Beitr. Ent.	Keltern	ISSN 0005 - 805X
57 (2007) 1	S. 37 - 80	30.06.2007

Revision of the New World Heteromeringia

(Diptera: Clusiidae: Clusiodinae)

With 63 figures on 24 plates and 5 maps

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Summary

The 18 New World species of Heteromeringia CZERNY, 1903 are revised, with 10 species described as new: H. apholis sp. n. (Mexico), H. aphotisma sp. n. (Brazil), H. decora sp. n. (Mexico), H. lateralis sp. n. (Costa Rica), H. mediana sp. n. (Brazil), H. nanella sp. n. (Brazil), H. nervosa sp. n. (Costa Rica), H. quadriseta sp. n. (Ecuador, Peru), H. volcana sp. n. (Costa Rica) and H. zophina sp. n. (Mexico). The Nearctic H. nitida nigripes Melander & Argo, 1924 is raised from subspecies to species. The H. nitida species group and the H. czernyi species group are erected, and species relationships are discussed for the latter (entirely neotropical) group. Sobarocephala subfasciata Curran, 1939 is included as a junior synonym of H. czernyi Kertesz, 1903. Heteromeringia dimidiata Hennig, 1938 is moved to Sobarocephala Czerny, 1903 comb. n. Heteromeringia tephrinos nomen n. is provided as a replacement name for the Afrotropical H. nigrifrons Lamb, 1914, which is a junior primary homonym of H. nigrifrons Kertesz, 1903. The biology of Heteromeringia is discussed, and a key is provided for all New World species. Agonistic interactions are described for this genus for the first time, with H. nitida Johnson, 1913 males recorded as using bicoloured forelegs to defend mating territories.

Key words

Heteromeringia, H. czernyi species group, H. nitida species group, Clusiidae, Diptera, New World, revision, new species, stat. n., syn. n., comb. n., nomen n., biology, behaviour.

Zusammenfassung

Die 18 neuweltlichen Arten von Heteromeringia CZERNY, 1903 werden revidiert inklusive Beschreibung von 10 neuen Arten (H. apholis sp. n. (Mexiko), H. aphotisma sp. n. (Brasilien), H. decora sp. n. (Mexiko), H. lateralis sp. n. (Costa Rica), H. mediana sp. n. (Brasilien), H. nanella sp. n. (Brasilien), H. nervosa sp. n. (Costa Rica), H. quadriseta sp. n. (Ecuador, Peru), H. volcana sp. n. (Costa Rica) und H. zophina sp. n. (Mexiko)). Die nearktische Unterart H. nitida nigripes Melander & Argo, 1924 wird zur Art erhoben. Die H. nitida-Artengruppe und die H. czernyi-Artengruppe werden aufgestellt, und die Verwandtschaftsverhältnisse der letzteren (ausschließlich neotropischen) Gruppe werden diskutiert. Sobarocephala subfasciata Curran, 1939 wird synonymisiert mit H. czernyi Kertesz, 1903. Heteromeringia dimidiata Hennig, 1938 wird in die Gattung Sobarocephala Czerny, 1903 comb. n. gestellt. Heteromeringia tephrinos nomen nov. wird als Ersatzname vorgeschlagen für die afrotropische H. nigrifrons Lamb, 1914, ein jüngeres primäres Homonym von H. nigrifrons Kertesz, 1903. Die Biologie von Heteromeringia wird diskutiert und ein Bestimmungsschlüssel für die neuweltlichen Arten wird vorgestellt. Zum ersten Mal wird aggressives Verhalten innerhalb der Gattung beschrieben: Männchen von H. nitida benutzen ihre zweifarbigen Vorderbeine zur Verteidigung von Paarungsrevieren.

Stichwörter

Heteromeringia, H. czernyi-Artengruppe, H. nitida-Artengruppe, Clusiidae, Diptera, Neue Welt, Revision, neue Arten, stat. n., syn. n., comb. n., nomen n., Biologie, Verhalten.

New species

Heteromeringia apholis sp. n., H. aphotisma sp. n., H. decora sp. n., H. lateralis sp. n., H. mediana sp. n., H. nanella sp. n., H. nervosa sp. n., H. quadriseta sp. n., H. volcana sp. n., H. zophina sp. n.

Introduction

Heteromeringia CZERNY, 1903 is a widespread genus of 61 species, 10 of which are described as new herein. The genus is characterized by relatively small external terminalia and an extremely long, coiled, black, double-ribbed distiphallus. Furthermore, because of the size of the phallus, the annulus (sternites 6-8) is also pocket-like ventrally so as to contain it when at rest. The male genitalia of Heteromeringia are the most distinct in the Clusiidae, but Heteromeringia is otherwise superficially similar to the sobarocephaline genera Sobarocephala CZERNY, 1903, Chaetoclusia Coquillett, 1904 and Procerosoma Lonsdale & Marshall, 2006a. These genera, however, have a smooth (not wrinkled and flat) scuttellum, Sobarocephala and Chaetoclusia have a dorsal preapical bristle on the mid tibia, and Procerosoma has an open cell bm (like most Sobarocephala) and a reduced mid fronto-orbital. All other New World Clusiidae have either interfrontal bristles, three long dorsocentral bristles, or a reclinate anterior fronto-orbital.

Heteromeringia has its centers of diversity in the New World and Old World tropics, particularly in the Oriental Region, with dozens of described (Sasakawa, 1966) and undescribed species. Eight species are known from Australia (McAlpine, 1960) and three are known from Africa and the Seychelles (Verbeke, 1968; Lamb, 1914). The relatively few species found in the Holarctic region include one species in Europe (H. nigrimana (Loew, 1864)), four species in Japan (H. quadrispinosa Sueyoshi, 2006, H. sexramifera Sueyoshi, 2006, H. crenulata Sueyoshi, 2006 and H. yamata Sueyoshi, 2006 (Sueyoshi, 2006)) and four species in North America (H. nitida Johnson, 1913, H. nigripes Melander & Argo, 1924, and the mostly neotropical H. czernyi Kertesz, 1903 and H. flavipes (Williston, 1896), which extend into Florida).

Eighteen species of *Heteromeringia* have been collected in the Neotropical Region, ten of which are described here as new. Of these 18 species, seven are placed in the newly erected "*H. czernyi* species group", which occurs throughout the Neotropics with two species ranging north to Florida. This group (described below) is well supported as monophyletic and easily recognized on the basis of a vibrissa-like anterior genal bristle.

Of the remaining ten species, seven are placed in what we here describe as the "Heteromeringia nitida species group". This large, widespread group occurs in all biogeographic regions except the eastern Palaearctic and is defined on the basis of a small, pale, disc-like structure on the male anepisternum (Fig. 9). The function of this disc is unknown, but it is positioned anterior and ventral to the anepisternal bristle, and is distinctly textured, circular, white to yellowish and approximately four to five times the width of the base of the anepisternal bristle. Mcalpine (1960) first noted this structure, finding it in most Australian species.

The remaining three New World *Heteromeringia* are currently unplaced because *H. apholis* sp. n. lacks the male anepisternal disk, and *H. decora* sp. n. and *H. nigrifrons* Kertesz, 1903 are known only from females.

Materials and methods

Over 1000 specimens were examined from, or deposited in, the following institutions: British Museum of Natural History, London (BMNH); California Academy of Sciences, San Francisco (CASC); Coleccion Boliviana de Fauna, La Paz (CBFC); Canadian National Collection, Ottawa (CNCI); University of Guelph Insect Collection (DEBU); Entomological Museum of Utah State, Logan (EMUS); Zoological Department of the Hungarian Natural History Museum, Budapest (HNHM); Instituto Nacional de Biodiversidad, Santo Domingo de Heredia (INBC); Coleccio Sistematica da Entomologia, Manaus (INPA); Museum of Comparative Zoology, Cambridge (MCZC); North Carolina State University, Raleigh (NCSU); Naturhistorische Museum Wien (NHMW); Muséum d'Histoire Naturelle, Genève (MHNC); Naturhistoriska Riksmuseet, Stockholm (NHRS); Museu Nacional, Quinta da Boa Vista, Rio de Janeiro (QBUM); Universidad Catolica del Ecuador, Quito (QCAZ); Royal Ontario Museum, Toronto (ROME); Staatlisches Museum für Tierkunde, Dresden (SMTD); Texas A&M University, College Station (TAMU); United States National Museum, Washington D. C. (USNM); Museum of Zoology, Lund University (UZMD); Zoologische Staatssammlung München (ZSMC). Preparation of specimens and morphological terminology follows that outlined in Lonsdale & Marshall (2006b). The M₁₊₂ ratio is defined as the length of the ultimate section of vein M divided by the length of the penultimate section. Body length and M₁₊₂ ranges include those for both sexes.

Heteromeringia CZERNY, 1903

Heteromeringia Czerny, 1903: 72. Kertesz, 1903: 567. Johnson, 1913: 98. Malloch, 1918: 7. Melander & Argo, 1924: 28. McAlpine 1960, 83-85. Sasakawa, 1966: 61-100. Type species: Heteromeringia nigrimana (Loew, 1864) (by monotypy).

Diagnosis

Outer angular extension on pedicel blunt and obtuse. Scutellum flattened and wrinkled dorsally. Subcostal break indistinct. Three or four fronto-orbital bristles, reclinate except for inclinate anterior bristle. Interfrontal bristle absent. One small lateral scutellar bristle (Fig. 8). Acrostichal bristle absent. Tibiae without dorsal preapical bristles. Distiphallus elongate, thin, with one pair of heavily-sclerotized lateral "ribs" and usually with accessory distal sclerites (Fig. 12). Ejaculatory apodeme elongate with apex fan-shaped (shown from different angles in Figs 24, 36 and 53).

Generic description

General. Body length 2.4-5.0 mm. Colour predominantly brown to black, sometimes yellow with variable dark pattern. Face flat and microsetulose. Arista sparsely plumose to pubescent. Outer angular extension on pedicel blunt and obtuse; inner extension absent. Antenna arising at midpoint of head. Frons almost always with medial pilose patch on anterior half or more (often reduced in females). Postcranium concave. Scutellum flattened dorsally and longitudinally wrinkled. Subcostal break indistinct. Wing clear to variably patterned. M_{1+2} ratio (length of the ultimate section of vein M_1 divided by length of penultimate section) 4.0-12.0 (usually 4.5-8.0). Fore tarsi usually with slight lateral compression (pronounced in some Old World species).

Chaetotaxy

Bristles black to brown. Three or four fronto-orbital bristles, reclinate except for inclinate anterior pair; anterior two bristles closely spaced near anterior margin of frons and hind pair positioned near posterior margin; fourth bristle sometimes present between anterior two pairs but less than 2/3 length of other bristles. Postvertical and ocellar bristles divergent, minute to large. Interfrontal bristle absent. Vibrissa well-developed. Usually five to seven short genal bristles (anterior bristle sometimes vibrissa-like). Two subgenal bristles. Pedicel with one outstanding dorsal bristle.

Occiput with row of short bristles behind eye margin. Two postsutural dorsocentral bristles, with anterior bristle usually 3/5-4/5 times length of posterior bristle; sometimes small additional bristle directly in front of anterior dorsocentral. Scutellum with one small lateral bristle and one long incurved apical bristle (Fig. 8). Acrostichal bristle absent. One postpronotal, two notopleural, two postsutural intra-alar and sometimes one small to minute intra post-alar bristle. 1-2 (Fig. 8) strong anepisternal and 1 katepisternal bristle. Tibiae without dorsal preapical bristles. Male fore and mid femora with ventral row of ctenidial bristles.

Male abdomen and terminalia

Tergite 1 narrow and fused to tergite 2; tergites 3-6 and sternites 2-5 well-developed, separate; sternite 1 reduced to thin strip; sternites 2-5 well-developed. Sternites 6-8 forming complete asymmetrical ring (= "annulus"); sternite 8 setose and dorsal with right lateral extension; sternite 7 on left side between sternites 6 and 8, heavily sclerotized anteriorly; sternite 6 fused to sternite 7 laterally, heavily sclerotized anteriorly, and weakly attached to sternite 8 ventrally; sternites 6 and 7 variably differentiated ventrally into weakly sclerotized, folded and/or widened regions, forming enlarged membranous "pocket" to enclose distiphallus when it is at rest. Spiracles in membrane ventral to tergites 1-5, (often) dorsolaterally between sternites 6 and 7, and ventrally between sternites 6 and 8. Epandrium dome-shaped, evenly bristled (Figs 10 and 11), and usually much narrower than abdomen. Surstylus variable in shape (Figs 10, 17, 33 and 51), but often less than 2/3 length of epandrium and rounded (very thin if longer); small rounded bristles apical on inner face. Cerci variable (Figs 11, 14, 18, 32 and 47), but usually less than half length of epandrium and often united. Hypandrium fused to pregonite (shape globose to triangular in profile) (Fig. 12), sparsely setose (bristles usually short and stout) and sometimes with distal setulae; hypandrial arm short and stout. Postgonite, epiphallus and lateral lobe of distiphallus absent. Phallapodeme 0.5-1.0 times length of hypandrium + pregonite. Basiphallus fused to distiphallus anteriorly. Distiphallus very elongate, dark, thin, with one pair of heavily-sclerotized lateral "ribs", and often with distal accessory sclerites. Ejaculatory apodeme elongate with apex fan-shaped.

Female abdomen and terminalia

Tergites 1 and 2 fused; tergites 3-6 and sternites 2-6 complete; sternite 1 reduced to thin anterior strip. Segments 7 and 8 narrowed into long, thin tube; terminal segments separated by long membranous area. Spiracles in membrane below tergites on segments 1 to 7. Cerci as long as sternite 10, length four times width. Spermatheca (one pair) pigmented (Figs 28-30 and 48-50); shape variable, but usually small, transversely wrinkled, cylindrical and telescoped. Genital chamber membranous and elongate. Spermathecal duct weakly sclerotized. Ventral receptacle sac-like (widest subapically), recurved, and with long, sometimes loosely coiled, subterminal flagellum (Fig. 29).

Key to the New World species of Heteromeringia.

Note: For specimens collected north of Mexico and southern Florida, start with couplet 11. Species placed in the *Heteromeringia nitida* species group are indicated by an asterisk (*), and species *incertae sedis* are indicated by an " Ω ".

1. Anterior genal bristle usually small, hair-like and not larger than remaining genal bristles. Arista short-pubescent. Three fronto-orbital bristles. Wing dusky, with small anterodistal cloud, or (rarely) clear. Palpus usually black, at least in part. Male usually with minute disc on an episternum (absent in *H. apholis*; males unknown for *H. nigrifrons* and *H. decora*)

-	(Fig. 9). Male terminalia: phallapodeme usually at least as long as hypandrium (Fig. 12); distiphallus usually with distal accessory sclerite(s); pregonite well-developed with two or more long, stout bristles (Fig. 12). Female terminalia (Figs 25-27): ventral receptacle small and sac-like; spermatheca much shorter than sternite 6, compact and telescoped; spermathecal duct not exceptionally long
2.	Notum yellow with brown pattern (Fig. 4). Anterior margin of frons black medially. Southern Mexico (Map 3)
-	Notum brown to black with postpronotum and notopleuron sometimes lighter. From mostly dark brown to black with anterior margin yellow to orange (at least medially), but sometimes lateral margins yellow anteriorly
3.	Fore tibia yellow. Mid tibia brown. Peru (Map 3) <i>H. nigrifrons</i> Kertesz, 1903 $^{\circ}$
-	Fore tibia black (sometimes yellow distally). Mid tibia sometimes light brown, brown on basal half, or with brown mottling
4.	Length 2.4-2.9 mm. Legs, including coxae, entirely brown. Wing clouded along anterior margin from R_1 to apex. Mexico (Map 3)
-	Length 2.8-4.3 mm. Legs yellow, at least in part. Wing clouded around apex of R_{2+3} or more extensively infuscated
5.	Face yellow. Palpus entirely brown. Distal 3/4 of first flagellomere dark brown (except on outer face). Gena nearly half height of eye. Male anepisternum without circular patch. Male cerci narrowing apically
	Face brown. Distal 1/3 of palpus yellow. First flagellomere lightly infuscated along inner-distal margin. Gena less than 1/3 height of eye. Male with small white circular patch on an episternum (Fig. 8). Male cerci widening apically
6.	Wing darkly clouded with pigment gradually fading to M_1 ; first radial cell evenly pigmented to R_1 (Fig. 57). Male cerci long, thin, and entirely united (Fig. 14). Neotropics (Map 2). Common
-	Wing dark to clear, with any pigment surrounding veins distinctly separated from each other (except at wing tip) by thin hyaline gap (Figs 54-56); if first radial cell dark, stripe interrupted distal to vein R_1 . Male cerci sometimes united, but never long and thin. Uncommon outside of United States.
7.	Fore femur yellow with apex dark brown. Male frons pilose, leaving only posterior half or wide spot around ocellar tubercle shiny; female frons sometimes as described for male, but pilosity usually restricted to small anterior spot. Male cerci well-developed and united (occasionally emarginate).

42 LONSDALE, O. & MARSHALL, St. A.: Revision of the New World Heteromeringia Fore femur entirely brown, at least on distal half, but rarely yellow with brown subapical band (some tropical specimens of *H. nigripes*). Anterior margin of male frons usually pilose medially on anterior 1/3 of frons or less (much reduced or absent in females). Male cerci 8. Postpronotum reddish. Fore tibia with brown mottling and yellow base. Mid tibia mottled with dark brown outer-apical spot. Hind femur with dark brown inner-apical spot. Face Notum entirely dark brown. Fore tibia brown. Mid tibia yellow. Hind femur dark brown. Femora entirely dark brown. First flagellomere yellow with orange spot at base of arista. 9. Male cerci and surstyli minute and triangular (Figs 16-18). Brazil (Map 3). Base of fore femur yellow (excluding some Mexican specimens), and mid and hind femora often predominantly yellow. First flagellomere entirely orange (female H. fucata), or extensively infuscated on inner face and anterior margin. Male cerci long and emarginate and Female first flagellomere orange. Male wing clear; female wing darkly clouded, excluding 10. region anterior to vein R, in front of basal cells and along posterior margin (Fig. 54). Ocellar bristle well-developed. Mid and hind femora yellow. Surstylus subtriangular in outline Female first flagellomere infuscated along anterior and inner-distal margins. Both sexes with wing darkly clouded on distal half along R_{2+3} and costa, and lightly clouded around R_{4.5} distally (Fig. 55). Ocellar bristle sometimes thin and weak. Mid and hind femora sometimes partly brown. Surstylus very thin on distal half and strongly acute. 11 11. Mid and hind coxae yellow, sometimes with dorsal margin brown; Mexican specimens with fore coxa, mid coxa, fore femur and hind femur entirely brown. Fore coxa white. Pedicel yellow. M_{1,2} ratio 5.0-7.5. Surstylus acute with apex rounded (Fig. 22). Spermatheca (Fig. 29) subcylindrical in shape with base narrowed; longer than wide. Spermathecal duct of nearly equal width along length. Southern Ontario, United States (mostly eastern, uncommon in Mid and hind coxae brown. Fore coxa light yellow. Fore femur brown with base yellow (nearctic and some neotropical specimens), or yellow with brown subapical band (Neotropics). Hind femur brown with base and apex yellow (North America), or yellow with brown dorsoapical spot (neotropical specimens outside Brazil). Pedicel sometimes brown. M_{1,2} ratio 4.0-5.0. Surstylus strongly pointed (Fig. 19). Spermatheca (Fig. 30) bell-shaped (broadly rounded apically and wide basally), and wider than long. Spermathecal duct abruptly swollen distally. United States (mostly southwestern, uncommon in the east), Mexico, Costa Rica, Honduras, southern Brazil (Map 1). One inclinate and two reclinate fronto-orbital bristles. Notum dark brown. Bristles brown. 12. Wing with strong to weak medial cloud (Fig. 59). Phallapodeme well-developed. Surstylus

brown. First flagellomere brown with base yellow. Wing with strong medial spot or bat (Fig. 59). Common. Florida to Argentina (Map 4)	-	One inclinate and three reclinate fronto-orbital bristles (anterior reclinate bristle small). Notum sometimes yellow to reddish with brown pattern. Bristles dark brown to black. Wing without separate medial cloud (Figs 60-63). Phallapodeme atrophied. Surstylus without scales
browned. Wing only lightly infuscated medially. Uncommon. Costa Rica, St. Vince (Map 5)	13.	Fore tarsi, fore tibia (usually), and sometimes mid tibia, hind tibia and tip of fore femure brown. First flagellomere brown with base yellow. Wing with strong medial spot or band (Fig. 59). Common. Florida to Argentina (Map 4) H. czernyi Kertesz, 1903
Thorax and legs yellow with variable brown pattern on thorax (Figs 2, 3, 5-7)	-	Legs yellow, sometimes with mid tibia brown. First flagellomere yellow with distal 1/3 browned. Wing only lightly infuscated medially. Uncommon. Costa Rica, St. Vincent (Map 5)
 15. Arista short-plumose. Postpronotum brown (Fig. 5), with colour sometimes faded (Fig. 6 Scutum sometimes with central postsutural stripe. Distal half of first flagellomere sometime brown. Bolivia, Brazil (Santa Catarina), Costa Rica, Ecuador, Honduras (Map 5)	14.	Thorax and legs (excluding hind coxae) dark brown. Brazil (Rio de Janeiro) (Map 5) H. aphotisma sp. n.
Scutum sometimes with central postsutural stripe. Distal half of first flagellomere sometime brown. Bolivia, Brazil (Santa Catarina), Costa Rica, Ecuador, Honduras (Map 5)	-	Thorax and legs yellow with variable brown pattern on thorax (Figs $2,3,5$ -7)
yellow or with orange tint. Scutum bivittate or entirely yellow. First flagellomere yellow white, sometimes with infuscation at base of arista	15.	Arista short-plumose. Postpronotum brown (Fig. 5), with colour sometimes faded (Fig. 6). Scutum sometimes with central postsutural stripe. Distal half of first flagellomere sometimes brown. Bolivia, Brazil (Santa Catarina), Costa Rica, Ecuador, Honduras (Map 5)
very faint). Scutum with one pair of thick stripes that connect anteriorly (Fig. 7). Subnot stripe brown. Tergite 1 and anterior half of tergite 2 yellow. Anterior margin of wing dark clouded into costal cell (Fig. 60). Costa Rica	-	Arista very short-plumose or pubescent. Lateral margin of scutum (including postpronotum) yellow or with orange tint. Scutum bivittate or entirely yellow. First flagellomere yellow to white, sometimes with infuscation at base of arista
reduced or absent. Subnotal stripe orange or absent. Tergites 1 and 2 dark brown. Anteri margin of wing clear on basal half	16.	Fore tarsi brown with basal segment yellow. From brown medially (sometimes pigment very faint). Scutum with one pair of thick stripes that connect anteriorly (Fig. 7). Subnotal stripe brown. Tergite 1 and anterior half of tergite 2 yellow. Anterior margin of wing darkly clouded into costal cell (Fig. 60). Costa Rica
distal half of R ₂₊₃ (Fig. 62). Ecuador, Peru (Map 5)	-	Fore tarsi yellow, sometimes with distal segment brown. Frons yellow. Notal markings reduced or absent. Subnotal stripe orange or absent. Tergites 1 and 2 dark brown. Anterior margin of wing clear on basal half
along anterior margin and around CuA ₁ (Fig. 63). Brazil (Amazonas) (Map 5)	17.	Scutellum yellow medially (Fig. 2). Tergites 6 to epandrium yellow. Wing clouded around distal half of R ₂₊₃ (Fig. 62). Ecuador, Peru (Map 5)
	-	along anterior margin and around CuA ₁ (Fig. 63). Brazil (Amazonas) (Map 5)

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Species descriptions.

Descriptions follow in alphabetical order within the *Heteromeringia nitida* group, the *H. czernyi* group and the unplaced species.

Heteromeringia nitida species group.

Heteromeringia fucata HENDEL, 1936

(Figs 10-12, 54, Map 3)

Heteromeringia fucata HENDEL, 1936: 89.

Description

Male

As described for female (see below) except as follows: minute bristle in front of anterior dorso-central; small white disc anterior and ventral to an episternal bristle; distal half of fore femur dark brown; hind tibia yellow; first flagellomere entirely yellow; infuscated regions on face, gena and parafacial dirty yellow to light brown (face otherwise yellow); palpus yellow with brownish base; frons pilose (excluding region around ocellar tubercle); wing clear.

Male terminalia (Figs 10-12)

Width and height of epandrium 1/3 greater than length. Cerci approximately 3/4 height of epandrium, widest subbasally, and with deep distal emargination. Surstylus nearly as high as epandrium, acutely triangular, curved inwards, slightly arched anteriorly, with minute setulae along outer surface apically and with small pointed bristles on inner-distal margin. Hypandrial complex similar to that of *H. nigripes* except pregonite with fewer distal setulae and no posterior setulae, and distal sclerites of distiphallus absent and basal sclerites somewhat widened and less heavily sclerotized at apex.

Female (Fig. 54)

Body length 4.3 mm. Bristles black. Two dorsocentral bristles. Ocellar bristle relatively long and well-developed. Genal bristles small and hair-like. Three fronto-orbital bristles. Arista pubescent. Thorax dark brown. Legs predominantly yellow with fore tarsi, fore tibia, hind tibia, distal 2/3 of fore femur and dorsal 2/3 of mid coxa dark brown. Head predominantly dark brown, although antenna (excluding arista) orange with anterior half of first flagellomere infuscated on inner face, anterior margin of frons orange medially, face yellow between antennal bases and tip of palpus yellow; upper-anterior margin of gena pilose (upper half of gena dirty yellow in female from Nova Teutonia); clypeus relatively wide laterally and thin medially. Abdomen dark brown with terminalia yellow. Wing darkly clouded excluding region anterior to vein R_1 in front of basal cells and along posterior margin. M_{1+2} ratio 4.8.

Female terminalia

Not dissected.

Holotype: BRAZIL. Unt. Amaz. Taperiuha, b. Santarem, 1-10.vi.1927, Zerny (1 \, \times, NHMW). Additional material examined: BRAZIL. Nova Teutonia, S.C., ix.1949, F. Plaumann (1 \, \times 1 \, \sigma, USNM).

Comments

The male of this unusually dimorphic species is described here for the first time on the basis of a specimen collected with a female identical to the holotype. Although the male of *Heteromeringia*

fucata does not closely resemble the female (see above description), both have yellow mid and hind femora in combination with a brown thorax, a relatively small M_{1+2} ratio and a pilose patch on the upper-anterior margin of the gena, separating them from neotropical congeners.

Heteromeringia fumipennis Melander & Argo, 1924

(Figs 9, 13-15, 28, 57, Map 2)

Heteromeringia fumipennis Melander & Argo, 1924: 30.

Description (Fig. 9)

Male

Body length 2.8-4.1 mm. Bristles black. Anterior dorsocentral bristle 1/2-4/5 length of posterior dorsocentral. Ocellar bristle relatively long and well-developed. All genal bristles small and hair-like. Three fronto-orbital bristles. Arista short-plumose. Male with small white disc anterior and ventral to anepisternal bristle. Thorax dark brown. Fore coxa white, and mid and hind coxae yellow (occasionally brown). Legs yellow except as follows: fore femur dark brown apically; mid femur sometimes dark brown on basal 4/5; hind femur dark brown apically (sometimes to distal half); fore tarsi, and fore and hind tibiae dark brown. Frons black with anterior margin orange; occiput and back of head dark brown; face and gena yellow to orange; palpus black with yellow tip (distal half or more sometimes yellow); one male and several females with palpus entirely black (this does not appear to correlate with any other variably coloured structures); antenna yellow with inner-distal margin dark brown; parafacial orange to brown or black; anterior 1/3 of frons pilose centrally; upper half of gena silvery tomentose anteriorly or along entire length. Wing darkly clouded excluding margin of anal lobe and (sometimes) basal 1/5; pattern occasionally as described for H. nitida. M_{1+2} ratio 4.0-4.5.

Holotype male with wing not as darkly infuscated, mid femur yellow, and palpus dark brown on basal 1/3.

Male terminalia (Figs 13-15)

Epandrial length 7/10 height and width and height subequal. Surstylus acutely triangular with posterior margin sinuate and height 7/10 that of epandrium; several small rounded bristles on inner face distally. Cerci thin, entirely united, and as high as surstylus. Hypandrium + pregonite globular with two stout bristles and several setulae; suture present on distal 1/5. Phallapodeme well-developed, swollen distally, and 1/5 longer than hypandrium + pregonite. Distiphallus with subapical break in one rib.

Female

As described for male except as follows: fore femur brown on distal 1/3-2/3 (one CNCI female from Nova Teutonia with base yellow); hind tibia occasionally yellow (two CNCI females from Nova Teutonia); frons entirely black; one Peruvian CNCI female with palpus only barely infuscated at base; face dark brown to black but always yellow beneath antennal base; gena dirty yellow to black; upper 1/3 of gena silvery tomentose anteriorly; segment 10 and cercus yellow.

One Mexican female (CNCI) with frons shiny, hind tibia with dorsal surface light brown, hind tibia and femur with one pair of dorsal and ventroapical spots, wing clouded along costa (distal to R_1) and around $R_{2,2}$, palpus black, and occiput and ventral half gena dark brown.

Female terminalia (Fig. 28)

Spermatheca 1/5 longer than wide (slightly narrower distally), strongly telescoped, densely covered with narrow transverse furrows, cross-section circular with four weak corners, and distally truncate with sunken apical cone. Spermathecal duct thin, weakly sclerotized, and twice length of spermatheca. Ventral receptacle small, recurved and with relatively short subterminal flagellum.

Distribution

Argentina, Bolivia, Belize, Brazil, Costa Rica, Dominican Republic, Ecuador, Guatemala, Guyana, Honduras, Jamaica, Mexico, Panama, Peru, Trinidad, Venezuela (Map 2).

Holotype: COSTA RICA. La Suiza de Turrialba, P. Schild (1 &, USNM).

Paratypes examined: COSTA RICA. Juan Vinas, 6.v.1910, near brook, forest edge, 2500', P.P. Calvert (1 °, USNM), Higuito, San Mateo, P. Schild (1 °, USNM), Turrialba, P. Schild (1 °, USNM), xi.1922 (2 ° °, USNM), La Suiza, 1922, P. Schild (2 ° °, USNM).

Paratype (Craspedochaeta concinna): COSTA RICA. Turrialba (1 &, USNM).

Additional material examined: 1569 ♀ 108♂♂ [BMNH, CASC, CBFC, CNCI, DEBU, EMUS, INBC, INPA, NHRS, QCAZ, USNM, ZSMC].

Comments

Heteromeringia fumipennis is a relatively common neotropical clusiid with hair-like genal bristles, darkly clouded wings and yellow fore femora with a dark brown apex (darker in females). The male genitalia are characterized by long, thin united cerci.

Heteromeringia nanella sp. n.

(Figs 16-18, Map 3)

Description

Male

Body length 3.5-4.0 mm. Bristles dark brown. Two dorsocentral bristles plus one short bristle in front of anterior dorsocentral. Ocellar bristle relatively long and well-developed. Genal bristles small and hair-like. Three fronto-orbital bristles. Arista pubescent. Male with small white disc anterior and ventral to anepisternal bristle. Thorax dark brown. Fore coxa white and silvery tomentose on anterior face, and mid and hind coxae light brown to yellow with upper margin light brown. Legs yellow with femora, fore tibia and fore tarsi dark brown; hind tibia sometimes dark brown. Frons dark brown with anterior margin and anterolateral corner yellow; first flagellomere yellow with orange spot at base of arista; back of head, occiput and posterior margin of gena dark brown; remainder of head yellow; parafacial silvery tomentose; gena pilose on anterodorsal margin; anterior half of frons pilose. Abdomen dark brown. Wing as described for *H. nitida*. M₁₊₂ ratio 4.7.

Male terminalia (Figs 16-18)

Sternites of annulus relatively thin ventrally. Epandrium small, rounded and shallow. Surstylus minute and triangular; inner face with six medial small rounded bristles. Cerci small and triangular (entirely united) with sides bulging. Hypandrial complex as described for *H. nitida* except as follows: hypandrium + pregonite with two strong medial and two strong distal bristles; phallapodeme significantly enlarged relative to remainder of hypandrial complex (2/5 longer than hypandrium + pregonite); ribs of distiphallus unequal in length.

Female

Unknown.

Etymology

The specific name refers to the small cerci and surstyli.

Holotype: BRAZIL. Dist. Fed. Planaltina, 1000m, cerradao, Malaise trap, 24.ix-6.x.1985, S.E. Miller (1 &, USNM).

Paratypes: BRAZIL. Same collection as holotype (4 & &, USNM; 1 &, DEBU).

Comments

Externally, *Heteromeringia nanella* is most easily characterized by brown femora and fore legs, but the most diagnostic characters are male genitalic: the annulus is reduced ventrally, the epandrium is small, and the cerci and surstyli are minute and triangular.

Heteromeringia nervosa sp. n.

(Fig. 56, Map 3)

Description

Male (Fig. 56)

Body length 4.1 mm. Bristles black. Two dorsocentral bristles. Ocellar bristle relatively long and well-developed. Genal bristles small and hair-like. Three fronto-orbital bristles. Arista pubescent. Male with small white circular structure anterior and ventral to an episternal bristle. Thorax dark brown with postpronotum reddish-brown. Coxae yellow with dorsal margin of mid coxa brown. Fore femur dark brown on distal 1/5; mid femur with dark brown inner-apical spot; hind femur with dark brown apex; fore tibia with dark brown mottling (excluding base); mid tibia with well defined dark brown outer-apical spot; fore tarsi dark brown; remainder of legs light yellow. Head yellow with frons dark brown (excluding thin border along posterior, lateral and anterior margin), first flagellomere dark brown on inner face (excluding base), and back of head and posterior half of occiput dark brown. Upper 2/3 of gena and anterodorsal margin of occiput silvery tomentose; anterior margin of frons with small triangular pilose patch. Abdomen dark brown. Wing darkly clouded on distal half around R_{2+3} ; remainder of wing with infuscation surrounding veins. M_{1+2} ratio 6.8.

Male terminalia

Not dissected, but external terminalia nearly twice as large as those of any other *Heteromeringia* (that is, terminalia wider than tergite 6). Epandrium approximately as wide as long and half as high as wide. Cerci small and triangular. Surstylus half length of epandrium with basal 2/5 parallel, distal 3/5 triangular, dorsal margin straight with apex slightly rounded, posterodistal margin slightly concave and inset, and inner face covered with short pointed bristles.

Female

Unknown.

Etymology

The specific name refers to the characteristic wing veins, which are surrounded by a thin infuscation.

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Holotype: COSTA RICA. Puntarenas: Monteverde, 1600 m, 22-27.ii.1991, B.J. Sinclair, at lights (1 o, CNCI).

Comments

Heteromeringia nervosa and H. volcana are both restricted to Costa Rica, and may form a natural group with H. fumipennis on the basis of reduced pilosity on the male frons and a predominantly yellow fore femur. Heteromeringia nervosa can be separated from other Heteromeringia by its characteristic wing pattern and its very large external male terminalia. The colouration of the wing and legs are similar to that of the nearctic H. nitida, but the wing pattern is slightly different medially and the terminalia (particularly the surstylus) are undoubtedly different.

Heteromeringia volcana, in comparison, has male terminalia similar to those of *H. nigripes*, which is also known from Costa Rica, but the genitalia differ as mentioned in the description. Furthermore, the palpus is yellow, the legs are predominantly yellow, the gena is yellow ventrally, the bristles are brown and the ocellar bristles are not as well developed.

Heteromeringia nigripes MELANDER & ARGO, 1924

(Figs 19-21, 30, Map 1)

Heteromeringia nitida var. nigripes Melander & Argo, 1924: 31.

Description

Male

Externally as described for *H. nitida* except as follows: NM paratype with additional reclinate bristle between mid and hind fronto-orbital bristles; fore coxa light yellow, and mid and hind coxae dark brown; mid tibia sometimes light brown; hind tibia variably coloured; femora dark brown with fore femur yellow basally, mid femur yellow on distal 1/3-1/2, and hind femur sometimes yellow at ends; pedicel yellow to dark brown; first flagellomere often with distal 2/3 of inner face and anterior margin dark brown, but occasionally with infuscation restricted to base of arista, or with distal margin of outer face also dark brown (some specimens from AZ); gena sometimes dark brown (some specimens from AZ and NM); palpus light brown (sometimes yellow on distal half, and male from Brazil with basal 3/4 of palpus brown). M_{1,2} ratio 4.0-5.0.

Males from Mexico and Honduras differ as follows: fore femur yellow with dark subapical band; mid femur yellow; hind femur with brown dorsoapical spot; hind tibia entirely brown (Mexico) or with wide apical and basal bands (Honduras); males in and south of Mexico usually with first flagellomere yellow on outer face; male from Honduras with palpus brown on basal 2/3.

Male terminalia (Figs 19-21)

Epandrium wide, shallow and narrowing basally. Surstylus as high as epandrium and strongly tapered apically; nearly bare and without small rounded bristles. Cerci widely emarginate apically. Hypandrial complex as described for *H. nitida* except as follows: phallapodeme as long as hypandrium + pregonite, but distinctly wider distally; distiphallus with one rib short, truncate and fringed, and other rib short and pointed with additional distal sclerite (sclerite usually wide basally and bifid on distal half, but male from Mexico with sclerites united and broad).

Female

As described for male except palpus brown to dark brown. One female from Brazil agrees with description of Brazilian male except fore coxa dark brown, femora brown (excluding distal 1/3 of mid femur and base of fore and hind femora) and anterior margin of first flagellomere dark brown.

Female terminalia (Fig. 30)

Spermathecal width 1/5 greater than length at widest point, strongly telescoped, densely covered with narrow, transverse wrinkles, rounded distally, circular in cross-section, and apex truncate with shallow inverted cone. Spermathecal duct at least five times longer than spermatheca and ending in wide thick-walled cylindrical chamber. Ventral receptacle small, recurved distally, saclike, narrow basally and with subterminal flagellum approximately two to three times length of spermathecal duct.

Distribution

Brazil (Santa Catarina), Costa Rica, Honduras, Mexico, United States (AZ, NJ, NM, UT, VA) (Map 1).

Holotype: UNITED STATES. NV: Las Vegas, "7.8" [year unknown], H.S. Barber (1 \, USNM). Paratypes: UNITED STATES. AZ: Mt Lemon, S Catalina Mts, 8000ft., 17.vii.19177 (19, USNM), Williams, 30.vi, H.S. Barber (13, USNM), NJ: Westville, 6.vi.1897 (13, USNM), NM: Las Vegas HS, 17.viii, Barber & Schwartz (1 &, USNM), VA: Mathias Pt., 1.ix.1915, R.C. Shannon (1 &, USNM). Additional material examined: BRAZIL. Estado Mato Grosso do Sul, road from Sete Placa/Victor, aspirated from car, 25.ii.1986, M. v.Tschirnhaus (19, ZSMC), Nova Teutonia, 27°11'S, 52°23'W, 300-500m, F. Plaumann, xi.1962 (1 &, CNCI). COSTA RICA. San Jose: Zurqui de Moravia, 1600m, v.1991, P. Hanson (1 &, DEBU). HONDURAS. F. Morazan, Cerro Uyuca, Malaise, 27.v.1994, 1800m, H. Howden (18, DEBU). MEXICO. Chiapas, San Cristobal, 7000', 30.v.1969, H.J. Teskey (1 &, CNCI), 24mi W La Cuidad, Dgo., 7000', 2.vii.1964, J.F. McAlpine (1&, CNCI), 10mi W El Salto, Dgo., 9000', 21.vi.1964, J.F. McAlpine (1 °, CNCI). UNITED STATES. AZ: Coconino Co., 20mi N Flagstaff, Bonito Pk., 5-8.viii.1984, 7000', B.V. Brown, sweeping ponderosa pine/meadow (3&&, USNM), Flagstaff, Oak crk., Can., 5900', 17-25.vii.1979, at Sterling Can., riparian woods (19, USNM), Malaise, S.&J. Peck (19, USNM), Cochise Co. Southwestern Research Stn., 8km W Portal, 1645m, 30.ix.1966, P.H. Arnaud Jr. (13, USNM), Portal S.W. Res. Sta., 5-9.vi.1972, W.W. Wirth, Malaise (1 \, 1 \, \text{USNM}), S.W.R.S., 5mi W Portal, Cochise Co., 5400', J.G. Rosen, D.K. Oliver, A.R. Molderke & J.A. Woods, 5.vii.1963 (3 \, \, \, V, USNM), 15.vii.1963 (1 \, \, USNM), 13.vii.1963 (19, USNM), NM: Catron Co., 8mi SE Luna, 7500', 9-14.vii.1979, S.&J. Peck, pond, pine at stream (3 & & 1 \, USNM), 5mi W Luna, 7400', 9-14.vii.1979, S.&J. Peck, San Francisco River, pond, pine-meadows (1 \, 1\, \text{USNM}), 5mi W Luna, 7400', 9-14.vii.1979, ponderosa pine/meadow, S.&J. Peck (3&&, DEBU), McKinley Co., Quaking Aspen, 6.4km S Fort Wingato, 9.vii.1966, 2440m, P.H. Arnaud Jr. (19, CASC), Los Alamos Co., Bandelier National Monument, Ponderosa campsite, 13.vii.1991, 2300m, Ilan Yarom, ex: Malaise trap (233 19, TAUI), UT: Cache Co., Tony Grove Jct. Malaise trap, 19-27.vii.1983 (2 ♀ ♀, EMUS), 11-25.vii.1984 (1 ♀, EMUS), W.J. Hanson, 12-19.vii.1983 (1 ♂, EMUS), Green Canyon, 15-19.vi.1985, N.N. Youssef (1 º, EMUS), Beaver Mtn., 27.vii-3.viii.1985 (1 º, EMUS), Summit Co., S slope Uinta Mts., 7525', hwy. 150 near Shingle Campground, 24.viii.1965, H.B. Leech (1 ♀, CASC).

Comments

Heteromeringia nigripes was originally described as a subspecies of *H. nitida*, but it varies significantly from *H. nitida* in external morphology, colouration and several structures of the male and female genitalia (listed in key). Both species, however, show some geographic variation in colour that could lead to misidentification unless genitalic characters are checked.

Heteromeringia nitida JOHNSON, 1913

(Figs 1, 22-24, 29, Map 1)

Heteromeringia nitida Johnson, 1913: 99. Malloch, 1918: 8. Melander & Argo, 1924: 31.

Description (Fig. 1)

Male

Body length 3.0-4.3 mm. Bristles black. Two dorsocentral bristles, sometimes with small bristle in front of anterior dorsocentral. Ocellar bristle occasionally smaller than postvertical. Genal bristles small and hair-like. Three fronto-orbital bristles. Arista short pubescent. Male with small white disc anterior and ventral to anepisternal bristle. Thorax dark brown. Fore coxa white and pilose on anterior surface, and mid and hind coxae yellow, sometimes with brownish basal infuscation (most prominent in specimens collected in and south of Virginia). Legs yellow except as follows: fore tibia, tarsi and distal half of fore femur dark brown; tip of hind femur usually dark brown (yellow in holotype); hind tibia usually with brown basal and apical bands (often faded). Frons dark brown with anterior and anterolateral margins orange-yellow; anterior margin of first flagel-lomere dark brown; face dirty orange, at least on dorsal half; back of head, occiput, gena (except above genal bristles), clypeus and mentum dark brown (sometimes gena dirty yellow to brownish); remainder of head yellow, with base of palpus occasionally brownish; upper 3/5 of gena silvery tomentose (tomentose band tapering past anterior half of eye); anterior half of frons pilose, usually including entire lateral margin. Abdomen dark brown. Wing darkly clouded on distal half along R₂₊₃ and costa, and lightly clouded around R₄₊₅ distally. M₁₊₂ ratio 5.0-7.5.

Male from Mexico more darkly coloured: fore femur entirely dark brown; mid femur dark brown on basal half; hind femur dark brown excluding base; mid tibia with basal half brown; hind tibia with basal 1/3 dark brown; mid and hind coxae brown; palpus brown on basal half.

Male terminalia (Figs 22-24)

Sclerites of annulus wide and weakly sclerotized. Epandrial height, length and width subequal. Surstylus acutely triangular, 7/10 height of epandrium, with posterior margin slightly sinuate and with several distal small rounded bristles. Cerci 2/3 height of surstylus, subquadrate and shallowly emarginate. Hypandrium + pregonite globular with three stout bristles and several small setulae; suture on distal 1/3. Phallapodeme well-developed and 1/5 longer than hypandrium + pregonite. Distiphallus with one rib extending into long, thin process. Male from Mexico with ejaculatory apodeme very large (distal "fan" approximately three times wider than average).

Female

Externally as described for male except palpus black with tip yellow and frons usually shiny; frons sometimes with minute pilose patch on anterior margin, but rarely as described for male.

Female terminalia (Fig. 29)

Spermatheca 1/5 longer than wide at widest point, strongly telescoped, densely covered with narrow, transverse wrinkles, circular in cross-section, and distally truncated with shallow inverted cone. Spermathecal ducts thin, several times length of spermatheca, and sometimes united along most of length. Ventral receptacle small, recurved, sac-like, narrow basally, and with long subterminal flagellum that is loosely coiled distally.

Distribution

Canada (southern ON), Mexico, United States (AL, AZ, DC, FL, GA, IL, MD, MI, MO, NC, NJ, NM, NY, SC, TN, TX, UT, VA, WV) (Map 1).

Holotype: UNITED STATES. NJ: L. Branch, 12.vi.1902 (1 &, MCZC).

Additional material examined: CANADA. ON: Essex Co., Point Pelee National Park, wooded area by W beach, Malaise/pan traps, 21.viii-10.ix.1999, O. Lonsdale (1 &, DEBU). MEXICO. 10mi E El Salto, Dgo., 9000', 21.vi.1964, J.F. McAlpine (1 &, CNCI). UNITED STATES. AL: Bon Secour NWR, 5-7.v.1994, mushroom trap in Oak, S.A. Marshall (1 9 1 8, DEBU), AZ: Montgomery Co., 20mi W Glenwood, T45 R27W, 15.vi-28.vii.1994, H.W. Robinson (1 ♀ 1 ♂, DEBU), CT: Putnam Pk., 24.vii.1939, A.L. Melander (15, USNM), East R., Hopk, 31.v.1917, Rehred, Par. Macremphytus, Cornus stolonifera, C.R. Ely (15, USNM), DC: Rock Creek Park, 26.v.1957, P.H. Arnaud Jr. (19, CASC), Reheboth, 18.vii.1976, W.W. Wirth, Malaise trap (1 9, USNM), FL: Alachua Co., Gainesville, W.W. Wirth, 27.iv.1970 (1 9, USNM), 27.iv.1970 (19, USNM), Withlacoochee St. Forest, Croom Reserve, 13.iv.1989, S.A. Marshall (388, DEBU), Royal Palm Park, 28.iv.1930, A.L. Melander (1 o, USNM), Sebring, Highlands Hamm. St. Pk., 15.iv.1970, W.W. Wirth, Malaise (19, USNM), GA: Athens, 28-31.v.1969, R.&J. Matthews, Malaise (13, EMUS), Liberty Co., St. Catherenes Isl., 24-28.iv.1972, Thompson & Picchi (233, USNM), IL: Mason Co. Sandridge State Park, 12.vi.1978, M.E. Irwin (19, EMUS), MD: Montgomery Co., Colesville, W.W. Wirth, 4.vii.1976 (1 \(\) 1 \(\), USNM), 11.vii.1974 (1 \(\) 1 \(\), USNM), 14.vi.1977 (2 \(\) \(\), USNM), 4.ix.1977, Malaise trap (2♀♀ 1♂, USNM), 14.vi.1975, Malaise trap (1♂, USNM), 3.viii.1975, Malaise trap (1 \, USNM), 7.viii.1975, Malaise trap (1 \, USNM), Bethseda, G. Steyskal, 17.v.1969 (1 \, USNM), 16.vii.1967 (18, USNM), Prince George Co., Rt. 4 nr. Patuxent Riv., 30.viii.1979, A. Freidberg (19, TAUI), MI: Wayne Co., Grosse Ile., G. Steyskal, 18.vi.1952 (2&&, USNM), 13.viii.1956 (1&, USNM), NC: Raleigh, 3.viii.1982, J. Jaenike (1 \, USNM), Cumberland Co., Fort Bragg, J.D. Birchim, 3-6.iv.1967 (19, CASC), 23-25.viii.1967 (10, DEBU), Raleigh, C.B.S. Brimley, 21.v.1924 (10, NCSU), Wake Co., 7 air mi SW of Raleigh off rd., C.S. Parron, Malaise trap 21.x.1985 (1 \, NCSU), 29.vii.1985 (1 \, NCSU), NH: White Mtns., Dolly Copp, 13.viii.1931, A.L. Melander (1 \, USNM), NJ: Orange, 5.vi.1932, C.H. Curran (2 & &, USNM), NY: Bear Mtn., 30.v.1941, A.L. Melander (1 &, USNM), Ulster Co., Cherrytown, 4mi NNW Kerhonkson, 15-30.vi.1971, P.B. Wygodzinsky (1♂, USNM), Flushing, 6.ix.1933 (1♀, USNM), Sta. Study Insects, Tuxedo, 26.vi.1928 (1 \, USNM), NY City, CortInd Pk., 6.vii.1926, A.L. Melander (1 \, \,), USNM), SC: Barnwell St. Pk., mushroom traps in Oak forest, 10-18.iv.1989, S.A. Marshall (USNM), Beaufort Co., Hilton Head Isl., forest preserve, ex. sweep over trail, 3.ix.1981, P.H. Adler (1 &, USNM), Georgetown Co. Hobcaw Barony, Belle Baruch Marine Field Lab, on slime mold on oak log, 26.iv-8.v.2004, S.A. Marshall (33 3 9 9, DEBU) [in alcohol], TN: Great Smoky Mtns. N.P., Cades Cove, 13.vi.1946, G. Steyskal (1 &, USNM), TX: Brazos Co., College Stn., 17.iv.1987, Wharton (1 \, TAMU), College Stn., ex. Malaise trap, R. Wharton & M. Hrncir, 9-23.iv.1982 (1 o, TAMU), 2-5.iv.1982 (1 o, TAMU), 21-25.iv.1981 (1 \, TAMU), Anderson Co. Salmon, 7.ix.1974, H.R. Burke, ex, Malaise (1 \, TAMU), 18.viii-6.ix.1974, H.R. Burke, ex. Malaise (1 \, TAMU), Bastrop Co. College Stn., Lick Crk. Park, 16-31.v.1988, R. Wharton (19, TAMU), College Stn., Lick Creek Park, Wharton & Praetorius, 2-16.v.1988 (1913, TAMU), 9-23.iv.1988 (19, TAMU), Montgomery Co., Jones St. Forest, 8mi S Conroe, 13-19.iv.1987, Wharton, Wang & Praetorius (3 & 3, TAMU), 16-23.viii.1987, Wharton, Steck & Carrol (1 9, TAMU), 28.vi-13.vii.1987, Wharton, Steck & Carrol (4&& 2 \, \varphi\), TAMU), Nacogdoches, iv.1958, M.R. Wheeler (2&&, USNM), VA: Great Falls, 21.vii.1962, G. Steyskal (1&, USNM), Fairfax Co., 2mi N Centreville, 11.vi.1972, G.F.&S. Hevel (1 &, USNM), Fairfax Co., West Springfield, Pohick Creek, 5.vi.1999, 38°46'N, 77°16'W, 550ft, C.F. Kassebeer (1 \, MHNC), WV: Kanawha Co., So. Charleston, 28.viii.1981, P.H. Adler, in copula, on fallen Oak (19 18, USNM) [single pin].

Comments

Heteromeringia nitida is a relatively common species in the eastern United States, ranging from the coast to Illinois and eastern Texas; several outlying specimens have been collected in New Mexico and Mexico. The range of this species extends northward almost to Maine, and we have

found a single specimen at the southern tip of Ontario in Point Pelee National Park. The other primarily nearctic species, *H. nigripes*, has a more southwestern distribution in Arizona, New Mexico and Utah, with occasional specimens collected south into Mexico, Honduras, Costa Rica and Brazil, and east into New Jersey and Virginia.

MCALPINE (1960) noted that the mid fronto-orbital bristles of *Heteromeringia pulla* MCALPINE, 1960 (and possibly *H. spinulosa* MCALPINE, 1960) were reclinate, but slightly incurved. Among New World species, we have found this state only in *H. nitida*, which also has a barely inclinate anterior fronto-orbital.

Heteromeringia volcana sp. n.

(Map 3)

Description

Male

Body length approximately 3.6 mm. Bristles black. Arista pubescent. Two dorsocentral bristles. Ocellar bristle relatively long and well-developed. All genal bristles small and hair-like. Three fronto-orbital bristles. Male with small white disc anterior and ventral to an episternal bristle. Thorax dark brown. Legs predominantly yellow, although fore tarsi dark brown, fore tibia dark brown with basal half yellow on dorsal margin, tip of fore femur dark brown, hind tibia dark brown and fore coxa white. Head mostly yellow with face and gena orange, distal half of inner face of first flagellomere lightly infuscated, clypeus, occiput and posterior 3/4 of frons (excluding lateral margins) dark brown, and frons orange centrally on anterior 1/4. Abdomen dark brown. Wing with light infuscation around all veins and with dark cloud around distal 1/3 of R_{2+3} . M_{1+2} ratio 4.6.

Male terminalia

As described for *H. nigripes* except cerci rounded distally and not tapering medially, hypandrium + pregonite with additional strong central bristle, and distiphallus with ribs asymmetrical (one extension half length of that found in *H. nigripes*, and other extension short, stout, and truncate).

Female

Unknown.

Etymology

The specific name is derived from the collection locality.

Holotype: COSTA RICA. Alajuela: Volcan Tenorio, N slope, trail to laguna, ~1000m, sweeping, 18.vi.2000, S.A. Marshall (1 σ, INBC).

Comments

See comments for Heteromeringia nervosa.

Heteromeringia zophina sp. n.

(Figs 25-27, Map 3)

Description

Male

Body length 2.9 mm. Bristles black. Three dorsocentral bristles; anterior bristle 3/5 length of median bristle, which is 3/5 length of posterior bristle. Ocellar bristle well-developed. Genal bristles small and hair-like. Right side of frons with additional reclinate fronto-orbital. Small white disc anterior and ventral to anepisternal bristle. Body brown except as follows: parafacial, gena and anterior half of buccal cavity dirty white; anterior margin of frons, scape, pedicel and first flagellomere orange; first flagellomere lightly infuscated along inner-distal margin; gena (excluding ventral margin) yellowish brown; distal 1/3 of palpus light yellow. Dorsal half of gena silvery tomentose (tomentose band tapering posteriorly). Height of gena slightly less than 1/3 that of eye. Frons pilose with wide shiny space around ocellar tubercle. Wing clouded along anterior margin from R₁ to apex. M_{1/2} ratio 8.5.

Male terminalia (Figs 25-27)

Epandrium 1/5 wider than high and length approximately 2/3 height. Cerci slightly tapering distally and shallowly emarginate. Surstylus thin, tapering, and weakly fused to epandrium; innerapical surface with several small rounded bristles, and outer surface with several minute setulae. Internal genitalia as described for *H. nitida* except as follows: hypandrium + pregonite with five stout bristles along anterior margin, only several setulae along ventral margin, suture absent and dorsal margin prominent; separation between basal and distal sclerites of distiphallus distinct; distal sclerite of phallus bifid with one thin tapered process, and one wide, flat truncated process.

Female

Unknown.

Etymology

The specific name is derived from the Greek for "darkness" (zophos).

Holotype: MEXICO. Durango. 9000', 10mi W El Salto, J.F. McAlpine, 30.vi.1964 (1 &, CNCI).

Comments

Heteromeringia zophina superficially resembles H. apholis, which is also small and dark, but H. zophina belongs to the H. nitida species group and has a male anepisternal disc. Heteromeringia zophina also has a strong additional pair of dorsocentral bristles, a light infuscation along the inner-distal margin of the first flagellomere, a brown face, a yellow tip on the palpus, a brown ventral stripe on the gena (narrowing anteriorly), and a gena that is no more than 1/3 the height of the eye. Furthermore, the surstylus is thin and mostly bare, the cerci are not as deeply incised, and the phallapodeme and distal sclerites of the distiphallus are much longer.

Heteromeringia czernyi species group.

Heteromeringia aphotisma sp. n.

(Map 5)

Description

Female

Body length 3.9 mm. Bristles black. Two dorsocentral bristles. Ocellar bristle relatively long and well-developed. One inclinate and three reclinate fronto-orbital bristles (anterior reclinate bristle small). Anterior genal bristle vibrissa-like. Arista short-plumose. Anepisternum with additional upcurved bristle in posterodorsal corner. Thorax dark brown. Legs yellow with fore and mid coxae dark brown, femora and tibiae dark brown with tips of femora yellow, and fore tarsi dark brown. Head yellow with frons, back of head, occiput and posterior margin of gena dark brown and inner face of first flagellomere with dark spot; anterodorsal margin of gena silvery tomentose; anterior half of frons pilose. Abdomen dark brown with tergite 1 white and terminalia yellow. Wing dusky, becoming darker towards costa. $M_{1,2}$ ratio 5.2.

Female terminalia

Not dissected.

Male

Unknown.

Etymology

The specific name is derived from the Greek for "without light" (*aphos*), referring to the dark colouration of this species with respect to the other *Heteromeringia* with four fronto-orbitals.

Holotype: BRAZIL. R.J. Nova Friburgo, 10km S, "Sitio Edelweiss", Malaise head, 1-28.ii.1990, S.A. Marshall (1 \, QBUM).

Comments

Within the *Heteromeringia czernyi* group, *H. aphotisma*, like *H. czernyi* and *H. flavipes*, has retained dark colouration and an upcurved bristle in the posterodorsal corner of the anepisternum. Unlike these two dark species, however, *H. aphotisma* also has an additional reclinate fronto-orbital bristle (synapomorphic of the rest of the group), entirely dusky wings, brown legs (excluding the mid and hind tarsi) and a much darker head, easily separating it.

Heteromeringia czernyi Kertesz, 1903

(Figs 8, 31-35, 48, 59, Map 4)

Heteromeringia czernyi Kertesz, 1903: 568. Melander & Argo, 1924: 29. Sobarocephala subfasciata Curran, 1939: 2.

Description (Figs 8, 59)

Male

Body length 2.8-3.9 mm. Bristles brown. Two dorsocentral bristles, but several specimens (including holotype) with minute bristle in front of anterior dorsocentral. Ocellar bristle relatively

long and well-developed. Anterior genal bristle vibrissa-like. Arista short-plumose. Anepisternum with additional upcurved bristle in posterodorsal corner. Thorax dark brown. Coxae white. Legs mostly yellow; fore tarsi and tibia brown (Central American specimens with fore tibia usually yellow with base and tip occasionally light brown); mid tibia often light brown to brown; hind tibia usually brown (sometimes excluding base); base of fore femur white; tip of hind femur sometimes brown. Frons brown centrally with anterior margin (occasionally anterior half or more) orange; back of head and occiput dark brown; first flagellomere brown with basal margin yellow (occasionally only apical 1/3 brown); face, gena, parafacial and mouthparts white; dorsal half of gena silvery tomentose; remainder of head yellow; anterior half of frons pilose. Abdomen dark brown. Wing dusky on distal 1/3 (fading posteriorly) and with cloud proximal to anterior cross-vein (sometimes restricted to first radial cell or forming distinct median band). M_{1+2} ratio 6.5-7.5. Nine males from Bolivia, Costa Rica and Ecuador with fore tibia and tarsi dark brown; two of these males (Naranjo, Costa Rica) with yellowish transverse stripe on scutum.

Male terminalia (Figs 31-35)

Annulus well-developed, if somewhat thin. Epandrium nearly as long as high, with width 1/5 greater than height. Surstylus small and subquadrate with short internal process; bristles sometimes forming "hand-shaped" scales on inner-distal margin of surstylus and internal process. Cerci small, entirely united and quadrate. Hypandrium + pregonite with thin medial extension (apically with stout, pointed bristle), and distal portion long and thin with one short, rounded subapical bristle. Phallapodeme stout and 2/5 length of hypandrium + pregonite. Basiphallus fused to distiphallus and with wide diamond-shaped posteroventral plate. Distiphallus relatively short (no more than three times length of hypandrium + pregonite) with loose apical fringe.

Female

As described for male except as follows: fore tibia and tip of fore femur dark brown (one female from Venezuela with fore tibia yellow); hind tibia sometimes light brown; gena and sides of face often variably dark brown; clypeus dark brown; frons often dark brown excluding lateral margins. Five females from Costa Rica with femora entirely yellow, three of which (Naranjo) also with antenna pale orange (tip brown), and face, gena, parafacial and mouthparts dark yellow. One female from Brazil with femora yellow and tibiae brown.

All Argentinean females, most Bolivian females and several Peruvian and Venezuelan females further differ as follows: tibiae dark brown (several specimens with mid tibia somewhat mottled with yellow or light brown); fore and hind femora with distal spot; lower half of gena and face light brown to orange (darkest in Argentinean specimens); frons dark brown excluding lateral margins (tinted with orange). Specimens from Trinidad and Tobago as above, but face, gena and basal 2/3 of mid tibia brown.

Female terminalia (Fig. 48)

Spermatheca as long as tergite 6 and untelescoped, basal section long and cylindrical, and apex wide with shallow inverted tip. Spermathecal duct short and thin. Ventral receptacle approximately 1/3 length of spermatheca, thin basally, wide and rounded distally (ie. wedge-shaped) and with long convoluted subterminal flagellum.

Distribution

Argentina, Belize, Bolivia, Brazil, Colombia, Costa Rica, Cuba, Dominica, Dominican Republic, Ecuador, Guatemala, Guyana, Honduras, Jamaica, Mexico, Panama, Peru, Puerto Rico, St. Lucia, Tobago, Trinidad, United States (FL), Venezuela (Map 4).

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Holotype (H. czernyi): PERU. Callanga (1º, HNHM).

Holotype (S. subfasciata): PANAMA. Barro Colorado Isld. Canal Zone, 5.i.1929, C.H. Curran (1 &, AMNH).

Paratype (S. subfasciata): PANAMA. Barro Colorado Isld. Canal Zone, 13.ii.1929, C.H. Curran (18, AMNH).

Additional material examined: 285 9 9 253 8 8 [BMNH, CBFC, CNCI, CASC, DEBU, EMUS, INBC, INPA, IZAV, NHRS, QCAZ, ROME, USNM, ZSMC].

Comments

The external genitalia of *Heteromeringia czernyi* are most similar to those of *H. flavipes* (Figs 36-38), but the distiphallus, in which both ribs end in separate fringes, resembles that of *H. flavifrons* (Fig. 39). The phalli of *H. quadriseta* and *H. mediana* (Figs 42 and 45) also end in fringes, but the ends of the ribs are fused; furthermore, the ribs of *H. quadriseta* are poorly defined and the phallus of *H. mediana* is interrupted medially, creating basal and distal sections.

Heteromeringia czernyi and H. fumipennis are the most commonly collected Heteromeringia in Central and South America. Heteromeringia czernyi is relatively easy to identify, being the only member of the H. czernyi species group with three fronto-orbitals, a brown thorax and brown fore tarsi. Heteromeringia fumipennis is significantly larger and darker, the wing is darkly clouded, all of the genal bristles are poorly developed and the male has an anepisternal disc.

Heteromeringia flavifrons HENNIG, 1938

(Figs 5, 6, 36-38, 49, 61, Map 5)

Heteromeringia flavifrons Hennig, 1938: 134.

Description (Figs 5, 6, 61)

Male

Body length 3.6-4.0 mm. Bristles black. Two dorsocentrals plus one minute bristle in front of anterior dorsocentral. Ocellar bristle relatively long and well-developed. Four fronto-orbital bristles with anterior reclinate bristle half length of remaining reclinate bristles. Anterior genal bristle vibrissa-like. Arista short pubescent. Scutum yellow with brown postpronotum (faded in most specimens) and light central postsutural stripe (narrowing anteriorly or strongly faded, sometimes reduced to basal spots); holotype with notopleuron also brown and notal stripe reduced to two ill-defined basal spots. Scutellum and laterotergites brown (light brown below lateral margins of scutellum). Pleuron and legs yellow with brown subnotal stripe; sometimes tarsomeres 2-5 brown on fore tarsi, and mid and hind tarsi with distal segments dirty yellow. Head yellow with anterior half of first flagellomere brown in specimens from Costa Rica, gena and face light brown to dirty white and ocellar spot brown; face and anterior half of frons pilose; upper 3/5 of gena silvery tomentose; INBC male with one pair of median brown stripes on posterior 3/4 of frons that do not touch posterior margin (notal stripe also faded). South American males with pigment on thorax much lighter and antenna more orange. Abdomen black. Wing darkly clouded along distal half of R_{2+3} and lightly clouded along distal half of R_{4+3} ; holotype with distal half of wing more darkly infuscated. M₁₊₂ ratio 5.8-6.0.

Male terminalia (Figs 36-38)

Epandrial length 3/5 height and width and height subequal. Cerci slightly more than half height of epandrium and rounded apically with medial emargination. Surstylus thin (laterally compressed), circular in outline, 2/3 length of epandrium and inner face densely setose (bristles on

distal half stout and pointed). Hypandrial complex as described for *H. czernyi* except hypandrium + pregonite without anterior projection, phallapodeme absent (or missing from dissected specimen), and distiphallus with one distal quadrate projection on left rib.

Female

Externally as described for male except as follows: notum reddish; notal stripe sometimes dark and well defined or entirely absent; from brownish on posterior 2/3.

Female terminalia (Fig. 49)

Spermatheca cylindrical, clavate, as long as sternite 6 and widest subapically; apex thinner, rounded, more heavily sclerotized and covered with minute bumps. Spermathecal duct weakly sclerotized; half as wide as spermatheca and 2/3 as long. Ventral receptacle as described for *H. czernyi*.

Distribution

Bolivia, Brazil (Santa Catarina), Costa Rica, Ecuador, Honduras (Map 5).

Holotype: BOLIVIA. Mapiri, S. Carlos, 800m, i.1903, Garlepp (1 &, SMTD).

Comments

Heteromeringia flavifrons resembles other pale Heteromeringia with four fronto-orbitals, but the hairs on the arista are longer, the antenna and postpronotum are darker and the scutum sometimes has a posteromedial stripe.

Heteromeringia flavipes (WILLISTON, 1896)

(Figs 39-41, Map 5)

Heteromeringia flavipes, Melander & Argo, 1924: 29-30.

Clusiodes flavipes, MALLOCH, 1918: 6.

Heteroneura flavipes Williston, 1896: 387; 1908: 319. Czerny, 1903: 101.

Description

Male

Body length 2.8 mm. Bristles brown. Two dorsocentral bristles. Ocellar bristle relatively long and well-developed. Anterior genal bristle vibrissa-like. Arista short-plumose. Anepisternum with additional upcurved bristle in posterodorsal corner. Thorax dark brown; Guanacaste male with faint yellowish arch in front of (and following) transverse suture. Coxae and legs light yellow with mid tibia sometimes brown; legs entirely yellow in types (one type severely damaged with mid legs missing). Frons dark brown with anterior half (or less) orange (yellow with posterior half

brownish-orange in Guanacaste male); antenna (excluding arista) yellow with distal 1/3 of first flagellomere brown; face, gena, parafacial and mouthparts white; remainder of head yellow; face pilose; upper 3/5 of gena silvery tomentose. Abdomen dark brown with cerci yellow and surstylus somewhat lighter medially and distally. Wing clouded around distal 1/4 of vein R_{2+3} and lightly clouded in base of first radial cell; male from Guanacaste and type specimens with distal 1/3-1/2 clouded, and with infuscation anterior to base of R_{2+3} . M_{1+2} ratio 5.7.

Male terminalia (Figs 39-41)

As described for *H. czernyi* except as follows: surstylus and epandrium smaller and more rounded; hypandrium + pregonite large, dorsally lobate, and without anterior bristle; distiphallus with both ribs shortened and terminating in long, thick accessory sclerites.

Female

None examined.

Distribution

Costa Rica, Nicaragua, St. Vincent, United States (FL) (Map 5).

Lectotype: ST. VINCENT. W.I., Leeward side, H.H. Smith (1 &, BMNH).

Paralectotypes: ST. VINCENT. same collection as lectotype (2 & &, BMNH).

Additional material examined: COSTA RICA. Guanacaste: Guanacaste N.P., Biol. Stn. Cacao, 13.ii.1995, screen sweeps, L. Masner (1 °, INBC), Puntarenas: San Vito de Coto Brus, Est. Biol. Las Alturas, 1500m, forest border, v.1992, P. Hanson (1 °, DEBU). ST. VINCENT. W.I., Mangaroo, 28.iii.1989, A. Freidberg (1 °, DEBU).

Comments

Two of the original five male cotypes WILLISTON designated for *Heteromeringia flavipes* (as *Heteroneura*) (WILLISTON, 1896) have been identified as pale phase males of *Craspedochaeta concinna* (WILLISTON, 1896). Of the remaining three male cotypes, one is here designated as the lectotype of *H. flavipes*. The single female cotype was not examined.

Heteromeringia lateralis sp. n.

(Figs 7, 50, 60, Map 5)

Description (Figs 7, 60)

Female

Body length 5.0 mm. Bristles black. Two dorsocentral bristles plus small bristle in front of anterior dorsocentral. Four fronto-orbital bristles with anterior reclinate bristle half as long as remaining reclinate bristles. Ocellar bristle relatively long and well-developed. Anterior genal bristle vibrissalike. Arista short pubescent. Scutum partly yellow with one pair of wide brown stripes outside dorsocentral rows that join anteriorly (emarginate behind suture); postpronotum and remainder of notopleuron brownish. Scutellum yellow with lateral corner brown. Katatergite and anatergite (below scutellum) brown. Pleuron yellow with subnotal stripe on dorsal half of anepisternum and anepimeron. Legs mostly yellow; base of hind tibia light brown; fore femur with light distal mark on inner face; fore tarsi brown with tarsomere 1 and base of tarsomere 2 yellow; mid and hind tarsi with tarsomeres 3-5 light brown. Head yellow except as follows: first flagellomere with infuscation at base of arista; distal 1/4 of palpus dark brown; frons brownish-orange (excluding lateral margins) with dark medial crescent-shaped spot; back of head with one pair of stripes; ocellar spot

brown. Parafacial and upper 3/5 of gena silvery tomentose. Abdomen brown with cerci yellow. Wing darkly clouded from costa to midpoint of second radial cell (distal to basal 1/3 of subcostal cell) and lightly clouded distally along R_{445} . M_{147} ratio 9.2.

Female terminalia (Fig. 50)

Spermatheca small and funnel-shaped (strongly concave distally with wide, rounded edge). Spermathecal duct weakly sclerotized, widened distally to surround base of spermatheca, and very long and wrinkled. Ventral receptacle as described for *H. czernyi*.

Male

Unknown.

Etymology

The specific name refers to the lateral stripes on the scutum and scutellum.

Holotype: COSTA RICA. Cartago: El Guarco, San Isidro, Madre Selva, Finca Los Lagos, 2600m, xii.1993, Trampa Malaise, M.M. Chavarria (1 \, NBC).

Comments

Although it is generally undesirable to describe a species on the basis of a single female, *Heteromeringia lateralis* is an easily diagnosed species distinct from all other congeners. It is characterized by an apically dark brown palpus, strong notal stripes that join anteriorly and continue along the sides of the scutellum posteriorly, and a strong band on the wing that extends along the costa into the costal cell.

Heteromeringia mediana sp. n.

(Figs 3, 42-44, 63, Map 5)

Description (Figs 3, 63)

Male

Body length 3.5 mm. Bristles black. Two dorsocentral bristles plus one minute bristle in front of anterior dorsocentral. Four fronto-orbital bristles with anterior reclinate fronto-orbital 2/3 length of remaining fronto-orbitals. Arista short-plumose. Ocellar bristle relatively long and well-developed. Anterior genal bristle vibrissa-like. Thorax yellow with katatergite, lateral margin of scutum and dorsal margin of pleuron in front of alar base with orange tinge, and scutellum with wide median brown stripe. Head yellow with median orange infuscation under tomentose patch on gena and ocellar tubercle brown. Legs yellow with elongate light brown subbasal spot on fore femur. Abdomen brown with tergite 1 and anterior half of tergite 2 yellow. Wing darkly clouded on distal half along costa, around R_{2+3} and R_{4+5} , and around basal section of CuA_1 ; lightly clouded in costal cell and around remaining veins. M_{1+2} ratio 12.0.

Male terminalia (Figs 42-44)

Annulus well-developed and bare. Epandrium 1/5 wider than long, and length half height with anterior margin curved. Cerci long, united and tapering apically with deep central emargination. Surstylus small and rounded with long, stout, pointed bristles along distal margin. Internal genitalia as described for *H. czernyi*, except hypandrium + pregonite without thin median process and minute setulae present distally.

LONSDALE, O. & MARSHALL, St. A.: Revision of the New World Heteromeringia

Female

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Unknown.

Etymology

The specific name refers to the median stripe of the scutellum.

Holotype: BRAZIL. Amazonas, 26km NE Manaus, Reserva Ducke, 22.xii.1988, J.A. Rafael, Arm. suspensa 1.5m (1 &, INPA).

Comments

Heteromeringia mediana differs from other New World Heteromeringia in having a median brown stripe on the scutellum and a very large M_{1+2} ratio. Its genitalia are similar to those of H. quadriseta, but the epandrium is shallower, the surstylus is slightly angulate, the hypandrium is more elongate and the phallapodeme is curved.

Heteromeringia quadriseta sp. n.

(Figs 2, 45-47, 62, Map 5)

Description (Figs 2, 62)

Male

Body length 2.9 mm. Bristles dark brown. Two dorsocentral bristles. Four fronto-orbital bristles with anterior reclinate bristle half length of remaining bristles. Ocellar bristle relatively long and well-developed. Anterior genal bristle vibrissa-like. Arista short-plumose. Thorax yellow with one pair of short thin postsutural stripes, lateral margin of scutum (excluding postpronotum) brownish and faded brownish stripe present below scutellum. Legs yellow with tarsomere 5 and distal edge of tarsomere 4 on fore tarsi brown. Head light yellow with ocellar spot brown and gena, face and mouthparts white; face, anterior 1/3 of frons and upper 3/5 of gena pilose. Abdomen predominantly yellow, although posterior margin of tergite 2 and tergites 3 and 4 brown, and tergite 5 with wide central stripe. Wing clouded around distal half of $R_{2,43}$. $M_{1,2}$ ratio 6.0.

Male terminalia (Figs 45-47)

Epandrium slightly wider than high and length 2/3 height. Surstylus small and rounded, distinctly wider than long and with stout pointed bristles on inner face. Cerci deeply sunken into epandrium, emarginate on distal 1/3 and with one pair of stout pointed apical bristles. Anterior face of hypandrium without process, dorsal margin strongly reclinate and terminal seta long and pointed (not rounded). Basiphallus fused to distiphallus and with wide diamond-shaped posteroventral plate. Phallapodeme as long as hypandrium + pregonite. Distiphallus relatively short with apex fringed.

Female

Unknown.

Etymology

The specific name refers to the four pairs of fronto-orbital bristles.

DOI: 10.21248/contrib.entomol.57.1.37-80

Holotype: PERU. Madre de Dios, Manu, Rio Manu, 250m, Pakitza, 12°07'S, 70°58'W, 9-23.ix.1988, A. Freidberg (1 &, USNM).

Paratype: ECUADOR. Napo Province, Yasuni National Park, PUCE Yasuni Research Station, rainforest, Malaise trap, 00°38'S, 76°36' W, 30.x-20.xi.1998, T. Pape (1 & , ZSMC).

Comments

Heteromeringia quadriseta is a pale eastern South American species with a medially yellow scutellum. Heteromeringia lateralis (also in the H. czernyi group) and H. decora (incertae sedis) also have a lighter scutellum, but these species are restricted to Central America, and they have a dark frons, a spot at the base of the arista and a predominantly brown scutellum.

Species incertae sedis.

Heteromeringia apholis sp. n.

(Figs 51-53, Map 3)

Description

Male

Body length 2.4 mm. Bristles black. Anterior dorsocentral bristle 2/3 length of posterior dorsocentral. Ocellar bristle well-developed. Genal bristles small and hair-like. Three fronto-orbital bristles. Anepisternum without disc. Body brown with face, parafacial, gena and anterior half of buccal cavity dirty white, antenna and anterior margin of frons orange and first flagellomere darkly infuscated on inner and distal faces. Occiput relatively wide and broadly rounded; gena nearly half height of eye. Dorsal half of gena silvery tomentose (tomentose band tapering posteriorly); frons pilose with wide shiny space along posterior margin enclosing ocellar tubercle. Wing clouded along anterior margin from R₁ to apex. M_{1,2} ratio 5.6.

Male terminalia (Figs 51-53)

Width and height of epandrium 1/3 greater than length. Cerci approximately 3/4 height of epandrium, widening distally and with deep triangular emargination. Surstylus 7/10 height of epandrium, acutely triangular, curved posteriorly, and with minute setulae along outer surface and numerous small pointed bristles distally on inner-apical surface. Internal genitalia as described for *H. nitida* except dorsal margin of hypandrium reclinate, suture absent, phallapodeme half as long, setulae on pregonite restricted to anterior and posteroventral patches, and distiphallus wide and membranous distally (without elongate apical process).

Female

Unknown.

Etymology

The specific name is derived from the Greek for "scale/spot", denoting the small circular structure found on the anepisternum of many *Heteromeringia* males; the prefix "a" indicates the absence of this structure.

Holotype: MEXICO. Durango. 9000', 10mi W El Salto, J.F. McAlpine, 5.vi.1964 (1&, CNCI).

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Comments

Heteromeringia apholis is a small, dark species, and the only New World Heteromeringia outside of the H. czernyi group (possibly aside from two species as yet unknown from males) without an anepisternal disc.

See comments for Heteromeringia zophina.

Heteromeringia decora sp. n.

(Figs 4, 58, Map 3)

Description (Figs 4, 58)

Female

Body length 4.9 mm. Bristles black. Two dorsocentral bristles. Ocellar bristle relatively long and well-developed. All genal bristles small and hair-like. Three fronto-orbital bristles. Arista pubescent. Thorax largely yellow; anterior 3/4 of presutural scutum brown (excluding small lateral emargination and wide truncate posterior emargination); remainder of notopleuron slightly brownish-orange; postsutural scutum with one pair of thin stripes outside dorsocentral rows (not touching posterior margin); scutellum yellow and subscutellum brown. Legs mostly yellow; fore coxa and basal half of femora white; fore femur with brown inner-apical spot; fore tibia brown laterally; fore tarsi dark brown laterally (remainder light brown); fore tibia and tarsi with slight lateral compression. Head yellow except as follows: frons brownish-orange (excluding lateral margins) with anterior half dark brown (velvety medially); first flagellomere with small spot around base of arista; back of head dark brown above foramen; face dirty yellow; distal half of palpus dark brown; gena brown medially on anterior half (fading posteriorly); gena silvery tomentose on dorsal 2/5 of anterior half. Abdomen brown with terminalia yellow. Wing darkly infuscated along R_{2+3} (excluding base) and along distal 2/5 around R_{4+5} ; lightly infuscated along all veins posterior to R_{4+5} . M_{1+2} ratio 8.3.

Female terminalia

Not dissected.

Male

Unknown.

Etymology

The specific name refers to the distinct colouration of this species.

Holotype: MEXICO. Chiapas: Montebello N.P., 5000', 31.v.1969, B.V. Peterson (Mal.) (19, CNCI).

Comments

Heteromeringia decora is easily separated from other New World Heteromeringia by its characteristic colouration, similar to that seen in some Indoaustralian species.

Heteromeringia nigrifrons Kertesz, 1903

(Map 3)

Heteromeringia nigrifrons Kertesz, 1903: 568. Melander & Argo, 1924: 30.

Description [translated from Kertesz (1903)]

Female

Black, with weak luster. Frons, face, gena and occiput black. Orbits from base of antenna to slightly beyond midpoint of frons narrowly brownish yellow. Antenna pale brownish yellow; third segment more or less reniform and with black apex; arista black, pubescent. Proboscis and palpus black, the latter reddish yellow in apical half. Bristles of head black. Genae ca. 1/6 as high as head. Vibrissa moderately long, behind it only very short setulae. Thoracic dorsum dull black, with appressed very short and weak ferruginous pubescence; bristles black. Pleura shining black. Legs reddish yellow. Front coxae pale yellow. Front femur with exception of basal half and knee, mid femur toward (i.e., excluding) apical fourth, and tibiae excluding knees yellow. Mid and hind tibiae with black [? ventral] apical spur. Femora with short bristles on ventral surface (bristles of hind femur longest). Front tibia and tarsi with short black setulae. Wing, excluding yellowish basis and hind margin, with smoky tinge; infuscation strongest at front margin. Third and fourth longitudinal veins parallel, last sector of fourth vein five times as long as penultimate sector. Halter yellowish white. Length: 4.3 mm; wing length: 3 mm.

Female terminalia

Not dissected.

Male

Unknown.

Holotype: PERU. Vilcanota (1 ♀, HNHM).

Comments

The holotypes of *Heteromeringia nigrifrons* and *H. flavifrons* were examined on our behalf by Dr. L. Papp in Hungary, allowing us to add the following notes to the above description: there is no upcurved bristle on posterodorsal surface of the anepisternum; the gena and occiput are shiny; the postvertical bristle is slightly shorter than the ocellar bristle; there are two pairs of dorsocentral bristles; the M_{1+2} ratio is 6.9. *Heteromeringia nigrifrons* is the only New World *Heteromeringia* outside of the *H. czernyi* group with yellow fore tibiae.

Recombinations

Two species previously treated as *Heteromeringia* are no longer included in the genus. *Heteromeringia* annulipes Johnson, 1913, described from North Carolina, was recently moved to *Craspedochaeta* Czerny, 1903 as a senior synonym of the predominantly neotropical *C. piceoflava* Sóos, 1962 (Lonsdale & Marshall, 2006b). The Peruvian *H. dimidiata* Hennig, 1938 (holotype label data: Peru. Ucayalifluss, Unini, 20.x.1903, Schnuse (19, SMTD)) belongs to a clade of neotropical *Sobarocephala* including *S. liturata* Melander & Argo, 1924 and is therefore treated here as *Sobarocephala dimidiata* (Hennig, 1938) comb. n. This species was mistakenly treated as *Heteromeringia* because its dark colouration gave it a resemblance to *H. fumipennis* Melander & Argo, 1924 (Hennig, 1938).

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Replacement names

A replacement name is here provided for the South African/Seychelles species *Heteromeringia ni-grifrons* LAMB, 1914, a primary junior homonym of the neotropical *H. nigrifrons* KERTESZ, 1903. The replacement name, *H. tephrinos* nomen nov., is Greek for "ash-coloured", in reference to the infuscated halter.

Relationships

Most New World *Heteromeringia* can be placed into one of two relatively common species groups: the widespread *H. nitida* group and the entirely Neotropical *H. czernyi* group. Three Neotropical species (*H. apholis*, *H. decora* and *H. nigrifrons*), and several species from Europe, Southeast Asia and Fiji, cannot be placed in either of the above species groups.

Heteromeringia czernyi species group. The H. czernyi group contains H. czernyi, H. flavipes, H. aphotisma, H. flavifrons, H. lateralis, H. quadriseta and H. mediana, and is defined by the following characters: anterior genal bristle vibrissa-like; anepisternum with additional upcurved bristle in posterodorsal corner (Fig. 8) (only retained in H. czernyi, H. flavipes and H. aphotisma); arista loosely pubescent or short-plumose; pregonite with rounded distal nub (Figs 34 and 35); basiphallus with diamond-shaped to (somewhat) rectangular posteroventral plate behind point of attachment to distiphallus; phallapodeme never longer than hypandrium + pregonite; ventral receptacle large and wedge-shaped (Figs 48-50); spermatheca not telescoped.

Heteromeringia flavipes and H. czernyi are basal in the group, characterized by brown bristles, one distal and one medial cloud on the wing, hand-shaped scales on the surstylus (Fig. 33) (absent in some specimens), a prominent process on the inner face of the surstylus, and an elongate sac-like spermatheca with distal sculpturing (Figs 48 and 49). Both species extend into Florida, but H. flavipes is not found south of Costa Rica, and H. czernyi is widespread in both Central and South America all the way to Tierra del Fuego, which is by far the most southern record of a clusiid in the New World. The remaining six species in the group form a clade defined by four fronto-orbital bristles and a dark infuscation from the costa to the midpoint of the second radial cell (reduced in H. quadriseta). Of these, H. aphotisma (southern Brazil) is the most ancestral because it retains dark colouration and an additional upcurved bristle in the posterodorsal corner of the anepisternum. The other four species are pale flies known either from Costa Rica (H. lateralis) or South America (*H. quadriseta:* Ecuador, Peru; *H. mediana:* Brazil)), although the widespread Heteromeringia flavifrons has been collected in Bolivia, Brazil, Costa Rica, Ecuador and Honduras. The two exclusively South American species form a clade characterized by small inset surstyli (Figs 44 and 47), an enlarged annulus (Figs 43 and 46), and cerci that are thin and widely incised with one pair of relatively short, stout apical bristles (Figs 44 and 47).

Heteromeringia nitida species group. The (single) defining synapomorphy of this widespread and species-rich group is the small, pale, disc-like structure on the male anepisternum (Fig. 9). This unusual character is unlikely to be subject to homoplasy and is an easily recognized synapomorphy. Many Heteromeringia belong to this group, but a World revision will be necessary to resolve its zoogeography and internal phylogeny, as well as the relationships between it and the remaining Heteromeringia.

Biology

Label data for New World specimens (mostly those we have collected in the Neotropics) suggest that some species of *Heteromeringia* aggregate around relatively open areas such as tree falls, forest borders, pastures and landslides. McAlpine (1960) also notes that while most Australian clusiids were taken in rainforests along creeks, *Heteromeringia* species were collected in more open forests.

We have collected *H. fumipennis*, *H. czernyi*, *H. nitida* and *H. flavifrons* with dung baits and dung traps. *Heteromeringia nitida* has also been collected using mushroom traps and has been observed on myxomycete sporocarps as described below. *Heteromeringia flavifrons* and *H. czernyi* have been collected from carrion. In Europe, *H. nigrimana* is known to be associated with dead wood in deciduous or mixed forests, predominantly on decaying logs (ROHÁČEK, 1995). Australian specimens of *H. norrisi* MCALPINE, 1960 have been bred from rotting wood and one female was collected "in [a] log with termites" (MCALPINE, 1960).

Agonistic behaviour

Like other clusiodine genera, including *Craspedochaeta* (Lonsdale & Marshall, 2006b), *Clusiodes* Coquillett, 1904 and *Hendelia* Czerny, 1903 (Marshall, 2000; McAlpine, 1976; Roháček, 1995), *Heteromeringia* males engage in agonistic interactions at lek sites on fallen trees. One of us (SM) observed *H. nitida* males visiting rotting oak logs in South Carolina over periods of several spring days in each of two consecutive years. Males appeared daily on bare patches of logs partially covered with myxomycete sporocarps, where each male seemed to patrol a territory of about six square cm. When two males appeared in the same territory, they folded their front legs back at the tibial-femoral joint before "boxing" with their elbows (Fig. 1). Females were observed going in and out of beetle burrows on the same logs, and although pairs were seen in copula on the lek sites, no premating behaviour was noted. Roháček (1995) speculated that a recently fallen lime-tree log was used as a mating place for *H. nigrimana*, as seven of the nine specimens he collected off of this log were males. Males of *H. pulla* have been observed moving their wings in a similar fashion to sepsids, platystomatids and tephritids on the fallen bark and limbs of *Eucalyptus* trees, where they were also observed copulating with females (McAlpine, 1960).

Acknowledgements

The loan of material from the following curators and institutions is gratefully acknowledged: N. Wyatt (BMNH); K. Ribardo and N. Penny (CASC); J. Cumming, J. O'Hara, J. R. Vockeroth and D. M. Wood (CNCI); W. Hanson (EMUS); M. von Tschirnhaus (Biological Collection, University of Bielefeld); M. Zumbado and M. Solis (INBC); A. Henriques (INPA); P. Perkins (MCZC); R. Blinn (NCSU); P. Sehnal and R. Contreras—Lichtenberg (NHMW); T. Pape (NHRS); D. C. Darling and D. Currie (ROME); U. Kallweit (SMTD); E. Riley and R. Wharton (TAMU); D. Furth, A. Norrbom and F. C. Thompson (USNM); R. Danielsson (UZMD). Comments provided by J. Roháček were very useful for improving this manuscript, as were notes on the Australian and Japanese Heteromeringia provided by D. K. McAlpine and M. Sueyoshi. M. Buck translated the abstract and the original description of H. nigrifrons. We would also like to thank L. Papp (HNHM) for examining the types of Heteromeringia nigrifrons and H. flavifrons on our behalf. This study was supported by an NSERC grant awarded to SM, and OGSST and NSERC grants awarded to OL.

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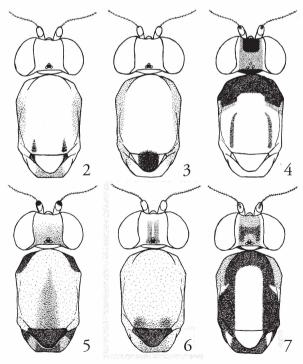
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Fig. 1: Agonistic interaction between *Heteromeringia nitida* Johnson males (South Carolina).



Figs 2-7: Dorsal colouration, head and thorax. 2 *H. quadriseta* sp. n., male; 3 *H. mediana* sp. n., male; 4 *H. decora* sp. n., female; 5-6 *H. flavifrons* Hennig, female; 7 *H. lateralis* sp. n., female.

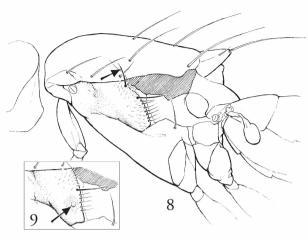
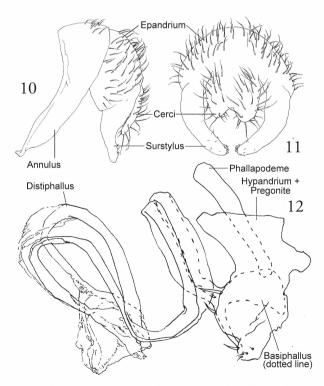
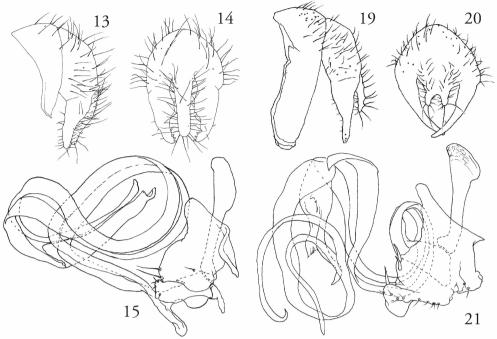


Fig. 8: Heteromeringia czernyi Kertesz, left lateral with detail of anepisternum and arrow indicating diagnostic upturned bristle. Fig. 9: H. fumipennis Melander & Argo, anepisternum with arrow indicating diagnostic lateral disc.

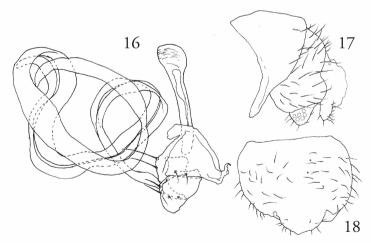


Figs 10-12: Heteromeringia fucata Hendel, genitalia. 10 external, left lateral; 11 external, posterior; 12 internal, left lateral. Ejaculatory apodeme omitted.

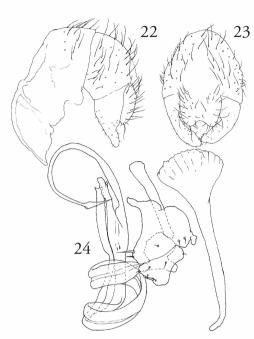


Figs 13-15: Heteromeringia fumipennis Melander & Argo, genitalia. 13 external, left lateral; 14 external, posterior; 15 internal, left lateral. Ejaculatory apodeme omitted.

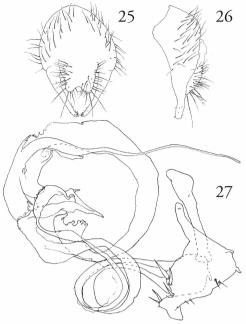
Figs 19-21: Heteromeringia nigripes Melander & Argo, genitalia. 19 external, left lateral; 20 external, posterior; 21 internal, left lateral. Ejaculatory apodeme omitted.



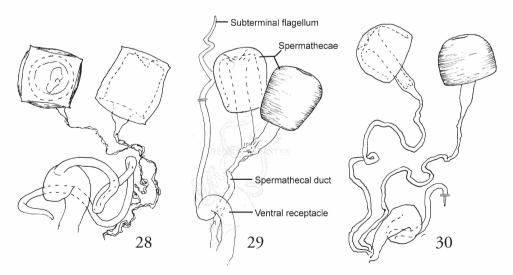
Figs 16-18: Heteromeringia nanella sp. n., genitalia. 16 internal, left lateral; 17 external, left lateral; 18 external, posterior. Ejaculatory apodeme omitted.



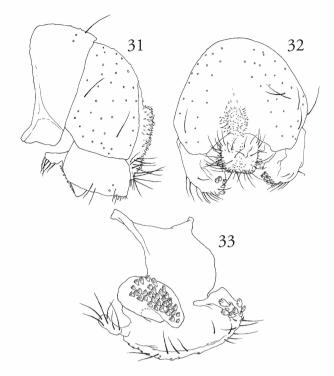
Figs 22-24: *Heteromeringia nitida* JOHNSON, genitalia. 22 external, left lateral; 23 external, posterior; 24 internal, left lateral.



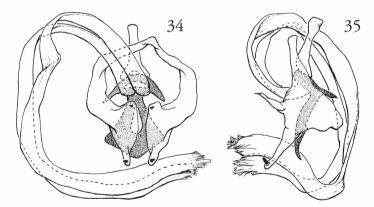
Figs 25-27: Heteromeringia zophina sp. n., genitalia. 25 external, posterior; 26 external, left lateral; 27 internal, left lateral. Ejaculatory apodeme and annulus omitted.



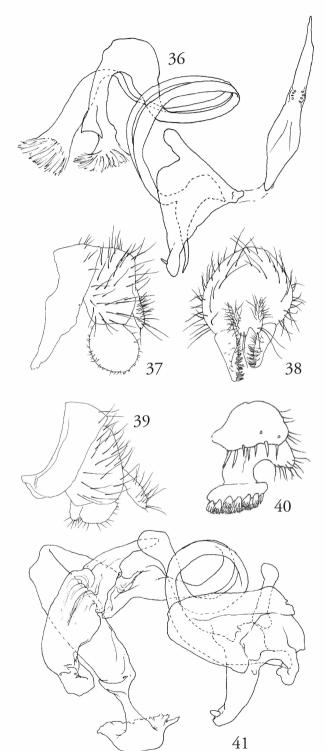
Figs 28-30: Female internal genitalia (spermathecae and ventral receptacle). 28 *Heteromeringia fumipennis* Melander & Argo; 29 *H. nitida* Johnson; 30 *H. nigripes* Melander & Argo.



Figs 31-33: Heteromeringia czernyi Kertesz, external terminalia. 31 left lateral; 32 posterior; 33 right surstylus, left lateral.

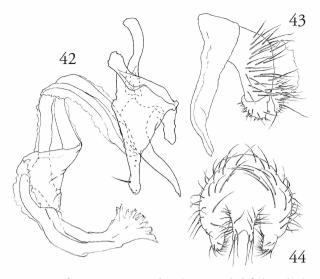


Figs 34-35: *Heteromeringia czernyi* Kertesz, internal genitalia, basiphallus shaded. 34 anterior; 35 left lateral. Ejaculatory apodeme omitted.

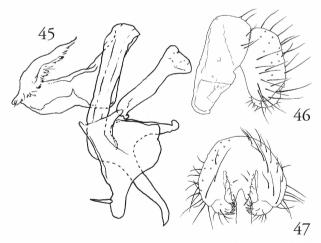


Figs 36-38: Heteromeringia flavifrons Hennig, genitalia. 36 internal, left lateral; 37 external, left lateral; 38 external, posterior. Phallapodeme missing from dissected specimen.

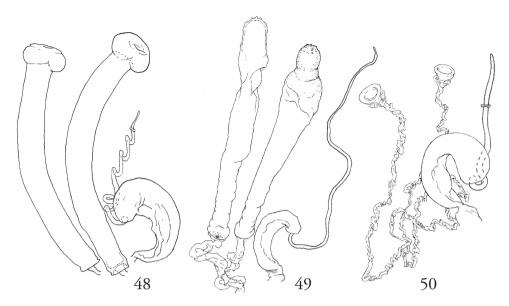
Figs 39-41: Heteromeringia flavipes (Williston), genitalia. 39 external, left lateral; 40 right surstylus, dorsal; 41 internal genitalia, left lateral. Ejaculatory apodeme omitted.



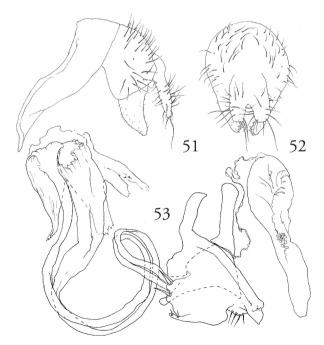
Figs 42-44: Heteromeringia mediana sp. n., genitalia. 42 internal, left lateral; 43 external, left lateral; 44 external, posterior. Ejaculatory apodeme omitted.



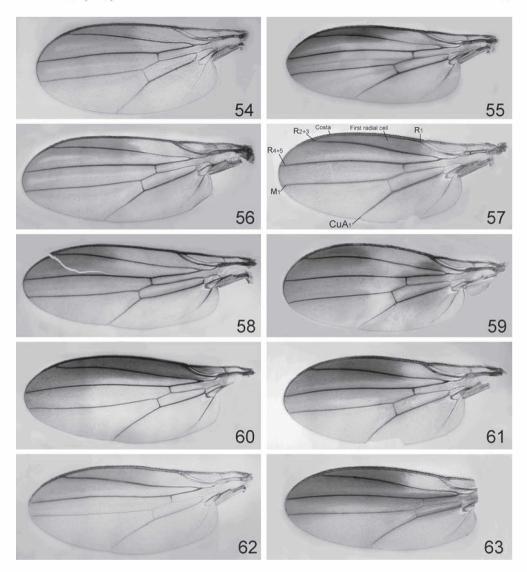
Figs 45-47: Heteromeringia quadriseta sp. n., genitalia. 45 internal, left lateral; 46 external, left lateral; 47 external, posterior. Ejaculatory apodeme omitted.



Figs 48-50: Female internal genitalia (spermathecae and ventral receptacle). 48 Heteromeringia czernyi Kertesz; 49 H. flavifrons Hennig; 50 H. lateralis sp. n.



Figs 51-53: Heteromeringia apholis sp. n., genitalia. 51 external, left lateral; 52 external, posterior; 53 internal, left lateral.



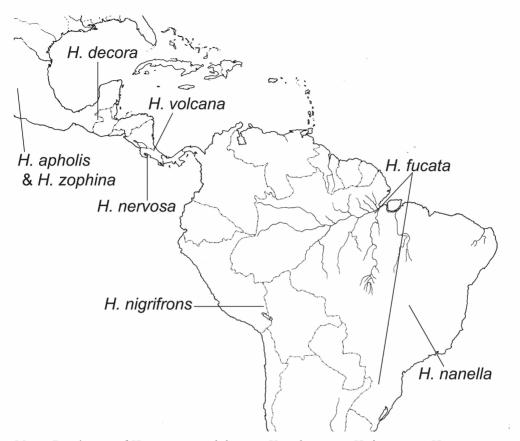
Figs 54-63: wings; 54: Heteromeringia fucata Hendel, 1936, female; 55: H. nitida Johnson, 1913, female; 56: H. nervosa sp. n., male; 57: H. fumipennis Melander & Argo, 1924, female; 58: H. decora sp. n., female; 59: H. czernyi Kertesz, 1903, female; 60: H. lateralis sp. n., female; 61: H. flavifrons Hennig, 1938, female; 62: H. quadriseta sp. n., male; 63: H. mediana sp. n., male.



Map 1: Distributions of $Heteromeringia\ nitida\$ Johnson (dot) and $Heteromeringia\ nigripes\$ Melander & Argo (circle). South American localities of $H.\ nigripes\$ not shown.



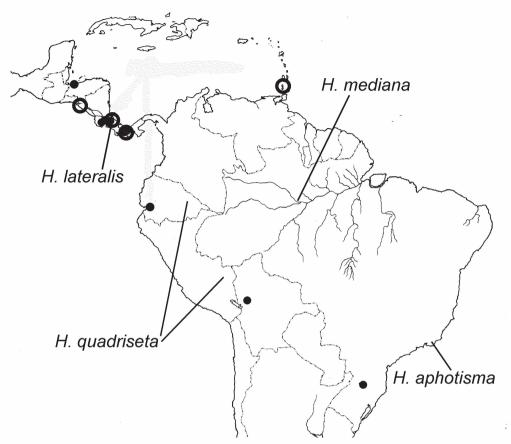
Map 2: Distribution of *Heteromeringia fumipennis* Melander & Argo.



Map 3: Distributions of *Heteromeringia apholis* sp. n., *H. zophina* sp. n., *H. decora* sp. n., *H. nervosa* sp. n., *H. volcana* sp. n., *H. nanella* sp. n., *H. nigrifrons* Kertesz, and *H. fucata* Hendel.



Map 4: Distribution of Heteromeringia czernyi Kertesz.



Map 5: Distributions of species in the *Heteromeringia czernyi* species group excluding *H. czernyi* Kertesz. Legend: *H. flavipes* (Williston), circle; *H. flavifrons* Hennig, dot.

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Autor(en)/Author(s): Lonsdale Owen, Marshall Stephen A.

Artikel/Article: Revision of the New World Heteromeringia (Diptera: Clusiidae:

Clusiodinae). 37-80