

Revision of the brachycistidine genus *Colocistis* Krombein, 1942 (Hymenoptera, Tiphidae)

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Abstract

Twelve species of the brachycistidine genus *Colocistis* Krombein, 1942 are reviewed and two new species, *Colocistis chemsaki* and *C. oaxacana*, are described from Baja California and Oaxaca, Mexico respectively. A key to the species and species distribution maps are provided.

Keywords

Oaxaca, Baja California, Mexico

Introduction

In 1917 Bradley recognized the relationship of males of several species he considered members of the genus *Brachycistis*. He placed these in what he named the *castanea* group. Malloch (1926) arranged the species of *Brachycistis* into groups according to structural criteria, proposed the *brevis* group consisting of three species and provided a key to the groups. Krombein (1942) described the male of a new species, *pilosa*, near the *castanea* group but because of its small compound eyes, small ocelli and black coloration he placed it in a new genus, *Colocistis*. In his nomenclatorial review of the brachycistidine genera, Wasbauer (1966) transferred all four of the species in the *castanea* group as well as two in the *brevis* group to *Colocistis*. In this work he also provided a key which separat-

ed *Colocistis* from the other male brachycistidine genera known at that time. The latest generic key was provided by Kimsey and Wasbauer (2006). Kimsey (2006) synonymized the female-based genus, *Aglyptacros* Mickel & Krombein (1942) with *Colocistis*. Ironically, the type of the genus *Colocistis*, *pilosa* Krombein is only known from the holotype specimen and the species may very well be extinct, as the type was collected in the vicinity of the City of San Diego, which is now highly urbanized.

The genus *Colocistis* occurs from southern Idaho and northern California south to Oaxaca, Mexico and east to Nebraska and eastern Texas.

Materials and methods

Type repositories and specimens studied below are indicated by the following acronyms: ANSP – Philadelphia Academy of Sciences, Pennsylvania, USA; BME – Bohart Museum of Entomology, University of California, Davis, USA; CAS – California Academy of Sciences, San Francisco, USA; CDFA – California State Arthropod Collection, California Department of Food and Agriculture, Sacramento; CUIC – Cornell University Insect Collection, Ithaca, New York, USA; EMEC – Essig Museum, University of California, Berkeley, USA; KSBS – University of Kansas, Lawrence, USA; LACM – Los Angeles County Museum of Natural History, California, USA; MCZ – Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; UCRC – Entomological Research Museum, University of California, Riverside, USA, and USNM – U.S. National Museum, Washington, D.C., USA.

Morphological terminology follows that used by Wasbauer (1966) is further illustrated in Figs 1, 10 and 14. The following acronyms are used in the descriptions below: LID = *lower interocular distance*, the narrowest distance between the eye margins across the face; OOL = *ocellocular length*, the distance between the hind ocellus and the nearest eye margin, and UID = *upper interocular distance*, the distance between the dorsal eye margins across the face.

Taxonomy

Colocistis Krombein

<http://species-id.net/wiki/Colocistis>

Colocistis Krombein, 1942 (April):65. Type species: *Colocistis pilosa* Krombein 1942:66.

Original designation.

Aglyptacros Mickel & Krombein, 1942 (November):669. Type species: *Glyptometopa eureka* Banks 1912. Original designation. Synonymized by Kimsey 2006.

Diagnosis. The genus *Colocistis* exhibits a number of unique traits in both sexes. Features in the female, include the ventrally angulate occipital carina, the ventrally angulate mid-

and hindtrochanters, hindcoxal carina on both the inner, ventral margin and dorsobasal surface. Because a number of these features, including the angulate occipital carina and hindcoxal carina are shared with males of *Colocistis* and the distributions of the two genera coincide *Aglyptacros* was made the junior synonym of *Colocistis* (Kimsey 2006).

Description. Male Body length 5–16 mm.

Head. Compound eyes and ocelli enlarged (except quite small in *chemsaki* and *pilosissima*); gular carina either not elevated or elevated gradually at level of posterior mandibular condyle, not suddenly produced apically, clypeal length versus width ratio not exceeding 0.35; maxillary and labial palpi not reduced, maxillary palpi six-segmented, exceeding posterior border of gular orifice by half length of palpus; labial palpi four-segmented.

Mesosoma. Fore wing with costa extending beyond stigma for a distance not over half length of stigma; forewing with two discoidal cells and two or three submarginal cells, second submarginal cell completely or almost completely underlying first submarginal cell, first transverse cubital vein arising at or before basal third of second submarginal cell (Fig. 14); hind wing with cubitus arcuately curved, longer than first transverse cubital vein and meeting it at an angle of less than 135 degrees; hind wing with jugal lobe shorter than submedial cell; forecoxa with admesal stridulatory area; hindcoxa with longitudinal carina on inner margin.

Metasoma. Sternum II without basal longitudinal carina (one species with transverse carina); digitus of genitalia without process extending distad of articulum; volsellar plate without spines or teeth, but with flexible hairs on mesal surface.

Description. Female Body length 5–12 mm.

Head. Mandible broadest subapically, with two distinct apical teeth, inner margin with large, obtuse tooth at broadest point, obtuse tooth obscured by scutate bristles, inner margin below tooth with three small teeth, outer carina obsolescent, ventral carina distinct, sharp; maxillary palp 5-segmented; occipital carina well-developed, angulate ventrolaterally, forming straight line ventrally, often subtended by secondary carina; vertex with submedial impressions, lateral setose groove represented by row of large punctures or foveae.

Mesosoma. Propleural ventral margin strongly elevated, with sharp, transverse carina; hindcoxa with longitudinal carina on inner margin; hindtibial calcar slightly curved and acute apically.

Metasoma. Sternum I with transverse subbasal carina well-developed and protruding, subtended by medial pit, and with two foveae basad; tergum I with well-developed lateral ridge.

Distribution. *Colocistis* species are found in southeastern California, southern Nevada, southern Arizona, southern Colorado, western Texas and as far south as Oaxaca, Mexico.

Key to species of *Colocistis*

- | | | |
|---|-----------------------------------------------|---|
| 1 | Wingless, metasoma 6-segmented; females | 2 |
| – | Winged, metasoma 7-segmented; males..... | 5 |

- 2 Gular carina strongly elevated or angulate on either side of midline, meeting occipital carina (as in Fig. 11); meso-metapleural suture obsolescent; metasomal sternum I with medial, longitudinal sulcus present on basal third **3**
- Gular carina linear or crenulate, not elevated or angulate on either side of midline, interrupted medially occipital carina incomplete laterally, not meeting gular carina (as in Fig. 12); meso-metapleural suture present, distinct; metasomal sternum I with medial, longitudinal sulcus present on more than half of length **4**
- 3 Gular carina interrupted medially, with strongly developed submedial tooth or angle, meeting occipital carina at distinct angle (Fig. 11); transverse carina posterior to gular carina medially interrupted, without curved angles or lobes; meso-metapleural suture absent or only faintly visible in certain views.....
- ***segredentata* Mickel & Krombein**
- Gular carina not interrupted medially, strongly developed submedial rounded lobe (Fig. 10); gular carina meeting occipital carina in even curve; transverse carina posterior to gular carina with two low, rounded prominences behind lobes of gular carina; meso-metapleural suture faint but distinct..... ***eureka* (Banks)**
- 4 Gular carina extending laterally considerably beyond where occipital carina would terminate if present (Fig. 12); vertex foveae linear, consisting of row of contiguous pits; metasomal sternum I medial, longitudinal sulcus extending complete length of sternum, sulcus narrow and deep anteriorly, broad and shallow posteriorly ***sulcata* Mickel & Krombein**
- Gular carina not extending laterally beyond where occipital carina would terminate if present; vertex foveae short, elliptical; metasomal sternum I medial, longitudinal sulcus same width throughout, deeper anteriorly than posteriorly ***paxillata* Mickel & Krombein**
- 5 Forewing with two submarginal cells (as in Fig. 13); hindcoxal carina low and indistinct **6**
- Forewing with three submarginal cells (as in Fig. 14); hindcoxal carina prominent **8**
- 6 Gular carina elevated anteriorly (as in Fig. 9) ***eremi* (Bradley)**
- Gular carina not elevated anteriorly, nearly linear **7**
- 7 OOL 1 ocellar diameter or less; vertex not visible behind ocelli in full frontal view (Fig. 1); gonostylar apical margin evenly curved to acute apex (Fig. 49) ***brevis* (Cresson)**
- OOL 2 ocellar diameters or more; vertex clearly visible behind ocelli in front view (Fig. 3); gonostylar apical margin truncate or slightly emarginate (Fig. 51)..... ***chemsaki* sp. n.**
- 8 Metasomal sternum II basally slightly raised and separated from posterior part by transverse declivity (as in Figs 19, 22) **9**
- Metasomal sternum II without raised area basally (as in Fig. 20)..... **10**
- 9 Head and body black; ocelli small, diameter of lateral ocellus 0.5× OOL (Fig. 7); clypeus with median tubercle (Fig. 7); aedeagus in lateral view evenly curved, simple at apex (Fig. 55) ***pilosa* Krombein**

- Head and body castaneus; ocelli enlarged, diameter of lateral ocellus at least 0.7× OOL (Fig. 4); clypeus without median tubercle (Fig. 4); aedeagus in lateral view suddenly decurved, apex with a dorsally projecting process (Fig. 52) ***crassa* (Bradley)**
- 10 Clypeus with a projecting tubercle, plainly visible above mandibles in full lateral view, area between tubercle and apex appearing beveled (Fig. 8); genitalia in lateral view with gonostyli straight or slightly concave at apex; aedeagus decurved before apex (Fig. 56) ***thermarum* (Bradley)**
- Clypeus somewhat flattened and depressed, not visible above mandibles in full lateral view, apex not beveled; genitalia in lateral view with gonostylus strongly excavate at apex; aedeagus not decurved before apex (as in Figs 50, 54) **11**
- 11 Integument of head, mesosoma and first metasomal segment lighter in color than remainder of metasoma; head in full frontal view (Fig. 6) with vertex arched far above ocelli; genitalia in lateral view (Fig. 54) with apex of gonostylus nearly straight ***oaxacana* sp. n.**
- Integument of entire body concolorous; head in full frontal view with vertex arched only slightly, if at all, above ocelli (Fig. 2); genitalia in lateral view (Fig. 50) with apex of gonostylus strongly excavate ***castanea* (Cresson)**

***Colocistis brevis* (Cresson)**

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

Figures 1, 33, 41, 49

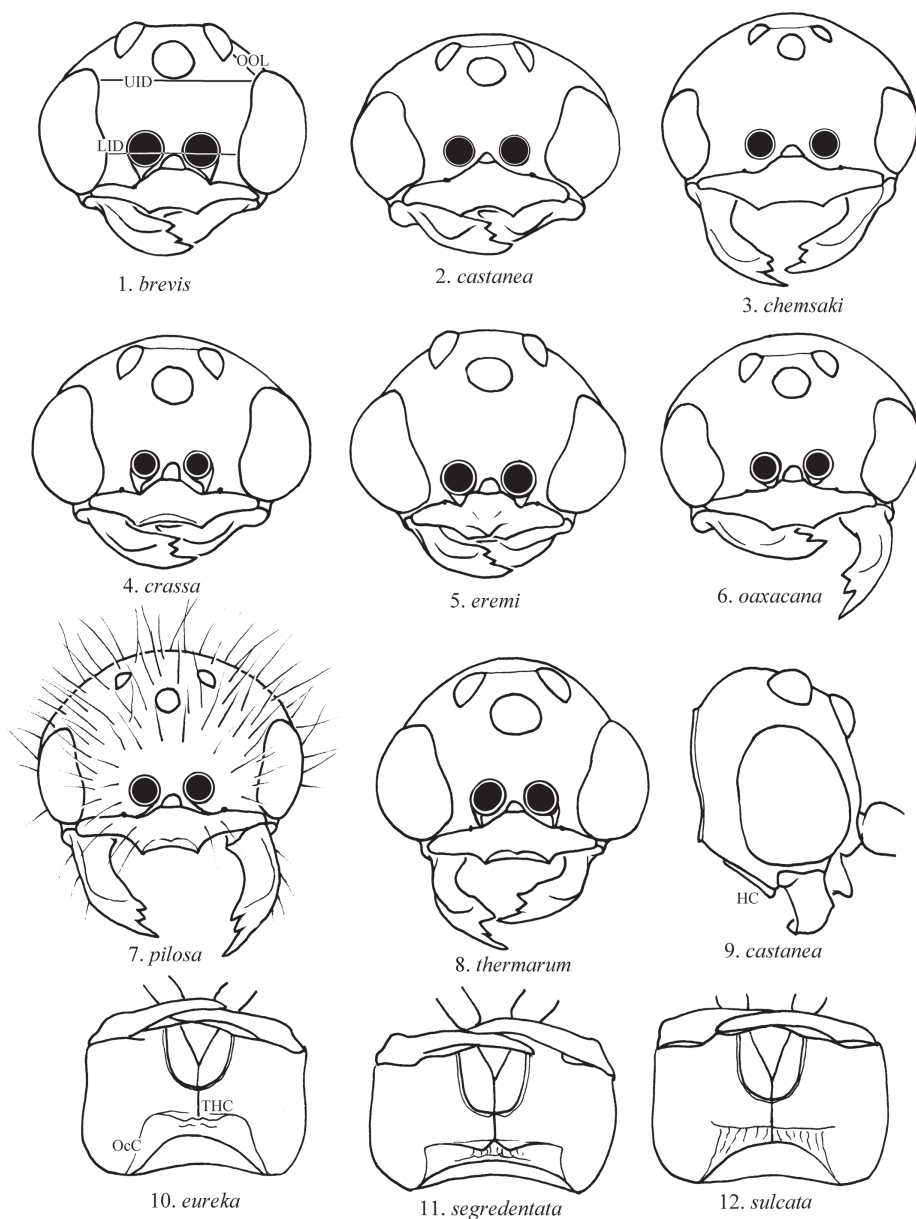
Brachycistis brevis Fox, 1899:285. Holotype male; USA: California (ANSP).

Diagnosis. This is one of three species in *Colocistis*, with two submarginal cells, including *eremi* and *chemsaki*, and one of two (*eremi*) with the costal vein not extending beyond the stigma. It can be distinguished from *eremi* by the hypostomal carina not elevated anteriorly (strongly elevated in *eremi*) and the aedeagus in lateral view slightly decurved (not decurved in *eremi*).

Description. Male.

Body length. 5–11 mm.

Head (Fig. 1). Compound eyes enlarged, extending laterally far beyond temples, inner margins somewhat emarginate; ocelli enlarged, diameter of lateral ocellus at least 0.7× OOL; vertex with impressed line between lateral ocelli absent or reduced to a row of punctures; postvertex not visible behind ocelli in frontal view; lateral ocelli separated from vertex by 0.5 or less one ocellar diameter in frontal view; clypeus raised medially and visible above mandibles in lateral view, apex not bounded laterally by strong teeth; gular carina gradually elevated anteriorly.; LID 0.8× UID; flagellomere I length 2.3–2.5× breadth; flagellomere II length 2.5× breadth; flagellomere IX length 5.5–6.0× breadth; occipital carina strong, complete ventrally, with strong carina extending from foramen magnum to hypostomal carina medially; mandible narrowest submedially.



Figures 1–12. 1–8 Front view of male head. 9 Lateral view of male head 10–12 Ventral view of female head. Abbreviations: LID = least interocular distance, OcC = occipital carina; OOL = ocellocular distance, THC = transverse hypostomal carina, UID = upper interocular distance.

Mesosoma. Pronotal punctures deep, contiguous; forefemur without stout spines; foretibia without spines except apically; basitarsus with three spines on outer surface; tibial spur as long as basitarsus; hindcoxa longitudinal dorsal carina basally angulate; mesopleural punctures contiguous; scutellum not strongly elevated above level of pro-

podeum; scutal and scutellar punctures 1–4 puncture diameters apart; postscutellum densely punctate; propodeum dorsal surface densely irregularly rugose, with irregular longitudinal submedial and sublateral carinae, posterior surface transversely, densely ridged, with large, dense punctures laterally; lateral surface impunctate ventrally becoming densely punctate dorsally; forewing with two submarginal cells, costa not extending along wing margin beyond stigma.

Metasoma. Tergum I without transverse carina; sternum II without raised area anteriorly.

Genitalia (Figs 42, 50). Gonostylus evenly curved to tip, aedeagus slightly de-curved in lateral view.

Color. Head and body concolorous castaneous; vestiture brown.

Female unknown.

Distribution (Fig. 33). USA: **Arizona**: Maricopa, Pima, Yuma counties; **California**: Imperial, Inyo, Riverside, San Bernardino, San Diego counties; **Nevada**: Lincoln, Nye counties; **Texas**: El Paso County; Mexico: **Baja California, Baja California Sur, Sonora**; 990 males were examined including the type (BME, EMEC, KSBS, LACM).

Colocistis castanea (Cresson)

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

Figures 2, 9, 14, 15, 17, 20, 34, 42, 50

Brachycistis castanea Cresson, 1865a:388. Holotype male; USA: California (ANSP).

Brachycistis stygia Bradley, 1917:276. Holotype male; USA: Arizona, Nogales (CUIC).

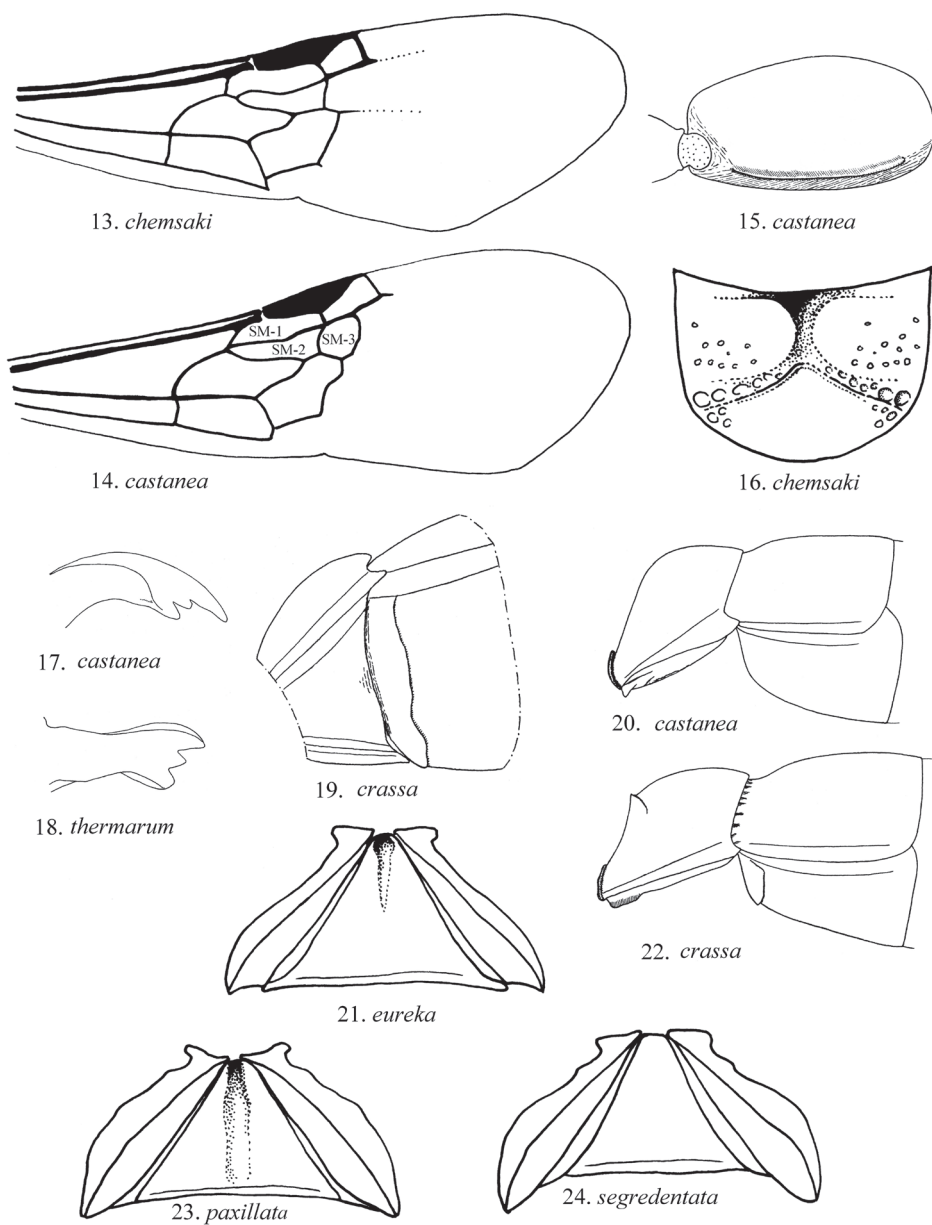
New synonymy.

Diagnosis. The simple second metasomal sternum distinguishes *castanea*, *oaxacana* and *thermarum* from other species of *Colocistis*. *Colocistis castanea* and *oaxacana* share a flattened clypeus in profile (elevated and tuberculate in *thermarum*). The concolorous body color and unmodified vertex will distinguish *castanea* from *oaxacana*. No structural features, only color could be found to distinguish *stygia* from *castanea*.

Description. Male.

Body length. 10–15 mm.

Head (Fig. 2). Head: compound eyes enlarged, extending laterally far beyond temples, inner margins somewhat emarginated; ocelli enlarged, diameter of lateral ocellus at least 0.7× OOL, removed from vertex by 0.5 or less one ocellar diameter in frontal view; impressed line present between lateral ocelli posteriorly; clypeus nearly flat, not visible above mandibles in lateral view, without projecting tubercle, apex not margined by strong teeth; antennal socket rim only slightly thickened ventrolaterally; LID 0.7× UID; flagellomere I length 2.3–2.5× breadth; flagellomere II length 2.5–2.6× breadth; flagellomere IX length 4.5–5.0× breadth; occipital carina strong but incomplete ventrally; mandible narrowest submedially, tapering apically toward ventroapical tooth (Fig. 17).



Figures 13–24. 13, 14 Male forewing. 15 Ventral view of male hindcoxa 16 Dorsal view of male propodeum 17 dorsal view of male mandible 18 lateral view of mandible 19 Ventral view of male metasomal sterna I-II 20, 22 Lateral view of male metasomal segments I and II 21, 23, 24 Ventral view of female metasomal sternum I. Abbreviations: SM-1, 2, 3 = submarginal cells 1–3.

Mesosoma. Pronotal punctures deep, contiguous, shoulders well developed, not produced laterally; forefemur without stout spines; foretibia without spines except apically; basitarsus with row of three spines on outer surface; tibial spur 0.9× length of

basitarsus; hindcoxa with longitudinal carina on ventral surface (Fig. 15), longitudinal dorsal carina not tooth-like; scutal, scutellar and mesopleural punctures large, separated by 1–3 puncture diameters; scutellum elevated above level of propodeum, with polished impunctate area medially; postscutellum densely punctate; propodeum dorsal surface coarsely rugose, with irregular, shallow, longitudinal medial groove, posterior surface separated from dorsal by transverse ridge, posterior surface polished, nearly impunctate, lateral surface dorsally with contiguous punctures becoming sparsely punctate to impunctate ventrally; forewing with 3 submarginal cells; costa continuing along wing margin beyond stigma.

Metasoma. Tergum I without transverse carina (Fig. 20); sternum II without raised area basally.

Genitalia (Figs 42, 49). Gonostylar apex arcuately excavate in lateral view; aedeagus not decurved before apex.

Color. Head and body concolorous castaneous to black; vestiture light brown.

Female unknown.

Distribution (Fig. 34). USA: **Arizona**: Cochise and Pima counties; **California**: Riverside, San Bernardino counties; **Nevada**: Clark County; **New Mexico**: Dona Ana, Eddy counties; **Texas**: Brewster, Culberson, Dimmit, Hudspeth, Maverick counties; MEXICO: **Baja California**, **Baja California Sur**, **Chihuahua**, **Coahuila**, **Sinaloa**, **Sonora**; 1727 males were examined (BME, CDFA, EMEC, LACM, UCRC).

***Colocistis chemsaki* Kimsey & Wasbauer, sp. n.**

<http://zoobank.org/DFA21F30-24D2-4BEA-8DD7-A3174EB2CD29>

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

Figures 3, 13, 16, 37, 43, 51

Holotype male. Mexico: Baja California Sur, La Paz, 21/ix.1967, J. A. Chemsak, on flowers during day (EMEC).

Paratypes. 1 male, 15 mi w La Paz, Michelbacher and Ross; 1 male, Santo (“San”) Domingo, Michelbacher and Ross (BME, CAS).

Diagnosis. This is one of three species, including *eremi* and *brevis*, with only two forewing submarginal cells. Unlike *eremi* the gular carina is simple, and unlike *brevis* the aedeagus is not decurved. This species shares several features with *pilosa*. The ocelli are small, about the size of the pedicel, whereas they are much larger than the pedicel in other *Colocistis*, and the eyes closely follow the head margins as opposed to bulging laterally. Unique features include the antenna darker than the rest of the body, whereas they are the same color in the other species, and the propodeum in *chemsaki* has two large elevated, ovoid areas on either side of the midline of the dorsal surface.

Description. Male.

Body length. 7–8 mm.

Head (Fig. 3). Compound eyes slightly enlarged, barely extending laterally beyond temples, inner margins somewhat emarginated; ocelli small, diameter subequal

to pedicel length; of lateral ocellus at least $0.7\times$ OOL, removed from vertex by 0.5 or less an ocellar diameter in frontal view; impressed line present between lateral ocelli posteriorly; clypeus nearly flat, not visible above mandibles in lateral view, without projecting tubercle, apex not margined by strong teeth; antennal socket rim only slightly thickened ventrolaterally; LID $0.9\times$ UID; flagellomere I length $2.3\times$ breadth; flagellomere II length $2.8\times$ breadth; flagellomere IX length $4.2\times$ breadth; occipital carina strong but incomplete ventromedially; mandible narrowest submedially, tapering apically toward ventroapical tooth.

Mesosoma. Pronotum nearly vertical anteriorly, punctures deep, contiguous close, shoulders well-developed, not produced laterally; foretibia without spines except apically; basitarsus with row of three spines on outer surface; tibial spur $0.9\times$ length of basitarsus; hindcoxal longitudinal dorsal carina elevated, angulate basally; mesonotal and mesopleural punctures deep, $0.5\text{--}1.0$ puncture diameter apart; scutellum elevated above level of propodeum, with polished impunctate area medially; postscutellum densely punctate; propodeum nearly impunctate, dorsal surface with shallow medial, longitudinal groove, dorsal surface separated from posterior surface by transverse ridge, ridge interrupted medially, lateral surface with punctures $1\text{--}2$ puncture diameters apart; forewing with 3 submarginal cells; costa continuing along wing margin beyond stigma.

Metasoma. Tergum I without transverse carina; sternum II without raised area basally.

Genitalia (Figs 43, 51). Gonostylar apex arcuately excavate in lateral view; aedeagus not decurved before apex.

Color. Head and body concolorous castaneous to black; vestiture brown.

Female unknown.

Distribution (Fig. 37).

Etymology. The species is named after the collector, John Chemsak.

***Colocistis crassa* (Bradley)**

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

Figures 4, 19, 22, 35, 44, 52

Brachycistis crassa Bradley, 1917:277. Holotype males; USA: California, Fresno County, Coalinga (CUIC).*

Diagnosis. *Colocistis crassa* and *pilosa* share a distinctive modification of metasomal sternum II, which has the basal area elevated and separated from the rest of the sternum by a transverse declivity. These two species can be separated by the castaneous body color in *crassa* (black in *pilosa*), clypeus with a well-developed medial tubercle (no tubercle in *pilosa*) and large compound eyes and ocelli (small in *pilosa*).

Description. Male.

Body length. 9–16 mm.

Head (Fig. 4). Compound eyes enlarged, extending well beyond temples; ocelli enlarged, diameter of lateral ocellus at least $0.7\times$ OOL; impressed line present between lateral ocelli; antennal socket rim thickened and carinate ventrolaterally; clypeus with median tubercle, visible above mandible in lateral view, apex not bounded laterally by strong teeth; gular carina not raised; LID $0.7\times$ UID; flagellomere I length $3.2\text{--}3.3\times$ breadth; flagellomere II length $2.7\text{--}2.8\times$ breadth; flagellomere IX length $5.7\text{--}5.8\times$ breadth; occipital carina strong, incomplete ventrally; hypostomal carina not raised; mandible narrowest submedially, tapering apically toward ventroapical tooth.

Mesosoma. Pronotum nearly vertical anteriorly, punctures separated by $0.5\text{--}1.0$ puncture diameters, shoulders well developed, not produced laterally; forefemur without stout spines; foretibia without spines except apically; basitarsus with two spines on outer surface; tibial spur $0.9\times$ length of basitarsus; hindcoxal longitudinal dorsal carina forming obtuse angle basally; scutal and mesopleural punctures $1\text{--}2$ puncture diameters apart; scutellum somewhat curved above level of propodeum, coarsely punctured with large, polished impunctate area medially; postscutellar punctures $1\text{--}2$ puncture diameters apart; propodeum with long dorsal surface, nearly impunctate, with wide medial, longitudinal trough, reaching carina separating dorsal from posterior surfaces, posterior surface with shallow punctures, $0.5\text{--}1.0$ puncture diameters apart, lateral surface punctures $0.5\text{--}1.0$ puncture diameters apart dorsally, nearly impunctate ventrally; forewing with 3 submarginal cells; costa extending along wing margin beyond stigma.

Metasoma. Tergum I with transverse carina at apex of frontal declivity (Fig. 22); sternum II with anterior portion slightly raised and separated from remainder of sternum by a transverse declivity (Figs 19, 22).

Genitalia (Figs 44, 52). Gonostylar apex somewhat excavate in lateral view; aedeagus abruptly decurved in lateral view, apex with dorsally projecting process.

Color. Head and body unicolorous, castaneous; vestiture pale brown.

Female unknown.

Distribution (Fig. 35). USA: **Arizona:** Cochise, Coconino, Gila, Graham, Maricopa, Pima, Pinal, Santa Cruz, Yuma counties; **California:** Alpine, Fresno, Imperial, Inyo, Kern, Kings, Lassen, Los Angeles, Madera, Merced, Mono, Monterey, Riverside, San Benito, San Bernardino, San Diego, San Luis Obispo, Santa Barbara, Santa Clara, Sonoma, Stanislaus, Tuolumne, Tulare, Ventura counties; **Idaho:** Ada, Elmore, Owyhee counties; **Kansas:** Stanton County; **Nevada:** Churchill, Esmeralda, Eureka, Humboldt, Lincoln, Nye, Pershing, Washoe counties; **New Mexico:** Dona Ana, Eddy, Hidalgo, Luna, Quay counties; **Texas:** Alpine, Brewster, Culberson, El Paso, Jeff Davis counties; **Utah:** Ogden County; Mexico: **Baja California, Baja California Sur, Chihuahua, San Luis Potosi, Sinaloa, Sonora;** 1250 males were examined (BME, CAS, CDFA, EMEC, KSBS, LACM, MCZ).

***Colocistis eremi* (Bradley)**

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

Figures 5, 36, 45, 53

Brachycistis eremi Bradley, 1917:279. Holotype male; USA: California, Imperial County, Calexico (CUIC).

Diagnosis. Only *brevis* and *eremi* have two submarginal cells and the costal vein not extending beyond the stigma. *Colocistis eremi* can be distinguished from *brevis* by the strongly elevated hypostomal carina and the aedeagus straight in lateral view as discussed under *brevis*.

Description. Male.

Body length. 5–12 mm.

Head (Fig. 5). Compound eyes enlarged, extending laterally far beyond temples; ocelli enlarged, diameter of lateral ocellus at least $0.7\times$ OOL; lateral ocellus removed from vertex by 0.5 or less one ocellar diameter; impressed line between lateral ocelli absent or reduced to row of punctures; clypeus raised medially and visible above mandibles in lateral view, apex not bounded laterally by strong teeth; gular carina raised anteriorly; LID $0.6\times$ UID; flagellomere I length $2.7\text{--}2.8\times$ breadth; flagellomere II length $3\times$ breadth; flagellomere IX length $3.6\text{--}3.7\times$ breadth; occipital carina strong, complete ventrally; mandible narrowest submedially, tapering apically toward ventroapical tooth.

Mesosoma. Pronotal punctures shallow, $0.5\text{--}1.0$ puncture diameters apart, shoulders well-developed, not produced laterally; forefemur without stout spines; foretibia without spines except apically; basitarsus with two spines on outer surface; tibial spur subequal to length of basitarsus; hindcoxa with longitudinal dorsal carina basally tooth-like; scutal punctures $1\text{--}2$ puncture diameters apart; mesopleural punctures nearly contiguous; scutellum slightly elevated above level of propodeum, punctures $1\text{--}3$ puncture diameters apart; postscutellum impunctate medially, densely punctate laterally; propodeum dorsal surface with longitudinal sublateral carinae, shallowly rugose, without transverse carina separating dorsal from posterior surface, posterior surface punctures deep, $1\text{--}3$ puncture diameters apart, lateral surface punctures $0.5\text{--}1.0$ puncture diameters apart dorsally, impunctate ventrally; forewing with two submarginal cells, costa not extending along wing margin beyond stigma.

Metasoma. Tergum I without transverse carina; sternum II without raised area anteriorly.

Genitalia (Figs 45, 53) in lateral view with gonostylus broadly curved to nearly straight at tip, aedeagus not decurved.

Color: Head and body unicolorous castaneous; vestiture pale brown.

Female unknown.

Distribution (Fig. 36): USA: **Arizona:** Coconino, Maricopa, Pima, Pinal, Yuma counties; **California:** Imperial, Inyo, Riverside, San Bernardino, San Diego Counties; Nevada: Lincoln, Nye counties; Mexico: **Baja California, Baja California Sur, Sonora;** 518 males were examined (BME, EMEC, KSBS, LACM).

***Colocistis eureka* (Mickel & Krombein)**

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

Figures 10, 21, 39

Glyptometopa eureka Banks, 1912:202. Holotype female; USA: Arizona, Palmerlee (MCZ).

Diagnosis. *Colocistis eureka* shares the strongly elevated gular carina with *segredentata*. However, in *eureka* the carina is strongly biangular or bidentate versus medially uninterrupted and the meso- metapleural sulcus is faint but distinct, versus absent or incomplete in *segredentata*.

Male unknown.

Description. Female.

Body length. 9.5–10.0 mm.

Head. Wider than long in anterior view; vertex with lateral foveae consisting of row of large, shallow punctures; occipital carina (Fig. 10) meeting transverse carina at obtuse angle, transverse carina irregular, notched medially between submedial teeth, subtended by irregular rugae toward occiput.

Mesosoma. Pronotal disk 0.4× as long as broad in dorsal view, nearly impunctate, with several scattered punctures; propleura densely punctured; foretibia with two spines laterally; basitarsus with two spines on outer surface; tibial spur 0.9× length of basitarsus; hindcoxa ventral carina extending 0.5 length of coxa, dorsal longitudinal carina broadly elevated basally.

Metasoma. Sternum I without medial groove (Fig. 21).

Color. Reddish brown; vestiture whitish to pale yellow.

Distribution (Fig. 39). USA: Arizona, Cochise County: Palmerlee; Santa Cruz County: Atascosa Mountain; two specimens were seen (BME, UCRC).

***Colocistis oaxacana* Kimsey & Wasbauer, sp. n.**

<http://zoobank.org/669E891B-4329-4EAD-B707-715EB06358EA>

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

Figures 6, 25, 26, 37, 46, 54

Diagnosis. Two unique features distinguish *oaxacana* from other species of *Colocistis*, the bicolored body and strongly elevated vertex. This species most closely resembles *castanea* but, in addition, to differences in the coloration and the elevated vertex, can be distinguished by the gonostylar apex strait or slightly curved but not excavate as in *castanea*.

Type material. Holotype male: Mexico: Oaxaca, 23 mi. south Matias Romero, iv/5/1962, F. D. Parker & L.A. Stange (BME). Paratypes (30 males): 6 males: same data as holotype; 4 males: iv/6/1962; 1 male, iv/8/1962; 1 male, iv/22/1962; 10 males: Tequisistlan, iv/6/1962, F. D. Parker & L.A. Stange; 4 males: 1 mi sw Tehuantepec, iv/5/53, E. I. Schlinger; 2 males: Ixtepec, iv/23/1962, F. D. Parker & L.A. Stange;



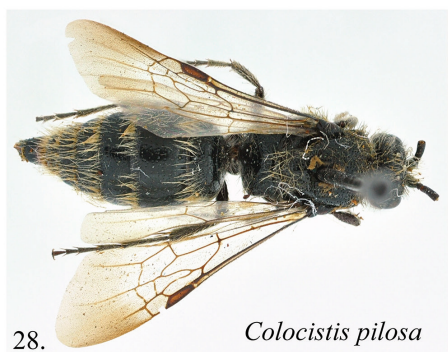
25.



27.



26.

Colocistis oaxacana

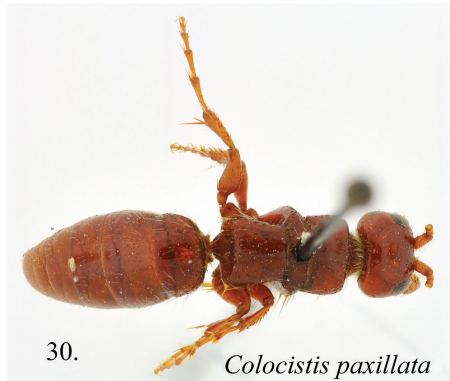
28.

Colocistis pilosa

29.



31.



30.

Colocistis paxillata

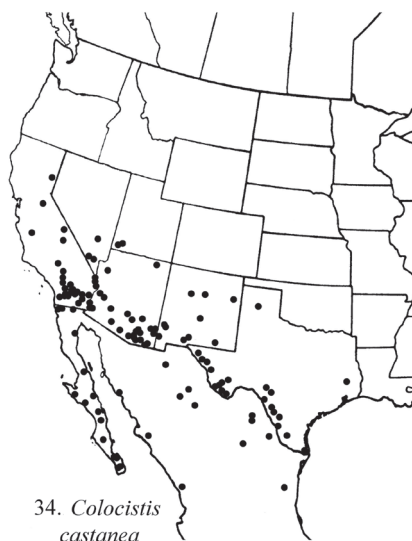
32.

Colocistis segredentata

Figures 25–32. 25–28. Males. 29–32 Females. 25, 27, 29, 31 Lateral view 26, 28, 30, 32 Dorsal view 25–30 are images of the holotypes.

1 male: 10 mi ne Juchitan, iv/15/1953, E. I. Schlinger; 2 males: Chiapas, 28 mi w Cintalapa (BME, EMEC).

Description. Male (Figs 25, 26).



Figures 33–36. Distribution maps of *Colocistis* species.

Body length. 9–11 mm.

Head (Fig. 6). Compound eyes enlarged, extending well beyond temples; ocelli enlarged, diameter of lateral ocellus at least $0.7\times$ OOL; lateral ocelli removed from vertex by nearly one ocellar diameter in frontal view; impressed line present between lateral ocelli; clypeus slightly convex but without projecting tubercle in lateral view, apex not



Figures 37–40. Distribution maps *Colocistis* species.

bounded laterally by strong teeth; antennal socket rim only slightly thickened ventro-laterally; LID $0.8\times$ UID; flagellomeres I-II length $2.7\text{--}2.8\times$ breadth; flagellomere IX length $5.2\text{--}5.5\times$ breadth; occipital carina strong but incomplete ventrally, without ca-

rina extending from foramen magnum to hypostomal carina medially; gular carina not raised; mandible narrowest submedially, tapering apically toward ventroapical tooth.

Mesosoma. Pronotum nearly vertical anteriorly, sloping posteriorly, punctures shallow and sparse medially, laterally deep and close, shoulders well developed, not produced laterally; forefemur without stout spines; foretibia without spines except apically; basitarsus with two spines on outer surface; tibial spur 0.9× length of basitarsus; hindcoxal longitudinal dorsal carina not tooth-like; scutal and mesopleural punctures separated by 0.5–1.0 puncture diameter; scutellum not arched dorsally above level of propodeum, punctures large, 0.5–1.0 puncture diameters apart, with polished impunctate area posteromedially; postscutellum impunctate medially; propodeum nearly impunctate, dorsal surface with shallow V-shaped trough medially, forming obtuse angle with posterior surface, separated from posterior surface by medially interrupted transverse carina, lateral surface with scattered punctures, 2–5 puncture diameters apart; forewing with 3 submarginal cells, costa extending long wing margin beyond stigma.

Metasoma. Tergum I without transverse carina; sternum I with narrow longitudinal medial groove extending most of length; sternum II without raised anterior portion.

Genitalia (Figs 46, 54). Gonostylus not excavate ventrally before apex and apical margin straight not excavate in lateral view; aedeagus broadest subapically and submedially, not decurved before apex in lateral view, apex simple.

Color. Head and mesosoma castaneous, metasoma darker, often nearly black; vestiture pale brown to black.

Female unknown.

Distribution (Fig. 37)

Etymology. The species is named after the collection locality, the state of Oaxaca, Mexico.

Discussion. *Colocistis oaxacana* is the southernmost species in the genus. The others are only recorded from as far south as Sinaloa, Mexico.

***Colocistis paxillata* (Mickel & Krombein)**

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

Figures 23, 29, 30

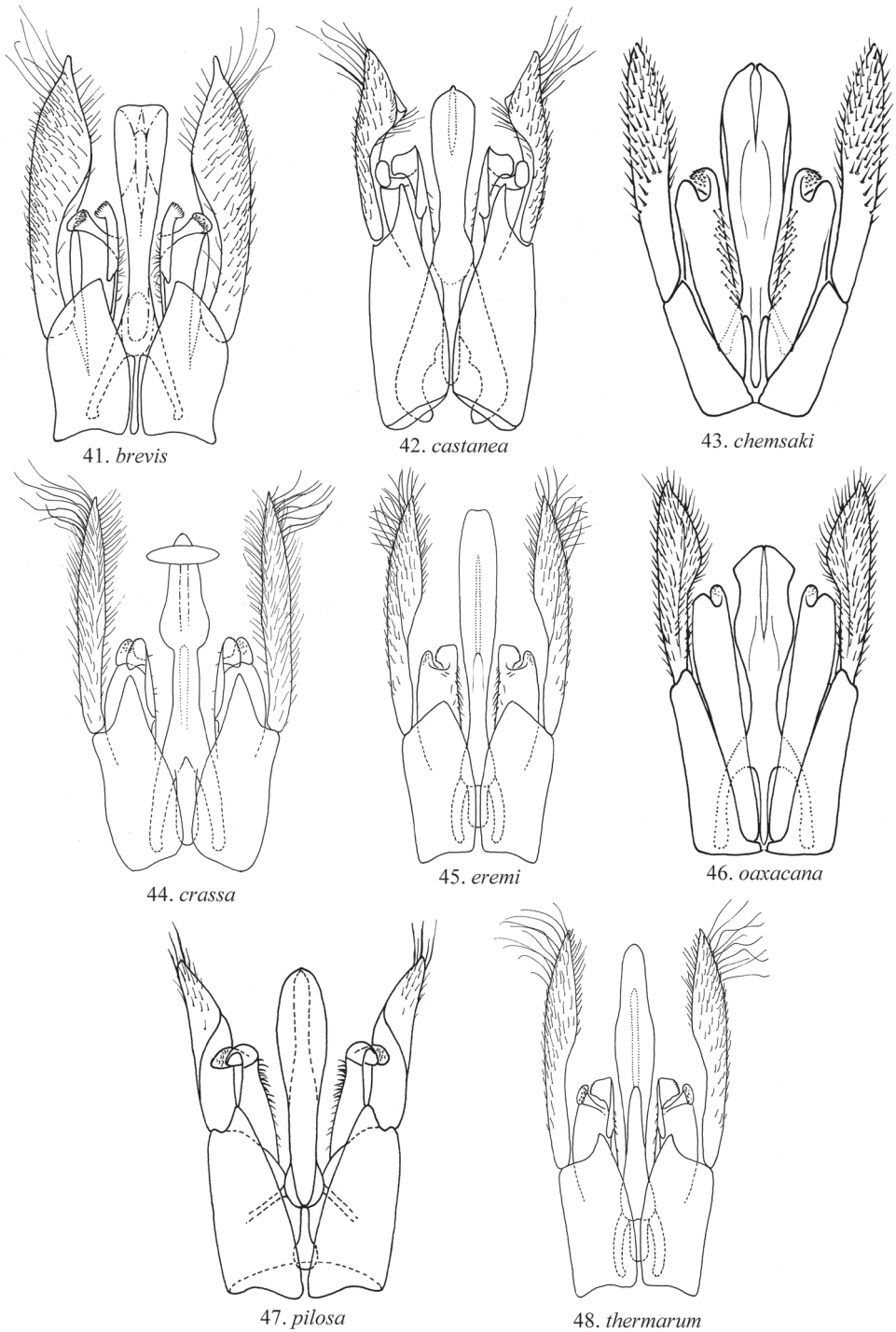
Aglyptacros paxillata Mickel & Krombein, 1942:673. Holotype female; USA: Colorado, La Junta (USNM).

Diagnosis. In *paxillata* and *sulcata* the gular carina is not elevated or angulate and does not meet the occipital carina. *Colocistis paxillata* can be distinguished from *sulcata* by the sulcus on metasomal sternum I extending the same width for the length of the sternum.

Male unknown.

Description. Female (Figs 29, 30).

Body length. 10.5 mm.



Figures 41–48. Ventral view of male genital capsule.

Head. 1.3× as wide as long (along midline) in anterior view; vertex with lateral foveae small, circular; occipital carina ending before hypostomal carina medially; transverse carina short and irregular on either side of midline.

Mesosoma. Pronotal disk 0.5× as long as broad in dorsal view, 1.8× as long as scutum; punctures 2–3 puncture diameters apart; propleura heavily punctured; forefemur without stout spines; foretibia without spines except apically; basitarsus with row of three spines on outer surface; tibial spur 0.9× length of basitarsus; hindcoxa ventral carina about half length of coxa, dorsal carina broadly lobate dorsally.

Metasoma. Sternum I with medial groove parallel-sided, extending to apical margin of sternum (Fig. 23).

Color. Reddish brown; vestiture pale yellow.

Distribution. USA: Colorado, Otero County; only the holotype female was seen.

***Colocistis pilosa* Krombein**

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

Figures 7, 27, 28, 37, 47, 55

Colocistis pilosa Krombein, 1942:66. Holotype male; USA: California, San Diego County, San Diego, June 22, 1890 (USNM).

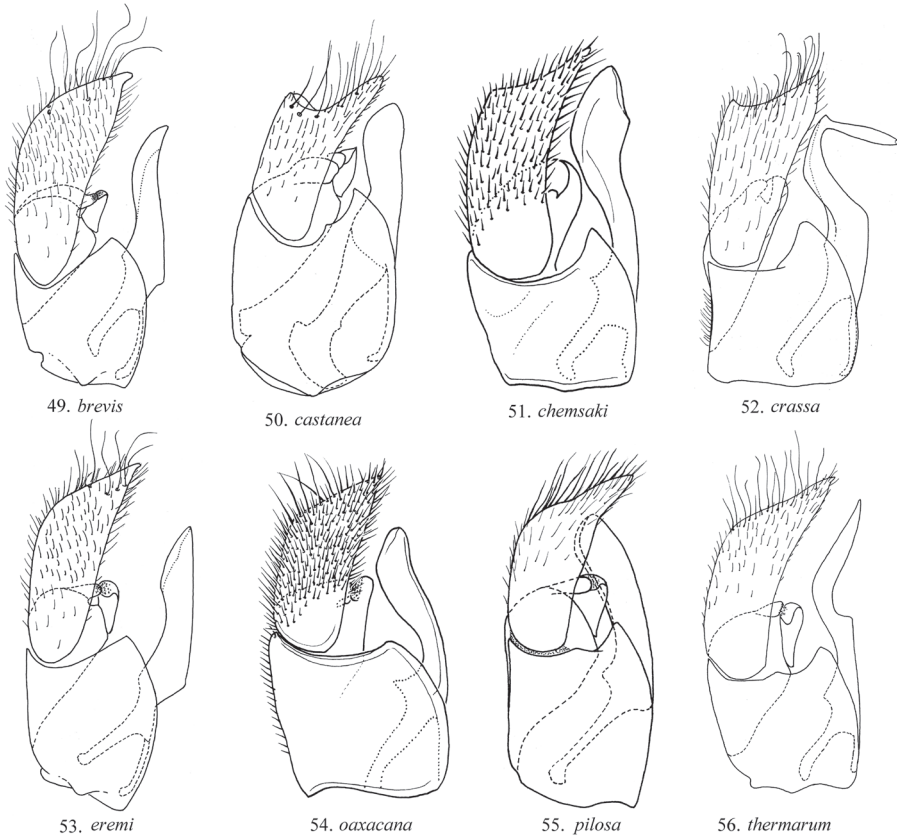
Diagnosis. *Colocistis pilosa* is only one of two species, including some specimens of *castanea*, with black body coloration. However, it shares with *crassa* the distinctive modification of metasomal sternum II, with the basal area elevated and separated from the rest of the sternum by a transverse declivity. These two species can be separated by the clypeus without a medial tubercle in *pilosa* (well-developed in *castanea*) and small compound eyes and ocelli (large in *castanea*), and long, dense, whitish pubescence.

Description. Male (Figs 27, 28).

Body length 11–12 mm.

Head (Fig. 7). Compound eyes not enlarged, barely extending beyond temples, inner margins slightly evenly curved; ocelli small, diameter of lateral ocellus 0.5× OOL; without impressed line between lateral ocelli; antennal socket rim slightly thickened ventrolaterally; clypeus with median tubercle visible in lateral view, apex bounded laterally by strong teeth; gular carina not raised; LID 0.85× UID; flagellomere I length 2.4× breadth; flagellomeres II–X missing; occipital carina strong but incomplete ventrally, with carina extending from foramen magnum to hypostomal carina medially; mandible narrowest submedially.

Mesosoma. Pronotum nearly vertical anteriorly, sloping posteriorly, punctures deep, largely contiguous, shoulders well-developed, not produced laterally; forefemur without stout spines; foretibia without spines, except apically; basitarsus with three spines on outer surface; tibial spur 0.9× length of basitarsus; hindcoxa without longitudinal dorsal carina tooth-like basally; mesonotal and mesopleural punctures contiguous; scutellum strongly arched dorsally much above level of propodeum, punctures 0.5–1.5 puncture diameters apart, with small, polished impunctate area medially; postscutellum punctures large, con-



Figures 49–56. Lateral view of male genital capsule.

tiguous; propodeum dorsal surface coarsely rugulose, separated from posterior face by distinct carina, posterior face punctures contiguous laterally, becoming more widely separated toward midline, except for small dorsomedial impunctate area, punctures becoming small toward petiole, laterally punctures 0.5 puncture diameter apart to contiguous; forewing with 3 submarginal cells, costa extending along wing margin beyond stigma.

Metasoma. Tergum I without transverse carina; sternum II with anterior portion slightly raised and separated from remainder of sternum by transverse declivity.

Genitalia (Figs 47, 55). Gonostylus slightly emarginate ventrally before tip in lateral view; aedeagus evenly curved, simple at apex in lateral view.

Color. Head and body unicolorous, black, with extensive long, erect pale, yellowish setae, setae more than half as long as eye height.

Female unknown.

Distribution (Fig. 37).

Discussion. *Colocistis pilosa* may be extinct; no specimens have been seen since the type was collected. The San Diego region where the type was collected has become increasingly urbanized since 1942 and is now highly urbanized with commercial and residential developments.

***Colocistis segredientata* (Mickel & Krombein)**

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

Figures 11, 24, 31, 32, 38

Aglyptacros segredientata Mickel & Krombein, 1942:671. Holotype female; USA: Arizona, Benson (MCZ).

Diagnosis. This might be the female of *castanea*. It shares a number of characteristics with *eureka* as discussed under that species. *Colocistis castanea* can be distinguished by the meso- metapleural suture absent or faint and incomplete and the medially interrupted transverse carina posterior to the gular carina.

Male unknown.

Description. Female (Figs 31, 32).

Body length 7.0–10.5 mm.

Head. Wider than long in anterior view; vertex with lateral foveae consisting of row of large, deep punctures; occipital carina meeting hypostomal carina at a right angle, hypostomal carina forming sharp angle on either side of midline; transverse carina short, irregular (Fig. 11).

Mesosoma. Pronotal disk 0.4× as long as broad in dorsal view; punctures widely separated, 2–10 puncture diameters apart; propleura coarsely rugosopunctate; forefemur without stout spines; foretibia without spines except apically; basitarsus with row of three spines on outer surface; tibial spur 0.9–1.0× as long as basitarsus; hindcoxa ventral, longitudinal carina extending half length of coxa; dorsal longitudinal carina broadly elevated and lobe-like basally.

Metasoma. Sternum I with medial groove short, not extending much beyond base of sternum, or absent (Fig. 24).

Color. Reddish brown; vestiture whitish to pale yellow.

Distribution (Fig. 38). USA: Arizona, Cochise County; California: Imperial, Inyo counties; Nevada: Nye County; 35 specimens were examined (BME, CDFA, UCRC).

***Colocistis sulcata* (Mickel & Krombein)**

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

Figures 12, 39

Aglyptacros sulcata Mickel & Krombein, 1942:674. Holotype female; USA: Texas, Valentine (KSBS).

Diagnosis. *Colocistis sulcata* most closely resembles *paxillata* based on the incomplete occipital carina and simple gular carina. It can be distinguished from *paxillata* by the gular carina extending laterally beyond where the occipital carina would join if extended and metasomal sternum I medial longitudinal trough narrow and deep anteriorly, becoming broad and shallow posteriorly; parallel-sided in *paxillata*.

Male unknown.

Description. Female.

Body length. 7–12 mm.

Head. Twice as wide as long in anterior view; vertex with lateral fovea a row of circular punctures; occipital carina meeting transverse carina at nearly right angle, transverse carina extending laterally further than occipital carina (Fig. 12).

Mesosoma. Notal punctures deep, scattered, 1–5 puncture diameters apart; pronotal disk 0.5× as long as broad in dorsal view, punctures 3–5 puncture diameters apart; propleura coarsely rugosopunctate; forefemur without stout spines; foretibia without spines except apically; basitarsus with row of three spines on outer surface; tibial spur as long as basitarsus; hindcoxa ventral carina extending half length of coxa; dorsal longitudinal carina broadly elevated and lobe-like basally; meso-metapleural suture at most indicated by faint indentation.

Metasoma. Sternum I with medial groove narrowest anteriorly, broadened posteriorly, extending length of sternum.

Color. Reddish brown; vestiture whitish to pale yellow.

Distribution (Fig. 39). USA: Arizona: Cochise County; Texas: Jeff Davis, Presidio counties; 4 specimens were examined (BME, EMEC).

***Colocistis thermarum* (Bradley)**

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

Figures 8, 18, 30, 40, 48, 56

Brachycistis thermarum Bradley, 1917:274. Holotype male; USA: Arizona, Hot Springs (CUIC).

Diagnosis. This is one of three species, including *castanea* and *oaxacana*, which have three submarginal cells and the second metasomal sternum simple. It can be distinguished from both by the tuberculate clypeus.

Description. Male.

Body length. 8–15 mm.

Head (Fig. 8). Compound eyes enlarged, extending well beyond temples; ocelli enlarged, diameter of lateral ocellus at least 0.7× OOL; impressed line present between lateral ocelli; antennal socket rim only slightly thickened ventrolaterally; clypeus with median tubercle visible above mandible in lateral view, apex not bounded laterally by strong teeth; gular carina not raised; LID 0.7× UID; flagellomeres I–II length 2.3–2.4× breadth; flagellomere IX length 5× breadth; occipital carina strong but, complete ventrally; hypostomal carina not raised; mandible narrowest submedially, apically broad and teeth subequal in length.

Mesosoma. Pronotum nearly vertical anteriorly, punctures deep, 0.5 puncture diameter apart to contiguous, shoulders well-developed, not produced laterally; forefemur without stout spines; foretibia without spines except apically; basitarsus with two spines on outer surface; tibial spur 0.9× length of basitarsus; hindcoxa without basally

tooth-like longitudinal dorsal carina; scutal punctures 0.5–2.0 puncture diameters apart; mesopleural punctures contiguous; scutellum flattened dorsally nearly planar with level of propodeum, punctures 0.5–1.0 puncture diameters apart, with small, polished impunctate area medially; postscutellum densely punctate; propodeal dorsal surface separated from posterior and lateral surfaces by carina, dorsal surface with longitudinal medial trough, surface shallowly rugose, posterior surface nearly impunctate, lateral surface densely punctate dorsally, impunctate ventrally; forewing with 3 submarginal cells; costa extending along wing beyond stigma.

Metasoma. Tergum I without transverse carina; sternum II without raised area basally.

Genitalia (Figs 48, 56). gonostylar apex nearly straight in lateral view; aedeagus abruptly decurved before apex, without dorsally projecting process.

Color. Head and body unicolorous, castaneous; vestiture whitish to pale yellow.

Female unknown.

Distribution (Fig. 40): USA: **Arizona**: Cochise, Maricopa, Pima, Pinal, Yuma counties; **California**: Imperial, Inyo, Riverside counties; **Texas**: Culberson, Dimmit, Jeff Davis counties; MEXICO: **Baja California**, **Baja California Sur**, **Sonora**; 370 males were examined (BME, CAS, CDFA, EMEC).

Acknowledgments

This study was made possible by all the individuals who provided specimens for the study, particularly Kevin Williams, Brian Harris, Alan Hardy and Fred Andrews.

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Morphology and function of the ovipositor mechanism in Ceraphronoidea (Hymenoptera, Apocrita)

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Abstract

The ovipositor of apocritan Hymenoptera is an invaluable source of phylogenetically relevant characters, and our understanding of its functional morphology stands to enlighten us about parasitoid life history strategies. Although Ceraphronoidea is one of the most commonly collected Hymenoptera taxa with considerable economic importance, our knowledge about their natural history and phylogenetic relationships, both to other apocritan lineages and within the superfamily itself, is limited. As a first step towards revealing ceraphronoid natural diversity we describe the skeletomuscular system of the ceraphronoid ovipositor for the first time. Dissections and Confocal Laser Scanning Microscopy 3D media files were used to visualize the ovipositor complex and to develop character concepts. Morphological structures were described in natural language and then translated into a character-character state format, whose terminology was linked to phenotype-relevant ontologies. Four unique anatomical phenotypes were revealed: 1. The first valvifer (gonangulum) of the genus *Trassedia* is composed of two articulating sclerites, a condition present only in a few basal insect taxa. The bipartition of the first valvifer in *Trassedia* is most likely secondary and might allow more rapid oviposition. 2. Ceraphronoids, unlike other Hymenoptera, lack the retractor muscle of the terebra; instead the egg laying device is retracted by the seventh sternite. 3. Also unlike other Hymenoptera, the cordate apodeme and the anterior flange of the second valvifer are fused and compose one ridge that serves as the site of attachment for the dorsal and ventral T9-second valvifer muscles. Overall, the ceraphronoid ovipositor system is highly variable and can be described by discrete, distinguishable character states. However, these differences, despite their discrete nature, do not reflect the present classification of the superfamily and might represent parallelisms driven by host biology.

Keywords

Skeletomusculature, second valvula, ovipositor sheath, *Aphanogmus*, *Ceraphron*, *Conostigmus*, *Megaspius*, *Dendrocerus*, *Lagynodes*, Hymenoptera Anatomy Ontology, Phenotypic Quality Ontology, Spatial Ontology

Introduction

Ceraphronoidea has, until recently, been one of the most neglected groups of parasitic Hymenoptera, despite their ubiquity in the environment and fascinating life history strategies, which span from primary to quaternary parasitism (hyper-hyper-hyperparasitism) (Haviland 1920). Since the establishment of Ceraphronoidea as a superfamily (Masner 1956, Masner and Dessart 1967) significant revisionary work has addressed Lagynodinae (Dessart 1977, 1987), species of *Conostigmus* Dahlbom (Dessart 1997) and species groups of *Dendrocerus* Ratzeburg (Dessart 1972, Fergusson 1980, Dessart 1985, Dessart 1995a, Dessart 1999, Dessart 2001). Records of parasitism by ceraphronoids cover a wide range of hosts, from at least eight insect orders: Hemiptera, Thysanoptera, Hymenoptera, Neuroptera, Coleoptera, Trichoptera, Diptera and Mecoptera (Austin 1984, Chiu et al. 1981, Cooper and Dessart 1975, Dessart 1967, 1992, Dessart and Bournier 1971, Evans et al. 2005, Fergusson 1980, Ghesquiere 1960, Ishii 1937, Luhman et al. 1999, Muesebeck 1979, Priesner 1936, Sinacori et al. 1992). Two species, *Dendrocerus carpenteri* (Curtis), and *Dendrocerus aphidum* (Rondani), serve as models for research concerning resource use and allocation by parasitoids (Araj et al. 2006), mate location (Schwörer et al. 1999), development and host interactions (Marris et al. 2000), sex determination of offspring (Chow and Mackauer 1996), host discrimination (Chow and Mackauer 1999), and behavioral evolution in bio-control systems (Müller et al. 1997).

The phylogenetic placement of Ceraphronoidea remains uncertain despite the recent efforts to resolve the Hymenoptera tree of life (Heraty et al. 2011, Sharkey et al. 2011). Using expressed sequence tag (EST) data and limited exemplars, Sharanowski et al. (2010) placed Ceraphronoidea as sister to Evanioidea, but with low support. Heraty et al. (2011), using data from four genetic loci, placed Ceraphronoidea as sister to Stephanidae or Stephanidae + Orussidae, depending on the analysis. Villhelmsen et al. (2010) found Ceraphronoidea to be sister to Megalyroidea within Evaniomorpha, based on morphological data. Sharkey et al. (2011) using molecular data and morphological data - based largely on Villhelmsen et al. (2010) - also suggested a sister relationship between Ceraphronoidea and Megalyroidea.

The most comprehensive review on the classification of the superfamily has proposed by Dessart and Cancemi (1987). Although this classification served as a template for further studies (Masner 1993, Dessart 1995a, b, Mikó and Deans 2009) the phylogenetic base has never been challenged. The utility of traditionally used morphological characters in Ceraphronoidea classification seems to be limited (Dessart 1995b,

c, 2001) and with the discovery of the first ceraphronid wasp with well-developed pterostigma even the family level classification of the superfamily has been challenged recently (Mikó and Deans 2009). Our recent observations on the genus *Trassedia* provide additional evidence that the current classification of the superfamily needs to be revised (Mikó et al. in press). The genus was erected by Cancemi (1996), who classified the type species within Megaspilinae and considered it to be closely related to *Conostigmus*. The original classification is supported by two distinct character states: the presence of a fore wing pterostigma (which has subsequently been found in Ceraphronidae; Mikó and Deans 2009) and the presence of 11 antennomeres (Ceraphronidae have 10). Our observations of multiple specimens of *Trassedia luapi* reveal numerous morphological character states that are specific to Ceraphronidae (Mikó and Deans 2009, Mikó et al. in press): absence of mesotibial apical spur, absence of narrow sclerite anterior to synsternum, presence of Waterston's evaporatorium, and numerous male genitalia characters. Based on these differences the genus has recently been transferred to Ceraphronidae (Mikó et al. in press), a classification we follow in this study.

It is evident that a comprehensive study using both morphological and molecular characters is necessary for the reevaluation of Ceraphronoidea systematics. Since traditionally used morphological characters have been phylogenetically inconsistent the utilization of unexplored character systems, such as the male and female terminalia might offer additional data relevant to more robustly estimate the phylogenetic history of this group.

Despite the extensive descriptive work done on comparative morphology of the Hymenoptera female terminalia (Oeser 1961, Smith 1970, Le Ralec et al. 1996, Quicke et al. 1992, Quicke et al. 1994, Quicke et al. 1999, Vilhelmsen 2000, Vilhelmsen et al. 2001), the available morphological data on the ceraphronoid female terminalia are restricted to the distal region of the terebra (Quicke et al. 1994, Le Ralec et al. 1996) and the accessory glands (Höller et al. 1993). The skeletomuscular system of ceraphronoid ovipositor remained, until now, relatively unexplored. The main aim of the present study is to describe morphological diversity of the female terminalia in Ceraphronoidea and compare its anatomical structures with that of other Hymenoptera taxa giving special emphasize on the skeletomuscular system. With this study, we establish a baseline for further phylogenetic analyses of the superfamily using ovipositor characters.

Materials and methods

Specimens used in this study (Table 1) were identified by Andrew Ernst (AFE) and István Mikó (IM). Megaspilinae was represented in our study by *Megaspilus armatus* (Say), *Dendrocercus spissicornis* (Hellén) and *Conostigmus abdominalis* (Boheman); Lagynodinae (Megaspilidae) by *Lagynodes* sp. (AFE); and Ceraphronidae by *Ceraphron* sp. (IM) (Fig. 5), *Aphanogmus* sp.1 (AFE), *Aphanogmus* sp. 2 (IM) and *Trassedia luapi* (Cancemi).

Table 1. Specimens observed for morphological description including specimen identifiers, preparation techniques, imaging method and collecting locality (verbatim collecting data are stored at figshare.com.).

Taxon	Specimen identifier	Imaging techniques	Locality	DOI of CLSM media files stored at http://figshare.com
<i>Aphanogmus</i> sp. 1	NCSU 0055648	brightfield	Hungary	
<i>Aphanogmus</i> sp. 1	NCSU 0002419	CLSM 40× water immersion	Hungary	doi: 10.6084/m9.figshare.156446 doi: 10.6084/m9.figshare.156439
<i>Aphanogmus</i> sp. 2	PSUCIM_5009	brightfield	Madagascar	
<i>Ceraphron</i> sp.	NCSU 0071198	brightfield	Madagascar	
<i>Ceraphron</i> sp.	NCSU 0071197	brightfield, CLSM 10×	Madagascar	doi: 10.6084/m9.figshare.156445
<i>Ceraphron</i> sp.	PSUCIM_5005, 5006	CLSM	Madagascar	doi: 10.6084/m9.figshare.156470 doi: 10.6084/m9.figshare.156469 doi: 10.6084/m9.figshare.156447
<i>Conostigmus abdominalis</i> (Boheman)	NCSU 0056302	brightfield	Sweden	
<i>Conostigmus abdominalis</i> (Boheman)	NCSU 0056301	brightfield	Sweden	
<i>Conostigmus abdominalis</i> (Boheman)	NCSU 0055647	brightfield, CLSM 20×	Sweden	doi: 10.6084/m9.figshare.156448 doi: 10.6084/m9.figshare.156433
<i>Dendrocercus spissicornis</i> Hellén	PSUCIM_5001, 5002	CLSM	Sweden	doi: 10.6084/m9.figshare.156452 doi: 10.6084/m9.figshare.156451 doi: 10.6084/m9.figshare.156450 doi: 10.6084/m9.figshare.156449
<i>Dendrocercus spissicornis</i> Hellén	PSUCIM_5010	CLSM	Sweden	doi: 10.6084/m9.figshare.156459 doi: 10.6084/m9.figshare.156453
<i>Lagynodes</i> sp.	NCSU 0055643	brightfield	USA	
<i>Lagynodes</i> sp.	NCSU 0056306	CLSM 20×, 40× water immersion	USA	doi: 10.6084/m9.figshare.156454 doi: 10.6084/m9.figshare.156443
<i>Lagynodes crassicornis</i>				
<i>Megaspilus armatus</i> (Say)	NCSU 0071199	brightfield	USA	
<i>Megaspilus armatus</i> (Say)	NCSU 0055645	brightfield, CLSM 20×	USA	doi: 10.6084/m9.figshare.156442 doi: 10.6084/m9.figshare.156434
<i>Megaspilus armatus</i> (Say)	NCSU 0056307	CLSM 40× water immersion	USA	doi: 10.6084/m9.figshare.156437
<i>Megaspilus armatus</i>	PSUCIM_5003	CLSM 20X	Canada	doi: 10.6084/m9.figshare.156458 doi: 10.6084/m9.figshare.156457 doi: 10.6084/m9.figshare.156456 doi: 10.6084/m9.figshare.156455
<i>Trassedia luapi</i> Cancemi	NCSU 0056318	brightfield, CLSM 10×	Madagascar	doi: 10.6084/m9.figshare.156440 doi: 10.6084/m9.figshare.156438 doi: 10.6084/m9.figshare.156436
<i>Trassedia luapi</i> Cancemi	NCSU_0071196	brightfield, CLSM 20×	Madagascar	doi: 10.6084/m9.figshare.156467 doi: 10.6084/m9.figshare.156444

Specimens used in the present study were stored in 95% ethanol. Some specimens were critical point dried and dissected on Blue-Tack (Blue Tack, Bostik inc.) medium. This method is mostly used to reveal the spatial relationships between muscles. Other specimens were dissected in glycerin on a concave microscope slide or were macerated in KOH to visualize the skeletal structures. Dissections and observations were made using an Olympus SZX16 stereomicroscope and an Olympus CX41 compound microscope.

Bright field images were taken using an Olympus CX41 compound microscope, equipped with an Olympus DP71 digital camera. Image stacks were combined using CombineZP (Hadley 2010) “do stack” command. SEM micrographs were made using a Hitachi S-3200 Scanning Electron Microscope (wd=23.5, av=5kV). Specimens were critical point dried and coated with palladium prior to examination. CLSM images were made on glycerin-stored specimens between 1.5 mm thick, 24×50 mm cover glasses with a Leica LSM 710 and Olympus Fluoview 1000 confocal laser scanning microscopes (CLSM) using the 488 nm laser to excite the sample. We collected the autofluorescence of insect anatomical structures between 500 and 700 nm with two channels (500–580; pseudocolor green and 580–700 pseudocolor red) using 106 and 206 Plan Achromat objectives. Volume rendered images and media files were generated by Imaris Bitplane (Bitplane, Zürich, Switzerland) and ImageJ (Schneider et al. 2012) software. Bright field and CLSM micrographs were edited with Adobe Photoshop CS4 (Adobe) changing “Gamma Correction” value, resize images to 7.3 cm width at 400 dpi resolution, standardize style and width of scale bars and create image annotations. Media files, SEM micrographs and bright field images are available from figshare.com (Table 1).

To verify the relationships between anatomical structures, serial transverse sectioning was carried out on a *Lagynodes* specimen (Table 1). The specimen was embedded in Araldit®, cut at 1 µm with a Microm microtome (HM 360), and stained with toluidine blue.

Anatomical terms used in the descriptions are linked to concepts in the Hymenoptera Anatomy Ontology (HAO; Hymenoptera Anatomy Portal (<http://portal.hymao.org>), Yoder et al. 2010), the Phenotypic Quality Ontology 1.2 (PATO; Gkoutos et al. 2004) and the Biospatial Ontology (Mungall 2013) via a table of uniform resource identifiers (URIs) (Appendix) following Seltsmann et al. 2012.

Towards semantic statements

Verbatim descriptions composed in natural language serve as the traditional way for communicating observations in insect morphology. However, these descriptions can be decoded only by morphology experts, are hardly accessible to non-expert researchers and cannot be reasoned over efficiently by text-mining applications (Vogt et al. 2010, Deans et al. 2012a, b, Vogt et al. 2013). Morphological descriptions, albeit they are arguably more complex, shares numerous similarities with taxonomic descriptions which

were the objects of recent efforts for altering the way of biodiversity descriptions into a more accessible format. Deans et al. (2012a) proposed a new description model for taxonomists applying semantic statements. These statements are written in a logic and queryable format and are linked to the concepts of biomedical ontologies. Semantic descriptions are therefore not only transparent for researchers unfamiliar with specific morphological jargon, but can be executed via an automated reasoning mechanism (Balhoff et al. in press, Mullins et al. 2012).

To meet the grand challenge of describing phenotypes in a semantic way, using Web Ontology Language (OWL; <http://www.w3.org/TR/owl-features/>) for example, one must be familiar with tools of the Semantic Web (e.g., Protégé, <http://protege.stanford.edu/> and Manchester Syntax, <http://www.w3.org/TR/owl2-manchester-syntax/>). Perhaps more importantly, one also has to provide a character/character state description with terms explicitly linked to ontologies.

We provide here an example of the transformation of our natural language descriptions to character/character state format and to link the terminology to relevant phenotype ontologies. Our goal is to make this product more accessible to future reasoning applications. During the “ontologization” procedure the describer is forced to provide strict, structure-based definitions for each anatomical concept, which itself enhances the readability, objectivity, consistency and comparability of the research product.

Results I: Natural language descriptions of anatomical structures in the ceraphronoid ovipositor assembly and S7

Integument

The first valvifer is dorsoventrally elongated in lateral view (ch1: 0; **1vf**: Figs 2E, 5A, E, 6A, D) with convex anterior (ch2:0) and straight (ch3:0; **p1v**: Figs 2D, 4A, 6A) or concave posterior margins (ch3:1; **p1v**: Fig. 3D) in all taxa except *Dendrocerus* where the posterior margin of the first valvifer is angled at the tergo-valviferal articulation (ch3:2; **p1v**: Fig. 4F). The first valvifer is not subdivided (ch4:1; **1vf**: Figs 2E, 5A, E, 6A, D) except in *Trassedia*, where the transvalvifer conjunctiva (ch4:0; **tv**: Fig. 3E) separates the elongate dorsal sclerite (ch5:0; **d1vf**: Fig. 3E) from the triangular ventral sclerite of the first valvifer (ch6:0; **v1vf**: Fig. 3E). The sclerites articulate with one another at the intravalvifer articulation (ch7:0; **iava**: Figs 3C, E), which is located anteriorly on the border between the two sclerites (ch8:0). The ventral margin of the dorsal sclerite (ch9:0) and the anterodorsal margin of the ventral sclerite are thickened relative to surrounding regions (ch10:0). The anterior flange of the first valvifer (**afl**: Fig. 1F) overlapping the second valvifer is present (ch11:0) in *Conostigmus*, *Dendrocerus* and *Megaspilus*, and *Lagynodes* but absent from Ceraphronidae (ch11:1). The first valvifer articulates with the second valvifer on its posteroventral corner (ch12:0; intervalvifer articulation, **iva**: Figs 1B, 2C, 3A–C, E, 4A, F, 5A, B, E, 6A, C, D) and with T9 on its posterior margin (ch13:0; tergo-valvifer articulation, **tva**: Figs 1B, 2C, 3B, C, E, 4A,

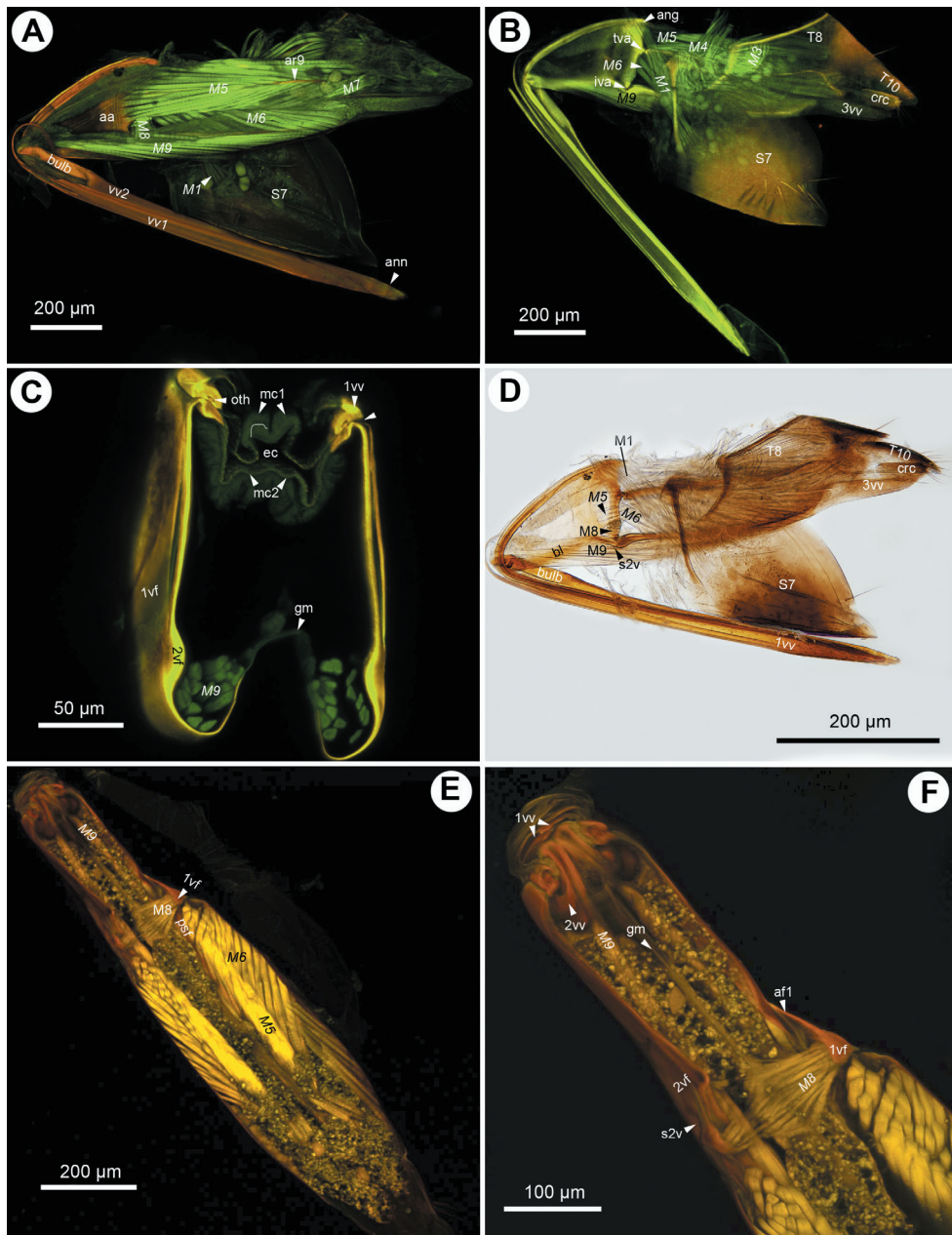


Figure 1. CLSM micrographs and bright field image showing the female terminalia of *Megaspilus armatus* (Say). **A** CLSM, medial view (doi: 10.6084/m9.figshare.156434) **B** CLSM, lateral view (doi: 10.6084/m9.figshare.156442) **C** CLSM, transverse section, white line indicates site of separation of median conjunctivae of the first valvulae (doi: 10.6084/m9.figshare.156437) **D** bright field, lateral view **E-F** CLSM, frontal section, dorsal view (doi: 10.6084/m9.figshare.156458; doi: 10.6084/m9.figshare.156457, doi: 10.6084/m9.figshare.156456, doi: 10.6084/m9.figshare.156455). All anterior to the left.

F, 5A, B, E, 6A, C, D). The tergo-valvifer articulation is in the middle of the posterior margin of the first valvifer in *Conostigmus* and *Lagynodes* (ch14:0; **tva**: Figs 2C, 4A), it is on the ventral half of the margin (ch14:1; **tva**: Figs 3B, C, E, 5A, B, E, 6D) in *Ceraphron*, *Aphanogmus* sp. 2 and *Trassedia*, where it is located ventrally on the posterior margin of the dorsal sclerite of the first valvifer (ch15:0; **tva**: Fig. 3B, C, E), it is in the upper half of the margin in *Megaspilus* and *Dendrocerus* (ch14:2; **tva**: Figs 1B, 4F) and adjacent to the anterior angle in *Aphanogmus* sp. 1 (ch14:3; **tva**: Figs 6A, C).

The anterior area of the second valvifer is expanded dorsally into a broad, flat, laterally directed surface (ch16:0; **aa**: Figs 1A, 2E). The basal line of the second valvifer (ch17:0) is a sharply defined ridge in *Ceraphron*, *Trassedia*, and *Aphanogmus* sp. 2 (ch18:0; **bl**: Figs 3B–D, 5A, E, 6D) but a thickening with diffuse margins in *Aphanogmus* sp. 1 and Megaspilidae (ch18:1; **bl**: Figs 1D, 2C, E, 4A, F). The dorsal projection of the second valvifer (ch19:0) is longer than the length of the anterior area of the second valvifer in *Ceraphron* and *Trassedia*, and *Aphanogmus* sp. 2 (ch20:1; **dp**: Figs 3C, E) whereas the projection is shorter than the length of the anterior area in other taxa examined (ch20:2; **dp**: Figs 2E, 4A). The anterior section of the dorsal flange of the second valvifer is sharply defined ridge in *Ceraphron*, *Aphanogmus* sp. 2, and *Trassedia* (ch21:0; **asf**: Figs 3B, C, D, 5A–E, 6D) but a thickening with diffuse margins in Megaspilidae and *Aphanogmus* sp. 1 (ch21:1; **asf**: Figs 2C, E, F, 4A, F). The posterior section of the dorsal flange of the second valvifer is sharply defined (ch22:0; **psf**: Figs 2C, E, 4A, D, 5A, E). The area of the second valvifer posterior to the intervalvifer articulation is elongate (ch23:0 **pa**: Figs 2C, E). The ventral margin of the second valvifer curves mediodorsally (ch24:0) encircling the posterior second valvifer-second valvula muscle (ch25:0. **2vf**, **M9**: Fig. 1C). The genital membrane of the second valvifers accommodates the terebra when it is retracted (ch26:0; **gm**: Fig. 1C). The venom gland reservoir is surrounded by the second valvifer is present in Ceraphronidae and *Lagynodes* (ch27:0; **res**: Figs 3A–E). The reservoir was not observed in other Megaspilidae (ch27:1). The content of the reservoir is yellowish, transparent and hard, resin-like (ch28:0; **res**: Fig. 5F) in critical point dried specimens.

The first valvula tapers distally in lateral view in *Ceraphron*, *Aphanogmus* sp. 2 and *Trassedia* (ch29:0; **1vv**: Figs 3B, 5A, F, 6D), whereas it is spatulate in Megaspilidae and *Aphanogmus* sp. 1 (ch29:1; **1vv**: Figs 1A, D, 2A, C, D, E, 4A, B, 6B, C). The banding pattern and annuli are missing from the first valvula (ch30:0; ch31:0).

The second valvulae are expanded proximally into the bulb (ch37:0; **bulb**: Figs 1A, D) and fused distal to the bulb (ch35:0). The dorsal valve tapers distally in dorsal view (ch36:0) and the anterior margin of the bulb is curved dorsally. The processus articularis is located laterally (ch32:0; **pra**: Figs 2F, 5D), the anterior notch of the dorsal valve anteriorly (ch33:0) and the processus muscularis anterodorsally on the bulb (ch34:0; **prm**: Fig. 2F). The anterior area of the second valvifer is 2.0 times as high as the bulb in lateral view in *Dendrocerus* and *Aphanogmus* sp. 1 (ch38:0; Figs 4E, 6B) whereas it is more than 2.0 times as high as the bulb in *Ceraphron* and Megaspilidae (ch39:1). Banding pattern is absent (ch39:0) whereas annuli are present on the dorsal valve in Megaspilidae (ch40:0; **ann**: Figs 1A, 2C) but absent in Ceraphronidae (ch40:1). The

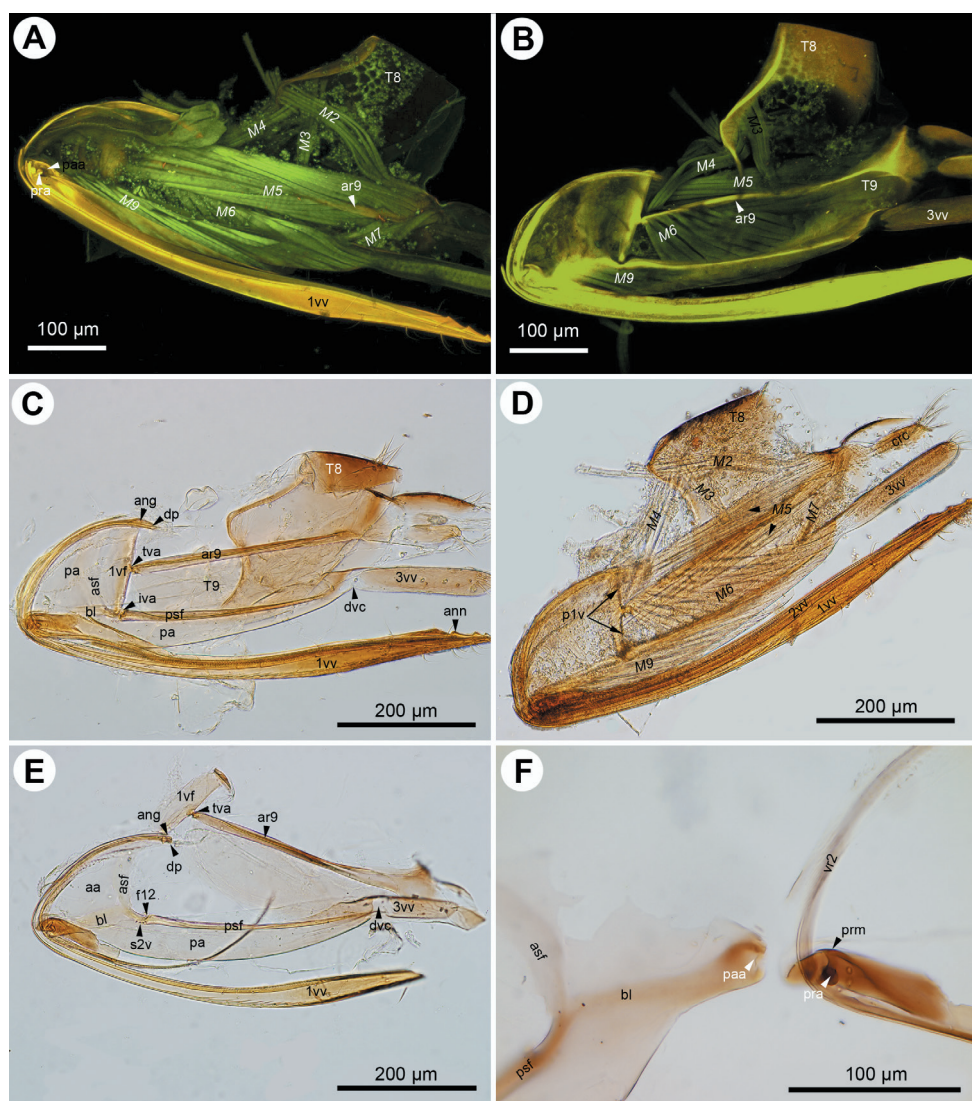


Figure 2. CLSM micrographs and bright field image showing the female terminalia of *Conostigmus abdominalis* (Boheman). **A** CLSM, medial view (doi: 10.6084/m9.figshare.156448) **B** CLSM, lateral view (doi: 10.6084/m9.figshare.156433) **C** bright field, medial view, muscles removed **D** bright field, medial view **E** bright field, medial view, first valvifer and T9 separated from second valvifer, muscles removed; **F**, bright field, second valvifer removed from second valvulae, muscles removed. All anterior to the left.

number of annuli is four (ch41:0) in *Conostigmus* and *Lagynodes* and six (ch41:1) in *Megaspilus*.

The third valvula and the second valvifer are fused at the median bridge (ch42:0; ch44:0; **mbr**: Figs 3C, E) connecting the opposite second valvifers at their posterior ends. A ventral, vertical conjunctiva marks the site of fusion of the two sclerites (ch43:1; **dvc**: Figs 2C, E, 3D, E, 4D). The third valvula tapers distally in lateral view

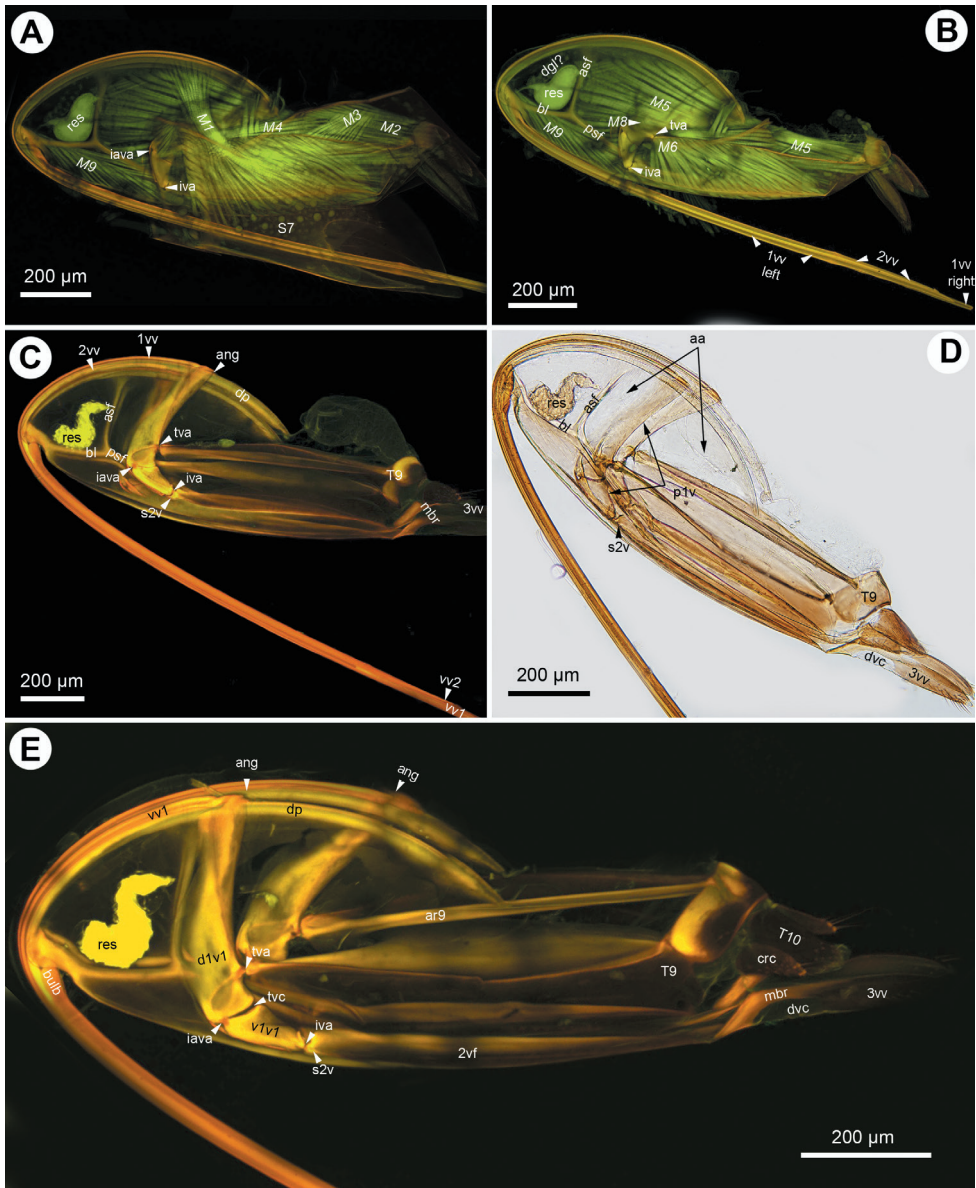


Figure 3. CLSM micrographs and bright field image showing the female terminalia of *Trassedia luapi* (Cancemi). **A** CLSM, lateral view, T8 intact (doi: 10.6084/m9.figshare.156440) **B** CLSM, lateral view, T8 removed (doi: 10.6084/m9.figshare.156438) **C** CLSM, lateral view, muscles removed (doi: 10.6084/m9.figshare.156444) **D** bright field, lateral view, muscles removed **E** CLSM, lateral view, muscles removed (doi: 10.6084/m9.figshare.156467). All anterior to the left.

(ch45:0; **3vv**: Figs 1B, 2B–E, 3C–E, 4D, F, 5E, F, 6A, B, F), its lateral wall is convex (ch46:0) and sclerotized (ch47:0) whereas its medial wall is concave (ch48:0; **3vv**: Fig. 3E) and membranous (ch49: 0; **3vv**: Fig. 3F).

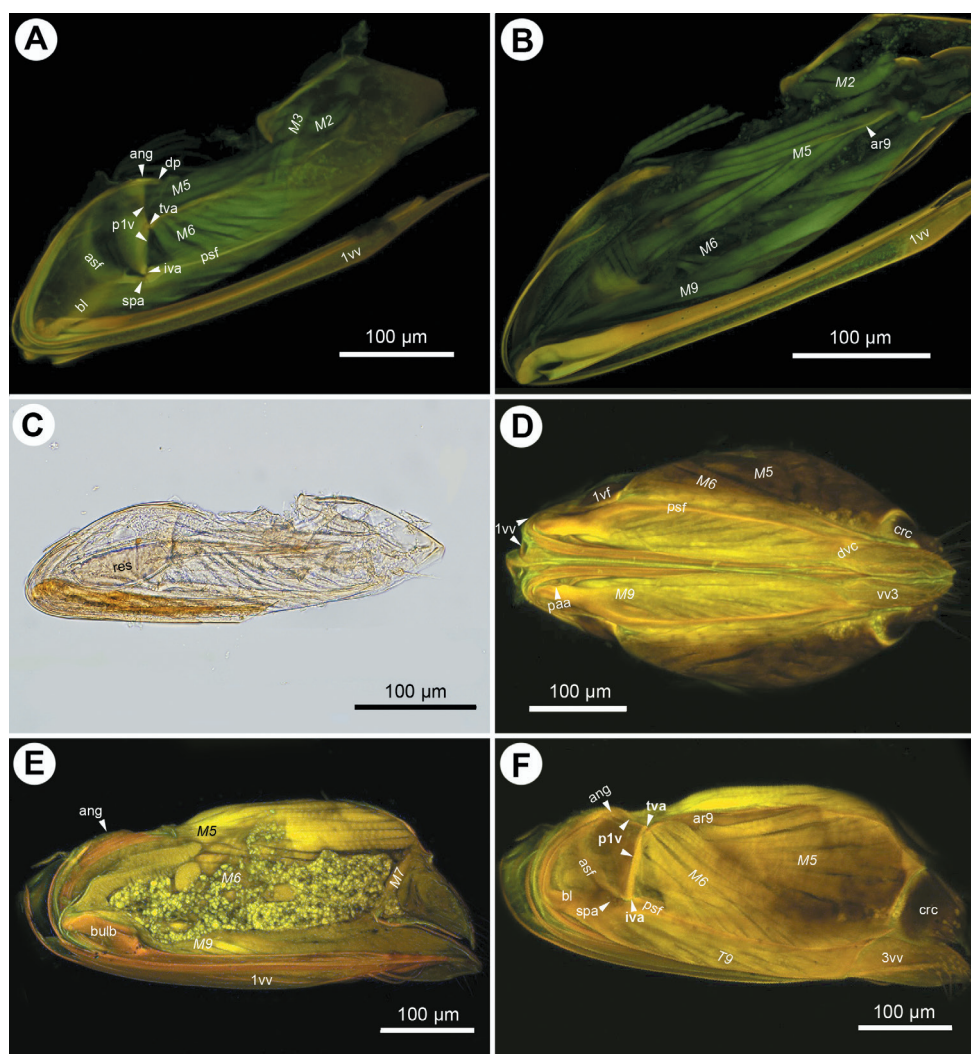


Figure 4. CLSM micrographs and bright field image showing the female terminalia of Megaspilidae. A–C: *Lagynodes* sp.: **A** CLSM, lateral view (doi: 10.6084/m9.figshare.156443) **B** CLSM, medial view (doi: 10.6084/m9.figshare.156454) **C** bright field, medial view. **D–F** *Dendrocerus spissicornis* (Hellén), CLSM: **D** ventral view (doi: 10.6084/m9.figshare.156451, doi: 10.6084/m9.figshare.156449) **E** medial view (doi: 10.6084/m9.figshare.156452) **F** lateral view (doi: 10.6084/m9.figshare.156459, doi: 10.6084/m9.figshare.156450). All anterior to left.

T9 is quadrangular in lateral view (ch50:0; T9: Figs 2B, C) and wider than long dorsomedially (ch51:0; T9: Figs 3D, E). The cordate apodeme and the anterior flange are continuous, composing the anterior ridge of T9 (ch52:0; ar9: Figs 2A–C, 3E, 4B), which is adjacent anteriorly with and separated posteriorly from the anterior margin of T9 (ch53:0.); the distance between the anterior margin of T9 and the ridge increases gradually posteriorly (ch54:0).

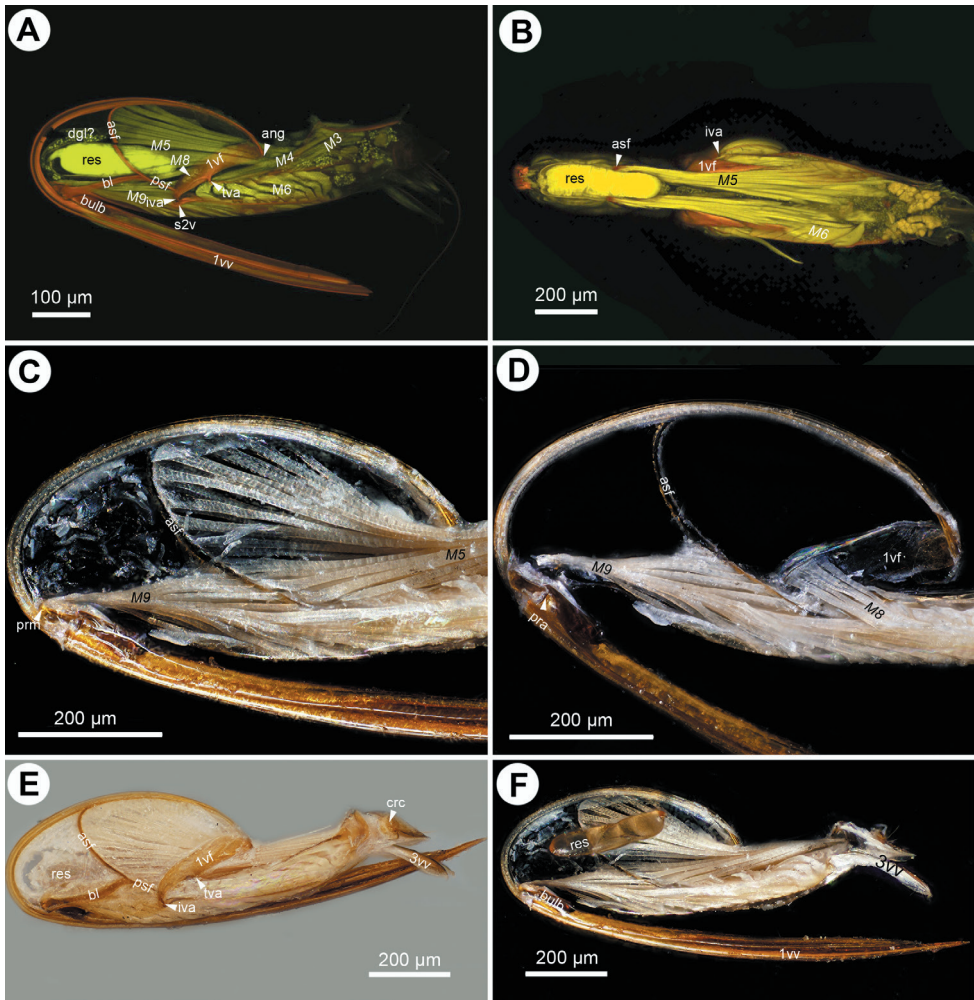


Figure 5. CLSM micrographs and bright field image showing the female terminalia of *Ceraphron* sp. **A** CLSM, lateral view (doi: 10.6084/m9.figshare.156445) **B** CLSM, frontal section, dorsal view (doi: 10.6084/m9.figshare.156447) **C** bright field, lateral view **D** bright field, medial view, dorsal T9-second valvifer muscle removed **E** bright field, medial view, dorsal T9-second valvifer muscle intact; **F**, bright field, medial view, venom gland reservoir intact. All anterior to left.

Muscles (numbered according to Vilhelmsen 2000)

S7-first valvula muscle (**M1**: Figs 1B, D, 3A) arises anteriorly from S7 (ch55:0) and inserts on the first valvula at the dorsal margin of the ovipositor adjacent to the border of the first valvula and the dorsal end of the first valvifer (ch56:0). The muscle is oriented posterodorsally (ch57:0). The dorsal T8-T9 muscle (**M2**: Figs 2A, 3A, 4A, B) arises from along the anterior margin of T8 (ch58:0) and inserts dorsally on the anterior margin of T9 (ch59:0). The lateral T8-T9 muscle (**M3**: Figs 1B, 2A, B, D,

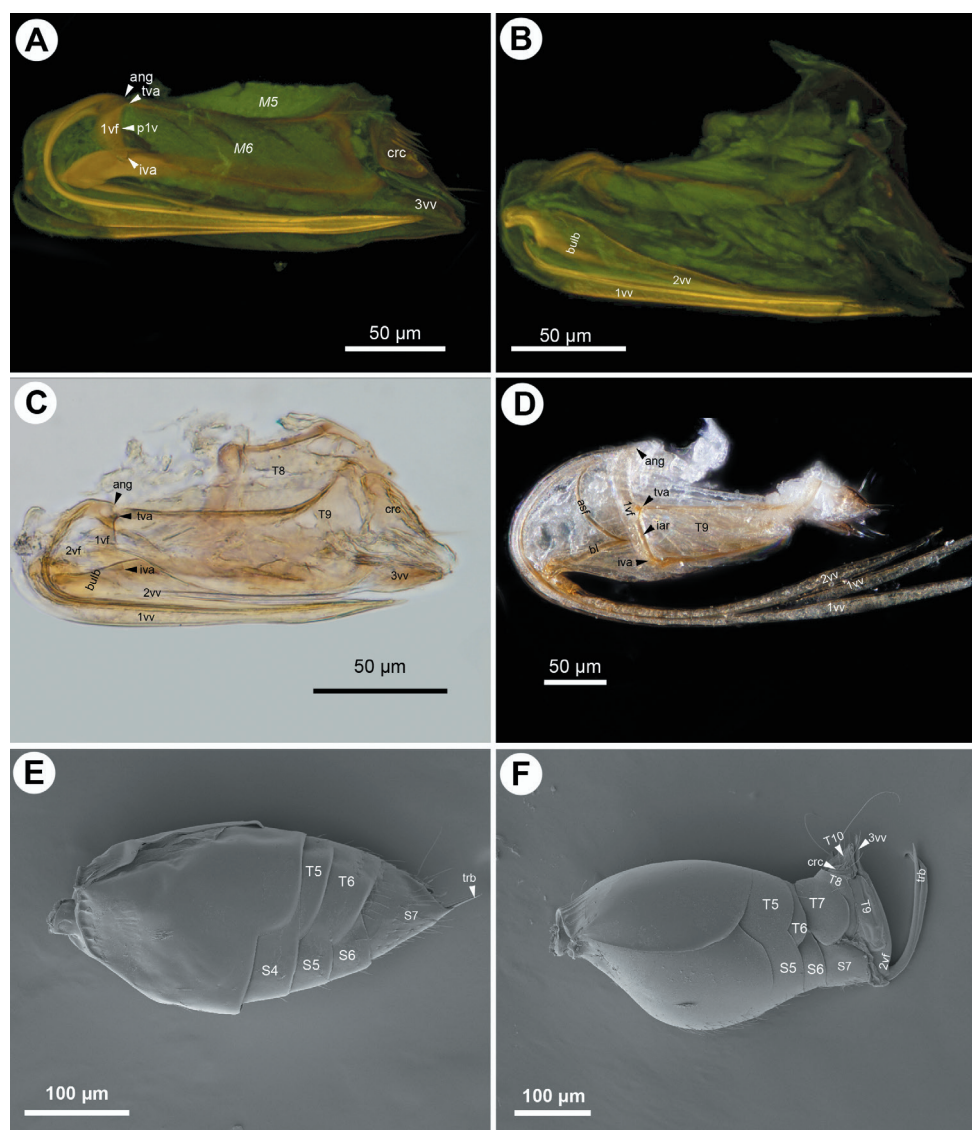


Figure 6. CLSM micrographs and bright field image showing the female terminalia of Ceraphronidae. **A–C:** *Aphanogmus* sp. 1: **A** CLSM, lateral view (doi: 10.6084/m9.figshare.156439) **B** CLSM, medial view (doi: 10.6084/m9.figshare.156446) **C** bright field, lateral view **D** *Aphanogmus* sp. 2, bright field, lateral view **E** *Synarsis* sp., SEM, lateral view **F** *Cyoceraphron* sp., SEM, lateral view. All anterior to left.

3A, 4A, 5A) arises from T8 posterodorsally of the dorsal T8-T9 muscle (ch60:0), and inserts on the anterior ridge of T9 (ch61:0). The T8-first valvifer muscle (**M4**: Figs 1B, 2A, 2B, 3A, 5A) arises from T8 dorsally of the site of attachment of the lateral T8-T9 muscle (ch62:0) and inserts on the first valvifer adjacent to the ninth tergal condyle of the first valvifer (ch63:0). The muscle inserts on the ventral sclerite of the first valvifer adjacent to the intravalvifer articulation (ch64:0; **M4**: Fig. 3A)

in *Trassedia*. The dorsal T9-second valvifer muscle (**M5**: Figs 1A, B, D, E, 2A, B, D, 3B, 4A, B, D, E, F, 5A–C, 6A) arises dorsally and ventrally from the anterior ridge of T9 with sites of origins extending ventrally and dorsally on the wall of the tergite (ch65:0) and inserts along the posterior margin of the anterior area of the second valvifer (ch66:0). The ventral T9-second valvifer muscle (**M6**: Figs 1A, B, D, E, 2A, B, D, 3B, 4A, B, D, F, 5A, B, 6A) is not subdivided (ch67:0) and arises from the medial side of the posterior area of the second valvifer (ch68:0). The site of insertion of the muscle extends along the anterior part of the anterior ridge of T9 in most taxa examined (ch69:0) except *Megaspilus*, and *Dendrocercus* where the muscle seemingly inserts partly on the interarticular ridge of the first valvifer (ch70:0; **M6**: Figs 1B, D, 4F). The posterior T9-second valvifer muscle (**M7**: Figs 1A, 2A, D, 4E) arises from the strap-like dorsal area of T9 (ch71:0) and inserts on the median bridge (ch72:0). The fan shaped first valvifer-genital membrane muscle (ch73:0; **M8**: Figs 1A, D, E, F, 3B, 5A, D) arises from the medial surface of the first valvifer near the intervalvifer articulation (ch74:0). The site of insertion of the muscle extends along the genital membrane (ch75:0). In *Trassedia* the muscle arises from the medial surface of the dorsal sclerite of the first valvifer (ch76:1; **M8**: Fig. 3B). The posterior second valvifer-second valvula muscle (**M9**: Figs 1A–F, 2A, B, D, 3A, B, 4B, D–F, 5A, C, D) arises from the medial side of the posterior area of the second valvifer (ch77:0), and inserts on the processus musculares (ch78:0). In *Ceraphron* and *Trassedia* some bands of the muscle arise from the anterior area of the second valvifer (ch.77:1; **M9**: Figs 3A, B, 5A, C, D). T9-genital membrane muscle (ch79:0), lateral T9-second valvifer muscle (ch80:0), second valvifer-genital membrane muscle (ch81:0) and the anterior second valvifer-second valvula muscles (ch82:0) are absent from Ceraphronoidea.

Results II: Semantically enhanced characters and character states for ceraphronoid female terminalia.

Integument

First valvifer: shape

(0) elongated in lateral view

Anterior margin of first valvifer: shape

(0) convex in lateral view

Posterior margin of first valvifer: shape

(0) straight in lateral view

(1) concave in lateral view

(2) bent at tergo-valvifer articulation

Transvalvifer conjunctiva: count

(0) present

(1) absent

Dorsal sclerite of the first valvifer: shape

(0) elongated in lateral view

Ventral sclerite of the first valvifer: shape

(0) triangular in lateral view

Intravalvifer articulation: count

(0) present

(1) absent

Intravalvifer articulation: position

(0) anterior region of first valvifer

Ventral margin of dorsal sclerite of the first valvifer: thickness

(0) thickened

Anterodorsal margin of ventral sclerite of the first valvifer: thickness

(0) thickened

Anterior flange of the first valvifer: count

(0) present

(1) absent

Second valviferal condyle of the first valvifer: position

(0) at the posteroventral corner of the first valvifer

Ninth tergal condyle of the first valvifer: position

(0) posterior margin of the first valvifer

Distance between tergo-valvifer articulation and intravalvifer articulation (D1): proportion to the distance between tergo-valvifer articulation and anterior angle of first valvifer (D2).

(0) $D1=D2$

(1) $D1<D2$

(2) $D1>D2$

(3) $D2=0$

Ninth tergal condyle of the first valvifer: position

(0) on dorsal sclerite of the first valvifer

Anterior area of the second valvifer: height vs. height of posterior area of second valvifer

(0) $3\leq 1$

Basal line of the second valvifer: count

(0) present

Basal line of the second valvifer: sharpness

(0) sharp

(1) blunt

Dorsal projection of the second valvifer: count

(0) present

Length of dorsal projection of second valvifer in lateral view (L1) vs. length of anterior area of second valvifer in lateral view (L2)

(0) $L1<L2$

(1) $L1>L2$

- Anterior section of dorsal flange of the second valvifer: sharpness
 (0) sharp
 (1) blunt
- Posterior section of dorsal flange of second valvifer: sharpness
 (0) sharp
- Posterior area of second valvifer: shape
 (0) elongated
- Ventral margin of the second valvifer: curvature
 (0) curved medially and curved dorsally in lateral view
- Ventral margin of the second valvifer: position
 (0) surrounds posterior second valvifer-second valvula muscle
- Genital membrane: position
 (0) surrounds terebra
- Venom gland reservoir of the second valvifer: count
 (0) present
 (1) absent
- Venom gland reservoir of the second valvifer: physical quality
 (0) resinous
- Distal region of first valvula: shape
 (0) tapered
 (1) spatulate
- Banding pattern on first valvula: count
 (0) absent
- Annuli on first valvula: count
 (0) absent
- Processus articularis: position
 (0) anterolateral region of the bulb
- Anterior notch of the dorsal valve: position
 (0) anterior region of the bulb
- Processus musculares: position
 (0) anterodorsal region of the bulb
- Distal notch of the dorsal valve: count
 (0) absent
- Distal region of the dorsal valve: shape
 (0) tapered in dorsal view
- Anterior region of dorsal margin of the bulb: curvature
 (0) curved dorsally in lateral view
- Bulb: height in lateral view vs. height of anterior area of the second valvifer in lateral view
 (0) =0.5
 (1) <0.5
- Banding pattern on dorsal valve: count
 (0) absent

Annuli on dorsal valve: count

(0) present

(1) absent

Annuli on dorsal valve: count value

(0) four

(1) six

Median bridge: count

(0) present

Distal vertical conjunctiva of the second valvifer-third valvifer complex: count

(0) present

Distal vertical conjunctiva of the second valvifer-third valvifer complex: overlap relationship with dorsal margin of second valvifer-third valvula complex

(0) does not overlap

Distal region of the third valvula: shape

(0) tapered in lateral view

Lateral region of the third valvula: shape

(0) convex in posterior view

Lateral region of the third valvula: entity

(0) is_a sclerite

Medial region of the third valvula: shape

(0) concave in posterior view

Median region of the third valvula: entity

(0) is_a conjunctiva

T9: shape

(0) quadrangular in lateral view

Dorso-median region of T9: width in dorsal view vs. length in dorsal view

(0) width > length

Anterior ridge of T9: count

(0) present

Anterolateral region of anterior ridge of T9: position

(0) adjacent to anterior margin of T9

Distance between Anterior ridge of T9 and anterior margin of T9: anterior-posterior gradient

(0) increasing

Muscles

Attachment site of S7-first valvula muscle (M1) on S7: position

(0) adjacent to the anterior margin of S7

Attachment site of S7-first valvula muscle (M1) on first valvula: position

(0) dorsal to second valvifer

Attachment site of S7-first valvula muscle on first valvula: position

(0) anterior to attachment site of S7-first valvula muscle on S7

Attachment site of dorsal T8-T9 muscle on T8: position

(0) adjacent to the anterior margin of T8

Attachment site of dorsal T8-T9 muscle on T9: position

(0) adjacent to anterior margin of the dorsomedial region of T9

Attachment site of lateral T8-T9 muscle on T8: position

(0) posterodorsal to the attachment site of dorsal T8-T9 muscle on T8

Attachment site of lateral T8-T9 muscle on T9: position

(0) adjacent to anterior ridge of T9

Attachment site of T8-first valvifer muscle on T8: position

(0) dorsal to the attachment site of lateral T8-T9 muscle on T8

Attachment site of T8-first valvifer muscle on first valvifer: position

(0) adjacent to the ninth tergal condyle of the first valvifer

Attachment site of T8-first valvifer muscle on first valvifer: position

(0) on ventral sclerite of the first valvifer adjacent to the intravalvifer articulation

Attachment site of dorsal T9-second valvifer muscle on T9: position

(0) adjacent to the anterior ridge of T9 and the region of T9 dorsal to and ventral to the anterior ridge of T9

Attachment site of dorsal T9-second valvifer muscle on second valvifer: position

(0) adjacent to the anterior section of the dorsal flange of the second valvifer

Ventral T9-second valvifer muscle: count value

(0) 1

Attachment site of ventral T9-second valvifer muscle on second valvifer: position

(0) posterior area of the second valvifer

Attachment site of ventral T9-second valvifer muscle on T9: position

(0) adjacent to anterior region of anterior ridge of T9

First valvifer-second valvifer muscle: count

(0) present

(1) absent

Attachment site of posterior T9-second valvifer muscle on T9: position

(0) on the dorsal region of T9

Attachment site of posterior T9-second valvifer muscle on second valvifer: position

(0) on the median bridge

First valvifer-genital membrane muscle: shape

(0) fan shaped in dorsal view

Attachment site of first valvifer-genital membrane muscle on first valvifer: position

(0) on the medial side of the first valvifer adjacent to the intervalvifer articulation

Attachment site of first valvifer-genital membrane muscle on genital membrane: position

(0) along the median line of the genital membrane

Attachment site of first valvifer-genital membrane muscle on first valvifer: position

(0) on the medial side of the dorsal sclerite of the first valvifer

Attachment site of posterior second valvifer-second valvula muscle on second valvifer:
position

(0) on the medial side of the posterior area of the second valvifer

(1) on the medial side of the posterior area of the second valvifer and the anterior area of the second valvifer

Attachment site of posterior second valvifer-second valvula muscle on second valvula:
position

(0) on the processus musculares

T9-genital membrane muscle: count

(0) absent

Lateral T9-second valvifer muscle: count

(0) absent

second valvifer-genital membrane muscle: count

(0) absent

anterior second valvifer-second valvula muscles: count

(0) absent

Discussion

The enormous diversity of ovipositor phenotype in Hymenoptera reflects the manner in which the female wasp finds feasible environments for her developing larvae. Host structure and location, as well as the different ways of storing the ovipositor, are arguably the principal factors driving the structural adaptation of these structures (Quicke et al. 1999, Vilhelmsen 2000, Vilhelmsen and Turrisi 2011). Major morphological characteristics of ceraphronoid ovipositors are most likely related to these influences.

Storage of terebra

The ceraphronoid ovipositor is stored in a horizontal position inside the metasoma, with its ventral part concealed by S7 (Fig. 6E). As the first oviposition movement, the contracting muscles between the apical metasomal tergites and sternites expose the ventral part of the ovipositor by rotating it and the ninth abdominal tergite posteriorly, from the resting, horizontal to the active, vertical position. This movement is common within Apocrita (Fig. 6F; Alam 1953, Copland 1976, Fergusson 1988).

The mechanism of the extension of the terebra from the second valvifer-third valvula complex is shared between Ceraphronoidea and most other Hymenoptera. The movement is facilitated by the posterior second valvifer-second valvula muscles (M9: Figs 1A–F, 2A, B, D, 3A, B, 4B, D–F, 5A, C, D; Vilhelmsen 2000). When the muscles contract they cause the bulb to pivot anteriorly at the basal articulation that is composed of the processus articularis and pars articularis (pra, paa: Figs 2A, 2F). As the bulb pivots, the distal end of the terebra move into an extended active position -

compare Fig. 1B (partially extended) with Fig. 2B (retracted). The terebra is held in the longitudinal axis during oviposition: <https://scholarsphere.psu.edu/files/r494vk42v>

At the end of the oviposition the terebra is retracted prior to the anterior rotation of the ovipositor/T9 complex into the resting, horizontal position. The retraction of the terebra, unlike its extension, seems to be unique for Ceraphronoidea. In other Hymenoptera the movement is accomplished by the contraction of the vertically oriented anterior second valvifer-second valvula muscle that arises from the anterodorsal margin of the second valvifer and inserts on the distal region of the bulb (King and Copland 1969, 1976, Vilhelmsen 2000, Fergusson 1988, Alam 1953). However, this muscle is absent from Ceraphronoidea, and thus we hypothesize a different mechanism for retracting the terebra. We observed a relatively large muscle arising from S7 and inserting dorsally on the first valvula in Ceraphronoidea (M1: Figs 1B, D, 3A). The position of the site of attachments of the muscle suggest that the S7-first valvula muscle (Figs 1B, 3A) aids in the retraction of the terebra. The presence of muscles arising from S7 and inserting on the first valvula has been reported only in some basal Hymenoptera (Dhillon 1966, Vilhelmsen 2000) and in one braconid species, *Stenobracon deesae* (Alam 1953). The S7-first valvulae muscle has an entirely different configuration in basal Hymenoptera. It arises from along the anterior margin of S7 and inserts on the proximal end of the ventral ramus of the first valvula and presumably contributes to the movement of the first valvula aiding the ventral T9-second valvifer muscle (Vilhelmsen 2000). In *Stenobracon*, however, the S7-first valvulae muscle has a very similar structure to that we reported in Ceraphronoidea (Alam 1953) suggesting the possible involvement of this muscle into the retraction of the terebra. Alam (1953) hypothesized that the muscle is involved in the movement of the median conjunctivae of the first valvulae (dorsal wall of the egg canal) influencing the egg movement along the egg canal. Although the anterior second valvifer-second valvulae muscle is present in all non-ceraphronoid Hymenoptera, it is possible that the S7-first valvulae muscle is involved in the retraction of the terebra in other Apocrita, and that this function is not an evolutionary novelty for Ceraphronoidea.

Egg laying mechanism

The paired first and second valvifers and T9, operated together by the dorsal and ventral T9-second valvifer muscles, form the ovipositor machinery that is responsible for “drilling” the terebra into a substrate and moving the egg along the egg canal (Vilhelmsen 2000).

As the dorsal T9-second valvifer muscle (M5: Figs 1A, B, D, E, 2A, B, D, 3B, 4A, B, D, E, F, 5A–C, 6A) contracts the first valvifer pivots posteriorly (in anterior to the left position) at the intervalvifer articulation while contraction of the antagonistic ventral T9-second valvifer muscle (M6: Figs 1A, B, D, E, 2A, B, D, 3B, 4A, B, D, F, 5A, B, 6A) pulls the first valvifer in the opposite direction (compare the position of the tergo-valvifer (tva) and intervalvifer articulations (iva) on Figures 3A and 3E). As this

movement is what slides the first valvula along the second valvulae, the distance the first valvifer moves determines the distance the first valvula moves. The left and right first valvulae slide back and forth alternately during the alternate contraction of the left and right T9-second valvifer muscle pairs (1vf left, 1vv right: Fig. 3B; Vilhelmsen 2000). This alternate movement is what is underlying the advance of the egg inside the egg canal and the drilling of the terebra into a substrate. The former function is facilitated by the presence of internal, posteriorly oriented cuticular modifications (Austin and Browning 1981) while the latter could be aided by anchoring structures on the first valvulae (Vilhelmsen 2000).

Adaptations effecting the alternate movements and configuration of the first valvulae might be mostly affected by the hardness of the substrate and constraints for fast oviposition. Oviposition into a concealed, and therefore relatively immobile host requires a robust system that has to be strong enough to drill or break the barrier. On the other hand, parasitization of an exposed, mobile but relatively soft host requires fast and perhaps less robust mechanism. Two major egg laying habits have been recorded within *Ceraphronoidea*: oviposition inside a mobile host and oviposition through a hard but relatively thin barrier enclosing the host, which has restricted movement (Dessart 1995b, c). *Ceraphron* and numerous *Aphanogmus* species were reported to parasitize free living Diptera larvae (Laborius 1972) whereas most *Dendrocerus* species and some *Aphanogmus* parasitize hosts hidden by the hardened integument of the primary host (Fergusson 1980), the wall of the cocoon (Peter and David 1990, Alam 1985) or galls (Bakke 1955) developed around the host.

The relative distance between the anterior angle of the first valvifer and the intervalvifer articulation (ang, iva: Figs 1B, 2C, E, 3C, E, 4A, E, F, 5A, 6A, C, D) is most probably positively correlated with the degree of the sliding motion of the first valvula (Prentice 1998). The posterior margin of the first valvifer angled at the tergo-valvifer articulation (**tv**a: Fig.) in most Hymenoptera (Oeser 1961, Vilhelmsen 2000). It is easy to see that the distance between the anterior angle of the first valvifer and the intervalvifer articulation and thus the degree of motion of the first valvula is larger with less acute angle at the tergo-valvifer articulation. A straight posterior margin of the first valvifer has been reported in a few Chalcidoidea (*Epidinocarsis*, Le Ralec et al. 1996; *Spalangia*, fig. 6 in Copland and King 1972) and in Apoidea (*Pryonx*, Prentice 1989). The only ceraphronoid taxon with a angled margin is *Dendrocerus*, while the rest have straight or concave (*Trassedia*) posterior margins. The location of the tergo-valvifer articulation on the posterior margin of the first valvifer seems to be also influenced by the way the first valvifer is moved. The closer the tergo-valvifer articulation is to the intervalvifer articulation and the further from the anterior angle, the further the first valvula will slide on the second valvula. The tergo-valvifer articulation is adjacent to the anterior angle of the first valvifer in *Aphanogmus* sp1. This indicates a first valvula sliding motion of very short distance but, considering the extended site of origin of the T9-second valvifer muscles, with relatively great power. The presence of an anterior angle corresponding to the tergo-valvifer articulation is unique in Hymenoptera.

Two ridges/apodemes are present on T9 in most Hymenoptera, the anterior flange of T9 and the cordate apodeme. The anterior flange extends along the anterior margin of the tergite and might be homologous with the antecosta of the ninth abdominal tergum of other insects because it receives the site of attachment of the dorsal T8-T9 muscle in *Macroxyela* (Vilhelmsen 2000). The dorsal T9-second valvifer muscle arises at least partly from the flange in the rest of Hymenoptera. The cordate apodeme is close to the tergo-valvifer articulation and receive the site of attachment of the ventral T9-second valvifer muscle. It is apophysis-like and extends internally in most basal hymenopterans but ridge-like and extended posteriorly in Siricoidea, Orussidae, and numerous Apocrita (“diagonal ridge” sensu Fergusson 1988). The apodeme is usually well separated from the anterior flange of T9 in Apocrita, except in *Bruchophagus*, where they are seemingly fused anteriorly (Copland and King 1971). Only one ridge, the anterior ridge of T9 extends along the anterior margin of T9 and receives the site of attachment of both the ventral and the dorsal T9-second valvifer muscles in Ceraphronoidea. This condition is unique in Hymenoptera. As described above, the dorsal and ventral T9-second valvifer muscles move the first valvifer indirectly. Host relationships of *Megaspilus* remain unknown, but it is possible that some bands of the ventral muscle insert on the interarticular ridge of the first valvula and thus the contraction of it might cause the direct movement of the sclerite.

The first valvifer is composed of two articulating sclerites in *Trassedia*. Although this condition is possibly plesiomorphic for Insecta (Klass et al. 2013) it is present only in a few taxa i.e. Archaeognatha, most ovipositor bearing Odonata and some Dermaptera (Klass *personal communication*). When the ventral T9-second valvifer muscle contracts the two sclerites of the first valvifer pivot anteriorly together as one unit. The two sclerites articulate with one another anteriorly, however, allowing the dorsal sclerite to pivot posteriorly on the ventral sclerite at the intravalvifer articulation when the dorsal T9-second valvifer muscle is contracted (Figs 3A–E). The first valvulae are thus enabled to slide a very long distance along the second valvulae in this unique system, probably allowing the egg to move quickly down the length of the ovipositor.

The presence or absence of annuli at the tip of the ovipositor may depend on the hardness of the substrate into which the wasp is ovipositing, as well as the circumstances under which oviposition is taking place (Quicke et al. 1999, Le Ralec et al. 1996, Gerling et al. 1998). Megaspilidae, similar to numerous other non-ichneumonoid apocritans do have annuli apically only on the second valvulae whereas Ceraphronidae lack them from both valvulae. In general it seems that the harder the substrate is, the more developed the ovipositor sculpture is (Le Ralec et al. 1996).

A minute gland (dgl?: Figs 3B, 5A) and a relatively larger gland reservoir (res: Figs 3A–E, 5A, B, E, F, 4C), enclosed by the second valvifers, have been detected in Ceraphronidae including *Trassedia* and *Lagynodes*. The Dufour’s gland and the venom gland reservoir has a similar location in some Chalcidoidea (Copland and King 1971) where it was hypothesized that the ventral second T9-second valvifer muscles might aid to discharge the reservoir (res: Fig. 5B). The gland extract of this possible venom reservoir is resin-like (hard, transparent and amber colored) in critical point dried *Cer-*

aphron specimens (res: Fig. 5F) implying its possible cement nature that might be used for coating the eggs or fastening them on a surface. *Ceraphron* and some *Aphanogmus* species are reported to be endoparasitoids (Cordero and Cave 1992) in which lifestyle the egg coating can be crucial for avoiding the host immune response. We did not observe any glands or resin containing reservoirs in Megaspilinae. Höller et al. (1993) identified the Dufour's gland in *Dendrocerus carpenteri* outside of the second valvifers and reported the absence of the venom gland in this taxon. Nevertheless, more accurate, TEM based examination of the accessory gland system of Ceraphronoidea is needed for clarifying the function of the gland and gland reservoir located inside the second valvifer.

In general, the ovipositors of *Ceraphron*, *Trassedia* and *Aphanogmus* sp. 2 are less robust and capable of a very large degree of motion, corresponding to the available data about ovipositing in exposed and active hosts. *Trassedia* represents, perhaps, a more extreme version of the "quickly into soft substrate" oviposition type. Megaspilidae, on the other hand, have a stronger, more robust ovipositor systems, which afford the smaller degree of motion required for handling a harder substrate concealing a static host. *Dendrocerus*, for example, exhibits extended sites of origins for muscles and a very small degree of motion for the first valvulae. *Aphanogmus* sp. 1, although it belongs to Ceraphronidae, shares numerous characteristics with *Dendrocerus* and therefore may represent the *Aphanogmus*-group that parasitizes hosts obscured by harder barrier, e.g., the wall of a plant gall, and thus is a case of parallelism driven by the same environmental constraints.

So far it is widely accepted that Ceraphronoidea is composed of two extant families, Ceraphronidae and Megaspilidae, plus two fossil families not treated here. The limits between the two families, however, have been challenged recently (Mikó and Deans 2009, Mikó et al. in press). Although the presence of the annuli in Megaspilidae and absence from Ceraphronidae supports the traditional classification, the location of a resin producing gland inside the second valvifers is shared by the megaspilid subfamily Lagynodinae and Ceraphronidae.

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Appendix

Anatomical terms used, cross-referenced to an ontological (formal) definition (Hymenoptera Anatomy Ontology; URI = Uniform Resource Identifier).

Abbreviation	Label	Concept	URI
	absent	A quality denoting the lack of an entity.	http://purl.obolibrary.org/obo/PATO_0000462
	adjacent to	A spatial quality inhering in a bearer by virtue of the bearer's being located near in space in relation to another entity.	http://purl.obolibrary.org/obo/PATO_0002259
ann	annulus, annuli	The carina that is transverse and extends across the lateral wall of the terebra.	http://purl.obolibrary.org/obo/HAO_0001173
ang	anterior angle of the first valvifer	The corner on the first valvifer that marks the posterior end of the first valvula.	http://purl.obolibrary.org/obo/HAO_0002168
aa	anterior area of the second valvifer	The area of the second valvifer which is anterior to the anatomical line that is the shortest distance from the first valvifer fossa of the second valvifer and the ventral margin of the second valvifer	http://purl.obolibrary.org/obo/HAO_0002169
	anterior flange of T9	The flange that extends along the anterolateral margin of female T9.	http://purl.obolibrary.org/obo/HAO_0001171
af1	anterior flange of the first valvifer	The flange that extends anteriorly on the first valvifer and overlaps with the posterior margin of the anterior area of the second valvifer.	http://purl.obolibrary.org/obo/HAO_0002166
	anterior margin	anatomical margin and (overlaps some anterior side)	http://purl.obolibrary.org/obo/BSPO_0000671
an2	anterior notch of the dorsal valve	The notch that is located anteriorly on the dorsal ramus of the second valvula that accommodates the ventral ramus of the second valvula and the first valvula.	http://purl.obolibrary.org/obo/HAO_0002178
	anterior region, anteriorly	anatomical region and (overlaps some anterior side)	http://purl.obolibrary.org/obo/BSPO_0000071
ar9	anterior ridge of T9	The ridge that extends along the anterior margin of female T9 and receives the site of origin of the ventral and the dorsal T9-second valvifer muscles.	http://purl.obolibrary.org/obo/HAO_0002182
	anterior second valvifer-second valvula muscle	The ovipositor muscle that arises from the anterodorsal part of the second valvifer and inserts subapically on the processus articulares.	http://purl.obolibrary.org/obo/HAO_0001166
asf	anterior section of dorsal flange of the second valvifer	The area of the dorsal flange of the second valvifer that is anterior to the site of origin of the basal line.	http://purl.obolibrary.org/obo/HAO_0002173
	anterior to	A spatial quality inhering in a bearer by virtue of the bearer's being located toward the front of an organism relative to another entity.	http://purl.obolibrary.org/obo/PATO_0001632

Abbreviation	Label	Concept	URI
	anterodorsal margin	anatomical margin and (overlaps some anterior side) and (overlaps some dorsal side)	http://purl.obolibrary.org/obo/BSPO_0000686
	anterolateral region	Anatomical region and (overlaps some anterior side) and (overlaps some lateral side)	http://purl.obolibrary.org/obo/BSPO_0000029
	apodeme	The process that is internal.	http://purl.obolibrary.org/obo/HAO_0000142
	attachement site	The area of the integument where muscles are attached to epidermal cells.	http://purl.obolibrary.org/obo/HAO_0002184
	banding pattern	The anatomical cluster that is composed of the strongly sclerotised areas corresponding with the annuli and less strongly sclerotised areas situated between them.	http://purl.obolibrary.org/obo/HAO_0001176
	basal articulation	The articulation that is part of the second valvifer-second valvula-third valvula complex and adjacent to the rhachis.	http://purl.obolibrary.org/obo/HAO_0001177
bl	basal line of the second valvifer	The line on the second valvifer that extends between the pars articularis and the dorsal flange of second valvifer.	http://purl.obolibrary.org/obo/HAO_0002171
	bent	A shape quality inhering in a bearer by virtue of the bearer's having one or more angle(s) in its length.	http://purl.obolibrary.org/obo/PATO_0000617
	blunt	A shape quality inhering in a bearer by virtue of the bearer's terminating gradually in a rounded end.	http://purl.obolibrary.org/obo/PATO_0001950
bulb	bulb	The anterior area of the dorsal valve that is bulbous.	http://purl.obolibrary.org/obo/HAO_0002177
	concave	A shape quality in a bearer by virtue of the bearer's curving inward.	http://purl.obolibrary.org/obo/PATO_0001857
	conjunctiva	The area of the integument that is weakly sclerotized, with thin exocuticle.	http://purl.obolibrary.org/obo/HAO_0000221
	convex	A shape quality that obtains by virtue of the bearer having inward facing edges; having a surface or boundary that curves or bulges outward, as the exterior of a sphere.	http://purl.obolibrary.org/obo/PATO_0001355
	cordate apodeme	The apodeme on the anterior margin of the abdominal tergum 9 that receives the ventral T9-second valvifer muscle.	http://purl.obolibrary.org/obo/HAO_0001585
	corner	The projection that is located at the intersection of two or more edges.	http://purl.obolibrary.org/obo/HAO_0000223
	count	The number of entities of this type that are part of the whole organism.	http://purl.obolibrary.org/obo/PATO_0000070
	count value		http://purl.obolibrary.org/obo/PATO_0000416
	curvature	A surface shape quality inhering in a bearer by virtue of the bearer's exhibiting a degree of bending.	http://purl.obolibrary.org/obo/PATO_0001591

Abbreviation	Label	Concept	URI
	curved dorsally	A curvature quality inhering in a bearer by virtue of the bearer's being curved towards the back or upper surface of an organism.	http://purl.obolibrary.org/obo/PATO_0001468
	curved medially	A curvature quality inhering in a bearer by virtue of the bearer's being curved towards the middle.	http://purl.obolibrary.org/obo/PATO_0002164
	distal notch of the dorsal valve	The notch that is distal on the dorsal valve.	http://purl.obolibrary.org/obo/HAO_0002179
	distal region	Anatomical region and (overlaps some distal side)	http://purl.obolibrary.org/obo/BSPO_0000078
dvc	distal vertical conjunctiva of the second valvifer-third valvifer complex	The conjunctiva that traverses the second valvifer-third valvula complex and is located distal to the median bridge of the second valvifer.	http://purl.obolibrary.org/obo/HAO_0002180
	distance	A quality that is the extent of space between two entities.	http://purl.obolibrary.org/obo/PATO_0000040
	dorsal margin	Anatomical margin and (overlaps some dorsal side).	http://purl.obolibrary.org/obo/BSPO_0000679
dp	dorsal projection of the second valvifer	The projection that is located on the second valvifer and corresponds to the proximal end of the rachis.	http://purl.obolibrary.org/obo/HAO_0002172
	dorsal region	anatomical region and (overlaps some dorsal side)	http://purl.obolibrary.org/obo/BSPO_0000079
d1vf	dorsal sclerite of the first valvifer	The sclerite of the first valvifer that is located dorsally of the transvalviferal conjunctiva.	http://purl.obolibrary.org/obo/HAO_0002163
M2	dorsal T8-T9 muscle	The abdominal muscle that arises from the anteromedian margin of female T8 and inserts on the anteromedian margin of the female T9.	http://purl.obolibrary.org/obo/HAO_0001571
M5	dorsal T9-second valvifer muscle	The ovipositor muscle that arises along the posterodorsal part of the anterior margin of female T9 and inserts on the anterior section of the dorsal flanges of the second valvifer.	http://purl.obolibrary.org/obo/HAO_0001569
	dorsal to	x dorsal_to y if x is further along the dorso-ventral axis than y, towards the back. A dorso-ventral axis is an axis that bisects an organism from back (e.g. spinal column) to front (e.g. belly).	http://purl.obolibrary.org/obo/BSPO_0000098
	dorsal valve	The area that is articulated with the right and left second valvifers at the basal articulation and bears the rhachies.	http://purl.obolibrary.org/obo/HAO_0001658
	dorsal view		http://purl.obolibrary.org/obo/BSPO_0000063
	dorsomedial region	anatomical region and (overlaps some dorsal side) and (overlaps some medial side)	http://purl.obolibrary.org/obo/BSPO_0000069

Abbreviation	Label	Concept	URI
ec	egg canal	The anatomical space that is between the left and right rhachises.	http://purl.obolibrary.org/obo/HAO_0002191
	elongated	A quality inhering in a bearer by virtue of the bearer's length being notably higher than its width.	http://purl.obolibrary.org/obo/PATO_0001154
	fan-shaped	A quality inhering in a bearer that is shaped in the form of a fan.	http://purl.obolibrary.org/obo/PATO_0002219
1vf	first valvifer	The area of the first valvifer-first valvula complex that is proximal to the aulax, bears the ninth tergal condyle of the first valvifer and the second valviferal condyle of the first valvifer and is connected to the genital membrane by muscle.	http://purl.obolibrary.org/obo/HAO_0000338
M8	first valvifer-genital membrane muscle	The ovipositor muscle that arises from the posterior part of the first valvifer and inserts anteriorly on the genital membrane anterior to the T9-genital membrane muscle.	http://purl.obolibrary.org/obo/HAO_0001746
	first valvifer-second valvifer muscle	The ovipositor muscle that arises from the first valvifer and inserts on the second valvifer.	http://purl.obolibrary.org/obo/HAO_0002189
1vv	first valvula, first valvulae	The area of the first valvifer-first valvula complex that is delimited distally by the proximal margin of the aulax.	http://purl.obolibrary.org/obo/HAO_0000339
gm	genital membrane	The conjunctiva that connects the ventral margins of the second valvifers.	http://purl.obolibrary.org/obo/HAO_0001757
	height	A 1-D extent quality inhering in a bearer by virtue of the bearer's vertical dimension of extension.	http://purl.obolibrary.org/obo/PATO_0000119
	increasing	quality and (increased_in_magnitude_relative_to some normal)	http://purl.obolibrary.org/obo/PATO_0002300
iar	interarticular ridge of the first valvifer	The ridge that extends along the posterior margin of the first valvifer between the inter-valvifer and tergovalvifer articulations.	http://purl.obolibrary.org/obo/HAO_0001562
iva	intervalvifer articulation	The articulation between the first valvifer and second valvifer.	http://purl.obolibrary.org/obo/HAO_0001558
iava	intravalvifer articulation	The articulation between the dorsal sclerite of the first valvifer and the ventral sclerite of the first valvifer.	http://purl.obolibrary.org/obo/HAO_0002165
	lateral region	anatomical region and (overlaps some lateral side)	http://purl.obolibrary.org/obo/BSPO_0000082
M3	lateral T8-T9 muscle	The ninth abdominal tergal muscle that arises from the anterolateral margin of female T8 and inserts on the anterolateral margin of female T9.	http://purl.obolibrary.org/obo/HAO_0001776
	lateral T9-second valvifer muscle	The muscle that arises from the posteroventral parts of the female T9 and inserts on the median bridge.	http://purl.obolibrary.org/obo/HAO_0002187

Abbreviation	Label	Concept	URI
	lateral view		http://purl.obolibrary.org/obo/BSPO_0000066
	length of anterior area of second valvifer	The anatomical line that is parallel with the longitudinal body axis and the shortest among the anatomical lines that extends between the anterior and posterior margins of the anterior area of the second valvifer.	http://purl.obolibrary.org/obo/HAO_0002240
	length of dorsal projection	The anatomical line that is parallel with the longitudinal body axis and the shortest among the anatomical lines that extends between the anterior and posterior margins of the dorsal projection.	http://purl.obolibrary.org/obo/HAO_0002193
	length of female T9	The anatomical line that is parallel with the longitudinal body axis and the shortest among the anatomical lines that extend between the anterior and posterior margins of female T9.	http://purl.obolibrary.org/obo/HAO_0002241
	medial side	a point in the centre of the organism (where the left-right axis intersects the midsagittal plane)	http://purl.obolibrary.org/obo/BSPO_0000067
	median bridge	The area that connects posterodorsally the second valvifers and is the site of attachment for the posterior T9-second valvifer muscle.	http://purl.obolibrary.org/obo/HAO_0001780
mc2	distal notch of the dorsal valve	The notch that is distal on the dorsal valve.	http://purl.obolibrary.org/obo/HAO_0002179
mc1	medial conjunctiva of the first valvulae	The conjunctiva that extends medially along the first valvula.	http://purl.obolibrary.org/obo/HAO_0002192
	median line	An axis that bisects an organism from head end to opposite end of body or tail.	http://purl.obolibrary.org/obo/BSPO_0000013
	medial region	anatomical region and (overlaps some medial side)	http://purl.obolibrary.org/obo/BSPO_0000083
	ninth tergal condyle of the first valvifer	The condyle that is located on the first valvifer and articulates with the first valviferal fossa of T9.	http://purl.obolibrary.org/obo/HAO_0002160
oth	olistheters	The anatomical cluster that is composed of the rhachis of the second valvula and the aulax of the first valvula.	http://purl.obolibrary.org/obo/HAO_0001103
	overlaps	x overlaps y if they have some part in common.	http://purl.obolibrary.org/obo/bspo%23overlaps
	ovipositor	The anatomical cluster that is composed of the first valvulae, second valvulae, third valvulae, first valvifers, second valvifers and female T9.	http://purl.obolibrary.org/obo/HAO_0000679
paa	pars articularis	The articular surface that is situated anteriorly on the ventral margin of the second valvifer and forms the lateral part of the basal articulation.	http://purl.obolibrary.org/obo/HAO_0001606

Abbreviation	Label	Concept	URI
	position	A spatial quality inhering in a bearer by virtue of the bearer's spatial location relative to other objects in the vicinity.	http://purl.obolibrary.org/obo/PATO_0000140
	posteriorly	anatomical gradient and (has_axis some anterior/posterior axis)	http://purl.obolibrary.org/obo/BSPO_0000052
pa	posterior area of the second valvifer	The area of the second valvifer that is posterior to the anatomical line that is the shortest distance from the first valviferal fossa of the second valvifer to the ventral margin of the second valvifer.	http://purl.obolibrary.org/obo/HAO_0002170
	posterior margin	anatomical margin and (overlaps some posterior side)	http://purl.obolibrary.org/obo/BSPO_0000672
p1v	posterior margin of first valvifer	The margin of the first valvifer that is posterior and extends between the intervalvifer articulation and the anterior angle of the first valvifer.	http://purl.obolibrary.org/obo/HAO_0002159
M9	posterior second valvifer-second valvula muscle	The ovipositor muscle that arises postero-ventrally from the second valvifer and inserts on the processus musculares of the second valvula.	http://purl.obolibrary.org/obo/HAO_0001815
psf	posterior section of dorsal flange of the second valvifer	The area of the dorsal flange of the second valvifer that is posterior to the to the site of origin of the basal line.	http://purl.obolibrary.org/obo/HAO_0002174
M7	posterior T9-second valvifer muscle	The ovipositor muscle that arises medially from the posterodorsal part of female T9 and inserts on the median bridge of the second valvifers.	http://purl.obolibrary.org/obo/HAO_0001813
	posterior view		http://purl.obolibrary.org/obo/BSPO_0000056
	postero-medial region	anatomical region and (overlaps some posterior side) and (overlaps some medial side)	http://purl.obolibrary.org/obo/BSPO_0000070
	posterodorsal to	A spatial quality inhering in a bearer by virtue of the bearer's being located toward the rear and upper surface of an organism relative to another entity.	http://purl.obolibrary.org/obo/PATO_0001916
	posteroventral corner of first valvifer	The corner of the first valvifer that is adjacent to the intervalvifer articulation.	http://purl.obolibrary.org/obo/HAO_0002239
	present	A quality inhering in a bearer by virtue of the bearer's existence.	http://purl.obolibrary.org/obo/PATO_0000467
pra	processus articularis	The process that extends laterally from the proximal region of the second valvula and forms the median part of the basal articulation, and corresponds to the site of attachment for the anterior second valvifer-second valvula muscle.	http://purl.obolibrary.org/obo/HAO_0001704

Abbreviation	Label	Concept	URI
prm	processus musculares	The apodeme that extends dorsally from the proximal part of the second valvula to the genital membrane and receives the site of attachment of the posterior second valvifer-second valvula muscle.	http://purl.obolibrary.org/obo/HAO_0001703
	proportion	A quality inhering in a bearer by virtue of the bearer's magnitude in respect to a related entity.	http://purl.obolibrary.org/obo/PATO_0001470
	quadrangular	A shape quality inhering in a bearer by virtue of the bearer's having four angles and four sides.	http://purl.obolibrary.org/obo/PATO_0001988
	region	A 3D region in space without well-defined compartmental boundaries; for example, the dorsal region of an ectoderm.	http://purl.obolibrary.org/obo/BSPO_0000070
	resinous	A physical quality inhering in a bearer by virtue of the bearer exhibiting molecular attraction to another entity in contact.	http://purl.obolibrary.org/obo/PATO_0002331
	ridge	The apodeme that is elongate.	http://purl.obolibrary.org/obo/HAO_0000899
	S7	The sternite that is connected to the first valvula via muscles.	http://purl.obolibrary.org/obo/HAO_0002185
	S7-first valvula muscle	The muscle that originates from the abdominal sternum 7 and inserts on the first valvula.	http://purl.obolibrary.org/obo/HAO_0001668
	sclerite, sclerites	The area of the integument where the cuticle is well sclerotised with thick exocuticle.	http://purl.obolibrary.org/obo/HAO_0000909
	second valvifer-genital membrane muscle	The ovipositor muscle that arises anteriorly from the dorsal flange of the second valvifer and inserts anteriorly on the dorsal part of the genital membrane.	http://purl.obolibrary.org/obo/HAO_0001672
2vf	second valvifer	The area of the second valvifer-second valvula-third valvula complex that is proximal to the basal articulation and to the processus musculares and articulates with female T9.	http://purl.obolibrary.org/obo/HAO_0000927
	second valvifer-genital membrane muscle	The ovipositor muscle that arises anteriorly from the dorsal flange of the second valvifer and inserts anteriorly on the dorsal part of the genital membrane.	http://purl.obolibrary.org/obo/HAO_0001672
	second valvifer condyle of the first valvifer	The condyle that is located on the first valvifer and articulates with the first valvifer fossa of the second valvifer.	http://purl.obolibrary.org/obo/HAO_0002167
	second valvifer-third valvula complex	The area of the second valvifer-second valvula-third valvula complex that is proximal to the basal articulation.	http://purl.obolibrary.org/obo/HAO_0002181
	2vv	second valvula, second valvulae	http://purl.obolibrary.org/obo/HAO_0000928
		The area of the second valvifer-second valvula-third valvifer complex that is distal to the basal articulation and to the processus musculares and is limited medially by the median body axis.	

Abbreviation	Label	Concept	URI
spa	sensillar patch	The patch that is composed of placoid sensilla adjacent to the intervalvifer articulation.	http://purl.obolibrary.org/obo/HAO_0001671
	shape	A morphological quality inhering in a bearer by virtue of the bearer's ratios of distances between its features (points, edges, surfaces and also holes etc).	http://purl.obolibrary.org/obo/PATO_0000052
	sharpness	A shape quality inhering in a bearer by virtue of the bearer's having a sharp or tapered end or point.	http://purl.obolibrary.org/obo/PATO_0000944
	sharp	A shape quality inhering in a bearer by virtue of the bearer's terminating in a point or edge.	http://purl.obolibrary.org/obo/PATO_0001419
	spatulate	A shape quality inhering in a bearer by virtue of the bearer's being oblong, with the lower end very much attenuated.	http://purl.obolibrary.org/obo/PATO_0001937
	straight	A shape quality inhering in a bearer by virtue of the bearer's being free of curves, bends, or angles.	http://purl.obolibrary.org/obo/PATO_0002180
	surrounds		http://purl.obolibrary.org/obo/BSPO_0000101
	T8	The tergite that is connected to female T9 by muscles.	http://purl.obolibrary.org/obo/HAO_0002188
	T8-first valvifer muscle	The ovipositor muscle that originates from the lateral part of female T8 and inserts on the dorsal margin of the first valvifer.	http://purl.obolibrary.org/obo/HAO_0001640
	T9	The tergite that is articulated with the first valvifer and second valvifer and is connected to the second valvifer via muscles.	http://purl.obolibrary.org/obo/HAO_0000075
	T9-genital membrane muscle	The ovipositor muscle that arises from the cordate apodeme and inserts dorsally on the proximal part of the genital membrane and on the opposite cordate apodeme.	http://purl.obolibrary.org/obo/HAO_0001639
	tapered	A shape quality inhering in a bearer by virtue of the bearer's being gradually narrower or thinner toward one end.	http://purl.obolibrary.org/obo/PATO_0001500
trb	terebra	The anatomical cluster that is composed of the first and second valvulae.	http://purl.obolibrary.org/obo/HAO_0001004
tva	tergo-valvifer articulation	The articulation that is located between the abdominal tergum 9 and the first valvifer and is composed of the ninth tergal condyle of the first valvifer and the first valviferal fossa of the ninth tergite.	http://purl.obolibrary.org/obo/HAO_0001636
	thickened	A thickness which is relatively high.	http://purl.obolibrary.org/obo/PATO_0000591
	thickness	A 1-D extent quality which is equal to the dimension through an object as opposed to its length or width.	http://purl.obolibrary.org/obo/PATO_0000915

Abbreviation	Label	Concept	URI
3vv	third valvula, third valvulae	The area of the second valvifer-third valvula complex that is posterior to the distal vertical conjunctiva of the second valvifer-third valvula complex.	http://purl.obolibrary.org/obo/HAO_0001012
tvc	transvalvifer conjunctiva	The conjunctiva that traverses the first valvifer and separates the dorsal and ventral sclerites of the first valvifer.	http://purl.obolibrary.org/obo/HAO_0002162
	triangular	A shape quality inhering in a bearer by virtue of the bearer's having three angles.	http://purl.obolibrary.org/obo/PATO_0001875
res	venom gland reservoir of the second valvifer	The gland reservoir that is between the second valvifers.	http://purl.obolibrary.org/obo/HAO_0002176
	ventral margin	anatomical margin and (overlaps some ventral side)	http://purl.obolibrary.org/obo/BSPO_0000684
vr2	ventral ramus of the second valvula	The area of the second valvifer-second valvula-third valvifer complex that bears the rhachis.	http://purl.obolibrary.org/obo/HAO_0001107
v1v	ventral sclerite of the first valvifer	The sclerite of the first valvifer that is ventral to the transvalviferal conjunctiva.	http://purl.obolibrary.org/obo/HAO_0002164
M6	ventral T9-second valvifer muscle	The ovipositor muscle that arises from the lateral region of female T9 and inserts along the posterior part of the dorsal flange of the second valvifer.	http://purl.obolibrary.org/obo/HAO_0001616
	ventral to	x ventral_to y if x is further along the dorso-ventral axis than y, towards the front. A dorso-ventral axis is an axis that bisects an organism from back (e.g. spinal column) to front (e.g. belly).	http://purl.obolibrary.org/obo/BSPO_0000102
	width	A 1-D extent quality which is equal to the distance from one side of an object to another side which is opposite.	http://purl.obolibrary.org/obo/PATO_0000921

Nesting behavior and ecological preferences of five Diphaglossinae species (Hymenoptera, Apoidea, Colletidae) from Argentina and Chile

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Abstract

The nests of *Cadequala albopilosa* (Spinola, 1851), *Diphaglossa gayi* Spinola, 1851, *Priloglossa tarsata* (Friese, 1900), *Priloglossa matutina* (Schrottky, 1904) and *Zikanapis tucumana* (Moure, 1945) (Colletidae, Diphaglossinae) from Argentina and Chile are described herein. They show similar features to those of other Diphaglossinae: they consist of a main tunnel, cells disposed radially, isolated or in pairs, and connected to the main tunnel by laterals ones. Main tunnels are mostly vertical in species nesting in soil surface but horizontal to inclined in *D. gayi*, which nests in banks. Cells are vertical with curved necks. The cells of *C. albopilosa* show less curved necks (less than 90°), whereas in the remaining four species the cell neck is highly curved (90° or more). Cells of *P. tarsata* have a spiral earthen closure and a wad cotton-like material, whereas in *P. matutina* only had the last one. In the remaining studied species any type of closure were found. Cocoons of *C. albopilosa* and *P. tarsata* are coriaceous showing a closure composed of three disks. *Zikanapis tucumana* and possibly *P. matutina* showed dim-light foraging. The remaining species are diurnal. The climate in their nesting sites is highly diverse, ranging from 8°C to 20°C in mean annual temperature, and from 250 mm to 3000 mm in mean annual precipitation. Only *C. albopilosa* and, to a lesser extent, *Z. tucumana* nested gregariously. *Zikanapis tucumana* and *P. tarsata* were observed visiting flowers of *Solanum*.

Keywords

Cadeguala albopilosa, *Diphaglossa gayi*, *Ptiloglossa tarsata*, *Ptiloglossa matutina*, *Zikanapis tucumana*, Caupolicanini, Diphaglossini, nest architecture, ecological preferences

Introduction

The Diphaglossinae include the largest and most robust Colletidae. They are known for being mostly crepuscular to nocturnal bees that are found in habitats ranging from deserts or near deserts to humid tropical rain forests (Rozen 1984, Almeida et al. 2012). Michener (2007) included nine genera in this subfamily distributed in three tribes, which are restricted to the New World. In contrast, Urban et al. (2012) considered this subfamily as a tribe divided in the subtribes Caupolicanina, Diphaglossina, and Dissoglottina, which include eleven genera. The genus *Zikanapis* is distributed in warm temperate areas of the continent (Compagnucci 2006) and includes five species from Argentina (Urban and Moure 2001, Michener et al. 2003, Compagnucci 2006, Urban et al. 2012). The genus *Ptiloglossa* includes 30 or more species ranging from Argentina to Texas and Arizona in USA (Michener 2007). The genus *Cadeguala* contains two species distributed from the Coquimbo region in northern Chile and Bolivia to Valdivia in southern Chile, and Río Negro province, Argentina (Michener 2007, Montalva et al. 2011). Finally, *Diphaglossa*, with only one species endemic to Chile, occurs from 30° to 50° of latitude in the continent and in the Chiloé island (Michener 2007, Montalva and Ruz 2010, Montalva et al. 2011).

The behavior and nest architecture of all Diphaglossinae is rather homogeneous and contrasts markedly with that of other colletid subfamilies (Janvier 1955, Roberts 1971, Rozen 1984). Typically, nesting behavior consists of the excavation of a vertical main tunnel by a single female and horizontal laterals ending in a large, vertically oriented cell with fluid provisions. Two of the most interesting features of diphaglossine biology are the construction of curved cells and the retention of a cocoon-spinning behavior and larval morphological features related to this behavior (Rozen 1984, Michener 2007). Most studies about the biology and nest architecture of the subfamily come from North American (Linsley 1962, Linsley and Cazier 1970, Roberts 1971, Rozen 1984, Rozen and Rozen 1986) and Central American species (Otis et al. 1983, Roubik and Michener 1984, Wuellner and Jang 1996). The knowledge of South American taxa corresponds to brief mentions by Schrottky (1906, 1907) about the biology of *Ptiloglossa ducalis* Smith and *P. matutina* from Brazil and Paraguay and observations of *Cadeguala albopilosa* and *Diphaglossa gayi* from Chile carried out by Claude-Joseph (1926) and Janvier (1933, 1955). Later, Rozen (1984) reinterpreted some aspects of the biology of *Cadeguala* and *Diphaglossa* species. Other studies on *Cadeguala occidentalis* were conducted by Torchio and Burwell (1987) and more recently by Montalva et al. (2011). The biology of some species of the genus *Caupolicana* was studied by Claude-Joseph (1926), Janvier (1933, 1955), Michener (1966), and Genise et al. (1990). The nesting biology of species of *Willinkapis*, *Cadegualina*, *Mydrosoma* and *Mydrosomella* is unknown.

Fossil bee cells with a curved shape attributed to *Diphaglossinae* have been recently recorded from the Cenozoic of Patagonia, Argentina (Sarzett et al. 2010). Herein is described the nest architecture and some data on the nesting biology of five South American species of *Diphaglossinae*, to enable in the future a more accurate comparisons with the fossil examples and to extract paleoenvironmental inferences from them.

In this contribution, novel nesting and biological observations are provided for three Caupolicanini species: *Ptiloglossa matutina* (Schrottky, 1904), *Ptiloglossa tarsata* (Friese, 1900), and *Zikanapis tucumana* Moure (1945); and two *Diphaglossini* species: *Cadeguala albopilosa* (Spinola, 1851) and *Diphaglossa gayi* Spinola (1851).

Materials and methods

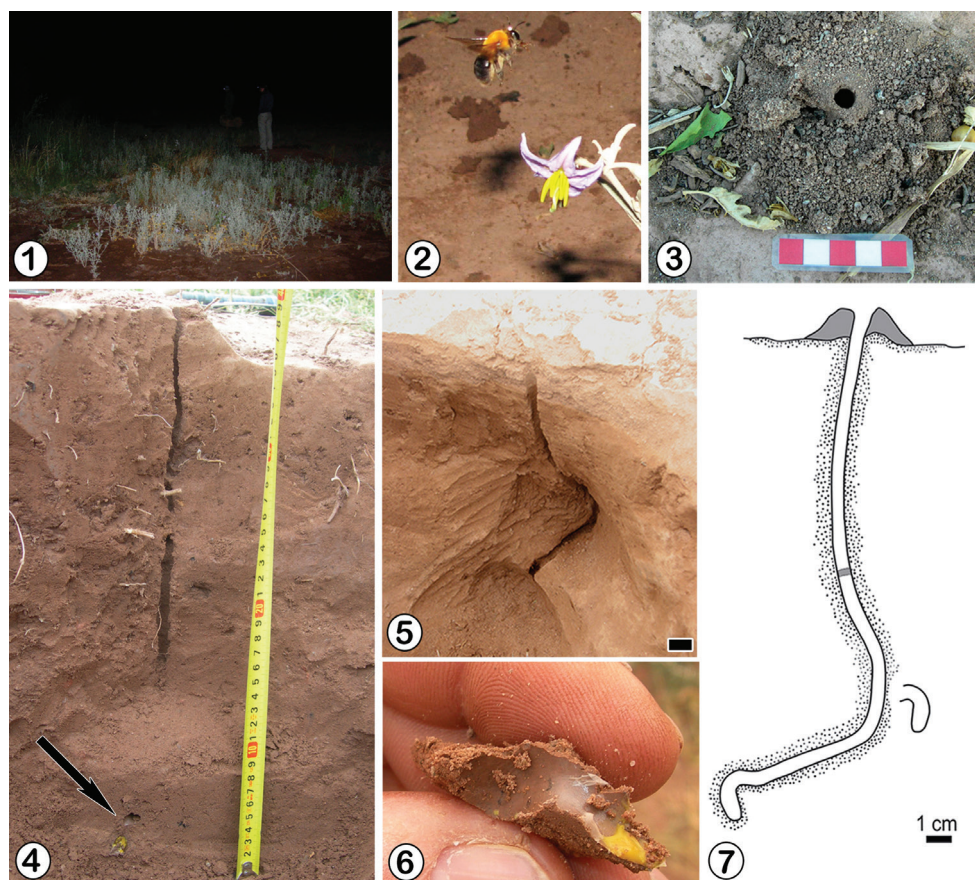
Excavations of nests were performed using plastic tubes to trace the tunnels downward while exposing a vertical section of the soil showing the whole structure of the nest when possible. The measures taken were: width and height of the tumulus, maximum diameter and length of the main tunnel and laterals, and number of cells. The length of the vertical part of the cell (from the bottom to the based of the neck), the maximum diameter of the cells, and the diameter of the neck were also measured. The larvae were boiled in water and maintained in alcohol 70%. Samples of soil surrounding nests were collected and carried to the laboratory for studying micromorphology. Collected bees were deposited in the entomological collection of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN-En), Buenos Aires (Argentina). Dr. Arturo Roig Alsina and Dr. Luis Compagnucci identified the bees. CT images were taken with Elscint SeleCT SP tomograph. 3D-reconstruction of one nest was prepared using computer program SLICER3 v.3.6.3, 2011. SEM images of cell operculum and cocoons were taken with a Philips XL30 SEM at the Museo Argentino de Ciencias Naturales.

Results

Zikanapis tucumana (Moure, 1945)

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

Localities and nesting sites. Observations on the biology and nest structure of this species were carried out during November 24th–30th, 2008 and through February 3rd–5th, 2009 at Vinchina (28°49.117'S, 68°11.433'W) and Anillaco (28°48.517'S, 66°55.867'W), both at La Rioja province, northwestern Argentina. The localities are included in xeric environments of the *Larrea*'s shrubland with a mean annual temperature (MAT) around 17° C and a mean annual precipitation (MAP) around 250 mm. Nest entrances were exposed in open areas and were never hidden by stones or shrubs. At Vinchina, nests formed an aggregation at the border of a formerly plowed open area frequently flooded by irrigation (Fig. 1). The ground surface was flat, compacted, and



Figures 1–7. *Zikanapis tucumana* (Moure, 1945). **1** General view of the nesting site at Vinchina (La Rioja province) before sunrise **2** Female of *Zikanapis tucumana* during foraging activity **3** Tumulus, turret and open nest entrance **4** Main and lateral tunnel showing one cell at the end (arrow) **5** General view of nest architecture, scale line: 1 cm **6** Remains of a cell with part of the provisions. Note the curvature of neck **7** Nest architecture.

devoid of rocks. The soil was composed principally of fine sand to silt bridged by sparse clayish material. The vegetation was sparse and basically comprising plants of *Solanum* sp. (10 to 20 cm tall) and grasses (Fig. 1). At Anillaco the nests were found at the surroundings of the CRILAR (Centro Regional de Investigaciones Científicas y Transferencia Tecnológica de Anillaco, La Rioja). The ground surface was flat, and the soil consisted of fine sand and numerous rocks of different sizes, which hindered excavation. The vegetation was sparse, consisting of some grasses, and scarce herbaceous plants, such as *Mirabilis ovata* and *Solanum* sp., some cacti, and trees (*Salix* sp. and *Prosopis* sp.). The nests at both localities were located among plants of *Solanum* sp. or near them.

Daily activity. *Zikanapis tucumana* was the only species in this study that clearly demonstrated dim-light, matinal foraging. At 04:30 am, still at night, the flower buds of *Solanum* sp. were still closed and no bee activity was observed. Females became

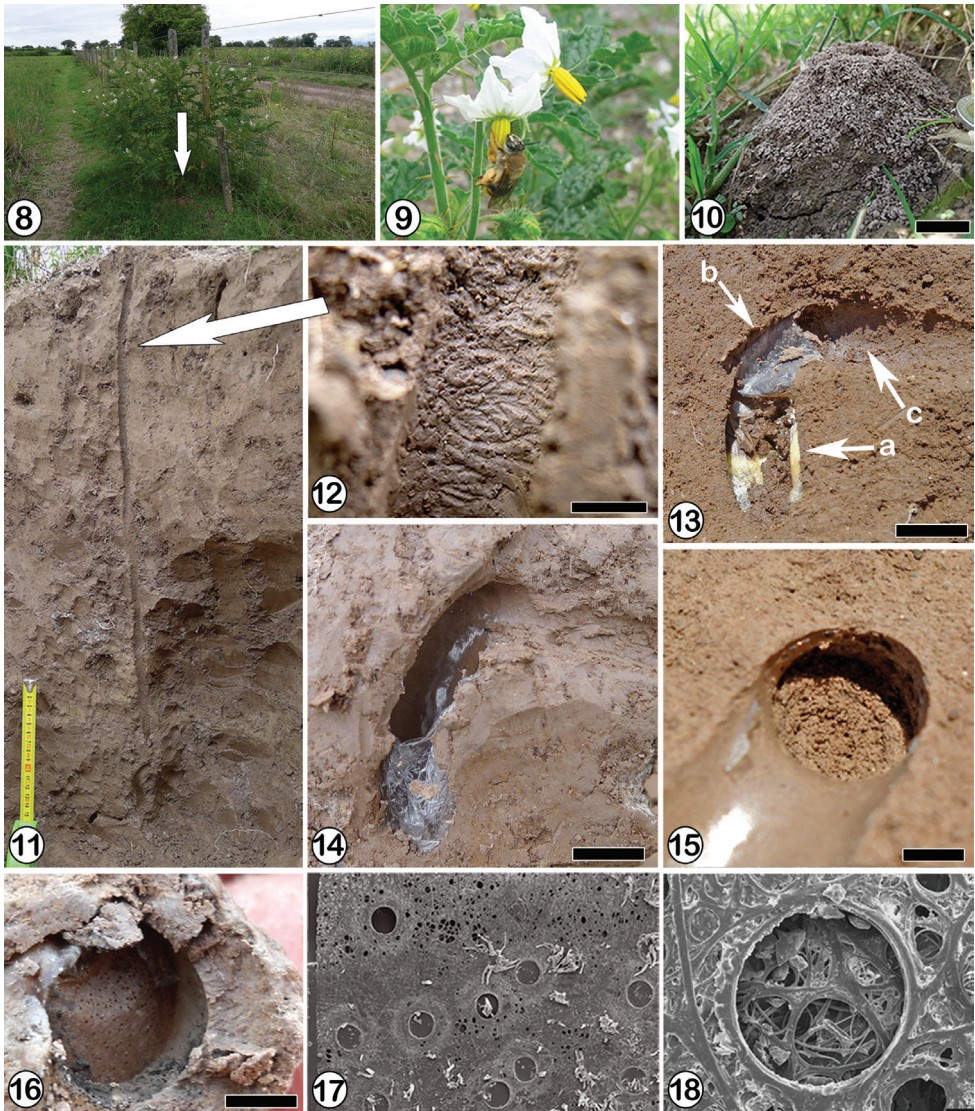
active around 05:00 am, still at night, when the flower buds of *Solanum* sp. began to open (Fig. 2). After 05:20 am, with twilight, females were completely active. With sunrise, around 07:00 am, the foraging activity of the bees ceased almost completely. The activity ended definitively around 07:30 with full daylight, when the entrance of nests were closed from inside with a soil plug. The number of foraging trips per bee during these 150 minutes for the five nests observed was around 8. The females with pollen remained inside nests about 2–3 minutes before leaving again. Their foraging trips lasted about 14 to 17 minutes. During November, males of *Z. tucumana* were also observed flying around nests 1–2 m above ground.

Description of nests. The entrance of nests was surrounded by a tumulus that ranged from 5 to 10 cm in diameter and 1 cm high (n: 6). Some nests also had a consolidated turret of 0.8 cm in maximum diameter and 1.7–2 cm high above the entrance (Fig. 3). The entrance, circular and 0.8 cm in diameter, was located at the center of the tumulus. The main tunnel, circular in cross section, was plugged with soil at approximately 10 cm from the entrance when the female was inside the nest. The main tunnel, 16–24 cm long (n: 9), was vertical and mostly straight at Vinchina but sinuous at Anillaco. Three nests had one cell and three other nests two cells. Cells, oriented vertically, were found at depths from 17 to 31 cm. They were disposed radially around the main tunnel, and connected with it by lateral tunnels 6–8 cm long. Lateral tunnels were subhorizontal or slightly inclined downwards and filled with soil when connected with closed cells. They ended in a raised, curved, entrance tunnel connected with the vertical portion of the cell (Figs 4, 5 and 7). Once lined and sealed, the distal part of the entrance tunnel became the curved neck of the cell. The vertical portion of the cells was 1.3–1.8 cm long and 0.9–1 cm in maximum diameter (n: 7). The neck was 0.7–0.8 cm in diameter (n: 2). The inner cell wall, including the neck, was smooth and lined with a whitish, semitransparent, cellophane-like material (Fig. 6). Two cells obtained during November from Vinchina contained eggs. The eggs, whitish, elongate, and slightly curved, were 2.3 mm long and 0.9 mm in maximum diameter. They were laid over the semiliquid provisions. The two cells collected during February at Anillaco contained an egg and a larva respectively. The larva, whitish, immobile and curved was located over a layer of remaining provisions at the base of the cell.

Ptiloglossa tarsata (Friese, 1900)

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

Locality and nesting site. The observations on the biology and nest structure were carried out during January 25th–30th; March 10th–16th, 2011; and January 4th–14th, 2012 at Paraje La Florida (25°0.817'S, 65°33.534'W), Salta province, Argentina. Two nests were excavated at this locality, which is in a transitional habitat between rain and dry forest with a MAT around 17 C° and a MAP between 700 to 800 mm (Baudino 1995). Two nests were found in a formerly plowed area in the surroundings of the establishment “La Florida”. The soil surface was flat and the cover was composed mostly

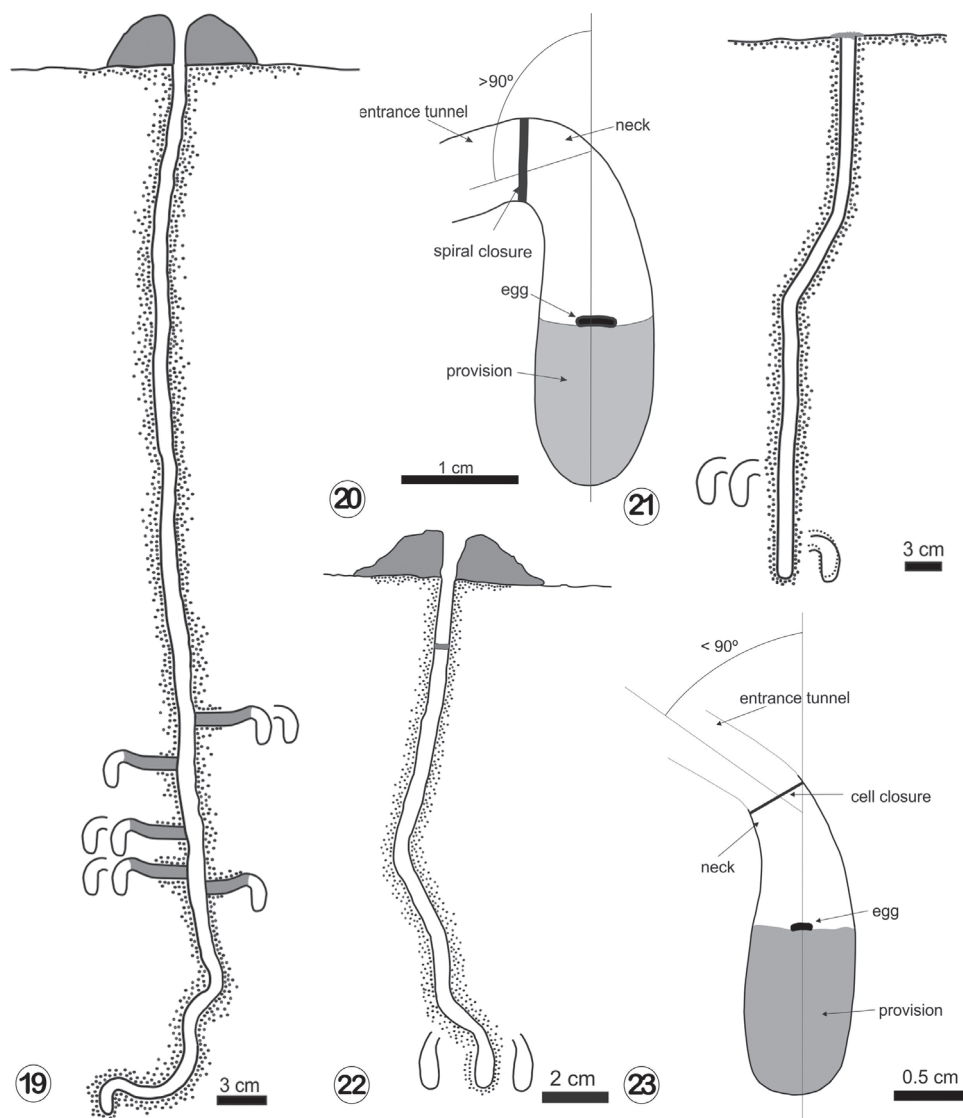


Figures 8–18. *Priloglossa tarsata* (Fries, 1900). **8** General view of the nesting site at “La Florida” (Salta province), the arrow indicates the location of the nest; **9** Female of *Priloglossa tarsata* foraging in a flower of *Solanum* sp. **10** Tumulus of unconsolidated soil, scale line: 1 cm **11** General view showing the nest architecture with a cell at the end of the main tunnel **12** Group of scratches probably produced by female’s mandibles. The arrow indicates their location in the main tunne; **13** (a) cell with cellophane-like lining and provisions, (b) neck and (c) entrance tunnel, scale line: 1 cm **14** One cell showing the cellophane-like lining on the wall, scale line: 1 cm **15** Spiral closure of one cell, scale line: 0.5 cm **16** Cocoon operculum with holes, scale line: 0.5 cm **17** Scanning electron micrograph of the cocoon operculum showing the fabric of silk threads with small circular holes, scale: 500 μ m **18** One circular hole surrounded by silk threads, scale: 50 μ m.

of grasses and plants of *Solanum* sp. and *Clematis* sp. (Fig. 8). The soil consisted of clayish to silty material and was devoid of rocks. The first nest was located next to a fence below a *Solanum* sp. plant, whereas the entrance of the second nest was partially covered by grasses.

Daily activity. The foraging activity started about 07:00 am, with full daylight, when females were observed visiting flowers of *Solanum* sp. (Fig. 9). One female made successive foraging trips, remaining inside the nest around 10 minutes after each trip. Foraging trips lasted around 20 minutes. This activity continued until 02:00 pm when the female closed the entrance from inside. The females were inside the main tunnels when the nests were excavated.

Description of nests. The entrance of the first nest, circular and 1 cm in diameter, was located at the center of a tumulus, 5.8 cm in maximum diameter and 4 cm high. The tumulus was composed of unconsolidated soil (Fig. 10). The main tunnel, vertical and slightly sinuous, was 40–61 cm long, and 1 cm in maximum diameter (Fig. 11). The inner surface of the main tunnel showed horizontal and densely grouped scratches 1–3 cm long and 0.2 cm wide. These scratches were probably made by the female mandibles (Fig. 12). The cells (n: 12), found at depths of 37–44 cm, were vertical and disposed radially around the main tunnel. Open cells were connected to the main tunnel by horizontal laterals, 5–7 cm long. Laterals ended in a raised, curved, entrance tunnel connecting with the vertical portion of the cell (Figs 11, 13c and 19). Once lined and sealed, the distal part of the entrance tunnel became the curved neck of the cell (Fig. 13b). Each lateral tunnel ended in one or two entrance tunnels connected with cells occurring at the same depth (Fig. 19). Entrance tunnels connected to closed cells were filled with soil (Fig. 19). The vertical portion of a cell was 1.9–2.0 cm long and 0.9–1 cm in maximum diameter (n: 12). The neck was 0.6–0.8 cm in diameter (n: 12). The inner walls of the cells and the neck were smooth and lined with a whitish, semitransparent cellophane-like material that extended up to the closure (Fig. 14). The cell closure, made with soil material, showed a spiral pattern composed of three coils on the inside (Fig. 15). Some cells contained a white wad of cotton-like material. The first nest excavated contained nine cells: three with eggs, three with young larvae, two with mature larvae, and one unfinished empty cell (Fig. 19). The second nest contained four cells, each with an egg. The eggs were whitish, cylindrical and lightly curved, 3 mm long and 0.8 mm wide. They lay on top of the semiliquid provisions (Fig. 20). Young larvae were also whitish, curved, and almost completely submerged in the provisions. Full grown larvae, more yellowish, were found inside cocoons made of a brown, thin, translucent, and slightly coriaceous material. The cocoon operculum is located at the base of the curved neck and consists of a circular disk of translucent, amber, semi-rigid material (Fig. 16). Below the operculum were two more disks of similar structure and composition to it. SEM observations indicated that these three disks were woven structures composed of crossed, coalescent silk threads of different thickness that leave small circular holes of 0.14–0.15 mm in diameter among them (Figs 17 and 18).



Figures 19–23. 19 Nest architecture of *Ptiloglossa tarsata* (Friese, 1900). 20 Cell with provisions and egg, cell neck, spiral closure, and entrance tunnel of *Ptiloglossa tarsata* 21 Nest architecture of *Ptiloglossa matutina* (Schrottky, 1904) 22 Nest architecture of *Cadequila albopilosa* (Spinola, 1851) 23 Cell with provisions and egg, cell neck, location of the cell closure and entrance tunnel of *Cadequila albopilosa*.

Ptiloglossa matutina (Schrottky, 1904)

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

Locality and nesting site. Observations were carried out during 2012 on March 11th and November 10th in the Karadya Bioreserve (25°52. 233'S, 53°58.167'W), near Andresito, Misiones province, Argentina (Fig. 24). The locality is included in the Upper

Paraná Atlantic Forest Region. The climate is warm subtropical, without a dry season, MAT around 20° C and a MAP around 2000 mm (Servicio Meteorológico Nacional, 2012). During March, 11th, males of *Ptiloglossa matutina* were collected, probably before their emergence, inside tunnels exposed in a soil vertical section. On November 10th, one nest was excavated in a patch of lateritic soil, altered by human activities, containing abundant roots, litter, and some rocks.

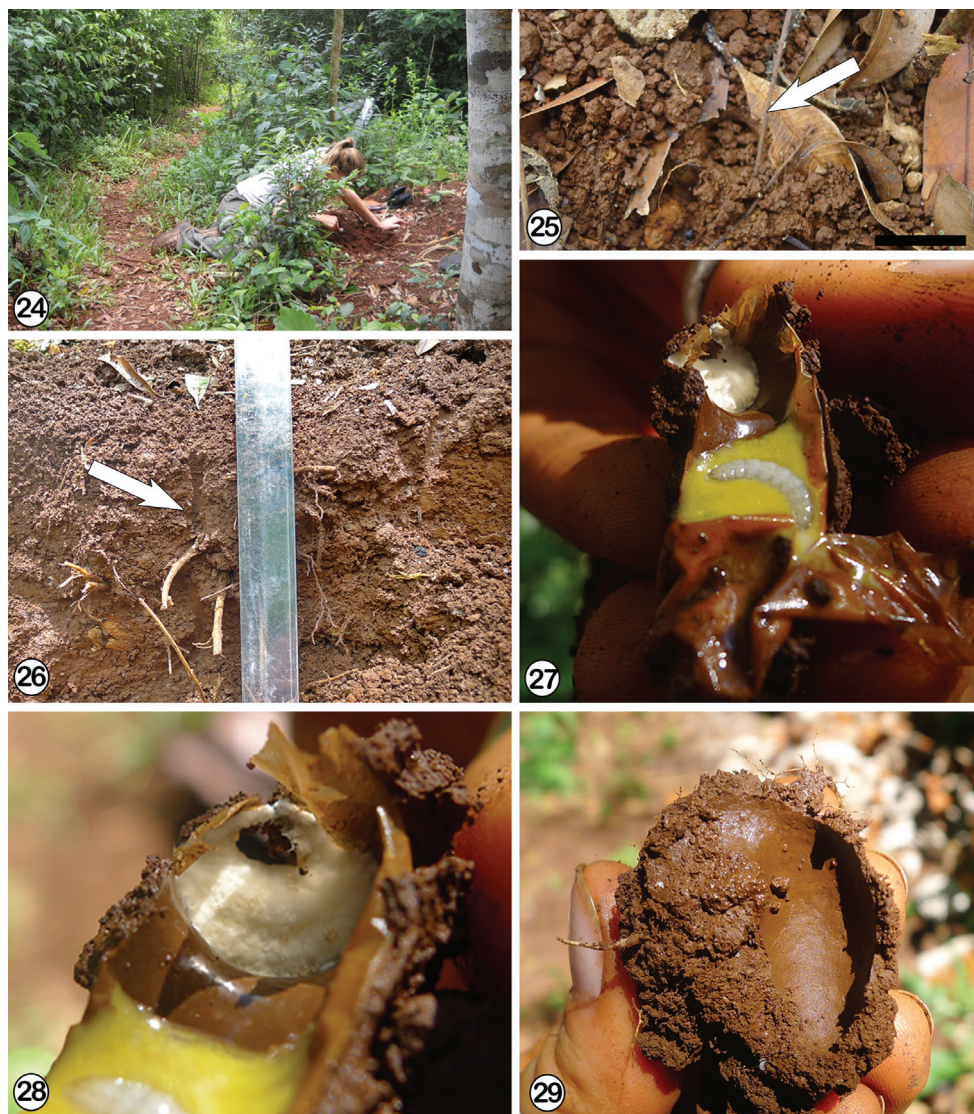
Daily activity. The nest was excavated at midday and the female was found inside the main tunnel. Some weeks ago, similar nests were observed with the entrance open and females flying close to them after 06:00 pm (Julián Baigorria, pers. comm.).

Description of the nest. The entrance was circular, 0.7 cm in diameter, without tumulus, and closed by a soil plug (Fig. 25). The main tunnel was circular in cross section, 25 cm long, nearly straight and slightly inclined downwards (Figs 21 and 26). It was 0.6–0.7 in maximum diameter. The nest contained four closed cells. One pair at a depth of 20 cm, were possibly connected to the main tunnel by a common tunnel filled with soil, 3 cm long. The other two cells, at a depth of 26 cm, were located at the other side of the main tunnel and also 3–4 cm of it (Fig. 26). The cells were vertical, rounded at the bottom and the neck was strongly curved (Figs 27 and 29). The vertical portion of the cell was 2.3 cm long and 1.3 cm in maximum diameter (n: 4). The neck was 0.8 cm in diameter (n: 4). The inner surface of cells and the neck were lined with a whitish semitransparent, cellophane-like material (Figs 27 and 28). Three cells contained eggs and one a young larva (Figs 27 and 28). The eggs, whitish, cylindrical and lightly curved, were 2.8 mm long and 0.4 mm wide. They laid on top of the yellow semiliquid provisions. The young larva was also whitish, curved, and almost submerged in the provisions. An earthen cell closure was not observed. Instead, a closure of white, cotton-like material that seems to be spirally arranged was observed (Fig. 28).

Cadeguala albopilosa (Spinola, 1851)

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

Locality and nesting site. The observations were carried out during November, 4th, 2009 and February, 17th, 2011 at Bahia Mansa (43°7.467'S, 71°39.95'W), Parque Nacional Los Alerces, Chubut province, Argentina (Fig. 30). On November, 9th, 2009 a nesting site was also found along the route 235 (43°26.142'S, 72°10.017'W), near Yelcho Lake, Palena province (Region de Los Lagos), Chile. The nests were studied at the xeric *Austrocedrus* forest of Bahia Mansa (Parque Nacional Los Alerces) with a MAT around 8 C° and MAP around 1200 mm. The nesting site at Bahia Mansa was slightly sloped and the soil subsurface contained a thin ash layer produced by the Chaiten eruption of May 2008 (Figs 30 and 32). The soil cover was composed of grasses and short herbs (Figs 30 and 31). The nests, around 20 and located among grasses, were distributed in an area of 5 × 7 m. The soil, containing many rocks, roots and grass rhizomes, was composed of silt to very fine sandy material. Nests of sweat bees, aestivation chambers of earthworms, and feeding chambers of cicadas were also present. The Chil-



Figures 24–29. *Priloglossa matutina* (Schrottky, 1904). **24** General view of the nesting site at Reserva Karadya, Andresito (Misiones province) **25** Nest entrance closed by a plug of soil (arrow), scale line: 1 cm **26** Soil with roots, litter, some rocks, and remains of the main tunnel (arrow) **27** Cell showing the larva partially submerged in provisions, cellophane lining, and the wad cotton-like material attached the cell closure, scale line: 0.5 cm **28** Detail of the cell closure with the cotton-like material **29** Cell and neck wall with the lining removed. Note the high curvature.

can locality along route 235 was a disturbed forest clearing composed of a dense grass cover. The area had some slopes with large rocks and trunks over the surface. Around 12 nests were distributed in an area of 6×1.5 m almost horizontal and partially covered by grasses. At both localities, closest nests were separated each other by 2–4 cm.

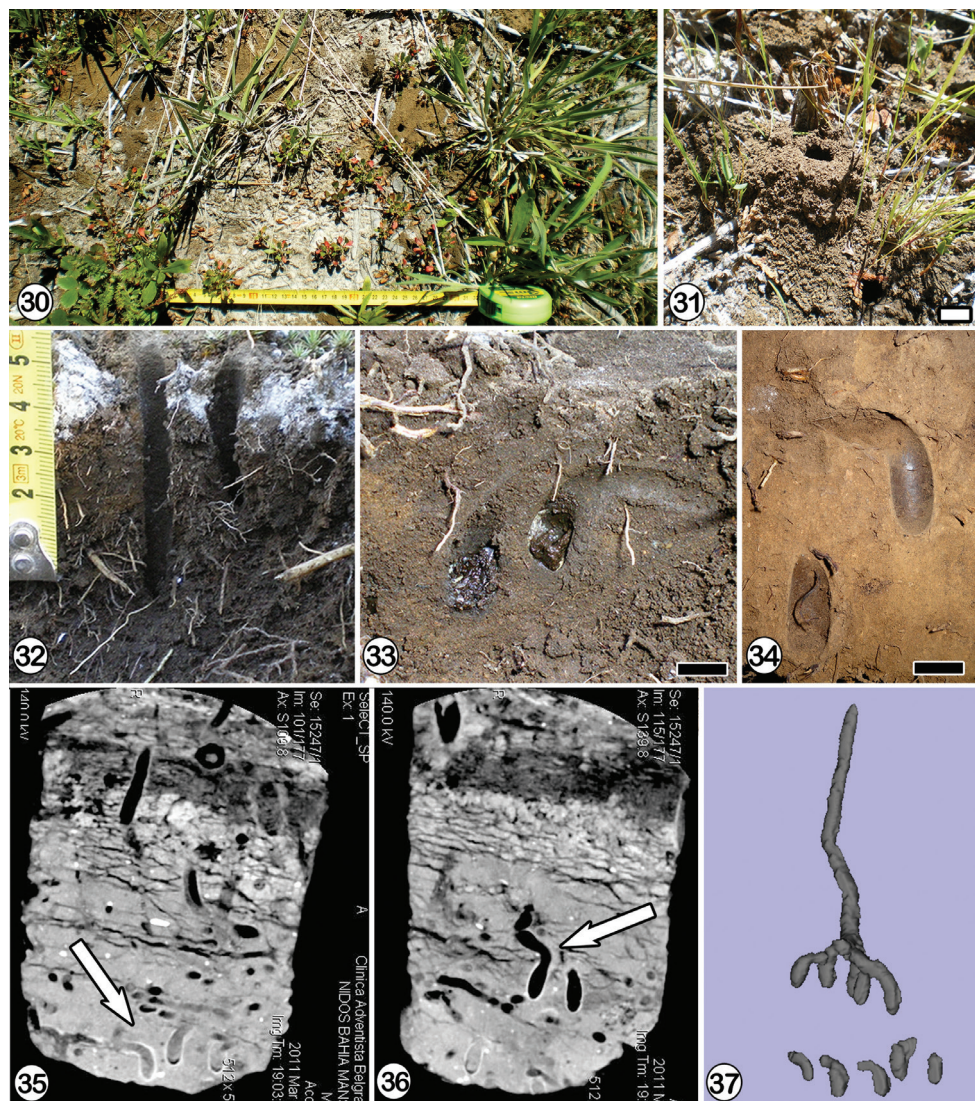
Daily activity. Bees were observed removing soil from the nests during November, 4th 2009 from 09:00 am to 05:00 pm. In the second field trip, during February 2011, no activity was observed.

Description of nests. Three nests were excavated during November 2009 when bees were active. The entrance, circular, 0.5 cm in maximum diameter was at the center of a large unconsolidated tumulus (Fig. 31). It was composed of a mixture of soil material and ash, 3–3.5 cm in maximum diameter and 2.5 cm high. During February 2011, when no activity of bees was observed, a piece of soil from the nesting site was extracted and taken to the laboratory for examination with a tomograph. The tomographic images provided a more precise picture of the nests and cells (Figs 35–37). The main tunnel, circular in cross section, was plugged with soil 2–3 cm below the entrance and descended vertically, straight or more sinuously among rocks (Fig. 22). It was 18–20 cm long and 0.5 cm in maximum diameter. The cells, found at a depth of 18–20 cm, were vertical and connected to the main tunnel by lateral ones, which were 2.5–3 cm long and mainly horizontal or gently curved (Fig. 23). They were filled with soil when connected to closed cells. At the distal end, lateral tunnels curved downwards, 90° or less, and were connected with the vertical portion of the cell. Once lined and sealed, the more distal curved part of the lateral tunnel connected to the cell became its curved neck (Figs 33 and 34). Each lateral tunnel ended in one or two cells occurring at the same depth (Fig. 22). The number of cells per nest ranged from 2 to 4 in the studied nests (n: 4). The vertical portion of the cells was 1.3–1.6 cm long and 0.6–0.9 cm in maximum diameter (n: 12). The neck was 0.5 cm in diameter (n: 5). The inner walls of the cells and the neck were smooth and lined with a whitish semitransparent cellophane-like material. Cells studied on November contained eggs laying on the surface of the semiliquid provisions. The eggs whitish, cylindrical and slightly curved were 2 mm long and 0.7 mm wide. Cells studied on February contained white pupae inside their cocoons. The cocoons were composed of a brown, translucent, thin, and slightly coriaceous material. The cocoon operculum, located at the base of the curved neck, was composed of one translucent, amber, and semi-rigid circular disk, 5.0–5.5 mm in diameter (n: 2). This disk was a woven structure composed of crossed silk threads of different thickness that leave small circular holes. Below the operculum there was a net of silk threads loosely arranged, similar to the filter-like structure observed by Rozen (1984) in the cocoon of various species of *Diphaglossinae*. Beneath the filter-like structure there was another disk with a similar microstructure to the operculum, but dome-shaped. It was called the ceiling of the pupation chamber by Rozen (1984).

Diphaglossa gayi Spinola, 1851

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

Localities and nesting sites. The observations were carried out during November 8th, 2009 and February 10th, 2011 beside the Río Negro Bridge (42°57.433'S, 72°39.233'W) and during November 9th, 2009 and February, 15th, 2011 at Lonconao (43°13.007'S,



Figures 30–37. *Cadeguala albopilosa* (Spinola, 1851). **30** General view of the nest site at Bahia Mansa, Parque Nacional Los Alerces (Chubut province) **31** tumulus of unconsolidated soil **32** two main tunnels and longitudinal view of the soil containing a thin ash layer **33** a pair of cells with provisions, necks and lateral tunnels, scale line: 1 cm **34** remains of cells of other nest, scale line: 1 cm **35–36** tomography images of one block of soil containing *Cadeguala albopilosa* nests, arrows indicate cells **37** 3D-reconstruction of one nest and isolate cells.

71°55.143'W), both localities from the Palena province (Region de Los Lagos, Chile). The nesting sites occur in the glades of hygrophilous evergreen forests with a MAT around 11° C and MAP around 2500–3000 mm. Two nests were excavated. The first nest was located in a steep slope in a farm beside the Río Negro Bridge (Fig. 38), where-



Figures 38–43. *Diphaglossa gayi* Spinola, 1851. **38** General view of the nesting site beside the Río Negro Bridge, Chile **39** general view of nesting site at Lonconao, Chile **40** tumulus of soil pellets and open entrance **41** main tunnel **42** nest architecture **43** cell, neck with lining, and egg laying on provisions.

as the second was excavated in a low vertical section of the soil in another farm at Lonconao (Fig. 39). At both localities, the soil, composed of silty to very fine sandy material and devoid of rocks, contained grass rhizomes, some roots, and earthworm burrows. The soil cover consisted of a combination of dense grasses and dicots (Fig. 38), and the subsurface contained a thin ash layer produced by the Chaiten eruption of May 2008.

Daily activity. On November 8th, 2009 the first nest was found around 06:00 pm and the female was observed entering the nest with pollen around 07:00 pm. On November 9th, 2009 the second nest was found also around 06:00 pm and the female was inside the main tunnel.

Description of nests. The Rio Negro nest showed an open circular entrance, 0.5 cm in diameter, which was surrounded by an eccentric tumulus, roughly 4.6 cm wide and 5.2 cm long. The tumulus was composed of soil pellets, probably of the recently deposited subsurface ash layer, which were paler than the soil surface (Fig. 40). The Lonconao nest was located in a vertical cut, thus the entrance, 0.7 in diameter, lacked a tumulus. Both nests share the same general structure. The main tunnel, circular in cross section, 32–38 cm long, was nearly straight and slightly inclined downwards, ending in a vertical segment 8 cm long (Figs 41 and 42). Its maximum diameter was 0.7–1.0 cm. Each nest contained four closed cells arranged in two pairs, one pair near the middle portion of the main tunnel, and the other near the end. It is possible that both cells were connected to the main tunnel by a common lateral, filled with soil when the nest was excavated (Fig. 42). The cells were vertical, rounded at the bottom, and the neck was strongly curved (Figs 42 and 43). The vertical portion of the cells was 2 cm long and 1 cm in maximum diameter (n: 8). The neck was 0.7 cm in diameter. The inner surface of cells and the neck was lined with a whitish semitransparent, cellophane-like material. The cells in both nests contained one egg laying on top of the semiliquid provisions. The cell closure was not observed.

Discussion

The five species studied herein share many ecological preferences, behaviors and features of nest architecture with each other, and with other Diphaglossinae, although some significant differences were also found during this study.

The broad ecological preferences of Diphaglossinae differ greatly among species as shown by its extended geographical distribution (Rozen 1984). Herein are provided values of mean annual temperature (MAT) and mean annual precipitation (MAP), along with vegetation types to understand more precisely this environmental diversity. The southern species, *Diphaglossa gayi* was found in glades of the hygrophilous evergreen forest (MAT = 11° C and MAP = 2500–3000 mm), whereas *Cadeguala albopilosa* nested in the xeric *Austrocedrus* forest (MAT = 8° C and MAP around 1200 mm). The northern species nested besides cultivated fields under warmer conditions (with a MAT between 17° C to 20° C at these localities). *Ptiloglossa tarsata* in an environment that originally corresponded to the more humid (MAP = 700–800 mm) transition between the drier Chaco and the Yungas and *Ptiloglossa matutina* habits the humid Paranaense Atlantic forest (MAP = 2000–2300 mm), while *Zikanapis tucumana* in a more xeric environment (MAP = 250 mm) of the *Larrea* shrubland.

Diphaglossinae were considered traditionally as dim-light bees (Rozen 1984, Michener 2007). However, among the species studied herein, only *Zikanapis tucuma-*

na and possibly *Ptiloglossa matutina* showed dim-light foraging. Wcislo and Tierney (2009) distinguished the following three types of dim-light foraging in bees: (1) matinal, if bees are active before sunrise; (2) vespertine, if bees are active in post-sunset twilight; and (3) crepuscular, if bees are active during both, evening and morning twilight. Females of *Zikanapis tucumana* showed matinal habits, starting the activity even at night (05:00 am), when the flowers of *Solanum* sp. began to open before twilight, which occurred at 05:20 am. Probably, during those 20 minutes there were some twilight, imperceptible for the human eye, which allows bees to fly, and the exposition of the flowers of *Solanum* sp. was synchronized with the start of flights. Females of *Ptiloglossa matutina* were observed flying after 06:00 pm (Julián Baigorria, pers. comm.), which indicates that this species may be vespertine. However, Schrottky (1907) captured *P. matutina* flying at 04:00 am in Paraguay. The observations presented herein indicate that *Ptiloglossa tarsata* is diurnal, starting their activity in the morning and continuing with foraging until 02:00 pm. After 02:00 pm the nests remained open with the female inside. A similar daily activity was recorded for *Cadeguala albopilosa*, which was active from the morning to 07:00 pm. *Diphaglossa gayi* was observed active after 06:00 pm with full sunlight. It was impossible to determine the previous daily activity because nests were found after 06:00 pm.

The proposed advantages of collecting pollen during twilight include: 1) reduction of competition for resources, 2) reduction of predators 3) reduction of nest parasites (e.g. Bohart and Youssef 1976, Roubik 1989, Wcislo et al. 2004, Kelber et al. 2005). In addition, dim-light bees are usually active at cooler temperatures during matinal or vespertine hours and this may reduce the exposure to unfavorable thermal conditions, mainly in those species that lives in xeric habits, montane regions, or higher latitudes (Hurd and Linsley 1970, Kelber et al. 2005, Wcislo and Tierney 2009). Among the three species described herein without dim-light foraging activity, *Diphaglossa gayi* and *Cadeguala albopilosa* inhabits cold-temperate and humid environments, while *Ptiloglossa tarsata* is found under warm and humid conditions. These species are active during the day when competition for food is higher. Accordingly, these species of Diphaglossinae seem to be not significantly affected by the factors mentioned previously. The species with dim-light foraging behavior, *Zikanapis tucumana* and *Ptiloglossa matutina*, inhabits environments as warm as that of *Ptiloglossa tarsata* suggesting that 1) this factor is not responsible for its daily activity, or 2) that *Zikanapis tucumana* and *Ptiloglossa matutina* may be more sensible to temperature than *Ptiloglossa tarsata*, or 3) that the influence of the xeric environment favors the matinal behavior of *Zikanapis tucumana*. Alternatively, the advantage of *Zikanapis tucumana* and *Ptiloglossa matutina* to nest during dim-light hours may be to reduce competitors, predators, or nest parasites.

Some aspects of the nest architecture, as the curvature of entrance tunnels and cell necks, were proposed as advantages to face floodings. For example, Roberts (1971) proposed for *Ptiloglossa guinnae* Roberts nests that the lateral tunnel rose just before the cell neck probably to prevent the entrance of rain water into the cell being provisioned by the female. However, it is difficult to corroborate this hypothesis for all the

species described herein. In nests of *Zikanapis tucumana*, *Ptiloglossa tarsata* and *Ptiloglossa matutina* the end of the lateral tunnels raised and then curved downwards (Figs 7, 19 and 21). The same can be inferred from the strongly curved neck of *Diphaglossa gayi* cells. In contrast, the short lateral tunnels of *Cadeguala albopilosa* nests, curved downwards without raising anteriorly (Fig. 23). Roberts' hypothesis (1971) could be corroborated only for *Diphaglossa gayi*, which nests under MAP around 2500 mm and *Ptiloglossa matutina*, which nests under MAP around 2300 mm, whereas *Cadeguala albopilosa*, which nests under MAP of 1200 mm lacks the raising of the entrance tunnels. In contrast, *Ptiloglossa tarsata* and *Zikanapis tucumana*, which nest under more xeric conditions, 750 mm and 250 mm respectively, show the raised tunnels. Beyond general xeric environmental conditions of the area, *Zikanapis tucumana* nested in a soil frequently flooded by irrigation suggesting that particular conditions of nesting sites may be also involved as a selective agent for this behavior.

There is a tendency of Diphaglossinae species to nest in aggregations of few to many bees (Rozen 1984). These aggregations can persist for more than one generation (Rozen 1984, Torchio and Burwell 1987, Montalva et al. 2011). Among the five species studied here only *Cadeguala albopilosa* and, to a lesser extent, *Zikanapis tucumana* showed aggregations. The nests of *Ptiloglossa tarsata*, *Ptiloglossa matutina*, and *Diphaglossa gayi* were found isolated.

A tumulus, mostly concentric, surrounded the nest entrances in species studied herein that nested in horizontal surfaces as *Zikanapis tucumana*, *Ptiloglossa tarsata*, and *Cadeguala albopilosa*. *Zikanapis tucumana* was the only species that constructed a consolidate tumulus, also observed in *Ptiloglossa arizonensis* Timberlake by Rozen (1984). The nest of *Ptiloglossa matutina* lacked this typical tumulus probably removed by the abundant precipitations. In *Diphaglossa gayi* that nested in sloping surfaces, the tumulus was eccentric or absent in vertical sections of soil. Similar conditions were observed in some species of *Caupolicana* and *Cadeguala* nesting in sloping surfaces (Rozen 1984).

The nest architecture of the species studied here was mostly similar to other Diphaglossinae described in the literature. The main and lateral tunnels were unlined and lack any particular surface texture in all species studied, with the exception of the main tunnel in nests of *Ptiloglossa tarsata*, which showed transverse scratches, probably produced by the female mandibles (Fig. 12).

Depending on the species studied herein, from the main tunnel arose 1 to 9 horizontal lateral tunnels connected with one cell as in *Zikanapis tucumana* or two cells as in *Ptiloglossa tarsata*, *Ptiloglossa matutina*, *Cadeguala albopilosa*, and probably *Diphaglossa gayi*. The presence of two cells connected to the same lateral is a novel feature for Diphaglossinae. In the five species studied here, the lateral tunnels were filled with soil when connected to closed cells. Janvier (1933) mentioned that the lateral tunnels in the nests of *Diphaglossa gayi* were unfilled. However, the closed cells of both nests of *D. gayi* recorded herein were not connected by an open lateral to the main tunnel.

The cell earthen closure of Diphaglossinae nests appears to be similar in all species, as in many bees, showing internally a spiral design (Rozen 1984, Almeida 2008).

This is consistent with the closure found in *Ptiloglossa tarsata* showing three coarse coils (Fig. 15). Similar closures were previously recorded also in *P. arizonensis*, *P. fulvopilosa* Cameron, *Caupolicana gaullei* Vachal, *C. albiventris* Friese, *Cadeguala occidentalis* (Haliday) and *C. albopilosa* (Rozen, 1984). In contrast, Janvier (1933) indicated that *Diphaglossa gayi* apparently lacks an earthen closure, and the same is true for *P. guinnae* Roberts (1971) and *Crawfordapis luctuosa* (Smith) (Rozen 1984). Roberts (1971) suggested that in *P. guinnae* Roberts the lack of a closure could have appeared to facilitate the elimination of CO₂ produced by fermentation of provisions. Similarly in the cells of *Zikanapis tucumana*, *Ptiloglossa matutina*, *Diphaglossa gayi* and *Cadeguala albopilosa* it was impossible to detect an earthen closure. Other character related to the closure was observed in *Ptiloglossa tarsata* and *P. matutina*, whose cells show a wad of cotton-like material of unknown origin (Fig. 28). The same structure was observed by Rozen (1984) in cells of *Ptiloglossa arizonensis* Timberlake. It seems that the presence of this material may be exclusive of *Ptiloglossa* species.

Rozen (1984) indicated that the most outstanding character of all nests of Diphaglossinae is the shape of their cells. These cells are unique among bees in having a curved neck. The shape of diphaglossine brood cells was discussed by Rozen (1984), who described two types of curved cells. Raised tunnels and more curved cells (90° or more degrees of curvature) were found in *Ptiloglossa tarsata*, *P. matutina*, *Zikanapis tucumana*, and *Diphaglossa gayi*, as previously described by Rozen (1984) for other species of *Ptiloglossa* and species of *Crawfordapis*. In contrast, in *Cadeguala albopilosa* (Fig. 23) the lateral tunnel is not raised and accordingly the curvature of cell neck is lesser than 90°, as in species of *Cadeguala* and *Caupolicana* (Rozen 1984). CT images were useful to confirm the curvature of cell necks of *Cadeguala albopilosa* observed in the field (Figs 35–37).

The Diphaglossinae are the only group among the Colletidae whose larvae spin cocoons (Rozen 1984, Michener 2007). Rozen (1984) described in great detail the cocoon structure of several species of the genus *Ptiloglossa* and *Crawfordapis luctuosa* (Smith), and redescribed that of *Cadeguala albopilosa*, previously described by Claude-Joseph (1926). Among the five species studied here, only the cocoons of *Ptiloglossa tarsata* and *Cadeguala albopilosa* were found. The cocoons of both species were similar to those described by Rozen (1984). Their walls were made of a brown, thin, translucent, and slightly coriaceous material. Cells with cocoons are closed by an operculum made of a disk of silk threads, whose fabric is different among species (Rozen 1984). Below the operculum it was described a structure named filter, composed of a net of silk threads that probably enables gas exchange (Roberts 1971, Rozen 1984, Almeida 2008). Immediately beneath the filter it was described another disk, similar in composition and structure to the operculum, but dome-shaped, which is called the ceiling (Rozen 1984). These structures were recognized only in cocoons of *Cadeguala albopilosa*. The observations in one cocoon of *Ptiloglossa tarsata* revealed the presence of one operculum and below it, two other circular disks of similar composition and fabric, which probably had the same function of the filter and the ceiling, but different microstructure.

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A new brachypterous species of *Heterospilus* Haliday (Braconidae, Doryctinae) from the Neotropical Region

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Abstract

A new species, *Heterospilus michaeli* Kula, from the Neotropical Region is described and differentiated from all other New World species of Doryctinae with brachypterous or apterous individuals. It is the first species of *Heterospilus* Haliday in the Neotropical Region known to exhibit brachyptery and the fourth described brachypterous species of *Heterospilus* worldwide. Errors and omissions in a recently published article on brachypterous and apterous doryctines in the New World are corrected.

Keywords

Apterous, aptery, brachyptery, Neotropical, parasitoid, taxonomy

Introduction

Kula (2011) described *Heterospilus belokobylskiji* Kula and *Heterospilus vincenti* Kula, the first New World species of *Heterospilus* Haliday known to exhibit either brachyptery or aptery. There were also two brachypterous species of *Heterospilus* known from the Palearctic Region, *Heterospilus brachyptera* (Jakimavicius, 1968) and *Heterospilus he-*

mipterus (Thomson, 1892), at that time. Belokobylskij and Kula (2012) synonymized the two aforementioned species. A new brachypterous species of *Heterospilus* from the Neotropical Region was discovered following the publication of Kula (2011). The new species is described herein, increasing the total number of brachypterous species of *Heterospilus* worldwide to four.

Belokobylskij and Kula (2012) provided thorough background on brachyptery and aptery in Braconidae. Kula (2011) discussed the New World doryctines that exhibit brachyptery and aptery and provided a table indicating wing conditions for each species. However, errors and omissions were discovered in the discussion and table after Kula (2011) was published; they are corrected in this article. Additionally, research carried out as part of Belokobylskij and Kula (2012) elucidated wing conditions previously unknown or not reported for certain species in table 1 of Kula (2011). Therefore, the table is updated and included in this article.

Materials and methods

Specimens of the new species described herein were borrowed from the University of Wyoming Insect Museum, Laramie, U.S.A. (ESUW). They were examined as in Kula (2009), and their placement in *Heterospilus* was determined through reference to Marsh (2002), Marsh (1997), and Seltmann and Sharkey (2007). Specimens of the new species were compared with the holotypes of *H. belokobylskiji* and *H. vincenti*, as well as the paratype of each species (all in the Smithsonian Institution National Museum of Natural History, Washington, DC, U.S.A. [USNM]). The new species was differentiated from *H. hemipterus* using data in Belokobylskij and Kula (2012). Additionally, specimens of all New World species of Doryctinae with brachypterous or apterous individuals except *Oroceguera andersoni* Seltmann & Sharkey and *Psenobolus triangularis* van Achterberg & Marsh were examined as part of research reported in Kula (2011). See Kula (2011) for details on the numbers and kinds of specimens examined. *Ecphylus caudatus*, known from the Palearctic and Oriental regions, was mistakenly included in the list of specimens examined in Kula (2011) instead of the Nearctic species *Ecphylus arcuatus* Muesebeck. However, the holotype and six paratypes of *E. arcuatus* (all in the USNM) were examined as part of that research. Additionally, the author does not consider *Ecphylopsis swezeyi* Beardsley a species of *Heterospilus* as suggested in Marsh (2002) based on examination of that species as discussed in Kula (2011).

Terminology for morphological features, setation, and surface sculpture follows references listed in the materials and methods of Kula (2011). Wing conditions in Table 1 are characterized as brachypterous, micropterous, or apterous as in Belokobylskij and Kula (2012). Measurements, abbreviations, and imaging are as in Kula (2011). The maxillary and labial palpi were obscured in both female specimens of the new species. Therefore, data on penultimate maxillary palpomere length:flagellomere 1 length ratio are not presented in the description of the female.

Table 1. Species of Doryctinae in the New World, excluding ypsistocerines, that exhibit brachyptery, microptery, or aptery.

Species	♀ wing condition	♂ wing condition
<i>Aptenobracon formicoides</i> Marsh	apterous	apterous
<i>Ecphylopsis costaricensis</i> Marsh	micropterous	micropterous
<i>Ecphylus arcuatus</i>	macropterous	micropterous
<i>Ecphylus lepturgi</i> Rohwer	apterous macropterous	apterous macropterous
<i>Ecphylus pacificus</i> Marsh	apterous macropterous	apterous
<i>Ecphylus schwarzii</i> (Ashmead)	apterous macropterous	apterous
<i>Heterospilus belokobylskiji</i> Kula	brachypterous	brachypterous
<i>Heterospilus michaeli</i> Kula, new species	brachypterous	brachypterous
<i>Heterospilus vincenti</i> Kula	brachypterous	brachypterous
<i>Oroceguera andersoni</i> Seltmann and Sharkey	apterous	unknown
<i>Pambolidea yuma</i> Ashmead	micropterous brachypterous macropterous	apterous micropterous
<i>Psenobolus ficarius</i> Ramirez and Marsh	macropterous	brachypterous
<i>Psenobolus parapygmaeus</i> Ramirez and Marsh	macropterous	brachypterous
<i>Psenobolus triangularis</i> van Achterberg and Marsh	unknown	brachypterous

Results and discussion

Heterospilus michaeli Kula, new species can be differentiated from some brachypterous or apterous doryctines in the New World (excluding ypsistocerines) by the condition of the wings (Table 1). Additionally, *H. michaeli* can be differentiated from all brachypterous or apterous New World species of Doryctinae using the same morphological features Kula (2011) used to differentiate *H. belokobylskiji* and *H. vincenti* from those species. *Ecphylus caudatus* was mistakenly included in both table 1 and the discussion of diagnostic features in Kula (2011) instead of *E. arcuatus*. However, as was reported under the name *E. caudatus* in Kula (2011), the metacoxa is round at the base in *E. arcuatus*; it has a tubercle at the base in *H. michaeli*.

Taxonomy

Heterospilus michaeli Kula, sp. n.

<http://zoobank.org/34A1D33D-49A6-4914-8FBC-619D6C47EC84>

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

Figs 1–2

Holotype female. Top label (white; partially handwritten, partially typewritten) = “Costa Rica: Guanacaste [:] Santa Rosa National Pk. [:] 300m, Malaise, Ian Gould

[sic] [:] 14.vi 1986". Second label (white; partially handwritten, partially typewritten) = "Bosque Humedo [:] mature dry forest [:] high proportion [:] evergreen species [:] Sun." Third label (white; typewritten) = "BH-11-0 [:] 14. Vi. 86" (ESUW).

Paratypes. 1 ♀ 9 ♂ same data as holotype (6 ♂ ESUW, 1 ♀ 3 ♂ USNM); 1 ♂ Costa Rica: Guanacaste Santa Rosa Natl. Park 300m, ex. [sic] Malaise trap Site #: Dates: 24.v–14.vi 1986 I.D. Gauld & D. Janzen [H] open regenerating woodland <10 years old [C] more or less fully shaded as possible (ESUW).

Diagnosis. The vertex is entirely strigate in *H. michaeli*; it is smooth except a pair of small strigulate areas posterolaterad the lateral ocelli in *H. belokobylskiji* and entirely coriaceous in *H. vincenti*. The frons is entirely strigate in *H. michaeli*; it is entirely coriaceous in *H. vincenti*. The head is yellow in *H. michaeli* (Fig. 1); it is brown in *H. belokobylskiji* (Kula 2011: figs 1–2) and reddish brown in *H. hemipterus* (Belokobylskij and Kula 2011: fig. 110). The forewing stigma is distinct in *H. belokobylskiji* (Kula 2011: fig. 2) and *H. hemipterus* (Belokobylskij and Kula 2011: fig. 110); it is indistinct in *H. michaeli*, with only thickened sclerotization at the wing apex. The hind wing stigma is located slightly apicad the middle of the wing in *H. michaeli* (Fig. 2); it is slightly basad the middle of the wing in *H. belokobylskiji* (Kula 2011: fig. 2) and at the wing apex in *H. vincenti* (Kula 2011: fig. 4). The flagellum is entirely yellow in *H. michaeli* females, and in males it transitions from yellow proximally to whitish yellow or white distally. The flagellum transitions from yellow proximally to brown distally in *H. belokobylskiji*, *H. hemipterus*, and *H. vincenti* females and males.

Description. Female (Fig. 1).

Body length. 2.10–2.51 mm.

Head. HL 0.72–0.74× HW, HW 1.09–1.11× TW, FW 1.73–1.85× FH, EL 0.77–0.83× EH, MSH 0.72× EH, F1L 0.87–0.94× F2L; antenna with 20 flagello-meres; mandible with two teeth, tooth closest to labiomaxillary complex shorter than other tooth, setiferous; malar space smooth, setiferous, malar suture absent; clypeus with roughly apical 1/3 setiferous and basal 2/3 glabrous; face entirely smooth or smooth mesally and rugulose laterally, glabrous mesally and setiferous laterally; frons strigulate, glabrous except one to two setae along margin of eye; vertex strigulate, setiferous; ocelli present and small but slightly larger than in *H. belokobylskiji* and *H. vincenti*; gena smooth with a few strigae posteriorly, setiferous; occiput smooth, glabrous except a few setae ventrally on both sides of head.

Mesosoma. ML 3.07–3.33× MW, ML 1.93–2.06× MH, MW 0.62–0.63× MH, SSL 0.40–0.45× SSW; pronotal collar with transverse carina or transverse rugosities, anterior portion rugulose and posterior portion crenulate, collar setiferous anteriorly and mesally, pronope absent, lateral portion of pronotum rugulose to rugose except pronotal groove crenulate, roughly setiferous along margins and glabrous mesally; notauli complete and meeting posteromesally, crenulate-rugose; mesoscutal midpit absent; mesoscutum (excluding lateral margin and notauli) coriaceous, setiferous along margins and notauli; scutellar sulcus with median longitudinal carina only or median longitudinal carina and pair of crenulae adjacent to carina; scutellar disc weakly coriaceous, setiferous along lateral and posterior margins; propodeum strongly carinate,



Figures 1–2. Lateral habitus images of *Heterospilus michaeli*, scale bars = 1.00 mm. **1** Holotype female
2 Paratype male.

setiferous, carinae forming hastate areola mesally, sculpture within areola areolate-rugose, basal 1/2 of propodeum divided into median and lateral areas by dorsal lateral carinae, median area coriaceous and lateral area rugose to areolate-rugose, apical 1/2 areolate-rugose; subalar groove crenulate; precoxal sulcus present in roughly anterior 1/2 of mesopleuron, crenulate; posterior mesopleural furrow crenulate; mesopleuron (excluding subalar groove, precoxal sulcus, and posterior mesopleural furrow) coriaceous, setiferous except glabrous area between subalar groove and precoxal sulcus; metapleuron areolate-rugose, setiferous; metacoxa with anteroventral basal tubercle.

Forewing. Brachypterous, extending slightly posteriad middle of propodeum (including fringe); hyaline; stigma absent but with thickened sclerotization at wing apex; venation limited to one tubular vein each along anterior and posterior margins (likely C+SC+R and 1A, respectively) and one tubular vein mesally (likely M+CU), vein along posterior margin converging with vein mesally slightly before wing apex, vein mesally converging with vein along anterior margin at wing apex.

Hind wing. Brachypterous, extending slightly posterior to middle of propodeum (including fringe); basal and subbasal cells enclosed by veins, with veins enclosing cells differing in width and sclerotization but especially wide and sclerotized mesally posterior to apex of subbasal cell.

Metasoma. T1L $0.91 \times$ T1W; subcylindrical; ovipositor with minute teeth ventrally, EOL about $2.07\text{--}2.21 \times$ T2+T3L; ovipositor sheaths setiferous, setae increasing in density anteriorly to posteriorly; T1 costate-rugose, dorsal carinae sharply defined in roughly anterior 1/4 of tergum then blending posteriorly with other sculpture on tergum, setiferous; T2 costate-rugose, setiferous; transverse groove between T2+T3 weakly impressed, one specimen with and one without smooth transverse band posteriad impression; T3 anterior 1/2 costate and posterior 1/2 smooth, setae forming single transverse row in middle of tergum; T4–T8 smooth, setae forming single transverse row in middle or posterior 1/2 of tergum.

Color. Head (excluding mouthparts and antenna) yellow, mouthparts whitish yellow except mandible yellow with teeth brown, antenna yellow; mesosoma brownish yellow to yellow; wing venation tan; legs yellow to brownish yellow; T1 brownish yellow to yellow, T2–T8 yellow.

Male (Fig. 2). As in female except:

Body length. 1.79–2.36.

Head. HL $0.71\text{--}0.76 \times$ HW, HW $1.09\text{--}1.14 \times$ TW, FW $1.50\text{--}1.90 \times$ FH, MSH $0.62\text{--}0.68 \times$ EH, PMPL $0.60\text{--}0.80 \times$ F1L; antenna with 17–20 flagellomeres; gena smooth with a few strigae posteriorly or entirely smooth.

Mesosoma. ML $3.00\text{--}3.27 \times$ MW, ML $2.08\text{--}2.25 \times$ MH, MW $0.64\text{--}0.70 \times$ MH, SSL $0.40\text{--}0.50 \times$ SSW; lateral portion of pronotum smooth with a few rugosities to rugose except pronotal groove crenulate; notauli crenulate-rugose to crenulate; scutellar disc weakly coriaceous or entirely smooth; mesopleuron (excluding subalar groove, precoxal sulcus, and posterior mesopleural furrow) rugulose to coriaceous.

Forewing. Brachypterous, extending roughly to middle or posterior margin of T1 (including fringe); one specimen with indistinct veins likely corresponding to 1RS,

1M, RS+M, and 1CU in addition to three distinct horizontal veins (likely C+SC+R, M+CU, and 1A).

Hind wing. Brachypterous, extending roughly to or slightly posteriad middle of T1 (including fringe); stigma slightly apicad middle of wing, subelliptical; basal and subbasal cells enclosed by tubular veins except delimited distally by stigma, basal cell delimited ventrally by M+CU vein, 1M vein absent; R1 vein tubular.

Metasoma. T1L 1.21–1.36× T1W; transverse groove between T2+T3 weakly impressed, with or without smooth transverse band posteriad impression; T3 anterior 1/2 costate to costate-rugulose and posterior 1/2 smooth; T4–T8 smooth except T4 sometimes (40%) with a few faint carinae mesally.

Color. Antenna yellow proximally transitioning to whitish yellow or white distally; metathoracic leg with coxa, femur, and tibia brown in one specimen; T3–T5 yellow with posterior edge brown or slightly darker.

Host. Unknown.

Etymology. This species is named for the author's son, Michael Alden Kula.

Acknowledgments

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Revision of the genus *Vadumasonium* Kammerer (Hymenoptera, Braconidae, Brachistinae)

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Abstract

The genus *Vadumasonium* Kammerer, 2006 (Braconidae: Brachistinae: Diospilini), formerly known only from the Nearctic region, is revised and a second species is described from England and Germany: *V. vardyorum* sp. n. The genus is new to the Palaearctic region and we report the first host record for the genus. A key to similar genera of the Diospilini and to both species is given.

Keywords

Vadum, *Vadumasonium*, biology, distribution, new species, key

Introduction

The genus *Vadumasonium* Kammerer, 2006 (Braconidae: Brachistinae: Diospilini) hitherto comprised only the type species: *Vadumasonium volatum* (Mason, 1987), known from Missouri and Texas (U.S.A.; Yu et al. 2012). It was originally described in the genus *Vadum* Mason, 1987, but this is a junior homonym of *Vadum* Strusz, 1983, and was renamed by Kammerer (2006) as *Vadumasonium*. The second author discovered a similar species from England and Germany amongst unidentified Braconidae in the collections of the Natural History Museum (London), which is described in this

paper. The main differences between the two known species concern the length of the ovipositor sheath, the shape of the clypeus and of the first metasomal tergite.

The biology of the type species is unknown but a pair of paratypes from Germany was reared from *Ptilinus pectinicornis* (Linnaeus, 1758) (Coleoptera: Anobiidae: Ptilininae). This agrees with what is known about host relationships of Diospilini, which are koinobiont endoparasitoids of coleopterous larvae (Shaw and Huddleston 1991). The tribe Diospilini Foerster, 1862, was traditionally included in the Helconinae s.l., but recent research (Sharanowski et al. 2011) suggests placement in a separate subfamily, Brachistinae Foerster, 1862, together with the former Blacinae Foerster, 1862.

Material and methods

For the terminology used in this paper, see van Achterberg (1988, 1993). For identification of the subfamily Helconinae s.l. and the tribe Diospilini, see van Achterberg (1993) and Sharkey (1997). For the genus *Vadumasonium* Kammerer, see Mason (1987; as *Vadum*) and Sharkey (1997; as *Vadum*). The specimens are deposited in the Natural History Museum, in London (BMNH), and in Naturalis Biodiversity Center, in Leiden (RMNH).

Taxonomy

Tribe Diospilini Foerster, 1862

Diospiloidae Foerster, 1862: 229.

Genus *Vadumasonium* Kammerer, 2006

<http://species-id.net/wiki/Vadumasonium>

Figs 1–16

Vadum Mason, 1987: 325–327 (not Strusz 1982). Type species (by original designation): *Vadum volatum* Mason, 1987 [examined].

Vadumasonium Kammerer, 2006: 269 (replacement name for primary homonym).

Diagnosis. Third antennal segment 0.8–0.9 times as long as fourth segment (Fig. 11); subapical antennal segments of female slender (Figs 3, 10); face short, strongly transverse (2.7–4.0 times wider than high; Fig. 5); ventral margin of clypeus medially with one small acute tooth (Fig. 5) or truncately protruding (Fig. 16); third maxillary palp segment and second labial segment distinctly widened (Fig. 13); labial palp with 4 segments; mandible with transverse basal groove (Fig. 5); medio-ventral sulcus of propleuron strongly widened anteriorly (occupying nearly entire propleuron anteri-

only) and reticulate; pronotum truncate medio-anteriorly; postpectal carina absent; hind wing with 3 distal hamuli; second submarginal cell of fore wing anteriorly narrowed and marginal cell of hind wing parallel-sided apically (Fig. 1); vein m-cu of fore wing antefurcal; first subdiscal cell of fore wing closed; vein 1-SR of fore wing absent and vein r distinctly longer than wide; vein cu-a of fore wing antefurcal, interstitial or narrowly postfurcal; vein 2A of fore wing slightly developed, short, area basal of vein largely glabrous (Fig. 8) and vein a absent (Fig. 1); tarsal claws simple (Fig. 12); first tergite parallel-sided or nearly so and dorsal carinae straight basally (Figs 4, 9); second tergite smooth or basally with some obsolescent sculpture.

Distribution. Holarctic (two species).

Notes. The genus *Vadumasonium* Kammerer belongs to a group of diospiline genera with vein 3-SR of fore wing shorter than vein 2-M (Fig. 1), resulting in an anteriorly narrowed (or trapezoidal) second submarginal cell; tarsal claws simple, without lobe or lamella (Fig. 12); dorsal carinae of first tergite strong in basal half of tergite and comparatively far from border of tergite (Figs 4, 9); hind wing with 3-5 distal hamuli; third antennal segment shorter than fourth segment (Fig. 11) or slightly longer. The genera can be separated as follows:

- 1 Medio-ventral sulcus of propleuron strongly widened anteriorly (occupying nearly entire propleuron anteriorly) and reticulate; mandible with transverse basal groove (Fig. 5); third antennal segment about 0.9 times as long as fourth segment (Fig. 11); ventral margin of clypeus with one small acute tooth (Fig. 5) or truncate protrusion (Fig. 16); third maxillary palp segment and second labial segment distinctly widened (Fig. 13); first tergite parallel-sided or nearly so (Figs 4, 9); hind wing with 3 distal hamuli; labial palp with 4 segments; subapical antennal segments of female slender (Figs 3, 10); Holarctic region ***Vadumasonium* Kammerer, 2006**
- Medio-ventral sulcus of propleuron at most moderately widened, parallel (occupying at most half of propleuron anteriorly) and crenulate; mandible without transverse basal groove; third antennal segment variable, if shorter than fourth segment (*Taphaeus*) then clypeus truncate ventrally; third maxillary palp segment and second labial segment weakly widened; first tergite more or less widened apically; hind wing with 5 distal hamuli; labial palp with 3 segments; subapical antennal segments of female more or less moniliform **2**
- 2 Third antennal segment slightly shorter than fourth segment; frons without median carina and slightly concave; vein r of fore wing hardly longer than wide; scutellum indistinctly micro-crenulate medio-posteriorly; first tergite contracted behind spiracles (cf. Fig. 4) and dorsal carinae curved basally; Holarctic and Australian regions ***Taphaeus* Wesmael, 1835**
- Third antennal segment slightly longer than fourth segment; frons with irregular medio-longitudinal crest and distinctly concave; vein r of fore wing distinctly longer than wide; scutellum with distinctly crenulate area

medio-posteriorly; first tergite not contracted behind spiracles and dorsal carina straight basally; Palaearctic and possibly Afrotropical and Australian regions.....***Aspicolpus* Wesmael, 1838**

Similar genera outside the Diospilini (*Hellenius* Tobias, 1982, in the Blacini) or the Brachistinae (*Plesiotypus* van Achterberg, 1992, in the Microtypinae) can be separated as they have vein 1-SR of the fore wing present, the ventral margin of the clypeus truncate or slightly convex and the precoxal sulcus absent or narrowly developed. In addition, *Hellenius* has the dorsal carinae of the first tergite curved basally and *Plesiotypus* has the pronotum concave medio-anteriorly and the face about 1.5 times wider than high medially.

Key to species of the genus *Vadumasonium* Kammerer

- 1 Length of ovipositor sheath about 1.6 times as long as fore wing; clypeus obtusely protruding medio-ventrally (Fig. 16); mesosoma brownish-yellow (except for largely dark brown prothorax and propodeum); length of first metasomal tergite about 3.5 times its apical width (Fig. 9); face without separate triangular area medially; frons smooth; malar suture largely absent; hind coxa largely smooth dorsally; antenna with 30–34 segments; Nearctic.....***V. volatum* (Mason, 1987)**
- Length of ovipositor sheath 1.2–1.3 times as long as fore wing (Figs 1, 14); clypeus with small acute tooth medio-ventrally (Fig. 5); mesosoma black or dark brown; length of first tergite about twice its apical width (Fig. 4); face with separate triangular area medially (Fig. 5); frons largely coriaceous (Figs 5, 6); malar suture present, except dorsal third (Fig. 5); hind coxa largely rugose dorsally (Fig. 7); antenna with 27–30 segments; Europe.....***V. vardyorum* sp. n.**

***Vadumasonium vardyorum* sp. n.**

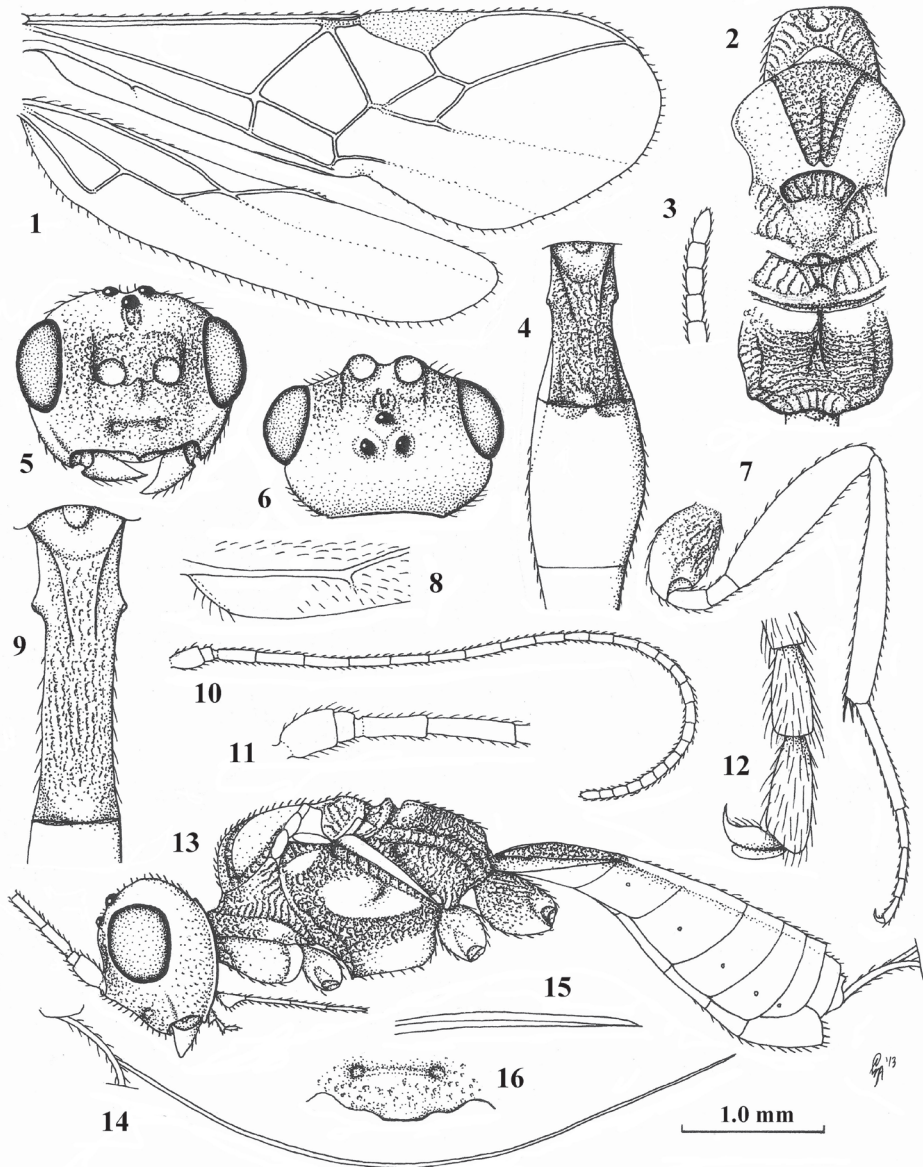
<http://zoobank.org/17104E30-0640-4364-9E5B-3A1656F1D0D8>

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

Figs 1–8, 10–15

Type material. Holotype, ♀ (BMNH), “England: Hants., Romsey, Awbridge, 1–14. viii.1981, C. & M. Vardy”, “Malaise trap at 5 m in dead *Larix*”, “*Aspigonus* sp., det. T. Huddleston, 1982”. Paratypes (2 ♀ + 1 ♂): 1 ♀ (RMNH), “England: Hants., New Forest, Minstead, 5.viii.[19]63. In cage with *Apatele alni*, L.W. Sigs”, “*Aspidogonus* sp., R.D. Eady det. 1967”; 1 ♀ + 1 ♂ (BMNH), “D. [= Germany], [near] Freiburg, Bechtaler Wald [= a strictly protected forest reserve near Weisweil in Baden-Württemberg], 1996”, “ex *Ptilinus pecticornis*”, “Hedqvist coll. BMNH(E) 2011-27”.

Diagnosis. Clypeus with small acute tooth medio-ventrally (Fig. 5); face 4.0 times wider than high medially and with separate triangular area medially (Fig. 5);



Figures 1–16. *Vadumasonium vardyorum* sp. n., ♀, holotype, but 9 and 16 of holotype of *V. volatum* (Mason), ♀. 1 wings 2 mesosoma dorsal 3 apex of antenna 4 first-third metasomal tergites dorsal 5 head frontal 6 head dorsal 7 hind leg lateral 8 detail of fore wing postero-basally 9 first tergite dorsal 10 antenna 11 base of antenna 12 inner hind claw 13 habitus lateral 14 ovipositor 15 apex of ovipositor lateral 16 clypeus frontal. 1, 7, 10, 13, 14: scale-line (= 1.0×); 2, 4–7: 1.7×; 3: 2.5×; 8, 9, 16: 2.0×; 11, 12, 15: 5.0×.

frons largely coriaceous (Figs 5, 6); malar suture present, except dorsal third (Fig. 5); hind coxa largely rugose dorsally (Fig. 7); mesosoma black or dark brown; length of first tergite about twice its apical width (Fig. 4); length of ovipositor sheath

1.2–1.3 times as long as fore wing (Figs 1, 14); length of fore wing 3.6–4.2 mm; antenna with 27–30 segments.

Description. Holotype, ♀, length of body 5.0 mm, of fore wing 4.2 mm.

Head. Antenna with 28 segments and 1.1 times as long as fore wing (Fig. 10); third segment 0.9 times as long as fourth segment, length of third, fourth and penultimate segments 3.6, 4.0 and 1.3 times their width, respectively; length of maxillary palp nearly equal to height of head; third segment of maxillary palp distinctly widened medially; second segment of labial palp wide, triangular with fourth segment inserted at lower corner (Fig. 13); occipital carina complete but medio-dorsally weakly developed; hypostomal carina narrow; length of eye in dorsal view 1.5 times temple (Fig. 6); frons moderately depressed and coriaceous medially, without median carina or groove and laterally slightly convex and punctate; face 4.0 times wider than high, slightly convex and punctate laterally and medially with triangular flat area (Fig. 5); clypeus convex and sparsely but distinctly punctate, its ventral margin thick and medio-ventrally with small tooth (Fig. 5); malar suture present, except dorsal 0.3 of malar space, malar space 1.2 times as long as basal width of mandible (Fig. 13); mandible with deep transverse groove basally (Fig. 5), ventral tooth about as wide as longer dorsal tooth.

Mesosoma. Length of mesosoma 1.5 times its height; dorsal pronope wide and moderately impressed, with pronotum truncate anteriorly (Fig. 2); antescutal depression absent, but with triangular flat area; pronotal sides largely punctate-rugose and medially crenulate; epicnemial area and complete precoxal sulcus widely reticulate-rugose and rest of mesopleuron (except dorsally) largely smooth; pleural sulcus crenulate; mesosternal sulcus wide and coarsely crenulate; notauli complete, crenulate and posteriorly wide (Fig. 2); middle lobe of mesoscutum densely punctate and posteriorly rugose, with a median carina, both lateral lobes largely smooth (Fig. 2); scutellar sulcus deep, wide and with irregular carinae; scutellum punctate and convex medially, with paired depressions medio-posteriorly (Fig. 2); surface of propodeum densely and coarsely rugose but anteriorly smooth, median carina short, posterior face hardly separated from dorsal face, lateral tubercles indistinct and areola absent.

Wings. Fore wing (Fig. 1): pterostigma triangular; first discal cell narrowly truncate anteriorly; 1-R1 ending before wing apex and 1.3 times as long as pterostigma; r:3-SR:SR1 = 9:13:74; 2-SR:3-SR:r-m = 28:13:22; 2-M nearly twice as long as 3-SR; r slender; 1-M and SR1 straight; cu-a interstitial; first subdiscal cell closed, CU1b short; M+CU1 sclerotized. Hind wing: M+CU:1-M = 24:15; cu-a straight.

Legs. Hind coxa densely rugose dorsally (Figs 7, 13); length of femur, tibia and basitarsus of hind leg 4.2, 8.7 and 8.4 times as long as wide, respectively; hind femur largely smooth; hind tibia slightly narrowed apically (Fig. 7); hind tibial spurs slender, apically acute and both 0.3 times as long as basitarsus.

Metasoma. First tergite 2.1 times as long as its apical width, surface largely rugose with straight dorsal carinae on basal 0.3 of tergite (Fig. 4); second suture absent; second and following tergites smooth; length of setose part of ovipositor sheath 1.18

times fore wing; upper valve of ovipositor depressed apically, without apical notch or nodus (Fig. 15); hypopygium truncate apically.

Colour. Black; antenna, clypeus, hind leg (but trochanter and trochantellus yellow), metasoma (but baso-ventrally yellowish-brown), pterostigma, parastigma and ovipositor sheath dark brown; remainder of legs (but middle coxa largely dark brown) and mandible brownish-yellow; veins brown; palpi, trochanters and trochantelli pale yellow; wing membrane slightly infuscate but somewhat darker near vein r of fore wing.

Male. The males do not differ from the females except for the sexual differences and a slightly higher number of antennal segments.

Variation. Length of body 5.0–5.3 mm, fore wing 3.6–4.2 mm; antenna of female with 27 (1) or 28 (1) segments and of male 30 (1); first tergite 1.9–2.2 times as long as its apical width; ovipositor sheath 1.18–1.31 times as long as fore wing; vein cu-a of fore wing interstitial or narrowly postfurcal; frons with or without an irregular median carina; second tergite smooth or with some obsolescent sculpture basally.

Biology. Reared from *Ptilinus pectinicornis* (Linnaeus, 1758) (Coleoptera: Anobiidae: Ptilininae).

Distribution. England, Germany.

Etymology. Named after Colin and Martha Vardy, for collecting the holotype and for their hospitality during visits by the senior author.

Acknowledgements

We thank Dr Henri Goulet and Mrs Caroline Boudreault (CNC, Ottawa) for the loan of the holotype of *Vadum volatum*.

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Revision of *Agathacrista* new genus (Hymenoptera, Braconidae, Agathidinae, Agathidini)

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Abstract

Based on a cladistic analysis, a new genus of Agathidini, *Agathacrista* Sharkey, is proposed and its phylogenetic position hypothesized. Two previously described (*Agathacrista cancellata*, *Agathacrista depressifera*) and three new species (*Agathacrista sailomi*, *Agathacrista winloni*, *Agathacrista krataeii*) are included. The distribution of *Agathacrista* is limited to the Oriental region and southern portion of the eastern Palearctic.

Keywords

Insecta, identification key, taxonomy, systematics

Introduction

Agathacrista, as proposed here, includes two previously described species, both of which were included in the paraphyletic concepts of *Bassus s.l.* and *Therophilus s.l.* This paper is part of a series that investigates these non-monophyletic taxa, while describing taxa from Thailand, Costa Rica, or more inclusive areas of the world.

Methods

Morphological terms: The length of the first metasomal tergite is measured from the apex of the tendon emanating from the propodeum to the posterior border of the tergite. Other terms are from Sharkey and Wharton (1997).

Museum acronyms

- HIC** Hymenoptera Institute Collection, University of Kentucky, Department of Entomology, Lexington, Kentucky, USA.
QSBG Queen Sirikit Botanic Gardens, Chiang Mai, Thailand.
TARI Taiwan Agricultural Research Institute, Entomology Collection, Taichung, Taiwan.

Species description format: Descriptions are of the holotype; variation is given in parentheses. In the species descriptions color is not extensively described because the images serve this purpose; however color characters that are variable or of diagnostic significance are detailed.

Species delimitation: The five species from Thailand treated here are very similar morphologically and are represented by only seven specimens. The seven specimens do not differ more than might be expected within one species of agathidine. In part, we relied on 28S sequence data to separate species. We did not employ any particular cut-off point in differences in 28S but rather calibrated the amount of sequence difference using species that exhibit significant morphological and host preference differences. This calibration comes from a large dataset of about 1,000 agathidine specimens for which we have 28S data. The three species of *Agathacrista* for which we have 28S sequences were identified according to this criterion. Morphological characters also played an important role in species delimitation. We examined ten specimens of *Agathacrista cancellata* (Enderlein, 1920), all from Taiwan. Body color varies considerably in this species, but wing color and the sculpture and dimensions of the first metasomal median tergite are uniform, suggesting that these are good species indicators within the genus. Therefore, these characters played an important role in our species concepts. *Agathacrista depressifera* (van Achterberg & Long, 2010) displays considerable variation in wing color-pattern. Despite the fact that we have some evidence to suggest that this species concept may include more than one species, our evidence is weak and not convincing enough to suggest changes. This revision of *Agathacrista* is very preliminary; many more specimens will be needed to fully understand species limits and species diversity.

Generic concepts: This is the fourth of a series of papers (Sharkey and Clutts 2011; Sharkey and Stoelb 2012; Sharkey et al. 2009) that reclassify what was once considered the genus *Bassus* (or *Microdus*, or *Agathis* s.l.). I (MJS) thought it best to give some details here on the criteria that were used to delineate generic limits. Most of these are stated in one manner or another in Backlund and Bremer (1998). The first considera-

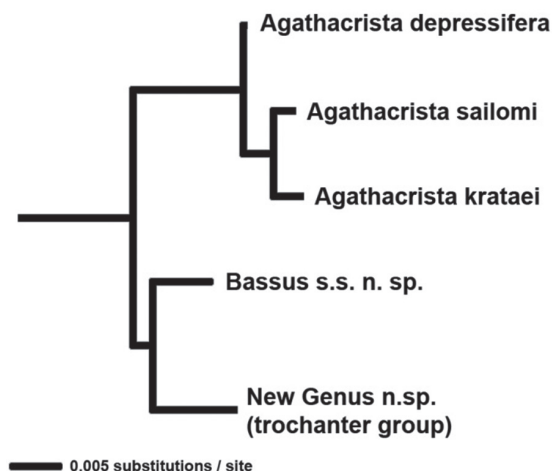


Figure 1. NJ tree showing 28S distances between species of *Agathacrista*.

tion is monophyly and this is why the polyphyletic concept of *Bassus s.l.* was rejected (Sharkey et al. 2009). The following criteria are in no particular order and may be more or less important depending on the genus.

Identifiability: *Agathacrista* is a good example of the utility of this criterion. *Agathacrista*, *Bassus s.s.* and a new genus to be described in a forthcoming paper, form a monophyletic group (Fig. 2). The only morphological synapomorphy to aid in the recognition of the group is the presence of small spines or pegs on the fore tibia; convergent in some members of *Earinus* and many other non-agathidines. If there was an easily observed character it might be best to expand the concept of *Bassus* to include *Agathacrista* and the new genus. Conversely, all three genera as here proposed have distinguishing characteristics. *Bassus s.s.* has long, simple claws that lack a basal lobe; *Agathacrista* has a crest between the antennae and the undescribed new genus has a distinct longitudinal carina on the hind trochanter, a character formerly thought to be restricted to some members of the Cremnoptini and Disophrini.

Biological information content: Typically the more that is known about organisms the more finely split the higher ranks are. This criterion has little application to any agathidines since we know so little about their natural history. Undoubtedly the morphological autapomorphies of the three genera referred to above will be shown to relate to unique behaviours.

Stability: This is somewhat tied to most other criteria and *Bassus s.l.* is a good example of an unstable concept. Over the years it has been included in the genus *Agathis s.l.* and numerous genera like *Camptothlipsis* and *Therophilus* have been included, or not. This instability has made information retrieval on any particular species rather cumbersome, as the number of different combinations they have been referred to is a minimum of three, i.e., *Microdus*, *Bassus*, *Agathis*, the foremost being a junior objective synonym of *Bassus*. Thus, generic concepts should be accompanied by solid phylogenetic evidence when such is available.

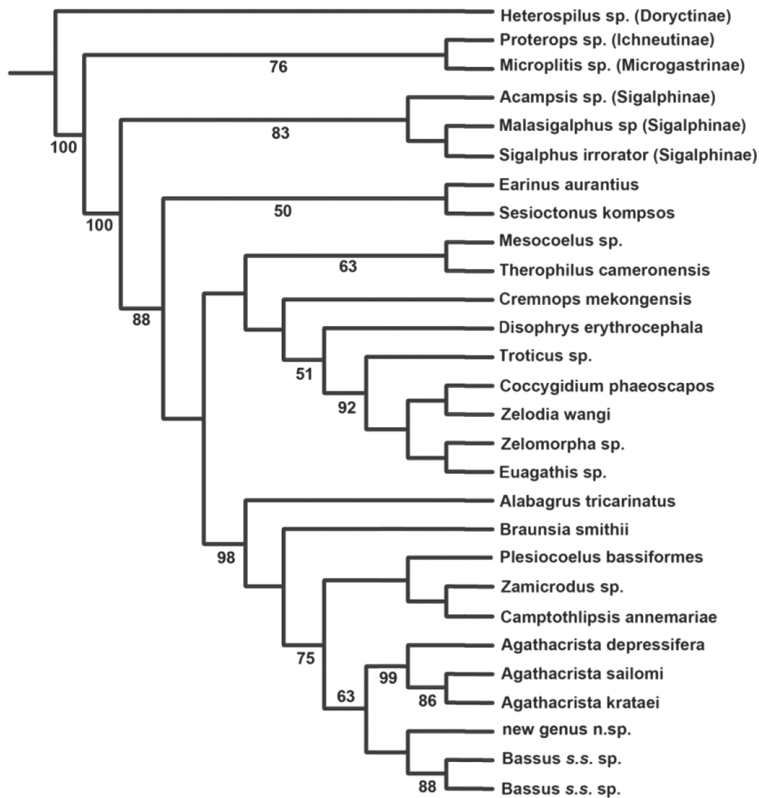


Figure 2. Maximum parsimony tree of some agathidine genera with a concentration near *Agathacrista* based on D2-D3 regions of 28S. Numbers below branches are bootstrap values; only values ≥ 50 are shown.

Phylogenetic evidence: This is directly related to stability. If new, but weak evidence suggests the non-monophyly of a well-recognized genus, it is usually best to wait for more data before making formal changes. In the case presented here, there is strong molecular phylogenetic evidence suggesting that the broad concept of *Bassus* (*Bassus s.l.*) is polyphyletic and there is significant morphological and molecular evidence for the monophyly of *Agathacrista*.

Specimen collection: As part of the inventory of Thai insects, 3 Malaise traps at each of 30 different localities throughout Thailand were operated from 2007-2010, comprising approximately 90 trap-years. The specimens dealt with here are primarily from these traps.

Phylogenetic methods: Regions D2-D3 of 28S rDNA (roughly 560 base pairs) were sequenced using the following primers: 28SD2hymF 5' - AGAGAGAGTTCAA-GAGTACGTG - 3' and 28SD3hymR 5' - TAGTTCACCATCTTTTCGGGTC - 3'. Sequences were edited using Geneious Pro v4.7.5 (Drummond et al. 2009) and aligned based on a secondary structure model for Ichneumonidea developed by Yoder and Gillespie (2004) and Gillespie et al. (2005). Regions of expansion and contraction

(RECs), regions of slipped-strand compensation (RSCs), and short regions of alignment ambiguity were further aligned/corrected by eye. Three of these regions (~30 base pairs) were deleted because they could not be aligned with confidence, i.e., there were multiple equally supported alignment options.

The NJ analysis (Fig. 1) was conducted with PAUP* (Swofford 2003) using default settings. The parsimony analysis (Fig. 2) was performed using TNT (Goloboff et al. 2008) [traditional search with 100 random addition sequences followed by branch-swapping, saving 100 trees per replication; 1000 bootstrap replications were used to estimate branch reliability].

Morphological terms used in this revision were matched to the Hymenoptera Anatomy Ontology (HAO; Yoder et al. 2010) (Appendix 4). Identifiers (URIs) in the format http://purl.obolibrary.org/obo/HAO_XXXXXXX represent anatomical concepts in HAO version <http://purl.obolibrary.org/obo/hao/2011-05-18/hao.owl>. They are provided to enable readers to confirm their understanding of the anatomical structures being referenced. To find out more about a given structure, including images, references and other metadata, use the identifier as a web-link, or use the HAO:XXXXXXX (note colon replaces underscore) as a search term at <http://glossary.hymao.org>.

All species are treated with a diagnosis and distributional data. They are illustrated with color photos using a JVC digital camera mounted on a Leica MZ16 microscope and Automontage® stacking software. Distributional data are listed for all species and a link to a Google map is included for all species. The descriptions are of holotypes and variation is given in parentheses.

Phylogenetic considerations

Sharkey et al. (2006) showed that the entities formerly referred to as *Bassus* s.l. fall into two widely disparate clades. One associated with the genus *Mesocoelus*, *Therophilus* and allies and the other with *Bassus* s.s., *Agathis*, *Alabagrus*, *Braunsia* and allies. *Agathacrista* falls into the latter lineage. It is sister to *Bassus* s.s. + a new genus to be described in another paper. All three genera are restricted to the Old World, and except for one species of *Bassus* s.s., *B. calculator* Fabricius, 1798, the type species, which is widely distributed throughout the Palearctic, all are restricted to the Oriental region, the northern, tropical parts of the Australian region, and the far eastern Palearctic.

Members of all three genera have distinct pegs on the anterior surface of the fore tibia (Fig. 3a), a synapomorphy. This character state is convergent in some members of the distantly related genus *Earinus* (Agathidinae), some Braconinae, most Doryctinae, and has rare and scattered appearances in other braconid subfamilies. Members of *Agathacrista* and *Bassus* have similar and rather unique color patterns (see Figs 4–8). The thin, acute, interantennal crest (Fig. 3b) is an autapomorphy for *Agathacrista* that is found convergently though rarely in a few other agathidine genera, e.g., a few members of *Therophilus*.

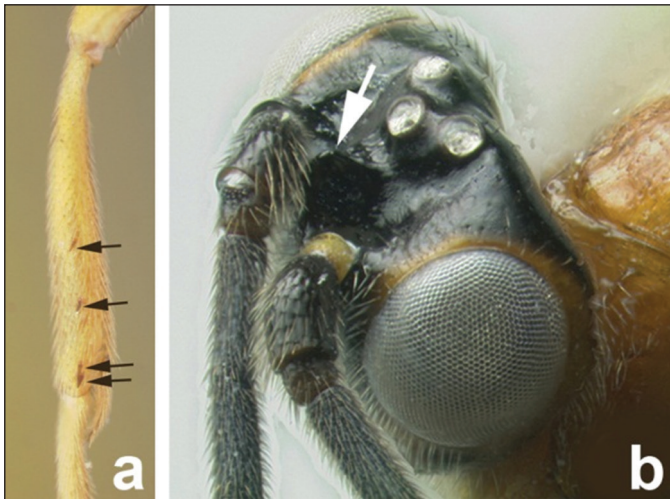


Figure 3. **a** fore leg of *Agathacrista* sp. showing pegs or spines **b** dorsolateral head of *Agathacrista* sp. showing interantennal crest.

Taxonomy

Agathacrista Sharkey, gen. n.

<http://zoobank.org/0E5C3C07-22D0-45B8-8B9A-4BA142EE1731>

<http://species-id.net/wiki/Agathacrista>

Type species. *Agathacrista winloni* Sharkey, sp. n.

Diagnosis. Interantennal space with longitudinal keel that is sharply declivous posteriorly (Figs 3b, 7d); ocelli elevated above surface of vertex; fore tibia with pegs (Fig. 3a); third metasomal median tergite lacking sculpture; basal lobe of tarsal claws large and right angled or slightly acute (Fig. 7a); fore wing partly or completely pigmented; hind wing vein CUB absent. Some members of a few other genera of Agathidini have a sharp keel between the antennae, but none of these have pegs on the fore tibia.

Description. Head. Lateral carina on frons (as in members of *Alabagrus*) absent; interantennal space with longitudinal keel that is sharply declivous posteriorly (Figs 3b, 7d); ocelli elevated above surface of vertex; gena not extended ventroposteriorly into sharp prominence (Fig. 6a); gena lacking sharp angle posteriad of eye; labial palpus with 4 segments, third segment less than $\frac{1}{2}$ as long as apical segment; apical antennomere acute but lacking nipple-like process. **Mesosoma.** Propleuron convex ventrally but lacking a sharp bump; notauli impressed and pitted, at least in part (Fig. 6c); posteroscutellar depression absent but sculpture usually present in this area; propodeum rugose to areolate-rugose (Fig. 7g); sclerite between hind coxal

cavities and metasomal foramen complete, its ventral margin situated ventral to dorsal margin of hind coxal cavities. **Legs.** Fore tibia with pegs (Fig. 3a); all tarsal claws with strong basal lobe and with right-angled or slightly acute angle (Fig. 7a). **Wings.** (Figs 6d, 8b). Fore wing RS+M vein mostly absent; second submarginal cell triangular; fore wing 3RSb straight and strong throughout; hind wing r and r-m cross veins absent; hind wing vein CUB absent; fore wing partially or completely pigmented, with yellow or melanic color. **Metasoma.** First median tergite longitudinally striate, with a slightly stronger pair of lateral striae and a medial stria (Fig. 7h, 8e), rarely striae reduced and sculpture mostly weakly rugose (see couplet 1 in the identification key); second median tergite with an elevated semi-circular area separated from the remainder of the tergite by a shallow groove (Fig. 8e); second median tergite from smooth to striate, usually smooth anteriorly with a few longitudinal striae in posterior half; median tergite 3 smooth; length of ovipositor rather uniform, as long as (Fig. 5) or slightly longer than body (Fig. 8c).

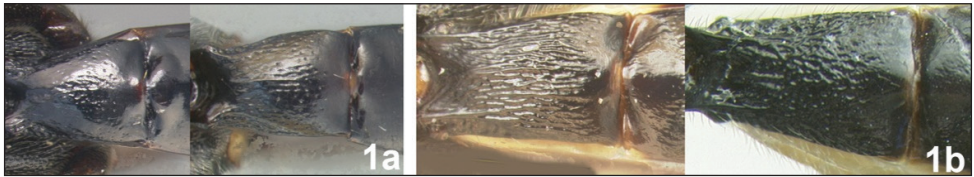
Biology. Unknown

Distribution. Restricted to the eastern Palearctic (Taiwan) and the Oriental region. For a distribution map, click [here](#).

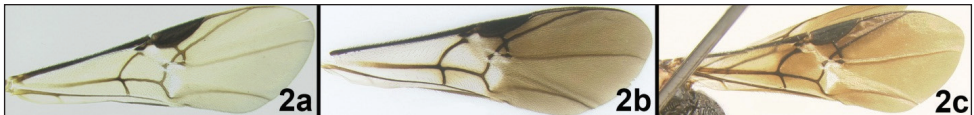
Etymology: From the Greek *agathis*, meaning “ball of thread”, and the Latin *crista*, meaning “crest”. Crest is in reference to the ridge between the antennal insertions. The gender is feminine.

Key

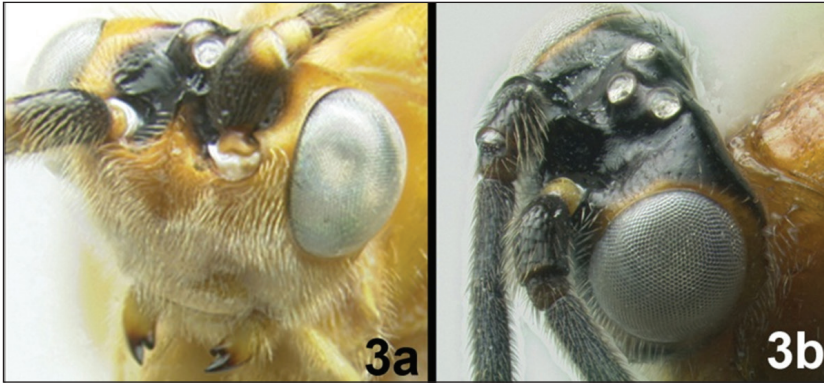
- 1a Median tergite 1 mostly smooth or weakly sculptured...*Agathacrista cancellata*
 1b Median tergite 1 mostly striate or rugosostriate.....2



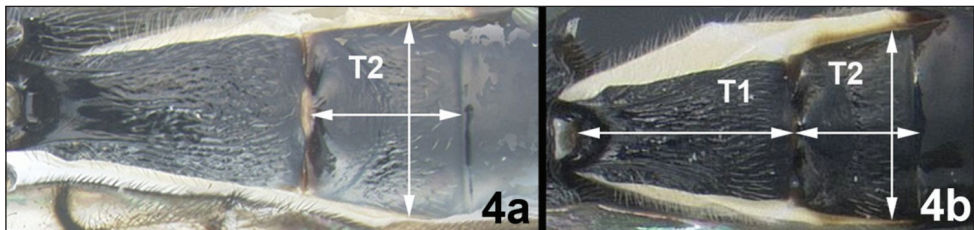
- 2a Fore wing uniformly yellow, at most slightly darker apically.....3
 2b Fore wing clear basally, infusate distally4
 2c Fore wing mostly evenly infusate, very slightly clearer at extreme base.....
 *Agathacrista depressifera*



- 3a Head mostly yellow, black color restricted to medial dorsal surface; larger specimens, ~ 9.6 mm *Agathacrista sailomi*
 3b Head mostly black, yellow color restricted to part of face and orbits of eyes; smaller specimens, ~ 6.2 mm *Agathacrista depressifera*



- 4a Median tergite 1 (T1) weakly converging anteriorly; T2 quadrate and ~1.3× wider than long..... *Agathacrista winloni*
 4b Median tergite 1 strongly converging anteriorly; T2 diverging posteriorly and ~1.5× wider than long..... *Agathacrista krataeii*



Species descriptions

Agathacrista cancellata (Enderlein), comb. n.

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

Fig. 4

Agathis cancellata Enderlein, 1920

Diagnosis. This species has the northern-most distribution and appears to be restricted to Taiwan where it is the only species present. Members come in two color morphs; one with the mesosoma bicolored and the other with the mesosoma entirely melanistic. *Agathacrista cancellata* differs from all other members of the genus by the relatively smooth surface of metasomal median tergite 1 (Fig. 1a in the identification key above).

Material examined. Taiwan: Female: “Kanshirei, 20 xi 1928, col. J Sonan” (HIC). “Kanshirei, 10 xi 1926, col. J Sonan” (TARI). Female: “Taichung, Wufeng,

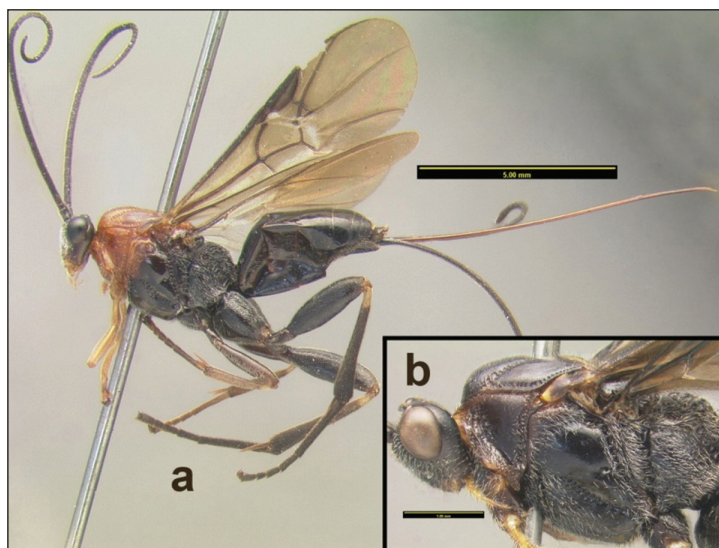


Figure 4. *Agathacrista cancellata*. **a** lateral habitus **b** lateral head and mesosoma.

Wanfeng, 2-7-v-1979, K.C. Chou" (HIC). Female: "Puli, Taichung. 16-19 v. 1956, K.S. Lin." (HIC). Female: "Taipei, 15.v.1964 K.S. Lin" (TARI). Male: "Shanti-men, Pingtung Hsien, 28.III.-1.IV.1981, C.C. Chen & C.C. Pang" (TARI). Female: "12.x.1952, Coll. S. C. Cheu" (TARI). Female: "Arisan, 5-VIII-1981, Col. T. Shiraki" (TARI). Female: "Chungho, 28.V.1963, Col. H.H. Tseng" (TARI). Female: "Suo-Suigen 24.VIII.1930, Col. J. Sonan" (HIC). For a distribution map, click here.

***Agathacrista depressifera* (Achterberg & Long), comb. n.**

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

Fig. 5

Therophilus depressiferus Achterberg & Long, 2010

Description. Length: 6.5 (7.8) mm. Antenna with 38 (42) flagellomeres. Number of spines on fore, mid, and hind tibiae 6(5), 8(11), 15(16). First median tergite 1.6 times longer than wide; second median tergite 1.2 times wider than long; median tergite 1 rugosostriate, except smooth near posterior margin, sculpture more reticulated than congeners; median tergite 2 smooth (weakly rugosostriate near midlength). Color: (melanic color of mesopleuron more extensive in the sole paratype.)

Material examined. **Vietnam:** Female: "Dak Lak Prov. Krong Bong, Chu Yan Sin NP, N12°31.303', E108°28.853', 28.vii.2008 MT" H7991 (QSBG). **Thailand:** Female: "Phetchabun, Khao Kho NP, 520m, 16°52.568'N, 101°08.104'E, 12-19.x.2006 Sintong leg. T807" H002 (HIC). For a distribution map, click here.

Molecular data. Genbank Accession KC556782 (H002).



Figure 5. *Agathacrista depressifera* lateral habitus.

***Agathacrista krataei* Sharkey, sp. n.**

<http://zoobank.org/FCDD9F11-0FF1-4B90-A7AB-5A75BE08A235>

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

Fig. 6

Description. Length: 8.4 mm. Antenna with 41 flagellomeres. Number of spines on fore, mid, and hind tibiae 6, 10, 13. First median tergite 1.5 times longer than wide; second median tergite 1.5 times wider than long; median tergite 1 entirely rugosostriate; median tergite 2 mostly weakly sculptured with striae, smooth posterolaterally.

Etymology. Named after Kratae Sanok a collector for the TIGER project at Pa Hin Ngam National Park.

Material examined. Holotype: Female: *Thailand*, “Sakon Nakhon, Phu Phan NP, Dry evergreen near house no. 1567, 16°48.628'N, 103°53.591'E, Malaise trap, vi.2007, Winlon Kongnara leg., T2502” H268 (QSBG). For a distribution map, click here.

Molecular data. Genbank Accession KC556781 (H268).

***Agathacrista sailomi* Sharkey sp. n.**

<http://zoobank.org/61CEE178-5F5E-4302-8A10-E4AE769CAF12>

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

Fig. 7

Description. Length: 9.6(9.3) mm. Antenna with 44 flagellomeres. Number of spines on fore, mid, and hind tibiae 4(3), 6, 6(13). First median tergite 1.6 times longer than wide; second median tergite 1.4 times wider than long; median tergite 1 rugosostriate, except smooth near posterior margin; median tergite 2 mostly smooth with a weak indication of longitudinal sculpture at midlength. Color: (Melanic color of head restricted to ocellar triangle in the sole paratype.)

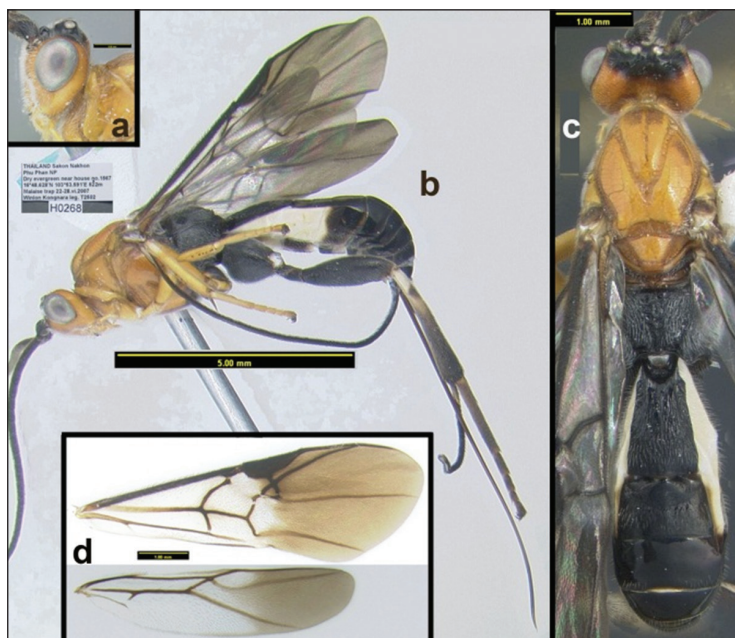


Figure 6. *Agathacrista krataei*. **a** lateral head **b** lateral habitus **c** dorsal habitus **d** wings.

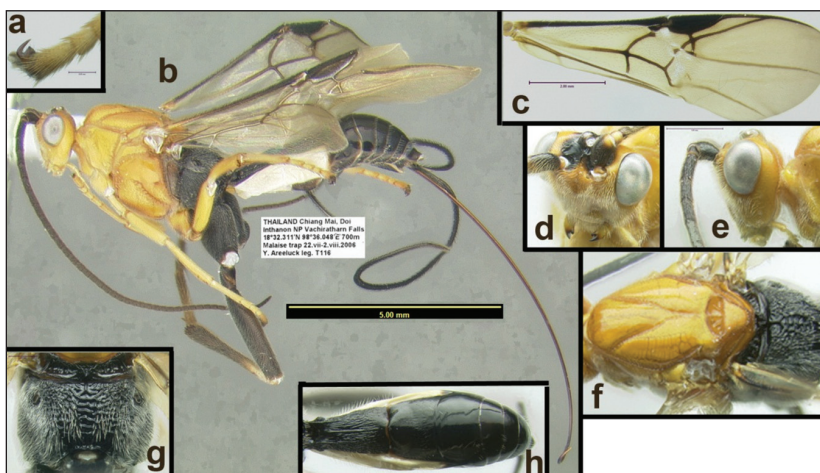


Figure 7. *Agathacrista sailomi*. **a** tarsal claw **b** lateral habitus **c** fore wing **d** anterolateral head **e** lateral head **f** dorsal mesosoma **g** dorsal propodeum **h** dorsal metasoma.

Etymology. Named after Sailom Tongbunchai a collector for the TIGER project at Phuphan National Park.

Material examined. Holotype: Female: **Thailand:** “Chiang Mai, Doi Inthanon NP, Vachiratharn Falls, 18°32.311'N. 98°36.048'E, 700m Malaise trap, 6–13.ix.2006 Y. Areeluck leg. T242” H013 (QSBG).

Molecular data. Genbank Accession KC556780 (H013).

Paratypes. Female: **Thailand:** “Chiang Mai, Doi Inthanon NP, Vachiratharn Falls, 18°32.311'N, 98°36.048'E, 700m Malaise trap, 22.vii–2.viii.2006 Y. Aree-luck leg. T116” H284 (HIC). Female: “Chiang Mai, 20.ix–20.x.(19)84, D. Jackson” H5904 (QSBG). For a distribution map, click [here](#).

***Agathacrista winloni* Sharkey, sp. n.**

<http://zoobank.org/3556862D-AC1D-428F-818D-B8CA315212D1>

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

Fig. 8

Description. Length: 8.4 (9.8) mm. Antenna with 43(45) flagellomeres. Number of spines on fore, mid, and hind tibiae 6, 8, 12(15). First median tergite 1.8 times longer than wide; second median tergite 1.2 times wider than long; median tergite 1

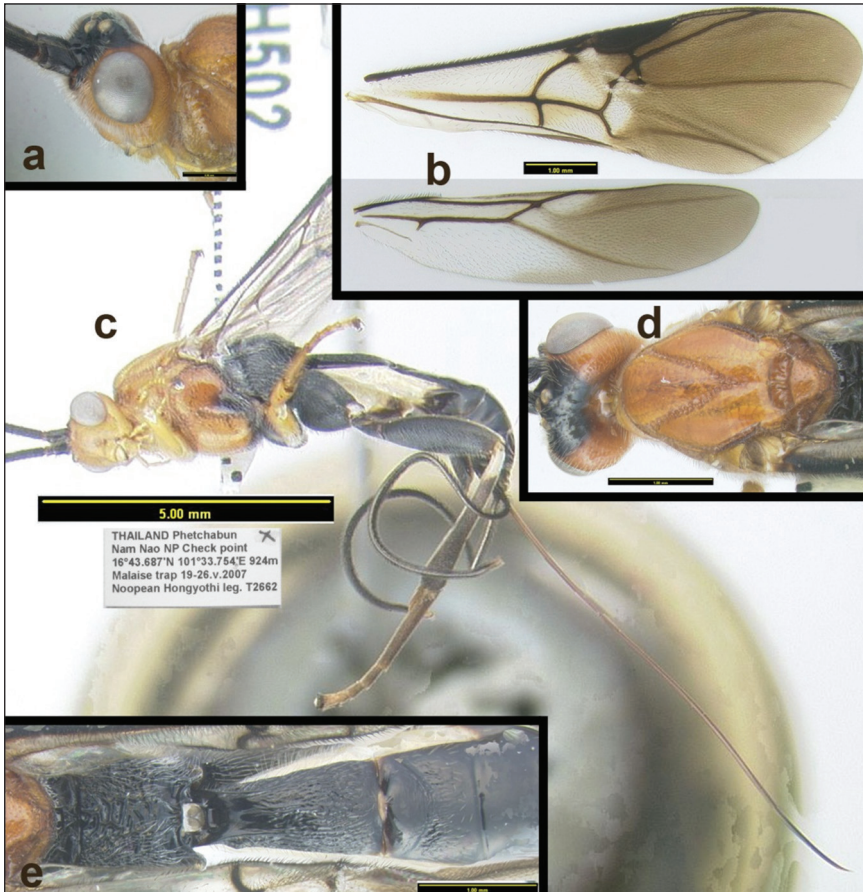


Figure 8. *Agathacrista winloni*. **a** lateral head **b** wings **c** lateral habitus **d** dorsal head and mesosoma **e** dorsal propodeum and metasomal median tergites 1–3.

rugosostriate, except smooth near posterior margin; median tergite 2 mostly smooth with a weak indication of longitudinal sculpture at midlength (almost entirely smooth). Color: (melanic color of mesopleuron more extensive in one paratype; mid femur melanic in basal half).

Etymology. Named after Winlon Kongnaka a collector for the TIGER project at Phuphan National Park.

Material examined. Holotype. Female: *Thailand*: “Phetchabun, Nam Nao National Park Check Point, 16°43.687'N, 101°33.754'E, 924m 19–26.v.2007 Noopean Hongyothi leg. T2662” H502 (QSBG).

Molecular data. Genbank Accession KC771135 (H502).

Paratypes. Female: *Thailand*: “Phetchabun, Nam Nao National Park Check Point, 16°43.687'N, 101°33.754'E, 924m 19–26.v.2007, Noopean Hongyothi leg. T2662” H501 (HIC). Female: “Phetchabun, Nam Nao NP Sam Makao forest, 16°41.067'N, 101°40.425'E, 540m, Malaise trap 4–11.ix.2006 Higgyothi & Janteab leg.” H466 (QSBG). Female: “800m, 180 km NE Bangkok Khao Yai Nat. Park 10–16.iv.1990 B.V. Brown, Moist evergreen for(est). MT.” (HIC). For a distribution map, click here.

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New synonymy of *Trissolcus halyomorphae* Yang

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Abstract

Trissolcus halyomorphae Yang **syn. n.** is treated as a junior synonym following examination of the holotype of *T. japonicus* (Ashmead).

Keywords

Halyomorpha halys, *Trissolcus japonicus*, *Trissolcus halyomorphae*, brown marmorated stink bug

Introduction

Halyomorpha halys (Stål) (Hemiptera: Pentatomidae), commonly called the brown marmorated stink bug, is a polyphagous invasive pest in the Mid-Atlantic United States and is recorded from 39 of the 48 contiguous states (Carter and Hoebeke 2003, Leskey et al. 2012). It has also become established in Switzerland (Wermelinger et al. 2008) and has been intercepted in New Zealand (Harris 2010). The distribution and abundance of this insect in both North America and Europe are expected to grow (Zhu et al. 2012), drawing increased attention to the need for management strategies, including biological control. Multiple species of egg parasitoid wasps in the genus *Trissolcus* (Hymenoptera: Platygasteridae) are currently the subject of a biological control

study by the Beneficial Insects & Introduction Unit (Newark, Delaware; USDA-ARS) for use against *H. halys*.

Yang et al. (2009) published a description of a new species, *Trissolcus halyomorphae* (Hymenoptera: Platygasteridae), reared from the eggs of *H. halys* in Northeastern China and provided information on its biology. Their diagnosis indicated that *T. halyomorphae* and *T. japonicus* were similar species and that the two could be separated by multiple characters. However, it appears that they did not examine the holotype of *T. japonicus*, and the specimens that formed the basis of their comparison must belong to a species other than *T. japonicus* with characters similar to those of *T. flavipes* (Thomson).

Examination of the holotype of *T. japonicus* revealed that the characters attributed to this species by Yang et al. (2009) are not present, and that *T. japonicus* and *T. halyomorphae* are conspecific. Specifically, in the holotype of *T. japonicus* the femora are not concolorous with the remainder of the legs, the antennal scrobe does not have rugulae that extend to the median ocellus, the posterior ocellus is separate from the inner orbit of the eye by less than one ocellar diameter, the orbits of the eyes (orbital furrows) are expanded ventrally, and the notaulus does not curve outward anteriorly.

Numerous attempts to borrow the holotype of *T. halyomorphae* were unsuccessful but we did procure two paratype females. These specimens, coupled with the images and description of Yang et al., enable us to confidently treat *T. halyomorphae* as a junior synonym of *T. japonicus*. We present this synonymy as a prelude to a full scale taxonomic revision of the Asian species of *Trissolcus* and to minimize confusion by eliminating future use of the name *T. halyomorphae* in literature regarding the biology of this species and its efficacy as a biological control agent.

The contributions of the authors are as follows: E.J. Talamas: species concept development, imaging, manuscript preparation; M. Buffington: manuscript preparation; K. Hoelmer: acquisition of paratype specimens.

Materials and methods

The locality data reported for primary types are not literal transcriptions of the labels: some abbreviations are expanded; additional data from the collectors are also included. The numbers prefixed with “USNM ENT” or “USNM Type No.” are unique identifiers for the individual specimens (note the blank space after the acronyms). Details on the data associated with these specimens may be accessed at the following link, purl.oclc.org/NET/hymenoptera/hol, and entering the identifier in the form. The taxonomic synopsis was generated by the Hymenoptera Online Database (hol.osu.edu).

Images were produced using Combine ZP and Cartograph extended-focus software. Full resolution images are archived at the image database at The Ohio State University (purl.oclc.org/NET/hymenoptera/specimage), MorphBank (www.morphbank.net), and Hymenoptera Holotypes of the Smithsonian Institution (usnmhymtypes.com).



Figures 1–3. *Trissolcus japonicus*, holotype female (usnm type no. 7127) **1** Head, anterior view **2** lateral habitus **3** dorsal habitus. Scale bars in millimeters.

Taxonomic part

Trissolcus japonicus (Ashmead)

urn:lsid:biosci.ohio-state.edu:osuc_concepts:3249

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

Dissolcus japonicus Ashmead, 1904: 73 (original description); Kieffer 1926: 124, 125 (description, keyed).

Asolcus plautiae Watanabe, 1954: 18, 22 (original description, keyed, synonymized by Hirashima and Yamagishi (1981)).

Trissolcus japonicus (Ashmead): Masner and Muesebeck 1968: 72 (type information, generic transfer); Hirashima and Yamagishi 1981: 153 (description, synonymy); Ryu and Hirashima 1984: 37, 43 (description, keyed).

Trissolcus plautiae (Watanabe): Kozlov 1968: 198 (keyed); Kozlov and Lê 1976: 658 (keyed); Kozlov and Lê 1977: 504 (keyed); Kozlov 1978: 629 (description); Hirashima and Yamagishi 1981: 153 (junior synonym of *Trissolcus japonicus*

(Ashmead)); Kozlov and Kononova 1983: 86 (description); Kononova 1995: 92 (keyed).

Trissolcus halyomorphae Yang, 2009: 40 (original description). **syn. n.**

Material examined. Holotype, female, *Dissolcus japonicus*: **JAPAN**: Kanagawa Pref., Ashigarashimo Dist., Hakone Town, Koebele, USNM Type No. 7127 (deposited in USNM). *Other material*: 2 paratype females of *Trissolcus halyomorphae*, **CHINA**: Xiangshan, Beijing 7-VIII-2001, reared from eggs of *Halyomorpha halys*, Yang, Z.-Q. Leg. USNM ENT 00872401-00872402 (USNM)

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Endnotes

- 1 urn:lsid:biosci.ohio_state.edu:osuc_pubs:97
- 2 urn:lsid:biosci.ohio_state.edu:osuc_pubs:944
- 3 urn:lsid:biosci.ohio_state.edu:osuc_pubs:310
- 4 urn:lsid:biosci.ohio_state.edu:osuc_pubs:602
- 5 urn:lsid:biosci.ohio_state.edu:osuc_pubs:688
- 6 urn:lsid:biosci.ohio_state.edu:osuc_pubs:326
- 7 urn:lsid:biosci.ohio_state.edu:osuc_pubs:364
- 8 urn:lsid:biosci.ohio_state.edu:osuc_pubs:1029
- 9 urn:lsid:biosci.ohio_state.edu:osuc_pubs:597
- 10 urn:lsid:biosci.ohio_state.edu:osuc_pubs:312
- 11 urn:lsid:biosci.ohio_state.edu:osuc_pubs:558
- 12 urn:lsid:biosci.ohio_state.edu:osuc_pubs:616
- 13 doi: 10.1603/008.102.0104
- 14 doi: 10.1371/journal.pone.0031246

