

Three new species of *Psyllipsocus* (Psocodea: 'Psocoptera': Psyllipsocidae) from Brazilian caves with description of a novel structure interpreted as a male accessory genital organ

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Three new species of *Psyllipsocus* (Psocodea: 'Psocoptera': Psyllipsocidae) from Brazilian caves with description of a novel structure interpreted as a male accessory genital organ. - The following closely related new species are described and illustrated: *Psyllipsocus chunjunctus* Lienhard n. spec., *P. serrifer* Lienhard n. spec., *P. similis* Lienhard n. spec. Within the genus they form a monophyletic species group characterized by the presence of an elaborate sclerotized clunial bridge medio-ventrally on the male abdominal apex. Based on morphological observations this novel structure is interpreted as an accessory genital organ, which is probably directly involved in copulation, partly replacing the primary male coupling organ (phallosome), which is strongly reduced in these species. The females of this species group are characterized by the presence of a cap-shaped spermapore sclerite and a sclerotized spermathecal blade. In the polyandrous species *P. serrifer* the spermathecal blade is saw-shaped and possibly serves as a "tin-opener" for thick-walled spermatophores. The function of this novel structure is presumably similar to that of the signum in the bursa copulatrix of some Lepidoptera.

Keywords: Brazil - cave fauna - new species - male genitalia - spermathecal signum.

INTRODUCTION

Psyllipsocus Selys-Longchamps is a very heterogeneous and probably ancient genus (Mockford, 2011) belonging to the suborder Trogiomorpha, infraorder Psyllipsocetae (Yoshizawa *et al.*, 2006). It comprises a total of 44 species, most of them described from North and Middle America and from the Aethiopian and Oriental regions (see Lienhard & Smithers, 2002 and Lienhard, 2011, 2012). 27 species are known from the New World (Lienhard & Smithers, 2002; Mockford, 2011, 2012) but only four species have been recorded from South America: *P. delamarei* Badonnel from Argentina (Badonnel, 1962), *P. variabilis* Badonnel from Colombia (Badonnel, 1986), *P. dubius* Badonnel from Venezuela (Badonnel, 1987) and *P. yucatan* Gurney from Brazil (García Aldrete & Mockford, 2009; Mockford, 2011; Lienhard *et al.*,

2012). Most of these species live on vegetation, especially on bark of trees, in soil litter or on lichen-covered rock outcrops; only a few species have been occasionally or exclusively recorded from caves (see Mockford, 2011; Badonnel, 1977a, b, 1987). A key to the 24 species known from North and Middle America was published by Mockford (2011).

This is the second contribution on *Psyllipsocus* resulting from a study on cave psocids from Brazil directed by the junior author. The first contribution (Lienhard *et al.*, 2012) reported *P. yucatan* from several Brazilian caves and treated the still enigmatic phenomenon of microcrystal deposits on the wing membranes of some living individuals of this species. Two contributions on the related family Prionoglarididae (Trogiomorpha: Prionoglaridetae) have also been published recently (Lienhard *et al.*, 2010; Lienhard & Ferreira, 2013).

At present we are aware of 17 *Psyllipsocus* species from Brazilian caves, most of them undescribed. Herein we describe three closely related species which form a monophyletic group characterized by several autapomorphies of male and female genitalia, in particular the presence of an elaborate sclerotized clunial bridge medioventrally on the male abdominal apex. This structure was incidentally discovered during routine dissection and slide-mounting of Brazilian *Psyllipsocus* specimens, soft tiny creatures with a body length of about 1.5 mm (see Fig. 1A). In some males, after separation of the hypandrium, it was not possible to flatten the dome-shaped abdominal apex by opening it ventrally between the paraprocts, for spreading the telson and the clunium (i. e. fused and well-sclerotized last two or three pretelsonic terga; see Mockford, 1993 and Lienhard, 1998). When using the standard method of dissection (see Lienhard, 1998: p. 62) the medioventral membrane at the base of the paraprocts can usually be cut by minute needles without any problem. In these males this zone resisted the usual mechanical treatment and finally showed to be differentiated as a sclerotized ventral connection between the hind corners of the clunium. Based on morphological observations this novel structure is here interpreted as an accessory genital organ, which is probably directly involved in copulation, partly replacing the primary male coupling organ (phallosome), which is strongly reduced in these species (see General Discussion).

MATERIAL AND METHODS

The material examined was collected by RLF (unless other collector mentioned) by hand-collecting in 32 caves situated in 20 municipalities and 5 states (see Fig. 1). In general only adults were studied. Nymphs are only mentioned if they were collected together with adults and therefore could be assigned to the same species as the latter. Dissection and slide-mounting followed the methods described by Lienhard (1998). 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).

The pilosity of wing veins is usually heavily damaged in the material studied. For the drawings it was reconstructed on the basis of the insertion points of the hairs, which are always visible in slide-mounted wings, and of the few hairs on each wing

which were not lost. The length of these hairs was considered as representative for the pilosity of the entire wing, based on the observation that in *Psyllipsocus* the length of wing ciliation is uniform over the whole wing.

Abbreviations used in the descriptions: BL = body length (in alcohol); F = hind-femur (length); FW = forewing (length); HW = hindwing (length); IO/D = shortest distance between compound eyes divided by longitudinal diameter of compound eye in dorsal view of head; P2 = second article of maxillary palp; P4 = fourth (terminal) article of maxillary palp; T = hindtibia (length); t1, t2, t3 = tarsomeres of hindtarsus (length, measured from condyle to condyle); v1, v2, v3 = first (ventral), second (dorsal) and third (external) ovipositor valvula respectively. Abbreviations of wing veins and cells are used according to Yoshizawa (2005).

Abbreviations for Brazilian states: BA = Bahia, GO = Goiás, MG = Minas Gerais, RN = Rio Grande do Norte, TO = Tocantins.

TAXONOMY

THE *CLUNJUNCTUS* SPECIES GROUP OF *PSYLLIPSOCUS*

DIAGNOSIS: Autapomorphies of male and female genitalia: Phallosome strongly reduced, lacking basal struts; endophallus closely applied to the inner (dorsal) surface of the hypandrium (Figs 2GH, 5A, 9CD), anteriorly with a pair of weakly sclerotized oval plates and posteriorly with some small lateral sclerotizations and a dorso-median pair of lobules bearing 2-3 placoid sensilla (their minute central sense pegs not always distinct). Male abdominal apex with an elaborate clunial bridge, i. e. hind corners of clunium ventrally prolonged and medially connected to each other by a sclerotized but laterally and medially somewhat flexible structure bearing in the middle a ventrally open papillate cavity facing the dorsal side of the distal lobe of the hypandrium (Figs 3A, 10). Opening of the spermathecal duct (spermapore) situated dorsally near the tip of a thick-walled conical or dome-shaped sclerotized cap surrounding the distal portion of the duct (Fig. 2C); in resting position this spermapore sclerite situated in a zone of multiply folded membranes (Fig. 6G). Spermathecal sac with a longitudinal sclerotized saw- or file-like blade on the inner side of its wall (Fig. 7A-G); base of this sclerite situated near opening of spermathecal duct (Fig. 7IJ).

Other characters: Both sexes macropterous (Fig. 4A) or brachypterous (Fig. 1A, 2AB); pterostigma of forewing almost triangular (i. e. crossvein between R1 and Rs situated at base of pterostigma or close to it); distal closed cell of forewing at least twice as long as wide; vein CuA1 only weakly curved; wing membranes hyaline. P2 with a stout sensillum in basal half (Fig. 4F); P4 slender, slightly broadening towards apex and bearing a shallow apical prominence (Fig. 4F); lacinial tip as in Fig. 4E; pedicel lacking microspades organ (sensu Mockford, 1993, 2011); antennal flagellomeres long and cylindrical (Fig. 4H). Pretarsal claws simple, symmetrical, with a small preapical denticle (Fig. 4G); hind legs with well-developed coxal organ (sensu Mockford, 2011), less distinct in brachypterous individuals. Epiproct simple. Paraproct with a basally not articulated long anal spine and a setal organ (sensu Mockford, 2011) consisting of a short fine seta and a longer, thicker seta (Figs 3A, 6BG, 8E); paraproctal sensorium in macropterous individuals usually with 6 fine trichobothria on basal florets and one stout seta (Fig. 6B), in brachypterous individuals number of tricho-

bothria often reduced. Female with three pairs of ovipositor valvulae, v1 and v2 weakly developed, membranous, v3 broad oval, slightly sclerotized and uniformly setose (Fig. 2F); subgenital plate simple, apically with a small and often indistinct median cleft (Fig. 6C). Hind corners of clunium in female ventrally not prolonged, connected to each other by a membranous zone (Fig. 8E). Apical lobe of hypandrium broadly rounded, with four dorsal placoid sensilla, each bearing a minute central sense peg (Figs 2GH, 5A, 9CD).

SPECIES OF THE *CLUNJUNCTUS* GROUP: *P. clunjunctus* Lienhard n. spec., *P. serrifer* Lienhard n. spec., *P. similis* Lienhard n. spec.

DISCUSSION: See General Discussion, below.

DESCRIPTIONS OF THE NEW SPECIES

Psyllipsocus clunjunctus Lienhard n. spec.

Figs 1A, 2, 3, 7G

HOLOTYPE: ISLA; ♂ (slide-mounted); BRAZIL (GO), Damianópolis, cave Lapa do Ribeirão dos Porcos, 27.vi.2002, leg. R. L. Ferreira.

PARATYPES: ISLA and MHNG, slide-mounted and/or in alcohol; BRAZIL, leg. R. L. Ferreira (unless other collector mentioned), from the following municipalities. 2♂, 1♀, São Desidério (BA), cave Gruta do Catitu, 24.vii.2006. 1♂, São Desidério (BA), cave Gruta do Sumidouro do João Baio, 29.vii.2006. – 1♀, Várzea Nova (BA), cave Gruta Jurema, 20.vii.2008. – 3♂, 2♀, 1 nymph, Damianópolis (GO), cave Lapa do Ribeirão dos Porcos, 29.vii.2001. 3♀ (one of them allotype), 1 nymph, Damianópolis (GO), cave Lapa do Ribeirão dos Porcos, 27.vi.2002. – 1♂, 1♀, Presidente Olegário (MG), cave Lapa Vereda da Palha, 13.x.2010. – 5♂, 4♀, 7 nymphs, Baraúna (RN), cave Caverna Britador, 11.vi.2010, leg. D. M. Bento. 2♀, 5 nymphs, Baraúna (RN), cave Caverna Cipós, 11.vi.2010, leg. D. M. Bento. 3♂, 1♀, 3 nymphs, Baraúna (RN), cave Caverna Escada, 27.i.2010, leg. D. M. Bento. 1♀, 1 nymph, Baraúna (RN), cave Caverna Esquecida, 17.vi.2010, leg. D. M. Bento. – 1♀, Felipe Guerra (RN), cave Lapa do Engano, 5.viii.2010, leg. D. M. Bento. 2♂, Felipe Guerra (RN), cave Caverna Rumana, 19.i.2010. 1♂, Felipe Guerra (RN), cave Caverna Rumana, 5.viii.2010, leg. D. M. Bento. 1♂, 1♀, Felipe Guerra (RN), cave Gruta da Catedral, 14.ix.2008. 1♀, Felipe Guerra (RN), cave Gruta Carrapateira, 24.iv.2007. – 4♂, 3 nymphs, Governador Dix-Sept Rosado (RN), cave Gruta do Lagedo Grande, 21.vii.2010, leg. D. M. Bento. – 3♀, Mossoró (RN), cave Caverna Trinta, 10.vi.2010, leg. D. M. Bento. – 1♂, 2♀, Aurora do Tocantins (TO), cave Gruta das Rãs, 8.i.2009, leg. R. A. Zampaulo.

DESCRIPTION: See diagnosis of the species group, with the following complements. General colouration whitish to light or medium brown. Head often with a characteristic pattern of brown hypodermal pigment (Fig. 2D), compound eyes dark brown to black. Tibiae lacking transversal bands. Abdomen whitish or with some brown hypodermal pigment, terminalia brown.

Both sexes brachypterous (Fig. 1A), in female (Fig. 2B) forewings at most reaching abdominal apex, in male (Fig. 2A) often somewhat projecting over tip of abdomen. Forewing venation with irregularities due to brachyptery, especially in the region of pterostigma and vein Rs (Fig. 2AB), the latter usually simple. Hindwings strongly reduced, often almost veinless (Fig. 2B). Compound eyes larger in weakly brachypterous specimens (IO/D about 2.6) than in strongly brachypterous ones (IO/D up to 3.9). Three ocelli present even in strongly brachypterous individuals. Antenna very long (more than twice body length) but usually damaged in preserved material; maximal number of articles observed: 29 (in a distally damaged antenna).

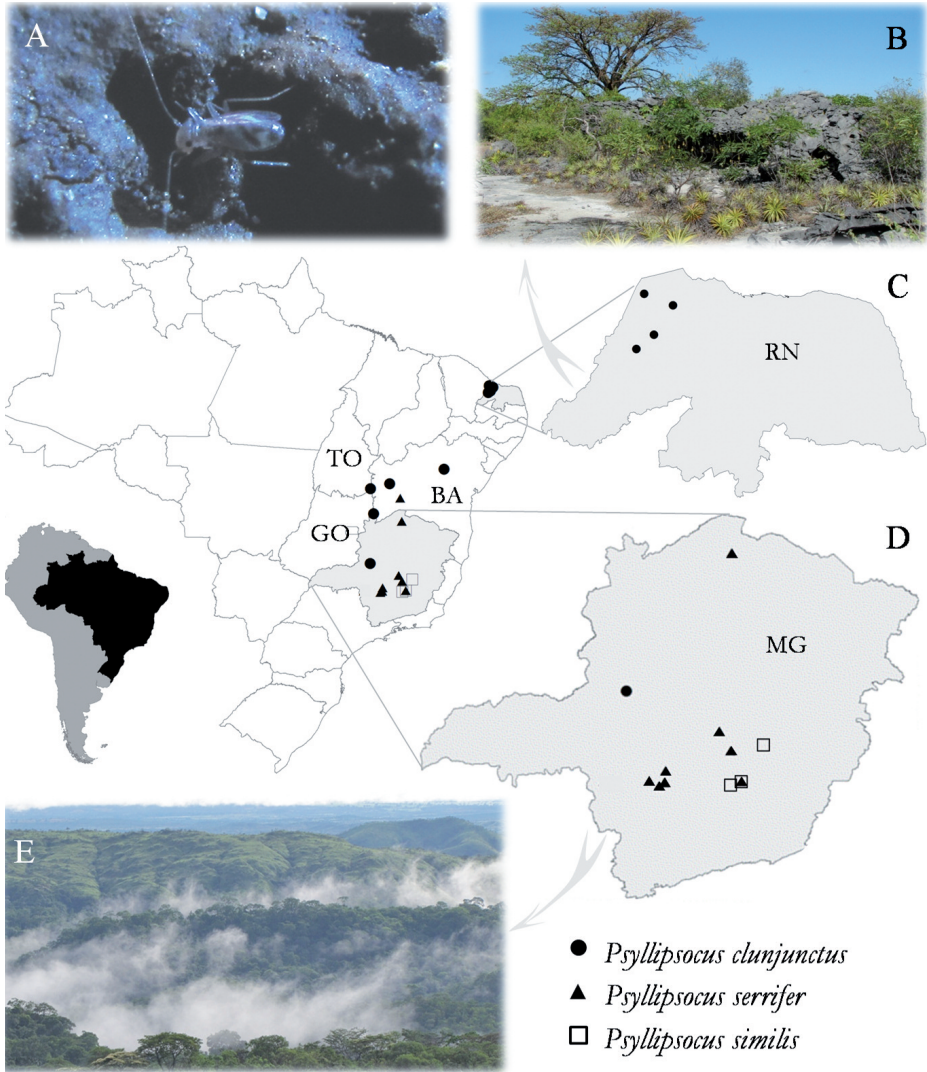


FIG. 1

Map of Brazil showing states and municipalities where specimens of the *Psyllipsocus clunijunctus* species group were collected. (A) *Psyllipsocus clunijunctus* Lienhard n. spec., habitus of brachypterous individual on guano (body length about 1.5 mm). (B) Caatinga formation (semi-arid) which exists in the areas near the caves in RN. (C) Collecting localities (municipalities) in RN. (D) Collecting localities (municipalities) in MG. (E) Cerrado formation (Brazilian Savanna) which exists in the areas near the caves in MG. – States: BA = Bahia, GO = Goiás, MG = Minas Gerais, RN = Rio Grande do Norte, TO = Tocantins.

Broad apical lobe of hypandrium (Fig. 2GH) with a distally rounded sclerotized median area, bearing 4-6 setae near its middle axis; pilosity of basal part of hypandrium as shown in Fig. 5A for *P. serrifer*; arrangement of the four dorsal placoid sensilla as shown in Fig. 2GH. Shape of latero-distal phallosomal sclerotizations and

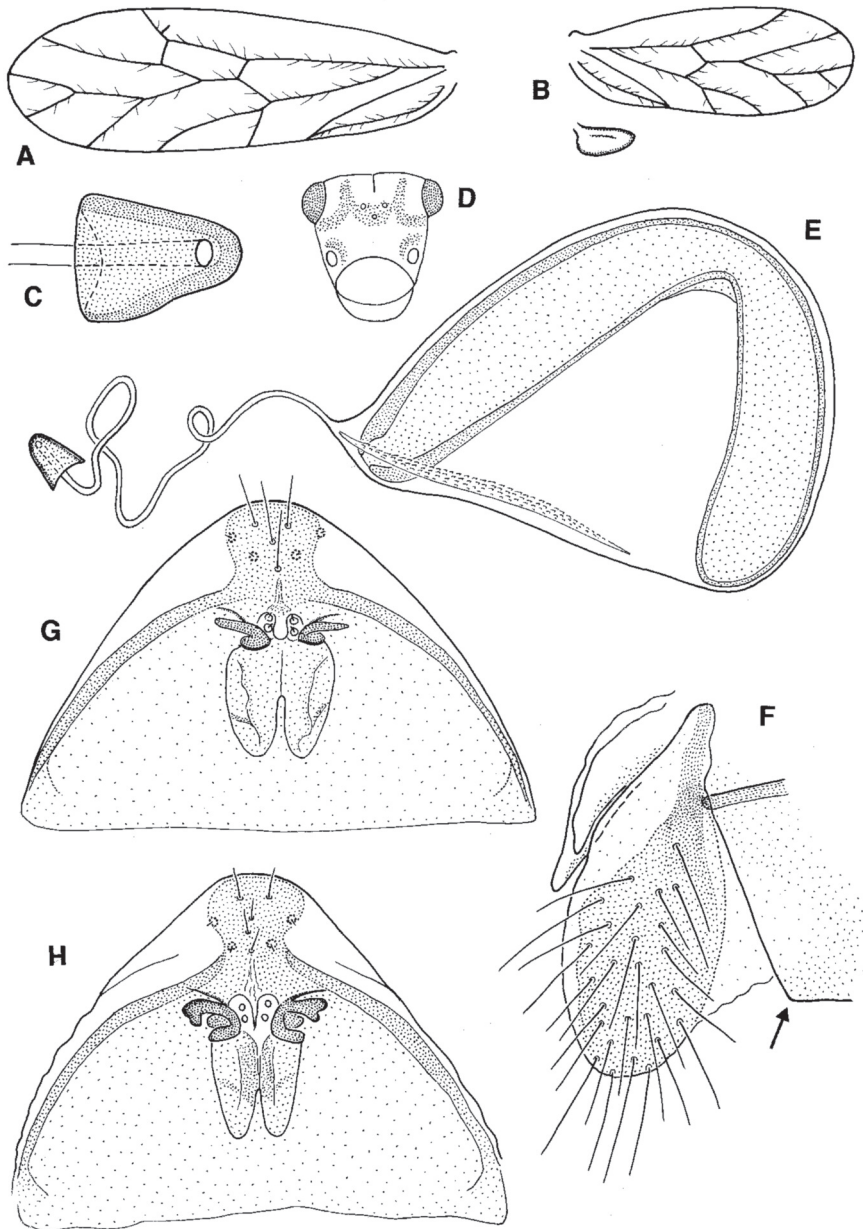


FIG. 2

Psyllipsocus clunjectus Lienhard n. spec. (A) Forewing of brachypterous male. (B) Forewing and hindwing of brachypterous female (same magnification as A). (C) Spermapore sclerite. (D) Head pattern of female from Baraúna (RN). (E) Spermatheca containing one spermatophore. (F) Hind corner of clunium (arrow) and left ovipositor valvulae. (G) Hypandrium and phallosome, ventral view (phallosome observed through ventral wall of hypandrium, pilosity of basal part of the latter not shown), male from São Desidério (BA). (H) Ditto, male from Damianópolis (GO).

of oval medio-distal phallosomal lobules somewhat variable, probably partly depending on position after slide-mounting; each lobule with two placoid sensilla (Fig. 2GH). Clunial bridge relatively simple, as shown in Fig. 3AB, central part seemingly articulated to the lateral parts by a partly membranous zone near the most narrow parts of the bridge (Fig. 3B). Central cavity laterally delimited by a rounded papillate border; these borders representing the ventralmost parts of the bridge. Clunial bridge on each side with a dorso-medially directed spur-like posterior prominence.

Spermopore sclerite of slightly variable shape and length (Figs 2C, 3C). Spermathecal blade slender, file-like, weakly sclerotized (Figs 2E, 7G). Spermathecal duct more than twice as long as spermathecal blade (Fig. 2E), occasionally with a weak thickening near spermathecal sac. Spermatophore long and slender, about 7-8 times longer than wide, sausage-shaped (Fig. 2E; in the spermatheca of one female three such spermatophores could be observed; this indicates that the species is polyandrous; see General Discussion, below).

MEASUREMENTS: Both sexes relatively small, body length usually 1.3-1.6 mm, exceptionally up to 1.8 mm in male and 2.0 mm in female. *Male holotype* (brachypterous): BL = 1.5 mm; FW = 1114 μ m; HW = 170 μ m; F = 386 μ m; T = 596 μ m; t1 = 320 μ m; t2 = 52 μ m; t3 = 66 μ m; IO/D = 2.8. – *Female allotype* (brachypterous): BL = 1.3 mm; FW = 733 μ m; HW = 166 μ m; F = 397 μ m; T = 607 μ m; t1 = 331 μ m; t2 = 50 μ m; t3 = 65 μ m; IO/D = 3.0.

ETYMOLOGY: The specific epithet refers to the clunial bridge joining the hind corners of the clunium to each other (Latin: *junctus*, -a, -um; joined).

DISTRIBUTION AND HABITAT: At present *P. clunjunctus* is known from 16 Brazilian caves situated in 9 municipalities (see Fig. 1). These caves are located in three limestone formations representing different ages and structures. The Bambuí group (upper Proterozoic), located in Minas Gerais, Goiás, Tocantins and Bahia states, comprises the biggest limestone group in Brazil, and contains a considerable proportion of the known caves in the country. The Una group (also upper Proterozoic) occurs in central Bahia state, and is spatially contiguous to the eastern “branch” of the Bambuí group; it is therefore plausible to assume subterranean continuities between these formations. The Apodi group, located in Rio Grande do Norte state, comprises younger limestones, dating from the Cretaceous. This formation is isolated from the previously cited groups.

The geographic distribution of *P. clunjunctus* is somewhat surprising, especially when considering its brachypterous condition, which limits dispersion. The contiguity between the Bambuí and Una limestone formations would explain most of the present distribution, except for the “unexpected” findings in Rio Grande do Norte state. However, many potential habitats between northern Bahia and Rio Grande do Norte (as granitic outcrops, full of fissures and spaces) have not been sampled, and the “distribution gap” observed is probably a sampling artefact.

The physical attributes of the caves inhabited by the different populations of *P. clunjunctus* are very heterogeneous and cave morphology or size are apparently not relevant factors determining the presence of these insects. On the other hand, the presence of guano, especially old piles from haematophagous bats, seems to be

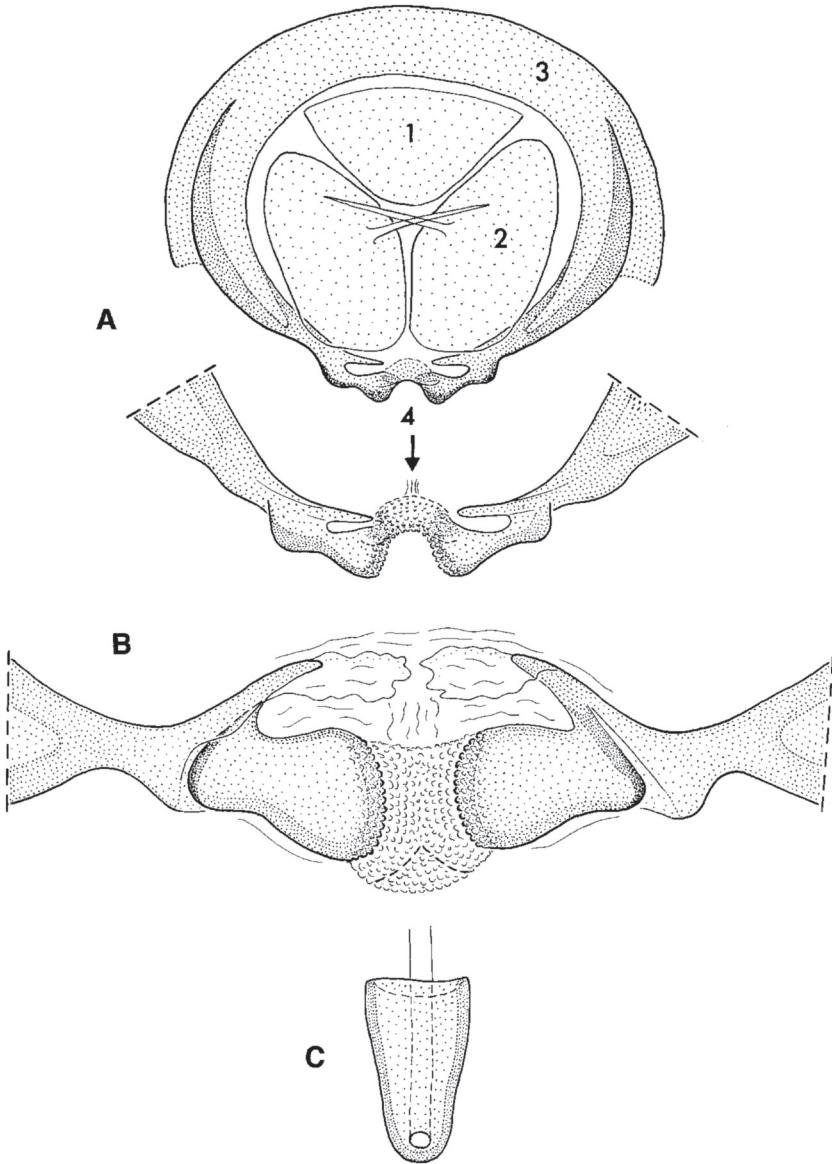


FIG. 3

Psyllipsocus clunijunctus Lienhard n. spec. (A) Schematic representation of slightly squashed male abdominal apex, with detail of clunial bridge, posterior view (1, epiproct; 2, paraproct; 3, clunium; 4 clunial bridge). (B) Clunial bridge, ventral view, posterior part upwards directed in the figure. (C) Spermapore sclerite of female (same magnification as B).

necessary for the occurrence of this species inside a cave. According to Ferreira & Martins (1999) and Ferreira *et al.* (2007) Psyllipsocidae generally prefer old guano piles in Brazilian caves and can be very abundant on this substrate.

DISCUSSION: This relatively small brachypterous species can easily be distinguished from both other species by the presence of a rounded sclerotized area on the distal lobe of the hypandrium, bearing some hairs in the middle, and by the characteristic arrangement of the four dorsal placoid sensilla of the hypandrium. The female is characterized by its particularly long spermathecal duct and the very large sausage-shaped spermatophore. The simple clunial bridge and the file-like spermathecal blade are similar to the corresponding structures in *P. similis*. See also General Discussion, below.

***Psyllipsocus serrifer* Lienhard n. spec.**

Figs 4-6, 7A-E, 7H-J

HOLOTYPE: ISLA; ♂ (slide-mounted); BRAZIL (MG), Pains, cave Gruta Paranoá, 15.i.2008, leg. R. L. Ferreira.

PARATYPES: ISLA and MHNG, slide-mounted and/or in alcohol; BRAZIL, leg. R. L. Ferreira (unless other collector mentioned), from the following municipalities. 2♀, 1 nymph, São Félix do Coribe (BA), cave PEA 377 (=BA 039), 10.v.2011, leg. S. S. Salgado. – 1♀, Arcos (MG), cave Gruta Labirinto, 28.i.2006. 1♀, Arcos (MG), cave Gruta da Bocaininha, 3.xii.2008. – 1♂, Cordisburgo (MG), cave Gruta do Salitre, 22.iv.2011. – 1♀, Doloresópolis (MG), cave Gruta P43, 9.xi.2003. – 1♂, Itabirito (MG), cave Gruta MP1, 29.viii.2005. – 1♀, Januária/Itacarambi (MG), cave Gruta Janelão, 28.vii.2003. – 1♂, Lagoa da Prata (MG), cave Gruta Salão de Festas, 4.v.2003. – 1♀, Matozinhos (MG), cave Gruta Pequenas III, 31.vii.2002. – 1♀, Pains (MG), cave Buraco do Nando, 12.x.2003. 1♀ (allotype), 1 specimen lacking abdomen, Pains (MG), cave Gruta Brasical, 28.ix.2003. 1♀, Pains (MG), cave Gruta do Sobradinho, 5.v.2001.

DESCRIPTION: See diagnosis of the species group, with the following complements. General colouration light to medium brown, exceptionally darker brown. Head often with a characteristic but rather variable pattern of brown hypodermal pigment (Fig. 6A), compound eyes dark brown to black. Tibiae uniformly brown, lacking transversal bands. Abdomen yellowish and usually with some red-brown hypodermal pigment, terminalia brown.

Both sexes macropterous (Fig. 4AB); one slightly brachypterous male has been observed, with vein Rs simple in both forewings (Fig. 4C). Three ocelli present; compound eyes relatively large, about same size in both sexes (IO/D 1.3-1.8). Antenna very long but usually damaged in preserved material.

Hypandrium (Fig. 5A) uniformly setose except for the glabrous and medially membranous apical lobe; the latter only bearing a transversal row of four short marginal setae; arrangement of the four dorsal placoid sensilla as shown in Fig. 5A. Shape of small postero-lateral sclerotizations of phallosome somewhat variable, probably partly depending on position after slide-mounting; phallosomal lobules posteriorly prominent, almost circular, each with two placoid sensilla (Fig. 5A). Clunial bridge relatively complex (Fig. 5BC), central part posteriorly with a movable membranous curtain held by a pair of sclerotized postero-lateral styli and, towards the middle of the cavity, by a sclerotized clip-like structure; the latter appears to be movable in dorso-ventral and antero-posterior directions. Lateral borders of the central papillate cavity representing the ventralmost parts of the clunial bridge, the antero-dorsal bulbous structure may be tendon-like, for insertion of muscles (Fig. 5B).

Spermopore sclerite of slightly variable shape and length (Figs 6D-F). Spermathecal blade saw-like, well-sclerotized, with many prominent sharp denticles;

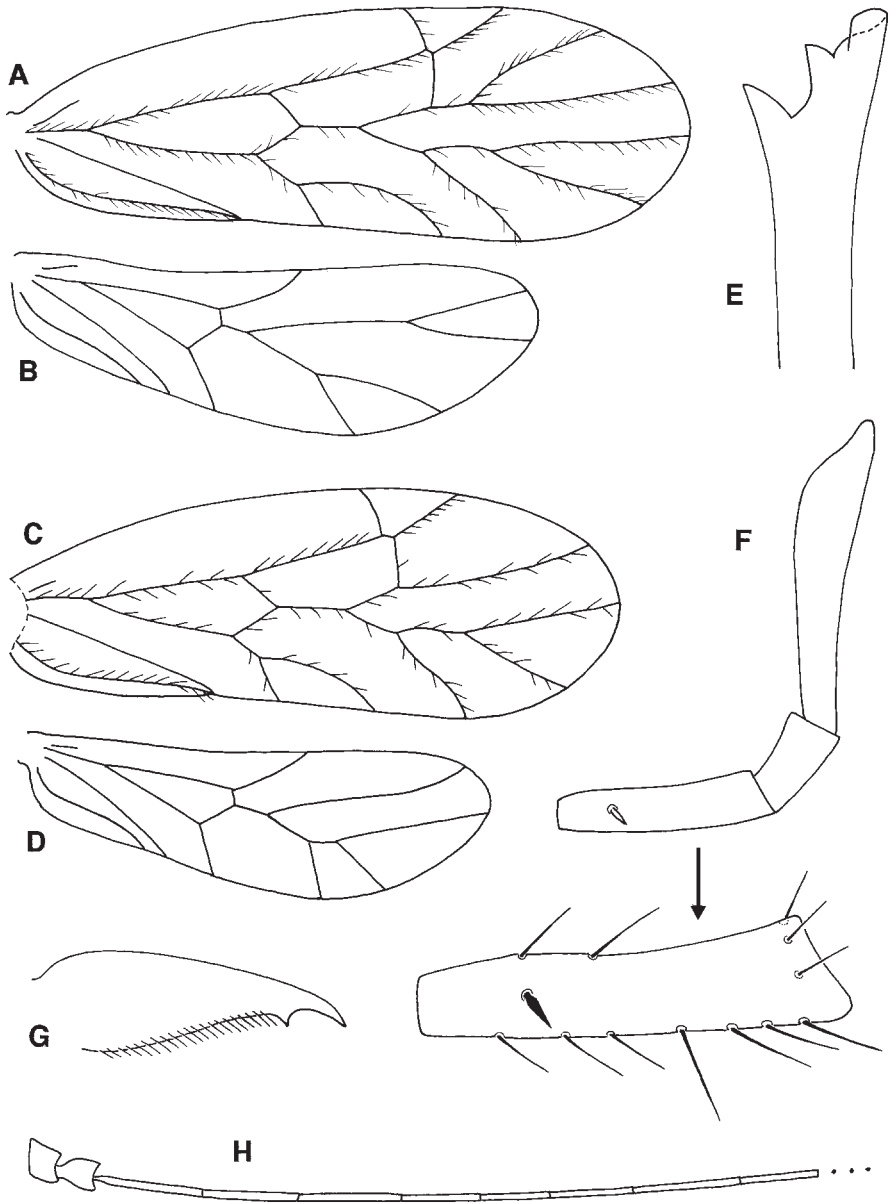


FIG. 4

Psyllipsocus serrifer Lienhard n. spec. A-B, E-H female; C-D male from Itabirito (MG). (A) Forewing. (B) Hindwing of the same specimen. (C) Forewing of slightly brachypterous male. (D) Hindwing of the same specimen. (E) Lacinal tip. (F) P2-P4 of maxillary palp, with detail of P2-chaetotaxy. (G) Pretarsal claw. (H) Scape, pedicel and the 8 basalmost antennal flagellomeres.

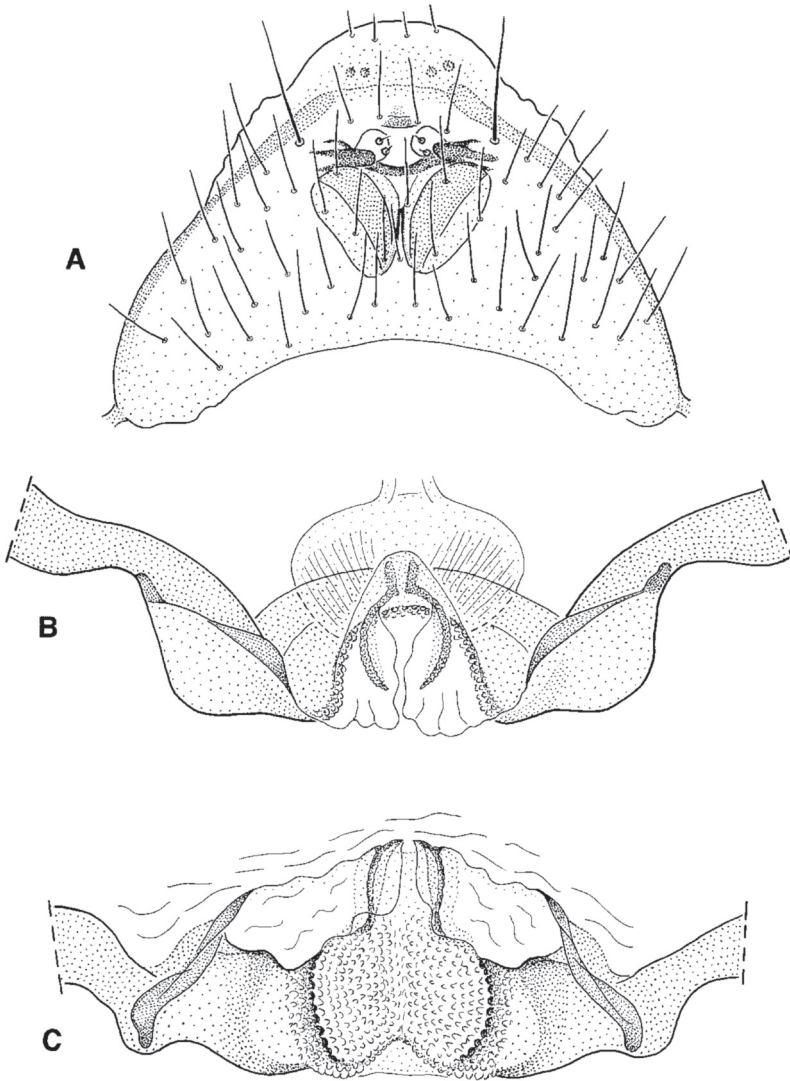


FIG. 5

Psyllipsocus serrifer Lienhard n. spec., male. (A) Hypandrium and phallosome, ventral view (phallosome observed through ventral wall of hypandrium). (B) Clunial bridge, posterior view. (C) Clunial bridge, ventral view, posterior part upwards directed in the figure (same magnification as B).

length and shape of sclerite and length of denticles rather variable [see Fig. 7A-E and Fig. 1: 7A-C correspond to the westernmost localities (Doresópolis and Pains), 7D corresponds to a locality situated towards central MG (Matozinhos) and 7E to the locality situated in northern MG (Gruta Janelão)]. In the females from northern MG

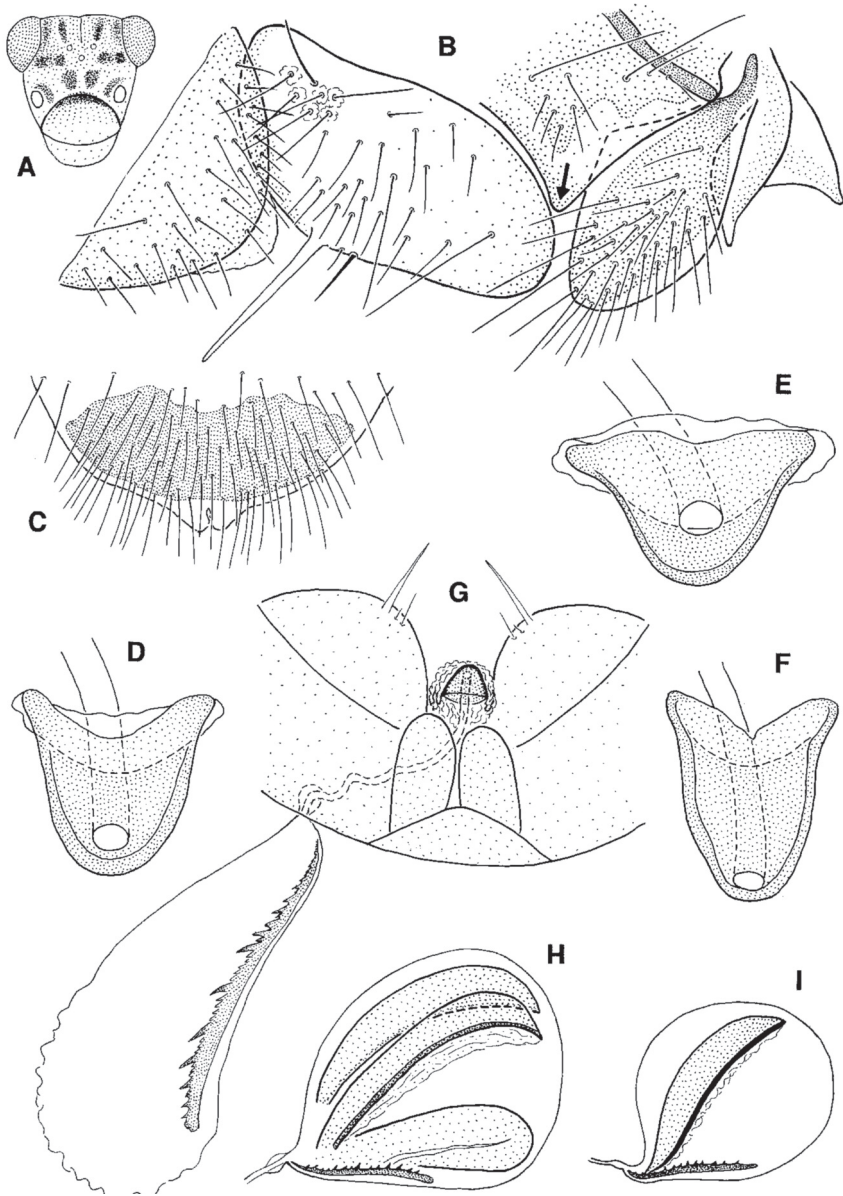


FIG. 6

Psyllipsocus serrifer Lienhard n. spec., female. (A) Head pattern. (B) Epiproct, right paraproct, right hind corner of clunium (arrow), right ovipositor valvulae. (C) Subgenital plate, ventral view. (D) Spermapore sclerite, female from Doresópolis (MG). (E) Ditto, female from Pains (MG), Brasical cave. (F) Ditto, female from Matozinhos (MG). (G) Schematic representation of spread abdominal apex of a virgin female, showing subgenital plate, the pair of v3, paraprocts, spermapore sclerite surrounded by multiply folded membrane and empty spermatheca. (H) Spermatheca with three spermatophores (see General Discussion). (I) Spermatheca with one spermatophore.

and from nearby BA (see Fig. 1) prominent sharp denticles of the saw shorter than in the other females (Fig. 7E). Spermathecal duct not longer than spermathecal blade (Figs 6G, 7J), near spermathecal sac surrounded by a thickening (Fig. 7I), the latter weakly developed in the females from northern MG and nearby BA. Spermatophore usually sickle-shaped (Figs 6HI, 7J; in the spermatheca of one female three spermatophores could be observed, see Fig. 6H; this indicates that the species is polyandrous; see General Discussion, below).

MEASUREMENTS: Both sexes of about same size, body length 2.0-2.7 mm. *Male holotype* (macropterous): BL = 2.0 mm; FW = 2850 µm; HW = 2170 µm; F = 564 µm; T = 1015 µm; t1 = 480 µm; t2 = 62 µm; t3 = 73 µm; IO/D = 1.5. – *Female allotype* (macropterous): BL = 2.5 mm; FW = 3040 µm; HW = 2360 µm; F = 606 µm; T = 1086 µm; hindtarsi broken; IO/D = 1.6.

ETYMOLOGY: The specific epithet refers to the saw-like spermathecal blade (Latin: *serra* – saw; suffix *-fer*, *-fera*, *-ferum* from *ferre* – to bear, carry).

DISTRIBUTION AND HABITAT: At present *P. serrifer* is known from 13 caves situated in 9 municipalities, mostly in southern and central Minas Gerais state, with one cave (Gruta Janelão) in northern Minas Gerais and one in nearby Bahia (see Fig. 1). Most of these caves are located in the southern part of the Bambuí limestone group; the two caves in northern Minas Gerais and Bahia states belong to the eastern branch of this formation. As with *P. clunijunctus*, the physical attributes of the caves inhabited by *P. serrifer* are very heterogeneous, but most of these caves are rich in old guano deposits.

DISCUSSION: This relatively large species is characterized by the presence of a saw-like spermathecal blade and by the complex clunial bridge, bearing a posterior membranous curtain which is laterally held by a pair of styli and medially by a clip-like sclerotized structure. The hypandrium is similar to that of *P. similis* except for the presence, in *P. serrifer*, of four marginal setae instead of two. The populations from northern MG and nearby BA slightly differ from the more southern populations of *P. serrifer* by two spermathecal characters (see description, above). A comparison of the characters of the clunial bridge between these populations was not possible because males are not yet known from the northern localities. See also General Discussion, below.

***Psyllipsocus similis* Lienhard n. spec.**

Figs 7F, 8-9

HOLOTYPE: ISLA; ♂ (slide-mounted); BRAZIL (MG), Itambé do Mato Dentro, cave Baixada dos Crioulos 2, 29.vii.2004, leg. R. L. Ferreira.

PARATYPES: ISLA and MHNG, slide-mounted and/or in alcohol; BRAZIL, leg. R. L. Ferreira, from the following municipalities. 1 ♀, Itabirito (MG), cave Gruta MP8, 8.ix.2005. – 3 ♂, 2 ♀ (one of them allotype), 2 specimens lacking abdomen, Itambé do Mato Dentro (MG), cave Baixada dos Crioulos 2, 29.vii.2004. – 1 ♂, Moeda (MG), cave SMS 19, 3.xii.2005.

DESCRIPTION: See diagnosis of the species group, with the following complements. General colouration yellowish to medium brown. Head often with some patches of brown hypodermal pigment, especially on frons, compound eyes dark brown to black. Tibiae uniformly brown, lacking transversal bands. Abdomen whitish to light brown, terminalia light brown.

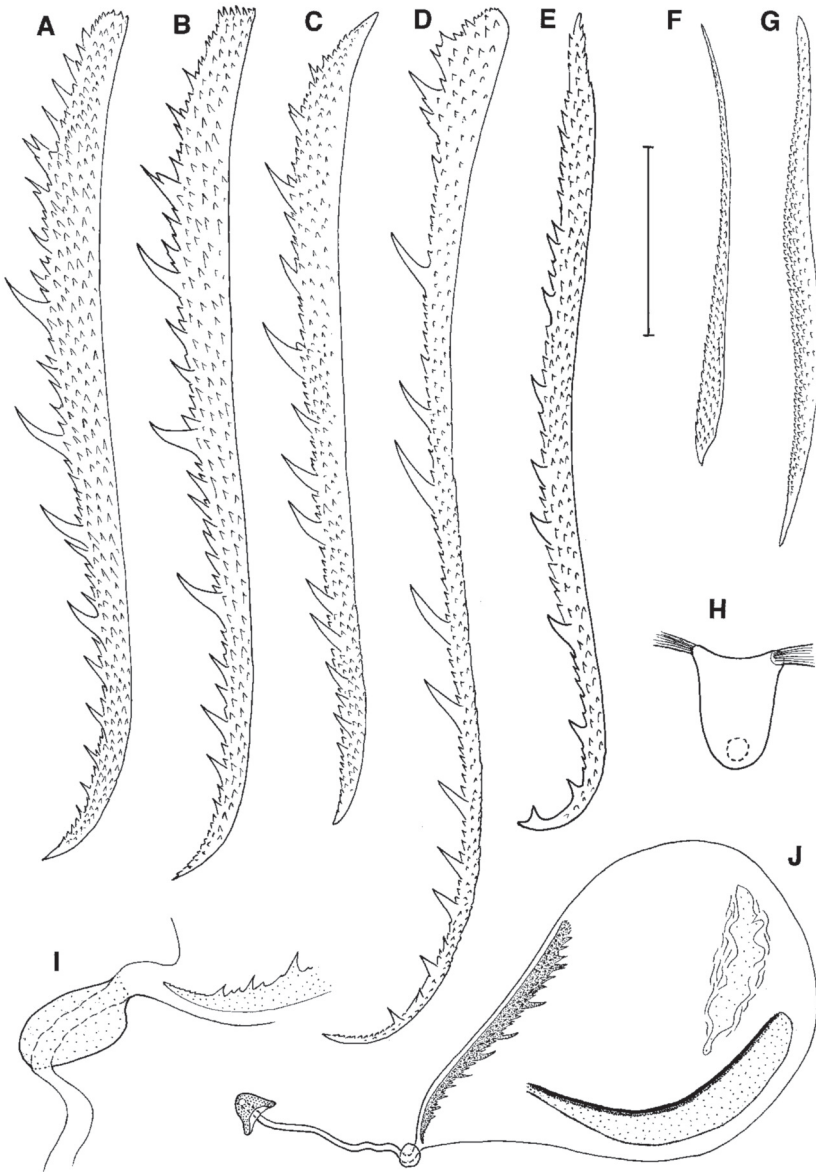


FIG. 7

Psyllipsocus spp., female. A-E: *Psyllipsocus serrifer* Lienhard n. spec. (A) Spermathecal blade, base downwards directed in the figure, female from Doresópolis (MG). (B) Ditto, female from Pains (MG), Brasical cave. (C) Ditto, female from Pains (MG), Sobradinho cave. (D) Ditto, female from Matozinhos (MG). (E) Ditto, female from Januária/Itacarambi (MG). (F) Ditto, *Psyllipsocus similis* Lienhard n. spec. (G) Ditto, *Psyllipsocus clunjectus* Lienhard n. spec. H-J: *Psyllipsocus serrifer* Lienhard n. spec. (H) Spermapore sclerite with insertion points of muscles. (I) Spermatheca, transition zone between duct and sac, with base of spermathecal blade. (J) Spermatheca containing one spermatophore. Scale bar = 0.1 mm (A-G).

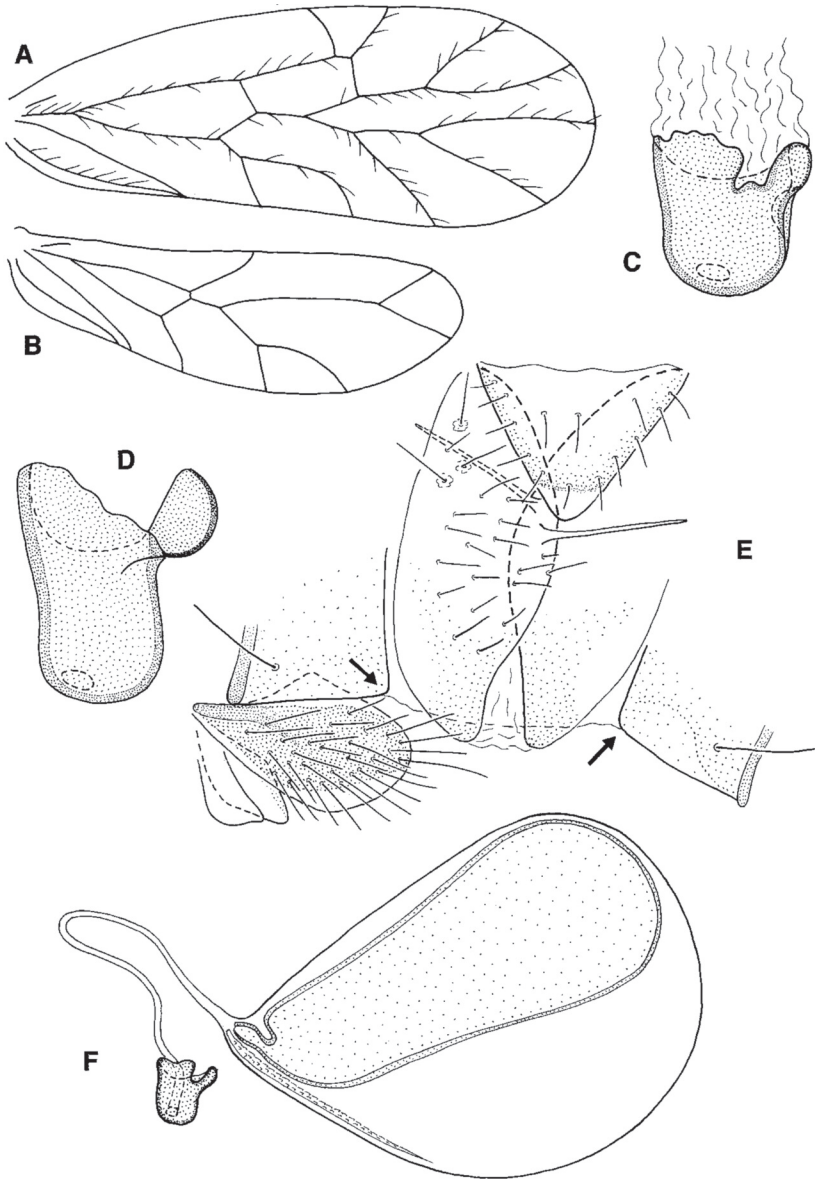


FIG. 8

Psyllipsocus similis Lienhard n. spec., female. (A) Forewing. (B) Hindwing of the same specimen. (C) Spermapore sclerite, female allotype from Itambé do Mato Dentro (MG). (D) Ditto, female from Itabirito (MG). (E) Epiproct, paraprocts (slightly overlapping due to slide-mounting), hind corners of clunium (arrows) and left ovipositor valvulae. (F) Spermatheca containing one spermatophore.

Both sexes macropterous (Fig. 8AB) or slightly brachypterous; in the forewing often some vein irregularities (e. g. Rs simple, M 2-branched). Three ocelli present; compound eyes of medium size in both sexes (IO/D 1.7-2.3). Antenna very long but usually damaged in preserved material.

Hypandrium (Fig. 9CD) uniformly setose except for the glabrous and medially membranous apical lobe (as shown in Fig. 5A for *P. serrifer*); the latter only bearing a pair of short marginal setae; arrangement of the four dorsal placoid sensilla as shown in Fig. 9CD. Shape of postero-lateral sclerotizations of phallosome and medio-distal semi-membranous microstructures somewhat variable, probably partly depending on position after slide-mounting; elongate oval phallosomal lobules not posteriorly prominent, situated between the lateral sclerotized bulges, each lobule with 2-3 placoid sensilla (Fig. 9CD). Clunial bridge relatively simple, somewhat flexible in middle and on each side at narrowest part (Fig. 9E), on each side with a dorso-medially directed spur-like posterior prominence; central cavity laterally delimited by a rounded papillate border, these borders representing the ventralmost parts of the bridge (Fig. 9AE).

Spermapore sclerite (Figs 8CDF, 9B) of slightly variable shape and length, its anterior border asymmetrically lobate. Spermathecal blade slender, file-like, weakly sclerotized (Figs 7F, 8F). Spermathecal duct about twice as long than spermathecal blade (Fig. 8F), no distinct thickening observed near spermathecal sac. Spermatophore broadly rounded, not much more than twice as long as wide, pear-shaped (Fig. 8F; in the spermatheca of one female two spermatophores could be observed; this indicates that the species is polyandrous; see General Discussion, below).

MEASUREMENTS: Both sexes of about same size, body length 1.7-2.2 mm. *Male holotype* (slightly brachypterous): BL = 1.7 mm; FW = 1600 μ m; HW = 1120 μ m; F = 480 μ m; T = 902 μ m; hindtarsi broken; IO/D = 2.0. – *Female allotype* (slightly brachypterous): BL = 1.7 mm; FW = 1640 μ m; HW = 1080 μ m; F = 475 μ m; T = 917 μ m; t1 = 392 μ m; t2 = 62 μ m; t3 = 75 μ m; IO/D = 2.1. – *Male paratype from Moeda* (macropterous): BL = 1.8 mm; FW = 1960 μ m; HW = 1500 μ m; F = 458 μ m; T = 846 μ m; t1 = 370 μ m; t2 = 69 μ m; t3 = 75 μ m; IO/D = 1.7.

ETYMOLOGY: The specific epithet (Latin: *similis*, *-is*, *-e*; similar) refers to the similarity of this species to the two other species of the *clunjunctus* species group, especially concerning the characters of the hypandrium (similar to *P. serrifer*) and of the clunial bridge and the spermathecal blade (similar to *P. clunjunctus*).

DISTRIBUTION AND HABITAT: At present *P. similis* is only known from three quartzite and iron ore caves situated in three municipalities in south-eastern Minas Gerais (see Fig. 1). Since there are macropterous specimens, which can easily disperse by flight, this narrow distribution may indicate some habitat specificity for this species. The three caves are located at higher altitudes (from 750 to 1550 m a.s.l.) than most of the caves in which the other species of the *clunjunctus* group usually occur. This may indicate some habitat preference (e. g. for low temperatures) that may explain the distribution and rarity of this species.

DISCUSSION: *P. similis* can be distinguished from both other species by the irregular anterior margin of the spermapore sclerite, by the broadly rounded pear-shaped

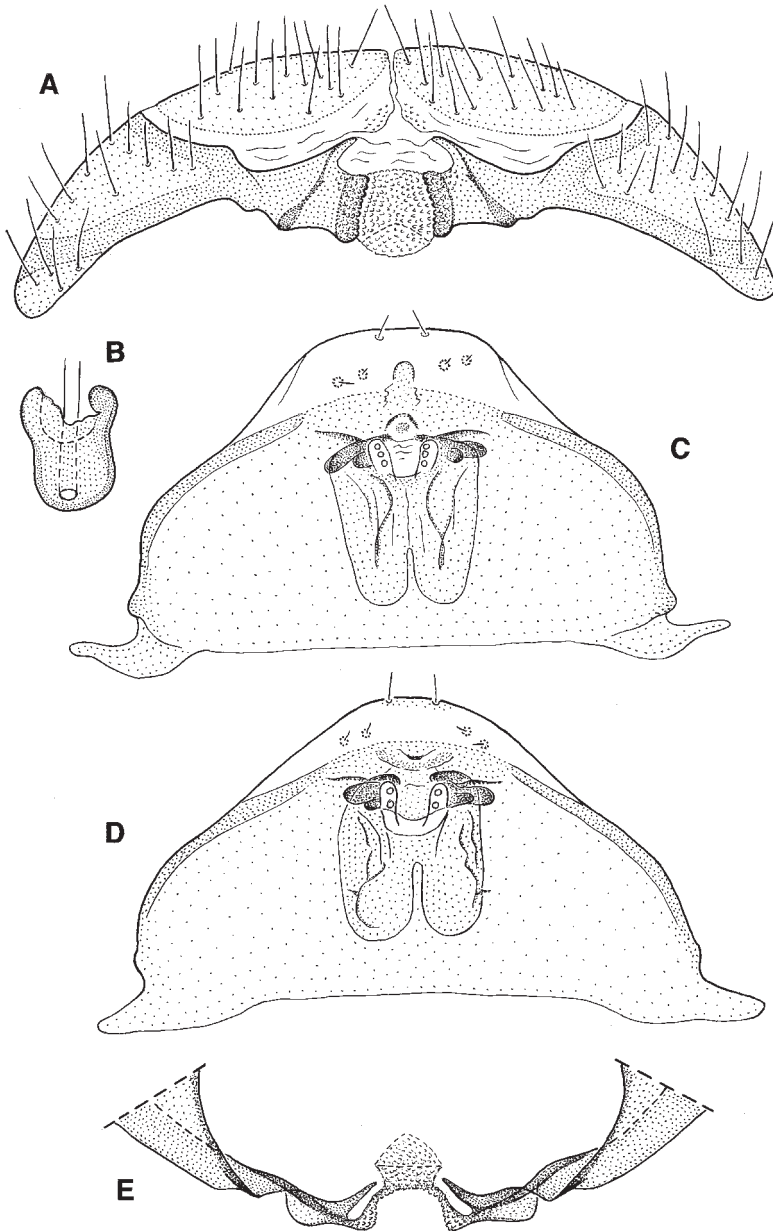


FIG. 9

Psyllipsocus similis Lienhard n. spec. (A) Male abdominal apex after separation of hypandrium, ventral view, slightly squashed, posterior part (i. e. paraprocts) upwards directed in the figure. (B) Spermaphore sclerite, female paratype from Itambé do Mato Dentro (MG). (C) Hypandrium and phallosome, ventral view (phallosome observed through ventral wall of hypandrium, pilosity of basal part of the latter not shown), male from Moeda (MG). (D) Ditto, male from Itambé do Mato Dentro (MG). (E) Clunial bridge, posterior view. Same magnification for A-E.

spermatophore and by the presence of only two short marginal setae on the broad membranous and otherwise glabrous distal lobe of the hypandrium. Its file-like spermathecal blade and its simple clunial bridge are similar to the corresponding characters of *P. clunjunctus*. In *P. similis* general size and relative length of the spermathecal duct are intermediate between the other two species of the *clunjunctus* group. See also General Discussion, below.

GENERAL DISCUSSION

FUNCTIONAL MORPHOLOGY

The members of the *Psyllipsocus clunjunctus* species group are characterized by four striking synapomorphies (for details see diagnosis of the species group): in the male by (1) the strong reduction of the phallosome with characteristic structure of the endophallus and (2) the presence of an elaborate sclerotized clunial bridge medio-ventrally on the abdominal apex; in the female by (3) the presence of a cap-shaped sclerite surrounding the distal end of the spermathecal duct, the opening of which (spermapore) is situated on the dorsal side of the cap near its tip, and by (4) the presence of a sclerotized file- or saw-like spermathecal blade. Based on our morphological observations we offer some hypotheses about the function of these structures.

The function of the weakly sclerotized file-like spermathecal blade is difficult to evaluate. This kind of blade, present in *P. clunjunctus* and *P. similis*, only bears small rounded or acute denticles (Fig. 7FG) and probably represents an initial stage in the evolution of the heavily sclerotized saw-like blade, present in *P. serrifer*, which bears a certain number of prominent sharp denticles (Fig. 7A-E). This saw is somewhat similar to a signum, the sclerotized sharp structure located in the bursa copulatrix of many Lepidoptera females, the main function of which is to break off the external wall of the spermatophore, thus allowing females access to the resources contained in it (Sanchez *et al.*, 2011). Up to 2-3 large and relatively thick-walled spermatophores have been observed in the spermatheca of each of the three species of the *clunjunctus* group (see species descriptions), which therefore can be considered as polyandrous. In *P. serrifer* the thick wall of the concave side of the sickle-shaped spermatophore always faces the signum-like saw (Figs 6HI, 7J). The presence, in the slide-mounted spermatheca shown in Fig. 6I, of an amorphous mass containing numerous spermatozoan filaments outside the spermatophore, along its concave side, may indicate that this spermatophore has been freshly slit longitudinally by contact with the saw-like sclerite serving as a "tin-opener". Probably the amorphous and partly filamentous mass in the spermatheca near the spermatophore shown in Fig. 7J also corresponds to some spermatophore content. In the third dissected female of *P. serrifer* where spermatophores could be observed the spermatheca contains two presumably slit superimposed sickle-shaped spermatophores (the filamentous content of one of them is still attached along its concave side) and one fresh spermatophore close to the saw-like sclerite on which the traces of presumed slitting are clearly visible (Fig. 6H). The rounded shape of this fresh spermatophore may indicate that the other spermatophores became sickle-shaped only after having been slit by the spermathecal signum. Such sickle-shaped spermatophores were never observed in *P. similis* and *P. clunjunctus*. In some polyandrous

Lepidoptera Sanchez *et al.* (2011) observed a positive correlation between the presence of a well-developed sclerotized signum and the thickness of the wall of the spermatophore as a result of sexually antagonistic coevolution. In these Lepidoptera males apparently evolved thick-walled spermatophores which delay further copulation of the females with other males, and as a reaction to this, females evolved sclerotized signa to break off these spermatophores more easily. Our morphological observations suggest that the spermathecal signum of *P. serrifer*, a novel structure in Psyllipsocidae, may have a similar function as the bursal signum in the Lepidoptera studied by Sanchez *et al.* (2011).

Our previous knowledge on copulation in trogiomorph psocids combined with the present morphological observations also suggests a quite plausible functional interpretation of the male clunial bridge and of the cap-like spermapore sclerite of the female which bears subapically, on its dorsal surface, the opening of the spermathecal duct. Klier (1956) described in detail the copulation of another trogiomorph psocid, *Trogium pulsatorium* (Linnaeus). In this species the spermapore is situated on the tip of a slightly sclerotized dome-shaped papilla (Klier, 1956: fig. 66, indicated by the abbreviation DRecMP). During copulation the forceps-like male parameres (a pair of lateral longitudinal struts of the phallosome) grasp the spermapore papilla for establishing the close contact between the opening of the male seminal duct and the opening of the spermathecal duct as a condition for successful transmission of the liquid spermatophore. Klier (1956: p. 264) makes an interesting statement (translated from German): "Because in this position [i. e. maximal intromission] the parameres cannot reach the spermapore papilla, which is situated in the vagina, we must assume that the spermapore papilla is actively erected by the female, maybe due to augmented pressure of body fluid".

In the species of the *P. clunijunctus* group the phallosome is strongly reduced and lacks the pair of longitudinal struts which are usually present in males of *Psyllipsocus* (see Mockford, 2011) and which are probably responsible for the function of the phallosome as an intromittent coupling organ. However, a novel structure has evolved ventrally on the male abdominal apex of these species, the clunial bridge (see diagnosis of the species group, above). We assume that the medially concave, rugose, vice-like part of the clunial bridge can hold the sclerotized spermapore cap of the female after intromission of the latter into the apicalmost part of the male abdomen (Fig. 10). In resting position the spermapore cap is surrounded by a thin, multiply folded membrane (Fig. 6G). This membrane is attached to the anterior margin of the cap (Fig. 8C) and may allow the erection, by injection of hemolymph, of a short penis-like intromittent prominence bearing the sclerotized cap at its distal end (Fig. 10). The erection of this female "micropenis" would be on a greater scale than that suggested by Klier (1956) for the simple spermapore papilla in *Trogium pulsatorium*, but based on the same hypothetical mechanism (see above). The muscles originating laterally on the anterior margin of the spermapore cap (see Fig. 7H) are probably responsible for withdrawing this sclerite after copulation. As observed by Edward Mockford (personal communication) genital coupling in *Psyllipsocus* occurs in a symmetric female-above position (sensu Huber *et al.*, 2007: p. 661), i. e. female on top, male below (wings raised), both facing same direction. In the species of the *clunijunctus* group the opening

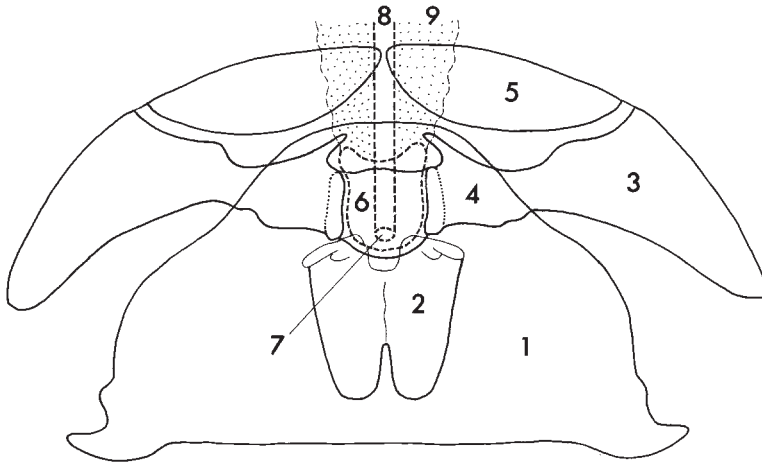


FIG. 10

Psyllipsocus similis Lienhard n. spec. Schematic representation of male and female genitalia in hypothetical coupling position, ventral view, based on Fig. 9A-C. Male: 1, hypandrium; 2, phallosome; 3, clunium; 4, clunial bridge; 5, paraproct. Female ("micropenis", interrupted line): 6, spermapore sclerite; 7, spermapore; 8, spermathecal duct; 9, hemolymph (dotted). For explanations see General Discussion: Functional Morphology.

of the spermathecal duct, situated dorsally (not terminally!) on the cap-like sclerite in resting position, would be ventrally directed in this coupling position, after intromission of the sclerite into the ventrally open median cavity of the clunial bridge. This vice-like flexible median part of the clunial bridge may catch the spermapore sclerite between its ventrally prominent jaws and firmly hold it during copulation (the thick and rigid wall of the spermapore sclerite prevents excessive squashing by the jaws). In this position the spermapore faces the distal end of the phallosomal structures situated on the dorsal side of the hypandrium (Fig. 10), and a close contact between the spermapore and the opening of the male seminal duct can be established. This hypothesis is quite plausible, though the opening of the male seminal duct has not been directly observed in the present study. The possibility of firmly holding the female spermapore sclerite for a long duration of genital coupling may be interpreted as an adaptation favouring the evolution of the particularly large and thick-walled spermatozoa observed in the species of the *clunjunctus* group, the production and transfer of which are probably rather time consuming. Indirectly this novel structure may thus also have favoured the evolution of the spermathecal signum in *P. serrifer* (see above).

It is interesting to compare these observations with the situation described for *Neotrogla* Lienhard (Trogioromorpha: Prionoglaridetae: Prionoglarididae), a recently discovered Brazilian genus of cave psocids (Lienhard *et al.*, 2010; Lienhard & Ferreira, 2013). The phallosome of *Neotrogla* is also strongly reduced and has lost its function as an intromittent coupling organ. However, in this genus it is not functionally replaced by a novel structure of the male but by an elaborate penis-like organ of the female, the gynosome, bearing the spermapore on its tip. In *Neotrogla*, the presence of a very long

spermathecal duct together with a longitudinal accessory sclerite (gynosomal rod) suggests the hypothesis that the gynosome can be deeply inserted into the male abdomen during copulation, to reach the opening of the seminal duct (ductus ejaculatorius) situated at the bottom of the male genital chamber (see Lienhard *et al.*, 2010: fig. 10c). The females of the *Psyllipsocus clunjunctus* group have a shorter spermathecal duct lacking any rod-like longitudinal accessory sclerite. Though the assumed intromission of the erected female “micropenis” must be deeper in these *Psyllipsocus* species than that of the simple spermapore papilla in *Trogium pulsatorium*, it is certainly less deep than that postulated for the gynosome in *Neotroglia*. While the gynosome is a strongly modified primary external genital organ of the female (spermapore papilla), the male clunial bridge is a completely novel structure, here interpreted as an accessory genital organ. This complex differentiation of the usually membranous last abdominal sternum is situated just ventrally of the paraprocts and forms a sclerotized but flexible connection between the ventrally prolonged hind corners of the clunium. It faces the phallosome and may functionally replace that organ's reduced parts (see above). In the other species of *Psyllipsocus* the hind corners of the male clunium are similar to those of the female (see arrows in Figs 2F, 6B, 8E), i. e. not prolonged ventrally and only connected to each other by a simple membranous zone which apparently has no function in genital coupling. As far as we know, this would be the only case in Psocoptera where the clunium is ventrally prolonged and gives rise to an elaborate accessory genital organ by fusion with the sclerotized medio-ventral zone of the last abdominal sternum. In the female this region of the abdominal apex probably has to remain membranous, constrained by the expansion needed during oviposition. In the male, however, an evolutionary potential apparently exists, realized in the males of the *Psyllipsocus clunjunctus* group by the differentiation of an elaborate clunial bridge.

DISTRIBUTION AND PHYLOGENY

The presently known distribution of the three species of the *Psyllipsocus clunjunctus* group is shown in Fig. 1 and has briefly been discussed for each species in the taxonomic part, above. *P. similis*, only known from three caves in south-eastern Minas Gerais state, seems to occupy a much more restricted area than the two other species. Never have two species been found in the same cave. Only in the municipality Itabirito (MG) more than one species were found: *P. serrifer* in the cave Gruta MP1 and *P. similis* in the cave Gruta MP8. While *P. clunjunctus* and *P. serrifer* have a clearly allopatric distribution, the much rarer *P. similis* seems to be sympatric with *P. serrifer*.

Within the genus *Psyllipsocus* the *clunjunctus* group is defined as a monophyletic clade by the four principal autapomorphies mentioned in the above discussion on functional morphology. At present it is not possible to present any hypothesis about a possible sister group relationship to other members of the genus *Psyllipsocus*. Within this species group, the usually macropterous *P. similis* appears to be most plesiomorphic due to the presence of a short and weakly sclerotized file-like spermathecal blade, a membranous hypandrial apex and simple pear-shaped spermatophores; the most recent common ancestor of the group could have been similar to this species. A first dichotomy gave probably rise to the brachypterous *P. clunjunctus*, characterized

by a somewhat longer spermathecal blade, a medio-apical hypandrial sclerotization and long sausage-shaped spermatophores. The sister-group of *P. clunjunctus* consists of the relatively primitive *P. similis* and the highly derived *P. serrifer*; the latter is characterized by the more elaborate clunial bridge, the well-sclerotized saw-like spermathecal blade and the sickle-shaped spermatophores. Hypandrial similarity between *P. serrifer* and *P. similis* is supposedly based on symplesiomorphy.

This phylogenetic hypothesis, together with the available distributional data, suggests an origin of the *clunjunctus* clade somewhere in central Minas Gerais state and a successful dispersal of *P. serrifer* and *P. clunjunctus* within the caves of the Bambuí group limestone formation and of the latter also towards north-eastern Brazil into the caves of the Una group and of the Apodi group (see Fig. 1 and remarks on *P. clunjunctus* in the taxonomic part, above). The very restricted area of *P. similis* may be interpreted as that of a relict population of this relatively plesiomorphic species.

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