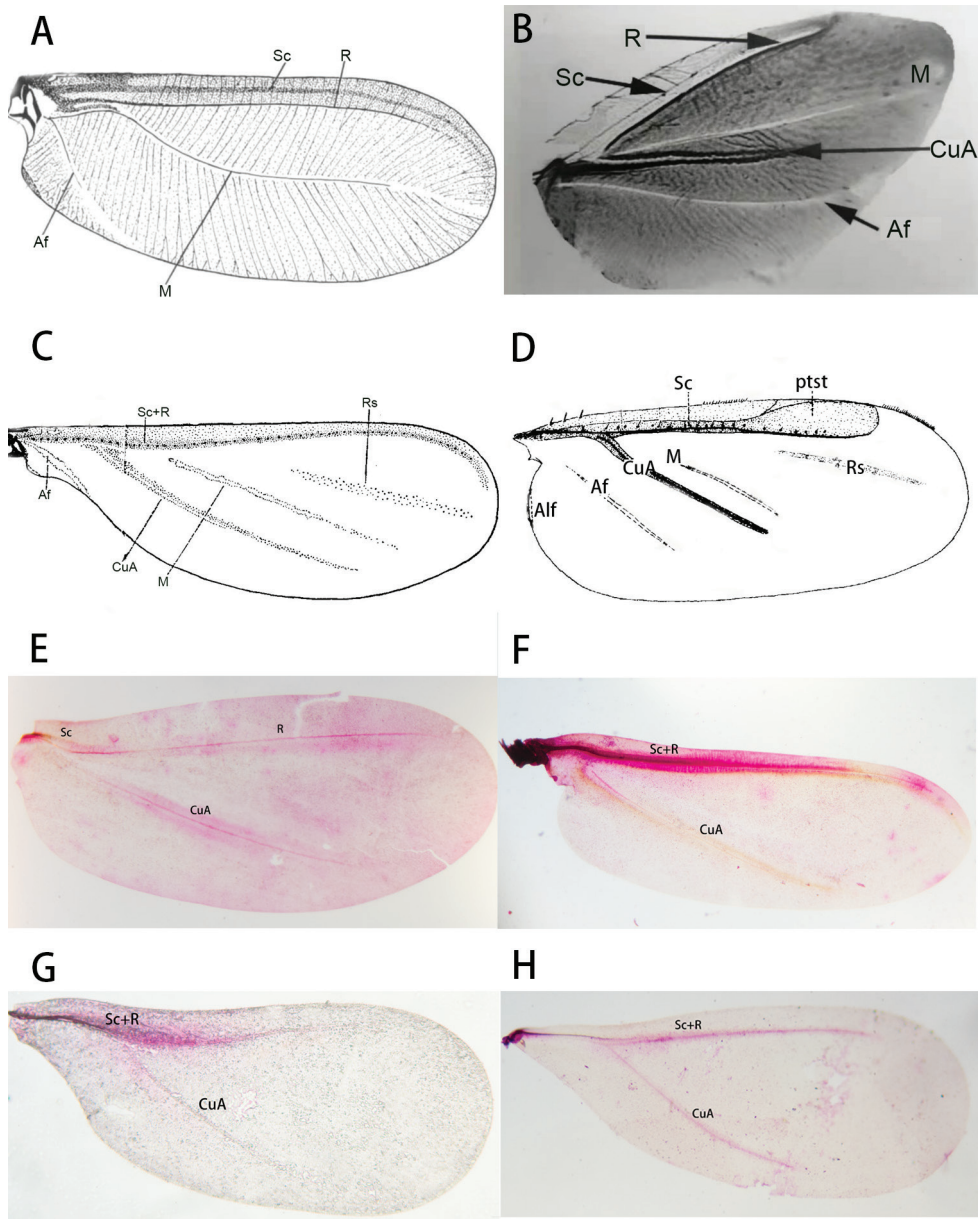


Figure 9. Wing venation of archaeococcoids and neococcoids **A** *Matsucoccus bisetosus* (Matsucoccidae) **B** *Drosicha* sp. (Monophlebidae) **C** *Orthezia urticae* (Ortheziidae) **D** *Weitschatus vysniauskas* (Weitschatiidae) **E** *Phenacoccus fraxinus* (Pseudococcidae) **F** *Parthenolecanium corni* (Coccidae) **G** *Asiacornococcus kaki* (Eriococcidae) **H** Diaspididae sp. Abbreviations: Af, Anal fold; Alf, Alar fold; CuA, Cubitus Anterior; M, Media; ptst, pterostigma; R, Radius; Rs, Radial sector; Sc, Subcosta; Sc+R, fusion of Subcosta and Radius.

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New species and new records of *Monohalea* Kieffer (Diptera, Ceratopogonidae) from Brazil

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Abstract

Two new Brazilian species of *Monohalea* Kieffer are described and illustrated based on male specimens, *Monohalea capixaba* **sp. nov.** from Espírito Santo and *Monohalea coimbrai* **sp. nov.** from Rio de Janeiro. New records for *M. aguirrei* Tavares & Souza, *M. archibaldoi* Tavares & Souza and *M. maculipennis* (Coquillett) are given based on specimens from Espírito Santo (all three species) and Amapá (*M. maculipennis* only). All specimens are deposited in the Ceratopogonidae Collection of Fundação Oswaldo Cruz, Brazil.

Keywords

Aquatic, biodiversity, Neotropical, predaceous midges, taxonomy

Introduction

The predaceous genus *Monohalea* Kieffer is distributed worldwide and includes 97 extant species (Borkent and Dominiak 2020; Borkent et al. 2022). Santarém and Felipe-Bauer (2021) recognized 25 species from the Neotropics, of which 16 are cited as present in Brazil. *Monohalea* is included in the tribe Ceratopogonini, the females of which are known to be predators of other small insects, mainly chironomids (Diptera,

Chironomidae) (Wirth and Grogan 1988). Downes (1978) reported females of *Monohalea* preying on swarming males of chironomids in Ontario, Canada. According to Wirth and Grogan (1981), the larvae are most frequently found in sphagnum moss and other bog-like habitats. Only a few species of *Monohalea* are known as immatures. Glukhova (1971, 1977) described the larva and discussed the habitat of species from Russia. Elson-Harris (1990) provided information about larva and pupa of *Monohalea* from Australia. Wirth and Grogan (1981) and Borkent (2014) described two pupae of the genus belonging to species from the United States (Maryland and New York), reared from sphagnum bog. Knowledge concerning the habitat of immature stages of *Monohalea* is lacking in the Neotropical region. The study of material deposited in the Ceratopogonidae Collection of Fundação Oswaldo Cruz (FIOCRUZ/CCER) revealed the presence of two undescribed species from the Brazilian States of Espírito Santo and Rio de Janeiro and new records of *Monohalea aguirrei* Tavares & Souza, *M. archibaldoi* Tavares & Souza for Espírito Santo and *M. maculipennis* (Coquillett) for Espírito Santo and Amapá.

With the addition of the new species and the new records, there are now 27 species of *Monohalea* known from the Neotropics, 18 from Brazil and 11 from the Brazilian Amazon region.

Materials and methods

Adult specimens were mounted on microscope slides in phenol-Canada balsam after the method described by Wirth and Marston (1968). Diagnostic characters were microphotographed using a NIKON Eclipse E 200 microscope with digital camera MOTICAM 2300, 3.0 MP, USB 2.0, and the plates were prepared using GIMP Portable 2.6. The general terminology is that employed in the paper on Brazilian *Monohalea* by Felipe-Bauer et al. (2017). Terms of the wing follow the system of the Manual of Central American Diptera (Borkent et al. 2009). All measurements are in micrometers, except those of the wings, which are in millimeters. This research is registered at SisGen (National System for the Management of Genetic Heritage and Associated Traditional Knowledge) under the number ABBD939. All specimens were deposited in the Ceratopogonidae Collection of Fundação Oswaldo Cruz (FIOCRUZ/CCER) and have been given a specimen registration number.

Monohalea capixaba Santarém & Felipe-Bauer, sp. nov.

<https://zoobank.org/B4C144D5-2EF4-42CF-876D-8860EC777758>

Figs 1, 2

Holotype. Male, on microscope slide, labeled “Holotype *Monohalea capixaba* Santarém and Felipe-Bauer”, “São Luiz de Baixo, Pancas, Espírito Santo, BRASIL, 19°12'34.43"S, 40°49'13.75"W, 14.XII.2010, CDC light trap, mata, Pinto, I.S. [leg.]” (CCER#3699).

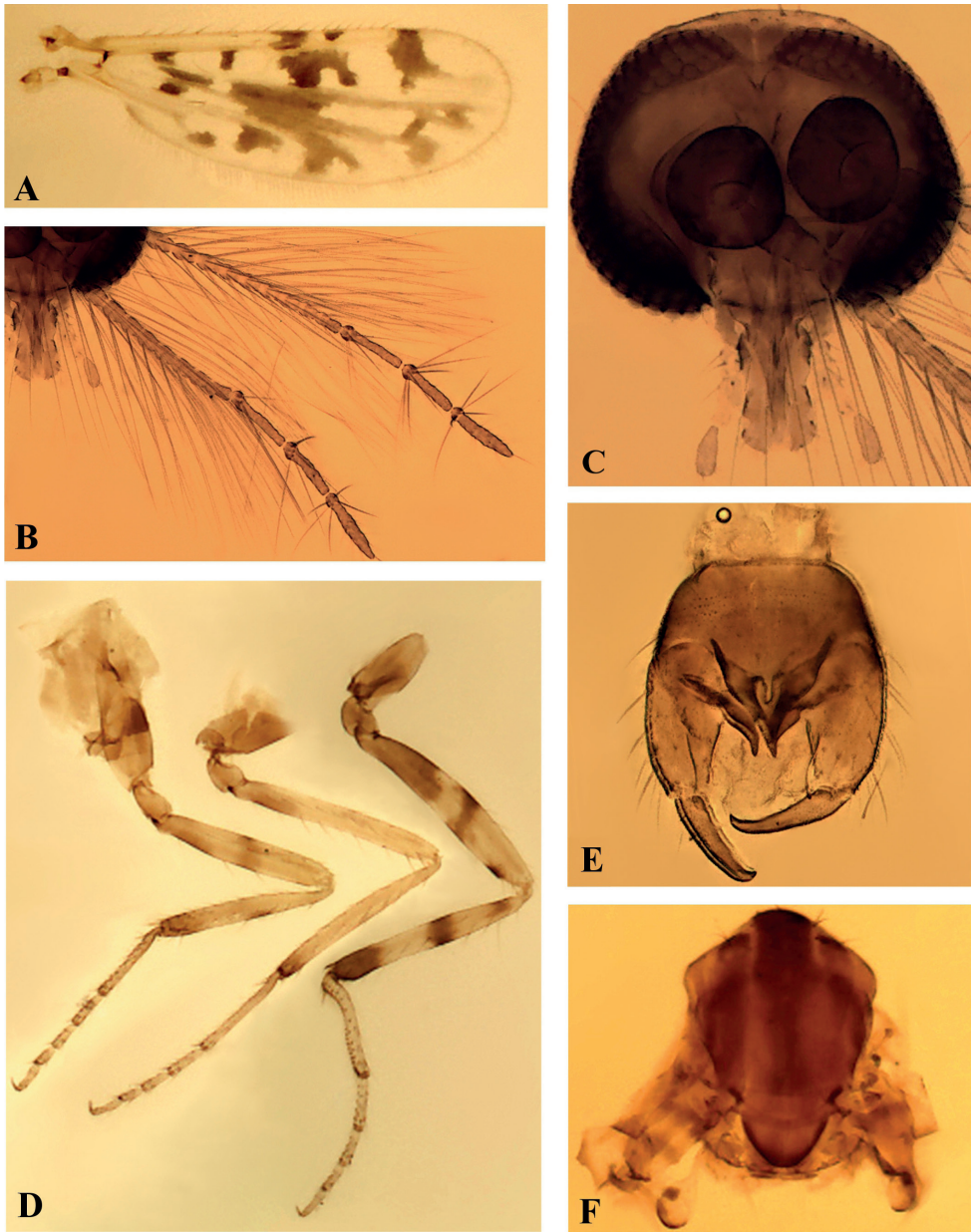


Figure 1. *Monobelea capixaba* sp. nov., male **A** wing **B** antenna **C** head, anterior view **D** fore-, mid-, hind legs (left to right), lateral view **E** genitalia, ventral view **F** thorax, dorsal view.

Diagnosis. Male adult: The only Neotropical species of *Monobelea* with legs yellowish, hind femur with basal brown band, mesal brown stripe and subapical ventral brown spot; parameres triangular, greatly expanded at single base, tapering distally, with apical portion simple and pointed apex. Female adult: unknown.

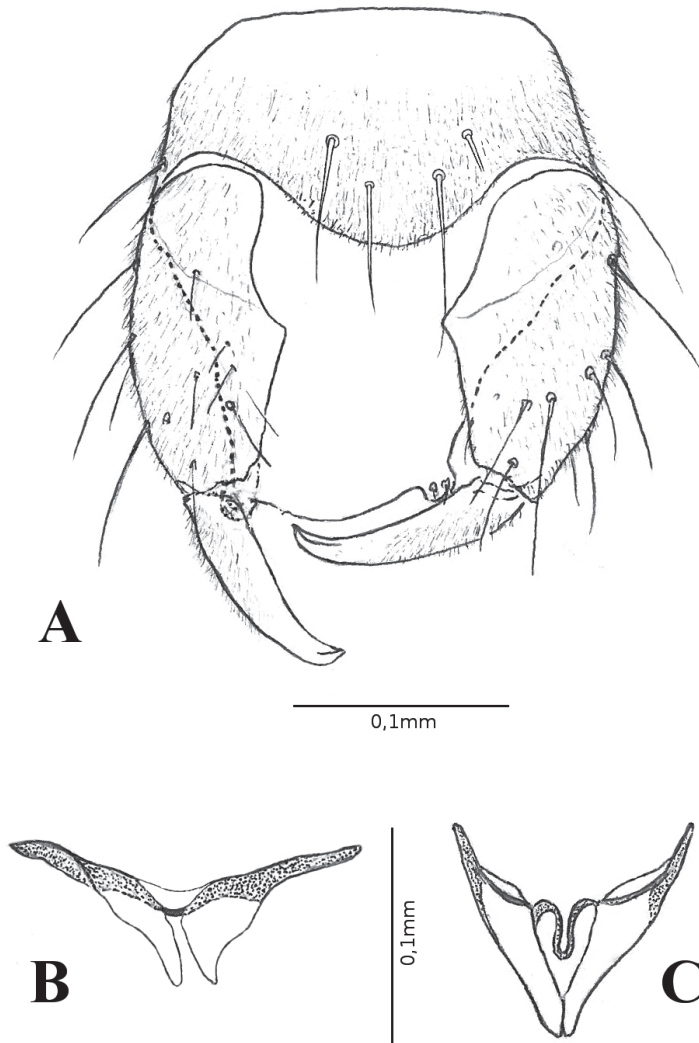


Figure 2. *Monobelea capixaba* sp. nov., male **A** terminalia, ventral view **B** parameres, ventral view **C** aedeagus, ventral view.

Description. Male. Head (Fig. 1C): eyes separated medially by a distance of 2 ommatidia. Antenna (Fig. 1B) brown; antennal ratio 0.95. Palpus pale brown, short; 3rd segment with small, shallow sensory pit, 5th segment darker, palpal ratio 1.29.

Thorax. Scutum brown, two median pale strips (Fig. 1F). Legs (Fig. 1D) yellowish; coxae and trochanters brown; forefemur with basal brown band and mesal brown stripe, midfemur with basal brown band, hind femur with basal brown band, mesal brown stripe and subapical ventral brown spot; tibiae brown apically; hind tibia with subbasal spot, mesal stripe; tibiofemoral joints yellowish; hind tibial comb with 5 bristles. Tarsi pale; fore-, hind tarsomere 1 with one basal, one apical spine; midtarsomere

1 with 2 basal, 2 apical spines; apical spines of tarsomeres 2–4 of fore-, mid-, hind legs: 1-1-1, 2-2-2, 1-1-1; basal spines absent; fore-, mid-, hind tarsal ratios 2.14, 2.43, 1.87; claws small, paired, equal-sized, 0.43–0.48× as long as 5th tarsomeres. Wing (Fig. 1A): macrotrichia present in wing margin; microtrichia absent; 2nd radial cell nearly 2× longer than 1st; wing length 0.77 mm, width 0.30 mm; costal ratio 0.68. Halter pale, distal portion of knob darker.

Abdomen. Pale brown. Genitalia brown (Figs 1E, 2A–C): sternite IX spiculate except on basal portion, posterior margin with a short, convex, median lobe with 4 long setae; tergite IX tapering, quadrate, with a pair of short apicolateral processes. Gonocoxite (Fig. 2A) moderately stout, nearly 2.06X longer than basal width, inner margin with mesal pointed protuberance; gonostylus (Fig. 2A) straight, tipped apex, 0.64 length of gonocoxite, basal 2/3 moderately pilose. Parameres (Fig. 2B) 0.91 length of aedeagus, triangular, greatly expanded at single base, tapering distally; apical portion simple, pointed apex. Aedeagus (Fig. 2C) triangular, composed of 2 pointed ventral plates; basal arms slightly expanded laterally.

Female. Unknown.

Distribution and bionomics. This species is known only from forested areas in Espírito Santo State, Brazil.

Etymology. This species name refers to the Portuguese gentilic name for the inhabitants of the Brazilian state of Espírito Santo, where the species occurs.

Taxonomic discussion. The male of this species has yellowish legs with a pattern of brown patches and the brown base of the hind femur. This pattern is similar to the Brazilian Amazonian species *M. patauateua* Felipe-Bauer & Trindade. Also, this species keys to couplet 22 (male) of *M. mayeri* Ortiz and *M. hieroglyphica* Kieffer in the key to Neotropical *Monohalea* by Lane and Wirth (1964). It can be easily distinguished from these three species by the peculiar aspect of the triangular parameres with a single base, without a mesal process.

***Monohalea coimbrai* Santarém & Felipe-Bauer, sp. nov.**

<https://zoobank.org/B09403A-C4DC-44E1-84E2-D046A0B39BDB>

Figs 3, 4

Holotype. Male, on microscope slide labeled “Holotype *Monohalea coimbrai* Santarém and Felipe-Bauer”, “Rio Cascatinha, sessão de 2^a ordem (acima da represa) 1470 m, drift Caledônia, Nova Friburgo, Rio de Janeiro, BRASIL, 24.VIII.1995, Fittkau, UFRJ, IOC [leg.]” (CCER#3075).

Diagnosis. Male adult: The only Neotropical species of *Monohalea* with legs pale, hind femur with large basal band slightly infuscated, mesal brown stripe, subapical ventral brown spot; gonostylus broad basally, tapering distally, deeply curved in distal 1/2; parameres stem swollen on proximal portion, curved, gradually tapering, internally directed, with small mesal pointed process, posteriorly directed arising from the swollen portion of the parameres. **Female adult:** unknown.

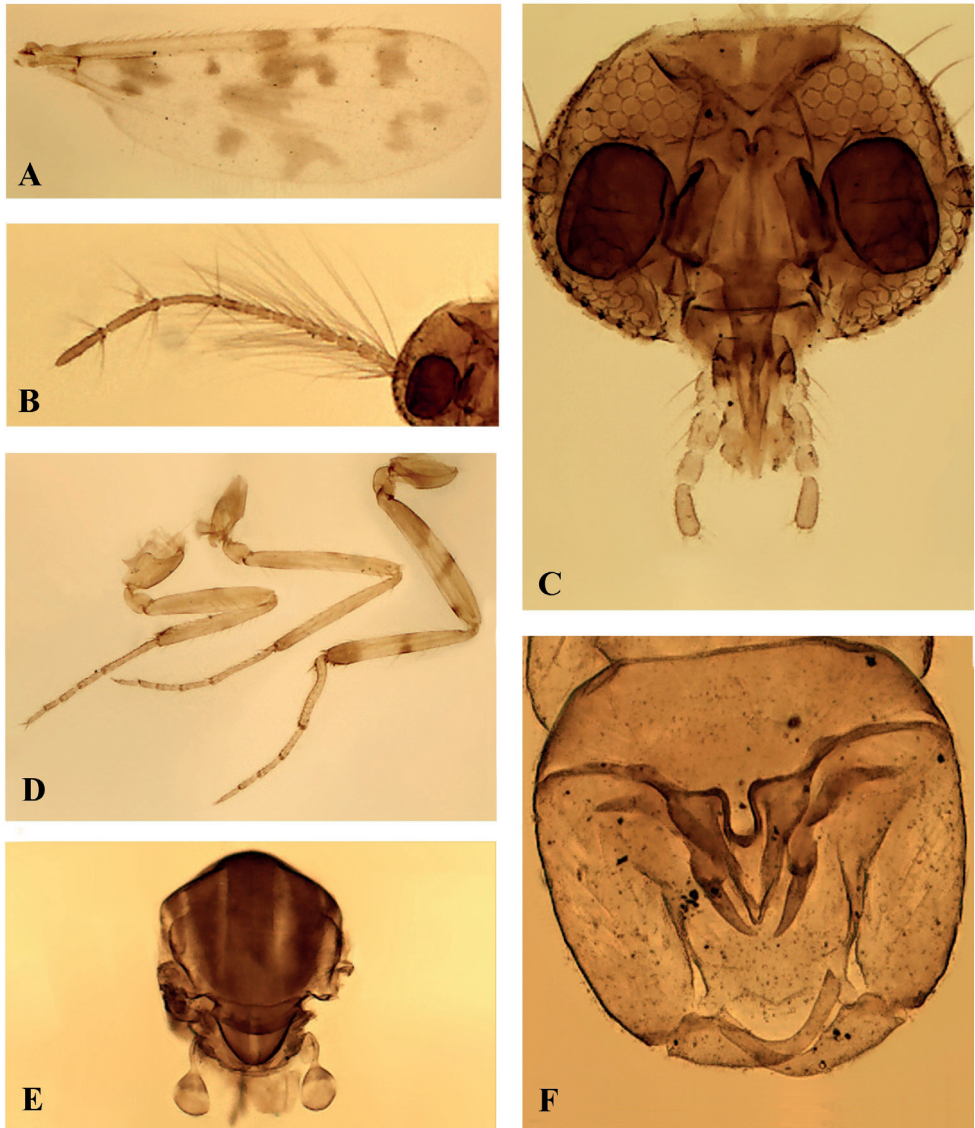


Figure 3. *Monobelea coimbrai* sp. nov., male **A** wing **B** antenna **C** head, anterior view **D** fore-, mid-, hind legs (left to right), lateral view **E** thorax, dorsal view **F** genitalia, ventral view.

Description. Male. Head (Fig. 3C): eyes separated medially by a distance of 2 ommatidia. Antenna (Fig. 3B) pale brown; antennal ratio 1.09. Palpus pale brown; 3rd segment with small, shallow, sensory pit; palpal ratio 1.50.

Thorax. Scutum (Fig. 3E) brown, pale brown laterally, two median pale strips. Legs (Fig. 3D) pale; coxae and trochanters pale; hind femur with large basal band slightly infuscated, mesal brown stripe and subapical ventral brown spot; hind tibia with mesal brown stripe, apical brown band; tibiofemoral joints yellowish; hind tibial

comb with 7 bristles. Tarsi pale; fore-, hind tarsomere 1 with one basal, one apical spine; midtarsomere 1 with 2 basal, 2 apical spines; apical spines of tarsomeres 2–4 of fore-, mid-, hind legs: 1-1-1, 2-2-2, 1-1-1; basal spines absent; fore-, mid-, hind tarsal ratios 2.12, 2.34, 1.91; claws small, paired, equal-sized, $0.38\text{--}0.42\times$ as long as 5th tarsomeres. Wing (Fig. 3A): infuscated, macrotrichia restricted to costa; microtrichia absent; 2nd radial cell nearly $2\times$ longer than 1st; wing length 0.92 mm, width 0.35 mm; costal ratio 0.81. Halter pale brown.

Abdomen. Yellowish. Genitalia (Figs 3F, 4A–C) yellowish: sternite IX spiculate except on basal portion, posterior margin with a short, convex, median lobe with 4 long setae; tergite IX tapering, with a pair of short apicolateral processes, each with 3 setae. Gonocoxite (Fig. 4A) moderately stout, nearly $2\times$ longer than basal width; gonostylus (Fig. 4A) broad basally, tapering distally, distal $\frac{1}{2}$ deeply curved, apex blunt, 0.74 length of gonocoxite, moderately pilose on basal $\frac{1}{2}$. Parameres (Fig. 4B) as

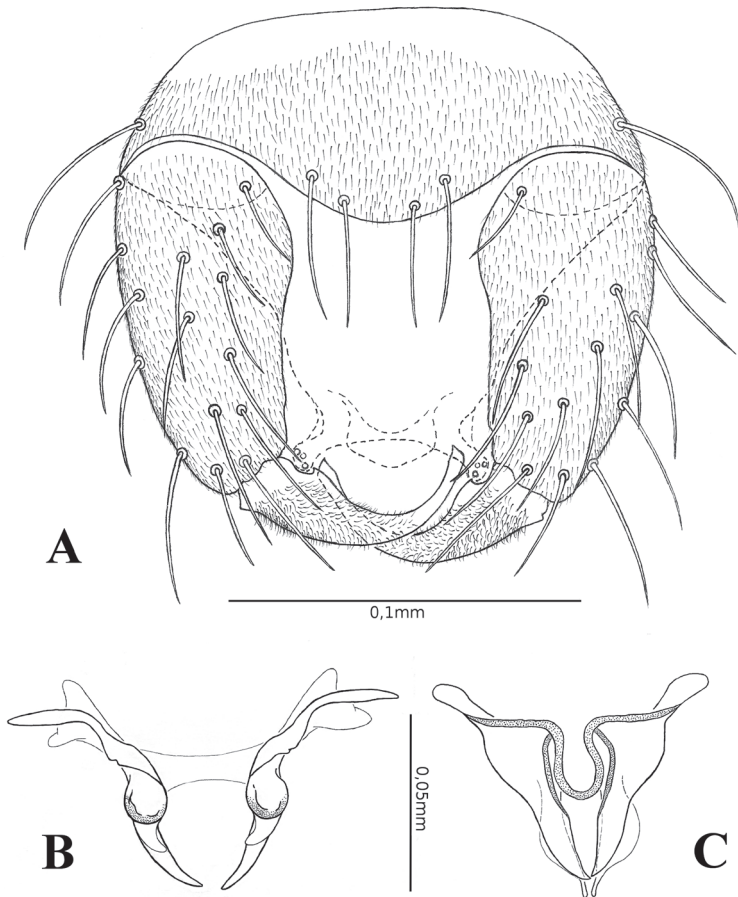


Figure 4. *Monohalea coimbrai* sp. nov., male **A** terminalia, ventral view **B** parameres, ventral view **C** aedeagus, ventral view.

long as aedeagus, fused at trilobed base, stem swollen, sclerotized on proximal portion, curved, gradually tapering, internally directed, with small inconspicuous mesal pointed process, tooth-shaped, posteriorly directed, arising from the swollen portion of the parameres. Aedeagus (Fig. 4C) triangular, composed of 2 pointed ventral plates, with slightly sclerotized dorsal structure, which arises in the middle way to aedeagus base and produced beyond the apices of ventral plates, ending as an apical projection; basal arms slender, broadly expanded laterally.

Female. Unknown

Distribution and bionomics. This species is known only from Rio de Janeiro, Brazil. It has been found in forested areas near rivers, up to 1470 m above sea level.

Etymology. This species is named in honor of Dr Ademar Coimbra-Filho (1924–2016), a biologist and primatologist. He was an enthusiast of biodiversity conservation and acted on several strategies to protect the biodiversity of Atlantic Forest, where this species has been found.

Taxonomic discussion. This species has pale legs with a pattern of brown patches and mesal processes in the parameres. It keys to couplet 19 in the key to Neotropical *Monohalea* by Lane and Wirth (1964), but it can be easily distinguished from *M. brasiliensis* Lane, *M. maculipennis* (Coquillett) and *M. poncai* Lane & Wirth by the presence of a unique, small inconspicuous mesal process of the parameres, tooth-shaped, posteriorly directed and arising from the swollen proximal portion. *Monohalea coimbrai* sp. nov. has a single deeply curved gonostylus that is unique in the Brazilian species of this genus.

New records

Monohalea archibaldoi Tavares & Souza, 1980

Monohalea archibaldoi Tavares & Souza, 1980: 98 (male, female, Brazil - Rio de Janeiro); Wirth and Grogan 1988: 69 (type locality); Borkent and Wirth 1997: 101 (in catalog); Borkent and Spinelli 2000: 50 (in catalog); Felipe-Bauer and Oliveira 2001: 1111 (type specimens); Borkent and Spinelli 2007: 83 (in catalog); Borkent and Dominiak 2020: 165 (in catalog); Santarém and Felipe-Bauer 2021: 18 (in Brazilian catalog).

Distribution. Brazil (Espírito Santo, Rio de Janeiro)

New records. 2 males, on microscope slides labeled “*Monohalea archibaldoi* Tavares & Souza, 1980”, “Comunidade de São Bento, Pancas, Espírito Santo, BRASIL, 19°13'44.0"S, 40°45'31.0"W, 06/II/2011, mata, CDC light trap, Pinto, I.S. [leg.]” (CCER#3700, CCER#3701).

Monohalea aguirrei Tavares & Souza, 1980

Monohalea aguirrei Tavares & Souza, 1980: 97 (in part; male, Brazil - Rio de Janeiro); Wirth and Grogan 1988: 69 (type locality); Borkent and Wirth 1997: 101 (in

catalog); Felipe-Bauer 1998: 223 (redescription); Borkent and Spinelli 2000: 50 (in catalog); Felipe-Bauer and Oliveira 2001: 1111 (type specimens); Borkent and Spinelli 2007: 83 (in catalog); Borkent and Dominiak 2020: 165 (in catalog); Santarém and Felipe-Bauer 2021: 18 (in Brazilian catalog).

Distribution. Brazil (Espírito Santo, Rio de Janeiro, Santa Catarina) and Argentina (Corrientes, Buenos Aires Province).

New records. 1 male, 1 female, on microscope slides labeled “*Monohalea aguirrei* Tavares & Souza, 1980”, “Palmital de Baixo, Pancas, Espírito Santo, BRASIL, 19°12'47.0"S, 40°47'20.0"W, 30/IX/2010, mata, CDC light trap, Pinto, I.S. [leg.]” (CCER#3702, CCER#3703); 1 male, same data except “Córrego Itauninhas, Mucurici, 18°04'11.8"S, 40°32'47.0"W, 02/IV/2010” (CCER#3704).

Monohalea maculipennis (Coquillett, 1905)

Ceratopogon maculipennis Coquillett, 1905: 64 (female, Fla.)

Monohalea maculipennis: Kieffer 1917: 312; Wirth 1953: 140 (redescr.; Mexico, Guatemala, Panama records; figs wing, female hind leg, male genitalia; discus.); Lane and Wirth 1964: 227 (distrib.; USA, Bahamas, Ecuador records; figs female hind leg, parameres; dimorphism); Wirth and Williams 1964: 308 (distrib.; fig. parameres; dimorphism); Wirth 1974: 41 (in catalog); Wirth and Grogan 1988: 69 (type locality); Borkent and Wirth 1997: 102 (in catalog); Felipe-Bauer 1998: 228 (Brazil records); Borkent and Spinelli 2000: 50 (in catalog); Borkent and Spinelli 2007: 83 (in catalog); Felipe-Bauer et al. 2017: 159 (Brazil - Pará record); Borkent and Dominiak 2020: 166 (in catalog); Santarém and Felipe-Bauer 2021: 18 (in Brazilian catalog).

Distribution. USA (Florida, Louisiana), Mexico (Tamaulipas, Yucatan), Bahamas, Guatemala, Panama, Brazil (Amapá, Pará, Espírito Santo, Rio de Janeiro).

New records. 1 male on microscope slide labeled “*Monohalea maculipennis* (Coquillett, 1905”, “Floresta Nacional do Rio Preto, Espírito Santo, BRASIL, 18°21'23.9"S, 39°50'41.4"W, 14/XII/2009, CDC light trap, Pinto, I.S. [leg.]” (CCER#3705); 2 males, same data except “Monumento Natural dos Pontões Capixabas, Palmital de Baixo, Pancas, 19°12'47.0"S, 40°47'20.0"W, 30/IX/2010, mata” (CCER#3706); “Córrego São Bento, Pancas, 19°13'50.0"S, 40°45'24.7"W, 18/X/2010, casa” (CCER#3707); 1 male on microscope slide labeled “*Monohalea maculipennis* (Coquillett, 1905”, “Redenção, Amapá, BRASIL, 24/II/1964, Lacombe D. col.” (CCER#3123).

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The immatures of the New World treehopper tribes Acutalini Fowler and Micrutalini Haupt (Hemiptera, Membracidae, Smiliinae)

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Abstract

The nymphs of *Acutalis* Fairmaire, *Bordoniana* Sakakibara, *Thrasymedes* Kirkaldy, and *Micrutalis* Fowler are described and illustrated (*Bordoniana* and *Thrasymedes* for the first time). The nymphs of all four genera are exceedingly cryptic. The nymphs of some species lack scoli on the head and pronotum but all have paired scoli on the meso- and metathoracic nota and abdominal segments III–IX. Some species also have lateral rows of enlarged chalazae on the abdomen, and even large scoli ventrolaterally—the latter condition is unique within Smiliinae. The eggs are deposited in stems (not in exposed masses) and nymphs are solitary and not ant-attended. The fifth instar nymphs of Micrutalini range in length from 3.0–3.5 mm, much smaller than the fifth instars of most other treehoppers.

Keywords

Acutalis, *Bordoniana*, immature stage, life history, *Micrutalis*, *Thrasymedes*

Introduction

Adult treehoppers (Membracidae, Aetalionidae, and Melizoderidae) are well known for their expanded pronotum present in adults of more than 430 genera and 3,350 species (McKamey 1998 and recent additions). But in immatures, the pronotum is

diminutive and accompanied by other structures, such as various arrangements of large spine-like structures (scoli) on the head and sometimes on the thoracic and abdominal segments, and enlarged setae with stalked or swollen bases (chalazae). We hypothesize that differences between adult and immature morphology may have evolved independently. Despite this wealth of potential diagnostic and systematically informative nymphal features, there have been few thorough descriptions of New World genera.

Besides the uniqueness of morphology of membracid nymphs, they also differ from nymphs of all other Auchenorrhyncha families in having the last visible abdominal segment (IX) fused ventrally, forming a tube containing the anal segments, which can be everted by the nymphs at will (McKamey and Brodbeck 2013). Behaviorally, membracid nymphs differ from those of most Auchenorrhyncha in being unable to jump (SHM pers. obs.).

The present paper is part of the larger effort to describe the immature stages of New World treehopper genera, which has so far covered the Caribbean genera *Antillotolania* Ramos, *Deiroideres* Ramos (McKamey and Brodbeck 2013), and tribe Quadrinareini (McKamey and Wallner 2022). The nymphs of the continental tribes Amastrini (McKamey et al. 2015) and Thuridini (McKamey and Porter 2016), and the membracine genus *Eunusa* Fonseca (McKamey 1992) have also been described. This work treats two more tribes of the New World subfamily Smiliinae: Acutalini and Micrutralini. The nymphs of all four genera described here are exceedingly cryptic (Figs 4–7, 42, 43). Both tribes occur throughout much of North and South America and the West Indies (McKamey 1998). The two tribes are grouped in this paper because of their small size and similar features in their nymphs and their adults. Adults of both tribes are commonly collected because they are often conspicuous with their black markings on the pronotum or wing veins (e.g., Figs 41, 43). In contrast, the nymphs of these tribes are rarely observed or collected.

Despite the scarcity of Acutalini and Micrutralini nymphs in collections, and their solitary nature and cryptic coloration and morphology, there has been some progress in nymphal descriptions. Quisenberry et al. (1978) illustrated and described, through a key, fifth instars of most genera of Membracidae present in Missouri, USA, including *Acutalis* and *Micrutralis*. They separated *Micrutralis* and *Acutalis* from other membracid genera based on the following features shared by both: paired median dorsal spines present on the abdomen but not on the head or pronotum, prothoracic tibia not dilated, anterior horn absent, and the outline of pronotum more or less rounded anteriorly. *Acutalis* was distinguished from *Micrutralis* based on a serrated dorsomedial line of the pronotum in *Acutalis* versus a smoothly rounded dorsomedial line of the pronotum and acute spines in *Micrutralis*. Tsai and Kopp (1981) described the life history, morphology, and phenology of *Acutalis tartarea* (Say), illustrating the adults, eggs, and all instars. They reported that eggs were laid in clusters of 12–15 eggs each, inserted into the epidermal tissues of the host plant, with about 1/3 of the egg exposed, usually into the axil area of a leaf. They also reported that the nymphs were gregarious near the terminal portion of the plant of two Asteraceae: ragweed (*Ambrosia artemisiifolia* L.) and China aster (*Callistephus chinensis* [L.] Nees, Asteraceae).

Deitz (1975) included three genera in Acutalini: *Acutalis* Fairmaire, *Euritea* Stål, and *Thrasymedes*. Generic additions since then include *Bordoniana* and *Cornutalis* (Sakakibara 1998, 1999a). Of these Acutalini genera, only nymphs of *Acutalis* have been described before now. The only host record for the genus *Cornutalis* is *Baccharis* sp., Asteraceae (Flórez-V. 2017).

Micrutralini only contains two genera: *Micrutralis* Fowler and *Trachytalis* Fowler. Several authors have contributed to our knowledge of micrutraline taxonomy and biology. For instance, Donald (1945) reported that *Micrutralis* sp. adults were “found in small numbers on *Cordia macrostachya* (Jacq.) R. & S.” (Boraginaceae) in Trinidad. In the present study, nymphs and adults of two *Micrutralis* species were also collected on *Cordia*, one in Ecuador and another in Nicaragua (see Material examined under *Micrutralis*). Sakakibara (1976) described two new species, Deitz (1983) referred one species to *Rhexia* Stål, and Sakakibara (1999b) provided a synopsis of *Micrutralis*, including 42 species. Nixon and Thompson (1987) described and illustrated nymphs of *M. calva* (Say) and listed many hosts, listed below. Amaro (2009) reported *M. calva* on *Leucaena leucocephala* (Lam.) de Wit (Fabaceae) in Cuba. Tsai and Brown (1991) provided a photograph of an *M. malleifera* Fowler nymph in a summary of pseudo-curly top virus in tomato (*Lycopersicon esculentum* Mill., Solanaceae). Flynn and Wheeler (2016) observed (but did not describe) nymphs of *Micrutralis*; they recorded adults of *M. pallens* Fowler on *Anisacanthus thurberi* [Torr.] A. Gray (Acanthaceae) but could not identify the observed nymphs because they were not reared to adults and there appeared to be two species on the host. Recently, however, Wheeler and Flynn (2021) described the nymphs of *M. discalis* (Walker) on mistletoe (Viscaceae), in general accordance with characters used in the aforementioned nymphal descriptions in this series.

In the present study, additional natural history information is provided as well as the descriptions of four genera of Acutalini and Micrutralini, two tribes of the New World subfamily Smiliinae. Nymphs of *Bordonia* and *Thrasymedes* have never been illustrated or described until now.

Materials and methods

Preserved specimens were either collected by the first author or found in the U.S. National Collection. Vouchers of all examined nymphs and their associated adults are deposited in the National Museum of Natural History, Smithsonian Institution, in Washington DC (USNM). They were collected in Ecuador, Mexico, Nicaragua, Peru, the United States, and Venezuela.

Photographs of dried specimens were taken with a Canon 5Dsr camera with an adjustable 65mm lens. Photos were taken using Capture One Pro v. 10.1.2, 64 bit, build 10.1.2.23 imaging software, aided by CamLift v. 2.9.7.1. The specimen was illuminated using two adjustable Dynalite MH2050 RoadMax flash heads, each attached to a Manfrotto 244 arm. The light was diffused using a simple, lampshade-style cone of translucent paper between the specimen and light sources. After individual “slices”

were photographed, they were compiled into a single, composite image using Zerene Stacker - USDA SI-SEL Lab Bk imaging system, v. 1.04, build T201706041920. Stacked images were enhanced and edited in Adobe Photoshop CSS Extended v. 12.0.

Results

Key tzo 5th instars of Acutalini genera (excluding *Euritea* and *Cornutalis*) and *Micrutalis*. Fifth instars differ from earlier instars in having a well-developed forewing pad that attains the posterior margin of the first visible abdominal segment (segment III) and usually overlaps part of the second visible segment (segment IV).

- | | | |
|---|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------|
| 1 | Total length 3.5 mm or less..... | <i>Micrutalis</i> |
| – | Total length 4.3–8.5 mm..... | 2 |
| 2 | Abdomen laterally glabrous, not setose; dorsal scoli directed posteriorly (Figs 3–7) | <i>Acutalis</i> |
| – | Abdomen laterally densely setose (Figs 8, 12, 18); dorsal scoli directed dorsally or dorsoposteriorly | 2 |
| 3 | Abdominal tergum IX distinctly shorter than length of remaining abdominal segments combined (Figs 12, 13); abdominal terga IV–VIII with or without large scoli ventrolaterally (Fig. 14); head and prothorax with or without scoli | <i>Bordoniana</i> |
| – | Abdominal tergum IX as long as remaining abdominal segments combined (Fig. 18); abdominal terga IV–VIII without scoli ventrolaterally; head and prothorax with scoli | <i>Thrasymedes</i> |

Acutalini Fowler

Quisenberry et al. (1978) found features for distinguishing *Acutalis*, which is the only acutaline genus represented in Missouri, and those features were sufficient for that fauna. Considered within the larger context of Smiliinae, those features also apply to the Amastrini genera *Bajulata* Ball, *Erosne* Stål, *Harmonides* Kirkaldy, and some *Amastris* Stål (McKamey et al. 2015). But these features do not apply to the acutaline genus *Bordoniana*, which has abdominal scoli directed dorsally, nor the genus *Thrasymedes*, which has scoli on the head and pronotum, or even some other *Acutalis*, which have scoli on the head (1 pair) and pronotum (2 pairs) (Fig. 3). We also found that nymphs of Acutalini are solitary and not ant-attended, and we speculate that eggs are not laid in exposed masses but instead within host tissue. Tsai and Kopp's (1981) report that the nymphs of *Acutalis* were gregarious near the terminal portion of ragweed host is interpreted here as a high population of solitary nymphs feeding at a preferred site with higher nitrogen. Nitrogen is recognized as an essential macronutrient for plant growth (Olas et al. 2019). Presumably, treehoppers feed on phloem, and plant nitrogen partitioning from source leaves to sinks occurs in the phloem (Tegeder and Masclaux-Daubresse 2017). Furthermore, Landrein et al. (2018) described a root-

borne cytokinin signal that transduces nitrate availability to the shoot apical meristem within a matter of days and controls the stem cell population and, hence, meristem size and growth. In other words, meristems and young leaves have a higher concentration of nitrogen than other plant parts, and this may be why meristems are preferred feeding sites of many treehopper adults and nymphs.

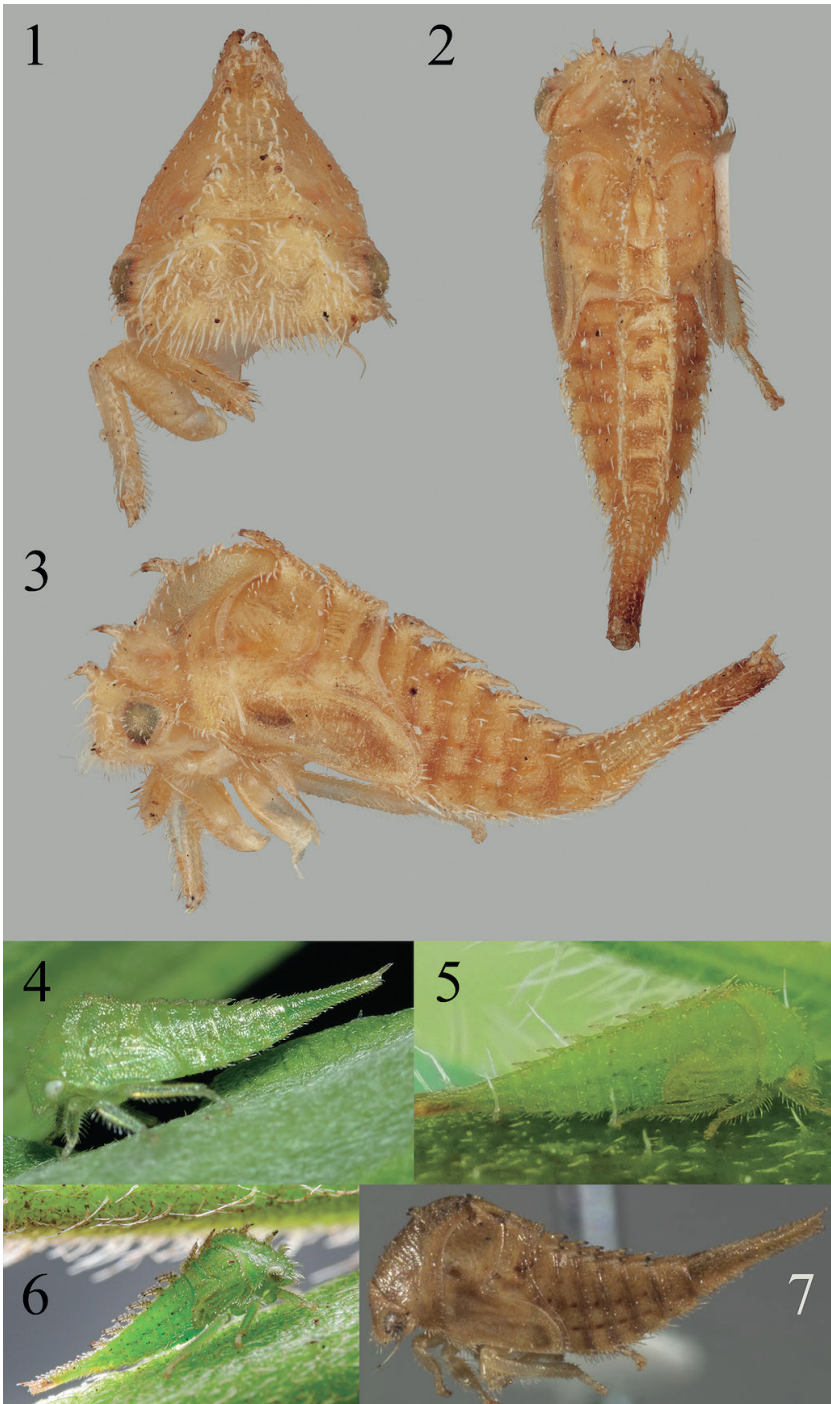
Nymphs are unknown for the acutaline genera *Cornutalis* Sakakibara and *Euritea* Stål.

***Acutalis* Fairmaire**

Figs 1–7

Nymph diagnosis. Body with full complement (9 pairs in total) of dorsal, short scoli from postmetopidium to last visible abdominal segment, and sometimes also 1 pair of scoli on head and 1 pair of scoli on premetopidium; metathoracic scoli directed forward, in opposite direction of abdominal scoli (backwards), low to tergal surface but not appressed; abdomen laterally with 3 rows of slightly enlarged chalazae but otherwise almost without setae.

Nymph description. Overall body. Fifth instar length 4.3 mm. Cross-section subtriangular; chalazae on thorax and abdomen, excluding those on scoli, sparse, almost absent; chalazal setae short; scoli parallel. **Head.** With simple conical scoli (except absent in *Acutalis tartarea*), directed anterad, length relative size to basal width about subequal; chalazal bases long-stalked; compound eye surface with setae; frontoclypeus with dense setae; enlarged chalazae absent between eyes, but present in front of ventral margin of eye and also adjacent to central or dorsal margin of eye; frons extending over central margin of eye. **Prothorax.** Premetopidium scoli present (except absent in *Acutalis tartarea*), directed anteriorly; postmetopidium scoli present, directed anteriorly; posterior extension of pronotum not surpassing anterior margin of metanotum; if present, premetopidial scoli length about 2–4× basal width; postmetopidial scoli length about 2–4× basal width. **Mesothorax.** Scoli bearing stalked chalazae; scoli directed dorsoanteriorly; forewing pad anterior costal margin straight; dorsal scoli length about 2–4× basal width; anterior basal side of scoli lacking cluster of enlarged chalazae; forewing pad surface chalazae absent; forewing pad costal chalazae present only on base of costal margin; meso- and metathorax without lateral rows on enlarged chalazae. **Metathorax.** Scoli bearing stalked chalazae; scoli directed dorsoanteriorly; dorsal scoli length about 2–4× basal width. **Legs.** Chalazae of tibia on anterior and posterior lateral margins, absent or very few on dorsal surface; prothoracic tibia form subcylindrical. **Abdomen.** Terga III–VIII ventrolateral margins each with row of four or more enlarged chalazae; terga III–VIII dorsal scoli subequal in size to each other; terga III–VIII tallest dorsal scoli length 2–4× basal width; tergum IV dorsal scoli directed preapically dorsally, apically posteriorly but not appressed; terga III–VIII lateral rows bearing 3 rows slightly enlarged chalazae; lamellae absent; scoli bearing stalked chalazae. Segment IX: dorsal length subequal to combined length remaining visible abdominal terga; preapically with paired enlarged setae dorsally, with 1 pair dorsal scoli apically.



Figures 1–7. *Acutalis* 1–3 *Acutalis fusconervosa* Fairmaire from Chiapas, Mexico in anterior, dorsal, and lateral views, respectively 4 *Acutalis* sp. from Durham, NC, courtesy of Margarita Lankford 5 *Acutalis* sp. from Hoover, AL, courtesy of Vitaly Charny 6 *Acutalis* sp. from Costa Rica, ex Asteraceae, courtesy of Kenji Nishida 7 *Acutalis tartarea*, courtesy of Mark Rothschild.

Material examined. *Acutalis fusconervosa*, 1 adult, 2 nymphs, MEXICO: Chiapas, 13 km S Pichucalco, 170 m alt., 17°26'38"N, 93°10'49"W, 2 November 2001, S.H. McKamey (USNM).

Note. There is a difference between Quisenberry et al.'s (1978) illustration of *A. tartarea* (Say) and the specimen of *A. fusconervosa* Fairmaire figured here (Fig. 7); the latter has a small pair of scoli on the pronotum, lacking in Quisenberry et al.'s illustration. This difference cannot be attributed to developmental changes because both are fifth instars deduced from wing pad size. Quisenberry et al.'s (1978) illustration was redrawn from Matusch (1912b).

***Bordoniana* Sakakibara**

Figs 8–17

Nymph diagnosis. Body densely setose; abdominal tergum IX distinctly shorter than length of remaining abdominal segments combined; abdominal terga IV–VIII sometimes with large scoli ventrolaterally; head and prothorax sometimes lacking scoli.

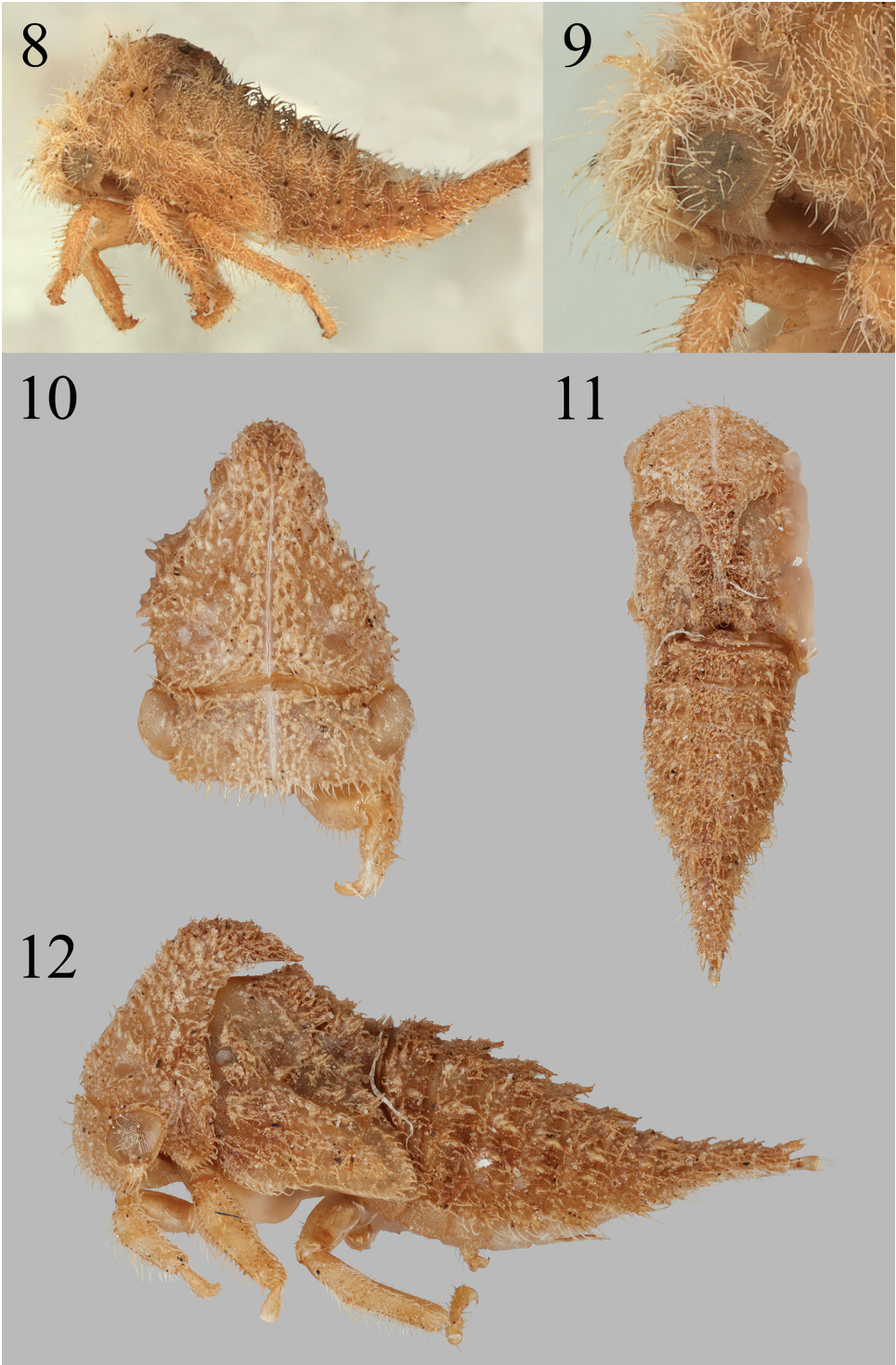
Nymph description. Overall body. Fifth instar length 5.1–6.5 mm. Cross-section subtriangular (except vertically depressed in *Bordoniana* sp. 2), chalazal dense on thorax and abdomen except scoli, obvious throughout body; chalazal setae long (except short in *Bordoniana* sp. 1), scoli parallel (except splayed or divergent away from each other in *B. virescens*). **Head.** Scoli pair absent (except with simple conical scoli in *B. virescens*); scoli projection directed anterad in *B. virescens*; chalazal bases variable (see Remarks below); compound eye surface with setae; between eyes, enlarged chalazae variable (see Remarks below); scoli length about 2–4× basal width in *B. virescens*; enlarged chalazae present in front of ventral margin of eye and also adjacent to central or dorsal margin of eye (except enlarged chalazae absent in *Bordoniana* sp. 1.); enlarged chalazae adjacent to central or dorsal margin of eye present (except absent in *Bordoniana* sp. 1); frons extending over central margin of eye. **Prothorax.** Premetopidium scoli present (except absent in *Bordoniana* sp. 1); premetopidium scoli directed dorsoanteriorly; postmetopidium scoli absent; posterior extension of pronotum not surpassing anterior margin of metanotum but does not attain posterior margin (except surpasses posterior margin of metanotum in *Bordoniana* sp. 1); premetopidial scoli length relative to basal width variable (see Remarks below). **Mesothorax.** Scoli bearing tuberculate chalazae (except bearing stalked chalazae in *B. virescens*); scolar direction variable (see Remarks below); forewing pad anterior costal margin sinuate (except straight in *B. virescens*); forewing pad chalazae short and dense, continuously covered (except densely covered in long setae in *Bordoniana* sp. 1); scoli length about 2–4× basal width (except scoli about as tall as basal width in *Bordoniana* sp. 1); anterior basal side of scoli lacking cluster of enlarged chalazae (except present in *B. virescens*); forewing pad costal chalazae present along entire costal margin (except present only at base of costal margin *B. virescens*); lateral rows, if present, with most medial row extending onto meso- and metathorax (except not extending onto thorax in *B. virescens*). **Metathorax.** Scoli bearing tuberculate chalazae (except bearing stalked chalazae in *B. virescens*); scoli directed dorsally

or almost so (except directed posteriorly in *Bordoniana* sp. 1); scoli length about 2–4× basal width (except scoli about as tall as basal width in *Bordoniana* sp. 1). **Legs.** Tibia with chalazae present on both lateral margins and dorsal surface; prothoracic tibia form subcylindrical (except foliaceus in *Bordoniana* sp. 1). **Abdomen.** Terga III–VIII ventrolateral margins variable (see Remarks below); terga III–VIII dorsal scoli subequal in length relative sizes to each other subequal (except scoli size decreasing posteriorly in *B. virescens*); terga III–VIII tallest dorsal scoli length about 2–4× basal width; tergum IV dorsal scoli directed preapically variable (see Remarks below); tergum IV dorsal scoli directed apically dorsoposteriorly (except posteriorly in *Bordoniana* sp. 1); terga III–VIII lateral rows bearing 2 rows enlarged chalazae (except not manifested in *B. virescens*); lamellae absent (except present with lateral margins converging, apex pointed in *Bordoniana* sp. 2); lamellae (if lamella present) bearing chalazae marginally and dorsally; scoli bearing tuberculate chalazae (except bearing stalked chalazae in *B. virescens*). Segment IX: dorsal length subequal to combined length of segments V–VIII (except subequal to combined lengths of segments VI–VIII in *Bordoniana* sp. 1); preapically with dorsal surface irregularly covered in chalazae.

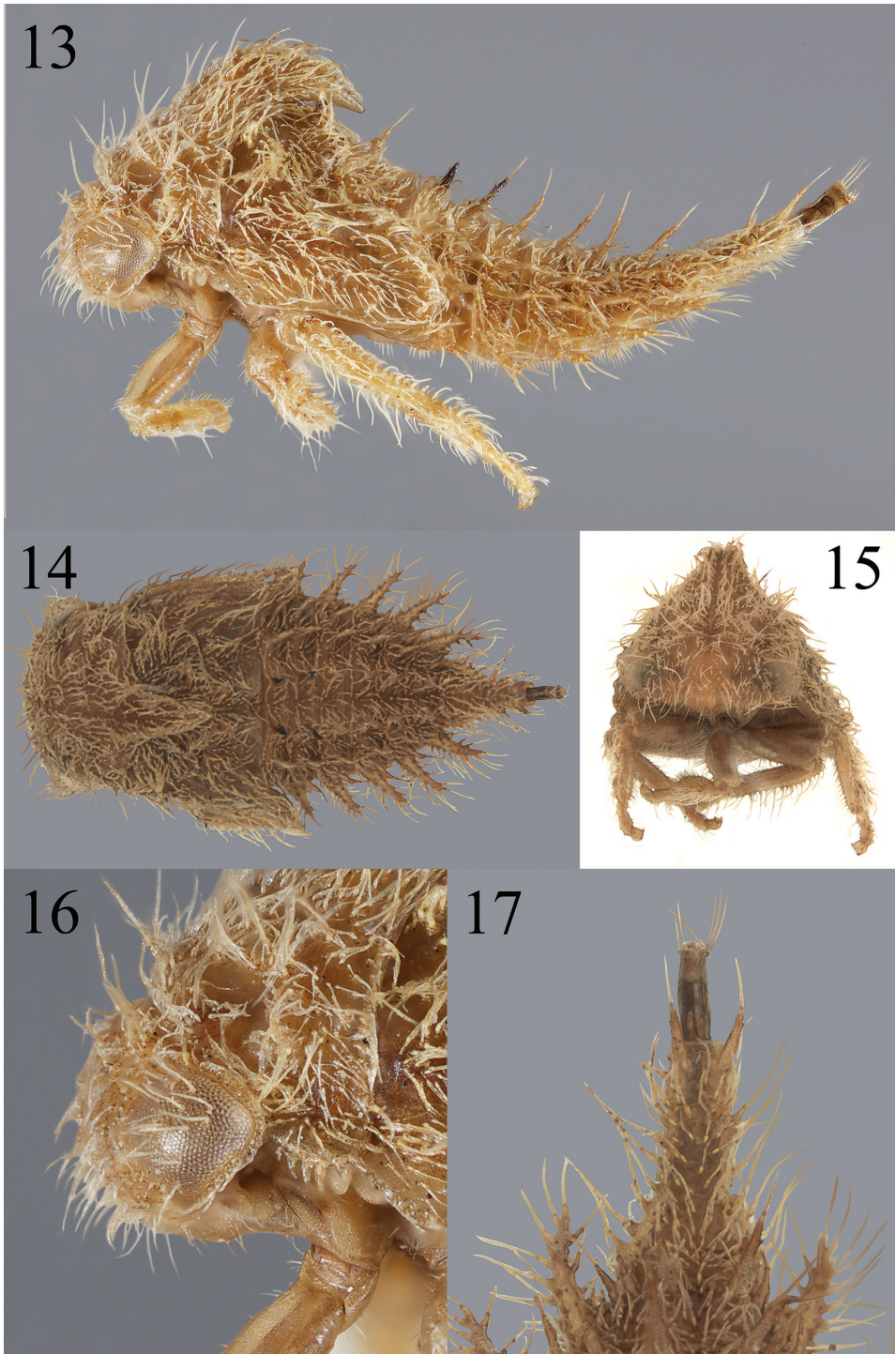
Material examined. *Bordoniana virescens* Sakakibara, 1 adult, 1 nymph, PERU: Acobamba, July 1940, W.D. Funkhouser Collection (USNM); *Bordoniana* sp. 1, 1 adult, 1 nymph, ECUADOR: Azuay, Baños, 2600 m alt., 23 May 1986, S.H. McKamey leg., lot# 05-23-23, 05-23-24 (USNM); *Bordoniana* sp. 2, 1 adult, 1 nymph, ECUADOR: Prov. Cañar. Ducur, via Cuenca-Guayaquil, 25-V-1986, ca 2520 m alt., S.H. McKamey leg., lot#86-0525-9, 86-0525-10 (USNM).

Remarks. Substantial morphological variation was found among the nymphs of the *Bordoniana* species examined. Specifically, the head and pronotum may have or lack scoli on the head and pronotum, and one species of undescribed *Bordoniana* has large scoli ventrolaterally on segments IV–VIII (Fig. 14); this is unique in Smiliinae and rare among other membracid nymphs (e.g., present in *Heteronotus* Laporte [figured in Deitz and Wallace 2010]).

We also discovered differences among the three species of *Bordoniana*. Head: chalazal bases tuberculate in *Bordoniana* sp. 1, short-stalked in *Bordoniana* sp. 2, and long-stalked in *B. virescens*; enlarged chalazae between eyes absent in *B. virescens*, present as a single pair in *Bordoniana* sp. 2, and present as pair of vertical rows in *Bordoniana* sp. 1. Prothorax: premetopidial scoli length relative to basal width about subequal to their basal widths in *Bordoniana* sp. 2, about 2–4× their basal widths in *B. virescens*, and scoli absent in *Bordoniana* sp. 1. Mesothorax: scoli directed dorsoanteriorly in *B. virescens*, dorsally or almost so in *Bordoniana* sp. 2, and directed posteriorly in *Bordoniana* sp. 1. Abdomen: terga III–VIII ventrolateral margins each with a single enlarged chalazae in *B. virescens*, with acuminate lateral extensions in *Bordoniana* sp. 2 (Fig. 14), and with a row of four or more enlarged chalazae in *Bordoniana* sp. 1; tergum IV scoli directed preapically dorsally or almost so in *B. virescens*, dorsoposteriorly in *Bordoniana* sp. 2, and posteriorly but not appressed in *Bordoniana* sp. 1. The most striking difference, described above, is that *Bordoniana* sp. 2 bears ventrolateral scoli, identical in placement but different in form to certain Centrotinae, Heteronotinae, Stegaspidinae, and *Procyrtia* Stål (Darninae) (SHM pers. observ.). No other smiliine nymphs have ventrolateral scoli.



Figures 8–12. *Bordoniana* 8, 9 *B. virescens* Sakakibara in lateral view, habitus and detail of head and portion of thorax, respectively 10–12 *Bordoniana* sp. 1 in anterior, dorsal, and lateral views, respectively.



Figures 13–17. *Bordoniana* sp. 2 **13–17** nymph in lateral, dorsal, and anterior views, respectively **16** detail of head and portion of prothorax, lateral view **17** detail of abdominal segment IX (last visible segment), dorsal view.

Thrasymedes Kirkaldy

Figs 18–22

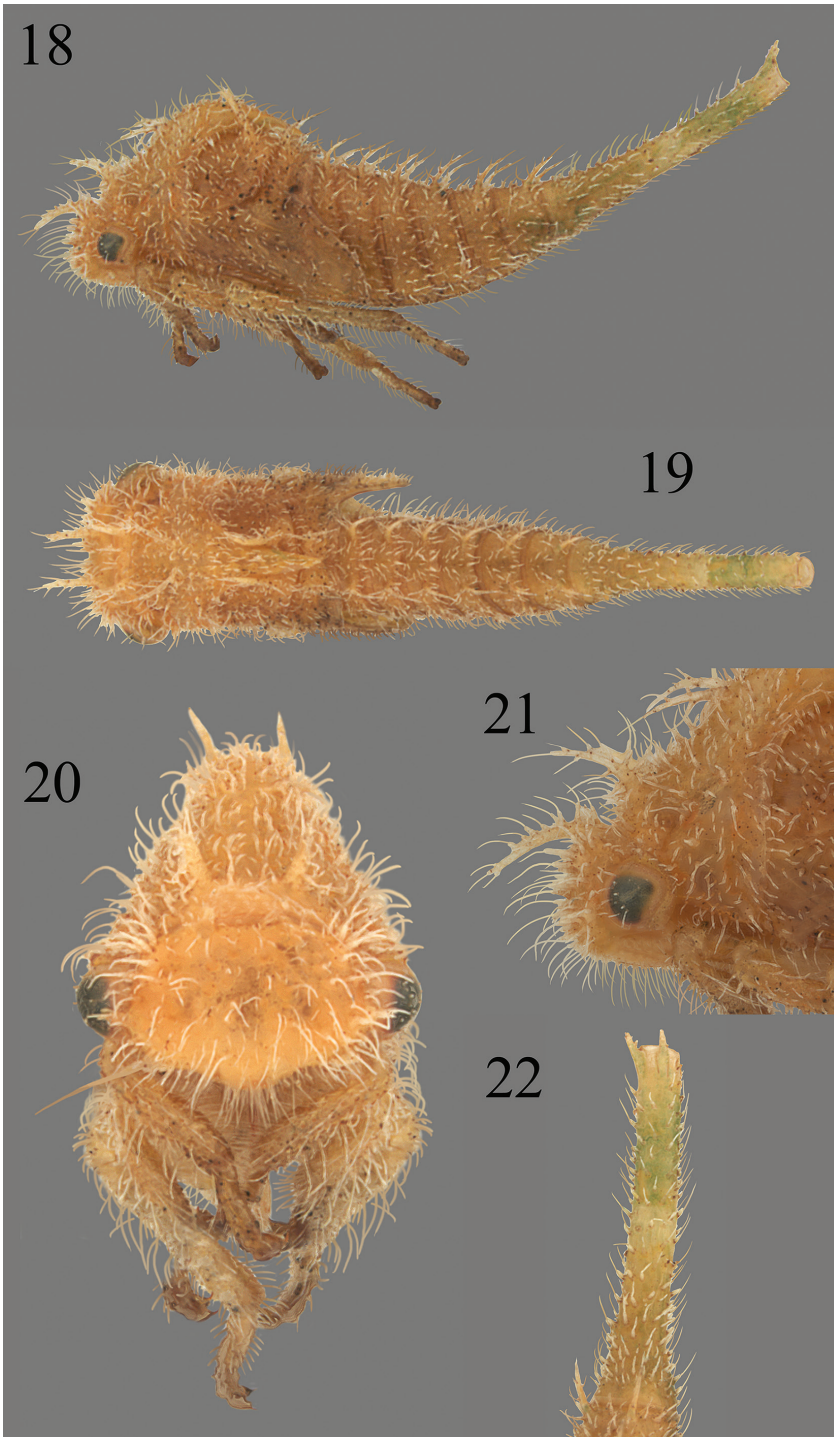
Nymph diagnosis. Body densely setose; with full complement of paired dorsal scoli from head to abdominal segment IX (12 pairs in total), though slender, not long and without stalked chalazae; abdominal segment IX as long as combined length of remaining abdominal terga; abdomen without scoli ventrolaterally.

Nymph description. Overall body. Fifth instar length 8.5 mm. Cross-section subtriangular; thorax and abdomen densely covered with chalazae, distinct throughout body; chalazal setae long; scoli parallel. **Head.** With simple conical scoli, directed anterad; chalazal bases long-stalked; compound eye surface with setae; enlarged chalazae between eyes present as pair of vertical rows; setae of frontoclypeus dense; scoli length about 5–7× basal width; enlarged chalazae in front of ventral margin of eye present; enlarged chalazae adjacent to central or dorsal margin of eye present; frons not extending over central margin of eye. **Prothorax.** Premetopidium scoli present, directed dorsoanteriorly; postmetopidium scoli present, directed anteriorly; posterior extension of pronotum surpasses anterior margin of metanotum, but does not attain its posterior margin; premetopidial scoli length about 5–7× basal width; postmetopidial scoli length about 5–7× basal width. **Mesothorax.** Dorsal scoli bearing stalked chalazae; scoli directed dorsoanteriorly and length about 5–7× basal width; anterior basal side of scoli lacking cluster of enlarged chalazae; forewing pad anterior costal margin straight; forewing pad surface densely covered by long chalazae; forewing pad costal chalazae along entire costal margin; lateral rows, if present, most medial row extending unto meso- and metathorax. **Metathorax.** Scoli bearing stalked chalazae; scoli directed dorsally or almost so; dorsal scoli length about 5–7× basal width. **Legs.** Chalazae of tibia present on both lateral margins and dorsal surface; prothoracic tibia form subcylindrical. **Abdomen.** Terga III–VIII ventrolateral margins each with 3 enlarged chalazae; terga III–VIII dorsal scoli length subequal to each other and bearing stalked chalazae; terga III–VIII tallest dorsal scoli length about 5–7× basal width; tergum IV dorsal scoli preapically directed dorsally or almost so, apically dorsoposteriorly; terga III–VIII bearing 1 lateral row of slightly enlarged chalazae; lamellae absent. Segment IX: longer than combined length of remaining abdominal terga, but shorter than length of rest of body; preapically with dorsal surface irregularly covered in chalazae.

Material examined. *Thrasymedes pallescens* (Stål): 39 adults, 1 nymph, 4 5th instar exuviae, MEXICO: Michoacán, Route 150, km 270, 40 km E Panindicuaró, 2150 m elev., 19°52'55"N, 101°24'45"W, 9 November 2001, S.H. McKamey leg. (USNM).

Micrutalini Haupt

As for Acutalini, Quisenberry et al. (1978) gave distinguishing features for *Micrutalis* in Missouri, and those features were sufficient for that fauna. Their illustration, redrawn from Matusch (1912a), is consistent with a photograph of the live specimen (Fig. 23). The illustration by Nixon and Thompson (1987) shows the abdominal scoli more elevated than those in the specimen (Fig. 23) and also more than those in the illustration by Matusch (1912a).



Figures 18–22. *Thrasymedes pallescens* (Stål) **18–20** nymph in lateral, dorsal, and anterior views, respectively **21** detail of head and portion of prothorax, in lateral view **22** detail of abdominal segment IX (last visible segment), in dorsal view.

Considered within the larger context of Smiliinae, however, the features described by Quisenberry et al. (1978) and Nixon and Thompson (1987) are insufficient to distinguish them from the amastrine genera noted above (McKamey et al. 2015) and do not apply to all Neotropical *Micrutralis* species examined in our study. For example, Neotropical species of *Micrutralis* (except *Micrutralis* sp. 2) have scoli on all thoracic segments, not just the abdomen. Nymphs of *Micrutralis* are solitary and not ant-attended, and eggs are not laid in exposed masses.

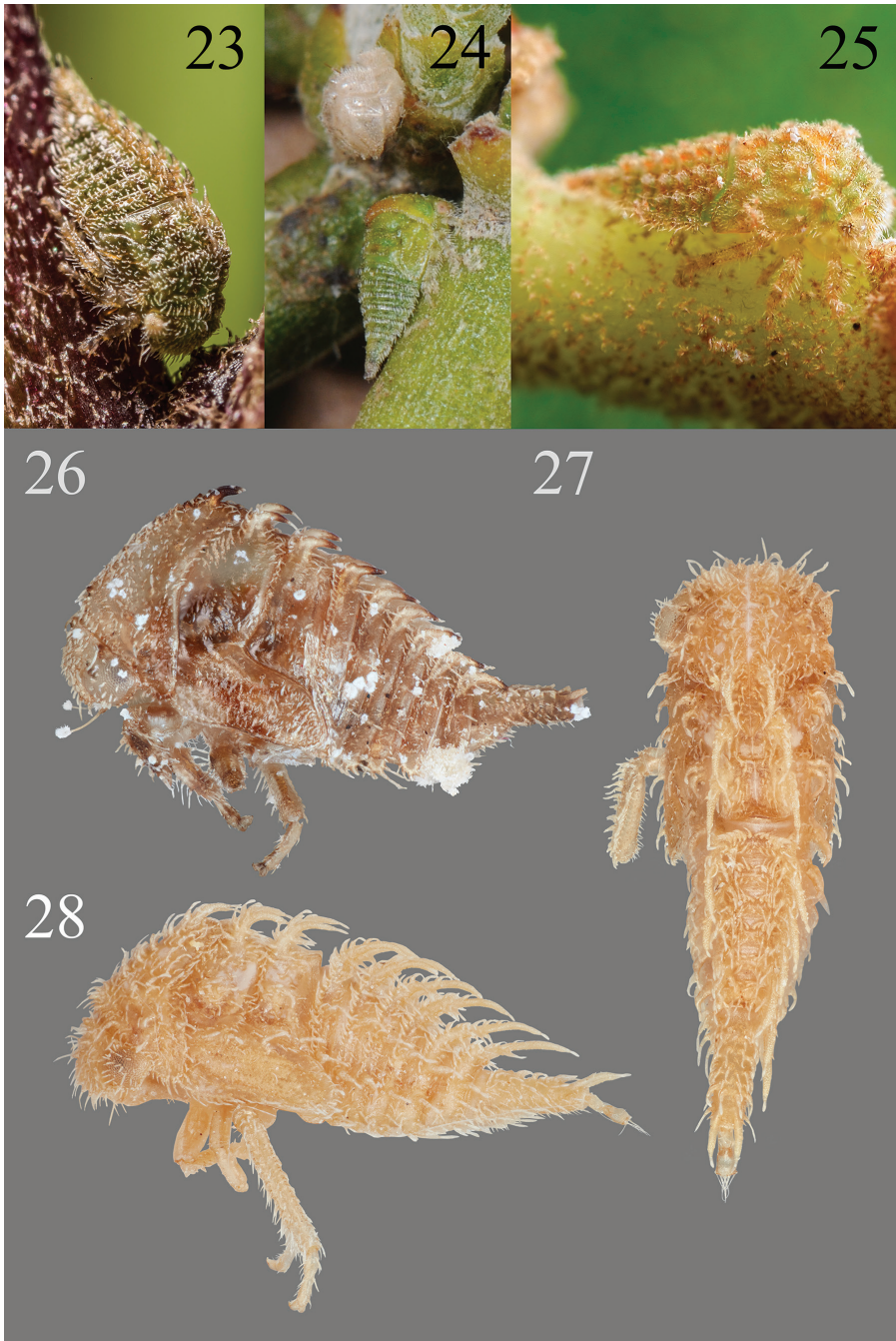
In comparing morphology of adults and nymphs, we found more uniformity among *Micrutralis* adults than in their nymphs. Nymphs have yet to be discovered for *Trachytalis* Fowler, the only other micrutraline genus.

***Micrutralis* Fowler**

Figs 23–43

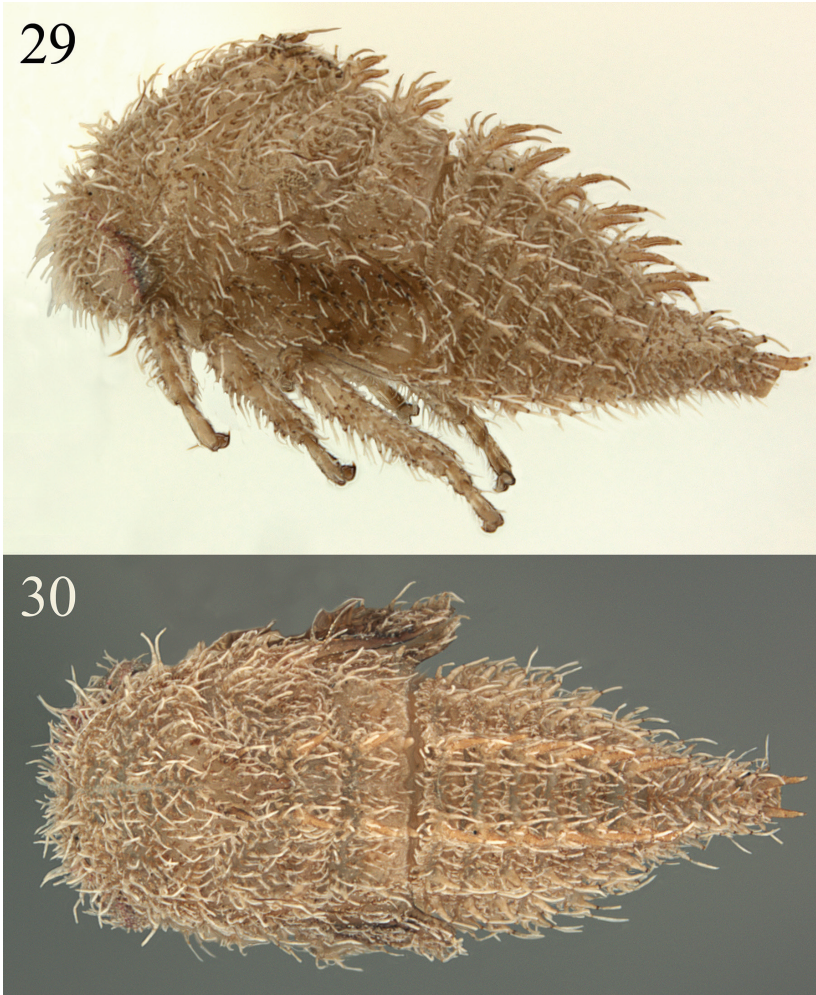
Nymph diagnosis. Fifth instar body length 3.0–3.5 mm; head and premetopidium lacking enlarged chalazae or scoli, postmetopidium with short scoli or enlarged chalazae; mesonotum to abdominal segment IX with small paired scoli; abdominal terga with 1 or 2 well-developed rows of enlarged chalazae or scoli; body densely setose, triangular in cross-section, not vertically compressed; abdomen lacking ventrolateral lamellae; wing pad costal margin linear or almost so; fused portion of abdominal segment IX directed posteriorly.

Nymph description. **Overall body.** Fifth instar length 3.0–3.5 mm. Cross-section subtriangular (except laterally compressed in *M. dubia* Fowler); chalazae on thorax and abdomen usually dense; chalazal setae long; no parts of body covered with wax-like substance; dorsal contour of abdomen in lateral view linear; scoli parallel; overall body in dorsal view elongate. **Head.** Lacking scoli; dorsal or anterior rounded protuberances absent; chalazal bases long-stalked (except tuberculate in *M. dubia*); chalazal setae simple, needlelike (except narrowly peltate in *M. dubia*) compound eye surface with setae; enlarged chalazae present or absent between eyes; setae of frontoclypeus scattered and sparse (except dense in *M. callangensis*); enlarged chalazae present in front of ventral margin of eye; enlarged chalazae present adjacent to central or dorsal margin of eye; frons extending over central margin of eye. **Prothorax.** Premetopidium lacking scoli; postmetopidium without dorsal paired structures or, if present (Fig. 33), with enlarged chalazae or small scoli directed dorsoposteriorly or dorsally then abruptly posteriorly; posterior extension of pronotum not surpassing anterior margin of metanotum, apex narrowly convex or acute; pronotal lateral margin rounded; postmetopidial scoli, if present, length about 2–4× basal width; metopidial sulcus not incised. **Mesothorax.** Dorsal structures consisting of paired scoli; scoli bearing stalked chalazae; scoli directed dorsoposteriorly or dorsally then abruptly posteriorly (except bluntly rounded in *M. callangensis*); forewing pad anterior costal margin form straight (except weakly sinuate in *M. dubia*); forewing pad surface chalazae sparse and with short setae (except densely covered in long setae in *M. callangensis*); scoli length about 2–4× basal width (except subequal to basal width in *M. callangensis*); anterior basal side of scoli lacking



Figures 23–28. *Microtalis* nymphs **23** *M. calva* from Allison Park, Allegheny Co, PA, courtesy of John Rosenfeld **24** *M. discalis* (Walker) on mistletoe from AZ, courtesy of Al Wheeler **25** *Microtalis* sp. from Costa Rica ex *Miconia calvescens* DC (Melastomataceae), courtesy of Kenji Nishida **26** *Microtalis* sp. from León, Nicaragua, lateral view **27**, **28** *M. dubia* Fowler, from Zona los Cinaros, Mérida State, Venezuela, in dorsal and lateral view, respectively.

cluster of enlarged chalazae; forewing pad costal chalazae present only on base of costal margin (except along entire costal margin *M. callangensis*); lateral rows of abdomen with most medial row extending onto meso- and metathorax. **Metathorax.** Dorsal structures consisting of paired scoli; scoli bearing short-stalked chalazae; scoli directed dorsoposteriorly or dorsally then abruptly posteriorly; dorsal scoli length about 2–4× basal width (except subequal to basal width in *M. callangensis*). **Legs.** Tibia with chalazae present on both lateral margins and dorsal surface; prothoracic tibia form subcylindrical; metathoracic tarsal length subequal to pro- and mesothoracic tarsal length; all first tarsomeres distinctly shorter than second tarsomeres. **Abdomen.** Terga III–VIII ventrolateral margins lacking scoli but each with 2 enlarged chalazae (except with a single enlarged chalazae in *M. callangensis*); terga III–VIII with dorsal scoli present, subequal in size to each other (2–4× basal width). directed dorsoposteriorly or dorsally



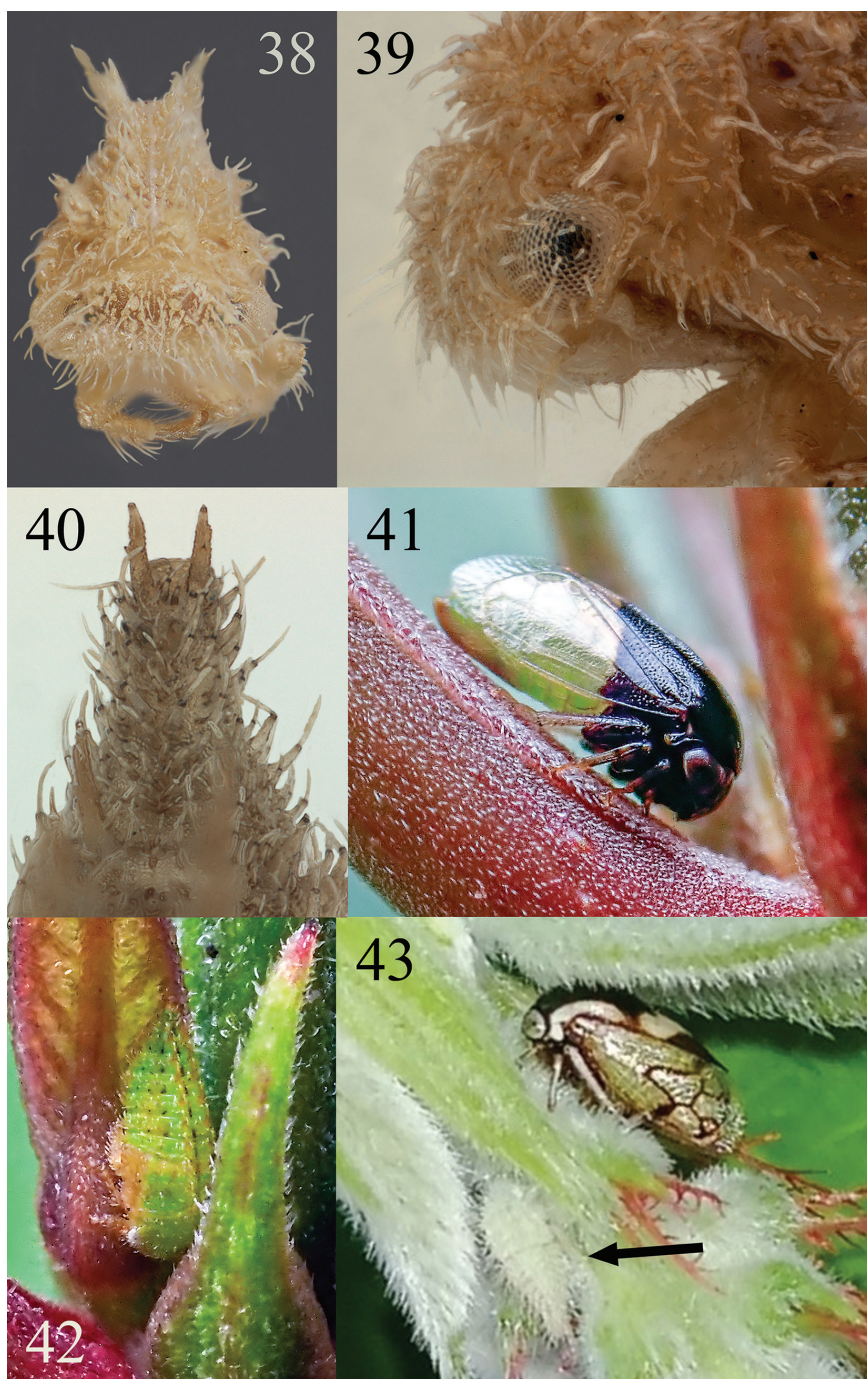
Figures 29, 30. *Micrutalis* sp. 2 from Loja, Ecuador in lateral and dorsal view, respectively.



Figures 31–34. *Micrutalis* sp. **31** habitus anterior view **32** detail posterior abdomen in dorsal view **33**, **34** habitus in lateral and dorsal views, respectively.



Figures 35–37. *Micrutralis callangensis* Goding in anterior, dorsal, and lateral views, respectively.



Figures 38–43. *Micrutalis* 38–40 *Micrutalis* sp. in anterior, detailed lateral head and portion of pronotum, and detailed abdomen, dorsal view, respectively 41, 42 *Micrutalis* undescribed sp., adult and nymph from Costa Rica, ex *Hamelia patens* Jacq. (Rubiaceae), courtesy of Kenji Nishida 43 *Micrutalis* undescribed sp., adult (upper right) and nymph (lower left, indicated by arrow) from San Juan, Bolivia by © Kozue Kawakami (CC BY).

then abruptly posteriorly; terga III–VIII with lateral 1 or 2 rows of enlarged chalazae (Fig. 33) or manifested as scoli (in *M. callangensis*); abdominal scoli bearing stalked chalazae (except bearing tuberculate chalazae in *M. dubia*). Segment IX: distal half tubular in cross-section; dorsal length subequal to length of segment V–VIII (except subequal to combined length of remaining visible abdominal terga in *M. callangensis*); preapical dorsal surface irregularly covered with chalazae; dorsal structures at apex consisting of paired scoli; ventral extension subequal to dorsal extension; fused portion of segment IX directed posteriorly and distal to unfused portion; unfused portion distally not bifurcate.

Material examined. *Micrutralis callangensis*, 1 adult, 1 nymph, ECUADOR: Cañar, Ducur, 25 May 1986, S.H. McKamey leg., lot # 86-0525-4, 86-0525-5 (USNM); *Micrutralis* undescribed species, 2 adults, 1 nymph, NICARAGUA: Leon Finca N.I.L., 8 [October] 1989, J.M. Maes leg., ex *Cordia* sp. (USNM); *M. dubia*, 1 adult, 2 nymphs, VENEZUELA: Ed. Merida, Zona Los Cinaros, 58 km SW Merida, 24 July 1984, S.H. McKamey leg., lot #1008, 1009 (USNM). *Micrutralis* sp. 2, 2 adults, 2 nymphs, ECUADOR: Loja, Loja, ca 2000 m alt., 30 May 1986, S.H. McKamey leg., lot #86-0530-7, 86-0530-8 (USNM); *Micrutralis* sp., 1 nymph (unassociated with adults), MEXICO: Animal and Plant Health Inspection Service (APHIS) intercept APSCA191974874004 at San Ysidro, California, 15-VII-2019, ex *Dysphania ambrosioides* (L.) Mosyakin & Clemants (Amaranthaceae; commonly known as espazote, Mexican tea, paico, and wormseed).

Hosts. The great majority of *Micrutralis* species lack host information. Nevertheless, there are some host records in the literature and among specimens examined in this study. Nixon and Thompson (1987) reported that *M. calva* was polyphagous, with adults feeding on wormwood, soapwort, sycamore, redbud, ironweed, alfalfa, ragweed, sunflower, black locust, and honey locust. Nixon and Thompson (1987) also reported that nymphs have been collected on ironweed, ragweed, sunflower, and honey locust (*Gleditsia triacanthos* L.); nymphs were collected on ironwood, ragweed, sunflower, and honey locust. The holotype of *M. henki* Sakakibara (1999b) was collected on *Luehea* [sic, for *Luehea*] *seemannii* Triana & Planch. Flynn and Wheeler (2016) recorded *M. pallens* on *Anisacanthus thurberi* [Torr.] A. Gray, Acanthaceae, but could not identify the *Micrutralis* species because the nymphs were not reared to adults. Wheeler and Flynn (2021) recorded *M. discalis* (Walker) from mistletoe (*Phoradendron californicum* Nutt., Viscaceae). The *M. dubia* from Ecuador in our study was collected on *Cordia* sp., Boraginaceae. The APHIS intercepted nymph was on *Dysphania ambrosioides* (L.) Mosyakin & Clemants (Amaranthaceae).

Remarks. Although Micrutralini adults are distinguished by their wing venation and genitalia, the small size of the fifth instars of *Micrutralis* sets them apart from most treehoppers. The only New World treehoppers that rival their small size are some *Bolbonota* Amyot & Serville, *Eunusa* Fonseca, some Tragopini, Thuridini, Quadrinareini, some *Amastris* Stål, Centrodontini, Endoiastinae, *Deiroides*, *Brachytalis* Metcalf & Bruner, *Brachybelus* Stål, and *Abelus* Stål. *Micrutralis* nymphs differ from the nymphs of all these small genera in one or more of the features listed above in the diagnosis of *Micrutralis*. In contrast to nymphs of *Micrutralis*, *Bolbonota* nymphs are covered with white wax-like exudate; *Eunusa* nymphs are covered with erect, stalked scoli and have the segment IX directed dorsally; nymphs of Tragopini, Thuridini, and Quadrinareini

lack scoli entirely; Centrodontini and Endoiastinae lack setae, *Brachytalis* nymphs have the posterior margin of the metathorax mesally lengthened; and *Deiroideres* and *Brachybelus* nymphs have ventrolateally flattened abdominal lamellae. The only genus among these for which the nymphs are unknown is *Abelus*. We presume these resemble those of the closely related *Ischnocentrus* Stål, which have the costal margin of the wing pad notched. The most unusual *Microtalis* species is *M. callangensis*, with its rounded meso- and metathoracic scoli, and its abdomen with lateral rows manifested as scoli rather than enlarged chalazae, and a proportionately longer segment IX.

Conclusions

Considering the great variability that we have observed, morphological variation within Acutalini and within Microtalini are underestimated. This situation is exacerbated by the absence of known nymphs for *Euritea* and *Cornutalis* (Acutalini) and *Trachytalis* (Microtalini). This is especially the case for *Microtalis*, for which only a few of the many species are known. For all genera in Acutalini and Microtalini, we expect that more species will reveal more variability than accounted for here. In this respect it is like any taxonomic revision; it represents only the species studied and becomes outdated when more are available for examination.

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