ZooKeys 494: 1–12 (2015)
doi: 10.3897/zookeys.494.9183
http://zookeys.pensoft.net

RESEARCH ARTICLE

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One new genus and two new species of oonopid spiders from Xishuangbanna Rainforest, southwestern China (Araneae, Oonopidae)

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Academic editor: *Y. Marusik* | Received 28 December 2014 | Accepted 19 March 2015 | Published 6 April 2015

http://zoobank.org/6506296F-5999-4EC8-83C1-47998F92F45E

Citation: Tong Y, Li S (2015) One new genus and two new species of oonopid spiders from Xishuangbanna Rainforest, southwestern China (Araneae, Oonopidae). ZooKeys 494: 1–12. doi: 10.3897/zookeys.494.9183

Abstract

A new genus, *Bannana*, is established for two new species that resemble those of the *Dysderoides* complex. Two new species are described, *B. crassispina* **sp. n.** and *B. parvula* **sp. n.** Morphological descriptions and illustrations of both new species are given.

Keywords

Taxonomy, goblin spider, diagnosis, morphology, tropical forest

Introduction

The "*Dysderoides* complex", including the genera *Dysderoides* Fage, 1946, *Himalayana* Grismado, 2014 and *Trilacuna* Tong & Li, 2007, was firstly proposed by Grismado et al. (2014). This Asian genera complex has a wide distribution, from Pakistan to Sumatra, and sharing the general morphology of the genitalia, chelicerae and labium.

When examining specimens collected from leaf litter in Xishuangbanna, Yunnan Province of China, two new species were recognized. They are very similar to those species of *Dysderoides*, having reduced eyes, deeply incised labium and complicated male palpal bulb, but without macrosetae on legs III and IV. Here a new genus belonging to the *Dysderoides* complex is established to accommodate these two new species.

Material and methods

Specimens in this study were mainly collected by pitfall-trapping and hand-collecting from leaf-litter in tropical rainforest in Xishuangbanna, Yunnan in 2006 and 2007. All specimens are deposited in the Institute of Zoology, Chinese Academy of Sciences in Beijing (IZCAS).

The specimens were examined using a Leica M205C stereomicroscope. Details were studied with the use of an Olympus BX51 compound microscope. All illustrations were made using a drawing tube and inked on ink jet plotter paper. Vulvae were cleared in lactic acid. Photos were made with a Canon EOS 550D zoom digital camera (18 megapixels). Images from multiple focal planes were combined using Helicon Focus (version 3.10) image stacking software. Descriptions were generated with the aid of the Planetary Biodiversity Inventory descriptive goblin spider database and shortened where possible. Measurements were taken using an Olympus BX51 compound microscope and are in millimeters.

Taxonomy

Family Oonopidae Simon, 1890

***Bannana* gen. n.**
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Type species. *Bannana crassispina* sp. n.

Etymology. The generic name is derived from the last a few letters of the type locality, 'Xishuangbanna', and is feminine in gender.

Diagnosis. The new genus is similar to *Dysderoides* but can be distinguished from the latter by the following combination of characters: 1) lacking macrosetae on legs III and IV; 2) having reticulate cuticle on the sternum and the sides of the carapace (Figs 1F, 3D, 4C, 5D), which is smooth in *Dysderoides*; 3) with radial furrows between coxae I–II, II–III, III–IV on the sternum, which is absent in *Dysderoides*; 4) females have large dorsal scutum (Figs 3A, B, 5E, F), which is absent or less than half of dorsum in *Dysderoides*. The new genus can be easily distinguished from *Trilacuna* and *Himalayana* by the reduced eyes (Figs 1F, 3D, 4C, 5D) and the reticulate cuticle on the sides of the carapace. Both *Trilacuna* and *Himalayana* have normal eyes and usually granulated or sometimes smooth on the sides of the carapace (Eichenberger 2011; Grismado et al. 2014; Tong and Li 2007, 2013). The new genus also can be distinguished from *Trilacuna* by the short postepigastric scutum in females (Figs 3G, 5G) and by having a furrow connecting the posterior tracheal spiracles in males (Figs 1G, 4F); can be distinguished from *Himalayana* by the absence of the acute projection in the prolateral dorsal part of the male bulb (see Grismado et al. 2014: fig. 62D–H) and the straight, stick-like sclerite in female genital area (Figs 2I, 6E).

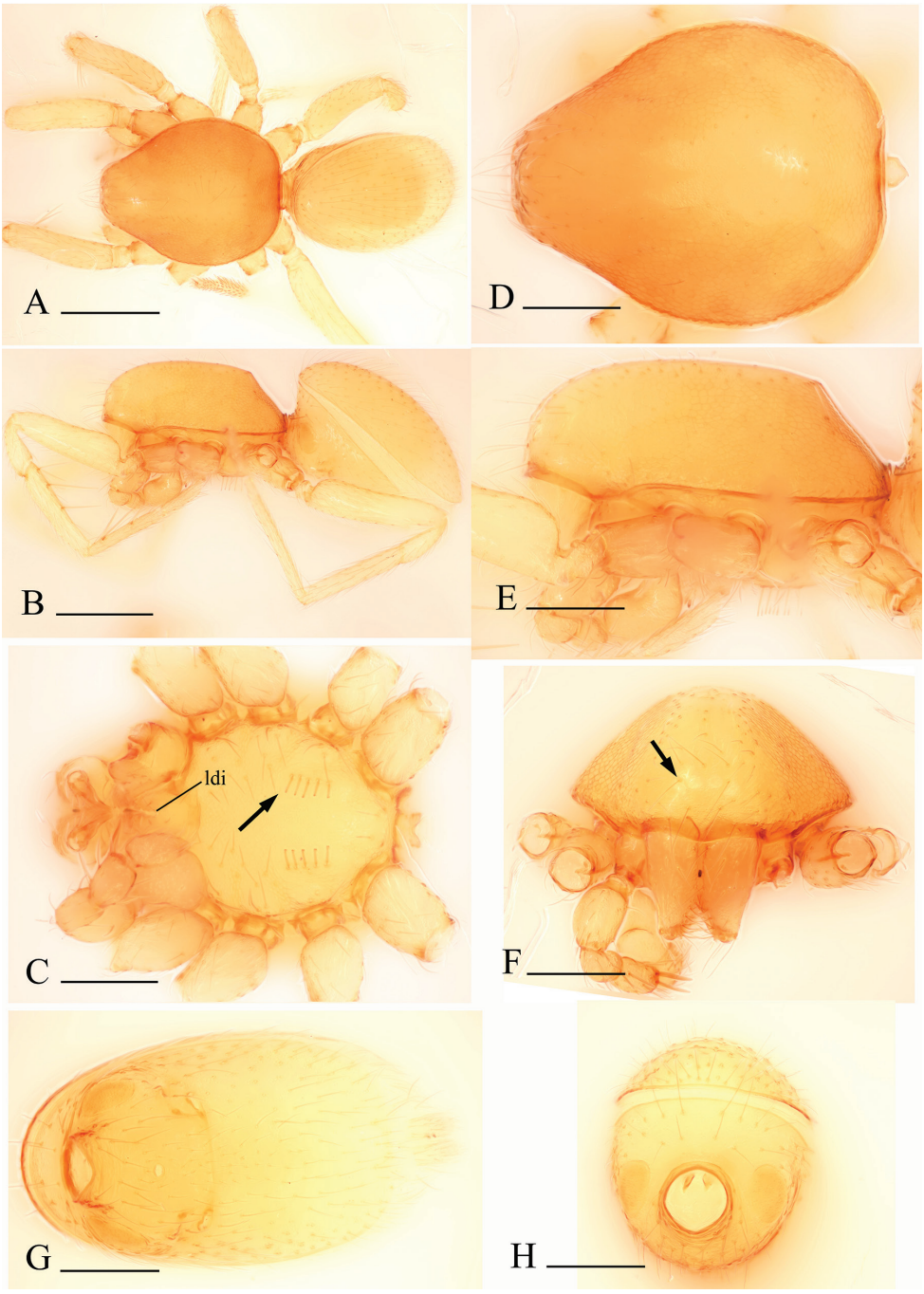

Figure 1. *Bannana crassispina* sp. n., male. **A, B** Habitus, dorsal and lateral views **C, D, E, F** Prosoma, ventral, dorsal, lateral and anterior views (arrows show the regular setae in Fig. C and the reduced eyes in Fig. F) **G, H** Abdomen, ventral and anterior views. Abbreviation: ldi = labium deep incision. Scales bar: **A, B** = 0.4 mm; **C–H** = 0.2 mm.

Description. Male: cephalothorax: *carapace* yellow, without any pattern, broadly oval in dorsal view, pars cephalica slightly elevated in lateral view, anteriorly narrowed to 0.49 times its maximum width or less, with rounded posterolateral corners, posterolateral edge without pits, posterior margin not bulging below posterior rim, anterolateral corners without extension or projections, posterolateral surface without spikes, surface of elevated portion of pars cephalica smooth, sides reticulated, thorax without depressions, fovea absent, without radiating rows of pits; lateral margin straight, smooth, rebordered, without denticles; marginal setae present. Clypeus margin unmodified, sinuous in front view, vertical in lateral view, median projection absent; setae light, needlelike. Chilum absent. Eyes absent (remnants still visible in *B. crassispina* sp. n.). *Sternum:* longer than wide, with radial furrows between coxae I–II, II–III, III–IV, uniform, not fused to carapace, median concavity absent, surface reticulated, microsculpture covering entire surface, anterior margin unmodified, posterior margin not extending posteriorly of coxae IV, anterior corner unmodified, distance between coxae approximately equal, lateral margins unmodified, without posterior hump; setae sparse, dark, needlelike, evenly scattered, without hair tufts (*B. crassispina* sp. n. has pairs of short setae in central part, as in Fig. 1C). *Mouthparts:* chelicerae straight, anterior face unmodified; without teeth on both promargin and retromargin; fangs without toothlike projections, directed medially, shape normal, without prominent basal process, tip unmodified; setae light, needlelike, evenly scattered; paturon inner margin with pairs of enlarged setae, distal region abruptly narrowed, posterior surface unmodified, promargin unmodified. Labium triangular, anterior margin deeply incised (as in Fig. 1C), same as sternum in sclerotization, not fused to sternum. Endites distally not excavated, anteromedian tip unmodified, posteromedian part unmodified, same as sternum in sclerotization. Abdomen: ovoid, rounded posteriorly. Dorsal scutum covering whole dorsum, strongly sclerotized, without color pattern. Epigastric scutum strongly sclerotized, surrounding pedicel. Postepigastric scutum strongly sclerotized, long, almost rectangular, covering nearly full length of abdomen length, anterior margin unmodified, without posteriorly directed lateral apodemes. Book lung covers large, smooth, anterolateral edge unmodified. Scutopedicel region unmodified, scutum not extending far dorsal of pedicel, plumose hairs absent. Posterior spiracles connected by groove. Spinneret scutum present, incomplete ring. Spinneret scutum without fringe of setae. Legs: pale, without color pattern; femur IV not thickened, same size as femora I–III, patella plus tibia I longer than carapace. Leg spines: tibiae I, II with 3 or 4 pairs of ventral spines each; metatarsi I, II with 2 pairs of ventral spines each, legs III and IV without spines. Genitalia: epigastric region with sperm pore large, oval, rebordered, situated in front of or at level of anterior spiracles. Palp normal size, not strongly sclerotized, right and left palps symmetrical, proximal segments yellow-brown; embolus light; trochanter normal size, unmodified; femur enlarged, attaching to patella basally; patella shorter than femur, not enlarged, setae unmodified; tibia not enlarged, distal part with modified setae in *B. crassispina* (Fig. 2A, D); cymbium yellow-brown, narrow in dorsal view, not fused with bulb, not extending beyond distal tip of bulb; bulb 1.5

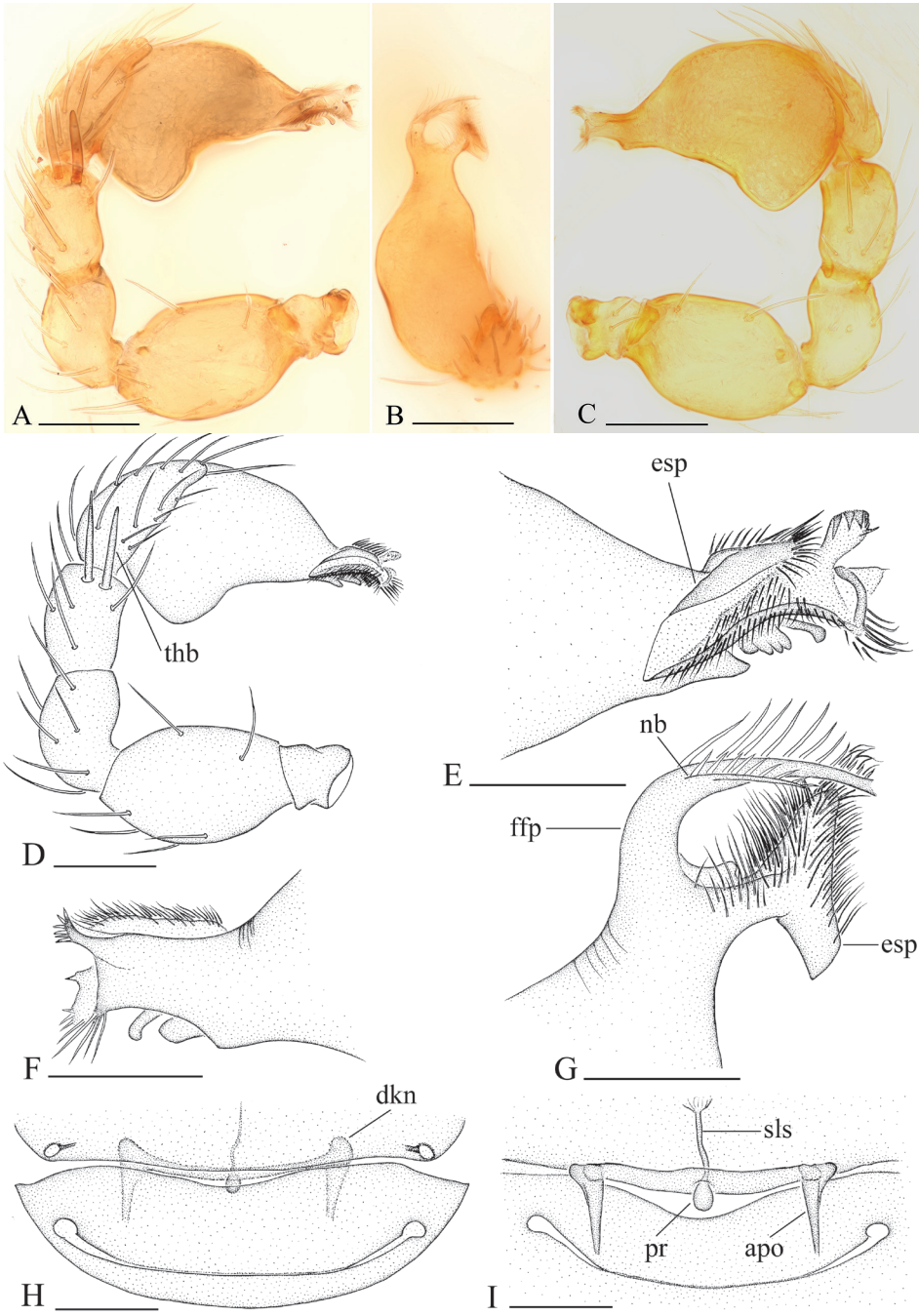

Figure 2. *Bannana crassispina* sp. n., **A–G** male **H, I** female **A, C, D** Left palp, prolateral (**A, D**) and retrolateral (**C**) views **B, E, F, G** Distal part of bulb, dorsal (**B, G**), prolateral (**E**) and retrolateral (**F**) views **H, I** Genital area, ventral and dorsal views. Abbreviations: apo = apodeme; dkn = dark brown knobs; esp = ear-shaped protrusion; ffp = filiform, curved projection; nb = narrow branch; pr = posterior receptacle; sls = stick-like sclerite; thb = thick bristles. Scales bar: **A–D, H, I** = 0.1 mm; **E–G** = 0.05 mm.

to 2 times as long as cymbium, tapering apically; distal part with several laminae that bear filiform projections surrounding the embolus.

Female: as in male except as noted. Palp without claw; spines absent. Abdomen: dorsal scutum large, covering more than 3/4 of dorsum (Figs 3A, 5E). Postepigastric scutum short, only around epigastric furrow, not fused to epigastric scutum (Figs 3G, 5G). Supraanal scutum absent. Postepigastric area setae needlelike. Genitalia: ventral view: without special external features; dorsal view: there are one transverse ventral plates, adjacent to a pair of short apodemes; posterior receptacle rounded to ovoid, extending anterior by a narrow, stick-like sclerite (Figs 2H, I, 6D, E).

Composition. *Bannana crassispina* sp. n. and *B. parvula* sp. n.

Distribution. China (Yunnan).

***Bannana crassispina* sp. n.**

http://zoobank.org/052CF748-1DF3-4D4F-BE90-B50BAA36F86B

Type material. Holotype: male (IZCAS Ar-25082), China: Yunnan Province, Mengla County, Menglun Nature Reserve, Secondary tropical seasonal moist forest (21°54.718'N, 101°16.940'E, Alt: 645 m), pitfall traps, 16–31 April 2007, G. Zheng and Z. Chen leg. **Paratypes:** 1 male (IZCAS Ar-25085), same data as holotype; 1 female (IZCAS Ar-25080), same data as holotype; 1 female (IZCAS Ar-25078), same data as holotype; 1 female (IZCAS Ar-25084), same locality as holotype, 16–31 March 2007; 1 female (IZCAS Ar-25083), same locality as holotype, 1–15 May 2007; 1 female (IZCAS Ar-25087), same locality as holotype, 1–15 May 2007; 1 female (IZCAS Ar-25077), same locality as holotype, 16–31 May 2007; 1 male (IZCAS Ar-25074), 21°54.607'N, 101°17.005'E, Alt: 633 m, pitfall traps, 16–31 May 2007; 2 males (IZCAS Ar-25073), same locality as above, searching, 4–11 May 2007; 1 female (IZCAS Ar-25075), 21°54.984'N, 101°16.982'E, Alt: 656 m, pitfall traps, 16–31 April 2007; 1 male (IZCAS Ar-25072), same locality as above, 16–24 November 2006; 1 male (IZCAS Ar-25076), same locality as above, 16–28 February 2007; 1 female (IZCAS Ar-25081), 16–31 May 2007; 1 female (IZCAS Ar-25086), 16–31 June 2007; 1 female (IZCAS Ar-25079), Secondary tropical seasonal rainforest (21°55.428'N, 101°16.441'E, Alt: 598 m), pitfall traps, 16–31 June 2007.

Etymology. The specific name is Latin, "crass-" = thick, and "spin-" = seta, referring to the thick bristles on male palpal tibiae.

Diagnosis. The males of the new species can be distinguished from *B. parvula* sp. n. by the thick bristles on palpal tibiae (thb in Fig. 2A, D) and rows of setae on the central part of sternum (Fig. 1C); females of the new species are similar to those of *Dysderoides synrang* Grismado & Deeleman, 2014, but can be distinguished by the absence of macrosetae on legs III and IV, and by the large dorsal abdominal scutum.

Description. Male. Body yellow, legs lighter. Habitus as in Fig. 1A, B. Body length 1.47; carapace 0.75 long, 0.49 wide; abdomen 0.85 long, 0.48 wide. Carapace broadly oval, *pars cephalica* slightly elevated in lateral view, dorsal surface smooth; sides

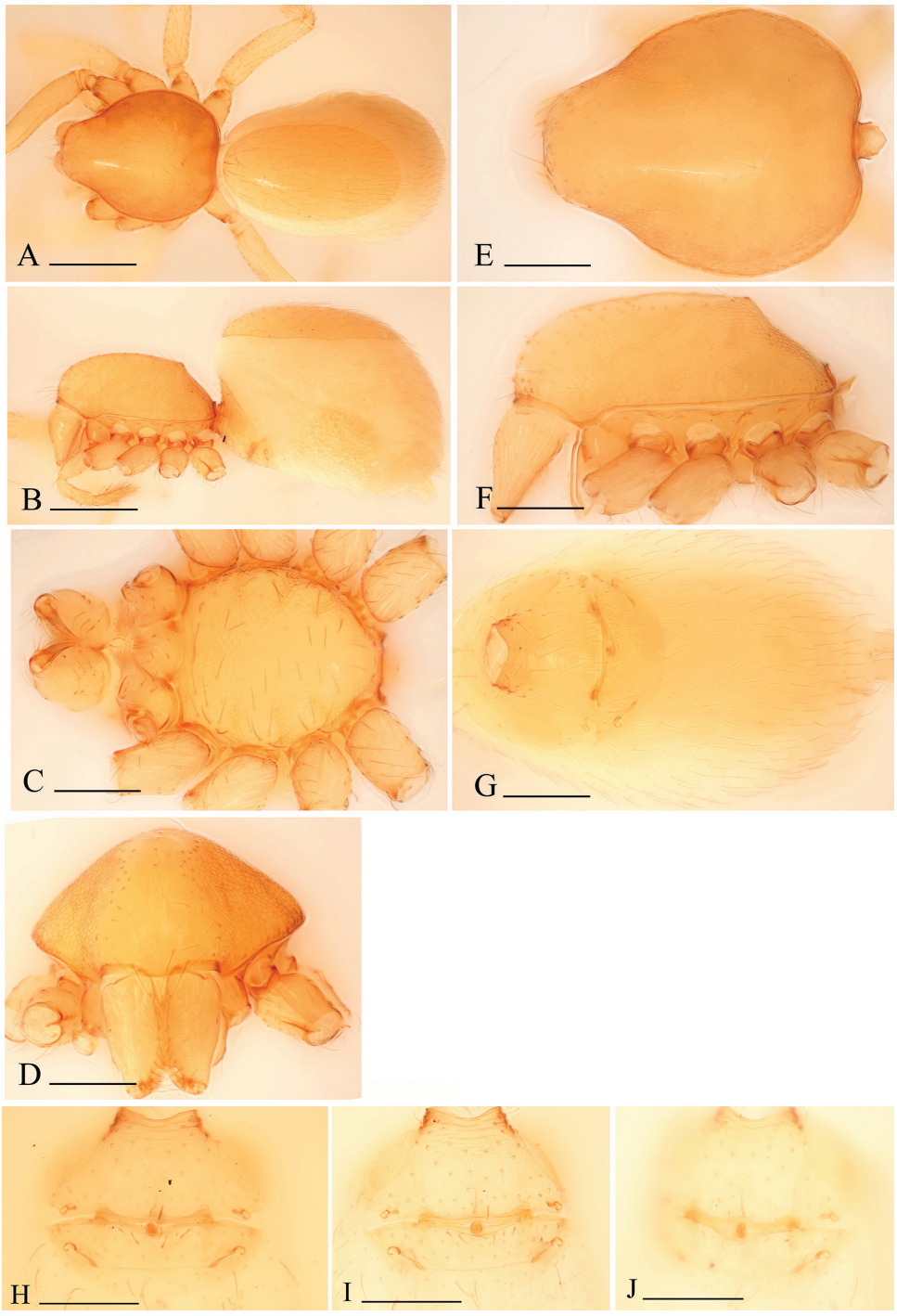

Figure 3. *Bannana crassispina* sp. n., female. **A, B** Habitus, dorsal and lateral views **C–F** Prosoma, ventral, anterior, dorsal and lateral views **G** Abdomen, ventral view **H–J** Genital area, ventral (**H, I**) and dorsal (**J**) views, **I, J** cleared in lactic acid. Scales bar: **A, B** = 0.4 mm; **C–J** = 0.2 mm.

reticulated; lateral margin rebordered; eyes reduced, only four eyes visible in frontal view (Fig. 1F). Mouthparts: chelicerae straight, paturon inner margin unmodified; labium anterior margin deeply incised (ldi) (Fig. 1C); endites slender, distally only slightly branched. Sternum: setae sparse, light, needle-like, evenly scattered; on the middle part of sternum with five pairs of short setae arranged in two rows (Fig. 1C). Abdomen: dorsal scutum covering full length of abdomen, no soft tissue visible from above, not fused to epigastric scutum. Pedicel tube short, unmodified. Book lung covers elliptical, surface smooth. Postepigastric and epigastric scutum fused, apodemes absent, posterior spiracles connected by groove (Fig. 1G). Leg spines: tibiae I, II with 4 pairs of ventral spines each; metatarsi I, II with 2 pairs of ventral spines each, legs III and IV without spines.

Male genitalia: epigastric region (Fig. 1G) with sperm pore small, oval, rebordered, situated in front of anterior spiracles. Palp (Fig. 2A–G): pale-orange; femur enlarged, attached to patella basally; tibia with two very strong, thick bristles (thb) on prolatero-distal part; cymbium not fused with bulb, with scattered setae; bulb pear shaped, basal-ventral area bulged, about twice as long as cymbium, stout, tapering apically; embolus system (Fig. 2E–G) complicated, with a wide, ear-shaped protrusion (esp) prolaterally, surface of the protrusion bearing numerous spinules, with a filiform, long and mesially curved projection (ffp) and a narrow branch (nb) retrolaterally.

Female: as in male except as noted. Habitus as in Fig. 3A, B. Slightly larger than male. Body length 1.78; carapace 0.73 long, 0.62 wide; abdomen 1.07 long, 0.69 wide. Abdomen: dorsal scutum covering about 3/4 of abdomen, about 2/3 of abdomen width (Fig. 3A). Sternum without characteristic setae. Postepigastric scutum short, boat-shaped, posterior margin smoothly curved, not fused to epigastric scutum (Fig. 3G).

Female genitalia: ventral view (Fig. 3H, I): posterior margin of epigastric scutum with two dark brown knobs (dkn); surface without external features. Dorsal view (Fig. 3J): with a elliptical posterior receptacle (pr), extending anterior by a narrow, stick-like sclerite (sls); with very short apodemes (apo).

Distribution. Known only from the type locality.

***Bannana parvula* sp. n.**
http://zoobank.org/29B780CE-957D-4DD2-ADDC-6083FB3AAFD0

Type material. Holotype: male (IZCAS Ar-25067), China: Yunnan Province, Mengla County, Menglun Nature Reserve, Secondary tropical seasonal moist forest (21°54.607'N, 101°17.005'E, Alt: 633 m), pitfall traps, 16–31 March 2007, G. Zheng and Z. Chen leg. **Paratypes:** 1 female (IZCAS Ar-25071), searching, same data as holotype; 1 male (IZCAS Ar-25068), Primary tropical seasonal rainforest (21°57.445'N, 101°12.997'E, Alt: 744 m), searching, 19–25 December 2006; 1 female (IZCAS Ar-25066), Secondary tropical seasonal moist forest (21°54.718'N, 101°16.940'E, Alt: 645 m), pitfall traps, 16–31 March 2007; 1 female (IZCAS Ar-25070), Rubber-tea plantation (21°55.551'N, 101°16.923'E, Alt: 561 m), searching, 19–26 May 2007; 1

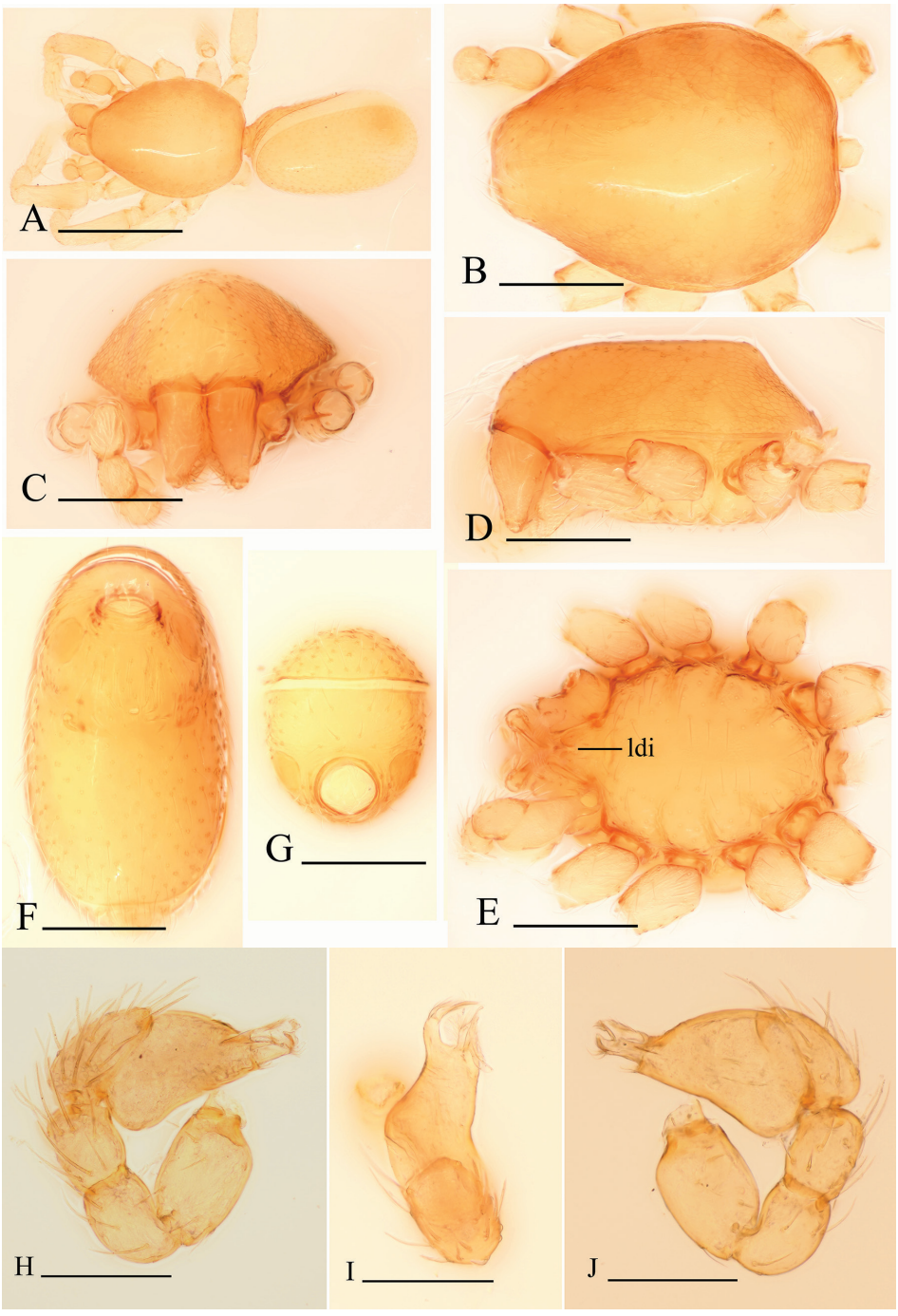

Figure 4. *Bannana parvula* sp. n., male. **A** Habitus, dorsal view **B, C, D, E** Prosoma, dorsal, anterior, lateral and ventral views **F, G** Abdomen, ventral and anterior views **H–J** Left palp, prolateral, dorsal and retrolateral views. Abbreviation: ldi = labium deep incision. Scales bar: **A** = 0.4 mm; **B–G** = 0.2 mm; **H–J** = 0.1 mm.

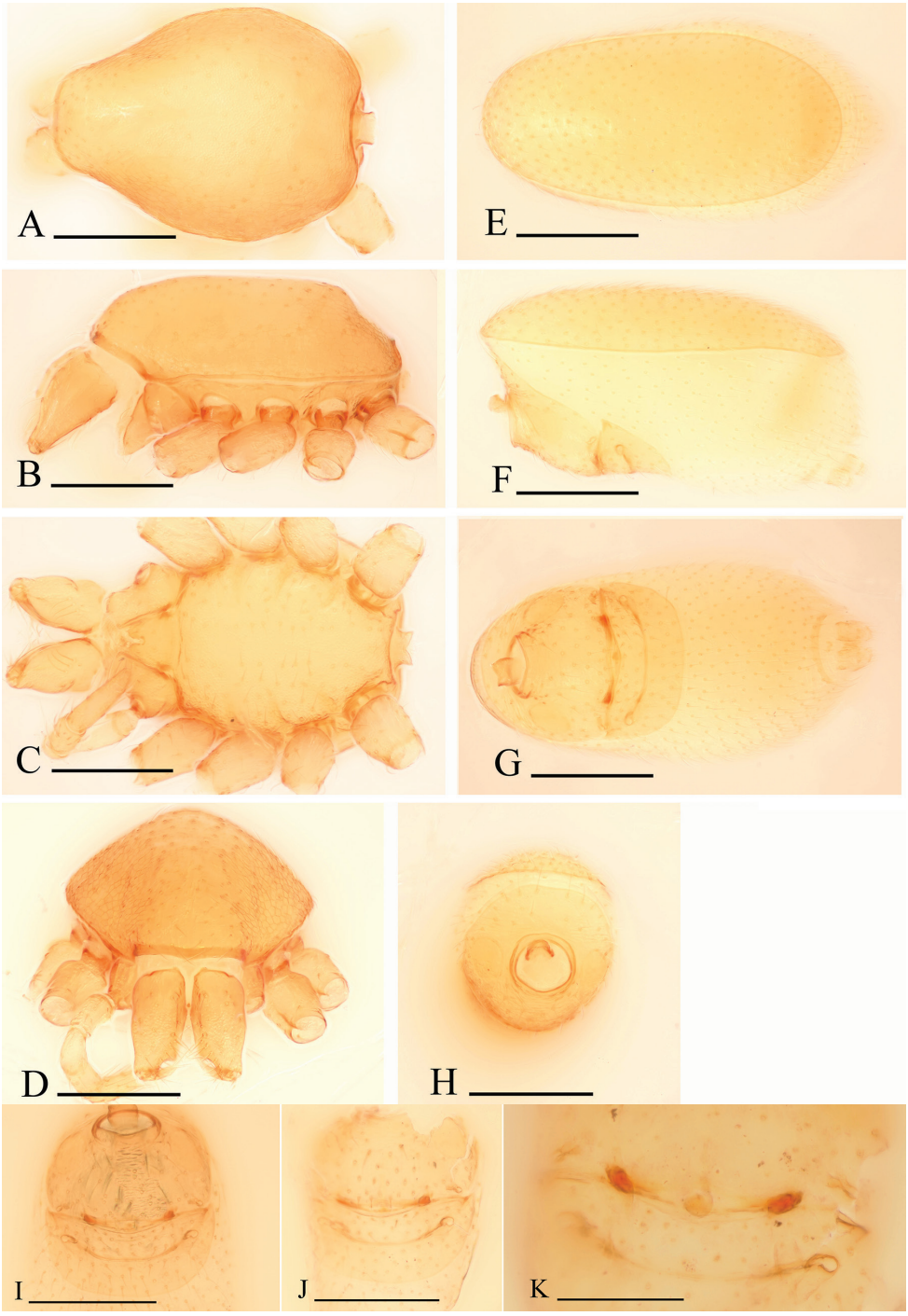

Figure 5. *Bannana parvula* sp. n., female. **A–D** Prosoma, dorsal, lateral, ventral and anterior views **E–H** Abdomen, dorsal, lateral, ventral and anterior views **I–K** Genital area, ventral (**I, J**) and dorsal (**K**) views **J, K** cleared in lactic acid. Scales bar: **A–J** = 0.2 mm; **K** = 0.1 mm.

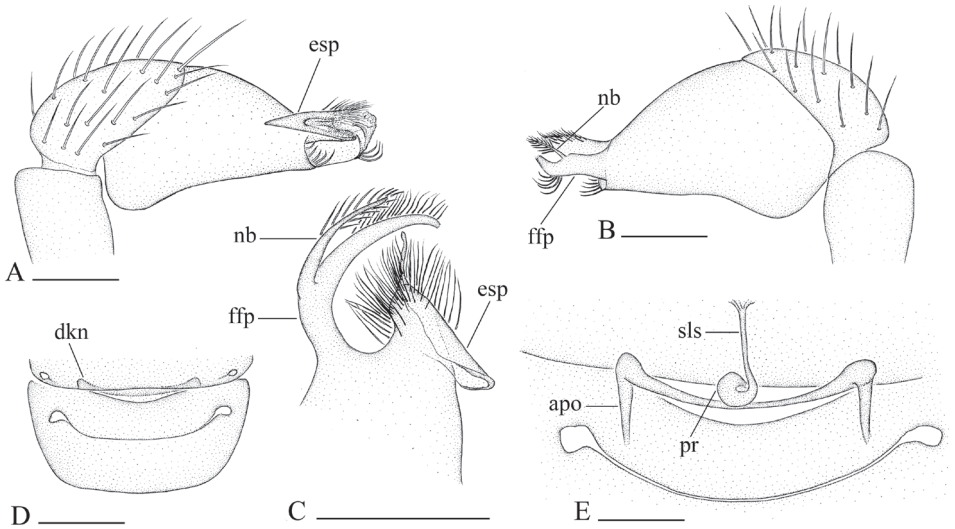

Figure 6. *Bannana parvula* sp. n. **A, B** Male bulb, prolateral and retrolateral views **C** Distal part of male bulb, dorsal view **D, E** Female genital area, ventral and dorsal views. Abbreviations: apo = apodeme; dkn = dark brown knobs; esp = ear-shaped protrusion; ffp = filiform, curved projection; nb = narrow branch; pr = posterior receptacle; sls = stick-like sclerite. Scales bar: **A, B, C, E** = 0.05 mm; **D** = 0.1 mm.

female (IZCAS Ar-25069), Rubber plantation (21°54.684'N, 101°16.319'E, Alt: 585 m), searching, 5–12 January 2007.

Etymology. The specific name is Latin, "parv-" = small, referring to the very small body size of this species.

Diagnosis. Males of the new species are similar to those of *Dysderoides kanoi* Grismado & Deeleman, 2014, but can be distinguished by the small size and the ear-shaped protrusion on distal part of bulb (compare Fig. 6A–C and Grismado et al. 2014: fig. 10G–I); females can be distinguished from *B. crassispina* sp. n. by the large dorsal abdominal scutum and the rectangular postepigastric scutum (Fig. 5E, I).

Description. Male. Body yellow, legs lighter. Habitus as in Fig. 4A. Body length 1.07; carapace 0.51 long, 0.38 wide; abdomen 0.62 long, 0.34 wide. Carapace oval, *pars cephalica* almost flat in lateral view, dorsal surface smooth; sides reticulated; lateral margin rebordered; no eye remnants visible (Fig. 4B, C). Mouthparts: chelicerae straight, paturon inner margin unmodified; labium anterior margin deeply incised (ldi) (Fig. 4E); endites slender, distally only slightly branched. Sternum: setae sparse, light, needle-like, evenly scattered. Abdomen: dorsal scutum covering full length of abdomen, no soft tissue visible from above, not fused to epigastric scutum. Pedicel tube short, unmodified. Book lung covers round, surface smooth. Postepigastric and epigastric scutum fused, apodemes absent, posterior spiracles connected by groove (Fig. 4F). Leg spines: tibiae I, II with 3 pairs of ventral spines each; metatarsi I, II with 2 pairs of ventral spines each, legs III and IV without spines.

Male genitalia: epigastric region (Fig. 4F) with sperm pore small, oval, rebordered, situated between anterior and posterior spiracles. Palp (Fig. 4H–J): pale-orange; femur

slightly enlarged, attached to patella basally; cymbium not fused with bulb, with scattered setae; bulb pear shaped, about twice as long as cymbium, stout, tapering apically; embolus system (Fig. 6A–C) complicated, with a narrow, ear-shaped protrusion (esp) prolaterally, surface of the protrusion bearing numerours spinules, with a filiform, long and mesially curved projection (ffp) and a narrow branch (nb) retrolaterally.

Female: as in male except as noted. Habitus as in Fig. 5A, B, E, F. Body length 1.12; carapace 0.50 long, 0.39 wide; abdomen 0.65 long, 0.32 wide. Abdomen: dorsal scutum covering about 5/6 of abdomen, about equal to the abdomen width (Fig. 5E). Postepigastric scutum rectangular, posterior margin nearly straight, not fused to epigastric scutum (Fig. 5G).

Female genitalia: ventral view (Figs 5I, J, 6D): posterior margin of epigastric scutum with two dark brown knobs (dkn); surface without external features. Dorsal view (Figs 5K, 6E): with a nearly round posterior receptacle (pr), extending anterior by a narrow, stick-like sclerite (sls); with short apodemes (apo).

Distribution. Known only from the type locality.

Acknowledgements

The manuscript benefited greatly from comments by Drs Yuri M. Marusik, Cristian J. Grismado and Darrell Ubick. This study was supported by the National Natural Science Foundation of China (NSFC-31071886/31172121/31372224/31372157), the Program for Liaoning Excellent Talents in University (LJQ2013114) for Yanfeng Tong.

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ZooKeys 494: 13–30 (2015)
doi: 10.3897/zookeys.494.8676
http://zookeys.pensoft.net

RESEARCH ARTICLE

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A new ladybird spider from Hungary (Araneae, Eresidae)

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Academic editor: *Jeremy Miller* | Received 1 October 2014 | Accepted 13 March 2015 | Published 6 April 2015

http://zoobank.org/E303FC86-F654-416C-A5D8-59C34044C60C

Citation: Kovács G, Prazsák I, Eichardt J, Vári G, Gyurkovics H (2015) A new ladybird spider from Hungary (Araneae, Eresidae). ZooKeys 494: 13–30. doi: 10.3897/zookeys.494.8676

Abstract

According to the most recent taxonomic literature, three species of the genus *Eresus* are known in Central Europe, *E. kollari*, *E. sandaliatus* and *E. moravicus*. We recognized a fourth distinctive species from Hungary, which is described as *Eresus hermani* **sp. n.** *Eresus hermani* has an early spring copulation period, females have a light grey (grizzled) cephalothorax due to a heavy cover of lightly colored setae, and an epigyne with large flat areas posterior to the epigynal pit, while males are distinguished by a broad and blunt terminal tooth of the conductor. An updated and modified comparative table of Řezáč et al. (2008) to include all four Central European *Eresus* species, and a simple key to the species group's species are given. Habitus, epigyne, vulva and conductor of *E. kollari*, *E. moravicus* and *E. sandaliatus* are also illustrated. An annotated list of papers illustrating *E. hermani* due to misidentifications is presented.

Keywords

Ladybird spiders, *Eresus*

Introduction

The velvet spiders (family Eresidae) are among the most attractive spiders in Europe. The family contains nine genera and 96 described species worldwide. The genus *Eresus*

Walckenaer, 1805 contains 15 valid species from Europe, Africa and Asia, of which nine occur in Europe (World Spider Catalog 2015).

According to the latest studies (Řezač et al. 2008, Miller et al. 2012) three species of the *Eresus sandaliatus* group, *Eresus kollari* Rossi, 1846, *E. sandaliatus* Martini & Goeze, 1778 and *E. moravicus* Řezáč, 2008, occur in Central Europe.

The long and complicated scientific history of the *Eresus sandaliatus* group *sensu* Miller et al. (2012) is discussed in detail in Řezač et al. (2008), so only the Hungarian perspective is described here. The nomenclatural chaos is well illustrated by the fact that *E. cinnaberinus* might become valid, possibly as a senior synonym of *E. kollari* (Azarkina and Trilikauskas 2012).

The Hungarian spider fauna was first studied in detail by Ottó Herman, who also gave a detailed description of the *Eresus* genus (Herman 1879). Herman indicated the presence of two species, *E. ruficapillus* C. L. Koch, 1846 (regarded as misidentification of *E. moravicus* by Řezač et al. 2008 due the "reddish-yellowish hairs on the female") and *E. kollari* (as *E. cinabarinus* Olivier), distinguishing *a*, *β*, and *γ* color variants, the latter corresponding to *E. moravicus*.

However, subsequent authors (e. g. Chyzer and Kulczynski 1918, Samu and Szinetár 1999) recognized only one species, *E. cinnaberinus*, with adults during the autumn.

Loksa (1969) mentioned a color form of female *Eresus* (*E. niger* var. *ruficapillatus* C.L. Koch) from the Mecsek hills and from the vicinity of lake Balaton, which has yellowish hairs on the carapace front, later identified as *E. moravicus* by Řezač et al. (2008).

Recently, Řezáč et al. (2008) considered *E. cinnaberinus* as *nomen dubium* [but see personal communication of Řezáč referred to in Azarkina and Trilikauskas (2012) as it might not] and proposed the name *E. kollari* Rossi, 1846 as valid. In this revision a distinct new species, *E. moravicus* was described (Řezač et al. 2008).

Eresus cinabarinus γ-color variant of Herman (1879), *E. ruficapillus* C.L. Koch and *E. niger* var. *ruficapillatus* (in Loksa 1969) were all identified as *E. moravicus* by Řezač et al. (2008). This means two Hungarian *Eresus* species, *E. moravicus* with a late spring–early summer copulation period, and *E. kollari* with populations mating in autumn (Kovács et al. 2010).

During an ongoing project aimed at mapping the distribution of Eresidae in Hungary, the presence of an *Eresus* species was observed with an early spring copulation period, which has unique morphological characters, and is described here as new to science.

Materials and methods

Specimens were either collected individually or by using pitfall traps, and stored in 70% ethyl-alcohol.

We studied 31 males, 15 females and 6 juveniles of *E. kollari*; 20 males, 25 females and 4 juveniles of *E. hermani* sp. n., and 19 males, 11 females and 3 juveniles of *E. moravicus*, and 2 males, 3 females and 2 juveniles of *E. sandaliatus*. All the measurements are given in millimeters (mm).

All specimens of the new species examined, including holotype and four paratypes, have been deposited in the Soil Zoological Collection (former Arachnoidea Collection) of the Department of Zoology, Hungarian Natural History Museum (HNHM) Budapest (curator Dr. László Dányi).

Specimens and copulatory organs were studied using a Leica MZ FL III stereomicroscope and photographed by Canon Q Imaging Micro 5.0 RTV at the Institute of Genetics, BRC. Scanning electron micrographs were taken with a Hitachi S-4700 microscope at the Department of Applied and Environmental Chemistry, University of Szeged, Hungary.

Abbreviations

Standard abbreviations of morphological terms follow Miller et al. (2012). Further abbreviations: **PME** = posterior median eyes, **PLE** = posterior lateral eyes, **Fe** = femur, **Pt** = patella, **Ti** = tibia, **Ta** = tarsus, **Mt** = metatarsus, **ML** = median lobe of epigyne, **L** = leg, **juv.** = juvenile.

HNHM	Hungarian Natural History Museum, Budapest;
NHMW	Naturhistorisches Museum, Wien;
PPI	Plant Protection Institute of the Hungarian Academy of Sciences, Budapest;
JLPC	private collection of Jørgen Lissner;
WPPC	private collection of Walter Pfliegler.

Translation of Hungarian geographical names in the description of collection material is *-hegy:* hill; *-völgy*: valley.

Results

Taxonomy

***Eresus hermani* sp. n.**
http://zoobank.org/CE9C2B06-FBAC-4246-BD75-EC716F94C34F
Figs 1A–B, 3A–C, 4A–B, 5A–B, 6A–B, 7A

Eresus cinnaberinus Szinetár 2006 p 22 fig. 3 (misidentified)
Eresus kollari Kovács et al. 2010 fig. 1C–F, 2D (misidentified)
Eresus kollari Miller et al. 2012 fig. 2A (misidentified)
Eresus kollari Szinetár et al. (2012): table 2, figure 6 (misidentified)

Material examined. Holotype: Female – HUNGARY, Budapest, Remete-hegy, N 47°32'26.3", E 19°00'24.1", singled, 23.04.2011., G. Kovács (HNHM, collection number: HNHM Araneae 7612).

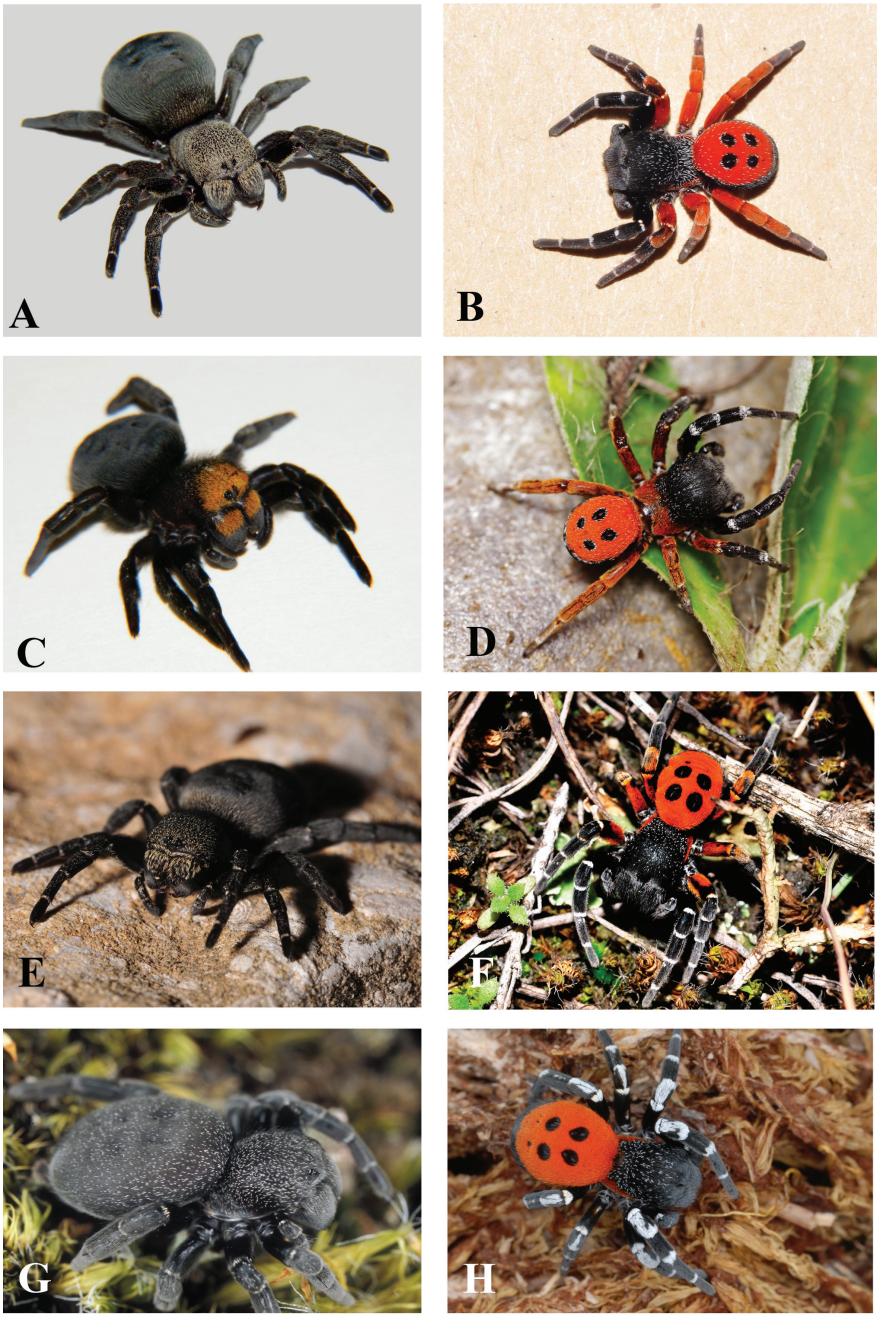

Figure 1. A–H Habitus of living *Eresus* species, photographs: **A–B** *Eresus hermani* **A** female (Remete-hegy, Budapest, Hungary) **B** male (Farkas-hegy, Budaörs, Hungary) **C–D** *Eresus moravicus* **C** female (Misina-hegy, Pécs, Hungary) **D** male (Dürnstein, Austria) **E–F** *Eresus kollari* **E** female (Paloznak, Hungary) **F** male (Kéleshalom, Hungary) **G–H** *Eresus sandaliatus* **G** subadult female (near to Silkeborg Langsø, Enebærbakken, Denmark) **H** male (Nørlund, Hallundbæk Stream, Denmark) (**D** courtesy of Walter Pfliegler **G–H** courtesy of Jørgen Lissner).

Paratypes: 2 females – HUNGARY, Budapest, Sas-hegy, N 47°28'47.2", E 19°01'04.4", singled, 02.10.2013., G. Kovács, H. Gyurkovics, G., Vári, A. Rákóczi (HNHM, collection number: HNHM Araneae-7630-31). – 2 males HUNGARY, Budapest, Remete-hegy, N 47°32'26.3", E 19°00'24.1", singled, 23.04.2011., G. Kovács, (HNHM, collection number: HNHM Araneae: 7632–33).

Remark. The genus *Eresus* in Central Europe has a long and difficult nomenclatural history. Some available "old names" were examined, such as *Eresus illustris* (presently considered *nomen dubium*, specimens are irretraceable), which is marked as possibly Hungarian (despite the fact Koch himself wrote "Vaterland: Unbekannt" [trans. Locality: Unknown]), but discarded it on the basis of the description and color image (Koch 1838, fig. 317), where the male has six black dots on the opisthosoma and only the dorsal side of hind femora as red, whereas *E. hermani* males have only four dots and clearly red hind legs patellae and tibiae, without any black, and tarsi and metatarsi are brownish grey (Fig. 1B). The female of *E. illustris* is unknown. The other possible candidate, *E. fulvus* Rossi 1846 (type specimens can no longer be found in NHMW), described by female specimens only, can also be excluded as a potential synonym, since they all have a large area covered by yellow/orange setae on the cephalothorax ["nitide fulvus" in the description of Rossi (1846)], whereas *E. hermani* females have no truly yellow setae on the prosoma at all; instead, its dorsal cephalothorax is light brownish-grey overall. According to Řezáč et al. 2008 (page 275.) *E. fulvus* Rossi differs from *E. moravicus* by "having spermatheca that are less lobed, and having copulatory ducts that are almost horizontal in the centre of the vulva." By contrast, spermathecae of *E. hermani* are rather conspicuously lobed, at least as much as in *Eresus moravicus* (Figs 4C, F and 5B, D).

Etymology. Dedicated to Ottó Herman (1835–1914), the Hungarian arachnologist and polymath, who first recognized color variants within Hungarian *Eresus* forms, to commemorate the 100th anniversary of his passing.

Diagnosis. Females of this species differ from all other *Eresus* females by the carapace's short, off-white to light brown hairs, intermingled with small clumps of long, black hairs, giving a light, grizzled appearance to the prosoma, and by an epigyne with a pair of flat plateaus adjoining the sides of the broad median lobe laterally. Males are characterized by the narrow groove and blunt, broad terminal tooth of the conductor, and distinguished from other *Eresus* species, except *E. moravicus*, by having almost entirely red hind legs. They differ from *E. moravicus* males by having red color on the thoracic dorsum only laterally, having a less prominent cephalic region with an almost flat area between PLE and PME, and by narrower strips of white setae on L I. This species has an early spring copulation period, and exhibits a marked difference in the sizes of the sexes: males are relatively small, while females are comparatively large among Central European *Eresus* spp. (Table 1).

Description. Male. Prosoma (Fig. 1B)**:** Length 2.9–4.1 (mean 3.4, N = 15) Prominent, color dark ferruginous brown, covered by long, black hairs intermingled with scattered, short, white ones. Cephalic region barely broader than thoracic part, weakly broadening towards the front, steeply raised posteriorly, but area between PME

Table 1. Distinguishing morphological characters of species belonging to *Eresus sandaliatus* group (in part after Řezáč et al. 2008).

	***Eresus kollari* Rossi, 1846 morphotype**	***Eresus sandaliatus* Martini & Goeze, 1778**
Females		
Prosoma length	3.6–6.1 (mean 4.7)	4.2–7.2 (mean 5.4)
Color of prosoma	black, sparsely sprinkled with off-white to light brown setae, more heavily anteriorly (Fig. 1E)	black, sparsely sprinkled with off-white to light brown setae, more heavily anteriorly (Fig. 1G)
Epigyne	(i) epigynal pit extending all the way to posterior epigyne (Figs 4G, H, 5E)	(i) epigynal pit extending all the way to posterior epigyne (Figs 4J, K, 5G)
	(ii) anterior 1/3 of fissures markedly incurvated sidewards, anterior tip usually not incurvated (Figs 4G,H, 5E)	(ii) anterior 1/3 of fissures slightly inclined sideways, anterior tip weakly bent (Figs 4J, K, 5G)
Vulva	(i) anterior section of copulatory ducts strongly sclerotized, usually elongated (Figs 4I, 5F)	(i) anterior section of copulatory ducts weakly sclerotized, usually globular Figs 4L, 5H)
	(ii) spermathecae distinctly lobed (Figs 4I, 5F)	(ii) spermathecae indistinctly lobed (Figs 4L, 5H)
Approximate ratio between greatest width of ML and that of epigyne	4:10	5:10
Males		
Prosoma length	2.6–4.2 (mean 3.6)	2.9–4.1 (mean 3.6)
Number of black spots on opisthosoma	usually 4	usually 6
White hairs on opisthosoma	usually present	usually absent
Color of hind legs	proximally red, distally black (Fig 1F)	black, exceptionally with some red on femur (Fig. 1H)
White transverse stripes on Leg I–II	narrow, covering only the distal edge of segments (Fig. 1 F)	very broad at the distal part of segments, widely extending into the proximal part of next segment (Fig. 1H)
Red color on thoracic dorsum	only on flanks, at most a few red hairs posteriorly (Fig. 1F)	only on flanks, at most a few red hairs posteriorly (Fig. 1H)
Conductor in lateral view	moderately wrinkled, much longer than wide (Fig. 3 H)	almost smooth, about as long as wide (Fig. 3K)
Terminal tooth of conductor	small, almost straight, pointed (Figs 3G, H, I)	strong, long, almost straight, tip cropped (Fig. 3J, K, L)
Groove of conductor in lateral view	shallow, V-shaped (Fig. 3 H.)	deep, U-shaped (Fig. 3K.)

Note: Without exception, the epigyne of *Eresus moravicus* specimens that we studied match those in Fig. 2L–P in Řezáč et al. (2008), but differ slightly from that shown in Fig. 2K (Řezáč et al. 2008), which seems to be depicted also as a drawing in Fig. 4H (Řezáč et al. 2008). The main difference is the direction of the anterior portion of fissures, which are typically directed slightly laterally, instead of medially. To aid differentiation of *E. moravicus*, we provide comparative photographs and a drawing of *E. moravicus* epigyne in Fig. 4D–E and Fig. 5C, which we believe to be typical of the species.

Table 1. Continued.

	Eresus hermani sp. n.	*Eresus moravicus* Řezáč, 2008
Females		
Prosoma length	6.6–9.9 (mean 8.2)	5.9–9.9 (mean 7.5)
Color of prosoma	entire prosoma grizzled light brown due to a heavy cover of off-white to light brown setae (Fig. 1A)	black, except orange anterior (Fig. 1C)
Epigyne	(i) flat plateaus between the posterior edge of epigynal pit and posterior of epigyne at sides of median lobe (Figs 4A, B, 5A, 6A)	(i) epigynal pit extending all the way to posterior epigyne (Figs 4D, 4E, 5C)
	(ii) anterior ½ of fissures parallel to midline, anterior tip strongly incurved (Figs 4A, B, 5A, 6A)	(ii) anterior ½ of fissures slightly diverging laterally, anterior tip strongly incurved–*see note* (Figs 4D, 5E, 5C)
Vulva	(i) anterior section of copulatory ducts weakly sclerotized, usually globular (Figs 4B, 5B, 6B)	(i) anterior section of copulatory ducts strongly sclerotised, usually elongated (Figs 4D, 5D)
	(ii) spermathecae strongly lobed (Figs 4C, 5B)	(ii) spermathecae strongly lobed (Figs 4D, 5B)
Approximate ratio between greatest width of ML and that of epigyne	6:10	5:10
Males		
Prosoma length	2.9–4.1 (mean 3.4)	3.5–5.6 (mean 4.6)
Number of black spots on opisthosoma	nearly always 4	nearly always 4
White hairs on opisthosoma	nearly always present	nearly always present
Color of hind legs	red, tarsal joints brownish grey (Fig. 1B)	red, tarsal joints brownish grey (Fig. 1D)
White transverse stripes on Leg I–II	narrow, covering only the distal edge of segments (Fig. 1B)	broad at the distal part of segments, usually extending to the proximal end of next segment (Fig. 1D)
Red color on thoracic dorsum	only on flanks, at most a few red hairs posteriorly (Fig. 1B)	extends to the middle, at least posteriorly (Fig. 1D)
Conductor in lateral view	wrinkled, clearly wider than long (Fig. 3B)	wrinkled, somewhat longer than wide (Fig. 3E)
Terminal tooth of conductor	strongly incurvated, broad and blunt (Fig. 3B, C)	strongly incurvated, narrows to a relatively pointed tip (Fig. 3E, F)
Groove of conductor in lateral view	deep, narrow, ν (Greek nu) or narrow U shaped (Fig. 3B.)	round (Fig. 3E.)

and PLE nearly flat. Thoracic part bordered laterally by narrow red stripes, never extending to posterior dorsum.

Chelicerae: Blackish-brown, covered by long, nearly adpressed black hairs; basal half with scattered white hairs on the front.

Legs: Legs I–II dark orange-brown with black hairs; Fe II and Pt II orange with red hairs, Ti II often with a dorsal patch of red hairs. Distal edges of Fe, Pt, Ti and Ta with narrow, white stripe dorsally, usually not extending to the proximal part of the next distal segment. Legs III and IV largely orange, covered with red hairs, Ta and Mt dull grayish-brown due to a mixture of reddish and black hairs, except for a proximodorsal patch of red on Mt.

Opisthosoma (Fig. 1B)**:** Dorsally red with scattered white hairs except for two pairs of black spots. Red area and black spots seamed by a more-or less continuous line of white hairs. Ventral side of opisthosoma black with the exception of some red hairs on the branchial opercula.

Palps (Fig. 3A–C)**:** Conductor broad, strongly wrinkled. Terminal tooth broad and blunt, somewhat longer than the lamella, with a strong, sudden bend at the base or somewhat more distally. Groove deep, narrow, ν (Greek nu) or narrow U shaped at the base in lateral view. Inner, spiny lamella high, about as high as terminal tooth.

Female. Prosoma (Fig. 1A)**:** Length 6.6–9.9 (mean 8.2, n = 21), prominent, especially the cephalic region, dark orange-brown with a heavy cover of short, off-white to light brown hairs and with scattered, small clumps of long, black hairs giving a grizzled appearance.

Chelicerae: Dark orange brown, front of basal 1/3–3/4 same color as prosoma.

Legs: Rusty red, Fe, Pt, Ti and Mt of all legs covered by black hairs with pale brown hairs scattered among them, the latter gradually decreasing in number from L I to L IV, usually clustering to form indistinct cross bands dorsally at the distal edge of each segments. Ta usually black, except for a small cluster of pale hairs basally.

Palps: Similar in color to L I.

Opisthosoma (Fig. 1A)**:** Brownish-black, covered by long black hairs with a scattering of short pale hairs at its anterior.

Epigyne (Figs 4A, 5A, 6A)**:** Moderately deep, median lobe broad (ratio between the greatest width of ML to the greatest width of epigyne: 6:10), considerably flared posteriorly, reaching well over the posterior margin of the epigynal pit. Posterior edge of the epigynal depression not reaching posterior epigyne, but followed by a pair of flat, somewhat wrinkled plateaus adjoining the fissures laterally. Posterior part of fissures inclined towards the midline, turning parallel to the longitudinal axis before the short, incurved anterior tips.

Vulva (Figs 4B, 5B, 6B)**:** Spermathecae distinctly lobed, reaching further laterally than copulatory ducts. Anterior part of copulatory ducts weakly sclerotized, usually circular, exceptionally elongated in outline.

Simplified key to the species of the *Eresus sandaliatus* group

Females

1 Anterior of cephalic region covered by bright yellow/orange setae..... ..... ***Eresus moravicus***

– No bright yellow/orange setae on prosoma **2**

2 Entire prosoma covered heavily by off-white to light brown setae; large..... ..... ***Eresus hermani* sp. n.**

– Prosoma sparsely sprinkled with lightly colored setae, somewhat more heavily on the front; smaller **3**

3 Anterior of fissures only slightly inclined sideways, as in Fig. 5G, spermathecae indistinctly lobed, anterior of copulatory ducts nearly round in outline, weakly sclerotized ..... ***Eresus sandaliatus***

– Anterior of fissures markedly incurvated sideways, as in Fig. 5F, spermathecae distinctly lobed, anterior of copulatory ducts elliptical, strongly sclerotized... ..... ***Eresus kollari***

Males

1 Terminal tooth of conductor strongly incurvated, hind legs almost entirely red **2**

– Terminal tooth of conductor nearly straight, at most weakly bent, red areas on hind legs not so extensive or entirely absent **3**

2 Conductor with a blunt terminal tooth and a narrow groove, prosoma barely broadens towards front ..... ***Eresus hermani* sp. n.**

– Conductor with a pointed terminal tooth and a round groove, prosoma strongly broadens towards front ..... ***Eresus moravicus***

3 Conductor with a strong, long and slightly bent terminal tooth and a U-shaped (in lateral view) groove, hind legs nearly devoid of red setae .... ***Eresus sandaliatus***

– Conductor with a short, straight terminal tooth and a V-shaped (in lateral view) groove, hind legs with extensive areas of red color ..... ***Eresus kollari***

Distribution.

Known from seven localities (Fig. 2): Budapest: Remete-hegy (*locus typicus*), Mátyás-hegy, Sas-hegy, Budaörs: Farkas-hegy, Érd: Fundoklia-völgy and Várpalota-Inota: Víztározó, Baglyas-hegy. With the exception of Érd: Fundoklia-völgy, *E. hermani* proved to be syntopic with *E. kollari*, whereas all three *Eresus* sp. occurring in Hungary, *E. hermani*, *E. kollari* and *E. moravicus* are syntopic at Várpalota-Inota: Baglyas-hegy.

Habitat. Edges of a local variety of downy oak scrub woodland (*Ceraso mahaleb-Quercetum pubescentis*) and the interim zone between calcareous open rocky grasslands (*Seselio leucospermi-Festucetum pallentis*) and degraded scrubland.

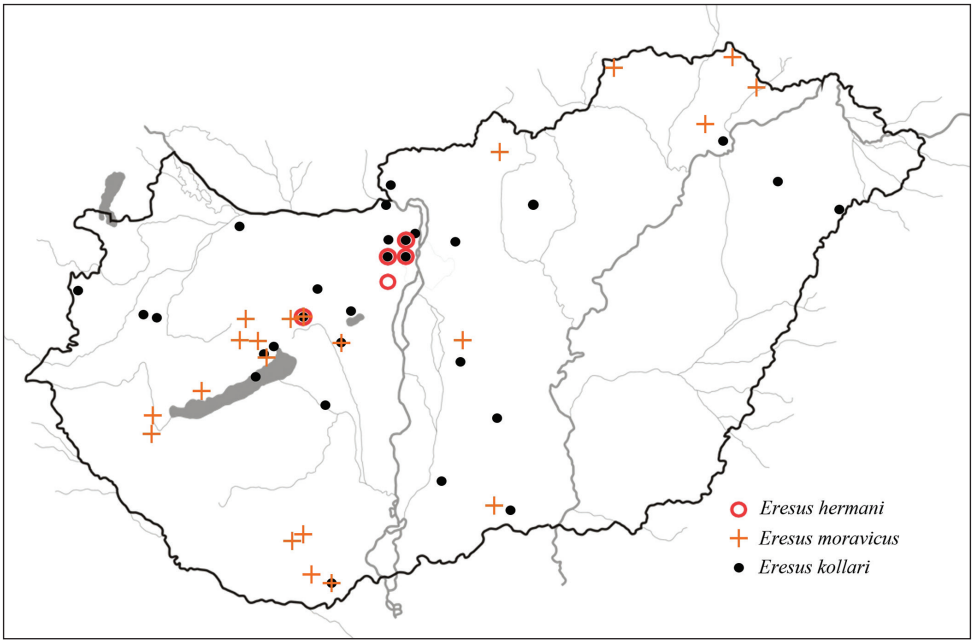

Figure 2. Known localities of all three *Eresus* species occurring in Hungary.

Phenology. *Eresus hermani* matures in August-September, wandering males can be found from the end of March to the end of April (inferred copulation period) and females lay eggs in June. This phenology clearly sets *Eresus hermani* apart from the other Hungarian *Eresus* species: *E. moravicus* matures in late spring and mates in early summer, while *E. kollari* matures in late summer – early autumn, immediately followed by a copulation period in autumn. The phenology of *Eresus hermani* is essentially the same as that of *E. sandaliatus* (Řezač et al. 2008), which, however, does not occur in Hungary or within the Carpathian Basin.

Additional material examined. Hungary: Remete-hegy, Budapest (1 ♀, 01.11.2008., G. Kovács, HNHM Araneae-7669); Remete-hegy, Budapest (1 ♀, 02.09.2008., G. Kovács, HNHM Araneae-7670); Remete-hegy, Budapest (3 ♀, 2 ♂, 05.04.2008., G. Kovács, HNHM Araneae-7671); Remete-hegy, Budapest (1 ♀, 1 juv., 18.04.2008., G. Kovács, HNHM Araneae-7672); Farkas-hegy, Budaörs (1 ♀, 22.09.2013., G. Kovács, H. Gyurkovics, G. Vári, D. V. Nagy, HNHM Araneae-7673); Farkas-hegy, Budaörs (2 ♂, 14.04.2013., H. Gyurkovics, G. Vári, HNHM Araneae-7674; Sas-hegy, Budapest (4 ♂, 07.04.2012., A. Rákóczi, HNHM Araneae-7675); Sas-hegy, Budapest (4 ♂, 25.03.2012., A. Rákóczi, HNHM Araneae-7676); Remete-hegy, Budapest (1 ♂, 16.04.2005., G. Kovács, HNHM Araneae-7677; Farkas-hegy, Budaörs (1 ♂, 13.04.2012., G. Kovács, HNHM Araneae-7678); Farkas-hegy, Budaörs (1 ♂, 21.04.2010., J. Bodor, HNHM Araneae-7679); Remete-hegy, Budapest (5 ♀, 16.09.2012., G. Kovács, HNHM Araneae-7680); Remete-hegy, Bu-

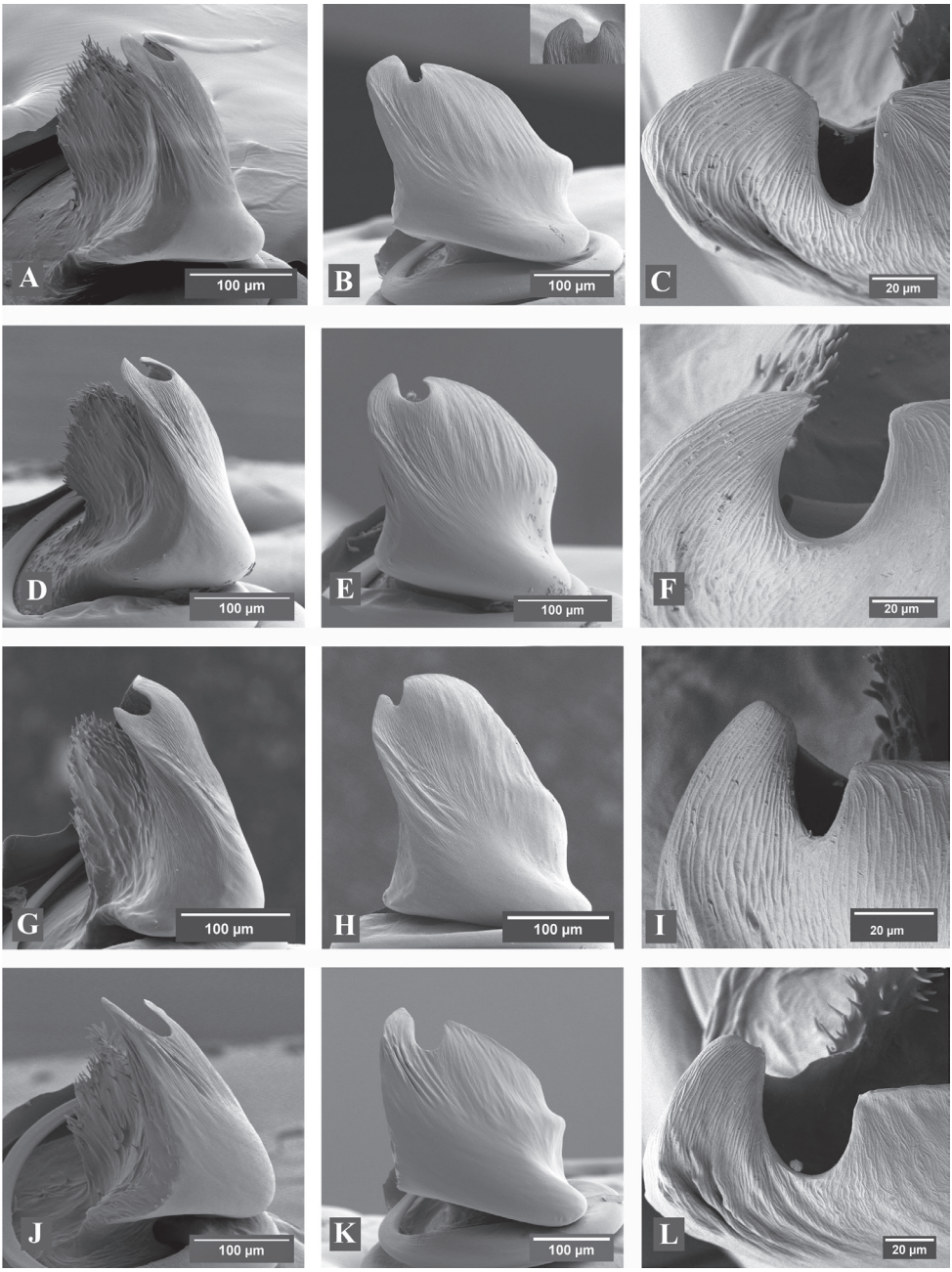

Figure 3. A–L Scanning electron micrographs of *Eresus* male palps: **A–C** *Eresus hermani* (Sas-hegy, Budapest, Hungary) **D–F** *Eresus moravicus* (Örkény-Táborfalva-Tatárszentgyörgy, Hungary) **G–I** *Eresus kollari* (Farkas-hegy, Budaörs, Hungary) **J–L** *Eresus sandaliatus* (Aulum, Denmark) **A, D, G, J** ventral **B, E, H, K** lateral and **C, F, I, L** apical view; inset in **B**: a variant of conductor tip with unusually wide groove (Sas-hegy, Budapest, Hungary).

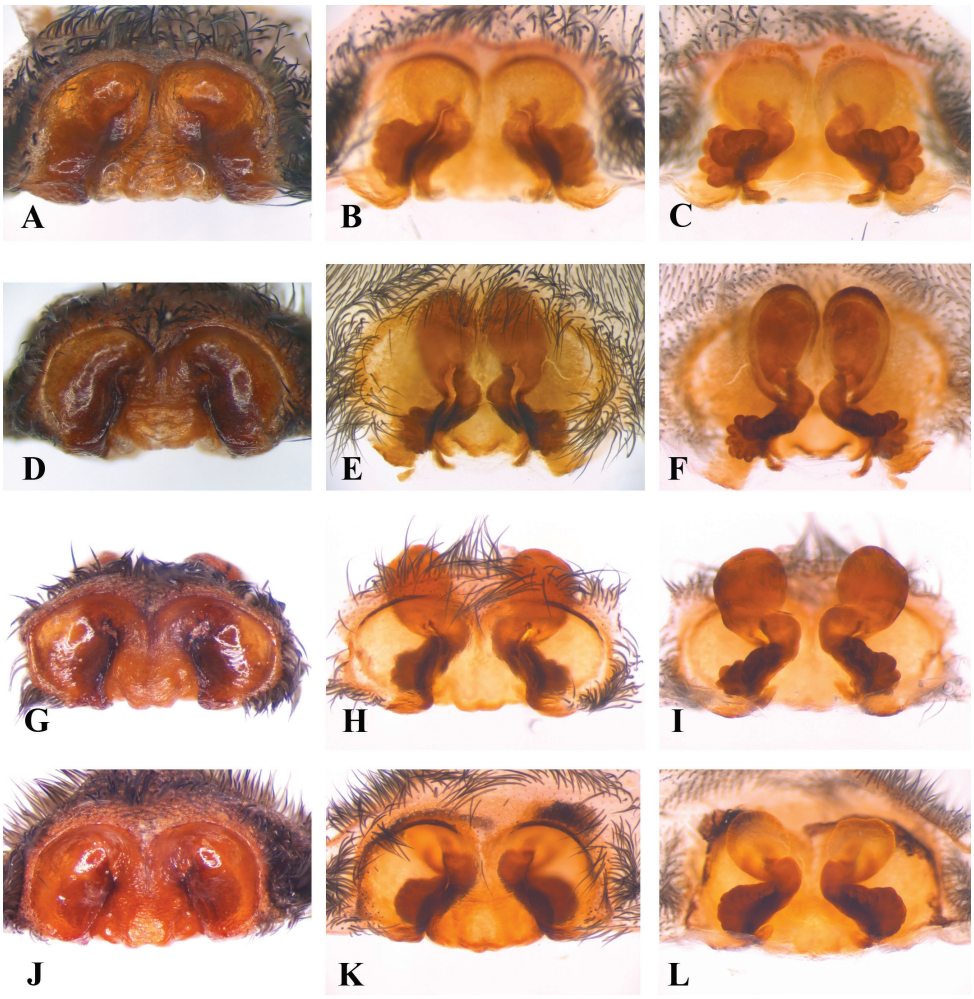

Figure 4. A–L Copulatory organs of *Eresus* adult females: **A–C** *Eresus hermani* (Sas-hegy, Budapest, Hungary) **D–F** *Eresus moravicus* (**D** Misina-hegy, Pécs, Hungary **E–F** Dürnstein, Austria) **G–I** *Eresus kollari* (Farkas-hegy, Budaörs, Hungary) **J–L** *Eresus sandaliatus* (near to Tranemose moor Northwest Jutland, Denmark) **A, D, G, J** epigyna **B, E, H, K** epigyna* **C, F, I, L** vulvae* (*: macerated).

dapest (1 ♀, 28.09.2008., G. Kovács, HNHM Araneae-7681); Remete-hegy, Budapest (3 ♀, 23.04.2011., G. Kovács, HNHM Araneae-7682); Remete-hegy, Budapest (1 ♀, 31.03.2011., G. Kovács, HNHM Araneae-7683); Sas-hegy, Budapest (6 ♀, 02.10.2013. H. Gyurkovics, A. Rákóczi, G. Vári, HNHM Araneae-7684); Érd, Fundoklia-völgy (1 ♀, 02.10.2013. G. Vári, HNHM Araneae-7685-86); Érd, Fundoklia-völgy, (1 ♀, 02.10.2013., G. Kovács, HNHM Araneae-7687); Várpalota-Inota (2 juv., 06.07.2014., G. Kovács, G. Vári, HNHM Araneae-7688), Mátyás-hegy, Budapest (5 ♂, 1933, G. Kolosváry, HNHM Araneae-2943).

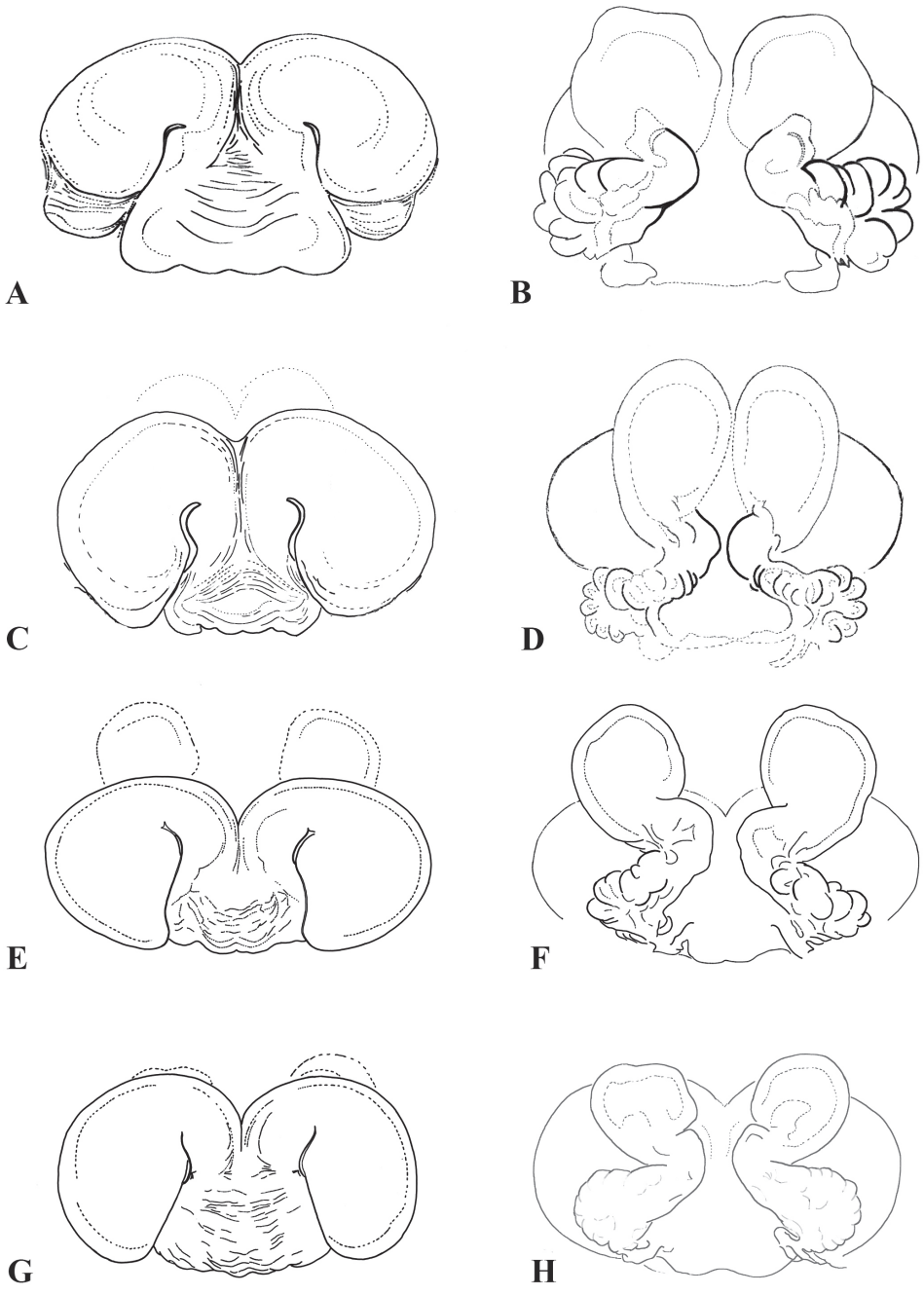

Figure 5. A–H Schematic drawings of *Eresus* female copulatory organs: **A–B** *Eresus hermani* (Sas-hegy, Budapest, Hungary) **C–D** *Eresus moravicus* (Dürnstein, Austria) **E–F** *Eresus kollari* (Farkas-hegy, Hungary) **G–H** *Eresus sandaliatus* (near Tranemose moor, Northwest Jutland, Denmark) **A, C, E, G** epigyna **B, D, F, H** vulvae.

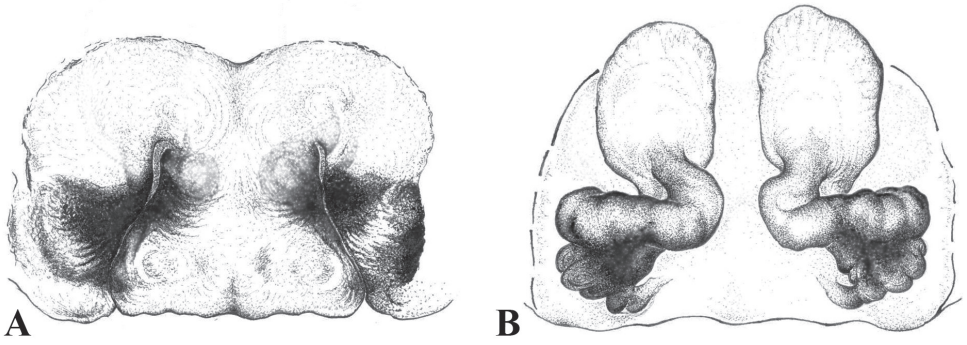

Figure 6. Drawings of *Eresus hermani* female copulatory organ, rare variant (Fundoklia-völgy, Érd, Hungary): **A** epigyne **B** vulva. Note the rounded anterior edge of the plateaus lateral to the median lobe in **A** and the elongated copulatory duct in **B**.

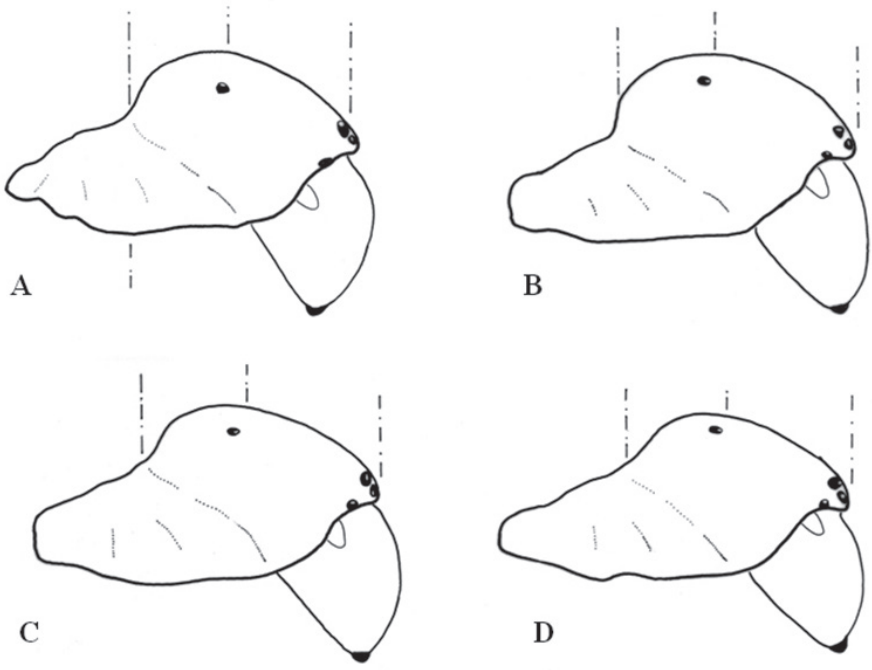

Figure 7. Outline of male prosomas of *Eresus* spp. belonging to the *Eresus sandaliatus* group, in lateral view **A** *Eresus hermani* **B** *Eresus moravicus* **C** *Eresus kollari* **D** *Eresus sandaliatus* (**B, C, D** after Fig 4. of Řezáč et al. 2008).

Remarks on misidentifications.

Cs. Szinetár (2006): p. 23. Fig. 3

The caption of this figure says "Female *Eresus cinnaberinus*", but, in fact, the picture shows a female *Eresus hermani* sp. n., as is evident from the heavy cover of light setae on the prosoma and the base of chelicerae.

Kovács et al. (2010): figure 1C–F figure 2D

According to captions, fig. 1C–F of this paper depict the genital organs of female *Eresus kollari*. However, the anterior part of fissures of the epigyna are nearly parallel, epigynal pits are followed by large flat plateaus at the sides of median lobes, anterior copulatory ducts are round and weakly sclerotized, spermathecae strongly lobed, all features that distinguish *Eresus hermani* sp. n. unambiguously. Additionally, the epigyne shown in fig. 1E is grossly malformed, having supernumerary rudiments of fissures, a kind of abnormality frequent among females raised in captivity. Figure 2D is labeled as female *Eresus kollari*. Again, this figure shows a female *Eresus hermani* sp. n., as evidenced by the dense cover of lightly colored setae on the cephalic region and basal segments of chelicerae. The reason for these misidentifications is that at the time of writing, the authors (including the corresponding author of the present paper) considered females of *Eresus hermani* sp. n. as merely an extreme local variant of *Eresus kollari*. (Note: by contrast, fig. 2F. indeed shows a female *Eresus kollari* next to a male of the same species, as can be judged by the sparsely distributed light setae on the prosoma.)

Miller et al. (2012): figure 2A

Figure 2. A. of this paper is mislabeled as *Eresus kollari*, whereas in fact it depicts a female *Eresus hermani* sp. n. Again, the true identity of the specimen shown in this picture is revealed by the light color of the prosoma and basal chelicerae. The obvious reason for the misidentification is that at the time of the completion of this Atlas, the concept of *Eresus hermani* sp. n. as a discreet species was not yet formed.

Szinetár et al. (2012): table 2, figure 6

In this paper, figure 6. shows a female *Eresus hermani* sp. n. mislabeled as *Eresus kollari*. Heavy cover of the prosoma by lightly colored hairs gives away the identity of the depicted specimen.

Acknowledgments

We wish to thank Csaba Szinetár, Tamás Szűts, Milan Řezáč, and an anonymous reviewer for their valuable advice on the manuscript. We would like to thank József Mihály (BRC Hungary) for his assistance with light microscopy and Ákos Kukovecz (University of Szeged) for his approval of the use of the scanning electron microscope. We are especially grateful to Jørgen Lissner and Walter Pfliegler for consenting to the use of their photographs in this manuscript. We thank the following colleagues, who generously provided us with specimens and locality data: András Rákóczi, Balázs Somogyi, Dávid Viktor Nagy, Edit Vadkerti, Gergely Ambrus, István Hahn, János Bodor, Krisztina Bleicher, Lilla Lajos, Ferenc Samu, Márton Szabó, Mónika Landy-Gyebnár, Jørgen Lissner, Péter Kovács, Róbert Gallé, László Somay, Tünde Rácz, Walter Pfliegler, Orsolya Szentjobbi and László Dányi (HNHM, Budapest). We are grateful to Jennifer Tusz for correcting the English of our manuscript.

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Appendix

Comparative materials examined

Eresus kollari. **Hungary:** Remete-hegy, Budapest (1 ♀, 19.09.2004., G. Kovács, HNHM Araneae-7689); Remete-hegy, Budapest (4 juv., 25.09.2005., G. Kovács, HNHM Araneae-7690); Remete-hegy, Budapest (2 ♂, 1 juv., 17.09.2006., G. Kovács, HNHM Araneae-7691); Remete-hegy, Budapest (1 ♀, 1 juv., 16.09.2007., G. Kovács, HNHM Araneae-7692); Remete-hegy, Budapest (3 ♀, 2 ♂, 03.10.2007., G. Kovács, HNHM Araneae-7693); Remete-hegy, Budapest (4 ♂, 02.09.2008., G. Kovács, HNHM Araneae-7694); Remete-hegy, Budapest (2 ♀, 3 ♂, 28.09.2008., G. Kovács, HNHM Araneae-7695); Kéleshalom (1 ♂, 14.11.2010., H. Gyurkovics, G. Vári, HNHM Araneae-7696); Remete-hegy, Budapest (1 ♀, 02.04.2011., G. Kovács, HNHM Araneae-7697); Budakalász (3 ♂, 01.09.2011., I. Hahn, L. Somay, HNHM Araneae-7698); Remete-hegy, Budapest (1 ♀, 09.04.2011., G. Kovács, HNHM Araneae-7699); Győrszentiván-Gönyü, Héricses (1 ♀, 28.11.2012., Cs. Szinetár, HNHM Araneae-7700); Farkas-hegy, Budaörs (2 ♀, 4 ♂, 15.09.2013., G. Kovács, HNHM Araneae-7701); Győrszentiván (1 ♂, 30.09.2013., P. Kovács, HNHM Araneae-7702); Sas-hegy, Budapest (3 ♂, 22.09.2010., E. Botos, PPI); Sas-hegy, Budapest (1 ♀, 16.07.2010., E. Botos, PPI); Sas-hegy, Budapest (1 ♀, 09.10.2010., E. Botos, PPI); Sas-hegy, Budapest (1 ♂, 07.10.1995., K. Bleicher, PPI); Gödöllő (1 ♂, 30.08.2012., G. Ambrus, HNHM Araneae-7703); Belsőbáránd (1 ♂, ?10.2010., Cs. Szinetár, HNHM Araneae-7704); Bugac (2 ♂, 24.09.2007., R. Gallé, HNHM Araneae-7705); Várpalota-Inota (1 ♀, 06.07.2014., G. Kovács, G. Vári, HNHM Araneae-7706), Ásotthalom (1 ♂, 20.10.2013., D. V. Nagy HNHM Araneae-7725), Mátyás-hegy, Budapest (2 ♂, 1933, G. Kolosváry, HNHM Araneae-2943).

Eresus moravicus. **Hungary:** Füzér, Castle hill (1 ♀, (juvenile at the time of collection), 07.10.2006., Cs. Szinetár, G. Kovács, HNHM Araneae-7707); Misina-hegy, Pécs (1 ♂, 22.04.2002., E. Vadkerti, HNHM Araneae-7708); Máriagyűd, Köves-máj (1 ♂, 08.05.2001, E. Vadkerti, HNHM Araneae -7709); Hárskút, Borostyán-hegy (1 ♂, 23.05.2011., L. Lajos, HNHM Araneae-7710); Misina-hegy, Pécs (3 ♂, 01.07.2011., E. Vadkerti, HNHM Araneae-7711); Felsőörs (1 ♂, 19.05.2011., M. Landy-Gyebnár, HNHM Araneae-7712); Cserkút (1 ♂, 26.05.2013., P. Kovács, HNHM Araneae-7713); Tatárszentgyörgy (4 ♂, 19.05.2013., H. Gyurkovics, G. Vári, HNHM Araneae-7714); Tatárszentgyörgy (2 ♀, 1 ♂, 19.05.2013., H. Gyurkovics, G. Vári, HNHM Araneae-7715); Tatárszentgyörgy (2 juv., 19.05.2013., H. Gyurkovics, G. Vári, HNHM Araneae-7716); Kelebia-Bácsborista (1 ♀, 1 ♂ (juvenile at the time of collection), 1 juv., 02.10.2011., H. Gyurkovics, G. Vári, HNHM Araneae-7717); Kelebia-Bácsborista (1 ♂, 30.05.2010., H. Gyurkovics, G. Vári, HNHM Araneae-7718); Misina-hegy, Pécs (3 ♀, 15.06.2012., G. Kovács, G. Vári, HNHM Araneae-7719); Szentgál, Tiszafás (1 ♂, 21.05.2012., M., Szabó, HNHM Araneae-7720); Kelebia-Bácsborista (1 ♂, 1 ♀, 06.06.2010., G.

Vári, HNHM Araneae-7721); Kelebia-Bácsborista (1 ♂, 24.05.2010., H. Gyurkovics HNHM Araneae-7723); Kelebia-Bácsborista (2 ♀, 06.06.2010., G. Kovács, HNHM Araneae-7724); Várpalota, Várvölgy (1 ♂, subadult at the time of collecting, 14.11.2014., G. Kovács, HNHM Araneae-7725). **Austria:** Dürnstein, (1 ♀, 07.06.2012., W. Pfliegler, WPPC).

E. sandaliatus. **Denmark:** Clasonsborg (1 juv., 12.05.2004, J. Lissner, JLPC); Tranemose moor, Northwest Jutland (1 ♀, 02.10.2006, J. Lissner, JLPC); Heather at Gindeskov Krat, Aulum (1 ♂, 06.08.2004, J. Lissner, JLPC); Heather at Stovbaek Krat near Aulum (1 juv., 08.06.2004, J. Lissner, JLPC); Norlund, north of Hallundbaek Stream (1 ♂, 28.10.2011, J. Lissner, JLPC); near the Danish-German border (1 ♀, 05.08.2006, J. Lissner, JLPC); Vind Hede (1 ♀, 30.09.2008, J. Lissner, JLPC).

ZooKeys 494: 31–50 (2015)
doi: 10.3897/zookeys.494.6837
http://zookeys.pensoft.net

RESEARCH ARTICLE

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Parachironomus Lenz from China and Japan (Diptera, Chironomidae)

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Academic editor: *V. Blagoderov* | Received 18 December 2013 | Accepted 9 March 2015 | Published 6 April 2015

http://zoobank.org/1AF03AFB-5B0A-4C0A-A2F2-3CC8D52CFA48

Citation: Yan C-C, Yan J, Jiang L, Guo Q, Liu T, Ge X-y, Wang X-H, Pan B-p (2015) *Parachironomus* Lenz from China and Japan (Diptera, Chironomidae). ZooKeys 494: 31–50. doi: 10.3897/zookeys.494.6837

Abstract

Members of the genus *Parachironomus* Lenz known from China and Japan are revised, and a key to their male adults is given. *Parachironomus poyangensis* **sp. n.** is described in this life stage. *Parachironomus frequens* (Johannsen) and *P. monochromus* (van der Wulp) are recorded from China for the first time, thus are redescribed from Chinese specimens. *Parachironomus kamaabeus* Sasa & Tanaka and *P. toneabeus* Sasa & Tanaka are new junior synonyms of *P. frequens*. Three Chinese or Japanese species formerly placed in *Parachironomus* are transferred to other genera, resulting in the new combinations *Cryptochironomus inafegeus* (Sasa, Kitami & Suzuki), *Demicryptochironomus* (*Irmakia*) *lobus* (Yan, Sæther, Jin & Wang), and *Microchironomus lacteipennis* (Kieffer). *Chironomus sauteri* Kieffer, *Parachironomus kisobilobalis* Sasa & Kondo and *P. kuramaexpandus* Sasa are removed from *Parachironomus*; the last of these three denotes a valid species of uncertain generic placement, the first two are *nomina dubia*.

Keywords

Chironomidae, *Parachironomus*, new species, new combinations, new synonyms, key

Introduction

The name *Parachironomus* was proposed by Lenz (1921) for a genus concept based on larval and pupal characters. Edwards (1929) gave the first brief diagnosis for male imagines. Townes (1945) treated Nearctic species which are now considered as *Parachironomus* in "*Harnischia* (*Harnischia*)", but his classification and nomenclature of Chironomini were very different from those in use today (e.g. Cranston et al. 1989; Makarchenko et al. 2006; Sæther and Spies 2013). However, Townes' designation of *Chironomus cryptotomus* Kieffer, 1915 as the type of *Parachironomus* has been accepted as formally valid, even though the taxonomic identity of that species is uncertain (*C. cryptotomus* Kieffer is a nomen dubium). Among the known genera in the *Harnischia* group, the genus *Parachironomus* is closer to *Demicryptochironomus* Lenz (1941); it is distinguished from the later in having long superior volsella with 2–3 distal setae usually arising from distinct pits, inferior volsella with blunt or pointed caudal projection, while in *Demicryptochironomus* usually no the setal pits of superior volsella and inferior volsella reduced or absent.

Freeman and Cranston (1980) synonymized *Kribiocryptus* Kieffer, 1921 and *Nilomyia* Kieffer, 1921 under *Parachironomus* Lenz, 1921. However, Spies and Sæther (2004) showed that any name available from Kieffer (1921b, published in June) would take precedence over any name available from Lenz (1921, October). In this situation, using *Parachironomus* as a valid name could comply with the current rules of nomenclature (ICZN 1999) only if a special ICZN ruling were to effect an exemption from priority in this case, or if *Kribiocryptus* and *Nilomyia* are no longer treated as synonymous with *Parachironomus*. The latter classification has been adopted by Sæther and Spies (2013), and is followed here.

Lehmann (1970) revised 17 European species and gave a generic diagnosis and key to species. Spies et al. (1994) revised members of the genus from the Neotropical Region, and modified the generic definition. Later, *Parachironomus supparilis* (Edwards, 1931) was split in three species: *P. longistilus* Paggi, 1977, *P. supparilis* (Edwards), and *P. valdiviensis* Spies (Spies 2008). Spies (2000) studied the Palaearctic *P. monochromus* (van der Wulp) and the Holarctic *P. tenuicaudatus* (Malloch) in all stages, and presented a provisional key to adult males from Nearctic Region.

Hashimoto et al. (1981) placed six species from Thailand in *Parachironomus*: *P. apicalis* (Kieffer), *P. calopunctus* Hashimoto, *P. truncatus* Hashimoto, *P. nakhonphanomensis* Hashimoto, *P. tener* (Kieffer), and *P. trisetifer* Hashimoto). However, if the partially incomplete published descriptions are correct, then all of these forms except possibly *P. calopunctus* obviously fall outside of the current diagnosis of *Parachironomus*. Moreover, the corresponding material is either lost or inaccessible. Under these circumstances, no species proposed in Hashimoto et al. (1981) is treated as valid in *Parachironomus* in the present work. Maheshwari and Agarwal (1993) published a *Parachironomus agraensis* from India, but insufficient description and inaccessible type material (M. Spies, pers. comm.) render this yet another nomen dubium in Chironomini.

Kikuchi and Sasa (1990) described a *P. tobaquartus* from Indonesia, but several hypopygial features of that species clearly rule out placement in *Parachironomus*. *Cryptochironomus lacteipennis* Kieffer and *C. sauteri* Kieffer were listed in *Parachironomus* by Sublette and Sublette (1973), along with *Chironomus primitivus* Johannsen. However, the assignment of genus names used in that work does not match that of today (for example, "*Parachironomus*" included *Microchironomus* Kieffer). Moreover, the original description of *C. sauteri* treats the adult female only; thus the name could not possibly be interpreted by Sublette and Sublette or any recent author without examination of the syntypes (at SDEI, Müncheberg, Germany).

Makarchenko et al. (2005) listed nine species from the Russian Far East: *P. biannulatus* (Staeger), *P. forceps* (Townes), *P. frequens* (Johannsen), *P. gracilior* (Kieffer) [sub *P. arcuatus* (Goetghebuer)]. *P. monochromus* (van der Wulp), *P. paradigitalis* Brundin, *P. parilis* (Walker), *P. pseudovarus* Zorina), and *P. vitiosus* (Goetghebuer); Zorina in Makarchenko et al. (2006) keyed eight of these species but omitted *P. forceps*.

From 1985–2001, Sasa and various co-authors, and Kobayashi and Suzuki (1999) recorded 11 species from Japan: *P. gracilior* (Kieffer) [sub *P. arcuatus* (Goetghebuer)], *P. harunasecundus* Sasa, *P. inafegeus* Sasa, Kitami & Suzuki, *P. inageheus* Sasa, Kitami & Suzuki, *P. kamaabeus* Sasa & Tanaka, *P. kisobilobalis* Sasa & Kondo, *P. kuramaexpandus* Sasa, *P. monochromus* (van der Wulp), *P. tamanipparai* (Sasa), *P. taishoabeus* Sasa & Tanaka, and *P. toneabeus* Sasa & Tanaka). Yamamoto (2010) keyed 7 species from Japan: *P. acutus*, *P. gracilior* [sub *P. arcuatus*], *P. kisobilobalis*, *P. kuramaexpandus*, *P. monochromus*, *P. swammerdami* (Kruseman) (which might also be *P. mauricii* (Kruseman) or an unnamed species), and *P. tamanipparai* (this belongs to *Saetheria* Jackson; M. Spies, pers. comm.). Based on the present examinations, only fpur or five true *Parachironomus* species appear to be known from Japan: *P. frequens* (Johannsen), *P. gracilior* (Kieffer), *P. monochromus* (van der Wulp), and *P. swammerdami* (Kruseman); *P. acutus* (Goetghebuer) is only provisionally placed in the genus at this time.

Wang et al. (1977) recorded *Cryptochironomus arcuatus* Goetghebuer, 1919 (= *P. gracilior* (Kieffer, 1918)) and *Cryptochironomus primitivus* Johannsen from Hubei Province, China. Wang (2000) listed both species in the genus *Parachironomus*. However, *Cryptochironomus primitivus* Johannsen has been treated as a synonym of *Microchironomus tener* (Kieffer) since Sæther (1977). Wang and Ji (2003) recorded *Parachironomus arcuatus* (= *P. gracilior*) in Oriental China (Fujian Province). In addition, Wang (2000) recorded *Parachironomus varus* (Goetghebuer) from Tianjin, but upon rechecking the specimen we are correcting that identification to *P. gracilior*. *Parachironomus lobus* Yan, Sæther, Jin & Wang was recorded by Yan et al. (2008b) from Hainan Province. According to an examination of type specimens by M. Spies, the species should be placed in the genus *Demicryptochironomus*.

Based on the known descriptions and material from China and Japan, the genus is reviewed, and one new species is described in the adult male stage. A key to adult males from China and Japan is provided.

Material and methods

The material examined was mounted on slides following the procedure outlined by Sæther (1969). The morphological nomenclature follows Sæther (1980) with the additions and corrections given by Sæther (1990). Measurements are given as ranges followed by the mean when more than three specimens were measured, followed by the number measured (n) in parentheses.

Type material studied is housed in the following institutions: Wang collection, Department of Biology, Life Science College, Nankai University, Tianjin, China (BDN); Sasa collection, National Science Museum, Tokyo, Japan (NSM).

Provisional key to adult males of *Parachironomus* from China and Japan

1 Tergite IX with shoulder-like caudal margin **2**
– Tergite IX with triangle caudal margin **4**
2 Gonostylus with distinct expansion basally; anal point parallel-sided ..... ***P. acutus* (Goetghebuer)**
– Gonostylus without distinct expansion basally or parallel-sided; anal point not parallel-sided **3**
3 Anal point with constriction proximal of apical swelling; gonostylus with constriction in middle ..... ***P. frequens* (Johannsen)**
– Anal point pointed; gonostylus parallel-sided ... ***P. swammerdami* (Kruseman)**
4 Gonostylus with distinct widening in distal 1/3; superior volsella slightly curved, swollen distally ..... ***P. monochromus* (van der Wulp)**
– Gonostylus widened basally or parallel-sided; superior volsella straightly, finger-like **5**
5 Frontal tubercles absent; mid and hind tibiae each with 1 spur; gonostylus parallel-sided ..... ***P. poyangensis* sp. n.**
– Frontal tubercles present; mid and hind tibiae each with 2 spurs; gonostylus widened basally ..... ***P. gracilior* (Kieffer)**

Species in *Parachironomus*

***Parachironomus frequens* (Johannsen)**
Figs 1–4

Chironomus frequens Johannsen, 1905: 230. – Malloch (1915: 452).
Chironomus (*Cryptochironomus*) *lhoneuxi* Goetghebuer, 1921b: 168.
Cryptochironomus longiforceps Kieffer, 1921d: 66.
Harnischia (*Harnischia*) *frequens* (Johannsen). – Townes (1945: 155).
Parachironomus frequens (Johannsen). – Lehmann (1970: 143); Pinder (1978: 132).

Parachironomus toneabeus Sasa & Tanaka, 1999: 38, **syn. n.**
Parachironomus kamaabeus Sasa & Tanaka, 2001: 45, **syn. n.**

Material examined. CHINA: 1 male, Hebei Province, Zunhua City, Dongling, Longmenkou Reservoir, 7. vii. 2001, Y. Guo; 1 male, Yunnan Province, Kunming City, Yiliang County, 2. vi. 1996, X. Wang; 1 male, Xizang Autonomous Region, Nyalam County, Zhangmu Town, 2400 m, a. s. l., 16. viii. 1987, light trap, C. Deng.

JAPAN: Holotype of *Parachironomus kamaabeus* Sasa & Tanaka, 2001 (No. 391: 45), male, Gunma Prefecture, Tone River, Taisho Bridge, light trap, 1. vii. 1999. -Paratype of *Parachironomus kamaabeus* Sasa & Tanaka, 2001 (No. 391: 47), male, Gunma Prefecture, Tone River, Taisho Bridge, light trap, 3. vii. 1999.

Diagnostic characters. The species is distinguished by the following combination of characters: mid and hind legs with dark brown rings, tergite IX with shoulder-like caudal margin; basal half of anal point with lateral setae, superior volsella finger-like.

Redescription (Chinese specimens). Male imago (n=3, unless otherwise stated). Total length 4.15–4.70, 4.46 mm. Wing length 1.98–2.54, 2.33 mm. Total length / wing length 1.78–2.10, 1.93. Wing length / length of profemur 2.20–2.47, 2.37.

Coloration. Thorax yellowish green to yellowish brown. Femora and tibiae of front legs yellowish green with distal 1/3 of tibiae and tarsi I dark brown, tarsi II with distal dark brown rings, tarsi III–V dark brown; femora and tibiae of mid and hind legs yellowish green, tarsi I, II of mid legs and tarsi I–III of hind legs pale with distal dark brown rings, tarsi III–V of mid legs and tarsi IV, V of hind legs completely dark brown (Fig. 1). Abdomen yellowish green to yellowish brown.

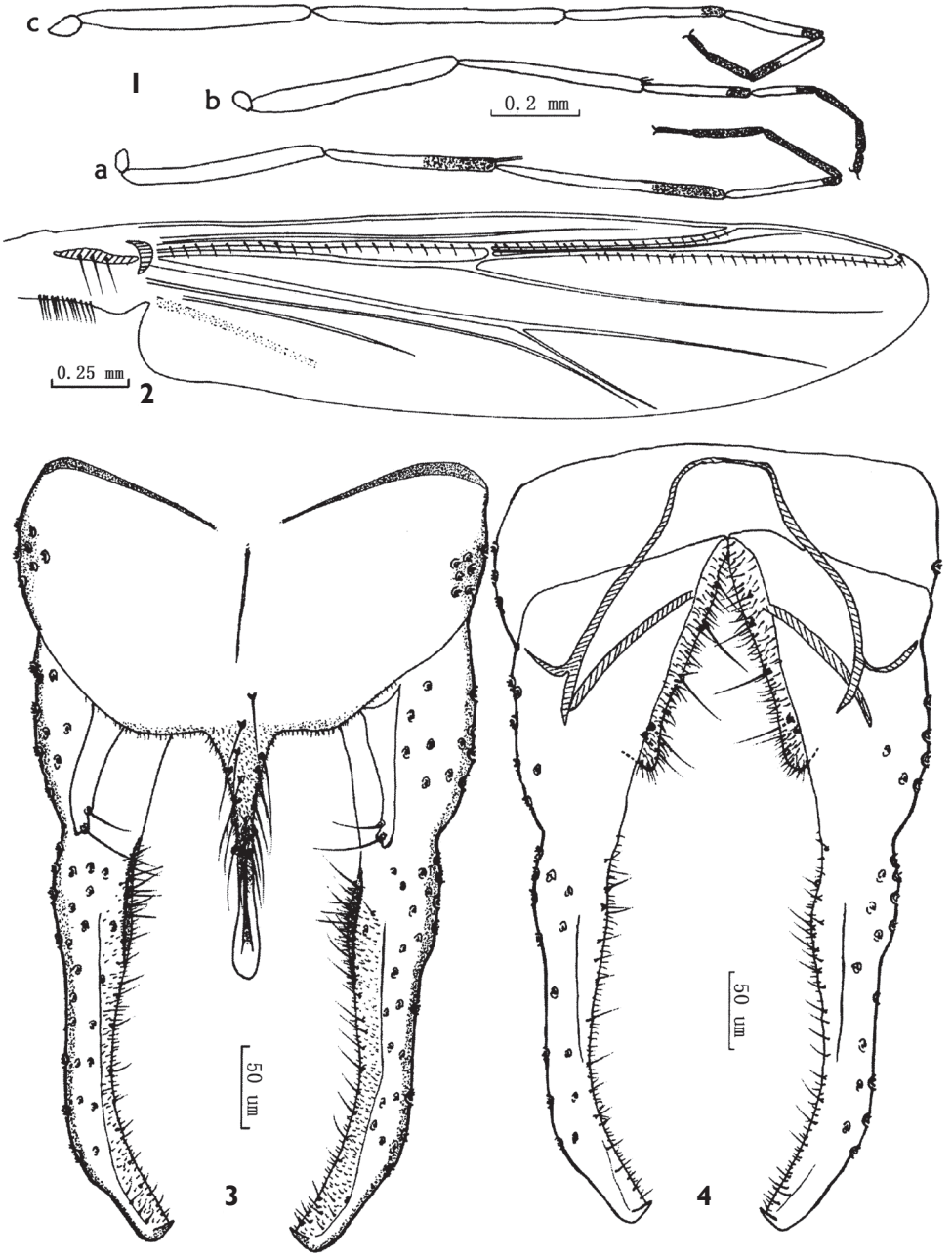
Head. AR 2.66–2.86, 2.79. Terminal flagellomere 850–1030, 960 mm long. Frontal tubercles absent. Temporal setae 16–17, 17, including 3–4, 4 inner verticals, 7–9, 8 outer verticals and 5–6, 5 postorbitals. Clypeus with 19–26, 22 setae. Tentorium 100–150, 133 mm long, 40–50, 47 mm wide. Palpomere lengths (in mm): 37–55, 47; 55–68, 59; 145–220, 184; 160–213, 181; 178–338, 255. Length ratio 5^{th} /3^{rd} palpomere 0.95–1.71, 1.40.

Thorax. Antepronotals 3–5 (2), acrostichals 5–9 (2), dorsocentrals 10–12 (2), prealars 5–9 (2). Scutellum with 18–20 (2) setae.

Wing (Fig. 2). VR 1.16–1.18, 1.17. R with 20–25, 22 setae, R_1 with 20–21, 21 setae, R_{4+5} with 22–26, 24 setae. Brachiolum with 3–4, 3 setae. Squama with 13 setae.

Legs. Front tibia with 3 subapical setae, 110 (1), 138–140 (2) and 150 (2) μm long; spurs of mid tibia 28–48, 36 and 33–50, 41 μm long, comb with 40–56, 47 teeth, 10–15, 12 μm long; spurs of hind tibia 33–55, 42 and 42–75, 56 μm long, comb with 56–68, 62 teeth, 10–15, 12 μm long. Tarsus 1 of mid leg with 22 sensilla chaetica, hind legs without sensilla chaetica. Lengths (in μm) and proportions of legs as in Table 1.

Hypopygium (Figs 3, 4). Laterosternite IX with 7–8 (2) setae. Anal tergite bands Y-shaped, fading far apart medially. Tergite IX with shoulder-like margin, bearing 2 setae at base of anal point. Anal point originating from caudal margin of anal tergite, bearing 14–22, 17 lateral setae in basal half, widened at base, constricted medially,



Figures 1–4. *Parachironomus frequens* (Johannsen), Chinese specimens. **1** Legs **a** front leg **b** mid leg **c** hind leg **2** Wing **3** Dorsal view of hypopygium **4** Ventral view of hypopygium.

slightly swollen apically, 130–155, 143 mm long, 30–35 (2) mm wide at base, 8–12 (2) mm wide in middle, 14–15 (2) mm wide at apex. Transverse sternapodeme 40–50, 46 mm long. Phallapodeme 95–118, 107 mm long. Superior volsella slightly curved,

Table 1. Lengths (μm) and proportions of adult male legs in *Parachironomus frequens* (Johannsen), (n=3).

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5	LR
p_1	900–1030, 980	800–960, 893	1080–1250 (2)	550–650 (2)	420–500 (2)	330–390 (2)	150–200 (2)	1.30–1.35 (2)
p_2	1030–1150, 1043	850–1060, 970	460–570, 523	280–350, 323	220–290, 260	150–190, 170	100–130, 116	0.54
p_3	1060–1300, 1183	1100–1350, 1242	670–820, 757	440–550, 500	350–440, 400	220–270, 243	120–160, 140	0.61

finger-like, slender distally, with an apical seta and a proximal lateral seta, both not arising in conspicuous pits. Inferior volsella with a moderately pointed caudal projection, covered with microtrichia, and reaching beyond anal tergite margin. Gonocoxite 148–175, 158 mm long, with 4–5 (2) strong medial setae. Gonostylus 230–275, 256 mm long with apical hook (2), slightly swollen at base, parallel-sided medially, curved distally, bearing 9–10 (2) setae along the basal inner margin and 12–14 (2) setae along the distal inner margin. HR 0.58–0.64, 0.62; HV 1.64–1.80, 1.74.

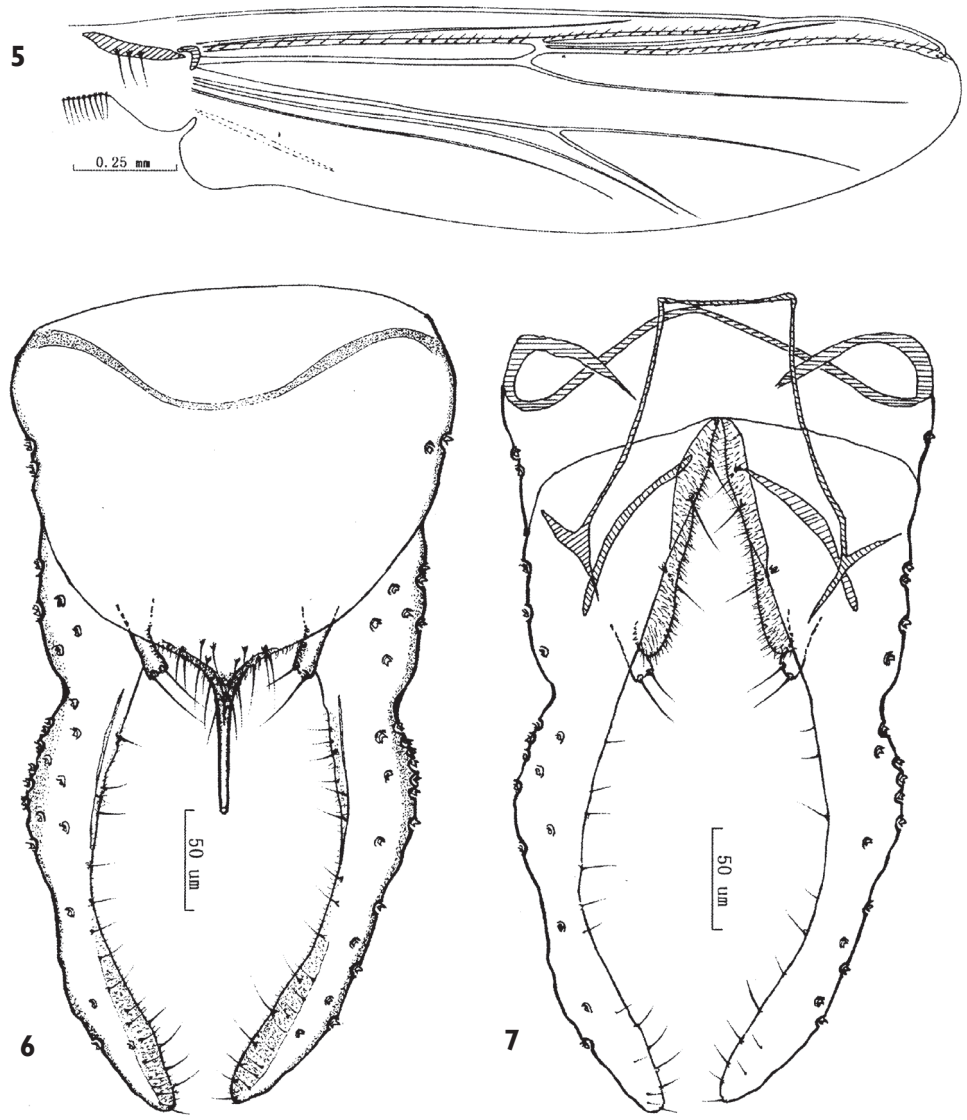
Distribution. Holarctic (Sæther and Spies 2013). The species is also known from Japan and China; the record for China is new.

Remarks. Sasa and Tanaka (1999) described *Parachironomus toneabeus* from Japan based on material collected at Kamakura Bridge, Ino River, Gunma Prefecture on 21 August 1998. The sample number was given as "391: 45–47". Sasa and Tanaka (2001) proposed *P. kamaabeus* according to material collected at Taisho Bridge, Tone River, Gunma Prefecture on 1 July 1999. However, the number of the specimen is also "391: 45–47". Based on the type specimens and the original descriptions and figures, we place both *P. toneabeus* and *P. kamaabeus* as new junior synonyms of *P. frequens* (Johannsen), due to distinct matches in leg color, shapes of the anal point, superior volsella and gonostylus, and the shoulder-like tergite IX margin.

Parachironomus gracilior **(Kieffer)**

Figs 5–7

Chironomus gracilior Kieffer, 1918: 49. – Goetghebuer (1921a: 42, 163).
Cryptochironomus arcuatus Goetghebuer, 1919: 66. – Wang et al. (1977: 230).
Tendipes (*Parachironomus*) *monotomus* (Kieffer). – Kruseman (1933: 193).
Tendipes (*Parachironomus*) *arcuatus* (Goetghebuer). – Kruseman (1933: 194).
Tendipes (*Cryptochironomus*) *arcuatus* (Goetghebuer). – Goetghebuer (1937 in 1937–1954: 43).
Parachironomus gracilior (Kieffer). – Lenz (1938: 711).
Parachironomus arcuatus (Goetghebuer). – Brundin (1947: 56); Lehmann (1970: 135); Pinder (1978: 132); Sasa (1985: 108); Sasa and Kawai (1987: 20); Sasa (1988: 56; 1989: 23, 849); Sasa and Kikuchi (1995: 102); Sasa (1996: 95; 1998: 30); Wang (2000: 645); Özkan (2002: 186); Wang and Ji (2003: 61); Makarchenko et al. (2005: 410).



Figures 5–7. *Parachironomus gracilior* (Kieffer), Chinese specimens. **5** Wing **6** Dorsal view of hypopygium **7** Ventral view of hypopygium.

Material examined. CHINA: 9 males, Tianjin City, Campus of Nankai University, 9 males, 12, 16. iv. 1985; 15. v. 1985; 20. iv. 1986, X. Wang; 1 male, Tianjin City, Shuanglin Farm, 20. vi. 1985, X. Wang; 1 male, Hebei Province, Qinhuangdao City, 1 male, vi. 1985, X. Wang; Hebei Province, Chicheng County, Yunzhou Reservoir, 21. vii. 2001, sweep net, Y. Guo and Y. Du. 1 male, Neimenggu Autonomous Region, Wuliangsuhai Lake, v. 1982, X. Wang; 1 male, Neimenggu Autonomous Region, Alashan League, Bayin, 30. vii. 1987, X. Wang; 1 male, Liaoning Province, Shenyang

City, 27. viii. 1990, J. Wang; 1 male, Jiangxi Province, Poyanghu Lake, Nanjishan, 12. vi. 2004, Sweep net, C. Yan. 1 male, Yunnan Province, Kunming City, Dianchi Lake, 23. v. 1986, X. Wang; 1 male, Yunnan Province, Lijiang City, School of Agriculture Reservoir, 2400 m a.s.l., 28. v. 1996, X. Wang.

Diagnostic characters. The species can be identified by the following combination of characters: anal point moderately narrow; frontal tubercles present; superior volsella bearing two apical setae, short cylindrical, often appearing more or less contracted, and with folds on inner margin; gonostylus with constriction at approximately mid-length.

Distribution. The species is widely distributed in the Palaearctic and extends into the Oriental Region (Sæther and Spies 2013). It occurs in China and Japan.

Remarks. The synonymy between *P. gracilior* and *P. arcuatus* was accepted in the past already (e.g. by Goetghebuer 1921a, Lenz 1938); thus we do not present it as a 'new synonymy' here. The holotype of *Chironomus gracilior* Kieffer (at SDEI) and non-type specimens identified as *Tendipes monotomus* by Kruseman (1933) have been examined by M. Spies, and found to be conspecific beyond any doubt (M. Spies, pers. comm.).

***Parachironomus monochromus* (van der Wulp)**

Figs 8–10

Chironomus unicolor van der Wulp, 1859: 5 (primary homonym of *C. unicolor* Walker, 1848).

Chironomus monochromus van der Wulp, 1875: 129 (replacement name for *C. unicolor* van der Wulp).

Chironomus (*Cryptochironomus*) *claviforceps* Edwards, 1929: 389.

Tendipes (*Parachironomus*) *monochromus* (van der Wulp). – Kruseman (1933: 192).

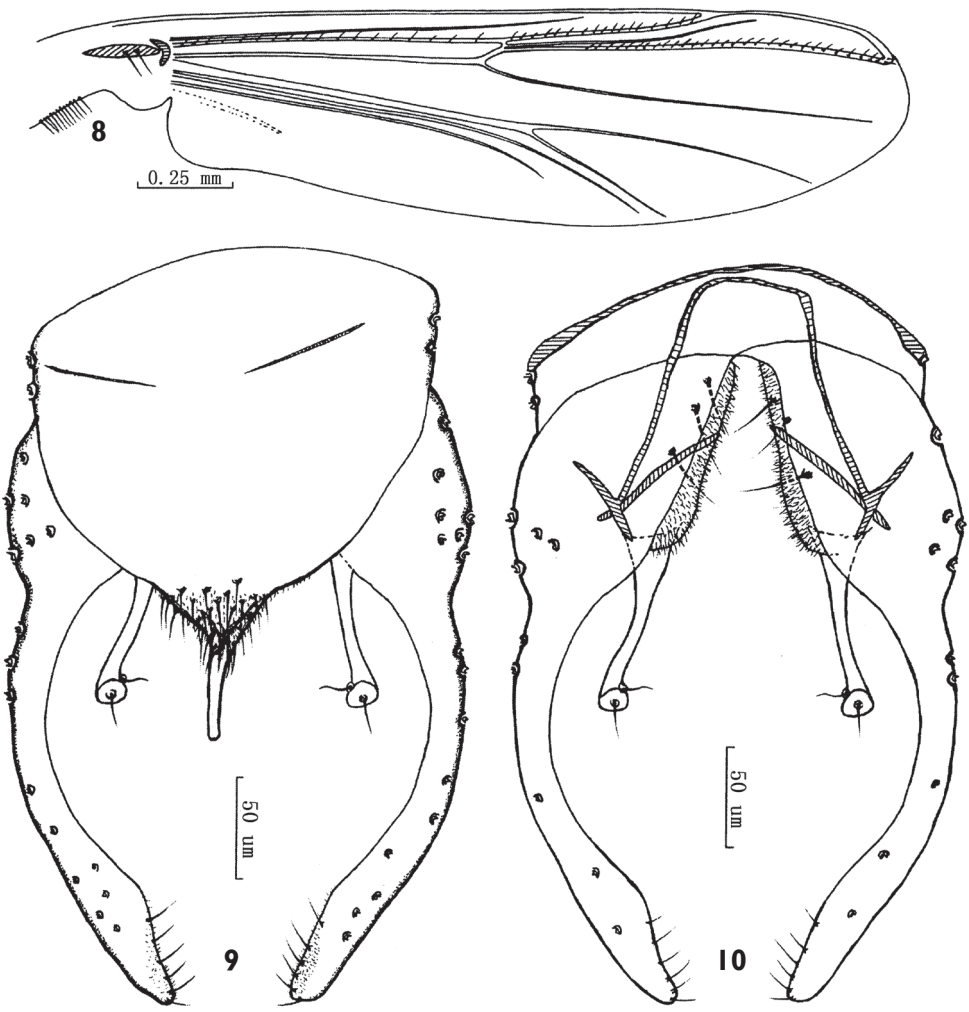
Tendipes (*Cryptochironomus* gr. *Parachironomus*) *monochromus* (van der Wulp). – Goetghebuer (1937 in 1937–1954: 46).

Parachironomus monochromus (van der Wulp). – Brundin (1947: 55); Lehmann (1970: 146); Pinder (1978: 130); Albu (1980: 131); Langton (1991: 274); Kobayashi and Suzuki (1999: 82); Spies (2000: 126).

Material examined. CHINA: 8 males, Tianjin City, Campus of Nankai University, 8 males, 12, 16. iv. 1985; 20. iv. 1986, X. Wang; 1 male, Hebei Province, Weichang County, Jixielinchang, 15. vii. 2001, sweep net, Y. Guo.

Diagnostic characters. The species is distinguished by the following combination of characters: anal tergite with distinct cluster of enlarged posterodorsal setae; anal point basal section intergrading with anal tergite, distal part strongly angled to ventral; superior volsella without apical or posterolateral projection; inferior volsella with lobe at least to median; gonostylus mostly slender, slightly curved, with distal widening to dorsal peaking around 2/3 of gonostylus length (excerpt from Spies 2000: 129).

Redescription (Chinese specimens). Male imago (n=9, unless otherwise stated). Total length 2.58–3.83, 3.38 mm. Wing length 1.30–1.98, 1.80 (8) mm. Total



Figures 8–10. *Parachironomus monochromus* (van der Wulp), Chinese specimens. **8** Wing **9** Dorsal view of hypopygium **10** Ventral view of hypopygium.

length/wing length 1.80–1.98, 1.88 (8). Wing length/length of profemur 2.28–2.57, 2.48 (8).

Coloration. Thorax yellowish green to dark brown. Front legs with femora yellowish green to dark brown, tibiae and tarsi dark brown except for tarsi I yellowish green in basal 4/5; mid and hind legs yellowish green to yellowish brown except for tarsi V dark brown. Abdomen yellowish green to dark brown.

Head. AR 1.86–2.27, 2.12. Terminal flagellomere 540–720, 673 μm long. Frontal tubercles absent (7) or present (2), cone-shaped, 15–22 μm high, 12–22 μm wide at

Table 2. Lengths (μm) and proportions of adult male legs in *Parachironomus monochromus* (van der Wulp) (n=9).

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5	LR
p_1	570–790, 727	420–620, 576	670–930, 863 (6)	340–460, 432 (6)	270–370, 342 (6)	210–270, 247 (6)	110–140, 133 (6)	1.45–1.64, 1.55 (6)
p_2	550–780, 728	480–710, 640	260–360, 326 (8)	140–310, 198 (8)	100–160, 140 (8)	70–110, 98 (8)	60–90, 85 (8)	0.44–0.54, 0.52 (8)
p_3	620–890, 818	610–950, 849	410–630, 557 (6)	210–350, 312 (6)	180–270, 247 (6)	110–150, 143 (6)	80–110, 104 (6)	0.66–0.70, 0.67 (6)

base. Temporal setae 18–22, 20, including 5–7, 6 inner verticals, 7–8, 8 outer verticals, and 5–8, 6 postorbitals. Clypeus with 14–20, 17 (8) setae. Tentorium 100–133, 120 μm long, 18–43, 33 μm wide. Palpomere lengths (in μm): 30–50, 40; 35–58, 51; 103–133, 110; 130–180, 153 (8); 178–220, 201 (8). Length ratio $5^{th}/3^{rd}$ palpomere 1.21–1.73, 1.58 (8).

Thorax. Antepronotals 2–5, 3 (8), acrostichals 10–14, 12 (8), dorsocentrals 8–14, 11, prealars 4–6, 5 (8). Scutellum with 6–10, 8 (7) setae.

Wing (Fig. 8). VR 1.11–1.17, 1.15 (8), R with 16–27, 20 (8) setae, R_1 with 10–17, 13 (8) setae, R_{4+5} with 21–29, 26 (8) setae. Brachiolum with 2–3, 2 (8) setae. Squama with 7–16, 12 (8) setae.

Legs. Front tibia with 3 subapical setae, 90–130, 104 (7), 98–133, 118 (6) and 120–138, 126 (3) μm long; spurs of mid tibia 24–33, 28 μm and 28–35, 31 μm long, comb with 30–42, 35 teeth, 10–12, 11 μm long; spurs of hind tibia 26–33, 31 μm and 28–35, 33 μm long, comb with 45–52, 48 teeth, 10–13, 12 μm long. Tarsus 1 of mid leg with 4–7, 6 (8) sensilla chaetica, hind leg without sensilla chaetica. Lengths (in μm) and proportions of legs as in Table 2.

Hypopygium (Figs 9, 10). Laterosternite IX with 2–3, 2 (8) setae. Anal tergite bands short, fading far apart medially. Tergite IX with 16–30, 21 (8) setae at base of anal point. Anal point 35–55, 48 (7) μm long, its base intergrading with conical tip of anal tergite; distal bare part narrow. Transverse sternapodeme 37–60, 52 (8) μm long. Phallapodeme 60–83, 73 (8) μm long. Superior volsella slightly curved, 70–95, 84 μm long, 13–25, 19 μm wide at base, 6–8, 7 μm wide in middle, 12–17, 15 μm wide at apex, without conspicuous apicolateral projection; median pit smaller than distal distinct pit and positioned a little proximal. Inferior volsella blunt with a low projection to posterior, not pointed, not reaching beyond anal tergite margin, and covered by microtrichia. Gonocoxite 88–118, 107 μm long, with 3–4, 3 strong medial setae. Gonostylus 158–213, 187 μm long, slender, curved and parallel-sided, with distinct expansion in distal 1/3, bearing 4–7, 6 (8) setae along distal inner margin. HR 0.49–0.68, 0.59, HV 1.63–2.01, 1.80.

Distribution. Palaearctic (Spies 2000). It also is recorded from Palaearctic China and Japan. The record for China is new.

***Parachironomus poyangensis* sp. n.**
http://zoobank.org/1E9205DA-EB68-420E-9EFC-7D45A851E307
Figs 11–13

Etymology. Named after the type locality. The species epithet is adjectival for the purposes of nomenclature.

Type material. Holotype male (BDN No. 21987). CHINA: Jiangxi Province, Poyanghu Lake, Nanjishan Natural Conservation area, 12. vi. 2004, sweep net, C. Yan. Paratypes: 2 males, data same as holotype.

Diagnostic characters. The new species is distinguished by the following combination of characters: body size small, thorax and abdomen yellowish green, wing cells without setae, mid and hind tibiae each with single spur, anal point nearly parallel-sided, superior volsella elongate digitiform, without distal swelling or projection, gonostylus nearly straight and of about even circumference throughout.

Description. Male imago (n=3). Total length 2.25–2.32, 2.28 mm. Wing length 1.08–1.11, 1.10 mm. Total length / wing length 2.08–2.09, 2.09. Wing length / length of profemur 2.20–2.30, 2.25.

Coloration. Thorax yellowish green. Femora of front legs yellowish green with distal parts brown, tibiae and tarsomeres dark brown; mid and hind legs yellowish green with tarsomeres IV, V dark brown. Abdomen yellowish green.

Head. AR 1.76–1.84, 1.80. Terminal flagellomere 450–470, 462 mm long. Frontal tubercles absent. Temporal setae 11–13, 12, including 3 inner verticals, 3–4, 3 outer verticals and 5–6, 5 postorbitals. Clypeus with 15–18, 17 setae. Tentorium 90–95, 92 mm long, 25–26, 25 mm wide. Palpomere lengths (in mm): 25–27, 26; 30–32, 31; 83–85, 84; 98–104, 100; 145–156, 151. Length ratio $5^{th}/3^{rd}$ palpomere 1.75–1.78, 1.77.

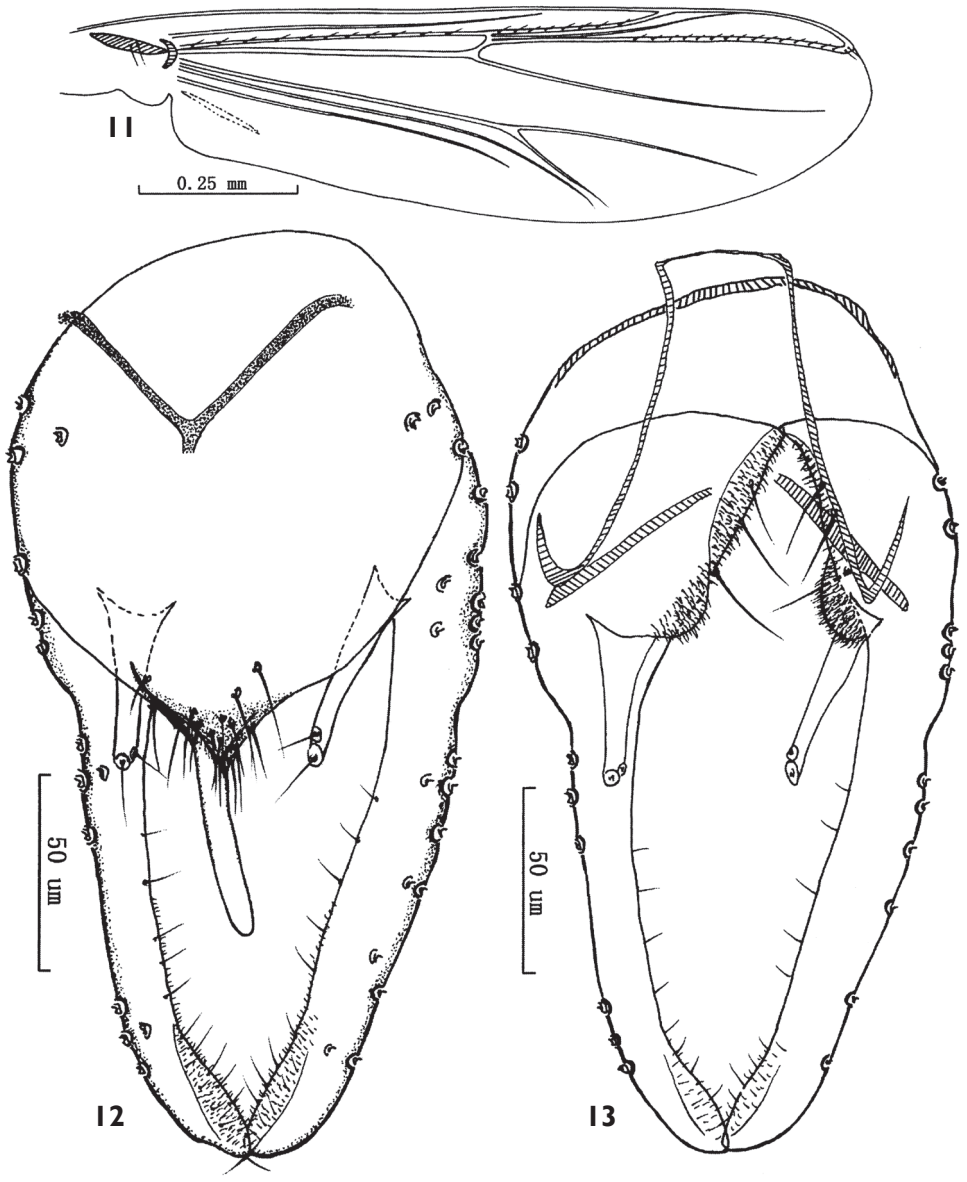
Thorax. Antepronotals 3–4, 3; acrostichals 8–9, 9; dorsocentrals 10–12, 11; prealars 3. Scutellum with 5–6, 5 setae.

Wing (Fig. 11). VR 1.15–1.17, 1.16. Cell surfaces without setae. R with 11–13, 12 setae, R_1 with 8–9, 8 setae, R_{4+5} with 17–18, 17 setae. Brachiolum with 2 setae. Squama with 10–12, 11 setae.

Legs. Front tibia with 2 subapical setae, 108–110, 109 and 118–130, 126 μm long, mid and hind tibiae each with a single spur, spur of middle tibia 20–22, 21 μm long, comb with 28–30, 31 teeth, 10 μm long; spur of hind tibia 28–30, 29 μm long, comb with 42–46, 44 teeth, 10–12, 11 μm long. Tarsus 1 of mid leg with 6–7, 7 sensilla chaetica, hind leg without sensilla chaetica. Lengths (in μm) and proportions of legs as in Table 3.

Table 3. Lengths (μm) and proportions of adult male legs in *Parachironomus poyangensis* sp. n. (n=3).

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5	LR
P_1	470–500, 490	310–330, 320	540–560, 550	340-380, 360	230–250, 243	160–180, 166	90–100, 93	1.69–1.74, 1.71
P_2	440–470, 456	350–380, 363	220–250, 233	120–140, 130	110–130, 120	70–80, 73	50–70, 60	0.63–0.66, 0.65
P_3	480–530, 503	490–520, 506	340–370, 353	200–220, 210	170–200, 183	100–130, 113	70–80, 73	0.70–0.74, 0.72



Figures 11–13. *Parachironomus poyangensis* sp. n. **11** Wing **12** Dorsal view of hypopygium **13** Ventral view of hypopygium.

Hypopygium (Figs 12, 13). Laterosternite IX with 3–4, 3 setae. Anal tergite bands V-shaped. Tergite IX with conical posterior margin, bearing 13–15, 14 setae at base of anal point. Anal point originating from caudal margin of anal tergite, parallel-sided, slightly pointed apically, 50–55, 52 mm long, 6–8, 7 mm wide at base, 4–5, 4 mm wide at apex. Transverse sternapodeme 27–32, 30 mm long. Phallapodeme 45–48, 46 mm long. Superior volsella straight, columnar, distal parts not widened, with an

apical seta and a subapical seta, both arising from distinct setal pits. Inferior volsella with a moderately blunt caudal projection, not reaching beyond caudal margin of anal tergite. Gonocoxite 75–80, 77 mm long, with 3–4, 3 strong medial setae. Gonostylus 112–115, 113 mm long, parallel-sided, curved distally, bearing 8–10, 9 setae along distal inner margin. HR 0.65–0.70, 0.67; HV 1.96–2.02, 1.99.

Distribution. The species is known only from the type locality in Oriental China.

Species removed from *Parachironomus*

Microchironomus lacteipennis (Kieffer), comb. n.

Cryptochironomus lacteipennis Kieffer, 1921a: 183.
Parachironomus lacteipennis (Kieffer) – Sublette and Sublette (1973: 405).

Remarks. Kieffer (1921a) described the species in the genus *Cryptochironomus*, which at that time included many species now treated in several separate genera. Sublette and Sublette (1973) placed it in *Parachironomus*. Based on the original description, which describes the inferior volsella as absent, the superior volsella as long and slender, the gonocoxite straight in the proximal 1/3, curved in the distal 2/3, distally attenuated and terminating in an incurved hooklet, *C. lacteipennis* clearly belongs to *Microchironomus* and not to *Parachironomus*. The placement by Sublette and Sublette (1973), and the earlier one in "*Tendipes* (*Parachironomus*)" by Kruseman (1939), likely are due to the fact that those authors did not treat *Microchironomus* as a separate genus.

Distribution. The species is recorded from Taiwan Province (Oriental China).

Chironomus sauteri Kieffer, *nomen dubium*

Chironomus (*Cryptochironomus*) *sauteri* Kieffer, 1921c: 583. – Tokunaga (1940: 301).
Parachironomus sauteri (Kieffer). – Sublette and Sublette (1973: 406).
Cryptochironomus sauteri (Kieffer). – Sasa (1989: 21).

Remarks. Kieffer (1921c) described the species based on females only, and without figures. Tokunaga (1940) described males and females from Taiwan Province, but illustrated only the male superior volsella. Sublette and Sublette (1973) transferred the species to "*Parachironomus*", but their use of this genus name was different from that of today (i.e., included *Microchironomus* Kieffer). Sasa (1989) examined Tokunaga's specimens and considered them as belonging to either *Cryptotendipes* or *Microchironomus*, but suggested that the status and placement of *C. sauteri* should be reserved for future clarification. We agree with Sasa's opinion, but have been unable to examine any of the syntypes; therefore, the species is not included in the present key.

Distribution. The species is known from Taiwan Province (Oriental China).

Parachironomus kisobilobalis Sasa & Kondo, *nomen dubium*

Parachironomus kisobilobalis Sasa & Kondo, 1994: 129. – Sasa and Kikuchi (1995: 102); Sasa (1998: 30); Sæther et al. (2000: 190).

Material examined. JAPAN: Holotype of *Parachironomus kisobilobalis* Sasa & Kondo, 1994 (No. A 224: 49), male, Aichi Prefecture, Kiso River in dammed-up middle reach near Nagoya City, "emerged from a sample", 26. ii. 1992.

Remarks. We have examined the holotype, but it was lacking the thorax, head except for antenna, tarsi of front legs, and half of the hypopygium. As the preserved parts do not suffice for placement of the species, we treat *P. kisobilobalis* as a *nomen dubium*. In any case, the original description calling the superior volsella "rod-like, with one apical seta and 4 short setae along inner margin" and the inferior volsella "semicircular, with 4 short marginal setae" (Sasa and Kondo 1994: 129; see also Figs 5i–5m) rules out that the species belongs to *Parachironomus*.

Distribution. The species has been recorded only from the type in a Palaearctic part of Japan.

Discussion

Among the many species previously reported in *Parachironomus* from Japan, only *P. frequens*, *P. gracilior*, *P. monochromus*, *P. swammerdami*, and possibly *P. acutus* (Original genus is *Chironomus*) are considered as valid records. Aside from the species treated in the present work, *Parachironomus harunasecundus* Sasa has been transferred to the genus *Demicryptochironomus* (Yan et al. 2008b); *P. inageheus* Sasa, Kitami & Suzuki, 2001 has been identified as a junior synonym of *Demicryptochironomus ginzancedeus* Sasa & Suzuki (Yan et al. 2008b). *Parachironomus inafegeus* Sasa, Kitami & Suzuki should be transferred to *Cryptochironomus* because of the prominent frontal tubercles, both superior and inferior volsellas carry long setae, the inferior volsella is completely covered by the superior volsella, and the gonostylus is short, rather broad and fused with the gonocoxite. *Parachironomus tamanipparai* (Sasa) was returned to *Paracladopelma* by Yan et al. (2008a), but the holotype (examined by M. Spies) and the published descriptions clearly show it to be a member of *Saetheria* (as recognized earlier, e.g. by Laville and Reiss 1988 and Makarchenko et al. 2006). *Parachironomus taishoabeus* Sasa & Tanaka is a junior synonym of *Saetheria tylus* (Townes) (Kobayashi 2007). *Parachironomus kuramaexpandus* Sasa (examined by M. Spies) probably belongs to an undescribed genus near *Rheomus*, but definitely not to *Parachironomus*.

Based on examination of the holotype and paratype of *Parachironomus lobus* Yan, Sæther, Jin & Wang by M. Spies, *P. lobus* is related to *Demicryptochironomus* (*Irmakia*) *latior*, but conclusive placement would require knowledge of the immature stages. The end of the superior volsella looks less expanded than in *D. latior*. For the moment we propose the new combination *Demicryptochironomus* (*Irmakia*) *lobus* and try to find at least the pupa of this species for further comparison with *D.* (*I.*) *latior* and other congeners.

Acknowledgements

We are pleased to acknowledge the considerable assistance of Dr. A. Shinohara (Department of Zoology, National Science Museum, Tokyo, Japan), who kindly enabled us to examine Sasa type specimens. We thank M. Spies (Zoologische Staatssammlung München, Germany), Dr. T. Kobayashi (Institute for Environmental and Social Welfare Sciences, Japan), and Dr. Eugenyi Makarchenko and Dr. Oksana Zorina (Institute of Biology and Pedology, Far Eastern Branch of Russian Academy of Sciences, Vladivostok, Russia), for providing much input at various levels of this work.

We are indebted to the late Prof. O.A. Sæther (Museum of Zoology, University of Bergen, Norway) for kindly checking specimens and offering valuable comments during his visit to our laboratory in 2005. Financial support received from the National Natural Science Foundation of China (NSFC), grant No. 31101653, 31272284, Natural Science Foundation of Tianjin (14JCQNJC14600), Tianjin City High School Science & Technology Fund Planning Project (20090608), Undergraduate Training Programs for Innovation and Entrepreneurship (201410065046), and from the Tianjin Normal University Talent Introduction Foundation (5RL104) is gratefully acknowledged.

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ZooKeys 494: 51–68 (2015)
doi: 10.3897/zookeys.494.9208
http://zookeys.pensoft.net

RESEARCH ARTICLE

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Revision of the genus *Eadmuna* Schaus, 1928 (Lepidoptera, Mimallonidae) with a description of a new species from French Guiana

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Academic editor: *D. Lafontaine* | Received 4 January 2015 | Accepted 15 March 2015 | Published 6 April 2015

http://zoobank.org/B3D52B14-1D97-41F0-87C0-3A28A89E1B13

Citation: St Laurent RA, Dombroskie JJ (2015) Revision of the genus *Eadmuna* Schaus, 1928 (Lepidoptera, Mimallonidae) with a description of a new species from French Guiana. ZooKeys 494: 51–68. doi: 10.3897/zookeys.494.9208

Abstract

The genus *Eadmuna* Schaus, 1928 is revised to include four species. *Eadmuna guianensis* **sp. n.**, is described from French Guiana and Guyana. The holotype of *Perophora pulverula* Schaus, 1896, currently placed in *Cicinnus* Blanchard, 1852, is determined to be a previously unrecognized female *Eadmuna,* and is transferred accordingly as *E. pulverula* **comb. n.**. *Eadmuna paloa* Schaus, 1933, **rev. status**, is removed from synonymy with the type species *E. esperans* (Schaus, 1905). *Eadmuna esperans*, *E. paloa*, and *E. pulverula* may be of conservation concern due to their limited extent of occurrence and endemicity to the highly imperiled Brazilian Atlantic forest.

Keywords

Brazilian Atlantic forest, *Cicinnus*, *Eadmuna guianensis*, Guyana

Introduction

The strictly New World and primarily Neotropical Mimallonoidea, comprised of the sole family Mimallonidae, presently consists of barely more than 200 described species in 28 genera (Herbin 2012). Phylogenetic relationships within the family Mimallonidae are not well understood, nor has there been a modern thorough treatment of the family

(Herbin 2012); Schaus (1928) was the last to treat the family as a whole. The two subfamilies proposed by Schaus, the Mimalloninae and the Lacosominae, were determined to be inadequately supported by both Pearson (1951, 1984) and Franclemont (1973) based on the fact that the trait originally used to separate the subfamilies (presence/absence of frenulum) was inconsistent, and the presence of the frenulum was deemed plesiomorphic by Herbin (2012). However, the subfamilies were maintained by Becker (1996). Until a sufficient monograph or generic revision of the family is completed, the relationships within the family will remain poorly understood; therefore, the subfamily classification used here follows Herbin (2012), without any currently recognized subfamilies.

Various genera in Mimallonidae lack well-defined unifying characters. *Cicinnus* Blanchard, 1852 and *Psychocampa* Grote & Robinson, 1866 in particular have been used by authors, essentially from Schaus until present, including Herbin (2012) and Herbin and Mielke (2014), to place newly described species of Mimallonidae without attempting to delineate synapomorphies for these genera. Additionally, the majority of genera in the family are small and frequently monotypic, half of the 28 currently recognized genera have fewer than three species. This is not surprising considering the variation in external wing morphology within the family, which was used by Schaus (1928) as the primary means for generic classification. Schaus (1928) provided a key to genera after separating them into the aforementioned subfamilies. The key relies primarily on venation and wing morphology traits, some of which are highly superficial and variable and are difficult to apply consistently in diagnoses, such as the appearance of the tornus. The basis of the subfamilies in the key, namely the presence or absence of the frenulum, was incorrectly reported by Schaus for a number of genera, thus the key lacks reliability. In addition to the issues presented by Schaus' key, Mimallonidae are frequently sexually dimorphic and this has resulted in the description of conspecific sexes as different species.

Currently the genus *Eadmuna* Schaus, 1928, contains a single species, *E. esperans* (Schaus, 1905). An additional species, *E. paloa* Schaus, 1933, was treated as a synonym of *E. esperans* by Becker (1996). The present work aims to determine the validity of names currently assigned to *Eadmuna* and a species assigned to the genus *Cicinnus.* Additionally, we will establish genus specific synapomorphies of *Eadmuna*, providing adequate support for placing a new species from French Guiana and Guyana within the genus.

Methods

Dissections were performed as in Lafontaine (1987), however, genitalia slides were not created in order to allow for three-dimensional analysis. Genitalia and abdomens are preserved in glycerol in microvials. Morphological, including genitalic, terminology follows Lemaire and Minet (1999). Wing venation terminology follows Franclemont (1973).

The holotypes of *Eadmuna paloa* and *Perophora pulverula* Schaus, 1896 were dissected and at least one specimen from each locality was dissected. In some cases only

one specimen from a given locality was available for study. The genitalia slide of the holotype of *E. esperans* was unavailable; however, topotypical *E. esperans* were dissected. All known *Eadmuna* specimens from the following institutions were examined:

AMNH	American Museum of Natural History, New York, New York, USA
CMNH	Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA
CNC	Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Ontario, Canada.
CUIC	Cornell University Insect Collection, Ithaca, New York, USA
FSCA	Florida State Collection of Arthropods, Gainesville, Florida, USA
MGCL	McGuire Center for Lepidoptera & Biodiversity, Gainesville, Florida, USA
USNM	National Museum of Natural History [formerly United States National Museum], Washington D.C., USA

Figures were manipulated with Adobe Photoshop CS4 (Adobe 2008). Images of adults were edited so that the best "half" is figured, and mirror images of the best half are figured so that the left half is shown for each specimen.

Maps were created with SimpleMappr (Shorthouse 2010) and edited with CS4. All geographical co-ordinates are approximate, and are based on the localities provided on specimen labels. GPS data was acquired with Google Earth.

Results

Eadmuna Schaus, 1928

Type species. *Cicinnus esperans* Schaus, 1905

Diagnosis. *Eadmuna* can be recognized by broad wings and silvery-gray ground color accented by varying degrees of brown. The forewing bears a discal cell as a hyaline or sub-hyaline patch bisected by the M_2 vein creating two separate windows. The hindwings lack any such hyaline markings. Although this marking is not unique within Mimallonidae, this character combined with the following two additional characters: the absence of any straight, continuous, vertical or diagonal postmedial lines and the presence of smooth wing margins; are diagnostic for the genus. Male genitalia are simple with a pointed, teardrop-shaped uncus, broad, ovoid tegumen with a pair of prominent, subtriangular, ridged lobes ventrally.

Description. Male. *Head*: Very small, scales on frons swept forward, eyes large comprising roughly two-thirds of head area, bordered posteriorly by darkbrown scales, border of darker scales continues down head reaching beneath labial palpi, labial palpi very small, segments smaller distally, hardly extending beyond frons, basal two segments tufted ventrally, dorsally covered in darkbrown scales greatly contrasting with overall straw coloration of head. Antenna bipectinate, scape and pedicel tufted. Ocelli and putative chaetosemata present. *Thorax*: Densely covered in long, hair-like scales

interspersed with widened, darker, petiolate scales giving a speckled appearance. *Legs:* Vestiture thick, scales long, especially on femur and tibia, coloration as for thorax, petiolate scales present. Tibial spurs about one fifth length of tibia, thick, triangular in cross section, ridged, ridges finely serrate along ventral length. *Forewing dorsum*: Forewing length: 16–20 mm, n=40. Triangular, convex outer margins becoming concave near apex in some species, apex accentuated. Silvery gray-brown ground color with extensive speckling due to dark, petiolate scales in similar manner to that of thorax. Discal spot prominent, hyaline or partially covered in translucent scales, with M_2 vein covered in dark scales separating hyaline patch into two distinct regions. Postmedial line usually present, though often faint, bulged in costal half, brown, dentate. Overall, scales become smaller and finer distally from wing base. *Forewing venter*: As for dorsum but usually lighter, postmedial lines generally more pronounced. *Hindwing dorsum*: Rounded, somewhat accentuated anal angle, essentially bearing same coloration and scale pattern as forewings though postmedial line usually fainter, if present. No hyaline patches present. Spatulate scales denser on inner margin. *Hindwing venter*: As for dorsum but usually lighter, postmedial lines generally more pronounced, frenulum with single bristle. *Wing venation*: As for *Cicinnus melsheimeri* (Harris, 1841) but R_4 + R_5 much shorter stalked. *Abdomen*: Somewhat compressed laterally, short, depth equal to that of thorax, rather triangular due to sudden truncation to slightly upturned tip, coloration a continuation of thoracic color, matching essentially dorsal wing coloration. *Genitalia*: Simple, uncus abruptly narrowed at base, extended apically. Tegumen broad, ovoid, with prominent, subtriangular, ridged lobes. Anal tube barely discernable, lightly sclerotized, with apex roughly halfway to distal tip of uncus. Valves simple, lightly sclerotized, basal half wider than distal half, sacculus half to one third width of valve at base, extending to half or two-thirds valve length. Juxta ventrally with quadrate lip and with two triangular arm-like spurs, one on either side of phallus. Juxtal spurs reach roughly midway along length of phallus. A small relatively quadrate sclerotized plate present dorsally to juxta/phallus. Vinculum broadly ovoid though flattened on dorsal and ventral margins, somewhat quadrate. Phallus simple, cylindrical, vesica sac-like or elongated with scobinate patch or with multidentate cornutus. **Female.** Similar to male except for: *Head*: Eyes greater than two thirds area of head, labial palpi smaller, region of brown scales bordering posterior of eyes thicker, extending to prothorax ventrally. *Legs*: Small scales nearly completely cover tibial spurs. *Forewing dorsum*: Forewing length range: 22–24 mm, n=3. Compared to male, forewing much broader overall, postmedial region lighter, more silvery gray than medial area, hyaline discal spot large, prominent. Postmedial line present, more pronounced than for male, brown, dentate, narrowly interrupted by veins, dark wedge where postmedial line meets costa. Antemedial lines present, bilobed, B-shaped. *Forewing venter*: As for dorsum, but lighter, postmedial line more contrasting. *Hindwing dorsum*: Broader, hardly accentuated anal angle, essentially bearing same coloration as forewings. Unlike males, entire hindwing, save for postmedial line, concolorous silvery gray, without a brown edge and without darker medial area present in forewings. Dentate postmedial line dark and well pronounced, narrowly interrupted by veins, slightly darker than that of

forewing. *Hindwing venter*: As for dorsum, but lighter, postmedial line more contrasting, frenulum rudimentary with numerous bristles hidden by hindwing scales. *Wing venation*: As for male but Rs appears to originate closer to middle of cell. *Abdomen*: Much broader than that of male. Coloration a continuation of thoracic color, though darkening somewhat distally. Two very elongated sclerotized plates present on venter of eighth segment. *Genitalia*: Papillae anales elongated or stocky, covered in fine setae, apophyses posteriores shorter or same length as apophyses anteriores. Ductus bursae short, ostium opening immediately into corpus bursae. Corpus bursae, round, with or without sclerotized structures reinforcing membrane, elongated appendix bursae.

Remarks. Despite Schaus' (1928) comment that *Eadmuna* genitalia are allied to those of *Psychocampa* (unspecified species), this has not been found when comparing *Eadmuna* genitalia to those of some representative *Psychocampa*. No *Eadmuna* genitalia resemble any of the *Psychocampa* genitalia figured in Herbin (2012), including *P. kohlii* Herbin which greatly resemble the genitalia of the type species *Psychocampa concolor* Grote & Robinson, 1866 (Herbin 2012).

Aceclosteria villaricensis (Schaus, 1933) was originally described in *Eadmuna*. Currently the genus *Aceclosteria* Vuillot, 1893 contains one species, *A. mus* Vuillot, 1893. Previously Schaus described a female *Aceclosteria* specimen as *Eadmuna villaricensis* due to it being allied with "*E. esperanza*," [sic] (Schaus, 1933) though the two species are quite dissimilar. For instance, *A. mus* has a continuous, non-dentate postmedial line. Additionally, in a single male genitalia dissection of *A. mus* from Rio Grande do Sul, Brazil (CUIC genitalia dissection 10-8-14:2), the genitalia were found to be highly complex structurally and asymmetrical, completely unlike *Eadmuna*. Becker (1996) synonymized *E. villaricensis* with *A. mus*. An external examination of the holotype of *E. villaricensis* supports Becker's synonymy.

One or two other undescribed species from Costa Rica are currently considered to belong to *Eadmuna* by Daniel Herbin (pers. comm.). These golden-colored species, superficially somewhat similar to *Eadmuna guianensis*, new species and *E. esperans*, have broad wings, dentate postmedial lines, and bisected forewing hyaline areas. However, the genitalia are very distinct (MGCL dissection number 9-24-14:1). In one of these undescribed species, the uncus is not truncate and is rather triangular and flattened apically, the juxta has two extremely long, curved tusk-like projections, pointed outwards above the phallus. Finally, somewhat triangular tegumen lobes are present, as in *Eadmuna*, but are significantly elongated and without numerous ridges as in *Eadmuna.* Thus, these species from Costa Rica cannot be considered *Eadmuna*.

The geographic distribution of the species *E. esperans* and *E. paloa*, and possibly *E. pulverula*, very clearly follows the Atlantic coastal rainforest of Brazil (see Figure 18) (IBGE). This biome is of particular conservation interest due to a massive loss of habitat, such that it has been estimated that only approximately 11% of the Brazilian Atlantic forest remains (Ribeiro et al. 2009). The association of these two or three species with this biome, along with the almost complete lack of recent material of these species in any of the visited collections, presents further justification for the conservation of this area of high species richness (Ribeiro et al. 2009).

Key to species of *Eadmuna

1 Antemedial and postmedial lines weakly defined, usually only postmedial line visible (Figs 1–6) (male)..... **2**
– Antemedial and postmedial lines well defined (Figs 7, 8) (female) **4**
2 Silvery-gray forewing elongated relative to hindwing (Figs 5, 6); with large hyaline areas, devoid of covering of scales, male vesica with a large straight cornutus that is fused to progressively smaller, parallel cornuti (Fig. 14) .... ***E. paloa*** **(part)**
– Silvery-brown to brown forewing not particularly elongated relative to hindwing (Figs 1–4); weakly to moderately falcate with small yellowish opaque hyaline discal markings, cornutus if present, not straight (Fig. 12)..... **3**
3 Wing silvery-brown, weakly falcate (Figs 1, 2), vesica with scobinate patch (Fig. 13), occurring in southern and southeastern Brazil..... ***E. esperans***
– Wing darker brown, more falcate (Figs 3, 4), vesica with curved, spiked cornutus (Fig. 12), occurring in northern South America (Guyana and French Guiana) ..... ***E. guianensis*** **sp. n.**
4 Forewing apex rounded, large hyaline discal mark (Fig. 7), corpus bursae firm, round, with heavily-sclerotized, internal bar-like structures reinforcing membrane (Figs 15, 16), venter of abdomen devoid of markings..... ***E. paloa*** **(part)**
– Forewing slightly falcate with smaller discal mark (Fig. 8), corpus bursae small, bag-like, without signum or cornuti (Fig. 17), dark longitudinal line on venter of abdomen..... ***E. pulverula***

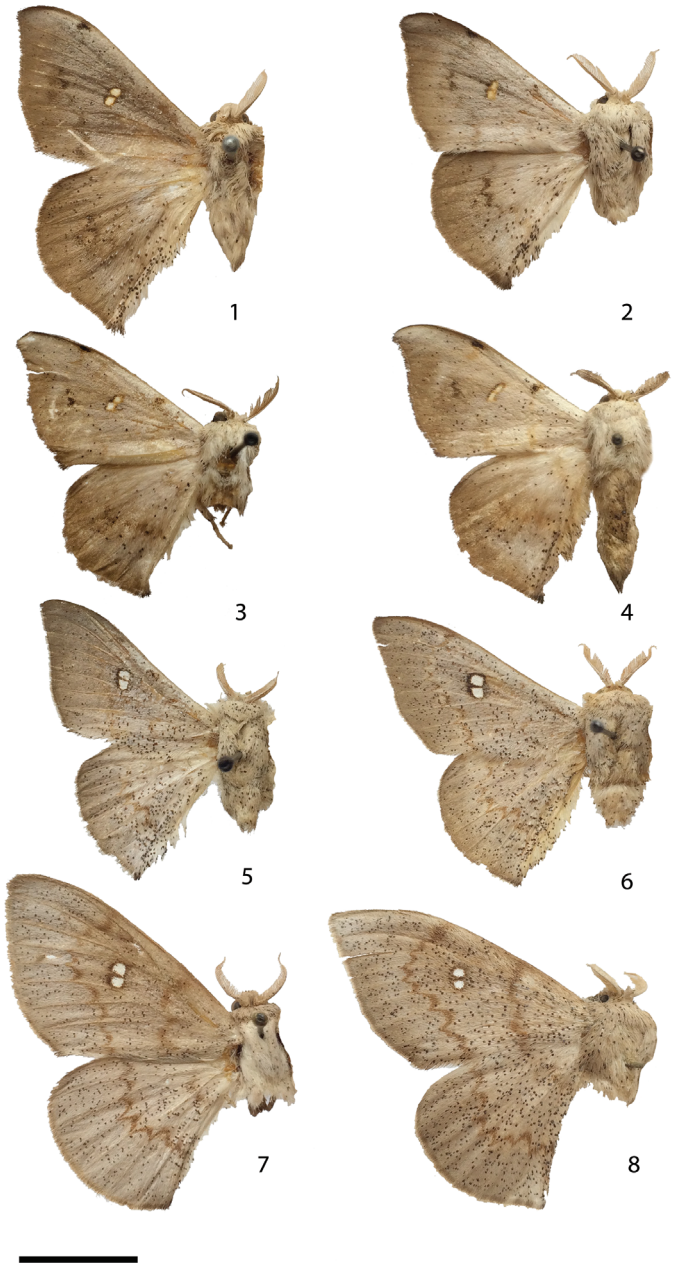
*Note: the male of *E. pulverula* and the females of *E. esperans* and *E. guianensis* are unknown

Eadmuna esperans **(Schaus, 1905)**
Figs 1, 2, 10, 13, 18

Cicinnus esperans Schaus, 1905
Eadmuna esperans; Schaus 1928
Eadmuna esperanza; Schaus 1933, misspelling
Eadmuna esperans; Becker 1996

Type material. Holotype: BRAZIL, Espírito Santo, Wm. Schaus collection, USNM holotype No.: 8893- genitalia diss: 86062, specimen examined, genitalia preparation not found [♂, USNM]. **Paratypes:** none. Type locality: BRAZIL, Espírito Santo.

Additional specimens examined. All males (21 total): **BRAZIL: Espírito Santo:** Linhares, 40 m, 25–30 i 1998, V.O. Becker coll, Col. Becker No.:113480- St Laurent diss: 11-1-14:9, 11-1-14:10 [4 ♂, USNM]; [no further data]- St Laurent genitalia diss: 11-1-14:6 [1 ♂, USNM]; **Santa Catarina:** "Saint Catherines"- St Laurent genitalia



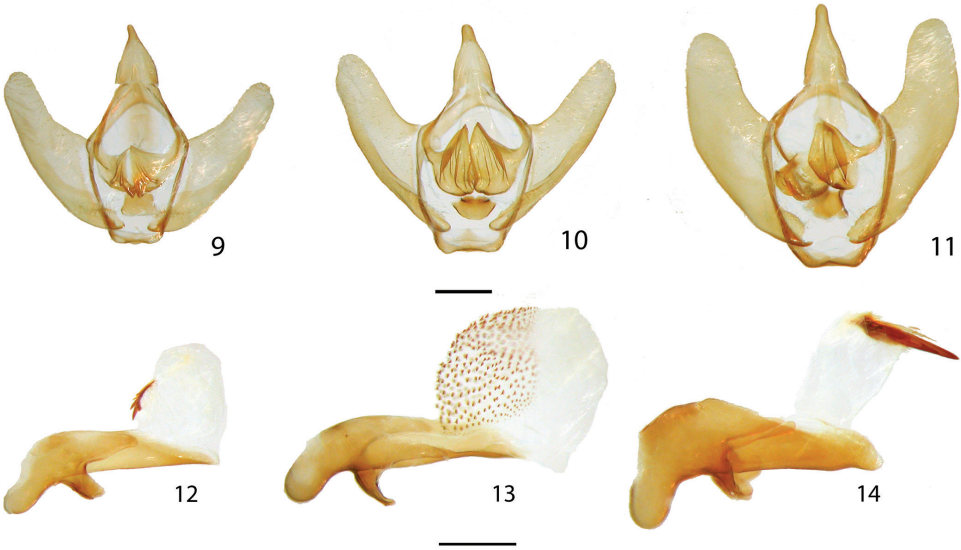
Figures 1–8. *Eadmuna* adults. **1** *E. esperans* holotype male, Espírito Santo, Brazil (image inverted laterally) [USNM] **2** *E. esperans* male, Jaraguá [do Sul], Santa Catarina, Brazil [CUIC] **3** *E. guianensis* holotype male, Mana River, French Guiana [CMNH] **4** *E. guianensis* paratype male, Mana River, French Guiana [CMNH] **5** *E. paloa* holotype male, São Paulo, Brazil (image inverted laterally) [USNM] **6** *E. paloa* male, Nova Bremen, Santa Catarina, Brazil (image inverted laterally) [CUIC] **7** *E. paloa* female, Rio Vermelho, Santa Catarina, Brazil (image inverted laterally) [AMNH] **8** *E. pulverula* holotype female, São Paulo, Brazil [USNM]. Scale bar = 1 cm.

diss: 11-1-14:2 [1 ♂, USNM]; F. Hoffman- St Laurent genitalia diss: 11-1:14:4 [2 ♂, USNM]; Jaraguá [do Sul], 10 x 1934, 14 x 1934, 17 ix 1934, coll. Fritz Hoffmann- St Laurent genitalia diss: 9-14-14:1, Franclemont genitalia slide: number 1763 [3 ♂, CUIC]; **Rio Grande do Sul:** Pelotas 15 v 1953, coll. C.M. de Biezanko no CB: 3503- St Laurent genitalia diss: 9-14-14:4 [1 ♂, CUIC]; **Rio de Janeiro:** Imbariê, 50 m, 21–27 viii 1955, coll. H. Ebert- St Laurent genitalia diss: 9-14-14:5 [1 ♂, CMNH]; "Itatiaya" [Itatiaia], 700 m, 5 x 1928, J.F. Zikan- St Laurent genitalia diss: 11-1-14:3 [1 ♂, USNM]; Zikan- St Laurent genitalia diss: 11-1-14:5 [1 ♂, USNM]; Itatiaia (Maromba), 17 viii 1952, No. 558, Pearson [1 ♂, USNM]; Itatiaia, (L 41, 1300 m) 5/8 iii 1951, Trav. & D. Albuquerque, No. 383- St Laurent diss: 11-1-14:12 [1 ♂, USNM]; PN. Itatiaia, Lago Azul 800(?)m, 12/13 xi 1956, H.R. & G.M. Pearson, No. HRP 1171- St Laurent diss: 11-1-14:13 [1 ♂, USNM]; **São Paulo:** Est. Biol. Boraceia, 850 m, near Salesopolis: 2 x 1971, E.G., I. & E.A. Munroe- St Laurent genitalia diss: 9-14-14:6 [1 ♂, CNC]; 26 ix 1971, E.G., I. & E.A. Munroe [2 ♂, CNC].

Diagnosis. The weakly falcate forewings distinguish *E. esperans* from the similar *Eadmuna guianensis*, new species, described below. Genitalia of *E. esperans* are unique among species in the genus in that the vesica has a large scobinate patch as opposed to a single cornutus.

Description. Male. *Head*: As for genus but border of darker scales that normally continues down head reaching beneath labial palpi somewhat reduced. *Thorax*: As for genus. *Legs*: As for genus but tibial spurs naked. *Forewing dorsum*: Forewing length: 17–20 mm, avg.: 18 mm, n=19. Triangular, rounded, convex margins becoming concave near subtly accentuated apex. Coloration light silvery brown, suffused with darker brown postmedially except near apex. Hyaline discal spot weakly pronounced, yellowish opaque rather than clear due to covering of yellowish scales, with M_2 vein separating hyaline patch into two distinct regions. Postmedial line bulging in costal half, scalloped, narrowly interrupted by veins, weaker on costal third except for dark wedge on costa. Occasionally dark diffuse spots between veins immediately beyond center of postmedial line. Antemedial line very weak except for dark chevron on costa. Fringe varies in coloration from dark brown to off white. *Forewing venter*: As for dorsum but lighter, postmedial line usually much darker, well-pronounced. *Hindwing dorsum*: Rounded, slightly falcate anal angle, bearing similar coloration and pattern as forewing though maculation usually somewhat fainter than on forewing and lacking a hyaline discal spot. *Hindwing venter*: As for dorsum but lighter, postmedial line usually much darker, well pronounced. *Wing venation*: As for genus. *Abdomen*: As for genus, concolorous with thorax. *Genitalia*: n=14. As for genus, simple, but distal end of teardrop-shaped uncus moderately thick, ventral lobes of tegumen subtriangular, with a central sclerotized ridge with three or four secondary ridges ventral to center of subtriangle. Sclerotized plate, dorsal to juxta and phallus, broad, especially on lower half. Phallus, simple, broad, cylindrical, vesica, sac-like with scobinate patch covering roughly half of everted vesica. **Female.** Unknown.

Distribution. This species is known from southeastern and southern Brazil in the states of Espírito Santo (type locality), Rio de Janeiro, São Paulo, Santa Catarina, and Rio Grande do Sul, apparently from relatively low to moderately high elevations (40 to



Figures 9–14. *Eadmuna* male genitalia, valves with phallus and juxta removed, and separated phallus and juxta. **9** *E. guianensis*, holotype, Mana River, French Guiana [St Laurent diss.: 9-14-14:3] **10** *E. esperans*, Est. Biol. Boraceia, 850 m, near Salesopolis, São Paulo, Brazil [St Laurent diss.: 9-14-14:6] **11** *E. paloa*, Nova Bremen, Santa Catarina, Brazil [St Laurent diss.: 9-14-14:8] **12** *E. guianensis*, holotype, Mana River, French Guiana [St Laurent diss.: 9-14-14:3] **13** *E. esperans*, Est. Biol. Boraceia, 850 m, near Salesopolis, São Paulo, Brazil [St Laurent diss.: 9-14-14:6] **14** *E. paloa*, Nova Bremen, Santa Catarina, Brazil [St Laurent diss.: 9-14-14:8]. Scale bars = 1 mm.

1300 m). This distribution coincides with both the pampa and Atlantic coastal forest biomes (IBGE 2004).

Remarks. *Eadmuna esperans*, the type species of the genus, was originally described under the genus *Cicinnus*, likely due to the early year of its description, a time when the author, Schaus, was placing many new species in this catch-all genus. It is only known to be sympatric with one congener, *E. paloa*, in Jaraguá [do Sul], Santa Catarina, Brazil, but can be readily separated by the genital characters mentioned above. *Eadmuna esperans* is most similar to the new species described below, but the latter has more falcate forewings and is known only from the Amazonian region of French Guiana and Guyana. The scobinate patch covering the vesica of *E. esperans* is unique in the genus.

***Eadmuna guianensis* St Laurent & Dombroskie, sp. n.**
http://zoobank.org/C5715C64-F209-4F6D-9A31-28E01275FDC2
Figs 3, 4, 9, 12, 18

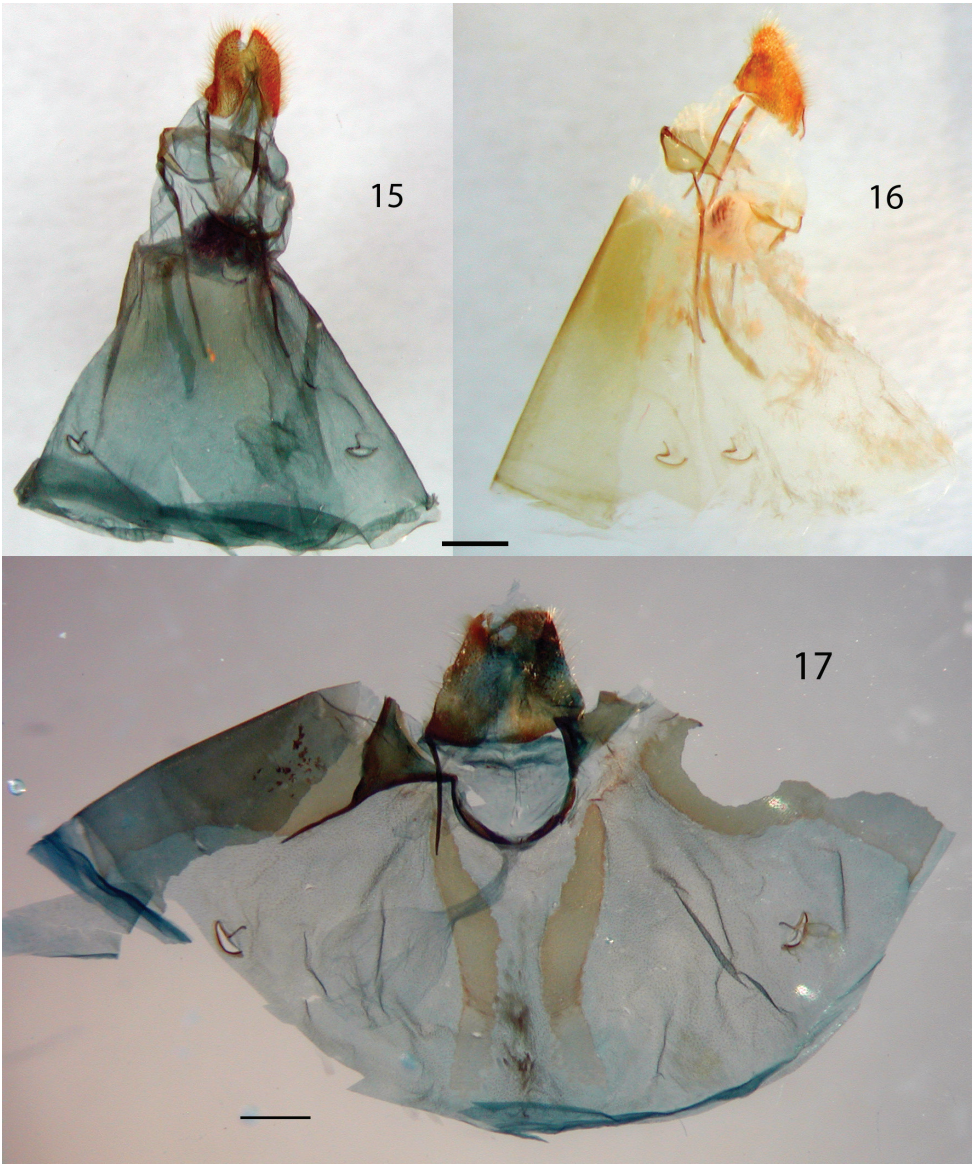
Type material. Holotype: Mana River, Fr. Guiana. May, 1917. Acc. 6008, "*Cicinnus esperans* Schaus," St Laurent diss.: 9-14-14:3, HOLOTYPE ♂ *Eadmuna guianensis* St

Laurent and Dombroskie, 2015 [handwritten red label]. Deposited Carnegie Museum of Natural History. Type locality: French Guiana, Mana River.

Paratypes: 4 males: **GUYANA:** 1 male: Tumatumari, Rio Potaro, Br. Guiana, Ac. 5615, St Laurent diss.: 10-27-14:1, PARATYPE ♂ *Eadmuna guianensis* St Laurent and Dombroskie, 2015 [yellow label]. Deposited American Museum of Natural History; **FRENCH GUIANA:** 3 males: Mana River, Fr. Guiana. May, 1917. Acc. 6008, "*C. esperans* Schaus," USNM-Mimal: 2510, St Laurent diss.: 11-1-14:1, PARATYPE ♂ *Eadmuna guianensis* St Laurent and Dombroskie, 2015 [yellow label]. Deposited National Museum of Natural History; Mana River, Fr. Guiana. May, 1917. Acc. 6008, PARATYPE ♂ *Eadmuna guianensis* St Laurent and Dombroskie, 2015 [yellow label]. Deposited Carnegie Museum of Natural History ; Mana River, Fr. Guiana. May, 1917. Acc. 6008, "*C. esperans* Schaus," illegible label, St Laurent diss: 9-14-14:2, PARATYPE ♂ *Eadmuna guianensis* St Laurent and Dombroskie, 2015 [yellow label]. Deposited Cornell University Insect Collection.

Diagnosis. Similar in general appearance to *E. esperans* but recognizable by darker overall brownish coloration, more acutely, slightly hooked forewing apex, and a vesica bearing a spiked, curved cornutus as opposed to a scobinate patch. The cornutus of *E. paloa*, unlike that of *E. guianensis*, is not curved. No other *Eadmuna* is known to occur in northern South America.

Description. Male. *Head*: As for genus. *Thorax*: As for genus. *Legs*: As for genus but tibial spurs slightly thinner, half to entirety of spurs covered in fine scales. *Forewing dorsum*: Forewing length: 18–20 mm, avg. 19 mm, n=5. Triangular, convex margins becoming concave near apex, apex accentuated. Brown coloration more predominant than silvery gray, especially distally from thorax, with less extensive speckling due to relative lack of dark, petiolate scales. Discal spot not prominent, elongated, hyaline, yellowish opaque, with M_2 vein separating hyaline patch into two distinct regions. Postmedial line bulging in costal half, scalloped, narrowly interrupted by veins, weaker on costal third except for dark wedge on costa. Antemedial line weak with dark chevron at costal margin. *Forewing venter*: Darker and lighter areas more finely defined though not particularly darker or lighter overall from dorsum. Postmedial line only somewhat slightly better defined than on dorsum. *Hindwing dorsum*: Rounded, with slightly pronounced anal angle, bearing similar coloration as forewings; postmedial line present, usually well developed, roughly parallel to outer margin, though angled slightly more inward on inner half than in other species. No hyaline patches present. *Hindwing venter*: Darker and lighter areas more finely defined though not particularly darker or lighter overall from dorsum. Postmedial line only somewhat better defined than on dorsum. *Wing venation*: As for genus but $R_4 + R_5$ slightly longer stalked. *Abdomen*: Coloration as for thorax, mostly concolorous with dorsal wing color. *Genitalia*: n=4. As for genus, simple but most structures thinner and weaker than other species. Uncus teardrop shaped, extended apically, very thin apically, highly truncated basally. Ventral lobes of tegumen subtriangular, ridged; ridges thicker and more pronounced than for *E. esperans*. Valves simple, relatively thin. Sclerotized plate, dorsal to juxta and phallus, broad, rounded dorsally.



Figures 15–17. *Eadmuna* female genitalia. **15** *E. paloa*, ventral, Rio Vermelho, Santa Catarina, Brazil [St Laurent diss.: 10-11-14:3] **16** *E. paloa*, lateral, Rio Vermelho, Santa Catarina, Brazil [St Laurent diss.: 11-1-14:8] **17** Damaged *E. pulverula*, holotype, ventral, São Paulo, Brazil [St Laurent diss.: 11-1-14:8]. Scale bars = 1 mm.

Phallus, simple, cylindrical, pointed when viewed ventrally/dorsally, vesica sac-like, bulbous with single curved cornutus bearing four or five spikes that increase in size distally. **Female.** Unknown.

Etymology. Named for the Guianas from where all the specimens were collected.

Distribution. This species is only known from Guyana and French Guiana and thus represents a significant disjunction in geographic distribution of the genus, the other three *Eadmuna* species being found in southern and southeastern Brazil.

Remarks. *Eadmuna guianensis* is known from the Amazon Rainforest, very distant from the range of its three congeners. This disjunction is unlikely to be due to an artefact of under-sampling in intervening areas because the Amazon region is well collected for Mimallonidae (R. St Laurent pers. obs.). Despite the seemingly geographic isolation and distance from the localities of the other species of *Eadmuna*, this species clearly belongs to this genus due to the characters of the genitalia, which are very similar to those of the type species and, surprisingly, bear aspects similar to *E. esperans* in wing pattern and valve structure and to *E. paloa* in the vesica.

Eadmuna paloa Schaus, 1933, rev. status

Figs 5–7, 11, 14–16, 18

Eadmuna esperans; Becker 1996, incorrect synonymy

Type material. Holotype: BRAZIL, São Paulo, "No. 71," USNM holotype No.: 34362- St Laurent diss: 11-1-14:7 [examined] [♂, USNM]. **Paratypes:** none. Type locality: BRAZIL, São Paulo.

Additional specimens examined. 22 males, 2 females: **BRAZIL: São Paulo:** Jacupiranga, 800m, 8 ii 1993, V.O. Becker, Col. Becker no. 87164- St Laurent diss: 11-1-14:11 [1 ♂, USNM]; **Santa Catarina:** Rio Vermelho: i 1957, A. Maller col., No. 1714 [1 ♂, USNM]; ii 1945, i 1944, leg. Anton Maller- St Laurent diss: 10-11-14:2 [2 ♂, AMNH]; ii 1945- leg Anton Maller- St Laurent diss: 10-11-14:3 [1 ♀, AMNH]; ii 1944, A. Maller Coll., Frank Johnson Donor- St Laurent diss: 11-12-14:1 [1 ♀, AMNH]; Hansa Humbolt [Corupá] [probably pre 1944] [1 ♂, USNM]; Jaraguá [do Sul], 29 xi 1934, 17 ix 1934, coll. Fritz Hoffmann- St Laurent genitalia diss: 9-14-14:7, Franclemont genitalia diss: 1769 [2 ♂, CUIC]; Nova Bremen, 7 xii 1936, 14 x 1936, 18 v 1936, 7 ix 1935 coll. Fritz Hoffmann- St Laurent genitalia diss: 9-14-14:8 [4 ♂, CUIC]; [no further data] [3 ♂, USNM]; F. Hoffman, No. 13791 [1 ♂, USNM]; F. Hoffman [1 ♂, USNM]; **Paraná:** Banhados (RR. from Curitiba to Paranaguá), 800 m, 14 ii 1972, E.G., I. & E.A. Munroe- St Laurent diss: 10-5-14-:1 [2 ♂, CNC]; **Minas Gerais:** Diamantina, Serrinha- X-IV, with X-IV crossed out, leg. E. Cohn- St Laurent diss: 10-11-14:1 [4 ♂, AMNH].

Diagnosis. *Eadmuna paloa* has more elongate forewings with larger hyaline areas than any other *Eadmuna* species. The vesica has a single, large, straight cornutus that is fused to progressively smaller, parallel cornuti that transition into a mane of long, clear, hair-like projections that originate from the vesica. Additionally, the lobes of the basal half of the tegumen are much more heavily sclerotized in all *E. paloa* examined than in other species in the genus. The female is larger than the male, with broader wings and darker, more pronounced antemedial and postmedial lines. The female of *E. paloa*

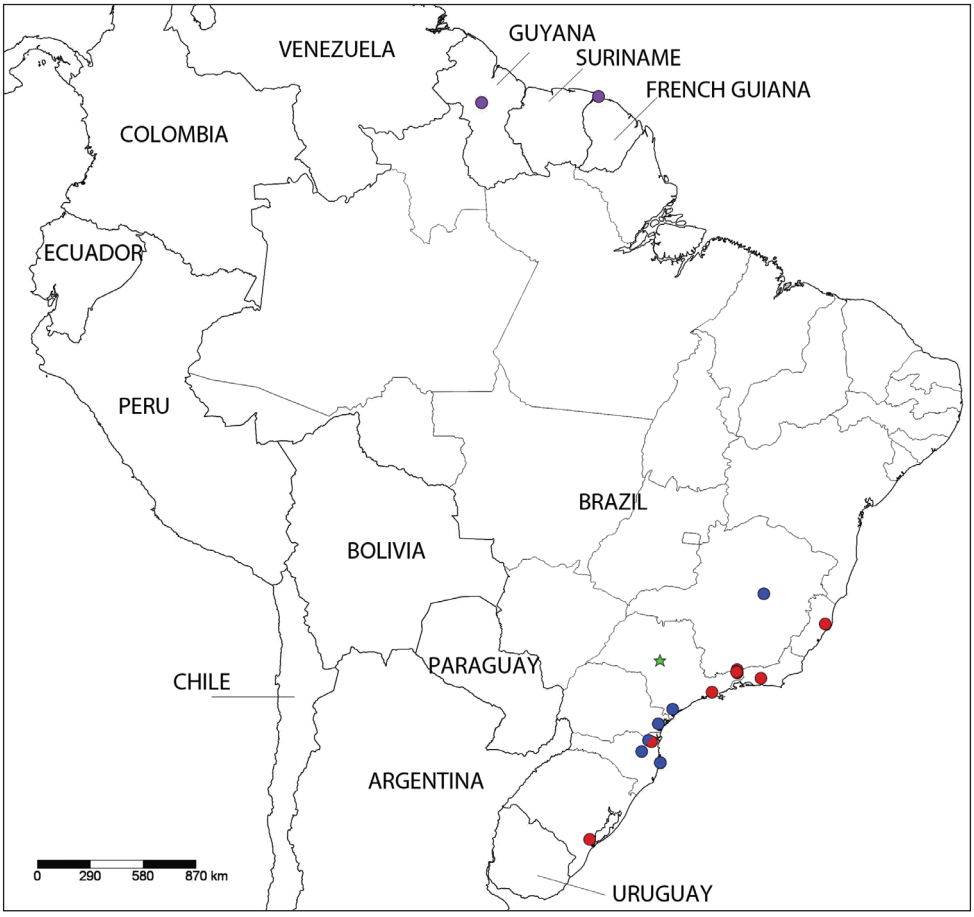


Figure 18. Distribution of *Eadmuna*. *E. esperans* (red circles), *E. guianensis* (purple circles), *E. paloa* (blue circles), *E. pulverula* (green star). Notes: red/blue circle represents the locality where both *E. esperans* and *E. paloa* have been collected, *E. pulverula* is represented by a star placed near the center of the Brazilian state of São Paulo because the type locality is "São Paulo," without further information regarding specific locality.

is similar to the female of *E. pulverula*, but the forewings are less falcate, with larger hyaline patches, and there is no longitudinal dark line on the venter of the abdomen.

The primary genital characters used to differentiate *E. esperans* and *E. paloa* are the vesica and cornutus. In *E. esperans* the vesica is sac-like and covered in a scobinate patch whereas the vesica of *E. paloa* is thinner and more cylindrical, and bears a single large cornutus. Aside from the very good genitalia characters, the two species can also be readily differentiated by wing morphology. *Eadmuna paloa* is generally more silvery in color with more acutely triangular forewings, has much larger forewing hyaline areas, and males have less pronounced postmedial lines.

Description. Male. *Head*: As for genus, but more off white in color rather than straw colored; dorsal surface of labial palpi and area surrounding eyes covered in contrasting brown scales. Labial palpi and antennal tufts smaller. *Thorax*: As for genus, but as on

head, scales of thorax lighter in coloration than in other species, thus darker petiolate scales more pronounced. *Legs*: As for genus, but tibial spurs clothed in small scales varying from covering proximal half to near entirety. *Forewing dorsum*: Forewing length: 16–20mm, avg. 18 mm, n=16. As for genus, but more acutely triangular, convex margins not concave near apex, lower quarter of forewing bows out slightly. Silvery gray brown with especially contrasting, extensive speckling due to dark, petiolate scales. Postmedial region roughly concolorous with rest of forewing, though silvery sheen lost near margin, so margin a singed-brown color. Hyaline discal spot prominent, large, very clear, not covered in scales, outlined by dark scales, M_2 separates hyaline patch into two distinct regions, creating a rough B-shape. Very faint postmedial line bulging in costal half, dentate, narrowly interrupted by veins, weaker on costal third except for darker wedge on costa. Antemedial line faint. Fringe white, contrasting with darker brown edge of wing. *Forewing venter*: As for dorsum, but lighter overall; postmedial line usually much darker. *Hindwing dorsum*: Rounded, slightly pronounced anal angle, bearing similar coloration to forewings. Postmedial line, when present, may be more strongly marked than on forewing. No hyaline patches present. Fringe as for forewing. *Hindwing venter*: As for dorsum, but lighter, postmedial line usually much darker. *Wing venation*: As for genus. *Abdomen*: As for genus, concolorous with thorax, but silvery instead of straw-colored. *Genitalia*: n=8. As for genus, uncus simple, teardrop shaped, extended apically with moderate thickness distally. Ridged ventral lobes of tegumen subtriangular, prominently sclerotized. Ridges thinner than for other species, and thus sharper and flatter, with central ridge especially pronounced. Valves simple, short and stocky for genus, bent upwards at a roughly ninety degree angle so distal ends of valves more in parallel with uncus than angled away. Sclerotized plate, dorsal to juxta and phallus, truncated dorsally with two heavily sclerotized points. Phallus, simple, cylindrical, distal end rounded, vesica elongated with single large cornutus fused to progressively smaller parallel cornuti transitioning into a mane of long, clear, hair-like projections that originate from vesica near base of cornutus, reaching outwards to surround cornutus. **Female.** *Head*: As for male, antennae bipectinate. *Thorax*: As for male. *Legs*: As for male, but small scales nearly completely cover tibial spurs. *Forewing dorsum*: Forewing length: 22–24 mm, avg. 23 mm n=2. As for male but much broader. Postmedial region lighter, more silvery-grey than medial area. Hyaline discal mark large, prominent. Postmedial line, more pronounced than for male, brown, dentate, narrowly interrupted by veins, dark wedge where postmedial line meets costa. Antemedial lines, bilobed, B-shaped. *Forewing venter*: As for dorsum, but lighter, postmedial line more contrasting. *Hindwing dorsum*: As for male, but broader, with hardly accentuated anal angle, essentially bearing same coloration as forewing. Unlike in male, entire hindwing, save for postmedial line, concolorous silvery gray, without a brown edge and without darker medial area on forewing. Dentate postmedial line dark and well pronounced, narrowly interrupted by veins, slightly darker than forewing ground color. No hyaline patches present. *Hindwing venter*: As for dorsum, but lighter, postmedial line more contrasting. *Wing venation*: As for genus. *Abdomen*: Much thicker than that of male. Color as for thorax, though darkening somewhat distally. *Genitalia*: n=2. Papillae anales elongated, covered in fine setae, apophyses posteriores about half length of apophyses anteriores, so

that when abdominal segments fully distended apophyses posteriores extend about to posterior margin of eighth segment. Ductus bursae short, ostium opening immediately into corpus bursae. Corpus bursae firm, round, with heavily-sclerotized, internal bar-like structures reinforcing membrane, appendix bursae elongated. Two very elongated, thin sclerotized plates on venter of eighth segment.

Distribution. This species is known only from southeastern and southern Brazil. São Paulo is the type locality, which was erroneously reported as Paraguay in Becker (1996). In southern Brazil, specimens were examined from the states of Santa Catarina and Paraná. *Eadmuna paloa* is also known from Diamantina, Minas Gerais from four specimens in the AMNH. This record is of considerable distance from the other localities closer to the coast and falls within the Cerrado biome (IBGE 2004). The only elevation data comes from the two Paraná specimens and the Jacupiranga, São Paulo locality, which are of moderate elevation, both localities sited at 800 m.

Remarks. *Eadmuna paloa* was synonymized with *E. esperans* by Becker (1996) without justification. The genitalia of the two species are shown to be substantially different, particularly the vesica and presence/absence of a cornutus. Both species are found to be sympatric, at least in Jaraguá [do Sul], Santa Catarina, Brazil.

This work describes the first female specimens to be attributed to *Eadmuna*. The two female specimens from the AMNH are part of a series of *E. paloa* from Rio Vermelho, Santa Catarina, Brazil, which includes two male specimens that, based on wing morphology and genitalia characteristics, match the male holotype of *E. paloa* from São Paulo. The wing morphology of the females is very similar to that of the males, particularly the silvery-gray coloration, highly dentate postmedial lines on all wings, and the presence of a large hyaline patch on the forewing. Additional support for associating these females with *E. paloa* is that the corpus bursae is highly sclerotized and strongly reinforced, potentially protecting the more membranous material of the corpus bursae from puncture due to the highly sclerotized and very sharp cornutus of the male (B. C. Schmidt pers. comm.). Males of *E. esperans* do not bear cornuti, only a scobinate patch on the vesica, thus relatively reduced sclerotization of the corpus would be expected in the female of *E. esperans*. The two females from Santa Catarina are therefore most reasonably associated with *E. paloa* males, which are much more frequent in collections.

***Eadmuna pulverula* (Schaus, 1896), comb. n.**
Figs 8, 17, 18

Perophora pulverula Schaus, 1896
Cicinnus pulverula; Schaus 1928
Cicinnus pulverula; Becker 1996

Type material. Holotype: BRAZIL, São Paulo, Wm. Schaus collection, USNM holotype No.:12563- St Laurent diss: 11-1-14:8 [examined] [♀, USNM]. **Paratypes:** none. Type locality: BRAZIL, São Paulo.

Diagnosis. Similar to female of *E. paloa* but the forewing apex is more falcate, the forewing discal hyaline patch slightly smaller, and with a distinct, thin dark line along the venter of the abdomen from the thorax to the distal end.

The papillae anales in *E. pulverula* are much broader and stockier than in *E. paloa*, the apophyses anteriores and posteriores are approximately the same length in *E. pulverula* whereas the apophyses posteriores are shorter than the apophyses anteriores in *E. paloa.* Sclerotized, ribbon-like plates are located on the venter of the eighth abdominal segments in both species, but those of *E. pulverula* are wider and angled inward toward each other medially, but are more parallel in *E. paloa*. Finally, the corpus bursae of *E. pulverula* lacks any sclerotized structure, but in *E. paloa*, this is the most distinctive trait of the genitalia.

Description. Female. *Head*: Antennae bipectinate. *Thorax*: As for female of *E. paloa*. *Legs*: As for female of *E. paloa*, but small scales nearly completely cover tibial spurs. *Forewing dorsum*: Forewing length: 24 mm, n=1. As for female of *E. paloa* but with slightly more pronounced apex and overall darker coloration and heavier speckling due to higher number of petiolate scales. Hyaline discal mark smaller. Postmedial line present, darker, thicker, brown, dentate, narrowly interrupted by veins, dark wedge where postmedial line meets costa. Antemedial lines present, bilobed, B-shaped, but straighter. *Forewing venter*: As for dorsum, postmedial line more contrasting. *Hindwing dorsum*: Coloration as for forewing though lighter overall, anal angle accentuated. Postmedial line dentate, dark, well pronounced, narrowly interrupted by veins, slightly lighter than that of forewing. No hyaline patches present. *Hindwing venter*: As for dorsum, but lighter, especially in antemedial area. *Wing venation*: As for genus. *Abdomen*: Very robust, color similar to that of thorax, though yellowing somewhat in holotype, likely due to age of specimen. Longitudinal dark line along middle of abdominal venter formed by darkbrown, thin, petiolate scales. *Genitalia*: n=1. Papillae anales stocky, somewhat triangular, covered in fine setae, apophyses posteriors and anteriores of similar length, though apophyses posteriors slightly thicker, only one of each apophysis present in holotype specimen due to damage. Ductus bursae short, corpus bursae small, baglike, without signum or cornuti. Remnants of appendix bursae visible. Wide, elongated, sclerotized plates present of venter of eighth segment, curving inward toward each other, roughly midway along their length. **Male.** Unknown.

Distribution. Known only from the type specimen, collected in São Paulo; no further locality information is available. Distribution is represented in Fig. 18 by a green placeholder star near the center of the state of São Paulo; however, it may be inferred from the distributions of *E. esperans* and *E. paloa* that *E. pulverula* likely ranges farther to the east in the state of São Paulo nearer to the coastal Atlantic Forest.

Remarks. The holotype of *Perophora pulverula* was determined to be a female of an *Eadmuna* species due to its close similarity to female *E. paloa* from Santa Catarina, Brazil. Despite the fact that female *Eadmuna* had not been recognized prior to this work, it can be reasonably determined that the females from Santa Catarina are in fact *E. paloa* (see remarks of *E. paloa*) whereas the female of *E. pulverula* most likely represent a distinct species based on differences in genitalia.

Unfortunately, the genitalia of the holotype of *E. pulverula* are not intact (see Fig. 17) and thus are not entirely available for study. However, the genitalia characters that are present are very distinct from either of the Santa Catarina *E. paloa* females, which were both similar to each other. The size differences between the two taxa are among the most striking. Although the overall size of the females of *E. paloa* and *E. pulverula* are very similar, the genitalia of *E. pulverula* are nearly twice as large as those of *E. paloa* in all respects.

It is possible that *E. pulverula* is the unidentified female of *E. esperans* due to process of elimination in that the only *Eadmuna* known to occur in southern and southeastern Brazil are *E. paloa* and *E. esperans* and the female of *E. paloa* has been identified. However, there is not enough evidence to support *E. pulverula* and *E. esperans* as being conspecific. A major problem with considering *E. pulverula* to be the female of *E. esperans* is the wing color. Females of *E. paloa* are so similar to conspecific males that one would expect the female of *E. esperans* also to be very similar to conspecific males, and not exhibit the extreme dimorphism that would be present if *E. pulverula* was considered conspecific with *E. esperans*. Extreme sexual dimorphism in wing color and pattern is not common in Mimallonidae, aside from the fact that females are usually larger than males, with much broader wings (R. A. St Laurent pers. obs.). In actuality, *E. pulverula* is very similar to female *E. paloa*, with major differences only in the genitalia.

The genitalia of *E. pulverula* are so distinct from the females of *E. paloa* that it becomes impossible to consider them the same entity which, based on wing morphology alone, would have been the most logical conclusion pending further evidence. The most conservative approach in dealing with the name *E. pulverula* is to transfer it to *Eadmuna* from *Cicinnus* due to the female holotype bearing a striking similarity to female *E. paloa*, but to maintain it as a valid species rather than trying to associate it with cryptic males currently considered *E. paloa* or attributing it to *E. esperans* by mere process of elimination. Until female *E. esperans* are accurately associated with the easily recognizable males, the current placement of *E. pulverula* remains somewhat inconclusive.

Acknowledgements

We thank B. C. Schmidt (CNC) for valuable discussion and loan of specimens; J. E. Hayden (FSCA) reviewed the manuscript and offered valuable feedback and facilitated the loan of specimens. J. Rawlins (CMNH), D. Grimaldi (AMNH), L. Thayer (AMNH), S. B. Rab Green (AMNH), and J. Brown (USNM) provided additional loans of specimens. J. D. Lafontaine (CNC) and an additional anonymous reviewer gave valuable contributions to the manuscript. R. McCarthy (Cornell University) offered assistance with graphical aspects of the paper, including support with CS4. A. P. S. Carvalho reviewed the manuscript numerous times and provided appreciated feedback and helpful insight to the biomes of Brazil, including recommending valuable sources. The Hunter R. Rawlings III Cornell Presidential Research Scholars program provided funding for this and ongoing research with Mimallonidae.

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ZooKeys 494: 69–106 (2015)
doi: 10.3897/zookeys.494.8748
http://zookeys.pensoft.net

RESEARCH ARTICLE

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Revision of the genus *Philonome* Chambers and its proposed reassignment to the family Tineidae (Lepidoptera, Tineoidea)

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Academic editor: *E. van Nieukerken* | Received 13 October 2014 | Accepted 10 March 2015 | Published 6 April 2015

http://zoobank.org/F73F468E-4DF7-479E-85C4-717466635BF9

Citation: Sohn J-C, Davis DR, Lopez-Vaamonde C (2015) Revision of the genus *Philonome* Chambers and its proposed reassignment to the family Tineidae (Lepidoptera, Tineoidea). ZooKeys 494: 69–106. doi: 10.3897/zookeys.494.8748

Abstract

The New World genus *Philonome* Chambers, 1874 is revised. This genus comprises twelve species, seven of which are described as new: two species, *P. nigrescens* **sp. n.** and *P. wielgusi* **sp. n.**, from the United States; four species, *P. albivittata* **sp. n.**, *P. curvilineata* **sp. n.**, *P. kawakitai* **sp. n.**, and *P. lambdagrapha* **sp. n.**, from French Guiana; and one species, *P. penerivifera* **sp. n.**, from Brazil. Lectotypes are designated for *Philonome clemensella* Chambers, 1874 and *P. rivifera* Meyrick, 1915. Partially on evidence of their head morphology and particularly from molecular evidence, the genus *Philonome*, previously associated with Bucculatricidae or Lyonetiidae, is reassigned to Tineidae. A possible systematic position of *Philonome* within Tineidae is discussed. *Eurynome* Chambers, 1875, is synonymized with *Argyresthia* Hübner, 1825 (Argyresthiidae). Photographs of adults and illustrations of genitalia, when available, are provided for all described species of *Philonome* and two species previously misplaced in *Philonome*, *Argyresthia luteella* (Chambers, 1875) and *Elachista albella* (Chambers, 1877). In addition, DNA barcodes were used for the delimitation of most species.

Keywords

Argyresthia, Argyresthiidae, Bucculatricidae, COI, DNA barcoding, *Eurynome*, Lyonetiidae, new species, New World

Introduction

The monobasic genus *Philonome* was proposed by Chambers in 1874 for *Philonome clemensella* Chambers. Chambers (1875) later proposed a supposedly allied genus, *Eurynome*, also based on a single species, *Eurynome luteella* Chambers, and in 1877, added another congener, *Eurynome albella* Chambers. *Eurynome*, however, was recognized as a homonym and later replaced by *Busckia* Dyar, 1903.

Chambers (1875, 1877, 1880) assigned *Philonome* to the Tineina, a conventional group name to accommodate primitive Microlepidoptera, and he further suggested that the genus is allied to *Bucculatrix* Zeller, 1839. The putative association between *Philonome* and *Bucculatrix* has been repeatedly expressed by subsequent researchers such as Meyrick (1915, 1920) and Forbes (1923). Barnes and McDunnough (1917) included *Philonome* under Lyonetiidae, together with *Bucculatrix*, followed by Forbes (1923), but they treated *Busckia* (= *Eurynome* Chambers) as a genus of Elachistidae. McDunnough (1939) transferred *Busckia* to Lyonetiidae and synonymized it with *Philonome*. Sohn et al. (2013) conducted a molecular phylogeny of Yponomeutoidea (to which Lyonetiidae belongs), including *Philonome clemensella*, and found that the species is nested within the Tineidae (Fig. 1). However, the tineid association of *Philonome* has been so far supported only by molecular data, not yet by morphological evidence.

Philonome currently includes six species, which occur exclusively in the New World: two from the Nearctic Region and four from the Neotropical Region. *Eurynome albella* Chambers (Figs 17, 70), known only from the unique holotype collected at Edgerton (38°57'24"N, 104°50'6"W; at ~ 6500 feet elevation), El Paso Co., Colorado, was once treated as *Philonome* (McDunnough 1939), but it was later assigned to *Elachista* of Elachistidae (Kaila 1999). Kaila (1999) found that the name *Elachista albella* (Chambers) had been preoccupied and hence he proposed a replacement name, *Elachista dasycara*. Chambers (1874, 1877) characterized *Philonome* and *Eurynome* on superficial appearance and wing venation. The adults resemble some species of *Bucculatrix* in wing pattern, notably *B. adelpha* Braun, 1963, or *B. angustata* Frey & Boll, 1876. However, *Philonome* differs from *Bucculatrix* in having an elongate, telescopic ovipositor and lacking an androconial scale pocket on the male abdomen (Braun 1963; Kobayashi et al. 2010). This suggests that their resemblance is due to convergence. The biology of *Philonome* is essentially unknown. Forbes (1923) stated that *P. clemensella* have been collected from hickory and linden trees. His statement, however, was based on the ambiguous label data of specimens from the United States National Museum of Natural History. No additional observation of the larvae of *P. clemensella* has been reported from these trees.

The goals of this paper are to redefine the generic characteristics of *Philonome*, to describe seven new species from the Nearctic and Neotropical Regions, to transfer a misplaced species, "*Philonome*" *luteella* to its correct genus, *Argyresthia*, and to provide morphological evidence of the tineid relationship of *Philonome*, which has been suggested from a recent molecular phylogenetic study (Sohn et al. 2013).

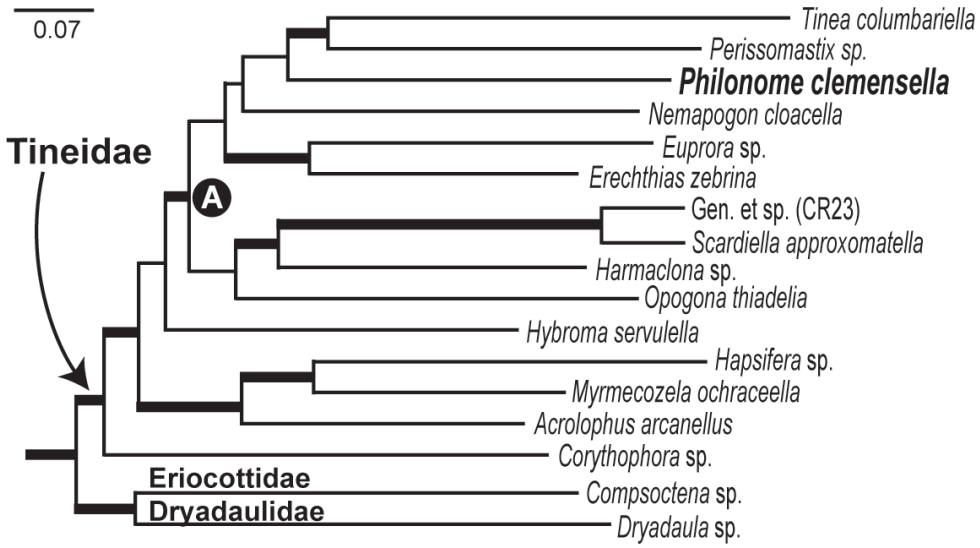


Figure 1. Maximum likelihood phylogeny of Tineidae *s. l.* extracted from Sohn et al. (2013), based on 27 nuclear genes. Branches in bold indicate the > 70% bootstrapping support from at least one analysis attempted by Sohn et al. (2013). The 'A' in closed circle represents a well-supported subclade of Tineidae in which *Philonome clemensella* is included.

Materials and methods

Pinned specimens from five institutional collections were examined. The abbreviations of these depositories are as follows:

BMNH Natural History Museum (formerly British Museum of Natural History), London, UK;
MCZ Museum of Comparative Zoology, Harvard University, Cambridge, USA;
MSU Mississippi Entomological Museum, Mississippi State University, Starkville, Mississippi, USA;
USNM National Museum of Natural History (formerly United States Museum of Natural History), Washington DC, USA;
VOB Vitor O. Becker, Instituto Uiraçu, Camacan, Brazil.

Other abbreviations include:

ex. example, the specimens whose sex cannot be determined;
Co. county;
GSN genitalia slide number;
WSN wing slide number.

Table 1. Specimens used for the DNA barcoding analysis. Both the Process ID and sample ID codes are unique identifiers linking the record in the BOLD database and the voucher specimen from which the sequence is derived. Additional collecting and specimen data are accessible in BOLD's data set (http://dx.doi.org/10.5883/DS-PHILONO) as well as GenBank (http://www.ncbi.nlm.nih.gov/genbank/).

Species	Process ID	Sample ID	Country	Accession number (NCBI, GENBANK)
Philonome clemensella	MEC875-04	jflandry0875	Canada	GU096008
Philonome clemensella	MNAL543-10	CNCLEP00035968	Canada	KP696787
Philonome clemensella	MNAI712-09	CNCLEP00038457	Canada	GU692620
Philonome clemensella	MNAI218-09	CNCLEP00042501	USA	GU693088
Philonome clemensella	MNAI241-09	CNCLEP00042524	USA	GU693064
Philonome curvilineata	LNOUA586-10	CLV68110	French Guiana	HQ571412
Philonome euryarga	LNOUA669-10	CLV76410	French Guiana	HQ571490
Philonome albivittata	LNOUA849-10	CLV94410	French Guiana	HQ571657
Philonome albivittata	LNOUA946-10	CLV104110	French Guiana	HQ571747
Philonome lambdagrapha	LNOUA928-10	CLV102310	French Guiana	HQ571730
Philonome kawakitai	GRANO044-11	AK0044	French Guiana	HQ571758
Philonome sp.	LNOUA958-10	CLV105310	French Guiana	KM224529

Selected specimens were dissected for genitalia and abdominal structures, following Clarke (1941), except that Chlorazol black was used for staining. Dissected genitalia were mounted on microscope slides in Euparal resin (BioQuip Products Inc.) or Canada balsam. Pinned specimens were examined under a Leica MZ APO stereoscope. Slide-mounted specimens were examined under a Leica LEITZ-DMRX microscope. All illustrations were drawn from dissections temporarily stored in glycerin, which were later permanently embedded in mounting medium. Terms for genitalia and wing venation follow Klots (1970) and Wootton (1979), respectively. The 8th abdominal segment is abbreviated as A8 in the descriptions. Verbatim label data are given for primary types. Additional data by the present authors are given in brackets.

DNA was extracted from hind legs of dried specimens. DNA barcodes (658 bp of the COI mitochondrial gene) were generated at the Canadian Centre for DNA Barcoding (CCDB, Guelph). A total of seven specimens were sequenced (Table 1), all collected in French Guiana by the third author (CLV). These newly generated barcodes were compared to five DNA-barcodes of *Philonome clemensella* (Table 1), one (jflandry0875) available at the Barcode of Life Data Systems (BOLD; www.boldsystems.org; also see Ratnasingham and Hebert 2007) and the other four unpublished. Barcode data were analysed using the analytical tools of BOLD such as Neighbour Joining and pairwise genetic distance matrix.

Details on the date and site of collection for each specimen, as well as a photograph are available through the DOI (http://dx.doi.org/10.5883/DS-PHILONO). The same DOI provides access to the sequence records and GenBank accession numbers (Table 1).

Systematic accounts

Philonome Chambers

Philonome Chambers, 1874: 96; Dyar 1903: 563; McDunnough 1939: 100; Davis 1983: 8; 1984: 25.

Type species: *Philonome clemensella* Chambers , 1874, by monotypy.

Phillonome [sic]: Chambers 1880: 196, 199. Incorrect subsequent spelling.

Phyllonome [sic]: Chambers 1882: 15. Incorrect subsequent spelling.

Adult. *Head* (Fig. 18): Vestiture of vertex rough with piliform scales; frons smooth with broad, flat, appressed scales; a band of broad, spatulate scales between the bases of the antennae, along the transfrontal suture, bounded both above and below by piliform scales. Antenna filiform in both sexes; antennal pecten absent; scape elongate, ~2.2–2.4× length of adjacent pedicel. Labial palpus without bristle-like setae; 2nd segment 2× longer than 1st, as long as 3rd. Maxillary palpus 5-segmented, longer than labial palpus. Proboscis naked, shorter than maxillary palpus.

Thorax: Foreleg epiphysis slender. Midfemur with apical tuft of elongate scales. Hind-tibia hairy dorsally. Forewing pattern elements (Fig. 2) including longitudinal fascia, costal fascia (absent in *P. euryarga*, *P. albivittata*, and *P. spectata*), subapical spot (present only in *P. cuprescens*, *P. wielgusi*, *P. nigrescens*, *P. clemensella*, and *P. lambdagrapha*), apical spot (present only in *P. cuprescens*, *P. wielgusi*, *P. nigrescens*, and *P. clemensella*), tornal patch, and dorsal bar (absent in *P. spectata*). Forewing venation (Fig. 20) with Rs 4-branched, all terminating on costa and arising from weak vein leading to M_1; M_2 and M_3 stalked; CuA as one branch. Hindwing venation (Fig. 20) with Sc terminating on basal 1/4 of costa; Rs, M_{2+3}, CuA weak, arising from weak vein leading to M_1; CuP and 1A+2A weak, stalked.

Abdomen: Coremata on male sternum VIII present posterolaterally, short and stiff (*P. albivittata* sp. n., *P. clemensella*, *P. euryarga*, and *P. wielgusi* sp. n.), long and hair-like (*P. lambdagrapha* sp. n.) or absent (*P. curvilineata* sp. n. and *P. rivifera*).

Male genitalia: Paired processes (uncus, Fig. 28) from tergum IX (tegumen) and often surrounding tuba analis either present or absent (*P. albivittata* sp. n. and *P. euryarga*); valva divided or deeply cleaved into two portions (*P. albivittata* sp. n., *P. clemensella*, *P. euryarga*, *P. penerivifera* sp. n., and *P. rivifera*) or entire; anellus funnel-shaped; basal ring of anellus moderately sclerotized; vinculum broad; saccus present.

Female genitalia: Ovipositor telescopic with two primary segments; papillae anales semi-elliptical, setose; lamella antevaginalis conical or cylindrical; additional protrusion behind ostium bursae present (*P. nigrescens* and *P. rivifera*) or absent; ductus bursae slender; corpus bursae obovate or elliptical; signum absent.

Biology. Chambers (1878) mentioned that he repeatedly collected *Philonome clemensella* from the type locality where *Gleditschia triacanthos* L., *Ulmus americana* L., *Prunus serotina* Ehrh., and *Celtis occidentalis* L. grow in the immediate vicinity. He then assumed

that the larvae may feed on some weeds or shrubs growing nearby. Forbes (1923) noted that the larvae of *P. clemensella* feed on hickory and linden. These records were, however, based on ambiguous label data which state only plant names without details and thus require verification. Nothing is known about the biology for other congeners of *P. clemensella*.

Included species (arranged by the similarities in the forewing pattern and the male genitalia):

Philonome cuprescens Walsingham, 1914
Philonome wielgusi sp. n.
Philonome nigrescens sp. n.
Philonome clemensella Chambers, 1874
Philonome lambdagrapha sp. n.
Philonome curvilineata sp. n.
Philonome euryarga Meyrick, 1915
Philonome albivittata sp. n.
Philonome penerivifera sp. n.
Philonome kawakitai sp. n.
Philonome rivifera Meyrick, 1915
Philonome spectata Meyrick, 1920
Philonome sp.

Keys to the species of *Philonome* based on external appearance

1	Forewing with longitudinal fascia extending near apex	**2**
–	Forewing with longitudinal fascia not extending beyond discal cell	**5**
2	Forewing ground color brown or reddish brown	**3**
–	Forewing ground color black	***nigrescens* sp. n.**
3	Forewing with costal fascia curved	**4**
–	Forewing with costal fascia straight	***wielgusi* sp. n.**
4	Yellow lining along costal fascia of forewing narrow	***clemensella* Chambers**
–	Yellow lining along costal fascia of forewing broad	***cuprescens* Walsingham**
5	Forewing with dorsal bar	**6**
–	Forewing without dorsal bar	***spectata* Meyrick**
6	Forewing with dorsal bar connected with longitudinal fascia	7
–	Forewing with dorsal bar separated from longitudinal fascia	**8**
7	Fore- and hindwing fringes pale grayish orange	***euryarga* Meyrick**
–	Fore- and hindwing fringes brownish gray	***albivittata* sp. n.**
8	Forewing with costal fascia	***lambdagrapha* sp. n.**
–	Forewing without costal fascia	***rivifera* Meyrick and allied species***

* Four species, *curvilineata* sp. n., *rivifera* Meyrick, *penerivifera* sp. n., and *kawakitai* sp. n., are indistinguishable from one another based on external appearance; see Table 2 for their differences in male genitalia (except *kawakitai* sp. n. whose males are unknown).

***Philonome cuprescens* Walsingham, 1914**
Figs 2, 21–25

Philonome cuprescens Walsingham, 1914: 346; Davis 1984: 25.

Adult (Fig. 2). *Head*: Vertex orange; space between antennal scapes lined with broad pale orange scales; frons brownish white with luster. Antenna 5/6 as long as forewing; scape orange dorsally, brownish white ventrally, pecten reddish brown; flagellomere dark brown on distal half, pale brownish gray on basal half. Labial palpus 1/4 as long as maxillary palpus, pale orange, pale orange. Maxillary palpus lustrous yellowish white dorsally, gray ventrally.

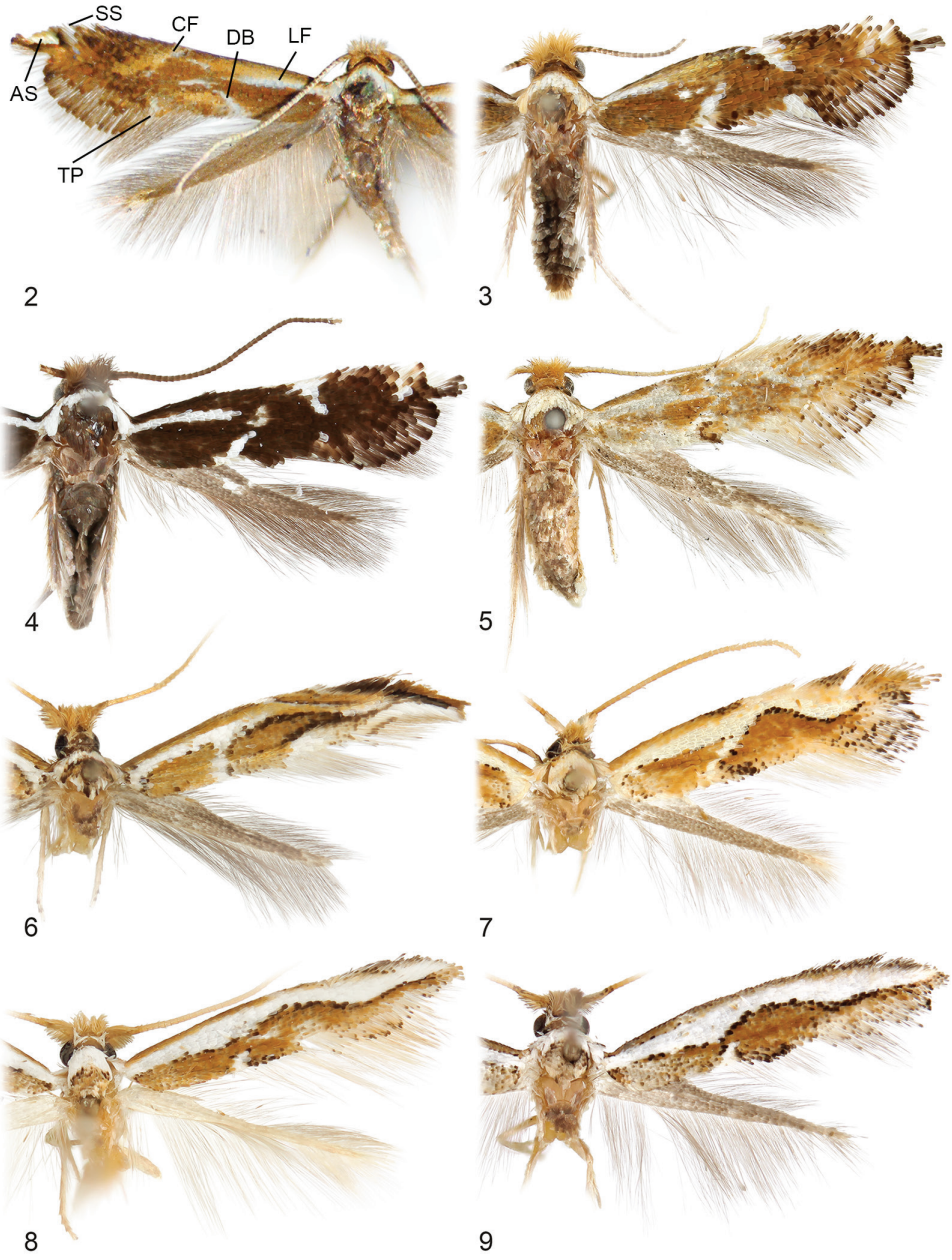
Thorax: Patagium orange; tegula white, tinged with brown basally, yellowish brown subbasally; mesonotum brown with white transverse band at anterior 1/5, lined with yellowish brown anteriorly. Foreleg with coxa, femur and tibia dark brown on exterior surface, lustrous pale reddish brown on interior surface; tarsomeres pale brown dorsally, pale orange ventrally. Midleg with coxa lustrous pale orange; femur lustrous pale orange, tinged with dark grayish brown apically; tibia dark brown dorsally, pale orange ventrally; tarsomeres pale reddish brown dorsally, pale orange ventrally. Hindleg with coxa pale orange; femur pale grayish brown, tinged with pale orange ventrobasally; tibia brown dorsally, pale orange ventrally, with mixture of pale orange and pale brown piliform scales of tuft ventrally; tarsomeres pale reddish brown dorsally, pale orange ventrally. Forewing length 2.8–3.9 mm (n = 2), brown, intermixed with dark brown scales in postmedian area; longitudinal fascia white, closer to costa than to dorsum, accompanied with yellowish brown fascia anteriorly; costal fascia yellowish brown, curved to apex at the middle, accompanied with narrow, white line along lower margin in costal 1/2; dorsal bar white, curved in terminal 1/4, accompanied with yellowish brown spreading in dorsal area, almost connected with longitudinal fascia; subapical spot white, narrow, curved; apical spot white, suffused with reddish brown costally; tornal patch very small; fringe elongate scales dark brown, hairy scales dark grayish brown. Hindwing and fringe dark grayish brown.

Abdomen: Terga lustrous, dark reddish brown; sterna lustrous, pale yellow.

Male genitalia (Figs 21–25): Tegumen rectangular, with subtrapezoidal protrusion apically and subtriangular process laterally; apical protrusion 1/2 as long as valva, with round depression ventro-subapically and triangular anterior extension. Valva elongate, digitate on distal half, setose subapically; costa convex at basal 2/5; sacculus as small, setose bulge. Vinculum broad, elliptical, anterior margin convex medially; saccus short, narrow-subtriangular. Phallus slightly curved at distal 1/3, of even width on distal 3/4, broadened on basal 1/4.

Female unknown.

Types. Holotype: male, “Type” [circular label with red borders], “Amula, 6000ft. GUERRERO MEXICO VIII 18 (H.H.Smith) (Gdm. Slvn) 66776”, “Walsingham Collection, 1910-427”, “*Philonome* ♂ *cuprescens* Wlsm. Biol. C. Am. Lep. Het. 4. p346, 1914 TYPE ♂ descr” [label with black marginal lines], BMNH. Paratypes:



Figures 2–9. Adults. **2** *Philonome cuprescens*, ♂ (3.1 mm), abbreviations: AS = apical spot; CF = costal fascia; DB = dorsal bar; LF = longitudinal fascia; SS = subapical spot; TP = tornal patch **3** *P. wielgusi*, ♂ holotype (2.8 mm) **4** *P. nigrescens*, ♂ holotype (2.8 mm) **5** *P. clemensella*, ♂ (4.0 mm) **6** *P. lambdagrapha*, ♂ holotype (3.0 mm) **7** *P. curvilineata*, ♂ holotype (2.8 mm) **8** *P. euryarga*, ♂ (2.7 mm) **9** *P. albivittata*, ♂ holotype (2.8 mm). (Forewing lengths in parentheses).

Same data as holotype: 1♂, 1 ex. [hindwing & abdomen missing], Type no. 66778 & 66779, [GSN] USNM 34210 (♂), USNM.

Material examined. Mexico: Same locality as holotype: 1♂, 2 ex., 18 September [no year] (HH Smith), BMNH.

Distribution. Mexico (Guerrero).

***Philonome wielgusi* Sohn & Davis, sp. n.**
http://zoobank.org/EDA70A5B-C1CD-4432-A242-EB7D19E71501
Figs 3, 26–30

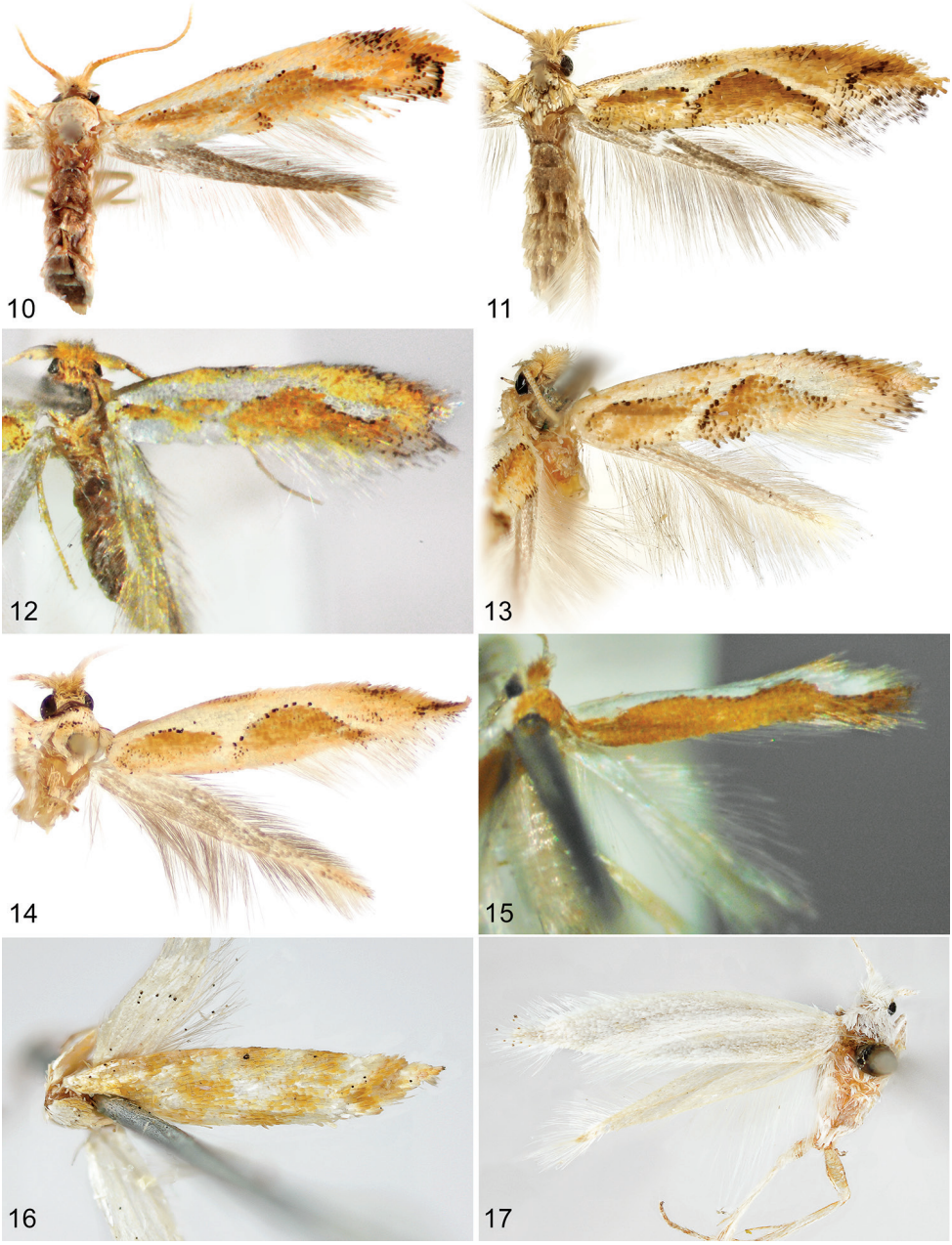
Diagnosis. This species is similar to *P. clemensella* in external appearance but can be distinguished from the latter in having shorter longitudinal fascia and straight costal fascia on the forewing. In the male genitalia, the lateral processes on the uncus are larger in *P. wielgusi* than in *P. clemensella* and the valvae are not divided at all in *P. wielgusi*.

Adult (Fig. 3). *Head*: Vertex yellowish brown, paler to frons; frons lustrous, pale yellowish gray. Antenna 2/3 as long as forewing; scape dark brown dorsally, with broad, lustrous, pale yellowish gray patch ventrally; first six flagellomeres dark brown dorsally, narrowly white ventrally; the remaining flagellomeres entirely dark brown. Labial palus straight, very small, 3/5 as long as antennal scape, pale orange, apex obtuse. Maxillary palpus 2× longer than labial palpus, yellowish gray; each segment tinged with pale orange apically.

Thorax: Patagium yellowish brown. Tegula dark yellowish brown on basal 1/4, pale grayish brown on distal 3/4, paler distad. Mesonotum lustrous white on anterior 1/3, dark grayish brown on posterior 2/3. Foreleg with coxa dark grayish brown laterally, silvery gray mesally; femur and tibia dark grayish brown, paler ventrad; tarsomere I to II pale orange, with narrow dark brownish gray patch dorsally, the remaining tarsomeres entirely dark grayish brown. Midleg with coxa and tibia dark grayish brown laterally, lustrous pale orange mesally; tibia dark brownish gray dorsally, lustrous pale orange ventrally; tarsi dark brownish gray. Hindleg with coxa and femur lustrous, pale orange; tibia lustrous, yellowish gray, sparsely hairy dorsally, with dense spiniform setae ventrally; tarsi dark brownish gray. Forewing length 2.3–3.0 mm (n = 8), brown, dorsum dark brownish gray basally; longitudinal fascia, white, extending from base to basal 1/3 of forewing, costal fascia white, at distal 2/5 of costa, oblique, adjacent to a slender dark brown line on anterior side; subapical and apical spots white; tornal patch white, triangular; dorsal bar white, oblique; fringe dark orange, each scale with dark brown tip. Hindwing and fringe gray.

Abdomen: Terga lustrous, gray; sterna lustrous, pale orange. Tergum VIII of male rectangular; sternum VIII subrectangular, broadly emarginated posteriorly, with oblique furrow laterally and short, stiff coremata posterolaterally.

Male genitalia (Figs 26–30): Tegumen subtrapezoidal, with semi-elliptical protrusion apically and falcate processes (uncus) laterally; apical protrusion with round opening dorsoposteriorly, connected with U-shaped groove basally; teguminal process 1/2 as long as valve. Valva elongate, broadened to base; apex obtuse, sparsely setose; sacculus



Figures 10–17. Adults. **10** *P. penerivifera*, ♀ paratype (3.6 mm) **11** *P. kawakitai*, ♀ holotype (3.8 mm) **12** *P. rivifera*, ♂ lectotype (3.4 mm) **13** *P. rivifera*, ♂ paralectotype (2.8 mm) **14** *P.* sp., CLV105310 (4.1 mm) **15** *P. spectata*, ♀ holotype (2.3 mm) **16** *Argyresthia luteella*, ♀ holotype (3.4 mm) **17** *Elachista dasycara* (= *Eurynome albella*),♀ holotype (4.0 mm). (Forewing lengths in parentheses).

broadened at basal 1/3, narrowed distally, nearly as long as valva. Anellus extending to basal 3/5 of phallus; juxta forming a ridge connected to anellus. Vinculum broad, smoothly angulate laterally, broadly triangular anteriorly, with setose bulge near base of valva; saccus short, subtriangular. Phallus narrowed to apex, slightly curved at middle.

Female unknown.

Types. Holotype: male, "ARIZONA: Cochise Co.: Sierra Vista 5131 Bannock 2 IX 1988", "Attracted to (E, Z) – 3 13 ODDOH @ 1615-1730 hrs.", "R. S. Wielgus Collector", USNM. Paratypes (78♂): **USA:** Arizona: Cochise Co.: Chiricahua Mountains., Sunny Flat Campground: 1♂, 28 July 1989, B & JF Landry, CNC . Sierra Vista: 5131 Bannock, 10♂, 31 August 1988 (RS Wielgus), on pheromone trap; 18♂, 1 September 1988, [GSN] USNM 31056; 12♂, 2 September 1988, [GSN] USNM 29950; 2♂, 5 September 1988; 1♂, 6 September 1988; 7♂, 9 September 1988; 1♂, 10 September 1988; 1♂, 14 September 1988; 3♂, 15 September 1988; 8♂, 16 September 1988; 4♂, 17 September 1988; 7♂, 18 September 1988, USNM. Graham Co.: Pinaleno Mountains: Wet Canyon: 3♂, 22 July 1989, B & JF Landry, CNC.

Distribution. Southwestern United States (Arizona).

Etymology. The species name is a patronym in honor of Mr. Ronald S. Wielgus, who collected nearly the entire type series.

Remarks. As reported by the collector, Ronald Wielgus, and indicated on specimen labels, nearly all moths were collected in the late afternoon, between 16:15 and 17:30 hours. All 157 adults collected thus far are males.

***Philonome nigrescens* Sohn & Davis, sp. n.**

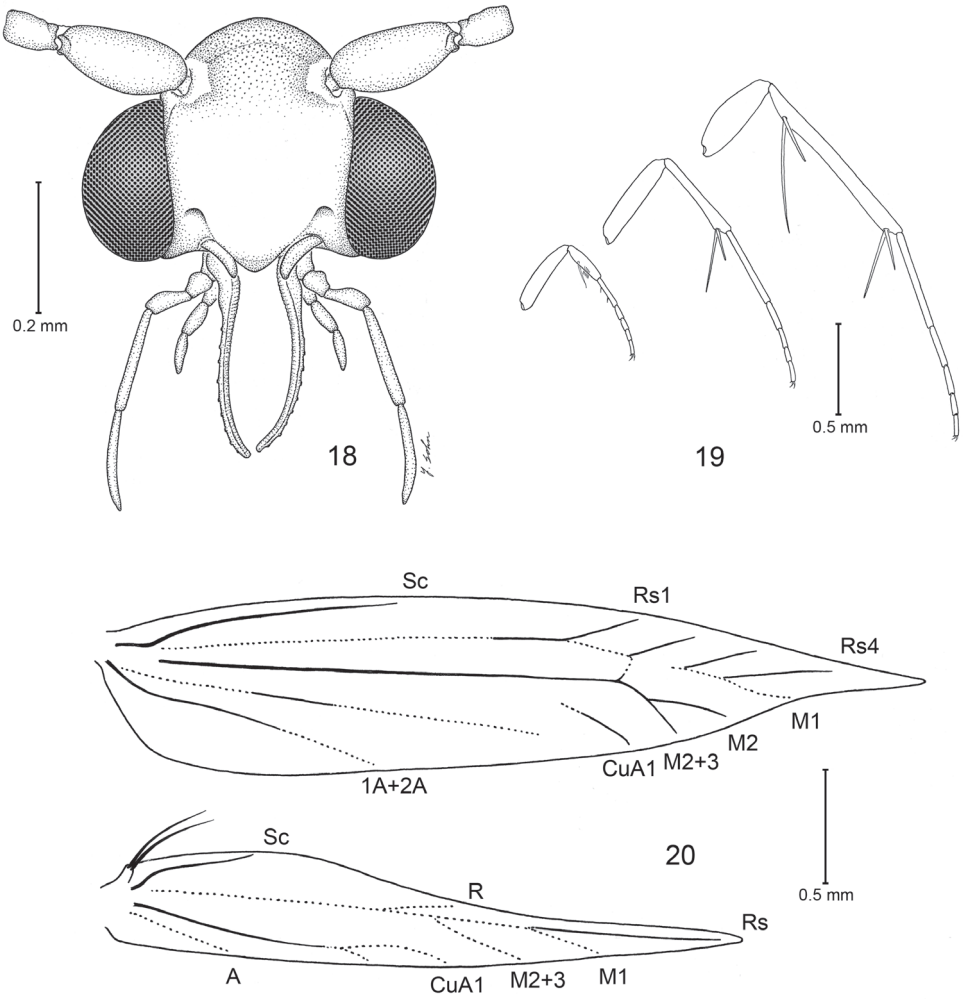
http://zoobank.org/8CF6C86B-3C26-48E6-B7F6-1366DC45017B

Figs 4, 31–33, 57–58

Diagnosis. This species is easily distinguished from all other congeners in possessing a black ground-color of the forewing and an elongate process on the transtila of the male genitalia.

Adult (Fig. 4). *Head*: Scales on vertex dark reddish brown, as long as antennal scape, directed forward; semicircular, dome-like scale cap on anterior vertex between antennal scapes, slightly concave anteriomedially, lustrous, pale yellowish gray; frons lustrous, yellowish gray. Antenna 3/5 as long as forewing; scape dark brown dorsally, reddish brown laterally, pale brownish gray ventrally, with flabellate, pale brownish gray scape cap anteroventrally and pecten; flagellomeres dark brown dorsally, pale brownish gray ventrally. Labial palpus straight, slender, conical, obtuse apically, small, 1/2 as long as antennal scape, lustrous, pale yellowish gray.

Thorax: Patagium white on distal half, dark brown on basal half; tegula white, tinged with dark brown basally; mesonotum dark brown with coppery luster. Foreleg with coxa to tarsomeres lustrous orange-white, narrowly tinged with gray dorsally. Midleg with coxa to tibia lustrous orange-white; femur with broad pale reddish brown patch dorsally; tibia broadly dark gray dorsally; tarsomeres dark gray, paler ventrally. Hindleg with coxa lustrous pale orange, tinged with brown basally; femur lustrous pale



Figures 18–20. *Philonome clemensella*, body morphology. **18** Head, frontal view **19** Legs **20** Wing venation.

orange; tibia and tarsomeres dark gray dorsally, lustrous pale orange ventrally; tibia spinose dorsally, with hair tufts ventrally. Forewing length 2.1–3.2 mm (n = 7), dark brown with coppery luster; longitudinal fascia white, extending from base to basal 1/3 of forewing; costal fascia white, straight, broadened at costa; dorsal bar white; subapical, apical and tornal spots white; fringe gray. Hindwing gray, paler to base; fringe gray.

Abdomen: Terga lustrous, dark grayish brown; sterna lustrous, yellowish gray ventrally.

Male genitalia (Figs 31–33): Tegumen trapezoidal, with digitate process posterolaterally; teguminal process 1/3 as long as valva, sparsely setose on dorsoapical 1/2; tuba analis arising between teguminal processes. Valva subtrapezoidal on basal half, digitate on distal half, densely setose apically and at middle, sparsely setose on distal half; sacculus

broadly swollen and granulate at basal 1/3, convex and setose at distal end. Transtilla with elongate process 3/4 as long as phallus. Juxta with semicircular bulge, connected to anellus.Vinculum broad, subquadrate; saccus quadrate, 1/2 as long as lateral process of tegumen. Phallus slightly curved, enlarged posteriorly; apex with linguiform carina.

Female genitalia (Figs 57–58): Apophyses posteriores 1.8× longer than apophyses anteriores. Lamella anteveginalis dome-shaped, slanted to ostium bursae. Sclerotized protrusion bearing ostium cylindrical, surrounded with conical membranous area. Ductus bursae as long as corpus bursae, narrow; inception of ductus seminalis at posterior 1/3 with a cylindrical sclerotization. Corpus bursae obovate.

Types. Holotype: male, "ARIZONA: Cochise Co. Sierra Vista 5131 Bannock 18 IX 1988", "R Wielgus Collector", "Attracted to 1988 Farchan (Z, Z)-3, 13 ODDA@1620hrs. in pheromone trap" [hand-written], USNM. Paratypes (8♂, 1♀): **USA**: Arizona: Cochise Co.: Same locality as holotype: 1♂, 13 May 1988, attracted to pheromone trap; 3♂, 28 August 1988 (R S Wielgus), attracted to pheromone trap; 1♂, 17 September 1988, all USNM. Pima Co.: Station Catalina: 1♂, ["iss"] 13 June 1913 (Hopk.), "from trunk of evergreen Oak", [GSN] USNM 16406, USNM. Santa Cruz Co.: Peña Blanca Campground: 2♂, 22 August 1988, attracted to pheromone trap, [WSN] USNM wing 29949, USNM. New Mexico: Grant Co.: Silver City: 1♀, 5 June 1974 (PM Jump), [GSN] USNM 34355, USNM.

Etymology. The species name is derived from the Latin verb 'nigrescere' meaning "verging on black" and refers to the black ground color of the forewing of this species.

Distribution. Southwestern United States (Arizona, New Mexico).

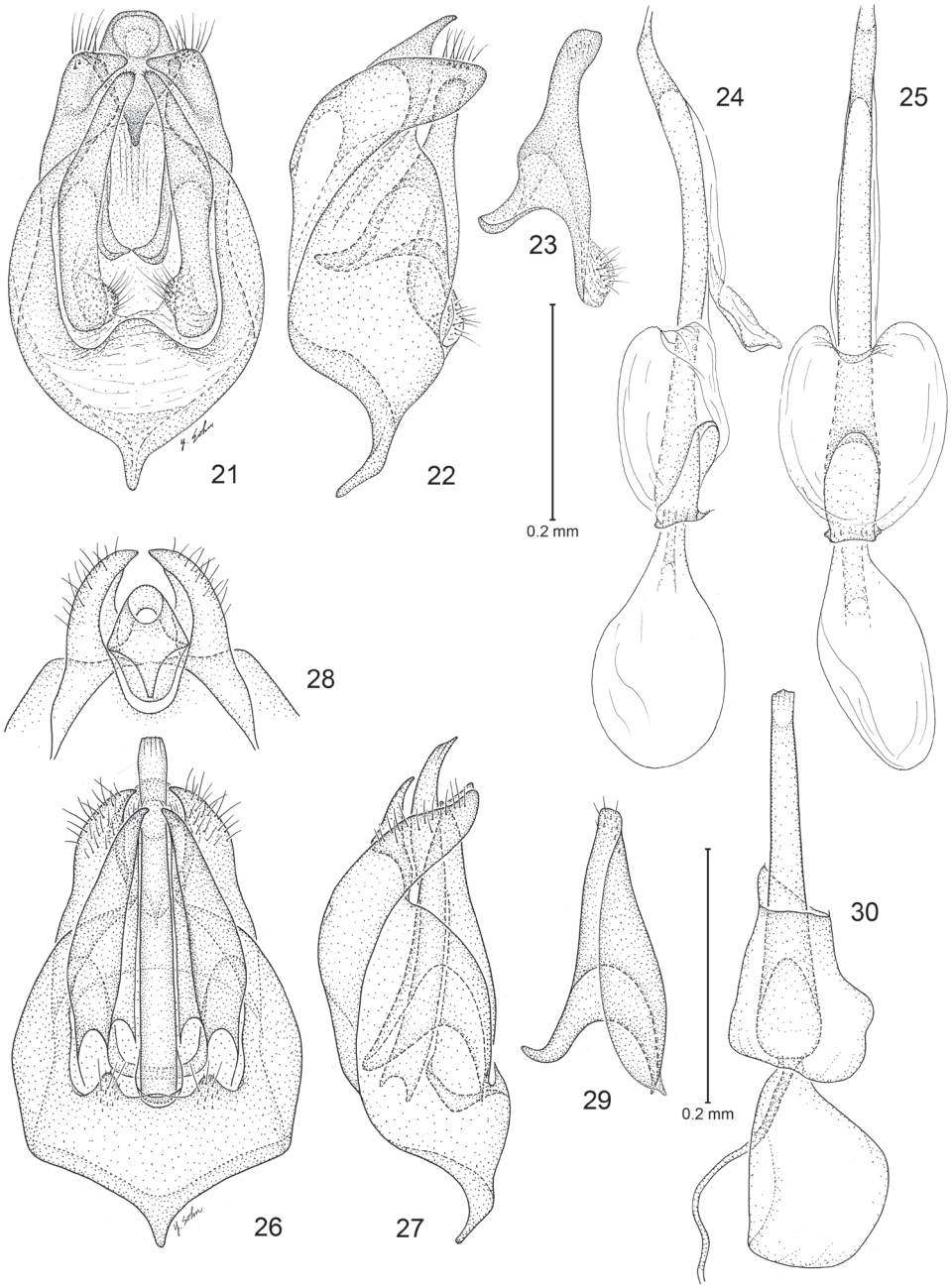
***Philonome clemensella* Chambers, 1874**

Figs 5, 34–36, 59–60

Philonome clemensella: Chambers 1874: 97; Dyar 1903: 563; McDunnough 1939: 100; Davis 1983: 8.
Philonome staintonella: Chambers 1876: 136. *Nomen nudum*

Adult (Fig. 5). *Head*: Vertex convex medially; scales on vertex orange, as long as antennal scape, slanted forward; semicircular, dome-like scale cap on anterior vertex between antennal scapes with compact appressed, lustrous pale yellow scales; frons smooth, lustrous pale yellow. Antenna 3/5 as long as forewing; scape reddish brown dorsally, lustrous pale yellow ventrally, with fan-shaped scale cap anterioventrally; flagellomeres dark reddish brown dorsally, lustrous pale yellow ventrally. Labial palpus straight, slender, very small, 1/2 as long as antennal scape, pale orange, apex acuminate. Maxillary palpus 3× longer than labial palpus, pale orange.

Thorax: Patagium reddish brown; tegula pale orange-white, suffused with reddish brown basally; mesonotum pale orange-white. Foreleg with coxa lustrous orange-white, tinged with gray dorsobasally; femur and tibia dark brownish gray dorsally, lustrous orange-white ventrally; tarsi orange-white, lustrous ventrally. Midleg with



Figures 21–30. *Philonome*, male genitalia. **21**–**25** *P. cuprescens*. **21** Ventral view of genital capsule **22** Lateral view **23** Lateral view of valva **24** phallus, lateral view **25** phallus, ventral view **26**–**30** *P. wielgusi*, male genitalia. **26** Ventral view of genital capsule **27** Lateral view **28** Ventral view of anellus and uncus **29** Lateral view of valva **30** Phallus. (Scale lengths in parentheses).

coxa lustrous orange-white; femur to tarsi pale orange dorsally, lustrous orange-white. Hindleg with coxa to tarsi lustrous orange-white; femur narrowly tinged with pale orange dorsally; tibia spinose dorsally, with hair-tufts ventrally. Forewing length 2.8–4.4 mm (n = 70), reddish brown; longitudinal fascia, white from base to the middle of forewing, often connected with white dorsal bar; costal fascia at distal 1/3 of costa, white, terminal 1/3 curved to apex, accompanying a row of dark brown scales caudad; subapical spot orange-white; tornal patch white, semicircular, borders blurred; elongate scales on apex, terminal 1/3 of costa, termen, with dark brown tips; fringe orange-white. Hindwing and fringe lustrous pale gray.

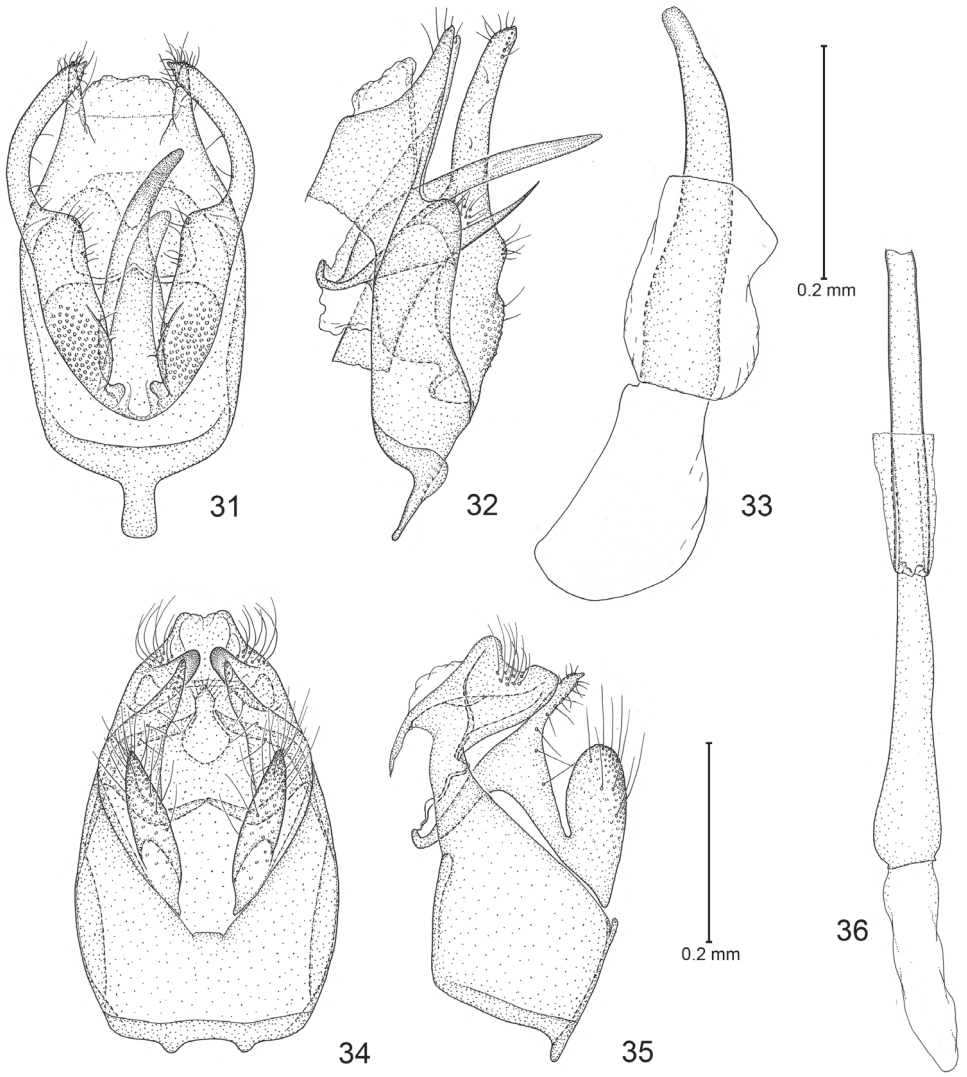
Abdomen: Terga lustrous, yellowish gray; sterna lustrous orange-white. Male tergum VIII trapezoidal; male sternum VIII subrectangular, broadly emarginated posteriorly, with oblique furrow laterally and short, stiff coremata posterolaterally.

Male genitalia (Figs 34–36): Tegumen trapezoidal, with subrectangular protrusion apically, strongly sclerotized, digitate process laterally, and short, lanceolate sclerite at center; long setae above teguminal process; tuba analis arising from dorsal area of apical protrusion. Valva deeply divided into two portions; costal portion triangular on basal half, elongate on distal half, sparsely setose, apex protruding; saccular portion elliptical, more densely setose to apex. Anellus extending to middle of phallus. Vinculum broadly sclerotized, capsulate, with a pair of small protrusions on distal margin. Phallus of even width except slightly-swollen at basal 1/6, slightly bifid apically.

Female genitalia (Figs 59–60): Apophyses posteriores 2× longer than apophyses anteriores. Elongate scales on posteroventral margin of A8. Lamella antevaginalis short, cylindrical, with ridge posterolaterally. Ductus bursae as long as corpus bursae, narrow on anterior 1/2; inception of ductus seminalis at middle of ductus bursae, bulged, with a sclerotized ring. Corpus bursae obovate.

Types. Lectotype (designated here): male, "48" [hand-written], "Type No. 522 U.S.N.M." [red label], "*Philonome clemmensella* [sic] K[entuck]y. 5961Lis1 Cham[bers]" [hand-written], USNM. Paralectotypes: **USA**: Kentucky: 4♀, 3 ex., June 14 [no year] (Chambers), Type no. 1311, MCZ.

Material examined. Canada: Ontario: Ottawa-Careton, Dunrobin: 1♀, 9 July 2007, CNCLEP00035968; 28 July, 2007, CNCLEP00038457, (L Scott). Quebec: 2♂, 21 July 2004, CNCLEP00006545, (JF Landry), CNC. **USA:** Alabama: Monroe Co.: Haines Island Park (31°43'23"N, 87°28'10"W): 2♂, 2♀, 26–27 May 1995 (R Brown, J MacGown & D Pollock), MSU. District of Columbia: Unspecified locality: 1♂, no date (Fernald); 1♂, 28 June 1885 (Fernald), "on oak"; 1♀, 21 June 1886 (Fernald); 1♂, 11 July 1896, "Hickory"; 3♀, 2–4 June 1897, "from Linden"; 1♀, September 1953, USNM. Florida: Pinellas Co.: Dunedin: Hammock Park: 1♂, 22 April 1987 (LC Dow), [GSN] USNM 96414, USNM. Kentucky: No specified locality: 1♂, no date & collector, USNM. Illinois: Macon Co.: Decatur: 1♂, 8–15 June [no year], USNM. Putnam Co.: 1♀, 30 June 1976 (MO Glenn), USNM. Maryland: Montgomery Co.: Takoma Park: 1♂, 1♀, 8 July 1986 (WE Steiner); 1♂, 7 July 1986, USNM. Wicomico Co.: 1km SW Sharptown at Plum Creek: 1♀, 12 July 1986 (JM Hill et al.), USNM. Massachusetts: Dukes Co.: Martha's Vineyard: 1♂, 13 July [no



Figures 31–36. *Philonome*, male genitalia. **31**–**33** *P. nigrescens* **31** Ventral view of genital capsule **32** Lateral view **33** Phallus **34**–**36** *P. clemensella*. **34** Ventral view of genital capsule **35** Lateral view **36** Phallus.

year] (FM Jones); 1 ex., 29 July [no year], all USNM. New Jersey: Burlington Co.: Medford: Lake Pine: 1♂, 13 July 1974 (DC Rentz), USNM. Essex Co.: Caldwell: 3♂, 2♀, 8 July 1900 (WD Kearfott), USNM. Essex County Park: 1♀, 20 May [no year] (WD Kearfott); 1♂, 7 July [no year], GSN: USNM 29977; 1♂, 12 July 1901; 1♂, 15 July [no year], USNM. Montclair: 1♀, 10 July [no year] (WD Kearfott), USNM; 1♂, 18 July [no year] (WD Kearfott), USNM. New York: Tompkins Co.: Ithaca: Six Mile Creek: 1♀, 23 July 1960 (RW Hodges), USNM. Unspecified locality: 1♀, "4971/ WLSM. 1906" (Beutenmueller), USNM. North Carolina: Craven Co.: Cherrypoint:

1♀, 3 July 1961 (SS Nicolay); 1♀, 12 July 1961; 1♀, 21 July 1961, all USNM. Harnett Co.: Spout Springs: 1♂, 25 August 1984 (WE Steiner et al.), USNM. Ohio: Hamilton Co.: Cincinnati, 1 ex., 23 June 1906 (A Braun); 1♂, 1♀, 27–28 June 1906, [GSN] USNM 16405 (♂); 1♀, 24 July 1907; 1♂, 3 August 1907; 1♂, 16 June 1908, all USNM. PENNSYLVANIA: Adams Co.: Arendtsville: 5♂, 6 July 1921 (SW Frost), USNM, GSN: USNM 29575. Allegheny Co.: Oak Station: 1♂, 6 July 1907 (F Marloff); 1♂, 11 July 1907, all USNM. Beaver Co.: New Brighton: 2♂, 11 July 1907 (Merrick Museum); 1♂, 23 July 1907; 1♂, 2♀, 26 July 1907, [GSN] USNM 34213 (♀), USNM. South Carolina: Charleston Co.: McClellanville: Wedge Plantation: 1♀, 11 May 1981 (RW Hodges), USNM, GSN: USNM 34212. Tennessee: Cocke Co.: Great Smoky Mt. National Park: Foothills Parkway (35°48'59"N, 83°13'11"W): 3♂, 1♀, 9 June 2002 (RL Brown & SM Lee), MSU. Texas: Harris Co.: 1♂, 20 May 1984 (Bellaire), [GSN] USNM 96415; 1♂, 2 April 1986, all USNM. Virginia: Fairfax Co.: 1km E Fairfax City: 1♂, 9 July 2005 (J Brown), USNM. Unspecified locality: 1♀, 27 June 1886, USNM. West Virginia: Morgan Co.: Sleepy Creek Forest: 2♂, 1 July 2010 (J Glaser); 1♂, 16 July 2011; 1♂, 19 July 2011; 1♂, 21 July 2011, USNM.

Distribution. Eastern Canada and the United States west to Texas.

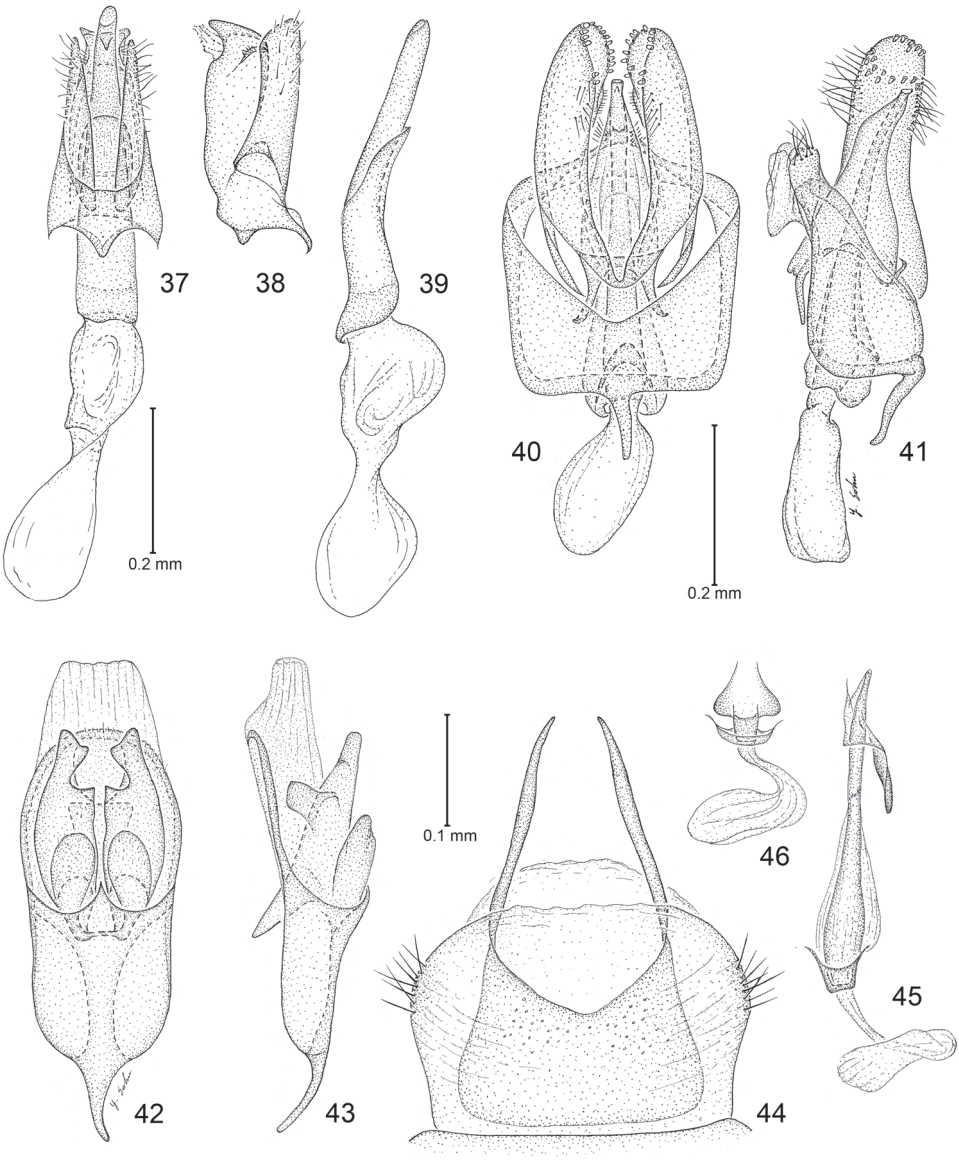
Host plants. Hickory (Juglandaceae: *Carya*) and linden (Tiliaceae: possibly *Tilia americana* L.) (Forbes 1923). These are from the label data in the USNM collection. The collection also includes a specimen whose label data states that it came from oak (Fagaceae: *Quercus*). The label data give no details other than plant common names. Therefore, it is not clear if these records refer to larval host plants or where the adults were collected.

***Philonome lambdagrapha* Sohn, Davis & Lopez-Vaamonde, sp. n.**
http://zoobank.org/E4E1964A-D664-4342-B555-DBC16C934821
Figs 6, 37–39

Diagnosis. This species is similar to *Philonome curvilineata* in external appearance but differs from the latter in having the longitudinal and costal fasciae separate (continuous in *P. curvilineata* and larger apical protrusion on the tegumen in the male genitalia.

Adult (Fig. 6). *Head*: Vertex orange on posterior 2/3, pale orange on anterior 1/3; scales on dorsum of occiput dark grayish brown; scales between antennal scapes lustrous pale orange; frons lustrous pale yellow. Antenna 4/5 as long as forewing; scape as long as diameter of eye, lustrous orange dorsally, lustrous pale yellowish gray laterally and ventrally, lustrous pale grayish brown apically; flagellomeres pale orange dorsally, lustrous pale yellow ventrally. Labial palpus 1/2 as long as antennal scape, lustrous pale yellowish gray.

Thorax: Patagium dark brown; tegula lustrous pale yellow, intermixed with orange scales basally; mesonotum silvery white with dark brown transverse band along anterior and posterior margins and at anterior 1/3, with orange transverse band at middle. Foreleg with coxa lustrous pale yellow; femur lustrous pale yellow, intermixed with pale gray-



Figures 37–46. *Philonome*, male genitalia. **37**–**39** *P. lambdagrapha* **37** Ventral view of genital capsule and phallus **38** Lateral view **39** Phallus **40**–**41** *P. curvilineata*. **40** Ventral view of genital capsule and phallus **41** Lateral view **42**–**46** *P. euryarga* **42** Ventral view of genital capsule **43** Ventral view **44** abdominal tergum VIII (caudal end directed upward) **45** Lateral view of phallus **46** Anterior base of phallus, ventral view.

ish brown laterally; tibia dark brown dorsally, pale grayish yellow ventrally; tarsomeres dark brown dorsally, pale orange ventrally. Midleg with coxa and femur lustrous pale yellow; tibia and tarsomeres grayish brown dorsally, pale yellow ventrally. Hindleg consumed for DNA extraction. Forewing length 3.0 mm (n = 1), reddish brown; costa black

in distal 1/3; longitudinal fascia extending to apical streak, straight, white on basal 1/2, juxtaposed with a slender, intermittent black line along lower border, sinuous, black on distal 1/2; costal fasciae slender, extending to apex; subapical streak white, juxtaposed with slender black line along lower border; apical streak white, connected with longitudinal fascia; dorsal bar white, juxtaposed with black along outer border; dorsal margin sparsely irrorated with black scales on basal 1/6 and at middle; tornal patch elongate, white, juxtaposed with black along upper border, irrorated with dark brown scales along outer border; marginal streak dark brown; fringe brown on distal 1/3 of costa, pale yellowish gray along termen. Hindwing brownish gray; fringe pale grayish brown.

Abdomen: Male tergum VIII and sternum VIII subquadrate; coremata piliform, as long as tergum VIII.

Male genitalia (Figs 37–39): Tegumen nearly as long as valva, semi-elliptical on basal 3/4, rectangular on distal 1/4, with small lateral protrusion dorsoposteriorly. Valva elongate, lobate, sparsely setose on outer surface. Juxta liguiform, 1/2 as long as valva. Vinculum broad, gradually broadened anteriorly, with medial and lateral protrusions along anterior margin; Phallus slightly curved at basal 2/5, broadened posteriorly.

Female unknown.

Type. Holotype: male, "ID#: CLV102310 [red letters] French Guiana: [Régina, Nouragues Research Station] [Lt:4.1 Ln:52/] Carlos Lopez Vaamonde 23-Jan-2010 DNA Barcode LNOUA928-10 [green letters in blue row]", "Nou68", "Genitalia slide DRD ♂ USNM 34621" [green label], USNM.

Distribution. French Guiana.

Etymology. The species name is derived from the Greek letter 'lambda' and a suffix derived from the Greek 'graphein' meaning "to write", and refers to the white fascia of the forewing resembling a lambda (λ).

***Philonome curvilineata* Sohn, Davis & Lopez-Vaamonde, sp. n.**
http://zoobank.org/992460F0-1A1B-4054-8818-2A32A56B77B6
Figs 7, 40–41

Diagnosis. This species is indistinguishable from *Philonome rivifera* Meyrick in external appearance but differs from the latter in having the apex of the valva in the male genitalia entire (*vs*. bifid in *P. rivifera*).

Adult (Fig. 7). *Head*: Scales of vertex orange on posterior 2/3, pale orange on anterior 1/3; scales on dorsum of occiput dark brown, orange on basal 1/4; scales between antennal scapes lustrous pale orange; frons very small, pale orange. Antenna 4/5 as long as forewing; scape as long as diameter of eye, pale orange, paler ventrad; flagellomeres pale orange dorsally, silvery white ventrally. Labial palpus 1/2 as long as antennal scape, lustrous pale orange.

Thorax: Scales of patagium orange with dark brown tips; tegula pale orange, intermixed with orange scales basally; mesonotum lustrous orange white, with pale orange transverse band along anterior and posterior margins and at middle. Foreleg with coxa

and femur lustrous pale orange; tibia orange, intermixed with dark brown scales dorsally, orange white ventrally; tarsomeres orange dorsally, pale orange ventrally; first tarsomere sparsely intermixed with dark brown scales dorsally. Midleg with coxa and femur lustrous pale orange; tibia brownish orange dorsally, lustrous orange white ventrally; tarsomeres pale orange dorsally, pale yellow ventrally. Hindleg consumed for DNA extraction. Forewing length 2.8 mm (n = 1), reddish brown, slightly paler along dorsal area; costal area yellowish brown on basal 1/2, brownish white above the curvature of longitudinal fascia, pale orange on distal 1/4, intermixed with black scales on middle and distal 1/4 of costa; longitudinal fascia continuous to near apex; convex at distal 1/3, white, juxtaposed with slender black line along lower border; dorsal bar straight, white, juxtaposed with slender, intermittent, black line along outer border; black irroration at middle of dorsal margin and on tornal area; fringe orange on distal costa and apex; scales of fringe along termen pale yellowish gray on basal 2/3, black on distal 1/3. Hindwing brownish gray; fringe pale grayish brown.

Abdomen: Male tergum VIII rectangular; male sternum VIII rectangular, broadly emarginated posteriorly.

Male genitalia (Figs 40–41): Tegumen rectangular, convex posteriorly, with sparsely setose, small bulge apically; tuba analis arising from dorsoposterior region of tegumen. Valva digitate, slightly enlarged on basal 1/2, flattened apically, with stout spiniform setae along edges of apical area and with piliform setae in inner surface of costal and saccular areas. Anellus conical, nearly as long as phallus. Vinculum broad, rectangular; saccus elongate, 1/4 as long as valva. Phallus slightly curved at distal 1/5, narrowing to apex, greatly broadened in basal 1/6.

Female unknown.

Type. Holotype: male, "ID#: CLV68110 [red letters] French Guiana: [Régina, Nouragues Research Station] [Lt:4.1 Ln:52/] Carlos Lopez Vaamonde 20-Jan-2010 DNA Barcode LNOUA586-10 [green letters in blue row]", "Nou37", "Genitalia slide DRD ♂ USNM 34620" [green label], USNM.

Distribution. French Guiana.

Etymology. The species name, an adjective, is derived from the Latin words 'curvus' and 'lineatus', together meaning "curved line" and refers to the curved longitudinal fascia on the forewing of this new species.

Philonome euryarga Meyrick, 1915

Figs 8, 42–46

Philonome euryarga Meyrick, 1915: 250.

Adult (Fig. 8). *Head*: Vertex reddish orange on posterior 2/3, pale orange on anterior 1/3; scales on interspace between antennal scapes yellowish white; frons lustrous, yellowish white; occipital area white. Antenna 3/5 as long as forewing; scape pale orange dorsally, pale yellowish gray; flagellomeres pale reddish orange dorsally, yellowish white

ventrally. Labial palpus as long as maxillary palpus, lustrous, pale yellowish gray, intermixed with dark brown scales apically. Maxillary palpus lustrous yellowish white.

Thorax: Patagium and tegulae white; mesonotum white in anterior 1/2, reddish brown in posterior 1/2, with a dark brown transverse band medially; mesoscutellum brownish gray. Foreleg lustrous yellowish white, with narrow brownish gray area dorsally. Midleg reddish orange dorsally, lustrous yellowish white ventrally. Hindleg pale orange dorsally, lustrous yellowish gray ventrally. Forewing length 2.7 mm (n=1), reddish brown; costa brown; longitudinal fascia white, spanning entire costal area except costa, lower margin sinuous, accompanied with narrow, dark brown line; dorsal bar white, at basal 1/3 of dorsum, dentiform, accompanied with dark brown bar along upper margin; marginal area dark brown; elongate scales of fringe pale reddish brown, with dark brown tips; hairy scales of fringe pale yellowish gray. Hindwing pale grayish orange; fringe yellowish gray.

Abdomen: Male tergum VIII sclerotized, subtrapezoidal, narrower caudally, emarginated posteriorly, with dense pores on posterior 1/3 and long process posterolaterally; male sternum VIII subrectangular, with short coremata posterolaterally.

Male genitalia (Figs 42–46): Tegumen round posteriorly, nearly parallel laterally, with an oval opening posteromedially; tuba analis as broad as vinculum. Valva divided into two portions; costal portion as long as tegumen, broad at basal 1/3, narrowed to cucullus, with a rectangular projection and a triangular projection at distal 2/5 of dorsal and ventral area respectively; cucullus digitate, with shallow bulge basally; saccular portion 1/2 as long as costal portion, obovate. Anellus extending to basal 5/8 of phallus. Vinculum elongate, subrectangular, as long as costal portion of valva, with T-shaped sclerotization medially; saccus 2/3 as long as vinculum, narrowed to apex. Phallus straight, broadened on basal 1/3.

Female genitalia not examined.

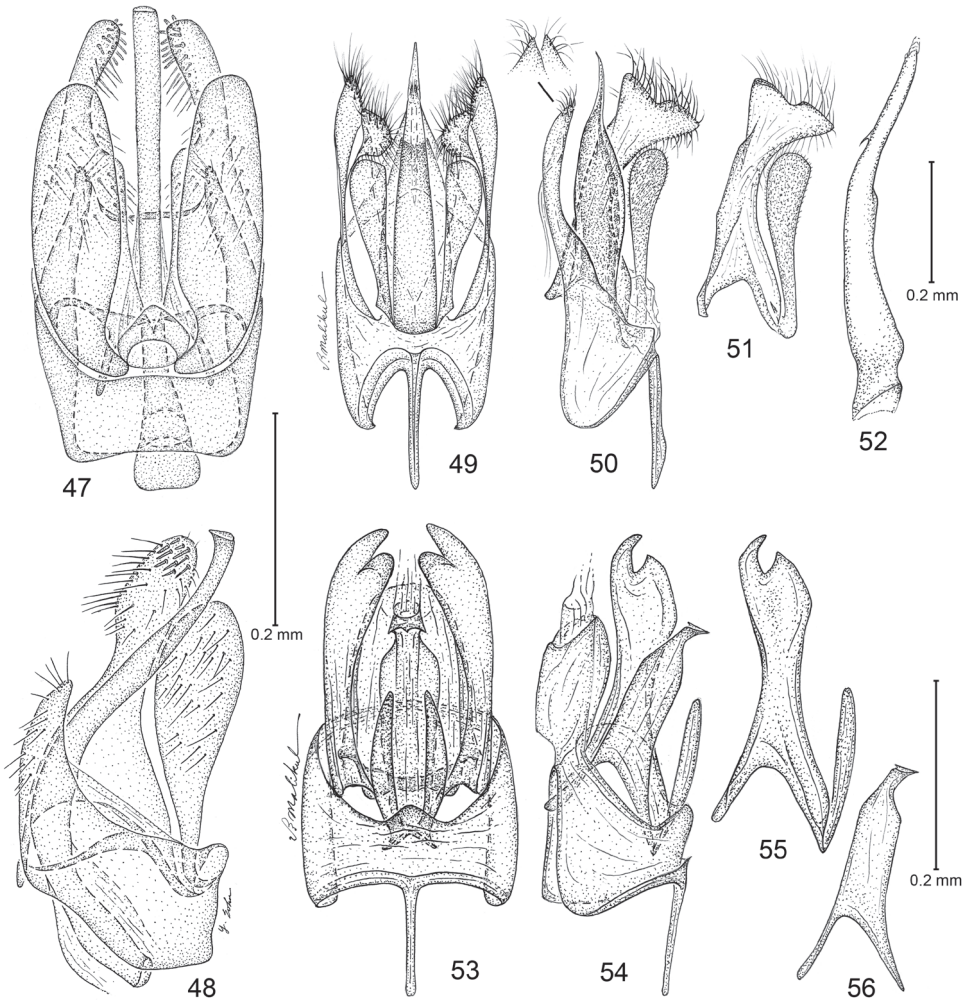
Type. Holotype: female, "Holo-type" [round label with red borders], "Bartica, Brit[ish] Guiana. Parish. 2.13", "*euryarga* Meyr." [hand-written], "*Philonome euryarga* 1/1 Meyr[ick] E. Meyrick det. in Meyrick Coll.", BMNH.

Material examined. French Guiana: Régina: Nouragues Research Station (Lt: 4.1, Ln: 52): 1♂, 19 January 2010 (C. Lopez-Vaamonde), DNA Barcode LNOUA669-10, ID#: CLV76410, [GSN] USNM 34622, USNM.

Distribution. Guyana and French Guiana.

***Philonome albivittata* Sohn, Davis & Lopez-Vaamonde, sp. n.**
http://zoobank.org/EC0040A3-49DF-48BF-AB11-B03C618B363B
Figs 9, 47–48

Diagnosis. This species is similar to another congener, *P. euryarga* Meyrick in overall external appearance, but differs from the latter in having darker hindwings. Their male genitalia possess several distinct differences including the tegumen with lateral projections in *P. albivittata*; the saccus present only in *P. euryarga*; and in the form of the costal portion of valva (Figs 41 *vs*. 46).



Figures 47–56. *Philonome*, male genitalia. **47**–**48** *P. albivittata* **47** Ventral view of genital capsule and phallus **48** Lateral view **49**–**52** *P. penerivifera* **49** Ventral view of genital capsule and phallus **50** Lateral view, with ventral detail of uncus **51** Lateral view of valva **52** Phallus **53–56** *P. rivifera*. **53** Ventral view of genital capsule and phallus **54** Lateral view **55** Lateral view of valva **56** Phallus.

Adult (Fig. 9). *Head*: Vertex orange, intermixed with pale orange scales anteriorly and posteriorly and with dark brown scales laterally; scales on dorsum of occiput dark brown, orange on basal 1/4; scales between antennal scapes lustrous pale orange. Frons silvery white, concave at center. Antenna 4/5 as long as forewing; scape as long as diameter of eye, orange dorsally, silvery white anterolaterally and ventrally, intermixed with grayish brown scales apically; flagellomeres pale orange dorsally, lustrous pale yellow ventrally; 1st and 2nd flagellomeres intermixed with grayish brown scales dorsoapically. Labial palpus 1/2 as long as antennal scape, lustrous pale yellow.

Thorax: Patagium lustrous pale yellow; tegula white, intermixed with pale orange scales basally; mesonotum white on anterior half, lustrous reddish brown on posterior half, with a dark brown transverse band medially. Foreleg with coxa lustrous pale yellow; femur lustrous dark grayish brown laterally, lustrous pale yellow mesally; tibia and tarsus dark brown dorsally, pale grayish yellow ventrally. Midleg with coxa lustrous pale yellow; femur lustrous pale orange dorsally, lustrous pale yellow laterally and ventrally; tibia pale orange, intermixed with dark brown scales dorsally; tarsomeres orange dorsally, pale orange ventrally. Hindleg with coxa and femur lustrous pale orange; tibia pale brownish orange dorsally, pale orange ventrally, with stiff piliform scales; tarsomeres pale orange. Forewing length 2.8–3.1 mm (n = 3); reddish brown; costa brown; longitudinal fascia white, spanning entire costal area except costa; lower margin sinuous, accompanied with narrow, dark brown line; dorsal bar white, at basal 1/3 of dorsum, dentiform, accompanied with dark brown bar along upper margin; marginal area dark brown; fringe brownish gray. Hindwing and fringe brownish gray.

Abdomen: Male tergum VIII rectangular; male sternum VIII subrectangular, with oblique furrow and short coremata laterally.

Male genitalia (Figs 47–48): Tegumen subtrapezoidal, with sparsely setose, digitate projection posterolaterally. Valva divided into two portions; costal portion 2× longer than tegumen, broad basally, narrowed to cucullus; cucullus spatulate, narrowly round apically, sparsely setose, with short, spiniform setae in apical 1/4; saccular portion 1.5× as long as tegumen, elongate, obovate, sparsely setose. Anellus funnel-shaped, broadened basally. Juxta with an ovate bulge and a ridge connected to anellus. Vinculum rectangular, slightly concave anteriorly. Phallus slender and of even diameter on posterior 4/5, enlarged subtriangularly around ductus ejaculatorius.

Female unknown.

Types. Holotype: male, "ID#: CLV10410 [red letters] French Guiana: [Régina, Nouragues Research Station] [Lt:4.1 Ln:52/] Carlos Lopez Vaamonde 16-Jan-2010 DNA Barcode LNOUA009 [sic: 946] -10 [green letters in blue row]", "Genitalia slide DRD ♂ USNM 34623" [green label], USNM. Paratype: **French Guiana:** Régina: Nouragues Research Station (Lt:4.1, Ln:52): 1♂, 20 January 2010 (C Lopez-Vaamonde), "ID#: CLV94410", "DNA Barcode LNOUA849-10", [GSN] 34625, USNM.

Distribution. French Guiana.

Etymology. The species name is derived from the Latin adjectives, 'albus' and 'vittatus', meaning "white" and "banded" respectively, and refers to the white longitudinal band on the forewing of this new species.

Philonome penerivifera **Sohn & Davis, sp. n.**

http://zoobank.org/48A07D44-E6AC-4D0B-AD2F-17863CB24E88
Figs 10, 49–52, 61–62

Diagnosis. This species is indistinguishable from *Philonome rivifera* in external appearance. Both species can be clearly distinguished from each other by the male genitalia (Table 2),

Table 2. Comparison of three similar species of *Philonome*, *P. curvilineata*, *P. penerivifera*, and *P. rivifera* in the male genitalia.

Characters	*curvilineata*	*penerivifera*	*rivifera*
Apical area of valva	entire	emarginated	bifid
Short spiniform setae on cucullus	present	absent	absent
Saccular portion of valva	not separate	separate	separate
Lateral area of vinculum	subtruncate	strongly protruding	slightly protruding
Saccus	1/4 as long as valva	3/5 as long as valva	1/2 as long as valva

including distal margin of cucullus shallowly concave in *P. penerivifera* but deeply emarginated in *P. rivifera*; tegumen triangular in *P. penerivifera* but subrectangular in *P. rivifera*; and lateral area of vinculum less protruding in *P. penerivifera* than in *P. rivifera*.

Adult (Fig. 10). *Head*: Vertex brownish white or pale orange on posterior 2/3, pale yellowish white on anterior 1/3; scales on interspace between antennal scapes yellowish white; frons lustrous yellowish white; scales on occiput pale orange, with dark brown tips dorsally, pale yellowish white laterally. Antenna 3/5 as long as forewing; scape pale grayish orange dorsally, lustrous yellowish white ventrally; flagellomeres pale orange dorsally, yellowish white ventrally. Labial palpus 1/2 as long as maxillary palpus, dark grayish brown laterally, lustrous yellowish white mesally. Maxillary palpus yellowish white.

Thorax: Scales of patagium pale orange, with dark brown tips; tegula reddish brown basally, paler to apex, pale orange apically; mesonotum pale orange, transversely intermixed with dark brown scales at middle. Fore- and midlegs with coxa lustrous yellowish white; femur, tibia, and tarsomeres dark brown dorsally, lustrous yellowish white laterally and ventrally. Hindleg pale brownish gray dorsally, lustrous yellowish white laterally and ventrally. Forewing length 3.2–3.6 mm (n = 2), coloration and patterns similar to *P. rivifera*. Hindwing dark brownish gray; fringe brownish gray on costal and apical area, yellowish gray along posterior margin.

Abdomen: Terga pale grayish orange or pale grayish brown; sterna lustrous, white or pale orange.

Male genitalia (Figs 49–52): Tegumen triangular, with bifid, setose apex; tuba analis arising from dorsoposterior area of tegumen. Valva divided into two portions; costal portion broadened in basal 1/2, triangular in distal 1/3; distal margin of cucullus slightly emarginated medially, with dense long setae; saccular portion elongate, spatulate, densely setose. Anellus conical, nearly as long as phallus, with minute thorns on interior wall. Vinculum elongate-subrectangular, with semi-elliptical emargination anteromedially; saccus elongate, as long as uncus. Phallus slightly curved at distal 1/3, broadened anteriorly.

Female genitalia (Figs 62–62): Apophyses posteriores 2.5× longer than apophyses anteriores. Lamella antevaginalis conical, obliquely truncate apically, setose posterolaterally. Ductus bursae as long as corpus bursae, narrow; inception of ductus seminalis at posterior 1/4 of ductus bursae; ductus seminalis coiled. Corpus bursae obovate, with scattered microscopic thorns.

Types. Holotype: male, "Holo-Type" [circular label with red border], "Para Brazil Parish 6 -19.", "*Philonome rivifera* 7/17 Meyr. E. Meyrick det. in Meyrick Coll." [old

label attached before this study], "Meyrick Coll. B.M. 1988-290.", "B.M. ♂ Genitalia slide No. 32828". Paratypes (1♂, 4♀, 1 ex.): **Brazil:** Amazonas: Munaos [= Manaus], 2♀, "11.19" (Parish), BMNH. Tefé, 1 ex., "1.20" (Parish), BMNH. Federal District: Planaltina (15°35'S, 47°42'W, alt. 1000m): 1♀, 3 May 1984 (VO Becker), "BECKER 56394", VOB; 1♀, 15 June 1985, "BECKER 57636", [GSN] USNM 34615, USNM. Pará: Óbidos, 1♂, "9.19" (Parish), BMNH.

Distribution. Brazil (Amazonas, Federal District, Pará).

Etymology. The species name is derived from the Latin prefix 'pene (= paene)', meaning "almost", and the preexisting species name, *rivifera*, and refers to the overall similarity of this species to *Philonome rivifera*.

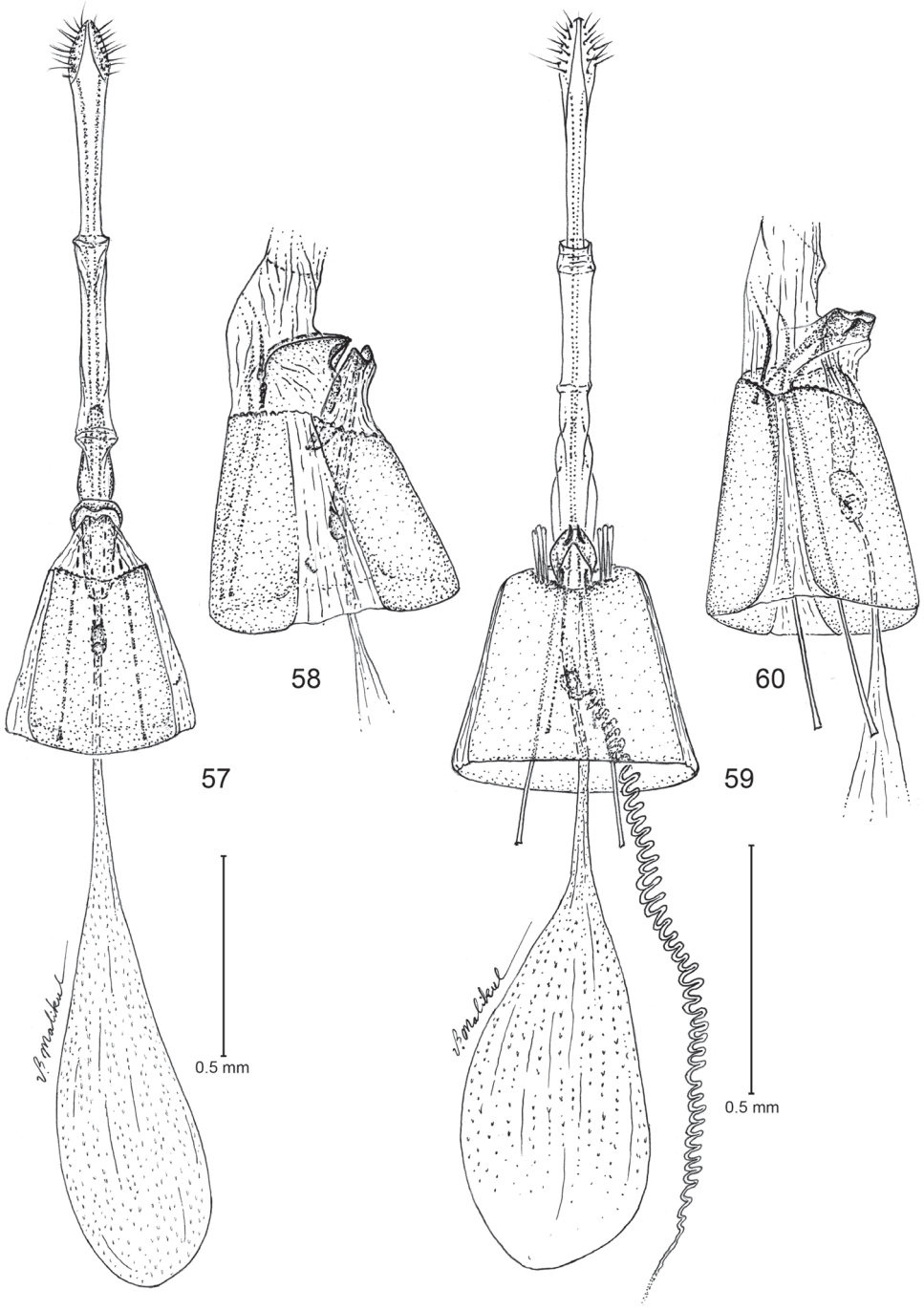
Remarks. The holotype and three paratypes of *Philonome penerivifera* in the BMNH collection were misidentified as *P. rivifera* by Edward Meyrick.

***Philonome kawakitai* Sohn, Davis & Lopez-Vaamonde, sp. n.**
http://zoobank.org/463A273D-CFFF-418E-8325-47B034B42A19
Figs 11, 63, 64

Diagnosis. The female genitalia of *P. kawakitai* is similar to those of *P. penerivifera* but differ from the latter in having the lamella antevaginalis of the seventh sternite more rounded (obliquely truncate posteriorly in *P. penerivifera*) and in the absence of microscopic spicules in the corpus bursae. *Philonome kawakitai* is distinguished from *P. curvilineata*, *P. penerivifera*, and *P. rivifera* in having the dorsal bar not reaching the dorsal margin and the complete subterminal line on the forewing.

Adult (Fig. 11). *Head*: Vertex pale brown, sparsely intermixed with dark brown scales posterolaterally, pale orange on anterior 1/3; frons lustrous pale grayish yellow. Antenna 8/9 as long as forewing; scape pale orange dorsally, lustrous yellowish white ventrally; first flagellomere dark brown dorsally, pale yellow ventrally; second to 9th flagellomeres pale orange dorsally, pale yellow ventrally; remaining flagellomeres pale grayish yellow. Labial palpus 1/2 as long as maxillary palpus, dark yellowish brown. Maxillary palpus dark yellowish brown.

Thorax: Scales of patagium pale orange, with dark brown tips; tegula pale brown on basal 1/3, pale orange on distal 2/3; mesonotum pale orange, sparsely intermixed with dark brown-tipped scales. Fore- and midlegs with coxa lustrous pale orange; femur, tibia, and tarsomeres dark brown mesally, lustrous yellowish white laterally. Hindleg with coxa pale orange; femur and tibia pale yellowish grayish dorsally, pale yellow ventrally; tarsomeres pale grayish yellow. Forewing length 3.8 mm (n = 2), reddish brown, paler along dorsal area; costal area pale orange, intermixed with dark brown scales densely on basal 1/3 and sparsely on distal 1/3; longitudinal fascia continuous to near termen, convex and narrowed at distal 1/3, white, juxtaposed with slender black line along lower border; dorsal bar as triangular patch on anterior half, combined to longitudinal fascia and as slender, intermittent, black line on posterior half; subterminal line connecting distal 1/8 of costa and tornus, dark brown, intermittent; fringe pale



Figures 57–60. *Philonome*, female genitalia. **57**–**58** *P. nigrescens* **57** Ventral view **58** Lateral view of segment 8 and sterigma **59**–**60** *P. clemensella* **59** Ventral view **60** Lateral view of segment 8 and sterigma.

brownish gray, with three dark brown, transverse lines. Hindwing dark brownish gray; fringe pale brownish gray.

Male unknown.

Female genitalia (Figs 63–64): Apophyses posteriores 2.2× longer than apophyses anteriores. Lamella antevaginalis conical and narrowly rounded caudally. Ductus bursae as long as corpus bursae, narrow; inception of ductus seminalis at posterior 1/8 of ductus bursae; ductus seminalis coiled in distal portion. Corpus bursae obovate, without signum or microscopic spicules.

Type. Holotype: female, "FRENCH GUIANA: Nouragues Nature Reserve Nouragues Research Station Sep[tember]-07-2010 collected by light trapping", "Genitalia slide DRD ♀ USNM 34652" [green label], USNM.

Distribution. French Guiana.

Etymology. The species name is a patronym in honor of Dr. Atsushi Kawakita who collected the holotype.

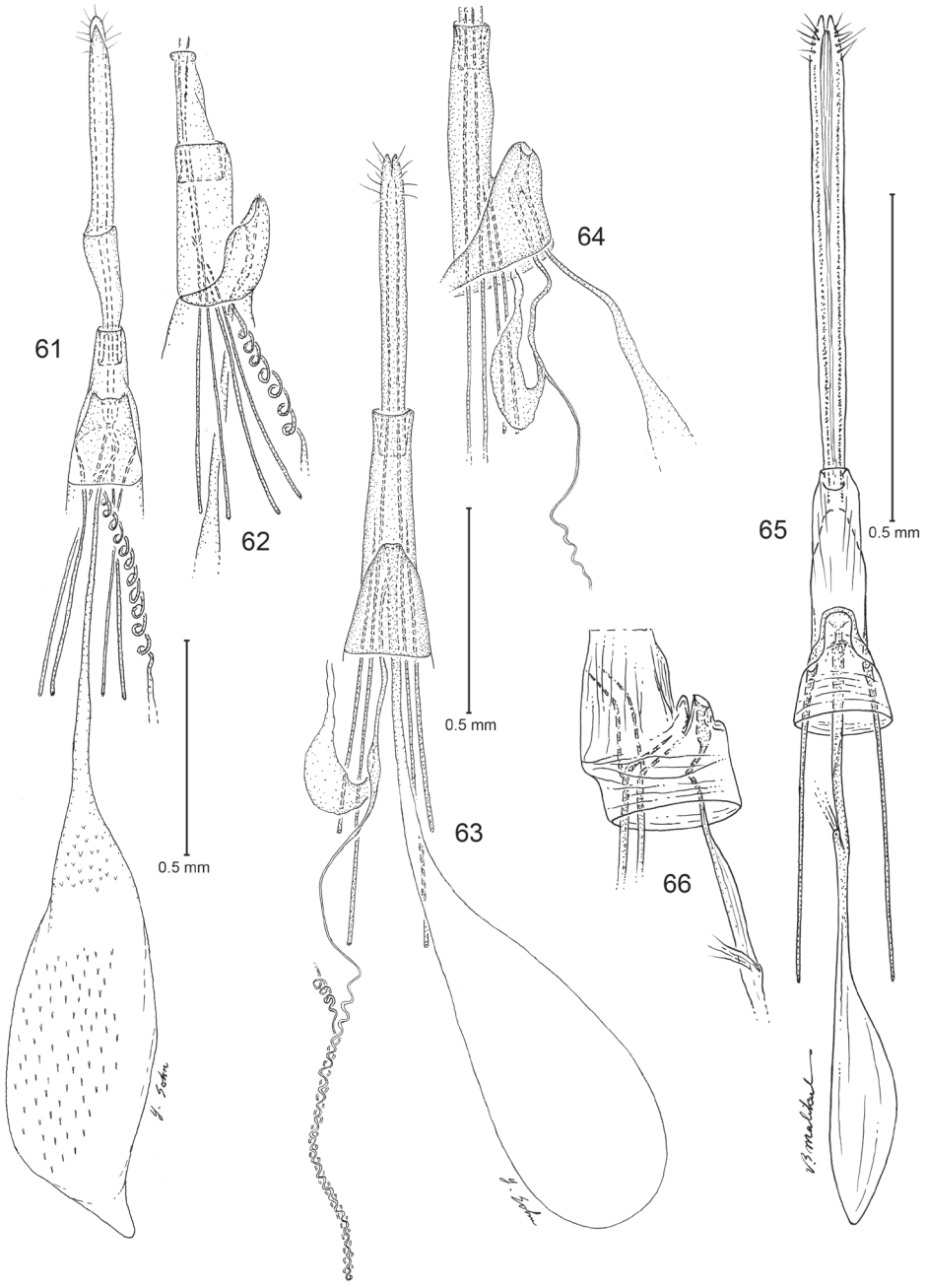
***Philonome rivifera* Meyrick, 1915**

Figs 12–13, 53–56, 65–66

Philonome rivifera Meyrick, 1915: 251.

Adult (Figs 12–13). *Head*: Vertex orange; frons lustrous pale orange, concave at center; scales on dorsum of occiput pale orange, dark purplish brown on apical 1/4; scales between antennal scapes, elongate, pale orange. Antenna 2/3 as long as forewing; scape as long as diameter of eye, lustrous pale orange, paler ventrad, narrowly suffused with orange dorsally; flagellomere I–VII pale reddish brown dorsally, lustrous pale orange ventrally; the remaining flagellomeres lustrous pale orange dorsally, paler ventrad. Labial palpus 3/4 as long as maxillary palpus, silvery white on interior surface, lustrous pale yellow on exterior surface, suffused with pale grayish orange apically. Maxillary palpus pale grayish brown.

Thorax: Patagium pale orange, tinged with dark brown distally; tegula lustrous pale yellow, intermixed with brown-tipped, orange scales basally; mesonotum pale orange, anterior 1/3 and posterior 1/3 lustrous pale yellow, with a narrow transverse band of dark brown-tipped scales. Fore- and midlegs with coxa lustrous pale yellow; femur pale orange dorsally, lustrous pale yellow laterally and ventrally; tibia and tarsomeres pale brown dorsally, pale orange ventrally. Hindleg with coxa and femur lustrous pale orange; tibia lustrous pale orange, with long piliform scales ventrally; tarsomeres orange dorsally, pale orange ventrally. Forewing length 2.8–4.6 mm (n = 3), reddish brown in medial area, orange in terminal 1/3 of costal area, pale orange in basal 2/3 of costal area and in basal 1/2 of dorsal area; longitudinal fascia white, continuing to subapical area, accompanied with a slender, dark brown line along lower margin, curved to costa at terminal 1/3; dorsal bar white, narrow, connected to white spreading on dorsum; distal area of costa, termen, and apical area densely irrorated with dark brown; elongate



Figures 61–66. *Philonome*, female genitalia. **61**–**62** *P. penerivifera* **61** Ventral view **62** Lateral view of segment 8 and sterigma **63**–**64** *P. kawakitai* **63** Ventral view **64** Lateral view **65**–**66** *P. rivifera* **65** Ventral view **66** Lateral view of segment 8 and sterigma.

scales of fringe pale grayish brown, with dark brown tip; piliform scales of fringe pale orange. Hindwing dark grayish brown; fringe purplish gray.

Abdomen: Terga grayish brown; sterna pale orange. Male tergum VIII rectangular; male sternum VIII subrectangular, broadly emarginated posteriorly; coremata absent.

Male genitalia (Figs 53–56): Tegumen 5/7 as long as valva, elliptical, convex anterolaterally, with round opening apically; tuba analis arising from apical opening. Valva divided into two portions; costal portion broadened in basal 1/3 and distal 1/3; cucullus divided into two projections apically, one falcate and the other small, triangulate; saccular portion narrow, digitate. Juxta trapezoidal. Vinculum wide, rectangular, convex posteromedially, with small protrusion laterally; saccus slender, as long as saccular portion of valva. Phallus of even width on basal 4/5, narrowed on distal 1/5, diverging into two projections basally.

Female genitalia (Figs 65–66): Papillae anales narrow, semi-elliptical; apophyses posteriores 1.2× longer than apophyses anteriores. Lamella postvaginalis quadrate. Lamella antevaginalis cylindrical. Ductus bursae narrow; inception of ductus seminalis present at middle of ductus bursae. Corpus bursae narrow, elliptical.

Types. Lectotype (designated here): male, "LECTO-TYPE" (round label with indigo boarders), "Bartica Brit[ish] Guiana Parish .2.13", "Meyrick Coll. B.M. 1938-290.", "*Philonome rivifera* 10/17 Meyr[ick] E. Meyrick det. in Meyrick Coll.", BMNH. Paralectotypes: **Guyana:** same data as lectotype: 1♂, 4♀, [GSN] BM 31892 (♂) & BM 32829 (♀), BMNH.

Distribution. Guyana.

Remarks. Meyrick (1915) described *Philonome rivifera*, based on eight specimens. Only six of those syntypes have been located in the BMNH. The specimen labels indicate that one of those was selected as the lectotype. This designation, however, has never been published, and the same specimen is designated here as the lectotype of *P. rivifera*.

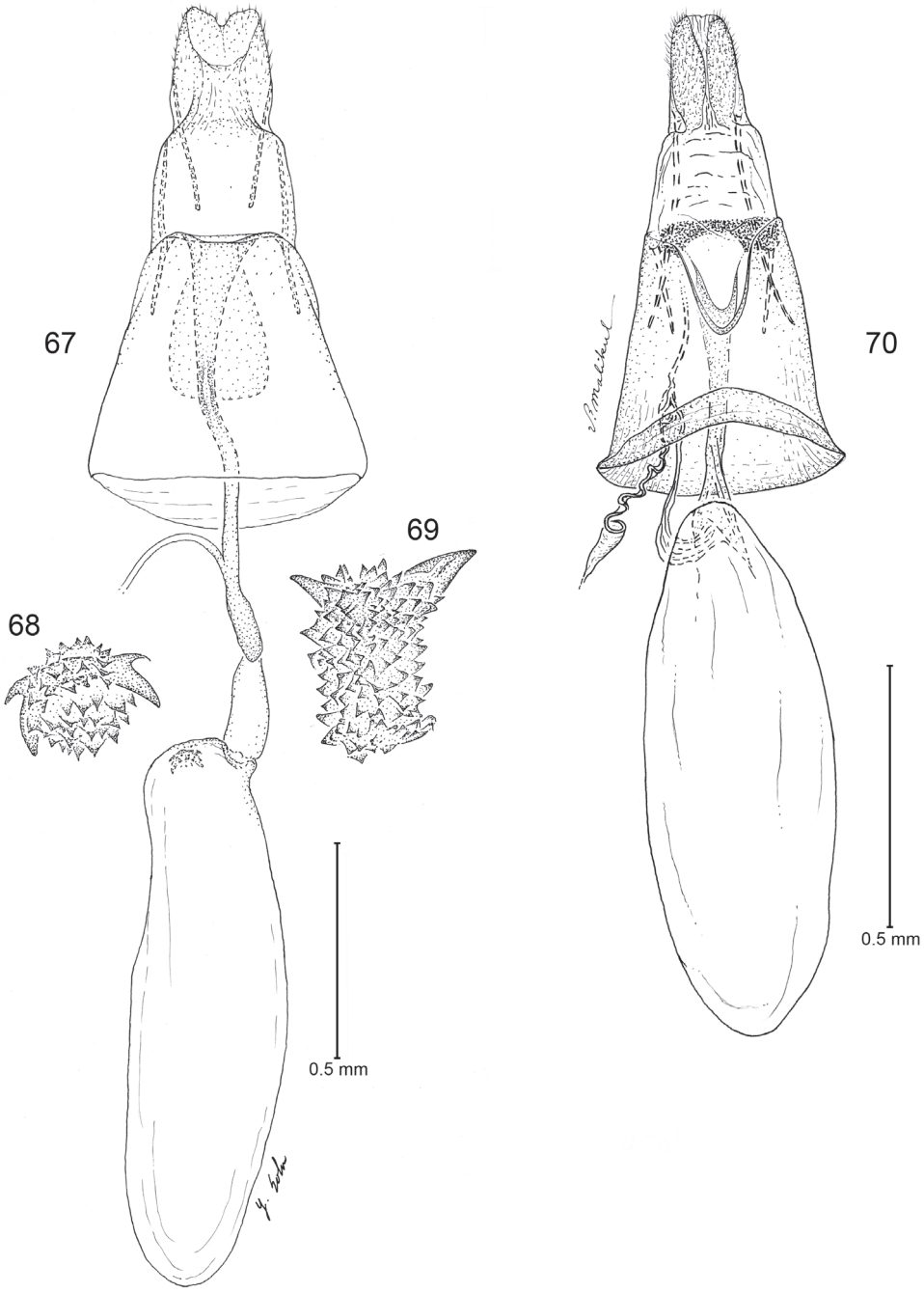
Philonome spectata **Meyrick, 1920**

Fig. 15

Philonome spectata Meyrick, 1920: 359; Davis 1984: 25.

Adult (Fig. 15). *Head*: Vertex reddish brown; frons pale orange. Antenna 3/4 as long as forewing; scape white, suffused with pale orange anterobasally; first five flagellomeres white; remaining flagellomeres pale grayish brown. Labial palpus and maxilary palpus pale orange.

Thorax: Patagium and mesonotum reddish brown; tegula white. Legs pale orange. Forewing length 2.3 mm (n = 1), reddish brown; longitudinal fascia white, covering most costal area, lower margin sinuous, accompanied with very narrow dark brown line; costa suffused with pale orange subbasally and in terminal 1/3; elongate scales of fringe around apex reddish brown with dark brown tips; piliform scales of fringe on



Figures 67–70. Female genitalia. **67**–**69** *Argyresthia luteella*. **67** Ventral view **68** Enlarged view of signum, ventral view **69** anterior view of Fig. 64 **70** *Elachista albella*, ventral view.

terminal 1/4 of costa and on tornal area yellowish brown with dark brown tips. Hindwing lustrous, yellowish gray, paler to base; fringe pale yellowish gray.

Abdomen: Terga and sterna lustrous white.

Female genitalia not examined.

Type. Holotype: female, "Holo-type" [round label with red borders], "Para Brazil Parish 7-19.", "Meyrick Coll. B.M. 1938-290.", "*Philonome spectata* 1/1 Meyr[ick] E. Meyrick det. in Meyrick Coll.", BMNH.

Distribution. Brazil (Pará).

Remarks. Only the holotype of *Philonome spectata* is known to exist. It was not possible to examine this specimen and to illustrate the genitalia. This species can be distinguished from other congeners in lacking the dorsal bar on the forewing.

***Philonome* sp.**

Fig. 14

Note. Forewing length 4.1 mm (n = 1). This species is indistinguishable from *P. rivifera* in superficial appearance. Our DNA-barcoding data show that it is distinct from other congeners from French Guiana and *P. clemensella,* and may be genetically closest to *P. kawakitai* (Fig. 71). The only specimen of this species has its abdomen missing. Its description is pending until additional specimens are found.

Material examined. French Guiana: Régina: Nouragues Research Station (Lt: 4.1, Ln: 52): 1♂, 24 January 2010 (C. Lopez-Vaamonde), DNA Barcode LNOUA958-10, ID#: CLV105310, USNM.

Distribution. French Guiana.

Revised status of *Philonome luteella* (Chambers)

Philonome luteella (Chambers) was originally the type species of *Eurynome* Chambers, 1875. The generic name was found to be preoccupied by *Eurynome* Leach, [1814] and was replaced with *Busckia* Dyar, 1903. McDunnough (1939) synonymized *Busckia* with *Philonome*. Our examination revealed that this species is actually a member of *Argyresthia* Hübner, [1825] (Argyresthiidae). Therefore, *Eurynome* Chambers, 1875 and its replacement name, *Busckia* Dyar, 1903, are here synonymized with *Argyresthia* Hübner, [1825].

***Argyresthia* Hübner, [1825]: 422.**

Type species. *Phalaena goedartella* Linnaeus, 1758, by subsequent designation by Busck (1907).

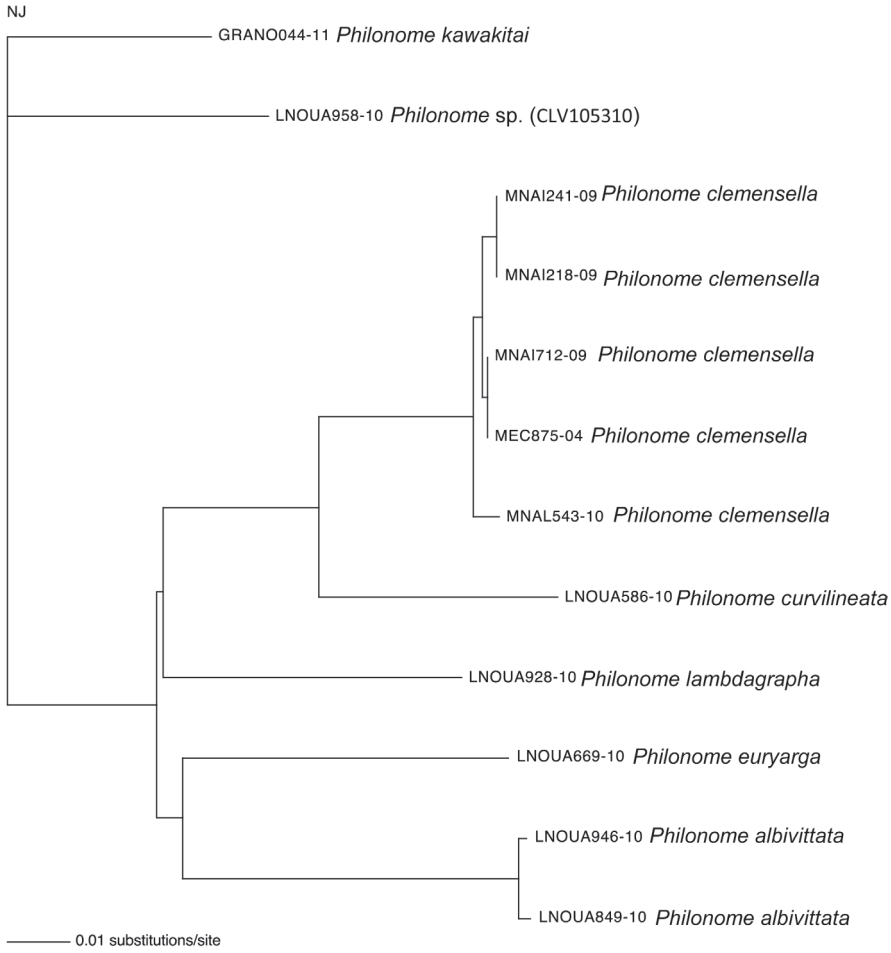


Figure 71. A Neighbor-Joining tree, generated under the K2P nucleotide substitution model, for the species of *Philonome*. Branch lengths represent the number of substitutions per site.

Eurynome Chambers, 1875: 304. A junior homonym of *Eurynome* Leach, [1814] [Crustacea]. **syn. n.** Type species: *Eurynome luteella* Chambers, 1875, by monotypy.

Busckia Dyar, 1903: 563. An objective replacement name of *Eurynome* Chambers, 1875. **syn. n.**

Argyresthia luteella (Chambers, 1875), comb. n.

Figs 16, 67–69

Eurynome luteella Chambers, 1875: 304.
Busckia luteella (Chambers): Dyar 1903: 563.
Philonome luteella (Chambers): McDunnough 1939: 100; Davis 1983: 8.

Adult (Fig. 16). Head missing from the holotype. Chambers (1875) stated that "head, eye caps and palpi white, the latter stained with yellowish".

Thorax: Patagium pale saffron yellow (Chambers 1875); mesonotum yellowish white, suffused with pale orange laterally and on posterior 1/3. Foreleg with coxa pale orange; other segments missing from holotype. Mid- and hindlegs with coxa, femur, and tibia pale orange dorsally, lustrous yellowish white ventrally; tarsomeres pale grayish brown dorsally, lustrous yellowish white ventrally. Forewing 3.4 mm (n = 1), lustrous yellowish white; basal and apical areas yellowish orange; antemedian, postmedian, and subterminal fasciae yellowish orange, oblique, indistinctly outlined; fringe yellowish orange on basal 1/3, purplish gray on distal 2/3. Hindwing lustrous yellowish white; fringe yellowish gray.

Male unknown.

Female genitalia (Figs 67–69): Papillae anales subrectangular, slightly protruding dorsolaterally. Apophyses posteriores nearly as long as apophyses anteriores including basal fork. Ostium bursae on posterior margin of sternite VIII. Ductus bursae as long as corpus bursae, funnel-shaped on posterior 2/5; antrum extending caudally over 1/3 of ductus bursae, cylindrical. Corpus bursae elongate, elliptical; signum at anterior area of corpus bursae, denticulate, with two diverging, large, spiniform sclerites posteriorly.

Type. Holotype: female, "Kentucky [sic] Chambers", "Type 14964" [red label], "*Eurynome luteella* Chambers" [hand-written on folded paper], "Genitalia slide MCZ-L122 Prep. by JC Sohn" [label with black border lines].

Distribution. Western United States (Colorado). Chambers (1875) stated "Spanish Bar", now Fall River in Larimer County, Colorado, as the collecting locality. On the label of the holotype of *P. luteella*, "Kentucky" was given as collecting locality with strikethrough mark indicating that the locality is not correct.

Remarks. The forewing pattern and the female genital morphology of *Eurynome luteella* suggest that it is not congeneric with *Philonome*. Its forewing pattern is similar to some species of *Argyresthia*, especially *A. cupressella* Walsingham, 1891, and *A. freyella* Walsingham, 1891. The female genitalia of *E. luteella* include a denticulate signum of which the shape is typical for *Argyresthia*. This species, consequently, has been reassigned to *Argyresthia*.

Discussion

Systematic position

Philonome has been associated frequently with *Bucculatrix*, since Chambers (1875). Both genera were placed in Lyonetiidae (Meyrick 1915, 1920; Barnes and McDunnough 1917; Forbes 1923). *Philonome* was retained within Lyonetiidae in recent checklists (e.g. Davis 1983; Poole and Gentili 1996), while *Bucculatrix* now constitutes its own family, Bucculatricidae (Davis and Robinson 1998). Heppner (1984, 2011) assigned *Philonome* to Bedelliinae (now Bedelliidae) without explanation. Recently,

Sohn et al. (2013) included *Philonome clemensella* as an outgroup in their phylogenetic analyses for Yponomeutoidea and they proposed that the genus belongs to Tineoidea (Fig. 1). In their resulting tree, *Philonome* was nested strongly within a monophyletic Tineidae *sensu* Regier et al. (2015). Several interrelationships of the genera included in the clade were unresolved from the study, but *Philonome* was further nested within a subclade of Tineidae (Fig. 1: A) that also included *Tinea* Linnaeus, 1758, *Perissomastix* Warren & Rothschild, 1905, *Nemapogon* Schrank, 1802, *Euprora* Busck, 1906, *Erechthias* Meyrick, 1880, *Scardiella* Robinson, 1986, *Harmaclona* Busck, 1914, and *Opogona* Zeller, 1853. The interrelationships of these genera were largely unresolved. In the best Maximum Likelihood tree constructed by Sohn et al. (2013), *Philonome* was grouped with a pair, *Tinea columbariella* Wocke, 1877 and *Perissomastix* sp., but this grouping was very weakly supported. Consequently, Sohn et al. (2013) identified *Philonome clemensella* as an unstable or rogue taxon.

Despite the strong support from molecular data, the tineid association of *Philonome* has never been addressed with morphological studies. Among the morphological characters associating *Philonome* with Tineidae are the reduced, naked haustellum with unassociated galeae, 5-segmented maxillary palpi, and vein Rs_4 terminating on costa before the forewing apex. It now appears that *Philonome* is most allied to the tineid subfamily Hieroxestinae also on the basis of morphological similarities. These include the wedge-shaped head (lateral view), vestiture of head partially consisting of appressed, laminate scales, and elongate scape without pecten. Previous association of this genus with *Bucculatrix* and Lyonetiidae was most likely decided largely by the presence of the broadly scaled antennal scape which forms an eyecap, a feature absent or poorly developed in Tineidae but typical for the latter two families. Eleven genera and 289 species are now recognized globally within Hieroxestinae, with 180 species assigned to *Opogona* (Robinson 2009). Within this subfamily, *Philonome* appears most similar morphologically to *Oinophila* Stephens, 1848, a holarctic genus currently restricted to two species. In particular, the head vestiture of both genera share unusual specializations not observed in other Hieroxestinae. The adult heads of Hieroxestinae typically possess a smooth, broad scaled frons and occiput, and a rough vertex consisting of a tuft of erect, piliform scales. The heads of *Philonome* and *Oinophila* are unusual in having the piliform scales of the vertex divided by a narrow, transverse band of broad, flat scales extending between the bases of the antennae (Davis 1978; Robinson and Tuck 1997). *Philonome* and *Oinophila* also possess similar wing venation, with the R vein lacking in the forewing and Rs with 4 branches. The heads of both genera possess a relatively raised vertex, and the rudimentary mandibles are better developed than in other genera of the subfamily. The antennal scape of *Oinophila* differs from that of *Philonome* in being more slender, smoothly scaled, and not formed into an eyecap. The female genitalia of *Philonome* differ from other known Hieroxestinae by lacking a signum in the corpus bursae.

Despite some possible synapomorphies between *Philonome* and the Hieroxestinae, we find them insufficient for a final taxonomic placement, and therefore leave the genus unplaced in Tineidae.

Table 3. Kimura 2-parameter (K2P) distances (%) for barcode DNA sequences of the seven analyzed species in genus *Philonome*. Minimal pairwise distances between species are given for each species pair. Values in square brackets represent maximal intraspecific distances.

	clemensella	***curvilineata***	***euryarga***	***albivittata***	***lambdagrapha***	**sp.**	***kawakitai***
clemensella	[0.9]						
curvilineata	6.9						
euryarga	11.5	13.3					
albivittata	12	13.2	11.7	[0.3]			
lambdagrapha	10.7	12.4	11.7	11.2			
sp.	13	14.1	13.9	14.1	12.1		
kawakitai	12.2	12.4	11.4	12.8	12.1	7.9	

DNA barcoding

Figure 71 shows a neighbor joining tree based on the DNA barcode sequences for 12 individuals of *Philonome* available at BOLD systems (www.barcodinglife.org). The resulting tree and the distance matrix (Table 3) indicate the presence of seven unique taxonomic units which can be assigned to the separate Barcode Index Numbers (BINs: Ratnasingham and Hebert 2013). These include two previously known species of *Philonome*; *P. clemensella* (five individuals) and *P. euryarga* (one individual); four species described in this paper, *P. albivittata*, *P. curvilineata*, *P. kawakitai*, and *P. lambdagrapha* (all except *P. albivittata* based on singleton); and one species (Fig. 14: CLV105310) from French Guiana which cannot be named due to the loss of the abdomen.

DNA barcodes of the seven species analysed are very distinctive (Fig. 71, Table 1). Indeed, DNA barcodes show high levels of interspecific genetic distance (Table 3). All species analysed show distinct DNA barcodes with a minimum interspecific pairwise genetic distance of 6.9% among all species. The maximum intraspecific genetic variation ranged from 0.9 to 0.3, much lower than interspecific distances, suggesting the existence of a barcode gap although current intraspecific sampling is too limited.

Acknowledgements

We would like to thank Kevin Tuck (retired) and Geoff Martin, both from the Natural History Museum, London, for allowing the first author to examine the museum collection under their responsibility. We are also grateful to David Adamski (Systematic Entomology Lab, US Department of Agriculture, Beltsville, Maryland) for checking some type specimens of *Philonome* and Atsushi Kawakita for donating one specimen for analysis. We are indebted to Young Sohn, Vichai Malikul, Donald Harvey, and Karolyn Darrow of the Department of Entomology, Smithsonian Institution, for their assistance preparing the illustrations, graphics, and plates used in this publication. We also thank colleagues at the Biodiversity Institute of Ontario, University of Guelph, Ontario, Canada for their assistance in the production of DNA barcodes.

Jean-François Landry of the Department of Entomology, Agriculture and Agri-Food Canada/Agriculture, Ottawa, kindly provided specimen data and allowed us to use four unpublished barcodes of *P. clemensella*. We would like to thank the editor Erik van Nieukerken and two anonymous reviewers for their valuable comments on our manuscript. Field work in French Guiana was funded by the CNRS program 'Amazonie', Nouragues research grants 2009 and 2010 to C.L.V. Funding for DNA barcoding was provided by the government of Canada through Genome Canada and the Ontario Genomics Institute in support of the International Barcode of Life project, and by NSERC. The first author especially appreciates the financial support from the Peter Buck Postdoctoral Fellowship (2013–2015), Smithsonian Institution.

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ZooKeys 494: 107–132 (2015)
doi: 10.3897/zookeys.494.8903
http://zookeys.pensoft.net

RESEARCH ARTICLE

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Three new species of woodlizards (Hoplocercinae, *Enyalioides*) from northwestern South America

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Academic editor: *J. Penner* | Received 6 November 2014 | Accepted 16 March 2015 | Published 6 April 2015

http://zoobank.org/90EEB2DA-E091-4545-BAF0-512E0BBBBBEA

Citation: Torres-Carvajal O, Venegas PJ, de Queiroz K (2015) Three new species of woodlizards (Hoplocercinae, *Enyalioides*) from northwestern South America. ZooKeys 494: 107–132. doi: 10.3897/zookeys.494.8903

Abstract

The discovery of three new species of *Enyalioides* from the tropical Andes in Ecuador and northern Peru is reported. *Enyalioides altotambo* **sp. n.** occurs in northwestern Ecuador and differs from other species of *Enyalioides* in having dorsal scales that are both smooth and homogeneous in size, a brown iris, and in lacking enlarged, circular and keeled scales on the flanks. *Enyalioides anisolepis* **sp. n.** occurs on the Amazonian slopes of the Andes in southern Ecuador and northern Peru and can be distinguished from other species of *Enyalioides* by its scattered, projecting large scales on the dorsum, flanks, and hind limbs, as well as a well-developed vertebral crest, with the vertebrals on the neck at least three times higher than those between the hind limbs. *Enyalioides sophiarothschildae* **sp. n.** is from the Amazonian slopes of the Cordillera Central in northeastern Peru; it differs from other species of *Enyalioides* in having caudal scales that are relatively homogeneous in size on each caudal segment, a white gular region with a black medial patch and several turquoise scales in males, as well as immaculate white labials and chin. A molecular phylogenetic tree of 18 species of hoplocercines is presented, including the three species described in this paper and *E. cofanorum*, as well as an updated identification key for species of Hoplocercinae.

Resumen

Reportamos el descubrimiento de tres especies nuevas de *Enyalioides* de los Andes tropicales en Ecuador y norte de Perú. *Enyalioides altotambo* **sp. n.**, del noroccidente de Ecuador, difiere de otras especies de *Enyalioides* por poseer escamas dorsales lisas y homogéneas en tamaño, iris café y por carecer de escamas circulares grandes y quilladas en los flancos. *Enyalioides anisolepis* **sp. n.** ocurre en las estribaciones amazónicas de los Andes al sur de Ecuador y norte de Perú, y se distingue de otras especies de *Enyalioides* por poseer escamas grandes y proyectadas dispersas en el dorso, flancos y extremidades posteriores, así como por su cresta vertebral bastante desarrollada, que a nivel del cuello es tres veces más alta que entre las extremidades posteriores. *Enyalioides sophiarothschildae* **sp. n.**, de las estribaciones amazónicas de la Cordillera Central al norte del Perú, difiere de otras especies de *Enyalioides* por poseer escamas caudales de tamaño similar en cada segmento caudal, una región gular blanca con una mancha medial negra y escamas turquesa en machos, así como la quijada y labiales de color blanco. También presentamos un árbol filogenético molecular de 18 especies de hoplocercinos, que incluye a las tres especies descritas en este artículo y a *E. cofanorum*, así como una clave de identificación actualizada para las especies de Hoplocercinae.

Keywords

Andes, Ecuador, *Enyalioides*, Hoplocercinae, Iguania, lizards, new species, Peru, systematics

Introduction

The iguanian lizard clade *Hoplocercinae* includes 16 currently recognized species assigned to *Enyalioides*, *Hoplocercus*, and *Morunasaurus* distributed from Panama to central Brazil (Torres-Carvajal et al. 2011). Woodlizards (*Enyalioides*) occupy lowland tropical rainforests including the Chocó and the western Amazon basin, with nine species (75%) occuring east of the Andes and three (25%) occuring west of the Andes.

With nearly 40% of the total number of species described in the last seven years from Ecuador and Peru (Torres-Carvajal et al. 2008; Torres-Carvajal et al. 2009; Venegas et al. 2011; Venegas et al. 2013), woodlizards represent one of the South American lizard groups with the highest species discovery rate (corrected for clade size) in the last decade. This is a striking fact given that woodlizards are among the largest and most colorful lizards in South American tropical forests and is most likely the result of recent fieldwork in poorly explored areas of the central and northern Andes. Here we contribute to this growing body of taxonomic knowledge with the description of three new species of *Enyalioides*, one from the Pacific slopes of the Andes in northern Ecuador, and the other two from the Amazonian slopes of the Andes in southern Ecuador and northern Peru.

Materials and methods

Snout-vent length (SVL) and tail length (TL) measurements were made with a ruler and recorded to the nearest millimeter. All other measurements (i.e., head width, length and height; rostral and mental width and height) were made with digital cali-

pers and recorded to the nearest 0.1 mm. Sex was determined by noting the presence of hemipenes or sexually dichromatic characters. The format of Torres-Carvajal et al. (2011) is followed for the descriptions of the new species, as well as the terminology of these authors for scutellational characters and measurements. Specimens of other species of *Enyalioides* examined in this study are listed in the Appendix. The distribution map was constructed in ArcMap 9.3 (ESRI, Inc.); WGS84 is the datum for all coordinates presented below. Institutional abbreviations correspond to Museo de Zoología, Pontificia Universidad Católica del Ecuador (QCAZ), Quito; Centro de Ornitología y Biodiversidad (CORBIDI), Lima, Peru; Museo de Historia Natural San Marcos (MUSM), Lima, Peru.

Phylogenetic analyses

Following laboratory protocols similar to those presented by Torres-Carvajal and de Queiroz (2009), we sequenced a continuous 1773 base fragment of mitochondrial DNA (mtDNA) that extends from the gene encoding subunit I of the protein NADH dehydrogenase (ND1) through the genes encoding $tRNA^{Ile}$, $tRNA^{Gln}$, $tRNA^{Met}$, subunit II of NADH dehydrogenase (ND2), $tRNA^{Trp}$, $tRNA^{Ala}$, $tRNA^{Asn}$, the origin of light-strand replication (OL), $tRNA^{Cys}$, $tRNA^{Tyr}$, to the gene encoding subunit I of the protein cytochrome c oxidase (COI). We added five new sequences from the new species described herein and one of *Enyalioides cofanorum* (QCAZ 8035) to the mtDNA dataset of Venegas et al. (2013). GenBank accession numbers for the new sequences are provided in Table 1.

Editing, assembly, and alignment of sequences were performed with Geneious 7.1.7 (Drummond et al. 2010). Genes were combined into a single dataset with four partitions, three corresponding to each codon position in protein coding genes and one to all tRNAs. The best partition strategy along with the corresponding models of evolution were obtained in PartitionFinder 1.1.1 (Lanfear et al. 2012) under the Bayesian information criterion.

Phylogenetic relationships were assessed under a Bayesian inference approach using MrBayes 3.2.2 (Ronquist et al. 2012) after partitioning the data as described above. To reduce the chance of converging on a local optimum, four runs were performed. Each consisted of five million generations and four Markov chains with default heating values. Trees were sampled every 1000 generations resulting in 5001 saved trees per analysis. Stationarity was confirmed by plotting the –ln *L* per generation in the program Tracer 1.6 (Rambaut et al. 2013). Additionally, the standard deviation of the partition frequencies and the potential scale reduction factor (Gelman and Rubin 1992) were used as convergence diagnostics for the posterior probabilities of bipartitions and branch lengths, respectively. Adequacy of mixing was assessed by examining the effective sample sizes (ESS) in Tracer, with ESS > 200 considered as satisfactory. After analyzing convergence, mixing, and sampling, the first 501 trees in the sample were discarded as "burn-in" from each run. We then confirmed that the four analyses

Table 1. Vouchers, locality data, and GenBank accession numbers of new DNA sequences obtained for this study.

Taxon	Voucher	Locality	GenBank number (ND4)	GenSeq nomenclature
E. altotambo	QCAZ 8073 (holotype)	Ecuador: Esmeraldas: Alto Tambo, 5 km on road to Placer	KP235211	genseq-1
E. anisolepis	QCAZ 8395	Ecuador: Zamora-Chinchipe: Chito, sector Los Planes	KP235213	genseq-2
E. anisolepis	QCAZ 8428	Ecuador: Zamora-Chinchipe: Chito	KP235214	genseq-2
E. anisolepis	QCAZ 8515	Ecuador: Zamora-Chinchipe: Chito, sector Los Planes	KP235215	genseq-2
E. cofanorum	QCAZ 8035	Ecuador: Orellana: 66 km on road Pompeya-Iro	KP235210	genseq-4
E. sophiarothschildae	CORBIDI 647 (holotype)	Peru: San Martín: Río Lejía on the trail La Cueva-Añazco Pueblo	KP235212	genseq-1

had reached stationarity at a similar likelihood score and that the topologies were similar and used the resultant 18,000 trees to calculate posterior probabilities (PP) for each bipartition on a 50% majority rule consensus tree.

Results

The taxonomic conclusions of this study are based on the observation of morphological features and color patterns, as well as the inferred phylogenetic relationships. This information is considered as species delimitation criteria following a general lineage or unified species concept (de Queiroz 1998; 2007).

***Enyalioides altotambo* sp. n.**
http://zoobank.org/4AE55600-2B8F-446B-B702-B55BDC3FF1EF
Proposed standard English name: Alto Tambo woodlizards
Proposed standard Spanish name: lagartijas de palo de Alto Tambo

Enyalioides oshaughnessyi (part) Torres-Carvajal et al. 2011: 23.

Type material. *Holotype*. QCAZ 8073 (Fig. 1), an adult male from Alto Tambo, 5 km on road to Placer, Bosque Integral Otokiki, 0.90600°N; -78.60600°W (DD), 620 m, Provincia Esmeraldas, Ecuador, collected on 2 May 2010 by I.G. Tapia, D. Almeida-Reinoso, J.M. Guayasamin and L.A. Coloma.

Paratype. ECUADOR: Provincia Esmeraldas: QCAZ 6671, adult female, Alto Tambo, Balthazar river, 0.90000°N; -78.61667°W, 645 m, collected on 5 November 2005 by F. Ayala-Varela and I.G. Tapia.

Diagnosis. *Enyalioides altotambo* differs from other species of *Enyalioides*, except for *E. oshaughnessyi*, in having dorsal scales that are both smooth and homogeneous in

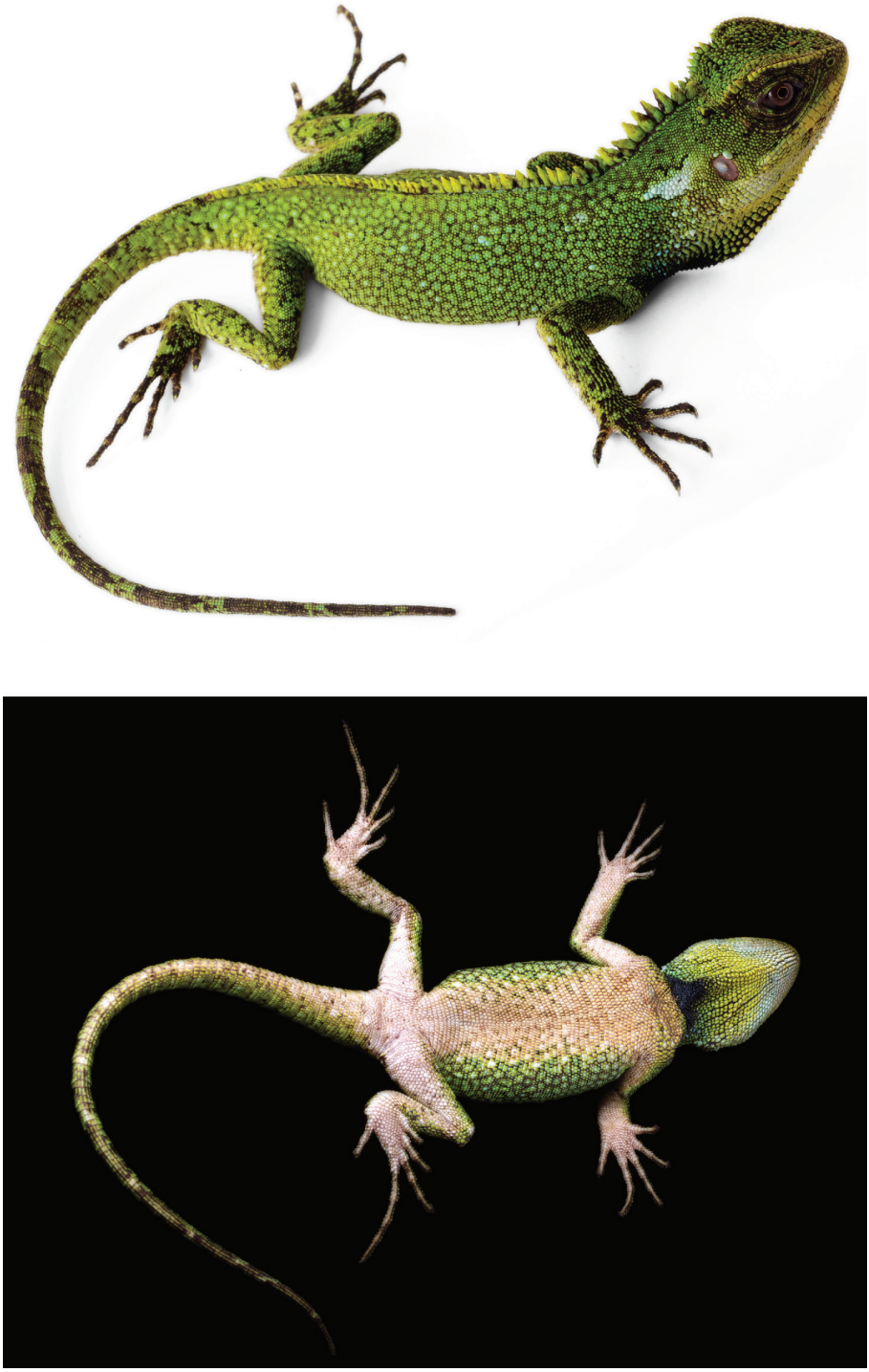

Figure 1. Holotype (QCAZ 8073, adult male, SVL = 119 mm) of *Enyalioides altotambo* in dorsal (top) and ventral (bottom) views. Photographs by Luis A. Coloma.

size. It can be distinguished from *E. oshaughnessyi* (character states in parentheses) by the following characters: iris brown in both sexes (iris bright red in both sexes); scales on lateral edge of skull roof just posterior to superciliaries strongly projected (moderately projected); adults of both sexes with light green spots on dorsum (if present, spots turquoise or blue); adult males with a black medial patch on gular region not extending dorsally to form an antehumeral bar (black patch under gular fold extending dorsally to form a short antehumeral bar); scales on flanks almost homogenous in size (flank scales heterogeneous in size, with a few enlarged, circular, keeled scales); pale postympanic stripe on lateral aspect of neck in both sexes (pale postympanic spot in both sexes), posterior surface of thighs without enlarged scales (scattered enlarged scales), tail length/total length 0.57–0.60 (0.59–0.62).

Description of holotype. Male (Fig. 1); SVL = 119 mm; TL = 160 mm; maximum head width = 21.9 mm; head length = 29.8 mm; head height = 20.3 mm; dorsal head scales keeled or multicarinate, projected dorsally; parietal eye present; eight scales immediately posterior to superciliaries conical, dorsolaterally projected, and conspicuously larger than adjacent scales; temporal scales small, pyramidal, low; one large conical pretympanic scale; superciliaries 17; canthals five; postrostrals three; supralabials 13 if counted to a point below middle of eye; rostral divided into three small scales, similar in size to adjacent supralabials; one longitudinal row of lorilabials between suboculars and supralabials at level of middle of eye, longitudinal rows of lorilabials anterior to this point two; loreal region with small, keeled, and juxtaposed scales; nasal at level of supralabials V–VI; infralabials 11 if counted to a point below middle of eye; mental (1.68 mm wide × 1.98 mm high) slightly wider and 1.5 times higher than adjacent infralabials; postmentals three; gulars ventrally projected and separated from each other by skin covered with tiny granular scales; gular fold complete midventrally, extending dorsally and posteriorly to form an antehumeral fold; neck with some oblique folds, and a dorsolateral row of enlarged scales; distal aspect of oblique fold immediately anterior to antehumeral fold with approximately six enlarged scales similar in size to gulars, but more than three or four times the size of adjacent fold scales.

Vertebral crest strongly projected and decreasing in size posteriorly, with vertebrals on neck at least four times higher than those between hind limbs; crest bifurcates at a point approximately 10 mm posterior to the cloaca, and extends onto tail about 1/3 its length; body flanks between fore and hind limbs with slight dorsolateral fold; scales on dorsolateral fold slightly larger than adjacent scales; dorsal and flank scales small, smooth, imbricate, more or less homogeneous in size; ventral scales imbricate, keeled, rectangular or rhomboid, with a posterolateral mucron; ventrals more than twice the size (area) of dorsals.

Limb scales keeled dorsally and keeled or feebly keeled ventrally; scales on dorsal and posterior aspects of thighs heterogeneous in size, with most scales less than half the size of those scales on anterior and ventral aspects, separated from each other by skin covered with tiny granular scales; subdigitals on finger IV 25; subdigitals on toe IV 29; femoral pores on each side one; tail laterally compressed and gradually tapering posteriorly; caudal scales smooth at the base of tail, becoming keeled and imbricate towards

Table 2. Summary of morphological characters and measurements (mm) of *Enyalioides altotambo*, *E. anisolepis* and *E. sophiarothschildae*. Range (first line) and mean ± standard deviation (second line) are given for quantitative characters, except when there was no variation.

Character	*E. altotambo N* = 2	*E. anisolepis N* = 15	*E. sophiarothschildae N* = 3
Dorsals in transverse row between dorsolateral crests at midbody	39–40 39.5 ± 0.71	28–35 32.00 ± 2.83	22–26 24.33 ± 2.08
Ventrals in transverse row at midbody	31–33 32.00 ± 1.41	23–29 26.53 ± 1.92	23–26 25.00 ± 1.73
Vertebrals from occiput to base of tail	50–51 50.50 ± 0.71	43–62 50.87 ± 6.27	51–57 54.00 ± 3.00
Gulars	47	30–35 31.71 ± 1.49	36
Infralabials	11	9	9–11 10.00 ± 1.00
Supralabials	13	10–12 10.77 ± 0.60	9–12 10.67 ± 1.53
Canthals	5	5–6 5.43 ± 0.51	5
Superciliaries	14–17 15.50 ± 2.12	13–18 15.57 ± 1.40	13–15 14.00 ± 1.00
Transverse rows of ventrals between fore and hind limbs	47–49 48.00 ± 1.41	38–46 41.27 ± 2.60	37–40 38.67 ± 1.53
Subdigitals finger IV	23–25 24.00 ± 1.41	15–20 18.36 ± 1.39	18–19 18.67 ± 0.58
Subdigitals toe IV	27–29 28.00 ± 1.41	24–27 25.14 ± 0.86	22–27 25.33 ± 2.89
Femoral pores	1–2 1.50 ± 0.71	0–3 1.64 ± 1.01	3–4 3.67 ± 0.58
Tail length/Total length	0.57–0.60 0.59 ± 0.02	0.59–0.71 0.62 ± 0.03	0.60–0.61 0.61 ± 0.01

tip, gradually increasing in size posteriorly on lateral and dorsal aspects of each caudal segment; caudals larger ventrally than dorsally; individual caudal segments three scales long ventrally and seven scales long dorsally.

Color in life of holotype (Fig. 1). Head light green with a few black and dark brown scales; superciliaries, canthals and labials yellow; bluish cream blotch, wider than high, behind tympanum; pretympanic scales bluish cream; dorsal body background light green with a fine dark brown reticulation and scattered bluish cream scales; vertebrals yellowish green; tail green with incomplete dark brown rings; black irregular marks on limbs, covering most of hands and feet; chin white; gular region bluish cream anterolaterally grading into yellowish green and then bluish green posteriorly, with a posteromedial black patch; ventral aspect of body, limbs and tail dirty cream; flank color pattern extending onto ventrolateral aspect of body; iris brown with golden ring around pupil.

Variation. Variation in meristic and morphometric characters of *Enyalioides altotambo* are presented in Table 2. The single female paratype (QCAZ 6671; Fig. 2) is

Figure 2. Paratype (QCAZ 6671, adult female, SVL = 132 mm) of *Enyalioides altotambo*. Photograph by Luis A. Coloma.

similar in lepidosis and color patterns to the holotype. It differs from the holotype in lacking a black gular patch, and in having a longer pale postympanic stripe, a yellow chin, and a yellow gular region. Furthermore, the scales on the lateral edge of the skull roof and those forming the vertebral crest are more projected in the female (Fig. 2); however, this variation could be ontogenetic rather than sexual because the female is larger (SVL = 134 mm) than the male (SVL = 119).

Distribution. *Enyalioides altotambo* is only known from two adjacent localities at 620–645 m in the Chocoan rainforests of northwestern Ecuador (Fig. 3). Female paratype QCAZ 6671 was found at 5:30 pm with its head facing up on a tree trunk.

Etymology. The specific epithet is a noun in apposition and refers to Alto Tambo, Provincia Esmeraldas, Ecuador, a village on the Ibarra-San Lorenzo road where *Enyalioides altotambo* was discovered.

Remarks. Although previously referred to *Enyalioides oshaughnessyi*, the possibility that the specimens here named *Enyalioides altotambo* represented a distinct species was recognized in previous studies. In a phylogenetic analysis of hoplocercine lizards, Torres-Carvajal and de Queiroz (2009) found "*E. oshaughnessyi*" to be paraphyletic relative to *E. touzeti* based on three samples of "*E. oshaughnessyi*". One of them corresponded to the paratype of *Enyalioides altotambo*, and was sister to a clade containing the sister taxa *E. touzeti* and *E. oshaughnessyi*. Torres-Carvajal et al. (2011) noted that the color of the iris in live specimens of "*E. oshaughnessyi*" from Alto Tambo was not bright red as in live specimens of "*E. oshaughnessyi*" from other localities and suggested that the two forms represented separate species. Nonetheless, these authors found no

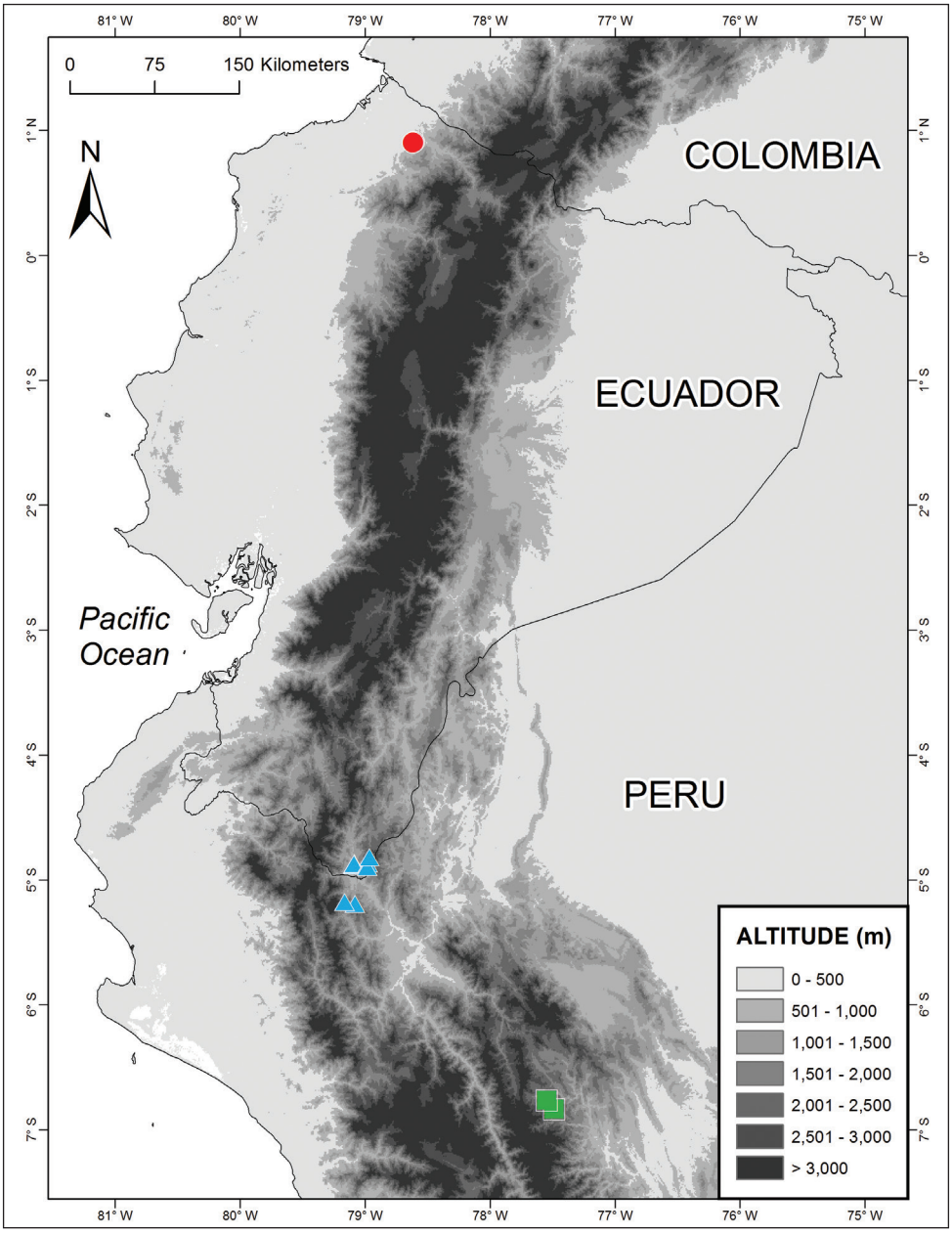

Figure 3. Distribution of *Enyalioides altotambo* (circles), *E. anisolepis* (triangles) and *E. sophiarothschildae* (squares).

other differences between the two potential species and refrained from associating the name *E. oshaughnessyi* with one versus the other because the type locality data of *E. oshaughnessyi* is vague ("Ecuador"), and the color of the iris was not recorded in its original description (Boulenger 1881). Here we recognize known populations other

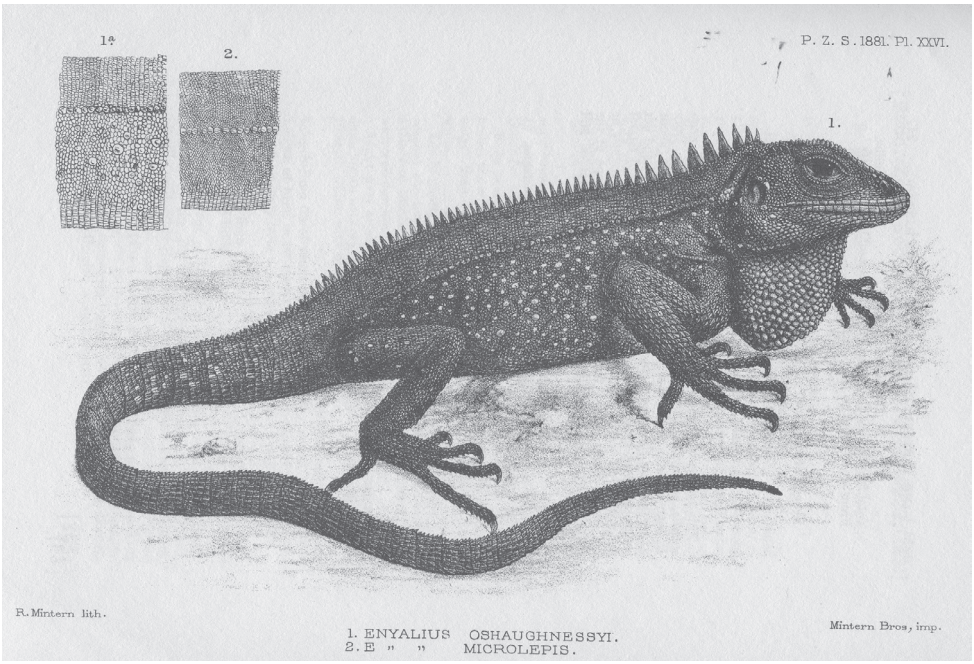

Figure 4. Holotype of *Enyalioides oshaughnessyi* (MRHN [Museum Royal d'Histoire Naturelle, Belgium] 2009, adult male). Illustration taken from original description (Boulenger 1881).

than that at Alto Tambo as *E. oshaughnessyi* based on the enlarged, circular and keeled scales scattered on the flanks of *E. oshaughnessyi* (absent in *E. altotambo*), as described and illustrated in its original description (Fig. 4; Boulenger 1881).

***Enyalioides anisolepis* sp. n.**
http://zoobank.org/6728260C-76AD-4C46-B97B-158C44BDA70C
Proposed standard English name: rough-scaled woodlizards
Proposed standard Spanish name: lagartijas de palo de escamas ásperas

Type material. *Holotype*. QCAZ 12537 (Fig. 5), an adult male from the eastern bank of the Mayo river, 4.5 km ESE Zumba, -4.88605°S, -79.08738°W (DD), 765 m, Provincia Zamora-Chinchipe, Ecuador, collected on 11 April 2014 by D.A. Paucar, D. Almeida-Reinoso, G. Galarza and D. Pareja.

Paratypes (14). ECUADOR: Provincia Zamora-Chinchipe: QCAZ 12521, juvenile with the same collection data as the holotype except -4.88673°S, -79.08744°W, 738 m; QCAZ 12527, adult male (Fig. 6) with the same collection data as the holotype except -4.87147°S, -79.08542°W, 738 m; QCAZ 12528, juvenile with the same collection data as the holotype except -4.87136°S, -79.08534°W, 738 m; QCAZ 12531, female with the same collection data as the holotype except -4.87808°S,

Figure 5. Holotype of *Enyalioides anisolepis* (QCAZ 12537, adult male, SVL = 130 mm). Top: dorsolateral view; middle: ventral view; bottom: lateral view of head. Photographs by Omar Torres-Carvajal.

-79.08956°W, 738 m; QCAZ 12535, juvenile (Fig. 6) with the same collection data as the holotype except -4.88658°S, -79.08747°W, 731 m; QCAZ 12536, juvenile with the same collection data as the holotype except -4.88622°S, -79.08737°W, 744 m; QCAZ 12552, female (Fig. 6) with the same collection data as the holotype except -4.87589°S, -79.08995°W, 741 m; QCAZ 12551, juvenile with the same collection data as the holotype except -4.87521°S, -79.08965°W, 724 m, collected on 12 April 2014; QCAZ 12517, adult male from Nuevo Paraíso, 700 m NW on road to Las Tres Aguas, -4,87109°S, -78,97579°W, 1742 m, collected on 10 April 2014 by the same collectors as the holotype; QCAZ 8395, female from Chito, sector Los Planes, -4.89814°S, -78.98095°W, collected on 16 February 2008 by S. Aldás-Alarcón; QCAZ

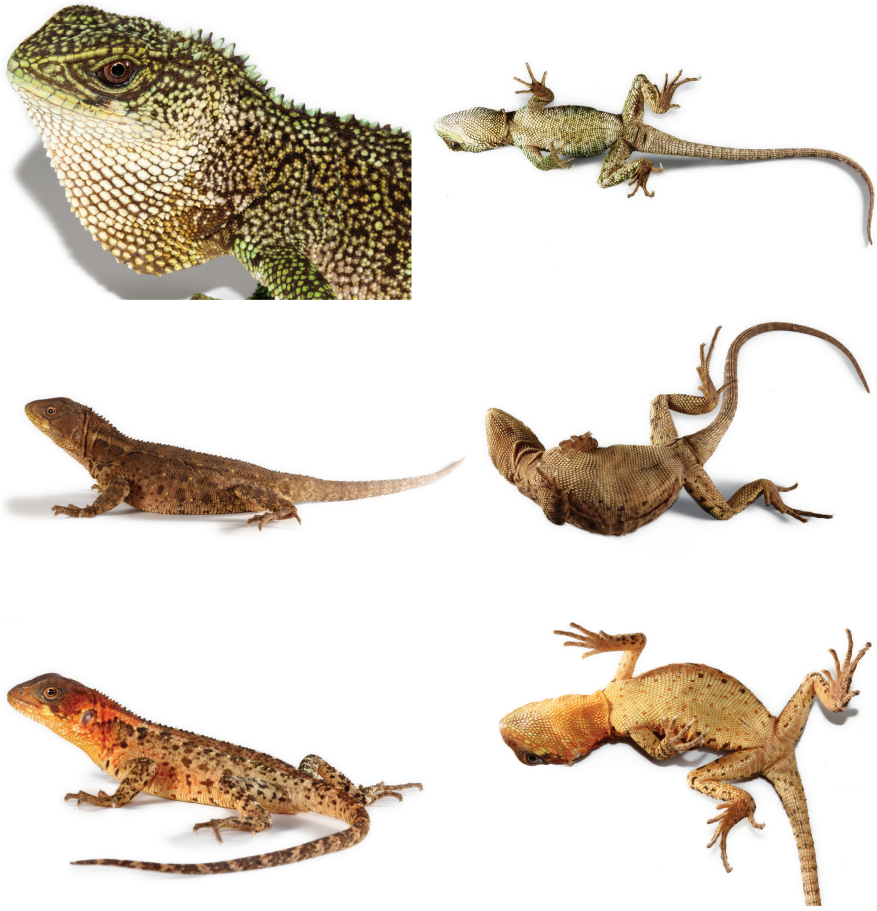

Figure 6. Paratypes of *Enyalioides anisolepis*. Lateral (left) and ventral (right) views of an adult male (top, QCAZ 12527, SVL = 111 mm), an adult female (middle, QCAZ 12552, SVL = 101 mm), and a juvenile (bottom, QCAZ 12535, SVL = 59 mm). Photographs by Omar Torres-Carvajal.

8515, female from Chito, sector Los Planes, -4.89726°S, -78.98191°W, collected on 18 February 2008 by S. Aldás-Alarcón; QCAZ 8428, female from Chito, 4.82037°S, -78.96247°W, 1724 m, collected on 14 February 2008 by S. Aldás-Alarcón. PERU: Provincia San Ignacio: Región Cajamarca: CORBIDI 870, female from Alto Ihuamaca-Namballe, -5.19448°S, -79.08048°W, 1616 m, collected on 26 August 2008 by M. Dobiey; MUSM 20675, adult female from El Sauce, Tabaconas Namballe National Sanctuary, -5.17897°S, -79.16347°W, 1600 m, collected in April 2003 by C. Aguilar.

Diagnosis. *Enyalioides anisolepis* can be distinguished from other species of *Enyalioides,* except for *E. heterolepis*, by having conical dorsal head scales (only in *E. anisolepis* and *E. heterolepis*) and scattered, projecting, large scales on the dorsum, flanks, and hind limbs (also in *E./Morunasaurus annularis* and *E./M. groi*), which are conspicuous in adults of both sexes (Fig. 7). Besides occurring on opposite sides of the Andes, *E. anisolepis* differs from *E.*

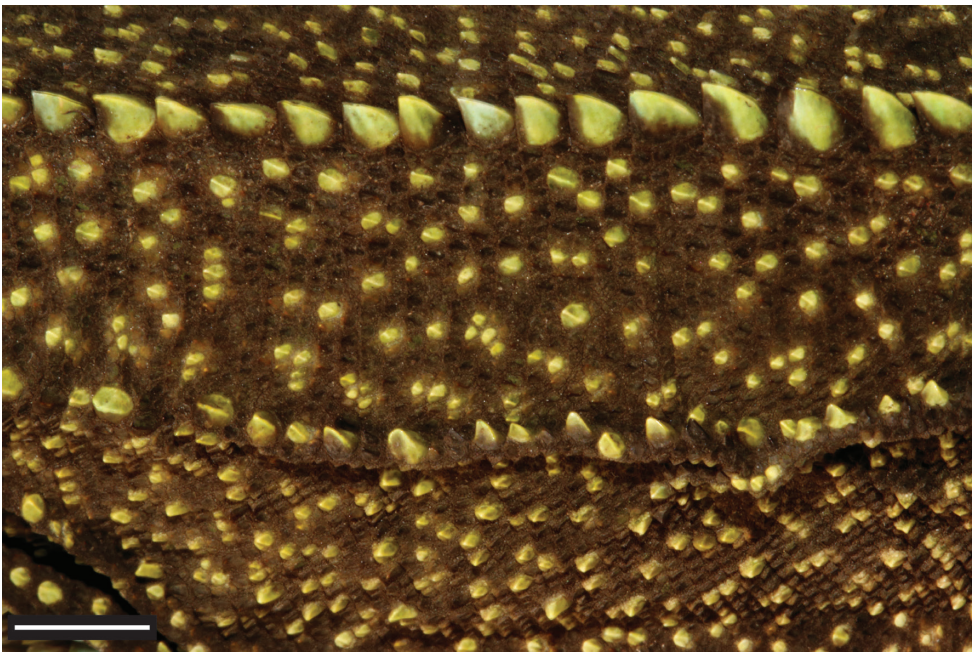

Figure 7. Close-up of left dorsum of *Enyalioides anisolepis* (QCAZ 12537, holotype) showing scattered enlarged scales. Scale bar = 5 mm. Photograph by Omar Torres-Carvajal.

heterolepis (character states from Torres-Carvajal et al. 2011 in parentheses) in having fewer vertebral scales, 43–62, 50.87 ± 6.27 (52–98, 74.61 ± 10.39), a higher vertebral crest with the vertebrals on neck at least three times higher than those between the hind limbs (vertebrals on neck maximum twice as high as those between hind limbs), scattered dark spots on belly in juveniles and adults of both sexes (belly without scattered dark spots, blackish medially in some adult males), tail in adult males moderately compressed laterally (strongly compressed), and a marked sexual dichromatism (Fig. 6), with the dorsal background color greenish in males and brownish in females (both sexes with a brownish background).

The only other species of *Enyalioides* with scattered, projecting dorsal scales is *E. cofanorum*, which differs from *E. anisolepis* in lacking projecting scales on the hind limbs, and in being smaller in size (maximum SVL in males and females of *E. cofanorum* 107 mm and 109 mm, respectively; 130 mm and 119 mm in *E. anisolepis*). Additionally, adults of both sexes of *E. cofanorum* have a brownish background (marked sexual dichromatism in *E. anisolepis*).

Description of holotype. Male (Fig. 5); SVL = 130 mm; TL = 220 mm; maximum head width = 28.7 mm; head length = 35.3 mm; head height = 24.6 mm; dorsal head scales keeled or multicarinate, those in the parietal region strongly projected dorsally; scales immediately posterior to superciliaries conical and dorsally projected, forming longitudinal row of ten (left) or nine (right) scales that extends posteriorly over supratemporal region; temporal scales small, tuberculate or keeled, juxtaposed; one enlarged pretympanic scale; superciliaries 17; canthals six; postrostrals three; su-

pralabials 11 if counted to a point right below middle of eye, and 16 if counted to commisure of mouth; rostral (2.6 mm wide × 1.5 mm high) about twice as wide as adjacent supralabials; single longitudinal row of lorilabials between suboculars and supralabials at level of middle of eye, longitudinal rows of lorilabials anterior to this point 2–4; loreal region with small, smooth and keeled, juxtaposed scales; nasal at level of supralabials III and IV; infralabials nine (left) or eight (right) if counted to a point right below middle of eye, and 13 (left) and 11 (right) if counted to commisure of mouth; mental (2.8 mm wide × 1.5 mm high) wider and higher than adjacent infralabials; postmentals two; gulars projected, low; gular fold complete midventrally; small dewlap present; neck with several longitudinal and oblique folds.

Vertebral crest strongly projected and decreasing in size posteriorly, with vertebrals on neck at least three times higher than those between hind limbs; crest bifurcates at a point approximately 10 mm posterior to the cloaca, and extends onto tail about ¼ its length; flanks between fore and hind limbs with dorsolateral and ventrolateral longitudinal folds, as well as several oblique folds; axillary region with three vertical folds; scales on dorsolateral folds slightly larger than adjacent scales giving the fold the appearance of a low crest; scales between dorsolateral folds and vertebral crest heterogeneous in size, prominently keeled, and imbricate, with largest scales twice as large as smallest ones; neck and scapular region with scattered, large conical scales; flank scales ventral to dorsolateral folds similar to those dorsal to folds, with largest scales four times as large as smallest ones (Fig. 7); axillary region with conical scales forming two short vertical folds; ventral scales imbricate, keeled, rhomboidal, with a posterior mucron; ventrals more than three times the area of smallest dorsals.

Limb scales keeled dorsally and ventrally, homogeneous in size on fore limbs; scales on dorsal and posterior aspect of thighs heterogeneous in size, with most scales less than half the size of those on anterior and ventral aspects; scales on dorsal surface of shanks heterogeneous in size, with granular scales between large keeled scales; subdigitals on finger IV 17; subdigitals on toe IV 25; three femoral pores on left leg, two on right leg; tail laterally compressed and gradually tapering posteriorly; caudal scales strongly keeled and imbricate, increasing in size posteriorly on lateral and dorsal aspects of each caudal segment; caudals larger ventrally than dorsally; individual caudal segments three scales long ventrally and six scales long dorsally.

Color in life of holotype (Fig. 5). Dorsal and lateral aspects of head with scattered black, brown, and pale green scales; labials greenish cream; dorsal background of body, limbs and tail brownish green with scattered pale green scales; vertebral crest pale green, the base and posterior surface of each vertebral scale dark brown; gular scales cream, the skin between them gray; orange patch on medial aspect of throat; chest and belly cream with a pale orange tint; ventral surface of limbs dirty cream with scattered brown spots; ventral surface of tail dirty cream proximally and brown distally; iris pale brown peripherally with dark brown reticulations, dark brown centrally; thin golden ring around pupil.

Variation. Variation in meristic and morphometric characters of *Enyalioides anisolepis* are presented in Table 2. Enlarged pretympanic scales are absent in more than half of the specimens; when present, they vary between 1–3. A few specimens have

smooth scales intermixed with the keeled dorsals. Ventrals are keeled except for an adult female specimen (QCAZ 8428) that has smooth ventrals, and an adult male specimen (QCAZ 12517) that has smooth ventrals anteriorly and feebly keeled ventrals posteriorly. Caudal segments are 6–8 scales long laterally.

This species has a marked sexual dichromatism in background colors (green in males, brown in females; see Fig. 6). Adult male paratypes are very similar in color patterns to the holotype, except for having dark spots on the belly. A subadult male (QCAZ 12517) has scattered black flecks on the gular region.

Adult females share similar color patterns with juveniles (Fig. 6): dorsal background of head, body, limbs and tail dark or pale brown; flanks dark or pale brown with scattered dark spots, blotches, or transverse bands (cream flecks in QCAZ 8428); diagonal subocular dark stripe extending from subocular region to commisure of mouth; faint cream stripe extending longitudinally from tympanum to scapular region, except in specimen QCAZ 8428, which has instead a cream blotch posterior to tympanum; limbs with faint brown transverse bands; throat, chest, belly and ventral surface of limbs and tail pale brown or cream, with scattered dark spots on belly and thighs (dark spots absent in QCAZ 8428). In addition, juveniles generally have dark brown transverse bands on dorsum, dark flecks on head, and transverse rows of dark brown blotches on flanks. The neck and sides of head have a bright orange tint in one specimen (QCAZ 12535).

Distribution and ecology. *Enyalioides anisolepis* is known to occur between 724–1742 m on the Amazonian slopes of the Andes in southern Ecuador and northern Peru (Fig. 3). It is known from Provincia Zamora-Chinchipe in extreme southern Ecuador and Región Cajamarca in northern Peru. Most specimens were found sleeping at night (7:00 pm–1:00 am) between 0.2–1.5 m above ground on stems, leaves, and tree roots in primary and secondary forests. Nine of the 15 known specimens were found within 5 m of small streams.

Etymology. The specific epithet *anisolepis* is a noun (in apposition) in the nominative singular and derives from the Greek words *anisos* (= unequal) and *lepis* (= scale). It refers to the heterogeneous scales on the dorsum, flanks and hind limbs of lizards of this species.

***Enyalioides sophiarothschildae* sp. n.**
http://zoobank.org/451884BA-28DE-4974-A7D1-FB4F77680FA7
Proposed standard English name: Rothschild's woodlizards
Proposed standard Spanish name: lagartijas de palo de Rothschild

Type material. *Holotype*. CORBIDI 647 (Fig. 8), an adult male from Río Lejía in the trail La Cueva-Añazco Pueblo, -6.83655°S; -77.48603°W (DD), 1700 m, Provincia Mariscal Cáceres, Región San Martín, Perú, collected on 2 February 2008 by P.J. Venegas.

Paratypes (2). PERU: Región San Martín: Provincia Mariscal Cáceres: MUSM 21883-84, adult males, El Dorado, -6.76666°S; -77.54500°W, 1600m, collected on 5 December 2003 by P.J. Venegas.

Figure 8. Holotype of *Enyalioides sophiarothschildae* sp. n. (CORBIDI 647, adult male, SVL = 135 mm). Top: dorsolateral view; middle: lateral view of head; bottom: ventral view. Photograph by Pablo J. Venegas.

Diagnosis. *Enyalioides sophiarothschildae* can be distinguished from other species of *Enyalioides*, except for *E. laticeps*, by having caudal scales that are relatively homogeneous in size on each caudal segment; in all other species of *Enyalioides*, the dorsal and lateral caudals increase in size posteriorly on each caudal segment, and the largest (posteriormost) caudals on each segment are mucronate or have some kind of projection (Torres-Carvajal et al. 2011). *Enyalioides sophiarothschildae* differs from *E. laticeps* (character states in parentheses) in color patterns: gular region in males white with a black medial patch scattered with turquoise scales (orange or dirty cream with longitudinal brown, reddish-brown, bluish, or orange streaks, and a large brown or black medial blotch at the level of the gular fold); chest in males grayish white with a turquoise tone (usually an orange tone); labials and chin immaculate white (cream or green in many tones, but never immaculate white).

Description of holotype. Male (Fig. 8); SVL = 135 mm; TL = 223 mm; maximum head width = 28.4 mm; head length = 34.7 mm; head height = 24.3 mm; dorsal head scales uni- or multicarinate, projected dorsally; parietal eye present; 3–4 scales immediately posterior to superciliaries conical, dorsolaterally projected, and slightly larger than adjacent scales; temporal scales small, multicarinate, separated from each other by tiny granular scales; no distinctly enlarged pretympanic scales; superciliaries 13; canthals six; postrostrals three; supralabials 10 if counted to a point below middle of eye; rostral (3.14 mm wide × 1.47 mm high) slightly wider than adjacent supralabials; single longitudinal row of lorilabials between suboculars and supralabials at level of middle of eye, two longitudinal rows of lorilabials anterior to this point; loreal region composed of small, smooth, and juxtaposed scales, some of which are separated from each other by tiny granular scales; nasal at level of supralabials III–IV; left and right infralabials nine if counted to a point below middle of eye; mental (2.77 mm wide × 2.60 mm high) slightly wider and 1.5 times higher than adjacent infralabials; postmentals two; gulars ventrally projected and separated from each other by skin covered with tiny granular scales; gular fold complete midventrally, extending dorsally and posteriorly to form antehumeral fold; neck with several oblique folds, and a dorsolateral row of enlarged scales; distal part of oblique fold immediately anterior to antehumeral fold with approximately 10 enlarged scales similar in size to gulars, but more than twice the size of adjacent fold scales.

Vertebral crest strongly projected and decreasing in size posteriorly, with vertebrals on neck at least four times higher than those between hind limbs; crest bifurcates posteriorly and extends onto tail less than ¼ its length; body flanks between fore and hind limbs with slight dorsolateral and ventrolateral longitudinal folds; scales on dorsolateral folds similar in size to adjacent scales; dorsal and flank scales small, keeled, imbricate, more or less homogeneous in size, and separated from each other by skin covered with tiny granular scales; ventral scales imbricate, smooth or slightly keeled, rectangular or rhomboid, with a posterolateral mucron; ventrals more than twice the area of dorsals.

Limb scales keeled dorsally and smooth or slightly keeled ventrally; scales on dorsal and posterior surfaces of thighs heterogeneous in size, with most scales less than half the size of those on anterior and ventral surfaces, separated from each other by skin covered

with tiny granular scales; subdigitals on finger IV 17; subdigitals on toe IV 25; femoral pores on each side four; tail laterally compressed and gradually tapering posteriorly; caudal scales strongly keeled and imbricate, not gradually increasing in size posteriorly on lateral and dorsal aspects of each caudal segment; caudals larger ventrally than dorsally; individual caudal segments three scales long ventrally and six scales long dorsally.

Color in life of holotype (Fig. 8). Head dark green with large black blotch between the eye and the tympanum; loreal region, nasal scale, labials and chin white; white blotch on posterior end of mandible; neck greenish brown dorsally and dark brown laterally, with a white rhomboidal blotch extending longitudinally from tympanum to scapular region; dorsal body background dark brown with scattered green scales and pale spots; limbs dark brown with green transverse bands; tail dark green with scattered dark brown marks; vertebral crest with intermixed green and dark brown scales; gular region white with a black posteromedial patch bearing scattered turquoise scales; chest grayish white with a turquoise tone anteriorly; belly grayish white with scattered, faint, pale brown blotches; ventral surface of limbs grayish white, with a longitudinal faint turquoise stripe along the thighs; tail grayish white; iris silver peripherally and dark brown centrally, with dark brown reticulations; silver ring around pupil.

Variation. Variation in meristic and morphometric characters of *Enyalioides sophiarothschildae* are presented in Table 2. One male paratype (MUSM 21883) differs from the holotype in having some scattered dark brown blotches on the throat.

Distribution and ecology. *Enyalioides sophiarothschildae* is known from the northeastern slopes of the Cordillera Central in Peru between 1600–1700 m (Fig. 3). This species is only known from two adjacent localities, the trail to La Cueva-Añasco Pueblo in the drainage of the Lejía river and El Dorado in the drainage of the Blanco river, both tributaries of the Huallabamba river in the northern part of the Huallaga river basin. This area corresponds to the Selva Alta (400–1000 m) and Yungas (300–2300 m) ecoregions (Brack 1986; Peñaherrera del Aguila 1989).

Individuals of *Enyalioides sophiarothschildae* were found active by day in primary forest. The holotype was found crossing a trail and tried to hide between the roots of a big tree when approached for capture. One of the paratypes climbed up a tree three meters above the ground when approached. The other paratype was found sitting on a big root.

Etymology. The specific epithet is a noun in the genitive case and is a patronym honoring Sophia Rothschild in recognition of her financial support for the improvement of the herpetological collection of CORBIDI through the BIOPAT Program.

Phylogenetic relationships

The phylogenetic tree inferred in this study (Fig. 9) is consistent with Torres-Carvajal and de Queiroz's (2009) phylogenetic hypothesis in that species of *Enyalioides* are split into two primary subclades: one containing *E. heterolepis* and *E. laticeps* as sister taxa,

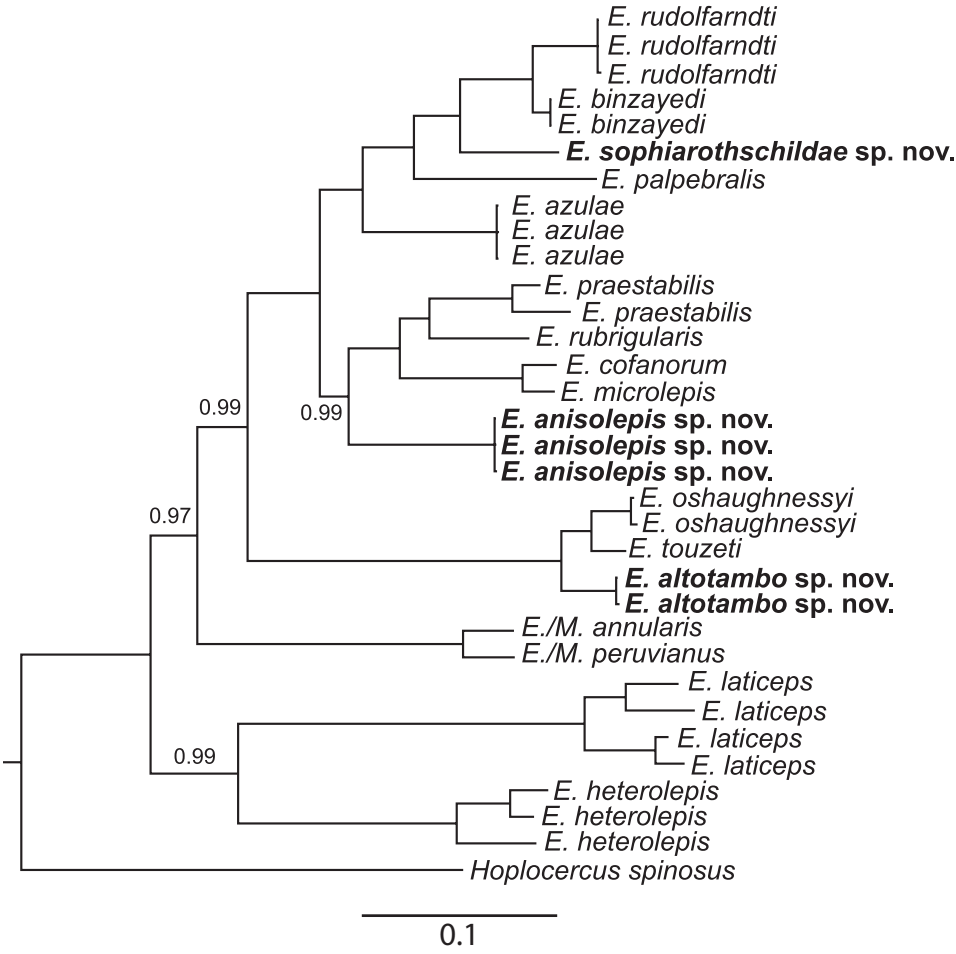

Figure 9. 50% Majority rule consensus tree of hoplocercine lizards (*E.* = *Enyalioides*, *M.* = *Morunasaurus*) based on a Bayesian analysis of mtDNA sequences. Posterior probabilities are equal to 1, unless otherwise noted by numbers next to branches. Outgroup taxa are not shown. The notation *E./M.* indicates that according to the phylogenetic definitions (de Queiroz and Gauthier 1990) of the names *Enyalioides* and *Morunasaurus* proposed by Torres-Carvajal et al. (2011), *Morunasaurus* is a subclade of *Enyalioides.*

and the other including all remaining species of *Enyalioides*, as well as possibly *Morunasaurus*. All species described in this paper are nested within the second clade.

Torres-Carvajal and de Queiroz (2009; see their Fig. 5) found *Enyalioides oshaughnessyi* to be paraphyletic relative to *E. touzeti* based on three samples of *E. oshaughnessyi* and one sample of *E. touzeti*. They hypothesized that either *E. oshaughnessyi* as previously circumscribed represents a single species, but its mtDNA has not yet become monophyletic relative to that of *E. touzeti*, or *E. oshaughnessyi* represents more than one species. Torres-Carvajal et al. (2011) found support for the latter hypothesis based on the color of

the iris, red in both sexes of most specimens of *E. oshaughnessyi* and reddish brown in two adult specimens from Alto Tambo (*E. altotambo* type specimens). Addition of sequence data from a second specimen from Alto Tambo further supports this hypothesis in that *E. oshaughnessyi* and *E. altotambo* are reciprocally monophyletic. *Enyalioides altotambo* is strongly supported as monophyletic (PP = 1) and, in agreement with previous phylogenetic hypotheses (Torres-Carvajal and de Queiroz 2009; Venegas et al. 2013), is sister (PP= 1) to a clade (PP = 1) formed by *E. touzeti* and *E. oshaughnessyi* (Fig. 9).

Enyalioides anisolepis is strongly supported (PP = 1) as monophyletic and is sister (PP = 0.99) to a clade (PP = 1) composed of *E. cofanorum*, *E. microlepis*, *E. rubrigularis*, and *E. praestabilis*. *Enyalioides sophiarothschildae* is sister (PP = 1) to a clade (PP = 1) composed of two recently discovered species, *E. binzayedi* and *E. rudolfarndti* (Venegas et al. 2011; Venegas et al. 2013) from Peru. Thus, the phylogenetic tree presented here strongly supports both referral of the three newly discovered species to *Enyalioides* and their status as different species from those recognized previously. Differences in morphology and color patterns presented above provide additional evidence for recognizing *E. altotambo*, *E. anisolepis* and *E. sophiarothschildae* as species.

Key to the 19 species of Hoplocercinae

The following key is artificial in the sense that its structure does not necessarily reflect the order of branching in the phylogeny.

1 Dorsal head scales flat, smooth, juxtaposed; vertebral crest absent or composed of a discontinuous row of enlarged scales that are longer than tall **2**

– Dorsal head scales conical; vertebral crest present, composed of projecting scales that are taller than long **5**

2 Tail depressed, short (tail length < snout-vent length), with enlarged spiny scales dorsally and laterally ..... ***Hoplocercus spinosus***

– Tail nearly round, moderate (tail length > snout-vent length), with rings of enlarged spiny scales **3**

3 Vertebral region of trunk without enlarged scales; tail with three scale rows separating the spiny whorls ventrally ..... ***Morunasaurus groi***

– Some vertebral scales in trunk region enlarged forming a discontinuous longitudinal row; tail with two scale rows separating the spiny whorls ventrally..... **4**

4 Usually two femoral pores on each leg; two postmentals; females without streaks on throat ..... ***M. annularis***

– Femoral pores 3–4 on each leg; usually four postmentals; females with dark streaks on throat ..... ***M. peruvianus***

5 Caudal scales homogeneous in size within each autotomic segment **6**

– Caudal scales increase in size posteriorly within each autotomic segment.... **7**

6 Gular region in males white with a black medial patch ..... ***Enyalioides sophiarothschildae***

– Gular region in males orange or dirty cream, with longitudinal brown, reddish-brown, bluish, or orange streaks, and a large brown or black medial blotch at the level of the gular fold.....***E. laticeps***

7 Lateral superciliary projection present; vertebral crest usually discontinuous (absent on posterior part of neck) .....***E. palpebralis***

– Lateral superciliary projection absent; vertebral crest continuous **8**

8 Scattered, conspicuous large scales on dorsum, flanks, and hind limbs present.....**9**

– Scattered, conspicuous large scales on dorsum, flanks, and hind limbs absent.....**10**

9 Scattered large scales tetrahedral in shape; vertebrals on neck maximum twice as high as those between hind limbs..... ***E. heterolepis***

– Scattered large scales strongly keeled, not tetrahedral in shape; vertebrals on neck at least three times higher than those between hind limbs....***E. anisolepis***

10 Ventrals smooth or slightly keeled **11**

– Ventrals conspicuously keeled.....**12**

11 Gulars in males cream or yellow without black margins; usually one femoral pore on each leg.....***E. praestabilis***

– Gulars in males bright orange or red, with black margins; usually two femoral pores on each leg.....***E. rubrigularis***

12 Dorsals heterogeneous in size, with scattered, tetrahedral, projecting scales (sometimes absent in males or juveniles); dorsolateral crests well developed between hind limbs.....***E. cofanorum***

– Dorsals homogeneous in size, without projecting scales; dorsolateral crests inconspicuous or absent between hind limbs **13**

13 Dorsals smooth or slightly keeled.....**14**

– Dorsals conspicuously keeled **15**

14 Scales on flanks heterogeneous in size, with a few enlarged, circular, keeled scales; iris bright red in both sexes; black patch under gular fold extending dorsally to form a short antehumeral bar in males.....***E. oshaughnessyi***

– Scales on flanks almost homogenous in size; iris brown in both sexes; black medial patch on gular region not extending dorsally to form an antehumeral bar in males .....***E. altotambo***

15 Dorsals in transverse row between dorsolateral crests at midbody 31 or fewer.....**16**

– Dorsals in transverse row between dorsolateral crests at midbody more than 31 .....**17**

16 Scales along the lateral edge of the skull roof strongly projected; dorsal scales homogeneous in size, with prominent median keel; antehumeral orange blotch in adult males absent.....***E. binzayedi***

– Scales along the lateral edge of the skull roof slightly projected; dorsal scales heterogeneous in size, without prominent median keel; distinct antehumeral orange blotch in adult males ..... ***E. rudolfarndti***

17 White or cream spot posterior to tympanum usually present; 41–54 (mean = 45.96 ± 3.49) dorsals in transverse row between dorsolateral crests at midbody; gular background in adult males light blue..... ***E. microlepis***

– White or cream spot posterior to tympanum absent; 37–47 (means = 41.63 ± 3.20 in *E. azulae*, 40.50 ± 1.90 in *E. touzeti*) dorsals in transverse row between dorsolateral crests at midbody; gular background in adult males cream or black..... **18**

18 Vertebral scales in neck region in adult males similar in size to vertebrals in pelvic region; 45–57 (mean = 51.13 ± 4.05) gulars ..... ***E. azulae***

– Vertebral scales in neck region in adult males more than twice as high as vertebrals in pelvic region; 42–48 (mean = 44.40 ± 2.22) gulars..... ***E. touzeti***

Acknowledgments

For the type specimens of the species described in this paper we thank all collectors for their help in the field. Venegas is indebted to R. Wagter for logistic support in the field. We thank A. Varela and P. Santiana for editing the photographs; L.A. Coloma for providing photographs of the type specimens of *E. altotambo*; and C. Aguilar and J. Amanzo for providing valuable information. Specimens of the new species described in this paper were collected under collection permits 005-14-IC-FAU-DNB/MA issued by Ministerio del Ambiente, Ecuador, and N°08 C/C-2008-INRENA-IANP; 110-2007-INRENA-IFFS-DCB; 118-2007-INRENA-IFFS-DCB issued by Instituto Nacional de Recursos Naturales, Peru. This research was funded by The Systematics Association´s Systematics Research Fund (OTC), a Restricted Endowment Award from the Smithsonian Institution (KdQ, OTC), the Secretaría de Educación Superior, Ciencia, Tecnología e Innovación del Ecuador (OTC), Pontificia Universidad Católica del Ecuador (OTC), UCUMARI (PJV), and Gobierno Regional de San Martín GORESAM (PJV).

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Appendix

Specimens examined

Enyalioides cofanorum.—**COLOMBIA:** *Amazonas*: Puerto Nariño, 3°46'13"S, 70°22'59"W, 110 m, ICN 4229; **ECUADOR:** *Orellana*: 4km N Anangu on Garza Cocha at Hosteria La Selva, 260 m, MCZ 174428–29; Cononaco, QCAZ 5975; SPF, QCAZ 2710; transecto PBT, Pozo Capiron 2, QCAZ 7563; Tiputini Biodiversity Station, 0°37'5"S, 76°10'19"W, 215 m, QCAZ 8006; Yasuni National Park, bloque Shiripuno, 0°43'35"S, 76°43'36"W, QCAZ 3521; *Sucumbíos*: La Selva lodge, 0°24'0"S, 76°39'0"W, QCAZ 2935, 2961, 3951, 3953; Limoncocha, MCZ 157697; Santa Cecilia, 0°5'6"N, 76°59'33"W, 340 m, KU 105342 [paratype], 112180–81 [paratypes], 122118 [paratype], 146658 [holotype], 147584–85 [paratypes], 175308; Tarapoa, 0°7'60"S, 76°25'0"W, 283 m, FHGO 5764; *Zamora Chinchipe*: cuenca del rio Jamboe, Sakantza, 1230 m, FHGO 2342; **PERU:** *Loreto*: Ampiyacu river, Distrito Pevas, 3°19'0"S, 71°51'0"W, 100 m, CAS 8323.

Enyalioides heterolepis.—**COLOMBIA:** *Antioquia*: Dabeiba, río Amparradó, campamento Ingeominas, 6°42'0"N, 76°27'0"W, 805 m, ICN unassigned numbers (2 specimens); Municipio Frontino, corregimiento La Blanquita (Murrí), 800 m, IND-R 4229; Municipio Frontino, Vereda Venados, Parque Nacional Natural Las Orquídeas, afluente de la quebrada El Retiro, 6°33'0"N, 76°18'25"W, 850–950 m, ICN 9143; *Cauca*: bajo Calima, granja de la Secretaría de Fomento, 3°59'47"N, 76°58'28"W, ICN 4231; Guapí, 2°33'23"N, 77°51'50"W, ICN 4232, 4234–35; Gorgona Island, 2°58'31"N, 78°12'27"W, 30–120 m, FMNH 165387–88, ICN 824, 826–27, 832–38, 1045, 1247–53, 1325–26, 4237–44, 4521, 6515, ICN unassigned numbers (2 specimens), KU 192676–77; Guapí, on road to pipeline between Chansará-Cantadelicia, ICN 4233, 4236; Municipio de Junta, headwaters río Guapi, IND-R 3570; Quebrada Guangui, ICN unassigned number (1 specimen); *Chocó*: 5 km NW Playa de Oro, IND-R 3556; Bahía Solano, Parque Nacional Natural Utría, ICN unassigned number (1 specimen); headwaters of río San Juan, ca. 800 m, FMNH 165224; Quibdo, San josé de Purré, río Cabi, IND-R 5035; Serranía del Baudo, Alto del Buey, 6°6'0"N, 77°13'0"W, ICN 4245–46; *Valle*: Virology Field Station, USNM 151610–12; *Valle del Cauca*: 8 km W Danubio, río Anchicaya, KU 169853; Buenaventura, Base Naval Málaga, quebrada Valencia, 3°58'0"N, 77°18'0"W, ICN unassigned numbers (2 specimens); Dagua, Vereda La Elsa, 3°34'47"N, 76°46'54"W, 980 m, ICN 9091; km 6 on road Buenaventura-río Calima, 3°53'36"N, 77°4'11"W, 0 m, FMNH 165181–82; km 22 on road Buenaventura-río Calima, FMNH 165223; Municipio Restrepo, Vereda Alegre, Campo Chanco, 3°38'14"N, 76°13'44"W, 460 m, ICN 9093; río Raposo, above caserío El Tigre, 3°42'0"N, 77°5'60"W, 11 m, ICN 1501–02; *no specific locality*: ICN 9092, 9801, 11313; **ECUADOR:** *El Oro*: Gualtaco, USNM 211076; *Esmeraldas*: Alto Tambo, 253 m, QCAZ 5523; Bosque Protector La Chiquita, 30 km E San Lorenzo on road to Ibarra, QCAZ 3839; Corriente Grande, 70 m,

QCAZ 3531; Jatun Sacha Field Station, Montañas Mache-Chindul, 41km W Quinindé, 0°21'21"N, 79°42'12"W, 600 m, FHGO 3200; Loma Linda, río Onzole, 95 m, QCAZ 3626; Mayronga, 100 m, QCAZ 2185–86, 2263–66; Reserva Ecológica Mache-Chindul, comunidad San Salvador, FHGO 4063; San Miguel de Cayapas, QCAZ 412; *Los Ríos*: Estación Biológica Río Palenque, 150-220 m, KU 146657, 164166, 180657–58, QCAZ 427, USNM 285451, 285454; *Manabí*: 38 km NW El Carmen, ca. El Carmen-Pedernales road, 330 m, KU 218380; *Pichincha*: 15 km NW La Florida, QCAZ 2844; La Perla, QCAZ 2025–26; Palma Real, USNM 211094; Puerto Quito, km 132 on road Calacalí-La Independencia, Hostería Selva Virgen, FHGO 4314; río Blanco, below mouth of río Toachi, USNM 211088; río Caoni, USNM 211095; río Toachi, between kms 100-110 on road to Santo Domingo de Los Colorados, USNM 211097–98; *Santo Domingo de los Tsáchilas*: km 30 Quinindé-Santo Domingo de los Colorados, USNM 211091; Santo Domingo de los Colorados, 600 m, KU 121090–91; PANAMA: *Colón*: Achiote, 40 m, KU 96688; *Darién*: Laguna, 820 m, KU 76050–53; ridge btw río Jaque & río Imamado, 730 m, KU 113490–94; SE slope Cerro Pirre, 1060 m, KU 96689–90; Tacarcuna, 550 m, KU 76047–48; *San Blas*: Armila, USNM 150121 *Veragua* (possibly Veraguas): MHNP 4067 [holotype].

Enyalioides laticeps.—**BRAZIL:** Fonteboa, upper Amazon, MHNP 6821 [holotype]; **COLOMBIA:** *Amazonas*: 50 km N Chorrera on Igará-Paraná, IND-R 1038–41; headwaters of río Caiwima, tributary of río Amacayacu, ca. 70 km NNE Puerto Nariño, MCZ 154482; Leticia, 4°12'55"S, 69°56'26"W, 83 m, ICN unassigned number (1 specimen); Parque Nacional Natural Amacayacu, cabaña Amacayacu, IND-R 4195; Parque Nacional Natural Amacayacu, río Amacayacu, Puerto Mogue, close to río Cabimas, IND-R 1037; Parque Nacional Natural Amacayacu, Mata-mata creek, 3 km W Mata-mata cabin, 3°41'0"S, 70°15'0"W, 150 m, ICN 9094; Puerto Rastrojo, río Miriti, IND-R 1920, 1929; río Amacayacu, tributary of río Amazonas, ca. 50km NNE Puerto Nariño, MCZ 156348; río Amacayacu-Caiwima, ca. 40km NNE Puerto Nariño, MCZ 154481; río Miriti Paraná, IND-R 1905; *Caquetá*: 30 km from mouth of río Cuemani, IND-R 1063–65; Florencia, MLS 117; Parque Nacional Natural Chiribiquete, río Mesay, Puerto Abeja, 0°5'27"N, 72°25'0"W, IAvH 4746; *Guaviare*: Chiribiquete, ICN unassigned number (1 specimen); *Meta*: río Guayabero, Angostura No.1, 2°17'0"N, 73°58'0"W, 300–350 m, ICN 1270; Cumaral, Vereda Juan Pablo II, 3°47'0"N, 73°55'0"W, ICN 7255; Guaguriba on road to Acacias, MCZ 156323; La Macarena, campamento Isama, río Duda, ICN 4230; La Macarena, Caño Guapayita, ICN 677; Las Salinas, 3 km NW Restrepo, 4°16'9"N, 73°35'9"W, 720 m, ICN unassigned number (1 specimen); La Macarena, río Duda, Parque Nacional Natural Los Tiniguas, campamento de primatología Puerto Chamuza, IND-R 4019–22, 4034; Serranía La Macarena, Caño Sardinata, 30 km W Vista Hermosa, IND-R 287; Villavicencio, 4°9'12"N, 73°38'6"W, 500 m, AMNH 35277, FMNH 30815, MLS 116; Villavicencio, Pozo Azul creek, 4°9'12"N, 73°38'6"W, 500 m, ICN 8341, ICN unsassigned numbers (2 specimens), MCZ 154334; *Putumayo*: ca. 10 km (airline)

S Mocoa, 700–800 m, AMNH 106631; no specific locality: FMNH 165208, 165211; *Vaupés*: Caparú, surroundings of lake Taraira, 1°8'46"S, 69°29'14"W, ICN 8058–61; Estación Biológica Caparú, IND-R 4382; **ECUADOR:** *Morona Santiago*: cantón Taisha, parroquia Macuma, centro Shuar Macuma, 2°8'6.6"S, 77°42'54"W, 720 m, FHGO 5460; Arapicos, 1°51'0"S, 77°57'0"W, 981 m, USNM 211111; *Napo*: Ahuano, QCAZ 7014; Ávila, río Napo, CAS-SUR 8261–62; Tena, QCAZ 6054; *Orellana*: 7 km S río Tiputini, KU 299832–33; Estación Científica Yasuní, QCAZ 7388; Loreto, 0°40'0"S, 77°19'0"W, 451 m, USNM 211121; Parque Nacional Yasuni, Tambococha, FHGO 3692; Parque Nacional Yasuni, Tiputini, Ishpingo, FHGO 5346; Río Napo, Añangu, south bank, QCAZ 9503; Sacha Lodge, QCAZ 8884; *Pastaza*: Alto río, USNM 211146; Lorocachi, QCAZ 3222; Palmira, río Pastaza valley, AMNH 37554; río Capahuari, USNM 211122; río Huiyayacu, USNM 211128; río Pindo, USNM 211143; río Shiripuno, 1°5'0"S, 76°50'0"W, FHGO 1624; Sarayacu, USNM 211124; Villano, 1°30'0"S, 77°29'0"W, 388 m, QCAZ 8118, 8262; *Sucumbíos*: 2 km W Lago Agrio, KU 299835; Lago Agrio, KU 299834, KU 299836; río Cuyabeno, USNM 211113; Santa Cecilia, 0°3'0'', N, 76°59'0'', 340 m, KU 122104–05, 122110–11, 147931, 147939–41, 152497; San Jose, S Tarapoa, FHGO 4839; San Pablo de Kantesiaya, 0°15'0"S, 76°25'30"W, 240 m, FHGO 850; Zancudococha, 0°25'0"S, 75°30'0"W, 220 m, FHGO 304; **PERU:** *Amazonas*: Caterpiza, USNM 568575; Galilea, USNM 568576–80; *Cusco*: Pagoreni, río Camisea, 11°42'23"S, 72°54'11"W, 465m; *Loreto*: Explorama Lodge, jct río Yanamono & río Amazonas, KU 220493; Intuto, río Tigre, AMNH 60575; San Jacinto, 175 m, KU 222164; *San Martin*: San Martin, 14 km ESE Shapaja, 360 m, KU 212627; *Ucayali*: río Calleria, Colonia Calleria, 15 km from Ucayali, CAS 95143. NO SPECIFIC LOCALITY: ICN 1231.

Enyalioides oshaughnessyi.—**ECUADOR:** *Esmeraldas*: Bilsa Ecological Reserve, 225 m, QCAZ 6866; *Guayas*: cerro Masvale, QCAZ 9893; *Los Ríos*: Estacion Biológica Río Palenque, 150–220 m, KU 152597, USNM 285456–57, Estación Biológica Jauneche, 50 m, QCAZ 6899; *Pichincha*: Finca Victoria, 37 km SE Santo Domingo de los Colorados, MCZ 80958; Hotel Tinalandia, 15 km SE Santo Domingo de los Colorados, MCZ 145269; Puerto Quito, MCZ 164509; Recinto Playa Rica, on road Nanegal-Selva Alegre, QCAZ 7426; Silanchi, río Blanco, USNM 211102; Tandapi, MCZ 164789; Unión del Toachi, 300 m, QCAZ 5326, 6682; *Santo Domingo de los Tsáchilas*: 1 km N, 2 km E Santo Domingo de los Colorados, 620 m, KU 179417; 2 km E, 1 km S Santo Domingo de los Colorados, 600 m, KU 179416; Finca La Esperanza, 5 km W Santo Domingo de los Colorados, USNM 211105; Finca La Esperanza, 5 km W Santo Domingo de los Colorados, USNM 211106–07; Santo Domingo de los Colorados, KU 109630, USNM 211103, 211109. NO SPECIFIC LOCALITY: USNM 22448, 22450.

ZooKeys 494: 133–154 (2015)
doi: 10.3897/zookeys.494.9352
http://zookeys.pensoft.net

REVIEW ARTICLE

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Community Next Steps for Making Globally Unique Identifiers Work for Biocollections Data

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Academic editor: *R. Mesibov* | Received 7 February 2015 | Accepted 17 March 2015 | Published 6 April 2015

http://zoobank.org/88A49A9D-612C-4BA7-93DB-B4A203346506

Citation: Guralnick RP, Cellinese N, Deck J, Pyle RL, Kunze J, Penev L, Walls R, Hagedorn G, Agosti D, Wieczorek J, Catapano T, Page EDM (2015) Community Next Steps for Making Globally Unique Identifiers Work for Biocollections Data. ZooKeys 494: 133–154. doi: 10.3897/zookeys.494.9352

Abstract

Biodiversity data is being digitized and made available online at a rapidly increasing rate but current practices typically do not preserve linkages between these data, which impedes interoperation, provenance tracking, and assembly of larger datasets. For data associated with biocollections, the biodiversity community has long recognized that an essential part of establishing and preserving linkages is to apply globally unique identifiers at the point when data are generated in the field and to persist these identifiers downstream, but this is seldom implemented in practice. There has neither been coalescence towards one single identifier solution (as in some other domains), nor even a set of recommended best practices and standards to support multiple identifier schemes sharing consistent responses. In order to further progress towards a broader community consensus, a group of biocollections and informatics experts assembled in

Stockholm in October 2014 to discuss community next steps to overcome current roadblocks. The workshop participants divided into four groups focusing on: identifier practice in current field biocollections; identifier application for legacy biocollections; identifiers as applied to biodiversity data records as they are published and made available in semantically marked-up publications; and cross-cutting identifier solutions that bridge across these domains. The main outcome was consensus on key issues, including recognition of differences between legacy and new biocollections processes, the need for identifier metadata profiles that can report information on identifier persistence missions, and the unambiguous indication of the type of object associated with the identifier. Current identifier characteristics are also summarized, and an overview of available schemes and practices is provided.

Keywords
Biocollections, identifiers, Globally Unique Identifiers, GUIDs, field collections, legacy collections, linked open data, semantic publishing

Introduction

The current biodiversity and genomic fields are characterized by large and rapidly growing digital datasets. While this trend in digitizing the global biodiversity knowledge base is valuable and important for accessing and synthesizing biodiversity information in the era of the Internet and Big Data, much of this information remains only loosely integrated. Efforts to cross-link otherwise disconnected silos of data (Page 2008, 2009) still rely on largely imprecise points of intersection, such as text-string taxon names (as proxies for taxon concepts), combinations of institution codes, collection codes, and catalog numbers (as labels for biological specimens and other samples), and aggregates of metadata that allow inferring equivalency (e.g., a combination of place, time, and participants for collecting events).

The necessary solution to build more connected, cross-linked and digitially accessible Internet content is to assign recognizable, persistent, globally unique, stable identifiers to biocollections specimens and data objects. While effort has been put forth on applicability statements for both Life Science Identifiers (LSIDs) and globally unique identifiers (GUIDs) (Pereira et al. 2007, Richards 2009), and on other fronts (Pyle 2006, Cryer et al. 2009, Baskauf 2010, Richards et al. 2011, TDWG 2013, Bouchout Declaration 2014), no single solution or clear best practice has taken hold in the biocollections community. To illustrate, Table 1 shows some example of identifiers associated with data mobilised by GBIF and includes LSIDs, URNs, HTTP-URIs (URLs) of various types, and DOIs (See Box 1 for explanations of abbreviations used in this article). The community has also struggled to define its view on identifier and dereferencing service persistence, and whether physical objects and abstract concepts should have identifiers that include embedded information on dereferencing services and protocols (a dereferenceable identifier contains an Internet protocol that directs a client to information about the resource it identifies), or whether functions of object identification and dereferencing should be decoupled. Further, and perhaps most important, the next steps towards a community-wide GUID solution are unclear.

Table 1. Examples of identifiers in use for biological samples in the GBIF database.

GBIF occurrence	Identifier type	Identifier	Catalog number	Collection
872747863	LSID	urn:lsid:biosci.ohio-state.edu:osuc_occurrences:OSUC__169968	OSUC 169968	C.A. Triplehorn Insect Collection
896421698	URN	urn:occurrence:Arctos:MVZ:Bird:157675:1526959	MVZ 157675	MVZ Bird Collection
784060956	URN	urn:catalog:UMMZ:Mammals:171041	UMMZ 71041	UMMZ Mammal Collection
575336458	HTTP URI	http://data.rbge.org.uk/herb/E00115694	E00115694	Royal Botanic Garden Edinburgh Herbarium
1050474791	HTTP URI	http://arctos.database.museum/guid/UAM:Ento:230092	UAM 230092	UAM Entomology Collection
1050474791	DOI	10.7299/X7VQ32SJ	UAM 230092	UAM Entomology Collection
624211191	UUID	EF0A4D3E-702F-4882-81B8-CA737AEB7B28	UF 161444	UF FLMNH Ichthyology
476850316	Darwin Core Triplet	MCZ:Mamm:8831	MCZ 8831	Museum of Comparative Zoology, Harvard University

Box 1. Abbreviations and the full spelled out version or more detailed meaning.

ABCD	Access to Biological Collections Data
ARK	Archival Resource Key
BCO	Biological Collections Ontology
DMP	Data Management Plan
DOI	Digital Object Identifier
EZID	A type of identifier & system run by California Digital Library
GBIF	Global Biodiversity Information Facility
GRBio	Global Repository of Biorepositories
GUID	Globally Unique Identifier
HTTP-URI	HTTP Uniform Resource Identifier
IGSN	International Geosample Number
LOD	Linked Open Data
LSID	Life Sciences Identifier
NEON	National Ecological Observatory Network
OCR	Optical Character Recognition
TDWG	Biodiversity Information Standards
URI	Uniform Resource Identifier
URL	Uniform Resource Locator
URN	Uniform Resource Name
UUID	Universally Unique Identifier

The application of identifiers to biocollections and the physical (and conceptual) objects they contain is complicated by both long and ingrained identifier curation practice, and a rapidly changing technology landscape. Legacy collections often have

a checkered past of provenance-tracking; as a result, essential linkages between data and collections have been lost due to lack of coordination and data practices predating digital recording. New, "born-digital" sampling methods promise to open floodgates of data and can make it easier to assign globally unique identifiers at the point of data creation. Thus, the optimal identifier solutions for new collections may be different than those for legacy data. Adding to the challenge, vast amounts of biodiversity data are in the scientific literature, which is the oldest form of biodiversity reporting. These data can be mined from the legacy literature but are largely "hidden" in non-semantic formats. In the future, advances in digital publishing will enable data to be more thoroughly linked to the literature, and vice-versa (Penev et al. 2010), thus laying the foundation for new best practices for citing datasets by means of identifiers.

In order to further progress on this critical issue, a group of biocollections and biodiversity informatics experts and stakeholders (Appendix 1) assembled at the Stockholm Museum of Natural History, 25–26 October 2014 to lay out a set of recommendations and next steps for community-wide approaches to globally unique identifier assignment, persistence, and dereferencing. After the opening discussions and compiling of key identifier characteristics (Box 2), the participants organized into four subgroups during the meeting: New biocollections, legacy biocollections, semantically enabled publications, and cross-cutting issues. In this paper we review the workshop results under those four headings and summarise consensus views on what should happen next.

Application of Identifiers to Newly Collected Field Biocollections

Field biocollections are extraordinarily diverse and continue to grow in scope and scale with the advent of novel technologies such as environmental DNA analyses (e.g., metagenomics), and new continental field-based endeavors such as the National Ecological Observatory Network (NEON; http://www.neoninc.org/) in the United States. Current practices in field collecting are highly heterogeneous and often based on traditional practices of local identifier assignment. Traditionally, "field numbers" are assigned prior to the specimen being fully accessioned. More permanent identifiers (which are also often only locally unique within an institution) are assigned when specimens are accessioned in a collection. In some cases, organizations and communities are already using globally unique identifier systems and even assigning permanent UUIDs for field collection objects while still in the field (as is planned by NEON). In contrast, the geology community has rallied around International Geo Sample Numbers (IGSNs; http://www.geosamples.org/igsnabout), which provide not just global uniqueness, but also minting authority, governance, and a set of services for resolving those numbers that are managed centrally. The lack of consistent practices in biological field sampling compared to what has been accomplished in geology is a lamentable drawback in biodiversity research.

The assignment of local identifiers (e.g., catalog numbers) to specimens for internal management purposes and for external referencing has been the standard practice

Box 2. Below the main characteristics of identifier schemes are listed. The list is not meant to be exhaustive but is intended to cover the major differences across different approaches.

Identifier Schemes:

- support **locally unique** (e.g., catalog numbers) and/or **globally unique** (e.g. DOIs, URLs or UUIDs) identifiers. Global uniqueness is vital to minimize ambiguity;
- provide identifiers that are **actionable.** Actionable identifiers may rely on special knowledge (e.g. for LSIDs, DOIs, or http services for plain identifiers) or they may rely on Internet standards (URIs);
- may require resolvers to support access to the **object** and to its **metadata**; for example, **content negotiation** (e.g., used by Linked Open Data) supports the provision of a human-readable object in one context and machine-readable metadata (e.g., RDF, JSON) in another context; additionally, **inflections** (e.g., ARK) let an ordinary user add to the identifier to request the object or its metadata
- may use **centralized** (e.g., purl.org, doi.org, n2t.net) or **decentralized dereferencing hosts** (e.g., an institutional site);
- may support **transparent identifiers** (e.g., identifier strings that contain information which can lead to semantic guesses by humans, such as collection numbers, collectors' initials, or institutional names) or **opaque identifiers**, e.g. strings of letters and digits created by software (counter, UUID generator, Noid minter);
- may come with **fees** for creation of an identifier (e.g. DOIs);
- may come with **fees** for the use of the resolver; these fees, which affect **scalability**, are separate from the time and effort required of end-providers no matter which identifier scheme they use (object curation, disk storage, updating resolver data as the object moves, etc.);
- may come with **metadata** requirements (e.g., DataCite DOIs) or guidelines; presence or absence of **citation** metadata can affect **visibility**;
- may come with administrative tools for central identifier **registration**; besides recording metadata, registration enters identifiers into a database so that the resolver host can look it up and forward requests to the object's current location; for example, user interfaces and APIs exist for EZID ARKs, DataCite DOIs, Handles, and PURLs

of biocollections for centuries. As long as humans need to communicate with other humans about specimens, this practice will (and should) continue. By themselves, however, such local identifiers ultimately lead to reduced value of specimens if they are used as the nexus to which all other derived, digitized data connect. The main problem is that local identifiers are not sufficient for linking data across the Internet; globally unique and persistent identifiers are a requirement for this. Thus, to maximize the value of specimens for both human-human communication and human-computer (as well as computer-computer) communication, globally unique identifiers should be issued to data objects together with local identifiers.

Roadblocks

Providing a chain of provenance for specimens and related data is a major challenge and has a set of roadblocks along multiple dimensions. Traditional field collecting methods are ingrained in many scientists. The informatics community needs to reach out more effectively and explain to scientists the limitations of existing workflows and why an identifier scheme built around global uniqueness is not only necessary from an

informatics standpoint, but would dramatically enhance the value of data for re-use, syntheses and analyses. Identifier solutions must support scientists' current practices and create minimal burden during the collecting process. The solution should provide incentives for adoption, both in the field and in downstream information systems. In particular, effort is needed to ensure perpetuation of field-assigned identifiers through to more permanent data curation steps. Whatever underlying identifier system is chosen, it needs to be robust in preventing the same identifiers from being assigned to different objects (and, ideally, reducing circumstances where the same object receives multiple identifiers).

An additional roadblock is a lack of clarity as to which classes of objects, concepts, or events identifiers should be assigned. Should GUIDs be associated with the actual, physical specimen or with the derived digital (e.g. images) or physical (e.g. tissues) derivatives? Focusing on biocollections specimens as material samples helps semantically clarify what bears the identifier, but many other modeling challenges relating measurement processes etc. to specimens still remain. Even for physical specimens, there are challenges in defining the types of entities that can constitute a specimen, which range from a distinct organism to a part of an organism, to a set of organisms, to abiotic samples containing specimens (e.g., a jar of seawater).

Next Steps

For newly collected samples, a highly desirable next step is the ability to assign globally unique identifiers directly to newly collected specimens or mixed samples in the field or shortly thereafter. In many cases, it may be desirable that these identifiers be pre-minted and written into a physical barcode or QR-Code, perhaps in conjunction with a human-friendly identifier. Figures 1 and 2 show different examples, the first representing a traditional biocollections object and the second depicting mass-labeling of tubes associated with collections samples. Assigning GUIDs to specimens at the time of collection allows field researchers to publish references to recently collected specimens without waiting for institutional identifiers that are assigned during the accession process. Beyond simply assigning unique identifiers in the field, it is critical that these identifiers persist perpetually with the objects they identify and all descendant samples, subsamples, analyses, data and publications referring to them, ensuring an unbroken chain of data provenance. In the best of all possible worlds, identifiers assigned in the field are retained as the permanent institutional identifier during accessioning.

It is not feasible (or, at this stage, even desirable) for the entire biodiversity community to adopt a single implementation for identifiers. However, evaluation of the available technical solutions is a high priority, and the scope of solutions includes IGSNs, DOIs, EZID ARKs, LOD-URIs and UUIDs (comparisons among many of the different options are shown in Table 2 and a comparison of more or less centrally managed mapping and redirection services is shown in Figure 3). The group explored

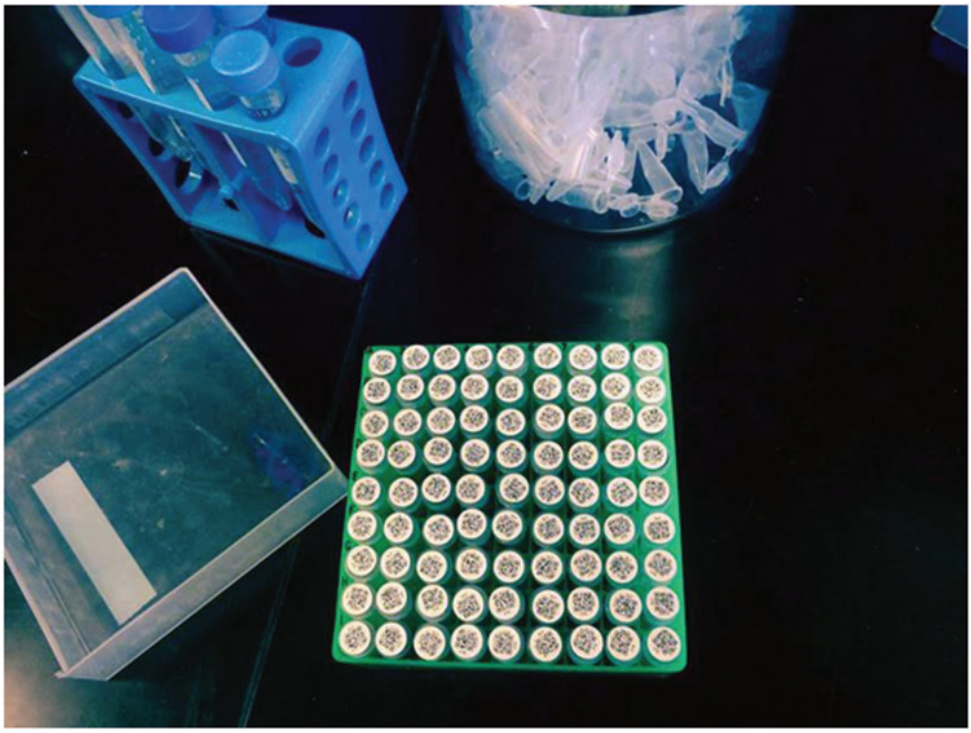

Figure 1. Example of UUIDs embedded within QR-Codes on microcentrifuge tube labels. The 5 mm × 5 mm QR-Codes (Version 2) are printed with a standard laser printer on sheets of self-adhesive 9 mm dots, and scan reliably with a standard barcode reader, while still providing room for a human-readable 5-character prefix + 5-digit number (the human-readable number and UUID are permanently cross-linked in the data management system). Photo: Robert K. Whitton.

several different viewpoints promoting the utilization of HTTP URIs for all identifiers and did not reach a consensus. HTTP URIs have the advantage that they provide a semantic web compatible default dereferencing method through the standard http protocol and can be flexibly constructed (Hagedorn et al. 2013). The advantage of many identifiers not being a HTTP URI is that the omission of a default dereferencing method avoids potential confusion and may allow for even greater flexibility. However, we recommend all identifiers have the ability to be dereferenceable through at least one http-based service, even if the http-form is not preferred.

The group strongly suggested that an immediate next step would be to prototype solutions to create persistent identifiers built on different, existing platforms. Such prototypes would engage stakeholders in testing and feedback in order to refine prototypes. The prototypes could also spawn key actions, including more focused workshops/hackathons, perhaps in the context of the Taxonomic Databases Working Group meetings (TDWG), with the goal of reporting outputs of such trials. TDWG, in particular, is a crucial stakeholder as an international standards organization for biodiversity objects and data.

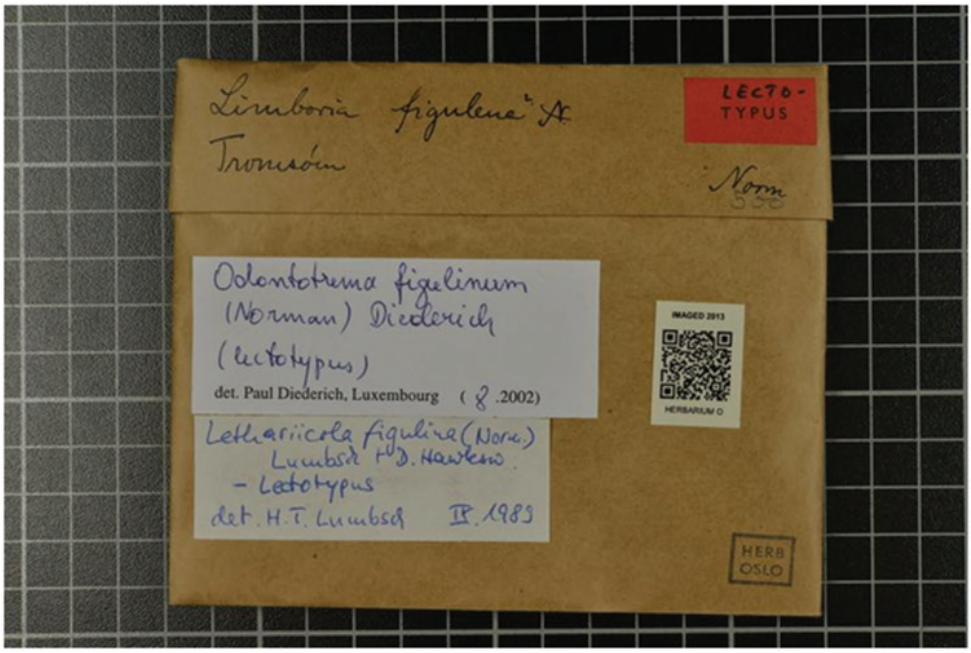

Figure 2. Example of a PURL-URI as a QR-Code, in this example attached to a digitised lichen type specimen in the Natural History Museum, University of Oslo. The QR-Code corresponds to http://purl.org/nhmuio/id/c1a8b878-a4f9-448b-be00-26cbad58b11c.

Scaling up to a larger system will require obtaining funding to support development. A fruitful path would be to align a few organizations that are working nationally or globally (e.g., NEON, iPlant (http://iplant.org), iDigBio, Critical Zone Observatories, Consortium of European Taxonomic Facilities) to adopt an early version of the system and to show interoperability and enhanced ability for tracking specimens and their derivatives as an outcome. For those more at the longer-tail of the specimen curation process, such as smaller biocollections or individual labs, incentives for adopting a system to replace the local numbering systems currently in practice could help coalesce efforts, and could further promote the value of such approaches when putting together data management plans (DMP) for funding agencies. In particular, identifier-specific DMP Tool (https://dmptool.org/) template content should be provided. Finally, with the strong growth of handheld devices, the biodiversity informatics community should work to produce tools for assigning identifiers with such devices.

A more detailed implementation proposal could be specified just for field collections, as part of a TDWG task group, leading to a community input and review process. This would be one key part of a larger effort to identify and reach out to national and international stakeholder groups, including collection managers, aggregators, publishers, scientists, funding agencies, downstream users of the data, and developers of software (e.g., Specify, http://specifyx.specifysoftware.org/; Symbiota, http://symbiota.org/docs/; and in-house software used by aggregators such as GBIF).

Table 2. Identifiers schemes according to key characteristics noted in part in Box 2.

Identifier characteristics	DataCite DOI	EZID ARK	OCLC PURL	Self-minted HTTP URI*	LSID	DwC Triplet	UUID
Globally Unique	yes	yes	yes	yes	yes	no	yes
Service Metadata Required for global uniqueness	yes	yes	yes	yes	yes	no	no
Per-identifier Cost	per id or subscription fee	yearly subscription fee	free	free	free	free	free
Identifier Issuance	registration	registration **	registration	local	local	local	local
Human-Friendly	provider dependent	provider dependent	provider dependent	provider dependent	provider dependent	high	low
Opacity	partial	partial	partial	provider dependent	provider dependent	low	high
Adoption by biodiversity informatics community	biodiversity publishing	low	low	high	low	collections community	variable
Adoption by broader informatics infrastructures	variable	low	variable	high	low	low	high
Dereferencing Service Integration	yes	yes	yes	yes	yes	no	no
Dereferencing Characteristics							
Dereferencing Type	central	central	central	distributed	distributed	N/A	N/A
Structured Identifier Responses directly from resolver ***	HTML, RDF/XML	HTML	HTML	provider dependent	yes	N/A	N/A
Redirection	yes	yes	yes	possible	possible	N/A	N/A
Clear Namespace policy and contract	yes	yes	no	no	no	N/A	N/A
Resolution service backed by institutions	yes	yes	no	provider dependent	no	****	****

* Self-minted HTTP URIs may include ARKs or PURLs as well

** ARKs have special mechanisms to extend scalability

*** Structured metadata responses may be available after redirection, depending on the provider (e.g. dublincore.org returns RDF/XML for PURLs)

**** Perhaps, if hosted by a general service (e.g. GrBio for Biocollections, GBIF for occurrence records, etc.)

Application of Identifiers to Legacy Data

Legacy specimens can be defined as material already stored in collections. The identifiers being considered here are those referring to collection objects, which may or may not persist in the collections, (e.g., living collections, tissue sample for DNA extraction, ecological specimens). A single physical collection object is a curatorial unit, which may represent only a part of a larger thing (e.g., mammal skeleton, fur, tissues), or may be an aggregate (e.g., lots, fossils with multiple organisms, herbarium sheets with multiple specimens). When aggregates are split (e.g., multiple taxa split

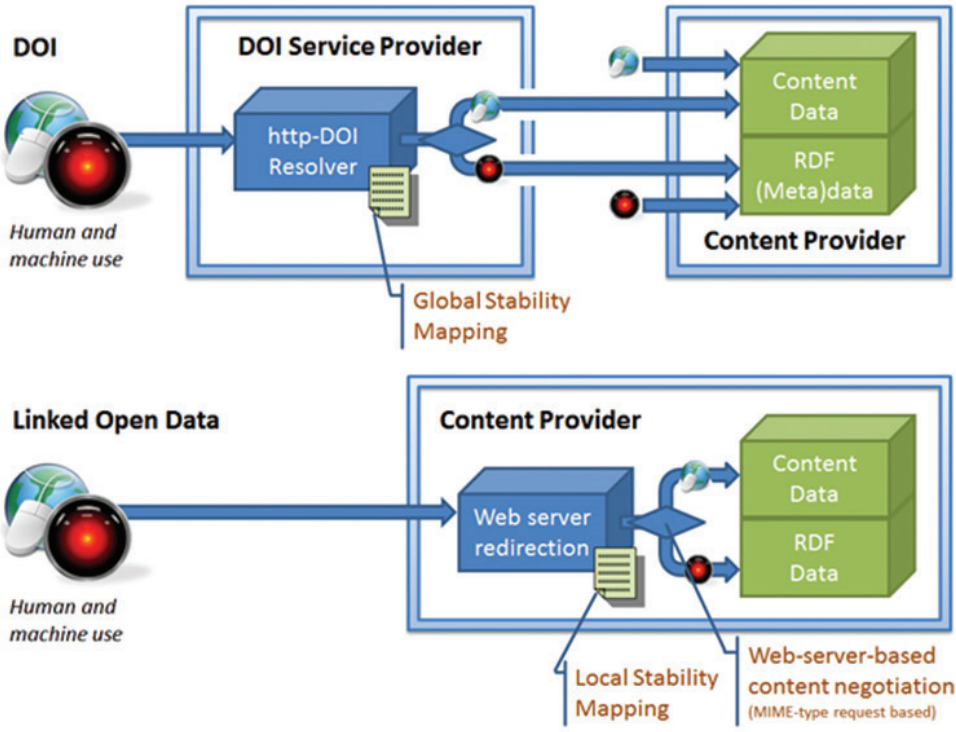

Figure 3. Identifier schemes differ in whether redirections and mappings to ensure stability are centrally managed or not. Top: a DOI dereferencing service like CrossRef or Datacite redirects to the actual content provider; the URIs of content data and RDF metadata are publicly visible and can be used as independent (albeit often unstable) identifiers. Bottom: A linked open data pattern, where each content provider assumes the responsibility for maintaining a stable mapping; the content negotiation is internal. Modified after Hagedorn 2013.

into different lots, parasites found on organisms, tissue samples removed), the original identifier generally relates to one of the elements and a new identifier is issued for the additional elements.

Most scientific journals, and even GenBank (http://www.ncbi.nlm.nih.gov/genbank/), make only vague recommendations about citing voucher specimens. The legacy identifier commonly used in the literature for botanical specimens over the last hundreds of years is the collector's name and collecting/field number, which often represents the collector's personal series number. The legacy identifier commonly used for zoological specimens is the institution acronym/catalog number. For example, the American Society of Mammalogists makes the following recommendation for the Journal of Mammalogy (http://www.mammalsociety.org/uploads/JM%20Author%20Instructions.pdf):

> "All DNA sequences must be submitted to GenBank, and accession numbers provided in the manuscript before publication. Museum catalogue numbers for all voucher specimens (including associated tissue) examined must be included in the manuscript (in an Appendix if numerous)."

Roadblocks

The single key roadblock with legacy data is the use of local identifiers at all steps during the collection and accessioning process. While these provide means for local provenance tracking, they are insufficient for managing across collections, and are hard to adapt and scale to an open platform for data discovery such as the Internet. A classic example is botanical "duplicates" that come from the same collecting event where different clippings of the same plant were sent to multiple museums. Similar issues can be found for cases where specimens were gifted from one collection to another. In these cases, linkages associating those specimens across collections were typically severed when biocollections were accessioned independently into institutional museum repositories. Those past associations can only be inferred from re-compiling data and looking for content-level matches related to the collections events.

Further, because most collections have effectively developed local curatorial practices, often based on regional and taxon-specific approaches, there is a wide variety of different legacy identifiers associated with specimens and their data. In sum, current practices were and remain highly heterogeneous and the information that could re-associate specimens across collections are lost and cannot be solved simply via post-hoc application of new GUIDs. Thus, the problems with legacy collections are managing both identifiers already in use and dealing with potential application of new ones.

Next Steps: As a pragmatic matter, the immediate next steps for legacy collections may not include broad application of globally unique identifiers. Instead, a short term next step is for biodiversity informaticians and collections staff to work together to standardize practices for assigning unique identifiers that are persistent (remain tightly associated with the objects they identify) and stable (continue to be actionable). At a minimum, institutions should clarify the identifier scheme being used locally via their own internal policies. Further development of community-wide best practices would be more effective because they would not only foster local curatorial practice, but also specify how those locally curated materials and their data eventually become part of the rapidly coalescing global, digital framework. These best practices need to be developed in the context of existing efforts and/or organizations such as the Global Registry of Biorepositories (GRBio; http://grbio.org/), which provides a needed framework for publishing repository-specific information like standard acronyms for institutions and collections. Curators should register their collections in GRBio and specify the adopted identifier scheme for the collection.

The legacy group also considered medium-term and longer-term goals, focusing more on broad informatics solutions than local identifier curation practices. One critical step is to assemble identifiers published by curators to aggregators such as GBIF and to assess identifier heterogeneity. This can feed into developing software for comparing identifiers (e.g., resolvers) that is better able to perform fuzzy matching on identifier strings (and fetch such variations), given that identifiers are sometimes expressed in unintended ways (e.g., added spaces or hyphens, capitalization, etc.). Using just a simple string comparison is insufficient and more robust systems should be set in place, which will then forward to the correct identifier. The same applies to whether a URI prefix should be part of the identifier or not.

Next, in order to avoid broken URIs, institution-independent resolvers (e.g., purl.org) or aggregators (e.g., GBIF) should check dereferenceable URIs at certain intervals and inform the responsible contact person when the target URIs return a 404 HTTP status code or are otherwise unavailable. Some providers, such as CrossRef (http://www.crossref.org/), offer services for policing broken URIs. With regards to the data records associated with specimens and published to aggregators such as GBIF, the legacy identifiers group strongly argued for the longer-term goal of inclusion of proper GUIDs in the occurrenceID (or materialSampleID) Darwin Core (Wieczorek et al. 2012) field, rather than some sort of concatenation of local identifiers, such as a Darwin Core triplet (Guralnick et al. 2014). Finally, we strongly encourage integration of identifier metadata into existing standard schemas (e.g., Darwin Core, ABCD; http://www.tdwg.org/activities/abcd/) as new concepts. Such metadata would include information regarding identifiers, persistence, rules for attribution (use, citation, reference) etc.. as is also discussed further in the "cross-cutting solutions" section.

The legacy biocollections group developed a list of immediate action items to most efficiently take the steps listed above. As a priority list, these include:

1) Assemble current identifiers from aggregate data as a means to determine current practices. Some of this work has already been accomplished as part of work by Guralnick et al. (2014) to evaluate Darwin Core Triplets and their current use as identifiers in different systems (e.g., VertNet, http://vertnet.org; Barcode of Life Data Systems, http://www.boldsystems.org/; GenBank), but further work focusing on GBIF datasets is needed. A critical assessment of current implementations will feed into the next step of generating more informed best practices or appropriate strategies that individual institutions can adopt based on their current GUIDs application.
2) Create best practice documentation on known identifier minting schemes. Document best practices with use cases, examples, and pros and cons.
3) As in the new field-collected biocollections group, there is a need to further clarify what exactly is being identified - MaterialSample vs. Organism vs. Occurrence; physical object vs. digital representation.
4) Clearly define the scope of the proposed identifying scheme and what benefits can be gained by it.
5) Demonstrate the implications for publishing in the primary literature.

Application of Biodiversity Data Identifiers In Publishing

Scientific publications are at the core of science communication and still one of the most powerful means for researchers to share their findings. Biodiversity oriented publications, including historical ones dated from the time of Linnaeus and before, provide one of the most important source of data and information, along with the means to quantitatively assess the impact of biocollections, institutions, and taxonomic groups. This enormous resource ultimately provides needed content for museums worldwide in their efforts to

secure continued funding for preserving and digitizing their specimen collections. Although the legacy literature is an essential resource and ultimate home for data derived from biocollections, it remains difficult to mine data from it, and provide the means to cite or track data usage. In the 21st century, these problems magnify as new digital systems are built to support registration of new data and provisioning of older content. By maintaining the currently prevailing model of publishing biodiversity information in formats not readable by machine or not readily harvestable, such as paper or PDF, we further impede efforts to convert data into fluid formats that support new science. One of the solutions to the problem is the wide adoption of identifiers for different data elements normally present in biodiversity publications. We present a set of use cases that would strongly benefit from a system of globally unique identifiers:

1) Use of identifiers for handling data across a registry (e.g., ZooBank), a publisher (e.g., Pensoft; http://www.pensoft.net) and a data aggregator (e.g., Plazi; http://plazi.org), thus providing linkages between all three.
2) Use of DOI identifiers for legacy literature allowing full citations from specimens to formal taxon treatments to other publications and vice versa.
3) Enabling of impact tracking of biological specimens, collections, institutions, and biodiversity data across journal articles.
4) Managing of information about specimens (e.g., occurrence records) in a similar way to publication and citation of data in the scholarly literature. For example, there is no current method to import (e.g., through an API) specimen records from resources such as GBIF into manuscripts, and ensure proper provenance and citations of these.
5) Import and citing of specimen records in publications with their own identifiers generated by the primary data providers or by aggregators (e.g., VertNet, GBIF, iDigBio; http://idigbio.org), paving the way to a wide array of future re-uses, including automated tracking of data usage and impact metrics.
6) Reconciliation of specimen label data with collection records published in literature (e.g., for transcription purposes or usage tracking of collections data) via the identifiers as a needed mechanism for linkage.
7) Aggregation of Web content from biodiversity data contained in publications. For example, articles that benefit from semantic markup allows for parsing and linking of independently published biodiversity data.
8) Use of identifiers to reference needed evidence: "In scholarly literature, whenever and wherever a claim relies upon data, the corresponding data should be cited" (http://www.force11.org/datacitation, principle 3).

Roadblocks

The difficulties in managing, tracking, and large-scale extracting of citations from any sources other than traditional publications are, in part, due to the paucity of widely adopted, persistent, globally unique and resolvable biodiversity data identifiers. Addi-

tionally, extracting specimen, taxon, and other biodiversity data from modern scholarly publications with unstructured formats and little to no markup is needlessly challenging. Another major obstacle is that information about specimens might be published in different places and with different levels of granularity. For example, a specimen might be cited as a holotype in a protologue, then georeferenced and published again in subsequent revisions, perhaps even under a synonym, with images and DNA data appearing separately in other publications. Unless the original specimen collection number is used consistently across all publications, it is difficult, if not impossible, to link together all the important digital derivatives independently generated from that specimen.

A final roadblock is the lack of adoption of advanced publishing approaches, including semantic markup, by almost all publishers in this domain. The TaxPub / Journal Archival Tag Suite provides (Catapano 2010, Penev et al. 2010, 2012) all the necessary functionality and has been successfully implemented by Pensoft in 14 journals, including the registration of the their articles in PubMed and PubMedCentral. However, it places the burden on publishers to adopt new technical approaches that are difficult to meet given a lack of resources and strong incentives for change.

Next Steps

The key next step is to establish the best practices to generate and assign identifiers as they either propagate from biocollections into the literature or are created during semantically enabled publishing processes. Such practices will assure that publications follow a set of principles ratified by various stakeholders and governments, and perhaps best described broadly in the Force11 data citation principles (https://www.force11.org/datacitation), and more directly for the biodiversity community in the Bouchout Declaration (Bouchout Declaration 2014, http://bouchoutdeclaration.org/). Tools are needed to retrieve identifiers assigned to biological names, taxonomic treatments associated with a name and specimen data discovered in the published records and/or stored in domain specific databases.

Below we summarize critical practices and principles for the use of identifiers in semantically enhanced publications:

1) Publishers should use GUIDs for formally cited or potentially relevant data (e.g., authors, books, articles, taxon names, taxonomic treatments, gene sequences, specimens, etc.) maintained in well- established and widely used external registries.
2) Publishers should issue GUIDs for data first made widely available through document publication (e.g., observation on a species published by an amateur naturalist with no GUID issued by or associated with an Institution).
3) Publishers should provide both human- and machine-readable content (Starr et al. 2015) through resolvable GUIDs for separate elements of an article (e.g., individual images, graphs, tables, supplementary materials, taxonomic treatments, checklists, etc.).

4) Resolvable GUIDs should be used as widely as possible to annotate published content; for example, adding a species to a published checklist should be identified by a GUID, which can be linked to the exact "place" within a published text (e.g., between two species in the checklist).
5) Publishers should use GUIDs and authority files for authors, e.g., ORCID (http://orcid.org/), VIAF (http://viaf.org/), authors of plant names (http://www.kew.org/data/authors.html), ZooBank authors (http://zoobank.org) or internal systems that unambiguously identify names of authors.
6) For the conversion of legacy literature, assign GUIDs to relevant elements that are widely used, resolve to content (e.g., articles, treatments, observation records) and can be a source for Linked Open Data. Whenever possible, use an existing identifier service (such as Plazi for treatments), rather than minting additional identifiers.
7) The identifier system(s) should be sustainable for the long term, highly reliable, and have an API as a backbone service.
8) We note a preference for identifiers used by indexing services (while such services use many kinds of identifiers, CrossRef and DataCite (http://datacite.org) DOIs are the most commonly used). Publishers should link data related to an article and the article itself through their GUIDs (CrossRef and DataCite DOIs cross-referencing service).
9) Identifiers and their metadata related to annotations in publications should be housed and made available by an independent party.

We discussed how systems can be built around identifiers that support all the different participants involved in publishing. Authors are critical participants and should better be able to cite usage of their data from semantically enhanced, rather than unstructured, formats. Publishers can assist authors by making all published data linkable/citable and contributing to specialized databases and/or permanent repositories (e.g. Dryad (http://datadryad.org/) or the Biodiversity Literature Repository (https://zenodo.org/collection/user-biosyslit)). Publishers can also provide authoring tools (such as the Pensoft Writing Tool (PWT) used by the Biodiversity Data Journal – see Smith et al. 2013) that assist authors with entry of structured data (i.e., upfront pre-submission markup and easy data import into the manuscript) to which new or existing identifiers can be assigned or included. Hence, easy data download and export to aggregators from the published paper can be achieved.

To serve the broader community (i.e., beyond authors), publishers can also provide tools to find cited data (e.g., http://refindit.org, which searches across CrossRef, DataCite, Mendeley (http://www.mendeley.com), RefBank (http://refbank.org), Global Names Usage Bank (http://www.globalnames.org/GNUB), Biodiversity Heritage Library (http://www.biodiversitylibrary.org/), Biodiversity Literature Repository (https://zenodo.org/collection/user-biosyslit) and others), as well as an ORCID lookup linked to data creators or owners. Contributing institutions can much more easily assess their institutional impact in biodiversity research output by tracking the usage of identifiers embedded in the articles, as well as better manage intellectual property. For example,

publishers can work with organizations such as GRBio to create identifiers for institutions so that all can be cited. Funding agencies can better argue that open access is not only a legal mandate but maximizes their return on investments in terms of products made available to the public. One possible step forward is to create identifiers for funding agencies (e.g., Fundref http://www.crossref.org/fundref/).

Cross-Cutting Issues and Needs

On the second day of the workshop, a subgroup met to broadly consider cross-cutting issues and needs, given the complexity of semantically interlinked publishing, legacy data, new biocollections, and connections to ecological, biomedical, and climate datasets. The group noted that many needed solutions are described in detail by the Cool URIs W3C Interest Group Note (http://www.w3.org/TR/cooluris/). In addition, the group suggested that promoting any particular approaches and standards apart from W3C efforts should be undertaken as part of the reinvigoration of the TDWG globally unique identifiers task group (http://www.tdwg.org/activities/guid/). Because identifier concerns are cross-cutting and involve research scientists, collectors, curators, publishers, and downstream users, collaboration with additional organizations focused on care of collections, such as the Society for Preservation of Natural History Collections, is needed. Shared responsibility among stakeholders can also break down barriers and enhance knowledge dissemination, helping to bridge the two worlds of physical and digital objects in curation of biocollections.

Defining the Target of the Identifier

Not all identifier schemes are unambiguous in declaring which identifier refers to an information resource and which to a physical object or abstract concept or event. For instance, an identifier referencing a photo of an eagle on a tree could be identifying the digital photo itself, a photographic print that was later scanned, a reference to the eagle as a physical specimen stored in a museum, the event of capturing the image, or a reference to an individual eagle that exists in nature. Distinguishing concepts such as “digital media”, “print media”, “individual”, and “specimen” is not trivial and ultimately relies on attaching formal descriptions from a biodiversity or biocollections ontology to the identified object. We encourage the use of the Darwin Core Basis Of Record term (http://rs.tdwg.org/dwc/terms/basisOfRecord) to describe the exact nature of the resource. There is a current proposal for tying values for the Basis Of Record term to ontology sources in the Biological Collections Ontology (Walls et al. 2014, Deck et al. in press) which will greatly help in clarifying the concepts underlying identified objects and their downstream use.

Standardizing Identifier Metadata Requests & Responses

Various identifier schemes behave differently when posting requests and receiving responses; standardized responses are urgently needed. An important example is the standardized content negotiation behavior in the semantic web; other examples are the unified content negotiation by CrossRef and DataCite (http://crosstech.crossref.org/2012/05/crossref_and_datacite_unify_su.html). Identifier metadata can be requested from the service provider not only using Linked Data patterns (which a user cannot do with just a web browser), but also by manipulating the URL endpoint directly, such as URL inflections (https://wiki.ucop.edu/display/Curation/ARK), alternate resolution prefixes, 303 re-directs or hashtags to denote physical objects, or parameter specification in the URL query string. The EZID system provides the ability to deliver DataCite, Dublin Core, CrossRef, or Dublin Core kernel (http://dublincore.org/groups/kernel/spec/) metadata profiles. **A strong recommendation is to create a biodiversity metadata profile to complement these existing profiles**.

Policy and Contracts

What intention goes into the creation of an identifier, including any contracts and technical specifications? The policies of identifier assigning authority provide information about the expectation of commitment, longevity, use, and re-use. Some identifier schemes require membership and fees in order to create identifiers while others are open and free. Some schemes mandate use of a particular table lookup technology while others do not. Each scheme has its unique history, community, and conditions of use (as described in more detail in Table 2). Whatever method is used for creating the identifier, it **should be publicized explicitly by the identifier authority**. Consumers need to know about the persistence mission of the agency and any potential contracts implied by use of the identifier.

Persisting GUIDs across Systems

The group discussed issues with contracts about retaining identifiers in downstream systems. **We strongly recommend creating community conventions when re-using data to place special importance on referencing and maintaining earlier identifiers**, especially those with clear policy and behaviour contracts. Use of such conventions provides significant value for data producers and consumers, such as data citation networks, analogous to those produced by CrossRef for journal publications.

Content Mutability

If a physical object is categorized as "organism" and is later changed to "bulk sample", does its associated identifier change with it? Does the identifier to a concept change if a spelling error or ambiguous wording is corrected in its definition? Does an information resource identifier change during versioning? Does an identifier guarantee binary identical results, or only identical core-content (which may be embedded in a modified template or formatted differently)? In some cases the answer may be a permanent single mutability policy of the identifier scheme itself, in other cases the identifier scheme may support multiple policies, and the mutability policy may be available as metadata on the identified object. **We recommend using, and where necessary, developing, a vocabulary to document mutability policies and conventions for various content types**.

Resolver Persistence

Dereferencing, or the automated process that a software tool (e.g., a web browser) employs to go from identifier to content or metadata access, starts with a URL. All identifiers, regardless of scheme, are resolved by a user agent if they are embedded in a URL. As for institutions that have long-term access in their mission, many people think that smaller, newer institutions' website hostnames will be short-lived compared to those of older, larger institutions (e.g., loc.gov, bnf.fr). Some people prefer to trust a hostname backed by a group of institutions, even if comparatively young (e.g., dx.doi.org), rather than by any one institution. Among such group or consortial arrangements, some people prefer to trust those committed to open access (e.g., gbif.org). Persistence missions can also far exceed current technological solutions. Will, for example, current http protocols look anything like the protocols used in 2065? **Forecasting about resolver persistence for 10, 20, 50, or 100 years is at best educated guesswork, but it should take into account such things as inevitable technological advances, resolver organization's mission, size, business model, openness, and current age**.

Identifier Ergonomics and Curation

Identifier readability and ease of transcription are concerns whenever identifiers are routinely recognized, typed, or written by human beings (e.g., on specimen labels). Non-opaque identifiers (containing recognizable strings) tend to be easy to read and to enter because humans can often spot transcription errors; however, it is difficult to mint them uniquely and quickly, and to keep them persistent (their structure makes them prone to "semantic rot"). It is easy to create UUIDs quickly and in large number, which can be especially useful for tracking instances of samples or events in aggregator databases. On the other hand, UUIDs rendered as hexadecimal characters (as opposed to embedded in QR-Codes) are opaque and long, and not as useful in situations where a UUID is

expected to be printed onto an insect pin, placed in a vial, or entered via a user interface by hand. There are other means of generating shorter unique opaque identifiers (e.g., Noid), but they have other disadvantages. **One solution to this dilemma is to maintain human-friendly identifiers (e.g., catalog numbers) when presenting content to humans in addition to computer-friendly identifiers (LOD, UUID, DOI, ARK, etc.) for electronic cross-linking**. Such a solution does require curation overhead to assure that both are managed for the long-term. Emerging services such as GRBio maps human-friendly Institution and Collection Codes to URIs for biocollections.

Conclusions and Planning For The Longer Term

Perhaps the most critical outcome of this workshop was general agreement about a key set of issues, listed below:

1) As opposed to discussing particular implementations, which is likely to be counter-productive, the group was much more interested in cross-cutting issues and the importance of delivery mechanisms that help machines and users interpret identifiers and metadata about them and the biodiversity data objects to which they point.
2) New field-based biocollections and legacy biocollections have different immediate and longer-term needs when it comes to identifier solutions. While there is every reason to assign a globally unique, persistent identifier to new data in biocollections, it may be less critical for legacy records. For legacy data, the problem of broken associations already exists and can only be repaired by spending effort to re-assert the relationships.
3) When a publisher creates records for a new derivative from a legacy collection, it should always copy in the "original" identifier field from the legacy record into the new record. Best practices and conventions for doing so still need to be developed.
4) Publications and data aggregators should not only honor existing identifiers and the metadata about those identifiers, but also follow practices that maximize interoperation with emerging digital library practices regarding data citation.
5) We see great value in reviving or establishing task groups in (and between) TDWG and SPNHC that can help implement some of the best practices and next steps discussed in this document, in particular the creation of a biodiversity metadata profile for identifiers, which can provide critical information about the type of biodiversity object to which the identifier points.

It is noteworthy that the assembled group represented people who have expressed sometimes opposing views on which identifier implementation is most likely to best support sharing and linking biodiversity data. The longer term is likely to see a whole suite of differing solutions, and Table 2 provides more details about differing identifier implementations and services. More important are the cross-cutting solutions, independent of any one identifier implementation, which can best facilitate a vibrant interconnected graph of specimens, samples, images, descriptions/traits, sequences and published content.

Acknowledgements

We would like to thank the National Science Foundation for supporting the BiSciCol (Biological Science Collections Tagging and Tracking; biscicol.org) project and all activities that took place during its development, including this workshop (DEB 0956371, DEB 0956350, and collaborative awards). We also note support from the Research Coordination Network for Genomic Standards Consortium (DBI-0840989), EAGER: An Interoperable Information Infrastructure for Biodiversity Research (IIS-1255035) who has supported travel and discussion related to this topic. The work of Pensot's and Plazi's teams was partly supported by the EU BON (Building the European Biodiversity Observation Network), an FP-7 (European Union Seventh Framework Programme, 2007-2013) grant (No 308454). We are grateful to all those who were involved in the project throughout the years for the constructive feedback and many discussions that took place throughout the course of developing outputs for the project. Robert Whitton provided Figure 1 and shared his insights on workflows involving field-assigned identifiers. We thank the Stockholm Natural History Museum for providing us with the venue and appreciate the coordination with the TDWG executive and organizing committees.

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Appendix 1

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