



Research paper

Description of unknown or poorly known pupae and adult males of Neotropical *Heteromyia* Say (Culicomorpha: Ceratopogonidae), with a specific key to pupae



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ABSTRACT

The pupae of four Neotropical species of *Heteromyia* Say, *H. clavata* Williston, *H. chaquensis* Duret and Lane, *H. correntina* Duret and Lane and *H. orellana* (Roback) are described, photographed and illustrated using dissecting and compound microscope Nikon Eclipse E200, and a key is presented for their identification. The adult male genitalia of *H. chaquensis* and *H. orellana* are also described. Studied specimens were collected in northeastern Argentina and in the Amazon region of Brazil and Peru. Differences and similarities between the described species are noted and discussed, and phylogenetic relationships between the species here treated and between genera in the tribe Heteromyiini are analyzed.

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Introduction

Heteromyia Say is a genus of the tribe Heteromyiini characterized by distinctive, large adult females with a greatly swollen forefemora with dense ventral spines and extremely elongate hind legs, each with a single, very long claw which they project upward when at rest (Borkent and Spinelli, 2007). The genus includes 13 extant species distributed in the Americas and one species from the Miocene of the Dominican Republic (Borkent, 2016). Borkent and Spinelli (2007) listed 11 extant species from the Neotropics and Borkent and Grogan (2009) listed two from the Nearctic region.

The genus is mainly known throughout the adults. Of the 13 known extant species, the pupae of only three, *H. woeki* Wirth and Grogan, *H. clavata* Williston and *H. prattii* Coquillett, were briefly described by Wirth and Grogan (1977, 1979), and the genus was

diagnosed and more fully described for pupae based on this three species by Borkent (2014).

In this paper we provide descriptions, photographs and illustrations of unknown or poorly known pupae of four species of Neotropical *Heteromyia*, as well as the adult male genitalia of *H. chaquensis* Duret and Lane and *H. orellana* (Roback), from material collected in northeastern Argentina and in the Amazon region of Brazil and Peru. We also present an analysis of the pupal characters to interpret the phylogenetic relationships within the tribe Heteromyiini.

Material and methods

Pupae of *H. clavata*, *H. chaquensis* and *H. correntina* Duret and Lane were collected from ponds associated with different macrophytes in Brazilian Amazonia. Pupae of *H. correntina* were also found in Argentina on the banks of a stream in Entre Ríos province. The pupa of *H. orellana* came from mud on the margin of an unnamed pond located nearby Iquitos, in Peruvian Amazonia.

Macrophytes or mud, were placed in a tray and the floating pupae collected with a pipette and transported to the laboratory

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isolated in a vial with a drop of water. They were reared to adults and were allowed to undergo sclerotization before preservation in 70% ethanol. Adults and pupal exuviae from Argentina and Peru were slide-mounted in Canada balsam following the technique of Wirth and Marston (1968), and those from Brazil following Borkent and Spinelli (2007). They were examined and measured with a compound microscope. The illustrations of diagnostic characters were prepared with the aid of an attached camera lucida. Photographs were taken with a digital camera Micrometrics SE Premium, through a Nikon Eclipse E200 microscope. Terminology and abbreviations of pupae follow Borkent (2012, 2014). The coordinates of the collecting sites were plotted in the program Google Earth, saved in shapefile format and mounted on maps using the QGIS program (version 2.4.0. Chugiak). After the maps compilation, a final image was assembled with the aid of the program Adobe Photoshop CS6 (version 13.0). Voucher specimens are deposited in the collections of the División Entomología, Museo de La Plata, Argentina (MLPA) and Instituto Nacional de Pesquisas da Amazônia, Brazil (INPA).

3. Results

3.1. Key of pupae of the Neotropical species of *Heteromyia* Say

Information on *H. wokei* obtained from Wirth and Grogan (1977)

1. Abdominal segment 9 with terminal process very long, slender, more or less spiculate, nearly straight, directed either nearly posteriorly or very divergent, apex moderately curved mesad, with their base separated by narrow, nearly transverse area (Figs. 2 J, 3 K, 4 J, N, 5 M); width of forefemur very wide compared to width of foretibia; dorsal apotome with one campaniform sensillum (DA-2-H) ventral to seta (DA-1-H) (Figs. 2 A, 3 A, 4 A, K, 5 A) <i>Heteromyia</i> Say	2	
-Abdominal segment 9 with terminal processes at most moderately elongate, directed posteriorly, apex pointed, evenly curved posteriorly, with their base separated by narrow or broad, nearly transverse area; width of forefemur not much wider than width of foretibia; dorsal apotome with one campaniform sensillum (DA-2-H) dorsal to seta (DA-1-H)		Other Heteromyiini
2. Labium entire or divided by apex of labrum; surface of dorsal apotome with stout knob-like tubercles; dorsal thoracic sensilla, D-1-T, D-2-T and D-5-T peg-like	3	
-Labium entire; surface of dorsal apotome smooth; dorsal thoracic sensilla, D-1-T, D-2-T and D-5-T elongate	5	
3. Labium entire; dorsal apotome with anterior margin with apex pointed; abdominal segment 9 with terminal process very slightly divergent		wokei Wirth and Grogan
-Labium divided by apex of labrum; dorsal apotome with anterior margin rounded; abdominal segment 9 with terminal process moderately divergent	4	
4. Abdominal segment 8 with two lateral sensilla (Fig. 5L); segment 9 equal in coloration to precedent segments (Fig. 1D)		orellana (Roback)
-Abdominal segment 8 with three lateral sensilla (Fig. 4I); segment 9 darkish than precedent segments (Fig. 1C)		correntina Duret and Lane
5. Dorsal apotome with dorsomedial notch (Fig. 2A); abdominal segment 9 with terminal process greatly divergent (Figs. 1 A, 2 J)		chaquensis Duret and Lane
-Dorsal apotome without dorsomedial notch (Fig. 3A); abdominal segment 9 with terminal process moderately divergent (Figs. 1 B, 3 K)		clavata Williston

Heteromyia chaquensis Duret and Lane (Figs. 1 A, 2 A–K, 6 A, 8 A–C, 9, 10)

Heteromyia chaquensis Duret and Lane, 1955: 37 (female; Argentina); Wirth, 1974: 47 (New World catalogue south of

USA); Borkent and Wirth, 1997: 114 (World catalogue); Borkent and Spinelli, 2000: 56 (New World catalogue south of USA); Borkent and Spinelli, 2007: 89 (Neotropical catalogue); Borkent, 2016: 145 (online World catalogue).

3.2. Brief description of adult female

Only Neotropical species with thorax reddish brown; wing with one radial cell, dark area in r_3 as transversal band behind mesal portion of radial cell, with a distinct dark, slender, longitudinal area beyond it, m_1 and m_2 with dark spot containing a conspicuous pale spot; legs yellow with a pair of dark, narrow, subapical bands on mid and hind femora, hind tibia entirely pale.

3.3. Male genitalia (Fig. 8A)

Yellowish. Sternite 9 2.5X wider than long with shallow, rounded, broad posteromedian excavation. Gonocoxite twice longer than wide, slightly tapering distally; gonostylus slender, as long as gonocoxite, moderately curved with recurved, pointed, dark tip. Parameres (Fig. 8C) narrowly fused at extreme base, each with basal arm stout, expanded; distal portion moderately stout basally, slender mesally, with slightly bulbous tip. Aedeagus (Fig. 8B) triangular; basal arch concave, extending to 1/5 of total length; lateral arms slender, well sclerotized; apex broadened at extreme tip, later bent, directed ventrally.

3.4. Female pupa (Figs. 1 A, 2 A–J, 6 A)

Total length 4.60 mm. Exuviae yellowish brown (Fig. 1A). *Head*: dorsal apotome (Fig. 2A) with disc 3.0 X broader than long, disc surface smooth, anterior margin deeply notched, forming two blunt lobes, each one with few stout knob-like tubercles, posterior margin nearly straight, posterolateral margin with broad raised areas bearing two dorsal apotome sensilla, DA-1-H short seta, DA-2-H campaniform sensillum (Fig. 2A); DAL 0.10 mm; DAW 0.36 mm; DAW/DAL 3.46. Mouthparts with mandible well developed, lacinia absent; palpus strong, extending to posterior margin of labium, labium entire, not divided medially. Sensilla: dorsolateral cephalic sclerite sensilla (Fig. 2C): DL-1-H short seta, DL-2-H campaniform sensillum; clypeal/labials (Fig. 2B): CL-1-H and CL-2-H long, thin setae, equal in size; oculars (Fig. 2B): O-1-H, O-3-H long, thin setae, O-2-H campaniform sensillum. *Thorax*: prothoracic extension wide, well developed, narrow dorsolaterally; respiratory organ (Figs. 1 A, 2 C, E) moderately elongate, nearly straight, slightly expanded at apex, with 16 apical pores arranged in single curved row, surface smooth; length 0.304 mm, wide 0.048 mm; pedicel short, length 0.044 mm, P/RO 0.144. Sensilla (Fig. 2D) as follows: 3 anteromedials, AM-1-T long seta, AM-2-T short, stout seta, AM-3-T campaniform sensillum; anterolateral AL-1-T short, stout seta on prominent tubercle; 5 dorsal setae (Fig. 2E) D-1-T, D-2-T, D-4-T, D-5-T elongate seta, all on rounded small tubercle, D-3-T campaniform sensillum; supraalar SA-2-T campaniform sensillum; two metathoracic campaniform sensilla, M-3-T (Fig. 2F) near anterior margin of metathorax. Cephalothorax rectangular, length 1.64 mm, width 1.16 mm, surface without rounded spicules, mesothorax without tubercles. *Abdomen*: segments with abundant spicules; tergite 1 with medial area with brown spot, and two small anterolateral spots; tergites 2–7 with medial area with brown spot, two crescent-shaped spots, two anterolateral spots; tergite 8 without medial spot; sternites 3–7 with medial spot, two anterolateral spots; sternite 8 without anterolateral spots. Sensilla: tergite 1 (Fig. 2F) with setae as follows: 6 dorsal sensilla, two anterior setae closely approximated, D-2-I short, stout seta, D-3-I long, thin seta, both located on the same tubercle, D-4-I, D-7-I campaniform sensilla, D-7-I situated anteriorly near D-3-I, two posterior

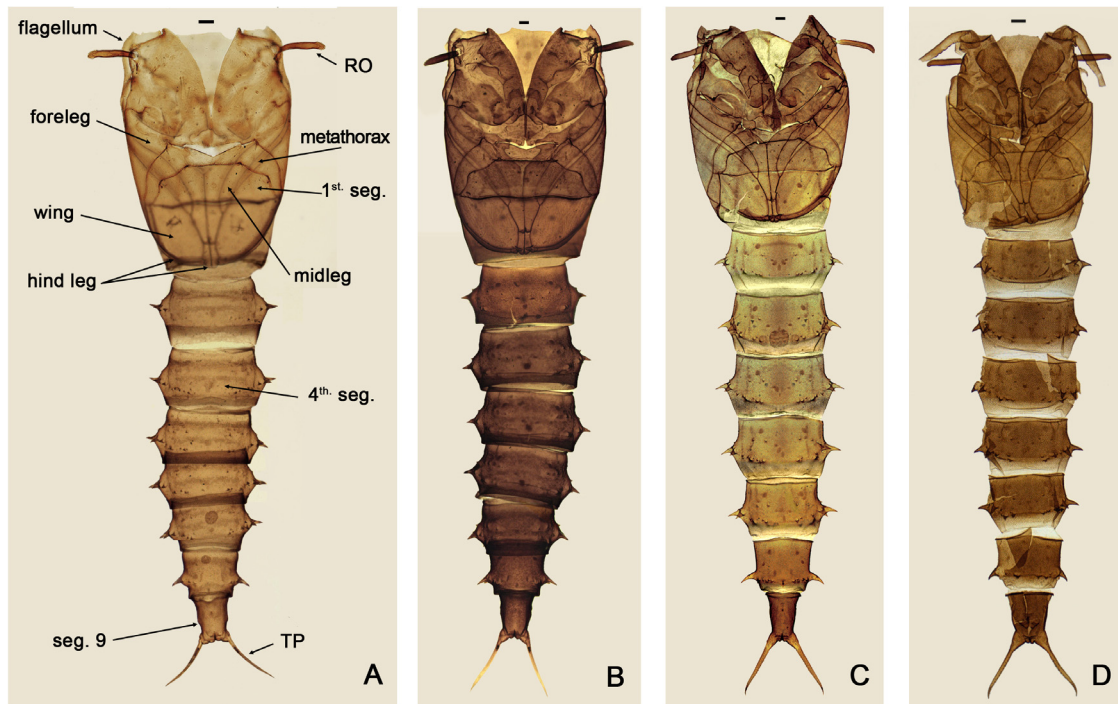


Fig. 1. *Heteromyia* Say, pupae. (A) *Heteromyia chaquensis* Duret and Lane, female. (B) *Heteromyia clavata* Williston, female. (C) *Heteromyia correntina* Duret and Lane, female. (D) *Heteromyia orellana* (Roback), male.

setae, D-8-I short, thin seta, D-9-I medium-sized, thin seta, 3 lateral sensilla, L-1-I elongate seta, L-2-I, L-3-I short setae, all setae on small tubercle; second abdominal segment similar to the first one except by a presence of seta D-5-II; segment 4 (Figs. 2 G-H, 6 A) with sensillar pattern as follows: D-2-IV, D-3-IV elongate, thin seta, both on small tubercles; D-5-IV, D-8-IV short, curved setae, D-9-IV elongate seta, D-4-IV, D-7-IV campaniform sensilla, D-7-IV situated near D-3-IV; D-5-IV on short tubercle, D-8-IV, D-9-IV on separate, closely pointed tubercles, posterior dorsal sensilla (D-5-IV, D-4-IV, D-8-IV, D-9-IV) arranged in transverse row; L-1-IV moderately elongate seta on small tubercle, just anterior to L-3-IV; L-2-IV, L-4-IV short setae on stout pointed tubercle, L-3-IV elongate seta on small tubercle; V-5-IV, V-7-IV medium-sized setae, V-6-IV moderately elongate seta, all on small pointed tubercles, V-5-IV, V-6-IV closely approximated; segment 8 (Fig. 2I) with sensillar pattern highly modified, without D-2-VIII, D-3-VIII, L-1-VIII. Segment 9 (Fig. 2J) with D-5-IX campaniform sensillum, D-6-IX not visible in available specimen, dorsal and ventral surface covered with abundant tiny spinules; length 0.78 mm, width 0.28 mm; terminal processes elongate, greatly divergent, each with small spicules along its entire extent, tapering to curved mesad, pointed apex; length 0.45 mm.

3.5. Male pupa (Fig. 2K)

Similar to female with usual sexual differences; total length 3.50 mm. Dorsal apotome with abundant stout wrinkles, DAL 0.096 mm; DAW 0.312 mm; DAW/DAL 3.25. Respiratory organ missing in available specimen. Cephalothorax length 1.48 mm, width 1.08 mm. Segment 9 (Fig. 2K) with abundant spicules, ventral genital lobe slightly globose, almost reaching posterior margin, surface smooth; length 0.30 mm, width 0.24 mm; terminal processes moderately elongate, slender and greatly divergent; D-5-IX present.

3.6. Distribution

Brazil (Amazonas), Argentina (Formosa, Chaco, Corrientes).

3.7. Specimens examined

Brazil, Amazonas, Iranduba, Ilha da Marchantaria, Lago Camaleão, 03°13'14.9"S, 59°56'52.6"W, 18-IV-2011, R. Torreias, 1 female (with pupal exuvium), from *Eichhornia crassipes* (Mart.) Solms; same data except 25-V-2011, 1 male (with pupal exuvium), from *Pistia stratiotes* Linnaeus; Argentina, Formosa, Estancia La Marcela, 35 km E El Colorado, 26°21'43.03"S, 59°23'59.79"W, 27/28-VII-2003, J. Williams, 1 female, luz (Fig. 10).

***Heteromyia clavata* Williston**
(Figs. 1 B, 3 A–K, 6 B, 9, 10)

Heteromyia clavata Williston, 1900: 225 (female; Mexico); Malloch, 1915: 361 (notes); Wirth, 1974: 47 (New World catalogue south of USA); Wirth and Grogan, 1977: 184 (adult diagnosis, pupa; synonymy; distribution); Borkent and Wirth, 1997: 114 (World catalogue); Borkent and Spinelli, 2000: 56 (New World catalogue south of USA); Borkent and Spinelli, 2007: 89 (Neotropical catalogue); Borkent, 2014: 77 (pupa description, in part); Borkent, 2016: 145 (online World catalogue).

Heteromyia rufa Kieffer, 1917: 325 (male; Colombia); Edwards, 1933: 87 (descriptive notes; Argentina); Duret and Lane, 1955: 36 (in key; Argentina).

Heteromyia caloptera Kieffer, 1919: 192 (unnecessary new name for *H. rufa* Kieffer, not Loew, 1861).

3.8. Brief description of adult female

Only Neotropical species with thorax reddish brown; wing with one, sometimes two radial cells, without isolated dark point in r_3 beyond the dark area behind second radial cell, m_1 with dark spot

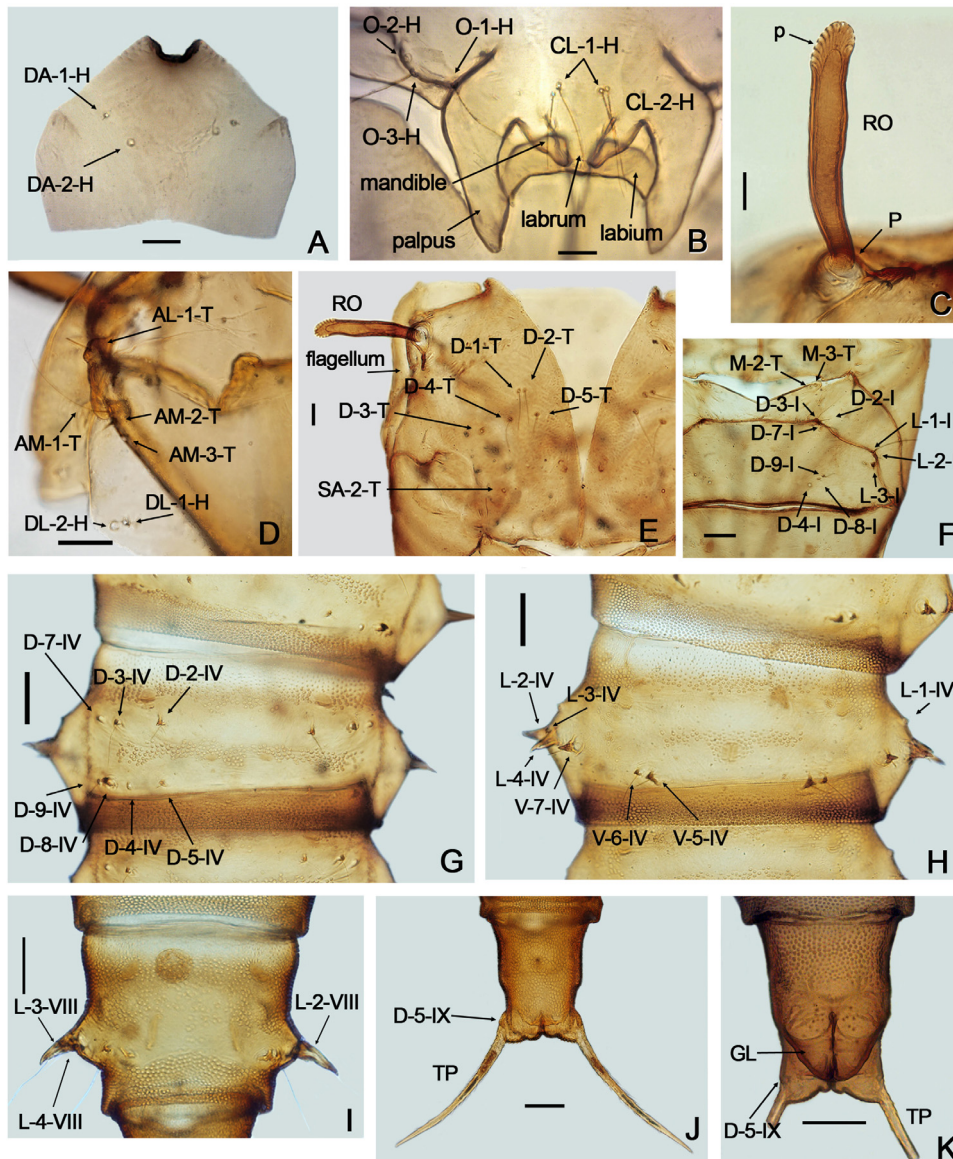


Fig. 2. *Heteromyia chaquensis* Duret and Lane: (A–J) female pupa, (K) male pupa. (A) Dorsal apotome, dorsal view. (B) Mouthparts with clypeal/labral and ocular sensilla, ventral view. (C) Respiratory organ, left side. (D) Cephalothoracic sensilla. (E) Dorsal thoracic sensilla, dorsal view and respiratory organ. (F) Metathorax and abdominal segment 1 chaetotaxy, dorsal view. (G) Abdominal segment 4 chaetotaxy, dorsal view. (H) Abdominal segment 4 chaetotaxy, ventral and lateral view. (I) Abdominal segment 8, dorsolateral view. (J–K) Segment 9, ventral view.

Anteromedial sensilla (AM-T); anterolateral sensillum (AL-1-T); campaniform sensillum of segment 9 (D-5-IX); clypeal/labral sensilla (CL-H); dorsal apotome sensilla (DA-H); dorsal sensilla of segment 1 (D-I); dorsal sensilla of segment 4 (D-IV); dorsal setae (D-T); dorsolateral cephalic sclerite sensilla (DL-H); genital lobe (GL); lateral sensilla of segment 1 (L-I); lateral sensilla of segment 4 (L-IV); lateral sensilla of segment 8 (L-VIII); metathoracic sensilla (M-T); ocular sensilla (O-H); pedicel (P); respiratory organ (RO); supraalar (SA-T); terminal processes (TP); ventral sensilla of segment 4 (V-IV).

containing a small pale spot; legs yellow with a pair of dark, narrow, subapical bands on mid and hind femora, hind tibia entirely pale.

3.9. Note

The male genitalia is not diagnosable at this time. The only available information about the male of this species is the original description of the holotype of *Heteromyia rufa* by Kieffer (1917), a species considered as a junior synonym of *H. clavata*. Unfortunately, this description is very brief and the only reference to the male genitalia is the following: “pince blanche, peu poilue, articles terminaux longs, subfiliformes et presque droits”. Moreover, the holotype, formerly deposited in the Hungarian Natural History Museum, Budapest, was destroyed by fire.

3.10. Female pupa (Figs. 1 B, 3 A–K, 6 B)

Total length 6.20–6.60 (6.40, n=2) mm. Exuviae dark brown (Fig. 1B). Head: dorsal apotome (Fig. 3A) with disc 3.3 X broader than long, disc surface smooth, anterior margin rounded, covered with few stout thorns with dark, triangular shaped projection, posterior margin slightly concave, posterolateral margin with broad raised areas, bearing two dorsal apotome sensilla (Fig. 3A), DA-1-H minute, hyaline seta, DA-2-H campaniform sensillum; DAL 0.104 mm; DAW 0.448 mm; DAW/DAL 4.307. Mouthparts with mandible well developed, lacinia absent; palpus strong, extending to posterior margin of labium, labium entire, not divided medially. Sensilla: dorsolateral cephalic sclerite sensilla (Fig. 3D): DL-1-H minute seta, DL-2-H campaniform sensillum; clypeal/labrals (Fig. 3B): CL-1-H and CL-2-H long, thin setae, equal in size; oculars

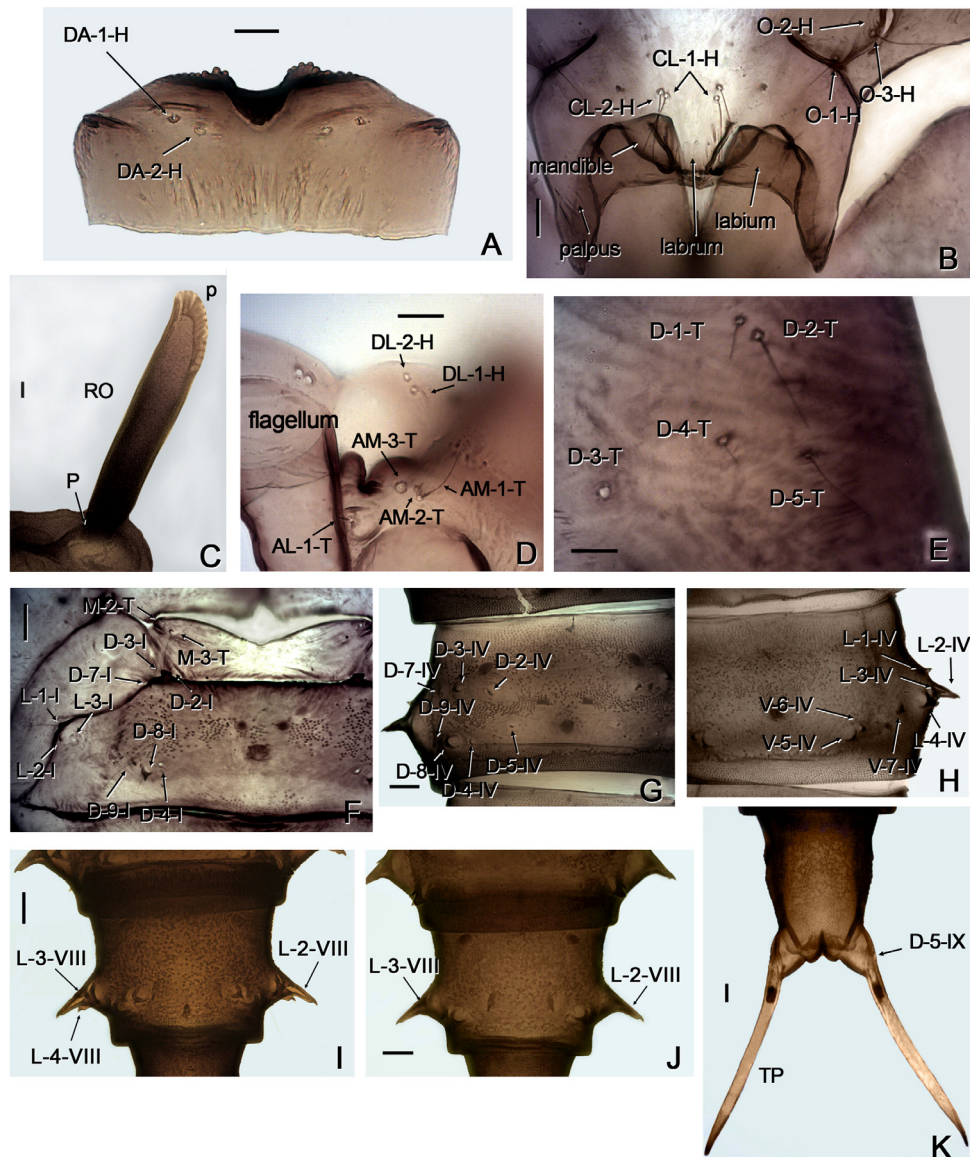


Fig. 3. *Heteromyia clavata* Williston: (A–K) female pupa. (A) Dorsal apotome. (B) Mouthparts with clypeal/labral and ocular sensilla, ventral view. (C) Respiratory organ, right side. (D) Cephalothoracic sensilla. (E) Dorsal thoracic sensilla. (F) Metathorax and abdominal segment 1 chaetotaxy, dorsal view. (G) Abdominal segment 4 chaetotaxy, dorsal view. (H) Abdominal segment 4 chaetotaxy, ventral and lateral view. (I–J) Abdominal segment 8, dorsolateral view. (K) Segment 9, ventral view.

Anteromedial sensilla (AM-T); anterolateral sensillum (AL-1-T); campaniform sensillum of segment 9 (D-5-IX); clypeal/labral sensilla (CL-H); dorsal apotome sensilla (DA-H); dorsal sensilla of segment 1 (D-I); dorsal sensilla of segment 4 (D-IV); dorsal setae (D-T); dorsolateral cephalic sclerite sensilla (DL-H); lateral sensilla of segment 1 (L-I); lateral sensilla of segment 4 (L-IV); lateral sensilla of segment 8 (L-VIII); metathoracic sensilla (M-T); ocular sensilla (O-H); pedicel (P); pore (p); respiratory organ (RO); terminal processes (TP); ventral sensilla of segment 4 (V-IV).

(Fig. 3B): O-1-H and O-3-H long, thin setae, O-2-H campaniform sensillum. **Thorax:** prothoracic extension wide, well developed, narrow dorsolaterally; respiratory organ (Fig. 3C) moderately elongate, straight, slightly expanded at apex with 13–20 apical pores arranged in single curved row; surface smooth; length 0.360–0.464 (0.408, $n=3$) mm, wide 0.064–0.080 (0.069, $n=3$) mm; pedicel short, length 0.056–0.072 (0.064, $n=3$) mm, P/RO 0.137–0.180 (0.157, $n=3$). Sensilla (Fig. 3D) as follows: 3 anteromedials, AM-1-T long seta, AM-2-T short, stout seta, AM-3-T campaniform sensillum; anterolateral (Fig. 3D) AL-1-T short, stout seta on prominent tubercle; 5 dorsal setae (Fig. 3E): D-1-T, D-2-T, D-5-T elongate setae, D-4-T short seta, all on small tubercles, D-3-T campaniform sensillum; supraalar SA-2-T campaniform sensillum; two metathoracic campaniform sensilla, M-3-T near anterior margin of metathorax (Fig. 3F). Cephalothorax rectangular, length 1.17–1.20 (1.18, $n=2$) mm, width 0.85–0.87 (0.86, $n=2$) mm, surface without

rounded spicules, mesothorax without tubercles. **Abdomen:** segments with abundant spicules; tergite 1 with medial area with brown spot, and two anterolateral spots; tergites 2–7 with medial area with dark spot; two crescent-shaped spots, two anterolateral spots; tergite 8 without medial spot; sternites 3–7 with medial spot, two anterolateral spots, sternite 8 without anterolateral spots. Sensilla: tergite 1 (Fig. 3F) with setae as follows: 6 dorsal sensilla, two anterior setae closely approximated, D-2-I short, stout seta, D-3-I long, thin seta, D-4-I, D-7-I campaniform sensilla situated anteriorly, near D-3-I; two posterior setae, D-8-I, D-9-I long, thin seta, D-9-I longer than D-8-I; 3 lateral sensilla: L-1-I elongate, thin seta, L-2-I, L-3-I short setae, all setae on small tubercle; second abdominal segment similar to the first one; segment 4 (Figs. 3 G–H, 6 B) with sensillar pattern as follows: D-2-IV short, thin seta, D-3-IV elongate, thin seta, both on small tubercle; D-5-IV short seta, D-8-IV peg-like seta, D-9-IV elongate seta, D-4-IV, D-7-IV campaniform

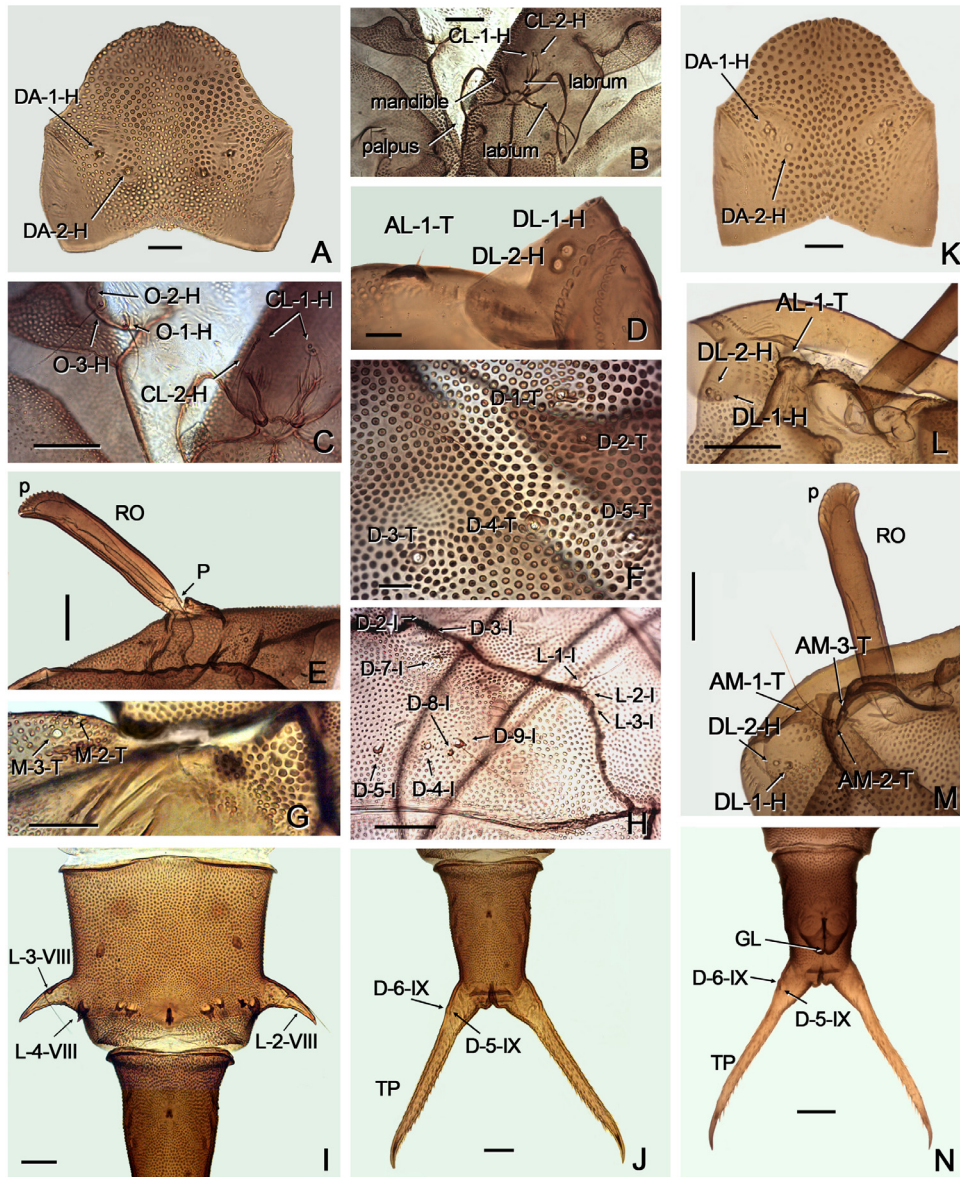


Fig. 4. *Heteromyia correntina* Duret and Lane: (A–J) female pupa, (K–N) male pupa. (A, K) Dorsal apotome. (B) Mouthparts and clypeal/labral sensilla. (C) Clypeal/labral and ocular sensilla, ventral view. (D, L) Anterolateral sensillum and dorsolateral cephalic sclerite sensilla. (E) Respiratory organ, left side. (F) Dorsal thoracic sensilla. (G) Metathorax chaetotaxy, dorsal view. (H) Abdominal segment 1 chaetotaxy, dorsal view. (I) Abdominal segment 8, dorsolateral view. (J, N) Segment 9, ventral view. (M) Respiratory organ, left side and cephalothoracic sensilla.

Anteromedial sensilla (AM-T); anterolateral sensillum (AL-1-T); campaniform sensilla of segment 9 (D-5-IX and D-6-IX); clypeal/labral sensilla (CL-H); dorsal apotome sensilla (DA-H); dorsal sensilla of segment 1 (D-I); dorsal setae (D-T); dorsolateral cephalic sclerite sensilla (DL-H); genital lobe (GL); lateral sensilla of segment 1 (L-I); lateral sensilla of segment 8 (L-VIII); metathoracic sensilla (M-T); ocular sensilla (O-H); pedicel (P); pore (p); respiratory organ (RO); terminal processes (TP).

sensilla, D-7-IV situated near D-3-IV; D-5-IV on short tubercle, D-8-IV, D-9-IV on closely separated, pointed tubercles; posterior dorsal sensilla (D-5-IV, D-4-IV, D-8-IV, D-9-IV) arranged in transverse row; L-1-IV moderately elongate seta on small, pointed tubercle, just anterior to L-3-IV; L-2-IV; L-4-IV short setae on stout pointed tubercles, L-3-IV elongate seta on small, pointed tubercle; V-5-IV, V-7-IV short peg-like setae, V-6-IV moderately elongate seta, all on small pointed tubercles, V-5-IV, V-6-IV closely approximated; segment 8 (Fig. 3I–J) with sensillar pattern highly modified, without D-2-VIII, D-3-VIII, L-1-VIII. Segment 9 (Fig. 3K) with D-5-IX campaniform sensillum, D-6-IX not visible in available specimens, dorsal surface entirely covered with spinules, ventral surface lacking spinules in central small area, length 1.01–1.12 (1.08, $n = 3$) mm, width 0.36–0.38 (0.37, $n = 3$) mm; terminal processes elongate,

divergent, each with small spicules along its entire extent tapering to curved mesad, pointed apex; length 0.61–0.68 (0.65, $n = 3$) mm.

3.11. Distribution

Mexico (Veracruz) to Colombia, Brazil (Amazonas), Argentina (Chaco, Corrientes).

3.12. Specimens examined

Brazil, Amazonas, Iranduba, Ilha da Marchantaria, Lago Grande, 03°14'43.9"S, 59°58'54.2"W, 4-IV-2011, R. Torreias, 2 females (with pupal exuviae) from *E. crassipes*; Iranduba, Ilha da Marchantaria, Lago Camaleão, 03°13'14.9"S, 59°56'52.6"W, 25-V-2011, R. Torreias, 1 female from *E. crassipes* (with pupal exuvium) (Fig. 10).

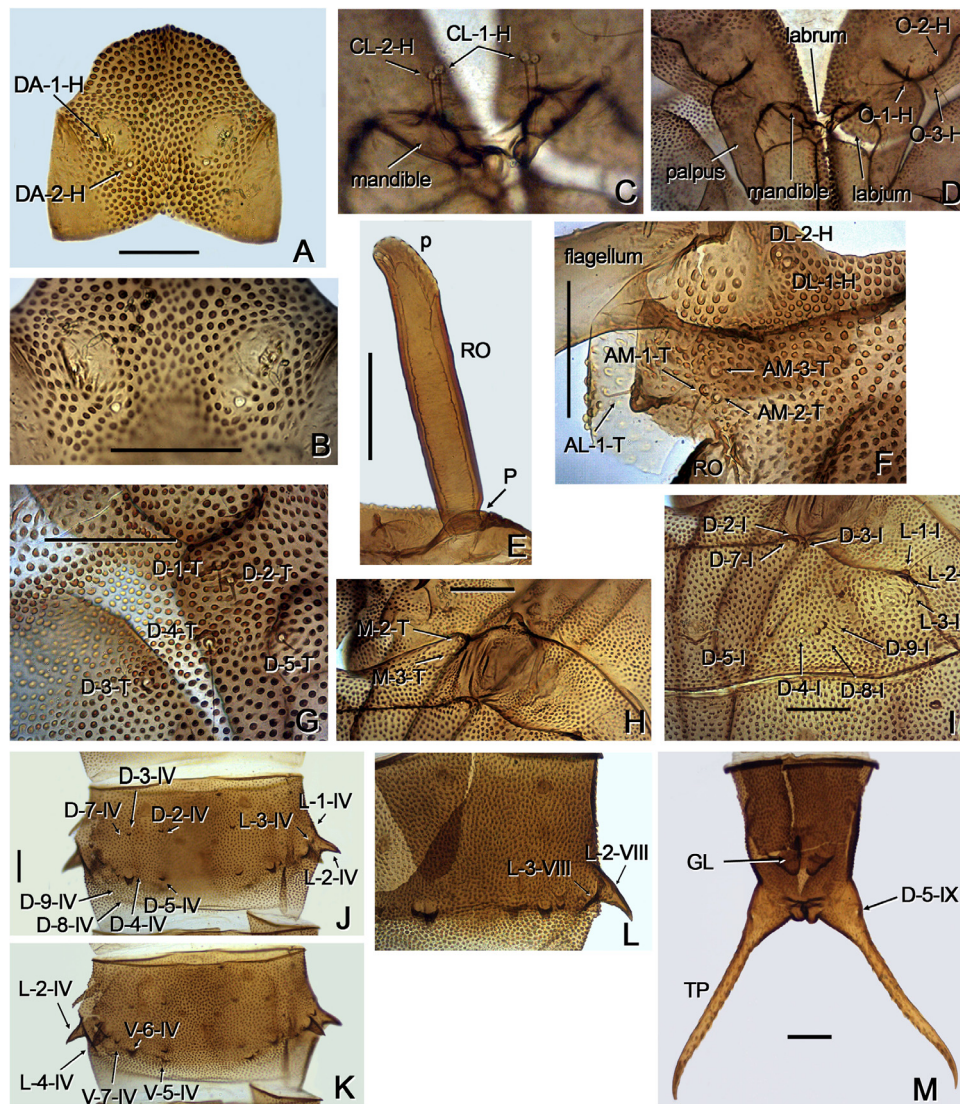


Fig. 5. *Heteromyia orellana* (Roback): (A–M) male pupa. (A) Dorsal apotome. (B) Dorsal apotomes. (C) Clypeal/labral sensilla, ventral view. (D) Mouthparts and ocular sensilla. (E) Respiratory organ, right side. (F) Cephalothoracic sensilla. (G) Dorsal thoracic sensilla. (H) Metathorax chaetotaxy. (I) Abdominal segment 1 chaetotaxy, dorsal view. (J) Abdominal segment 4, dorsal and lateral view. (K) Abdominal segment 4, ventral and lateral view. (L) Abdominal segment 8, dorsolateral view. (M) Segment 9, ventral view. Anteromedial sensilla (AM-T); anterolateral sensillum (AL-1-T); campaniform sensillum of segment 9 (D-5-IX); clypeal/labral sensilla (CL-H); dorsal apotome sensilla (DA-H); dorsal sensilla of segment 1 (D-I); dorsal sensilla of segment 4 (D-IV); dorsal setae (D-T); dorsolateral cephalic sclerite sensilla (DL-H); genital lobe (GL); lateral sensilla of segment 1 (L-I); lateral sensilla of segment 4 (L-IV); lateral sensilla of segment 8 (L-VIII); metathoracic sensilla (M-T); ocular sensilla (O-H); pedicel (P); pore (p); respiratory organ (RO); terminal processes (TP); ventral sensilla of segment 4 (V-IV).

Heteromyia correntina Duret and Lane
(Figs. 1 C, 4 A–N, 7 A, 9, 10)

Heteromyia correntina Duret and Lane, 1955: 39 (female, male; Argentina); Wirth, 1974: 47 (New World catalogue south of USA); Spinelli et al., 1995: 166 (Brazil, Rondônia); Borkent and Wirth, 1997: 114 (World catalogue); Borkent and Spinelli, 2000: 56 (New World catalogue south of USA); Borkent and Spinelli, 2007: 89 (Neotropical catalogue); Borkent, 2016: 145 (online World catalogue).

3.13. Brief description of adult

Only Neotropical species with thorax yellowish brown; wing with one radial cell, dark area in r_3 restricted to a transversal band behind radial cell, without isolated dark point beyond it, m_1 with dark spot containing a conspicuous pale spot; apical 1/3 of mid and

hind femora slightly swollen, hind tibia entirely dark brown. Male sternite 9 with shallow, rounded, broad posteromedial excavation.

3.14. Female pupa (Figs. 1 C, 4 A–J, 7 A)

Total length 7.00 mm. Exuviae yellowish brown (Fig. 1C) except segment 9 brown. Head: dorsal apotome (Fig. 4A) with disc 1.85 X broader than long, disc surface covered with stout thorns, anterior margin rounded without subapical tubercle; posterior margin concave, posterolateral margin with broad raised areas devoid of thorns; bearing two dorsal apotome sensilla, DA-1-H short, stout seta, DA-2-H campaniform sensillum (Fig. 4A); DAL 0.160 (n=2) mm; DAW 0.376–0.384 (0.380, n=2) mm; DAW/DAL 2.35–2.40 (2.375, n=2). Mouthparts (Fig. 4B) with mandible well developed, lacinia absent; palpus strong, extending to posterolateral margin of labium, labium divided. Sensilla: dorsolateral cephalic sclerite sensilla (Fig. 4D): DL-1-H minute seta, DL-2-H campaniform sensillum; clypeal/labrals (Fig. 4B–C): CL-1-H, CL-

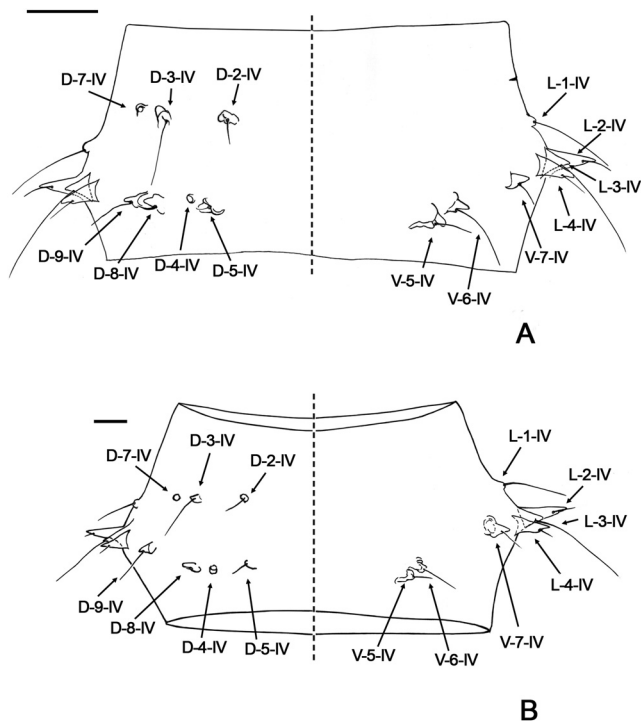


Fig. 6. Female pupae, abdominal segment 4 chaetotaxy (A–B). (A) *Heteromyia chaquensis* Duret and Lane. (B) *Heteromyia clavata* Williston. Dorsal sensilla of segment 4 (D-IV); lateral sensilla of segment 4 (L-IV); ventral sensilla of segment 4 (V-IV).

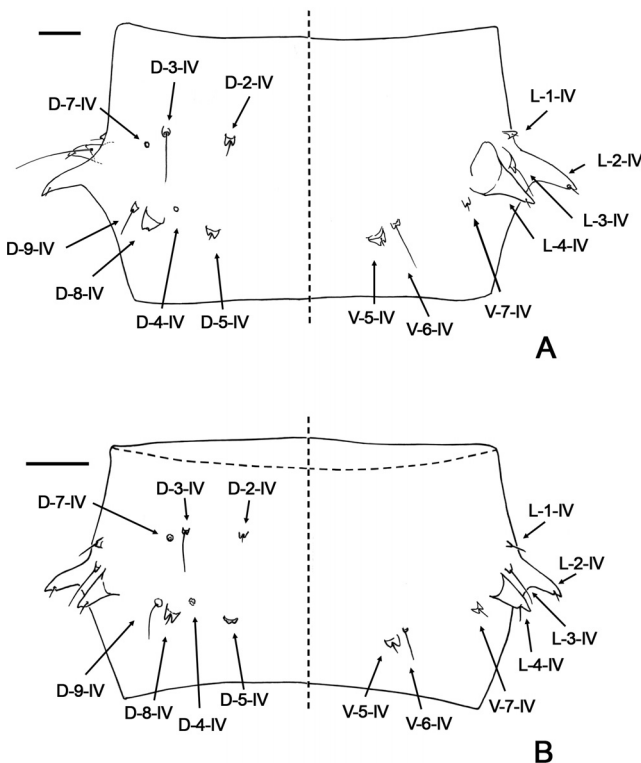


Fig. 7. Pupae, abdominal segment 4 chaetotaxy (A–B). (A) *Heteromyia correntina* Duret and Lane, female pupa. (B) *Heteromyia orellana* (Roback), male pupa. Dorsal sensilla of segment 4 (D-IV); lateral sensilla of segment 4 (L-IV); ventral sensilla of segment 4 (V-IV).

2-H long, thin setae, CL-1-H slightly longer than CL-2-H; oculars (Fig. 4C): O-1-H, O-3-H long, thin setae, O-2-H campaniform sensillum. *Thorax*: prothoracic extension wide, well developed, narrow dorsolaterally; respiratory organ (Fig. 4E) moderately elongate, brown, straight, slightly expanded at bent apex with 16–18 apical pores, arranged in single curved row; surface smooth; length 0.416 (n=2) mm, wide 0.064–0.072 (0.068, n=2) mm; pedicel (Fig. 4E) short, length 0.030 (n=2) mm, P/RO 0.072 (n=2). Sensilla as follows: 3 anteromedials, AM-1-T long seta, AM-2-T short seta, AM-3-T campaniform sensillum; anterolateral (Fig. 4D): AL-1-T medium-sized, stout seta; 5 dorsal setae (Fig. 4F): D-1-T, D-2-T and D-5-T short setae, D-3-T campaniform sensillum, D-4-T elongate seta, all on rounded tubercle; supraalar SA-2-T campaniform sensillum; two metathoracic (Fig. 4G) campaniform sensilla, M-3-T near anterior margin of metathorax. Cephalothorax rectangular, length 2.14 mm, width 1.70 mm, surface covered with abundant rounded spicules, and brown, triangular tubercle located on mesothorax. *Abdomen*: segments with abundant spicules; tergite 1 (Fig. 4H) with medial area with brown spot, and two or three anterolateral spots, tergites 2–7 with medial area with stripe, two spots, two anterolateral spots; tergite 8 without stripe; sternites 3–7 with medial spot, two anterolateral spots; sternite 8 without medial spot. Sensilla: tergite 1 (Fig. 4H) with setae as follows: 7 dorsal sensilla, two anterior setae, D-2-I short, stout seta, D-3-I long, thin seta, D-4-I, D-7-I campaniform sensilla situated anteriorly, near D-3-I; three posterior setae: D-5-I, D-8-I short, stout setae, D-9-I long, thin seta; 3 lateral sensilla: L-2-I, L-3-I short, stout setae, L-1-I long, thin seta, all setae on small tubercle; second abdominal segment similar to the first one; segment 4 (Fig. 7A) with sensillar pattern as follows: D-2-IV minute seta, D-3-IV elongate, thin seta on short, quadrangular tubercles; D-4-IV campaniform sensillum, D-5-IV, D-8-IV short setae, D-9-IV elongate, thin seta, D-7-IV campaniform sensillum near D-3-IV; D-5-IV on short tubercle, D-8-IV, D-9-IV on closely separated, short tubercles; posterior dorsal sensilla (D-5-IV, D-4-IV, D-8-IV, D-9-IV) arranged in transverse row; L-1-IV short seta on small pointed tubercle, just anterior to L-3-IV; L-2-IV, L-4-IV short setae on stout pointed tubercles, L-3-IV moderately elongate seta on small, pointed tubercles; V-5-IV, V-7-IV minute setae, V-6-IV moderately elongate seta, all on small pointed tubercles, V-5-IV, V-6-IV closely approximated; segment 8 (Fig. 4I) modified, without D-2-VIII, D-3-VIII, L-1-VIII. Segment 9 (Fig. 4J) with D-5-IX, D-6-IX campaniform sensilla, dorsal surface covered with abundant tiny spinules, ventral surface with medial spot, length 1.17–1.19 (1.18, n=2) mm, width 0.34–0.38 (0.36, n=2) mm; terminal processes very elongate, slender with abundant spicules along its entire extent tapering to curved mesad, darkish, pointed apex; length 0.69–0.72 (0.70, n=2) mm.

3.15. Male pupa (Fig. 4K–N)

Similar to female with usual sexual differences. Total length 4.32–5.48 (4.84, n=5) mm. Dorsal apotome (Fig. 4K) with abundant stout thorns, DAL 0.096–0.112 (0.105, n=6) mm; DAW 0.288–0.320 (0.297, n=6) mm; DAW/DAL 2.57–3.08 (2.83, n=6). Respiratory organ (Fig. 4M), RO length 0.272–0.376 (0.304, n=6) mm, RO width 0.048–0.056 (0.049, n=6) pedicel short, length 0.014–0.020 (0.016, n=6) mm, P/RO 0.049–0.064 (0.055, n=6); 2 dorsolaterals, DL-1-H minute seta, DL-2-H campaniform sensillum (Fig. 4L–M), 3 anteromedials AM-1-T long, thin seta, AM-2-T minute seta and AM-3-T campaniform sensillum (Fig. 4M), anterolateral AL-1-T short, stout seta as in Fig. 4L. Cephalothorax length 1.42–1.62 (1.50, n=5) mm, width 0.98–1.16 (1.07, n=5) mm. Two metathoracic campaniform sensilla, M-3-T near anterior margin of metathorax. Segment 9 (Fig. 4N) apically truncate, dorsal surface with abundant tiny spinules; genital lobe short, not reaching posterior margin of segment, surface smooth; length 0.82–1.07 (0.92, n=6) mm, width

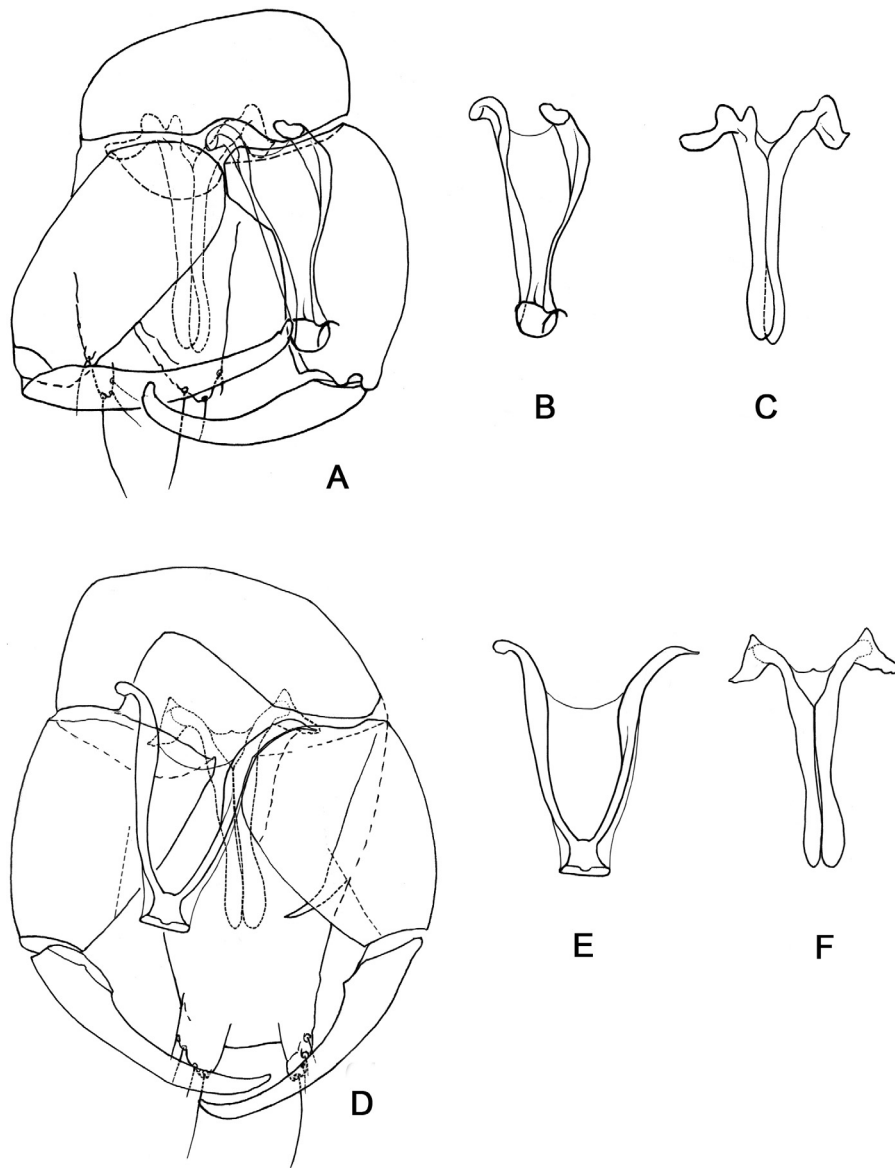


Fig. 8. *Heteromyia*, adult male genitalia (A–F): (A–C) *Heteromyia chaquensis* Duret and Lane, (D–F) *Heteromyia orellana* (Roback). (A, D) Genitalia. (B, E) Aedeagus. (C, F) Parameres.

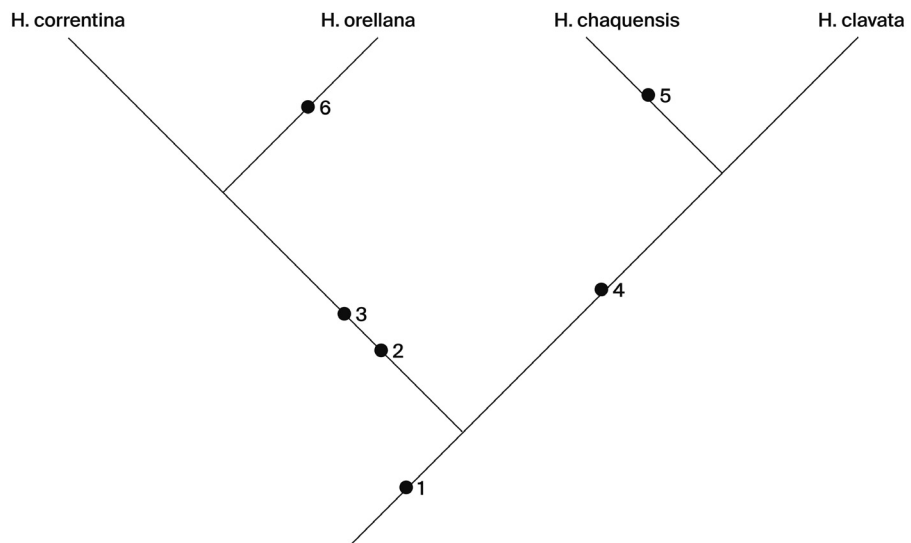


Fig. 9. Cladogram of studied species.

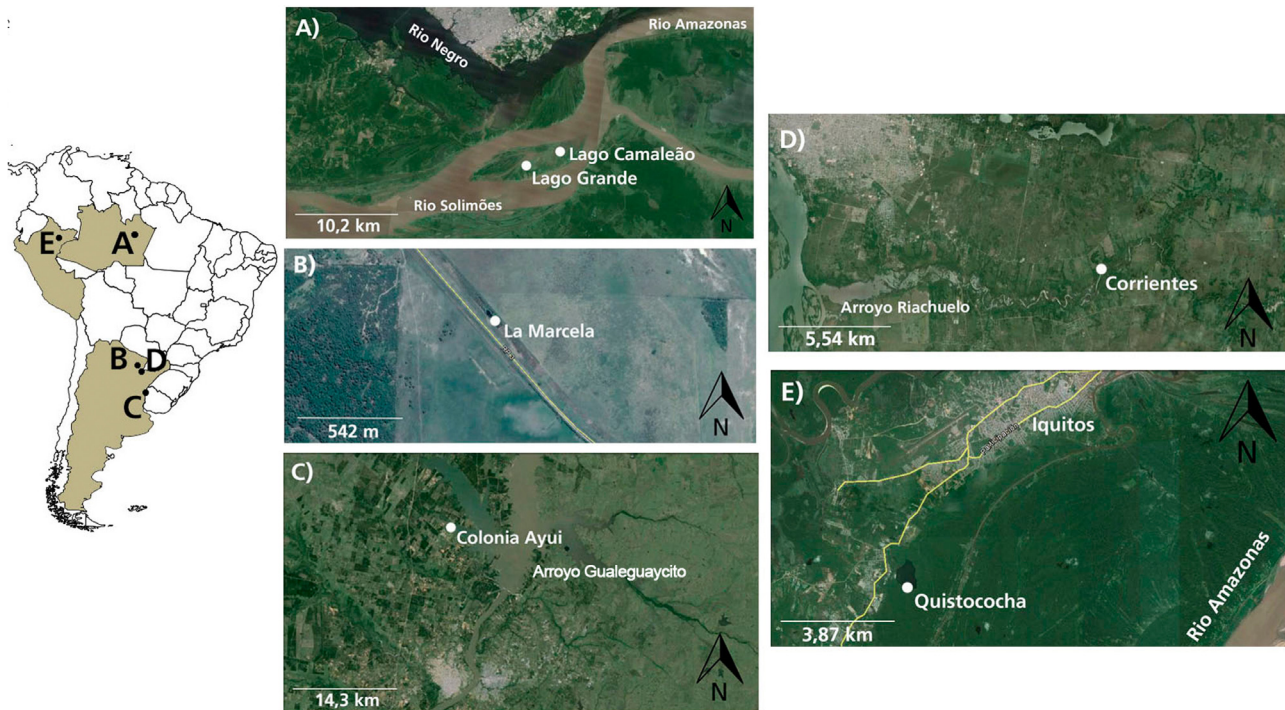


Fig. 10. Collecting sites (A–D). (A) *Heteromyia clavata* Williston. (B) *Heteromyia chaquensis* Duret and Lane. (C–D) *Heteromyia correntina* Duret and Lane. (E) *Heteromyia orellana* (Roback). Shaded areas indicate country (B–E) and state (A).

0.22–0.35 (0.28, n=6) mm; terminal processes thin, elongate with pointed tip, D-5-IX and D-6-IX present; length 0.48–0.61 (0.54, n=6) mm.

3.16. Distribution

Panama, Brazil (Rondônia, Amazonas), Argentina (Chaco, Corrientes, Entre Ríos).

3.17. Specimens examined

Brazil, Amazonas, Iranduba, Ilha da Marchantaria, Lago Camaleão, 03°13'14.9"S, 59°56'52.6"W, 26-VII-2010, Díaz – Marino, 1 male (with pupal exuvium) from *Pontederia cordata* Linnaeus; same data except 25-V-2011, R. Torreias, 1 male (with pupal exuvium) from *P. stratiotes*; Iranduba, Ilha da Marchantaria, Lago Grande, 03°14'43.9"S, 59°58'54.2"W, 28-VII-2010, Díaz – Marino, 2 males (with pupal exuviae); same data except 4-IV-2011, R. Torreias, 1 male (with pupal exuvium) from *E. crassipes*. Argentina, Formosa, Estancia La Marcela, 35 km E El Colorado, 26°21'43.03"S, 59°23'59.79"W, V-2005, F. Brusa, 1 male, luz; Corrientes, Estación Biológica Corrientes (EBCo), 27°32'50.5"S, 58°40'49.5"W, 53 m, 30-IX-2012, Díaz – Marino, 1 female (with pupal exuvium); Entre Ríos, arroyo Gualeguaycito, Colonia Ayuí, 31°11'55.60"S, 58°1'9.05"W, 10-XI-1984, Spinelli – Balseiro, 1 male, 1 female (with pupal exuviae) (Fig. 10).

Heteromyia orellana (Roback)

(Figs. 1 D, 5 A–M, 7 B, 8 D–F, 9, 10)

Palpomyia orellana Roback, 1957: 1 (female; Peru).

Heteromyia orellana: Wirth, 1974: 47 (New World catalogue south of USA; combination); Borkent and Wirth, 1997: 114 (World catalogue); Borkent and Spinelli, 2000: 56 (New World catalogue south of USA); Borkent and Spinelli, 2007: 89

(Neotropical catalogue); Borkent, 2016: 145 (online World catalogue).

3.18. Brief description of adult female

Only Neotropical species with thorax yellowish or yellowish brown; wing with one radial cell, dark area in r_3 restricted to a transversal band behind distal portion of radial cell, without isolated dark point beyond it, m_1 with dark spot containing a very small, slender, pale spot, hind tibia entirely dark brown.

3.19. Male genitalia (Fig. 8D) yellowish

Yellowish. Sternite 9 twice wider than long with V-shaped posteromedial excavation. Gonocoxite stout, 1.4 X longer than wide, tapering distally; gonostylus slender, slightly longer than gonocoxite, moderately curved with recurved, pointed, dark tip. Parameres (Fig. 8F) narrowly fused at base, each with basal arm stout, expanded; distal portion stout basally, slender mesally, with slightly bulbous tip. Aedeagus (Fig. 8E) triangular, twice longer than wide; basal arch concave, extending to 1/3 of total length; lateral arms slender, well sclerotized; apex broadened at extreme tip, latter bent, directed ventrally.

3.20. Male pupa (Figs. 1 D, 5 A–M, 7 B)

Total length 5.16 mm. Exuviae yellowish brown (Fig. 1D). Head: dorsal apotome (Fig. 5H) with disc 2.0 X broader than long, disc surface covered with stout knob-like tubercles, anterior margin rounded without subapical tubercle; each side of mesal area with smooth raised area; posterior margin concave, posterolateral margin with broad raised areas devoid of knob-like tubercles, bearing two dorsal apotome sensilla (Fig. 5H–I): DA-1-H short, stout seta, DA-2-H campaniform sensillum; DAL 0.11 mm; DAW 0.30 mm; DAW/DAL 2.64. Mouthparts (Fig. 5D) with mandible well devel-

oped, lacinia absent; palpus strong, extending to posterolateral margin of labium; labium divided. Sensilla: dorsolateral cephalic scleritesensilla (Fig. 5B): DL-1-H short seta, DL-2-H campaniform sensillum; clypeal/labials (Fig. 5E): CL-1-H and CL-2-H elongate, thin setae, CL-1-H slightly longer than CL-2-H; oculars (Fig. 5D): O-1-H and O-3-H elongate, thin setae, O-2-H campaniform sensillum. *Thorax*: prothoracic extension wide, well developed, narrow dorso-laterally; respiratory organ moderately elongate, brown, straight, slightly expanded at bent apex with 16 apical pores arranged in single curved row; surface smooth; length 0.288 mm, wide 0.048 mm; pedicel short, length 0.020 mm, P/RO 0.069 (Fig. 5A). Sensilla as follows: 3 anteromedials (Fig. 5B): AM-1-T long seta, AM-2-T short seta, AM-3-T campaniform sensillum; anterolateral (Fig. 5B) AL-1-T medium-sized, stout seta; 5 dorsal setae (Fig. 5C): D-1-T, D-2-T, D-5-T short, stout setae, D-3-T campaniform sensillum, D-4-T elongate, thin seta, all on rounded tubercle; supraalar SA-2-T campaniform sensillum; two metathoracic campaniform sensilla, M-3-T (Fig. 5F) near anterior margin of metathorax. Cephalothorax rectangular, length 1.50 mm, width 1.10 mm, surface covered with abundant rounded spicules, and brown, triangular tubercle located on mesothorax. *Abdomen*: segments with abundant spicules; tergite 1 with medial area with brown spot and two or three anterolateral spots, tergites 2–7 with stripe, two spots, two anterolateral spots; tergite 8 without stripe; sternites 3–7 with medial spot, two anterolateral spots; sternite 8 without medial spot. Sensilla: tergite 1 (Fig. 5G) with setae as follows: 7 dorsal sensilla, two anterior setae, D-2-I short, stout seta, D-3-I long, thin seta, D-4-I, D-7-I campaniform sensilla, D-7-I situated anteriorly, near D-3-I; three posterior setae: D-5-I, D-8-I short, thin setae, D-9-I long, thin seta; 3 lateral sensilla, L-1-I long, thin seta, L-2-I, L-3-I short, stout setae, all setae on small tubercles; second abdominal segment similar to the first one; segment 4 (Figs. 5 J–K, 7 B) with sensillar pattern as follows: D-2-IV short, stout seta, D-3-IV elongate, thin seta on short, quadrangular tubercles; D-5-IV, D-8-IV minute setae, D-9-IV elongate, thin seta, D-4-IV, D-7-IV campaniform sensilla, D-7-IV situated near D-3-IV, D-5-IV on short tubercle, D-8-IV, D-9-IV on closely separated, short tubercles, posterior dorsal sensilla (D-5-IV, D-4-IV, D-8-IV, D-9-IV) arranged in transverse row; L-1-IV short seta on small pointed tubercle, just anterior to L-3-IV; L-2-IV, L-4-IV short setae on stout pointed tubercles, L-3-IV moderately elongate seta on small, pointed tubercles; V-5-IV, V-7-IV peg-like setae, V-6-IV moderately elongate seta, all on small pointed tubercles, V-5-IV, V-6-IV closely approximated; segment 8 (Fig. 5L) modified, without D-2-VIII, D-3-VIII, D-5-VIII, L-1-VIII and L-4-VIII. Segment 9 (Fig. 5M) with D-5-IX, D-6-IX campaniform sensilla, dorsal and ventral surface covered with abundant tiny spicules, ventral surface with medial spot; length 0.91 mm, width 0.36 mm; genital lobes short, not reaching posterior margin of segment, surface smooth; terminal processes elongate, slender with abundant posteriorly directed spicules along its entire extent tapering to curved mesad, pointed apex; length 0.52 mm.

3.21. Distribution

Peru (Iquitos).

3.22. Specimens examined

Peru, Iquitos, Quistococha, 03°49'42.13"S, 73°19'17.68"W, 13-VIII-1996, G. Spinelli, 1 male (with pupal exuvium), from mud at pond margin (Fig. 10).

4. Taxonomic discussion

It is worth remarking the position of the DA-2-H sensillum in the four species herein studied. It is located ventral to DA-1-H.

This is coincident with the illustration of the female dorsal apotome of *Heteromyia wokei* provided by Borkent (2014), which also shows the same localization of the dorsal apotomal sensilla. This is a synapomorphy and a new diagnostic feature for the genus.

Based on the observations carried out during this study, a couple of discrepancies arise with the generic description by Borkent (2014) for the pupa of *Heteromyia*:

- 1) Anteromedial sensilla (AM): Borkent (2014) mentioned two setae, one short (AM-2-T) and one long (AM-1-T). The four species herein studied also show these two setae plus an additional one, a campaniform sensillum (AM-3-T). The latter is located near AM-2-T in *H. chaquensis*, *H. clavata* and *H. correntina* (Figs. 2 C, 3 B, 4 K), and near AM-1-T in *H. orellana* (Fig. 5B). Borkent (2014) lightly overlooked this sensillum. This character is only shared with *Pellucidomyia* Macfie within the Heteromyiini.
- 2) Sensilla of abdominal segment 8: Borkent (2014) mentioned the absence of one dorsal sensillum (D-3-VIII) and one lateral sensillum (L-1-VIII). Our study reveals that the absence of dorsal sensilla is more variable, e.g., the four studied species lack D-2-VIII and D-5-VIII and *H. orellana* also lacks L-4-VIII.

With regard to differences and similarities of the species described during this study, *H. clavata* and *H. chaquensis* are very similar by virtue of the dorsal apotome surface very smooth, the labium entire, the D-2-T sensillum large and the abdominal segment 1 lacking the D-5-I sensillum. On the other hand, the dorsal apotome surface is tuberculate in *H. correntina* and *H. orellana*; the labium is divided; the D-2-T sensillum is short and the D-5-I sensillum is present in the abdominal segment 1.

Heteromyia chaquensis differs from *H. clavata* by its smaller size and yellowish coloration (dark brown coloration in *H. clavata*), the anterior margin of the dorsal apotome deeply notched (rounded with a dark, mesal triangular shaped projection in *H. clavata*) and the terminal processes of segment 9 much more divergent.

Heteromyia correntina differs from *H. orellana* by its larger size and segment 9 darker than preceding ones. The habitats where they were collected also differ, *H. correntina* is associated with floating macrophytes and *H. orellana* was present in mud at a pond margin.

Currently there are six species of *Heteromyia* known as pupae, being their larvae unknown. The description of the habitats of the pupae here may provide the necessary clues to discover them in the future.

As a rule, the association between some taxonomic structures with immature habitats is evident. The long terminal processes of the pupae of this genus are typical of ceratopogonids that inhabit in large environments and are associated with floating vegetation.

5. Phylogenetic relationships

Our analysis of features of the pupae of four species of *Heteromyia* shows only one synapomorphy (character 1) (Fig. 9). The characters 2 and 3 are plesiomorphic in *H. correntina* and *H. orellana*, while the character 4 is apomorphic for *H. chaquensis* and *H. clavata*. The characters 5 and 6 are derived conditions.

5.1. Character states in the studied species

1. Dorsal apotome with one seta and a campaniform sensillum (Figs. 2 A, 3 A, 4 A, K, 5 A–B). The DA-2-H campaniform sensillum is located ventral to DA-1-H seta, something unique in the family. Some *Dasyhelea* Kieffer and some *Austroconops* Wirth and Lee have the DA-2-H nearly lateral to each other or slightly ventral

to DA-1-H. This is a synapomorphy and a new diagnostic feature for the genus.

2. Thorax with five dorsal setae; D-1-T, D-2-T and D-5-T present as peg-like setae in *H. correntina* (Fig. 4F) or short setae in *H. orellana* (Fig. 5G). This condition also occurs in *Clinohelea* Kieffer (plesiomorphic condition). *Heteromyia chaquensis* and *H. clavata* have D-1-T, D-2-T and D-5-T elongate setae (Figs. 2 E, 3 E) as in *Pellucidomyia* (derived condition).
3. Pupal mouthparts with labium entire or divided by labrum is present in *Heteromyia* (plesiomorphic condition). *Heteromyia correntina* and *H. orellana* (Figs. 4 B, 5 D) have a labium divided by labrum. This character state is shared with *Clinohelea* and *Pellucidomyia*, but the presence of labium entire is present in *H. chaquensis* and in *H. clavata*.
4. Pupal dorsal apotome surface is tuberculate in *H. correntina* and in *H. orellana* (Figs. 4 A, K, 5 A–B). This feature is the unique synapomorphy which indicates that these two species are sister species. *Heteromyia chaquensis* and *H. clavata* show the dorsal apotome surface smooth (Figs. 2 A, 3 A). This derived condition is unique within *Heteromyia*, but similar to observed in *Pellucidomyia*.
5. Pupal dorsal apotome without dorsomedial notch is present in most species of *Heteromyia* (Figs. 4 A, K, 5 A) (plesiomorphic condition). The plesiomorphic condition also occurs in *Clinohelea* and in *Pellucidomyia*. *Heteromyia chaquensis* (Fig. 2A) shows the anterior margin of the dorsal apotome with dorsomedial notch. This derived condition is nearly unique within the *Heteromyiini*, but *H. clavata* has puzzling intrageneric variation (Fig. 3A).
6. Pupal abdominal segment 8 with three lateral sensilla is present in *Clinohelea*, *Pellucidomyia* and most species of *Heteromyia* (Figs. 2 I, 3 I–J, 4 I) (apomorphic condition). *Heteromyia orellana* (Fig. 5L) has two lateral sensilla in the abdominal segment 8. This second derived state is unique within the *Heteromyiini*.

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