ZooKeys 1063: 1–21 (2021)
doi: 10.3897/zookeys.1063.69942
https://zookeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
ZooKeys
Launched to accelerate biodiversity research

Revision of the Chinese species of subgenus *Koreonialoe* (Coleoptera: Carabidae: *Pterostichus*), with descriptions of two new species

Wen-Qi Yin[1], Hong-Liang Shi[1], Hong-Bin Liang[2]

1 *College of Forestry, Beijing Forestry University, Beijing 100083, China* **2** *Key Laboratory of Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China*

Corresponding author: Hong-Liang Shi (shihl@bjfu.edu.cn)

Academic editor: Borislav Guéorguiev | Received 9 June 2021 | Accepted 9 September 2021 | Published 18 October 2021

http://zoobank.org/3687D722-9CD6-4D82-ACF8-D6701E399F4B

Citation: Yin W-Q, Shi H-L, Liang H-B (2021) Revision of the Chinese species of subgenus *Koreonialoe* (Coleoptera: Carabidae: *Pterostichus*), with descriptions of two new species. ZooKeys 1063: 1–21. https://doi.org/10.3897/zookeys.1063.69942

Abstract

The Chinese species of subgenus *Koreonialoe* Park & Kwon, 1996 of the genus *Pterostichus* are revised, including four species from the eastern part of Jilin and Liaoning provinces. Two new species are described: *Pterostichus* (*Koreonialoe*) *micropoides* **sp. nov.** (type locality: Jilin, Changbai county), and *Pterostichus* (*Koreonialoe*) *tetralobatus* **sp. nov.** (type locality: Liaoning, Xiuyan county). *Pterostichus* (*Koreonialoe*) *bellatrix* (Tschitschérine) is newly recorded from China (Jilin). The subgenus *Koreonialoe* is classified into two groups on account of their differences on the endophallus, and all Chinese species accord with the *microps* group defined herein. A key to all six species in the *microps* group is provided.

Keywords

Endophallus, genitalia, ground beetles, new species, Northeast China

Introduction

The subgenus *Koreonialoe* includes a group of pterostichine beetles with large heads, elongate mandibles, opaque elytra, and the male sternum unmodified. They are distributed in the Korean Peninsula and adjacent areas (including the Northeast China, Primorskiy Kray, and Tsushima). This group was initially recognized as the *opacipennis* group under subgenus *Nialoe* by Nemoto (1988), who revised this group containing seven species from the Korean Peninsula and Tsushima (Japan). Park and Kwon (1996) erected the subgenus *Koreonialoe* to accommodate species in the *opacipennis* group and described three species and one subspecies from South Korea. The first Chinese species in this group, *P. syleus* was described by Kirschenhofer (1997), but this species was initially placed in the subgenus *Nialoe* until Sasakawa et al. (2013) assigned it to the subgenus *Koreonialoe*. Subsequently, three new species were described (Sasakawa et al. 2008; Li and Zhang 2014), and *P. togyusanus* was upgraded to the species level (Park et al. 2013) from a subspecies of *P. bellatrix*.

The subgenus *Natalianoe* was erected by Berlov and Plutenko (1997) for its type species *P. microps* Heyden (distributed in Russia, Primorskiy Kray) and other similar macrocephalic species from Korea and Japan. Most of these species mentioned by Berlov and Plutenko (1997) are now placed in subgenus *Koreonialoe* and in the *P. macrogenys* group of *Nialoe* (Sasakawa 2005b). *Pterostichus microps* is morphologically very similar to some species in *Koreonialoe* and was placed in *Koreonialoe* by Lafer (2005) and Sundukov (2013), but it was not treated in recent important revisions (Sasakawa et al. 2013; Park and Park 2013).

Prior to the present study, there was a total of 16 species in *Koreonialoe*, with one species from Russia, Primorskiy Kray (*P. microps*), one from Japan, Tsushima (*P. opacipennis*), one from China, Liaoning (*P. syleus*), and the other 13 from the Korean Peninsula. The single Chinese *Koreonialoe* species, *P. syleus* has been rarely collected and is known only from its type locality, Sifangding, Liaoning. During expeditions to Northeast China in recent years, a large number of specimens belonging to this subgenus were collected from different localities of the eastern part of Jilin and Liaoning provinces (Fig. 36). Although these specimens are almost identical in their external features, detailed studies on the endophallus of male genitalia show that four different species are present in China: two of them were undescribed and *P. bellatrix* is recorded from China for the first time.

The present study describes two new species from Northeast China, newly records *P. bellatrix* from China (Jilin), and provides a key for all six species with ventrally directed endophallus of male genitalia. All new species are amply described and illustrated, especially for their endophallic characters.

Materials and methods

The present study is mainly based on the examination of specimens from Northeast China. All specimens examined, including types of new species, are deposited in the collections of the Institute of Zoology, Chinese Academy of Sciences, Beijing, China (IZAS).

The body length (BL) was measured from the apical margin of the labrum to the elytral apex; body width (BW) was measured along the elytral greatest width; the width of head (HW) was measured along the greatest transverse distance of head including eyes. The pronotum width (PW) was measured along its greatest width; pronotum length (PL) was measured along its median line; basal width (PBW) was measured along its posterior margin; apical width (PAW) was measured along its apical margin. Elytra length (EL) was measured along the suture from the base of the scutellum to the elytra apex.

The terminology of the endophallic lobes of male genitalia follows Sasakawa et al. (2005a, 2013). The abbreviations used in the endophallus are as follows: left apical lobe (**la**, = lobe β in Nemoto 1988; Park and Kwon 1996), left preapical lobe (**lp**, = lobe α (part) in Nemoto 1988; Park and Kwon 1996), right apical lobe (**ra**), gonopore (**gp**), gonopore lobe (**gpl**). In some species from China, the median lobe of aedeagus has a tubercle (**tu**) on the left ventral side. Other terms used, dissection techniques, endophallus everting procedures, and photography follow Shi et al. (2013).

Taxonomy

Subgenus *Koreonialoe* Park & Kwon, 1996

Koreonialoe Park & Kwon, 1996: 93. Type species: *Pterostichus teretis* Park & Kwon, by original designation. Park and Park 2013: 66. Bousquet 2017: 717.
Natalianoe Berlov & Plutenko, 1997: 4. Type species: *Pterostichus microps* Heyden, by original designation. Sundukov 2013: 130 (as junior synonym of *Koreonialoe*).
"*opacipennis* species-group" of *Nialoe*: Nemoto 1988: 39. Sasakawa et al. 2008: 174. Sasakawa et al. 2013: 430.

Diagnosis. Medium to large-sized *Pterostichus*; head large and thick, with elongate mandibles; eyes small, temporae swollen, a little wider than width across outer margins of eyes; pronotum cordate with posterior angles nearly rectangular; elytra entirely opaque; sternite VI or VII of males without secondary sexual modification.

Comparison. *Koreonialoe* species all share two external morphological features not found in other *Nialoe* species (= *Nialoe sensu lato*: Kasahara 1988; Sasakawa 2005a): elytra entirely opaque from dense, ISODIAMETRIC microsculpture; males without secondary sexual modification of sternite VII. *Koreonialoe* is considered to be a clade sister to the *macrogenys* species group (Sasakawa 2005b). These two groups are similar in their enlarged head with elongate mandibles and swollen temporae. But the latter group differs in the dorsal surface of elytra shiny and sternite VII of males is more or less concave.

Subgeneric characters. Body robust, medium to large size, body length 12–25 mm, elongate and macrocephalic. Dorsally black, dark brown or reddish brown; pronotum finely punctate, more or less opaque; elytra entirely opaque, without metallic luster. Palpi and tarsi brown, other parts of legs similar color as elytra. Head large and thick; eyes small and convex, tempora strongly swollen, generally a little longer than length of eyes; frons with shallow and sparse punctures throughout; frontal grooves shallow and wide, reaching midpoint of eyes. First antennomere shorter than combined length of following two segments. Mandibles long, outer surface nearly straight, apex hooked; apical margin of labrum and clypeus deeply emarginate; terminal segment of labial palpus fusiform, a little dilated in males; mentum tooth bifid, mentum with a pair of longitudinal depressions, submentum with two setae on each side. Pronotum strongly cordate, widest near anterior third, one-sixth to one-fifth wider than length. Surface more or less opaque, with fine punctures, sub-anterior transversal sulci well defined, strongly curved. Lateral margins slightly arched from anterior angles to the middle, strongly sinuate and then nearly straight before posterior angles; posterior angles nearly rectangular; posterior margin strongly emarginate at middle. Mid-lateral setae present near anterior fifth of lateral margins; lateral expansions narrow, equally wide at anterior and posterior portions. Basal foveae with inner and outer grooves faintly defined and partly fused, forming deep depression between them; outer groove slightly shorter than inner one (definition of pronotal inner and outer grooved see Shi et al. 2013: 103); middle area between two basal foveae with strong transverse wrinkles or heavy punctures. Elytra entirely opaque, length a little greater than one-half of width, widest a little behind middle. Shoulders widely rounded; basal ridge and lateral margins forming obtuse angle; striae regular, parascutellar dorsal pore present on the end of first stria; two or three discal pores on third interval, all adjoining to second stria. Umbilicate series on ninth interval continuous, sparse at middle. Ventral side: metepisternum slightly shorter than basal width, nearly smooth; stermite VII with one seta on each side in males, with two in female, male sternite VI or VII without secondary sexual modification. Mesofemora with two setae; metacoxae with two setae; metatrochanters without setae; fifth tarsomere glabrous or setose ventrally. Male genitalia with median lobe of aedeagus stout, curved at basal one-third to one-fourth; right paramere short and straight. Endophallus straight or directed ventrally, with two or more lobes at anterior part. Female genitalia: Gonocoxite II of ovipositor falciform in ventral view, length ca. three times basal width; outer margin with two or three short and fine ensiform setae irregularly arranged, inner margin without ensiform setae; apex strongly compressed, rounded in lateral view, with two nematiform setae in a groove (Figs 28–31). Spermatheca with seminal canal and receptaculum differentiated, receptaculum digitate, shortly branched at base, seminal canal much slenderer than receptaculum, three to five times length of receptaculum; spermathecal gland inserted on the base of receptaculum (Figs 32–35).

Distribution. A total of 18 species distributed along the Korean Peninsula and adjacent areas, including the eastern part of Jilin and Liaoning (China), Primorskiy Kray (Russia), Tsushima Island (Japan).

Remarks. Different species of the subgenus *Koreonialoe* are extremely similar in their external appearances. All known species are almost indistinguishable from each other by external characters, and even difficult to differentiate by the sclerotized part of male genitalia. Thus previous species delimitation under this subgenus was mainly based on the male endophallic characters, especially the number, location, and shape of apical lobes (Nemoto 1988; Park and Kwon 1996; Sasakawa et al. 2008).

The endophallus of male genitalia is also important for inferring phylogeny (Sasakawa 2005a). Previous studies showed that most species (11 of 14) in *Koreonialoe* have their endophallus short and straight, but the remaining three species (*P. bellatrix*, *P. syleus*, and *P. togyusanus*) have the endophallus more elongate and clearly directed ventrally (Sasakawa et al. 2013). In the present study, we found that the ventrally directed and elongate endophallus present in all four species distributed in China, as well as in *P. microps* which was not treated by Sasakawa et al. (2013).

To better interpret the infra-subgeneric taxonomy of *Koreonialoe*, names of two groups are introduced: 1) the *opacipennis* group (*sensu stricto*, *nec.* Nemoto 1988): containing twelve species distributed in the Korean Peninsula and Tsushima, with a short and straight endophallus, gonopore that opens apically to the aedeagus, the ostium very weakly turn left. 2) the *microps* group: containing six species in Northeast China, the Korean Peninsula, and Primorskiy Kray, with elongate and ventrally directed endophallus, gonopore that opens basally to the aedeagus, aedeagal apex more or less deflected ventrally, the ostium more evidently turned left. Although these two groups included in the subgenus *Koreonialoe* are not based on a phylogenetic analysis, it seems likely that the *opacipennis* group (sensu strict) could be monophyletic for their highly specialized endophallus.

The determination of female specimens of *Koreonialoe* is very difficult sometimes. In most subgenera of *Pterostichus*, sibling species usually can be differentiated by the outline of pronotum, pronotal basal foveal characters, including the punctuation, length and depth of basal foveal grooves, chaetotaxy on elytra and legs, elytral striae depth and punctation, microsculpture, and male modification on the sternum. But in *Koreonialoe*, these important characters are always identical for most species. Moreover, the female ovipositor and reproductive tracts also do not help in species determination (Figs 28–35). In a few cases, the body size and color are helpful, for example in the two sympatric species *P. micropoides* and *P. bellatrix*, the latter one is always much larger and darker in color. But many allopatric species are usually extremely similar to each other. In these cases, females can be determined only through the males collected in exactly the same locality. Therefore, in the present study, the key to species is mainly based on the characters of male genitalia, and this key does not help determine females. But under each Chinese species, we provide comparisons to similar species on external features as well.

Key to species of subgenus *Koreonialoe* (Part of males)

1 Endophallus short and straight, gonopore opened apically on aedeagus (Sasakawa 2005: Fig. 3J); aedeagal apex usually not deflected ventrally, ostium very weakly turned left.. ***opacipennis* group**

– Endophallus elongate and directed ventrally, gonopore opened basally to aedeagus (Figs 22–27); aedeagal apex more or less deflected ventrally, ostium more evidently turned left (***microps* group**)... **2**

2 Median lobe of aedeagus with ventral margin more or less tumid (Figs 9–12) **3**

– Median lobe of aedeagus with ventral margin not tumid (Figs 7, 8)........... **5**

3 Median lobe of aedeagus with a large conic tubercle near middle of ventral margin (Fig. 12); apical portion of median lobe gradually deflected ventrally; left apical lobe of endophallus hooked .... ***P. bellatrix* Tschitschérine**

– Median lobe of aedeagus slightly tumid before middle of ventral margin (Figs 9–11); apical portion abruptly deflected ventrally; left apical lobe of endophallus not hooked.. **4**

4 Endophallus with four lobes, left apical lobe divided into two sub-lobes (Fig. 26).. ***P. tetralobatus* sp. nov.**

– Endophallus with three lobes, left apical lobe not divided (Figs 24, 25) .... ***P. syleus* Kirschenhofer**

5 Dorsally nearly black; endophallus with three lobes, right apical lobe present; left preapical lobe with apex conic (Sasakawa et al. 2013: Fig. 2A)................ .... ***P. togyusanus* Park & Kown**

– Dorsally dark reddish brown; endophallus with two lobes, right apical lobe absent; left preapical lobe with apex spherical (Figs 21, 22, 23).................... **6**

6 Endophallus directed ventrally; left apical lobe a little smaller than left preapical lobe; lp and la both spherical (Figs 22, 23).... ..... ***P. micropoides* sp. nov.**

– Endophallus directed dorsal-ventrally; left apical lobe strongly compressed, much smaller than left preapical lobe (Fig. 21)................ ***P. microps* Heyden**

1. ***Pterostichus* (*Koreonialoe*) *micropoides* sp. nov.**

http://zoobank.org/F3B14AEA-5732-494E-9CA9-BA042FEE15B9

Figs 1, 2, 7, 8, 13, 14, 22, 23, 30, 34

Type locality. China, Jilin province: Baishan city, Changbai county, Changsongling (41.74N, 128.02E, alt 1330 m).

Type material. *Holotype*: male, “Jilin province, Baishan City, Changbai County, E of Changsongling tunnel; mixed forest, 41.7398N, 128.0221E, 1330m”; “pitfall trap, 2019.VIII.9, Shi HL & Liu YZ lgt. Exp. BJFU 2019”; “HOLOTYPE ♂ *Pterostichus* (*Koreonialoe*) *micropoides* sp. nov., des. Yin & Shi. 2021” [red label]. ***Paratypes*** (a total of 164 males and 104 females): 1 male and 2 females, the same data as holotype but labeled as paratype; 2 males and 2 females, “Jilin province, Baishan City, Changbai County, Manjiang Changsong Village; mixed forest, 42.8527N, 127.8287E, 107m”; “pitfall trap; 2019.VIII.9, Liu YZ, Wang C, Zhu PZ & Wu JY lgt.”; 5 males and 5 females, “Jilin province, Yanbian City, Antu County, Laoling along G334, Anhe view point; 42.5153N, 128.6744E, 1300m”; “pitfall trap; 2019. VII.31-2019.VIII.2, Liu YZ, Wang C, Wu JY & Zhu PZ lgt.”; 1 male, “Jilin province, Hunchun City, Jingxin county, Daxiutiandong Village; fagus forest, 42.6448N, 130.3486E, 30m”; “pitfall trap; 2019.VIII.10, Shi HL & Liu YZ lgt.”; 1 male, “Jilin province, Antu County, north slope of Changbai mountain, Tianchi waterfall meadow; 42.0373N, 128.0544E, 1959m”; “2019.VIII.7, Shi HL, Liu YZ & Wang C lgt.”; 2 males and 1 female, “Jilin province, Antu county, north slope of Changbai mountain, W to the waterfall; alpine meadow, 42.0477N, 128.0517E, 2117m"; "pitfall trap; 2019.VIII.7, Shi HL, Liu YZ & Wang C lgt."; 4 males and 1 female, "Jilin province, Baishan city, Fusong county, W of Changsongling tunnel; mixed forest, 41.7798N, 127.9400E, 1577m"; "pitfall trap; 2019.VIII.9, Shi HL & Liu YZ lgt."; 17 males and 18 females, "China Jilin province, Antu County, north slope of Changbai mountain, 42.0797N, 128.0637E, 2000m, 2011.VII-VIII, Zou Y lgt."; 9 males and 3 females, "China Jilin province, Antu County, north slope of Changbai mountain, 42.0877N, 128.0738E, 1820m, 2011.VII-VIII, Zou Y lgt."; 6 males and 3 females, "China Jilin province, Antu County, north slope of Changbai mountain, 42.0885N, 128.0696E, 1950m, 2011.VII-VIII, Zou Y lgt."; 11 males, "China Jilin province, Antu County, north slope of Changbai mountain, 42.0888N, 128.0703E, 1750m, 2011.VII-VIII, Zou Y lgt."; 9 males and 5 females, "China Jilin province, Antu County, north slope of Changbai mountain, 42.0947N, 128.0675E, 1740m, 2011.VII-VIII, Zou Y lgt."; 12 males and 5 females, "China Jilin province, Antu County, north slope of Changbai mountain, 42.1192N, 128.1047E, 1730m, 2011.VII-VIII, Zou Y lgt."; 3 males and 1 female, "China Jilin province, Antu County, north slope of Changbai mountain, 42.1797N, 128.1375E, 1520m, 2011.VII-VIII, Zou Y lgt."; 3 males and 2 females, "China Jilin province, Antu County, north slope of Changbai mountain, 42.0573N, 128.0669E, 1990m, 2012.VII-VIII, Zou Y lgt."; 15 males and 12 females, "China Jilin province, Antu County, north slope of Changbai mountain, 42.0575N, 128.0656E, 1960m, 2012.VII-VIII, Zou Y lgt."; 26 males and 10 females, "China Jilin province, Antu County, north slope of Changbai mountain, 42.0797N, 128.0637E, 2000m, 2012.VII-VIII, Zou Y lgt."; 3 males and 5 females, "China Jilin province, Antu County, north slope of Changbai mountain, 42.0877N, 128.0738E, 1820m, 2012.VII-VIII, Zou Y lgt."; 7 males and 3 females, "China Jilin province, Antu County, north slope of Changbai mountain, 42.0885N, 128.0696E, 1950m, 2012.VII-VIII, Zou Y lgt."; 3 males and 6 females, "China Jilin province, Antu County, north slope of Changbai mountain, 42.0888N, 128.0703E, 1750m, 2012.VII-VIII, Zou Y lgt."; 9 males and 3 females, "China Jilin province, Antu County, north slope of Changbai mountain, 42.0947N, 128.0675E, 1740m, 2012.VII-VIII, Zou Y lgt."; 11 males and 10 females, "China Jilin province, Antu County, north slope of Changbai mountain, 42.1192N, 128.1047E, 1730m, 2012.VII-VIII, Zou Y lgt."; 1 male and 3 females, "China Jilin province, Antu County, north slope of Changbai mountain, 42.1209N, 128.1073E, 1620m, 2012.VII-VIII, Zou Y lgt."; 1 male and 1 female, "China Jilin province, Antu County, north slope of Changbai mountain, 42.1714N, 128.1347E, 1600m, 2012.VII-VIII, Zou Y lgt."; 1 male and 2 females, "China Jilin province, Antu County, north slope of Changbai mountain, 42.1797N, 128.1375E, 1520m, 2012.VII-VIII, Zou Y lgt."; 1 female, " Jilin province, the Changbai mountain Tianchi, 2000m, 1987.VII.22, Yu Peiyu lgt."; 1 male, "20100818, OH-15-S56".

Diagnosis. Small sized species in this subgenus; body dark reddish brown; fifth tarsomere without seta on ventral side; median lobe of aedeagus stout, ventral surface without tubercle, apical portion simple, not distinctly deflected to venter or left; endophallus strongly directed ventrally, gonopore opened to the ventral-base of aedeagus; two endophallic lobes present, both spherical; lp a little larger than la.

Comparison. *Pterostichus micropoides* sp. nov. is most similar to *P. microps* Heyden in its external and aedeagal features: both species have the median lobe of aedeagus without ventral tubercle and not apically dilated. But these two species also differ in their male genitalia: in *P. micropoides* sp. nov., the median lobe of aedeagus is only very slightly deflected ventrally at the apical fourth (Figs 7, 8), while in *P. microps* it is more distinctly deflected ventrally at the apical fourth (Fig. 20). The endophallus of these two species is also very similar: they both curved ventrally with only two endophallic lobes present. But they are different in the orientation of endophallus and shape of lobes: in *P. micropoides* sp. nov., the endophallus is generally directed ventrally, gonopore opened to the ventral-basal direction; the endophallic lobes with la and lp both spherical, lp a little larger than la (Figs 22, 23); while in *P. microps*, the endophallus directed apical-ventrally, gonopore opened to the basal direction; the endophallic lobes with la strongly compressed, much smaller than lp (Fig. 21).

From the external features, *P. micropoides* sp. nov. can be readily distinguished among all Chinese species of *Koreonialoe* for its smaller size (BL 13.7–15.7 mm versus 16.8–21.6 mm in other species) and dorsally reddish brown (a little darker in *P. syleus*, much darker in other two species). Besides, *P. micropoides* sp. nov. is a little different from other three Chinese species in the pronotum punctures: in *P. micropoides* sp. nov., pronotum disc with sparser fine punctures, area anterior to the transversal sulci completely impunctate; but in other species, pronotum disc with much denser fine punctures, area anterior to the transversal sulci distinctly punctate.

Description. BL 13.7–15.7 mm, BW 5.4–6.7 mm. Body form robust, dorsally dark reddish brown, elytra opaque, without metallic luster. Head large, widest at temporae; frons smooth; frontal grooves shallow; temporae strongly swollen, a little longer than eyes; eyes small and hemispherical. Pronotum strongly cordate, disc with relative sparse fine punctures, area anterior to sub-anterior transversal sulci impunctate; PW/HW = 1.31–1.36, PW/PL = 1.42–1.46, widest near anterior third; anterior margin slightly wider than posterior margin, PAW/PBW = 1.14–1.18. Lateral margins slightly arched from anterior angles to the middle, strongly sinuate and then nearly straight before posterior angles; posterior angles rectangular; mid-lateral setae present at anterior fifth of lateral margins; lateral expansions equal width at anterior and posterior portion. Basal foveae with inner and outer grooves faintly defined and partly fused, forming deep depression between them, outer groove slightly shorter than inner one; middle area between two basal foveae longitudinal rugose. Elytra oblong, shoulders widely rounded; basal ridge and lateral margin forming an obtuse angle; elytra 1.53–1.65 times longer than wide. Usually three discal pores present on third interval, all adjoining the second stria: the first one before middle, position of the second one variable, the last one at apical fifth to eighth. Umbilicate series on ninth interval continuous, sparse at middle. Ventral side: metepisternum near smooth; sternite VII of males without secondary sexual modification. Fifth tarsomere without ventral seta. Male genitalia: median lobe of aedeagus gradually curved at basal third; ventral surface without a conspicuous tubercle, apical portion not dilated, gradually deflected ventrally (Figs 7, 8); apical lamella very short, rounded-triangular, nearly straight in dorsal view (Figs 13, 14). Endophallus (Figs 22, 23) long, straightly directed ventrally, gonopore opened to ventral-basal direction of aedeagus; two distinct lobes recognized: left apical lobe (**la**) small, spherical, apex not hooked; left preapical lobe (**lp**) larger than la, similar shape as la. Female genitalia typical in this subgenus.

Distribution. This species is relatively widespread along the Changbai mountain range of Jilin province, the border between China and North Korea. (Fig. 36, green)

Etymology. The name of this new species is derived from *P. microps* from the Far East of Russia and a Greek suffix "-oides" meaning alike. It alludes to its similarity to this species.

2. *Pterostichus* (*Koreonialoe*) *tetralobatus* sp. nov.

http://zoobank.org/09F795C5-1F7F-4215-AE25-608CF1272D8C
Figs 5, 11, 17, 26, 31, 35

Type locality. China, Liaoning province: Anshan city, Xiuyan county, Laopingding (40.41N, 123.72E, alt 632m).

Type material. ***Holotype*:** male, "Liaoning province, Anshan City, Xiuyan County, Laopingding mountain, mixed forest; 40.4109N, 123.7252E, 632m"; "pitfall trap; 2019.VIII.11, Zhu PZ, Wu JY & Wang C lgt."; "HOLOTYPE ♂ *Pterostichus* (*Koreonialoe*) *tetralobatus* sp. nov., des. Yin & Shi. 2021" [red label]. ***Paratypes*:** 1 male and 2 females, the same data as holotype but labeled as paratype.

Diagnosis. Dorsal side nearly black; fifth tarsomere without ventral seta. Median lobe of aedeagus stout, ventral margin slightly tumid forming an inconspicuous tubercle. Endophallus long and thick, directed basal-ventrally; four lobes present: la divided into two sub-lobes, la1 and la2 both cylindrical, la2 smaller than la1, adnate to la1; ra apically hooked.

Comparison. This new species is peculiar among all the Chinese species of subgenus *Koreonialoe* for the endophallus has four distinct lobes, while all other species have two or three lobes. The left apical lobe divided into two lobes: la2 much smaller than la1, and adnate to la1. *P. tetralobatus* sp. nov. is very similar to *P. syleus* in the sclerotized part of male genitalia, but quite different in their endophallus.

From the external features, *P. tetralobatus* sp. nov. can be distinguished from *P. micropoides* sp. nov. and *P. syleus* for its larger size (BL 20.2–21.6 mm versus 13.7–19.7 mm in other two species) and dorsally nearly black (versus dark brown in other two species). But, the females of *P. tetralobatus* sp. nov. are completely identical to that of *P. bellatrix*. They can be determined only by the allopatric distributions (Fig. 36).

Description. BL 20.2–21.6 mm, BW 7.2–7.6 mm. Body form robust, dorsal surface nearly black, elytra opaque, without metallic luster. Head large, widest at temporae; frons smooth; frontal grooves shallow; temporae strongly swollen, a little shorter than eyes; eyes small and hemisphere; terminal segment of labial palpus fusiform. Pronotum strongly cordate, disc evenly and densely covered with fine punctures, area anterior to sub-anterior transversal sulci well punctate; PW/HW = 1.27–1.31, PW/PL = 1.58–1.62, widest near anterior third; anterior margin a little wider than posterior margin, PAW/PBW = 1.09–1.14. Lateral margins slightly arched from anterior angles to the middle, strongly sinuate and then nearly straight before posterior angles; posterior angles rectangular; mid-lateral setae present at anterior fifth of lateral margins; lateral expansions equal width anteriorly and posteriorly. Basal foveae with inner and outer grooves faintly defined and partly fused, forming deep depression between them, outer groove slightly shorter than inner one; middle area between two basal foveae longitudinal rugose. Elytra oblong, shoulders widely rounded; basal ridge and lateral margin forming an obtuse angle; elytra 1.58–1.65 times longer than wide. Usually three discal pores present on third interval, all adjoining the second stria; the first one before middle, position of the second one variable, the last one at apical fifth to eighth. Umbilicate series on ninth interval continuous, sparse at middle. Ventral side: metepisternum nearly smooth; sternite VII of males without secondary sexual modification. Fifth tarsomere without ventral seta. Male genitalia: median lobe of aedeagus stout, gradually curved at basal fourth, strongly dilated near middle, apical portion abruptly deflected ventrally; ventral surface shallowly tumid near middle, forming an inconspicuous tubercle (Fig. 11); apical lamella narrow, apex rounded-triangular, slightly oblique to the left in dorsal view (Fig. 17). Endophallus (Fig. 26) long and thick, strongly directed basal-ventrally, gonopore opened to ventral-basal direction of aedeagus; four distinct lobes recognized: left apical lobe (**la**) divided into two sub-lobes, left apical lobe I (**la1**) cylindrical, larger than all other three lobes; left apical lobe II (**la2**) same shape as la1 but smaller, adnate to la1; left preapical lobe (**lp**) oblate and small, located behind la1, well separated from it; right apical lobe (**ra**) small, orbicular, apically hooked. Female genitalia typical in this subgenus.

Distribution. This species was only found in the type locality, Anshan, Liaoning Province, Laopingding mountain. (Fig. 36, red)

Etymology. The scientific name of the new species is composed of two Greek root: "*tetr-*" meaning four and "*lobat-*" meaning lobe. The new species is named for its endophallus with four lobes which is special in this subgenus.

3. *Pterostichus* (*Koreonialoe*) *syleus* Kirschenhofer, 1997

Figs 3, 4, 9, 10, 15, 16, 24, 25, 29, 33

Pterostichus (*Koreonialoe*) *syleus* Kirschenhofer, 1997: 694 (Holotype deposited in Naturhistorisches Museum Wien; type locality: "Shi-fang Ding", sg. *Nialoe*); Sasakawa et al. 2013: 430 (based on the misidentification of an unknown species).

Material examined. (8 males and 16 females): 4 males, "China, Liaoning, Dandong city, Saima town; Mixed forest, 41.0143N, 124.3020E"; "Day, 2008.VIII.15, pitfall trap, Shan HC lgt."; 1 male, "Liaoning province, Dalian City, Snake island; 2012, Shi

JS lgt."; 2 males, "China, Liaoning, Benxi City, Guanmenshan mountain; 41.5644N, 123.5779E, 530m, 2011.VIII.20, night, Huang XL lgt."; 1 male, "China, Liaoning province, Benxi City, Benxi county, Guanmenshan mountain; 41.5644N, 123.5779E, 530m, 2011.VIII.23, day, Huang XL lgt."; 2 males and 5 females, "China, Liaoning province, Zhuanghe City, Buyunshan mountain; 40.0862N, 122.7234E, pitfall trap, 1133m"; "2019.VIII.15, Zhu PZ & Wang C lgt."; 6 females, "China, Liaoning, Fushun city, Qingyuan county, Nankouqian town; mixed forest; 2020.VIII, local collector."; 2 females, "Liaoning province, Baishilazi, 40.9394N, 124.8025E, 567m, 2015.VIII.14, mixed forest"; 1 female, "Liaoning province, Baishilazi, 40.9385N, 124.7891E, 713m, 2015.VIII.15, broadleaved mixed forest"; 2 females, "Liaoning province, Baishilazi, 40.9412N, 124.7986E, 591m, 2015.IX.12, mixed forest".

Diagnosis. Dorsally dark reddish brown; fifth tarsomere without ventral seta. Median lobe of aedeagus stout, ventral surface slightly tumid forming an inconspicuous tubercle. Endophallus elongate, directed basal-ventrally, gonopore opened to the ventral-basal direction of aedeagus; three lobes present: la and lp both oblate, without hook at apex, similar in size and well separate.

Comparison. From the sclerotized features of male genitalia, *P. syleus* is most similar to *P. tetralobatus* sp. nov. for they both have an inconspicuous tubercle on the ventral margin of median lobe. But they are quite different in the endophallus. *P. syleus* is distinguishable from *P. tetralobatus* sp. nov. for the endophallus with la not divided and ra only very faintly defined, while in the latter species with la divided into two sub-lobes, and ra well defined.

From the external features, *P. syleus* can be distinguished from *P. micropoides* by its slightly larger size (BL 16.8–19.7 mm versus 13.7–15.7 mm), and from *P. bellatrix* and *P. tetralobatus* by the smaller size (BL 16.8–19.7 mm versus 19.7–21.6 mm) and lighter color (dark reddish brown versus nearly black).

Description. BL 16.8–19.7 mm, BW 6.7–7.2 mm. Body form robust, dorsally dark reddish brown, elytra opaque, without metallic luster. Head large, widest at temporae; frons smooth; frontal grooves shallow; temporae strongly swollen, a little shorter than eyes; eyes small and hemisphere; terminal segment of labial palpus fusiform. Pronotum strongly cordate, disc evenly and densely covered with fine punctures, area anterior to sub-anterior transversal sulci well punctate; PW/HW = 1.26–1.32, PW/PL = 1.46–1.51, widest near anterior third; anterior margin a little wider than posterior margin, PAW/PBW = 1.19–1.21. Lateral margins slightly arched from anterior angles to the middle, strongly sinuate and then nearly straight before posterior angles; posterior angles rectangular; mid-lateral setae present at anterior fifth of lateral margins; lateral expansions equal width anteriorly and posteriorly. Basal foveae with inner and outer grooves faintly defined and partly fused, forming deep depression between them, outer groove slightly shorter than inner one; middle area between two basal foveae longitudinal rugose. Elytra oblong, shoulders widely rounded; basal ridge and lateral margin forming an obtuse angle; elytra 1.59–1.64 times longer than wide. Usually three discal pores present on third interval, all adjoining the second stria; the first one before middle, position of the second one variable, the last one at apical sixth to eighth.

Umbilicate series on ninth interval continuous, sparse at middle. Ventral side: metepisternum nearly smooth; sternite VII of males without secondary sexual modification. Fifth tarsomere without ventral seta. Male genitalia: median lobe of aedeagus stout, gradually curved at basal third, slightly dilated near middle, apical portion abruptly deflected ventrally; ventral surface shallowly tumid near middle, forming an inconspicuous tubercle (Figs 9, 10); apical lamella narrow, apex rounded-triangular, very faintly oblique to the left in dorsal view (Figs 15, 16). Endophallus (Figs 24, 25) long, directed basal-ventrally, gonopore opened to ventral-basal direction of aedeagus; three endophallic lobes recognized: right apical lobe (**ra**) faintly defined, close to gonopore; left apical lobe (**la**) oblate, apex not hooked; left preapical lobe (**lp**) similar shape and size as la, these two lobes well separated. Female genitalia typical in this subgenus.

Distribution. Widely distributed in the eastern part of Liaoning province, along the Qianshan mountain range. (Fig. 36, blue)

Remarks. Sasakawa et al. (2013) redescribed this species and illustrated its endophallus based on a specimen from the type locality (Shi-Fang-Ding, the highest peak of Baishilazi nature reserve). However, their description and illustrations do not accord with the original literature (Kirschenhofer 1997) or our examined specimens from the type locality (Baishilazi). Sasakawa et al. (2013) indicated that *P. syleus* is the only species of *Koreonialoe* with the fifth tarsomeres setose beneath, but in the original description Kirschenhofer (1997) mentioned this species has: "*Klauenglieder unterseits glatt*". Moreover, compared with the line drawing of the male genitalia of *P. syleus* (Kirschenhofer 1997: Fig. 23), specimen described by Sasakawa et al. (Sasakawa et al. 2013: Fig. 2D) is different in the sclerotized part of male genitalia in the ventral tubercle a little larger and the apical portion of median lobe less deflected ventrally in lateral view. Thus, although the specimen described by Sasakawa et al. (2013) is exactly from the type locality of *P. syleus*, we thought it should belong to an unknown new species different from *P. syleus* and all other known species of *Koreonialoe*. Besides the differences mentioned above, these two species are also different in their endophallus: *P. syleus* has the endophallus more strongly directed ventro-basally, and lp is oblate, with apex not hooked (Figs 24, 25); but the species by Sasakawa et al. (2013) has endophallus less directed ventral-basally, and lp is coniform, with distinctly hooked apex (Sasakawa et al. 2013: Fig. 2D).

4. ***Pterostichus* (*Koreonialoe*) *bellatrix* (Tschitschérine, 1895)**

Figs 6, 12, 18, 27, 28, 32

Pterostichus (*Koreonialoe*) *bellatrix* Tschitschérine, 1895: 169 (Syntypes deposited in Zoological Institute, Russian Academy of sciences, St Petersburg, Russia; type locality: North Korea, sg. *Feronia*); Jedlička 1962: 271 (misspelled as *P. bellator*, sg. *Lianoe*); Kwon and Lee 1986: 28 (misspelled as *P. bellator*, sg. *Nialoe*); Park and Kwon 1996: 96 (misspelled as *P. bellator*); Sasakawa 2005a: 1209 (misspelled as *P. bellator*); Sasakawa et al. 2013: 430; Park and Park 2013: 66. **New record from China**

Pterostichus klickai Jedlička, 1931: 104. (Holotype deposited in Narodni Muzeum Prirodovedecke Muzeum, Prague, Czech Republic, Type locality: Seishin, Korea); Cho 1957: 194; Jedlička 1962: 272 (sg. *Lianoe*); Kwon and Lee 1986: 28; Nemoto 1988: 40; Bousquet 2003: 497 (synonymized with *P. bellatrix*).

Material examined. (6 males and 1 female): 1 male, "China Jilin province, Baishan City, Changbai County, E of Changsongling tunnel; Mixed forest, 41.7398N, 128.0221E, 1330m"; "pitfall trap; 2019.VIII.9, Shi HL & Liu YZ lgt."; 4 males and 1 female, "China Jilin province, Baishan City, Fusong county, W of Changsongling tunnel; mixed forest, 41.7798N, 127.9400E, 1577m"; "pitfall trap, 2019.VIII.9, Shi HL & Liu YZ lgt."; 1 male, "Jilin province, Changbai Mountain Hot Spring, 1982. VII.13, Liao Suyi lgt.".

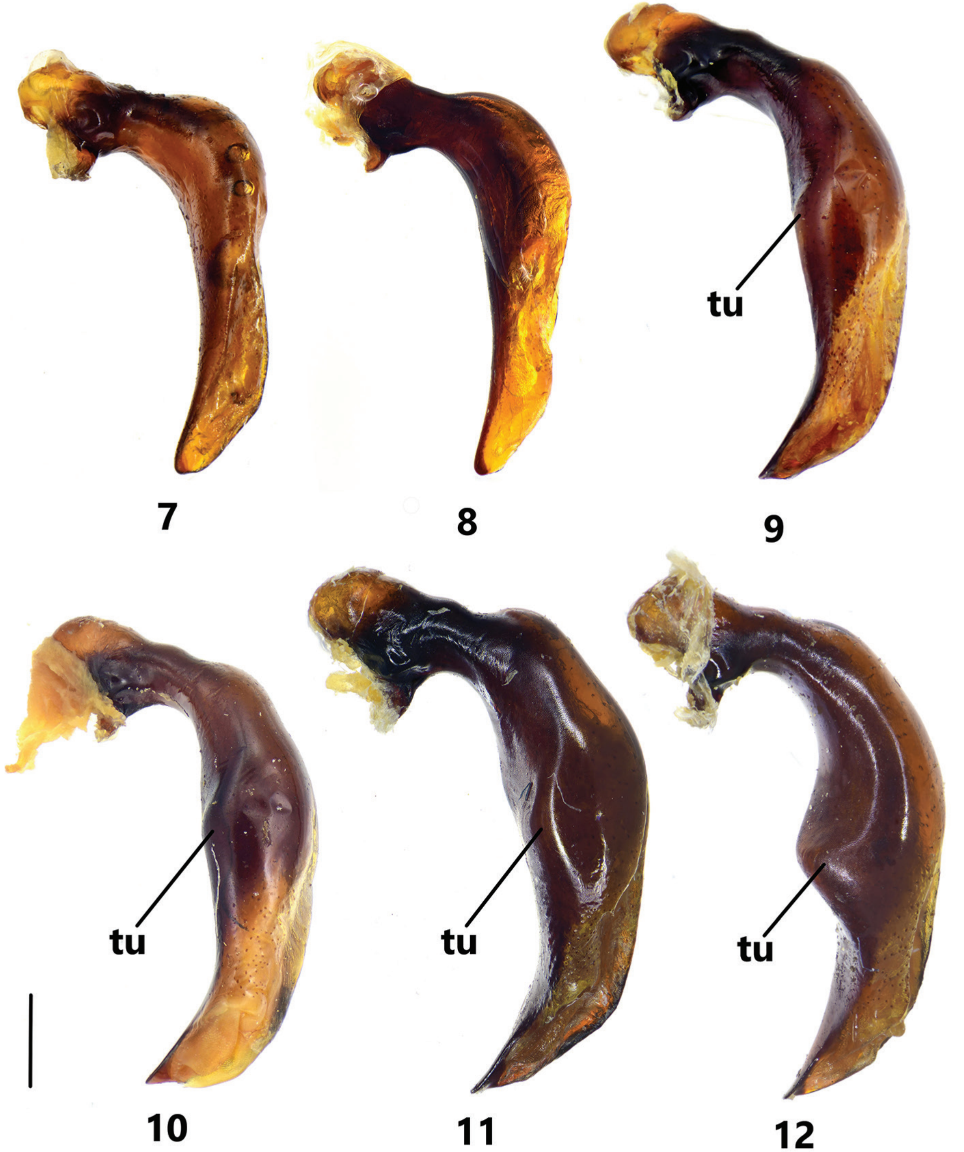
Diagnosis. Dorsal surface nearly black; fifth tarsomere without ventral seta. Median lobe of aedeagus stout, ventral margin strongly tumid forming a conspicuous cuneate tubercle anterior to middle. Endophallus directed basal-ventrally, gonopore opened to the ventral-basal direction of aedeagus; three lobes present: la and lp similar in size, la a little hooked apically, ra faintly defined.

Comparison. *P. bellatrix* is similar to *P. syleus* and *P. tetralobatus* in their external features, but can be distinguished from the latter two species by the more conspicuous ventral tubercle on male genitalia. Another species, *P. woongbii* from South Korea, also has a conspicuous ventral tubercle on male genitalia, but is quite different from *P. bellatrix* in the ventral tubercle located near base of median lobe, and endophallus short and straight.

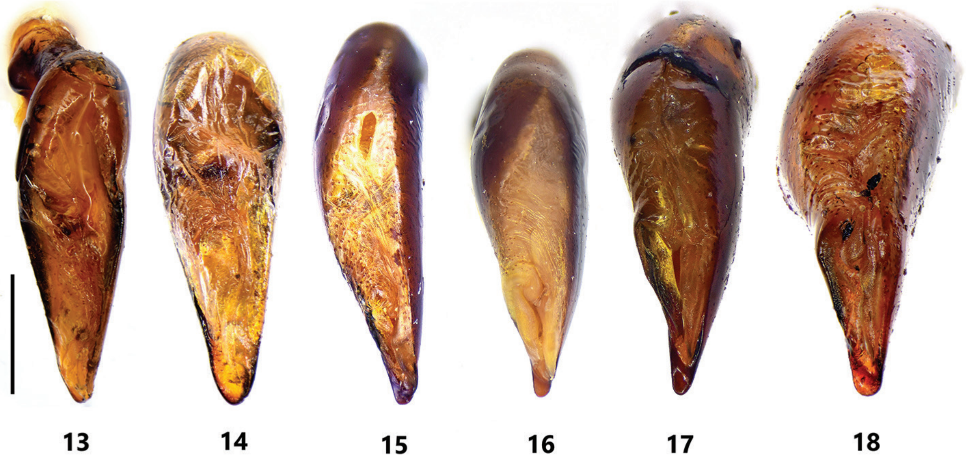
From the external features, *P. bellatrix* can be distinguished from *P. micropoides* sp. nov. and *P. syleus* for its larger size (BL 19.7–21.2 mm versus 13.7–19.7 mm in other two species) and dorsally nearly black (versus dark reddish brown in other two species). But, the females of *P. bellatrix* are completely identical to that of *P. tetralobatus* sp. nov. They can be determined only by the allopatric distributions (Fig. 32).

Description. BL 19.7–21.2 mm, BW 6.3–6.6 mm. Body form robust, dorsally dark brown, nearly black, elytra opaque, without metallic luster. Head large, widest at temporae; frons smooth; frontal grooves shallow; temporae strongly swollen, a little shorter than eyes; eyes small and hemispherical; terminal segment of labial palpus fusiform. Pronotum strongly cordate, disc evenly and densely covered with fine punctures, area anterior to sub-anterior transversal sulci well punctate; PW/HW = 1.23–1.27, PW/PL = 1.53–1.56, widest near anterior third; anterior margin a little wider than posterior margin, PAW/PBW = 1.16–1.18. Lateral margins slightly arched from anterior angles to the middle, strongly sinuate and then nearly straight before posterior angles; posterior angles rectangular; mid-lateral setae present at anterior fifth of lateral margins; lateral expansions equal width anteriorly and posteriorly. Basal foveae with inner and outer grooves faintly defined and partly fused, forming deep depression between them, outer groove slightly shorter than

Figures 1–6. Habitus of Pterostichus (Koreonialoe) spp. from China **1** *P. micropoides* sp. nov., Holotype. **2** *P. micropoides* sp. nov., male, Paratype from Hunchun city, Jilin **3** *P. syleus* Kirschenhofer, a male from Fengcheng city, Liaoning **4** *P. syleus* Kirschenhofer, a female from Zhuanghe city, Liaoning 5 *P. quadrilobatus* sp. nov., Holotype **6** *P. bellatrix* Tschitschérine, a male from Changbai county, Jilin. Scale bar: 5mm.



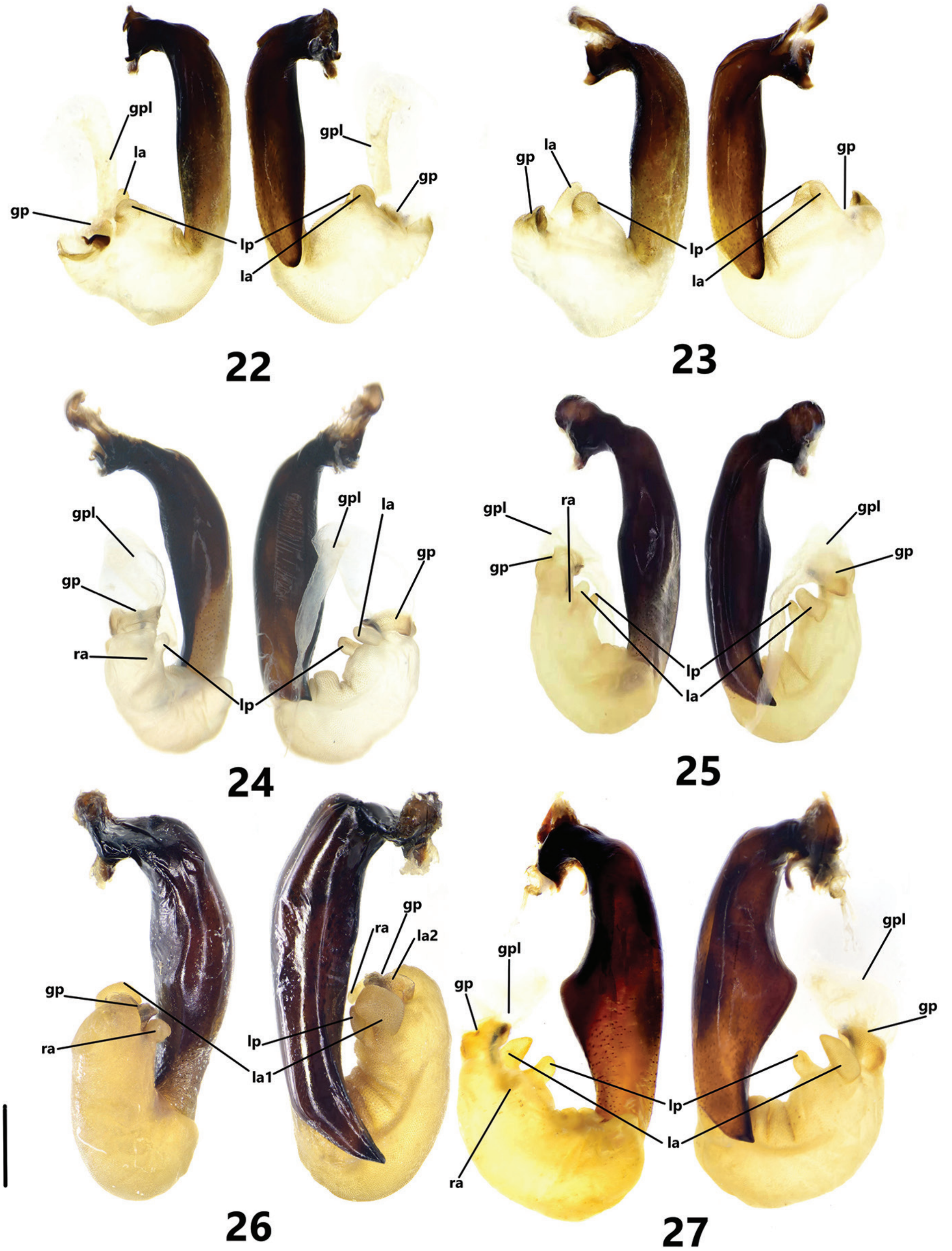
Figures 7–12. Male genitalia of *Pterostichus* (*Koreonialoe*) spp. from China, left lateral view of median lobe of aedeagus **7** *P. micropoides* sp. nov., Holotype **8** *P. micropoides* sp. nov., Paratype from Changbai county, Jilin **9** *P. syleus* Kirschenhofer, a male from Fengcheng city, Liaoning **10** *P. syleus* Kirschenhofer, a male from Shedao Island, Liaoning **11** *P. quadrilobatus* sp. nov., Holotype **12** *P. bellatrix* Tschitschérine, a male from Changbai county, Jilin. Scale bar: 1 mm.



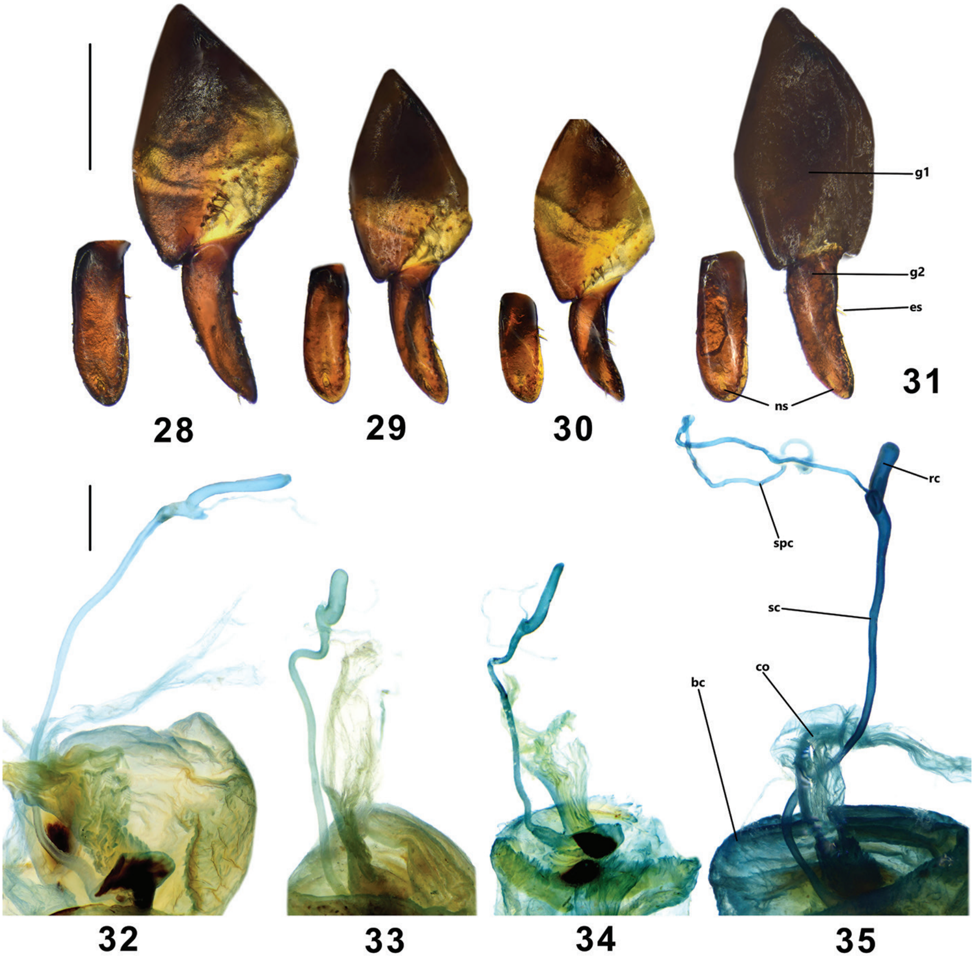
Figures 13–18. Male genitalia of *Pterostichus* (*Koreonialoe*) spp. from China, dorsal view of median lobe of aedeagus **13** *P. micropoides* sp. nov., Holotype **14** *P. micropoides* sp. nov. Paratype from Changbai county **15** *P. syleus* Kirschenhofer, a male from Fengcheng city, Liaoning **16** *P. syleus* Kirschenhofer, a male from Shedao Island, Liaoning **17** *P. quadrilobatus* sp. nov., Paratype from Laopingding, Liaoning **18** *P. bellatrix* Tschitschérine, a male from Changbai county, Jilin. Scale bar: 1 mm.

Figures 19–21. *Pterostichus* (*Koreonialoe*) *microps* Heyden, a male labeled as "Russia, Primorye Terr. Lazovsky reserve, Krodon America, 2002.IV.25, J. Sundukov leg" **19** habitus **20** male genitalia, dorsal view of median lobe, scale bar: 1 mm **21** endophallus, left lateral view and right lateral view. Scale bars: 5 mm (**a** for Fig. 19); 1 mm (**b** Figs 21, 22).

inner one; middle area between two basal foveae longitudinal rugose. Elytra oblong, shoulders widely rounded; basal ridge and lateral margin forming an obtuse angle; elytra 1.53–1.56 times longer than wide. Usually three discal pores present on third interval, all adjoining the second stria; the first one before middle, position of the



Figures 22–27. Endophallus of *Pterostichus* (*Koreonialoe*) spp. from China, left lateral view and right lateral view **22** *P. micropoides* sp. nov., Paratype from Antu city, Jilin **23** *P. micropoides* sp. nov., Paratype from Changbaishan mt., Jilin **24** *P. syleus* Kirschenhofer, a male from Fengcheng city, Liaoning **25** *P. syleus* Kirschenhofer, a male from Shedao Island, Liaoning **26** *P. quadrilobatus* sp. nov., Holotype **27** *P. bellatrix* Tschitschérine, a male from Changbai county, Jilin. Scale bar: 1 mm.



Figures 28–35. Female genitalia of *Pterostichus* (*Koreonialoe*) spp. from China, Figs **28–31** ventral view and inner lateral view of ovipositor. Figs **32–35** female reproductive system. **28, 32** *P. tetralobatus*, Paratype from Laopingding, Liaoning **29, 33** *P. syleus*, a female from Baishilazi, Liaoning **30, 34** *P. micropoides*, female, Paratype from Antu county, Jilin **31, 35** *P. bellatrix*, a female from Fusong county, Jilin. Scale bar: 0.5 mm. Abbreviations: g1: gonocoxite I; g2:gonocoxite II; es: ensiform setae; ns, nematiform setae; bc: bursa copulatrix; co: common oviduct; sc: seminal canal; rc: receptaculum; spc: spermathecal canal.

second one variable, the last one at apical sixth to eighth. Umbilicate series on ninth interval continuous, sparse at middle. Ventral side: metepisternum nearly smooth; sternite VII of males without secondary sexual modification. Fifth tarsomere without ventral seta. Male genitalia: median lobe of aedeagus stout, gradually curved at basal third, apical portion gradually deflected ventrally; ventral surface strongly tumid near middle, forming a conspicuous cuneate tubercle a little anterior to the middle (Fig. 12); apical lamella short and wide, apex rounded, not oblique to the

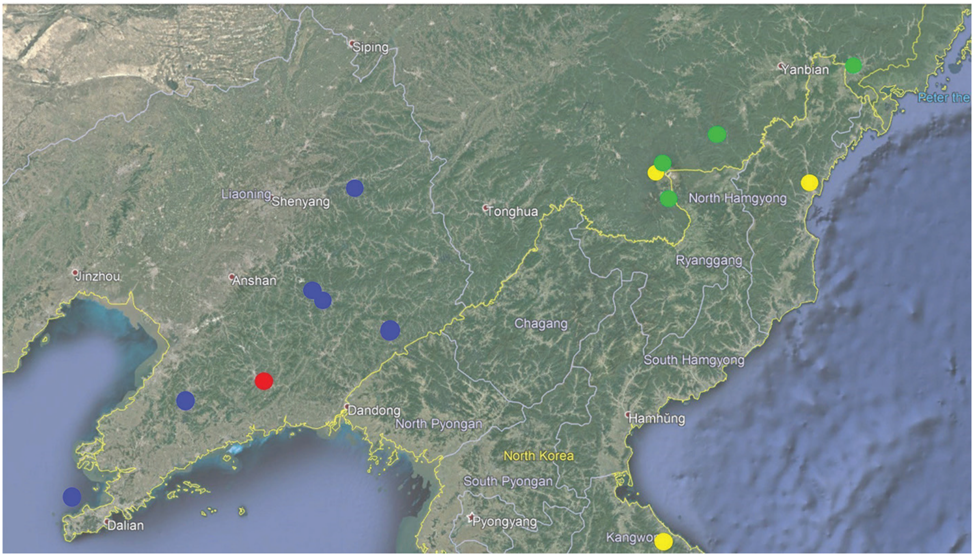


Figure 36. Confirmed distribution of *Pterostichus* (*Koreonialoe*) spp. in China: Green: *P. micropoides* sp. nov.; Red: *P. tetralobatus* sp. nov.; Yellow: *P. bellatrix* Tschitschérine; Blue: *P. syleus* Kirschenhofer.

left in dorsal view (Fig. 18). Endophallus (Fig. 27) long, directed basal-ventrally, gonopore opened to the ventral-basal direction of aedeagus; three endophallic lobes recognized, all placed near gonopore: left apical lobe (**la**) oblate, apex slightly hooked, forming an oblique upper surface; left preapical lobe (**lp**) similar size as la, apex rounded, well separate from la; right apical lobe (**ra**) faintly defined, nearly spherical. Female genitalia typical in this subgenus.

Distribution. This species is widespread from the southeastern part of Jilin province to South Korea, along the eastern mountains in the Korean Peninsula. (Fig. 36, yellow, distributions in South Korea not shown)

Acknowledgements

We wish to thank Mr. Yizhou Liu (BJFU), Mr. Pingzhou Zhu (IZAS), Mr. Chen Wang (BJFU) and Ms. Jingyu Wu (BJFU) for their help when collecting the types of new species. We are also grateful to Dr. Han Xu (BJFU), Mr. Tai Gao (BJFU), Mr. Weifeng Yan (BJFU), Ms. Zibo Liu (BJFU) and Mr. Haohan Mao (BJFU) for their help during our study work. We thank Dr Kipling Will (Berkeley, USA) and Dr Riccardo Sciaky (Milano, Italy) for their valuable comments and linguistic improvement on this paper. This study was supported by the General Program of National Natural Science Foundation of China (31770687) and Forestry Science and Technology Innovation Special of Jiangxi Forestry Department (201912).

References

Berlov O, Plutenko A (1997) Two new subgenera of the genus *Pterostichus* (Coleoptera, Carabidae) from the Far East of Russia. Vestnik Irkutskoy Gosudarstvennoy Selskokhozyaystvennoy Akademii 5: 47–51.

Bousquet Y (2003) Tribe Pterostichini Bonelli, 1810. In: Löbl I, Smetana A (Eds) Catalogue of Palaearctic Coleoptera. Archostemata-Myxophaga-Adephaga, 1. Apollo Books, Stenstrup, 469–520.

Bousquet Y (2017) Tribe Pterostichini Bonelli, 1810. In: Löbl I, Löbl D (Eds) Catalogue of Palaearctic Coleoptera, Volume 1: Archostemata-Myxophaga-Adephaga. EJ Brill, Denmark, 717.

Cho PS (1957) A systematic catalogue of Korean Coleoptera. Human Immunology Korea University 2: 173–338.

Jedlička A (1931) Noví Carabidi z jižní Číny-Yunnanu. (II. díl.) Neue Carabiden aus Süd-China. (II. Teil.). Časopis Československé Společnosti Entomologické 28: 102–108.

Jedlička A (1962) Monographie des Tribus Pterostichini aus Ostasien (Pterostichi, Trigonotomi, Myadi) (Coleoptera-Carabidae). Entomologische Abhandlungen und Berichte aus dem Staatlich Museum für Tierkunde in Dresden 26: 177–346.

Kasahara S (1988) Distribution pattern and speciation of pterostichine carabid beetles in Japan. In: Satô M (Ed.) The Beetles of Japan, with Special Reference to Their Origin and Speciation. Tôkai University Press, Tokyo, 52–65. [in Japanese]

Kirschenhofer E (1997) Neue Arten der Gattungen *Pterostichus* Bonelli 1810, *Synuchus* Gyllenhal 1810, *Lesticus* Dejean 1828 und *Trigonotoma* Dejean 1828 aus Ost- und Südostasien (Coleoptera, Carabidae: Pterostichinae). Linzer Biologische Beiträge 29: 689–714.

Kwon YJ, Lee SM (1986) Check list of superfamily Caraboidea from Korea. Insecta Koreana, 6: 1–56.

Lafer GS (2005) A check-list of ground beetles (Coleoptera: Cicindelidae, Carabidae) of the Muravjev-Amursky Peninsula, Primorskii Krai. Far Eastern Entomologist 151: 1–8.

Li JK, Zhang XP (2014) [new species]. In: Li JK, Zhang XP, Gao MX, Lin L, Wang XY (Eds) Nouvelles espèces et nouvelle citation de coléoptères d'Asie (Hydrophilidae- Carabidae-Cantharidae). Le Coléoptériste17: 182–184.

Nemoto K (1988) *Pterostichus opacipennis* Jedlička and its allied species of South Korea and Japan (Coleoptera, Carabidae). Bulletin of the Biogeographical Society of Japan 43: 39–46.

Park JK, Kwon YJ (1996) A new subgenus of the *Pterostichus* from Korea (Coleoptera: Harpalidae). Korean Journal of Entomology 26(1): 93–103.

Park JK, Park JY (2013) Insect Fauna of Korea, Volume 12, Number 13: 1–98.

Park JK, Lyu DP, Park JY (2013) Two new species of the genus *Pterostichus* (Coleoptera: Carabidae) from Korea. Journal of Asia-Pacific Entomology, 16: 385–388. https://doi.org/10.1016/j.aspen.2013.04.012

Sasakawa K (2005a) Phylogenetic studies of the subgenus *Nialoe* (s. lat.) (Coleoptera, Carabidae, genus *Pterostichus*), Part 1: homology of the component parts of male genitalia and higher phylogeny. Zoological Science 22: 1205–1216. https://doi.org/10.2108/zsj.22.1205

Sasakawa K (2005b) *Pterositchus macrogenys* Bates, 1883 (Coleoptera, Carabidae) and its allied species of northern Japan. Biogeography 7: 69–78.

Sasakawa K, Kim JK, Kim JK, Kubota K (2013) Notes on the ground beetle *Pterostichus togyusanus* (Coleoptera: Carabidae): Phylogenetic evidence for species status and new distribution record. Journal of Asia-Pacific Entomology, 2013, 16(4): 429–431. https://doi.org/10.1016/j.aspen.2013.05.003

Sasakawa K, Kim JL, Kim JK, Kubota K (2008) Taxonomic studies of *Pterostichus ishikawai* Nemoto (Coleoptera: Carabidae). Entomological Science 11: 173–178. https://doi.org/10.1111/j.1479-8298.2008.00261.x

Shi HL, Sciaky R, Liang HB, Zhou HZ (2013) A new subgenus *Wraseiellus* of the genus *Pterostichus* Bonelli (Coleoptera, Carabidae, Pterostichini) and new species descriptions. Zootaxa 3664 (2): 101–135. https://doi.org/10.11646/zootaxa.3664.2.1

Sundukov YN (2013) Annotirovannyi katalog zhuzhelits (Coleoptera: Caraboidea) Sikhote-Alinya. [An annotated catalogue of the ground beetles (Coleoptera: Caraboidea) of Sikhote-Alin]. Vladivostok, Dalnauka: 1–270.

Tschitschérine T (1895) Supplément à la faune des carabiques de la Corée. Horae Societatis Entomologicae Rossicae 29[1894-1895]: 154–188.

ZooKeys 1063: 23–48 (2021)
doi: 10.3897/zookeys.1063.69580
https://zookeys.pensoft.net

CHECKLIST

A peer-reviewed open-access journal
ZooKeys
Launched to accelerate biodiversity research

Amphibians of the equatorial seasonally dry forests of Ecuador and Peru

Diego Armijos-Ojeda[1,2,3], Diana Székely[1,3], Paul Székely[1,3], Dan Cogălniceanu[4], Diego F. Cisneros-Heredia[5,6,7,8], Leonardo Ordóñez-Delgado[1,2,3], Adrián Escudero[9], Carlos Iván Espinosa[1]

1 *Laboratorio de Ecología Tropical y Servicios Ecosistémicos (EcoSs-Lab), Departamento de Ciencias Biológicas y Agropecuarias, Universidad Técnica Particular de Loja, Loja 110107, Ecuador* **2** *Programa de Doctorado en Conservación de Recursos Naturales, Escuela Internacional de Doctorado, Universidad Rey Juan Carlos, 28933 Móstoles, Madrid, Spain* **3** *Museo de Zoología, Universidad Técnica Particular de Loja, San Cayetano Alto, calle París s/n, Loja, Ecuador* **4** *Faculty of Natural and Agricultural Sciences, Ovidius University Constanța, 900470, Constanța, Romania* **5** *Colegio de Ciencias Biológicas y Ambientales COCIBA, Universidad San Francisco de Quito USFQ, Quito 170901, Ecuador* **6** *Museo de Zoología & Laboratorio de Zoología Terrestre, Instituto de Biodiversidad Tropical iBIOTROP, Universidad San Francisco de Quito USFQ, Quito, Ecuador* **7** *Department of Geography, King's College, London, UK* **8** *Instituto Nacional de Biodiversidad INABIO, Quito, Ecuador* **9** *Department of Science, Rey Juan Carlos University, 28933, Móstoles, Madrid, Spain*

Corresponding author: Diana Székely (dszekely@utpl.edu.ec)

Academic editor: Luis Ceríaco | Received 7 June 2021 | Accepted 20 August 2021 | Published 18 October 2021

http://zoobank.org/7CAAD4A9-4036-4199-B8CD-CC55557528C2

Citation: Armijos-Ojeda D, Székely D, Székely P, Cogălniceanu D, Cisneros-Heredia DF, Ordóñez-Delgado L, Escudero A, Espinosa CI (2021) Amphibians of the equatorial seasonally dry forests of Ecuador and Peru. ZooKeys 1063: 23–48. https://doi.org/10.3897/zookeys.1063.69580

Abstract

Seasonally dry forests (SDFs) are one of the most challenging ecosystems for amphibians, fueling the diversity of this group of vertebrates. An updated inventory of native amphibians present in the Equatorial SDF is provided, which extends along the Pacific coast of Ecuador and northwestern Peru. The study is based on an extensive field sampling (two thirds of the total records) carried out throughout the Equatorial SDF, along with a compilation of the available information on distribution of amphibians in the region from published scientific papers, museum collections and on-line databases. The final dataset included 2,032 occurrence records for 30 amphibian species, belonging to eight anuran families. Additionally, data regarding conservation status, habitat use, spawn deposition site, reproductive mode, and body size, along with an identification key for all encountered species are provided. The results indicate a strong sampling bias with a deficit in the Peruvian part of the study area, and a need for urgent inventories targeted at under-sampled areas, using modern taxonomic methods. The study emphasizes the conservation priorities in the Equatorial SDF, based on the distribution, conservation status and life-history data. This information should be useful for the local authorities and institutions involved in the management and conservation of biodiversity in SDF.

Keywords
Annotated list, Anura, Conservation, Distribution, Herpetofauna, Life-history

Introduction

Seasonally dry forests (hereafter SDFs) have been recently recognized as a coherent biome distributed across South America (Prado and Gibbs 1993; Pennington et al. 2000; Pennington et al. 2006; Linares-Palomino et al. 2011). They consist of tree- or shrub-dominated ecosystems with deciduous or semideciduous vegetation, occurring in frost-free areas with mean annual temperatures higher than 17 °C, high seasonal rainfall that sums less than 1,600 mm/year, and at least 5–6 months annually with less than 100 mm/month (Murphy and Lugo 1986; Pennington et al. 2000; Prado 2000; Espinosa et al. 2012). Although animal diversity of Neotropical SDFs has received relatively little attention (Sánchez-Azofeifa et al. 2005), a general trend of lower species richness is apparent when compared to neighboring moister forest ecosystems such as rainforests and cloud forests (Espinosa et al. 2011; Hanson 2011; Jenkins et al. 2013; Guedes et al. 2018). This trend is quite evident in amphibians, organisms that are highly dependent of humid conditions. The harsher climate conditions typical for the SDF act as strong limiting factors for amphibian diversity (Duellman 1988; Székely et al. 2016). Even so, survey efforts carried out in these habitats have revealed high levels of amphibian endemism, and diverse behavioral and physiological adaptations allowing most of these species to endure long periods of low food availability and hydric stress (Ceballos 1995; Chazdon et al. 2011; Stoner and Timm 2011).

In the Neotropics, there are at least four distinct phytogeographic groups of SDF: Caribbean-Mesoamerican, Ecuadorian-Peruvian, Brazilian Caatinga, and Central South American (Prado 2000; Linares-Palomino 2004a). Among them, the Ecuadorian-Peruvian SDF has the smallest extent, aggregating coastal SDFs from western Ecuador and northwestern Peru (Pennington et al. 2000; Peralvo et al. 2007), but excluding the seasonal habitats from Huancabamba and Marañon, which, although relatively close spatially, are considered to be biogeographically distinct due to the fact that the Andes mountain-range represents a dispersal barrier (Linares-Palomino 2004b). Chapman (1926) was the first to recognize the high levels of biodiversity and endemism of the Ecuadorian SDF, using the term Tropical Arid Fauna. Later, the name Tumbesian Centre of Endemism has been extensively used (Cracraft 1985; Best and Kessler 1995; Stattersfield et al. 1998) for this biogeographic region, recognized as a center of endemism at a global scale taking into consideration the better studied taxa, i.e., birds (Best and Kessler 1995) and vascular plants (Davis et al. 1997) and, consequently, a global priority for conservation (DryFlor 2016) and a hotspot for biodiversity (Myers et al. 2000). Other authors have referred to this area under different (complete or partially synonym) names: Ecuadorian Subcentre (Müller 1973), Guayas Province (Ringuelet 1975), Ecuadorian Pacific Dry Forest (Udvardy 1975), Pacific Equatorial Dominion (Ab'Saber 1977), Tumbesian Centre (Cracraft 1985), Ecuadorian Dry Forest and Western Ecuador Moist Forest (Dinnerstein 1995), Western Ecuador Province (Morrone 1999), Arid Ecuadorian and Túmbes-Piura Provinces (Morrone 2001), Equatorial Pacific Area (Porzecanski and Cracraft 2005), Western Ecuador and Ecuadorian Provinces (Morrone 2014), and there is currently a lack of consensus about the precise position and extent of the SDF in Ecuador and Peru. These diverse definitions are usually based on endemism patterns of either vascular plants or birds, so they tend to include neighboring moist habitats, ranging from mangroves to montane cloud forests (Best and Kessler 1995), merging different ecosystems which are often not characterized by seasonality. As a result, these delimitations are less effective when applied to more water-dependent taxa such as amphibians, which show quite different patterns of diversity and endemism.

The amphibian diversity in the SDF of the coastal areas of Ecuador and Peru has been scarcely explored, with only a small number of localities being inventoried (Almendáriz and Carr 1992, 2012; Venegas 2005; Cisneros-Heredia 2006; Armijos-Ojeda and Valarezo 2010; Amador and Martinez 2011; Székely et al. 2016; Sánchez-Nivicela et al. 2015; Cuadrado et al. 2020). Several factors influence this lack of information, including bias caused by researchers' preference for the more biodiverse tropical rain and cloud forests, logistic limitations imposed by site accessibility, and the short and unpredictable rainy season when amphibians are active and can be detected.

The first step in the development of any effective management and conservation strategy for amphibians is the completion of regional inventories, especially in the context of rapid biodiversity loss and climate changes. Understanding species distribution is especially urgent in the case of amphibians, the most threatened vertebrate group worldwide (Catenazzi 2015). In this context, our aim was to update the list of amphibian species and their distribution in the coastal SDF of Ecuador and Peru, through extensive fieldwork and the compilation of all available information, to prioritize conservation actions, promote public awareness and focus further inventory efforts towards areas where gaps remain.

Materials and methods

Study area

For the purpose of the study, we use the definition of the Ecuadorian Province (Morrone 2014), including all seasonally dry forests (**SDFs**) in this biogeographical region and excluding neighboring moist habitats that are likely to promote amphibian communities of different origin and with different characteristics. Henceforth, we will use the term Equatorial SDF for this area, which has a finer resolution than the one of Ecuadorian Province; also, we consider the term to be more adequate to denominate territories in both Ecuador and Peru. To generate the map layer used in the analysis, we used Quantum GIS (QGIS) environment 3.4.13 (QGIS.org 2021). To delimit our study area, we used as a basis the national digital maps of ecosystem types for Ecuador (MAE 2013) and Peru (MINAM 2019). These two cartographic databases are currently the most precise available for the area, due to their spatial resolution (scale 1:100,000). In both cases, the ministries of environment in the respective countries define the types of ecosystems according to vegetation cover, bioclimate, biogeography, physiography, altitude, and land use cover. The final map for the Equatorial SDF included ecosystem types with a characteristic of seasonal distribution of precipitation and a semi-deciduous and deciduous vegetation (forests, shrublands), and excluded the Marañón dry forests (Suppl. material 1: Table S1). We added the "Anthropical" and "No data" categories situated in areas of historical distribution of those ecosystems. The resulting shape was manually corrected, fixing geometry problems and filling gaps with the dedicated tool of QGIS to reduce the noise and obtain a more accurate area. The final area covers 55,680.5 km^2 (of which 36.5% in Ecuador and 63.5% in Peru), with an altitudinal range between 0 and 1631 m a.s.l., and consists of a narrow band (3–150 km wide) bordering the Pacific Ocean, extending from the Ecuadorian province of Esmeraldas in the north, to the Peruvian department of Lambayeque in the south.

The climate in the Equatorial SDF region is characterized by a striking seasonality, with a dry season lasting between five and eight months (Escribano-Ávila 2016), a fairly stable high temperature throughout the year, and annual rainfall varying between 500–1,500 mm, while the average monthly rainfall varies between 10 mm to more than 200 mm (Murphy and Lugo 1986; Espinosa et al. 2012). The vegetation is dominated (>50%) by deciduous or semi-deciduous trees. The region is delimited by neighboring ecosystems characterized by a higher rainfall input, such as the transition zones to the Andean mountain range (foothills) in the eastern region and transition zones to the Choco rainforest in the north.

Data collection

The distribution records were compiled from the following sources:

1. Field surveys. Field data were collected and geo-referenced by the authors between 2000 and 2021. Sampling was carried out at various locations (Fig. 1 – Field data), using visual / auditory encounter surveys and active searches (Heyer et al. 1994). Specific methodologies varied, but consisted in both diurnal and nocturnal extensive surveys carried out mainly during the rainy season, and included searches of suitable terrestrial refugia, netting, torching, pitfall traps and call surveys, unconstrained by time or area.
2. Literature review. We carried out search routines between January and April 2021 on the online search engines Google Scholar (https://scholar.google.com/), SciELO (https://scielo.org/), Web of Science (http://webofknowledge.com/), retrieving

papers by using the following search terms: “amphibian”, “Anura”, “herpetofauna”, and “Tumbesian”, “Ecuadorian dry forest”, “Peruvian dry forest”, and reviewing the first 200 results for each search. We included articles in peer-reviewed journals, as well as theses and reports that included relevant information regarding the species distribution, where locations were either geo-referenced or precise enough to permit the assignation of coordinates, and identification was done to species level (Fig. 1 – Literature).

3. Museum biological collections housed at Instituto Nacional de Biodiversidad, Quito, Ecuador (DHMECN), and Museo de Zoología, Universidad San Francisco de Quito, Ecuador (ZSFQ).

4. Publicly available species distribution data on the Global Biodiversity Information Facility (https://www.gbif.org/), which includes the iNaturalist platform data, accessed April 2021 (https://doi.org/10.15468/dl.55dnar). These data were manually curated, removing all vague locality descriptors, likely erroneous species identification, and exotic species records (Zizka et al. 2020). We also filtered for duplicated records (same species at the same coordinates at the same moment).

Regardless of source, we standardized the species list using the taxonomy of Amphibian Species of the World (Frost 2021). Only specimens that could be identified to species level were included in the dataset. Non-native species records were removed (i.e., the bullfrog *Lithobates catesbeianus*). For each species, we indicate the extinction risk status at the global level based on the IUCN Red List of Threatened Species (IUCN 2021).

To characterize species life-history traits, we carried out a literature search for each species in peer-reviewed articles or books and completed with field observations whenever available (Suppl. material 2). We selected four relevant traits which reflect ecological strategies, niche, and functional roles in the ecosystem (Oliveira et al. 2017) and adopted some rather coarse categories to accommodate for the lack of ecological information for most of the species present in the region. Species habitat use, defined as the overall vertical foraging stratum preferred by the adult, resulted in four broad categories: terrestrial/fossorial (foraging mostly on the ground or in leaf-litter, galler-

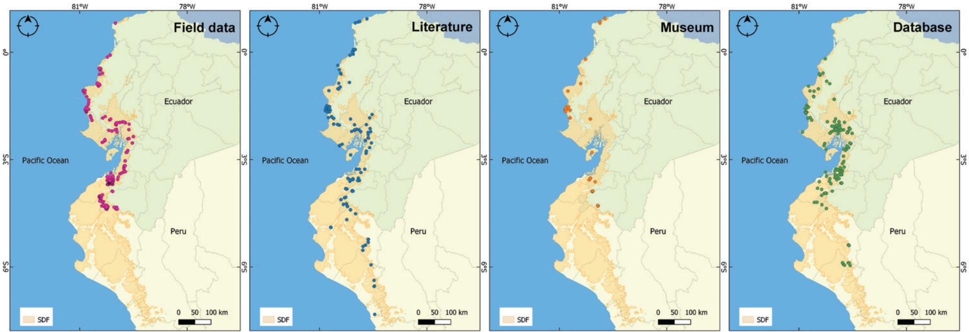


Figure 1. Distribution of amphibian occurrence records in the Equatorial Seasonally Dry Forest (SDF). Maps are provided depending on the data source: Field data, Literature, Museum, Database.

ies, crevices, or holes on the floor), arboreal (predominantly perching on leaves in trees, bushes, phytotelmata, grasses, including riparian vegetation), terrestrial/riparian (found in terrestrial habitats close to or around bodies of water), and aquatic/riparian (semi-aquatic species living in streams or ponds). We also reported the reproductive mode (either larval or direct development), as well as the spawn site, the microhabitat where eggs are deposited (either aquatic, terrestrial, or arboreal). As a morphological character, body size was defined as the maximum snout-vent length (**SVL**) value known for the species, and we report the value separately for females and males. Finally, we generated an identification key, based on morphological characters. However, it is worth mentioning that in some taxa (e.g., the case of *Engystomops* spp.) the reliable identification usually requires additional information (such as mating calls).

Specimen collection

In the case of voucher specimens, individuals were photographed, after which they were euthanized using 20% benzocaine, fixed in 10% formalin, and stored in 70% ethanol. Tissue samples for genetic analyses were preserved in 96% ethanol. Specimens are deposited at Museo de Zoología, Universidad Técnica Particular de Loja (MUTPL), and Museo de Zoología, Universidad San Francisco de Quito (ZSFQ) Ecuador. Information on these specimens is included as field data since it was generated by the authors during fieldwork.

Research permits were issued by Ministerio del Ambiente del Ecuador. This study was evaluated and approved by the Ethics Committee of Universidad Técnica Particular de Loja (UTPL-CBEA-2016-001).

Results

The final dataset consists of 2,032 distribution records spread throughout the Equatorial SDF region. Seventy-seven records are from Peru, and 1,955 are from Ecuador (Fig. 1). Our field records constitute most of the data points (Fig. 1 – Field data), i.e. 1,374 records (67.6%). The literature revision produced 285 records (14%) from 29 publications (Fig. 1 – Literature), while the museum collections of INABIO and ZSFQ included 87 records (4.3%, Fig. 1 – Museum). The online databases GBIF and iNaturalist contributed 286 data points, representing 14.1% of the dataset (Fig. 1 – Database).

Overall, we report 30 amphibian species for the Equatorial SDF, belonging to 14 genera and eight families (Figs 2–6); all 30 species were present in Ecuador, of which 16 were also encountered in Peru (Suppl. material 1: Table 2S). The best represented family was Leptodactylidae (genera *Engystomops* and *Leptodactylus*) with eight species. Five species (*Ceratophrys stolzmanni*, *Engystomops montubio*, *E. puyango*, *E. randi* and *Lithobates bwana*) are endemic to the Equatorial SDF. Two, *Epipedobates anthonyi* and *Leptodactylus labrosus*, have a distribution mostly restricted to the Equatorial SDF, with few occurrences in adjacent habitats, characterized by higher humidity/altitude. The remaining 23 species have a wider distribution.

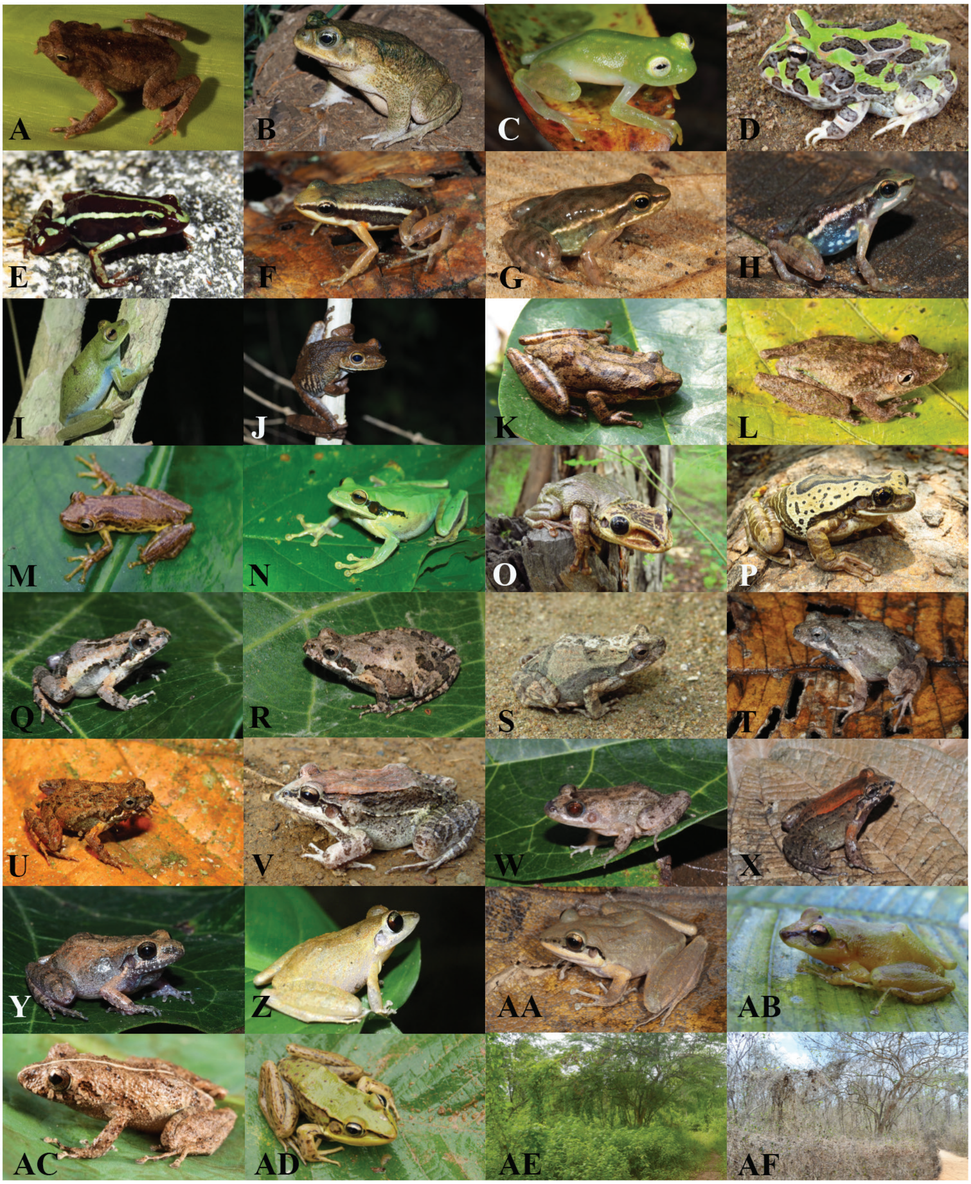


Figure 2. Amphibian species of the Equatorial Seasonally Dry Forest **A** *Rhinella alata* (photo by Silvia Aldás, https://bioweb.bio) **B** *Rhinella horribilis* **C** *Hyalinobatrachium tatayoi* **D** *Ceratophrys stolzmanni* **E** *Epipedobates anthonyi* **F** *Epipedobates machalilla* **G** *Hyloxalus elachyhistus* **H** *Hyloxalus infraguttatus* **I** *Boana pellucens* **J** *Boana rosenbergi* **K** *Scinax quinquefasciatus* **L** *Scinax sugillatus* (photograph by Santiago R. Ron, https://bioweb.bio) **M** *Scinax tsachila* **N** *Smilisca phaeota* **O** *Trachycephalus jordani* **P** *Trachycephalus quadrangulum* **Q** *Engystomops guayaco* **R** *Engystomops montubio* **S** *Engystomops pustulatus* **T** *Engystomops puyango* **U** *Engystomops randi* **V** *Leptodactylus labrosus* **W** *Leptodactylus melanonotus* **X** *Leptodactylus ventrimaculatus* **Y** *Barycholos pulcher* **Z** *Pristimantis achatinus* **AA** *Pristimantis lymani* **AB** *Pristimantis subsigillatus* **AC** *Pristimantis walkeri* (photograph by Santiago R. Ron, https://bioweb.bio) **AD** *Lithobates bwana*. Habitat seasonal change (Reserva Ecológica Arenillas) **AE** april (rainy season) **AF** december (dry season).

Regarding the global extinction risk status (IUCN 2021), one (*C. stolzmanni*) is classified as Vulnerable, and three are Near Threatened (*E. anthonyi*, *Hyalinobatrachium tatayoi*, and *Hyloxalus infraguttatus*). Two are Data Deficient (*Rhinella alata* and *Engystomops guayaco*) and another three (*R. horribilis*, *Scinax tsachila* and *Trachycephalus quadrangulum*) are currently Not Evaluated, while the remaining 21 species have a Least Concern IUCN status (Table 1).

Life-history characteristics

In terms of amphibian species habitat use, 17 (56.7%) are terrestrial / fossorial, nine (30%) are arboreal, two are aquatic / riparian (6.7%), and two are terrestrial / riparian (6.7%) (Table 1). Most species have larval development (25 species, 83.3%), and the five species of Strabomantidae have a direct development (16.7%). Amphibians living in Equatorial SDF exhibit several reproductive strategies for egg deposition; the most common behavior was to deposit eggs directly in the water (17 species, 56.6%, amongst which the five *Engystomops* species which produce foam nests), terrestrial deposition (12 species, 40%), and one species lays egg clutches on leaves overhanging water (*Hyalinobatrachium tatayoi*). The range of body sizes is wide, with maximum adult size varying between 16 mm (*Epipedobates machalilla*) and 130 mm (*Rhinella horribilis*).

Changes in distribution range

We report here the extension of the distribution ranges of four amphibian species detected during fieldwork.

Ceratophrys stolzmanni (Pacific horned frog). This species is endemic to the lowland Equatorial SDF (Ortega-Andrade et al. 2021), with a distribution extending from its type locality, Tumbes, Peru (Steindachner 1882), in the south, up to La Seca (Manabí, Ecuador), in the north. Distribution follows the Pacific coast, the innermost point being 50 km from the coast (Cuadrado et al. 2020), but all previously recorded locations were at low altitudes (up to 130 m a.s.l.). In the present study, we extend the known distribution of this species by adding several new locations (Fig. 3). Amongst them, the record from Manabí, Ecuador (1.0679°S, 80.8308°W), in the vicinity of the El Aromo oil refinery, at 380 m a.s.l., is the highest altitude reported for the species. We also encountered the Pacific horned frog in Progreso, Reserva Cazaderos (4.0259°S, 80.4497°W, 221 m a.s.l.) and Mangahurco, Área de Conservación Municipal Los Guayacanes (4.1611°S, 80.4388°W, 360 m a.s.l.), these being the first records for the Loja province (Ecuador). They also represent the most continental records for this species, being located at more than 70 km from the Pacific coast. Another important observation is that the locations in Loja province, despite being spatially close to the Tumbes region, are actually separated by the Cerro de Amotape mountain range, which was until now considered a barrier for this typically lowland, burrowing amphibian.

Table 1. Life-history characteristics and conservation status for the amphibians of the Equatorial Seasonally Dry Forest. IUCN Status – extinction risk status according to IUCN (2021): NE - Not Evaluated, DD - Data Deficient, LC - Least Concern, NT - Near Threatened, VU - Vulnerable. Reproductive modes: LDv - Larval Development, DDv - Direct Development. * indicates species with a distribution restricted to Equatorial Seasonally Dry Forest. References are given in Suppl. material 2. FD - unpublished information collected by the authors during fieldwork.

Family	Species	IUCN Status	Habitat	Spawn site	Reproductive mode	Maximum size (males) mm	Maximum size (females) mm	References
Bufonidae	*Rhinella alata*	DD	Terrestrial / fossorial	Aquatic	LDv	43.3	56.2	FD; (1)
	Rhinella horribilis	NE	Terrestrial / fossorial	Aquatic	LDv	130.0	160.0	FD; (2); (3); (4)
Centrolenidae	*Hyalinobatrachium tatayoi*	NT	Arboreal	Arboreal	LDv	26.8	31.1	FD; (5); (6)
Ceratophryidae	*Ceratophrys stolzmanni**	VU	Terrestrial / fossorial	Aquatic	LDv	70.4	75.9	FD; (7); (8); (9)
Dendrobatidae	*Epipedobates anthonyi*	NT	Terrestrial / fossorial	Terrestrial	LDv	25.0	27.0	FD; (10); (11)
	Epipedobates machalilla	LC	Terrestrial / fossorial	Terrestrial	LDv	16.0	17.6	FD; (12); (13)
	Hyloxalus elachyhistus	LC	Aquatic / riparian	Terrestrial	LDv	24.1	24.8	FD; (12); (14)
	Hyloxalus infraguttatus	NT	Terrestrial / fossorial	Terrestrial	LDv	20.5	23.4	FD; (12); (15); (16)
Hylidae	*Boana pellucens*	LC	Arboreal	Aquatic	LDv	52.9	61.0	(17); (18); (19); (20); (21); (22)
	Boana rosenbergi	LC	Arboreal	Aquatic	LDv	90.0	93.2	(19); (23); (24); (25)
Hylidae	*Scinax quinquefasciatus*	LC	Arboreal	Aquatic	LDv	38.2	38.9	(26); (27)
	Scinax sugillatus	LC	Arboreal	Aquatic	LDv	42.0	45.5	(27); (28)
	Scinax tsachila	NE	Arboreal	Aquatic	LDv	34.2	36.4	FD
	Smilisca phaeota	LC	Arboreal	Aquatic	LDv	66.0	78.0	(29)
	Trachycephalus jordani	LC	Arboreal	Aquatic	LDv	95.4	111.3	FD; (28); (30)
	Trachycephalus quadrangulum	NE	Arboreal	Aquatic	LDv	76.9	80.8	FD; (28); (31)
Leptodactylidae	*Engystomops guayaco*	DD	Terrestrial / fossorial	Aquatic	LDv	19.38	20.98	FD
	*Engystomops montubio**	LC	Terrestrial / fossorial	Aquatic	LDv	22.8	19.71	FD
	Engystomops pustulatus	LC	Terrestrial / fossorial	Aquatic	LDv	32.3	36.5	FD
	*Engystomops puyango**	LC	Terrestrial / fossorial	Aquatic	LDv	30.5	32.6	FD; (13); (32)
	*Engystomops randi**	LC	Terrestrial / fossorial	Aquatic	LDv	18.7	19.7	(13); (33)
	Leptodactylus labrosus	LC	Terrestrial / fossorial	Terrestrial	LDv	67.4	71.2	FD; (34); (35); (36)
	Leptodactylus melanonotus	LC	Terrestrial / riparian	Terrestrial	LDv	43.4	48.1	(35); (37); (38)
	Leptodactylus ventrimaculatus	LC	Terrestrial / riparian	Terrestrial	LDv	55.4	59.3	FD
Strabomantidae	*Barycholos pulcher*	LC	Terrestrial / fossorial	Terrestrial	DDv	26.9	30.5	(39); (40)
	Pristimantis achatinus	LC	Terrestrial / fossorial	Terrestrial	DDv	36.2	46.1	(19); (41); (42)
	Pristimantis lymani	LC	Terrestrial / fossorial	Terrestrial	DDv	45.3	72.9	FD; (43); (44)
	Pristimantis subsigillatus	LC	Terrestrial / fossorial	Terrestrial	DDv	28.5	33.4	FD; (45)
	Pristimantis walkeri	LC	Terrestrial / fossorial	Terrestrial	DDv	18.5	25.3	FD
Ranidae	*Lithobates bwana**	LC	Aquatic / riparian	Aquatic	LDv	63	95	FD; (46)

Engystomops puyango (Puyango dwarf frog). This small amphibian was recently described from the Puyango Petrified Forest, in south-western Ecuador (Ron et al. 2014), and was until now known from a small number of localities. We contribute several new reports in the region; its presence in Casacay (3.3383°S, 79.7268°W, 146 m a.s.l.), El Oro province, more than 72 km from the type locality, constitutes the farthest record from the known distribution (Fig. 4).

Engystomops randi (Rand's dwarf frog). Another recently described leptodactylid species, which has a wider distribution, encompassing most of the Equatorial SDF close to the coast (Ron et al. 2014). We report for the first time its presence in Peru, Tumbes Reserve (3.7743°S, 80.2249°W, 53 m a.s.l.) (Fig. 4).

Trachycephalus quadrangulum (Chocoan milk frog). This is a large tree frog, mostly known from the coastal Ecuadorian region (Ron et al. 2016). We contribute a new locality for Loja province in Ecuador, close to Bolaspamba (4.1823°S, 80.3692°W, 416 m a.s.l.) (Fig. 5).

Key to the amphibian species of the Equatorial seasonally dry forests of Ecuador and Peru

1	Digit tips not expanded	**2**
–	Digit tips expanded	**13**
2	Keratinized metatarsal spade present; extremely wide head and mouth	***Ceratophrys stolzmanni***
–	Keratinized metatarsal spade absent	**3**
3	Parotoid glands present	**4**
–	Parotoid glands absent	**10**
4	Cranial crests present; adults medium or large: SVL > 40 mm; flank glands absent	**5**
–	Cranial crests absent; adults small: SVL < 40 mm; flank glands present	**6**
5	Large sized, SVL of adults > 70 mm; parotoid glands large; tarsal fold present	***Rhinella horribilis***
–	Medium sized, SVL of adults < 60 mm; parotoid glands small; tarsal fold absent	***Rhinella alata***
6	SVL of adults > 23 mm; lateral fringes on toes absent	7
–	SVL of adults < 23 mm; lateral fringes on toes present	**8**
7	SVL of adults > 25 mm; larger tubercles on the dorsum	***Engystomops pustulatus***
–	SVL of adults > 23 mm; smaller and fewer tubercles on the dorsum	***Engystomops puyango***
8	SVL of adults 15–20 mm; lateral fringes on toes broad; webbing between toes basal	***Engystomops guayaco***
–	Lateral fringes on toes narrow, webbing between toes absent	**9**
9	SVL of adults 17–22 mm; proportionately shorter flank and parotoid glands	***Engystomops montubio***
–	SVL of adults 17–20 mm; proportionately longer flank and parotoid glands	***Engystomops randi***
10	Extensive webbing between the toes; subarticular tubercles low	***Lithobates bwana***
–	Webbing between the toes absent; subarticular tubercles well developed	**11**
11	Males with black horny thumb spines; toes with well-developed lateral fringes	***Leptodactylus melanonotus***
–	Males without thumb spines; toes without developed lateral fringes	**12**

12 Posterior surface of tarsus with many white tubercles; sole of foot with white tubercles .... ***Leptodactylus ventrimaculatus***

– Posterior surface of tarsus usually without white tubercles; sole of foot usually lacking white tubercles.. ***Leptodactylus labrosus***

13 Expanded discs bearing a pair of scute-like fleshy structures on the dorsal surface of digit tips...**14**

– Expanded discs without dorsal scute-like fleshy structures on tips of digits... **17**

14 Broad, light middorsal stripe present........................***Epipedobates anthonyi***

– Middorsal stripe absent...**15**

15 Venter immaculate (without white spots)............. ***Epipedobates machalilla***

– Venter with white spots...**16**

16 Extensive webbing between the toes..........................***Hyloxalus elachyhistus***

– Limited webbing between the toes ....***Hyloxalus infraguttatus***

17 Venter transparent with the white peritonea and lungs visible, dorsal surfaces green with yellow spots .... ***Hyalinobatrachium tatayoi***

– Venter not transparent and internal organs not visible, dorsal surfaces brown, grey or green **18**

18 Fingers lacking webbing...**19**

– Webbing present between fingers **26**

19 Toe III longer than Toe V; digit tips just slightly expanded (swollen); well defined white glands posterior to angle of jaw............... ***Barycholos pulcher***

– Toe V longer than Toe III **20**

20 Toes lacking extensive webbing...**21**

– Webbing present between toes **24**

21 Finger I longer than Finger II; dorsolateral folds present...........................**22**

– Finger I shorter than Finger II; dorsolateral folds absent **23**

22 Discs on fingers relatively small; inner surface of tarsus bearing long fold; posterior surfaces of the thighs black with white spots or reticulations; SVL of adults 25–73 mm ....***Pristimantis lymani***

– Discs on fingers broad; inner tarsal tubercle small; posterior surfaces of the thighs brown with small cream flecks; SVL of adults 23–46 mm ....***Pristimantis achatinus***

23 Snout bearing papilla at tip; heel with small conical tubercle; SVL of adults 19–33 mm...***Pristimantis subsigillatus***

– Snout without papilla at tip; heel lacking tubercles; groin black with yellow spots; SVL of adults 13–25 mm.................................***Pristimantis walkeri***

24 Lower jaw with a row of tubercles; snout long; black and blue mottling in the groin and on the anterior and posterior surfaces of the thighs...***Scinax sugillatus***

– Lower jaw without a row of tubercles...**25**

25 Shank bones visible through the skin, white to bluish-white; dorsum with scattered to abundant small tubercles....................***Scinax quinquefasciatus***

– Shank bones visible through the skin, green; dorsum without tubercles ....***Scinax tsachila***

26 Top of the head co-ossified and rough (integumentary-cranial co-ossified skull); iris golden with irregular black spots; SVL of adults 65–111 mm .... ***Trachycephalus jordani***
– Top of the head not co-ossified **27**
27 Skin on dorsum tuberculate; webbing between the fingers extensive; dorsal coloration usually brown .... ***Boana rosenbergi***
– Skin on dorsum smooth; webbing between fingers basal to moderate **28**
28 Pronounced calcar on the heel; webbing between the fingers moderate; dorsal coloration usually green; iris yellowish .... ***Boana pellucens***
– Calcar on heel absent **29**
29 Webbing between the fingers moderate; iris golden with irregular black spots; thick, glandular skin on the head and back . ***Trachycephalus quadrangulum***
– Webbing between the fingers basal; characteristic dark postorbital mark and white labial stripe .... ***Smilisca phaeota***

Clave para las especies de anfibios del bosque estacionalmente seco Ecuatorial de Ecuador y Perú

1 Terminaciones de los dedos no expandidas **2**
– Terminación de los dedos expandidas **13**
2 Presencia de espádices metatarsiales queratinizados; cabeza y boca extremadamente anchas .... ***Ceratophrys stolzmanni***
– Espádice metatarsial queratinizado ausente **3**
3 Presencia de glándulas parotoideas **4**
– Glándulas parotoideas ausentes **10**
4 Presencia de crestas craneales; adultos medianos o grandes: LHC > 40 mm; glándulas del flanco ausentes **5**
– Crestas craneales ausentes; adultos pequeños: LHC < 40 mm; glándulas del flanco presentes **6**
5 Tamaño grande, LHC de adultos > 70 mm; glándulas parotoideas grandes; pliegue tarsal presente .... ***Rhinella horribilis***
– Tamaño mediano, LHC de adultos < 60 mm; glándulas parótidas pequeñas; pliegue tarsal ausente .... ***Rhinella alata***
6 LHC de adultos > 23 mm; flecos laterales en los dedos de los pies ausentes 7
– LHC de adultos < 23 mm; flecos laterales en los dedos de los pies presentes **8**
7 LHC de adultos > 25 mm; tubérculos más grandes en el dorso .... ***Engystomops pustulatus***
– LHC de adultos > 23 mm; menos tubérculos y de tamaño menor en el dorso .... ***Engystomops puyango***
8 LHC de adultos de 15 a 20 mm; flecos laterales en los dedos de los pies anchas; membrana entre los dedos de los pies basal .... ***Engystomops guayaco***
– flecos laterales en los dedos del pie estrechos; membranas entre los dedos del pie ausentes **9**

9 LHC de adultos de 17 a 22 mm; glándulas parotoideas y del flanco proporcionalmente más pequeñas .... ***Engystomops montubio***

– LHC de adultos de 17 a 20 mm; glándulas parotoideas y del flanco proporcionalmente más largas .... ***Engystomops randi***

10 Extensas membranas entre los dedos de los pies; tubérculos subarticulares bajos .... ***Lithobates bwana***

– Membranas entre los dedos de los pies ausentes; tubérculos subarticulares bien desarrollados **11**

11 Machos con espinas córneas negras en los pulgares; dedos de los pies con flecos laterales bien desarrollados .... ***Leptodactylus melanonotus***

– Machos sin espinas pulgares; dedos de los pies sin flecos laterales desarrollados **12**

12 Superficie posterior del tarso con muchos tubérculos blancos; planta del pie con tubérculos blancos .... ***Leptodactylus ventrimaculatus***

– Superficie posterior del tarso generalmente sin tubérculos blancos; planta del pie generalmente sin tubérculos blancos .... ***Leptodactylus labrosus***

13 Discos expandidos que llevan un par de estructuras carnosas en forma de escudos en la superficie dorsal de las puntas de los dedos **14**

– Discos expandidos sin estructuras carnosas en forma de escudos dorsales en las puntas de los dedos **17**

14 Presencia de una franja media dorsal clara y ancha .... ***Epipedobates anthonyi***

– Franja media dorsal ausente **15**

15 Vientre inmaculado (sin manchas blancas) .... ***Epipedobates machalilla***

– Vientre con manchas blancas **16**

16 Membrana extensa entre los dedos de los pies .... ***Hyloxalus elachyhistus***

– Membrana limitada entre los dedos .... ***Hyloxalus infraguttatus***

17 Vientre transparente con el peritoneo blanco y los pulmones visibles, superficies dorsales verdes con manchas amarillas .... ***Hyalinobatrachium tatayoi***

– Vientre no transparente y órganos internos no visibles, superficies dorsales marrón, gris o verde **18**

18 Dedos de la mano sin membranas interdigitales **19**

– Membranas interdigitales presentes entre los dedos de la mano **26**

19 Dedo III del pie más largo que el Dedo V; puntas de los dedos solo ligeramente expandidas (hinchadas); glándulas blancas bien definidas posteriores al ángulo de la mandíbula .... ***Barycholos pulcher***

– Dedo V del pie más largo que el Dedo III **20**

20 Dedos del pie que carecen de membranas extensas **21**

– Membranas interdigitales presentes entre los dedos de los pies **24**

21 Dedo I del mano más largo que el Dedo II; pliegues dorsolaterales presentes **22**

– Dedo I del mano más corto que el Dedo II; pliegues dorsolaterales ausentes. **23**

22 Discos en los dedos relativamente pequeños; superficie interna del tarso con pliegue largo; superficies posteriores de los muslos negras con manchas o reticulaciones blancas; LHC de adultos 25–73 mm .... ***Pristimantis lymani***

– Discos en los dedos anchos; tubérculo tarsal interno pequeño; superficies posteriores de los muslos marrones con pequeñas manchas color crema; LHC de adultos 23–46 mm... ***Pristimantis achatinus***

23 Hocico con papila en la punta; talón con pequeño tubérculo cónico; LHC de adultos 19–33 mm.. ***Pristimantis subsigillatus***

– Hocico sin papila en la punta; talón sin tubérculos; ingle negra con manchas amarillas; LHC de adultos 13–25 mm .... ***Pristimantis walkeri***

24 Mandíbula inferior con una hilera de tubérculos; hocico largo; moteado negro y azul en la ingle y en las superficies anterior y posterior de los muslos.... .... ***Scinax sugillatus***

– Mandíbula inferior sin una hilera de tubérculos **25**

25 Huesos de las patas visibles a través de la piel, de color blanco a blanco azulado; dorso con pequeños tubérculos, dispersos a abundantes .... ***Scinax quinquefasciatus***

– Huesos de las patas visibles a través de la piel, verdes; dorso sin tubérculos.... .... ***Scinax tsachila***

26 Parte superior de la cabeza co-osificada y rugosa (cráneo co-osificado tegumentario-craneal); iris dorado con manchas negras irregulares; LHC de adultos 65–111 mm .... ***Trachycephalus jordani***

– Parte superior de la cabeza no co-osificada **27**

27 Piel en el dorso tuberculada; membrana extensa entre los dedos de la mano; coloración dorsal generalmente marrón............................ ***Boana rosenbergi***

– Piel lisa en el dorso; membrana entre los dedos basal a moderada............. **28**

28 Calcar pronunciado en el talón; membrana entre los dedos de la mano moderada; coloración dorsal generalmente verde; iris amarillento .... ***Boana pellucens***

– Calcar en el talón ausente **29**

29 Membrana entre los dedos de la mano moderada; iris dorado con manchas negras irregulares; piel glandular gruesa en la cabeza y dorso .... ***Trachycephalus quadrangulum***

– Membrana entre los dedos de la mano basal; marca postorbital oscura característica y franja labial blanca .... ***Smilisca phaeota***

Discussion

We provide the first comprehensive amphibian species checklist for the Equatorial SDF, including 30 species. In addition to compiling the available data from published sources, museum collections and online databases, we contribute a large amount of original information generated through extensive field surveys (two thirds of all reported informa-

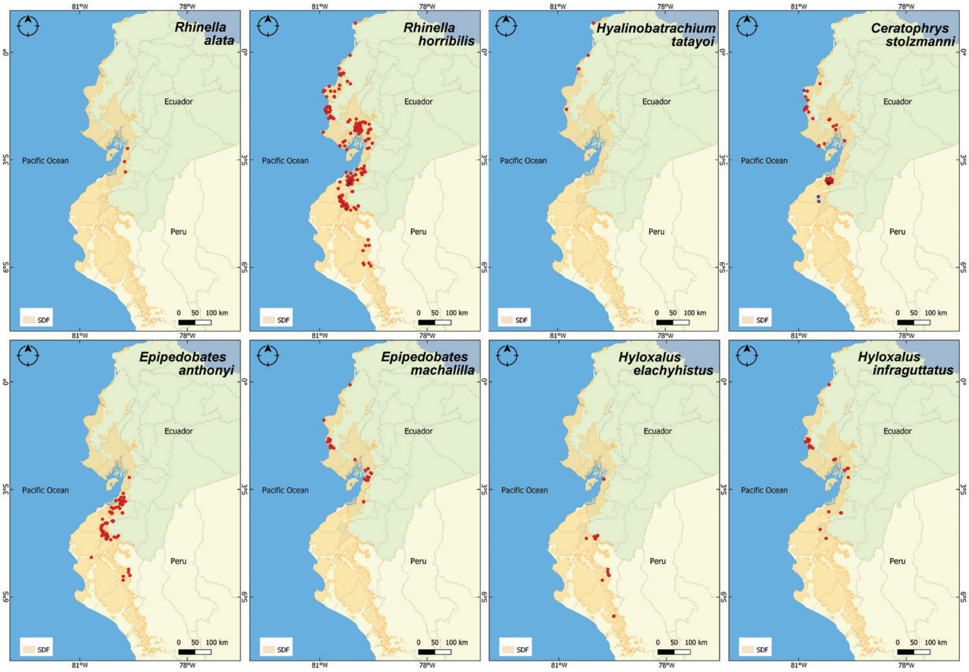


Figure 3. Distribution records of Bufonidae, Centrolenidae, Ceratophryidae and Dendrobatidae in the Equatorial Seasonally Dry Forest (SDF). Maps are given for the families Bufonidae (*Rhinella alata*, *R. horribilis*), Centrolenidae (*Hyalinobatrachium tatayoi*), Ceratophryidae (*Ceratophrys stolzmanni*) and Dendrobatidae (*Epipedobates anthonyi*, *E. machalilla*, *Hyloxalus elachyhistus*, *H. infraguttatus*). For *Ceratophrys stolzmanni*, blue points represent new distributional records for the species, the two southernmost localities and the highest altitude, respectively.

tion for the area). Although the records reported here significantly add to our previous understanding of tropical amphibian communities in South American seasonally dry habitats, the dataset probably underestimates the actual amphibian diversity in the area.

Although the Equatorial SDF has been overall understudied, the lack of information is most evident in the Peruvian part of this ecoregion. For a better understanding, further efforts to disseminate currently unpublished amphibian distribution records of Peruvian researchers and taxonomically clarify the identity of amphibians which are currently assigned only at genus level (e.g., Venegas 2005) are necessary. From the total dataset, less than 4% of the records were from Peru, although 63.5% of Equatorial SDF area corresponds to this country. A lower amphibian richness is expected in certain Peruvian regions, such as the area bordering the Sechuran desert, due to the hostile environmental conditions. The bibliographic search and a comparison with similar habitats in Ecuador suggest that the lack of data regarding amphibian diversity in the Peruvian part of the Equatorial SDF is due to sampling bias rather than accurately reflecting the absence of this taxa. Even in Ecuador, where sampling was carried out more homogenously throughout the study area, there is still a shortage of adequate amphibian

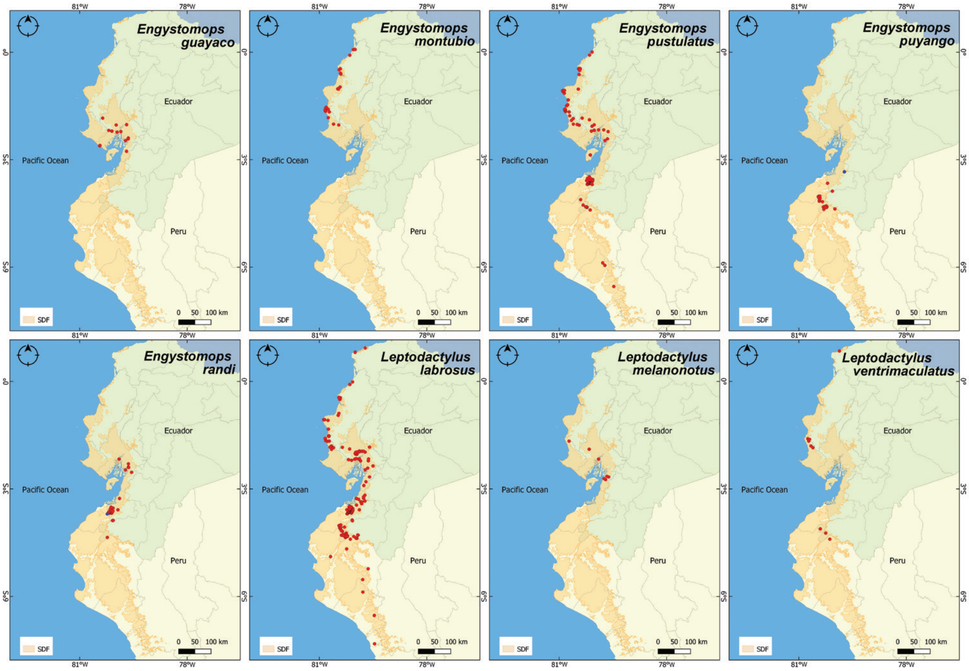


Figure 4. Distribution records for the Leptodactylidae family in the Equatorial Seasonally Dry Forest (SDF). In blue, distribution range extensions: for *Engystomops puyango*, the northernmost locality is more than 70 km from the previously known distribution; for *E. randi*, the first record in Peru.

inventories, especially outside protected areas (Ortega-Andrade et al. 2021). Further efforts to inventory the extensive underexplored areas to correctly evaluate the amphibian community status should constitute a priority (Ortega-Andrade et al. 2021).

The fact that, out of the 30 species present in the Equatorial SDF, five have been described as new for science in the last 20 years (*Scinax tsachila*, *Engystomops guayaco*, *E. montubio*, *E. puyango*, *E. randi*) further emphasizes the need for intense and focused research targeted at undersampled locations. The list of amphibians present in the Equatorial SDF can change in the future because of updated taxonomic studies based on modern integrative techniques that use morphological, molecular, and behavioral data. It is the case of the cane toads (*R. horribilis*), for which a recent study indicates that the species present in these forests might be phylogenetically distinct from the rest of the range (Pereyra et al. 2021). Similarly, a species of milk frog (*Trachycephalus quadrangulum*) was resurrected after being included in the *T. typhonius* species complex for 50 years, as was the toad *Rhinella alata*, after being synonymized to *R. margaritifera*. It is likely that a similar fate awaits species in the genera *Pristimantis*, *Leptodactylus* and *Hyloxalus*, for which taxonomical delimitation is currently based on morphological characters only, allowing for the existence of cryptic taxa.

We include the information on important life history characteristics for all amphibian species present in the Equatorial SDF. It is recommended that prioritization of

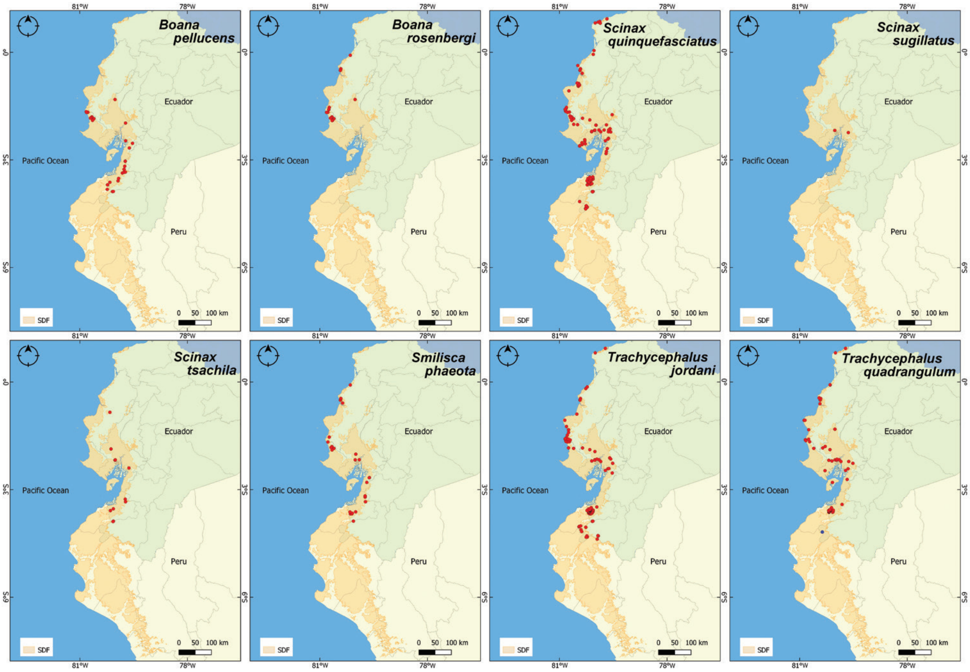


Figure 5. Distribution records for the Hylidae family in the Equatorial Seasonally Dry Forest (SDF). In blue, the first report of *Trachycephalus quadrangulum* in Loja province.

conservation measures should consider functional diversity of an assemblage, not only species richness, since species make differential contribution to the functioning of their ecosystem (Campos et al. 2017; Bolochio et al. 2020). Currently, research conducted on life-history is scarce for most of the 30 amphibian species. As more information becomes available, the inclusion of additional traits, might offer a more complete image of the native amphibian communities and their capacity to withstand landscape changes. The current insufficient knowledge regarding Equatorial SDF species threats and risks, in addition to the fact that some have been only recently (re)described, results in the five species that are lacking a global conservation status assessment.

Seven of the 30 species (23.3%) have a distribution exclusively or almost-exclusively restricted to the Equatorial SDF. Although amphibian species living in tropical dry forests are inherently more tolerant to high temperatures and desiccation, they are still expected to be vulnerable to the predicted climate changes because they are already exposed to conditions at the limit of their physiological tolerance (Catenazzi et al. 2014; Székely et al. 2018). No studies modelling the sensitivity to climate change scenarios have been carried out for the species endemic to the Equatorial SDF. Some of the species have adapted to anthropized environments, and in some cases their distribution extends to other ecosystems adjacent to the dry forest. However, the small extent and fragmented limits of the Equatorial SDF, coupled with the land-use change that affects this ecoregion, represent a risk that, in the case of climate change, these species face a re-

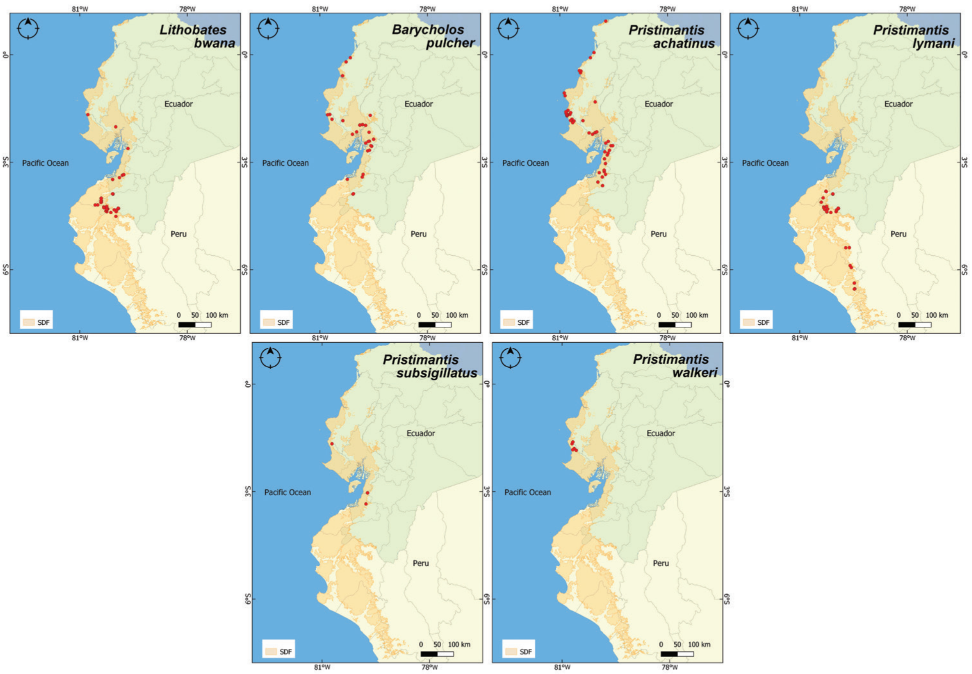


Figure 6. Distribution records of Ranidae and Craugastoridae in the Equatorial Seasonally Dry Forest (SDF). Maps are given for Ranidae (*Lithobates bwana*) and Craugastoridae (*Barycholos pulcher*, *Pristimantis achatinus*, *P. lymani*, *P. subsigillatus*, and *P. walkeri*).

duction of suitable habitat (Nowakowski et al. 2017), even if currently they also occur in protected areas. This emphasizes the need for the species with a narrow distribution to be targeted for urgent monitoring and conservation measures (Sodhi et al 2008).

Conservation aspects

The current loss of biodiversity in the study area is the synergic result of a multitude of factors, the most important being habitat loss, fragmentation, pollution, introduction of alien species and unsustainable use of resources (Ceballos and Ortega-Baes 2011). The Equatorial SDF is under severe anthropic pressure (Jara-Guerrero et al. 2019), experiencing a dramatic loss in area in the quality of these forests, exacerbating the biodiversity losses that occurred during the last century, mainly because of agricultural and urban expansion (Mittermeier et al. 1999; Sierra 2013). Originally, 35% of coastal Ecuador was naturally covered with Equatorial SDF, but this ecosystem was reduced to less than 2% by the 1990s (Dodson and Gentry 1991). This alarming situation has catalyzed an effort to protect the last remnants and isolated patches of tropical dry forest (Gentry 1977; Parker and Carr 1992; Best and Kessler 1995; Espinosa et al. 2012; Sierra 2013; Tapia-Armijos et al. 2015). Estimated yearly rate of deforestation in the area was on average of 1.6% between

2000 and 2010 (Sierra 2013). Making matters worse is the fact that the remnants are highly fragmented, reducing their potential of regeneration (Tapia-Armijos et al. 2015). In this context, there is an urgent need for future research evaluating the efficiency of protected areas for the conservation of Equatorial SDF amphibians, under different scenarios of global change.

The level of protection for Equatorial SDF is extremely low (Rivas et al. 2020), less than 5% of its territory being included in nationally protected areas in Ecuador and Peru (Escribano-Avila et al. 2017). To alleviate this aspect, several private entities and local communities are taking steps forward to protect key areas in the region (Escribano-Avila et al. 2017). However, the conservation of this and other ecosystems cannot and should not be the exclusive responsibility of NGOs. The governments of Ecuador and Peru, the civil society of each country (including universities and research centers), and the international community must become more involved in these processes. An essential part of this support is providing the correct information and analysis regarding species distribution, ecology, and status of conservation.

Acknowledgements

Research permits were issued by Ministerio del Ambiente, Agua y Transición Ecológica del Ecuador: MAE-DNB-CM-2015-0016, granted to Universidad Técnica Particular de Loja; MAAE-ARSFC-2020-0727 granted to Paul Székely; MAAE-ARSFC-2020-0960, granted to Diego Armijos-Ojeda; 009-IC-FAN-DPEO-MAE, granted to Diego F. Cisneros-Heredia, Universidad San Francisco de Quito.

Fieldwork was partially funded by The Rufford Foundation (grant no. 30020-1 "Protecting the tropical dry forest, home to unique amphibians").

DFCH's work was possible thanks to financial support granted to different research projects by Gobierno Autónomo Descentralizado Provincial de El Oro GADPEO, Universidad San Francisco de Quito USFQ, Fundación Natura, Biósfera Gestión Ambiental, Sun Conservation S.A., and Secretaría de Educación Superior, Ciencia, Tecnología e Innovación SENESCYT (Programa Becas de Excelencia).

We are grateful to Claudia Koch and Matthew Metcalf for their constructive comments that helped to improve our manuscript.

We thank all the persons who, through their contribution in terms of logistics and lodgings, have helped us during fieldwork at various sites: rangers in Reserva Ecologica Arenillas, Sandro Trigrero (Comunidad Dos Mangas), Silvano Quimiz (Comunidad Rio Blanco), Mariela Loor (Reserva Lalo Loor), Belarmino Camacho and his wife (Mangahurco), Felipe Sánchez and Elsita Castillo (Cabeza de Toro), Guilbert Olaya, Mayely Aponte and Mrs. Astrid (Cazaderos), Mikaela Soto and her husband (Hotel Los Guayacanes), Darwin Martínez (NCI Zapotillo), park rangers and officers of the Ministerio del Ambiente in Puyango, Ítalo Encalada (Bosque Petrificado de Puyango), park rangers and officers of the Ministerio del Ambiente in Machalilla, Carlos Zambrano, Andrés Baquero, Diego Mosquera, Galo Echeverría (Parque Nacional Machalilla). We are grateful to the persons who have contributed their field data: Mario Yánez, Fausto Siavichay, Patricia Bejarano, Daniela Sánchez, Juan Carlos Sánchez, and Luis Oyagata. Special thanks to Judit Vörös, María Fernanda Burneo, Ana Paula Cabrera, and Pamela Aponte, for their help during fieldwork, and Ivonne González for her support with the spatial analyses process.

DFCH thanks María Elena Heredia, Laura Heredia, Jonathan Guillemot, Nicole Acosta, Mateo Dávila, Emilia Peñaherrera, Alejandro Montalvo, Diego Mosquera, Andrés Baquero, Galo Echeverría, Italo Encalada, Pablo Beltrán, Daniela Proaño, Karina Dammer, Kelly Swing, Jean-Marc Touzet, and Francisco Vintimilla for their valuable support during fieldwork and lab work.

References

Ab'Sáber AN (1977) Os domínios morfoclimáticos na América do Sul. Primeira aproximaçao. Geomorfología 52: 1–21.

Almendáriz A, Carr JL (1992) Amphibians and reptile list; January-February trip. In: Parker TA III, Carr JL (Eds) Status of forest remnants in the Cordillera de la Costa and adjacent areas of southwestern Ecuador. Conservation International, Washington DC, 128–130.

Almendáriz A, Carr J (2012) Lista actualizada de los anfibios y reptiles registrados en los remanentes de bosque de la Cordillera de la Costa y áreas adyacentes del suroeste del Ecuador. Revista Politécnica 30: 184–194.

Amador LA, Martínez CC (2011) Anfibios presentes en cuatro localidades de la Cordillera Chongón-Colonche, Ecuador. Boletín Técnico, Serie Zoológica 10: 55–68.

Armijos-Ojeda D, Valarezo K (2010) Diversidad de anfibios y reptiles de un bosque seco en el sur occidente del Ecuador. Ecología Forestal 1: 30–36.

Best BJ, Kessler M (1995) Biodiversity and Conservation in Tumbesian Ecuador and Peru. BirdLife I. BirdLife International, Cambridge, 218 pp.

Bolochio BE, Lescano JN, Cordier JM, Loyola R, Nori J (2020) A functional perspective for global amphibian conservation. Biological Conservation 245: e108572. https://doi.org/10.1016/j.biocon.2020.108572

Campos FS, Lourenço-de-Moraes R, Llorente GA, Solé M (2017) Cost-effective conservation of amphibian ecology and evolution. Science Advances 3: e1602929. https://doi.org/10.1126/sciadv.1602929

Catenazzi A (2015) State of the world's amphibians. Annual Review of Environment and Resources 40: 91–119. https://doi.org/10.1146/annurev-environ-102014-021358

Catenazzi A, Lehr E, Vredenburg VT (2014) Thermal physiology, disease, and amphibian declines on the eastern slopes of the Andes. Conservation Biology 28: 509–517. https://doi.org/10.1111/cobi.12194

Ceballos G (1995) Vertebrate diversity, ecology, and conservation in Neotropical dry forests. In: Bullock SH, Mooney HA, Medina E (Eds) Seasonally dry tropical forests. Cambridge University Press, Cambridge, 195–207. https://doi.org/10.1017/CBO9780511753398.008

Ceballos G, Ortega-Baes P (2011) La sexta extinción: La pérdida de especies y poblaciones en el Neotrópico. In: Simonetti J, Dirzo R (Eds) Conservación Biológica: Perspectivas desde América Latina. Editorial Universitaria, Santiago de Chile, 95–108.

Chapman FM (1926) The distribution of bird-life in Ecuador. Bulletin of the American Museum of Natural History 55: 1–784.

Chazdon R, Harvey C, Martínez-Ramos M, Balvanera P, Stoner KE, Schondube JE, Avila Cabadilla LD, Flores-Hidalgo M (2011) Seasonally dry tropical forest biodiversity and conservation value in agricultural landscapes of Mesoamerica. In: Dirzo R, Young HS, Mooney HA, Ceballos G (Eds) Seasonally Dry Tropical Forests: Ecology and Conservation. Island Press, Washington, 195–219. https://doi.org/10.5822/978-1-61091-021-7_12

Cisneros-Heredia DF (2006) Amphibians, Machalilla National Park, province of Manabí, western Ecuador. Check List 2: 45–54. https://doi.org/10.15560/2.1.45

Cracraft J (1985) Historical biogeography and patterns of differentiation within the South American avifauna: areas of endemism. Ornithological Monographs 36: 49–84. https://doi.org/10.2307/40168278

Cuadrado SS, Loor YA, Narváez AE (2020) Herpetofauna of Engabao, Playas Canton, Ecuador, with notes on the occurrence of *Ceratophrys stolzmanni* (Steindachner, 1882). Check List 16: 665–674. https://doi.org/10.15560/16.3.665

Davis S, Heywood VH, Hamilton AC (1997) Centres of plant diversity, vol. 3: the Americas. IUCN, Gland, 576 pp.

Dinerstein E, Olson DM, Graham DJ, Webster AL, Primm SA, Bookbinder MP, Ledec G (1995) A conservation assessment of the terrestrial ecoregions of Latin America and the Caribbean. World Bank, Washington DC, 129 pp. https://doi.org/10.1596/0-8213-3295-3

Dodson CH, Gentry AH (1991) Biological extinction in western Ecuador. Annals of the Missouri Botanical Garden 78: 273–295. https://doi.org/10.2307/2399563

Duellman WE (1988) Patterns of species diversity in anuran amphibians in the American tropics. Annals of the Missouri Botanical Garden 75: 79–104. https://doi.org/10.2307/2399467

Dryflor, Banda K, Delgado-Salinas A, Dexter KG, Linares-Palomino R, Oliveira-Filho A, Prado D, Weintritt J (2016) Plant diversity patterns in neotropical dry forests and their conservation implications. Science 353: 1383–1387. https://doi.org/10.1126/science.aaf5080

Escribano-Ávila G (2016) El bosque seco neotropical de la provincia Ecuatoriana: un pequeño gran desconocido. Revista Ecosistemas 25: 1–4. https://doi.org/10.7818/ECOS.2016.25-2.01

Escribano-Avila G, Cervera L, Ordóñez-Delgado L, Jara-Guerrero A, Amador L, Paladines B, Briceño J, Parés-Jiménez V, Lizcano D, Duncan D, Espinosa CI (2017) Biodiversity patterns and ecological processes in Neotropical dry forest: the need to connect research and management for long-term conservation. Neotropical Biodiversity 3: 107–116. https://doi.org/10.1080/23766808.2017.1298495

Espinosa CI, Cabrera O, Luzuriaga AL, Escudero A (2011) What factors affect diversity and species composition of endangered Tumbesian dry forests in southern Ecuador? Biotropica 43: 15–22. https://doi.org/10.1111/j.1744-7429.2010.00665.x

Espinosa CI, de la Cruz M, Luzuriaga A, Escudero A (2012) Bosques tropicales secos de la región Pacífico Ecuatorial: diversidad, estructura, funcionamiento e implicaciones para la conservación. Revista Ecosistemas 21: 167–179. https://doi.org/10.7818/re.2014.21-1-2.00

Frost DR (2021) Amphibian Species of the World: an online reference. Version 6.1. Electronic Database. https://amphibiansoftheworld.amnh.org/index.php [Accessed on 31 May 2021]

Guedes TB, Sawaya RJ, Zizka A, Laffan S, Faurby S, Pyron RA, Bérnils RS, Jansen M, Passos P, Prudente ALC, Cisneros-Heredia DF, Braz HB, Nogueira CC, Antonelli A (2018) Patterns, biases and prospects in the distribution and diversity of Neotropical snakes. Global Ecology and Biogeography 27: 14–21. https://doi.org/10.1111/geb.12679

Gentry A (1977) Endangered plant species and habitats of Ecuador and Amazonian Peru. In: Prance GT, Elias TS (Eds) Extinction is forever. The New York Botanical Garden, New York, 136–149.

Hanson PE (2011) Insect diversity in seasonally dry tropical forests. In: Dirzo R, Young HS, Mooney HA, Ceballos G (Eds) Seasonally dry tropical forests: ecology and conservation. Island Press, Washington, 71–84. https://doi.org/10.5822/978-1-61091-021-7_5

Heyer WR, Donnelly MA, McDiarmid RW, Hayek LAC, Foster MS (1994) Measuring and monitoring biological diversity - standard methods for amphibians. Smithsonian Institution Press, Washington, 364 pp.

IUCN (2021) The IUCN Red List of Threatened Species. Version 2021–1. https://www.iucnredlist.org [Accessed on 31 May 2021]

Jara-Guerrero A, Maldonado-Riofrío D, Espinosa CI, Duncan D (2019) Beyond the blame game: a restoration pathway reconciles ecologists' and local leaders' divergent models of seasonally dry tropical forest degradation. Ecology and Society 24: e22. https://doi.org/10.5751/ES-11142-240422

Jenkins CN, Pimm SL, Joppa LN (2013) Global patterns of terrestrial vertebrate diversity and conservation. Proceedings of the National Academy of Sciences 110: E2602–E2610. https://doi.org/10.1073/pnas.1302251110

Linares-Palomino R (2004a) Los bosques tropicales estacionalmente secos: I. El concepto de los bosques secos en el Perú. Arnoldia 11: 85–102.

Linares-Palomino R (2004b) Los bosques tropicales estacionalmente secos: II. Fitogeografía y composición florística. Arnoldia 11: 103–138.

Linares-Palomino R, Oliveira-Filho AT, Pennington RT (2011) Neotropical seasonally dry forests: diversity, endemism, and biogeography of woody plants. In: Dirzo R, Young HS, Mooney HA, Ceballos G (Eds) Seasonally dry tropical forests: ecology and conservation. Island Press, Washington, 3–21. https://doi.org/10.5822/978-1-61091-021-7_1

MAE [Ministerio del Ambiente del Ecuador] (2013) Sistema de clasificación de los ecosistemas del Ecuador continental. Subsecretaría de Patrimonio Natural: Ministerio del Ambiente, Quito, 136 pp.

MINAM [Ministerio del Ambiente] (2019) Mapa nacional de ecosistemas del Perú: memoria descriptiva. Negrapata, Lima, 124 pp.

Mittermeier RA, Myers N, Mittermeier CG (1999) Biodiversidad amenazada. Las ecorregiones terrestres prioritarias del mundo. CEMEX, México, 430 pp.

Morrone JJ (1999) Presentación preliminar de un nuevo esquema biogeográfico de América del Sur. Biogeographica 75: 1–16.

Morrone JJ (2001) Biogeografía de América latina y el Caribe. Cyted, Zaragoza, 148 pp.

Morrone JJ (2014) Biogeographical regionalisation of the Neotropical region. Zootaxa 3782: 1–110. https://doi.org/10.11646/zootaxa.3782.1.1

Müller P (1973) The dispersal centres of terrestrial vertebrates in the Neotropical realm: a study in the evolution of the Neotropical biota and its native landscapes. Junk, The Hague, 244 pp.

Murphy PG, Lugo AE (1986) Ecology of tropical dry forest. Annual Review of Ecology and Systematics 17: 67–88. https://doi.org/10.1146/annurev.es.17.110186.000435

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403: 853–858. https://doi.org/10.1038/35002501

Nowakowski AJ, Watling JI, Whitfield SM, Todd BD, Kurz DJ, Donnelly MA (2017) Tropical amphibians in shifting thermal landscapes under land-use and climate change. Conservation Biology 31: 96–105. https://doi.org/10.1111/cobi.12769

Oliveira BF, São-Pedro VA, Santos-Barrera G, Penone C, Costa GC (2017) AmphiBIO, a global database for amphibian ecological traits. Scientific Data 4: e170123. https://doi.org/10.1038/sdata.2017.123

Ortega-Andrade HM, Rodes Blanco M, Cisneros-Heredia DF, Guerra Arévalo N, López de Vargas-Machuca KG, Sánchez-Nivicela JC, Armijos-Ojeda D, Cáceres Andrade JF, Reyes-Puig C, Quezada Riera AB, Székely P, Rojas Soto OR, Székely D, Guayasamin JM, Siavichay Pesántez FR, Amador L, Betancourt R, Ramírez-Jaramillo SM, Timbe-Borja B, Laporta MG, Webster Bernal JF, Oyagata Cachimuel LA, Chávez Jácome D, Posse V, Valle-Piñuela C, Padilla Jiménez D, Reyes-Puig JP, Terán-Valdez A, Coloma LA, Pérez Lara B, Carvajal-Endara S, Urgilés S, Yánez Muñoz MH (2021) Red List assessment of amphibian species of Ecuador: A multidimensional approach for their conservation. PLoS ONE 16: e0251027. https://doi.org/10.1371/journal.pone.0251027

Parker TA, Carr JL (1992) Status of forest remnants in the Cordillera de la Costa and adjacent areas of southwestern Ecuador. Conservation International, Washington DC, 178 pp.

Pennington T, Prado DE, Pendry CA (2000) Neotropical seasonally dry forests and Quaternary vegetation changes. Journal of Biogeography 27: 261–273. https://doi.org/10.1046/j.1365-2699.2000.00397.x

Pennington RT, Lewis GP, Ratter JA (2006) An overview of the plant diversity, biogeography and conservation of neotropical savannas and seasonally dry forests. In: Pennington RT, Lewis GP, Ratter JA (Eds) Neotropical savannas and seasonally dry forests. CRC Press, Boca Raton, 31 pp. https://doi.org/10.1201/9781420004496

Peralvo M, Sierra R, Kenneth R, Ulloa C (2007) Identification of biodiversity conservation priorities using predictive modeling: an application for the Equatorial Pacific region of South America. Biodiversity and Conservation 16: 2649–2675. https://doi.org/10.1007/s10531-006-9077-y

Pereyra MO, Blotto BL, Baldo D, Chaparro JC, Ron SR, Elias-Costa AJ, Iglesias PP, Venegas PJ, Thomé MTC, Ospina-Sarria JJ, Maciel NM, Rada M, Kolenc F, Borteiro C, Rivera-Correa M, Rojas-Runjaic FJM, Moravec J, De La Riva I, Wheeler WC, Castroviejo-Fisher S, Grant T, Célio, Haddad FB, Faivovich J (2021) Evolution in the genus *Rhinella*: a total evidence phylogenetic analysis of Neotropical true toads (Anura: Bufonidae). Bulletin of the American Museum of Natural History 447: 1–156. https://doi.org/10.1206/0003-0090.447.1.1

Porzecanski AL, Cracraft J (2005) Cladistic analysis of distributions and endemism (CADE): Using raw distributions of birds to unravel the biogeography of the South American aridlands. Journal of Biogeography 32: 261–275. http://dx.doi.org/10.1111/j.1365-2699.2004.01138.x

Prado DE (2000) Seasonally dry forests of tropical South America: from forgotten ecosystems to a new phytogeographic unit. Edinburgh Journal of Botany 57: 437–461. https://doi.org/10.1206/0003-0090.447.1.1

Prado DE, Gibbs PE (1993) Patterns of species distributions in the dry seasonal forests of South America. Annals of the Missouri Botanical Garden 1: 902–927. https://doi.org/10.2307/2399937

QGIS.org (2021) QGIS Geographic Information System. QGIS Association, Zurich. http://www.qgis.org

Ringuelet RA (1975) Zoogeografía y ecología de los peces de aguas continentales de la Argentina y consideraciones sobre las áreas ictiológicas de América del Sur. Ecosur 2: 1–122.

Rivas CA, Navarro-Cerillo RM, Johnston JC, Guerrero-Casado J (2020) Dry forest is more threatened but less protected than evergreen forest in Ecuador's coastal region. Environmental Conservation 47: 79–83. https://doi.org/10.1017/S0376892920000077

Ron SR, Narváez A, Romero G (2014) Reproduction and spawning behavior in the frog, *Engystomops pustulatus* (Shreve 1941). Amphibian & Reptile Conservation 8: 25–32.

Ron SR, Venegas PJ, Ortega-Andrade HM, Gagliardi-Urrutia LAG, Salerno PE (2016) Systematics of *Ecnomiohyla tuberculosa* with the description of a new species and comments on the taxonomy of *Trachycephalus typhonius* (Anura, Hylidae). ZooKeys 630: 115–154. https://doi.org/10.3897/zookeys.630.9298

Sánchez-Azofeifa GA, Quesada M, Rodríguez JP, Nassar JM, Stoner KE, Castillo A, Garvin T, Zent EL, Calvo-Alvarado JC, Kalacska ME, Fajardo L (2005) Research priorities for Neotropical dry forests. Biotropica: The Journal of Biology and Conservation 37: 477–485. https://doi.org/10.1046/j.0950-091x.2001.00153.x-i1

Sánchez-Nivicela JC, Yánez-Muñoz MH, Cisneros-Heredia DF (2015) Herpetofauna. Bosques Secos de Tierras Bajas. In: INABIO-GADPEO (Eds) Anfibios, reptiles y aves de la provincia de El Oro: Una guía para la identificación de especies del páramo al manglar. Serie de Publicaciones GADPEO-INABIO 11. INABIO-GADPEO, Quito.

Sierra R (2013) Patrones y factores de deforestación en el Ecuador continental, 1990–2010 y un acercamiento a los próximos 10 años. Conservación Internacional Ecuador y Forest Trends, Quito, 57 pp.

Sodhi NS, Bickford D, Diesmos AC, Lee TM, Koh LP, Brook BW, Sekercioglu CH, Bradshaw CJ (2008) Measuring the meltdown: drivers of global amphibian extinction and decline. PLoS ONE 3: e1636. https://doi.org/10.1371/journal.pone.0001636

Stattersfield AJ, Crosby MJ, Long AJ, Wege DC (1998) Endemic bird areas of the world: priorities for biodiversity conservation. BirdLife Conservation Series. No. 7. BirdLife International, Cambridge, 846 pp.

Steindachner F (1882) Batrachologische Beiträge. Sitzungsberichte der Akademie der Wissenschaften in Wien. Mathematisch-Naturwissenschaftliche Klasse 85: 188–194.

Stoner K, Timm R (2011) Seasonally dry tropical forest mammals: adaptations and seasonal patterns. In: Dirzo R, Young HS, Mooney HA, Ceballos G (Eds) Seasonally dry tropical forests: ecology and conservation. Island Press, Washington, 100–121. https://doi.org/10.5822/978-1-61091-021-7_6

Székely D, Szekely P, Stănescu F, Cogălniceanu D, Sinsch U (2018) Breed fast, die young: demography of a poorly known fossorial frog from the xeric Neotropics. Salamandra 54: 37–44.

Székely P, Székely D, Armijos-Ojeda D, Jara-Guerrero A, Cogălniceanu D (2016) Anfibios de un bosque seco tropical: Reserva Ecológica Arenillas, Ecuador. Revista Ecosistemas 25: 24–34. https://doi.org/10.7818/ECOS.2016.25-2.04

Tapia-Armijos MF, Homeier J, Espinosa CI, Leuschner C, de la Cruz M (2015) Deforestation and forest fragmentation in South Ecuador since the 1970s-losing a hotspot of biodiversity. PLoS ONE 10: e0133701. https://doi.org/10.1371/journal.pone.0133701

Udvardy MDF (1975) A classification of the biogeographical provinces of the world. International Union for Conservation of Nature and Natural Resources Occasional Paper 18, Morges, 49 pp.

Venegas PJ (2005) Herpetofauna del bosque seco ecuatorial de Perú: taxonomía, ecología y biogeografía. Zonas áridas 9: 9–24. http://dx.doi.org/10.21704/za.v9i1.565

Zizka A, Antunes Carvalho F, Calvente A, Rocio Baez-Lizarazo M, Cabral A, Coelho JFR, Colli-Silva M, Fantinati MR, Fernandes MF, Ferreira-Araújo T, Gondim Lambert Moreira F, Santos NMC, Santos TAB, dos Santos-Costa RC, Serrano FC, Alves da Silva AP, de Souza Soares A, Cavalcante de Souza PG, Calisto Tomaz E, Vale VF, Vieira TL, Antonelli A (2020) No one-size-fits-all solution to clean GBIF. PeerJ 8: e9916. https://doi.org/10.7717/peerj.9916

Supplementary material 1

Tables S1, S2

Authors: Diego Armijos-Ojeda, Diana Székely, Paul Székely, Dan Cogălniceanu, Diego F. Cisneros-Heredia, Leonardo Ordóñez-Delgado, Adrián Escudero, Carlos Iván Espinosa

Data type: species data

Explanation note: List of ecosystem types included in the Equatorial Seasonally Dry Forest, based on MAE 2013 and MINAM 2019. Presence of amphibian species in the provinces (Ecuador) or departments (Peru) throughout the Equatorial Seasonally Dry Forest.

Link: https://doi.org/10.3897/zookeys.1063.69580.suppl1

Supplementary material 2

Appendix 1. Reference list for life-history characteristics of amphibians of the Equatorial Seasonally Dry Forest (Table 1)

Authors: Diego Armijos-Ojeda, Diana Székely, Paul Székely, Dan Cogălniceanu, Diego F. Cisneros-Heredia, Leonardo Ordóñez-Delgado, Adrián Escudero, Carlos Iván Espinosa

Data type: reference list

Link: https://doi.org/10.3897/zookeys.1063.69580.suppl2

Supplementary material 3

Dataset including amphibian species occurence information, museum specimen numbers, source of data

Authors: Diego Armijos-Ojeda, Diana Székely, Paul Székely, Dan Cogălniceanu, Diego F. Cisneros-Heredia, Leonardo Ordóñez-Delgado, Adrián Escudero, Carlos Iván Espinosa

Data type: species data

Link: https://doi.org/10.3897/zookeys.1063.69580.suppl3

ZooKeys 1063: 49–104 (2021)
doi: 10.3897/zookeys.1063.71180
https://zookeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
ZooKeys
Launched to accelerate biodiversity research

Revision of the genus *Niphta* (Diptera, Thaumaleidae) Theischinger of South America, with descriptions of nine new species and a new immature morphotype

Robert J. Pivar[1], Bradley J. Sinclair[2], John K. Moulton[1]

1 The University of Tennessee, Department of Entomology and Plant Pathology, 2505 E.J. Chapman Drive, 370 Plant Biotechnology Building, Knoxville, Tennessee, 37996, USA **2** *Canadian National Collection of Insects and Canadian Food Inspection Agency, K.W. Neatby Building, C.E.F., 960 Carling Avenue, Ottawa, Ontario, Canada K1A 0C6*

Corresponding author: John K. Moulton (jmoulton@utk.edu)

Academic editor: Art Borkent | Received 6 July 2021 | Accepted 22 August 2021 | Published 19 October 2021

http://zoobank.org/2792B13C-D577-416C-B83D-1C8043701C78

Citation: Pivar RJ, Sinclair BJ, Moulton JK (2021) Revision of the genus *Niphta* (Diptera, Thaumaleidae) Theischinger of South America, with descriptions of nine new species and a new immature morphotype. ZooKeys 1063: 49–104. https://doi.org/10.3897/zookeys.1063.71180

Abstract

The *Niphta* Theischinger fauna of South America is revised to include 11 species, nine of which are described as new to science (*N. acus* Pivar, **sp. nov.**, *N. bifurcata* Pivar & Moulton, **sp. nov.**, *N. bispinosa* Pivar & Sinclair, **sp. nov.**, *N. brunnea* Pivar, **sp. nov.**, *N. courtneyi* Pivar, **sp. nov.**, *N. daniellae* Pivar, **sp. nov.**, *N. downesi* Pivar, **sp. nov.**, *N. eurydactyla* Pivar, **sp. nov.**, *N. mapuche* Pivar, **sp. nov.**). The genus *Niphta* is redefined, both previously described Chilean species are redescribed, *N. halteralis* (Edwards) and *N. nudipennis* (Edwards), and females are described or redescribed where possible. The first descriptions of the immature stages of South American *Niphta* are provided, which represent a new larval morphotype in Thaumaleidae, as larvae and pupae possess ventral adhesive structures. Furthermore, these larvae were collected from vegetation rather than rocky substrates. Illustrations and micrographs are provided for all species, and scanning electron microscopy images are included for select immatures. A key to species, distribution maps, and discussions regarding phylogenetic affinities and habitat are also included.

Keywords

Andes, Chile, diversity, madicolous, midge, seepages

Introduction

Thaumaleidae, or madicolous midges, consist of nearly 200 species classified in seven genera. They have no known medical or economic importance to humans, and are considerably less studied than their presumptive sister family, Simuliidae (black flies) (Moulton 2000; Bertone et al. 2008; Wiegmann et al. 2011; Borkent 2012; Kutty et al. 2018). Adults are commonly collected from rock-face seepages, margins of waterfalls and splash zones of cascading streams (Sinclair 2000; Pivar et al. 2018a, b; Pivar et al. 2020). Thaumaleid larvae are restricted to madicolous habitats, or substrates with a thin film of water flowing over them (Mackie 2004; Shimabukuro and Trivinho-Strixino 2018). Until this study, larvae were thought to be limited to rocky substrates.

South America has eight described species of Thaumaleidae in three genera prior to this study, known from only three countries: *Austrothaumalea* Tonnoir (five species, Chile and Argentina), *Neothaumalea* Pivar, Moulton and Sinclair (one species, Brazil) and *Niphta* Theischinger (two species, Chile). Edwards (1930) was the first to describe thaumaleids from South America, including three species of *Austrothaumalea* and two species of *Niphta*. Schmid (1970) later described an additional species of *Austrothaumalea*. The first record of the family from Brazil was published by Pivar et al. (2018b), where they described the new genus and species, *Neothaumalea atlantica* Pivar & Pinho. Pivar et al. (2020) described an additional species of *Austrothaumalea*, synonymised *Oterere* McLellan with *Austrothaumalea* and provided a key to South American genera and species of *Austrothaumalea*. In addition to the described species above, Röder (1886) noted an undescribed species from the Ecuadorian Andes, though this record remains unverified by the authors despite attempts to locate the specimen.

The focus of this study is the South American *Niphta*, a small genus with two described species in Chile (Edwards 1930) and three in Australia (Theischinger 1986). The original descriptions by Edwards were brief and illustrations rudimentary, both severely lacking in detail. Discussions regarding relationships and keys were lacking, and immature stages unknown. Herein, *Niphta* is redefined, nine new species are described, Edwards' species are redescribed and females are described or redescribed for all available species. Genitalic illustrations are included for all species and available sexes. Additionally, immature stages of South American *Niphta* are described for the first time. Distribution maps, keys to species (see Pivar et al. 2020 for key to genera), and discussions regarding phylogenetic affinities, faunal patterns and habitat are also provided.

Materials and methods

Efforts were made to recollect fresh material from as near as possible to the perceived type localities. Adults were collected using an aerial net to sweep above the madicolous substrate and adjacent riparian vegetation. Sweeping for adults should be attempted first, if possible, to avoid having to sweep less accessible areas if they try to escape when searching for larvae. Immatures were collected by using forceps to pull them off the substrate, or by pouring water over the substrate and flushing immatures into a white pan (Sinclair and Saigusa 2002). In addition to examining rocks, vegetation (including leaves, stems, branches, etc.) in the splash zone should be carefully examined for larvae and pupae. This also includes inspecting any debris collected while sweep netting for adults, as it may contain immatures. Once collected, all life stages were placed directly into 75% non-denatured ethanol for morphological studies or 95% non-denatured ethanol for molecular studies.

Adult genitalia were cleared with hot 85% lactic acid. Representative adults and immatures were also cleared with the GeneJET Genomic DNA Purification Kit #K0722 (ThermoScientific, Waltham, MA) to maintain important membranous and lightly sclerotised structures, and to extract DNA for subsequent molecular study. The GeneJET lysate preparation protocol was followed and cleared voucher specimens were stored in 70% non-denatured ethanol. Positive identifications of females and immatures were made by comparing their DNA sequences to those of identified males. Specimens identified through molecular means are denoted by an asterisk (*) in the Type material and Additional material examined sections. Pinned specimens were dried using Brown's (1993) hexamethyldisilazane (HMDS) method. Cleared terminalia were preserved in glycerine-filled microvials pinned beneath the specimen.

Specimens were viewed using a Meiji Techno RZ stereomicroscope mounted with a Progres Gryphax Naos 22-megapixel camera (Jenoptik, Jena, Germany) and aided by iSolution Lite x64 software (Focus Precision Industries, Victoria, MN, USA) to take light micrographs of pinned adults and immatures in alcohol. Image stacks were created using Helicon Focus 6.7.1 (HeliconSoft, Roseau Valley, Dominica). Cleared terminalia and larval head capsules in glycerine were viewed with an Olympus BH-2 compound microscope equipped with DIC and images were taken following the same methods as above. Line drawings were first traced from stacked micrograph images captured using the compound microscope, structures were re-evaluated by closely re-examining specimens (as stacking failed to clearly differentiate critical internal structures), then line drawings were inked and digitised for publication. The left gonocoxite and gonostylus were intentionally omitted for male *Niphta nudipennis* group species to allow for clearer visualisation of remaining genitalic characters.

Samples were prepared for scanning electron microscopy by transferring specimens from 95% non-denatured ethanol into a 12 mm × 30 μm microporous specimen capsule (Electron Microscopy Services, Hatfield, PA). Capsules were then subjected to the following HMDS dehydration series, each step lasting 20 minutes: 100% ethanol, 1:1 ethanol to HMDS, 1:75 ethanol to HMDS, then two steps of 100% HMDS. Dried specimens were mounted on carbon tape affixed to 45°/90° aluminium stubs and sputter-coated with gold for 10 sec at 20 μA in a SPI-Module Sputter Coater (West Chester, PA). Specimens were viewed with a Hitachi TM3030 electron microscope (Tokyo, Japan) at a voltage of 15 kV.

Terms used for adult structures follow Cumming and Wood (2017). Homology of the male terminalia follows Sinclair (1992). Terms used for larval and pupal structures follow those of Courtney et al. (2000) and Borkent (2012), respectively. The numbering system for larval head capsule setae and sensory pits follows Sinclair and Stuckenberg (1995). Distribution maps were created with SimpleMappr (Shorthouse 2010).

Specimens are deposited in the following repositories: Canadian National Collection of Insects, Ottawa, Canada (**CNC**); Instituto de Entomología, Universidad Metropolitana de Ciencias de la Educación, Santiago, Chile (**UMCE**); Museo Nacional de Historia Natural, Santiago, Chile (**MNNC**); National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA (**USNM**); Robert J. Pivar, private collection, Ancaster, Ontario, Canada (**RJP**); University of Tennessee, Knoxville, Tennessee, USA (**UTK**).

Label data for primary types are presented exactly as they appear. Data are listed from the top downward on the staging pin, with data from each label enclosed in quotation marks; lines are delimited by a forward slash mark. Repository is given in parentheses and USNM database numbers are listed.

Taxonomy

A key to adults of South American genera of Thaumaleidae is provided in Pivar et al. (2020).

Genus *Niphta* Theischinger

Niphta Theischinger, 1986: 314. Type-species: *Niphta bickeli* Theischinger (original designation).

Diagnosis. *Niphta* is characterised as follows: presence of a distinct antealar ridge; proepisternal setae absent; microtrichia of $R_1(+R_{2+3})$ confined to base near humeral crossvein; R_{2+3} crossvein situated closer to apex of $R_1(+R_{2+3})$ than to origin of R_{4+5}; R_1 and $R_1(+R_{2+3})$ with three weakenings or depigmented gaps; R_{4+5} often with arch not strongly produced; basal spur of CuA absent; gonocoxites broad, not much longer than wide; hypandrium absent; gonocoxal plate extended posterodorsally forming a medial process; parameres fused medially, emerging from gonocoxal plate complex.

Redescription. *Adult*. Eye bridge broad, comprising more than five facets. Scutum clothed in both short and long setae; scutellum with row of long, black marginal setae. Supra-alar region produced into distinct antealar ridge (Fig. 9H); ridge with setae. Proepisternal setae absent. Wing tip narrowly rounded; membrane lacking macrotrichia; C with sparse macrotrichia, more so on remaining wing margin; Sc incomplete; microtrichia of $R_1(+R_{2+3})$ confined to base near humeral crossvein; R_{2+3} crossvein situated closer to origin of R_{4+5} than to apex of $R_1(+R_{2+3})$; R_1 and $R_1(+R_{2+3})$ with three weakenings or depigmented gaps; R_{4+5} often with arch not strongly produced; R_{4+5} and M_1 running parallel toward margin; M_1 straight; M_2 with gentle bend in apical third; M_4 with slight bend; CuA angulate near base; basal spur of CuA absent. *Male Termina-*

lia: Hypandrium absent. Gonocoxites broad, not much longer than wide; gonocoxal plate extended posterodorsally, forming medial process, acting as aedeagal guide; parameres fused medially, emerging from gonocoxal plate complex.

Distribution. Chile and Australia.

Species groups. Prior to this study, only five described species of *Niphta* were known from all regions and few phylogenetic affinities had been discussed. Theischinger (1986) suggested that the Australian *N. farecta* Theischinger was more closely allied to the Chilean *N. nudipennis* (Edwards) than the other Australian species. With the additional nine species described herein, it is now possible to better assess relationships based upon morphology. Species groups are proposed below for the genus *Niphta*.

The *N. bickeli* group: This group is characterised by the following features: broad gonocoxites extending to the posterior epandrial margin and lacking projections; long gonostyli; parameres fused medially, then separating into two arms that do not project anteriorly; a pair of apodemes from base of parameres extend to posterior margin of epandrium, on either side of the anus; cerci inconspicuous, thinly sclerotised and unpigmented; females lack projection at base of hypogynial valves. This group is greyish black in colouration. Additionally, immatures of *N. collessi* Theischinger lack ventral adhesive structures and protuberances on the larval head capsule (Sinclair 2000); these are tentatively seen as important characters uniting this species group until further Australian immatures are discovered and accurately associated with the adults (see discussion below comparing *Niphta* immatures). The *N. bickeli* group is found in Australia and includes the following species: *N. bickeli* Theischinger, *N. collessi*, and *N. farecta*.

The *N. halteralis* group: This group is characterised by the following features: gonocoxites extending to midpoint of epandrium, lacking pointed projections; short and narrow gonostyli; parameres fused throughout; prominent cerci projecting anteriorly, extending well beyond posterior epandrial margin; females lack projection at base of hypogynial valves. This group is darkly coloured, mostly black and grey. Immature stages have ventral adhesive structures, are collected from rocky substrates and larval head capsules have many protuberances. The *N. halteralis* group is known from Chile and includes the following species: *N. acus* sp. nov., *N. downesi* sp. nov., *N. halteralis* (Edwards), and *N. mapuche* sp. nov.

The *N. nudipennis* group: This group is characterised by the following features: gonocoxites extending, at most, to midpoint of epandrium, and bearing pointed projections; broad, short gonostyli cheliform or finger-like; parameres fused medially. separated into two arms that project anteriorly and may be flexed or extended; cerci small, projecting anteroventrally; females possess distinct blunt or pointed projection at base of hypogynial valves; sternite 8 highly modified (genital fork and lateral arms); Female sternite 9 greatly expanded and heavily sclerotised, presumably reflecting the highly modified male genitalia. This group tends to be lighter in colouration. Immature stages have ventral adhesive structure, are collected from vegetation in splash zones, and larval head capsules have many protuberances. The *N. nudipennis* group is known from Chile and includes: *N. bifurcata* sp. nov., *N. bispinosa* sp. nov., *N. brunnea* sp. nov., *N. courtneyi* sp. nov., *N. daniellae* sp. nov., *N. eurydactyla* sp. nov. and *N. nudipennis*.

Key to adult males of South American species of *Niphta*[*]

1 Gonocoxite subquadrate or conical, with posteromedial projection broad, rounded, projecting posteriorly (Fig. 2). Parameres fused medially to apex (Figs 2, 3). Body typically dark in colour (Fig. 4) .... **2 (*N. halteralis* group)**

– Gonocoxite oblong, with posteromedial projection narrow, pointed, projecting medially (Figs 5, 6). Parameres fused medially then separating into two raptorial-like apical arms (Figs 7, 8). Body typically light in colour (Figs 9, 10) .... **5 (*N. nudipennis* group)**

2 Paramere with hooked apex. Gonostylus straight (Figs 2C, 3C) .... ***N. halteralis* (Edwards)**

– Paramere without hooked apex. Gonostylus arched outwards **3**

3 Gonostylus bifurcate apically. Paramere with abrupt, strongly tapered, off-centred needle-like apex (Figs 2A, 3A) .... ***N. acus* Pivar, sp. nov.**

– Gonostylus tapered to single apex. Paramere evenly tapered throughout **4**

4 Paramere, in lateral view, divided into two filaments; dorsal filament, at most, nearly reaching posterior margin of epandrium; ventral filament not extended beyond apex of gonostylus, not easily visible (Figs 2D, 3D) ..... ***N. mapuche* Pivar, sp. nov.**

– Paramere, in lateral view, divided into three filaments; dorsal filament extended beyond posterior margin of epandrium; paired ventral filaments extended beyond apex of gonostylus, easily visible (Figs 2B, 3B) .... ***N. downesi* Pivar, sp. nov.**

5 Gonostyli cheliform or bearing a finger-like projection (Figs 5B, C, 6) **6**

– Gonostyli not cheliform, without projections; broad at base, tapered to pointed apex (Figs 5A, 7A) .... ***N. daniellae* Pivar, sp. nov.**

6 Gonostyli with finger-like projection (Fig. 5B, C) 7

– Gonostyli cheliform, resembling crab claw (Fig. 6) **8**

7 Gonostyli with projection broad, tapered slightly at apex, without bend (Figs 5B, 7B) .... ***N. eurydactyla* Pivar, sp. nov.**

– Gonostyli with projection narrow throughout, bent at midpoint (Figs 5C, D, 7C, D) .... ***N. nudipennis* (Edwards)**

8 Gonostyli with posterior apex bifurcate (Fig. 6A, B) **9**

– Gonostyli with posterior apex bearing single apex (Fig. 6C, D) **10**

9 Gonocoxites with two projections, anterior one bifurcate (Figs 6A, 8A). Body brown to dark brown in colour (Figs 9E, 10E) .... ***N. bifurcata* Pivar & Moulton, sp. nov.**

– Gonocoxites with three separate projections (Figs 6B, 8B). Body yellow in colour (Figs 9B, 10B) .... ***N. courtneyi* Pivar, sp. nov.**

10 Gonocoxites with two projections; anterior one long, bifurcate; posterior one small, tooth-like (Figs 6C, 8C). Body yellowish brown in colour (Figs 9G, 10G) .... ***N. bispinosa* Pivar & Sinclair, sp. nov.**

– Gonocoxites with three projections, two anterior (one small and inconspicuous at base of large one), one posterior; posterior projection slender, about as long as

---

[*] see Fig. 1 for micrograph of wing with pertinent structures labelled

larger anterior projection (Figs 6D, 8D). Body dark brown in colour (Figs 9A, 10A) ....***N. brunnea*** **Pivar, sp. nov.**

Key to adult female species groups of South American *Niphta*

1 Sternite 8 with distinct projection between hypogynial valves (Figs 11, 12) .. ..***N. nudipennis*** **group**

– Sternite 8 without distinct projection between hypogynial valves (Fig. 13) ... . ***N. halteralis*** **group**

Species diagnoses and descriptions of South American *Niphta*

The *N. halteralis* group

Niphta acus Pivar, sp. nov.

http://zoobank.org/4E68FECD-24B7-4E34-9F20-0F8FCC80EDBD

Figs 2A, 3A, 4A, 13A, B, 14C, 15C, 16C, 17C, 18C, 19C, 20A, B, 25, 27C

Type material. ***Holotype*:** ♂, glued to point with abdomen in glycerine microvial pinned beneath, labelled: "Chile: Region VIII (Bío Bío)/ Rte. Q-61, Estero Agua/ Blanca, 8.xii.2016/ 37°46'30.8"S 71°42'03.9"W/ elev. 552 m, vegetation near/ splash zones, J.K. Moulton &/ R.J. Pivar"; "HOLOTYPE/ *Niphta*/ *acus*/ Pivar [red label]" (CNC). ***Allotype*:** ♀, same label data as holotype (CNC). ***Paratypes*:** Chile: Region RM (Santiago): Quebrada el Cinco Mil, 17.xii.2016, 33°31'30.4"S 70°13'52.6"W, elev. 1308 m, creek, J.K. Moulton & R.J. Pivar (3♀*); Region V (Valparaíso): Rte. 60, 18.xii.2016, 32°54'31.3"S 70°18'21.5"W, elev. 1423 m, creek, J.K. Moulton & R.J. Pivar (2♂); Region VIII (Bío Bío): Rte. N-55, 16.xii.2016, 36°55'02.7"S

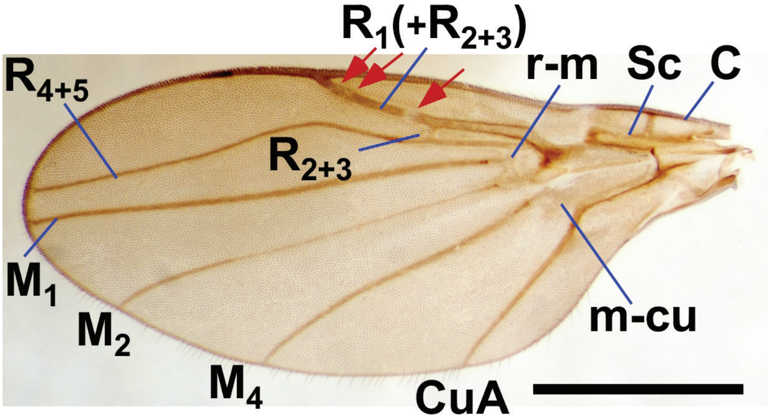


Figure 1. Left wing of *Niphta nudipennis* with arrows indicating three depigmented gaps. Abbreviations: C, costa; CuA, anterior branch of cubital vein; M, medial veins; m-cu, medial-cubital crossvein; R, radial veins; r-m, radial-medial crossvein; Sc, subcosta. Scale bar: 1.0 mm.

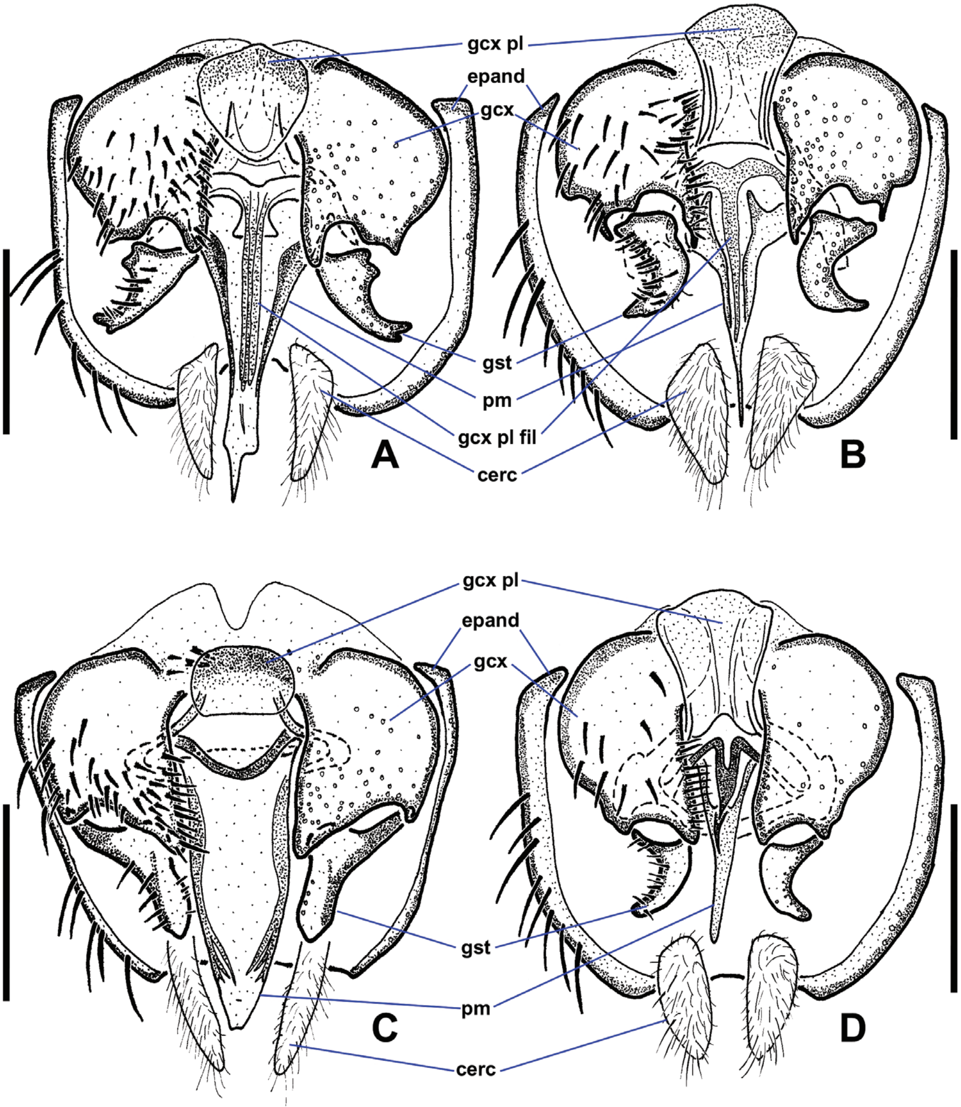


Figure 2. Ventral views of male *Niphta halteralis* group terminalia **A** *N. acus* sp. nov. **B** *N. downesi* sp. nov. **C** *N. halteralis* **D** *N. mapuche* sp. nov. Abbreviations: cerc, cercus; epand, epandrium; gcx, gonocoxite; gcx pl, gonocoxal plate; gcx pl fl, gonocoxal plate filament; gst, gonostylus; pm, paramere. Scale bars : 0.1 mm.

71°25'49.6"W, elev. 1449 m, roadside seep, J.K. Moulton & R.J. Pivar (25♂); same label data as previous except, collected from rockface (8 larvae*, 5 pupae*, 8 pupal exuviae); Rte. Q-61, Estero Agua Blanca, 8.xii.2016, 37°46'30.8"S 71°42'03.9"W, elev. 552 m, vegetation near splash zones, J.K. Moulton & R.J. Pivar (41♂, 10♀*, 1 larva*); Rte. Q-61, 8.xii.2016, 37°48'34.7"S 71°40'30.0"W, elev. 390 m, roadside seep, J.K. Moulton & R.J. Pivar (2♂, 1♀*).

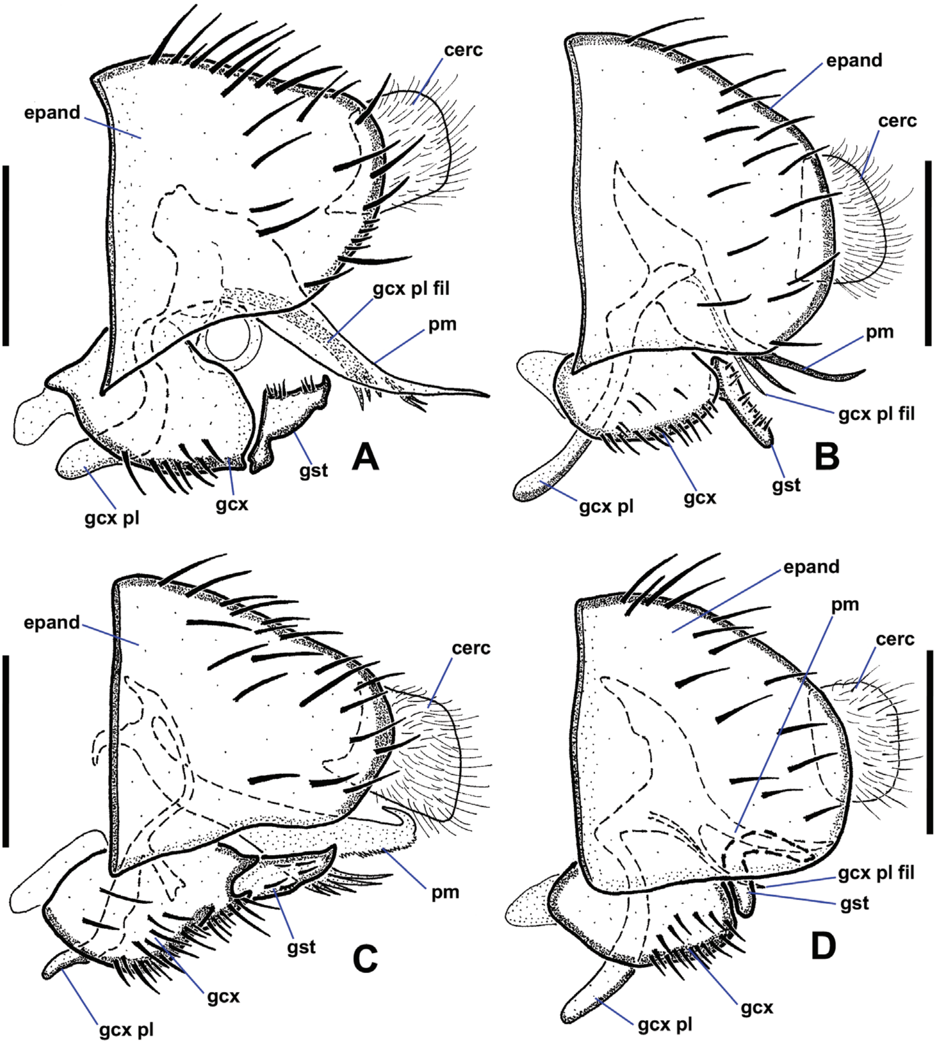


Figure 3. Lateral views of male *Niphta halteralis* group terminalia **A** *N. acus* sp. nov. **B** *N. downesi* sp. nov. **C** *N. halteralis* **D** *N. mapuche* sp. nov. Abbreviations: cerc, cercus; epand, epandrium; gcx, gonocoxite; gcx pl, gonocoxal plate; gcx pl fl, gonocoxal plate filament; gst, gonostylus; pm, paramere. Scale bars: 0.1 mm.

Recognition. *Niphta acus* is recognised by the bifurcated apex of the gonostylus and the strongly apically tapered parameres, giving the appearance of a needle-like tip.

Description. Male. *n* = 71.

Length 1.6–2.5 mm.

Colouration (Fig. 4A). Head dull, blackish brown; pronotum and postpronotum dark brown; postpronotal lobe brown with dark brown markings, light brown around anterior spiracle; prescutum, mesoscutum and pleura shiny, blackish brown; scutellum and mediotergite shiny, blackish brown; katepisternum dark brown with blackish brown markings, remaining pteropleuron mainly blackish brown with dispersed markings of brown to light brown; base of halter black, knob creamy yellow; legs greyish brown, apex of tarsi darker; abdomen blackish brown; terminalia concolourous with abdomen.

Head. Eyes above antennae broadly joined, with small triangular frons visible above antennae; frons with three to five strong setae. Flagellomeres 1–3 subquadrate, with flagellomere 1 expanded, 3 × as wide as next segment, equal to lengths of 2 and 3 combined; flagellomeres 4–10 cylindrical, becoming progressively thinner and elongate. Vertex with black setae of uniform length, with longer, black orbital setae.

Thorax. Mesoscutum with prominent antealar ridge, bearing thee pronounced setae. Scutum clothed dorsally in short, black setulae; notopleural, supra-alar and postsutural setae long, black. Pteropleuron bare. All legs with tarsi simple.

Wing. Wing length: 1.8–2.5 mm. Dark, infuscate throughout, apex somewhat narrowed; C fringed in small setulae, with a few microtrichia scattered throughout; posterior wing margin with closely spaced fringe of microtrichia; Sc incomplete; R_1 and $R_1(+R_{2+3})$ with three weakenings or depigmented gaps, first slightly beyond R_{2+3}, second and third closely approximated, near C; microtrichia of $R_1(+R_{2+3})$ confined to base near humeral crossvein, remaining veins bare; R flexed into cell br; R_{2+3} distinct, situated in basal third of $R_1(+R_{2+3})$; bend in R_{4+5} gentle; R_{4+5} and M_1 running parallel toward margin; M_1 straight; M_2 with gentle bend in apical third; M_4 with slight bend.

Abdomen. Abdominal sternite 1 narrow, spectacle-shaped; sternite 2 reduced to slender median sclerite, a few setae restricted to laterad on posterior third and medially beneath sclerite; sternites 3–7 rectangular, lacking distinct sclerites, setae restricted to posterior two-thirds; sternite 8 strongly reduced, anterior margin well sclerotised, arched slightly into preceding segment, lacking setae.

Terminalia (Figs 2A, 3A). Epandrium quadrate in ventral view, posterior margin rounded with large, medial indentation; long, extending well beyond gonostyli; without lobes or projections. Gonocoxites conical, one-third longer than wide, anterior margin rounded, expanded dorsally behind gonocoxal plate, nearly meeting medially, extended anteriorly toward sternite 8; posterior inner margin produced into rounded projection, outer margin without notch; inner margin densely setose. Gonostylus short, three-quarters length of cercus, strongly curved laterally throughout; widest at base, tapered toward bifurcated apex; outer margin bearing laterally directed setae. Parameres fused at gonocoxal apodeme, widest at point of fusion; extended beyond cerci; forming canal-like structure, flattened apically, tapered to off-centre sharp point (occasionally specimens with broken apex). Gonocoxal plate well sclerotised; tongue-like plate extended anteroventrally; hollow medially, pitcher plant-like; gonocoxal apodeme with secondary structure comprising three arms fused medially, running along interior of paramere canal, flaring into three or four filaments, projected ventrally at apex, with pair of lateral flanges near point of fusion. Cercus large, prominent; subquadrate; projected posteriorly; situated within epandrial indentation.

Female. *n* = 15.

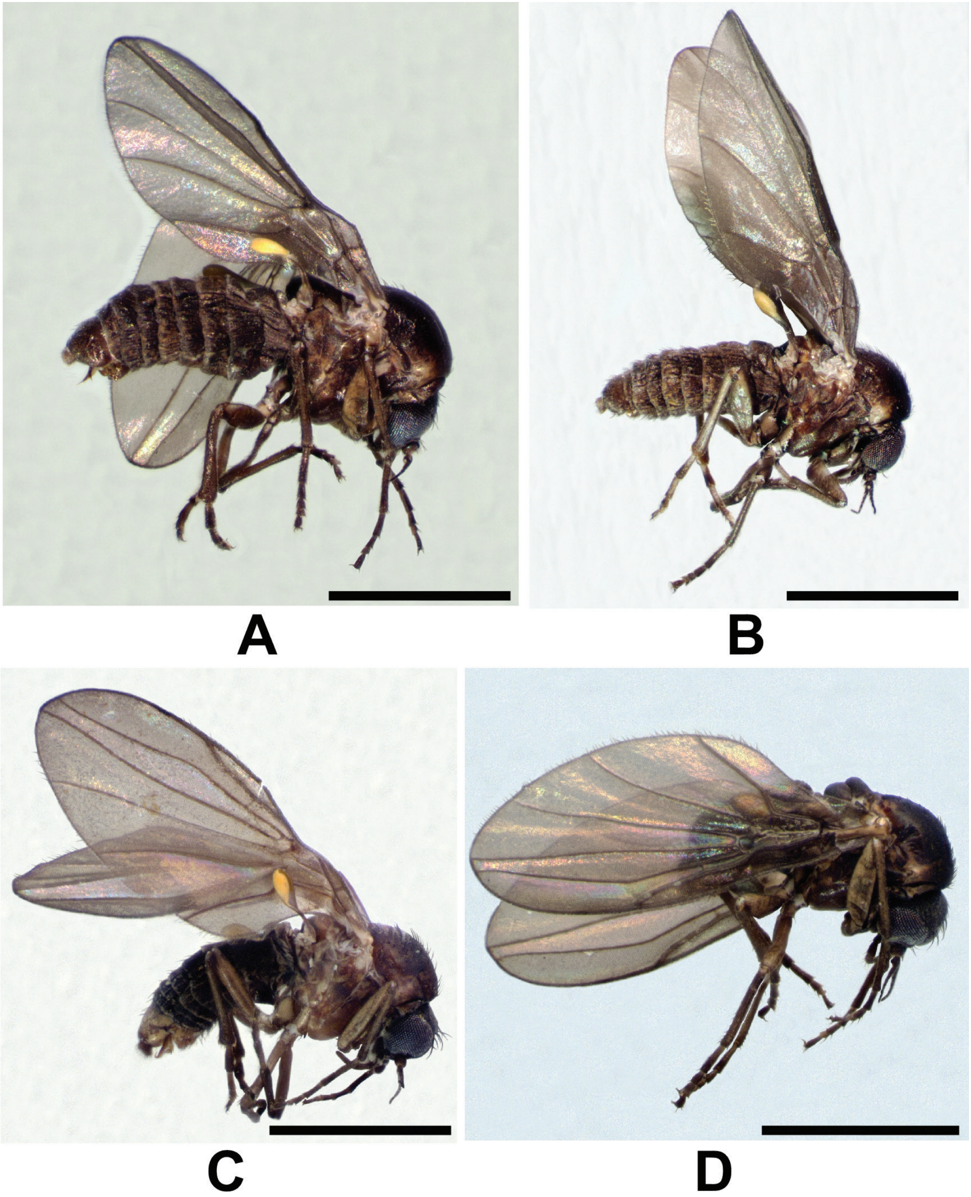


Figure 4. Adult male lateral habitus micrographs of the *Niphta halteralis* group **A** *N. acus* sp. nov. **B** *N. downesi* sp. nov. **C** *N. halteralis* **D** *N. mapuche* sp. nov. Scale bars: 1.0 mm.

Similar to male except as follows: *Terminalia* (Fig. 13A, B). Hypogynial valve not projecting beyond tergite 9; posterior margin deeply emarginated in ventral view, nearly dividing sternite in half, forming two subtriangular lobes; lobes densely setose. Tergite 9 subtriangular in lateral view, 3 × as wide as tergite 8, lacking lateral projections; posterior margin heavily sclerotised at base of cerci. Sternite 9 (genital fork) slender,

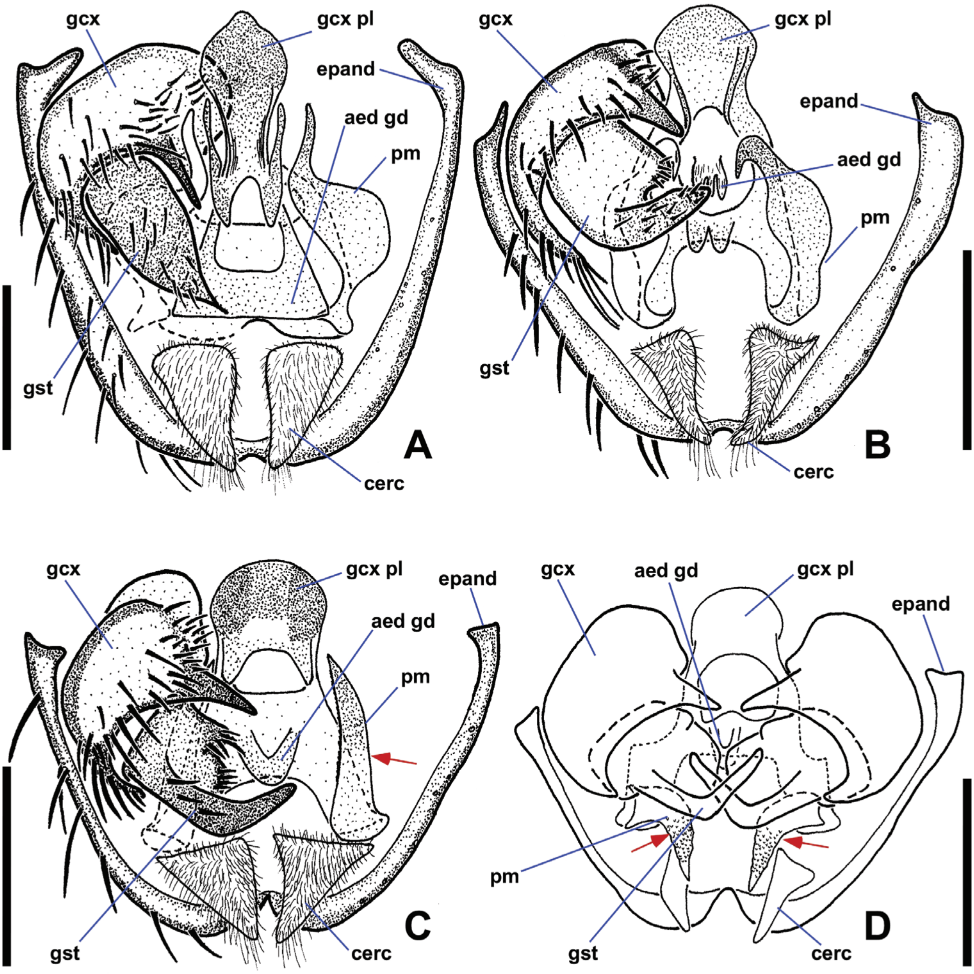


Figure 5. Ventral views of male *Niphta nudipennis* group terminalia **A** *N. daniellae* sp. nov. **B** *N. eurydactyla* sp. nov. **C** *N. nudipennis* with parameres retracted **D** *N. nudipennis* with parameres extended. Arrows indicate range of motion of parameres. Abbreviations: aed gd, aedeagal guide; cerc, cercus; epand, epandrium; gcx, gonocoxite; gcx pl, gonocoxal plate; gst, gonostylus; pm, paramere. Scale bars: 0.1 mm.

Y-shaped anteriorly and posteriorly; lateral arms extended slightly beyond hypogynial valve, divergent toward apex. Hypoproct sclerotised, narrow. Cercus rounded, projected posteroventrally; bearing numerous setae.

Pupa. *n* = 8 (Figs 14C, 15C, 16C).

Length 3.0–4.0 mm.

Colouration. Brown; with black spot above eye in developing adult.

Head. Maxillary sheath short, posteromedially directed; gently tapered toward truncate apex; apices of palpi separated medially. Three short, slender setae above black spot over eye.

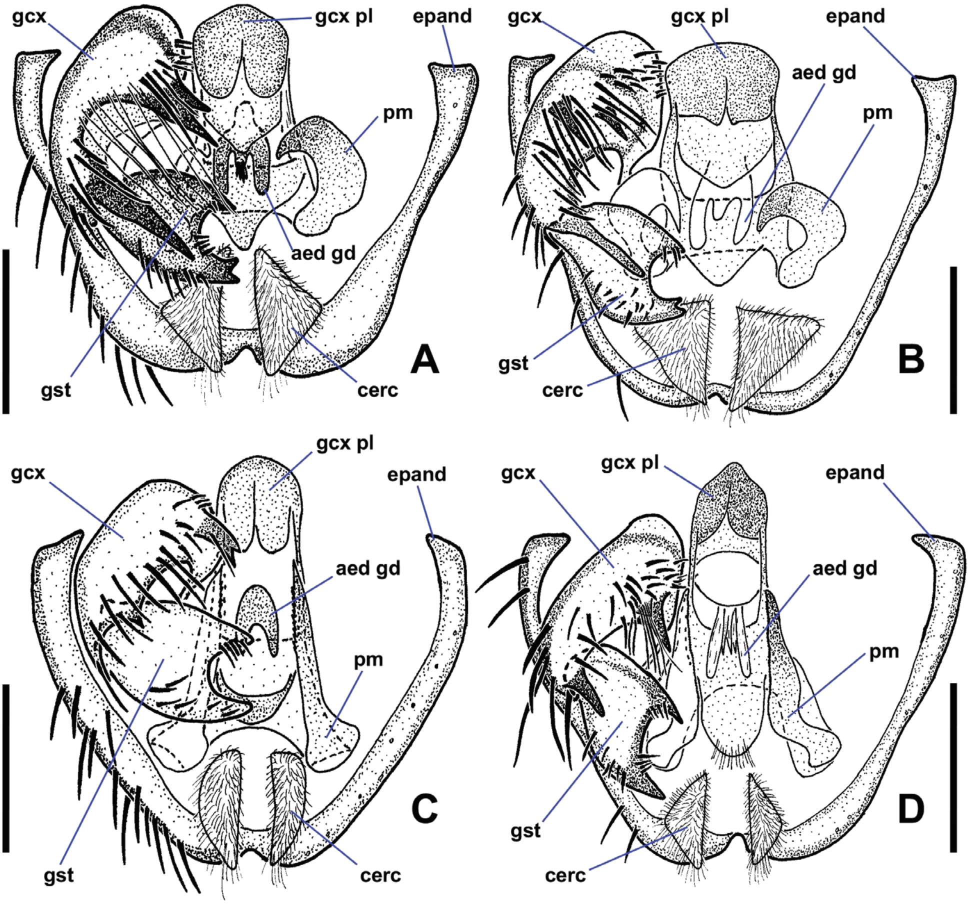


Figure 6. Ventral views of male *Niphta nudipennis* group terminalia **A** *N. bifurcata* sp. nov. **B** *N. courtneyi* sp. nov. **C** *N. bispinosa* sp. nov. **D** *N. brunnea* sp. nov. Abbreviations: aed gd, aedeagal guide; cerc, cercus; epand, epandrium; gcx, gonocoxite; gcx pl, gonocoxal plate; gst, gonostylus; pm, paramere. Scale bars: 0.1 mm.

Thorax. Width nearly subequal to abdomen at widest point. Foreleg sheath projecting straight, slightly longer than wing sheaths, reaching posterior margin of sternite 2; anterior half of midleg visible anterior to wing sheath, then hidden behind foreleg, slightly shorter than foreleg; hind leg concealed behind wing sheath, only apex visible between apex of foreleg and wing sheath, shorter than foreleg. Wing sheaths not reaching posterior margin of abdominal sternite 2; large tubercle at base bearing pair of short, slender setae. Respiratory organ short and squat, much shorter than maxillary sheath, broadest subapically; bulbous; spiracular openings encircling apex; stalk wide, emerging from small tubercle. Tubercle situated posterodorsally to respiratory organ, rounded, projected slightly laterally; apex nearly touching or touching respiratory organ. Tubercle situated posterolaterally to respiratory organ crenulate, projected

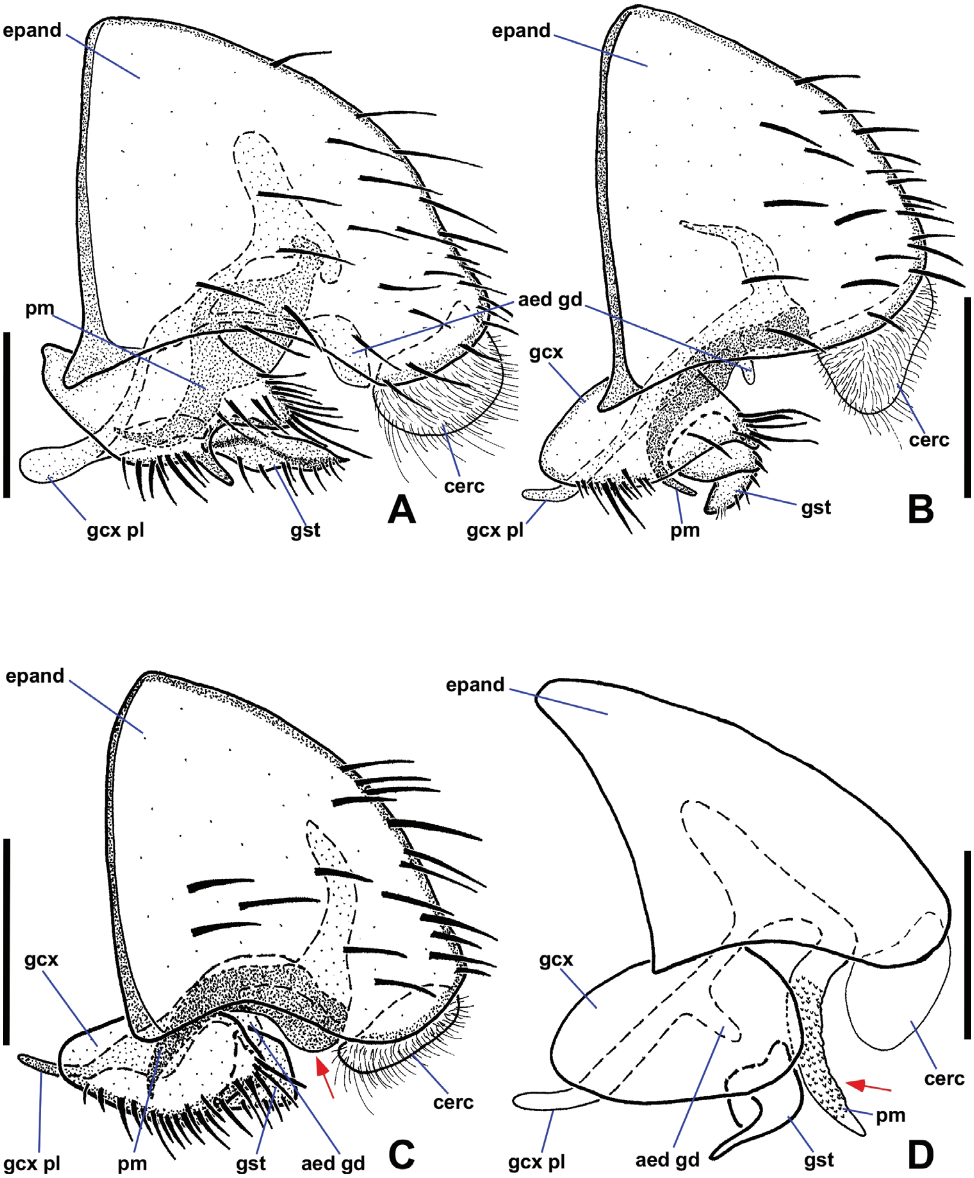


Figure 7. Lateral views of male *Niphta nudipennis* group terminalia **A** *N. daniellae* sp. nov. **B** *N. eurydactyla* sp. nov. **C** *N. nudipennis* with parameres retracted **D** *N. nudipennis* with parameres extended. Arrows indicate range of motion of parameres. Abbreviations: aed gd, aedeagal guide; cerc, cercus; epand, epandrium; gcx, gonocoxite; gcx pl, gonocoxal plate; gst, gonostylus; pm, paramere. Scale bars: 0.1 mm.

slightly anteriorly. Ridge located anteroventrally to respiratory organ with single, thin midlateral seta; mesothorax with group of four short, slender dorsocentral setae near ridge; single seta on humeral lobe.

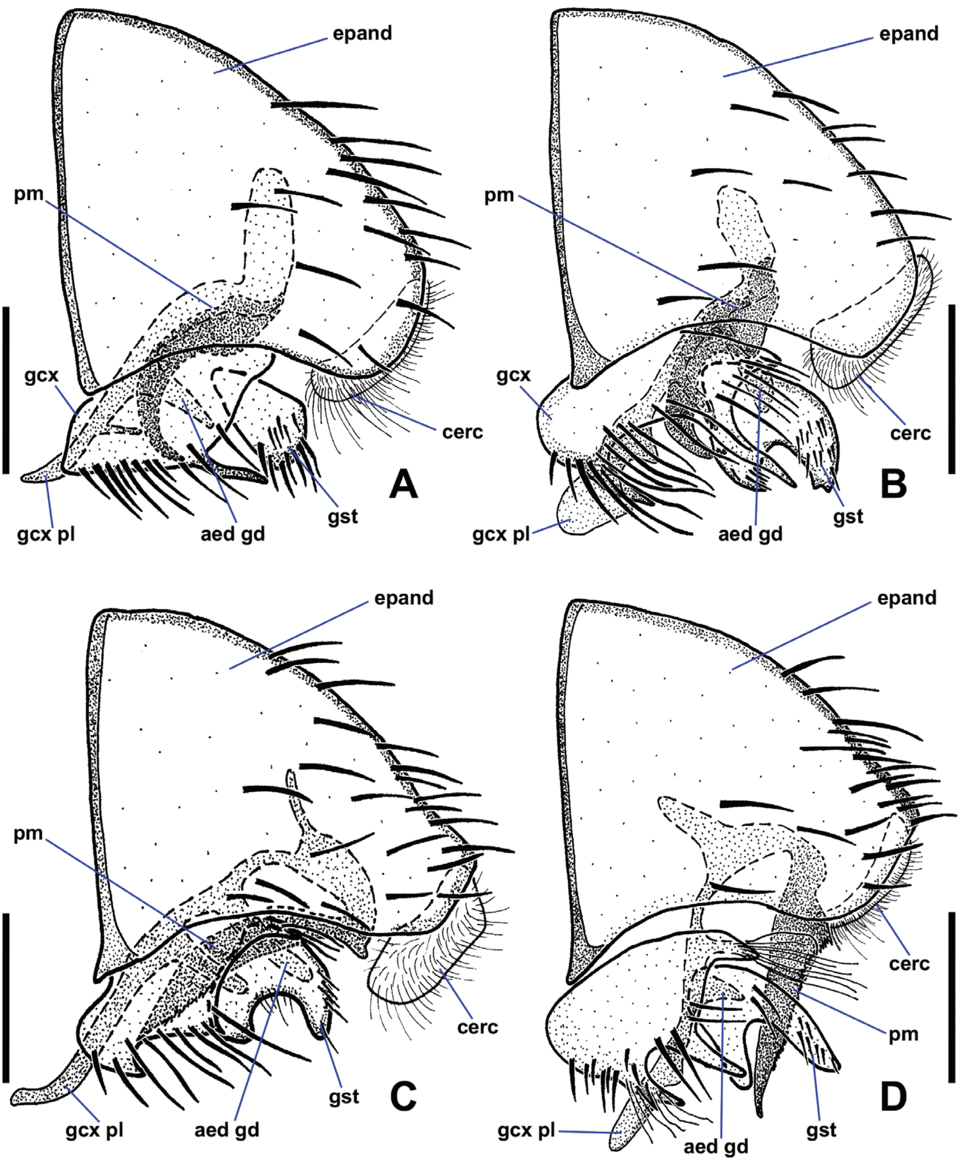


Figure 8. Lateral views of male *Niphta nudipennis* group terminalia **A** *N. bifurcata* sp. nov. **B** *N. courtneyi* sp. nov. **C** *N. bispinosa* sp. nov. **D** *N. brunnea* sp. nov. Abbreviations: aed gd, aedeagal guide; cerc, cercus; epand, epandrium; gcx, gonocoxite; gcx pl, gonocoxal plate; gst, gonostylus; pm, paramere. Scale bars: 0.1 mm.

Abdomen. Subcylindrical, strongly tapered at caudal segment. Spiracles weakly developed, not projected or distinctly visible. Tergites 1–8 rectangular, without ridges; bearing pair of slender lateral setae above lateral margins and pair of slender dorsolateral setae. Tergite 9 rounded, posterior with dorsolateral ridges bearing pair of lateral setae and hind margin emarginated; projection directed posteriorly in lateral view. Sternites 3–8 rectangular, without row of faint setulae along anterior margin; lateral margins crenulate, bearing a few thin, short setae. Sternites 3 and 4 bearing pair of small lateral adhesive structures, sternite 5 bearing pair of large lateral adhesive structures on lateral margin. Caudal sternite subquadrate, with pair of posteriorly projected medial lobes; posterior margin with pair of medial ridges, curved dorsally forming small, dorsally projected tubercle in lateral view; without distinct caudal hooks.

Larva. *n* = 8 (Figs 17C, 18C, 19C, 20A, B).

Length of final instar 6.2–6.7 mm.

Colouration. Head capsule usually black or dark brown, sometimes black with light brown markings. Body mottled with various shades of grey and brown.

Head capsule (Fig. 20A, B). Two large, circular eye spots, elevated on tubercle; antenna on largest tubercle, with three finger-like processes; with five pairs of tubercles outside of ecdysial lines (not including antennal and ocular tubercle), two outermost tubercles bifurcate; single tubercle between ecdysial line, bi- or trifurcate; 15 pairs of unbranched setae; five pairs of sensory pits (13, 14, 18, 20, 21), sensory pit 13 above antennal tubercle.

Thorax. Prothorax with pair of anterodorsolateral protuberances bare; anterolateral protuberances with one long and two short setae; spiracular protuberance bearing two protuberances, inner protuberance with pair of setae, outer with single seta; pair of midlateral setae below anterolateral protuberance; three closely approximated setae near base of prothoracic leg (Keilin's organ). Mesothorax and metathorax with pair of dorsolateral protuberances bearing pair of closely approximated setae, one thickened, one slender; mesothorax with additional seta beneath protuberance; lateral protuberance on both segments bearing four setae; one long seta slightly ventral to lateral protuberance; three mid-ventrolateral setae directed ventrally. Prothorax bearing proleg, posterior half with rectangular adhesive structure; meso- and metathoracic sternites with rectangular adhesive structures.

Abdomen. Sternites 1–7 modified into circular, suction cup-like adhesive structures; sternite 8 with quadrate adhesive structure, extending over sternite 9; sternite 9 smooth, bearing anal proleg. Tergites 1–7 with single anterolateral protuberance on each side with single seta, and pair of posterodorsolateral protuberances, each bearing two closely approximated short, thin setae; lateral adhesive structure swelling bearing four setae, two lateral, two basal; additional single seta located anterior to lateral swelling. Segment 8 with dorsolateral protuberance on either side of posterior spiracular plate, each bearing pair of small setae; lateral protuberance with three setae; single short ventrolateral seta; ventral surface bearing pair of setae. Posterior spiracular plate with sclerite encircling procerci; procercus shorter than length of spiracular plate, bearing four setae, two thick, two slender; without cone-like protuberance on either side of procerci. Terminal segment with anterior dorsal protuberance bare; pair of posterior lateral protuberances with pair of setae; five lateral setae; two pairs of long setae on posterior margin, above pair of anal papillae; ventral sternite bearing single pair of setae.

Additional material examined. Known only from the type series.

Distribution. Known from the south-central Andes of Chile (Fig. 24A); this species includes the northern-most record for *Niphta* in South America.

Etymology. The species name is from the Latin *acu* (needle, pin) in allusion to the needle-like tip of the paramere.

Bionomics. This species was collected at higher elevations than any other species in this publication. Larvae and pupae have ventral adhesive structures and were collected only from rocky substrates (Fig. 25). All immatures were collected from the margin of waterfalls, where water flow was quite slow.

Niphta downesi Pivar, sp. nov.

http://zoobank.org/11210E93-FC16-4315-BD7A-8974A93E782C
Figs 2B, 3B, 4B, 24A, 27A

Type material. ***Holotype*:** ♂, glued to point with abdomen in glycerine microvial pinned beneath, labelled: "Chile: Region XIV (Los Ríos)/ Rte. T-85, 13.xii.2016/ 40°19'58.6"S 72°16'56.1"W/ elev. 95 m, roadcut seep, J.K./ Moulton & R.J. Pivar"; "HOLOTYPE/ *Niphta*/ *downesi*/ Pivar [red label]" (CNC). ***Paratypes*:** Chile: Region X (Los Lagos): Ensenada, nr. Baños de Petrohué, 12.i.1985, J.A. Downes (1♂, CNC); Region XIV (Los Ríos): same data as holotype (1♂); Rte. T-85, 13.xii.2016, 40°19'58.7"S 72°16'54.8"W, elev. 145 m, foliage around waterfalls, J.K. Moulton & R.J. Pivar (12 ♂).

Recognition. This species is recognised by both filaments of the paramere and the aedeagal guide being easily visible in lateral view, giving it a tri-filamentous appearance. Also, the bend in the gonostylus is slightly stronger than that of *N. mapuche*.

Description. The description of *N. downesi* differs from that of *N. acus* in the following regards:

Male. $n = 3$.

Length 1.9–2.4 mm.

Colouration (Fig. 4B). Head dull, black; pronotum and postpronotum black; postpronotal lobe, prescutum and mesoscutum shiny, blackish brown, lateral face of postpronotal lobe brown, creamy around anterior spiracle; scutellum blackish brown dorsally, light brown ventrally; mediotergite shiny, blackish brown; pteropleuron mainly brown with dispersed markings of black and dark brown; base of halter blackish, knob creamy yellow; abdomen blackish brown.

Head. Frons with two strong setae. Flagellomeres 1–3 subquadrate, expanded, 1.5 × as wide as next segment, as long as 2 and 3 combined.

Thorax. Antealar ridge bearing single pronounced, medial seta flanked by two smaller setae.

Wing. Wing length: 2.2–2.4 mm. C and posterior wing margin with fringe of microtrichia.

Abdomen. Sternites 3–7 with setae restricted to posterior two-thirds and laterad; sternite 8 strongly arched into preceding segment, lacking setae.

Terminalia (Figs 2B, 3B). Gonocoxite subquadrate, posterior inner margin produced into pointed projection, outer margin notched. Gonostylus short, slightly more than half-length of cercus, strongly arched outwards; apex pointed. Parameres distally fused, widest medially, as wide as gonocoxite; extended past posterior margin of epandrium; lateral margins curved ventrally, canal-like medially in ventral view, then tapered rapidly to filamentous, pointed apex projected posterodorsally, extended beyond epandrium; medial structure cradled within canal, protruded ventrally; in lateral view ending at halfway point of longest filament. Gonocoxal apodeme with secondary structure comprising single filament, running along interior of paramere canal, projected ventrally at apex. Cercus trapezoidal; projected posteroventrally; situated within epandrial indentation.

Female. Unknown.

Immature stages. Unknown.

Additional material examined. Known only from the type series.

Distribution. Known from the foothills of the southern Andes in Chile (Fig. 24A).

Etymology. *Niphta downesi* is named in honour of veterinary and medical entomologist J.A. Downes, who collected the first specimen of this species in 1985.

Niphta halteralis (Edwards)

Figs 2C, 3C, 4C, 13C, D, 24A, 27F

Austrothaumalea halteralis Edwards, 1930: 114. Stuardo, 1946: 42 (catalogue); Stone, 1966: 1 (catalogue); Arnaud, 1977: 284 (distribution).

Niphta halteris (Edwards): Theischinger 1986: 316 (*lapsis calami*, new combination); McLellan, 1988: 563 (moved to genus *Niphta* by Theischinger (1986)).

Type material examined. ***Holotype*:** ♂, minuten pinned with abdomen mounted in resin, labelled: "Casa Pangue./ 4–10.xii.1926."; "Austrothaumalea/ halteralis Edw./ F.W. Edwards/ det. 1930."; "S. Chile:/ Llanquihue prov./ F. & M. Edwards./ B.M. 1927 – 63."; "HOLO-/ TYPE [white label with red margin]"; "NHMUK010210689".

Recognition. This species is recognised by its distinct hook-tipped paramere.

Redescription. The redescriptions of *N. halteralis* differ from that of *N. acus* in the following regards:

Male. *n* = 44.

Length 1.3–2.0 mm.

Colouration (Fig. 4C). Head dull, dark brown to black; postpronotal lobe, prescutum and mesoscutum shiny, brown, middle of postscutum light brown; scutellum and mediotergite shiny, light brown; pteropleuron light brown with dispersed dark brown markings; base of halter light brown, knob creamy yellow; legs pale brown, tarsi darker; abdomen dark brown, hind margins of tergites whitish; terminalia light brown.

Head. Frons with two strong setae. Flagellomeres 1–3 subquadrate, slightly expanded, 0.25 × as wide as next segment, slightly shorter than 2 and 3 combined. Vertex with yellow setae of uniform length, with longer, black orbital setae.

Thorax. Antealar ridge bearing single pronounced medial seta flanked by two smaller setae.

Wing. Wing length: 2.0–2.9 mm. C and posterior wing margin with fringe of microtrichia; R_{2+3} distinct, situated slightly before middle of $R_1(+R_{2+3})$; M_1 and M_2 straight.

Abdomen. Sternites 3–7 rectangular, lacking distinct sclerites, setae restricted to posterior half; sternite 8 strongly arched into preceding segment, lacking setae.

Terminalia (Figs 2C, 3C). Gonocoxite subquadrate; posterior inner margin produced into pointed projection; inner margin densely setose; outer margin without notch. Gonostylus short, about as long as cercus, widest at base, strongly tapered along outer margin with rounded apex; apex slightly flanged outward, appearing pointed in lateral view; distal half bearing setae along outer apical margin, a few setae on inner margin. Parameres fused at gonocoxal apodeme, widest medially, as wide as gonocoxite; extended past posterior margin of epandrium; lateral margins curved ventrally forming canal-like structure with median 'wings' projected posteriorly, margins feathered; apex with pointed hook-like projection, recurved and projected anteriorly to left. Gonocoxal plate well sclerotised; tongue-like plate extended anteroventrally; gonocoxal apodeme with secondary bridge connected with base of paramere. Cercus trapezoidal; projected posteroventrally.

Female. *n* = 6.

Similar to male except as follows: *Abdomen*. Tergite 9 noticeably more sclerotised than preceding tergites; sternite 8 well sclerotised.

Terminalia (Fig. 13C, D). Hypogynial valve with posterior margin deeply emarginated in ventral view, forming two triangular lobes. Tergite 9 oblong in lateral view, twice as wide as tergite 8. Sternite 9 (genital fork) slender, T-shaped; lateral arms not extended beyond hypogynial valve, Y-shaped; with ventral sclerite in hypogynial valve cleft. Two sclerotised, tube-like structures (perhaps spermathecal pumps) dorsal to base of lateral arms in lateral view; spermathecal receptacles and ducts not observed.

Immature stages. Unknown.

Additional material examined. Chile: Region X (Los Lagos): Camino de Penetracion @ Hwy. 7 sign, 16.xii.2013, 42°07'57.5"S 72°27'45.3"W, seep, sweeping veg., G.R. Curler (1♂, 1♀*); Camino de Penetracion @ km post 125.600, 16.xii.2013, 42°03'33.3"S 72°27'07.4"W, rock seep, G.R. Curler (1♂); Casa Pangue, Llanquihue, 12.1926, R&E Shannon, USNMENT01115811 (1♂, USNM); Ensenada, nr. Baños de Petrohué, 12.i.1985, J.A. Downes (2♂, CNC; 1♂, USNM (USNMENT01115812)); Rte. 215, 12.xii.2016, 40°40'32.4"S 72°17'35.6"W, elev. 252 m, trickle falls, J.K. Moulton & R.J. Pivar (1♂); Rte. U-99, 10.xii.2016, 41°08'09.6"S 72°35'43.3"W, elev. 81 m, roadside falls, J.K. Moulton & R.J. Pivar (15♂; 4♀*); Rte. U-99, 10.xii.2016, 41°08'28.2"S 72°35'16.8"W, elev. 101 m, roadside seeps/creek, J.K. Moulton & R.J. Pivar (11♂, 1♀*); Rte. V-69, 12.xii.2016, 41°26'37.7"S 72°17'42.2"W, elev. 34 m, cascading stream, J.K. Moulton & R.J. Pivar (1♂); Rte. V-69, Puente El Salto, 12.xii.2016, 41°31'29.2"S 72°17'14.6"W, elev. 37 m, splash zone above falls, J.K. Moulton & R.J. Pivar (2♂); Region XIV (Los Ríos): Antilhue, Rte. T-35, 9.xii.2016, 39°49'09.8"S 72°56'22.6"W, elev. 40 m, roadside creek, J.K. Moulton & R.J. Pivar (3♂); Valdivia, Los Ulmos Rd., 15.i.1985, J.A. Downes (5♂, CNC).

Distribution. Known from both the Andes and Chilean Coastal Range in southern Chile (Fig. 24A).

Bionomics. This species appears restricted predominantly to low elevations in the Valdivian temperate rain forest.

Niphta mapuche Pivar, sp. nov.

http://zoobank.org/DD325D3C-7AAF-4FB5-9060-42CBCD462511

Figs 2D, 3D, 4D, 13E, F, 20C, D, 24A

Type material. ***Holotype*:** ♂, glued to point with abdomen in glycerine microvial pinned beneath, labelled: "Chile: Region IX (Araucanía)/ Rte. S-365, 14.xii.2016/ 38°46'27.0"S 71°36'51.0"W/ elev. 809 m, creek/small falls/ J.K. Moulton & R.J. Pivar"; "HOLOTYPE/ *Niphta*/ *mapuche*/ Pivar [red label]" (CNC). ***Allotype*:** ♀, same label data as holotype (CNC). ***Paratypes*:** Chile: Region VIII (Bío Bío): Rte. Q-61, 8.xii.2016, 37°48'22.8"S 71°40'46.6"W, elev. 379 m, cascading creek, J.K. Moulton & R.J. Pivar (2♂, 1♀*); Rte. Q-689, 8.xii.2016, 37°54'55.6"S 71°35'43.2"W, elev. 552 m, cascading creek, J.K. Moulton & R.J. Pivar (2♀*); Region IX (Araucanía): nr. Tolhuaca N.P., Rte. 71, 15.xii.2016, 38°13'23.5"S 71°49'07.8"W, elev. 934 m, stream, J.K. Moulton & R.J. Pivar (1♂); Rte. S-365, 14.xii.2016, 38°46'27.0"S 71°36'51.0"W, elev. 809 m, creek/small falls, J.K. Moulton & R.J. Pivar (4♂, 1♀*); Salto El Léon (spray zone at base), 2.xii.2013, 39°25'10.9"S 71°45'42.3"W, elev. 760 m, madicolous habitats, G.W. Courtney (CH13080) (3♀*, 4 pupal exuviae); same label data as previous except, 3.x.2007 (8 larvae); upper Rio Malleco @ Rd Xing, 25.xii.2013, 38°13'20.0"S 71°44'40.8"W, elev. 1040 m, from riffle rocks, G.W. Courtney (CH13–030) (7 larvae*); Region X (Los Lagos): Parque Nacional Alerce Andino, culvert falls above Sargazo GS, 1.xii.2008, 41°30'31.8"S 72°37'13.8"W, elev. 335 m, G.W. Courtney (CH08–23) (4 larvae*); Region XIV (Los Ríos): Estero Altura Pazas on Cosh-Liq Rd., 1.xii.2013, 39°44'43.8"S 71°56'22.14"W, elev. 385 m, on wetted rock, G.W. Courtney (CH13–079) (6 larvae*); Rte. T-29, Puente Altura Pazas, 14.xii.2016, 39°44'43.6"S 71°56'24.4"W, elev. 363 m, cascading creek, J.K. Moulton & R.J. Pivar (2♂, 2♀*).

Recognition. This species is recognised by the paramere being mostly hidden within the epandrium in lateral view, giving the paramere a two-filament appearance. The gonostylus is less recurved than that of *N. downesi*.

Description. The descriptions of *N. mapuche* differ from that of *N. acus* in the following regards:

Male. $n = 10$.

Length 1.4–2.5 mm.

Colouration (Fig. 4D). Head dull, black; pronotum and postpronotum brown; prescutum and mesoscutum shiny, blackish brown, pleura brown; katepisternum brown with blackish brown margins; base of halter light brown turning black medially, knob creamy yellow; legs ranging from pale brown to blackish brown; abdomen blackish brown, posterior margins creamy; terminalia variable in colour from blackish brown to grey.

Head. Flagellomeres 1–3 subquadrate, 1 expanded, 2 × as wide as next segment, as long as 2 and 3 combined.

Abdomen. Abdominal sternite 2 with few setae restricted to laterad on posterior third; sternites 3–7 with setae restricted to lateral margins and middle third; sternite 8 with three or fewer setae medially and on lateral margins.

Terminalia (Figs 2D, 3D). Gonocoxite subquadrate; posterior inner margin slightly produced into pointed projection, outer margin notched. Gonostylus short, less than half-length of cercus, strongly curved lateroventrally throughout; apex pointed; outer margin bearing laterally directed setae. Parameres distally fused, widest at point of fusion; not reaching posterior margin of epandrium; dividing into two pointed, filamentous projections medially; shorter ventral filament not extended beyond gonostyli, apex directed posteriorly; longer dorsal filament not extended to posterior margin of epandrium, at most slightly beyond base of cercus, apex projected slightly posterodorsally. Gonocoxal plate broad, well sclerotised, tongue-like plate extending anteroventrally; gonocoxal apodeme with secondary structure comprising single short, indistinct filament, running along interior of paramere, ending before apical margin of gonostylus. Cercus trapezoidal.

Female. *n* = 10.

Similar to male except as follows: *Terminalia* (Fig. 13E, F). Hypogynial valve not projected beyond tergite 9; posterior margin deeply emarginated in ventral view, forming two triangular lobes; lateral margin sclerotised at base. Tergite 9 triangular in lateral view. Sternite 9 (genital fork) slender, Y-shaped; lateral arms not extended beyond hypogynial valve, fused distally forming rounded posterior margin; lightly sclerotised ventral plate at base of hypogynial valve. Two sclerotised, tube-like structures dorsal to genital fork, spermathecal pumps perhaps; spermathecal receptacles and ducts not observed.

Pupa. *n* = 4 (not figured due to condition of specimens).

Length 3.5–4.0 mm.

Head. Setae not observed.

Thorax. Hindleg concealed behind wing sheath, only apex visible between apex of foreleg and wing sheath, slightly shorter than foreleg, but longer than wing sheath. Wing sheaths with large tubercle at base, setae not visible.

Abdomen. Setae not visible on tergites 1–8.

Larva. *n* = 17.

Length of final instar 6.3–6.7 mm.

Colouration. Head capsule variable, ranging from light brown to black. Body mottled brown and grey, possibly pale brown to creamy; cream coloured ventrally.

Head capsule (Fig. 20C, D). Tubercles below and beside eye bifurcate; two tubercles between ecdysial line, upper tubercle bi- or trifurcate.

Abdomen. Tergites 1–7 with lateral adhesive structure swelling bearing five setae, two lateral, three basal.

Additional material examined. Known only from the type series.

Distribution. Known from the southern Andes of Chile (Fig. 24A).

Etymology. This species is named after the Mapuche (*mapu*, land, *che*, people) indigenous peoples, who since ~ 500 B.C., have inhabited the regions of southern Chile, where *N. mapuche* is known.

Bionomics. This is a mid-elevation species. Adults were observed flying around and resting on leaf tips, roughly two meters from the nearest splash zones. Larvae and pupae have ventral adhesive structures and were collected only from rocky substrates at the margin of a waterfall.

The *N. nudipennis* group

Niphta bifurcata Pivar and Moulton, sp. nov.

http://zoobank.org/2C174B79-C941-4878-9A41-AC43414033FC

Figs 6A, 8A, 9A, 10A, 11A, 12A, 24B

Type material. ***Holotype*:** ♂, glued to point with abdomen in glycerine microvial pinned beneath, labelled: "Chile: Region XIV (Los Ríos)/ Antilhue, Rte. T-35, 9.xii.2016/ 39°49'09.8"S 72°56'22.6"W/ elev. 40 m, roadside creek,/ J.K. Moulton & R.J. Pivar"; "HOLOTYPE/ *Niphta*/ *bifurcata*/ Pivar & Moulton [red label]" (CNC). ***Allotype*:** ♀*, same data as holotype (CNC). ***Paratypes*:** Chile: Region XIV (Los Ríos): same data as holotype (2♂).

Recognition. This species is recognised by the bifurcate, posterior apex of the cheliform gonostylus and the bifurcate anterior projection of the gonocoxite. It is darker in colouration compared to the closely related *N. courtneyi*.

Description. Male. *n* = 3.

Length 1.7–1.9 mm.

Colouration (Figs 9A, 10A). Head dull, dark brown; pronotum and postpronotum dark brown; postpronotal lobe and lateral margins of prescutum light brown; scutum shiny with three distinct dark brown stripes, pleura light brown; postscutum brown; scutellum shiny, light brown; mediotergite shiny, anterior half light brown, posterior half brown; katepisternum mainly dark brown, light brown near coxa 1; paratergite brown; remaining pteropleuron mainly brown with dispersed light brown and black markings; base of halter pale brown, knob pale yellow; legs pale brown, apex of tarsi darker; abdomen brown; terminalia pale brown.

Head. Eyes above antennae broadly joined, with small triangular frons visible above antennae; frons with two strong setae. Flagellomeres 1–3 subquadrate, 1 expanded, twice as wide as next segment, shorter in length than 2 and 3 combined; flagellomeres 4–10 cylindrical, becoming progressively thinner and elongate. Vertex with black setae of uniform length, with longer, black orbital setae.

Thorax. Mesoscutum with prominent antealar ridge, bearing three setae, middle seta most pronounced. Scutum clothed dorsally in short, black setulae; notopleural, supra-alar and postsutural setae long, black. Pteropleuron bare. All legs with tarsi simple.

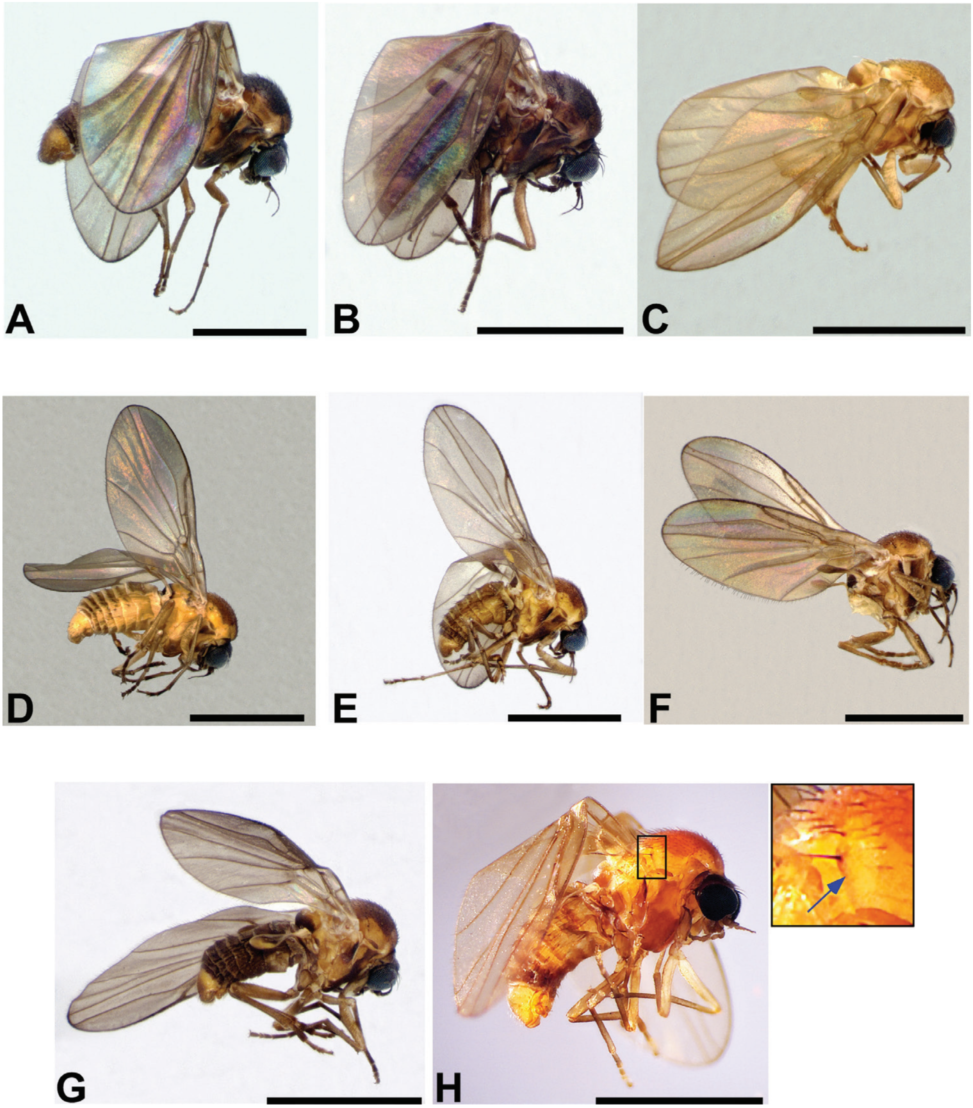


Figure 9. Adult lateral habitus micrographs of the *Niphta nudipennis* group **A** *N. bifurcata* sp. nov. (♂) **B** *N. brunnea* sp. nov. (♂) **C** *N. courtneyi* sp. nov. (♀), abdomen dissected **D** *N. daniellae* sp. nov. (♂) **E** *N. eurydactyla* sp. nov. (♂) **F** *N. bispinosa* sp. nov. (♂), abdomen dissected **G** *N. nudipennis* (♂) **H** *N. courtneyi* sp. nov. (♂), inset with arrow indicating antealar ridge. Scale bars: 1.0 mm.

Wing. Wing length: 2.1–2.4 mm. Infuscate throughout, apex somewhat narrowed; C fringed in small setulae, with widely spaced microtrichia; posterior wing margin with closely spaced fringe of microtrichia; Sc incomplete; R_1 and $R_1(+R_{2+3})$ with three weakenings or depigmented gaps, first slightly beyond R_{2+3}, second and third closely approximated, near C; microtrichia of $R_1(+R_{2+3})$ confined to base near humeral cross-vein, remaining veins bare; R flexed into cell br; R_{2+3} distinct, situated in basal third

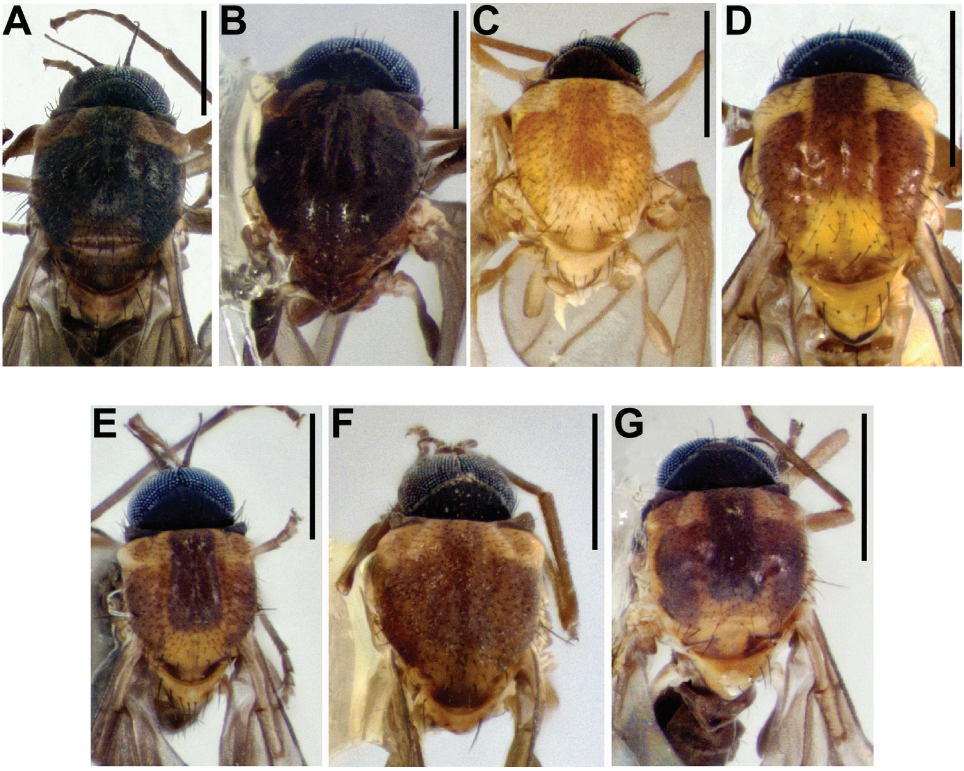


Figure 10. Adult dorsal habitus micrographs of the *Niphta nudipennis* group **A** *N. bifurcata* sp. nov. (♂) **B** *N. brunnea* sp. nov. (♂) **C** *N. courtneyi* sp. nov. (♀), abdomen dissected **D** *N. daniellae* sp. nov. (♂) **E** *N. eurydactyla* sp. nov. (♂) **F** *N. bispinosa* sp. nov. (♂), abdomen dissected **G** *N. nudipennis* (♂) Scale bars: 1.0 mm.

of $R_1(+R_{2+3})$; bend in R_{4+5} strong; R_{4+5} and M_1 running parallel toward margin; M_1 straight; M_2 with gentle bend in apical third; M_4 with slight bend.

Abdomen. Abdominal sternite 1 narrow, spectacle-shaped; sternite 2 reduced to slender median sclerite, a few setae restricted to posterior third; sternites 3–7 rectangular, lightly sclerotised, setae restricted to posterior half; sternite 8 strongly reduced, anterior margin well sclerotised, arched slightly into preceding segment, a few setae restricted to laterad.

Terminalia (Figs 6A, 8A). Epandrium quadrate in ventral view, posterior margin rounded, with medial cleft; long, extended beyond gonostyli; without lobes or projections. Gonocoxites oblong, longer than wide; anterior margin rounded, somewhat expanded dorsally behind gonocoxal plate, not closely approximated; with two spine-like projections; anterior projection wide, bifurcate; posterior projection long, slender, slightly sinuous, tapered to single apex, nearly twice as long as anterior projection; inner margin with numerous long, thin setae. Gonostylus cheliform, dorsoventrally flattened anteriorly, swollen posteriorly; anterior apex with a few setae; posterior apex bifurcate,

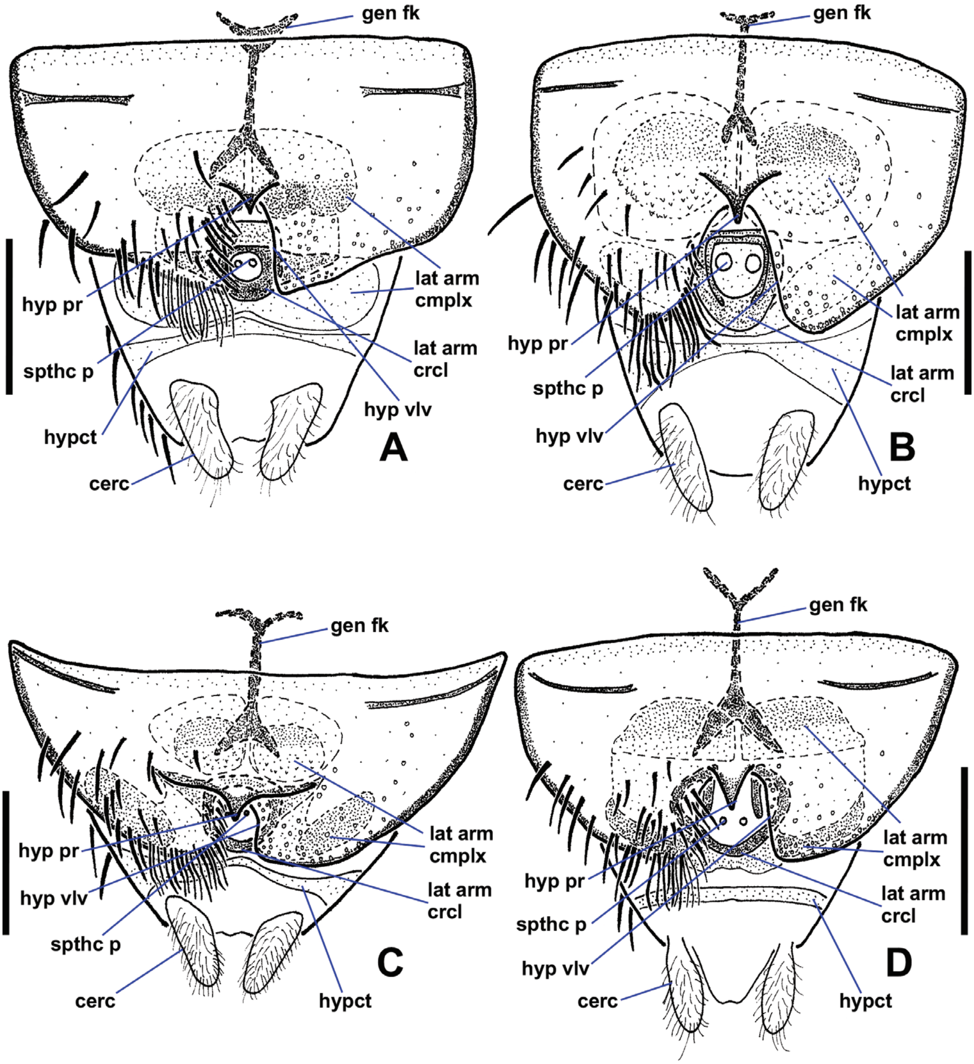


Figure 11. Ventral views of female *Niphta nudipennis* group terminalia **A** *N. bifurcata* sp. nov. **B** *N. courtneyi* sp. nov. **C** *N. bispinosa* sp. nov. **D** *N. nudipennis*. Abbreviations: cerc, cercus; gen fk, genital fork; hyp pr, hypogynial protuberance; hyp vlv, hypogynial valve; hypct, hypoproct; lat arm crcl, lateral arm circle; lat arm cmplx, lateral arm complex; spthc p, spermathecal pump. Scale bars: 0.1 mm.

setose. Parameres medially fused, attached basally to arms of gonocoxal plate; divided distally into dorsal parameral apodeme and ventral arm; ventral arm projected anteroventrally toward gonocoxal plate, strongly curved anteriorly, sickle-shaped, surface textured with tiny bumps, except for smooth apex; ventral arm extends posteroventrally presumably to aid in copulation; when retracted, rests ventrally between dorsal arm of gonocoxal plate and dorsal to anterior gonocoxal projection. Gonocoxal plate broad, well sclerotised; anterior margin subquadrate, basal margin cleft; pair of dorsal arms

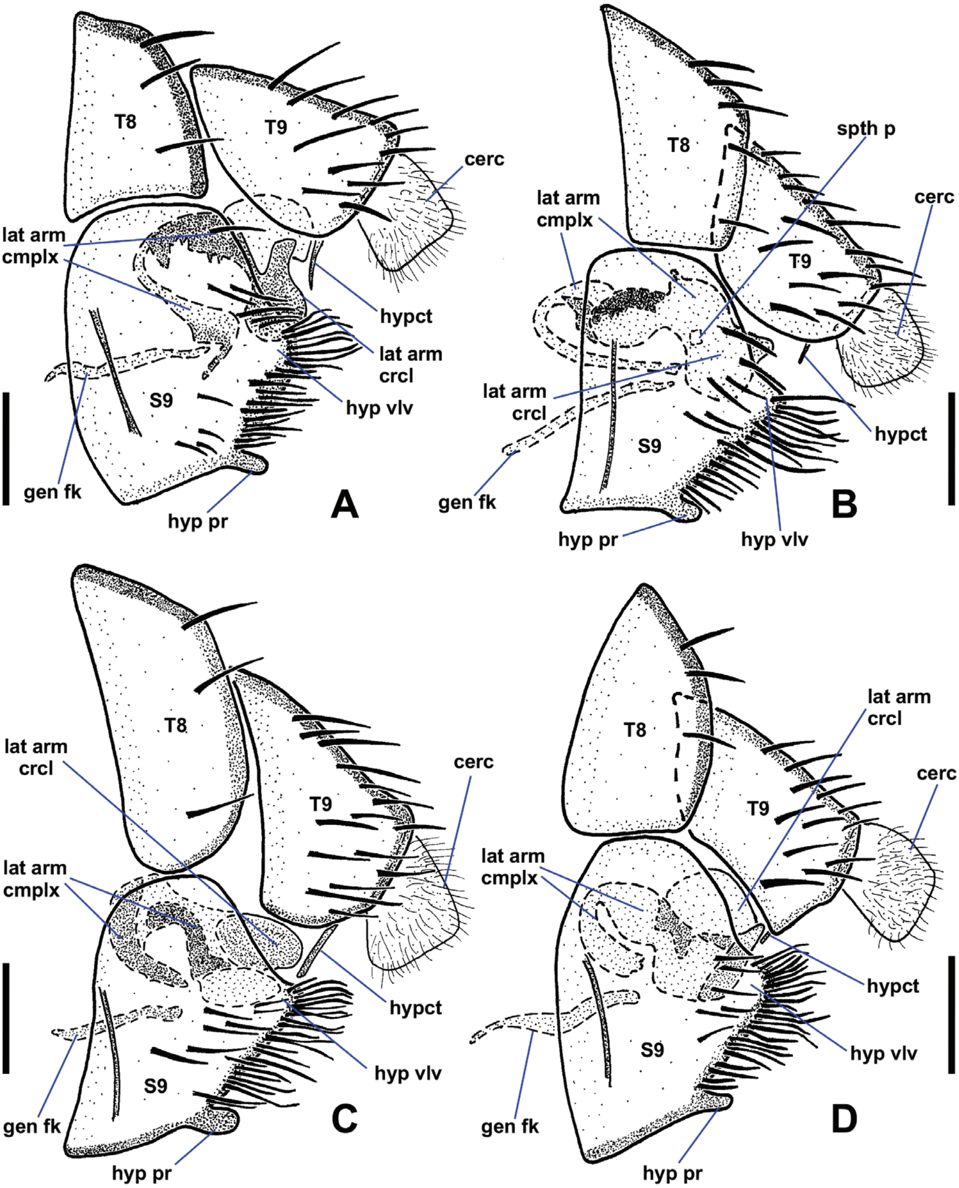


Figure 12. Lateral views of female *Niphta nudipennis* group terminalia **A** *N. bifurcata* sp. nov. **B** *N. courtneyi* sp. nov. **C** *N. bispinosa* sp. nov. **D** *N. nudipennis*. Abbreviations: cerc, cercus; gen fk, genital fork; hyp pr, hypogynial protuberance; hyp vlv, hypogynial valve; hypct, hypoproct; lat arm crcl, lateral arm circle; lat arm cmplx, lateral arm complex; S, sternite; spthc p, spermathecal pump; T, tergite. Scale bars: 0.1 mm.

connected to parameres; medial aedeagal guide projected ventrally between posterior margins of gonocoxites, well sclerotised, comprising two parts: anterior Y-shaped structure with five finger-like projections protruded from posterior margin and dorsal triangular plate. Cercus ovoid, only slightly visible in lateral view; projected anteroventrally; situated within epandrial indentation.

Female. $n = 1$.

Similar to male except as follows: *Abdomen*. Tergite 9 noticeably more sclerotised than preceding tergites; sternite 8 well sclerotised, with distinct blunt projection at base of hypogynial valve. *Terminalia* (Figs 11A, 12A). Hypogynial valve not projected beyond tergite 9; posterior margin deeply cleft in ventral view, forming two triangular lobes; lobes densely setose, with both stout, thickened setae and thinner, long setae with slight apical bend; hypogynial protuberance between valves. Tergite 9 subquadrate in lateral view, 1.5 × as wide as tergite 8, lacking lateral projections. Sternite 9 (genital fork) slender, Y-shaped at both ends; lateral arms forming complex of highly modified structures: medial heavily sclerotised circular opening, dorsal to posterior cleft of hypogynial valve, with pair of lateral sclerotised triangular expansions; triangular expansions expanded dorsally into pair of circular plates, those further expanded anteriorly into pair of heavily sclerotised plates, strongly recurved posteroventrally toward circular opening, remaining dorsal to genital fork; dorsal surface of recurved plates with tiny grooves and indentations. Hypoproct lightly sclerotised, narrow. Cercus quadrate, projected posteroventrally; bearing numerous setae. Spermathecae not observed; two spermathecal ducts visible in centre of lateral arm circle.

Immature stages. Unknown.

Additional material examined. Known only from the type series.

Distribution. Known only from the type locality in the Chilean Coastal Range (Fig. 24B).

Etymology. *Niphta bifurcata* is named in reference to the posterior apex of the gonostylus and the anterior projection of the gonocoxite, both of which are bifurcate.

Niphta bispinosa **Pivar and Sinclair, sp. nov.**

http://zoobank.org/9A9B5605-3AD0-4019-8019-BF8C47828DA5
Figs 6C, 8C, 9F, 10F, 11C, 12C, 24B, 27B, D

Type material. ***Holotype***: ♂, glued to point with abdomen in glycerine microvial pinned beneath, labelled: "Chile: Region VII (Maule)/ Los Queñes, Rte. J-25,/ 6.xii.2016, 34°59'46.7"S 70°49'19.2"W/ elev. 679 m, cascading creek,/ J.K. Moulton & R.J. Pivar"; "HOLOTYPE/ *Niphta/ bispinosa/* Pivar & Sinclair [red label]" (CNC). ***Allotype***: ♀*, same data as holotype (CNC). ***Paratype***: Chile: Region VII (Maule): Los Queñes, Rte. J-25, 6.xii.2016, 34°59'48.8"S 70°48'37.0"W, elev. 684 m, seep, J.K. Moulton & R.J. Pivar (1♀*).

Recognition. This species is recognised by the cheliform gonostylus with non-bifurcate apices and the gonocoxite with two projections, the anterior one long and bifurcate, the posterior one small, tooth-like. It is lighter in colouration than the closely related *N. brunnea*.

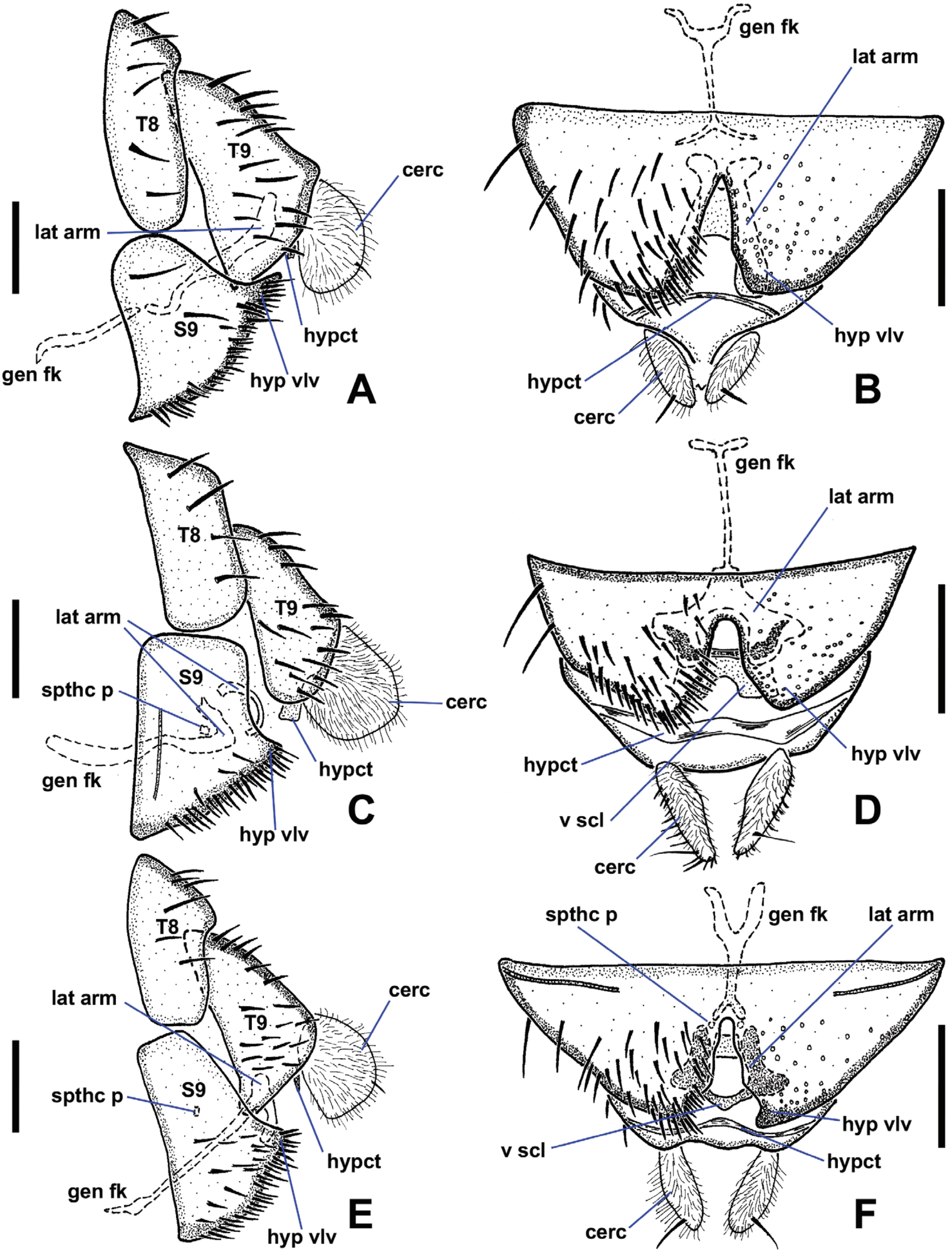


Figure 13. Female terminalia of the *Niphta halteralis* group **A** lateral, *N. acus* sp. nov. **B** ventral, *N. acus* sp. nov. **C** lateral, *N. halteralis* **D** ventral, *N. halteralis* **E** lateral, *N. mapuche* sp. nov. **F** ventral, *N. mapuche* sp. nov. Abbreviations: cerc, cercus; gen fk, genital fork; hyp vlv, hypogynial valve; hypct, hypoproct; lat arm, lateral arm; S, sternite; spthc p, spermathecal pump; T, tergite; v scl, ventral sclerite. Scale bars: 0.1 mm.

Description. The descriptions of *N. bispinosa* differ from that of *N. bifurcata* in the following regards:

Male. *n* = 1.

Length 1.9–2.4 mm.

Colouration (Figs 9F, 10F). Pronotum and postpronotum brown; postpronotal lobe and lateral margins of prescutum pale yellow; remaining scutum shiny, brown, pleura yellow; postscutum with medial brown spot above scutoscutellar suture, encircled by yellowish brown margin; scutellum shiny, yellow; mediotergite shiny, dark brown except anterior margin yellow; katepisternum mainly brown, lighter near anterior spiracle; remaining pteropleuron mainly pale yellow with dispersed brown markings; base of halter yellow, distal half of stalk and knob grey; legs pale yellow, apex of tarsi darker; terminalia light brown.

Head. Frons with three strong setae. Flagellomere 1 expanded, 1.5 × as wide as next segment, equal in length to 2 and 3 combined.

Wing. Wing length: 2.0–2.4 mm. Lightly infuscate throughout; bend in R_{4+5} gentle.

Terminalia (Figs 6C, 8C). Posterior margin of epandrium rounded, with narrow medial cleft. Gonocoxites oblong, wider than long; anterior margin rounded, somewhat expanded dorsally behind gonocoxal plate, not closely approximated; with two spine-like projections; anterior projection bifurcate, projected posteriorly, 3 × longer than posterior projection; posterior projection short, tooth-like; margin around gonostylus setose. Gonostylus cheliform, dorsoventrally flattened, margins concave creating bowl-like appearance; anterior apex with a few indistinct setae, posterior apex with strong setae. Parameres medially fused, attached basally to arms of gonocoxal plate; divided distally into dorsal parameral apodeme and ventral arm; ventral arm projected anteroventrally toward gonocoxal plate, strongly curved anteriorly, blade-like, ventral margin serrate; ventral arm extended posteroventrally presumably to aid in copulation; when retracted, rests ventrally between dorsal arm of gonocoxal plate and inner margin of gonocoxite, apex reaching base of anterior gonocoxal projection. Gonocoxal plate broad, well sclerotised; anterior margin subquadrate, basal margin cleft; pair of dorsal arms connected to parameres; medial aedeagal guide projected ventrally between gonostyli, well sclerotised, comprising two parts: anterior Y-shaped structure and posterior triangular plate. Cercus prominent, ovoid.

Female. *n* = 2.

Similar to male except as follows: *Terminalia* (Figs 11C, 12C). Posterior margin of hypogynial valve deeply cleft in ventral view, forming two quadrate lobes. Tergite 9 twice as wide as tergite 8. Sternite 9 (genital fork) slender, Y-shaped at both ends; lateral arms forming complex of highly modified structures: medial heavily sclerotised circular opening, dorsal to posterior opening of hypogynial valve, with pair of lateral sclerotised triangular expansions. Spermathecae not observed.

Immature stages. Unknown.

Additional material examined. Known only from the type series.

Distribution. Known only from the type locality in central Chile (Fig. 24B).

Etymology. *Niphta bispinosa* is named in reference to the two projections from the gonocoxite.

Niphta brunnea Pivar, sp. nov.

http://zoobank.org/ED8B78EE-F799-4B34-B465-E47C578BC679
Figs 6D, 8D, 9B, 10B, 14A, 15A, 16A, 17A, 18A, 19A, 21A, B, 22, 23, 24B, 26A–C

Type material. ***Holotype*:** ♂, glued to point with abdomen in glycerine microvial pinned beneath, labelled: "Chile: Region IX (Araucanía)/ Rte. 71, 15.xii.2016/ 38°14'20.6"S 71°53'46.6"W,/ elev. 953 m, roadside seeps,/ J.K. Moulton & R.J. Pivar"; "HOLOTYPE/ *Niphta*/ *brunnea*/ Pivar [red label]" (CNC). ***Paratypes*:** Chile: Region VIII (Bío Bío): Rte. Q-61, 8.xii.2016, 37°49'14.2"S 71°40'34.1"W, elev. 366 m, creek, J.K. Moulton & R.J. Pivar (1♂); Rte. Q-61, Estero Agua Blanca 8.xii.2016, 37°46'30.8"S 71°42'03.9"W, elev. 552 m, vegetation near splash zones, J.K. Moulton & R.J. Pivar (1♂); Region IX (Araucanía): same data as holotype (3♂); same data as holotype except, larvae/pupae on foliage in splash zone (6 larvae*, 5 pupae, 3 pupal exuviae).

Recognition. This species is recognised by the cheliform gonostylus bearing non-bifurcate apices and the gonocoxite with three projections: two that are nearly equal in size and the third, much smaller and inconspicuous, situated at the base of the anterior one. It is darker in colouration compared to the closely related *N. bispinosa*, and the darkest of the *N. nudipennis* group.

Description. The descriptions of *N. brunnea* differ from that of *N. bifurcata* in the following regards:

Male. *n* = 5.

Length 1.6–1.9 mm.

Colouration (Figs 9B, 10B). Pronotum and postpronotum brown; remaining scutum shiny, brown, pleura light brown; scutellum shiny, brown; mediotergite shiny, anterior half light brown, posterior half dark brown; katepisternum mainly brown, lighter near anterior spiracle; remaining pteropleuron mainly brown with dispersed markings of dark/light brown; base of halter creamy, distal half of stalk and knob light brown; abdomen brown; terminalia light brown.

Head. Flagellomere 1 expanded, 1.5 × as wide as next segment, shorter in length than 2 and 3 combined.

Wing. Wing length: 1.9–2.2 mm.

Terminalia (Figs 6D, 8D). Epandrium quadrate in ventral view, posterior margin rounded, with narrow medial cleft; long, extended beyond gonostyli; without lobes or projections. Gonocoxites oblong, longer than wide; anterior margin rounded, somewhat expanded dorsally, not closely approximated; with three spine-like projections; large anterior projection nearly equal in length to posterior projection, gradually tapered toward apex; smaller anterior projection positioned somewhat anterior to large tooth, may be small and inconspicuous in some specimens; posterior projection

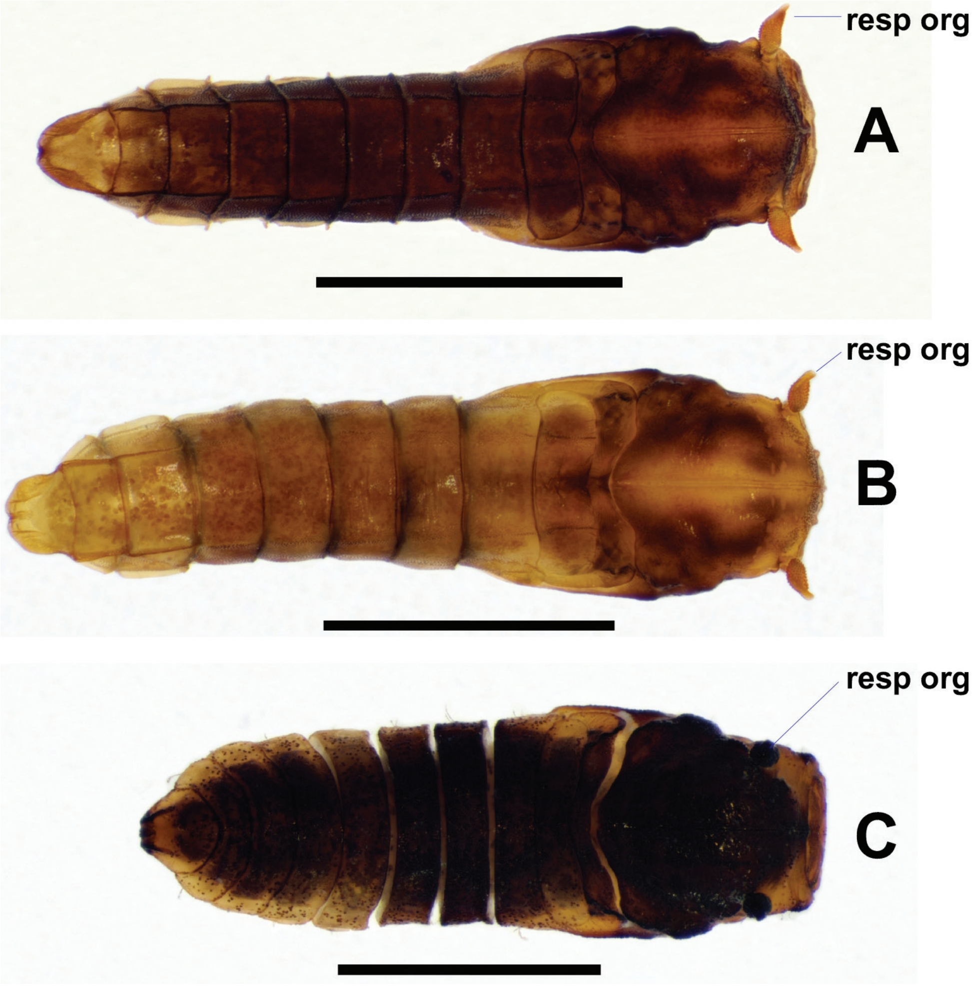


Figure 14. Dorsal views of *Niphta* pupae **A** *N. brunnea* sp. nov. **B** *N. nudipennis* **C** *N. acus* sp. nov. Abbreviations: resp org, respiratory organ. Scale bars: 1.0 mm.

strongly tapered toward apex, some specimens with second basal tooth on outer margin of projection; margin around anterior projection with long, thin setae. Gonostylus cheliform, dorsoventrally flattened, margins concave creating bowl-like appearance; anterior apex with a few indistinct setae, posterior margin with strong setae. Parameres medially fused, attached basally to arms of gonocoxal plate; divided distally into dorsal parameral apodeme and ventral arm; ventral arm projected anteroventrally toward gonocoxal plate, knife-shaped, ventral margin serrate; when retracted, resting ventrally between dorsal arm of gonocoxal plate and inner margin of gonocoxite, apex reaching base of anterior gonocoxal projection. Gonocoxal plate broad, well sclerotised; anterior margin triangular, basal margin cleft; pair of dorsal arms connect to parameres; medial

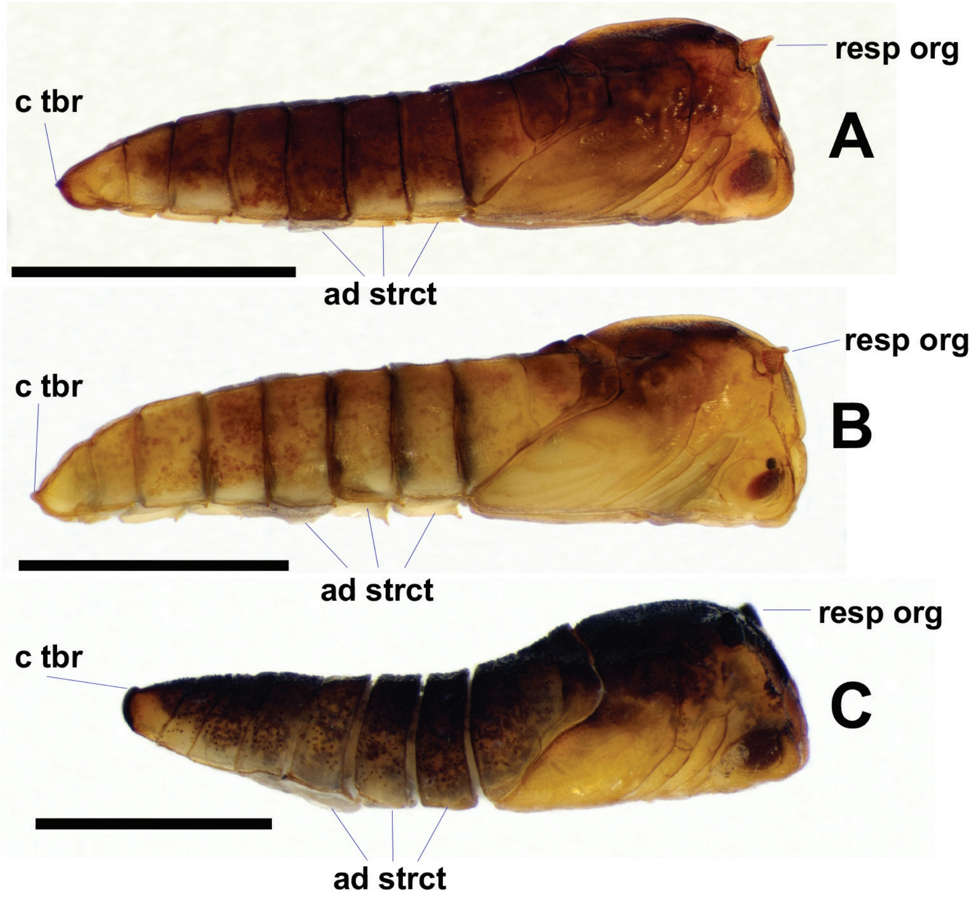


Figure 15. Lateral views of *Niphta* pupae **A** *N. brunnea* sp. nov. **B** *N. nudipennis* **C** *N. acus* sp. nov. Abbreviations: ad strct, adhesive structure; c tbr, caudal tubercle; resp org, respiratory organ. Scale bars: 1.0 mm.

aedeagal guide projected ventrally between gonostyli, well sclerotised, consisting of two parts, anterior structure with five projections and posterior rounded plate bearing minute setulae. Cercus ovoid, only slightly visible in lateral view; projected anteroventrally; situated within epandrial indentation.

Female. Unknown.

Pupa. *n* = 6 (Figs 14A, 15A, 16A, 22).

Length 2.7–2.9 mm.

Colouration. Brown; sometimes with black spot above eyes in developing adult.

Head. Maxillary sheath short, posteromedially directed, gently tapered toward truncate apex, apices of palpi separated medially; devoid of tubercles and setae.

Thorax. 1.5 × wider than abdomen at widest point. Foreleg sheath projected straight and slightly beyond wing sheaths, reaching hind margin of sternite 2; anterior half of midleg visible anterior to wing sheath, then hidden behind foreleg, not projected beyond wing sheath; hindleg concealed beneath wing sheath, only small

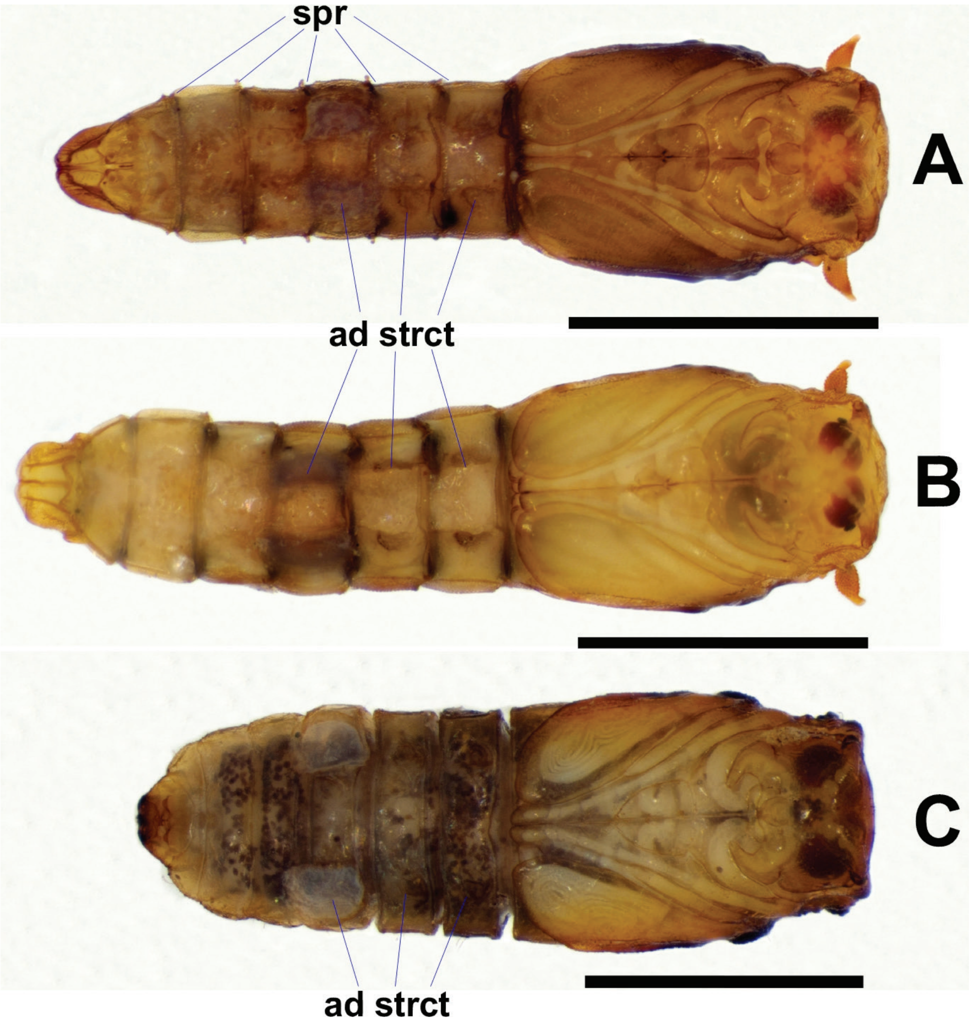


Figure 16. Ventral views of *Niphta* pupae **A** *N. brunnea* sp. nov. **B** *N. nudipennis* **C** *N. acus* sp. nov. Abbreviations: ad strct, adhesive structure; spr, spiracle. Scale bars: 1.0 mm.

triangular apex visible between apex of foreleg and wing sheath, not extended beyond wing sheath. Wing sheath extended to posterior margin of abdominal sternite 2. Respiratory organ slightly shorter than maxillary sheath, broadest subapically; ovate, slightly arched medially, tapered toward apex; spiracular openings encircling apex; stalk thin, emerging from small tubercle. Tubercle situated posterodorsally to respiratory organ, rounded, projected laterally; apex nearly touching or touching respiratory organ. Thorax devoid of setae.

Abdomen. Subcylindrical, evenly tapered toward caudal segment. Spiracles well developed, distinct on segments 3–7, projected anterodorsolaterally; all bearing minute spine-like setulae. Segment 8 with short lateral projection, less than half length of pre-

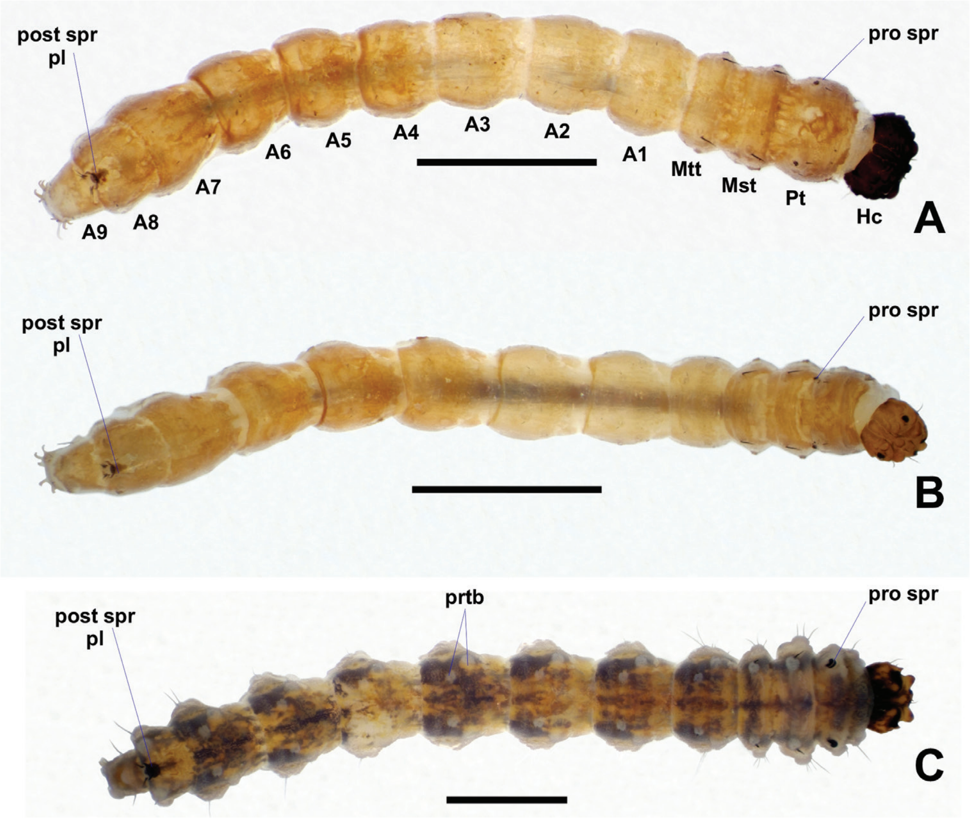


Figure 17. Dorsal views of *Niphta* larvae **A** *N. brunnea* sp. nov. **B** *N. nudipennis* **C** *N. acus* sp. nov. Abbreviations: A, abdominal segment; Hc, head capsule; Mst, mesothorax; Mtt, metathorax; Pt, prothorax; pro spr, prothoracic spiracle; prtb, protuberance; post spr pl, posterior spiracular plate. Scale bars: 1.0 mm.

ceding spiracles, projected dorsolaterally. Tergites 1–8 quadrate, devoid of setae, with pair of dorsolateral ridges and faint medial transverse groove, groove not meeting dorsolateral ridges. Tergite 9 rounded, posterior margin emarginated, laterally compressed compared to preceding segments; small, rounded projection pointing posteriorly in lateral view. Sternites 3–8 rectangular, with row of faint setulae along anterior margin, not connecting to lateral margin; lateral margins crenulate, lacking setae. Sternites 3 and 4 bearing pair of small lateral adhesive structures, sternite 5 bearing pair of large lateral adhesive structures on lateral margin. Caudal sternite triangular, with medial sclerotised groove and pair of medial rounded, posteromedially projected lobes; posterior margin with medial longitudinal ridge; without distinct caudal hooks.

Larva. *n* = 6 (Figs 17A, 18A, 19A, 21A, B, 23).

Length of final instar 4.8–5.1 mm.

Colouration. Head capsule pale brown, anterolateral margin of ecdysial line black. Body creamy brown.

Figure 18. Lateral views of *Niphta* larvae **A** *N. brunnea* sp. nov. **B** *N. nudipennis* **C** *N. acus* sp. nov. Abbreviations: anl prl, anal proleg; pro prl, prothoracic proleg. Scale bars: 1.0 mm.

Head capsule (Fig. 28A, B). Two large, circular eye spots, elevated on tubercle; antenna with three finger-like processes, elevated on largest tubercle; with five pairs of smaller tubercles outside of ecdysial lines (not including antennal and ocular tubercle); single tubercle between ecdysial lines, about same size as ocular tubercle; 15 pairs of unbranched setae; six sensory pits (13, 14, 18, 19, 20, 21), sensory pit 13 above antennal tubercle.

Thorax. Prothorax with single pair of protuberances bearing single spiracle; spiracular protuberance bearing one pair of dorsal setae anterior to spiracle and single dorsolateral seta; three mid-lateral setae, two long, one short and fine; two closely approximated setae near base of prothoracic leg (Keilin's organ). Mesothorax and metathorax with pair of small dorsolateral protuberances and pair of large lateral protuberances; mesothoracic dorsolateral protuberance bearing single thickened seta, metathoracic lateral protuberance bearing pair of closely approximated setae, anterior seta thickened and longer than posterior seta; lateral protuberance on both

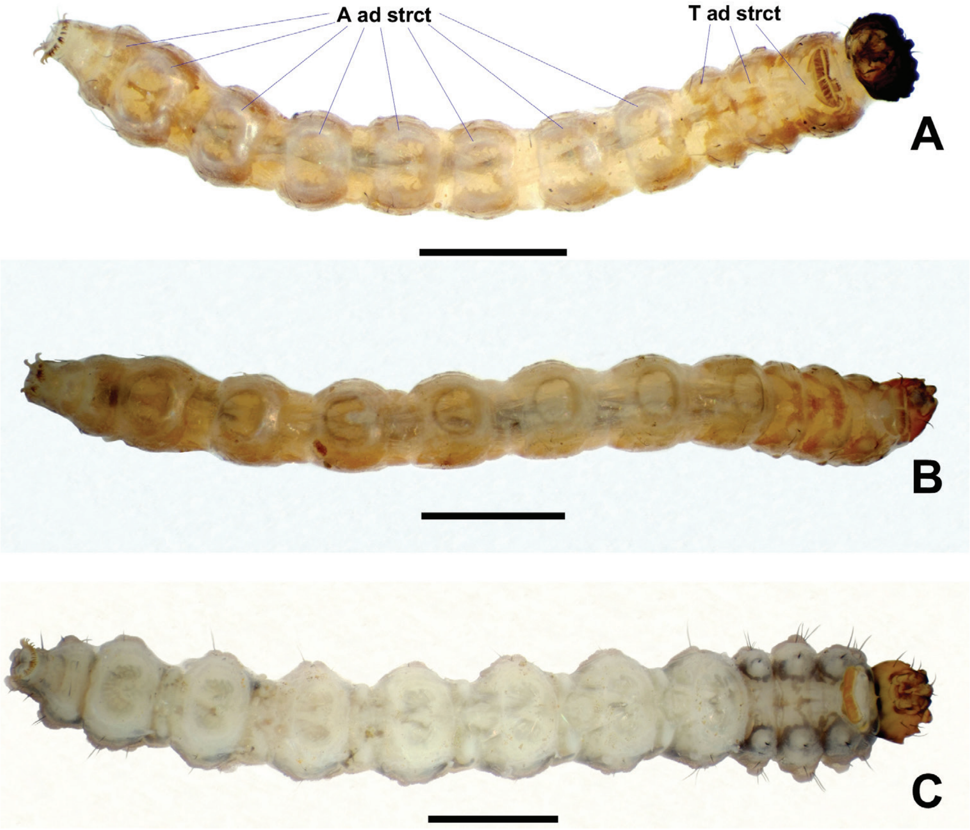


Figure 19. Ventral views of *Niphta* larvae **A** *N. brunnea* sp. nov. **B** *N. nudipennis* **C** *N. acus* sp. nov. Abbreviations: A ad strct, abdominal adhesive structure; T ad strct, thoracic adhesive structure. Scale bars: 1.0 mm.

segments bearing three setae, two short, one long; single long seta slightly ventral to lateral protuberance; one pair of mid-ventrolateral setae. Prothorax bearing proleg, posterior half with rectangular adhesive structure; meso- and metathoracic sternites with rectangular adhesive structure.

Abdomen. Sternites 1–7 modified into circular, suction cup-like adhesive structure; sternite 8 with quadrate adhesive structure; sternite 9 smooth, bearing anal proleg. Segments 1–7 lacking distinct protuberances, at most, pair of dorsolateral swellings bearing single or paired short, thin setae; single seta situated anterolaterally; lateral adhesive structure swelling bearing numerous setae, two anterolateral, two midlateral, four basalateral. Segment 8 with small dorsolateral protuberance on either side of posterior spiracular plate, each bearing pair of small setae; lateral protuberance with single seta; single short ventrolateral seta; ventral sternite bearing pair of setae. Posterior spiracular plate with sclerite encircling procerci;

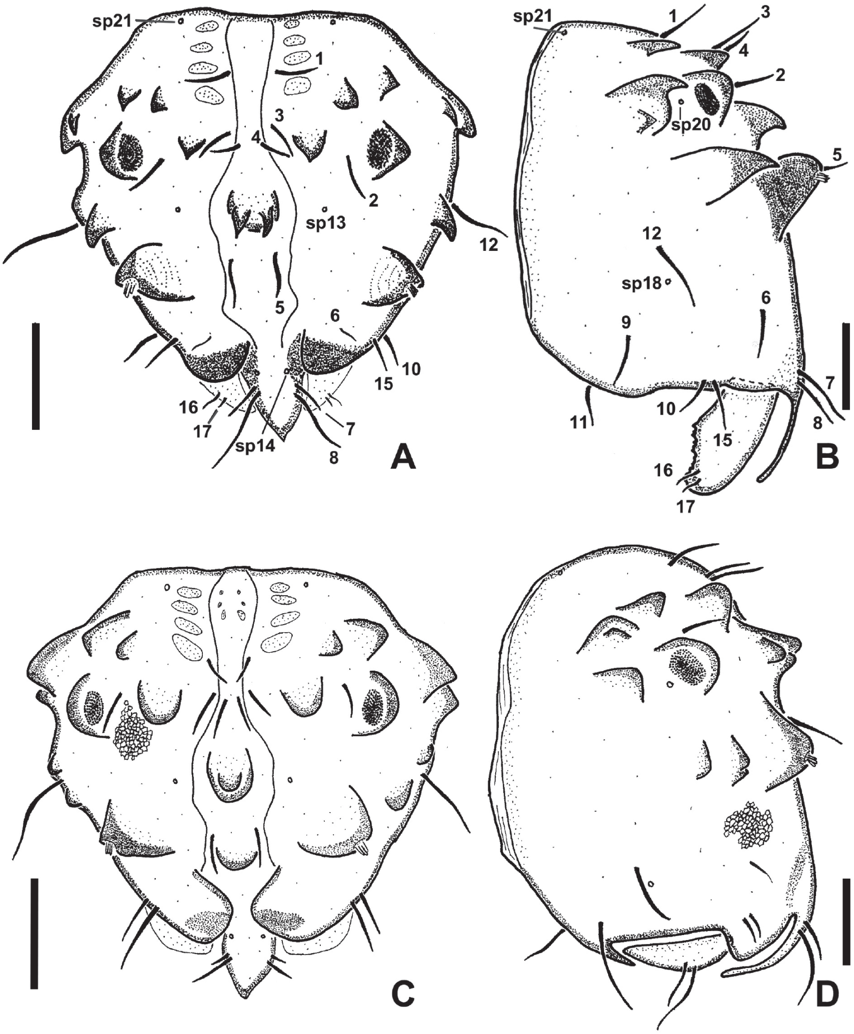


Figure 20. *Niphta halteralis* group larval head capsules with setae and sensory pits numbered **A** anterior, *N. acus* sp. nov. **B** lateral, *N. acus* sp. nov. **C** anterior, *N. mapuche* sp. nov. **D** lateral, *N. mapuche* sp. nov. Abbreviations: sp, sensory pit. Scale bars: 0.1 mm.

procercus shorter than length of spiracular plate, bearing four setae, two thick, two slender; without cone-like protuberance on either side of procerci. Terminal segment with pair of protuberances, no setae; pair of dorsolateral setae; five lateral setae; two pairs of long setae on posterior margin, above pair of anal papillae; ventral sternite lacking setae.

Additional material examined. Known only from the type series.

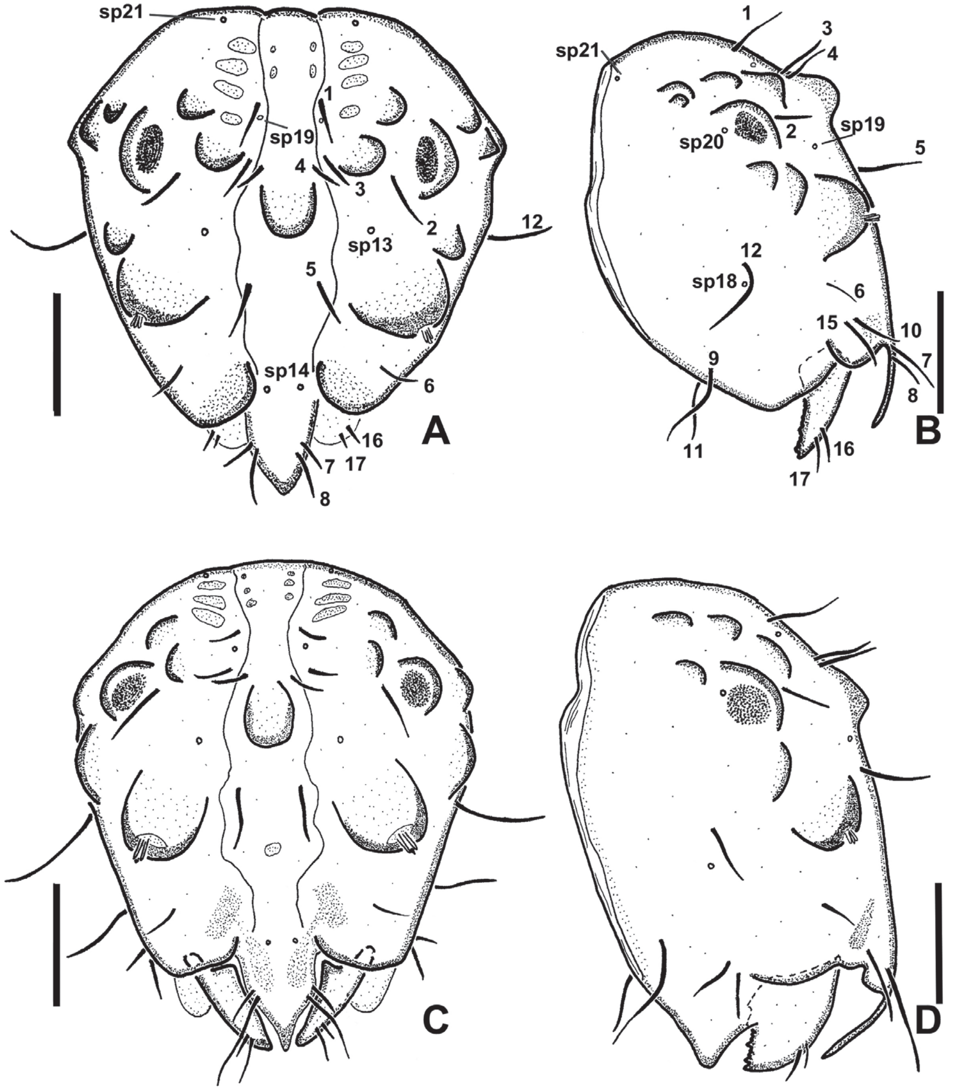


Figure 21. *Niphta nudipennis* group larval head capsules with setae and sensory pits numbered **A** anterior, *N. brunnea* sp. nov. **B** lateral, *N. brunnea* sp. nov. **C** anterior, *N. nudipennis* **D** lateral, *N. nudipennis*. Abbreviations: sp, sensory pit. Scale bars: 0.1 mm.

Distribution. Known only from two localities in the Andes of southern Chile (Fig. 24B).

Etymology. *Niphta brunnea* is from the Latin *brunneus* (brown) in allusion to its brown colouration, the darkest of the *N. nudipennis* group.

Bionomics. The larvae and pupae both possess the ventral adhesive structures seen in other known immature stages of South American *Niphta*. Immatures were

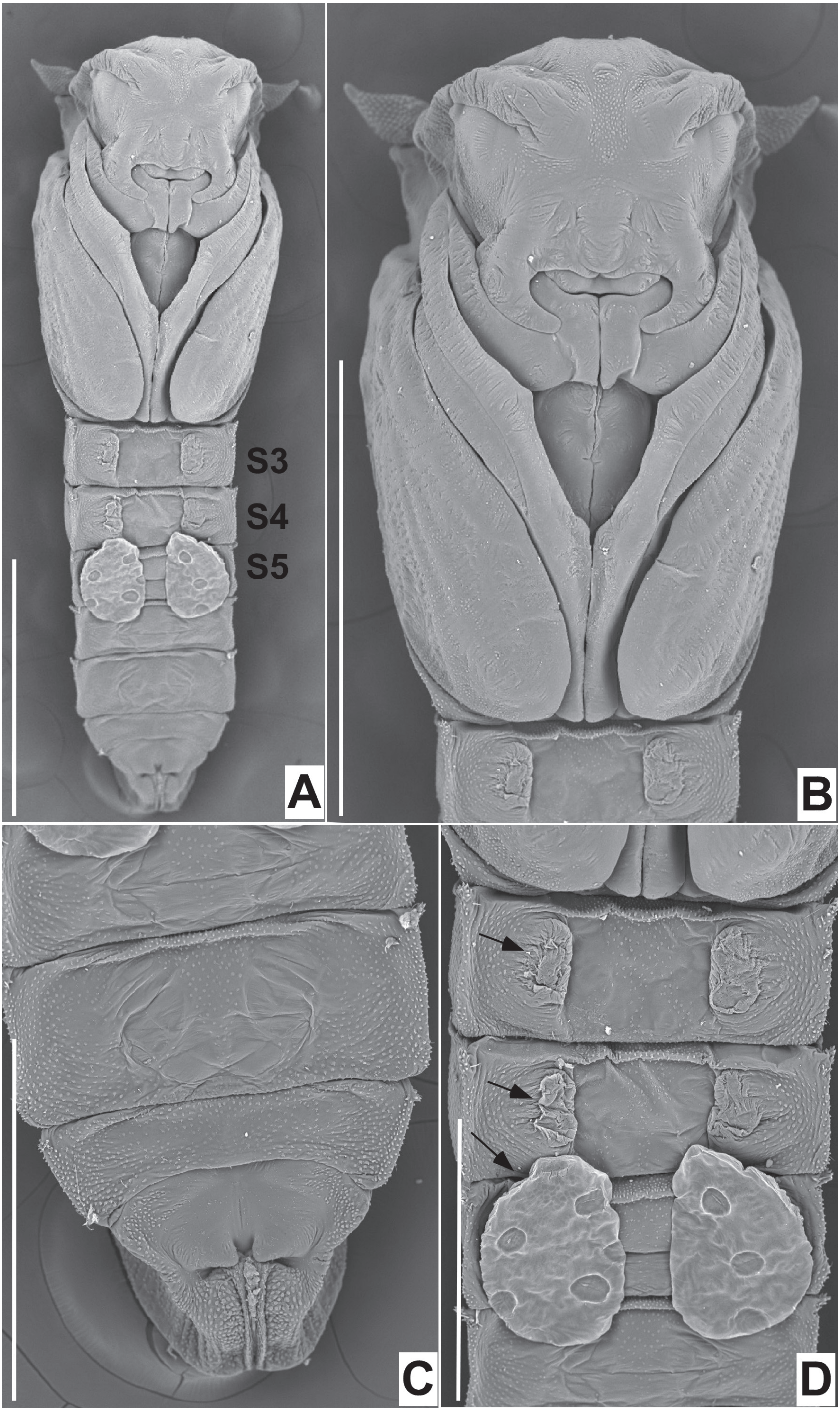


Figure 22. Scanning electron micrographs of ventral view of pupae of *Niphta brunnea* sp. nov. **A** habitus (scale bar: 1.0 mm) **B** head and thorax (scale bar: 1.0 mm) **C** posterior segments (scale bar = 0.5 mm) **D** adhesive structures (scale bar: 0.5 mm). Abbreviations: S, sternite.

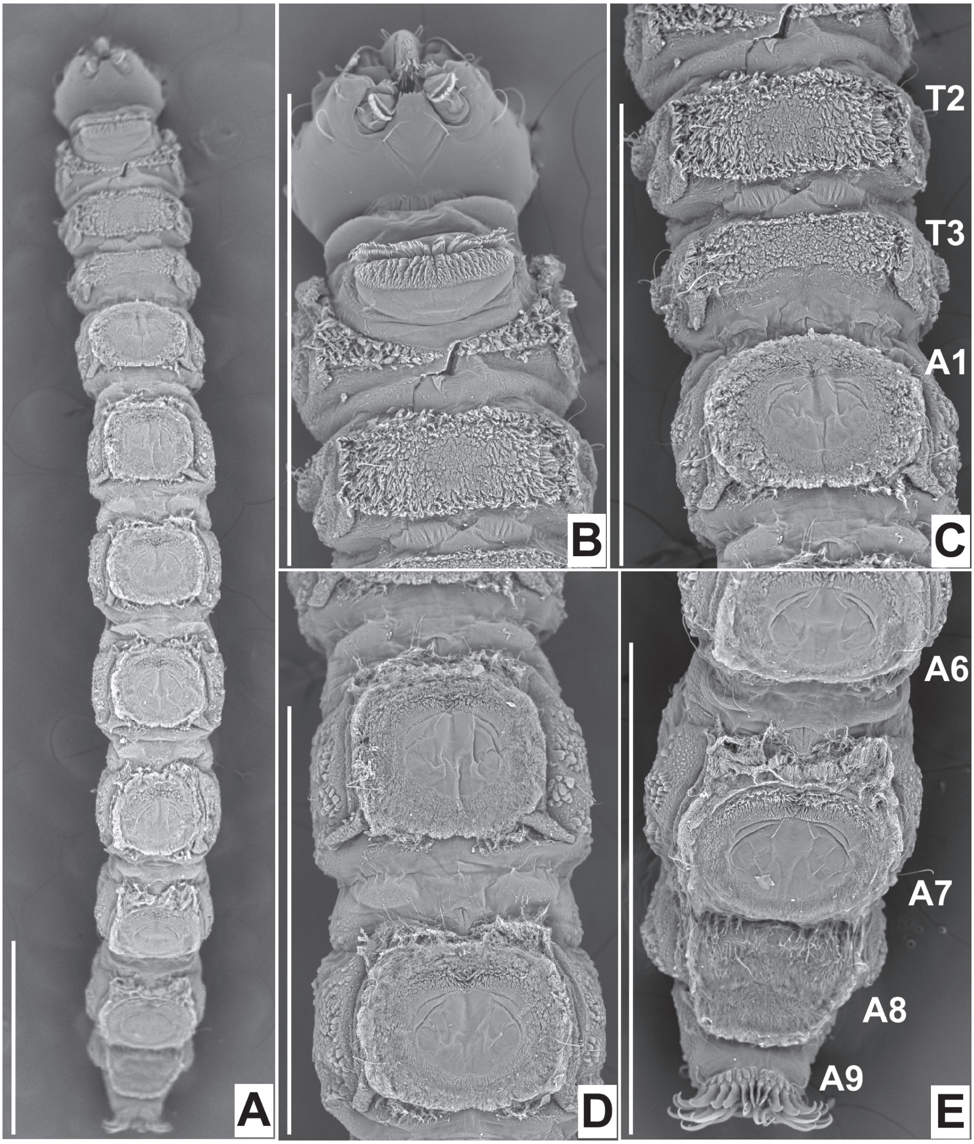


Figure 23. Scanning electron micrographs of ventral view of larvae of *Niphta brunnea* sp. nov. **A** habitus **B** head and thoracic segments 1 & 2 **C** thoracic segments 2 & 3 and abdominal segment 1 **D** abdominal segments 2 & 3 **E** abdominal segments 6, 7, 8 & 9. Abbreviations: A, abdominal segment; T, thoracic segment. Scale bars: 1.0 mm.

collected from wetted vegetation in the splash zones, never from rocks (Fig. 26A–C). Vegetation included both living and dead plant material, including smooth leaves and herbaceous stems. The vegetation was not in the direct flow of water, but rather lightly splashed by water droplets that maintained enough moisture for the immatures to survive.

Niphta courtneyi Pivar, sp. nov.

http://zoobank.org/AE13E1F7-1030-4B4F-9492-92515EE9F67E
Figs 6B, 8B, 9C, H, 10C, 11B, 12B, 24B

Type material. ***Holotype*:** ♂, glued to point with abdomen in glycerine microvial pinned beneath, labelled: "Chile, Region X (Los Lagos)/ East side Lago Llanquihue/ small falls on road (nr PN/ VPR) 41°08.47'S 72°35.28'W/ ≈ 100 m 2.xii.2008 GW/ Courtney (CH08–30)"; "HOLOTYPE/ *Niphta/ courtneyi/* Pivar [red label]" (CNC). ***Allotype*:** ♀*, same data as holotype (CNC). ***Paratypes*:** Chile: Region X (Los Lagos): Rte. U-99, 10.xii.2016, 41°08'28.2"S 72°35'16.8"W, elev. 101 m, roadside seeps/ creek, J.K. Moulton & R.J. Pivar (1♀*).

Recognition. This species is recognised by the bifurcate posterior apex of the cheliform gonostylus and the presence of three gonocoxal projections. It is lighter in colouration than the closely related *N. bifurcata*.

Description. The descriptions of *N. courtneyi* differ from that of *N. bifurcata* in the following regards:

Male. $n = 1$.

Length 2.1–2.3 mm.

Colouration (Figs 9C, 10C). Head dull, brown; pronotum and postpronotum brown; postpronotal lobe and lateral margins of prescutum yellow; scutum shiny with three distinct dark brown stripes, pleura yellow; postscutum yellow, two lateral brown spots above scutoscutellar suture; scutellum shiny, yellow; mediotergite shiny, anterior half yellow, posterior half brown; katepisternum mainly pale brown, yellow near fore coxa; remaining pteropleuron mainly yellow with dispersed brown markings; halter creamy yellow; legs pale yellow, apex of tarsi darker; abdomen brown; terminalia yellow.

Head. Frons with three strong setae. Flagellomere 1 expanded, 1.5 × as wide as next segment, shorter in length than 2 and 3 combined.

Wing. Wing length: 1.9–2.2 mm. Lightly infuscate throughout.

Terminalia (Figs 6B, 8B). Epandrium quadrate in ventral view, posterior margin rounded, with narrow medial cleft; long, extended beyond gonostyli; without lobes or projections. Gonocoxites oblong, longer than wide; anterior margin rounded, somewhat expanded dorsally, not closely approximated; with three spine-like projections; two anterior projections, with inner projection shorter than outer; posterior projection long, slender, tapered to single apex, 3.5 × longer than shortest projection; margin around gonostylus with long, dense thin setae. Gonostylus cheliform, dorsoventrally flattened anteriorly, swollen posteriorly; anterior apex with a few setae; posterior apex bifurcate, setose. Parameres medially fused, attached basally to arms of gonocoxal plate; divided distally into dorsal parameral apodeme and ventral arm; ventral arm projected anteroventrally toward gonocoxal plate, strongly curved anteriorly, sickle-shaped, surface textured with tiny bumps, except for smooth apex; ventral arm, when retracted, rests ventrally between dorsal arm of gonocoxal plate and inner margin of gonocoxite. Gonocoxal plate broad, well sclerotised; anterior margin subquadrate, basal margin cleft; pair of dorsal arms connected to parameres; medial aedeagal guide projected ven-

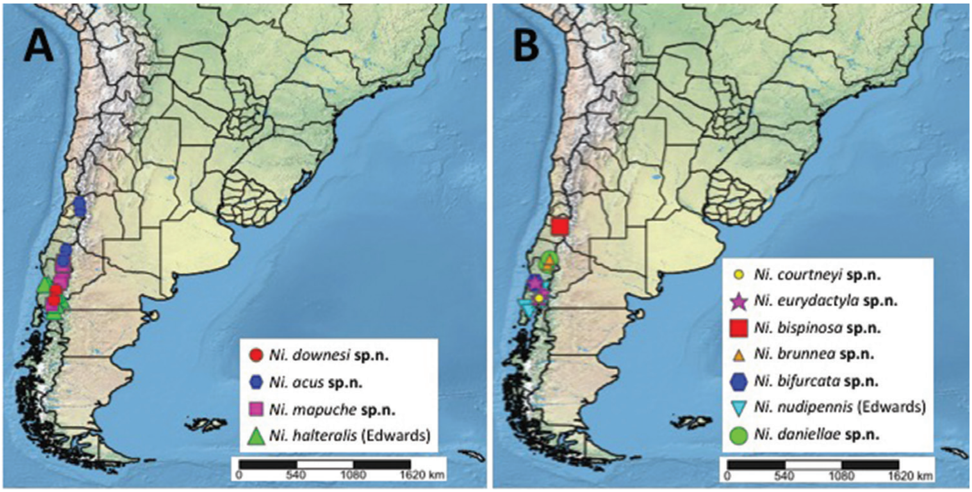


Figure 24. Known distribution of Chilean *Niphta* **A** *N. halteralis* group **B** *N. nudipennis* group.

trally between posterior margins of gonocoxites, well sclerotised, consisting of two parts: anterior Y-shaped structure and posterior triangular plate. Cercus ovoid, only slightly visible in lateral view; projected anteroventrally; situated within epandrial indentation.

Female. *n* = 2.

Similar to male except as follows: *Terminalia* (Figs 11B, 12B). Tergite 9 subquadrate in lateral view, 2 × as wide as tergite 8, lacking lateral projections.

Immature stages. Unknown.

Additional material examined. Known only from the type series.

Distribution. Known only from the type locality, the East side of Lago Llanquihue in Southern Chile (Fig. 24B).

Etymology. *Niphta courtneyi* is named in honour of its collector, Gregory W. Courtney (Iowa State University). Courtney collected three new species of Thaumaleidae from Chile (*A. fredericki* Pivar, *N. courtneyi*, and *N. mapuche*), as well as immature material, prompting us to further investigate the Chilean fauna.

Niphta daniellae Pivar, sp. nov.

http://zoobank.org/2974B173-08B9-4832-991A-A0DD52A1929B
Figs 5A, 7A, 9D, 10D, 24B, 26A

Type material. ***Holotype*:** ♂, glued to point with abdomen in glycerine microvial pinned beneath, labelled: "Chile: Region IX (Araucanía)/ Rte. 71, 15.xii.2016/ 38°14'20.6"S 71°53'46.6"W/ elev. 953 m, roadside seeps/ J.K. Moulton & R.J. Pivar"; "HOLOTYPE/ *Niphta*/ *daniellae*/ Pivar [red label]" (CNC). ***Paratypes*:** Chile: Region VIII (Bío Bío): Rte. Q-61, 8.xii.2016, 37°48'22.8"S 71°40'46.6"W, elev. 379 m, cascading creek, J.K. Moulton & R.J. Pivar (1♂).

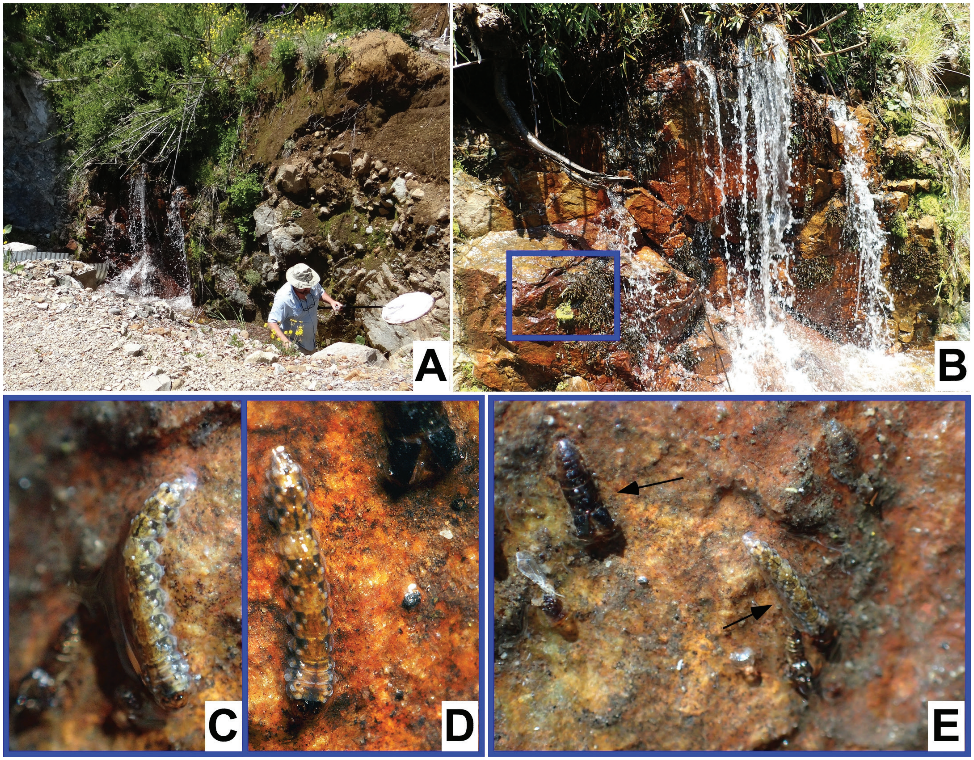


Figure 25. Habitat and larvae of *Niphta acus* sp. nov. (36°55'02.7"S 71°25'49.6"W) **A** Moulton shown next to the falls for scale **B** close up of falls with box indicating where immatures were captured (Note: they were not found in high flow zones) **C** lateral view of larva, with adhesive structures visibly in contact with substrate **D** dorsal view of larva illustrating camouflage **E** larva and pupal exuviae on rock face.

Recognition. This species is recognised by the sharply pointed, tapered gonostylus with no projections and not cheliform, unlike all remaining species in the *N. nudipennis* group. The gonocoxal plate also has a pair of lateral arms projected anteriorly.

Description. The description of *N. daniellae* differs from that of *N. bifurcata* in the following regards:

Male. *n* = 2.

Length 1.7–2.0 mm.

Colouration (Figs 9D, 10D). Postpronotal lobe and lateral margins of prescutum yellow; scutum shiny with three distinct brown stripes, pleura yellow; postscutum yellow, two lateral brown spots above scutoscutellar suture; scutellum shiny, yellowish; mediotergite shiny, anterior half yellow, posterior half brown; katepisternum dark brown, except yellow at base of fore coxa; anepisternum and paratergite brown; remaining pteropleuron yellow; halter entirely creamy yellow; legs yellowish brown, tarsi dark brown; abdominal tergites brown, posterior margin pale brown, sternites mainly yellow with scattered brown markings; terminalia yellowish brown.

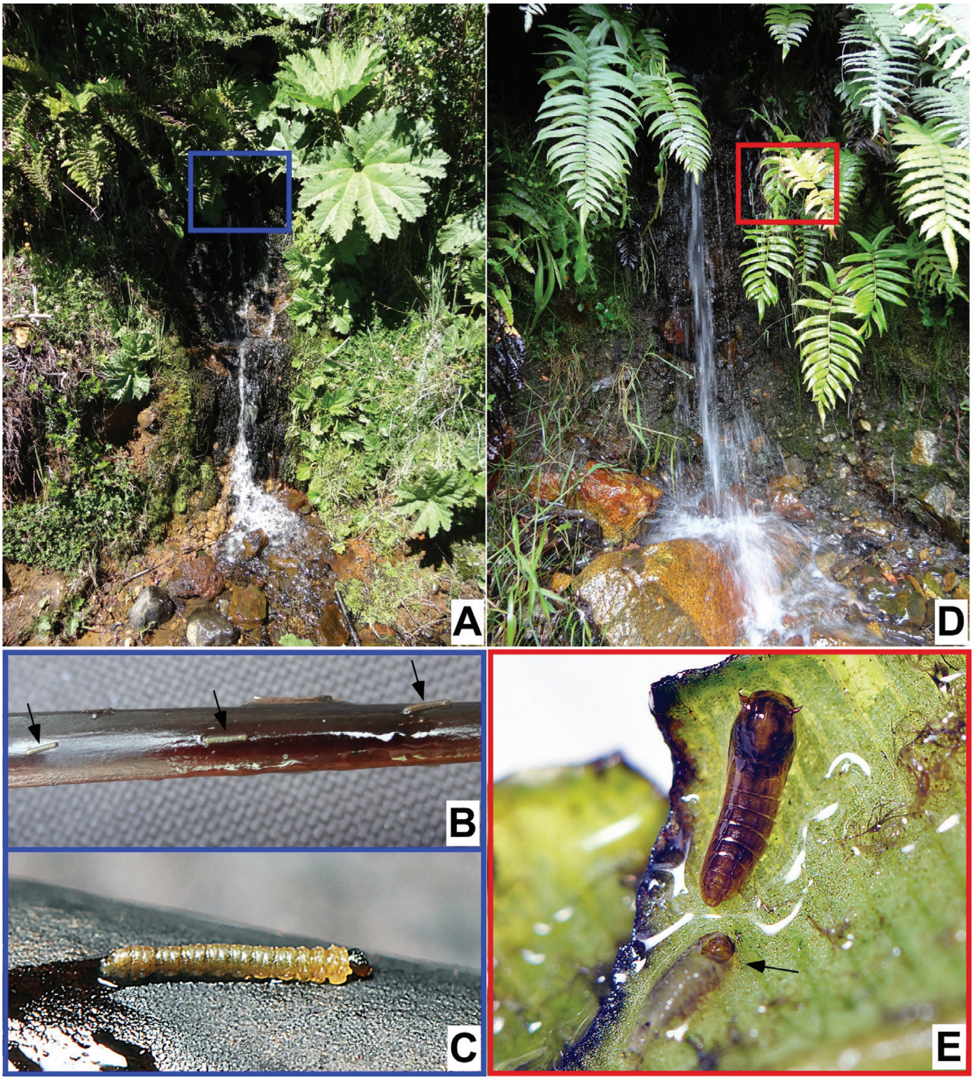


Figure 26. Habitat and immatures of members of the *Niphta nudipennis* group **A** type locality of *N. brunnea* sp. nov. and *N. daniellae* sp. nov., box indicating where plant stem in images **B, C** was taken from (38°14'20.6"S 71°53'46.6"W) **B** larvae of *N. brunnea* sp. nov. on plant stem from splash zone **C** close up of *N. brunnea* sp. nov. larva, adhesive structure visibly in contact with substrate **D** habitat of *N. nudipennis*, box indicating foliage in splash zone where immatures were found **E** pupa of *N. nudipennis* affixed to leaf with final instar larval exuviae visible.

Head. Frons with two to three strong setae. Flagellomere 1 expanded, 1.5 × as wide as next segment, subequal in length to 2 and 3 combined.

Wing. Wing length: 2.2–2.3 mm. Lightly infuscate throughout; bend in R_{4+5} gentle; M_4 with slight apical bend.

Abdomen. Abdominal sternite 2 reduced to slender median sclerite, lacking setae; sternites 3–7 rectangular, setae restricted to posterior two-thirds; sternite 8 strongly reduced, lacking setae.

Terminalia (Figs 5A, 7A). Epandrium quadrate in ventral view, posterior margin rounded, with narrow medial cleft; long, extended beyond gonostyli; without lobes or projections. Gonocoxites oblong, longer than wide, inner margin setose, expanded anterodorsally above gonocoxal plate, closely approximated but not fused; two posteromedially directed spine-like projections, one anterior to gonostylus, one posterior; anterior projection pointed, bare; posterior projection blunt, setose. Gonostylus longer than wide, distal half strongly tapered to pointed apex; dorsoventrally compressed, margins curved slightly ventrally, scoopula-like, heavily sclerotised; a few setae scattered throughout, apex bare. Parameres medially fused, attached basally to arms of gonocoxal plate; surface textured with tiny bumps, except for smooth apex; divided medially into dorsal parameral apodeme and ventral arm; ventral arm projected anteroventrally, expanded medially, apical third rapidly tapered to pointed apex, sharply curved anterodorsally; ventral arm, when retracted, rests ventrally between lateral margin of gonocoxal plate and gonocoxite. Gonocoxal plate broad, well sclerotised; anteroventral margin subtriangular, basal margin cleft forming two ventrally directed projections; pair of dorsal arms connect to parameres; with median expansion projected ventrally between posterior margins of gonocoxites. Cercus ovoid, visible in lateral view; projected anteroventrally; situated within epandrial indentation.

Female. Unknown.

Immature stages. Unknown.

Additional material examined. Known only from the type series.

Distribution. Known from two localities in the Andes of south-central Chile (Fig. 24B).

Etymology. This species is named in honour of RJP's wife, Danielle Lombardi, for her support during Pivar's graduate research and entomological endeavours, and for playing an important role in organising the Chilean expedition. Raised in northern Chile (Arica), Danielle's Spanish skills were critical for translating all communications with government and national park contacts, as well as translating our requests for collecting permits.

Niphta eurydactyla Pivar, sp. nov.

http://zoobank.org/3F67511B-97D8-4C71-ADF7-29936A99D333

Figs 5B, 7B, 9E, 10E, 24B, 27A

Type material. ***Holotype***: ♂, glued to point with abdomen in glycerine microvial pinned beneath, labelled: "Chile: Region X (Los Lagos)/Rte. U-99, 10.xii.2016/ 41°08'28.2"S 72°35'16.8"W/ elev. 101 m, roadside seeps/ and creek, J.K. Moulton & R.J./ Pivar"; "HOLOTYPE/ *Niphta*/ *eurydactyla*/ Pivar [red label]" (CNC). ***Paratypes***: Chile: Region X (Los Lagos): Rte. 215, 12.xii.2016, 40°40'32.4"S 72°17'35.6"W,

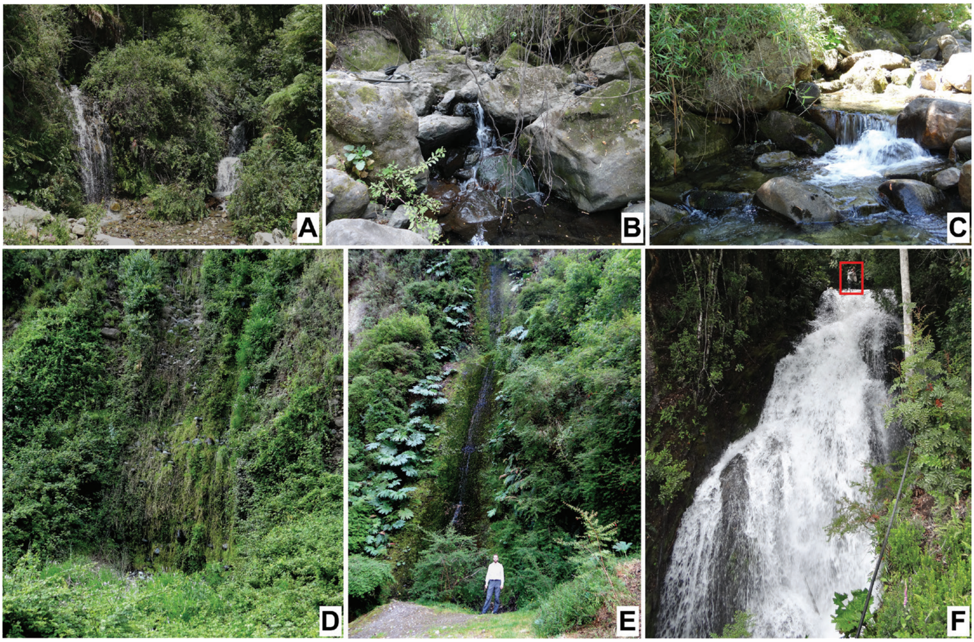


Figure 27. Examples of thaumaleid habitats in Chile **A** waterfalls where *Niphta downesi* sp. nov., *N. eurydactyla* sp. nov. and *N. nudipennis* were collected by sweeping adjacent foliage (40°19'58.7"S 72°16'54.8"W) **B** collection site of *N. bispinosa* sp. nov. (34°59'48.8"S 70°48'37.0"W) (after Pivar *et al.* 2020) **C** type locality of *N. acus* sp. nov., specimens were mainly collected from plants on left (37°46'30.8"S 71°42'03.9"W) **D** rock face seep, type locality of *N. bispinosa* sp. nov. (34°59'46.7"S 70°49'19.2"W) **E** Chiloé, *N. nudipennis* was collected at a small waterfall next to the larger Cascada Tocoihue, Pivar is shown for scale (42°18'20.3"S 73°26'08.9"W); F, Puente El Salto, *N. halteralis* was collected above the falls, Pivar is shown above the falls for scale (41°31'29.2"S 72°17'14.6"W).

elev. 252 m, trickle falls, J.K. Moulton & R.J. Pivar (1♂); Rte. U-99, 10.xii.2016, 41°08'09.6"S 72°35'43.3"W, elev. 81 m, roadside falls, J.K. Moulton & R.J. Pivar (1♂); Rte. U-99, 10.xii.2016, 41°08'28.2"S 72°35'16.8"W, elev. 101 m, roadside seeps/creek, J.K. Moulton & R.J. Pivar (9♂); Region XIV (Los Ríos): Antilhue, Rte. T-35, 9.xii.2016, 39°49'09.8"S 72°56'22.6"W, elev. 40 m, roadside creek, J.K. Moulton & R.J. Pivar (1♂); Rte. T-29, 14.xii.2016, 39°43'03.4"S 71°55'31.6"W, elev. 340 m, seepage, J.K. Moulton & R.J. Pivar (1♂); Rte. T-85, 13.xii.2016, 40°19'58.7"S 72°16'54.8"W, elev. 145 m, foliage around waterfalls, J.K. Moulton & R.J. Pivar (3♂).

Recognition. This species is recognised by a broad, straight, finger-like projection on the gonostylus.

Description. The description of *N. eurydactyla* differs from that of *N. bifurcata* in the following regards:

Male. *n* = 17.

Length 1.5–1.8 mm.

Colouration (Figs 9E, 10E). Variable colouration, even among specimens from the same population; base colouration of thorax either yellow or orange as follows: postpronotal lobe and lateral margins of prescutum orangey/yellowish brown; scutum shiny with three distinct brown stripes, pleura yellow to yellowish brown; postscutum orangey/yellowish brown, two lateral brown spots above scutoscutellar suture; scutellum shiny, orangey/yellowish brown; mediotergite shiny, anterior half orangey/yellowish brown, posterior half brown; katepisternum mainly pale brown with scattered orange/yellow and black markings, or mostly yellowish brown with brown lateral markings above mid coxae; paratergite brown; remaining pteropleuron mainly orangey-brown to yellowish brown with dispersed markings of brown and black; base of halter creamy grey, knob pale yellow; legs pale brown, apex of tarsi darker; abdomen brown; terminalia pale brown.

Thorax. Antealar ridge bearing three to four setae, middle seta most pronounced.

Wing. Wing length: 1.8–2.2 mm.

Abdomen. Abdominal sternites with setae restricted to posterior two-thirds.

Terminalia (Figs 5B, 7B). Epandrium quadrate in ventral view, posterior margin rounded, with narrow medial cleft; long, extended beyond gonostyli; without lobes or projections. Gonocoxites oblong, longer than wide, large C-shaped scallop where gonostyli inserted; anterior margin rounded, somewhat expanded dorsally, not closely approximated; anterior inner margin with stout spine-like projection; margin around gonostylus setose. Gonostylus subquadrate; with finger-like projection emerging from posterolateral corner, gently tapered toward apex, bearing a few setae; inner anterior margin with small, rounded projection bearing a few fine setae. Parameres medially fused, attached basally to arms of gonocoxal plate; divided distally into dorsal parameral apodeme and ventral arm; ventral arm projected anteroventrally toward gonocoxal plate, strongly curved anteriorly, sickle-shaped, surface textured with tiny bumps, except for smooth apex; ventral arm, when retracted, rests ventrally between lateral margin of gonocoxal plate and gonostylus. Gonocoxal plate broad, well sclerotised; anterior margin rounded; pair of dorsal arms connect to parameres; median aedeagal guide trident-shaped, weakly sclerotised. Cercus prominent; ovoid; projected anteroventrally; situated within epandrial indentation.

Female. Unknown.

Immature stages. Unknown.

Additional material examined. Known only from the type series.

Distribution. Known from both the Chilean Coastal Range and Andes of southern Chile (Fig. 24B).

Etymology. The specific name is from the Greek *eury* (broad, wide) and *daktylos* (finger), in allusion to the broad, finger-like projection on the gonostylus.

Niphta nudipennis **(Edwards)**

Figs 1, 5C, D, 7C, D, 9G, 10G, 11D, 12D, 14B, 15B, 16B, 17B, 18B, 19B, 21C, D, 24B, 26D, E, 27A, E

Austrothaumalea nudipennis Edwards, 1930: 113. Stuardo, 1946: 42 (catalogue); Stone, 1966: 1 (catalogue); Arnaud, 1977: 284 (distribution).

Niphta nudipennis (Edwards): Theischinger 1986: 316 (new combination); McLellan 1988: 563 (comments).

Type material examined. ***Holotype*:** ♂, minuten pinned with abdomen mounted in resin, labelled: "Ancud./ 17–19.xii.1926."; "Austrothaumalea/ nudipennis Edw./ F.W. Edwards/ det. 1930."; "S. Chile:/ Chiloe I./ F. & M. Edwards./ B.M. 1927 – 63."; "HOLO-/ TYPE [white label with red margin]"; "NHMUK010210690". ***Allotype*:** ♀, same label data as holotype (NHMUK). ***Paratypes*:** same data as holotype (4♂, 4♀, NHMUK).

Recognition. This species is recognised by a long, narrow, finger-like projection on the gonostylus that has a medial bend.

Redescription. The adult and immature descriptions of *N. nudipennis* differ from those of *N. bifurcata* and *N. brunnea*, respectively in the following regards:

Male. *n* = 22.

Length 1.5–2.3 mm.

Colouration (Figs 9G, 10G). Postpronotal lobe and lateral margins of prescutum orangey-brown; scutum shiny with three distinct brown stripes, pleura orangey-brown (sometimes scutal stripes concolourous with pleura); postscutum orangey-brown, two lateral brown spots above scutoscutellar suture; scutellum shiny, yellowish brown; mediotergite shiny, anterior half yellowish brown, posterior half brown; katepisternum variable in colour, may be mostly brown with orange markings, or mostly yellowish brown with brown lateral markings above mid coxa; remaining pteropleuron mainly orangey-brown to yellowish brown with dispersed brown to light brown markings; base of halter pale yellow, turning brown, knob yellowish orange; terminalia light brown.

Head. Flagellomere 1 subequal in length to 2 and 3 combined.

Wing (Fig. 1). Wing length: 2.0–2.9 mm.

Abdomen. Abdominal sternite 2 with a few setae restricted to laterad on posterior third; sternites 3–7 with setae restricted to posterior two-thirds; sternite 8 lacking setae.

Terminalia (Figs 5C, 7C). Epandrium quadrate in ventral view, posterior margin rounded, with narrow medial cleft; long, extended beyond gonostyli; without lobes or projections. Gonocoxites oblong, wider than long, large C-shaped scallop where gonostyli inserted; anterior margin rounded, somewhat expanded dorsally, not closely approximated, extended anteriorly toward sternite 8; anterior margin with stout spine-like projection; inner margin anterior to spine setose with short, fine setulae; margin around gonostylus setose. Gonostylus quadrate basally; with pointed, finger-like projection emerging from posterolateral corner, bent 45° at midpoint, bearing a few setae at base; inner anterior margin with small, rounded projection bearing a few fine setae; posterior margin with fringe of setae. Parameres medially fused, attached basally to gonocoxal plate; divided medially into dorsal parameral apodeme and ventral arm; ventral arm projected anteroventrally toward gonocoxal plate, strongly curved anteriorly, sickle-shaped, surface textured with tiny bumps, except for smooth apex; ventral arm extends posteroventrally presumably to aid in copulation (Figs 5D, 7D); when retracted, rests ventrally between lateral margin of gonocoxal plate and gonostylus; when extended, gonostyli move inward, finger-like projections crossing and forming an 'X' allowing parameres to extend ventrally. Gonocoxal plate broad, well sclerotised; anterior margin rounded, basal margin cleft; pair of dorsal arms connected to parameres; with median expansion projected ventrally between gonostyli, weakly sclerotised. Cercus ovoid, slightly visible in lateral view; projected anteroventrally; situated within epandrial indentation.

Female. *n* = 6.

Similar to male except as follows: *Abdomen*. Tergite 9 noticeably more sclerotised than preceding tergites; sternite 8 well sclerotised, with distinct blunt projection at base of hypogynial valve.

Terminalia (Figs 11D, 12D). Hypogynial valve not projected beyond tergite 9; posterior margin deeply cleft in ventral view, forming two subquadrate lobes; lobes densely setose, with both stout, thickened setae and thinner, long setae with slight apical bend; elongate hypogynial protuberance between valves. Tergite 9 subquadrate in lateral view, 2 × as wide as tergite 8, lacking lateral projections. Hypoproct lightly sclerotised, narrow. Cercus quadrate, projected posteroventrally; bearing numerous setae.

Pupa. *n* = 4 (Figs 14B, 15B, 16B).

Length 3.0–3.1 mm.

Colouration. Light brown; with black spot above eyes in developing adult.

Thorax. 1.25 × wider than abdomen at widest point. Foreleg sheath projected straight, slightly shorter than wing sheaths; anterior half of midleg visible anterior to wing sheath, then hidden behind foreleg, apices visible, slightly longer than foreleg; hindleg concealed beneath wing sheath, only apex visible between apex of foreleg and wing sheath, longer than foreleg, extended slightly beyond wing sheath but not reaching hind margin of sternite 2. Wing sheaths not reaching posterior margin of abdominal sternite 2. Respiratory organ slightly longer than maxillary sheath, broadest subapically. Tubercle situated posterodorsally to respiratory organ, rounded, projected slightly posterolaterally; apex well separated from respiratory organ. Thorax devoid of setae.

Abdomen. Sternite 8 with small, indistinct lateral projection, directed slightly anterolaterally. Tergites 1–8 quadrate, devoid of setae, with pair of dorsolateral ridges (indistinct on tergites 1–6). Caudal sternite subquadrate, lacking medial lobes; posterior margin with medial longitudinal groove; without distinct caudal hooks.

Larva. *n* = 27 (Figs 17B, 18B, 19B).

Length of final instar 4.7–5.4 mm.

Colouration. Head capsule pale brown (sometimes dark brown). Body creamy brown.

Head capsule (Fig. 21C, D). Five pairs of tubercles outside of ecdysial lines (not including antennal and ocular tubercle), all smaller than ocular tubercle; 2 tubercles between ecdysial lines, upper tubercle larger than lower.

Thorax. Spiracular protuberance bearing one pair of dorsal setae anterior to spiracle and single lateral seta.

Abdomen. Segments 1–7 with lateral adhesive structure inflatted bearing four setae, two midlateral, two basalateral. Terminal segment with pair of protuberances bearing pair of setae; four lateral setae, two long, two short and fine.

Additional material examined. Chile: Region X (Los Lagos): Chiloé, Cascada Tocoihue, 10.xii.2016, 42°18'20.3"S 73°26'08.9"W, elev. 32 m, smaller falls, J.K.

Moulton & R.J. Pivar (2♂, 4♀*); Ensenada, nr. Baños de Petrohué, 12.i.1985, J.A. Downes (13♂, 2♀, CNC); Isla Chiloé, Ancud, 12.1926, R. & E. Shannon, USNMENT01115824 (1♂, USNM) [Note: There is an additional USNM specimen identified as *N. nudipennis* from this same collection event; however, abdomen is missing and species identification cannot be confirmed (USNMENT01115825)]; Rte. V-69, 12.xii.2016, 41°19'51.5"S 72°24'40.0"W, elev. 129 m, roadside seep, J.K. Moulton & R.J. Pivar (2♂); Rte. V-69, 12.xii.2016, 41°31'48.8"S 72°17'31.2"W, elev. 39 m, trickling creek, J.K. Moulton & R.J. Pivar (5♂); same data as previous except, larvae/pupae on foliage in splash zone (27 larvae*, 4 pupae, 3 pupal exuviae); Region XIV (Los Ríos): Rte. T-85, 13.xii.2016, 40°19'58.7"S 72°16'54.8"W, elev. 145 m, foliage around waterfalls, J.K. Moulton & R.J. Pivar (1♂).

Distribution. Known from both the Chilean Coastal Range and the Andes of southern Chile (Fig. 24B).

Bionomics. *Niphta nudipennis* is a low-elevation species inhabiting the Valdivian temperate rainforest. Adults were collected mainly from foliage around splash zones (Figs 26D, 27A, F). The larvae possess the ventral adhesive structures found in the *N. halteralis* group; however, they were only collected from overhanging vegetation in the splash zone. Vegetation included both living and dead plant tissue, on textures spanning smooth leaf surfaces, to more textured fern fronds and herbaceous stems (Fig. 26E). Pupae were collected from the same habitats and also possess adhesive structures. The amount of water splashing on the vegetation appeared to be just enough to keep it damp enough to keep the immatures alive.

Discussion and conclusions

Immature stages of South American *Niphta*

Pivar et al. (2018b) described the first immatures for South American thaumaleids, where the larva and pupa of *Neothaumalea atlantica* were described. Sinclair (2000) described the larva and pupa of *N. collessi*, an Australian species and the first for the genus. The remarkable immatures described herein are the first for South American *Niphta* and reveal unique evolutionary adaptations for the family. Unlike other described thaumaleid species, including *N. collessi*, immature South American *Niphta* are equipped with ventral adhesive structures, resembling suction cups. They are present on nearly all segments of the larva and on segments 3–5 of the pupa, and presumably aid in maintaining their position within the flow of water. The known immatures of the *N. halteralis* species group (*N. acus* and *N. mapuche*) were both collected from rocky substrates (Fig. 25), whereas the known immatures of the *N. nudipennis* species group (*N. brunnea* and *N. nudipennis*) were collected from vegetation in the splash zones, the first such observation for the family (Fig. 26).

Each group's morphology is well adapted to their microhabitat. On a rock face, immatures have to contend with debris being washed down from the substrate above. Pupae of the *N. halteralis* group were collected from exposed microhabitats on the rock face, with no protection from flowing debris. Their stout and stocky body shape, hidden spiracles and small respiratory organs that do not extend far from the body, likely help in withstanding any potential debris impact and reduce breakage of exposed appendages. Both pupae and larvae are mottled and much darker in colouration than the pupae of the *N. nudipennis* group, offering greater camouflage from predators on the exposed rock face. Larvae have the added vestiture of dorsal tubercles, which help to break up the outline of the body. Immatures of the *N. halteralis* group also bear more setae than species of the *N. nudipennis* group, perhaps for sensing debris or predators that may be nearby.

Immatures of the *N. nudipennis* group were all collected from plant material, either living or dead, but always directly in the splash zone. They were collected from both smooth leaf surfaces and more textured vegetation, such as ferns and herbaceous plant stems. They were found on both upper and lower leaf surfaces, depending on which surface was in the splash zone. Contrary to a rock face, the amount of debris flowing down a leaf is likely minimal. Pupae of the *N. nudipennis* group are conoid, with a broad head and thorax and a narrow abdomen, protruding spiracles, and large, laterally projecting respiratory organs. All of these features are indicative of life in a habitat where debris does not pose a problem of displacement, breakage, or blockage of the respiratory organ. The leaf habitats were generally shaded and hidden from direct view, and coupled with constant splashing, individuals may experience less predation than on a rock face, thereby reducing the need for the dark, mottled colouration and tubercles. Eggs on vegetation were not observed, nor was oviposition by the adults, but they are presumably laid on the vegetation surface.

The presence of the adhesive structures is associated with behavioural traits that differ from those of other Thaumaleidae. The typical thaumaleid larva will exhibit a characteristic quick, sidewinding motion to evade predation (Thienemann 1909; Sinclair 2000; Pivar et al. 2018a). Chilean *Niphta* are much slower when trying to escape, almost caterpillar-like in movement, with slow, undulating motions. The thoracic adhesive structures are rectangular in shape and are more mobile than those of the abdominal segments, which are circular (Fig. 23).

Despite the discovery of this new larval morphotype, specimens were never collected in areas of extremely high flow or aggressive splash zones; rather, they were collected in typical thaumaleid habitat consisting of slow flowing, thin films of water. Perhaps antecedents originated in environments with higher water flow, such as in a river, and the extant species are a result of having adapted to the more familiar recent habitats. Alternatively, these slow flowing zones may be subject to torrential flooding after rainfall. The continued presence of the adhesive structures suggests a continuing evolutionary advantage in their present-day habitat.

Comparison of *Niphta* immatures

Immatures of the Australian *N. collessi* (Sinclair 2000) differ from Chilean *Niphta* most notably in the absence of the ventral adhesive structures. Several other characters also warrant discussion.

The pupa of *N. collessi* has caudal hooks, much like in *Neothaumalea atlantica*; however, the Chilean species lack caudal hooks or any other projections. There is also a significant reduction in setae, both in number and length. *Niphta collessi* has numerous setae, many of which are long, while members of the *N. halteralis* group have very few, short setae. Pupae of the *N. nudipennis* group lack abdominal setae altogether. The respiratory organs of *N. collessi* are similar in appearance to those of the *N. nudipennis* group, where they are broadest subapically and project laterally, whereas those in the *N. halteralis* group are shorter and barely project laterally. The spiracles of *N. collessi* and the *N. nudipennis* group are also similar; well developed on sternites 3–7 and mounted on long, narrow, lateral tubercles. The spiracles are barely visible in the *N. halteralis* group.

The larvae also exhibit some significant differences and similarities. The most apparent difference, aside from the adhesive structures, is in the sculpture of the head capsule. All described Chilean *Niphta* have protuberances and large antennal tubercles, similar to those of *Neothaumalea atlantica*; *Niphta collessi* lacks protuberances and the antennae are on short tubercles. Also, much as in the pupae, Chilean *Niphta* larvae exhibit a reduction in setae compared to *N. collessi*. Another significant difference is the presence of cauliflower-like protuberances on both thoracic and abdominal tergites. These protuberances are especially prominent in the *N. halteralis* group, and are reduced but still present in *Ni. nudipennis* group. Based on Sinclair's (2000) description, it appears that *N. collessi* lacks all protuberances and is more reminiscent of *Austrothaumalea* larvae. Similarities between the two faunas are: larval head-capsule with sensory pit 13 near dorsal margin of antenna, head-capsule only with simple setae and the caudal lobes flanking posterior spiracular plate are absent. Since descriptions of the immature stages of *N. collessi* are based on a single pupa and attached larval exuviae, additional collections of the immature stages are needed urgently to verify our comparisons.

Larvae with ventral adhesive structures have been collected in Australia. Though they have not been reared, nor identification confirmed via DNA fingerprinting (attempts to fingerprint were made, but with no success), morphology indicates these larvae are likely a member of *Niphta*. They appear very similar to members of the *N. halteralis* group: presence of distinct thoracic and abdominal protuberances, darker colouration, long abdominal setae (longer and more abundant than *N. halteralis* group) and pronounced head-capsule protuberances (not as large as *N. halteralis* group, but larger than *N. nudipennis* group). The adhesive structures appear very similar between all species: thoracic segments rectangular, adhesive structures felt-like; abdominal segments 1–7 circular, margins felt-like with smooth interior; abdominal segment 8 quadrate, felt-like (Fig. 23). Continued sampling on both continents will provide further insight into the evolution of *Niphta*.

Faunal patterns and habitat

South American thaumaleid diversity has now increased to 17 described species. Additionally, there is the likely new species to be discovered in Ecuador, plus three more new species from Chile that were collected by the authors, but not yet described because they are represented by females only. Since males possess readily recognised genitalic features, the authors have decided to wait until further material is collected before describing these species. Both morphological and molecular data (Pivar, unpublished data) support the presence of these new species. Of the described South American species, only *Neothaumalea atlantica* is not found in the Andes Range and is recorded from the Atlantic Forest of southeastern Brazil, in the Serra Geral mountains (Pivar et al. 2018b). The remaining species range along a roughly 2000 km stretch of the south-central Chilean Andes, with only three records from the Argentinian side, all from Bariloche. The Andes are the longest mountain range in the world at roughly 7000 km long, running from the southern tip of Chile, north to Venezuela. There are only 16 described species from ~20% of sampled mountain range. The South American fauna is undoubtedly more diverse than is presently known and current numbers are reflective of under sampling.

In Chile, thaumaleid diversity increases as one moves south. Beginning in central Chile and progressing south, the following are the known diversity of species per region (including the three undescribed females): Valparaíso (1 sp.), Santiago (2 spp.), O'Higgins (1 sp.), Maule (2 spp.), Bío Bío (5 spp.), Araucanía (7 spp.), Los Ríos (6 spp.), Los Lagos (8 spp.) and Aysén (1 sp.). These numbers are reflective of both the amount of time spent collecting in certain regions and regions sampled; some regions have likely never been sampled (particularly in northern Chile). Available habitat is also a large contributor to diversity. From Bío Bío to Los Lagos, specimens were collected in Valdivian temperate rainforests, characterised by high rainfall and cooler temperatures. Vegetation types include southern beech, laurel and broadleaved forest, bamboo and ferns. With an abundance of mountain streams and waterfalls, similar to the Nearctic Pacific Northwest (Pivar et al. 2018a), there is ample habitat for thaumaleids. From Valparaíso to Maule, habitat availability begins to drop drastically, in particular from Valparaíso to O'Higgins. These regions are part of the Chilean Matorral ecoregion of central Chile, characterised by a temperate Mediterranean climate and sclerophyllous shrubs and trees, and cacti (Meserve et al. 2019). Summers are dry and hot, and madicolous habitats scarce, as suggested by the diversity listed above. The western slopes of the Andes, from Santiago in central Chile to northern Peru, become extremely dry as they transition into the Atacama Desert. Suitable habitat is scant in these areas, though the eastern slopes of Argentina, Bolivia and Peru may contain more suitable habitat as they receive more moisture.

Most Chilean species are found in temperate rainforest regions, but some are found in both wet and dry climates (*A. chilensis* Edwards, *N. acus*). The type of madicolous habitat (i.e., creek, rock face seep, stream, waterfall, *etc*.) (Fig. 27) does not seem to dictate where a particular species may be found; oftentimes, species were collected in multiple habitat types. Multiple species and genera were frequently collected together, both within the same species group and mixed groups.

Future collections should focus on all areas of the Andes, with an emphasis on the northern sections to provide insight into the northern limits of the family and genera. Currently, the southern-most Nearctic species is *Androprosopa zempoala* Sinclair and Huerta from central Mexico (Sinclair and Huerta 2010) and the northern-most South American species is the undescribed specimen from Ecuador. Thaumaleids are not recorded from Central America (Brown et al. 2009), so what is the northern limit of the South American genera? Does one genus become more abundant than the other at higher/lower latitudes or elevations? Other mountain ranges on the continent should be explored, such as the Sierras de Córdoba (central Argentina), the Sierra Nevada de Santa Marta (northern Colombia), and continued studies in Brazil will surely lead to new discoveries. Focused collecting efforts in these regions will answer these questions, as well as divulge the true breadth of South American thaumaleid diversity.

Acknowledgments

The authors would like to thank colleagues who provided fresh material for this study: Gregory Courtney, Greg Curler and Isai Madriz. Additionally, Duncan Sivell (NHMUK), Torsten Dikow (USNM) and Michelle Trautwein (CAS) facilitated specimen loans. Thank you to Gary Phillips for providing assistance producing the SEM photos. Thanks are also due to Danielle Lombardi, whose Spanish skills were invaluable when communicating with Chilean government and national park officials, as well as translating all our permit materials both to and from Spanish. Christian Gonzalez (UMCE) provided information regarding collecting sites throughout Southern Chile. Art Borkent and an anonymous reviewer provided helpful comments to improve this paper. La Corporación Nacional Forestal (CONAF) and Servicio Agrícola y Ganadero (SAG) of Chile granted collecting permits (#036/2016) and provided information for exporting specimens. Funding for this research was provided from the following sources: United States National Science Foundation awards DEB-1146290 and DEB-1949813, Smithsonian Institution S.W. Williston Diptera Research Fund (RJP), Hatch Projects TEN00479 and TEN00558 from the USDA National Institute of Food and Agtriculture, and the University of Tennessee Department of Entomology and Plant Pathology.

References

Arnaud Jr, PH (1977) Thaumaleidae. In: Hurlbert SH (Ed.) Biota Acuática de Sudamérica Austral. San Diego State University, San Diego, California, 283–285.

Bertone MA, Courtney GW, Wiegmann BM (2008) Phylogenetic and temporal diversification of the earliest true flies (Insecta: Diptera) based on multiple nuclear genes. Systematic Entomology 33: 668–687. https://doi.org/10.1111/j.1365-3113.2008.00437.x

Borkent A (2012) The pupae of Culicomorpha – morphology and a new phylogenetic tree. Zootaxa 3396: 1–98. https://doi.org/10.11646/zootaxa.3396.1.1

Brown BV (1993) A further chemical alternative to critical-point-drying for preparing small (or large) flies. Fly Times 11: 10.

Brown BV, Borkent A, Cumming JM, Wood DM, Woodley NE, Zumbado M (Eds) (2009) Manual of Central American Diptera, vol. 1, NRC Research Press, Ottawa, Canada, 714 pp.

Courtney GW, Sinclair BJ, Meier R (2000) Morphology and terminology of Diptera larvae. In: Papp L, Darvas B (Eds) Contributions to a manual of Palaearctic Diptera (with special reference to flies of economic importance), vol. 1 General and applied dipterology. Science Herald, Budapest, Hungary, 85–161.

Cumming JM, Wood DM (2017) [Chapter] 3. Adult morphology and terminology. In: Kirk-Spriggs AH, Sinclair BJ (Eds) Manual of Afrotropical Diptera, vol. 1. Introductory chapters and keys to Diptera families. Suricata 4, South African National Biodiversity Institute, Pretoria, South Africa, 89–133.

Edwards FW (1930) Part II: Bibionidae, Scatopsidae, Cecidomyiidae, Culicidae, Thaumaleidae (Orphnephilidae), Anisopodidae (Rhyphidae). In: Diptera of Patagonia and South Chile based on material in the British Museum (Natural History). British Museum of Natural History, London, 2: 111–114.

Mackie GL (2004) Applied aquatic ecosystem concepts, 2nd edn. Kendall Hunt Publishing, Dubuque, Iowa, 374 pp.

McLellan ID (1988) A revision of New Zealand Thaumaleidae (Diptera: Nematocera) with descriptions of new species and a new genus. New Zealand Journal of Zoology 15: 563–575. https://doi.org/10.1080/03014223.1988.10422636

Meserve PL, Gómez-González S, Kelt DA (2020) The Chilean Matorral: Characteristics, Biogeography, and Disturbance. In: Goldstein M, DellaSala D (Eds) Encyclopedia of the World's Biomes. Elsevier, 594–601. https://doi.org/10.106/B978-0-12-409548-9.11985-2

Moulton JK (2000) Molecular sequence data resolves basal divergences within Simuliidae (Diptera). Systematic Entomology 25: 95–113. https://doi.org/10.1046/j.1365-3113.2000.00097.x

Pivar RJ, Moulton JK, Sinclair BJ (2018a) Revision of the western Nearctic *Androprosopa* (Diptera: Thaumaleidae) and descriptions of three new species. Insect Systematics and Evolution 50 (2019): 346–406. https://doi.org/10.1163/1876312X-00002189

Pivar RJ, Sinclair BJ, Moulton JK (2020) Revision of the South American species of *Austrothaumalea* Tonnoir (Diptera: Thaumaleidae). Zootaxa 4853 (4): 509–526. https://doi.org/10.11646/zootaxa.4853.4.2

Pivar RJ, Pinho LC, Klingeman WE, Moulton JK, Sinclair BJ (2018b) A new genus and species, and first record of the family Thaumaleidae (Diptera) from Brazil. The Canadian Entomologist 150: 481–494. https://doi.org/10.4039/tce.2018.29

Röder V von (1886) Dipteren von den Cordilleren in Columbien. Gesammelt durch Herrn Dr. Alphons Stübel. Entomologische Zeitung herausgegeben von dem Entomologischen Vereine zu Stettin 47: 257–270.

Schmid F (1970) Quelques Thaumaléides nouvelle ou peu connues (Diptera, Thaumaleidae). Le Naturaliste Canadien 97: 499–510.

Shorthouse DP (2010) SimpleMappr, an online tool to produce publication-quality point maps. www.simplemappr.net. [Accessed 24 October, 2020]

Sinclair BJ (1992) A new species of *Trichothaumalea* (Diptera: Thaumaleidae) from eastern North America and a discussion of male genitalic homologies. The Canadian Entomologist 124: 491–499. https://doi.org/10.4039/Ent124491-3

Sinclair BJ (2000) Immature stages of Australian *Austrothaumalea* Tonnoir and *Niphta* Theischinger (Diptera: Thaumaleidae). Australian Journal of Entomology 39: 171–176. https://doi.org/10.1046/j.1440-6055.2000.00162.x

Sinclair BJ, Huerta H (2010) A new species of *Androprosopa* from Mexico (Diptera: Thaumaleidae). The Canadian Entomologist 142: 443–447. https://doi.org/10.4039/n10-035

Sinclair BJ, Saigusa T (2002) A new species of the seepage midge genus *Trichothaumalea* Edwards from Japan. Insect Systematics and Evolution 33: 175–184. https://doi.org/10.1163/187631202X00127

Sinclair BJ, Stuckenberg BR (1995) Review of the Thaumaleidae (Diptera) of South Africa. Annals of the Natal Museum 36: 209–214.

Shimabukuro EM, Trivinho-Strixino S (2018) Madicolous Chironomidae from the Brazilian Atlantic Forest: A checklist with notes on altitudinal distributions (Diptera, Insecta). ZooKeys 751: 41–73. https://doi.org/10.3897/zookeys.751.20611

Stuardo C (1946) Catalogo de los Dipteros de Chile. Imprenta Universitaria, Santiago de Chile, Chile, 253 pp.

Stone A (1966) 13. Family Thaumaleidae (Orphnephilidae). A Catalogue of the Diptera of the Americas South of the United States. Departamento de Zoologia, Secretaria da Agricultura, São Paulo, Brazil, 1–2.

Thienemann A (1909) *Orphnephila testacea* Macq. Ein beitrag zur kenntnis der fauna hygropetrica. Annales de Biologie Lacustre 4: 53–87.

Theischinger G (1986) Australian Thaumaleidae (Insecta: Diptera). Records of the Australian Museum 38: 291–317. https://doi.org/10.3853/j.0067-1975.38.1986.184

Wiegmann BM, Trautwein MD, Winkler IS, Barr NB, Kim JW, Lambkin C, Bertone MA, Cassel BK, Bayless KM, Heimberg AM, Wheeler BM, Peterson KJ, Pape T, Sinclair BJ, Skevington JH, Blagoderov V, Caravas J, Kutty SJ, Schmidt-Ott U, Kampmeier GE, Thompson FC, Grimaldi DA, Beckenbach AT, Courtney GW, Friedrich M, Meier R, Yeates DK (2011) Episodic radiations in the fly tree of life. Proceedings of the National Academy of Sciences 108: 5690–5695. https://doi.org/10.1073/pnas.1012675108

ZooKeys 1063: 105–120 (2021)
doi: 10.3897/zookeys.1063.71914
https://zookeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
ZooKeys
Launched to accelerate biodiversity research

Gelechia omelkoi sp. nov. – a new species from the Russian Altai Mountains related to the Nearctic *Gelechia mandella* Busck, 1904 (Lepidoptera, Gelechiidae), with a synopsis of *Gelechia* from the Altai Republic of Russia

Oleksiy Bidzilya[1], Peter Huemer[2], Jean-François Landry[3], Jan Šumpich[4]

1 *Institute for Evolutionary Ecology of the National Academy of Sciences of Ukraine, 37 Academician Lebedev str., 03143, Kyiv, Ukraine* **2** *Tiroler Landesmuseen Betriebsges.m.b.H., Natural History Collections, Krajnc-Str. 1, A-6060 Hall in Tirol, Austria* **3** *Canadian National Collection of Insects, Arachnids, and Nematodes, Agriculture and Agri-Food Canada, Ottawa Research and Development Centre, C.E.F., Ottawa, Ontario K1A 0C6, Canada* **4** *National Museum, Department of Entomology, Cirkusová 1740, CZ-193 00 Praha 9 – Horní Počernice, Czech Republic*

Corresponding author: Oleksiy Bidzilya (olexbid@gmail.com)

Academic editor: Mark Metz | Received 21 July 2021 | Accepted 30 August 2021 | Published 19 October 2021

http://zoobank.org/E898EEB5-16A5-4954-A6FC-4A5BC164D7CA

Citation: Bidzilya O, Huemer P, Landry J-F, Šumpich J (2021) *Gelechia omelkoi* sp. nov. – a new species from the Russian Altai Mountains related to the Nearctic *Gelechia mandella* Busck, 1904 (Lepidoptera, Gelechiidae), with a synopsis of *Gelechia* from the Altai Republic of Russia. ZooKeys 1063: 105–120. https://doi.org/10.3897/zookeys.1063.71914

Abstract

Gelechia omelkoi sp. nov. is described from the Ukok plateau and South Chuisky ridge in the Altai Mountains of Russia. The adult of the new species, including its male genitalia, is illustrated and compared with species most similar in morphology and DNA barcodes—*G. sororculella* (Hübner, 1817) and *G. jakovlevi* Krulikovsky, 1905 from the Palaearctic region, as well as *G. mandella* Busck, 1904 from Canada. This last species is redescribed based on adult specimens, including the genitalia of both sexes, and a lectotype is designated. *Gelechia sirotina* Omelko, 1986 is recorded from the Altai Republic for the first time. An updated list of six species of *Gelechia* from the Altai Mountains of Russia is given. Dorsal habitus photographs of all species are provided. The male genitalia of the lectotype of *G. jakovlevi* is illustrated for the first time.

Keywords

Canada, distribution, DNA barcoding, Nearctic Region, new records, Palaearctic Region, Russia

Introduction

During a collecting trip to the Altai Mountains in 1995, the first author collected a short series of uniformly greyish-black Gelechiidae. Despite some differences in the male genitalia and external appearance, they were identified by OB as *G. sororculella* (Hübner, 1817), and introduced under this name in a list of Lepidoptera collected on the Ukok plateau (Bidzilya et al. 2002). Six years later, seven additional males were collected in the same locality, and two males of *G. sororculella* were found in adjacent territories in the Kosh-Agach region. In 2016, two additional males were collected in Ukok by PH, and in 2017 another five males were collected at South Chuiski ridge, within the Kosh-Agach district, by JŠ. DNA barcoding of one of these specimens indicated that specimens from the Ukok plateau represented a new species (Huemer et al. 2017), with 5.94% minimum distance to the nearest Palaearctic species, *G. sororculella*, and 2.88% minimum distance to the nearest Nearctic species, *G. mandella* Busck, 1904. This last species was described from British Columbia, Canada, but it had since then not been treated in the taxonomic literature. The examination of adults during this study, particularly their genitalia, indicated its similarity to the new species from Altai as well as to *G. sororculella* and *G. jakovlevi* Krulikovsky, 1905. The new species from the Altai Mountains of Russia is described here as *G. omelkoi* sp. nov. A lectotype is designated for *G. mandella*, which is redescribed based on additional material, with male and female genitalia illustrated for the first time. Both species are compared with the Palaearctic species *G. sororculella* and *G. jakovlevi*. We also provide an updated list of *Gelechia* species known from the Altai Republic of Russia, with additional distributional information including the first record of *G. sirotina* Omelko, 1986.

Material and methods

Specimens of the new species were collected at light as well as by sweeping during daytime or at early sunrise around shrubs of *Salix* spp. JŠ collected all specimens with portable light traps equipped with 8W ultraviolet lamps.

The studied material is deposited in the following collections:

CBG	Centre for Biodiversity Genomics, University of Guelph, Ontario, Canada
CNC	Canadian National Collection of Insects, Arachnids, and Nematodes, Ottawa, Canada
NMPC	National Museum, Prague, Czech Republic
TLMF	Tiroler Landesmuseum Ferdinandeum, Innsbruck, Austria
USNM	United States National Museum,Washington, D.C., USA
ZIN	Zoological Institute, Russian Academy of Sciences, Saint-Petersburg, Russia
ZMKU	Zoological Museum, Kyiv National Taras Shevchenko University, Kyiv, Ukraine

Male and female genitalia were dissected and prepared using standard methods for Gelechiidae (Landry 2007; Huemer and Karsholt 2010). Slide-mounted genitalia were prepared and photographed as described by Landry et al. (2013) and Bidzilya et al. (2020).

The descriptive terminology largely follows Huemer and Karsholt (1999), except cucullus instead of valva and phallus instead of aedeagus.

DNA Barcoding

A tissue sample from a specimen of *Gelechia omelkoi* sp. nov. was successfully processed at the Canadian Centre for DNA Barcoding (CBG, Biodiversity Institute of Ontario, University of Guelph) (deWaard et al. 2008), resulting in a 658 base-pair full DNA barcode segment of the mitochondrial COI gene (cytochrome c oxidase 1). Complementary public sequences of *G. mandella* (n=13), *G. sororculella* (n=17) and *G. rhombella* (n=10) from BOLD systems v. 4.0. (http://www.boldsystems.org; Ratnasingham and Hebert 2007) were used for analysis (Table 1). Degrees of intra- and interspecific variation of DNA barcode fragments were calculated under the Kimura 2-parameter model of nucleotide substitution using the analytical tools of BOLD. A neighbor-joining tree of DNA barcode data of selected taxa (Table 1) was constructed using MEGA 6 (Tamura et al. 2013) under the Kimura 2 parameter model for nucleotide substitutions.

Results

***Gelechia omelkoi* sp. nov.**

http://zoobank.org/831C091D-D8DD-44C0-A3E5-9732381EBA22
Figures 2, 6, 7, 14–16

Material examined. Holotype [Russia] • ♂; Altai, Kosh-Agatch distr., Ukok plateau; 2200 m; 19 Jul 2001; Bidzilya leg.; ZMKU.

Paratypes. Russia • 6 ♂; same collection data as for holotype; 1, 10, 20, 24, 25 Jul 2001; [genitalia slide number] 286/20, O. Bidzilya • 3 ♂; same collection data as for holotype; 22 Jul 1995 [genitalia slide number] 62/03, O. Bidzilya, all ZMKU• 2 ♂; Altai Republic, Kosh-Agatch distr., Northern part of Ukok plateau, Zhumaly river basin; 2400–2500 m; 4–6 Aug 2016; P. Huemer and B. Wiesmair leg. [Barcode identification number] TLMF Lep 20453; TLMF • 4 ♂♂; Altai, Belyashi [Dzhazator] env. (25 km NW), confluence of Argut and Karagem rivers; 49.865°N, 87.173°E; 1400 m; rocky steppe; 27–28 Jul 2017 [genitalia slide number] 21257, J. Šumpich; J. Šumpich leg. • 1 ♂; Altai, Belyashi (Dzhazator) env. (56 km SE), Dzhazator valley, 49.63°N, 88.20°E, mountain meadows near Tara river; 2300 m; 25–26 Jul 2017; [genitalia slide number] 21261, J. Šumpich; J. Šumpich leg.; all NMPC.

Table 1. Analysed specimens of *Gelechia* spp. from BOLD

Species	Sample ID	Process ID	GenBank	BIN
Gelechia mandella	08BBLEP-02943	LPAB601-08	KM542545	BOLD:AAG0039
	08BBLEP-02962	LPAB620-08	KM549242	BOLD:AAG0039
	08BBLEP-03043	LPAB701-08	KM542418	BOLD:AAG0039
	BIOUG22954-B10	GMOCL291-15	MG358112	BOLD:AAG0039
	BIOUG23126-F09	GMOLH046-15	MG360795	BOLD:AAG0039
	BIOUG23265-E04	GMOLH161-15	MG363316	BOLD:AAG0039
	BIOUG44827-B07	GMOLF029-19		BOLD:AAG0039
	BIOUG44827-B08	GMOLF030-19		BOLD:AAG0039
	BIOUG44827-B10	GMOLF032-19		BOLD:AAG0039
	BIOUG44832-B12	GMORG046-19		BOLD:AAG0039
	CNCLEP00067704	MNAJ551-09		BOLD:AAG0039
	CNCLEP00067705	MNAJ552-09		BOLD:AAG0039
	CNCLEP00100431	CNCLA1217-13		BOLD:AAG0039
Gelechia rhombella	MM02568	LEFIB736-10	HM871614	BOLD:AAE6372
	MM09529	LEFIE614-10	HM874337	BOLD:AAE6372
	MM03481	LEFIC137-10	HM871983	BOLD:AAE6372
	TLMF Lep 15352	ABOLA330-14	MN805653	BOLD:AAE6372
	TLMF Lep 15357	ABOLA335-14	MN805882	BOLD:AAE6372
	TLMF Lep 16781	ABOLA821-15	MN803821	BOLD:AAE6372
	TLMF Lep 24269	LEAST911-17	MN805984	BOLD:AAE6372
	KLM Lep 08814	LEAST1479-18	MN803550	BOLD:AAE6372
	KLM Lep 12426	LEAST1671-18	MN806057	BOLD:AAE6372
	MM05043	LEFIJ14972-20		BOLD:AAE6372
Gelechia sororculella	MM13873	LEFIA945-10	HM387078	BOLD:AAC8633
	MM00668	LEFIB214-10	HM871118	BOLD:AAC8633
	MM00669	LEFIB215-10	HM871119	BOLD:AAC8633
	MM09008	LEFIE419-10	HM874143	BOLD:AAC8633
	TLMF Lep 03819	PHLAD644-11	JN271047	BOLD:AAC8633
	TLMF Lep 05290	PHLAF120-11	MN804563	BOLD:AAC8633
	TLMF Lep 07445	PHLAG766-12	MN806665	BOLD:AAC8633
	TLMF Lep 08880	PHLAI385-13	MN804332	BOLD:AAC8633
	TLMF Lep 09231	PHLAI669-13	MN806319	BOLD:AAC8633
	TLMF Lep 12390	LEATC408-13	MN804176	BOLD:AAC8633
	TLMF Lep 11904	LEATE492-13	MN803907	BOLD:AAC8633
	TLMF Lep 16768	ABOLA808-15	MN803611	BOLD:AAC8633
	TLMF Lep 17098	ABOLB093-15	MN806268	BOLD:AAC8633
	TLMF Lep 21377	LEKOB014-16	MN804141	BOLD:AAC8633
	KLM Lep 12406	LEAST1651-18	MN806454	BOLD:AAC8633
	KLM Lep 14931	LEASV1480-19		BOLD:AAC8633
	KLM Lep 14936	LEASV1485-19		BOLD:AAC8633
Gelechia omelkoi	TLMF Lep 20453	LEALT230-16		BOLD:ADD9926

Diagnosis. The new species differs externally from most other Palaearctic species of *Gelechia* by the uniformly blackish-grey forewing without markings. *Gelechia mandella* and *G. sororculella* are similarly dark but without glossy forewings and with at least some indication of paler markings. The male genitalia are similar to those of *G. mandella*, *G. sororculella* and *G. jakovlevi*. The differences among these taxa are summarized in Table 2.

Table 2. Characters separating *G. omelkoi* sp. nov., *G. mandella*, *G. sororculella* and *G. jakovlevi*.

Characters	*omelkoi*	*mandella*	*sororculella*	*jakovlevi*
Apex of phallus	Short, weakly pointed	Elongate, pointed, broad at base	Elongate, pointed, narrow at base	Elongate, pointed, narrow at base
Ratio middle part of phallus /caecum	0,5	0,7	0,7	0,5
Fultura superior	Weakly divided, not extended to anteromedial emargination of tegumen	Weakly divided, not extended to anteromedial emargination of tegumen	Weakly divided, not extended to anteromedial emargination of tegumen	Deeply divided, extended to anteromedial emargination of tegumen
Sacculus	3/4–4/5 length of cucullus	2/3–3/4 length of cucullus	4/5 length of cucullus	4/5 length of cucullus
Posterior margin of uncus	Straight	Straight	Straight	Weakly emarginate

Description. Adult (Figs 2, 15, 16). Forewing length 6.5–7.2 mm (mean = 6.7, n=10). Wingspan 13.8–15.0 mm. (mean = 14.4, n=10). Head, thorax and tegulae black, with rare grey-tipped scales on frons, labial palpus black mixed with white, underside of palpomere 2 with brush of long scales separated by medial gap, white on the inner side, scape black, flagellomeres black, ringed with grey, densely ciliated beneath, forewing overall matt, covered with grey brown- or grey-tipped scales, without markings, fringe grey, brown-tipped; hindwing grey, veins mottled with brown.

In male, sternum VIII rounded, anterior part narrow, reverse-trapezoid; tergum VIII elongate, tongue-shaped, with paired long coremata (Fig. 14).

Male genitalia (Figs 6, 7). Uncus broadly rounded, two times broader than long, posterior margin weakly serrated, edged with long setae, distal sclerite of gnathos absent, lateral sclerites slender, short, culcitula broad, pillow-shaped, fultura superior extended anteriorly to about 2/3 length of tegumen, not reaching anteromedial emargination of tegumen, tegumen nearly parallel-sided, 2.5 times longer than broad at base; cucullus slender, of even width, extended to apex of uncus, sacculus in its broadest part 2–3 times as broad as cucullus, apex tapered, curved inwards, extended to 3/4–4/5 length of cucullus, vinculum broad, medial processes rounded, broadly separated; saccus tapered, extended far beyond apex of pedunculi; phallus slightly shorter than tegumen, medial section nearly parallel-sided, caecum distinctly inflated, about 2 times as broad as phallus, apex short, weakly pointed, lateral lobe reverse V-shaped, lateral process short, thorn-shaped, medial sclerite slender, elongate; bulbus ejaculatorius moderately long, sack-shaped, with small irregularly shaped lamina.

Female genitalia. Unknown.

Biology. Part of the type series, including the holotype, was collected by netting during early sunrise around dwarf willows (*Salix glauca* and others) at altitudes from 2200 to 2500 m. It is highly likely that one of these *Salix* species is a host plant for the larvae, and that the new species is restricted in its distribution to mountain areas where its possible host plant occurs. Other specimens were attracted to light in the

Figure 1. Neighbor-Joining tree of *Gelechia omelkoi* sp. nov. and nearest European and North American *Gelechia* spp. in BOLD, with the generic type species *Gelechia rhombella* as outgroup (Kimura 2-parameter, constructed with MEGA 6 cf. Tamura et al. 2013), only sequences >500 bp considered. The scale bar only applies to internal branches between species. Width of triangles represents sample size, depth represents genetic variation within the cluster. Source: DNA Barcode data from BOLD (Barcode of Life Database, cf. Ratnasingham and Hebert 2007).

same habitats, in mountains meadow or rocky steppe from 1400 to 2500 m (Figs 23, 24). *Gelechia sororculella* is also known from neighboring territories of Altai, but was observed in river valleys (Chuya, Chagan). This species is associated with several species of *Salix* (Huemer and Karsholt 1999), but not with the dwarf willows presumed to be the host for *G. omelkoi* sp. nov.

Molecular data. BIN: BOLD:ADD9926 (n=1). The minimum distance to the nearest neighbour, the North American *G. mandella*, is 2.88%, whereas it is 5.94% distant from the nearest Palaearctic *G. sororculella* (Fig. 1).

Distribution. Russia: Altai Republic, Ukok plateau and South Chuisky ridge.

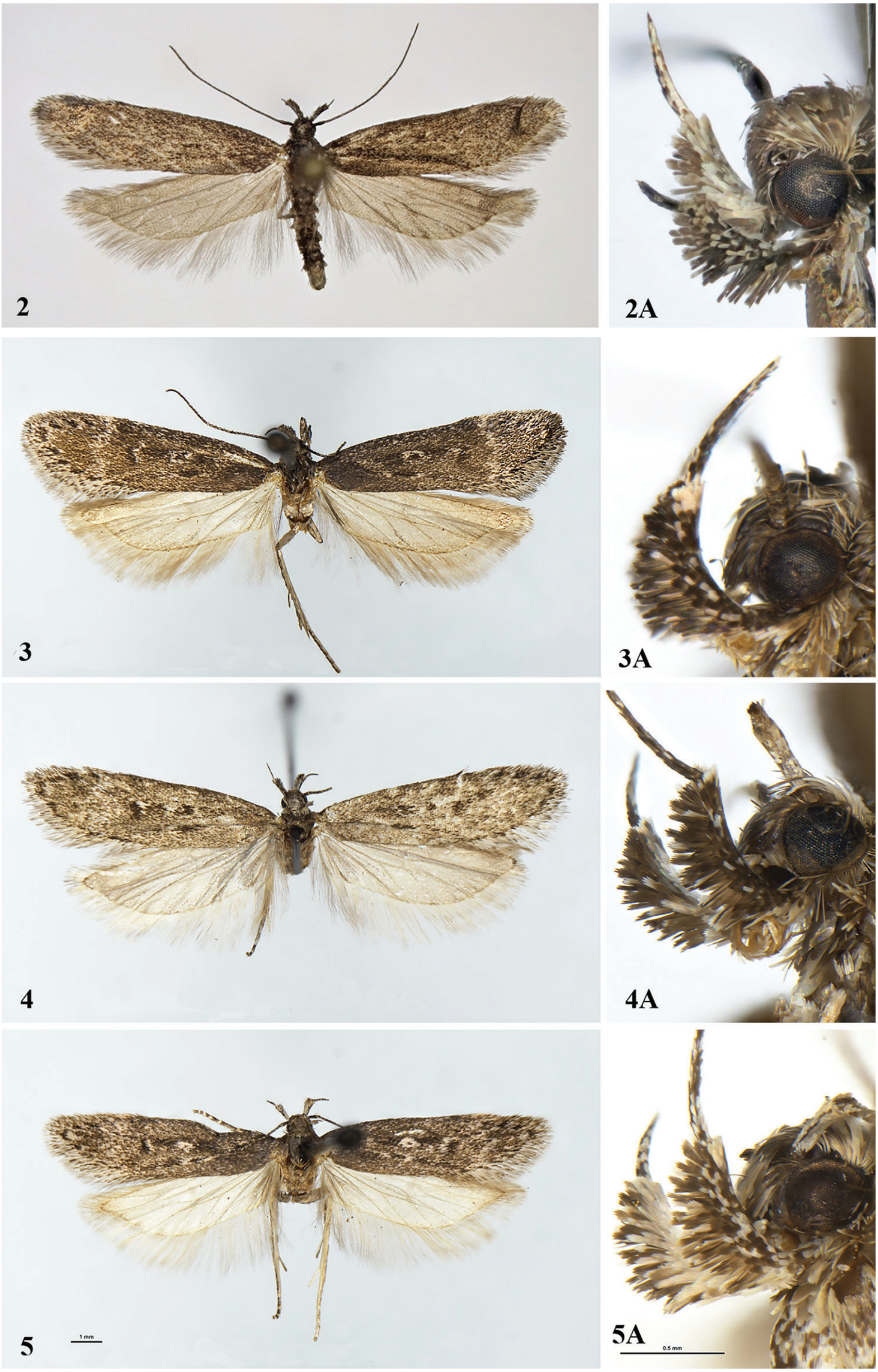
Etymology. The new species is named in honour of Mikhail M. Omelko (Federal Scientific Center of East Asia Terrestrial Biodiversity, Far Eastern Branch, Russian Academy of Sciences, Vladivostok, Russia), in recognition of his contribution to the study of Gelechiidae, and the genus *Gelechia* in particular. The species name is a noun in the genitive case.

Gelechia mandella Busck, 1904

Figs 3–5, 8, 9, 12, 13

Gelechia mandella Busck, 1904. – Proceedings of the United States National Museum 27 (1375): 759. Type locality: Kaslo, British Colombia, Canada.

Material examined. [Canada] • 16 ♂; Alberta, Nordegg, [54.470°N, 116.075°W], various dates from 29 Jun – 6 Aug 1921; [barcoded male 4 Jul 1921]; bred from larva on Willow; J. McDunnough leg. [specimen number] CNCLEP00100431; [genitalia slide number] MIC 8484; [other males numbers] CNCLEP00100430–100433, CNCLEP00127961–127973 • 1 ♀; same collection data as for proceeding, 10 Jul 1921 [specimen number] CNCLEP00127968; [genitalia slide number] MIC 8485 • 2 ♂;



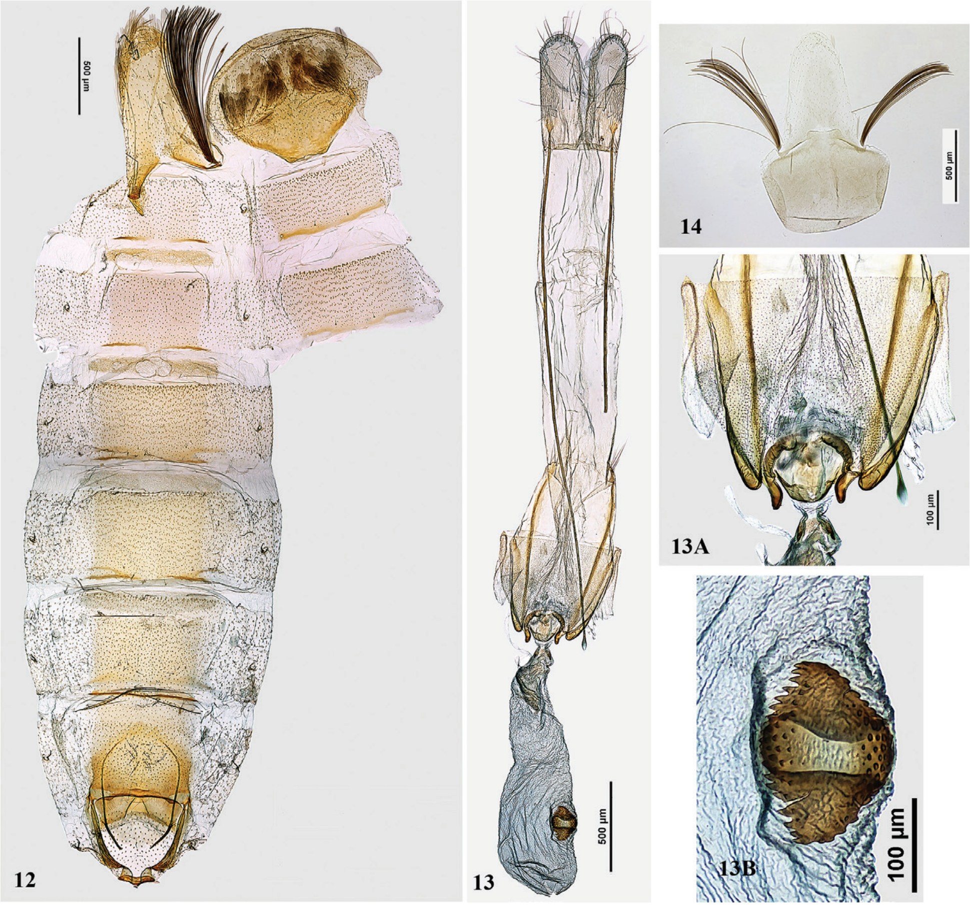
Figures 2–5. *Gelechia* spp. Adults. **2, 2A** *Gelechia omelkoi* sp. nov. **2** adult, holotype **2A** head, paratype **3–5** *G. mandella* **3, 3A** male, Alberta **3** adult **3A** head **4, 4A** male, Yukon **4** adult **4A** head **5, 5A** female Alberta **5** adult **5A** head.

Figures 6–11. *Gelechia* spp., male genitalia. **6, 7** *G. omelkoi* sp. nov., paratypes **6** genitalia slide 286/20, O. Bidzilya **7** genitalia slide 62/03, O. Bidzilya **8, 9** *G. mandella* **8** Alberta, genitalia slide MIC 8484 **9** Yukon, genitalia slide MIC 8486 **10** *G. sororculella*, genitalia slide 287/20, O. Bidzilya **11** *G. jakovlevi*, lectotype, genitalia slide 309/20, O. Bidzilya.

Yukon, km 140.5 Dempster Hwy, [65.069°N, 138.129°W], 900 m, 28 Jul 1980; D. Wood and J. Lafontaine leg.; [specimen number] CNCLEP00067704–67705; genitalia slide number [MIC 8486]; all in CNC.

Diagnosis. *Gelechia mandella* is a blackish-grey, medium-sized species with a black streak interrupted by diffuse white spots in the middle of the forewing, a black streak in fold and a diffuse white subapical fascia. The wing pattern resembles that of the Holarctic species *Gelechia sabinellus* (Zeller, 1839), but it is darker and predominantly black rather than grey. Additionally, *G. sabinellus* has strikingly differently coloured scales on the labial palps. The Palaearctic *G. sororculella* looks nearly indistinguishable externally (Fig. 19).

Redescription. Adult (Figs 3–5). Forewing length 7.8–9.4 mm (mean = 8.6, n=18). Wingspan 15.9–18.7 mm (mean = 17.1, n=16). Head, thorax and tegulae greyish



Figures 12–14. *Gelechia* spp., genitalia and abdomen. **12, 13** *G. mandella*. **12** abdomen, male, genitalia slide MIC 8484 **13A, B** Female genitalia, slide MIC 8485 13A segment VIII (enlarged) **13B** Signum (enlarged) **14** *G. omelkoi* sp. nov., male segment VIII, genitalia. slide 62/03, O. Bidzilya.

black, labial palpus black mixed with white, palpomere 2 underside with brush of long scales divided by medial gap, inner side entirely white in some specimens, scape black, flagellomeres black, ringed with light grey, forewing greyish black, sparsely mixed with white-tipped scales, fold with black medial streak edged with white from both ends, indistinct black streak in middle 2/3 interrupted by large white spot at 1/2 and much smaller white spot at 2/3, diffuse white fascia at about 3/4, termen black-spotted, cilia white, black-tipped; hindwing light grey with grey cilia and distinctly darkened veins.

In male, sternum VIII rounded in distal part, reverse trapezoid basally; tergum VIII elongate, tongue-shaped, with paired, long coremata (Fig. 12).

Male genitalia (Figs 8, 9). Uncus broadly rounded, twice wider than long, posterior margin weakly serrated, edged with long setae, distal sclerite of gnathos absent, lateral sclerites slender, short, culcitula slightly wider than uncus, pillow-shaped, fultura superior extended anteriorly to about 2/3 length of tegumen, not reaching anteromedial emargination of tegumen, tegumen nearly parallel-sided, 2.5 times as long as broad at base; cucullus slender, of even width, extended to apex of uncus, sacculus in its broadest part 1.5–2.0 times as broad as cucullus, apex tapered, curved inwards, extended to 2/3–3/4 length of cucullus, vinculum broad, medial processes rounded, broadly separated; saccus weakly or distinctly narrowed apically, extended far beyond apex of pedunculi; phallus slightly shorter than tegumen, medial portion nearly straight or with dorsal side slightly curved, caecum weakly inflated, about 1.5 times as broad as phallus, apex moderately elongate, triangularly pointed with comparatively broad base, dorsal lobe beak-shaped and recurved, lateral process short, thorn-shaped, medial sclerite slender, elongate; bulbus ejaculatorius elongate, sack-shaped, with small, irregularly shaped lamina.

Female genitalia (Figs 13, 13A, 13B). Papillae anales elongate, subovate, with straight anterior margin; apophyses posteriores three times as long as segment VIII, apophyses anteriores reduced to melanized bands fused to lateral wall of sternum VIII; sternum VIII three times longer than broad, with narrow, sclerotized lateral rods, wrinkled along medial membranous zone, with strongly sclerotized short anterolateral drop-shaped processes confluent with apices of apophyses anteriores; subgenital plate small, band-shaped, with short, pointed anterior protrusions near anterior margin of sternum VIII; ostium rounded, with distinct posterolateral edging connected anteriorly with base of apophyses anteriores; antrum cylindrical, colliculum short, trapezoid, laterally sclerotized; ductus bursae very short, broadened into corpus bursae, with indistinct transition, corpus bursae as long as and slightly wider than adjacent part of ductus bursae, signum plate subovate, with serrate margins and broad transverse medial groove.

Biology. Adults have been collected from late June to early August in Alberta and in late July in Yukon. Two specimens from Nordegg, Alberta were reared from an unspecified willow.

Molecular data. BIN: BOLD:AAG0039. The intraspecific average distance of the barcode region is 0.14% (n=13, data from BOLD). The minimum distance to the nearest neighbour, the Palaearctic *G. omelkoi* sp. nov., is 2.88% (Fig. 1).

Distribution. Canada: British Columbia, Alberta, Yukon (new record), Northwest Territories (new record). Two alleged records from Montana, USA in SCAN (2021) are represented by photographs taken on 14–15 May 2018 near the town of Missoula in the mountainous western part of the state. Although the superficial appearance of the moths on the photos makes it possible that this be *G. mandella*, their identity remains unverified. The same website also shows two Northwest Territories records, which are actually sourced from two BOLD public records analyzed here (BIOUG23265-E04 and BIOUG23126-F09 deposited in CBG; see Table 1). The record from Quebec in Pohl et al. (2018) was based on a female specimen in CNC from Forestville (specimen # CNCLEP00100429), which has since been barcoded and belongs to a different BIN (BOLD:AAH6283). It is here excluded and likely represents a different species.

Remarks. Busck (1904) described *Gelechia mandella* from an unspecified number of specimens, as indicated by a size range accompanying the original description. There is a series of specimens of *G. mandella* identified by Busck in the collection of USNM. We assume four of them, with red type labels, are from Busck's original series. None of these syntypes has a locality label, only a Dyar field number, which corresponds with Kaslo, British Columbia (Canada). This series comprises two females collected 15.08.1903 (USNM slide #6773 (genitalia), USNMENT01480487 and USNM slide #6779 (wings), USNMENT01480485); one specimen without an abdomen, collected 13.08.1903 (USNMENT01480486); and one dissected male collected 5.08.1903. This last specimen, labelled "type No. 7859, U.S.N.M", "Genitalia Slide 6775, by AB, ♂, USNM", "*Gelechia mandella* Busck, Type" (USNMENT00835335) was incorrectly published as the "holotype" by Brown et al. (2004). Photographs of the specimen, its labels, and the genitalia are available online (https://collections.nmnh.si.edu/search/ento/?ark=ark:/65665/38eb1f15df800489fac64727ff945379c). At one time, the USNMENT00835335 specimen was labelled with "Mesilla, NM [New Mexico]." This was likely due to a mix-up when labels were removed from the pins to be photographed and the Mesilla label belongs to another type, possibly *Gelechia malindella* Busck, 1910 [a junior synonym of *Friseria cockerelli* (Busck, 1903)]. The label error for the USNMENT00835335 specimen is now corrected. Here, we designate the USNMENT00835335 specimen among the likely syntypes as lectotype of *G. mandella*, to stabilize nomenclature.

The CNC series from Nordegg, Alberta collected in 1921 was identified as *G. mandella* by Annette Braun. Despite the difficulty to interpret some characters of the male genitalia from the photo of the lectotype slide of *G. mandella*, visible features match those of the barcoded specimens. Taking also into consideration the similarity in external appearance, we are confident that specimens from Yukon and Alberta represent *G. mandella*.

Discussion

The genus *Gelechia* is represented by 22 species in Europe, and the European fauna was revised and studied in detail by Huemer and Karsholt (1999). In North America, 40 valid species are recognized, but the genus has never been the object of any revision and several names remain of uncertain identity (Lee et al. 2009). In Russia, the genus was revised for the Far East (Omelko 1986), and the data on the distribution of 24 species throughout the country were summarized (Ponomarenko 2019). Until recently, 10 species were recorded from Siberia, including the rather unexpected finding of *Gelechia repetitrix* Meyrick, 1931 from the Omsk region (Ponomarenko and Knyazev 2020). Currently, six species of *Gelechia* are known from the Altai, but records of additional species (e.g., *G. turpella* ([Denis & Schiffermüller], 1775) are expected. Below, we provide a list of *Gelechia* species known from the Altai Republic of Russia, with updated information on their distribution and corresponding references.

Gelechia sororculella (Hübner, [1817])

Figs 10, 19

Records. Bidzilya et al. 2002: 207. Misidentification of *G. omelkoi* sp. nov.

Material examined. Russia • 1 ♂; Altai Republic, Shebalino distr., Cherga env.; 17 Jul 1995; P. Ustjuzhanin leg.; ZMKU • 1 ♂, Russia, Altai, Kosh-Agatch distr., 15 km from Beltir. vil. up on Tchagan river; steppe; 2200 m; 13 Aug 2000; O. Bidzilya leg.; [genitalia slide number] 287/20, O. Bidzilya; ZMKU • 1 ♂; Altai, Kosh-Agatch env., Tchuja river bank; on trunk of Salix sp.; 17 Aug 2000; O. Bidzilya leg.; ZMKU.

Kyrgyzstan • 1 ♂; 5 km S of At-Bashi, Narynskaya oblast; 15 Aug 1981; S. Sinev leg.; ZIN.

Remarks. The previous record of this species from Ukok plateau in Altai (Bidzilya et al. 2002: 207) refers to *G. omelkoi* sp. nov.

Distribution. Palaearctic Region from Spain to Russian Far East (Huemer and Karsholt 1999; Ponomarenko 2019); Kyrgyzstan (new record).

Gelechia omelkoi sp. nov.

Material examined. (see above).

Distribution. Russia (Altai Mts).

Gelechia jakovlevi Krulikovsky, 1905

Figs 11, 17, 18

Records. Bidzilya 2002: 69.

Material examined. Russia • 1 ♀; Altai, Ongudai distr., 15 km from Iodro vil. down on Tchuja river; 6 Aug 2000; O. Bidzilya leg.; [genitalia slide number] 293/20, O. Bidzilya; ZMKU • 1 ♂, Russia, Altai, Belyashi (Dzhazator) env. (25 km NW), confluence of Argut and Karagem rivers; rocky steppe; 49.865°N, 87.173°E; 1400 m; 27–28 Jul 2017 [genitalia slide number] 21265, J. Šumpich; J. Šumpich leg.; NMPC.

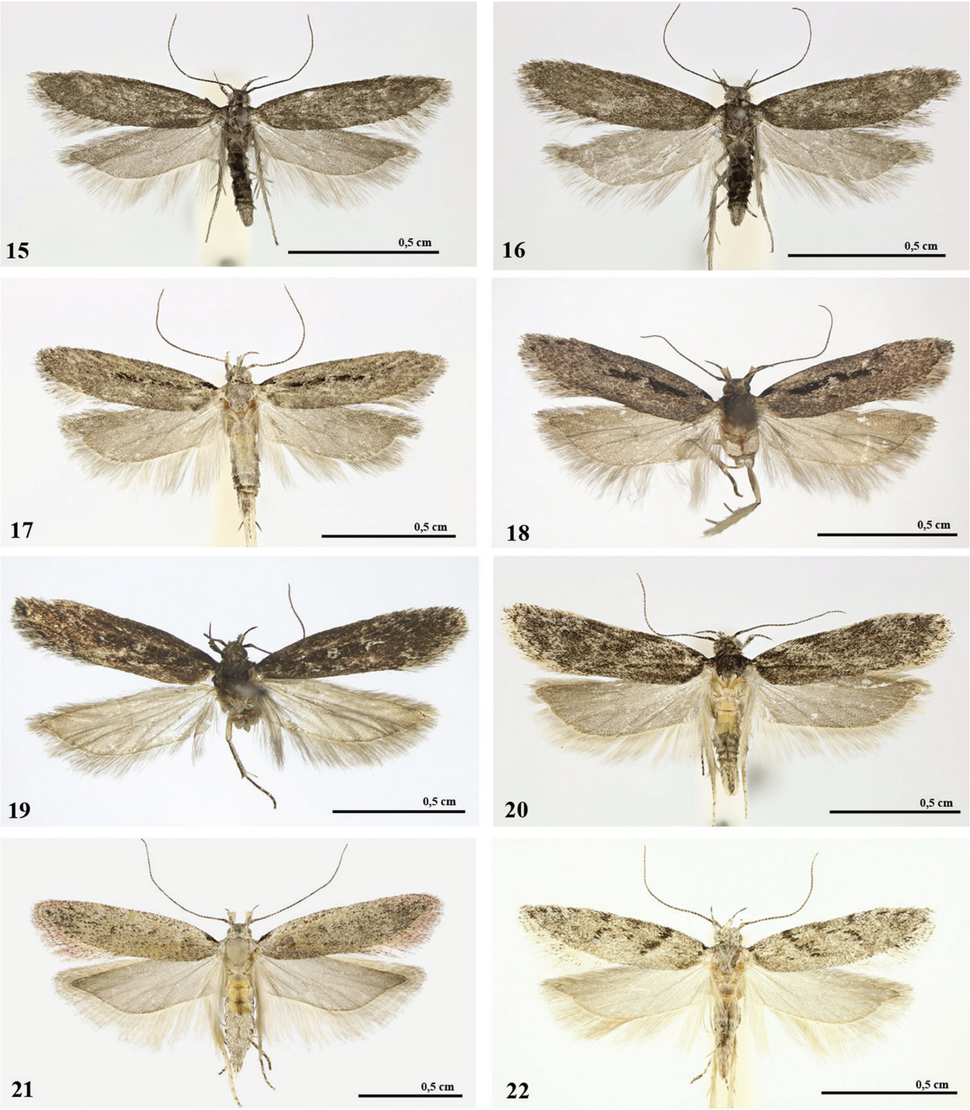
Distribution. Northern and eastern Europe, Russia: European part, Tomsk region, Altai, Buryatia (Huemer and Karsholt 1999; Ponomarenko 2019); Mongolia (ssp. *mongoliae* Emeljanov & Piskunov, 1982).

Remarks. *Gelechia jakovlevi mongoliae* was described based on a female from Songino, western Mongolia. The status of this taxon needs clarification after examination of a male, which is unknown to us.

Gelechia muscosella Zeller, 1839

Fig. 20

Records. Bidzilya 2002: 68.



Figures 15–22. *Gelechia* spp., adults. **15, 16** *G. omelkoi* sp. nov., paratypes, males. **15** Dzhazator. **16** Karagem. **17, 18** *G. jakovlevi*. **17** Male, Karagem. **18** Female, Iodro **19** *G. sororculella*, male, Cherga **20** *G. muscosella*, male, Aktash **21** *G. hippophaella*, female, Karagem **22** *G. sirotina*, male, Karagem.

Material examined. Russia • 1 ♂; Gornoaltaisk; 15 Jul 1997; A. Lvovsky leg.; ZIN • 1 ♂; Altai, Aktash vill.; grassy steppe, rocks; 50.320°N, 87.60°E; 1400 m; 11 Jul 2014; J. Šumpich leg.; NMPC.

Distribution. Palaearctic Region from Great Britain to Far East of Russia and China: Qinghai, Gansu, Shaanxi (Huemer and Karsholt 1999; Li 2002).

Figures 23, 24. Habitats of *Gelechia omelkoi* sp. nov. **23** Steppe near the confluence of Argut and Karagem rivers **24** mountain steppe near Dzhazator (photographs by Jan Šumpich).

Gelechia hippophaella (Schrank, 1802)

Fig. 21

Records. Piskunov 1981: 669.

Material examined. Russia • 1 ♀; Altai, Belyashi (Dzhazator) env. (25 km NW), confluence of Argut and Karagem rivers; rocky steppe; 49.865°N, 87.173°E; 1400 m; 27–28 Jul 2017 J. Šumpich leg.; NMPC.

Distribution. Northern, central and south-eastern Europe; Siberia: Altai, Tuva, Buryatia; China: Ningxia (Huemer and Karsholt 1999; Li 2002; Ponomarenko 2019), unconfirmed record from Mongolia (Piskunov 1990).

Gelechia sirotina Omelko, 1986

Fig. 22

Material examined. Russia • 1 ♂; Altai, Belyashi (Dzhazator) env. (25 km NW), confluence of Argut and Karagem rivers; rocky steppe; 49.865°N, 87.173°E; 1400 m; 27–28 Jul 2017 [genitalia slide number] 19922, J. Šumpich; J. Šumpich leg.; NMPC.

Distribution. Belarus; Tajikistan (Piskunov 1989); Russia: Altai (new record), Tuva, Zabaikalskiy krai, Primorskiy krai (Ponomarenko 2019).

Acknowledgements

The work was supported by the Ukrainian State Budget Program "Support for the Development of Priority Areas of Scientific Research" (Code: 6541230) (O. Bidzilya) and by the Ministry of Culture of the Czech Republic (DKRVO 2019−2023/5.I.c, National Museum, 00023272) (J. Šumpich). PH would like to thank Roman Yakovlev for organization of the expedition to the Altai Mountains, and Benjamin Wiesmair for assistance during field work. We are thankful to Sangmi Lee and Ole Karsholt for valuable comments on the manuscript. Our special thanks to Mark A. Metz (Systematic Entomology Laboratory—USDA) for clarifying the status of the primary types of *G. mandella*, providing information on and images of the Busck material, and editorial suggestions concerning the manuscript.

References

Bidzilya OV (2002) On the distribution of Gelechiid Moths (Lepidoptera, Gelechiidae) in the Southern Siberia. Contribution 1. The Kharkov Entomological Society Gazette 9(1–2) [2001]: 64–72. [In Russian]

Bidzilya OV, Budashkin YI, Klyuchko ZF, Kostjuk IY (2002) A contribution to the knowledge of the Lepidoptera fauna of the Ukok plateau in south-eastern Altai, Russia. Entomofauna 23(17): 201–218.

Bidzilya O, Budashkin Y, Yepishin V (2020) Review of the tribe Anerastiini (Lepidoptera: Pyralidae: Phycitinae) from Ukraine. Zootaxa 4718(1): 1–24.

Brown J, Adamski D, Hodges RW, Bahr SM (2004) Catalogue of the type specimens of Gelechioidea (Lepidoptera) in the collection of the National Museum of Natural History, Smithsonian Institution, Washington, DC. Zootaxa 510: 3–160.

Busck A (1904) Tineid Moths from British Columbia, with Descriptions of New Species. Proceedings of the United States National Museum 27 (1375): 745–778.

deWaard JR, Ivanova NV, Hajibabaei M, Hebert PDN (2008) Assembling DNA Barcodes: Analytical Protocols. Pp. 275–293 In: Martin CC (Ed.) Methods in Molecular Biology: Environmental Genomics. Humana Press Inc., Totowa, USA, 364 pp.

Emelyanov IM, Piskunov VI (1982) New data on the fauna of the gelechiid and anarsiid moths (Lepidoptera: Gelechiidae, Anarsiidae) of Mongolia, the USSR and North China. Nasekomye Mongolii 8: 366–407. [In Russian]

Huemer P, Karsholt O (1999) Gelechiidae I (Gelechiidae: Gelechiinae, Teleiodinae). In: Huemer P, Karsholt O, Lyneborg L (Eds) Microlepidoptera of Europe. Vol. 3. Apollo Books, Stenstrup, 356 pp.

Huemer P, Karsholt O (2010) Gelechiidae II (Gelechiinae: Gnorimoschemini). In: Huemer P, Karsholt O, Nuss M (Eds) Microlepidoptera of Europe. Vol. 6. Apollo Books, Stenstrup, 586 pp.

Huemer P, Wieser Ch, Wiesmair B, Sinev SYu, Wieser Ch, Yakovlev RV (2017) Schmetterlinge (Lepidoptera) des Altai-Gebirges (Südsibirien, Russland) – Eindrücke einer internationalen Expedition im Spätsommer 2016. Carinthia II n 207./127. Jahrgang n Seiten 527–564 n Klagenfurt 2017.

Landry J-F (2007) Taxonomic review of the Leek Moth genus *Acrolepiopsis* (Lepidoptera: Acrolepiidae) in North America. The Canadian Entomologist 139(3): 319–353.

Landry J-F, Nazari V, deWaard JR, Mutanen M, Lopez-Vaamonde C, Huemer P, Hebert PDN (2013) Shared but overlooked: 30 species of Holarctic Microlepidoptera revealed by DNA barcodes and morphology. Zootaxa 3749(1): 1–93.

Lee S, Hodges RW, Brown RL (2009) Checklist of Gelechiidae (Lepidoptera) in America North of Mexico. Zootaxa 2231: 1–39.

Omelko MM (1986) Gelechiid moths of the genus *Gelechia* (Lepidoptera, Gelechiidae) of the Southern Primorie. Akademia Nauk SSSR. Issledovanija po systematiki tcheshuekrylykh nasekomykh fauny SSSR. Trudy Zoologichesko Instituta [USSR Academy of Sciences. Proceedings of the Zoological Institute, Studies on systematics of lepidopterous insects of the fauna of the USSR] 145: 84–109. [In Russian]

Piskunov VI (1981) 50. Fam. Gelechiidae. In: Medvedev GS (Ed.) Key to the insects of the European part of USSR 4(2): 659–48. Leningrad, Nauka. [In Russian]

Piskunov VI (1989) Fauna vyemchatokrylykh molei (Lepidoptera, Gelechiidae) Belorusskoi SSR po resultatam issledovanii 1978–1988 gg [Gelechiid Moths of Belarussia based on study in 1978–1988]. Dinamica zootsenozov, problemy ochrany i ratsionalnogo ispol'zovaniaya zhivotnogo mira Belorussii. VI Zoological Conference, Theses of reports (19–21 September 1989), Vitebsk. Nauka i technika, Minsk, 100–101. [In Russian]

Piskunov VI (1990) Second addition to the fauna of the gelechiid moths (Lepidoptera, Gelechiidae) of Mongolia. Nasekomye Mongolii 11: 285–316. [In Russian]

Pohl GR, Landry J-F, Schmidt BC, Lafontaine JD, Troubridge JT, Macaulay AD, van Nieukerken EJ, deWaard JR, Dombroskie JJ, Klymko J, Nazari V, Stead K (2018) Annotated checklist of the moths and butterflies (Lepidoptera) of Canada and Alaska. Series Faunistica. Pensoft, 580 pp.

Ponomarenko MG (2019) Gelechiidae. In: Sinev SYu (Ed.) Katalog cheshuekrylykh (Lepidoptera) Rossii [Catalogue of the Lepidoptera of Russia]. Edition 2. Saint Petersburg: Zoological Institute of the Russian Academy of Sciences, 91–112. [In Russian]

Ponomarenko MG, Knyazev SA (2020) On the fauna of Gelechiid Moths from the Omsk region. Amurian Zoological Journal 12(3): 275–285. [In Russian]

Ratnasingham S, Hebert PDN (2007) BOLD: The Barcode of Life Data System (http://www.barcodinglife.org). Molecular Ecology Notes 7: 355–364.

SCAN (2021) SCAN. https://scan-bugs.org/portal/taxa/index.php?taxauthid=1&taxon=275451&cl=104 [Accessed 14 June 2021]

Tamura K, Stecher G, Peterson D, Filipski A, Kumar S (2013) MEGA6: Molecular Evolutionary Genetics Analysis version 6.0. Molecular Biology and Evolution 30: 2725–2729.

ZooKeys 1063: 121–137 (2021)
doi: 10.3897/zookeys.1063.73094
https://zookeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
ZooKeys
Launched to accelerate biodiversity research

A new species of *Pseudosinella* Schäffer, 1897 (Collembola, Entomobryidae) from Hungary and Romania, with redescription of the related species *Pseudosinella huetheri* Stomp, 1971

Daniel Winkler[1], Márton Tamás Németh[2], Cristina Fiera[3]

1 University of Sopron, Faculty of Forestry, Institute of Wildlife Management and Wildlife Biology, Bajcsy–Zs. str. 4, H–9400 Sopron, Hungary **2** *University of Sopron, Forest Research Institute, Paprét 17., H–9400 Sopron, Hungary* **3** *Institute of Biology Bucharest of Romanian Academy, 296 Splaiul Independenţei, P.O. Box 56–53, 060031, Bucharest, Romania*

Corresponding author: Daniel Winkler (winklerdanielandras@gmail.com)

Academic editor: L. Deharveng | Received 17 August 2021 | Accepted 19 September 2021 | Published 20 October 2021

http://zoobank.org/4A798206-7211-4790-9802-72A52646CA97

Citation: Winkler D, Németh MT, Fiera C (2021) A new species of *Pseudosinella* Schäffer, 1897 (Collembola, Entomobryidae) from Hungary and Romania, with redescription of the related species *Pseudosinella huetheri* Stomp, 1971. ZooKeys 1063: 121–137. https://doi.org/10.3897/zookeys.1063.73094

Abstract

A new species of the genus *Pseudosinella* Schäffer, 1897 from Hungary and Romania is described and illustrated. *Pseudosinella hartnerae* **sp. nov.** belongs to the group with 5+5 eyes, and can be identified by its unique labial chaetotaxy ($M_1m_2rel_1L_2$) within this group. *Pseudosinella huetheri* Stomp, 1971, the closest related species sharing the same dorsal macrochaetae formula ($R_0R_1R_2$001/00/0101+2), is also redescribed here based on the holotype. Comparative analysis between the two species and among other related species is provided.

Keywords

Chaetotaxy, *Pseudosinella hartnerae* sp. nov., springtails, taxonomy

Introduction

Pseudosinella Schäffer, 1897 is the largest collembolan genus, represented by 382 described species worldwide (Bellinger et al. 2021), inhabiting a wide range of habitats from xerophilic areas (e.g., Traser et al. 2006) through caves (e.g., Gisin and Gama 1969; Cipola et al. 2020) to wetlands like alluvial forests (e.g., Buşmachiu et al. 2017; Winkler and Mateos 2018).

As a part of soil biodiversity surveys in Hungary, the Bátorliget Pasture Nature Conservation Area was revisited in 2017. Among the collected Collembola material, a new species of *Pseudosinella* Schäffer, 1897 was discovered and is described in the present paper. Around the same time, Collembola samplings were carried out in Romania Mohoş Nature Reserve, from where the same *Pseudosinella* species was also found. The genus was previously represented by 17 species in Hungary (Dányi and Traser 2008; Winkler and Mateos 2018) and 24 species in Romania (Fiera 2013). However, its richness is probably underestimated and doubtless destined to increase with further taxonomic efforts in both countries.

The new species belongs to the group of species with 5+5 eyes. With the help of the computer assisted Delta identification key using the combination of chaetotaxic and other characters, originally designed by Christiansen et al. (1990) and regularly updated by Jordana et al. (2021), *Pseudosinella huetheri* Stomp, 1971 was found to be its closest related species. Therefore, on this occasion, *Pseudosinella huetheri* was also examined and redescribed from the holotype preserved in the Natural History Museum of Geneva (Switzerland).

Material and methods

In October 2017, soil samplings were carried out in the Bátorliget Pasture Nature Conservation Area (East Hungary). A month later, soil mesofauna samplings were carried out also in Romania, around St. Ana Lake (Mohoş Nature Reserve). Springtails were extracted from the hand collected litter and soil samples within 14 days using a modified Berlese–Tullgren apparatus (without light or heating devices). The specimens were cleared using Nesbitt fluid and then mounted on permanent slides in Hoyer's medium. The slides were examined under a Leica DM2500 LED microscope with conventional bright light and phase contrast.

Abbreviations used in text and figures are:

Abd	abdominal tergite;
accp	accessorial p–sensilla;
Ant	antennal segment;
a.s.l.	above sea level;
HNHM	Hungarian Natural History Museum, Budapest;
IBB	Institute of Biology Bucharest, Romanian Academy;

NHMG	Natural History Museum of Geneva;
Mac	macrochaeta;
mic	microchaeta;
psp	pseudopore;
Th	thoracic tergite.

Symbols used in figures:

open circle	Mac;
black dots	mic;
x	trichobotria.

Terminology

Dorsal head chaetotaxy follows Gisin (1967), Jordana and Baquero (2007) and also the "AMS" nomenclature of Soto-Adames (2010). Clypeal chaetotaxy follows Yoshii and Suhardjono (1992). For the labial palp, the notation of Fjellberg (1999) was used. For labial chaetotaxy, Gisin's nomenclature (1964) was applied, while for postlabial chaetotaxy, the notations of Chen and Christiansen (1993) and Cipola et al. (2018) were used. Dorsal chaetotaxy schemes of thoracic and abdominal segments follow Gisin (1967) and Szeptycki (1972, 1979), except for chaeta m_7a on Abd III (following Wang et al. 2003) and chaeta p_8p on Abd III (following Mateos 2008). The tergal specialized chaetae (S–chaetae) pattern follows Zhang and Deharveng (2015).

Taxonomy

Class Collembola Lubbock, 1873
Order Entomobryomorpha Börner, 1913
Family Entomobryidae Schäffer, 1896
Subfamily Lepidocyrtinae Wahlgren, 1906
Genus *Pseudosinella* Schäffer, 1897

Pseudosinella hartnerae Winkler & Fiera, sp. nov.

http://zoobank.org/EC5FA909-3CA5-4164-AAB2-E0AAFC5D989C
Figures 1–5

Type material. *Holotype*: Hungary. ♀ on slide (Nr. HNHM collpr-896), Bátorliget, Szabolcs–Szatmár–Bereg county, 161 m a.s.l., 47°46'11"N, 22°16'19"E, from litter, hand collecting, 8 Oct. 2017, leg. D. Winkler. ***Paratypes*:** Two ♀ and one ♂ on slide (Nr. HNHM collpr-896); two ♀ and one specimen with sex not visible (Nr.: HNHM collpr-897); two ♀ (Nr. WD–coll–113 and WD–coll–114); same data as holotype. The holotype and four paratypes are deposited in the Hungarian Natural History Mu-

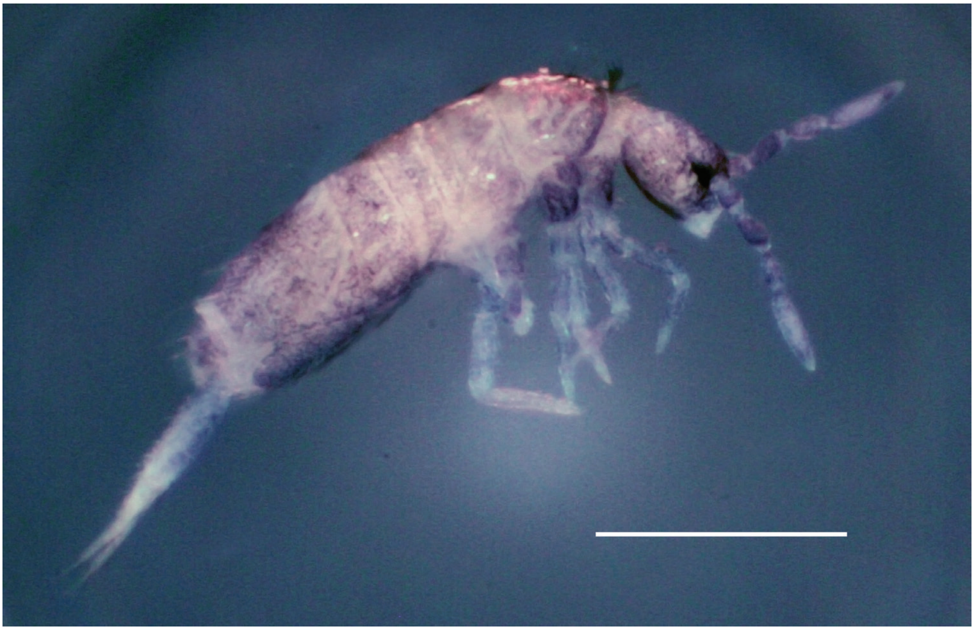


Figure 1. *Pseudosinella hartnerae* sp. nov. Habitus. Scale bar: 0.5 mm.

seum (HNHM), Budapest. Two paratypes are preserved in the first author's collection at the University of Sopron, Faculty of Forestry, Sopron, Hungary; one paratype is kept in C. Fiera's collection (IBB).

Other material. Romania. Seven specimens (one ♂ on slide, Nr.: IBB Coll-12544; and six specimens of sex not determined in ethyl alcohol, vial Nr. IBB–26), Lake Saint Ana, Harghita County, Romania, 984 m a.s.l., 46°7'33"N, 25°53'28"E, 2 Nov. 2017, mixed forest with beech and fir, from litter, hand collecting, leg. C. Fiera.; 4 specimens (one ♀ on slide, Nr. IBB Coll–12545; and three specimens of sex not determined in ethyl alcohol, vial Nr. IBB–26), Mohoş peat bog, 1050 m a.s.l., 46°8'6"N, 25°53'59"E, 2 Nov. 2017, Scots pine forest, from peat moss *Sphagnum*, hand collecting, leg. C. Fiera. Preserved in the last author's collection (IBB).

Diagnosis. 5+5 ocelli. Colour bluish-grey. Labial chaetotaxy $M_1m_2rel_1L_2$, r vestigial. Dorsal macrochaetae formula $R_0R_1R_2001/00/0101+2$. Abd II chaetotaxy: $paBq_1q_2$. Abd IV accessory chaeta s, anteriorly to trichobothrial complex, absent. Antennae and legs without scales. Unguis inner side with two paired basal teeth and one unpaired tooth. Unguiculus outer lamella smooth.

Description. ***Habitus*** (Fig. 1). Body length (without head and furca) 1.01–1.27 mm (holotype: 1.08 mm). Colour: Head, antennae, trunk and legs bluish-grey, blue shades also on manubrium and ventral tube. Eye patches dark blue.

Head. With 5+5 eyes (ABCDH, with H only slightly smaller). Dorsal cephalic main macrochaetae formula $R_0R_1R_2P$ (according to AMS notation A_0, A_2, A_3 and Pa_5) (Fig. 2A). Maximum number of macrochaetae "An" on head 9+9. Antennal length to head diagonal length (measured from cervical edge to apex of labrum) ratio 1.2–1.4

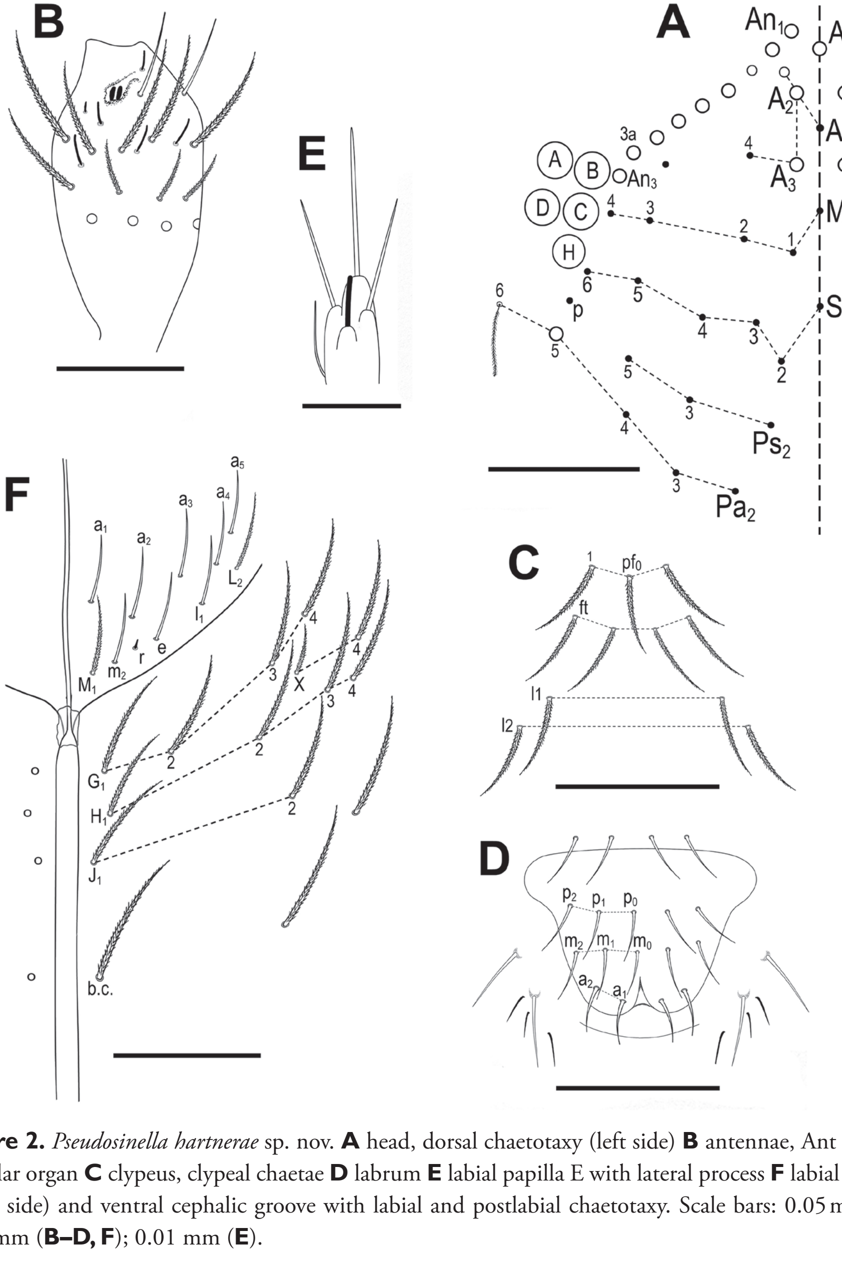


Figure 2. *Pseudosinella hartnerae* sp. nov. **A** head, dorsal chaetotaxy (left side) **B** antennae, Ant III with sensillar organ **C** clypeus, clypeal chaetae **D** labrum **E** labial papilla E with lateral process **F** labial triangle (right side) and ventral cephalic groove with labial and postlabial chaetotaxy. Scale bars: 0.05 mm (**A**); 0.03 mm (**B–D, F**); 0.01 mm (**E**).

(holotype: 1.3). Relation of antennal segments I–IV as 1 : 1.7 : 1.5 : 2.9 (holotype). Ant III sensillary organ composed of two rod-like sensilla partially behind a cuticular fold, guarded by three sensilla, one of them short, with spiny morphology (Fig. 2B). Ant IV without apical bulb. Clypeus with eleven subequal ciliated chaetae (three in row pf, four in row ft, two in row l1 and two in row l2) (Fig. 2C). Arrangement of chaetae on labrum 4/554, prelabral chaetae smooth; first (p), second (m) and apical (a) rows of labral chaetae also smooth, chaetae of p and m series about the same in size, not enlarged, a_1–a_2 thicker but not enlarged; labral edge with no differentiated papillae (Fig. 2D). Outer maxillary palp with two smooth chaetae and three smooth main sublobal hairs. Lateral process (*sensu* Fjellberg 1999) on papilla E finger-shaped, barely reaching the top of papilla (Fig. 2E). Labial anterior row with five smooth chaetae (a_1–a_5); formula of basal row $M_1m_2rel_1L_2$ with M_1 and L_2 ciliated and all other chaetae smooth (Fig. 2F). Chaeta r short (ratio of r/m_2 0.2–0.3). Ventral chaetotaxy with about 15 ciliate chaetae, postlabial formula 4 (G1–4), 2 (X, X4), 4 (H1–4), and 2 (J1–2) chaetae; b.c. present (Fig. 2F).

Body. Body dorsal macrochaetae from Th II to Abd IV 00/0101+2. Mesothorax without macrochaetae. Two anterolateral S-chaetae (al and ms) present. Th III without Mac, anterolateral sensillum al present. Abd I with lateral S-microchaeta (ms). Chaetotaxy of Abd II–III as in Fig. 3A, B. Abd II chaetotaxy between two dorsomedial trichobothria $paBq_1q_2$ using Gisin's symbols (Gisin 1967); following Szeptycki's (1979) notation p=a_2p, a=a_2, B=m_3, q_1=m_3e and q_2=p_4. Chaeta a as ciliated mic. Abd III chaeta d_3 present. Chaetotaxy and trichobothrial complex on Abd IV as in Fig. 4A, B. Mac B_5, B_6, C_1, E_2, E_3, F_1 and F_2 broader with broad sockets, D_2, D_3, De_3, E_4, E_4p, E_4p_2, F_3, F_3p, Fe_4, Fe_5, T_6 and T_7 thinner with smaller sockets. Abd IV with five fan-shaped chaetae (D_1, a, m, p_e and p_i) associated with two trichobothria. Accessory chaeta s, associated with trichobotrium T_2, absent. Nine S-chaetae (as, ps,

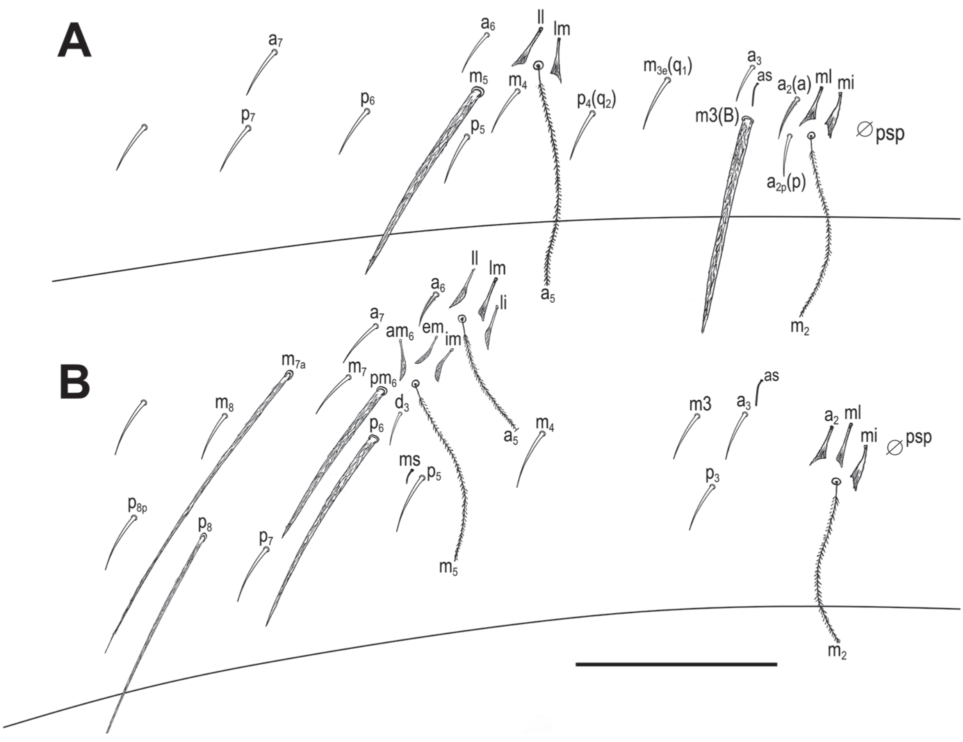


Figure 3. *Pseudosinella hartnerae* sp. nov. Abdomen dorsal chaetotaxy: **A** Abd II (left side) **B** Abd III (left side). Scale bar: 0.03 mm (**A, B**).

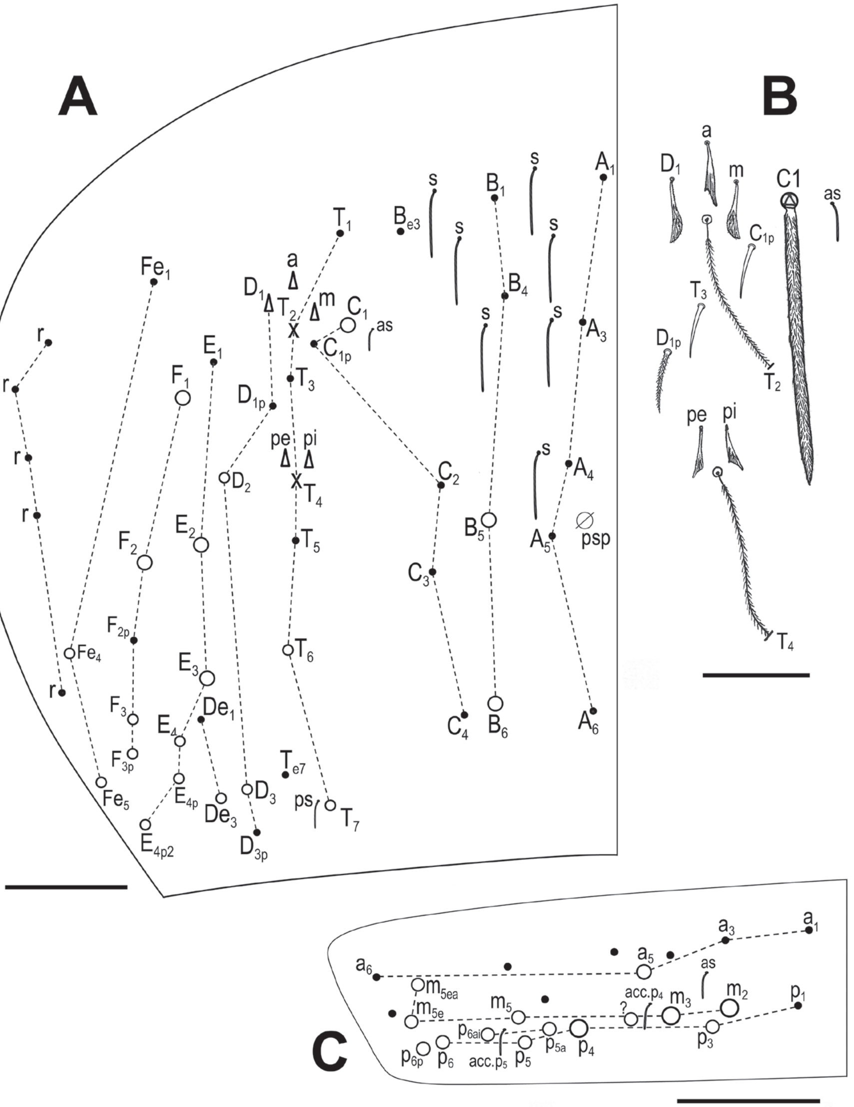


Figure 4. *Pseudosinella hartnerae* sp. nov. Abdomen dorsal chaetotaxy: **A** Abd IV (left side) **B** Abd IV trichobothrial complex (left side) **C** Abd V. Scale bars: 0.05 mm (**A**); 0.02 mm (**B**); 0.03 mm (**C**).

and seven long dorsal S-chaetae) present. Dorsal chaetotaxy of Abd V as in Fig. 4C. Three S-chaetae (as, acc.p4 and acc.p5) typical for *Pseudosinella* present. Legs without scales. Trochanteral organ with up to 12 smooth spiny chaetae forming a V-shaped pattern (Fig. 5A). Unguis and unguiculus as in Fig. 5B. Unguis with subequal paired basal teeth at 35% from inner edge, and with a median unpaired inner tooth at 60% from inner edge, apical tooth absent. Outer side with paired lateral teeth and a short external tooth. Unguiculus lanceolate, external lamella smooth. Tibiotarsal tenent hair clavate, supraempodial chaeta on tibiotarsus III smooth and acuminate. Ratio

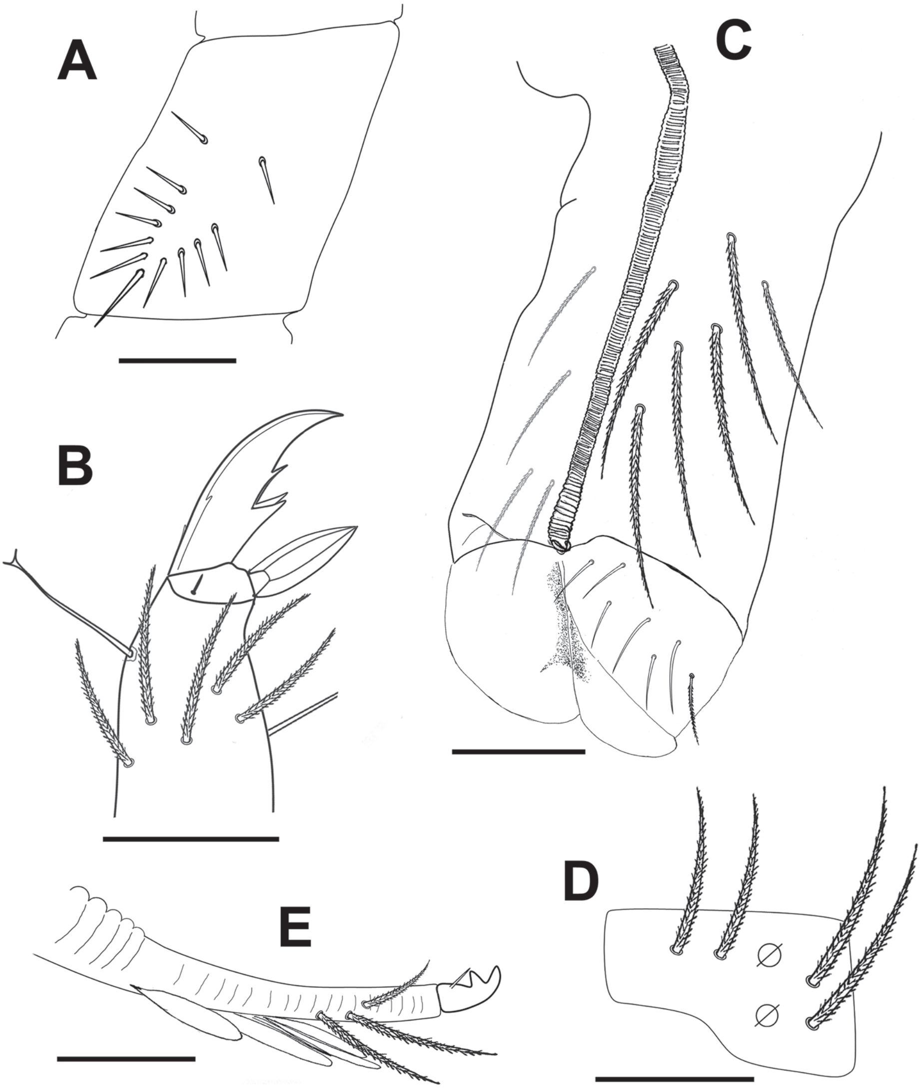


Figure 5. *Pseudosinella hartnerae* sp. nov. **A** trochanteral organ **B** leg III unguis and unguiculus **C** ventral tube anterior view (right side) and posterior view (left side) **D** manubrial plate **E** mucro and apical part of dens. Scale bars: 0.02 mm (**A, B, D, E**); 0.03 mm (**C**).

of supraempodial chaeta / unguiculus around 0.9. Ventral tube without scales; with 6+6 subequal ciliated chaetae on anterior side and 4+4 subequal ciliated chaetae on posterior side; lateral flap with 1 ciliated and a maximum of 6 smooth chaetae (Fig. 5C). Manubrium ventrally with scales and 2+2 terminal ciliated chaetae. Manubrial plate with 2 larger inner chaetae and 2 chaetae external to the 2 pseudopores (Fig. 5D). Length of not ringed terminal dens about 4 times the length of mucro. Mucro with distal tooth equal to anteapical one; basal spine reaching tip of anteapical tooth (Fig. 5E). Ratio manubrium/dens/mucro as 16:15:1.

Ecology and distribution. The type locality (Bátorliget Pasture Nature Conservation Area, Szabolcs–Szatmár–Bereg county, Hungary) of *Pseudosinella hartnerae* sp. nov. is a special relict mire and forest area with high biodiversity. The new species was collected from the upper layer and litter of a forest clearing with pioneer vegetation including silver birch (*Betula pendula*) trees. Specimens in Romania were collected from litter in the surrounding forest of the volcanic lake Saint Ana, and from peat mosses in the nearby Mohoș bog. Both Romanian sites are located in the Mohoş Nature Reserve, Harghita County. This new *Pseudosinella* is a phytodetriticolous, bryophilous and hygrophilous species.

Etymology. The name of the new species is dedicated to former zoologist colleague and friend Dr. Anna Fenyősiné Hartner (1965–2006), an excellent specialist in myrmecology.

Pseudosinella huetheri **Stomp, 1971**

Figures 6–10

Material examined. ***Holotype*:** Luxembourg. sex not visible, on slide, preserved in NHMG (Fig. 6A), Berdorf, "Zigzagschloeff" rocks, 357 m a.s.l., 49°49'33"N, 6°20'21"E, beech forest (*Fagetum*), from litter, 11.Aug.1965, leg. N. Stomp.

Diagnosis. 5+5 ocelli. Colour yellowish white. Labial chaetotaxy $M_1m_2Rel_1L_2$, R ~ 0.5 of M. Dorsal macrochaetae formula $R_0R_1R_2$001/00/0101+2. Abdominal tergite II chaetotaxy: –aBq_1q_2. Abd IV accessory chaeta s, anteriorly to trichobothrial complex, absent. Antennae and legs without scales. Unguis inner side with two paired basal teeth and one unpaired tooth, unguiculus outer lamella smooth.

Redescription. ***Habitus*** (Fig. 6B). Body length (without head and furca) 1.2–1.5 mm (Stomp 1971), holotype length 1.46 mm. Colour (after Stomp 1971): yellowish white, without any trace of pigment, neither on tergites and coxae nor on antennae. A few spots of blue pigment distributed in small dots around eyes. Eye patches blue.

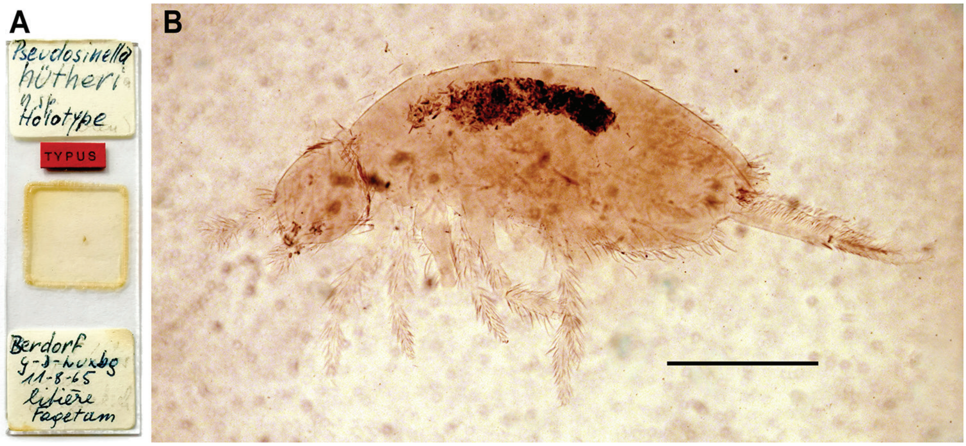


Figure 6. *Pseudosinella huetheri* Stomp, 1971. **A** Photograph of the slide of the holotype from the NHMG Switzerland) **B** Habitus, holotype. Scale bar: 0.05 mm (**B**).

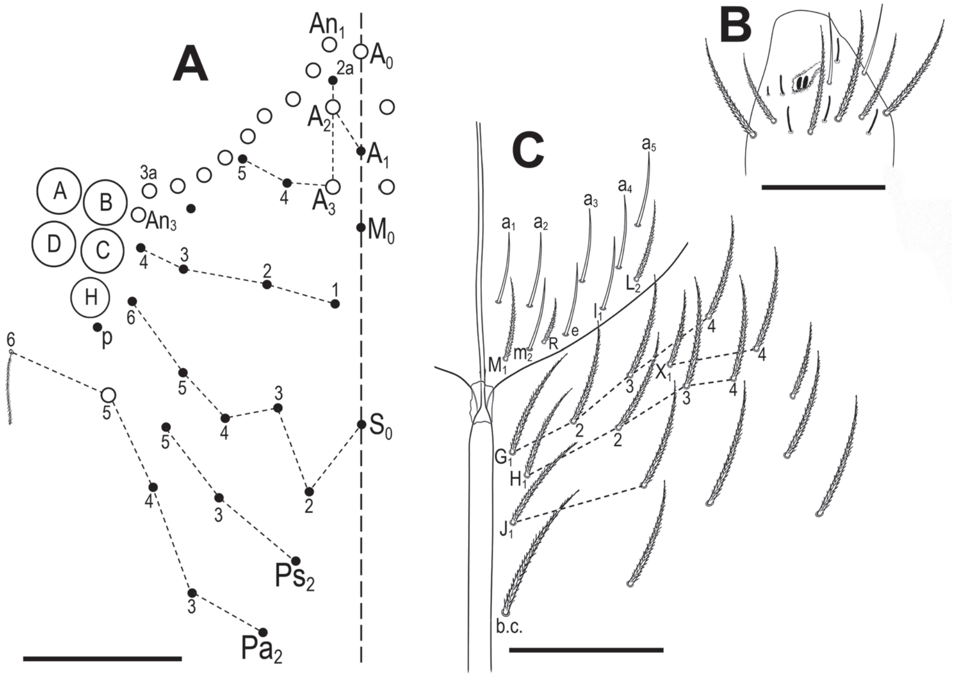


Figure 7. *Pseudosinella huetheri* Stomp, 1971 **A** head, dorsal chaetotaxy (left side) **B** antennae, apex of Ant III with sensillar organ **C** labial triangle (right side) and ventral cephalic groove with labial and postlabial chaetotaxy. Scale bars: 0.05 mm (**A**); 0.03 mm (**B, C**).

Head. With 5+5 eyes (ABCDH, with H only slightly smaller) (Fig. 7A; see also fig. 2 in Stomp 1971). Dorsal cephalic main macrochaetae formula $R_0R_1R_2P$ (according to AMS notation A_0, A_2, A_3 and Pa_5). Number of macrochaetae "An" on head 10+10 (Fig. 7A). Antennal length to head diagonal length ratio 1.4 (head diagonal measured from cervical edge to apex of labrum). Relation of antennal segments I–IV as 1 : 1.7 : 1.5 : 3.0. Ant III sensillary organ composed of two rod-like sensilla partially behind a cuticular fold, guarded by three sensilla, one of them shorter, spine-like (Fig. B). Ant IV without apical bulb. Arrangement of chaetae on labrum 4/554; prelabral chaetae smooth, first (p), second (m) and apical (a) rows of labral chaetae also smooth, chaetae of p and m series about the same in size, not enlarged, a_1–a_2 thicker but not enlarged; labral edge with no differentiated papillae (as in Fig. 2D). Outer maxillary palp with two smooth chaetae and three smooth main sublobal hairs. Lateral process (*sensu* Fjellberg 1999) on papilla E finger-shaped, barely reaching the top of papilla (see Fig. 2E). Labial anterior row formed by 5 smooth chaetae (a1–a5); formula of basal row $M_1m_2Rel_1L_2$ with M_1, R and L_2 ciliated and all other chaetae smooth (Fig. 7C). Chaeta R reduced (ratio of R/m_2 0.5). Ventral postlabial chaetotaxy with about 18 ciliate chaetae, postlabial formula 4 (G1–4), 2 (X, X4), 4 (H1–4), and 2 (J1–2) chaetae; b.c. present (Fig. 7C).

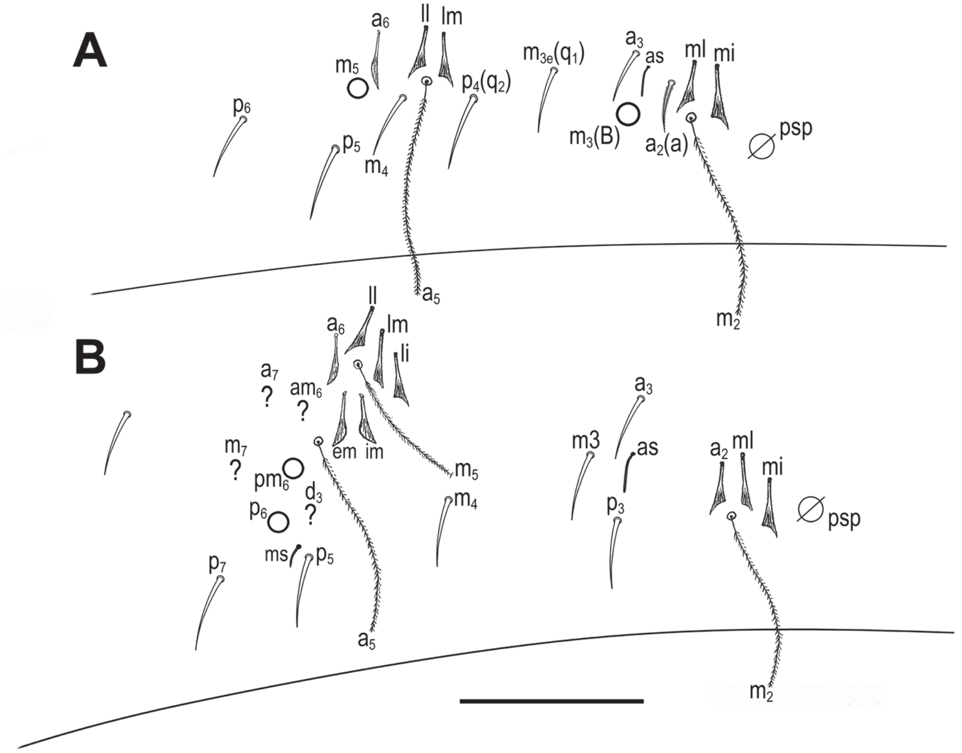


Figure 8. *Pseudosinella huetheri* Stomp, 1971. Abdomen dorsal chaetotaxy: **A** Abd II (left side) **B** Abd III (left side). ? indicates the estimated position of chaetae that were not observed in the holotype due to the condition of the slide, but their presence is assumed. Scale bar: 0.05 mm (**A, B**).

Body. Body dorsal macrochaetae from Th II to Abd IV 00/0101+2. Mesothorax without Mac. Two anterolateral S-chaetae (al and ms) present. Th III without Mac, anterolateral sensillum al present. Abd I with lateral S-microchaeta (ms). Chaetotaxy of Abd II–III as in Fig. 8A, B. Abd II chaetotaxy between two dorso-medial trichobothria –aBq_1q_2 using Gisin's symbols (Gisin 1967); following Szeptycki's (1979) notation a=a_2, B=m_3, q_1=m_3e and q_2=p_4. Chaeta a as ciliated mic. Abd IV chaetotaxy as in Fig. 9A. Mac B_5, B_6, C_1, D_3, E_2, E_3, F_1, F_2 and F_3 broader with broad sockets, D_2, De_3, E_4, E_4p, E_4p_2, F_3p, Fe_4, Fe_5, T_6 and T_7 thinner with smaller sockets. Chaeta E_1 not visible, its morphology unknown. Abd IV chaetae associated with the two trichobotria (m, p_e and p_i) fan-shaped (chaeta a not visible, but with great certainty also fan-shaped) (see also Hüther 1969). Accessory chaeta s, associated with trichobotrium T_2, absent. Five S-chaetae (as, ps, and three long dorsal S-chaetae) present. Dorsal chaetotaxy of Abd V as in Fig. 9B. Three S-chaetae (as, acc.p4 and acc.p5) typical for the genus present. Legs without scales. Trochanteral organ with 14 smooth spiny chaetae forming a V-shaped pattern (Fig. 10A). Unguis and unguiculus as in fig. 3 in Stomp (1971). Unguis with subequal paired basal teeth at 45% from inner edge, and with a median

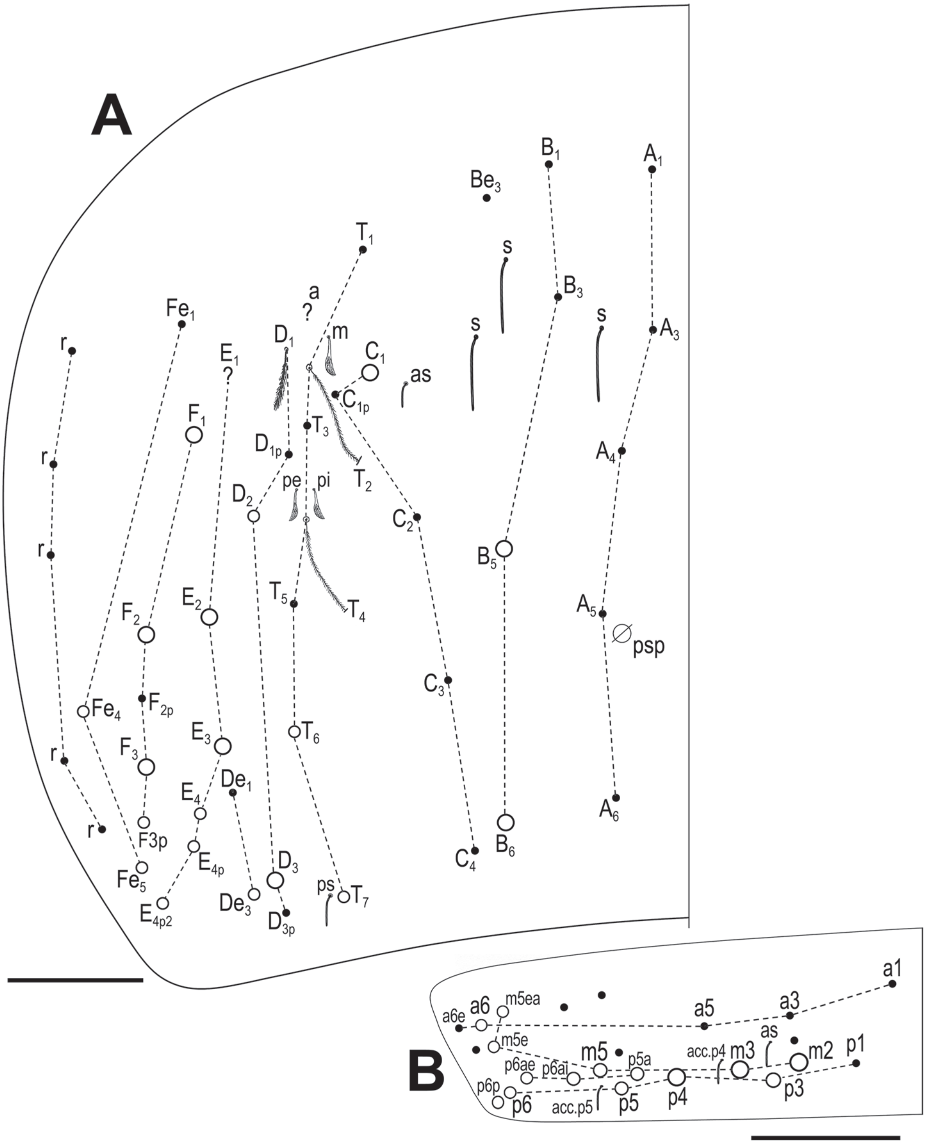


Figure 9. *Pseudosinella huetheri* Stomp, 1971. Abdomen dorsal chaetotaxy: **A** Abd IV (left side) **B** Abd V. ? indicates the estimated position of chaetae that were not observed in the holotype due to the condition of the slide, but their presence is assumed. Scale bars: 0.05 mm (**A, B**).

unpaired inner tooth at 65% from inner edge, apical tooth absent. A short external tooth also present. Unguiculus lanceolate, external lamella smooth. Tibiotarsal tenent hair spatulate, supraempodial chaeta on tibiotarsus III smooth and acuminate. Ratio of supraempodial chaeta / unguiculus ~0.9. Ventral tube without scales; with 8+8 subequal ciliated chaetae on anterior side and 5+5 subequal ciliated chaetae on posterior

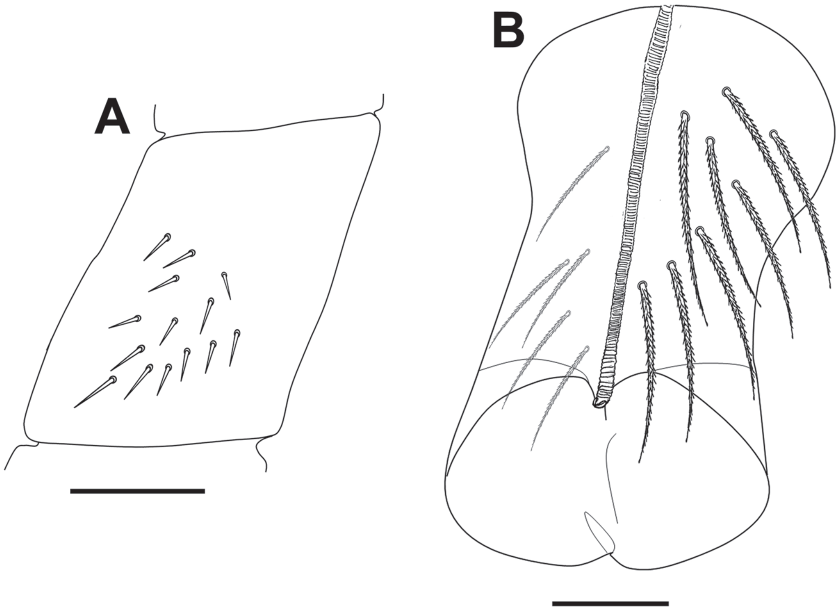


Figure 10. *Pseudosinella huetheri* Stomp, 1971. **A** trochanteral organ **B** ventral tube anterior view (right side) and posterior view (left side). Scale bars: 0.03 mm (**A, B**).

side (Fig. 10B); lateral flap with 4 ciliated and 7 smooth chaetae. Manubrium ventrally with scales and 2+2 terminal ciliated chaetae. Manubrial plate with 2 inner chaetae and 2 chaetae external to the 2 pseudopores (as in Fig. 5D). Length of not ringed terminal dens about 4 times the length of mucro. Mucro with distal tooth equal to anteapical one; basal spine reaching tip of anteapical tooth (as in Fig. 5E). Ratio manubrium/dens/mucro as 12:13:1.

Ecology and distribution. *Pseudosinella huetheri* was described from Luxembourg, from a beech forest near Berdorf (Stomp 1971). The original description reported the species also from Germany and Switzerland. Later, the species was found in Austria (Bretschko and Christian 1989), France (Ponge 2004) and Slovakia (Raschmanová et al. 2008). Dányi et al. (2006) collected a species close to *P. huetheri* in Romania, listed as "*Pseudosinella* cf. *huetheri*", but without any differential character being mentioned.

Discussion

Considering the number of eyes (5+5) and the similar dorsal main macrochaetae distribution (R000/00/0101+2 or R001/00/0101+2), *Pseudosinella hartnerae* sp. nov. is close to *P. altamirensis* Baquero, Jordana, Labrada & Luque, 2020; *P. horaki* Rusek, 1985; *P. huetheri*; *P. mauli* Stomp, 1972; *P. mucronata* Gouze & Deharveng, 1987; and *P. sandelsorum* Gruia, 1977 (Table 1). The new species is, however, characterized by a

Table 1. Comparison of *P. hartnerae* sp. nov. with related species with 5+5 eyes and similar dorsal macrochaetae distribution.

Species	Ch1	Ch2	Ch3	Ch4	Ch5	Ch6	Ch7	Ch8	Ch9	Ch10	Ch11	Ch12
P. altamirensis	pale with blue pigmentation	$M_1m_2Rel_1l_2$	R000/00/0101+2	1.6–2.2	–	+	3	35%	40%	1	2+7–12	2
P. horaki	pale greyish blue	$M_1M_2REL_1L_2$	R001/00/0101+2	1.6	+	–	3	50%	75%	2	U	1
P. huetheri	yellowish white	$M_1m_2Rel_1L_2$	R001/00/0101+2	1.4	–	–	3	45%	65%	2	2+2	1
P. mauli	bluish black	$M_1M_2rEL_1L_2$	R001/00/0101+2	1.3	+	+	3	~45%	65%	2	2+3	1
P. mucronata	diffuse pigmentation	$m_1(M_1)$ $m_2Rel_1l_2$	R000/00/0101+2	1.8–2.0	–	–	3	~45%	60%	1	U	2
P. sandelsorum	dark blue pigment on Ant and legs	$M_1M_2REL_1L_2$	R001/00/0101+2	1.3	+	–	4	~50%	70%	2	2+4–10	1
P. hartnerae sp. nov	bluish-grey	$M_1m_2rel_1L_2$	R001/00/0101+2	1.2–1.4	+	–	3	35%	60%	2	2+2	1

Legend. **Ch1**: body colour. **Ch2**: basal labial chaetotaxy formula. **Ch3**: body dorsal macrochaetae formula. **Ch4**: antennal length to head diagonal length ratio. **Ch5**: Abd II chaeta **p**: (+) present or (–) absent. **Ch6**: Abd IV supplementary chaeta **s**: (+) present or (–) absent. **Ch7**: number of teeth of inner unguis. **Ch8**: distance of distal paired claw tooth from the base as a % of total claw length. **Ch9**: distance of distal unpaired claw tooth from the base as a % of total claw length. **Ch10**: tenent hair shape: (1) acuminate, (2) clavate. **Ch11**: number of inner and outer chaetae on manubrial plate. **Ch12**: habitat: (1) surface, (2) cave. "U", unknown.

unique basal labial chaetotaxy. While *P. horaki*, *P. mauli* and *P. sandelsorum* have M_1, M_2, E, L_1 and L_2 as ciliated chaetae, in *P. hartnerae* sp. nov. only M_1 and L_2 are ciliated, and m_2, r, e, and l_1 are smooth. *Pseudosinella altamirensis* bears two ciliated labial chaetae (M_1 and R), and *P. mucronata* has R and occasionally also M_1 as ciliated chaetae, while all other chaetae are smooth. Only *P. huetheri* shows a similar morphology of labial chaetae, with the exception of chaeta R present as a fairly developed ciliated chaeta (r smooth and reduced in *P. hartnerae* sp. nov). The new species differs from *P. huetheri* also by the colour pattern and by the presence of Abd II chaeta p (a_{2p}). The new species differs from *P. altamirensis* and *P. mucronata* also by the presence of subocular cephalic marcrochaeta Pa_5. The new species differs from *P. altamirensis* and *P. mauli* by the absence of accessory chaeta s on Abd IV. Besides, the new species differs from *P. sandelsorum* by the number of teeth of the inner unguis. *Pseudosinella hartnerae* sp. nov. and *P. huetheri* share the number of chaetae (2) external to the pseudopores on the manubrial plate, which is greater for *P. altamirensis* (7–12), *P. mauli* (3) and *P. sandelsorum* (4–10).

Acknowledgements

We would like to thank Edit Horváth (HNHM) for his assistance with the deposition of the type material of the new species; Peter Schwendinger and Lionel Monod for providing the holotype of *Pseudosinella huetheri* from the NHMG. We are greatly indebted to editor Louis Deharveng and two anonymous reviewers for their valuable comments and suggestions improving the manuscript. C. Fiera acknowledges the support by a grant of the Ministry of Research, Innovation and Digitization, CNCS/CCCDI – UEFISCDI, project number PN-III-P1-1.1-TE-2019-0358, within PNCDI III".

References

Baquero E, Jordana R, Labrada L, Luque CG (2020) A new species of *Pseudosinella* Schäffer, 1897 (Collembola, Entomobryidae) from Altamira Caves (Cantabria, Spain). ZooKeys 989: 39–54. https://doi.org/10.3897/zookeys.989.52361

Bellinger PF, Christiansen KA, Janssens F (2021) Checklist of the Collembola of the World. http://www.collembola.org [Accessed on: 11.09.2021]

Börner C (1913) Die Familien der Collembolen. Zoologischer Anzeiger 41: 315–322.

Bretschko G, Christian E (1989) Collembola in the bed sediments of an Alpine gravel stream (RITRODAT-Lunz Study Area, Austria). Internationale Revue der gesamten Hydrobiologie und Hydrographie 74(5): 491–498. https://doi.org/10.1002/iroh.19890740504

Buşmachiu G, Kováč Ľ, Miklisová D, Weiner WM (2017) Riparian Collembola (Hexapoda) communities of northern Moldova, Eastern Europe. ZooKeys 724: 119–134. https://doi.org/10.3897/zookeys.724.12478

Chen J-X, Christiansen KA (1993) The genus *Sinella* with special reference to *Sinella* s. s. (Collembola: Entomobryidae) of China. Oriental Insects 1993, 27(1): 1–54. https://doi.org/10.1080/00305316.1993.10432236

Christiansen K, Bellinger P, Gama MM da (1990) Computer Assisted Identification of Specimens of *Pseudosinella* (Collembola: Entomobryidae). Revue d'Écologie et de Biologie du Sol 27(2): 231–246.

Cipola NG, Arbea J, Baquero E, Jordana R, Morais JW, Bellini BC (2018) The survey *Seira* Lubbock, 1870 (Collembola, Entomobryidae, Seirinae) from Iberian Peninsula and Canary Islands, including three new species. Zootaxa 4458: 1–66. https://doi.org/10.11646/zootaxa.4458.1.1

Cipola NG, Oliveira JVLC, Bellini BC, Ferreira AS, Lima ECA, Brito RA, Stievano LC, Souza PGC, Zeppelini D (2020) Review of Eyeless *Pseudosinella* Schäffer (Collembola, Entomobryidae, and Lepidocyrtinae) from Brazilian Caves. Insects 11(3): e194. [141 pp.] https://doi.org/10.3390/insects11030194

Dányi L, Traser G (2008) An annotated checklist of the springtail fauna of Hungary (Hexapoda: Collembola). Opuscula Zoologica 38: 3–82.

Dányi L, Traser G, Fiera C, Radwanski JM (2006) Preliminary data on the Collembola fauna of the Maramureş (Romania). Studia Universitatis Vasile Goldis Arad, Seria Stiintele Vietii 17: 47–51.

Fiera C (2013) Species of the genus *Pseudosinella* (Collembola: Entomobryidae) in Romanian fauna. Acta Oecologica Carpatica 6: 53–66.

Fjellberg A (1999) The labial palp in Collembola. Zoologischer Anzeiger 237: 309–330.

Gisin H (1964) Collemboles d'Europe VII. Revue Suisse de Zoologie 71(4): 649–678. https://doi.org/10.5962/bhl.part.75615

Gisin H (1967) Espèces nouvelles et lignées évolutives de *Pseudosinella* endogés (Collembola). Memórias e Estudos do Museu Zoologico da Universidade de Coimbra 301: 1–25.

Gisin H, Gama MM da (1969) Espèces nouvelles de *Pseudosinella* cavernicoles (Insecta, Collembola). Revue suisse de Zoologie 76(6): 143–181. https://doi.org/10.5962/bhl.part.146030

Gouze A, Deharveng L (1987) Deux espèces nouvelles de *Pseudosinella* cavernicoles du Var (Coll.). Bulletin de la Société Entomologique de France 91(3–4): 65–68.

Gruia M (1977) Collemboles euédaphiques de la Vallé Motru Sec. Travaux de l'Institut de Spéologie "Émile Racovitza" 16: 77–84.

Hüther W (1969) Über einige bemerkenswerte Ur-Insekten aus der Pfalz und benachbarter Gebiete (Protura, Diplura, Collembola). Mitteilungen der Pollichia des Pfälzischen Vereins für Naturkunde und Naturschutz 16: 135–148.

Jordana R, Baquero E (2007) New species of *Pseudosinella* Schäffer, 1897 (Collembola, Entomobryidae) from Spain. Zootaxa 1465: 1–14. https://doi.org/10.11646/zootaxa.1465.1.1

Jordana R, Baquero E, Ariño AH (2021) Continuously updated: Collembola DELTA database. University of Navarra. http://www.unav.es/unzyec/collembola/ [Accessed on 14.02.2021]

Lubbock J (1873) Monograph of the Collembola and Thysanura. Ray Society, London, 276 pp. https://doi.org/10.5962/bhl.title.11583

Mateos E (2008) The European *Lepidocyrtus* Bourlet, 1839 (Collembola: Entomobryidae). Zootaxa 1769: 35–59. https://doi.org/10.11646/zootaxa.1769.1.2

Ponge JF (2004) Effets des composés organiques sur la faune du sol: perturbation des communautés et recolonisation des substrats pollués. Technial report. Muséum National d'Histoire Naturelle, CNRS UMR 7179, 42 pp.

Raschmanová N, Kováč L, Miklisova D (2008) The effect of mesoclimate on Collembola diversity in the Zádiel Valley, Slovak Karst (Slovakia). European Journal of Soil Biology 44: 463–472. https://doi.org/10.1016/j.ejsobi.2008.07.005

Rusek J (1985) New Palearctic *Lepidocyrtus* and *Pseudosinella* species (Collembola: Entomobryidae). Vestnik Ceskoslovenske Spolecnosti Zoologicke 49: 132–146.

Schäffer C (1896) Die Collembolen der Umgebung von Hamburg und benachbarter Gebiete. Mitteilungen aus dem Naturhistorischen Museum Hamburg 13: 149–216.

Schäffer C (1897) Apterygoten. Hamburger Magalhaensische Sammelreise Apterygoten 8: 1–48.

Soto-Adames FN (2010) Two new species and descriptive notes for five *Pseudosinella* species (Hexapoda: Collembola: Entomobryidae) from West Virginian (USA) Caves. Zootaxa 2331: 1–34.

Stomp N (1971) Contribution à l'étude des *Pseudosinella* endogés. Espèces européennes de *Pseudosinella* à 5+5 yeux. Revue d'écologie et de biologie du sol 8: 173–184.

Stomp N (1972) Deux nouvelles espèces de *Pseudosinella* endogés d'Europe (Collemboles, Entomobryides). Revue Suisse de Zoologie 79: 279–286. https://doi.org/10.5962/bhl.part.97128

Szeptycki A (1972) Morpho-systematic studies on Collembola III. Body chaetotaxy in the first instars of several genera of the Entomobryomorpha. Acta Zoologica Cracoviensia 17: 341–372.

Szeptycki A (1979) Morpho-systematic studies of Collembola. IV. Chaetotaxy of the Entomobryidae and its phylogenetical significance. Polska Akademia Nauk, Zakład Zoologii Systematycznej i Doświadczalnej, Państwowe Wydawnictwo Naukowe, Warszawa and Kraków, 218 pp.

Traser G, Szűcs P, Winkler D (2006): Collembola diversity of moss habitats in the Sopron Region, NW-Hungary. Acta Silvatica et Lignaria Hungarica 2: 69–80.

Wahlgren E (1906) Apterygoten aus Ägypten und dem Sudan nebst Bemerkungen zur Verbreitung und Systematik der Collembolen. Results of the Swedish Zoological Expedition to Egypt and the White Nile 1901 under the Direction of L.A. Jägerskiöld, Uppsala, 72 pp.

Wang F, Chen J-X, Christiansen K (2003) Taxonomy of the genus *Lepidocyrtus* s.l. (Collembola: Entomobryidae) in East and Southeast Asia and Malaysia, with description of a new species from the People's Republic of China. The Canadian Entomologist 135: 823–837. https://doi.org/10.4039/n02-106

Winkler D, Mateos E (2018) New species of *Pseudosinella* Schäffer, 1897 (Collembola, Entomobryidae) from Hungary. Zootaxa 4382(2): 347–366. https://doi.org/10.11646/zootaxa.4382.2.7

Yoshii R, Suhardjono YR (1992) Collembolan fauna of Indonesia and its affinities III: Collembola of Timor Island. AZAO 1992, 2: 75–96.

Zhang F, Deharveng L (2015) Systematic revision of Entomobryidae (Collembola) by integrating molecular and new morphological evidence. Zoologica Scripta 44(3): 298–311. https://doi.org/10.1111/zsc.12100