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Revision of *Ooctonus* in the Neotropical region and comparison with *Boudiennyia* (Hymenoptera: Mymaridae)

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Abstract

Ooctonus Haliday (Hymenoptera: Mymaridae) contains four species in the Neotropical Region: *O. clebschi* Huber, **sp. n.**, *O. costaricensis* Huber, **sp. n.**, *O. woolleyi* Huber, **sp. n.**, and *O. zolnerowichi* Huber, **sp. n.** *Ooctonus costaricensis* represents the furthest south *Ooctonus* has been recorded in the New World. An illustrated identification key to females is given. The genus is compared with *Boudiennyia* Girault, known only from Australia and New Caledonia. Despite many similarities, *Ooctonus* is treated as a somewhat isolated clade whereas *Boudiennyia*, apparently the most similar genus to *Ooctonus*, is treated as the basal clade of Mymarini *sensu* Annecke and Doutt. Reduction in tarsal number has occurred at least four times in three distantly related clades of extant Mymaridae: in *Eoforesteria* Mathot and *Ptilomymar* Annecke & Doutt, the latter newly placed in the *Camptoptera*-group of genera, in *Kikiki* Huber & Beardsley in the *Anagrus* group of genera, and in Mymarini except for *Boudiennyia*, and perhaps also *Ooctonus*.

Key words: Chalcidoidea, Mymarini, egg parasitoid, Mexico, Costa Rica

Introduction

This is the concluding paper of a series on *Ooctonus* Haliday (Hymenoptera: Mymaridae), a primarily Northern Hemisphere genus. Huber *et al*. (2010) treated the few species known from the Southern Hemisphere (South Africa and one adventive European species in New Zealand) and Huber (2012) the species from America north of Mexico, whereas Triapitsyn (2010) treated the species from the Palaearctic and Oriental regions. Guzmán-Larralde *et al*. (2001) first reported *Ooctonus* from Mexico, but without naming species. The species revised here are so far known only from Mexico and Costa Rica. They are treated as being from the Neotropical region although those examined from Mexico were collected at high elevation in habitats that are essentially Nearctic. The genus is compared with *Boudiennyia* Girault, known only from Australia and New Caledonia.

Material and methods

About 100 specimens were examined, 65 of them males. Photographs were taken with a digital scanning camera attached to a microscope, and the resulting layers combined electronically using Zerene Stacker® and retouched as needed with Adobe® Photoshop. Measurements are given in micrometers (µm). Body length was measured from critical point dried specimens; the remaining measurements are from cleared and slide mounted specimens. Structural terms and abbreviations are according to Huber (2012), who provided a generic diagnosis. A few corrections to that paper are made. The term 'marginal' or 'marginal/stigmal' vein was used in several species descriptions and for all of them the length measured was from the base of parastigma to the apex of stigmal vein. However, in the illustrations (Huber 2012, figs 9, 10, Table 1) the 'marginal' vein is correctly labelled as the parastigma. The parastigmas is defined as the distance from the base of the obviously sclerotized part of the parastigma just basal to the proximal macrochaeta (and posterior to the apex of the submarginal vein) to the distal macrochaeta. This definition matches the one in Heraty et al. (2013: 8) but differs slightly from the accompanying

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image (fig. 6m) where the apex of the parastigma is shown as extending to the campaniform sensilla labelled 'psts?'. The stigmal vein is measured from the distal macrochaeta to the apex of the venation. The correct term, parastigma, is used in the species descriptions below. In the list of abbreviations (Huber 2012, table 1) 'mtp' should be the mesotrochantinal plate, not metatrochantinal plate. Finally, abbreviations with subscripts appear correctly on the figures themselves but incorrectly (without subscripts) in the table. CO1 barcodes were obtained from three of five specimens using the protocols summarized in Huber (2012). Abbreviations used below are: fl = funicle segment; gt_1 = gastral tergum one.

Specimens are deposited in the following institutions:

CNC	Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Ontario.
ROM	Royal Ontario Museum, Toronto, Ontario.
TAMU	Texas A&M University, College Station, Texas.
UCRC	University of California, Riverside, California.

Key to *Ooctonus* species in the Neotropical region. Females.

1 Propodeum with median areole almost touching dorsellum, with extremely short and thick carinae (Figs 13, 14); clava without bullae (Figs 8, 9) . . . . *O. costaricensis*, **sp. n.**

\- Propodeum with median areole clearly separated from dorsellum by a median carina (Figs 15–17); clava with at least one group of at least 2 bullae (Figs 7, 10, 11) 2

2(1) Flagellum with fl_5 and fl_6 both without mps (Fig. 10); clava with bullae in 3 usually distinctly separate groups (Fig. 10), though apical two groups sometimes close together . . . . *O. woolleyi*, **sp. n.**

\- Flagellum with at least 1 mps on at least one of fl_5 and fl_6 or if exceptionally both without mps then clava with at most two groups of bullae (Fig. 7) 3

3(2) Flagellum with 2 mps on each of fl_5 and fl_6 (Fig. 11); clava at least 244 µm and with one group of 2 bullae just beyond middle of clava (Fig. 11) . . . . *O. zolnerowichi*, **sp. n.**

\- Flagellum with fewer mps on fl_5 and fl_6, either 2 and 1, 1 and 1, or 1 and 0 mps (Fig. 7); clava shorter, at most 230 µm, and with two groups of at least 3 bullae (usually more) beyond middle and near apex (Fig. 7) . . . . *O. clebschi*, **sp. n.**

Ooctonus clebschi **Huber, sp. n.**

(Figs 1, 2, 7, 15, 18, 22)

Type material. Holotype ♀ in CNC, on slide (Fig. 22) with two labels: 1. "Mexico: Oaxaca Llano de las Flores, 15 mi NE. Ixtlan de Juarez 21.vii.1985, J. Woolley & G. Zolnerowich". 2. "Ooctonus clebschi Huber Holotype ♀ dorsal".

Paratypes (5 ♀). **MEXICO**. **Michoacán**. 6 mi. N. Cheran, 8.vii.1985, J. Woolley, G. Zolnerowich (1♀, CNC). **Oaxaca**. Same data as holotype (2♀, CNC, UCRC); 1.4 mi NE La Cumbre, 18.vii.1985, J. Woolley, G. Zolnerowich (1♀, CNC); Santiago Comaltepec, hwy 17 km 108, Cerro Humochico, 2948m, 17.58° N 96.51° W, H. Clebsch, dense oak/pine forest, YPT (1♀, CNC).

Diagnosis. Clava with a cluster of 4–6 (rarely as few as 3) bullae just beyond middle and another near apex (Fig. 7); clava at most 230 µm long.

Females of *O. clebschi* are very similar to those of *O. zolnerowichi* except the clava is shorter and has far more bullae. Because females of the two species cannot be distinguished unless the bullae on the clava can be examined their correct identification requires cleared, slide mounted specimens. As a consequence, body length and colour cannot be described from critical point dried specimens because their identity is uncertain.

Description. **Female**. Body length and colour probably as for *O. woolleyi* (see below). *Head*. Width 306–393 (n=5). Vertex without stemmaticum (Fig. 1). Mid ocellus diameter 23–27. *Antenna*. Length/width measurements (n=6): scape 226–283, pedicel 67–82, fl_1 72–107, fl_2 78–115, fl_3 70–96, fl_4 54–70, fl_5 56–76, fl_6 41–66, fl_7 61–75, fl_8 57–71, clava 177–230. Flagellum (Fig. 7) total length 496–635; with 2 or, less often, 1 or rarely 0 mps on fl_5, 0 or 1 or rarely 2 mps on fl_6, and 2 mps on fl_7 and fl_8; fl_2 the longest funicle segment; fl_1–fl_6 length/width ratios (n=6): fl_1

4.26–4.90, fl_2 4.06–4.95, fl_3 3.09–3.93, fl_4 2.20–2.59, fl_5 1.99–2.42, fl_6 1.55–1.99; clava 3.04–3.83× as long as wide, slightly longer than fl_6– fl_8 together, with 7 mps and (internally) with two clusters of bullae. *Mesosoma*. Pronotum with collar moderately short (Fig. 15) but visible in dorsal view, with well defined transverse carina. Mesoscutal midlobe with engraved meshes; scutellar seta long, extending posteriorly to medially slightly concave frenal line; axilla reticulate, lateral panel of axilla and axillula smooth; frenum entirely reticulate. Metanotum with dorsellum smooth and lateral lobes with 2 longitudinal carinae (Fig. 15). Propodeum (Fig. 15) smooth between carinae; anterior margin with propodeal stub slightly lateral to lateral margin of dorsellum; median areole separated from dorsellum by a short carina; plica straight, its anterior limit in line with apex of stub. *Wings*. Fore wing (Fig. 18) length 1321–1642, width 453–632, length/width 2.55–2.92, and longest marginal setae 100–114, at most about 0.2× as long as greatest wing width (n=6). Hind wing (Fig. 18) length (n=6) 969–1253, width 54–82, and longest marginal setae 113–154. *Metasoma*. Petiole shorter than metacoxa + metatrochantellus. Gaster with ovipositor length 435–549 (n= 6), 0.92–1.06× as long as metatibia length (404–574), and projecting slightly beyond gastral apex.

Male. Unidentifiable to species, but probably present in material examined.

Etymology. The species is described in honour of Hans Clebsch, a professional French horn player with the Cleveland Orchestra and an amateur taxonomist who collected one of the females.

Hosts and Habitat. Hosts unknown; one specimen was collected in dense oak/pine forest.

Ooctonus costaricensis Huber, sp. n.

(Figs 3, 4, 8, 9, 13, 14, 19, 23)

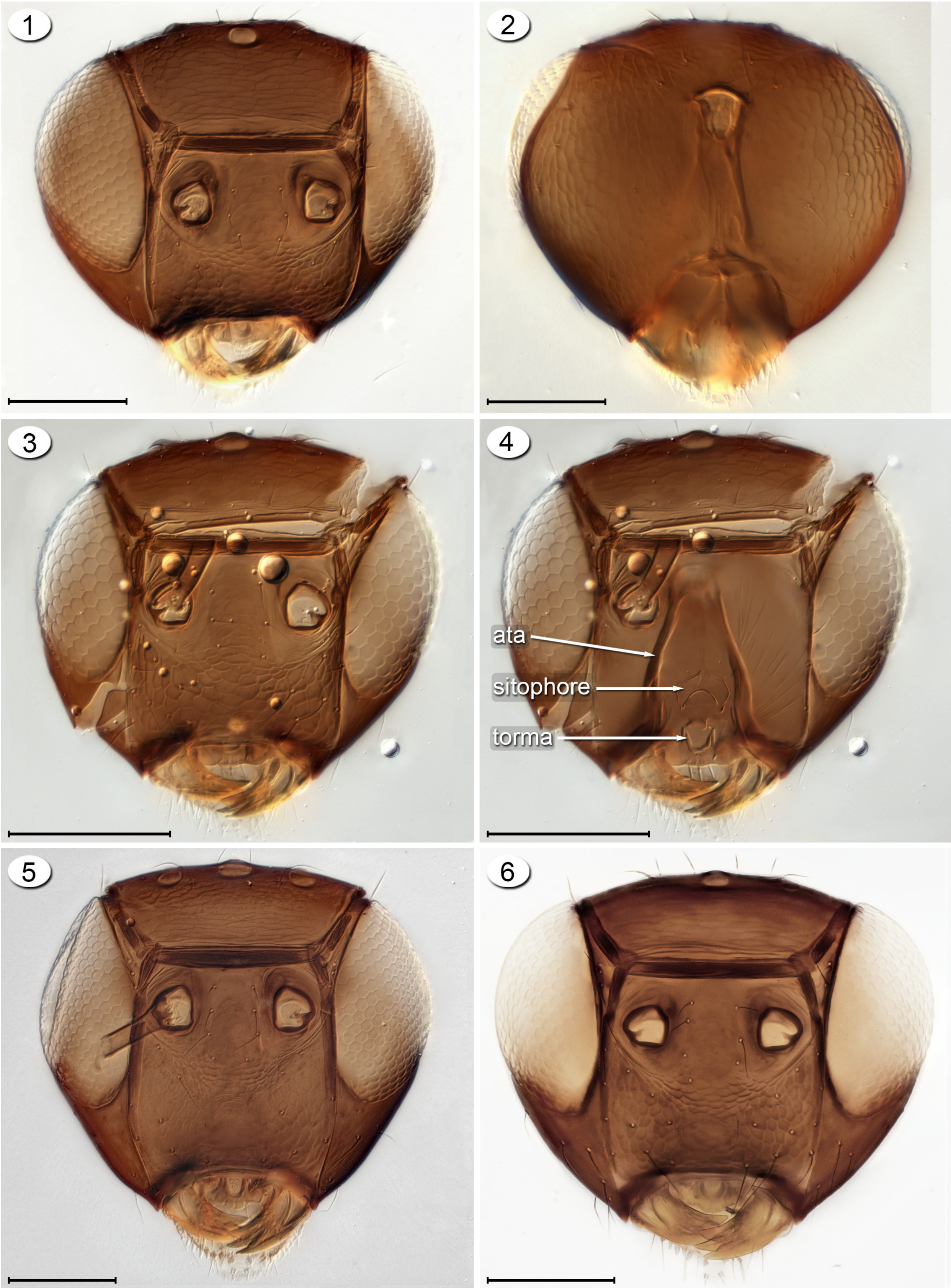
Type material. Holotype ♀ in UCRC, on slide (Fig. 23) with four labels: 1. "Costa Rica: San José Zurqui de Moravia 10.05ºN. 84.02ºW. vi.1995. P. Hanson Malaise trap. 1600m". 2. "UCRC Mounted at UCR/ERM by V.V. Berezovskiy 2008 in Canada balsam lateral". 3. "Univ. Calif. Riverside Ent. Res. Museum UCRC ENT 296747". 4. "Ooctonus costaricensis Huber ♀ Holotype dry body length 0.86 mm."

Paratypes (6 ♀). **COSTA RICA**. **Alajuela**. Rio Barranca, S. of Zarcerco, 12.xii.1987, P. Hanson, screen sweep, ROM 878012 (1 ♀, ROM). **San José**. Zurquí de Moravia, 1600m, v and viii.1995, P. Hanson (4 ♀, CNC, UCRC); San Antonio de Escazú, 700m, ix.1996, P. Hanson, C. Flores (1 ♀, CNC).

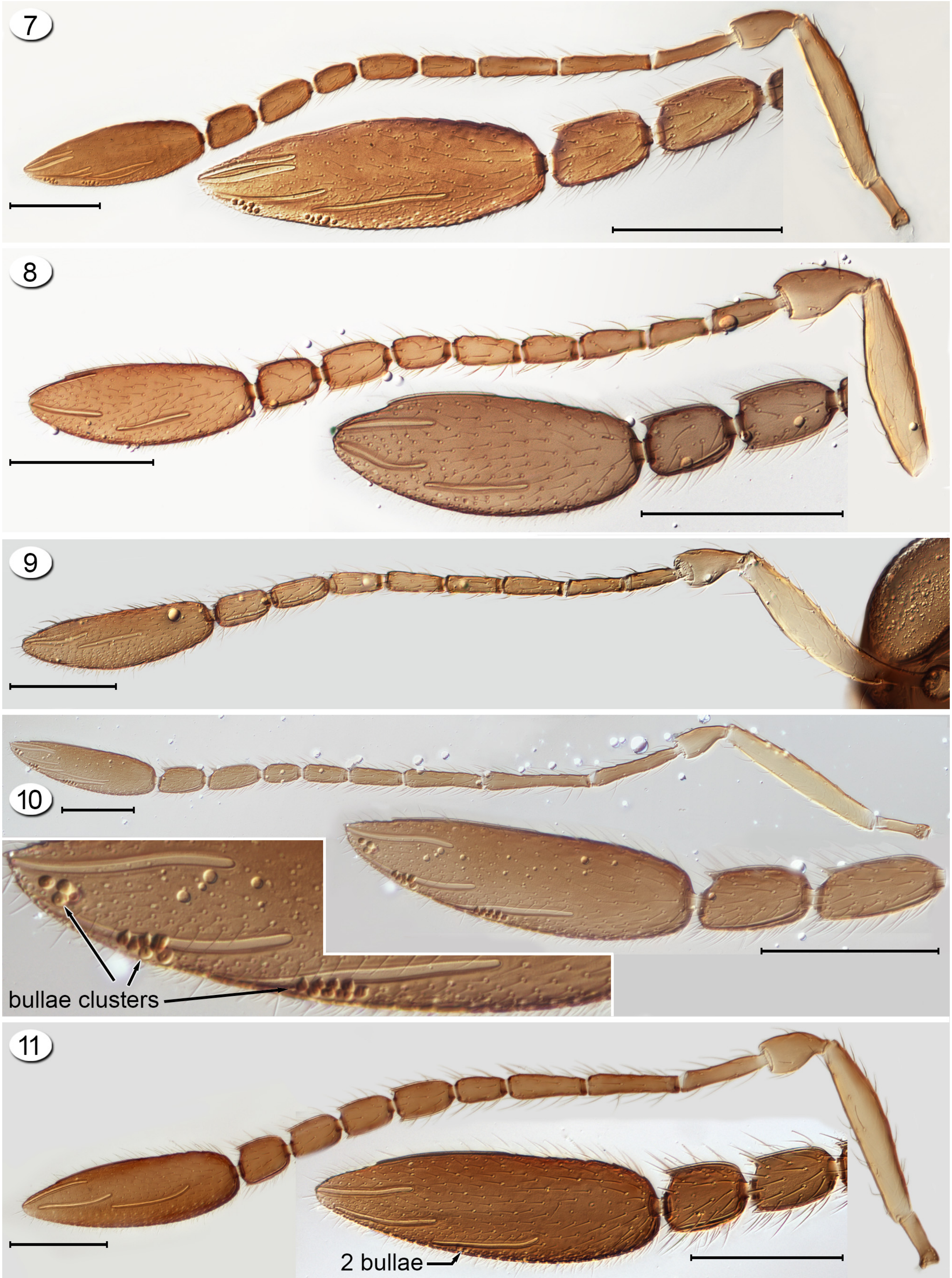
Diagnosis. Propodeum without a median carina so the pentagonal areole is almost in contact with the dorsellum (Figs 13, 14).

Females of *O. costaricensis* are most similar to those of *O. vulgatus* Haliday and *O. notatus* from America North of Mexico. They differ from *O. vulgatus* by the absence of claval bullae (a row of several bullae in *O. vulgatus*) and entirely reticulate frenum (medially smooth frenum in *O. vulgatus*), and from *O. notatus* by the lack of mps on fl_5 (two mps on fl_5 in *O. notatus*).

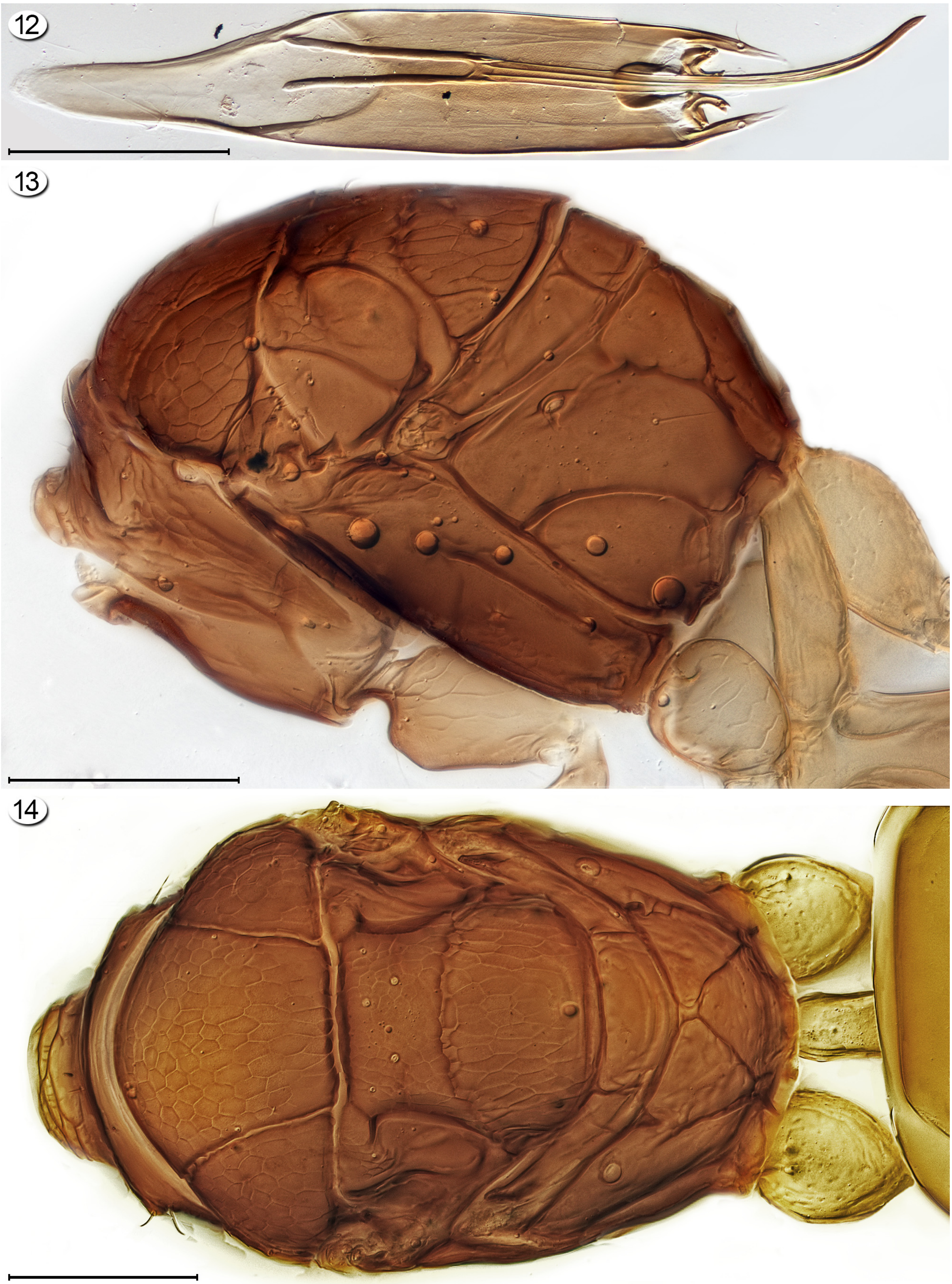
Description. Female. Body length 845–973 μm (critical point dried, n=5). Head except mouthparts and mesosoma almost black; metasoma mostly yellow or light brown, sometimes with ovipositor and surrounding area brown or apical half dorsally brown; procoxa and mouthparts brown; antenna dark brown except scape and pedicel laterally and ventrally yellow; petiole and legs except procoxa and apical tarsomere, yellow with brown on much of femora dorsally and laterally. Fore wing (Fig. 19) with distinct brown suffusion in basal half, especially along posterior margin. *Head*. Width (n=2) 262–306. Vertex without stemmaticum (Figs 3, 4). Mid ocellus diameter 23–27. *Antenna*. Measurements (length/width, n=2): scape 189–207/34–43, pedicel 68–74/36–37, fl_1 56–67/17, fl_2 46–64/18–19, fl_3 50–56/20–22, fl_4 40–52/21–22, fl_5 48–60/22–23, fl_6 44–45/24–25, fl_7 53–65/30, fl_8 49–57/32–34, clava 162–188/59. Flagellum (Figs 8, 9) total length 385–476; with 2 mps on fl_7 and fl_8; fl_1 slightly the longest funicle segment; fl_1–fl_6 length/width ratios (n=2): fl_1 3.31–4.00, fl_2 2.64–3.38, fl_3 2.43–2.56, fl_4 1.92–2.43, fl_5 2.13–2.57, fl_6 1.85–2.23; clava 2.75–3.19× as long as wide, slightly longer than fl_6–fl_8 together, with 7 mps and without bullae (Fig. 8, inset). *Mesosoma*. Pronotum (Figs 13, 14) with collar moderately short, with well defined transverse carina. Mesonotum midlobe with engraved meshes; scutellar seta moderately long, not quite extending posteriorly to medially straight frenal line; axilla reticulate, lateral panel of axilla and axillula smooth; frenum entirely reticulate. Metanotum with dorsellum smooth and lateral lobes with at most 1 longitudinal carina (Figs 13, 14). Propodeum (Fig. 14) slightly rugose between carinae; anterior margin with propodeal stub distinctly lateral to lateral margin of dorsellum; median areole almost abutting dorsellum, separated only by carina almost as wide as



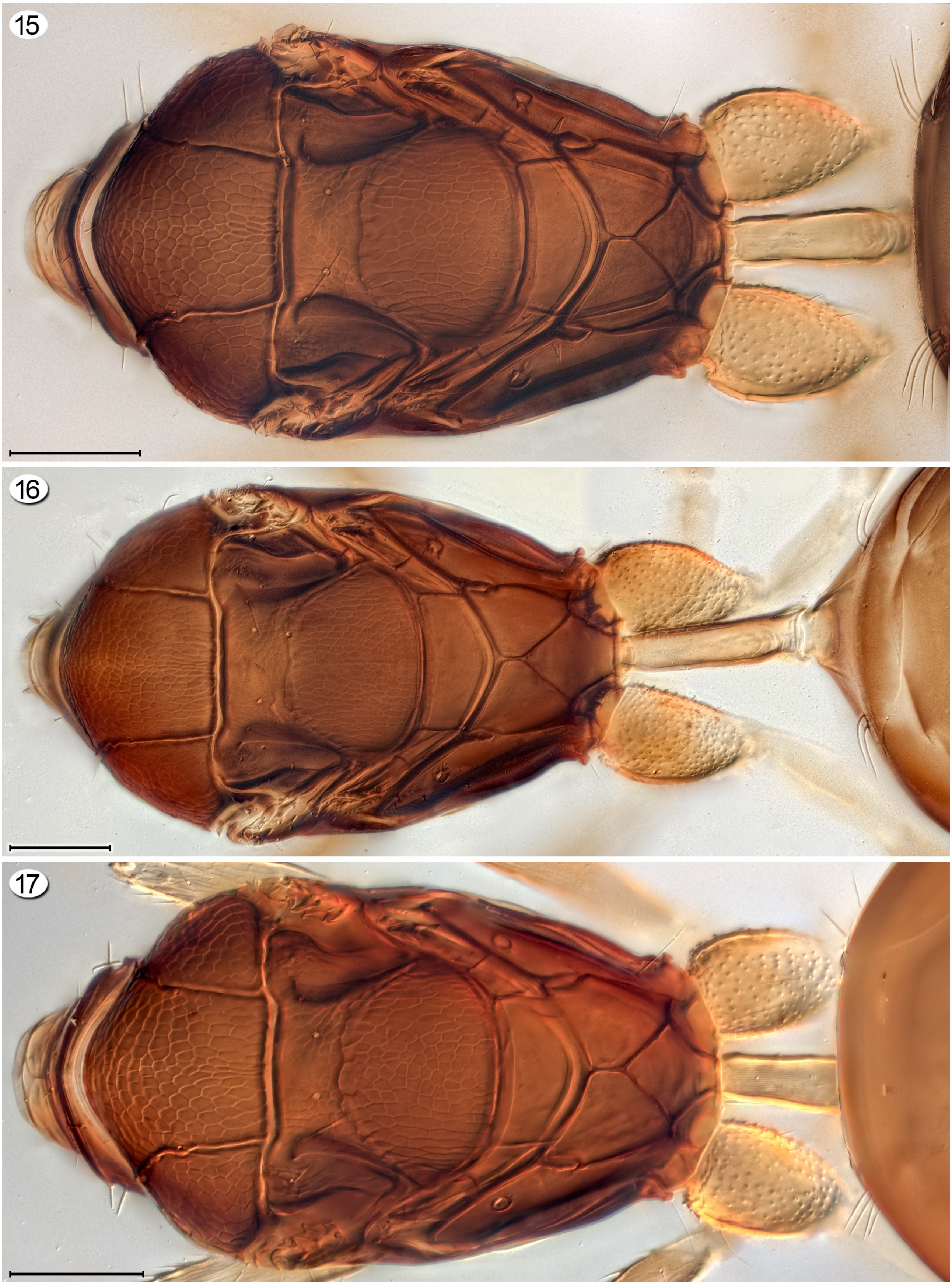
FIGURES 1–6. *Ooctonus* spp., head, holotypes. 1, *O. clebschi*, anterior; 2, *O. clebschi*, posterior; 3, *O. costaricensis*, anterior; 4, *O. costaricensis*, internal, showing tentorium, base of labrum with torma, and sitophore; 5, *O. woolleyi*, anterior; 6, *O. zolnerowichi*, anterior. **ata** = anterior tentorial arm. Scale bars are 100 µm.



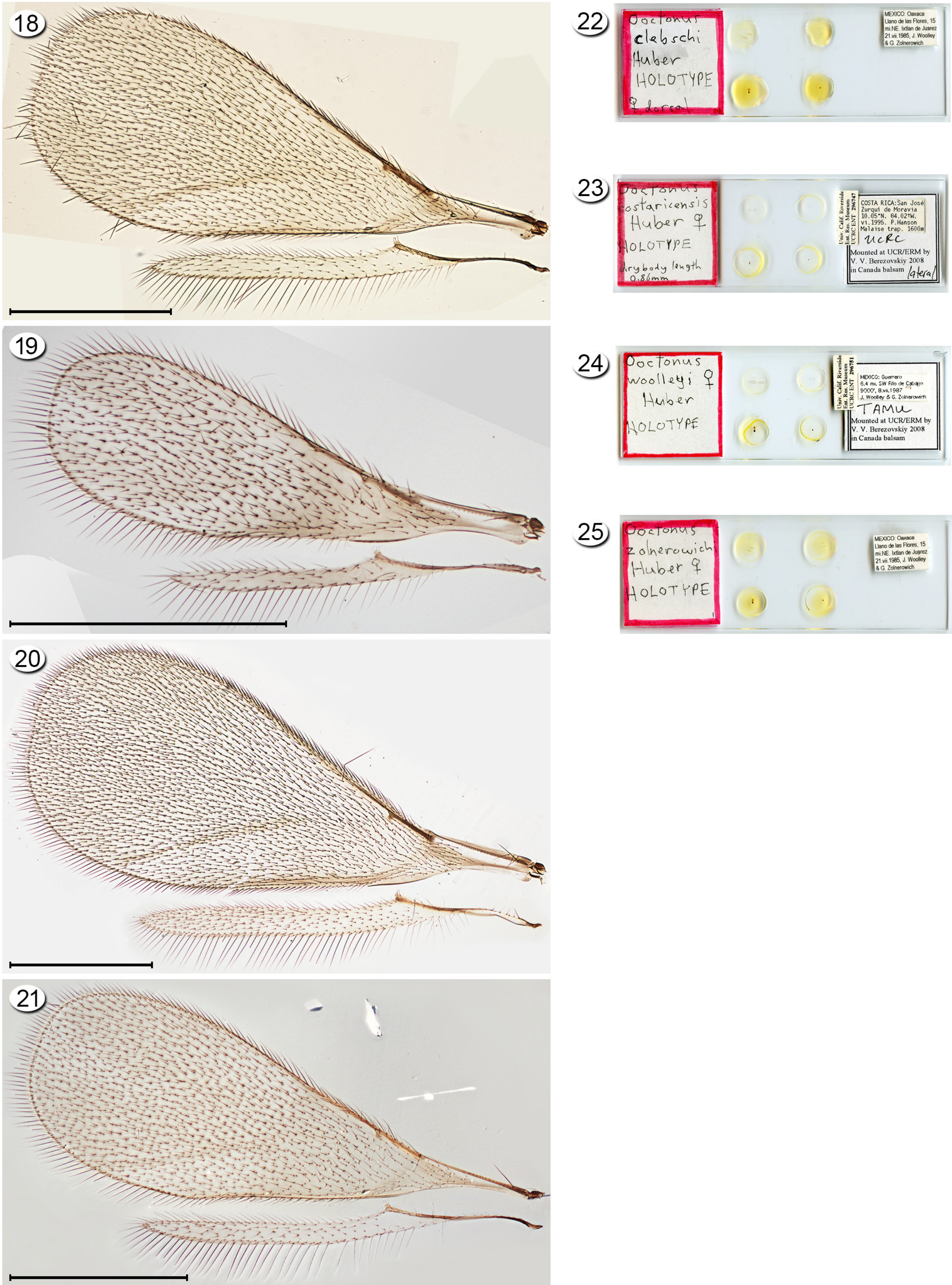
FIGURES 7–11. *Ooctonus* spp., female antenna (insets show clava – usually with bullae – and $fl_7 + fl_8$). 7, *O. clebschi,* holotype; 8, *O. costaricensis,* holotype; 9, *O. costaricensis*, paratype; 10, *O. woolleyi*, holotype; 11, *O. zolnerowichi*, holotype. Scale bars are 100 µm.



FIGURES 12–14. *Ooctonus* spp. 12, *O. woolleyi*, male genitalia; 13, *O. costaricensis*, mesosoma lateral, holotype; 14, *O. costaricensis*, mesosoma dorsal, paratype. Scale bars are 100 µm.



FIGURES 15–17. *Ooctonus* spp., mesosoma, dorsal. 15, *O. clebschi*, holotype; 16, *O. woolleyi*, holotype; 17, *O. zolnerowichi*, holotype. Scale bars are 100 µm.



FIGURES 18–25. *Ooctonus* spp., 18–21, wings; 22–25, type slides. 18, *O. clebschi*, holotype; 19, *O. costaricensis*, holotype; 20, *O. woolleyi*, holotype; 21, *O. zolnerowichi*, holotype; 22, *O. clebschi*; 23, *O. costaricensis*; 24, *O. woolleyi*; 25, *O. zolnerowichi*. Scale bars are 500 µm.

long; plica almost straight, its anterior apex clearly lateral to apex of propodeal stub and not extending to anterior margin. *Wings*. Fore wing (Fig. 19) length 902–1103, width 295–382, length/width 2.89–3.05, and longest marginal setae 90, 0.08–0.10× as long as greatest wing width (n=2). Hind wing (Fig. 19) length 682–834, width 41–52, and longest marginal setae 84–89 (n=2). *Metasoma*. Petiole shorter than metacoxa + metatrochantellus. Gaster with ovipositor length 441–450 (n=2), 1.14–1.37× as long as metatibia length (328–388) and projecting slightly beyond gastral apex.

Male. Unknown.

Etymology. The species is named after the country, Costa Rica, in which all the specimens were collected.

Hosts and Habitat. Unknown.

Ooctonus woolleyi **Huber, sp. n.**

(Figs 5, 10, 12, 16, 20, 24)

Type material. Holotype ♀ in TAMU, on slide (Fig. 24) with three labels: 1. "Mexico: Guerrero 6.4 mi. SW. Filo de Cabajjo [sic] 9000' 8.vii.1987, J. Woolley & G. Zolnerowich TAMU Mounted at UCR/ERM by V.V. Berezovskiy 2008 in Canada balsam". 2. "Univ. Calif. Riverside Ent. Museum UCRCENT 296751". 3. "Ooctonus woolleyi Huber & Holotype".

Paratypes (23 ♀, 8♂). **MEXICO**. **Guerrero**. Same data as holotype (8♂, TAMU, UCRC); 6.6 mi. SW Filo de Caballos, 12.vii.1985, J. Woolley & G. Zolnerowich (7 ♀, CNC, UCRC); 5 mi. SW Filo de Caballos, ca. 8000', 7.vii.1984, J.B.Woolley (1 ♀, CNC); 10.3 km SW Filo de Caballos, 2700m, 13 and 17.vii.1992, R.S. Anderson, oak/pine/fir forest (wet) (3 ♀, CNC). **Michoacan**. 6 mi. N. Cheran, 8.vii.1985, J. Woolley & G. Zolnerowich (2 ♀, CNC). **Oaxaca**. 1.4 mi. NE. La Cumbre, 18.vii.1985, J. Woolley, G. Zolnerowich (3 ♀, CNC).

Only the males from the type locality are designated paratypes. Males from elsewhere are not because at least some of them may be males of either *O. clebschi* or *O. zolnerowichi*, females of which were collected at some of the same locations as *O. woolleyi*.

Diagnosis. Flagellum with fl_5 and fl_6 lacking mps and clava with three clusters of bullae (other species with at most two sets of bullae), the basal cluster with two rows of about 4 bullae each and well separated from the subapical clusters, the latter with 4 or 3 bullae each and clearly separated (Fig. 10) or almost together; head slightly narrower (Fig. 5) than for females of other species.

Among the species North of Mexico, females of *O. vulgatus* only have several claval bullae, but these are in a single cluster (Huber 2012).

Description. Female. Body length 1400–1500 µm (critical point dried, n=5). Head except mouthparts and mesosoma very dark brown, almost black, metasoma and procoxa dark brown; antenna dark brown except scape and pedicel laterally and ventrally yellow; petiole and legs except procoxa, yellow with some brown on most of femora dorsally and laterally and on tibiae and apical tarsomere. *Head*. Width 311–364 (n=3). Vertex without stemmaticum (Fig. 5). Mid ocellus diameter 25–34. *Antenna*. Measurements (length/width, n= 4 or 5): scape 218–322/38–42, pedicel 68–80/36–42, fl_1 78–130/20–25, fl_2 96–154/22–28, fl_3 70–115/25–28, fl_4 48–76/24–27, fl_5 43–64/25–28, fl_6 41–57/26–30, fl_7 56–77/31–36, fl_8 48–70/33–44, clava 174–210/51–60. Flagellum (Fig. 10) total length 480–743; with 2 mps on fl_7, and fl_8; fl_2 the longest funicle segment; fl_1–fl_6 length/width ratios (n=5): fl_1 3.58–5.58, fl_2 4.14–5.70, fl_3 2.84–4.19, fl_4 1.92–3.08, fl_5 1.71–2.50, fl_6 1.60–2.01; clava 3.33–3.59× as long as wide, longer than fl_6– fl_8 together, with 7 mps and (internally) three clusters of bullae (Fig. 10, inset). *Mesosoma*. Pronotum (Fig. 16) with collar moderately short, with well defined transverse carina. Mesonotum midlobe with engraved meshes; scutellar seta moderately long, not quite extending posteriorly to medially slightly concave frenal line; axilla reticulate anteriorly, smooth posteriorly; frenum entirely reticulate. Metanotum with dorsellum smooth and lateral lobes smooth except for 1 (Fig. 16) or 2 longitudinal carinae. Propodeum (Fig. 16) smooth between carinae; anterior margin with propodeal stub just lateral to lateral margin of dorsellum; median areole separated from dorsellum by short median carina; plica almost straight, its anterior limit in line with propodeal stub apex, and with a short median branch extending to anterior margin of propodeum. *Wings*. Fore wing (Fig. 20) length 1388–1862, width 565–778, length/width 2.39–2.61, and longest marginal setae 69–98, about 0.13× as long as greatest wing width (n=5). Hind wing (Fig. 20) length (n=5) 1062–1400, width 66–105, and longest marginal setae 110–150. *Metasoma*. Petiole shorter than metacoxa + metatrochantellus. Gaster with ovipositor length 506–619 (n=5), 0.99–1.04× as long as metatibia length (446–628) and projecting slightly beyond gastral apex.

Male. Unidentifiable to species. The males from the same collecting event as the females are assumed to be conspecific with the female. Its genitalia are illustrated (Fig. 12).

Etymology. The species is described in honour of Jim Woolley, a good colleague at Texas A&M University, who collected some of the specimens.

Hosts and Habitat. Primary cloud forest of deciduous trees and conifers.

Ooctonus zolnerowichi **Huber, sp. n.**
(Figs 6, 11, 17, 21, 25)

Ooctonus sp.: Huber, 2012: 104 (barcoded).

Type material. Holotype ♀ in CNC, on slide (Fig. 25) with two labels: 1. "Mexico: Oaxaca Llano de las Flores, 15 mi NE. Ixtlan de Juarez 21.vii.1985, J. Woolley & G. Zolnerowich". 2. "Ooctonus zolnerowichi Huber ♀ holotype".

Paratypes (6 ♀, 1 ♂). **MEXICO**. **Oaxaca**. Same data as holotype (2♀, 1♂, CNC—2 specimens barcoded: CNCHYM07520 and CNCHYM07521); Santiago Comaltepec, hwy 17 km 108, Cerro Humochico, 2948 m, 17.58º N 96.51º W, H. Clebsch, dense oak/pine forest, YPT (3♀, CNC, UCRC); Cerro Pelón, km 108.5, 2945m, 17º34.73'N 96º30.43'W, 27–28.vi.2006, alpine fir (1♀, CNC).

Diagnosis. Clava with one cluster of 2 bullae just beyond midpoint and at least 240 µm long.

Females of *O. zolnerowichi* are very similar to those of *O. clebschi*, as discussed under the later species. Body length and colour of the male are described from the single, card-mounted male whose barcode matches that of the female (CNCHYM07521 [Genebank Accession Number KC 157693]). The specimen was soaked in a solution to extract DNA for barcoding prior to colour description so its colour may have been modified slightly. The only female that gave a useful barcode was slide mounted so its colour is not described.

Description. Female. *Head*. Width 348–387 (n=5). Vertex without stemmaticum (Fig. 6). Mid ocellus diameter 22–27. *Antenna*. Measurements (length/width, n=7): scape 262–286/37–44, pedicel 70–78/41–44, fl_1 73–101/21–24, fl_2 88–107/23–25, fl_3 75–89/26–30, fl_4 58–67/27–37, fl_5 70–79/35–40, fl_6 52–65/30–40, fl_7 62–72/38–46, fl_8 63–71/43–52, clava 244–272/73–79. Flagellum (Fig. 11) total length 550–634; with 2 mps (exceptionally 1 on one antenna) on fl_5, 1 mps (sometimes 2, exceptionally 0 on one antenna) on fl_6, 2 mps on fl_7 and fl_8; fl_2 the longest funicle segment; fl_1–fl_6 length/width ratios (n=6): fl_1 3.80–4.36, fl_2 3.75–4.67, fl_3 2.95–3.15, fl_4 1.82–2.46, fl_5 1.74–2.11, fl_6 1.36–1.74; clava 3.12–3.68× as long as wide, and longer than fl_6– fl_8 and sometimes even fl_5–fl_8, with 7 mps and one cluster of 2 bullae submedially. *Mesosoma*. Pronotum (Fig. 17) with collar moderately short, with well defined transverse carina. Mesonotum midlobe with reticulate sculpture; scutellar seta long, extending posteriorly slightly past medially fairly straight frenal line; axilla reticulate, lateral panel of axilla and axillula smooth; frenum entirely reticulate. Metanotum with dorsellum smooth and lateral lobes with 1–3 longitudinal carinae (Fig. 17). Propodeum (Fig. 17) smooth between carinae; anterior margin with a stub slightly lateral to lateral margin of dorsellum; median areole separated from dorsellum by a short carina; plica slightly curved anteriorly, its anterior limit in line with apex of stub. *Wings*. Fore wing (Fig. 21) length 1438–1738, width 507–674, length/width 2.58–2.82, and longest marginal setae 98–116, about 0.16–0.22× as long as greatest wing width (n=7). Hind wing (Fig. 21) length 1078–1338 (n=7), width 66–80, and longest marginal setae 134–157. *Metasoma*. Petiole shorter than metacoxa + metatrochantellus. Gaster with ovipositor length 518–603 (n=5), 0.09–1.16× as long as metatibia length (498–575) and projecting slightly beyond gastral apex.

Male. Body length 1280 µm (critical point dried, barcode CNCHYM07520 [Genebank Accession Number KC157694]). Head except mouthparts and mesosoma very dark brown, almost black, metasoma and procoxa brown; antenna dark brown except scape and pedicel laterally and ventrally yellow; petiole and legs except procoxa, yellow with a little brown on most of femora dorsally and laterally and on tibiae and apical tarsomere. Mid ocellus diameter 30. *Antenna*. Length (slide mounted after barcoding): scape 205, pedicel 70, fl_1 135, fl_2 140, fl_3 140, fl_4 140, fl_5 140, fl_6 135, fl_7 135, fl_8 130, fl_9 130, fl_{10} 130, fl_{11} 135. Total flagellar length 1490; fl_6 length/width 4.5.

Etymology. The species is described in honour of Greg Zolnerowich, a colleague at Kansas State University who collected some of the specimens.

Hosts and Habitat. Hosts are unknown. Specimens were collected in dense oak/pine forest and one was from a habitat with alpine fir.

Discussion Although the number and distribution of mps on one or two funicle segments of the left and right antenna can differ in the same specimen, this does not happen with the bullae of the clava. The distribution and number of claval bullae thus seem to be reliable features for distinguishing females of some *Ooctonus* species. In fact, females of two of the species treated here, *O. clebschi* and *O. zolnerowichi*, can only be separated reliably based on the distribution of bullae. Claval length is the only other feature that might be used to separate them. The two species are sympatric, having been collected together in at least two different Mexican localities. *Ooctonus woolleyi* was also collected in the same localities as *O. clebschi*. Again, the fact they are sympatric suggests they are good species. Had this not been the case the value of bullae numbers and distribution would be compromised, because it could be argued that the different locations and habitat in which the specimens were collected may be the reason for the differences. Additional barcoding of freshly collected females should confirm that *O. clebschi* and *O. zolnerowichi* are distinct species.

At least 14 *Ooctonus* species from outside the Neotropical region (Afrotropical, Nearctic, Palearctic) also have claval bullae. However, except for *O. vulgatus*, which has a row of several bullae, the bullae were not noticed by Huber (2012) or other authors because they are almost always only two of them, located together medially or submedially. Exceptions are *O. novickyi* Soyka with 3 bullae and *O. triapitsyni* Huber with 2–4 bullae. Two South African species are unusual. In *O. capensis* Huber the two bullae are U-shaped, different from the spherical bullae of most other species, whereas in *O. infuscatus* Huber there are 3 bullae so close together at the claval apex that they appear to be one large bulla. It would be interesting to find out more about their structure and function, and whether their number and distribution is always constant within a species.

Three Mexican specimens that yielded barcodes are clearly different morphologically and genetically from species found north of Mexico (Huber 2012, fig. 200). Two of the specimens [CNCHYM07520, CNCHYM07521] are included in *O. zolnerowichi*. The third specimen [CNCHYM07518] yielded a 121 bp barcode. When the two barcodes from *O. zolnerowichi* and CNCHYM07518 were aligned, five differences in base pairs were found. This indicates the presence of two species, which is supported by morphology. The pentagonal alveole in CNCHYM07518 abuts the dorsellum, as in *O. costaricensis*, but it is clearly a different species. Unfortunately, it is known only from males: from Puebla, 3.7 mi S. Zacapoaxtla (1 ♂, CNC), and Michoacan, 2 mi. S. Carapan (10 ♂, CNC) and 6 mi. S. Cheran (12 ♂, CNC). It cannot be described meaningfully until females are collected. Two other specimens [CNCHYM07517, CNCHYM07519] yielded no barcode and a trace barcode, respectively.

Boudiennyia Girault

(Figs 26–64)

Boudiennyia Girault, 1937: 2; Lin *et al.*, 2007: 11, 15 (key), 27 (diagnosis).

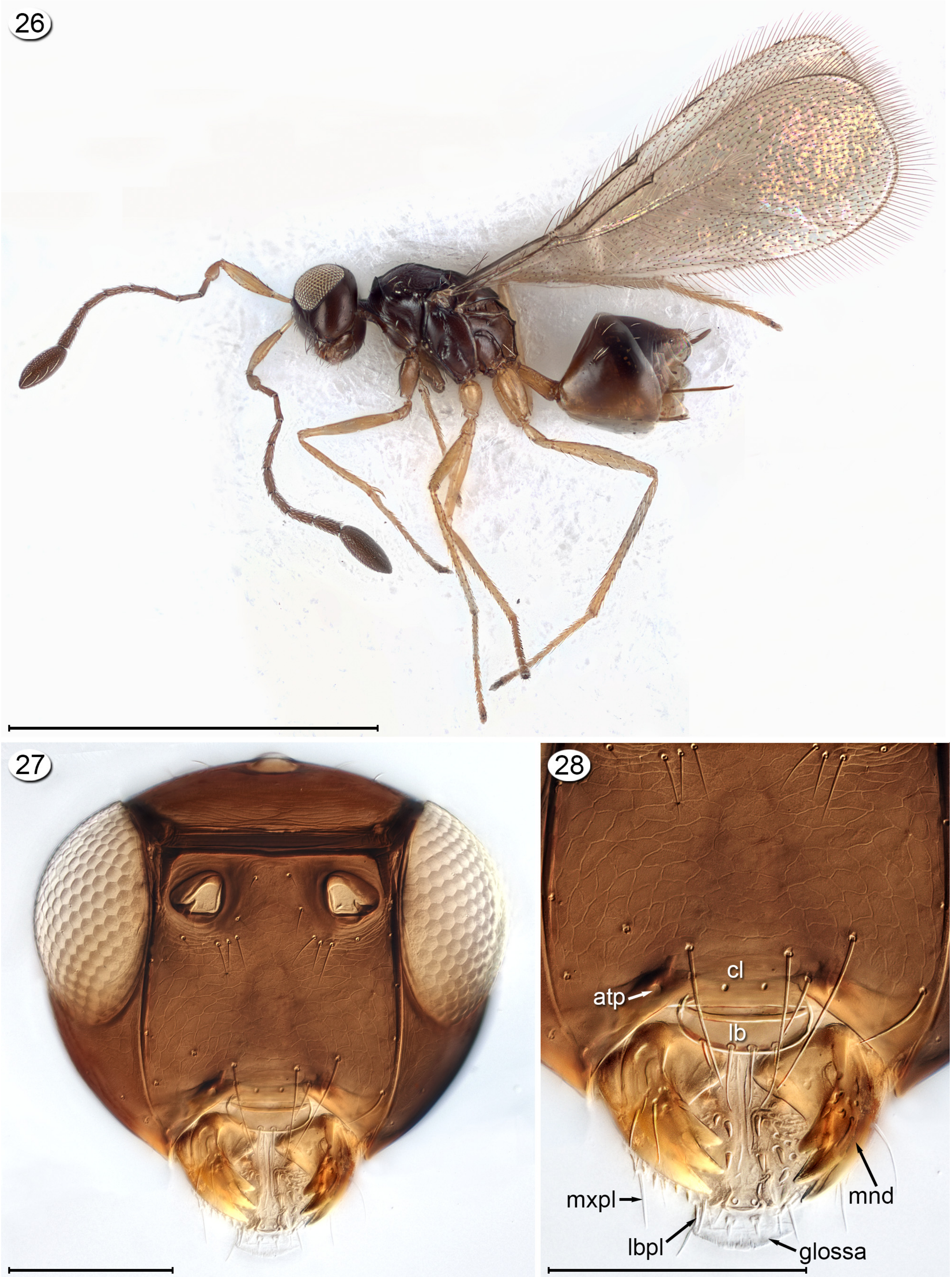
Diagnosis. *Boudiennyia* is distinguished from *Ooctonus* and all other mymarid genera by the scutellum with paired, star-shaped internal structures posterior to the placoid sensilla (visible only in cleared slide mounts) (Fig. 33), and the propodeum with a quadrate median areole (Figs 33, 50) bounded by distinct carinae and well separated from the dorsellum by slightly diverging sublateral carinae that extend from the dorsolateral corner of the areole and flare laterally to extend parallel with posterior margin of the metanotum to the anterolateral apex of the propodeum. Other features that distinguish the two genera are listed in Table 1.

Superficially, *Ooctonus* and *Boudiennyia* are similar in general appearance (Fig. 26, and Huber 2012, figs 2–5). They have the same body colour, with dark brown body and light coloured petiole (as in various *Polynema*-group genera), a well sclerotized gaster that does not collapse significantly when air dried, and a wide and apically truncate fore wing with a distinct oblique hair line that extends from near the venation apex toward the posteroapical margin of the wing (Figs 26, 36). Structural features that appear to unite *Ooctonus* + *Boudiennyia* are: 8-segmented female clava; 5-segmented tarsi, pronotum with transverse carina separating collar from neck; hypochaeta next to proximal macrochaeta (as in most mymarid genera); venation parallel with fore wing margin; long and narrow petiole; gt_1 much the largest tergum (the latter two features as in most Mymarinae, sensu Annecke and Doutt 1961); and a group or row of setae on gt_1 anterolaterally (Figs 32, 37, 38). But many features are different between the two genera (Table 1).

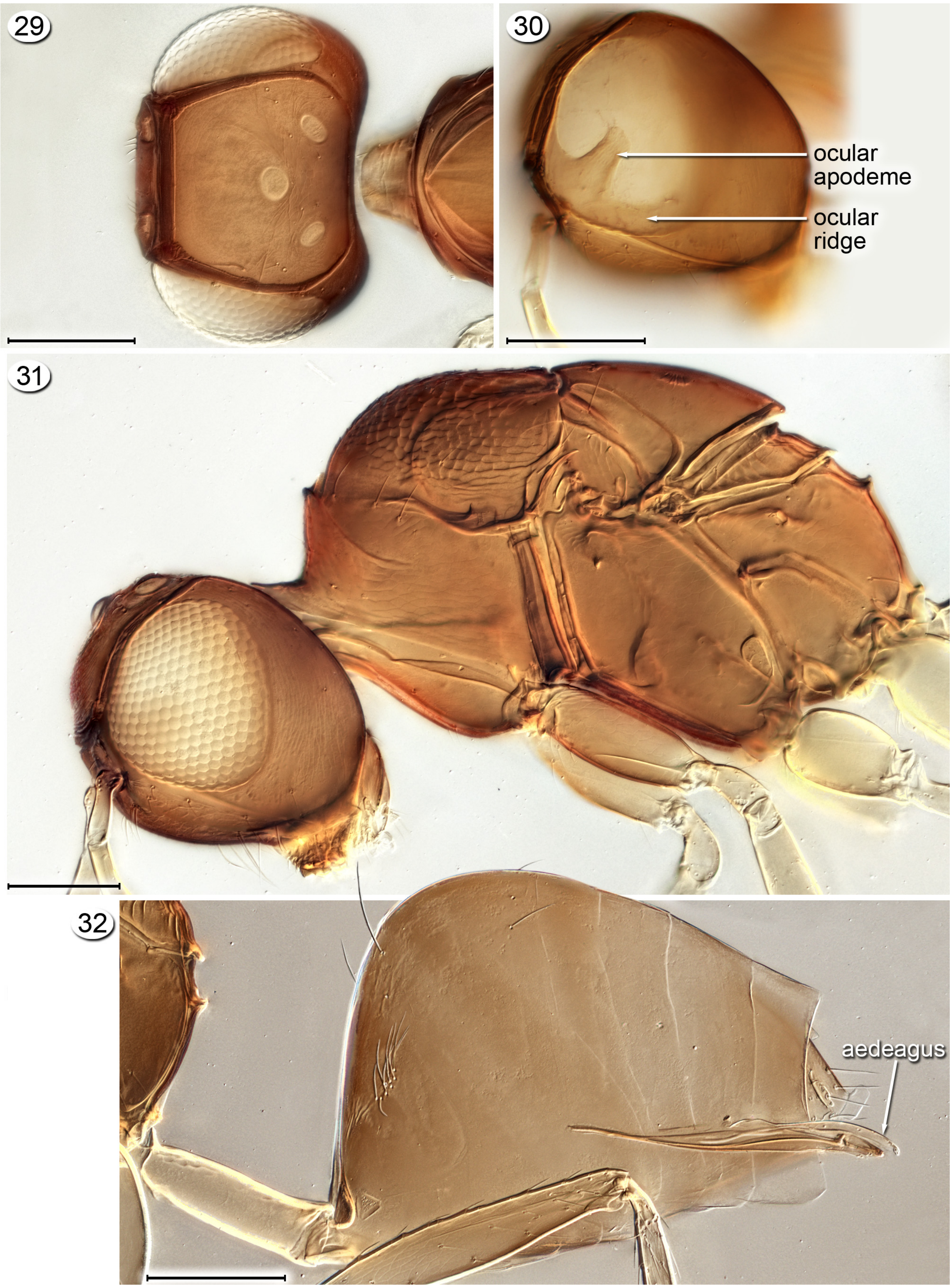
TABLE 1. Contrast of morphological features in specimens of *Ooctonus* and *Boudiennyia*. Figures with a lower case 'f' are from Huber (2012); otherwise they are in the present paper.

Character	*Ooctonus*	*Boudiennyia*
Labral setae	5	4 (Fig. 28)
Setae above clypeus	Usually short	Long (Figs 27, 28)
Anterior tentorial pits	Hidden (barely visible)	Clearly visible (Figs 27, 46)
Ocular apophysis	Longer (fig. 62)	Shorter (Fig. 30)
Claval mps	7 (rarely 8) (Figs 7–11)	10 (Fig. 33)
Propleura	Short median line of junction (fig. 197)	Long median line of junction (Fig. 49)
Prosternum	Large (fig. 197)	Small (Fig. 49)
Notauli	Well defined (Figs 13–17)	Poorly defined (Fig. 47)
Scutellum	Sculptured (Figs 14–17)	Smooth (Fig. 47)
Fenestra	Short and narrow, triangular (fig. 109)	Large, circular (Fig. 33)
Frenum	Clearly separate (Figs 13–17)	Undefined (Figs 47, 48)
Axillula	Not extending to lateral lobe of mesoscutum (Figs 13–17)	Extending to lateral lobe of mesoscutum (Figs 33, 47, 48)
Mesodiscrimen	Distinct (fig. 197)	Indistinct (Fig. 49)
Mesofurcal pit	Large, circular (fig. 197)	Small, linear (Fig. 49)
Parastigma	Shorter; venation 0.35 wing length (Figs 18–21)	Longer; venation 0.50 wing length (Fig. 36)
Lateral panel of metanotum	With few carinae (Figs 13–17)	With many carinae (Figs 48, 50)
Metapleural pit	Absent (fig. 6)	Present (Fig. 48)
Metadiscrimen	Absent	Present (Fig. 49)
Mesopectus (= mesosternum) in ventral view	Merging smoothly laterally with mesepisternum (Fig. 197)	Separated laterally from mesepisternum by ridge (Fig. 49)
Propodeal stub	Usually present (Figs 13–17)	Absent (Fig. 50)
Petiole	Ventrally with partial longitudinal suture (fig. 198)	Ventrally without longitudinal suture (Fig. 57)
Gt_1 setae	Cluster of 3; no setae dorsomedially (figs 195, 196)	Row of 2 to several, and 1–3 dorsomedially (Figs 32, 37, 38)
Gt_1 shape in dorsal view	Posterior margin straight medially (fig. 196)	Posterior margin strongly V- shaped (Fig. 54)
Male genitalia	Aedeagal apodemes diverging, not united anteriorly (Fig. 12)	Aedeagal apodemes converging, united anteriorly (Fig. 40)

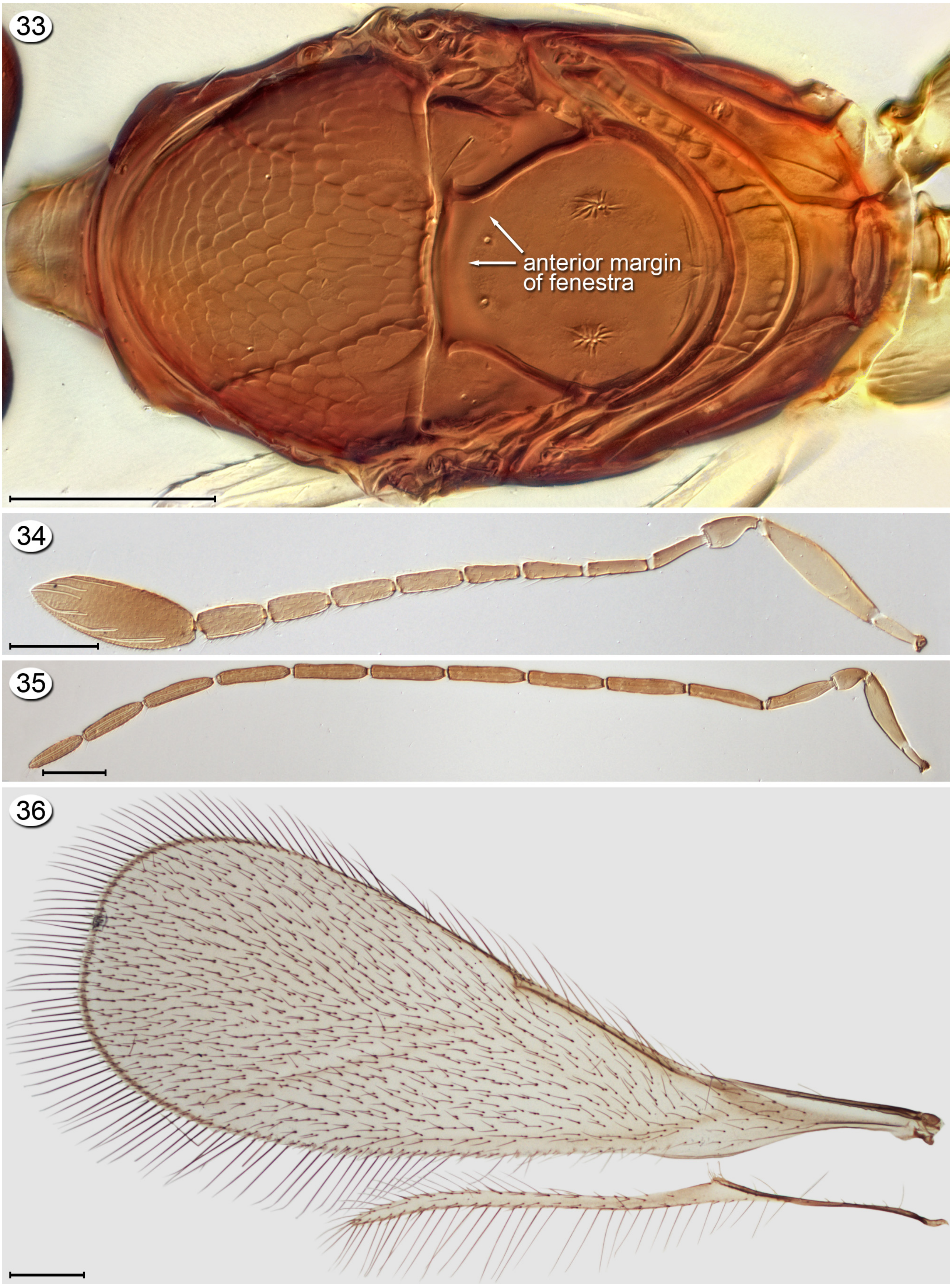
Discussion Under their treatment of *Gonatocerus* Nees (as *Lymaenon* Walker), Annecke & Doutt (1961) noted some important differences between *Cosmocomoidea* Howard, originally proposed as a subgenus of *Gonatocerus* but synonymized under *Ooctonus* by two previous workers, and *Ooctonus*. The differences they noted were position of the hypochaeta and structure of the petiole, which has a different type of junction with gt_2. However, they still placed *Ooctonus* together with *Gonatocerus* and somewhat similar genera in Ooctonini. They did not mention *Boudiennyia* at all, which is known only from Australia and New Caledonia and was unknown except as a name to most mymarid taxonomists. Consequently, they could not comment upon its defining features or its relationships. Based on morphology, Schauff (1984) treated *Ooctonus* as the sister group of *Gonatocerus*. He did not treat *Boudiennyia* because his study was limited to the Nearctic fauna. Because the defining features used for *Gonatocerus* + *Ooctonus* are plesiomorphies, as Schauff (1984) acknowledged, they are inadequate to support a



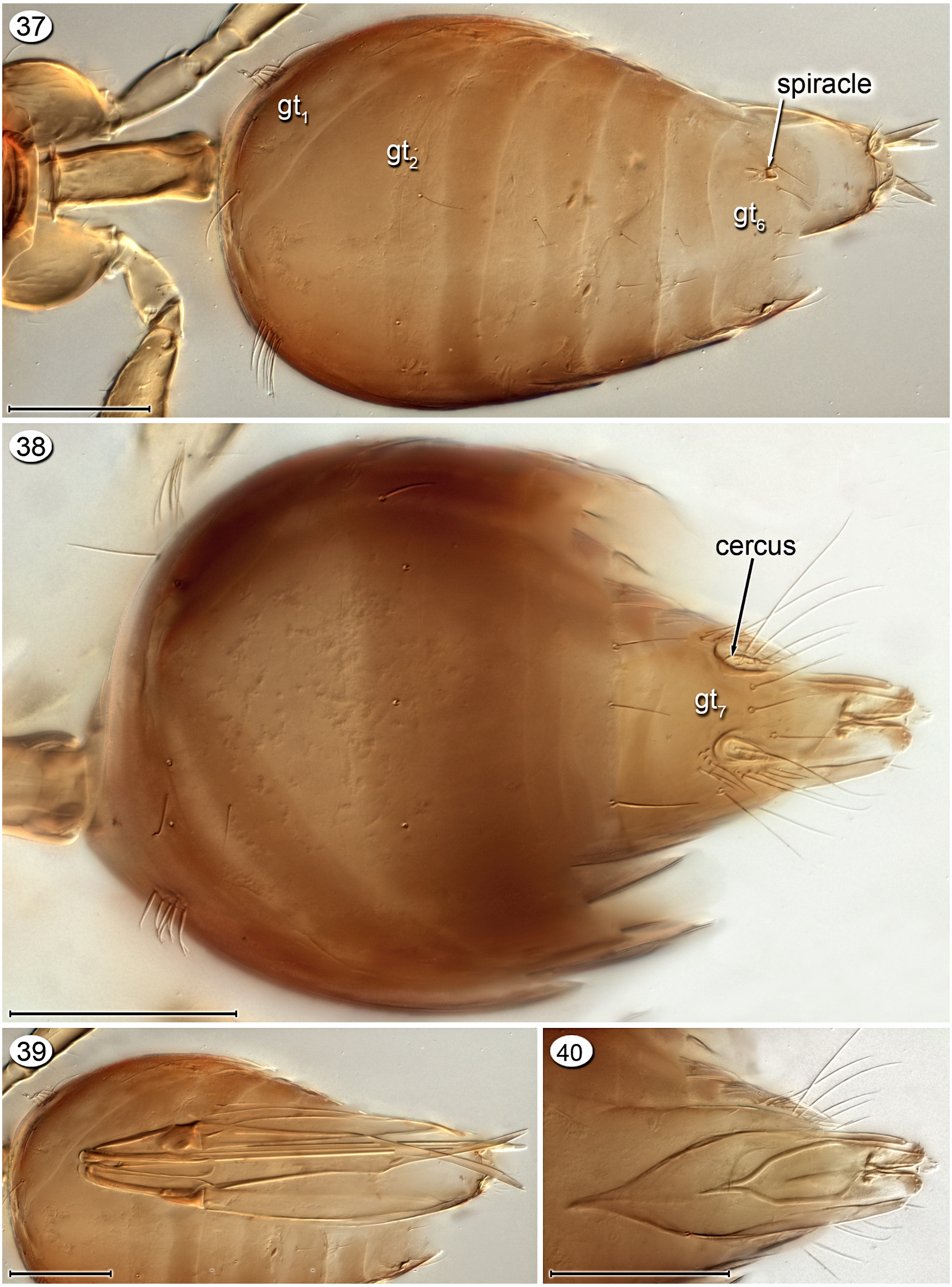
FIGURES 26–28. *Boudiennyia* sp. 26, female habitus; 27, head, anterior; 28, mouthparts, anterior. **atp** = anterior tentorial pit, **cl** = clypeus, **lb** = labrum, **lbpl** = labial palpus, **mnd** = mandible, **mxpl** = maxillary palpus. Scale bar for 26 = 1000 µm; for 27 and 28 = 100 µm.



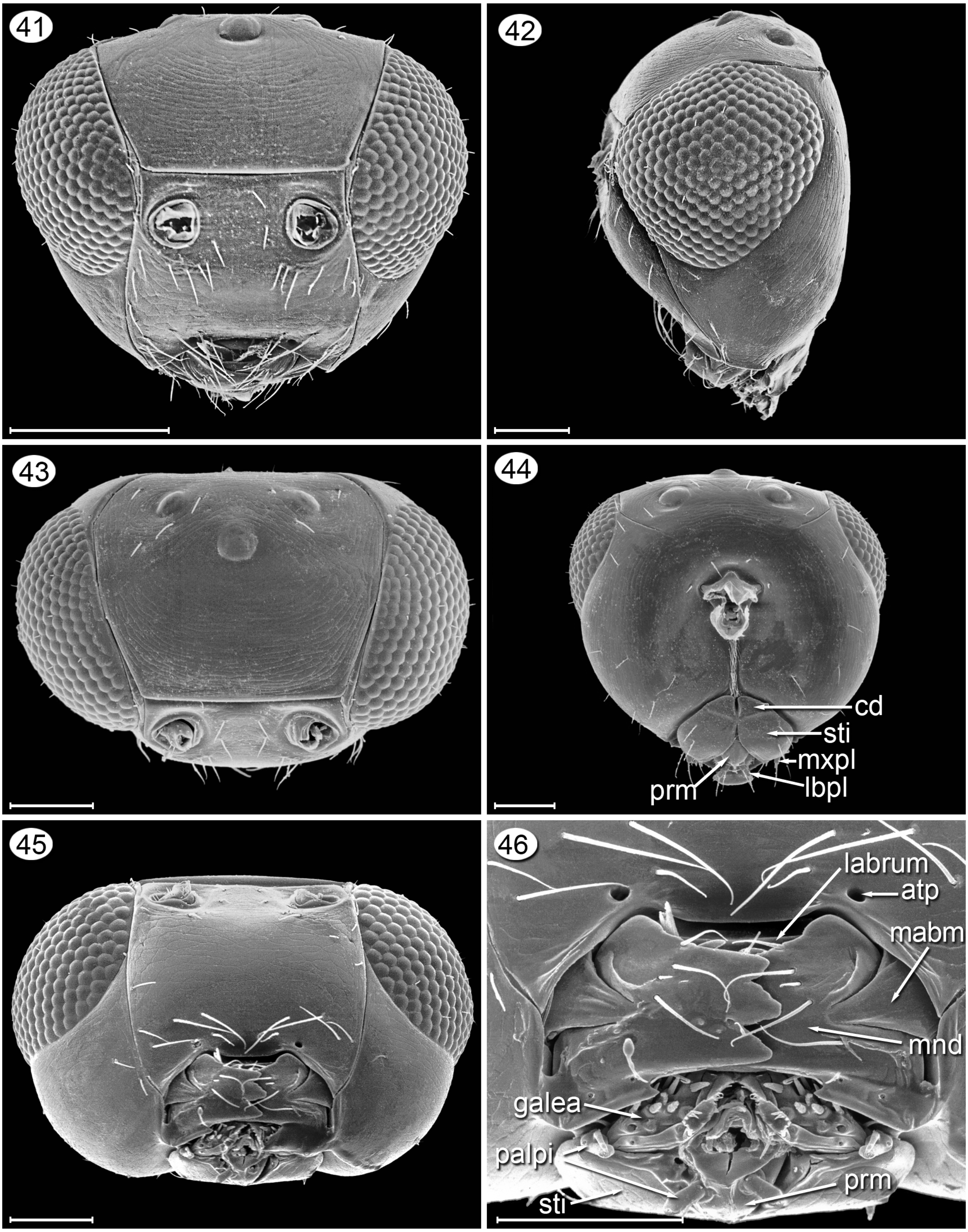
FIGURES 29–32. *Boudiennyia* sp. 29, head, dorsal, female; 30, head, lateral (internal), male; 31, head + mesosoma, lateral, male; 32, metasoma, lateral, male. Scale bars are 100 µm.



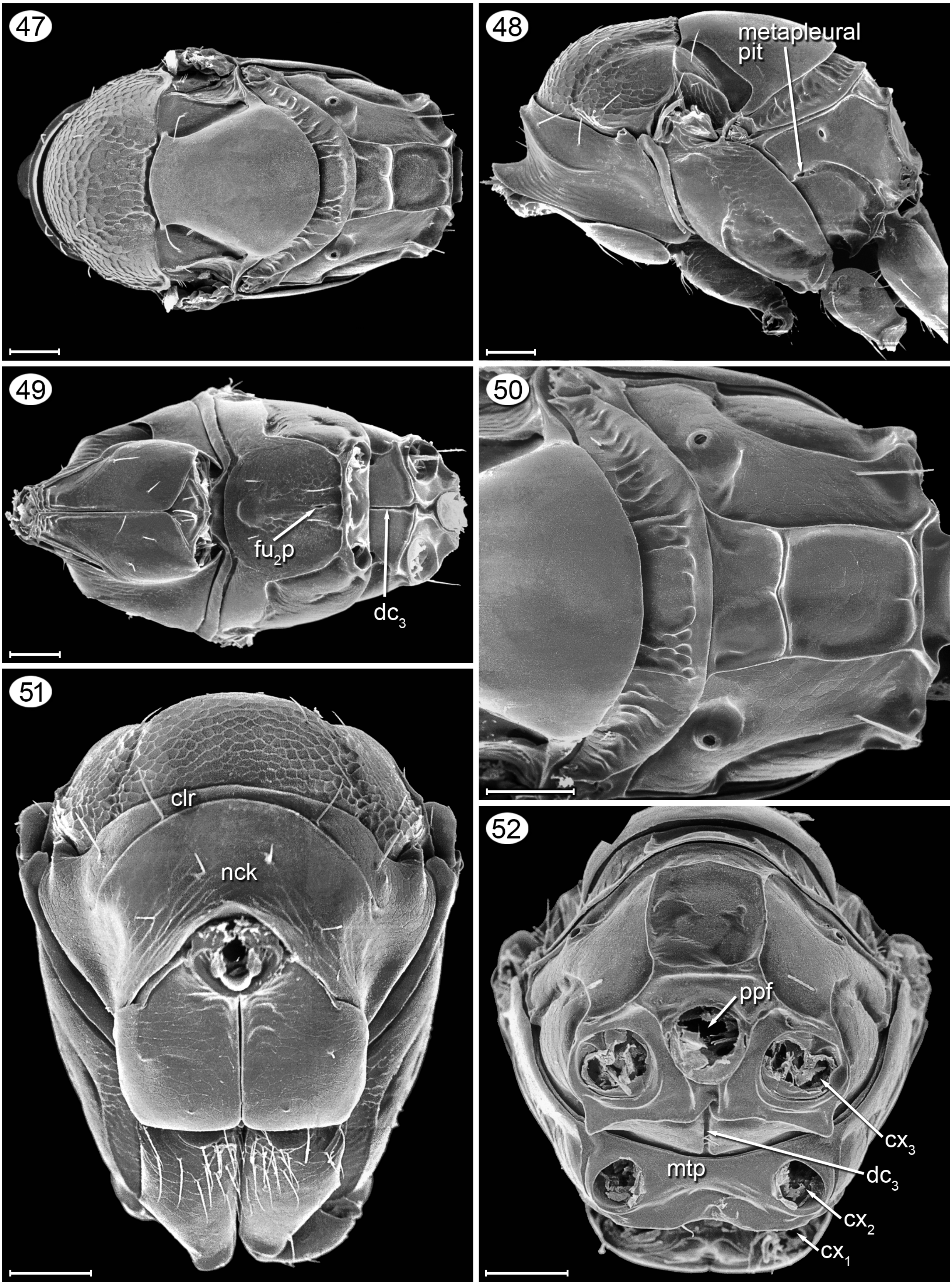
FIGURES 33–36. *Boudiennyia* sp. 33, mesosoma, dorsal, female; 34, antenna, female; 35, antenna, male; 36, wings, female. Scale bars are 100 µm.



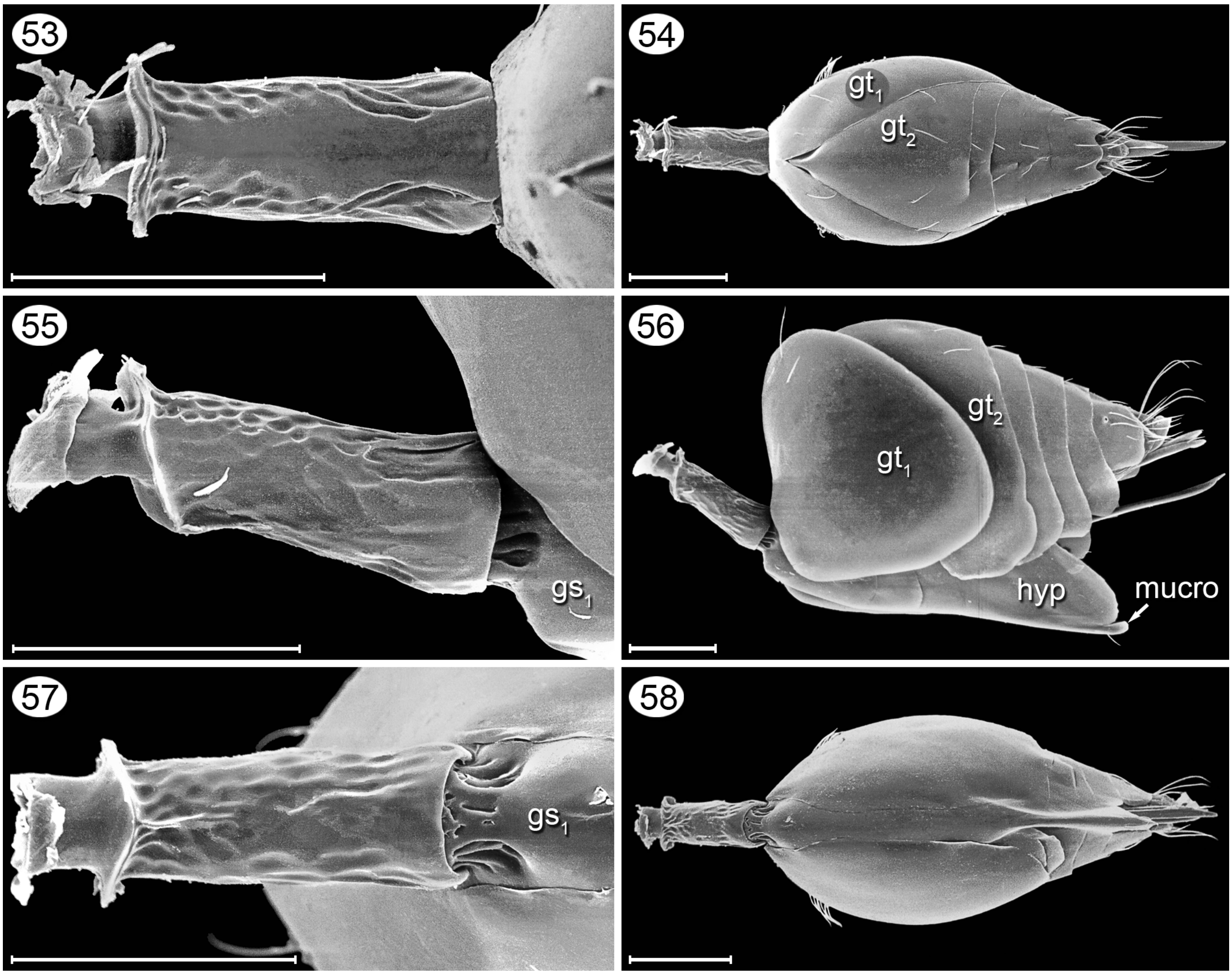
FIGURES 37–40. *Boudiennyia* sp. 37, metasoma, dorsal (gt_7 detached from gt_6); 38, gaster, male; 39, ovipositor (seen through gaster); 40, genitalia, male (seen through gaster). **gt** = gastral tergum. Scale bars are 100 µm.



FIGURES 41–46. *Boudiennyia* sp., female except 44, scanning electron micrographs (SEM). 41, head, anterior; 42, head, lateral; 43, head, dorsal; 44, head, posterior; 45, head, ventral; 46, mouthparts. **atp** = anterior tentorial pit, **cd** = cardo, **mabm** = mandibular abductor muscle, **mnd** = mandible, **sti** = stipes, **prm** = prementum. Scale bars are 50 µm.



FIGURES 47–52. *Boudiennyia* sp., female except 49, SEM. 47, mesosoma, dorsal; 48, mesosoma, lateral; 49, mesosoma, ventral; 50, frenum–propodeum, dorsal; 51, mesosoma, anterior; 52, mesosoma, posterior. **clr** = collar, **cx** = coxal foramen, **dc** = discrimen, **fu_2p** = mesofurcal pit, **mtp** = mesotrochantinal plate, **nck** = neck, **ppf** = propodeal foramen. Scale bars are 50 µm.



FIGURES 53–58. *Boudiennyia* sp., petiole and entire mesosoma, female, SEM. 53 and 54, dorsal; 55 and 56, lateral; 57 and 58, ventral. **gs** = gastral sternum, **gt** = gastral tergum, **hyp** = hypopygium. Scale bars are 100 µm.

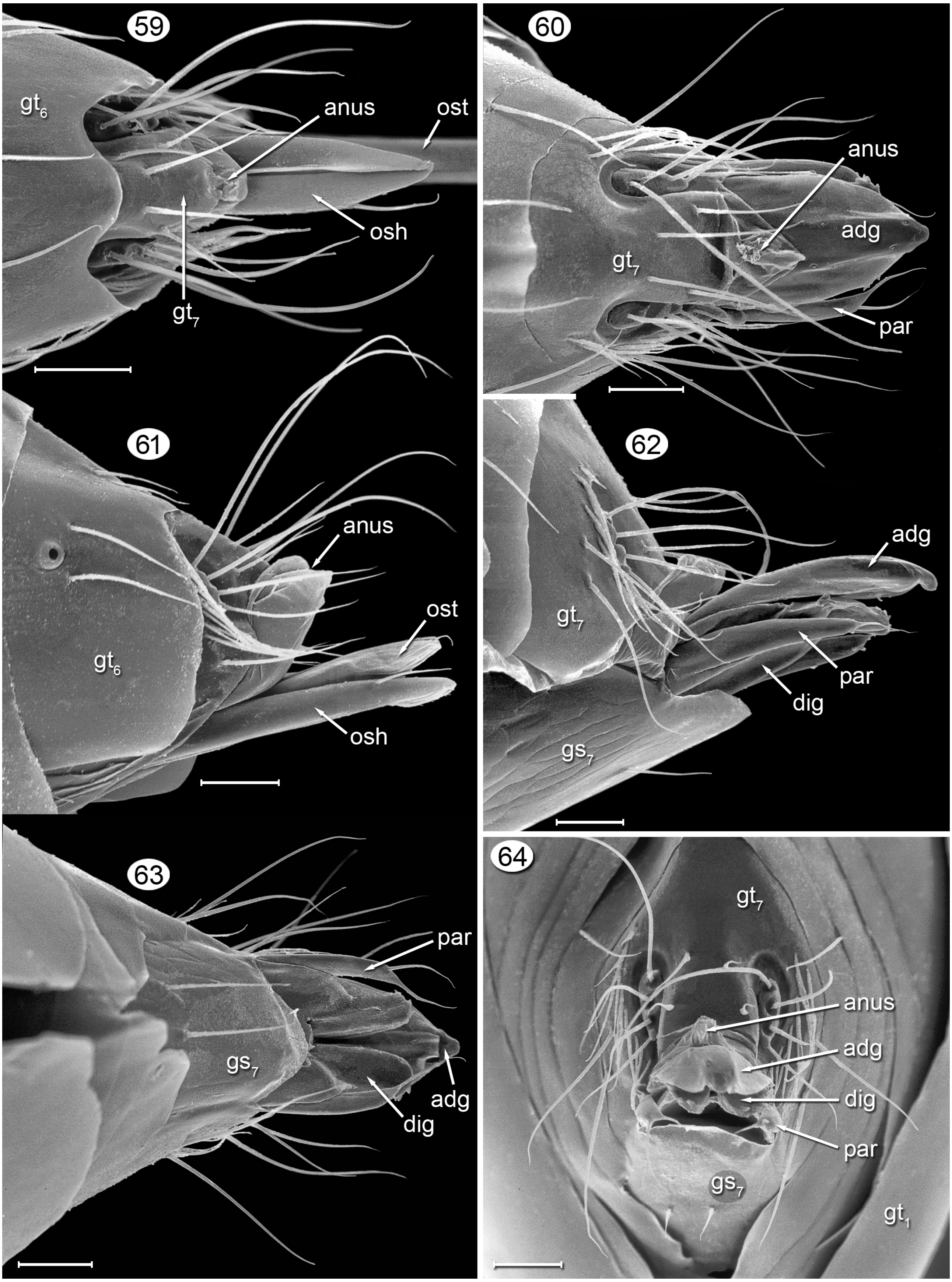
sister-group relationship. Schauff noted only one apomorphy for *Gonatocerus*, namely, the parastigma (his 'submarginal' vein or the 'marginal' vein of most other authors) towards the base slants away from the wing margin whereas in other genera, including *Ooctonus*, it is parallel to the wing margin and at its base usually bends up towards the submarginal vein ('subcosta' of Schauff). Noyes & Valentine (1989) also placed *Ooctonus* and *Gonatocerus* together in their *Gonatocerus* group. Based on male genitalia, Viggiani (1989) placed *Ooctonus* and *Gonatocerus* each in its own tribe and in different subfamilies. Zeya & Hayat (1995) noted the different structure of the cerci in the two genera and summarized other differences, including the unique structure of the male genitalia. *Ooctonus* was grouped together with *Gonatocerus* and two other genera based on molecular evidence (Munroe *et al*. 2011), and combined molecular and morphological evidence (Heraty *et al*. 2013). In the latter paper, *Ooctonus* appeared as sister group to *Borneomymar* Huber in the morphology-based cladogram (fig. 8) and sister group to *Gonatocerus* in the combined morphology/molecular-based cladogram (fig. 9). In both cases *Ooctonus* was indicated as related to other genera with 5-segmented tarsi (not 4-segmented, as inadvertently stated in Munroe *et al*. 2011, p. 21). Huber (2002) showed putative relationships of major lineages of Mymaridae in an intuitive cladogram (p. 44, fig. 7) and suggested that the sister genus of *Ooctonus* was *Boudiennyia*. If stems 7 and 9 on the cladogram in that paper are reversed so that *Ooctonus* + *Boudiennyia* are next to Mymarini *sensu* Annecke & Doutt (1961) the relationships seem to make better sense, as shown here (Fig. 65). The two clades share a long, narrow petiole of type 2, as described by Schauff (1984), in which the base of the gaster extends slightly into the apex of the petiole. The *Ooctonus* + *Boudiennyia* clade would then be defined by two similarities: pronotum with a transverse carina and propodeum with a complete set of carinae. This clade would be separated from the Mymarini clade, distinguished by three apomorphies, the first two of which are homoplasies, as they occur in other lineages within Mymaridae: females with fewer funicle segments (6 instead of 8), both sexes with fewer tarsal segments (4 instead of 5), and venation short, with parastigma short or absent.

Although superficially similar, *Ooctonus*, *Gonatocerus*, and *Boudiennyia* differ from one another in many features, suggesting they are quite distantly related. There are sufficient morphological differences between *Ooctonus* and *Gonatocerus* that I agree with Viggiani's (1989) view in placing *Ooctonus* and *Gonatocerus* in different subfamilies. *Ooctonus* differs sufficiently from *Boudiennyia* that they should perhaps be placed in different tribes but the same subfamily. The most significant difference is that *Boudiennyia* (Table 1) has a large fenestra occupying most of the scutellum, as in the *Polynema*-group of genera within Mymarini. So instead of treating *Ooctonus* + *Boudiennyia* as sister genera (Huber 2002), I propose here that *Boudiennyia* alone is likely the sister group to all remaining Mymarini (Fig. 66), and is separated from them by two plesiomorphies: funicle 8-segmented, and tarsi 5-segmented. Interestingly, Annecke and Doutt (1961, p.14) had pointed out the similarity of petiole structure between *Ooctonus* and two genera of Mymarini, *Mymar* Curtis and *Polynema* Haliday, but did not realize its significance.

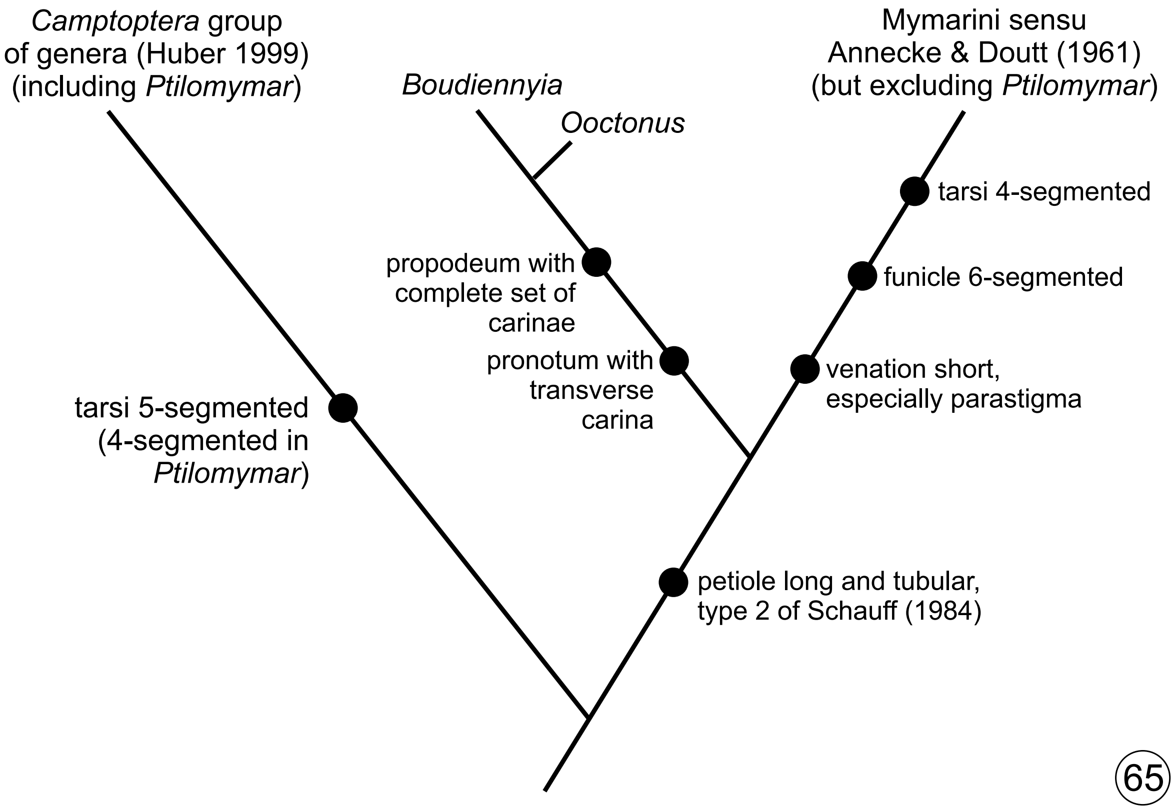
If *Ooctonus* were placed in its own lineage near *Gonatocerus* or in a lineage together with *Gonatocerus* and similar genera, the numerous features it shares with *Boudiennyia* and other genera within Mymarini, particularly the *Polynema* group of genera, would then have to be treated as independently derived; they would represent convergences with members of Mymarini. In contrast, if *Ooctonus* and *Boudiennyia* are included as sister genera in a sister clade to Mymarini then only two losses (two female funicle segments and one tarsal segment) and one reduction (parastigmal vein length) would be sufficient to explain their relationship to Mymarini Fig. 64). However, if *Ooctonus* and *Boudiennyia* are indeed correctly placed each in their own tribe (Fig. 65) and these are more closely related to groups of genera with 4-segmented tarsi, then the number of tarsal segments can no longer be used to define major lineages within extant Mymaridae because tarsal number reduction would have occurred independently at least three times.

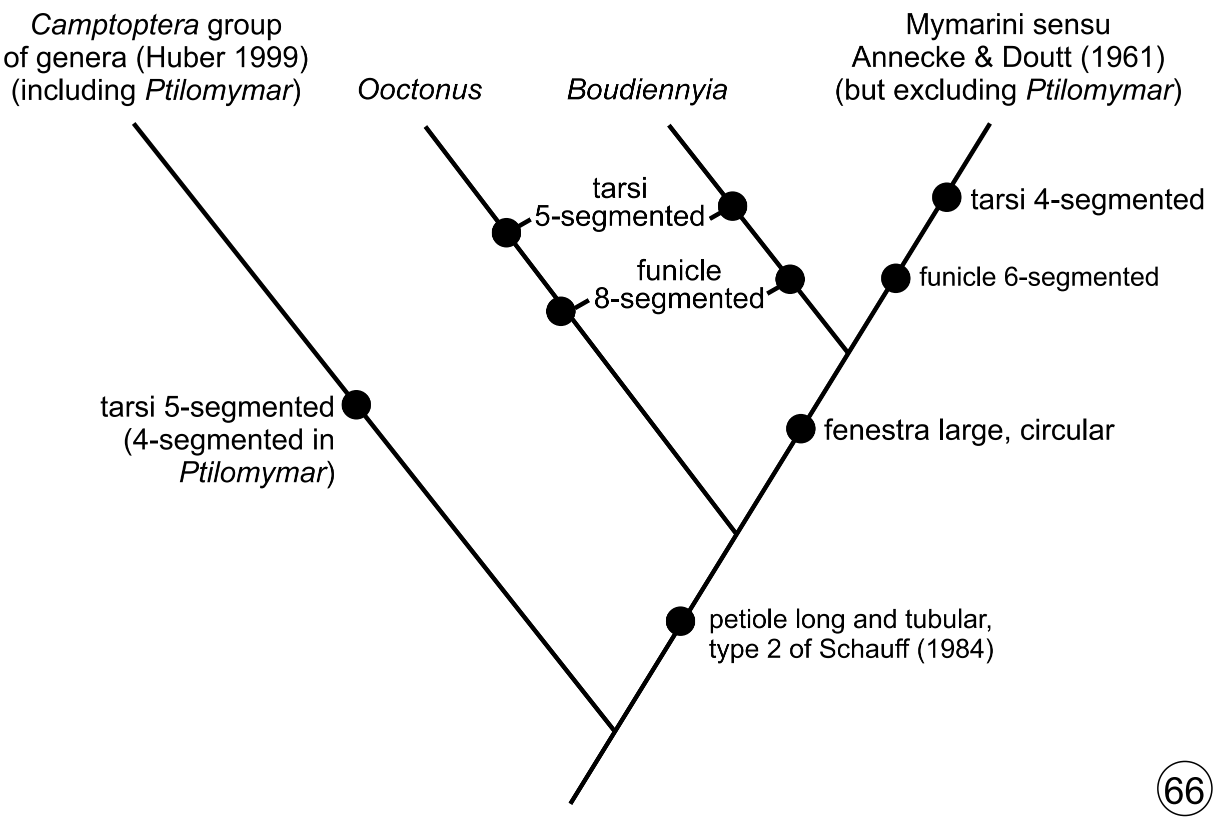
The two other, unrelated clades in which tarsal number reduction occurs are in the *Camptoptera*-group and *Anagrus*-group of genera. In the *Camptoptera*-group, tarsal number reduction occurs in *Eofoersteria* as a result of fusion of the apical two tarsomeres (Huber & Lin 1999). The second reduction in the *Camptoptera* group has not been discussed previously. Annecke & Doutt (1961) placed *Ptilomymar* in Mymarini because it has 4-segmented tarsi, but it is better placed in the *Camptoptera* group based on at least two features, the short but distinct petiole and the female antenna with at least 7 funicle segments. Within the *Camptoptera* group, *Ptilomymar* has the propodeum with translucent flanges, as in *Stephanocampta* Mathot, but a large, smooth gt_1, as in *Litus* (which should probably also be placed in the *Camptoptera* group). Tarsal reduction in *Ptilomymar* is also due to fusion of the last two tarsomeres. In the *Anagrus* group of genera, reduction occurs from 4 to 3 in *Kikiki*, due to loss of one tarsomere (Huber 2013). The fact that reduction in tarsal number, either through fusion or loss, occurs at all in the same or different lineages within Mymaridae is not surprising. Such a reduction occurred already among the five Cretaceous genera of Mymaridae, where *Enneagmus* Yoshimoto has three tarsal segments and the other four genera have five (Poinar and Huber 2011). Reduction in segment number also occurs in flagellar segments of females and/or males in various genera of Mymaridae through loss or, occasionally, fusion, resulting in the same number of segments in otherwise unrelated lineages.

I consider the generic relationships of Mymaridae not to be resolved well enough to classify genera correctly based on evolutionary relationships into formal tribes and subfamilies. However, I agree with Viggiani (1989) that the best solution for classifying *Ooctonus* is to place it in its own group that is either related to other genera with 5-segmented tarsi except *Gonatocerus*, or related to genera with 4-segmented tarsi and a long gastral petiole of type 2. I would classify *Boudiennyia* in its own group as well, and place it as the basal genus to the rest of Mymarini, whose genera all have 4-segmented tarsi. I exclude *Ptilomymar* from Mymarini sensu Annecke & Doutt (1961), as noted above, and would exclude *Anneckia* Subba Rao and *Omyomymar* Schauff from Mymarini *sensu* Viggiani (1989). Other genera may also be better placed elsewhere than in Mymarini. If *Boudiennyia* is correctly placed either as the basal genus within Mymarini or as sister clade to Mymarini it would be the first evidence for linking genera with 8-funicle segments in females and 5-segmented tarsi to genera with 6-segmented funicle, 4-segmented tarsi and a long gastral petiole of type 2. It would be most interesting to obtain fresh specimens of *Boudiennyia* for molecular study to determine which one of relationships discussed above is correct.



FIGURES 59–64. *Boudiennyia* sp., apex of gaster. 59, female, dorsal; 60, male, dorsal; 61, female, lateral; 62, male, lateral; 63, male, ventral; 64, male, posterior. **adg** = aedeagus, **dig** = digitus, **gs** = gastral sternum, **gt** = gastral tergum, **osh** = ovipositor sheath (3rd valvula), **ost** = ovipositor stylets (1st + 2nd valvulae), **par** = paramere. Scale bars are 20 µm.





FIGURES 65–67. Hypothesized relationships of *Ooctonus* and *Boudiennyia*. 65, both genera in same group; 66, each genus in different group. Character distribution shown without indication of polarity. Most character states are likely homoplasies.

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