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Further studies on water mites from Korea, with description of two new species (Acari, Hydrachnidia)

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Abstract

New records of water mites (Acari: Hydrachnidia) from streams in South Korea are presented. Two species are described as new to science: *Torrenticola neodentifera* **sp. n.** (Torrenticolidae) and *Atractides ermilovi* **sp. n.** (Hygrobatidae). Five species are reported as first records for Korea: *Wandesia* (*Wandesia*) *reducta* Tuzovskij, 1987, *W.* (*Wandesia*) cf. *rara* Tuzovskij, 1990, *Sperchon* (*Sperchon*) *orientalis* Tuzovskij, 1990, *Feltria* (*Feltria*) *kuluensis* Tuzovskij, 1988 and *Atractides* (*Atractides*) *constrictus* (Sokolow, 1934). The latter species is redescribed and elevated to species rank based on new material from the Russian Far East.

Keywords

Acari, Hydrachnidia, new species, new records, running waters

Introduction

Recently, the senior author (Pešić 2014) published a checklist of water mites from Korea, listing 74 species, in 32 genera and 13 families. However, the water mite fauna of Korea is still insufficiently known. This is one of the limnic groups of invertebrates for which studies have been published only very recently, as the first paper on water mites in South Korea was published as late as the last decade of the 20th century (Chung and Kim 1991). For a full bibliography see Pešić (2014).

The water mites of this study mainly were collected by the senior author during his trip in South Korea in May, 2013. The paper aims to describe this material in order to prepare the way towards the production of an identification key of this important group of freshwater invertebrates.

Material and methods

Water mite were collected by hand netting, sorted on the spot from the living material, fixed in Koenike-fluid and dissected as described elsewhere (e.g., Gerecke et al. 2007). Holotype and paratypes of the new species will be deposited in the National Institute of Biological Resources, Korea (NIBR); material from the Russian Far East is deposited in the research collections of the Institute of Biology and Soil Science, Vladivostok, Russia (IBSS).

In the section 'Material examined' collecting site abbreviations derive from the geographical database Pešić. The composition of the material is given as: males/females/deutonymphs. All measurements are given in µm. For a detailed description and discussion of the characteristics of the genus *Atractides* and a detailed methodological introduction, see Gerecke (2003).

The following abbreviations are used: Ac-1 = first acetabulum, asl = above sea level, Cx-I = first coxae, Cxgl-4 = coxoglandularia of fourth coxae, Dgl-1-4 = dorsoglandularia, dL = dorsal length, H = height, L = length, Lgl-1-4 = lateroglandularia, I-L-6 = Leg 1, sixth segment (tarsus), mL = medial length, n = number of specimens examined, NP = National Park, P-1 = palp, first segment, Preoc. = preoculare; pregen = pregenital sclerite, Postoc. = postoculare; S-1 = proximal large ventral seta at I-L-5, S-2 = distal large ventral seta at I-L-5, Vgl-1 = ventroglandularia 1, vL = ventral length, W = width.

Systematic part

Family Hydryphantidae Piersig, 1896

Subfamily Wandesiinae Schwoerbel, 1961

Genus *Wandesia* Schechtel, 1912

Wandesia (*Wandesia*) *reducta* Tuzovskij, 1987

Fig. 1

Synonymy. *Wandesia reducta* Tuzovskij 1987: 39.

Material examined. SOUTH KOREA: CR22 Gangwon Province, Chiaksan NP, Silim town, stream shaded, substrate: stones, gravels; 37°17.081'N, 128°15.389'E, 25.v.2013 Pešić & Karanović 0/1/0 (mounted).

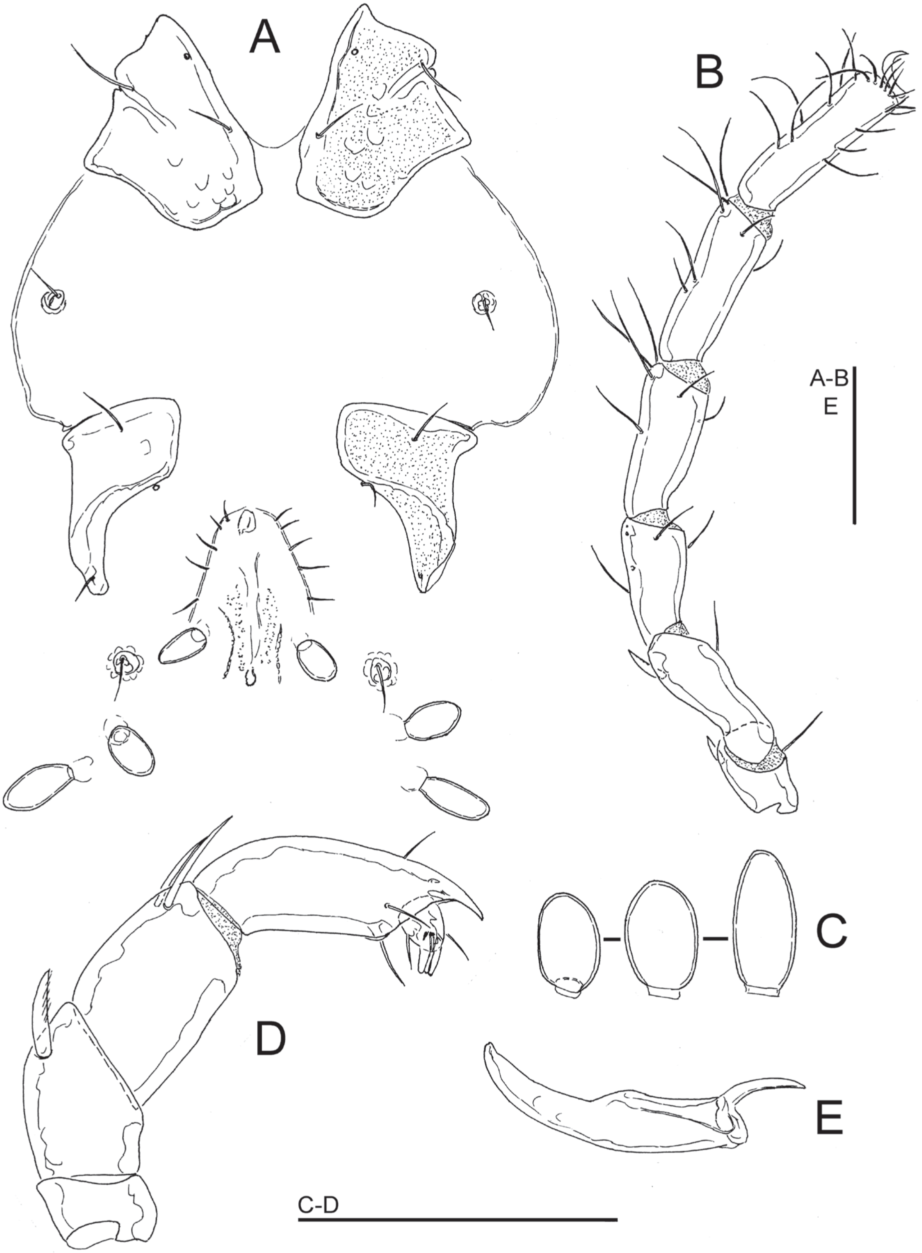

Figure 1. *Wandesia reducta* Tuzovskij, 1987, female, Chiaksan NP, Korea: **A** coxal and genital field **B** I-Leg **C** acetabula (Ac-1-3, from left to right) **D** palp, medial view **E** chelicera. Scale bars = 100 µm.

Remarks. The single female from this study matches the general morphology of *Wandesia reducta* Tuzovskij, 1987. This species was described by Tuzovskij (1987) from Magadan region in the Russian Far East, based on three females and a larva.

Here we give measurements of the specimen from Korea. Idiosoma L 1800, Cx-I+II total L 138, W 113, Cx-III+IV lateral L 131; Ac-1 L 31, L/W 1.5, Ac-2 L 34 L/W 1.5, Ac-3 L 43, L/W 2.2; gnathosoma vL 146, chelicera total L 206, H 42, L/H ratio 5.0, basal segment L 154, claw L 59, L basal segment/claw ratio 2.6; palp: total L 248, dL/H, dL/H ratio: P-1, 20/34, 0.59; P-2, 60/40, 1.5; P-3, 55/42, 1.3; P-4, 91/26, 3.56; P-5, 22/12, 1.9; length P-2/P-4 ratio 0.66; dL of I-L: 44, 75, 91, 106, 109, 88.

Distribution. Far East of Russia (Tuzovskij 1987; Semenchenko 2010). New for the fauna of Korea.

***Wandesia* (*Wandesia*) cf. *rara* Tuzovskij, 1990**

Fig. 2

Synonymy. *Wandesia rara* Tuzovskij 1990: 67.

Material examined. SOUTH KOREA: CR16 Gyeongsangbuk Province, Juwangsan NP, Woroe-ri, Cheong song-eup, Dalgikpo, waterfall, 36°26.499'N, 129°08.114'E, 23.v.2013 Pešić & Karanović 0/1/0 (mounted).

Morphology. Idiosoma L 1800, coxae and genital field: Fig. 2A, Cx-I+II total L 144-146, W 111-125, Cx-III+IV lateral L 144-145; number of coxal setae: Cx-I, 3, Cx-II, 0, Cx-III, 1, Cx-IV, 1; genital field with three pairs of Ac and three setae on a transparent sclerotized strip on each side; gonopore L 106; Ac-1 L 29, L/W 1.28, Ac-2 L 32, L/W 1.5, Ac-3 L 30, L/W 1.2.

Gnathosoma vL 189, chelicera (Fig. 2C) total L 223, H 39, L/H ratio 5.8, basal segment L 150, claw L 60, L basal segment/claw ratio 2.5. Palp: dL/H, dL/H ratio: P-2, 63/41.5, 1.5; P-3, 56/45, 1.26; P-4, 94/27, 3.5; P-5, 25/12, 2.1; L P-2/P-4 ratio 0.67; palp setation as given in Fig. 2B.

Legs: setation as given in Fig. 2E–H; dorsal margin of I-L-6 and II-L-6 strongly concave (Fig. 2E–F); dL of I-L-3-6: 95, 118, 123, 123; II-L-3-6: 92, 111, 120, 122; III-L-3-6: 71, 191, 109, 121; IV-L-3-6: 108, 129, 122, 123.

Remarks. With regard to similar setation of coxae, P-5 without a flagelar seta and dorsal margin of the tarsus of I-L and II-L strongly concave, the new species resembles *Wandesia rara* Tuzovskij, 1990 a species described from the Primory Territory in the Russian Far East on the basis of a single deutonymph (Tuzovskij 1990). The difference is found in more elongated Ac (L/W 2.0, calculated from figure 38-1, of Tuzovskij (1990)) in the deutonymph of *W. rara*. Thus, our assignment of specimen from Korea is tentative. Only with more material in the future, and finding of a adults from the *locus typicus* it will be possible to decide whether the specimen from Korea is conspecific with *W. rara* or a species new for science.

Distribution. Far East of Russia (Primory Territory – Tuzovskij 1990). New for the fauna of Korea.

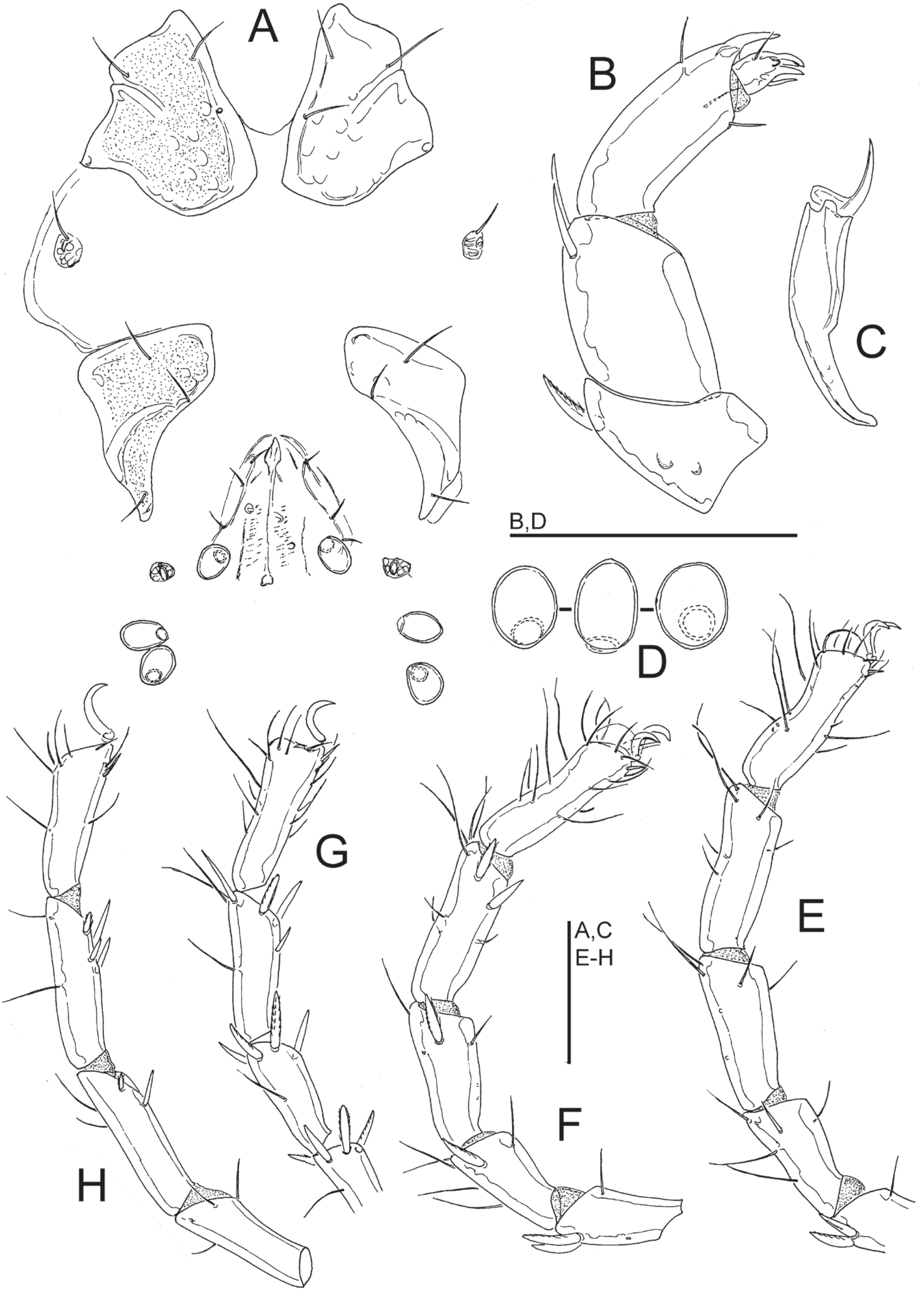

Figure 2. *Wandesia* cf. *rara* Tuzovskij, 1990, female, Juwangsan NP, Korea: **A** coxal and genital field **B** palp, lateral view (P-1 lacking) **C** chelicera **D** acetabula (Ac-1-3, from left to right) **E** I-L-3-6 **F** II-L-2-6 **G** III-L-4-6 **H** IV-L-3-6. Scale bars = 100 µm.

Family Sperchontidae Thor, 1900
Genus *Sperchon* Kramer, 1877

Sperchon (*Sperchon*) *orientalis* Tuzovskij, 1990
Fig. 3

Synonymy. *Sperchon orientalis* Tuzovskij 1990: 99.

Material examined. SOUTH KOREA: CR20 Chungcheongbuk Province, Mt. Vorak, Deokjusanseong, stream, 36°51.705'N, 128°06.030'E, 25.v.2013 Pešić & Karanović 2/1/0 (1/0/0 mounted).

Remarks. The specimens examined from South Korea matches the general morphology of *Sperchon orientalis* Tuzovskij, 1990, a species described from the Primory Territory in the Russian Far East (Tuzovskij 2008). Due to the general shape of idiosoma (Cx-I medially separated, excretory pore surrounded by a sclerotized ring, see Fig. 3B) and palp (P-4 ventral setae strongly developed and projecting, dividing this segment in three equal parts in size, Fig. 3C–D), *S. orientalis* closely resembles *S. glandulosus* Koenike, 1886, from which it differs by the eye capsule longer than diameter of Postoc., a higher number of dorsal setae on P-2 and -3 and less densely arranged dorsal setae on IV-L-3-5 (Tuzovskij 2008).

Chung and Kim (1991) reported and illustrated *Sperchon fluviatilis* Uchida, 1934 from Korea. However, the excretory pore in *S. fluviatilis* is smooth (see Uchida 1934, fig. 12–13), not sclerotized as in the illustrated male specimen from Korea. As their illustrations (Chung and Kim 1991: fig. 3A–D) show a general conformity with *S. orientalis*, it is likely that the specimens attributed to *S. fluviatilis* refer to *S. orientalis*.

Distribution. Far East of Russia, eastern Siberia (Tuzovskij 2008; Semenchenko et al. 2010). New for the fauna of Korea.

Family Torrenticolidae Piersig, 1902
Subfamily Torrenticolinae Piersig, 1902
Genus *Torrenticola* Piersig, 1896

Torrenticola (*Torrenticola*) *neodentifera* sp. n.
http://zoobank.org/094C3931-DDEF-4E80-83F0-8A6C1F55BFB4
Figs 4–6

Synonymy. *Torrenticola dentifera* Pešić et al. 2013: 25, figs 2, 7B.

Type series. Holotype male (NIBR), dissected and slide mounted, SOUTH KOREA: CR21 Chungcheongbuk Province, Woraksan NP, Jungseonam, River exposed to sunlight, sand, gravel substrate, 36°52.644'N, 128°17.784'E, 25.v.2013 Pešić & Kara-

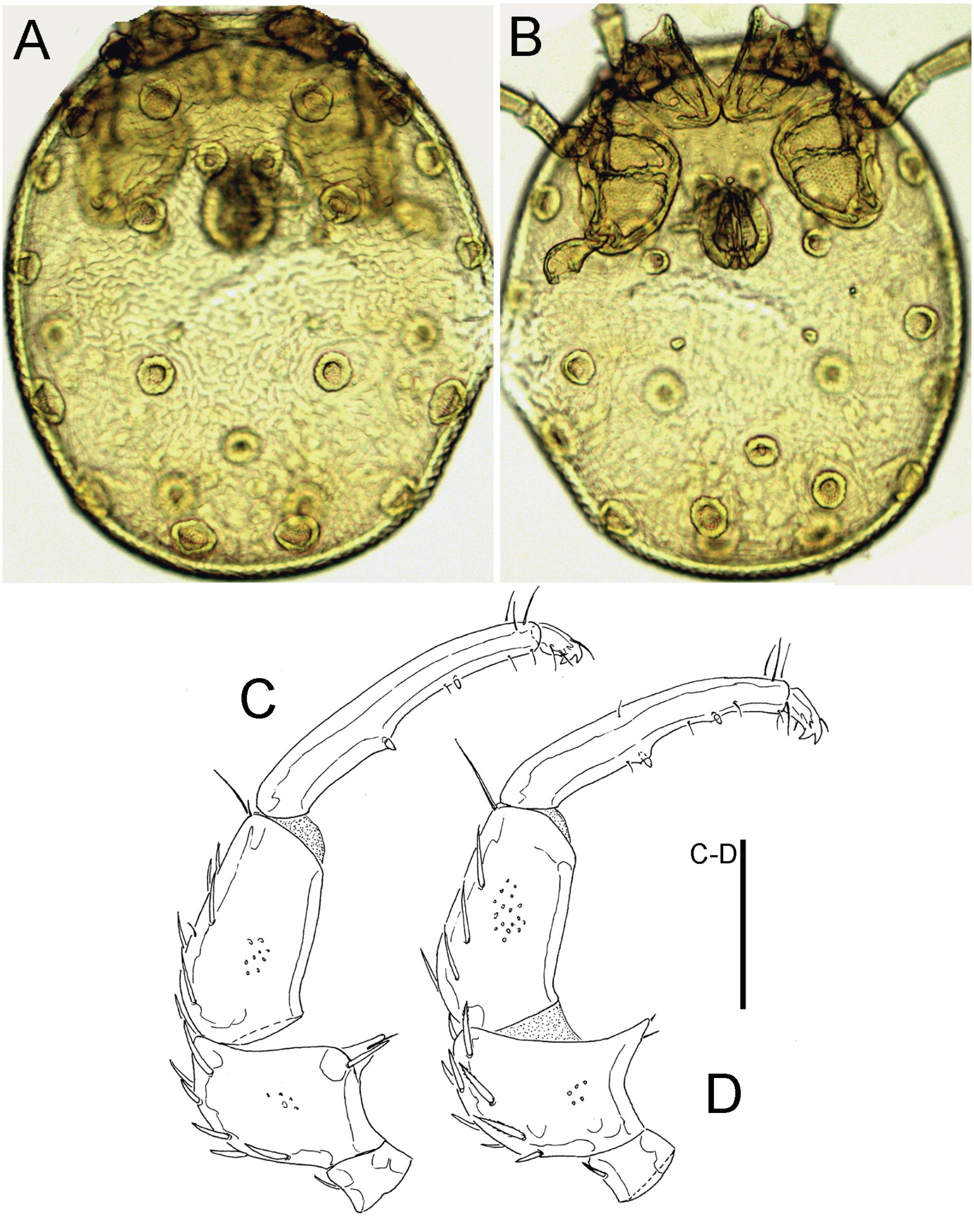

Figure 3. *Sperchon orientalis* Tuzovskij, 1990, male, Deokjusanseong, Korea (**A–B** photograph, **C–F** line drawing): **A** idiosoma, dorsal view **B** idiosoma, ventral view **C** palp, lateral view **D** palp, medial view. Scale bar = 100 µm (**C–D**).

nović. Paratype (NIBR): one female, CR22 Gangwon Province, Chiaksan NP, Silim town, stream shaded, stones, gravels, 37°17.081'N, 128°15.389'E, 25.v.2013 Pešić & Karanović, dissected and slide mounted.

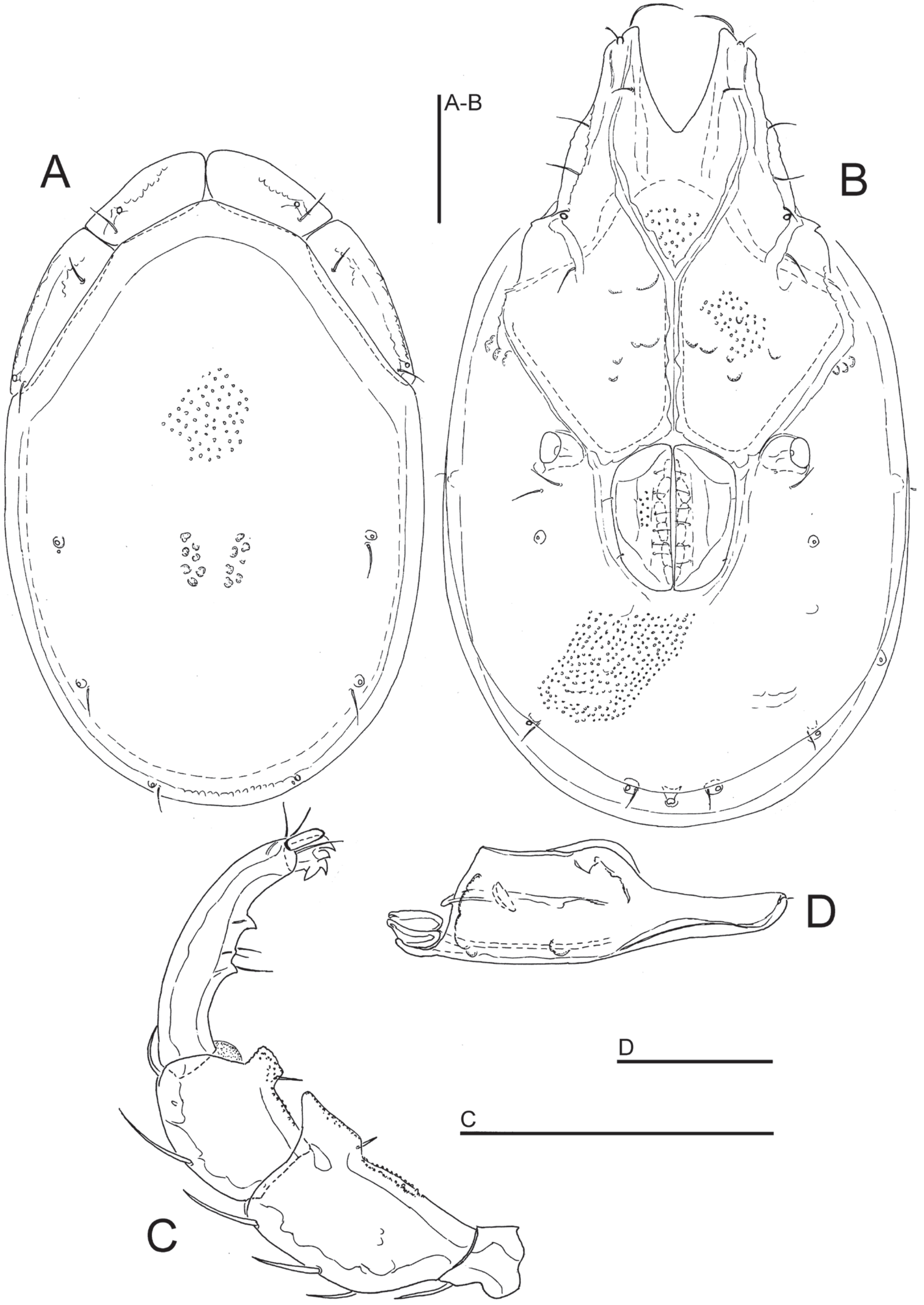

Figure 4. *Torrenticola neodentifera* sp. n., male holotype, Woraksan NP, Korea: **A** dorsal shield **B** ventral shield **C** palp, medial view **D** gnathosoma. Scale bars = 100 µm.

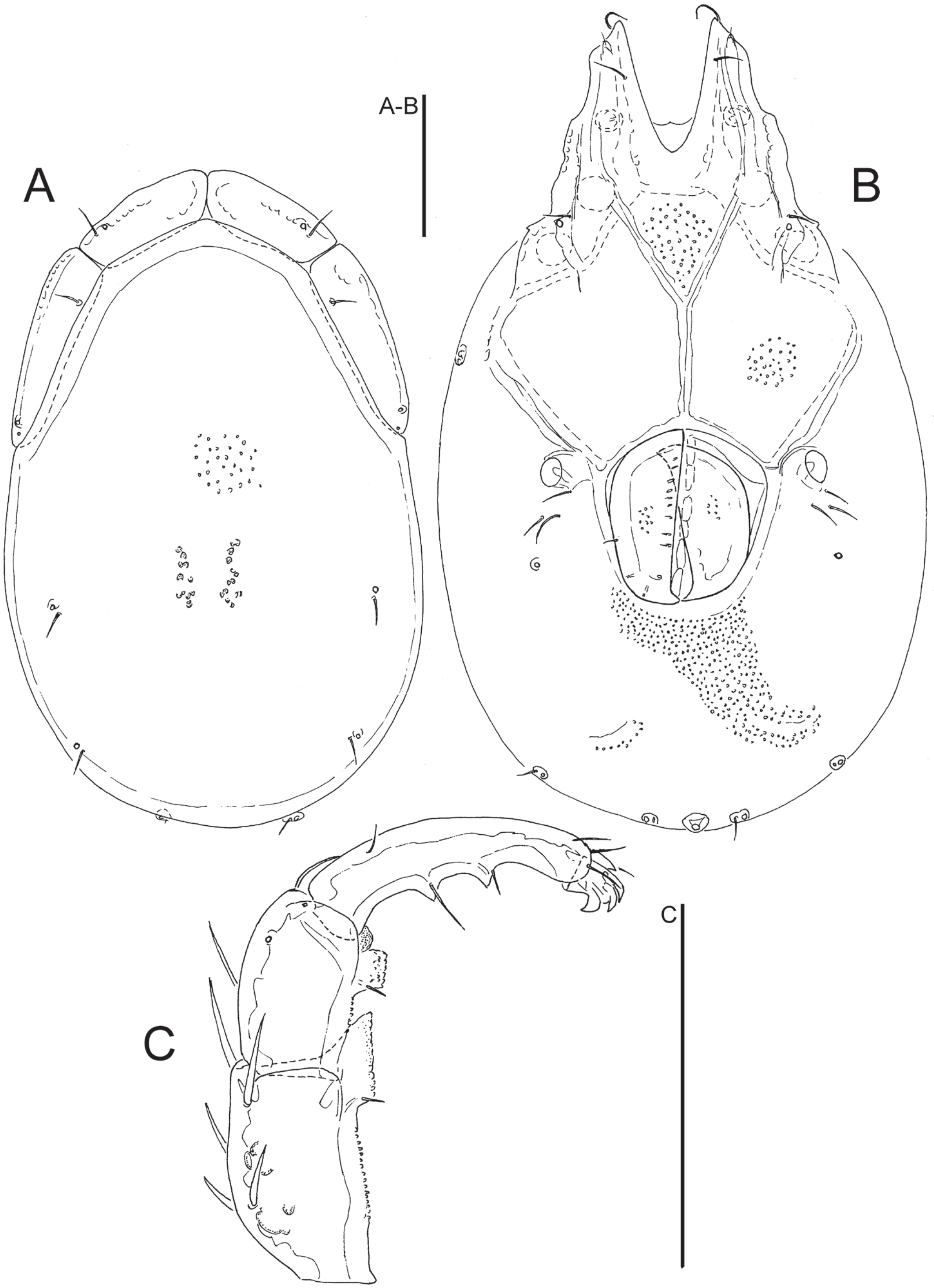

Figure 5. *Torrenticola neodentifera* sp. n., female, Chiaksan NP, Korea: **A** dorsal shield **B** ventral shield **C** palp, lateral view. Scale bars = 100 µm.

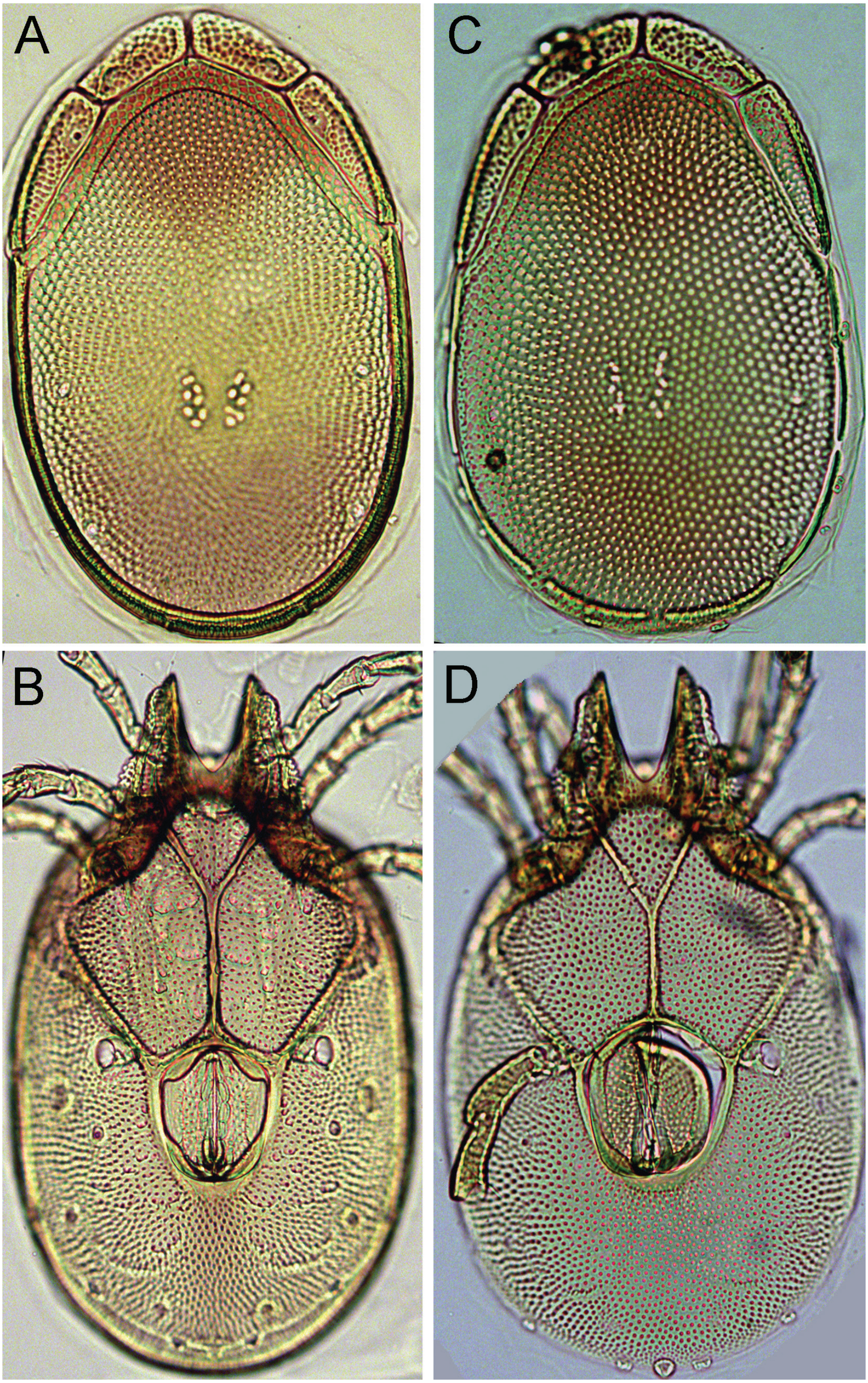

Figure 6. Photographs of *Torrenticola neodentifera* sp. n. (**A–B** male holotype, **C–D** female paratype): **A, C** = dorsal shield **B, D** = ventral shield.

Diagnosis. Idiosoma dimensions relatively large (L 580-630); dorsal shield with colour pattern as illustrated in Fig. 5A; P-2 with a laterally compressed, anteriorly directed ventrodistal extension; P-3 with a broad, subrectangular ventrodistal projection.

Description. *General features* — Idiosoma elongated; dorsal shield with colour pattern as illustrated in Fig. 6A,C; frontal platelets anteriorly bulging (Figs 4A, 5A); gnathosomal bay V-shaped; Cxgl-4 subapical, only slightly posterior of Cx-I tips; medial suture line of Cx-II+III long; posterior suture line of Cx-IV in its medial part perpendicular to the longitudinal body axis, laterally distinctly curving anteriorly; excretory pore and Vgl-2 on the line of primary sclerotization near posterior idiosoma margin; gnathosoma ventral margin only slightly curved, rostrum well developed; P-2 shorter than P-4, ventral margin of P-2 with a fine denticulation also in proximal half of the segment, distally with a laterally compressed, anteriorly directed hyaline extension and a very short, denticle-like seta laterally at base of projection; P-3 with a broad, subrectangular, apically serrated ventrodistal projection with a fine denticles, and a short seta laterally at base of projection; P-4 ventral tubercles well developed and separated (Figs 4C, 5C). *Male*. Genital field subrectangular; ejaculatory complex conventional in shape (Fig. 2D in Pešić et al. 2013). *Female*. The short postgenital area and caudal position of the excretory pore (Fig. 5B) in the specimen from Korea are due to the obviously juvenile age (indicated by weak sclerotization and absence of eggs); genital field pentagonal in shape.

Measurements. Male — Idiosoma (ventral view: Figs 4B, 6B) L 628, W 365; dorsal shield (Figs 4A, 6A) L 516, W 331, L/W ratio 1.56; dorsal plate L 477; shoulder platelet L 141-143, W 41-44, L/W ratio 3.2-3.5; frontal platelet L 106-109, W 46-47, L/W ratio 2.3; shoulder/frontal platelet L ratio 1.29-1.35. Gnathosomal bay L 81, Cx-I total L 200, Cx-I mL 118, Cx-II+III mL 127; ratio Cx-I L/Cx-II+III mL 1.58; Cx-I mL/Cx-II+III mL 0.93. Genital field L/W 116/98, ratio 1.18; ejaculatory complex L 162; distance genital field-excretory pore 162, distance genital field-caudal margin 184. Gnathosoma vL 256; chelicera total L 270; palp: total L 239, dL/H, dL/H ratio: P-1, 22/21, 1.05; P-2, 65/39, 1.7; P-3, 49/35, 1.4; P-4, 86/19, 4.6; P-5, 17/11, 1.6; P-2/P-4 ratio 0.76.

Female — Idiosoma (ventral view: Figs 5B, 6D) L 581, W 353; dorsal shield (Figs 5A, 6C) L 472, W 303, L/W ratio 1.56; dorsal plate L 439; shoulder platelet L 144-150, W 38-42, L/W ratio 3.4-4.0; frontal platelet L 103-105, W 44-56, L/W ratio 1.8-2.4; shoulder/frontal platelet L ratio 1.37-1.46. Gnathosomal bay L 94, Cx-I total L 206, Cx-I mL 110, Cx-II+III mL 87; ratio Cx-I L/Cx-II+III mL 2.37; Cx-I mL/Cx-II+III mL 1.26. Genital field L/W 116/126, ratio 0.92; distance genital field-excretory pore 150. Gnathosoma vL 252; chelicera total L 258-262; palp: total L 225, dL/H, dL/H ratio: P-1, 19/20, 0.95; P-2, 63/37, 1.7; P-3, 49/32, 1.54; P-4, 79/20, 4.0; P-5, 15/10, 1.5; P-2/P-4 ratio 0.8.

Etymology. Named for its similarity with *T. dentifera* Wiles, 1991.

Remarks. Pešić et al. (2013) collected a single male from a stream in Naebyeansan National Park, South Korea and assigned it to *Torrenticola dentifera*. This specimen is in perfect agreement with specimens examined in our study. In the original description of *T. dentifera*, a species described on the basis of two males from Selangor, Peninsular Malaysia (Wiles 1991), no information on colour pattern of dorsal shield and shape of ejaculatory complex are given. At the present state of art, males of *Torrenticola dentifera* can be distinguished from the new species by smaller dimensions of idiosoma and palps, and a more slender ventrodistal projection on P-3.

Habitat. A permanent sandy/bouldary stream, shaded by riparian vegetation (Fig. 13C–D).

Distribution. Korea ("*Torrenticola dentifera*" Pešić et al. 2013, this study).

Family Hygrobatidae Koch, 1842

Genus *Hygrobates* Koch, 1837

Hygrobates (*Rivobates*) cf. *microepimeratus* (Sokolow, 1934)

Fig. 7

Synonymy. *Rivobates microepimeratus* Sokolow 1934: 356.

Material examined. SOUTH KOREA: CR20 Chungcheongbuk Province, Mt. Vorak, Deokjusanseong, stream, 36°51.705'N, 128°06.030'E, 25.v.2013 Pešić & Karanović 0/1/0 (mounted).

Remarks. The single female from this study matches the general morphology of *Hygrobates microepimeratus* (Sokolow, 1934) a species described from the Primory Territory in the Russian Far East (Sokolow 1934), and later on reported by Chung and Kim (1997) from Korea. This species is known from a female only making it difficult to separate from other similar species, i.e. *H. ezoensis* Uchida, 1934 (Russia: Sakhalin, Japan: Hokkaido) and *H. taniguchii* Imamura, 1954 (Japan, Hokkaido). In the original description Sokolow (1934, 1940), in addition to more slender P-3 (compared with *H. diversiporus*), gave particular weight to the smaller dimensions of coxae which occupy one third of venter. According to Imamura (1954) *H. taniguchii* differs from *H. microepimeratus* in larger coxae. *Hygrobates ezoensis* differs in P-2 with a more pronounced and acute ventrodistal projection and stouter P-3 (see Matsumoto et al. 2005).

Distribution. Far East of Russia (Primory Territory – Sokolow 1934), Korea (Chung and Kim 1997, this study).

Genus *Atractides* Koch, 1837

Atractides (*Atractides*) *constrictus* (Sokolow, 1934), stat. n.

Figs 8–10

Synonymy. *Megapus nodipalpis constrictus* Sokolow 1934: 361.

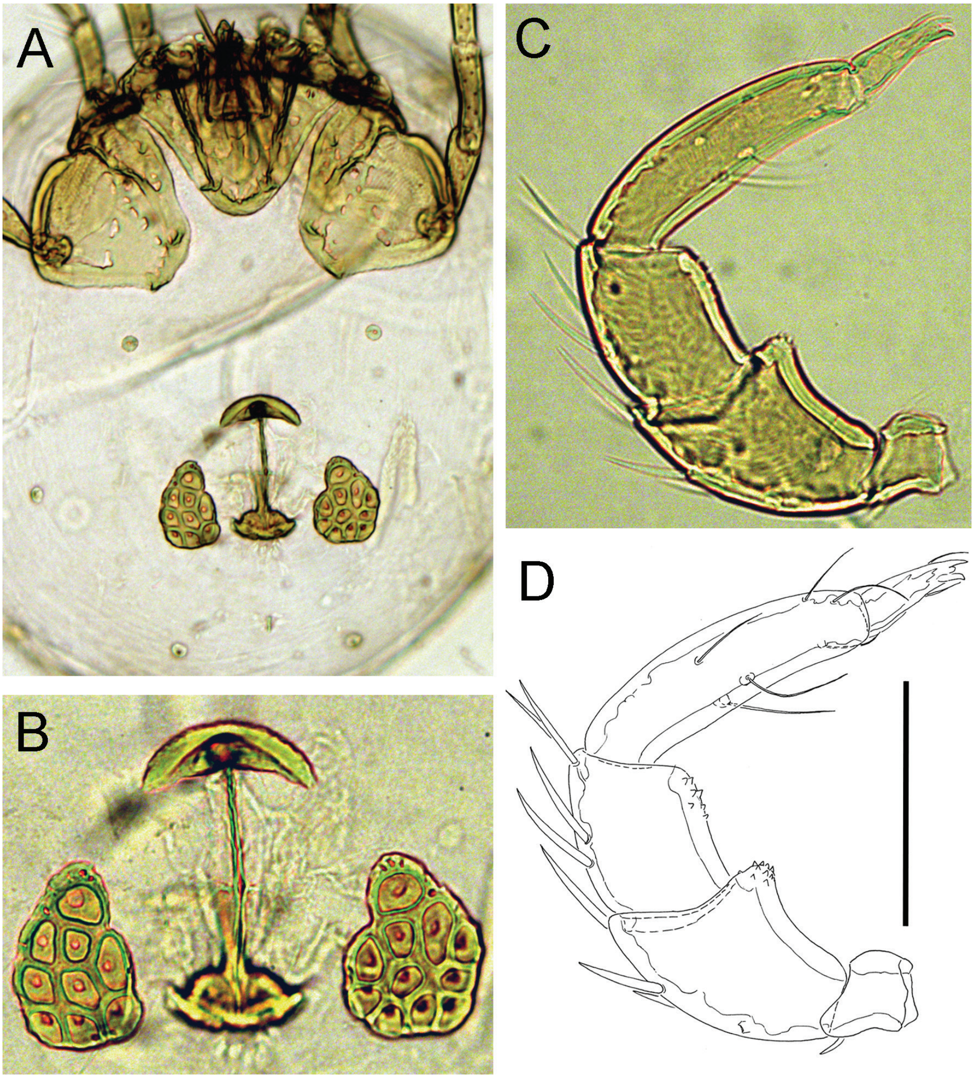

Figure 7. *Hygrobates* (*Rivobates*) cf. *microepimeratus* (Sokolow, 1934), female, Deokjusanseong, Korea (**A–C** photographs, **D** line drawing): **A** idiosoma, ventral view **B** genital field **C–D** palp. Scale bar = 100 µm (**D**).

Material examined. SOUTH KOREA: CR22 Gangwon Province, Chiaksan NP, Silim town, stream (shaded, stones and gravel substrate), 37°17.081'N, 128°15.389'E, 25.v.2013 Pešić & Karanović 5/0/0 (1/0/0 mounted). RUSSIA: Primory Territory, Khasansky District, "Kedrovaya Pad National Nature Biosphere Reserve", Sea of Japan basin, Kedrovaya River (depth 12–50 cm; substrate: boulders, cobbles, pebbles), 43°06.056'N; 131°33.310'E; 27.vi.1993 Tiunova 4/15/0 (2/2/0 mounted); Primory Territory, Partizansky District, Partizanskay River basin, Tigrovaya River (substrate: cobbles, pebbles, sand), 43°11.401'N; 133°12.660'E, 12.vi.2010 Semenchenko & Sidorov 2/3/2 (1/1/2 mounted).

General features. *Adults.* Integument striated, muscle insertions unsclerotized. Setae Dgl-1, Dgl-3, Dgl-4 and Lgl-2 longer than other dorsal setae; Preoc. and Postoc. without glandularia (Fig. 9A–C). Coxal field: caudal margin Cx-I convex, apodemes of Cx-II directed laterally (Figs 8A, 9D). Excretory pore smooth; Vgl-1 fused to Vgl-2, separate in juvenile specimens. Gnathosoma elongated (Figs 9F). Palp with strong sexual dimorphism in P-2 and -4, P-4 sword seta between ventral setae. Legs without swimming setae, posterior legs slender (Fig. 9I). Leg claws with near-equal denticles (Fig. 9J). I-L-5: S-1 longish, blunt, S-2 basally enlarged, pointed; I-L-6 curved, basally thickened (Figs 8B, 9H, 10C). *Male.* Genital field: both anterior and posterior margins deeply indented, Ac in a triangle, Ac-3 strongly enlarged (Figs 8A, 9E). Palp: P-2 with strong ventrodistal protrusion consisting of a bluntly pointed medial hump and a convex lateral thickening; P-3 ventral margin concave; P-4 maximum H near proximoventral seta, sword seta between ventral setae (Figs 8C–D, 9G). *Female.* Ac arranged in an obtuse angle (Fig. 10A). Palp: P-2 ventrodistal edge rounded; P-3 ventral margin straight or slightly concave; P-4 slender, slightly protruding near proximoventral seta (Fig. 10B).

Deutonymphs. Setae Dgl-1, Dgl-3, Dgl-4 and Lgl-2 longer than other dorsal setae; Preoc. and Postoc. without glandularia (Figs 10D–F). Coxal field: covers about one half of ventral surface. Caudal margin of Cx-I convex. Excretory pore smooth; Vgl-1 fused to Vgl-2 (Fig. 10G). Genital field: 2 pairs of acetabula placed on fused anteriorly genital plates, each bearing 3 thin setae (Fig. 10H). Palps: P-2 with 1 proximal and 2 distal setae; P-3 with 2 distal setae; P-4 slightly convex, sword seta between ventral setae (Fig. 10I). Setation on I-L-5-6 similar to adults (Fig. 10J).

Measurements. Male (from CR22, in parentheses specimen from Russia, Tigrovaya River) — Idiosoma L/W 600/538 (560/476); coxal field: L 369 (336); Cx-III W 409 (383); Cx-I+II mL 138 (135), lL 263 (238); genital field L/W 129 (109)/ 157 (122), L Ac 1-3: 40-42 (37-42), 51-52 (39-40), 72 (50-51); ejaculatory complex L 127 (106).

Palp: Total L 317 (275), dL/H: P-1, 29/34 (29/36, 0.81); P-2, 77/55 (65/56); P-3, 75/48 (56/46); P-4, 97/29 (93/38); P-5, 39/15 (32/16); L P-2/P-4 ratio 0.79 (0.69). Gnathosoma vL 153 (127).

Legs: I-L-5 dL 218 (174), vL 142 (151), dL/vL ratio 1.53 (1.44), maximum H 59 (49), dL/maximum H 3.7 (4.45), S-1 L 105 (84), L/W ratio 8.5 (12), S-2 L 74 (73), L/W ratio 5.4 (9.1), distance S-1-2, 24 (16), L ratio S-1/2, 1.42 (1.15); I-L-6 dL 139 (120); central H 21 (20), dL/central H ratio 6.7 (6); dL I-L-5/6 ratio 1.57 (1.45).

Female (from Kedrovaya River, Russia, in parentheses specimen from Tigrovaya River) — Idiosoma L/W 765/730 (730/600); coxal field: L 405 (369); Cx-III W 402 (468); Cx-I+II mL 138 (139), lL 290 (264); genital field L/W 162 (142)/197 (174), genital plate L 137 (118); pregen W 65 (62); L Ac 1-3: 50 (47), 56 (50), 54 (51).

Palp: Total L 400 (368), dL/H: P-1, 38/51 (43/29); P-2, 89/76 (72/44); P-3, 116/56 (105/43); P-4, 124/35 (116/29); P-5, 33/19 (32/16); L P-2/P-4 ratio 0.72 (0.62). Gnathosoma vL 160 (147).

Legs: I-L-5 dL 248 (221), vL 170 (156), dL/vL ratio 1.46 (1.42), maximum H 79 (56), dL/maximum H 3.1 (3.9), S-1 L 124 (108), L/W ratio 12.4 (13.5), S-2 L 97 (82),

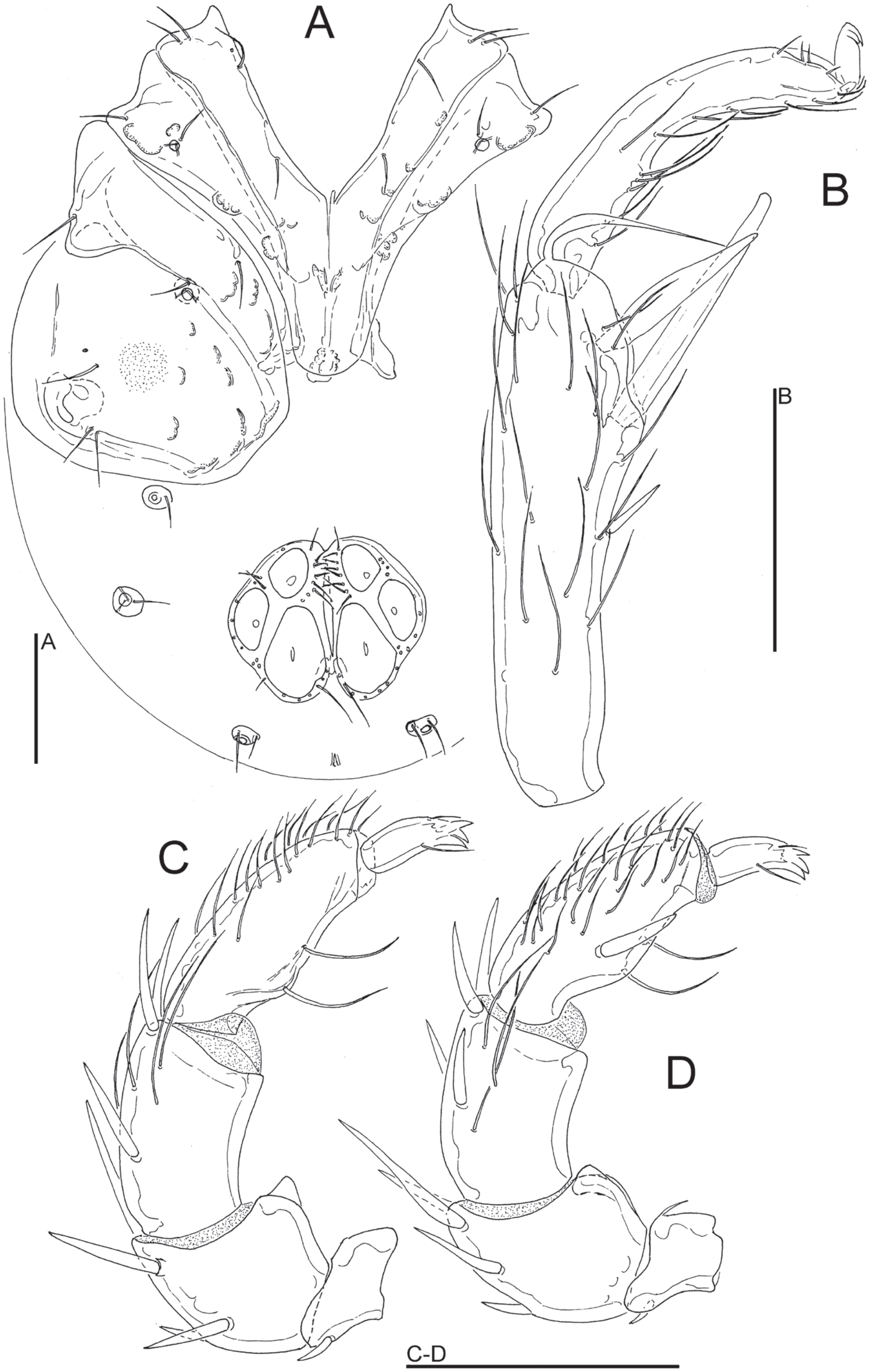

Figure 8. *Atractides constrictus* (Sokolow, 1934), male, Chiaksan NP, Korea: **A** idiosoma, ventral view **B** I-L-5 and -6 **C** palp, lateral view **D** palp, medial view. Scale bars = 100 µm.

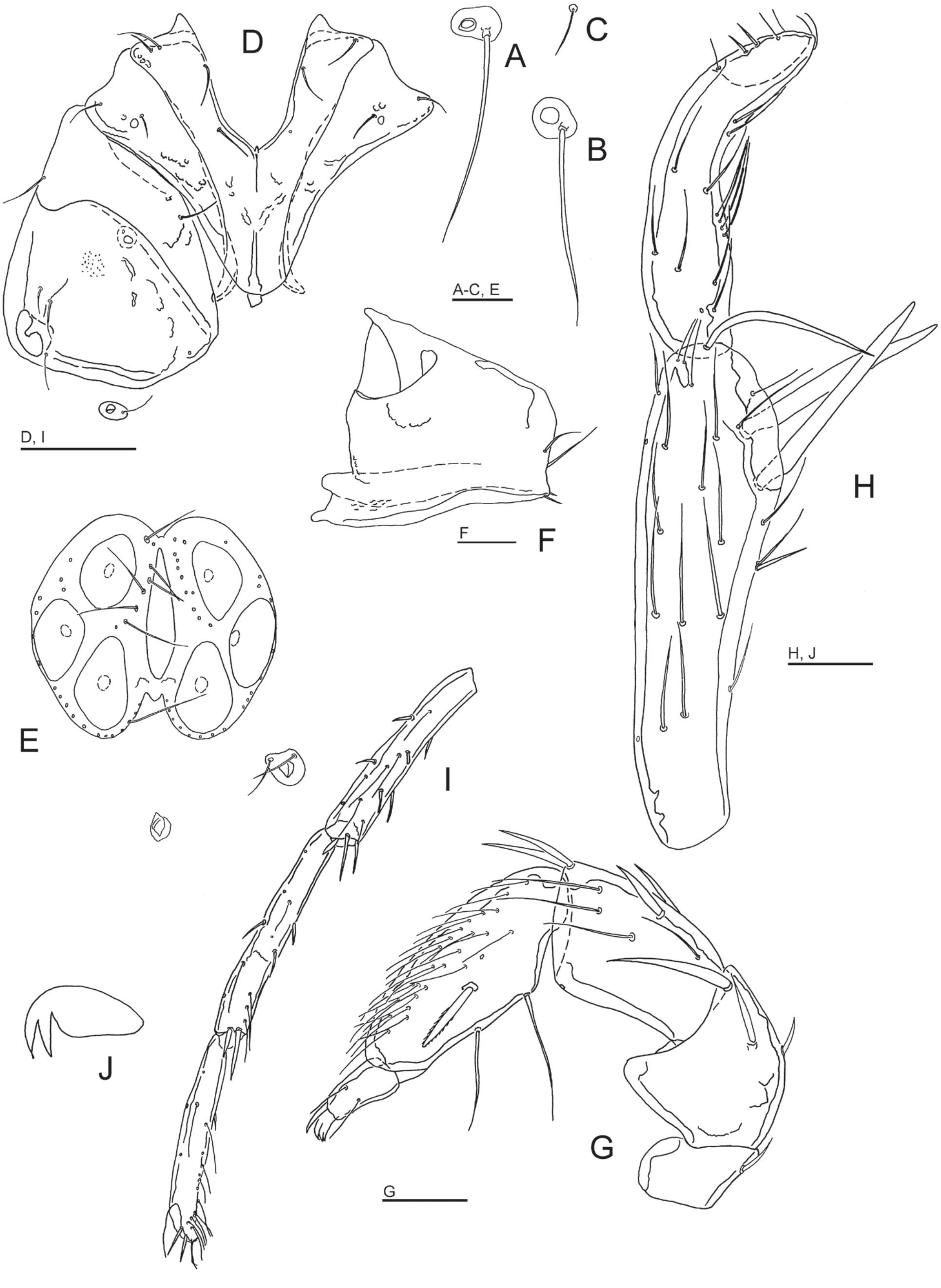

Figure 9. *Atractides constrictus* (Sokolow, 1934), male, Tigrovaya River, Russia: **A** seta Dgl-1 **B** seta Dgl-4 **C** Postoc. **D** coxal field **E** genital field, excretory pore and Vgl-1 fused to Vgl-2 **F** gnathosoma **G** palp, medial view **H** I-L-5 and -6 **I** IV-L-4-6 **J** legs claw. Scale bars = 100 µm (**D, I**), 25 µm (**A–C, E–H, J**).

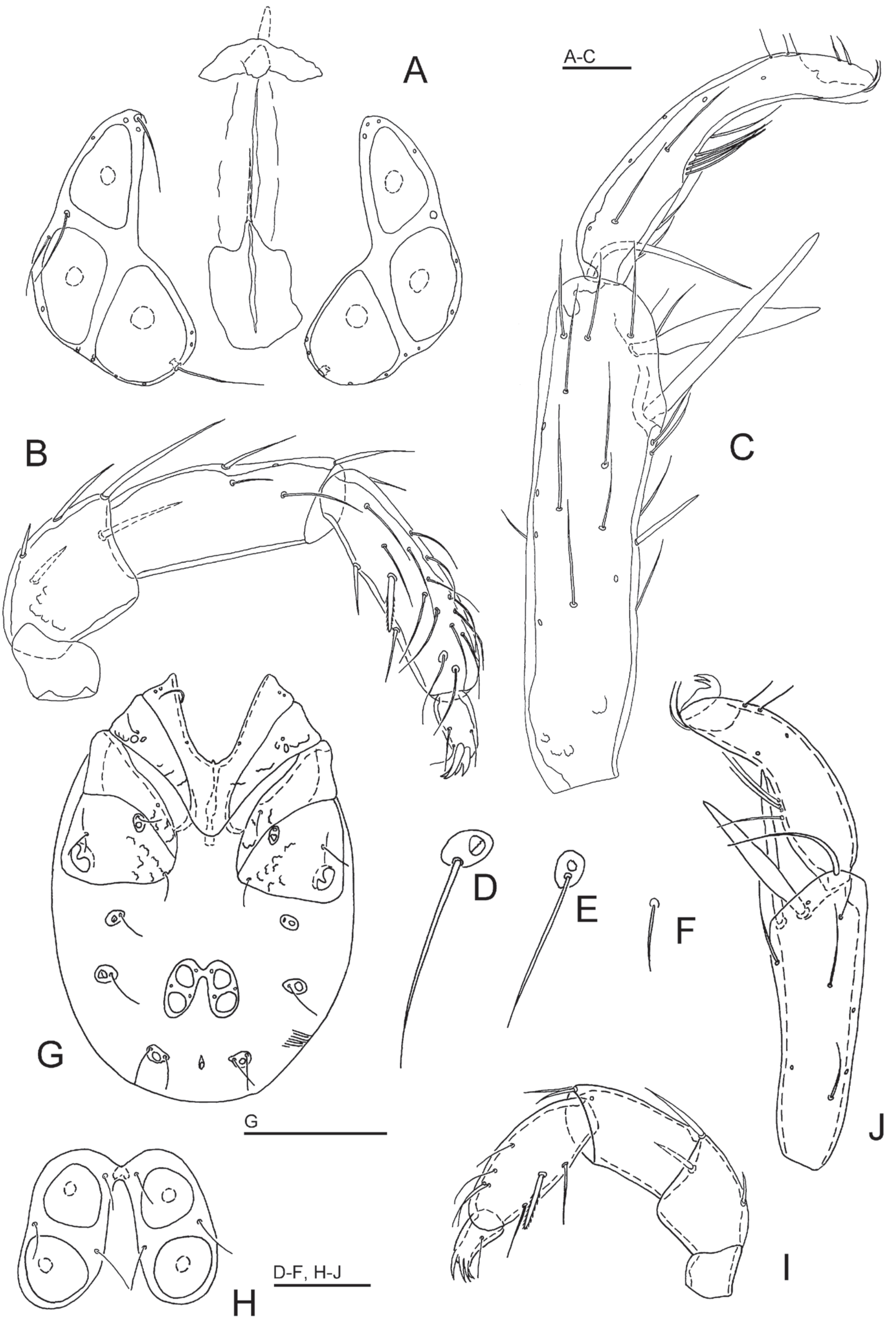

Figure 10. *Atractides constrictus* (Sokolow, 1934), Tigrovaya River, Russia (**A–C** female, **D–J** deutonymph): **A** genital field **B** palp, medial view **C** I-L-5 and -6 **D** seta Dgl-1 **E** seta Dgl-4 **F** Postoc. **G** idiosoma, ventral view **H** genital field **I** palp, medial view **J** I-L-5 and -6. Scale bars = 100 µm (**G**), 25 µm (**A–F, H–J**).

L/W ratio 7.5 (8.2), distance S-1-2, 28 (24), L ratio S-1/2, 1.29 (1.32); I-L-6 dL 179 (156); central H 22 (20), dL/central H ratio 8.1 (7.8); dL I-L-5/6 ratio 1.36 (1.42).

Deutonymph — Idiosoma L/W 323/237); coxal field: L 173; Cx-III W 191; Cx-I+II mL 62, lL 119; genital plate L/W 49/28; L Ac 1-2: 19, 17.

Palp: Total L 165, dL/H: P-1, 18/18; P-2, 37/30; P-3, 43/22; P-4, 49/21; P-5, 18/10; L P-2/P-4 ratio 0.75. Gnathosoma vL 81.

Legs: I-L-5 dL 96, vL 76, dL/vL ratio 1.3, maximum H 31, dL/maximum H 1.5, S-1 L 47, L/W ratio 11.8, S-2 L 46, L/W ratio 9.2, distance S-1-2, 2.5, L ratio S-1/2, 1.02; I-L-6 dL 70; central H 16, dL/central H ratio 4.4; dL I-L-5/6 ratio 1.36.

Remarks. *Atractides constrictus* was originally described by Sokolow (1934) from the Primory Territory in the Russian Far East as a 'variety' of *A. nodipalpis*. In the original description Sokolow (1934, 1940) gave particular weigt to the shape of P-4 in males: strongly thickened near proximoventral seta, basally strongly narrowed, ventral setae more closely approaching to each other. However, there is no reason to support the placement of this taxon as a subspecies of *A. nodipalpis*, as from the latter species, *A. constrictus* can easily be distinguished by the fused Vgl-1 and -2. Males examined from Korea show a general conformity with material from the Far East of Russia. Differences are found in a more enlarged Ac-3, a larger S-1/2 interspace and I-L-6 relatively longer compared to I-L-5 in specimens from Korea.

Distribution. Far East of Russia (Primory Territory – Sokolow 1934). New for the fauna of Korea.

Atractides (*Atractides*) *gracilis* (Sokolow, 1934)

Synonymy. *Megapus gracilis* Sokolow 1934: 366.

Material examined. SOUTH KOREA: CR17 Gyeongsangbuk Province, Hupo-Myeon, shadded stream, 36°40.996'N, 129°25.201'E, 24.v.2013 Pešić & Karanović 0/1/0; CR18 Gyeongsangbuk Province, Haenggok-ri, river, exposed to sunlight, 36°57.182'N, 129°17.670'E, 24.v.2013 Pešić & Karanović 0/1/0.

Distribution. Far East of Russia (Arsenyevka River basin – Sokolow 1934); Japan; Korea (Kim and Chung 1991, Pešić 2014, this study).

Atractides (*Atractides*) *ermilovi* sp. n.

http://zoobank.org/ABC02400-8864-4BAD-B3E8-F7AAD7B9DBDE

Fig. 11

Type series. Holotype male (NIBR), dissected and slide mounted, SOUTH KOREA: CR19 Chungcheongbuk Province, Sobaeksan NP, shaded stream, 36°57.660'N, 128°25.534'E, 24.v.2013 Pešić & Karanović.

Diagnosis (Female unknown). Median suture line relatively Cx-I+II long (> 100 µm); acetabula large (maximum diameter > 50 µm) in triangular position; ven-

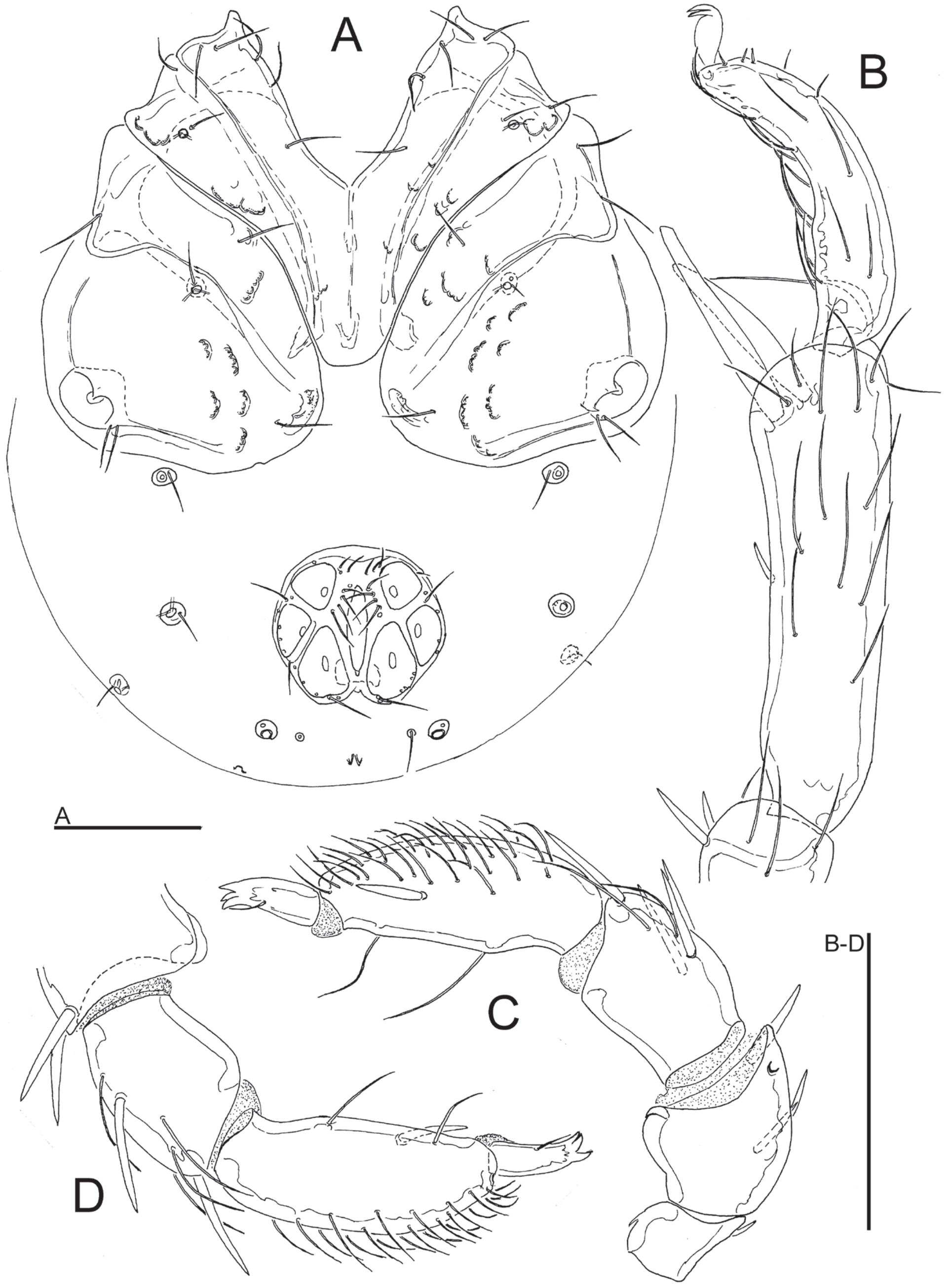

Figure 11. *Atractides ermilovi* sp. n., male, CR19 Sobaeksan NP, Korea: **A** idiosoma, ventral view **B** I-L-5 and -6 **C** palp, medial view **D** palp (P-3-5), lateral view. Scale bars = 100 µm.

trodistal protrusion of P-2 conus- shaped; S-1 distally truncated, S-2 thicker and shorter, small setal interspace (8 µm): I-L-6 short (L I-L-5/6 ratio 1.59) and stout (L/H ratio 5.0).

General features. Integument striated, muscle insertions unsclerotized. Coxal field: caudal margin Cx-I straight, apodemes of Cx-II directed laterally. Genital field: anterior margin of primary sclerotization slightly concave, but secondary sclerotization forming narrow semicircular border, posterior margin slightly indented, Ac in triangular position (Fig. 11A). Excretory pore smooth; Vgl-1 not fused to Vgl-2. Palp (Fig. 11C–D): strong ventrodistal protrusion of P-2; P-3 weakly concave proximally; P-4 sword seta between ventral setae, but approached to distoventral seta. I-L-5 (Fig. 11B): dorsal and ventral margins subparallel basally and centrally but diverging near the distal edge, S-1 and -2 close together, S-1 distally truncated, S-2 thicker and shorter, bluntly pointed; I-L-6 stout and curved, basally thickened, distally equally narrowed.

Measurements — Idiosoma L/W 550/425; coxal field: L 319; Cx-III W 366; Cx-I+II mL 121, lL 231; genital field L/W 112/120, L Ac 1-3: 34, 42, 51-55.

Palp: Total L 289, dL/H, dL/H ratio: P-1, 31/25, 1.25; P-2, 66/51, 1.3; P-3, 62/44, 1.39; P-4, 96/26, 3.67; P-5, 34/13, 2.5; L P-2/P-4 ratio 0.96.

Legs: I-L-5 dL 171, vL 132, dL/vL ratio 1.3, maximum H 48, dL/maximum H 3.59, S-1 L 77, L/W ratio 8.4, S-2 L 65, L/W ratio 6.0, distance S-1-2, 8, L ratio S-1/2, 1.19; I-L-6 dL 108, central H 22, dL/central H ratio 5.0; dL I-L-5/6 ratio 1.59.

Female: unknown.

Etymology. Named after Dr Sergey Ermilov (Tyumen, Russia), for his contribution to the taxonomy of oribatid mites.

Remarks. The new species resembles *Atractides samsoni* (Sokolow, 1936) in the small S-1/2 interspace, I-L-6 stocky, postgenital area with smooth excretory pore and unfused Vgl-1/2 and a palp with a conus shaped ventrodistal protrusion in male. The latter species can be distinguished by the shorter medial suture line of Cx-I, smaller acetabula, more slender S-1 and -2, and I-L-6 only weakly curved and longer (see Gerecke 2003). Males of *A. constrictus* (Sokolow, 1934), a species similar in the shape of palp (double ventral protrusion on P-2), a larger Ac (maximum diameter > 39 µm), and I-L-6 relatively short compared to I-L-5 (L I-L-5/6 ratio 1.4-1.6), differ in wider setal interspace on I-L-5, I-L-6 more slender and more narrow centrally, P-4 ventral setae inserted more closely to each other and genital field deeply indented both anteriorly and posteriorly.

Habitat. A permanent sandy/bouldary stream, shaded by riparian vegetation (Fig. 13B).

Distribution. Korea, only known from the locus typicus.

Family Feltriidae K.Viets, 1926
Genus *Feltria* Koenike, 1892

Feltria (*Feltria*) *kuluensis* Tuzovskij, 1988
Fig. 12

Synonymy. *Feltria kuluensis* Tuzovskij 1988: 226.

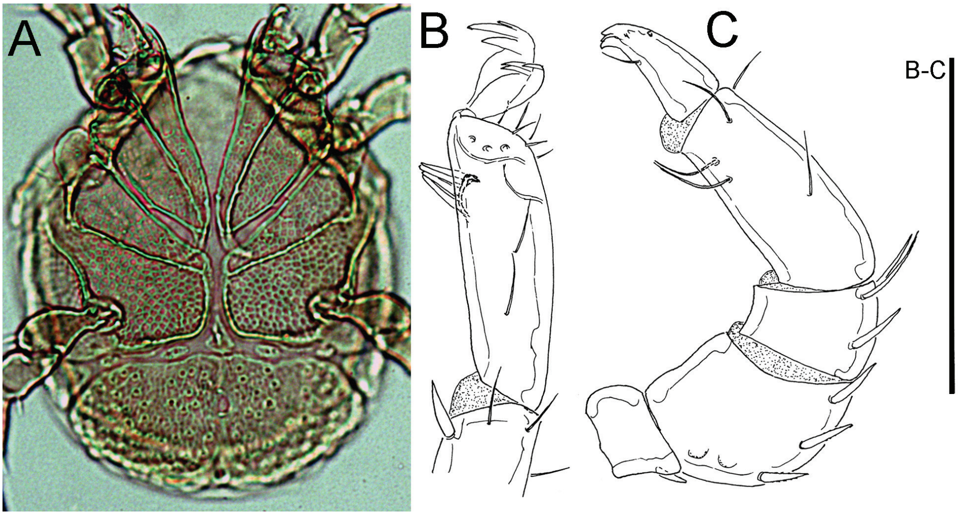

Figure 12. *Feltria kuluensis* Tuzovskij, 1988, male, Juwangsan NP, Korea (**A** photograph, **B–C** line drawing): **A** idiosoma, ventral view **B** IV-L-6 **C** palp. Scale bar = 100 μm (**B–C**).

Material examined. SOUTH KOREA: CR16 Gyeongsangbuk Province, Juwangsan NP, Woroe-ri, Cheong song-eup, Dalgikpo, waterfall, 36°26.499'N, 129°08.114'E, 23.v.2013 Pešić & Karanović 1/0/0 (mounted).

Remarks. The single male from this study matches the general morphology of *Feltria kuluensis* Tuzovskij, 1988, a species described from the Magadan region in the Russian Far East (Tuzovskij (1988). This species closely resembles *F. minuta* Koenike, 1892, a species known from central, northern and western Europe, due to the following features: dorsum in male with a large shield (including Postoc. and Dgl-1-3) and Dgl-4 on paired, transverse, laterally pointed posterodorsal platelets (fig. 7-1, in Tuzovskij 1988), genital plate in male with undulating or straight anterior margin, gonopore in central position, and more than 50 pairs of Ac scattered over the whole plate (Fig. 12A), and male IV-L-6 with a digitiform ventrolateral extension directed to distal part of segment (Fig. 12B). *Feltria minuta* differs in relatively more slender palp, P-4 with both ventral setae on slightly elevated, parallel longitudinal extensions, and male IV-L-6 relatively more shorter with ventrolateral extension bearing one fine seta and two enlarged, transparent setae, adpressed to each other and directed ventrally (Gerecke et al. 2009).

Chung and Kim (1991) reported and illustrated *Feltria ishikariensis* Imamura, 1954 from Kangreung, Korea. This species was described orginally by Uchida (1934) as *F. rotunda* based on three specimens (probably, by mistake assigned to a male, see figs 48–49 in Uchida 1934). Later on, Imamura (1954) described and illustrated the female of *F. ishikariensis* from Hokkaido, Japan. *Feltria ishikariensis* clearly differs from the species illustrated by Chung and Kim (1991) by the lower number of acetabula (< 50 pairs of Ac). As their illustrations (Chung and Kim 1991: Figs 6G–I, 7A–C) show a general conformity with *F. kuluensis* in all abovementioned characters, it is very likely that the specimens attributed to *F. ishikariensis* refer to *F. kuluensis*.

Figure 13. Photographs of selected sampling sites. **A** CR16 (Juwangsan NP , Dalgikpo waterfall, sampling site of *Wandesia* cf. *rara* and *Feltria kuluensis*) **B** CR19 (Sobaeksan NP, stream, type locality of *Atractides ermilovi* sp. n.) **C** CR21 (Woraksan NP, stream, type locality of *Torrenticola neodentifera* sp. n.) **D** CR22 (Chiaksan NP, stream, sampling site of *Wandesia reducta*, *Torrenticola neodentifera* sp. n. and *Atractides constrictus*).

In the same paper, Chung and Kim (1991) assigned two female specimens collected from Kangreung to *F. minuta* Koenike, 1892. As mentioned by Pešić (2014), because the important characters are restricted to males, this assignment is uncertain, and probably refer to female of *F. kuluensis*.

Distribution. Far East of Russia (Tuzovskij 1988). New for fauna of Korea.

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The senior author thanks Dr Tomislav Karanovic (from the Hanyang University, Seoul) for his assistance with the field work. We express deep gratitude to Dr D.A. Sidorov and Dr T.M. Tiunova (Institute of Biology and Soil Science, Russia) for collecting some of the material examined in this study. This study was undertaken with financial support of the discovery project of endemic species in Korea [Invertebrate part excluding insects] sponsored by NIBR Korea (NIBR No. 2013-02-001).

References

Chung K-S, Kim I-H (1991) Water mites (Acari) from the vicinity of Kangreung, Korea. Journal of Natural Sciences Research of the Institute KANU 7: 49–83. [In Korean]

Chung K-S, Kim I-H (1997) Eight species of water mites (Acari) new to Korean fauna. Journal of Natural Sciences Research of the Institute KANU 13(2): 117–135. [In Korean]

Gerecke R (2003) Water mites of the genus *Atractides* Koch, 1837 (Acari: Parasitengona: Hygrobatidae) in the western Palaearctic region: A revision. Zoological Journal of the Linnean Society 138(2-3): 141–378. doi: 10.1046/j.1096-3642.06-0.00051.x

Gerecke R, Weigmann G, Wohltmann A, Wurst E (2007) Order Acari – General introduction and key to major groups. In: Gerecke R (Ed.) Chelicerata, Acari II. Süßwasserfauna von Mitteleuropa, 7, 2–1. Elsevier GmbH, Spektrum Akademischer Verlag, Heidelberg, 14–57.

Gerecke R, Schatz H, Wohltmann A (2009) The mites (Chelicerata: Acari) of the CRENODAT project: faunistic records and ecological data from springs in the autonomous province of Trento (Italian Alps). International Journal of Acarology 35(4): 303–333. doi: 10.1080/01647950903059452

Imamura T (1954) Studies on water mites from Hokkaido. Journal of the Faculty of Sciences, Hokkaido University, Sapporo, Section B, Supplement 1: 1–148.

Matsumoto N, Dick MH, Mawatari SF (2005) Water mites of the genus *Hygrobates* Koch, 1837 (Acari: Parasitengona: Hygrobatidae) from Hokkaido, northern Japan. Journal of Natural History 39: 1893–1945. doi: 10.1080/00222930400023727

Pešić V (2014) Checklist of the water mites (Acari, Hydrachnidia) of Korea, with description of one new subgenus and two new species. Ecologica Montenegrina 1(4): 204–230.

Pešić V, Semenchenko K, Lee W (2013) Torrenticolid water mites from Korea and the Russian Far East. ZooKeys 299: 21–48. doi: 10.3897/zookeys.299.5272

Semenchenko KA (2010) Water mites (Acari: Hydrachnidia) from the south of the Far East. PhD thesis, Institute of Biology and Soil, Vladivostok, 274 pp. [In Russian]

Semenchenko KA, Abé H, Boeskorov GG (2010) New data on water mite fauna (Acari, Hydrachnidia, Halacaroidea) of Sakha Republic (Yakutia). Zoologicheskii Zhurnal 89(2): 167–177. [In Russian]

Sokolow I (1934) Beiträge zur Kenntnis der Hydracarinenfauna des Ussuri Gebietes II. Hydracarinen der fließenden Gewässer. Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere 65: 309–388.

Sokolow I (1940) Hydracarina (1re partie: Hydrachnellae). Faune de l'URSS. Arachnides, 5(2). Edition de l'Academie des Sciences de l' URSS, Moscou–Leningrad, 511 pp. [In Russian]

Tuzovskij PV (1987) Novye vidy vodjanych klescej roda *Wandesia* (Hydryphantidae, Acariformes) iz Magadanskoj Oblasti. Biolgicheskie Nauki, Moskva 3: 36–44.

Tuzovskij PV (1988) Novyje vidy vodjanych klescej roda *Feltria* Koenike (Acariformes, Feltriidae). Entomologicheskoe Obozrenie 67(1): 218–230.

Tuzovskij PV (1990) Key to deutonymphs of water mites. Nauka, Moscow, 1–238. [In Russian]

Tuzovskij PV (2008) The Morphology of three species of adult water mites of the genus *Sperchon* (*S. kuluensis*, *S. prosperoides*, and *S. orientalis*, Acariformes, Sperchontidae). Entomological Review 88(2): 139–149. doi: 10.1134/S0013873808020024

Uchida T (1934) Some rheophilous water mites from Japan. Journal of the Faculty of Sciences, Hokkaido University, Sapporo, Series 6, Zoology 3(2): 67–116.

Wiles PR (1991) Rheophilic watermites (Acari: Hydrachnidia) from mainland Malaysia. Acarologia 32: 41–56.

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RESEARCH ARTICLE

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Discovery of the genus *Formosiepyris* Terayama, (Hymenoptera, Bethylidae) in Vietnam, with a description of a new species

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Abstract

Formosiepyris vietnamensis **sp. n.** (Hymenoptera: Bethylidae) is described based on material collected from Da Lat, southern Vietnam. This is the first record of *Formosiepyris* Terayama from Vietnam. The new species can be distinguished from other *Formosiepyris* species by a narrow and rounded clypeus; a mandible with three teeth; a second metasomal tergite having small, sparsely distributed punctures and smooth interspaces, except for anterior 2/5, which is microreticulate; and a head length : width aspect ratio of 10 : 11. A key to the Oriental species of *Formosiepyris* is provided.

Keywords

Epyrinae, key, new record, Oriental region

Introduction

The genus *Formosiepyris* Terayama, 2004 (Hymenoptera: Bethylidae: Epyrinae) was initially described based on three species, namely, *F. marishi* Terayama, 2004 from Thailand, *F. shiva* Terayama, 2004 from India and *F. takasago* Terayama, 2004 from Taiwan (Terayama 2004). Subsequently, *F. rugulosus* Xu & He, 2005 was described from Fujian Province, China, (Xu and He 2005). While all of these species are distributed in the Oriental region, Mugrabi and Azevedo (2010) and Azevedo et al. (2010) recorded several unidentified species of *Formosiepyris* in the United Arab Emirates and Madagascar, implying that the distribution and diversity of this genus require clarification.

In the course of our study on the hymenopteran fauna of Vietnam, we collected a male *Formosiepyris* specimen from Da Lat, Lam Dong Province, in southern Vietnam. Here we describe a new *Formosiepyris* species based on this male, and provide an updated key to the Oriental species.

Material and methods

The terminology follows that of Evans (1964), Azevedo (2001), and Terayama (2006). The following abbreviations were used in the description: HL, head length; HW, head width; WF, width of frons; LM, length of mesosoma; LPD, length of propodeal disc; WPD, width of propodeal disc; FWL, forewing length; TL, total body length; EL, eye length; POL, minimum distance between posterior ocelli; AOL, minimum distance from a posterior ocellus to nearest eye margin; OOL, minimum distance from a posterior ocellus to nearest eye margin; WOT, distance across and including posterior ocelli.

The holotype of *F. takasago* deposited in the National Museum of Nature and Science Tsukuba, Japan, and a paratype of *F. marishi* in the Terayama Collection were also examined for comparison. Character evaluations of the other two species, *F. shiva* and *F. rugulosus*, were based on the original descriptions (Terayama 2004; Xu and He 2005).

The holotype designated in this study has temporarily been deposited in the Laboratory of Entomology, Faculty of Agriculture, Tokyo University of Agriculture Atsugi, Japan, but it will be transferred to the Vietnam National Museum of Nature, Hanoi, Vietnam.

Taxonomy

Genus *Formosiepyris* Terayama, 2004

Formosiepyris Terayama, 2004: 91. Type species: *F. marishi* Terayama, 2004.

Diagnosis. Head rounded; mandible with three or four teeth; median lobe of clypeus rounded or triangular; lateral lobe of clypeus undeveloped; eye covered with minute setae, large and convex; antenna with 13 antennomeres; posterior margin of pronotal disc and mesoscutum with transverse groove; posterolateral corner of propodeal disc with two pairs of small projections (Terayama 2004).

Distribution. Oriental region and Afrotropical region (Species listed in the latter are not identified) (Terayama 2004; Xu and He 2005; Mugrabi and Azevedo 2010; Azevedo et al. 2010).

Host. Unknown (Terayama 2004; Xu and He 2005).

Formosiepyris vietnamensis **Tsujii, Mita, Terayama, Pham & Okajima, sp. n.**

http://zoobank.org/BDE59050-88E1-4EC3-93C0-556D41100590

Figs 1–5

Type. Holotype: male, Vietnam, Lam Dong Prov., Da Lat, near Tuyen Lam Lake, 11°53'00.1"N, 108°24'29.9"E, ca. 1420m, 15. III. 2013, collected by yellow pan trap, K. Tsujii leg.

Diagnosis. Mandible with three teeth; anterior margin of clypeus rounded (Fig. 1); surface between median carina and inner submedian carina of propodeum without longitudinal striae; second metasomal tergite with sparse small punctures, and with smooth interspaces except anterior 2/5 sparsely microreticulate (Fig. 5).

Description of male. Measurements. HL 0.99 mm; HW 1.10 mm; WF 0.58 mm; LM 1.96 mm; LPD; 0.65 mm; WPD, 0.78 mm; FWL 2.78 mm; TL 4.90 mm. EL 0.56 mm; Malar space 0.89 mm. Hind wing 2.08 mm. Hind leg 2.68 mm.

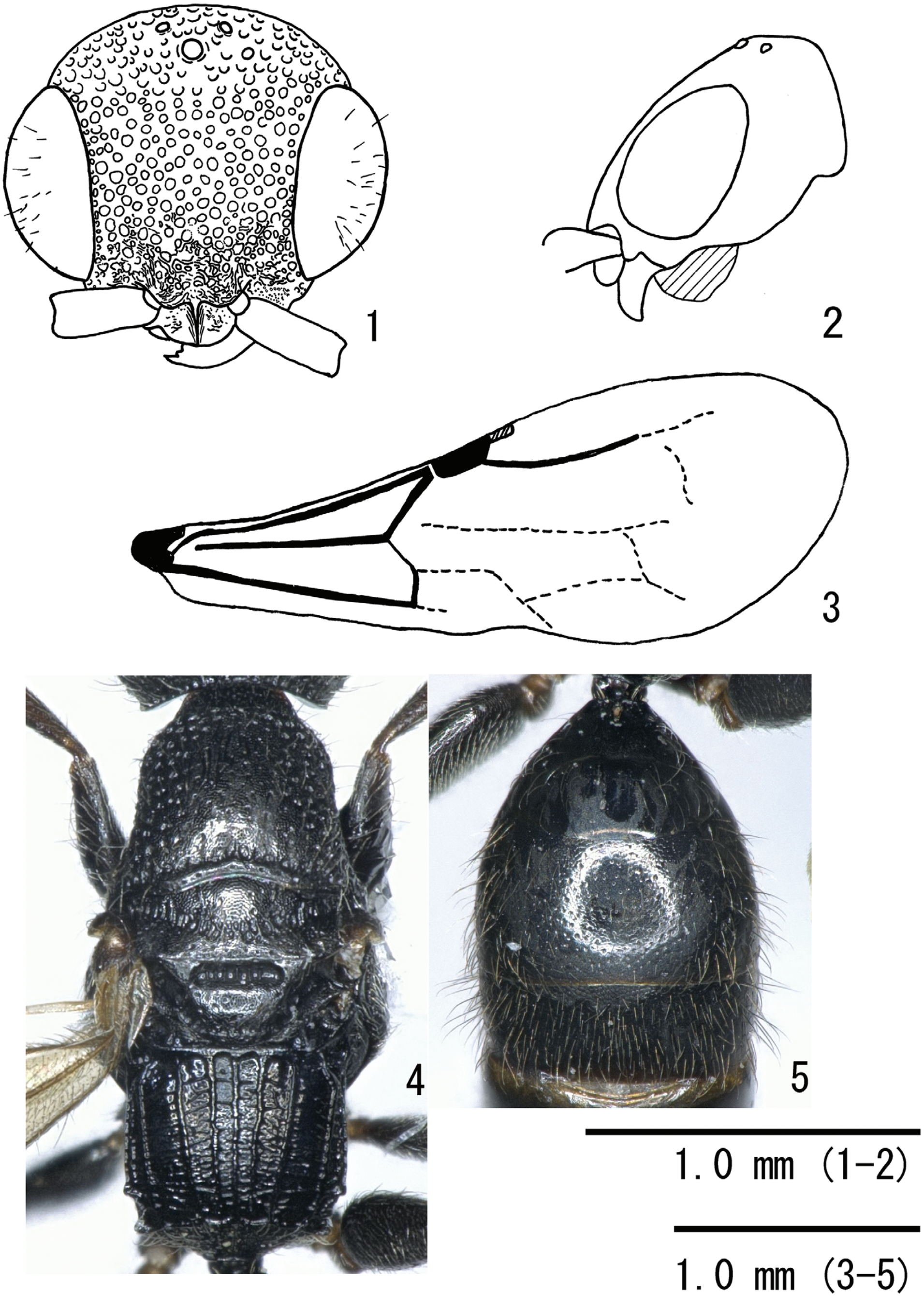
Coloration. Body black, except dark brown apical half of mandible and yellowish brown tarsi. Wings faintly tinged with brown.

Head. Head 0.9 times as long as wide, with convex posterior margin in frontal view; frons and vertex densely and strongly punctated and microreticulate interspaces; maximum diameter of punctures ca. 0.3–0.5 mm. Posteroventral corner of gena forming dully projection (Fig. 2). Mandible with three teeth (Fig. 1). Anterior margin of clypeus rounded. The ratio of first five antennomeres as follows; 16: 7: 11: 11: 11. WF 1.05 times EL. Ocelli forming obtuse triangle; OOL 1.24 times WOT.

Mesosoma (Fig. 4). Pronotum punctated with microreticulate interspaces; punctures sparser than head; median longitudinal carina absent. Scutum punctated with microreticulate interspaces. Propodeal disc 0.83 times as long as wide, with five discal carinae; surfaces between carinae of propodeum without longitudinal striae; posterolateral corner of propodeal disc with two pairs of distinct projection; sublateral carina present. Hind femur 5.6 times as long as wide in lateral view. Hind leg with two tibial spurs as long as half of first tarsomere. Tarsal claws simple. Fore wing with short metacarpus, 0.4 times as long as pterostigma; transverse-median vein convex posteriorly.

Metasoma. First tergite 0.5 times as long as wide, smooth; second tergite 0.5 times as long as wide; second and third tergites punctated with sparsely located small punctures and smooth interspaces except microreticulated anterior 2/5 (Fig. 5).

Female. Unknown.



Figures 1–5. *Formosiepyris vietnamensis* sp. n., holotype male. **1** Head in full face view **2** head in lateral view **3** forewing in dorsal view **4** mesosoma in dorsal view **5** metasoma in dorsal view.

Etymology. The specific name is from the type locality, Vietnam.

Hosts. Unknown.

Distribution. Oriental region: Vietnam (Lam Dong Province).

Remarks. This species is similar to *F. marishi* based on the convex posterior margin of the head in full-face view; having a punctated pronotum with microreticulate interspaces; punctures on pronotum sparser than those on head; and absence of longitudinal striae on propodeum surface between median carina and inner submedian carina. However, this species can be distinguished from *F. marishi* by having a weakly rounded anterior margin of the clypeus; head wider than long; ocelli forming an obtuse triangle; second antennomere shorter than third antennomere; and second and third tergites with small sparsely located punctures and smooth interspaces, except for microreticulated anterior 2/5.

Key to species of Oriental *Formosiepyris*

Female (females of *F. takasago* and *F. vietnamensis* are unknown)

1 Anterior margin of clypeus triangular .... ***F. marishi* Terayama, 2004**
– Anterior margin of clypeus rounded **2**
2 Mandible with three teeth; posterior margin of head convex in full-face view; second antennomere as long as third antennomere; surface between median carina and inner submedian carina of propodeum with longitudinal striae ... . ***F. shiva* Terayama, 2004**
– Mandible with four teeth; posterior margin of head straight in full-face view; second antennomere shorter than third antennomere; surface between median carina and inner submedian carina of propodeum without longitudinal striae .... ***F. rugulosus* Xu & He, 2005**

Male (males of *F. shiva* and *F. rugulosus* are unknown)

1 Anterior margin of clypeus triangular; ocelli forming a right triangle in full-face view .... ***F. marishi* Terayama, 2004**
– Anterior margin of clypeus rounded; ocelli forming an obtuse triangle in full-face view **2**
2 Head as long as wide, with posterior margin straight in full-face view; second metasomal tergite densely punctate .... ***F. takasago* Terayama, 2004**
– Head wider than long, with posterior margin convex in full-face view (Fig. 1); second metasomal tergite sparsely punctated except anterior 2/5 covered with microreticulate (Fig. 5) .... ***F. vietnamensis* sp. n.**

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References

Azevedo CO (2001) Systematics of the Neotropical Dissomphalus Ashmead (Hymenoptera, Bethylidae) of the bicavatus group. Revista Brasileira de Entomologia 45(3): 173–205.

Azevedo CO, Alencar IDCC, Barbosa DN (2010) Order Hymenoptera, family Bethylidae. Arthropod Fauna of UAE 3: 388–411.

Evans HE (1964) A synopsis of the American Bethylidae (Hymenoptera: Aculeata). Bulletin of the Museum of Comparative Zoology 132(1): 1–222.

Mugrabi DF, Azevedo CO (2010) Insecta, Hymenoptera, Bethylidae: Range extension and filling gaps in Madagascar. Check List 6: 62–63.

Terayama M (2004) *Formosiepyris*, a new genus of the family Bethylidae (Hymenoptera, Chrysidoidea) from the Oriental Region, with a proposal of a new synonymy of genus. The Research Bulletin of Kanto Gakuen University, Liberal Arts 12: 91–99.

Terayama M (2006) The Insects of Japan: Bethylidae (Hymenoptera). Touka Shobo, Fukuoka, 319 pp.

Xu Z, He J (2005) A new species of *Formosiepyris* Terayama, 2004 (Hymenoptera: Bethylidae) from China. Zootaxa 959: 1–4.

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RESEARCH ARTICLE

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Four new species of Cerambycidae (Coleoptera) from Paraguay

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Abstract

Four new species of Cerambycidae are described from Paraguay: *Eranina tomentilla* (Hemilophini); *Mimasyngenes concolor* (Desmiphorini); *Recchia drechseli* (Aerenicini); and *Microibidion bimaculatum* (Neoibidionini). The new species are included in known keys.

Keywords

Cerambycinae, key, Lamiinae, South America, taxonomy

Introduction

Bates (1866) described *Erana* to include a single species: *E. cincticornis* Bates, 1866. Still in the 19th Century, Bates (1874, 1881, 1885) described nine other species in this genus. In the 20th Century, 14 species were described, and one was transferred to *Erana*. More recently, in this century, 12 new species were described. Monné (2005) proposed *Eranina* to replace *Erana* Bates, 1866, preoccupied by *Erana* Gray, 1840 (Aves). Currently *Eranina* includes 36 species, distributed in North (Mexico), Central and South America. Martins and Galileo (2014) reviewed the 18 South American species and provided a key to them.

Mimasyngenes Breuning, 1950 includes 14 species, apparently occurring only in South America. A single species was recorded for Costa Rica (*Mimasyngenes icuapara* Galileo & Martins, 1996) by Swift et al. (2010), but Monné (2014) considered the record as doubtful: "Costa Rica ?, Brazil (São Paulo), Argentina (Misiones)." Clarke (2007) revised the species of *Mimasyngenes* occurring in Bolivia, and provided a key to the ten species known at that time. After the publication of that key, four new species were described in *Mimasyngenes*.

Recchia Lane, 1966 is a predominantly South American genus, with a single species also occurring in Central America: *Recchia hirsuta* (Bates, 1881). Currently *Recchia* includes 22 species. From those species, seven were transferred from *Aerenica* Dejean, 1835, of which two were originally described in *Saperda* Fabricius, 1775. Galileo and Martins (1992) synonymized *Trichohippopsides* Breuning, 1980 with *Recchia*, and the type species of the former, *T. albicans* Breuning, 1980, with *Recchia albicans* (Guérin-Méneville, 1844). Martins and Galileo (1998) considered *Coruparana* Lane, 1966 as a new synonym of *Recchia*. Thus, two more species were added to *Recchia*.

Microibidion Martins, 1962 is exclusively South American, and includes six species. The latest species was described from Bolivia 43 years ago. Martins (2009) revised the species of this genus and provided a key to them.

Material and methods

Photographs were taken with Canon EOS Rebel T3i DSLR camera, Canon MP-E 65mm f/2.8 1–5× macro lens, controlled by Zerene Stacker AutoMontage software.

The collection acronyms used in this study are as follows:

MZSP	Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil.

Systematics

Lamiinae Latreille, 1825
Hemilophini Thomson, 1868

Eranina tomentilla sp. n.

http://zoobank.org/ACFC97FC-8369-4A8F-AC34-02AA1591385C
Figs 1, 2, 3

Description. Integument black; the following parts orange: frons, most of clypeus, most of lateral side of mandibles, maxillary palpomeres I–III, base of maxillary palpomere IV, ventral side of head, area under lower eye lobes, base of antennomere III, base and nearly all ventral side of antennomere IV, base of antennomeres V–VII, large central "V-like" area on pronotum, parts of lateral side of prothorax, lateral longitudinal band on basal half of elytra (reaching lateral margin on basal fourth), basal two-thirds of profemora, basal half of mesofemora, basal third of metafemora; the following brown-yellowish: vertex, about central two-fourths of dorsal side of antennomere III; parts of lateral side of prothorax; tarsal claws; brown longitudinal band on basal half of elytra, between orange band and black area; ventral side of scape dark-brown.

Head. Frons transverse, coarse, abundantly punctate (most punctures obliterated by pubescence); pubescence yellow, dense, mixed with long, sparse setae. Coronal suture well-marked from clypeus to anterior edge of prothorax. Area between antennal tubercles depressed, coarse punctate; pubescence sparser than on anterior region of frons; laterally with long setae. Antennal tubercles with yellow pubescence on base, dark-brown on remaining surface; with long, abundant setae. Vertex with yellow, dense pubescence. Area behind lower eye lobes coarse, abundantly punctate; pubescence, moderately dense on narrow band close to eyes, very sparse towards anterior edge of prothorax. Genae with yellow pubescence, mixed by long, sparse setae. Distance between upper eye lobes equal to 0.2 times the length of scape; distance between lower eye lobes, in frontal view, equal to 0.6 times the length of scape. Antennae as long as 1.2 times the elytral length; almost reaching elytral apex; scape, pedicel and antennomere III with abundant, moderately long erect setae, mixed with also abundant very long setae throughout; antennomere IV with setae as on III, but sparser; antennomeres V–XI dorsally with sparse, moderately long setae, ventrally with very long, sparse setae; antennal formula based on antennomere III: scape = 0.77; pedicel = 0.14; IV = 0.44; V = 0.25; VI = 0.23; VII = 0.21; VIII = 0.21; IX = 0.19; X = 0.19; XI = 0.21.

Thorax. Prothorax cylindrical, transverse. Pronotum moderately coarse, abundantly punctate; pubescence yellow on area with orange integument, directed towards center, forming elongated tuft; on each side of anterior half, spot of yellowish-white pubescence; remaining surface with very short, slightly conspicuous brownish-yellow pubescence; with long, sparse setae. Lateral sides of prothorax moderately coarse, abundant punctate; pubescence brownish-yellow, dense on areas with light integument, brown on areas with dark integument. Metasternum laterally pubescent, very sparsely pubescent towards middle. Elytra: coarse, abundantly punctate on basal half, gradually finer, sparser punctate towards apex; pubescence dense, very conspicuous on area with orange integument, dark-brown, very short on remaining surface; with moderately long, abundant erect setae throughout; apex individually rounded. Legs: femora pubescent, with long, moderately abundant setae (mainly ventrally).

Abdomen. Ventrites I–IV laterally pubescent, distinctly sparser towards center, interspersed with long, sparse setae. Ventrite V trapezoidal, 1.5 times as long as IV, with long sparse setae, distinctly denser near apex, laterally pubescent; apex rounded.

Type material. Holotype female: PARAGUAY, San Pedro: La Florida (56°59'W, 24°29'S), 27.IV.2012, U. Drechsel col. (MZSP).

Dimensions in mm (female). Total length, 8.0; length of prothorax at center, 1.2; anterior width of prothorax, 1.3; posterior width of prothorax, 1.4; humeral width, 1.9; elytral length, 5.8.

Figures 1–16. **1–3** *Eranina tomentilla*, holotype female (length, 8.0 mm): **1** Dorsal habitus **2** Lateral habitus **3** Head, frontal view **4–6** *Mimasyngenes concolor*, holotype female (length 4.2 mm): **4** Dorsal habitus **5** Lateral habitus **6** Head, frontal view **7–10** *Recchia drechseli*, holotype male (11.6 mm): **7** Dorsal habitus **8** Lateral habitus **9** Head, frontal view **10** Upper eye lobes **11** *Recchia goiana*, male, upper eye lobes **12–15** *Microibidion bimaculatum*: **12** Holotype male (5.7 mm), dorsal view **13** Holotype male, lateral view **14** Paratype female (6.6 mm), ventral view **15** Holotype male, head, frontal view **16** *Microibidion exculptum*, paratype male, dorsal view.

Etymology. Latin, *tomentum* = pubescence consisting of moderately long, soft, entangled hairs; *illa* = suffix, added to feminine nouns to denote a diminutive form. Relating to the hairy look of the species.

Remarks. *Eranina tomentilla* sp. n. differs from *E. argentina* (Bruch, 1911) as follows (comparison with syntype female deposited at MZSP): distance between upper eye lobes equal to 0.2 times the length of scape; setae on antennomere III distinctly more abundant; antennomere III 2.2 times longer than IV; basal integument of antennomeres V–VII orange. In *E. argentina* the distance between upper eye lobes is equal to 0.35 times length of scape, the setae on antennomere III are sparser (mainly the shorter ones), antennomere III is 1.7 times as long as IV, and antennomeres V–VII are entirely dark. It can be separated from females of *E. porangaba* (Galileo & Martins, 1998) by antennae not reaching elytral apex (surpassing in *E. porangaba*), and by antennomere III longer than twice length of IV (distinctly shorter than twice the length of IV in *E. porangaba*).

Eranina tomentilla can be included in the alternative of couplet “16”, from Martins and Galileo (2014) (translated; couplet 15 modified):

15(13) Elytra without yellow macula on humeri; antennomere IV white with basal ring black. French Guiana, Brazil (Amazonas)...***E. cincticornis* (Bates, 1866)**
– Elytra with yellow macula on humeri; antennomere IV basally yellowish ... **16**
16(15) Elytra mostly yellowish with circum-scutellar region and distal third reddish-brown; antennomere III shorter than twice the length of IV; antennomeres V–VII entirely dark. Paraguay, Argentina ....***E. argentina* (Bruch, 1911)**
– Elytra mostly dark; antennomere III longer than twice the length of IV; antennomeres V–VII orange on base. Paraguay ....***E. tomentilla* sp. n.**

Desmiphorini Thomson, 1860

Mimasyngenes concolor sp. n.

http://zoobank.org/33412AE4-55CE-4D84-B1C5-D8289CD33A88
Figs 4, 5, 6

Description. Integument black, with labrum and palpi reddish-brown; pubescence white; setae dark-brown.

Head. Frons transverse, coarse, moderately abundantly punctate; pubescence sparse, distinctly not obliterating integument, slightly more concentrated along coronal suture and margin of eyes; setae long, sparse. Sculpture and pubescence of vertex as on frons. Coronal suture marked from clypeus to anterior edge of prothorax. Area behind eyes with sparse pubescence. Genae with sparse pubescence towards clypeus, glabrous towards apex. Distance between upper eye lobes equal to 0.6 times the length of scape; distance between lower eye lobes, in frontal view, equal to 0.8 times the length of scape. Antennae as long as 1.3 times the elytral length; reaching elytral apex; antennal segments sparsely pubescent; scape, pedicel and antennomeres III–VII with sparse, very long setae throughout (ventrally longer and more abundant on antennomeres); antennomeres VIII–X with moderately long setae near apex; antennal formula based on antennomere III: scape = 0.96; pedicel = 0.33; IV = 1.08; V = 0.75; VI = 0.75; VII = 0.67; VIII = 0.58; IX = 0.46; X = 0.42; XI = 0.42.

Thorax. Prothorax transverse, distinctly wider between lateral tubercles and anterior margin. Pronotum coarse, deeply, abundantly punctate; pubescence sparse, slightly longer between lateral tubercles of prothorax and anterior margin; with long, sparse setae. Lateral sides of prothorax with sculpture, pubescence and setae as on pronotum; lateral tubercle spiny, curved upwards. Elytra: coarse, deeply, abundantly punctate (punctures aligned in rows); pubescence sparse, forming rows placed between rows of punctures; with long, sparse setae; lateral sides slightly expanded after middle; apex together rounded. Legs: Femora and tibiae with sparse pubescence, dorsally with long, sparse setae.

Abdomen. Ventrites pubescent. Ventrite V trapezoidal, 3.3 times as long as IV, depressed at center of distal third; apex concave.

Type material. Holotype female: PARAGUAY, Canindeyú: Carapa, (54°23'W, 24°22'S), 22.XI.2003, U. Drechsel col. (MZSP).

Dimensions in mm (female). Total length, 4.20; length of prothorax at center, 0.85; anterior width of prothorax, 0.85; posterior width of prothorax, 0.80; largest width of prothorax, 1.05; humeral width, 1.20; elytral length, 2.95.

Etymology. Latin, *concolor* = of the same color. Relating to the uniform color of the body.

Remarks. *Mimasyngenes concolor* sp. n. is similar to *M. icuapara* Galileo & Martins, 1996, but differs mainly by the spiny lateral tubercle of prothorax being notably smaller, and by antennomere III shorter than IV. In *M. icuapara* the lateral tubercle of prothorax is distinctly longer and antennomere III is about as long as IV.

Mimasyngenes concolor can be included in the alternative of couplet "5", from Clarke (2007) (modified):

5	Lateral tubercle simple, with blunt tooth. Bolivia, Brazil (Maranhão, Pernambuco, Goiás), Argentina .... ***M. lineatipennis* Breuning, 1950**
–	Lateral tubercle with curved spine .... **5'**
5'(5)	Pronotum and elytra finely punctate. Brazil (São Paulo), Bolivia .... ***M. quiuira* Galileo & Martins, 1996**
–	Pronotum and elytra coarsely punctate. Paraguay .... ***M. concolor* sp. n.**

Aerenicini Lacordaire, 1872

Recchia drechseli sp. n.

http://zoobank.org/F3B626CF-F8B2-43F9-9D56-65D072A9ABCC
Figs 7, 8, 9, 10

Description. Integument dark-brown; basal two-thirds of antennomeres III–XI, mostly metatarsomere I, and basal two-thirds of tarsomeres V reddish-brown; meso- and metatibiae mostly brown.

Head. Frons trapezoidal, microsculptured, moderately fine, abundantly punctate (mainly towards clypeus); pubescence abundant, yellowish-brown, not obliterating integument (slightly whitish on some areas); with long, abundant setae. Antennal tubercles microsculptured, sparse, finely punctate (punctures sparser towards apex); pubescence as on frons. Coronal suture distinct from clypeus to anterior edge of prothorax. Vertex moderately fine, abundantly punctate; pubescence somewhat denser than on frons. Area behind eyes densely pubescent from upper eye lobes to about middle of lower eye lobes; from middle of lower eye lobes to its apex with narrow band of pubescence close to eyes, and glabrous towards anterior edge of prothorax. Genae sparsely pubescent towards eyes, glabrous towards apex. Distance between upper eye lobes equal to 0.3 times the length of scape; distance between lower eye lobes, in frontal view, equal to 0.5 times the length of scape. Antennae as long as 1.9 times the elytral length; reaching elytral apex at base of antennomere VIII; scape and pedicel with long setae throughout; antennomere III with long, moderately abundant setae on ventral side, with moderately short, abundant setae on basal half of dorsal side; antennomeres IV–XI ventrally with long, sparse setae (sparser towards distal antennomeres); antennal formula based on antennomere III: scape = 1.40; pedicel = 0.21; IV = 0.88; V = 0.88; VI = 0.83; VII = 0.81; VIII = 0.74; IX = 0.71; X = 0.62; XI = 0.64.

Thorax. Prothorax cylindrical, slightly longer than wide; lateral sides distinctly narrower at basal third. Pronotum moderately coarse, abundantly punctate (most punctures obliterated by pubescence); pubescence yellowish-white, except for a large "V-like" central area and lateral sides with yellowish-brown pubescence; with long, sparse setae. Pubescence of lateral sides of prothorax yellowish-brown; pubescence close to pronotum, gradually more yellowish-white towards prosternum. Pro- and mesosternum mostly with dark-brown pubescence. Mesepisternum with dark-brown pubescence on half close to mesosternum, yellowish-white on half close to humerus. Mesepimeron with yellowish-white pubescence. Metepisternum and lateral sides of metasternum with dense, yellowish-white pubescence; remaining surface of metasternum with pubescence less dense. Elytra: coarse, abundantly punctate on basal third, gradually finer, sparser towards apex; pubescence yellowish-white (more yellowish on some areas), not forming distinct drawing; with long, sparse setae; apex individually rounded. Legs: pubescence on femora distinctly not obliterating integument.

Abdomen. Ventrites with yellowish-brown pubescence, interspersed with long, sparse setae. Ventrite V trapezoidal, 1.4 times as long as IV; apex rounded.

Type material. Holotype male: PARAGUAY, Canindeyú: Armisticio (54°32'W, 24°34'S), 30.XI.2009, U. Drechsel col. (MZSP).

Dimensions in mm (male). Total length, 11.6; length of prothorax at center, 1.9; anterior width of prothorax, 1.9; posterior width of prothorax, 1.9; humeral width, 2.7; elytral length, 8.3.

Etymology. The species is named for Ulf Drechsel, collector of the holotype.

Remarks. *Recchia drechseli* sp. n. differs from *R. goiana* Martins & Galileo, 1985 as follows: dorsal pubescence less compact; upper eye lobes wider (Fig. 10), largest width larger than basal width of scape; distance between upper eye lobes equal to about 2.3 times the largest width of one lobe. In *R. goiana* the dorsal pubescence is more compact, the upper eye lobes are narrower (Fig. 11), with largest width about as wide as basal width of scape, and the distance between upper eye lobes is equal to 3.0 times the largest width of one lobe. It differs from *R. flaveola* Martins & Galileo, 1985 mainly by the femora being darker (reddish in *R. flaveola*), and by the elytra without distinct contrasting areas of pubescence (present in *R. flaveola*).

Recchia drechseli can be included in the alternative of couplet "19", from Martins and Galileo (1998) (translated; modified):

19(18) Integument dark-brown on femora and pro- and mesosternum .... **19'**

– Integument reddish on femora and pro- and mesosternum. Brazil (Goiás, Federal District, Mato Grosso do Sul, Minas Gerais, São Paulo), Paraguay .. .. ***R. flaveola* Martins & Galileo, 1985**

19'(19) Largest width of upper eye lobes about as wide as basal width of scape; distance between upper eye lobes is equal to 3.0 times the largest width of one lobe. Bolivia, Brazil (Goiás, Mato Grosso, Mato Grosso do Sul, São Paulo), Paraguay .... ***R. goiana* Martins & Galileo, 1985**

– Largest width of upper eye lobes larger than basal width of scape; distance between upper eye lobes equal to about 2.3 times the largest width of one lobe. Paraguay.. ***R. drechseli* sp. n.**

Neoibidionini Monné, 2012

Microibidion bimaculatum sp. n.

http://zoobank.org/F92DA9A9-C03F-4EEB-8238-16EDC9E7C10B
Figs 12, 13, 14, 15

Description. Male. Integument dark-brown, except for: palpi reddish; large, yellowish, sub-rounded spot on each elytron near middle, not reaching lateral side and suture.

Head. Frons transverse, coarse, abundantly, confluently punctate; pubescence yellowish, sparse, absent on narrow band around coronal suture. Antennal tubercles elevated, with sculpture and pubescence as on frons. Coronal suture distinct from clypeus to about anterior edge of eyes. Vertex moderately fine, densely, confluently punctate; pubescence sparser than on frons. Area behind eyes coarse, sparsely punctate; pubescence very sparse. Genae fine, abundantly punctate, with sparse short setae. Distance between upper eye lobes equal to 0.60 times the length of scape; distance between lower eye lobes, in frontal view, equal to 0.85 times the length of scape. Antennae as long as 1.8 times the elytral length; reaching elytral apex about apex antennomere IX; scape, pedicel and antennomeres with withish-yellow pubescence; antennomeres VII–XI somewhat curved (mainly VII–VIII); antennal formula based on antennomere III: scape = 0.76; pedicel = 0.28; IV = 0.67; V = 0.88; VI = 0.88; VII = 0.88; VIII = 0.85; IX = 0.82; X = 0.73; XI = 0.79.

Thorax. Prothorax narrower at base than anteriorly; with constriction at middle of basal half. Pronotum moderately coarse, sparsely punctate; disc with three small tubercles about middle (central more conspicuous); pubescence moderately yellowish, sparse, except for three large longitudinal glabrous areas (central longest). Lateral side of prothorax sparsely punctate; with short, very sparse setae. Pubescence on metepisterna and metasternum abundant, but not dense. Scutellum with dense, yellowish pubescence. Elytra: moderately coarse, abundantly punctate; nearly all punctures with small, fine setae; with sparse, thick, yellow, moderately long setae, somewhat aligned in three rows on basal two-thirds; apex individually rounded. Legs: pubescence on femora yellowish-brown, distinctly not obliterating integument.

Abdomen. Ventrites with pubescence as on lateral side of metasternum. Ventrite V about as long as IV; apex truncate.

Paratype female. Antennae as long as 1.5 times elytral length; slightly surpassing elytral apex. Ventrite V trapezoidal; about as long as IV; apex rounded.

Type material. Holotype male: PARAGUAY, Presidente Hayes: Lolita (Laguna Yaragui, 59°37'W, 23°05'S), I.2005, U. Drechsel col. (MZSP). Paratype female: PARAGUAY, Alto Parana: Estancia Dimas (55°13'W, 25 33'S), II.2005, U. Drechsel col. (MZSP).

Dimensions in mm (male/female). Total length, 5.70/6.60; length of prothorax at center, 1.20/1.30; anterior width of prothorax, 0.85/0.95; posterior width of prothorax, 0.75/0.85; humeral width, 1.15/1.30; elytral length, 3.70/4.10.

Etymology. Latin, *bi* = two; *maculatus* = spotted. Relating to the two spots on elytra.

Remarks. *Microibidion bimaculatum* sp. n. is similar to *M. exculptum* Martins, 1962, but differs as follows: antennae dark-brown; antennomeres somewhat thicker in both sexes; antennomeres X and XI about as long as IV; basal antennomeres without long, sparse setae on ventral side; thick setae on basal two-thirds of elytra aligned in three rows. In *M. exculptum* (Fig. 16) the antennae are reddish, the antennomeres are slender, antennomeres X and XI are shorter than IV, the basal antennomeres have long, sparse setae on ventral side, and the thick setae on basal two-thirds of elytra are aligned in 4/5 rows.

Microibidion bimaculatum can be included in the alternative of couplet "3", from Martins (2009) (translated):

3(2) Head, prothorax and elytra reddish; upper eye lobes with two rows of ommatidia. Brazil (Espírito Santo to Santa Catarina) .... ***M. muticum* (Martins, 1962)**
– Head, prothorax and elytra dark-brown or black; upper eye lobes with three rows of ommatidia .... **3'**
3'(2) Antennomeres X and XI shorter than IV; basal antennomeres ventrally with long, sparse setae; thick setae on elytra aligned in 4/5 rows on basal two-thirds. Brazil (São Paulo to Rio Grande do Sul), Paraguay, Argentina (Misiones, Buenos Aires)... ***M. exculptum* Martins, 1962**
– Antennomeres X and XI about as long as IV; basal antennomeres ventrally without long setae; thick setae on elytra aligned in 3 rows on basal two-thirds. Paraguay .... ***M. bimaculatum* sp. n.**

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References

Bates HW (1866) XLV. Contributions to an Insect Fauna of the Amazons Valley. Coleoptera: Longicornes. The Annals and Magazine of Natural History17(3): 425–435.

Bates HW (1874) Supplement to the longicorn Coleoptera of Chontales, Nicaragua. The Transactions of the Entomological Society of London 1874: 219–235.

Bates HW (1881) Insecta, Coleoptera, Lamiidae. Biologia Centrali-Americana 5: 153–224.

Bates HW (1885) Supplement to Longicornia. Biologia Centrali-Americana, Insecta, Coleoptera 5: 249–436.

Clarke ROS (2007) Synopsis of the Bolivian species of *Mimasyngenes* Breuning, 1950 (Coleoptera, Cerambycidae, Desmiphorini) with two new species. Papéis Avulsos de Zoologia 47(26): 359–368. doi: 10.1590/S0031-10492007002600001

Galileo MHM, Martins UR (1992) Neotropical Cerambycidae (Coleoptera) of the Canadian Museum of Nature, Ottawa. III. Aerenicini (Lamiinae). Insecta Mundi 6(3-4): 141–144.

Martins UR, Galileo MHM (1998) Revisão da tribo Aerenicini Lacordaire, 1872 (Coleoptera, Cerambycidae, Lamiinae). Arquivos de Zoologia 35(1): 1–133. doi: 10.11606/issn.2176-7793.v35i1p1-133

Martins UR (2009) Tribo Ibidionini. Subtribo Compsina. In: Martins UR (Org.) Cerambycidae Sul-Americanos (Coleoptera). Taxonomia. Curitiba, Sociedade Brasileira de Entomologia v. 10, 1–199.

Martins UR, Galileo MHM (2014) Subfamília Lamiiinae. Hemilophini Thomson, 1868. Parte I. In: Martins UR (Org.) Cerambycidae Sul-Americanos (Coleoptera). Taxonomia. Curitiba, Sociedade Brasileira de Entomologia v. 13, 3–231.

Monné MA (2005) Catalogue of the Cerambycidae (Coleoptera) of the Neotropical Region. Part. II. Subfamily Lamiinae. Zootaxa 1023: 1–759.

Monné MA (2014) Catalogue of the Cerambycidae (Coleoptera) of the Neotropical Region. Part II. Subfamily Lamiinae. http://www.cerambyxcat.com/ [accessed 30 September 2014]

Swift IP, Bezark LG, Nearns EH, Solís A, Hovore FT (2010) Checklist of the Cerambycidae (Coleoptera) of Costa Rica. Insecta Mundi 131: 1–68.

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A new leafminer on grapevine and *Rhoicissus* (Vitaceae) in South Africa within an expanded generic concept of *Holocacista* (Insecta, Lepidoptera, Heliozelidae)

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Abstract

A grapevine leafminer found recently in table grape orchards and vineyards in the Paarl region (Western Cape, South Africa) is described as *Holocacista capensis* **sp. n.** It has also been found on native *Rhoicissus digitata* and bred on that species in the laboratory. It is closely related to *Holocacista salutans* (Meyrick, 1921), **comb. n.** (from *Antispila*), described from Durban in KwaZulu-Natal, but widespread in southern Africa and a native leafminer of various Vitaceae: *Rhoicissus tomentosa*, *R. digitata*, *R. tridentata* and *Cissus cornifolia*. *Holocacista capensis* has been found on *Vitis vinifera* both in Gauteng and Western Cape, the earliest record being from 1950 in Pretoria. The initial host shift from native Vitaceae to *Vitis* must have occurred much earlier. The species is sometimes present in high densities, but hitherto no sizeable damage to the crops has been noted. The genus *Holocacista* Walsingham & Durrant, 1909, previously known from the single European grapevine leafminer *H. rivillei* (Stainton, 1855), is expanded and redescribed and for the first time reported from Africa, East and South-East Asia and Australia. It comprises seven named species and at least 15 unnamed species. The following species are also recombined with *Holocacista*: transferred from *Antispilina*: South-African *H. varii* (Mey, 2011), **comb. n.**, feeding on *Pelargonium*, transferred from *Antispila*: the Indian species *H. micrarcha* (Meyrick, 1926), **comb. n.** and *H. pariodelta* (Meyrick, 1929), **comb. n.**, both feeding on *Lannea coromandelica*, and *H. selastis* (Meyrick, 1926), **comb. n.** on *Psychotria dalzelii*. We also remove the following from *Antispila*: *Heliozela anna* (Fletcher, 1920), **comb. n.** and *H. argyrozona* (Meyrick, 1918), **comb. n.**, whereas the following Indian Vitaceae feeding species are confirmed to belong in *Antispila* s. str.: *Antispila argostoma* Meyrick, 1916 and *A. aristarcha* Meyrick, 1916. *Holocacista salutans* and *H. varii* are redescribed and diagnosed against *H. capensis* and other South African Heliozelidae. DNA barcodes are provided for 13 species of *Holocacista*.

Keywords
Host shift, leafminers, Vitaceae, viticulture, table grapes, *Rhoicissus*, *Cissus*, DNA barcode, genitalia, *Holocacista*, *Antispilina*, *Antispila*, Afrotropics, South Africa, Zimbabwe, India

Introduction

The occurrence of leafmining Lepidoptera on cultivated grapevine has until recently been a minor economic problem, with just some damage in European viticulture by the native *Holocacista rivillei* (Stainton, 1855) (Camporese and Marchesini 1991; Alma 1995). In the last decades two cases have been reported of damage by grapevine leafminers introduced from North America into Europe: *Phyllocnistis vitegenella* Clemens, 1859 (family Gracillariidae) and *Antispila oinophylla* Van Nieukerken & Wagner, 2012 (family Heliozelidae) (Marchesini et al. 2000; van Nieukerken et al. 2012b). In Japan a native *Vitis*-feeding heliozelid infested cultivated grapevine: *Antispila uenoi* Kuroko, 1987 (Kuroko 1987; Ueno et al. 1987). In North America there are few reports of damage to cultivated grapes (e.g., Mcgiffen and Neunzig 1985), despite the rich Vitaceae-feeding fauna of heliozelids (van Nieukerken et al. 2012b). The recent infestations on cultivated grapevine with heliozelids were unexpected and in both situations required a new species to be described, despite the fact that Vitaceae as a hostplant for this family was a long-known fact, even recorded in the 18th century (Godeheu De Riville 1750; van Nieukerken et al. 2012b).

In 1990 some cocoons of an unknown leafminer infesting vines grown on the experimental farm in Roodeplaat, Pretoria, were submitted by Miss S. Marais to HG. Together with moths reared in March 1998 from urban vines in Oudtshoorn (Western Cape), these were examined during a visit in March 1999 by Dr. Vári in Pretoria, who identified them tentatively as a possible species of *Antispila* Hübner, 1825, on the basis of the type of mine and external features. After Dr J. De Waal (Dow Chemicals) brought some infested vine leaves from a commercial table grape farm near Paarl, a visit by HG showed considerable infestations in local table grape orchards, ranging from Somerset-West to Paarl in the Western Cape. As the presence of the moth, especially on grapes destined for export, could pose serious economic problems, even though the infestation did not yet result in real damage to the crop, its potential future risks required further study of the identity of the leafminer and of its life history and infestation ecology.

The Heliozelidae are a small family of primitive Monotrysian moths, of which most species make leafmines as larvae, with 124 named species globally (van Nieukerken et al. 2012b). Taxonomically the family is poorly studied, with only the Japanese fauna relatively well known (Lee and Hirowatari 2013), and a recent description of the primitive South American genus *Plesiozela* Karsholt & Kristensen, 2003, based on the unpublished generic revision by Nielsen (1980) (Karsholt and Kristensen 2003). The discovery of two North American species that invaded Europe and attacked commercially grown crops led to a revival of taxonomic and phylogenetic studies, with extensive DNA barcoding (van Nieukerken et al. 2012b; van Nieukerken et al. 2013;

Bernardo et al. 2015). One of the surprising results from these studies is the possibility that Vitaceae may form the ancestral hostplants of at least a large part of the family.

The African fauna of Heliozelidae is virtually unknown, only four species have been named to date, three of which are from South Africa. The fourth, *Antispila merinaella* Paulian & Viette, 1955, described from Madagascar (Paulian and Viette 1955), is misplaced and in fact belongs to Elachistidae (J. Minet personal communication), which also better fits the hostplant family Commelinaceae, on which several species of the genus *Elachista* Treitschke, 1833 occur (Kaila 2011). The South African species are *Antispila argyrozona* Meyrick, 1918, *A. salutans* Meyrick, 1921, both with unknown host (Kroon 1999; Vári et al. 2002) and the recently described *Antispilina varii* Mey, 2011, reared from leafmines on *Pelargonium* L.'Hérit. in the Western Cape (Mey 2011).

The late Lajos Vári (Pretoria) devoted a large part of his life to the study of leafmining Lepidoptera of southern Africa, which he extensively collected and reared between 1950 and 2007 (Kroon 2011). He only published on a limited part of this fauna, mainly Nepticulidae and Gracillariidae (Vári 1955; 1961; 1963), but did not describe the Heliozelidae that he collected. In fact, he had already discovered a *Vitis*-feeding heliozelid in 1950 in Pretoria as appears both from his notebooks and collection in Pretoria, but another record on *Vitis* L. has also been published somewhat hidden in a list as *Antispila* sp. (Kroon 1999). By studying Vári's collection, it soon appeared that a small but diverse fauna of heliozelids is present in southern Africa, with the majority feeding on native Vitaceae. As observed before (van Nieukerken et al. 2012b), many species placed in *Antispila* probably do not belong to that genus, which can be regarded as a dumping ground for heliozelids with bright spots and fascia (van Nieukerken et al. 2012b). This is also true for the Southern African species, the majority of which belong to the previously monotypic genus *Holocacista* Walsingham & Durrant, 1909, and only one of the unnamed species belongs in *Antispila* s. str. Although a revision of the South African fauna would be desirable, we here limit ourselves to the identity and taxonomy of the grapevine miner, which will be described as a new species, and compared with *Holocacista salutans* (Meyrick, 1921), comb. n. and *H. varii* (Mey, 2011), comb. n., both now re-described. We also describe its biology, provide DNA barcodes, and discuss a potential hostplant shift. Because the genus *Holocacista* previously only comprised the type species *H. rivillei*, the genus is diagnosed and re-described here as well. In Appendix A we provide brief notes on other South African Heliozelidae.

Material and methods

Material

Larvae, cocoons and adults of *Holocacista capensis* were collected in various table grape orchards, vineyards and weedy growth of grapevine in the Paarl region, several other localities in the Western Cape and at Roodeplaat, north of Pretoria. We selected the Holotype from our recent reared material, so that the name unequivocally refers to the grapevine leafminer, and to couple its morphology with DNA data. Although the description is based on multiple specimens, we refrain from selecting paratypes as they have no name-bearing function (International Commission on Zoological Nomenclature 1999). The many specimens reared by us will be divided among the collections in Leiden (Naturalis), Stellenbosch (USEC), Pretoria (ARC-PPRI and TMSA), and Cape Town (Iziko).

The extensive collections in the Ditsong Museum of Natural History (formerly Transvaal Museum, Pretoria) formed the basis for most of the present taxonomic studies, together with our newly collected material. The majority of the Pretoria material was collected and reared by Lajos Vári. The material comprises three important sources:

1. *Dry pinned collection of adults.* These are usually rather poorly labelled, with only a locality name (often in capitals), sometimes followed by a second indication of the locality, the handwritten date of emergence of the adult, sometimes the name of the collector followed by an Ac. no. [Accession number] followed by a handwritten number. There are no further details, no hostplant names nor original collection dates (unless it has been collected as an adult). In the collection, which is organised in unit trays, often a single example of a leaf with mines is pinned next to the reared moths, usually with a handwritten number on the leaf.
2. *Herbarium of leafmines*. The original collection was stored in simple open envelopes with a number, sometimes with a small label inside, but often not. The majority of this collection has later been mounted by collection staff onto herbarium sheets, partly glued to the sheet and mounted with white strips. The Ac. numbers are also written on these sheets, sometimes with additional information.
3. *Notebooks of Lajos Vári.* This is an essential source to reconstruct the hostplant data, detailed localities and collection data. They also give insight in Vári's concepts of the species he collected; he often gave manuscript names, sometimes changed subsequently and referring to earlier numbers when he considered hostplants or moth species to be identical. The Ac. numbers from the labels provide access to the notes; these numbers only refer to Vári's material and are not a general numbering for the museum.

The data we present under material and in Suppl. material 1 are the label data, supplemented with details from these notebooks.

For understanding the generic composition of the genus *Holocacista*, we studied several Heliozelidae available to us, and examined a number of Indian species described by Meyrick, that were potential candidates to belong to this genus.

Details on all studied specimens, including those sequenced, are given as an Excel sheet in Suppl. material 1.

Abbreviations for depositories etc.

ARC-PPRI	Agricultural Research Council – Plant Protection Research Institute, Pretoria, South Africa

BMNH	Natural History Museum, London, UK [for slides only the abbreviation BM is used]
EvN	E.J. van Nieukerken [for slide and rearing numbers]
HG	Personal collection of H. Geertsema, Stellenbosch, South Africa
ISAM	Iziko South African Museum, Cape Town, South Africa
JCK	J.C. Koster [for slide numbers]
MHUB	Museum für Naturkunde, Berlin, Germany
RMNH	Naturalis Biodiversity Center, Leiden, The Netherlands
TMSA	Ditsong National Museum of Natural History (formerly Transvaal Museum), Pretoria, South Africa [for slides only the abbreviation TM is used]
USEC	University Stellenbosch Entomology Collection, Stellenbosch, South Africa.

Rearing

Leaves with active mines were cut to smaller pieces and placed in small plastic containers for rearing. After the shields had been exscinded and the larvae had left the mines, the leaves were removed to avoid moulding, and examples of leafmines were dried in a plant press. Often the larvae in their shields needed some 'assistance' with forceps in order to remove them from the leaf fragments, probably because the low turgor pressure in the leaf fragments made it difficult to exit in the natural fashion, where a higher turgor pressure facilitates the release of the shield. The larval shields and the resulting cocoons were kept with some paper tissue in closed containers, and a little moisture added from time to time until emergence of the moths. Emergence from cocoons kept in this way was abundant.

Morphology

Methods for preparation of the genitalia follow van Nieukerken et al. (2012b). Male genitalia and wings were stained with phenosafranin and mounted in Euparal, often after studying material first in glycerine; for some specimens, genitalia were stored in glycerine in small vials; female genitalia were stained with Chlorazol black. Venation was studied in descaled wings that were stained with phenosafranin, after cleaning in ethanol 70% and embedded in Euparal. Whole body preparations of adults were prepared from specimens in ethanol, largely following Lee and Brown (2006) and also stained with phenosafranin.

Morphological terminology follows other recent treatments of Heliozelidae (Karsholt and Kristensen 2003; van Nieukerken et al. 2012b), the generic description follows the format set for *Plesiozela* (Karsholt and Kristensen 2003), and partly also follows Nielsen's unpublished thesis (Nielsen 1980). We also include information extracted from Nielsen's manuscript description of *Holocacista*, compared with our material and more species. Compared to the 2012 treatment (van Nieukerken et al. 2012b), the labelling of wing veins has slightly been changed; also since then we realised that antennal flagellomeres of Heliozelidae have two annuli of scales, and thus the number of antennal segments given then was incorrect and about twice the actual number (van Nieukerken et al. 2012b; Bernardo et al. 2015).

Photographs of mounted moths were prepared using an AxioCam digital camera attached to a motorized Zeiss SteREO Discovery V12, using the Module Extended Focus in the Carl Zeiss AxioVision software to prepare a picture in full focus from a Z-stack of about 10 to 25 individual photos. Leafmines and live adults were photographed with a similar camera on a manually operated Zeiss Stemi SV11 stereomicroscope, without extended focus, or with extended focus prepared from just a few exposures. Genitalia and wing slides were photographed with a similar camera on a manually operated Zeiss Axioskop H, usually with just a single exposure. Leafmines were examined and photographed with dark field illumination. Field photographs were taken with a Canon EOS camera.

Photographs were edited with Adobe Photoshop®, avoiding any change to the real object, but backgrounds were cleaned from excess debris; also some protruding scales were digitally removed from the denuded wings in Figs 29–36. Photos of wing venation were taken in sections, and combined with the photomerge tool in Photoshop. This was also done for some large leafmines. Drawings of genitalia were prepared using a drawing tube attached to the Zeiss Axioskop H. Some photos and drawings are given here as mirror image, in order to get all figures in a comparable orientation.

Host plant names of South African plants follow Germishuizen and Meyer (2003) and identifications of Vitaceae were checked and updated with Palgrave and Palgrave (2002). Other plant names were checked with The Plant List (2013).

Molecular analysis

DNA was extracted non-destructively from larvae in ethanol 96% or adult abdomens (Knölke et al. 2005). Larvae were cut with a scalpel at three positions: one in the anterior region behind the head, one in the middle region of the body and one in the posterior region. One side of the body was cut to save the larval cuticle. After lysis, larval pelts were temporarily kept in ethanol 70% to allow future mounting on slide, abdomens and genitalia were dissected and mounted on slides or stored temporarily in glycerine. Extraction was carried out with the Qiagen DNEasey Blood and Tissue kit.

A 665 bp or a 658 bp fragment of the mitochondrial CO1 gene, the DNA barcode, was amplified. PCR conditions and primers are described in our earlier studies (van Nieukerken et al. 2012a; van Nieukerken et al. 2012b; Doorenweerd et al. 2015). Sequencing was outsourced to Macrogen Corporation, Amsterdam or BaseClear B.V., Leiden.

The sequence data generated and used in this study have been deposited in the public BOLD dataset "Holocacista leafminers [DS-HOLOCAC]" [http://dx.doi.

org/10.5883/DS-HOLOCAC] and GenBank, they are listed with all details in the table with all studied specimens (Suppl. material 1). All specimens used for DNA barcodes and larvae stored as tissue samples in ethanol 96% and kept in a minus 80 freezer, received a RMNH.INS registry number, irrespective whether the original specimen belongs to the Naturalis collections or not. EvN 4-digit Genitalia slide numbers translate into a 5-digit RMNH.INS. number by adding 20,000; thus genitalia slide EvN4622 is associated with specimen and DNA extract RMNH.INS.24622.

Neighbor joining trees were prepared with the tools provided on the Boldsystems website (Ratnasingham and Hebert 2007), using "Pairwise Distance" as distance model. Further model based phylogenetic analyses were not carried out, since the CO1 gene does not have sufficient information for phylogeny. Analyses of several genes for the whole family are currently being studied and will be published elsewhere.

Field observations

Monthly field visits to the infected vineyard at De Akker (Paarl South) were conducted between February 8 and May 11, 2012, and again from November 2012 to May 2013. From 2013 the vineyard at De Heuvel estate was also visited regularly. At monthly intervals, leaf samples (n = 100) were randomly collected from selected vineyards. Leaves were classified into three size groups, viz. large (older), medium and small (young), and numbers of mines (developing, containing shields or larvae, or holes) were noted to determine any preference for the major table grape cultivars and to determine variation in the population density throughout the grape season.

During 23–25 March 2012, a survey of vineyards between Worcester and Swellendam was carried out, as well as a search for signs of heliozelid leafmines on *Rhoicissus* Planch. species present on the periphery of indigenous temperate forest in the Swellendam district. Search for those mines was repeated in 2013 and 2014, but no live moths were found or reared.

Results

Identification

Moths reared from the grapevine leafmines were compared with other available adult Heliozelidae, and the similarity with European *Holocacista rivillei* became immediately apparent, particularly by the remarkable curved spine on the phallus, but also by venation and colour pattern. Comparison with the three named South African species also showed similarity to the species *Antispila salutans* Meyrick, 1921 and *Antispilina varii* Mey, 2011, and for some time we used the name "*Holocacista salutans*". However, a detailed analysis of genitalia and comparison with material reared by Lajos Vári, made it clear that our grapevine feeder was neither of these species, but closely resembled a single population reared by Vári from leafmines on *Rhoicissus digitata* (L.f.) Gilg. & M.Brandt. On the basis of the morphological similarity with *Holocacista rivillei* (genitalia and wing venation) and an initial molecular phylogeny (data not presented here), it was clear that the new species belongs to the same clade as *H. rivillei* and not to the clade that comprises either the type species of *Antispila* Hübner, [1825] (viz. *A. metallella* ([Denis & Schiffermüller], 1775) or the clade with the type species of *Antispilina* Hering, 1941 (*A. ludwigi* Hering, 1941). Since this clade comprises several moths with similar morphology, we enlarge the genus *Holocacista* here and describe the grapevine leafminer as a new species. We therefore also redefine the genus *Holocacista* here and newly combine several species with it.

Taxonomy

Genus *Holocacista* Walsingham & Durrant

Holocacista Walsingham & Durrant, in Walsingham 1909: xxix. Type species (by original designation and monotypy): *Elachista rivillei* Stainton, 1855: 89.
Holocacista; Nielsen (1980): 105 [re-description in unpublished thesis].

Differential diagnosis. Very small moths, wingspan between 3 and 5 mm, usually with a pattern of metallic-silvery spots, but in some species not metallic, typically comprising a dorsal and costal spot at 1/4 sometimes united into a fascia and a postmedial fascia, which also may be broken into two spots. In some species part of this pattern is absent. Males never with androconial scales or hair-pencils. Separated from externally somewhat similar *Antispila* species by the reduced venation (Figs 29–34); in *Antispila* the discoidal cell is present and more veins are retained (Fig. 35); also most *Antispila* species are larger and have more antennal segments. Separated from most *Heliozela* species by more extensive colour pattern, the few *Heliozela* that do have more spots can be separated also by the venation with discoidal cell (Fig. 36), also *Heliozela* species have more antennal segments. Species of *Antispilina* and some in the "*Antispila*" *ampelopsifoliella* group have a very similar venation and are more difficult to separate; most *Holocacista* differ in the male genitalia by the usually long appendix on the phallus, moreover they have a small epiphysis, which is absent in the other genera with reduced venation.

Description. Adults. Very small moths, forewing length ca. 1.5–2.5 mm (wingspan ca. 3–5 mm).

Head (Figs 21–24). Almost oval in outline. Eyes in latero-ventral position , ventral margin not reaching lower margin of head. Eye phragma narrow, weakly melanised. No sutures present. Anterior tentorial arms very slender, prominently curved laterally before converging towards frons. Vestiture comprising lamellar scales, firmly appressed on head, in dry specimens scales on vertex sometimes raised, probably an artefact as a result of drying. Mouthparts: labrum narrow, pilifers absent. Mandibles small, as long as broad, relatively well sclerotised (Fig. 23). Maxilla with galea well developed and longer than head; maxillary palp reduced to a single segment. Labial palp well developed, 3-segmented, drooping, slightly shorter than head capsule; distal segment from slightly longer to 1.5× second segment; depression for Organ von Rath not seen. Antenna (Fig. 24) ca. half length of forewing with 14–20 segments [best counted in denuded specimens on slides], no sexual dimorphism. Scape and pedicel of equal length, slightly shorter than flagellomeres. Flagellomeres cylindrical, longer than wide, each with two annuli of scales, often differently coloured, resulting in visible dark and pale rings from above. Pecten present, but not easily visible; Nielsen (1980) counted 4–6 hairs in *H. rivillei*.

Thorax. Vestiture of appressed lamellar scales, usually concolorous with ground colour of forewings. Foreleg with small but distinct epiphysis of about 36–48 µm in *H. rivillei* (Fig. 26) to 50–82 µm in *H. capensis* (Fig. 25), distinctly smaller than in *Heliozela* (Fig. 27) (150–165 µm in two measured European specimens) and without the microtrichia along the inner side, which probably serve as antennal cleaning apparatus. In *Antispila*, *Antispilina* (Fig. 28) and *Coptodisca* epiphysis completely lacking.

Wings. Male retinaculum a series of 7–12 hook-shaped bristles, arising from a thickened serrate portion of Sc. Frenulum in male a strong curved bristle (e.g., Fig. 30), in female two bristles present (Figs 29, 34); no pseudofrenular bristles in male. Humeral field with scattered microtrichia, otherwise restricted on wing membrane to area just posterior of retinaculum, arranged in longitudinal rows. Scale sockets regularly spaced, not in distinct rows.

Venation in forewing (Figs 29–34) with Sc to middle of costa. R unbranched, a separate vein, to costa. Rs with M and CuA, ending in 3–4 branches, interpreted as Rs1+2 to costa, Rs3+4 to termen, M and CuA to dorsum; in one species, *H.* sp._*Terminalia_SA*, tentatively placed here, Rs+M+Cu even more reduced, with only 2 branches. Hindwing with Sc+R to costa, Rs+ M with 2–3 branches, Rs to costa, 1 or 2 branches of M to termen and dorsum; CuA a separate vein to dorsum.

Wing pattern (Figs 1–16). On forewing typically comprising a pair of opposite pale, often metallic spots at 1/3 and a similarly coloured fascia or opposite spots at 2/3 on a dark background, brown to black, or brassy and shining. Variation exists in relative size, whether spots are joined to a fascia, or fascia is broken, or spots may be absent (e.g., Figs 11, 14, 16). Many species show sexual dimorphy in pattern, with females having more or larger pale elements than male. Only a single species from Arabian Peninsula has a different pattern with much yellow, probably as an adaptation to the desert habitat (Fig. 13). A fringe line often available, with fringe scales pale. Hindwings uniform grey. Androconial scales absent in all species examined.

Pregenital abdomen. Abdominal sclerites weakly sclerotised. Anterior sternum II subtriangular, free.

Male genitalia. Vinculum (S IX) very long, anteriorly often reaching beyond anterior margin of segment VI, almost cylindrical; tegumen (TIX) narrow, usually with a medial posterior process, probably a composite structure with uncus. Gnathos absent. Valva rather narrow, with stalked pectinifer halfway to inner margin, pecten comprising 6–12 blunt sensilla; transtilla typically with medial anterior projection, sublateral processes long. Phallocrypt (manica) with some to many strongly-sclerotised conical spines, often arranged in an asymmetric fashion, or with many smaller spines. Phallus outer tube often with remarkable ventrally-curved appendix on phallus, or appendices of different sizes and shapes. Juxta present and often bilobed or reduced to narrow ventral process.

Female genitalia. SVIII pointed, T VIII deeply indented. Oviscapt with few lateral cusps. Anterior and posterior apophyses subequal in length. Spermathecal papilla usually with circular sclerotisation. Ductus spermathecae with many coils.

Larva. Larvae yellow or whitish, usually with darker head capsule. Larva of *H. rivillei* described in detail by Grandi (1931) and Marchi (1956). Head prognathous, legs and prolegs absent, but paired ambulatory calli on T2 and 3 (ventral and dorsal) and fused ventro-medial – calli on A3–6. Larvae with four feeding instars and a fifth non-feeding instar that constructs the case in which it pupates.

Biology. Hostplants. Several species feed on Vitaceae and Rubiaceae, a few species on Anacardiaceae, and single species each on Balsaminaceae, Dilleniaceae, Geraniaceae and Plumbaginaceae. A species feeding on Combretaceae is tentatively added, but this requires confirmation.

Life history. Eggs are inserted in leaf tissue, often near a vein or leaf margin. All species construct leafmines (Figs 70–75, 79, 83–93), usually starting as a narrow linear mine, later usually widening into a blotch, or sometimes remaining an irregularly wide gallery, and cut out an oval shield, comprising the epidermal layers, during the penultimate instar. Frass is deposited in a central line in the mine or filling the mine, later often scattered in the blotch or pushed by the larva to one side. The shields (Figs 76–78), later forming the cocoons, are more or less flat, without the raised ridge that is characteristic for *Antispila*. They attach this cocoon to any surface (trunks, leaves, leaf litter, etc.) where the non-feeding final instar larva pupates. Adults are usually day flying (Figs 80–82), and rarely come to light.

Distribution. Mainly Old World tropics and subtropics: Afrotropical, Oriental and Australian regions, north to Taiwan and southern Europe (type species). Some DNA barcodes suggest that the genus also occurs in South and Central America, but no adults have yet been studied from this area.

Composition. The species listed in the checklist below, both named ones and unnamed ones, share the external and venation characters described above, and those dissected also the male genitalia characters. Those species that we have been able to sequence form a well-supported clade in a phylogenetic analysis (both Bayesian and Maximum Likelihood) of the Heliozelidae based on four genes (unpublished study in progress), as part of a larger clade of genera with reduced venation (including also *Antispilina* Hering, 1941, *Coptodisca* Walsingham, 1895 and the "*Antispila*" *ampelopsifoliella* group). While checking several Indian species described by Meyrick, we could also change the following generic assignment: *Heliozela anna* (Fletcher, 1920), comb. n. (from *Antispila*, feeding on Myrtaceae) (Figs 20, 36), whereas the following remain in their original genus: *Antispila argostoma* Meyrick, 1916 (Figs 18, 35) and *A. aristarcha* Meyrick, 1916 (Fig. 19), both feeding on Vitaceae. While we assign an unnamed species feeding on *Impatiens* from Vietnam to *Holocacista* here (Figs 16, 34), the Indonesian *Microplitica metadesmia* (Meyrick, 1934) that likewise feeds on *Impatiens*, has a completely different venation, more similar to *Heliozela* Herrich-Schäffer, 1853.

Pending further study of this species and the type species of *Microplitica* Meyrick, 1935 (*Microplitis desmophanes* Meyrick, 1922), we leave it in *Microplitica* for now.

In the checklist below we provide the original genus in brackets, type locality, and the hostplant of the types. The species are listed geographically, first the named ones, then the unnamed ones.

Checklist

Palearctic species
H. rivillei (Stainton, 1855): p. 89 (*Elachista*)
    Malta, *Vitis vinifera* L. [type species]

African species
H. capensis van Nieukerken & Geertsema, sp. n.
    South Africa, Western Cape, Paarl, *Vitis vinifera* L.
H. salutans (Meyrick, 1921): p. 108, comb. n. (*Antispila*)
    South Africa, [Kwazulu Natal], Durban, [*Rhoicissus* sp.]
H. varii (Mey, 2011): p. 156, comb. n. (*Antispilina*)
    South Africa, Western Cape, Cape Town, *Pelargonium cucullatum* (L.) L'Hérit.

Asian species
H. micrarcha (Meyrick, 1926): p. 261, comb. n. (*Antispila*)
    India, [Karnataka], Karwar, *Lannea coromandelica* (Houtt.) Merr. (=*Odina wodier* Roxb., Anacardiaceae)
H. pariodelta (Meyrick, 1929): p. 541, comb. n. (*Antispila*)
    India, Bihar, Pusa, *Lannea coromandelica* (Houtt.) Merr. (=*Odina wodier* Roxb., Anacardiaceae)
H. selastis (Meyrick, 1926): p. 261, comb. n. (*Antispila*)
    India, [Karnataka], Karwar, *Psychotria dalzellii* Hook.f. (Rubiaceae)

Unnamed species:

Palearctic species
sp. *Dyerophytum*_UAE
    United Arab Emirates, Fujairah, *Dyerophytum indicum* (Gibbs ex Wight) Kuntze (Plumbaginaceae)

African species [see also Appendix A]
sp. *Rhoicissus_tridentata*
    South Africa, *Rhoicissus tridentata* (L.f.) Wild & R.B.Drumm. subsp. *cuneifolia* (Eckl. & Zeyh.) Urton, *R. tomentosa* (Lam.) Wild & R.B.Drumm. (Vitaceae)
sp. *Rhoicissus_tomentosa*
    South Africa, *Rhoicissus tomentosa* (Lam.) Wild & R.B.Drumm. (Vitaceae)

sp. *Rhoicissus*_PundaMilia
  South Africa, *Rhoicissus digitata* (L.f.) Gilg. & M.Brandt (Vitaceae)
sp. *Cissus_integrifolia*
  South Africa, *Cissus integrifolia* (Baker) Planch. (Vitaceae)
sp. *Lannea*_SA
  South Africa, *Lannea discolor* (Sond.) Engl. (Anacardiaceae)
sp. *Terminalia*_SA [placement tentative]
  South Africa, *Terminalia prunioides* M.A. Lawson (Combretaceae)

Asian species
sp. *Leea*_Borneo
  Indonesia, Kalimantan Timur, *Leea indica* (Burm.f.) Merr. (Vitaceae)
sp. *Impatiens*_Vietnam
  Vietnam, Cuc Phuong NP, *Impatiens clavigera* Hook. f. (Balsaminaceae)
sp. *Lasianthus*_Borneo
  Indonesia, Kalimantan Timur, *Lasianthus* Jack sp. (Rubiaceae)
sp. *Lasianthus*_Sabah
  Malaysia, Sabah, *Lasianthus* Jack sp. (Rubiaceae)
sp. *Paedaeria*_Taiwan
  Taiwan, *Paederia foetida* L. (Rubiaceae)

Australian species
sp. *Psychotria*_Australia
  Australia, Queensland, *Psychotria simmondsiana* F.M.Bailey (Rubiaceae)
sp. *Morinda*_Australia
  Australia, Queensland, *Morinda jasminoides* A.Cunn. (Rubiaceae)
sp. *Hibbertia*_Australia
  Australia, West Australia, *Hibbertia* Andrews (Dilleniaceae)

***Holocacista rivillei* (Stainton)**

Figs 9, 21, 23, 24, 26, 29, 87, 88, 105

Elachista rivillei Stainton, 1855: 89.
Holocacista rivillei; van Nieukerken et al. (2012b): 62 [redescription]; Cean (2014): 385 [record Rumania, description]

Note. The type species of *Holocacista* has recently been diagnosed in the context of a study of European (and North American) Vitaceae miners (van Nieukerken et al. 2012b), when the genus was still considered monotypic. Here we briefly diagnose it against other species in the genus, without a full redescription. It should be noted that only material from Italy and Bulgaria has been examined in detail. Morphological details (Figs 21, 23, 24, 26) and venation (Fig. 29) are described under the generic treatment. For a full synonymy we refer to van Nieukerken et al. (2012b).

Differential diagnosis (Fig. 9)**.** Wingspan 4.0–4.5 mm. Antenna ringed, 15 segments; head and thorax bronze grey. Forewing fuscous to black, with golden silvery pattern consisting of four spots, costals distal to dorsals, the first costal and dorsal sometimes united as oblique fascia; a distinct fringe line, fringe silvery white. Differs from South African *H. capensis* and *H. salutans* by more golden shining spots and distinct first costal spot (almost absent or reduced in other species); from *H. varii* and other species by distinct fringe line and ringed antenna.

Male genitalia (Fig. 105, and Figs 48–50 in van Nieukerken et al 2012b). Total length vinculum + tegumen 630–720 µm, phallus 575–630 µm. Pecten with 8–10 teeth. Juxta more elaborate than in South African Vitaceae miners, deeply bifurcate. Phallus without spines on phallocrypt, wrinkled. Female genitalia illustrated by van Nieukerken et al (2012b, Figs 51–52) and Cean (2014).

Biology. Host plants. Vitaceae: *Vitis vinifera*, wild and cultivated, possibly also on cultivated *Parthenocissus* Planch. (new record from Russia, Kalmykiya).

Leafmines (Figs 87, 88). The egg is inserted usually close to a major vein, probably on leaf underside. The mine is first a gallery, turning from once to several times around the oviposition site and then extends, often along a vein as a rather straight linear mine, occasionally as a serpentine mine; distally enlarging into a small blotch. The frass is black forming a broken line, often not exactly in the middle of the mine; in thicker leaves it may be wider; in the blotch the frass is dispersed; the larva cuts out a case of about 3.3–4 mm × 2.0–2.5 mm.

Distribution. Widespread in southern Europe, Turkey and Central Asia (van Nieukerken et al. 2012b), now also recorded in Romania (Cean 2014). Probably only native in eastern part of its current distribution area.

Material examined. Adults and leafmines: **Bulgaria**: 1♂, 7 adults [sex not determined], Sliven, 5.iv.1928, P. Tschorbadjiev, Genitalia slide JCK7867 (coll. Natural History Museum Sofia). **Italy**: 28 adults (4♂, 1♀ dissected), Vicenza, Borghetto, experimental vineyard, leafmines on *Vitis vinifera*, 2007, emerged i–ii.2009, M. Baldessari (RMNH); 1♂ (dissected), 7♀, many leafmines, larvae, ibidem, 19.viii.2013, EvN2013904, emerged 11.ix–3.x.2013, M. Baldessari (RMNH). **Russia**: leafmines only, Kalmykiya, Elista, Citypark, 26.ix.2000, leafmines on *Parthenocissus*, V. Zolotuhin (coll. Zolotuhin).

***Holocacista capensis* sp. n.**

http://zoobank.org/1455B935-A7E5-4247-8BAB-47825BAF3048

Figs 1–3, 22, 25, 30, 37–53, 70–82, 94–96, 107–110, 115, 116

Antispila sp. Kroon (1999): 83, 120 [on *Vitis* sp.].

Type material. Holotype male, South Africa (Western Cape), Paarl NW, De Heuvel estate, 180 m, 16.i.2013, leafmines on *Vitis vinifera* cv ‘Regal’, EvN2013004, emerged

27.i.2013, E.J. van Nieukerken & H. Geertsema, Genitalia slide EvN4622, DNA extracted (RMNH.INS.24622) (RMNH).

Differential diagnosis. Externally *Holocacista capensis* is almost inseparable from other South African Vitaceae-feeding *Holocacista* species, including *H. salutans*. Absence or reduction of the first costal spot in the male, however, may be an indication that the specimen might be *H. capensis*; only study of genitalia allows a firm identification. For differences with *H. varii*, see there. The only South African Vitaceae-feeding "real" *Antispila* species is much larger and has more antennal segments (ca. 26). In male genitalia the configuration of the small number of spines on phallocrypt in combination with the ventrally curved phallus appendix is characteristic, otherwise very similar to *H. salutans* and some of the unnamed *Rhoicissus* miners. Leafmines characterised by the very contorted first part of the mine, which is straighter or shorter in the other species; currently the only known leafminer on *Vitis* in South Africa.

Description. *Male* (Figs 1, 3). Head face and vertex covered with appressed, metallic, silvery-white scales, more brownish grey on vertex. Palpi porrect, white; base of proboscis covered with white scales. Antenna with 16 segments, ringed, each flagellomere with a basal fuscous scale ring and apical white scale ring on upper side, scales on underside all white. Legs grey, tarsi mostly yellowish white, especially on underside. Thorax and forewings ground colour grey brown, slightly irrorate, caused by scales being dark tipped and paler at base. A silver-white pattern on forewing consists of a triangular dorsal spot at 1/4, usually associated with a minor spot of just a few scales at costa, that may be joined to dorsal spot, or even completely absent; a second triangular dorsal spot at 1/2, reaching almost to middle of wing; a triangular costal spot just beyond middle, always separate; fringe line very distinct, demarcated by dark-tipped scales. Terminal fringe silvery white. Hindwings pale grey. Underside of wings fuscous, with white spots visible. Abdomen lead coloured, including vestiture on external genitalia.

Female (Fig. 2). Antenna with 16 segments. Colour pattern distinct from male: scales almost uniformly dark fuscous with purplish tinge, resulting in darker, velvety wing colour and contrasting silvery-white pattern; first costal and dorsal spots joined to form a narrow fascia, wider at dorsum; second dorsal and costal spots as in male; fringe line distinct, scales forming cilia line with slightly paler bases. Abdomen almost black, narrowly pointed posteriorly.

Measurements. Male: forewing length 1.8–2.3 mm (2.0 ± 0.1, 20) (1 dwarf of 1.55 mm forewing length excluded), wingspan: 3.9–4.9 mm. Female: forewing length 1.9–2.1 mm (2.0 ± 0.1, 14), wingspan 4.0–4.6 mm.

Male genitalia (Figs 37–49, 94–96, 107–110, 115). Total length vinculum + tegumen 425–625 µm. Vinculum (S IX) long, reaching anterior margin of segment VI. Tegumen (Figs 41, 46, 110) well sclerotised, with medial, slightly-bilobed posterior projection, one sensilla on each lobe; tegumen dorsally with groups of microtrichia, and two lateral lobes with setae or sensilla; a poorly-sclerotised structure below tegumen may be a reduced uncus. Valva (Figs 40, 43, 108) narrow, apex blunt, with stalked pectinifer halfway to inner margin, pecten comprising 8–11 blunt sensilla, usually same number on both valvae, but sometimes a difference of one. Valva length (without transtilla) 200–230 µm. Transtilla (Figs 41, 109) with long sublateral processes and medial spatulate posterior process, with rounded corners. Juxta elongate, as a narrow ventral process of phallus, attached on phallus near phallocrypt spines (Fig. 48). Phallus (Figs 39, 42, 44, 45, 48, 49, 94–96, 107) long and narrow, ca. 340–425 µm long. Phallocrypt (manica) with some strongly-sclerotised conical spines, arranged asymmetrically; in lateral view (Figs 44, 94–96) one dorsally, curved ventrad, a similar strong one ventrally curved dorsad, latter with 3–4 smaller spines in a row anteriorly; in ventrally mounted specimens spines appear mostly on right side, where phallus is constricted. Phallus outer tube with ventrally-curved appendix ca.103–150 µm long (measured along curve).

Female genitalia (Figs 50–53). Length of anterior apophyses 800–900 µm (n=5), posterior apophyses 880–935 µm (n=5). Oviscapt with 5–6 cusps on either side (Figs 51, 52). Ductus spermathecae with many wide convolutions, spermathecal papilla with circle-shaped sclerotisation (Fig. 50).

Biology. Host plants. Vitaceae: *Rhoicissus digitata* (L.f.) Gilg. & M. Brandt and various South African grown cultivars of *Vitis vinifera* (e.g., Chardonnay, Chenin Blanc, Red Globe, Régal).

Leafmines (Figs 70–75, 79). The egg is inserted on the leaf underside, usually within 1–2 mm from a vein, rarely slightly farther. Freshly expanded foliage is preferentially selected for oviposition, but as egg laying proceeds from early spring to late autumn, it also oviposits on older leaves, even those showing previous feeding. The majority of the mines on *Vitis* (75% of 160 mines from six samples) start at the leaf edge, but even there the egg is always near the vein in the tip of a lobe; some mines originate close to the leaf midrib. Also, the few studied mines on *Rhoicissus* start at the leaf(let) tip. The mine starts as a much contorted narrow gallery, often first in a zigzag pattern with U-turns, eventually enlarging into an irregular wide gallery or a blotch. The frass is brown in the early mine, later black, in a rather thin line in the centre of the gallery; later the frass is in clumps in a wider central line. The whole mine occupies a small area of ca. 12–15 mm long, of which the size depends on leaf thickness; in thin leaves mines are appreciably longer and wider. Mines are very often clustered in groups of 3–5 or even more. The larva cuts out an elliptic case of about 2.5–4.1 mm (3.4 ± 0.3, n=34) × 1.5–3.1 mm (2.3 ± 0.3, n=34) mm wide, ratio 1.2–1.8 (1.5 ± 0.1).

Voltinism and habits. The moth is multivoltine; the first adults appear during early spring (September to October) and a single generation lasts from three to four weeks; peak numbers are reached during February and March at the height of the grape picking season. Moths are still present in April; the last were seen early May; many cocoons overwinter in leaf litter, dropping to the ground and pupating amongst leaf litter or attached to stems and trellises from April onwards, and yielding moths from September onwards. Larvae are present almost continuously from November to early May when the leaves start to wither and drop. Larvae have only once been collected on *Rhoicissus*, these in March. When fully grown, larvae descend from the mines to attach their cocoons upon landing on a variety of objects such as other leaves, berries of grape bunches, trellises or on the bark of the vine itself (Fig. 76).

Moths aggregate and mate in the heat of the day (1100–1400 hrs) on exposed vine foliage, but prefer to oviposit in the shaded canopy conditions under which table grapes are grown; wine grapes, grown in an open cultivation system and fully exposed to the sun are rarely, or at least less seriously attacked.

Distribution (Fig. 115)**.** On native *Rhoicissus* as yet only found once: South Africa, Western Cape (Wilderness). On cultivated *Vitis* from South Africa: Western Cape, Northern Cape and Gauteng.

DNA barcode. We barcoded eight specimens, including the Holotype. All barcodes belong to Barcode Identification Number (BIN):ACG9027, the largest intraspecific distance is 1.4%, between one specimen collected in Gauteng and the rest, collected in the Western Cape.

DNA-Barcode of Holotype, HELA103-14 (658 basepairs):

AACTTTATATTTTATTTTTTGGTATTTGAGCGGGATTAGTAGGAACATCAATAAGTTTATTAATTCGTGCTGAATTAGGAATCCCTGGGTCCTTAATTTCTAATGATCAAATTTATAATACTATTGTTACAGCTCATGCATTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTTCCGTTAATATTAGGAGCCCCAGATATAGCATTTCCTCGTCTTAATAATATAAGTTTTTGACTCCTTCCCCCATCTTTAACATTATTAATTTCAAGAAGATTAGTTGAAATGGGATCAGGAACTGGATGAACTGTCTATCCACCTTTATCTTCCAATATTGCCCATATGGGAACTTCTGTGGATTTAACTATTTTTTCTTTACATTTGGCTGGAATTTCATCTATTTTAGGAGCTGTAAATTTTATTACAACAATTATTAATATAAAACCAGTTAGAATAATATATAATCAACTTTCTTTATTTGTTTGATCTGTGGGTATTACAGCTTTATTACTATTATTATCTTTACCTGTATTAGCTGGAGCTATTACTATATTATTAACTGATCGAAATTTAAATACTTCTTTTTTTGACCCTATGGGAGGAGGAGACCCTATTCTATATCAACATTTATTT

Remarks. The only wild *Rhoicissus* on which mines of *H. capensis* were collected, was identified by Vári in his notebook as *R. revoilii*. The single leaf we studied could belong to this species or to *R. digitata*, which is very similar. On the basis of the distribution (Palgrave and Palgrave 2002), we conclude that the latter is the most likely, since *R. revoilii* is not known to occur in the Western Cape.

Several reared adults were used in 2013 for a rearing experiment on potted plants of *Rhoicissus rhomboidea* (E.Mey. ex Harv.) Planch., bought in the Netherlands. Although the adults lived for several days, no traces of mines were found. Either the species is unsuitable as a hostplant, or these potted plants contained remnants of insecticides. Later, we were more successful with rearing larval offspring from *Vitis*-grown adults from Wellington on potted *Rhoicissus digitata* in the laboratory in Stellenbosch (for resulting leafmines see Fig. 79). The main aim of this preliminary study was to detect whether moths reared on *V. vinifera* would readily breed on (caged) *R. digitata*; moths emerging from grapevine leaf litter or sampled foliage were released into the caged *Rhoicissus*. The latter was readily infested, often resulting in the entire leaf being consumed by the larvae.

Other live cocoons were sent in 2013 to Lund, Sweden, emerged there, and have been used for pheromone studies (Wang et al. 2015).

Material examined. Adults and leafmines: **South Africa, Gauteng**: 3♂, Pretoria, Roodeplaat, 1245 m, leafmines *Vitis vinifera*, emerged 10–12.x.1990, S. Marais, Genitalia slide EvN4264, DNA extracted (RMNH.INS.24264) (HG, RMNH); 3♂, 5♀, same locality, emerged 4–14.iv.2012, D. Visser (HG, RMNH); 2♀ [5 more specimens in TMSA], Pretoria, emerged 2–6.xi.1950, L. Vári, Genitalia slide TM6830, Wing slide TM 2414 (TMSA); 1♀ [1 more specimen in TMSA], 1 herbarium sheet with 6 leafmines on 4 leaves, Pretoria, 8.iii.1953, Ac. no. 660, leafmines on *V. vinifera*, emerged 10–31. iii.1953, L. Vári (TMSA); 1♂, 1♀, 1 herbarium sheet with ca. 13 leafmines in 4 leaves, Pretoria, in own garden, 21.x.1953, Ac. no. 866, leafmines on *V. vinifera*, emerged 26.x–3.xi.1953, L. Vári (TMSA); 1♂, larvae and leafmines, Roodeplaat exp. Farm, 1168 m, 23.i.2013, leafmines *V. vinifera*, EvN2013025–026, E.J. van Nieukerken & S. Richter, 1 larva DNA extracted (RMNH.INS.29586) . **Northern Cape**: 9♂, 14♀ [unmounted], Vaalhartz Research Stn., Jan Kempdorp near Kimberly, 27.ii.1980 [emergence date?], W. v.d. Westhuyzen (TMSA). **Western Cape**: 2♂, 3♀, Cape Town, Woodstock, cocoons collected on *V. vinifera*, 26.ii.2012, emerged 5–13.iii.2012, M. Wohlfarter; 1♂, Oudtshoorn, March 1998, on urban vine, H. Geertsema (HG); 81♂, 58♀, Paarl, nr Windmeul, 168 m, leafmines/cocoons on *V. vinifera*, emerged 1.ii–30.iii.2012, H. Geertsema, Genitalia slides EvN4260♂, 4261♀, 4262♂, 4263♀; complete adults on slide EvN4445♂, 4446♂, 4447♂, DNA extracted (RMNH.INS.24260, 24261, 24262, 24263, 24445, 24446, 24447) (HG, RMNH); 3♂, 2♀, Paarl NW, Nelson estate, 125 m, 15.i.2013, leafmines on *Vitis vinifera* cv 'Chenin Blanc', EvN2013002, emerged 18.i–1.ii.2013, E.J. van Nieukerken & H. Geertsema; 6♂, 10♀, 4 larvae, ibidem, 130 m, leafmines on *V. vinifera* cv ''Chardonnay', EvN2013003, emerged 24.i–5.ii.2013, Genitalia slide EvN4624♀, DNA extracted (RMNH.INS.24624), larvae RMNH.INS.2956265; 6♂, 11♀, 6 larvae, Paarl NW, De Heuvel estate, 180 m, 16.i.2013, leafmines on *V. vinifera* cv 'Regal', EvN2013004, emerged 20–27.i.2013, E.J. van Nieukerken & H. Geertsema, larvae RMNH.INS.29578–83; 2♂, 3♀, ibidem, leafmines on *V. vinifera* cv 'Red globe', EvN2013005, emerged 26.i–4.ii.2013; 1♂, 3♀, ibidem, 25.i.2013, leafmines on *V. vinifera* cv 'Red globe', EvN2013030, emerged 1–6.ii.2013, E.J. van Nieukerken & H. Geertsema (RMNH, HG); 5 adults, Somerset, 23.ii.2012, cocoons collected on *V. vinifera*, emerged 27.ii–5.iii.2012, O. Lotter; 1♀, Wellington, emerged 25.xii.2014, leafmines on *V. vinifera*, L. Torrance (HG). 3♂, 1♀ [8 more specimens in TMSA], 1 leaf with 6 mines, Wilderness, Kaaimans River, 15.iii.1954, Ac. no. 1093, leafmines on *Rhoicissus digitata* [in notebook Vári as *R. revoilii*], emerged 4–5.iv.1954, L. Vári, Genitalia slide EvN4381♂, DNA extracted (RMNH.INS.24381) (TMSA).

Additional data [leafmines and larvae collected, no adults kept in collection]. **South Africa, Western Cape**: 11♂, 21♀ [reared from 50 cocoons in Lund, Sweden and used for pheromone studies], Paarl NW, De Heuvel estate, 180 m, 25.i.2013, leafmines on *Vitis vinifera* cv 'Regal', EvN2013029, emerged 2–15.ii.2013, E.J. van Nieukerken & H. Geertsema; several adults, Wellington, emerged xii.2014, ex *V. vinifera* laboratory bred on R. *digitata*, L. Torrance (HG).

Holocacista salutans **(Meyrick), comb. n.**

Figs 4, 54–58, 65, 66, 85, 86, 97–100, 111, 113, 115

Antispila salutans Meyrick, 1921: 108. 5 Syntypes ♂♀: South Africa, [KwaZulu Natal], Durban, x.[19]18/19, v.d. Merwe (TMSA, BMNH) [partly examined].

Antispila salutans; Vári and Kroon (1986): 154; Vári et al. (2002): 10; De Prins and De Prins (2014): database.

Differential diagnosis. Externally *H. salutans* hardly differs from *H. capensis*, but the male usually has a costal spot at 1/3 from base, albeit very small. The only consistent characters to separate it from *H. capensis* are in the male genitalia: the row of larger spines dorsally on the phallocrypt, whereas *H. capensis* has a row ventrally and just a single spine ventrally; also the shape of the transtilla *H. salutans* differs from that in *capensis*. The leafmines of *H. salutans* have the gallery mine with wider frass, more clumped and not zigzag as in *H. capensis*.

Description. *Male* (Fig. 4). Head: face and vertex covered with appressed, metallic, silvery-white scales, more brownish grey on vertex. Palpi porrect, white; base of proboscis covered with white scales. Antenna with 16 segments, ringed, each flagellomere with a basal fuscous scale ring and apical white scale ring on upper side, scales on underside all white. Legs grey, tarsi mostly yellowish white, especially on underside. Thorax and forewings ground colour grey brown, slightly irrorate, caused by scales being dark tipped and paler at base. A silver-white pattern on forewing consists of a triangular dorsal spot at 1/4 from base, a smaller spot at costa, sometimes joined to dorsal spot as a narrow fascia; a second triangular dorsal spot at 1/2, reaching almost to middle of wing; a triangular costal spot just beyond middle, always separate; fringe line very distinct, demarcated by dark-tipped scales. Terminal fringe silvery white. Hindwings pale grey. Underside of wings fuscous, with white spots visible. Abdomen lead grey, including vestiture on external genitalia.

Female. Antenna with 16 segments. Colour pattern distinct from male: scales almost uniformly dark fuscous with purplish tinge, resulting in darker, velvety wing colour and contrasting silvery-white pattern; first costal and dorsal spots always joined to form a narrow fascia, wider at dorsum; second dorsal and costal spots as in male; fringe line distinct, scales forming cilia line with slightly paler bases. Abdomen almost black, narrowly pointed posteriorly.

Measurements. Male: forewing length 1.7–2.3 mm (2.0 ± 0.2, 6), wingspan: 4.0–5.0 mm. Female: forewing length ca. 2.0 mm (n=3), wingspan ca. 4.5 mm.

Male genitalia (Figs 54–58, 97–100, 111, 113). Total length vinculum + tegumen ca. 460–490 µm (n=3). Vinculum (S IX) long, reaching anterior margin of segment VI. Tegumen and uncus well sclerotised, with two medial projections, probably representing tegumen and uncus, dorsalmost projection very similar to tegumen of *H. capensis*, ventral one truncate, slightly excavated posteriorly, with serrate margins. Valva narrow, apex blunt, with stalked pectinifer halfway along inner margin, pecten comprising 8–10 blunt sensilla. Valva length (without transtilla) ca. 165–215 µm.

Transtilla with long sublateral processes and medial spatulate posterior process, with produced lateral corners (Fig. 111). Juxta (Fig. 56) elongate, as a narrow ventral process of phallus, attached to phallus near phallocrypt spines. Phallus (Figs 56, 97–100) long and narrow, ca. 390–430 µm long. Phallocrypt (manica) with two rows of strongly-sclerotised conical spines, arranged symmetrically; in lateral view seen dorsally, all curved ventrad, more than 6–7 spines in a row; a group of small spines posterior to these. Phallus outer tube not constricted, with ventrally-curved appendix of ca. 105–125 µm long (measured along curve).

Female genitalia (Figs 65, 66). Length of anterior apophyses 850 µm (n=1), posterior apophyses 890 µm (n=1). Oviscapt not yet studied in ventral view. Ductus spermathecae with many wide convolutions, spermathecal papilla with circle-shaped sclerotisation (Fig. 66).

Biology. Host plants. Vitaceae: *Rhoicissus digitata* (L.f.) Gilg. & M. Brandt, *R. revoilii* Planch., *R. tomentosa* (Lam.) Wild. & R.B. Drumm. and *Cissus cornifolia* (Baker) Planch. Records from *R. tridentata* (L.f.) Wild. & R.B. Drumm. subsp. *cuneifolia* (Eckl. & Zeyh.) Urton require confirmation (see below).

Leafmines (Figs 85, 86)**.** The egg is inserted on the leaf underside, usually close to a vein; some mines start at the leaf edge. The mine starts as a much contorted narrow gallery with all convolutions close to each other, hardly leaving leaf tissue between them. Later, the mine enlarging into an irregular wide gallery or a blotch. The frass is black throughout, clumped and almost filling the gallery, but with space between the clumps. Mines are very often clustered in groups. The larva cuts out an elliptic case of about 3 mm long and 2 mm wide.

Voltinism. Larvae have been found from March to June, in September and again from December to January; adults usually emerge between 3–8 weeks after collecting of leafmines; probably multiple overlapping generations.

Distribution (Fig. 115)**.** South Africa: KwaZulu-Natal, Limpopo and Zimbabwe: Masvingo. Records from Gauteng (Pretoria) need confirmation, several leafmines from *Rhoicissus tridentata* resemble those of *H. salutans* on other hosts, but we have yet no proof from adults that they are this species.

Remarks. Meyrick (1921) described *Antispila salutans* from five specimens from "Natal, Durban, in October (Janse)." They were part of a much larger series, of which the labels in the Ditsong Museum (former Transvaal Museum) give more information: all from Durban, collected by v.d. Merwe, Coll. Janse. Some are dated 10.10.18 [in hand], others x.19 or xi.19 [in print], those dated x.19 also have a label with the text "Ac. n. 453" [Accession number 453]. Many specimens have a cocoon added, showing that they have been reared. The five specimens in London are merely labelled (in Meyrick's hand) "Durban, Natal, AJTJ, 10 [or 11].19". Meyrick usually replaced original labels of specimens that he kept for his own collection with shorter ones in his own hand or print (Clarke 1955). Meyrick (1921) wrote in the introduction of his paper: "The types of those new species received from Mr A. J. T. Janse are contained in his collection, …." Three specimens of *Antispila salutans* are placed in the type collection in Pretoria under the type numbers 109–111. In addition to the locality label, they have a type label in red ink, with name and type number, and an additional label, printed in black, with a 4-digit number, split in two rows. Such labels are always attached to Janse specimens studied by Meyrick, but no registry book is available in Pretoria with more information (Martin Krüger, personal communication). So if we regard these as real syntypes, even though one of these was labelled with 'xi', thus from November, only two of the specimens in London can be regarded as the remaining syntypes, and all other specimens are just topotypical, but not types (see also Razowski and Krüger 2007). For the time being we cannot make a decision as to which specimens in London are actual syntypes, and suggest that the male specimen in the type collection in Pretoria with "Type No. 109" is probably the best candidate to be selected as Lectotype, preferably during a full revision. For now a Lectotype selection does not seem necessary.

Unfortunately, we have not been able to find information on the rearing and hostplant of van der Merwe's series. The Accession number 453 on some labels had previously been misinterpreted as a number of Vári, who labelled all his reared material with such numbers [probably following up on Janse's system, but with new numbers]. The leaf with mines that was pinned in the *salutans* box belongs to *Bridelia cathartica* Bert. (Euphorbiaceae), has probable Coleoptera mines, and has Vári's number 453. Obviously, this has nothing to do with the heliozelid. There are no notebooks of Janse left that could shed light on this number (Martin Krüger, personal communication).

Unfortunately, we did not find recent material of this species and are therefore as yet unable to give the DNA barcode.

Material examined. Syntypes. **South Africa, KwaZulu-Natal**: 1♂, "DURBAN / 10.10 / v.d. Merwe 18/ Coll. Janse" [black print, date in hand, black cadre]; "24 / 93" [black print] ; "Antispila /salutans /Type No. 109"[hand, red ink, "Type No" in print] . 1♂, "DURBAN / 10.10 / v.d. Merwe 18/ Coll. Janse" [black print, date in hand, black cadre]; "24 / 93" [black print];"Antispila /salutans /Cotype No. 111" [hand, red ink, "Cotype No" in print]. 1 adult, "DURBAN / v.d. Merwe xi.19/ Coll. Janse" [black print, black cadre]; "29/ 28" [black print]; "Antispila /salutans /Cotype No. 110" [hand, red ink, "Cotype No" in print]. 4 specimens including 2 possible Syntypes in London, not examined.

Non-type material. Adults and leafmines: **South Africa, Kwazulu-Natal**, 2♂, 1♀, Durban, emerged x and xi.1919, van der Merwe [ex coll. Janse], genitalia slide TM4023 (♂), wing slide TM1585 (♀); 5♂, 3♀, 1 leaf with 8 mines, Jozini Dam [Pongolapoortdam] , Lebombo Mts., 14.i.1965, Ac. no 2788, leafmines on *Rhoicissus tomentosa*, emerged 27.i–5.ii1965, L. Vári, genitalia slides EvN4384 (♂),EvN4668 (♀); 1♂, 2♀, Umhlanga Rocks, 9–16.vi.1968, Ac. no 2944, leafmines on *Rhoicissus revoilii*, emerged 2–5.viii.1968, L. Vári; 1♂, 1♀, Umhlanga Rocks, 25.iii.1975, Ac. no 3342, leafmines on *Rhoicissus revoilii*, emerged 10–11.iv.1975, L. Vári, genitalia slide EvN4383 (♂); **Limpopo**: 1♂, 1♀, 1 leaf with 3 mines, Cyprus Farm, nr. Ofcolaco, 20.ix.1960, Ac. no 2247, leafmines on *Rhoicissus tomentosa*, emerged 11–13.x.1960, L. Vári; 6 leafmines on 6 leaves, Debengeni, De Hoek, Waterfalls, 15.vi.1954, Ac. no. 1329, leafmines on *Rhoicissus revoilii*, L. Vári; 1♂, 5 mines on 2 leaves, Louis Trichardt, 17.iii.1964, Ac. no 2693, leafmines on *Rhoicissus tomentosa*, emerged 31.iii–5.iv.1964, L. Vári. **Zimbabwe, Masvingo**: 2♂, 11 mines on 11 leaves, Lundi, 22.iv.1956, Ac. no 1916, leafmines on *Cissus cornifolia*, emerged 1–30.vi.1956, L. Vári; genitalia slide EvN4386 (♂) (all TMSA).

Holocacista varii **(Mey, 2011), comb. n.**

Figs 5, 6, 59–64, 67–69, 89, 90, 104, 112, 114, 116

Antispilina varii Mey, 2011: 156. Holotype ♂ RSA, Cape Town, 26.3.1954, bred from *Pelargonium cucullatum* from slopes of the Table Mtn., Vári Ac. No. 1047, leg. 4.3.1954, L. Vári, genitalia slide Mey (TMSA) [not examined].

Differential diagnosis. *Holocacista varii* is the only species similar to *H. capensis* that occurs probably commonly in the natural habitats near the grape growing areas of Western Cape and thus could potentially be confused with it. It is distinctly larger, and the forewings are more shining bronze than those of *H. capensis*. Moreover, the male and female have a complete fascia at 1/3 from forewing base that is not narrower at the costa and the antennae are not ringed. In male genitalia, *H. varii* lacks the larger spines on the phallocrypt, and has a more developed juxta; further, the dorsal row of spines on the tegumen is characteristic and the shape of the transtilla differs. The female genitalia have more elaborate sclerotisations, and the apophyses are longer.

Redescription. *Male* (Fig. 5). Head face and vertex covered with appressed, metallic, pale-bronze scales. Palpi porrect, white; base of proboscis covered with white scales. Antenna with ca. 20 segments, uniform bronze brown, scales on underside all white. Legs grey, tarsi mostly yellowish white, especially on underside. Thorax and forewings grey brown with some bronze lustre, with silver-white patterning; an oblique fascia at 1/4, hardly narrower at costa; a slightly triangular dorsal spot at 1/2, not reaching middle of wing; a triangular or squarish costal spot just beyond middle; fringe line not very distinct, demarcating scales not conspicuously dark tipped. Terminal fringe silvery white. Hindwings pale grey. Underside of wings fuscous. Abdomen lead grey, including vestiture on external genitalia.

Female (Fig. 6). Antenna with ca. 19 segments. Colour pattern different from male: scales more uniformly bronze brown, with strong lustre, and contrasting silvery-white pattern.

Measurements. Male: forewing length 2.4–2.8 mm (2.5 ± 0.1, 6), wingspan: 5.0–5.7 mm. Female: forewing length 2.1–2.6 mm (n=3), wingspan 4.5–5.6 mm.

Male genitalia (Figs 59–64, 104, 112, 114). Total length vinculum + tegumen ca. 670 µm. Vinculum (S IX) long, reaching anterior margin of segment VI. Tegumen (Figs 60, 61, 114) well sclerotised, with medial, blunt posterior projection, with several setae; tegumen dorsally with a transverse keel with many strong spines in posterior direction. Valva (Fig. 63) narrow, basally wider, apex blunt, with stalked pectinifer halfway along inner margin, pecten comprising 7 or 8 blunt sensilla. Valva length (without transtilla) ca. 265 µm. Transtilla (Figs 64, 112) with relatively long sublateral processes and medial spatulate posterior process, indented posteriorly. Juxta (Fig. 62) well developed, split into an elongate process ventral to phallus and a furcate process dorsal to phallus. Phallus (Figs 62, 104) long and narrow, ca. 540 µm long. Phallocrypt (manica) slightly spinulose posteriorly, no strong spines present. Phallus in lateral view a distinctly-curved outer tube with ventrally-curved appendix, the latter almost straight, ca. 120 µm long (measured as curve).

Female genitalia (Figs 67–69). Length of anterior apophyses ca. 935 µm (n=1), posterior apophyses 1020 µm (n=1). Oviscapt with 4 or 5 cusps at either side (Fig. 69). Ductus spermathecae with many wide convolutions, spermathecal papilla with circle-shaped sclerotisation, other elaborate sclerotisations in vestibulum.

Biology. Host plants. Geraniaceae; most commonly found on *Pelargonium cucullatum* (L.) L'Hérit., a common plant in Fynbos of Cape Peninsula and the western part of the Western Cape; single records on *P. panduriforme* Eckl. & Zeyh., *P. hispidum* Willd. and *P. citronellum* J.J.A. Van der Walt.

Leafmines (Figs 89–90)**.** The egg is inserted at any place of the leaf underside, usually not far from a vein. The mine starts towards a vein and then follows the vein as a narrow gallery of ca. 2 cm, eventually rather suddenly enlarging into a more or less triangular or elongate blotch, usually after the mine makes a turn of 180°. In thin leaves the blotch can be very elongated. The frass in the early mine is a narrow black line, in the blotch the frass is typically clumped near the entrance. Mines occur either singly or with a few together on one leaf. The larva cuts out an elliptic case of about 3.4–3.7 mm long × 1.6–2.2 mm wide. The larva probably descends with its cocoon into leaf litter before pupation.

Voltinism. Larvae are found between mid-September and April, and are apparently absent in winter; adults usually emerge between 3–6 weeks after collecting the larvae, suggesting there are multiple overlapping generations. The specimen from Worcester (October) is the only record of an adult taken in the wild.

Distribution (Fig. 116)**.** South Africa: Western Cape, Eastern Cape (new record). The species is abundant on Table Mountain and in the Cape Peninsula, but it is here also recorded from other Fynbos localities around Stellenbosch and Worcester, and Vári also reared it from Zuurberg Pass in Eastern Cape, so we assume a wide distribution in Western and Eastern Cape.

DNA barcode. We barcoded four specimens (three from Table Mountain, one from Stellenbosch), with a maximum intraspecific distance of 1.55%, within the same population on Table Mountain. The BIN is BOLD:ACG8941.

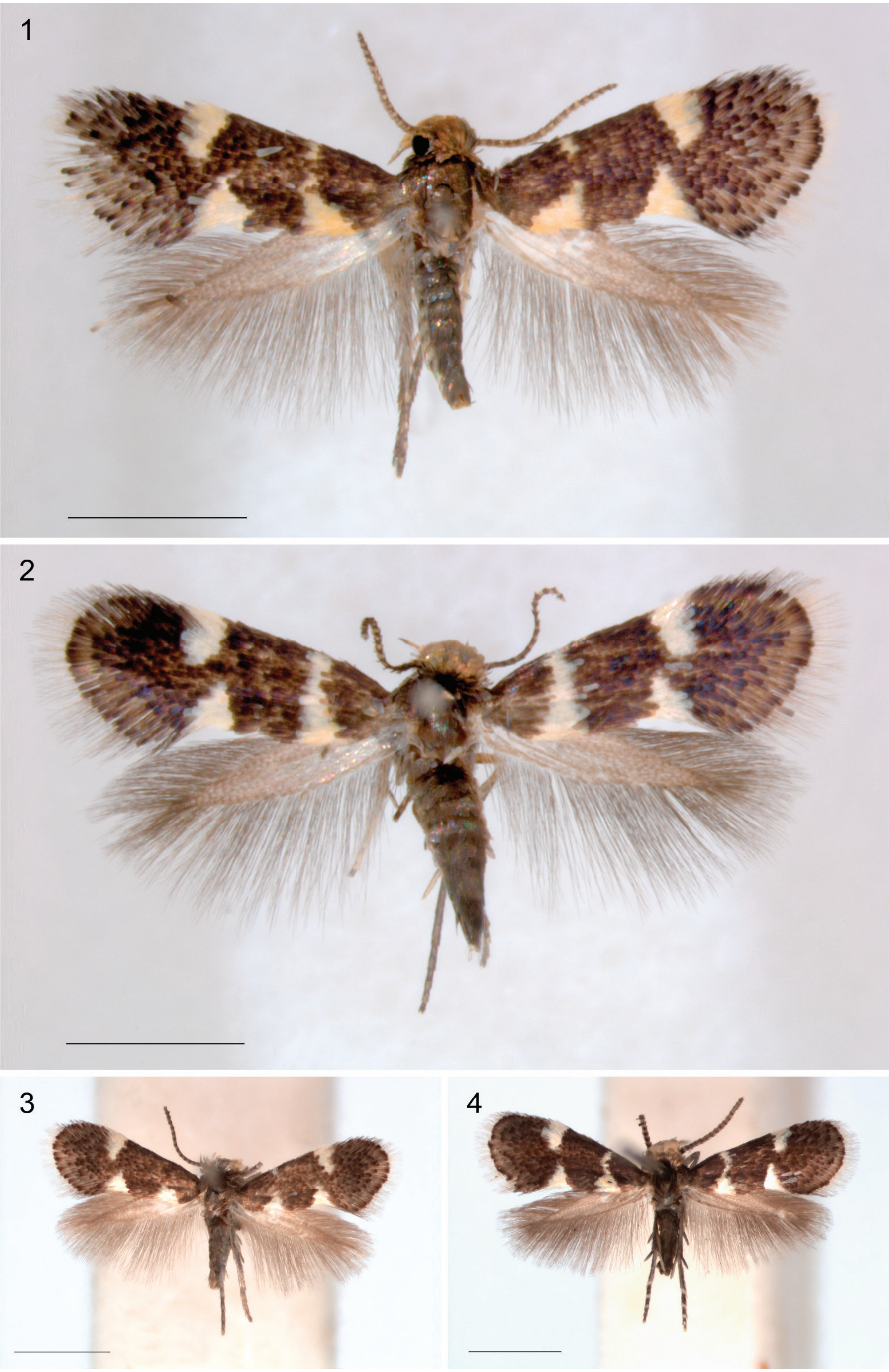
Remarks. In the original description Mey (2011) mentioned that the valval pecten has 13–15 spines, a number that we cannot confirm from the few specimens studied. He further considered the phallus appendix as a cornutus. This appendix, however, is not attached to the vesica, but is an unmovable extension of the phallic tube. Mey (2011) placed this species in *Antispilina* on the basis of its venation, overlooking the fact that *Holocacista* has the same venation. *Antispilina* is a small Palearctic genus, feeding on Polygonaceae, with some new species in the course of description (B.W. Lee et al. in preparation). The placement of this species in *Holocacista*, which is diverse in Africa, makes much more sense. Possibly the ancestor of *H. varii* shifted hosts from Vitaceae to *Pelargonium*.

Many of the specimens listed under material have only been briefly examined by EvN during his visit to the Ditsong Museum, hence the absence of indication of sex.

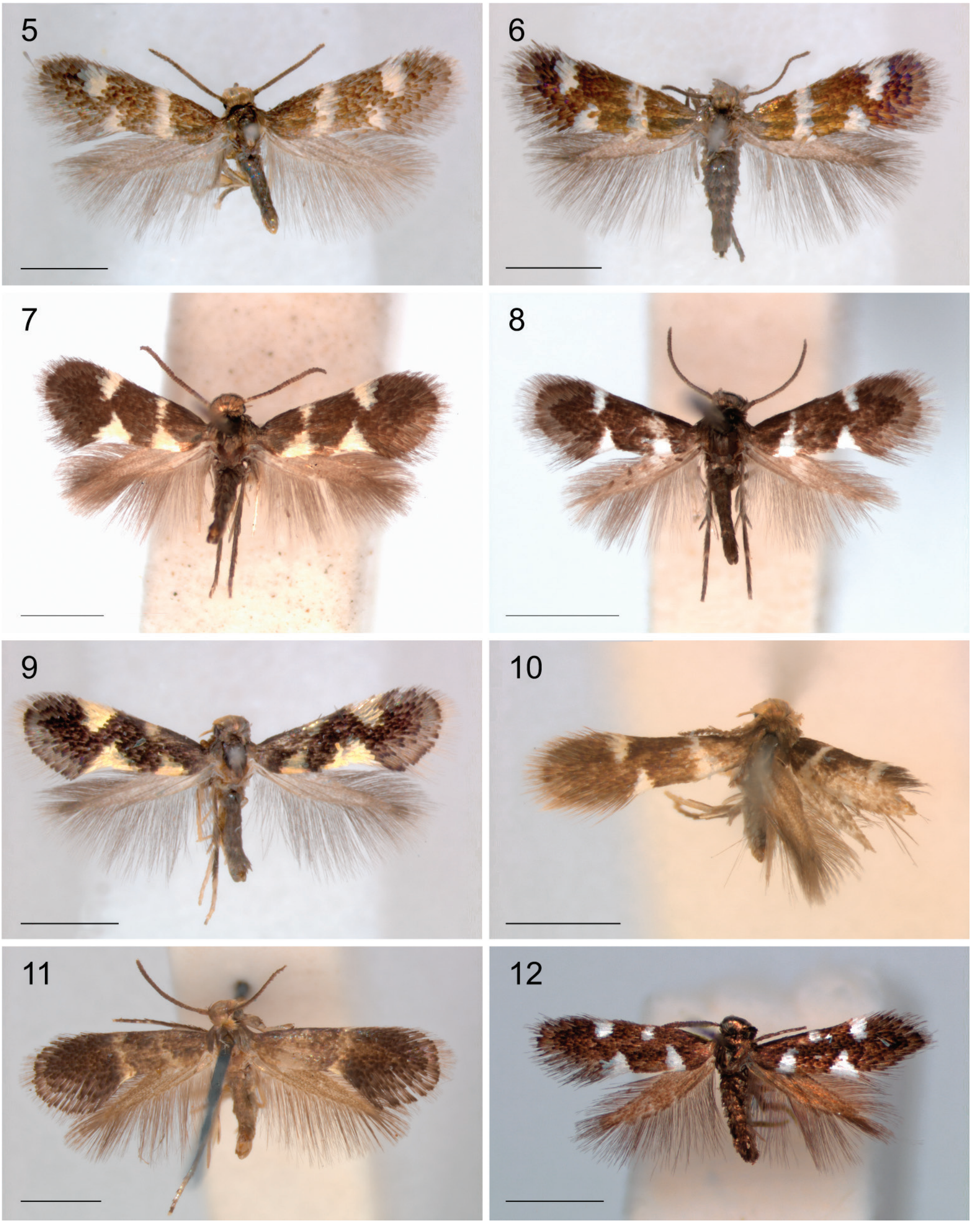
Material examined. Eastern Cape: 1 adult, Zuurberg Pass, south slopes, 22.iii.1954, 11 mines, Pelargonium sp., 1 adult emerged 20.iv.1954, L. Vári (TMSA). **Western Cape**: 5 adults, Bloubergstrand, 3.x.1974, Ac. no. 3308, leafmines on *Pelargonium*, emerged 26–30.x.1974, L. Vári (TMSA); 2 adults, ibidem, 13.x.1975, Ac. no. 3496, leafmines on *Pelargonium*, emerged 14.xi.1975, L. Vári (TMSA); 6 adults, Cape of Good Hope Nature Reserve, 26.x.1966, Ac. no. 2851, leafmines on *Pelargonium*, emerged 21–23.xi.1966, L. Vári (TMSA); 8 adults, ibidem, Ac. no. 288527.x.1967, emerged 20–22.xi.1967, L. Vári (TMSA); 4 adults, Cape Peninsula, Bakoven, 29.x.1975, Ac. no. 3499, leafmines on *Pelargonium*, emerged 17–19.xi.1975, L. Vári (TMSA); 5 adults, Cape Peninsula, Hout Bay, 11.xi.1954, Ac. no. 1357 leafmines on *Pelargonium cucullatum*, emerged 7–21.xii.1954, L. Vári (TMSA); 2 adults (paratypes), ibidem, 14.ix.1966, Ac. no. 2846, emerged 21.xi.1966, L. Vári (TMSA); 10 adults (paratypes), Cape Peninsula, nr. Muizenberg, Steenberg, 10.xi.1979, Ac. no. 3764, leafmines on *Pelargonium*, emerged 15.xi–10.xii.1979, L. Vári (TMSA); 1♂, 1♀, 1 adult (paratypes), Cape Town, Kirstenbosch, 17.xi.1954, Ac. no. 1365, leafmines on *Pelargonium cucullatum*, emerged 11–14.xii.1954, L. Vári (MHUB, TMSA); 1 adult, ibidem, emerged 5–29.xii.1954, A.J.T. Janse (TMSA); 2 adults (paratypes), ibidem, 14.ix.1962, Ac. no. 2535, emerged 1–17.x.1962, L. Vári (TMSA); 1♂, 1♀, ibidem, 23.xi.2014, leafmines on *P. citronelium*, emerged 11.xii.2014, L. Torrance & H. Geertsema (USEC); 1♂, 1♀, ibidem, 23.xi.2014, leafmines on *P. cucullatum*, emerged 11–14.xii.2014, L. Torrance & H. Geertsema (USEC).

6♂, 4♀ (paratypes), 1 adult, Cape Town, slopes Table Mt., 4.iii.1954, Ac. no. 1047, leafmines on *Pelargonium cucullatum*, emerged 26.iii–3.iv.1954, L. Vári (TMSA); 9 adults, Noordhoek, leafmines on *Pelargonium*, pupa 10–14.v.1984, emerged 28–31.v.1984, H. Geertsema (TMSA); leafmines, Stellenbosch, Botanical Garden, 122 m, 27.i.2013, EvN2013032, leafmines on *Pelargonium panduriforme*, E.J. van Nieukerken (RMNH); 1 larva, ibidem, 27.i.2013, EvN2013033, leafmines on *Pelargonium hispidum*, E.J. van Nieukerken (RMNH); 3 larvae, Stellenbosch, Jonkershoek, 390 m, 18.i.2013, EvN2013017, leafmines on *Pelargonium cucullatum*, E.J. van Nieukerken & H. Geertsema (RMNH); 3♂, 4♀, 3 larvae, Table mountain NP, Cecilia, nr Klaasenskop, 385 m, 19.i.2013, EvN2013022, leafmines on *Pelargonium cucullatum*, emerged 11–22.ii.2013, E.J. van Nieukerken (RMNH); 1♂, 1♀, 1 larva, Table mountain NP, Cecilia, parking lot, 180 m, 19.i.2013, EvN2013024, leafmines on *Pelargonium cucullatum*, emerged 24.i–12.ii.2013, E.J. van Nieukerken & H. Geertsema (RMNH); 1♂, Worcester, Fairy Glen, 15–19.x.1966, L. Vári & Potgieter (TMSA).

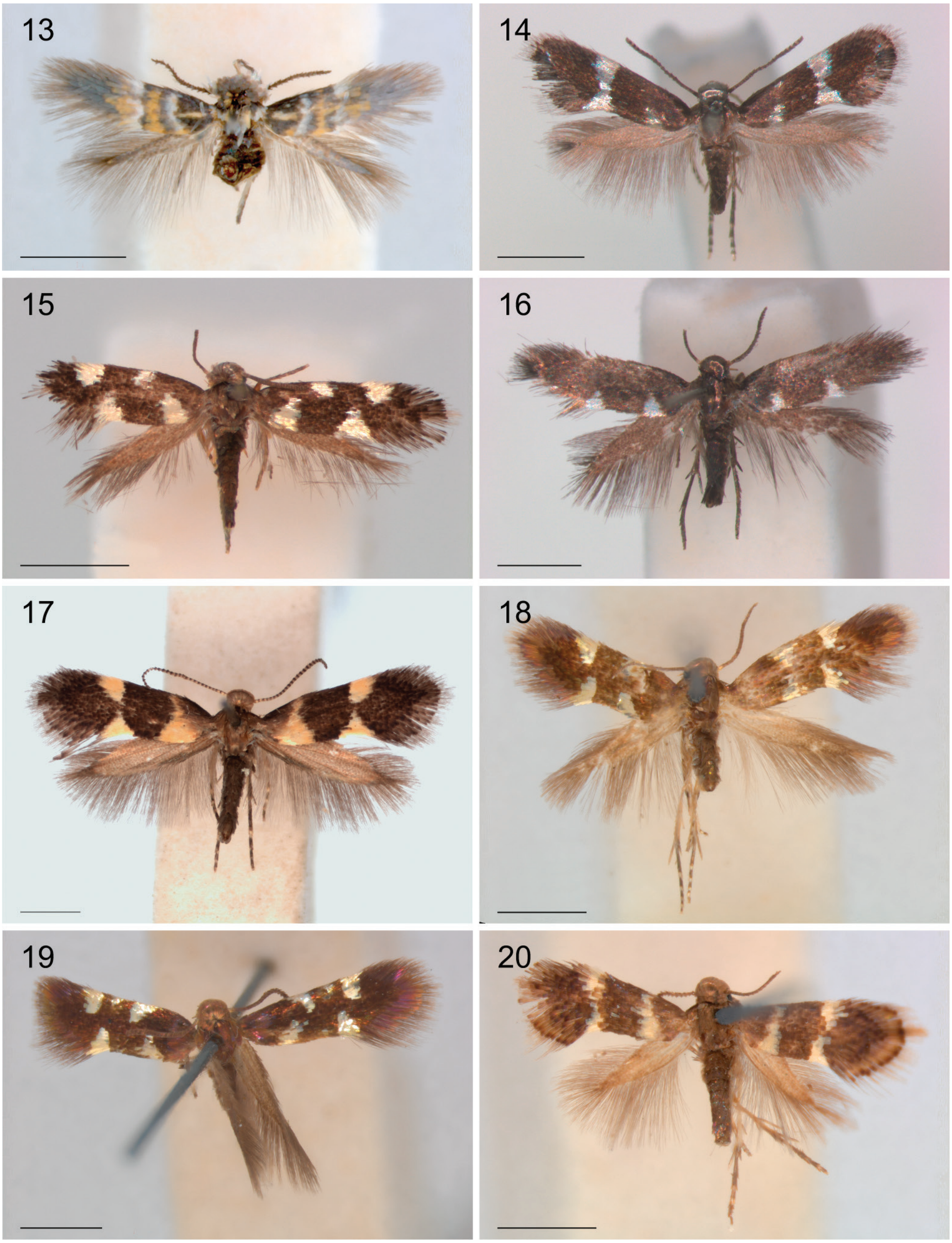
Other material. Leafmines, observation, Western Cape, Ashton, 2014, L. Torrance & H. Geertsema.



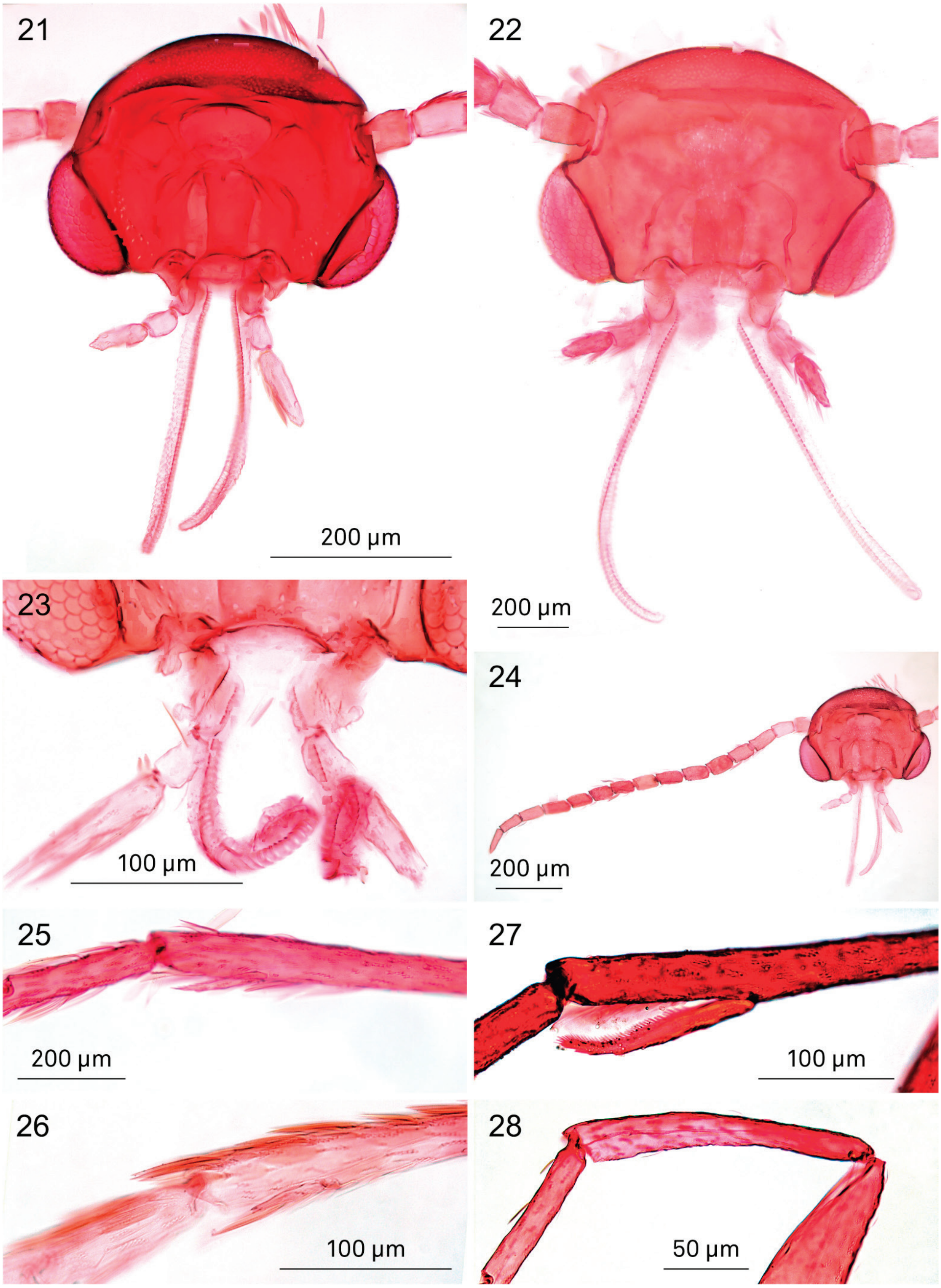
Figures 1–4. *Holocacista* species, adult habitus. **1–3** *Holocacista capensis*: **1** Male holotype, RMNH.INS.24622 **2** Female, Western Cape, Paarl, RMNH.INS.24624 **3** Male, Western Cape, Wilderness, reared from *Rhoicissus digitata*, Genitalia slide EvN4381 **4** *H. salutans*, male, Kwazulu-Natal, Umhlanga Rocks, reared from *R. revoilii*, Genitalia slide EvN 4383. Scales 1 mm.



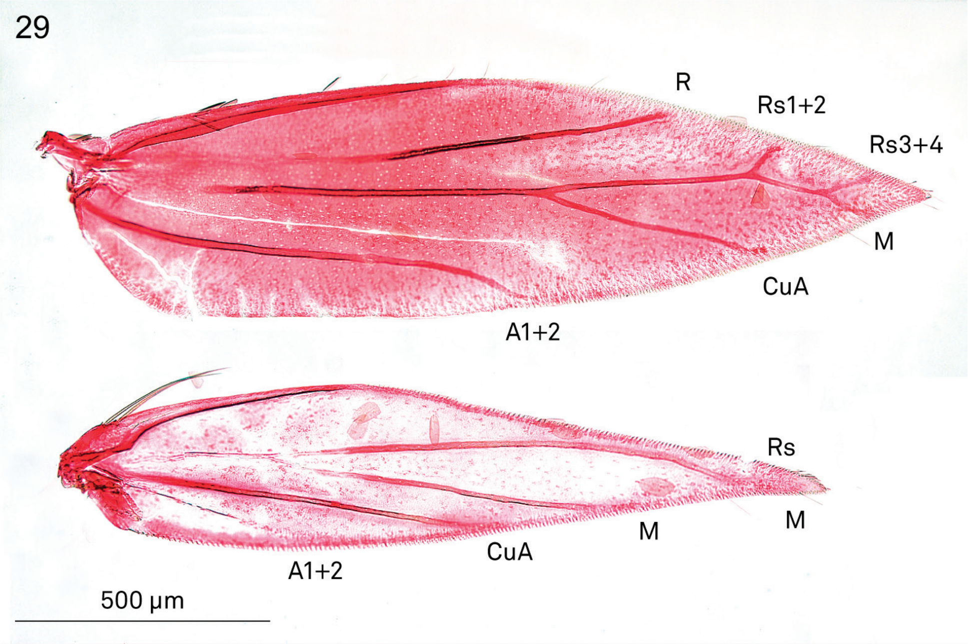
Figures 5–12. *Holocacista* species, adult habitus. **5, 6** *H. varii*, Western Cape, Table mountain NP **5** Male, RMNH.INS.24623 **6** Female RMNH.INS.24625 **7** *H.* sp. *Rhoicissus_tridentata*, male, Zimbabwe, Mt. Selinda, Genitalia slide EvN4385 **8** *H.* sp. *Cissus_integrifolia*, male, Zimbabwe, Lundi, Genitalia slide EvN4387 **9** *H. rivillei*, male, Italy, Borghetto, RMNH.INS.24626 **10** *H. micrarcha*, male **11** *H. selastis*, male **12** *H. Leea_Borneo*, male, Indonesia, Kalimantan Timur, Gunung Lumut, RMNH.INS.24158. Scales 1 mm.



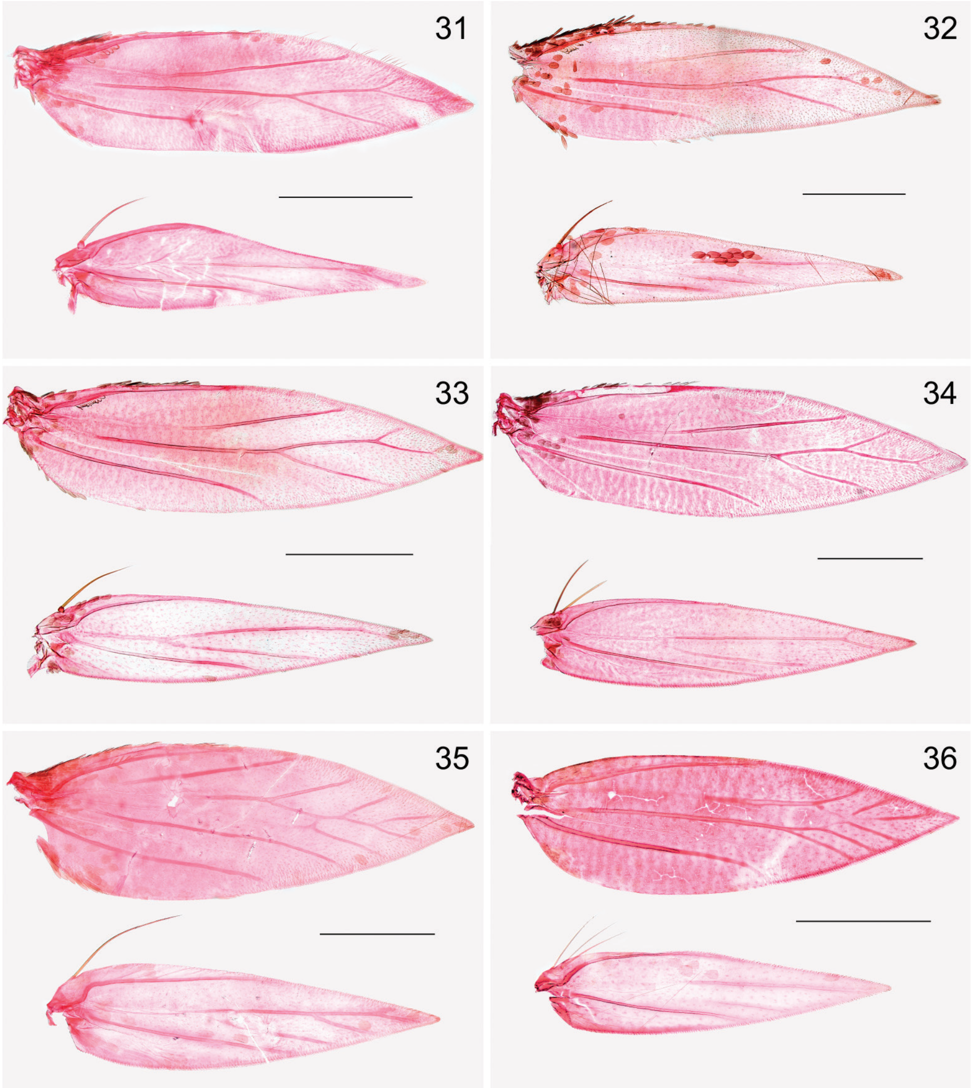
Figures 13–20. Heliozelidae species, adult habitus. **13** *Holocacista* sp. *Dyerophytum*_UAE, Male, UAE, Fujairah, RMNH.INS.24628 **14** *H.* sp. *Psychotria*_Australia, male, Australia, Queensland, RMNH.INS.24367 **15** *H.* sp. *Lasianthus*_Borneo, female, Indonesia, Kalimantan Timur, Gunung Lumut, RMNH.INS.24159 **16** *H.* sp. *Impatiens*_Vietnam, male, Vietnam, Cuc Phuong NP, RMNH.INS.24361 **17** *Antispila* sp. *Rhoicissus*_SA, male, South Africa, Limpopo, Louis Trichard, Genitalia slide EvN4379 **18** *A. argostoma*, male, India **19** *A. aristarcha*, female, India **20** *Heliozela anna*, female, India. Scales 1 mm.



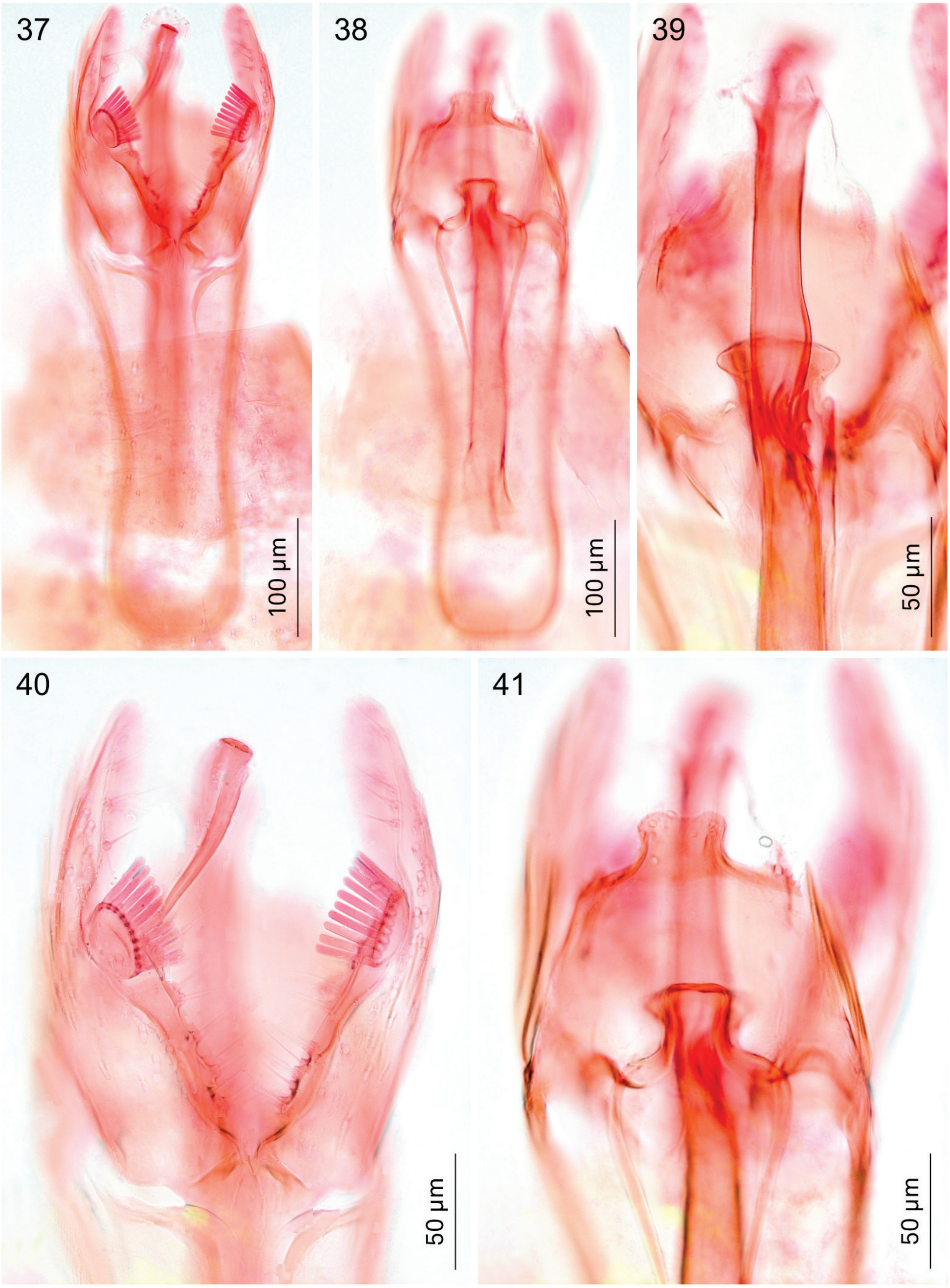
Figures 21–28. Heliozelidae species, details of adult morphology. **21** *Holocacista rivillei*, male, denuded head, RMNH.INS.24300 **22** *H. capensis*, male, denuded head, RMNH.INS.24445 **23** *H. rivillei*, male, detail mouthparts, RMNH.INS.24443 **24** *H. rivillei*, male, head and antenna, showing 15 segments, RMNH.INS.24300 **25–28** Male foretibia with or without epiphysis: **25** *H. capensis*, small epiphysis, RMNH.INS.24445 **26** *H. rivillei*, small epiphysis, RMNH.INS.24443 **27** *Heliozela sericiella*, large epiphysis, RMNH.INS.24451 **28** *Antispilina ludwigi*, epiphysis absent, RMNH.INS.24448.



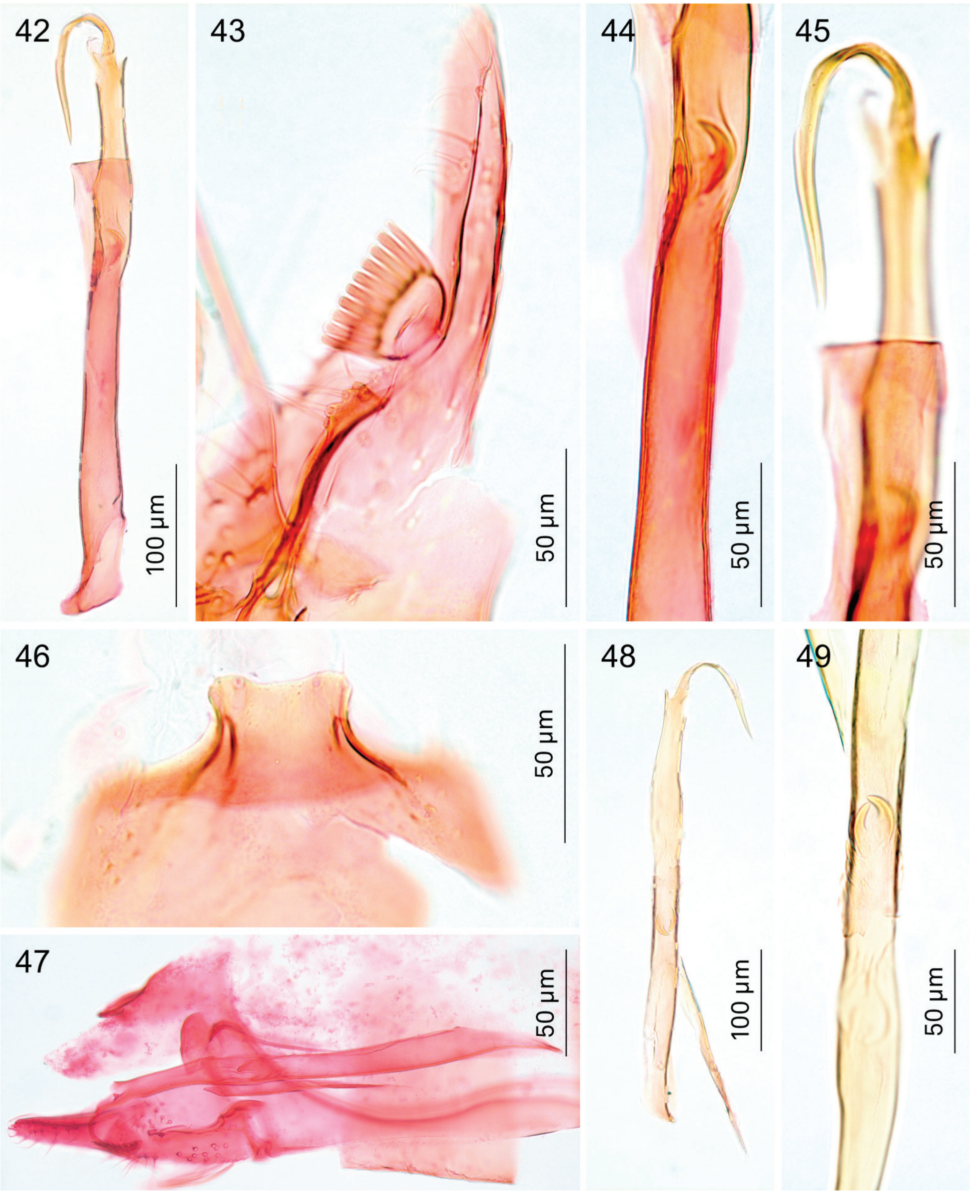
Figures 29, 30. *Holocacista* species, wing venation. **29** *Holocacista rivillei*, female, veins labelled, RMNH.INS.24259 **30** *H. capensis*, male, RMNH.INS.24260.



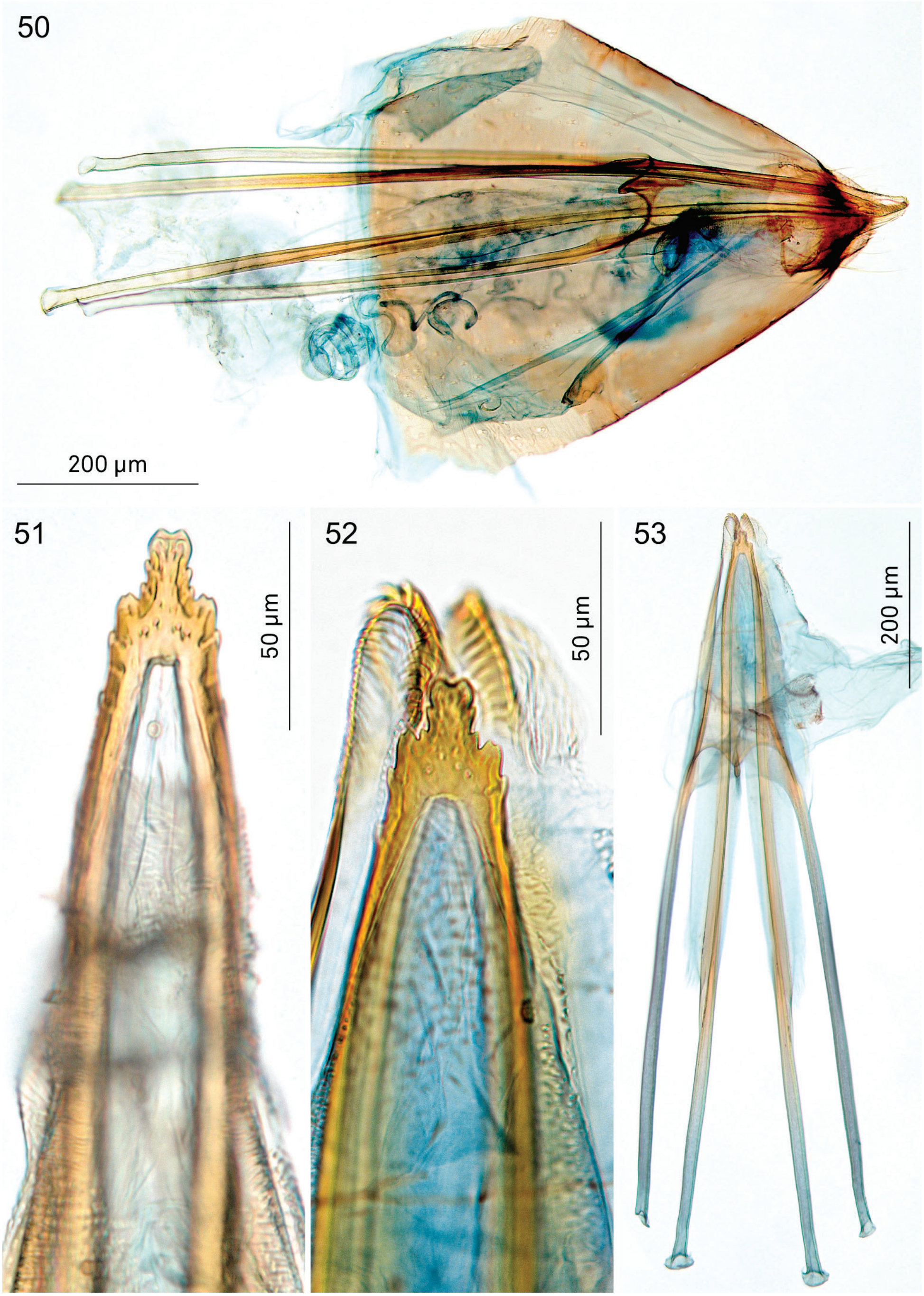
Figures 31–36. Heliozelidae species, wing venation **31** *Holocacista micrarcha*, male, BM34300 **32** *H. selastis*, male, BM34299 **33** *H.* sp. *Psychotria*_Australia, male, RMNH.INS.24367 **34** *H.* sp. *Impatiens*_ Vietnam, female, RMNH.INS.24368 **35** *Antispila argostoma*, male, BM34298 **36** *Heliozela anna*, female, BM34301. Scales 0.5 mm.



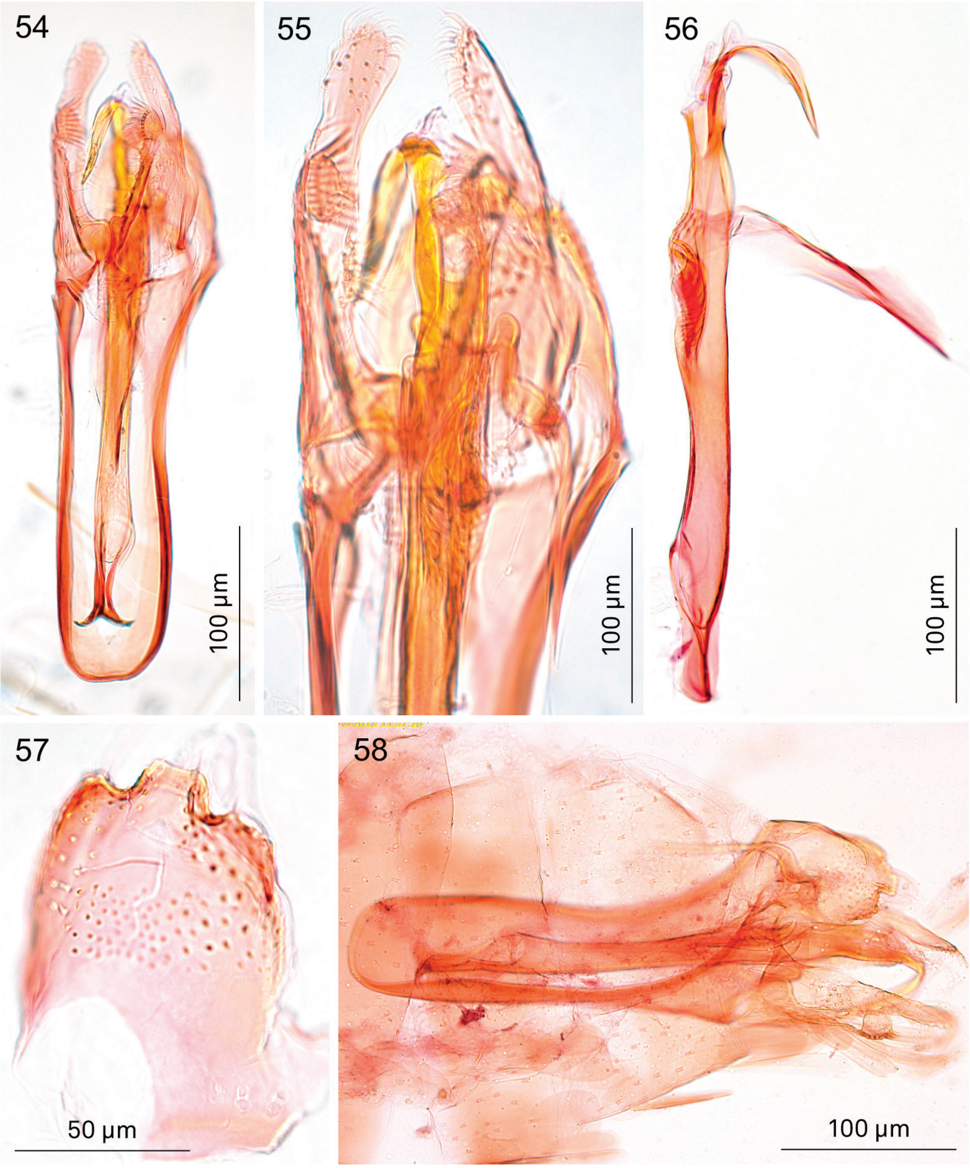
Figures 37–41. *Holocacista capensis*, male genitalia in ventral view, RMNH.INS.24445; **37** and **40** focussed on ventral side, showing valvae and phallus tip; others more dorsally, showing tegumen and transtilla.



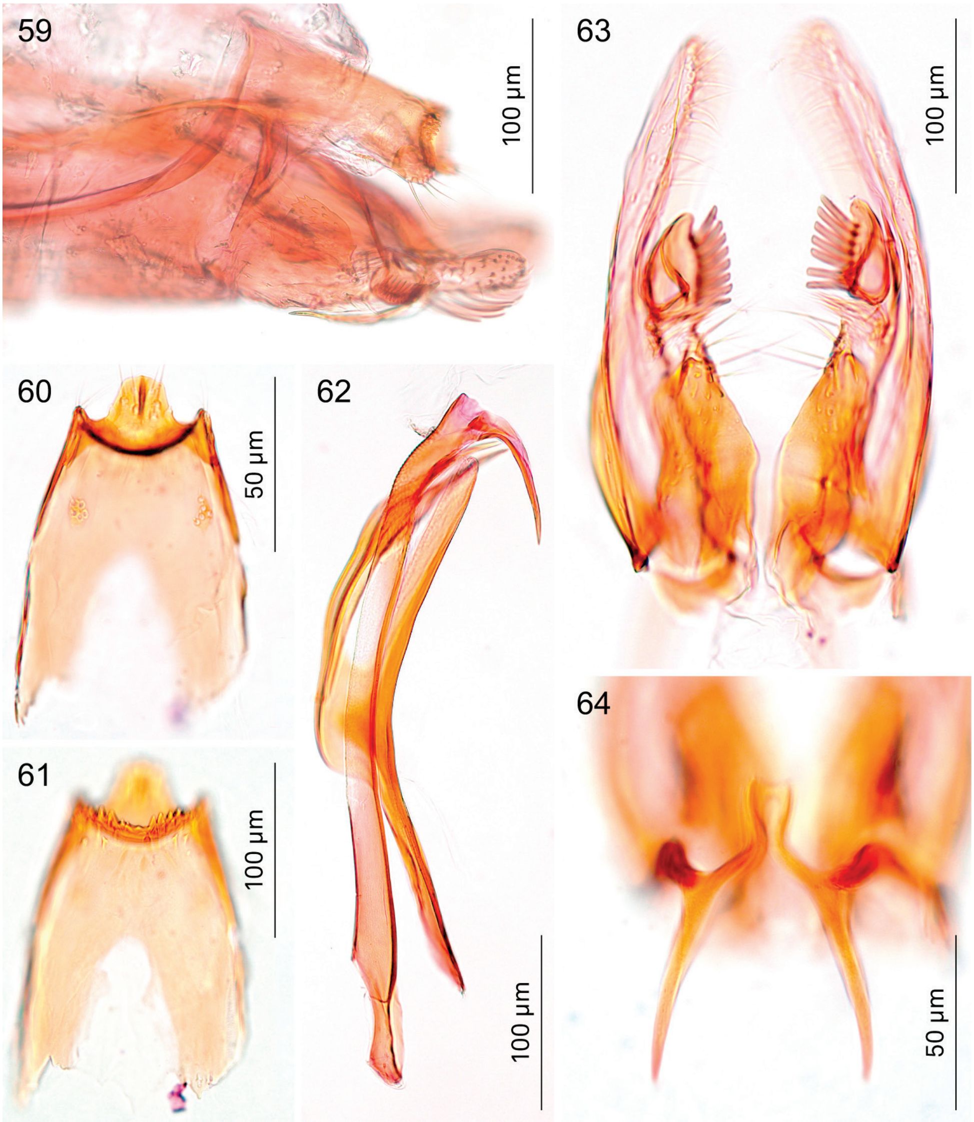
Figures 42–49. *Holocacista capensis*, male genitalia, details. **42–46** Holotype, RMNH.INS.24642, phallus in ventro-lateral view (42, 44, 45); valva in ventral view (43); tegumen in dorsal view (46) **47** Genitalia in lateral view, RMNH.INS.24446 **48, 49** phallus and juxta, lateral view, slide JCK7813.



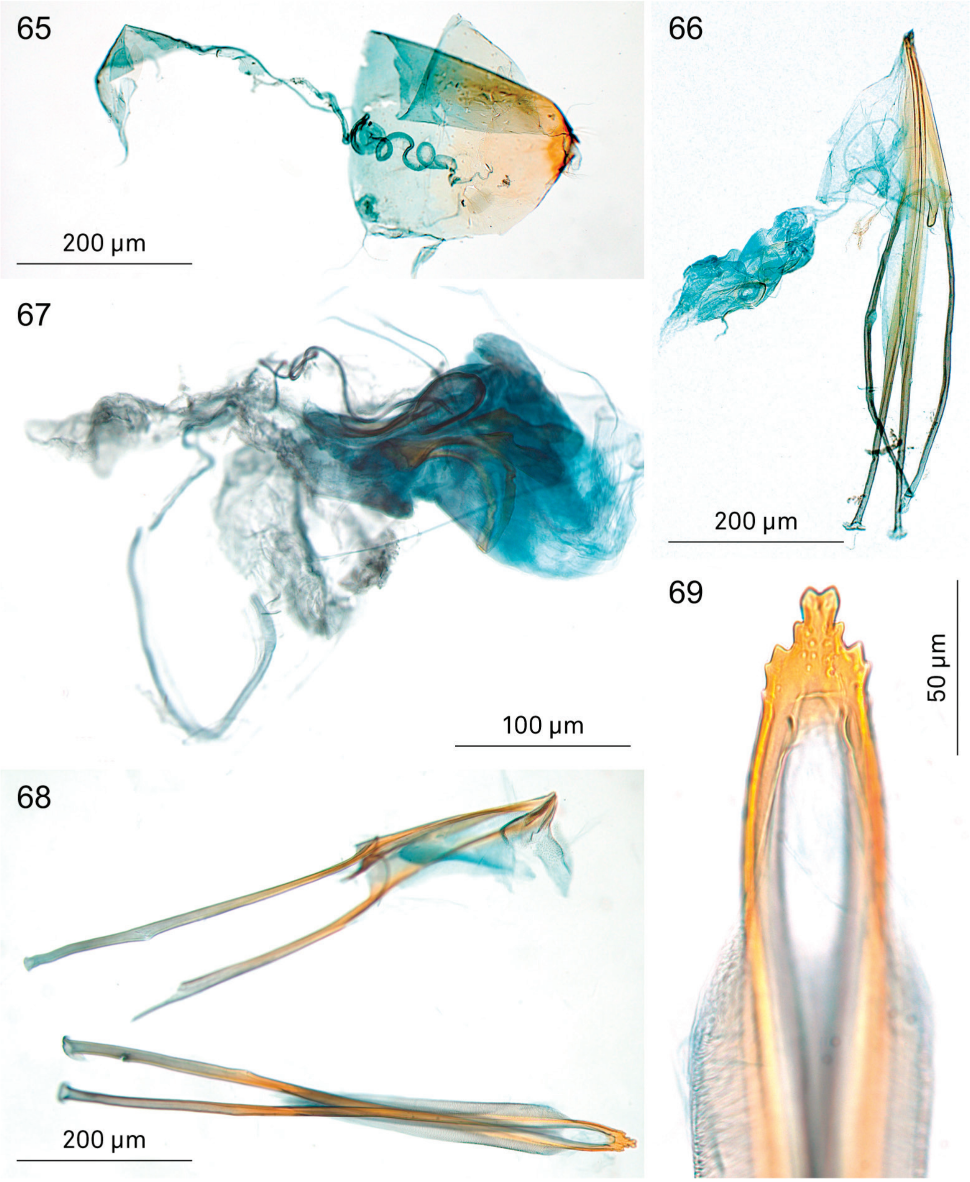
Figures 50–53. *Holocacista capensis*, female genitalia. **50** lateral view, RMNH.INS.24261 **51–53** Oviscapt detail (**51, 52**) or complete apophyses in ventral view, RMNH.INS.24625 (**51**), RMNH.INS.24624 (**52, 53**).



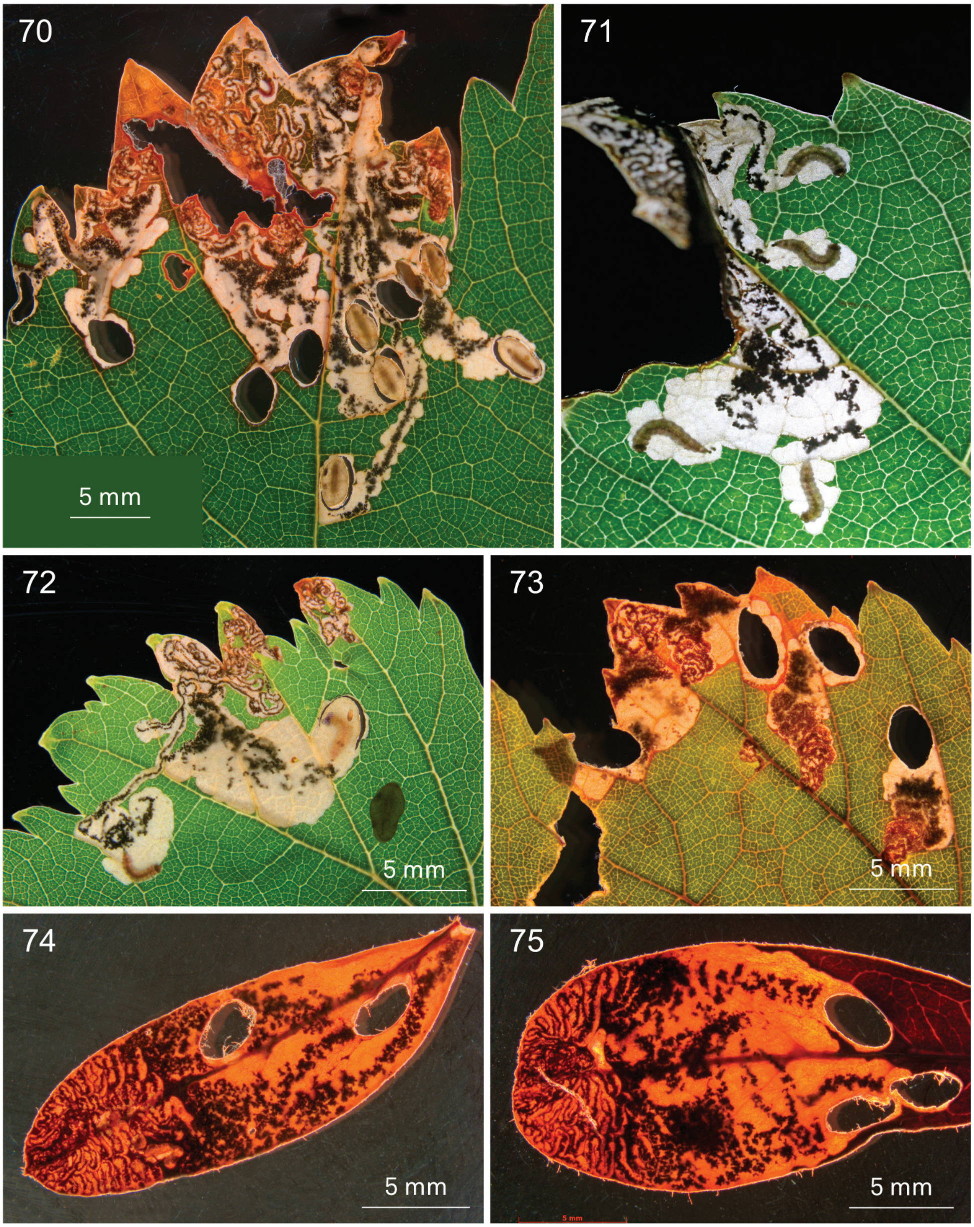
Figures 54–58. *Holocacista salutans*, male genitalia. **54, 55** ventro-lateral view, Genitalia slide EvN4383 **56** phallus in lateral view, Genitalia slide EvN4384 **57** tegumen in almost dorsal view, Genitalia slide EvN4384 **58** possible syntype in lateral view, Genitalia slide TM4023.



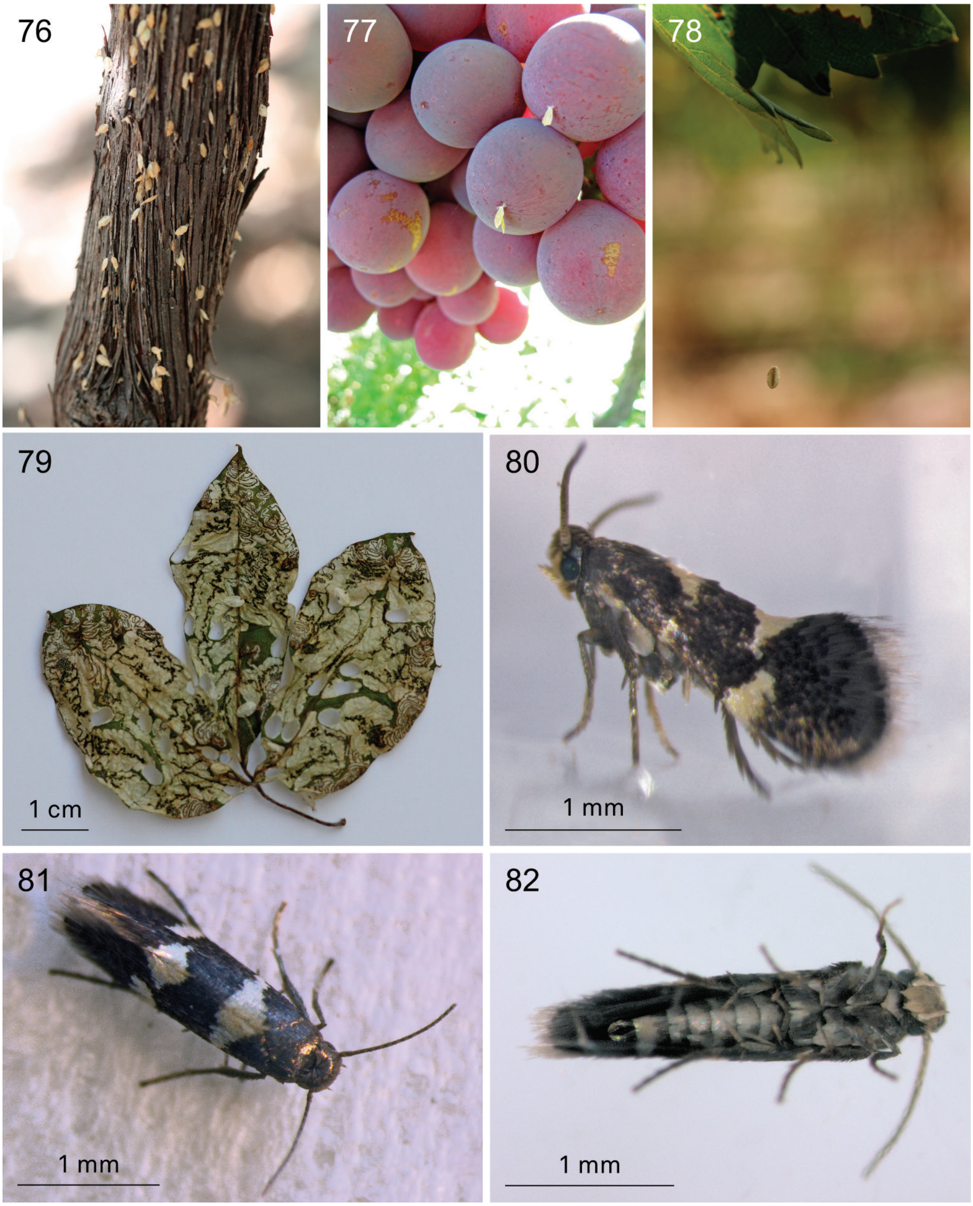
Figures 59–64. *Holocacista varii*, male genitalia. **59** ventral view, photographed in glycerin, Genitalia slide EvN4388 **60–64** details, RMNH.INS.24623 **60, 61** tegumen, respectively more ventrally and dorsally focussed **62** phallus and juxta in lateral view **63** valvae in ventral view **64** transtilla ventral view, focussed more dorsally.



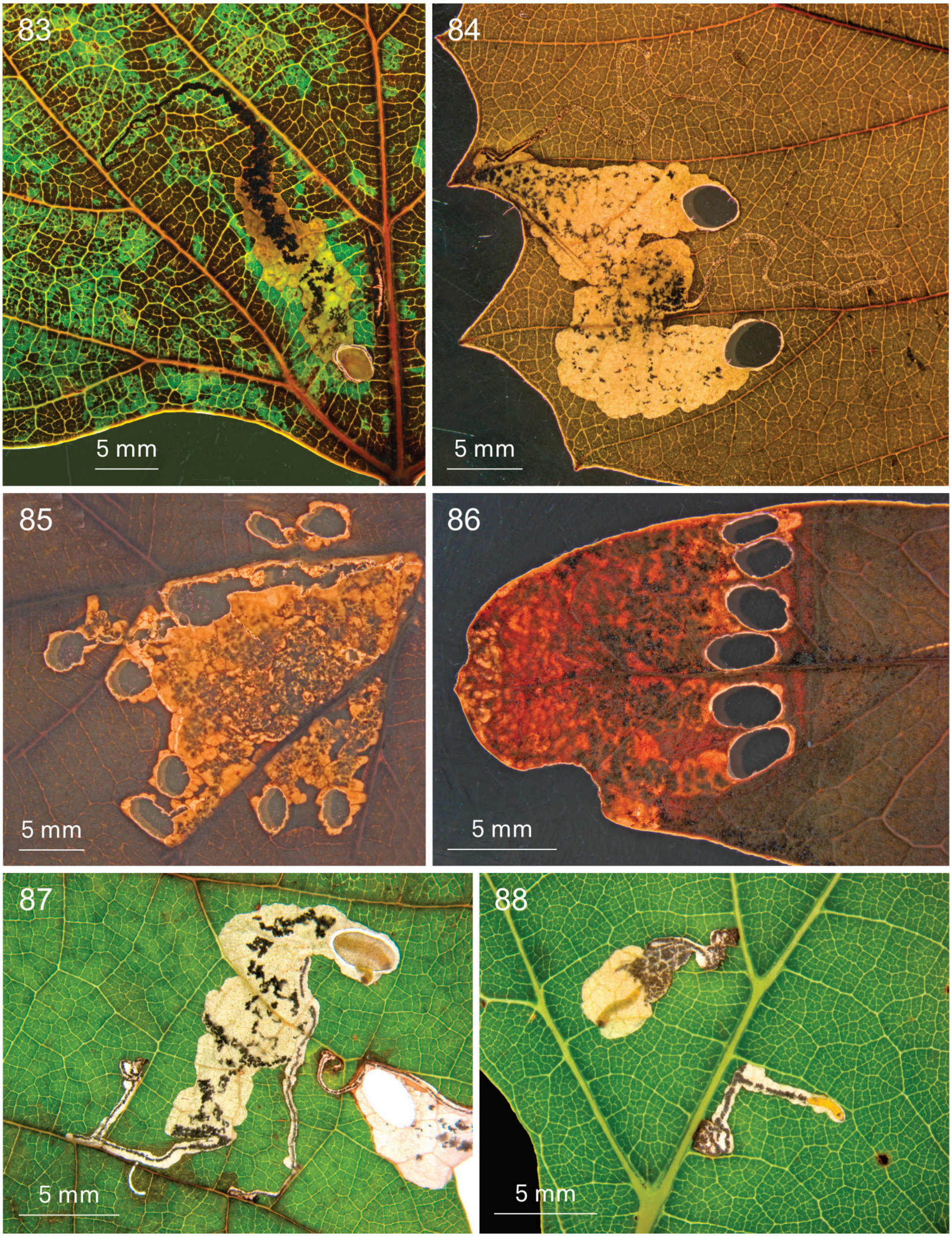
Figures 65–69. *Holocacista* species, female genitalia. **65, 66** *H. salutans*, lateral view, RMNH.INS.24668 **67–69** *H. varii*, RMNH.INS.24625: **67** internal genitalia in lateral view **68** apophyses in more or less ventral view **69** oviscapt detail, ventral view.



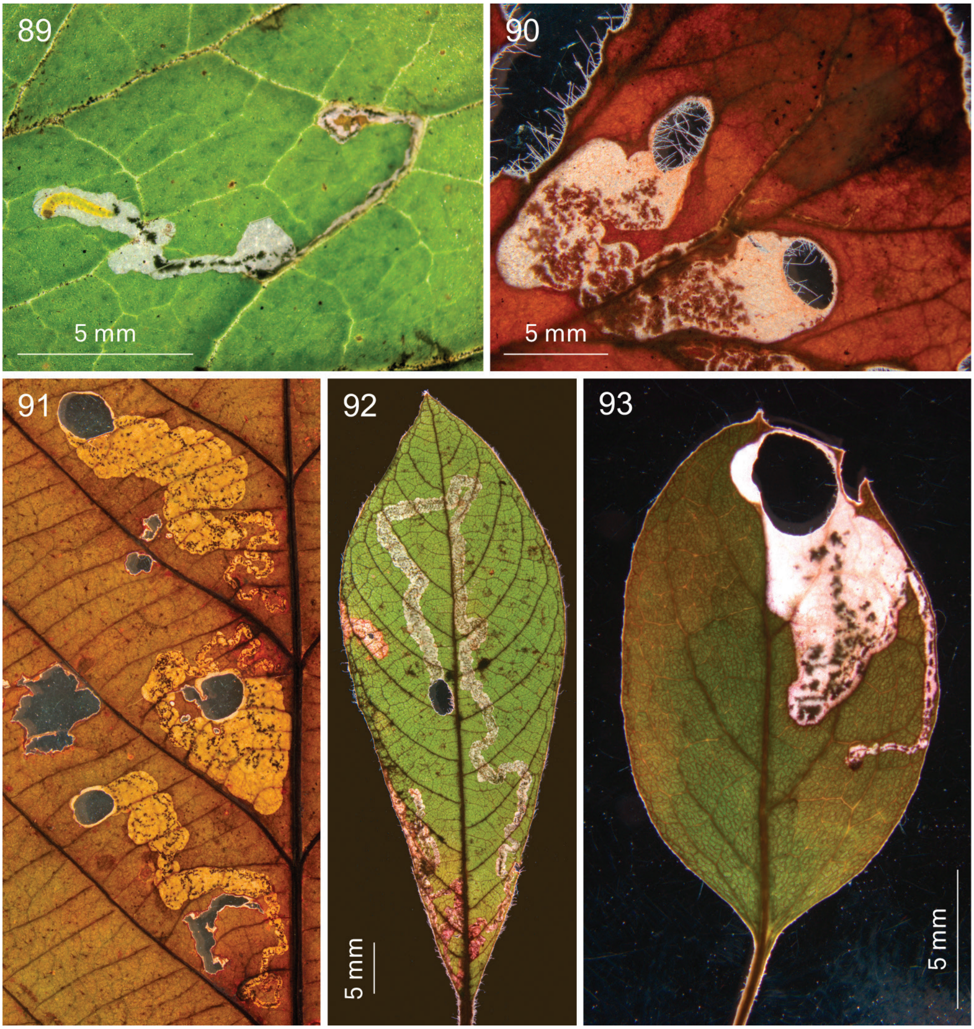
Figures 70–75. *Holocacista capensis*, leafmines on *Vitis vinifera*, Paarl (70–73) and *Rhoicissus digitata*, Wilderness (74, 75) **70** EvN2013029, 25 January 2013 **71** 16 January 2013 **72** EvN2013029, 25 January 2013 **73** 2013003, 15 January 2013 **74, 75** Vári Ac. No. 1093, 15.iii.1954 (dried leafmines).



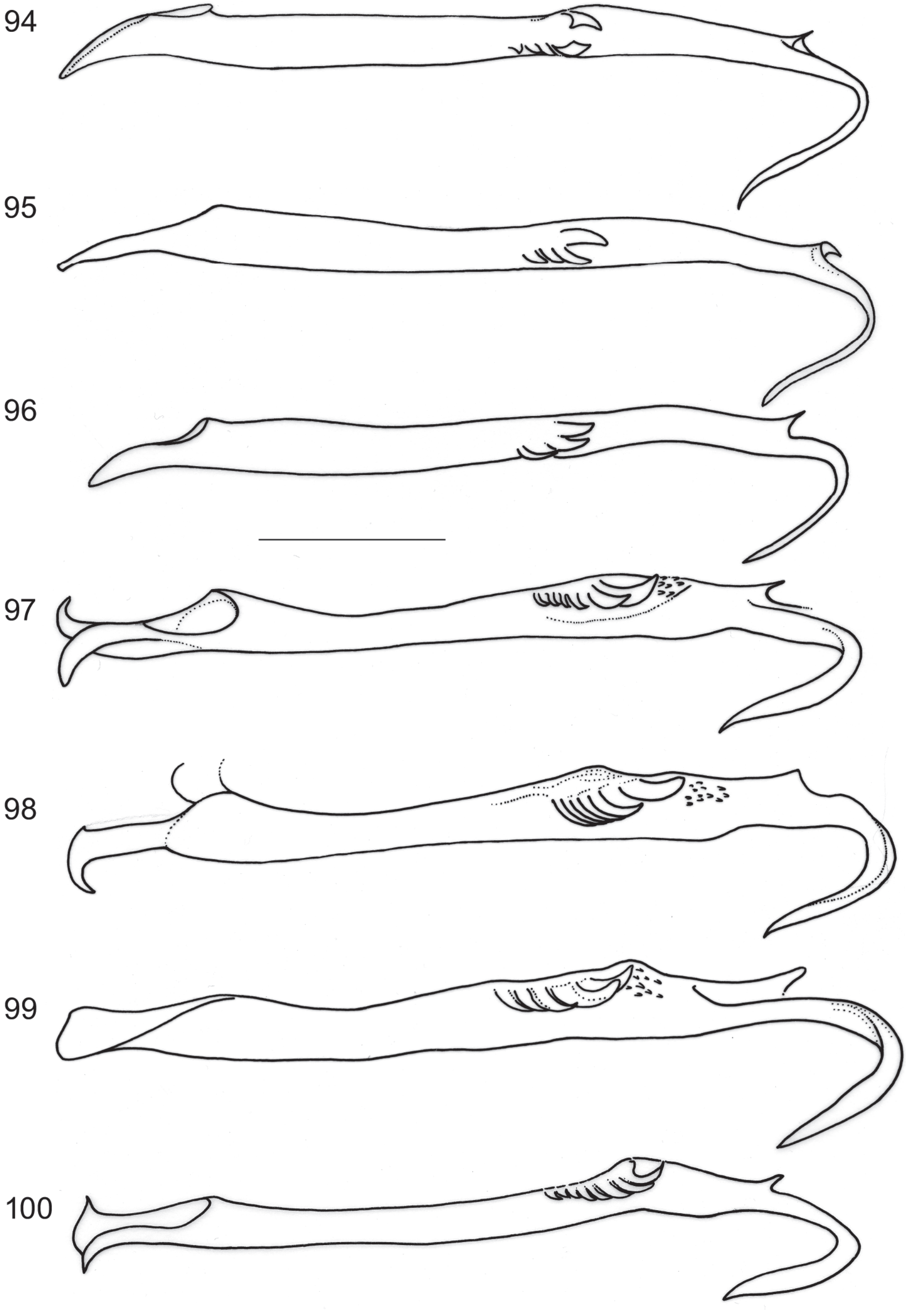
Figures 76–82. *Holocacista capensis*, life history. **76** Trunk of *Vitis* with many cocoons with exuviae, De Anker, Paarl, 14 February 2013 **77** grapes with fresh cocoons attached, Paarl, 25 January 2013 **78** larva in cocoon, going down on silken thread, Paarl, 16 January 2013 **79** Leafmines in *Rhoicissus digitata*, reared in laboratory from adults that originated on *Vitis* from Wellington, 2014 **80–82** Live adult males, reared from *Vitis vinifera*, from Paarl **80** EvN2013004, 28 January **81** Windmeul, reared in Leiden, 23 February 2012 **82** EvN2013005, 4 February.



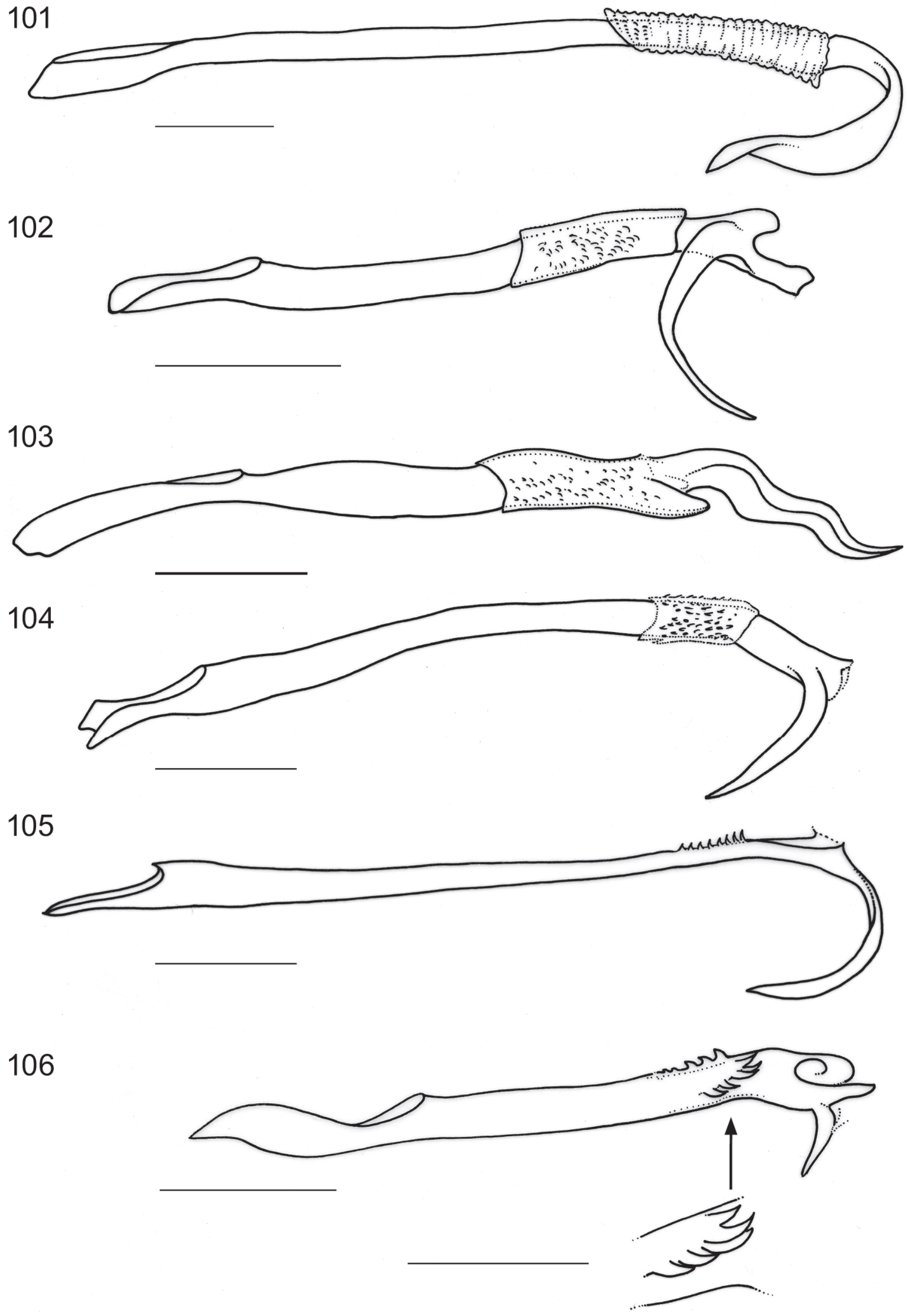
Figures 83–88. *Holocacista* species, leafmines on Vitaceae. **83** *H.* sp. *Rhoicissus_tomentosa*, fresh mine, larva cutting out shield, Swellendam, EvN2014901, larva RMNH.INS.30313 **84** *H.* sp. *Rhoicissus_tridentata*, dried mines, Vari 1225 **85** *H. salutans* on *Rhoicissus tomentosa*, dried mines, Vari 2788 **86** *H. salutans* on *Rhoicissus digitata*, dried mines, Vari 3342 **87, 88** *H. rivillei*, fresh mines with larvae on *Vitis vinifera*, in 87 two larvae next to each other, one in cocoon, EvN2013904.



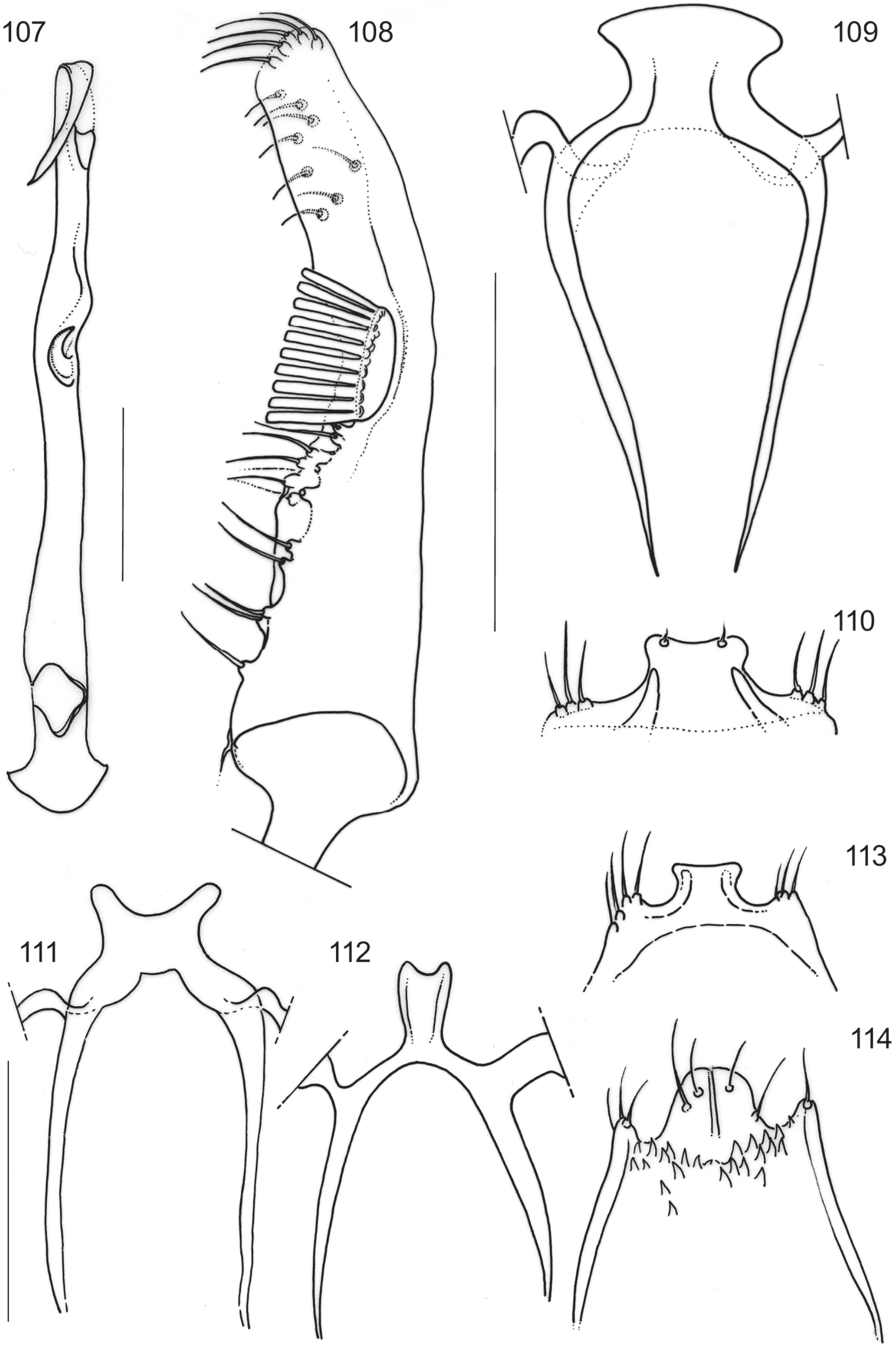
Figures 89–93. *Holocacista* species, leafmines on various plants **89** *H. varii*, fresh mine with larva on *Pelargonium*, EvN2013033 **90** *H. varii*, dried mine on *Pelargonium cucullatum*, EvN2013021 **91** *H.* sp. *Leea*_Borneo, dried mines on *Leea indica*, EvN2005252 **92** *H.* sp. *Lasianthus*_Borneo, dried mine on *Lasianthus* sp., EvN2005255 **93** *H.* sp. *Paederia*_Taiwan, dried mine on *Paederia*, EvN2012314.



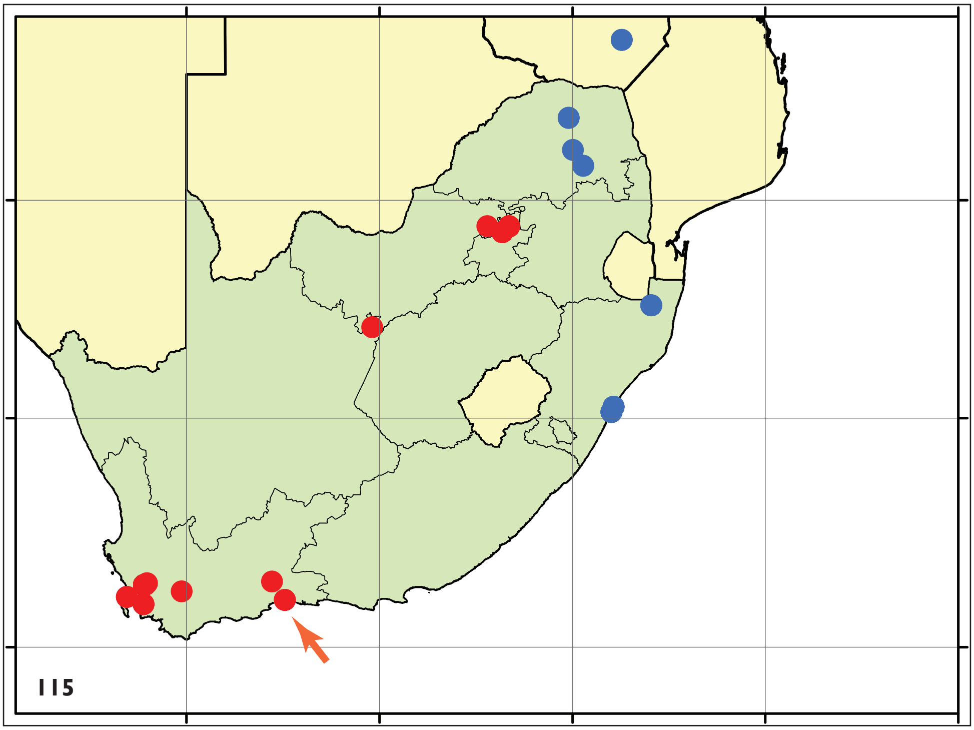
Figures 94–100. *Holocacista* species, male phallus in lateral view, scale 100 µm. **94–96** *H. capensis*, Genitalia slides resp. EvN4264, EvN4446 [mirrored], EvN4381 **97–100** *H. salutans*, Genitalia slides resp. TM4023 [type locality], EvN4383, EvN4384. All on same scale.

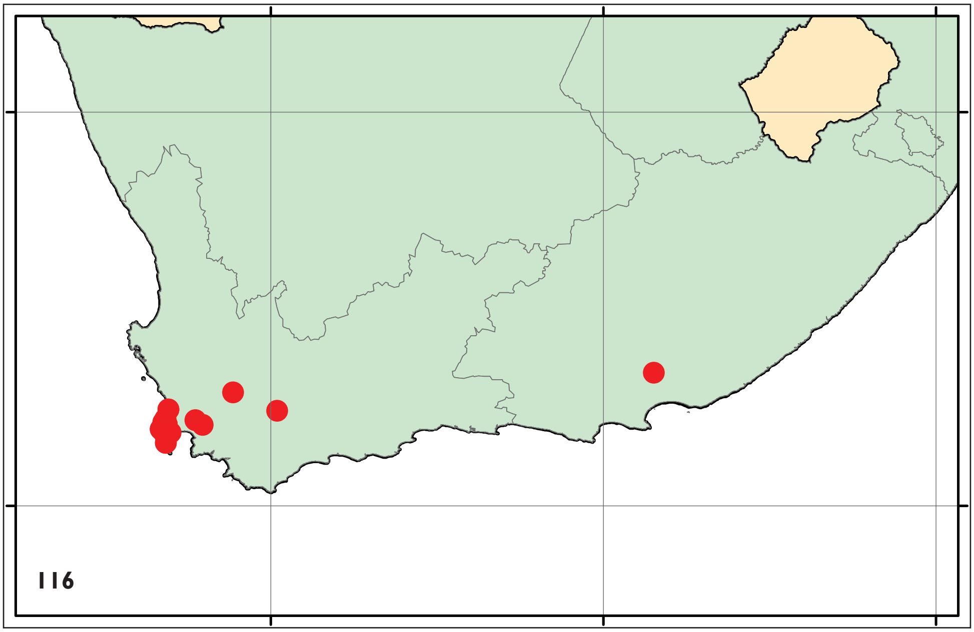


Figures 101–106. *Holocacista* species, male phallus in lateral view, scales 100 µm. **101** *H.* sp. *Rhoicissus_tridentata*, Genitalia slide EvN4380 [mirrored] **102** *H.* sp. *Rhoicissus*_PundaMilia, Genitalia slide EvN4382 **103** *H.* sp. *Cissus_integrifolia*, Genitalia slide EvN4387 **104** *H. varii,* Genitalia slide EvN4623 **105** *H. rivillei*, Genitalia slide EvN4443 [mirrored] **106** *H.* sp. *Dyerophytum*_UAE , Genitalia slide EvN4628. 104 and 105 on the same scale.



Figures 107–114. *Holocacista* species, male genitalia, details, scales 100 µm. **107–110** *H. capensis*, Holotype, Genitalia slide EvN4622 **111, 113** *H. salutans*, Genitalia slide EvN4383 **112, 114** *H. varii* Genitalia slide EvN4623 108–110, same scale; 111–114 same scale.





Figures 115–116. Distribution records of southern African *Holocacista* species. **115** *H. capensis* (red dots) and *H. salutans* (blue dots); arrow points at Wilderness, only locality where *H. capensis* was found on native *Rhoicissus digitata* **116** *H. varii*.

DNA barcoding and species relationships of *Holocacista capensis*

Barcode analysis

We sequenced eight specimens of *H. capensis* and compared those with 24 sequences of other *Holocacista* species and several other heliozelid barcodes, sequenced for previous studies (van Nieukerken et al. 2012b; Bernardo et al. 2015). The NJ tree is presented in Fig. 117. The barcodes of *H. capensis* group clearly together and can only be divided in three haplotypes, two from the Paarl region, which just differ in a single substitution on position 59 (C or T), whereas the single sequenced specimen from Gauteng has a difference of 1.4% (9 nucleotides). The nearest neighbours are a specimen of *H. varii* and a specimen of *H. rivillei*, each with a distance of 11.2%. The three sequenced larvae from *Rhoicissus* represent two barcode clusters: respectively the two larvae from *R. tridentata* in North West province (12.0–12.2% distance from *H. capensis*), and the single sequence of a larva from *R. tomentosa* in Western Cape (11.9% distance). We failed in amplifying DNA from collection specimens of South African Heliozelidae stored in TMSA, also when using primers for smaller parts of the CO1 gene.

Most *Holocacista* barcodes group together in the NJ tree, but a few Asian ones cluster at different parts of the tree.

Infestation of Grapevine in South Africa by *Holocacista capensis*

Since its initial discovery in 2011 on table grape vines in Paarl, the moth is now reported from Cape Town, Somerset-West, Stellenbosch and Wellington; in all cases reports were in conjunction with damage reported on the foliage of table grape or wine grapevines. Various cultivars have been affected, but no single preference for a particular cultivar was obvious. Infestations, as indicated by the number of mines per leaf or descending larvae from the canopy, range from small to extensive. Thus far, no reports have been received of its presence in the Hex River Valley, the major table grape producing region of South Africa, although a report has been received from Robertson, close to that region.

The very first record of its presence on vines now appears to be that of Dr Lajos Vári, breeding the moth from an urban grape vine in his own garden in Pretoria. In 1980, moths were bred in Northern Cape, Vaalhartz Research Station and later, infested vine leaves from Roodeplaat yielded moths in 1990. The first records from the Western Cape were moths, bred from infested urban vine foliage collected in March 1998 from Oudtshoorn. Although it was first noticed in commercial table grape vines in 2011 in the Western Cape, field observations indicate that it must have occurred much earlier in the region on grape vines. All collections made of leafmines in 2011 to date, have yielded larval or pupal parasites, an indication of a longer presence of the moth. Reports from field workers indicated that they had noticed the scale-like larval

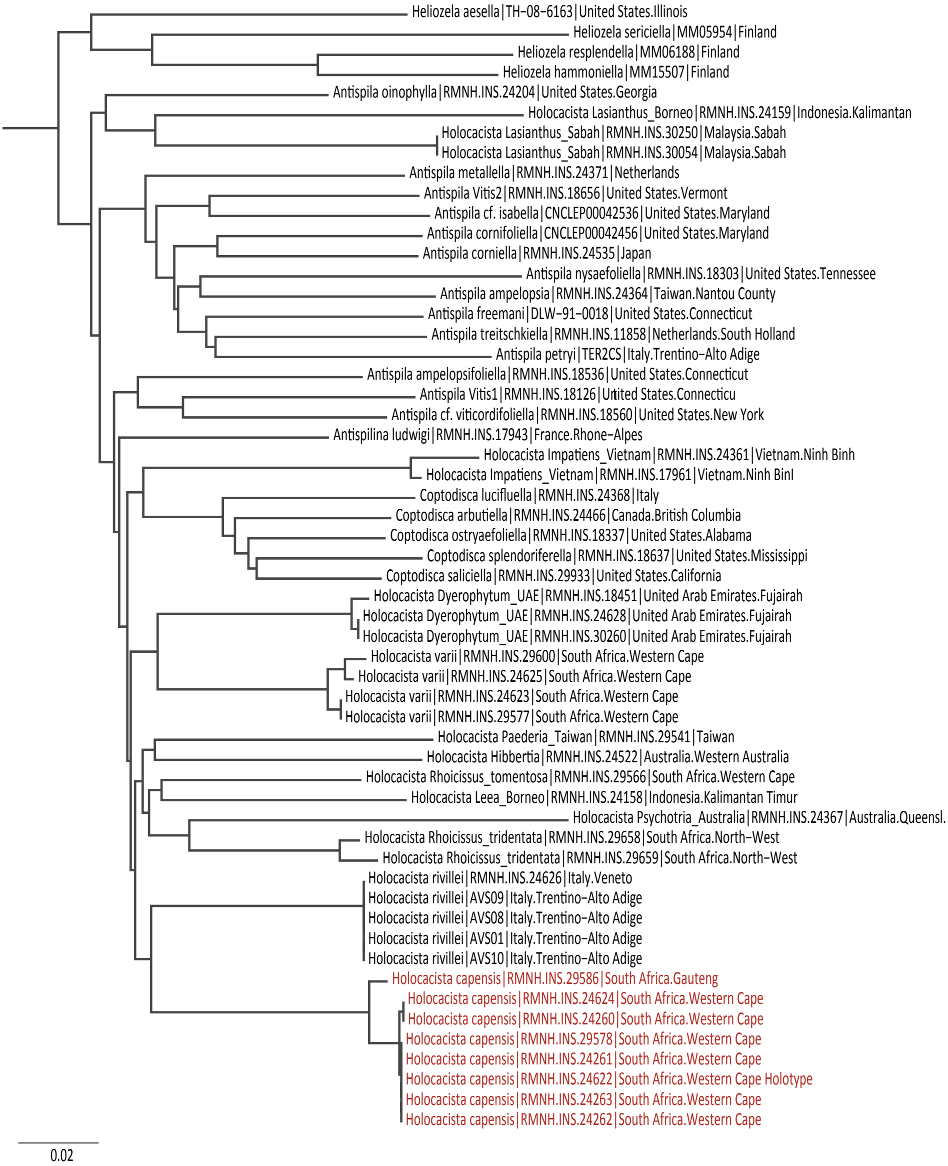


Figure 117. Neighbor Joining Tree, based on DNA barcodes of *Holocacista* species and other Heliozelidae.

or cocoon shields earlier on grape vines, but were then of the opinion that these were either discarded scale insect exuviae or plant debris.

At present, the moth is widespread in the grape vine regions of the Western Cape, but mainly restricted to that region south of the Cape Fold Mountain range, although one record is known from Robertson, north of that range. In the northern part of South Africa, it occurs in high population numbers in the table grape region at Brits, east of Pretoria. Records also exist of its occurrence in the Vaalhartz region (Northern Cape) and in Oudtshoorn (Western Cape).

The effect of the leafmines on the grape vine itself appears to be limited. At the height of the moth season, most table grape vines are under irrigation and lost leaf growth is quickly replaced with new foliage throughout the growing season. Collateral damage by the larvae, when at high population numbers, may be more serious, especially when larvae descend from the vine canopy to form a dense curtain of suspended larvae. This not only harasses the harvesters themselves and contaminates the grape bunches, but in some cases, the radiators of tractors collecting the grape bunches became completely blocked by this curtain (in one case, this occurred in a distance of less than 200 m), requiring constant removal of the larvae.

Discussion

Taxonomy and identification

As in previous studies on unexpected infestations of grapevine and walnuts by Heliozelidae (van Nieukerken et al. 2012b; Bernardo et al. 2015), the lack of a taxonomic framework of this family made the identification difficult, and required a detailed taxonomic study. For Africa, the situation was in fact worse than in the cited examples from North-America, where at least an extensive literature on leafminers exists. Here only a single species had been described in recent years according to modern taxonomic methodology, with details on genitalia (Mey 2011); in addition to two very short – now useless – descriptions nearly a century old. Only by detailed study of material borrowed from the collections in Pretoria could we reach the conclusion that our species was unnamed and belongs to the genus *Holocacista*, which was hitherto only known from a single Mediterranean species. Thanks to the long lasting efforts of the former curator of the Transvaal Museum, Lajos Vári, who reared and collected leafminers from many different species throughout southern Africa between 1950 and 1990, there was a firm basis available for this study in the collections in Pretoria, even though nothing on this particular group had been published previously. We cannot stress enough the importance of maintaining and enlarging such collections for studies such as the present one.

While redescribing the genus *Holocacista*, we could also assign various other South African, Asian and Australian species to the genus. This further showed that also in those areas the family Heliozelidae has been poorly studied.

Unfortunately, the failure of amplifying DNA from the South African collection specimens has prevented a comparative usage of DNA barcodes. Our research has also shown that still many unnamed species exist, and additional revisionary taxonomic work on this fauna and on other leafminers, including fieldwork, is highly important, where the possibility exists that this and other economic important plants could become infested.

Origin and host shift of the grapevine miner

In our study we were only able to associate the new species with a single population feeding on native *Rhoicissus digitata*. Up to now we do not have any match yet of DNA barcodes of native *Rhoicissus* feeders, of which we sequenced two possible (new) species. Interestingly, the only *Rhoicissus*-feeding population of *Holocacista capensis* has been found in the Western Cape, from where also the majority of the grapevine miner records originate. This could be an indication that the host shift from *Rhoicissus* to *Vitis* may have taken place in the Western Cape. We assume that in the past the natural vegetation with *Rhoicissus* was much more widespread and more often close to vineyards, making such a shift far easier. However, this would mean that the shift may have taken place more than a century ago or even longer. Grapevine has been grown in the Western Cape since the Dutch settled at the Cape in the 17th century (http://en.wikipedia.org/wiki/History_of_South_African_wine). If that is the case, the miner has apparently been able to occur in low densities without being spotted before Lajos Vári recorded it first from his own garden in Pretoria in 1950 (this study). The occurrence in Gauteng and the Northern Cape could in that scenario be explained by a later infestation from the Western Cape. The Paarl-Wellington region is the major cultivation area of vine nursery stock in South Africa. Major cultivars are propagated and dispatched in large quantities to commercial farms and nurseries throughout the country. Rootstock in the form of hardwood cuttings, harvested during late autumn and winter, is obtained from a variety of sources before being grafted with the desired cultivar. This may explain the infestation of other areas with the moth. Visits to home garden nurseries in the Western Cape detected many grape vines being infested with the leafminer.

The 1.4% barcode difference between the single sequenced Gauteng specimen and the Paarl specimens could be an indication for a genetic variation between the Gauteng and Western Cape populations, although the genetic variation in a single population of *H. varii* that we observed is in fact larger. Still, genetic variation could have been caused by repeated host shifts from *Rhoicissus* to *Vitis* from genetically different populations. The fact that we easily could rear offspring of *Vitis* reared adults onto *Rhoicissus digitata* also supports this hypothesis. This would mean that the barcode variation represents the original variation of this species on its native hosts. This is not so unlikely, since several of the Vitaceae-feeding Heliozelidae appear to have wider host ranges than a single genus, and may occur on e.g., both *Vitis* and *Parthenocissus*, such as *Antispila oinophylla* (van Nieukerken et al. 2012b); whereas in that paper we reported this double host association only from Italy, it has since also been observed in North America (J.F. Landry, personal communication), or sharing *Vitis* and *Ampelopsis* in *Antispila ampelopsia* Kuroko (Kuroko 1961). In Japan a comparative shift from native to cultivated hosts also occurred, but then within the genus *Vitis*: *Antispila uenoi* Kuroko shifted from native *Vitis coignetiae* Pulliat ex Planch. to the cultivated North American *V. labrusca* L. and became a pest (Kuroko 1987; Ueno et al. 1987). However, within a rather uniform genus such as *Vitis*, such a shift is hardly surprising, since most species share leaf structure and chemistry, and usually also share the same herbivores. It seems that a shift from *Rhoicissus* to *Vitis* would require more adaptation; whereas most *Rhoicissus* are evergreen, *Vitis* is deciduous, and in South Africa its leaves fall in May. Moths that emerge late will not be able to find an oviposition place and will perish. Our observations during the winter seasons of 2012–2013 show that moths only start emerging from early September onwards in synchrony with the appearance of grapevine foliage. It is possible that the life history of the native moths feeding on *Rhoicissus* in the Western Cape was already synchronised with the cooler winter climate, and therefore emergence of moths was rare in the winter. Another indication for this could be that the closely related *Holocacista* species in the Highveld of Gauteng also hibernate in their cocoons during the cold winter months. However, differences in leaf texture between *Rhoicissus* and *Vitis* may require further adaptation, although it is possibly easier for a species that feeds on tougher leaves to adapt to softer leaves than vice versa.

Another case of host shift by a heliozelid is the recent infestation of walnut in Italian orchards by the North American *Coptodisca lucifluella* (Bernardo et al. 2015). It seems that this species shifted host from its original American host, the genus *Carya*, to *Juglans*, possibly after its introduction.

Where the origin of the grapes planted in South Africa is almost universally European (http://en.wikipedia.org/wiki/History_of_South_African_wine), it is not very likely that *H. capensis* originated somewhere other than in South Africa. Its close relationship to several other South African Vitaceae miners makes it very plausible that *H. capensis* indeed is a native South African insect. For tracing the origin of the host shift, a larger scale inventory of South African Vitaceae miners with detailed DNA analysis is required.

There are only few other insects known that feed both on *Rhoicissus* and *Vitis*, but at least two hawk moths (Sphingidae) are reported from both genera: *Hippotion celerio* (Linnaeus, 1758), that is more polyphagous (in the Western Cape during the winter months its larvae feed on *Zantedeschia aethiopica* (L.) Spreng.), and *Theretra capensis* (Linnaeus, 1764), that seems to be specialised on Vitaceae (Kroon 1999). However, external-feeding large caterpillars, such as these hawk moths, require different adaptations compared to leafminers. On *Rhoicissus* we also noted leafmines belonging to the genus *Phyllocnistis* Zeller, 1848 (Gracillariidae) that may belong to an undescribed species.

Infestation of vineyards and table grape plantations

It is apparent that *Holocacista capensis*, as shown by the presence of larval and pupal parasites, must have been present for some time in the vineyards in this region. Only when moth densities reached alarmingly high numbers, was identification called for. Although damage by the larvae to the grapevine foliage itself is limited, the reported collateral damage by the larvae can be serious. Also, contamination of grapes with cocoons is cumbersome, since they need to be removed manually before the grapes can be sold or exported.

A first step needed to control the insects is assessing its density, by measuring the number of mines per leaf, infested leaves per vine, and particularly by setting out pheromone traps (Wang et al. 2015). This should be organised in selected vineyards in the vine growing regions of the greater Western Cape. Currently, already some of this research is planned.

Control of the moth itself appears to be difficult. It appears that all cultivars of table grapes, especially those grown under a dense canopy cover, are attacked; wine grape cultivars are not that seriously affected and the mines are of little concern to the wine producer, but the moth can maintain populations in the vineyards that could infest table grape plantations. Moth densities are highest at the time of table grape harvest, with the result that no chemical control is feasible. Larvae are well protected within the leaf itself, ruling out the use of a systemic insecticide at the time when grape berries are developing and ripening. Although parasitoids are present, their numbers are low and only reach higher numbers near the end of the grape season. Ants could be efficient predators, but their numbers are controlled by the vine farmers. In two cases, numbers of moths were drastically reduced when insecticides were applied for the control of some other pests during October-November, the start of the vine growing season; investigations on this aspect are at present being carried out. Another measure that resulted in much lower densities was manual removal of cocoons from trellises and trunks during winter, but this is a time consuming method. Further research is also needed to see if mating disruption with pheromones is a serious possibility.

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References

Alma A (1995) Bio-ethologic and epidemiologic researches on *Holocacista rivillei* Stainton (Lepidoptera Heliozelidae). Ricerche bio-etologiche ed epidemiologiche su *Holocacista rivillei* Stainton (Lepidoptera Heliozelidae). Redia 78: 373–378.

Bernardo U, Nieukerken EJ van, Sasso R, Gebiola M, Gualtieri L, Viggiani G (2015) Characterization, distribution, biology and impact on Italian walnut orchards of the invasive North-American leafminer *Coptodisca lucifluella* (Lepidoptera: Heliozelidae). Bulletin of Entomological Research 105: 1–15. doi: 10.1017/S0007485314000947

Camporese P, Marchesini E (1991) Nota preliminare sulla minatrice delle foglie di vite *Holocacista rivillei* (Stainton) (Lepidoptera: Incurvariidae Heliozelinae) nel Veneto. Atti del Congresso Nazionale Italiano di Entomologia 16: 663–668.

Cean M (2014) *Holocacista rivillei* (Stainton, 1855) (Lepidoptera Heliozidae) – a leafminer species recorded on *Vitis vinifera* L. from southern Romania Scientific Papers Series A Agronomy 57: 385–388. http://agronomyjournal.usamv.ro/pdf/2014/art69.pdf

Clarke JFG (1955) Catalogue of the types specimens of Microlepidoptera in the British Museum (Natural History) described by Edward Meyrick, volume 1. Trustees of the British Museum (Natural History), London, 1: vii, 332 pp. http://www.biodiversitylibrary.org/bibliography/68439

De Prins J, De Prins W (2014) Afromoths, online database of Afrotropical moth species (Lepidoptera). http://www.afromoths.net/

Doorenweerd C, Nieukerken EJ van, Menken SBJ (2015) A global phylogeny of leafmining *Ectoedemia* moths (Lepidoptera: Nepticulidae): exploring host plant family shifts and allopatry as drivers of speciation. PLoS ONE 10: e0119586. doi: 10.1371/journal.pone.0119586

Germishuizen G, Meyer NL (2003) Plants of southern Africa: an annotated checklist. Strelitzia 14: 1–1231. http://planet.botany.uwc.ac.za/NISL/Biodiversity/Attachments/Plants%20of%20SA.pdf

Godeheu de Riville (1750) Histoire d'une chenille mineuse des feuilles de vigne extraite d'une lettre écrite de Malte à M. de Reaumur. Mémoires de Mathématique et de Physique présentés a l'Académie Royale des Sciences 1: 177–189. http://biodiversitylibrary.org/page/28958314

Grandi G (1931) Morfologia ed etologia comparata di insetti a regime specializzato. I. La morfologia comparata di alcuni stati larvali di 20 Microlepidotteri minatori. Bollettino del Laboratorio di Entomologia del Reale Istituto Superiore Agrario di Bologna 4: 223–336.

International Commission on Zoological Nomenclature (1999) International Code of Zoological Nomenclature. Fourth edition. Adopted by the International Union of Biological Sciences. The International Trust for Zoological Nomenclature, London, xxix + 306 pp.

Kaila L (2011) Elachistine Moths of Australia (Lepidoptera: Gelechioidea: Elachistidae). CSIRO, Collingwood, Monographs on Australian Lepidoptera Series 11: 456 pp.

Karsholt O, Kristensen NP (2003) *Plesiozela*, gen. n. from temperate South America: apparent sister-group of the previously known Heliozelidae (Lepidoptera: Incurvarioidea: Heliozelidae). Invertebrate Systematics 17: 39–46. doi: 10.1071/IS02047

Knölke S, Erlacher S, Hausmann A, Miller MA, Segerer AH (2005) A procedure for combined genitalia dissection and DNA extraction in Lepidoptera. Insect Systematics and Evolution 35: 401–409. doi: 10.1163/187631204788912463

Kroon D (2011) Lajos Vári (27 September 1916 – 21 April 2011): obituary. African Entomology 19: 741–743. doi: 10.4001/003.019.0315

Kroon DM (1999) Lepidoptera of Southern Africa: Host-Plants & other associations. A Catalogue. Lepidopterists' Society of Africa, x, 159 pp.

Kuroko H (1961) The genus *Antispila* from Japan, with descriptions of seven new species (Lepidoptera, Heliozelidae). Esakia 3: 11–24, pls 14–19. http://hdl.handle.net/2324/2347

Kuroko H (1987) Three new species of the genus *Antispila* (Lepidoptera: Heliozelidae) from Japan. Tinea 12: 109–117.

Lee B-W, Hirowatari T (2013) Heliozelidae. In: Hirowatari T, Nasu Y, Sakamaki Y, Kishida Y (Eds) Nihon-san garui hyojun zukan. The standard of moths in Japan vol. 3. Gakken Kyoiku Shuppan, Tokyo, 99–102, pl. 103–106.

Lee S, Brown RL (2006) A new method for preparing slide mounts of whole bodies of Microlepidoptera. Journal of Asia-Pacific Entomology 9: 249–253. doi: 10.1016/S1226-8615(08)60299-X

Marchesini E, Posenato G, Sancassani GP (2000) Parassitoidi indigeni della minatrice americana della vite. L'Informatore Agrario 10: 93–96.

Marchi G (1956) Ricerche su un Lepidottero Eliozelide, l' "*Holocacista rivillei*" Staint., minatore delle foglie della Vite. Bollettino del Laboratorio di Entomologia del Reale Istituto Superiore Agrario di Bologna 22: 247–276.

McGiffen KC, Neunzig HH (1985) A guide to the identification and biology of insects feeding on muscadine and bunch grapes in North Carolina. North Carolina Agricultural Research Service, North Carolina State University, Raleigh, North Carolina, iv, 93 pp.

Mey W (2011) Basic pattern of Lepidoptera diversity in Southwestern Africa. Wissenschaftlicher Verlag – Peks, Schwanfeld, Esperiana Memoir 6: 1–316, 340 pls.

Meyrick E (1918) Descriptions of South African Micro-Lepidoptera. Annals of the Transvaal Museum 6: 7–59. http://content.ajarchive.org/cdm4/doc_viewer.php?CISOROOT=/00411752&CISOPTR=794&CISOBOX=0

Meyrick E (1921) Descriptions of South African Micro-Lepidoptera. Annals of the Transvaal Museum 8: 49–148. http://content.ajarchive.org/cdm4/document.php?CISOROOT=/00411752&CISOPTR=781&REC=6

Meyrick E (1926) Exotic Microlepidoptera 3: 257–288.

Meyrick E (1929) Exotic Microlepidoptera 3: 513–544.

Nielsen ES (1980) The Incurvarioid Genera of the World. Unpublished thesis, University of Copenhagen, Copenhagen, 318 pp.

Nieukerken EJ van, Doorenweerd C, Stokvis FR, Groenenberg DSJ (2012a) DNA barcoding of the leaf-mining moth subgenus *Ectoedemia* s. str. (Lepidoptera: Nepticulidae) with COI and EF1- α: two are better than one in recognising cryptic species. Contributions to Zoology 81: 1–24. http://www.contributionstozoology.nl/vol81/nr01/a01

Nieukerken EJ van, Wagner DL, Baldessari M, Mazzon L, Angeli G, Girolami V, Duso C, Doorenweerd C (2012b) *Antispila oinophylla* new species (Lepidoptera, Heliozelidae), a new North American grapevine leafminer invading Italian vineyards: taxonomy, DNA barcodes and life cycle. ZooKeys 170: 29–77. doi: 10.3897/zookeys.170.2617

Nieukerken EJ van, Doorenweerd C, Vijverberg R (2013) Heliozelidae phylogeny and hostplant relationships. In: Programme and Abstracts XVIII European Congress of Lepidopterology. Pensoft Publishers, Blagoevgrad, 59–60.

Palgrave KC, Palgrave MC (2002) Trees of Southern Africa, new edition. Struik, Cape Town, 1212 pp.

Paulian R, Viette P (1955) Essai d’un catalogue biologique des Lépidoptères Hétérocères de Tananarive. Mémoires de l’Institut Scientifique de MadagascarTananarive, Série E, Entomologie 6: 141–281.

Ratnasingham S, Hebert PDN (2007) BOLD: The Barcode of Life Data System (www.barcodinglife.org). Molecular Ecology Notes 7: 355–364. doi: 10.1111/j.1471-8286.2007.01678.x

Razowski J, Krüger M (2007) An illustrated catalogue of the type specimens of Tortricidae in the Transvaal Museum, Pretoria(Lepidoptera: Tortricidae) (parte A). SHILAP Revista de Lepidopterologia 35: 103–157. http://www.redalyc.org/pdf/455/45513802.pdf

Stainton HT (1855) On some of the difficulties of entomological students, as exemplified by recent experience in the genus *Elachista*. Transactions of the Entomological Society of London 3: 84–89. doi: 10.1111/j.1365-2311.1855.tb02664.x

The Plant List (2013) The Plant List, a working list of all known plant species. Version 1.1. Royal Botanic Gardens, Kew & Missouri Botanical Garden. http://www.theplantlist.org/

Ueno W, Hayasaka T, Endo S, Shibahasi T (1987) Ecology and control of *Antispila* sp. (Lepidoptera: Heliozelidae) infesting grape leaves. Bulletin of the Yamagata Horticultural Experimental Station 6: 1–18.

Vári L (1955) South African Lepidoptera 1. Descriptions of new leafmining Tineina. Annals of the Transvaal Museum 22: 331–351.

Vári L (1961) South African Lepidoptera, 1. Lithocolletidae. Transvaal Museum Memoir 12, i-xix, 1–238, plates 231–112.

Vári L (1963) South African Lepidoptera, 3. Descriptions of new Stigmellidae. Koedoe 6: 66–75. doi: 10.4102/koedoe.v6i1.813

Vári L, Kroon D (1986) Southern African Lepidoptera. A series of cross-referenced indices. Lepidopterists Society of Southern Africa & The Transvaal Museum, Pretoria, i-x, 198 pp.

Vári L, Kroon DM, Krüger M (2002) Classification and checklist of the species of Lepidoptera recorded in Southern Africa. Simple Solutions, Chatswood, Australia, xxi, 384 pp.

Walsingham L (1909) Rediscovered Micro-Lepidopteron from the south of France. Transactions of the Entomological Society of London 1909: xxix. http://biodiversitylibrary.org/page/14686330

Wang H-L, Geertsema H, Nieukerken EJ van, Löfstedt C (2015) Identification of the female-produced sex pheromone of the leafminer *Holocacista capensis* (Lepidoptera: Heliozelidae) infesting grapevine in South Africa. Journal of Chemical Ecology. [submitted]

Appendix A

Southern African Heliozelidae

The following tentative checklist and short diagnoses are based on the collections in the Ditsong Museum in Pretoria, mostly gathered during extensive rearing of leafmines by Lajos Vári and a few other records, including our own. For most Vitaceae feeders some genitalia have been dissected, and for all taxa adults and leafmines have been examined. In all, 12 species are recognized, but differences in mines and variation in genitalia suggest there are more. Additionally, even more may be expected in parts of southern Africa where Vári rarely collected. A revision of this group should preferably include collecting of new material and molecular analyses.

Genus *Heliozela* Herrich-Schäffer, 1853

Heliozela argyrozona (Meyrick, 1918), comb. n.

Antispila argyrozona Meyrick, 1918: 35. Holotype ♂: South Africa, [KwaZulu Natal], Eshowe, 4.i.[19]16, A.J.T. Janse; "29 51"; Type No. 108 (TMSA) [examined].

Wingspan ca. 4.0–4.5 mm. Uniformly dark bronze, male with a white medial costal spot, female with a medial fascia and usually a small costal spot at 1/3. A typical *Heliozela*, with distinct epiphysis and complex venation. Assignment of the reared series to *H. argyrozona* is tentative and based on external resemblance of the females with the holotype; no genitalia have been examined.

Hostplant. *Syzygium cordatum* Hochst. ex Krauss (Myrtaceae). Mine a sinuous gallery on leaf upperside, gradually becoming wider.

Distribution. Kwazulu-Natal, Limpopo.

Material examined. South Africa: 34 adults, mines on 10 leaves, Limpopo, Louis Trichardt, 6–8.v.1953, Ac. no. 740, 743, leafmines on *Syzygium cordatum,* emerged 2.vi.–4.ix.1953, L. Vári, Genitalia slide TM3825; 1 adult, KwaZulu-Natal, Umdoni park, 15.v.1974, Ac. no. 3286, leafmines on *Syzygium,* emerged 17.vii.1974, L. Vári.

Heliozela sp. 2

Resembles *H. argyrozona*, but has two fasciae.

Hostplant. unknown.

Distribution. Limpopo.

Material examined. South Africa: 1 ♀, Limpopo, Woodbush, 14–16.ix.1960, van Son & Vári.

Genus *Antispila* Hübner, 1825

Antispila sp.

This is the largest South African heliozelid with a wingspan of 7–7.5 mm and large yellowish fascia and spots (Fig. 17). The antennae are distinctly ringed and have 26 segments. The male has a conspicuous large patch of yellow and black androconial scales on the forewing and hindwing underside.

Hostplant. *Rhoicissus rhomboidea* (Vitaceae). Mines are conspicuous large blotches and have a large cut out of about 6 mm long, which separates them easily from the *Holocacista* mines.

Distribution. Eastern Cape, Limpopo. Only three specimens and three herbarium sheets in TMSA.

Material examined. South Africa: 1 moth, 1 sheet with mines, Eastern Cape, Grahamstown, 2.xii.1954, Ac. no. 1471, leafmines on *Cissus rhomboideus*, emerged 30.xii.1954, L. Vári; 1♂, 1♀, 2 sheets with mines, Limpopo, Louis Trichardt, 2.v.1953, Ac. no. 674, leafmines on *Cissus rhomboideus*, emerged 14.vii–30.viii.1953, L. Vári, Genitalia slide ♂ EvN4379.

Genus *Holocacista* Walsingham & Durrant, 1909

Holocacista capensis van Nieukerken & Geertsema, sp. n.

See above.

Holocacista salutans (Meyrick, 1921), comb. n.

See above.

Holocacista varii (Mey, 2011), comb. n.

See above.

Holocacista sp. *Rhoicissus_tridentata*

Wingspan ca. 4.0–4.8 mm. Differs from *H. capensis* and *H. salutans* by smoother bronze scaling, costal and tornal spots about same size, antennae hardly ringed, fringe line not pronounced. In male genitalia very long phallus, without spines, but a folded sleeve (Fig. 101).

Hostplant. *Rhoicissus tridentata* subsp. *cuneifolia* (Vitaceae). Possibly also on *R. rhomboidea*, and *R. tomentosa*, but this needs to be verified. Mines characterised by long initial linear gallery filled with frass (Fig. 84). Larvae from October to June, those from May and June hibernate and moths emerge in September and October.

Distribution. Gauteng, KwaZulu-Natal, North West, Zimbabwe: Harare.

Remarks. The majority of specimens reared from *R. tridentata* leafmines, as listed below are probably this species as characterised by the described externals, phallus and leafmine, but at least *H. salutans*, or a closely related species and *H. Rhoicissus_PundaMilia*, also occur on this host and there may be more hidden in this material. Vári used at least three manuscript names in his notebooks for specimens from this host, indicating he also considered not all to belong to one species: "*Antispila denticola*," "*A. cuneifoliella*" and "*A. hartwigi*". We associate tentatively the two DNA barcodes with this species, but this requires confirmation.

Material examined. South Africa, Gauteng: 7 adults, 2 sheets with mines, Pretoria, Wonderboom Zuid, 1.iv.1950, Ac. no. 298, leafmines on *Rhoicissus tridentata*, emerged 12.x–30.xi.1950, L. Vári, Genitalia slides ♂ TM6767, ♀ TM6769; 12 adults, 1 sheet with mines, ibidem, 16.xii.1950, Ac. no. 298, emerged 29.xii.1950–10.i.1951; 26 adults, 2 sheets with mines [mixed with mines of *H.* cf. *salutans*, Pretoria, Meintjeskop, 7.vi.1951, Ac. no. 339, 340, 341, leafmines on *R. tridentata*, emerged 19.ix–9.x.1951, L. Vári, Genitalia slides TM6768, TM6770, ♀ TM6829, ♂ TM10347; 17 adults, ibidem, 27.v.1953, Ac. no. 833, emerged 27.ix–6.xi.1953; 1♂, 1♀, Suikerbosrand, 21–24.x.1975, Ac. no 3472, leafmines on *Rhoicissus* sp., emerged 24.x–10.xi.1975, M.J. Scoble. **KwaZulu-Natal**: 4 adults, 1 envelope with leafmines, Mt. Edgecombe, 31.iii.1954, Ac. no. 1225, leafmines on *R. tridentata*, emerged 21–26.iv.1954, L. Vári, Genitalia slide ♂ EvN4380. **North-West**: 2 larvae (RMNH.INS.29658, 29659), Kgaswane Nature Reserve, Rustenburg, 27.i.2013, EvN2013901, leafmines on *R. tridentata*, M. Stiller. **Zimbabwe**, **Harare**: 1♂, Mt. Selinda, 8.iv.1956, Ac. no. 1784, leafmines on *R. tridentata*, emerged 29.iv.1956, L. Vári, Genitalia slide EvN4385.

Holocacista sp. *Rhoicissus_tomentosa*

We have no adults that we can associate with certainty with the distinctive mine of this species. We barcoded two larvae (RMNH.INS.29566, 30313). The samples with leafmines from the Vári collection often show several mine types, apart from this species also including *H. salutans* and possibly the previous species or others. Further work is needed to differentiate these taxa.

Hostplant. *Rhoicissus tomentosa* (Vitaceae). Mine a gallery, first filled with frass, later an elongate gallery-like blotch with central clumped frass (Fig. 83).

Distribution. Limpopo, Western Cape, Zimbabwe: Harare.

Material examined. South Africa, Limpopo: ??? adults, 2 sheets with mines (mixed), Louis Trichardt, 17.iii.1964, Ac. no. 2694, leafmines on *Rhoicissus tomentosa*, adults emerged 7–10.iv.1964, L. Vári. **Western Cape**: 1 larva, RMNH.INS.29566, leafmines, Swellendam E, Zuurbraak, 17.i.2013, EvN2013007, leafmines on *R. tomentosa*, E.J. van Nieukerken & H. Geertsema; 1 larva, RMNH.INS.30313, leafmines, ibidem, 16.vi.2014, EvN2014009, H. Geertsema. **Zimbabwe, Harare**: 1 adult?, 1 sheet with mines, Mt. Selinda, 8.iv.1956, Ac. no. 1783, leafmines on *R. tomentosa*, emerged 4.v.1956, L. Vári. **Zimbabwe, Masvingo**: 1 sheet with mines, Vumba, Mareh, 7.iii.1964, Ac. no. 2649, L. Vári.

Holocacista sp. *Rhoicissus*_PundaMilia

Wingspan 3.0–4.0 mm, very small species. Externally inseparable from *H. salutans*. Male genitalia characterised by very different, recurved phallus appendage (Fig. 102).

Hostplant. *Rhoicissus digitata* and *R. tridentata* subsp. *cuneifolia* (Vitaceae). Mines a narrow gallery with medial linear frass, gradually enlarging into a wide gallery, rather different from those of *H. capensis* and *salutans* on *R. digitata*.

Distribution. Gauteng, Limpopo.

Material examined. South Africa, Gauteng: 1♂, Pretoria, Meintjeskop, 7.vi.1951, Ac. no. 339, leafmines on *Rhoicissus tridentata*, emerged 8.x.1951, L. Vári, Genitalia slide TM6828. **Limpopo**: 2 adults, Punda Milia, K.N.P. Survey [Kruger National Park Survey], 23.xi.1961, Ac. no. 2362, leafmines on *Rhoicissus digitata*, emerged 11.xii.1961, L. Vári; 5 adults, 1 sheet with 10 mines, ibidem, 4.xii.1964, Ac. no. 2712, leafmines on *R. digitata*, emerged 21.xii.1964, Genitalia slide EvN4382.

Holocacista sp. *Cissus_integrifolia*

Wingspan 3.5–4.0 mm, small species. Externally similar to *H.* sp. *Rhoicissus_tridentata*, with bronze wings, and antennae not ringed. Male genitalia characterised by the phallus appendage that is not curved backwards, but sinuous (Fig. 103).

Hostplant. *Cissus integrifolia* (Vitaceae). Mines very compact, start with spiral gallery, later becoming an elongate blotch with frass in zigzag pattern.

Distribution. Zimbabwe: Masvingo.

Material examined. Zimbabwe, Masvingo: 11 adults, 1 sheet with 15 mines, Lundi, Lundi river, 4.iii.1964, Ac. no. 2646, leafmines on *Cissus integrifolia*, emerged 21–25.iii.1964, L. Vári, Genitalia slide ♂ EvN4387.

Holocacista sp. *Lannea*_SA

Wingspan 4–5 mm. Wings bronze fuscous with shining fascia and costal and tornal spots, rather similar to *H.* sp. *Rhoicissus_tridentata*. Antennae not ringed. Genitalia not examined.

Hostplant. *Lannea discolor*, *Lannea* sp. (Anacardiaceae). Mine very compact, somewhat resembling those of *H. capensis*. Initial gallery with zigzag turns, closely to each other, later completely enclosed in blotch.

Distribution. Gauteng.

Remarks. Vári gave the manuscript name "*Antispila lanneivora*".

Material examined. South Africa, Gauteng: 1♂, Pretoria, behind garden Prof. J[anse], 16.i.1951, Ac. no. 317, leafmines on *Lannea discolor*, emerged 2.ii.1951, L. Vári; 4 adults, 1 sheet with 12 mines, Pretoria, above Pierneef St., 16.i.1951, Ac. no. 618, leafmines on *L. discolor*, emerged 9–12.ii.1951, L. Vári; 5 adults, Pretoria, Magalies Mountain, 26.xii.1953, Ac. no. 1016, leafmines on *Lannea* sp., emerged 8–11.i.1951, L. Vári.

Holocacista sp. *Terminalia*_SA

Wingspan 3.0–3.7 mm, very small moths. Wings greyish or brown with narrow medial fascia. Venation extremely reduced, forewing with 4 veins only, Rs, R+M, CuA and A.

Hostplant. *Terminalia prunioides* (Combretaceae). Mine a narrow gallery, suddenly enlarging into a roundish blotch.

Distribution. Namibia: Erongo

Remarks. Placement in *Holocacista* is tentative.

Material examined. Namibia, Erongo: 2 adults, 2 leaves with 2 mines, Karabib, 20.v.1959, Ac. no. 2108, leafmines on *Terminalia prunioides*, emerged 15.vi.1959, L. Vári, Genitalia slide ♂ EvN4387.

Supplementary material 1

All material examined and used for DNA barcoding

Authors: Erik J. van Nieukerken, Henk Geertsema

Data type: Excel spreadsheet (xlsx).

Explanation note: The dataset comprises all material examined and identified to a certain extent for this study. All specimens used for the descriptions of genus and listed species are included, as are all DNA barcoded specimens, including those that were published earlier.

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REVIEW ARTICLE

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Captive breeding of pangolins: current status, problems and future prospects

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Abstract

Pangolins are unique placental mammals with eight species existing in the world, which have adapted to a highly specialized diet of ants and termites, and are of significance in the control of forest termite disaster. Besides their ecological value, pangolins are extremely important economic animals with the value as medicine and food. At present, illegal hunting and habitat destruction have drastically decreased the wild population of pangolins, pushing them to the edge of extinction. Captive breeding is an important way to protect these species, but because of pangolin's specialized behaviors and high dependence on natural ecosystem, there still exist many technical barriers to successful captive breeding programs. In this paper, based on the literatures and our practical experience, we reviewed the status and existing problems in captive breeding of pangolins, including four aspects, the naturalistic habitat, dietary husbandry, reproduction and disease control. Some recommendations are presented for effective captive breeding and protection of pangolins.

Keywords

Pangolin, captive breeding, dietary husbandry, disease, conservation

Introduction

Pangolins, also known as scaly anteaters, are eutherians, and unique placental mammals. Despite fulfilling a similar ecological niche as anteaters and armadillos of the order Xenarthra, they are taxonomically distinct. There are eight existing species of pangolins in the world, and all are the class Mammalia, order Pholidota, family Manidae, and genus *Manis*. Pangolins mainly distribute in Eastern, Southeastern and Southern Asia, as well as most of Africa. Four species of pangolins are native to Africa, including the Cape Pangolin (*Manis temmincki*), Giant Pangolin (*Manis gigantean*), Long-tailed or Black-bellied Pangolin (*Manis tetradactyla*) and Tree or African White-bellied Pangolin (*Manis tricuspis*). The other four pangolins are native to Asia, including the Chinese Pangolin (*Manis pentadactyla*), Indian Pangolin (*Manis crassicaudata*), Malayan Pangolin (*Manis javanica*) and Palawan Pangolin (*Manis culionensis*), a new species identified in 2005 (Gaubert and Antunes 2005).

As predators preying on ants and termites, pangolins have a specialized diet and perform an important ecological role in regulating insect populations. It has been estimated that an adult pangolin can consume more than 70 million insects annually, and has a significant impact on the control of forest termites (Shi and Wang 1985). Besides its ecological values, pangolins are extremely important economic animals, valued for both medicine and food. Pangolin's scales are used as a common ingredient in traditional Asian medicines; for example, the Chinese Pangolin's scales had been used as an ingredient in traditional Chinese Medicine for thousands of years, and had been recorded in several ancient books of Chinese Medicine. Generally, the pangolin's scales were thought to have the functions of promoting blood circulation, accelerating milk secretion, detumescence and apocenosis *etc*. But there is no too much progress in determining the scale's active ingredients. The scales of Indian Pangolin, Malayan Pangolin and Cape Pangolin are also used as medicine by local residents while pangolin's meat is considered as delicacy and tonic in some Chinese and Vietnamese cultures.

Because of pangolin's economic values, illegal hunting and illegal trade take place frequently. For example, approximately 24 tons and 14 tons of frozen pangolins were seized in Vietnam and Indonesia in March 2008 and July 2008, respectively (Shepherd 2009); about nine tons and ten tons of frozen pangolins were seized in China and Philippines in December 2012 and April 2013, respectively (GuangzhouDaily 2012; HuanqiuNet 2013). This massive poaching has rapidly exhausted wild pangolin population. Besides illegal hunting, habitat destructions also drastically decreases wild populations (Wu et al. 2002). All extant species of pangolin are listed in Appendix II of CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora). At the 11th meeting of the Conference of the Parties to CITES in 2000, a zero export quota was established for the Three Asian Pangolin species (Malayan Pangolin, Chinese Pangolin and Indian Pangolin), for specimens removed from the wild and traded for primarily commercial purposes. In 2007, a zero export quota was also established for the Palawan Pangolin following its recognition as a species distinct from the Malayan Pangolin. In 2007, International Union for Conservation of Nature and Natural Resources (IUCN) and Conservation International (CI) adjusted Chinese Pangolin and Malayan Pangolin from low-risk (LR) level to endangered (EN) level (Zhang et al. 2010). In addition, pangolins are also protected in their range states by domestic wildlife laws, for example, Chinese Pangolin is listed in class II national key-protected species in China (Wu et al. 2002).

With the exhaustion of wild populations, captive breeding becomes an important way to protect pangolins from extinction; however, there still exist many technical barriers for the captive breeding programs because of pangolin's specialized behavior and dependence on natural ecosystems. According to literature, over the past 150 years, more than 100 zoos or organizations have attempted to maintain pangolins. Most captive pangolins died within six months, although some were held for two to three years, a few cases lived for 12–19 years. Zoo records for pangolins in captivity from 1877 to 2001 had been reviewed by Yang (Yang et al. 2007). Currently, a range of pangolin researches and conservation projects are underway both in Asia and Africa, including investigations into illegal trade, ecology, behavior, genetics, rehabilitation, and release. The institutes working on pangolin captive breeding in the last decade were summarized in Table 1. With the accumulation of ecological studies and husbandry techniques, some institutes have made progress in captive breeding programs, and some records of pangolin births have been reported recently. For example, by solving the digestive problems, the Taipei Zoo successfully bred Chinese Pangolins in captivity (Yang et al. 2007); a newborn Malayan Pangolin was reported in the Research Base for Pangolin Domestication and Breeding from South China Normal University in 2011 (SCNU 2011). Although the newborn cases of captive pangolins are encouraging, the captive breeding of pangolins is still difficult, and there is no successful reproduction report of filial generation. More work is needed to improve the livability, growth rate and reproduction rate of the captive pangolins. In this paper, based on the existing literature and our practical experience, we reviewed the status and existing problems in captive breeding of pangolins, and some recommendations are presented for effective captive breeding and protection of pangolins.

Naturalistic habitat for captive pangolins

Pangolins occupy a variety of habitats in the wild, ranging from tropical to sub-tropical, from cleared and cultivated areas, savannah grasslands to mixed forest, broadleaf forest, secondary forest, *etc.* (Lim 2008b; Wu et al. 2004a), but they have poor adaptability to captive environments. By analyzing their wild habitat and finding the key ecological factors, pangolin's artificial habitats had been improved a lot. A naturalistic habitat can greatly reduce animal's stress from changing environments, and keep them comfortable in captivity.

Pangolins are divided into two types: terrestrial and arboreal. Most of the pangolins are terrestrial and they dig burrows or live in other animal's deserted dens for nesting and shelter. The rest of the pangolins are arboreal, living in hollow trees or on tree

Table 1. Institutes (programs) holding pangolins in captivity in the last decade.

Institutes/Programs	Species	Status
Taipei Zoo	Chinese pangolin	They improved artificial diet, and had a new-born record in captivity (Yang et al. 2007).
Research Base for Pangolin Domestication and Breeding from South China Normal University, China	Chinese pangolin, Malayan pangolin	The habitat, diet and management of captive pangolins were improved a lot, and had several new-born records in captivity (SCNU 2011).
Yunnan Wild Animals Park, China	Chinese pangolin	Successfully mated pangolins in captivity, and had a newborn record, but the cub died within three days (YunnanNet 2008).
Guangdong Provincial Wildlife Rescue Center; South China Institute of Endangered Animals, China	Malayan pangolin	Supplied pangolins with naturalistic habitats, optimized artificial diet, and kept pangolins for more than 500 days (Programs carried out by ourselves).
Night Safari, Singapore	Malayan pangolin	They can breed and raise the Malayan pangolins in captivity (Vijayan et al. 2008).
Conservation International (CI); Forestry Administration (FA), Cambodia	Malayan pangolin	CI together with the FA have recently set up the Pangolin Rehabilitation Center, to provide care and treatment to animals rescued from the wildlife trade (PangolinSG 2013).
Cuc Phuong National Park, Vietnam; Cat Tien National Park/ Carnivore & Pangolin Conservation Programme (CPCP)	Malayan pangolin	Some pangolins have kept alive over six years, and got two new-born records in captivity; one of the cubs kept alive for nine months (Visited by ourselves in November 2011).
Cu Chi Wildlife Rescue Station, Vietnam	Malayan pangolin	Some pangolins have kept alive over two years, and got two new-born records in captivity (Visited by ourselves in November 2011).
Cambodia/Angkor Centre for Conservation of Biodiversity (ACCB)	Malayan pangolin	ACCB is a pangolin program that has been running since 2004. They have the longest living Malayan pangolin ever to be hand-reared in captivity (SavePangolins 2013).
Indonesian Institute for Sciences (LIPI), Indonesia	Malayan pangolin	LIPI is undertaking research into the rescue and captive-breeding of pangolins in addition to conducting molecular studies (PangolinSG 2013).
Breeding center for pangolins, Nandan Kanan Zoological Park, India	Indian pangolin	The special program is aimed at documenting the behavioral pattern and reproductive characteristic of the Indian pangolin. They had a newborn record at 2007 (ZeeNews 2007).
Tikki Hywood Trust; Zimbabwe Parks; Wildlife Management Authority, Zimbabwe	Cape pangolin	They are working with the Cape pangolin for captive breeding and re-introduction purposes (PangolinSG 2013).
San Diego Zoo, USA	Tree pangolin	One Tree pangolin lives in the San Diego Zoo for visiting (SanDiegoZoo 2013).

branches (Chang 2004). But the distinction between them is not absolute, the terrestrial pangolins also climb tree sometimes. For example, the field study on the ecology of a single female Malayan Pangolin and her young in their natural habitat proved that hollows of large trees were associated with all of their three dens (Lim and Ng 2007). Burrows are extremely important in the terrestrial pangolin's life history because a suitable burrow could satisfy pangolin's requirements for food sources, concealment and temperature, but only few studies about pangolin's burrows were reported (Bao et al. 2013; Jiang et al. 1988; Liu and Xu 1981; Wu et al. 2004b). Chinese Pangolin mainly chooses the soil that is moist, rich and with soft layer thickness to dig burrows. Pangolins' burrows are blind holes, with no branches. The size of the entrance is generally 14.20 ± 2.79 cm for long diameter, 12.50 ± 2.83 cm for short diameter (Wu et al. 2004b). Interestingly, pangolins' burrows change with seasons and food resources (Liu and Xu 1981). In summer, the number of burrows is less than in winter, and the burrow is shallower (0.32 ± 0.11 m), including the entrance and tunnel. In winter, the burrow is deeper (1.44 ± 0.73 m). This is probably related to ant's activities under surface and pangolin's special requirements for temperature in winter (Wu et al. 2004a; Wu et al. 2004b). In addition, the slope of pangolin's burrows varies from 30° to 60°, and the openings of burrows often face the sun, probably to make the digging more easily and to maintain the cave temperature in winter. Pangolins' habitat location is understood to be linked with their key prey species in the wild (Wu et al. 2004a; Wu et al. 2003), and their burrows are always close to ant or termite nests, probably for feeding easily. So a suitable artificial cave or digging condition is believed to be a key factor in the naturalistic habitat for territorial pangolins.

Suitable temperature is another key factor for pangolins' naturalistic habitat, since pangolins have slower metabolism and little body hair to keep warm. When temperatures were 12–15 °C inside the pangolin cage, pangolins may suffer shivering and a runny nose (Heath and Vanderlip 1988). If they catch a cold, they will be susceptible to pneumonia, which often leads to death (Chang 2004). Determinations of the burrow temperature for the Chinese Pangolin in winter show that the temperature fluctuated between 17.8 °C and 21.0 °C, even the air temperature outside the burrow fluctuated dramatically (during 4.6–38.3 °C). The temperature changes outside the burrow had almost no significant influence on thermal conditions inside the burrow (Bao et al. 2013). Therefore, it was proposed by Bao that the most optimum ambient temperature for Chinese Pangolins in winter is not less than 18 °C.

Most pangolins are nocturnal creatures, occasionally active during the day, and are generally shy and timid (Wu et al. 2004a; Wu et al. 2004b). By analyzing the video records, we found that pangolins prefer to hide in their artificial caves most of the time, except for foraging, suggesting captive pangolins may be always under great stress in captivity. Stress is thought to be one of the major causes of fatality among captive pangolins, and they could be the combined results of the inappropriate environmental factors, including the new surroundings, new diets, too much human interference or handlings, *etc*. Hence, less disturbance, better concealment and reducing pangolin's stress as much as possible in captive may be other key factors for the naturalistic habitat, and we believe that appropriate burrows or digging conditions in the naturalistic habitat may also be helpful in keeping concealment.

Dietary husbandry of pangolins

In addition to a suitable accommodation, artificial diet is another critical limiting factor for captive pangolins. Pangolins have adapted to a highly specialized diet of ants and termites making it difficult to replace their natural food completely with artificial food.

Field studies show that except for ants and termites, pangolin's diet also includes ant larvae, bees (pupas), flies, worms, crickets, and some of other insect larvae, and sometimes sand and grass will be swallowed in the intake process. A pangolin of three kilogram can consume up to 300–400 g of termites per feeding (Coulson 1989; Lim 2008a). Different pangolin species have differences in their diet compositions. Chinese Pangolin's food includes 15 species, including nine species of termites and six species of ants (Liu and Xu 1981; Shi and Wang 1985; Wu et al. 2005). Cape Pangolin's food contains more species, including 15 species of ants and five species of termites (Coulson 1989; Jacobsen et al. 1991; Richer et al. 1997; Swart et al. 1999; Sweeney 1956). Diet composition of pangolins is particularly relevant with different latitudes. At the same time, diet composition is also associated with seasonal change. In summer, ants are usually found on ground while termites hide in subsurface tunnels, so ants are the main food source. In winter, ants move into underground nests because of the low temperature, pangolins prefer to choose termites nest for its greater biomass than the ants'. The nutritional components of the ants and termites preyed by pangolins in the wild were analyzed, and the results indicated that the component ratio differs significantly between different ants or termite species. For example, the crude protein, fat, and ash content in three ants species (*Dolichoderus affinis*, *Crematogaster macaoensis*, *Oecophylla smaragdina*) preyed by Chinese Pangolins ranged from 32.65% to 66.85%, 10.85% to 27.26% and 1.91% to 4.81%, respectively (Li et al. 2010). So it is believed that the nutritional differences among their prey could be guidance for pangolins' food choice. It is interesting that some ants are unacceptable to pangolins, for example, Chinese Pangolin do not like *Paratrechina bourbonica* and *Odontotermes zunyiensis*. An explanation is that except the nutrient components, palatability and safety may also be considered by pangolins.

According to their natural food compositions, a number of artificial diets for captive pangolins had been developed, ingredients including eggs, meat (minced beef, horse meat, fish), milk, milk powders, canned feline diet, orchid leaves, commercial chows, psyllium seeds, carrots, yeasts, multivitamins, and insects *etc.* (Heath and Vanderlip 1988; Tenaza and Schultz 1977; Wilson 1994; Yang et al. 2007). Wu et al. reported that pangolins enjoy high protein, high fat, high calorie food, because of their strong digestion and absorption in their small intestine (Wu et al. 1999). Ke et al. (1999) found that the epidermis of ants have chitin which is suitable for the pangolin's digestion characteristics. Vijayan et al. believed that Vitamin K is pivotal in treatment of fecal occult blood of pangolins (Vijayan et al. 2008). It is worth mentioning that the Taipei Zoo had made lots of improvements in Chinese Pangolin's diet by summarizing the previous experiences, and got satisfactory results. The digestive disorders are common diseases for pangolins feeding with artificial food, and the animal's feces

Table 2. Some diet formulas fed to pangolins in captivity.

Species	Formulas and remarks
Chinese pangolin	Formula 1: Horsemeat (150 g), milk (180 ml), egg yolk (1), cooked cereal (5 g), milk powder (5 g), calcium powder (1 g), vitamin complex (0.2 ml). Feeding after grinding, mixing, heating. Female pangolin gave birth to a cub. The baby was weaned after 89 days. Both of them survived more than six months (Masui 1967).
	Formula 2: Canned feline diet (2 tin), milk powder (2 tablespoons), flaxseed Meal (2 tablespoons), egg yolk (2). Total feeding quantity of two pairs of pangolin a day. Both of the two female have gave birth, one cub each. A male pangolin survived for 212 days, others more than 460 days (Heath and Vanderlip 1988).
	Formula 3: Bee larvae (100 g), egg yolks (10 g), apple lump (65 g), meal worm larvae (45 g), yeast powder (2.7 g), coconut powder (1.4 g), calcium carbonate (0.9 g), added powdered supplement (1.5 g), vitamin supplements (5 ml), soil (5 g). According to previous formulas, after improvements, the Taipei Zoo developed this formula. Except improved the food intake and digestive disorders, they also got a newborn record in captivity. (Yang et al. 2007).
Malayan pangolin	Formula1: Egg (hard boiled) (2 tablespoons), multi-vitamin liquid (2 tablespoons), horse meat (120 g), water (350 ml), mealworm (150 g), insectivore pellets (80 g), salmon Oil (1 pump), powdered termite mound (4 tablespoons). mixed into a paste, feeding at night (Vijayan et al. 2008).
Indian pangolin	Formula 1: Warm water (1 cup), ant eggs (1/2 cup). There are three pangolins, each had survived for 2, 4, 30 months respectively (Crandall 1964).
	Formula 2: Dry dog food (400 g), horsemeat (200 g), biolac (1/2 tin), raw eggs (2), multiple vitamins (5 drops). A female survived for more than one years, has produced a cub, which only survived for three days (Ogilvie and Bridgwater 1967).
Cape pangolin	Formula1: Minced meat (1/2 pound), maize paste (1/2 pound), raw eggs (2), milk (2 pint), termites (2 pound). Stir the food without termites, and feeding with termites at 11 am and feeding feed at eight pm. The first pair survived for 28 months, and gave birth to one cub. The cub survived for ten months; The other pair survived for 38 months with one cub born. (van Ee 1966).
Giant pangolin	Formula 1: Chopped bovine heart meat (2 cup), cooked cereal milk powder (2 cup). Feeding in the dusk, add raw egg and wheat germ, sometimes. One survived for four years, the other two survived for two years (Crandall 1964).
Tree pangolin	Formula1: Minced beef. Without water, adding vitamin, mixing into wetting powder. A female pangolin lived for two years, gave birth to a cub which lived for seven months (Menzies 1963; 1966).

are always fluid. By improving the diet ingredients, the animals' feces turned from yellow-brown to dark brown and assumed a conical shape. In addition to solving the digestion problems, the diet also significantly improved the survival rate, and they have got a newborn record of Chinese Pangolin in captivity. They also suggested that a certain proportion of the chitin may be the key to pangolin's artificial diet, this inference agreed with Ke's study (Ke et al. 1999; Yang et al. 2007), but more studies are needed to further prove it.

Some recipes for captive pangolins were summarized in Table 2, and most of them had been proved effective; they could be good references in pangolin husbandry practice. However, these recipes still need to be improved. Nutrition, palatability, and cost of material should to be fully considered, and in particular, the function of chitin in pangolin's diet needs to be symmetrically surveyed.

Reproduction study of captive pangolins

Reproductive disturbance is another technical barrier for captive pangolins. Only a few newborn records were reported in the last decade. This is an understandable situation, because without a successful diet, even survival and growth are problems for captive pangolins, not to mention successful reproduction. Except for poor adaptation to captive environments, poor understanding of pangolin's reproductive biology is another limiting factor in pangolin's captive breeding. In the past, the understanding of pangolin reproductive biology has been limited, owing to fragmentary reproductive records, which are primarily from interviewing with hunters, birthing records of rescued individuals in shelters, and a handful of dead fetus anatomy records. So, the reproduction parameters of pangolins are quite inaccurate. At present only few reproductive traits, including pangolin's time of birth, estrus, gestation period and litter size were reported (Chin et al. 2011).

Typically, pangolins are solitary except in mating season. May to July is their preferred mating seasons. Male pangolins often fight each other for females in the mating seasons. The winner will mate with the female pangolin, with the mating period generally lasting three to five days. Female pangolins have two to five estrous cycles during the mating season, and each will last for 11-26 days, until pregnancy (Cen et al. 2010). Different species of pangolin have different gestation periods, Cape Pangolin's gestation period is about 139 days (van Ee 1966), the gestation periods of the Tree Pangolin and Long-tail Pangolin are close to the Cape Pangolin's; the Indian Pangolin's gestation period is shorter, just 65–70 days (Hayssen and Van Tienhoven 1993). The pregnancy period of the Chinese Pangolin is about 101–169 days (Wu 1998b; Yang et al. 2007), but by monitoring the concentration of the serum progesterone, Chin et al. believed that the gestation period of the Chinese Pangolin was 318 to 372 days (Chin et al. 2011), which is significantly different from the results of Wu's and Yang's observations (Wu 1998b; Yang et al. 2007), suggesting that more systematic and quantitative analysis are needed to determine pangolin's reproduction parameters. Pangolins are believed to give birth to one young each time, but twins are known (Lim 2008a). The cubs will stay with their mother for six months before they leave. There are suggestions that new-born pangolins reach sexual maturity in one or two years, though there is no consensus on this.

Generally, regarding the pangolin's reproduction, little information has been known. This situation greatly limits the application of artificial reproductive technology in pangolin's artificial propagation, suggesting more work is needed to overcome the pangolin's reproductive disturbance in captivity.

Disease control for captive pangolins

Because of their poor adaptability to captive environment and a weak immune system, pangolins are easily to get sick. Gastrointestinal disease, pneumonia, skin disease, parasites, *etc.* are the most common causes of death for captive pangolins (Cen et al. 2010; Chang 2004; Clark et al. 2008). Over 50 percent of captive pangolins' died of hemorrhagic gastric ulcers and pneumonia (Chin and Yang 2008). It is believed that the directing causes of the gastric ulcers are the stress and unsuccessful artificial diet. Under stress, pangolins are easy to develop stomach ulcers and die (Chin and Yang 2008; Chin et al. 2006). To provide an appropriate habitat and reduce the stress may be helpful to improve the health of captive pangolins.

It is documented that almost all the wild animals have parasites, such as ticks and mites, especially for the pangolins seized from illegal trade (Hafiz et al. 2012). Due to the mess and dirty transportation process, most of the individuals have had high parasite burdens, and a very high percentage of animals shed gastrointestinal worm eggs in their feces (Clark et al. 2008). According to the autopsy results of 17 Malayan Pangolin seized from the illegal marketing (10 females, 7 males) in December 2013 (Figure 1, anatomical study of the pangolin), 16 individuals carried ticks with an average intensity of 9 and ranged from 1–24 (unpublished data). These parasites probably cause pangolins anemic, wasting, infectious disease, loss of immunity, and even death. Unfortunately, because of lacking of animal samples we can still not conduct detailed research on pangolins' diseases.

Lessons from our practical experiences

Since 2010, in order to protect the seized pangolins, a plan of *ex* situ conservation with captive-breeding has been carried out by South China Institute of Endangered Animals and Guangdong Provincial Wildlife Rescue Center (Guangzhou, China). From 2010–2013, we had kept 35 seized pangolins (2 Chinese Pangolins, 33 Malayan Pangolins) (Figure 2, pangolins in captivity). Based on field survey of the habitats of the both pangolin species, we created an artificial habitat for these pangolins. This artificial habitat is created in a room including caves for resting and breeding, feeding area with food bowls, and play area with dry tree trunks. In winter, the caves are covered by dry straw and cotton quilt to keep the temperature stability. Air conditioners are also used to adjust the temperature. Every day we offer pangolins food (milk and suckling pig feed as major food, and termite as supplementary feed) and clear water and observe the food consumption. A video monitoring system is used to record the activities of pangolins. With this method, although most of pangolins have died of gastrointestinal disease and other unknown diseases, we had kept 2 pangolins (1 Chinese Pangolin, 1 Malayan Pangolin) for over 600 days, and 3 Malayan Pangolins for about 380 days, 12 Malayan Pangolins for about 200 days.

Figure 1. Anatomical study of the pangolin.

Based on three years of work, we got some practical experiences and lessons: (1) Keep the temperature stable in the pangolin's rooms. The sharp change of temperature has serious effect on pangolins' health. For a case in 2012, when the cold came suddenly, the temperature dropped from 20 °C to 5 °C in one night, such temperature change caused 6 Malayan Pangolins death within 15 hours. (2) Different species, different sources and different body-sized individuals should be kept in deferent rooms to avoid fighting and to minimize the propagation of disease.

Based on the review of current knowledge and our own experience, we give some recommendations for the future practice of captive pangolins, wishing to improve the successful rate of captive breeding of pangolins.

1) Optimize and quantify the environmental parameters. Naturalistic habitat which could simulate their wild microenvironment is the best choice for captive pangolins. It seems that we have achieved some progress in constructing pangolin's artificial habitat, for example, moderate temperatures, less disturbance, better concealment, supplying an artificial cave or a mound for digging burrows *etc*. Nevertheless, the detail parameters of the habitat need to be quantified and further optimized in the future, such as the indoor temperature and humidity, area, animal density, light intensity, litter type and height *etc*. Moreover, reducing the stress level of pangolins in captivity must be noted, and installing a closed-circuit television in their habitat will be convenient to observe their activities without interference.

Figure 2. Pangolins in captivity.

2) Analyze pangolin's digestive system and improve their artificial diets. Appropriate artificial diet is another key factor for captive breeding of pangolins. Although there are lots of diet formulas developed, and some of them seem successful, more work is needed to improve their artificial diet in the future, because even the most successful artificial diet can't replace natural food completely. Generally, artificial diet must match their digestive system and satisfy their nutritional needs. This requires us to understand the physiology of pangolin's digestive system comprehensively. There are some anatomical analysis of pangolin's digestive system recently (Adeniyi et al. 2012; Munyala et al. 2011; Ofusori et al. 2008), but it is still unknown why pangolin selectively preys on ants and termites. Analyzing pangolin's digestive enzyme composition and identifying its critical categories may provide us some clues. Further analyzing the nutrition components of the ants and termites preyed by pangolins may help us to understand their nutritional needs. It is particularly worth mentioning that finding the function of the chitin in pangolin's food is an interesting topic, whether it is the crucial element for pangolin's nutrition requirements needs more studies. The information about pangolin's digestive enzyme components and food components may contribute to the further improvement of their diet formulas.

3) Determine the reproductive parameters. Although there are successful breeding records of captive pangolins in the past, they are just individual cases. Improving the reproduction rate is the ultimate aim of the pangolin captive programs, so more reproductive parameters need to be determined in the future. Besides the descriptions for the reproductive traits, such as estrus cycle, gonad activity cycle, mating time, pregnancy period *etc*. Quantitative analysis of hormone concentrations during the reproductive cycle needs more attentions, including testosterone concentration and male sexual behavior, estrogen concentration and estrus, follicle-stimulating hormone (FSH) concentration and ovulation, *etc*. These studies could provide reference for artificial regulation of reproductions in practice.
4) Disease control. Prevention is much more efficient than treatment in disease control. Supplying a suitable environment or using preventive actions to reduce the chance of illness will be the preferred choices for captive pangolins. For example, suitable temperature and humidity is essential to prevent pneumonia, and appropriate artificial diet is essential to prevent gastrointestinal diseases. Pesticides such as thiabendazole can be used regularly to get rid of parasites. At the same time, more case studies need to be strengthened to find the prevalence of disease in pangolins, and to provide references for future treatments.

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References

Adeniyi T, Tijani A, Adekomi D, Abayomi T (2012) A comparative study of the lateral geniculate body of rat (*Rattus Norvegicus*), bat (*Eidolon Helvum*) and pangolin (*Manis Tricuspis*). Global Journal of Health Science 4: 118–125. doi: 10.5539/gjhs.v4n4p118

Bao F, Wu S, Su C, Yang L, Zhang F, Ma G (2013) Air temperature changes in a burrow of Chinese pangolin, *Manis pentadactyla*, in winter. Folia Zoologica 62: 42–47.

Cen L, Xu L, Xu H, Xiang Y, Xue Z (2010) Protection and cultivated technology of pangolin. Asia-Pacific Traditional Medicine 6: 12–15. [In Chinese]

Chang CY (2004) Study on the apparent digestibility of diet on Formosan pangolin. National Taiwan University, Taipei, Taiwan. [In Chinese]

Chin SC, Lien CY, Chan YT, Chen CL, Yang YC, Yeh LS (2011) Monitoring the gestation period of rescued Formosan pangolin (*Manis pentadactyla pentadactyla*) with progesterone radioimmunoassay. Zoo Biology 31: 479–489. doi: 10.1002/zoo.20413

Chin SC, Yang CW (2008) Formosan pangolin rescue, rehabilitation and conservation. In: Pantel S, Chin SY (Eds) Proceedings of the Workshop on Trade and Conservation of Pangolins Native to South and Southeast Asia. TRAFFIC Southeast Asia, Singapore Zoo, Singapore, 108–110.

Chin SC, Liu CH, Guo JC, Chen SY, Yeh LS (2006) A 10-year review of autopsy of rescued Formosan pangolin (Manis pentadactyla pentadactyla) in Taipei zoo. Proceedings of AZWMP 2006: 43.

Clark L, Van Thai N, Phuong TQ (2008) A long way from home: the health status of Asian pangolins confiscated from the illegal wildlife trade in Viet Nam. In: Pantel S, Chin SY (Eds) Proceedings of the Workshop on Trade and Conservation of Pangolins Native to South and Southeast Asia. TRAFFIC Southeast Asia, Singapore Zoo, Singapore, 111–118.

Coulson I (1989) The pangolin (*Manis temmincki* Smuts, 1835) in Zimbabwe. African Journal of Ecology 27: 149–155. doi: 10.1111/j.1365-2028.1989.tb00938.x

Crandall LS (1964) The management of wild mammals in captivity. University of Chicago Press, Chicago, 195–199.

Gaubert P, Antunes A (2005) Assessing the taxonomic status of the Palawan pangolin *Manis culionensis* (Pholidota) using discrete morphological characters. Journal of Mammalogy 86: 1068–1074. doi: 10.1644/1545-1542(2005)86[1068:attsot]2.0.co;2

Guangzhou Daily (2013) 2032 smuggling pangonlins were seized in Shantou. http://gzdaily.dayoo.com/html/2012-12/28/content_2092636.htm [accessed 28 October.2013] [In Chinese]

Hafiz SM, Marina H, Afzan AW, Chong J (2012) Ectoparasite from confiscated Malayan pangolin (*Manis javanica* Desmarest) in Peninsular Malaysia. In: UMT 11th international annual symposium on sustainability science and management. Terengganu, Malaysia, 1225–1229.

Hayssen VD, Van Tienhoven A (1993) Asdell's patterns of mammalian reproduction: a compendium of species-specific data. Cornell University Press, Ithaca, New York, 658–659.

Heath ME, Vanderlip SL (1988) Biology, husbandry, and veterinary care of captive Chinese pangolins (*Manis pentadactyla*). Zoo Biology 7: 293–312. doi: 10.1002/zoo.1430070402

HuanqiuNet (2013) Chinese fishing boat harbouring 10 tons of pangolins stranded in Philippines. http://world.huanqiu.com/exclusive/2013-04/3833367.html [accessed 28 October.2013] [In Chinese]

Jacobsen NHG, Newbery RE, Dewet MJ, Viljoen PC, Pietersen E (1991) A contribution of the ecology of the steppe pangolin *Manis-temminckii* in the Transvaal. International Journal of Mammalian Biology 56: 94–100.

Jiang H, Feng M, Huang J (1988) Preliminary observation on pangolin's active habits. Chinese Journal of Wildlife 9: 11–13. [In Chinese]

Ke YY, Chang H, Wu SB, Liu Q, Fong GX (1999) A study on Chinese pangolin's main food nutrition. Zoological Research 20: 394–395. [In Chinese]

Li X, Zhou Jl, Guo Zf, Guo Aw, Chen F-f (2010) The analysis on nutrition contents of ants preyed on by *Manis pentadactyla*, Xishuangbanna of China. Sichuan Journal of Zoology 29: 620–621. [In Chinese]

Lim NTL (2008a) Autecology of the sunda pangolin (*Manis javanica*) in Singapore. National University Of Singapore, Singapore.

Lim NTL (2008b) Ecological research and conservation of Sunda pangolin *Manis javanica* in Singapore. In: Pantel S, Chin SY (Eds) Proceedings of the Workshop on Trade and Conservation of Pangolins Native to South and Southeast Asia. TRAFFIC Southeast Asia, Singapore Zoo, Singapore, 90–93.

Lim NTL, Ng PKL (2007) Home range, activity cycle and natal den usage of a female Sunda pangolin Manis javanica (Mammalia: Pholidota) in Singapore. Endangered Species Research 3: 1–8.

Liu ZH, Xu LH (1981) Pangolin's habits and its resource protection. Chinese Journal of Zoology 16: 40–41. [In Chinese]

Masui M (1967) Birth of a Chinese pangolin *Manis pentadactyle* at Ueno Zoo, Tokyo. International Zoo Yearbook 7: 114–116. doi: 10.1111/j.1748-1090.1967.tb00340.x

Menzies J (1963) Feeding pangolins (*Manis* spp) in captivity. International Zoo Yearbook 4: 126–128. doi: 10.1111/j.1748-1090.1963.tb03644.x

Menzies J (1966) A note on the nutrition of the tree pangolin *Manis tricuspis* in captivity. International Zoo Yearbook 6: 71–71. doi: 10.1111/j.1748-1090.1966.tb01694.x

Munyala R, Liumsiricharoen M, Pongket P, Prapong T, Suprasert A (2011) Glycoconjugates in the secretory epithelium of the mandibular salivary gland of Malayan pangolin (*Manis javanica*). KKU Veterinary Journal 19: 162–170.

Ofusori D, Caxton-Martins E, Keji S, Oluwayinka P, Abayomi T, Ajayi S (2008) The microarchitectural adaptations in the stomach of African tree pangolin *Manis tricuspis*. International Journal of Morphology 26: 701–705. doi: 10.4067/S0717-95022008000300031

Ogilvie PW, Bridgwater DD (1967) Notes on the breeding of an Indian pangolin *Manis Crassicaudats* at Oklahoma Zoo. International Zoo Yearbook 7: 116–118. doi: 10.1111/j.1748-1090.1967.tb00341.x

PangolinSG (2013) Conservation and research projects being conducted by PangolinSG members. http://www.pangolinsg.org/conservation/current-projects/ [accessed 20, December.2013]

Richer R, Coulson IAN, Heath M (1997) Foraging behaviour and ecology of the Cape pangolin (*Manis temminckii*) in north-western Zimbabwe. African Journal of Ecology 35: 361–369. doi: 10.1111/j.1365-2028.1997.101-89101.x

SanDiegoZoo (2013) Tree pangolin. http://animals.sandiegozoo.org/animals/tree-pangolin [accessed 20, December.2013]

SavePangolins (2013) Rescue and rehabilitation centers. http://savepangolins.org/conservation/ [accessed 10, December.2013]

SCNU (2013) First record of a newborn Malayan pangolin (*Manis javanica*) in captivity. http://sky.scnu.edu.cn/news/201110139559837.htm [accessed 28 October.2013] [In Chinese]

Shepherd CR (2009) Overview of pangolin trade in Southeast Asia. In: Pantel S, Chin SY (Eds) Proceedings of the Workshop on Trade and Conservation of Pangolins Native to South and Southeast Asia, 6–9.

Shi YQ, Wang YG (1985) Food habits on pangolin. Chinese Journal of Wildlife 6: 42–43. [In Chinese]

Swart JM, Richardson PRK, Ferguson JWH (1999) Ecological factors affecting the feeding behaviour of pangolins (*Manis temminckii*). Journal of Zoology 247: 281–292. doi: 10.1111/j.1469-7998.1999.tb00992.x

Sweeney R (1956) Some notes on the feeding habits of the Ground Pangolin, *Smutsia Temminckii* (Smuts). The Annals & Magazine of Natural History 9: 893–896. doi: 10.1080/00222935608655913

Tenaza R, Schultz T (1977) Natural and synthetic diets for Pholidota. In: Rechcigl M (Ed.) CRC handbook series in nutrition and food. CRC Press, Cleveland, 549–553.

van Ee CA (1966) A note on breeding the Cape pangolin *Manis temniincki* at Bloemfontein zoo. International Zoo Yearbook 6: 163–164. doi: 10.1111/j.1748-1090.1966.tb01734.x

Vijayan M, Yeong C, Ling D (2008) Captive management of Malayan pangolins *Manis javanica* in the Night Safari. In: Pantel S, Chin SY (Eds) Proceedings of the Workshop on Trade and Conservation of Pangolins Native to South and Southeast Asia. TRAFFIC Southeast Asia, Singapore Zoo, Singapore, 119–129.

Wilson AE (1994) Husbandry of pangolins *Manis* spp. International Zoo Yearbook 33: 248–251. doi: 10.1111/j.1748-1090.1994.tb03578.x

Wu S (1998a) Classification and distribution of pangolin and its protection status in the world. In: Hu J, Wu Y (Eds) Resource and Conservation of Vertebrate. Sichuan Publishing House of Science and Technology, Chengdu, 130–138. [In Chinese]

Wu S (1998b) Notes on a newborn Chinese pangolin (*Manis pentadactyla aurita*). Journal of Qinghai Normal University (Natural Science), 40–42. [In Chinese]

Wu S, Liu N, Li Y, Sun R (2005) Observation on food habits and foraging behavior of Chinese pangolin (*Manis pentadactyla*). Chinese Journal of Applie Environmental Biology 11: 337–341. [In Chinese]

Wu S, Liu N, Ma G, Tang M, Chen H, Xu Z (2004a) A current situation of ecology study on pangolins. Chinese Journal of Zoology 39: 46–52.

Wu S, Liu N, Ma G, Xu Z, Chen H (2003) Studies on habitat selection by Chinese pangolin (*Manis pentadactyla*) in winter in Dawuling natural reserve. Acta Ecologica Sinica 23: 1079–1086. [In Chinese]

Wu S, Liu Q, Feng G, Ke Y (1999) Preliminary study on food nutrient contents of Chinese pangolin (*Manis pentadactyla*). Journal of Zhanjiang Normal College (Natural Science) 20: 74–76. [In Chinese]

Wu S, Ma G, Chen H, Xu Z, Li Y, Liu N (2004b) A preliminary study on burrow ecology of *Manis pentadactyla*. Chinese Journal of Applied Ecology 15: 401–407. [In Chinese]

Wu S, Ma G, Tang M, Chen H, Liu N (2002) The status and conservation strategy of pangolin resource in China. Journal of Natural Resources 17: 174–180. [In Chinese]

Yang CW, Chen S, Chang CY, Lin MF, Block E, Lorentsen R, Chin JSC, Dierenfeld ES (2007) History and dietary husbandry of pangolins in captivity. Zoo Biology 26: 223–230. doi: 10.1002/zoo.20134

Yu M, Li N, Hu L, Lin Z (2009) Integrated study of the pharmic-animal, pangolin. Jilin Journal of Traditional Chinese Medicine 29: 514–517. [In Chinese]

YunnanNet (2013) First captive breeding record of pangolin in Yunnan Wild Animals Park. http://www.yunnan.cn/html/2008-11/19/content_140986.htm [accessed 30 October.2013] [In Chinese]

ZeeNews (2013) Captive breeding of pangolin successful in Nandankanan zoo. http://zeenews.india.com/news/eco-news/captive-breeding-of-pangolin-successful-in-nandankanan-zoo_407963.html [accessed 20, December.2013]

Zhang L, Li Q, Sun G, Luo S (2010) Population and conservation status of pangolins. Bulletin of Biology 45: 1–5. [In Chinese]

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RESEARCH ARTICLE

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Taxonomic revision of the genus *Prionopelta* (Hymenoptera, Formicidae) in the Malagasy region

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Abstract

In this study we revise the taxonomy of the genus *Prionopelta* for the Malagasy region, treating seven species, six of which are newly described (*P. laurae* **sp. n.**, *P. seychelles* **sp. n.**, *P. subtilis* **sp. n.**, *P. talos* **sp. n.**, *P. vampira* **sp. n.**, *P. xerosilva* **sp. n.**), and one redescribed (*P. descarpentriesi* Santschi). One species, *P. seychelles*, is restricted to Seychelles, while the six remaining species treated are endemic to Madagascar.

Keywords

Afrotropical region, Madagascar, equatorial rainforest, taxonomy, Amblyoponinae, *Prionopelta*

Introduction

The genus *Prionopelta* Mayr, 1866 contains 21 species, including six that are newly described here. In his species-level treatment of the genus, Brown (1960) recognized ten species scattered throughout the Old and New World tropics, and later returned *P. marthae* to the genus after an erroneous removal based on mislabeled specimens (Brown 1965). Subsequently, Terron described two new species from the Afrotropics (1974), and Shattuck described two new Indo-Pacific species and clarified diagnoses and geographic distributions for *P. kraepelini* and *P. opaca* (2008). Total species counts to date are thus: five from the New World tropics (*P. punctulata* Mayr, *P. antillana*

Forel, *P. marthae* Forel, *P. modesta* Forel, and *P. amabilis* Borgmeier), six from the Indo-Pacific region: (*P. majuscula* Emery, *P. opaca* Emery, *P. kraepelini* Forel, *P. brocha* Wilson, *P. media* Shattuck, and *P. robynmae* Shattuck), three from the tropics of Africa (*P. amieti* Terron, *P. humicola* Terron, *P. aethiopica* Arnold), and seven from the Malagasy region (*P. descarpentriesi* Santschi, *P. laurae* **sp. n.**, *P. seychelles* **sp. n.**, *P. subtilis* **sp. n.**, *P. talos* **sp. n.**, *P. vampira* **sp. n.**, *P. xerosilva* **sp. n.**). Interestingly, *Prionopelta* is thus one of four genera, along with *Mystrium*, *Euponera*, and *Leptogenys*, where described species numbers from the Malagasy region are greater than those from the Afrotropics.

Material and methods

The present contribution includes all specimens of *Prionopelta* collected from the arthropod survey project conducted in Madagascar by B.L. Fisher and the members of the Madagascar Biodiversity Center from 1992 through 2013 (Fisher 2005). This revision also integrates specimens from the Philip S. Ward Collection at the University of California Davis, CA, U.S.A. (PSWC). Observations were carried out with a Leica MZ125 microscope. Digital color montage images were created using a JVC KY-F75 digital camera and Syncroscopy Auto-Montage software (version 5.0), or a Leica DFC 425 camera in combination with the Leica Application Suite software (version 3.8). All images presented here are available online at AntWeb (http://www.antweb.org). Distribution maps for each species were produced with the software R (R Core Team 2015). Measurements were performed using a Mitutoyo digital, dual-axis stage micrometer. Measurements were recorded to the thousandth of a millimeter, but values presented are rounded to the nearest hundredth of a millimeter. For each species, measurements are presented as minimums and maximums with means following in parentheses. The following measurements and indices are reported, largely following Shattuck (2008):

HW	Head width: maximum head width in full-face (dorsal) view.
HL	Head length: maximum head length in full-face (dorsal) view, measured from the anteriormost point of the clypeal margin to the posteriormost point of the head proper.
SL	Scape length: length of the scape (first antennal segment) excluding the basal neck and condyle.
WL	Weber's length: diagonal length of mesosoma in lateral view from the posteroventral margin of propodeal lobe to the anteriormost point of pronotal slope, excluding the neck.
PetL	Petiole length: midline length of the petiolar node (excluding the anterior peduncle) in dorsal view.
PetW	Petiole width: width of the petiolar node in dorsal view.
T1W	First gastral segment width: width of first gastral (third abdominal) tergite in dorsal view.

CI	Cephalic index: HW/HL × 100
SI	Scape index: SL/HW × 100
PI	Petiolar index: PetW/PetL × 100

Abbreviations of depositories

Collection abbreviations follow Bolton (1980) and Evenhuis (2009). The material upon which this study is based is located, or deposited at the following institutions:

BMNH	The Natural History Museum (British Museum, Natural History), London, U.K.
CASC	California Academy of Sciences, San Francisco, California, U.S.A.
MCZC	Museum of Comparative Zoology, Cambridge, Mass. U.S.A.
MHNG	Muséum d'Histoire Naturelle, Geneva, Switzerland
NHMB	Naturhistorisches Museum, Basel, Switzerland
PBZT	Parc Botanique et Zoologique de Tsimbazaza, Antananarivo, Madagascar
PSWC	Philip S. Ward Collection at the University of California Davis, CA, U.S.A.

The role of sculpture in identifying species of Malagasy *Prionopelta*

Sculpture of the head and dorsum of the mesosoma is of high diagnostic value in identifying Malagasy *Prionopelta*. In describing sculpture we use the same terminology as Harris (1979) and Shattuck (2008). We use the term "foveae" to refer to the shallow, circular, flat-bottomed depressions present on the integument, and the terms "punctations" or "punctures" to mean minute, point-like depressions in the surface of the integument that appear as tiny pinpricks even under high magnification. All Malagasy *Prionopelta* have foveae that vary in both size and density on both head and mesosoma, and most species also have punctations on the dorsum of the mesosoma. Additionally, all taxa possess a band devoid of foveae on the head that runs medially and longitudinally. This area, extending from just posterior to the antennal sockets to near the posterior margin of the head, varies in size and shape among species. Throughout the text, this area is excluded from consideration when statements are made concerning the density and extent of sculpture on the head. In some individuals a linear, scarlike, coronal suture is present in this region running longitudinally along the dorsum of the head.

When identifying Malagasy *Prionopelta*, it is helpful to recognize three qualitative conditions concerning the arrangement of foveae on the head. The first condition occurs when foveae are relatively equally spaced from one another at a distance that is greater than the diameter of an individual fovea, with smooth, shining integument present between foveae (Fig. 1A, B). The next condition is one of variable foveal placement, with some foveae as described above but others directly adjacent to one another (Fig. 1C). At low magnification, these adjacent foveae appear to touch directly, whereas under high magnification they appear very close together (much closer together than the diameter of an individual fovea), causing the area between each fovea to form a distinct raised margin that rises above what would otherwise be the smooth surface of the integument. There is a general tendency in both of the above-described conditions for cephalic foveae to increase in density moving laterally to medially in full-face view. In the final of these three general conditions, foveae are placed extremely densely on the head so that virtually no shining integument is present between foveae (except for the median cephalic band mentioned above). In this condition, foveae appear as a dense system of directly adjacent pits with only netlike boundaries of thin, raised margins separating individual fovea (Fig. 1D).

Taxonomy

Prionopelta Mayr, 1866

Prionopelta can be recognized from other Malagasy genera through the following combination of characters: petiole which lacks a posterior face due to its broad attachment to the gaster; elongate, subtriangular mandibles with three teeth positioned distally on a distinct mandibular face; apical tooth the longest, and second tooth the shortest with a mid-length third tooth; antennal segments variable (either 9 or 12 for Malagasy species) but always with a four-segmented club; body overall never more than 3 mm in length.

Synopsis of Malagasy *Prionopelta*

Prionopelta descarpentriesi Santschi, 1924
Prionopelta laurae **sp. n.**
Prionopelta seychelles **sp. n.**
Prionopelta subtilis **sp. n.**
Prionopelta talos **sp. n.**
Prionopelta vampira **sp. n.**
Prionopelta xerosilva **sp. n.**

Identification key for Malagasy *Prionopelta* species (workers)

1 Nine antennal segments present, palest and smallest of the Malagasy *Prionopelta* (HL < 0.4 mm and HW < 0.3 mm); entire body pale yellow (Fig. 7).. .... ***P. laurae***

– Twelve antennal segments present; not as small as above (HL > 0.4 mm and HW > 0.3 mm); varying in size and color **2**

2 Cephalic foveae widely and evenly spaced such that they are only extremely rarely adjacent to one another; all cephalic foveae appear as if scooped out of a flat, shining surface, and completely lack raised margins at their perimeter (Fig. 1A, B)..**3**

– Cephalic foveae of variable spacing but never as sparse as above; at a minimum, head with several clusters of two or more foveae which are directly adjacent in full-face view (Fig. 1C) and often with many to most foveae on the head directly adjacent to one another (Fig. 1D); integument between adjacent foveae appears to bulge, and when foveae are densely placed, these bulged areas form a network of raised margins (Fig. 1D) **4**

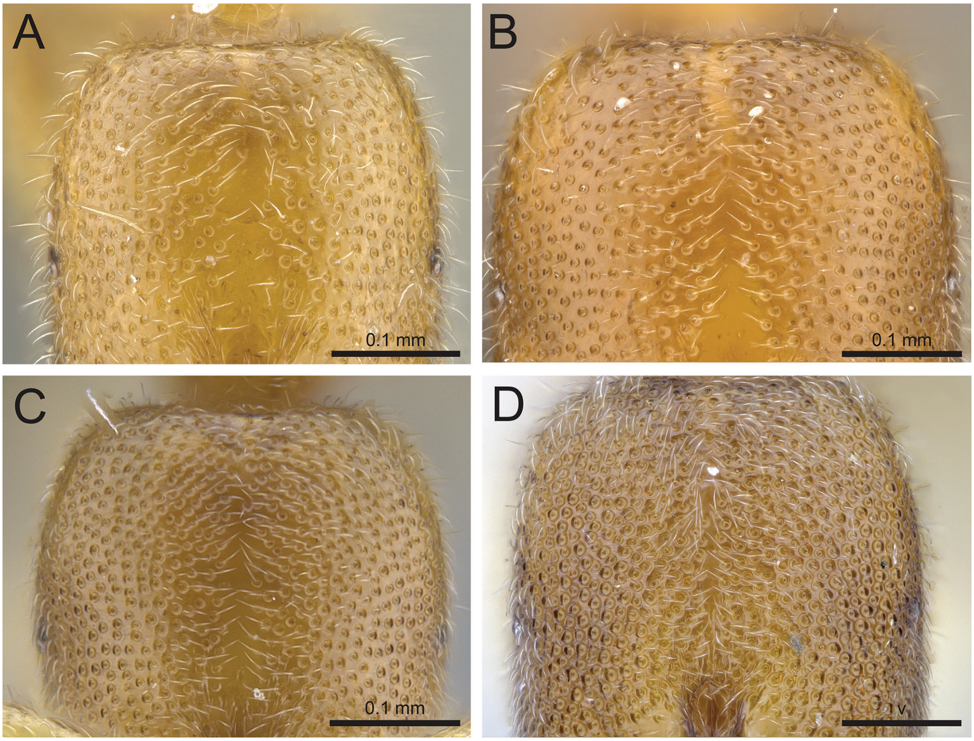

Figure 1. Head in full-face view. **A** *P. xerosilva* (CASENT0157254) **B** *P. vampira* (CASENT0461978) **C** *P. descarpentriesi* "morphotype-A" (CASENT0034837) **D** *P. descarpentriesi* "morphotype-C" (CASENT0191895).

3 Metanotal suture absent in dorsal view, in its place a smooth surface with no clear boundary dividing mesonotum and propodeum; posterior margin of the propodeum convex and crescent-shaped in dorsal view (Fig. 2A); lamellae of the posterior propodeum present; apical tooth of the mandible extremely long (Fig. 2C)...***P. vampira***

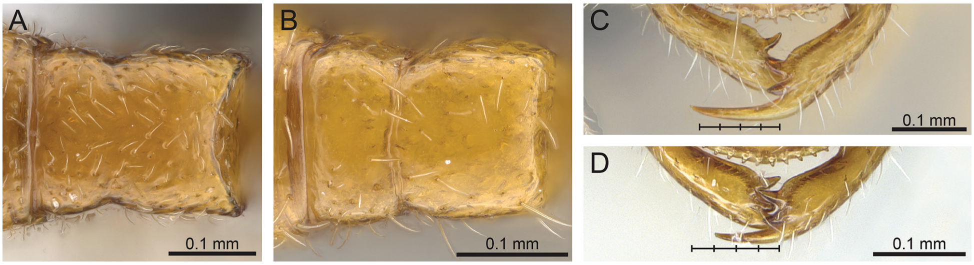

Figure 2. A, **B** Mesonotum and propodeum in dorsal view. **A** *P. vampira* (CASENT0461978) **B** *P. xerosilva* (CASENT0157254) **C** mandibles of *P. vampira*, demonstrating that apical tooth is greater than four times the length of third tooth (CASENT0461978) **D** mandibles of *P. xerosilva*, demonstrating that apical tooth is less than four times the length of third tooth (CASENT0157254).

– Metanotal suture present; posterior margin of the propodeum relatively straight in dorsal view (Fig. 2B); lamellae absent; apical tooth intermediate in length (Fig. 2D); known only from tropical dry forests of western Madagascar..... ***P. xerosilva***

4 Vast majority of cephalic foveae densely positioned so they are directly adjacent to one another; vein-like ridges present running between foveae producing the appearance of a netlike pattern across the entire head (Fig. 3A, B, C, D); areas of shining integument devoid of foveae are present only at the extreme posterolateral corners of the head...**5**

– Cephalic foveae variable in their spacing, but always with some foveae directly adjacent and others isolated from one another; usually with the frequency of adjacent foveae increasing laterally to medially (Fig. 1C) 7

5 Coronal suture present on head which appears as a uniformly thin, linear scar that swells above the surrounding integument under high magnification (Fig. 3A, B); sculpture on pronotum weak, consisting of shallow foveae which are much larger and more widely spaced than those on the head, and are interspersed with minute punctures. ....***P. subtilis***

– Coronal suture absent on head; median cephalic band wider and more irregular, never uniformly swelling above the surface of the surrounding integument as a suture, appearing instead as a shining area devoid of foveae (Fig. 3C); if band is narrow (Fig. 3D), then surface of the pronotum always covered in large, deep, regularly-spaced foveae, similar in size to those on the head................. **6**

6 Cephalic foveae small and densely positioned so that the vast majority are directly adjacent to one another with swollen ridges between; median cephalic band devoid of foveae is wide, usually wider at its base and narrowing posteriorly (Fig. 3C); foveae of the pronotum much larger than that of the head, ranging from shallow to deep, and interspersed with punctures; known only from Seychelles...***P. seychelles***

– Cephalic foveae large, deep, and densely placed, joining to form a network of tall, jagged ridges; median cephalic band lacking foveae is usually thin and

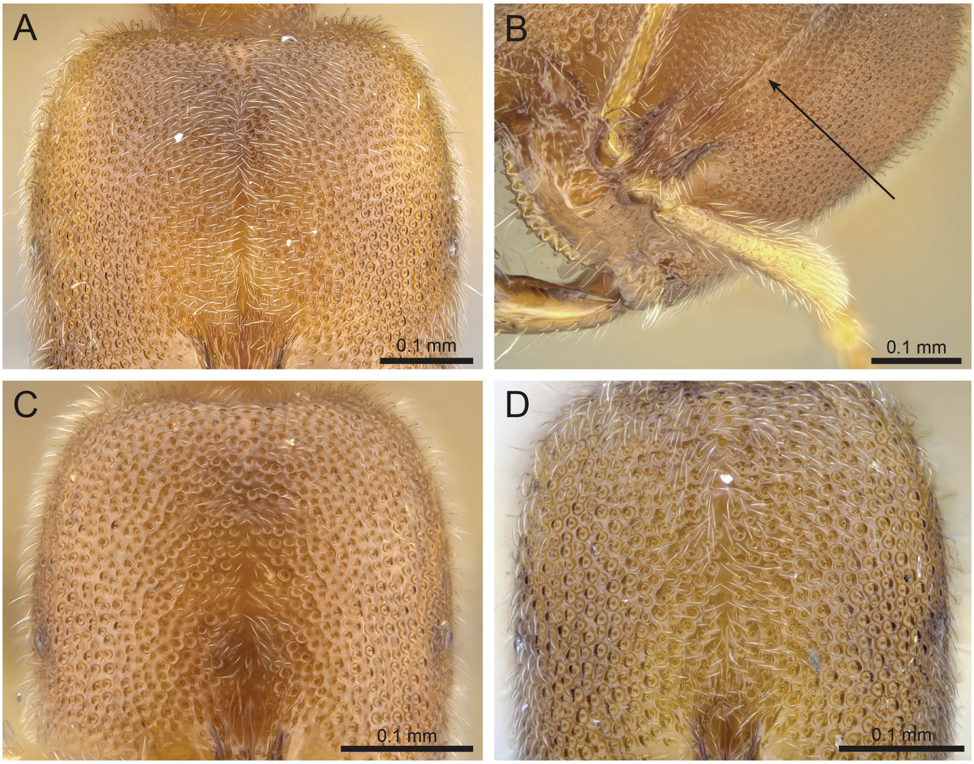

Figure 3. Head in full-face view. **A** *P. subtilis* (CASENT0033641) **B** *P. subtilis* (CASENT0151601) specimen rotated to demonstrate raised coronal suture **C** *P. seychelles* (CASENT0161311) **D** *P. descarpentriesi* "morphotype-C" (CASENT0191895).

narrow, but its boundaries are irregular and jagged (Fig. 3D); pronotum lacking punctures and possessing deep, regularly-spaced foveae which are similar-sized to those on the head .... ***P. descarpentriesi*** (in part)

7 Distinctly tricolored body with dark brown, uniformly colored head, lighter brown body, and pale yellow legs (Fig. 10B); large, globular eyes which project spherically from the head; at high magnification, eyes composed of several overlapping globular sections delineated by sutures (Fig. 4A, D); known only from the Anjanaharibe-Sud Reserve of Madagascar ....***P. talos***

– Not distinctly tricolored as above; some individuals possess dark brown on head but always at least with lighter brown present at the posterolateral corners of the head which resembles the color of the mesosoma (Fig. 5A, B); eyes ranging in size from almost absent (Fig. 4C, F) to dark, irregular circles that are almost flush with the surrounding integument (Fig. 4B, E); eyes never globular and never composed of several visible globular sections .... ***P. descarpentriesi*** (in part)

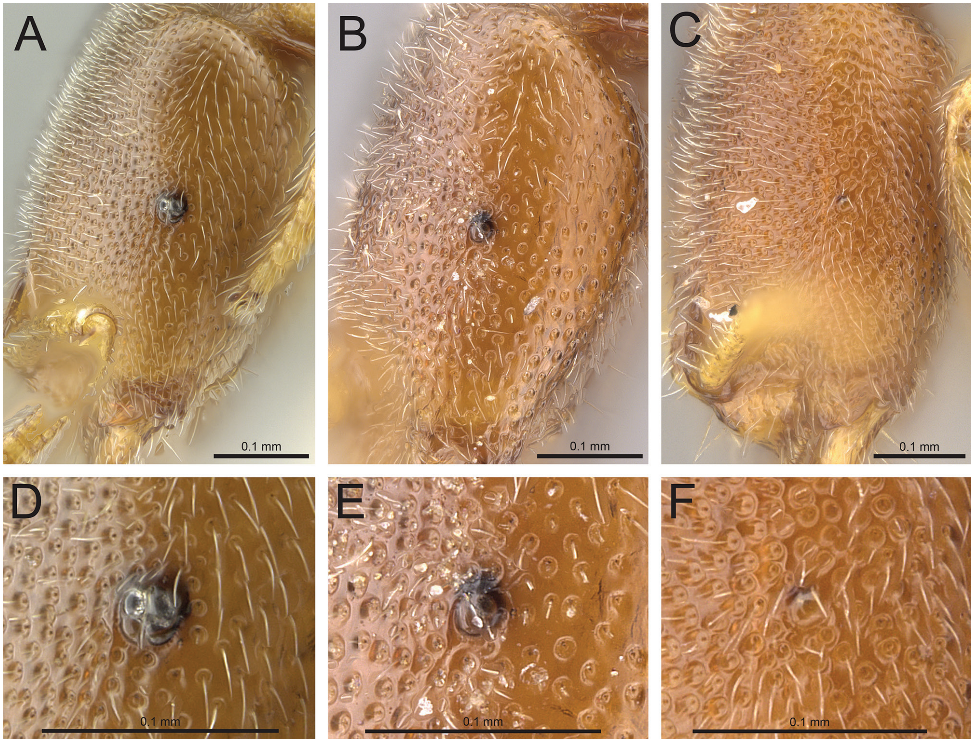

Figure 4. A, B, C Head in profile. **A** *P. talos* (CASENT0339229) **B** *P. descarpentriesi* "morphotype-A" (CASENT0168970) (photo: Michele Esposito 2014) **C** *P. descarpentriesi* "morphotype-C" (CASENT0042668) (photo: Michele Esposito 2014) **D, E, F** close-up of eye. **D** *P. talos* (CASENT0339229) **E** *P. descarpentriesi* (CASENT0168970) (Michele Esposito 2014) **F** *P. descarpentriesi* (CASENT0042668) (Michele Esposito 2014).

Prionopelta descarpentriesi Santschi

Figs 1C, D, 3D, 4B, C, E, F, 5, 6

Prionopelta descarpentriesi Santschi, 1924b:195.

Type material. Lectotype, pinned worker, CASENT0101548 [designated here], MADAGASCAR, Ikelivia, 30.ix.1923 (*Descarpentries*) (NHMB) [examined]. **Paralectotypes**, one pinned worker CASENT0101547 with same data as lectotype (NHMB) [examined].

Diagnosis. *P. descarpentriesi* can be identified by the following combination of characters: twelve antennal segments; median cephalic band lacking a thin suture that is swollen above the surrounding integument; placement of cephalic foveae ranging from sparse to dense, but always at minimum, with at least several clusters of foveae directly adjacent to one another (if nowhere else, then medially in full-face view); if all foveae on the head are directly adjacent so that no flat, shining space is present between foveae, then foveae are large and accompanied by pronotal sculpture which is characterized as being both similar in size to that on the head and not consisting of smaller foveae or punctures; eye appearing as either an asymmetrical dark patch which appears to be a stain in the cuticle that is flush with its surrounding integument, or a single, slightly rounded glob with no definable subunits.

Worker measurements (N=25). HL 0.42–0.53 (0.48); HW 0.32–0.43 (0.38); SL 0.22–0.3 (0.26); WL 0.46–0.6 (0.52); PetL 0.11–0.2 (0.16); PetW 0.17–0.26 (0.22); T1W 0.29–0.37 (0.33); CI 74.64–85.1 (79.6); PI 118.23–173.29 (141.94); SI 61.46–72.38 (67.31).

Worker description. Posterior margin of the head straight to weakly concave in full-face view; spacing of cephalic foveae highly variable, ranging from individuals with dense, directly adjacent foveae covering the entire head (known only from far eastern and northern Madagascar, see morphotype descriptions below), to individuals with foveae more widely spaced so that shining areas are visible between; median cephalic band devoid of foveae ranging from wide to extremely narrow but never appearing as a linear suture that is uniformly swollen above the level of the surrounding integument; apical tooth intermediate in length; evenly-space pronotal foveae range from shallow to deep; shallow foveae present on mesonotum and propodeum.

Distribution and ecology. This widespread species has been collected from leaf litter from 10–1860 meters of elevation. While found most commonly in rainforest and montane rainforest, it has also been collected in Uapaca woodland, littoral rainforest, and tropical dry forest (Fig. 13). *P. descarpentriesi* has been collected in forest litter, under moss, rocks, and logs, as well as inside rotten logs and underground in soil.

Taxonomic notes. Three generalized morphotypes can be distinguished within this taxon; these vary in density of cephalic foveae and other co-occurring traits (Fig. 6). In morphotype A, the majority of foveae are equidistantly spaced and separated by a span of shining integument of around one foveal diameter (Figs 1C, 5A, 6A). These foveae appear cleanly scooped from the surface of the integument and largely lack raised margins. Morphotype B, which is intermediate between A and C, has denser cephalic foveae covering almost the entire head, however foveae are smaller and more delicate than those of morphotype C and raised ridges between foveae are less pronounced (Fig. 6B). Pronotal sculpture in morphotype B usually consists of several sizes of foveae along with some punctures. Morphotype C possesses large, dense cephalic foveae that cover the entire head, accompanied by a pronounced network of raised, jagged ridges between foveae (Figs 1D, 3D, 4C, 6C). Morphotype C additionally has large, deep, and evenly spaced pronotal foveae that are similar in size to those on the head, and this morphotype lacks smaller foveae or punctures on the pronotum. Width of the median cephalic band devoid of foveae is widest in morphotype A and narrowest in morphotype C.

P. descarpentriesi is much more morphologically variable than the other species treated in this revision and very possibly represents a species complex. This could explain why *P. descarpentriesi* is abundant, geographically widespread, and morphologically variable. Morphotype C, which is restricted to a band bordering the coast of eastern and northern Madagascar (Fig. 14), is recognizably distinct from the majority of individuals from interior populations of the species. At several localities where morphotype C is present, individuals from morphotype A and B are also present with little to no evidence of character blending between morphotypes: Galako, Makirovana, Morojejy Nature Reserve, and Sahafina. However, at other locales such as Ambohijanahary, Montagne d'Ambre, and Vohemar, a bewildering array of intermediate forms have been collected, blurring the lines between the three morphotypes. Collecting nest series from the aforementioned locations to determine whether this population-level variation is intra- or intercolonial is an important first step in ultimately understanding how morphological variation is partioned in this taxon as currently dilineated.

Under the above scheme, the lectotype and paralectotype of *P. descarpentriesi* would be considered morphotype A. Jules Descarpentries (1881–1927) collected the types for this species on 30 September 1923 and the collection locale was subsequently noted as "Ikelivia", making it difficult to determine a more precise location based on modern place names. Historical records indicate that Descarpentries resided in Tulear, and worked as a topographic surveyor and entomologist. According to records, he was active around Tsaratanana and Fianarantsoa (specifically Andringitra) and often traveled with H. Perrier de la Bâthie. Given that morphotype A is reasonably widespread across Madagascar, including Tsaratanana and Andringitra, it is possible that the type specimens from "Ikelivia" were collected in either of these localities. To further complicate matters, most of Descarpentries's specimens, which were destined to the Paris Museum, were sold on the side by a member of the staff. Before the specimens were sold, the labels were changed to hide their true ordinance (Jeannel 1951, (Anonymous 1970)).

Non-type material. MADAGASCAR: Antananarivo, Ankalalahana, 19.0066°S, 47.1122°E, 1375 m, Uapaca woodland, 29.iii.2011 (*B.L.Fisher et al.*); Antananarivo, Forêt de galerie, Andranorovitra, 24.0 km NNE Ankazobe, 18.1124°S, 47.1976°E, 1491 m, disturbed gallery montane forest, 2.vi.2008 (*B.L.Fisher et al.*); Antananarivo, Navoatra I Non Protected Area, 7.64 km NW Arivonimamo, 18.9781°S, 47.1193°E, 1373 m, Uapaca woodland, 6.v.2010 (*Andrianjaka Ravelomanana*); Antananarivo, Réserve Naturelle Sohisika, Sohisika 24.6 km NNE Ankazobe, 18.1032°S, 47.1869°E, 1464 m, gallery montane forest, 1.vi.2008 (*B.L.Fisher et al.*); Antananarivo, Réserve Spéciale d'Ambohitantely, 18.2244°S, 47.2774°E, 1490 m, montane forest, 9.iii.2012 (*B.L.Fisher et al.*); Antananarivo, Réserve Spéciale d'Ambohitantely, Forêt d'Ambohitantely, 20.9 km 72° NE d'Ankazobe, 18.2253°S, 47.2868°E, 1410 m, montane rainforest, 17.iv.2001 (*Fisher, Griswold et al.*); Antananarivo, Réserve Spéciale d'Ambohitantely, Forêt d'Ambohitantely, Jardin Botanique, 24.1 km 59° NE d'Ankazobe, 18.1714°S, 47.2818°E, 1620 m, montane rainforest, 17.iv.2001 (*Fisher, Griswold et al.*); Antananarivo, Tsimbazaza, 18.928°S, 47.527°E, 1300 m, park/garden, 16.xii.2006 (*B.L.Fisher et al.*); Antsiranana, 6.5 km SSW Befingotra, Rés. Anjanaharibe-Sud, 14.75°S, 49.5°E, 875 m, rainforest, 19.x.1994 (*B.L.Fisher*); Antsiranana, 9.2 km WSW Befingotra, Rés. Anjanaharibe-Sud, 14.75°S, 49.4667°E, 1280 m, montane rainforest, 5.xi.1994 (*B.L.Fisher*); Antsiranana, Ambondrobe, 41.1 km 175° Vohemar, 13.7153°S, 50.1017°E, 10 m, littoral rainforest, 29.xi.2004 (*B.L.Fisher*); Ant-

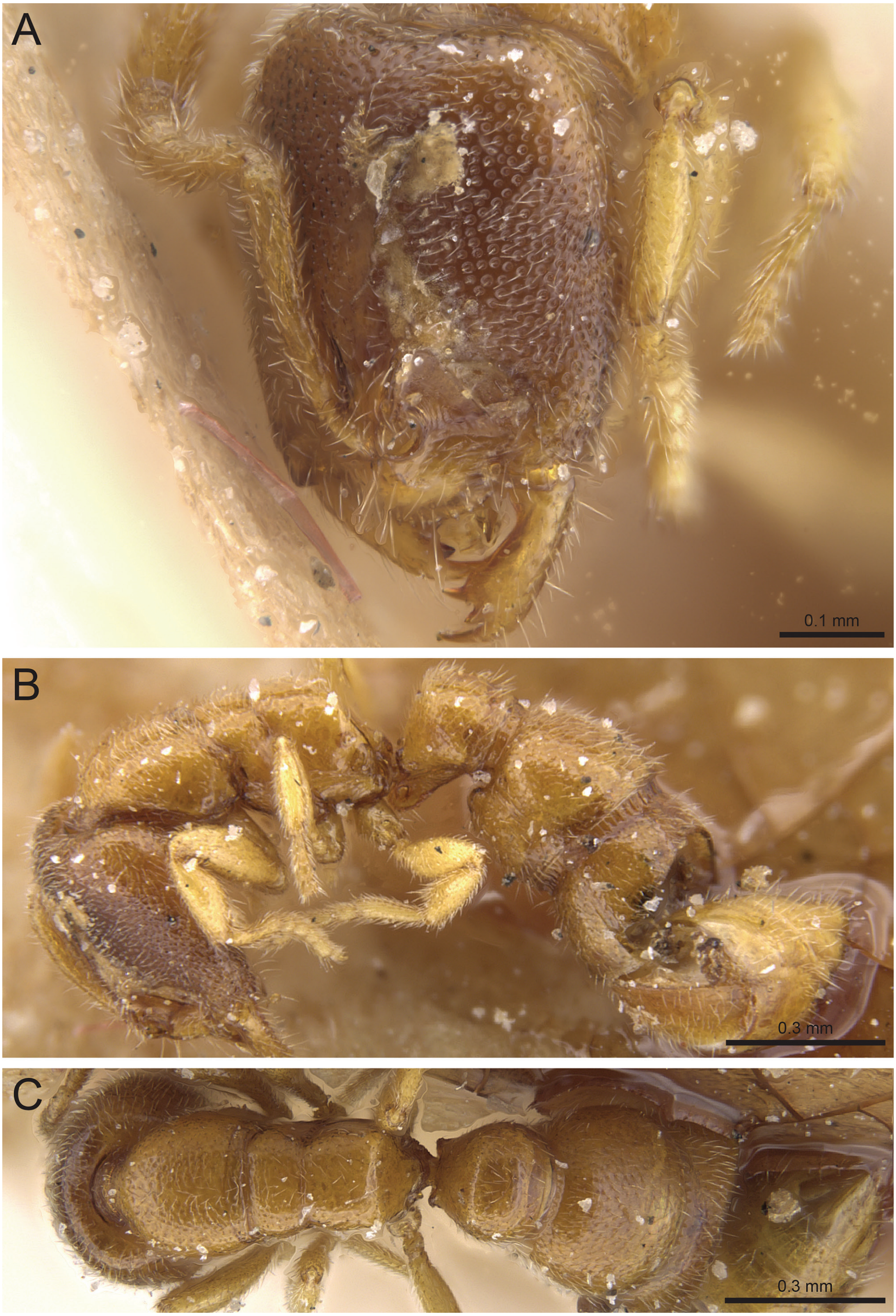

Figure 5. *P. descarpentriesi* lectotype worker (CASENT0101547). **A** Head in full-face view **B** Body in profile **C** Body in dorsal view.

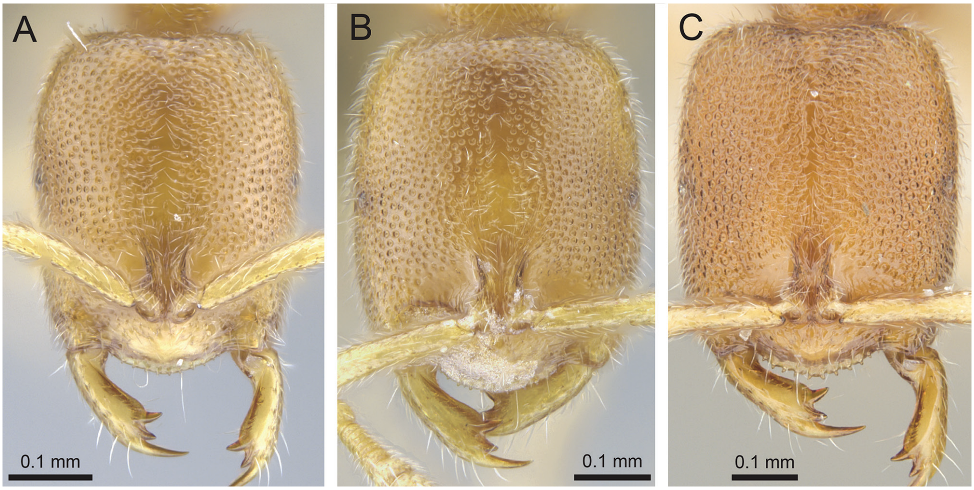

Figure 6. A, B, C Head in full-face view displaying variation in *P. descarpentriesi* for cephalic sculpture. **A** (CASENT0034837) "morphotype-A" **B** (CASENT0480792) "morphotype-B" **C** (CASENT0191895) "morphotype-C".

siranana, Ampasindava, Andranomatavy Forest, 13.669°S, 47.9877°E, 149 m, disturbed dry forest, 6.x.2013 (*B.L.Fisher et al.*); Antsiranana, Ampasindava, Andranomatavy Forest, 13.663°S, 47.9794°E, 543 m, disturbed dry forest, 6.x.2013 (*B.L.Fisher et al.*); Antsiranana, Binara Forest, 13.2621°S, 49.6067°E, 559 m, degraded rainforest, 18.x.2013 (*B.L.Fisher et al.*); Antsiranana, Binara Forest, 13.2621°S, 49.605°E, 692 m, rainforest, 18.x.2013 (*B.L.Fisher et al.*); Antsiranana, Binara Forest, 13.2639°S, 49.5992°E, 1065 m, rainforest, 18.x.2013 (*B.L.Fisher et al.*); Antsiranana, Forêt Ambanitaza, 26.1 km 347° Antalaha, 14.6793°S, 50.1837°E, 240 m, rainforest, 26.xi.2004 (*B.L.Fisher*); Antsiranana, Forêt d' Andavakoera, 21.4 km 75° ENE Ambilobe; 4.6 km 356° N Betsiaka, 13.1183°S, 49.23°E, 425 m, rainforest, 15.xii.2003 (*B.L.Fisher*); Antsiranana, Forêt d' Antsahabe, 11.4 km 275° W Daraina, 13.2117°S, 49.5567°E, 550 m, tropical dry forest, 12.xii.2003 (*B.L.Fisher*); Antsiranana, Forêt d'Ampondrabe, 26.3 km 10° NNE Daraina, 12.97°S, 49.7°E, 175 m, tropical dry forest, 10.xii.2003 (*B.L.Fisher*); Antsiranana, Forêt de Bekaraoka, 6.8 km 60° ENE Daraina, 13.1667°S, 49.71°E, 150 m, tropical dry forest, 7.xii.2003 (*B.L.Fisher*); Antsiranana, Forêt de Binara, 7.5 km 230° SW Daraina, 13.255°S, 49.6167°E, 375 m, tropical dry forest, 1.xii.2003 (*B.L.Fisher*); Antsiranana, Forêt de Binara, 9.1 km 233° SW Daraina, 13.2633°S, 49.6033°E, 800 m, rainforest, 3.xii.2003 (*B.L.Fisher*); Antsiranana, Forêt de Binara, 9.4 km 235° SW Daraina, 13.2633°S, 49.6°E, 1100 m, montane rainforest, 5.xii.2003 (*B.L.Fisher*); Antsiranana, Galoko chain, Mont Galoko, 13.5936°S, 48.7316°E, 1100 m, montane forest, 22.ii.2013 (*B.L.Fisher et al.*); Antsiranana, Galoko chain, Mont Galoko, 13.5888°S, 48.7286°E, 980 m, montane forest, 22.ii.2013 (*B.L.Fisher et al.*); Antsiranana, Galoko chain, Mont Galoko, 13.5849°S, 48.7182°E, 520 m, rainforest, 16.ii.2013 (*B.L.Fisher et al.*); Antsiranana, Galoko chain, Mont Kalabenono, 13.6418°S, 48.6728°E, 643 m, rainforest, 10.x.2013 (*B.L.Fisher et al.*); Antsiranana, Galoko chain, Mont Kalabenono, 13.64°S, 48.6737°E, 498 m, rainforest, 10.x.2013 (*B.L.Fisher et al.*); Antsiranana, Galoko chain, Mont Kalabenono, 13.6461°S, 48.6773°E, 937 m, rainforest, 10.x.2013 (*B.L.Fisher et al.*); Antsiranana, Makirovana forest, 14.1604°S, 49.9522°E, 550 m, rainforest, 1.v.2011 (*B.L.Fisher et al.*); Antsiranana, Makirovana forest, 14.1651°S, 49.9477°E, 900 m, montane rainforest, 30.iv.2011 (*B.L.Fisher et al.*); Antsiranana, Makirovana forest, 14.1667°S, 49.95°E, 715 m, rainforest, 1.v.2011 (*B.L.Fisher et al.*); Antsiranana, Makirovana forest, 14.1707°S, 49.9541°E, 415 m, rainforest, 28.iv.2011 (*B.L.Fisher et al.*); Antsiranana, Parc National de Marojejy, Antranohofa, 26.6 km 31° NNE Andapa, 10.7 km 318° NW Manantenina, 14.4433°S, 49.7433°E, 1325 m, montane rainforest, 18.xi.2003 (*B.L.Fisher*); Antsiranana, Parc National de Marojejy, Manantenina River, 27.6 km 35° NE Andapa, 9.6 km 327° NNW Manantenina, 14.435°S, 49.76°E, 775 m, rainforest, 15.xi.2003 (*B.L.Fisher et al.*); Antsiranana, Parc National de Marojejy, Manantenina River, 28.0 km 38° NE Andapa, 8.2 km 333° NNW Manantenina, 14.4367°S, 49.775°E, 450 m, rainforest, 12.xi.2003 (*B.L.Fisher et al.*); Antsiranana, Parc National Montagne d'Ambre, 12.2 km 211° SSW Joffreville, 12.5964°S, 49.1595°E, 1300 m, montane rainforest, 2.ii.2001 (*Fisher, Griswold et al.*); Antsiranana, Parc National Montagne d'Ambre, 3.6 km 235° SW Joffreville, 12.5344°S, 49.1795°E, 925 m, montane rainforest, 20.i.2001 (*Fisher, Griswold et al.*); Antsiranana, Prov.Antsiranana R.S. Manongarivo 17.3 km 218° SW Antanambao, 14.0217°S, 48.4183°E, 1580 m, montane rainforest, 27.x.1998 (*B.L.Fisher*); Antsiranana, R.S. Manongarivo, 10.8 km 229° SW Antanambao, 13.9617°S, 48.4333°E, 400 m, rainforest, 8.xi.1998 (*B.L.Fisher*); Antsiranana, R.S. Manongarivo, 12.8 km 228° SW Antanambao, 13.9767°S, 48.4233°E, 780 m, rainforest, 11.x.1998 (*B.L.Fisher*); Antsiranana, R.S. Manongarivo, 14.5 km 220° SW Antanambao, 13.9983°S, 48.4283°E, 1175 m, montane rainforest, 20.x.1998 (*B.L.Fisher*); Antsiranana, R.S. Manongarivo, 20.4 km 219° SW Antanambao, 14.0467°S, 48.4017°E, 1860 m, montane rainforest, 3.xi.1998 (*B.L.Fisher*); Fianarantsoa, 28 km. SSW Ambositra, Ankazomivady, 20.775°S, 47.1683°E, 1670 m, grassland, 11.i.1998 (*B.L.Fisher*); Fianarantsoa, 3 km W Ranomafana, nr. Ifandiana, 21.25°S, 47.4167°E, 950 m, forest, 27.iv.1989 (*P.S.Ward*); Fianarantsoa, 43 km S Ambalavao, Rés. Andringitra, 22.2333°S, 47°E, 825 m, rainforest, 5.x.1993 (*B.L.Fisher*); Fianarantsoa, 45 km S. Ambalavao, 22.2167°S, 47.0167°E, 785 m, rainforest, 25.ix.1993 (*B.L.Fisher*); Fianarantsoa, 7.6 km 122º Kianjavato, Forêt Classée Vatovavy, 21.4°S, 47.94°E, 175 m, rainforest, 6.vi.2005 (*B.L.Fisher et al.*); Fianarantsoa, 9.0 km NE Ivohibe, 22.4267°S, 46.9383°E, 900 m, rainforest, 12.xi.1997 (*B.L.Fisher* (*Sylvain*)); Fianarantsoa, Ampangabe I Non Protected Area, 21.4 km W Itremo, 20.6111°S, 46.6069°E, 1414 m, savannah woodland, 21.iii.2010 (*Andrianjaka Ravelomanana*); Fianarantsoa, Antapia I Non Protected Area, 26.43 km SW Ambositra, 20.7197°S, 47.0868°E, 1495 m, Uapaca woodland, 3.ii.2010 (*Andrianjaka Ravelomanana*); Fianarantsoa, Antohatsahomby V Non Protected Area, 22.63 km NW Itremo, 20.5672°S, 46.5792°E, 1726 m, Uapaca woodland, 18.iii.2010 (*Andrianjaka Ravelomanana*); Fianarantsoa, Forêt d'Atsirakambiaty, 7.6 km 285° WNW Itremo, 20.5933°S, 46.5633°E, 1550 m, montane rainforest, 22.i.2003 (*Fisher, Griswold et al.*); Fianarantsoa, Mampiarika I Non Protected Area, 28.08 km SW Ambositra, 20.7344°S, 47.0836°E, 1480 m, Uapaca woodland, 31.i.2010 (*Andrianjaka Ravelomanana*); Fianarantsoa, Mampiarika III Non Protected Area, 28.93 km SW Ambositra, 20.7358°S, 47.084°E, 1487 m, Uapaca woodland, 1.ii.2010 (*Andrianjaka Ravelomanana*); Fianarantsoa, Parc National Befotaka-Midongy, Papango 27.7 km S Midongy-Sud, Mount Papango, 23.8352°S, 46.9637°E, 940 m, rainforest, 13.xi.2006 (*B.L.Fisher et al.*); Fianarantsoa, Parc National d'Isalo, 9.1 km 354° N Ranohira, 22.4817°S, 45.4617°E, 725 m, gallery forest, 27.i.2003 (*Fisher, Griswold et al.*); Fianarantsoa, Parc National de Ranomafana, Vatoharanana River, 4.1 km 231° SW Ranomafana, 21.29°S, 47.4333°E, 1100 m, montane rainforest, 27.iii.2003 (*Fisher, Griswold et al.*); Fianarantsoa, Parc Nationale Ranomafana: Talatakely, 21.2483°S, 47.4267°E, in guava forest, 9.iv.1998 (*CE Griswold, DH Kavanaugh, ND Penny, MJ Raherilalao, JS Ranorianarisoa, J Schwei*); Fianarantsoa, R.S. Ivohibe, 7.5 km ENE Ivohibe, 22.47°S, 46.96°E, 900 m, rainforest, 7.x.1997 (*B.L.Fisher* (*Sylvain*)); Fianarantsoa, Réserve Forestière d'Agnalazaha, Mahabo, 42.9 km 215° Farafangana, 23.1938°S, 47.723°E, 20 m, littoral rainforest, 19.iv.2006 (*B.L. Fisher et al.*); Fianarantsoa, Soanierenana I Non Protected Area, 25.33 km SW Ambositra, 20.7214°S, 47.1099°E, 1723 m, savannah grassland, 6.ii.2010 (*Andrianjaka Ravelomanana*); Mahajanga, Réserve Spéciale Marotandrano, Marotandrano 48.3 km S Mandritsara, 16.2832°S, 48.8144°E, 865 m, transition humid forest, 6.xii.2007 (*B.L.Fisher et al.*); Toamasina, 16 km S Moramanga, 19.0833°S, 48.2333°E, 950 m, rainforest, 18.xi.1990 (*P. S. Ward*); Toamasina, 19 km ESE Maroantsetra, 15.4833°S, 49.9°E, 350 m, rainforest, 22.iv.1989 (*P. S. Ward*); Toamasina, 5.3 km SSE Ambanizana, Andranobe, 15.6713°S, 49.974°E, 425 m, rainforest, 19.xi.1993 (*B.L.Fisher*); Toamasina, 6.3 km S Ambanizana, Andranobe, 15.6813°S, 49.958°E, 25 m, rainforest, 14.xi.1993 (*B.L.Fisher*); Toamasina, 6.9 km NE Ambanizana, Ambohitsitondroina, 15.5851°S, 50.0095°E, 825 m, rainforest, 2.xii.1993 (*B.L.Fisher*); Toamasina, Ambanizana, Parc National Masoala, 15.5717°S, 50.0061°E, 925 m, montane rainforest, 26.ii.2003 (*D. Andriamalala, D. Silva, et al.*); Toamasina, Ambatovy, 12.4 km NE Moramanga, 18.8496°S, 48.2947°E, 1010 m, montane rainforest, 3.iii.2007 (*B.L.Fisher et al.*); Toamasina, Ambatovy, 12.4 km NE Moramanga, 18.8394°S, 48.3084°E, 1080 m, montane rainforest, 4.iii.2007 (*B.L.Fisher et al.*); Toamasina, Analamay, 18.8062°S, 48.3371°E, 1068 m, montane rainforest, 21.iii.2004 (*Malagasy ant team*); Toamasina, Corridor Forestier Analamay-Mantadia, Ambatoharanana, 18.8042°S, 48.4008°E, 968 m, rainforest, 12.xii.2012 (*B.L.Fisher et al.*); Toamasina, Corridor Forestier Analamay-Mantadia, Ambohibolakely, 18.779°S, 48.3638°E, 918 m, rainforest, 23.xi.2012 (*B.L.Fisher et al.*); Toamasina, Corridor Forestier Analamay-Mantadia, Tsaravoniana, 18.7612°S, 48.4213°E, 939 m, rainforest, 2.xii.2012 (*B.L.Fisher et al.*); Toamasina, Corridor Forestier Analamay-Mantadia, Tsaravoniana, 18.7646°S, 48.4194°E, 1039 m, rainforest, 2.xii.2012 (*B.L.Fisher et al.*); Toamasina, Forêt Ambatovy, 14.3 km 57° Moramanga, 18.8508°S, 48.32°E, 1075 m, montane rainforest, 21.iii.2004 (*Malagasy ant team*); Toamasina, Ile Sainte Marie, Forêt Kalalao, 9.9 km 34° Ambodifotatra, 16.9225°S, 49.8873°E, 100 m, rainforest, 24.xi.2005 (*B.L.Fisher et al.*); Toamasina, Montagne d'Akirindro 7.6 km 341° NNW Ambinanitelo, 15.2883°S, 49.5483°E, 600 m, rainforest, 17.iii.2003 (*Fisher, Griswold et al.*); Toamasina, Montagne d'Anjanaharibe, 18.0 km 21° NNE Ambinanitelo, 15.1883°S, 49.615°E, 470 m, rainforest, 8.iii.2003 (*Fisher, Griswold et al.*); Toamasina, Montagne d'Anjanaharibe, 19.5 km 27° NNE Ambinanitelo, 15.1783°S, 49.635°E, 1100 m, montane rainforest, 12.iii.2003 (*Fisher, Griswold et al.*); Toamasina, Parc National de Zahamena, Onibe River, 17.7591°S, 48.8547°E, 780 m, rainforest, 21.ii.2009 (*B.L.Fisher et al.*); Toamasina, Parc National de Zahamena, Tetezambatana forest, near junction of Nosivola and Manakambahiny Rivers, 17.743°S, 48.7294°E, 860 m, rainforest, 18.ii.2009 (*B.L.Fisher et al.*); Toamasina, Parc National Mananara-Nord, 7.1 km 261° Antanambe, 16.455°S, 49.7875°E, 225 m, rainforest, 14.xi.2005 (*B.L.Fisher et al.*); Toamasina, Parcelle K7 Tampolo, 17.2833°S, 49.4167°E, 10 m, littoral forest, 16.iv.2004 (*Malagasy ant team*); Toamasina, Parcelle K9 Tampolo, 17.175°S, 49.268°E, 10 m, littoral forest, 19.iv.2004 (*Malagasy ant team*); Toamasina, Res. Ambodiriana, 4.8 km 306°Manompana, along Manompana river, 16.6723°S, 49.7012°E, 125 m, rainforest, 18.xi.2005 (*B.L.Fisher et al.*); Toamasina, Reserve Betampona, Camp Vohitsivalana, 37.1 km 338° Toamasina, 17.8867°S, 49.2025°E, 520 m, rainforest, 1.xii.2005 (*B.L.Fisher et al.*); Toamasina, Réserve Spéciale Ambatovaky, Sandrangato river, 16.8175°S, 49.295°E, 360 m, rainforest, 25.ii.2010 (*B.L.Fisher et al.*); Toamasina, S.F. Tampolo, 10 km NNE Fenoarivo Atn., 17.2825°S, 49.43°E, 10 m, littoral rainforest, 4.iv.1997 (*B.L.Fisher*); Toamasina, Sahafina forest 11.4 km W Brickaville, 18.8145°S, 48.962°E, 140 m, rainforest, 13.xii.2007 (*B.L.Fisher et al.*); Toamasina, Torotorofotsy, 18.8708°S, 48.3474°E, 1070 m, montane rainforest, marsh edge, 24.iii.2004 (*Malagasy ant team*); Toliara, 10 km NW Enakara, Rés. Andohahela, 24.5667°S, 46.8167°E, 430 m, rainforest, 22.xi.1992 (*B.L.Fisher*); Toliara, 11 km NW Enakara, Rés. Andohahela, 24.5667°S, 46.8333°E, 800 m, rainforest, 17.xi.1992 (*B.L.Fisher*); Toliara, 2.7 km WNW 302° Ste. Luce, 24.7717°S, 47.1717°E, 20 m, littoral rainforest, 9.xii.1998 (*B.L.Fisher* (*J.-Baptiste*)); Toliara, Anosy Region, Distric of Amboasary, 58Km SW of Fort Dauphin, 08 Km NW of Amboasary, Berenty Special Reserve, 25.0067°S, 46.3033°E, 85 m, Galery forest, 25.v.2003 (*Rin'ha, Mike*); Toliara, Forêt Classée d'Analavelona, 29.2 km 343° NNW Mahaboboka, 22.675°S, 44.19°E, 1100 m, montane rainforest, 18.ii.2003 (*Fisher, Griswold et al.*); Toliara, Forêt Classée d'Analavelona, 29.4 km 343° NNW Mahaboboka, 22.675°S, 44.1867°E, 1050 m, montane rainforest, 21.ii.2003 (*Fisher, Griswold et al.*); Toliara, Forêt Ivohibe 55.6 km N Tolagnaro, 24.5617°S, 47.2002°E, 650 m, rainforest, 4.xii.2006 (*B.L.Fisher et al.*); Toliara, Grand Lavasoa, 25.9 km W Tolagnaro, 25.0877°S, 46.749°E, 450 m, rainforest, 30.xi.2006 (*B.L.Fisher et al.*); Toliara, Mandena, 8.4 km NNE 30° Tolagnaro, 24.9517°S, 47.0017°E, 20 m, littoral rainforest, 20.xi.1998 (*B.L.Fisher*); Toliara, Parc National Andohahela, Col de Tanatana, 33.3 km NW Tolagnaro, 24.7585°S, 46.8537°E, 275 m, rainforest, 22.xi.2006 (*B.L.Fisher et al.*); Toliara, Rés. Andohahela, 6 km SSW Eminiminy, 24.7333°S, 46.8°E, 330 m, rainforest, 4.ii.1993 (*P. S. Ward*); Toliara, Réserve Spéciale d'Ambohijanahary, Forêt d'Ankazotsihitafototra, 34.6 km 314° NW Ambaravaranala, 18.26°S, 45.4183°E, 1100 m, montane rainforest, 16.i.2003 (*Fisher, Griswold et al.*); Toliara, Réserve Spéciale d'Ambohijanahary, Forêt d'Ankazotsihitafototra, 35.2 km 312° NW Ambaravaranala, 18.2667°S, 45.4067°E, 1050 m, montane rainforest, 13.i.2003 (*Fisher, Griswold et al.*); Toliara, Réserve Spéciale Kalambatritra, Ampanihy, 23.4635°S, 46.4631°E, 1270 m, montane rainforest, 9.ii.2009 (*B.L.Fisher et al.*); Bongolava Prefec. de Tsiroanomandidy, 6.xii.1974 (*A.Peyrieras*).

Prionopelta laurae **Overson & Fisher, sp. n.**

http://zoobank.org/7FC54F7E-4F21-4714-A6C1-D4F6757A7999
Fig. 7

Type material. Holotype, pinned worker, MADAGASCAR, Antsiranana, Parc National de Marojejy, Manantenina River, 28.0 km 38° NE Andapa, 8.2 km 333° NNW Manantenina, 14.43667°S, 49.775°E, 450 m, rainforest, sifted litter (leaf mold, rotten wood), collection code: BLF08722, 12.xi.2003 (*B.L. Fisher et al.*) (CASC: CASENT0046149). **Paratypes**, nine pinned workers with same data as holotype (BMNH: CASENT0046153; CASC: CASENT0046141; CASENT0046142; CASENT0046143; CASENT0046147; CASENT0046151; MCZC: CASENT0046150; MHNG: CASENT0046140; NHMB: CASENT0046148).

Diagnosis. *P. laurae* is the only Malagasy *Prionopelta* with workers that possess nine antennal segments (all others possess twelve). Additionally, it is the smallest of all the Malagasy species with HL < 0.4 mm and HW < 0.3 mm (HL and HW of all other species is greater than 0.4 mm and 0.3 mm respectively).

Worker measurements (N=16). HL 0.33–0.38 (0.35); HW 0.24–0.27 (0.26); SL 0.16–0.18 (0.17); WL 0.34–0.4 (0.38); PetL 0.09–0.11 (0.1); PetW 0.13–0.15 (0.14); T1W 0.19–0.23 (0.21); CI 67.55–75.64 (72.71); PI 120.18–152.75 (135.44); SI 61.62–69.05 (65.06).

Worker description. Head much longer than wide with lowest cephalic index on average of all Malagasy *Prionopelta* (mean CI 72.71); posterior head margin straight in full-face view; cephalic foveae small and very dense, with no space for additional cephalic foveae present; median cephalic band devoid of foveae is long and thin and appears slightly swollen or raised above the surrounding integument, forming a scarlike suture; apical tooth of the mandible over four times the length of third tooth in full-face view; nine antennal segments; eye greatly reduced, appearing as a tiny, dark gray patch; majority of marks on pronotum are densely spaced, tiny punctures; mesonotum and propodeum consisting of tiny shallow foveae; metanotal groove visible dorsally; smallest of the *Prionopelta* from Malagasy region; body distinctly pale yellow in color.

Etymology. The name of this species is a patronym dedicated to Laura D. Steger for her continual support during the course of this work and her either completely genuine—or expertly feigned—enthusiasm for being endlessly bombarded by information about ants.

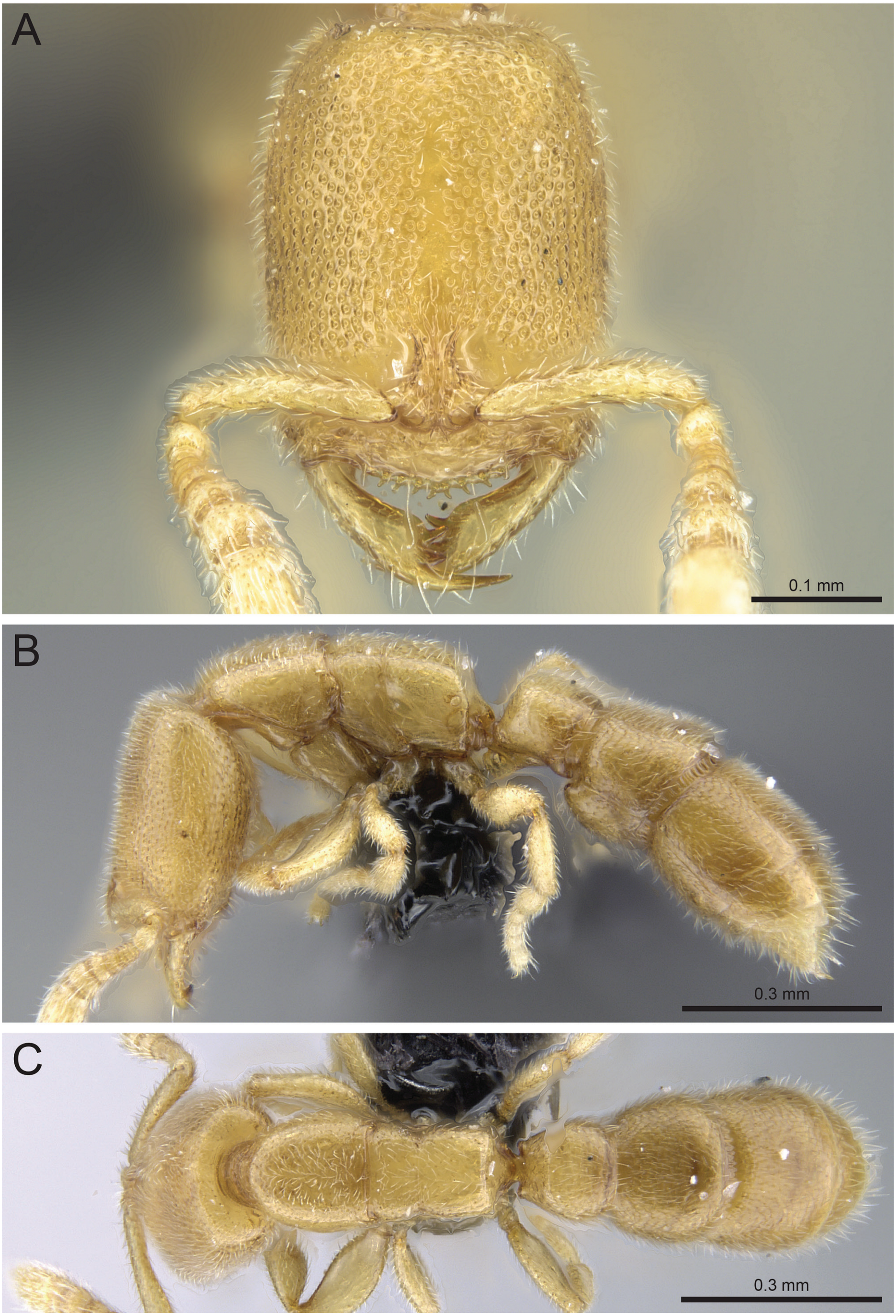

Figure 7. *P. laurae* paratype worker (CASENT0046151). **A** Head in full-face view **B** Body in profile **C** Body in dorsal view.

Distribution and ecology. This species has been collected in leaf litter primarily in rainforest with some collections from littoral rainforest and one in tropical dry rainforest, at elevations between 10–600 meters. Its range is restricted to eastern Madagascar and is seemingly disjunct, with most individuals collected from the northeast and only two locales known from the southeast near the coast. No individuals have been collected between Sahafina Forest in the north and Mahabo forest in the south, a distance of 500 km (Fig. 13). The current range of *P. laurae* is such that it may once have been distributed along the entire eastern coast of Madagascar.

Taxonomic notes. This species of *Prionopelta* is unmistakable as it is the only Malagasy species with nine antennal segments. It is also the smallest known species of Malagasy *Prionopelta* and is a distinct pale yellow color, which is much lighter than the fully-sclerotized workers of any other Malagasy species.

Non-type material. MADAGASCAR: Antsiranana, Ambondrobe, 41.1 km 175° Vohemar, 13.7153°S, 50.1017°E, 10 m, littoral rainforest, 29.xi.2004 (*B.L.Fisher*); Antsiranana, Forêt Ambanitaza, 26.1 km 347° Antalaha, 14.6793°S, 50.1837°E, 240 m, rainforest, 26.xi.2004 (*B.L.Fisher*); Antsiranana, Forêt de Binara, 7.5 km 230° SW Daraina, 13.255°S, 49.6167°E, 375 m, tropical dry forest, 1.xii.2003 (*B.L.Fisher*); Fianarantsoa, Réserve Forestière d'Agnalazaha, Mahabo, 42.9 km 215° Farafangana, 23.1938°S, 47.723°E, 20 m, littoral rainforest, 19.iv.2006 (*B.L. Fisher et al.*); Toamasina, 19 km ESE Maroantsetra, 15.4833°S, 49.9°E, 350 m, rainforest, 22.iv.1989 (*P. S. Ward*); Toamasina, Montagne d'Akirindro 7.6 km 341° NNW Ambinanitelo, 15.2883°S, 49.5483°E, 600 m, rainforest, 17.iii.2003 (*Fisher, Griswold et al.*); Toamasina, Nosy Mangabe, 15.5°S, 49.7667°E, 300 m, rainforest, 18.iv.1989 (*P. S. Ward*); Toamasina, Parc National Mananara-Nord, 7.1 km 261° Antanambe, 16.455°S, 49.7875°E, 225 m, rainforest, 14.xi.2005 (*B.L.Fisher et al.*); Toamasina, Reserve Betampona, Camp Rendrirendry 34.1 km 332° Toamasina, 17.924°S, 49.1997°E, 390 m, rainforest, 28.xi.2005 (*B.L.Fisher et al.*); Toamasina, Reserve Betampona, Camp Vohitsivalana, 37.1 km 338° Toamasina, 17.8867°S, 49.2025°E, 520 m, rainforest, 1.xii.2005 (*B.L.Fisher et al.*); Toamasina, Réserve Spéciale Ambatovaky, Sandrangato river, 16.7727°S, 49.2655°E, 450 m, rainforest, 20.ii.2010 (*B.L.Fisher et al.*); Toamasina, Réserve Spéciale Ambatovaky, Sandrangato river, 16.8175°S, 49.295°E, 360 m, rainforest, 25.ii.2010 (*B.L.Fisher et al.*); Toamasina, Sahafina forest 11.4 km W Brickaville, 18.8145°S, 48.962°E, 140 m, rainforest, 13.xii.2007 (*B.L.Fisher et al.*); Toliara, 2.7 km WNW 302° Ste. Luce, 24.7717°S, 47.1717°E, 20 m, littoral rainforest, 9.xii.1998 (*B.L.Fisher, J.-Baptiste*).

Prionopelta seychelles Overson & Fisher, sp. n.

http://zoobank.org/8DB94B93-AD69-4D75-B5A4-2561EC02622B
Figs 3C, 8

Type material. Holotype, pinned worker, SEYCHELLES, Silhouette Island, ridge from Mont Corgat to Mont Cocos Marrons, 4.50126°S, 55.23985°E, 455 m, forest, sifted litter (leaf mold, rotten wood), collection code BLF23364, 24.ii.2010 (*B.L. Fisher et al.*) (CASC: CASENT0161311). **Paratypes**, eight pinned workers with same data as holotype (BMNH: CASENT0161314; CASC: CASENT0161310; CASENT0161312; CASENT0161313; CASENT0161315; CASENT0161316; CASENT0161317; CASENT0161319).

Diagnosis. *P. seychelles* is the only known species from Seychelles. It can be distinguished from all other Malagasy *Prionopelta* through the following characters: twelve antennal segments; densely arranged cephalic foveae with virtually no space for additional foveae and no shining integument visible between; pronotum consisting of shallow foveae much larger in diameter than those on the head with punctures between; median cephalic band which is devoid of foveae not swelling above the surrounding integument, and often characterized as being wider anteriorly and narrower posteriorly.

Worker measurements (N=15). HL 0.44–0.48 (0.46); HW 0.33–0.37 (0.35); SL 0.22–0.26 (0.24); WL 0.47–0.54 (0.5); PetL 0.13–0.17 (0.14); PetW 0.17–0.21 (0.18); T1W 0.29–0.31 (0.3); CI 73.63–80.41 (76.39); PI 106.92–144.44 (128.7); SI 64.56–73.43 (69.77).

Worker description. Twelve antennal segments; posterior margin of the head weakly concave in full-face view; small cephalic foveae densely positioned so that no flat, shining integument is present between; median cephalic band which is devoid of foveae does not appear to swell above the surrounding integument, but rather appears as a smooth, shining surface which is widest anteriorly, narrowing posteriorly; apical tooth intermediate in length; pronotum with foveae which range from shallow to deep and are interspersed regularly with punctures; mesonotum and propodeum consisting of large, shallow foveae; metanotal groove strongly visible, and mesopropodeal suture visible to barely visible, but some depression always present; posterior propodeal edge viewed dorsally is straight or only very slightly concave; no protruding lamellae of the posterior propodeum.

Etymology. This species is named after the Seychelles archipelago, to which it is endemic. The species epithet is a noun in apposition, and thus invariable.

Distribution and ecology. This species is known only from Seychelles and is found between 15–660 meters of elevation on the islands of Mahé, Conception, Thérèse, Silhouette, Praslin, La Digue, Félicité Island, and the Little Sister island group. It does not appear to have strict habitat preferences as it has been collected in mixed forest, littoral forest, non-native forest, palm forest, and coastal scrub. *P. seychelles* has also been collected from a diversity of microhabitats including from leaf litter, inside rotten logs, under rocks, under moss on live trees, and under root mats.

Taxonomic notes. *P. seychelles* is most likely to be confused with *P. subtilis*, as both have very small cephalic foveae that are densely arranged on the head. However, the two species are not sympatric, as *P. seychelles* is known only from Seychelles, and *P. subtilis* only from Madagascar. The median cephalic bands contrast markedly between these taxa, as that of *P. seychelles* is wide anteriorly, often tapering posteriorly, with an interrupted border caused by aberrantly placed foveae which break up the margins which define the smooth shining area (Fig. 8A). That of *P. subtilis*, on the other hand,

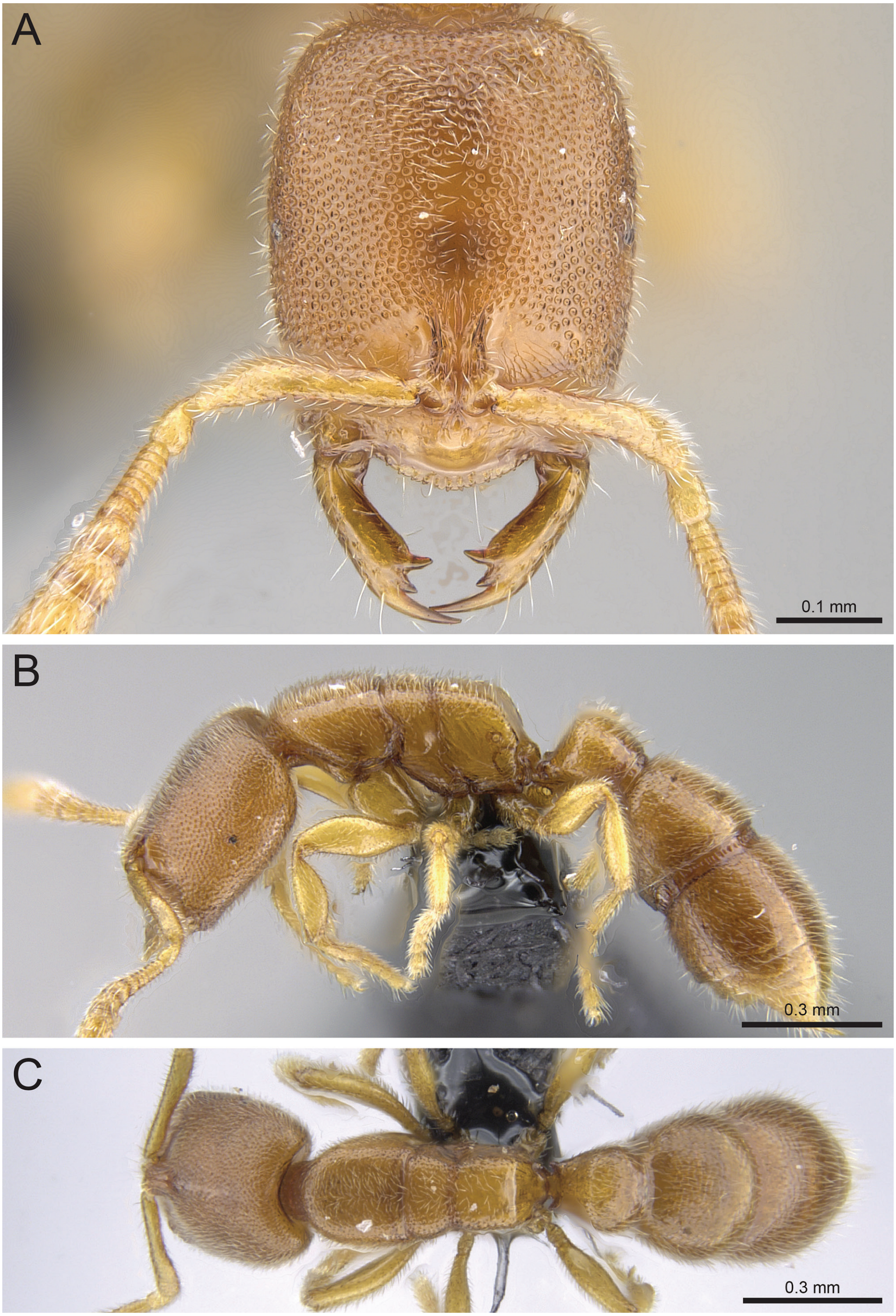

Figure 8. *P. seychelles* paratype worker (CASENT0161319). **A** Head in full-face view **B** Body in profile **C** Body in dorsal view.

is very thin throughout its length, with clearly defined borders which are swollen above the surrounding integument (Fig. 3A, B) On average, *P. subtilis* also has a wider head than *P. seychelles*: 0.39–0.45 (0.42) vs. 0.33–0.37 (0.35), respectively. Additionally, the cephalic foveae of *P. subtilis* are smaller and the cephalic sculpture overall appears more delicate than that of *P. seychelles*.

Non-type material. SEYCHELLES: Conception Island, 4.6631°S, 55.3682°E, 65 m, mixed forest, 12.ii.2010 (*B.L.Fisher et al.*); Félicité Island, 4.3258°S, 55.8698°E, 120 m, forest, 1.ii.2010 (*B.L.Fisher et al.*); La Digue Island, 4.3561°S, 55.8433°E, 300 m, forest, 31.i.2010 (*B.L.Fisher et al.*); La Digue Island, Veuve Réserve, 4.357°S, 55.8279°E, 15 m, littoral forest, 2.ii.2010 (*B.L.Fisher et al.*); Mahé Island, Casse Dent, Morne Seychellois National Park, 4.6528°S, 55.4374°E, 465 m, mixed forest, 11.ii.2010 (*B.L.Fisher et al.*); Mahé Island, Morne Blanc, 4.6574°S, 55.4333°E, 660 m, mixed forest near glacis, 10.ii.2010 (*B.L.Fisher et al.*); Mare Aux Cochon, Mahé Island, 30.vii.2002 (*J. Gerlach*); Praslin Island, 4.3546°S, 55.748°E, 25 m, coastal scrub, 6.ii.2010 (*B.L.Fisher et al.*); Praslin Island, Praslin tower, 4.3409°S, 55.7451°E, 370 m, mixed forest, 3.ii.2010 (*B.L.Fisher et al.*); Praslin Island, Vallée de Mai, 4.331°S, 55.7389°E, 200 m, palm forest, 2.ii.2010 (*B.L.Fisher et al.*); Silhouette Island, above Jardin Marron on crest to Mont Plaisir and Pot à Eau, 4.4867°S, 55.2341°E, 520 m, forest, 20.i.2010 (*B.L.Fisher et al.*); Silhouette Island, Gratte Fesse, 4.4917°S, 55.2389°E, 450 m, forest, 6.iv.2009 (*J. Gerlach*); Silhouette Island, Jardin Marron, 4.4864°S, 55.2363°E, 395 m, non native forest, 27.i.2010 (*B.L.Fisher et al.*); Silhouette Island, Jardin Marron, 4.4864°S, 55.2364°E, 390 m, 24.iii.2009 (*J. Gerlach*); Silhouette Island, La Passe, 4.4847°S, 55.2508°E, 20 m, park/garden, 12.vii.2001 (*J. Gerlach*); Silhouette Island, on path to Anse Mondon, 4.4689°S, 55.2294°E, 255 m, forest, 23.i.2010 (*B.L.Fisher et al.*); Silhouette Island, on plateau toward Gratte Fesse, 4.4879°S, 55.2342°E, 490 m, forest, 22.i.2010 (*B.L.Fisher et al.*).

Prionopelta subtilis **Overson & Fisher, sp. n.**

http://zoobank.org/A5A3CDAC-71AF-48E1-914A-5086872539F0
Figs 3A, B, 9

Type material. Holotype, pinned worker, MADAGASCAR, Toamasina, Montagne d'Anjanaharibe, 18.0 km 21° NNE Ambinanitelo, 15.18833°S, 49.615°E, 470 m, rainforest, sifted litter (leaf mold, rotten wood), BLF08002, 8.iii.2003 (*B.L. Fisher et al.*) (CASC: CASENT0033641). **Paratypes**, 23 pinned workers with same data as holotype (BMNH: CASENT0033585; CASC: CASENT0033582; CASENT0033586; CASENT0033588; CASENT0033590; CASENT0033591; CASENT0033596; CASENT0033597; CASENT0033598; CASENT0033599; CASENT0033600; CASENT0033601; CASENT0033603; CASENT0033606; CASENT0033610; CASENT0033611; CASENT0033613; CASENT0033614; CASENT0033615; CASENT0033644; MCZC: CASENT0033604; MHNG: CASENT0033584; NHMB: CASENT0033643).

Diagnosis. *P. subtilis* can be recognized by the following combination of characters: twelve antennal segments; minute, densely placed cephalic foveae with raised margins where foveae touch so that the entire head is covered in a delicate mosaic of connected foveae with ridges between; well-defined, uniformly narrow, coronal suture that swells above the level of the surrounding integument; shallow foveae on the pronotum are much larger than those on the head, and more widely spaced, with tiny punctures between.

Worker measurements (N=20). HL 0.47–0.57 (0.52); HW 0.39–0.45 (0.42); SL 0.26–0.32 (0.29); WL 0.5–0.67 (0.58); PetL 0.14–0.18 (0.16); PetW 0.19–0.26 (0.22); T1W 0.31–0.4 (0.35); CI 76.55–86.41 (80.5); PI 126.32–150.69 (139.98); SI 61.34–71.39 (68.14).

Worker description. Posterior head margin slightly concave with a noticeable notch medially; cephalic foveae dense and minute; virtually no area of the head lacking foveae in full-face view except at the extreme posterolateral corners; median cephalic band devoid of foveae is thin, linear, and slightly but uniformly swells above the surrounding integument; apical tooth intermediate in length; foveae on the pronotum are shallow, as well as more widely spaced and obviously larger than those on the head, with punctures present between; mesonotum and propodeum consisting of shallow foveae and punctures; metanotal groove visible dorsally, and mesopropodeal suture strongly visible in lateral view.

Etymology. The name of this species comes from the Latin adjective meaning "fine", "thin", or "slender" and refers to the very delicate, net-like patterns produced by the sculpture on the head.

Distribution and ecology. This common and widespread species is found in rainforest, montane rainforest, lowland rainforest, tropical forest, littoral forest, degraded forest, and marsh edge from 5–1325 meters of elevation (Fig. 13). On the ground it has been collected from inside rotten logs and sticks, as well as under moss, rocks, logs, and in litter. It has also been collected from above-ground sites including canopy moss and leaf litter, as well as inside above-ground twigs and branches.

Taxonomic notes. *P. subtilis* is easy to recognize at a glance under high magnification once several individuals have been observed, as the very small and delicate foveae covering the entire surface of the head produce a unique visual appearance among the Malagasy *Prionopelta*. The only other confusable species with dense, directly adjacent foveae across the entire head (besides *P. laurae*, which would not be mistaken for *P. subtilis*) are *P. seychelles*, and some *P. descarpentriesi*. Unlike *P. subtilis*, *P. seychelles* does not possesses a coronal suture medially on the head. Some individuals of *P. descarpentriesi* have a dense pattern of touching foveae with a network of ridges between them across the entire head, but these foveae are much larger and deeper than in *P. subtilis*. Additionally, this trait in *P. descarpentriesi* is accompanied by sculpture on the pronotum that consists almost entirely of large foveae which are similar in size to those on the head, whereas *P. subtilis* has much larger foveae on its pronotum than on its head, and these foveae are interspersed with punctures.

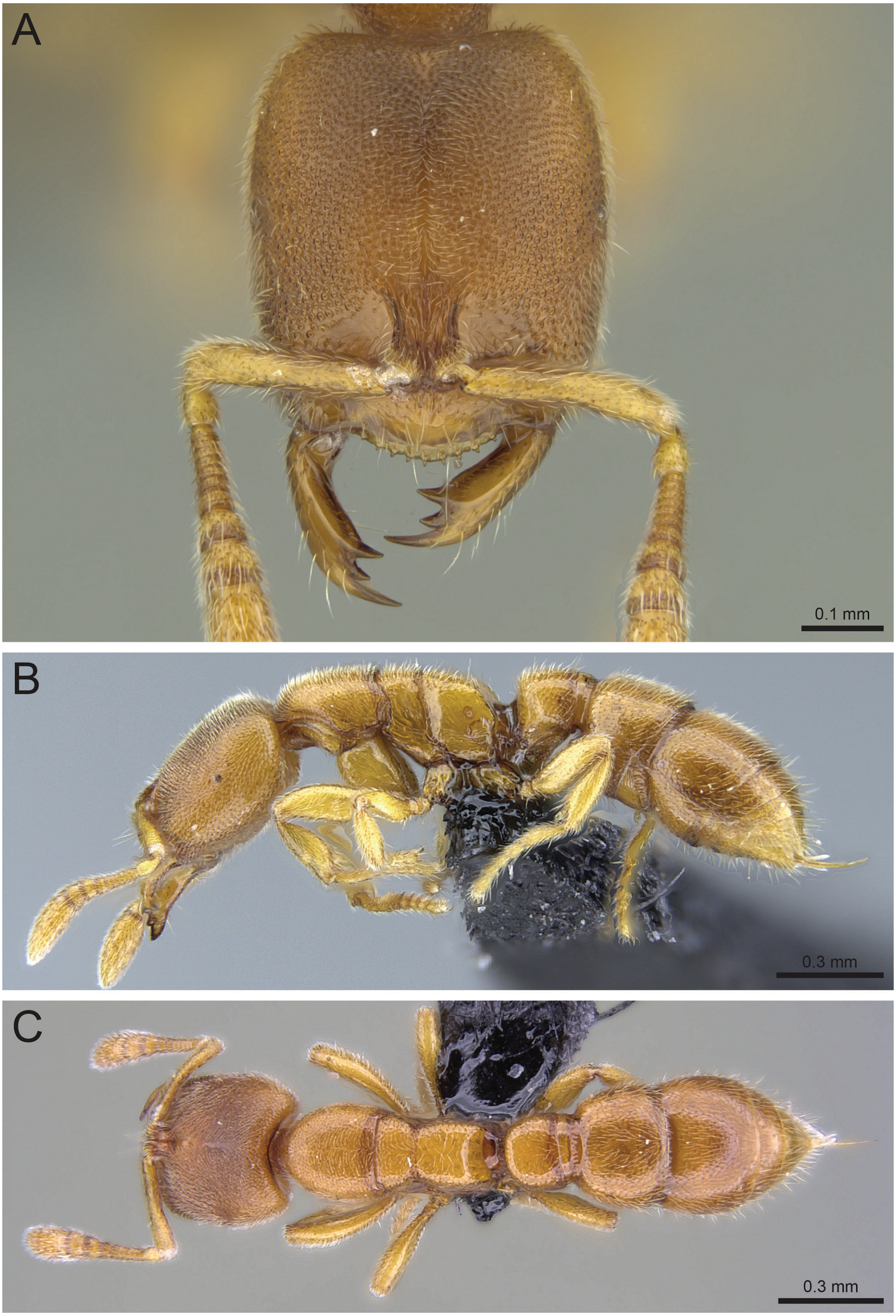

Figure 9. *P. subtilis* holotype worker (CASENT0033641). **A** Head in full-face view **B** Body in profile **C** Body in dorsal view.

Non-type material. MADAGASCAR: Andasibe, Mantadia NP, 7.i.2006 (*A.Ballerio*); Antsiranana, 6.5 km SSW Befingotra, Rés. Anjanaharibe-Sud, 14.75°S, 49.5°E, 875 m, rainforest, 19.x.1994 (*B.L.Fisher*); Antsiranana, 9.2 km WSW Befingotra, Rés. Anjanaharibe-Sud, 14.75°S, 49.4667°E, 1200 m, montane rainforest, 9.xi.1994 (*B.L.Fisher*); Antsiranana, Betaolana Forest, along Bekona River, 14.53°S, 49.4404°E, 880 m, rainforest, 4.iii.2009 (*B.L.Fisher et al.*); Antsiranana, Binara Forest, 13.2639°S, 49.5992°E, 1065 m, rainforest, 18.x.2013 (*B.L.Fisher et al.*); Antsiranana, Forêt de Binara, 9.4 km 235° SW Daraina, 13.2633°S, 49.6°E, 1100 m, montane rainforest, 5.xii.2003 (*B.L.Fisher*); Antsiranana, Makirovana forest, 14.1651°S, 49.9477°E, 900 m, montane rainforest, 30.iv.2011 (*B.L.Fisher et al.*); Antsiranana, Makirovana forest, 14.1667°S, 49.95°E, 715 m, rainforest, 2.v.2011 (*B.L.Fisher et al.*); Antsiranana, Makirovana forest, 14.1604°S, 49.9522°E, 550 m, rainforest, 1.v.2011 (*B.L.Fisher et al.*); Antsiranana, Makirovana forest, 14.1707°S, 49.9541°E, 415 m, rainforest, 29.iv.2011 (*B.L.Fisher et al.*); Antsiranana, Parc National de Marojejy, Antranohofa, 26.6 km 31° NNE Andapa, 10.7 km 318° NW Manantenina, 14.4433°S, 49.7433°E, 1325 m, montane rainforest, 18.xi.2003 (*B.L.Fisher*); Antsiranana, Parc National de Marojejy, Manantenina River, 27.6 km 35° NE Andapa, 9.6 km 327° NNW Manantenina, 14.435°S, 49.76°E, 775 m, rainforest, 15.xi.2003 (*B.L.Fisher et al.*); Antsiranana, Parc National de Marojejy, Manantenina River, 28.0 km 38° NE Andapa, 8.2 km 333° NNW Manantenina, 14.4367°S, 49.775°E, 450 m, rainforest, 12.xi.2003 (*B.L.Fisher et al.*); Antsiranana, Parc National Montagne d'Ambre, 12.5178°S, 49.1796°E, 1000 m, montane rainforest, 4.iii.2011 (*B.L.Fisher et al.*); Antsiranana, Parc National Montagne d'Ambre, 12.5139°S, 49.1778°E, 984 m, montane rainforest, 25.ii.2011 (*B.L.Fisher et al.*); Antsiranana, Parc National Montagne d'Ambre, 12.5231°S, 49.179°E, 1100 m, montane rainforest, 11.iii.2011 (*B.L.Fisher et al.*); Antsiranana, Parc National Montagne d'Ambre, 12.5342°S, 49.1761°E, 1325 m, montane rainforest, 12.iii.2011 (*B.L.Fisher et al.*); Antsiranana, Parc National Montagne d'Ambre, 12.5247°S, 49.1724°E, 1235 m, montane rainforest, 10.iii.2011 (*B.L.Fisher et al.*); Antsiranana, Parc National Montagne d'Ambre, 3.6 km 235° SW Joffreville, 12.5344°S, 49.1795°E, 925 m, montane rainforest, 20.i.2001 (*Fisher, Griswold et al.*); Antsiranana, Parc National Montagne d'Ambre, Mahasarika, 12.5318°S, 49.1766°E, 1135 m, montane rainforest, 19.xi.2007 (*B.L.Fisher et al.*); Antsiranana, Parc National Montagne d'Ambre, Petit lac, 12.5366°S, 49.1741°E, 1130 m, montane rainforest, 17.xi.2007 (*B.L.Fisher et al.*); Antsiranana, Parc National Montagne d'Ambre, Roussettes, 12.5257°S, 49.1724°E, 1025 m, montane rainforest, 15.xi.2007 (*B.L.Fisher et al.*); Fianarantsoa, 43 km S Ambalavao, Rés. Andringitra, 22.2333°S, 47°E, 825 m, rainforest, 5.x.1993 (*B.L.Fisher*); Fianarantsoa, 45 km S. Ambalavao, 22.2167°S, 47.0167°E, 785 m, rainforest, 25.ix.1993 (*B.L.Fisher*); Fianarantsoa, Forêt d'Ambalagoavy Nord, Ikongo, Ambatombe, 21.8275°S, 47.3389°E, 625 m, 1.xii.2000 (*R. Harin'Hala & M.E. Irwin*); Fianarantsoa, Forêt de Vevembe, 66.6 km 293° Farafangana, 22.791°S, 47.1818°E, 600 m, rainforest, transition to montane forest, 24.iv.2006 (*B.L. Fisher et al.*); Fianarantsoa, Réserve

Forestière d'Agnalazaha, Mahabo, 42.9 km 215° Farafangana, 23.1938°S, 47.723°E, 20 m, littoral rainforest, 19.iv.2006 (*B.L. Fisher et al.*); Fianarantsoa, Réserve Spéciale Manombo 24.5 km 228° Farafangana, 23.0158°S, 47.719°E, 30 m, rainforest, 22.iv.2006 (*B.L. Fisher et al.*); Mahajanga, Réserve Spéciale Marotandrano, Marotandrano 48.3 km S Mandritsara, 16.2832°S, 48.8144°E, 865 m, transition humid forest, 7.xii.2007 (*B.L.Fisher et al.*); Toamasina, 16 km S Moramanga, 19.0833°S, 48.2333°E, 950 m, rainforest, 18.xi.1990 (*P. S. Ward*); Toamasina, 5.3 km SSE Ambanizana, Andranobe, 15.6713°S, 49.974°E, 425 m, rainforest, 21.xi.1993 (*B.L.Fisher*); Toamasina, 6.3 km S Ambanizana, Andranobe, 15.6813°S, 49.958°E, 25 m, rainforest, 14.xi.1993 (*B.L.Fisher*); Toamasina, 6.9 km NE Ambanizana, Ambohitsitondroina, 15.5851°S, 50.0095°E, 825 m, rainforest, 2.xii.1993 (*B.L.Fisher*); Toamasina, 6.9 km NE Ambanizana, Ambohitsitondroina, 15.5667°S, 50°E, 1000 m, montane rainforest, 8.xii.1993 (*B.L.Fisher*); Toamasina, 6 km ESE Andasibe (=Perinet), 18.95°S, 48.4667°E, 900 m, rainforest, 17.xi.1990 (*P. S. Ward*); Toamasina, Ambanizana, Parc National Masoala, 15.5717°S, 50.0061°E, 925 m, montane rainforest, 26.ii.2003 (*D. Andriamalala, D. Silva, et al.*); Toamasina, Ambanizana, Parc National Masoala, 15.5722°S, 50.0069°E, 1020 m, montane rainforest, 2.iii.2003 (*D. Andriamalala, D. Silva, et al.*); Toamasina, Ambatovy, 12.4 km NE Moramanga, 18.8394°S, 48.3084°E, 1080 m, montane rainforest, 8.iii.2007 (*B.L.Fisher et al.*); Toamasina, Ambatovy, 12.4 km NE Moramanga, 18.8496°S, 48.2947°E, 1010 m, montane rainforest, 3.iii.2007 (*B.L.Fisher et al.*); Toamasina, Analamay, 18.8062°S, 48.3371°E, 1068 m, montane rainforest, 21.iii.2004 (*Malagasy ant team*); Toamasina, Ankerana, 18.4067°S, 48.8228°E, 681 m, degraded forest, 28.i.2012 (*B.L.Fisher et al.*); Toamasina, Ankerana, 18.4064°S, 48.8025°E, 1108 m, montane forest, 19.i.2012 (*B.L.Fisher et al.*); Toamasina, Ankerana, 18.4104°S, 48.8189°E, 855 m, rainforest, 25.i.2012 (*B.L.Fisher et al.*); Toamasina, Ankerana, 18.4017°S, 48.806°E, 1035 m, montane forest, 24.i.2012 (*B.L.Fisher et al.*); Toamasina, Ankerana, 18.4006°S, 48.8131°E, 865 m, rainforest, 17.i.2012 (*B.L.Fisher et al.*); Toamasina, Ankerana, 18.4083°S, 48.8211°E, 750 m, rainforest, 21.i.2012 (*B.L.Fisher et al.*); Toamasina, Ankerana, 18.4061°S, 48.8203°E, 725 m, rainforest, 16.i.2012 (*B.L.Fisher et al.*); Toamasina, Bevolota 17.1 km N Andasibe, 18.7707°S, 48.4316°E, 995 m, montane rainforest, 12.xii.2007 (*B.L.Fisher et al.*); Toamasina, Corridor Forestier Analamay-Mantadia, Ambatoharanana, 18.8042°S, 48.4008°E, 968 m, rainforest, 12.xii.2012 (*B.L.Fisher et al.*); Toamasina, Corridor Forestier Analamay-Mantadia, Ambatoharanana, 18.8039°S, 48.4051°E, 1013 m, rainforest, 12.xii.2012 (*B.L.Fisher et al.*); Toamasina, Corridor Forestier Analamay-Mantadia, Ambatoharanana, 18.804°S, 48.4036°E, 1064 m, rainforest, 12.xii.2012 (*B.L.Fisher et al.*); Toamasina, Corridor Forestier Analamay-Mantadia, Ambatoharanana, 18.8044°S, 48.4074°E, 960 m, rainforest, 12.xii.2012 (*B.L.Fisher et al.*); Toamasina, Corridor Forestier Analamay-Mantadia, Ambohibolakely, 18.779°S, 48.3638°E, 918 m, rainforest, 23.xi.2012 (*B.L.Fisher et al.*); Toamasina, Corridor Forestier Analamay-Mantadia, Ambohibolakely, 18.7791°S, 48.3663°E, 1014 m, rainforest, 23.xi.2012 (*B.L.Fisher et al.*); Toamasina, Corridor Forestier Analamay-Mantadia, Ambohibolakely, 18.7609°S, 48.3713°E, 1044 m, rainforest, 29.xi.2012 (*B.L.Fisher et al.*); Toamasina, Corridor Forestier Analamay-Mantadia, Ambohibolakely, 18.7613°S, 48.3644°E, 983 m, rainforest, 26.xi.2012 (*B.L.Fisher et al.*); Toamasina, Corridor Forestier Analamay-Mantadia, Tsaravoniana, 18.7612°S, 48.4213°E, 939 m, rainforest, 2.xii.2012 (*B.L.Fisher et al.*); Toamasina, Corridor Forestier Analamay-Mantadia, Tsaravoniana, 18.7637°S, 48.4203°E, 984 m, rainforest, 2.xii.2012 (*B.L.Fisher et al.*); Toamasina, Corridor Forestier Analamay-Mantadia, Tsaravoniana, 18.7646°S, 48.4194°E, 1039 m, rainforest, 4.xii.2012 (*B.L.Fisher et al.*); Toamasina, Corridor Forestier Analamay-Mantadia, Tsaravoniana, 18.7574°S, 48.423°E, 1018 m, rainforest, 8.xii.2012 (*B.L.Fisher et al.*); Toamasina, F.C. Andriantantely, 18.695°S, 48.8133°E, 530 m, rainforest, 4.xii.1998 (*H.J.Ratsirarson*); Toamasina, F.C. Didy, 18.1983°S, 48.5783°E, 960 m, rainforest, 16.xii.1998 (*H.J.Ratsirarson*); Toamasina, F.C. Sandranantitra, 18.0483°S, 49.0917°E, 450 m, rainforest, 18.i.1999 (*H.J.Ratsirarson*); Toamasina, Forêt Ambatovy, 14.3 km 57° Moramanga, 18.8508°S, 48.32°E, 1075 m, montane rainforest, 12.iv.2005 (*B.L.Fisher*); Toamasina, Montagne d'Akirindro 7.6 km 341° NNW Ambinanitelo, 15.2883°S, 49.5483°E, 600 m, rainforest, 17.iii.2003 (*Fisher, Griswold et al.*); Toamasina, Montagne d'Anjanaharibe, 18.0 km 21° NNE Ambinanitelo, 15.1883°S, 49.615°E, 470 m, rainforest, 8.iii.2003 (*Fisher, Griswold et al.*); Toamasina, Montagne d'Anjanaharibe, 19.5 km 27° NNE Ambinanitelo, 15.1783°S, 49.635°E, 1100 m, montane rainforest, 12.iii.2003 (*Fisher, Griswold et al.*); Toamasina, Nosy Mangabe, 7.43 km S Maroantsetra, 15.4973°S, 49.7622°E, 5 m, littoral rainforest edge, 25.vii.2007 (*B.L.Fisher et al.*); Toamasina, P.N. Mantadia, 18.7917°S, 48.4267°E, 895 m, rainforest, 25.xi.1998 (*H.J.Ratsirarson*); Toamasina, Parc National de Zahamena, 17.7336°S, 48.7263°E, 950 m, rainforest, 19.ii.2009 (*B.L.Fisher et al.*); Toamasina, Parc National de Zahamena, Besaky River, 17.7524°S, 48.8532°E, 760 m, rainforest, 22.ii.2009 (*B.L.Fisher et al.*); Toamasina, Parc National de Zahamena, Onibe River, 17.7591°S, 48.8547°E, 780 m, rainforest, 21.ii.2009 (*B.L.Fisher et al.*); Toamasina, Parc National de Zahamena, Sahavorondrano River, 17.7526°S, 48.8573°E, 765 m, rainforest, 23.ii.2009 (*B.L.Fisher et al.*); Toamasina, Parc National de Zahamena, Tetezambatana forest, near junction of Nosivola and Manakambahiny Rivers, 17.743°S, 48.7294°E, 860 m, rainforest, 18.ii.2009 (*B.L.Fisher et al.*); Toamasina, Reserve Betampona, Camp Rendrirendry 34.1 km 332° Toamasina, 17.924°S, 49.1997°E, 390 m, rainforest, 29.xi.2005 (*B.L.Fisher et al.*); Toamasina, Reserve Betampona, Camp Vohitsivalana, 37.1 km 338° Toamasina, 17.8867°S, 49.2025°E, 520 m, rainforest, 2.xii.2005 (*B.L.Fisher et al.*); Toamasina, Réserve Nationale Intégrale Betampona, Betampona 35.1 km NW Toamasina, 17.918°S, 49.2007°E, 500 m, rainforest, 15.xii.2007 (*B.L.Fisher et al.*); Toamasina, Réserve Spéciale Ambatovaky, Sandrangato river, 16.7702°S, 49.2664°E, 470 m, rainforest, 23.ii.2010 (*B.L.Fisher et al.*); Toamasina, Réserve Spéciale Ambatovaky, Sandrangato river, 16.7747°S, 49.2655°E, 355 m, rainforest along river, 21.ii.2010 (*B.L.Fisher et al.*); Toamasina, Réserve Spéciale Ambatovaky, Sandrangato river, 16.7633°S, 49.2669°E, 520 m, rainforest, 22.ii.2010 (*B.L.Fisher et al.*); Toamasina, Réserve Spéciale Ambatovaky, Sandrangato river, 16.7727°S, 49.2655°E, 450 m, rainforest, 20.ii.2010 (*B.L.Fisher et al.*); Toamasina, Réserve Spéciale Ambatovaky, Sandrangato river, 16.7691°S, 49.267°E, 475 m, rainforest, 21.ii.2010 (*B.L.Fisher et al.*); Toamasina, Réserve Spéciale Ambatovaky, Sandrangato river, 16.8175°S, 49.295°E, 360 m, rainforest, 25.ii.2010 (*B.L.Fisher et al.*); Toamasina, S.F. Tampolo, 10 km NNE Fenoarivo Atn., 17.2825°S, 49.43°E, 10 m, littoral rainforest, 5.iv.1997 (*B.L.Fisher*); Toamasina, Sahafina forest 11.4 km W Brickaville, 18.8145°S, 48.962°E, 140 m, rainforest, 13.xii.2007 (*B.L.Fisher et al.*); Toamasina, Torotorofotsy, 18.8708°S, 48.3474°E, 1070 m, montane rainforest, marsh edge, 24.iii.2004 (*Malagasy ant team*); Toamasina, Torotorofotsy, 18.7705°S, 48.4304°E, 1005 m, montane rainforest, 12.iii.2012 (*B.L.Fisher et al.*); Toliara, Parc National Andohahela, Col de Tanatana, 33.3 km NW Tolagnaro, 24.7585°S, 46.8537°E, 275 m, rainforest, 28.xi.2006 (*B.L.Fisher et al.*); Toliara, Parc National d'Andohahela, Manampanihy River, 5.4 km 113° ESE Mahamavo, 36.7 km 343° NNW Tolagnaro, 24.7639°S, 46.7668°E, 650 m, rainforest, 24.i.2002 (*Fisher-Griswold Arthropod Team*); Toliara, Rés. Andohahela, 6 km SSW Eminiminy, 24.7333°S, 46.8°E, 330 m, rainforest, 4.ii.1993 (*P.S.Ward*); Toliara, Réserve Spéciale d'Ambohijanahary, Forêt d'Ankazotsihitafototra, 35.2 km 312° NW Ambaravaranala, 18.2667°S, 45.4067°E, 1050 m, montane rainforest, 13.i.2003 (*Fisher, Griswold et al.*).

Prionopelta talos **Overson & Fisher, sp. n.**

http://zoobank.org/D7559E6C-40E3-47A5-B43A-5D5E14828003

Figs 4A, D, 10

Type material. Holotype, pinned worker, MADAGASCAR, Antsiranana, 9.2 km WSW Befingotra, Rés. Anjanaharibe-Sud, 14.75°S, 49.46667°E, 1260 m, montane rainforest, canopy moss and leaf litter, collection code BLF01217, 11.xi.1994 (*B.L. Fisher et al.*) (CASC: CASENT0009472). **Paratypes**, six pinned workers with same data as holotype (CASC: CASENT0009473; CASENT0009474; CASENT0191885; CASENT0339228; CASENT0339229; CASENT0339230).

Diagnosis. *P. talos* can be recognized by the following combination of characters: twelve antennal segments; large globular eye which appears as a half-sphere emerging from the surface of the head, composed of several asymmetrical subunits visible under high magnification; pronounced, tricolored body with a dark brown head, light brown body, and yellow/pale legs; known only from the Anjanaharibe-Sud Reserve in northeastern Madagascar.

Worker measurements (N=9). HL 0.5–0.53 (0.52); HW 0.39–0.43 (0.41); SL 0.28–0.3 (0.28); WL 0.52–0.62 (0.56); PetL 0.14–0.16 (0.15); PetW 0.21–0.24 (0.23); T1W 0.35–0.38 (0.36); CI 77.07–81.19 (79.06); PI 143.95–163.83 (152.84); SI 67.23–72.59 (69.8).

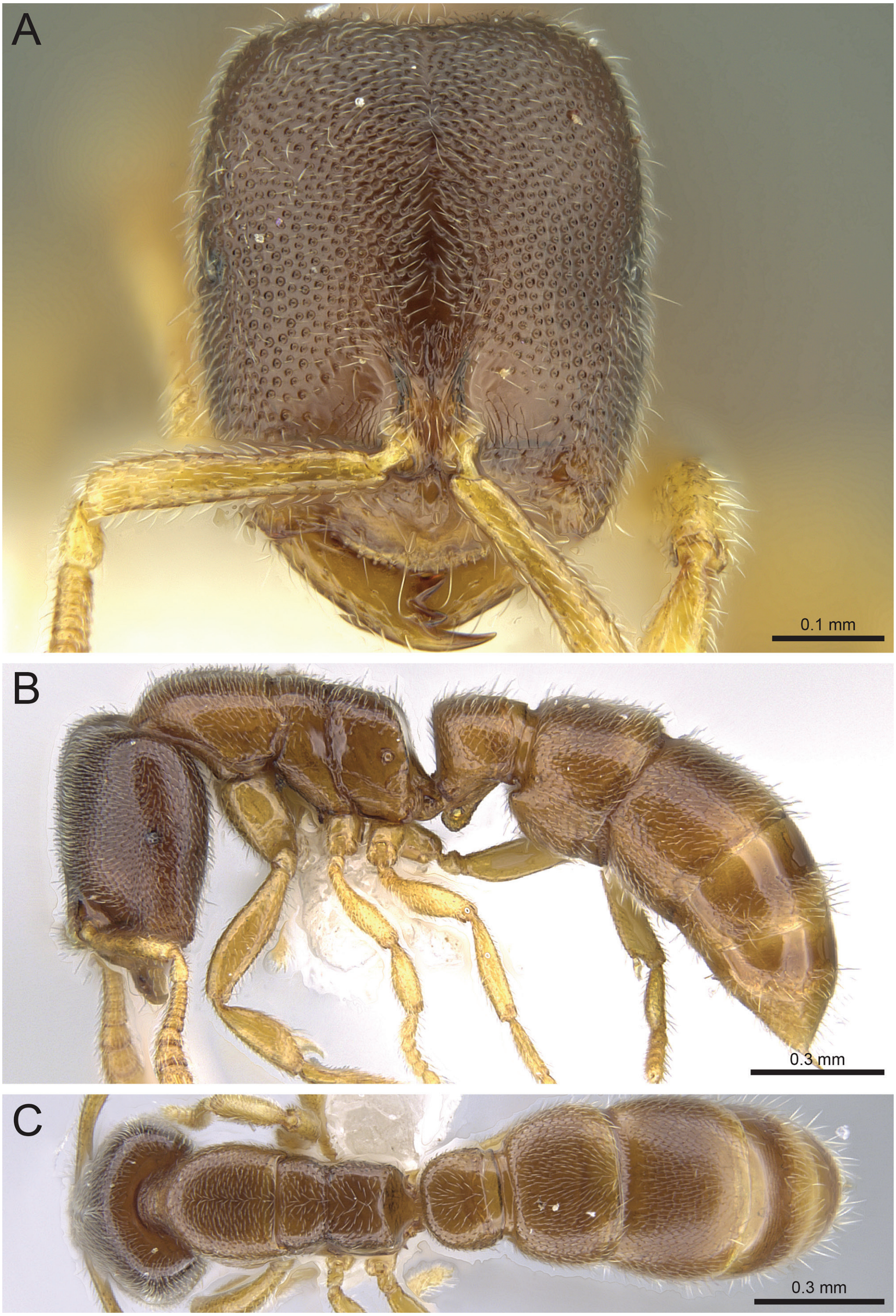

Figure 10. *P. talos* holotype worker (CASENT0009472). **A** Head in full-face view **B** Body in profile **C** Body in dorsal view.

Worker description. In full-face view, cephalic foveae become denser medially, so that laterally, foveae are separated by more than the diameter of one fovea, and medially, many foveae are directly adjacent and tend to form longitudinal chains of connected foveae; areas between foveae dark brown and shining; median cephalic area devoid of foveae not swelling above the surface of the surrounding integument and characterized as being widest anteriorly, narrowing posteriorly; apical tooth relatively short in length; eyes largest of all Malagasy *Prionopelta*, uniformly globular in shape, and under very high magnification, appear to be composed of several subunits which form a conglomerate half-sphere; both large, shallow foveae and small punctures present on pronotum and mesonotum; propodeal surface possesses only large shallow foveae; strong metanotal groove in dorsal view; strong mesopropodeal suture; distinctly tricolored body with uniformly dark brown head, tan mesosoma and gaster, and pale yellow legs and antennae.

Etymology. The rich brown color of the shiny integument of this taxon inspired the name "Talos", after the living bronze statue that protected Europa from invaders in Greek mythology. The species epithet is an arbitrary combination of letters, and thus invariant.

Distribution and ecology. This rare ant is known from a single locality in the Anjanaharibe-Sud Reserve in the province of Antsiranana (Fig. 13). It is found in montane rainforest at an elevation of 1260 meters.

Taxonomic notes. *P. talos* is most likely to be confused with *P. descarpentriesi* as it has a similar arrangement of cephalic foveae to some individuals of *P. descarpentriesi* (morphotype A). However, *P. talos* has distinctly shaped and larger eyes and a striking color pattern that distinguishes it quite easily from all Malagasy congeners.

Prionopelta vampira Overson & Fisher, sp. n.

http://zoobank.org/4B5C917A-C3A8-4CFC-8E25-0F50321B0F67
Figs 1B, 2A, C, 11

Type material. Holotype, pinned worker, MADAGASCAR, Antsiranana, Forêt d'Analabe, 30.0 km 72° ENE Daraina, 13.08333°S, 49.90833°E, 30 m, littoral rainforest, sifted litter (leaf mold, rotten wood), collection code BLF09426, 27.xi.2003 (*B.L. Fisher et al.*) (CASC: CASENT0041504). **Paratypes**, three pinned workers with same data as holotype (CASC: CASENT0041500; CASENT0041501; CASENT0041502).

Diagnosis. *P. vampira* is the only member of the genus from the Malagasy region in which workers entirely lack any visible metanotal suture when viewed dorsally; additionally the posterior propodeal edge is noticeably more concave in dorsal view than any other Malagasy *Prionopelta*.

Worker measurements (N=8). HL 0.49–0.53 (0.5); HW 0.41–0.45 (0.42); SL 0.27–0.31 (0.28); WL 0.55–0.62 (0.58); PetL 0.19–0.23 (0.21); PetW 0.24–0.26 (0.25); T1W 0.35–0.39 (0.37); CI 81.78–85.31 (83.78); PI 103.96–130.2 (120.71); SI 64.25–69.36 (67.33).

Worker description. Highest cephalic index on average of Malagasy *Prionopelta* (CI 81.78–85.31 (83.78); posterior margin of the head with slight notch medially in full-face view; cephalic foveae shallow, large, and widely spaced; directly adjacent cephalic foveae either completely lacking, or very rare; if any foveae are adjacent, then always with only 2–3 foveae connected, and these usually always medially on the head in full-face view; majority of cephalic foveae separated by 1–3 foveal diameters, appear cleanly scooped from the shining integument, and lack raised margins; median cephalic band devoid of foveae is uniformly broad, and not swelling above the integument; apical tooth very long, longest of all Malagasy *Prionopelta*, over four times the length of the third apical tooth measured from base to tip (Fig. 2C); sculpture of the dorsum of the mesosoma consisting of large, shallow foveae which are widely spaced at 2–3 foveal diameters with punctures present between foveae; no metanotal suture present in dorsal view, but rather a shining surface with no clear distinction between propodeum and mesonotum; in a few specimens, a slightly perceptible depression is sometimes visible at the site of the metanotal suture, with associated notches on the lateral edges of the dorsum of the mesosoma, but this depression always lacks scarring; in lateral view, mesopropodeal suture weak, appearing as a gradual depression rather than a scar; posterior propodeal edge seen dorsally strongly concave; sharp lamellae of the posterior propodeum present.

Etymology. The name of this species is inspired by the vampire-like nature of its exceptionally long apical tooth. The species epithet is a Latinized adjective of the German and Hungarian word “vampir”.

Distribution and ecology. This species is almost entirely restricted to northern Madagascar where it is found in litter in rainforest, littoral rainforest, and montane rainforest from 25–1200 meters of elevation. Intriguingly, *P. vampira* has also been collected at a single, highly disjunct site in far southeastern Madagascar 1048 km to the south near Enakara in the province of Toliara (Fig. 13).

Taxonomic notes. This species, which has similar cephalic scupturing to *P. xerosilva*, is otherwise unmistakable due to its extremely long apical tooth, lack of a metanotal suture, and strongly concave posterior propodeal edge when viewed dorsally.

Non-type material. MADAGASCAR: Antsiranana, Ampasindava, Andranomatavy Forest, 13.669°S, 47.9877°E, 149 m, disturbed dry forest, 6.x.2013 (*B.L.Fisher et al.*); Antsiranana, Ampasindava, Andranomatavy Forest, 13.663°S, 47.9794°E, 543 m, disturbed dry forest, 6.x.2013 (*B.L.Fisher et al.*); Antsiranana, Forêt Ambato, 26.6 km 33° Ambanja, 13.4645°S, 48.5517°E, 150 m, rainforest, 8.xii.2004 (*B.L.Fisher*); Antsiranana, Forêt d’ Andavakoera, 21.4 km 75° ENE Ambilobe; 4.6 km 356° N Betsiaka, 13.1183°S, 49.23°E, 425 m, rainforest, 15.xii.2003 (*B.L.Fisher*); Antsiranana, Forêt d’Ampombofofo, 12.0995°S, 49.3387°E, 25 m, littoral forest, 21.xi.2007 (*B.L.Fisher et al.*); Antsiranana, Forêt d’Analabe, 30.0 km 72° ENE Daraina, 13.0833°S, 49.9083°E, 30 m, littoral rainforest, 27.xi.2003 (*B.L.Fisher*); Antsiranana, Makirovana forest, 14.1707°S, 49.9541°E, 225 m, rainforest, 4.v.2011 (*B.L.Fisher et al.*); Antsiranana, Nosy Be, Réserve Naturelle Intégrale de Lokobe, 6.3 km 112° ESE Hellville, 13.4193°S, 48.3312°E, 30 m, rainforest, 19.iii.2001 (*Fisher, Griswold et al.*); Toliara, 11 km NW Enakara, Rés. Andohahela, 24.5667°S, 46.8333°E, 800 m, rainforest, 17.xi.1992 (*B.L.Fisher*).

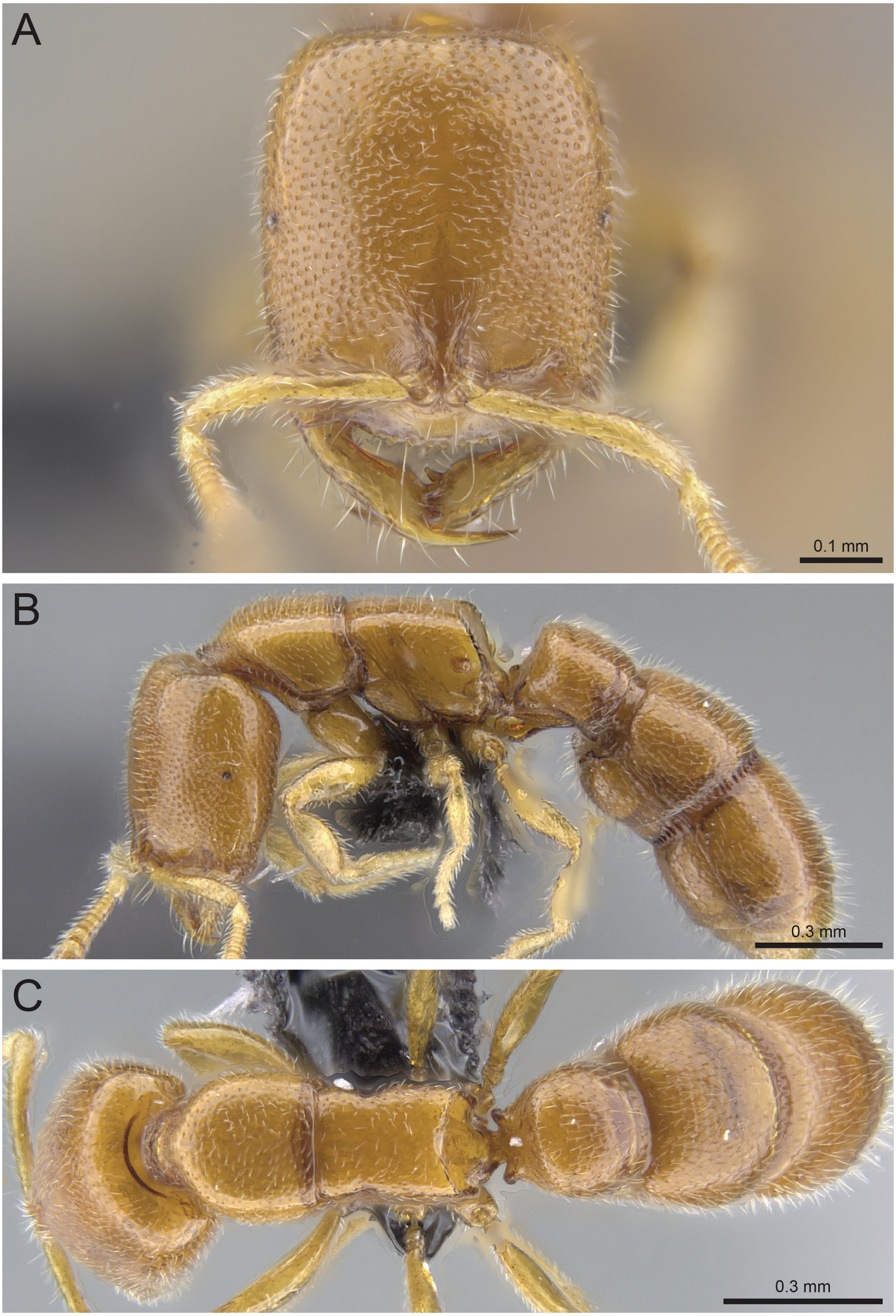

Figure 11. *P. vampira* holotype worker (CASENT0041504). **A** Head in full-face view **B** Body in profile **C** Body in dorsal view.

Prionopelta xerosilva Overson & Fisher, sp. n.

http://zoobank.org/794FF570-F328-49F0-A5D7-44775B31A230

Figs 1A, 2B, D, 12

Type material. Holotype, pinned worker, MADAGASCAR, Mahajanga, Réserve Forestière Beanka, 50.7 km E Maintirano, 17.88021°S, 44.46877°E, 140 m, tropical dry forest on tsingy, sifted litter (leaf mold, rotten wood), BLF22999, 29.x.2009 (*B.L. Fisher et al.*) (CASC: CASENT0157254). **Paratypes**, six pinned workers with same data as holotype (CASC: CASENT0157257; CASENT0157258; CASENT0157260; CASENT0157262; CASENT0157701, CASENT0157702).

Diagnosis. *P. xerosilva* is identifiable from the following combination of characters: cephalic foveae consistently and widely separated by 1–3 foveal diameters, with foveae directly adjacent only extremely rarely, including at the posterolateral corners of the head; metanotal suture strongly visible in dorsal view.

Worker measurements (N=6). HL 0.43–0.46 (0.45); HW 0.34–0.36 (0.35); SL 0.23–0.25 (0.24); WL 0.45–0.5 (0.48); PetL 0.14–0.15 (0.15); PetW 0.19–0.21 (0.2); T1W 0.31–0.33 (0.32); CI 74.35–81.82 (77.85); PI 126.8–148.18 (138.76); SI 65.51–71.88 (69.77).

Worker description. Cephalic foveae shallow, large, and most widely spaced of the Malagasy *Prionopelta*; directly adjacent cephalic foveae either completely lacking, or very rare; if any foveae are adjacent, then always with only 2–3 foveae connected, and these usually located medially on the head in full-face view; majority of cephalic foveae are separated by 1–3 foveal diameters, appear cleanly scooped from shining integument, and lack any raised margins at their perimeter; median cephalic band devoid of foveae is wide along its length, not tapering posteriorly; coronal suture absent medially on the head; apical tooth intermediate in length, never more than 4 times as long as the third tooth from base to tip (Fig. 2D); very weak, shallow, foveae present on the pronotum which are noticeably less dense than those of other Malagasy *Prionopelta*; foveae of the dorsum of the mesosoma interspersed with punctures; pronounced metanotal suture visible in dorsal view, mesopropodeal suture weaker but present; posterior edge of the propodeum straight or only very slightly concave in dorsal view; protruding lamellae of the posterior propodeum absent.

Etymology. The name of this new species is a combination of the Greek adjective “xero” meaning dry and the Latin noun “silva” for forest, as this species is known only from tropical dry forests in western Madagascar.

Distribution and ecology. *P. xerosilva* is known only from tropical dry forests in the province of Mahajanga in western-central Madagascar (Fig. 13). It has only been collected from forest litter and ranges between 50–300 meters of elevation.

Taxonomic notes. With its uniformly and widely spaced cephalic foveae, *P. xerosilva* could only be confused with *P. vampira*. However, the latter lacks a metanotal suture and possesses a very long apical tooth, a strongly concave posterior edge of the propodeum in dorsal view, and lamellae protruding from the posterior propodeum, all of which *P. xerosilva* lacks.

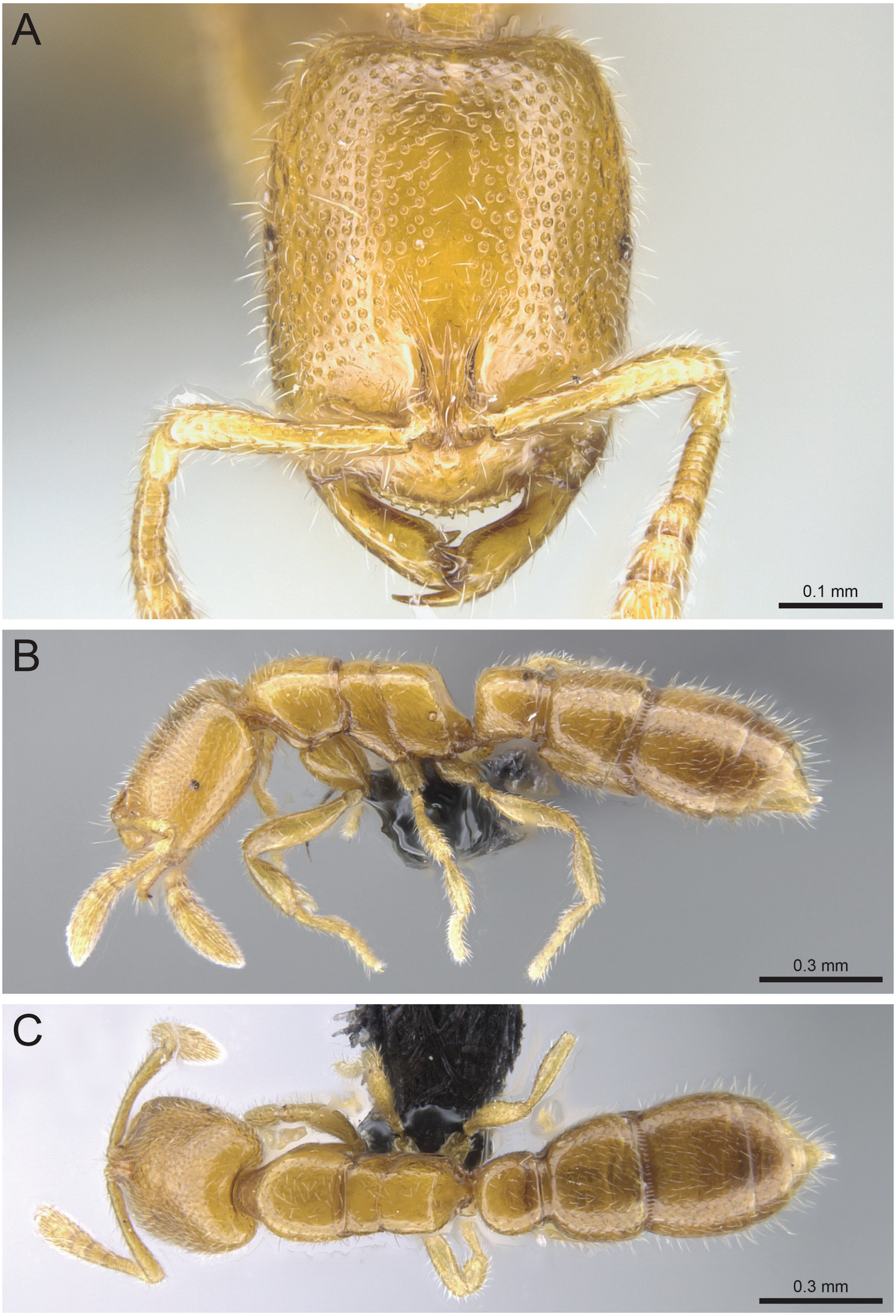

Figure 12. *P. xerosilva* holotype worker (CASENT0157254). **A** Head in full-face view **B** Body in profile **C** Body in dorsal view.

Figure 13. Geographic distributions for Malagasy *Prionopelta*. White diamonds represent type localities whereas dark circles represent non-type localities. Type locality for *P. descarpentriesi* is unknown. *P. seychelles*, known only from Seychelles, is not pictured here.

Non-type material. MADAGASCAR: Mahajanga, Parc National Tsingy de Bemaraha, 10.6 km ESE 123° Antsalova, 18.7094°S, 44.7182°E, 150 m, tropical dry forest on Tsingy, 16.xi.2001 (*Fisher-Griswold Arthropod Team*); Mahajanga, Parc National Tsingy de Bemaraha, 2.5 km 62° ENE Bekopaka, Ankidrodroa River, 19.1322°S,

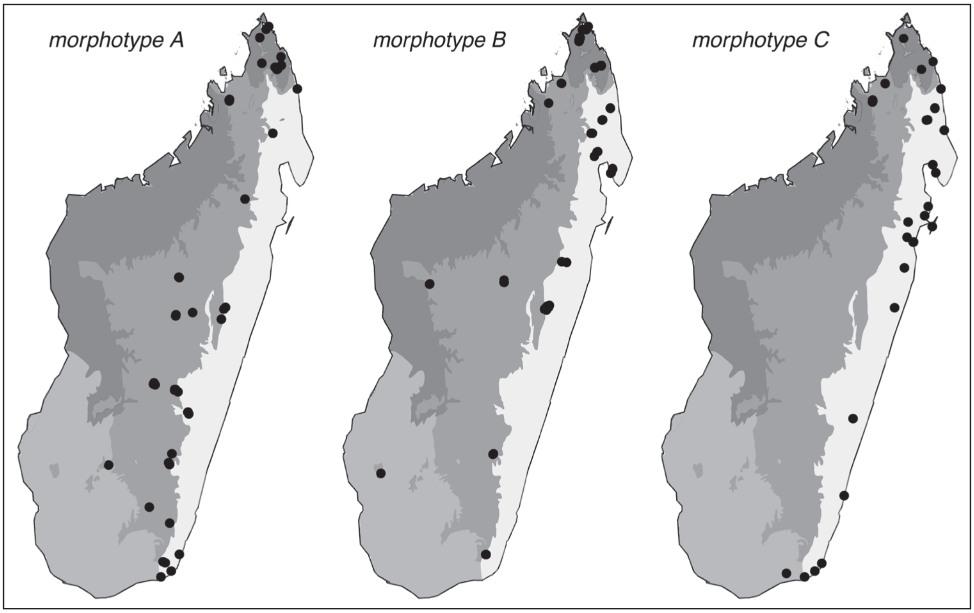

Figure 14. Geographic distributions for morphotypes of *P. descarpentriesi*.

44.8147°E, 100 m, tropical dry forest on Tsingy, 11.xi.2001 (*Fisher-Griswold Arthropod Team*); Mahajanga, Parc National Tsingy de Bemaraha, 3.4 km 93° E Bekopaka, Tombeau Vazimba, 19.1419°S, 44.828°E, 50 m, tropical dry forest, 6.xi.2001 (*Fisher-Griswold Arthropod Team*); Mahajanga, Réserve forestière Beanka, 50.2 km E Maintirano, 18.0265°S, 44.0505°E, 250 m, tropical dry forest on tsingy, 19.x.2009 (*B.L.Fisher et al.*); Mahajanga, Réserve forestière Beanka, 52.7 km E Maintirano, 18.0622°S, 44.5259°E, 300 m, tropical dry forest on tsingy, 24.x.2009 (*B.L.Fisher et al.*).

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References

Anonymous (1970) Nouvelles données scientifiques sur le massif du Tsaratanana (Madagascar): résultats de la mission concertée de novembre 1966. Armée française-ORSTOM, Mémoire Orstom n°37, Paris, 251.

Brown WL (1960) Contributions toward a reclassification of the Formicidae, III. Tribe Amblyoponini (Hymenoptera). Bulletin of the Museum of Comparative Zoology 122: 143–230.

Brown WL (1965) Contributions to a reclassification of the Formicidae. IV. Tribe Typhlomyrmecini (Hymenoptera). Psyche 72: 65–78. doi: 10.1155/1965/36792

Fisher BL (2005) A model for a global inventory of ants: A case study in Madagascar. Proceedings of the California Academy of Sciences 56: 86–97.

Harris RA (1979) A glossary of surface sculpturing. California Department of Food and Agriculture, Bureau of Entomology 28: 1–31.

Jeannel R (1951) Revision des Anchomenini de la région malgache (Col. Pterostichidœ). Mémoires de l'Institut Scientifique de Madagascar, Série A, 5: 285–351.

Mayr GL (1866) Myrmecologische Beiträge. Sitzungsberichte der Koenigliche Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe 53: 484–517.

Santschi F (1924) Descriptions de nouveaux Formicides africains et notes diverses II. Revue Zoologique Africaine 12: 195–224.

Shattuck SO (2008) Revision of the ant genus *Prionopelta* (Hymenoptera: Formicidae) in the Indo-Pacific region. Zootaxa 1846: 21–34.

R Core Team (2014) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org [accessed 18 October 2014]

Terron G (1974) Découverte au Cameroun de deux espèces nouvelles du genre *Prionopelta* Mayr (Hym., Formicidae). Annales de la Faculté des Sciences, Université Fédérale du Cameroun 17: 105–119.