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Review of the genus *Aphaereta* Förster, 1863 (Hymenoptera, Braconidae, Alysiinae) from the Afrotropical region, with description of three new species

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Abstract

The *Aphaereta* Förster, 1863 species of the Afrotropical region (including Madagascar) are reviewed. Three new species, *A. elongata* **sp. n.** (Kenya), *A. hararensis* **sp. n.** (Zimbabwe) and *A. mosselensis* **sp. n.** (South Africa) are described and illustrated. Re-descriptions of *A. basirufa* Granger, 1949 (Madagascar) and *A. sarcophagensis* Shenefelt, 1974 (South Africa) are added.

Keywords

Endoparasitoids, Braconidae, Alysiinae, *Aphaereta*, Afrotropical Region, key

Introduction

The Alysiinae is a conspicuously diverse subfamily within the Braconidae (Dolphin and Quicke 2001) with more than 2000 described species from two large and polymorphic tribes Alysiini and Dacnusini (Shenefelt 1974, Yu et al. 2012). Species of Alysiini are parasitoids of different groups of Diptera-Cyclorrhapha, but members of Dacnusini are almost exclusively specialised on leaf- and stem-miners, predominantly of the families Agromyzidae, Ephydridae and Chloropidae.

The genus *Aphaereta* Förster, 1863 can be recognised amongst the genera of the tribe Alysiini by the following characters: mandible simple and with three teeth, its

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ventral and diagonal ridges well developed; first flagellar segment sometimes only slightly shorter than second segment; pterostigma of fore wing narrow, merging imperceptibly with R1 in most species; fore wing RS+M absent; 2RS shorter than 3RSa; first subdiscal cell open; 2CU interstitial or nearly so; hind wing with m-cu absent, if rarely cu-a present, then r-m and M+CU much shorter than 1M; ovipositor sheath sparsely setose throughout (Wharton 2002).

This genus includes about 40 species around the world wide, of which two species were known in the Afrotropical region including Madagascar (Yu et al. 2012). In this paper, three new Afrotropical species of the genus *Aphaereta* are described and illustrated, viz. *A. elongata* sp. n. from Kenya, *A. hararensis* sp. n. from Zimbabwe and *A. mosselensis* sp. n. from South Africa. Moreover, re-descriptions of *A. basirufa* Granger, 1949 from Madagascar and *A. sarcophagensis* Shenefelt, 1974 from South Africa are given. Finally, a key for the identification of *Aphaereta* species from the Afrotropical region (with Madagascar) is provided.

Material and methods

For the terminology of the morphological features and sculpture, measurements and wing venation nomenclature see Sharkey and Wharton (1997) and HAO (Hymenoptera Anatomy Ontology Portal: http://portal.hymao.org/) (Yoder et al. 2010). For measurements of the length and width of mandibles and abbreviations for ocellar proportions see Peris-Felipo et al. (2013). The following terms are equivalent between this paper and Peris-Felipo et al. (2013):

Gena: temples.
Anterior tentorial pit: paraclypeal fovea.
Mesoscutal midpit: mesoscutal pit.
Scutoscutellar sulcus: prescutellar depression.
Mesopectus: mesopleuron.
Mesepimeral sulcus: posterior mesopleural furrow.
Marginal cell: radial cell.
Nervulus: vein cu-a.
Second submarginal cell: brachial cell.

The external morphology of the Alysiinae parasitoids was studied and illustrated using Leica© S8 APO stereomicroscope equipped with a Nikon© D700 digital camera, and Hitachi© S–4800 scanning electron microscopes in the Electron Microscopy Service of the University of Valencia (SCSIE) with a beam of 2 kV and without sputter coating for SEM pictures was used. The types of newly described species are deposited in the collection of the Natural History Museum (London, UK; BMNH). Other abbreviation used in the text is MNHN for “Muséum National d’Histoire Naturelle” (Paris, France).

Taxonomic part

Aphaereta basirufa Granger, 1949
Figs 1–2

Aphaereta basirufa Granger 1949: 405; Shenefelt 1974: 957; Fischer 1994: 773; Yu et al. 2012.

Type material. Holotype: female, Madagascar, Ankaratra, Terra typica, ii.1938, alt 1800, Mém. Inst. sci. Madagascar 2A: 405 (A. Seyrig) (MNHN) (not examined).

Material examined. 3 females, Madagascar, Tamatave, Perinet, 27.iv–3.v.1983 (J.S. Noyes and M.C. Day leg.) (BMNH).

Re-description. Female.

Head entirely smooth; in dorsal view 1.6–1.8 times as wide as median length, 1.4 times as wide as mesoscutum, with rounded gena behind eye. Eye in lateral view as high as wide and twice as wide as temple medially. POL 1.6 times OD; OOL 4.3 times OD. Face twice as wide as high; inner margins of eyes subparallel. Clypeus slightly curved ventrally, 2.4–3.0 times as wide as high; its upper margin striated. Mandible widened towards apex, 1.3 times as long as its maximum width. Upper tooth of mandible longer than lower tooth, rounded apically; middle tooth very long, wide basally and narrowed towards apex, rounded apically; lower tooth pointed apically. Antenna longer than body, 22–25-segmented. Scape about 3.0 times as long as pedicel. First flagellar segment 3.7–4.0 times as long as its apical width; second segment 5.0–5.6 times as long as its maximum width, 1.5 times as long as first segment. Third flagellar segment 4.5 times as long as its width. Fourth to seventh flagellar segments 3.4–3.5 times, eight to penultimate segments 3.0 times, and apical segment 3.8 times as long as their maximum width accordingly.

Mesosoma 1.1 times as long as high (lateral view). Mesoscutum 1.2 times as long as its maximum width. Notauli mainly absent on vertical surface of mesoscutum. Mesoscutal midpit absent. Prescutellar depression smooth, without lateral carinae. Precoxal suture present, reaching anterior margin of mesopectus and not reaching posterior margin of mesopectus. Mesepimeral sulcus crenulate below. Propodeum sculptured, with long median longitudinal carina, with apical half densely sculptured. Propodeal spiracle relatively small.

Wings. Length of fore wing 3.0 times its maximum width. Marginal cell reaching apex of wing, 5.2 times as long as its maximum width. Vein 3RSa about 2.0–2.1 times as long as 2RS, 3.3–3.4 times as long as r, 0.3–0.4 times as long as 3RSb. Second submarginal cell 2.45 times as long as its maximum width. Hind wing 6.8 times as long as its maximum width.

Legs. Hind femur 5.0–5.5 times as long as its maximum width. Hind tibia weakly widened towards apex, 10.4 times as long as its maximum subapical width, as long as hind tarsus. First segment of hind tarsus (basitarsus) twice as long as second segment.

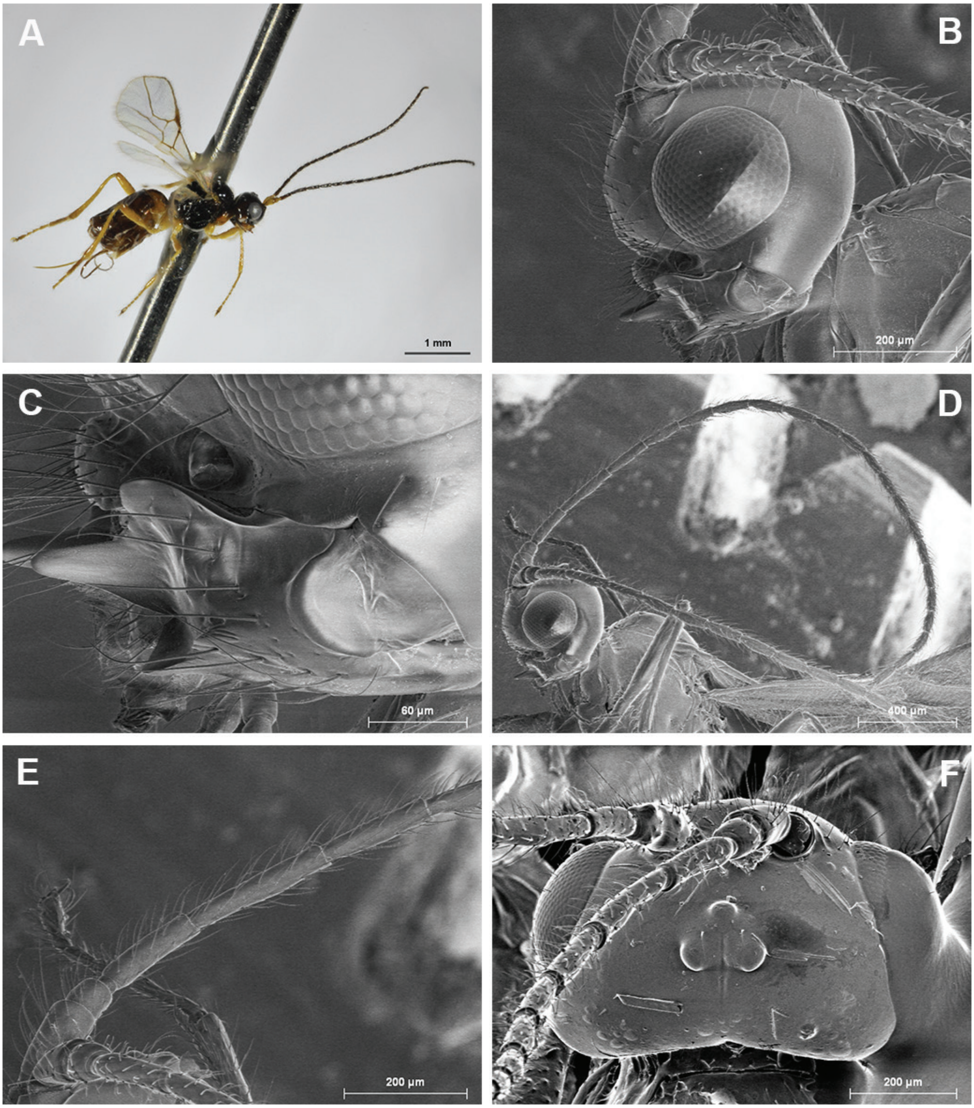

Figure 1. *Aphaereta basirufa* Granger (female) **A** Habitus, lateral view **B** Head, lateral view **C** Mandible **D** Antenna **E** Basal segments of antenna **F** Head, dorsal view.

Metasoma distinctly compressed. First tergite with two median carinae, striate inside them, and smooth on lateral area; weakly widened towards apex; as long as its apical width. Ovipositor 3.4 times as long as first tergite, nearly as long as metasoma, 1.8 times as long as hind femur.

Colour. Body dark brown. Scape, pedicel, mandible, legs and ovipositor yellow. In dorsal view, head and mesosoma dark brown; first metasomal tergite yellow, paler than brown second and third tergites. Wings hyaline. Pterostigma brown.

Body length 2.7–3.0 mm; fore wing length 3.8–3.9 mm.

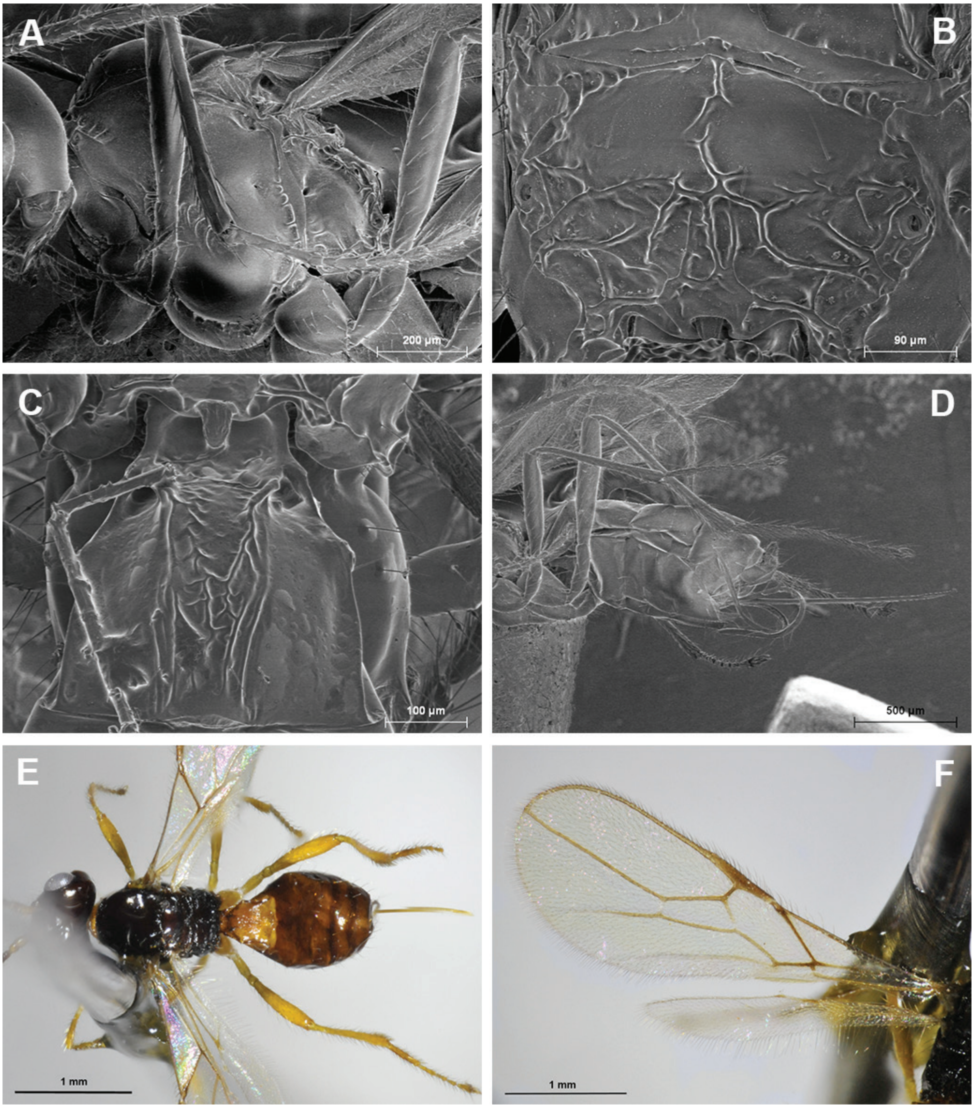

Figure 2. *Aphaereta basirufa* Granger (female) A. Mesosoma, lateral view **B** Propodeum, dorsal view **C** First metasomal tergite **D** Metasoma, hind leg and ovipositor, lateral view **E** Habitus, dorsal view **F** Fore and hind wings.

Male. Unknown.

Comparative diagnosis. This species is similar to *A. sarcophagensis* Shenefelt, 1974 from South Africa, but differs in having the first metasomal tergite paler than second and third tergites (similar colouration in *A. sarcophagensis*), hind femur 5.0–5.5 times as long as its maximum width (4.5 times in *A. sarcophagensis*), first flagellar segment 3.7–4.0 times as long as its maximum width (3.0 times in *A. sarcophagensis*); second segment 5.0–5.6 times (4.6 times in *A. sarcophagensis*); third segment 4.5 times (3.3 times in *A. sarcophagensis*), face twice as wide as high (1.6 times in *A. sarcophagensis*), and clypeus 2.4–3.0 times as wide as high (3.5 times in *A. sarcophagensis*).

Aphaereta elongata Peris-Felipo, sp. n.

http://zoobank.org/93BE1E4A-3FD0-4F0E-ACD4-C02C8AA0106C
Figs 3–4

Etymology. Named after its long second submarginal cell.

Type material. Holotype: female, Kenya, NE Kisumu (Nr. Lake Victoria), 15 mts, xi.1979 (M.D. Croft leg.) (BMNH). Paratypes: 2 females, same data as holotype (BMNH).

Description. Female (holotype).

Head entirely smooth; in dorsal view 1.5 times as wide as median length, 1.4 times as wide as mesoscutum, with rounded gena behind eye. Eye in lateral view 1.2 times as high as wide and 1.9 times as wide as temple medially. POL 1.25 times OD; OOL 2.7 times OD. Face 1.25 times as wide as high; inner margins of eyes subparallel. Clypeus slightly curved ventrally, 2.6 times as wide as high. Mandible widened towards apex, 1.8 times as long as its maximum width. Upper tooth of mandible longer than lower tooth; middle tooth wide basally and narrowed towards apex, rounded apically; lower tooth rounded apically. Antenna longer than body, 16-segmented. Scape as long as pedicel. First flagellar segment 4.5 times as long as its apical width; second segment 6.4 times as long as its maximum width; 1.3 times as long as first segment. Third flagellar segment 5.1 times as long as its width: fourth to fifteenth segments 4.4–4.5 times, and sixteenth (apical) segment 5.0 times as long as their maximum width accordingly.

Mesosoma 1.5 times as long as high (lateral view). Mesoscutum 1.2 times as long as its maximum width. Notauli mainly absent on vertical surface of mesoscutum. Mesoscutal midpit absent. Prescutellar depression smooth, without lateral carinae. Precoxal suture smooth, not reaching anterior and posterior margins of mesopectus. Mesepimeral sulcus smooth. Propodeum sculptured, with pentagonal areola in apical half. Propodeal spiracle relatively small.

Wings. Length of fore wing 2.9 times its maximum width. Marginal cell reaching apex of wing, 4.8 times as long as its maximum width. Vein 3RSa 4.5 times as long as 2RS, 9.0 times as long as r, 0.5 times as long as 3RSb. Second submarginal cell distinctly narrowed distally, 5.5 times as long as maximum width. Hind wing 7.2 times as long as its maximum width.

Legs. Hind femur 4.4 times as long as its maximum width. Hind tibia weakly widened towards apex, about 10.5 times as long as its maximum subapical width, as long as hind tarsus. First segment of hind tarsus (basitarsus) twice as long as second segment.

Metasoma distinctly compressed. First tergite mostly smooth, finely striate in middle part, weakly widened towards apex, 1.6 times as long as its apical width.

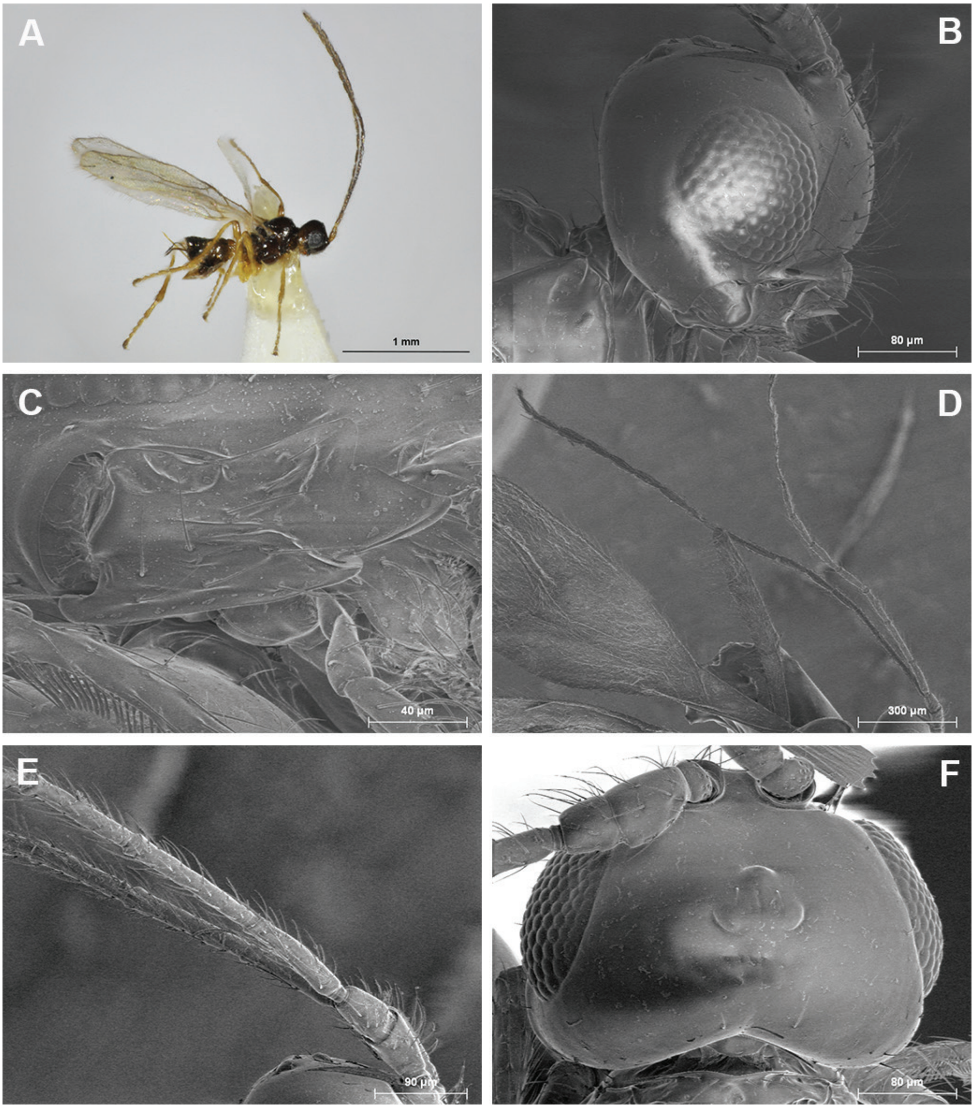

Figure 3. *Aphaereta elongata* Peris-Felipo, sp. n. (female) **A** Habitus, lateral view **B** Head, lateral view **C** Mandible **D** Antenna **E** Basal segments of antenna **F** Head, dorsal view.

Ovipositor 2.2 times as long as first tergite, distinctly shorter than metasoma, as long as hind femur.

Colour. Body dark brown. Antenna brown. Legs and ovipositor yellow. In dorsal view, head and mesosoma dark brown; metasoma light brown. Wings hyaline. Pterostigma light brown.

Body length 1.2 mm; fore wing length 1.8 mm.

Variations. All specimens are identical.

Male. Unknown.

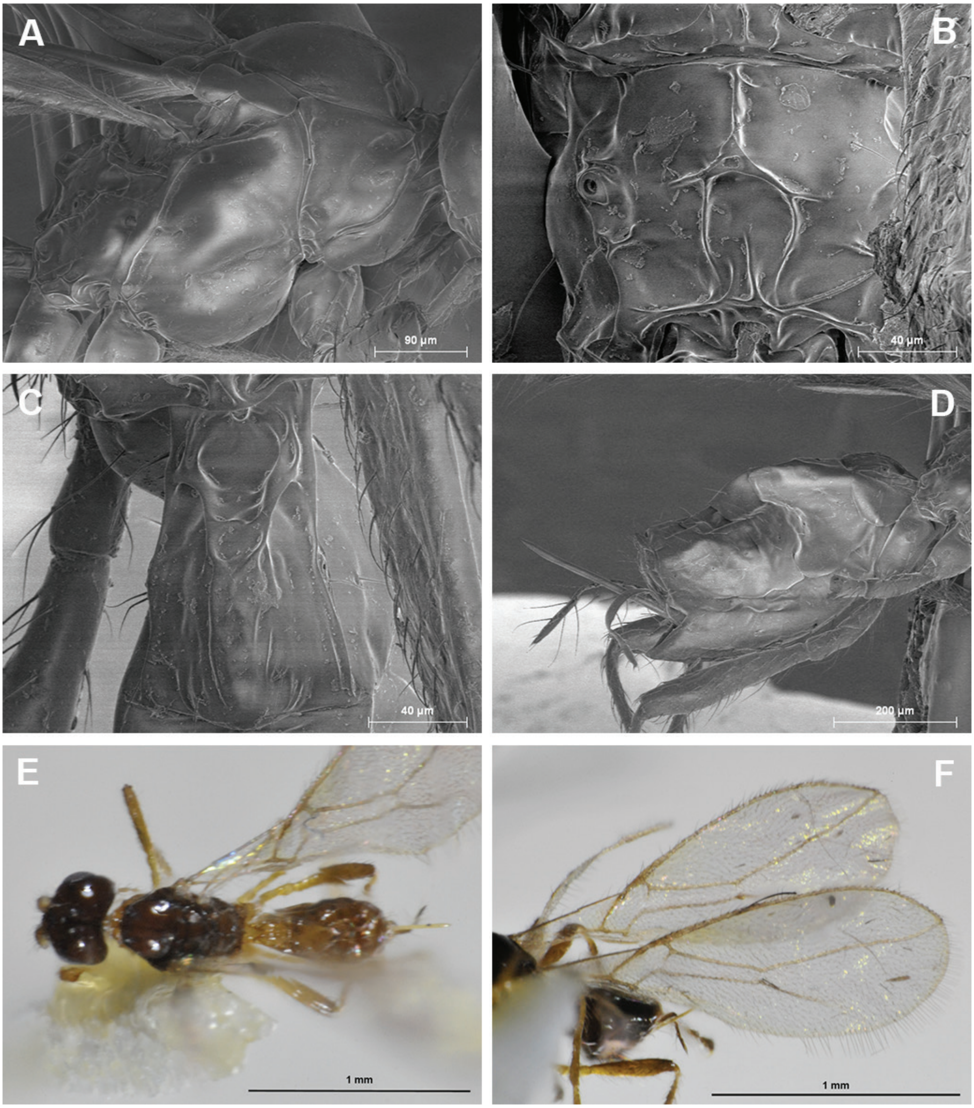

Figure 4. *Aphaereta elongata* Peris-Felipo, sp. n. (female) **A** Mesosoma, lateral view **B** Propodeum, dorsal view **C** First metasomal tergite **D** Metasoma, hind leg and ovipositor, lateral view **E** Habitus, dorsal view **F** Fore and hind wings.

Comparative diagnosis. This new species is similar to *A. mosselensis* Peris-Felipo, sp. n., but differs in having the eye in lateral view 1.9 times as wide as temple medially (1.2 times in *A. mosselensis*), clypeus 2.6 times as wide as high (4.0 times in *A. mosselensis*), mandible 1.8 times as long as its maximum width (1.4 times in *A. mosselensis*), first flagellar segment 4.5 times as long as its apical width (2.8 times in *A. mosselensis*), second flagellar segment 6.4 times as long as its maximum width (4.0 times in *A. mosselensis*), third flagellar segment 5.1 times as long as its width (3.0 times in *A. mosselensis*), hind femur 4.4 times as long as its maximum width (5.0 times in *A. mosselensis*), and precoxal suture smooth, not reaching anterior and posterior margins of mesopectus (crenulate, reaching anterior margin of mesopectus in *A. mosselensis*).

Aphaereta hararensis Peris-Felipo, sp. n.

http://zoobank.org/B045F991-9C47-4A1B-9135-69D8D03FB45F
Figs 5–6

Etymology. Named after Harare, the type locality of this new species.

Type material. Holotype: female, Zimbabwe, nr Harare, vii.1982 (Watsham leg.) (BMNH). Paratypes: 2 females, same data as holotype (BMNH).

Description. Female (holotype).

Head entirely smooth; in dorsal view 1.8 times as wide as median length, 1.3 times as wide as mesoscutum, with rounded gena behind eye. Eye in lateral view as high as wide and 1.75 times as wide as temple medially. POL 1.5 times OD; OOL 3.0 times OD. Face 1.45 times as wide as high; inner margins of eyes subparallel. Clypeus slightly curved ventrally, 3.0 times as wide as high; its upper margin crenulate. Mandible widened towards apex, 1.5 times as long as its maximum width. Upper tooth of mandible longer than lower tooth; middle tooth wide basally and narrowed towards apex, rounded apically; lower tooth shorter than upper tooth, rounded apically. Antenna shorter than body, 19-segmented. Scape 1.5 times as long as pedicel. First flagellar segment 3.4 times as long as its apical width; second segment 4.7 times as long as its maximum width; 1.5 times as long as first segment. Third flagellar segment 2.9 times as long as its width. Fourth to sixth flagellar segments 2.7 times, seventh to tenth segments 2.4–2.5 times, eleventh to eighteenth segments 1.5–1.6 times, and nineteenth (apical) segment 3.6 times as long as their maximum width accordingly.

Mesosoma 1.2 times as long as high (lateral view). Mesoscutum 1.2 times as long as its maximum width. Notauli mainly absent on vertical surface of mesoscutum. Mesoscutal midpit absent. Prescutellar depression smooth, with lateral carinae. Precoxal suture present, reaching anterior margin of mesopectus and not reaching posterior margin of mesopectus. Mesepimeral sulcus crenulate below. Propodeum sculptured, with long median longitudinal carina, with apical half densely sculptured. Propodeal spiracle relatively small.

Wings. Length of fore wing 2.6 times its maximum width. Marginal cell reaching apex of wing, 3.4 times as long as its maximum width. Vein 3RSa 1.6 times as long as 2RS, 3.75 times as long as r, 0.45 times as long as 3RSb. Second submarginal cell 2.3 times as long as maximum width. Hind wing 5.1 times as long as its maximum width.

Legs. Hind femur 4.6 times as long as its maximum width. Hind tibia weakly widened towards apex, about 8.0 times as long as its maximum subapical width, as long as hind tarsus. First segment of hind tarsus (basitarsus) 2.25 times as long as second segment.

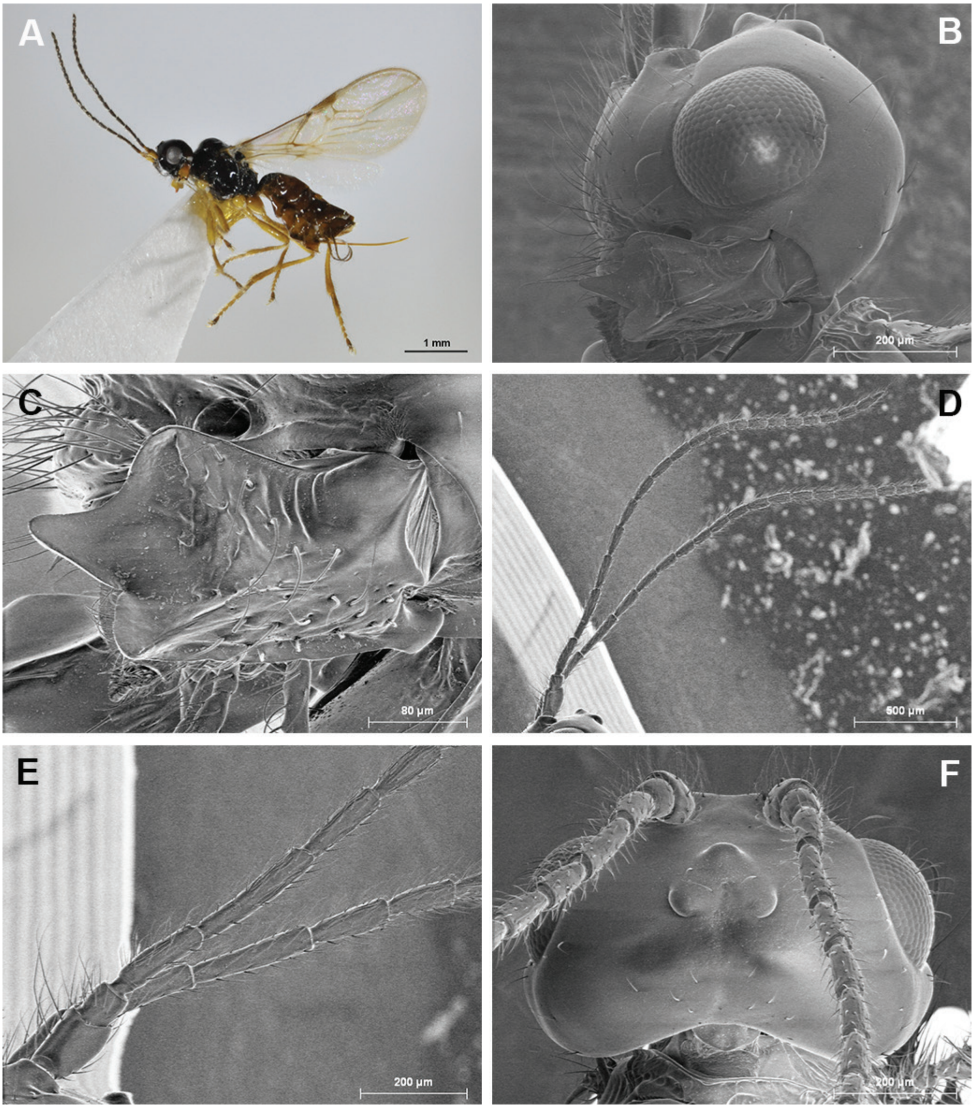

Figure 5. *Aphaereta hararensis* Peris-Felipo, sp. n. (female) **A** Habitus, lateral view **B** Head, lateral view **C** Mandible **D** Antenna **E** Basal segments of antenna **F** Head, dorsal view.

Metasoma distinctly compressed. First tergite striated in middle part, weakly widened towards apex, 1.25 times as long as its apical width. Ovipositor 2.9 times as long as first tergite, distinctly shorter than metasoma, 1.6 times as long as hind femur.

Colour. Head and mesosoma dark brown. Antenna and metasoma brown. Scape, pedicel, mandible, legs and ovipositor light brown to yellow. In dorsal view, head, mesosoma and first metasomal tergite dark brown; second and third tergites brown. First metasomal tergiter darker than second and third tergites. Wings hyaline. Pterostigma light brown to brown.

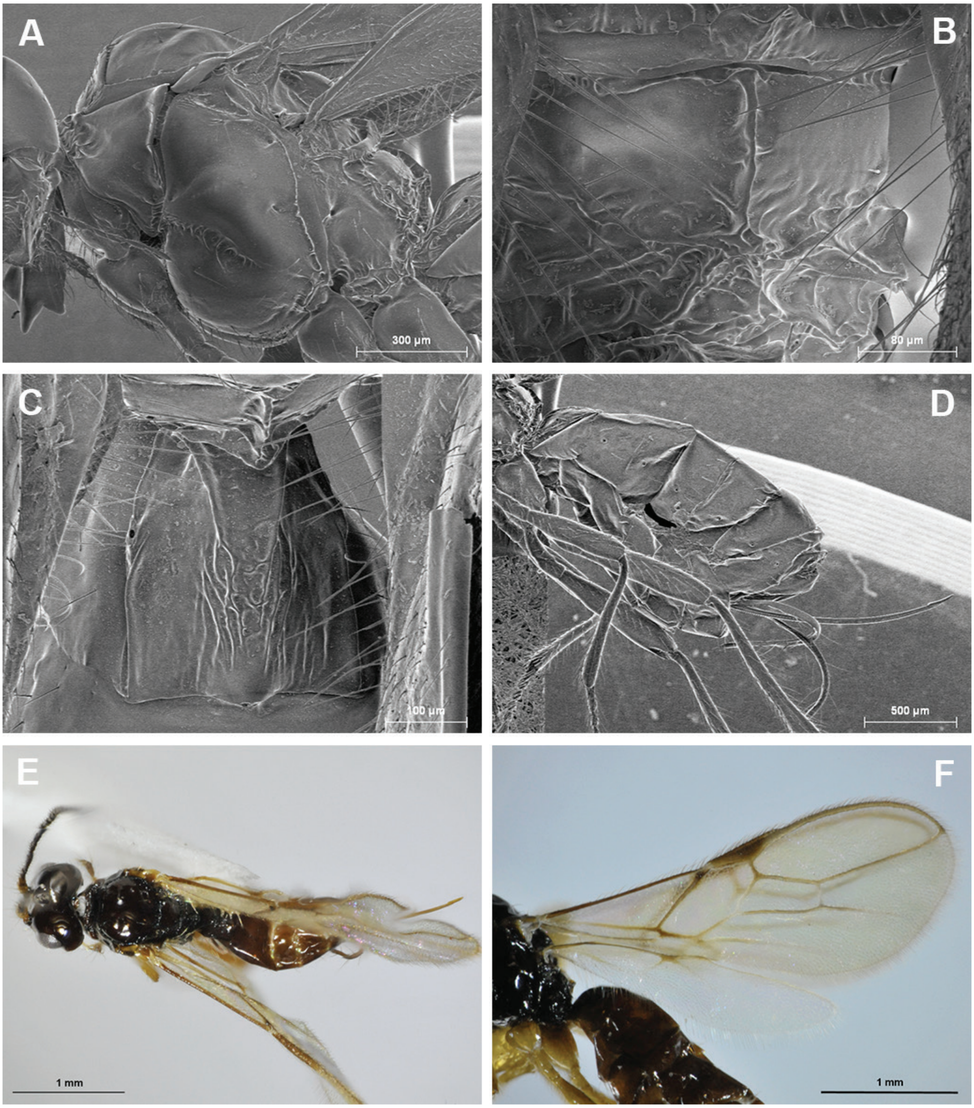

Figure 6. *Aphaereta hararensis* Peris-Felipo, sp. n. (female) **A** Mesosoma, lateral view **B** Propodeum, dorsal view **C** First metasomal tergite **D** Metasoma, hind leg and ovipositor, lateral view **E** Habitus, dorsal view **F** Fore and hind wings.

Body length 3.3 mm; fore wing length 3.2 mm.

Variation. Body length 3.3–3.4 mm; fore wing length 3.2–3.3 mm. Antenna 18–19-segmented. Vein 3RSa 1.5–1.6 times as long as 2RS, 3.7–3.8 times as long as r, 0.4–0.5 times as long as 3RSb.

Male. Unknown.

Comparative diagnosis. This new species is similar to *A. mosselensis* Peris-Felipo, sp. n. but differs in having the head, mesosoma and first metasomal tergite with similar colour; second and third metasomal tergites paler than head, mesosoma and first tergite (head, mesosoma and first, second and third metasomal tergites with same colour in *A. mosselensis*), first flagellar segment 3.4 times as long as its maximum width (2.75 times in *A. mosselensis*); second segment 4.7 times (4.0 times in *A. mosselensis*), hind femur 4.6 times as long as its maximum width (5.0 times in *A. mosselensis*), head in dorsal view 1.8 times as wide as median length (1.5 times in *A. mosselensis*), eye in lateral view 1.75 times as wide as temple medially (1.15–1.20 times in *A. mosselensis*), clypeus 3.0 times as wide as high (4.0 times in *A. mosselensis*), Mesepimeral sulcus crenulate below (smooth in *A. mosselensis*), prescutellar depression with lateral carinae (without in *A. mosselensis*), and ovipositor 2.9 times as long as first tergite (2.15 times in *A. mosselensis*).

Aphaereta mosselensis Peris-Felipo, sp. n.

http://zoobank.org/02E7089D-8C76-454B-A5FC-A85CDB310FFB
Figs 7–8

Etymology. Named after Mossel Bay, the type locality of this new species.

Type material. Holotype: female, South Africa, Cape province, Mossel Bay, 5–31.viii.1921, Brit. Mus. 1921–315 (R.E. Turner leg.) (BMNH). Paratype: 1 female, same locality as holotype but v.1932, Brit. Mus. 1932–206 (BMNH).

Description. Female (holotype).

Head entirely smooth; in dorsal view 1.5 times as wide as median length, 1.4 times as wide as mesoscutum, with rounded gena behind eye. Eye in lateral view 1.2 times as high as wide and 1.2 times as wide as temple medially. POL 2.0 times OD; OOL 3.5 times OD. Face 1.5 times as wide as high; inner margins of eyes subparallel. Clypeus slightly curved ventrally, 4.0 times as wide as high; its upper margin striated. Mandible widened towards apex, 1.4 times as long as its maximum width. Upper tooth of mandible longer than middle and lower tooth; middle tooth wide basally and narrowed towards apex, rounded apically; lower tooth shorter than upper tooth, rounded apically. Antenna as long as body, 16-segmented. Scape 1.4 times as long as pedicel. First flagellar segment 2.75 times as long as its apical width; second segment 4.0 times as long as its maximum width; 1.7 times as long as first segment. Third flagellar segment 3.0 times as long as its width. Fourth to fifth flagellar segments 2.5 times, sixth to eight segments 2.3 times, ninth to fifteenth segments 2.1 times, and sixteenth (apical) segment 2.6 times as long as their maximum width accordingly.

Mesosoma 1.2 times as long as high (lateral view). Mesoscutum 0.9 times as long as its maximum width. Notauli mainly absent on vertical surface of mesoscutum. Mesoscutal midpit absent. Prescutellar depression smooth, without lateral carinae. Precoxal suture present, reaching anterior margin of mesopectus and not reaching posterior margin of mesopectus. Mesepimeral sulcus smooth. Propodeum sculptured, with long median longitudinal carina, with emerging carinae in the middle part reaching propodeal edges and thin areola in posterior half. Propodeal spiracle relatively small.

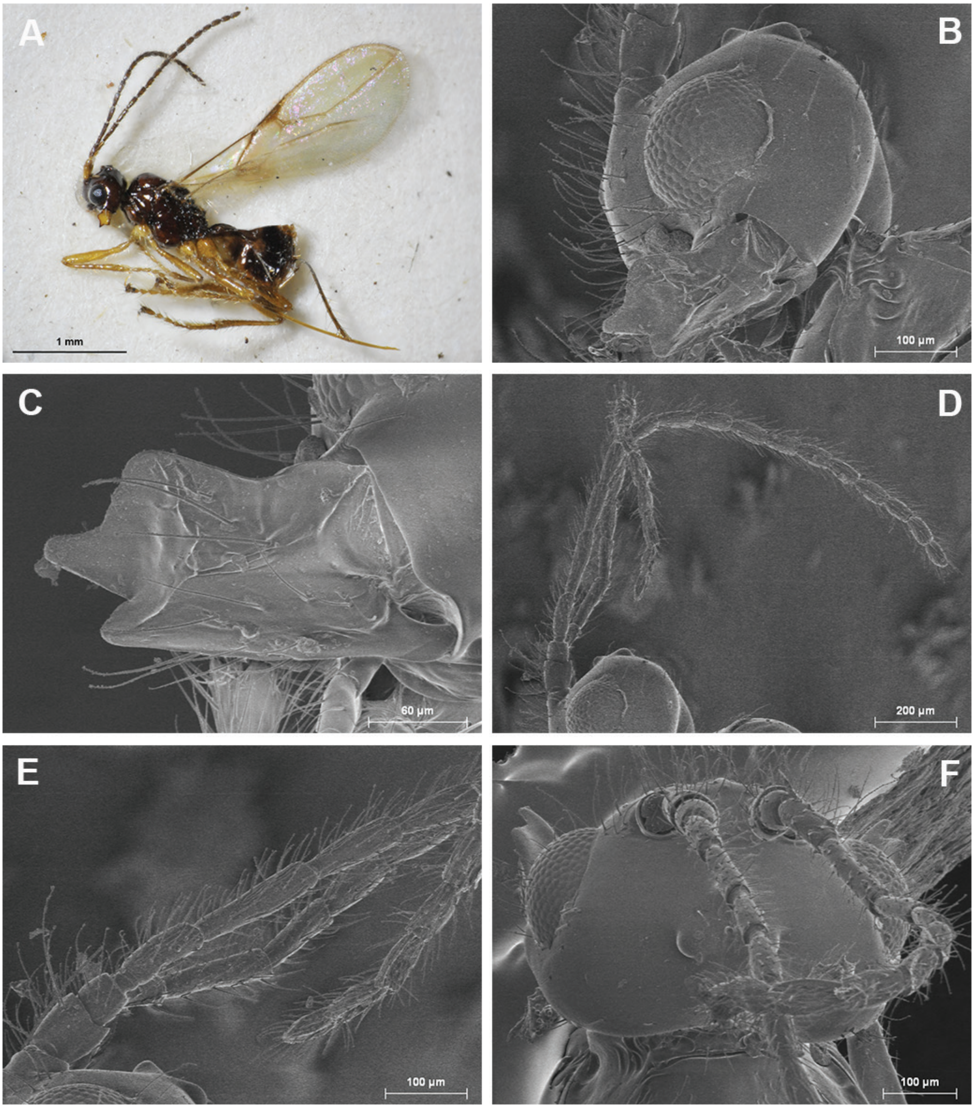

Figure 7. *Aphaereta mosselensis* Peris-Felipo, sp. n. (female) **A** Habitus, lateral view **B** Head, lateral view **C** Mandible **D** Antenna **E** Basal segments of antenna **F** Head, dorsal view.

Wings. Length of fore wing 2.8 times its maximum width. Marginal cell reaching apex of wing, 4.0 times as long as its maximum width. Vein 3RSa 2.3 times as long as 2RS, 5.5 times as long as r, 0.4 times as long as 3RSb. Second submarginal cell 3.6 times as long as maximum width. Hind wing 9.3 times as long as its maximum width.

Legs. Hind femur 5.0 times as long as its maximum width. Hind tibia weakly widened towards apex, about 10.0 times as long as its maximum subapical width, as long as hind tarsus. First segment of hind tarsus (basitarsus) 1.5 times as long as second segment.

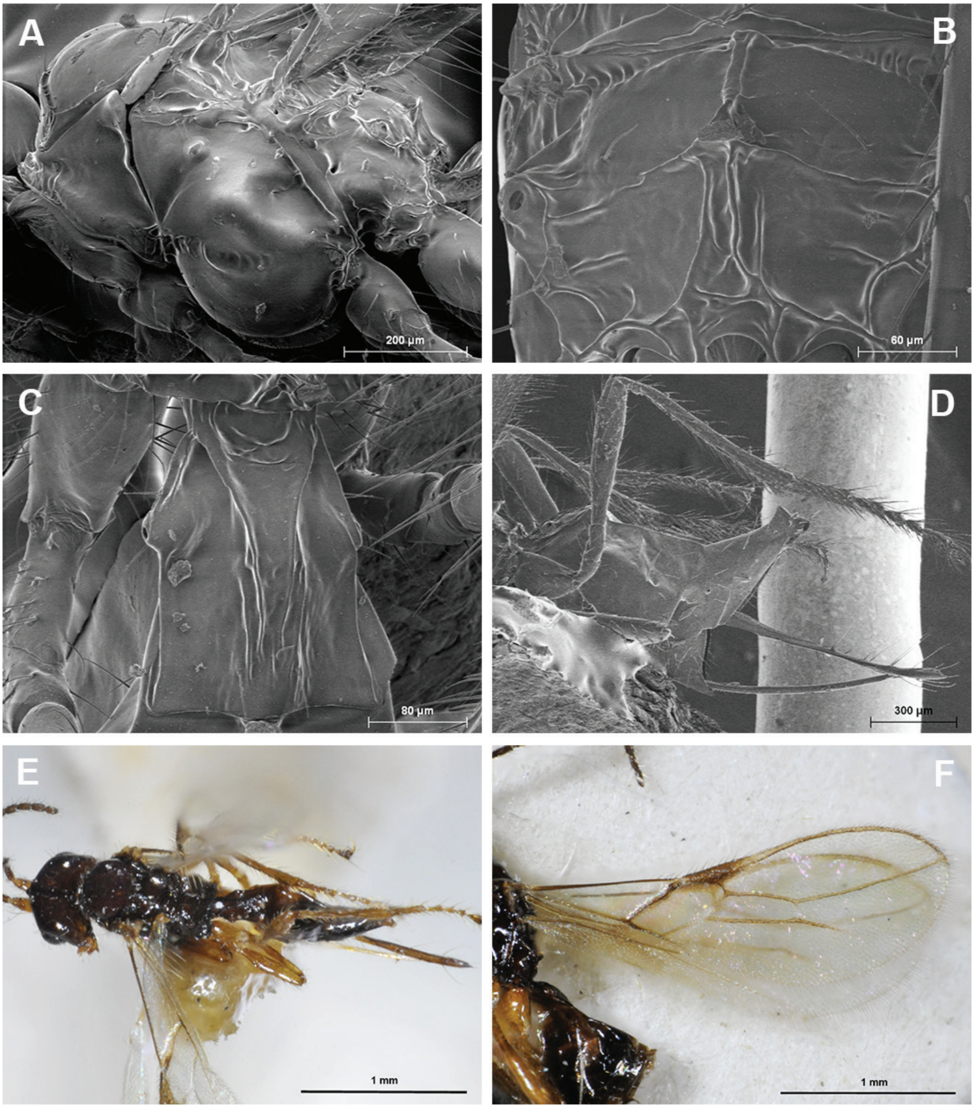

Figure 8. *Aphaereta mosselensis* Peris-Felipo, sp. n. (female) **A** Mesosoma, lateral view **B** Propodeum, dorsal view **C** First metasomal tergite **D** Metasoma, hind leg and ovipositor, lateral view **E** Habitus, dorsal view **F** Fore and hind wings.

Metasoma distinctly compressed. First tergite striated in the middle part, weakly widened towards apex, 1.5 times as long as its apical width. Ovipositor 2.2 times as long as first tergite, distinctly shorter than metasoma, 1.3 times as long as hind femur.

Colour. Body brown to dark brown. Scape, pedicel, mandible, legs and ovipositor brown light. In dorsal view, head, mesosoma and metasoma dark brown. Wings hyaline. Pterostigma light brown to brown.

Body length 2.0 mm; fore wing length 2.5 mm.

Variation. Body length 1.9–2.0 mm; fore wing length 2.5–2.6 mm. Antenna 15–16–segmented. Eye in lateral view 1.1–1.2 times as wide as temple medially.

Male. Unknown.

Comparative diagnosis. This new species is similar to *A. elongata* sp. n. and *A. hararensis* sp. n. Differences between these species are listed after description of the latter species.

Aphaereta sarcophagensis Shenefelt, 1974

Figs 9–10

Aphaereta sarcophagae Bridwell 1919: 177 [junior homonym]; Brues 1924: 149; 1926: 423; Thompson 1953: 89.

Aphaereta sarcophagensis Shenefelt 1974: 962; Fischer 1988: 95; Yu et al. 2012.

Type material. Holotype: locality of the type specimen is unclear (not examined).

Material examined. 2 females, South Africa, Cape province, Mossel Bay, 5–31.vii.1921, Brit. Mus. 1921–315 (R.E. Turner leg.) (BMNH); 2 females, same locality but 15–28.iii.1922, Brit. Mus. 1922–153 and iv.1921, Brit. Mus. 1921–294 (BMNH).

Re-description. Female.

Head entirely smooth; in dorsal view 1.85–2.00 times as wide as median length, 1.4 times as wide as mesoscutum, with rounded gena behind eye. Eye in lateral view as high as wide and 1.8–1.9 times as wide as temple medially. POL 1.75 times OD; OOL 2.9 times OD. Face 1.6 times as wide as high; inner margins of eyes subparallel. Clypeus slightly curved ventrally, 3.5 times as wide as high; its upper margin striated. Mandible widened towards apex, 1.5 times as long as its maximum width. Upper tooth of mandible longer than lower tooth; middle tooth wide basally and narrowed towards apex, pointed apically; lower tooth shorter than upper tooth, rounded apically. Antenna shorter than body, 18–20-segmented. Scape 1.4 times as long as pedicel. First flagellar segment 3.0 times as long as its apical width; second segment 4.7 times as long as its maximum width; 1.5 times as long as first segment. Third flagellar segment 3.3 times as long as its width. Fourth to ninth flagellar segments 2.4–2.5 times, tenth to eighteenth (apical) segments 2.1 times as long as their maximum width accordingly.

Mesosoma 1.3 times as long as high (lateral view). Mesoscutum 1.2 times as long as its maximum width. Notauli mainly absent on vertical surface of mesoscutum. Mesoscutal midpit absent. Prescutellar depression smooth, without lateral carinae. Precoxal suture present, long, reaching anterior margin of mesopectus and not reaching posterior margin of mesopectus. Mesepimeral sulcus slight crenulate below. Propodeum sculptured, with long median longitudinal carina, with apical half densely sculptured. Propodeal spiracle relatively small.

Wings. Length of fore wing 2.6 times its maximum width. Marginal cell reaching apex of wing, 3.4 times as long as its maximum width. Vein 3RSa 2.0–2.1 times as long

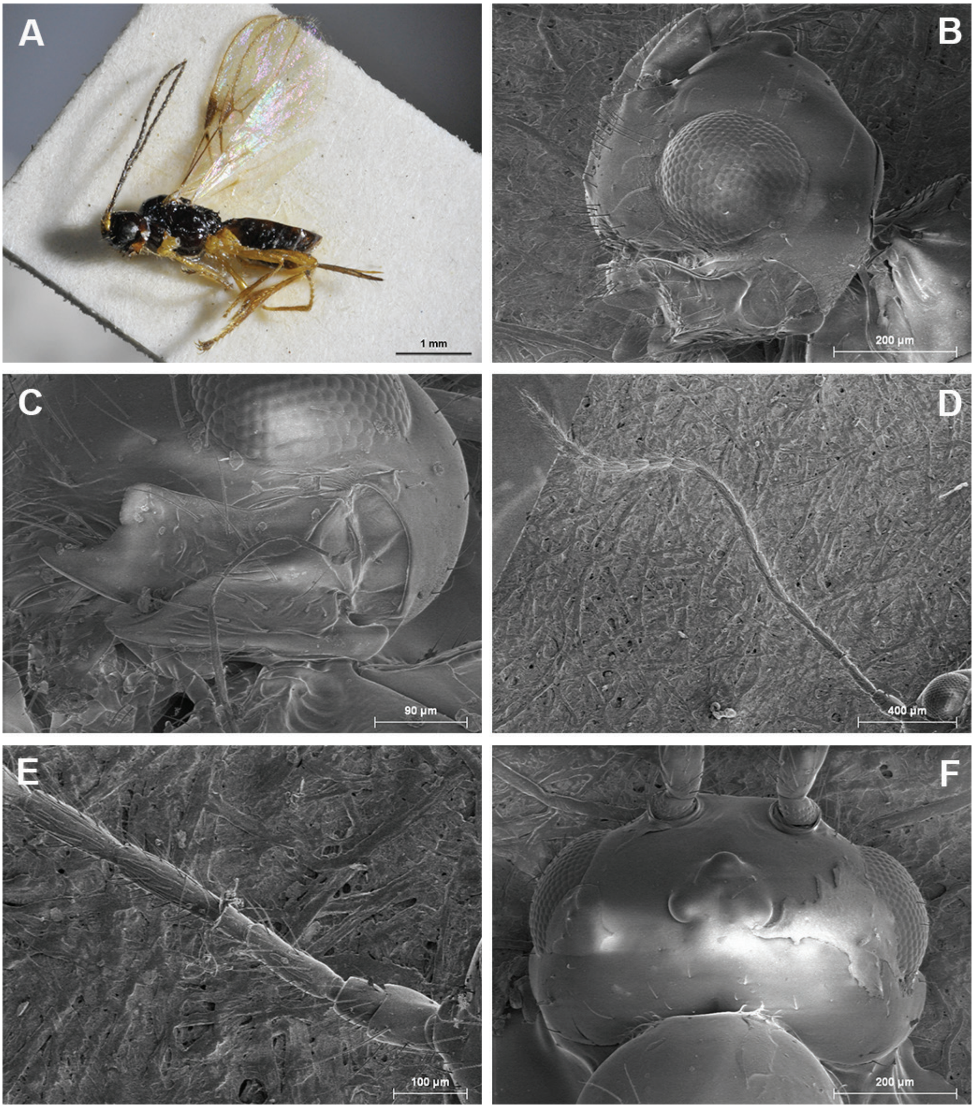

Figure 9. *Aphaereta sarcophagensis* Shenefelt (female) **A** Habitus, lateral view **B** Head, lateral view **C** Mandible **D** Antenna **E** Basal segments of antenna **F** Head, dorsal view.

as 2RS, 4.7 times as long as r, 0.4–0.5 times as long as 3RSb. Second submarginal cell 2.6 times as long as maximum width. Hind wing 4.8 times as long as its maximum width.

Legs. Hind femur 4.5 times as long as its maximum width. Hind tibia weakly widened towards apex, about 9.7 times as long as its maximum subapical width, 0.95 times as long as hind tarsus. First segment of hind tarsus (basitarsus) twice as long as second segment.

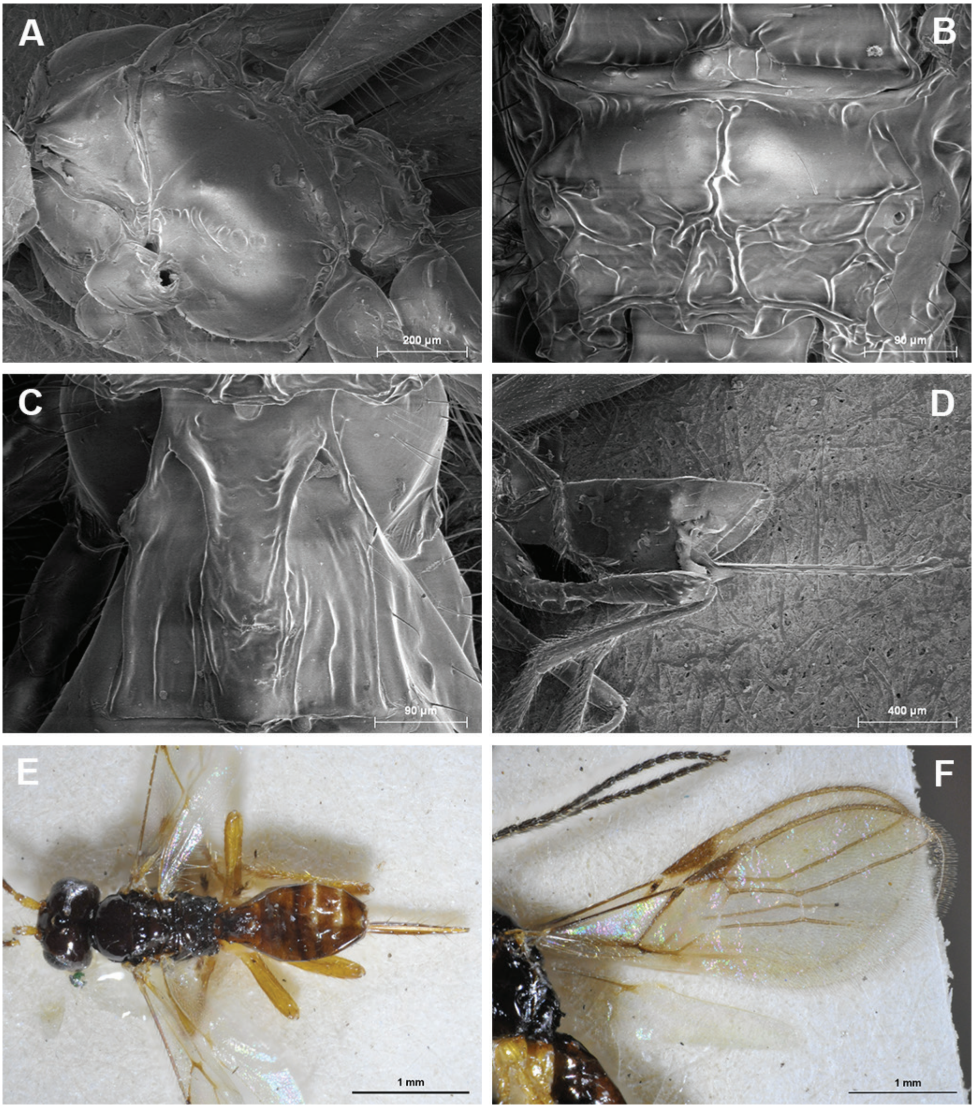

Figure 10. *Aphaereta sarcophagensis* Shenefelt (female) **A** Mesosoma, lateral view **B** Propodeum, dorsal view **C** First metasomal tergite **D** Metasoma, hind leg and ovipositor, lateral view **E** Habitus, dorsal view **F** Fore and hind wings.

Metasoma distinctly compressed. First tergite finely striated, weakly widened towards apex as long as its apical width. Ovipositor 3.4 times as long as first tergite, near as long as metasoma, 1.6 times as long as hind femur.

Colour. Body dark brown. Scape, pedicel, mandible, and legs brown light. In dorsal view, head and mesosoma dark brown; metasoma light brown. Wings hyaline. Pterostigma light brown – brown.

Body length 2.9–3.0 mm; fore wing length 3.2–3.3 mm.

Male. Unknown.

Comparative diagnosis. This species is similar to *A. basirufa* Granger. Differences between these species are listed after description of the latter species.

Key to Afrotropical (including Madagascar) species of the genus *Aphaereta* Förster

1 Second submarginal cell 5.5 times as long as maximum width (Fig. 4F). First flagellar segment 4.5 times, second segment 6.4 times and third segment 5.1 times as long as their maximum width accordingly (Fig. 3E). Mandible 1.8 times as long as its maximum width (Fig. 3C). Upper part of the clypeus not striate. Mesosoma (lateral view) 1.5 times as long as high (Fig. 4A). Precoxal suture smooth, not reaching anterior margin of mesopectus (Fig. 4A). Ovipositor as long as hind femur (Fig. 4D). Antenna 16-segmented. Body length 1.2 mm. Kenya .... ***A. elongata* sp. n.**

– Second submarginal cell 2.3–3.6 times as long as maximum width. First flagellar segment 2.75–3.70 times, second segment 4.6–5.6 times and third segment 3.0–4.5 times as long as their maximum width accordingly. Mandible 1.3–1.5 times as long as its maximum width. Upper part of the clypeus striate. Mesosoma (lateral view) 1.1–1.3 times as long as high. Precoxal suture crenulate, reaching anterior margin of mesopectus. Ovipositor 1.3–1.8 times as long as hind femur **2**

2 First metasomal tergite as long as its apical width. Propodeum without areola **3**

– First metasomal tergite 1.25–1.50 times as long as its apical width. Propodeum with areola **4**

3 First metasomal tergite paler than second and third tergites (Fig. 2E). Hind femur 5.0–5.5 times as long as its maximum width (Fig. 2D). First flagellar segment 3.7–4.0 times, second segment 5.0–5.6 times and third segment 4.5 times as long as their maximum width accordingly (Fig. 1E). Head in dorsal view 1.6–1.8 times as wide as median length (Fig. 1F). Face twice as wide as high. Clypeus 2.4–3.0 times as wide as high. Antenna 22–25-segmented. Body length 2.7–3.0 mm. Madagascar......................... ***A. basirufa* Granger**

– Three basal tergites similarly coloured (Fig. 10A). Hind femur 4.5 times as long as its maximum width (Fig. 10D). First flagellar segment 3.0 times, second segment 4.6 times and third segment 3.3 times as long as their maximum width accordingly (Fig. 9E). Head in dorsal view 1.85–2.00 times as wide as median length (Fig. 9F). Face 1.6 times as wide as high. Clypeus 3.5 times as wide as high. Antenna 18-segmented. Body length 2.9–3.0 mm. South Africa... ***A. sarcophagensis* Shenefelt**

4 Second and third metasomal tergites paler than first tergite (Fig. 6E). First flagellar segment 3.4 times and second segment 4.7 times as long as their

maximum width accordingly (Fig. 5E). Hind femur 4.6 times as long as maximum width (Fig. 6D). Head in dorsal view 1.8 times as wide as median length (Fig. 5F). Eye in lateral view 1.75 times as wide as temple medially (Fig. 5B). Clypeus 3.0 times as wide as high. Mesepimeral sulcus crenulate below (Fig. 6A). Prescutellar depression with lateral carinae. Ovipositor 2.9 times as long as first tergite (Fig. 6D). Antenna 18–19-segmented. Body length 3.3–3.4 mm. Zimbabwe ....***A. hararensis* sp. n.**

– Three basal tergites similarly coloured (Fig. 8A). First flagellar segment 2.75 times and second segment 4.0 times as long as their maximum width accordingly (Fig. 7E). Hind femur 5.0 times as long as maximum width (Fig. 8D). Head in dorsal view 1.5 times as wide as median length (Fig. 7F). Eye in lateral view 1.15–1.20 times as wide as temple medially (Fig. 7B). Clypeus 4.0 times as wide as high. Mesepimeral sulcus entirely smooth (Fig. 8A). Prescutellar depression without lateral carinae. Ovipositor 2.15 times as long as first tergite (Fig. 8D). Antenna 15–16-segmented. Body length 1.9–2.0 mm. South Africa ....***A. mosselensis* sp. n.**

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References

Bridwell JC (1919) Descriptions of new species of Hymenopterous parasites of Muscoid Diptera, with notes on their habits. Proceedings of the Hawaiian Entomological Society 4: 166–179.

Brues CT (1924) Some South African parasitic Hymenoptera of the families Evaniidae, Braconidae, Alysiidae and Plumariidae in the South African Museum with a catalogue of the known species. Annals of the South African Museum 19: 1–150.

Brues CT (1926) Studies on Ethiopian Braconidae with a catalogue of the African species. Proceedings of the American Academy of Arts and Sciences 61: 206–436. doi: 10.2307/20026158

Dolphin K, Quicke DLJ (2001) Estimating the global species richness of an incompletely described taxon: an example using parasitoid wasps (Hymenoptera: Braconidae). Biological Journal of the Linnean Society 73: 279–286. doi: 10.1111/j.1095-8312.2001.tb01363.x

Fischer M (1988) Einzelheiten zur taxonomic exotischer Alysiinae der Gattungen Aphaereta Foerster, Asobara Foerster, Coelalysia Cameron und Phaenocarpa Foerster (Hymenoptera, Braconidae). Annalen des Naturhistorischen Museums in Wien 90: 93–130.

Fischer M (1994) Beitrag zur Kenntnis der Kieferwespen der Welt (Hymenoptera, Braconidae, Alysiinae: Alysiini). Linzer biologische Beiträge 26(2): 763–806.

Granger C (1949) Braconides de Madagascar. Memoires de l'Institut Scientifique de Madagascar (A) 2: 1–428.

Peris-Felipo FJ, Fischer M, Jiménez-Peydró R (2013) Five new Dinotrema species from Spain with mesoscutal pit and medially sculptured propodeum. Bulletin of Insectology 66(1): 59–71.

Shenefelt RD (1974) Pars 11. Braconidae 7. Alysiinae. In: Van der Vecht J, Shenefelt RD (Eds) Hymenopterorum Catalogus (nova edition). Dr. W. Junk. B. V. Junk, The Hague, 937–1113.

Sharkey MJ, Wharton RA (1997) Morphology and terminology. In: Wharton RA, Marsh PM, Sharkey MJ (Eds) Manual of the New World Genera of the Family Braconidae (Hymenoptera). International Society Hymenopterists, Washington D.C., 19–37.

Thompson WR (1953) Host of the Hymenoptera (Agaonidae to Braconidae). A catalogue of the parasites and predators of insect pests 2(2): 1–190.

Wharton RA (2002) Revision of the Australian Alysiini (Hymenoptera: Braconidae). Invertebrate Systematics 16: 7–105. doi: 10.1071/IT01012

Yoder MJ, Mikó I, Seltmann KC, Bertone MA, Deans AR (2010) A Gross Anatomy Ontology for Hymenoptera. PLoS ONE 5(12): e15991. doi: 10.1371/journal.pone.0015991

Yu DS, Achterberg C van, Horstman K (2012) Taxapad 2012, Ichneumonoidea 2011. Database on flash-drive. Ottawa, Ontario, Canada.

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RESEARCH ARTICLE

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Notes on the biology, morphology, nomenclature and classification of *Pseudavga flavicoxa* Tobias, 1964 (Hymenoptera, Braconidae, Rhysipolinae), a genus and species new to Britain parasitizing *Bucculatrix thoracella* (Thunberg) (Lepidoptera, Bucculatricidae)

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Abstract

The solitary parasitoid *Pseudavga flavicoxa* has been reared, in some numbers, from cocoons of the bucculatricid moth *Bucculatrix thoracella* collected as larvae descending from *Tilia* × *vulgaris* to form their cocoons, at Jealott's Hill, Berkshire, England. The taxonomic confusions and complications bedevilling its determination are outlined, and the recognition of the genus *Pseudavga* Tobias, 1964 is proposed. Egg placement in this koinobiont ectoparasitoid and the related genus *Rhysipolis* is discussed.

Keywords

Cantharoctonus, *Rhysipolis*, *Pachystigmus*, France, Croatia

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Introduction

Among parasitoids of Lepidoptera reared during 2010 and 2011 by IS and sent to MRS for determination was a small (2.2 mm) predominantly straw-orange female specimen of a cyclostome braconid of the subfamily Rhysipolinae. It had been reared, probably in spring 2011 [found dead], from a cocoon of the bucculatricid moth *Bucculatrix thoracella* (Thunberg) collected at Jealott's Hill, Berkshire, England on 13.ix.2010 as a larva descending from *Tilia* × *vulgaris* to spin up. The parasitoid was instantly recognised for what it was, as there are several similar specimens in the National Museums of Scotland (NMS) at the time provisionally standing over the incorrect name *Rhysipolis rustus* Papp, some of which were also reared from *Bucculatrix* in mainland Europe. However, no other British record or specimen had been seen, and nor had MRS been able to place them satisfactorily to genus within the tangled classification of Rhysipolinae. Further specimens reared from *B. thoracella* at Jealott's Hill have subsequently been obtained.

As well as simply bringing forth and figuring this species as a British insect (Figures 1–6), in this paper we review some of the taxonomic and nomenclatural morass surrounding its determination as *Pseudavga flavicoxa* Tobias, and propose the reinstatement of the generic name *Pseudavga* Tobias, 1964. In a work on Braconidae of the Russian Far East, Belokobylskij (1998) cites *Bucculatrix ulmella* Zeller (in fact from Moldavia) and (more surprisingly, in view of its different feeding habit) *Leucoptera malinifoliella* (Costa) as hosts of *flavicoxa* (as *Noserus*), but rearing records of *P. flavicoxa* in Western Europe have not previously been given.

In addition, some preliminary observations on the biology of *P. flavicoxa* are recorded, and both morphological and biological comparisons with *Rhysipolis* Foerster, 1862 are made. While the generic classification within Rhysipolinae remains in need of a wider review, morphological notes on the New World genus *Cantharoctonus* Viereck, 1912 are also given.

Materials and methods

All *B. thoracella* that produced *P. flavicoxa* were collected as descending larvae at Jealott's Hill, Berkshire, England (see "Biological observations" below). Experimental exposures involved wild *B. thoracella* larvae of various ages collected from *Tilia* × *vulgaris* in Edinburgh.

Figures 1–6 were made using a Leica MZ16 microscope and phototube with an Olympus C-5060 camera, with multiple images stacked using ZereneStacker. Figures 7, 8 and 10–13 were taken as single images on a hand-held Canon Powershot S110 directly down one arm of a Wild M5A stereomicroscope, and Figure 9 was taken with a Fuji Finepix S and Brunnel SP100 trinocular microscope. Figure 14 was originally obtained on colour transparency film using a Contaflex camera and close-up lenses, with other details not recalled, and scanned.

Figures 1–6. *Pseudavga flavicoxa*, female. **1** habitus, lateral **2** propodeum and 1st metasomal tergite, dorsal **3** mesosoma, dorsal **4** head, dorsal **5** face **6** antennae.

Reared British material in NMS

Following the rearing of a single ♀ from *B. thoracella* collected in 2011 (see above), IS attempted to rear further specimens from this host from the same *Tilia* × *vulgaris* trees in the autumn of 2012, collecting around 150 host larvae. However, owing to a communication failure, only approximately half-grown larvae were collected, and only moths resulted. The following year, from 4.ix–19.x.2013, 92 fully grown descending larvae produced 2 ♀, 1 ♂ of *P. flavicoxa* in x. 2013, and a further ♀ was found dead by iv.2014; otherwise practically all cocoons produced moths in 2014. In autumn 2014, in preparation for more detailed research on the biology of the parasitoid proposed for 2015, a large number of descending larvae were collected from the same *Tilia* trees in the period 9.ix–4.x.2014, and the resulting cocoons were kept indoors until being dispatched to Edinburgh, where they were received on 10.x.2014. By that date around 20 *P. flavicoxa* (both sexes equally) had emerged from the earliest made collections (9–10.ix.2014), but the remaining *Bucculatrix* cocoons were immediately placed in an outdoor rearing shed (cf. Shaw 1997) and, apart from 1 ♂ on 16.x.2014 from the same early collections, no further emergences occurred (by 23.xii.2014): it is of course unclear whether or not more will emerge in 2015, but it is presumed that they will as the behaviour of the living adult females did not suggest preparation for hibernation. The range of antennal segments in the British material seen so far is ♀ 22–24; ♂ 24–26.

Continental material in NMS

Additional specimens, clearly congeneric with the British material and some reared from a further two species of *Bucculatrix*, are in NMS as follows:

CROATIA: 1 ♂, Oputija, ex *Bucculatrix frangutella* (Goeze), final instar larva coll. x.1988, em. x/xi.1988 (J.L. Gregory).

FRANCE: 1 ♀, Côte d'Or, Abbey de la Bussière, at light 21.vii.2003 (M.R. Shaw); 1 ♀, 1 ♂, Dordogne, La Barrière, 15 km S Riberac, at light 4–12.viii.2007 (M.R. Shaw;) and 1 ♀, same data but ex *Bucculatrix ulmella* on *Quercus*, coll. and em. viii.2007 (M.R. Shaw).

Results

Identity and nomenclature

A specimen from France present in NMS that is very similar to (certainly congeneric and provisionally regarded as conspecific with) the British reared specimens had been determined by MRS in 2003 as the nominal taxon *Rhysipolis rustus* Papp, based on the original description (Papp 1991). However by then Papp (2002) had placed his species in synonymy with what he referred to as *Noserus flavicoxa* (Tobias), the generic placement resulting presumably because Belokobylskij and Tobias (1986) had (incorrectly) synonymised *Pseudavga* Tobias, 1964 (type species *P. flavicoxa* Tobias, 1964) with *Noserus*. This incorrect generic synonymy caused identification problems: the genus *Noserus* Foerster, 1863 (not 1862—see Foley et al. 2003) has been interpreted in various ways in the literature, but its type species *Noserus facialis* Foerster, 1863 was redescribed and figured by Whitfield and van Achterberg (1987) and clearly bore no relation to the reared British specimens, although *Noserus facialis* has been recorded from *Bucculatrix ulmella* (Tobias 1976, Belokobylskij and Tobias 1986, Belokobylskij 1998—the last two probably merely a reiteration of the first). However, when rearing records appear to have been transcribed from one work to another several times without clarification or further detail it is difficult to treat them with confidence, especially when the application of names to the parasitoid(s) has been inconsistent over that time. Thus the reliability of the parasitoid determination for this host record is possibly in doubt because Belokobylskij and Tobias (1986) and Belokobylskij (1998) incorrectly regarded *Pseudavga* as a synonym of *Noserus*, and this might conceivably underlie the citation of *B. ulmella* as host of both *flavicoxa* and *facialis* (which seems inherently unlikely to be the case) by Belokobylskij (1998), who keys *flavicoxa*, *facialis* (with the synonym *brevicauda*, but see below) and two Eastern Palaearctic species, *occipitalis* Belokobylskij, 1986 and *olgensis* Belokobylskij, 1994, all as species of *Noserus* (regarding both *Pachystigmus* and *Pseudavga* as synonyms). It was in a footnote that Belokobylskij and Tobias (1986) first stated that *Pachystigmus* Hellén, 1927 (type species *Pachystigmus nitidulus* Hellén, 1927, described from a single male) was a synonym of *Noserus*, and Whitfield and van Achterberg (1987) formalised the latter synonymy. Foley et al. (2003) showed that *Noserus* Foerster, 1863 (not 1862) is a junior homonym of *Noserus* LeConte, 1862, which is applied in Coleoptera, with the result that the name *Pachystigmus* has been resurrected and used subsequently (e.g. in *Fauna Europaea*).

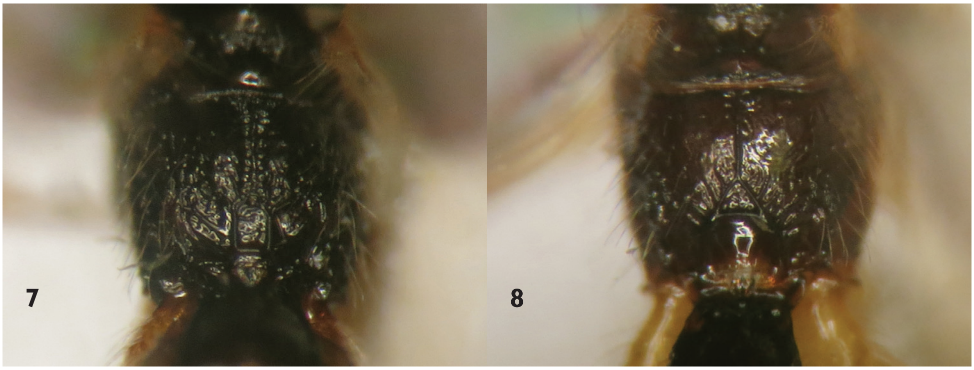
In their attempt to clarify the application of the generic names *Cantharoctonus*, *Noserus* (now *Pachystigmus*, which has a different type species) and *Pseudavga*, Whitfield and van Achterberg (1987) stated that the type species of *Noserus*, *Pachystigmus*, *Pseudavga* and *Rhysipolis* had all been seen by van Achterberg. However, the paper then went on to diagnose and figure "*Pseudavga*" by reference not to the type species *flavicoxa* Tobias (Tobias 1964a), but to another nominal species that was at that time placed in *Pseudavga* (but incorrectly so), *Oncophanes brevicauda* Tobias, 1964, a nominal species (Tobias 1964b) now regarded as belonging in *Pachystigmus* and therefore congeneric with the nominal *Noserus facialis* (the proposed synonymy of *brevicauda* with *facialis* by Belokobylskij and Tobias (1986) has not been followed or accepted by van Achterberg (pers. comm.), and consequently both are listed as valid species of *Pachystigmus* in *Fauna Europaea*). This error in the recognition and diagnosis of *Pseudavga* was another major impediment to correctly identifying the reared British specimens as *Pseudavga flavicoxa*.

Generic placement

In *Fauna Europaea*, *flavicoxa* is listed as a species of *Rhysipolis* Foerster, although no formal synonymy of *Pseudavga* with *Rhysipolis* has been proposed. The propodeum is broadly similar in the two genera, with a clear median carina anteriorly, and with an areola and a petiolar area more or less defined medioposteriorly. In *Rhysipolis* there is a wide divergence in the shape and relative sizes of the two latter areas: for example, in the type species *R. meditator* (Haliday) (Figure 7) the areola is moderately large, narrow, parallel-sided posteriorly with the short converging anterior sides to complete the pentagon being all but obscured in general rugosity, and the area petiolaris is almost unnoticeably small; while in *R. decorator* (Haliday) (Figure 8) the areola is very small, more or less reduced to a triangle, and the area petiolaris is by comparison massive. The propodeum of *P. flavicoxa* (Figure 2), with its relatively large pentagonal areola and small area petiolaris, sits fairly comfortably within these wide limits, closest to *R. meditator,* and it is presumably largely on account of the similar propodeum (in particular its anterior median carina) that van Achterberg placed *flavicoxa* in *Rhysipolis* in *Fauna Europaea*. However, *Pseudavga* has a significantly larger and wider areola and, unlike the situation in most *Rhysipolis* species, this has strong costulae. *Pseudavga* also differs from *Rhysipolis* in having a weak but distinct pronope (Figure 3) and in its legs bearing numerous long upstanding setae; furthermore, the spiracle of the second metasomal tergite is more deeply into the epipleuron (laterotergite) than in *Rhysipolis*. Perhaps even more obviously, *Rhysipolis* species have a longer ovipositor, commensurate with parasitizing hosts that are concealed in leaf mines and folds (Shaw 1983), whereas the short ovipositor of *Pseudavga* (Figure 1) is compatible with parasitism of fully exposed hosts (as reported here). Although the circumstantial evidence is that *Pseudavga* may have developmental biology similar to, or possibly identical with, that of *Rhysipolis*, these morphological differences justify its recognition as a genus distinct from *Rhysipolis*.

Sergey A. Belokobylskij (pers. comm.) has agreed with the present conclusion that *Pseudavga* is a genus distinct from *Pachystigmus*, regarding the reduced prepectal carina in *Pseudavga*, which is present only laterally [but variable; in some British specimens more extensive], as the most important difference. We have not seen the type of *Pachystigmus nitidulus* and consequently can offer no further opinion, but the original description (Hellén 1927) makes it clear that it is substantially different from *Pseudavga flavicoxa*, for example in the swollen male pterostigma of *nitidulus* (although this may not be a consistent generic character for *Pachystigmus*), and the figures given by Whitfield and van Achterberg (1987) of two further *Pachystigmus* species (*facialis* (as *Noserus*) and *brevicauda* (as *Pseudavga*)) also appear profoundly dissimilar.

However, whether or not *Pseudavga* should be retained as a genus distinct from the New World genus *Cantharoctonus* seems more doubtful, although in *Cantharoctonus* (to judge from the four undetermined N. American specimens in NMS) the complete prepectal carina appears to be much stronger than in *Pseudavga flavicoxa*, in which it is only weakly present. Whitfield and van Achterberg (1987) did not note similarities, but this must have been only because they misinterpreted *Pseudavga*, as in fact the two genera are in many respects extremely similar and both are parasitoids of *Bucculatrix*. Whitfield and van Achterberg (1987: Fig. 45) also seem to have misinterpreted the disposition of the hypostomal and occipital carinae in *Cantharoctonus*, in which (as in *Pseudavga*) in reality the carinae fail to meet, though converging towards the mandibular base, as the former peters out just before the mandible rather than, as Whitfield and van Achterberg (1987) state and figure, meeting well before the base of the mandible.



Figures 7, 8. *Rhysipolis* species, propodeum. **7** *R. meditator* **8** *R. decorator*.

(In fact it is apparent from detached heads of *Pseudavga flavicoxa* that the lower part of the hypostomal carina is not only extremely weak but also dissociates into a series of diverging ridges, the uppermost of which does more or less run into (or gives out just before) the very strong occipital carina before the mandibular base, but the lower and stronger of which runs on to the level of the mandible without meeting the occipital carina.) As well as an almost indistinguishable general facies, the two nominal genera also share the general arrangement of carinae on the propodeum (*Cantharoctonus*: Figs 8 and 47 in Whitfield and van Achterberg 1987), and the position (in the epipleuron) of the spiracle of the second metasomal tergite. One of the particular features of *Cantharoctonus* is a transverse and more or less crenulate groove across the extreme anterior edge of the propodeum, and in specimens in which this is well developed it is indeed quite striking. However, it seems to be rather variable in *Cantharoctonus*, and is to at least some extent discernible, if weak, on all the material of *Pseudavga* detailed in this paper. While a rather weak pronope is present in *Pseudavga flavicoxa* (Figure 3) it is stated to be absent in *Cantharoctonus* (Whitfield and van Achterberg 1987), but this may not have much significance (the dorsum of the pronotum is visible in only one of the specimens of *Cantharoctonus* in NMS). The legs of both genera bear long rather upright setae; somewhat less pronounced in *Pseudavga* (in which the setae on the hind tibia are almost as decumbent as in *Rhysipolis meditator*, the type species of *Rhysipolis*, unlike the specimens of *Cantharoctonus* seen). Whether the similarities between the two nominal genera are of greater significance than their differences might best be considered in the course of a thorough review of generic relationships in Rhysipolinae as a whole, as certainly seems to be needed.

Variation

Taken together, the available material of *Pseudavga* in NMS is very variable (e.g. in respect of colour, position of the radius on the pterostigma, shape and sculpture of the first metasomal tergite, detail of carination and sculpture of the propodeum, lengths of antennal segments and perhaps ovipositor sheath) and may represent more than one (possibly up to three) species. However, even though from a single population, there is enough variation in the British material (which must surely belong to only one species) to lead us to conclude that there is insufficient material at hand to assess possible species limits in the wider material in NMS, so provisionally we regard it as all belonging to a single variable species, *P. flavicoxa*.

Biological observations

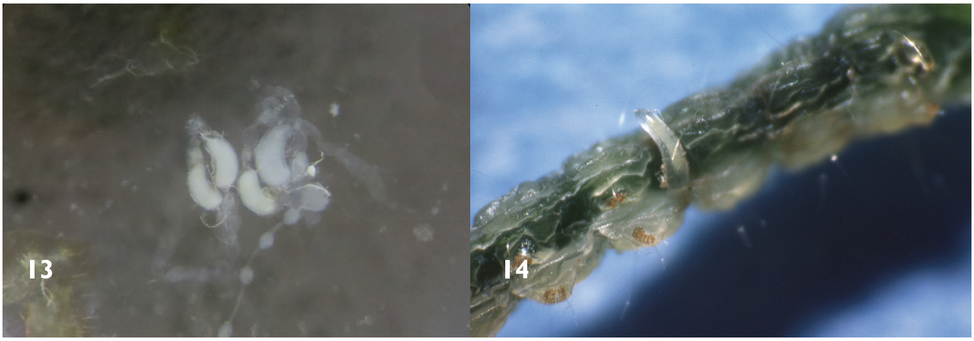
The host of the British specimens, *Bucculatrix thoracella*, has greatly increased its range and abundance in Britain over the past 40 years, probably both through broadening its foodplant tolerance from *Tilia cordata*, a native but local and restricted woodland tree, to include the widely planted *Tilia* × *vulgaris*, and by becoming thoroughly plurivoltine (Emmet 1984). Thus from formerly being a local, uncommon and apparently univoltine denizen of mainly SW England, it is today widespread and common, especially in suburban environments where *Tilia* × *vulgaris* is frequently planted, over most of mainland Britain (including Edinburgh, where it is profoundly plurivoltine). After a brief period as a leaf miner, the larva of *B. thoracella* feeds on the parenchyma of *Tilia* leaves from the leaf underside, leaving a windowed pattern of damage visible from the upperside. To accomplish its moults, the larva constructs a temporary small and dense silken shelter, in which ecdysis occurs. When fully fed, the larva descends from the leaf on a silken thread, and spins its characteristic ribbed cocoon upon landfall.

One of the descending *B. thoracella* larvae intercepted by IS on 2.x.2014 was being grappled by a small orange insect which (although it escaped) was almost certainly *P. flavicoxa*, and inspection of some other descending larvae revealed the presence of single eggs, 0.2 mm long and in each case (7 observations) transversely placed (sub) dorsally along the intersegmental membrane behind the first thoracic segment (Figures 9–11; from alcohol preserved specimens, 10–11 then air dried). The egg is rounded at both ends; the small dark point visible at the narrow (presumably caudal) end in Figure 9 is part of the host.

In Edinburgh, indoors at room temperature (18–22 °C), 1–2 mid-final instar host larvae were kept, on strips of *Tilia* × *vulgaris* leaf, in 2.5 × 7.5 cm corked glass tubes with a single (probably mated) female *P. flavicoxa* (6 replicates), with diluted honey smeared on the glass, from 13.x.2014 (after 3 days of feeding in the absence of hosts) until the females died (the last one on 25.x.2014). At times, hosts in moulting cocoons were also added. The hosts were inspected twice daily, and replaced as they formed cocoons; all cocoons were opened and the larvae within also inspected. No ovipositions resulted, and indeed (including during the initial period of inspection afforded to each female being newly introduced to hosts) no interest whatsoever in the hosts or their traces was observed (Figure 12). Most deaths of *P. flavicoxa* resulted from being gummed up in the traces of honey provided as food, and/or other

Figures 9–12. *Pseudavga flavicoxa* with final instar larval host *Bucculatrix thoracella*. **9–11** egg on intersegmental membrane behind prothorax of host **12** adult female parasitoid ignoring host.

fluid that appeared in the tube, and three adults suffering this fate were dissected (8, 9 and 12 days after 10.x.2014, when they had started to feed on dilute honey). The dissections hardly differed, each showing a single egg nearing maturity in each of the two ovarioles of the paired ovaries (i.e. 4 eggs in advanced ovigenesis, Figure 13), but with little sign that other eggs would follow. No egg had entered the oviduct per se, and it was unclear whether they were ready for oviposition or, conceivably, being resorbed. It does, however, seem certain that if eggs were going to be ready for oviposition from these females in October 2014, the period from 10.x.14 to (maximally) 25.x.2014, during which they had been warm, fed ad libitum, and given access to hosts, was long enough for them to have become so. Thus it was surprising that no ovipositions were obtained, especially as the adult female parasitoids showed no sign of behaviour suggesting that they might overwinter as adults (it has not, however, escaped notice that none of the adults of *Pseudavga* seen has unequivocally overwintered in a host cocoon).



Figures 13, 14. 13 *Pseudavga flavicoxa*, partial dissection of 12 day old female showing one almost mature egg in each of four ovarioles **14** *Rhysipolis decorator*, egg artificially partly detached from freeze-killed and stretched larva of *Caloptilia* sp.

Comparison with the biology of *Rhysipolis*

Although the act of oviposition per se has not been seen in either *Rhysipolis* or *Pseudavga*, there are some comparisons that can be drawn simply from observation of the eggs. In *Rhysipolis* the egg is similarly placed transversely across a host intersegmental membrane, though with much greater flexibility as to the segments concerned (Shaw 1983, reporting on three studied species), but the egg is much slenderer than that of *Pseudavga* (compare Figures 9 and 14). The eggs of *Rhysipolis* spp. presumably have to travel down the (relatively longer) ovipositor shaft because the host is concealed beneath plant tissue, and are consequently relatively slender; some flexibility regarding exact placement is likely also to be a consequence of host concealment. But the apparently more exact placement, and especially the less elongate egg shape, in *Pseudavga* raises the question of how, or whether at all, the ovipositor might be involved in egg placement. In particular, Shaw and Wahl (2014) have drawn attention to the possible universality of the egg (or at any rate the bulk of the egg) not travelling down the ovipositor shaft in all arthropod-consuming apocritan Hymenoptera whose larvae feed from an external position (the relevant ectoparasitoids and all carniveroid Aculeata) in which the female is able to make direct bodily contact with the host or prey at the time of oviposition. For this reason, microscopic observation of the moment of oviposition by *Pseudavga* would be of considerable interest.

Studied *Rhysipolis* species (Shaw 1983) employ a venom which, in addition to causing temporary paralysis aiding host-handling by the parasitoid, switches the host to a prepupal state of arrested development at the end of the instar attacked, precociously if the host is in its penultimate instar at the time of attack. In some cases, therefore, a given *Rhysipolis* species may develop on a nominally penultimate host. Although we have not seen suggestively undersized cocoons of the host (which, however, are uncommonly seen in the hosts of wild *Rhysipolis* populations), it would be of interest to know whether or not such a venom is employed by *Pseudavga*, and the unexplained failure to obtain attacks on the host in the autumn of 2014 was extremely disappointing.

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References

Belokobylskij SA (1998) [Subfam. Exothecini]. In: Lehr PA (Ed.) [Key to insects of the Russian Far East. Neuropteroidea, Mecoptera, Hymenoptera]. Dal'nauka, Vladivostok, 4, part 3: 111–159. [In Russian]

Belokobylskij SA, Tobias VI (1986) Doryctinae. In: Medvedev GS (Ed.) Opredelitel Nasekomych Eurospeiskoi Tsasti SSSR 3, Peredpondatokrylye 4. Opredelitel Faune SSSR 145: 21–72. [In Russian, translated 1995 Science Publishers, Lebanon]

Emmet AM (1984) *Bucculatrix thoracella* (Thunberg) (Lep.: Lyonetiidae). Entomologist's Record and Journal of Variation 96: 130–131.

Fauna Europaea http://www.faunaeur.org [accessed 30.x.2014]

Foley IA, Ivie MA, Spies M (2003) *Pachystigmus* Hellén, 1927, a substitute name for *Noserus* Foerster, 1863 (Hymenoptera: Braconidae), not *Noserus* LeConte, 1862 (Coleoptera: Zopheridae). Insecta Mundi 17: 103–106.

Hellén W (1927) Zur Kenntnis der Braconiden (Hym.) Finnlands. 1. Subfam. Braconinae (part.), Rogadinae und Spathiinae. Acta Societatis pro Fauna et Flora Fennica 56(12): 1–59.

Papp J (1991) Second survey of the braconid wasps in the Bátorliget Nature Conservation Areas, Hungary (Hymenoptera: Braconidae). In: Mahunka S (Ed.) The Bátorliget Nature Reserves – after forty years. Hungarian Natural History Museum, Budapest 2: 639–674.

Papp J (2002) The braconid wasps (Hymenoptera: Braconidae) of the Fertö-Hanság National Park (NW Hungary). In: The fauna of the Fertö-Hanság Nationl Park. Hungarian Natural History Museum, Budapest, 557–581.

Shaw MR (1983) On[e] evolution of endoparasitism: the biology of some genera of Rogadinae (Braconidae). In: Gupta VK (Ed.) Studies on the Hymenoptera. Contributions of the American Entomological Institute 20: 307–328.

Shaw MR (1997) Rearing parasitic Hymenoptera. Amateur Entomologist's Society, Orpington. 46 pp.

Shaw MR, Wahl DB (2014) Biology, early stages and description of a new species of *Adelognathus* Holmgren (Hymenoptera: Ichneumonidae: Adelognathinae). Zootaxa 3884(3): 235–252. doi: 10.11646/zootaxa.3884.3.3

Tobias VI (1964a) Novye vidy i rod brakonid iz Tadzhikistana (Hymenoptera, Braconidae). [New braconid species and genus from Tajikistan (Hymenoptera, Braconidae)]. Izvestiya Otdeleniva Biologicheskih Nauk Akademii Nauk Tadzhikskoy SSR 2(16): 58–65. [In Russian]

Tobias VI (1964b) Novye vidy i rod brakonid (Hymenoptera, Braconidae) iz Kazahstana. [New species and genus of braconids (Hymenoptera, Braconidae) from Kazakhstan]. Trudy Zoologicheskogo Instituta Akademii Nauk SSSR 34: 177–234. [In Russian]

Tobias VI (1976) [Braconids of the Caucasus (Hymenoptera, Braconidae]. Opredelitel Faune SSSR 110. Nauka, Leningrad, 286 pp. [In Russian]

Whitfield JB, van Achterberg C (1987) Clarification of the taxonomic status of the genera *Cantharoctonus* Viereck, *Noserus* Foerster and *Pseudavga* Tobias (Hymenoptera: Braconidae). Systematic Entomology 12: 509–518. doi: 10.1111/j.1365-3113.1987.tb00221.x

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RESEARCH ARTICLE

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Aenictus yangi sp. n. – a new species of the *A. ceylonicus* species group (Hymenoptera, Formicidae, Dorylinae) from Yunnan, China

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Abstract

In this study we present a taxonomic update for the *Aenictus ceylonicus* group. A recent survey of the leaf litter ant fauna of Xingshuangbanna (Yunnan, China) yielded material of a hitherto unknown member of the group, which we describe here as *Aenictus yangi* **sp. n.** The new species is clearly distinguishable from the other species of the *A. ceylonicus* group based on differences in mandibular dentition, the development of the metanotal groove, the shape of the propodeum and subpetiolar process, as well as surface sculpture on the mesosoma and waist segments. In order to integrate *A. yangi* **sp. n.** into the taxonomic system created by Jaitrong and Yamane (2013) we provide an update to the identification key provided in the latter revision, as well as a diagnostic discussion and high-quality illustrations of important species and morphological characters.

Keywords

Army ants, *A. ceylonicus* species group, China, taxonomy, Yunnan

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Introduction

The ant genus *Aenictus* Shuckard, 1840 is widely distributed throughout the tropics and subtropics of the Old World. *Aenictus* species can be found from the Mediterranean and most of Africa through the Middle East to the Oriental, Indo-Australian, and Australasian regions, whereas they are completely absent in the New World, Madagascar, most of the Palaearctic, and the Pacific east of New Guinea (e.g. Wilson 1964; Gotwald 1995; Shattuck 2008). Currently, there are 180 valid species of *Aenictus* (Bolton, 2014) rendering it one of the larger genera among ants. Historically, the systematic placement of *Aenictus* was a question of debate with most authors treating it as a genus within the subfamily Dorylinae (e.g. Mayr 1865; Dalla Torre 1893; Emery 1895; Borgmeier 1954). In the last decades it was mostly considered as the only genus of the subfamily Aenictinae (Bolton 1990, 1995; Baroni Urbani et al. 1992) until the recent molecular phylogeny of Brady et al. (2014), which showed that *Aenictus* belongs to a monophyletic group containing all dorylomorph genera now placed in the subfamily Dorylinae.

All species of *Aenictus* are considered as "true army ants" (Wilson 1964), which means that they possess a combination of behavioural and reproductive traits defined as the "army ant syndrome" (Schneirla 1971; Gotwald 1995; Brady 2003). This syndrome includes obligate group foraging, nomadism, highly modified (dichthadiiform) queens, and establishment of new colonies through colony fission. Based on the available data, most *Aenictus* seem to be specialised predators of other ants, social wasps, and termites, but there are also reports of some species preying on non-social insects or, more rarely, gathering honeydew (Arnold 1915; Santschi 1933; Gotwald 1995; Shattuck 2008; Staab 2014). Shattuck (2008) noted that despite being widespread the genus is comparatively rarely collected. Nevertheless, all known species nest and usually perform their mass raids in the soil stratum, and only occasionally above ground, which might account for the relative uncommonness.

With the exception of the Afrotropical region, the taxonomy of *Aenictus* is in a relatively good state compared to other dorylomorph genera. The first modern, comprehensive taxonomic treatment was that of Wilson (1964) who revised the army ants of the Indo-Australian region. In the decades since taxonomic contributions consisted mainly of single species descriptions or small regional treatments (e.g. Terayama and Yamane 1984, 1989; Xu 1994; Wu and Wang 1995; Zhou and Chen 1999; Yamane and Hashimoto 1999; Wang 2006). Fortunately, in the last decade there were several contributions aiming to treat broader regions and to improve the subgeneric classification. Aktaç et al. (2004) provided the first taxonomic overview of the southwestern Palaearctic, Sharaf et al. (2012) treated the Middle East, and Shattuck (2008) revised the Australian *Aenictus* fauna. Concerning the South East Asian species, there were numerous recent contributions. Initially focusing on particular species assemblages and describing few additional species (e.g. Jaitrong and Eguchi 2010; Jaitrong and Yamane 2010; Jaitrong et al. 2010), the situation changed significantly with the diagnoses and definitions of species groups presented by Jaitrong and Yamane (2011). The latter publication provided workable hypotheses for twelve species groups with an easy-to-use identification key to the established groups, as well as revisions for two species groups (*A. currax* and *A. laeviceps* groups). More recently Wiwatwitaya and Jaitrong (2011) revised the *A. hottai* group, Jaitrong and Hashimoto (2012) the *Aenictus minutulus* group, and Jaitrong and Yamane (2012) treated the *Aenictus javanus* and *Aenictus philippinensis* groups. Finally, Jaitrong and Yamane (2013) revised the *A. ceylonicus* group, which is the largest group known so far.

As already outlined in detail by Wilson (1964), there are two taxonomic systems for *Aenictus*, as well as for other army ants: one based on workers and one on males. The males of *Aenictus* are relatively large and often encountered in light traps, whereas they are seldom collected together with workers (Wilson 1964). So, the main problem is the lack of association between both systems. Wilson (1964) suggested ignoring the male-based names and establishing a sound worker-based taxonomy until males are found together with workers and the different taxonomic names can be harmonised. Jaitrong and Yamane (2011, 2013) concur with that approach and state that male-based names will eventually be matched with worker-based names using DNA information.

In this study we describe a new *Aenictus* species from the *A. ceylonicus* species group. The material was collected in Xingshuangbanna, Yunnan, China, during a recent survey of the local myrmecofauna (Guenard et al. 2013, Liu et al. in review). Despite being clearly a member of the *A. ceylonicus* group, our detailed morphological analysis did not allow us to fit it to any of the described group members. In addition, the material did not key out with the recent identification key provided by Jaitrong and Yamane (2013) in their revision of the *A. ceylonicus* group. Consequently, we consider the material as new and describe it herein as *A. yangi* sp. n. on the basis of the worker caste. We also integrate it into the taxonomic system created by Jaitrong and Yamane (2011, 2013) by updating their key to species of the *A. ceylonicus* group and providing a diagnostic discussion and high-quality illustrations of important species and morphological characters.

Abbreviations of depositories

The collection abbreviations follow Evenhuis (2014) and Jaitrong and Yamane (2013). The material upon which this study is based is located and/or was examined at the following institutions:

BMNH	The Natural History Museum, London, U.K.
CAS	California Academy of Sciences, San Francisco, U.S.A.
ISAS	Kunming, Kunming Institute of Zoology, Yunnan, China
HLMD	Hessisches Landesmuseum Darmstadt, Darmstadt, Germany
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.
MHNG	Muséum d'Histoire Naturelle de la Ville de Genève, Geneva, Switzerland
NHMB	Naturhistorisches Museum, Basel, Switzerland
PUPAC	Punjabi University Patiala Ant Collection, Patiala, India
SKYC	SKY Collection at Kagoshima University, Japan
THNHM	Natural History Museum of the National Science Museum, Thailand

Material and methods

The material used for this study was collected during an inventory of the ant fauna of Xingshuangbanna, Yunnan, China, in 2013, which yielded approximately 240 species/morphospecies (Liu et al. in review). The main focus of that study was to assess the ground and leaf litter ant fauna, and the new *Aenictus* species treated here was also collected from two leaf litter samples. All available workers were mounted, analysed, and measured. Morphological observations and measurements were done with a Leica M165 C stereomicroscope equipped with an orthogonal pair of micrometres at a magnification of 100×. Measurements were recorded in mm to three decimal places and rounded to two decimal places for presentation. The measurements and indices used in this study follow Jaitrong and Yamane (2011, 2013):

CI	Cephalic index: HW / HL × 100.
HL	Maximum head length in full-face view, measured from the anterior clypeal margin to the midpoint of a line drawn across the posterior margin of the head. [Note: the anterior clypeal margin in species on the *A. ceylonicus* group is sometimes concave, which is the case in *A. yangi*, and measuring as defined above reduces the maximum head length].
HW	Maximum head width in full-face view.
ML	Mesosomal length measured from the point at which the pronotum meets the cervical shield to the posterior margin of metapleuron in profile.
PL	Petiole length measured from the anterior margin of the peduncle to the posterior-most point of the tergite.
SI	Scape index: SL / HW × 100.
SL	Scape length, excluding the basal constriction and condylar bulb.
TL	Total length, roughly measured from the anterior margin of head to the tip of the gaster in stretched-out specimens.

In general, the morphological terminology used in this study follows Hölldobler and Wilson (1990), Bolton (1994), and for key characters of the genus *Aenictus* Jaitrong and Yamane (2011).

Results

The *Aenictus ceylonicus* species group

Diagnosis. The group was first diagnosed by Wilson (1964) and recently redefined by Jaitrong and Yamane (2011, 2013). The following definition is taken from the latter studies:

Antenna ten-segmented; with head in full-face view scape extending beyond half of head length, but not reaching the occipital corner of head; mandible linear, its basal and external margins almost parallel; masticatory margin with large apical tooth followed by medium-sized subapical tooth, 0–6 small denticles present between subapical tooth and basal tooth; with mandibles closed, a gap present between mandibles and anterior margin of clypeus; anterior clypeal margin weakly concave or almost straight, lacking denticles; frontal carina short and thin reaching to or slightly extending beyond the level of posterior margin of torulus; with head in full-face view curved anterior extension of frontal carina reaching to or extending beyond the level of anterior clypeal margin; parafrontal ridges absent; promesonotum usually convex dorsally and sloping gradually to propodeum (rarely with almost straight dorsal outline); subpetiolar process developed. Head and first gastral tergite smooth and shiny. Body yellowish, reddish or dark brown; typhlatta spot absent.

Notes. The *A. ceylonicus* group under the above definition contains 33 species (Jaitrong and Yamane 2013) and is clearly the most species-rich group in the genus. It is widespread in the southeastern Palaearctic, Oriental, Indo-Australian and Austral-Asian regions (Wilson 1964; Shattuck 2008; Jaitrong and Yamane 2011, 2013). Its distinction from other groups is very straightforward on the basis of the linear mandible, the distinct gap between the mandibles and the anterior margin of the clypeus when the mandibles are closed, the almost straight or feebly concave anterior clypeal margin, and the lack of clypeal denticles. Some or most of the African *Aenictus* might be members of the group also (Wilson 1964), but due to the lack of revisions or other modern taxonomic treatment their affinities remain unclear.

Update to the identification key of the *A. ceylonicus* group

The identification key to the South East Asian species provided by Jaitrong and Yamane (2013) contains 22 key couplets for 23 species. The new species described here needs to be included, thus in the following we slightly modify the first few key couplets without altering the remainder of the key.

1 Mandibles with 2–6 teeth/denticles between subapical and basal teeth (mandibles with more than 4 teeth/denticles in total) (Fig. 4D)......................... **2**

– Mandibles with 0–1 tooth/denticle between subapical and basal teeth (mandibles with 3–4 teeth/denticles in total) (Fig. 1A, B)................................ **15**

2a Dorsal face of propodeum mostly smooth and shiny; lateral face of propodeum partly smooth and shiny (Fig. 2A); postpetiole usually entirely smooth and shiny, rarely reticulate-punctate basally **2b**

– Propodeum entirely sculptured (Fig. 2B); postpetiole entirely sculptured or with smooth and shiny small area on dorsal face **6**

2b Metanotal groove noticeably present but weak; propodeal junction noticeably angulate with distinct tooth; subpetiolar process relatively elongate, subrectangular, and slightly projecting anteroventrally (Fig. 3A) .... ***A. yangi***

– Character combination never as above; metanotal groove usually absent or strongly reduced, but always weaker than above; propodeal junction rounded to angulate without/with small tooth; subpetiolar process variable, ranging from strongly reduced and rounded to subrectangular, but never as elongate as above (Fig. 3B–E) 3

From couplet 3 onwards there are no changes to the key presented by Jaitrong and Yamane (2013) and we refer to that publication.

Aenictus yangi sp. n.

http://zoobank.org/EF119658-0F74-48A9-8E5A-0CD76CF97143

Figs 3A, 4A–D

Type material. Holotype, pinned worker, China, Yunnan, Xishuangbanna, Man Sai village, 21°51'34.4"N, 101°16'39.6"E, 680m, young rain forest, leaf litter, 12.IIV.2013 (*B. Blanchard, B. Guénard & C. Liu*) (ISAS: CASENT0735503).

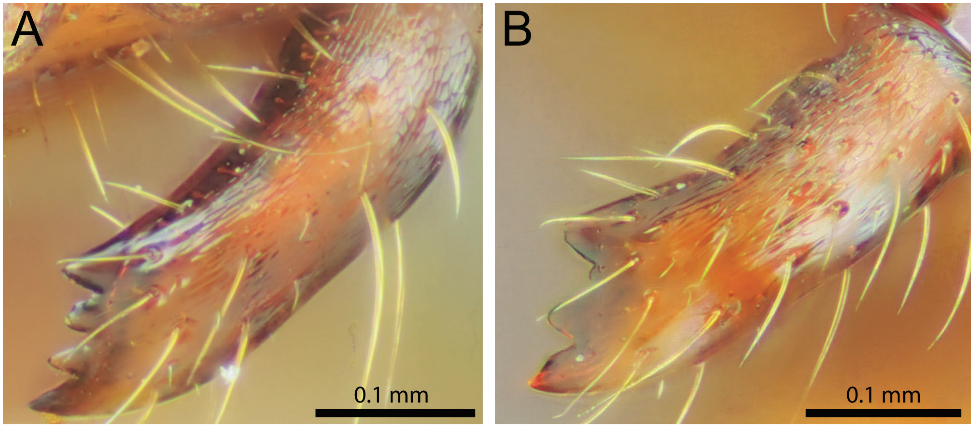

Figure 1. Mandible showing masticatory margin. **A** *A. maneerati* Jaitrong & Yamane **B** *A. watanasiti* Jaitrong & Yamane. Images are from Jaitrong and Yamane (2013).

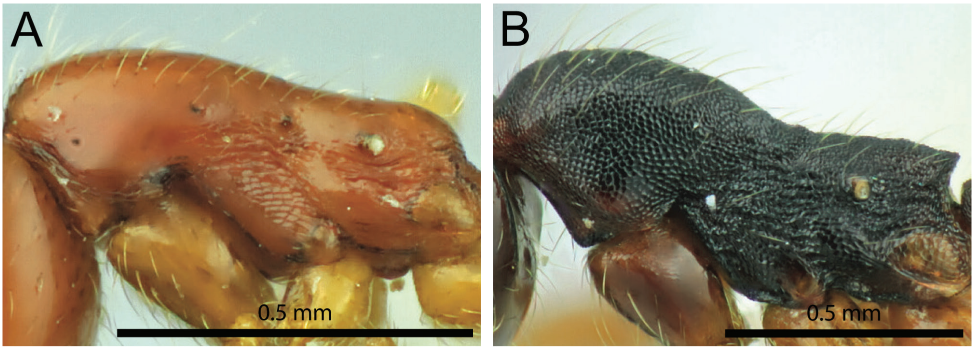

Figure 2. Mesosoma in profile. **A** *A. longicephalus* Jaitrong & Yamane **B** *A. pinkaewi* Jaitrong & Yamane. Images are from Jaitrong and Yamane (2013).

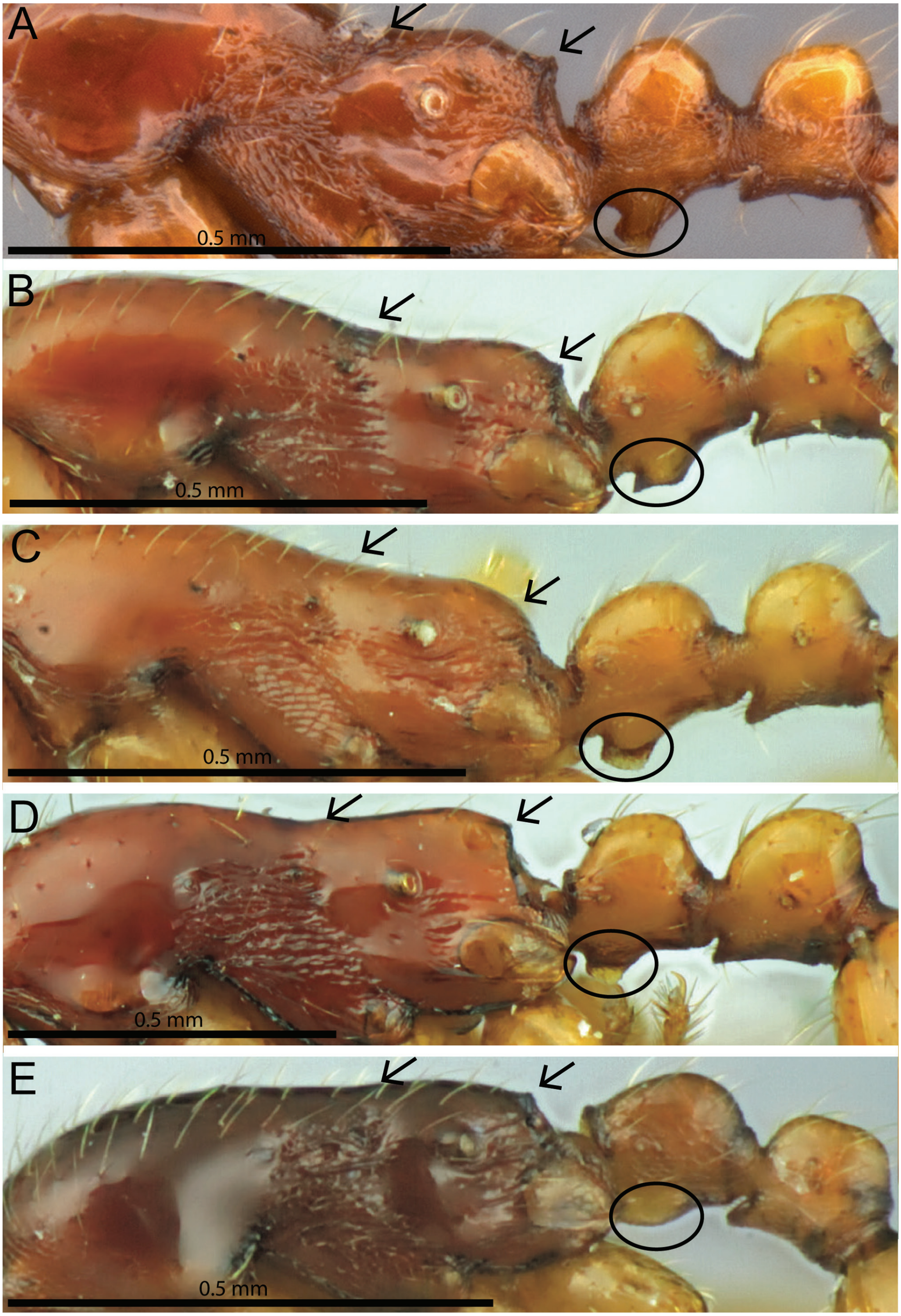

Figure 3. Mesosoma and waist segments in profile (black arrows indicate metanotal groove and propodeal junction, black ellipse subpetiolar process). **A** *A. yangi* sp. n. **B** *A. baliensis* Jaitrong & Yamane **C** *A. longicephalus* Jaitrong & Yamane **D** *A. minipetiolus* Jaitrong & Yamane **E** *A. wiwatwitayai* Jaitrong & Yamane. Images except figure 3A are from Jaitrong and Yamane (2013).

Paratypes, 14 pinned workers, China, Yunnan, Xishuangbanna, Man Sai village, 21°51'34.4"N, 101°16'39.6"E, 680m, young rain forest, leaf litter, 12.IIV.2013 (*B. Blanchard, B. Guénard & C. Liu*) (BMNH: CASENT0717204; CAS: CASENT0735506; CASENT0735508; HLMD: CASENT0735507; ISAS: CASENT0717203; CASENT0735495; CASENT0735496; CASENT0735498; MCZ: CASENT0735505; MHNG: CASENT0735504; NHMB: CASENT0735501; PUPAC: CASENT0735500; SKYC: CASENT0735499; THNHM: CASENT0735497).

Non-type material. China, Yunnan, Xishuangbanna, Man Sai village, 21°51'34.4"N, 101°16'39.6"E, 680m, young rain forest, leaf litter, 12.IIV.2013 (*B. Blanchard, B. Guénard & C. Liu*).

Diagnosis. *Aenictus yangi* differs from other South East Asian members of the *A. ceylonicus* group by the following combination of characters: head in full-face view distinctly longer than broad (CI 82–90); masticatory margin of mandible with seven teeth/denticles; antennal scapes relatively long (SI 76–86); metanotal groove noticeably present but weak; propodeal junction noticeably angulate with distinct tooth; subpetiolar process relatively elongate, subrectangular, and slightly projecting anteroventrally; propodeum laterally mostly smooth and shiny, weakly irregularly rugulose at base, and weakly reticulate-punctate near propodeal junction; petiole and postpetiole mostly smooth and shiny with lower portions reticulate-punctate.

Worker measurements (N=17). TL 2.21–2.60; HL 0.51–0.57; HW 0.43–0.50; SL 0.33–0.42; ML 0.69–0.87; PL 0.17–0.20; CI 82–90; SI 76–86.

Worker description. Head in full-face view distinctly longer than broad (CI 82–90), sides convex, posterior head margin straight to very weakly convex; occipital margin bearing a distinct carina. Antennal scapes relatively long (SI 76–86), extending beyond 2/3 of head length but not reaching posterior head margin. Frontal carinae relatively short and indistinct, reaching the level of posterior margin of torulus. Parafrontal ridges absent. Anterior clypeal margin weakly to moderately concave, not concealed by curved anterior extension of frontal carina. Masticatory margin of mandible with large acute apical tooth followed by one medium-sized subapical tooth, one small denticle, one medium-sized tooth, two smaller denticles, and medium-sized basal tooth, reaching total of seven teeth/denticles; basal margin straight. Maximum width of gap between anterior clypeal margin and mandibles about 1.0 to 1.4 times broader than maximum width of mandible. Promesonotum convex dorsally and sloping gradually to metanotal groove; metanotal groove noticeably present but weak; mesopleuron relatively long, clearly demarcated from metapleuron by weak groove; metapleural gland bulla relatively large, its maximum diameter about 1.7 to 2.1 times longer than distance between propodeal spiracle and metapleural gland bulla. Propodeum in profile with feebly convex dorsal outline; propodeal junction noticeably angulate with distinct tooth; declivity of propodeum moderately concave and encircled by strongly developed rim. Petiole in profile higher than long, its dorsal outline strongly convex; subpetiolar process relatively elongate, subrectangular, and slightly projecting anteroventrally. Postpetiole slightly smaller than petiole, its dorsal outline strongly convex. Head including antennal scape entirely

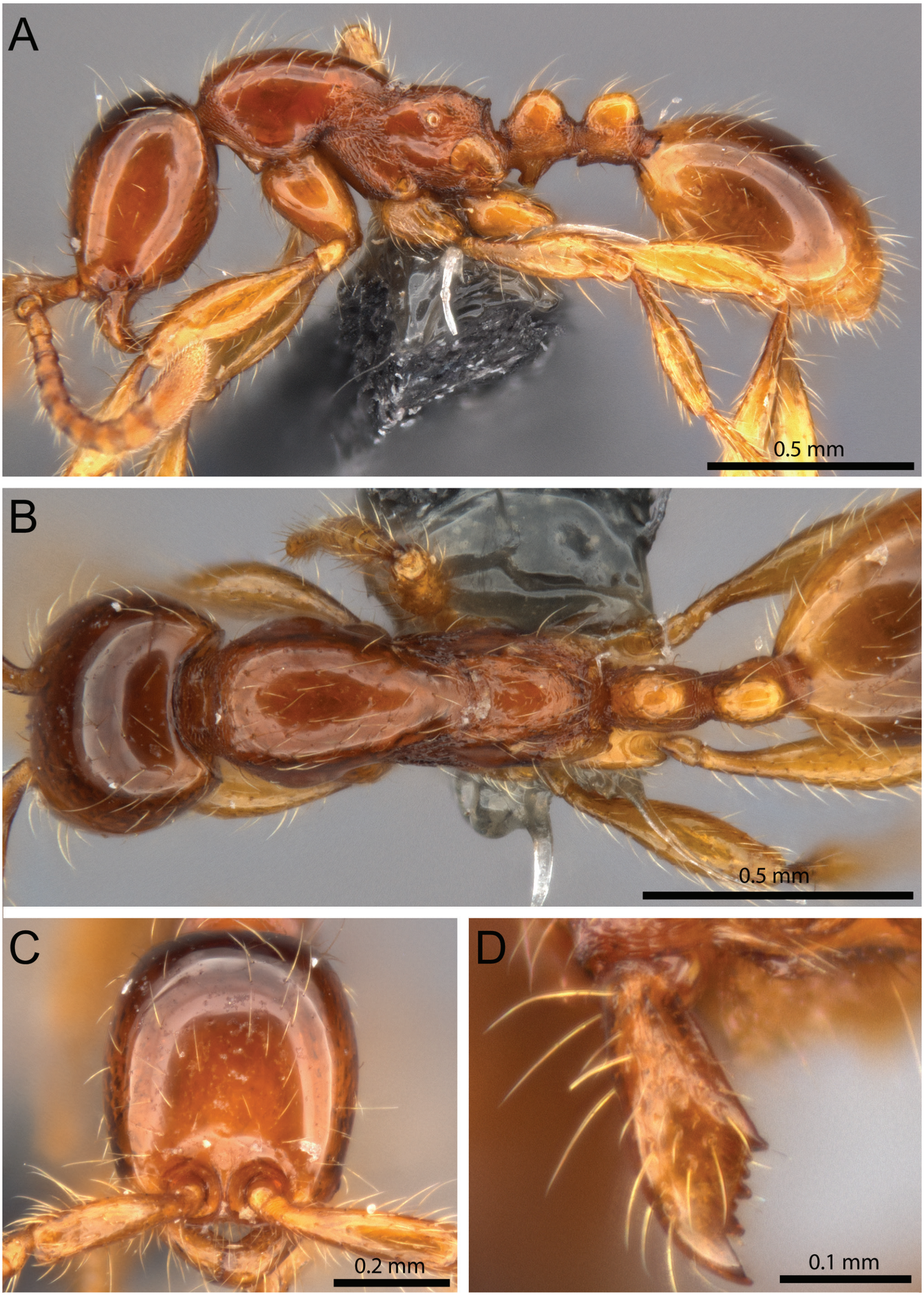

Figure 4. *Aenictus yangi* sp. n. (CASENT0735503). **A** Body in profile **B** Body in dorsal view **C** head in full-face view **D** right mandible in frontal view.

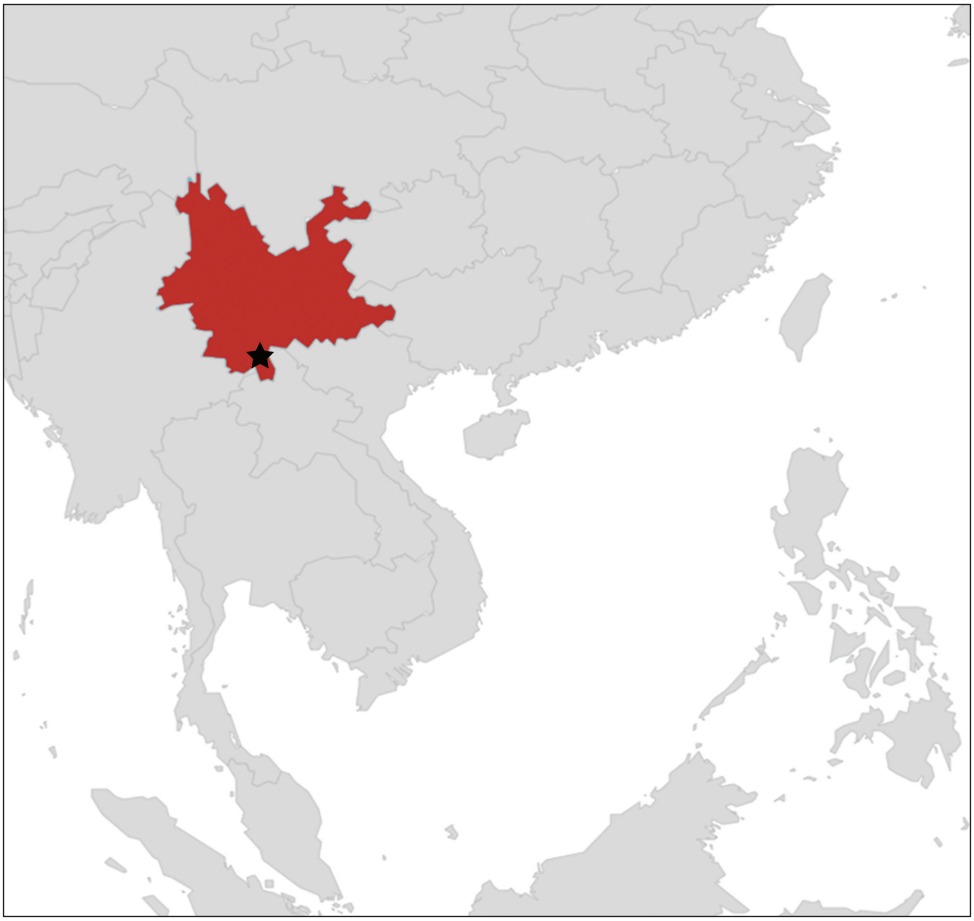

Figure 5. Map of South East Asia showing the type locality of *A. yangi* sp. n. (black star), red indicates Yunnan Province, China.

smooth and shiny. Mandibles predominantly unsculptured, smooth and shiny with weak, superficial striation basally. Promesonotum entirely smooth and shiny; mesopleuron and metanotal groove irregularly rugulose; propodeum laterally mostly smooth and shiny, weakly irregularly rugulose at base, and weakly reticulate-punctate near propodeal junction. Petiolar node and postpetiole mostly smooth and shiny with lower portions reticulate-punctate. Head and mesosoma dorsally with abundant erect to subdecumbent hairs. Head, mesosoma, and gaster usually reddish brown, always distinctly darker than yellow to light yellowish brown mandibles, antennae, petiole, postpetiole, and legs.

Etymology. The new species is dedicated to Da-Rong Yang from the Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences. We want to thank him for his great support of the first author's studies in the area.

Distribution and ecology. At present, the new species is only known from Xishuangbanna in southern Yunnan. The type locality is a tropical lowland rainforest situated at an elevation of around 550 m. The new species was only collected twice, both times through leaf litter extraction. Nevertheless, as for most *Aenictus*, we strongly suspect that *A. yangi* has a more hypogaeic lifestyle and might be more abundant in the soil stratum. The use of specific collection techniques that target subterranean army ants, such as subterranean oil baiting (Weissflog et al. 2001), will likely yield additional material of this species. Unfortunately, due to the limited available material there is no additional information about its ecology.

Taxonomic notes. The identification of *A. yangi* within the *A. ceylonicus* species group can be easily performed with the updated identification key provided above. The new species is morphologically most similar to *A. baliensis* Jaitrong & Yamane, 2013 (Bali), *A. longicephalus* Jaitrong & Yamane, 2013 (Lombok), *A. minipetiolus* Jaitrong & Yamane, 2013 (Lombok), and *A. wiwatwitayai* Jaitrong & Yamane, 2013 (Thailand). However, *A. yangi* can be immediately separated from these by the development of the metanotal groove, the shape of the propodeum and the subpetiolar process, and the sculpture on the mesosoma and waist segments (see Fig. 3 for details). *Aenictus yangi* can be easily separated from *A. brevipodus* Jaitrong & Yamane, 2013 (Thailand), and *A. formosensis* Forel, 1913 (Taiwan) by the number of mandibular teeth, shape of the head, the shape and punctate of petiole and postpetiole, and the shape of subpetiolar process.

Acknowledgements

We would like to thank Benoit Guénard and Benjamin Blanchard for their assistance in collecting the new species. The first author also wants to thank Da-Rong Yang from the Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences for his cooperation and help in organizing the field survey. The authors acknowledge the support of OIST and an NSF grant to EPE (NSF DEB-1145989).

References

Aktaç N, Radchenko AG, Kiran K (2004) On the taxonomy of the west Palaearctic Aenictinae (Hymenoptera: Formicidae). Annales Zoologici 54: 361–364.

Arnold G (1915) A monograph of the Formicidae of South Africa. Part I. Ponerinae, Dorylinae. Annals of the South African Museum 14: 1–159.

Baroni Urbani C, Bolton B, Ward PS (1992) The internal phylogeny of ants (Hymenoptera: Formicidae). Systematic Entomology 17: 301–329. doi: 10.1111/j.1365-3113.1992.tb00553.x

Bolton B (1990) Army ants reassessed: the phylogeny and classification of the doryline section (Hymenoptera, Formicidae). Journal of Natural History 24: 1339–1364. doi: 10.1080/00222939000770811

Bolton B (1994) Identification guide to the ant genera of the world. Harvard University Press, Cambridge, Massachusetts, 222 pp.

Bolton B (1995) A new general catalogue of the ants of the world. Harvard University Press, Cambridge, Massachusetts, 504 pp.

Bolton B (2014) An online catalog of the ants of the world. http://antcat.org [accessed 27 October 2014]

Borgmeier T (1954) Aenictini n. trib. und die Tribus-Einteilung der Dorylinen (Hym. Formicidae). Zoologischer Anzeiger 153: 211–214.

Brady SG (2003) Evolution of the army ant syndrome: the origin and long-term evolutionary stasis of a complex of behavioral and reproductive adaptations. Proceedings of the National Academy of Sciences 100: 6575–6579. doi: 10.1073/pnas.1137809100

Brady SG, Fisher BL, Schultz TR, Ward PS (2014) The rise of army ants and their relatives: diversification of specialized predatory doryline ants. BMC Evolutionary Biology 14: 93, 14 pp.

Dalla Torre KW (1893) Catalogus Hymenopterorum hucusque descriptorum systematicus et synonymicus. Vol. 7. Formicidae (Heterogyna). W. Engelmann, Leipzig, 289 pp.

Emery C (1895) Die Gattung *Dorylus* Fab. und die systematische Eintheilung der Formiciden. Zoologische Jahrbücher. Abteilung für Systematik, Geographie und Biologie der Tiere 8: 685–778.

Evenhuis NL (2014) The insect and spider collections of the world website. http://hbs.bishopmuseum.org/codens [accessed 1 October 2014]

Gotwald WH (1995) Army ants: the biology of social predation. Cornell University Press, Ithaca and London, 320 pp.

Guénard B, Blanchard B, Liu C, Yang DR, Economo EP (2013) Rediscovery of the rare ant genus *Bannapone* (Hymenoptera: Formicidae: Amblyoponinae) and description of the worker caste. Zootaxa 3734: 371–379. doi: 10.11646/zootaxa.3734.3.6

Hölldobler B, Wilson EO (1990) The ants. Harvard University Press, Cambridge, Massachusetts, 732 pp. doi: 10.1007/978-3-662-10306-7

Jaitrong W, Eguchi K (2010) A new army ant of the genus *Aenictus* from Thailand (Hymenoptera: Formicidae). The Thailand Natural History Museum Journal 4: 13–17.

Jaitrong W, Yamane S (2010) The army ant *Aenictus silvestrii* and its related species in Southeast Asia, with a description of a new species (Hymenoptera: Formicidae: Aenictinae). Entomological Science 13: 328–333. doi: 10.1111/j.1479-8298.2010.00385.x

Jaitrong W, Yamane S, Wiwatwitaya D (2010) The army ant *Aenictus wroughtonii* (Hymenoptera: Formicidae: Aenictinae) and related species in the Oriental Region, with descriptions of two new species. Japanese Journal of Systematic Entomology 16: 33–46.

Jaitrong W, Yamane S (2011) Synopsis of *Aenictus* species groups and revision of the *A. currax* and *A. laeviceps* groups in the eastern Oriental, Indo-Australian, and Australasian regions (Hymenoptera: Formicidae: Aenictinae). Zootaxa 3128: 1–46.

Jaitrong W, Hashimoto Y (2012) Revision of the *Aenictus minutulus* species group (Hymenoptera: Formicidae: Aenictinae) from Southeast Asia. Zootaxa 3426: 29–44.

Jaitrong W, Yamane S (2012) Review of the Southeast Asian species of the *Aenictus javanus* and *Aenictus philippinensis* species groups (Hymenoptera, Formicidae, Aenictinae). ZooKeys 193: 49–78. doi: 10.3897/zookeys.193.2768

Jaitrong W, Yamane S (2013) The *Aenictus ceylonicus* species group (Hymenoptera, Formicidae, Aenictinae) from Southeast Asia. Journal of Hymenoptera Research 31:165–233. doi: 10.3897/jhr.31.4274

Mayr G (1865) Formicidae. In: Novara Expedition 1865. Reise der Österreichischen Fregatte "Novara" um die Erde in den Jahren 1857, 1858, 1859. Zoologischer Theil. Bd. II. Abt. 1. K. Gerold's Sohn, Wien, 119 pp.

Santschi F (1933) Contribution à l'étude des fourmis de l'Afrique tropicale. Bulletin et Annales de la Société Entomologique de Belgique 73: 95–108.

Sharaf MR, Aldawood SA, El-Hawagry MS (2012) First record of the ant subfamily Aenictinae (Hymenoptera, Formicidae) from Saudi Arabia, with the description of a new species. ZooKeys 228: 39–49. doi: 10.3897/zookeys.228.3559

Shattuck SO (2008) Review of the ant genus *Aenictus* (Hymenoptera: Formicidae) in Australia with notes on *A. ceylonicus* (Mayr). Zootaxa 1926: 1–19.

Shuckard WE (1840) Monograph of the Dorylidae, a family of the Hymenoptera Heterogyna. Annals of Natural History 5: 258–271. doi: 10.1080/00222934009496821

Schneirla TC (1971) Army ants. A study in social organization. W. H. Freeman & Co., San Francisco, 349 pp.

Staab M (2014) The first observation of honeydew foraging in army ants since 1933: *Aenictus hodgsoni* Forel, 1901 tending *Eutrichosiphum heterotrichum* (Raychaudhuri, 1956) in Southeast China. Asian Myrmecology 6: 115–118.

Terayama M (1984) A new species of the army ant genus *Aenictus* from Taiwan. Bulletin of the Biogeographical Society of Japan 39: 13–16.

Terayama M, Yamane S (1989) The army ant genus *Aenictus* (Hymenoptera, Formicidae) from Sumatra, with descriptions of three new species. Japanese Journal of Entomology 57: 597–603.

Wang W (2006) A new species of the genus *Aenictus* Shuckard from China (Hymenoptera, Formicidae). Acta Zootaxonomica Sinica 31: 637–639.

Weissflog A, Sternheim E, Dorow WHO, Berghoff S, Maschwitz U (2001) How to study subterranean army ants: a novel method for locating and monitoring field populations of the South East Asian army ant *Dorylus* (*Dichthadia*) *laevigatus* Smith, 1857 (Formicidae, Dorylinae) with observations on their ecology. Insectes Sociaux 47: 317–324. doi: 10.1007/PL00001723

Wilson EO (1964) The true army ants of the Indo-Australian area (Hymenoptera: Formicidae: Dorylinae). Pacific Insects 6: 427–483.

Wiwatwitaya D, Jaitrong W (2011) The army ant *Aenictus hottai* (Hymenoptera: Formicidae: Aenictinae) and related species in Southeast Asia, with a description of a new species. Sociobiology 58: 557–565.

Wu J, Wang C (1995) The ants of China. China Forestry Publishing House, Beijing, 214 pp.

Xu Z (1994) A taxonomic study of the ant subfamily Dorylinae in China (Hymenoptera: Formicidae). Journal of Southwest Forestry College 14: 115–122.

Yamane S, Hashimoto Y (1999) A remarkable new species of the army ant genus *Aenictus* (Hymenoptera, Formicidae) with a polymorphic worker caste. Tropics 8: 427–432. doi: 10.3759/tropics.8.427

Zhou S, Chen Z (1999) The ant genus *Aenictus* Shuckard from Guangxi (Hymenoptera: Formicidae). Guangxi Science 6: 63–64.

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Eurytoma serratulae and *E. robusta* (Hymenoptera, Eurytomidae): complementary host exploitation strategies of coexisting parasitoids and their impact on the host *Urophora cardui*

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Abstract

Our study investigates the host exploitation strategies of *Eurytoma serratulae* and *E. robusta* (Chalcidoidea, Eurytomidae), two parasitoid species that co-occur in gall populations of the tephritid *Urophora cardui* on *Cirsium* spp. The endoparasitoid *E. serratulae* detects the host larvae before an externally visible gall is formed. It profits from large galls, as its parasitization rate increases with increasing numbers of chambers per gall. Oviposition by the ectoparasitoid *E. robusta* does not occur until a distinct gall with chambers has been formed. Its parasitization rate reaches highest values in medium-sized galls. *Eurytoma robusta* is the dominant parasitoid in host populations with low and moderate gall densities, whereas *E. serratulae* is the superior exploiter of host populations with high gall densities. Within single galls *E. robusta* is an important hyperparasitoid of *E. serratulae*, but *E. serratulae* has no adverse influence on *E. robusta*. Parasitism by *E. serratulae* induces host larvae to promote gall growth, an effect that is profitable to both the parasitoid and the remaining host larvae in the gall. Parasitism by *E. robusta* often leads to smaller galls, as cases of unsuccessful parasitization result in empty gall cells.

Keywords

Urophora cardui galls, coexistence of *Eurytoma*, parasitoid-interactions, stimulation of gall growth

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Introduction

A competitive coexistence of generalists and specialists is a common and well-studied feature of parasitoid guilds exploiting phytophagous hosts (e.g. Smith 1929, Zwölfer and Kraus 1957, Fisher 1961, Askew 1968, Godfray 1994). A particular case is the coexistence of pairs of competing congeners, a situation found in *Eurytoma* species (Chalcidoidea, Eurytomidae) associated with gall forming tephritids: thus *Eurytoma compressa* (Fabricius) (= *curta* (Walker)) and *E. robusta* Mayr coexist in hosts living in Cardueae flower head galls (Zwölfer and Arnold-Rinehart 1993), and *Eurytoma obtusiventris* Gahan and *E. gigantea* Walsh in stem galls of North American *Solidago* spp. (Abrahamson and Weis 1997). The parasitoids *Eurytoma serratulae* (Fabricius) and *E. robusta* regularly co-occur in gall populations of the tephritid *Urophora cardui* (Linnaeus) on shoots of Creeping Thistle (*Cirsium arvense*). Information on the biology of *E. serratulae* and *E. robusta* has been published by Claridge (1961), Redfern (1983), Redfern and Askew (1992) and Zwölfer (1979, 1988). In view of considerable differences in its larval biology *E. robusta* has been placed in a separate species group of *Eurytoma* (e.g. Zerova and Seryogina 2006). Both species are solitary parasitoids.

Our study investigates the mechanisms that make the coexistence of the two *Eurytoma* species possible. The characteristics of the multilocular gall of *U. cardui* allow comparing the behaviour of the two *Eurytoma* species on the level of the microhabitat of individual galls and on the macrohabitat level of the gall populations. For both levels we compare the exploitation strategies of *E. serratulae* and *E. robusta* using our large basis of field-collected data that allow the statistical evaluation of "natural experiments". We analyse the influence of gall size and gall densities in the field on the incidence, degree of parasitism and the exploitation pattern of the two *Eurytoma* species. In conclusion we compare the effect of *E. serratulae* and *E. robusta* on the growth of *U. cardui* galls and we discuss how the characteristic features of the multilocular galls of *U. cardui* and the specialized oviposition behaviour safeguard *E. serratulae* against an overexploitation of its resource.

Methods and material

Collections. For our study we combined cage observations on the behaviour of *E. serratulae* with the statistical analysis of field collected gall populations. For the evaluation of our field data we disposed of 693 gall samples (16 732 galls) of *C. arvense* and nine samples (374 galls) of *C. creticum*. The *C. arvense* galls were collected between the years 1969 and 2006 in France, Switzerland, northern Italy, Germany, Austria, Slovakia, southern England, and western Poland, the *C. creticum*-galls in 1984 and 1990 in northern Greece. Galls were collected from September / October to March / April. *Urophora cardui* populations frequently occur in the form of metapopulations (Eber and Brandl 1994), i.e. as a network of single demes (Saccheri and Hanski 2006). We treated a thistle patch with *U. cardui* galls as a "population" if it was separated from a neighbouring patch with galls by at least 200 m. We counted the number of thistle shoots and galls / patch in the field, estimated the total number of shoots / patch and dissected the galls under a stereomicroscope. We assessed the gall content (living or dead larvae or pupae of *U. cardui*, *E. serratulae*, *E. robusta* and other parasitoids, empty chambers, eggs of *E. robusta*) and gall size (cell number and gall diameter). All data were assessed in SPSS files by the program DATA ENTRY and analysed by IBM SPSS statistics 21. For the path analysis we followed Sokal and Rohlf (1981).

Host ranges and distribution of *Eurytoma serratulae* and *E. robusta*. *Eurytoma serratulae* is an endoparasitoid of *Urophora cardui*. Claridge (1961) showed that *E. tristis* Mayr, which Mayr (1878) and other authors recorded from galls of *U. cardui,* is synonymous with *E. serratulae*. All reliable host records of *E. serratulae* refer to *U. cardui*, a tephritid whose host plants are *Cirsium arvense* (Claridge 1961), *C. creticum* (Zwölfer 1988) and *C. setosum* (Frenzel et al. 2000). The ectoparasitoid *Eurytoma robusta* can so far only be identified as a morphospecies, the host records in the literature may actually pertain to a cluster of undescribed siblings. Claridge (1961) describes *E. robusta* as attacking "a wide range of tephritid galls on Cardueae host plants". Zwölfer and Arnold-Rinehart (1993) list *E. robusta* from 14 Palearctic *Urophora* species on 22 Cardueae host plant species.

Both parasitoids have been reared from *U. cardui* galls on *C. arvense* in England (Claridge 1961), Switzerland, France, Germany and Austria (Zwölfer 1979, 1994), and Finland (Vikberg 2005). Additional records from *U. cardui* on *C. arvense* are from northern Italy, western Poland and Slovakia (H. Zwölfer, unpublished). The two *Eurytoma* species also coexist in *U. cardui* galls on *C. creticum* in northern Greece (Zwölfer 1988) and in *U. cardui* galls on *C. setosum* originating from the Ural Mountains (Frenzel et al. 2000). Thus, the two *Eurytoma* species attack *Urophora cardui* on all 3 host plants and in almost all regions where galls have been analysed. An exception is Denmark and Schleswig-Holstein (northern Germany), where Johannesen and Seitz (2003a, b) as well as we (H. Zwölfer, unpublished) found only *E. robusta* in *U. cardui* galls. There, the examined thistle patches with *U. cardui* may have been recently recolonized by *U. cardui* (Johannesen and Seitz 2003b). Parasitoids of minor importance in *U. cardui* galls are the ectoparasitoids *Torymus chloromerus* (Walker) (Torymidae) and *Pteromalus elevatus* (Walker) (Pteromalidae).

Biology of *Eurytoma serratulae* and *E. robusta*

Eurytoma serratulae is a koinobiont (Askew and Shaw 1986) endoparasitoid. Oviposition takes place in early summer, shortly after the start of the oviposition period of *U. cardui*. The *E. serratulae* females detect the host larvae in thistle shoots, before a visible growth of the gall had occurred (Zwölfer 1979) and deposit their eggs into the young host larvae. This early attack on the hosts has the advantage that there is no constraint on the length of the ovipositor (Price and Clancy 1986). The young *E. serratulae* larva remains in developmental stasis within the growing *U. cardui* larva until the host larva is full-grown in early autumn. Then, the parasitoid larva consumes its host and induces a sclerotization of the cuticula of the host (Claridge 1961). This process might provide some protection against hyperparasitoids or predators penetrating into the gall. The mature parasitoid larva spends the winter within this mummy, which externally resembles a pupated *U. cardui* larva. Pupation of *E. serratulae* occurs in the following spring, emergence of the adults in early summer.

Eurytoma robusta is an idiobiont (Askew and Shaw 1986). Its females lay their eggs into the chambers of more advanced stages of *U. cardui* galls. The hatching larvae exploit the host larvae as an ectoparasitoid. The mature larvae hibernate within the gall chambers, they pupate in spring and the adults emerge 2–3 weeks later than those of *E. serratulae*. *Eurytoma robusta* is a hyperparasitoid of *E. serratulae*, if it consumes a host larva already attacked by a young larva of the congener. Within an individual gall an *E. robusta* larva may feed on and kill more than one host. Due to poor synchronization young host larvae are often killed and consumed before they have developed enough biomass to allow the maturation of the *E. robusta* larva. If nutritive gall tissue is still available, the *E. robusta* larvae may switch to it, thus acting as an inquiline (Redfern and Askew 1992). *Eurytoma robusta* often suffers from a high incidence of superparasitism. Zwölfer et al. (2007) give a detailed description of the biology of *E. robusta* and the part it plays in the population dynamics of its host *U. cardui*.

Results

E. serratulae and *E. robusta*: the influence of gall size (number of cells)

To assess the role of gall size for the parasitization pattern we use data from 260 gall samples with a total of 7,064 galls collected from 1976 to 1993 in eastern France, southern Germany and eastern Austria. The number of cells / gall ranged from one to 18 (mean + SE = 3.807+0.045, median = 3). A total of 25% of the galls had more than five cells and 10% more than 6 cells. Incidence of parasitism (% galls attacked) by *E. serratulae* increases steadily with increasing gall size, whereas attack rate by *E. robusta* reaches a maximum at intermediate gall sizes (Fig. 1). A corresponding pattern exists, if the average number of *Eurytoma* larvae / gall is examined (Fig. 2). The different trends of parasitization by *E. serratulae* and *E. robusta* are also recognizable in Fig. 3, which compares the average content of single galls of the different size classes. The graph includes the galls with empty cells, which usually are caused by *E. robusta* (Zwölfer et al. 2007). This species is represented together with a small (< 5%) proportion of *Pteromalus elevatus,* a rare ectoparasitoid of *U. cardui.* The clear winner of an increasing gall size is the host, *U. cardui* (Freese and Zwölfer 1996). Because of interactions with other mortality factors of *U. cardui*, the correlation of *E. serratulae* with gall size (cells / gall) is weak (Spearman rank correlation: $r_s = 0.236$, $T = 20.72$,

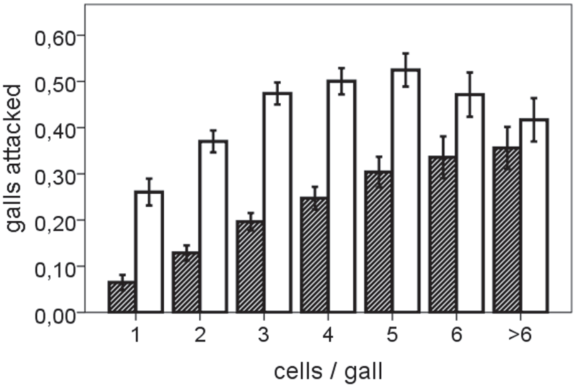

Figure 1. Average attack rate of galls by *E. serratulae* (black) and *E. robusta* (white) as function of cell numbers per gall. Analysed material: 260 gall samples with a total of 7,064 galls collected from 1976 to 1993 in eastern France, southern Germany and eastern Austria.

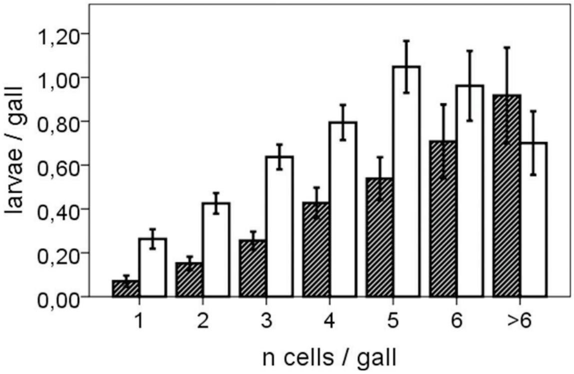

Figure 2. Average frequency of *E. serratulae* (black) and *E. robusta* (white) larvae as function of cell numbers per gall. Analysed material: 260 gall samples with a total of 7,064 galls collected from 1976 to 1993 in eastern France, southern Germany and eastern Austria.

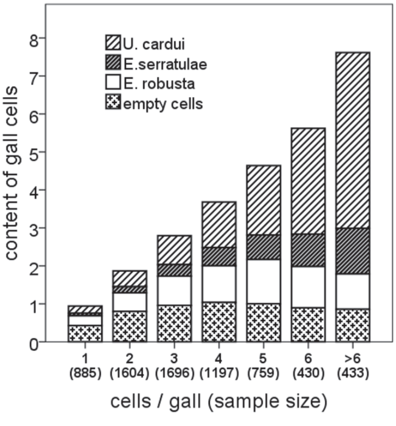

Figure 3. Average content of galls as a function of cell numbers / gall. (In parentheses: number of galls examined).

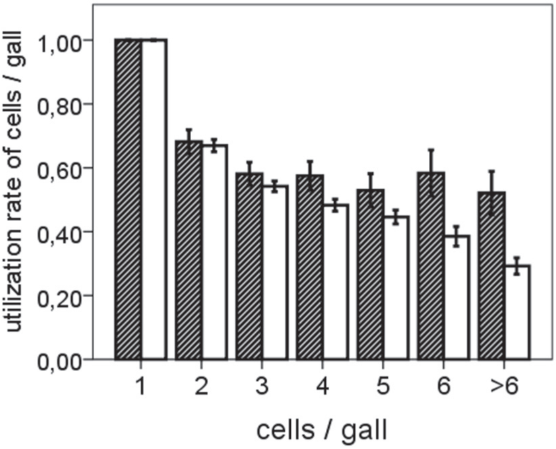

Figure 4. Average exploitation rate of galls attacked by *E. serratulae* (black) and/or *E. robusta* (white) as a function of gall size (cells / gall). Material: *E. serratulae*: 1407 galls; *E. robusta:* 1509 galls.

$p < 0.001$, $N = 6971$). It becomes much stronger ($r_s = 0.604$, $T = 12.305$, $p < 0.001$, $N = 270$), if the analysis is restricted to galls parasitized by *E. serratulae* without other mortality factors (e.g. *E. robusta* or empty chambers).

The mean exploitation rate of the cells of a gall drops in both *Eurytoma* species with an increasing number of cells / gall (Fig. 4). In *E. robusta* it decreases from 60–70% in small galls to 20% in galls with more than seven chambers. In *E. serratulae* the trend remains constant with a rate of about 40% in medium-sized and large galls. Therefore *E. serratulae* profits from *U. cardui* populations with large galls more than *E. robusta.* The difference between the two species is significant ($p < 0.001$).

E. serratulae and *E. robusta*: interactions at the level of single galls

Since *E. robusta* oviposits later than *E. serratulae*, we expected an asymmetric relationship between the two *Eurytoma* species. For a statistical test the effect of gall size on the rate of parasitization had to be removed. If galls occupied by *E. serratulae* without its congener are compared with galls jointly occupied by both species together (Fig. 5), the presence of *E. robusta* in a gall leads to a lower proportion of *E. serratulae* larvae (means of 1.87 vs 2.18 larvae / gall, ANOVA: $F = 16.5$, DF = 1 / 1405, $p < 0.001$). We interpret the difference as loss of *E. serratulae* due to hyperparasitism by *E. robusta*. For *E. robusta* the presence of *E. serratulae* has no significant effect (means of 1.74 and 1.75 larvae / gall, ANOVA: $F = 0.11$, DF = 1 / 2979, $p = 0.743$). Since cases in which all *E. serratulae* larvae have been eliminated by *E. robusta* could not be assessed, the data in Fig. 5 do not represent the entire extent of mortality of *E. serratulae* due to *E. robusta*.

Figure 5. Asymmetric interaction between the *E. serratulae* (black) and *E. robusta* (white): Average numbers of *E. serratulae*/gall without *E. robusta* (381 galls); *E. serratulae* together with *E. robusta* (324 galls); *E. robusta* without *E. serratulae* (2454 galls).

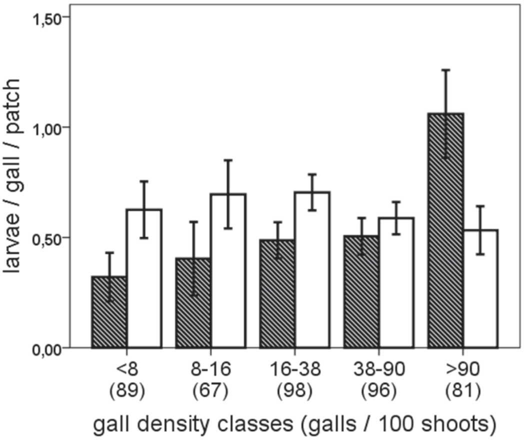

Figure 6. The influence of gall density / thistle patch (= galls / 100 thistle shoots) on *E. serratulae* (black) and *E. robusta* (white). (In parentheses: number of galls examined).

E. serratulae and *E. robusta*: comparison of gall populations

Our material allows comparing the two *Eurytoma* spp. with regard to gall density / thistle patch, which is a rough estimate of the quantity of galls in a thistle patch (*E. serratulae* = 688 samples; *E. robusta* = 1093 samples). The analysed samples represent average densities of locally and temporally fluctuating parasitoid-host complexes (Zwölfer 1994, Zwölfer et al. 2007). If analysed for five classes of sample sizes (Fig. 6) the average parasitism of *E. serratulae* and *E. robusta* is significantly different only in populations with low and high gall densities. In isolated galls and small clusters of galls *E. robusta* reaches larval densities twice as large as *E. serratulae*. The opposite situation occurs in thistle patches where the host population has reached peak gall densities. The rate of parasitism by *E. serratulae* increases steadily with increasing gall densities (Spearman correlation: $r_s = 0.399$, $N = 670$ populations, $p < 0.001$), whereas *E. robusta*

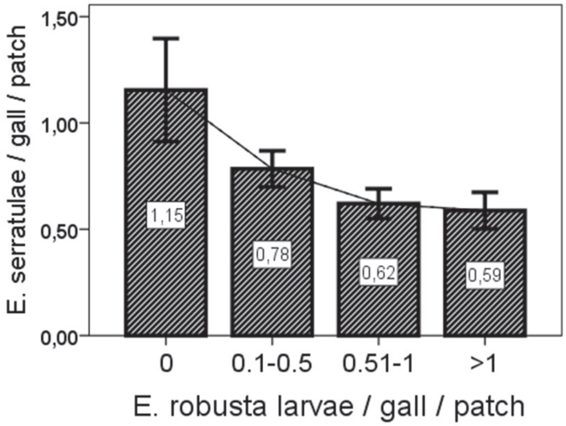

Figure 7. Average numbers of *E. serratulae* larvae / gall in *U. cardui* populations with different parasitization rates of *E. robusta.* (Sample sizes: 227, 332, 295, 209 gall populations).

reaches highest values in patches with intermediate gall densities (F = 3.589, DF = 4 / 437, p = 0.007). *Eurytoma serratulae* profits from phases with high gall density, while *E. robusta* takes over at low and intermediate gall densities. The pattern suggests differences in the host searching behaviour of the two species, but an additional effect that favours *E. serratulae* at high host densities may be the reduced load of hyperparasitism by *E. robusta*. A general linear model was used to disentangle the effects of sample size and gall density. Sample size is statistically not significant (*E. serratulae*: DF = 4, F = 0.577, p = 0.679; *E. robusta*: DF = 4, F = 0.500, p = 0.736), but the effect of gall density is highly significant (*E. serratulae*: DF = 4, F = 10.428, p < 0.001; *E. robusta*: DF = 4, F = 3.739, p < 0.001), and the interaction between the two factors is weak (*E. serratulae:* DF = 15, F = 1.740, p = 0.040; *E. robusta*: DF = 15, F = 1.774, p = 0.035).

Fig. 7 shows that the average number of *E. serratulae* larvae / gall / sample reaches the highest value in gall populations without *E. robusta* and sinks significantly with increasing numbers of *E. robusta* larvae (N samples: 227, 332, 295, 209, DF = 3, F = 4.723, p = 0.003). We interpret the data as an average mortality of 40–50% due to hyperparasitism and empty cells caused by *E. robusta*. If the average density of *E. robusta* larvae is compared for samples without (N = 357) and with (N = 691) *E. serratulae*, there is an increase of 0.57 to 0.65 *E. robusta* larvae /gall / sample. This weak statistical effect (DF = 1, F = 4.033, p = 0.045) with the factor "*E. serratulae*" is due to the fact that *E. serratulae* has the tendency to occur in higher numbers in galls with more chambers, which favour also *E. robusta*.

Hyperparasitism by *E. robusta* masks in most gall populations the superior capacity of *E. serratulae* to use the cells of the multilocular *U. cardui* galls. In 119 gall populations with less than 0.011 *E. robusta* larvae / gall / sample an average of 27.9% of the available cells where parasitized by *E. serratulae*, whereas *E. robusta* (605 populations with low or without parasitism by *E. serratulae*) used only 21.8%. The difference is significant (T-test: p < 0.001).

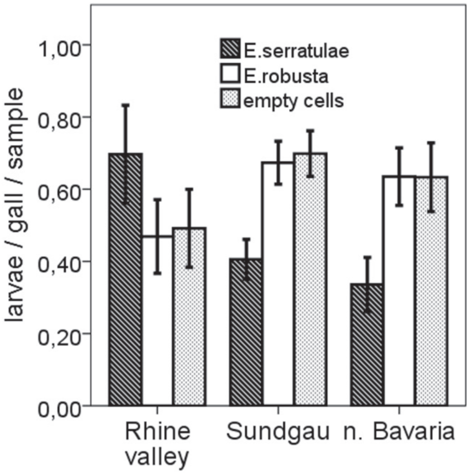

Figure 8. Parasitization of *U. cardui* samples by *E. serratulae* and *E .robusta* in 3 different regions of western Europe. Sundgau (France, region of Belfort): 307 samples, 6463 galls (1970–2004); Upper Rhine Valley (region n.w. Freiburg): 78 samples, 1885 galls (1972–1992); North eastern Bavaria (region s.e. Bayreuth): 216 samples, 4131 galls (1978–2004).

E. serratulae and *E. robusta:* regional differences

The parasitization rates of *E. serratulae* and *E. robusta* vary temporally and locally with the population dynamics of *U. cardui* (Zwölfer et al. 2007). These fluctuations are superimposed by regional differences (Fig. 8). Examples are the *U. cardui* populations in the floodplain forests of the upper Rhine Valley, where the host occurs in relatively stable source-sink systems. In these forests the average density / gall / sample of *E. serratulae* (mean = 0.744, SE = +0.069 was distinctly higher than that of *E. robusta* (mean = 0.427, SE = +0.052). In northern Bavaria (Bayreuth – Pegnitz) *U. cardui* occurs in a fragmented, agriculturally influenced landscape in mostly short-living population systems and metapopulations. Here *E. robusta* dominated with a mean density of 0.661, SE = +0.04 over *E. serratulae* (mean = 0.364, SE = +0.043). The Belfort-Sundgau region holds an intermediate position (*E. serratulae*: mean = 0.459, SE = +0.031. *Eurytoma robusta*: mean = 0.638, SE = +0.027). If our whole material collected in western and central Europe (*E. serratulae* = 772 gall samples, *E. robusta* = 755 gall samples) is compared, the average mortality of *U. cardui* due to *E. robusta* plus the empty cell factor (= 38.9%) is more than twice as high as that of *E. serratulae* (14.8%).

Effect of *E. serratulae* and *E. robusta* on gall growth

In galls of *U. cardui* the number of *E. serratulae* larvae / gall is positively correlated with the gall diameter (r = 0,428, p < 0.001, N = 1407). But the variable "*E. serratulae* larvae / gall" is also correlated with the variable "cells / gall" (r = 0,481, p < 0.001, N

Table 1. The effect of cells / gall and *E. serratulae* larvae / gall on gall diameter. Multiple regression: dependent variable: gall diameter, N = 2.733, multiple R = 0.67115, adjusted $R^2 = 0.45024$, SE = 3.02533.

Variable	B	SE (B)	Beta	*T*	Sign
cells / gall	1.15157	0.02496	0.6606	46.147	< 0.001
E. serratulae / gall	0.18681	0.04095	0.0653	4.562	< 0.001
(Constant)	9.00247	0.11135		80.851	< 0.001

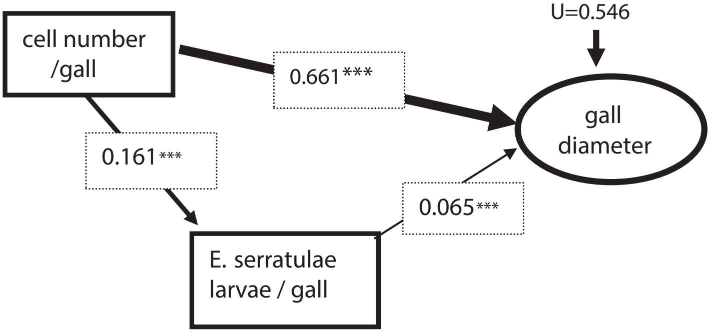

Figure 9. Direct and indirect effects between cells / gall, *E. serratulae* / gall and gall diameter. Path diagram: all three path coefficients (beta values) are significant at $p < 0.001$. Multiple $R^2 = 0.4546$. U (coefficient of non-determination) = 0.5456 ($N = 2{,}733$ *U. cardui* galls with *E. serratulae*).

= 2733), which in turn strongly affects the gall diameter ($r = 0{,}674$, $p < 0.001$, $N = 2733$). Together the two variables account for about 45% of the variation of the gall diameter ($R^2 = 0.454$). A multiple regression (Table 1) and a path analysis allow to separate the effect of the two variables and to calculate the impact of the variable "*E. serratulae* larvae / gall". Fig. 9 shows the three path coefficients (= standard partial regression coefficients). A comparison of the strength of the coefficients affecting the gall diameter allows the conclusion that the parasitoid larvae / gall can contribute about 10% to the gall diameter. Since *E. serratulae* attacks the *U. cardui* larvae before the gall is formed, this effect is not due to the selection of larger galls but to a stimulatory influence on gall growth.

An independent additional test is the comparison of galls with and without parasitoids (Fig. 10). Multivariate tests (GLM, Wilks-Lamda) for the gall size classes 2–5 (2 = 158, 3 = 158, 4 = 84, 5 = 45 galls, DF = 441) indicate ($F = 14.364$ and $p < 0.001$) a high statistical significance: Galls parasitized exclusively by *E. serratulae* have larger diameters than unparasitized galls and galls parasitized exclusively by *E. robusta* have lesser diameters than galls without parasitoids. This negative effect of *E. robusta* is not due to an ovipositional preference for smaller galls but to a premature elimination of young *Urophora* larvae that results in empty cells (Johannesen and Seitz 2003a, Zwölfer et al. 2007).

Table 2. Correlation of body weight of unparasitized *U. cardui* and *E. serratulae* larvae within *U. cardui* mummies with gall parameters.

	***U. cardui* (*N* = 66)**	***E .serratulae* (*N* = 15)**
Weight (mg) vs gall length (mm)		
r	0.0892 (*p* = 0.464)	**0.8452 (*p* = 0.0001)**
slope	0.048 (SE = 0.067)	0.2253 (SE = 0.0395)
Weight (mg) vs gall diameter (mm)		
r	0.1701 (*p* = 0.1722)	**0.6233 (*p* = 0.013)**
slope	0.1972 (SE = 0.1428)	0.4503 (SE = 0.1561)
Weight (mg) vs cell sum/gall		
r	0.0679 (*p* = 0.588)	**0.5633 (*p* = 0.0393)**
slope	-0.2201 (SE = 0.4043)	1.1746 (SE = 0.5127)

In a subsample of 81 galls we assessed larval biomass of the host and *E. serratulae,* gall diameter and length, and cell sum / gall. The average fresh weight of 66 mature unparasitized third instar larvae of *U. cardui* was 13.465 mg (SE = +0.545 mg) and that of 15 full grown *E . serratulae* larvae (inclusive of the sclerotized host skins) 5.207 mg (SE = +0.452 mg). Gall length (mean 24.302 mm, SE = +0.88 mm) ranged from 14.8 to 35.2 mm. Gall diameters (mean 13.82 mm, SE = +0.408 mm) ranged from 7.9 to 20.3 mm. Correlations of larval weight of *E. serratulae* in sclerotized host skins with the gall parameters diameter, length, and cell sum produced positive correlations (Table 2). We interpret this difference as another indication that host larvae, under the influence of the endoparasitoid *E. serratulae*, stimulate gall growth more strongly than *U. cardui* larvae without the endoparasitoid.

Discussion

Mechanisms allowing a balance in multi-parasitoid systems are compensations between intrinsic and extrinsic superiorities (Smith 1929). Examples can be found in most parasitoid complexes where parasitoid species with different life histories competitively coexist (e.g. Zwölfer and Kraus 1957, Askew 1968, Godfray 1994). Another important aspect is the temporal niche divergence of coexisting parasitoids, i.e. the exploitation of different host stages (e.g. Pschorn-Walcher and Altenhoffer 1989) or different developmental phases of plant galls (e.g. Askew 1975). Simulation models (Hassell 1986, 2000) demonstrate that patchy host distributions, metapopulation structures and host refuges may stabilize parasitoid-host interactions and contribute to prevent overexploitation of host populations.

In our study we show that the particular characteristics of multilocular plant galls provide an additional stabilizing mechanism for competing parasitoid species, since the two *Eurytoma* species exploit the cells of an individual gall in different ways. *Eurytoma robusta* is intrinsically superior, i.e. where its larva comes into contact with an *U. cardui* larva containing a young *E. serratulae*, it eliminates both. An advantage is also the capacity of the *E. robusta* larva to feed as an inquiline on the nutritive tissues of the gall. For its oviposition *E. robusta* is dependent on galls with fully developed cells, where synchronisation problems can lead to mortality of the young host larvae and starvation of the *E. robusta* larvae. Frequent and often high superparasitism of *E. robusta* (Zwölfer et al. 2007) can result in a considerable waste of eggs. As an initiator of empty cells *E. robusta* is an important mortality factor of *U. cardui* (Fig. 8). Parasitism by *E. robusta* and empty cells due to host killing without successful development of the parasitoid larva can cause up to 100% host mortality of small *U. cardui* populations. In experimental *U. cardui* populations in the Swiss Jura (Zwölfer 1994) and in several of our monitored populations in Northern Bavaria (Zwölfer et al. 2007) an overexploitation by *E. robusta* resulted in the complete breakdown of local *U. cardui* subpopulations and the associated monophagous parasitoid *E. serratulae*. In such cases its relatively broad host range allows *E. robusta* to switch to other host species. With regard to its host *U. cardui*, *E. robusta* is a poorly adapted generalist parasitoid but nevertheless an important mortality factor.

The life history of its congener *E. serratulae* is perfectly integrated with that of *U. cardui*. The female of *E. serratulae* detects the young host larvae already before an externally visible gall is formed and is able to parasitize a greater proportion than *E. robusta* of the host larvae available in an individual gall. In this way *E. serratulae* profits from grown up *U. cardui* populations with large multi-chambered galls. The capability to induce a sclerotization of host cuticula, once the host larva is consumed, provides a certain protection of the hibernating *E. serratulae* larva, e.g. against hyperparasitoids or predators. The emergence of adults is well synchronized with the emergence of the host flies. The increasing parasitism by *E. serratulae* in thistle patches with higher gall densities (Fig. 6) indicates a host searching behaviour influenced by the concentration of the host resource. Within a local host population galls with more cells contain over proportionally more *E. serratulae* larvae. This relationship suggests that thistle shoots with larger clutch sizes of *Urophora* are better recognizable and more attractive for *E. serratulae* females. The positive density dependence on the macrohabitat and microhabitat levels relieves the host *U. cardui* at low densities and contributes to stabilize a host-parasitoid system (Hassell 2000). Within individual galls the exploitation rate of *E. serratulae* is inversely density-dependent, making possible an increasing host refuge for *U. cardui* with increasing numbers of cells / gall (Fig. 3). The reason for this inverse relationship may be egg limitation of the *E. serratulae* females leading to some sort of "predator satiation" and/or the difficulty to locate all the tiny host larvae of a large clutch. The survival advantage of *U. cardui* larvae in galls with higher cell numbers can be important for the population dynamics of the host; as such galls contribute considerably more to the reproductive fitness of *U. cardui* than small galls (Freese and Zwölfer 1996). Since the absolute numbers of *E. serratulae* / gall also increase, larger galls with higher cell numbers are ultimately profitable to both the parasitoid and the host. Tabuchi and Amano (2004) report a similar relationship for the gall midge *Asteralobia sasakii* and its parasitoids on *Ilex*.

A particular feature of *E. serratulae* is its capacity to contribute to the growth of *U. cardui* galls (Table 1, Fig. 10). Host manipulation by endoparasitoids is a common

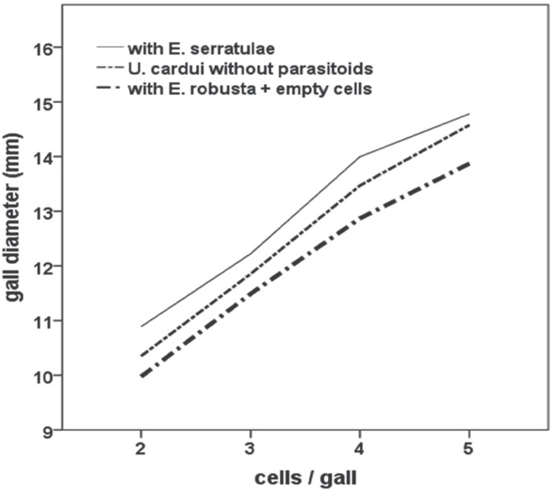

Figure 10. Average gall diameter in galls with *E. serratulae* (3512 galls), with unparasitized *U. cardui* (3449 galls) and with *E .robusta* plus empty cells (4288 galls).

phenomenon, as parasites tend to alter their hosts in ways beneficial to their own fitness. A special type of this manipulation consists in the prolongation of the feeding stages of the host, which allows the parasitoid larva to accumulate additional food resources (Beckage and Riddiford 1983, Slansky 1986, Godfray 1994). We assume that *E. serratulae* larvae stimulate *U. cardui* larvae to produce additional gall growth in a comparable way. Since larger galls provide better protection and possibly also an improved nutritional situation for *U. cardui* (Freese and Zwölfer 1996) they are profitable for both *U. cardui* and *E. serratulae.* The life history of *E. serratulae*, and the fact that it was able to follow its host to all three host plants and to cover the whole distribution area of *U. cardui*, indicate that the parasitism of *U. cardui* by *E. serratulae* forms an evolutionarily ancient and stable association.

It is interesting to compare *E. serratulae* with *Eurytoma obtusiventris* Gahan, the monophagous and highly specialised parasitoid of another gall-inducing tephritid, *Eurosta solidaginis* (Fitch), on North American *Solidago* spp. (Uhler 1951, Abrahamson et al. 1989, Abrahamson and Weis 1997). Both parasitoid species are koinobiont endoparasitoids, both attack the young host larvae of a gall-maker before gall formation starts, both are more frequent in large host galls and both are exposed to congeneric hyperparasitoids (*E. robusta* and *E. gigantea* Walsh, respectively), which deposit their eggs later into the galls. An important difference between the two parasitoid-host systems lies in the gall structure. The multi-chamber gall of *U. cardui* can secure the survival of some host larvae, whereas the single-chamber gall of *E. solidaginis,* once attacked, provides no chance of a host-escape. Differences exist also in the exploitation strategies of the two parasitoids. No influence on gall growth is described for *E. obtusiventris*; its higher frequency in larger galls is interpreted as a mere result of interactions with other mortality factors of the *Eurosta* galls (Abrahamson et al. 1989). It might, however, be worthwhile checking whether *E. obtusiventris* larvae could manipulate *Eurosta* larvae to produce larger goldenrod galls in a comparable way as *E. serratulae* influences the growth of *U. cardui* galls.

Our study shows that the specialised *E. serratulae* in its closely-knit and evolutionarily stable parasitoid-host system with *U. cardui* follows a "sustainable" exploitation strategy, which is absent in the poorly adapted generalist *E. robusta*.

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References

Abrahamson WG, Sattler JF, McCrea KD, Weis AE (1989) Variation in selection pressures on the golden rod gall fly and the competitive interactions of its natural enemies. Oecologia 79: 15–22. doi: 10.1007/BF00378234

Abrahamson WG, Weis AE (1997) Evolutionary ecology across three trophic levels, goldenrods, gallmakers, and natural enemies. Princeton University Press, Princeton, New Jersey.

Askew RR (1968) A survey of leafminers and their parasites on laburnum. Transactions of the Royal Entomological Society of London 120: 1–37. doi: 10.1111/j.1365-2311.1968.tb00335.x

Askew RR (1975) The organisation of chalcid-dominated parasitoid communities centred upon endophytic hosts.In: Price PW (Ed.) Evolutionary strategies of parasitoids. Plenum Press, New York, 130–153.

Askew RR, Shaw MR (1986) Parasitoid communities: their size, structure and development. In: Waage J, Greathead D (Eds) Insect parasitoids. Academic Press, London, 225–264.

Beckage NE, Riddiford LM (1983) Growth and development of the endoparasitic wasp *Apanteles congregatus*, dependence on host nutritional status and parasitoid load. Physiological Entomology 8: 231–241. doi: 10.1111/j.1365-3032.1983.tb00355.x

Claridge MF (1961) Biological observations on some eurytomid (Hym. Chalcidoidea) parasites associated with Compositae, and some taxonomic implications. Proceedings of the Royal Entomological Society of London (A) 36: 153–158. doi: 10.1111/j.1365-3032.1961.tb00261.x

Eber S, Brandl R (1994) Ecological and genetic spatial patterns of *Urophora cardui* (Diptera: Tephritidae) as evidence for population structure and biogeographical processes. Journal of Animal Ecology 63: 187–199. doi: 10.2307/5594

Fisher RC (1961) A study in insect multiparasitism. II the mechanism and control of competition for possession of the host. Journal of experimental Biology 38: 605–628.

Freese G, Zwölfer H (1996) The problem of optimal clutch size in a tritrophic system: the oviposition strategy of the thistle gall fly *Urophora cardui* (Dipt. Tephritidae). Oecologia 108: 293–302. doi: 10.1007/BF00334654

Frenzel M, Eber S, Klotz S, Brandl R (2000) Ecological comparisons across geographical distributions: the thistle gall fly *Urophora cardui* (Diptera: Tephritidae) on different *Cirsium* hosts. European Journal of Entomology 97: 183–189. doi: 10.14411/eje.2000.035

Godfray HCJ (1994) Parasitoids. Behavioural and Evolutionary Ecology. University Press, Princton.

Hassell MP (1986) Parasitoids and population regulation. In: Waage KJ, Greathead D (Eds) Insect parasitoids. Academic Press, London, 201–224.

Hassell MP (2000) The Spatial and Temporal Dynamics of Host-parasitoid Interactions. Oxford University Press.

Johannesen J, Seitz A (2003a) Larval distributions of the ectoparasitoid wasp *Eurytoma robusta* relative to the host tephritid gall fly *Urophora cardui*. Entomologia experimentalis et applicata: 107: 47–55. doi: 10.1046/j.1570-7458.2003.00040.x

Johannesen J, Seitz A (2003b) Comparative population genetic structures of the fruit fly *Urophora cardui* and its primary parasitoid *Eurytoma robusta*. Entomologia experimentalis et applicata 107: 149–157. doi: 10.1046/j.1570-7458.2003.00077.x

Mayr G (1878) Arten der Chalcidier-Gattung *Eurytoma* durch Zucht erhalten. Verhandlungen der zoologisch-botanischen Gesellschaft Wien 28: 297–334.

Price PW, Clancy KM (1986) Interactions among three trophic levels: galls size and parasitoid attack. Ecology 6: 1539–1600.

Pschorn-Walcher H, Altenhofer E (1989) The parasitoid community of leaf-mining sawflies (Fenusini and Heterarthrini): A comparative analysis. Zoologischer Anzeiger 222: 37–57.

Redfern M (1983) Insects and thistles. Naturalists' Handbooks 4, Press Syndicate of the University of Cambridge.

Redfern M, Askew RR (1992) Plant Galls. Naturalists' Handbooks 17, Press Syndicate of the University of Cambridge.

Saccheri I, Hanski I (2006) Natural selection and population dynamics. Trends in Ecology and Evolution 21: 341–347. doi: 10.1016/j.tree.2006.03.018

Slansky F (1986) Nutritional ecology of endoparasitic insects and their hosts: an overview. Journal of Insect Physiology 32: 255–261. doi: 10.1016/0022-1910(86)90036-3

Smith HS (1929) Multiple parasitism: its relation to the biological control of insect pests. Bulletin of Entomological Research 20: 141–149. doi: 10.1017/S0007485300021040

Sokal RR, Rohlf FJ (1981) Biometry, second edition. Freeman and Company, San Francisco.

Tabuchi K, Amano H (2004) Impact of differential parasitoid attack on the number of chambers in multilocular galls of two closely related gall midges (Diptera: Cecidomyiidae). Evolutionary Ecology Research 6: 695–707.

Uhler LD (1951) Biology and ecology of the golden rod gall fly, *Eurosta solidaginis* (Fitch). Memoir 300, Cornell University Agricultural Experiment Station, Ithaca, New York, 1–51.

Vikberg V (2005) Orakärpänen (*Urophora cardui*) ja sen kiilukaisloiset Etelä-Suomessa (Hymenoptera: Chalcidoidea: Eulophidae, Eupelmidae, Eurytomidae, Pteromalidae, Torymidae). Sahlbergia 10: 30–49.

Zerova MD, Seryogina LY (2006) A review of the Palaearctic species of the genus *Eurytoma*, belonging to the *E. robusta* species group (Hymenoptera, Eurytomidae), with description of two new species. Entomological Review 86:695–705. doi: 10.1134/S001387380606008X

Zwölfer H (1979) Strategies and counterstrategies in insect population systems competing for space and food in flower heads and plant galls. Fortschritte der Zoologie 25: 331–353.

Zwölfer H (1988) Evolutionary and ecological relationships of the insect fauna of thistles. Annual Review of Entomology 33: 103–22. doi: 10.1146/annurev.en.33.010188.000535

Zwölfer H (1994) Structure and biomass transfer in food webs: stability, fluctuations, and network control. In: Schulze (Ed.) Flux control in biological systems from enzymes to populations and ecosystems. Academic Press Inc., San Diego, 365–419.

Zwölfer H, Arnold-Rinehart J (1993) The evolution of interactions and diversity in plant-insect systems. The *Urophora-Eurytoma* food web in galls on Palearctic Cardueae. Ecological Studies, Springer, Berlin, Heidelberg, New York 99: 211–233.

Zwölfer H, Böheim M, Beck E (2007) *Eurytoma robusta* (Hymenoptera: Eurytomidae), a local key factor in the population dynamics of *Urophora cardui* (Diptera: Tephritidae): A comparative analysis. European Journal of Entomology 104: 217–224. doi: 10.14411/eje.2007.034

Zwölfer H, Kraus M (1957) Biocoentic studies on the parasites of two fir- and two oak-tortricids. Entomophaga 2: 173–196. doi: 10.1007/BF02372436

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Revision of the *Crematogaster ranavalonae*-group in Asia, with description of two new species (Hymenoptera, Formicidae)

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Abstract

The Asian members of the *Crematogaster ranavalonae*-group are revised and twelve species, including two new species, *C. hashimi* **sp. n.** and *C. imperfecta* **sp. n.** are recognized. The members are distinguished from the other Asian *Crematogaster* in having smooth, shiny bodies with short appressed setae on the surface. *Crematogaster sikkimensis* Forel, 1904 is raised to the species level, and the following new synonyms are established: *C. aberrans* Forel, 1892 = *C. aberrans assmuthi* Forel, 1913, **syn. n.** = *C. aberrans inglebyi* Forel, 1902, **syn. n.** = *C. soror* Forel, 1902, **syn. n.**; *C. ebenina* Forel, 1902 = *C. ebenina corax* Forel, 1902, **syn. n.** A key to the species based on the worker caste is provided.

Keywords

Asia, *Crematogaster ranavalonae*-group, Formicidae, new species, *Oxygyne*, taxonomy, ventrolateral katepisternal ridge

Introduction

The hyperdiverse ant genus *Crematogaster* had been subdivided into sixteen subgenera (Emery 1922; Wheeler 1922). Recently a molecular phylogenetic analysis has suggested that most of these subgenera are non-monophyletic, and that the subgenus *Oxygyne* is monophyletic (Blaimer 2012c). Subsequently Blaimer (2012b) established

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the *Crematogaster ranavalonae*-group to accommodate the former subgenus *Oxygyne* in her subgeneric revision of this genus.

Members of the *Crematogaster ranavalonae*-group have been differentiated based on characters found in the worker and queen castes (Blaimer 2012a, 2012b). Although workers of the Asian members also posses the taxonomic characters identified by her, the propodeal spines in some of the Asian species are not well developed, appearing instead as small tubercles. However, I have identified a unique character among the members of the Asian *C. ranavalonae*-group; that is, while the ridge separating the lateral and ventral portions of the mesopleuron is distinct in most *Crematogaster* species, it is not distinct in the Asian members of the *C. ranavalonae*-group. Furthermore, the queen caste of some members of the species group has falcate mandibles, suggesting the occurrence of temporal social parasitism in those species (Forel 1910; Santschi 1934; Hölldobler and Wilson 1990; Blaimer 2012a). However, among the Asian fauna, falcate mandibles are found only in the queen of *C. augusti* and are unknown in other species due to the rarity with which they are encountered in the field. In this study, I do not treate the queen caste because it is not represented in my collections.

The *Crematogaster ranavalonae*-group consists of twenty-two species, including eleven species from Africa and Madagascar, ten from Asia, and one from New Guinea (Blaimer 2012b). Among the Asian fauna (ten species and four subspecies), four species and three subspecies have been described from India. It is considered that India is the center of diversity in this species-group, but this may be an overestimate attributable to the rarity of this species group in the field. This paper provides a revision of the Asian members of *C. ranavalonae*-group, based on the morphological characters of the worker caste.

Materials and methods

Sources of material

Specimens were examined and/or deposited in the collections listed below. Codes for public institutions mainly follow those in Brandão (2000). Nest series samples, most of which were recently collected, are represented as colony codes, e.g., "SH12-Tha-01."

BMNH	The Natural History Museum, London, U. K.
CASC	California Academy of Sciences, San Francisco, CA, USA
FRIM	Forest Research Institute Malaysia, Kepong, 52109 Kuala Lumpur, Malaysia.
IEGG	Istituto di Entomologia "Guido Grandi", Bologna, Italy.
KUM	Kyushu University, Fukuoka, Japan.
MCSN	Museo Civico di Storia Naturale "Giacomo Doria", Genoa, Italy.
MCZC	Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA.
MHNG	Musée d'Histoire Naturelle, Geneva, Switzerland.

MBBJ	Museum Zoologicum Bogoriense, Cibinong, Java, Indonesia.
NHMB	Naturhistorisches Museum, Basel, Switzerland.
NHMW	Naturhistorisches Museum Wien, Wien, Austria.
SKYC	Sk. Yamane Collection, Kagoshima University, Japan.
THNHM	Thailand Natural History Museum, Technopolis, Khlong Luang, Pathum Thani, Thailand.

Methods

Most observations were made on an Olympus SZX12 stereomicroscope. The scanning electron micrographs (SEM) were prepared with a JSM-5600LV scanning electron microscope. Color images were taken using a Canon EOS 50D with a Canon MP-E 65 mm 1–5× macro lens, then processed using Combine ZM.

The relative position of propodeal spiracles was observed in lateral view, with the mesosoma carefully tilted to the position with the true maximum of Weber's length.

Measurements and indices

Measurements were made under an Olympus SZX12 stereomicroscope using micrometers. All measurements are expressed in millimeters, recorded to the second decimal place. The measurements for petiole and postpetiole follow Longino (2003).

Head Width (HW): Maximum width of head in full-face view, excluding the eyes (Fig. 1).

Head Length (HL): Perpendicular distance from vertex margin to line tangent to anteriormost projections of clypeus in full-face view (Fig. 1).

Cephalic Index (CI): HW/HL × 100.

Scape Length (SL): Length of the first antennal segment, excluding the neck and basal condyle (Fig. 2).

Scape Index (SI): SL/HW × 100.

Eye Length (EL): Maximum length of the compound eye (Fig. 1).

Pronotal Width (PW): Maximum width of the pronotum in dorsal view (Fig. 3).

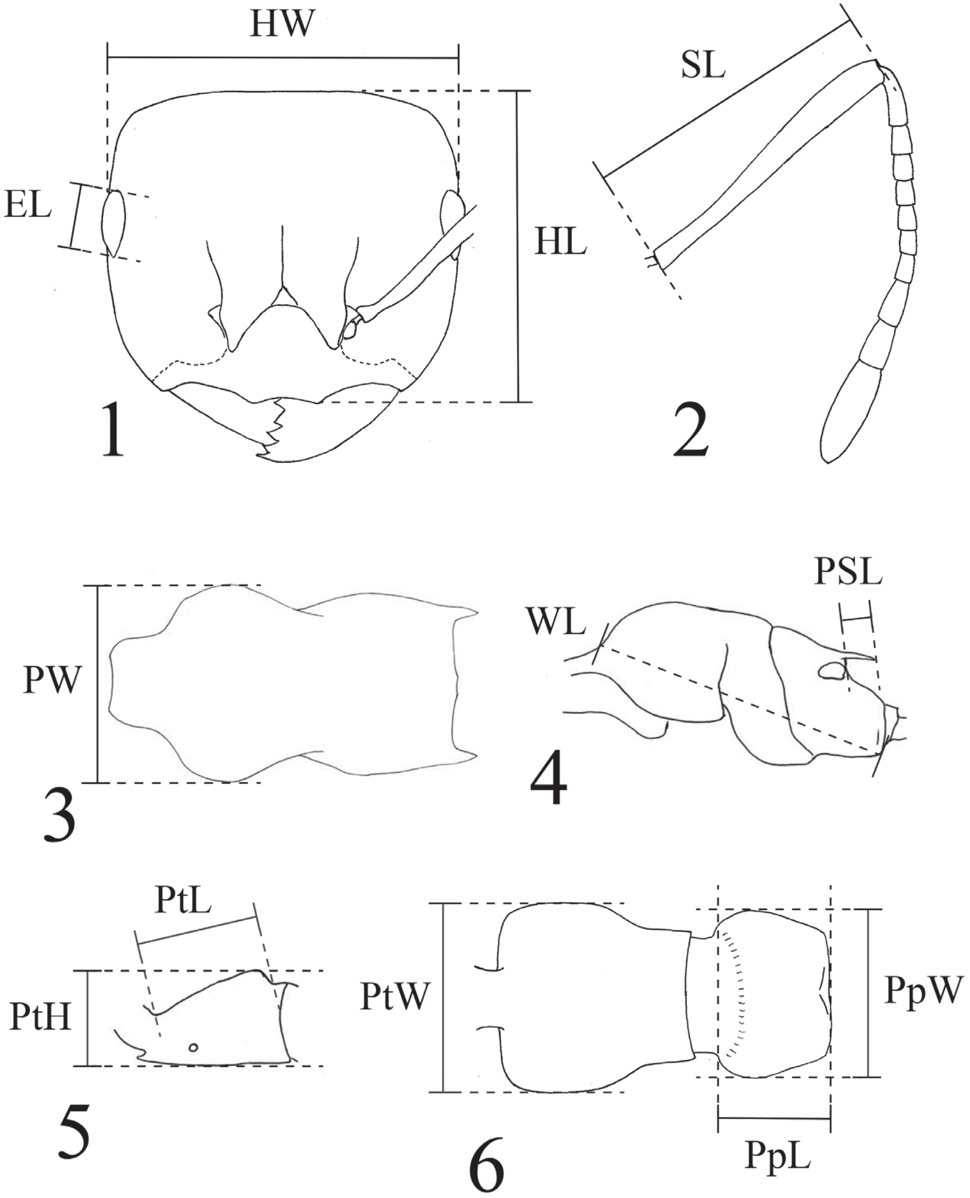
Weber's Length of the mesosoma (WL): Diagonal length, measured in lateral view from the anterior margin of the pronotum (excluding the collar) to the posterior extremity of the propodeal lobe (Fig. 4).

Propodeal Spine Length (PSL): measured from tip of propodeal spine to closest point on outer rim of propodeal spiracle (Fig. 4).

Petiole Length (PtL): Length of the petiole in lateral view (Fig. 5) (see Longino 2003, fig. 2).

Petiole Width (PtW): Maximum width of petiole in dorsal view (Fig. 6).

Petiole Height (PtH): Height of the petiole in lateral view (Fig. 5) (see Longino 2003, fig. 2).



Figures 1–6. Measurements of workers. **1** Head width, head length and eye length **2** Scape length **3** Pronotal width **4** Weber's length and propodeal spine length **5** Petiole length and petiole height **6** Petiole width, postpetiole length and postpetiole width.

Postpetiole Length (PpL): Length of the postpetiole in dorsal view (Fig. 6) (see Longino 2003, fig. 2).

Postpetiole Width (PpW): Maximum width of postpetiole in dorsal view, excluding the helcium (Fig. 6).

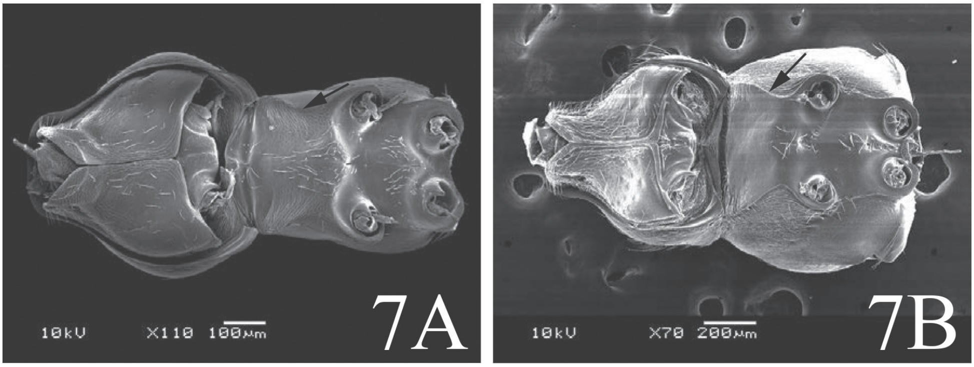


Figure 7. Ventrolateral katepisternal ridge from ventral portion in mesosoma (legs removed). Arrow indicates the ridge. **A** *Crematogaster hashimi* **B** *Crematogaster physothorax*.

Petiole Height Index (PtHI): PtH/PtL × 100.
Petiole Width Index (PtWI): PtW/PtL × 100.
Postpetiole Width Index (PpWI): PpW/PpL × 100.
Waist Index (WI): PpW/PtW × 100.

An important character in the Asian *Crematogaster ranavalonae*-group is explained below.

Ventrolateral katepisternal ridge (Fig. 7). The ridge separates the mesopleuron lateral surface from ventral surface. Most Asian *Crematogaster* species have a well-defined ridge separating the two surfaces (Fig. 7B), but in some species the ridge is absent or vestigial (Fig. 7A). The ridge is visible in pinned specimens from lateral or ventrolateral view.

Asian *Crematogaster ranavalonae*-group

The Asian members of the *Crematogaster ranavalonae*-group not only have the morphological features diagnosed by Blaimer (2012a, 2012b), but also show the additional features below.

(i) Pronotum steeply raised in lateral view.
(ii) Ventrolateral katepisternal ridge indistinct, but weakly developed anteriorly in some species.
(iii) Integument essentially smooth and shiny.
(iv) Erect pilosity almost absent. Some erect setae are developed on the clypeus or dorsal surface of petiole and postpetiole, but absent on the dorsum of head, mesosoma and fourth to seventh abdominal tergites.
(v) Dorsum of head, mesosoma and fourth abdominal tergite with short and appressed setae.

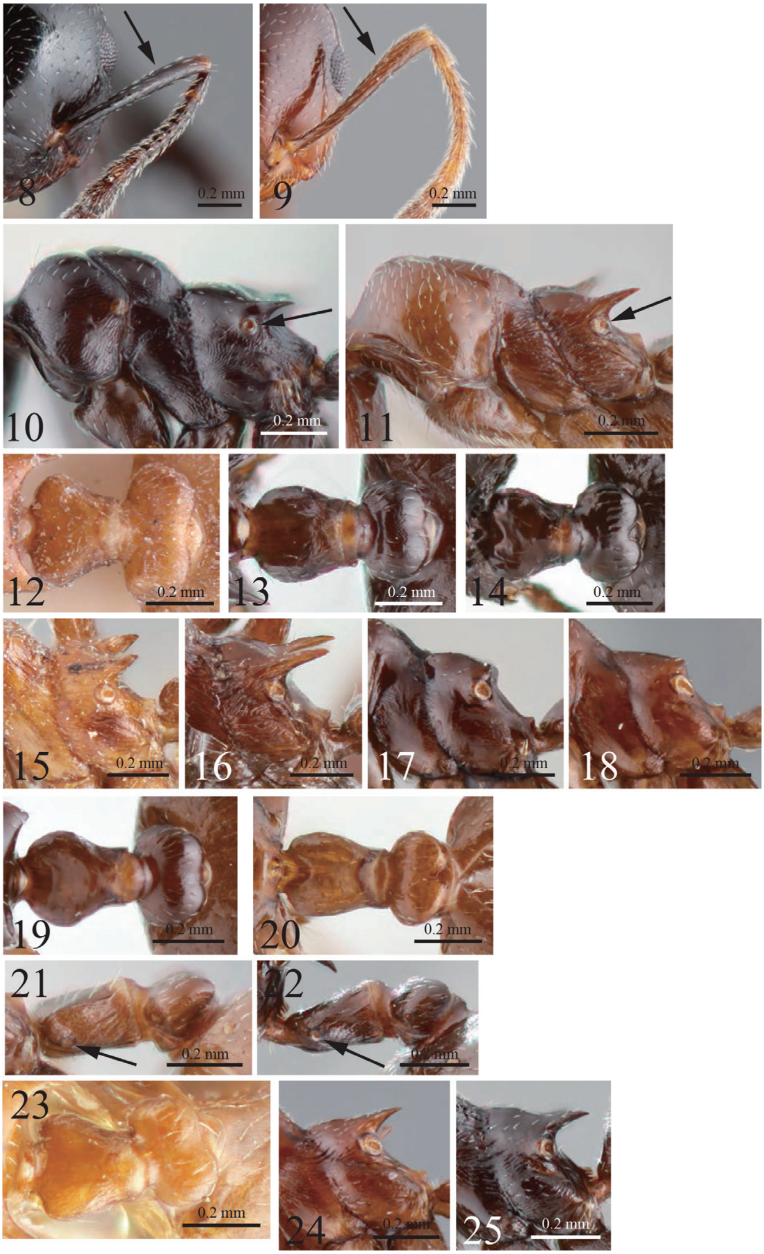
This species group is easily defined from other Asian *Crematogaster* in having a steeply raised pronotum, smooth and shiny body surface, and short and appressed body setae.

Synonymic list of the Asian *Crematogaster ranavalonae*-group

aberrans Forel, 1892.
  = *aberrans assmuthi* Forel, 1913, **syn. n.**
  = *aberrans inglebyi* Forel, 1902, **syn. n.**
  = *soror* Forel, 1902, **syn. n.**
augusti Emery, 1895.
butteli Forel, 1913.
daisyi Forel, 1901.
dalyi Forel, 1902.
ebenina Forel, 1902.
  = *ebenina corax* Forel, 1902, **syn. n.**
hashimi **sp. n.**
imperfecta **sp. n.**
pia Forel, 1911.
sikkimensis Forel, 1904. **stat. n.**
tumidula Emery, 1900.
vandermeermohri Menozzi, 1930

Key to species based on the worker caste (not included are *C. augusti*, known only from the queen caste, and *C. vandermeermohri* whose type specimens were not examined)

1 Scape with sparse setae (Fig. 8). Propodeal spiracles as small as mesothoracic spiracles (Fig. 10) .... ***aberrans***
– Scape with abundant setae (Fig. 9). Propodeal spiracles large; diameter ca. 2 × as large as mesothoracic spiracles (Fig. 11) **2**
2 Postpetiole markedly bilobed laterally, more than 2 × as broad as long (PpWI 212–236) (Fig. 12) **3**
– Postpetiole moderately bilobed laterally, generally ca. 1.2 to 2 × as broad as long (PpWI 125-200) (Figs 13, 14) **4**
3 Propodeal spines short; their length equal to or shorter than diameter of propodeal spiracles (Fig. 15) .... ***dalyi***
– Propodeal spines long; distinctly longer than diameter of propodeal spiracles (Fig. 16) .... ***sikkimensis***
4 Propodeal spines not developed, reduced to small tubercles (Figs 17, 18) ... **5**
– Propodeal spines developed (Fig. 11) **6**
5 Propodeal spiracles circular (Fig. 17). Petiole about as broad as or broader than long (PtWI 96–109) (Fig. 19) .... ***hashimi***
– Propodeal spiracles elliptical (Fig. 18). Petiole longer than broad (PtWI 88-92) (Fig. 20) .... ***imperfecta***
6 Anterolateral portion of petiole developed laterally and spiracles on petiole located on lower position and directed ventrally (Fig. 21) .... ***daisyi***



Figures 8–25. Worker characters of Asian *Crematogaster ranavalonae*-group. **8** left scape (*C. aberrans*) **9** left scape (*C. daisyi*) **10** propodeal spiracle (*C. aberrans*) **11** propodeal spiracle (*C. daisyi*) **12** petiole and postpetiole (*C. dalyi*) **13** petiole and postpetiole (*C. ebenina*) **14** petiole and postpetiole (*C. pia*) **15** propodeal spine (*C. dalyi*) **16** propodeal spine (*C. sikkimensis*) **17** propodeal spiracle and reduced propodeal spine (*C. hashimi*) **18** propodeal spiracle and reduced propodeal spine (*C. imperfecta*) **19** petiole and postpetiole (*C. hashimi*) **20** petiole and postpetiole (*C. imperfecta*) **21** spiracle on petiole (*C. daisyi*) **22** spiracle on petiole (*C. ebenina*) **23** petiole and postpetiole (*C. butteli*) **24** propodeal spine (*C. tumidula*) **25** propodeal spine (*C. ebenina*).

– Anterolateral portion of petiole developed laterally, but spiracles on petiole located on middle portion and directed laterally (Fig. 22)..........................**7**

7 Anterolateral corners of petiole angulate, anterior face developed (Fig. 23) . ***butteli***

– Anterolateral corners of petiole rounded, anterior face sinuate (Fig. 13)......**8**

8 Propodeal spines short and stout; as long as diameter of propodeal spiracles (Fig. 24)...***tumidula***

– Propodeal spines long; distinctly longer than diameter of propodeal spiracles (Fig. 25)...**9**

9 Anterolateral corners of petiole undeveloped, tapering anteriorly (Fig. 13). Postpetiole generally as wide as petiole in dorsal view (WI 96–100) ... ***ebenina***

– Anterolateral corners of petiole developed (Fig. 14). Postpetiole wider than petiole in dorsal view (WI 103-115) ....***pia***

Species accounts

Crematogaster aberrans Forel

Fig. 26

Crematogaster aberrans Forel, 1892: 532-534. Type locality: India, Thana. Combination in *C.* (*Oxygyne*) by Forel, 1901: 375; in *C.* (*Crematogaster*) by Blaimer, 2012b: 55.

Crematogaster (*Oxygyne*) *aberrans* var. *assmuthi* Forel, 1913: 662. Type locality: India, Bombay. **syn. n.**

Crematogaster (*Oxygyne*) *aberrans* var. *inglebyi* Forel, 1902: 201. Type locality: India, Travancore. **syn. n.**

Crematogaster (*Oxygyne*) *soror* Forel, 1902: 200. Type locality: India, Poona and Bombay. Combination in *C.* (*Crematogaster*) by Blaimer, 2012b: 55. **syn. n.**

Type material examined. *Crematogaster aberrans*: lectotype worker (top specimen of three on one pin) by present designation and five paralectotype workers from India, Thana (MHNG, examined); one syntype worker from India, Thana (NHMB, examined). *Crematogaster* (*Oxygyne*) *aberrans* var. *assmuthi*: one syntype worker from India, Bombay (*M. Assmuth*) (MHNG, examined). *Crematogaster* (*Oxygyne*) *aberrans* var. *inglebyi*: three syntype worker from India, Travancore (*Ferguson* and *Ingleby*) (MHNG, examined). *Crematogaster* (*Oxygyne*) *soror*: five syntype workers from India, Poona (*Wroughton*) and Bombay (*Rothney*) (MHNG, examined); one syntype worker from India, Bombay (*Rothney*) (NHMB, examined).

Non-type material examined. THAILAND: 8 workers, Doi Chiang Dao (500-600m alt.), nr Chiang Mai, N. Thailand. 2.iv.2005 (TH05-SKY-22) (*Sk. Yamane*); 5 workers, Ngao, Lampang, 17.ii.1991 (*No collector's name*); 4 workers, Maegar, Phayao, 30.iii.1991 (*No collector's name*).

Measurements and indices (workers, n = 10). HW 0.82-0.96; HL 0.78-0.93; CI 102-109; SL 0.64-0.74; SI 75-82; EL 0.18-0.21; PW 0.50-0.58; WL 0.90-1.05; PSL

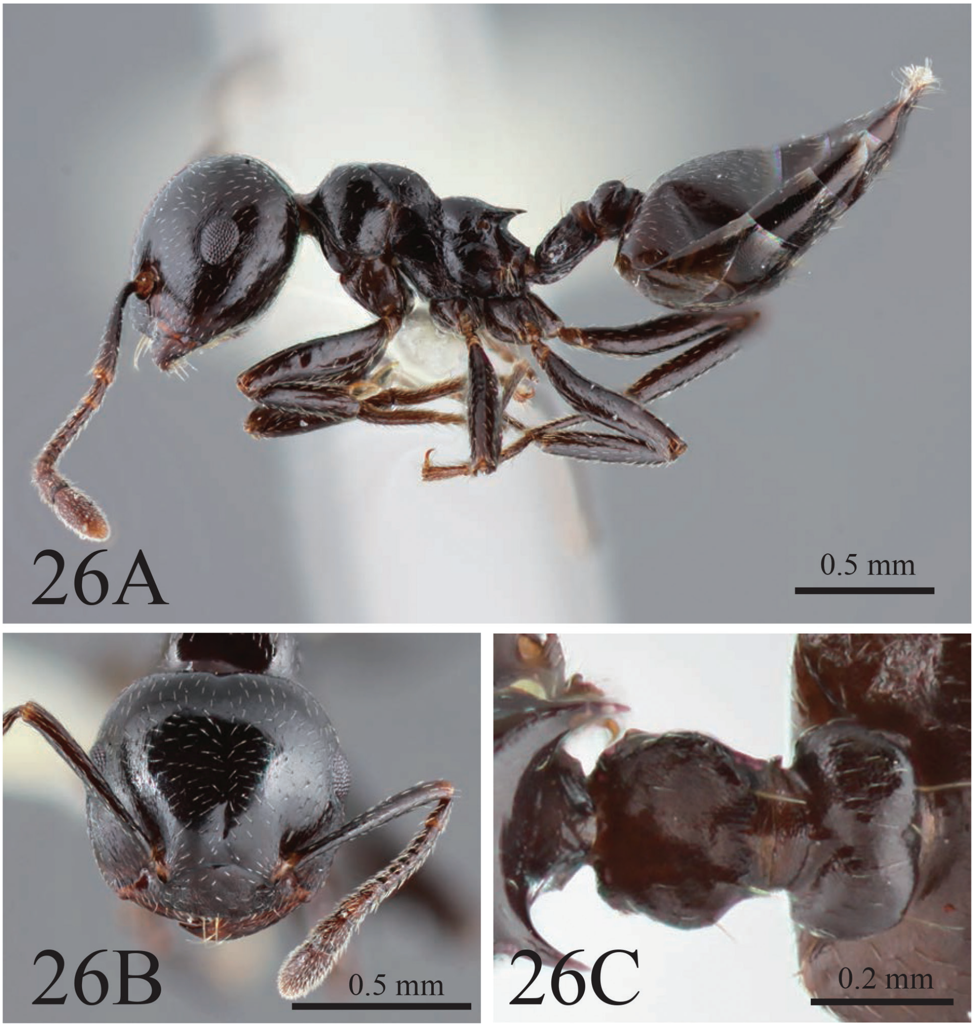


Figure 26. *Crematogaster aberrans* [Doi Chiang Dao, nr. Chiang Mai, N. Thaiand]. **A** Lateral view of body **B** Full face view **C** Dorsal view of petiole and postpetiole.

0.09-0.12; PtL 0.25-0.30; PtW 0.25-0.32; PtH 0.17-0.20; PpL 0.15-0.19; PpW 0.25-0.33; PtHI 61-76; PtWI 97-116; PpWI 167-213; WI 100-114.

General description of worker. Head appearing rounded in front view. Mandible indistinctly striate, with four teeth, apical and subapical teeth large, basal two teeth smaller. Scape exceeding posterior corner of head, with sparse appressed setae, each of which is about as long as scape diameter. Compound eye slightly projecting beyond lateral margin of head in full face view.

Mesonotum highly convex in lateral view. Ventrolateral katepisternal ridge indistinct. Propodeal spine short and stout; the length variable, but generally as long as propodeal spiracle, dorsum not higher than anterior propodeum in lateral view. Propodeal spiracle as large as mesothoracic spiracle pit, situated apart from the propodeal declivity in lateral view, directed laterally.

In dorsal view, shape of petiole scoop with convex side, as long as broad. Petiole with anterolateral corner angulate. Petiolar spiracle big, as wide as half of propodeal spiracle in diameter, directed laterally. Postpetiole bilobed, with slight longitudinal median sulcus. Postpetiole slightly wider than petiole in dorsal view.

Integument essentially smooth and shiny. Clypeus generally smooth and shiny, but weakly striated with faint rugulae. Malar region with feeble longitudinal rugulae. Dorsal surface of promesonotum weakly punctuated. Lateral surface of pronotum shiny, but weakly punctuated. Mesopleuron weakly punctuated. Dorsal surface of propodeum smooth and shiny. Lateral propodeum smooth and shiny.

Erect pilosity almost absent. Dorsum of head, clypeus and mesosoma with short and appressed, sparse setae. Clypeus without pair of longer setae on anteriormost portion. Anterior clypeal margin with one single longer seta and one pair of longer setae on median portion, mixed with some shorter setae on side. One to three pairs of short, erect setae on pronotal shoulder. Posterolateral tubercle with two pairs of erect setae. Ventral surface of petiole with longer appressed setae. Postpetiole with two pairs of longer setae posteriorly. Fourth abdominal tergite with appressed setae.

Body color reddish brown.

Distribution. This species is distributed in India and Thailand.

Comments. This species is unique among Asian *Crematogaster ranavalonae*-group in having the scape with sparse setae and smaller propodeal spiracles, situated apart from the propodeal declivity.

The syntype workers of *C. aberrans assmuthi* match well with syntype workers of *C. aberrans*. I treated *C. aberrans assmuthi* as a junior synonym of *C. aberrans*. The syntype workers of *C. aberrans inglebyi* match well with syntype workers of *C. aberrans*, but with only the following small difference: the former has right brown colored body (cf. Forel 1902). I concluded that *C. aberrans inglebyi* is a junior synonym of *C. aberrans*. The syntype workers of *C. soror* match well with syntype workers of *C. aberrans*. In Forel's original description (Forel 1902), he mentioned that the head is subquadratic. However, the posterior margin of head is not angulate, appearing rounded in front view. Thus I here synonymize *C. soror* with *C. aberrans*.

***Crematogaster augusti* Emery**

Crematogaster augusti Emery, 1895: 31, pl. 2, figs. 19, 20. Type locality: Indonesia, Marang, Sumatra. Combination in *C.* (*Oxygyne*) by Emery, 1922: 157; in *C.* (*Crematogaster*) by Blaimer, 2012b: 55.

Type material examined. *Crematogaster augusti*: one syntype queen from Indonesia, Marang, Sumatra (MCSN, examined).

Comments. Emery's original description was based on a single queen. Our collections are limited to worker specimens, but two unique features are found in the type. First, the propodeal spines are not developed, as they are in the queen of *C. agnetis* Forel from Madagascar (Blaimer 2012a). Second, the body surface appearing smooth and shiny. The taxonomic status will remain uncertain until nest series become available.

Crematogaster butteli Forel

Fig. 27

Crematogaster (*Oxygyne*) *butteli* Forel, 1913: 78. Type locality: Indonesia, Soengei Bamban, Sumatra. Combination in *C.* (*Crematogaster*) by Blaimer, 2012b: 55.

Type material examined. *Crematogaster* (*Oxygyne*) *butteli*: lectotype worker (top specimen of two on one pin) by present designation and four paralectotype workers from Indonesia, Soengei Bamban, Sumatra (MHNG, examined); one syntype worker from Indonesia, Soengei Bamban, Sumatra (NHMB, examined).

Measurements and indices (type workers, n = 5). HW 0.80-0.85; HL 0.76-0.80; CI 103-107; SL 0.64-0.67; SI 79-84; EL 0.16-0.17; PW 0.48-0.52; WL 0.91-0.96; PSL 0.12-0.14; PtL 0.21-0.22; PtW 0.22-0.24; PtH 0.15-0.16; PpL 0.14-0.15; PpW 0.24-0.25; PtHI 68-76; PtWI 95-114; PpWI 167-179; WI 100-119.

General description of worker. Head appearing subquadratic in front view. Mandible weakly striate, with four teeth, apical and subapical teeth large, basal two teeth smaller. Scape exceeding posterior corner of head, with appressed setae, each of which is as long as width of scape. Compound eye large and slightly projecting beyond lateral margin of head in full face view.

Ventrolateral katepisternal ridge indistinct posteriorly. Propodeal spine long and stout, longer than spiracle diameter, directed upward, dorsum higher than anterior propodeum in lateral view. Propodeal spiracle large, situated on lateral surface of propodeum and close to propodeal declivity in lateral view.

In dorsal view, shape of petiole scoop with tapering side posteriorly, longer than broad. Petiole with anterolateral corner angulate. Petiolar spiracle big, as wide as half of propodeal spiracle in size. Postpetiole bilobed but without longitudinal median sulcus. Postpetiole as wide as petiole in dorsal view.

Integument essentially smooth and shiny. Clypeus smooth and shiny without rugulae. Malar region generally smooth, with feeble rugulae. Dorsal surface of promesonotum smooth and shiny. Lateral surface of pronotum smooth and shiny. Mesopleuron shiny, but with longitudinal rugulae. Dorsal surface of propodeum smooth and shiny. Lateral propodeum shiny, but with longitudinal rugulae.

Erect pilosity almost absent. Dorsum of head, clypeus and mesosoma with sparse, short and appressed setae. Clypeus with one pair of longer setae on anteriormost portion, directed medially. Anterior clypeal margin with two pairs of longer setae on

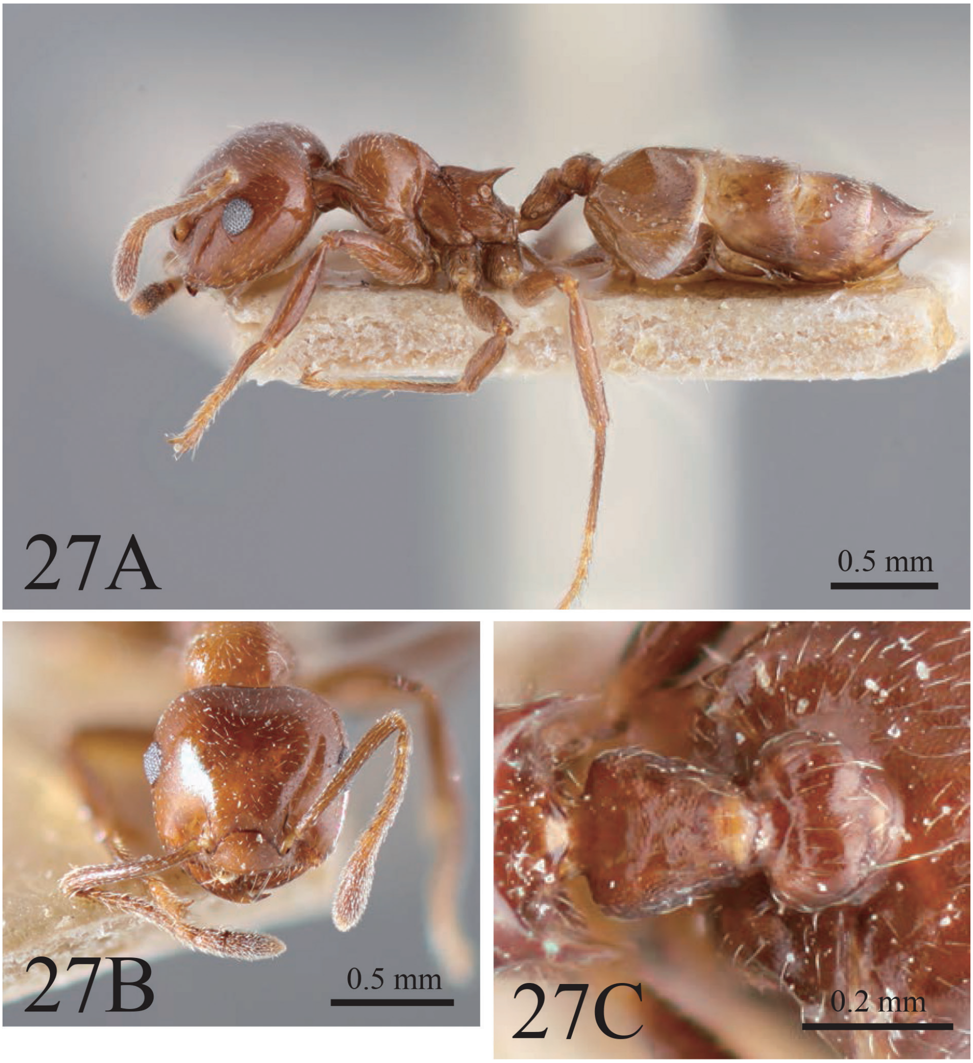


Figure 27. *Crematogaster butteli* [Soengei, Bamban, Sumatra, Indonesia]. **A** Lateral view of body **B** Full face view **C** Dorsal view of petiole and postpetiole.

median portion, mixed with some shorter setae on sides. No erect setae on pronotal shoulder. Posterolateral tubercle with some appressed setae. Ventral surface of petiole with appressed setae. Postpetiole with one pair of longer erect setae posteriorly. Fourth abdominal tergite with appressed setae.

Body color reddish brown.

Distribution. This species is known only from the type locality in Sumatra.

Comments. This species is similar to *C. tumidula* but can be distiguished in having angulate anterolateral corners of the petiole .

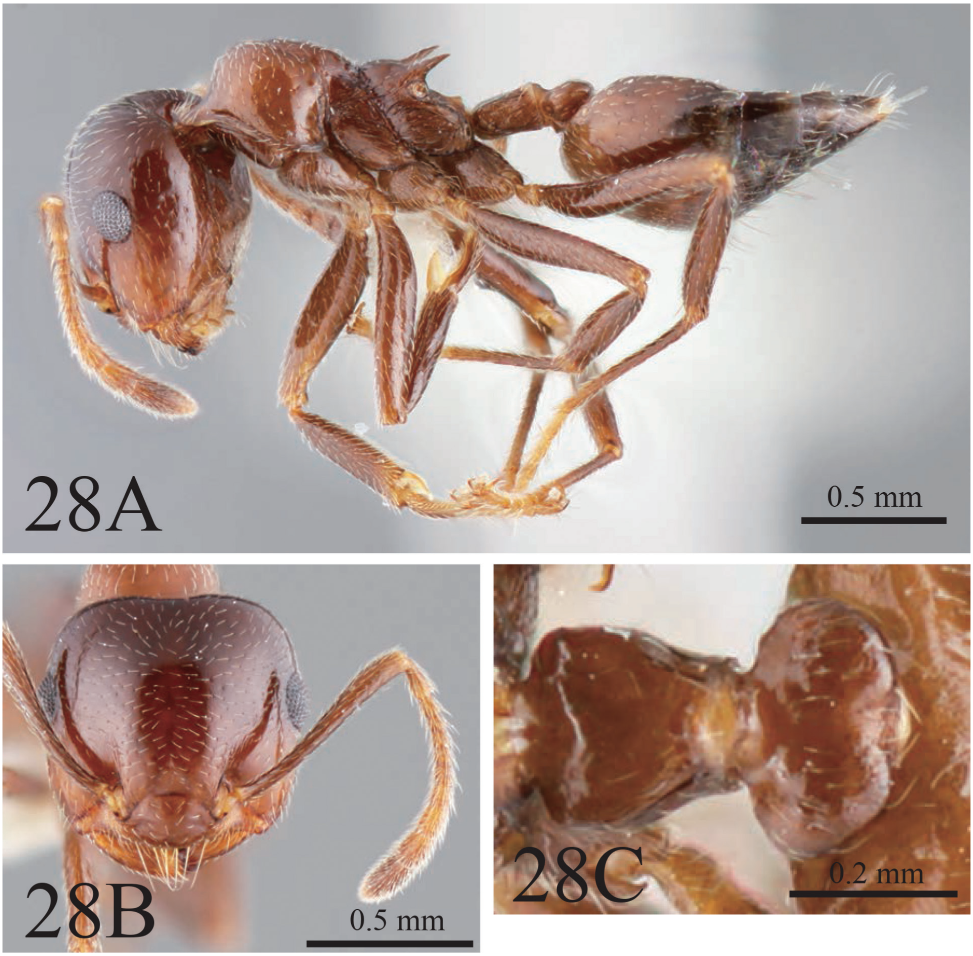


Figure 28. *Crematogaster daisyi* [Tasek Merimbun, Brunei]. **A** Lateral view of body **B** Full face view **C** Dorsal view of petiole and postpetiole.

Crematogaster daisyi Forel

Fig. 28

Crematogaster (*Oxygyne*) *daisyi* Forel, 1901: 376. Type locality: Malaysia, Sarawak, Borneo. Combination in *C.* (*Crematogaster*) by Blaimer, 2012b: 55.

Type material examined. *Crematogaster* (*Oxygyne*) *daisyi*: lectotype worker (bottom specimen of three on one pin) by present designation and five paralectotype workers from Malaysia, Sarawak, Borneo (*Haviland*) (MHNG, examined); three syntype workers from Malaysia, Sarawak (NHMW, examined); three syntype workers from Malaysia, Sarawak (*Haviland*) (NHMB, examined).

Non-type material examined. MALAYSIA: 1 worker, Lambir National Park, Miri, Sarawak, Borneo, 2.i.1998, (*Sk. Yamane*); **BRUNEI**: 1 worker, Tasek Merimbun, 11.ii.1999 (Eg99-BOR-011) (*K. Eguchi*); 1 worker, Tasek Merimbun, 17.ii.1999 (Eg99-BOR-155) (*K. Eguchi*).

Measurements and indices. (workers, n = 6). HW 0.79-0.88; HL 0.74-0.83; CI 101-107; SL 0.68-0.76; SI 86-90; EL 0.17-0.18; PW 0.49-0.54; WL 0.91-0.97; PSL 0.11-0.15; PtL 0.22-0.24; PtW 0.22-0.26; PtH 0.13-0.15; PpL 0.15-0.17; PpW 0.27-0.33; PtHI 59-68; PtWI 100-130; PpWI 169-200; WI 107-136.

General description of worker. Head appearing subquadratic in front view. Mandible weakly striate, with four teeth, apical and subapical teeth large, basal two teeth smaller. Scape exceeding posterior corner of head, with appressed setae, each of which is as long as width of scape. Compound eye large and slightly projecting beyond lateral margin of head in full face view.

Ventrolateral katepisternal ridge indistinct posteriorly. Propodeal spine long and stout; length greater than spiracle, directed upward, dorsum higher than anterior propodeum in lateral view. Propodeal spiracle large, touching to propodeal declivity in lateral view, directed laterally.

In dorsal view, shape of petiole scoop with convex side, longer than broad. Petiole with subparallel side on anterior half in dorsal view. Petiolar spiracle large, as large as half of propodeal spiracle, directed downward. Postpetiole bilobed with longitudinal median sulcus. Postpetiole wider than petiole in dorsal view.

Integument essentially smooth and shiny. Clypeus smooth and shiny without rugulae. Malar regions generally smooth. Dorsal surface of promesonotum smooth and shiny. Lateral surface of pronotum smooth and shiny. Mesopleuron and lateral propodeum generally shiny, but with feable rugulae. Dorsal surface of propodeum smooth and shiny.

Erect pilosity almost absent. Dorsum of head, clypeus and mesosoma with short and appressed setae sparsely. Clypeus with one pair of longer setae on anteriormost portion, directed medially. Anterior clypeal margin with two pairs of longer setae, mixed with some shorter setae on sides. No erect setae on pronotal shoulder. Posterolateral tubercle with some decumbent to appressed shorter setae. Ventral surface of petiole with appressed setae. Postpetiole with some shorter setae posteriorly. Fourth abdominal tergite with appressed setae.

Body color reddish brown.

Distribution. This species is only known from Malaysia (Borneo).

Comments. This species is similar to *C. sikkimensis*, but differs in having the spiracles on the petiole located on the lower position in lateral view.

***Crematogaster dalyi* Forel**

Fig. 29

Crematogaster (*Oxygyne*) *dalyi* Forel, 1902: 201. Type locality: India, Coonoor. Combination in *C.* (*Crematogaster*) by Blaimer, 2012b: 55.

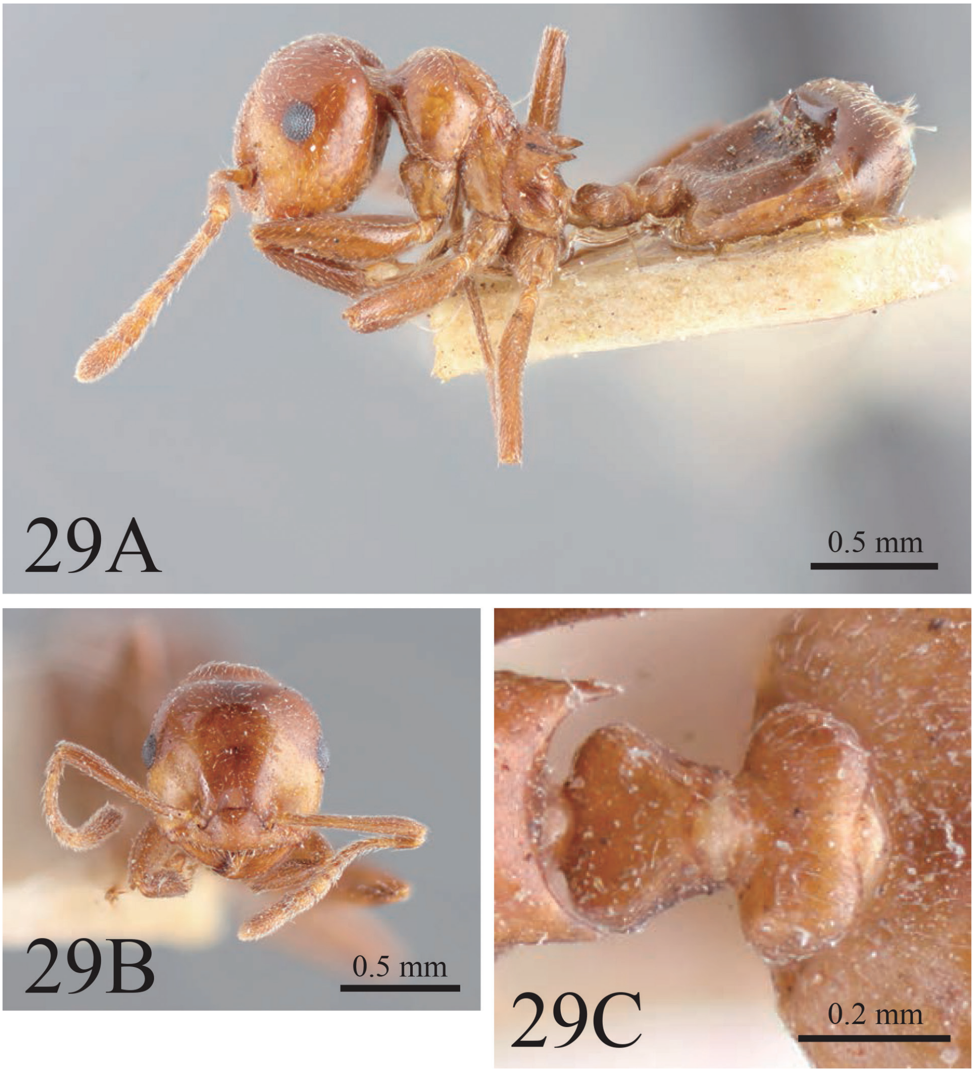


Figure 29. *Crematogaster dalyi* [Coonoor, India]. **A** Lateral view of body **B** Full face view **C** Dorsal view of petiole and postpetiole.

Type material examined. *Crematogaster* (*Oxygyne*) *dalyi*: lectotype worker (middle specimen of three on one pin) by present designation and two paralectotype workers from India, Coonoor (*Daly*) (MHNG, examined).

Measurements and indices. (type workers, n = 3) HW 0.86-0.92; HL 0.85-0.87; CI 99-108; SL 0.74-0.75; SI 80-87; EL 0.16-0.18; PW 0.55-0.58; WL 1.02-1.03; PSL 0.1-0.12; PtL 0.25-0.26; PtW 0.30-0.33; PtH 0.16-0.17; PpL 0.17-0.18; PpW 0.37-0.39; PtHI 64-65; PtWI 115-132; PpWI 217-229; WI 118-126.

General description of worker. Head appearing subquadratic in front view. Mandible weakly striate, with four teeth, apical and subapical teeth large, basal two

teeth smaller. Scape exceeding posterior corner of head, with dense appressed setae, each of which is less than width of scape. Compound eye slightly projecting beyond lateral margin of head in full face view.

Ventrolateral katepisternal ridge indistinct posteriorly. Propodeal spine short and stout; length longer than spiracle, directed upward; dorsum as high as anterior propodeum in lateral view. Propodeal spiracle situated close to propodeal declivity in lateral view, directed laterally.

In dorsal view, shape of petiole scoop, longer than broad. Petiolar spiracle big, as wide as half of propodeal spiracle in size. Postpetiolar spiracle big and distinct, located anteriorly on lateral surface. In dorsal view, postpetiole broader than long, strongly bilobed but without longitudinal median sulcus. Postpetiole distinctly wider than petiole in dorsal view.

Integument essentially smooth and shiny. Clypeus generally smooth and shiny, but with feable rugulae. Malar region smooth and shiny. Dorsal surface of promesonotum smooth and shiny. Lateral surface of pronotum generally smooth and shiny, but with longitudinal rugulae on anterior portion. Mesopleuron and lateral propodeum generally smooth and shiny, but with weak longitudinal rugulae. Dorsal surface of propodeum smooth and shiny.

Erect pilosity absent. Dorsum of head, clypeus and mesosoma with short and appressed setae. Clypeus with one pair of longer setae on anteriormost portion, directed medially. Anterior clypeal margin with one single longer setae and two pairs of longer setae on the median portion, mixed with some shorter setae on sides. No erect seate on pronotal shoulders. Posterolateral tubercle without appressed setae. Ventral surface of petiole with appressed setae. Postpetiole without setae posteriorly. Fourth abdominal tergite with short and appressed setae.

Body color brown.

Distribution. This species is only known from the type locality in India.

Comments. This species is similar to *C. sikkimensis*, but differs in having short propodeal spines.

Crematogaster ebenina Forel

Fig. 30

Crematogaster (*Oxygyne*) *ebenina* Forel, 1902: 199. Type locality: India, Thana, Kanara, Poona, Belgaum. Combination in *C.* (*Crematogaster*) by Blaimer, 2012b: 55.

Crematogaster ebenina var. *corax* Forel, 1902: 200. Type locality: Myanmar, Moulmain. **syn. n.**

Type material examined. *Crematogaster* (*Oxygyne*) *ebenina*: lectotype worker (bottom specimen of three on one pin) by present designation and five paralectotype workers from India, Kanara (*Wroughton*) (MHNG, examined); one syntype worker from India, Poona (*Wroughton*) (NHMW, examined). *Crematogaster ebenina* var. *corax*: six syntype workers from Myanmar, Moulmain (*Hodgson*) (MHNG, examined).

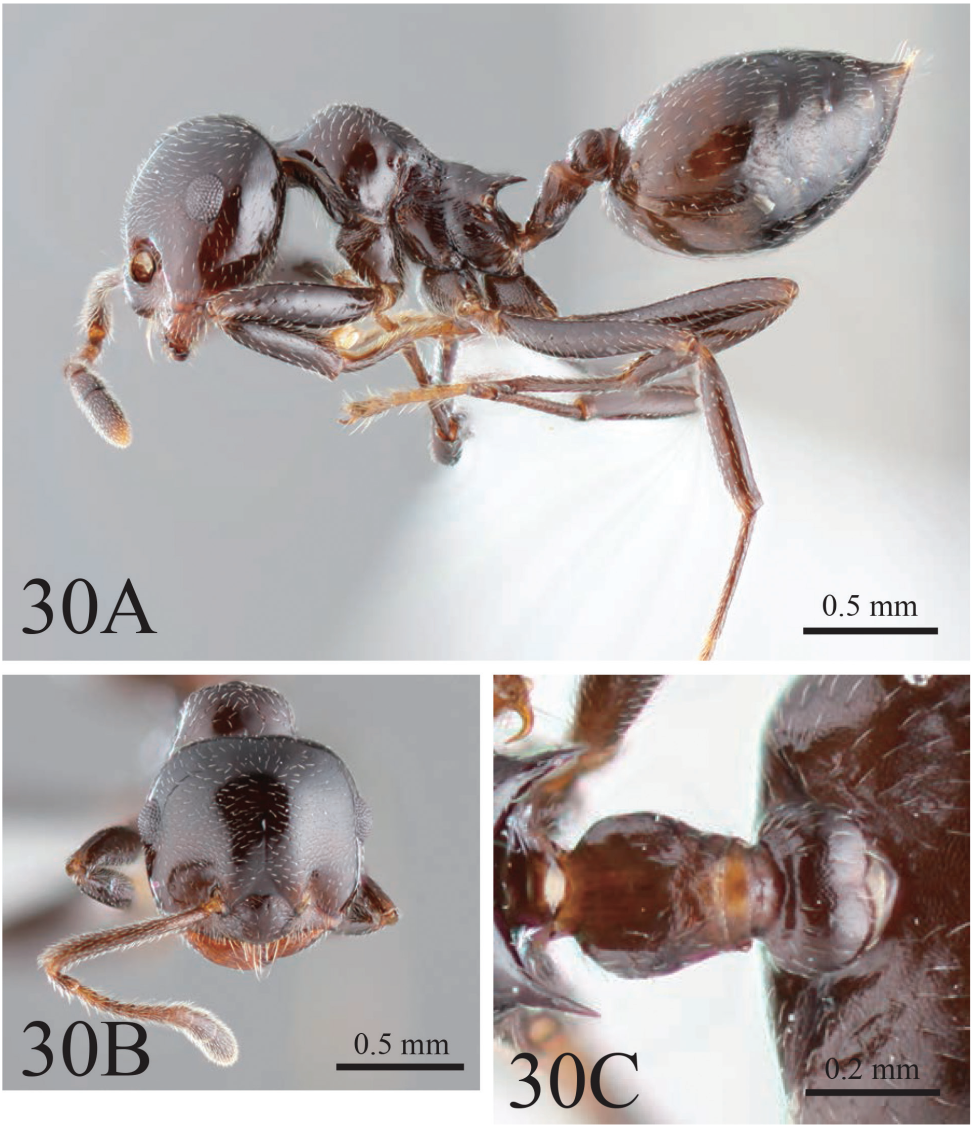


Figure 30. *Crematogaster ebenina* [Gandhi National Park, India]. **A** Lateral view of body **B** Full face view **C** Dorsal view of petiole and postpetiole.

Non-type material examined. INDIA: 4 workers, Mumbai, 16.x.2007 (*S. Hosoishi*).

Measurements and indices. (workers, n = 4) HW 0.85-0.94; HL 0.81-0.86; CI 105-109; SL 0.69-0.76; SI 78-82; EL 0.18-0.19; PW 0.51-0.56; WL 0.98-1.05; PSL 0.11-0.13; PtL 0.24-0.26; PtW 0.24-0.27; PtH 0.16-0.17; PpL 0.14-0.16; PpW 0.24-0.26; PtHI 64-67; PtWI 100-113; PpWI 162-173; WI 96-100.

General description of worker. Head appearing subquadratic in front view. Mandible weakly striate, with four teeth, apical and subapical teeth large, basal two

teeth smaller. Scape exceeding posterior corner of head, with appressed setae, each of which is less than or as long as width of scape in length. Compound eye large and slightly projecting beyond lateral margin of head in full face view.

Ventrolateral katepisternal ridge indistinct. Propodeal spine long and stout; length equal to slightly greater than diameter of propodeal spiracle, directed upward, dorsum as high as anterior propodeum. Propodeal spiracle large and situated close to propodeal declivity in lateral view, directed posterolaterally.

In dorsal view, shape of petiole scoop with convex side, longer than broad. Anterolateral corner of petiole undeveloped, tapering anteriorly. Petiolar spiracle big, as large as half of propodeal spiracle in diameter. Postpetiole weakly bilobed but without longitudinal median sulcus. Petiole slightly wider than, or as wide as postpetiole in dorsal view.

Integument essentially smooth and shiny. Clypeus generally smooth and shiny, but with feable rugulae. Malar region smooth and shiny without rugulae. Dorsal surface of promesonotum smooth and shiny. Lateral surface of pronotum smooth and shiny. Mesopleuron and lateral propodeum generally shiny, but with feable rugulae. Dorsal surface of propodeum smooth and shiny.

Erect pilosity almost absent. Dorsum of head, clypeus and mesosoma with short and appressed sparse setae. Clypeus without longer setae on anteriormost portion. Anterior clypeal margin with one single longer setae and two pairs of longer setae, mixed with some shorter setae on the side. No erect setae on pronotal shoulder. Posterolateral tubercle with some decumbent to appressed shorter setae. Ventral surface of petiole with appressed setae. Postpetiole with some shorter setae posteriorly. Fourth abdominal tergite with appressed setae.

Body color reddish brown.

Distribution. This species is distributed in India and Myanmar.

Comments. This species is unique in Asian *C. ranavalonae*-group in having a slender petiole. This species is similar to *C. tumidula*, but distinguished in having the petiole without anterolateral corners.

The syntype workers of *C. ebenina corax* agree well with syntype workers of *C. ebenina*. Thus I treated *C. ebenina corax* as a junior synonym of *C. ebenina*.

Crematogaster hashimi sp. n.

http://zoobank.org/520D115A-F486-43F2-8520-E9114103C9EF
Fig. 31

Type material examined. Holotype. MALAYSIA: Worker from Ulu Gombak, Selangor [N3°19', E101°45'] 15.iii.2010, leg. S. Hosoishi, SH10-Mal-67 (FRIM: KUMANT012). **Paratypes.** Seven workers, same data as holotype (CASC: KUMAN013; KUM: KUMANT014; BMNH: KUMANT015, MCZC: KUMANT016; MHNG: KUMANT017; MBBJ: KUMANT018; THNHM: KUMANT019).

Non-type material examined. THAILAND: Maeklong, 29.xi.2003, leg. Watana Sakchoowong, TUS 15min, WS3 (KUM).

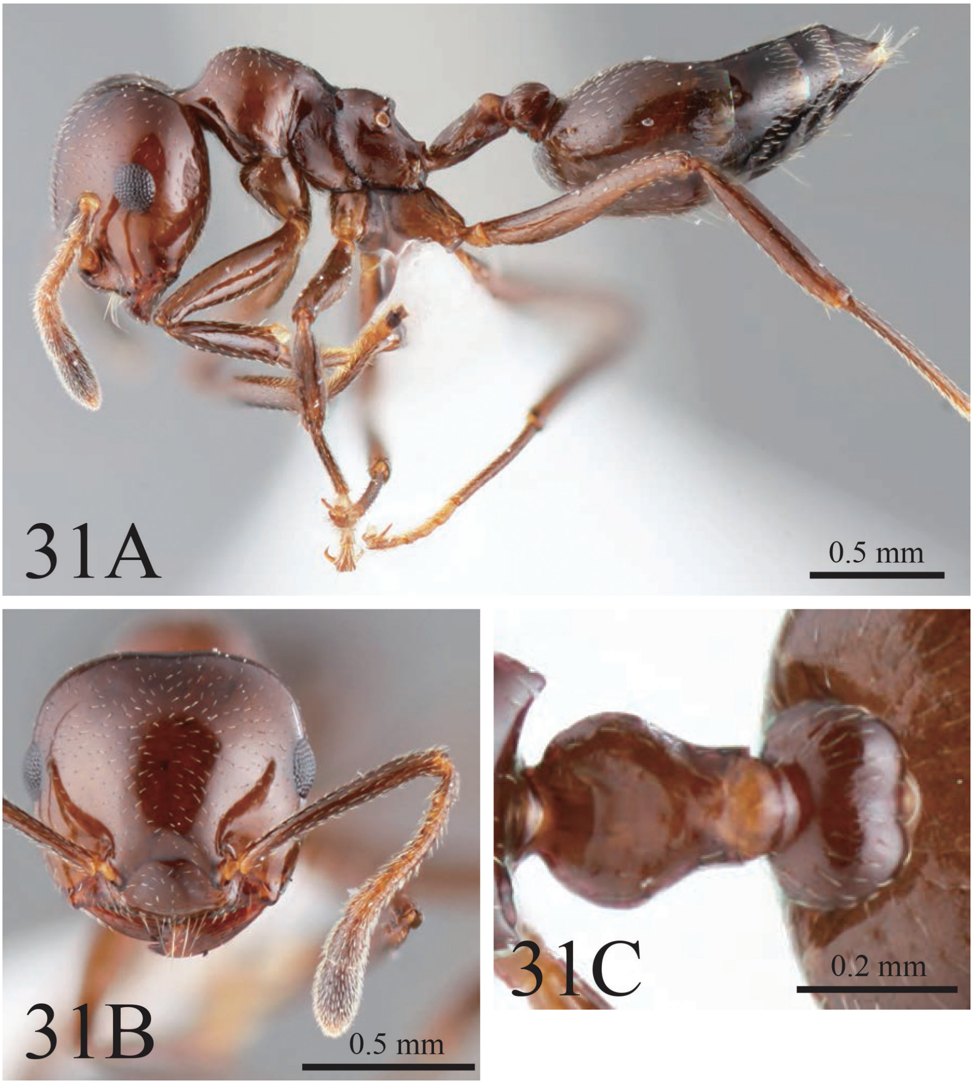


Figure 31. *Crematogaster hashimi* [Ulu Gombak, Selangor, W. Malaysia]. **A** Lateral view of body **B** Full face view **C** Dorsal view of petiole and postpetiole.

Measurements and indices. (type and non-type workers, n = 12). HW 0.80-0.88; HL 0.77-0.82; CI 100-109; SL 0.67-0.75; SI 82-89; EL 0.16-0.18; PW 0.48-0.56; WL 0.87-0.98; PSL 0.03-0.06; PtL 0.23-0.26; PtW 0.22-0.26; PtH 0.13-0.15; PpL 0.15-0.17; PpW 0.24-0.28; PtHI 54-61; PtWI 96-109; PpWI 153-167; WI 96-108.

General description of worker. Head appearing subquadratic in front view. Mandible weakly striate, with four teeth, apical and subapical teeth large, basal two teeth smaller. Scape exceeding posterior corner of head, with appressed setae, each of which is less than width of scape in length. Compound eye large and slightly projecting beyond lateral margin of head in full face view.

Ventrolateral katepisternal ridge indistinct posteriorly. Propodeal spine undeveloped, but as small tubercule in some workers; length distinctly shorter than propodeal spiracle. Propodeal spiracle large and circular, situated close to propodeal declivity in lateral view, directed laterally.

In dorsal view, shape of petiole scoop with convex side, longer than broad. Anterolateral corner of petiole rounded. Petiolar spiracle small, less than half of propodeal spiracle in size. In dorsal view, postpetiole slightly broader than long. Postpetiole weakly bilobed, but without longitudinal median sulcus. Postpetiole as wide as petiole in dorsal view.

Integument essentially smooth and shiny. Clypeus smooth and shiny without rugulae. Malar region smooth and shiny. Dorsal surface of promesonotum smooth and shiny. Lateral surface of pronotum smooth and shiny. Mesopleuron smooth and shiny. Dorsal surface of propodeum smooth and shiny. Lateral propodeum smooth and shiny.

Erect pilosity almost absent. Dorsum of head, clypeus, mesosoma and fourth abdominal tergite with short and appressed sparse setae . Clypeus without longer setae on anteriormost portion. Anterior clypeal margin with two or three pairs of longer setae on median portion, with some shorter setae on side. No erect setae on pronotal shoulder. Posterolateral tubercle with some appressed setae. Ventral surface of petiole without setae. Postpetiole without longer erect setae posteriorly. Fourth abdominal tergite with appressed setae.

Body color reddish brown.

Etymology. The species is dedicated to Dr. Rosli Hashim, University of Malaya, who helped with field surveys in Malaysia.

Distribution. This species is distributed in Thailand and Malaysia (Peninsula).

Comments. This species is similar to *C. imperfecta*, but differs in having circular propodeal spiracles and broader petiole.

This species inhabits well-developed forests, and forage on trees.

Crematogaster imperfecta sp. n.

http://zoobank.org/B9AB38B4-BF0A-44FF-BA07-7E8CFE33FEBB
Fig. 32

Type material examined. Holotype. MALAYSIA: Worker from Sg. Kalang, 800–1000 m alt., Sabah, Borneo, 23.ii.1997, leg. Sk. Yamane (ITBC: KUMANT020). **Paratypes.** Three workers, same data as holotype (CASC: KUMANT021; KUM: KUMANT022; SKYC: KUMANT023). Two workers from MALAYSIA: Tower Region, Lambir NP, Miri, Sarawak, 26.i.1983, leg. Sk. Yamane, Canopy Ecol. (BMNH: KUMANT024; THNHM: KUMANT025).

Measurements and indices. (type workers, n = 6). HW 0.77-0.87; HL 0.72-0.81; CI 103-108; SL 0.63-0.71; SI 78-83; EL 0.16-0.18; PW 0.48-0.54; WL 0.86-0.95; PSL 0.02-0.04; PtL 0.24-0.26; PtW 0.21-0.23; PtH 0.13-0.15; PpL 0.14-0.16; PpW 0.22-0.26; PtHI 54-60; PtWI 88-92; PpWI 156-167; WI 104-114

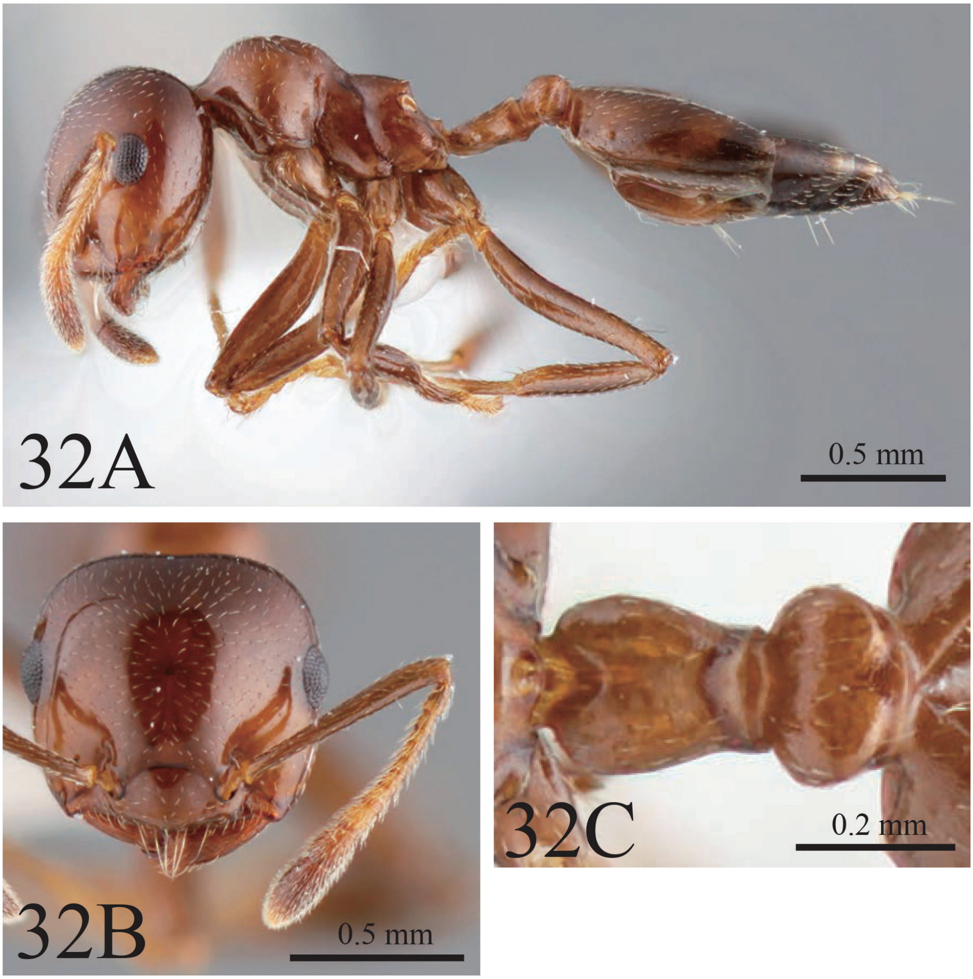


Figure 32. *Crematogaster imperfecta* [Sg. Kalang, Tenom, Sabah, Borneo, E. Malaysia]. **A** Lateral view of body **B** Full face view **C** Dorsal view of petiole and postpetiole.

General description of worker. Head appearing subquadratic in front view. Mandible weakly striate, with four teeth, apical and subapical teeth large, basal two teeth smaller. Scape exceeding posterior corner of head, with appressed setae, each of which is less than width of scape in length. Compound eye large and slightly projecting beyond lateral margin of head in full face view.

Ventrolateral katepisternal ridge indistinct posteriorly. Propodeal spine undeveloped, but as small tubercule in some workers; length distinctly shorter than propodeal spiracle. Propodeal spiracle large, situated close to the propodeal declivity in lateral view, directed laterally.

In dorsal view, shape of petiole scoop with convex side, longer than broad. Anterolateral corner of petiole developed. Petiolar spiracle small, less than half of propodeal spiracle in size. In dorsal view, postpetiole slightly broader than long. Postpetiole weakly bilobed, but without longitudinal median sulcus. Postpetiole as wide as petiole in dorsal view.

Integument essentially smooth and shiny. Clypeus smooth and shiny without rugulae. Malar region smooth and shiny. Dorsal surface of promesonotum smooth and shiny. Lateral surface of pronotum smooth and shiny. Mesopleuron smooth and shiny. Dorsal surface of propodeum smooth and shiny. Lateral propodeum smooth and shiny.

Erect pilosity almost absent. Dorsum of head, clypeus, mesosoma and fourth abdominal tergite with short and appressed sparse setae. Clypeus with longer setae on anteriormost portion, directed medially. Anterior clypeal margin with two pairs of longer setae on median portion, with some shorter setae on side. No erect setae on pronotal shoulder. Posterolateral tubercle with some appressed setae. Ventral surface of petiole without setae. Postpetiole without longer erect setae posteriorly. Fourth abdominal tergite with appressed setae.

Body color reddish brown.

Etymology. The specific name refers to the undeveloped propodeal spines.

Distribution. This species is known from Malaysia (Borneo).

Comments. This species is very similar to *C. hashimi*, but differs in having elliptical propodeal spiracles and a slender petiole.

Crematogaster pia Forel

Fig. 33

Crematogaster tumidula subsp. *pia* Forel, 1911: 384. Type locality: Malaysia, Berhentian Tingi, Nigri Sembilan, Malacca. Combination in *C.* (*Acrocoelia*), and raised to species by Emery, 1922: 151; in *C.* (*Crematogaster*) by Blaimer, 2012b: 55.

Type material examined. *Crematogaster tumidula* subsp. *pia*: lectotype worker (top specimen of three on one pin) by present designation and five paralectotype workers from Malaysia, Berhentian Tingi, Nigri Sembilan, Malacca (*R. Matrin*) (MHNG, examined); five syntype workers from Malaysia, Berhentian Tingi, Nigri Sembilan, Malacca (*R. Matrin*) (NHMB, examined).

Non-type material examined. THAILAND: 4 workers, Maegar, Phayao, 21.iii.1990 (*No collector's name*); 6 workers, Thachai Sukhothai, 1.iii.1991 (*No collector's name*); 21 workers, Ban Krang Camp, Kaeng Krachan National Park, Phet Buri [N12°47', E99°27'] 23.xii.2012 (SH12-Tha-01) (*S. Hosoishi*); 14 workers, Evergreen For., Khlong Naka WS, Ranong Prov., S. Thailand, 12.viii.2009, (WJT09-TH2045) (*W. Jaitrong*).

Measurements and indices. (workers, n = 11). HW 0.90-0.96; HL 0.88-0.92; CI 102-108; SL 0.79-0.87; SI 83-94; EL 0.18-0.21; PW 0.54-0.59; WL 1.05-1.13; PSL 0.14-0.17; PtL 0.25-0.27; PtW 0.25-0.30; PtH 0.16-0.18; PpL 0.15-0.19; PpW 0.28-0.31; PtHI 59-69; PtWI 96-115; PpWI 158-187; WI 103-115.

Figure 33. *Crematogaster pia* [Ban Krang Camp, Kaeng Krachang National Park, Phet Buri, Thailand]. **A** Lateral view of body **B** Full face view **C** Dorsal view of petiole and postpetiole.

General description of worker. Head appearing subquadratic in front view. Mandible weakly striate, with four teeth, apical and subapincal teeth large, basal two teeth smaller. Scape exceeding posterior corner of head, with appressed setae, each of which is as long as width of scape in length. Compound eye large and slightly projecting beyond lateral margin of head in full face view.

Ventrolateral katepisternal ridge indistinct posteriorly. Propodeal spine long and stout; length longer than spiracle, dorsum as high as anterior propodeum in lateral view; basal width larger than spiracle in diameter. Propodeal spiracle large, situated close to propodeal declivity in lateral view, directed laterally.

In dorsal view, shape of petiole scoop with convex side, as broad as long. Anterolateral corner of petiole angulate. Petiolar spiracle big, as wide as half of propodeal spiracle in diameter, directed laterally. In dorsal view, postpetiole broader than long, bilobed but without longitudinal median sulcus. Postpetiole slightly wider than petiole in dorsal view.

Integument essentially smooth and shiny. Clypeus smooth and shiny without rugulae. Malar region smooth and shiny. Dorsal surface of promesonotum smooth and shiny. Lateral surface of pronotum smooth and shiny. Mesopleuron and lateral propodeum generally shiny, but with feable rugulae. Dorsal surface of propodeum smooth and shiny; anterior dorsum with feable rugulae.

Erect pilosity almost absent. Dorsum of head, clypeus and mesosoma with short and appressed sparse setae. Clypeus with one pair of longer setae on anteriormost portion, directed medially. Anterior clypeal margin with two or three pairs of longer setae on median portion, mixed with some shorter setae on side. No erect setae on pronotal shoulder. Posterolateral tubercle with some decumbent to appressed shorter setae. Ventral surface of petiole with appressed setae. Postpetiole with some shorter setae posteriorly. Fourth abdominal tergite with appressed setae.

Body color reddish brown to brownish.

Distribution. This species is distributed in Thailand and Malaysia (Peninsula).

Comments. This species is similar to *C. butteli* and *C. tumidula*, but differs from *C. butteli* in having an anterolaterally developed petiole, and from *C. tumidula* in having long propodeal spines.

This species inhabits well-developed forests, make a carton nest and forage on trees.

Crematogaster sikkimensis Forel, stat. n.

Fig. 34

Crematogaster (*Oxygyne*) *dalyi* var. *sikkimensis* Forel, 1904: 24. Type locality: India, Sikkim.

Type material examined. *Crematogaster* (*Oxygyne*) *dalyi* var. *sikkimensis*: lectotype worker (top specimen of three on one pin) by present designation and three paralectotype workers from India, Sikkim (*Möller*) (MHNG, examined).

Measurement and indices. (type workers, n = 4). HW 0.82-0.91; HL 0.80-0.88; CI 102-103; SL 0.72-0.78; SI 83-89; EL 0.17-0.19; PW 0.50-0.56; WL 0.92-1.07; PSL 0.14-0.17; PtL 0.25-0.26; PtW 0.27-0.30; PtH 0.14-0.17; PpL 0.14-0.17; PpW 0.33-0.36; PtHI 60-65; PtWI 108-116; PpWI 212-236; WI 120-130.

General description of worker. Head appearing subquadratic in front view. Mandible weakly striate, with four teeth, apical and subapincal teeth large, basal two teeth smaller. Scape exceeding posterior corner of head, with appressed setae, each of

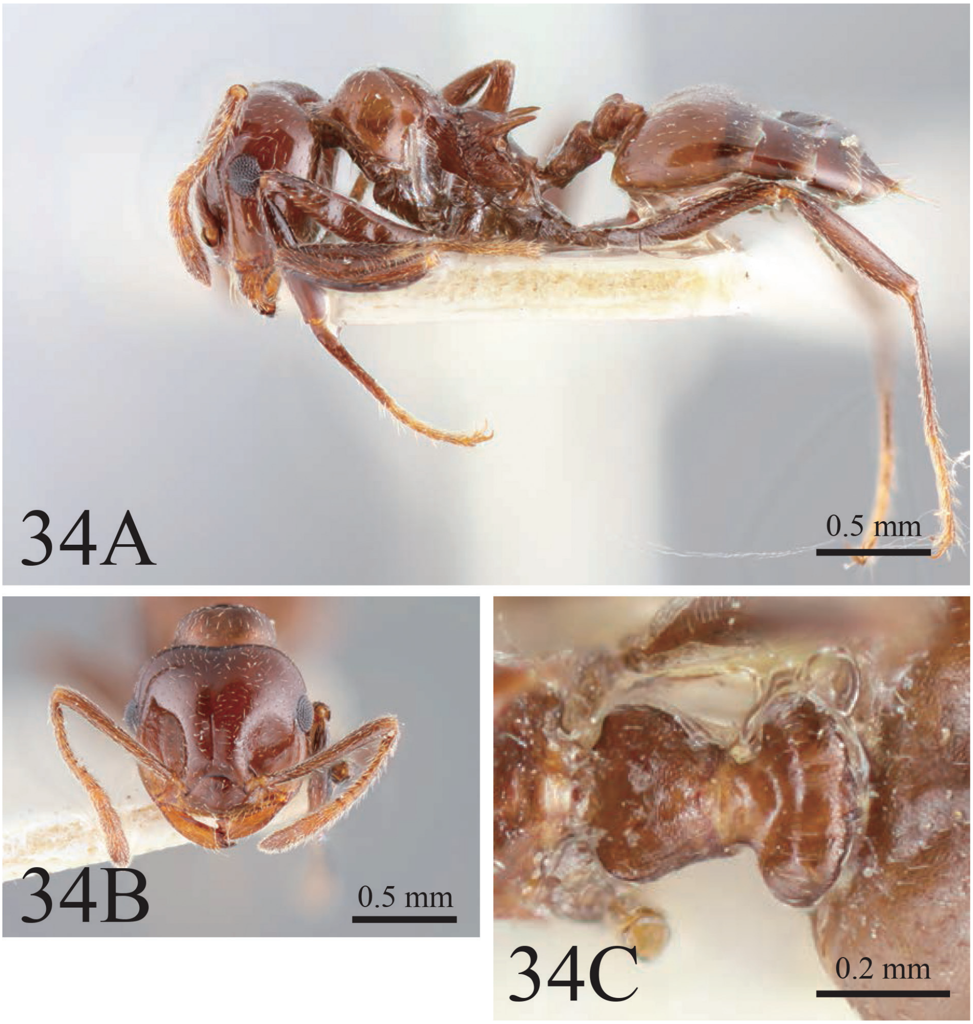


Figure 34. *Crematogaster sikkimensis* [Sikkim, India]. **A** Lateral view of body **B** Full face view **C** Dorsal view of petiole and postpetiole.

which is as long as width of scape in length. Compound eye large and slightly projecting beyond lateral margin of head in full face view.

Ventrolateral katepisternal ridge appearing indistinct posteriorly. Propodeal spine long and slender; length longer than spiracle, directed upward; dorsum higher than anterior propodeum. Propodeal spiracle large, situated close to propodeal declivity in lateral view, directed laterally.

In dorsal view, shape of petiole scoop with convex side, as long as broad. Petiolar spiracle big, as wide as half of propodeal spiracle in diameter. In dorsal view, postpetiole broader than long, strongly bilobed laterally, but without longitudinal median sulcus. Postpetiole wider than petiole in dorsal view.

Integument essentially smooth and shiny. Clypeus smooth and shiny without rugulae. Malar region with feable rugulae. Dorsal surface of promesonotum smooth and shiny. Lateral surface of pronotum smooth and shiny. Mesopleuron and lateral propodeum generally shiny, but with longitudinal rugulae. Dorsal surface of propodeum smooth and shiny.

Erect pilosity almost absent. Dorsum of head, clypeus and mesosoma with short and appressed sparse setae. Clypeus with one pair of longer setae on anteriormost portion, directed medially. Anterior clypeal margin with two pairs of longer setae, mixed with some shorter setae on side. No erect setae on pronotal shoulder. Posterolateral tubercle with some decumbent to appressed shorter setae. Ventral surface of petiole with appressed setae. Postpetiole with some shorter setae posteriorly. Fourth abdominal tergite with appressed setae.

Body color brown.

Distribution. This species is only known from the type locality in India.

Comments. This species is similar to *C. daisyi* and *C. dalyi*, but differs from *C. daisyi* in having the spiracles on the petiole located on the middle position in lateral view, and from *C. dalyi* in having long propodeal spines.

Top specimen of three on one pin was designated as lectotype worker here, but it is noted that the body of the middle specimen was lost from the card point.

Crematogaster tumidula Emery

Fig. 35

Crematogaster tumidula Emery, 1900: 689, fig. 8. Type locality: Indonesia, Pangherang-Pisang, Sumatra. Combination in *C.* (*Physocrema*) by Emery, 1922: 140; Donisthorpe 1941: 226; in *C.* (*Oxygyne*) by Hosoishi & Ogata, 2009: 33; in *C.* (*Crematogaster*) by Blaimer, 2012b: 55.

Type material examined. *Crematogaster tumidula*: lectotype worker by present designation and one paralectotype worker from Indonesia, Pangherang-Pisang, Sumatra (*E. Modigliani*) (MCSN) [examined].

Non-type material examined. MALAYSIA: 2 workers, Old Tower R., Lambir N. P., Miri, Sarawak, 30.xii.1997, (SR97-SKY-106) (*Sk. Yamane*); 3 workers, Bt. Pantu, Lambir N. P., Miri, Sarawak, 13.viii.1995, (*Sk. Yamane*); 1 worker, Tower Region, Lambir N. P., Miri, Sarawak, 21.i.1993, (*Sk. Yamane*); **INDONESIA**: 1 worker, Sangkimah, Kutai N. P., Kalimantan, 17.ix.1993, (*Sk. Yamane*).

Measurements and indices. (workers, n = 10). HW 0.73-0.88; HL 0.72-0.86; CI 101-107; SL 0.60-0.77; SI 80-88; EL 0.15-0.19; PW 0.43-0.53; WL 0.80-0.97; PSL 0.08-0.12; PtL 0.20-0.26; PtW 0.23-0.27; PtH 0.14-0.18; PpL 0.14-0.22; PpW 0.20-0.28; PtHI 54-68; PtWI 89-113; PpWI 125-178; WI 88-118.

General description of worker. Head appearing subquadratic in front view. Mandible weakly striate, with four teeth, apical and subapical teeth large, basal two

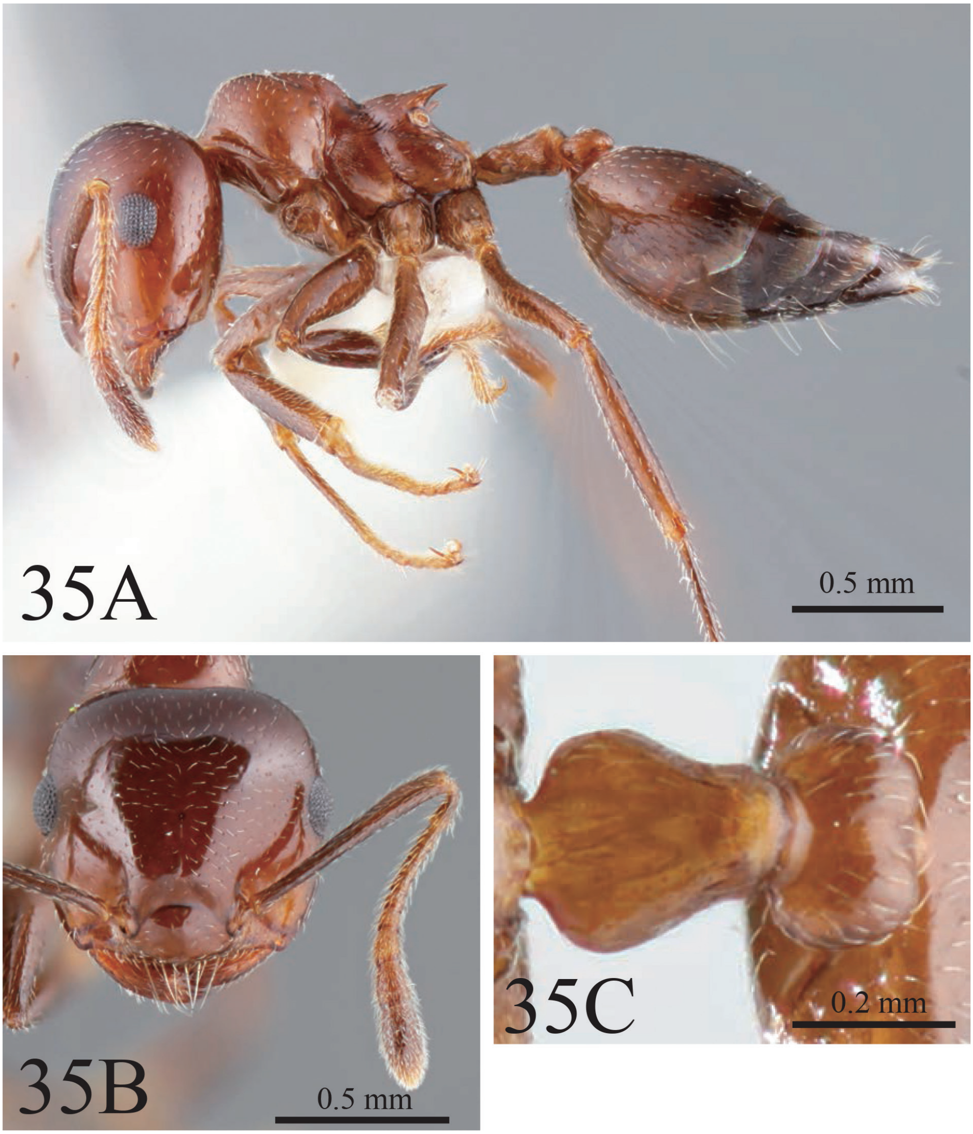


Figure 35. *Crematogaster tumidula* [Lambir National Park, Sarawak, Borneo, E. Malaysia]. **A** Lateral view of body **B** Full face view **C** Dorsal view of petiole and postpetiole.

teeth smaller. Scape exceeding posterior corner of head, with appressed setae, each of which is less than width of scape in length. Compound eye large and slightly projecting beyond lateral margin of head in full face view.

Ventrolateral katepisternal ridge indistinct posteriorly. Propodeal spine short and stout; length as long as spiracle, directed posteriorly, dorsum as high as anterior propodeum; basal width smaller than spiracles in diameter. Propodeal spiracle large, situated close to propodeal declivity in lateral view, directed laterally or posterolaterally.

In dorsal view, shape of petiole scoop with convex side, longer than broad. Anterolateral corner of petiole developed. Petiolar spiracle as large as half of propodeal spiracle in diameter, directed laterally. Postpetiole bilobed but without longitudinal median sulcus. Postpetiole as wide as petiole in dorsal view.

Integument essentially smooth and shiny. Clypeus smooth and shiny without rugulae. Malar region smooth and shiny. Dorsal surface of promesonotum smooth and shiny. Lateral surface of pronotum smooth and shiny. Mesopleuron and lateral propodeum generally smooth, but with feable rugulae. Dorsal surface of propodeum smooth and shiny; anterior dorsum smooth without rugulae.

Erect pilosity almost absent. Dorsum of head, clypeus and mesosoma with short and appressed sparse setae. Clypeus with one pair of longer setae on anteriormost portion, directed medially. Anterior clypeal margin with two pairs of longer setae on median portion, mixed with some shorter setae on side. No erect setae on pronotal shoulder. Posterolateral tubercle with some appressed shorter setae. Ventral surface of petiole with appressed setae. Postpetiole with some appressed setae. Fourth abdominal tergite with appressed setae.

Body color reddish brown.

Distribution. This species is known from Malaysia (Borneo) and Indonesia (Kalimantan, Sumatra).

Comments. This species is similar to *C. ebenina*, but differs in having developed anterolateral corners of the petiole. It is also similar to *C. pia*, but differs in having short and stout propodeal spines and the basal portion with smooth surface.

***Crematogaster vandermeermohri* Menozzi**

Crematogaster (*Paracrema*) *vandermeermohri* Menozzi, 1930: 1, fig. 1. Type locality: Indonesia, Toetoepan, Sumatra. Combination in *C.* (*Crematogaster*) by Blaimer, 2012b: 55.

Type material. *Crematogaster* (*Paracrema*) *vandermeermohri*: syntype worker from Indonesia, Toetoepan, Sumatra (probably in IEGG, not seen).

Comments. I have not been able to examine type-material of *C. vandermeermohri*. Judging from the original description and figure, this species is close to *C. hashimi* and *C. imperfecta*. Menozzi (1930) described the following features: (1) propodeal spines small and blunt, inflated near the base; (2) postpetiole slightly narrower than petiole in dorsal view. The two features are not found in the related species. The postpetiole is as wide as or wider than petiole in *C. hashimi* and *C. imperfecta*.

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References

Blaimer B (2012a) Untangling complex morphological variation: taxonomic revision of the subgenus *Crematogaster* (*Oxygyne*) in Madagascar, with insight into the evolution and biogeography of this enigmatic ant clade (Hymenoptera: Formicidae). Systematic Entomology 37: 240–260. doi: 10.1111/j.1365-3113.2011.00609.x

Blaimer B (2012b) A subgeneric revision of *Crematogaster* and discussion of regional species-groups (Hymenoptera: Formicidae). Zootaxa 3482: 47–67.

Blaimer B (2012c) Acrobat ants go global-Origin, evolution and systematics of the genus *Crematogaster* (Hymenoptera: Formicidae). Molecular Phylogenetics and Evolution 65: 421–436. doi: 10.1016/j.ympev.2012.06.028

Bolton B (1995) A New General Catalogue of the Ants of the World. Harvard University Press, Cambridge, Massachusetts, 504 pp.

Brandão CRF (2000) Major regional and type collections of ants (Formicidae) of the world and sources for the identification of ant species. In: Agosti D, Majer JD, Alonso LE, Schultz TR (Eds) Ants: Standard methods for measuring and monitoring biodiversity. Smithsonian Institution Press, Washington & London, 172–185.

Brown WL Jr (1973) A comparison of the Hylean and Congo-West African rain forest ant faunas. In: Meggers BJ, Ayensu ES, Duckworth WD (Eds) Tropical Forest Ecosystems in Africa and South America: a Comparative Review. Washington D.C., 161–185.

Donisthorpe H (1941) Description of a new species of *Crematogaster* Lund, subgenus *Physocrema* Forel, with a list of, and a key to, the known species of the subgenus. Entomologist 74: 225–227.

Emery C (1895) Voyage de M. E. Simon dans l'Afrique australe (janvier-avril 1893). Formicides. Annales de la Société Entomologique de France 64: 15–56.

Emery C (1900) Formiche raccolte da Elio Modigliani in Sumatra, Engano e Mentawei. Annali del Museo Civico di Storia Naturali di Genova (2) 20 [40]: 661–722.

Emery C (1922) Hymenoptera, Fam. Formicidae, subfam. Myrmicinae. In: Genera Insectorum. Fasc. 174B. Bruxelles, 95–206.

Forel A (1892) Nouvelles espèces de formicides de Madagascar. (Récoltées par M. Sikora.) Annales de la Société Entomologique de Belgique 36: 516–535.

Forel A (1901) Variétés myrmécologiques. Annales de la Société Entomologique de Belgique 45: 334–382.

Forel A (1902) Myrmicinae nouveaux de l'Inde et de Ceylan. Revue Suisse de Zoologie 10: 165–249.

Forel A (1904) Miscellanea myrmécologiques. Revue Suisse de Zoologie 12: 1–52.

Forel A (1910) Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Südafrika ausgeführt in den Jahren 1903–1905 von Dr. Leonard Schultze. Vierter Band. Systematik und Tiergeographie. D) Formicidae. Denkschriften der Medizinsch-Naturwissenschaftlichen Gesellschaft Jena 16: 1–30.

Forel A (1911) Fourmis nouvelles ou interessantes. Bulletin de la Société Vaudoise des Sciences Naturelles 47: 331–400.

Forel A (1913) Quelques fourmis des Indes, du Japon et d'Afrique. Revue Suisse de Zoologie 21: 659–673.

Forel A (1913) Wissenschaftliche Ergebnisse einer Forschungsreise nach Ostindien, ausgefuhrt im Auftrage der Kgl. Preuss. Akademie der Wissenschaften zu Berlin von H. v. Buttel-Reepen. 2. Ameisen aus Sumatra, Java, Malacca und Ceylon. Gesammelt von Herrn Prof. Dr. v. Buttel-Reepen in den Jahren 1911–1912. Zoologische Jahrbucher. Abteilung fur Systematik, Geographie und Biologie der Tiere 36: 1–148.

Forel A (1917) Cadre synoptique actuel de la faune universelle des fourmis. Bulletin de la Société Vaudoise des Sciences Naturelles 51: 229–253.

Hölldobler B, Wilson EO (1990) The Ants. Harvard University Press, 732 pp. doi: 10.1007/978-3-662-10306-7

Hosoishi S, Ogata K (2009) A taxonomic revision of the Asian endemic subgenus *Physocrema* of the genus *Crematogaster* (Hymenoptera: Formicidae). Zootaxa 2062: 15–36.

Longino JT (2003) The *Crematogaster* (Hymenoptera, Formicidae, Myrmicinae) of Costa Rica. Zootaxa 151: 1–150.

Santschi F (1934) Deux nouveaux *Crematogaster* intéressants. Bulletin Vaudoise des Sciences Naturelles 58: 187–191.

Smith DR (1979) Formicoidea. In: Krombein KV, Hurd PD Jr, Smith DR, Burks BD (Eds) Catalog of Hymenoptera in America North of Mexico 2 Apocrita (Aculeata). Washington D.C., 1323–1467.

Soulié J (1964) Sur la répartition géographique des genres de la tribu des Crematogastrini. Bulletin de la Société d'Histoire Naturelle de Toulouse 99: 397–409.

Wheeler WM (1911) A list of the type species of the genera and subgenera of Formicidae. Annals of the New York Academy of Sciences 21: 157–175. doi: 10.1111/j.1749-6632.1911.tb56932.x

Wheeler WM (1922) The ants of the Belgian Congo. Bulletin of the American Museum of Natural History 45: 1–1139.

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REVIEW ARTICLE

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Polistinae biogeography in the Neotropics: history and prospects

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Abstract

Discussions regarding Polistinae biogeography in the last two decades rarely associated current patterns of distribution with environmental changes. This well-known and very diverse group of insects is highly endemic in the Neotropics, but environmental factors influencing the enormous biological diversity in the region are not well established. Exploring evidence on the two main hypotheses concerning the origins and early colonization processes of paper wasps we position in favor of the Gondwanan hypothesis and discuss change-promoter processes in the Neotropics whose effects might have altered the distributions and facilitated the speciation of Polistinae in the region. Furthermore, based on recent advances in biogeography, mostly in the integration of ecological and evolutionary information, we highlight directions for future biogeographical research within the group.

Keywords

Biological richness, ecology, evolution, paper wasps, speciation, species distribution

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Introduction

It is surprising how young the biogeography of Polistinae is. Many questions remain unsolved or have never been posed for this subfamily. This gap in our knowledge is partially due to the absence of discussions linking variations (e.g., morphological, molecular and physiological) with historical processes. Exciting themes such as colonization routes, population genetics and phylogeography have not been featured in discussions of paper wasps' biology, thereby seriously limiting our ability to draw evolutionary conclusions. Furthermore, many recent advances in science have not been applied to the study of these insects. For example, it is not known how distributions of Polistinae species have changed during the Late Cenozoic or if existed and where refuges were located for forest-dwelling species during periods of extreme cold (i.e., the ice ages). These issues have already been explored and explanations have been proposed for some amphibians (Carnaval et al. 2009), birds (Batalha-Filho et al. 2012; Maldonado-Coelho 2012), ants (Resende et al. 2010) and plants (Pinheiro et al. 2013). Also, population relationships and historical demography are unknown for the subfamily Polistinae.

Compared with Africa, Europe and Asia, regions where paper wasps are abundant, an endemism of nearly 70% (~630 species) is recorded in the Americas (Richards 1978, Jeanne 1991, Silveira 2008) and most of the species are restricted to the Neotropics. In fact, these insects constitute a well-represented group in the Neotropical region, both in terms of abundance and richness. In addition, differences regarding both nest and body morphological traits and behavioral strategies (e.g., necrophilia, cyclic oligogyny) indicate that the region is the main hotspot for Polistinae or, using the words of O. W. Richards, is "the metropolis of social wasps" (Evans and West-Eberhard 1970).

Despite this richness, biogeographic studies related to Polistinae are not common. In fact, discussions regarding the origins and distribution patterns of this subfamily were not discussed by almost two decades; the last study on this subject before Silva and Noll (2014) was published by Carpenter (1996). However, factors related to the current distribution and success of paper wasps are typically associated with environmental conditions (e.g., Dejean et al. 2011). In addition, the historical reasons regarding the irradiation of these insects in the Neotropics – i.e., the explosion of species richness, likely during the Cenozoic – have not been discussed.

Many unanswered questions regarding the biogeography of these interesting insects can be posed: (1) what evidence exists supporting the biogeographical hypotheses on the origins of Polistinae and colonization of the New World?, (2) what are the primary ecological and environmental constraints shifting the distributions of the wasps and promoting changes in the Neotropics that make it "the metropolis of social wasps"? and (3) how did these wasps proceed while colonizing the New World? In this work we focus on the first two questions; the later is the theme of another ongoing study. In order to address these questions, we provide a brief review of the two main hypotheses regarding Polistinae biogeography (i.e., the Beringian and Gondwanan hypotheses) and associate historical processes such as climatic-vegetational changes, orogeny and global temperature oscillations with the promotion of changes in Polistinae diversity and distribution in the Neotropics. In the last section of the text, we highlight some perspectives that are, in our opinion, critical for a deeper understanding of Polistinae biogeography. We maintain that these perspectives will drive future knowledge in this field. If we are able to influence ecological and evolutionary integrative discussions about these wasps, our goals in this work will certainly be achieved.

Biogeographical hypotheses: origins of Polistinae and colonization of the Neotropics

Early biogeographical hypotheses stated that paper wasps originated in the tropics based on the high diversity of such insects in the region (Wheeler 1922, Richards and Richards 1951). The sympatric and restricted occurrence in the oriental tropics of the three social subfamilies of Vespidae (Stenogastrinae, Vespinae and Polistinae) and the presence of ancestral forms in nest architecture (West-Eberhard 1969) and basal morphological traits (Van der Vecht 1965) support assumptions that the Vespinae/Polistinae split likely occurred in southeastern Asia (Van der Vecht 1965, Richards 1971). According to these assumptions, the dispersion of paper wasps into the New World occurred twice through the Bering Strait in the Middle Tertiary and the current distribution therein was likely reached after the last ice age (Richards 1978).

Carpenter (1981) criticized the relation between center of diversity and center of origin and suggested that the distribution pattern of paper wasps is "widely Gondwanan." It was also suggested by Carpenter (1993) that the separation between Africa and South America in the Early Cretaceous (120–100 million years ago; Mya) was an important event in the evolutionary history of the group. Carpenter (1996) also reviewed the two main hypotheses of Polistinae biogeography and performed Component Analyses for *Polistes* Latreille subgenera. Area cladograms presented in that work supported the Gondwanan distribution of subgenera and rejected the expected dispersion through the Bering Strait (as defended by Van der Vecht 1965, Richards 1971, 1978).

Other data also support the Gondwanan distribution of paper wasps and we reviewed some of these studies, focusing on paleontological, phylogenetic and divergence time evidence.

Fossil records

There are few data related to the paleodistribution of paper wasps based on fossil records. Despite this fact, important evidence that permits inferences about the biogeographic hypotheses was obtained by Brown (1941a) with a specimen from the Upper Cretaceous: a wasp nest comb of *Brownichnus favosites* (previously treated as genus *Celliforma*) from Utah, United States. The specimen shows traits comparable to papery nests, just like those of *Polistes*. This finding defined the presence of social behavior in insects earlier than that predicted in that time, from the Eocene to the Cretaceous, but Brown (1941a) was unable to determine the relationships of the specimen with today's social wasps.

After some discussions regarding the classification of such a comb in Bequaert and Carpenter (1941) and Brown (1941b), Wenzel (1990) confirmed that the comb is indeed from a social wasp. Despite the fact that Wenzel (1990) has not been conclusive about the relationships of *B. favosites* with present-day groups, the author advocated that the comb is certainly from a Vespinae or a Polistinae. Moreover, he defended that if *B. favosites* is an ancient *Polistes*, the vicariance hypothesis (i.e., Gondwanan) "should remain intact."

Phylogeny

Phylogenetic inferences have provided important information about the evolutionary history of Polistinae. Carpenter (1991) carried out the first cladistic analysis of the relationships among the genera of subfamily based on morphological and nest architecture characters. This analysis placed the cosmopolitan Polistini as the sister group to the other tribes. Ropalidiini (Old World), Mischocyttarini and Epiponini were grouped in a polytomy. Wenzel and Carpenter (1994) solved the polytomy by placing Mischocyttarini as an intermediate group and Ropalidiini and Epiponini as more derived groups. Pickett and Carpenter (2010), however, reviewed several molecular and morphological characters of Vespidae and placed Ropalidiini as the most basal group, followed by Mischocyttarini and Polistini + Epiponini as sister tribes.

The evolutionary history of *Polistes* has been the most thoroughly studied by phylogenetic assessments. We reviewed five of the main studies (Carpenter 1996, Zhu et al. 2000, Arévalo et al. 2004, Pickett and Wenzel 2004, Pickett et al. 2006) and noted that the Old World subgenera are invariably those at the base of the trees and that the New World subgenera are derived. We consider this settlement as a strong evidence for a more recent colonization in the western tropics. Likewise, considering that Mischocyttarini and Epiponini only occur in the Neotropics, and that no fossils of these groups were recorded outside of this region [following the suggestion of Carpenter and Grimaldi (1997) in not considering the misidentifications of two *Polybia* Lepeletier found in Burnham (1978) from England] and if genus *Paleopolistes* from France is not an Epiponini (Perrard & Carpenter, 2014) we are tempted to give credit to the hypothesis that both tribes arose in the New World after the separation of Africa and South America (120 Mya).

Divergence time estimates

Ezenwa et al. (1998) raised assumptions that even though the oldest known paper wasp fossil dates from the Cretaceous (Brown 1941a), the Vespinae/Polistinae split likely occurred in the Middle Jurassic (about 175 Mya) and the four tribes arose between 175 and 80 Mya. These assumptions, although not tested empirically, strengthen the hypothesis of a possible colonization of the Americas in a Gondwanan scenario due the exclusivity of Mischocyttarini and Epiponini in this region.

Based on these data, we tend to give credence to the Gondwanan hypothesis as a reasonable and convincing assumption able to explain the origins and colonization processes of the worldwide Polistinae distribution, as well as early colonization routes.

The life in the metropolis

Distinct from other regions of the globe, the Neotropics are composed of large, humid forests that have undergone several changes (Hoorn et al. 2010). These forests harbor most of the paper wasp fauna in the region (Richards 1978). The causes for the high biodiversity levels in these rainforests have been recurrently associated with environmental changes and hypotheses regarding extrinsic processes (non-genetic mechanisms) that facilitate speciation in the biota, mostly in the Amazonian region, have also been explored in previous studies. Haffer (1997, 2008) provided extensive reviews concerning these hypotheses and argued that several of them are relevant to speciation processes in different geological periods of the Cenozoic.

Although environmental processes have not been commonly explored to explain the diversity of paper wasps in the Neotropics, historical and recurrent events have certainly provided evolutionary scenarios for adaptive irradiation of this group in the region. Richards (1978) recognized that climate and vegetation changes in South America have mixed the distribution of paper wasps during the geologically recent past of Brazil. Dejean et al. (2011) associated the fluctuation of species richness to climatic phenomena such as El Niño and La Niña in French Guiana. However, empirical analyses and theoretical assumptions regarding environmental factors able to induce putative alterations in populations of paper wasps have not been sufficiently discussed. Here, we provide a quick review of the main hypotheses concerning speciation processes in the Neotropics. We aim to highlight the major environmental events that we consider to have been involved in the Neotropical irradiation of Polistinae during the Cenozoic. Other proposals can be found in the reviews of Haffer (1997, 2008), including the Gradient, Canopy-density and Museum hypotheses; we opted not to include these hypotheses in this work because the arguments used to explain speciation processes are less general in these hypotheses than in those presented here.

Climatic-vegetational changes: the Refuge hypothesis

The Refuge hypothesis predicts the occurrence of putative forest refuges – regions where forests remain unaltered irrespective of global temperature oscillations – during the Cenozoic and before, i.e., more than 60 Mya (Haffer 1997, 2008). Even so, Haffer (1969) proposed initially that climatic-vegetational changes during the Pleistocene (1.8–0.1 Mya) were the main causes for novelties and speciation processes to arise in the Amazonian rainforest. This idea suffered criticisms (e.g., Bush and Oliveira 2006) and was not supported by many studies that contested the short timespan for speciation events predicted initially by the author since most of the Neotropical groups likely arose before the Pleistocene (e.g., Zink and Slowinski 1995, Costa 2003, Geurgas et al. 2008).

Haffer modified his earlier ideas based mainly on Bennett's (1990) assumptions regarding the influences of Milankovitch cycles on communities over a time scale of 20–100 thousand years, or ky. These cycles, caused by alterations in the Earth's orbit, would have affected population structures and caused disruptive events in the Neotropical communities and might be the main factors responsible for oscillating the climate of the planet due to its influence on glacial/interglacial cycles (see Bennett (1990) for complete explanations on the Milankovitch cycles). In summary, the Refuge hypothesis (Haffer 1997, 2008) is particularly based on the effects of dry/humid periods of the Cenozoic on the speciation events in the Amazonian rainforest.

Some refuges have also been proposed for the Brazilian Atlantic Forest (e.g., Carnaval and Moritz 2008, Carnaval et al. 2009), suggesting that these areas might have indeed served as stable forest patches for many forest-dwelling taxa throughout climatic-vegetational changes. Moreover, because each species has its own ecological niche, idiosyncratic responses to alterations as well as different distribution of refuges are expected for different species.

Richards (1978) considered that climatic-vegetational changes could have affected the distribution of species but pointed out that paper wasps had not showed clear evidence for refuge areas. Indeed, there are no empirical data concerning this matter, but distribution of some species denote that the retraction of South American rainforests during dry periods disrupted populations of *Epipona media* Cooper, *Synoeca septentrionalis* Richards and *Angiopolybia pallens* (Lepeletier) (Menezes et al. 2010, 2011, Carvalho et al. 2014).

Phylogeographic analyses carried out with the extinction-threatened ant *Dinoponera lucida* Emery (Resende et al. 2010) and with orchid bees (López-Uribe et al. 2014) indicated that, in fact, different size refuges were important for the creation and maintenance of hymenopterans' diversity in the Neotropical rainforests. For paper wasps, however, there are no studies on this matter.

Paleogeography and River hypotheses

According to these hypotheses, different models are expected to have caused geographic separation and speciation of the animal populations in the Amazonian rainforest that are related to worldwide sea level changes, uplifts of plateaus and flooding of plains. The emergence of islands (Island Model (Emsley 1965, Croizat 1976)), archs (Arch Model (Morell 1996)), lagoons (Lagoon Model (Marroig and Cerqueira 1997)) and rivers (River hypothesis (Sick 1967)) in the Amazonian basin were recognized as historical events that putatively shifted species' distribution ranges, facilitating their differentiation.

Despite Haffer (2008) arguing that some of these inferences are highly speculative and contain several missing links, it is possible that such alterations in the geography of the Amazonian region, if they occurred during the Cenozoic, would have provided a great variety of environments for diversification of paper wasps. Furthermore, it is not surprising that large bodies of water might act as barriers to the flow between disrupted populations of land species. For wasps, that would not be different. Indeed, swarms have great difficulty in dispersing across water (Jeanne 1981). This fact possibly affected the decline of paper wasps in the Caribbean, for example, due to limitations of the chemical trail system, but might not be a very convincing overall explanation since the subfamily is present throughout Southeast Asia, the Philippines, and Australia (Carpenter and Grimaldi 1997), for example.

Mainland species in turn might also have had their distributions altered during landscape changes in the Cenozoic caused by both water barriers and tectonic events. As showed by Silva and Noll (2014), phylogenetics and distribution data call attention to the importance of land bridges connecting the Northern and Southern Hemispheres to the cladogenesis of basal species of genus *Brachygastra* Perty. Unfortunately, although these alterations have influenced substantially the distribution of some land organisms (Croizat 1976, Hershkovitz 1977), it is not possible to our knowledge to quantify precisely how much these changes have contributed to extinction, disruptions and speciation events of paper wasps.

Disturbance-Vicariance hypothesis

This hypothesis regards the influence of cold/warm cycles (not dry/humid, as proposed by the Refuge hypothesis) as selecting Amazonian lineages throughout temperature oscillations during the Pleistocene (Colinvaux 1993, Bush 1994). Invasion, counter-invasion and competitive interactions are seen in this model as events affecting distributions and abundances of species. According to these assumptions, the presence of invading and cold-adapted taxa could have resulted in local extinctions, favoring isolation of genotypes and allopatric speciation of some taxa.

There is a regional focus of this hypothesis on the peripheral areas of the Amazonian rainforest due to the high faunal endemism in such areas. Such regions are recognized by the model as being rich in endemic taxa due to their supposed environmental instability. Indeed, temperature oscillations during the Pleistocene might have influenced the distribution of taxa and genotypes, but speciation events are mostly expected to have occurred before 1.8 Mya (Zink and Slowinski 1995, Costa 2003).

The Quaternary is undoubtedly a short time to explain the huge diversity of paper wasp species in the Neotropics. Both temperature oscillations and the short period, however, are apparently sufficient for population structuring mainly of widely disrupted taxa. Polistinae species might have undergone their distribution to optimal locations during such changes in the temperature and environmentally related genotypes might have been frequently selected. Such alterations might also have influenced both behavioral and physiologic traits, including feeding habits, defense, nest building, resistance to diseases and predators and adaptive strategies against cold or warm climate. Future researches are undoubtedly needed for accurate detailing.

Future directions

Since ecological and phylogenetic information can comprise very useful frameworks for raising hypotheses on historical biogeography in scenarios constantly in change, to explore the different impact of variables on the distribution of Polistinae is an important subject to be discussed. Furthermore, the knowledge of environmental and geological constraints that affect distribution of species can help predictions about extrinsic mechanisms shifting large-scale distributional patterns. In addition, to resolve important questions like the causes of some clades disperse to some areas but not to others is the major challenge in historical biogeography (Wiens and Graham 2005) and define the favorable and unfavorable conditions that unbalance population density over time figures as a crucial factor to describe distribution of any group (Haldane 1956). However, understanding how extrinsic factors alter distribution we can determine environmental and ecological constraints that species can tolerate or not and, likewise, which regions these species might occupy by dispersal events.

A very promising group of paper wasps for start this kind of research is that composed by forest-dwelling species. Using data regarding current distribution, one can propose past and present distributions of acceptable conditions for a clade to occur, based on ecological niche modelling, for example (e.g., Hugall et al. 2002, Carnaval et al. 2009). Since the bioclimatic conditions that maintain the distribution of humid forests have changed in the Neotropics during ice ages and since forest-dwelling species depend on forest coverage to nest and forage, the distribution of these wasps has likely responded in a convergent manner to these alterations. Thinking about the biogeographic research of paper wasps in the next years, the formulation of potential paleodistribution models might be considered a cornerstone that will drive population genetics hypotheses, mostly based on phylogeographic frameworks, in studies of these insects.

Specialized literature related to the distribution or phylogenetics is very common for different clades of paper wasps. However, a fine-scale distribution pattern of Neotropical Polistinae could be more precisely understood by reviewing specialized literature; i.e., species by species. Also, tests of hypotheses using these data for making inferences about the ecological and evolutionary causes of the success or failure of Polistinae in colonizing certain regions have been rarely done. For example, the Tropical Niche Conservatism hypothesis (Wiens and Graham 2005) could explain the tendency of paper wasps to inhabit tropical areas instead of temperate regions since the subfamily was originated in a similar environment (i.e., tropical Asia). A strategy for testing such a hypothesis could be based on the integration of physiological responses, such as thermoregulation, and population relationships in the study of dry-adapted lineages of paper wasps. Since niche conservatism predicts that unaltered lineages are not likely to habit areas characterized by conditions different from fundamental niches, lineages of a clade showing thermoregulatory responses different from their ancestral populations would be expected to be adapted to local climatic alterations as a result of niche expansion.

Many recent studies have shown that integrative approaches linking climatic and phylogeny-based information to explain biogeographical patterns might be very useful for testing explicit hypotheses of causation by particular, mostly environmental, events (Hugall et al. 2002, Waltari et al. 2007, Carnaval et al. 2009). Moreover, recent discussions have drawn attention to the strong connection between evolutionary processes (e.g., ecological specialization) and environmental events such as climatic-vegetational changes in shaping the distribution of organisms over time (Wiens 2004, Hoorn et al. 2010). Quantifying the different impacts of each of these factors in the evolutionary history of Polistinae should be regarded as the main challenge in the future of biogeography and speciation research of the subfamily. The study of biogeographical processes using such wasps as models can also aid in our understanding of significant events that have influenced the distribution, historical demography and extinctions of the Neotropical biota, including the disjunction between Amazonia and Atlantic Forest and the demographic retraction of populations adapted to rainforest conditions during glacial periods, for example.

Despite Ezenwa et al. (1998) have proposed possible periods for the arising of the Polistinae tribes, current techniques are more precise for inferring divergence times. Based on a molecular clock model, which permits dating putative splits between lineages using fossil-calibrated phylogenetic trees, the proposal of the geological periods in which the subfamily Polistinae and its four tribes arose, as well as temporal concentration of speciation events, would be more convincing. Such research could also be conducted to test hypotheses regarding the influence of geological events such as river formation and land uplifts on the separation of lineages since the periods in which these events occurred are known.

In light of the differences regarding life histories, occupied niches, huge diversity, etc., the Neotropical paper wasps represent an interesting group to be used as model in a wide range of studies. However, biogeographic patterns as colonization routes and causes behind alterations on the distribution have not been sufficiently discussed using advanced analyses. We expect that by focusing on some of the challenges presented in this work, the study of biogeography with these wasps will progress in the forthcoming years.

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References

Arévalo E, Zhu Y, Carpenter JM, Strassmann JE (2004) The phylogeny of the social wasp subfamily Polistinae: evidence from microsatellite flanking sequences, mitochondrial COI sequence, and morphological characters. BioMed Central Evolutionary Biology 4: 8. doi: 10.1186/1471-2148-4-8

Batalha-Filho H, Cabanne GS, Miyaki CY (2012) Phylogeography of an Atlantic forest passerine reveals demographic stability through the last glacial maximum. Molecular Phylogenetics and Evolution 65: 892–902. doi: 10.1016/j.ympev.2012.08.010

Bequaert JC, Carpenter JM (1941) The antiquity of social insects. Psyche 48: 50–55. doi: 10.1155/1941/64162

Bennett KD (1990) Milankovitch cycles and their effects on species in ecological and evolutionary time. Paleobiology 16: 11–21.

Brown RW (1941a) The comb of a wasp nest from the Upper Cretaceous of Utah. American Journal of Science 239: 54–56. doi: 10.2475/ajs.239.1.54

Brown RW (1941b) Concerning the antiquity of social insects. Psyche 48: 105–110. doi: 10.1155/1941/76070

Burnham L (1978) Survey of social insects in the fossil record. Psyche 85: 85–134. doi: 10.1155/1978/80816

Bush MB (1994) Amazonian speciation: a necessarily complex model. Journal of Biogeography 21: 5–17. doi: 10.2307/2845600

Bush MB, Oliveira PE (2006) The rise and fall of the Refugial Hypothesis of Amazonian Speciation: a paleoecological perspective. Biota Neotropica 6, 17 pp.

Carnaval AC, Hickerson MJ, Haddad CFB, Rodrigues MT, Moritz C (2009) Stability predicts genetic diversity in the Brazilian Atlantic Forest Hotspot. Science 323: 785–789. doi: 10.1126/science.1166955

Carnaval AC, Moritz C (2008) Historical climate modelling predicts patterns of current biodiversity in the Brazilian Atlantic forest. Journal of Biogeography 35: 1187–1201. doi: 10.1111/j.1365-2699.2007.01870.x

Carpenter JM (1981) The phylogenetic relationships and natural classification of the Vespoidea (Hymenoptera). Systematic Entomology 7: 11–38. doi: 10.1111/j.1365-3113.1982.tb00124.x

Carpenter JM (1991) Phylogenetic relationships and the origin of social behavior in the Vespidae. In: Ross KG, Matthews RW (Eds) The social biology of wasps. Cornell University, Ithaca, 7–32.

Carpenter JM (1993) Biogeographic patterns in the Vespidae (Hymenoptera): two views of Africa and South America. In: Goldblatt P (Ed.) Biological relationships between Africa and South America. Yale University, New Haven, 139–155.

Carpenter JM (1996) Phylogeny and biogeography of *Polistes*. In: Turillazzi S, West-Eberhard MJ (Eds) Natural history and evolution of paper wasps. Oxford University, New York, 18–57.

Carpenter JM, Grimaldi DA (1997) Social Wasps in Amber. American Museum Novitates 3203: 7 pp.

Carvalho AF, Santos GMM, Menezes RST, Costa MA (2014) Genetic diversity of *Angiopolybia pallens* (Lepeletier) (Hymenoptera, Vespidae, Polistinae) explained by the disjunction of South American rainforests. Genetics and Molecular Research 13: 89–94. doi: 10.4238/2014.January.8.7

Colinvaux P (1993) Pleistocene biogeography and diversity in tropical forests of South America. Biological relationships between Africa and South America. Yale University, New Haven, 473–499.

Costa LP (2003) The historical bridge between the Amazon and the Atlantic forest of Brazil: a study of molecular phylogeography with small mammals. Journal of Biogeography 30: 71–86. doi: 10.1046/j.1365-2699.2003.00792.x

Croizat L (1976) Biogeografía analítica y sintética ("Panbiogeografía") de las Américas. Bibliotéca de la Academia de Ciencias Físicas, Matemáticas y Naturales, Caracas, 1–890.

Dejean A, Céréghino R, Carpenter JM, Corbara B, Hérault B, Rossi V, Leponce M, Orivel J, Bonal D (2011) Climate change impact on Neotropical social wasps. PLoS ONE 6: e27004. doi: 10.1371/journal.pone.0027004

Emsley MG (1965) Speciation in *Heliconius* (Lep. Nymphalidae): Morphology and geographic distribution. Zoologica 50: 191–254.

Evans HE, West-Eberhard MJ (1970) The wasps. University of Michigan, Ann Arbor, 1–265.

Ezenwa VO, Peters JM, Zhu Y, Arévalo E, Hastings MD, Seppa P, Pedersen JS, Zacchi F, Queller DC, Strassmann JE (1998) Ancient conservation of trinucleotide microsatellite loci in polistine wasps. Molecular Phylogenetics and Evolution 10: 168–177. doi: 10.1006/mpev.1998.0528

Geurgas SR, Rodrigues MT, Moritz C (2008) The genus *Coleodactylus* (Sphaerodactylinae, Gekkota) revisited: a molecular phylogenetic perspective. Molecular Phylogenetics and Evolution 49: 92–101. doi: 10.1016/j.ympev.2008.05.043

Haffer J (1969) Speciation in Amazonian forest birds. Science 165: 131–137. doi: 10.1126/science.165.3889.131

Haffer J (1997) Alternative models of vertebrate speciation in Amazonia: an overview. Biodiversity and Conservation 6: 451– 476. doi: 10.1023/A:1018320925954

Haffer J (2008) Hypotheses to explain the origin of species in Amazonia. Brazilian Journal of Biology 68(Supplement 4): 917–947. doi: 10.1590/S1519-69842008000500003

Haldane JBS (1956) The relationship between density regulation and natural selection. Proceedings of the Royal Society of London B 145: 306–308. doi: 10.1098/rspb.1956.0039

Hernandez PA, Graham CH, Master LL, Albert DL (2006) The effect of sample size and species characteristics on performance of different species distribution modeling methods. Ecography 29: 773–785. doi: 10.1111/j.1472-4642.2008.00482.x

Hershkovitz P (1977) Living New World monkeys (Platyrrhini). University of Chicago, Chicago.

Hoorn C, Wesselingh FP, ter Steege H et al. (2010) Amazonia through time: Andean Uplift, Climate Change, Landscape Evolution, and Biodiversity. Science 330: 927–931. doi: 10.1126/science.1194585

Hugall A, Moritz C, Moussalli A, Stanisic J (2002) Reconciling paleodistribution models and comparative phylogeography in the Wet Tropics rainforest land snail *Gnarosophia* *bellendenkerensis* (Brazier 1875). Proceedings of the National Academy of Sciences USA 99: 6112–6117. doi: 10.1073/pnas.092538699

Jeanne RL (1981) Chemical communication during swarm emigration in the social wasp *Polybia sericea* (Olivier). Animal Behaviour 29: 102–113. doi: 10.1016/S0003-3472(81)80157-1

Jeanne RL (1991) The swarm-founding Polistinae. In: Ross KG, Matthews RW (Eds) The social biology of wasps. Cornell University, Ithaca, 191–231.

López-Uribe MM, Zamudio KR, Cardoso CF, Danforth BN (2014) Climate, physiological tolerance and sex-biased dispersal shape genetic structure of Neotropical orchid bees. Molecular Ecology 23: 1874–1890. doi: 10.1111/mec.12689

Maldonado-Coelho M (2012) Climatic oscillations shape the phylogeographical structure of Atlantic Forest fire-eye antbirds (Aves: Thamnophilidae). Biological Journal of the Linnean Society 105: 900–924. doi: 10.1111/j.1095-8312.2011.01823.x

Marroig G, Cerqueira R (1997) Plio–Pleistocene South American history and the Amazon Lagoon hypothesis: a piece in the puzzle of Amazonian diversification. Journal of Comparative Biology 2: 103–119.

Menezes RST, Carvalho AF, Raw A, Costa MA (2010) *Epipona media* Cooper (Hymenoptera: Vespidae), a social wasp new to the Brazilian Atlantic Forest. Neotropical Entomology 39: 1046–1047. doi: 10.1590/S1519-566X2010000600031

Menezes RST, Andena SR, Carvalho AF, Costa MA (2011) First records of *Synoeca septentrionalis* Richards, 1978 (Hymenoptera, Vespidae, Epiponini) in the Brazilian Atlantic Rain Forest. ZooKeys 151: 75–78. doi: 10.3897/zookeys.151.1882

Morell V (1996) Amazonian diversity: a river doesn't run through it. Special news report. Science 273: 1496–1497. doi: 10.1126/science.273.5281.1496b

Perrard A, Nel A, Carpenter JM (2014) A new paper wasp from Late Eocene of France (Hymenoptera: Vespidae: Polistinae). Zootaxa 3753: 542–548. doi: 10.11646/zootaxa.3753.6.2

Pickett KM, Wenzel JW (2004) Phylogenetic analysis of the New World *Polistes* (Hymenoptera: Vespidae, Polistinae) using morphology and molecules. Journal of the Kansas Entomological Society 77: 742–760. doi: 10.2317/E-18.1

Pickett KM, Carpenter JM (2010) Simultaneous analysis and the origin of eusociality in the Vespidae (Insecta: Hymenoptera). Arthropod Systematics and Phylogeny 68: 3–33.

Pickett KM, Carpenter JM, Wheeler WC (2006) Systematics of *Polistes* (Hymenoptera: Vespidae), with a phylogenetic consideration of Hamilton's haplodiploidy hypothesis. Annales Zoologici Fennici 43: 390–406.

Pinheiro F, Cozzolino S, Barros F, Gouveia TMZM, Suzuki RM, Fay MF, Palma-Silva C (2013) Phylogeographic structure and outbreeding depression reveal early stages of reproductive isolation in the Neotropical orchid *Epidendrum denticulatum*. Evolution 67: 2024–2039. doi: 10.1111/evo.12085

Resende HC, Yotoko KSC, DeLabie JHC, Costa MA, Campiolo S, Tavares MG, Campos LAO, Fernandes-Salomão TM (2010) Pliocene and Pleistocene events shaping the genetic diversity within the central corridor of the Brazilian Atlantic Forest. Biological Journal of the Linnean Society 101: 949–960. doi: 10.1111/j.1095-8312.2010.01534.x

Richards OW, Richards MJ (1951) Observations on the social wasps of South America (Hymenoptera, Vespidae). Transactions of the Royal Entomological Society of London 102: 1–170. doi: 10.1111/j.1365-2311.1951.tb01241.x

Richards OW (1971) The biology of the social wasps (Hymenoptera, Vespidae). Biological Reviews 46: 483–528. doi: 10.1111/j.1469-185X.1971.tb01054.x

Richards OW (1978) The social wasps of the Americas excluding the Vespinae. British Museum Natural History, London.

Sick H (1967) Rios e enchentes na Amazônia como obstáculo para a avifauna. Atas Simpósio sobre a Biota amazônica 5: 495–520.

Silva M, Noll FB (2014) Biogeography of the social wasp genus *Brachygastra* (Hymenoptera: Vespidade: Polistinae). Journal of Biogeography: 1–10. Article first published online: 22 SEP 2014. doi: 10.1111/jbi.12417

Silveira OT (2008) Phylogeny of wasps of the genus *Mischocyttarus* de Saussure (Hymenoptera, Vespidae, Polistinae). Revista Brasileira de Entomologia 52: 510–549. doi: 10.1590/S0085-56262008000400004

Van der Vecht J (1965) The geographical distribution of the social wasps (Hymenoptera, Vespidae). Proceedings of the XII International Congress of Entomology: 440–441.

Waltari E, Hijmans RJ, Peterson AT, Nyári ÁS, Perkins SL, Guralnick RP (2007) Locating Pleistocene Refugia: Comparing Phylogeographic and Ecological Niche Model Predictions. PLoS ONE 7: e563. doi: 10.1371/journal.pone.0000563

Wenzel JW (1990) A social wasp's nest from the Cretaceous period, Utah, USA, and its biogeographical significance. Psyche 97: 21–29. doi: 10.1155/1990/24696

Wenzel JW, Carpenter JM (1994) Comparing methods: adaptative traits and tests of adaptation. In: Eggleton P, Vane-Wright R (Eds) Phylogenetics and Ecology. London Academic Press, London, 79–101.

West-Eberhard MJ (1969) The Social Biology of Polistine Wasps. Miscellaneous publications, Museum of Zoology, University of Michigan 140: 1–101.

Wheeler WM (1922) Social life among the insects. Lecture II. Part 2. Wasps solitary and social. The Scientific Monthly 15: 119–131.

Wiens JJ (2004) Speciation and ecology revisited: phylogenetic niche conservatism and the origin of species. Evolution 58: 193–197. doi: 10.1111/j.0014-3820.2004.tb01586.x

Wiens JJ, Graham CH (2005) Niche conservatism: integrating evolution, ecology, and conservation biology. Annual Review of Ecology and Systematics 36: 519–539. doi: 10.1146/annurev.ecolsys.36.102803.095431

Zhu Y, Queller D, Strassmann JE (2000) A phylogenetic perspective on sequence evolution in microsatellite loci. Journal of Molecular Evolution 50: 324–338. doi: 10.1007/s002399910036

Zink RM, Slowinski JB (1995) Evidence from molecular systematics for decreased avian diversification in the Pleistocene Epoch. Proceedings of the National Academy of Sciences USA, 92: 5832–5835. doi: 10.1073/pnas.92.13.5832