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Review of Brazilian cave psocids of the families Psyllipsocidae and Prionoglarididae (Psocodea: 'Psocoptera': Trogiomorpha) with a key to the South American species of these families

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Abstract: Data on Brazilian cave psocids (Insecta) of the families Psyllipsocidae and Prionoglarididae are summarized, as a synthesis of the results of the most important investigation on cave psocids ever realized. Prionoglarididae are represented by 4 species of the endemic cavernicolous genus *Neotrogla*, Psyllipsocidae by 17 species of *Psyllipsocus* (15 of them endemic) and 2 widely distributed species of *Psocathropos*. These 19 recently described Brazilian endemic *Neotrogla* and *Psyllipsocus* were discovered in the course of the project, based on the examination of about 400 adult psyllipsocids and prionoglaridids collected in 124 caves situated in 59 municipalities and 13 Brazilian states. Some augmentations to the descriptions of the widely distributed *Psyllipsocus ramburii, Psyllipsocus yucatan, Psocathropos lachlani* and *Psocathropos pilipennis* are given and the following new synonymies are proposed: *Psyllipsocus ramburii* Selys-Longchamps (*P. variabilis* Badonnel n. syn., *P. dubius* Badonnel n. syn.), *Psyllipsocus yucatan* Gurney (*P. collarti* Badonnel n. syn., *P. decui* Badonnel n. syn.), *Psocathropos lachlani* Ribaga (*Vulturops termitorum* Townsend n. syn., *Dorypteryx astizi* Brèthes n. syn.). The distribution of the 23 species of psyllipsocids and prionoglaridids known from Brazilian caves is analysed and some evolutionary aspects are discussed. A key to the 25 South American species of these families is given, including two other previously known species: *Psyllipsocus delamarei* from Argentina and the troglobitic prionoglaridid *Speleopsocus chimanta* from Venezuela.

Keywords: Brazil - cave fauna - endemism - male genitalia - new synonymies.

INTRODUCTION

All over the world, representatives of the psocid families Psyllipsocidae and Prionoglarididae, belonging to the suborder Trogiomorpha (Yoshizawa *et al*., 2006), are regularly found in caves (Badonnel & Lienhard, 1994; Lienhard, 2000, 2002, 2004a, 2007; Lienhard *et al*., 2010a). But both families are poorly known from South America (Lienhard & Smithers, 2002; Lienhard, 2004b, 2011). We present here a synthesis of the results of a study of these families as they are represented in Brazilian caves. This study is a part of a long-term research project of the junior author on Brazilian cave invertebrates.

Since 1996 some 800 caves have been visited by the junior author and collaborating biospeleologists. Psocids of the above mentioned families (especially Psyllipsocidae) were observed in about 300 caves, mostly nymphs, but sometimes also adults. While the identification of the nymphs was not possible, the roughly 400 adult individuals of Psyllipsocidae (Fig. 1A) and Prionoglarididae (Fig. 1BC) submitted to the senior author could be identified down to species level. This material was collected in 124 Brazilian caves situated in 59 municipalities and 13 states (Appendix 2). A total of 23 species belonging to three genera could be distinguished, 19 of them new to science (Appendix 1). These new species were described by Lienhard *et al.* (2010b) and Lienhard & Ferreira (2013a, b, 2014), whilst the four previously known non-endemic species are treated below. All psyllipsocids and prionoglaridids presently known from South America are listed (Appendix 1) and keyed. General observations on the distribution of the Brazilian cave species are also presented and some evolutionary aspects are discussed.

This is the most important investigation on cave psocids ever realized (for a bibliography on cave psocids see Badonnel & Lienhard, 1994 and Lienhard, 2002, 2014). It revealed an unexpected diversity for two families which were almost unknown from South America, not only from caves but also from non-subterranean habitats. Some particularly interesting results of this

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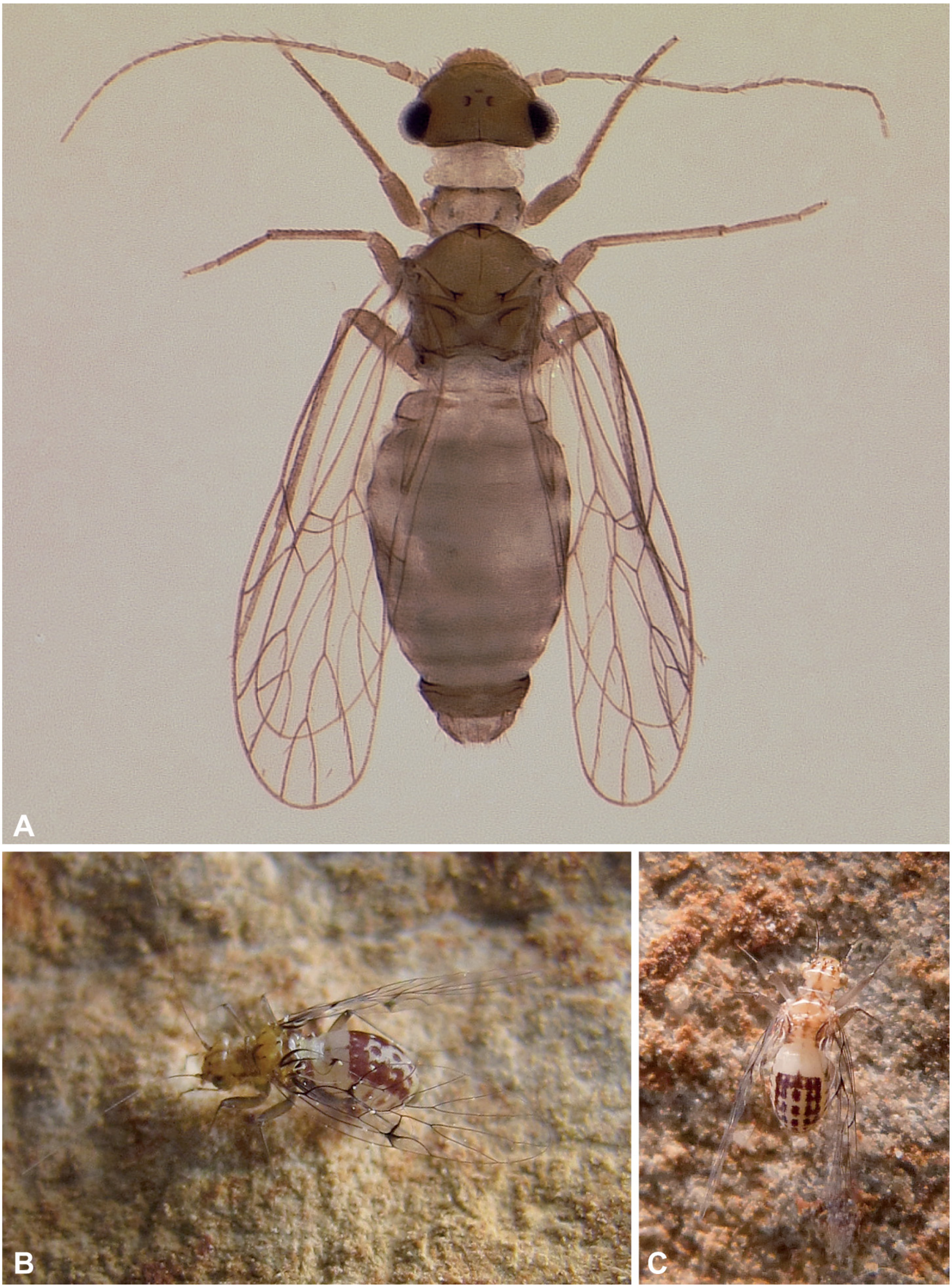

Fig. 1. (A) *Psyllipsocus yucatan*, habitus in dorsal view (in alcohol), body length 1.5 mm (from head to abdominal tip) (after Lienhard *et al.,* 2012). (B) *Neotrogla curvata*, habitus in dorso-lateral view (alive, in cave), body length 3.5 mm. (C) *Neotrogla aurora*, habitus in dorsal view (alive, in cave), body length 2.8 mm.

study have already been presented in two special papers: the enigmatic presence of microcrystals on the wings of some specimens of *Psyllipsocus yucatan* by Lienhard *et al*. (2012) and the spectacular coupling role reversal (reversed intromittent organs) in the genus *Neotrogla* by Yoshizawa *et al.* (2014).

MATERIAL AND METHODS

The material examined was collected by RLF (unless other collector mentioned) by hand-collecting (for collecting data, see Appendix 2). Dissection and slide-mounting followed the methods described by Lienhard (1998). For general remarks and morphological abbreviations used in the descriptions, see Lienhard & Ferreira (2014).

The material examined is deposited in the following institutions: Universidade Federal de Lavras, Departamento de Biologia (Coleção de Invertebrados Subterrâneos), Lavras, Brazil (ISLA); Muséum d'histoire naturelle, Geneva, Switzerland (MHNG); Systematic Entomology, Hokkaido University, Sapporo, Japan (SEHU) (some specimens of *Neotrogla* spp.).

Abbreviations used in the key (nomenclature of wing veins according to Yoshizawa, 2005): A1 = first anal vein; AP = areola postica (a marginal cell in forewing formed by veins CuA1 and CuA2); CuA1 = first branch of cubitus anterior; CuA2 = second branch of cubitus anterior; CuP = cubitus posterior; FW = forewing (length); FWw = forewing (greatest width); M = media; M1-M3 = branches of media; m1 = medial cell anteriorly delimited by M1; m2 = medial cell anteriorly delimited by M2; P2 = second article of maxillary palp; R = radius; Rs = radial sector (undivided basal part of R2-R5); R1 = first branch of radius; r1 = radial cell anteriorly delimited by R1; R2+3 = first branch of radial sector; r3 = radial cell anteriorly delimited by R2+3; R4+5 = second branch of radial sector; r5 = radial cell anteriorly delimited by R4+5; Sc = subcosta; v3 = third (external) valvula of the ovipositor.

Abbreviations for Brazilian states: AL = Alagoas, AM = Amazonas, BA = Bahia, CE = Ceará, ES = Espírito Santo, GO = Goiás, MG = Minas Gerais, MT = Mato Grosso, PI = Piauí, RN = Rio Grande do Norte, RS = Rio Grande do Sul, SP = São Paulo, TO = Tocantins.

TAXONOMIC PART

Non-endemic Psyllipsocidae from Brazil

All South American species of the families Psyllipsocidae and Prionoglarididae are listed in Appendix 1, based on previously published data (Badonnel, 1962; Lienhard *et al*., 2010a, b; Lienhard & Ferreira, 2013a, b, 2014) and on the following data concerning four widely distributed Brazilian species, not treated in detail before. At present, these four species are the only non-endemics known from Brazil. The 15 endemic species of *Psyllipsocus* were treated by Lienhard & Ferreira (2013b, 2014) and the 4 endemic species of *Neotrogla* by Lienhard *et al.* (2010b), Lienhard & Ferreira (2013a) and Yoshizawa *et al.* (2014). The South American fauna of these families comprises 25 species, 23 of which are known from Brazil (*Psyllipsocus delamarei* only known from Argentina and *Speleopsocus chimanta* from Venezuela). See also the identification key for the South American species, presented below.

Psyllipsocus ramburii Selys-Longchamps, 1872

Figs 2-3

Psyllipsocus ramburii Selys-Longchamps, 1872: 146.
Psyllipsocus variabilis Badonnel, 1986: 182. **Syn. nov.**
Psyllipsocus dubius Badonnel, 1987: 173. **Syn. nov.**
For further synonymy see Lienhard & Smithers (2002).

Material examined: ISLA and MHNG; numerous females, most of them micropterous (slide-mounted and in alcohol), collected by R. L. Ferreira in caves situated in the following Brazilian municipalities. – Castelo (ES), Gruta do Limoeiro cave, 7.i.2005. – Arcos (MG), Caverna do Alinhamento cave, 1.vi.2002. – Cordisburgo (MG), Gruta de Maquiné cave, 10.vii.2000. – Cordisburgo (MG), Gruta Santo Amaro 1 cave, 28.ix.2010. – Coromandel (MG), Gruta João do Pó cave, 5.x.2000. – Coromandel (MG), Gruta Ronan cave, 3.x.2000. – Coromandel (MG), Gruta Ronan II cave, 4.x.2000. – Diamantina (MG), Gruta do Salitre cave, 13.xii.2007. – Itumirim (MG), Gruta Santo Antônio cave, 25.x.2002. – João Pinheiro (MG), Gruta do Sapecado cave, 15.x.2010. – Lagoa Santa (MG), Gruta da Lapinha cave, 12.vi.2002. – Matozinhos (MG), Gruta dos Irmãos Piriás cave, 28.vii.2000. – Matozinhos (MG), Gruta Lavoura cave, 28.+29.v.1997, 26.vi.1997, 19.ii.2000. – Matozinhos (MG), Meandro Abismante cave, 6.vii.2002. – Matutina (MG), Gruta 9 cave, 10.x.2010. – Moeda (MG), cave SMS 29, 11.xii.2005. – Pains (MG), Gruta do Capão cave, 5.v.2001. – Pains (MG), Gruta Paranoá cave, 15.i.2008. – Pains (MG), Gruta Retiro cave, 27.xi.1999. – Paracatu (MG), Gruta da Fazenda Tamanduá II cave, 14.x.2010. – Paracatu (MG), Lapa do Brocotó cave, 16.ix.2010. – Paracatu (MG), Lapa de Santo Antônio cave, 13.vii.2010. – Santa Maria do Suaçuí (MG), Gruta do Rio Suaçuí cave, 19.vii.2002. – Sete Lagoas (MG), Gruta Rei do Mato cave, 3.+4.xi.2011. – Vazante (MG), Lapa da Delza cave, 12.vii.2010. – Torres (RS), Furna da Lagoa de Itapeva cave, 20.v.2008. – Altinópolis (SP), Gruta do Itambé cave, 27.ii.2006. – Altinópolis (SP), Gruta Olho de Cabra cave, 2.iii.2006. – Altinópolis (SP), Gruta do Paraná cave, 1.iii.2006. – Itirapina (SP), Gruta da Toca cave, 22.x.2004.

Further description: *P. ramburii* is the type species of the genus *Psyllipsocus*; it is polymorphic and occurs in three forms: macropterous, brachypterous

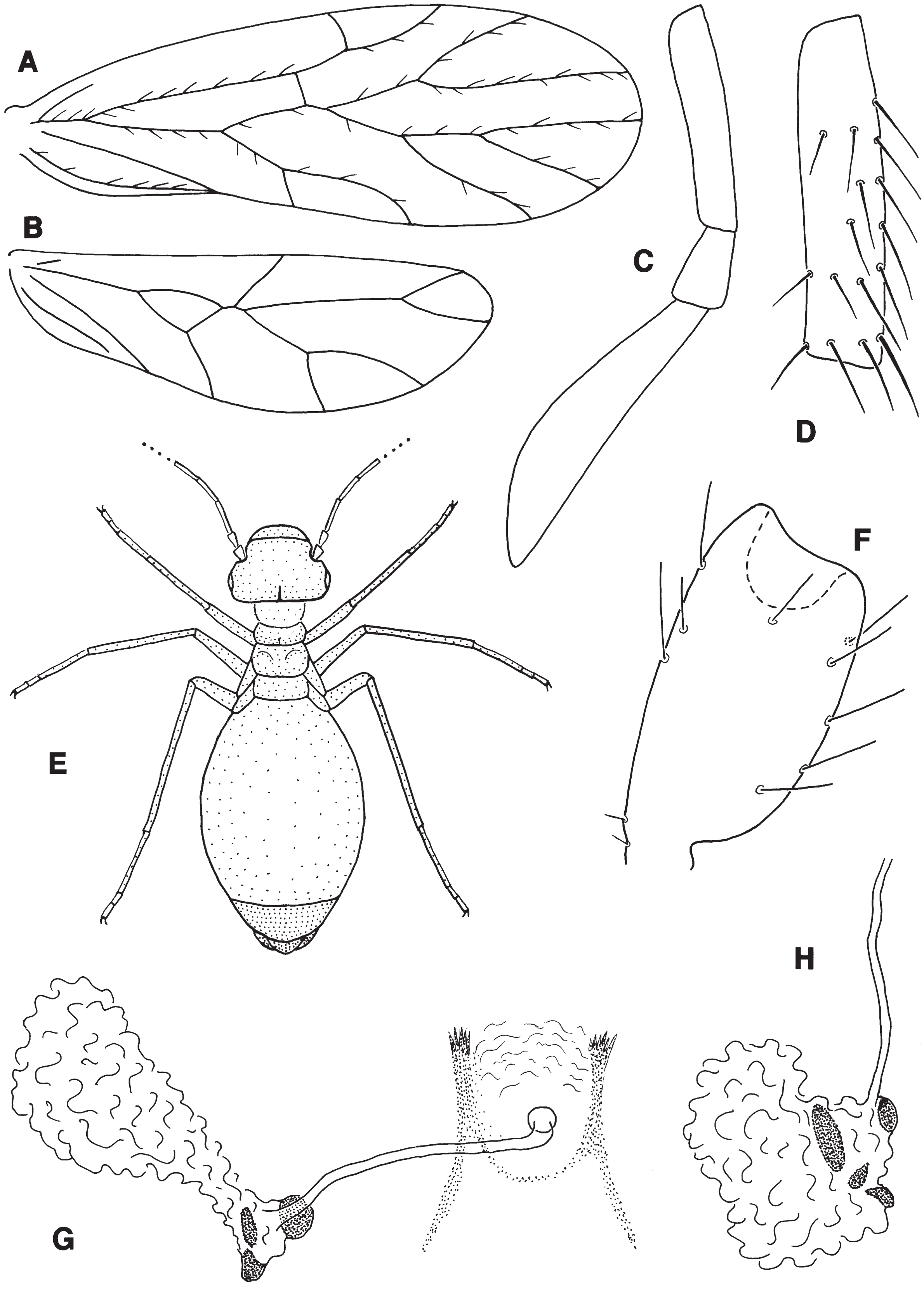

Fig. 2. *Psyllipsocus ramburii*, from Brazilian caves, macropterous female MHNG 7929 from Gruta Santo Antônio (A-D, H), micropterous female MHNG 7954 from Gruta do Rio Suaçuí (E-G). (A) Forewing. (B) Hindwing. (C) P2-P4 of maxillary palp. (D) P2-chaetotaxy. (E) Habitus (body length 1.7 mm). (F) Pedicel, showing absence of microspades organ (compare with Fig. 7D). (G) Spermapore plate and spermatheca. (H) Spermatheca.

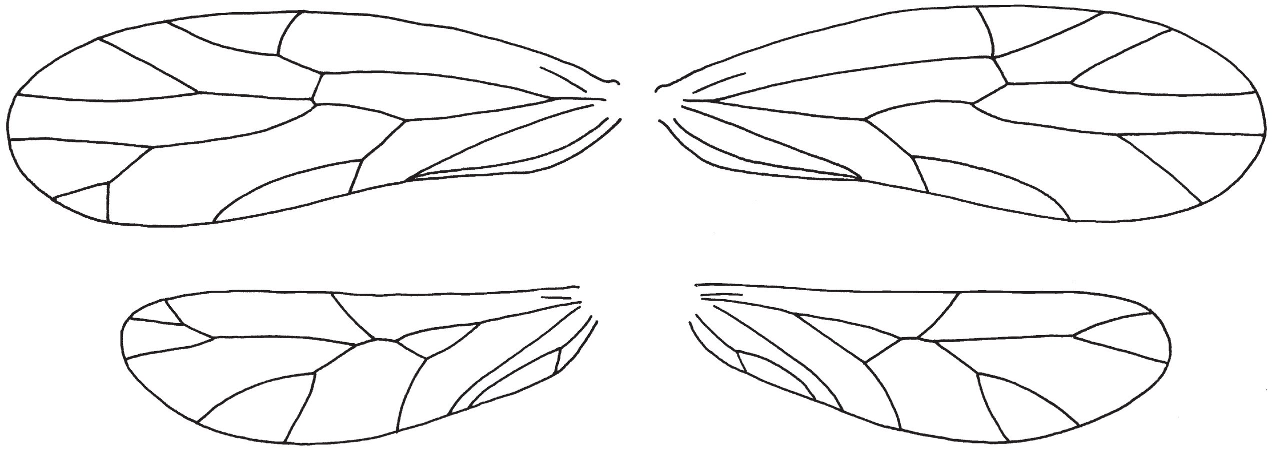

Fig. 3. *Psyllipsocus ramburii*, macropterous female (MHNG 8125) with slightly shortened wings, from Gruta João do Pó cave (Brazil, MG, Coromandel). Forewings and hindwings (pilosity not shown).

and micropterous; the existence of an apterous form is somewhat doubtful and has yet to be confirmed (see Key and Discussion, below). For detailed descriptions see Mockford (1993) and Lienhard (1998). Two characters are also especially noted by Mockford (2011): "macropterous form lacking distal closed cell in forewing; setal organ at base of paraproctal spine consisting of one very long and one short seta." Here we note the following additional characters (Figs 2-3, see also Key): pedicel lacking microspades organ (Fig. 2F); P2 lacking stout sensillum (Fig. 2D); spermatheca small and crumpled (due to parthenogenesis), with 3-4 small and irregularly shaped sclerites near duct (Fig. 2GH; see also Lienhard, 1998: fig. 37e and Badonnel, 1986: fig. 22); spermapore region with a characteristic pair of more or less sclerotized longitudinal straps (Fig. 2G; see also Mockford, 1993: fig. 62 and Badonnel, 1986: fig. 22); macropterous form occasionally with slightly shortened wings (not as short as in the typical brachypterous form, see Lienhard, 1998: figs 37c, 38c) and rather variable venation (Fig. 3, see also Badonnel, 1986: figs 14-18); in micropterous form length of minute wing rudiments variable, relatively long and bearing some vein rudiments (Lienhard, 1998: fig. 37a, g) or very short and veinless (Fig. 2E).

Biology: *P. ramburii* is a parthenogenetic species (thelytoky) and only one single (accidental?) male is known (Lienhard, 1977, 1998). The phallosome of the male is equipped with a pair of well-developed basal struts, as they are present in all psyllipsocids (Mockford, 2011) except for most of the Brazilian cave endemics (Lienhard & Ferreira, 2014; see also Evolutionary Considerations, below).

Distribution: *P. ramburii* is a widespread species (Lienhard & Smithers, 2002), often domicole but also regularly found in caves all over the world (Badonnel & Lienhard, 1994). Previously published South American records can be found in the following references: Strinati, 1971 (Uruguay); Badonnel, 1972 (Chile); Badonnel, 1986 (Colombia, as *P. variabilis*); Badonnel, 1987 (Venezuela, as *P. dubius*); Cammousseight & New, 1994 (Chile).

Discussion: The presence, in the macropterous specimens from Brazil, of a variability of wing venation similar to that described by Badonnel (1986) for *P. variabilis* from Colombia, and the absence of other distinctive characteristics, support synonymizing the latter with *P. ramburii*.

The case of *P. dubius* is more complex. This apterous species was described from Venezuela by Badonnel (1987), based on the holotype female from cacao ground litter and a second (non-paratype) female from a cave. The microscopical slides of both specimens, mounted by André Badonnel himself, are deposited in the MHNG and were examined. Unfortunately the thorax of the holotype had been damaged and only the prothorax is present on the slide. Thus, the absence of wing rudiments could not be confirmed for this specimen. The second specimen is better preserved; it is complete, though its thorax was deformed by slide-mounting. Surprisingly it bears wing rudiments which are very similar to those of the micropterous form of *P. ramburii*; in this female, they are particularly small and completely veinless (as in the female from a Brazilian cave figured in Fig. 2E). This specimen of *P. dubius* has clearly to be assigned to *P. ramburii*. In the original description of *P. dubius*, Badonnel insists on the complete apterism of this species and does not mention any variability of wing development. He also mentions that the only morphological difference between *P. ramburii* and *P. dubius* is the complete absence of wing rudiments in the latter. Even though the holotype might really be apterous, we are convinced that synonymy of *P. dubius* with *P. ramburii* is justified. The terminalia of the holotype correspond exactly to *P. ramburii*; in particular the spermapore region with the typical pair of sclerotized longitudinal straps clearly visible. However, the quite plausible existence of an apterous form of this polymorphic species is not yet definitively confirmed with this synonymization. It is possible that Badonnel did not realize that the part of the broken thorax of the holotype present on the slide was only the prothorax and misinterpreted the absence of wing rudiments on this part as apterism, while he probably overlooked the small wing rudiments present on the deformed slide-mounted thorax of the second female. Alternatively, it is also possible that he had already observed the absence of wing rudiments in the holotype before dissecting the specimen; impressed by this unusual character he might have overlooked their presence in the second female.

Psyllipsocus yucatan Gurney, 1943

Figs 1A and 4-6

Psyllipsocus yucatan Gurney, 1943: 212.
Psyllipsocus collarti Badonnel, 1946: 140. **Syn. nov.**
Psyllipsocus decui Badonnel, 1977: 340. **Syn. nov.**

Material examined: ISLA and MHNG; numerous males and females (slide-mounted and in alcohol), collected by R. L. Ferreira (unless other collector mentioned) in caves situated in the following Brazilian municipalities. – Murici (AL), Toca da Raposa 1 cave (granite), 13.i.2007. – Murici (AL), Toca da Raposa 2 cave (granite), 13.i.2007. – Campo Formoso (BA), Toca da Tiquara cave, 8.i.2008, i.2009, xii.2010. – Santa Maria da Vitória (BA), cave PEA 343, 15.v.2011, leg. S. S. Salgado. – Ubajara (CE), Gruta dos Mocós cave, 3.i.2007. – Ubajara (CE), Gruta do Morcego Branco cave, 3.i.2007. – Ubajara (CE), Gruta de Ubajara cave, 30.xii.2006. – Castelo (ES), Gruta do Limoeiro cave, 7.i.2005. – Arinos (MG), Lapa do Salobo cave, 18.vii.2010. – Santa Maria do Suaçuí (MG), Gruta do Rio Suaçuí cave, 19.vii.2002. – Teófilo Otoni (MG), Lapa da Vaca Parida cave, 26.i.2005. – Felipe Guerra (RN), Caverna Trapiá cave, 6.i.2010, 4.viii.2010, leg. D. M. Bento. – Ilha Bela (SP), Gruta da Serraria cave, 22.iv.2006.

Further description: This species is always macropterous. For detailed descriptions see Gurney (1943) and the augmented description given by Mockford (2011). Here we note the following characters (Figs 4-6, see also Key). Forewing usually with a subtle but typical colouration (Fig. 4G), as described by Gurney (1943: p. 212): "membrane faintly tinged with fuscous, a clear spot at posterior margin of wing between apex of Cu2 [= CuA2] and apices of anal veins [= CuP and A1]." P2 lacking clearly differentiated stout sensillum (Fig. 4D). Epiproct characteristically pigmented (Fig. 4BF). Paraproctal setal organ consisting of a minute hair and a longer and thicker seta; anal spine replaced by a stout, relatively short and basally articulated seta (not much longer than long seta of setal organ) (Fig. 4BF); female paraproct simple, male paraproct ventrally with a small concave protuberance ("fossette inférieure" of Badonnel, 1946) (Fig. 4F). Pigmentation of hypandrium interrupted in middle of anterior margin (Fig. 6AB); aspect of distal phallosome sclerites somewhat variable, depending on view (dorsal/ ventral) and on position after slide-mounting (Fig. 6A similar to fig. 5 in Badonnel, 1946; Fig. 6B similar to fig. 107 in Mockford, 2011). Sclerotization of ovipositor v1 and v2 variable; sclerotized median axis of v1 weakly developed or absent; median axis of v2 usually well-sclerotized (Fig. 5A), but weakly developed or completely absent in pale individuals (so observed in several pale specimens from Brazil, Antigua and Thailand). Spermapore plate weakly sclerotized but characteristic (Fig. 5B); spermathecal sac with complex sclerotizations near origin of duct (Fig. 5DE); spermatophores not sclerotized, somewhat variable in shape, but always similar to that figured in Fig. 5C; the spermatheca of a female may contain up to about a dozen spermatophores (see legend to Fig. 5B).

Biology: In general, *P. yucatan* seems to be a cave species and it was explicitly indicated as living on vegetation only once (Badonnel, 1948: on leaves of an orange tree), with no domicole population known. The presence of up to about a dozen spermatophores in the spermatheca of one single female indicates that the species is polyandrous.

Distribution: *P. yucatan* was originally described from a Mexican cave by Gurney (1943). Previously published South American records can be found in the following references: García Aldrete & Mockford, 2009 (Brazil, probably same record as that mentioned by Mockford, 2011); Mockford, 2011 (Brazil, in an artificial cave); Lienhard *et al.*, 2012 (Brazil, in caves). The species is also known from a cave in Cuba (Badonnel, 1977, as *P. decui*) and from caves in Jamaica, Aruba and Antigua (MHNG, unpublished). African specimens are known from Congo (Badonnel, 1946, 1948, as *P. collarti,* on vegetation), Kenya and Senegal (MHNG, unpublished). Some specimens of *P. yucatan* have also been collected in a cave in Thailand (MHNG, unpublished). The species seems to be widely distributed in the tropics.

Discussion: The only difference between *P. yucatan* and *P. decui* indicated by Mockford (2011) is the absence of the sclerotized median axis of v2. The above mentioned variability shows that this character cannot be used to separate these species. The absence of a sclerotized v2-axis in the palest specimens examined corresponds to the situation described by Badonnel (1977) for the very pale holotype of *P. decui* from Cuba, where v1 and v2 are completely hyaline. Therefore *P. decui* is here considered as a junior synonym of *P. yucatan*.

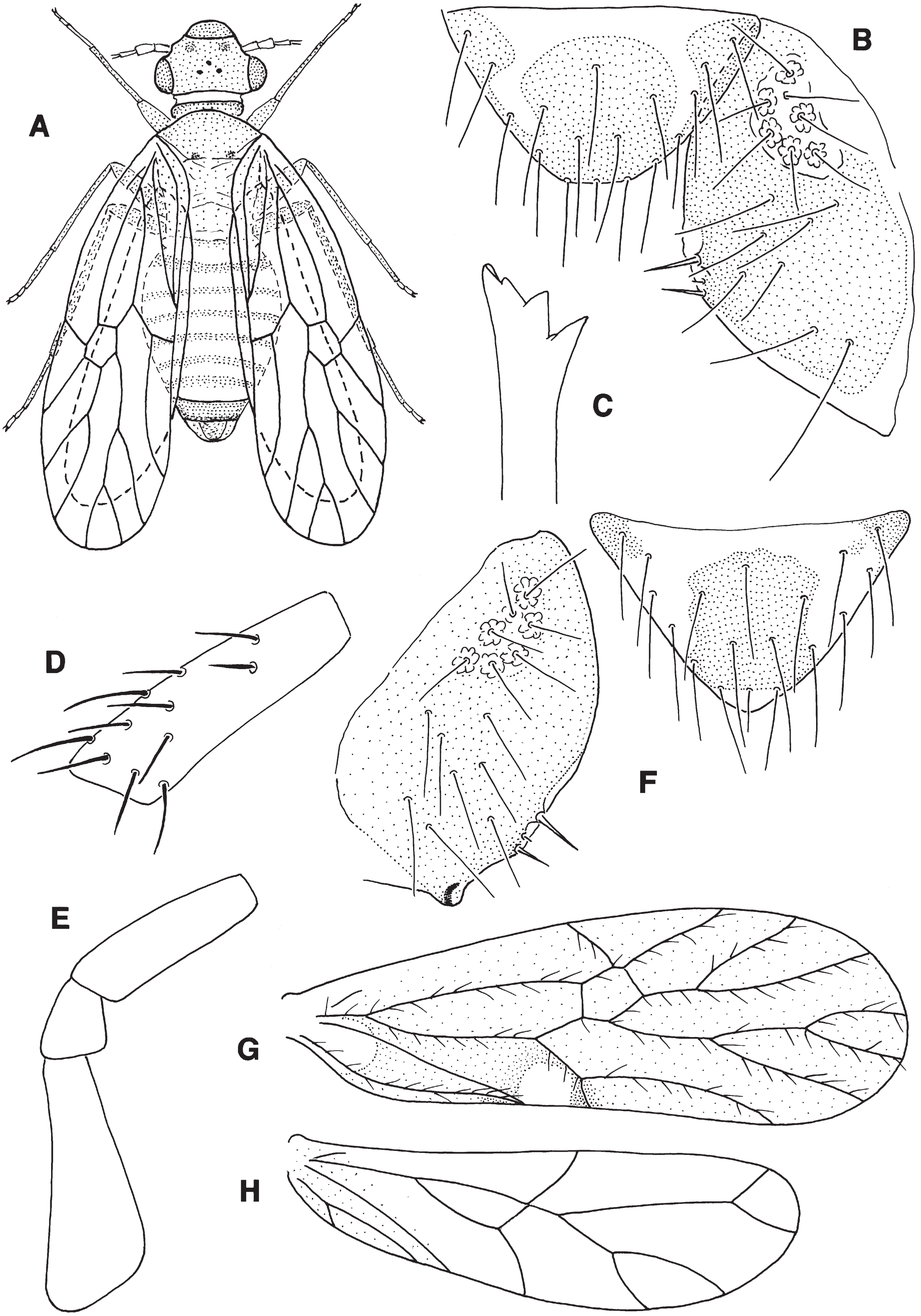

Fig. 4. *Psyllipsocus yucatan*, from Brazilian caves, general morphology. (A) Habitus, male. (B) Epiproct and right paraproct, female. (C) Lacinial tip, female. (D) P2-chaetotaxy, female. (E) P2-P4 of maxillary palp, female. (F) Epiproct and left paraproct, male. (G) Forewing, male. (H) Hindwing, male.

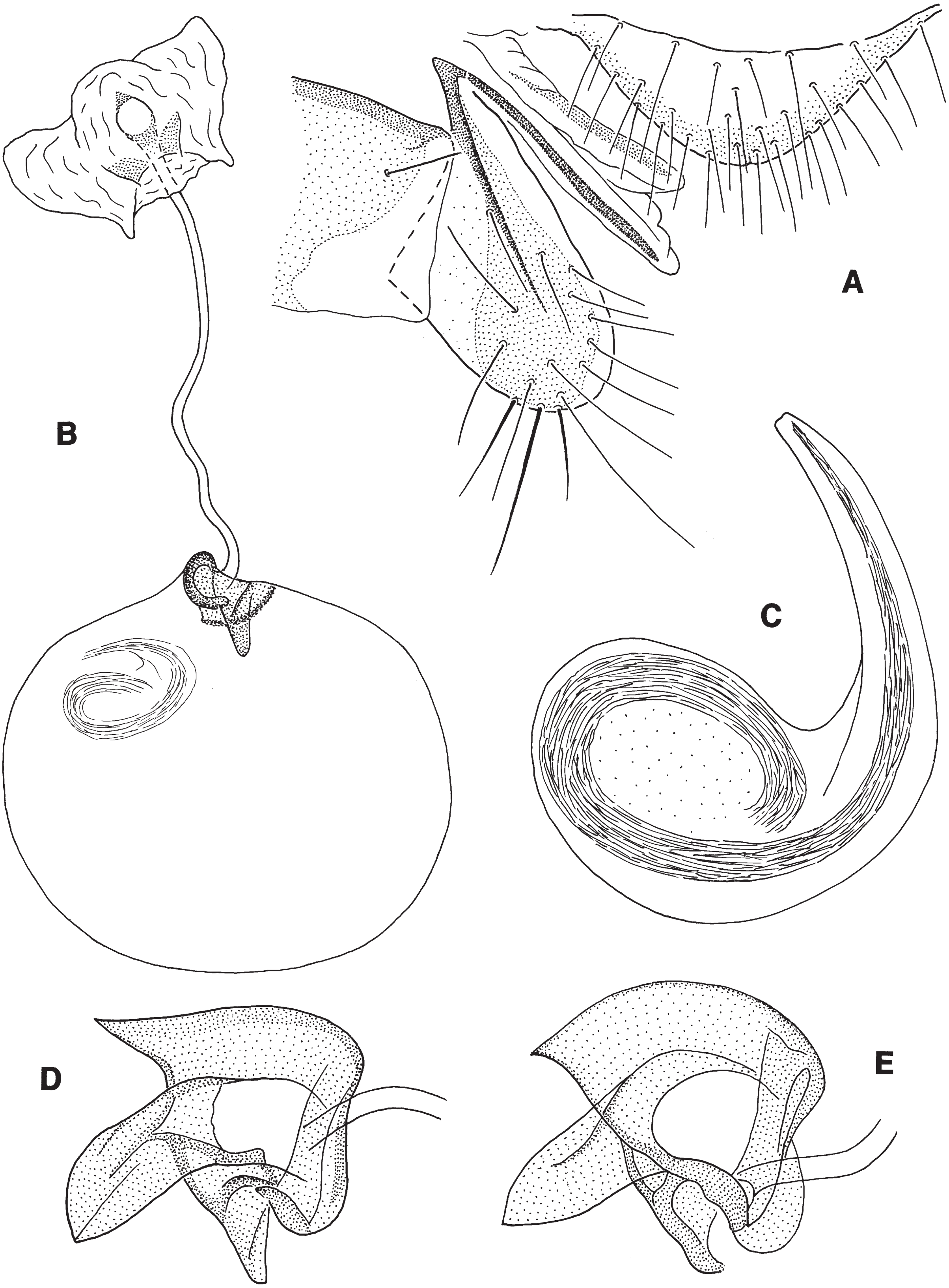

Fig. 5. *Psyllipsocus yucatan*, from Brazilian caves, female genitalia. (A) Subgenital plate, right ovipositor valvulae and right hind corner of clunium. (B) Spermapore plate and spermatheca (the latter contains about a dozen spermatophores, only one of them shown). (C) Spermatophore (not same female as B). (D) Spermathecal sclerotizations and proximal part of spermathecal duct, specimen MHNG 7990 from Toca da Raposa 2, AL. (E) Ditto, specimen MHNG 8000 from Gruta de Ubajara, CE.

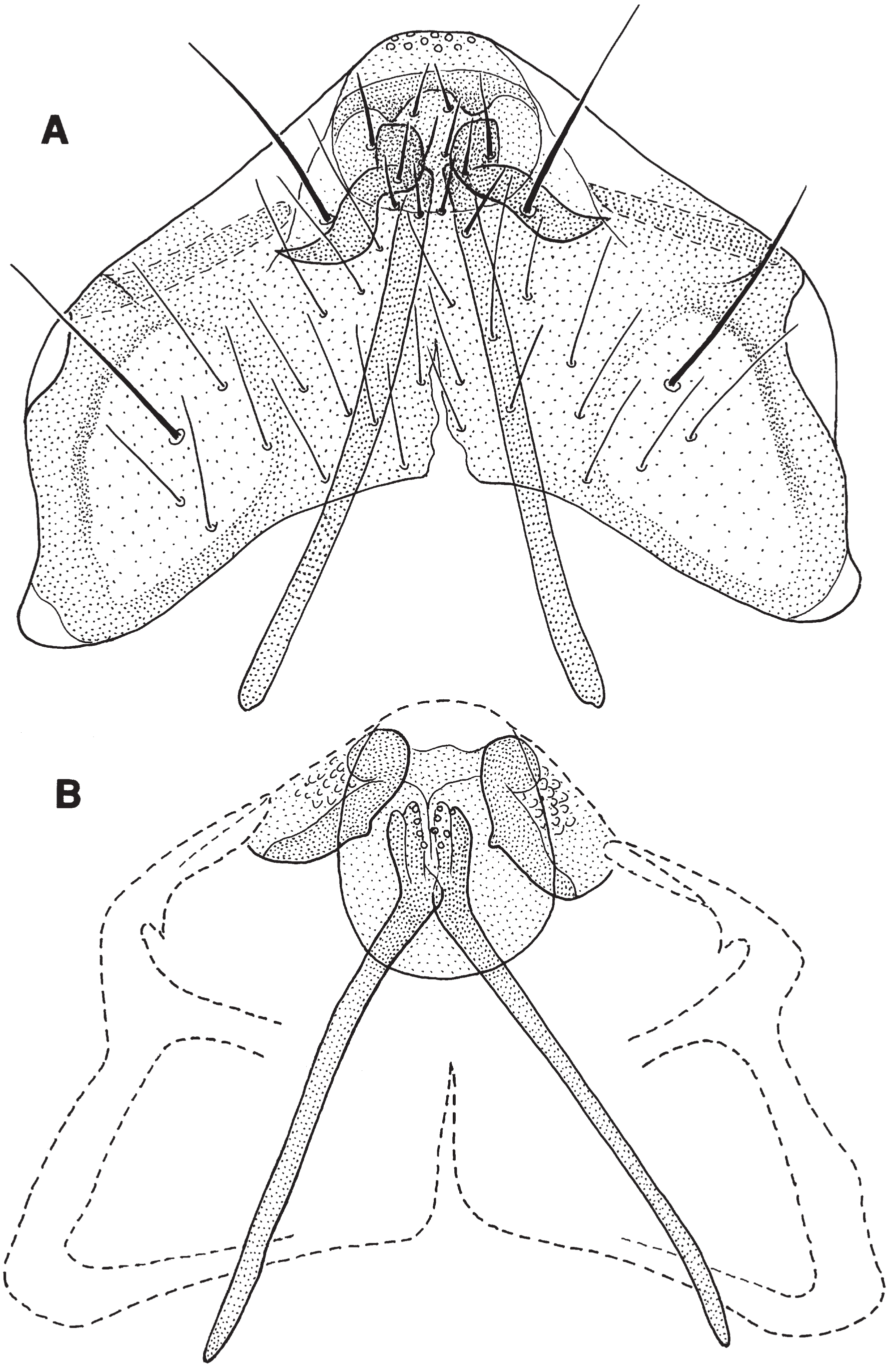

Fig. 6. *Psyllipsocus yucatan*, from Brazilian caves, male genitalia. (A) Hypandrium and phallosome, ventral view. (B) Ditto, dorsal view, other specimen than in A (hypandrium schematically shown by interrupted lines).

Badonnel (1948, 1977) and Mockford (2011) noted the close proximity of *P. yucatan* and the African *P. collarti*. CL has examined the series of syntypes of *P. collarti* (1 female and 1 male slide-mounted by Badonnel, the latter on two separate slides, and several specimens in alcohol, some of them badly damaged, all deposited in the Musée Royal de l'Afrique Centrale, Tervuren, Belgium). No significant difference between the African and the Brazilian specimens could be observed. The structure figured by Badonnel (1946: fig. 10, labeled vv) as a sclerotized distal appendage of v1 is only visible on one side of the slide-mounted terminalia; it is evident that this is an artefact (probably a particle of detritus adhering to the membranous v1). *P. collarti* is here considered as a junior synonym of *P. yucatan*.

Psocathropos lachlani Ribaga, 1899

Fig. 7

Psocathropos lachlani Ribaga, 1899: 157.
Vulturops termitorum Townsend, 1912: 269 (type species of *Vulturops*). **Syn. nov.**
Psocathropos termitorum (Townsend); Roesler, 1944: 134 (*Vulturops* considered as a junior synonym of *Psocathropos*).
Dorypteryx astizi Brèthes, 1923: 117. **Syn. nov.**
Psocathropos astizi (Brèthes); Lienhard, 1977: 435 (new combination suggested).
Psocathropos astizi (Brèthes); Lienhard & Smithers, 2002: 43.
For further synonymy see Lienhard & Smithers (2002).

Material examined: ISLA and MHNG; several males and females (slide-mounted and in alcohol), collected by R. L. Ferreira in caves situated in the following Brazilian municipalities. – Delmiro Gouveia (AL), Gruta Morcego cave, 23.iv.2006. – Curaçá (Patamuté) (BA), Toca d'agua de Patamuté cave, 6.i.2008. – Ubajara (CE), Gruta de Ubajara cave, 30.xii.2006. – Santa Teresa (ES), Gruta do André Huscki cave, 4.i.2005. – Cordisburgo (MG), Gruta de Maquiné cave, 10.vii.2000 and 18.v.2010. – Montalvânia (MG), Gruta Nossa Senhora do Perpétuo Socorro cave, 14.vii.2007. – Nacip Raydan (MG), Gruta Manga de Pedra cave (granito), 21.vii.2002. – Teófilo Otoni (MG), Lapa da Vaca Parida cave, 26.i.2005. – Altinópolis (SP), Gruta do Itambé cave, 27.ii.2006.

Further description: *P. lachlani* is the type species of the genus *Psocathropos*; it is usually brachypterous. The wings of the rare macropterous form (see Key) were first described by Mockford (1993); two macropterous females from a laboratory culture (Jamaica: Kingston, leg. B. D. Turner, 1971) are deposited in the MHNG. For detailed descriptions see Mockford (1993) and Lienhard (1998); some important characters are also mentioned by Badonnel (1967, see Discussion below) and in the key given by Mockford (1991). Here we note the following characters (Fig. 7, see also Key). Length of forewing of brachypterous form variable, usually not reaching abdominal tip; venation of forewing also somewhat variable, but Rs always simple (Fig. 7A). Hindwing of brachypterous form always reduced to a minute bare and veinless flap (Fig. 7B). P2 lacking stout sensillum. Pedicel with well-developed microspades organ (Fig. 7E). Paraproctal trichobothria with weakly differentiated basal florets; setal organ consisting of one minute hair and one somewhat thicker and longer seta; anal spine not differentiated, replaced by a normal seta which is not much longer than the ventral seta of the setal organ (Fig. 7FG). Epiproct and paraproct of female with some conspicuous cylinder setae (Fig. 7F). Setae of male epiproct and paraproct normal, but paraproct ventrally pointed due to the presence of a conspicuous posteroventral sclerotized ridge which is ventrally linked to fine membranes (Fig. 7G); depending on slide-mounting this structure may appear like a free-ending appendix (see Badonnel, 1967: fig. 58; Mockford, 1993: fig. 467; Lienhard, 1998: fig. 36j). Hypandrium and phallosome as in Fig. 7H, hypandrium shorter than its basal width, phallic cradle well differentiated; longitudinal struts in middle connected to each other by a V-shaped sclerite, pores on apical part of longitudinal struts present but not visible in Fig. 7H (only visible in strongly squashed genitalia; see Badonnel, 1967: fig. 57). Spermatheca as in Fig. 7D, with a sclerotized globular vesicle near duct, spermapore lacking sclerotization, spermathecal sac with a narrowed zone towards opening of duct, spermatophore about pear-shaped.

Biology: In relatively warm regions, *P. lachlani* is often domicole, as was the type population from southern Italy (Ribaga, 1899); in the tropics it is also regularly found in ground litter and sometimes in caves (Lienhard, 2002). Brèthes (1923) and Townsend (1912) recorded the species indoors (as *P. astizi* and *P. termitorum* respectively; see Discussion, below), the latter especially in houses infested with termites. The presence of one "fresh" spermatophore and debris of about three "old" spermatophores in the female figured (Fig. 7D) indicates that the species is polyandrous.

Distribution: *P. lachlani* is widespread (Lienhard & Smithers, 2002). Previously published South American records can be found in the following references: Townsend, 1912 (Peru, as *P. termitorum*); Brèthes, 1923 (Argentina, as *P. astizi*); New, 1984 (Brazil); Mockford, 1993 (Colombia); García Aldrete & Mockford, 2009 (Brazil). In adddition to the Brazilian specimens mentioned above, some unpublished material from Paraguay (MHNG) was also examined. Other specimens examined (MHNG) are from the following countries: Guatemala, Guadeloupe, Jamaica, Ascension Island, Cabo Verde, Madeira, Liberia, Togo, Rwanda, Mozambique, Morocco, Israel, Reunion, India, Malaysia, Singapore, Indonesia, Thailand, Fiji.

Discussion: The detailed descriptions and the forewing figures given by Townsend (1912) and Brèthes (1923) for *P. termitorum* and *P. astizi* respectively fit very well the widely distributed *P. lachlani*; therefore we propose here to consider these two names as junior synonyms of the latter.

Under the synonym *P. microps* (Enderlein), Badonnel (1967: p. 27) gives excellent figures of the forewing and the male terminalia of *P. lachlani*, but it has to be noted that in the legend (not in the text!) his figure 58 is erroneously assigned to *P. pilipennis*.

Psocathropos pilipennis (Enderlein, 1931)

Fig. 8

Gambrella pilipennis Enderlein, 1931: 221.
Psocathropos pilipennis (Enderlein); Menon, 1942: 35.

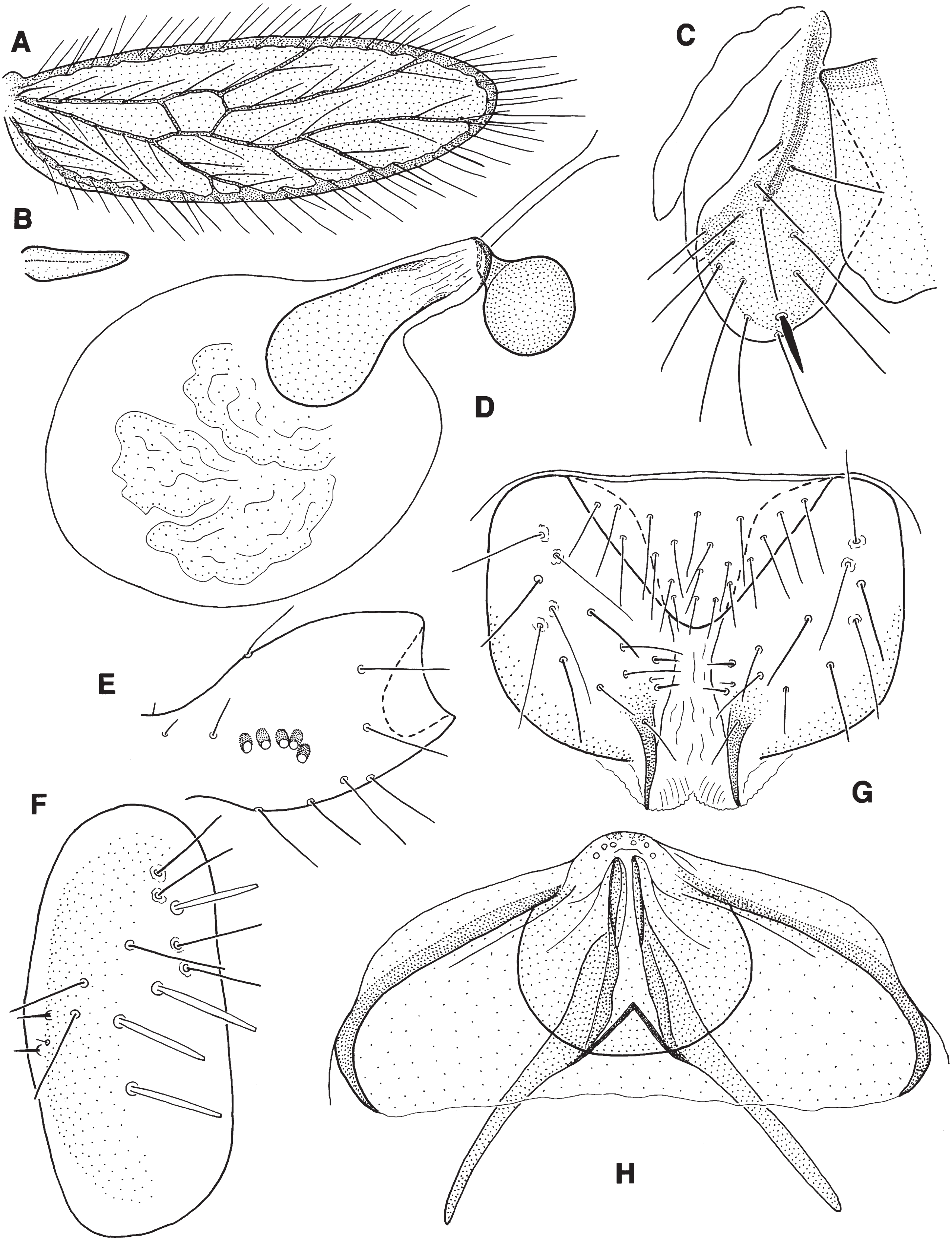

Fig. 7. *Psocathropos lachlani*, from Brazilian caves. (A) Forewing, female. (B) Hindwing, female. (C) Left ovipositor valvulae and left hind corner of clunium. (D) Spermatheca containing one "fresh" spermatophore and debris of three "old" spermatophores. (E) Pedicel with microspades organ, female. (F) Right paraproct, female. (G) Epiproct and paraprocts, male. (H) Hypandrium and phallosome, ventral view (pilosity not shown).

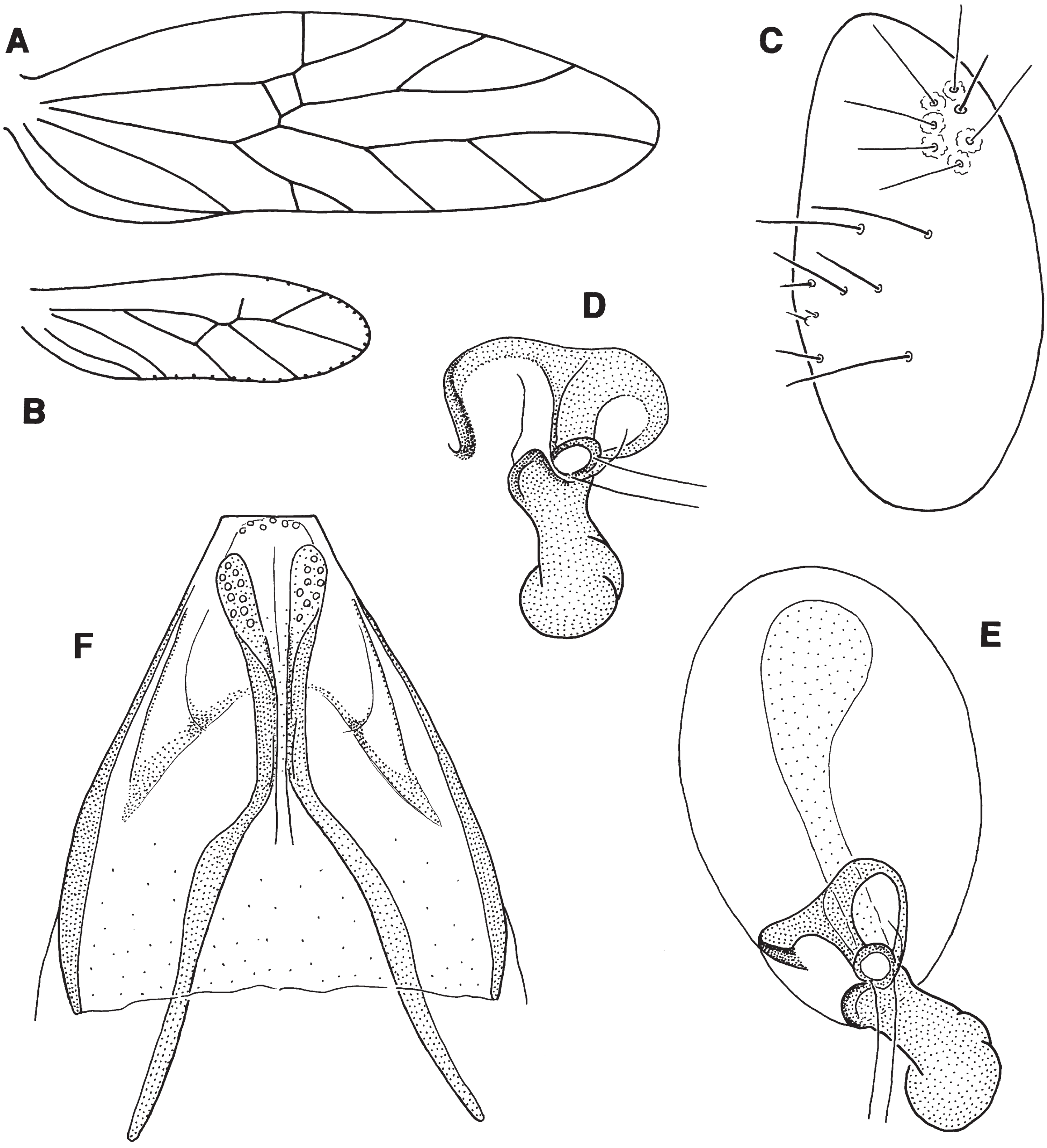

Fig. 8. *Psocathropos pilipennis*, from Brazilian caves. (A) Forewing, male (pilosity not shown). (B) Hindwing, male, showing venation and insertion points of setae. (C) Right paraproct, female. (D) Spermathecal sclerotizations and proximal part of spermathecal duct, specimen MHNG 8148 from Toca do Garrincho, PI. (E) Spermatheca (duct incomplete) containing one spermatophore, specimen MNHG 8150 from Gruta do Araticum, CE (sclerotizations less squashed than in D). (F) Hypandrium and phallosome, ventral view (pilosity not shown).

Material examined: ISLA and MHNG; 4 males and 4 females (slide-mounted and in alcohol), collected by R. L. Ferreira in caves situated in the following Brazilian municipalities. – Ubajara (CE), Gruta do Araticum cave, 1.i.2007. – Coronel José Dias (PI), Toca do Garrincho cave, 11.ix.2008. – Felipe Guerra (RN), Gruta Roncador cave, 1.vi.2006. – Jandaíra (RN), Gruta Aroeira cave, 11.i.2006.

Further description: This species is always brachypterous. For general descriptions see Enderlein (1931: female) and Badonnel (1967: male, see also Discussion below); some important characters are also mentioned in the key given by Mockford (1991) and in Mockford (1993: p. 51). Here we note the following characters (Fig. 8, see also Key). Body length 1.4-1.6 mm. Colouration similar to *P. lachlani*, but usually less pigmented, sometimes hypodermal pigment almost absent. Forewing slightly tapering towards apex, usually almost reaching tip of abdomen or slightly surpassing it (especially in males); venation of forewing somewhat variable, but Rs always bifurcate (Fig. 8A). Hindwing strongly shortened but always with some clearly differentiated veins and several long marginal setae (Fig. 8B). P2 and pedicel as in *P. lachlani*. Epiproct and paraproct simple in both sexes (i.e. no cylinder setae in female and no paraproctal posteroventral ridge in male), anal spine replaced by a normal seta, setal organ as in *P. lachlani* (Fig. 8C). Hypandrium and phallosome as in Fig. 8F, hypandrium longer than its basal width, apically truncate, phallic cradle not clearly differentiated; longitudinal struts lacking V-shaped connecting sclerite, apically with clearly visible pores. Spermatheca as in Fig. 8E, sclerotizations near duct more complicated than in *P. lachlani* and vesicle slightly elongate (Fig. 8DE). Spermapore lacking sclerotization, spermathecal sac oval, lacking narrowed zone towards opening of duct, spermatophore elongately pear-shaped (Fig. 8E).

Biology: In houses (Menon, 1942; Badonnel, 1967; Mockford, 1991), in ground litter and on low vegetation (New, 1977), in caves.

Distribution: Published records are from the Seychelles (Enderlein, 1931), India (Menon, 1942), Madagascar (Badonnel, 1967) and the Aldabra Islands (New, 1977). In addition to the Brazilian material, some specimens from the following countries have also been examined (MHNG): Honduras (in cave), Curaçao (in cave), Singapore (ground litter and/or in houses), Malaysia (on fungi in forest), Vietnam (ground litter), Thailand (domicole?). The species seems to be widespread in the tropics, though less common than *P. lachlani*. However, it is not excluded that some published records of the latter comprise also undiscovered material of *P. pilipennis* (e.g. Menon, 1942; see Discussion below). Badonnel (1967) also indicates that both species were taken together in a house in Madagascar.

Discussion: Menon (1942) synonymizes the genus *Gambrella* Enderlein with *Psocathropos* Ribaga and gives a description of its type species, *P. pilipennis*. However, his material apparently consisted of a mixture of both species, *P. pilipennis* and *P. lachlani*. Therefore he mentions a variability of wing morphology (hindwing sometimes “totally wanting” and forewing sometimes relatively short with simple Rs, see figures 25-26) which we have never observed in *P. pilipennis*. In our opinion, his figures 25 and 26 illustrate forewings of *P. lachlani*, while his figures 23, 24 and 27 illustrate wings of *P. pilipennis*, and his figure 28 the male genitalia of the latter. Badonnel (1967) gives excellent figures of the wings and the male genitalia, but it has to be noted that his figure 58 does not illustrate epiproct and paraproct of *P. pilipennis*, as erroneously indicated in the legend, but of *P. lachlani* (= *P. microps*), as correctly indicated in the text on the latter species (p. 27).

Key to the South American species of Psyllipsocidae and Prionoglarididae

This key allows species identification of adult South American psocids belonging to the families Psyllipsocidae and Prionoglarididae. In addition to the characters mentioned in the key, these species are characterized among Psocoptera by their 3-segmented tarsi, the absence of scales on body and wings, the absence of a thickened and distinctly opaque pterostigma (sometimes slightly opaque in Prionoglarididae) and the presence, in the forewing, of a simple anal vein and a nodulus (i.e. veins CuP and A1 joining at wing margin). Their body is never dorsoventrally flattened and, if present, their forewings are membranous, never coriaceous, though sometimes slightly vaulted (elytriform).
For abbreviations see Material and Methods, above.

1 Forewing normally developed (macropterous) or slightly shortened, usually extending well beyond tip of abdomen, not tapering towards apex but broadly rounded, with normal venation 2
– Apterous, micropterous or clearly brachypterous (forewing usually not reaching tip of abdomen or tapering towards apex), venation at least slightly reduced 3
2 Forewing: basal portion of Sc developed as a slightly curved vein joining R1 just basally of pterostigma (Lienhard & Ferreira, 2013a: fig. 1a). Body length: 2.5 to 3.7 mm .... Prionoglarididae: *Neotrogla* 11
– Forewing: basal portion of Sc rudimentary, ending in membrane, not joining R and usually not extending beyond base of basal closed cell (Fig. 2A). Body length: 1.0 mm (*Psyllipsocus didymus*) to 2.7 mm (*P. serrifer*), mostly about 1.5 mm .... Psyllipsocidae 14
3 Apterous, without wing rudiments; ocelli completely reduced 4
– Micropterous or brachypterous 5
4 Pretarsal claw without preapical tooth. Eye minute, consisting of a single ommatidium. Paraproct without anal spine .... Prionoglarididae: *Speleopsocus chimanta*
Note: This species is a troglobite known from a cave in south eastern Venezuela (see Lienhard *et al.,* 2010a).
– Pretarsal claw with a small preapical tooth. Eye differentiated as a small compound eye, with several ommatidia. Paraproct with a long anal spine .... *Psyllipsocus ramburii*

Note: This is the rare (or potential?) apterous form of *P. ramburii*, corresponding to *P. dubius* Badonnel which is here considered as a junior synonym of the latter (see Discussion of *P. ramburii*, above). For micropterous, brachypterous and macropterous forms, see couplets 5, 10 and 15.

5 Forewing flat or slightly vaulted (elytriform), reaching posterior half of abdomen and bearing some clearly differentiated veins 6

– Forewing strongly reduced, just reaching basal abdominal segments and lacking clearly differentiated veins (Fig. 2E). Paraproct with a long anal spine .... *Psyllipsocus ramburii*

Note: This is the micropterous form of *P. ramburii*; for apterous, brachypterous and macropterous forms, see couplets 4, 10 and 15.

6 Forewing margin with long setae (their length several times width of marginal vein) (Fig. 7A). Paraproct lacking a conspicuous anal spine (Figs 7FG, 8C) .... *Psocathropos* 7

– Forewing margin bare (except for some microscopic hairs which are much shorter than width of marginal vein). Paraproct with a long anal spine (Lienhard & Ferreira, 2014: fig. 1F) .... *Psyllipsocus* 8

7 Forewing Rs simple (Fig. 7A); hindwing strongly reduced, bare and veinless (Fig. 7B). Hypandrium shorter than its basal width (Fig. 7H). Male paraproct ventrally pointed, with a posteroventral sclerotized ridge (Fig. 7G). Female paraproct and epiproct with some conspicuous cylinder setae (Fig. 7F) .... *Psocathropos lachlani*

Note: This is the brachypterous form of *P. lachlani*; for the rare macropterous form, see couplet 14.

– Forewing Rs bifurcate (Fig. 8A); hindwing much shortened but with some clearly differentiated veins and some long marginal setae (Fig. 8B). Hypandrium longer than its basal width (Fig. 8F). Male paraproct as in female (Fig. 8C), ventrally rounded, lacking sclerotized ridge. Female paraproct and epiproct lacking cylinder setae .... *Psocathropos pilipennis*

Note: Macropterous form unknown in this species.

8 Forewing with a brown transversal band about in middle (Lienhard & Ferreira, 2014: fig. 1C) .... *Psyllipsocus spinifer*

Note: For the much rarer macropterous form of this species, see couplet 22.

– Forewing unmarked 9

9 P2 with a stout sensillum in basal half (Lienhard & Ferreira, 2013b: fig. 4F) .... *Psyllipsocus clunjunctus*

Note: Macropterous form of this species not known.

– Stout P2-sensillum not differentiated (Fig. 2D) 10

10 Forewing slightly vaulted (elytriform), hindwing a tiny membranous flap only reaching hind margin of first abdominal tergite .... *Psyllipsocus delamarei*

Note: This species is only known from one female from Argentina (see Badonnel, 1962); it seems to be very close to the brachypterous form of *P. ramburii*.

– Forewing not elytriform, hindwing with some veins, not much shorter than half length of forewing .... *Psyllipsocus ramburii*

Note: This is the brachypterous form of *P. ramburii*; for apterous, micropterous and macropterous forms, see couplets 4, 5 and 15.

11 Female: distal part of gynosome strongly curved (Lienhard & Ferreira, 2013a: fig. 1d) .... *Neotrogla curvata*

– Female: distal part of gynosome straight or only slightly curved (Lienhard *et al*., 2010b: figs 2df, 8c) 12

12 Female: membranous part of gynosome not lobate (Lienhard *et al*., 2010b: fig. 8c) .... *Neotrogla truncata*

– Female: membranous part of gynosome with a spiny dorsal lobe and a pair of spiny lateral lobes (Lienhard *et al*., 2010b: fig. 2f) 13

13 Female: distal lobe of subgenital plate (egg-guide) apically with a large bare median lobe and a pair of minute pilose lateral lobes (Lienhard *et al*., 2010b: fig. 1c) .... *Neotrogla brasiliensis*

– Female: pilose lateral lobes of egg-guide not much smaller than bare median lobe (Lienhard *et al*., 2010b: fig. 5) .... *Neotrogla aurora*

14 Forewing and hindwing with numerous long marginal setae (their length several times width of marginal vein) (Mockford, 1993: figs 462, 463) .... *Psocathropos lachlani*

Note: This is the rare macropterous form of *P. lachlani*; for the brachypterous form, see couplet 7.

– Wing margins bare (except for some microscopic hairs which are shorter than width of marginal vein) 15

15 Distal closed cell in forewing absent (i.e. no crossvein between R1 and Rs) (Fig. 2A) .... *Psyllipsocus ramburii*

Note: This is the relatively rare macropterous form of *P. ramburii*; for apterous, micropterous and brachypterous forms, see couplets 4, 5 and 10.

– Distal closed cell present, distally delimited by a crossvein between R1 and Rs (Fig. 4G) 16

16 In forewing Rs and M joined by a crossvein (Lienhard & Ferreira, 2014: fig. 3A) 17

– In forewing Rs and M fused for a length (Fig. 4G) 19

17 Forewing unmarked .... *Psyllipsocus falcifer*

– Forewing with some pigmented areas 18

18 AP flat, its marginal length more than twice its height, patches of wing pattern associated to veins (Lienhard & Ferreira, 2014: fig. 5A) .... *Psyllipsocus marconii*

– AP tall, its marginal length not much exceeding its height, an isolated longitudinal patch present in middle of cells r1, r3 and r5 (Lienhard & Ferreira, 2014: fig. 7A) .... *Psyllipsocus thaidis*

19 First portion of pterostigmal R1 not longer than half length of R1-Rs crossvein (Fig. 4G) 20

– First portion of pterostigmal R1 clearly longer than half length of R1-Rs crossvein, often longer than this crossvein 22

20 Distal closed cell almost twice as long as marginal length of pterostigma; paraproct with a long, basally non-articulated anal spine (Lienhard & Ferreira, 2013b: figs 4A, 6B) 21

– Distal closed cell only about half as long as marginal length of pterostigma (Fig. 4G); anal spine of paraproct replaced by a stout, relatively short and basally articulated seta (Fig. 4BF) .... *Psyllipsocus yucatan*

21 Female: spermatheca with a conspicuous longitudinal saw-like sclerite (Lienhard & Ferreira, 2013b: fig. 7J). Male: abdominal apex with a complex clunial bridge, hypandrium with four apical setae (Lienhard & Ferreira, 2013b: fig. 5) .... *Psyllipsocus serrifer*

– Female: spermatheca with a slender file-like sclerite (Lienhard & Ferreira, 2013b: fig. 8F). Male: abdominal apex with a simple clunial bridge, hypandrium with two apical setae (Lienhard & Ferreira, 2013b: fig. 9) .... *Psyllipsocus similis*

22 Forewing and hindwing with a brown transversal band in basal half (Lienhard & Ferreira, 2014: fig. 1AB) .... *Psyllipsocus spinifer*

Note: This is the relatively rare macropterous form of this species; for the brachypterous form, see couplet 8.

– Wings unmarked or wing pattern different 23

23 Forewing particularly narrow, FW/FWw > 3 24

– Forewing of normal shape, FW/FWw ≤ 3 25

24 Forewing with narrow pigment bands bordering most of veins (Lienhard & Ferreira, 2014: fig. 16A). Male: postero-median V-shaped incision of phallosome not deeper than length of antero-median part of phallosome sclerite (Lienhard & Ferreira, 2014: fig. 17AB) .... *Psyllipsocus angustipennis*

– Pigment bands broader in apical half of forewing, covering more than half of the surface of cells m1 and m2 (Lienhard & Ferreira, 2014: fig. 17C). Male: postero-median V-shaped incision of phallosome deeper than length of antero-median part of phallosome sclerite (Lienhard & Ferreira, 2014: fig. 17F) .... *Psyllipsocus proximus*

25 Forewing anal vein with a brown spot at the base of each hair; exceptionally forewings completely unmarked (see pale specimens of *P. subtilis*, couplet 28) 26

– Forewing anal vein lacking such spots; distal end of forewing veins bordered by brown pigment (Lienhard & Ferreira, 2014: figs 14A, 15A) .... *Psyllipsocus punctulatus* (and female spec. cf. *punctulatus*)

26 Height of AP exceeding its marginal length; forewing with a conspicuous U-shaped or V-shaped brown patch covering most of cell r1 (Lienhard & Ferreira, 2014: fig. 13A) .... *Psyllipsocus radiopictus*

– AP lower than its marginal length; pigmentation of cell r1 different 27

27 Forewing with a broad brown band bordering apical portion of R1 and R1-Rs crossvein, forming a conspicuous angulate patch which borders cell r1 basally (Lienhard & Ferreira, 2014: fig. 12A) .... *Psyllipsocus fuscistigma*

– At most narrow pigment bands bordering apical portion of R1 and R1-Rs crossvein 28

28 Forewing with four narrow pigment stripes parallel to veins R2+3 and R4+5, situated in cells r1 (one stripe), r3 (two stripes) and r5 (one stripe); these stripes clearly separated from the narrow pigmented zones bordering these veins. In very pale specimens forewings unmarked. Male: clunium simple, lacking clunial rods. Female: v3 with a marginal row of thick setae, clearly thicker than other v3-setae of similar length (Lienhard & Ferreira, 2014: fig. 11AE) .... *Psyllipsocus subtilis*

– Forewing with a dark brown drop-shaped spot or stripe or a light brown diffuse patch in middle of cells r1 and r3. Male: clunial rods present. Female: v3-pilosity uniform 29

29 Forewing with a dark brown spot or stripe in middle of cells r1 and r3. Male: phallic cradle of hypandrium anteriorly broadly rounded (Lienhard & Ferreira, 2014: figs 8, 9) .... *Psyllipsocus clunioventralis*

– These cells only with a light brown diffuse patch covering most of their surface. Male: phallic cradle of hypandrium anteriorly truncate (Lienhard & Ferreira, 2014: fig. 10) .... *Psyllipsocus didymus*

GENERAL DISCUSSION

Analysis of distribution

This analysis is based on the data presented in Appendix 2. Detailed considerations concerning each of the 19 endemics (15 *Psyllipsocus* spp., 4 *Neotrogla* spp.) have already been published by Lienhard *et al.* (2010b) and Lienhard & Ferreira (2013a, b, 2014) when describing these previously unknown species. During this project, about 400 adult individuals of 23 species of Psyllipsocidae and Prionoglarididae from 124 Brazilian caves were identified (Table 1). The total number of caves wherein each species was recorded and the number of caves wherein it was associated with another species of these families are presented in Table 2. The proportion of Brazilian caves occupied by these families is unknown; because of uneven sampling effort their absence cannot be assumed for caves where they are not currently recorded. This discussion only concerns caves with identified adults; caves with nymphs that cannot be identified are not included (see also Introduction).

As previously observed by Lienhard & Ferreira (2014) and Yoshizawa *et al.* (2014), these insects live predominantly in dry resource-poor caves. Two closely related species of *Psyllipsocus* or two species of *Neotrogla* have never been found in the same cave. In most of the caves only one species was present, rarely two species (23 caves), exceptionally three species (viz. Gruta de Ubajara, CE: *Psoc. lachlani, P. spinifer, P. yucatan*; Gruta Janelão, MG: *N. brasiliensis, P. serrifer, P. spinifer*; Gruta do Lagedo Grande, RN: *P. clunjunctus, P. spinifer, P. subtilis*). In most caves with two or three species, only one of them is a Brazilian endemic; in seven caves two endemics were found and in two caves three endemics live together (Gruta Janelão and Gruta do Lagedo Grande, see above). In three caves (cave PEA 343, BA; Gruta Caboclo, MG; Gruta Janelão, MG) specimens of both genera, *Neotrogla* and *Psyllipsocus*, were present simultaneously. Among the 15 endemics of *Psyllipsocus*, 8 species were recorded from a single cave each (Table 2). Thus, very strict local endemism appears to be high in this genus.

The cosmopolitan and often domicole species *P. ramburii* is the most common cave *Psyllipsocus* in Brazil (present in 30 caves, in 23 of them exclusively). In about 40% of the caves at least one of the non-endemics *P. ramburii, P. yucatan, Psoc. lachlani* or *Psoc. pilipennis* is present; 32% of the caves are exclusively inhabited by non-endemics. The high frequency of the opportunistic, parthenogenetic (thelytokous) and often domicole *P. ramburii* indicates that this species is a particularly good disperser; but it may sometimes have been introduced by human activities.

In all 9 caves with two or three Brazilian endemics at least one of them is *P. spinifer* or *P. clunjunctus.* Together with *P. serrifer*, these are the most widely distributed endemics. *P. spinifer* is known from 20 caves (19 municipalities, 8 states), *P. clunjunctus* from 16 caves (9 municipalities, 5 states) and *P. serrifer* from 13 caves (9 municipalities, 2 states) (for the distribution of the latter two species, see also map in Lienhard & Ferreira, 2013b). *P. spinifer* is very often associated with other species, being found alone in only five caves. It is interesting to see that the non-domicole, non-parthenogenetic endemic *P. spinifer*, the second most common Brazilian cave species, is much more often associated with a probably more specialized local endemic than the most common, cosmopolitan, domicole and parthenogenetic *P. ramburii* (Table 2). It cannot be excluded that the presence of this opportunistic generalist contributes to the elimination of locally endemic specialists. Only in two of 30 caves *P. ramburii* has been recorded together with a Brazilian endemic (*P. falcifer, P. serrifer*).

Some evolutionary considerations

This rather speculative discussion follows the short remarks that we made in the recent paper wherein most of the endemic cave species of *Psyllipsocus* were described (Lienhard & Ferreira, 2014). Rather than as a discussion of concrete results we consider this part as an outlook on possible future research perspectives concerning the fascinating cave psocids of the families Psyllipsocidae and Prionoglarididae.

The only clearly troglobitic representative of these families from the New World is the prionoglaridid *Speleopsocus chimanta* known from a humid cave in south eastern Venezuela (see Key and Appendix 1). All other species are winged, have well developed compound eyes and are relatively well-pigmented, except for the cosmopolitan and often domicole pale and

Table 1. Species richness, rate of endemism and distribution for Brazilian genera of Psyllipsocidae and Prionoglarididae based on adult specimens collected in caves.

	species	endemics	caves	municipalities	states
Psocathropos	2		13	12	8
Psyllipsocus	17	15 (88%)	102	51	13
Neotrogla	4	4 (100%)	19	9	3
Total	**23**	**19 (83%)**	**124**	**59**	**13**

Table 2. Brazilian cave species of Psyllipsocidae (*Psocathropos, Psyllipsocus*) and Prionoglarididae (*Neotrogla*) with **total number** of caves wherein adults of each species were collected and, on corresponding line or column, number of caves where the species was associated with another one.

	species	total	*P. lachlani*	*P. pilipennis*	*P. ramburii*	*P. yucatan*	*P. angustipennis*	*P. clunioventralis*	*P. clunjunctus*	*P. didymus*	*P. falcifer*	*P. fuscistigma*	*P. marconii*	*P. proximus*	*P. punctulatus*	*P. radiopictus*	*P. serrifer*	*P. similis*	*P. spinifer*	*P. subtilis*	*P. thaidis*	*N. aurora*	*N. brasiliensis*	*N. curvata*
non-endemics	*Psocathropos lachlani*	**9**			2	2							1						2					
	Psocathropos pilipennis	**4**																	1					
	Psyllipsocus ramburii	**30**	2			2					1						1		2					
	Psyllipsocus yucatan	**13**	2		2											1			2					1
endemics	*Psyllipsocus angustipennis*	**3**																						
	Psyllipsocus clunioventralis	**1**																	1					
	Psyllipsocus clunjunctus	**16**																	3	2				
	Psyllipsocus didymus	**1**																						
	Psyllipsocus falcifer	**8**			1														1					
	Psyllipsocus fuscistigma	**1**																	1					
	Psyllipsocus marconii	**1**	1																					
	Psyllipsocus proximus	**1**																						
	Psyllipsocus punctulatus	**1**																	1					
	Psyllipsocus radiopictus	**1**				1																		
	Psyllipsocus serrifer	**13**			1														1				1	
	Psyllipsocus similis	**3**																						
	Psyllipsocus spinifer	**20**	2	1	2	2		1	3		1	1			1		1			1			2	
	Psyllipsocus subtilis	**6**							2										1					
	Psyllipsocus thaidis	**1**																						
	Neotrogla aurora	**6**																						
	Neotrogla brasiliensis	**3**															1		2					
	Neotrogla curvata	**7**				1																		
	Neotrogla truncata	**3**																						

wingless forms of *Psyllipsocus ramburii*, with reduced but still multifacetted eyes (see Key). The only character interpreted as a cave adaptation (Lienhard, 2000) is the presence of leg trichobothria in the prionoglaridid subfamiliy Speleketorinae, to which the Brazilian genus *Neotrogla* belongs (Lienhard, 2004a; Lienhard *et al.,* 2010b). This genus is only known from caves. However, most of the *Psyllipsocus* species known from North and Middle America live on the bark of trees, in soil litter or on lichen-covered rock outcrops (Mockford, 2011). Unfortunately, all available data on Brazilian *Psyllipsocus* concern material collected in caves, though some species of this genus might also live in other microhabitats in Brazil, outside of caves, as in the northern parts of the New World. It would be of particular interest to discover non-cavernicolous populations of the endemic species or of species closely related to them.

Most of the local endemics are only known from one cave or from some caves situated close together (often in the same municipality or neighbouring municipalities). Some isolated relict populations of formerly more widely distributed species might be at the origin of this high diversity of cave endemics. These ancestors were probably not strictly cavernicolous. The relatively wide distribution of *P. spinifer, P. clunjunctus* and *P. serrifer* may be the result of secondary dispersal of these endemics out of their region of origin.

The endemic cave *Psyllipsocus* form a heterogeneous assemblage of isolated species or small groups of species. However, except for the most common endemic *P. spinifer*, they all show some kind of reduction of the phallosome, apparently due to homoplasy (Lienhard & Ferreira, 2014) (Note: males of *P. thaidis* and *P. radiopictus* are not known). All known Brazilian prionoglaridids (i.e. the four species of the endemic cave genus *Neotrogla*) show also a strong reduction of the phallosome (Lienhard *et al.,* 2010b; Lienhard & Ferreira, 2013a; Yoshizawa *et al.,* 2014). Therefore we proposed the speculative hypothesis that the locally endemic cave species of these genera might have evolved under a particular selection pressure favouring reduction of male primary external genitalia (Lienhard & Ferreira, 2014). This selection pressure could be similar to that favouring reduction of the phallosome in the African cave prionoglaridid *Afrotrogla*, known from caves in semidesertic regions of Namibia and South Africa (Lienhard, 2007). All these psocids live in dry resource-poor caves and are the only known representatives of the suborder Trogiomorpha with reduced phallosomes. For the genus *Neotrogla*, Yoshizawa *et al.* (2014) showed that this reduction of the male intromittent organ is very probably related to reversed sexual selection. The only psocid species where reversed sexual selection has clearly been documented at present, *Lepinotus patruelis*, also belongs to the suborder Trogiomorpha but is not cavernicolous and has normal male genitalia (Wearing-Wilde, 1995, 1996; Yoshizawa *et al.,* 2014). It would be interesting to elucidate the influence of a subterranean mode of life in dry caves on sexual selection. Miller & Svensson (2014: p. 427) "suggest that deeper ecological perspectives on sexual selection may alter some of the fundamental assumptions of sexual selection theory and rapidly lead to new discoveries". Prionoglarididae and Psyllipsocidae could play a key role in future research in this field. We suggest that adaptations to life in dry, resource-poor cave environments could affect sexual selection and thus promote sexual role reversal in these insects.

However, the absence of data on non-cavernicolous representatives of these families from Brazil makes it impossible to estimate the pertinence of the supposed correlation between a subterranean mode of life and the presence of reduced male genitalia. The most widely distributed endemic cave species is *P. spinifer*, the only endemic with a normal male phallosome, like that of all non-cavernicolous species of the genus. Thus, this species may also live outside of caves in Brazil. For the local endemics with reduced phallosome it may be speculated that they evolved as cave refugees from populations which were not competitive under out-of-cave conditions.

In the trogiomorphan species with the most striking reduction of the phallosome (i.e. all species of *Neotrogla* and *Afrotrogla* and of the *Psyllipsocus clunjunctus* species group), females have evolved novel differentiations of the spermapore region. Yoshizawa *et al.* (2014) showed that, in *Neotrogla*, the novel female organ functions as an intromittent organ during copulation. Such a function was also suggested hypothetically for the novel female organs in *Afrotrogla* (Lienhard, 2007) and the *Psyllipsocus clunjunctus* group (Lienhard & Ferreira, 2013b). Among the Brazilian endemics with a reduced phallosome there are two particularly successful species, in terms of their distribution range, *P. clunjunctus* and *P. serrifer*, both belonging to the *clunjunctus* species group. They are not only characterized by the almost complete absence of phallosome sclerites and the presence of a novel female "micropenis", but they also have evolved a novel male accessory genital organ, the clunial bridge (Lienhard & Ferreira, 2013b). Might these novel structures be the reason of their success?

It is difficult to ascribe to pure coincidence these varied phenomena relating to similar modifications of genital morphology and reproductive behaviour in species that are not particularly closely related but which share a cavernicole life history. Perhaps we are here confronted with a new category of adaptations to a life in caves different to the classical troglomorphic adaptations (reduction of wings, pigmentation and eyes; see Dethier & Hubart, 2005), and as yet, not directly explained.

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APPENDIX 1: Checklist of South American Psyllipsocidae and Prionoglarididae, with indication of general distribution (only known from caves, except for *Psocathropos* spp., *Psyllipsocus delamarei, P. ramburii* and *P. yucatan*).

Psyllipsocidae

Psocathropos Ribaga, 1899: 156; type species: *P. lachlani* Ribaga.

Psocathropos lachlani Ribaga, 1899: 157. Widely distributed in the tropics (often domicole).

Psocathropos pilipennis (Enderlein, 1931: 221). Widely distributed in the tropics (sometimes domicole).

Psyllipsocus Selys-Longchamps, 1872: 145; type species: *P. ramburii* Selys-Longchamps.

Psyllipsocus angustipennis Lienhard, 2014; in: Lienhard & Ferreira, 2014: 239. Brazil.

Psyllipsocus clunioventralis Lienhard, 2014; in: Lienhard & Ferreira, 2014: 225. Brazil.

Psyllipsocus clunjunctus Lienhard, 2013; in: Lienhard & Ferreira, 2013b: 424. Brazil.

Psyllipsocus delamarei Badonnel, 1962: 187. Argentina.

Psyllipsocus didymus Lienhard, 2014; in: Lienhard & Ferreira, 2014: 229. Brazil.

Psyllipsocus falcifer Lienhard, 2014; in: Lienhard & Ferreira, 2014: 216. Brazil.

Psyllipsocus fuscistigma Lienhard, 2014; in: Lienhard & Ferreira, 2014: 233. Brazil.

Psyllipsocus marconii Lienhard, 2014; in: Lienhard & Ferreira, 2014: 220. Brazil.

Psyllipsocus proximus Lienhard, 2014; in: Lienhard & Ferreira, 2014: 242. Brazil.

Psyllipsocus punctulatus Lienhard, 2014; in: Lienhard & Ferreira, 2014: 236. Brazil.

Psyllipsocus radiopictus Lienhard, 2014; in: Lienhard & Ferreira, 2014: 234. Brazil.

Psyllipsocus ramburii Selys-Longchamps, 1872: 146. Cosmopolitan (often domicole).

Psyllipsocus serrifer Lienhard, 2013; in: Lienhard & Ferreira, 2013b: 429. Brazil.

Psyllipsocus similis Lienhard, 2013; in: Lienhard & Ferreira, 2013b: 433. Brazil.

Psyllipsocus spinifer Lienhard, 2014; in: Lienhard & Ferreira, 2014: 212. Brazil.

Psyllipsocus subtilis Lienhard, 2014; in: Lienhard & Ferreira, 2014: 229. Brazil.

Psyllipsocus thaidis Lienhard, 2014; in: Lienhard & Ferreira, 2014: 223. Brazil.

Psyllipsocus yucatan Gurney, 1943: 212. Widely distributed in the tropics.

Prionoglarididae

Neotrogla Lienhard, 2010; in: Lienhard *et al*., 2010b: 612; type species: *N. brasiliensis* Lienhard.

Neotrogla aurora Lienhard, 2010; in: Lienhard *et al*., 2010b: 619. Brazil.

Neotrogla brasiliensis Lienhard, 2010; in: Lienhard *et al*., 2010b: 614. Brazil.

Neotrogla curvata Lienhard & Ferreira, 2013a: 4. Brazil.

Neotrogla truncata Lienhard, 2010; in: Lienhard *et al*., 2010b: 622. Brazil.

Speleopsocus Lienhard, 2010; in: Lienhard *et al*., 2010a: 186; type species: *S. chimanta* Lienhard.
Speleopsocus chimanta Lienhard, 2010; in: Lienhard *et al*., 2010a: 187. Venezuela.

APPENDIX 2: Comprehensive list of Brazilian caves wherein adults of Psyllipsocidae and Prionoglarididae were collected (leg. R. L. Ferreira unless other collector mentioned)

P. = *Psyllipsocus*; *Psoc.* = *Psocathropos*; ***in bold type*** = non-endemic species (widely distributed in the tropics or cosmopolitan)

Alagoas (AL)
Delmiro Gouveia (AL), Gruta Morcego, 23.iv.2006: ***Psoc. lachlani***
Murici (AL), Toca da Raposa 1 (granite), 13.i.2007: *P. radiopictus*, ***P. yucatan***
Murici (AL), Toca da Raposa 2 (granite), 13.i.2007: ***P. yucatan***

Amazonas (AM)
Apuí (AM), Gruta Apiacá 1, Parque Nacional do Juruena, 13.ix.2011: *P. proximus*

Bahia (BA)
Campo Formoso (BA), Toca do Angico, 9.i.2008: *P. spinifer*
Campo Formoso (BA), Toca do Morrinho, i.1997: *P. spinifer*
Campo Formoso (BA), Toca do Pitu, 10.vii.2008: *Neotrogla truncata*
Campo Formoso (BA), Toca da Tiquara, 8.i.2008, i.2009, xii.2010: ***P. yucatan***
Curaçá (Patamuté) (BA), Toca d'agua de Patamuté, 6.i.2008: ***Psoc. lachlani***, *P. spinifer*
Ourolândia (BA), Toca dos Ossos, 31.vii.2007, 10.vi.2012, i.2013: *Neotrogla truncata*
Palmeiras (BA), Gruta Ioiô, 1.i.2008: *Neotrogla truncata*
Santa Maria da Vitória (BA), cave PEA 341, x.2012: *Neotrogla curvata*
Santa Maria da Vitória (BA), cave PEA 342, x.2012: *Neotrogla curvata*
Santa Maria da Vitória (BA), cave PEA 343, 15.v.2011, leg. S. S. Salgado: *Neotrogla curvata*, ***P. yucatan***
São Desidério (BA), Gruta do Catitu, 24.vii.200: *P. clunjunctus*
São Desidério (BA), Gruta do Sumidouro do João Baio, 29.vii.2006: *P. clunjunctus, P. spinifer*
São Félix do Coribe (BA), cave PEA 377, 10.v.2011, leg. S. S. Salgado: *P. serrifer*
São Félix do Coribe (BA), cave PEA 378, x.2012: *Neotrogla curvata*
São Félix do Coribe (BA), cave PEA 380, 21.vii.2011, leg. S. S. Salgado: *Neotrogla curvata*
São Félix do Coribe (BA), cave PEA 381, 18.vii.2011, leg. S. S. Salgado: *Neotrogla curvata*
São Félix do Coribe (BA), cave PEA 383, 18.vii.2011, leg. S. S. Salgado: *Neotrogla curvata*
Várzea Nova (BA), Gruta Jurema, 20.vii.2008: *P. clunjunctus*

Ceará (CE)
Araripe (CE), Gruta do Brejinho, 1.v.2007: *P. spinifer*
Tejuçuoca (CE), Gruta do Veado Campeiro, 16.ix.2008: *P. fuscistigma, P. spinifer*
Ubajara (CE), Gruta do Araticum, 1.i.2007: ***Psoc. pilipennis,*** *P. spinifer*
Ubajara (CE), Gruta dos Mocós, 3.i.2007: ***P. yucatan***
Ubajara (CE), Gruta do Morcego Branco, 3.i.2007: *P. spinifer,* ***P. yucatan***
Ubajara (CE), Gruta de Ubajara, 30.xii.2006: ***Psoc. lachlani***, *P. spinifer,* ***P. yucatan***

Espírito Santo (ES)
Castelo (ES), Gruta do Limoeiro, 7.i.2005: ***P. ramburii, P. yucatan***
Santa Teresa (ES), Gruta do André Huscki, 4.i.2005: ***Psoc. lachlani***

Goiás (GO)
Damianópolis (GO), Lapa do Ribeirão dos Porcos, 29.vii.2001, 5.x.2001, 27.vi.2002: *P. clunjunctus, P. spinifer*

Minas Gerais (MG)
Arcos (MG), Caverna do Alinhamento, 1.vi.2002: ***P. ramburii***
Arcos (MG), Gruta da Bocaininha, 3.xii.2008: *P. serrifer*
Arcos (MG), Gruta Labirinto, 28.i.2006: *P. serrifer*
Arinos (MG), Lapa do Salobo, 18.vii.2010: ***P. yucatan***
Cordisburgo (MG), Gruta de Maquiné, 10.vii.2000, 18.v.2010: ***Psoc. lachlani***, ***P. ramburii***
Cordisburgo (MG), Gruta do Salitre, 22.iv.2011: *P. serrifer*
Cordisburgo (MG), Gruta Santo Amaro 1, 28.ix.2010: ***P. ramburii***
Cordisburgo (MG), Gruta Tão Lucas, 14.xi.2010: *P. falcifer*
Cordisburgo (MG), Lapinha do Atamis, 13.xi.2010: *P. falcifer*
Coromandel (MG), Gruta João do Pó, 5.x.2000: ***P. ramburii***
Coromandel (MG), Gruta Ronan, 3.x.2000: ***P. ramburii***
Coromandel (MG), Gruta Ronan II, 4.x.2000: ***P. ramburii***
Diamantina (MG), Gruta do Salitre, 13.xii.2007: ***P. ramburii***
Doresópolis (MG), Gruta P43, 9.xi.2003: *P. serrifer*
Itabirito (MG), Gruta MP1, 29.viii.2005: *P. serrifer*
Itabirito (MG), Gruta MP8, 8.ix.2005: *P. similis*
Itacarambi (MG), Gruta Bonita, 19.iii.2003: *P. angustipennis*
Itambé do Mato Dentro (MG), Baixada dos Crioulos 2, 29.vii.2004: *P. similis*
Itumirim (MG), Gruta Santo Antônio, 25.x.2002: ***P. ramburii***
Januária (MG), Gruta Caboclo, 27.vii.2003: *Neotrogla brasiliensis, P. spinifer*
Januária (MG), Gruta Ossos, vii.2003, iii.2013: *Neotrogla brasiliensis*
Januária / Itacarambi (MG), Gruta Brejal, 25.vii.2003: female cf. *P. punctulatus*
Januária / Itacarambi (MG), Gruta Janelão, 28.vii.2003: *Neotrogla brasiliensis, P. serrifer, P. spinifer*
Januária / Itacarambi (MG), Gruta Preguiça, 26.vii.2003: *P. angustipennis*
João Pinheiro (MG), Gruta do Sapecado, 15.x.2010: ***P. ramburii***
Lagoa da Prata (MG), Gruta Salão de Festas, 4.v.2003: *P. serrifer*
Lagoa Santa (MG), Gruta da Lapinha, 12.vi.2002: ***P. ramburii***
Matozinhos (MG), Gruta dos Irmãos Piriás, 28.vii.2000: ***P. ramburii***
Matozinhos (MG), Gruta Lavoura, 28.+ 29.v.1997, 26.vi.1997, 19.ii.2000: ***P. ramburii***
Matozinhos (MG), Gruta Pequenas III, 31.vii.2002: *P. serrifer*
Matozinhos (MG), Meandro Abismante, 6.vii.2002: ***P. ramburii***
Matutina (MG), Gruta 9, 10.x.2010: ***P. ramburii***
Moeda (MG), SMS 19, 3.xii.2005: *P. similis*

Moeda (MG), SMS 29, 11.xii.2005: ***P. ramburii***
Montalvânia (MG), Gruta Nossa Senhora do Perpétuo Socorro, 14.vii.2007: ***Psoc. lachlani***, *P. marconii*
Nacip Raydan (MG), Gruta Manga de Pedra (granito), 21.vii.2002: ***Psoc. lachlani***
Pains (MG), Buraco do Nando, 12.x.2003: *P. serrifer*
Pains (MG), Gruta Brasical, 28.ix.2003: *P. serrifer*
Pains (MG), Gruta do Capão, 5.v.2001: ***P. ramburii***
Pains (MG), Gruta dos Estromatólitos, 7.xi.2000: *P. falcifer*
Pains (MG), Gruta Paiol de Milho, 13.x.2003: *P. falcifer, P. spinifer*
Pains (MG), Gruta Paranoá, 15.i.2008: ***P. ramburii***, *P. serrifer*
Pains (MG), Gruta Retiro, 27.xi.1999: ***P. ramburii***
Pains (MG), Gruta Ronco, 28.xi.1999: *P. falcifer*
Pains (MG), Gruta do Sobradinho, 5.v.2001: *P. serrifer*
Paracatu (MG), Gruta da Fazenda Tamanduá II, 14.x.2010: ***P. ramburii***
Paracatu (MG), Lapa do Brocotó, 16.ix.2010: ***P. ramburii***
Paracatu (MG), Lapa de Santo Antônio, 13.vii.2010: ***P. ramburii***
Presidente Olegário (MG), Lapa Vereda da Palha, 13.x.2010: *P. clunjunctus*
Santa Maria do Suaçuí (MG), Gruta do Rio Suaçuí, 19.vii.2002: ***P. ramburii, P. yucatan***
Sete Lagoas (MG), Gruta Rei do Mato, 3.+4.xi.2011: *P. falcifer,* ***P. ramburii***
Teófilo Otoni (MG), Lapa da Vaca Parida, 26.i.2005: ***Psoc. lachlani***, ***P. yucatan***
Vazante (MG), Gruta da Escarpa, xi.2008: *P. falcifer*
Vazante (MG), Lapa da Delza, 12.vii.2010: ***P. ramburii***
Vazante (MG), Lapa das Urtigas, 16.ix.2010: *P. falcifer*

Mato Grosso (MT)
Apiacás (MT), Casa de pedra do Navalha, Parque Nacional do Juruena, 9.ix.2011: *P. angustipennis*
Chapada dos Guimarães (MT), Gruta Kiogo Brado, 27.x.2006: *P. clunioventralis, P. spinifer*
Paranaíta (MT), Gruta da Pedra Preta, 19.ix.2011: *P. didymus*

Piauí (PI)
Coronel José Dias (PI), Coroa de Frade, ix.2008: *P. thaidis*
Coronel José Dias (PI), Toca do Garrincho, 11.ix.2008: ***Psoc. pilipennis***
Coronel José Dias (PI), Toca do Inferno, 12.ix.2008: *P. punctulatus, P. spinifer*
Coronel José Dias (PI), Toca das Moendas, 10.ix.2008: *P. spinifer*

Rio Grande do Norte (RN)
Baraúna (RN), Caverna Britador, 11.vi.2010, leg. D. M. Bento: *P. clunjunctus*
Baraúna (RN), Caverna Cipós, 11.vi.2010, leg. D. M. Bento: *P. clunjunctus*
Baraúna (RN), Caverna Escada, 27.i.2010, leg. D. M. Bento: *P. clunjunctus*
Baraúna (RN), Caverna Esquecida, 17.vi.2010, leg. D. M. Bento: *P. clunjunctus*
Felipe Guerra (RN), Caverna Arapuá, 3.viii.2010, leg. D. M. Bento: *P. subtilis*
Felipe Guerra (RN), Caverna Beira-Rio, 19.iii.2010, leg. D. M. Bento: *P. subtilis*
Felipe Guerra (RN), Caverna Rumana, 19.i.2010, 5.viii.2010, leg. D. M. Bento: *P. clunjunctus, P. subtilis*
Felipe Guerra (RN), Caverna Trapiá, 6.i.2010, 4.viii.2010, leg. D. M. Bento: ***P. yucatan***
Felipe Guerra (RN), Gruta Carrapateira, 24.iv.2007: *P. clunjunctus*
Felipe Guerra (RN), Gruta da Catedral, 14.ix.2008: *P. clunjunctus*
Felipe Guerra (RN), Gruta Roncador, 1.vi.2006: ***Psoc. pilipennis***
Felipe Guerra (RN), Lapa do Engano, 5.viii.2010, leg. D. M. Bento: *P. clunjunctus*
Governador Dix-Sept Rosado (RN), Caverna Capoeira do João Carlos, 3.vi.2010, leg. D. M. Bento: *P. subtilis*
Governador Dix-Sept Rosado (RN), Gruta do Lagedo Grande, 21.vii.2010, leg. D. M. Bento: *P. clunjunctus, P. spinifer. P. subtilis*
Governador Dix-Sept Rosado (RN), Gruta do Marimbondo Caboclo, 20.vii.2010, leg. D. M. Bento: *P. subtilis*
Jandaíra (RN), Gruta Aroeira, 11.i.2006: ***Psoc. pilipennis***
Mossoró (RN), Caverna Trinta, 10.vi.2010, leg. D. M. Bento: *P. clunjunctus*

Rio Grande do Sul (RS)
Torres (RS), Furna da Lagoa de Itapeva, 20.v.2008: ***P. ramburii***

São Paulo (SP)
Altinópolis (SP), Gruta Edgar 1, 28.ii.2006: *P. spinifer*
Altinópolis (SP), Gruta do Itambé, 27.ii.2006: ***Psoc. lachlani***, ***P. ramburii***
Altinópolis (SP), Gruta Olho de Cabra, 2.iii.2006: ***P. ramburii****, P. spinifer*
Altinópolis (SP), Gruta do Paraná, 1.iii.2006: ***P. ramburii****, P. spinifer*
Ilha Bela (SP), Gruta da Serraria, 22.iv.2006: ***P. yucatan***
Itirapina (SP), Gruta da Toca, 22.x.2004: ***P. ramburii***

Tocantins (TO)
Arraias (TO), cave Ponto 008, 4.-6.x.2010, leg F. Pellegatti *et al.*: *Neotrogla aurora*
Arraias (TO), cave Ponto 014, 4.-6.x.2010, leg F. Pellegatti *et al.*: *Neotrogla aurora*
Aurora do Tocantins (TO), Gruta Asa Branca 1, 7.i.2009, leg. R. A. Zampaulo: *Neotrogla aurora*
Aurora do Tocantins (TO), Gruta Biritite, 5.i.2009, leg. R. A. Zampaulo: *Neotrogla aurora*
Aurora do Tocantins (TO), Gruta Couve-Flor, 7.i.2009, leg. R. A. Zampaulo: *Neotrogla aurora*
Aurora do Tocantins (TO), Gruta das Rãs, 8.i.2009, leg. R. A. Zampaulo: *P. clunjunctus*
Dianópolis (TO), Gruta Imperial, iii.2013: *Neotrogla aurora*