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# Six new species of *Paraleia* Tonnoir (Diptera, Mycetophilidae): amphinotic elements at the northern range of the Andes

SARAH SIQUEIRA OLIVEIRA<sup>1,3</sup> & DALTON DE SOUZA AMORIM<sup>1,2</sup>

<sup>1</sup>Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Av. Bandeirantes 3900, 14040-901 Ribeirão Preto SP BRAZIL

<sup>2</sup>*E*-mail: dsamorim@usp.br, CNPq Research Fellowship, partially developed under FAPESP Grant 2003/10.274-9 <sup>3</sup>Corresponding author. *E*-mail: oliveira.sarahcv@gmail.com (FAPESP Grant 2008/52324-6)

## Abstract

*Paraleia* was originally described by Tonnoir for *P. fulvescens*, known from Australia. More recently, eleven Neotropical species were added to the genus—nine of which are from Chile and southern Argentina, one from Bolivia, and one from Peru. This distribution pattern is typical of many mycetophilid genera. Six new Neotropical species of *Paraleia* from the Andean Colombia and Ecuador are herein described. Male terminalia of *P. bolivari* **sp. n.**, *P. denticulata* **sp. n.**, *P. fumosa* **sp. n.**, and *P. tonnoiri* **sp. n.**, as well as female terminalia of *P. bolivari* **sp. n.**, *P. denticulata* **sp. n.**, *P. fumosa* **sp. n.**, *P. fumosa* **sp. n.**, *P. sharkeyi* **sp. n.**, and *Paraleia* **sp.** are illustrated. High-resolution photos of wings for all species are presented. An identification key for world species of *Paraleia* is provided.

Key words: Paraleia, Mycetophilidae, Diptera, Neotropics, taxonomy

## Introduction

The Mycetophilidae (fungus gnats) contain about 151 extant genera and 4,100 species worldwide (Thompson & Pape 2011) and there was considerable diversification of the family in the Cretaceous (Blagoderov & Grimaldi 2004). The known Neotropical diversity of the family is close to 1,000 species now (Thompson & Pape 2011).

There is a consensus about the monophyly of the Mycetophilidae (Søli 1997, Tozoni 1998, Amorim & Rindal 2007, Rindal *et al.* 2009), but a robust phylogeny for the family is still wanting. Most recent classifications of the Mycetophilidae include as subfamilies Sciophilinae, Gnoristinae, Mycomyiinae, Leiinae, Manotinae, Allactoneurinae, and Mycetophilinae (Tuomikoski 1966, Hennig 1973, Väisänen 1984, Matile 1989, Rindal *et al.* 2009). The "Metanepsiinae", erected by Matile (1971) as a tribe of Gnoristinae, has an uncertain position within the family and is sometimes treated as subfamily (Väisänen 1984, Ševčík & Hippa 2010). It most certainly constitutes a smaller clade of the Gnoristinae and without a phylogeny of the subfamily it would possibly make the "Gnoristini" paraphyletic (Kallweit 1998).

The delimitation of the Leiinae is still not well established in the literature. Edwards (1925) indicated two features to define the group, a short  $R_1$  and a rather longitudinal r-m. Despite exceptions among the leiine genera, a sinuous CuA has been also taken as a synapomorphy for the subfamily (Baxter & Poinar 1994, Jaschhof & Kallweit 2009). This set of characters, however, corresponds to synapomorphies at different levels, some of them of more inclusive groups. The discussion about the subfamily composition, hence, is recurrent (e.g., Søli 1997, Søli *et al.* 2000, Hippa *et al.* 2005, Jaschhof & Kallweit 2009), suggesting that the monophyly of the Leiinae in a wider sense may be questionable. The delimitation of the group proposed by Edwards (1925), Hackman *et al.* (1988), Søli (1997), and Kurina (2004) comprises 32 recent genera and almost 550 species. The fossil record assigned to the subfamily is considerably rich, with eight genera in Cretaceous amber and 54 extinct species (Evenhuis 1994, Baxter & Poinar 1994, Blagoderov 1998, Blagoderov & Grimaldi 2004).

There is no doubt about the placement of *Paraleia* within the Leiinae. The genus has the typical displacement of the base of the radial sector to a more distal position in the wing, with a consequent shortening of  $R_1$  (Edwards

1925). In Jaschhof & Kallweit's (2009) paper on the *Cycloneura* group of genera in New Zealand, they accept a delimitation of the "Leiini" (= Leiinae, e.g. Chandler 2009) including *Leia* Meigen, *Clastobasis* Skuse, *Anomalo-myia* Hutton, *Acrodicrania* Skuse, *Indoleia* Edwards, *Ateleia* Skuse, *Leiella* Enderlein, and the group of genera around *Cycloneura*. Despite not making reference to *Paraleia*, the genus obviously fits in delimitation of the sub-family.

The genus *Paraleia* was originally described by Tonnoir (1929) for a species from Australia, *P. fulvescens* Tonnoir. Edwards (1933) published the first records of the genus for the Neotropical region, describing *P. caudata*, from Bolivia, and *P. peruviana*, from Peru. Freeman (1951) described four additional species from southern Argentina—*P. castanea*, *P. cinerea*, *P. falcigera*, *P. funerea* (plus a species not formally described, *Paraleia* sp.)—and Duret (1984) described *P. martinici*, from Chile. *Paraleia nubilipennis* (Walker 1837), originally described in *Leia*, *P. nephrodops* (Enderlein 1940), described in the genus *Selkirkius* (synonymized to *Paraleia* by Freeman 1954), and *P. antarctica* (Bigot 1888), described as *Leia*—the former two from Chile, the last from Argentina—also belong in the genus, summing up eleven species.

In this paper, we formally describe six new species of *Paraleia* plus one additional species only informally referred to, from areas in elevations above 2,000 m in the Andes of Colombia and Ecuador, increasing the diversity of the genus to 17 formally described species in the world. An identification key for the world species of *Paraleia* is also furnished.

## Material and methods

The specimens examined in this paper belong to collection of *Instituto de Investigación de Recursos Biológicos* Alexander von Humboldt (IAvH), Colombia, to the Diptera collection of the Museu de Zoologia da Universidade de São Paulo (MZUSP), Brazil, and to the Diptera collection of the Australian Museum (AMSA), Sydney, Australia. Most of the holotypes and some paratypes are allocated in the IAvH, and one holotype and some paratypes were deposited at the MZUSP collection.

Wings and the terminalia were separated from the rest of the body. The wings are mounted in permanent Canada balsam slide preparations. The terminalia were heated in KOH solution, neutralized, dehydrated and mounted in permanent Canada balsam slide preparations. Photographs were taken using a Leica DC camera attached to a Leica MZ16 stereomicroscope and a DM2500 Leica compound microscope. Photos were produced using the Auto-Montage software. Initial drawings were made using a camera lucida and then redrawn with Adobe Illustrator 11.0. Morphology terminology and wing venation follows Søli (1997) and Amorim & Rindal (2007). For species with more than one specimen available, measurements in the descriptions correspond to average values.

Some of the males with the terminalia illustrated in this paper have one of the gonostyle represented rotated, so its dorsal face could have its spines properly visualized. Regarding the female terminalia, all the species are very similar in a ventral view. So, one of them is illustrated in this perspective and the other ones in a lateral view, that are more informative and emphasizes the diagnostic features for all species.

Most species are described here from males and females collected together at least in one locality and that fit basically in the same description. One of the species is described based only in males, while two species that do not fit the description of any of the remaining species are described based only in females. The differences in details of the wing, color and details of the female terminalia are enough to justify the description of species based only in females. A group of female specimens that have very similar morphology of the terminalia but some variation in the coloration of the body could be conspecific with one of the species described based only on a male, but the specimens were not collected together, so they are referred here only as "*Paraleia* **sp**.".

Abbreviations used are: ae, aedeagus; anp, anepisternum; ce, cercus; ce1, first cercomere of female terminalia; ce2, second cercomere of female terminalia; cxI, fore coxa; cxII, mid coxa; cxIII, hind coxa; gcap, gonocoxal apodeme; gcx, gonocoxite; gs, gonostyle; ktp, katepisternum; ltg; laterotergite; mes, metepisternum; mep, mesepimeron; mtg, mediotergite; par, parameres; pem, proepimeron; pes, proepisternum; pnt, pronotum; S, sternite; sc, scutum; sctl, scutellum; T, tergite.

## Paraleia Tonnoir

Paraleia Tonnoir, 1929: 611. Type-species, Paraleia fulvescens Tonnoir, by original designation.

**Diagnosis.** C extending slightly beyond  $R_5$ ,  $R_5$  ending rather close to wing apex; Sc complete, ending at C on basal third of wing length; h, Sc, sc-r, Rs and  $M_{1+2}$  without macrotrichia, other veins with dorsal macrotrichia; first sector of Rs transverse or almost transverse; r-m long, almost longitudinal, aligned with second sector of  $R_5$ , this r-m/ $R_5$  system pretty much separated from  $R_1$ . Medial and cubital forks complete, CuA slightly concave,  $A_1$  absent on distal third. Laterotergite and mediotergite bare. Gonocoxite with an extension distal to the base of gonostyle, the inner face typically with numerous short spines; gonostyle elongated, with combs of short spines and a long, pre-apical spine. *Paraleia* is unequivocally separated from its closeby relatives in the Leiinae—e.g., *Leia*, *Leiella*, *Indoleia*, *Clastobasis*, *Rondaniella* Johannsen, *Neoclastobasis* Ostroverchova, and *Greenomyia* Brunetti—by the r-m/ $R_5$  complex largely displaced from the anterior margin, actually a uniquely derived feature of the genus. The distal projection of the gonocoxite, posterior to the insertion of the gonostyles, bearing a number of spines, sometimes forming combs, also present in the gonostyle, is also a very distinctive of the species of *Paraleia*.

## Identification key to world species of Paraleia

1.	Body entirely yellow, no brownish areas (Australia) P. fulvescens Tonnoir
-	Body with at least some brownish areas (South America)
2(1).	Scutum and most pleural sclerites of thorax predominantly yellow, brownish areas, if present, restricted to longitudinal bands
	or undefined latero-posterior brownish maculae
-	Thorax entirely or predominantly brown, yellow areas restricted in extension, generally to the anterior corners or as longitudi-
	nal bands
3(2).	Tip of wing with a light brown macula (Fig. 10), laterotergite yellowish P. nidorosa sp. n.
-	Wing entirely hyaline (e.g., Fig, 12), laterotergite brownish
4(3).	Hind coxa entirely brownish, flagellomeres entirely light brown
-	Hind coxa yellow with a brown distal spot, flagellomeres 1–3 yellow at base
5(2).	Scutum entirely brown
-	Scutum brown with yellow longitudinal bands
6(5).	Wing membrane not entirely hyaline, with a rank area close to up of $K_5$
- 7(6).	Gonostyle with few long apical setae, distally with angle of about 90° (Freeman 1951: fig. 147) <i>P. cinerea</i> Freeman
-	Gonostyle with tew long apical setae, distanty with angle of about 90 (Freeman 1991, hg. 147)
8(7).	Gonostyle without a group of long apreal sette, graduary curved distanty
-	Gonostyle wider at basal 2/3, with an inner indentation midway to apex (Duret 1984: fig. 8) <i>P. martinici</i> Duret
9(5).	Wing membrane hyaline (e.g., Fig. 12)
-	Wing membrane with maculae (e.g., Figs. 3–8, 11)
10(9).	
	spine (Fig. 20) <i>P. tonnoiri</i> <b>sp. n.</b>
-	Gonocoxite dorsal projection shorter than the gonostyle, with small denticulate spines, but no elongated spine 11
11(10)	). Denticulate spines along the dorsal margin of the gonocoxite dorsal projection (Freeman 1951: fig. 150)
-	Denticulate spines scattered along the apex of the gonocoxite dorsal projection (Freeman 1951: fig. 149)
12(0)	Wing membrane with incomplete or weakly defined transversal maculae (e.g., Figs. 5–8, 11)
12(9).	Wing membrane with incomplete or weakly defined transversal maculae (e.g., Figs. 5–8, 11)
-	). Hind coxa entirely yellow
-	Hind coxa entirely yellow
14(13)	). Wing maculae very weak across medial veins and at anal cell; CuA not sinuous (Figs. 5, 6)
-	Wing maculae more distinct across medial veins, stronger on the first section of Rs and apex of $R_s$ , and at anal cell; CuA
	slightly sinuous
15(13	). Wing membrane inconspicuous maculated at the first section of Rs and at the wing apex (Figs. 7, 8). Female sternite 8 wide,
	with a shallow distal incision in lateral view (Fig. 19) P. denticulata sp. n.
-	Wing membrane stronger maculated just after the first section of Rs, apex of $R_5$ , and around base of cubital fork (Fig. 11).
	Female sternite 8 slender, with a deep distal incision in lateral view (Fig. 22)
16(12	). Wing with two marks along line of $r-m+R_5$ (Freeman 1951: fig. 306). Male gonostyle with an external crest before apex bear-
	ing a row of short spines (Freeman 1951: fig. 146) P. antarctica (Bigot)

- Wing with three marks along line of r-m+ $R_5$ (e.g., Figs. 3–4). No external crest on male gonostyle	
17(16). Gonostyle rounded distally (Fig. 13)	
- Gonostyle bifid or trifid at apex	
18(17). Gonostyle bifid at apex (Freeman 1951: fig. 145, Freeman 1954: fig. a) P. nubilipennis (Walker)	
- Gonostyle trifid at apex (Freeman 1954: fig. c) <i>P. nephrodops</i> (Enderlein)	

## Paraleia bolivari, sp. n.

(Figs. 2–4, 13–15)

**Diagnosis.** Three ocelli. Three dark brown maculae across the wing. Gonostyle round apically, with a row of short spines on distal half, and a long spine at apex. Female sternite 8 round apically, with a fringe of brown setae.

**Material examined.** Holotype ♂, COLOMBIA, State of Cundinamarca, PNN Chingaza, Bosque Palacio, 04°31'N 73°54'W, 2,939 m, 17.i–04.ii.2001, M1258 (E. Niño Leg.) (IAvH). Paratypes: 1♀, same data as holotype (IAvH); 1♀, COLOMBIA, State of Cundinamarca, PNN Alto de la Bandera, 04°31'N 73°45'W, 3,660 m, 04–16.ii.2001, M1261 (L. Cifuentes Leg.) (MZUSP).

Description. Male. Head (Fig. 2). Vertex brown, with scattered, whitish, longer bristles. Mid ocellus smaller, lateral ocelli close to but not touching eye margin. Frons light brown, covered with setulae, clypeus light yellow; labella yellow; maxillary palpus whitish yellow, five palpomeres, last palpomere almost twice length of penultimate, first two palpomeres short. Scape shorter than pedicel, both yellow, first flagellomere light brown on distal half, lighter on basal half, second and third flagellomeres brown, with basal fourth lighter, remaining flagellomeres brown. Thorax (Fig. 2). Pronotum yellowish-brown, with five strong yellow setae, dorsal three stronger, ventral two shorter. Scutum basically brown, dark yellow on anterior corners, above wings, and long dorso-centrals, covered with short scattered setae, stronger dorso-centrals and supra-alars. Scutellum yellow, with four scutellar bristles. Proepisternum light-brown, proepimeron slightly darker, bare. Meso and metapleura brown, entirely bare. Haltere whitish, setose. Fore leg with coxa whitish-yellow, trochanter brown, femur light yellow, except for a brown ventro-basal macula, tibia and tarsus light brown; mid and hind coxae light yellow, with a brown mesal macula, mid femur light yellow, darker ventrally, hind femur light yellow, brown at apical fifth, mid and hind tibiae and tarsi light brown, darker to apex. Tibial spurs 1:2:2, brown, spurs almost twice tibial diameter at apex. Some few dark apical setae on fore tibia, mid and hind tibiae with long, strong, black setae. Wing (Fig. 3). Length, 4.9 mm, width, 1.6 mm. Membrane without macrotrichia, light yellowish brown, darker brown bands at basal third, mid and apex of wing, darker at base of Rs; sc-r present, close to apex of Sc; C extending slightly beyond R<sub>5</sub> apex, almost reaching wing tip; Sc complete, reaching C at wing basal third. R<sub>1</sub> less than twice r-m length, reaching C at distal third of wing; Rs almost vertical; R5 reaching C close to the wing tip, almost straight; r-m almost longitudinal, about seven times length of base of Rs.  $M_{1+2}$  slightly shorter than r-m;  $M_1$  and  $M_2$  more than twice length of  $M_{1+2}$ ; CuA depressed midway to apex; A1 incomplete on distal third. M1, M2, M4, apical third of second sector of CuA and A<sub>1</sub> distally with macrotrichia. Abdomen. Tergites 1–6 brown, tergites 2 and 3 lighter; sternites 1–6 whitish yellow mesally, brownish laterally; segment 7 brown, with numerous yellowish setulae. Terminalia yellowish. Termi**nalia** (Fig. 13). Gonocoxite yellowish with brown margins, with extensions distally to the base of the gonostyle, rounded distally, with many short spines at ventral surface; gonostyle long, round distally, with a row of short spines, and a single, long spine at apex; aedeagus thin, long, bifid at distal half; parameres well developed, more sclerotized at apex, involving the aedeagus; cercus covered with setulae; tergite 9 weakly sclerotized, round apically.

**Female.** As males, except as follows. **Wing** (Fig. 4). Length, 4.4 mm, width, 1.5 mm. Brown maculae slightly lighter. Vertex lighter ventrally. Mid and hind coxae and femora darker. Abdominal tergites brown, with lateral margins lighter. **Terminalia** (Figs. 14–15). Terminalia yellowish-brown, distal margin of sternite 8 round, with a fringe of brown setae; cercus longer than rest of terminalia, basal cercomere longer than apical one.

**Etymology.** This species is named after Simon Bolivar (1783–1830), born in Venezuela and responsible for the independence of Bolivia, Ecuador, Peru, Colombia, Venezuela, and Panama.

**Comments.** One of the *P. bolivari* **sp. n.** females has the wing maculae lighter than the others, but the shape of sternite 8 is similar, so they are considered here as conspecific. The wing pattern in this species is quite similar to that of *P. denticulata* **sp. n.** and *P. sharkeyi* **sp. n.** regarding the disposition of the maculae on the wing membrane, but it is stronger and more conspicuous than in that from the other species, especially on the first section of Rs. The

presence of a long gonostyle, with a row of short spines and a single long apical one (Fig. 13) also differentiate *P. bolivari* **sp. n.** from *P. denticulata* **sp. n.**, where the gonostyle shows an irregular row of short spines, as well as a single subapical one (Fig. 18). In the female terminalia, the distal margin of the sternite 8 is very particular in each one of these species: round with a fringe of brown setae in *P. bolivari* **sp. n.** (Figs. 14, 15); wide with a distal incision, brown and long setae in *P. denticulata* **sp. n.** (Fig. 19); and with a deep lateral incision, quite strongly setose in *P. sharkeyi* **sp. n.** (Fig. 22).



FIGURE 1. Habitus. Female paratype of Paraleia fumosa sp. n., lateral view. Scale 1 mm.



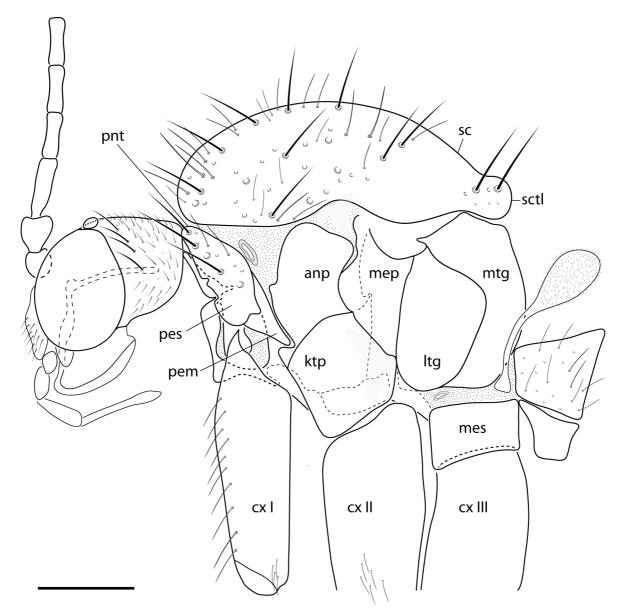


FIGURE 2. Lateral view of head, thorax and first abdominal segment. Male paratype of Paraleia bolivari sp. n. Scale 1 mm.

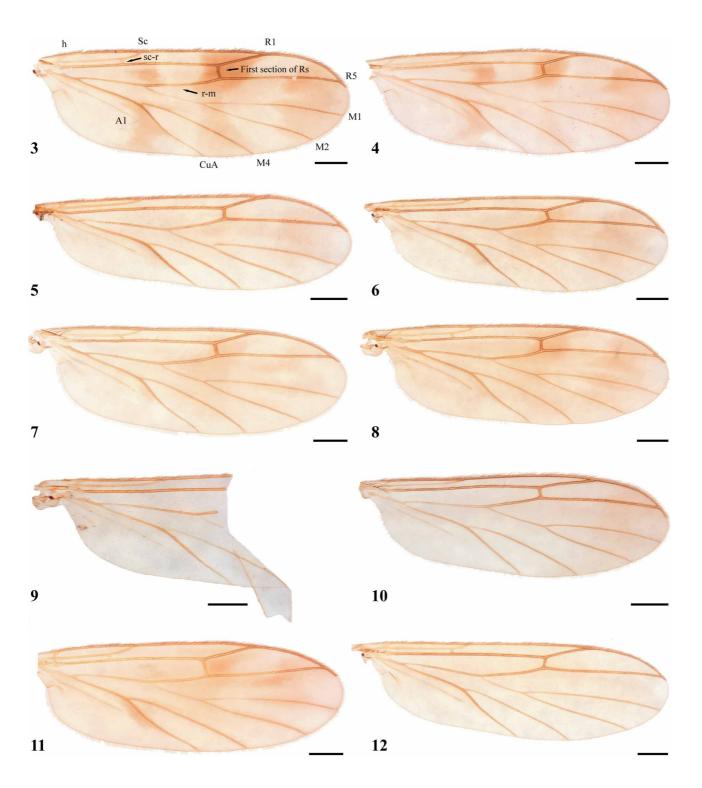
*Paraleia fumosa*, **sp. n.** (Figs. 1, 5–6, 16–17)

**Diagnosis.** Two ocelli. Wings brown maculae rather inconspicuous,  $R_5$  straight. Gonostyle folded distally, with a single spine at apex and a subapical row of spines, gonocoxite projection distal to base of gonostyle with a distal and a ventral rows of spines.

**Material examined.** Holotype ♂, ECUADOR, E. Papallacta (Quito/Baeza), 2,900 m, 12–15.i.1971 (L.E. Peña Col.) (MZUSP). Paratypes: 1♂ 2♀ COLOMBIA, State of Huilla, PNN Cueva de los Guácharos, Mun. Acevedo, 01°37'N 76°06'W, 2,150 m, 15–19.vi.2003, M3787 (J. Lopes leg.) (IAvH).

**Description**. **Male. Head.** Vertex brown, with scattered, whitish, longer bristles. Two ocelli close to but not touching eye margin, mid ocellus absent. Frons light brown, covered with setulae, clypeus light yellow; labella yellow, maxillary palpus whitish yellow, five palpomeres, last palpomere as long as penultimate, first two palpomeres short. Scape and pedicel of equal length, yellow, first flagellomere yellow on basal half, remaining flagellomeres brown. **Thorax.** Pronotum yellow, with four strong bristles. Scutum brown, yellow on anterior corners until the middle of scutum, as an anterior-posterior line. Scutellum yellow, four scutellar bristles. Mediotergite and lateral

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FIGURES 3–12. Wings of *Paraleia*. 3. *Paraleia bolivari* sp. n., male paratype. 4. *Paraleia bolivari* sp. n., female paratype. 5. *Paraleia fumosa* sp. n., male paratype. 6. *Paraleia fumosa* sp. n., female paratype. 7. *Paraleia denticulata* sp. n., male paratype. 8. *Paraleia denticulata* sp. n., female paratype. 9. *Paraleia tonnoiri* sp. n., male holotype. 10. *Paraleia nidorosa* sp. n., female holotype. 11. *Paraleia sharkeyi* sp. n., female paratype. 12. *Paraleia* sp., female paratype. Scale 0.5 mm.

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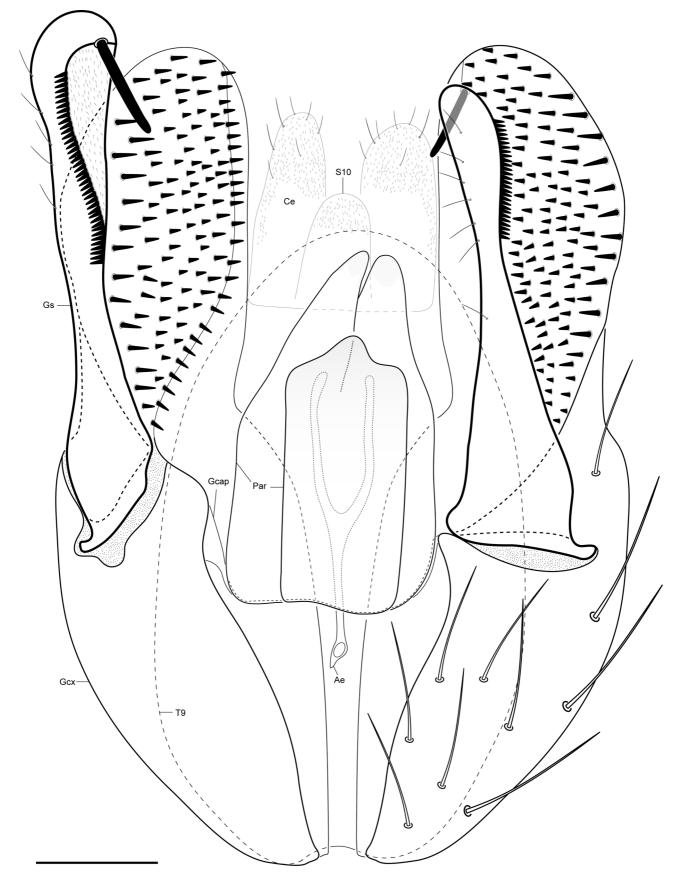


FIGURE 13. Male terminalia of Paraleia bolivari sp. n., ventral view. Paratype. Scale 0.1 mm.

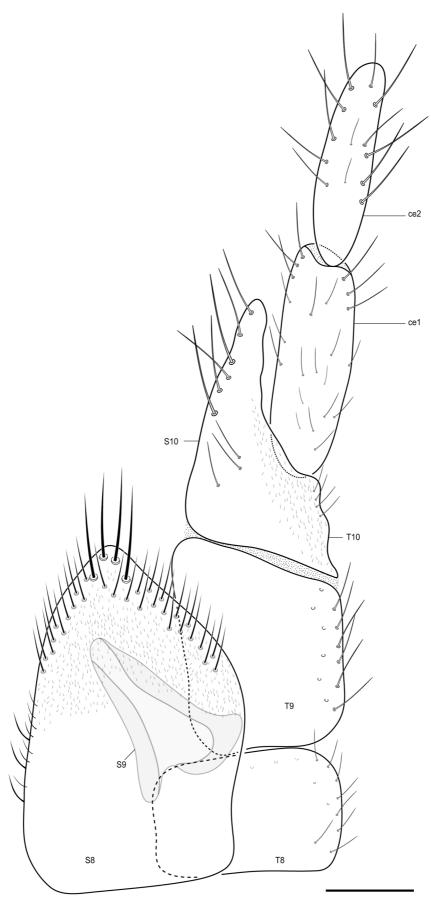


FIGURE 14. Female terminalia of Paraleia bolivari sp. n., lateral view. Paratype. Scale 0.1 mm.

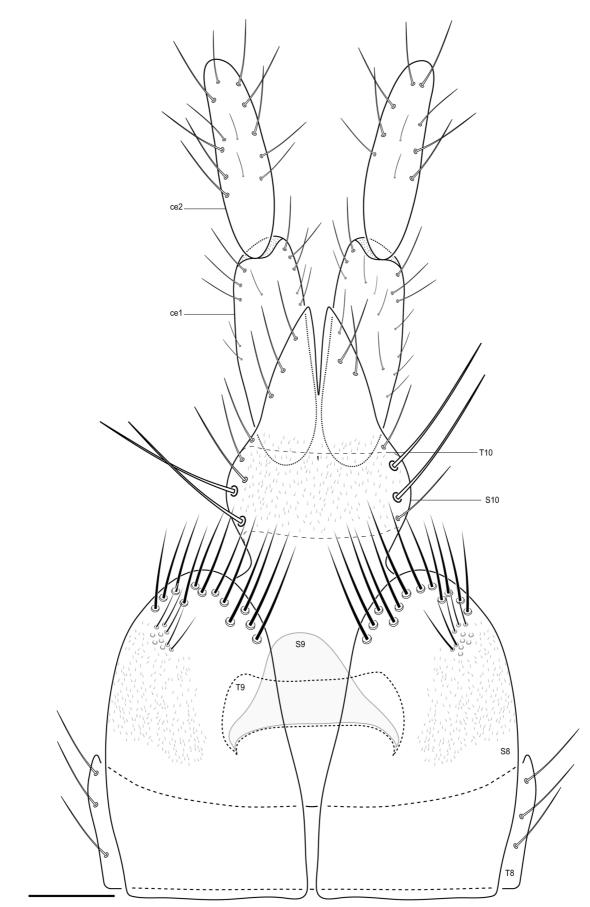


FIGURE 15. Female terminalia of Paraleia bolivari sp. n., ventral view. Paratype. Scale 0.1 mm.



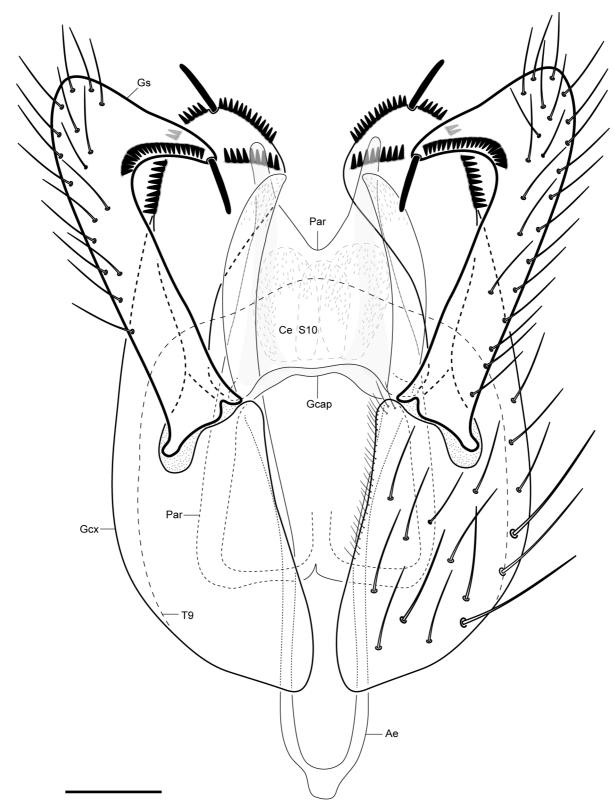


FIGURE 16. Male terminalia of Paraleia fumosa sp. n., ventral view. Holotype. Scale 0.1 mm.

sclerites bare, brown. Pleural membranae yellow, bare. Haltere whitish, knob slightly brownish, setose. Legs yellow. Tibial spurs 1:2:2, spurs almost twice width of tibial apex. Some few dark apical setae on fore tibia, mid and hind tibiae with long, strong, black setae. **Wing** (Fig. 5). Length, 4.2 mm, width, 1.2 mm. Membrane without macrotrichia, translucent, brown maculae rather inconspicuous across mid and apex of wing, a slightly darker area just posterior to  $A_1$ . Sc-r present, not strongly sclerotized; C extending slightly beyond  $R_5$  apex; Sc complete, reaching

C on distal third of wing.  $R_1$  shorter than r-m length, reaching C at distal third of wing; Rs transverse;  $R_5$  straight, reaching C close to wing apex; r-m almost longitudinal, about seven times Rs length.  $M_{1+2}$  shorter than r-m length;  $M_1$  and  $M_2$  more than twice length of  $M_{1+2}$ ; CuA slightly depressed midway to apex;  $A_1$  incomplete on distal third.  $M_1$ ,  $M_2$ ,  $M_4$ , second sector of CuA and  $A_1$  setose. **Abdomen.** Abdomen pubescent. Tergites 1–7 brown, tergites 2–4 with a yellowish distal band; sternites 1–4 yellow, sternite 5 yellow on the basal half, brownish distally, sternites 6–7 brown. Terminalia yellowish on basal half, brownish apically. **Terminalia** (Fig. 16). Gonocoxite yellow, with brown margins, extending beyond base of gonostyle, with a row of short spines along distal margin, an additional transverse row of short spines ventrally, and one long spine at apex; gonostyle long, with a distal fold inwards, a row of short spines ventrally close to apex and a single, long spine at apex; aedeagus thin, long, bifid since its base, with small setulae apically; parameres well developed, more sclerotized apically, involving the aedeagus; cercus covered with setulae; tergite 9 less sclerotized, short mesal projection along distal margin.

**Female** (Fig. 1). As male, except as follows. **Wing** (Fig. 6). Length, 4.6 mm, width, 1.4 mm. R-m six times length of Rs first sector. Abdominal tergites 2–5 with apical yellow band; sternites 1–6 yellow, lateral margins brownish, sternite 7 brownish. **Terminalia** (Fig. 17). Terminalia brownish, distal margin of sternite 8 rounded, with a fringe of brown, long setae; cercus almost as long as rest of terminalia, basal cercomere longer than apical one.

**Etymology.** The specific epithet is Latin adjective *fumosus*, meaning smoky, in reference to the weakly defined, light wing maculae.

**Comments.** The holotype wing has the base of vein  $M_1$  nearly separated from  $M_{1+2}$ , but is otherwise identical to the females.  $R_5$  in all specimens analyzed is particularly straight. The general body coloration of this species is quite similar to *P. peruviana* Edwards, known from Mamara, Peru. In the Edwards original description of *P. peruviana* there are no illustrations of male and female terminalias, but it is possible at this moment to note some differences in the wing maculation. In *P. fumosa* **sp. n.**, the wing membrane shows very weak maculae across medial veins and at anal cell (Figs. 5, 6) and the CuA is not sinuous. On the other hand, in *P. peruviana* the wing membrane is maculated at the medial veins; stronger on the first section of Rs, apex of  $R_5$ , and anal cell; and the CuA is slightly sinuous.

## Paraleia denticulata, sp. n.

(Figs. 7-8, 18-19)

**Diagnosis.** Three ocelli. Wing with a pair of pretty well defined brown maculae at the mid and apex of the wing, plus a weaker marking distal to  $A_1$ . Gonostyle widening to the apex, inner surface with a distal row of short spines and a long apical spine, gonocoxite projection distal to the base of gonostyle with an irregular row of short spines and scattered short apical spines. Female sternite 8 with apical border mesally depressed laterally, with short spines distally.

**Material examined.** Holotype  $3^{\circ}$ , COLOMBIA, State of Cundinamarca, PNN Sumapaz Bocatoma, Cerro El Zapato, 04°14'N 74°12'W, 3,560 m, 06–20.xi.2002, M3444 (A. Patiño Leg.) (IAvH). Paratypes  $23^{\circ}$  same data as holotype (IAvH);  $13^{\circ}$  idem, but 18.xi–04.xii.2002, M3443 (MZUSP);  $43^{\circ} 2^{\circ}$  idem, but 02–17.i.2003, M3442 (IAvH/MZUSP).

**Description**. **Male. Head.** Vertex brown, with scattered, whitish long bristles. Mesal ocellus small, lateral ocelli close to but not touching eye margin. Frons and clypeus light brown, covered with setulae; labella yellow; maxillary palpus whitish yellow, with five palpomeres, last palpomere almost twice length of penultimate, first two palpomeres short. Scape and pedicel of similar lenght, yellow, first flagellomere lighter on the basal third, second and third flagellomeres brown with lighter basal fourth, remaining flagellomeres brown. **Thorax.** Pronotum yellow, with five strong yellow setae, four of them stronger dorsally and one smaller ventrally. Scutum brown, dark yellow on anterior corners, above base of wing, and along dorso-centrals; scutum covered with scattered short setae, stronger dorso-centrals and supra-alars. Scutellum yellow, brownish at margins, with four scutellar bristles. Pleural sclerites brown, bare. Pleural membranae yellowish. Haltere whitish, setose. Legs yellow, mid and hind coxae with a brown mesal macula. Tibial spurs 1:2:2, brown, spurs almost twice tibia diameter at apex. Some few dark apical setae on fore tibia, mid and hind tibiae with long, strong black setae. **Wing** (Fig. 7). Length, 4.5 mm, width, 1.5 mm. Membrane without macrotrichia, yellowish, with one brownish macula across mid of wing and an additional, less well defined mark close to apex, a third inconspicuous mark posterior to  $A_1$ . C extending slightly

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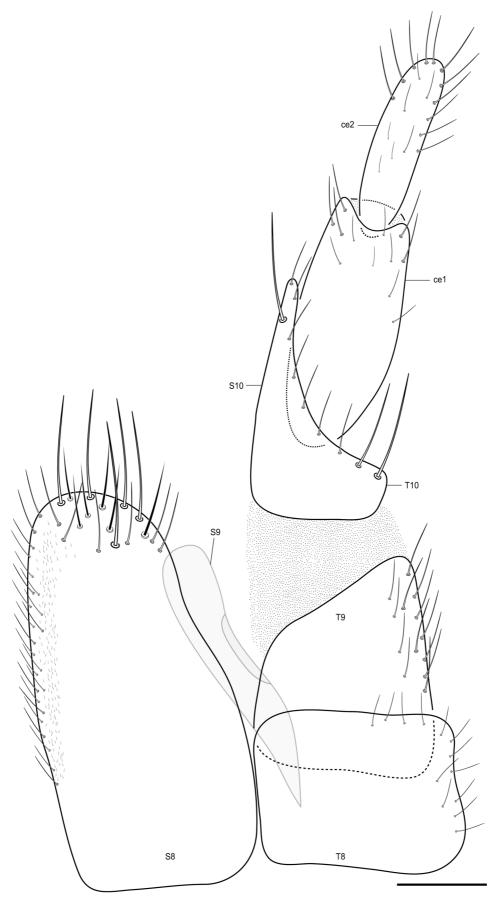


FIGURE 17. Female terminalia of Paraleia fumosa sp. n., lateral view. Paratype. Scale 0.1 mm.

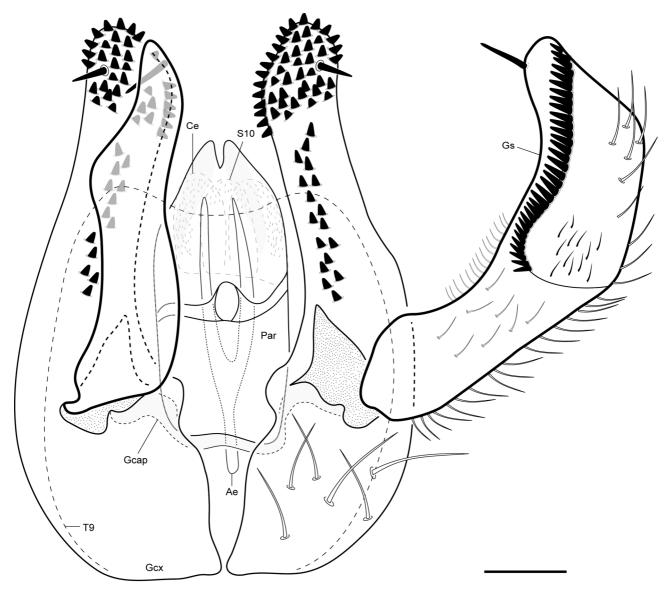


FIGURE 18. Male terminalia of Paraleia denticulata sp. n., ventral view. Paratype. Scale 0.1 mm.

beyond  $R_5$  apex; sc-r present; Sc complete, ending in C at wing basal third.  $R_1$  less than twice r-m length, reaching C at distal third of wing; Rs nearly transverse;  $R_5$  reaching C close to wing tip, nearly straight; r-m almost longitudinal, about six times length of first sector of Rs.  $M_{1+2}$  shorter than r-m length;  $M_1$  and  $M_2$  twice length of  $M_{1+2}$ ; CuA depressed midway to apex.  $M_1$ ,  $M_2$ ,  $M_4$ , second sector of CuA setose and  $A_1$  setose. **Abdomen.** Abdomen covered with numerous yellowish setulae. Tergites 1–7 brown, tergites 2–4 lighter than remaining; sternites 1–4, whitish yellow mesally, brownish laterally; sternites 5–6, brownish; sternite 7, brown. Terminalia yellowish basally, brownish apically, tergite 9 yellow, with a brown mesal, transverse band. **Terminalia** (Fig. 18). Gonocoxite extension distal to base of gonostyle with an irregular row of short spines along basal two thirds, scattered short spines at apex, as well as a single, subapical spine; gonostyle long widening to the apex, inner surface with a row of short spines along distal margin, besides a long, subapical spine; aedeagus thin, bifid at distal two thirds; parameres well developed, more sclerotized at apex, involving aedeagus; cercus covered with setulae; tergite 9 weakly sclerotized, with a shallow mesal depression at distal margin.

**Female.** As male, except as follows. **Wing** (Fig. 8). Length, 4.6 mm, width, 1.6 mm. Wing maculae slightly less conspicuous. All coxae with a brown mesal maculae. Abdominal tergites 2–4 brown with a light transverse, distal stripe. **Terminalia** (Fig. 19). Terminalia yellow, sternite 8 wide, distal margin wide, with a distal incision, with some brown, long setae along distal margin, and some short spines at laterals; cercus almost as long as rest of terminalia, basal cercomere longer than apical one.

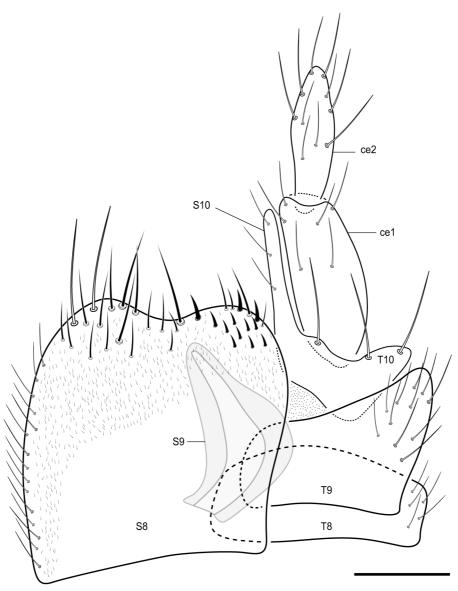


FIGURE 19. Female terminalia of Paraleia denticulata sp. n., lateral view. Paratype. Scale 0.1 mm.

**Etymology.** The specific epithet is Latin adjective *denticulatus*, meaning bearing small teeth, in reference to the short spines at apex of gonocoxite projection.

**Comments.** Some specimens have a more inconspicuous maculae and  $A_1$  weaker. The male gonocoxite and gonostyle of this species are in somewhat similar to those *P. bolivari* **sp. n.** *Paraleia denticulata* **sp. n.** has a single subapical spine at gonocoxite apex and a gonostyle widening to the apex, with an irregular row of short spines, as well as a single subapical one (Fig. 18). On the other hand, *P. bolivari* **sp. n.** doesn't have the subapical spine at gonocoxite apex and shows a long gonostyle, with a row of short spines and a single long apical one (Fig. 13).

## Paraleia tonnoiri, sp. n.

(Figs. 9, 20)

**Diagnosis.** Two ocelli. Wings without clear markings. Gonocoxite distal extension with an irregular row of short spines on distal two thirds at inner surface, two regular, parallel, longitudinal rows of short spines near apex, short spines distributed around the apex, and a long subapical spine. Gonostyle long, pointed at apex, with a longitudinal row of short spines at distal fourth, two short rows of spines and a long, subapical spine.

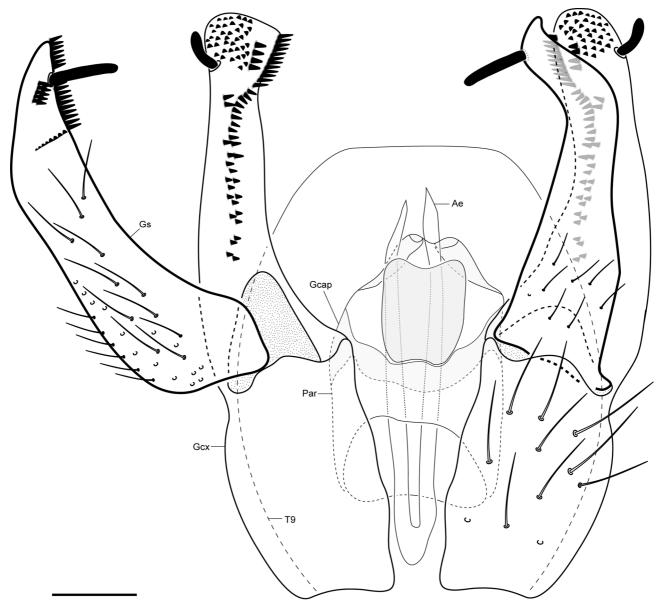


FIGURE 20. Male terminalia of Paraleia tonnoiri sp. n., ventral view. Holotype. Scale 0.1 mm.

**Material examined.** Holotype ♂, COLOMBIA, State of Magdalena, PNN Santa Marta, San Lorenzo, 10°48'N 73°39'W, 2,500 m, 15–30.i.2001, M1186 (J. Cantillo Leg.) (IAvH).

**Description**. **Male. Head.** Vertex brown, with scattered, whitish, longer bristles. Two ocelli close to, but not touching eye margin, mid ocellus absent. Frons and clypeus light brown, with scattered setulae; labella yellow, maxillary palpus whitish yellow, five palpomeres, last palpomere almost twice length of penultimate, first two palpomeres short. Scape and pedicel of equal length, yellow, first flagellomere yellow at basal half, light brown distally, second and third flagellomeres light brown, with basal fourth lighter, distal flagellomeres light brown (flagellomeres 9–14 missing). **Thorax.** Pronotum yellow, with five strong bristles, three anterior and two mesal. Scutum light brown, two narrow yellow bands beginning on anterior corners and joining in the median region of scutum. Scutellum yellow, four scutellar bristles. Mediotergite and lateral sclerites light brown, bare. Pleural membrane yellow. Haltere whitish, setose. Legs yellow. Tibial spurs 1:2:2, spurs almost twice width of tibia apex. Mid and hind tibiae with long and strong setae. **Wing** (Fig. 9). Width, 2.4 mm. Membrane without macrotrichia, yellow-ish, no clear markings. Sc complete, ending in C; sc-r absent; CuA slightly curved midway to apex; A<sub>1</sub> weakly sclerotized, absent on distal third. M<sub>4</sub>, second sector of CuA and A<sub>1</sub> setose. **Abdomen.** Abdomen pubescent. Tergite 1 light brown, tergites 2–6 light brown with a distal yellow band, tergite 7 yellow. Sternites yellow, sternites 6 and 7 with brownish spots. **Terminalia** (Fig. 20). Terminalia yellow, gonostyle and gonocoxite with brownish distal mar-

gin. Gonocoxite distal extension with an irregular row of short spines on distal two thirds at inner surface, two regular, parallel, rows of short spines near apex, and additional short spines around the apex, besides a long subapical spine. Gonostyle long, pointed apically, with a longitudinal row of short spines at distal fourth on inner surface, two short transversal rows of spines, and a long, subapical spine; aedeagus thin, entirely bifid; parameres well developed, more sclerotized at apex, involving aedeagus; cercus not visualized; tergite 9 weakly sclerotized, straight at distal margin.

Female. Unknown.

**Etymology.** The specific epithet is formed after the Belgian entomologist André Léon Tonnoir (1885–1940), who described a large number of species and genera of Mycetophilidae from Australia and New Zealand region, including the first known species of *Paraleia*.

**Comments.** One of the wings of the only specimen known is entirely missing and the other wing has the distal part missing. The aedeagus is bifid from its base to the apex, the presence of only two ocelli and the regular rows of short spines at the apex of gonostyle clearly approximate this species to *P. fumosa* **sp. n.** However the gonocoxite distal extension and wing maculation are very particular in each of these species. The gonocoxites of *P. tonnoiri* **sp. n.** show an irregular longitudinal row of short spines at their inner surface and one apical spine longer and curved (Fig. 20); the wing membrane seems do not have maculation (Fig. 9). In *P. fumosa* **sp. n.** the gonocoxites have a row of short spines along distal margin, with one very long; an additional transverse row of short spines ventrally (Fig. 16); the wing membrane shows maculae brown close to the wing apex and just posterior to  $A_1$  (Figs. 5, 6).

## Paraleia nidorosa, sp. n.

(Figs. 10, 21)

**Diagnosis.** Three ocelli. Wing with a brown macula apically. Female sternite 8 rounded apically, a little depressed at inner margin dorsally, with long setae apically.

**Material examined.** Holotype  $\bigcirc$ , COLOMBIA, State of Huilla, PNN Cueva de los Guácharos, Mun. Acevedo, 01°37'N 76°06'W, 2150 m, 15–19.xi.2003, M3788 (J. Lopes Leg.) (IAvH).

Description. Male. Unknown.

Female. Head. Vertex brownish, with scattered bristles. Three ocelli, mid ocellus small, lateral ones close to but not touching eye margin. Frons and clypeus yellow, covered with short setulae; labella yellow; maxillary palpus whitish yellow, five palpomeres, last palpomere almost twice length of penultimate, first two palpomeres short. Scape and pedicel subequal, yellow, with setulae; flagellomeres 1–4 with basal half yellow, distal half light brown, remaining flagellomeres light brown. Thorax. Thorax predominantly yellow. Pronotum yellow, with three strong bristles near posterior margin. Scutum yellow, with three longitudinal brownish bands, mesal band with a yellow narrow line anteriorly. Scutellum yellow, with four scutellar bristles. Mediotergite brownish, bare, remaining pleural sclerites yellow, bare, pleural membrane yellowish. Haltere with brownish knob and whitish pedicel, setose. Legs yellow, mid and hind tibiae with long, strong black setae. Tibial spurs 1:2:2, spur length almost twice tibial width at apex. Wing (Fig. 10). Length, 4.0 mm, width, 1.3 mm. Membrane without macrotrichia, translucent, with a light brown, rather indefinite macula close to wing apex. C extending slightly beyond  $R_s$  apex; Sc complete, reaching C at wing basal third; sc-r absent; R<sub>1</sub> about as long as r-m, reaching C beyond distal third of wing; first sector of Rs transverse;  $R_5$  reaching C close to wing tip, with a very gentle curve on distal half; r-m almost longitudinal, about six times length of first sector of Rs.  $M_{1+2}$  longer than r-m length;  $M_1$  and  $M_2$  almost twice  $M_{1+2}$  length; CuA nearly straight along its entire length. M<sub>1</sub> and M<sub>2</sub> with setae, M<sub>4</sub>, second sector of CuA and A<sub>1</sub> apically with macrotrichia. Abdomen. Abdomen pubescent, covered with setulae. Tergites 1-7 brown. Sternites 1-3 yellow, sternites 4-6 yellow with brownish lateral margins, sternite 7 brownish; distal margin of sternite 8 rounded. Terminalia (Fig. 21). Terminalia brownish, gonapophysis 8 rounded distally, not wide; cercus length subequal to that of rest of terminalia, basal cercomere longer than apical one.

**Etymology.** The specific epithet is Latin adjective *nidorosus*, meaning steam, in reference to the apical inconspicuous macula in the wing membrane.

**Comments.** Considering the other female species described here, differences in the wings and shape of the sternite 8 are enough to erect *P. nidorosa* **sp. n.** as a new species despite missing the male specimen. *Paraleia nidorosa* **sp. n.** shows the wing membrane with only a brown macula rather indefinite close to wing apex (Fig. 10) and

a female sternite 8 rounded apically, little depressed at inner dorsal margin, with long setae apically (Fig. 21). *Paraleia bolivari* **sp. n.**, *P. fumosa* **sp. n.**, *P. denticulata* **sp. n.**, and *P. sharkeyi* **sp. n.**, besides the macula on the wing apex, show wing membrane patterned in other regions (Figs. 4, 6, 8, 11) and *Paraleia* **sp.** has the wing hyaline (Fig. 12). The distal margin of sternite 8 of *P. bolivari* **sp. n.** is round with fringe of setae, not depressed at inner dorsal margin (Figs. 14, 15); in *P. fumosa* **sp. n.** it is rounded with a fringe of long setae (Fig. 17); in *P. denticulata* **sp. n.** it is wide with a distal incision, brown and long setae (Fig. 19); in *P. sharkeyi* **sp. n.** (Fig. 22) it has a deep lateral incision and is quite strongly setose; in *Paraleia* **sp.** is pointed with black setulae along its distal margin.

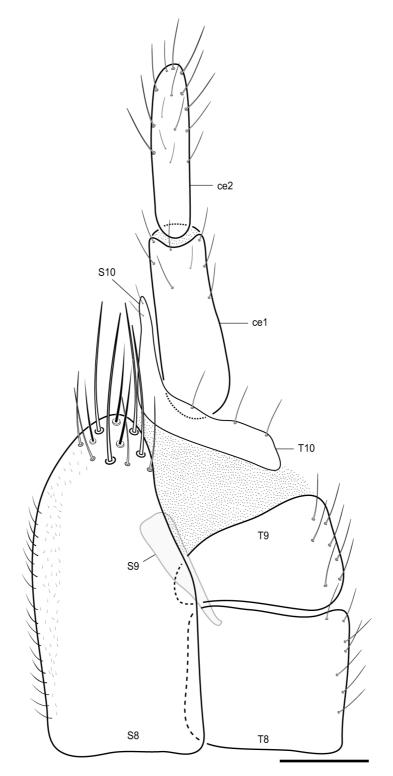


FIGURE 21. Female terminalia of Paraleia nidorosa sp. n., lateral view. Holotype. Scale 0.1 mm.

### Paraleia sharkeyi, sp. n.

(Figs. 11, 22)

**Diagnosis.** Three ocelli. Wing with brown, undefined markings. Female sternite 8 distal border with deep lateral incisions at each side, quite strongly setose.

**Material examined.** Holotype  $\bigcirc$ , COLOMBIA, State of Cundinamarca, PNN Chingaza, Alto de La Bandera, 04°31'N 73°45'W, 3,660 m, 04–10.v.2002, M3218 (A. Garcia Leg.) (IAvH). Paratype. 1 $\bigcirc$ , same data as holotype, 15.xi–01.xii.2001, M2600 (L. Cifuentes Leg.) (MZUSP).

## Description. Male. Unknown.

Female. Head. Vertex brown, with scattered, whitish, longer bristles. Mesal ocellus small, lateral ocelli close to but not touching eye margin. Frons and clypeus brown, with scattered setulae; labella yellow; maxillary palpus whitish yellow, five palpomeres, length of last palpomere almost twice the penultimate, first two palpomeres short. Scape and pedicel subequal in length, yellow, apical half of first flagellomere light brown, basal half lighter, second and third flagellomeres brown with lighter basal fourth, remaining flagellomeres brown. Thorax. Pronotum yellow, with four strong yellow setae, three stronger, dorsally, one smaller, ventrally. Scutum brown, dark yellow on anterior corner, above wings, along line of dorso-centrals. Scutum with short scattered setae, stronger dorso-centrals, and supra-alars. Scutellum yellow, with four scutellar bristles. Pleural sclerites brown, bare. Pleural membranae brown. Haltere whitish, setose. Legs yellow, mid and hind coxae with a brown mesal macula. Tibial spurs 1:2:2, brown, spurs almost twice width of tibial apex. Some few dark apical setae on fore tibia, mid and hind tibiae with long, strong black setae. Wing (Fig. 11). Length, 4.5 mm, width, 1.6 mm. Membrane with few macrotrichia scattered on anal cell, brown rather undefined transverse markings at basal third, around base of cubital fork, mid of wing, distal to first sector of Rs and base of medial fork, and across distal third of  $R_s$ , besides an inconspicuous macula anteriorly to r-m. C extending considerably beyond apex of R<sub>5</sub>; Sc complete, ending in C at wing basal third; sc-r present.  $R_1$  clearly shorter than r-m, reaching C at distal third of wing; Rs almost transverse;  $R_5$  relatively short, reaching C before level of  $M_1$ ; r-m almost longitudinal, about seven times length of first sector of Rs.  $M_{1+2}$ almost as long as r-m length; length of M1 and M2 more than twice M1+2 length; CuA clearly depressed midway to apex.  $M_1$  and  $M_2$ , apical half of  $M_4$  and second sector of CuA setose,  $A_1$  bare. Abdominal tergites brown, sternites light brown. Terminalia (Fig. 22). Terminalia yellow. Distal border of the sternite 8 with deep lateral incisions at each side, quite strongly setose; cercus longer than rest of terminalia, basal cercomere longer than apical one.

Etymology. This species is named after the American entomologist Michael Sharkey.

**Comments.** There is some minor variation at wing maculation between the specimens of the type series. This species is very similar morphologically to *P. bolivari*, **sp. n.** and *P. denticulata* **sp. n.**, with differences in the wing maculation and in the shape of sternite 8. *Paraleia sharkeyi* **sp. n.** has stronger maculae on wing membrane just after the first section of Rs, apex of  $R_5$ , and around base of cubital fork (Fig. 11), and sternite 8 with a deep lateral incision, which is quite strongly setose (Fig. 22). *Paraleia bolivari* **sp. n.** has the wing membrane strongly at the first section of Rs, at wing apex, at base and apex of cubital fork (Figs. 5, 6), and a sternite 8 round with fringe of setae (Figs. 14, 15); in *P. denticulata* **sp. n.** the wing membrane is inconspicuous maculated at the first section of Rs and at the wing apex (Figs. 7, 8), and the sternite 8 is wide with a distal incision, brown and long setae (Fig. 19).

## Paraleia sp.

(Figs. 12, 23)

**Diagnosis.** Two ocelli. Wing nearly translucent. Female sternite 8 pointed, with some black setulae along distal margin.

**Material examined.** 1 $\bigcirc$ , COLOMBIA, State of Cundinamarca, PNN Chingaza, Bosque Palacio, 04°31'N 73°54'W, 2,939 m, 17.i–04.ii.2001, M1258 (E. Niño Leg.) (IAvH). 1 $\bigcirc$  State of Boyacá, SFF Iguaque, Cabana Mammaramos, 05°25'N 73°27'W, 2,855 m, 23.v–08.vi.2000, M146 (P. Reina Leg.) (IAvH). 2 $\bigcirc$  State of Huilla, PNN Curva de los Guácharos, Mun. Acevedo, 01°37'N 76°06'W, 2,150 m, 15–19.vi.2003, M3787 (J. Lopes Leg.) (MZUSP).

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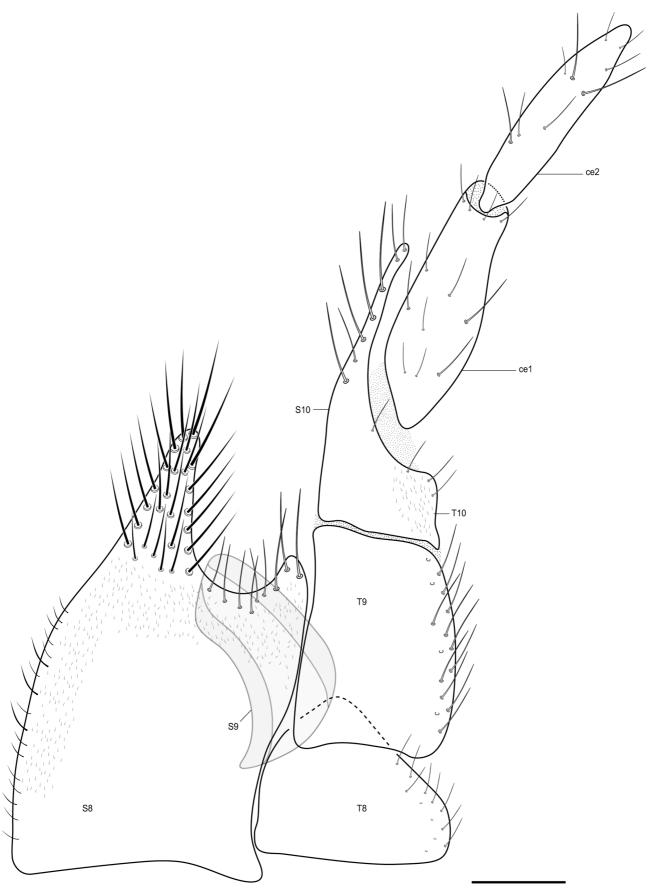


FIGURE 22. Female terminalia of *Paraleia sharkeyi* sp. n., lateral view. Paratype. Scale 0.1 mm.

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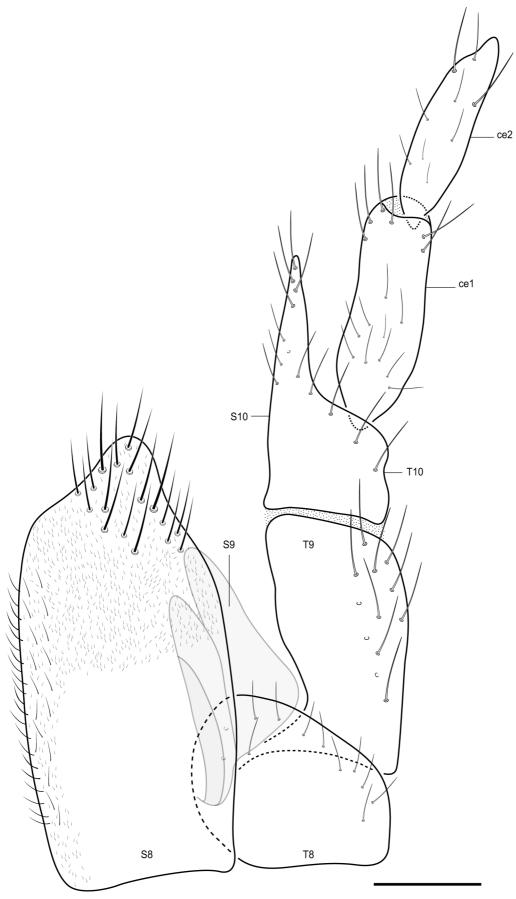


FIGURE 23. Female terminalia of Paraleia sp., lateral view. Paratype. Scale 0.1 mm.

Description. Female. Head. Vertex lighter ventrally, with scattered, whitish, longer bristles. Two ocelli close to but not touching eye margin, mid ocellus absent. Frons light brown, covered with scattered setulae, clypeus light yellow; labella yellow; maxillary palpus whitish yellow, five palpomeres, last palpomere length almost twice penultimate, first two palpomeres short. Scape smaller than pedicel, both yellow, apical half of first flagellomere light brown, basal half lighter, second and third flagellomeres brown with lighter basal fourth, remaining flagellomeres brown. Thorax. Pronotum yellowish-brown, five strong yellow setae, three stronger, dorsally, and two smaller, ventrally. Scutum dark yellow, with a small, undefined latero-posterior brown macula. Scutellum yellow mesally, brownish at margins, with four scutellar bristles. Antepronotum and proepisternum light yellow, bare. Pleural sclerites brown, bare, katepisternum, mesepimeron and laterotergite each with a yellowish mesal macula, metepisternum light yellow. Legs light yellow, darker to apex, hind coxa with a brown mesal macula. Tibial spurs 1:2:2, brown, spurs almost twice width of tibial apex. Some few dark apical setae on fore tibia, mid and hind tibiae with long, strong, black setae. Haltere whitish, setose. Wing (Fig. 12). Length, 4.8 mm, width, 1.7 mm. Membrane without macrotrichia, hyaline. C extending slightly beyond R<sub>5</sub>; Sc complete, reaching C at basal third of wing; sc-r present. R<sub>1</sub> pretty shorter than r-m length, reaching C beyond distal third of wing; first sector of Rs almost transverse, directed basalwards distally; R<sub>5</sub> reaching C close to wing tip; r-m almost longitudinal, about five times length of first sector of Rs. M<sub>1+2</sub> obviously shorter than r-m length; medial fork long, M<sub>1</sub> and M<sub>2</sub> more than twice length of M<sub>1+2</sub>; CuA slightly depressed midway to apex. M<sub>1</sub> and M<sub>2</sub>, M<sub>4</sub>, second sector of CuA and A<sub>1</sub> setose. Abdomen. Abdominal tergites 1–7 brown, with a whitish band at distal margin, and yellow brown lateral bands on tergites 2– 7. Sternites almost entirely whitish yellow, with slender, irregular brown bands laterally. Terminalia (Fig. 23). Terminalia yellow. Sternite 8 pointed, with some black setulae along the distal margin; cercus almost longer than rest of terminalia, basal cercomere longer than apical one.

**Comments.** In most of the *Paraleia* species studied here, there is not much color variation between males and females, but there are a few exceptions. The female specimens included here as *Paraleia* **sp.** show some variation concerning the presence of a brown spot basally at the hind coxa (which is missing in some specimens), and yellowish spots may be present or absent on the brownish anepisternum and katepisternum. Interestingly, all these females have identical female terminalia, suggesting that, despite some variation in coloration, these specimens may be conspecific. These females, on the other hand, are similar to the male of *P. tonnoiri* **sp. n.** for most details of the morphology, including the number of ocelli, but were collected in different localities in Colombia. In *P. tonnoiri* **sp. n.** the coloration of the scutum is brown with two narrow yellow bands joining posteriorly, a feature present in one of the specimens of *Paraleia* **sp.**, less evident in the remaining females. At this stage, the fact that the distal part of the wing is missing in *P. tonnoiri* **sp. n.** and that there are no males collected together with the females included here under *Paraleia* **sp.** makes it advisable not to propose a separate species name for these latter specimens.

## Taxonomic and biogeographical considerations

The presence of *Paraleia* in Colombian Andes is particularly noteworthy—it constitutes the northern most occurrence of a taxon with amphinotic distribution (*sensu* Matile 1990), i.e., present only in Australia and South America. This is not a common pattern, but also happens, e.g., with the Leiinae genus *Procycloneura* (Oliveira *et al.* 2007).

The wide r5 cell, with displacement of the R<sub>5</sub>-r-m system of veins away from the anterior margin, is unique in Leiinae and gives a characteristic aspect to the wing venation of *Paraleia*, strongly suggesting that the genus is monophyletic. All new species show this feature, as well as the remaining diagnostic characters. Long spines apically at the gonostyle and subapically at the gonocoxite distal extension are shared by *P. fulvescens* and most of the Neotropical species, but combs of shorter spines in the gonostyles are present only in Neotropical clade of the genus. The evolution of the wing maculation, on the other hand, is not easy to interpret throughout the evolution of the subfamily or even within the genus. In the only known Australian species of the genus, *Paraleia fulvescens*, a typical maculation pattern is absent and there is only a darkening of the membrane along the anterior margin. Some of the Neotropical species miss a clear maculation pattern in the wing (e.g., *P. martinici* Duret, *P. falcigera* Freeman, *P. funerea* Freeman, *P. castanea* Freeman, and *Paraleia* **sp.** from this paper), but the presence of maculae in most of the genera in the subfamily suggests that this could represent a secondary loss.

The presence in Colombia and Ecuador of species with both obvious wing patterns and no maculation at all as it is also observed in Chile— suggests that there are species in the northern range of *Paraleia* belonging to different clades within the genus.

The opening of the southern Atlantic Ocean, breaking up Gondwana, began in early Cretaceous, 145 mya (Raven & Axelrod 1974), while New Zealand, Australia and South America were connected until Late Cretaceous, 70 mya (McCarthy 2003, 2005). The final disruption between Australia and South America occurred only in the second half of the Cenozoic, about 35 mya (McLoughlin 2001), meaning that there has been a lasting connection between Australia and South America with Antarctica since the Cretaceous to the mid Cenozoic. This explains why amphinotic distributions are a widespread biogeographical pattern—and, hence, originated through vicariance, not transoceanic dispersal—but with an age of disruption not compatible with the initial division of Gondwana (Amorim *et al.* 2009).

Indeed, in a study on colletid bees (Hymenoptera, Colletidae), molecular divergence between clades with amphinotic distribution point to a mid Oligocene disjunction, 33–35 mya (Almeida *et al.* in press). This is pattern is remarkably similar to what found in *Paraleia*. In fact, there may be a group of leiine and sciophiline genera that compose a clade within each of these subfamilies that have, as in the case of the colletid bees, multiple lineages each with amphinotic distribution, with representatives in South America and Australia.

The first cladogenesis in the genus, therefore, with the separation of the Australian and South American components, hence, would have been in the Late Eocene–Early Oligocene, at a time when the Andean cordillera was already formed in the south. The presence of *Paraleia* species in the northern extreme of the Andes with both patterned and non-patterned wing membrane suggests that early events in the evolution of the genus, whatever the topology, resulted in clades that extended to the north together with the uplift of the northern half of the Andes itself.

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