RESEARCH ARTICLE



Trigonalidae (Hymenoptera) of Madagascar

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Abstract

Seven species of the primarily hyperparasitoid family Trigonalidae are reported from Madagascar: Orthogonalys brevis Smith & Tripotin, **sp. n.**, Orthogonalys gigantea Benoit, 1951; O. hova Bischoff, 1933; O. maculata Bischoff, 1933; Orthogonalys parahova Smith & Tripotin, **sp. n.**, O. seyrigi Bischoff, 1933; and Trigonalys natalensis Kriechbaumer, 1894. Diagnoses and a key to species are given.

Keywords

Afrotropical, hyperparasitoids

Introduction

Other than original descriptions and catalogs, no work has been done on the trigonalid fauna of Madagascar. In the most recent list by Carmean and Kimsey (1998), three species of *Orthogonalys* Schulz and one species of *Trigonalys* Westwood are listed. About 200 specimens were collected during the survey of Madagascar by the California Academy of Sciences, San Francisco. Study of this material, as well as the types and type series of the described species, has resulted in the recognition of six species of *Orthogonalys* and one species of *Trigonalys*. Two main problems in *Orthogonalys* included the validity *O. gigantea* Benoit, which appeared to be only a large form of *O. hova* Bischoff (Carmean and Kimsey 1998), and *O. seyrigi* form *maculata* Bischoff, which has been considered as a synonym or as a subspecies of *O. seyrigi* Bischoff (Weinstein and Austin 1991). Here, we recognize both *O. gigantea* and *O. maculata* as valid species. In addition, two new species of *Orthogonalys* are described. Illustrations and a key to species for Madagascar are provided.

Trigonalidae are hyperparasitoids mostly of Ichneumonidae (Hymenoptera) and Tachinidae (Diptera) parasitizing Lepidoptera caterpillars and social wasps (Weinstein and Austin 1991, Carmean 1991, Carmean and Kimsey 1998, Murphy et al. 2009). However, two species of *Taeniogonalos* in Australia have been reared directly from saw-fly hosts (Raff 1934, Carne 1969). The only records of hosts for Madagascar are by Benoit (1951), who mentioned that *Orthogonalys hova* was obtained from rearing of a limacodid moth, and Schultz (1910), who stated that *Trigonalys natalensis* was reared from an unidentified lepidopteran pupa.

Trigonalids have been recorded from the provinces of Antsiranana, Fianarantsoa, Majunga, Toamasina, and Toliara and probably occur throughout Madagascar.

Materials and methods

Images were obtained using an EntoVision Imaging Suite that included a firewire JVC KY-75 3CCD digital camera mounted to a Leica M16 zoom lens via a Leica z-step microscope stand. Multiple focal planes were merged using Cartograph 5.6.0 (Microvision Instruments, France) software.

Specimens used in this study are deposited in the California Academy of Sciences, San Francisco, USA (CAS); Museum für Naturkunde, Humboldt-Universität, Berlin, Germany (MNHU); Muséum National d'Histoire Naturelle, Paris, France (MNHN); National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM); and the collection of Pierre Tripotin, Mont Saint-Aignan, France (PT).

Locality data are recorded essentially as they appear on the specimen labels. Characterization of genera and validity of generic names was treated by Carmean and Kimsey (1998). Terminology is based on Huber and Sharkey (1993).

Madagascar previously was divided into six provinces and 22 regions. The 22 regions became the highest subdivisions in 2007 (http://en.wikipedia.org/wiki/Madagascar). All label data, as well as distributions reported in the literature, are according to the original six provinces, which are used in this paper.

Results

Key to species

1	Antenna black; mesosoma and metasoma predominantly black; wings dark-
	ened (Fig. 40) Trigonalys natalensis
_	Antenna with white central band; mesosoma and usually metasoma predomi-
	nantly orange to yellow, metasoma commonly partly black dorsally; wings
	hyaline (Figs 1, 8, 14, 15, 21, 29, 35) (Orthogonalys)2
2	Mesosoma black posterior to transscutal articulation, mesoscutellum and
	metascutellum white (Figs 23, 36)
-	Mesosoma orange, mesoscutellum and metascutellum may be yellow (Figs 3,
	10, 16, 30)
3	Mesoscutellum slightly longer than broad, anterior width about $0.8\times$ medial
	length (Fig. 23); hind tibia brown to black, darker than orange femur and tar-
	sus (Figs 21, 22); only about 3 or 4 central antennomeres completely white
	(Fig. 26); first metasomal tergum partly black (Fig. 23); paramere of male geni-
	talia oval, about 1.5× as long as broad, white (Figs 27, 28)
-	Mesoscutellum about as long as broad, anterior width about $1.1\times$ medial
	length (Fig. 36); hind legs orange (Fig. 35); about 6 central antennomeres
	completely white (as in Figs 2, 14); first metasomal tergum orange (Figs 35,
	36); paramere of male genitalia short, almost round and as long as broad,
	brown (Fig. 39)
4	Frons completely white, not interrupted in center by broad, black band (Fig. 4)
	or interrupted by a very narrow black line; gena black (Figs 1, 2); paramere of
	male genitalia short, round, slightly broader than long, brown (Fig. 6), less than
	half length of gonostipes (Fig. 7); about 5–8 mm long O. brevis sp. n.
-	Frons interrupted in middle by broad black stripe (Figs 11, 17, 31); gena
	mostly white (Figs 8, 14, 29); paramere of male genitalia elongate, 1.4–1.8×
	as long as broad, white or dark orange (Figs 13, 20, 33), more than half length
	of gonostipes (Fig. 19); size various
5	Propodeum with transverse carinae (Fig. 10); paramere of male genitalia or-
	ange brown, about 1.4× as long as broad, rounded at apex (Fig. 13); large,
	14–15 mm long O. gigantea
-	Propodeum with irregular reticulate sculpture (Figs 16, 30); paramere of male
	genitalia white, about 1.5× as long as broad, tapering to acutely rounded apex
	(Fig. 20) or about 1.8× as long as broad and broadly rounded at apex (Fig.
,	33); small, 4–11 mm long6
6	Mesoscutellum slightly broader than long, anterior width 1.2× medial length
	(Fig. 30); about 4 central antennomeres completely white; clypeus white;

Orthogonalys brevis Smith & Tripotin, sp. n.

urn:lsid:zoobank.org:act:B4FFC8CA-72FF-43FB-854B-E8C5E9E58802 http://species-id.net/wiki/Orthogonalys_brevis Figs 1–7

Holotype. male, labeled "PROVINCE TOAMASINA: Montagne d'Anjanaharibe, 18.0 km 21° NNE Ambinanitelo, elev 470 m, 8–12 Mar 2003, 15°11'18"S, 049°36'54"E", "California Acad. of Sciences, coll. Fisher, Griswold et al., Malaise trap, in rainforest, collection code BLF8011" (CAS).

Paratypes. Same data as for holotype (1 ♀, 1 ♂, CAS, USNM); "PROVINCE ANTSIRANANA: Marojejy Nat'l Park, 5 km W Manantenina village, Camp Mantella, 28 April – 7 May 2005, 14°26.29'S, 49°46.44'E", "California Academy of Sciences, coll: M. Irwin, R. Harin'Hala, Malaise trap, low altitude rainforest, elev. 490 m, MA-31-20" (1 ♂, CAS), same except "26 Sept.- 4 Oct. 2005, MA-31-32" (3 ♂, CAS, USNM); same except "28 Aug. – ll Sept. 2005, MA-31-29" (1 ♂, USNM). "PROV-INCE ANTSIRANANA: Parc National de Marojejy, Manantenina River, 26.6 km 35° NNW Manantenina, 11–14 Dec 2005, 14°26'06"S, 049°45'36"E," "California Acad. of Sciences, coll. B. L. Fisher et al., elev. 775 m, Malaise trap, rainforest, collection code BLF 13385" (3 ♂, CAS, USNM, PT). "PROVINCE ANTSIRANANA: Parc National de Marojejy, Manantenina River, 28.0 km 38° NE Andapapa, 8.2 km 333° NNW Manantenina, el 450 m, 12–25 November 2003," "14°26'12"S, 049°46'30"E, California Acad. of Sciences, coll. B. L. Fisher et al., B. L. Fisher et al., Malaise trap in rainforest, BLF 8723" (1 ♂, CAS).

Description. Female (Fig. 1). Length. 7.0 mm. Similar to male except for penultimate metasomal segment and sheath black, and genitalic characters.

Male. (Fig. 2). Length. 5.0–8.0 mm. Antenna black, antennomeres 9–16 and sometimes 17 white. Head white with vertex and gena black, black extending anteriorly as V-shaped mark in front of ocelli; broad black median stripe on clypeus (Figs 4, 5). Mesosoma pale orange. Legs pale orange with hind tibia and tarsus darker to black. Wings hyaline, veins brown, costa more orange toward base; stigma brown to orange with anterior margin black. Genitalia brown.



Figures 1–3. Orthogonalys brevis. I Female paratype, lateral view. 2 Male paratype, lateral view. 3 Mesosoma and metasoma, male, dorsal view.



Figures 4–7. *Orthogonalys brevis*, male paratype. 4 Head, front view. 5 Head, dorsal view. 6 Apex of abdomen and genitalia, lateral view. 7 Genitalia, dorsal view.

Antenna with 28 antennomeres. Head from above slightly concave behind, distance behind eyes about $0.7 \times$ eye length (Fig. 5). Metascutellum broader than long, anterior breadth about $1.3 \times$ medial length; metascutellum about $2.0 \times$ broader than long (Fig. 3). Dorsum of mesosoma shiny, with widely spaced small punctures farther apart than $2-3 \times$ puncture diameters. Propodeum coarsely reticulate (Fig. 3). Male genitalia with paramere short, $1.6 \times$ broader than long, broadly rounded at apex, about $0.5 \times$ length of gonostipes (Figs 6, 7).

Distribution. Madagascar: Antsiranana, Toamasina.

Etymology. The specific name is from the Latin *brevis*, referring to the short parameres of the male genitalia.

Remarks. The short parameres of the male genitalia place this species close to *O. seyrigi*; however, the parameres of *O. brevis* are shorter and broader than long whereas those of *O. seyrigi* are about as broad as long (Figs 6, 39) The color of *O. brevis* is entirely different than in *O. seyrigi* and more similar to that of *O. hova* with the almost entirely orange mesosoma and metasoma. The color of the head is consistently different than in other *Orthogonalys* species with more white across the frons, which is not interrupted with black, except sometime for a very narrow medial line, and the entirely black gena (Figs 4, 5). The metasoma of *O. brevis* is almost entirely orange with only apical segment white and the penultimate segment mostly black.

Orthogonalys gigantea Benoit

http://species-id.net/wiki/Orthogonalys_gigantea Figs 8–13

Orthogonalos gigantea Benoit, 1951: 143.-Paulian 1961: 206, fig. 79.

Orthogonalys gigantea: Weinstein and Austin 1991: 422.-Carmean and Kimsey 1998: 53, 54.

Type material. Holotype female at MNHN, labeled "Muséum Paris," "Madagascar, Mgn l'Ambre," "Muséum Paris 1.34 A. Seyrig," "TYPE [red]," "Orthogonalys gigantea sp. n. holotype \mathcal{Q} , det. P. L. G. Benoit 1951." Benoit (1951) described the species from "Madagascar: Montagne d'Ambre I.1934 (A. Seyrig \mathcal{Q} holotype, au Muséum National d'Histoire Naturelle de Paris." The antennae are missing except first three antennomeres of left and first antennomere of right and parts are glued onto a piece of cardboard on the pin.

Additional specimen examined. PROVINCE ANTSIRANANA: "Madagascar Nord, dct Diégo-Suarez, Analamerana, 80 m, 50 km SE Diégo, I-59, Andria R." (1 ⁽¹⁾, MNHN).

Description. Female (Fig. 8). Length, 14 mm. Head black; inner orbits broadly from top of eye through malar area and gena, clypeus except for median V-shaped stripe, and mandible except apex white (Figs 11, 12). Mesosoma orange with hind corners of pronotum, lower anterior corner of pronotum, and metascutellum yellow. Legs dark orange; hind tibia and tarsus darker, nearly black. Metasoma dark orange with black spot at center of 1st tergite, small faint black spot at center of 2nd tergite, lateral and posterior bands on 3rd tergite, and most of tergite 4 except for white posterior margin; tergite 5 white; laterally and ventrally mostly yellow with black spot on 6^{rh} sternite and sheath black.

Antenna missing (see male). Head from above nearly straight behind, behind eyes slightly expanded, distance behind eyes about equal to eye length (Fig. 12). Anterior



Figures 8-9. Orthogonalys gigantea. 8 Female holotype, dorsolateral view. 9 Male, dorsolateral view.

width of mesoscutellum $0.8\times$ medial length. Metascutellum $2\times$ broader than long (Fig. 10). Mesonotum shiny with closely set punctures, mostly separated by shiny interspaces $1-2\times$ puncture diameters. Propodeum with almost straight transverse carinae (Fig. 10).

Male. (Fig. 9). Length, 15 mm. Antenna black; antennomeres 11–16 and basal half of 17 white. Similar to female except apex of mesoscutellum more yellowish, metasoma mostly black above with reddish brown at apex of tergite 1 and on most of tergites 2 and 3, tergites 1–3 laterally and ventrally orange yellow and tergites 4–6 with white spots. Paramere dark orange.



Figures 10–13. Orthogonalys gigantea. 10 Mesosoma, dorsal view, male. 11 Head front view, female holotype. 12 Head, dorsal view, female holotype. 13 Male paramere, lateral view (appearance is due to hairs matted against the surface).

Antenna with 28 antennomeres, otherwise similar to female. Paramere oval, about 1.4× as long as broad, broadly rounded at apex (Fig. 13).

Distribution. Madagascar: Antsiranana.

Remarks. The status of this species has been questionable. Carmean and Kimsey (1998) thought that it might be only a large form of *O. hova*. Benoit (1951) described the species from a single female. He separated *O. gigantea* from *O. hova* by its large size (14 mm) and by the following: teeth of mandibles broad but not very long, the inferior tooth directed downwards; clypeus very thickened; antennal sockets closer together; punctation of scutellum sparser but stronger; propodeum broader than long, with transverse carinae complete and regular (not tangled and less strong); color identical except the white "atténué" on the head and sides of abdomen. We have not seen additional females but have

examined one male that compares in color and structure with the holotype female and was collected not far from the type locality, and we consider them to be the same species.

After study of both sexes, we note a number of characters that justify treating *O. gigantea* as a valid species. Size cannot be regarded as a valid character in trigonalids. However, in comparison to *O. hova*, the specimens examined are consistently larger. The female holotype of *O. gigantea* is 14 mm and the male is 15 mm, whereas the largest *O. hova* female is 9 mm and males 5.0–9.5 mm, with most in the 7 mm range. We are not sure about the clypeus, mandible, punctation of the scutellum, and closeness of the antennal sockets as Benoit described; these do not seem significant. However, we emphasize the following characters: the sculpture of the propodeum of *O. gigantea* is more transverse (Fig. 10) than the more reticulate sculpture of *O. hova* (Fig. 16) and other *Orthogonalys* species; the color of both are similar, except that *O. gigantea* has the metascutellum yellow and the male has the metasomal tergites mostly black whereas the metascutellum of *O. hova* is orange and the metasomal tergites of the male are considerably orange; and the parameres of *O. gigantea* are dark orange and rounded at the apex (Fig. 13), whereas those of *O. hova* are white and more acute at the apex (Fig. 20).

This species is known only from northern Madagascar. The holotype and associated male were collected in the same area, around Diego Suarez, the two localities only about 50 km apart.

Orthogonalys hova Bischoff

http://species-id.net/wiki/Orthogonalys_hova Figs 14–20

Orthogonalos hova Bischoff, 1933: 485.-Bischoff 1938: 6.

Orthogonalos nova (sic): Benoit 1951: 143. Misspelling.

Orthogonalys hova: Weinstein and Austin 1991: 422, 429. –Carmean and Kimsey 1998: 54.

Type material. Bischoff (1933) stated "Eine Anzahl \Im von Madagaskar, Rogez, IX.30, X.30, X.-XI. 31, XII.32, sowie 2 \Im von Ambalavao, XII.30 und Ankaratra, I.31 (Seyrig S.)" and "Als Typus bezeichne ich ein Männchen von Rogez, X.31, als Allotypus das Weibchen von Ankaratra. Paratypen auch in Museum Paris." The holotype at MNHU is labeled "O. –Madagaskar, Rogez 10.31, Seyrig S "Orthogonalos hova Bisch. \Im Type 1933, det. Bischoff," "TYPUS," "Zool. Mus. Berlin." Also at MNHU there are six male paratypes and a female allotype as follows: same data as holotype (1 \Im), same data as holotype except 11.32 (2 \Im); "Madagascar, Rogez, X-30, A. Seyrig" and Bischoff det label "Paratype \Im " (1 \Im), same except IX.30 (1 \Im); "Madagascar, Ankasatan [?] 1.31, A. Seyrig" Υ "allotype 1933" ALLOTYPUS" (1 \Im), same except XII-30 without allotype label (1 \Im). Six paratypes were found at MNHN, all males from Rogez "X-30" (2), "X-31" (2), "XII.32" (1), "IX-30" (1).



Figures 14-15. Orthogonalys hova. 14 Female, lateral view. 15 Male, dorsolateral view.

Additional specimens examined. PROVINCE FIANARANTSOA: Parc National Ranomafana, Belle Vue at Talatakely, elev. 1020 m, 10–21 March 2003, 21°15.99'S, 47°25.21'E, coll. M. Irwin, R. Harin'Hala, California Acad. of Sciences, Malaise, sec-



Figures 16–20. *Orthogonalys hova*, male. 16 Mesosoma, dorsal view. 17 Head, front view. 18, Head, dorsal view. 19 Genitalia, dorsal view. 20 Apex of abdomen and genitalia, lateral view.

ondary tropical forest, MA-02-09C-56 (5 ♂); same data except following dates and code numbers: 15–28 May 2003, MA-02-09C-61 (6 3); 21 March – 12 April 2003, NA-02-09C-57 (4 3); 12–23 April 2003, MA-02-09C-58 (1 3); 28 May – 6 June 2003, MA-02-09C-62 (7 ♂); 6–18 June 2003, MA-02-09C-63 (3 ♂); 12–23 April 2003, MA-02-09C-58 (1 3); 16-26 February 2003, MA-02-09C-54 (3 3); 8-15 November 2001, MA-02-09C-02 (4 3); 28 Nov. – 8 Dec. 2001, MA-02-09C-05 (3 3); 15–21 Dec. 2001, MA-02-09C-07 (1 ♂); 16 Oct. – 8 Nov. 2001, MA-02-09C-01 (6 ්); 14–24 July 2002, MA-02-09C-35 (1 ්); 28 April – 5 May 2002, MA-02-09C-27 (2 ♂). Parc National Ranomafana, radio tower at forest edge, elev. 1130 m, 18–29 June 2003, 21°15.05'S, 47°24.43'E, coll.: M. Irwin, R. Harin'Hala, California Acad. of Sciences, Malaise, mixed tropical forest, MA-02-09B-64 (4 $\vec{\alpha}$); same data except following dates and code numbers: 7–18 June 2003, MA-02-09B-63 (5 Å); 7–17 May 2003, MA-02-09B-60 (4 ♂); 27 April – 7 May 2003, MA-02-09B-59 (5 ♂); 3–16 April 2003, MA-02-09B-57 (1 3); 20 March – 3 April 2003, MA-02-09B-56 (3 3); 9-20 March 2003, MA-02-09B-55 (8 ♂); 18-27 February 2003, MA-02-09B-53 (10 ♂); 27 June – 7 July 2003, MA-02-09B-65 (5 ♂); 6–17 July 2003, MA-02-09B-66 (8 중); 17-30 May 2003, MA-02-09B-61 (10 중); 15-27 April 2003, MA-02-09B-58 (8 중); 27 Feb. – 9 March 2003, MA-02-09B-64 (2 중); 14–24 June 2002, MA-02-09B-32 (3 ð). Manombo Special Reserve, camp site, 32 km SSE of Farafangana, 20 Jan - 2 Feb. 2005, 23°01.31'S, 47°43.20'E, California Acad. of Sciences, coll: M. Irwin, R. Harin'Hala, Malaise trap, lowland rainforest, elev. 36 m, MA-28-11 (1 3). Ranomafana JIRAMA waterworks, 15–22 November 2001, 21°14.91'S, 47°27.13'E, coll.: M. Irwin, R. Harin'Hala, California Acad. of Sciences, Malaise trap near river, elev. 690 m, MA-02-09D-03 (1 3); Parc National Ranomafana, Vohiparara, at broken bridge, 1110 m, 15-25 July 2002, 21°13.57'S, 47°22.19E, coll: M. Irwin, R. Harin'Hala, California Acad. of Sciences, Malaise trap in high altitude rainforest, MA-02-09A-35 (2 3); same data except following dates and code numbers: 14–21 January 2002, MA-02-09A-12 (1 3); 15–21 December 2001, MA-02-09A-07 (1 9, 1 3). PROVINCE TOAMASINA: Rogez (type locality; holotype and paratypes). PROV-INCE TOLIARA: Parc National de Zombitse, 19.8 km 84° E Sakaraha, elev. 770 m, 5–9 Feb. 2003, 22°50'36"S, 044°42'36"E, coll. Fisher, Griswold et al., California Acad of Sciences Malaise trap, in tropical dry forest, coll. Code BLF 7506 (1 \Im). Réserve Spéciale, Kalambatritra, Ampenihy, 23°27'49"S, 046°27'47"E, 9–10 February 2009, Calif. Acad. of Sciences, coll: B. L. Fisher et al., Malaise trap, montane rainforest, elev. 1270 m, BLF 21564 (1 d). Deposited at CAS, USNM, PT, MNHU, MNHN.

Description. Female (Fig. 14). Length, 7.0–9.0 mm Similar to male except metasoma more extensively white; mostly black on tergites 1 and 2, with decreasing amount of black toward apex.

Male. (Fig. 15). Length, 4.0–9.5 mm. Antenna black, antennomeres 9–15 white and sometimes apex of 8. Head white with vertex black, with black extending to dorsal margins of eyes, partly down outer orbits, down outer margin of gena and broad stripe medially to antennal sockets (Figs 17, 18). Clypeus with median broad black stripe (Fig. 17). Mesosoma orange. Legs orange. Wings hyaline with veins and stigma

black. Metasoma with tergites 1-3 orange to reddish brown, tergites 4 and 5 black and narrowly white at apices of tergites 5-7; tergites 2-5 with white lateral spots; sternites white except 4 and 5 with narrow black anterior margins. Male genitalia with gonostipes brown, paramere white.

Antenna with 26–28 antennomeres. Head from above almost straight behind, distance behind eyes about 0.8× eye length, with scattered fine punctures (Fig. 18). Mesoscutellum with anterior width slightly shorter than medial length. Metascutellum 2× broader than long. Propodeum with coarse reticulate sculpture (Fig. 16). Mesonotum shiny with small punctures separated by flat shiny interspaces mostly 2× or more puncture diameters. Male genitalia with paramere about 1.5× as long as broad, narrowing to acutely rounded apex (Fig. 20), about 0.8× length of gonostipes (Fig. 19).

Host. Benoit (1951) mentioned that a specimen was obtained by Seyrig from rearing of a limacodid moth.

Distribution. Madagascar: Antananarivo (Ankaratra, Benoit 1951), Fianarantsoa, Mahajanga (Andreba, Benoit 1951), Toamasina, Toliara Tanzania (Carmean and Kimsey 1998).

Remarks. See discussion under *O. gigantea* for characters separating the two species. This is the most commonly collected species in Madagascar and occurs from the lowlands to high altitude rainforests. We have examined about 130 specimens.

Orthogonalys maculata Bischoff

http://species-id.net/wiki/Orthogonalys_maculata Figs 21–28

Orthogonalos seyrigi f. maculata Bischoff, 1933: 485.-Bischoff 1938: 6.-Benoit 1951: 143.

Orthogonalys seyrigi maculata: Weinstein and Austin 1991: 422.

Type material. Holotype male at MNHU, labeled "O. –Madagaskar, Rogez 11.32, Seyrig S." "Orthogonalos seyrigi f. maculata Bisch. Type ♂ 1933, det. Bischoff" "TY-PUS" "Zool. Mus. Berlin." Bischoff (1933) stated "Als f. maculata n. f. bezeichne ich ein grosses Männchen aus Rogez, XI.32."

Additional specimens examined. PROVINCE ANTSIRANANA: Marojejy Nat'l Park, 5 km W Manantenina village, Camp Mantella, 18–30 May 2005, 14°26.29'S, 49°46.44'E, California Academy of Sciences, coll: M. Irwin, R. Harin'Hala, Malaise trap, low altitude rainforest, elev. 490 m, MA-31-22 (1 ♂); same data except 4–16 April 2005, MA-31-18 (1 ♂). PROVINCE FIANARANTSOA: Parc National Ranomafana, Belle Vue at Talatakely, elev. 1020 m, 16 Oct – 8 Nov. 2001, 21°15.99'S, 47°25.21'E,



Figures 21–22. Orthogonalys maculata. 21 Female, lateral view. 22 Male holotype, lateral view.



Figures 23–28. Orthogonalys maculata, male. 23 Mesosoma, dorsal view. 24 Head, front view. 25 Head, dorsal view. 26 Antenna. 27 Apex of abdomen and genitalia, lateral view. 28 Genitalia, dorsal view.

coll. M. Irwin, R. Harin'Hala, California Acad. of Sciences, Malaise, secondary tropical forest, MA-02-09C-01 (3 \Diamond); same data except follow dates and code numbers: 19–26 February 2002, MA-02-09C-17 (2 \Diamond); 21 March – 12 April 2003, MA-02-09C-57 (3 \Diamond); 10–21 March 2003, MA-02-09C-56 (1 \Diamond); 6–18 June 2003, MA-02-09C-63 (1 \Diamond). Parc National Ranomafana, radio tower at forest edge, elev. 1130 m, 6–17 July 2003, 21°15.05'S, 47°24.43'E, coll.: M. Irwin, R. Harin'Hala, California Acad. of Sciences, Malaise, mixed tropical forest, MA-02-09B-66 (1 \Diamond); same data except following dates and code numbers: 20 March – 3 April 2003, MA-02-09B-56 (1 \Diamond); 7–17 May 2003, MA-02-09B-60 (1 \Diamond). Ranomafana JIRAMA waterworks, 10–14 January 2002, 21°14.91'S, 47°27.13'E, coll.: M. Irwin, R. Harin'Hala, California Acad. of Sciences, Malaise trap near river, elev. 690 m, MA-02-09D-11 (1 \Diamond). PROVINCE TOAMASINA: Rogez (type locality, holotype \Diamond). Deposited in CAS, USNM, PT, MNHU.

Description. Female (Fig. 21). Length, 14 mm. Similar to male except metasoma white laterally and ventrally and tergites 1–4 mostly black dorsally, 5 and 6 black anteriorly.

Male. (Fig. 22). Length, 8.5–12.0 mm. Antenna black with antennomere 10 white at apex, 11–12 completely white, and 13–15 partly brown on lower surface and white on upper surface (Fig. 26) or 11–14 completely white. Head white with vertex black, black extending to dorsal margin of eyes, down posterior margin of gena, and anteriorly onto frons to antennal sockets (Figs 24, 25). Mesosoma anterior to transscutal articulation red, posterior to transscutal articulation black with mesoscutellum and metascutellum white; pronotum with anterolateral margins white and laterally white with broad black intermediate stripe; mesopleuron and mesosternum mostly white with black on dorsal margin and margins of mesepimeron black; metapleuron mostly white. Legs orange with hind tibia and basal half of basitarsomere darker, hearly black. Wings hyaline; veins and stigma black. Metasoma mostly orange; tergite 1 mostly black, tergites 2–6 orange with black spots at apices of tergites 5 and 6 and sometimes laterally on tergites 2 and 4, and apical tergite white. Male genitalia with gonostipes brown and paramere white.

Antenna with 28–29 antennomeres. Head from above nearly straight behind; distance behind eyes about $0.7 \times$ eye length (Fig. 25). Mesoscutellum as long as broad, anterior width $0.8 \times$ medial length; metascutellum about $1.4 \times$ broader than long. Propodeum with coarse reticulation anteriorly, 4 or 5 irregular transverse carinae posteriorly (Fig. 23). Mesonotum shiny, with fine punctures mostly separated by shiny interspaces $3 \times$ or more than puncture diameters. Male genitalia with paramere about $1.5 \times$ as long as broad, broadly rounded apically (Fig. 27); subequal to length of gonostipes (Fig. 28).

Distribution. Madagascar: Antsiranana, Fianarantsoa, Toamasina.

Remarks. The color of *O. maculata* is almost identical to *O. seyrigi*, which probably led to its description only as a form of that species by Bischoff (1933). Color differences in *O. maculata* include only 2–4 central antennomeres completely white, darker to black hind tibia and tarsus, and mostly black first metasomal tergite. *Orthogonalys seyrigi* has more antennomeres completely white, usually 6, orange hind tibiae and tarsi concolorus with the rest of the legs, and the first metasomal tergite orange. Other differences in *O. maculata* are the narrower mesoscutellum, which is slightly as long as broad (Fig. 23), and the paramere of the male genitalia which is long and white (Fig. 27), much more like the parameres of *O. gigantea* and *O. hova*, rather than the short, brown paramere of *O. seyrigi* (Fig. 39). Because of the similar male genitalia, we regard this species more closely related to *O. gigantea* and *O. hova* rather than to *O. seyrigi*.

Orthogonalys parahova Smith & Tripotin, sp. n.

urn:lsid:zoobank.org:act:99FB8068-7C7D-4C21-B2C8-EE08997CD0FA http://species-id.net/wiki/Orthogonalys_parahova Figs 29–34

Holotype. Male, labeled "Madagascar, Fianarantsoa, Parc National Ranomafana, Belle Vue at Talatakely, elev. 1020 m, 15–28 May 2003," "21°15.99'S, 47°25.21'E, coll. M. Irwin, R. Harin'Hala, California Acad. of Sciences, Malaise, secondary tropical forest, MA-02-09C-61" (CAS).

Paratype. "Madagascar, Fianarantsoa, Miandritsara Forest, 40 km S Ambositra, 20°47.56'S, 47°10.54'E, 5–19 March 2005," "California Acad. of Sciences, coll: M. Irwin, R. Harin'Hala, Malaise trap, in low altitude rainforest, elev. 825 m, MA-29-11" (1 ♂, CAS).

Description. Female. Unknown.

Male (Fig. 29). Length, 10.0 -11.0 mm. Antenna black; antennomeres 11 at apex, 12–15, and base of 16 white. Head white with vertex and upper frons black, black extending to dorsal margins of eyes and medially to near antennal sockets (Figs 31, 32); clypeus white. Mesosoma orange with posterior lateral angles of pronotum white and metascutellum yellow; pleura and sterna lighter orange than dorsum. Legs orange with hind tibia and tarsus black. Wings hyaline with veins and stigma black. Metasoma with tergite 1 mostly black, tergites 2–4 orange, tergite 5 mostly black, and tergites 6 and 7 white, narrow lateral edges of tergites white and sternites mostly white; genitalia with gonostipes brown and paramere white.

Antenna with 28–29 antennomeres. Head from above slightly emarginated behind; head behind eyes about $0.8 \times$ eye length (Fig. 32). Anterior width of mesoscutellum about $1.2 \times$ medial length; shallow, median longitudinal groove on posterior half (Fig. 30). Metascutellum $2 \times$ broader than long. Mesonotum shiny with closely set punctures, mostly separated by shiny interspaces $1 - 2 \times$ puncture diameters. Propodeum with irregular transverse carinae at center, more reticulate on sides (Fig. 30). Paramere of male genitalia about $1.8 \times$ as long as broad, broadly rounded at apex (Fig. 33), subequal in length to gonostipes (as in Fig. 28).

Etymology. From the species name "*hova*" with the Greek prefix "*para*" meaning resembling *O. hova*.



Figures 29-30. Orthogonalys parahova, holotype male. 29 Dorsolateral view. 30 Mesosoma and metasoma, dorsal view.

Remarks. This species is similar to *O. hova*, and initially we considered the two males as large specimens of that species. However, the following differences justify its recognition as a distinct species: antenna with only about 4 central antennomeres completely white; clypeus white; genae almost completely white; posterior angles of pronotum white; mesoscutellum with anterior width about longer than medial length and with distinct median furrow in posterior half (Fig. 30); and paramere of male genitalia longer, about 1.8 times as long as broad and rounded at its apex (Fig. 33). The parameres resemble the long, rounded parameres of *O. maculata*.



Figures 31–34. Orthogonalys parahova, holotype male. 31 Head, front view. 32 Head, dorsal view. 33 Apex of abdomen and male genitalia, lateral view. 34, Mandibles.

Orthogonalys seyrigi Bischoff

http://species-id.net/wiki/Orthogonalys_seyrigi Figs 35–39

Orthogonalos seyrigi Bischoff, 1933: 483.–Bischoff 1938: 6.–Benoit 1951: 143. Orthogonalys seyrigi seyrigi: Weinstein and Austin 1991: 422.

Type material. Bischoff (1933) stated "Eine Anzahl $\Im \Im$ und $\Im \Im$ liegen vo von [?] Madagaskar, Rogez, IX-XII. 30, II. 31, II. 32, X. 32, XI. 32 Seyrig S." and "Als Typus bezeichne ich ein Männchen von Rogez, II.31, als Allotypus ein Weibchen vom gleichen Fundort und Datum. Paratypen auch in Museum Paris." The holotype male at MNHU is labeled "Madagascar, Rogez, 11.31, A. Seyrig" "Orthogonalos seyrigi Bisch. Type \Im 1933, det. Bischoff" "TYPUS" "Zool. Mus. Berlin." There are also seven paratype males, five with the same data as the holotype except



Figures 35-36. Orthogonalys seyrigi, male. 35 Lateral view. 36 Mesosoma, dorsal view.

XII.30 (4) and II.31 (1), and two males labeled "O. –Madagaskar, Rogez 11.32, Seyrig S."

There are five paratypes at MNHN from Rogez, most in bad condition. Two are males, one with the antennae missing; one is a female, probably the only female in the



Figures 37–39. Orthogonalys seyrigi, male. 37 Head, front view. 38 Head, dorsal view. 39 Apex of abdomen and genitalia, lateral view.

original type series and the allotype designated by Bischoff, and is missing the head; two others are probably males but have the head and metasoma missing.

Description. Female. Known by female allotype as designated by Bischoff (1933) in MNHN. The head is missing but otherwise similar to male.

Male. (Fig. 35). Length, 8.0 - 9.0 mm. Antenna black with apex of 9th antennomere and antennomeres 10–15 completely white. Head white with vertex black, black narrowly extending to dorsal margin of eyes and as broad stripe anteriorly to antennal sockets; small medial black spot on dorsal margin of clypeus (Figs 37, 38). Mesosoma white laterally and ventrally with central dark stripe on pronotum; area anterior to transscutal articulation red, posterior to transscutal articulation black with mesoscutellum and metascutellum white. Legs orange with hind tibia and tarsus sometimes slightly darker orange than rest of legs. Wings hyaline; veins and stigma black. Metasoma mostly orange, base of first tergite black; lateral margins of tergites and posterior margins of sternites whiter. Male genitalia brown.

Antenna with 26 - 28 antennomeres. Head from above with posterior margin slightly concave; head behind eyes subequal to eye length (Fig. 38). Mesoscutellum with anterior width $1.1 \times$ medial length; metascutellum about $1.5 \times$ broader than long (Fig. 36). Dorsum of mesosoma shiny, with large punctures separated by $2-3 \times$ puncture diameters. Propodeum coarsely reticulate anteriorly, irregularly transversely cari-

nate posteriorly (Fig. 36). Genitalia with paramere short, about as long as broad and broadly rounded posteriorly (Fig. 39).

Distribution. Madagascar: Mahajanga (Andreba) (Benoit 1951); Toamasina. Tanzania (tentative identification, Carmean and Kimsey 1998).

Remarks. Bischoff (1933) described the species from both sexes. All types at MNHU are males, and all except one of those at MNHN are apparently males. The one female at MNHN is probably the allotype, but it has the head missing and therefore we cannot characterize the female. We have not seen specimens other than the type series.

The short parameres of the male genitalia (Fig. 39) relate this species to *O. brevis* (Fig. 6) but in *O. seyrigi* the parameres are about as long as broad, the genae are white, the white on the frons is interrupted by a broad median black stripe, and the meso-soma is red anterior to the transscutal articulation, and black posterior to it with the mesoscutellum and metascutellum white.

Trigonalys natalensis (Kriechbaumer)

http://species-id.net/wiki/Trigonalys_natalensis Fig. 40

Trigonalis Natalensis Kriechbaumer, 1894:318.

Trigonalys natalensis: Carmean and Kimsey 1998: 70.

Discenea natalensis madegassa Bischoff, 1933: 485.–Bischoff 1938: 9.–Benoit 1951: 141.–Paulian 1961: 207.–Weinstein and Austin 1991: 413.

Type material. Not examined. Kriechbaumer described this species from a female from "Port Natal 24.4.93", now Durban, South Africa. The holotype of *D. natalensis madegassa* Bischoff is in MNHU "8 QQ liegen vor von Madagaskar, Bekily, I., III, IV. 1932 und Ihosy, II.-III.1933 (Seyrig S.)" "Als Typus bezeichne ich ein Stück von Bekily, IV.1932." Three paratypes are in MNHN.

Specimen examined. PROVINCE FIANARANTSOA: Parc National Ranomafana, Belle Vue at Talatakely, elev. 1020 m, 5–13 May 2002, 21°15.99'S, 47°25.21'E, coll. M. Irwin, R. Harin'Hala, California Acad. of Sciences, Malaise, secondary tropical forest, MA-02-09C-28 (1 ♂, CAS)

Description. Female (Fig. 40). Length, 10.0 mm. Black with clypeus, area below antennal sockets, lower inner orbits, malar area, genae, large spots on 2nd metasomal tergite, small lateral spots on 3rd metasomal tergite, and posterior part of 2nd metasomal sternite white. Wings evenly lightly infuscated.

Male. Not seen.

Distribution. Madagascar: Fianarantsoa, Toliara (type locality of *D. natalensis madegassa*). Angola, Kenya, South Africa, Zimbabwe (Carmean and Kimsey 1998).

Host. Schultz (1910) stated that this was reared from an unidentified lepidopteran pupa.



Figure 40. Trigonalys natalensis, lateral view.

Remarks. We have seen only one specimen and do not characterize this species further. It is readily separated from the *Orthogonalys* species by its black antennae, mostly black body, and infuscated wings. Two subspecies may occur in Madagascar, the typical subspecies from Madagascar, without locality, and *T. natalensis madegassa* from only the two localities given by Bischoff (1933). We see no reason to distinguish subspecies at present.

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References

- Benoit PLG (1951) La systématique des Trigonaloidae (Hym.) éthiopiens. Revue de Zoologie et de Botanique Africaines 44 (2): 141–147.
- Bischoff H (1933) Beiträge zur Kenntnis der Trigonaloiden. Mitteilungen aus dem Zoologischen Museum in Berlin 19: 480–496.
- Bischoff H (1938) Trigonaloidae. In: Hedicke H (Ed) Hymenopterorum Catalogus, Pars 5. Dr.W. Junk, Gravenhage, 18 pp.
- Carmean D (1991) Biology of the Trigonalyidae (Hymenoptera), with notes on the vespine parasitoid *Bareogonalos canadensis*. New Zealand Journal of Zoology 18: 209–214.
- Carmean D, Kimsey L (1998) Phylogenetic revision of the parasitoid wasp family Trigonalidae (Hymenoptera). Systematic Entomology 23(1): 35–76. doi: 10.1046/j.1365-3113.1998.00042.x
- Carne PB (1969) On the population dynamics of the *Eucalyptus*-defoliating sawfly *Perga affinis affinis* Kirby (Hymenoptera). Australian Journal of Zoology 17: 113–141. doi: 10.1071/ZO9690113
- Huber JT, Sharkey MJ (1993) Structure, pp. 13–59. In: Goulet H, Huber JT (Eds) Hymenoptera of the World: An Identification Guide to Families. Research Branch, Agriculture Canada, Publication 1894E, 668 pp.
- Kriechbaumer J (1894) Hymenoptera Ichneumonoidea a medico nautico Dr. Joh. Brauns in itinere secundo ad oras Africae lecta. Berliner Entomologische Zeitschrift 39: 297–318. doi: 10.1002/mmnd.18940390215
- Murphy SM, Lil JT, Smith DR (2009) A scattershot approach to host location: Uncovering the unique life history of the trigonalid hyperparasitoid *Orthogonalys pulchella* (Cresson). American Entomologist 55: 82–87.
- Paulian R (1961) La zoogéographie de Madagascar et des iles voisines. Faune de Madagascar 13, Publications de l'Institut de Recherche Scientifique Tananarive – Tsimbazaza, 484 pp.
- Raff JW (1934) Observations on sawflies of the genus *Perga*, with notes on some reared primary parasites of the families Trigonalidae, Ichneumonidae, and Tachinidae. Proceedings of the Royal Society of Victoria 47: 54–77.
- Schulz WW (1910) Ein Beitrag zur Kenntnis der Lebensweise, Systematik und geographischen Verbreitung der Trigonaloiden. Entomologisk Tidskrift 31: 103–108.
- Weinstein P, Austin AD (1991) The host relationships of trigonalid wasps (Hymenoptera: Trigonalyidae), with a review of their biology and catalogue to world species. Journal of Natural History 25(2): 399–433. doi: 10.1080/00222939100770281

RESEARCH ARTICLE



Nesting habits, alternative nesting tactics and female territoriality of the cockroach-hunting solitary wasp *Penepodium luteipenne* (Hymenoptera, Sphecidae)

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Abstract

The nesting behaviour of the cockroach-hunting solitary wasp *Penepodium luteipenne* (Fabricius, 1804) is described, including five different nesting tactics: digging of new nests, use of pre-existing burrows in the soil, brood parasitism of open nests, brood parasitism of closed nests, and nest usurpation. Observations of a peculiar female territorial behaviour are also provided. Knowledge of the behaviour of other species of the tribe Podiini is summarized and compared with the behaviour of *P. luteipenne*. This study is based on nesting females observed in the Biological Reserve of Poço das Antas, an area in southeastern Brazil covered by Atlantic Forest.

Keywords

Behaviour, biology, cleptoparasitism, Podiini

Introduction

The genus *Penepodium* Menke, together with the genera *Podium* Fabricius, *Trigonopsis* Perty and *Dynatus* Lepeletier form a monophyletic group of Neotropical cockroach-hunting sphecid wasps (Bohart and Menke 1976, Ohl 1996a, b), currently classified as the tribe Podiini (Pulawski 2011a). The biology of the Podiini is known from short

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notes on some species (see Pulawski 2011b) and a few more extensive studies (e.g., Williams 1928, Eberhard 1974, Ribeiro and Garófalo 2010). In the present paper the nesting behaviour of *Penepodium luteipenne* (Fabricius, 1804) is described, including five alternative nesting tactics and a peculiar female territorial behaviour. Some aspects of the knowledge on the behaviour of the Podiini, especially motor patterns concerning nesting activity, are summarized, and compared with the behaviour of *P. luteipenne*. Larval behaviour and development of *P. luteipenne* was described by Buys (2009a). The presently studied species (the same as that previously studied by Buys 2001; 2009a; b) may not be the same as the species studied by Williams (1928) in Amazonian Brazil, as *P. luteipenne* (S.T. Amarante, personal communication). Even so, I here use the name *P. luteipenne* to refer to both of these biological entities, pending the completion of a revisionary study of the genus.

Methods

The study was carried out in the Biological Reserve of Poço das Antas (20°30'S, 42°15'W; cities of Silva Jardim and Casimiro de Abreu, Rio de Janeiro State), an area in southeastern Brazil covered by the Atlantic Forest. The area was visited every month from December 1994 to February 1997, with additional, sporadic, observations in 2001 and 2002. The complete construction and provisioning of about 90 nests of *Penepodium luteipenne* was observed, and several other nesting females were observed during various phases of the nesting cycle. Some females were marked with rapid dry enamel to facilitate individual observation. Coloured dots were placed on the dorsum or on the legs of the wasps with a small paintbrush while they were digging or closing their nests. It was almost always possible to mark the wasps without interrupting their activities. Prey items were measured with a micrometer and weighed with a digital balance while still alive. The prey items were put in transparent plastic sacs and carefully compressed in order to immobilize them for measurement. Voucher specimens of adult P. luteipenne and its prey items, as well original field notes and photographs, were deposited in the entomological collection of the Instituto Oswaldo Cruz (Rio de Janeiro, RJ) (Sandor Buys Collection - SB). Additional voucher specimens were deposited at the Museu Nacional - Universidade Federal do Rio de Janeiro (Rio de Janeiro, RJ) and the Museu de Zoologia - Universidade de São Paulo (São Paulo, SP).

Results

Habitat, nest structure and daily nesting activity

Nesting females were found at horizontal sites, without litter or low vegetation, on unpaved roads that crossed forested areas. The nests consisted of single celled burrows 3–5cm deep (n=15), with a narrower entrance tunnel 5–10mm in height (n=5). In cross section, the cells were circular with 12–15mm (n=8) in diameter, and the entrance tunnels were elliptical, the major axis with 9–12mm (n=16) and the minor axis with 6.5–8.5mm (n=16). Females usually appeared on the nesting site between 8:00–10:00 hrs and ceased activity from 16:00–18:00 hrs. They commonly remained rested on the ground at sites exposed to the sun before initiating activity, presumably to warm up.

Nesting site selection

Females selecting a nest site initially walked on the ground antennating the soil. They initially dug in several sites, and inspected crevices and other soil irregularities with their mandibles. Occasionally they entered nests of conspecific females or, more rarely, the nests of other ground-nesting wasp species. Usually, the females dug a number of short burrows before digging a nest. They did not close these abandoned tentative burrows.

Digging of new nests

When digging a nest a female *Penepodium luteipenne* cut the soil with her mandibles, accumulating lumps of earth in their mouthparts. She then stepped aside about 2–4 cm and tossed the earth a short distance with a flip of her head. A female would dig from opposite sides on the same axis. After digging for a few minutes on one side, she turned 180° and continued the excavation on the opposite side. The excavated earth thus formed two semi-circular mounds around the nest entrance (Fig. 1). Females periodically interrupted their excavations and left to gather water, which they regurgitated on the excavation site, apparently to soften the earth.

Nesting in pre-existing burrows in the ground

Female *Penepodium luteipenne* commonly reused pre-existing burrows. These almost always were old nests of conspecific females. The females usually found the old nests partially filled with earth, the remains of prey, and an empty cocoon. They spent some time excavating the burrows to recondition them. Although it was not possible to securely define the frequency of reuse of pre-existing burrows during this study, I estimate at least 25% of the observed nests were reused nests of conspecifics, and quite possibly more. Reused nests were recognisable because remains of cockroaches and the characteristic cocoons of *P. luteipenne* (see Buys 2001, 2009 for cocoon morphology) were found in the mounds of excavated earth left around the entrance.



Figures 1–5. Nesting behaviour of Penepodium luteipenne **1** Digging of the nest, the accumulated lose earth around the nest entrance is the earth excavated from the burrow **2** stinging of the prey **3** oviposition (setae in the wasp's front leg) **4** placement of the prey into the nest **5** female pushing a prey stuck in the nest entrance, using both the front and mid legs, and the opened mandibles.

Brood parasitism in open nests

Brood parasitism in open nests was observed twice. In the first case the female entered the nest of another female while she was absent and found prey items. She reacted quickly, moving her body and antennae, and performed the following behavioural sequence: (1) grasped one cockroach with her mandibles, (2) pulled the cockroach

outside the burrow, (3) stung it, (4) ate the egg of the host wasp, (5) laid her egg on the prey, (6) reinserted the cockroach into the nest and (7) departed. The host female later closed the nest apparently without perceiving the violation of her nest.

In the second case, the female followed the same behavioural sequence described above, but differed in that when she checked the base of the forelegs of the prey taken from the nest she did not find an egg of the host female, she laid her own egg on the prey and departed. Later the host female arrived at the nest with one more prey item and oviposited on it. The parasitized nest was thus left with two prey items bearing eggs.

Brood parasitism in closed nest

Brood parasitism in closed nests was observed three times. The cleptoparasitic females found recently closed, provisioned nests of other females. They opened the nest plug and followed the same behavioural sequence described above for brood parasitism in open nests (inclusive of eating the host egg), with the additional step that the cleptoparasitic female closed the nest herself.

Nest usurpation

Effective nest usurpation was observed only once, but agonistic behaviour among nesting females that apparently were attempts at nest usurpation was often observed. In the one unequivocal case of nest usurpation, the usurping female repeatedly approached a nesting female, who had been marked with enamel on one leg. Both wasps reacted aggressively, charging each other and sometimes rolling with each other on the ground. The resident female had placed two prey items into the nest, one of them with her egg, but she finally abandoned the nest, apparently due to the persistent aggression of the usurping female. The usurping female did not remove the original prey items from the nest but instead placed two more cockroaches in the nest, on one of which she laid an egg. The nest was thus left with four prey items, two of which bore eggs.

Nest provisions

The prey items from 64 nests were collected: 31 nests with one prey item, 23 nests with two prey items, seven nests with three prey items, and three nests with four prey items. A total of 109 epilamprine cockroaches (Blattodea: Blaberidae) was collected from the nests: 19 adults of *Poeciloderrhis catharina* (Shelford, 1910); 10 adults of *P. basistriga* (Walker, 1868); five adults of *Poeciloderrhis* sp.; 69 nymphs probably of *P. catharina*; and six nymphs probably of *P. basistriga*. Morphometric features taken from live prey items are summarized Table 1.

	Length	Ν	Width	Ν	Biomass (g)	Ν
Poeciloderrhis catharina	(21.7) 24.3 (25.5)	08	(10.4) 11.0 (12.2)	08	(0.26) 0.40 (0.68)	19
Poeciloderrhis basistriga	(14.0) 18.1 (25.0)	05	(07.0) 9.7 (11.8)	05	(0.13) 0.30 (0.46)	08
<i>Epilampra</i> sp.	(23.1) 24.5 (26.0)	02	(10.0) 10.6 (11.3)	02	(0.15) 0.26 (0.37)	02
Nymph type 1 (<i>P. catharina</i> ?)	(13.0) 18.3 (27.5)	46	(06.0) 10.2 (12.0)	46	(0.09) 0.21 (0.36)	66
Nymph type 2 (<i>P. basistriga</i> ?)	(17.5) 17.9 (18.3)	02	(09.5) 09.6 (09.7)	02	(0.16) 0.25 (0.36)	05

Table 1. Length, width and biomass of prey species found in nests of Penepodium luteipenne (minimum, mean and maximum in millimetre).

Prey transport

When transporting prey, a female *Penepodium luteipenne* initially grasped the antennae of the cockroach with her mandibles and dragged it, its body on ground, while walking forwards. The prey remained under the wasps' body, usually venter up. The females sometimes flew while carrying their prey, but the flights were rather clumsy and usually only in straight lines. On these occasions, a female would grasp the antennae of its prey with her mandibles and appeared to hold its body with her legs. The length of the flights seemed to be related to the distance of the prey from the nest and to the size of the prey. Usually longer distances were traversed in flight, especially when it is necessary to pass over areas with vegetation or abundant litter. On the other hand, the females had difficulty flying with larger prey items, so flight length decreased with increasing prey size. Thus, large prey items usually were carried on the ground or with a set of short flights, while small prey items were commonly carried by long flights.

Prey paralysis

The duration of the effects of the wasp's venom on its prey was relatively brief as cockroaches collected from nests just after closure were able to walk. Although the prey items transported by females apparently are always under the effect of its venom, suggesting that they sting the prey during the hunt, a female commonly stung again its prey at the nest site before placing it into the burrow. When stinging its prey a female grasped the pronotum of the cockroach with her mandibles, and stung the roach in different points on the ventral surface of its body (Fig. 2). Small prey specimens were immediately paralysed after the sting but females frequently needed to repeatedly sting larger prey items to subdue them before ovipositing on their body and placing them in the nest.

Oviposition

A female laid its egg on its prey before inserting it into the nest. This usually was done within 20cm of the entrance. Oviposition involved the following stereotypical behavioural sequence (Fig. 3): (1) the paralysed cockroach is placed dorsal side up; (2) the female wasp faces the cockroach; (3) she grasps the cockroach with her front and/or the mid legs; (4) she extends her hind legs, raising the anterior portion of the prey in a manner so that the prey body makes an acute angle to the ground; (5) she bends her gaster so that the tip of her metasoma reaches the region between the forelegs of the cockroach; and finally (6) oviposits behind one forecoxa. The eggs were always laid on the last prey item brought to the nest. Oviposition on this sheltered place probably reduces the probability of the cockroach dislodging the egg when it wakes from paralysis.

Placement of the prey into the nest

The females inserted the prey into the nest with its head inward. They positioned the head of the cockroach at the nest entrance and, extending their long hind legs, pushed the prey into the nest (Figs 4–5). The females use their front legs and mandibles to manipulate the prey, and their hind legs to maintain their own body on the ground (Figs 4–5). The cockroaches were difficult to maneuver within the nest because their widths were almost as broad as that of the nest cells (see Table 1). Frequently, the width of the cockroach was too large and they became stuck in the nest entrance. On these occasions, the females usually spent a long time attempting to push the prey into the nest. The wasp pushed with its mandibles open, using both its front and mid legs as well as vigorously beating its wings, apparently to increase its strength (Fig. 5). If this attempt failed, they tried to pull the cockroach out by grasping one of its legs, wings or the tip of its abdomen. If this was unsuccessful, they alternated pushing and pulling the prey. A total of 28 abandoned nests were found with cockroaches stuck in the entrance, some of these bearing a wasp's egg.

Nest closure and transport of water

Females quarried lumps of earth in the ground, usually from within 15cm of the nest entrance, and accumulated them in their mouthparts when closing their nests. The females carefully selected the site to quarry the earth, avoiding very compacted earth. They apparently were unable to accumulate loose soil in their mouthparts as they rarely used the loose soil near the entrance left from the nest excavation when closing their nests. On one occasion, a female was observed regurgitating water on loose earth which allowed her to accumulate the moistened soil in her mouthparts. The females placed the lumps of earth on the nest entrance without loosening them. They then regurgitated water, dissolving the earth lumps so that they perfectly fit the nest entrance. While females regurgitated water, their entire body vibrated, and they emitted a characteristic pulsing, buzzing sound. These vibrations apparently aided in dissolving the soil. Sometimes females returned repeatedly to the same site to quarry earth, but they did not form distinguishable accessory burrows. Sometimes the females removed little stones and leaf fragments that came with the lump of earth, after they placed the lumps on the nest entrance. Female wasps were often observed gathering water from the central tanks of bromeliads (Bromeliaceae) within five meter from the nest, but the most of the time it was not possible to determine the sources of water because they were in inaccessible places inside the forest. One female was observed collecting water in a temporary rain pool in an unpaved road while another female gathered water accumulated in a dried leaf fallen on the midst of a road, 175cm from her nest. Females commonly used the same water sources when digging and closing multiple, successively constructed nests.

During nest closure a female made 10-13 flights (n = 15) to gather water. Each load of water was used to wet 4–8 lumps of earth (n = 15). After the nest plug became level with the surface of the ground, the females usually added smaller lumps of earth, which they did not wet, and then placed over the nest entrance fallen leaves, chips, small stones, lumps of dried earth or other debris collected near to the nest. This made the nest entrance visually indistinguishable from the surrounding soil. On one occasion, a female regurgitated a few drops of water soon after concluding the nest closure, apparently to discard excess water. Females never made temporary nest closures. Some nests remained open through the night despite containing prey items.

Defence of the nest

Females of *Penepodium luteipenne* drove away other insects, both those walking within about 20–30 cm of the nests, and flies hovering over the nest entrance, throughout the nesting cycle. Females with open mandibles aggressively charged small objects (such as a stylus) placed near open nests. However, females did not defend nests after closing them. Several times nests were excavated to collect the prey items immediately after closure and the nearby female did not react.

Defence of the nesting site

Female *Penepodium luteipenne* typically dig a series of single celled nests, each within 5–50cm of one another. Occasionally during the nest cycle a female would traverse the site where she had constructed several nests and aggressively charge any other wasps she encountered, conspecific or not. This behaviour allowed her to monopolize

a particular nest area. This defensive behaviour was observed primarily during the following phases of the nesting cycle: (1) searching for a nesting site; (2) nest digging, when females often interrupted digging to walk around the nest site on repetitive routes; (3) foraging, when the female returned to the nest without prey, she usually checked the nest interior, and then walked about the nest site. Aggressive encounters among conspecific females were most frequent, but females of *P. luteipenne* also attacked other species such as *Eremnophila binodis* (Fabricius, 1789) (Sphecidae), *Trypoxylon aestivale* Richards, 1934 (Crabronidae), *Cerceris* sp. (Crabronidae), and *Pepsis* sp. (Pompilidae).

Discussion

Nest provisions

The prey species and number of prey items per nest in the tribe Podiini is summarized in the Table II. As a rule, Podiini use cockroaches to provision their nests, but crickets (Orthoptera: Gryllidae) were reported as prey of *Trigonopsis grylloctonus* Richards, 1937 (Richards 1937: unidentified grylids) and *Trigonopsis rufiventris* (Fabricius, 1804) (Vardy 1978: *Anaxipha* sp.) (Table 2). Females of the genera *Penepodium* and *Dynatus*, in general, use larger prey species than females of the genera *Podium* and *Trigonopsis* (Table 2).

Temporary closing of the nest

Penepodium luteipenne is similar to some other Podiini who do not construct temporary nest plugs [*Penepodium haematogastrum* (Spinola, 1851): Williams 1928; *Podium rufipes* Fabricius, 1805: Krombein 1970]. However, some other Podiini have been observed constructing temporary nest closures when nest provisioning is not completed in one day [*Trigonopsis cameronii* (Kohl, 1902): Eberhard 1974; *Podium denticulatum* F. Smith, 1856: Ribeiro and Garófalo 2010]. *Penepodium luteipenne* leave their nests open even on occasions when provisioning is not completed in one day.

Prey paralysis

Temporary paralysis of prey, as described here for *Penepodium luteipenne*, has been observed in several previously studied species of the genus [*P. fumipenne* (Taschenberg, 1869): Genise 1981; *P. gorianum* (Lepeletier de Saint Fargeau, 1845): Garcia and Adis 1993; *P. latro* (Kohl, 1902): Buys 2006; and Amazonian *P. luteipenne*: Williams 1928]. However, species of *Podium* and *Trigonopsis* seem to more permanently paralyze their prey (*P. fulvipes* Cresson, 1865: Genaro 1994; *P. luctuosum*

Podiini species	odiini species Prey species		Source
Dynatus nigripes	Eublaberus distanti (Kirby, 1903) Archimandrita tessellata (Rehn, 1903)	15	Kimsey 1978
	Hyporhicnoda (or near genus)	7	Cooper 1980
Penepodium fumi- penne	Unidentified cockroaches	4	Genise 1981
Penepodium goria- num	<i>Eunyctibora</i> sp.	1-4	Garcia and Adis 1993
Penepodium latro	Poeciloderrhis sp.	1	Buys 2006
Penepodium lu-	<i>Poeciloderrhis basistriga</i> (Walker, 1868) <i>Poeciloderrhis catharina</i> (Shelford, 1910)	1-4	Buys 2001, 2009a
teipenne	Epilampra abdomennigrum (De Geer, 1773)	-	Williams 1928
	Epilampra abdomennigrum (De Geer, 1773)	1-5	Richards 1937
Podium luctuosum	Parcoblatta uhleriana (Saussure, 1862)	5-7	Krombein 1967
Podium denticu-	<i>Cahita borero</i> Rehn, 1937 <i>Pseudomops neglecta</i> Shelford, 1906	2-11	Camilo et al. 1996
latum	Unidentified cockroaches	2-10	Ribeiro and Garófalo 2010
Podium fulvipes	<i>Euthlastoblatta</i> spp. <i>Cariblata</i> sp. <i>Latiblattella rehni</i> Herbard, 1917 <i>Epilampra</i> sp. <i>Plectoptera</i> sp.	-	Genaro 1994
	Parcoblatta pennsylvanica (De Geer, 1773)	1-3	Rau 1937
Podium rufipes	Chorisoneura texensis Saussure & Zehntner, 1893 Cariblatta lutea Saussure & Zehntner, 1893 Latiblattella rehni Herbard, 1917 Parcoblatta sp. Cariblatta minima Herbard, 1916 Eurycotis floridana (Walker, 1868)	3-6	Krombein 1967
	Chorisoneura texensis Saussure & Zehntner, 1893 Latiblattella rehni Herbard, 1917 Chorisoneura sp. Eurycotis floridana (Walker, 1868)	1-3	Krombein 1970
Trigonopsis came- ronii	ame- Riatia fulgida (Saussure, 1862) Chorisoneura translucida (Saussure, 1864) Amazonina sp.		Eberhard 1974
Trigonopsis cyclo- cephalus	onopsis cyclo- valus Poroblatta sp.		Vardy 1978
Trigonopsis gryl- loctonus	Unidentified crickets (Orthoptera: Gryllidae) ¹		Richards 1937
Trigonopsis rufiven- tris	Anaxipha sp. (Orthoptera: Gryllidae) ² Chorisoneura sp. Anaplecta sp. Calhypnorna sp.	-	Vardy 1978

Table 2. Summary of prey species and number of prey items per nest in species of the tribe Podiini.

^{1,2} These are unique cases of non-cockroach prey items found in Podiini nests
Smith, 1856: Krombein 1967; *P. rufipes*: Krombein 1967, 1970; and *T. cameronii*: Eberhard 1974).

Oviposition on the last hunted prey item

Oviposition on the first prey item stored in the nest has been observed among most of the Podiini studied to date (*Penepodium gorianum*: Garcia and Adis 1993; *Podium denticulatum*: Ribeiro and Garófalo 2010; *Podium rufipes*: Krombein 1970; and *Trigonospis cameronii*: Eberhard 1974). Only *P. luteipenne*, in this study, and the Amazonian *P. luteipenne* studied by Williams (1928), oviposit on the last hunted prey item.

Oviposition posture

The stereotypic oviposition posture observed in *Penepodium luteipenne* is similar to that of *Penepodium haematogastrum*, as illustrated by Williams (1928: fig. 188), and of *Trigonospis cameronii*, as illustrated by Eberhard (1974: fig. 4). However, the prey items used by *T. cameronii* are much smaller than those used by *P. luteipenne* and *P. haematogastrum*, and it uses only its front legs to hold its prey (see Eberhard 1974: fig. 4).

Oviposition outside the nest

Penepodium luteipenne, as well as other Podiini (Amazonian *P. luteipenne*: Williams 1928, *T. cameronii*: Eberhard 1974), is distinct in ovipositing on its prey outside the nest. An exception was observed by Ribeiro and Garófalo (2010) who found that *P. denticulatum* oviposited sometimes before and sometimes after placing its prey in the nest. The behaviour of ovipositing outside the nest may be due to the lack of space inside the nest such that the female cannot assume the characteristic oviposition posture necessary for her to oviposit on a forecoxa of her prey.

Placement of the egg on the prey body

Placement of the egg under one prey forecoxa, as described for *Penepodium luteipenne*, was found in previously studied species of Podiini [*Dynatus nigripes* (Westwood, 1852): Cooper 1980, Kimsey 1978; Amazonian *Penepodium luteipenne*: Williams 1928; *P. gorianum*: Garcia and Adis (1993); *P. latro*: Buys 2006; *Podium denticulatum*: Camilo et al. 1996, Ribeiro and Garófalo 2010; *P. luctuosum*: Krombein 1967; *P. rufipes*: Krombein 1970; *Trigonopsis rufiventris*: Williams 1928, Arlé 1933]. Garcia and Adis (1993) and Cooper (1980) observed, in *P. gorianum* and *D. nigripes* respectively, that the position of the egg under one forecoxa of the prey prevents the cockroaches from

dislodging the eggs. Furthermore, Podiini larvae partially penetrate the prey body at the point where the egg is laid and remain immobile during early development (Williams 1928, Krombein 1970, Garcia and Adis 1993, Buys 2009). This point must be a suitable place for the early instar larva to penetrate the prey and feed. Interestingly, the cockroach-hunting crabronid wasps (Hymenoptera: Crabronidae) *Tachysphex fanuiensis* Cheesman, 1928 (Williams 1945) and *Tachysphex inconspicuus* (W.F. Kirby, 1890) (Buys 2007) also lay their eggs under one prey forecoxa just as do the Podiini. This can be interpreted as an adaptive convergence.

Position of the prey inside the nest

Placement of the prey headfirst into the nest as observed in *Penepodium luteipenne*, was also found in all previously studied species of Podiini (*Penepodium gorianum*: Garcia and Adis 1993; *Podium denticulatum*: Camilo et al. 1996; *P. fulvipes*: Genaro 1994; *P. rufipes*: Krombein 1970; *P. luctuosum*: Krombein 1967; and *Trigonopsis cameronii*: Eberhard 1974). In *P. luteipenne*, the position of the prey inside the nest, coupled with the elliptical shape of the nest opening tunnel, which is narrower than the cell, apparently aids in preventing the cockroaches from escaping from the open nests after waking from paralysis.

Alternative nesting tactics

Intraspecific parasitism has been recorded for relatively few species of sphecid wasps (review in Field 1992b, see also Bohart and Menke 1976). However, as more detailed behavioural studies are performed on sphecid wasps, including observations with individually marked females, a number of distinct types of intraspecific parasitism have been found. Intraspecific parasitism may be widespread among sphecids, but it currently remains veiled by the paucity of studies. This seems to be the case for the tribe Podiini, in which distinct types of intraspecific parasitism were observed in *Penepodium luteipenne* and *Trigonopsis cameroni*, two species with detailed studies including individually marked females.

Female territoriality

The defensive behaviour of the females of *Penepodium luteipenne* at their nests can be interpreted as territorial because they monopolize their nesting sites and defend them against other wasps. Female territorial behaviour has been rarely observed among sphecids or related families. Territorial behaviour identical to those of *P. luteipenne* was observed in the ammophiline caterpillar-hunting wasp *Podalonia valida* (Cresson, 1865) (Hymenoptera: Sphecidae) (Steiner 1975) and in the spider-hunting *Anoplius viaticus* (Linnaeus,

1758) (Hymenoptera: Pompilidae) (Field 1992a). As these three species belong to distantly related lineages, this behaviour appears to be convergently evolved in these species. The evolution of this kind of territorial behaviour in *P. luteipenne* may be correlated with monopolization of an area rich in resources and defence of the nest against intraspecific parasitism. The nesting habitat of *P. luteipenne* is structurally complex, being composed of integrated parts with valuable resources relatively near one another. These include sites where the females search for suitable soil to dig (bare portions of compacted mud soil), sources of water (central cups of bromeliads), and prey items (areas covered with litter where the females can finds cockroaches). Although each of these resources may separately be locally common, a site with all these resources available nearby may not be easily found. At the same time, several clustered nests of one female could represent a form of resource concentration to cleptoparasitic conspecific wasps against which resident females must defend their nest areas. It is thus probable that once a female finds a suitable site, it will be advantageous to maintain it for some time, despite the energetic costs of defending it.

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References

- Arlé R (1933) Sobre a nidificação, a biologia e os parasitos de *Sceliphron (Trigonopsis) abdominalis*, Petry. Anais da Academia Brasileira de Ciências 5: 205–212.
- Bohart RM, Menke AS (1976) Sphecidae wasps of the world: a generic revision. University of California Press, 665 pp.
- Buys SC (2001) Last instar larva of *Penepodium dubium* (Hymenoptera: Sphecidae). Revista de Biología Tropical 49 (1): 327–330.
- Buys SC (2006) Observations on the biology and description of the last instar larva of *Penepodium latro* (Kohl, 1902) (Hymenoptera, Sphecidae). Arquivos do Museu Nacional 64: 121–124.

- Buys SC (2007) Comparative behavioural study of *Tachysphex inconspicuus* (Hymenoptera: Crabronidae) in two locations in the southeast Brazil. Neotropical Entomology 3: 327– 330. doi: 10.1590/S1519-566X2007000300001
- Buys SC (2009a) Larval behaviour and development of *Penepodium luteipenne* (Fabricius, 1804). Mitteilungen des Internationalen Entomologischen Vereins 34: 33–40.
- Buys SC (2009b) Sphecidae (Hymenoptera: Apoidea) of Rio de Janeiro State (Southeast Brazil): inventory of species and notes on biology and distribution. Arquivos do Museu Nacional 67: 275–282.
- Camillo E, Garófalo CA, Assis JMF, Serrano JC (1996) Biologia de *Podium denticulatum* Smith em ninhos armadilhas (Hymenoptera: Sphecidae: Sphecinae). Anais da Sociedade Entomológica Brasileira 25: 439–450.
- Cooper M (1980) Notes on the biology of *Dynatus nigrepes* (West.) and *Penepodium albovillosum* (Cam.) (Hym., Sphecidae). Entomologist's Monthly Magazine 116: 87–89.
- Eberhard WG (1974) The natural history and behaviour of the wasp *Trygonopsis cameronii* Kohl (Sphecidae). Transactions of the Royal Entomological Society of London 125: 295–328. doi: 10.1111/j.1365-2311.1973.tb00545.x
- Field J (1992a) Intraspecific parasitism and nest defence in the solitary pompilid wasp Anoplius viaticus (Hymenoptera: Pompilidae). Journal of Zoology 228: 341–350. doi: 10.1111/ j.1469-7998.1992.tb04613.x
- Field J (1992b) Intraspecific parasitism as an alternative reproductive tactic in nest-building wasps and bees. Biological Reviews 67: 79–127. doi: 10.1111/j.1469-185X.1992. tb01659.x
- Garcia MVB, Adis J (1993) On the biology of *Penepodium goryanum* (Lepeletier) in wooden trap-nests (Hymenoptera, Sphecidae). Proceedings of the Entomological Society of Washington 95: 547–553.
- Genaro JA (1994) Inquilinos de *Sceliphron assimile*, con enfase en *Podium fulvipes* (Hymenoptera: Vespidae, Sphecidae, Megachilidae). Caribbean Journal of Science 30: 270–272.
- Genise JF (1981) Utilización de excrementos de herbivoros en la nidificación de *Penepodium fumipenne* (Tacsh.) (Hymenoptera, Sphecidae). Ecosur 8: 51–52.
- Kimsey LS (1978) Nesting and male behavior in *Dynatus nigripes spinolae* (Lepeletier) (Hymenoptera, Sphecidae). Pan-Pacific Entomologist 54: 65–68.
- Krombein KV (1967) Trap-nesting Wasps and Bees: Life Histories, Nests and Associates. Smithsonian Institute Press, 570 pp. doi: 10.5962/bhl.title.46295
- Krombein KV (1970) Behavioral and life-history notes on three Floridian solitary wasp (Hymenoptera: Sphecidae). Smithsonian Contributions to Zoology 46: 1–26. doi: 10.5479/ si.00810282.46
- Ohl M (1996a) Die phylogenetischen Beziehungen der Sphecinae (Hymenoptera: Apoidea: "Sphecidae") aufgrund morphologischer Merkmale dos Exosckellets. Zoologische Beiträge, Neue Folge 37: 3–40.
- Ohl M (1996b) The Phylogenetic Relationships within the Neotropical Podiinae with Special Reference to *Podium* Fabricius (Hymenoptera: Apoidae: "Sphecidae"). Deutsche Entomologische Zeitschrift 43: 189–218. doi: 10.1002/mmnd.19960430204

- Pulawski WJ (2011a) Family group names and classification. Available from http://www.calacademy.org/research/entomology/Entomology_Resources/Hymenoptera/Sphecidae/ Family_group_names_and_classification.pdf [accessed on 16.06.2011]
- Pulawski WJ (2010b) Catalog of Sphecidae sensu lato. Available from: http://www.calacademy. org/research/entomology/Entomology_Resources/Hymenoptera/sphecidae/Genera_and_ species_PDF/introduction.htm [accessed on 12.07.2011]
- Rau P (1937) A note on the nesting habits of the roach-hunting wasp *Podium* (*Parapodium*) *carolina* Rohwer. Entomological News 48: 91–94.
- Ribeiro F, Garófalo CA (2010) Nesting behavior of *Podium denticulatum*. Neotropical Entomology 39: 885–891. doi: 10.1590/S1519-566X2010000600006
- Richards OW (1937) Results of the Oxford University expedition to British Guiana, 1929. Hymenoptera, Sphecidae and Bembecidae. Transactions of the Royal Entomological Society of London 86: 101–118. doi: 10.1111/j.1365-2311.1937.tb00427.x
- Steiner AL (1975) Description of the territorial behaviour of *Podalonia valida* (Hymenoptera, Sphecidae) females in southwest Arizona, with remarks on digger wasp territorial behaviour. Quaestiones Entomologicae 11: 113–127.
- Vardy CR (1978) A revision of the Neotropical wasp genus *Trigonopsis* Perty (Hymenoptera: Sphecidae). Bulletin of the British Museum of Natural History (Entomology) 37: 117– 152.
- Williams FX (1928) Studies in tropical wasps their host and associates. Bulletin of the Experimental Station of Hawaiian sugar Planter's Association (Entomological Series) 19: 1–179.
- Williams FX (1945) The aculeate wasps of New Caledonia, with natural history notes. Proceedings of the Hawaiian Entomological Society 12: 407–452.

SHORT COMMUNICATION



Wing wear is a poor estimate of age in Cerceris fumipennis (Hymenoptera, Crabronidae)

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The native, ground nesting, beetle hunting philanthine wasp *Cerceris fumipennis* Say is in development as a biosurveillance tool to detect Emerald Ash Borer (Agrilus planipennis) and other pest Buprestidae threatening the forests of North America (Marshall et al. 2005; Careless and Marshall 2010; Nalepa and Swink 2011). As part of that effort the North Carolina (NC) Department of Agriculture & Consumer Services has been working to determine the phenology and life history of C. fumipennis in the state, primarily to determine its activity overlap with prey species of interest. An examination of specimens in the NC State University Insect Museum indicated that C. fumipennis had been collected in Wake County, NC, as early as 24 May and as late as 22 September between 1921 and 1982, and Kurczewski and Miller (1984) noted that C. fumipennis probably has a partial second brood in the south. Observations of wing wear of C. fumipennis females in Wake County during 2009 suggested that there may be either an extended emergence of a single generation, or that more than one generation per year occurs in the state. During the third week of July, females with completely intact wings as well as females with severely damaged wing margins were both present in the same nesting aggregation. In 2010 a study was conducted at that aggregation, a baseball diamond in the Raleigh City Parks system, to determine if wing wear in C. fumipennis may be positively correlated with female age.

Shortly after nests began appearing at the site (30 May), females were captured and given a unique mark on the thorax using DecoColor opaque paint markers (Fig. 1a). A picture of each marked female's right wing was taken with a Sony Cybershot

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Figure 1. Technique used in attempting to determine number of *Cerceris fumipennis* generations per year based on wing wear. **A** Marked female; **B** Field photograph of right wing, showing reference points for analysis; **C**₁ Undamaged wing of Female #2 (30 May); **C**₂ Damaged wing 18 days later. **D** Plot of percent wing damage over time in 9 females, based on pixel counts of before (baseline) vs. after wings.

camera, and the wasp was then released. Subsequently, 11 visits were made to the site over the active season, and during each, an attempt was made to capture and examine all active wasps. If a female hadn't been previously captured, she was marked and her wing condition recorded. In all recaptured females, wing condition was documented if it had been more than 5 days since she was last seen. Four site visits were made during the first week of wasp activity; subsequently, visits were made at least every 2 weeks until the end of the active season at that site (26 July).

A total of 32 females were marked between 30 May and 12 July, and in 23 (72%) the wing was completely undamaged when the female was first captured. Nearly half (47%) of marked females were never recovered. Eight females were recaptured between 10 and 18 days after initial marking. One was found dead on the field 4 days after marking, an apparent casualty of a human foot. Wing damage in these nine wasps was analyzed using the before (baseline) and after photographs, based on the technique of Lehnert (2010). A standard portion of the wing was delineated in Adobe Photoshop^{*}

(Version 9.0.2) by drawing a line through two reference points: where vein Cu_{1b} meets the wing margin, and at the junction of M and 3r-m (Fig. 1b). That portion of the image was excised, the color removed, and the contrast adjusted so that the wing appeared black on a white background (Fig. 1c). ImageJ software (National Institute of Health, public domain) was then used to obtain pixel counts in the before and after wing tips to estimate percent wing damage. Percent damage was plotted against the number of days elapsed between the before and after photographs to determine if wing damage could be correlated with a given female's age.

The relationship between days elapsed and percent wing damage was inconsistent (Fig. 1d). A few females contributed to a trend of increased damage with time, but in others, the wings remain intact or nearly so over the same period. The wings of two females were completely unchanged over a 10-12 day interval. The results indicate that wing damage is of little use in assessing C. fumipennis age and consequently the number of generations of the wasp in central NC. Wing damage probably results primarily from digging and maintaining a nest and intraspecific aggression, and is therefore likely to be associated with behavioral variation. Females of C. fumipennis obtain nests by re-using their natal nest, digging a new one, or usurping one from another female; contention of nest ownership may involve brief fights (Mueller et al. 1992). A female that digs a nest in hard substrate, then defends it from a number of conspecifics would be prone to more wing wear than one that claims ownership of a relatively uncontested existing nest. Both substrate characteristics and nesting strategy, then, would contribute to variation in wing wear. Although not examined in the present study, mandibular wear may exhibit similar behavior dependent variation. In conclusion, wing wear is not an appropriate measure of female age in C. fumipennis, but the Lehnert (2010) technique may be of use in other hymenopteran taxa.

Acknowledgements

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References

- Careless P, Marshall SA (2010) Working with the smoky-winged beetle bandit. Bulletin de la Société d'entomologie du Canada 42: 25–29. [http://www.cerceris.info/pdf/esc_bulle-tin_%20careless&marshall.pdf]
- Kurczewski FE, Miller RC (1984) Observations on the nesting of three species of *Cerceris* (Hymenoptera: Sphecidae). Florida Entomologist 67: 146–154. doi: 10.2307/3494114
- Lehnert M (2010) New protocol for measuring Lepidoptera wing damage. Journal of the Lepidopterist's Society 1: 29–32.

- Marshall SA, Paiero SM, Buck M (2005) Buprestid sampling at nests of *Cerceris fumipennis* (Hymenoptera: Crabronidae) in southern Ontario: the first Canadian records of three buprestids (Coleoptera: Buprestidae). Canadian Entomologist 137: 416–419. doi: 10.4039/ n05-016
- Mueller UG, Warneke AF, Grafe TU, Ode PR (1992) Female size and nest defense in the digger wasp *Cerceris fumipennis* (Hymenoptera: Sphecidae: Philanthinae). Journal of the Kansas Entomological Society 65: 44–52.
- Nalepa C, Swink W (2011) Hemlock borers collected by the native wasp *Cerceris fumipennis* in the North Carolina mountains. North Carolina Pest News 26 (11): 7. http://ipm.ncsu. edu/current_ipm/pest_news.html

RESEARCH ARTICLE



A new species of *Hadrocryptus* (Hymenoptera, Ichneumonidae, Cryptinae), with the first account of the biology for the genus

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Abstract

A new species of the cryptine genus *Hadrocryptus* is described based on specimens reared from bamboo trap nests in Hong Kong. *Hadrocryptus perforator* sp. n. is an ectoparasitoid of aculeate Hymenoptera larvae and prepupae of the families Vespidae (Eumeninae) and Sphecidae. These are the first host records for this genus.

Keywords

Xenorhynchium, Zethus, Isodontia diodon, taxonomy, host, Sphecinae

Introduction

The subfamily Cryptinae is the largest subfamily of Ichneumonidae, with about 400 genera described to date (Yu et al. 2005; subsequent publications) and species of cryptine may be encountered commonly throughout much of the world. Where known, most species are idiobiont ectoparasitoids of prepupae or pupae of holometabolous in-

sects enclosed in cocoons or plant tissues, although the vast majority of species remain unknown biologically. Although individual species tend to have restricted host ranges (Schwarz and Shaw 1998), known hosts across the subfamily are varied and include members of Lepidoptera, Coleoptera, Diptera, Neuroptera, Raphidioptera and Hymenoptera as well as egg sacs of some Pseudoscorpionida and Araneae.

Hadrocryptus Cameron, 1903 belongs to a group of genera in the tribe Cryptini that are often referred to as the sub-tribe Gabuniina. Where known, gabuniines parasitise wood-boring beetles (Townes and Townes 1962), however there are no host records for most of the genera, including *Hadrocryptus* previously. Here we report on the biology of *Hadrocryptus perforator* sp. n. as a parasitoid of a common eumenine in Hong Kong, *Xenorhynchium* sp., and as an occasional parasitoid of another eumenine, *Zethus* sp., and a sphecid, *Isodontia diodon* (Kohl), in trap nests.

There are six described species of *Hadrocryptus*, found in India, Bhutan, the Philippines, Indonesia and Malaysia (Gupta and Gupta 1983); however, the species that was reared in Hong Kong represents an undescribed taxon.

Taxonomy

Morphological terminology follows Gauld (1991) but the species description is modelled on those provided by Gupta and Gupta (1983), who provide a key to the species of *Hadrocryptus* then known. Images of pinned specimens were taken with a Canon EOS 450D digital camera attached to a Leica MZ 16 stereomicroscope. Several partially focused images were combined using Helicon Focus v. 4.80 software. Trap nest content pictures were taken at various stages of the host and parasitoid development with a Nikon D200 equipped with a Nikorr 60mm macro lens and Sunpak R12 ring flash, a stainless steel ruler was placed in the frame to determine scale at editing. Pictures were edited using Nikon Capture NX and Adobe Photoshop CS2 softwares. Collection acronyms: BMNH – Natural History Museum, London; BPC – Barthélémy, private collection.

Recognition of Hadrocryptus

Apical flagellomere with truncate hammer. Face with horn just below and between antennal sockets. Clypeus with median tooth. Mandible with lower tooth longer than upper. Epomia short and weak. Mesoscutum short, slightly wider than long and no longer than area of propodeum behind anterior transverse carina. Groove between metapleurum and propodeum wide, crossed by carinae. Propodeum lacking pleural carina between anterior transverse carina and hind coxa. Propodeal spiracle elongate. Fore tibia swollen. First tergite with pronounced basal, lateral teeth; with elongate, dorsal depression at level of spiracles. Second tergite strongly punctate. Ovipositor lower valve with vertical teeth, dorsal lobe enclosing upper valve. Fore wing vein *cu-a* far basal to Rs+M. Hind wing with abscissa of *Cu* between *M* and *cu-a* longer than *cu-a*.

Hadrocryptus perforator Broad & Barthélémy, sp. n.

urn:lsid:zoobank.org:act:42AA95D5-15E8-40F5-913C-8A813439968E http://species-id.net/wiki/Hadrocryptus_perforator

Holotype. Female, exact label data: 'Pak Sha O, HK 50Q KK 242 849. 70m C. Barthélémy, 22.iii.10 Ref: 0386.A.Hy.1', 'Hong Kong Ex *Xenorhynchium* sp. in bamboo trap nest, coll. 7.2009, em. 3.2010 BMNH(E) 2010-74 AQ', BMNH. Paratypes: 1 female, same data as holotype but '20.iii.10 Ref: 0384.A.Hy.1', 1 male, same data as holotype but '13.vi.10 Ref: 0414.A.Hy.1' and 'Ex *Isodontia diodon* in bamboo nest em. 6.2010', both BMNH; 1 female same data as holotype, 1 female same data as holotype but '20.iii.10, ref.: 0383.A.Hy.1', 2 males same data as holotype but ' 03.iv.11 ref.: 0432.A.Hy.1' and ' Ex. *Zethus* sp.', all BPC.

Female. First flagellomere 7.0× as long as apically wide (basal 'annellus' section excluded). Frons largely polished, with weak punctures ventral to ocelli and some oblique wrinkling in a V-shape ventral to anterior ocellus. Vertex with conspicuous punctures, separated by more than twice their diameter. Facial horn, just below and between antennal sockets, large, pointed oval in dorsal view, protruding by distance slightly greater than inter-antennal distance (Fig. 1a). Face and clypeus closely punctate, punctures becoming confluent medially on face. Clypeus apically concave with obtuse, low median tooth.

Pronotum mostly smooth, transversely striate lateromedially with short transverse striae along posterior edge. Mesoscutum polished, weakly granulate anteriorly, with isolated punctures anteriorly, medially. Notauli strong to level of anterior edge of notauli, fading then. Scutellum with punctures on smooth background, separated by about their own diameter. Mesopleuron densely punctate, punctures small and separated by about their diameter, except transversely striate anterodorsally and medially, speculum and subalar prominence weakly punctate on smooth background. Metapleuron strongly punctate posterodorsally, sparsely punctate medially. Pleural carina absent except basally. Juxtacoxal carina strong but with narrow interruptions anteriorly and posteriorly. Submetapleural carina complete. Propodeum with area anterior of anterior transverse carina polished, punctate in posterior half; anterior transverse carina strong, complete; remainder of dorsal surface reticulate, transversely striate medially (Fig. 1c). First tergite polished, punctate on apical half, punctures coalescing medially, apically (Fig. 1c). Lower edge of first sternite with weak teeth, separated by more than their width. Second tergite with semicircular basal, median area defined by depression behind this; third tergite with basal area defined by shallower curve; second and third tergites densely punctate, punctures faint on successive tergites. Ovipositor (measured from tip of hypopygium) 2.1× length of hind tibia.

Mainly black with copious ivory/white markings (Fig. 1b). The following ivory: several median flagellomeres, face, clypeus (except for small basal, median black patch), horn on upper face, inner orbits to vertex, outer orbits to dorsal 0.7 of eye, central, median part of pronotum, lateral corners of median lobe of mesoscutum, central area on mesoscutum, tegula, short section of lateral carina of mesoscutum immediately anterior



Figure 1. Holotype female of *Hadrocryptus perforator* sp. n.; **a** head, dorsal view, showing horn; **b** whole body, dorsal view; **c** propodeum and base of metasoma, dorsal view.

to scuto-scutellar groove, subalar prominence, posteroventral patch on mesopleurum, scutellum, metascutellum, median longitudinal stripe on propodeum, interrupted posterior to transverse carina, widened posteriorly, metapleurum dorsally, posteriorly, fore and mid coxae (except tiny lateral black spot), extensive dorsal, posterior area on hind coxa, all trochanters (with brown dorsal stripe on mid and hind trochanters), fore and mid trochantelli, ventral patch on hind trochantellus, outer surface of fore and mid tarsomeres 1 to 3, all of hind tarsus except for apical patch on 5th, posterior bands on 1st to 7th tergites dull yellow or cream. Fore and mid femora and tibiae orange with dark brown dorsal stripes, fading to cream ventrally, hind tibia orange, apical 0.18 black, hind femur orange, apically and basally black-ringed.

Male. Similar to female, differs (in addition to the obvious sexual differences) only in the more extensive ivory area on the mesopleuron, extending anteriorly as lateral and median stripes on the mesosternum, and in the less modified antenna tip (simply pointed).

Remarks. *Hadrocryptus* is an easily recognised genus of the *Gabunia* genus-group (Gabuniina of Townes 1970), with its prominent facial tubercle in combination with several other characters (e.g. lateral, basal teeth on the first tergite, absence of the pleural carina). Gupta and Gupta (1983) revised the species of *Hadrocryptus*, which are restricted to the Oriental region. In Gupta and Gupta's key, *Hadrocryptus perforator* sp. nov. will key out to *H. ditissimus* (Tosquinet), from which it differs most obviously in the much weaker ventral teeth on the first sternite and the centrally white pronotal collar.

Biology of Hadrocryptus perforator

Materials and methods

Hadrocryptus perforator was reared from six trap nests placed in and collected from three locations in Hong Kong: (1) Ng Tung Chai, UTM 50Q KK 042 840, 140m asl, trap referenced as NTC-028.A4, set adjacent to a healthy 60+ year old forest on the slopes of Hong Kong's highest peak; (2) Sha Lo Tong, UTM 50Q KK 100 886, 180m asl, trap referenced as SLT-025.A1 and SLT-025.A4 of the same bundle, set adjacent to a Fung Shui wood behind an abandoned village; and (3) Pak Sha O, UTM 50Q KK 242 849, 70m asl, trap referenced as PSO-093.A3, PSO-117.A2 and PSO-117.A6 set in the first author's garden adjacent to a healthy secondary growth forest. All locations were in shaded environments.

The traps consisted of hollow bamboo canes of varied length and diameter that were cut so that one end was closed by a nodal septum. Clusters of four to seven cut canes were bundled together and hung from low branches on various bushes and trees. Dimensions of traps are given in Table 1

Upon collection, segments were placed in Ziploc^{*} bags and opened in the laboratory for content examination, the data are summarised in Table 2.

Trap reference	Date set	Date collected	Trap diameter (mm)	Trap length (mm)
SLT.025.A1	17-Apr-09	22-Feb-10	10	250
SLT.025.A4	17-Apr-09	22-Feb-10	10.5	253
NTC.028.A4	17-Apr-09	10-Jul-09	11	250
PSO-093.A3	12-Apr-10	03-Jun-10	7.5	165
PSO-117.A2	23-Jun-10	26-Sep-10	9	225
PSO-117.A6	23-Jun-10	31-Oct-10	8	225

Table 1. Trap physical dimensions and dates of Collection.

Observations & Discussion

At opening on 10 July 2009, trap NTC-028.A4 contained a single cell with a prepupal larva of *Xenorhynchium* sp., a gravid female mite (Acari) and a single egg of *Hadrocryptus* (Fig. 2), laid 4-5 mm from the host prepupal larva. The egg was slightly arched, 2.4 mm long with a more or less constant diameter of 0.46 mm. Upon hatching, the cryptine larva had to reach its host and probably fed externally on it. It took 21 days for the parasitoid to complete development, emerging as a male.

At opening on 22 February 2010, trap SLT-025.A1 contained seven cells with four prepupal larvae of *Xenorhynchium* sp. (Vespidae: Eumeninae) in cells 2, 4, 5 and 7 and three cocoons of *Hadrocryptus* in cells 1, 3 and 6 (Fig. 3). The desiccated integuments of the host larvae were also found in the parasitised cells. All three parasitoids were females. The first author witnessed the emergence of *Hadrocryptus perforator* from cell 1 and it took approximately three minutes for the cryptine to breach its cocoon (Fig. 5); the individual in cell 3 followed minutes afterwards.

Trap SLT-025.A4 contained six cells with five pre-pupal larvae of *Xenorhynchium* sp. and one cocoon of *Hadrocryptus* (Fig. 4) in cell 4 which also contained the desic-cated integument of the host larva. The single individual emerged as a female on 20 March 2010 when the first author inspected the trap content. The cryptine took approximately five minutes to breach the cocoon.

Trap PSO-093.A3 contained three cells fabricated by *Isodontia diodon* (Sphecidae: Sphecinae), a single male parasitoid emerged. Trap PSO-117.A2 contained two cells of *Xenorhynchium* sp., of which one was parasitised by *Hadrocryptus perforator*. Emergence of the parasitoid has not been witnessed at drafting of this paper. Trap PSO-117. A6 contained five cells of *Zethus* sp. (Vespidae: Eumeninae), of which two were parasitised. At opening there were five prepupal larvae of the host and two small larvae of the parasitoid in cell 1 and cell 3 (Fig. 7). Both emerged as males.

In all cases the parasitoid pupae were positioned head towards the trap entrance. By 14 March 2010, the *Hadrocryptus* pupae showed clear colour markings through the cocoon in both SLT-025.A1 and A4 traps (Fig. 6).

Four out of six parasitised nests were of *Xenorhynchium* sp., although a different eumenine was also host to the parasitoid and more surprisingly a sphecid. Data are too limited to say whether there is any taxonomic host preference. With development as an

Pre-pupal larva of Xenorhynchium sp.



Figure 2. Trap NTC-028.A4 at opening.



Figure 3. Trap SLT.025.A1 at opening.



Figure 4. Trap SLT.025.A4 at opening.



Figure 5. The emergence sequence of an adult *Hadrocryptus perforator* from trap SLT-025.A4.

Trap reference	Host sub- family	Host species	No. of host cells	No. of cells parasitized	Parasitoid emergence date	Males	Females
SLT.025.A1	Eumeninae	Xenorhynchium sp.	7	3	20-Mar- 2010 & 22- Mar- 2010		3
SLT.025.A4	Eumeninae	Xenorhynchium sp.	6	1	20-Mar-10		1
NTC.028.A4	Eumeninae	Xenorhynchium sp.	1	1	01-Aug-09	1	
PSO-093.A3	Sphecinae	Isodontia diodon	3	1	13-Jun-10	1	
PSO-117.A2	Eumeninae	Xenorhynchium sp.	2	1	?	?	?
PSO-117.A6	Eumeninae	Zethus sp.	5	2	3-Apr- 2011 & 04- Apr- 2011	2	
		Totals	24	9		4	4

Table 2. Contents of each trap.



Figure 6. Cell 4 of trap SLT-025.A4 showing the coloration of the pupa inside the cocoon.

idiobiont ectoparasitoid, it is probable that a variety of aculeate Hymenoptera in stem nests will be suitable as hosts.

The parasitoid's cocoons were 15.7-18.4 mm long (mean = 17.6 mm; n = 5) and 4.1-6.4 mm in diameter (mean = 5.3; n = 5). They were composed of a thin single layer of finely spun silk (0.06 mm thick; measured with a precision s/s calliper), shiny and brownish in colour yet translucent, affixed to the cell walls with numerous silk strands (Fig. 6). The meconium was discharged by the pupating larva internally at the anal end of the cocoon along with the shed integument.

There was no apparent spatial determinism in the location of the parasitised cells. Additionally, both male and female eumenine wasps emerged from the two SLT traps, so there was no apparent host sexual preference by the parasitoid.

Xenorhynchium sp. fashions cell partitions out of fine clay/soil with inclusion of sand grains, approximately 2-3 mm thick; however, *Hadrocryptus perforator* managed to per-



Figure 7. Larva of Hadrocryptus perforator feeding on prepupal larva of Zethus sp., trap PSO-117.A.6.

forate this obstacle without any apparent difficulty, creating an opening approximately 4 mm in diameter. Although *Zethus* sp. constructs thin cell partitions probably composed of glandular secretions, the first parasitoid to emerge from trap PSO-117.A6 did so by chewing its way through the trap walls (bamboo), rather than through the cell partitions.

As evidenced by trap NTC-028.A4 and PSO-117.A6, *Hadrocryptus* lays its egg well after the nest has been closed and sealed by the host. It does so by ovipositing through the trap walls (bamboo) and not by physically entering the nest, as shown by the intact partitions at tube opening. From the very limited data (tube SLT-025.A1 only) it seems that the parasitoid located in the outermost cell emerges first.

There was a 1:1 female to male ratio (n = 8) in the reared specimens.

The emergence of *Hadrocryptus perforator* was from March to August and its development time is approximately three weeks, therefore it can be inferred that this cryptine



Figure 8. Habitus of female *Hadrocryptus perforator*.

is multivoltine in Hong Kong, with the last generation overwintering as prepupal larvae or pupae. In fact the voltinism of this species might coincide with that of its hosts.

Conclusion

Although most host records of gabuniines are from wood-boring Coleoptera, reliable host records are in short supply and parasitism of stem-nesting aculeates may have evolved more frequently, as has been the case in Pimplinae (Gauld et al. 2002). The limited observations presented here are relevant as nothing was previously known about the biology of this genus. Further nest trapping of Aculeata may answer critical questions such as development time, voltinism and sex ratio, and particularly the mechanisms at play in host selection.

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References

- Gauld ID (1991) The Ichneumonidae of Costa Rica, 1. Memoirs of the American Entomological Institute 47: 1–589.
- Gauld ID, Wahl DB, Broad G (2002) The suprageneric groups of the Pimplinae (Hymenoptera: Ichneumonidae): a cladistic re-evaluation and evolutionary biological study. Zoological Journal of the Linnean Society 136: 421–485. doi: 10.1046/j.1096-3642.2002.00031.x
- Gupta S, Gupta VK (1983) Ichneumonolgia Orientalis, Part IX. The tribe Gabuniini (Hymenoptera: Ichneumonidae). Oriental Insects Monograph 10: 1–313.
- Schwarz M, Shaw MR (1998) Western Palaearctic Cryptinae (Hymenoptera: Ichneumonidae) in the National Museums of Scotland, with nomenclatural changes, taxonomic notes, rearing records and special reference to the British check list. Part 1. Tribe Cryptini. Entomologist's Gazette 49: 101–127.
- Townes HK (1970) The genera of Ichneumonidae, Part 2. Memoirs of the American Entomological Institute 12: 1–537.
- Townes HK, Townes M (1962) Ichneumon-flies of America north of Mexico: 3. Subfamily Gelinae, tribe Mesostenini. United States National Museum Bulletin 216: 1–602+i-viii.
- Yu DS, van Achterberg C, Horstmann K (2005) World Ichneumonoidea 2004. Taxonomy, biology, morphology and distribution. CD/DVD. Taxapad, Vancouver, Canada.

RESEARCH ARTICLE



A new species-group of Camptothlipsis (Braconidae, Agathidinae) from South Africa, with notes on the evolution of long mouthparts

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Abstract

A new species-group of *Camptothlipsis* (Hymenoptera: Braconidae: Agathidinae), Lingualongis, endemic to the Western Cape of South Africa is proposed and three new species are described, i.e., *Camptothlipsis lingualongis, Camptothlipsis aagota* and *Camptothlipsis inertusursus*. Phylogenetic analyses support this as a distinct monophyletic group within *Camptothlipsis*. The phenomenon of elongate mouthparts in Hymenoptera and the unusual multiple evolution of such within the agathidines is briefly discussed.

Keywords

Agathidinae, lingualongis, long mouthparts, systematics, phylogeny, endemism.

Introduction

Agathidinae (Hymenoptera: Braconidae) is an unusual subfamily of hymenopterans. It is found all over the world in most terrestrial habitats, has widely variable life history traits, and has been used several times for biological control (Sharkey et al. 2006). What makes this subfamily most unusual, however, is multiple, independent evolution of elongate mouthparts. Adult mouthparts have multiple functions within Hymenoptera including: emergence facilitation, phoretic copulation, defense, host handling, and nest excavation and construction (Jervis 1998). However, the most common use of hymenopteran mouthparts is to feed on nectar (Jervis 1998, Krenn et al. 2005). Long mouthparts, used for nectar extraction, only occur in a handful of families within Hymenoptera outside of Aculeata, i.e., Tenthredinidae, Pergidae, Braconidae, and Ichneumonidae (Jervis 1998, Krenn et al. 2005). Within Braconidae, elongate mouthparts occur in few subfamilies other than Agathidinae, i.e., Braconinae, Cardiochilinae, and Cheloninae (Jervis 1998, Krenn et al. 2005). As uncommon as the trait of long mouthparts appears to be, it is remarkable that agathidines have independently evolved elongate mouthparts at least five times including *Disophrys*, *Agathis*, *Lytopylus* (formerly part of *Bassus*), *Agathirsia* and Cremnoptini (Sharkey et al. 2006, Jervis 1998).

Here we report, a new species-group of *Camptothlipsis* with elongate mouthparts, the Lingualongis species-group, which is endemic to the Western Cape of South Africa (Fig. 1). Members of the Lingualongis species-group have mouthparts (both maxilla and labium) that are 1 to 1.5 times as long as their heads are high. We suggest two hypotheses in this paper to explain the extreme elongation of mouthpart in this group: 1) they are highly specialized nectar feeders and dependent on the flower of the plant on which their host lepidopterans feed or 2) that the long mouthparts facilitate the extraction of nectar from a wide variety of flowers with both shallow and deep nectaries.

Methods

The data from the specimens used to produce the cladogram in Fig. 2, with the exception of the new species-group specimen data, are from the data sets of Sharkey et al. (2006) and Sharkey et al. (2011). The *Camptothlipsis* specimens in this analysis are a subset of the total available sequences, representing all parts of the genus, in an effort to keep the data set small and manageable for this project.

Most of the material for this study was collected in Malaise traps set up throughout the Western Cape of South Africa, along with a few specimens from sweep samples, with dates ranging from 1997 to 2009. Specimens were sent to the Sharkey Lab in Lexington, Kentucky where they were treated in hexamethyldisilazane (HMDS), mounted, and labeled. Morphological terminology follows Sharkey and Wharton (1997). Images for this study were taken with an automontage imaging system, Archimed 5.2.2, mounted on a Leica Z16 ZP0 stereomicroscope and edited using Adobe Photoshop CS4.

Regions D2–D3 of 28S rDNA were sequenced using the following primers: 28SD2hymF 5' – AGAGAGAGTTCAAGAGTACGTG – 3' and 28SD3hymR 5' – TAGTTCACCATCTTTCGGGTC – 3'. Sequences were edited using Geneious Pro v4.7.5 (Drummond et al. 2009) and aligned based on a secondary structure model for Ichneumonoidea developed by Yoder and Gillespie (2004-present) and Gillespie et al. (2005). Regions of expansion and contraction (RECs), regions of slipped-strand



Figure 1. Mouthparts of *Camptothlipsis lingualongis*, a member of the species-group Lingualongis (left) compared with the mouthparts of a representative of the rest of the genus (right).

compensation (RSCs), and short regions of alignment ambiguity were further aligned/ corrected by eye (see supplementary file 1).

Phylogenetic trees were constructed using maximum parsimony and Bayesian analyses. Maximum parsimony analyses were performed using PAUP (Swofford 2002). A standard search of 1,000 replicates with 25% of trees saved was performed. The Bayesian analysis was performed using MrBayes v3.1.2 (Ronquist and Huelsenbeck 2003). Best-fitting DNA substitution models were determined using MrModeltest2.2 (Nylander 2004). The general time reversible model of evolution with a parameter for invariant sites and rate heterogeneity modeled under a gamma distribution (GTR+I+G) was determined as the best-fitting model.

Each Bayesian analysis consisted of two independent Bayesian runs initiated from different random starting trees. The analysis ran for 2,000,000 generations, reaching a topological similarity criterion of 0.005; trees were sampled every 200 generations. 25% of the trees from each run were removed as burn-in upon topological convergence.



Figure 2. A partial maximum parsimony cladogram of the subfamily Agathidinae. Consistency (**CI**) and retention (**RI**) index values are given at bottom left; branch support values are posterior probabilities/ bootstrap values.

See Appendix 1 for the data used to perform this analyses.

Specimen depository codes: HIC: Hymenoptera Institute Collection, University of Kentucky. SAMC: Natural History Department, Iziko South African Museum.

Results

The maximum parsimony and Bayesian analyses produced almost identical cladograms (the *Braunsia* clade varying with more or less polytomies). Branch support values (bsv) for the phylogenetic analyses are given as Bayesian posterior probabilities and parsimony bootstrap values, respectively, in Fig. 2, e.g., 63/56. Within the Lingualongis species-group, three different species are indicated in the molecular analysis, i.e. *Camptothlipsis inertusursus, Camptothlipsis lingualongis*, and *Camptothlipsis aagota. C. aagota* is strongly supported molecularly (bsv 0.99/73), and morphological characters (deep, foveolate no-taulus, long foveolate sternaulus, deeply punctuate propodeum and granulate first tergite) suggest further evidence for the species. *C. inertusursus* and *C. lingualongis* are more weakly supported as species molecularly (bsv -/- and 0.63/56 respectively), but distinct morphological characters (very long malar space, foveolate sternaulus, rugose propodeum, and smooth first metasomal tergite, vs. short malar space, smooth notauli, smooth sternaulus, and weak propodeal texturing, respectively) suggest independent species.

The clade containing the Lingualongis species-group is strongly supported molecularly (bsv 1.0/100) and morphological characters (distinctive long mouthparts) suggest further evidence for the species-group. Phylogenetic analyses place the new species-group within the genus *Camptothlipsis* (Fig. 2). However, since the support values that suggest this placement are rather weak (bsv 0.53/64), more molecular markers are necessary to falsify the hypothesis that the Lingualongis species-group does not deserve generic status as the sister clade to *Camptothlipsis*.

While almost 60 specimens were tested for viable DNA, only eight 28S sequences were obtained. The degradation of viable DNA could be due to unfavorable conditions, e.g. extreme heat, and/or improper storage conditions before specimens were obtained by the Sharkey Lab. Although not much can be done about the former, if the later is the problem, this can be avoided in the future by proper training and instruction to those tasked with storing specimens before distribution. Due to this inability to obtain viable DNA, and thus 28S sequences, from a larger range of specimens and the high variability of morphological characteristics, only three species are described in this paper. All other potential species (we expect there are approximately 10 of these) are lumped as "undescribed species" in the key.

Taxonomy

Lingualongis new species-group

Figs 3.a–3.e

Description. *Head* (Figs 3.c - 3.e) - Lateral carina of frons absent; lateral ocellus raised; interantennal space raised, converging into a single distinct anteromedial carina; antennal depression deep; scape simple; 20–35 flagellomeres, apical flagellomere slightly rounded; gena rounded posteroventrally; malar length slightly short-



Figure 3. Lingualongis species-group a wings b hind claw c anterior head d mouthparts e mandible.

er to 1½ times as long as the height of the compound eye in lateral profile; anterior tentorial pits deep and distinct; mandible with two teeth; galea 1.0–1.5 times as long as height of head; maxillary palpus five segmented, the fourth segment somewhat reduced, length of palp as long or longer than galea; labium slightly longer than galea, and slightly longer than head to 1.5 times longer; labial palpus four segmented, third segment highly reduced.

Mesosoma - Subpronopes separate, and shallow; notauli present; scutellar sulcus present, with numerous longitudinal carinae; metanotum smooth or with carinae; propodeum lightly granulate to deeply pitted to rugose; mesopleuron with mesopleural groove (sternaulus) present; metapleuron slightly rugose ventrally with a rounded point anteroventrally.

Metasoma - Median tergite 1 lacking pair of longitudinal carinae, distal width roughly 1 to 2 times basal width; median syntergum 2 + 3 smooth, with transverse depression separating terga 2 and 3; ovipositor length as long as metasoma + most of mesosoma to as long as entire body.

Wings (Fig. 3.a) - Fore wing: second submarginal cell absent; m-cu broken; 3RSb straight to slightly sinuate. Hind wing: R1 and r-m present; RS nebulous or spectral and sinuate; cu-a not tubular throughout, broken; CUb present as a nebulous or spectral vein.

Legs (Fig. 3.b) - Tarsal claws simple with a pointed basal lobe and 3–5 basal pectines; mid tibia with apical and sometimes subapical spines; hind tibia with apical spines.

Hosts/Biology. Unknown. Presumably they are koinobiont endoparasitoids of lepidopteran larvae. More specifically, caterpillars of the family Gelechiidae, many of which are agricultural pests, are good candidates for this group's hosts because, to date, the only host records for members of the genus *Camptothlipsis* are on Gelechiidae larvae (Sharkey et al. 2009). Judging from the long length of their ovipositors, the group's hosts, which are probably also endemic, are most likely concealed deeply within the host plant tissue.

Distribution. South Africa, Western Cape.

Etymology. From the Latin, *lingua* (tongue), and *longis* (long). The name refers to the very long mouthparts of this species-group.

Comments. Within this species-group the morphology and color are highly variable. The malar length range from slightly shorter to much longer than the height of the compound eye; the anterior face of the head ranges from wider than long to longer than wide; the notauli ranges from V-shaped to Y-shaped, distinctly foveolate to completely smooth; the scutellar sulcus is partitioned into 5 to about 9 sections. These can be almost rectangular to round; the lateral metanotum ranges from smooth to ridged; the sternaulus ranges from ½ to 3⁄4 the length of the mesopleuron, straight to wavy or curved, and can be foveolate to completely smooth; the propodeal sculpture ranges from almost smooth with some slight granulation, to deeply pitted, to rugose; the first metasomal tergite ranges from square-shaped to distinctly elongate, and although the sculpture is usually granulate, it can also be slightly rugose with some specimens being completely smooth. Body length ranges from 2mm to 8mm. Color ranges from completely black to completely orange-yellow with every combination in-between. Three species are described in this paper; however, there are most likely many more species in this species-group that remain to be described.

Key to species of the Lingualongis Species-Group







Species Descriptions

Descriptions are of the holotype, with species' variation given within parentheses, e.g., 33 (31–35).

Camptothlipsis lingualongis Tucker & Sharkey, sp. n. urn:lsid:zoobank.org:act:D9B7511B-DC36-453A-BCE3-CD6AB0BA3BFD http://species-id.net/wiki/Camptothlipsis_lingualongis Figs 4.a-4.i

Diagnosis. This is the largest and most distinctive species in the Lingualongis species-group. It is easily distinguished by its very long malar space, foveolate sternaulus, rugose propodeum, and its smooth or almost smooth first metasomal tergite

3



Figure 4. *Camptothlipsis lingualongis* **a** lateral habitus **b** lateral head **c** mesopleuron **d** dorsal habitus **e** dorsal thorax **f** propodeum **g** anterior head **h** hind tibial spines **i** first median tergite of metasoma.

(Figs 4.a - 4.i). It is also one of the few members of the group that is all or almost all orange.

Description. Holotype female; length: 7.5mm (4.7–7.5mm).

Head (Figs 4.b, 4.g) – 33 (28–33) flagellomeres; malar length about $1.1 \times$ eye height; glossa as long as head height (3.3 vs. 3.3mm); anterior face about as wide as high; ventral-most anterior edge of face shorter than greatest interantennal space; lightly covered with pale setae.

Mesosoma (Figs 4.c, 4.e, 4.f) - Median mesonotal lobe smooth except for faint beginnings of a carina anteromedially; notauli smooth, slightly extended posteriorly after joining medially; scutellar sulcus partitioned into 7 sections by longitudinal carinae; metanotum almost smooth, very faintly rugose; propodeum distinctly rugose, becoming almost areolate rugose posteromedially; sternaulus about ³/₄ length of mesopleuron, foveolate and slightly sinuate; metapleuron with some carinae, but mostly smooth, and lightly to densely covered with pale setae.

Metasoma (Fig. 4.i) - First median tergite slightly longer than wide (1.2mm vs. 0.96mm), apical width 2× basal width, sculpture smooth with some very faint beginnings of rugosity basally; ovipositor as long as mesosoma + metasoma.

Legs (Fig. 4.h) - Mid leg with 2 apical spines; hind femur length about $3.5 \times$ its width at widest point, hind tibia with 7 (7–10) apical spines, entire leg covered with pale setae.

Color - Orange-yellow except black as follows: median vertex of head, median mesonotal lobe apicomedially, posterolateral edges of mesoscutum, most of metanotum, apicomedial part (to all) of propodeum, 1st metasomal tergite basomedially, apical most part of last tergite, labrum and mouthparts, mesosternum and ovipositor sheath; antenna and wings brown, wing veins slightly darker brown.

Etymology. From the Latin, *lingua* (tongue), and *longis* (long). The name refers to the long mouthparts.

GenBank accession numbers. JN564494; JN564495.

Material Examined. HOLOTYPE: female, South Africa: Western Cape: Koeberg Nature Reserve, 33°37.62'S, 18°24.26'E, 3–31 Oct. 1997, S. van Noort, Malaise trap KO97-M12 (SAMC). PARATYPES: 1 female, South Africa: Western Cape: Kogelberge Nature Reserve, 34°16.48'S, 19°01.03'E, 16 Nov – 16 Dec 1999, S. van Noort, Malaise trap, KO98-M48 (HIC). 1 female, 2 males, South Africa: Western Cape: Mt. Rochelle, 5km S. of Franschoek, sweep, 10.i.2006, M. Buffington (HIC and SAMC) (accession number JN564495).

Camptothlipsis aagota Tucker & Sharkey, sp. n.

urn:lsid:zoobank.org:act:5515E4C5-1A8E-4F03-9A53-E9E716340FA8 http://species-id.net/wiki/Camptothlipsis_aagota Figs 5.a–5.i

Diagnosis. This species is distinguished by its deep, foveolate notaulus, long, foveolate sternaulus, deeply punctate propodeum, and granulate first median tergite (Figs 5.a - 5.i).

Description. Holotype female; length: 3.7mm (3.5–4.5mm)

Head (Figs 5.b, 5.g) – 23 (23–26) flagellomeres; malar length about 1x eye height; glossa slightly longer than head height (0.87 vs. 0.88mm); anterior face about as wide as high or slightly wider (0.83 vs. 0.80mm); ventral-most anterior edge of face shorter than greatest interantennal space; lightly covered with pale setae.

Mesosoma (Figs 5.c, 5.e, 5.f) - Median mesonotal lobe smooth with very faint, shallow pitting; notauli deep and foveolate (sometimes slightly extending posteriorly after joining medially); scutellar sulcus partitioned into 6 (5–9) sections by longitudinal carinae; metanotum very faintly rugose; propodeum moderately to deeply punctate; sternaulus about $\frac{4}{5}$ ($\frac{4}{5}$ - $\frac{3}{4}$) length of mesopleuron, foveolate and slightly sinuate; metapleuron $\frac{1}{2}$ ($\frac{1}{2}$ - $\frac{3}{4}$) punctate, somewhat densely covered by pale setae.

Metasoma (Fig. 5.i) - First median tergite slightly longer than wide (0.55 vs. 0.46mm), apical width 2x basal width, sculpture granulate; ovipositor as long as entire body.

Legs (Fig. 5.h) - Mid leg with 2 apical and 2 subapical spines; hind femur length about $3 \times$ as long as wide, hind tibia with 5 (5–8) apical spines, entire leg covered with pale setae.



Figure 5. *Camptothlipsis aagota* **a** lateral habitus **b** lateral head **c** mesopleuron **d** dorsal habitus **e** dorsal thorax **f** propodeum **g** anterior head **h** mid and hind tibial spines **i** first median tergite of metasoma.

Color - Head - Orange-yellow except black as follows: vertex, spot on dorsomedial face, clypeal pit area, labrum, and mouthparts. Antenna and mandible brown. *Meso-soma -* Black except orange-yellow as follows: pronotum, edges of notauli, two thick medial longitudinal bands on mesoscutum, posteromedial scutellum, longitudinal band above sternaulus, dorsomedial spot on metapleuron. *Metasoma -* Terga mostly black with some orange-yellow highlights, ovipositor yellow, ovipositor sheath black. *Wings -* Translucent to pale yellow-brown, veins brown to light brown. *Legs -* Yellow, except brown as follows: trochanter, basal patch on hind femur, apical tibia and tarsal segments. Hind coxa mostly black.

Etymology. The species is named after the first author's mother, Ågot Marga. **GenBank accession number.** JN564488; JN564489.

Material Examined. HOLOTYPE: female, South Africa: Western Cape: Anyskop Farm, (5.5 km 290°W Langebaanweg), Malaise trap 32°57.39'S 18°05.32'E, 8–25. ix.2002, S. van Noort, LW02-N7-M47, Sand Plain Fynbos (SAMC) (accession num-

ber JN564489). PARATYPES: 2 females, same locality data as holotype with dates 9–16.x.2002 and code LW02-N7-M98 (HIC and SAMC).

Camptothlipsis inertusursus Tucker & Sharkey, sp. n. urn:lsid:zoobank.org:act:746C4EC3-62DD-4432-ABCC-FDDF29C77FC5 http://species-id.net/wiki/Camptothlipsis_inertusursus Figs 6.a–6.i

Diagnosis. This species is distinguished by its short malar space, smooth notauli, smooth or almost smooth sternaulus, weak propodeal sculpture, and mostly black coloration (Figs 6.a - 6.i).

Description. Holotype female; length: 3.6mm (3.5–4.5mm).

Head (Figs 6.b, 6.g) - 22 (22-27) flagellomeres; malar length shorter than eye height (0.26 vs. 3.6mm); glossa longer than head height (0.80 vs. 0.70mm); anterior face about as wide as high; ventral-most anterior edge of face about same length as greatest interantennal space; lightly covered with pale setae.

Mesosoma (Figs 6.c, 6.e, 6.f) - Median mesonotal lobe smooth; notauli smooth, ending posteriorly where joined medially; scutellar sulcus partitioned into 7 (5–8) sections by longitudinal carinae; metanotum weakly to very weakly pitted; propodeum very weakly rugose, often appearing almost smooth, with a weak anteromedial carina; sternaulus about ³/₄ length of mesopleuron, smooth to very weakly foveolate; metapleuron mostly smooth with some weak rugosity around the ventral edges, moderately covered with pale setae.

Metasoma (Fig. 6.i) - First median tergite longer than wide (0.45 vs. 0.34mm), apical width slightly less than $2 \times$ basal width, sculpture granulate; ovipositor slightly longer than mesosoma + metasoma.

Legs (Fig. 6.h) - Mid leg with 3 (3–5) apical and 2 (2–3) subapical spines; hind femur length about 3x as long as wide, hind tibia with 10 (6–12) apical spines (occasionally 1 subapical spine), entire leg covered with pale setae.

Color - Black except yellow to orange as follows: longitudinal band on malar space, apex of antennal pedicel, base of first flagellomere, labrum, mandible, tegula, legs, 2^{nd} and 3^{rd} metasomal terga and ovipositor, coxa brown-black; wings translucent with brown to light brown veins.

Etymology. From the Latin *inertus* (lazy), and *ursus* (bear). The species is named for the first author's father, whom she thought would be amused by the name.

GenBank accession numbers. JN564490; JN564491; JN564492; JN565593.

Material Examined. HOLOTYPE: female, South Africa: Western Cape, 10km S. Clanwilliam, 32°13.39'S 18°50.50'E, 140m, 5–25.X.2004, sand plain fynbos, ME Irwin, FD Parker, M Hauser, MT, LW02-N2-M207 (SAMC). PARATYPES: 2 females, same locality and date data as holotype (HIC and SAMC) (accession number JN565593).



Figure 6. *Camptothlipsis inertusursus* **a** lateral habitus **b** lateral head **c** mesopleuron **d** dorsal habitus **e** dorsal thorax **f** propodeum **g** anterior head **h** mid tibial spines **i** first median tergite of metasoma.

Discussion

This species-group has type 1 mouthparts, i.e., the glossa extracts nectar and then in retracted within the galeae, which close around it and allow the liquid to be sucked into the alimentary canal (Pucci and Sharkey 2004). The extreme elongation of mouthparts in this group suggests two possibilities: 1) they are highly specialized nectar feeders and dependent on the flower of the plant on which their host lepidopterans feed or 2) that the long mouthparts facilitate the extraction of nectar from a wide variety of flowers with both shallow and deep nectaries. The first hypothesis is supported by the biology of *Agathis malvacearum* Latreille, adults of which commonly feed on the same plant as their hosts *Metzneria lappella* Linnaeus (Lepidoptera: Gelechiidae) i.e., burdock, *Arctium minus* Bernh (Juhala 1967). The second hypothesis is supported by bees such as *Apis mellifera* Linnaeus that feed on a wide variety of plants with multiple nectary morphologies.

Our preferred hypothesis is the first and we suggest that, like *A. malvacearum*, members of the Lingualongis species-group may have an obligate and symbiotic rela-

tionship with their host flowers, in that the host plant provides nectar and host lepidopterans, and the wasp pollinates and protects the plant by keeping host lepidopteran populations in check.

The Western Cape of South Africa is a biodiversity hotspot and its long term environmental stability allows for the survival of large concentrations of relict species, such as the stag beetle *Colophon montisatris* Endrödy-Younga, and encourages organisms to radiate and differentiate morphologically (Fjeldsa and Lovett 1997, National World Heritage Serial Site 2005). South Africa also has a huge number of smaller endemic organisms including 46 invertebrate families, 150 species of Apoidea, and over 6,000 species of plants (Picker and Samways 1996, Kuhlmann 2009, National World Heritage Serial Site 2005). Due to its endemism, the species-group is undoubtedly parasitic on an endemic group of moths, which most likely feed on host plants that are also endemic.

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References

- Drummond AJ, Ashton B, Cheung M, Heled J, Kearse M, Moir R, Stones-Havas S, Thierer T, Wilson A (2009) Geneious v4.7. http://www.geneious.com
- Fjeldsa J, Lovett JC (1997) Geographical patterns of an old and young species in African forest biota: the significance of specific montane areas as evolutionary centres. Biodiversity and Conservation 6: 325–346. doi: 10.1023/A:1018356506390
- Gillespie JJ, Munro JB, Heraty JM, Yoder MJ, Owen AK, Carmichael AE (2005) Secondary structural model of the 28S rDNA expansion segments D2 and D3 for chalcidoid wasps (Hymenoptera: Chalcidoidea). Molecular Biology and Evolution 22: 1593–1608. doi: 10.1093/molbev/msi152
- Jervis M (1998) Functional and evolutionary aspects of mouthpart structure in parasitoid wasps. Biological Journal of the Linnaean Society 63: 461–493. doi: 10.1111/j.1095-8312.1998.tb00326.x
- Juhala C (1967) Notes on parasitic Hymenoptera associated with a Gelechiid moth, *Metzneria lappella*, in the Common Burdock, and description of a new species of *Agathis* (Braconidae). Annals of the Entomological Society of America 60(1): 95–97.
- Krenn HW, Plant JD, Szucsich NU (2005) Mouthparts of flower-visiting insects. Arthropod Structure & Development 34: 1–40. doi: 10.1016/j.asd.2004.10.002
- Kuhlmann M (2009) Patterns of diversity, endemism and distribution of bees (Insecta: Hymenoptera: Anthophila) in southern Africa. South African Journal of Botany 75: 726–738. doi: 10.1016/j.sajb.2009.06.016
- National World Heritage Serial Site (2005) Cape floral region protected areas Western Cape & Eastern Cape provinces South Africa. United Nations Environmental Programme World Conservation Monitoring Centre.
- Nylander JAA (2004) MrModeltest v2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University.
- Picker MD, Samways MJ (1996) Faunal diversity and endemicity of the cape peninsula, South Africa – a first assessment. Biodiversity and Conservation 5: 591–606. doi: 10.1007/ BF00137611
- Pucci T, Sharkey M (2004) A revision of *Agathirsia* Westwood (Hymenoptera: Braconidae: Agathidinae) with notes on mouthpart evolution. Journal of Hymenoptera Research 13: 64–107.
- Ronquist F, Huelsenbeck JP (2003) MrBayes 3: Bayesian Phylogenetic inference under mixed models. Bioinformatics 19: 1572–1574. doi: 10.1093/bioinformatics/btg180
- Sharkey MJ, Laurenne NM, Sharanowski B, Quicke DLJ, Murray D (2006) Revisions of the Agathidinae (Hymenoptera: Braconidae) with comparisons of static and dynamic alignments. Cladistics 22: 546–567. doi: 10.1111/j.1096-0031.2006.00121.x
- Sharkey MJ, Parys KA, Clutts SA (2011) A new genus of Agathidinae with the description of a new species parasitic on *Samea multiplicalis* (Guenee). Journal of Hymenoptera Research (submitted). doi: 10.3897/jhr.23.1100
- Sharkey M, Yu D, van Noort S, Seltmann K, Penev L (2009) Revision of the Oriental genera of Agathidinae (Hymenoptera, Braconidae) with an emphasis on Thailand and interactive keys to genera published in three different formats. ZooKeys 21: 19–54. doi: 10.3897/ zookeys.21.271
- Sharkey MJ, Wharton RA (1997) Morphology and Terminology. In: Wharton RA, Marsh PM, Sharkey MJ (Eds) Manual of the new world genera of Braconidae (Hymenoptera). Special publication of the International Society of Hymenopterists, Washington, DC, 19–37
- Swofford DL (2002) PAUP version 4.0b10 for Macintosh. Sinauer Associates, Inc. Publishers, Sunderland, Massachusetts.
- Yoder M, Gillespie J (2004-present) jRNA Exploring insect phylogeny using RNA secondary structure. http://hymenoptera.tamu.edu/rna

Appendix I

Data used to perform the analyses. (doi: 10.3897/JHR.24.1909.app1). File format: NEXUS file (NEX).

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RESEARCH ARTICLE



Redescription of Mononeuron duguetiae Fischer (Braconidae, Doryctinae), a gall associated species on Duguetia furfuracea (St. Hil.) (Annonaceae)

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Abstract

We redescribe the poorly known, gall associated doryctine wasp *Mononeuron duguetiae* Fischer (Braconidae) based on museum and recently collected material. This species shares various morphological features with the members of the also gall associated *Allorhogas* Gahan, suggesting their close relationship. A Bayesian phylogenetic analysis using mitochondrial (COI) and nuclear (28S) markers recovered *M. duguetiae* within a clade with another five gall associated doryctine genera + *Heterospilus* Haliday. Surprisingly, *M. duguetiae* was recovered, though with low support, as the sister taxon of a *Monitoriella* Hedqvist + *Labania* Hedqvist clade, and not closely related to *Allorhogas*. Information is provided about the galls on *Duguetia furfuracea* (St. Hil.) (Annonaceae) where the specimens of *M. duguetiae* were reared.

Keywords

redescription, Braconidae, Doryctinae, gall associated, Mononeuron

Introduction

The braconid subfamily Doryctinae is a cosmopolitan, highly diverse group of parasitoid wasps containing more than 1,300 described species (Yu et al. 2005), although this probably only represents half of its actual species diversity (Jones et al. 2009). Species of this subfamily are grouped into about 200 recognized genera, some of which are considerably species rich with wide geographical distributions (e.g. *Heterospilus* Haliday, *Spathius* Nees, *Notiospathius* Matthews and Marsh, *Allorhogas* Gahan).

The doryctine genus *Mononeuron* Fischer was erected by Fischer (1981) to contain a single species, *M. duguetiae* Fischer, reared from galls on *Duguetia furfuracea* (St. Hil.) (Annonaceae) at a locality in the state of São Paulo, Brazil. In this work, Fischer distinguished *Mononeuron* from other doryctine genera by its reduced hind wing vein cu-a, first metasomal tergite without wing-like projections, and remaining metasomal tergites without grooves. These features, however, are also present in other doryctine genera. *Mononeuron duguetiae* instead appears to be morphologically very similar to the species of the mainly New World *Allorhogas* Gahan, which are also known to be gall associated.

Here, we redescribe *M. duguetiae* based on museum (including the holotype specimen) and recently collected material, and provide information about the galls where the species was reared. We also employed one mitochondrial (mt) [cytochrome oxidase I (COI)] and one nuclear [28S ribosomal (r) RNA gene] marker to elucidate the phylogenetic affinities of this taxon.

Methods

All the specimens examined in this study were collected in the type locality of the species, the vegetation of which consists of the remains of Brazilian savannah ('cerrado') forest owned by the Universidade Federal de São Carlos, in São Carlos, São Paulo, Brazil. Some of the specimens were reared from galls on *D. furfuracea* in February of 2011. The specimens were preserved in 100% ethanol and kept at -20°C until they were mounted or processed for DNA sequencing. The examined material is deposited in the Departamento de Ecologia e Biologia Evolutiva, Universidade Federal de São Carlos, São Carlos, SP, Brazil (DCBU), the Colección Nacional de Insectos, Instituto de Biología, Universidad Nacional Atónoma de México (CNIN IB-UNAM), and the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina (MACN).

The terminology employed follows Sharkey and Wharton (1997), except for the surface sculpture, which follows Harris (1979). Colour digital photographs were taken and edited with a Leica[®] Z16 APO-A stereoscopic microscope, a Leica[®] DFC295/DFC290 HD camera, and the Leica Application Suite[®] program. Digital SEM photographs were taken with a FEI QuantaTM 250 SEM in low vacuum mode.

Phylogenetic affinities of Mononeuron based on DNA sequence data

The phylogenetic placement of *Mononeuron* was assessed using DNA sequences of one fast evolving (629 bp of the COI mtDNA gene) and one slow evolving [-650 bp of

the second and third domain regions of the 28S rRNA gene] gene marker. Two COI and one 28S sequence were generated from specimens of *M. duguetiae* (COI: Gen-Bank accession nos JQ320372-3; 28S: GenBank accession no. JQ320371). Protocols for genomic DNA extraction of the samples (using a non-destructive technique) and amplification of the PCR products were the same as those employed by Ceccarelli et al. (2012). Amplification of the COI and 28S products employed the LepF1/LepRI (Hebert et al. 2004) and the 28Sfwd/28Srev primers (Belshaw and Quicke 1997; Mardulyn and Whitfield 1999), respectively. PCR products were sent directly to the High-Throughput Genomics Unit at the University of Washington (http://www.ht-seq.org/index.html) for sequencing. All sequences were edited using Sequencher 4.1.4 (Gene Codes Corp.).

COI genetic distances between the two sequenced specimens of *M. duguetiae* and among these and previously published sequences of species belonging to *Heterospathius*, *Heterospilus* and to the gall associated doryctine genera *Allorhogas* Gahan, *Labania* Hedqvist, *Monitoriella* Hedqvist, *Percnobracon* Kieffer & Jörgensen and *Psenobolus* Reinhard were calculated using the K2P distance model (Kimura 1980) with PAUP version 4.0b10 (Swofford 2002). GenBank accession numbers for the above taxa are found in Zaldívar-Riverón et al. (2008). *Heterospilus* was recovered in previous studies as the sister group of a clade with the species of the above gall associated doryctine genera (Zaldívar-Riverón et al. 2007, 2008). The phylogenetic affinities of *M. duguetiae* were assessed by including the 28S and COI sequences of one specimen of *M. duguetiae* in a previously published COI+28S matrix (Zaldivar-Riverón et al. 2008) composed of 94 species belonging to 64 different doryctine genera. This matrix excluded the regions of ambiguous alignment detected for the 28S marker from the analyses performed.

A Bayesian MCMC partitioned analysis was run with MrBayes version 3.1.2 (Ronquist and Huelsenbeck 2003) through the University of Oslo bioportal (http://www.bioportal.uio.no/). The analysis employed two simultaneous runs of 10 million generations each, using four chains, default priors, and four partitions, one for 28S and three for COI according to its first, second and third codon positions. The evolutionary model employed for each partition was obtained with MrModeltest version 2.3 (Nylander 2004) and PAUP version 4.0b10 (Swofford 2002) using the Akaike information criterion. The first five million sampled trees of each run were deleted and the remaining trees were pooled to build a majority rule consensus tree, considering posterior probability (PP) of clades \geq 0.95 as significantly supported (Huelsenbeck and Ronquist 2001).

We used a Bayesian approach (Buckley et al. 2002; Reeder 2003) to test for an alternative topology not present in the 50% majority rule consensus trees derived from the two simultaneous analyses. This alternative topology places the three included specimens of *Allorhogas* and *M. duguetiae* as monophyletic. Details about this approach are found in Zaldívar-Riverón et al. (2008).

Results

Phylogenetic relationships

Corrected COI genetic distances between the two specimens of *M. dugetiae* and among the latter specimens and the species belonging to other gall associated genera were of 0.5% (3 bp) and of 13.5 to 16.5% (71 to 86 bp), respectively. Corrected COI distances among species of the above gall associated taxa and species of *Heterospilus* varied from 14.4 to 21.1 % (79 to 111 bp). Our Bayesian phylogram recovered the same major doryctine clades obtained in Zaldívar-Riverón's (2008) phylogenetic study: a South American, an Australian, a Holcobraconini, and an African-Holarctic-Madagascan clade. Within the South American clade, *M. duguetiae* is nested within a significantly supported clade (PP= 1.0) composed of members belonging to the five gall associated doryctine genera and the included species of *Heterospilus* Haliday (Fig. 1). This latter clade is composed of two subclades, one (PP = 0.92) with *Perconobracon* at the base of a monophyletic *Allorhogas* (PP = 0.96) that are sister to a cluster containing *M. duguetiae* and *Monitoriella* + *Labania* (PP = 0.94), and a second one with a *Heterospilus* + *Heterospathius cluster* that is sister to *Psenobolus* (PP = 0.95).



0.2 subst./site

Figure 1. Part of the Bayesian phylogram obtained in this study showing the phylogenetic affinities of *M. duguetiae* Fischer with respect to other gall associated doryctine genera (see results for details of the complete reconstructed topology). Numbers near clades represent posterior probabilities.

The Bayesian test showed that the alternative topology with the three included specimens of *Allorhogas* and *M. duguetiae* as monophyletic is present in some of our 95% credible set of trees sampled from Bayesian analysis. We therefore cannot statistically reject the paraphyly of *Allorhogas* with respect to *M. duguetiae*.

Taxonomy

Mononeuron Fischer

http://species-id.net/wiki/Mononeuron

Mononeuron Fischer, 1981: 47–51 (original description); Marsh 1997: 214 (Key); Yu et al. 2005 (catalogue).

Type species. Mononeuron duguetiae Fischer

Diagnosis. *Mononeuron* may be distinguished from the remaining doryctine genera by having the following combination of features: frons excavated; occipital carina meeting hypostomal carina; propodeum with semicircular or subtriangular shaped basal median areas (Fig. 2C); fore wing vein r-m present (Fig. 3C); first subdiscal cell of fore wing open at apex (Fig. 3C); hind wing vein SC+R absent (Fig. 3D); hind wing vein cu-a absent or spectral (Fig. 3D); hind wing vein 1A incomplete (Fig. 3D); hind wing vein M+CU equal to or slightly greater than vein 1M (Fig. 3D); hind wing vein m-cu slightly curved toward wing apex or straight to wing margin but never angled toward wing base (Fig. 3D); hind coxa with a distinct baso-ventral tubercle; basal sternal plate of first metasomal tergum less than 0,25 length of tergum; metasoma sculptured on first three terga (Fig. 2C); ovipositor apex strongly sclerotized and with a single nodus (Fig. 2D).

Mononueuron is morphologically similar to *Allorhogas*, but it can be distinguished from members of this genus by having the vertex at least partially striate (Fig. 2B) (coriaceous in all described species of *Allorhogas*); hind wing vein SC+R absent (present in all described species of *Allorhogas* except *A. ingavera* Marsh); hind wing vein cu-a absent or spectral (sclerotized or nebulose in most described species of *Allorhogas*, only spectral in *A. argentinus* Brèthes and *A. shawi* Marsh); hind wing vein 1A incomplete (always reaching vein cu-a in other described species of *Allorhogas*); ovipositor long, about 1.5 times length of metasoma (Fig. 3B) (generally shorter than metasoma in most of the described species of *Allorhogas*, longer than metasoma in *A. gallicola* Gahan).

Mononeuron duguetiae Fischer, 1981: 47–51.

http://species-id.net/wiki/Mononeuron_duguetiae

Description. Female. *Colour*: Body and first three flagellomeres honey yellow, remaining flagellomeres, fifth tarsomeres and ovipositor sheath light brown (Fig. 3B). *Body*



Figure 2. *Mononeuron duguetiae* Fischer (holotype, female) **A** head and mesosoma, lateral view **B** head and mesoscutum, dorsal view **C** metasoma, dorsal view **D** ovipositor.

length: 2.5 mm; ovipositor 2.5 mm. Head: Clypeus smooth, face and frons smooth, frons slightly excavated, vertex slightly striate laterally and anteriorly, smooth posteriorly (Fig. 2B), temple and gena smooth (Fig. 2A); eye 1.45 times higher than wide (lateral view); malar space 0.45 times eye height (lateral view); temple 0.46 times eye width (dorsal view); ocular-ocellar distance 3.3 times diameter of lateral ocellus; length of scape 1.4 times its width (frontal view); antenna with 20 flagellomeres. Mesosoma: Length of mesosoma 1.5 its maximum height; pronotum smooth laterally, pronotal collar short (Fig. 2A); pronotal groove weakly scrobiculate, propleuron smooth; mesoscutal lobes coriaceous; notauli shallow but distinct, obscured before scutellum at middle of mesoscutum in a costate-rugose area (Fig. 2B); scutellar disc slightly coriaceous; median length of scutellar sulcus 0.33 times median length of scutellar disc, with six carinae (Fig. 2B); mesopleuron coriaceous, weakly coriaceous medially (Fig. 2A); subalar groove scrobiculate; precoxal sulcus wide, smooth, 0.5 length of mesopleuron; venter of mesosoma slightly coriaceous; metapleuron strongly rugose; propodeum with a pentagonal areola diverging at the base of propodeum, areolar area rugose, basal median areas coriaceous (Fig. 2C). Wings: Fore wing length 2.75 times its maximum width, length of pterostigma 3.2 times its maximum width, vein r about 0.5 times length of vein 3RSa, vein 3RSb reaching the wing margin as a tubular vein; vein m-cu interstitial to vein 2RS, vein 1cu-a distinctly postfurcal with vein 1M (Fig. 3C); hind wing vein SC+R absent; vein cu-a absent (Fig. 3D); vein m-cu nebulous (Fig. 3D); vein 1A reduced, only present basally; vein M+CU about equal length of vein 1M (Fig. 3D). *Legs*: Fore tibia with a row of 12 spines; hind femur weakly coriaceous, length 3.86 times its maximum width; hind coxa weakly striate dorsally, coriaceous laterally, with a distinct basal tubercle. *Metasoma*: Length of first metasomal tergum 0.9 times its apical width, median area slightly coriaceous basally, costate-rugose laterally, with complete longitudinal lateral carinae; dorsope present, acrosternite 0.2 times length of first metasomal median tergite; second metasomal median tergite longitudinally costate (Fig. 2C); third metasomal median tergite costate on basal half, smooth on apical half (Fig. 2C); remaining metasomal median tergites smooth; ovipositor 1.8 times length of metasoma. Ovipositor strongly sclerotized apically, with a single nodus (Fig. 2D).

Male. Slightly smaller than female. Body length 2.0–2.5 mm; hind femur swollen, length 2.35 times its maximum width.

Variation. Females: Antenna with 16–21 flagellomeres; scutellar sulcus with 5–6 carinae.

Biology. We collected 20 leaves of *D. furfuracea* infested with galls at the type locality of *M. duguetiae* in February of 2011. All leaves were placed in a plastic bag and maintained at room temperature. Each of the collected leaves had between three to 10 spheroidal galls with a maximum diameter of approximately 1 cm (Fig. 3A). Twenty five specimens of *M. duguetiae* emerged from the galls a few days after being collected, and two or more individuals were observed to emerge from each gall. Moreover, two specimens of an unidentified cecydomiid species and the following wasp taxa emerged after most of the specimens of *M. duguetiae* had emerged: Torymidae (six specimens belonging to an unidentified species), Eurytomidae (13 specimens of an unidentified species), Eulophidae (21 individuals of an unidentified species), and Diapriidae (one unidentified species), whereas others are generally phytophagous (e.g. Eurytomidae). We could not confirm that *M. duguetiae* is the species that induces the above galls, though its early emergence suggests that it might be cecidogenic.

Comments. The genus *Mononeuron* has been mainly characterised by the absence of hind wing vein cu-a. This feature was employed to distinguish the genus in the key to New World doryctine genera provided by Marsh (1997). We found that some of the examined specimens of *M. duguetiae* have hind wing vein cu-a spectral (*sensu* Mason 1986) but present. Some described species of *Allorhogas* also have a nebulous or even spectral hind wing vein cu-a (e.g. *A. argentinus, A. shawi*; Marsh 2002).

In our Bayesian analysis, *M. duguetiae* was more closely related to *Monitoriella* and *Labania* than to the species of *Allorhogas*, although with marginally non- significant support. This contrasts with our morphological examinations, which show that there are various external morphological features in *M. duguetiae* shared with species of *Allorhogas*. The latter genus is a mainly Neotropical and Nearctic group with 33



Figure 3. A Galls on *Duguetia furfuracea*. B–D *Mononeuron duguetiae* Fischer (holotype, female).B Habitus, lateral view C fore wing D hind wing.

described and an undetermined number of undescribed species. Among the features shared by *M. duguetiae* and members of *Allorhogas* are an excavated frons, hind wing vein r-m present, pronotal collar very short or absent, propodeum usually with semicircular or subtriangular shaped basal median areas, basal sternal plate of first metasomal tergum less than 0.25 length of tergum; metasoma sculptured on first three terga, hind coxa with small but distinct basal tubercle, fore wing vein r-m present, first subdiscal cell open at apex, and hind wing vein m-cu usually curved toward wing apex, often straight to wing margin but never angled toward wing base. Further molecular phylogenetic studies employing additional markers and more taxa, especially for the species of *Allorhogas*, will confirm the relationships of *M. duguetiae* with respect to other gall associated doryctine genera.

We also examined various specimens assigned to *M. duguetiae* deposited in the DCBU collection that show some morphological differences, and which might represent an undescribed species. These specimens were collected in the type locality of *M. duguetiae* and all of them were reared from the same type of galls on *D. furfuracea*. They differ from our concept of *M. duguetiae* by having the vertex, mesopleuron and basal areas of propodeum mostly smooth, and the first metasomal median tergite smooth and with brown colour. Further molecular data will allow us to confirm whether this represents an undescribed species of *Mononeuron* or intraspecific variation within *M. duguetiae*.

Examined material. Holotype (DCBU).–Female. Brazil, São Carlos, São Paulo, geschlüpft von Gallen von *Duguetia furfuracea* ST. HILL. (Annonaceae). Other examined material: 31 specimens, 12 males, 19 females. Twelve specimens: Brazil, SP, São Carlos, UFSCar, Cerrado forest, 21°58'7.96"S, 47°53'9.68"W, ex. *Duguetia furfuracea*

galls, 26 January 2011, A. Zaldívar-Riverón and J. Nunes coll. Nineteen specimens: same locality as above, 18 March to11 April 2008, A. M. Penteado-Dias, coll.

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References

- Belshaw R, Quicke DLJ (1997) A molecular phylogeny of the Aphidiinae (Hymenoptera: Braconidae). Molecular Phylogenetics and Evolution 7: 281–293. doi: 10.1006/ mpev.1996.0400
- Buckley TR, Arensburger P, Simon C, Chambers GK (2002) Combined data, Bayesian phylogenetics, and the origin of the New Zealand cicada genera. Systematic Biology 51: 4–18. doi: 10.1080/106351502753475844
- Ceccarelli FS, Sharkey MJ, Zaldívar-Riverón A (2012) Species identification in the taxonomically neglected, highly diverse, Neotropical parasitoid wasp genus *Notiospathius* (Braconidae: Doryctinae) based on an integrative molecular and morphological approach. Molecular Phylogenetic and Evolution 62: 485–495. doi: 10.1016/j.ympev.2011.10.018
- Fischer M (1981) Versuch einer systematischen Gliederung der Doryctinae, insbesondere der Doryctini, und Redeskription nach Material aus den Naturwissenschaftlichen Museum in Budapest (Hymenoptera: Braconidae). Polskie Pismo Entomologiczne 51: 41–99.
- Harris RA (1979) A glossary of surface sculpturing. Occasional Papers in Entomology 28: 1–31.
- Hebert PDN, Penton EH, Burns JM, Janzen DH, Hallwachs W (2004) Ten species in one: DNA barcoding reveals cryptic species in the neotropical skipper butterfly *Astraptes fulgerator*. Proceedings of the National Academy of Sciences 101: 14812–14817. doi: 10.1073/ pnas.0406166101
- Huelsenbeck JP, Ronquist FR (2001) MRBAYES: Bayesian inference of phylogenetic trees. Bioinformatics 17: 754–755. doi: 10.1093/bioinformatics/17.8.754

- Jones OR, Purvis A, Baumgart E, Quicke DLJ (2009) Using taxonomic revision data to estimate the geographic and taxonomic distribution of undescribed species richness in the Braconidae (Hymenoptera: Ichenumonoidea). Insect Conservation and Biodiversity 2: 204–212. doi: 10.1111/j.1752-4598.2009.00057.x
- Kimura M (1980) A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. Journal of Molecular Evolution 16: 111–120. doi: 10.1007/BF01731581
- Mardulyn P, Whitfield JB (1999) Phylogenetic signal in the COI, 16S, and 28S genes for inferring relationships among genera of Microgastrinae (Hymenoptera; Braconidae): evidence of a high diversification rate in this group of parasitoids. Molecular Phylogenetics and Evolution 12: 282–294. doi: 10.1006/mpev.1999.0618
- Marsh PM (1997) Doryctinae. In: Wharton RA, Marsh PM, Sharkey MJ (Eds) Manual of the New World genera of the family Braconidae (Hymenoptera). International Society of Hymenopterists, Special Publication 1: 207–233.
- Marsh PM (2002) The Doryctinae of Costa Rica (excluding the genus *Heterospilus*). Memoirs of the American Entomological Institute 70: 1–319.
- Mason WRM (1986) Standard drawing conventions and definitions for venational and other features of wings of Hymenoptera. Proceedings of the Entomological Society of Washington 88: 1–7.
- Nylander JAA (2004) MrModeltest v2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University, Sweden.
- Reeder TW (2003) A phylogeny of the Australian Sphenomorphus group (Scincidae: Squamata) and the phylogenetic placement of the crocodile skinks (*Tribolonotus*): Bayesian approaches to assessing congruence and obtaining confidence in maximum likelihood inferred relationships. Molecular Phylogenetics and Evolution 27: 384–397. doi: 10.1016/S1055-7903(02)00448-7
- Ronquist F, Huelsenbeck JP (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19: 1572–1574. doi: 10.1093/bioinformatics/btg180
- Sharkey MJ, Wharton RA (1997) Morphology and Terminology. In: Wharton RA, Marsh PM, Sharkey MJ (Eds) Manual of the New World genera of the familiy Braconidae (Hymenoptera). Special publication of the International Society of Hymenopterists, no. 1: 19–37.
- Swofford DL (2002) Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. In. Sunderland, Massachusetts: Sinauer Associates.
- Yu D, van Achterberg K, Horstmann K (2005) World Ichneumonoidea. 2004. Taxonomy, Biology, Morphology and Distribution. Taxapad, Vancouver, Canada.
- Zaldívar-Riverón A, Belokobylskij SA, León-Regagnon V, Martínez JJ, Briceño R, Quicke DLJ (2007) A single origin of gall association in a group of parasitic wasps with disparate morphologies. Molecular Phylogenetics and Evolution 44: 981–992. doi: 10.1016/j. ympev.2007.05.016
- Zaldívar-Riverón A, Belokobylskij SA, León-Regagnon V, Briceño-GR, Quicke DLJ (2008) Molecular phylogeny and historical biogeography of the cosmopolitan parasitic wasp subfamily Doryctinae (Hymenoptera: Braconidae). Invertebrate Systematics 22: 345–363. doi: 10.1071/IS07028

RESEARCH ARTICLE



Two new species of *Pambolus* (Hymenoptera, Braconidae) from Jamaica

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Abstract

Pambolus albospina **sp. n.** and *Pambolus rastafari* **sp. n.** are described from Jamaica. *Pambolus rastafari* can be distinguished from all other Neotropical species of the genus by its antennal color pattern and the smooth sculpture of the head and mesoscutum. *Pambolus albospina* is morphologically close to *P. hemitaeniatus* van Achterberg, from which it can be distinguished by the number of white antennal segments and the sculpture on the first metasomal tergite. These two new species constitute the first records of the genus for the Caribbean Islands.

Keywords

Caribbean, Hormiinae, Pambolinae, Taxonomy

Introduction

Pambolus Haliday is a braconid genus with 42 currently valid species from all biogeographic regions (Yu et al. 2005). It has been included in the subfamily Hormiinae (Whitfield and Wharton 1997) or in the small subfamily Pambolinae (van Achterberg 1995; Braet and van Achterberg 2003; van Achterberg and Braet 2004; Yu et al. 2005). In this paper we follow the latter classification since Whitfield and Wharton's (1997) concept of Hormiinae includes a heterogeneous array of genera and does not represent a natural group as revealed by a previous phylogenetic study of the cyclostome subfamilies of Braconidae (Zaldívar-Riverón et al. 2006). Currently, two subgenera are recognized within *Pambolus*, the typic subgenus includes all species with reduced wings, whereas *Phaenodus* gathers all macropterous forms (Braet and van Achterberg 2003).

In the Neotropical Region, *Pambolus* includes 12 described mainland species that are distributed from Honduras to northern Argentina (Yu et al. 2005). Specimens of *Pambolus* are fairly commonly observed in hymenopteran samples, though its species are not particularly abundant (Shaw and Huddelston 1991). Nine of the twelve recognized Neotropical species were described based on single females, and only one, *P. hebes* Papp, is known from both sexes (Papp 1996). The biology of species of *Pambolus* is largely unknown. Shaw and Huddelston (1991) report that a European species of *Pambolus* has been associated with chrysomelids (Coleoptera), although this information needs to be confirmed. The aim of this work is to describe two new species of *Pambolus* recently collected in Jamaica, which represent the first records of the genus for the Caribbean Islands.

Methods

Specimens were collected using yellow pan traps at two localities in Jamaica.

Morphological terminology follows Sharkey and Wharton (1997), surface sculpture terminology follows Harris (1979). Descriptions of the new species are organized following the basic format of recent descriptions of *Pambolus* species (Braet and van Achterberg 2003; van Achterberg and Braet 2004) in order to facilitate comparisons. Photographs were taken and edited using a Leica[®] Z16 APO-A stereoscopic microscope, a Leica[®] DFC295/DFC290 HD camera, and the Leica Application Suite[®] program. DNA Barcode sequences [-650 bp of the cytochrome oxidase I (COI) mitochondrial DNA gene; Hebert et al. 2003] were generated for specimens of the two new species using the same DNA extraction and amplification protocols employed by Ceccarelli et al. (in press).

Specimens are deposited at Colección Nacional de Insectos (CNIN), Instituto de Biología, Universidad Nacional Autónoma de México, and at Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina (MACN).

Results

Pambolus albospina sp. n.

urn:lsid:zoobank.org:act:19BA7908-B656-4B6E-A661-F9C68582B370 http://species-id.net/wiki/Pambolus_albospina Figures 1–6

Diagnosis. Following the key to Neotropical species (Braet and van Achterberg 2003), the female of this new species runs to *P. hemitaeniatus* van Achterberg, but differs from



Figures 1–6. *Pambolus albospina* sp. n. **I** Habitus of female (lateral view) **2** head (anterior view) **3** head, mesosoma and first metasomal segment (dorsal view) **4** head, mesosoma and first metasomal segment (lateral view) **5** antenna (dorsal view) **6** wings.

the latter and all other Neotropical species of the subgenus *Phaenodus* by having an entirely smooth first metasomal tergite without striations, and by its entirely white propodeal spines. Males, however, are difficult to relate to those of the other species. They can be distinguished from *P. longicornis* (Enderlein)-the only neotropical species of the subgenus *Phaenodus* with known males- also by the color of the propodeal spines and the smooth first metasomal tergite.

Female. *Color:* Mostly reddish brown (fig. 1); scape and base of pedicel pale yellow, apex of pedicel and first five flagellomeres honey yellow, sixth to eleventh flagellomeres gradually darkening from brownish yellow to black, further flagellomeres (12th to 24th) entirely white. Palpi white; lower area of temple, gena, face, clypeus and labrum reddish brown; frons, vertex and upper area of temple orange brown, ocellar triangle darkened. Mesoscutum, scutellum and propodeum except propodeal spines, orange brown; pronotum, mesopleuron and metapleuron darker, rusty brown; propodeal spines entirely white. First metasomal tergite reddish brown, reminder of metasoma brown. Coxae, trochanters and trochatelli white, femora white basally and brown on apical third fourth, tibiae whitish, tarsi light brown. Fore wing with faint infuscate bands, hind wing hyaline, pterostigma and veins brown, except vein r-m and junction of veins 2RS and 2M, which are not pigmented.

Head: Antenna (fig. 5) with 24 flagellomeres, first flagellomere 1.1 times longer than second, first and second flagellomeres 5.5 and 5.0 times longer than their maximum width respectively. Scapus oblique apically; in dorsal view (fig. 3) length of eyes 1.9 times temple; POL 1.5 times OD and 0.7 times OOL; in dorsal view width of head 1.7 times its maximum length; face flattened and clypeus weakly convex in lateral view; face (fig. 2) weakly coriaceous near toruli, turning smooth near clypeus; clypeus largely smooth; anterior tentorial pit big and circular; frons, vertex and temple rugulose; gena smooth and shining (fig. 4); malar space 1.5 times basal width of mandible; occipital carina complete, meeting hypostomal carina ventrally.

Mesosoma: Length of mesosoma 1.4 times its maximum height and 1.6 times its maximum width; mesosoma setose; pronotum largely smooth, pronotal furrow deep and scrobiculate; propleuron convex and weakly coriaceoous; mesopleuron smooth (fig. 4), precoxal sulcus deep and scrobiculate, occupying two thirds length of mesopleuron, posterior mesopleural furrow strongly scrobiculate; subalar area rugose; episternal scrobe deep; prepectal and postpectal carinae strongly developed; metapleuron reticualte; mesoscutum (fig. 3) acinose-coriaceous; notauli wide and scrobiculate anteriorly, rather obscured in a median area posteriorly; scutellum coriaceous and slightly convex; scutellar sulcus with five carinae, its median length 0.6 times as long as scutellum; propodeum areolate rugose, with a long and narrow areola medially (fig. 3), areola irregularly rugose anteriorly and with four transverse carinae posteriorly, spines of propodeum 0.8 times as long as fore basitarsus.

Wings: Wings (fig. 6) densely setose. Fore wing: veins r and 3RSa basally widened; r:3RSa:3RSb = 2:5:16; 2RS:2M:r-m = 6:10:3; vein (RS+M)a straight; vein cu-a just interstitial and almost indistinct; first subdiscal cell open. Hind wing: vein cu-a oblique, directed towards wing base; M+CU:1-M = 2:5.

Legs: Hind coxa unsculptured dorsally; length of femur, tibia and basitarsus of hind leg 4.4, 7.6 and 6.0 times their width, respectively; hind femur very weakly coriaceous.

Metasoma: Length of first tergite 0.7 times its apical width, its median area well delimited by carinae but entirely smooth, lateral areas also smooth (fig. 3); second metasomal tergum with a few basal striations, otherwise smooth, remaining terga completely smooth; combined length of second and third tergites as long as their maximum width; length of ovipositor sheath 0.4 times the length of metasoma.

Male Similar to female, except for its slightly lighter body color and its much longer antennae, with 31 flagellomeres, five apical flagellomeres entirely white.

Etymology. The specific epithet refers to the white propodeal spines of this species.

Material examined. Holotype female: Jamaica, Trelawny, Windsor, 18.35752, -76.66406, 82m, 19–21.xi.2010, yellow pan traps, F. S. Ceccarelli col. GenBank accession no. JQ268751. (CNIN IB-UNAM) Paratypes: three males, Jamaica, Saint Andrew, New Castle, 18.06840, -76.7119, 860m, 11.xi.2010, F. S. Ceccarelli col. (CNIN IB-UNAM, MACN); GenBank accession no. JQ268752.

Pambolus rastafari sp. n.

urn:lsid:zoobank.org:act:76DBA72C-1920-4BF3-860E-860B88A1739F http://species-id.net/wiki/Pambolus_rastafari Figures 7–15

Diagnosis. Following the keys to Neotropical species of *Pambolus* (Braet and van Achterberg 2003; van Achterberg and Braet 2004), *P. rastafari* runs to couplet three due to the presence of a white basal antennal band; however, it can easily be distinguished from *P. duplotaeniatus* van Achterberg, *P. granulatus* van Achterberg and *P. microstriatus* van Achterberg by the basal white band being composed of a single white flagellomere. The three aforementioned species have a white band composed of at least three flagellomeres. This new species also differs from the above three species by its entirely smooth and polished head and mesoscutum.

Female. *Color:* Mostly chestnut brown (fig. 7); palpi, pedicel, second flagellomere, coxae, trochanters and trochantelli, all femora and all tibiae basally ivory white; flagellomeres beyond 12th and fore tarsus light brown; annellus of first flagellomere and apex of all trochantelli distinctly orange-brown; wings almost entirely infuscate, with subhyaline areas at junction of veins 2RS and 2M and along vein r-m; remaining veins light brown.

Head: Antenna broken, 13 flagellomeres remaining, first flagellomere 1.2 times longer than second, first and second flagellomeres 5.0 and 3.9 times longer than their maximum width, respectively. Scapus oblique apically. In dorsal view (fig. 9) length of eyes 1.9 times the length of temple; POL as long as OD and 0.4 times OOL; in dorsal view width of head 0.6 times its median length; face rather flattened and clypeus weakly convex in lateral view (fig. 10); face smooth and setose (fig. 8); clypeus smooth; anterior tentorial pit big and circular; frons smooth and slightly concave; vertex, tem-



Figures 7–13. *Pambolus rastafari* sp. n. 7 habitus of female (lateral view) 8 head (anterior view) 9 head (dorsal view) 10 head and basal antennomeres (lateral view) 11 mesosoma (lateral view) 12 mesoscutum and sctuellum (dorsal view) 13 propodeum and first metasomal segment (dorsal view).



Figures 14-15. Pambolus rastafari sp. n. 14 fore wing 15 hind wing.

ple and gena also smooth and shining; malar space 2.0 times basal width of mandible; occipital carina complete, strongly developed, meeting hypostomal carina ventrally.

Mesosoma: Length of mesosoma 1.4 times its maximum height and 1.6-1.7 times its maximum width; mesosoma setose; pronotum largely smooth, slightly coriaceous anteriorly, pronotal furrow present only medially and scrobiculate; propleuron convex and smooth; mesopleuron smooth (fig. 11), precoxal sulcus deep and scrobiculate, occupying two thirds the length of the mesopleuron, subalar and posterior mesopleural furrows scrobiculate; prepectal and postpectal carinae strongly developed; metapleuron irregularly rugose; mesoscutum smooth and shining (fig. 12); notauli wide and crenulate on anterior edge of mesoscutum, indistinct posteriorly; mesoscutum with a median V-shaped posterior pit; scutellar disc smooth; scutellar sulcus with five coarse and oblique carinae, its median length 0.5 times as long as scutellar disc; propodeum (fig. 13) areolate rugose, with a long and narrow areola medially, areola with a median longitudinal carina anteriorly and with three transverse carinae posteriorly, spines of propodeum 0.7 times as long as fore basitarsus.

Wings: Wings densely setose. Fore wing (fig. 14): veins r and 3-SR basally widened; r:3RSa:3RSb = 3:8:12; 2RS:2M:r-m = 9:17:5; veins (RS+M)b and r-m unpigmented; vein (RS+M)a straight; vein cu-a insterstitial; first subdiscal cell open. Hind wing (fig.15): vein cu-a vertical; M+CU:1-M = 2:5.

Legs: Hind coxa largely finely striate dorsally; length of femur, tibia and basitarsus of hind leg 4.4, 8.4 and 5.3 times their width, respectively; hind femur very weakly coriaceous.

Metasoma: Length of first tergite 0.8 times its apical width, its median area wide and coarsely longitudinally striate (fig. 13), lateral areas smooth; remaining terga completely smooth and shining; combined length of second and third tergites as long as their maximum width; length of ovipositor sheath 0.4-0.5 times the length of metasoma.

Male. Unknown.

Etymology. The specific epithet refers to the religious and social movement from Jamaica.

Material examined. Holotype female: Jamaica, Saint Andrew, New Castle, 18.06840, -76.7119, 860m, 11.xi.2010, F. S. Ceccarelli col. (CNIN IB-UNAM); Gen-Bank accession no. JQ268750. Paratype: one female, same data as holotype (MACN).

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References

- Achterberg C van (1995) Generic revision of the subfamily Betylobraconinae (Hymenoptera: Braconidae) and other groups with modified fore tarsus. Zoologische Verhandelingen 298: 1–242.
- Achterberg C. van, Braet Y (2004) Two new species of *Pambolus* Haliday (Hymenoptera: Braconidae: Pambolinae) from Argentina. Zoologische Mededelingen 78: 337–344.
- Braet Y, Achterberg C van (2003) New species of *Pambolus* Haliday and *Phaenocarpa* Foerster (Hymenoptera: Braconidae: Pambolinae, Alysiinae) from French Guyana, Suriname and Panama. Zoologische Mededelingen Leiden 77: 153–179.
- Ceccarelli FS, Sharkey MJ, Zaldivar-Riverón A (in press) Species identification in the taxonomically neglected, highly diverse, neotropical parasitoid wasp genus *Notiospathius* (Braconidae: Doryctinae) based on an integrative molecular and morphological approach. Molecular Phylogenetics and Evolution.
- Harris RA (1979) A glossary of surface sculpturing. Occasional Papers of Entomology, California Department of Food and Agriculture, no. 28, 31 pp.

- Hebert PDN, Ratnasingham S, deWaard JR (2003) Barcoding animal life: cytochrome c oxidase subunit 1 divergences among closely related species. Proceedings of the Royal Society B 270: S96–S99. doi: 10.1098/rsbl.2003.0025
- Papp J (1996) On the genus *Pambolus* (Hymenoptera: Braconidae: Pambolinae), with description of four new tropical species. Acta Zoologica Academiae Scientiarum Hungaricae 42: 41–57.
- 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). Special Publication of the International Society of Hymenopterists no 1, p. 19–37.
- Shaw MR, Huddleston T (1991) Classification and biology of braconid wasps (Hymenoptera: Braconidae). Handbooks for the Identification of British Insects 7: 1–126.
- Whitfield JB, Wharton RA (1997) Subfamily Hormiinae. In: Wharton RA, Marsh PM, Sharkey MJ (Eds) Manual of the New World genera of the family Braconidae (Hymenoptera). Special Publication of the International Society of Hymenopterists no. 1, p. 291–307.
- Yu DSK, Achterberg C van, Horstmann K (2005) World Ichneumonoidea 2004. Taxonomy, Biology, Morphology and Distribution [CD/DVD]. Taxapad, Vancouver.
- Zaldívar-Riverón A, Mori M, Quicke DLJ (2006) Systematics of the cyclostome subfamilies of braconid parasitic wasps (Hymenoptera: Ichneumonoidea): a simultaneous molecular and morphological Bayesian approach. Molecular Phylogenetics and Evolution 38: 130–145. doi: 10.1016/j.ympev.2005.08.006

RESEARCH ARTICLE



The genus Quartinia Ed. André, 1884 (Hymenoptera, Vespidae, Masarinae) in Southern Africa. Part VI. New and little known species both with complete and incomplete venation

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Abstract

In this publication, the sixth of a projected series revising the Afrotropical species of the genus *Quartinia* Ed. André, 1884 (Hymenoptera: Vespidae: Masarinae), 11 species (8 with complete venation and 3 with incomplete venation) are dealt with.

Two new species, *carpenteri* and *latigena* are described, as are the hitherto unknown males of *artemus* Richards and *luteomandibulata* Gess.

Quartinia atlantica Gess, 2011, for which only the female was known, is sunk into synonymy with Q. namaquensis Gess, 2007, for which only the male was known, females previously erroneously ascribed to the latter (Gess 2011a) being those of Q. conchicola Gess, 2007. Augmented collecting data and, in most instances, flower visiting records are given for arenaria Gess, artemis Richards, bonaespei Gess, luteomandibulata Gess, namaqua Gess, namaquensis Gess, niveopicta von Schulthess, propinqua von Schulthess and vagepunctata von Schulthess.

Keywords

Southern Africa, taxonomy, floral associations

Introduction

The background to the present state of knowledge of the taxonomy of the genus *Quartinia* Ed. André, 1884 has been fully stated in Gess (2007).

Desirable as it might be to undertake a complete revision of the genus, this is at present not practicable. Rather than to get bogged down in a study which might never be completed and published, it is intended to publish a series of papers describing new species as well as reviewing some known species. It is envisioned that a new key to species will complete the series. To date Parts I–V have been published as Gess (2007), Gess (2008), Gess (2009) and Gess (2011a and b).

Species of *Quartinia* range in length from a little over 2 mm to 7 mm. In comparison with the great majority of species of other genera of Masarinae even the largest *Quartinia* are relatively small. In view of the considerable range in size shown by species of *Quartinia* and in order to express relative size, categories based on length have been established for species of the genus. These are minute (1.5 - 2.5 mm); small (2.5 – 3.5 mm); medium (3.5 – 4.5mm); large (4.5 – 5.5 mm); very large (5.5 – 6.5 mm) and gigantic (6.5 – 7.5 mm).

The present paper deals both with species with complete venation (2m-cu present and as thick as other veins) and with incomplete venation (2m-cu present but attenuate and interrupted).

Acronyms for institutions in which material is housed are: AMG = Albany Museum, Grahamstown, South Africa; AMNH = American Museum of Natural History, New York; BMNH = Natural History Museum, London, England.

Taxonomy

A. Species with complete venation

Quartinia arenaria Gess

http://species-id.net/wiki/Quartinia_arenaria

Quartinia arenaria Gess, 2011a: 2, figs 1 - 7. \bigcirc , \bigcirc . Holotype \bigcirc , South Africa: Western Cape: S, of Yserfontein (AMG), geographic distribution, floral associations.

Additional material examined. SOUTH AFRICA; WESTERN CAPE: Melkbosstrand, Duynefontein (33.42S, 18.26E), 3 – 16.x.2010 (D. W., G. T. and G. M. Gess), 18 \bigcirc 2, 26 \bigcirc (7 \bigcirc \bigcirc , 8 \bigcirc \bigcirc on sand beneath *Trachyandra* sp., Asphodelaceae; 1 \bigcirc on flower of large pink mesem, Aizoaceae: Mesembryanthema); Koeberg Nature Reserve (33.38S, 18.24E), 9 – 30.x.2010 (D. W., G. T. and G. M. Gess), 74 \bigcirc 2, 106 \bigcirc (28 \bigcirc \bigcirc , 82 \bigcirc \bigcirc on sand beneath *Trachyandra* sp., Asphodelaceae; 3 \bigcirc \bigcirc visiting white flowers of *Capnophyllum africanum* (L.) W. D. J. Koch, Apiaceae; 24 \bigcirc \bigcirc , 2 \bigcirc \bigcirc on ground); same locality, 29 – 30.x.2010 (F.W. and S. K. Gess), 52 \bigcirc \bigcirc , 11 \bigcirc (3 $\bigcirc \bigcirc$, 6 $\bigcirc \bigcirc$ visiting purple flowers of *Senecio* cf. *arenarius* Thunb., Asteraceae; 1 \bigcirc , 1 \bigcirc visiting yellow flowers of *Senecio* sp., Asteraceae; 14 $\bigcirc \bigcirc$, 4 $\bigcirc \bigcirc$ visiting yellow flowers of "helichrysum", Asteraceae; 5 $\bigcirc \bigcirc$ visiting yellow flowers of *Carpobrotus* sp., Aizoaceae:Mesembryanthema; 7 $\bigcirc \bigcirc$ visiting white flowers of *Capnophyllum africanum*; 22 $\bigcirc \bigcirc$ on ground) – [all AMG].

Augmented floral associations. To the previously recorded Aizoaceae: Mesembryanthema (*Conocosia* sp. and *Drosanthemum* sp.) are added *Carpobrotus* sp. and "large pink mesem"; Apiaceae (*Capnophyllum africanum* (L.) W. D. J. Koch) and Asteraceae (*Senecio* spp. and "helichrysum")

Quartinia artemis Richards

http://species-id.net/wiki/Quartinia_artemis Figs 1–6

Quartinia artemis Richards, 1962: 156, ♀. Holotype: ♀, South Africa: Calvinia (BMNH); Gess, S. K. 1996: 245 (flower visiting); Carpenter, 2001: 23 (listed); Gess and Gess, 2003: 58 (flower visiting).

Diagnosis. Medium sized (3.6 - 4.3 mm) but large on the basis of Richards' measurement (\mathcal{Q} about 5.0 mm). Fore wing with Cu1a and 2*m-cu* complete and as thick as other veins. Tegula with inner posterior corner inwardly produced, acute. Angle of propodeum very markedly posteriorly produced into thick, non-translucent lamella. Posterior face of propodeum with ventral third shiny, contrasting markedly with closely punctured upper two thirds; shiny part laterally covering inner surface of lamella and passing upwards into a well marked pit.

Description. *Female* (previously adequately described) (Figs 1, 3, 5). The present material agrees well with the description but some of the specimens, less melanistic than the type, differ in having the pale markings (yellow, usually suffuged with ferruginous at the edges) slightly more extensive. Thus the pronotum may have a pair of small transverse streaks antero-medially in addition to the minute spot at the postero-dorsal angle; the scutellum may have the lamella pale in addition to the marking (present in some specimens only) at the centre of the posterior margin; and the gaster has posterior bands on all the terga.

Male (hitherto undescribed) (Figs 2, 4, 6): Easily associated with the female on account of the uniquely developed propodeal angles. Pale markings are more extensive than those of females from the same localities. Black. The following are yellowish-white: small spot submarginally on each side of clypeus (in one specimen only); underside of more proximal flagellomeres of club; narrow transverse band (entire or narrowly interrupted) medially on anterior margin of pronotum; streak on humeral angle and spot on postero-dorsal angle; tegula (except for ferruginous median area); transverse mark postero-medially on scutellum; scutellar lamella (usually medially suffused with ferruginous); posterior bands on terga I – VI (that of T I markedly wider than progres-



Figures 1–6. *Quartinia artemis* $| \uparrow \uparrow$, lateral view (× 9) $2 \circ$, lateral view (× 12) $3 \uparrow$, dorsal view (× 10) $4 \circ$, dorsal view (× 11) $5 \uparrow$, head, front view (× 32) $6 \circ$, head, front view (× 30).

sively narrower bands of terga II – VI). Various shades of ferruginous are: mandibles distally; labrum; upper surface of antennae; upper and outer lateral surfaces of propodeal lamella (to variable degree); terga I – V laterally; in most specimens tergum VI medially and tergum VII entirely; posterior bands on sterna. Legs as described for female.

Tergum VII with disk noticeably convex; apical margin with a V-shaped slit; lobes flanking slit rounded. Fore legs unmodified; sterna atuberculate.

Mesosoma more closely and finely punctured than that of female.

Length 3.6 - 4.0 mm; length of fore wing 2.6 mm.

Material examined. SOUTH AFRICA: NORTHERN CAPE: Carnarvon (30.59S, 22.07E), 24.ix.2009 (F. W. and S. K. Gess), $4 \bigcirc \bigcirc$ (visiting yellow flowers of blue/violet

rayed capitula of *Felicia dubia* Cass., Asteraceae); 15 km N[orth] of Nieuwoudtville on road to Loeriesfontein [Skuinshoogte Pass] (31.16S, 19.08E), 3-8.x.1989 (F. W. and S. K. Gess), 1 \bigcirc (visiting flowers of *Leysera tenella* DC., Asteraceae); Sutherland District, Bo-Visrivier road (32.25S, 20.39E), 6.x.2009 (F. W. and S. K. Gess), 4 $\bigcirc \bigcirc$ (visiting yellow flowers of *Chrysocoma* sp., Asteraceae); Sutherland District, W[est] of Ouberg Pass (32.26S, 20.19E), 28.ix.2009 (F. W. and S. K. Gess), 1 \bigcirc , 4 $\bigcirc \bigcirc$ (1 \bigcirc , 1 \bigcirc visiting yellow flowers of blue/violet rayed capitula of *Felicia dubia* Cass., Asteraceae; 3 $\bigcirc \bigcirc$ visiting yellow flowers of "button" capitula, Asteraceae); Sutherland District, Rooikloof Farm (32.26S, 20.39E), 10.x.2009 (D. W.Gess), 1 \bigcirc (visiting yellow flowers of *Chrysocoma* sp., Asteraceae); between Sutherland and Matjiesfontein (33.04S, 20.35E), 2.x.2009 (F. W. and S. K. Gess), 1 \bigcirc (visiting yellow flowers of *Chrysocoma* sp., Asteraceae); 1 \bigcirc kitting yellow flowers of *Chrysocoma* sp., Asteraceae); WESTERN CAPE: 10 km E[ast] of Laingsburg, Geelbeksbrug Farm (33.09S, 20.59E), 13.x.2009 (F. W. and S. K. Gess), 2 $\bigcirc \bigcirc$ (1 \bigcirc visiting yellow flowers of *Leysera tenella*, Asteraceae; 1 \bigcirc visiting yellow flowers of *Chrysocoma* sp., Asteraceae) – [all AMG].

Geographic distribution. Known from the seven localities in the Northern Cape and one in the Western Cape, all being in the western part of the Great Karoo. The southernmost locality for *Q. artemis* is separated by the Klein Swartberg from the localities in the Little Karoo recorded below for *Q. carpenteri*.

Floral associations. Asteraceae (*Chrysocoma, Felicia, Leysera,* "button" capitula). Nesting. Unknown.

Quartinia bonaespei Gess

http://species-id.net/wiki/Quartinia_bonaespei Figs 7–12

Quartinia bonaespei Gess, 2007: 213, figs 1, 7, ♀, ♂. Holotype: ♂, South Africa: Western Cape: on coast 4 km north of Bloubergstrand (AMG), geographic distribution, floral associations, nesting; Gess, 2009: 279 (additional material examined).

Additional material examined. SOUTH AFRICA; WESTERN CAPE: Koeberg Nature Reserve (33.38S, 18.24E), 9 – 30.x.2010 (D. W., G. T. and G. M. Gess), 7 \bigcirc (2 \bigcirc \bigcirc on sand beneath *Trachyandra* sp., Asphodelaceae; 3 \bigcirc \bigcirc on ground); same locality, 29.x.2010 (F. W. and S. K. Gess), 5 \bigcirc \bigcirc (4 \bigcirc \bigcirc visiting purple flowers of *Senecio* cf. *arenarius* Thunb., Asteraceae); Melkbosstrand, Duynefontein (33.42S, 18.26E), 3 – 16.x.2010 (D. W., G. T. and G. M. Gess), 32 \bigcirc \bigcirc 4 \bigcirc \bigcirc (1 \bigcirc on flowers of *Trachyandra* sp.; 1 \bigcirc on flowers of "purple daisy with yellow centre" [probably *Senecio* cf. *arenarius*]), 26 \bigcirc \bigcirc 2 \bigcirc \bigcirc on sand beneath *Trachyandra* sp.); Melkbosstrand, Holgat to Kreefbaai (33.46S, 18.27E), 24 – 28.ix.2010 (D. W., G. T. and G. M. Gess), 38 \bigcirc (7 \bigcirc \bigcirc on flowers of *Trachyandra* sp.; 31 \bigcirc \bigcirc on sand beneath *Trachyandra* sp.) [all AMG].

Augmented floral associations. To the previously recorded Asphodelaceae (*Tra-chyandra divaricata* (Jacq.) Kunth., for which eight more records are added), and Aizoaceae: Mesembrianthema (including *Conicosia* and *Drosanthemum*), are added five



Figures 7–12. *Quartinia bonaespei* **7** \bigcirc , lateral view (× 7) **8** \bigcirc , lateral view (× 7) **9** \bigcirc , dorsal view (× 7) **10** \bigcirc , dorsal view (× 7) **11** \bigcirc , head, front view (× 21) **12** \bigcirc , head, front view (× 19).

records for Asteraceae (*Senecio* cf. *arenarius* Thunb.). It would appear that *Trachyandra* is a favoured forage flower and it is for this reason that so many specimens, both females and males, of the wasp have been caught resting on the sand beneath these plants.

Quartinia carpenteri sp. n.

urn:lsid:zoobank.org:act:AA57E93C-7846-4A55-8041-8B1BB8458316 http://species-id.net/wiki/Quartinia_carpenteri Figs 13–18

Holotype. \mathcal{O} , SOUTH AFRICA: WESTERN CAPE: Bergendal Farm (33.30S, 21.19E), 4 km E[ast] of Ladismith, 2.xi.2010 (F. W and S. K. Gess), (visiting yel-



Figures 13–18. *Quartinia carpenteri* **13** \bigcirc , lateral view (× 8) **14** \bigcirc , lateral view (× 9) **15** \bigcirc , dorsal view (× 8) **16** \bigcirc , dorsal view (× 9) **17** \bigcirc , head, front view (× 23) **18** \bigcirc , head, front view (× 23).

low flowers of semi-prostrate mesem, *Malephora* sp., Aizoaceae: Mesembryanthema) [AMG].

Paratypes. SOUTH AFRICA: WESTERN CAPE: same data as holotype, 12 $\bigcirc \bigcirc$, 2 $\bigcirc \bigcirc$; 5 km S[outh] of Ladismith on R62 (33.32S, 21.15E), 9.xi.2010 (F. W. and S. K. Gess), 2 $\bigcirc \bigcirc$ (visiting yellow flowers of semi-prostrate mesem, *Malephora* sp. Aizoaceae: Mesembryanthema) [AMG]; 3 km S[outh] of Meiringspoort (33°28'S, 22°32'E) (500m), 11.xii.1996 (J. Carpenter & A. Davidson), 4 $\bigcirc \bigcirc$ [AMNH].

Diagnosis. Large (4.8–5.4 mm). Fore wing with Cu1a and 2*m-cu* complete and as thick as other veins. Tegula with inner posterior corner inwardly produced, acute. Angle of propodeum postero-ventrally produced into rounded, marginally translucent lamella. Posterior face of propodeum with ventral third shiny, contrasting markedly with closely punctured upper two thirds; shiny part laterally covering inner surface of lamella but smoothly concave and **not** passing upwards into a well marked pit as in

Q. artemis. Male with clypeus and labrum yellowish-white; with posterior margin of tergum VII shallowly emarginate and with sterna atuberculate.

Description. *Female* (Figs 13, 15, 17): Black. The following are yellowish-white: underside of antenna; short transverse band medially on anterior margin of pronotum, small mark (effaced in one specimen) on humeral angle, minute spot at postero-dorsal angle; tegula (except for ferruginous median area); scutellar lamella (usually medially suffused with ferruginous); posterior bands, not attaining sides and progressively narrower and shorter on terga I – V; apex of femur and streak on dorsal aspect of tibia of fore leg; apex of femur and base of tibia of middle and hind legs. Various shades of ferruginous are: distal half of mandible; upper aspect of antenna; translucent posterior margin of propodeal lamella; terga laterally; diffuse posterior bands on sterna; most of femur, tibia and tarsomeres of all legs. Wings lightly browned; veins brown.

Length 5.0 – 5.4 mm; length of fore wing 3.5 mm (average of 3); hamuli 5.

Head in front view $1.23 \times as$ wide as long; POL: OOL = 1: 0.8. Clypeus $1.3 \times as$ wide as long; anterior margin shallowly emarginate; antero-lateral angle rounded.

Clypeus, frons and vertex moderately coarsely and closely punctured with microsculptured (shagreened) interstices; punctures on pronotum, mesonotum, scutellum and dorsum of propodeum larger than those on head, discrete, on mesonotum separated variously by less than their diameter to about four times their diameter. Gaster closely punctured; terga I and II coarsely so, remaining terga progressively more finely punctured.

Angle of propodeum postero-ventrally produced into rounded, marginally translucent lamella. Posterior face of propodeum with ventral third shiny, contrasting markedly with closely punctured upper two thirds; shiny part laterally covering inner surface of lamella but smoothly concave and not passing upwards into a well marked pit as in *Q. artemis.*

Male (Figs 14, 16, 18): Black. The following are yellowish-white: variably sized spot (effaced in one specimen) on base of mandible; labrum; clypeus (except immediately below antennal socket); scape and pedicel (except dorsally); underside of intermediate flagellomeres and of proximal flagellomeres of club; transverse band on anterior margin of pronotum, either fused with marking on humeral angle or narrowly separated from it; minute spot at postero-dorsal angle; two minute dots at top of mesopleuron (in one specimen only); tegula (except for ferruginous median area); transverse mark of variable length posteriorly on scutellum; scutellar lamella (medially suffused with ferruginous); small streak edging upper part of propodeal lamella; posterior bands, not attaining sides and progressively narrower and shorter on terga I – VI and small crescent-shaped band margining emargination on VII; apex of femur and base of tibia of all legs. Various shades of ferruginous are: distal half of mandible; upper aspect of antenna; translucent posterior margin of propodeal lamella; terga laterally; diffuse posterior bands on sterna; most of femur, tibia and tarsomeres of all legs. Wings lightly browned; veins brown.

Length circa 4.8 mm; length of fore wing 3.0 mm; hamuli 5.

Head in front view $1.36 \times$ as wide as long; POL: OOL = 1: 0.8. Clypeus $1.45 \times$ as wide as long; anterior margin shallowly emarginate; antero-lateral angles rounded.

Punctation similar to that of female except that on mesoscutum and scutellum it is courser and closer.

Angles of propodeum and posterior face of the latter identical with that of female. Posterior margin of tergum VII shallowly emarginate, not slit-like. Sterna atuberculate.

Etymology. Named after James Carpenter of the American Museum of Natural History, New York, co-collector with Amy Davidson of the first specimens of the present species, cladist of the Masarinae, and much esteemed colleague and friend.

Geographic distribution. Known from three localities, not very far distant from each other, in the Little Karoo of the Western Cape. Its close congener, *Q. artemis*, appears, from the available records (see above), to be a species of the western Great Karoo.

Floral associations. Aizoaceae: Mesembryanthema (*Malephora* sp.). **Nesting.** Unknown.

Quartinia luteomandibulata Gess

http://species-id.net/wiki/Quartinia_luteomandibulata Figs 19–21

Diagnosis. – Large (4.7 - 5.6 mm). Fore wing with Cu1a and 2m-cu complete and as thick as other veins. Tegula with posterior inner corner inwardly produced. Female with mandible at least in part pale yellow, contrasting strikingly with totally black clypeus. Male with mandible, labrum, clypeus, large dorsally widened supra-clypeal marking (in some specimens extended laterally to fuse with streak at bottom of ocular sinus), para-ocular streak, yellow.

Description. *Male* (hitherto undescribed) (Figs 19, 20, 21): Black. The following are pale yellow: mandible (except ferruginous apex); scape, pedicel, underside of proximal flagellomeres; labrum; clypeus (except beneath antennal socket); large dorsally widened supra-clypeal marking on lower half of frons (this marking in some specimens widened and extended laterally to fuse with streak at bottom of ocular sinus, in which case entire ocular sinus is filled; in a few specimens an intermediate condition is present in which one or more spots of variable size are present between the dorso-lateral corners of the supra-clypeal mark and the streak at the bottom of the ocular sinus); narrow paraocular streak (in specimens with unexpanded supraclypeal marking confined to lower orbit; in specimens with supra-clypeal marking

Quartinia luteomandibulata Gess, 2011a: 12, figs 25 – 27, ♀. Holotype ♀, South Africa: Western Cape: Lamberts Bay (AMG).



Figures 19–21. *Quartinia luteomandibulata* **19** $\stackrel{\circ}{\mathcal{O}}$, lateral view (× 9) **20** $\stackrel{\circ}{\mathcal{O}}$, dorsal view (× 9) **21** $\stackrel{\circ}{\mathcal{O}}$, head, front view (× 22).

extended into ocular sinus narrowly fused with infilling of sinus, leaving a narrow outwardly curved black streak above antennal socket); streak (in some specimens effaced) of variable length on temple behind top of eye; pair of wedge-shaped markings (meeting or very narrowly separated medially) on anterior margin of pronotum and extreme postero-dorsal angle of same; large mark on humeral angle (in some specimens fused with marking on anterior margin); mark of variable extent (large or broken up into a number of small spots or totally effaced) on mesopleuron; tegula (except for ferruginous median area); spot basally on each side of scutellum (in a minority of specimens only); scutellar lamella (interrupted posteriorly); marking on propodeal angle (varying from most of dorsal and lateral surfaces to small spot on dorsum to total effacement); posterior bands not or almost reaching sides on terga I, II, III, IV,V or VI (depending on degree of melanism); band on tergum I widest, those on subsequent terga progressively narrower but all bands (particularly if well developed) medially and laterally anteriorly produced; streak on apical half of femur, most of tibia and in some specimens most of tarsomeres of legs. Light ferruginous are: apex of mandible; antennal club (dorsally a little darker); tarsomeres (if not pale yellow). Darker ferruginous are: median area of tegula; parameres; claws. Wings very lightly browned, almost hyaline; veins brown.

Length 4.7 - 5.3 mm (average of 3: 5.1 mm); length of fore wing 3.2 mm (average of 3); hamuli 6.

Head in front view $1.4 \times as$ wide as long; POL: OOL = 1: 0.6. Clypeus $1.6 \times as$ wide as long; anterior margin widely and shallowly emarginate; antero-lateral corners obtusely rounded.

Punctation similar to that of female but microreticulation (shagreening) of mesosoma less obvious and integument consequently somewhat more shiny.

Tergum VII with disk slightly depressed medially; apical margin with a median V-shaped slit; lobes flanking slit wide, smoothly rounded. Sterna atuberculate.

Melanistic females. In comparison with some females of the type series from further north along the west coast and in particular with sympatric females from Koeberg, several females from this latter locality exhibit some degree of melanism affecting the pale yellow markings of the head and mesosoma. Thus the markings on the lower half of the frons and in the ocular sinus may be greatly reduced or even totally effaced. Also, the streak on the temple may be greatly reduced or totally absent (though it may be absent also in specimens with well developed markings on the frons). The spot basally on each side of the scutellum may be reduced or effaced (as in the paratype from Lamberts Bay) and the marking on the propodeal angle may be reduced (as in the paratype from Lamberts Bay) or may be effaced. All these specimens, however, exhibit the characteristic pale yellow (at least in part) mandible contrasting strikingly with the totally black clypeus, the large pale yellow marking on the humeral angle, and the pale yellow apex of the femur and most of the tibia of all legs.

Additional material examined. SOUTH AFRICA: WESTERN CAPE: Koeberg Nature Reserve (33.38S, 18.24E), 9.x.2010, 4 \Im (on sand beneath *Trachyandra* sp., Asphodelaceae); same locality, 17.x.2010, 9 \Im , 12 \Im ; same locality, 24.x.2010, 7 \Im , 19 \Im (1 \Im visiting white flowers of Apiaceae); same locality, 30.x.2010, 10 \Im , 6 \Im (1 \Im visiting flowers of large white mesem, Aizoaceae: Mesembryanthema; all other specimens on ground) – (all D. W., G. T. and G. M. Gess); same locality, 29.x.2010, 3 \Im (1 \Im visiting flowers of purple *Senecio* cf. *arenarius* Thunb., Asteraceae; other specimens on ground); same locality, 30.x.2010, 4 \Im , 4 \Im (1 \Im , 1 \Im , visiting white flowers of *Capnophyllum africanum* (L.) W. D. J. Koch, Apiaceae; other specimens on ground) – (all F. W. and S. K. Gess) [all AMG].

Extended geographic distribution. The present material from the Koeberg Nature Reserve (33.38S, 18.24E) establishes a southward extension of the hitherto known distribution of *Q. luteomandibulata.* Previously the species was known from the Koingnaas Mines (30.10S, 17.14E) in the Northern Cape and from Lamberts Bay (32.05S, 18.19E) in the Western Cape. All three localities are in the Strandveld of the West Coast of Acocks (1953).

Augmented floral associations. To the previously recorded Aizoaceae: Mesembryanthema (*Conicosia* sp.) (Gess 2011a: 12) may be added: Aizoaceae: Mesembryan-

thema (large white mesem); Asteraceae (*Senecio* cf. *arenarius* Thunb.); Apiaceae (*Capnophyllum africanum* (L.) W. D. J. Koch).

Nesting. Unknown.

Quartinia namaqua Gess

http://species-id.net/wiki/Quartinia_namaqua

Quartinia namaqua Gess, 2007: 219, ♀, ♂. Holotype: ♂, South Africa: Northern Cape: Inland of Hondeklip Bay (30.19S, 17.17E) (AMG), geographic distribution, floral associations, nesting.

Additional material examined. SOUTH AFRICA: Northern Cape: Koingnaas Mines (30.14S, 17.15E), ix.2007 (from pan trap) (C. Lyons & J. Mingo), 1 $\stackrel{\circ}{\circ}$ [AMG]. The above record, for the second male known, is from slightly north of the type locality.

Quartinia namaquensis Gess

http://species-id.net/wiki/Quartinia_namaquensis

- *Quartinia namaquensis* Gess, 2007: 222, figs 3, 9. ♂. Holotype ♂, South Africa: Northern Cape: Leliefontein (AMG), geographic distribution, nesting; Gess, 2011a (additional material: ♂; not ♀♀ = *Q. conchicola* Gess).
- *Quartinia atlantica* Gess, 2011a: 5, figs 8 10. ♀. Holotype ♀, South Africa: Western Cape: Blaauwberg Melkbosstrand (AMG), geographic distribution. syn. n.

Notes. *Quartinia atlantica* Gess, 2011 was described from the holotype \Im from Blaauwberg – Melkbosstrand, collected on 5.x.2005 by F. W. and S. K. Gess and from an assemblage of a further 57 \Im \Im from the Koeberg Nature Reserve, the latter obtained by S. van Noort from yellow pan traps during the period 13. vi. – 28.xi.1997.

Subsequent collecting at Koeberg Nature Reserve by D. W., G. T. and G. M. Gess during the period 9 - 30.x.2010 and by F. W. and S. K. Gess during the period 29 - 30.x.2010 yielded a further $64 \ \bigcirc \ \bigcirc \$ and $25 \ \bigcirc \ \bigcirc \$ respectively. A total of $147 \ \bigcirc \ \bigcirc \$ was therefore collected, however no males which could be ascribed to the species were found.

Persistent and diligent collecting by D. W., G. T. and G. M. Gess at the Koeberg Nature Reserve at the beginning of following season, on 30 and 31 July 2011, was rewarded with the capture of both females of *Q. atlantica* and of associated clearly conspecific males.

Examination of these males showed them to be conspecific, though showing some degree of melanism, with the type material of *Q. namaquensis* Gess, 2007, described from Leliefontein and from west of Wallekraal as also with the single male recorded (Gess 2011a) from Sutherland.

In the light of the present association of males and females from Koeberg, it is clear that the females recorded (Gess 2011a) from Sutherland as also those from Leliefontein and Remhoogte were erroneously assigned to *namaquensis* and described as such and that they are *conchicola* (Gess, 2007). As stated (Gess 2011a) these specimens are "virtually indistinguishable from the female of *Q. conchicola* Gess, the differences being subtle". Re-examination of the material suggests that rather than subtle the differences are illusory!

Establishment of the present synonymy means that for *Q. namaquensis* both male and true female are now known, as are an extended distribution down the west coast, floral associations and nesting.

Description. *Male* (previously adequately described from Leliefontein and from west of Wallekraal: see Gess, 2007: 222, figs 3, 9; further illustrated in Gess, 2011a, figs 29, 31, 33 and 34).

The recently collected males from Koeberg share with the type material and with the subsequently recorded male from Sutherland the following diagnostic characters: fore femur greatly swollen, its posterior surface in proximal half markedly concavely excavate, smooth and very shiny, its baso-ventral region angulate and sublamellate; tergum VII drawn out apico-medially into robust, pointed, dorsally flattened and apically narrowly pointed process; antennae noticeably attenuated.

In comparison with the type material, the specimens are to some degree melanistic in so far that the posterior bands on terga I–V are reduced, being narrower and not reaching sides; that the band on tergum VI is absent; that the middle and hind femora and tibiae (except at the "knees") are predominantly black and that the tarsomeres of these legs are dark brown.

Female (previously adequately described from Koeberg as Quartinia atlantica

Gess (see Gess, 2011a: 5, figs 8 – 10), here sunk into synonymy.

If the females from Koeberg follow the same tendency towards melanism as shown by the males from that locality in comparison with those from further north, then they may likewise in the north have more extensive pale markings and pale legs.

Additional material examined. SOUTH AFRICA; WESTERN CAPE: Koeberg Nature Reserve (33.38S, 18.24E), 9 – 30.x.2010 (D. W., G. T. and G. M. Gess), 64 QQ (10 QQ on sand beneath *Trachyandra* sp., Asphodelaceae; 23 QQ on ground; 3 QQ visiting white flowers of *Capnophyllum africanum* (L.) W. D. J. Koch, Apiaceae); same locality, 29 – 30.x.2010 (F. W. and S. K. Gess), 25 QQ (14 QQ visiting purple flowers of *Senecio* cf. *arenarius* Thunb., Asteraceae; 2 QQ visiting yellow flowers of "helichrysum", Asteraceae; 4 QQ visiting yellow flowers of *Capnophyllum africanum*; 3 QQ on ground); same locality, 30 & 31.vii.2011 (D. W., G. T. and G. M. Gess), 7 QQ, 9 dd (on ground) – [all AMG].

Floral associations. Aizoaceae: Mesembryathema (*Carpobrotus* sp.); Apiaceae (*Capnophyllum africanum* (L.) W. D. J. Koch,); Asteraceae (*Senecio* sp. and "helichrysum"). To these may be added the record for the male from Sutherland: Cam-

panulaceae (*Wahlenbergia* near *polyclada* A.DC.). [The records for the females from Sutherland, erroneously assigned to *Q. namaquensis,* pertain to *Q. conchicola.*]

Nesting. West of Wallekraal one specimen, a male, freshly eclosed and with

wings not yet fully hardened, was extracted from a cell of a nest in a sand-filled shell of the desert snail *Trigonephrus* sp. (Mollusca: Gasteropoda; Pulmonata: Dorcasii-dae) (Gess 2007: 221). Such sand-filled shells occur also at Koeberg and it is likely that there too *Q. namaquensis* utilises them for nesting.

Discussion. In the key to species of *Quartinia* nesting in sand-filled snail shells (Gess 2007: 227–228) the then unknown female of *namaquensis* was not included.

In the key the missing female of *namaquensis* (as now identified from Koeberg) runs down to *australis* Gess, the characters given in the key being common to the females of both species, which indeed bear a close resemblance to one another though the relevant males are very different. The females may be distinguished, however, by the following characters. Though the tegulae are similarly marked and both have the inner posterior corner inwardly produced, that of *namaquensis* is relatively longer (1.5 × longer than wide) and more acutely pointed posteriorly than that of *australis* (1.3 × longer than wide). The mesoscutum of *namaquensis* is very obviously and finely microsculptured (shagreened) with fine, discrete punctures; that of *australis* less obviously shagreened with moderately coarse, close, at times subconfluent punctures. As far as is known, the areas of distribution of *namaquensis* and of *australis* are well separated.

Quartinia vagepunctata von Schulthess

http://species-id.net/wiki/Quartinia_vagepunctata

Quartinia vegepunctata von Schulthess 1929: 504 (key), ♀. Holotype ♀: South Africa: Little Karroo (*sic*), 38 m[iles] E of Ceres (BMNH). – von Schulthess 1935: 386 (key); Richards 1962: 132 (key), 169 (redescription of female); Gess and Gess 1992 (nesting); Gess, S. K. 1996 (nesting , flower visiting); Carpenter 2001: 29 (listed); Gess and Gess 2003: 64 (flower visiting); Gess 2011a: 32, figs 84-90 (description of male, key, flower visiting).

Augmented floral associations. To the previously recorded very marked association with Asteraceae (Gess 2011a: 36) may be added *Felicia* spp.
B. Species the with incomplete venation

Quartinia latigena sp. n.

urn:lsid:zoobank.org:act:E1DC02A8-81DB-47D4-8A2C-6D909171EDDD http://species-id.net/wiki/Quartinia_latigena Figs 22–27

Holotype. ♂, SOUTH AFRICA: NORTHERN CAPE: Nuwerus (31.08S, 18.22E), 17.x.2000 (F. W. and S. K. Gess) (visiting yellow flowers of *Pteronia* sp., Asteraceae) [AMG].

Paratypes. SOUTH AFRICA: NORTHERN CAPE: same data as holotype, 5 $\Im \Im$ [AMG].

Diagnosis. Small to medium sized (3.2 - 3.6 mm long). Fore wing with Cu1a and 2m-cu thin, the latter interrupted before reaching M. Tegula with posterior inner corner inwardly produced, anteriorly and posteriorly yellowish-white, medially usually dark ferruginous. POL: OOL= $1: \ge 1$. Temple unusually wide. Male with clypeus markedly contrasting and set off from frons by striking juxtaposition and sharp separation at suture of yellowish-white (of clypeus) and black (of frons); with broad paraocular streak carried upwards and narrowing to join (in some specimens) with crescent at bottom of ocular sinus. Sterna atuberculate.

Description. *Female* (Figs 22, 24, 26): Black. Yellowish-white (tending to be suffused with ferruginous) are: basi-lateral area of mandible; narrow crescent at bottom of ocular sinus; streak of variable size (almost effaced in one specimen) on temple; pair of variably sized streaks (almost effaced in two specimens) anteriorly on pronotum; postero-dorsal angle of pronotum; minute spot at top of mesopleuron (in two specimens only); tegula (except medially where ferruginous); postero-medial spot on scutellum; medially interrupted scutellar lamella; posterior bands, medially anteriorly produced and progressively narrower, on terga I – IV; apex of femur, most of tibia and basal four tarsomeres of all legs. Various shades of ferruginous are: mandibles (other than basilateral area); labrum; anterior border of clypeus (in some specimens only); antennae (dark above, light beneath); tegula medially; markings on femor, fifth tarsomere and claws of all legs.

Length 3.5 - 3.6 mm; length of fore wing 2.1 mm.

Head in front view $1.1 \times as$ wide as long. POL: OOL = 1: 1.03. Temple unusually wide. Clypeus $1.68 \times as$ wide as long; distal margin shallowly emarginate.

Head, mesosoma and gaster microsculptured (shagreened), moderately shiny; frons and vertex with small, well separated, inconspicuous punctures; pronotum and mesoscutum with punctures slightly larger and more conspicuous than those on head; gaster with small, inconspicuous punctures.

Male (Figs 23, 25, 27): Black. Yellowish-white are: basi-lateral area of mandible; underside of first two flagellomeres of antennal club and basal part of third; clypeus (except small area below antennal socket, pair of indefinite ferruginous spots on up-



Figures 22–27. *Quartinia latigena* **22** ♀, lateral view (× 14) **23** ♂, lateral view (× 13) **24** ♀, dorsal view (× 14) **25** ♂, dorsal view (× 13) **26** ♀, head, front view (× 39) **27** ♂, head, front view (× 33).

per half of disk and narrow broken transverse ferruginous line on lower half of disk) [clypeus markedly set off from frons by striking juxtaposition of yellowish-white and black at suture]; broad paraocular streak carried upwards and narrowing to join (in two specimens) with crescent at bottom of ocular sinus; large streak on temple; short, transverse anterior band drawn back along posterior margin of pronotum to postero-dorsal angle; streak on humeral angle; spot at top of mesopleuron; tegula (except medially where testaceous to ferruginous); postero-medial spot on scutellum; medially interrupted scutellar lamella; small spot to elongate streak on propodeal angle; posterior bands, laterally and medially anteriorly produced and progressively narrower, on terga I – VI; poorly defined posterior bands on most of sterna; apex of femur, most of tibia and basal four tarsomeres of all legs. Various shades of ferruginous are: mandibles (other than

basi-lateral area); labrum; antennae (other than parts listed above); tegula medially; markings on femor, fifth tarsomere and claws of all legs. Ground colour of gaster varying from black to dark brown with ferruginous last tergum, sternum and parameres.

Length 3.2 mm; length of fore wing 2.0 mm.

Head in front view $1.26 \times as$ wide as long. POL: OOL = 1: 1.15. Temple unusually wide. Clypeus $1.9 \times as$ wide as long; distal margin slightly down turned and narrowly lamellate, very widely and shallowly emarginate. Labrum without any indication of median carina, pointed apically.

Tergum VII with disk evenly convex; with V-shaped apical incision and the lobes defining it rounded. Sterna atuberculate.

Surface sculpture as in female.

Etymology. The name *latigena* serves to draw attention to the unusually wide temple in both the male and the female.

Geographic distribution. Known only from the type locality in southern Namaqualand, in the Succulent Karoo of Acocks (1953).

Floral associations. Asteraceae (Pteronia).

Nesting. Unknown.

Quartinia niveopicta von Schulthess

http://species-id.net/wiki/Quartinia_niveopicta Figs 28–30

- *Quartinia niveopicta* von Schulthess, 1930: 327, 329-380, ♀. Holotype: ♀, South Africa: Matjesfontein (BMNH); Turner, 1939: 1 (flower visiting); Carpenter, 2001: 26 (listed); Gess and Gess, 2003: 61 (flower visiting).
- *Quartinioides niveopicta* (von Schulthess): Richards, 1962: 176, 177 (key), 198 (redescription of ♀; description of ♂); Gess, S. K. 1996: 253 (flower visiting).

Diagnosis. Small to medium sized (presently studied females 3.2 - 3.6 mm). Fore wing with Cu1a and 2m-cu present but attenuate, much thinner than other veins, and with 2m-cu interrupted before reaching M. Tegula with posterior inner corner absolutely rounded. Female (Figs 28, 29, 30) with ground colour of head and mesosoma black, that of gaster reddish. Yellowish-white markings extensive, distributed as follows: on mandible (basally); on clypeus (apico-laterally and baso-medially); on frons (a spot in each ocular sinus and two more medially between latter; spots fused in most specimens to form a medially interrupted or even complete transverse band); on temple; on pronotum (anterior transverse band carried down to humeral angle; hind margin to postero-dorsal angle); on mesopleuron; on mesoscutum (two small antero-lateral spots and a larger postero-medial spot); on most of tegula; on scutellum (trilobed posterior band); on scutellar lamella; on propodeal angle; on gaster (posterior bands anteriorly produced medially and laterally); and on apex of femur, on tibia and on proximal tarsomeres of all legs. Male (unknown to present author;



Figures 28–30. *Quartinia niveopicta* **28** \bigcirc , lateral view (× 12) **29** \bigcirc , dorsal view (× 12) **30** \bigcirc , head, front view (× 36).

characters here given from Richards,1962: 199) with trochanters and proximal half of femora with dense, rather long, "woolly" setae; tergumVII with a well marked angular emargination; sterna 7 + 8 flat, ending in a narrow black central process. Coloured similarly to female but labrum, entire clypeus yellowish-white.

Material examined. SOUTH AFRICA: NORTHERN CAPE: Williston (31°20'S, 20°54'E) (1078m), 3.II.2006 (Carpenter & Davidson), $3 \ Q \ Q$ [AMNH]; WESTERN CAPE: 43 km ENE of Ceres on road to Sutherland [= Karoopoort] (33.12S, 19.44E), 2 – 3.xii.1989 (S. K. Gess), 1 $\ Q$ (on flowers of *Limonium* sp., Plumbaginaceae); SSE of Calitzdorp at bridge over Remhoogte River (33.34S, 21.43E), 8.xi.2010 (F.W. and S. K. Gess), 1 $\ Q$ (visiting flowers of *Peliostomum leucorrhizum* E. Mey. ex Benth., Scrophulariaceae); EASTERN CAPE: Fullerton, [33.11S, 23.50E], 30.x.1967 (C. Jacot-Guillamod), 3 $\ Q \ Q \ =$ [all AMG].

Provenance of material examined by Richards (1962). WESTERN CAPE: Matjesfontein [33.14S, 20.35E]; EASTERN CAPE: Willowmore [33.18S, 23.30E].

Geographic distribution. Known from a limited number of localities, all in the karroid areas of the Northern Cape, the Western Cape and Eastern Cape.

Floral associations. Plumbaginaceae (*Limonium*) and Scrophulariaceae (*Peli-ostomum*). Turner (1939) recorded the species from Aizoaceae: Mesembyanthema ("*Mesembryanthemum*").

Quartinia propinqua von Schulthess

http://species-id.net/wiki/Quartinia_propinqua

- *Quartinia propinqua* von Schulthess, 1932: 526, figs 2, 3, 4. ♀, ♂. Lectotype: ♀, Namibia: Aus (BMNH) designated by von Schulthess; Carpenter, 2001: 27 (listed); Gess and Gess, 2003: 62 (flower visiting); Gess, 2009: 265 (diagnosis, geographic distribution, floral associations).
- *Quartinioides propinqua* (von Schulthess): Richards, 1962: 199; Gess and Gess, 1989: 128 (flower visiting); Gess, S. K. 1996: Appendices 1 and 2 (flower visiting).
- *Quartinioides* sp. G: Gess and Gess, 1989: 128 (flower visiting); Gess, S. K. 1996: Appendices 1 and 2 (flower visiting).

Diagnosis. See Gess (2009: 265).

Additional material examined. SOUTH AFRICA: NORTHERN CAPE: Richtersveld National Park, Koeroegabvlakte (28.11S, 17.03E), 17–21& 24.ix.1995 (F. W., S. K. and R. W. Gess), 1 \bigcirc (on yellow flowers of *Gorteria* sp., Asteraceae); Augrabies (28.36S, 20.21E), 26.ii.2000 (F. W. and S. K. Gess), 10 $\bigcirc \bigcirc$ (visiting yellow flowers, Asteraceae); 25 km N[orth] of Kamieskroon (30.01S, 17.53E), 17.x.2000 (F. W. and S. K. Gess), 1 \bigcirc (visiting yellow flowers of 'gazania'', Asteraceae) – [all AMG]; Williston (31°20'S, 20°54'E) (1078m), 6.ii.2006 (Carpenter & Davidson), 1 \bigcirc ; Calvinia (31°28'S, 19°46'E) (981m), 5.ii.2006 (Carpenter & Davidson), 17 $\bigcirc \bigcirc$, 1 \bigcirc ; WESTERN CAPE: Vanrhynsdorp (31°36'S, 18°45'E) (112m), 4.ii.2006 (Carpenter & Davidson), 1 \bigcirc – [all AMNH].

Discussion. The data associated with the additional specimens slightly augment the known wide distribution of the species and reinforce the already demonstrated very strong association with Asteraceae.

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References

Acocks JPH (1953) Veld types of South Africa. Memoirs of the Botanical Survey of South Africa 29: i–iv, 1–192.

André Ed (1884) Spécies des Hyménoptères d'Europe et Algérie. Vol. 2. André and André, Beaune. Carpenter JM (2001) Checklist of the subfamily Masarinae (Hymenoptera: Vespidae. Ameri-

- can Museum Novitates 3325: 1–39. doi: 10.1206/0003-0082(2001)325<0001:COSOTS >2.0.CO;2
- Gess FW (2007) The genus *Quartinia* Ed. André, 1884 (Hymenoptera: Vespidae: Masarinae) in southern Africa. Part I. Description of new species with complete venation. Journal of Hymenoptera Research 16: 211–233.
- Gess FW (2008) The genus *Quartinia* Ed. André, 1884 (Hymenoptera: Vespidae: Masarinae) in southern Africa. Part II. A new species with complete venation and with a deeply excised antennal club in the male. Journal of Hymenoptera Research 17: 83–5.
- Gess FW (2009 The genus *Quartinia* Ed. André, 1884 (Hymenoptera: Vespidae: Masarinae) in southern Africa. Part III. New and little known species with incomplete venation. Journal of Hymenoptera Research 18: 244–281.
- Gess FW (2011a) The genus *Quartinia* Ed. André, 1884 (Hymenoptera, Vespidae, Masarinae) in southern Africa. Part IV. New and little known species with complete venation. Journal of Hymenoptera Research 21: 1–39. doi: 10.3897/JHR.21.870

- Gess FW (2011b) The genus *Quartinia* Ed. André, 1884 (Hymenoptera, Vespidae, Masarinae) in southern Africa. Part V. New and little known species with incomplete venation. Journal of Hymenoptera Research 22: 29–43. doi: 10.3897/jhr.22.871
- Gess FW, Gess SK (1992) Ethology of three southern African ground nesting Masarinae, two Celonites species and a silk spinning Quartinia species, with a discussion of nesting by the subfamily as a whole (Hymenoptera: Vespidae). Journal of Hymenoptera Research 1: 145–155.
- Gess SK (1996) The Pollen Wasps: Ecology and Natural History of the Masarinae. Harvard University Press, Cambridge, Massachusetts, 340 pp.
- Gess SK, Gess FW (1989) Flower visiting by masarid wasps in southern Africa (Hymenoptera: Vespoidea: Masaridae). Annals of the Cape Provincial Museums (Natural History) 18: 95–134.
- Gess SK, Gess FW (2003) A catalogue of flower visiting records for aculeate wasps and bees in the semi-arid to arid areas of southern Africa. Department of Entomology, Albany Museum, Grahamstown, 529 pp.
- Richards OW (1962) A revisional study of the masarid wasps (Hymenoptera, Vespoidea). British Museum (Natural History), London, 294 pp.
- Schulthess A von (1929) Contribution to the knowledge of African Masaridae (Vespoidea). Annals and Magazine of Natural History (10) 3: 498–511. doi: 10.1080/00222932908673003
- Schulthess A von (1930) Some more South African Masaridae (Vespoidea). Annals and Magazine of Natural History (10) 5: 326–330. doi: 10.1080/00222933008673140
- Schulthess A von (1935) Some more South African Masaridae (Vespoidea). Annals and Magazine of Natural History (10) 16: 383–390. doi: 10.1080/00222933508655058
- Schulthess A von, Scott H (1932) Some more South African Masaridae (Vespoidea), with notes on the mouthparts of the genera *Quartinia* and *Quartiniella*. Annals and Magazine of Natural History (10) 10: 525–536. doi: 10.1080/00222933208673605
- Turner RE (1939) Notes on the Masarid Wasps of the Genus *Quartinia*. Annals of the Transvaal Museum 20: 1–4.