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The Neotropical genera *Parasphen* Enderlein, 1922 and *Ptilosphen* Enderlein, 1922 (Diptera, Micropezidae, Taeniapterinae)

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Abstract. The Neotropical genera *Parasphen* Enderlein, 1922 and *Ptilosphen* Enderlein, 1922 are revised. *Parasphen rufipes* (Fabricius, 1805) is given as a new combination, *Parasphen frontalis* Cresson, 1930 and *Parasphen amazonicus ruficauda* Curran, 1932 are treated as new synonyms of *Parasphen rufipes* comb. nov., *Ptilosphen rufifrons* Enderlein, 1922 is treated as a new junior synonym of *Ptilosphen cyaneiventris* (Macquart, 1846), and *Ptilosphen viriolatus* Enderlein, 1922 and *Ptilosphen albibasis* Enderlein, 1922 are treated as new junior synonyms of *Ptilosphen callichroma* (Bigot, 1886). The following 14 new species of *Ptilosphen* are described: *Pt. boroboro* Marshall sp. nov., *Pt. crassus* Marshall sp. nov., *Pt. dellarum* Marshall sp. nov., *Pt. elongatus* Marshall sp. nov., *Pt. inconueniens* Marshall sp. nov., *Pt. manu* Marshall sp. nov., *Pt. notatus* Marshall sp. nov., *Pt. rafaeli* Marshall sp. nov., *Pt. ramosus* Marshall sp. nov., *Pt. xanthicoxa* Marshall sp. nov., *Pt. xestos* Marshall sp. nov., *Pt. yasuni* Marshall sp. nov., *Pt. yauae* Marshall sp. nov., and *Pt. zonalis* Marshall sp. nov. Lectotypes are designated for *Ptilosphen conveniens* (Wulp, 1897) and *Pt. viriolatus* Enderlein, 1922. The species of *Parasphen* and *Ptilosphen* are keyed and CO1 neighbour-joining and maximum likelihood trees are given for 18 of the 26 species of *Ptilosphen*.

Keywords. New species, new synonyms, new combinations, Neotropical.

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Introduction

The 26 species of *Ptilosphen* Enderlein, 1922 and the two species of *Parasphen* Enderlein, 1922 are the only New World Micropezidae Loew, 1861 with a long and pointed anal cell (*cup* or *cua*) and an entirely long-haired (as opposed to bare, pubescent or bipectinate) arista (Marshall 2010). Both genera further differ from other Micropezidae with a long anal cell, traditionally grouped as the tribe Taeniapterini Cresson, 1938, in lacking postocellar bristles and both differ from most other Taeniapterini (other than *Poecilotylus* Hennig, 1934) in having parallel-sided palpi with rounded tips. Despite these shared characters and a general superficial similarity, *Parasphen* and *Ptilosphen* differ widely in many features, especially those of the male and female terminalia. Both *Parasphen* and *Ptilosphen* are probably more

closely related to the genera traditionally treated as the tribe Rainieriini Cresson, 1938 (=Grallipezini Aczél, 1951), otherwise characterized by a short anal cell, than to other genera with an elongate anal cell (tribe Taeniapterini).

Although some species of *Ptilosphen* appear to be narrowly endemic, several are widespread and common enough to place the genus among the most frequently noticed Neotropical Micropezidae. The relatively large adult flies are often seen on low foliage where, as in many other micropezids, their forelegs (partially white in many species) are routinely extended in front of the body in a way that resembles the antennae of sympatric ichneumonoid wasps. At least one species (*Pt. callichroma* (Bigot, 1886)) exhibits elaborate mating and defensive behaviours, including nocturnal aggregations. Courtship in *Ptilosphen* species can include precopulatory inflation of parts of the male abdominal pleuron, oral exchange of liquid nuptial gifts and characteristic dancing and stroking. The detailed description of the biology of *Pt. callichroma* (as *Pt. variolatus* Enderlein, 1922) provided by Ortiz (2003) renders it one of the most thoroughly documented of all micropezid species. Eggs of this species, and probably other members of the genus, are deposited in small batches in soft, decomposing leaf litter or rotting wood where the larvae develop in the decaying plant material. Adults of *Ptilosphen* are attracted to various kinds of decomposing matter, such as dead insects and bird droppings, and can be readily collected using dung baits. Many of the specimens examined for this study were collected individually using small dung baits; other specimens were taken in Malaise traps. A couple of species (the Central American *Pt. dellarum* Marshall sp. nov., the South American *Pt. mimicus* Cresson, 1930 and possibly the South American *Pt. inconveniens* Marshall sp. nov.) are characteristic of cloud forest habitats above 1000 m a.s.l., but most collection records for *Ptilosphen*, and all records of *Parasphen*, are from lower elevation forests. *Ptilosphen* species are found throughout the neotropics from Mexico south to Bolivia, but *Parasphen* appears to be restricted to Amazonia.

Although *Ptilosphen* and *Parasphen* are superficially similar, they are separately characterized by the morphological characters outlined in the diagnoses and descriptions below, and each genus is also supported by published and unpublished sequence data. Lindsay & Marshall (2023) included *Parasphen amazonicus* Enderlein, 1922 and five *Ptilosphen* species among the outgroup taxa in a molecular phylogeny of the *Scipopus* group and related species. Their maximum likelihood tree using CO1–5', CO1–3', 12S and 28S–2, 28S–3 and 28S–5 (Lindsay & Marshall 2023: fig. 2) recovered the five *Ptilosphen* species together as the sister group to a branch made up of several genera of Rainieriini, including *Grallipeza* Rondani, 1850 and *Calosphen* Hennig, 1934 but excluding the *Scipopus* group. *Parasphen* was recovered outside the *Ptilosphen/Grallipeza/Calosphen* clade. Unpublished CO1 (barcode) maximum likelihood trees of New World Micropezidae also show *Ptilosphen* and *Parasphen* as widely separated branches but consistently recover *Ptilosphen* as a single branch closely related to *Grallipeza*. *Parasphen* is weakly supported as deep within the Taeniapterini on barcode trees, but morphological characters other than the Taeniapterini-like anal cell suggest a relationship between *Parasphen* and *Mesoconius* Enderlein, 1922.

Two other published molecular phylogenies included *Ptilosphen* but not *Parasphen*. Ferro *et al.* (2021) included two species of *Ptilosphen*, *Pt. dellarum* Marshall sp. nov. and *Pt. crassus* Marshall sp. nov. (as “*Ptilosphen* n. spp.”), in their analysis (using CO1, CAD, EF-1 α , 16S and 28S) of selected Taeniapterinae Cresson, 1930, finding that they clustered with the *Scipopus* group (a major clade of Rainieriini treated by Lindsay & Marshall (2023) as the genus *Scipopus* Enderlein, 1922). Jackson *et al.* (2015) included a specimen of *Ptilosphen cyaneiventris* (Macquart, 1846) in a majority rule consensus cladogram (using 12S, CO1, wingless and CAD), recovering it as the sister species to *Cardiacephala harenosa* (Cresson, 1930) (as *Plocoscelus harenosus* Cresson, 1930).

Although *Ptilosphen* can be conveniently divided into orange species and black species for identification purposes, this is an artificial division and apparently does not reflect relationships.

Material and methods

Specimens were borrowed from, examined at, or deposited in the following institutions:

- AMNH = American Museum of Natural History, New York, New York, U.S.A.
ANSP = Academy of Natural Sciences, Philadelphia, Pennsylvania, U.S.A.
BIOUG = Biodiversity Institute of Ontario, Guelph, Ontario, Canada
CBFC = Colección Boliviana de Fauna, La Paz, Bolivia
CMNH = Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A.
CNCI = Canadian National Collection of Insects, Arachnids & Nematodes, Ottawa, Ontario, Canada
CUIC = Cornell University Insect Collection, Cornell, New York, U.S.A.
DEBU = University of Guelph Insect Collection, Guelph, Ontario, Canada
FMNH = Field Museum of Natural History, Chicago, Illinois, U.S.A.
IAVH = Instituto Alexander von Humboldt, Villa de Leyva, Colombia
INPA = Coleção Entomológica, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil
MECN = INABIO, Instituto Nacional de Biodiversidad, Quito, Ecuador
MLUH = Martin-Luther-Universität, Zentralmagazin Naturwissenschaftlicher Sammlungen, Zoologische Sammlung, Halle (Saale), Germany
MNBG = Museum für Naturkunde, Berlin, Germany
MNCR = Museo Nacional de Costa Rica, San José, Costa Rica (including the collections of INBio, the Instituto Nacional de Biodiversidad = INBC)
MUSM = Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru
NHMUK = Natural History Museum (British Museum (Natural History)), London, United Kingdom (=BMNH)
NHMW = Naturhistorisches Museum Wien, Vienna, Austria
OXUM = Hope Entomological Collections, University Museum, Oxford, England
QCAZ = Departamento de Biología, Pontificia Universidad Católica del Ecuador, Quito, Ecuador
ROME = Royal Ontario Museum, Toronto, Ontario, Canada
SMTD = Staatliches Museum für Tierkunde, Dresden, Germany
SNOW = Snow Entomological Museum, Lawrence, Kansas, U.S.A.
TAUI = Zoological Museum of Tel Aviv University, Tel Aviv, Israel
USNM = United States National Museum (National Museum of Natural History), Washington D.C., U.S.A.
ZMUC = Zoological Museum, National Museum of Denmark, Copenhagen
ZMUH = Zoological Museum, University of Helsinki, Finland

Diagnoses of species known only from types in MNBG are based on notes and photographs taken by S.A.M. during a visit to Berlin in 2001.

Label data are mostly given verbatim, but some abbreviations are entered as full terms and presentation of dates and elevations are standardized.

Morphological terminology and methodology follow Marshall (2019), with key structures labelled on Figs 1–2. Tergites, sternites and abdominal pleura are abbreviated T, S and P respectively. Abdominal lengths vary widely according to preservation method, so approximate body lengths are given as the distance between antennal base and wing apex (antennal base to wing base + wing length). The orbital plate, which extends far behind the ocelli in Taeniopterinae, is divided into the epicephalon and paracephalon (following Cresson 1930); the paracephalon is the outer portion and extends from the eye to the outer vertical bristle, the epicephalon is the inner part between the paracephalon and the posterior part of the frontal vitta and extends forward from the inner vertical bristle to an angled upper margin of the frontal plate. The upper fronto-orbital bristle (orbital bristle, rarely absent) is on the lower part of the epicephalon; the single lower fronto-orbital bristle (frontal bristle, rarely absent) is on the frontal plate. The part of the frontal vitta posterior to the ocelli is the postocellar frontal vitta, the part in front of the

ocelli is the preocellar frontal vitta; these areas are usually continuous but are sometimes broken by a band across the ocelli. Sexually dimorphic characters include the cervical sclerite, which is enlarged and centrally concave in females of some species; the scapular setae or suprahumeral setae, which are sometimes strongly developed only in females; and abdominal characters including tergal sclerotization and pleural pigmentation.

Male abdomens and female oviscapes were cleared in either hot lactic acid or (more often) hot potassium hydroxide; specimens cleared in potassium hydroxide were later neutralized in acetic acid and rinsed in distilled water prior to storage in glycerin. Female terminalia were usually stained with lignin pink prior to temporarily teasing out the spermathecae and associated ducts, usually either through the anterior opening of the oviscape or through an incision on the side of the oviscape, although for species with exceptionally delicate spermathecal ducts the oviduct and spermathecal complex were extracted by pulling off the ovipositor tip. The spermathecal ducts, stems and bodies vary widely interspecifically but are intraspecifically consistent; for most species they provide a reliable set of diagnostic characters and for some clades they offer persuasive synapomorphies.

Some colour characters traditionally used in *Ptilosphen* descriptions and keys show intraspecific variation. Frontal vitta colour and the conspicuous banding of the mid and hind femora, for example, are traditionally used as key characters but sometimes vary within and between populations of the same species. Abdominal pigmentation, on the other hand, seems to be consistent within species. Like many other taeniapterines, *Ptilosphen* species usually have a prominently pigmented abdominal pleuron, usually with one or more vertical black bands. Abdominal pigmentation is sometimes sexually dimorphic and can be diagnostic at the species level although the pleuron is often obscured or discoloured on older or shriveled specimens. Most *Ptilosphen* (but apparently not *Parasphen*) males have a pleural sac, a more or less circular and apparently inflatable patch of membrane, taking up much of P2 but sometimes only visible on fresh or living specimens; males of *Pt. callichroma* also inflate P4–5 as part of precopulatory behaviour (Ortiz 2003).

Molecular data

Specimens of seventeen species of *Ptilosphen* were sent to the Canadian Centre for DNA Barcoding (Guelph, Ontario) for assessment of the ‘barcode’ region of cytochrome oxidase I (CO1), and CO1 data for further *Ptilosphen* specimens (of which most were *Pt. callichroma*) were accessed through BOLD (Barcode of Life Database: <http://boldsystems.org/>, Ratnasingham & Hebert 2007). From this material, a dataset of *Ptilosphen* taxa was created by selecting a single representative of each barcode index number (BIN; Ratnasingham & Hebert 2013) or, in cases where BINs are not yet assigned, the sequence of a given species with the highest number of base pairs (bp) (Table 1, with sequence and BIN information). The selected sequences were first aligned using the automatic BOLD aligner (an amino acid Hidden Markov Model), then further visually aligned in Mesquite (Maddison & Maddison 2025) to ensure consistent gap placement with the sequences. Neighbour-joining tree and maximum likelihood (using GTR+G+I) analyses were run using NINJA (Wheeler 2009) and RAxML (Stamatakis 2014), respectively; bootstrap values for maximum likelihood were calculated with 1000 replicates.

Results

Class Insecta Linnaeus, 1758
Order Diptera Linnaeus, 1758
Superfamily Neriioidea Hendel, 1916
Family Micropezidae Loew, 1861
Subfamily Taeniapterinae Cresson, 1930

Genus *Parasphen* Enderlein, 1922

Parasphen Enderlein, 1922: 226 (type species *Parasphen amazonicus* Enderlein, 1922 (orig. des.)).

Table 1. Barcode Index Numbers (BINs) and cytochrome c oxidase subunit 1 (barcode) sequence data used to generate the neighbour-joining and maximum likelihood trees (Fig. 30) for *Ptilosphen* Enderlein, 1922 with links to the sequence and BIN data. *Grallipeza nebulosa* (Loew, 1866) is included as an outgroup.

Species	Sequence used (process id)	Sequence length (bp)	BIN (if assigned)
<i>Grallipeza nebulosa</i> (Loew, 1866)	MYCRO200-15	661	BOLD:AAN8610
<i>Ptilosphen callichroma</i> (Bigot, 1886)	DEBUA289-17	658	BOLD:AAX7275
<i>Pt. comis</i> Cresson, 1930 (Ecuador)	DEBUA310-17	658	BOLD:ACS3585
<i>Pt. comis</i> (Guyana)	MYCRO941-22	658	BOLD:AFA0486
<i>Pt. comis</i> (Peru)	MYCRO942-22	658	BOLD:AFA1407
<i>Pt. conveniens</i> (Wulp, 1897)	CROAD47638-22	653	BOLD:AEW3356
<i>Pt. crassus</i> Marshall sp. nov.	DEBUA311-17	658	BOLD:ADC6988
<i>Pt. cyaneiventris</i> (Macquart, 1846)	UGIC085-08	658	BOLD:AAX7282
<i>Pt. dellarum</i> Marshall sp. nov.	MYCRO181-15	658	BOLD:ACW1480
<i>Pt. dubius</i> Hennig, 1934	MYCRO884-21	658	BOLD:AAX7287
<i>Pt. enderleini</i> Cresson, 1930 (Ecuador)	DEBUA291-17	658	BOLD:ADG5872
<i>Pt. facetus</i> Enderlein, 1922	MYCRO943-22	658	BOLD:ADC8802
<i>Pt. fulvus</i> (Walker, 1849)	MYCRO952-22	204	(not assigned)
<i>Pt. gentilis</i> Cresson, 1930	DEBUA293-17	658	BOLD:ADG6967
<i>Pt. gentilis</i>	CRBAC15370-22	671	BOLD:AES7116
<i>Pt. insignis</i> (Wiedemann, 1830)	MYCRO885-21	658	BOLD:AEF1992
<i>Pt. manu</i> Marshall sp. nov. (Peru)	PERMS13883-24	658	BOLD:AGJ4000
<i>Pt. manu</i> Marshall sp. nov. (Peru)	PERMQ48399-24	658	BOLD:AGH1496
<i>Pt. mimicus</i> Cresson, 1930 (Bolivia)	MYCRO283-16	658	BOLD:ADC7536
<i>Pt. mimicus</i> (Colombia)	DEBUA292-17	658	BOLD:ADG4110
<i>Pt. notatus</i> Marshall sp. nov.	MYCRO946-22	128	(not assigned)
<i>Pt. rafaeli</i> Marshall sp. nov.	MYCRO955-22	658	BOLD:AFA0487
<i>Pt. ramosus</i> Marshall sp. nov.	MYCRO959-22	267	(not assigned)
<i>Pt. tetrastigma</i> (Schiner, 1868)	MYCRO956-22	658	BOLD:AFA0485
<i>Pt. xestos</i> Marshall sp. nov.	PERPT3736-23	652	BOLD:AFG0141
<i>Pt. yasuni</i> Marshall sp. nov.	MYCRO945-22	658	BOLD:AFA0488
<i>Pt. yauae</i> Marshall sp. nov.	PERMU26539-24	658	BOLD:AFN3992

Parasphen – Curran 1934a: 450; 1934b: 305. — Hennig 1934: 70, 312–313. — Aczél 1949: 335; 1951: 517. — Steyskal 1968: 10. — Schumann 1988: 115. — Marshall 2010: 809. — Ferro & de Carvalho 2014: 53.

Diagnosis

Parasphen includes just two, relatively large (length 15–18 mm), darkly pigmented species with neither dorsocentral nor frontal bristles and further characterized by a uniformly textured and pigmented frons covered with small black setulae, a short third costal sector (approximately $0.3 \times$ second costal sector), almost concolorous legs, a distiphallus terminating in a large phallic bulb, and reduction of spermathecal number from three to two.

Description

HEAD. Antenna with first flagellomere about $1.5 \times$ as long as wide, elongate oval with a dorsal depression distal to arista base; arista long-haired in basal $\frac{3}{4}$, bare distally. Postocellar bristle absent, inner vertical present, outer vertical present. Frontal vitta entirely orange, not differentiated from frontal plate; lower frons with scattered small black setulae. Frontal vitta behind ocelli broad, almost parallel-sided, depressed between slightly swollen and shiny epicephala. Ocellar triangle closer to vertex than to anterior margin of frons. One small to very small upper fronto-orbital bristle flanking vitta just anterior to level of ocelli. Palpus broad, spatulate, orange to reddish brown, parallel-sided, with scattered, uniformly short black setulae. Face and parafacial pale, dull, orange on upper half and white on lower half; subantennal depression and parafacial silvery microsetulose.

THORAX. Prosternum bare. Cervical sclerite simple, convex. Dorsocentral bristles absent, anterior and posterior notopleural bristles strong, supraalar and postalar bristles well developed; scutellum with one pair of apical bristles. Katatergite convex, slightly swollen. Scutum shiny blue-black with an indistinct pattern of silvery pruinosity. Fore tarsomeres 2–5 completely dark, tarsomere 1 mostly yellow to white but distally darkened; fore tibia dark. Mid and hind tibiae flattened and sulcate in basal half and cylindrical in distal half, basal half with a single row and distal half with a loose double row of small anterodorsal bristles. All femora uniformly pigmented, orange to dark brown. Wing almost entirely clear (*P. rufipes* (Fabricius, 1805) comb. nov.) or strongly banded (*P. amazonicus* Enderlein, 1922). Last (third) costal sector shorter than section of M between r-m and dm-cu. Anal cell long and tapered towards wing margin, entirely bare, surrounded by microtrichose areas; veins A1+CuA2 and CuA1 reaching wing margin.

ABDOMEN. Male abdomen with P1–2 dark but without an obvious pleural sac, pleuron otherwise mostly pale except along dorsal margin.

FEMALE TERMINALIA. Ventral receptacle small. Two large spermathecae on an elongate single duct arising centrally on a small, compact bursa copulatrix.

MALE TERMINALIA. S5 with genital fork large, divided into two short, thick, relatively straight arms; inner face of each arm densely packed with dense, short, stout spines. S6 small, bare, shining; epandrium short; cercus large. Basiphallus small, distinct from base of distiphallus. Distiphallus short, broad and dorsoventrally flattened, terminating in a very large and complex phallic bulb, distal distiphallus absent. Hypandrium broad and scoop-like anteriorly, with a well-developed and dorsally complete dorsal bridge connecting to anterior margin of phallic plate. Postgonite minute, inconspicuous.

Genus *Ptilosphen* Enderlein, 1922

Ptilosphen Enderlein, 1922: 166, 222 (type species: *Calobata insignis* Wiedemann, 1830 (orig. des.)).

Ptilosphen – Frey 1927: 68. — Cresson 1930: 345. — Curran 1934a: 450. — Hennig 1934: 70, 313. — Aczél 1949: 335; 1951: 517. — Steyskal 1968: 13. — Schumann 1988: 115. — Marshall 2010: 809. — Ferro & de Carvalho 2014: 53. — Martinez-Alava & Serna 2015: 343. — Marshall *et al.* 2016: 542.

Diagnosis

Relatively robust Taeniapterinae (length 11–20 mm), colour orange to black. Frons with strongly differentiated but variably coloured frontal vitta anteriorly tapered to a point at or near anterior margin of frons. Third costal sector 0.5–0.7 × second costal sector, at least as long as section of M between r-m and dm-cu. Three or (rarely) four spermathecae. Distiphallus divided into basal distiphallus, phallic bulb and distal distiphallus. Dorsocentral bristles present or (rarely) absent, frontal bristles present or (rarely) absent.

Description

HEAD. Antenna with first flagellomere oval, about 1.2 × as long as wide; arista long-haired in basal $\frac{3}{4}$, bare or almost bare distally. Postocellar bristle absent. Inner vertical present, outer vertical present (most species) or absent (two species). Fronto-orbital bristles usually in two pairs, a small lower (frontal) pair on the margin of the midpoint of the frontal vitta and a larger upper (orbital) pair at or above the level of ocelli but one or both fronto-orbitals sometimes absent. Ocellar triangle closer to vertex than to anterior margin of frons. Palpus parallel sided with rounded apex, 3–6 × as long as wide, uniformly yellow to orange or (usually) darker on basal half. Frontal vitta flat to slightly elevated in front of ocelli, oval to teardrop-shaped, usually strongly tapered anteriorly and variably tapered posterior to ocelli. Lower face usually pale; subantennal depression and parafacial silvery microsetulose.

THORAX. Prosternum bare or with sparse or dense setulae. Cervical sclerite variable, often centrally concave in female only. Postsutural dorsocentral bristles usually present as a single prescutellar pair (absent in some species). Scapular (suprahumeral) setae present or absent in one or both sexes, sometimes forming a strong cluster near anteromedial corner of postpronotum. Two notopleural bristles, anterior bristle usually relatively small (rarely absent). Supraalar and postalar bristles present. Katatergite convex but not distinctly swollen. Mid and hind femora often pale basally, hind femur, and usually mid femur, also with a median or distomedian pale ring. Mid and hind tibia weakly sulcate and often slightly flattened on basal third to half (more so on larger species), usually with sparse rows of small anterodorsal bristles. Wing clear or (usually) patterned, basal band present or absent, discal band usually prominently V-shaped or triangular but sometimes reduced to a spot or narrow band, preapical band present or absent, apex of wing usually at least weakly pigmented. Anal cell (= cell *cup*, cell *cua*) bare, not microsetulose like the rest of the wing membrane, long and tapered towards wing margin; veins A1+CuA2 and CuA1 reaching wing margin.

ABDOMEN. Pleural membrane with conspicuous black markings, often sexually dimorphic and usually including a vertical band on P2 and P3 and extensive pigmentation on at least dorsal part of P4, P5, and P6. Male pleuron often with an apparent pleural sac on P1–2 and sometimes on P4–5 (often difficult to discern on dry specimens). Middle abdominal tergites reduced or desclerotized in some species, tergal sclerotization sometimes sexually dimorphic.

FEMALE TERMINALIA. Bursa copulatrix small, often with an elongate apical extension or common spermathecal duct apparently continuous with primary spermathecal duct; secondary duct usually arising laterally at or near base of primary duct; ventral receptacle very small or (usually) apparently absent. Three or (rarely) four spermathecae on two ducts, primary duct usually larger than secondary (single) duct (smaller in two species, equal in one) and ending in two spermathecae usually on distinctively developed stems often separated from the corresponding duct by extremely narrow, threadlike

constrictions. Secondary or single duct normally leading to a single spermatheca without a distinct broad stem; single spermatheca usually much smaller than the primary or paired spermathecae but sometimes equal, rarely larger and different in form. Form of ducts and spermathecal dimensions variable between species.

MALE TERMINALIA. S5 with a prominent genital fork on a large base, arms usually finger-like but sometimes broad and scoop-like or elaborated with additional long or short processes. S6 large, plate-like. Epandrium small, narrow and somewhat compressed. Cercus setose, simple and relatively prominent. Hypandrium with a band-like to broad and scoop-like anterior loop and a dorsally incomplete dorsal bridge, posterior arms of hypandrium bent dorsally at apex of anteroventral epandrial extension and extending to or almost to phallopodeme and anterolateral margin of phallic plate (thus forming a phallic guide); subepandrial sclerite often with sclerotized margins (=bacilliform sclerites); phallic plate well developed, usually striate. Postgonite small but distinct, usually broadly rounded, posteriorly spinulose and apically with a few anterior setulae. Basiphallus usually dome-like and shiny, often projecting conspicuously beyond base of distiphallus but sometimes barely differentiated from basal distiphallus. Basal distiphallus relatively broad and short, separated from a narrower distal distiphallus by a simple bipartite phallic bulb; phallic bulb usually comprising two overlapping chambers including a proximal chamber (a terminal swelling of the ejaculatory duct in the basal distiphallus) and a more heavily sclerotized and generally much smaller distal chamber usually continuous with the base of the distal distiphallus (Fig. 6K); distal distiphallus long or short, with or without a terminal swelling or expanded (funnel-like) apex. Ejaculatory apodeme smaller than epandrium, sperm pump robust with large lateral lobes or apodemes.

Key to the species of *Ptilosphen* Enderlein, 1922 and *Parasphen* Enderlein, 1922

1. Frontal vitta and frontal plate not differentiated from one another, similar in orange colour and texture; lower frons covered with small black setae (Fig. 1E). Notum dark brown with blue metallic highlights. Third (last) costal sector (between R_{2+3} and R_{4+5}) conspicuously short, one third or less than length of second costal sector. Distiphallus broad and short, terminating in a large phallic bulb (Fig. 1D). Two spermathecae 2 *Parasphen* Enderlein, 1922
 - Frontal vitta duller than frontal plate and usually different in color, lower frons not covered with small black bristles; if frons uniformly orange then notum similar in color (Fig. 4G), without blue highlights. Third costal sector longer than one third length of second costal sector. Distiphallus elongate, distal and basal portions separated by a small and simple phallic bulb with two distinct chambers (Fig. 6K). Three or (rarely) four spermathecae 3 *Ptilosphen* Enderlein, 1922
2. Mid and hind femora brown to black, terminalia dark. Wing with a dark, clearly delimited discal band. Arms of genital fork slender and incurved (Fig. 1C). Ejaculatory apodeme smaller than epandrium. Spermathecae spherical (Fig. 1G) *Parasphen amazonicus* Enderlein, 1922 (Brazil, Colombia, Ecuador, Peru)
 - Mid femur, hind femur and terminalia reddish brown to orange. Wing with a diffuse discal band, barely distinguishable from surrounding membrane. Arms of genital fork thick, short and divergent (Fig. 2C). Ejaculatory apodeme larger than epandrium. Spermathecae elongate and goblet-like (Fig. 2A) *Parasphen rufipes* (Fabricius, 1805) comb. nov. (Brazil, French Guiana, Guyana)
3. Mesothorax reddish brown to orange 4
 - Mesothorax blue-black or very dark brown 13
4. Mid and hind femora uniformly orange or with weak to indistinguishable white rings (Fig. 15) and abdominal pleuron white, without bands. Frontal vitta uniformly orange, not extending to anterior margin of frons. Anterior and posterior notopleural bristles subequal in length (anterior bristle thinner). Length greater than 15 mm *Ptilosphen fulvus* (Walker, 1849) (Brazil, French Guiana), male unknown

- Hind and mid femora variable in colour, usually with one or more distinct white rings (exceptions have a prominently banded abdominal pleuron). Frontal vitta variable in colour but usually brown or black and tapered to anterior margin of frons. Anterior notopleural bristle smaller, usually less than half as long as posterior bristle (rarely absent). Length variable..... 5
5. Dorsocentral, anterior notopleural and outer vertical bristles absent. Discal and pre-apical wing bands narrow and distinct (Fig. 10A). Female with dense group of scapular (suprahumeral) bristles and a large, distinctly bilobed cervical sclerite; male with weak scapular setae and an indistinctly bilobed cervical sclerite. Female abdominal P3–5 black on dorsal half and P2 entirely black, pleuron thus without vertical bands posterior to P2; male abdomen with a narrow vertical band on P3. Mid and hind femora black with white bands..... *Ptilosphen dellarum* Marshall sp. nov. (Costa Rica)
- Prescutellar dorsocentral, anterior notopleural and outer vertical bristles present. Wing with apex infusate but without a distinct pre-apical wing band (Fig. 5D), discal band variable. Scapular setae absent and cervical sclerite not bilobed. P3 with a distinct vertical black band in both sexes. Mid and hind femora orange to brown, with white bands 6
6. Fore tarsus with at least 4th and 5th tarsomeres black or dark brown (Fig. 4F); mid and hind femora with well-defined white rings, often margined by a darker area. Wing with discal band triangular, linear, dot-like or subquadrate, not forming a deep V (Figs 5B, 9A). Postocellar frontal vitta tapered to a point or very narrow apex. Oviscape mostly orange, pruinose laterally, without a distinct preapical black band 7 (Central and South America)
- Fore tarsus completely white or very pale brown (tarsomeres 4 and 5 sometimes with dark setulae) (Figs 11A, E, 18D); white rings on mid and hind femora variable, sometimes incomplete or weakly defined. Wing with discal band usually forming a deep V (Fig 11A), often weakly developed, rarely subquadrate. Postocellar frontal vitta broad, with a rounded apex. Oviscape variable in colour, usually silvery microsetulose laterally and often with a distinct, broad preapical black band..... 8 (South America)
7. Wing with discal band dot-like or subquadrate (height and length approximately equal) with a thin anterodistal branch arising at right angle (Fig. 9A). Abdominal P3 with black area broadly fused with dark part of P4 dorsally (Fig. 9G). Female with paired (primary) spermathecal duct slightly narrower than spermathecae. Tarsomere three of foreleg all or mostly white; first tarsomere of hind leg mostly brown, sometimes white basally. Basal white band of hind femur usually less than 2 × as long as wide..... *Ptilosphen cyaneiventris* (Macquart, 1846) (Colombia, Panama, Venezuela)
- Wing with discal band transverse, evenly tapered anteriorly or thin and triangular; without an anterodistal branch (Fig. 5B, D). Abdominal P3 with black area almost entirely separate from pigmented area of P2 (Fig. 5E). Female with paired (primary) spermathecal duct very broad, much broader than spermathecae (Fig. 5G). Tarsomere three of foreleg mostly black, first tarsomere of hind leg entirely or almost entirely pale. Basal white band of hind femur usually more than 3 × as long as wide..... *Ptilosphen callichroma* (Bigot, 1886) (Belize, Costa Rica, Guatemala, Mexico)
8. Frontal vitta broken into two dark areas separated by broad orange band crossing ocelli (Fig. 21B). Black bands of abdominal P2 and P3 tapered ventrally with posterior margin straight and vertical (Fig. 21A, F). Male genital fork with a U-shaped basal cleft. Paired (primary) spermathecae goblet-shaped, stems short and densely studded with narrow tubercles. Oviscape orange except at apex..... *Ptilosphen notatus* Marshall sp. nov. (Brazil, French Guiana)
- Frontal vitta not conspicuously divided by an orange band across the ocelli. Black band of abdominal P2 usually angled posteriorly (Fig. 18C), sometimes covering entire pleuron. Basal cleft of male genital fork either linear (Fig. 18G) or deeply V-shaped (Fig. 11B). Spermathecal stems elongate and sometimes sinuate, not studded with tubercles. Oviscape dark at least dorsally 9

9. Distal distiphallus much longer than basal distiphallus (Fig. 27F). Pronotum entirely orange and male genital fork with slender, strongly incurved arms. Spermathecae of known females elongate oval, not expanded distally, paired spermathecae with simple stems (Fig. 27H). Males with a well-developed pleural sac on P2. Wing with a small, subquadrate discal band mostly confined to between R_{4+5} and M (Fig. 27B), often indistinct. Mid femur either uniformly orange, or orange to brown with an indistinct median pale ring 10
- Distal distiphallus much shorter than basal distiphallus (Fig. 11D). If pronotum entirely orange, then male genital fork with arms almost parallel, not incurved. Paired (primary) spermathecae goblet-shaped or oval, stems elongate with conspicuously swollen basal half and sinuate distal half (Figs 11F, 18F). Males without a distinct pleural sac on P2. Discal band usually V-shaped or almost completely crossing wing (Fig. 11A) but sometimes greatly reduced. Mid femur with a distinct but sometimes incomplete median pale ring, usually margined by dark seams 12
10. Mid and hind femora with pale medial and basal bands, sometimes indistinct. Anterior (preocellar) frontal vitta uniformly pruinose. Epandrium all or mostly dark brown. Abdominal P3 mostly pale, dark only along posterior margin in male, dark only dorsally in female (Fig. 27A, G) 11
- Mid and hind femora uniformly pigmented beyond base. Anterior frontal vitta with a central pruinose band. Epandrium orange. Anterior half of abdominal P3 black, forming part of a dark band encircling the abdomen (Fig. 29B) *Ptilosphen zonalis* Marshall sp. nov. (Brazil), female unknown
11. Mid and hind legs reddish brown, with relatively indistinct yellow bands basally and centrally. Wing with discal band extending from R_{4+5} to CuA_1 . Epandrium all or mostly dark brown. Male genital fork without elevated basomedial processes (basal lobe). Female with paired spermathecae on elongate relatively smooth stems, single spermatheca with a very long string-like base longer than spermatheca (Fig. 27)
 *Ptilosphen yasuni* Marshall sp. nov. (Ecuador, Colombia, Peru, Venezuela)
- Mid and hind legs brown, with distinct white bands subbasally and centrally, and with a black basal mark. Wing with discal band greatly reduced to a spot over M_1 . Epandrium dark brown except for a pale dorsal strip. Male genital fork with elevated basomedial processes longer than wide. Female with elongate and conspicuously bumpy paired spermathecae, single spermatheca with a short string-like base (Fig. 28) *Ptilosphen yauae* Marshall sp. nov. (Peru)
12. Prothorax and cervical sclerite black to dark brown, female cervical sclerite black with swollen posteroventral angle. Oviscape mostly black, white pruinose laterally in anterior $\frac{3}{4}$, otherwise bare, apex orange. Male genital fork with a deep V-shaped cleft at base, arms strongly incurved distally, base with a quadrate pale area medially (Fig. 11B). Abdomen of female with first pleural band much broader than second band *Ptilosphen dubius* Hennig, 1934 (Bolivia, Peru)
- Cervical sclerite orange and prothorax all or mostly orange, posterior part of cervical sclerite only slightly elevated. Oviscape orange laterally on basal half, with a dark preapical ring. Male genital fork with a narrow, linear cleft at base, arms thick and almost straight (Fig. 18G). Abdomen of female with first pleural band narrowly tapered ventrally, similar in width to second band
 *Ptilosphen insignis* (Wiedemann, 1830) (Bolivia, Brazil, Colombia, French Guiana, Guyana, Trinidad & Tobago)
13. Wing pigmentation broken into two small, staggered discal patches and two preapical spots (Fig. 24F). Females with a row of at least five strong scapular setae. Female T3–4 sclerotized but pale yellow, contrasting with adjacent dark upper pleurae (Fig. 24A)
 *Ptilosphen tetrastigma* (Schiner, 1868) (Brazil, Colombia, Peru, Venezuela)
- Wing with an undivided discal band; preapical band variable. Scapular setae usually absent in both sexes where known, at most represented by 2–4 small setae. If female T3–4 pale, then desclerotized and adjacent pleurae also pale (females unknown for *Pt. elongatus* Marshall sp. nov.) 14

14. Outer vertical and dorsocentral bristles absent 15
 – Outer vertical present, dorsocentral bristles present or absent 16
15. Notopleuron with two bristles. Wing with strong transverse basal and preapical bands and a triangular discal band (Fig. 7B). Mid and hind femora with a pale band at or before mid point. Female abdomen with T3–4 membranous, forming a pale area continuous with extensive pale area on pleuron (Fig. 7B)..... *Ptilosphen conveniens* (Wulp, 1897) (Costa Rica, Panama)
 – Notopleuron with only a posterior bristle. Wing with a broad, parallel-sided discal band and a preapical band barely distinguishable from apical infuscation; basal band present but indistinct (Fig. 12D). Mid and hind femora with a pale band in distal third, far beyond mid point
 *Ptilosphen elongatus* Marshall sp. nov. (Costa Rica), female unknown
16. Dorsocentral bristle absent or greatly reduced and wing evenly infuscate, without discal band or other distinct dark areas (Fig. 26G) *Ptilosphen xestos* Marshall sp. nov. (Peru)
 – Dorsocentral bristles usually present, but if absent then with distinct wing banding..... 17
17. Wing with a discal band or spot (sometimes indistinct) and usually a dark apex, preapical band absent. Fore tarsus entirely pale (tarsomeres 1–3 white, tarsomeres 4 and 5 white to yellowish brown or with a few dark bristles); mid femur either without a white band or with a band near middle (not in apical third)..... 18
 – Wing with a preapical band between discal band and apical infuscation (Fig. 20D). At least distal two tarsomeres of foreleg black or brown. Mid femur with a white band in apical third 24
18. Fore coxa bright orange and fore femur black with a narrowly orange base. Palpus and clypeus entirely yellow (Fig. 22C)..... *Ptilosphen rafaeli* Marshall sp. nov. (Brazil), male unknown
 – Fore coxa yellow or (usually) brown to black with heavy silver pruinosity. Fore femur either entirely black or at least basal third orange or yellow-orange. Palpus or clypeus at least partially black to brown 19
19. Fore femur distinctly bicolored, basal one third to one half yellow to tawny, distal half brown to black. Mid and hind femora black between well-developed basal and median white bands, brown distal to median white band (Fig. 13A). Wing mostly smoky, with an isolated, sometimes indistinct, discal spot or cloud in cell r_{4+5} about midway between crossveins, sometimes with a weak extension reaching R_{2+3} 20 *Ptilosphen enderleini* species complex
 – Fore femur uniformly colored. Distal and proximal halves of hind and mid femora similarly pigmented (median band often absent on mid femur) (Fig. 8H). Wing with a distinct triangular (Fig. 6B) or V-shaped (Fig. 23C) discal band..... 22
20. Fore coxa and basal third of fore femur yellowish, similar in colour (Fig. 25E). Katepisternum partially reddish brown. Single spermathecal duct arising near base of swollen basal third of paired duct; paired spermathecal stems long with a large multituberculate swelling at midpoint, separated from spermatheca by a constriction (Fig. 25A)
 *Ptilosphen xanthicoxa* Marshall sp. nov. (Brazil, Colombia)
 – Fore coxa much darker than the orange basal third to half of fore femur. Katepisternum uniformly dark. Single spermathecal duct either arising near apex of broad common duct or at the very base of a slightly swollen and mostly parallel-sided paired duct. Stem of paired duct entirely thickened, without isolated swollen part at midpoint (Fig. 13B) 21
21. Wing with a weak, indistinct, discal band reaching R_{2+3} . Abdominal P3 dark, continuous with dark P2. Male with basal distiphallus distinctly shorter than distal distiphallus. Female with paired and single spermathecal ducts arising independently from bursa; paired duct slightly swollen, much broader than single duct and parallel sided until tapered in distal fifth (Fig. 19B)..... *Ptilosphen manu* Marshall sp. nov. (Brazil, Colombia, Peru)

- Wing mostly smoky, with an isolated, sometimes indistinct, discal spot or cloud in cell r4+5. Abdominal P3 mostly pale. Male with basal distiphallus distinctly longer than distal distiphallus. Female with paired and single spermathecal ducts arising from apex of a bulbous common duct about half as long as paired duct; paired and single ducts similar in diameter beyond apex of basal swollen part or common duct (Fig. 13B) ... *Ptilosphen enderleini* Cresson, 1930 (Peru, Colombia, Ecuador)

- 22. Discal wing band broadly triangular (Fig. 6B). Frontal plate, and usually frontal vitta, red or reddish; frontal vitta less than half of frontal width at maximum (Fig. 6A). Distal distiphallus twice as long as basal distiphallus (Fig. 6F). Abdominal pleuron of males, but not females, with a complete vertical band on P3 *Ptilosphen comis* Cresson, 1930 (Bolivia, Brazil, Colombia, Ecuador, French Guyana, Guyana, Peru, Venezuela)
- Discal wing band narrow, in a broad U or V shape (Fig. 8A). Frons all or mostly black to dark brown, maximum width of frontal vitta at least $\frac{3}{4}$ of frontal width (Fig. 23E). Distal distiphallus shorter than basal distiphallus (Fig. 23H). Abdominal pleuron of both sexes with a complete vertical band on posterior half of P3 (Fig. 23F) 23

- 23. Mid femur brown with a broad and distinct white band near midpoint. Wing with discal band weak, especially at apices; area surrounding apex of anal cell clear. Male genital fork very long, distally branched into a short, blunt basal lobe and a long, curved distal lobe (Fig. 23A) *Ptilosphen ramosus* Marshall sp. nov. (Colombia)
- Mid femur usually uniformly dark brown or black except for extreme base, sometimes with an indistinct or incomplete medial band. Wing with discal band of uniform width and uniformly pigmented to anterior wing margin; apex of anal cell in a small pigmented spot. Genital fork with two very short and broad arms with inner surface flat and entirely covered with short spines, without inner basal lobes (Fig. 8C)..... *Ptilosphen crassus* Marshall sp. nov. (Colombia, Ecuador, Peru)

- 24. Tarsomeres 2–5 of foreleg dark brown. Wing with two dark bands (basal band absent or reduced to indistinct spot, discal band v-shaped or parallel-sided, preapical band linear). Frontal vitta black. Female with secondary spermathecae small and paired, primary spermathecae larger and fused into a bilobed structure (Figs 17F, 20C) 25
- Tarsomere 2 of foreleg all or mostly white. Wing with three dark bands (basal band crossing most of wing, discal band solid triangular, preapical band linear). Frontal vitta at least partly orange. Female with secondary spermatheca single and much smaller than paired (primary) spermathecae (Fig. 14I) 26

- 25. Prescutellar dorsocentral bristle present. Wing with large and elongate discal band extending into basal quarter of wing (Fig. 17D). Female with abdominal T3 and adjacent pleuron white, desclerotized *Ptilosphen inconveniens* Marshall sp. nov. (Colombia), male unknown
- Dorsocentral bristles absent. Wing with discal band short, not extending into basal quarter of wing (Fig. 20D). Female with T3 unmodified and adjacent pleuron with a prominent vertical black band..... *Ptilosphen mimicus* Cresson, 1930 (Bolivia, Colombia, Ecuador, Peru)

- 26. Tarsomere three of foreleg all or mostly white. Genital fork of male with a prominent inner process on each arm, thus with four arms (Fig. 16I). Distiphallus and main spermathecal duct greatly elongated (Fig. 16C–D)..... 27
- Entire third tarsomere of foreleg brown. Genital fork with only two arms (Fig. 14D). Distal distiphallus shorter than epandrium (Fig. 14C), spermathecal ducts not strikingly elongate (Fig. 14I)..... *Ptilosphen facetus* Enderlein, 1922 (Colombia, Ecuador)

27. Preapical wing band almost straight, central part not shifted basally (Fig. 16J). Distal two tarsomeres of foreleg black to dark brown. Genital fork with inner arm short, less than $3\times$ as long as wide and less than half as long as outer arm *Ptilosphen gentilis* Cresson, 1930 (Costa Rica, Nicaragua)
- Preapical wing band staggered, central part shifted basally (Fig. 3D). Distal two tarsomeres of foreleg pale brown. Genital fork with inner arm long, more than $4\times$ as long as wide and more than half as long as outer arm *Ptilosphen boroboro* Marshall sp. nov. (Colombia)

Species accounts

The species descriptions below begin with the two species of *Parasphen*, followed by the species of *Ptilosphen* in alphabetical order.

***Parasphen amazonicus* Enderlein, 1922**

Fig. 1

Parasphen amazonicus Enderlein, 1922: 226.

Parasphen amazonicus – Hennig 1934: 313. — Aczél 1949: 335. — Steyskal 1968: 10. — Schumann 1988: 86. — Ferro & de Carvalho 2014: 57.

Type material

Holotype

BRAZIL • ♀; Upper Amazon region; MNBG.

Other material examined

BRAZIL • 2 ♀♀; Amazon; H.W. Bates leg.; NHMUK (a third specimen apparently from the same series but with neither abdomen nor collector label has a handwritten label “*Parasphen amazonicus* Enderlein”).

COLOMBIA • 1 ♀; Putumayo, Orito, Reserva Natural La Isla Escondida; 0.65547° N, 77.07302° W; 850 m a.s.l.; 18 Aug. 2024; Pollet and De Braekeleer leg.; sweep net; IAVH, Life on Trees: LOT00-40018/S72.

ECUADOR • 2 ♀♀, 1 ♂; Prov. Napo, Jatun Sacha Res., 6 km E of Misahualli; 1°4' S, 77°37' W; 450 m a.s.l.; 30 Apr.–8 May 2002; S.A. Marshall leg.; varzea; DEBU (terminalia of male missing) • 1 ♀; Napo, Tiputini Biodiversity Station; May 2011; S.A. Marshall leg.; DEBU • 1 ♂; Napo, Tiputini Biodiversity Station, lot 2077, transect 8; 216 m a.s.l.; T. Erwin *et al.* leg.; insecticidal fogging of mostly green leaves, some with bryophytes or moss; USNM.

PERU • 1 ♀; Prov. Loreto, Campamento San Jacinto; 175–215 m a.s.l.; Jun. 1993; R. Leschen leg.; DEBU • 1 ♀; Cuzco, Villa Carmen Field Station; 22–24 May 2011; Bennett and Razuri leg.; yellow pan traps; USNM.

Redescription (see generic description for head and thorax chaetotaxy)

LENGTH. 17–18 mm.

COLOUR (Fig. 1A–B, E–F). Head almost entirely orange, epicephalon slightly darkened. Notum black to dark brown with metallic blue highlights; with a very narrow central strip flanked by narrow silver vittae and a transverse silver pruinose strip along suture. Legs, abdominal tergites and terminalia mostly dark brown to black, tarsomere one of foreleg white except at apex. Wing with an elongate-triangular basal band, a thick dark discal band, and lightly infuscated tip.

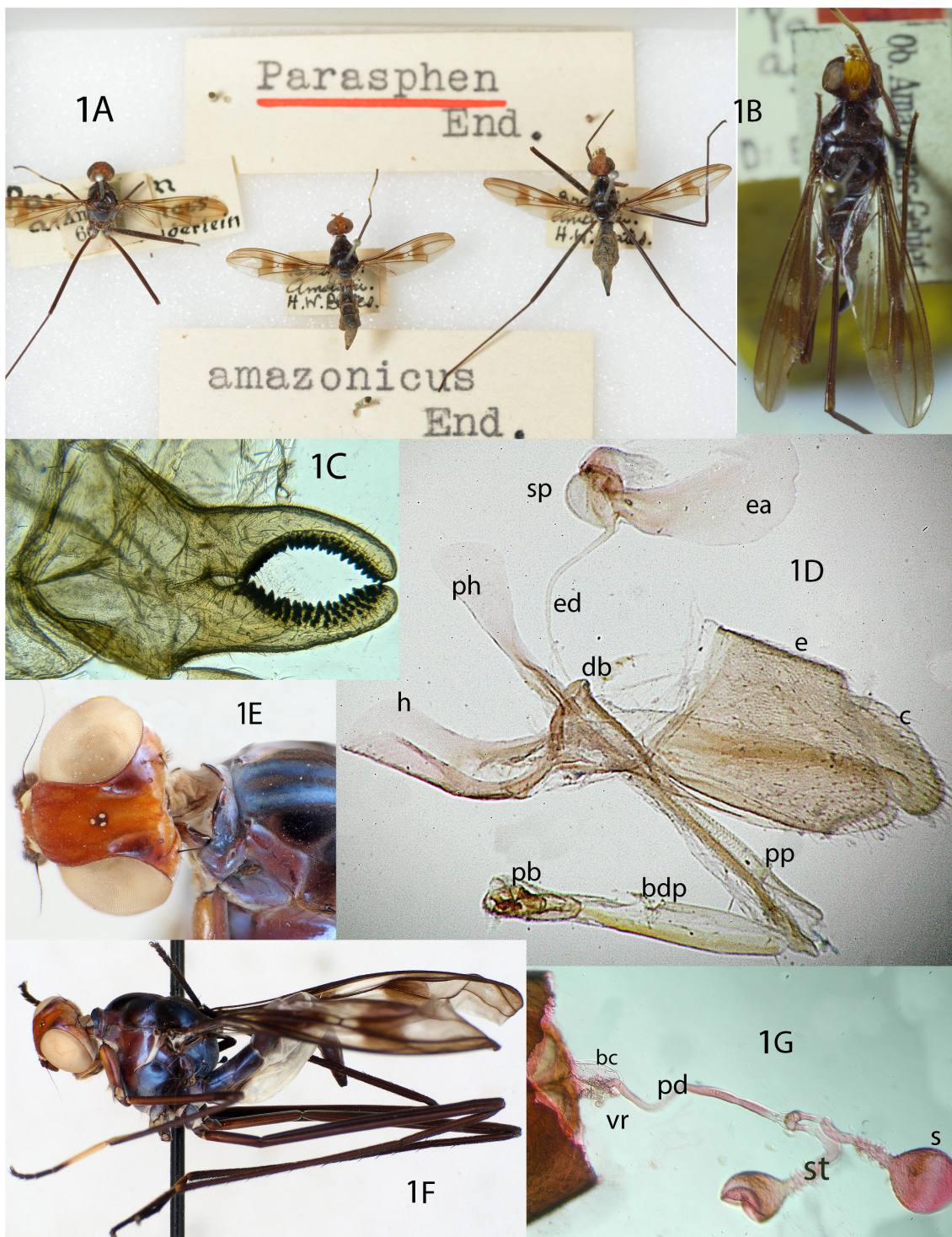


Fig. 1. *Parasphen amazonicus* Enderlein, 1922. **A.** ♀♀, specimens collected by Henry Walter Bates and a specimen of unknown sex (NHMUK). **B.** Holotype (MNBG). **C.** ♂, sternite 5 (genital fork), Ecuador (DEBU). **D.** ♂, terminalia, left lateral view (DEBU). **E.** ♀, head and anterior thorax, Ecuador (DEBU). **F.** ♀, lateral view, Ecuador (DEBU). **G.** Spermathecae and associated structures, Ecuador (DEBU). Abbreviations: bc=bursa copulatrix; bdp=basal distiphallus; c=cercus; db=dorsal bridge; e=epandrium; ea=ejaculatory apodeme; ed=ejaculatory duct; h=hypandrium; pb=phallic bulb; pd=paired spermathecal duct; ph=phallapodeme; pp=phallic plate; s=spermatheca; st=spermathecal stem; vr=ventral receptacle.

FEMALE TERMINALIA (Fig. 1G). Ventral receptacle very small, basally constricted and distally bulbous. Two spherical spermathecae on a single duct, with elongate stems studded with conspicuous tubercles on distal half. Spermathecal duct of uniform width, slightly narrower than stems and only slightly longer than stem + spermathecae.

MALE TERMINALIA (Fig. 1C–D). Genital fork with two short, thick, relatively straight arms; inner face of each arm with about 30 short, stout spines covering distal ¾ of arm but absent in V-shaped base of fork between arms. Distiphallus broad and relatively short, terminating in an elongate phallic bulb. Hypandrium with a scoop-like anterior bridge and a narrow dorsal bridge continuous with a broad, transverse striate phallic plate. Ejaculatory apodeme about half the size of the hypandrium, sperm pump robust.

Remarks

This Amazonian species is distinguished from its only congener, *Pa. rufipes* comb. nov., by its dark legs and terminalia, distinctly banded wings, and the male and female genitalia (short genital fork, spherical spermathecae). Curran described a variety “*ruficauda*” for specimens from Guyana that he thought fit the description of *Pa. amazonicus* except for their reddish terminalia, but the distribution, habitus and the reddish terminalia of the specimens he examined were typical of *Pa. rufipes* Fabricius. *Parasphen amazonicus ruficauda* Curran, 1932 is therefore here treated as a junior synonym of *Pa. rufipes* and considered further under that species.

Parasphen rufipes (Fabricius, 1805) comb. nov.

Fig. 2

Calobata rufipes Fabricius, 1805: 261.

Parasphen frontalis Cresson, 1930: 336.

Parasphen amazonicus var. *ruficauda* Curran, 1932: 2. **Syn. nov.**

Parasphen ruficauda Curran, 1934b: 302 (wing figure caption only).

Calobata rufipes – Wiedemann 1830: 537. — Hennig 1934: 313. — Steyskal 1968 (as unplaced Taeniapterinae).

Systellapha rufipes – Enderlein 1922: 189.

Parasphen frontalis – Hennig 1934: 313 (tentatively synonymized with *Calobata rufipes*). — Aczél 1949: 335. — Steyskal 1968: 10. — Roback 1969: 538.

Parasphen amazonicus var. *ruficauda* – Curran 1934a: 295, 454.

Type material

Holotype of *Parasphen rufipes*

BRAZIL? • ♀; “America merid.”; ZMUC.

Holotype of *Parasphen frontalis*

GUYANA (as BRITISH GUIANA) • ♀; Kartabo, Bartica District; 11 Mar. 1922; AMNH (not examined).

Paratypes of *Parasphen frontalis*

GUYANA (as BRITISH GUIANA) • 1 ♀; Parish; USNM • 1 ♀; Kamakusa, H. Long (Bequaert); USNM.

Holotype (♂) and 2 paratypes (♀♂) of *Parasphen amazonicus* var. *ruficauda*

GUYANA (as BRITISH GUIANA) • 1 ♀, 2 ♂♂; Kartabo; 26–27 Mar. and 28 May 1924; AMNH.

Other material examined

BRAZIL • 1 ♂; Prov. Benevides, Para; 1918; S.M. Klages leg.; CMNH • 1 specimen without abdomen; Para; H.W. Bates leg.; NHMUK.

FRENCH GUIANA • 2 ♀♀; Prov. Mana River; May 1917; CMNH • 1 ♀; Prov. Barticon; 1961; USNM.

GUYANA (as BRITISH GUIANA) • 5 specimens, one labelled as “examined by Hennig 1937”; NHMUK • 2 ♀♀; Kartabo, Bartica District; A.L. Melander collection; USNM (one badly damaged with one leg and one wing).

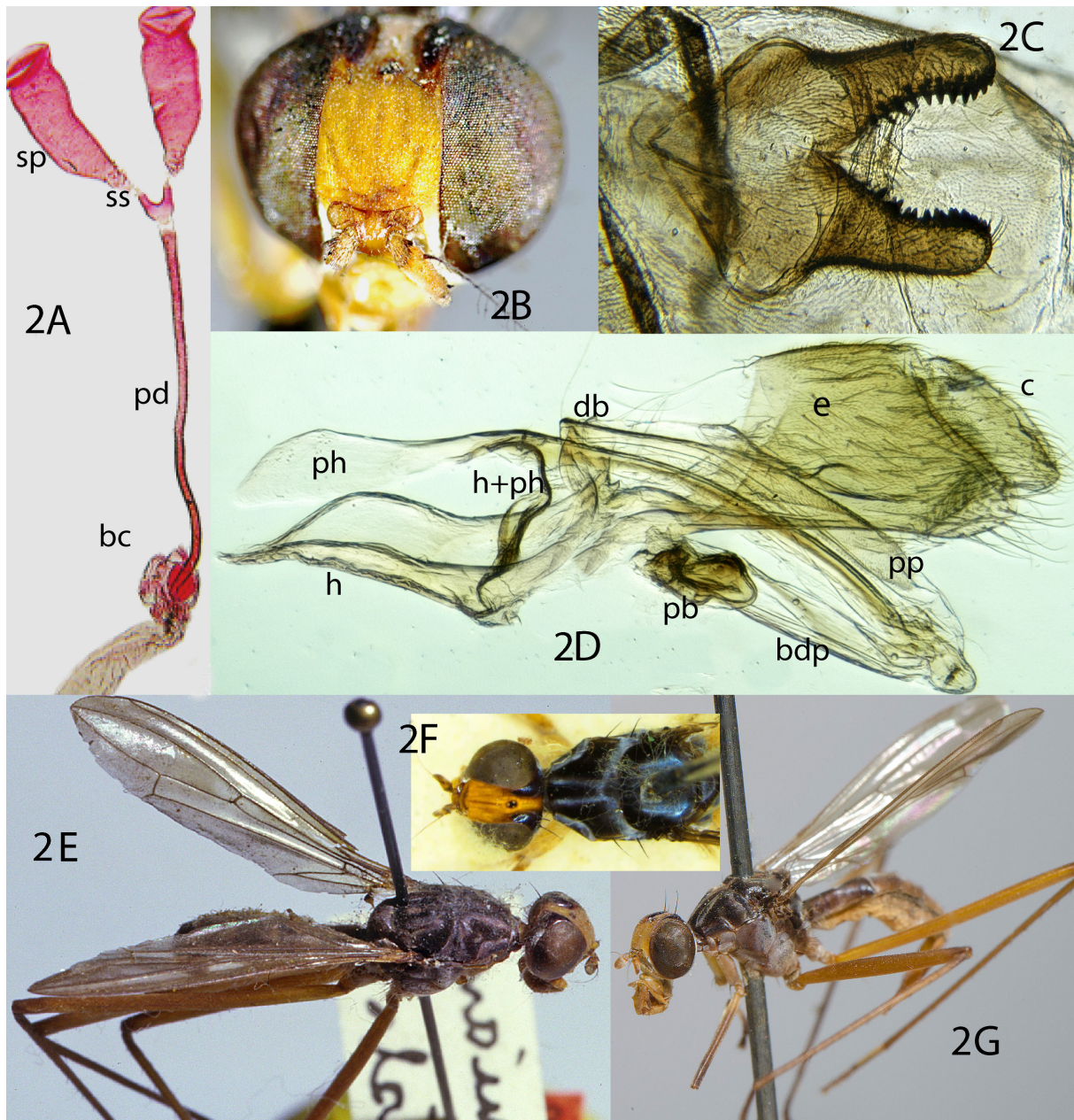


Fig. 2. *Parasphen rufipes* (Fabricius, 1805) comb. nov. **A.** Spermathecae and associated structures, French Guiana (CMNH). **B.** ♂, head, French Guiana (CMNH). **C.** ♂, sternite 5 (genital fork), French Guiana (CMNH). **D.** ♂, terminalia, left lateral view, French Guiana (CMNH). **E.** Paratype of *Pa. frontalis* (USNM). **F.** ♀, head and thorax, dorsal view, Brazil (NHMUK). **G.** Holotype of *Pa. rufipes* (ZMUC). Abbreviations: bc = bursa copulatrix; bdp = basal distiphallus; c = cercus; db = dorsal bridge; e = epandrium; h = hypandrium; h+ph = linkage between hypandrium and phallapodeme; pb = phallic bulb; pd = paired spermathecal duct; ph = phallapodeme; pp = phallic plate; sp = spermatheca; ss = spermathecal stem.

Redescription (see generic description for head and thorax chaetotaxy)

LENGTH. 15–16 mm.

COLOUR (Fig. 2B, E–G). Epicephalon and paracephalon shining brown to shining blue-black, contrasting sharply with orange frontal vitta. Notum dark with distinct metallic blue highlights around postpronotal lobe and forming a pair of narrow vittae flanking a central dark strip; pleuron reddish at least on ventral half. Legs, including at least basal half of fore femur and all of mid and hind femora, orange to reddish brown. Wing without distinct bands, entire wing transparent with a very faint discal band. Male terminalia, abdominal tergites posterior to T2 and female oviscape orange.

FEMALE TERMINALIA (Fig. 2A). Bursa copulatrix small, ventral receptacle not visible. Two very large, elongate spermathecae, with an expanded and round-rimmed apex and tuberculate basal portion, stems thin and short connecting to a sclerotized U-shaped base. Duct long and simple.

MALE TERMINALIA (Fig. 2C–D). Genital fork with two short, thick, relatively straight arms; inner face of each arm flat and densely packed with about 70 short black spines, spinose area extending to base of arm; base of fork between arms with narrow cleft. Phallus subequal in length to epandrium, terminating in a very large phallic bulb; basal distiphallus with ventral sclerotization Y-shaped, phallic bulb between the arms of the Y. Hypandrium with a broad, ribbon-like sclerotized process connecting the posteromedial margin of the anterior hypandrium with the phallapodeme just anterior to the dorsal hypandrial bridge; anterior hypandrium broad and scoop-like. Phallic plate continuous with dorsal hypandrial bridge, broad, and densely transverse-striate. Ejaculatory apodeme large, similar in size to epandrium; sperm pump about $\frac{1}{3}$ size of apodeme.

Remarks

Curran (1932) described two males and one female from Kartabo District, Guyana, as a new variety of *Pa. amazonicus*, stating that they agree with the description of *Pa. amazonicus* except that “the apex of the abdomen and the genitalia of the male are reddish and the ovipositor of the female is reddish yellow”. But those same characters are diagnostic for *Pa. frontalis* (a junior synonym of *Pa. rufipes* comb. nov.), which Cresson described two years earlier from the same locality (Kartabo District). Photographs of the type specimens of *Parasphen amazonicus* var. *ruficauda* (provided by David Grimaldi, AMNH) show all of the external diagnostic features of *Pa. rufipes* (wing with a diffuse discal band, femora and terminalia reddish brown to orange, epicephalon and paracephalon contrasting sharply in colour with upper frontal vitta). *Parasphen amazonicus* var. *ruficauda* is therefore here recognized as a synonym of *Pa. rufipes*.

The terminalia of the only male specimen of *Pa. rufipes* available for dissection has a broad, ribbon-like sclerotized median process connecting the posteromedial margin of the anterior hypandrium with the phallapodeme, just anterior to the dorsal hypandrial bridge (Fig. 2D, h+ph). This structure is probably homologous with the phallic guide of some other nerioids, including other micropezid subfamilies (McAlpine 1998) and some *Ptilosphen*, but more material is needed to confirm this.

Ptilosphen boroboro Marshall sp. nov.

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Fig. 3

Etymology

This species name is a noun in apposition derived from the type locality.

Type material

Holotype

COLOMBIA • ♂; Prov. Choco, Utria Natl. Pk., Boroboro; 6°1'9" N, 77°20'55" W; 10 m a.s.l.; 19–27 Jul. 2000; J. Pérez leg.; IAVH,debu00402411.

Paratypes

COLOMBIA • 1 ♀; Prov. Choco, Utria National Park; 6°1'9" N, 77°20'55" W; 20 m a.s.l.; 7–28 Sep. 2000; J. Pérez leg.; IAVH • 1 ♀; same data as for preceding; DEBU • 1 ♂; Choco, Parque Nacionales Naturales Utria Cocalito; 26 Dec. 2000–1 Feb. 2001; J. Perez leg.; IAVH • 1 ♀; same data as for preceding; 30 Jul.–16 Aug. 2000; IAVH • 1 ♀; same data as for preceding; 50 m a.s.l.; 5–19 Jul. 2000; Malaise trap; IAVH • 1 ♀; same data as for preceding; 0–10 m a.s.l.; IAVH • 2 ♀♀, 4 ♂♂; Prov. Valle del Cauca, Farallones de Cali Alto, Anchicaya; 3°26' N, 76°48' W; 730 m a.s.l.; Jan.–Sep. 2000; S. Sarria leg.; Malaise traps; IAVH • 3 ♀♀, 3 ♂♂; same data as preceding; sequence MYCRO958-22; DEBU • 1 ♀; Aljibes, Providencia, cf. 33 km SW of Zaragoza, Antioquia; 22 Dec. 1970; “Bench B”; USNM.

Description

LENGTH. 14–15 mm.

COLOUR (Fig. 3A, C–E, G–H). Dark shiny blue-black to brown except as follows: frontal vitta dull orange, darkened towards anterior margin and well defined; frontal plate dull reddish brown; ocellar triangle, epicephalon and paracephalon dark reddish brown, shiny except for a microtrichose area between inner vertical bristles and on postociput. Palpus yellow in apical third, otherwise brown; scape, first flagellomere, lunule and face orange; subantennal depression brown; clypeus black and entirely setulose. Notum mostly silvery pruinose with an incomplete central brown vitta and blue highlights dorsally, black laterally. Fore tarsomeres 1–3 white, distal two tarsomeres pale brown; foreleg otherwise dark brown. Mid tarsus and tibia brown; mid and hind femora brown with white rings at distal third; mid femur with a white base 1–3 × width of femur, hind femur with white ring 2–4 × width of femur; hind tibia and tarsus brown. Wing with a broadly triangular complete discal band, a narrow and staggered preapical band, and an infuscated apex. Abdominal tergites dark brown with patterns of silvery pruinosity as follows: female with T1–2 silvery except for a bare triangle with truncate points touching the middle of the hind margin and the middle of the side margins of the syntergite, T3 and T4 silvery along anterior margins, T5 silvery on anterior and posterior margins, T6 entirely silvery, oviscapae brown, mostly silvery pruinose except for a narrow bare dorsal strip and a bare, shiny apical fifth; male tergites similar but S8 and epandrium entirely pruinose. Abdominal P1 of female brown on anterior half, P2 entirely black except for posterior margin, P3 mostly black except for anterior margin, black area of P3 continuous with black area of P4 dorsally; P4 with a broad band on upper half only, P5–6 entirely black. Male pleural pigmentation similar to female on segments 1–3, P4–5 with dense white microsetulosity covering ventral $\frac{2}{3}$ of pleuron.

HEAD. Two fronto-orbital bristles, upper (orbital) large. Frontal vitta gradually tapered to a point both anteriorly and posteriorly, 0.6 × as wide as frons at maximum width, postocellar part narrow. Outer vertical bristle present.

THORAX. Prosternum bare except for minute scattered setulae. Cervical sclerite finely microtrichose except at anterior margin; female with centre part of cervical sclerite depressed and pit-like, posterior part slightly but distinctly convex; male cervical sclerite with centre and posterior parts almost uniformly convex. Scapular setae not differentiated from anterior dorsocentral setulae. Postpronotum microsetulose dorsally, bare laterally, with a few scattered setulae. Two notopleural bristles, anterior 0.5 × as long as posterior. Katepisternum with one vertical row of strong setae preceded by a vertical row of about 6 fine lower setae and scattered small, fine and pale upper setae. Dorsocentral bristle present.

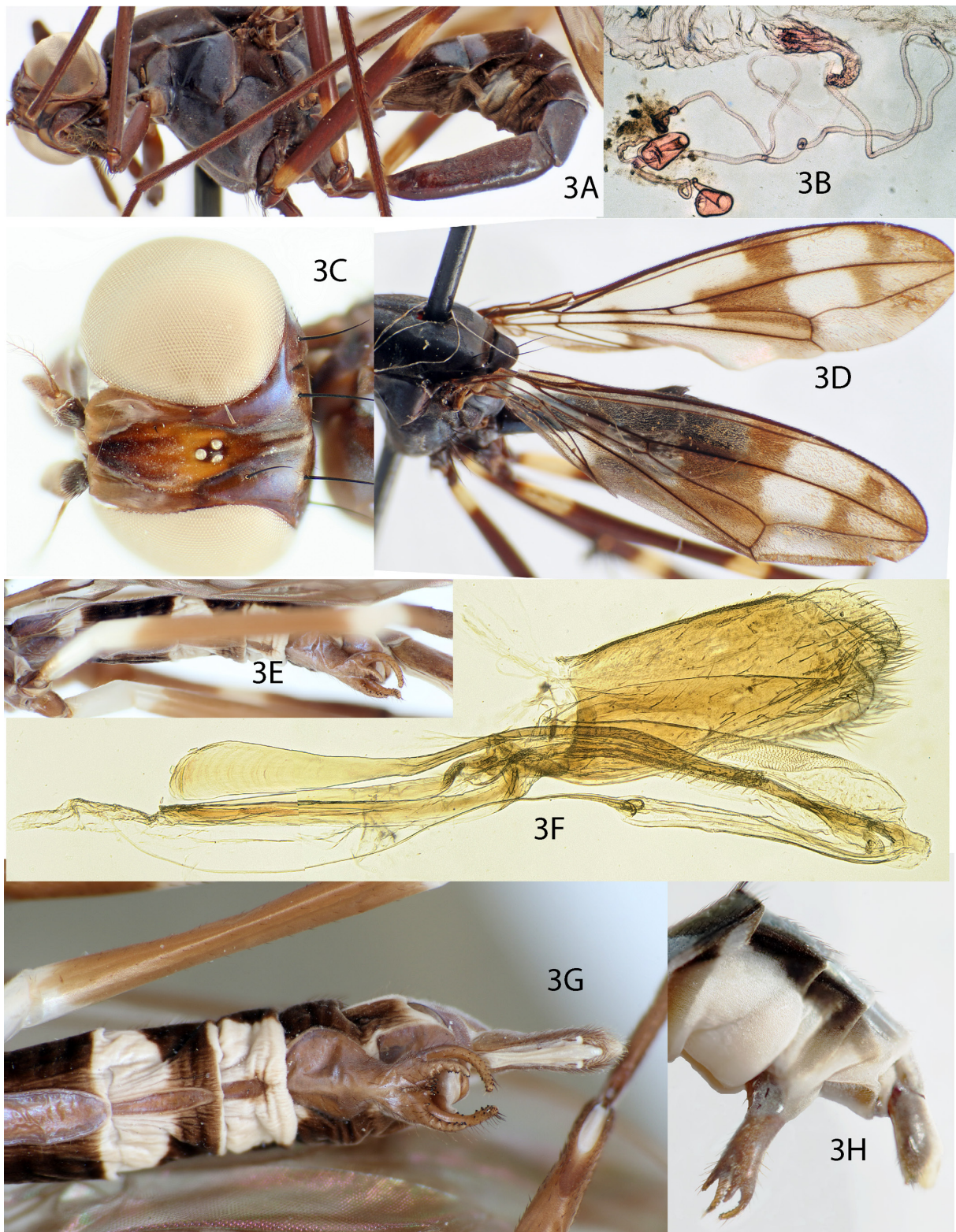


Fig. 3. *Ptilosphen boroboro* Marshall sp. nov., Colombia (IAVH). **A.** ♀. **B.** Spermathecae and associated structures. **C.** Head, dorsal view. **D.** ♀, left dorsolateral view to show wing pigmentation. **E.** ♂, abdomen, ventrolateral view to show structure of genital fork. **F.** ♂, terminalia, left lateral view. **G.** ♂, abdomen, ventral view. **H.** ♂, abdomen, left lateral view.

FEMALE TERMINALIA (Fig. 3B). Three spermathecae; paired spermathecae on a very long, uniform-width primary duct arising from the apex of an elongate common duct; apex of primary duct slightly swollen where it divides into two long, sinuate stems each ending in an elongate funnel-shaped and strongly recurved spermatheca. Secondary spermathecal duct arising from side of common duct, smaller and shorter than primary duct, ending in a very small acorn-shaped spermatheca.

MALE TERMINALIA (Fig. 3E–H). Genital fork with two pairs of long arms separated by a basal cluster of 6–8 stout teeth, upper arm strongly arched downward and with a few short dark distal teeth; lower arm shorter but almost reaching distal tip of upper arm, with dark teeth forming a double row along mesal surface. Basiphallus small, projecting slightly beyond distiphallus base. Basal distiphallus broad, subequal in length to epandrium, distal distiphallus very long, threadlike and extending anteriorly beyond phallapodeme, apparently reaching anterior apex of hypandrium. Anterior bridge of hypandrium elongate. Phallic bulb small, about half the distal width of the basal distiphallus, with proximal chamber oval and twice as large as the distal chamber. Postgonite very small and short, with a broad, posteriorly spinulose apex and a few small setulae on anterior surface.

Remarks

Ptilosphen boroboro Marshall sp. nov. is closely related to the Central American species *Pt. gentilis* Cresson, 1830, which also has a four-armed genital fork. In *Pt. gentilis*, however, the lower arms are much less than half as long as the upper arms, in contrast to the relatively long lower arms of *Pt. boroboro*. Both species resemble the South American *Pt. facetus* Enderlein, 1922 in external features other than pigmentation of the fore tarsus.

Ptilosphen callichroma (Bigot, 1886) resurrected nominal species
Figs 4–5

Calobata callichroma Bigot, 1886: 373.

Ptilosphen albibasis Enderlein, 1922: 224. **Syn. nov.**

Ptilosphen viriolatus Enderlein, 1922: 225. **Syn. nov.**

Calobata callichroma – Giglio-Tos 1895: 63. — van der Wulp 1897: 368, 375. — Aldrich 1905: 616. — Cresson 1908: 5, 8. — Enderlein 1922: 224 (treated as a synonym of *Ptilosphen cyaneiventris* (Macquart, 1846)).

Ptilosphen albibasis – Hennig 1934: 314, 317. — Aczél 1949: 336. — Steyskal 1968: 13. — Schumann 1988: 84.

Ptilosphen viriolatus – Hennig 1934: 315, 317. — Aczél 1949: 339. — Steyskal 1968: 14. — Schumann 1988: 113.

Type material

Syntypes of *Calobata callichroma*

“MEXICO” • 2 ♂♂; OXUM (photographs provided by Zoe Simmons).

Holotype of *Pt. albibasis*

MEXICO • ♀; Oaxaca, Deppe; MNBG.

Lectotype of *Pt. viriolatus* (here designated)

GUATEMALA • ♂; Tumbador; 12 Nov. 1912; Riedel leg.; MNBG.

(Both syntypes of *Pt. viriolatus* were examined in MNBG in 2002 but only the above Guatemala specimen was photographed and sketched. The second specimen, from Costa Rica, was noted as damaged. The specimen from Guatemala is therefore here treated as lectotype).

Other material examined**Typical form** (linear wing band)

BELIZE • 3 ♀♀, 2 ♂♂; Prov. San Ignacio, Maya Mtn. Lodge; Jan. 1991; S.A. Marshall leg.; dung trap; DEBU • 1 ♀; 1 ♂; Middlesex; 125 m a.s.l.; 8 Apr. 1965; E.C. Welling leg.; CNCI.

GUATEMALA • 1 spec. (no abdomen); Puente Samala, J. Bml. NB. San Felipeo; 25 Jul. 1966; K.U. Survey Course leg.; SNOW.

MEXICO • 1 ♀, 4 ♂♂; Prov. Chiapas, Yaxoquintela; 560 m a.s.l.; Sep. 1978; J.E. Rawlins leg.; CMNH • 2 ♀♀; Prov. Veracruz, 33 km NE of Catemaco, Los Tuxtlas Biol. Stn; 160 m a.s.l.; Jul.–Aug. 1983; S. and J. Peck leg.; CMNH • 3 ♂♂; Veracruz, 32 km N of Catemaco UNAM Preserve; 4–9 Jan. 1982; E.M. May leg.; Malaise trap; SNOW • 1 ♂; Veracruz, Cordoba; 13 Aug. 1964; P.J. Spangler leg.; USNM • 2 ♀♀, 6 ♂♂; Sontecompan; Jun. 1969; W.R.M. Mason leg.; CNCI • 1 ♂; Sontecompan; Jun. 1969; B.V. Peterson leg.; CNCI • 1 ♀, 1 ♂; Sontecompan, U. Mex. Biol. Res; 400 ft a.s.l.; Jun. 1969; W.R.M. Mason leg.; CNCI • 1 ♀, 1 ♂; Catemaco; 1100 ft a.s.l.; Jun. 1969; W.R.M. Mason leg.; CNCI • 1 ♂; Chiapas, Palenque; 600 ft a.s.l.; 22–23 Jun. 1969; W.R.M. Mason leg.; CNCI • 1 ♀; Chiapas, Palenque Ruins; 23 Jun. 1969; B.V. Peterson leg.; CNCI • 1 ♀; Veracruz, Lake Catemaco; 18 Jun. 1969; B.V. Peterson leg.; CNCI • 1 ♀; Guerrerá, near Tierra Colorado; 29 May 1963; USNM.

Costa Rican form (broad wing band)

COSTA RICA • 1 ♂; Guanacaste, ACG, Pailas Dos; 9–16 Feb. 2017; D. Janzen and W. Halwachs leg.; BIOUG • 1 ♂; same data as preceding; 6–13 Jun. 2019; BIOUG • 1 ♂; same data as preceding; 16–23 Jan. 2020; BIOUG • 8 ♀♀, 1 ♂; Heredia, Estac. Biol. La Selva; 1993–1995; Malaise trap; CO1 specimen DEBU0554; INBC • 2 ♀♀, 1 ♂; Rara Aves Nat. Res., 12 km S of Las Horquetas; 10°17'0" N, 84°2'50" W; 700 m a.s.l.; Feb. 2005; S.A. Marshall leg.; DEBU • 1 ♀, 1 ♂; same data as preceding; MNCR • 3 ♀♀, 2 ♂♂; Santo Domingo; Oct. 1999; S.A. Marshall and M. Buck leg.; DEBU • 3 ♂♂; Sto. Domingo, INBioParque; 19 Aug. 2001; S.A. Marshall leg.; CO1 specimen DEBUA289-17; DEBU • 6 ♀♀; Pandora, Estrella Valley; Mar. 1984; G.V. Manley and H.F. Howden leg.; DEBU • 4 ♀♀; San José, Pérez Zeledón, Rivas; 820 m a.s.l.; Dec. 1998–Jan. 1999; B.D. Gill leg.; DEBU • 3 ♀♀; Alajuela, Volcan Tenorio, N Slope, trail to laguna; 800–900 m a.s.l.; Jun. 2000; S.A. Marshall leg.; rainforest; DEBU • 1 ♀, 1 ♂; Prov. Puntarenas, Corcovado Natl. Pk, San Pedrillo; 8°37'15" N, 83°44'6" W; 5–50 m a.s.l.; Aug. 2001; S.A. Marshall leg.; DEBU • 1 ♀, 2 ♂♂; Punta Leona, forest around hotel; Feb. 2001; P.D. Careless leg.; DEBU • 1 ♂; San Vito, Las Cruces; 1200 m a.s.l.; Jul. 1983; B. Gill leg.; CNCI • 1 ♀; Prov. Turrialba; 640 m a.s.l.; Oct. 1981; R. Davidson leg.; CMNH • 2 ♂♂; Prov. Guanacaste; 700 m a.s.l.; 1994; C. Moraga leg.; DEBU • 1 ♂; Cacao; 750 m a.s.l.; Feb. 1996; S.A. Marshall leg.; DEBU • 1 ♂; Prov. Cartago; 1100 m a.s.l.; Oct. 1994; G. Fonseca leg.; DEBU • 2 ♀♀, 1 ♂; Prov. Alajuela, Soltis Research Centre; 10°22'59" N, 84°37'3" W; 27 Apr.–12 May 2018; S.A. Marshall and S.M. Paiero leg.; DEBU • 1 ♀, 1 ♂; same data as preceding; 26 Apr.–13 May 2022; S.A. Marshall leg.; DEBU • 3 ♀♀; Tapanti National Park; 8 Aug. 2013; S.A. Marshall leg.; MNCR • 2 ♀♀, 1 ♂; San Jose, Farm La Caja; 1942; H. Schmidt leg.; USNM.

Redescription

LENGTH. 12–14 mm.

COLOUR (Figs 4, 5A–E, H). Body mostly pale orange. Frontal vitta and frontal plate reddish to dark brown. Lunule orange; clypeus microtrichose, sparsely so medially, yellow except for a dark basal median patch. Palpus pale yellow, white along apical margin. Pleuron with a broad vertical white pollinose band on posterior half of anepisternum. Fore tarsomeres 4 and 5 completely dark, tarsomere 3 variable but usually mostly dark, tarsomeres 1 and 2 white; fore tibia brown; fore femur yellow basally, dark brown distally. Mid tarsus and tibia brown; mid femur orange-brown with basal and medial white

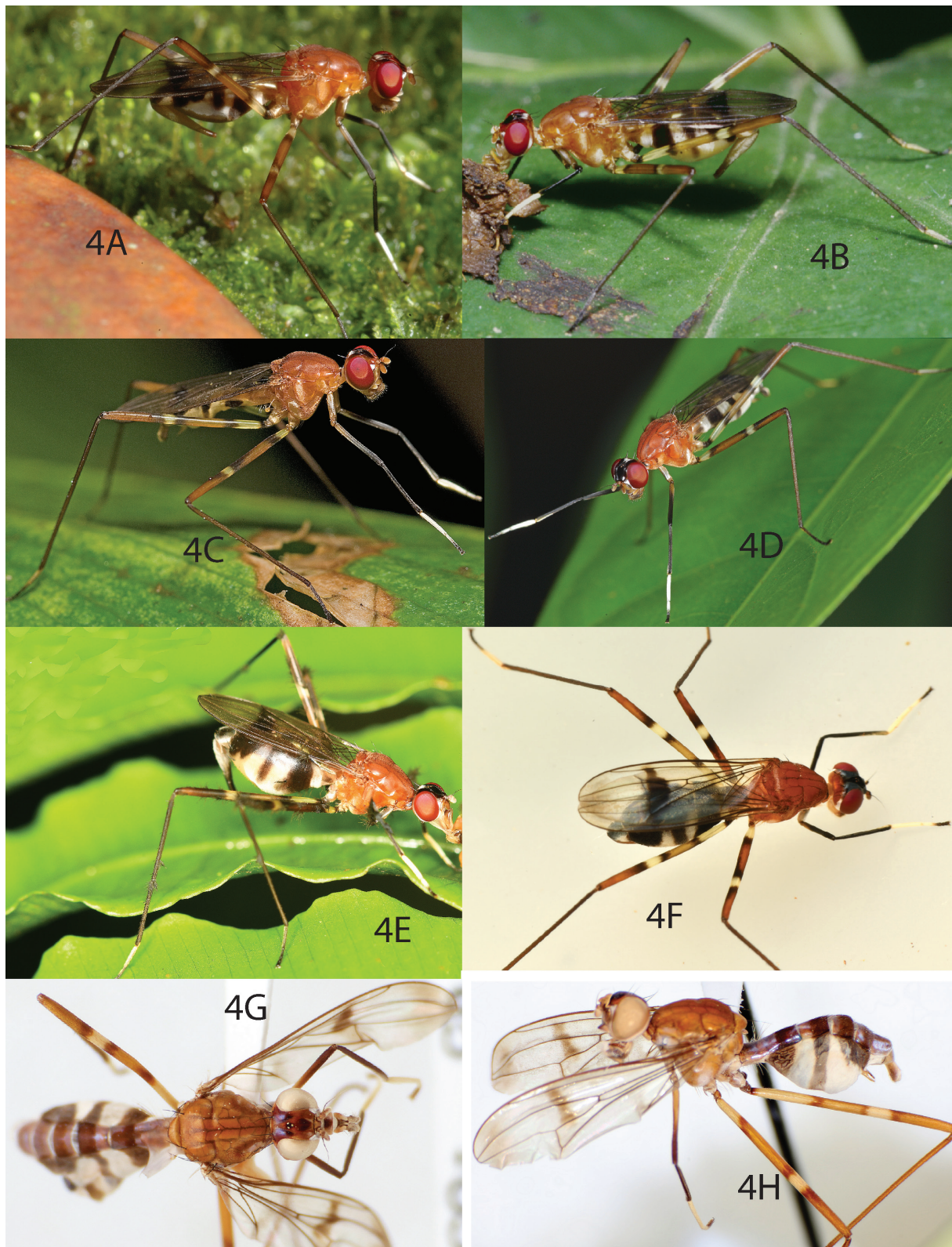


Fig. 4. *Ptilosphen callichroma* (Bigot, 1886), part one. **A–B.** Living ♀♀, Costa Rica (DEBU). **C–D.** Living ♂♂, Costa Rica (DEBU). **E.** ♀, with fungi on legs, abdomen and wing, Volcan Arenal, Costa Rica (DEBU). **F.** Living ♀, Costa Rica, showing broad wing pigmentation (DEBU). **G–H.** ♂, Mexico, to show typical narrow wing pigmentation (CMNH).

rings 1–2 × width of femur, margins of rings usually distinctly darkened. Hind femur orange-brown with basal white ring 3–4 × width of femur and medial white ring 2 × width of femur; hind tibia brown; hind tarsomeres 2–5 brown, tarsomere 1 white. Abdomen with T1+2 microtrichose except for a bare posteromedial patch, T1 pale; T2 darker, with black posterior corner; T3–4 brown, microtrichose on basal half only; pleural pigmentation distinct: P1 pale, P2 almost entirely black except for anterior margin, P3 with a black band covering posterior half, and upper part of P4–5 with dark area increasing in extent towards posterior margin. Oviscape brown dorsally and apically, yellow laterally.

HEAD. Frontal vitta convex, broadly tapered anteriorly and narrowly tapered posteriorly, 0.4 × width of frons at maximum. Outer vertical bristle present.

THORAX. Prosternum microsetulose and with a few fine setae along anterior margin. Cervical sclerite in both sexes prominent, elevated but not bilobed, narrowest posteriorly. Scapular setae very small to absent. Katepisternum with one main posterior row of strong yellow bristles, setae anterior to row fine and pale. Dorsocentral bristle present. Wing with discal band transverse, parallel-sided and narrow in typical form, more triangular in Costa Rican specimens; apex of wing indistinctly pigmented.

FEMALE TERMINALIA (Fig. 5G). Single and paired or primary spermathecae similar in size and shape, expanded apically; primary duct arising from apex of bursa extension or common duct and conspicuously broad, 4–5 × as wide and twice as long as single (secondary) duct; primary spermathecal stems long and sinuate, greatly constricted at base; single spermathecal stem greatly reduced. Single spermathecal duct arising just before apex of long common duct or thin extension of the bursa.

MALE TERMINALIA (Fig. 5E–F). Inner face of each genital fork arm with short, stout spines forming a loose cluster of 6–7 around mid point and a tight cluster of 3–4 at base; apex of each arm with or without a single inner short spine; base of fork between arms with a deep V-shaped cleft. Basiphallus prominent, projecting posteriorly as a rounded lobe. Distiphallus longer than epandrium, distal distiphallus straight, half as wide and twice as long as basal distiphallus, apex expanded into a broad funnel with a central seta-like process. Anterior bridge of hypandrium short and scoop-like. Phallic bulb weakly differentiated, with distal chamber only slightly smaller than proximal chamber. Ejaculatory apodeme similar in size to epandrium.

Remarks

Ptilosphen callichroma was treated as a junior synonym of *Pt. cyaneiventris* by Enderlein (1922), Hennig (1934) and Steyskal (1968) but syntypes of *Pt. callichroma* in OXUM seem to be conspecific with types of *Pt. albibasis* Enderlein, 1922 and *Pt. viriolatus* Enderlein, 1922 rather than *Pt. cyaneiventris*. Hennig (1934: 315) separated *Pt. albibasis* from *Pt. viriolatus* (and *Pt. cyaneiventris*) on the basis of the more extensive basal white ring on its hind femur, but the proportions of the white parts of the hind femur vary intraspecifically and have similar dimensions in the types of *Pt. albibasis* and *Pt. viriolatus* (it is usually narrower in *Pt. cyaneiventris*). *Ptilosphen cyaneiventris* also differs from *Pt. callichroma* in wing pigmentation and other characters, but the two species are closely related and show as sister species on the CO1 trees (Fig. 30). Specimens of *Ptilosphen callichroma* from Mexico, Belize, Guatemala and Honduras have a characteristic wing pigmentation in which the discal band is narrow and straight, almost parallel-sided, and never tapered anteriorly; they also usually have a reddish brown frontal vitta. Specimens from Costa Rica, where *Pt. callichroma* is arguably the most frequently encountered micropezid species, have the discal band tapered anteriorly to form a more or less triangular band, and usually have a darker frontal vitta. Male and female genitalia of these geographical variants are identical and both variants barcode in a single BIN; they are therefore treated as a single species.

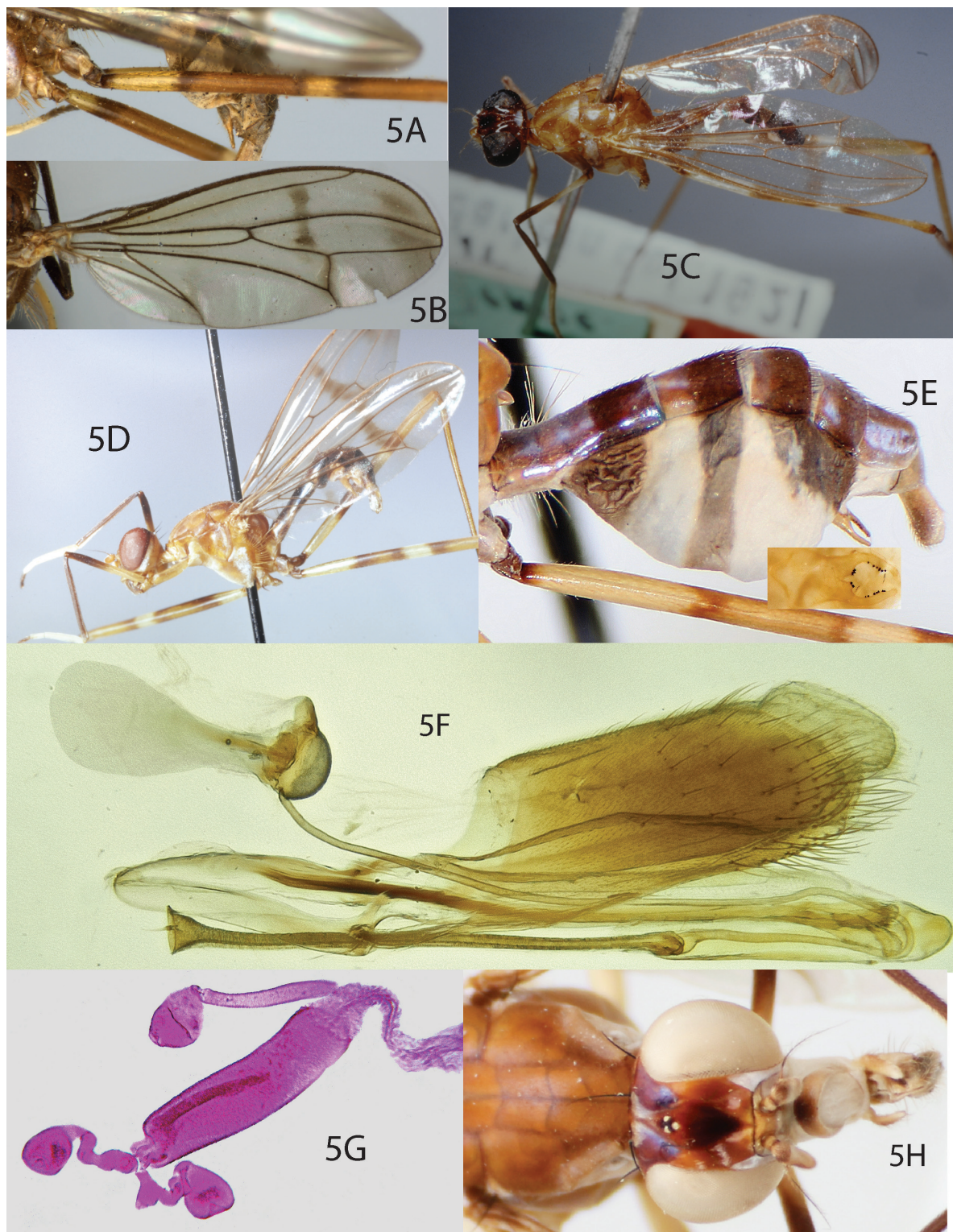


Fig. 5. *Ptilosphen callichroma* (Bigot, 1886) and junior synonyms, part two. **A–B.** Syntype of *Pt. callichroma*, Mexico, leg, abdomen, wing (OXUM, photos by Zoe Simmons). **C.** Holotype of *Pt. albibasis* Enderlein, 1922, ♀, Mexico (MNBG). **D.** Lectotype of *Pt. viriolatus* Enderlein, 1922 (here designated), ♂, Guatemala (MNBG). **E.** ♂, abdomen, left lateral view, Mexico (inset shows genital fork in ventral view) (CMNH). **F.** ♂, terminalia, left lateral view, Guatemala (SNOW). **G.** Spermathecae and associated structures, Costa Rica (DEBU). **H.** Head and thorax, Costa Rica (DEBU).

Ptilosphen comis Cresson, 1930

Fig. 6

Ptilosphen comis Cresson, 1930: 347.

Ptilosphen subgentilis Hendel, 1936: 71 (Brazil). Synonymized with *Pt. comis* by Hennig (1938: 14).

Ptilosphen comis – Curran 1934a: 295, 457. — Hennig 1934: 315, 318. — Aczél 1949: 336. — Steyskal 1968: 13. — Roback 1969: 533. — Albuquerque 1991: 4. — Ferro & de Carvalho 2014: 59. — Marshall *et al.* 2016: 543.

Type material

Holotype of *Ptilosphen comis*

GUYANA • ♂; Kamakusa; H. Lang leg.; ANSP.

Paratypes of *Ptilosphen comis*

GUYANA (as BRITISH GUIANA) • 2 ♀♀; same data as for holotype (not examined); ANSP.

Other material examined

BOLIVIA • 3 ♀♀; Prov. S. Inicua, Riv. Alto Beni; 1100 m a.s.l.; Jan. 1976; L. Peña leg.; CNCI.

BRAZIL • 1 ♀, 3 ♂♂ (see Remarks); Prov. Roraima, Serra Pacaraima, BR-174; 4°27'04" N, 61°07'56" W; 800 m a.s.l.; 1–7 Sep. 1995; J.A. Rafael, A.L. Henriques and J. Vidal leg.; arm, Malaise; INPA.

COLOMBIA • 4 ♀♀, 1 ♂; Prov. Amazonas, Leticia; 185 m a.s.l.; Feb. 1972; P. Ward and A. Forsyth leg.; CNCI.

ECUADOR • 13 ♀♀, 8 ♂♂; Prov. Napo, Jatun Sacha Res., 6 km E of Misahualli; 1°4' S, 77°37' W; 450 m a.s.l.; Apr.–May 2002; S.A. Marshall leg.; DEBU • 13 ♀♀, 8 ♂♂; same data as for preceding; QCAZ • 2 ♀♀; same data as for preceding; S.M. Paiero leg.; QCAZ • 1 ♂; same data as for preceding; J. Boone leg.; QCAZ • 1 ♂; same data as for preceding; J. Lapierre leg.; QCAZ • 1 ♀; same data as for preceding; T. Eles leg.; QCAZ • 1 ♀; same data as for preceding; J. Steiner leg.; QCAZ • 1 ♂; same data as for preceding; C. Thickett leg.; QCAZ • 4 ♀♀, 1 ♂; Yasuni Ntl. Pk, Yasuni Research Station; Apr.–May 2009; S.A. Marshall leg.; DEBU • 5 ♀♀; same data as for preceding; QCAZ; 1 ♀; same data as for preceding; M. Morno leg; CO1 specimen DEBUA310-17; DEBU • 2 ♂♂; same as for preceding; D. Verkindt leg.; QCAZ; 2 ♀♀, 3 ♂♂; same as for preceding; M.D. Jackson leg.; DEBU • 2 ♀♀; Yasuni Ntl. Pk, Yasuni Research Station; 0°38' S, 76°36' W; Nov. 1998; T. Pape and B. Viklund leg.; DEBU • 1 ♀, 2 ♂♂; Tiputini Biodiv. Stn, vic. Yasuni Ntl. Pk.; Feb. 1998; D.C. Darling leg.; ROME • 1 ♀; Res. Ethnica Waorani, 1 km S of Onkone Gare Camp; 0°39'10" S, 76°26'0" W; Oct. 1994; T.L. Erwin leg.; USNM • 2 ♀♀, 1 ♂; Napo, vicinity of Misahualli; 1°2' S, 77°40' W; 27–31 Oct. 2002; E.M. Fisher leg.; DEBU • 1 ♀; Coca; 250 m a.s.l.; May 1965; L. Peña leg.; CNCI.

FRENCH GUIANA • 1 ♀; Regina, Kaw Kaw Mtns., Point Rd 30; 3–27 Mar. 2007; K. Sarv leg.; rainforest/plantations Malaise trap; DEBU • 1 ♀; Cayenne, Kaw Mt., Relaise de Patawa; 300 m a.s.l.; Feb. 2006; Malaise; J.A. Cerda leg.; CO1 specimen MYCRO944-22; DEBU.

GUYANA • 6 ♀♀, 6 ♂♂; Potaro-Siparuni, Mount Wokomung; 21–26 Oct. 2004; B. Hubley leg.; dung trap in primary forest; CO1 specimens MYCRO941-22; DEBU • 6 ♀♀, 7 ♂♂; same data as for preceding; ROME..

PERU • 1 ♀, 2 ♂♂; Prov. Loreto; 175–300 m a.s.l.; Jul. 1993; R. Leschen leg.; DEBU • 6 ♀♀, 4 ♂♂; Cusco, Villa Carmen Biological Station; Oct. 2012–Apr. 2014; Norrbom, Steck, Sutton, Rodriguez, Choque, Forster leg.; Malaise traps and multilure traps; USNM • 1 ♂; Puculpa; 14 Dec. 1950; Schunke leg.; USNM • 1 ♀, 1 ♂; Madre de Dios, Tambopata; 16 Aug. 1982; J. Anderson leg.; human feces; USNM • 1 ♀, 1 ♂; Loreto, Campamento San Jacinto; 175–215 m a.s.l.; 4 and 11 Jul. 1993; R. Leschen leg.; flight intercept trap; DEBU.

VENEZUELA • 1 ♀; Akuriman, Gran Sabana EB; Nov.–Dec. 1940; USNM.

Redescription (from topotypic material, variation noted below)

LENGTH. 10–15 mm, usually 14–15 mm.

COLOUR (Fig. 6A–D, G). Frons reddish, epicephalon and frontal vitta pruinose and varying from orange to dark reddish brown; epicephalon shining. Lunule orange, face and parafacial white to silvery pruinose. Clypeus brown, entirely microsetulose. Palpus yellow-brown distally, darker basally. Thorax and abdomen black to dark brown, notum indistinctly vittate with narrow central reddish strip separating broader silvery vittae, pleuron with extensive pruinosity forming diffuse vertical bands, anterior part of katepisternum and anepisternum bare. Legs mostly brown, mid and hind femora with basal white bands and distomedian white bands (often indistinct or absent on mid femur), basal white band usually twice as long as distomedian band. Fore tarsus entirely white, with white setulae on tarsomeres 1–2, black setulae on tarsomeres 4–5 and at least ventral side of tarsomere 3 (distal tarsomeres thus appearing dark). All coxae black with a heavy white pruinosity; fore trochanter and femur uniformly brown-black. Wing with a large, distinctly triangular discal wing band, anterior corner of discal band extending to costa; apical pigmentation diffuse but extensive. Abdominal tergites dark brown to blue-black, entirely pruinose. Abdominal pleuron boldly banded in black and white, with narrowly separated complete black bands on P1 and P2, P3 with dark area tapering ventrally from posterior part of T3, the P3 band complete and narrow in males, broader, incomplete and often continuous with the P4–6 pigmentation in females; P4–6 usually with dorsal pigmentation and sometimes entirely pigmented. Oviscape brown with darker apex, microsetulose except for apex and at least basal dorsal area.

HEAD. Two fronto-orbital bristles, upper strong. Anterior frontal vitta mostly parallel-sided, abruptly tapered to anterior frontal margin, half as wide as frons at maximum width. Postocellar frontal vitta broad, almost parallel sided. Outer vertical bristle present.

THORAX. Prosternum microsetulose, with a few inconspicuous fine setulae along anterior margin. Cervical sclerite broad, posterior part convex, indistinctly microsetulose. Postpronotum bare or almost so. Two notopleural bristles, anterior slightly smaller. Dorsocentral bristle present.

FEMALE TERMINALIA (Fig. 6E). Oviscape elongate triangular and slightly longer than T4–6, strongly flattened in dried specimens. Paired spermathecae elongate goblet-shaped, apically flat and normally invaginate; stems and spermathecal base thick and studded with short protuberances; single spermatheca smaller, with a short, simple stem. Ducts and stems separated by a short, inconspicuous constriction. Spermathecal ducts long, thin, parallel-sided, ringed by transverse striae; single duct $\frac{1}{2}$ as long as and slightly narrower than primary duct; ducts arising at apex of long common duct or thin extension of the bursa.

MALE TERMINALIA (Fig. 6F, H–K). Arms of genital fork long, thin, inwardly arched with fine hairs along entire outer surface; inner face of arms with about 12 small stout spines on distal half; inner basal lobes subquadrate and each with an apical compact cluster of stout spines; base of fork with deep, narrowly U-shaped cleft (cleft V-shaped in Ecuadorian specimens examined). Epandrium long and narrow, twice as long as high. Basiphallus prominent, projecting posteriorly as a rounded lobe. Basal distiphallus very short, dorsoventrally flattened, about half as long as epandrium and less than a third as long as the narrow, cylindrical and transverse striate distal distiphallus. Phallic bulb small, proximal chamber twice as large as distal chamber. Anterior bridge of hypandrium short scoop-like. Phallic plate with transverse rows of minute microtrichiae. Postgonite small but bulbous, with three minute setulae anteroventrally, posterior surface evenly covered with minute bumps. Ejaculatory apodeme unusually small, only slightly larger than sperm pump, sperm pump with broad, flat lateral extensions.

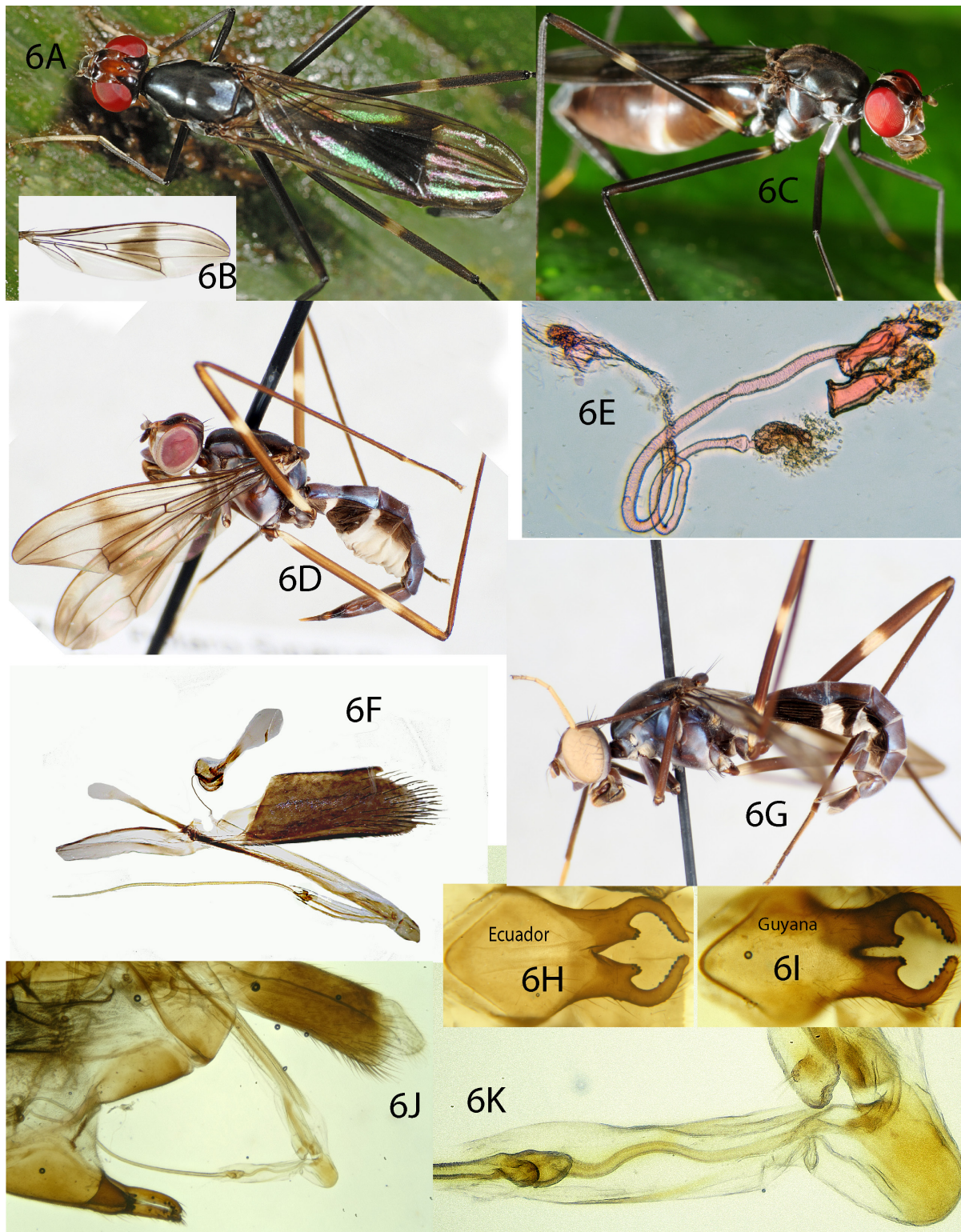


Fig. 6. *Ptilosphen comis* Cresson, 1930 (DEBU). **A.** ♀, dorsal view, Ecuador. **B.** ♀, wing, Ecuador. **C.** ♀, lateral view, Ecuador; discoloration on ventral half of P4–6 and complete lack of a middle ring on mid femur are atypical. **D.** ♀, Guyana. **E.** Spermathecae and associated structures, Guyana. **F.** ♂, terminalia, Ecuador. **G.** ♂, Guyana. **H–I.** ♂, sternite 5 (genital fork), Ecuador and Guyana. **J.** ♂, terminalia, left lateral view, Guyana. **K.** Postgonite, basiphallus, basal distiphallus and phallic bulb, Guyana (twisted into dorsal view).

Remarks

The widespread and common South American *Pt. comis* exhibits considerable variability in head and leg pigmentation but can be reliably recognized, at least to the species complex level, by the solid triangular discal wing band in combination with the red or reddish brown frontal plate. The redescription above is based on material from Guyana (type locality) and French Guiana; specimens from other countries differ slightly in female pleural pigmentation, male genital fork shape, size, and head colour. Andean specimens (15 mm in length) are slightly larger than specimens from Guyana (14 mm) and Ecuadorian specimens have a V-shaped cleft between the inner basal lobes of the genital fork, in contrast with the almost parallel-sided cleft of other specimens. The four specimens examined from Brazil are significantly smaller, at about 10 mm. All specimens dissected were uniform for the characteristic spermathecal characters and for details of the internal male genitalia. The CO1 analysis shows members of the complex on a single branch, with specimens from different countries in three different BINS (Fig. 30). They are treated as a single named species here although “*Pt. comis*” is probably a species complex. More material is needed to reconsider the status of the Andean and Brazilian populations relative to the typical northeastern South American populations. In the meantime, “*Pt. comis*” is an easily diagnosed clade.

Ptilosphen conveniens (Wulp, 1897)

Fig. 7

Calobata conveniens van der Wulp, 1897: 368, 373, pl. 9 fig. 27.

Ptilosphen conveniens – Enderlein 1922: 223, 225. — Cresson 1930: 348. — Hennig 1934: 315, 318. — Aczél 1949: 336. — Steyskal 1968: 13.

Type material

Lectotype (here designated)

PANAMA • ♀; Bugaba; 800–1500 ft. a.s.l.; Champion leg.; NHMUK (labelled as “cotype”, B.C.A. [Biologia Centrali-Americana] Dipt. II *Calobata conveniens*).

Paralectotypes

PANAMA • 4 ♂♂, one partial specimen (sex unknown); same label data as for lectotype; NHMUK.

Other material examined

COSTA RICA • 2 ♂♂; Prov. Puntarenas, Osa Pen., Corcovado Natl. Pk; 500–600 m a.s.l.; Aug. 1996; Pape and Viklund leg.; DEBU • 1 ♀, 1 ♂; Osa Peninsula, 2.5 km S of Rincon; 8°42'1" N, 83°30'50" W; Aug. 2001; S.A. Marshall leg.; DEBU • 1 ♂; Drake; 8°41'25" N, 83°40'3" W; 5 m a.s.l.; Aug. 2001; S.A. Marshall leg.; DEBU • 1 ♀; Corcovado Natl. Pk, San Pedrillo; 8°37'15" N, 83°44'6" W; 5–50 m a.s.l.; Aug. 2001; S.A. Marshall leg.; DEBU • 1 ♀; P.N. Corcovado, Sirena; Jan. 2000; P. Orítz leg.; DEBU • 1 ♀; Proyecto Campaniero de Osa, N of San Pedrillo; Feb. 2005; P. Careless leg.; DEBU • 1 ♀; Prov. Puntarenas, Fila Matajambre Osa; 300–740 m a.s.l.; May 1994; M.A. Zumbado leg.; INBC • 1 ♂; Estacion Sirena; 1–100 m a.s.l.; Mar. 1995; M.A. Zumbado leg.; INBC • 1 ♂; Prov. San José, Carlos, Rios Paraiso Reserve, Pecari Stn, 16 km NNE of Quepos; 9°33'53" N, 84°07'32" W; 400 m a.s.l.; 12–15 Apr. 2006; S.A. Marshall leg.; DEBU • 1 ♀, 1 ♂; same data as for preceding; 15 Feb. 2003; DEBU • 1 ♂; same data as for preceding; 22–27 Feb. 2006; MNCR • 1 ♂; same data as for preceding; 23–26 Feb. 2006; S.M. Paiero leg.; CO1 specimen MYCRO957-22; DEBU • 2 ♀♀, 1 ♂; same data as for preceding; MNCR..

Note

Wulp (1897) indicated that he described a female but also examined four males and another female. There are six specimens labelled as cotypes in the NHMUK. Four specimens are males, one specimen

is damaged beyond recognition (one leg, no head, no abdomen), and one specimen is a relatively intact female that also has only one leg (left foreleg), but which shows the characteristic abdominal pigmentation. The intact female (illustrated in Fig. 7) is presumably the one used for Wulp's description, and is therefore here designated as lectotype.

Redescription

LENGTH. 12–13 mm.

COLOUR (Fig. 7A–E). Dark shiny blue-black except as follows: frontal vitta dull orange and well defined, frontal plate shiny orange; ocellar triangle, epicephalon and paracephalon reddish brown with a microtrichose area between inner vertical bristles and on postocciput. Palpus yellow and antenna orange, clypeus and face pale, clypeus entirely pale setulose. Fore tarsomeres 3–5 yellowish white to light brown, tarsomeres 1 and 2 white; fore tibia dark brown; fore femur white to yellow basally and dark brown distally. Mid tarsus and tibia brown; mid and hind femora brown with medial white rings and a reddish apex; mid femur with a white base $1-3 \times$ width of femur, hind femur with white ring $2-4 \times$ width of femur; hind tibia brown; hind tarsomeres 2–5 brown, tarsomere 1 pale ventrally. Wing with transverse basal and preapical bands and triangular discal band. Female abdomen with tergites dark except for pale posterior half of T2 and pale and unsclerotized T3–4; P1 with a narrow vertical white stripe, upper half of P3–4 extensively yellow to white so that side of abdomen seems to have large white spot continuous with the pale middle tergites. Male tergites uniformly dark but pleuron with vertical black and white stripes: P1 brown on anterior half, otherwise white, P2 with a broad black band, P3 with a narrow black band on posterior half, and P4–5 dark dorsally.

HEAD. Two pairs of fronto-orbital bristles, upper pair large. Frontal vitta gradually tapered to a point both anteriorly and posteriorly, maximum width half of frontal width. Outer vertical bristle normally absent (present on one side on one specimen), inner vertical bristles usually present and single but doubled on one female specimen.

THORAX. Prosternum anteriorly with dense golden setulae. Cervical sclerite densely microsculptured and microtrichose except at margin, centre part strongly differentiated, white and prominent in female, weakly convex and brown in male. Female with 2–3 inconspicuous scapular setae in a more or less transverse row, male with scapular setae not differentiated from anterior dorsocentral setulae. Postpronotum with a few scattered setulae. Two notopleural bristles, anterior $0.5 \times$ as long as posterior. Katepisternum with one vertical row of strong setae preceded by a vertical row in which only the lower six setae are long and dark, and the upper setae are small, fine and pale. Dorsocentral bristles absent.

FEMALE TERMINALIA (Fig. 7I). Three spermathecae similar in size but different in shape and surface sculpture, primary and secondary ducts arising together at apex of bursa extension or common duct; primary duct long with basal $\frac{2}{3}$ greatly expanded and distal third narrow and parallel sided, with paired spermathecae smooth and oval, each on a narrow and distally expanded stem about as long as spermatheca. Secondary (single) duct slightly shorter than primary spermathecal duct and $\frac{1}{3}$ as wide as basal $\frac{2}{3}$ of primary spermathecal duct, base of duct threadlike, greatly constricted; single spermatheca broader than paired spermathecae, rough-surfaced, flattened and irregularly anvil-shaped.

MALE TERMINALIA (Fig. 7F–H). Genital fork with two short, thin, arched arms with fine hairs along entire inner and outer surface; inner face of arms with short, small spines extending entire length of arm and in two compact basal clusters; base with shallow groove. Basiphallus prominent, projecting posteriorly as a rounded lobe. Distiphallus shorter than phallopodeme; basal distiphallus short; distal distiphallus long and thin, narrower and twice as long as basal distiphallus, with weak transverse striations and expanded goblet-like apex. Phallic bulb broad, clearly divided into long proximal chamber and short

distal chamber. Anterior bridge of hypandrium long, tongue-like. Postgonite very small and short, with a round and weakly spinulose apex.

Remarks

Ptilosphen conveniens, known from Costa Rica and Panama, and the South American species *Pt. tetrastigma* (Schiner, 1868) and *Pt. inconviens* Marshall sp. nov. all show similar sexual

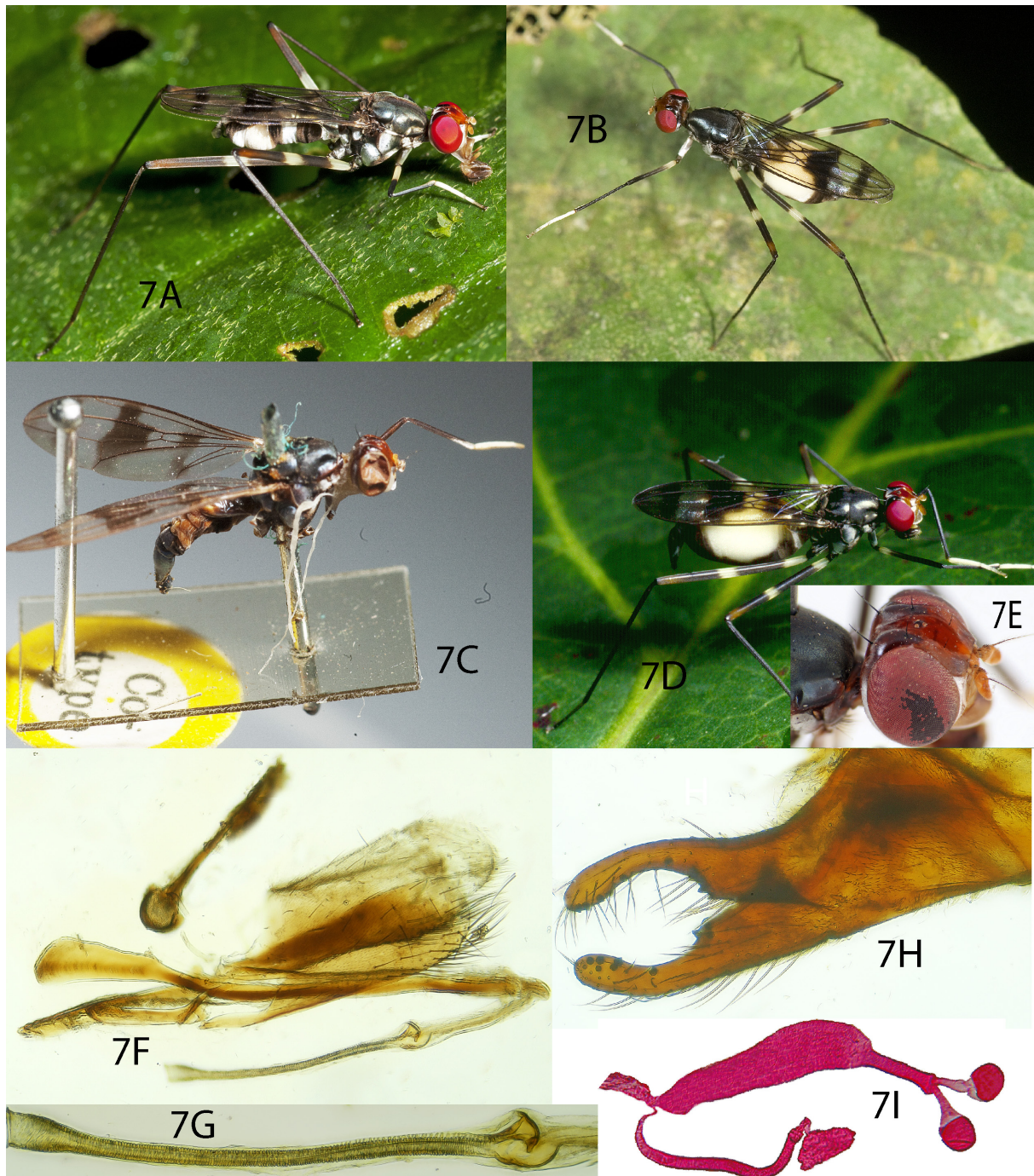


Fig. 7. *Ptilosphen conveniens* (Wulp, 1897), Costa Rica except C (DEBU and MNCR). A. ♂. B, D. ♀, dorsal and lateral views. C. Lectotype (here designated), Panama. E. ♀, head. F. ♂, terminalia, left lateral view. G. Distal distiphallus and phallic bulb. H. ♂, sternite 5 (genital fork). I. Spermathecae and associated structures.

dimorphism in abdominal colour and sclerotization. Females of *Pt. tetrastigma* have T3–4 white in contrast to adjacent black-banded pleurae; however, while *Pt. conveniens* and *Pt. inconveniens* have a similar large white pleural area adjacent to a desclerotized or pale T3 (*Pt. inconveniens*) or T3–4 (*Pt. conveniens*). This seems to be convergent similarity; however, since several characters (the absence of outer vertical and dorsocentral bristles, the distinct narrow preapical wing band, and the unusual spermathecal complex with a swollen duct and an anvil-shaped single spermatheca) suggest a closer relationship between *Pt. conveniens* and *Pt. dellarum* Marshall sp. nov. This relationship is recovered in the neighbour-joining tree (Fig. 30) but not the maximum likelihood tree. *Ptilosphen conveniens* is a Central American species, and there are no verified records from South America. According to Hennig (1934) the female specimens of *Pt. conveniens* recorded by Enderlein (1922) from Brazil are *Pt. comis*.

Ptilosphen crassus Marshall sp. nov.

[urn:lsid:zoobank.org:act:8525D018-64FD-46F2-929E-BE1912575061](https://zoobank.org/act:8525D018-64FD-46F2-929E-BE1912575061)

Fig. 8

Etymology

The species name refers to the stout male genital fork (Lat. ‘*crassus*’ = ‘fat’).

Type material

Holotype

ECUADOR • ♂; Prov. Napo, Jatun Sacha Res., 6 km E of Misahualli; 1°4' S, 77°37' W; 450 m a.s.l.; 30 Apr.–8 May 2002; S.A. Marshall leg.; varzea; QCAZ.

Paratypes

ECUADOR • 9 ♀♀, 10 ♂♂; same data as for holotype; QCAZ • 1 ♀; same data as for holotype; M. Buck leg.; DEBU • 1 ♀; same data as for holotype; 2–7 May 2002; M. Buck leg.; DEBU • 1 ♀; same data as for holotype; 5 May 2002; M. Buck leg.; DEBU • 1 ♀; same data as for holotype; 4 May 2002; M. Buck leg.; DEBU • 1 ♀; same data as for holotype; 2 May 2002; O. Lonsdale leg.; DEBU • 1 ♀; same data as for holotype; 30 Apr.–7 May 2002; Buck *et al.* leg.; landslide in forest, Malaise; DEBU • 1 ♀; same data as for holotype; 1–2 May 2002; Buck and Lonsdale leg.; dung pans; DEBU • 1 ♀; same data as for holotype; 7 May 2002; S.A. Marshall leg.; tower trail; DEBU • 1 ♀, 1 ♂; same data as for holotype; S.M. Paiero leg.; DEBU • 2 ♀♀; same data as for holotype; Z. Fitzgerald leg.; DEBU • 1 ♀; same data as for holotype; G. Reisinger leg.; DEBU • 1 ♀; same data as for holotype; P. Careless leg.; DEBU • 1 ♀, 1 ♂; same data as for holotype; P. Mikoda leg.; DEBU • 4 ♀♀, 1 ♂; Tiputini Biodiversity Station; May 2011 and Jan. 2013; S.A. Marshall and P. Careless leg.; CO1 specimen DEBUA311-17; DEBU • 2 ♂♂; Puerto Orellana, Tiputini Biodiversity Station, M. Kotrba; Aug. 1999; DEBU • 14 ♀♀, 9 ♂♂; Yasuní Natl. Pk., Yasuní Research Station; 28 Apr.–8 May 2009; S.A. Marshall leg.; DEBU • 2 ♀♀, 1 ♂; same data as for preceding; H. Cumming, M. Buck and L. Hewitt leg.; DEBU • 3 ♀♀; same data as for preceding; 3–20 Nov. 1998; T. Pape and B. Viklund leg.; DEBU • 1 ♀, 1 ♂; Pompeya, Pastaza; 14–22 May 1965; L. Peña leg.; CNCI • 1 ♀; Coca, Napo; 250 m a.s.l.; May 1965; L. Peña leg.; CNCI • 1 ♀, 1 ♂; Napo, vic. Misahualli; 27–31 Oct. 2002; E. Fisher leg.; DEBU • 1 ♀; Zamora, Podocarpus National Park; 19–22 Feb. 2003; C. Darling leg.; human dung; ROME • 8 ♀♀, 4 ♂♂; Napo, Narupa Yacu Reserve; 0°40'50" S, 76°24'2" W; 250 m a.s.l.; May 2019, S.A. Marshall and K. Lindsay leg.; DEBU • 3 ♀♀, 3 ♂♂; Prov. Napo, Parque Nacional Sumaco; 1500 m a.s.l.; 18–21 Jan. 2024; S. Luk and S.A. Marshall leg.; MECN • 1 ♂; Prov. Pastaza, Mera, Centro de Investigacion Sumak Kawsay; 1400 m a.s.l.; 23–26 Jan. 2024; S.A. Marshall leg.; MECN.

PERU • 2 ♀♀; Prov. Loreto, Teniente López, 1.5 km N; 230–305 m a.s.l.; 18 Jul. 1993; R. Leschen leg.; flight intercept trap; DEBU • 2 ♀♀; same data as for preceding; 22 Jul. 1993; DEBU • 1 ♂; same data as for preceding; 24 Jul. 1993; DEBU • 2 ♀♀; Depto Loreto, Campamento San Jacinto; 175–215 m a.s.l.; 5–10 Jul. 1993; R. Leschen leg.; DEBU • 1 ♀; Prov. Loreto, 1.5 km N of Taniente Lopez; 230–305 m a.s.l.; 26 Jul. 1993; R. Leschen leg.; DEBU • 1 ♀; Iquitos; Mar.–Apr. 1911; R.C. Shannon leg.; USNM.

Other material examined

COLOMBIA • 11 ♀♀; Prov. Putumayo, Parque Nacionales Naturales La Paya Cabaña La Paya; 0°2' S, 75°12' W; 330 m a.s.l.; 5–25 Dec. 2001; E. Lozano leg.; Malaise trap; IAVH • 1 ♀; Putumayo, Orito, RN La Isla Escondida; 0.65547° N, 77.07302° W; 850 m a.s.l.; 18–22 Aug. 2024; Pollet and De Braekeleer leg.; yellow pan traps; IAVH, Life on Trees: LOT00-39007/Y1-1 • 1 ♀; same data as for preceding; yellow pan traps; IAVH, Life on Trees: LOT00-39005/Y1-1 • 1 ♀; same data as for preceding; white pan traps; IAVH, Life on Trees: LOT00-39005/W1-1.

Description

LENGTH. 12–14 mm.

COLOUR (Fig. 8A–B, E, H, J). Frons black to dark brown, frontal vitta entirely black and well defined, pruinose except for ocellar triangle; epicephalon and paracephalon shiny and smooth. Lunule, face and parafacial white to silvery pruinose, subantennal depression shining black. Clypeus brown to black with lower rim pale, palpus yellowish distally, slightly darker on basal third. Thorax and abdomen black to dark brown, notum indistinctly vittate with narrow anteriorly tapered central reddish strip incomplete anteriorly but otherwise separating broader silvery vittae, pleuron with extensive pruinosity forming broad silvery vertical bands. Legs mostly dark brown to black, mid femur with a narrow white base, hind femur with an extensive white base and broad distomedian white band. Fore tarsus entirely white, with white setulae except for a few darker setulae on distal tarsomeres. Fore coxa white pruinose at least dorsally, fore femur uniformly brown-black. Wing with V-shaped or broadly U-shaped discal band, uniform in width and usually strong to anterior wing margin. Tergites of female abdomen black with bluish pruinosity except on posterior half of T3, margins of T4–5, and middle part of T2, oviscape black with silvery lateral pruinosity and orange apex. Male similar but non-pruinose part of T3 more extensive. Abdominal pleuron similar in both sexes: boldly banded in black and white, with separate bands on P1, P2, and posterior half of P3 and dorsal pigmentation on P4–6, P2 band covering all of P2, P3 band very narrow and parallel sided.

HEAD. Frontal vitta broad, maximum width $0.7 \times$ frontal width, tapered to a point anteriorly, broad and parallel-sided behind ocelli with a broadly rounded posterior apex. Two strong, subequal fronto-orbital bristles. Outer vertical bristle present.

THORAX. Prosternum bare and shiny except for a narrow microsetulose anterior margin. Cervical sclerite simple in both sexes. Postpronotal and scapular setae absent. Katepisternum with one vertical row of bristles. Two notopleural bristles, anterior small. Dorsocentral bristle present.

FEMALE TERMINALIA (Fig. 8I). Spermathecae with a minutely tuberculate surface; primary (paired) spermathecal stem elongate, bulbous and broader than spermathecae on basal half, distally weakly differentiated from the small spermathecae, stems separated from duct by a moderate constriction. Single spermatheca bean-shaped, separated from duct by a constriction but without an obvious stem, duct $0.7 \times$ as long as and half as wide as paired spermathecal duct. Spermathecal ducts transverse striate, slightly swollen on basal half, both arising from apex of narrow extension of bursa or common duct.

MALE TERMINALIA (Fig. 8C–D, F–G). S5 with genital fork half as long as anterior part of sternite, inner faces of short, stout, thick, slightly incurved arms with dense, short spines over entire length and with compact clusters of stout, short spines on medioventral swellings basally. Hypandrium with a broad, scoop-like anteromedial bridge. Basiphallus prominent but narrow, projecting posteriorly as a parallel-sided lobe. Distal distiphallus narrower and $0.8 \times$ as long as basal distiphallus, with a slightly expanded funnel-like apex; phallic bulb with an elongate but weakly differentiated proximal chamber and a small, spherical distal chamber. Ejaculatory apodeme smaller than epandrium, with a stout sperm pump.

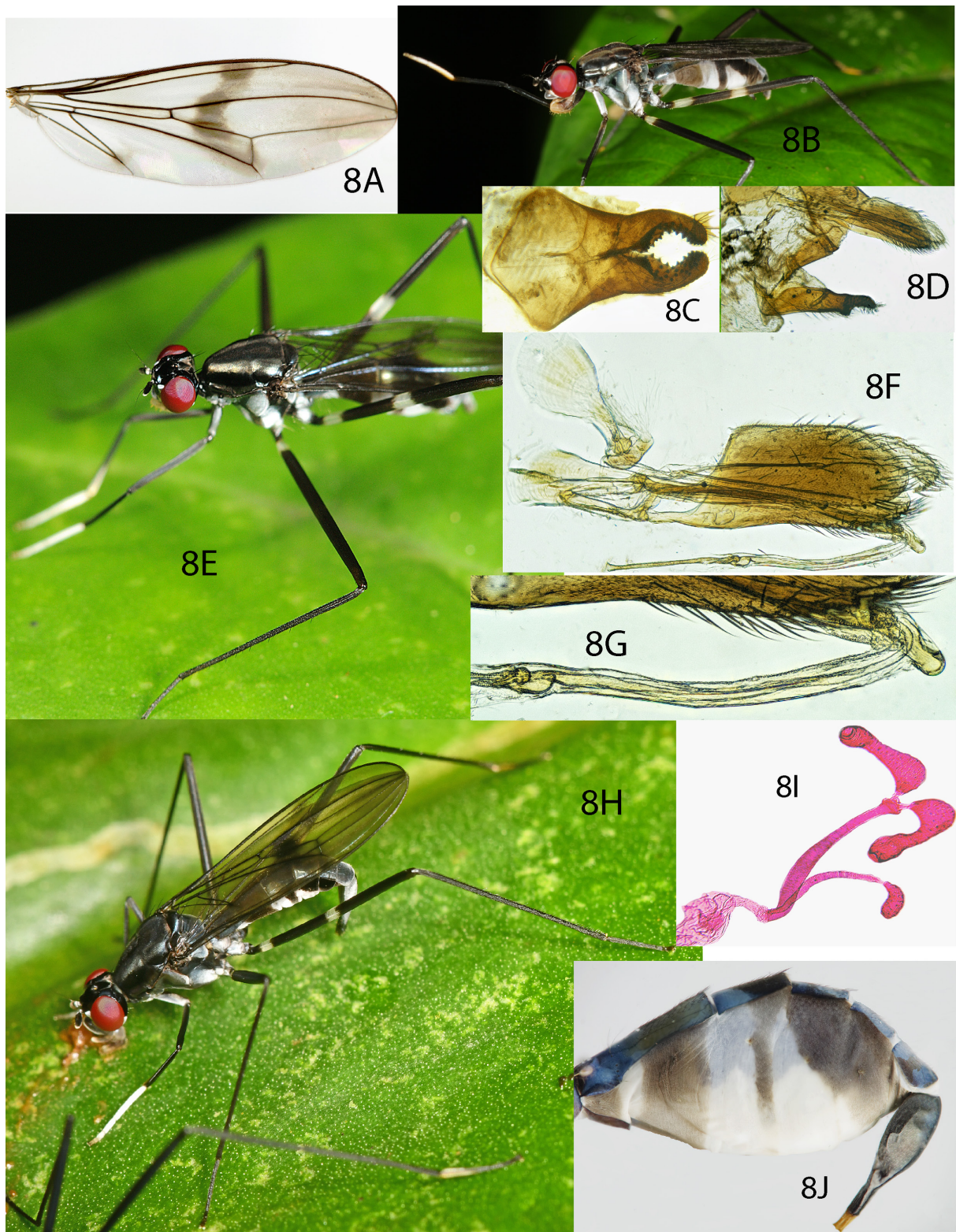


Fig. 8. *Ptilosphen crassus* Marshall sp. nov., Ecuador (DEBU). **A.** Wing. **B, E.** ♂, lateral and dorsal views. **C.** ♂, sternite 5 (genital fork). **D.** ♂, abdominal apex, left lateral view. **F.** ♂, terminalia, left lateral view. **G.** Base of phallus showing basal distiphallus and phallic bulb. **H.** Living ♀. **I.** Spermathecae and associated structures. **J.** ♀, abdomen, left lateral view.

Remarks

The partially sympatric *Pt. crassus* Marshall sp. nov. and *Pt. ramosus* Marshall sp. nov. are very difficult to distinguish without recourse to male genitalic characters, although the distinctive and widely different genitalia of these species leave no doubt that they are valid species. Males of both species can be easily recognized by the genital fork, even on the basis of dried specimens.

Ptilosphen cyaneiventris (Macquart, 1846)

Fig. 9

Calobata cyaneiventris Macquart, 1846: 343.

Ptilosphen rufifrons Enderlein, 1922: 224. **Syn. nov.**

Calobata cyaneiventris – Schiner 1868: 252. — van der Wulp 1883: 50.

Ptilosphen cyaneiventris – Enderlein 1922: 223–224. — Cresson 1930: 346. — Czerny 1932: 285. — Curran 1934a: 457. — Hennig 1934: 315, 316. — Aczél 1949: 336. — Steyskal 1968: 13. — Marshall *et al.* 2016: 543.

Ptilosphen rufifrons – Hennig 1934: 314, 317; 1937: 523. — Aczél 1949: 338. — Steyskal 1968: 13. — Schumann 1988: 106. — Ferro & de Carvalho 2014: 59. — Marshall *et al.* 2016: 543 (noted as a probable synonym of *cyaneiventris*).

Type material

Holotype of *Ptilosphen cyaneiventris*

COLOMBIA • 1 ♀; “Collection de M. Robyns, de Bruxelles” (not examined; see Remarks below).

Syntypes of *Ptilosphen rufifrons*

COLOMBIA • ♀, ♂; Cordillieren, terra caliente; MNBG.

Other material examined

Typical specimens with a dark frontal vitta

COLOMBIA • 1 ♀; Cacaguslito, Santa Maria; H. Smith leg.; CMNH • 2 ♀♀; Providencia, Algipes, 33 km SW of Zaragoza, Antioquia; 1 Dec. 1970; R. Pinger leg.; USNM • 4 ♀♀, 2 ♂♂; Magdalena, Tayrona N. Pk., Canaveral; Apr.–Aug. 2000; R. Henriquez leg.; Malaise traps; CO1 specimen MYCRO 953-22; IAVH.

PANAMA • 1 ♀, 1 ♂; Alhajuelo; 19 Feb. and 12 Mar. 1912; A. Busck leg.; USNM • 1 ♀; Canal Zone, Juan Galegos Isl.; Jun. 1981; B. Gill leg.; CNCI • 13 ♀♀, 13 ♂♂, 1 no abdomen; Canal Zone, Barro Colorado Isl.; Feb.–Aug. 1956; C.W. and M.E. Rettenmeyer leg.; 2254; SNOW • 1 ♀; Canal Zone, Barro Colorado Isl.; 7 Jan. 1971; G.W. Beyers leg.; SNOW • 1 ♀; Canal Zone, Barro Colorado Isl.; Jul. 1967; W.W. Wirth leg.; USNM • 1 ♀; Canal Zone, Barro Colorado Isl.; 20 May–11 Jun. 1981; B. Gill leg.; DEBU • 2 ♀♀; Canal Zone, Barro Colorado Island; 4–11 Dec. 1996; J. Pickering leg.; DEBU • 1 ♀; same data as for preceding 23 Apr.–5 May 1996 • 1 ♀; same data as for preceding; 11–19 May 1996 • 1 ♀; same data as for preceding; 16–23 Oct. 1996; CO1 specimen MYCRO954-22.

VENEZUELA • 1 ♂; Prov. Aragua, Rancho Grande Biol. Stn, Henri Pittier Nat. Park, La Cumbra; 8 Mar. 1995; S.A. Marshall leg.; DEBU • 1 ♀, 2 ♂♂; Prov. Aragua, Henri Pittier Nat. Park: Pico Periquito; 1680 m a.s.l.; Nov. 1997; T. Pape leg.; Malaise trap; CO1 specimen DEBU0555; DEBU • 1 ♀; Carabobo, Henri Pittier Nat. Park, Portachuelo Pass; 13 Sep. 2008; J. Skevington leg.; DEBU • 3 ♀♀; Carabobo, “Valle Seco, Jan. 40”; P. Anduze leg.; USNM • 1 ♀; Lara, Barquisimeto; R. Urtiaga leg.; “in laboratory”; USNM • 2 ♂♂; Puerto la Cruz; Dec. 1928; E. Holt leg.; CMNH.

Specimens with a red frontal vitta (“*rufifrons*”)

COLOMBIA • 1 ♀; Magdalena, Tayrona N. Pk., Canaveral; 14–29 Jun. 2000; R. Henriquez leg.; Malaise traps; IAVH • 1 ♀; Cacagusalito, Stn Marta; H.H. Smith leg.; CMNH.

PANAMA • 2 ♀♀; Trinidad River; 25 Mar. 1912; A. Busck leg.; [determined as *Pt. cyaneiventris* by Cresson, 1923]; USNM • 1 ♂; Canal Zone, Barro Colorado Isl.; 1 Aug. 1956; C.W. and M.E. Rettenmeyer leg.; 2254; SNOW.

Redescription

LENGTH. 12–14 mm.

COLOUR (Fig. 9A–B, G–H). Orange except as follows: frontal vitta usually entirely brown and well defined, sometimes uniformly orange (see Remarks below about *Ptilosphen rufifrons*). Lower frons orange, lunule orange-yellow, clypeus brown, entirely microsetulose. Palpus orange-brown, paler in apical quarter. Fore tarsomeres 4 and 5 completely dark, tarsomeres 1–3 white; fore tibia brown; fore femur yellow basally, dark brown distally. Mid tarsus and tibia brown, mid and hind femora orange-brown with white basal and distomedian rings 1–3 × width of femur, margins of rings usually not distinctly darkened (but darkened in the type). Hind tarsomeres brown except tarsomere 1 white ventrally. Wing with a small subquadrate discal band with a thin anterior branch extending anteriorly and a less distinct branch along dm-cu. Abdomen with T1 reddish brown, tergites otherwise dark brown, T2 with black posterior corners. Pleural pigmentation distinct: P1 pale, P2 black on dorsal margin and posterior half, P3 with a black band broad dorsally and tapered ventrally, distinctly separated from black part of P3 but broadly fused with the black upper half of P4–5; black area more extensive on female. Oviscape brown and shiny dorsally and apically, yellowish and densely silver microsetulose laterally.

HEAD. Frontal vitta broad, maximum width approximately $0.7 \times$ frontal width, abruptly tapered to a point anteriorly and posteriorly. Two strong fronto-orbital bristles, upper (orbital) inserted just above level of upper ocelli. Outer vertical bristle present.

THORAX. Cervical sclerite prominent in both sexes, elevated but not bilobed, narrowest posteriorly. Scapular setae very small to absent. Katepisternum with one main posterior row of strong golden bristles, setae anterior to row fine and pale. Dorsocentral bristle present.

FEMALE TERMINALIA (Fig. 9I). Paired (primary) spermathecal duct broad and parallel-sided, slightly narrower than spermathecae; paired spermathecal stems elongate and twisted, very narrow at base, paired spermathecae small, broad at one end and tapered at other, stem arising from side of narrowed end. Single spermatheca oval and tuberculate, on a very short and very narrow stem separated from duct by a threadlike constriction, single (secondary) duct $\frac{1}{2}$ as long as and $\frac{1}{4}$ as wide as paired spermathecal duct. Spermathecal ducts arising from a long apical extension of the bursa copulatrix; secondary duct apparently arising laterally from base of primary duct.

MALE TERMINALIA (Fig. 9C–F). Genital fork with two long, thin, arched arms with long, fine hairs along entire outer surface; inner face of each arm with short, stout spines forming a cluster in distal half and smaller cluster at apex; base of fork narrowly and shallowly cleft with short, blunt stout spines flanking cleft. Distal distiphallus longer than epandrium, basal distiphallus less than one third as long and $3 \times$ as wide as distal distiphallus and apparently fused with a broadly rounded basiphallus. Phallic bulb very small and simple, much narrower than apex of basal distiphallus; proximal chamber elongate but weakly differentiated, distal chamber very small but distinct. Distal distiphallus straight, apex flared into a small funnel $2\text{--}3 \times$ diameter of distal distiphallus. Anterior bridge of hypandrium short scoop-like. Ejaculatory apodeme similar in size to epandrium.

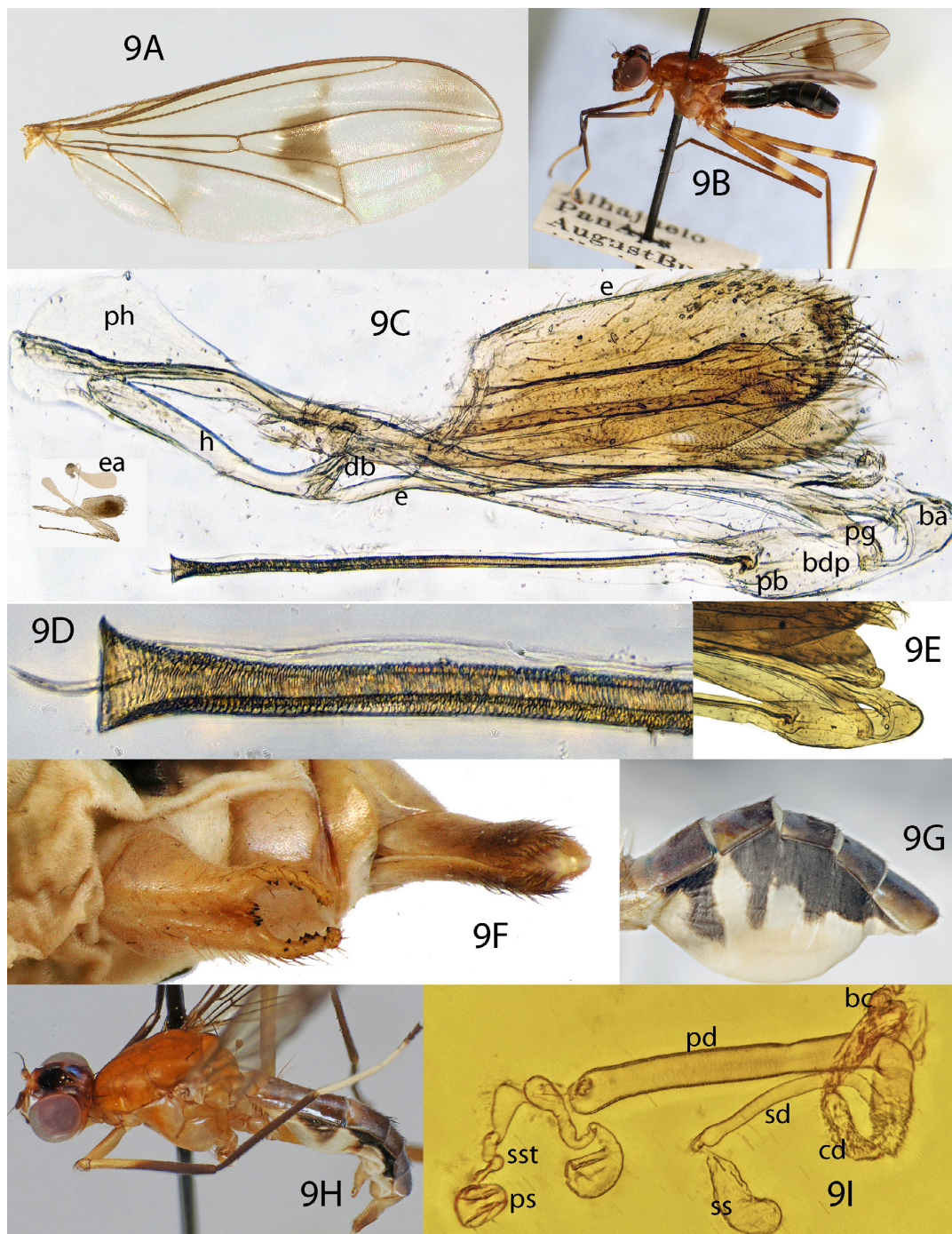


Fig. 9. *Ptilosphen cyaneiventris* (Macquart, 1846). **A.** Wing, Colombia, ♀, IAVH. **B.** ♀, Panama (USNM). **C.** ♂, terminalia, left lateral view, Panama (USNM), with inset showing relative size of ejaculatory apodeme. **D.** Apex of distiphallus, Panama (USNM). **E.** Base of phallus. showing the very short basal distiphallus, Panama (USNM). **F.** ♂, abdomen, ventral, Venezuela (DEBU). **G.** ♀, abdomen (without oviscapes) lateral view, Panama (DEBU). **H.** ♂, Venezuela (DEBU). **I.** Spermathecae and associated structures, Colombia (DEBU). Abbreviations: ba=basiphallus; bc=bursa copulatrix; bdp=basal distiphallus; cd=common duct; db=dorsal bridge; e=epandrium (also labeled on anteroventral extension); ea=ejaculatory apodeme; h=hypandrium; pb=phallic bulb; pd=paired spermathecal duct; pg=postgonite; ph=phallapodeme; ps=paired spermathecae; sd=single spermathecal duct; ss=single spermatheca; sst=spermathecal stem.

Remarks

Ptilosphen cyaneiventris is closely related to the Central American species *Pt. callichroma*, from which it can be distinguished by the white third fore tarsomere, the characteristically shaped discal wing band and by the broadly joined pigmented portions of P3 and P4–5, as well as minor differences in male terminalia and the female spermathecal complex. *Ptilosphen cyaneiventris* has a more southerly distribution than *Pt. callichroma*, with a known distribution extending from Panama to Colombia and Venezuela.

Ptilosphen rufifrons is here treated as a synonym of *Pt. cyaneiventris*, although *Pt. rufifrons* was named for specimens with a red frontal vitta, contrasting with the usual dark frontal vitta of *Pt. cyaneiventris*. Male and female syntypes of *Pt. rufifrons* (Colombia; examined at MNBG) otherwise match the above description of *Pt. cyaneiventris* and correspond exactly to one of the specimens listed above from Magdalena, Colombia. The two specimens from Trinidad River, Panama differ slightly in that the anterior extension of the discal cell is slightly displaced forward from the posterior corner. The male from Barro Colorado Island was dissected and confirmed as identical to typically coloured *Pt. cyaneiventris*.

The type of *Pt. cyaneiventris* was not located, but the description above is consistent with Hennig's (1934) diagnosis of this species. Barcoding recovers *Pt. cyaneiventris* (including specimens with a reddish frontal vitta) as a close sister group to *Pt. callichroma*.

Hennig (1934) lists "*Ptilosphen cyaneiventris* Czerny" as a junior synonym of *Pt. viriolatus* (a species here treated as a junior synonym of *Pt. callichroma* Bigot), based on Czerny's (1932) identification of specimens from Costa Rica and Venezuela as *Pt. cyaneiventris* (Macquart). Czerny's Costa Rican specimens are likely to be *Pt. callichroma*, but his Venezuelan specimen is probably *Pt. cyaneiventris*.

***Ptilosphen dellarum* Marshall sp. nov.**

[urn:lsid:zoobank.org:act:7B148F14-B520-4B87-8577-39F4C4FC3481](https://zoobank.org/act:7B148F14-B520-4B87-8577-39F4C4FC3481)

Fig. 10

Etymology

The species name honours Evelyn and Rose Dell, who helped with this project as undergraduate students in 2004.

Type material**Holotype**

COSTA RICA • ♀; Nectandra Cloud Forest Reserve; 10°11'8.61" N, 84°30'32.91" W; 1200 m a.s.l.; 19 Aug. 2022; S.A. Marshall leg.; MNCR

Paratypes

COSTA RICA • 1 ♀, 1 ♂; same data as for holotype; MNCR • 2 ♀♀; Prov. Puntarenas, Monteverde Biol. Stn, lower trail; 11 Jun. 2000; S.A. Marshall leg.; cloud forest; MNCR • 2 ♀♀; same data as for preceding; 11–13 Jun. 2000; S.A. Marshall and M. Buck leg.; DEBU • 2 ♀♀; Monteverde Biol. Stn, upper trail; 14–18 Aug. 2010; S.A. Marshall leg.; MNCR • 1 ♀; Monteverde Biol. Stn; 1500 m a.s.l.; 1 Jun. 2000; M. Buck leg.; white pans in kitchen compost; DEBU • 1 ♂, 1 ♀; Monteverde; 25–28 May 1998; E. Fisher leg.; DEBU • 1 ♂; San Luis, Monteverde; 1000–1350 m a.s.l.; Apr. 1994; Z. Fuentes leg.; MNCR • 1 ♀; Est. La Casina, Monteverde; 1520 m a.s.l.; Feb. 1994; N. Obando leg.; MNCR • 5 ♀♀, 1 ♂; Prov. Alajuela, San Ramón Biol. Res.; 900 m a.s.l.; Apr.–May 2000; P. Hanson leg.; MNCR • 1 ♀; Volcán Tenorio, N. slope nr. Bijagua Biol. Stn; 700 m a.s.l.; 16–20 Jun. 2000; S.A. Marshall leg.; rainforest; DEBU • 1 ♂; Prov. Cartago, Tapantí Natl. Pk.; 8 Aug. 2013; S.A. Marshall leg.; DEBU • 2 ♀♀; Tapantí Natl. Pk., Ranger Stn; 1200 m a.s.l.; 8–11 Oct. 1999; M. Buck leg.; pans in kitchen refuse; DEBU • 1 ♂; Río San Lorenzo, Tierras Morenas; 1050 m a.s.l.; Mar. 1993; G. Rodríguez leg.; MNCR • 1 ♂; Prov. Heredia, Rara Avis Nat. Res., 12 km S of Las Horquetas; 10°17'0" N, 84°2'50" W; 700 m a.s.l.; 22–27 Feb. 2005; S.A. Marshall leg.; DEBU • 2 ♀♀; Prov. San José, Moravia, Zurquí de Moravia;

1600 m a.s.l.; 5–9 Aug. 2013; S.A. Marshall leg.; hand collected during ZADBI bioblitz; MNCR • 1 ♀; Moravia, Zurquí de Moravia; 1600 m a.s.l.; ZADBI project leg.; 21 Oct. 2012; bait trap with chicken; MNCR • 2 ♀♀, 1 ♂; same data as for preceding; 24 Sep. 2012; bait trap; MNCR • 1 ♂; same data as for preceding; 3–10 May 2012, Malaise trap; MNCR • 1 ♂; same data as for preceding; 3–10 Nov. 2013, Malaise trap; MNCR • 1 ♀; Prov. Alajuela, Quesada, Albergue Pozo Verde; 10°15'15" N, 84°22'18" W; 1800 m a.s.l.; 21 Apr. 2023; S.A. Marshall leg.; DEBU.

Description

LENGTH. 15–16 mm.

COLOUR (Fig. 10A–B, D–E, I). Thorax orange except for black pronotum, cervical sclerite and ventral margin of proepisternum; katepisternum silvery pruinose anteriorly and posteriorly. Head, including antenna and clypeus, mostly black; frontal vitta velvety black but head otherwise dull pruinose dorsally. Lunule brown, face pale. Parafacial silvery pruinose; palpus pale yellow to white except for brown basal quarter. Legs with all trochanters black; fore tarsomeres 4 and 5 completely dark, tarsomeres 1–2 white, tarsomere 3 black distally; fore coxa orange with heavy silvery pruinosity, fore femur and tibia black. Mid tarsus and tibia brown; mid and hind femora black with white base slightly longer than width of femur and distomedian white ring 1–2 × width of femur. Hind tarsomeres 1 and 2 white, tarsomeres 3–5 black. Wing with narrow and transverse discal band and a similarly dimensioned preapical band broken by clear areas over R4+5 and M1. Abdominal tergites brown, lightly pruinose. Male abdomen with P1 dark on anterior half, white posteriorly, P2 entirely black, P3 with a ventrally tapered black band along posterior margin, distinctly separated from black part of P2 but broadly fused with the black upper half of P4–5. Female abdomen similar to male on P1–2, otherwise dark on dorsal half and white ventrally. Oviscape dark brown except for orange apical half, bare dorsally, silvery pruinose laterally on basal half.

HEAD. Outer vertical and fronto-orbital bristles normally absent but holotype (*Nectandra*) with an outer vertical on one side only. Anterior frontal vitta flat, almost straight-sided in front of ocelli and then gradually tapered to a point anteriorly, half of frontal width at maximum; postocellar frontal vitta gradually tapered to a rounded apex posteriorly.

THORAX. Cervical sclerite of female deeply concave at middle and projecting at posterior margin (Fig. 10C); cervical sclerite of male simple. Scapular (suprahumeral) setae forming a dense tuft of 5–6 stout bristles at anterolateral corner of female postpronotum; male with only small and inconspicuous scapular setae. Anterior notopleural and dorsocentral bristles absent. Katepisternum with one main posterior row of strong golden bristles, setae anterior to row fine and pale.

FEMALE TERMINALIA (Fig. 10E–F). Oviscape broad and bulbous on basal half, strongly narrowed distally. Three spermathecae on two ducts arising separately from a broad extension of the bursa copulatrix; surface of bursa extension densely covered with small processes. Paired spermathecae on a long, broad duct greatly inflated in distal third before dividing into two very short, narrow stems each leading to an elongate-cylindrical spermatheca. Single spermathecal duct very short and narrow, single spermatheca relatively large, broadly triangular and somewhat flattened, on a very short and narrow stem.

MALE TERMINALIA (Fig. 10G–H). Genital fork with two long, thin arms, incurved and almost touching apically and with long, fine hairs along entire ventral surface; inner face of each arm with short, stout spines scattered along inner margin and forming a cluster at apex; base of fork narrowly and shallowly cleft. Postgonite minute, subquadrate; upper apex minutely granulose, lower apex with cluster of seven small setulae. Basiphallus prominent, projecting posteriorly as a rounded lobe. Distiphallus twice as long as epandrium, distal distiphallus half as wide and 3 × as long as the broad basal distiphallus, with indistinct transverse striae and a slightly expanded apex. Phallic bulb short but broader than apex of basal distiphallus, proximal chamber forming a bulbous expansion of the ejaculatory duct, distal chamber forming a hemispherical cap about half as large. Anterior bridge of hypandrium ribbon-like. Ejaculatory apodeme very small, much smaller than epandrium.

Remarks

Several characters suggest that *Pt. dellarum* Marshall sp. nov. is closely related to *Pt. conveniens*, despite the superficially different appearances of the black *Pt. conveniens* and the mostly orange *Pt. dellarum*. Apparent synapomorphies shared by these species include the unusual spermathecal complex and the loss of dorsocentral and outer vertical bristles. The spermathecal complex of both species includes a strongly modified flattened-triangular single spermatheca and a strongly swollen paired spermathecal

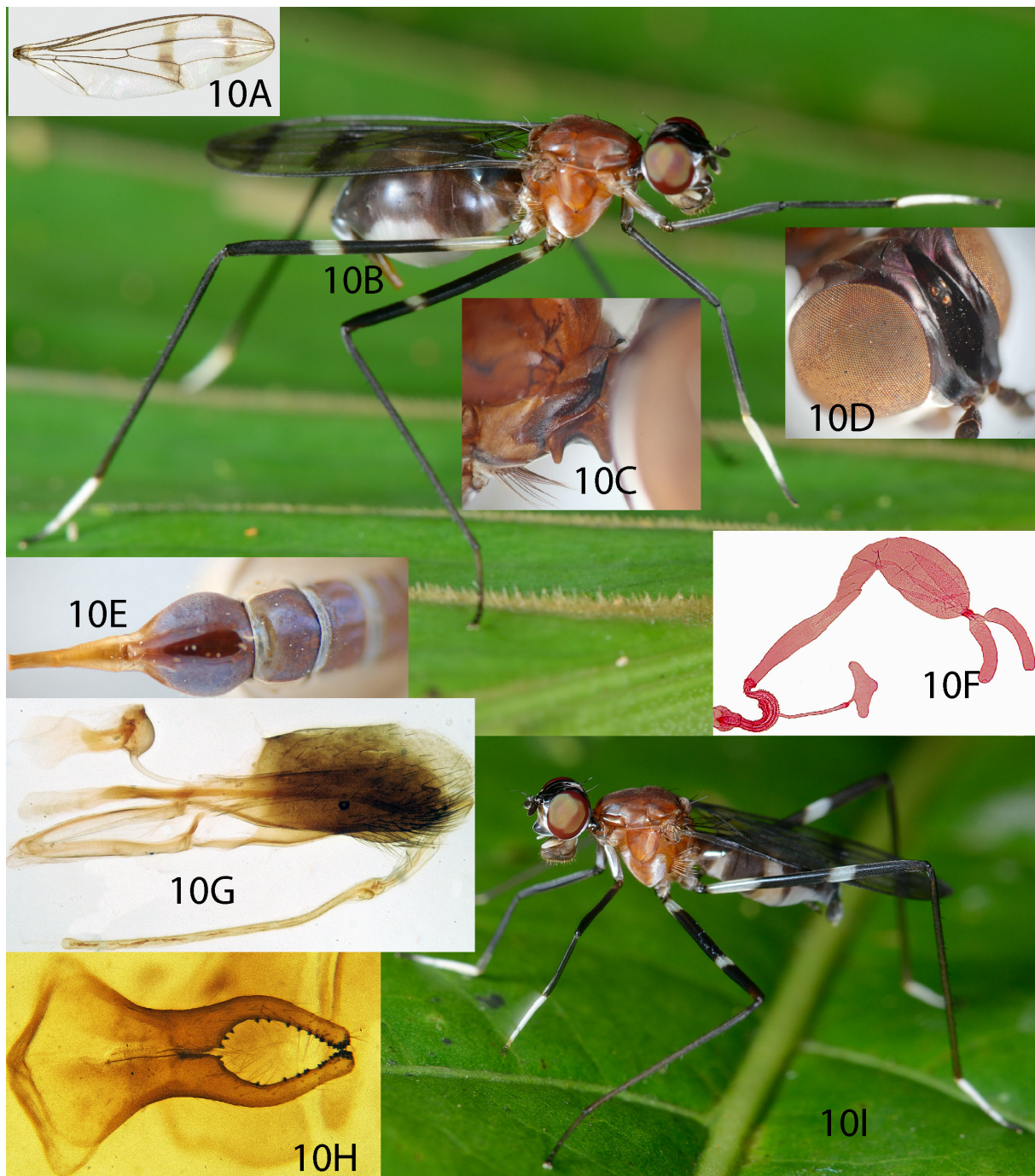


Fig. 10. *Ptilosphen dellarum* Marshall sp. nov., Costa Rica (MNCR). **A.** Wing. **B.** Living ♀. **C.** ♀, cervical sclerite. **D.** ♀, head. **E.** ♀, oviscape. **F.** Spermathecae and associated structures. **G.** ♂, terminalia, left lateral view. **H.** ♂, sternite 5 (genital fork). **I.** Living ♂.

duct with smooth paired spermathecae (spherical in *Pt. conveniens*, elongate in *Pt. dellarum*) on short stems. Both species appear to be restricted to Central America. *Ptilosphen elongatus* Marshall sp. nov., another species known only from Costa Rica, has also lost the frontal, outer vertical, dorsocentral and anterior notopleural bristles and has a similar pattern of transverse wing bands. Females of *Pt. elongatus* remain unknown and no sequence data are available.

Ptilosphen dubius Hennig, 1934

Fig. 11

Ptilosphen dubius Hennig, 1934: 316.

Ptilosphen dubius – Aczél 1949: 337. — Steyskal 1968: 13. — Albuquerque 1991: 4. — Ferro & de Carvalho 2014: 59.

Type material

Holotype

BOLIVIA • ♀; Mapiri, Sarampioni; 700 m a.s.l.; 18 Feb. 1900; W. Schnuse leg.; SMTD.

Paratypes

BOLIVIA • 1 ♂; Mapiri, San Ernesto; 800 m a.s.l.; 28 Mar. 1903; SMTD • 1 ♀; Sarampioni; 13 Feb. 1903; SMTD • 1 ♂; San Antonio; 1000 m a.s.l.; 23 Feb. 1903; SMTD • 1 ♀; San Carlos; 800 m a.s.l.; 1903; SMTD.

PERU • 1 ♀; Urubambatl; 12 Sep. 1903; SMTD.

Other material examined

BOLIVIA • 3 ♀♀, 1 ♂; Prov. La Paz, San Antonio, ca 8 km S of Mapiri; 15°20'56" S, 68°13'31" W; Apr. 2001; S.A. Marshall leg.; DEBU • 4 ♀♀, 1 ♂; same data as for preceding; CBFC • 9 ♀♀; Heath River Wildlife Centre, 21 km SSW of Puerto Heath; 12°40' S, 68°42' W; 29 Apr.–12 May 2007; S.A. Marshall leg.; DEBU • 2 ♀♀, 1 ♂; same data as for preceding; S. Paiero, J. Kits and M. Jackson leg.; CO1 specimen MYCRO-0947-22; DEBU • 5 ♀♀; San Juanito, nr. Teoponte; 15°29'42" S, 67°47'48" W; 500 m a.s.l.; Apr. 2001; S.A. Marshall leg.; CO1 specimens DEBU-0549, MYCRO-0948-22; DEBU • 1 ♀; Carasco National Park entrance, 2 km E, 12 km SW of Villa Tunari; 17°4.28' S, 65°29.257' W; 517 m a.s.l.; 16 Dec. 2016; A. Borkent leg.; USNM • 1 ♀; Prov. S. Inicua, Riv. Alto Beni; 1100 m a.s.l.; Jan. 1976; L.E. Peña leg.; CNCI.

PERU • 4 ♀♀, 3 ♂♂; Prov. Cuzco, Quincemil; 700 m a.s.l.; Nov. 1962; L. Peña leg.; CNCI • 1 ♀; Prov. Cuzco, Villa Carmen Biological Station; May 2011; T. Forster, Bennet and Razuni leg.; blue pans, Malaise trap; USNM • 5 ♀♀, 2 ♂♂; Prov. Madre de Dios, Los Amigos Biological Station; 2–14 Jun. 2006; Paiero and Klymko leg.; DEBU • 4 ♀♀, 1 ♂; Prov. Madre de Dios, Avispas; 400 m a.s.l.; Dec. 1962; L. Peña leg.; CNCI • 1 ♀; Cock of the Rock Lodge; 13°03'21" S, 71°32'46" W; 1380 m a.s.l.; 6 Dec. 2011; S.A. Marshall leg.; DEBU.

Redescription

LENGTH. 11–16 mm, usually 14–15 mm.

COLOUR (Fig. 11A, E, G). Head mostly dark reddish brown to black; lower face, parafacials and central postoccipt orange; posterior frontal vitta and parafacials densely silvery microsetulose; gena, clypeus, palpus and postgena yellow. Thorax mostly orange, sparsely microsetulose; pronotum, cervical sclerite and ventral margin of proepimeron black. Katepisternal bristles orange. Fore tarsomeres 1–3 white,

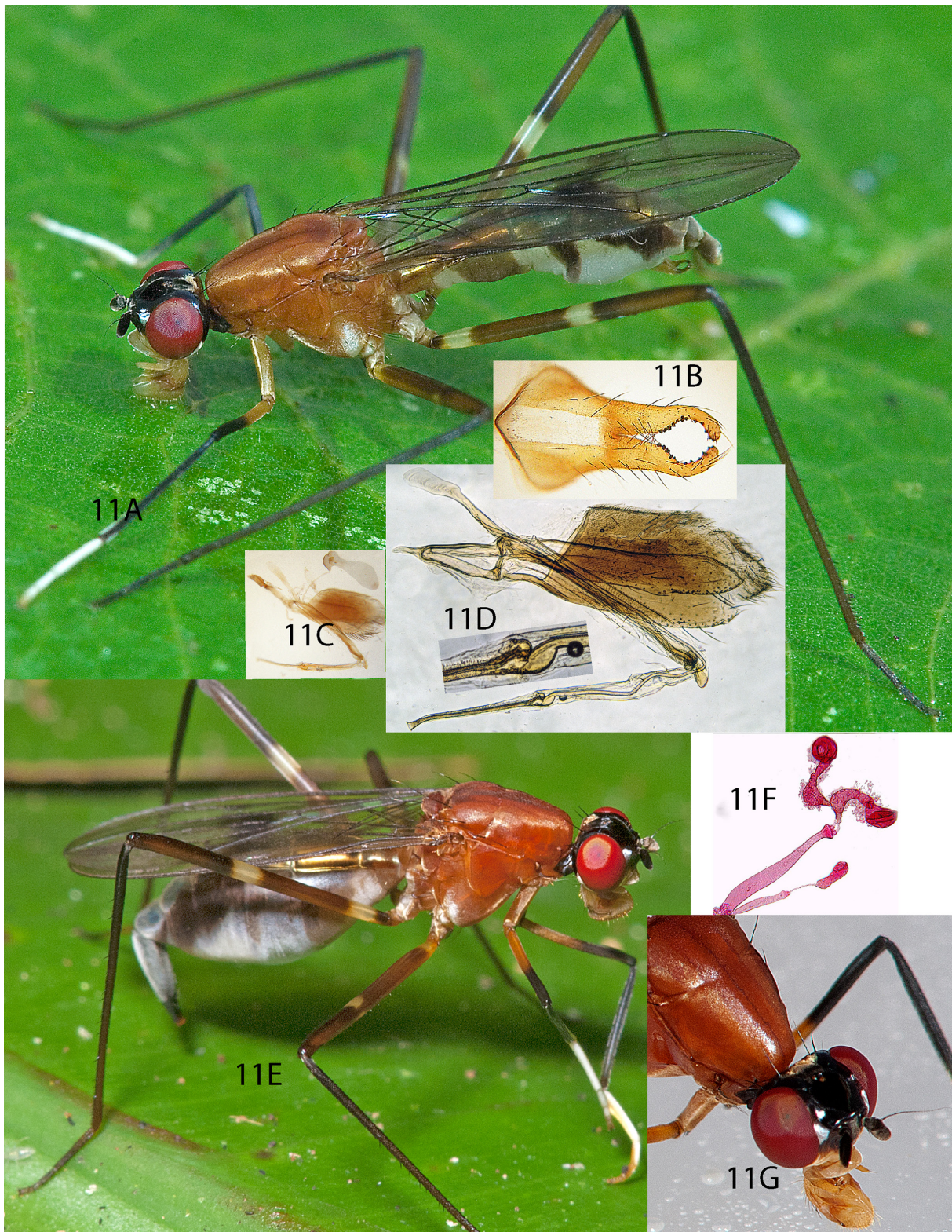


Fig. 11. *Ptilosphen dubius* Hennig, 1934, Bolivia (DEBU). **A.** Living ♂. **B.** ♂, sternite 5 (genital fork). **C.** ♂, terminalia with ejaculatory apodeme, left lateral view. **D.** ♂, terminalia, left lateral view, phallic bulb as inset. **E.** Living ♀. **F.** Spermathecae and associated structures. **G.** Head and thorax, dorsal view.

tarsomeres 4–5 white to yellowish brown with a few black setulae; fore tibia black; fore femur orange on basal half, black on distal half. Mid tarsus and tibia dark brown; mid femur and hind femur yellow-brown with medial white rings 1–2 × width of femur, mid femur with a short white basal ring, hind femur with a longer white subbasal ring. Hind tibia and hind tarsomeres brown. Abdominal tergites of male brown except for black posterior corners of T2; abdominal pleuron of male boldly banded in brown and white, with separate bands on P1, P2, and P3; the P2 band complete and broad; P4–5 dark on dorsal half. Abdomen of female with T1 brown, other tergites black; oviscape mostly dark brown, silvery microsetulose laterally and basally, dorsally and distally bare and shining, apex yellow. Pleuron of female with P2 mostly dark, P3 with a weak dark band on posterior half and P4–5 dark on dorsal half. Wing with a weak V-shaped discal band.

HEAD. Two strong fronto-orbital bristles, inner and outer vertical bristles well developed. Anterior frontal vitta broad, 0.6–0.7 × frontal width, slightly elevated and sharply tapered to a point anteriorly, postocellar frontal vitta very broad, depressed, almost parallel sided until broadly rounded apex. Frontal plate with sharp longitudinal striae. Orbital plate smooth, shiny except for microsetulose strip between inner verticals and postocellar frontal vitta.

THORAX. Cervical sclerite evenly swollen in male, female with central area flattened or concave, differentiated from sides, posterior part slightly elevated. Postpronotum microsetulose with a few pale, small and indistinct dorsal setulae. Female with a few minute scapular setae in a row of three or four; male without scapular setae. Katepisternum with one main vertical row of orange bristles. Dorsocentral bristle present.

FEMALE TERMINALIA (Fig. 11F). Three spermathecae, paired spermathecal duct slightly swollen in basal half, ending in a small swelling followed by a short threadlike constriction leading to a long, thick spermathecal stem swollen in basal half and distally narrowed to the small spherical spermathecae. Single spermathecal duct very short, ending in a long threadlike constriction leading to a small peanut-shaped spermatheca (or stem plus spermatheca) that is 1.5 × as long as duct.

MALE TERMINALIA (Fig. 11B–D). Genital fork with bases of arms broad and tubular, divided by a deep V-shaped cleft, arms distally narrow, short and strongly incurved, inner surface with sparse short spines densely packed near base and evenly spaced distally; inner basal arms absent. S5 centrally desclerotized, thus with a broad longitudinal pale area. Epaandrium long and narrow, almost 3 × as long as wide. Basiphallus small but prominent, projecting posteriorly as a tapered, apically rounded lobe. Distiphallus 1.5 × length of epaandrium, basal distiphallus broad and almost as long as epaandrium, indistinctly swollen at apex to form proximal chamber of phallic bulb, distal chamber of phallic bulb very small; distal distiphallus with transverse striations, 0.8 × length of basal distiphallus, apex funnel-shaped. Hypaandrium with narrow, tongue-like anterior bridge. Postgonite small but bulbous, with three minute setulae anteroventrally, posterior surface densely granulate. Ejaculatory apodeme narrower and shorter than epaandrium.

Remarks

Ptilosphen dubius Hennig, 1934 differs consistently from the otherwise similar species *Pt. insignis* Wiedemann, 1830 by its mostly black pronotal collar and cervical sclerite, by its darker oviscape and by differences in the male and female genitalia. The strikingly modified male sternite 5 with a clear basal area and the basally tubular, distally narrowed incurved genital fork arms of *Pt. dubius* (Fig. 11B) contrast with the broad, straight arms of the *Pt. insignis* genital fork (Fig. 18G). The *Pt. dubius* paired spermathecal stems are simpler and the spermathecae are more elongate than in *Pt. insignis*.

We have labelled a series of six specimens from Pucallpa, Peru collected in 1951 (USNM) as “near *Pt. dubius*” because they differ from *Pt. dubius* in having almost clear wings, with pigmentation absent or restricted to a small area below R₄₊₅. Male and female genitalia seem to match *Pt. dubius*. As noted below in the remarks under *Pt. insignis*, specimens of *Pt. insignis* collected with *Pt. dubius* at the Heath

River Wildlife Centre in Bolivia were recovered in the same CO1 BIN as *Pt. dubius*. Those specimens, however, match *Pt. insignis*, not *Pt. dubius*, in morphology. CO1 data from other specimens suggest that *Pt. dubius* is more closely related to the dark-bodied species *Pt. enderleini* Cresson, 1930 and *Pt. crassus* Marshall sp. nov. than to *Pt. insignis*.

Ptilosphen elongatus Marshall sp. nov.

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Fig. 12

Etymology

The specific name refers to the elongate abdominal structures including the genital fork, epandrium and distiphallus.

Type material

Holotype

COSTA RICA • ♂; San Jose, Est. Santa Elena, Viejo, Las Nubes; 1210 m a.s.l.; 4–15 Jan. 1996; E. Alfaro leg.; Amarilla L S 371750-507800 #6864; MNCR.

Paratype

COSTA RICA • 1 ♂; San Jose, Est. Santa Elena, Sendero El Llano; 1500 m a.s.l.; 9 Jan. 1996; E. Alfaro leg.; Amarilla L S 371300-509200 #6863; MNCR.

Description

LENGTH. 13 mm.

COLOUR (Fig. 12A–B). Dark brown to black except as follows: frontal vitta entirely dull orange and well defined, frontal plate shiny orange; ocellar triangle, epicephalon and paracephalon reddish brown with a microtrichose area between inner vertical bristles and on postoccipt. Antenna with pedicel and distal part of first flagellomere reddish brown, basal part of first flagellomere orange, subantennal depression black and microsetulose. Palpus yellow, lunule and lower face pale; clypeus brown, entirely pale setulose. Fore tarsomeres 3–5 and apex of tarsomere 2 light brown with black setulae, tarsomeres 1 and 2 otherwise white with white setulae. Mid and hind femora with white ring in distal third and a reddish apex; mid femur with a white base $3 \times$ width of femur, hind femur with white ring $4 \times$ width of femur; hind tibia brown; hind tarsomeres 2–5 brown, tarsomere 1 with dense short white setulae ventrally. Wing with indistinct transverse basal and preapical bands, the latter continuous with weak apical infuscation, and a broad, parallel sided discal band. Abdominal tergites mostly black with a metallic blue tinge. Pleuron with a distinct pattern of black microsetulose bands: P1 white, P2 entirely black, P3 black on posterior half, P4–6 black on dorsal third.

HEAD. Fronto-orbital bristles apparently absent (no sockets visible). Frontal vitta broad anteriorly, $0.6 \times$ frontal width at maximum, abruptly tapered to a point at anterior margin of frons, narrow posteriorly and gradually tapered to a rounded point between the inner verticals. Outer vertical bristle absent.

THORAX. Prosternum microsetulose, anteriorly with a few marginal setulae. Posterior cervical sclerite densely microtrichose except on anterior quarter, weakly convex. Postpronotum entirely microsetulose, dorsal surface flat or somewhat depressed. Five stout but small and inconspicuous scapular setae in a more or less transverse row. One posterior notopleural bristle, anterior notopleural bristle absent. Pleuron almost entirely microsetulose except for a small bare area on the anteroventral corner of the anepisternum. Katepisternum with one vertical row of strong setae preceded by a vertical row in which only the lower 6 setae are long and dark and the upper setae are small, fine and pale. Dorsocentral bristles absent.

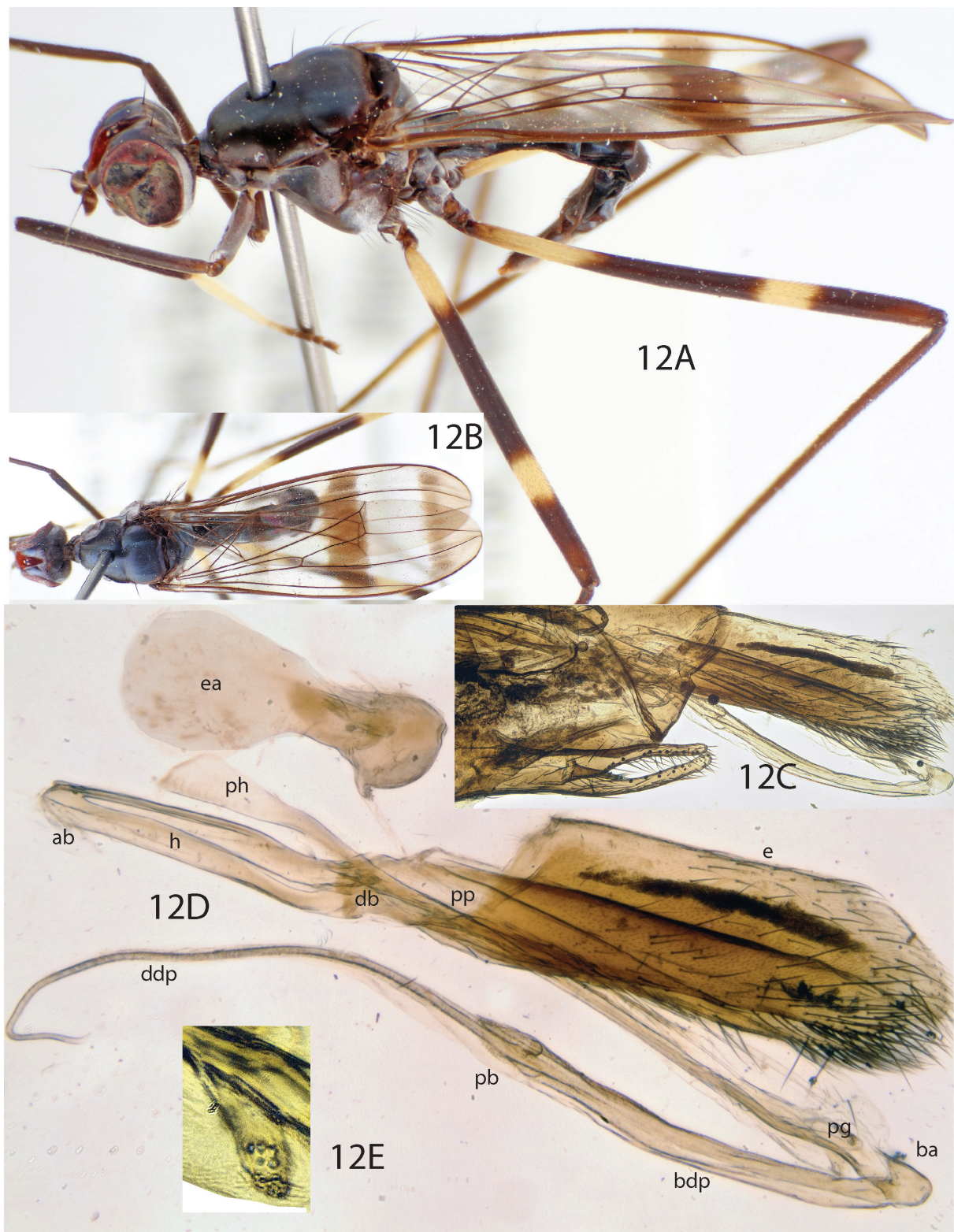


Fig. 12. *Ptilosphen elongatus* Marshall sp. nov., holotype, ♂, Costa Rica (MNCR). A–B. Habitus. C. Abdominal apex, left lateral view. D. Terminalia, left lateral view. E. Detail of left postgonite. Abbreviations: ab=anterior bridge of hypandrium; ba=basiphallus; bdp=basal distiphallus; db=dorsal bridge of hypandrium; ddp=distal distiphallus; e=epandrium; ea=ejaculatory apodeme; h=hypandrium; pb=phallic bulb; pg=postgonite; ph=phallapodeme; pp=phallic plate.

FEMALE TERMINALIA. Female unknown.

MALE TERMINALIA (Fig. 12C–E). Genital fork strikingly elongate, with a long base and two long very slightly incurved arms with long setae along the inner ventral surfaces and a few short, stout cone-like spinules along the ventral surface. Basiphallus small, barely distinguishable from base of distiphallus, slightly projecting posteriorly (Fig. 12H). Distiphallus very long, basal distiphallus as long as epandrium; phallic bulb elongate, with a weakly differentiated basal chamber and a relatively large distal chamber apparently overlapping the base of a long, thin, curved distal distiphallus ringed by weak striae. Subepandrial sclerite uniformly sclerotized, postgonite very small but narrow and finger-like, with a patch of distal spinules and a few small apical setulae.

Remarks

Although it is known from only two male specimens, *Pt. elongatus* is a distinctive species, distinguished from congeners on the basis of several characters in addition to its uniquely elongated abdominal structures. Like the similar and probably closely related *Pt. conveniens*, also known from Costa Rica, *Pt. elongatus* lacks outer vertical and dorsocentral bristles. Unlike *Pt. conveniens*, *Pt. elongatus* lacks an anterior notopleural bristle and apparently lacks frontal bristles as well. The distinctive transverse discal wing band of *Pt. elongatus* is markedly different from the triangular discal band of *Pt. conveniens*.

Ptilosphen enderleini Cresson, 1930

Fig. 13

Ptilosphen enderleini Cresson, 1930: 346.

Ptilosphen enderleini – Hennig 1934: 315, 318. — Hendel 1936: 72. — Aczél 1949: 337. — Steyskal 1968: 13. — Roback 1969: 536. — Ferro & de Carvalho 2014: 59. — Marshall *et al.* 2016: 543.

Type material

Holotype

PERU • ♂; Puerto Bermudez, Rio Pichis; 12–19 Jul. 1920; Cornell Univ. Exped., Lot 569; CUIC (examined at CUIC, 2012).

Paratypes

PERU • 3 ♀♀; same data as for holotype; CUIC.

Other material examined

COLOMBIA • 1 ♀, 1 ♂; Prov. Putumayo, Parque Nacional Naturale La Paya Cabana La Paya; 330 m a.s.l.; 5–25 Dec. 2001; E. Lozano leg.; Malaise trap; DEBU • 1 ♀, 1 ♂; same data as for preceding; 20 Nov.–5 Dec. 2001; IAVH.

ECUADOR • 3 ♀♀, 6 ♂♂; Prov. Napo, Jatun Sacha, Res., 6 km E of Misahualli; 1°4' S, 77°37' W; 450 m a.s.l.; May 2002; Marshall and Buck leg.; CO1 specimen DEBUA291-17; DEBU • 4 ♀♀, 6 ♂♂; same data as for preceding; QCAZ • 2 ♀♀, 3 ♂♂; Yasuni Natl. Pk, Yasuni Research Station; 28 Apr.–8 May 2009; S.A. Marshall leg.; DEBU • 1 ♀, 2 ♂♂; Tiputini Biodiv. Stn, vic. Yasuni Ntl. Pk.; 14–18 Feb. 1999; D.C. Darling leg.; ROME • 1 ♀, 1 ♂; Tiputini Biodiv. Stn; May 2011; S.A. Marshall leg.; DEBU • 1 ♀; Coca; 250 m a.s.l.; May 1965; L. Peña leg.; CNCI • 1 ♂; Prov. Zamora, Jumboe Riv.; 1200 m a.s.l.; Apr. 1965; L. Peña leg.; CNCI • 2 ♀♀; Napo, Narupa Yacu Reserve; 0°40'50" S, 76°24'2" W; 250 m a.s.l.; May 2019; K. Lindsay leg.; DEBU.

Redescription

LENGTH. 11–13 mm.

COLOUR (Fig. 13A, D–E, J–K). Frons black, frontal vitta pruinose and dull, sometimes reddish at anterior apex only; paracephalon, lower epicephalon and frontal plate shiny, upper epicephalon and posterior frontal vitta silvery microsetulose. Lunule reddish and setulose; scape, pedicel and base of first flagellomere reddish brown, antenna otherwise black; upper face brown, lower face yellow, parafacial white to silvery pruinose, subantennal depression shiny black. Clypeus yellow to orange, entirely microsetulose. Palpus orange in distal quarter, otherwise brown. Notum black, indistinctly vittate with incomplete golden-brown microsetulose central vitta separating broader silvery microsetulose vittae, pleuron with extensive pruinosity forming vertical bands. Fore coxa reddish brown, densely microsetulose; fore tarsus white; fore tibia dark brown; fore femur orange basally, dark brown distally. Mid coxa reddish brown, heavily silvery microsetulose. Mid tarsus and tibia brown; mid femur with basal and medial white rings $1\text{--}2 \times$ width of femur, otherwise dark brown to black proximal to distomedian white band, brown to reddish brown distal to distomedian white band. Hind coxa reddish brown, silvery microsetulose on posterior half. Hind femur brown with basal or subbasal and medial white rings $1\text{--}2 \times$ width of femur, base of femur with a narrow or obsolete dark area; hind tibia and tarsus brown. Wing with a small, relatively indistinct dot-like discal wing band mostly contained in cell r_{4+5} . Abdominal tergites blue-black, lightly silvery pruinose on central part of T1–2 and almost all of T3, otherwise heavily pruinose, oviscape silvery pruinose basally and laterally, leaving a bare dorsal strip. Pleuron boldly banded in black and white, with separate bands on P1, P2, and P3 and dorsal pigmentation on P4–6, P3 largely pale, with dark band complete and narrow in males, broader, incomplete and continuous with the P4–6 pigmentation in females.

HEAD. Two large fronto-orbital bristles, upper inserted at level of upper ocelli. Frontal vitta broad, $0.5 \times$ frontal width at maximum, sharply tapered anteriorly and mostly parallel sided posteriorly, rounded at posterior apex. Outer vertical bristle present.

THORAX. Prosternum entirely microsetulose, with a deep central pit. Cervical sclerite broad, slightly depressed medially in male, deeply depressed medially and thus distinctly bilobate in female. Postpronotum uniformly microsetulose with a few scattered small setulae. Scapular setae absent. Notopleuron with two bristles, anterior small. Dorsocentral bristle present.

FEMALE TERMINALIA (Fig. 13B–C). Bursa copulatrix narrow, terminating in a bulbous, bottle-like common duct about half as long as the paired spermathecal duct; paired (primary) spermathecal duct and single spermathecal duct arising separately at apex of common duct. Primary duct with a distal swelling followed by narrow constriction basal to broad, tuberculate stems similar in width to the elongate oval paired spermathecae. Secondary (single) spermathecal duct shorter but similar in diameter to primary duct, with a smaller distal swelling and a very narrow constriction between duct and simple, round spermatheca covered with small circular indents.

MALE TERMINALIA (Fig. 13F–I). Genital fork with a long base and two long, thin, arched arms with fine hairs along entire outer surface; inner face of arms with dense, short spines extending entire length of arm; two compact clusters of stout, medial spines at base where arms converge; base of fork between arms with shallow groove. Epandrium long and narrow, $2.5 \times$ as long as wide. Basiphallus well sclerotized and distinct from distiphallus, short and broadly rounded. Basal distiphallus equal in length to epandrium, slightly longer than the narrower distal distiphallus; distal distiphallus with transverse striae and a broadened and funnel-shaped apex. Phallic bulb small, with a small proximal chamber and a slightly smaller distal chamber. Postgonite bulbous and densely covered with small teeth posteriorly, with three minute setulae anteroventrally. Ejaculatory apodeme slightly smaller than epandrium. Margin of subepandrial sclerite heavily sclerotized to form distinct bacilliform sclerite. Hypandrium with a long, tongue-like anterior bridge and a narrow, sinuate dorsal bridge, phallic plate with transverse rows of minute microtrichiae.

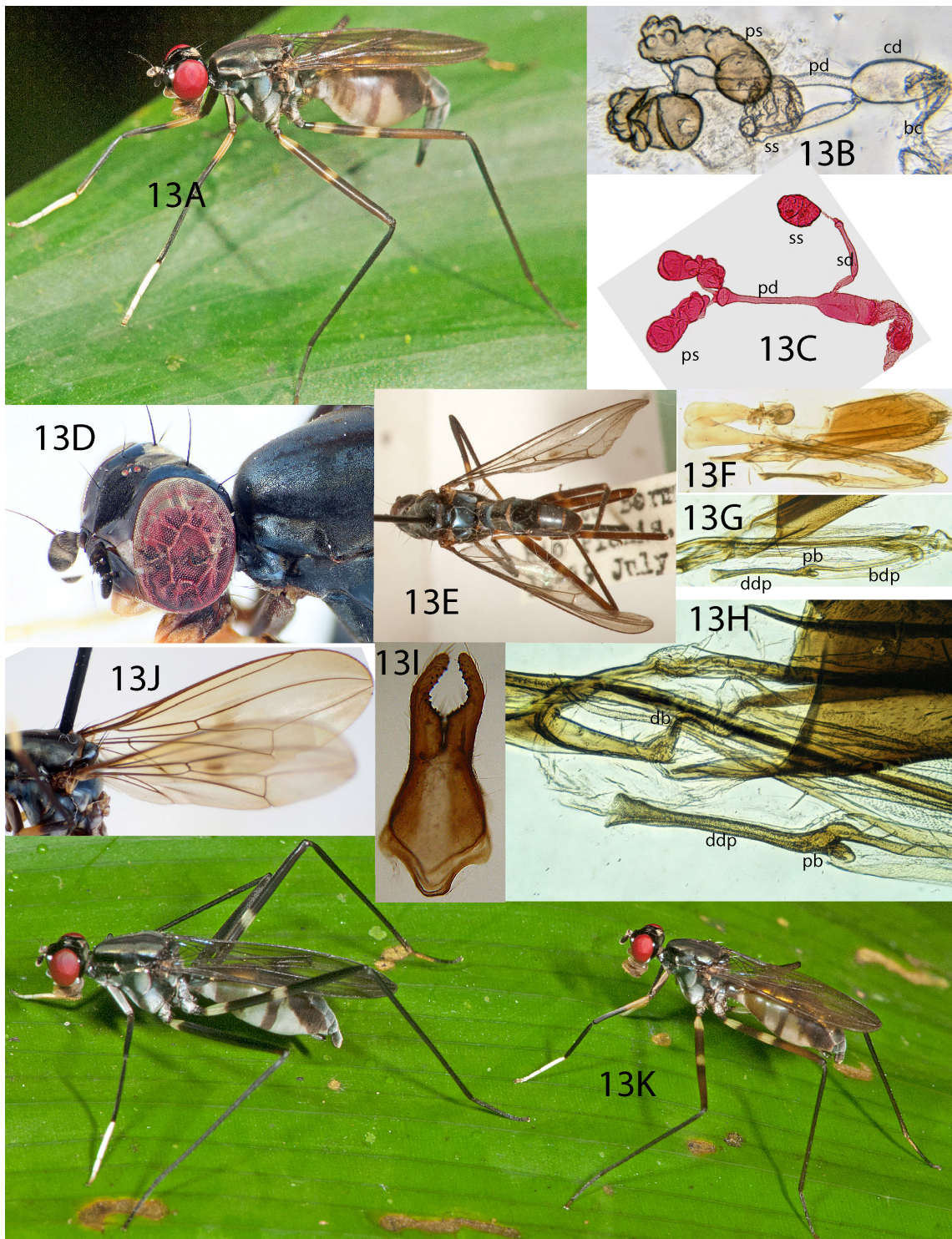


Fig. 13. *Ptilosphen enderleini* Cresson, 1930, Ecuador (DEBU) unless otherwise indicated. **A.** Living ♀. **B–C.** Spermathecae and associated structures. **D.** ♂, head. **E.** Holotype, ♂, Peru (CUIC). **F–H.** ♂, terminalia, left lateral and left dorsolateral views detail. **I.** ♂, sternite 5 (genital fork). **J.** ♂, wings. **K.** ♂ (right), with larger ♂ *Pt. crassus* Marshall sp. nov. (left). Abbreviations: bc=bursa copulatrix; bdp=basal distiphallus; cd=common duct; db=dorsal bridge; ddp=distal distiphallus; pb=phallic bulb; pd=paired (primary) spermathecal duct; ps=paired spermatheca; sd=single (secondary) spermathecal duct; ss=single spermatheca.

Remarks

Cresson's (1930) original description of this species is brief and fits both *Pt. enderleini* and *Pt. manu*, while Hennig's (1934) concept of the species explicitly encompassed material corresponding to both species, writing that a topotypic specimen in Dresden had "the wing spot only faintly indicated" (typical of *Pt. enderleini*) whereas in a specimen from elsewhere in Peru (Pichis-Weg) "the wing spot is sharply defined and brightly colored (typical of *Pt. manu*)". Hennig also determined three specimens in the BMNH, collected by H.W. Bates in Brazil ("Amazonas"), as *Pt. enderleini* although they also have a sharply defined discal band ("wing spot") with a diffuse extension to R_{2+3} as is typical for *Pt. manu*. The other two Brazilian specimens identified as *Pt. enderleini* by Hennig, both in MLUH, have not been re-examined and we have seen no other *Pt. enderleini* from Brazil.

The two species cluster together in both CO1 analyses (Fig. 30). In the ML analysis (Fig. 30B), *Pt. enderleini* is recovered, with weak support, between the two sequences of *Pt. manu* Marshall sp. nov., but there are morphological characters that support the treatment of them as distinct species, and the distance between the two *Pt. manu* sequences is shorter than to *Pt. enderleini* (as in Fig. 30A). Despite the close external similarity between *Pt. enderleini* and *Pt. manu*, their female spermathecal complex and male distiphallus differ widely (in *Pt. manu* the basal distiphallus is very short and the primary spermathecal duct has a long and gently tapered swollen part). *Ptilosphen xanthicoxa* Marshall sp. nov., from Brazil and Colombia (no available sequence data), is also closely related to *Pt. enderleini*, from which it differs in details of the spermathecal complex (the basally inserted single spermathecal duct and constricted paired spermathecal stems).

Ptilosphen facetus Enderlein, 1922

Fig. 14

Ptilosphen facetus Enderlein, 1922: 223, 225.

Ptilosphen facetus – Hennig 1934: 315, 319. — Aczél 1949: 337. — Steyskal 1968: 13. — Schumann 1988: 93. — Marshall *et al.* 2016: 543.

Type material

Holotype

ECUADOR • ♂; Balzapamba; R. Haensch leg.; MNBG.

Other material examined

COLOMBIA • 2 ♀♀; Prov. B'ventura, Anchicaya; 400 m a.s.l.; Feb. 1970; D.M. Wood leg.; CNCI.

ECUADOR • 2 ♀♀, 3 ♂♂; Prov. Pichincha, Maquipucuna Bio. Res; 1200 m a.s.l.; 27 Oct. 1999; S.A. Marshall leg.; DEBU • 8 ♀♀, 4 ♂♂; same data as for preceding; 28 Apr. 2002; S.A. Marshall and M. Buck leg.; QCAZ • 3 ♀♀, 3 ♂♂; same data as for preceding; CO1 specimens MYCRO943-22, DEBU290-17; DEBU • 1 ♀; Sto. Domingo; 600 m a.s.l.; June 1965; L. Peña leg.; CNCI.

Redescription

LENGTH. 13–16 mm.

COLOUR (Fig. 14A–B, E–H). Dark shiny blue-black except as follows: frontal vitta entirely dull orange and well defined, frontal plate shiny reddish brown; ocellar triangle, epicephalon and paracephalon reddish brown with a microtrichose area between inner vertical bristles and on postocciptus. Palpus yellow

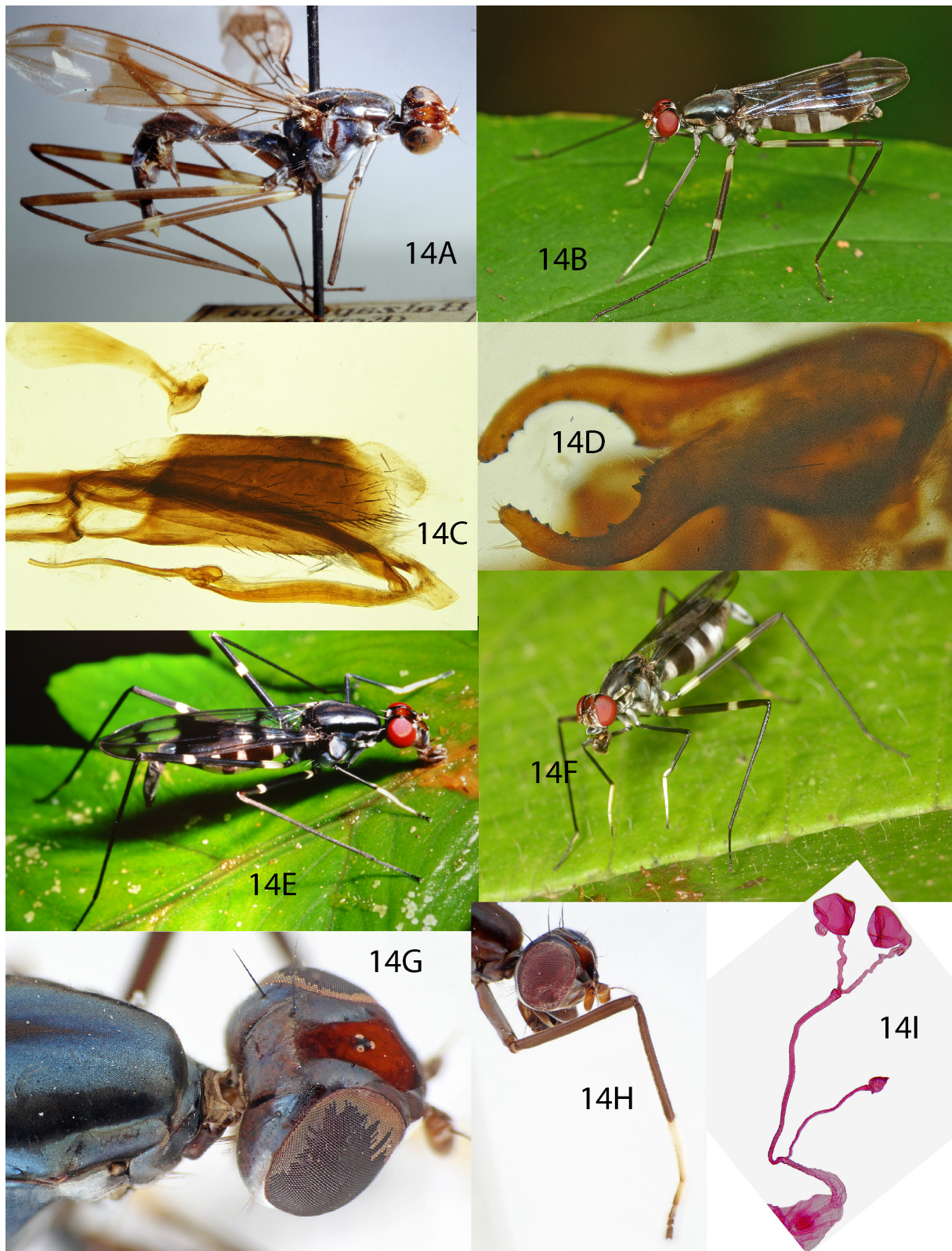


Fig. 14. *Ptilosphen facetus* Enderlein, 1922, Ecuador (DEBU except holotype). **A.** Holotype, ♂ (MNBG). **B.** Living ♂. **C.** ♂, terminalia, left lateral view. **D.** ♂, sternite 5 (genital fork). **E–F.** Living ♀. **G.** ♀, head and thorax, dorsal view. **H.** ♀, head and foreleg. **I.** Spermathecae and associated structures.

in apical third, otherwise brown; antenna and lunule orange, face brown, clypeus black and entirely setulose. Notum mostly silvery pruinose dorsally but with a narrow and anteriorly tapered incomplete brown medial vitta; black dorsolaterally. Fore tarsomeres 3–5 and apex of tarsomere 2 brown, tarsomeres 1 and 2 otherwise white; foreleg otherwise dark brown. Mid tarsus and tibia brown; mid and hind femora brown with white rings at distal third; mid femur with a white base $1\text{--}3 \times$ width of femur, hind femur with white basal ring $2\text{--}4 \times$ width of femur; hind tibia and tarsus brown. Wing with transverse basal and preapical bands and broadly triangular discal band, preapical band staggered with part in cell r4+5 more basal. Abdominal T1–2 blue-black except for dull black anterior margin of T1 and dull black middle of T2, other tergites blue-black along anterior third, T5 with a narrow blue-black longitudinal line and a narrow blue-black posterior margin, tergites otherwise dull black. Abdominal P1 of female black on anterior half, P2 entirely black, P3 with a broad vertical band, P4 with a broad band on upper half only, P5–6 entirely black; oviscape brown, mostly silvery pruinose except for a narrow bare dorsal strip and a bare, shiny apical fifth. Male abdomen with pleural pigmentation similar to female on segments 1–3, P4–5 with dense white microsetulosity covering ventral $\frac{2}{3}$ of pleuron; epandrium brown and entirely microsetulose.

HEAD. Two pairs of fronto-orbital bristles, upper pair large. Frontal vitta convex, gradually tapered to a point both anteriorly and posteriorly, $0.7 \times$ width of frons at maximum. Outer vertical bristle present.

THORAX. Prosternum bare except for minute scattered setulae. Cervical sclerite finely microtrichose except at anterior margin, female with centre part depressed, strongly differentiated and divided from anterior part, posterior part strongly convex; male cervical sclerite with centre and posterior parts almost uniformly convex. Scapular setae not differentiated from anterior dorsocentral setulae. Postpronotum microsetulose dorsally, bare laterally, with a few scattered setulae. Two notopleural bristles, anterior $0.5 \times$ as long as posterior. Katepisternum with one vertical row of strong setae preceded by a vertical row of about six fine lower setae and scattered small, fine and pale upper setae. Dorsocentral bristle present.

FEMALE TERMINALIA (Fig. 14I). Three spermathecae, paired spermathecae on a long, uniform-width primary duct arising from the apex of an elongate common duct, apex of primary duct slightly swollen where it divides into two long, sinuate stems each ending in a broadly cup-shaped spermatheca. Single spermathecal duct arising from side of common duct, smaller and shorter than primary duct, ending in a very small acorn-shaped spermatheca.

MALE TERMINALIA (Fig. 14C–D). Genital fork with two strongly incurved arched arms with fine hairs distally on outer surface and short, small spines scattered along length of inner surface and in a loose basal cluster and on a slightly raised inner basal process; base with shallow groove. Basiphallus prominent, much wider than basal distiphallus and projecting posteriorly as a subquadrate lobe. Basal distiphallus broad, slightly shorter than epandrium, distal distiphallus narrower and slightly shorter, ringed by fine striae, weakly sinuate and not expanded at apex. Phallic bulb broad, proximal chamber about twice the size of the inconspicuous distal chamber. Hypandrium with a scoop-like anterior bridge. Subepandrial sclerite uniformly sclerotized. Postgonite very small and short, with a tapered and weakly spinulose apex and a few small setulae on anterior surface.

Remarks

Ptilosphen facetus is externally similar to and apparently closely related to *Pt. gentilis* (Central America) and *Pt. boroboro* Marshall sp. nov. (Colombia), both of which differ from *Pt. facetus* in having a four-branched male genital fork. CO1 data supports a close relationship between *Pt. facetus* and *Pt. gentilis* (Fig. 30).

Ptilosphen fulvus (Walker, 1849)

Fig. 15

Calobata fulva Walker, 1849: 1050.

Ptilosphen ochraceus Enderlein, 1922: 225. Synonymized with *fulvus* by Steyskal (1967: 77).

Ptilosphen ochraceus – Hennig 1934: 314, 317. — Aczél 1949: 338. — Schumann 1988: 103.

Calobata fulva – Hennig 1934: 321.

Ptilosphen fulvus – Steyskal 1967: 77; 1968: 13. — Ferro & de Carvalho 2014: 59.

Type material

Holotype of *Ptilosphen fulvus*

BRAZIL • ♀; “Amaz // round green-ringed label // type // *Calobata fulva* Walk.”; NHMUK, NHMUK010579826 (labelled as holotype by D. Whitmore in 2016).

Paratype of *Ptilosphen fulvus*

BRAZIL • 1 ♀; Para; (labels read “Amaz. // one of Walker’s series so named, E.A.W. // *Calobata fulva* Walk.”); NHMUK.

Syntypes of *Ptilosphen ochraceus*

BRAZIL • 2 ♀♀; Para, Sieber; MNBG.

Other material examined

BRAZIL • 1 ♀; Prov. Amazon, S. Pedru da Agua Branca, F. Sta Rosa; 5°07'07" S, 48°15'19" W; Dec. 2001; Rafael, Oliveira and Vidal leg.; INPA • 2 ♀♀ (one dissected); Upper Rocana, N. Para; Jul. 1918; S.M. Klages leg.; CMNH.

FRENCH GUIANA • 1 ♀; Mitaraka, on trail between inserberg and swamp; M. Pollett leg.; dissected and illustrated, sequenced for CO1 MYCRO952-22; MNHN.

LOCALITY UNKNOWN • 1 ♀; labelled “*Calobata testacea*” (no locality or collector; *C. testacea* is a *Poecilotylus*, as confirmed by examination of the type in ZMUC, but this specimen is certainly a *Ptilosphen* and probably *Pt. fulvus*); OXUM.

Redescription

LENGTH. 16–18 mm.

COLOUR (Fig. 15A–C). Orange except as follows: parafacial and posterior genal margin silvery pruinose. Anterior margin of pronotum narrowly dark brown. Fore tarsomeres 4–5 reddish brown, tarsomeres 1 and 2 and base of tarsomere 3 white; fore tibia and apex of fore femur dark brown to black. Mid tarsomeres and mid tibia brown; mid and hind femora uniformly orange (hind tibia with indistinct yellowish area at distal third on some specimens, including holotype); hind tibia and hind tarsomeres dark brown. Wing with discal pigmentation diffuse, elongate, surrounding most of vein M between r-m and dm-cu. Abdominal tergites mostly shiny brown with a blue tinge on some specimens, posterolateral corners of T2 darkened, base of T1+2 pale; pleural pigmentation indistinct on all available specimens, upper part of P3–5 apparently darkened.

HEAD. Frontal vitta tapered anteriorly to a point above lower margin of frons, half as wide as frons; one small frontal bristle at widest point of vitta; postocellar part of frontal vitta gradually tapered. Outer vertical bristle present.

THORAX. Prosternum bare except for microsetulose anterior margin. Cervical sclerite quadrate, depressed and differentiated at middle and thus slightly bilobed. Postpronotal lobe microsetulose but without setae. Scapular setae absent. Katepisternal bristles golden. Notopleuron with two equal bristles. Dorsocentral bristle present.

FEMALE TERMINALIA (Fig. 15D). Paired spermathecae suboval with a deeply inverted (everted in some preparations) apex and an elongate, thick stem with small conical protuberances, stem separated from apex of primary duct by a very narrow and elongate constriction; duct long, thin with tight transverse striations. Single spermatheca similar but smaller and without the elongate stem, single duct $\frac{3}{4}$ as long as, and of equal width to, primary spermathecal duct; both ducts arising at apex of a very narrow common duct or bursa extension.

MALE TERMINALIA. Male unknown.

Remarks

This species is characterized by an almost entirely orange body, an unmarked abdominal pleuron and a relatively large size. With such limited material, and without male specimens, it is difficult to fully characterize the species, and there are no obvious close relatives. The only available CO1 sequence is too short to provide strong support for relationships. Walker's description of *Pt. fulvus* suggests that it is "nearly allied to *C. testacea*", but *C. testacea* is a *Poecilotylus*.

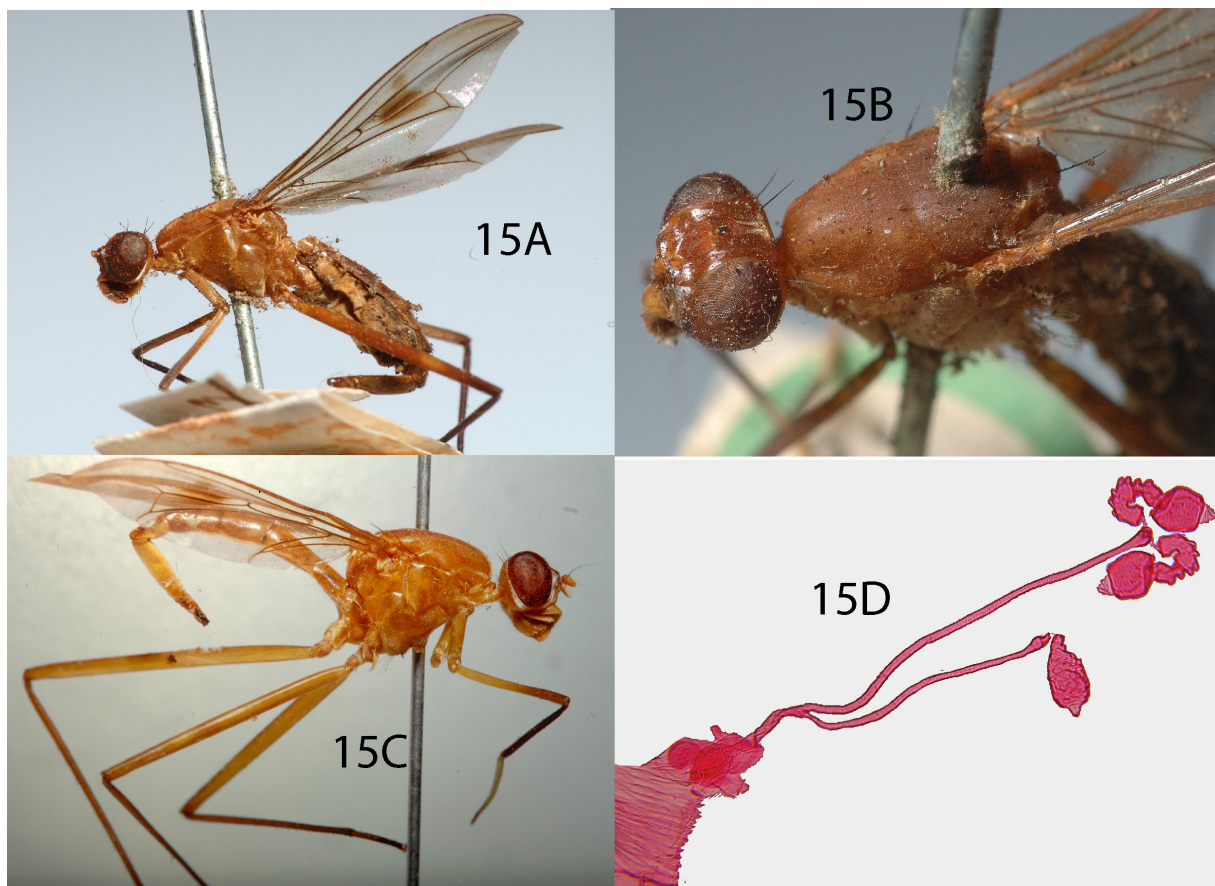


Fig. 15. *Ptilosphen fulvus* (Walker, 1849). **A.** Holotype, ♀, Brazil, lateral view (NHMUK). **B.** Holotype, ♀, dorsolateral view. **C.** Syntype of *Pt. ochraceus* Enderlein, 1922, Brazil (MNBG). **D.** Spermathecae and associated structures, French Guiana (MNHN).

Ptilosphen gentilis Cresson, 1930

Fig. 16

Ptilosphen gentilis Cresson, 1930: 348.

Ptilosphen gentilis Hennig 1934: 315, 318. — Aczél 1949: 337. — Steyskal 1968: 13. — Roback 1969: 539. — Albuquerque 1991: 4. — Marshall *et al.* 2016: 543.

Type material

Holotype

COSTA RICA • ♂; San Carlos; Schild and Burgdorf leg.; USNM.

Paratypes

COSTA RICA • 4 ♀♀, 2 ♂♂; same data as for holotype; USNM (not examined).

Other material examined

COSTA RICA • 10 ♂♂; Prov. Limón, Siquerres, Pacuarito, Los Brisas; 200–500 m a.s.l.; 1996; B. Viklund leg.; DEBU • 5 ♀♀, 8 ♂♂; Prov. Heredia, Rara Avis Nat. Res., 12 km S of Las Horquitas; 10°17'0" N, 84°2'50" W; 700 m a.s.l.; Feb. 2005; S.A. Marshall leg.; CO1 specimen DEBU293-17; DEBU • 1 ♀, 2 ♂♂; La Selva; 2000; E.M. and C.F. Fischer leg.; DEBU • 1 ♀, 1 ♂; La Selva, Biol. Res.; Feb. 2003; M. Pollet leg.; DEBU • 4 ♀♀, 4 ♂♂; Prov. Alajuela, Volcan Tenorio; Mar. 2000; Buck and Marshall leg.; DEBU • 5 ♀♀, 5 ♂♂; San Juan de Peñas Blancas, San Ramón, Soltis Research Centre; 17 Aug. 2013, Apr.–May 2018, Apr.–May 2022; S.A. Marshall leg.; DEBU • 1 ♀; Prov. Guanacaste, Estacion Pitilla, 9 km S of Santa Cecilia; Feb. 1996; S.A. Marshall leg.; DEBU • 1 ♂; Prov. Puntarenas, Punta Leona; Feb. 2001; P.D. Careless leg.; DEBU • 1 ♀, 3 ♂♂; Area Conservation Central Parque Nacional Braulio Carillo, Quebrada Gonzalez; 13 Aug. 2013; S.A. Marshall leg.; DEBU (alcohol) • 1 ♀, 3 ♂♂; Area Conservation Central Parque Nacional Braulio Carillo Sector El Ceibo; 600 m a.s.l.; 29 Jul.–5 Aug. 2019; D. Janzen *et al.*; CO1 specimen BIOUG77721-F01; BIOUG • 1 ♀; Area Conservation La Amistad; 306 m a.s.l.; 7–14 Feb. 2021; D. Janzen *et al.* leg.; CO1 specimen BIOUG80754-C04; BIOUG • 1 ♂; Alajuela, Arenal National Park; 25 Aug. 2022; S.A. Marshall leg.; DEBU.

NICARAGUA • 1 ♀; Rio San Juan Prov., Refugia Bartola Res., 5 mi. E of El Castillo; 3–8 May 2008; J. Wilson and K. Williams leg.; DEBU.

Redescription

LENGTH. 13–16 mm.

COLOUR (Fig. 16A–B, G–J). Dark brown to black except as follows: frontal vitta entirely dull velvety orange and well defined, darker anteriorly, posterior apex within a densely silvery microsetulose area extending between inner vertical bristles; frontal plate bare, reddish; ocellar triangle, epicephalon and paracephalon black and bare except for microsetulose area between inner vertical bristles. Palpus yellow in apical third, otherwise brown; lunule orange, face brown with dark lower margin, densely microsetulose except for bare subantennal depression; clypeus black and entirely silvery microsetulose with setulosity densest laterally; parafacial densely silver microsetulose. Antenna mostly orange but first flagellomere black distally and on dorsal third. Notum blue-black, mostly silvery pruinose dorsally but with a narrow and anteriorly tapered incomplete black medial vitta; black dorsolaterally. Fore tarsomeres 1–3 white, tarsomeres 4–5 brown; foreleg otherwise dark brown. Mid tarsomeres and mid tibia brown; mid and hind femora brown with white rings at distal third; mid femur with a white base 1–3 × width of femur, hind femur with white ring 2–4 × width of femur; hind tibia and tarsus brown. Wing with transverse basal and preapical bands and broadly triangular discal band; preapical band straight, not

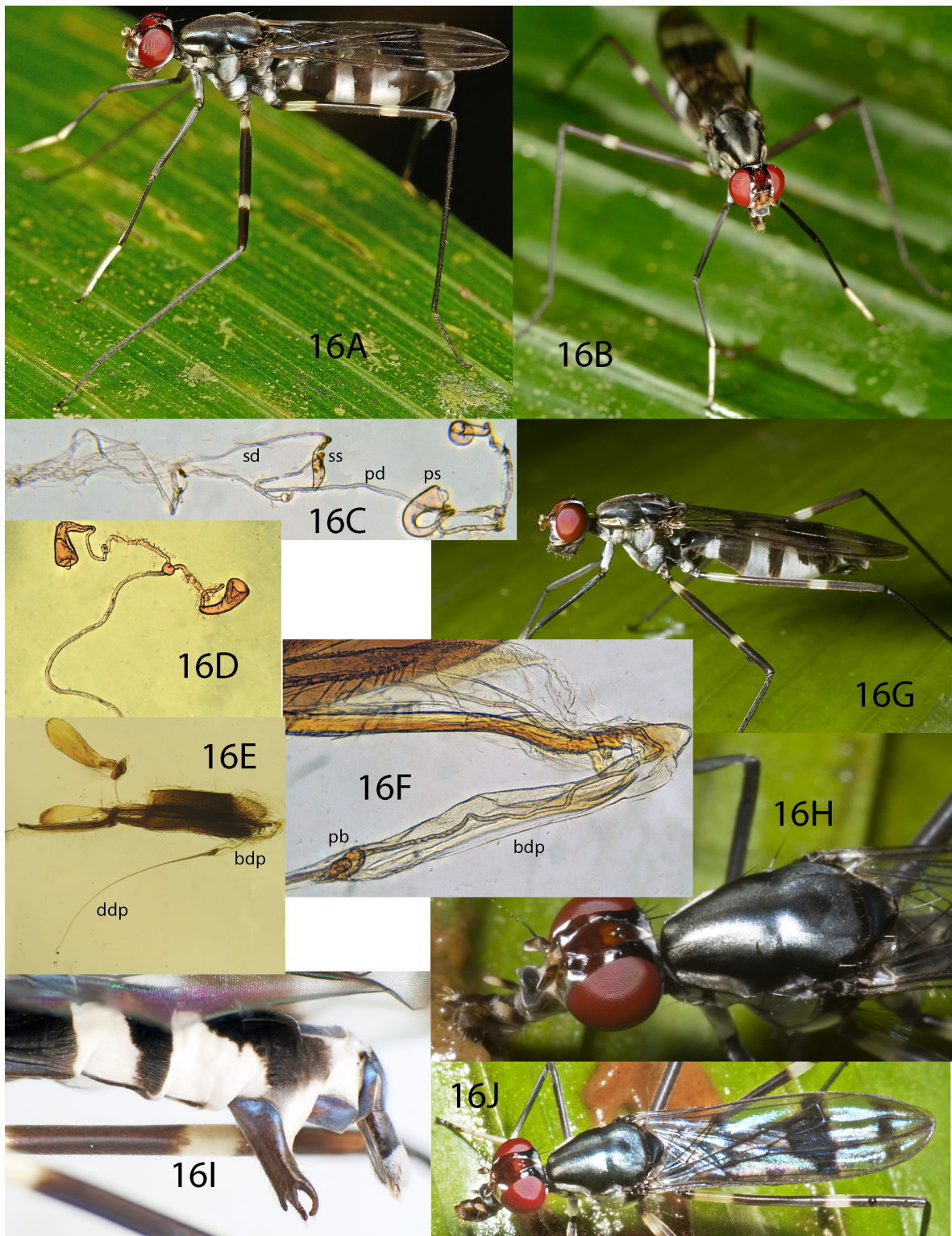


Fig. 16. *Ptilosphen gentilis* Cresson, Costa Rica (DEBU). **A–B.** Living ♀. **C–D.** Spermathecae and associated structures with detail of paired spermathecae. **E.** ♂, terminalia, left lateral view. **F.** ♂, terminalia, left lateral view, detail to show basal distiphallus, phallic bulb, postgonite. **G.** Living ♂. **H.** ♀, head and thorax. **I.** ♂, abdomen, lateral view. **J.** ♀, dorsal view. Abbreviations: bdp=basal distiphallus; ddp=distal distiphallus; pb=phallic bulb; pd=paired (primary) spermathecal duct; ps=paired spermathecae; sd=single (secondary) spermathecal duct; ss=single spermatheca.

conspicuously staggered at middle as in related species. Abdominal T1–2 blue-black pruinose except for dull black anterior margin of T1 and dull black middle of T2, T3–5 blue-black along anterior quarter, T6 entirely blue-black pruinose, female ovipositor pruinose basally, bare distally. Abdominal P1 of female black on anterior half, P2 entirely black, P3 with a broad vertical band, P4 with a broad band on upper half only, P5–6 entirely black; oviscape brown, mostly silvery pruinose except for a narrow bare dorsal strip and a bare, shiny apical fifth. Male pleural pigmentation similar to female on segments 1–3, P4–5 with dense white microsetulosity covering ventral $\frac{2}{3}$ of pleuron; epandrium brown and entirely microsetulose.

HEAD. Two pairs of large fronto-orbital bristles. Frontal vitta gradually tapered to a point both anteriorly and posteriorly, about half as wide as frons at widest point. Outer vertical bristle present.

THORAX. Prosternum bare except for minute scattered setulae. Cervical sclerite finely microtrichose except at anterior margin, female with centre part depressed, strongly differentiated and divided from anterior part, posterior part strongly convex; male cervical sclerite with centre and posterior parts almost uniformly convex. Scapular setae not differentiated from anterior dorsocentral setulae. Postpronotum microsetulose dorsally, bare laterally, with a few scattered setulae. Two notopleural bristles, anterior $0.8\times$ as long as posterior. Katepisternum with one vertical row of strong setae preceded by a vertical row of about six fine lower setae and scattered small, fine and pale upper setae. Dorsocentral bristle present.

FEMALE TERMINALIA (Fig. 16C–D). Three spermathecae; paired spermathecae on an extremely long, uniformly narrow primary duct arising from the apex of an elongate common duct; apex of primary duct distinctly swollen where it divides into two very long, narrow, sinuate stems, each ending in an elongate, basally bent cone-shaped spermatheca. Single spermathecal duct arising from side of common duct, smaller and shorter than primary duct, ending in a very small elongate spermatheca.

MALE TERMINALIA (Fig. 16E–F, I). Genital fork elongate with a short basal arm and a long, strongly incurved arched arm with fine hairs distally on outer surface and short, small spines scattered along length of inner surface and in a loose basal cluster and on a slightly raised inner basal process; base with shallow groove between arms. Basiphallus small but prominent, narrower than basal distiphallus and slightly projecting posteriorly as a tapered lobe. Basal distiphallus broad, shorter than epandrium, distal distiphallus narrower, long and whip-like, reaching or exceeding anterior margin of the long hypandrium. Phallic bulb small, proximal chamber distinct and about double the size of the small distal chamber. Hypandrium with narrow, tongue-like anterior bridge. Subepandrial sclerite uniformly sclerotized. Postgonite very small and short, with a tapered and weakly spinulose apex and a few small setulae on anterior surface.

Remarks

Ptilosphen gentilis is a Central American species currently known mostly from Costa Rica, where it is commonly encountered. Records of *Pt. gentilis* from South America (Albuquerque 1991) cited in catalogues (Steyskal 1967; Marshall *et al.* 2016) are probably all misidentified *Pt. facetus* or *Pt. boroboro* Marshall sp. nov. *Ptilosphen gentilis* is closely related to *Pt. boroboro*, which also has a four-armed genital fork, but the lower arms of the *Pt. gentilis* genital fork are shorter (much less than half as long as the upper arms) and the basal distiphallus is much shorter. There were no CO1 sequences of *Pt. boroboro* available, but the analysis supports a close relationship between *Pt. facetus* and *Pt. gentilis*. Females of these species are similar. Costa Rican specimens of *Pt. gentilis* fell into two CO1 BINs, but morphology suggests that they are the same species.

Ptilosphen inconveniens Marshall sp. nov.

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Fig. 17

Etymology

The species name is a modification of the name of the misleadingly similar *Pt. conveniens* and reflects the inconvenience of dealing with such an interesting species on the basis of only a single female specimen.

Type material

Holotype

COLOMBIA • ♀; Nariño R.N, La Planada Via Hondón; 1°15' N, 78°15' W; 1930 m a.s.l.; 2–16 Nov. 2000; G. Oliva leg., 1411; Malaise; IAVH.

Description (female only)

LENGTH. 15 mm.

COLOUR (Fig. 17A–E). Dark shiny blue-black except as follows: frontal vitta velvety black, frontal plate shining brown, reddish along eye; antenna brown, parafacial silvery pruinose, vertex entirely microsetulose. Palpus brown, orange apically; clypeus pruinose blue-black, face mostly pale. Fore

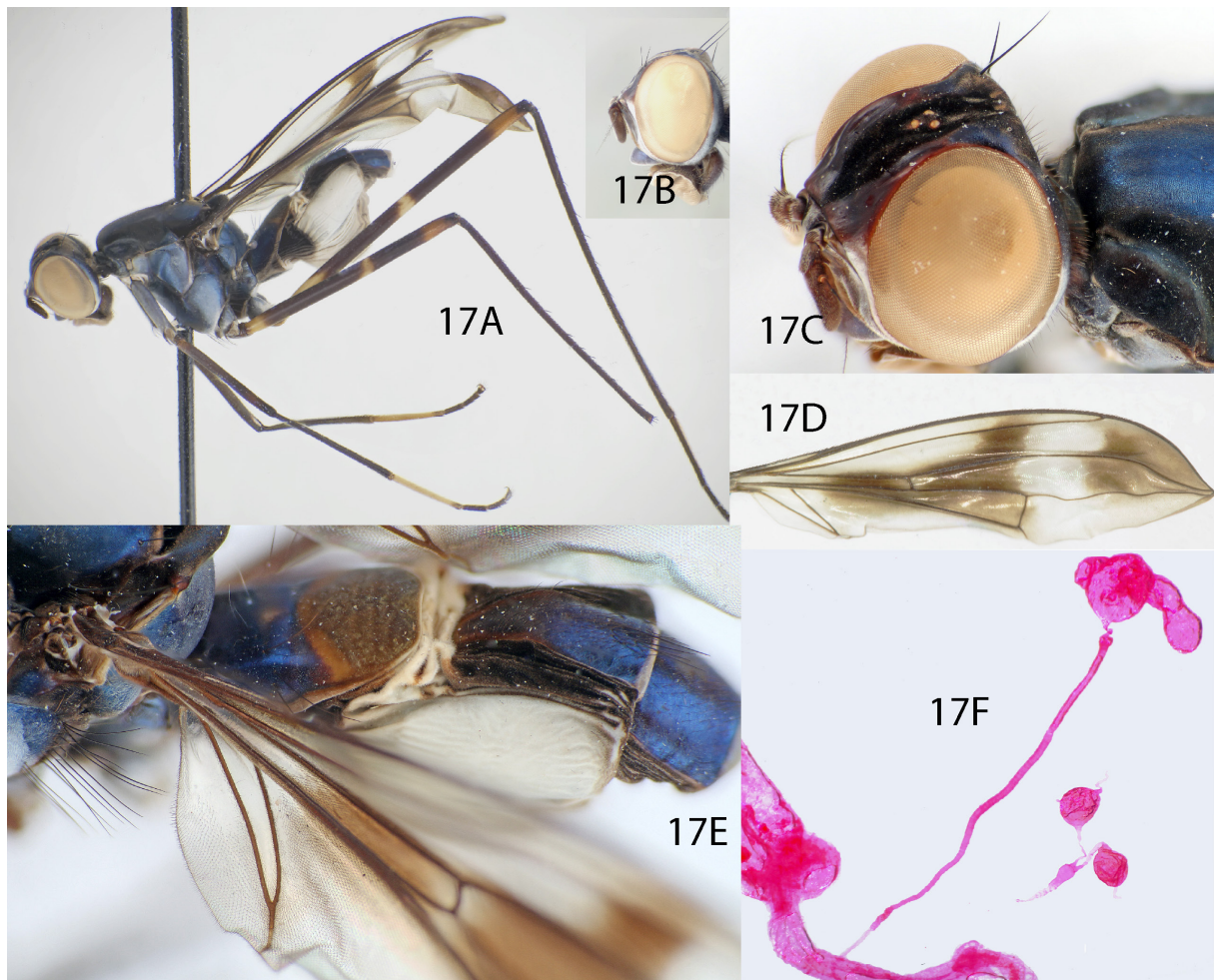


Fig. 17. *Ptilosphen inconveniens* Marshall sp. nov., holotype, ♀, Brazil (INPA). **A.** Habitus. **B–C.** Head. **D.** Wing. **E.** Abdomen, dorsolateral view. **F.** Spermathecae and associated structures.

tarsomeres 2–5 dark, tarsomere 1 white except for dark apex; fore tibia and fore femur entirely dark brown. Mid tibia brown; mid femur brown with basal white ring as long as width of femur, a midventral white ring half as long as femoral width and a preapical orange ring twice as long as femoral width; hind femur similar but with a longer basal white part; hind tibia brown; hind tarsus brown. Wing with an unusually extensive elongate triangular discal band extending from near wing base to dm-cu and extending anteriorly to wing margin; apex of wing also heavily pigmented from M to anterior wing margin. Abdomen with tergites shining blue-black except for pale brown posterior half of T2, white and unsclerotized T3 (wrinkled and not totally visible on unique holotype) and brown anterior third of T4; pleuron with a large white inflated area on P2–4 and flanked by black P2, a black upper quarter of P4, a black P5, and a slightly darkened ventral area.

HEAD. Two fronto-orbital bristles. Outer vertical bristle present. Frontal vitta about half as wide as frons at widest point, very slightly elevated, parallel sided except for the gradually tapered anterior quarter; posterior part of vitta only slightly tapered to a broad apex.

THORAX. Prosternum inconspicuously setulose. Cervical sclerite subquadrate and almost flat. Scapular setae absent. Postpronotum with a few scattered inconspicuous setulae. Notopleuron with two bristles, anterior thinner and shorter than posterior. Katepisternum with one posterior vertical row of black bristles preceded by a similar row along ventral fifth of row and below, upper setae of anterior row fine and hair-like. Dorsocentral bristle present.

FEMALE TERMINALIA (Fig. 17F). Paired spermathecal duct very small and arising distally on bursa extension, leading to a small swelling before dividing into narrow stems each ending in a balloon-like spermatheca. Secondary spermathecal duct much longer and thicker, arising laterally from common duct (or bursa extension), narrow basally and terminating in a very short, coiled constriction leading to a very large bulbous swelling that branches into two fat arms with a bulbous apex.

MALE TERMINALIA. Male unknown.

Remarks

Ptilosphen inconveniens Marshall sp. nov. and *Pt. mimicus* are apparently closely related and differ widely from other *Ptilosphen* species in having the paired (primary) spermathecal duct greatly reduced and arising apically from the bursa, while the much larger single (presumably secondary) spermathecal duct arises low on the bursa and leads to a large bifurcate single spermatheca. Both species are also characterized by black fore tarsomeres 2–5, unlike other *Ptilosphen* species, but *Pt. inconveniens* is distinguished from *Pt. mimicus* by its large and elongate discal wing band (extending into the basal quarter of the wing), the distinctive desclerotization of female T3 and the retention of prescutellar dorsocentrals and two fronto-orbital bristles. Males of *Pt. inconveniens* remain unknown.

Ptilosphen insignis (Wiedemann, 1830)

Fig. 18

Calobata insignis Wiedemann, 1830: 533.

Calobata nigrifrons Bigot, 1886: 374. Type-locality: “Brazil”. Synonymized with *Pt. insignis* by Hennig (1934: 315).

Ptilosphen insignis – Enderlein 1922: 223–224. — Frey 1927: 72. — Curran 1934a: 295, 457. — Hennig 1934: 314. — Hendel 1936: 72. — Aczél 1949: 337. — Steyskal 1968: 13. — Schumann 1988: 98. — Albuquerque 1991: 4. — Ferro & de Carvalho 2014: 59. — Marshall *et al.* 2016: 543.

Ptilosphen nigrifrons – Enderlein 1922: 223–224.

Type material

Type material of *Ptilosphen insignis*

BRAZIL • ♀ (HT?); MNGB.

Note: the only putative type material of *Ptilosphen insignis* examined is a male specimen in MNBG labelled as a type by Enderlein, but according to Wiedemann (1830), the description is based on a female. Enderlein also lists specimens from Colombia and Guyana as follows:

COLOMBIA • ♀♀; Cordillieren, Terra Caliente; Prof. Dr Thieme.

GUYANA • ♀♀; Schomburg.

Type material of *Calobata nigrifrons* was not examined (deposition unknown, not in the Bigot collection at Oxford).

Other material examined

BOLIVIA • 12 ♀♀, 6 ♂♂; Heath River Wildlife Centre, 21 km SSW of Puerto Heath; 12°40' S, 68°42' W; 29 Apr.–12 May 2007; S.A. Marshall and S. Paiero leg.; CO1 specimens MYCRO949-22, MYCRO950-22 (see Remarks); DEBU.

BRAZIL • 1 ♀; Prov. Amazonas, Amazonas, 50 km N of Manaus, km 934 BR 174, km 14 ZF-2; 13 Jan. 2020; Rafael and Marshall leg.; INPA • 2 ♀♀; Presidente Figueiredo, Cachoeira Iracema, nr parking lot; 29 Jan. 2020; Rafael and Marshall leg.; INPA • 1 ♀, 5 ♂♂; Prov. Amazonas; A. Roman leg.; FMNH • 1 ♀, 1 ♂; Campus Universitario, Manaus; 1988; Castilho and Binda leg.; INPA • 2 ♀♀; Embrapa; 1992; Albuquerque and Binda; INPA • 1 ♀; S. Izabel. R. Negro Maturaca; 1990; J.A. Rafael leg.; arm, Malaise; INPA • 1 ♀; Rio Jau, Meriti Mun. Novo Airao; 1994; J.A. Rafael leg.; INPA • 1 ♂; Manaus, 174 km 41 Res. 1501; 2°27'26" S, 59°45'00" W; 1995; Roche and Silva leg.; INPA • 1 ♀; Coari, Rio Urucu, Petrobras, RUC; 1994; Roche and Silva leg.; INPA • 1 ♀; Vegetacao; 1983; R.Y. Harada leg.; INPA • 1 ♀; Prov. Rondonia, Ouro Preto do Oeste, Igarapé; Jul. 1995; Mandi leg.; INPA • 1 ♂; Guajara-Mirim, Rio Ouro Preto; 1995; Rafael and Henriques leg.; Malaise; INPA • 1 ♀, 2 ♂♂; Prov. Rio Negro; A. Roman leg.; FMNH • 4 ♀♀; Parna do Jau, Lago do Miratuca; 1993; L.S. Aquino leg.; INPA • 3 ♀♀; Pacaraima; 1988; J.A. Rafael leg.; INPA • 1 ♀; S. Pedro da Agua Branch, F. Sta Rosa; 2001; J.A. Rafael, F.L. Oliveira and J. Vidal leg.; INPA • 1 ♀; Prov. Para Tucuruí, R. Tocantins; 1981; INPA • 1 ♀; 5 mi. SE of Manaus; Mar. 1973; B.V. Peterson leg.; CNCI • 2 ♂♂; Umarituba, Rio Negro; Expedition Roman; ZMUH • 1 ♀; Rio Negro, San Gabriel; ZMUH • 1 ♀, 2 damaged specimens without abdomens; Rio Urapes, Tararacua and Manaus; ZMUH • 1 ♀, 1 ♂; Rio Autaz; ZMUH.

FRENCH GUIANA • 5 ♀♀, 4 ♂♂; Mitaraka; 283–306 m a.s.l.; 26 Jan.–10 Mar. 2015; M. Pollett, J. Touroult and E. Poirier leg., PROJECT MITARAKA; tropical moist rainforest, yellow pan traps and flight intercept traps; MNHN • 15 ♀♀, 7 ♂♂; Mana River; May 1917; CMNH • 2 ♀♀, 5 ♂♂; Roura, road D6m; 17–23 Nov. 2018; G. Ferro leg.; rainforest trail, human dung; DEBU • 1 ♀; Monsinery, “Emerald Jungle”, Carrefour de Gallion; 1 Jan. 2003; M. Kotrba leg.; DEBU • 2 ♀♀; Cayenne, Kaw Mtn, Relais de Patawa; Jan. 2006; J-A. Cerda leg.; Malaise; CO1 specimen MYCRO 0885-21; DEBU.

GUYANA • 17 ♀♀, 7 ♂♂; Potaro-Siparuni, Mount Wokomung; 21–26 Oct. 2004; B. Hubley leg.; dung trap in primary forest; DEBU • 18 ♀♀, 7 ♂♂; same data as for preceding; ROME • 1 ♀, 1 ♂; Kabocalli, Iwokrama Forest Reserve; 60 m a.s.l.; 3–5 Jun. 2001; Brooks and Falin leg.; flight intercept trap; DEBU • 1 ♀; Mazaruni-Potari District, Takutu Mtns; 13 Dec. 1983; Earthwatch Research Expeditions, Warner and Steiner leg.; USNM.

TRINIDAD & TOBAGO • 3 ♀♀, 2 ♂♂; Trinidad, Prov. Tabaquite; 1902; H.D. Chipman leg.; CMNH.

Redescription

LENGTH. 13–15 mm.

COLOUR (Fig. 18A–D). Head mostly dark reddish brown except darker frontal vitta and yellow lower face, parafacials, gena, clypeus, palpus and postgena and central postoccipt; postocellar frontal vitta and parafacials densely silvery microsetulose. Subantennal depression black, pedicel, scape and extreme base of first flagellomere reddish, first flagellomere otherwise dark brown. Vitta entirely dark. Thorax mostly orange, sparsely microsetulose; at most anterior margin of pronotum black to brown. Katepisternal bristles orange. Fore tarsomeres mostly white although distal one or two tarsomeres sometimes yellowish; fore tibia dark brown; fore femur distally dark brown, yellow to orange on basal half. Mid tarsus and tibia brown; mid femur and hind femur yellow-brown with medial white rings 1–2 × width of femur (pale rings on mid tibia obsolete on some specimens, basal half of mid tibia often pale on posterior half), mid femur and hind femur with a pale basal ring (often indistinct). Hind tibia and tarsus brown. Wing with a small subquadrate to triangular discal band extending from middle of cell dm to beyond R4+5, often with an indistinct anterodistal extension to or beyond R2+3.

Abdominal tergites of male brown except for black posterior corners and anterior margin of T2; abdominal pleuron of male boldly banded in black and white, with separate bands on P1, P2, and P3; the P3 band complete and broad; P2 usually with a distinct pleural sac in upper half; P4–5 white and sometimes delineated as an apparent inflatable sac. Abdomen of female with T1 orange, other tergites dark brown to black, pruinose; oviscape orange and heavily silvery microsetulose laterally, dorsally and distally brown, bare and shining, apex yellow. Pleuron of female with P2 and P3 with ventrally tapered dark bands, P4–5 dark on dorsal half.

HEAD. Frontal vitta entirely black to dark brown and well defined, slightly elevated and teardrop-shaped, strongly tapered to anterior point and about 0.7 × frontal width at maximum. Two strong fronto-orbital bristles. Palpus 5 × as long as wide with long, thin, light hairs extending length of one side. Outer vertical bristles present.

THORAX. Prosternum microsetulose. Cervical sclerite evenly swollen in male, female with central area slightly depressed. Postpronotum microsetulose but without differentiated setulae. Scapular setae absent in both sexes. Katepisternum with one main vertical row of orange bristles. Dorsocentral bristle present.

FEMALE TERMINALIA (Fig. 18F). Oviscape reaching almost to anterior margin of P2. Three spermathecae, primary spermathecal duct slightly broader in basal half, terminating in a distinct swelling before splitting into two long ducts with a greatly swollen basal half and a coiled distal half, spermatheca expanded to a cup-like apex. Secondary spermathecal duct much smaller and less than half as long, ending in an indistinct swelling, a very small stem and a single spermatheca.

MALE TERMINALIA (Fig. 18E, G–H). Genital fork with thick, straight arms, inner surface concave near base with sparse short spines evenly spaced; inner basal arms absent, base deeply cleft by a very narrow, almost linear cut. Epandrium long and narrow, almost 3 × as long as wide. Basiphallus smaller than base of distiphallus, barely projecting posteriorly as a subquadrate lobe. Distiphallus 1.5 × length of epandrium, basal distiphallus broad and almost as long as epandrium; phallic bulb short, with proximal and distal chambers equally distinct and similar in size; distal distiphallus with transverse striations, 0.8 × length of basal distiphallus, apex funnel shaped. Hypandrium with narrow, tongue-like anterior bridge. Postgonite small but bulbous, with 3 minute setulae anteroventrally, posterior surface evenly covered with minute bumps. Ejaculatory apodeme broad, slightly shorter than epandrium.

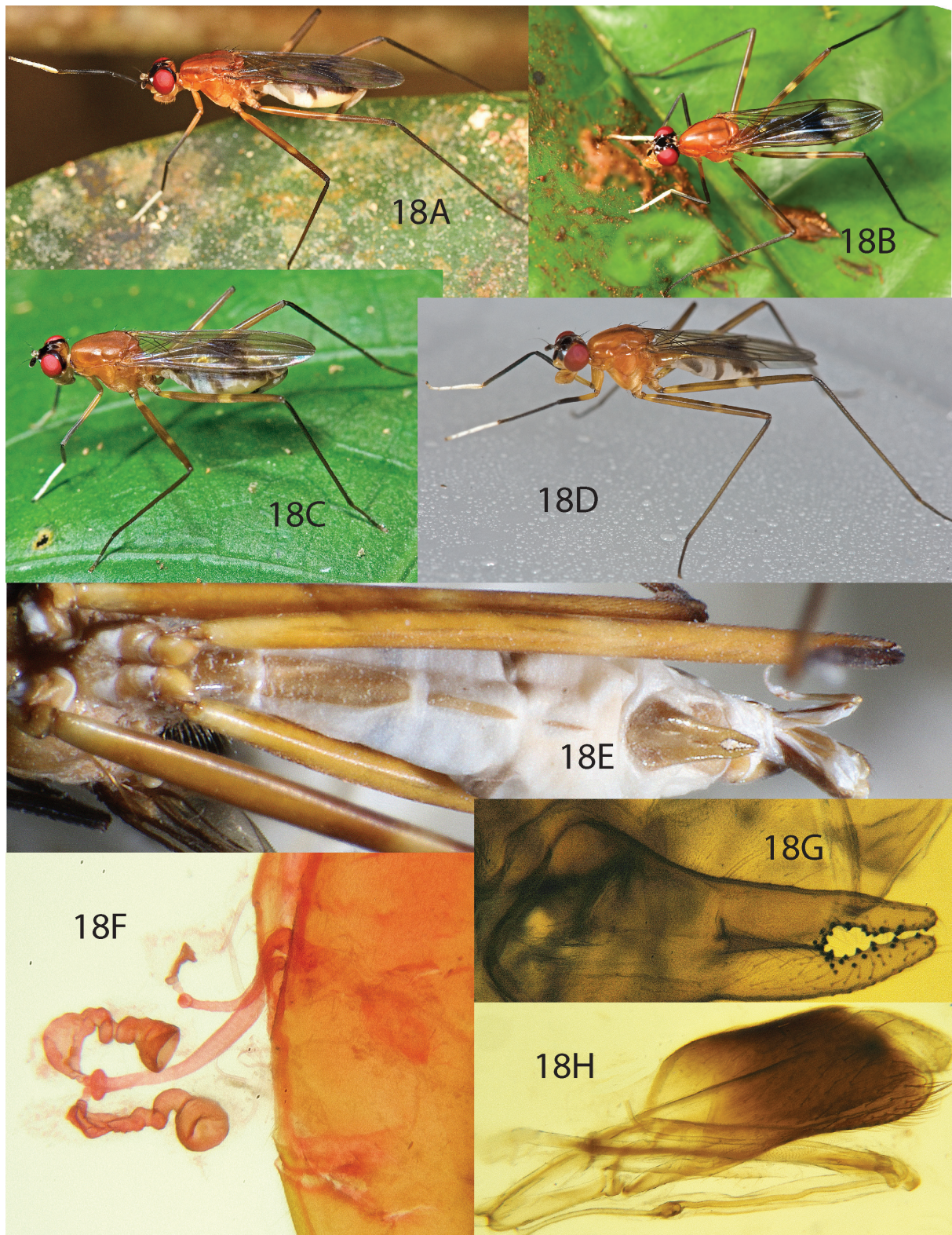


Fig. 18. *Ptilosphen insignis* (Wiedemann, 1830). A–B. Living ♀ and ♂, Brazil (INPA). C–D. Living ♀ and ♂, Bolivia (DEBU). E. ♂, abdomen, ventral view, French Guiana (DEBU). F. Spermathecal complex and left side of oviscapae, Peru (DEBU). G. ♂, sternite 5 (genital fork), Guyana (DEBU). H. ♂, terminalia, left lateral view, Guyana (DEBU).

Remarks

Ptilosphen insignis can be distinguished from the similar *Pt. dubius* by the broad and straight arms of the male genital fork and, to a lesser extent, pronotal colour, oviscape colour and the characteristically shaped female spermathecae and spermathecal stems.

Some specimens of *Pt. insignis* vary in discal wing band pigmentation (distinct to faint) and size and could easily be misidentified as *Pt. yasuni* Marshall sp. nov. (the probable sister species to *Pt. insignis*) without examination of abdominal characters. One female specimen from Brazil (Presidente Figueiredo, Cachoeira Iracema, nr parking lot, 29 Jan. 2020; Rafael and Marshall; INPA) has the discal band divided into two separate oblong oval spots, one over M and one over R₄₊₅. This specimen might represent a separate species, but male specimens are required to confirm its status. The five specimens listed above from Trinidad are also atypical in having almost no wing pigmentation, however both male and female terminalia suggest that they are *Pt. insignis*.

Two of the specimens identified as *Pt. insignis* from Heath River, Bolivia, barcoded into the same BIN as *Pt. dubius*, widely separated from other specimens of *Pt. insignis* from Guyana and French Guyana. Collections from Heath River included 18 specimens identified as *Pt. insignis* and 12 identified as *Pt. dubius*. All specimens, including the two *Pt. insignis* that sequence with *Pt. dubius*, were re-checked and are correctly identified according to the multiple diagnostic features mentioned above.

***Ptilosphen manu* Marshall sp. nov.**

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Fig. 19

Etymology

The species name reflects the type locality, Manu National Park, and is treated as a noun in apposition.

Type material**Holotype**

PERU • ♀; Cuzco, Paucartambo, Kosnipata, Estacion Biologica Manu, Platanal; 12.900481° S, 71.4045° W; 519 m a.s.l.; 24 Feb.–4 Mar. 2023; MANU ICFC leg.; Malaise trap; MUSM, CBG A48535-A07.

Paratypes

COLOMBIA • 1 ♂; Putumayo, Orito, RN La Isla Escondida; 0.65547° N, 77.07302° W; 850 m a.s.l.; 5 Aug. 2024; Pollet and De Braekeleer leg.; sweep net; IAVH, Life on Trees: LOT00-40007/S20.

PERU • 1 ♀; Cuzco, Paucartambo, Kosnipata, Estacion Biologica Manu, Mandala 2; 12.895102° S, 71.40271° W; 513 m a.s.l.; 9–16 Nov. 2022; MANU ICFC leg.; Malaise trap; CO1 specimen PERMQ48399-24; DEBU • 1 ♀; same data as for preceding; MUSM • 1 ♂; Cuzco, Paucartambo, Kosnipata, Estacion Biologica Manu, Mandala 2; 12.895102° S, 71.40271° W; 513 m a.s.l.; 4–11 Mar. 2023; MANU ICFC leg.; Malaise trap; CO1 specimen PERMS13883-24; MUSM • 8 ♀♀, 2 ♂♂; Prov. Cuzco, Quincemil; 700 m a.s.l.; Sep. 1962; L. Peña leg.; CNCI (det. as *Pt. enderleini* by L. Albuquerque, dissected and confirmed as *Pt. manu*) • 6 ♀♀; Prov. Madre de Dios, Avispas; 400 m a.s.l.; Oct. 1962; L. Peña leg.; CNCI (det. as *Pt. enderleini* by L. Albuquerque, dissected and confirmed as *Pt. manu*).

Note: Estacion Biologica Manu is the same locality referred to on older labels (thus elsewhere in this paper) as Villa Carmen.

Other material examined

BRAZIL • 2 ♂♂, 1 ♀; Amazon, H.W. Bates leg.; NHMUK. These specimens were determined as *Pt. enderleini* by Hennig and listed as *Pt. enderleini* in Hennig (1934). One is an intact female, one has no abdomen or legs, and the third (illustrated here; Fig. 19E) lacks terminalia.

Although not examined by the authors, the specimen of “*Pt. enderleini*” mentioned in Hennig (1934) from Pichis-Weg (Peru) is presumably also this species.

Description

LENGTH. 12–13 mm.

COLOUR (Fig. 19E–G). Frons black with anterior margin reddish, frontal vitta pruinose and dull; paracephalon, lower epicephalon and frontal plate shiny, upper epicephalon and posterior frontal vitta silvery microsetulose. Lunule, scape, pedicel and base of first flagellomere orange, antenna otherwise black; lower face yellow, parafacial white to silvery pruinose, subantennal depression shiny black. Clypeus reddish brown and almost bare at middle, otherwise black, densely microsetulose. Palpus yellow-orange distally, brown basally. Notum black, indistinctly vittate with incomplete golden-brown microsetulose central vitta separating broader silvery microsetulose vittae, pleuron with extensive pruinosity forming broad, weakly differentiated vertical bands. Fore coxa reddish brown, densely microsetulose on inner surface; fore femur yellow basally, dark brown distally. Mid coxa reddish brown, heavily silvery microsetulose. Mid tarsus and tibia brown; mid femur with basal and medial white rings 1–2 × width of femur, otherwise dark brown proximal to distomedian white band, brown to reddish brown distal to distomedian white band. Hind coxa reddish brown, silvery microsetulose on posterior half. Hind femur brown with subbasal and medial white rings 1–3 × width of femur, base of femur brown at least on external surface with length of brown basal area exceeding femur width; hind tibia and tarsus brown. Wing with a distinct subquadrate discal wing band crossing cell r4+5 and extending as a weaker band almost to costa. Abdominal tergites blue-black, golden pruinose on central part of T2 and anterior margin of T3, remainder of T3 bare, tergites and most of oviscapae otherwise silvery pruinose, oviscapae with a bare distal dorsal and distal area. Pleuron of female boldly banded in black and white, P1 dark on anterior $\frac{3}{4}$, P2 pale anteriorly but otherwise dark, P3 entirely dark but with white setulosity, P5 almost entirely dark and P4 yellow at least on ventral half (male paratype with pleuron obscured but apparently as in female).

HEAD. Two large fronto-orbital bristles, upper inserted at level of upper ocelli. Frontal vitta broad, 0.5 × frontal width at maximum, sharply tapered anteriorly and mostly parallel sided posteriorly, rounded at posterior apex. Outer vertical bristle present.

THORAX. Prosternum entirely microsetulose, with a deep central pit. Cervical sclerite broad, slightly depressed medially in male, deeply depressed medially and distinctly bilobate in female. Postpronotum uniformly microsetulose with a few scattered small setulae. Scapular setae absent. Notopleuron with two bristles, anterior small. Dorsocentral bristle present.

FEMALE TERMINALIA (Fig. 19D). Paired and single spermathecal ducts arising independently from bursa, paired duct swollen, much broader than single duct and parallel sided until tapered in distal fifth. Primary duct with a distal swelling followed by a narrow constriction basal to broad, tuberculate stems slightly narrower than the elongate oval paired spermathecae. Secondary (single) spermathecal duct shorter and half the diameter of the primary duct, with a smaller distal swelling and a very narrow constriction between duct and an irregular tuberculate spermatheca.

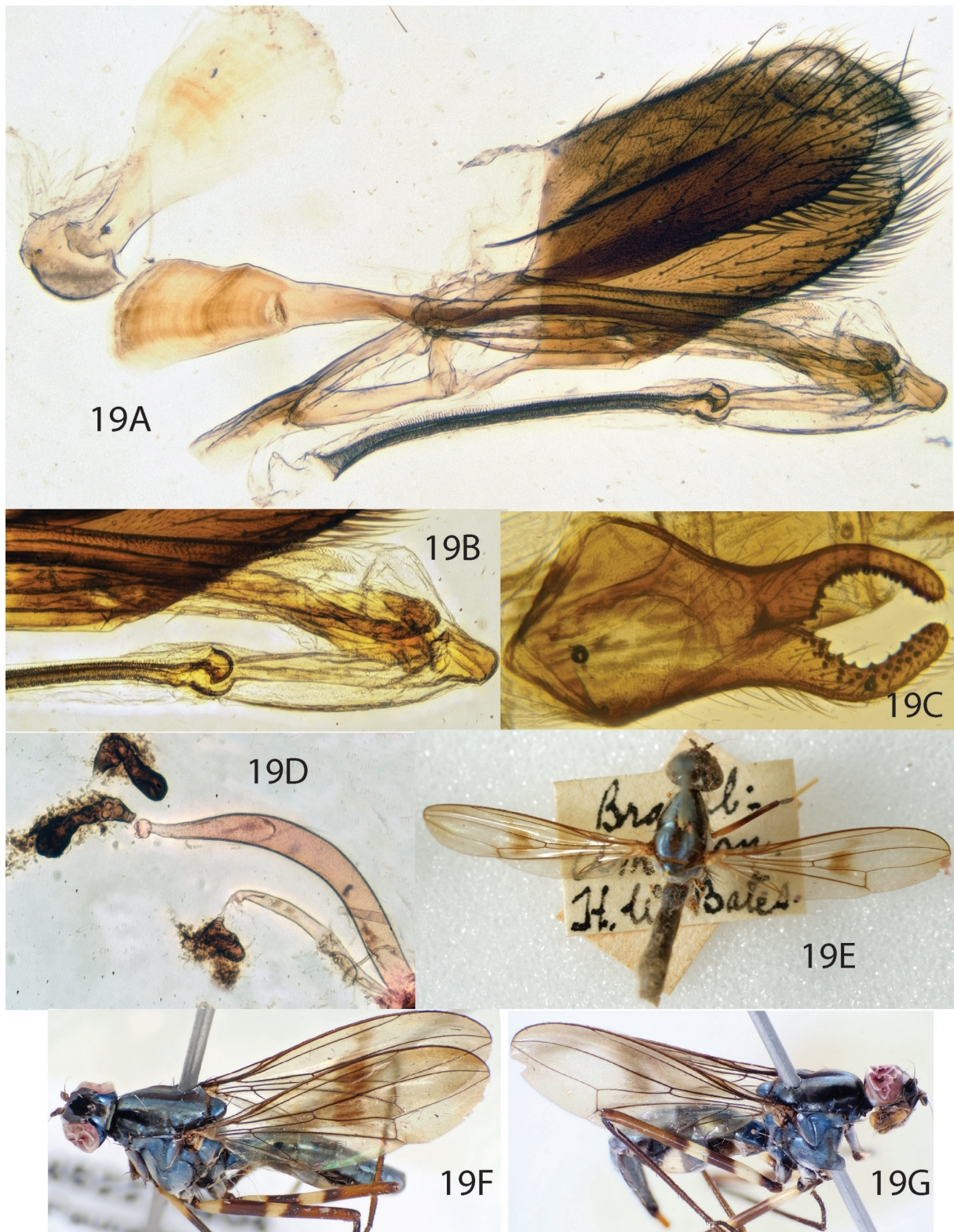


Fig. 19. *Ptilosphen manu* Marshall sp. nov., ♂, Peru (MUSM). **A.** ♂, terminalia, left lateral view. **B.** ♂, terminalia, left lateral view detail to show basal distiphallus, phallic bulb, postgonite. **C.** ♂, sternite 5 (genital fork). **D.** Spermathecae and associated structures. **E.** H.W. Bates specimen from Brazil, sex unknown. **F.** ♀, left lateral view, Peru. **G.** ♀, right lateral view, Peru.

MALE TERMINALIA (Fig. 19A–C). Genital fork with a long base and two long, thin, arched arms with fine hairs along entire outer surface; inner face of arms with dense, short spines extending entire length of arm; base of fork between arms with a narrow V-shaped cleft. Epandrium about twice as long as wide. Basiphallus well sclerotized and distinct from distiphallus, broadly rounded; basal distiphallus half as long as distal distiphallus, distal distiphallus with transverse striae and a broadened and funnel-shaped apex. Phallic bulb small, distinctly divided into two chambers, with ejaculatory duct expanding into the larger of the two chambers. Postgonite bulbous and densely covered with small teeth posteriorly, with three minute setulae anteroventrally. Ejaculatory apodeme slightly smaller than epandrium. Margin of subepandrial sclerite heavily sclerotized to form distinct bacilliform sclerite. Hypandrium with a long, tongue-like anterior bridge and an incomplete dorsal bridge, phallic plate with transverse rows of minute microtrichiae.

Remarks

Ptilosphen manu is externally similar to *Pt. enderleini*, from which it can be distinguished by the very faint discal wing banding extending almost to the costa. The male and female terminalia of these species are distinctly different, with the primary spermathecal duct of *Pt. manu* mostly broad and parallel-sided and the basal distiphallus very short.

Ptilosphen mimicus Cresson, 1930

Fig. 20

Ptilosphen mimicus Cresson, 1930: 348.

Ptilosphen mimicus – Hennig 1934: 315, 319. — Aczél 1949: 338. — Steyskal 1968: 13. — Roback 1969: 546. — Marshall *et al.* 2016: 543.

Type material

Holotype

PERU • ♀; Piches and Perene Valleys; 200–300 ft. a.s.l.; Soc. Geog. De Lima leg.; USNM.

Paratypes

PERU • 2 ♀♀; same data as for holotype; USNM.

Other material examined

BOLIVIA • 3 ♀♀, 5 ♂♂; Prov. La Paz, Cumbre Alto Beni; 15°40'31" S, 67°29'21" W; 1400 m a.s.l.; Apr. 2001; S.A. Marshall leg.; CBFC • 2 ♀♀, 4 ♂♂; same data as for preceding; DEBU • 10 ♀♀, 1 ♂; Caranavi; 15°46'35" S, 67°35'48" W; 1400 m a.s.l.; Apr. 2001; S.A. Marshall leg.; DEBU • 1 ♀; Prov. Cochabamba, Cochabamba; 1400 m a.s.l.; Feb. 1999; F. Génier leg.; DEBU.

COLOMBIA • 1 ♀; Prov. Huila, Parque Nacional Natural Cueva del los Guacharos Cueva del Indio; 1°37' N, 76°6' W; 1990 m a.s.l.; 28 Nov.–1 Dec. 2001; D. Campos leg.; CO1 specimen DEBUA292-17; DEBU • 1 ♀; Prov. Huila, Parque Nacional Natural Cueva del los Guacharos Mirador; 1980 m a.s.l.; 7–21 Dec. 2001; Malaise trap; J. Fonseca leg.; IAVH • 1 ♀; same data as preceding; 22 Dec. 2001; C. Cortes leg.; IAVH.

ECUADOR • 3 ♀♀; El Chaco; 1750 m a.s.l.; Nov. 1999; S.A. Marshall leg.; DEBU • 1 ♂; Prov. Napo, Parque Nacional Sumaco; 1500 m a.s.l.; 21 Jan. 2024; S.A. Marshall leg.; MECN • 1 ♀, 1 ♂; Pastaza, Mera, Centro de Investigación Sumac Kawsay; 1°24'6.24" S, 78°3'57.80" W; 23–26 Jan. 2024; S.A. Marshall leg.; DEBU • 2 ♀♀; same data as for preceding; MECN.

PERU • 4 ♀♀; Cock of the Rock Lodge; 13°3'21" S, 71°32'46" W; ~1380 m a.s.l.; 6 Dec. 2011; S.A. Marshall leg.; DEBU.

Redescription

LENGTH. 14–16 mm.

COLOUR (Fig. 20A–B, D–E). Black to dark brown except as follows: frontal vitta velvety brown to black, frontal plate shiny brown, antennae brown with ventrobasal part of first flagellomere orange, lunule

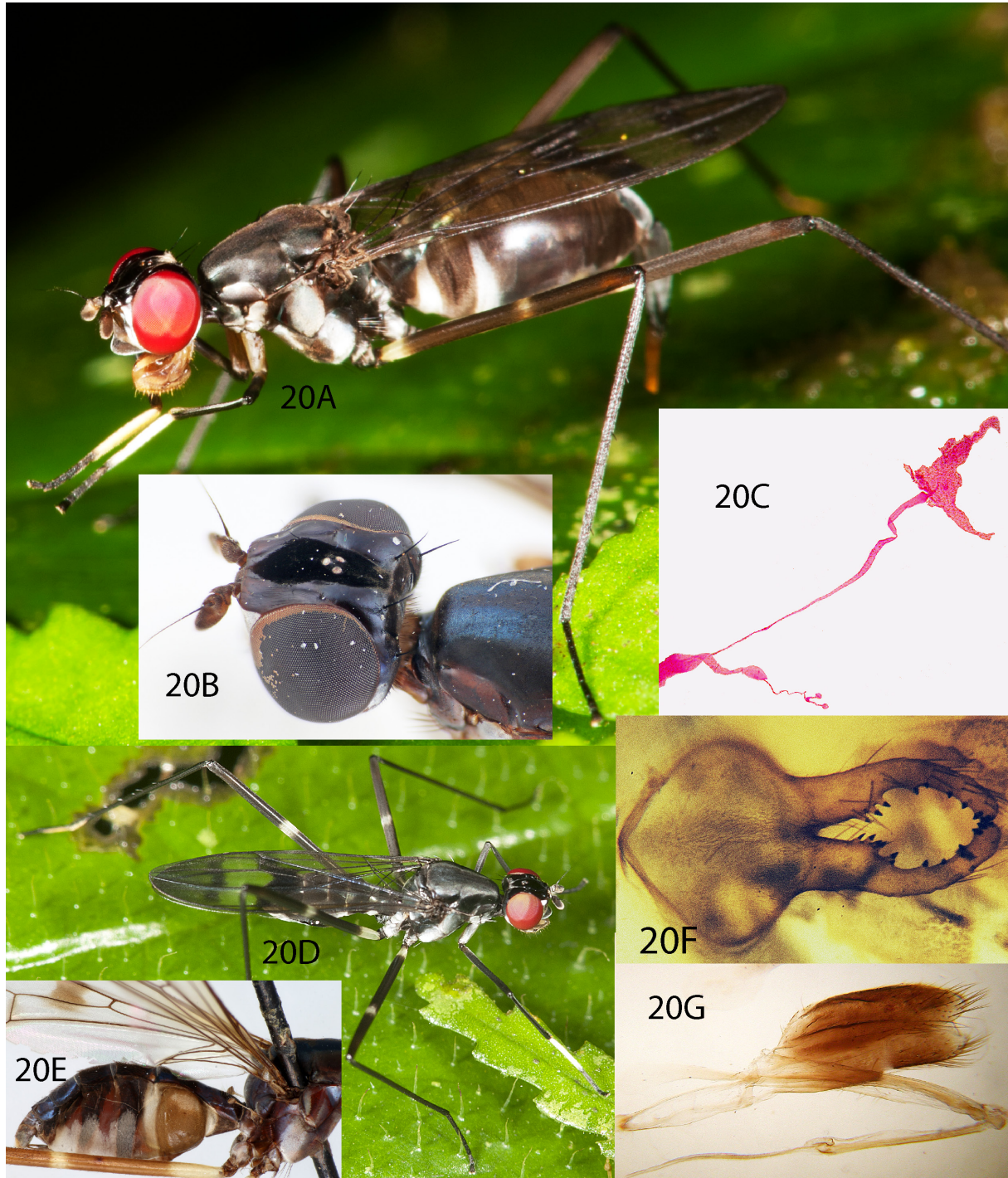


Fig. 20. *Ptilosphen mimicus* Cresson, 1930, Bolivia (DEBU) **A.** Living ♀. **B.** ♀, head and anterior thorax. **C.** Spermathecae and associated structures. **D.** Living ♂. **E.** ♂, right lateral view. **F.** ♂, sternite 5 (genital fork). **G.** Aedeagus and associated structures.

orange brown, parafacial and subantennal depression silvery pruinose, vertex microsetulose between inner verticals. Palpus orange; clypeus brown, microsetulose, face mostly pale. Fore tarsomeres 2–5 dark, tarsomere 1 white except for black apex; fore tibia and fore femur entirely dark brown to black. Mid tibia brown; mid femur brown with basal white ring as long as width of femur, a middle white ring less than half as long as femoral width and an indistinct or incomplete preapical orange ring; hind femur similar but with a longer basal white part and a longer middle ring; hind tibia brown; hind tarsus mostly brown but tarsomere 1 pale ventrally with white setae. Scutum black, postpronotal lobe and pleuron reddish brown; pleuron with central broad silvery pruinose vertical band. Wing with a V-shaped discal band extending from cell dm to anterior margin and a narrow transverse preapical band extending from vein M to anterior margin. Abdominal tergites brown with a pattern of silvery pruinosity crossing junctions between T1–2 and T2–3; T4 bare, T5, T6 and sides of female oviscape densely silvery pruinose, oviscape dorsally with a broad shiny dorsal strip. Pleuron of female abdomen with P1 dark and much of P2 forming a belt-like black vertical band apparently surrounding abdomen; upper part of P3–5 dark. Male abdomen with a large pale brown pleural sac on P2 and with a black vertical band on P3, dark area on P4–5 restricted to dorsal half.

HEAD. Frontal vitta slightly expanded to half of frontal width anterior to ocelli, then tapered to a point at anterior margin; posterior frontal vitta gently tapered to a broad apex. One pair of fronto-orbital bristles, upper pair (orbital bristles) absent. Outer vertical bristle present.

THORAX. Prosternum bare centrally, microsetulose and with fine setulae anteriorly and anterolaterally. Cervical sclerite of female pale ventrally and greatly expanded on anterior half; male cervical sclerite evenly swollen. Postpronotal lobe bare. Notopleuron with two subequal bristles. Katepisternum with a vertical row of about eight bristles anteroventral to main vertical row. Dorsocentral bristle absent.

FEMALE TERMINALIA (Fig. 20C). Three spermathecae, larger and single (presumably secondary) spermatheca on a long, slightly distally expanded duct arising from side of bursa, stem short and narrow, main body large and divided into two tapered arms. Paired (presumably primary) spermathecal duct much smaller, very short and narrow, arising from apex of a long extension of the bursa, branching into short ducts leading to two small spherical spermathecae.

MALE TERMINALIA (Fig. 20F–G). Genital fork with two long, thin, incurved arms with fine hairs along entire outer surface and widely spaced short spines on mesal surface; 3–4 spines concentrated into a cluster at base; base of fork between arms with a deep groove dividing broad bases of arms. Basiphallus smaller than base of distiphallus, barely projecting posteriorly as a subquadrate lobe. Distiphallus elongate, twice as long as epandrium; distal distiphallus long and thin, slightly longer than and less than half as wide as basal distiphallus at base, distally tapered to a narrow apex. Phallic bulb small and simple, with proximal chamber weakly developed and distal chamber very small and short. Hypandrium elongate, forming a long anterior bridge approximately corresponding to the distal distiphallus, anterior margin narrowed with a short anterior tongue. Ejaculatory apodeme small, about $\frac{1}{3}$ of epandrium size.

Remarks

The similar spermathecal complex of *Pt. mimicus* and *Pt. inconveniens* Marshall sp. nov. differ widely from other *Ptilosphen* and strongly suggest a close relationship between these species. In contrast to almost all other micropezids, the secondary spermathecae of these species seem to be fused with a thick stem to form a single bifurcate mass.

Ptilosphen notatus Marshall sp. nov.

[urn:lsid:zoobank.org:act:D2071641-9F1F-43AD-BCFC-B24DFDFDF92A](https://doi.org/10.21203/rs.3.rs-10000000)

Fig. 21

Etymology

This species is named for the characteristically marked frontal vitta.

Type material

Holotype

FRENCH GUIANA • ♀; Mitaraka; 2°14'17.8" N, 54°27'8.2" W; 352 m a.s.l.; 3–8 Mar. 2015; M. Pollett leg.; MITARAKA/154; tropical moist rainforest, yellow pans traps; MNHN.

Paratypes

BRAZIL • 1 ♀; Amazonas, 50 km N of Manaus, km 934 BR 174, km 14 ZF-2; 13 Jan. 2020; Rafael and Marshall leg.; INPA.

FRENCH GUIANA • • 1 ♀; same locality as for holotype; 352 m a.s.l.; 25 Feb.–3 Mar. 2015; M. Pollett leg.; white pan trap; MNHN • 1 ♂; same locality as for holotype; 433 m a.s.l.; 2–8 Mar. 2015; M. Pollett leg.; white pan trap; DEBU • 1 ♀, 1 ♂; same locality as for holotype; 352 m a.s.l.; 3–8 Mar. 2015; M. Pollett leg.; tropical moist forest, yellow pan trap; MNHN • 1 ♂; same locality as for holotype; 445 m a.s.l.; 7 Mar. 2015; M. Pollett leg.; vegetation along small swamp; DEBU • 1 ♂; same locality as for holotype; 352 m a.s.l.; 25 Feb.–3 Mar. 2015; M. Pollett leg.; tropical moist forest, yellow pan trap; MNHN • 1 ♀; same data as for holotype; 373 m a.s.l.; 2–8 Mar. 2015; M. Pollett leg.; tropical moist forest, white pan trap; MNHN.

Description

LENGTH. 14–15 mm.

COLOUR (Fig. 21A–B, E–F). Head mostly reddish brown; lower face and clypeus yellow, parafacial and gena silvery microsetulose. Pedicel and inner scape surface orange, first flagellomere black. Subantennal depressions and frontal vitta mostly black; anterior and postocellar frontal vitta separated by a broad orange band crossing the ocelli, postocellar frontal vitta parallel sided until vertex, anterior frontal vitta tapered to a broad apex widely separated from anterior margin of frons by a pale anterior area. Fore femur yellow anteriorly, brown posteriorly; fore tarsus white but distal two tarsomeres with dark setulae. Mid and hind femora reddish brown with pale base and indistinct pale band at or just beyond middle. Hind tarsus dark brown, concolorous with tibia. Thorax yellow-brown, without a distinct pattern. Wing with a narrow discal band, indistinctly U-shaped. Abdominal pleuron of female with distinct pigmentation on dorsal half, pigmented areas of P2–3 tapered anteriorly and with a vertical posterior margin; P4 with an almost straight ventral margin; male pleuron similar but with a lightly brown pigmented pleural sac along ventral margin of pigmented area of P2. Female abdomen with T1 brown, T2–5 pruinose dark brown with blue-black highlights, T6 pruinose basally and laterally only; oviscape yellow with black tip, pruinose laterally and shiny dorsally. Male with tergites entirely pruinose, terminalia yellow to pale brown.

HEAD. Frontal vitta strongly convex, half as wide as frons at maximum, broadly tapered anteriorly and parallel sided posteriorly. Two fronto-orbital bristles, a large upper (orbital) at level of upper ocelli and a small lower (frontal). Frontal plate indistinctly striate, orbital plate smooth and mostly shiny but upper epicephalon microsetulose from inner vertical to posterior vitta. Outer vertical bristle present.

THORAX. Prosternum microsetulose with a few scattered fine setulae. Cervical sclerite simple. Postpronotum microsetulose but without setulae or setae. Scapular setae absent. Notopleural bristles strong, anterior about half the size of posterior. Katepisternum with one main vertical row of orange bristles and a short row of about 12 weaker bristles anteroventral to main row. Dorsocentral bristle present.

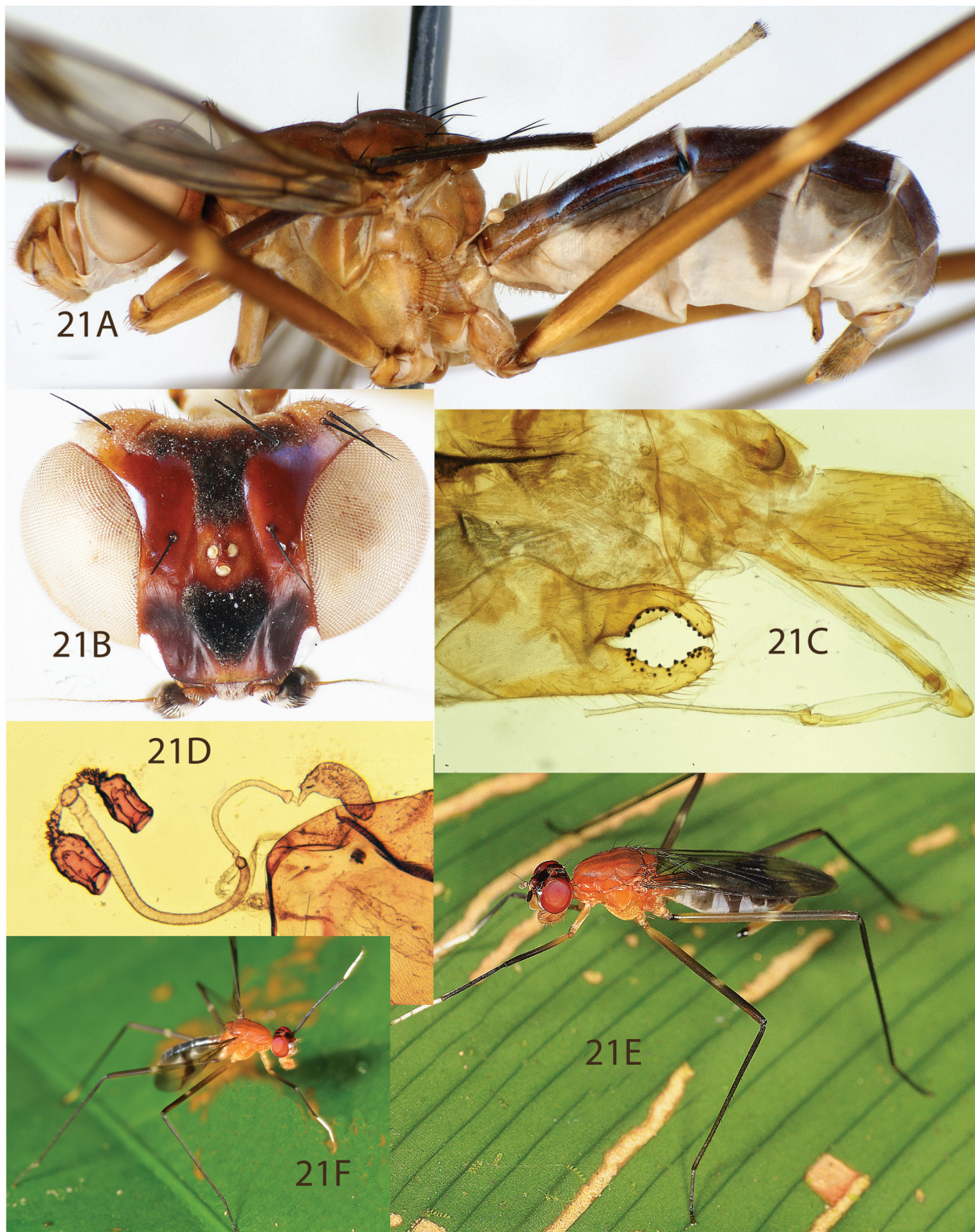


Fig. 21. *Ptilosphen notatus* Marshall sp. nov., French Guiana (MNHN) except for E and F. **A.** ♂. **B.** Head. **C.** Genital fork (male sternite 5), epandrium, aedeagus. **D.** Spermathecae and associated structures. **E.** Living ♀, Brazil (INPA). **F.** Living ♂, Brazil (not collected).

FEMALE TERMINALIA (Fig. 21D–E). Both spermathecal ducts arising together at the apex of a short apical extension of the bursa. Single and paired spermathecae similar in size, paired spermathecae goblet-shaped with a broad invaginated apex, all spermathecae with small surface tubercles; primary duct parallel-sided, twice as wide and $1.5 \times$ as long as single duct, ending in a small bulb just before paired spermathecal stems with a simple basal half and a densely tuberculate distal half. Single spermathecal duct with an apical bulb, apically separated from the short-stemmed spermatheca by a very short threadlike constriction.

MALE TERMINALIA (Fig. 21C). Epandrium with a densely long setose posteroventral corner. Cerci prominent. Genital fork arm mostly cylindrical but incurved with short, stout spines on inner surface; spines most densely packed at base and apex; base of fork between arms about twice as long as arms, with a median groove and a deep narrow cleft. Postgonite broad and rounded, almost hemispherical, but very short and inconspicuous. Basiphallus larger than base of distiphallus, projecting posteriorly as a rounded lobe. Distiphallus longer than epandrium, distal distiphallus almost straight, with distinct transverse striations or rings, $0.25 \times$ as wide and $1.5 \times$ as long as basal distiphallus, apex forming a narrow funnel. Phallic bulb short and weakly differentiated, proximal chamber elongate and distal chamber very small and barely distinguishable from base of distal distiphallus. Hypandrium with a ribbon-like anterior bridge. Ejaculatory apodeme greatly reduced, narrower and about twice as long as sperm pump.

Remarks

Ptilosphen notatus Marshall sp. nov. is one of several orange species with a superficial similarity to *Pt. insignis*. It most resembles *Pt. yasuni* Marshall sp. nov. in male genitalic characters, especially the long distal distiphallus. The only available CO1 sequence for *Pt. notatus* is short, and preliminary analyses recovered this species, with poor support, closer to the *facetus-gentilis* clade than to either *Pt. yasuni* or *Pt. insignis*. *Ptilosphen notatus* can be recognized by the distinct division of the frontal vitta into upper and lower black parts separated by a broad orange band over the ocelli and by the separation of the black lower frontal vitta from the anterior frontal margin by a broad pale area. Males of *Pt. notatus* differ markedly from the common sympatric species *Pt. insignis* by the genital fork with narrow incurved arms (Fig. 21C), in contrast with the thick straight arms of *Pt. insignis* (Fig. 18G).

Ptilosphen rafaelli Marshall sp. nov.

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Fig. 22

Etymology

This species name is a patronym honouring esteemed colleague Jose Albertino Rafael, the co-collector of the type specimen.

Type material

Holotype

BRAZIL • ♀; Amazonas, Novo Airão, AM 352 km 10; 2°42'45" S, 60°57'12" W; Jan. 2020; Rafael and Marshall leg.; INPA, debu00402571.

Paratype

BRAZIL • 1 ♀; same data as for holotype; barcode specimen MYCRO955-22; INPA.

Description (females only)

LENGTH. 13 mm.

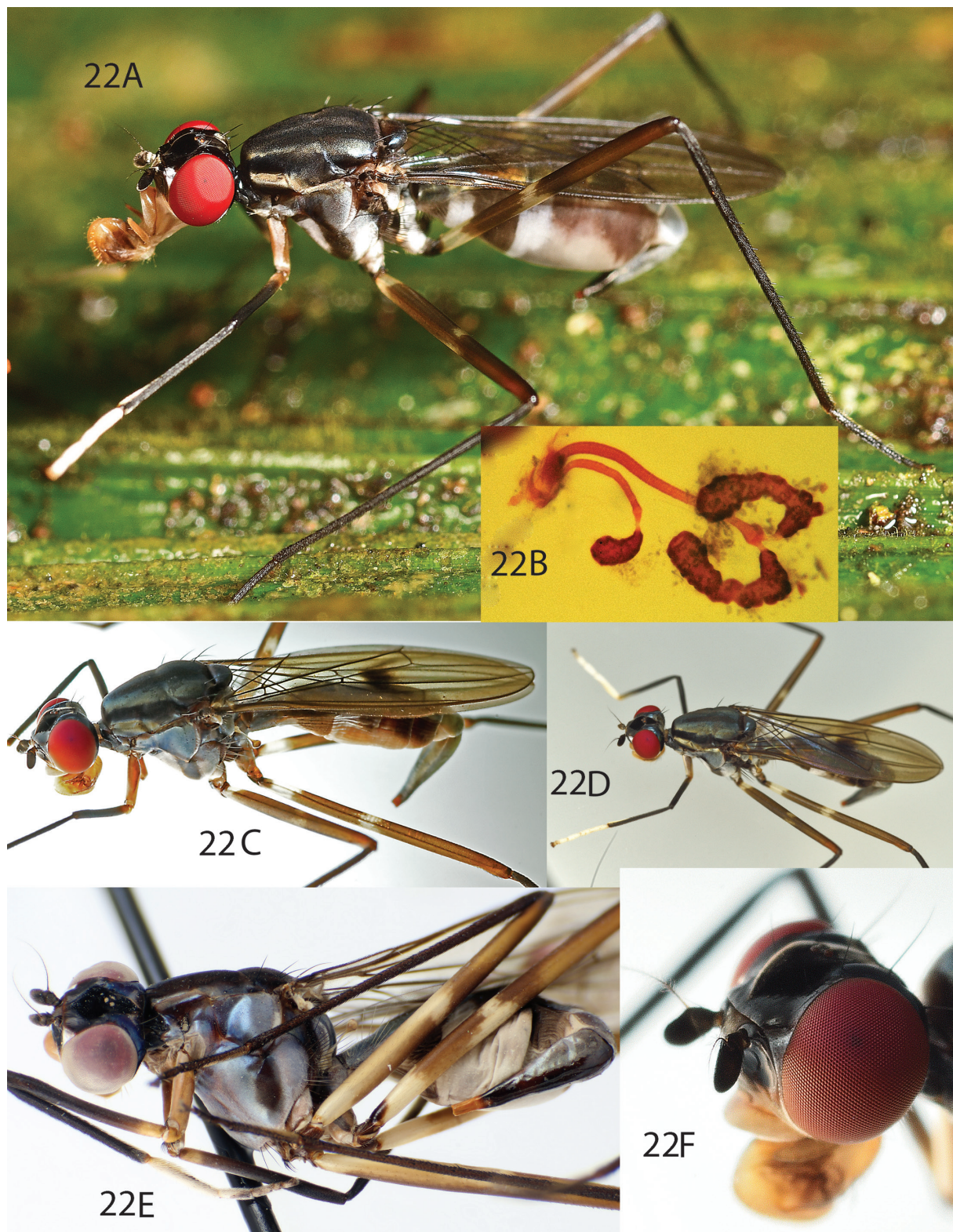


Fig. 22. *Ptilosphen rafaeli* Marshall sp. nov., Brazil (INPA). **A, C–D.** Living ♀. **B.** Spermathecae and associated structures. **E.** Holotype (INPA), habitus. **F.** Holotype (INPA), head.

COLOUR (Fig. 22A, C–F). Frons, antenna and subantennal depression black: frontal vitta velvety black except for pruinose ocellar triangle, epicephalon brassy pruinose, paracephalon shiny blue-black. Clypeus, palpus and lower face margin bright yellow-orange. Parafacial silvery pruinose. Thorax and abdomen black to dark brown, notum indistinctly vittate with narrow central black strip separating broader silvery vittae, pleuron white pruinose except for a vertical black band at centre of katepisternum. Coxa, trochanter and basal part of fore femur orange, fore tarsus mostly white and white setulose but distal three tarsomeres slightly darkened. Mid femur brown with a narrow basal white band and an irregular white band at middle; hind femur similar but with a subbasal white band beyond a narrow brown base; mid and hind trochanters, tibiae and tarsus black. Wing generally infusate with small subquadrate discal patch, without apical or preapical band. Abdominal P1 and P2 with broad vertical black bands separated by a white area, P3 white on anterior half, and P4–6 dark on dorsal half and slightly darkened ventrally. Abdominal T1–2 broadly pruinose at junction and laterally, dorsal part of T2 bare; T3 pruinose on anterior margin and laterally; T4 pruinose anteriorly, laterally and posteromedially; T5–7 entirely pruinose. Oviscape black except orange apex, silvery pruinose laterally on basal $\frac{3}{4}$; dorsal strip and preapical area shiny black.

HEAD. Frontal vitta broad and convex, $0.75 \times$ width of frons at maximum width, strongly tapered anteriorly, broad and gradually tapered to a rounded apex posteriorly. Two fronto-orbital bristles, upper strong. Outer vertical bristle present.

THORAX. Prosternum microsetulose with scattered weak setulae. Pronotum with a prominent transverse groove on lateral parts. Cervical sclerite broad and convex posteriorly, distinctly microsetulose. Postpronotum microsetulose, with several small erect setae. Two notopleural bristles, anterior small. Dorsocentral bristle present.

FEMALE TERMINALIA (Fig. 22B). Oviscape elongate triangular, length $2.7 \times$ maximum width. Paired spermathecal stems elongate and strongly tuberculate, gradually expanded apically to spermathecae that are little differentiated from the stems, with a short and thin constriction separating the duct from a swollen apex of the primary (paired) duct; single spermatheca similar but much smaller and less elongate. Spermathecal ducts long, thin, parallel-sided, single duct $\frac{1}{2}$ as long as and slightly narrower than primary spermathecal duct; ducts arising separately on broad bursa apex.

MALE TERMINALIA. Male unknown.

Remarks

Although this black-bodied species is known only from females, it seems to be distinctive and easily recognized by the orange clypeus, palpus and fore coxa. The apparent lack of preapical and apical pigmentation in the wing is also unusual in the genus. The spermathecae and associated structures resemble those of the similar black-bodied species *Pt. ramosus* and the orange-bodied species *Pt. insignis* and *Pt. dubius*; CO1 data place *Pt. rafaeli* next to *Pt. insignis*.

Ptilosphen ramosus Marshall sp. nov.

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Fig. 23

Etymology

The species name is from the Latin for ‘branched’, referring to the branched arms of the genital fork.

Type material

Holotype

COLOMBIA • ♂; Prov. Amazonas, Parque Nacionales Naturales Amacayacu, San Martin; 3°23' S, 70°6' W; 150 m a.s.l.; 5–19 Dec. 2001; D. Chota leg.; Malaise trap; IAVH.

Paratypes

COLOMBIA • • 1 ♀; same data as for holotype; 2–16 Apr. 2001; CO1 specimen MYCRO959-22; DEBU • 1 ♀; 12–26 Feb. 2001; DEBU • 1 ♀; 26 Feb.–12 Mar. 2001; DEBU • 1 ♀; 24 Aug.–1 Sep. 2001; B. Amado leg.; DEBU • • 1 ♀; same data as for holotype; 14–22 Jan. 2001; B. Amado leg.; IAVH • 1 ♂; same data as for preceding; 15–23 Feb. 2001; IAVH • 1 ♀; same data as for preceding; 22–30 Apr. 2000; IAVH • 2 ♀♀; Amazonas, Parque Nacionales Naturales Amacayacu Matamata; 3°23' S, 70°6' W; 9–30 Jul. 2000; D. Chota leg.; IAVH • 1 ♀; Parque Nacionales Naturales Amacayacu Matamata; 3°23'1" S, 70°6'1" W; 300 m a.s.l.; 14–21 Aug. 2000; A. Parente leg.; IAVH • 1 ♀; Parque Nacionales Naturales Amacayacu Matamata; 3°23' S, 70°6' W; 150 m a.s.l.; 19 Nov. 2001; D. Chota leg.; IAVH • 1 ♂; same data as for preceding; 17 SEP. 2001; IAVH • 1 ♀; same data as for preceding; 17 Sep.–1 Oct. 2001; Malaise trap; DEBU • 1 ♀; same data as for preceding; IAVH • 1 ♀; Amazonas, Amacayacu National Park, Sector Matamata; 150 m a.s.l.; 11–24 Apr. 2000; A. Felix leg.; Malaise trap; DEBU • 1 ♂ (damaged); PNN Amacayacu Matamata; 17 Sep. 2001; D. Chota leg.; CO1 specimen MYCRO276-16; DEBU • 1 ♂ (badly damaged, one leg remaining); Prov. Leticia, Amazonas; 185 m a.s.l.; 19–26 Feb. 1972; D. Ward and A. Forsyth leg.; CNCI.

Description

LENGTH. 12–13 mm.

COLOUR (Fig. 23A–C, E–F). Body mostly black. Frontal vitta velvety black, frontal plate and face reddish brown, top of head heavily golden microtrichose behind, between and just beside and in front of inner verticals, epicephalon and paracephalon otherwise shiny black or dark brown; clypeus dull orange and entirely microsetulose, palpus yellow distally. Notum silvery microsetulose with narrow dark central and dorsolateral vittae, postpronotum and notopleuron silvery. Fore tarsus white; fore tibia and femur dark brown; mid tarsus and tibia brown; mid femur brown with medial and basal white rings subequal to width of femur (ring near midpoint sometimes weak or incomplete). Hind femur brown with basal and medial white rings $2 \times$ width of femur; hind tibia and hind tarsus brown. Wing with faint brown V-shaped discal band, indistinct apical infuscation and an indistinct infuscated spot in basal third. Abdominal T1–2 silvery microsetulose except for a narrow dark median strip on T1 and posterior half of T2; anterolateral margins of T3 silvery microsetulose. Pleuron with a broad dark band on anterior half of P1 and most of P2, a narrow band on the posterior part of P3 and increasingly extensive dorsal dark portions of P4–5 with P4 dark on dorsal half and P5 entirely dark.

HEAD. Frontal vitta strongly convex anterior to ocelli, $0.6 \times$ frontal width at maximum, abruptly tapered to a point anteriorly; postocellar frontal vitta almost level, broad and almost parallel sided until an abrupt taper to a rounded point between postocellars. Two strong fronto-orbital bristles, outer vertical bristle present.

THORAX. Prosternum bare centrally, microsetulose anteriorly. Cervical sclerite simple, posterior part almost flat, slightly depressed at middle. Postpronotum entirely microsetulose, with a few scattered fine setulae. Scapular setae absent. Two notopleural bristles, anterior weakest. Katapisternum with one main row of dark bristles. Dorsocentral bristle present.

FEMALE TERMINALIA (Fig. 23D, G). Oviscape broad and short, expanded basally and half as wide as long, bare distally and along dorsal strip. Three spermathecae on two ducts with smaller single duct arising from side of primary duct at its origin at the apex of a narrow extension of the bursa, primary duct twice as long and thick as single duct and ending in a distinct swelling followed by a short constriction at base of the two thick, prominently tuberculate spermathecal stems that are very little differentiated from the spermathecae. Single spermatheca much smaller, on a short stem separated from single duct apex by a distinct threadlike constriction.

MALE TERMINALIA (Fig. 23A, H–I). Genital fork with four arms: one pair long and thin, one pair short and thick; inner face of arms with dense, short spines extending entire length of arm; base of fork between

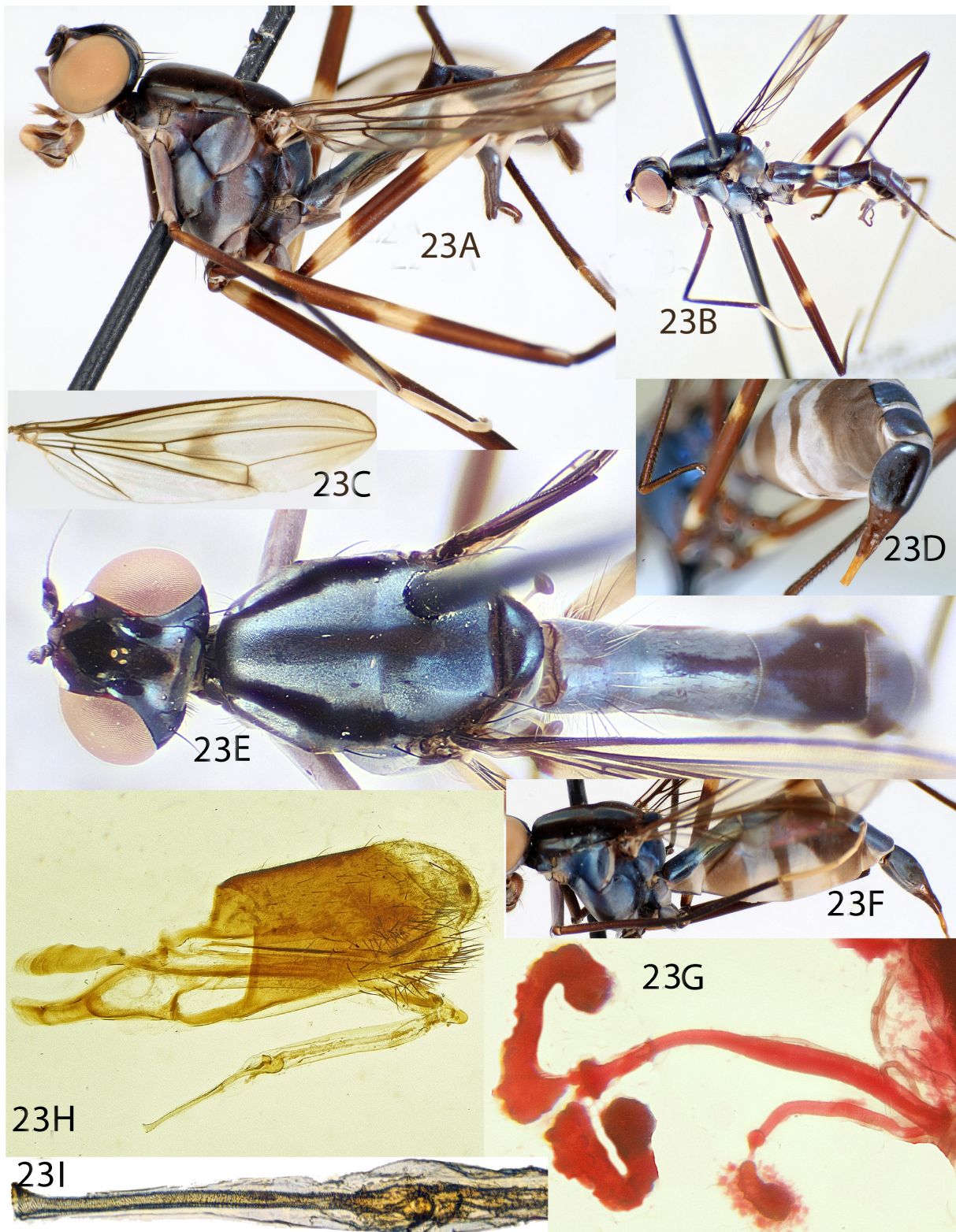


Fig. 23. *Ptilosphen ramosus* Marshall sp. nov., Colombia (IAVH). **A–B.** ♂, lateral and dorsolateral views. **C.** ♂, wing. **D.** ♀, abdomen, posterior view. **E.** ♀, dorsal view. **F.** ♀, left lateral view. **G.** Spermathecae and associated structures. **H.** ♂, terminalia, left lateral view. **I.** Phallus left lateral view.

arms deeply grooved. Basiphallus small but prominent, similar in width to basal distiphallus, projecting posteriorly as a narrow rounded lobe. Distiphallus relatively short, with basal distiphallus slightly shorter than epandrium and twice as long and thick as distal distiphallus, distal distiphallus ringed by weak striae and with a slightly expanded and funnel-like apex. Postgonite small, distal part broadly rounded, mitt-like and entirely spinulose, anterodistal surface finely spinulose. Phallic bulb distinct and similar in width to the basal distiphallus, with proximal chamber elongate and distal chamber short and cap like. Hypandrium with a long, broadly tongue-like anterior bridge.

Remarks

Males of this species have a highly distinctive, prominently branched male genital fork, each arm with an elongate, curved distal part arising at an acute angle to a short, blunt inner basal part. Females have a relatively short, basally expanded oviscape. *Ptilosphen gentilis* has a similarly elaborate genital fork but with a long, tapered and toothed inner basal arm; these species are otherwise dissimilar and not likely to be confused with one another. *Ptilosphen crassus* Marshall sp. nov. resembles *Pt. ramosus* Marshall sp. nov. in most external characters, but males of *Pt. crassus* have a different genital fork with a single pair of short, broad, scooped arms and females have a relatively long, slender oviscape. Most specimens of *Pt. ramosus* have at least a partial white band near the middle of the mid femur, and most specimens of *Pt. crassus* have the middle part of the femur uniformly brown, but there are a few exceptions so the species cannot be reliably separated on femoral pigmentation alone. The internal female genitalia of *Pt. crassus* and *Pt. ramosus* appear to be identical and pleural banding patterns are also the same. Both sequenced specimens of *Pt. ramosus* yielded only short sequences which were not included in the CO1 analyses here but, unsurprisingly, they do come out as closest to *Pt. crassus* in CO1 neighbour-joining trees in queries to the BOLD database.

Ptilosphen tetrastigma (Schiner, 1868)

Fig. 24

Calobata tetrastigma Schiner, 1868: 252.

Ptilosphen cinctiventris Enderlein, 1922: 225. Synonymized with *Pt. tetrastigma* by Hennig 1934: 319 (note that the accidental deletion of the line for *Pt. tetrastigma* following the line for *Pt. rufifrons* in the list of Colombian species by Marshall *et al.* (2016) seemed to place *Pt. cinctiventris* under *Pt. rufifrons* although it is clearly a synonym of *Pt. tetrastigma*).

Ptilosphen tetrastigma – Enderlein 1922: 223, 225. — Frey 1927: 72. — Cresson 1930: 347. — Hennig 1934: 315, 319. — Aczél 1949: 338. — Steyskal 1968: 13. — Schumann 1988: 90. — Ferro & de Carvalho 2014: 59.

Type material

Probable syntypes

VENEZUELA • 5 ♀♀, 3 ♂♂; 1864; Alexander Lindig leg.; NHMW (see Remarks below).

Other material examined

BRAZIL • 3 ♀♀, 7 ♂♂; Rio de Janeiro; 1938; R.C. Shannon leg.; USNM • 2 ♀♀, 1 ♂; São Sebastião; 12–13 Oct. 1976; J. Kugler leg.; TAU. A photo of a female *Pt. tetrastigma* from Tapiraí, State of São Paulo, 18180-000, Brazil, appears on INaturalist <https://www.inaturalist.ca/observations/104770382>.

COLOMBIA • 1 ♀; Prov. Meta, 23 km NW of Villaviencio Qbda., Susamuco; 1000 m a.s.l.; Mar. 1972; S. and J. Peck leg.; CNCI • 1 ♂; Carteguatatuba; J.W. Boyes leg.; CNCI.

PERU • 1 ♀; Junin. Pampa Hermosa Lodge; 1220 m a.s.l.; 24–27 Dec. 2007; D. Brzoska leg.; flight intercept trap; DEBU.

VENEZUELA • 1 ♀; Lara, Sabana Grande; 1282 m a.s.l.; 4 Sep. 2008; M.D. Jackson leg.; CO1 specimen MYCRO956-22; DEBU.

Redescription

LENGTH. 10–15 mm, usually 14–15 mm.

COLOUR (Fig. 24A–B, F). Frons orange except reddish brown upper half of frontal vitta; upper part of head mostly shiny brown, microtrichose area between inner vertical bristles tapering forward almost to ocelli. Lunule pale orange, face and parafacial white to silvery pruinose. Clypeus yellow, entirely setulose. Palpus yellow, paler at apex. Thorax blue-black, densely silvery microtrichose with an indistinct vittate pattern in some lights. Fore tarsus white, 4th and 5th tarsomeres with thick dark bristles; fore tibia dark brown; fore femur distally dark brown and basally yellow. Mid tarsus and tibia brown; mid femur and hind femur yellow-brown with medial white rings 1–2 × and basal white rings 2–3 × width of femur. Hind tibia and tarsus brown. Wing with two separate and staggered discal dots, two faint and almost contiguous preapical dots and a weakly pigmented area over crossvein dm-cu. Abdominal tergites of male brown except for black posterior corners of T2; abdominal pleuron of male boldly banded in black and white, with separate bands on P1, P2, and P3; the P3 band complete and broad; P4–5 white. Abdomen of female with T3–4 white to yellow, other tergites dull brown. T3 with long golden setae on posterior half. Oviscape with apex yellow, otherwise brown with apical quarter and dorsal strip shining, base and sides pruinose. Pleuron of female abdomen dark on dorsal half.

HEAD. Frontal vitta flat or depressed, narrow, about a third of frontal width at maximum. Frontal setae absent. Outer vertical bristle present.

THORAX. Prosternum centrally bare with a deep central pit, with long, fine setae anteriorly and anterolaterally. Cervical sclerite evenly swollen in male, female with central area flattened or concave, differentiated from sides. Postpronotum with a few weak dorsal setulae. Female with scapular setae strong, in a distinct row of 7–9; male without scapular setae. Katepisternum with one main vertical row of dark bristles, additional row anterior to main row fine and pale. Dorsocentral bristle present.

FEMALE TERMINALIA (Fig. 24C). Oviscape slightly shorter than T4–6. Four spermathecae, one pair elongate funnel-shaped and one pair subspherical; both on long, thin ducts, one duct (presumably the secondary duct) arising laterally low on a broadly swollen common duct (or a broad base of the primary duct); the other (primary duct) arising at the tapered apex of the swollen common duct or duct base. Each spermatheca on a narrow stem, stems of secondary spermathecae longer and thinner.

MALE TERMINALIA (Fig. 24D–E, G). Genital fork with thin, strongly incurved arms with long fine hairs along entire surface; inner face of arms with clusters of short, stout spines at base and apex and a few scattered spines in between; inner basal arms absent, base deeply cleft. Distiphallus slightly longer than epandrium, basal distiphallus broad and almost as long as epandrium, phallic bulb with proximal chamber apparently weakly developed; distal chamber darker, transverse. Distal distiphallus short, stout, tapered to a simple apex and with strong transverse striations. Postgonite small but bulbous, with three minute setulae anteroventrally, posterior surface evenly covered with minute bumps. Hypandrium with narrow, tongue-like anterior bridge. Ejaculatory apodeme broad but shorter than epandrium.

Remarks

Ptilosphen tetrastigma is easily recognized by the four wing marks referred to in the species name, but its striking sexual dimorphism apparently led Enderlein (1922) to describe the females as a different species (*Pt. cinctiventris*). The Central American species *Pt. conveniens* and *Pt. inconveniens* Marshall sp. nov. show similar dimorphism, with females having depigmented or desclerotized middle abdominal tergites. *Ptilosphen tetrastigma* is the only species in the genus with four large and distinct spermathecae (two pairs), although the secondary spermatheca is bifurcate and could be interpreted as divided in *Pt. mimicus* and *Pt. inconveniens*. Similar duplication of the secondary (normally single) spermatheca crops up independently in small lineages of several other genera.

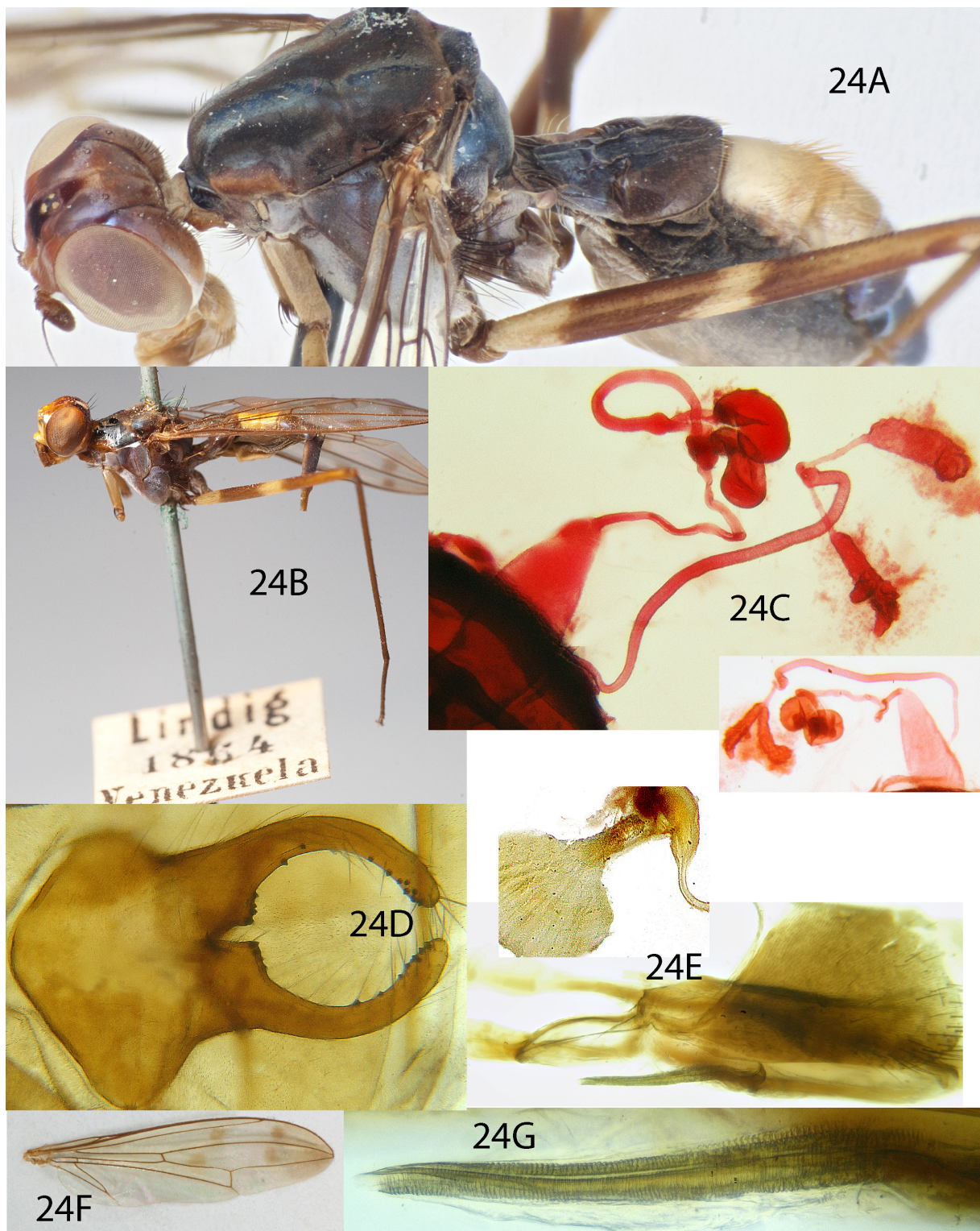


Fig. 24. *Ptilosphen tetrastigma* (Schiner, 1868). **A.** ♀, dorsolateral view, Peru (DEBU). **B.** Syntype, ♀, Venezuela (NHMW), lateral view. **C.** Spermathecae and associated structures, Peru (DEBU; inset shows origin of secondary duct on side of bursa). **D.** ♂, sternite 5 (genital fork), Brazil (TAUI). **E.** ♂, terminalia, lateral view, Brazil (TAUI; inset shows ejaculatory apodeme). **F.** ♂, wing, Brazil (TAUI). **G.** Distal distiphallus, Brazil (TAUI).

Schiner (1868) described this species on the basis of nine cotypes from “South America”, in a paper dealing mostly with material collected during the voyage of the Austrian frigate “*Novara*” (1857–1859), but the specimen labels on the probable type series (eight specimens) in NHMW indicate that they were collected in Venezuela by Alexander Lindig in 1864. No specimen in the series is labelled as a cotype or type and the female illustrated in Fig. 24 was determined by F. Hendel as *Ptilosphen cinciventris* (below the label reading “*tetrastigma* Alte Sammlung”). Males and females in the series, however, are clearly the same species and correspond to Schiner’s description of *Pt. tetrastigma* as well as the description above.

Ptilosphen xanthicoxa Marshall sp. nov.

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Fig. 25

Etymology

The species name is a noun in apposition referring to the diagnostic bright yellow fore coxa of this species.

Type material

Holotype

COLOMBIA • ♀; Prov. Putumayo, La Paya Fca. Charapa; 0°8' S, 74°57' W; 330 m a.s.l.; 1–15 Oct. 2001; R. Cobete leg.; M2442; IAVH.

Paratypes

BRAZIL • 1 ♀; Prov. Amazonas, Parnajau Rio Papagaio; Jun. 2001; Henriques, Vidal and Silva leg.; INPA.

COLOMBIA 1 ♂; Prov. Amazonas, Amacayacu, Matamata; 3°23' S, 70°6' W; 150 m a.s.l.; July 2001; D. Chota leg.; Malaise; IAVH • 2 ♀♀; Prov. Amazonas, Amacayacu, San Martin; 3°23' S, 70°6' W; 150 m a.s.l.; 2–16 Apr. 2001; D. Chota leg.; IAVH • 1 ♀; same locality as for preceding; 24 Aug.–1 Sep. 2000; B. Amado leg.; DEBU 00402360.

Description

LENGTH. 12–13 mm.

COLOUR (Fig. 25C–F). Frons black with anterior margin reddish, frontal vitta pruinose and dull; paracephalon, lower epicephalon and frontal plate shiny, upper epicephalon and posterior frontal vitta silvery microsetulose. Lunule, scape, pedicel and base of first flagellomere dark reddish brown; antenna otherwise black; lower face yellow, parafacial white to silvery pruinose, subantennal depression shiny black. Clypeus yellow and almost bare at middle, otherwise black, densely microsetulose. Palpus yellow-orange distally, brown basally. Notum black, indistinctly vittate with incomplete dark central vitta separating broader silvery microsetulose vittae; pleuron with extensive reddish areas and with extensive pruinosity forming broad, weakly differentiated vertical bands. Fore coxa yellow, densely microsetulose on inner surface; fore femur yellow basally, dark brown distally. Mid coxa reddish brown, heavily silvery microsetulose. Mid tarsus and tibia brown; mid femur with basal and medial white rings subequal to width of femur, otherwise orange-brown. Hind coxa reddish brown, silvery microsetulose on posterior half. Hind femur orange-brown with basal or subbasal and medial white rings 1–3 × width of femur, base of femur brown on anterior surface only; hind tibia and tarsus brown. Wing with indistinct discal band in base of cell r4+5. Abdomen with T1–2 mostly reddish brown with a golden pruinosity except for central part of T2, remaining tergites mostly brown, golden pruinose laterally, oviscapae black with a bare dorsal and distal area, apex orange. Pleuron with P1 brown at base and with brown vertical bands on posterior halves of P2 and P3, P4–5 entirely dark on dorsal half.

HEAD. Two large fronto-orbital bristles, upper inserted at level of upper ocelli. Frontal vitta broad, $0.6\times$ frontal width at maximum, sharply tapered anteriorly and mostly parallel sided posteriorly, tapered to posterior apex. Outer vertical bristle present.

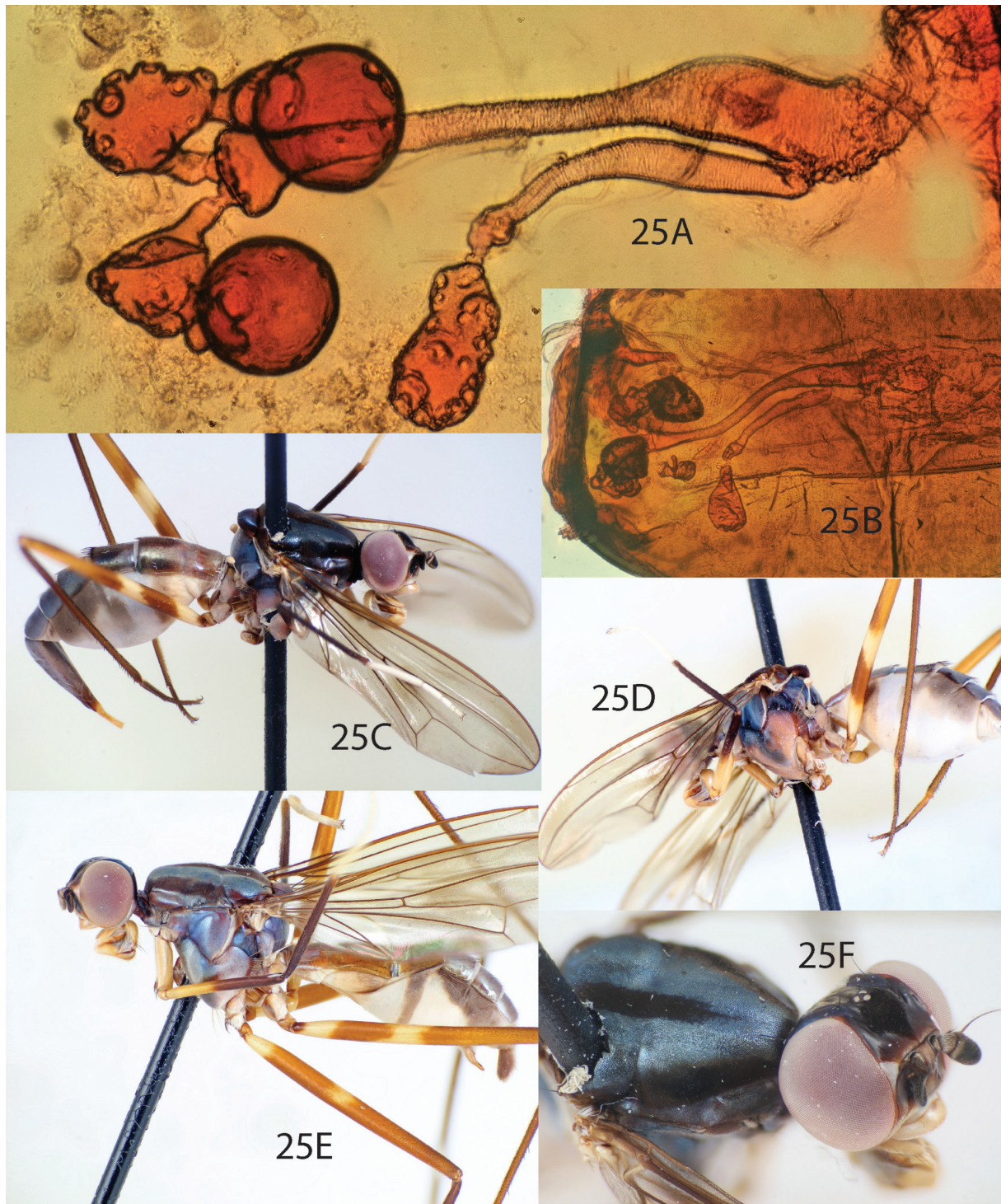


Fig. 25. *Ptilosphen xanthicoxa* Marshall sp. nov., Colombia (IAVH). A–B. Spermathecae and associated structures (B within oviscape). C. ♀, right lateral view. D. ♂, left lateral view. E. ♂, left lateral view. F. ♂ head and thorax.

THORAX. Prosternum entirely microsetulose, with a deep central pit. Cervical sclerite broad, slightly depressed medially in male, deeply depressed medially and distinctly bilobate in female. Postpronotum uniformly microsetulose with a few scattered small setulae. Scapular setae absent. Notopleuron with two large bristles. Dorsocentral bristle large, exceeding scutellum apex.

FEMALE TERMINALIA (Fig. 25A–B). Paired spermathecal duct with basal third conspicuously swollen but parallel sided, gradually tapering to a mostly parallel-sided and transverse striate distal $\frac{2}{3}$ and ending in a broadened but flat-topped apex before splitting into two long spermathecal stems, each with a large, oval, conspicuously tuberculate swelling at midpoint; paired spermathecae spherical with a smooth surface. Single spermathecal duct arising laterally near base of swollen part of paired duct, apparently at the end of a short common duct continuous with base of paired duct; similar in width to most of paired duct and about half as long; single spermatheca club-shaped on a narrow stem and ornamented with circular tubercles similar to those on the stems of the paired spermathecae.

MALE TERMINALIA. As described for *Pt. enderleini*.

Remarks

Ptilosphen xanthicoxa Marshall sp. nov. is very similar to the sympatric *Pt. enderleini*, although it differs in having a yellow fore coxa, more extensive reddish thoracic pigmentation, and an almost clear wing. Male terminalia of these species are apparently identical, however the species can be distinguished by body colour and wing pigmentation. The spermathecal configuration of *Pt. xanthicoxa* is clearly homologous with, but consistently different from, that of *Pt. enderleini*, most obviously in the basal insertion point of the single spermathecal duct but also in details of the primary duct and the constricted paired spermathecal stems.

Ptilosphen xestos Marshall sp. nov.

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Fig. 26

Etymology

The name, in apposition from the Greek for stripped, refers to the absence of dorsocentral bristles.

Type material

Holotype

PERU • ♀; Prov. Madre de Dios, Tambopata, Laberinto, EBLA-B1BJ; 12.555° S, 70.093° W; 9 Jul. 2021; EBLA ICFC leg.; yellow pan traps; COI specimen PERPT3736-23; MUSM.

Paratype

PERU • 1 ♂; Madre de Dios, Tambopata, Laberinto, EBLA-B2CP; 12.556° S, 70.081° W; 16 Aug. 2021; EBLA ICFC leg.; yellow pan traps; COI specimen PERPT7661-23; MUSM.

Description

LENGTH. 13–14 mm.

COLOUR (Fig. 26A, F–G). Frons black to dark brown except for reddish brown anterior margin and posterior margin of frontal vitta; frontal vitta pruinose and dull; paracephalon, lower epicephalon and frontal plate shiny, upper epicephalon and posterior frontal vitta silvery microsetulose. Postocular area sharply divided into a black shiny upper part and a white pruinose lower part. Lunule reddish and setulose; face orange, lower face pale with dark margin, parafacial white to silvery pruinose, subantennal

depression shiny black with yellow ventral border. Clypeus orange, bare centrally, microsetulose laterally. Palpus yellow. Notum black with broad silvery pruinose vittae, an incomplete dark central vitta separating broader silvery microsetulose vittae, pleuron with extensive pruinosity forming vertical bands, cervical sclerite of female holotype orange except for dark, setulose dorsal margin (male cervical sclerite entirely black). Posterior katapisternum slightly reddish, with vertical row of bristles yellow. Fore coxa reddish brown; fore tarsus white; fore tibia dark brown; fore femur (missing from holotype) pale yellow on basal third, dark brown distally. Mid coxa heavily silver pruinose. Mid tarsus and tibia brown; mid femur with basal and medial white rings $1\text{--}2 \times$ width of femur, otherwise pale brown; brown area between white rings twice as long as basal white area. Hind coxa reddish brown with a darker strip, silvery microsetulose on posterior half. Hind femur brown with a narrow brown base preceding subbasal and medial white rings $1\text{--}2 \times$ width of femur, brown area separating white rings slightly longer than white area; hind tibia and tarsus brown. Wing almost evenly and lightly infuscate, with only an indistinct small cloud just beyond crossvein r-m. Abdominal tergites blue-black, lightly silvery pruinose on central part of T1–2 and almost bare on all of T3 except anterolateral margin, otherwise heavily pruinose, oviscape dark but silvery pruinose basally and laterally, leaving a bare dorsal strip and a bare area basal to orange apex. Pleuron boldly banded in black and white, with separate bands on P1, P2, and P3 and dorsal pigmentation on P4–6, males with a large dark pleural sac on P2 and with P3 band complete and narrow, females with P2 band broad dorsally but incomplete ventrally, P3 band narrow ventrally but continuous with the P4–6 pigmentation dorsally.

HEAD. Lower fronto-orbital bristles well developed, paratype with a single upper fronto-orbital on one side, other side apparently without bristle or socket; holotype without trace of upper fronto-orbital bristle or socket. Frontal vitta broad, $0.5 \times$ frontal width at maximum, sharply tapered anteriorly, broad and almost parallel sided posteriorly, rounded at posterior apex. Outer vertical bristle present.

THORAX. Prosternum entirely microsetulose, with a deep central pit. Cervical sclerite of male broad anteriorly and narrow posteriorly with a flat outer face; female cervical subquadrate, shallowly depressed medially and indistinctly bilobate. Postpronotum uniformly microsetulose with a few scattered small setulae. Scapular setae absent. Notopleuron with two bristles, anterior small. Dorsocentral bristle absent.

FEMALE TERMINALIA (Fig. 26H). Paired and single spermathecal ducts arising together at apex of narrow bursa, single duct short and narrow, ending in a club-shaped spermatheca on a narrow stem. Paired duct broad, transverse striate and almost parallel sided until abruptly tapering to a narrow distal fifth; paired spermathecae separated from duct by long, thread-like constrictions, spermathecae club-shaped with strongly tuberculate stems.

MALE TERMINALIA (Fig. 26B–E). Genital fork with a long base and two long, thin, arched arms with fine hairs along entire outer surface; inner face of arms with dense, short spines extending entire length of arm; two compact clusters of stout, medial spines at base where arms converge; base of fork between arms with shallow groove. Epandrium long and narrow, $2.5 \times$ as long as wide. Basiphallus well sclerotized and distinct from distiphallus, projecting posterior to base of distiphallus. Basal distiphallus half as long as epandrium, $0.7 \times$ as long as the narrower distal distiphallus; distal distiphallus with transverse striae and a slightly broadened and funnel-shaped apex. Phallic bulb small, with a small proximal chamber and a smaller distal chamber. Postgonite bulbous and densely covered with small teeth posteriorly and ventrally. Ejaculatory apodeme much smaller than epandrium. Margin of subepandrial sclerite heavily sclerotized to form distinct bacilliform sclerite. Hypandrium with a long, tongue-like anterior bridge and a narrow, incomplete dorsal bridge, phallic plate with transverse rows of minute microtrichiae.

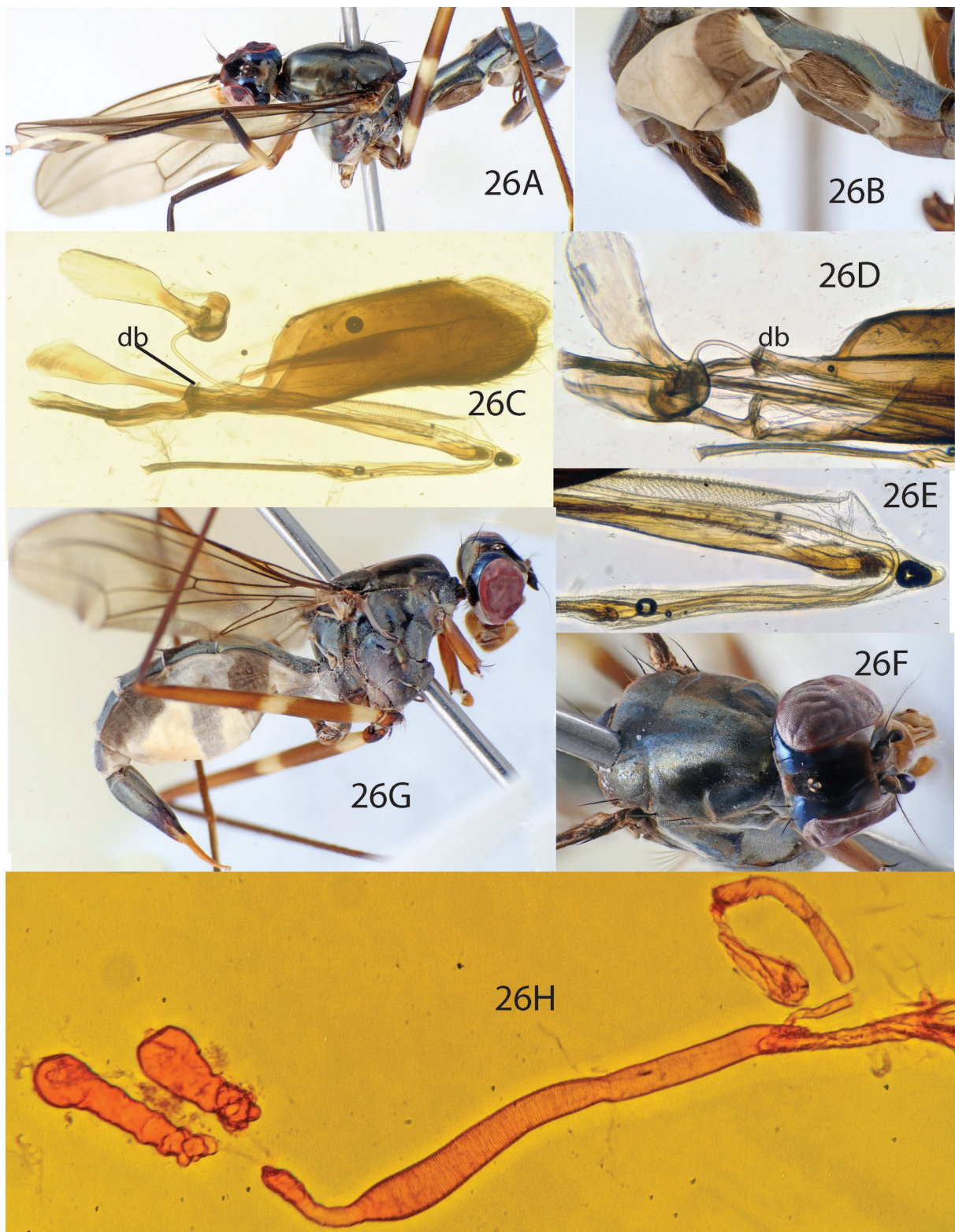


Fig. 26. *Ptilosphen xestos* Marshall sp. nov., Peru (MUSM). A. ♂, left lateral view. B. ♂, abdomen, right side. C. ♂, terminalia, lateral view. D. ♂, terminalia, anterior part, dorsal view. E. ♂, base of phallus, left lateral view. F. ♀, head, dorsal and anterior views. G. ♀, right lateral view. H. Spermathecae and associated structures (single spermathecal duct broken near base). Abbreviation: db=dorsal bridge of hypandrium.

Remarks

The bicolored fore femur in combination with the limited wing pigmentation and relatively small body size gives this species a superficial similarity to *Pt. enderleini*, from which it is easily distinguished by the absence of dorsocentral bristles and strikingly different spermathecal complex. The epandrium is longer and the flare at the end of the distal distiphallus is narrower than in the superficially similar *Pt. enderleini*, but otherwise the male genitalia are similar. The CO1 analysis (Fig. 30) strongly supports the placement of *Pt. xestos* Marshall sp. nov. on a branch with *Pt. yauae* Marshall sp. nov., an orange species superficially dissimilar from *Pt. xestos*.

Ptilosphen yasuni Marshall sp. nov.

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Fig. 27

Etymology

The name is a noun in apposition taken from the type locality.

Type material

Holotype

ECUADOR • ♂; Prov. Orellano, Yasuni Natl. Pk., Yasuni Research Station; 0°40'S, 76°24'W; 250 m a.s.l.; 25 Apr.–8 May 2009; S.A. Marshall leg.; CO1 specimen MYCRO945-22; QCAZ.

Paratypes

COLOMBIA • 1 ♀, 1 ♂; Putumayo, Parque Nacionales Naturales La Paya Caban Viviano Varzea; 320 m a.s.l.; 15–20 Oct. 2011; R. Cobete leg.; Malaise; IAVH.

ECUADOR • 1 ♀, 4 ♂♂; same data as for holotype; CO1 specimen MYCRO945-22; QCAZ • 4 ♂♂; same data as for holotype; DEBU • 3 ♀♀, 4 ♂♂; same data as for holotype; V. Belluz and C. McCreary leg.; DEBU • 1 ♀; same data as for preceding; 14–19 Feb. 1998; D.C. Darling leg.; DEBU • 3 ♀♀; Prov. Orellano, Tiputini Biodiversity Station; Aug. 1999; M. Kotrba leg.; USNM • 1 ♀; same data as for preceding; W.N. Mathis, A. Baptista and M. Kotrba leg.; USNM • 1 ♀; Yasuni Ntl. Pk, Yasuni Research Station; 0°38' S, 76°36' W; Nov. 1998; T. Pape and B. Viklund leg.; Malaise trap, rain forest; DEBU..

Other material examined

COLOMBIA • 1 ♀; Prov. Putumayo, La Paya Fca, Charapa; 0°8' S, 74°57' W; 330 m a.s.l.; Oct. 2001; R. Cobete leg.; IAVH • 1 ♀; Prov. Caqueta, Serrania de Chiribiquete Rio Cunaré, bos. Tierra; 0°32' N, 72°38' W; 330 m a.s.l.; Nov. 2000; Gonzalez and Ospina leg.; IAVH.

ECUADOR • 4 ♂♂; same data as for holotype, excluded from paratype series because they have an apparently atypical pale pleural sac; DEBU.

VENEZUELA • 1 ♀; Bolivar. Rio Grande Research Station, 26 km E of Palmar; 700 m a.s.l.; 24–25 Mar. 1978; J.B. Heppner leg.; rainforest; USNM.

Description

LENGTH. 13–15 mm.

COLOUR (Fig. 27A, D–E, G). Pale orange except as follows: preocellar frontal vitta mostly velvety black to dark reddish brown but orange at anterior margin; postocellar frontal vitta and adjacent epicephalon densely silvery pruinose but sometimes with a narrow bare and shiny area immediately behind ocelli;



Fig. 27. *Ptilosphen yasuni* Marshall sp. nov., Ecuador (DEBU) **A.** ♂, left lateral view. **B.** ♂, abdomen and wing. **C.** ♂, sternite 5 (genital fork). **D–E.** Head, dorsal and anterolateral views. **F.** ♂, terminalia, left lateral view. **G.** ♀, right lateral view. **H.** Spermathecae and associated structures.

frontal plate shiny brown with distinct longitudinal striae; paracephalon shiny brown. Lunule orange; face sometimes with a black patch anteromedially; clypeus densely pale microtrichose, yellow. Antenna and subantennal depression black; subantennal depression bare, shiny. Palpus yellow to pale orange. Thorax orange, posterior margin of anepisternum with a silvery pruinose patch. Fore tarsus white; fore femur orange on basal half, dark brown distally, fore tibia brown. Mid tarsus and tibia dark brown; mid femur with a pale base, otherwise uniformly orange or with an indistinct medial pale ring; hind femur with a pale subbasal area $2\text{--}3 \times$ femoral width and a weak medial pale ring subequal to femoral width; margins of rings not distinct or darkened; hind tibia and tarsus dark brown. Wing with discal band small and subquadrate, extending from R4+5 to CuA1; apex of wing indistinctly pigmented. Male abdomen with T1 orange; T2–6 black to brown sometimes with weak central orange strip, T7 orange-brown; T5 entirely microsetulose, T3 silvery microsetulose laterally but almost bare centrally from anterior to posterior margin, T4 microsetulose but weakly so dorsally and epandrium dark. Pleural pigmentation distinct: female with P1 pale reddish brown, P2 with a broad diagonal dark brown strip slightly tapering ventrally, P3 with a brown dorsal third, and upper part of P4–5 with dark area increasing in extent towards posterior margin. Abdominal pleuron of male with a densely microsetulose elongate oval pleural sac occupying most of P2 and dark band of P3 encircling posterior margin of segment; pleural sac usually dark and longer than high (as in type specimen) but pale and higher than long in some specimens (two such specimens were dissected and matched the type in other features). Oviscape with a broad preapical black ring and an orange apex, heavily silvery pollinose dorsally and basally, orange laterally.

HEAD. Frontal vitta convex, $0.6 \times$ as wide as frons at maximum, sharply tapered to anterior margin and gently tapered to a broadly rounded posterior margin. Two fronto-orbital bristles, a large upper (orbital) at level of upper ocelli and a small lower (frontal). Frontal plate with about six distinct striae, orbital plate smooth and mostly shiny but upper epicephalon microsetulose from inner vertical to posterior vitta. Outer vertical bristle present.

THORAX. Prosternum microsetulose and with scattered fine setulae anteriorly. Cervical sclerite of female with a slightly concave middle part and a strongly lobate posterior quarter; male cervical sclerite only slightly convex on posterior half. Scapular setae absent. Katepisternum with one main posterior row of strong yellow bristles, setae anterior to row fine and pale.

FEMALE TERMINALIA (Fig. 27H). Single and paired spermathecae similar in size and shape, elongate oval with an evaginated apex in available dissections; primary (paired) duct parallel-sided, twice as wide and $1.5 \times$ as long as single duct, ending in a small bulb separated from the long, sinuate paired spermathecal stems by a thin, threadlike constriction about as long as duct width. Single spermathecal duct without an apical bulb, apically separated from the very short-stemmed spermatheca by a remarkably long threadlike constriction as long as the spermatheca and its short stem. Spermathecal ducts arising together at apex of narrow bursa extension.

MALE TERMINALIA (Fig. 27B–C, F). Genital fork arm mostly cylindrical but incurved to a slightly swollen apex, with short, stout spines on inner surface most densely packed at base and apex; base of fork between arms about twice as long as arms, with a median groove and a deep narrow cleft. Postgonite broad, larger than basiphallus and distinctly longer than in congeners, with strongly spinulose posterodistal surface. Basiphallus smaller than base of distiphallus, barely projecting posteriorly as a rounded lobe (Fig. 27F). Distiphallus longer than epandrium, distal distiphallus almost straight, with distinct transverse striations or rings, $0.3 \times$ as wide and $1.3 \times$ as long as basal distiphallus, apex forming a broad funnel. Phallic bulb elongate, appearing mostly as a simple swelling between basal and distal distiphallus, distal chamber small and cap like. Hypandrium with tongue-like anterior bridge. Ejaculatory apodeme slightly smaller than epandrium.

Remarks

Ptilosphen yasuni Marshall sp. nov. belongs to the *Pt. insignis* species group, members of which can be difficult to distinguish on the basis of external morphology. It resembles *Pt. notatus* Marshall sp. nov. in having a long distal distiphallus and strongly incurved genital fork arms, but the spermathecal complex differs conspicuously between these species. The maximum likelihood analysis (Fig. 30) shows *Pt. yasuni* next to a clade including *Pt. insignis* and *Pt. crassus* Marshall sp. nov.

***Ptilosphen yauae* Marshall sp. nov.**

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Fig. 28

Etymology

This species is named after our colleague and nerioid expert Tiffany Yau.

Type material**Holotype**

PERU • ♂; Cuzco, Paucartambo, Kosnipata, Estacion Biologica Manu, Bambu; 12.892715° S, 71.41099° W; 522 m a.s.l.; 18–25 Mar. 2023; MANU ICFC leg.; Malaise trap; MUSM, CBG-A25882C02.

Paratypes

PERU • 1 ♀, 1 ♂; Cuzco, Paucartambo, Kosnipata, Estacion Biologica Manu, Bambu; 12.892715° S, 71.41099° W; 522 m a.s.l.; 18–25 Mar. 2023; MANU ICFC leg.; Malaise trap; MUSM • 1 ♂; same data as for preceding; 29 Apr.–6 May 2023; CO1 specimen PERMU26539-24; DEBU • 1 ♀; same data as for preceding; 14–21 Jun. 2023; MUSM • 1 ♀; Cuzco, Paucartambo, Kosnipata, Estacion Biologica Manu, Cana brava; 12.893167° S, 71.399376° W; 513 m a.s.l.; 9–16 Nov. 2022; MANU ICFC leg.; Malaise trap; MUSM • 1 ♂; Cuzco, Paucartambo, Kosnipata, Estacion Biologica Manu, Copoazu; 12.899883° S, 71.40479° W; 521 m a.s.l.; 23 Nov.–2 Dec. 2022; MANU ICFC leg.; Malaise trap; DEBU • 1 ♀; Cuzco, Paucartambo, Kosnipata, Estacion Biologica Manu, Mandala 2; 12.895102° S, 71.40271° W; 513 m a.s.l.; 6–12 Jul. 2023; MANU ICFC leg.; Malaise trap; MUSM • 1 ♂; Cuzco, Paucartambo, Kosnipata, Estacion Biologica Manu, Pastizal; 12.892787° S, 71.404144° W; 518 m a.s.l.; 23 Nov.–2 Dec. 2022; MANU ICFC leg.; Malaise trap; MUSM • 1 ♂; same data as for preceding; 27 Oct.–3 Nov. 2022; DEBU • 1 ♀, 1 ♂; Cuzco, Villa Carmen; 534 m a.s.l.; Jan. 2015; E. Rodriguez leg.; Malaise; USNM.

Other material examined

PERU • 1 ♀; Madre de Dios, Manu, Estacion Biologica Manu, Trocha 12 (700 m); 12.873081° S, 71.40999° W; 690 m a.s.l.; 10 Nov. 2022; MANU ICFC leg.; Malaise Trap; MUSM • 1 ♂; Cuzco, Paucartambo, Kosnipata, Estacion Biologica Manu, Mandala 2; 12.895102° S, 71.40271° W; 513 m a.s.l.; 29 May 2023; MANU ICFC leg.; Malaise trap; MUSM • 1 ♀; same data as for preceding; 24 Feb. 2023; MUSM • 2 ♀♀; Cuzco, Paucartambo, Kosnipata, Estacion Biologica Manu, Bambu; 12.892792° S, 71.41099° W; 523 m a.s.l.; 25 Mar. 2023; MANU ICFC leg.; Malaise trap; MUSM • 1 ♀; Cuzco, Paucartambo, Kosnipata, Estacion Biologica Manu, Cana brava; 12.893167° S, 71.399376° W; 513 m a.s.l.; 14 May 2023; MANU ICFC leg.; Malaise trap; MUSM • 1 ♀; Cuzco, Paucartambo, Kosnipata, Estacion Biologica Manu, Platanal; 12.900481° S, 71.4045° W; 519 m a.s.l.; 16 Nov. 2022; MANU ICFC leg.; Malaise trap; MUSM • 1 ♂; Cuzco, Paucartambo, Kosnipata, Estacion Biologica Manu, Bambu; 12.892715° S, 71.41099° W; 523 m a.s.l.; 16 Nov. 2022; MANU ICFC leg.; Malaise trap; MUSM • 1 ♀; same data as for preceding; 2 Dec. 2022; MUSM • 1 ♀; same data as for preceding; 29 Apr. 2023; MUSM • 2 ♀♀; same data as for preceding; 29 May 2023; MUSM • 1 ♂; same data as for preceding; 21 Jun. 2023; MUSM • 5 ♀♀, 6 ♂♂; same data as for preceding; (no date given); MUSM.

Description

LENGTH. 13–15 mm.

COLOUR (Fig. 28B–C, G). Pale orange except as follows: preocellar frontal vitta black; postocellar frontal vitta dark, ocellar triangle dark but in an indistinct orange band crossing vitta. Epicephalon mostly shiny black; frontal plate shiny black. Lunule brown; clypeus densely pale microtrichose, yellow. Antenna and subantennal depression black; subantennal depression bare, shiny. Palpus yellow. Thorax orange, posterior margin of anepisternum with a narrow silvery pruinose strip, katepisternum silvery pruinose except for an anterior bare strip. Fore tarsus white; fore femur orange on basal third, black distally, fore tibia black. Mid tarsus and tibia dark brown; mid femur brown with a white subbasal area $2\text{--}3 \times$ femoral width and a white medial ring subequal to femoral width (sometimes incomplete); hind femur brown with a narrowly dark brown base, a broad subbasal white band and a complete white medial band. margins of rings not distinct or darkened; hind tibia and tarsus dark brown. Wing with discal band greatly reduced, forming a spot over M1; apex of wing indistinctly pigmented. Male abdomen with T1 orange; remaining tergites shiny blue black. Pleural pigmentation of female partially obscured on type material but with P1 apparently partly pale reddish brown, P2 entirely black on dorsal half, P3 with a strong black vertical strip near middle and upper part of P4–5 dark. Abdominal pleuron of male with a densely microsetulose elongate oval pleural sac occupying most of P2 and dark band of P3 in posterior quarter of segment. Oviscape black with orange apex, mostly microsetulose but a distal bare dorsal strip and small distal lateral bare areas.

HEAD (Fig. 28C). Frontal vitta convex, $0.6 \times$ as wide as frons at maximum, sharply tapered to a point before anterior margin of frons and gently tapered to a broadly rounded posterior margin. Two strong fronto-orbital bristles, an upper (orbital) at level of upper ocelli and a lower (frontal). Frontal plate with indistinct striae, orbital plate smooth and mostly shiny but posterior margin microsetulose. Outer vertical bristle present.

THORAX. Prosternum densely setulose. Cervical sclerite of female with a slightly concave middle part and a strongly lobate posterior quarter; male cervical sclerite only slightly convex on posterior half. Scapular setae absent. Katepisternum with one main posterior row of strong yellow bristles, setae anterior to row fine and pale. Dorsocentral bristles absent.

FEMALE TERMINALIA (Fig. 28E–F). Paired spermathecae larger than single spermatheca, elongate oval with an invaginated apex in available dissections, stem with a short narrow base and a long, thick conspicuously tuberculate part almost as thick as the spermatheca; primary (paired) duct very broad on basal $\frac{2}{3}$ and tapered to a narrow distal third ending in a bulb-like swelling from which the spermathecal stems arise; single duct arising from base of primary duct at apex of bursa, very short but thickened in middle section and tapered to a very short stem leading to a small oval single spermatheca.

MALE TERMINALIA (Fig. 28A, D). Genital fork arm mostly cylindrical but incurved to a slightly swollen apex, with short, stout spines on inner surface most densely packed on the subquadrate apex of a prominent basal lobe at the base of each arm; base of fork between arms about twice as long as arms, with a median groove and a deep narrow cleft. Postgonite broad and rounded with strongly spinulose posterodistal surface. Basiphallus strongly projecting posteriorly with an upturned apex (Fig. 28D). Distiphallus longer than epandrium, distal distiphallus almost straight, with distinct transverse striations or rings, as wide as but shorter than basal distiphallus, apex forming a broad funnel. Phallic bulb elongate and only slightly swollen, appearing as an overlap between the apex of the basal distiphallus and the base of the distal distiphallus. Hypandrium with a broad tongue-like anterior bridge, incomplete dorsal bridge apparently connected to phallopodeme. Ejaculatory apodeme slightly smaller than epandrium.

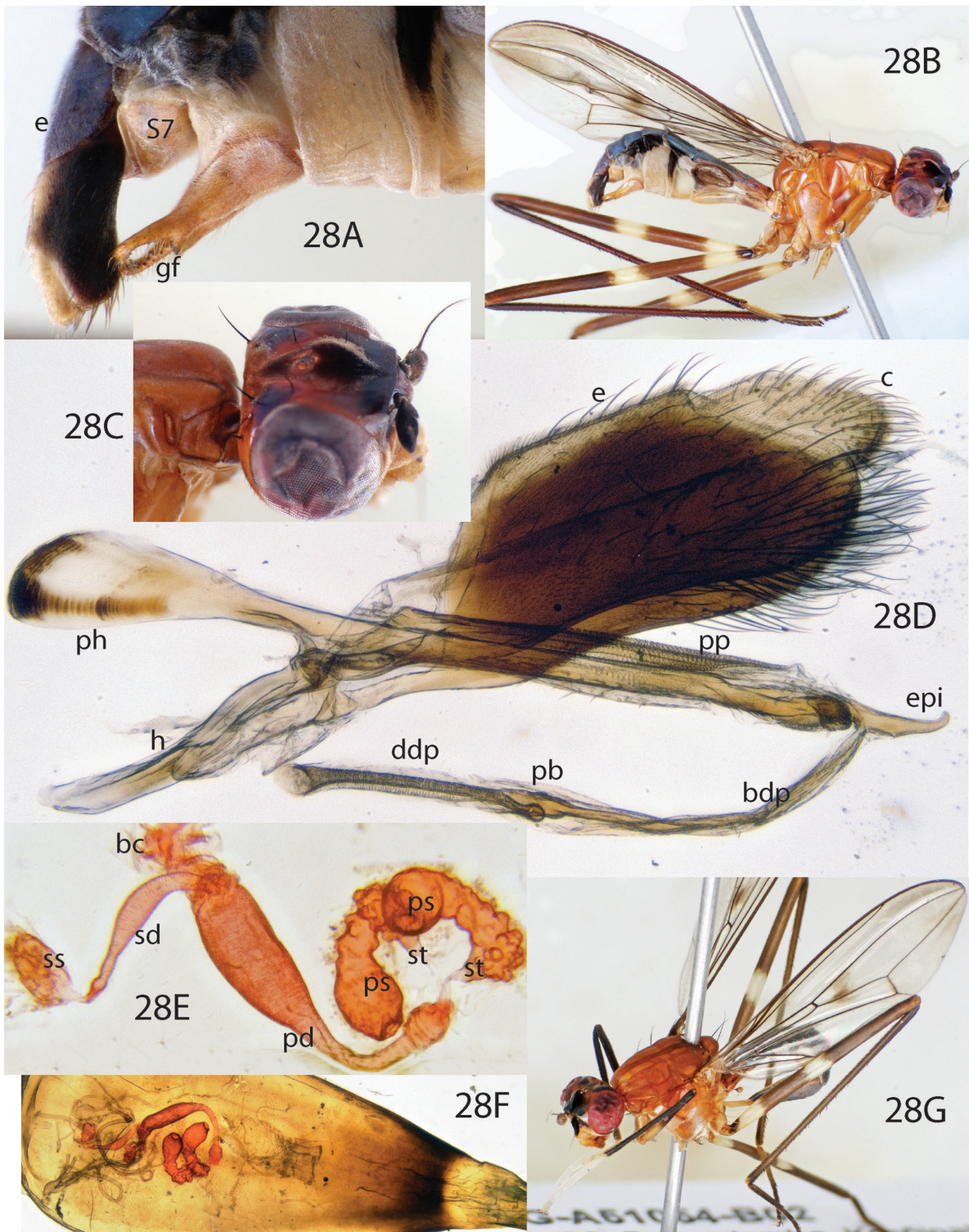


Fig. 28. *Ptilosphen yauae* Marshall sp. nov., Peru (MUSM) **A.** ♂, abdominal apex, right lateral view. **B.** ♂, right lateral view. **C.** ♂, head, dorsolateral view. **D.** ♂, terminalia, left lateral view. **E.** Spermathecae and associated structures. **F.** Oviscape containing stained spermathecal complex. **G.** ♀, left dorsolateral view. Abbreviations: bc=bursa copulatrix; bdp=basal distiphallus; c=cercus; ddp=distal distiphallus; e=epandrium; epi=epiphallus; gf=genital fork; h=hypandrium; pb=phallic bulb; pd=paired spermathecal duct; ps=paired spermatheca; ph=phallapodeme; pp=phallic plate; sd=single spermathecal duct; ss=single spermatheca; st =spermathecal stem; S7=sternite 7.

Remarks

Ptilosphen yauae Marshall sp. nov. belongs to the *Pt. insignis* species group, members of which can be difficult to distinguish on the basis of external morphology. It resembles *Pt. notatus* Marshall sp. nov. and *Pt. yasuni* Marshall sp. nov. in having a long distal distiphallus and strongly incurved genital fork arms but is readily distinguished from these species by its distinct spermathecal complex and prominent basal lobes of the male genital fork.

Ptilosphen zonalis Marshall sp. nov.

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Fig. 29

Etymology

The name is from the Latin for ‘belted’ and refers to the dark bands of pigment entirely encircling the male abdomen.

Type material

Holotype

BRAZIL(?) • ♂; “S. Gabriel, Sv. Amaz. Exp., 28 Dec” (presumably São Gabriel da Cachoeiras, on the Rio Negro River, in the Cabeça do Cachorro region, Amazonas state, Brazil); ZMUH.

Description

LENGTH. 12 mm.

COLOUR (Fig. 29A–C, F). Head and thorax orange except as follows: preocellar (anterior) frontal vitta velvety reddish brown except for a yellowish orange area at anterior margin and a straight-sided silvery pollinose strip filling the central third of the vitta. Lunule yellow-orange; face reddish brown with a lower yellow area; clypeus densely pale microtrichose, yellow. Antenna and subantennal depression black; subantennal depression bare, shiny. Palpus pale, almost white, with dense white setulosity. Thorax orange with two vertical silvery microsetulose areas separated by bare vertical strips. Fore tarsus yellowish white; fore femur orange on basal half, dark brown distally, fore tibia brown. Mid and hind femora uniformly orange; mid tibia and tarsus brown (hind tibia and tarsus missing on type). Wing with discal band small and very indistinct, extending from R4+5 to CuA1; apex of wing clear. Abdominal tergites black to blue-black except for T2, which is dark reddish brown; T3 with silvery-bluish pruinosity anteriorly and laterally. Pleural pigmentation very dark with P1 mostly dark but separated from P2 by a white strip, dark band of P2 encircling segment and surrounding a large, circular, yellowish, densely microsetulose pleural sac. Segment 3 entirely circled by a broad, parallel-sided black band on anterior half, band partially crossed by an angled orange band on upper third of P3. Posterior part of P3 and all of P4 mostly white, with black dorsal area. Segment 4 ventrally with a narrow central black strip continuous with black strip on posterior quarter of segment 3. Anteroventral margin of segment 5 black, P5 and S5 otherwise orange, including genital fork; T8 and epandrium orange.

HEAD. Frontal vitta convex, $0.7\times$ as wide as frons at maximum, gradually tapered to anterior margin and gently tapered to a broadly rounded posterior margin. Two fronto-orbital bristles, a large upper (orbital) above level of upper ocelli and a small lower (frontal). Frontal plate indistinctly striate, orbital plate smooth and mostly shiny but upper epicephalon microsetulose from inner vertical to posterior vitta. Outer vertical bristle present.

THORAX. Prosternum inconspicuously microsetulose, with a few fine setulae anterolaterally. Cervical sclerite with posterior section broad, microsetulose and centrally depressed. Postpronotum microsetulose

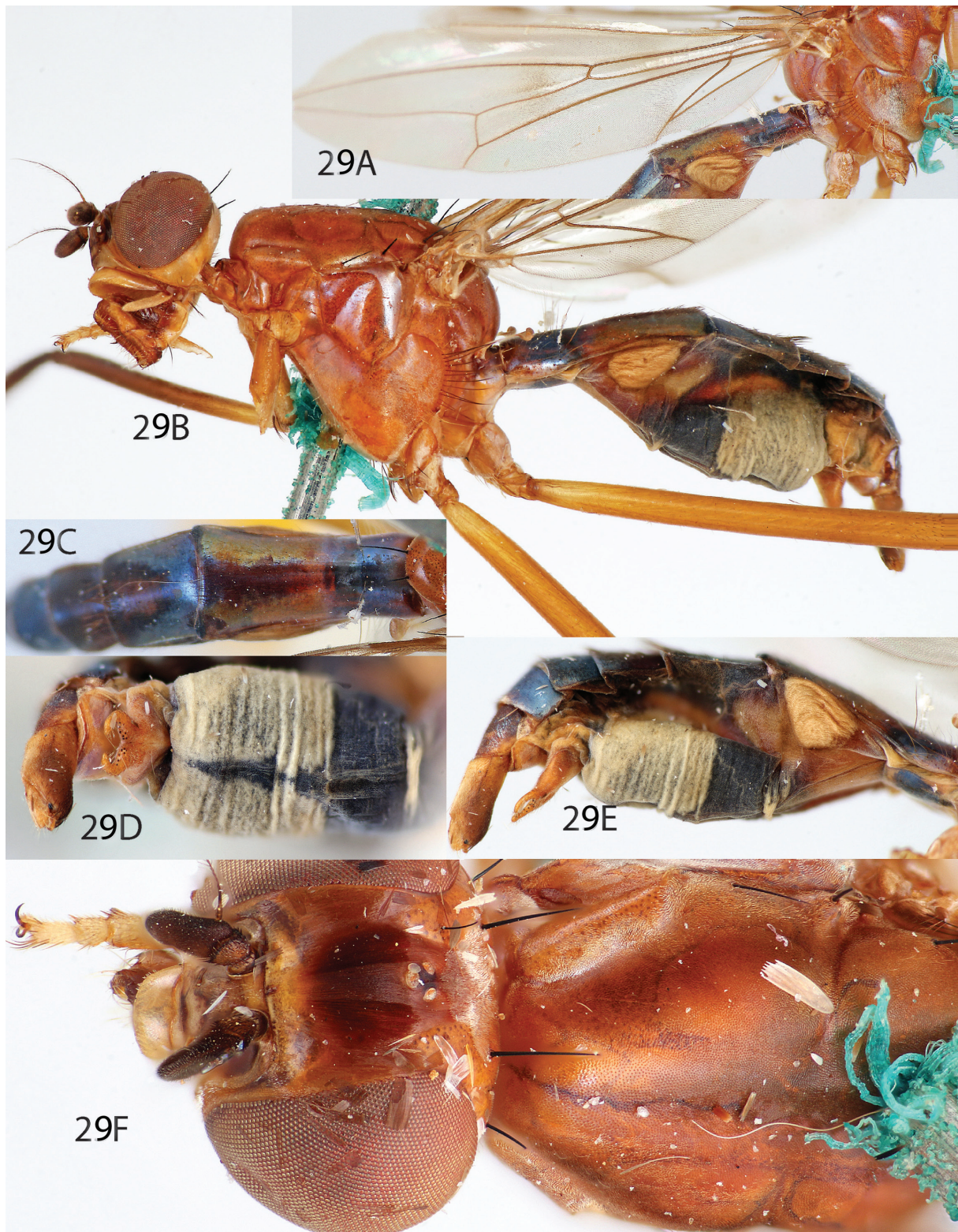


Fig. 29. *Ptilosphen zonalis* Marshall sp. nov., holotype, ♂, Brazil (ZMUH) A. Wing. B. Left lateral view. C. Abdomen, dorsal view. D. Abdomen, ventral view. E. Abdomen, right lateral view. F. Head and thorax.

on dorsal surface only, otherwise bare except for a few small setulae. Scapular setae absent. Notopleuron with two bristles, anterior smaller. Katepisternum with one main posterior row of strong bristles; setae anterior to row fine and pale. Dorsocentral bristle present.

FEMALE TERMINALIA. Female unknown.

MALE TERMINALIA (Fig. 29D–E). Genital fork arm mostly cylindrical but incurved to a slightly swollen apex, with short, stout spines on inner surface most densely packed at base and apex; base of fork about twice as long as arms, with a median groove and a deep narrow cleft. Internal genitalia not observed.

Remarks

The distinctive abdominal pigmentation of the holotype of *Ptilosphen zonalis* Marshall sp. nov., with a broad dark belt of pigmentation circling the third abdominal segment, differs markedly from other named species of *Ptilosphen*. Based on external characters, *Ptilosphen zonalis* belongs to the difficult group of *Pt. insignis*-like species and is most similar to *Pt. yasuni* Marshall sp. nov. It differs most obviously from that species in the pigmentation of the abdominal pleuron and the uniformly pigmented mid and hind femora, although the unique pruinosity pattern of the frontal vitta is also likely to be a reliable character for this species. The abdominal pigmentation, although striking, is not entirely unique. A male specimen from Peru (CNCI) has similar extensive dark abdominal pigmentation but it lacks the unusual frontal vitta pruinosity, it has banded femora as in most congeners and the white pleural sac is smaller and perfectly circular. That specimen, which is mouldy and damaged, is labelled as “*Ptilosphen* n. sp. near *zonalis*”.

Species previously treated as Ptilosphen

Poecilotyclus leucomelas (Walker, 1853)

Calobata leucomelas Walker, 1853: 392.

Calobata varipes Walker, 1853: 392. Synonymized with *leucomelas* by Steyskal (1967: 80).

Grallomyia leucomelas – Enderlein 1922: 218.

Rainieria leucomelas – Czerny 1932: 276.

Rainieria varipes – Czerny 1932: 276

Ptilosphen leucomelas – Hennig 1934: 314, 320. — Aczel 1949: 338.

Ptilosphen varipes – Hennig 1934: 314, 320. — Aczel 1949: 338.

Poecilotyclus leucomelas – Steyskal 1967. — Jackson *et al.* 2015: 424. — Ferro & Marshall 2020: 40.

Type material

Holotype of *Calobata varipes* (no abdomen, two remaining legs)

SOUTH AMERICA • “A.R. Wallace // Dvir 68.4”; NHMUK (round green label “Type”). Another two specimens in NHMUK are labelled “*Ptilosphen varipes* determined by Willi Hennig 1938”.

Holotype ♂ of *Calobata leucomelas*

SOUTH AMERICA • ♂; NHMUK (round green label “Type”). Another 8 specimens in NHMUK are labelled “*Ptilosphen leucomelas*, Walk. determined by Willi Hennig 1938”.

Other material examined

BRAZIL • 1 ♀, 2 ♂♂; Nova Teutonia; CNCI.

Remarks

Hennig (1934) treated this species as a *Ptilosphen* and confirmed this opinion in determinations of NHMUK specimens compared to the type in 1938, presumably because of the short-plumose basal third

of the arista and the single frontal bristle, but Steyskal (1967) synonymized *Calobata leucomelas* and *Calobata varipes*, transferring them to the genus *Poecilotylus* (as *Poecilotylus leucomelas*). *Poecilotylus leucomelas* differs from species of *Ptilosphen* in its unmarked wings, well-developed postocellar bristles (clearly visible on the type material in NHMUK and on the Halle (MLUH) specimen of *Pt. varipes* determined by Hennig) and its mostly bare arista. It is therefore retained in the large, probably paraphyletic genus *Poecilotylus*, as in Jackson *et al.* 2015 and Ferro & Marshall 2020.

Hennig keyed out *varipes* and *leucomelas* (now synonyms) as the only “*Ptilosphen*” with postvertical (postocellar) bristles and a largely bare arista although he indicated that the postverticals were absent in his description of *Pt. varipes* (they are clearly present on the type). In his generic key (1934), *Ptilosphen* and *Poecilotylus* (as *Poecilomyia*) are separated on the basis of the arista (bare in *Poecilotylus*, haired in *Ptilosphen*) and the frontal bristles (one in *Ptilosphen*, two in *Poecilotylus*). The number of fronto-orbitals varies from 0–2 in *Ptilosphen* (almost always 2: one orbital and one frontal) and 2–3 in *Poecilotylus* (normally three: one orbital and two frontal); *Po. leucomelas* has a single frontal bristle as in *Ptilosphen*. The arista is mostly bare but there are hairs in the basal third of the arista unlike most other *Poecilotylus*. There is another, undescribed, species of *Poecilotylus* with a similar character combination but with the arista short-haired throughout.

***Poecilotylus varipes* variety *aequifemur* (Hennig, 1934)**

Ptilosphen varipes variety *aequifemur* Hennig, 1934: 320.

Remarks

Steyskal (1968) expressed the opinion that the specimens Hennig (1934) referred to as *varipes*, including *Pt. varipes* variety *aequifemur*, “are probably 1 or 2 species of *Ptilosphen*, for which the name *aequifemur* is available”. As noted above, the NHMUK specimens housed with the type of *Pt. varipes* and determined by Hennig as *Pt. varipes* belong in *Poecilotylus*, not *Ptilosphen*. Hennig used the name *aequifemur* for two female specimens from Venezuela in MLUH that he considered to differ from typical *varipes* only in that the middle femora have the same white distomedian rings as the hind limbs. According to Karla Schneider (email to S.A.M., May 2005), the only specimen of *Pt. varipes* in MLUH is determined as *Pt. varipes* by Hennig, but not as “variety *aequifemur*”. Her photos of that specimen do not show distomedian rings on the mid femur, so it cannot be a type of *Pt. varipes aequifemur*. The two syntypes appear to be lost. There is no reason to consider *aequifemur* to be a *Ptilosphen* (as defined here) and it is here treated as a *Poecilotylus* and a probable synonym of *Poecilotylus varipes*. Colour of the mid and hind femora seems to be highly variable in this species.

***Poecilotylus ichneumoneus* (Brauer, 1885)**

Calobata ichneumonea Brauer, 1885: 388.

Ptilosphen ichneumoneus – Enderlein 1922: 223.

Grallomyia ichneumonea – Frey 1927: 72. — Cresson 1930: 344. — Czerny 1932: 283.

Taeniptera ichneumonea – Hennig 1934: 75, 95. — Aczél 1949: 316. — Steyskal 1968: 17.

Mitromyia ichneumoneus – Jackson *et al.* 2015: 424.

Remarks

Calobata ichneumoneus Brauer and related undescribed species belong in an undescribed genus; however, they are here provisionally treated as *Poecilotylus* because they run to *Poecilotylus* using current keys. Enderlein was clearly in error treating *ichneumoneus* as a *Ptilosphen*.

Molecular data

Sequences of CO1 were available for 21 species of *Ptilosphen*, with 18 named taxa represented by sequences over 600 bp and three species (*Pt. fulvus*, *Pt. notatus* Marshall sp. nov. and *Pt. ramosus* Marshall sp. nov.) represented by only short sequences (< 300 bp); the species represented by short sequences were not included in the analyses. The CO1 analysis of the 18 named species of *Ptilosphen* are summarized here as nearest neighbour and maximum likelihood trees (Fig. 30) with bootstrap values > 50 % noted on the maximum likelihood tree. Two variable South American species, *Pt. comis* and *Pt. mimicus*, probably represent species complexes; in each case specimens from different countries were recovered on the same branch but in different BINs (three BINs with 4.6 to 7.4 % differences, and two BINs with 2.6 % difference, respectively). Sequences for *Pt. gentilis* were recovered on a single

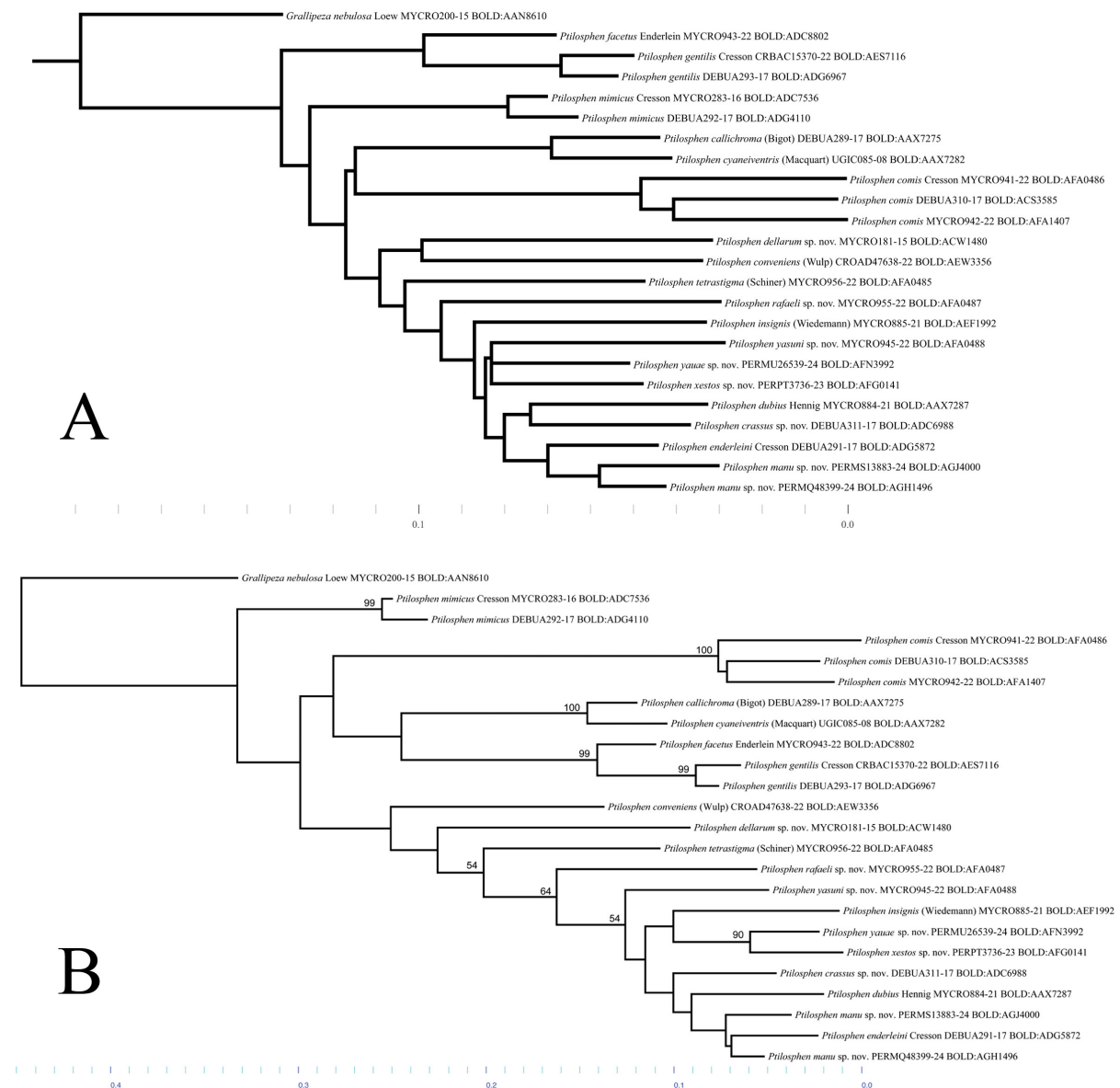


Fig. 30. Sequenced species of *Ptilosphen* Enderlein, 1922, with *Grallipeza nebulosa* (Loew, 1866) as outgroup. **A.** Neighbour-joining analysis. **B.** Maximum likelihood analysis. Order of information is species name, process id and barcode index number (BIN). Bootstrap values > 50% are noted on the ML tree. Scale bars show percentage difference (0.1 = 10%).

branch divided into two BINs (2.7 % difference), but the specimens used (all from Costa Rica) seem to be morphologically identical. As noted, assessment of further specimens from throughout the range of these species is needed to test species concepts.

Discussion

This paper revises two superficially similar genera of taeniapterine Micropezidae: the relatively infrequently collected genus *Parasphen*, including two species associated with lowland Amazonian rainforest, and the large and common genus *Ptilosphen*, including 26 species associated primarily with low to mid elevation forests in Central and South America. Although *Parasphen* and *Ptilosphen* are among the largest and most readily diagnosed micropezid genera, and although many *Ptilosphen* are among the most abundant and easily collected neotropical micropezid species, the material considered here includes 14 previously undescribed species. Three species (*Pt. fulvus*, *Pt. inconveniens* Marshall sp. nov., and *Pt. rafaeli* Marshall sp. nov.) remain known from females only and two species (*Pt. zonalis* Marshall sp. nov. and *Pt. elongatus* Marshall sp. nov.) remain known only from males. Two variable and widespread South American species, *Pt. comis* and *Pt. mimicus*, probably represent species complexes; more specimens from across their extensive ranges are needed to decide whether splitting them into multiple species is justified. Although more collecting at a wider range of Neotropical localities is likely to yield a few further species and will allow for a better understanding of intraspecific variability, *Ptilosphen* is now one of the better documented micropezid genera.

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References

Aczél M.L. 1949. Catalogo de la familia de las "Tylidae" (Calobatidae + Micropezidae + Neriidae, Diptera) en la region neotropical. *Acta Zoologica Lilloana* 8: 309–389.

- Aczél M.L. 1951. Morfología externa y division sistemática de las “Tanypezidiformes” con sinopsis de las especies argentinas de “Tylidae” (“Micropezidae”) y “Neriidae” (Diptera). *Acta Zoologica Lilloana* 11: 482–589.
- Albuquerque L.P. de 1991. Taeniapterinae (Diptera, Micropezidae) da Ilha de Maracã e da localidade de Pacaraima, Roraima, Brasil. *Acta Amazonica* 21 (1): 3–13. <https://doi.org/10.1590/1809-43921991211013>
- Aldrich J.M. 1905. A catalogue of North American Diptera (or two-winged flies). *Smithsonian Miscellaneous Collections* 46: 1–680. <https://doi.org/10.5962/bhl.title.1681>
- Bigot J.M.F. 1886. Diptères nouveaux ou peu connus. 29^e partie (suite) (1). XXXVII. 2^e: *Annales de la Société entomologique de France* 6: 369–392, 592.
- Brauer F. 1885. Systematisch-zoologische Studien. *Sitzungsberichte der Akademie der Wissenschaften in Wien* (1) 91: 237–413.
- Cresson R.T. Jr. 1908 Dipterological notes. I. Micropezidae. *Transactions of the American Entomological Society* 34: 1–12.
- Cresson E.T. Jr. 1930. Notes on and descriptions of some neotropical Neriidae and Micropezidae (Diptera). *Transactions of the American Entomological Society* 56: 307–362.
- Curran C.H. 1932. New species of Calobatidae from British Guiana. *American Museum Novitates* 559: 1–4.
- Curran C.H. 1934a. The Diptera of Kartabo, Bartica District, British Guiana, with descriptions of new species from other British Guiana localities. *Bulletin of the American Museum of Natural History* 66: 287–532.
- Curran C.H. 1934b. *The Families and Genera of North American Diptera*. Ballou Press, New York. <https://doi.org/10.5962/bhl.title.6825>
- Czerny L. 1932. Tyliden und Neriiden des Zoologischen Museums in Hamburg (Dipt.). *Stettiner Entomologische Zeitung* 93: 267–302.
- Enderlein G. 1922. Klassifikation der Micropeziden. *Archiv für Naturgeschichte Serie A* 88: 140–229.
- Fabricius J.C. 1805. *Systema antliatorum secundum ordines, genera, species*. C. Reichard, Brunsvigae [=Brunswick]. <https://doi.org/10.5962/bhl.title.15806>
- Ferro G.B. & de Carvalho C.J.B. 2014. A pictorial key and diagnosis of the Brazilian genera of Micropezidae. *Revista Brasileira de Entomologia* 58 (1): 52–62. <https://doi.org/10.1590/S0085-56262014000100009>
- Ferro G.B. & Marshall S.A. 2020. A redefinition of *Paragrallomyia* Hendel (Diptera: Micropezidae, Taeniapterinae) and a revision of the *P. albibasis* complex. *Zootaxa* 4822 (1): 39–70. <https://doi.org/10.11646/zootaxa.4822.1.2>
- Ferro G.B., Skevington J.H., Marshall S.A. & Kelso S. 2021. Systematic relationships of the Taeniapterini (Diptera: Micropezidae, Taeniapterinae). *Zootaxa* 5004 (2): 370–384. <https://doi.org/10.11646/zootaxa.5004.2.6>
- Frey R. 1927. Zur Systematik der Diptera Haplostomata. III. Fam. Micropezidae. *Notulae Entomologicae* 7: 65–76.
- Giglio-Tos E. 1895. Ditteri del Messico. Parte IV. Muscidae Calypteratae, Muscinae, Anthomyiinae. Muscidae Acalypteratae, Scatophaginae, Helomyzinae, Tatanocerinae, Ortalinae, Ulidinae, Sapromyzinae, Trypetinae, Sepsinae, Tanypezinae, Psilinae, Chloropinae, Ephydrinae, Drosophilinae. *Memorie della Reale accademia delle scienze di Torino* (2) 45 (1896): 1–73.

- Hendel F. 1936. Ergebnisse einer zoologischen Sammelreise nach Brasilien insbesondere in das Amazonasgebiet ausgeführt von Dr. J. Zerny. X. Teil. Diptera: Muscidae acalyptratae (excl. Chloropidae). *Annalen des Naturhistorischen Museums in Wien* 47: 61–106.
- Hennig W. 1934. Revision der Tyliden (Dipt., Acalypt.), 1 Teil: Die Taeniapterinae Amerikas. *Stettiner Entomologische Zeitung* 95: 65–108, 294–330.
- Hennig W. 1937. Tylidae (Micropezidae, Diptera), aus der Sammlung des British Museum of Natural History. Nachträge zur “Revision der Tyliden-II”. *Annals and Magazine of Natural History Series* 10, 19: 521–523.
- Hennig W. 1938. Neue Beiträge zur Systematik der Richardiiden und Tyliden (Diptera, Acalyptrata). *Arbeiten über morphologische und taxonomische Entomologie aus Berlin-Dahlem* 5 (1): 8–15.
- Jackson M.D., Marshall S.A. & Skevington J.H. 2015. Molecular phylogeny of the Taeniapterini (Diptera: Micropezidae) using nuclear and mitochondrial DNA, with a reclassification of the genus *Taeniaptera* Macquart. *Insect Systematics & Evolution* 46: 1–20. <https://doi.org/10.1163/1876312X-45032125>
- Lindsay K. & Marshall S.A. 2023. A revision of *Scipopus* Enderlein including the subgenera *Scipopus* s. str., *Phaeopterina* Frey and *Parascipopus* subgen. nov. (Diptera, Micropezidae, Taeniapterinae). *European Journal of Taxonomy* 904: 1–189. <https://doi.org/10.5852/ejt.2023.904.2323>
- Macquart J. 1846. Diptères exotiques nouveaux ou peu connus. *Mémoires de la Société royale de Sciences, Agriculture, Arts Lille* (1844): 133–364.
- Maddison W.P. & Maddison D.M. 2025. Mesquite: a modular system for evolutionary analysis. Version 4.01. Available from <https://www.mesquiteproject.org> [accessed 10 Feb. 2026].
- Marshall S.A. 2010. Micropezidae. Chapter 5. In: Brown B.V., Borkent A., Cumming J.M., Wood D.M., Woodley N.E. & Zumbado M.A. (eds) *Manual of Central American Diptera, Volume 2*: 805–813. NRC Research Press, Ottawa.
- Marshall S.A. 2019. A revision of the genus *Mesoconius* Enderlein (Diptera, Micropezidae, Taeniapterinae). *European Journal of Taxonomy* 548: 1–126. <https://doi.org/10.5852/ejt.2019.548>
- Marshall S.A., Cardona A. & Wolff M. 2016. Family Micropezidae (Catalogue of Micropezidae of Colombia). *Zootaxa* 4122 (1): 538–548. <https://doi.org/10.11646/zootaxa.4122.1.40>
- Martinez-Alava J.O. & Serna F. 2015. Managing insect collections. Micropezidae (Diptera: Neriioidea) of the Entomological Museum UNAB. *Agronomía Colombiana* 33 (3): 339–347. <https://doi.org/10.15446/agron.colomb.v33n3.52432>
- McAlpine D.K. 1998 Review of the Australian stilt flies (Diptera: Micropezidae) with a phylogenetic analysis of the family. *Invertebrate Taxonomy* 12: 55–134. <https://doi.org/10.1071/IT96018>
- Ortiz P. 2003. *Historia natural, sitios de apareamiento, comportamiento sexual y posible función de la alimentación nupcial en Ptilosphen viriolatus (Diptera: Micropezidae)* M.Sc. Thesis, Universidad de Costa Rica.
- Ratnasingham S. & Hebert P.D. 2007. BOLD: The Barcode of Life Data System. *Molecular Ecology Notes* 7 (3): 355–364. <https://doi.org/10.1111/j.1471-8286.2007.01678.x>
- Ratnasingham S. & Hebert P.D.N. 2013. A DNA-based registry for all animal species: the Barcode Index Number (BIN) system. *PLoS ONE* 8 (7): e66213. <https://doi.org/10.1371/journal.pone.0066213>
- Roback S.S. 1969. The genera, subgenera and species described by E.T. Cresson, Jr. 1906–1949. *Transactions of the American Entomological Society* 95 (4): 517–569.

Schiner J.R. 1868. Diptera. In: von Wüllerstorff-Urbair B. (ed.) *Reise der österreichischen Fregatte Novara um die Erde in den Jahren 1857, 1858, 1859 unter den Befehlen des Commodore B. Von Wüllerstorff-Urbair. Zoologischer Theil. Vol. 2. Abt. I.* Karl Gerold & Sons, Vienna. Available from <https://biodiversitylibrary.org/page/1221403> [accessed 31 Jul. 2023].

Schumann H. 1988. Die Micropeziden-Typen der Dipteren-Sammlung des Zoologischen Museums in Berlin. *Mitteilungen aus dem Zoologischen Museum Berlin* 64 (1): 83–115.
<https://doi.org/10.1002/mmnz.19880640104>

Stamatakis A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30: 1312–1313. <https://doi.org/10.1093/bioinformatics/btu033>

Steyskal G.C. 1967. Notes on some older types of Neotropical Micropezidae with descriptions of new species (Diptera, Acalyptratae). *Papeis Avulsos de Zoologia* 20: 75–84.
<https://doi.org/10.11606/0031-1049.1967.20p75-84>

Steyskal G.C. 1968. Family Micropezidae. In: Papavero *et al.* (eds) *A Catalog of the Diptera of the Americas South of the United States* 48: 1–33. Departamento Zoologia, Secretaria da Agricultura, São Paulo.

Walker F. 1849. *List of the Specimens of Dipterous Insects in the Collection of the British Museum.* Part II, [iii]+231–484, Part III: [iii]+485–687, Part IV. [iii] + 689–1172 + [2]. British Museum (Natural History), London.

Walker F. 1853. Diptera. Part IV. In: Saunders W.W. (ed.) *Insecta Saundersiana: or Characters of Undescribed Insects in the Collection of William Wilson Saunders, Esq., F.R.S., F.L.S., & c.* Vol. 1: 253–414, pls. 7–8. Van Voorst, London.

Wheeler T.J. 2009. Large-scale neighbor-joining with NINJA. In: Salzberg S.L. & Warnow T. (eds) *Proceedings of the 9th Workshop on Algorithms in Bioinformatics*: 375–389. WABI 2009.
https://doi.org/10.1007/978-3-642-04241-6_31

Wiedemann C.R.W. 1830. *Aussereuropäische zweiflügelige Insekten. Als Fortsetzung des Meigenschen Werks. Zweiter Theil.* Schulz, Hamm.

Wulp F.M. van der. 1897. Group Calobatinae. In: Godman F.D. & Salvin O. (eds) *Biologia Centrali-Americana. Insecta. Diptera* 2: 363–376. Taylor & Francis, London.

Wulp F.M. van der. 1883. Amerikaansche Diptera (1882–1883) [No. 3.]. *Tijdschrift voor Entomologie* 26: 1–60.

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