

**Descriptions of two new *Pseudophacopteron* species
(Hemiptera: Psylloidea: Phacopteronidae)
inducing galls on *Aspidosperma* (Apocynaceae) in Brazil**

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Abstract. Two new species of the large pantropical jumping plant-louse genus *Pseudophacopteron* Enderlein, 1921 (Hemiptera: Psylloidea: Phacopteronidae) are described from dry woodland habitats in the Midwest, Southeast and South of Brazil. *Pseudophacopteron aspidospermi* sp. nov. is associated with *Aspidosperma australe*, *P. longicaudatum* sp. nov. has been found on *Aspidosperma macrocarpon* and *A. tomentosum* (Apocynaceae). Both species induce intralaminar lenticular galls on the leaves of their host trees which have been the subject of several structural, histochemical and ecological publications. Adult males and females, fifth instar immatures and galls are illustrated including diagnostic morphological details, and compared with other Neotropical and Old World species of *Pseudophacopteron* and Phacopteronidae. The distribution of *Pseudophacopteron* in the Neotropical Region is briefly discussed.

Key words. Sternorrhyncha, jumping plant-lice, psyllids, phytophagous insects, taxonomy, morphology, zooecidia, Gentianales, cerrado, South America, Neotropical Region

Introduction

Induction of galls on plants by arthropods appears to be the most complex form of phytophagy (SHORTHOUSE et al. 2005). Relationships between the gall inducing organisms and their host plants are often very specific and involve a number of biological, physiological and morphological adaptations. Galls and their inducers represent a frequent object of studies addressing general evolutionary and ecological questions such as coevolution, adaptive radiation and global biodiversity patterns, as well as biochemical and histological processes associated with the formation of galls at the cell level (e.g. SHORTHOUSE & ROHFRIETSCH 1990, CSÓKA et al. 1997, RAMAN et al. 2005, SHORTHOUSE et al. 2005, DAMASCENO et al. 2010). Although widespread and evolved in several unrelated arthropod groups on virtually all orders of spermatophytes, the ability to induce galls is restricted to particular taxa (RAMAN et al. 2005), and the distribution of galls and their inducers is not even but shows general geographical patterns with gradients of diversity partly differing among individual gall-inducing groups (PRICE et al. 1998, REDFERN 2011).

Jumping plant-lice or psyllids (Hemiptera: Sternorrhyncha: Psylloidea) include many gall-inducing species which are narrowly host-specific, and are most species-rich in the tropics and south temperate regions (HODKINSON 1984, BURCKHARDT 2005). Also, within the Psylloidea, gall-inducing species can be found in several not closely related groups, being particularly frequent in some taxa while some other large groups do not induce galls at all (BURCKHARDT 2005). The small pantropical family Phacopteronidae is one of the groups with a high proportion of gall-inducing species (MALENOVSKÝ et al. 2007). It currently includes 48 valid extant species described from the Afrotropical, Neotropical, and Oriental Regions (BROWN & HODKINSON 1988, MALENOVSKÝ & BURCKHARDT 2009, YANG et al. 2009, LI 2011, OUVARD 2015), and at least as many undescribed species from these and the Australasian Region (HOLLIS 2004; unpublished BMNH, NHMB and USNM data). As far as known, species of Phacopteronidae are strictly monophagous or narrowly oligophagous on various species or genera of Sapindales (= Rutales) with the exception of a few species of the large pantropical genus *Pseudophacopteron* Enderlein, 1921, which are associated with the unrelated Apocynaceae (Gentianales) (HODKINSON 1986, BROWN & HODKINSON 1988, HOLLIS 2004, MALENOVSKÝ et al. 2007, MALENOVSKÝ & BURCKHARDT 2009). Members of Apocynaceae, a species-rich plant family that includes some 5100 species of trees, shrubs, herbs, stem succulents, and vines, distributed mainly in the tropics and subtropics worldwide, many of which contain milky latex and are poisonous (NAZAR et al. 2013), are otherwise used as host plants only by a small number of psyllid taxa, particularly by several species of *Diaphorina* (Liviidae), and perhaps also some Triozidae (HOLLIS 1987, MALENOVSKÝ & BURCKHARDT 2014, OUVARD et al. 2015, and further references cited in OUVARD 2015).

The Neotropical Region is considered to have a very diverse psyllid fauna which has been, however, only poorly explored so far. This is particularly true for Brazil from where 76 psyllid species have been recorded but ten times as many or more can be expected (BURCKHARDT & QUEIROZ 2012, 2013; BURCKHARDT et al. 2013). Many psyllid species in Brazil are probably confined to tropical rain forests, but also dry woodland and savanna biomes seem to support a distinct and diverse psyllid fauna (D. Burckhardt & D. L. Queiroz, pers. observ.). Xeric habitats like the Brazilian cerrado are particularly rich in gall-inducing insects in general (PRICE et al. 1998, FERNANDES et al. 2005).

Aspidosperma Mart. & Zucc. (Apocynaceae) includes approximately 70 species of deciduous or evergreen trees found from Mexico to Argentina, growing in a variety of habitats from the dry campos and cerrado of south central Brazil to the inundated river margins of the Amazon basin (WOODSON 1951, HASSLER 2014). Many species are used as important local source of timber (WOODSON 1951) and contain pharmaceutically interesting compounds (e.g. indole alkaloids; DOLABELA et al. 2012, COUTINHO et al. 2013).

Psyllid galls on leaves of *Aspidosperma* were first reported from Brazil over a century ago (RÜBSAAMEN 1907) and later associated with *Pseudophacopteron* (BROWN & HODKINSON 1988, BURCKHARDT & QUEIROZ 2012). Partly due to their great abundance on *Aspidosperma australe* in the campus of the Universidade Federal de Minas Gerais in Belo Horizonte in south-eastern Brazil, the gall system *Pseudophacopteron-Aspidosperma australe* has served as a model for detailed anatomical, ultrastructural, chemical, and histochemical studies (CHRISTIANO 2002, OLIVEIRA & ISAIAS 2010, OLIVEIRA et al. 2011), as well as for comparative studies of phenology between the gall-inducer and its host plant (CAMPOS et al. 2010). Synchrony between the psyllid and the host plant has also been recently studied in *Pseudophacopteron* sp. on *Aspidosperma macrocarpon* in rupestrian cerrado in central Brazil (CASTRO et al. 2013). However, the identity of *Aspidosperma* psyllids at species level has not been elucidated yet. Based on a study of available specimens from museum collections and recent field work in Brazil, we conclude that the material from *Aspidosperma* belongs to two undescribed *Pseudophacopteron* species which we formally name and describe in this paper.

Material and methods

Material from the following collections was examined or is cited:

- BMNH Natural History Museum, London, United Kingdom;
- MMBC Moravian Museum, Brno, Czech Republic;
- MZSP Museu de Zoologia da Universidade de São Paulo, SP, Brazil;
- LEEF Laboratório Entomológico, Embrapa Florestas, Colombo, PR, Brazil;
- NHMB Naturhistorisches Museum, Basel, Switzerland;
- NMPC National Museum, Prague, Czech Republic;
- USNM National Museum of Natural History, Smithsonian Institution, collections deposited in the Systematic Entomology Laboratory, United States Department of Agriculture, Beltsville, Maryland, United States;
- ZMHB Museum für Naturkunde, Berlin, Germany.

Measurements and figures were made from slide-mounted specimens. Parts of slide-mounted specimens were also used to prepare photographs of fore wings and hind legs (using an Olympus BX 41 microscope associated with an Olympus Camedia 5060 WZ digital camera and QuickPHOTO PRO software). Habitus photographs were taken with a Leica DFC 295 digital camera on a Leica Z16 APO macroscope and the Leica Application Suite v. 3.7 software; the details of metatibial spurs were taken with a Philips XL 30 ESEM scanning electron microscope.

Morphological terminology used in the descriptions is combined from HOLLIS (1976), BROWN & HODKINSON (1988), and OSSIANNILSSON (1992). The nomenclature of host plants follows HASSLER (2014).

Taxonomy

Pseudophacopteron aspidospermi sp. nov.

(Figs 1, 3, 5, 7, 9, 10, 12–16, 20, 21, 23, 25, 27, 29–35, 41–43)

“Psyllidengalle” [= psyllid gall]: RÜBSAAMEN (1907): 111.

Pseudophacopteron sp.: ISAIAS et al. (2000), CHRISTIANO (2002), CHRISTIANO et al. (2003), CAMPOS et al. (2010), OLIVEIRA & ISAIAS (2010), OLIVEIRA et al. (2011), BURCKHARDT & QUEIROZ (2012).

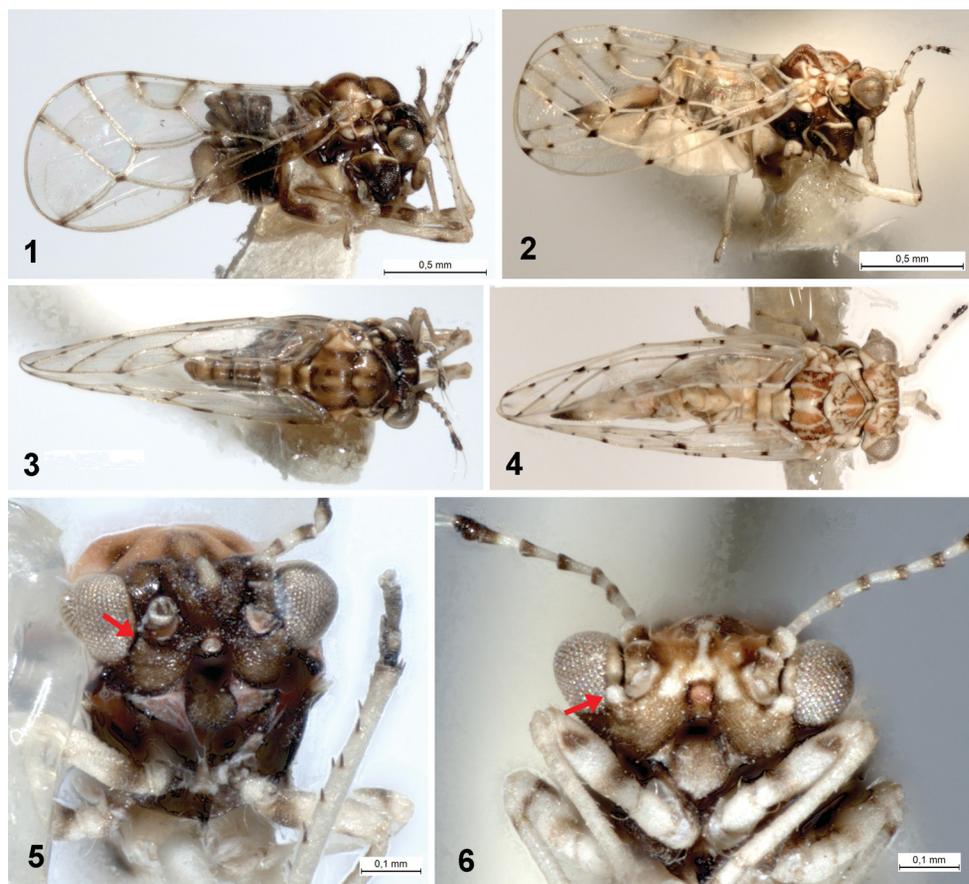
Type locality. Brazil, Minas Gerais: Belo Horizonte, Pampulha Campus of Universidade Federal de Minas Gerais, approx. 19°52'18"S, 43°52'00"W, 820 m a.s.l.

Type material. HOLOTYPE: ♂, BRAZIL: MINAS GERAIS: ‘Belo Horizonte, Pampulha Campus of Universidade Federal de Minas Gerais, 12 April 1998, on *Aspidosperma australe*, J. C. S. Christiano leg.’ (BMNH, dry-mounted). PARATYPES: BRAZIL: MINAS GERAIS: 4 ♂♂ 6 ♀♀, same data as holotype (BMNH, MMBC, NHMB, dry- and slide-mounted); 3 fifth instar immatures, same data but 17 June 2014; 2 fifth, 3 fourth and 3 third instar immatures, same data but 3 July 2014; 5 fifth instar immatures, same data but 10 September 2014, all R. M. S. Isaias leg. (MMBC, NHMB, slide-mounted and preserved in ethanol); 1 ♀, Lavras, 21°14'S 45°00'W, 900 m, 1–6 June 2010, D. Burckhardt leg. #1 (NHMB, dry-mounted). SANTA CATARINA: 1 ♂, Nova Teutonia, 6 August 1943, F. Plaumann leg.; 1 ♀, same data but 29 June 1943 (BMNH, dry-mounted).

Additional material examined. BRAZIL: RIO DE JANEIRO: Tijuca, July 1899, a twig of *Aspidosperma australe* with galls on leaves (coll. E. H. Rübсаamen, ZMHB, dry herbarium sample, Figs 41–43).

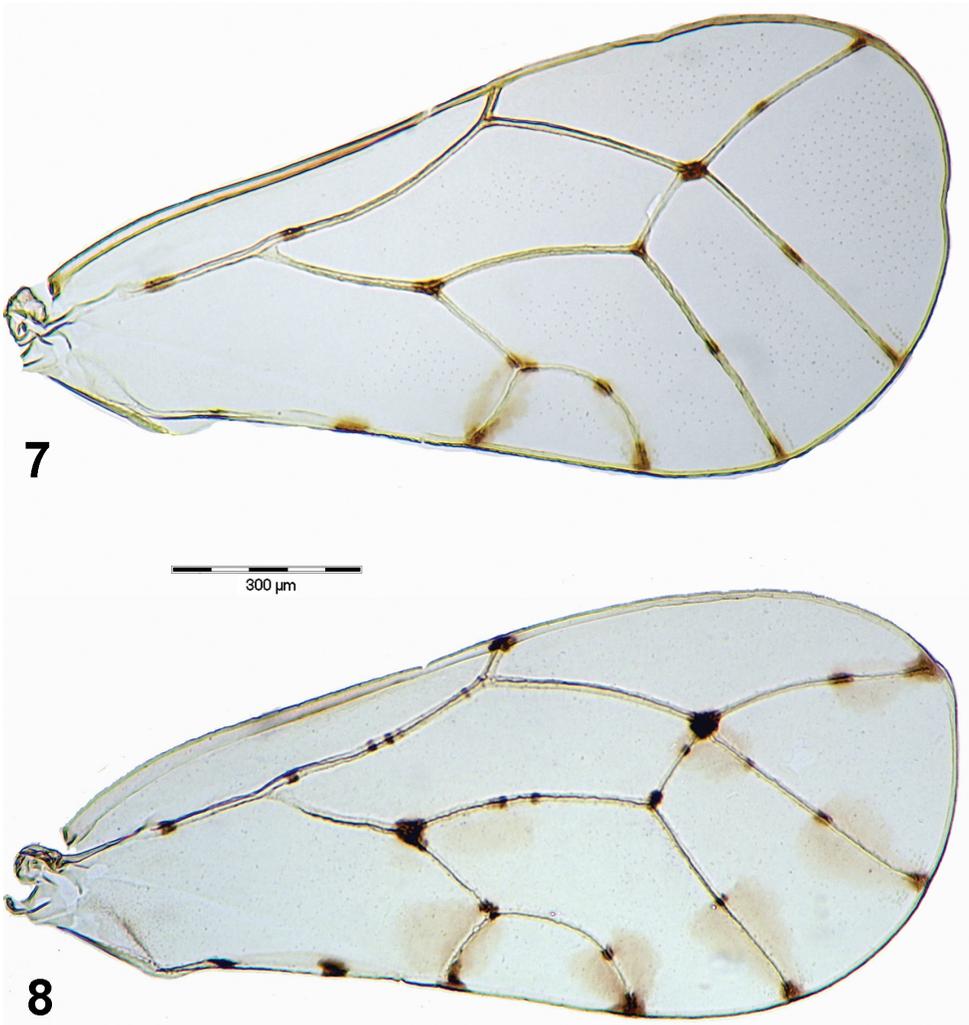
Description. Adult. Coloration. Vertex dark brown with midline pale ochreous; genae, frons and clypeus uniformly dark brown (Fig. 5). Pronotum dark brown with midline and lateral tubercles pale ochreous; mesopraescutum orange brown with anterior margin dark brown or entirely dark brown with a pale ochreous patch at base medially; mesoscutum orange brown to dark brown with four pale ochreous stripes; mesoscutellum pale ochreous to dark brown; pleural sclerites dark brown with pale yellow markings (Figs 1, 3). Antenna off-white, segments 1–2 basally, segments 4–8 apically and segments 9–10 entirely dark brown (Figs 1, 5, 25). Legs off-white to pale ochreous; profemur with a dark brown transverse streak basally (Fig. 5), mesofemur with two dark brown streaks basally and subapically; metacoxa extensively dark brown on posterior and ventral margins, metafemur with a small dark brown patch on dorsal side subapically; metatibia with lateral and apical spurs dark brown; metatarsus infuscate (Figs 5, 10). Fore wing membrane clear with indistinct light brown infuscations along veins Cu_{1b} and apex of Cu_{1a} ; veins off-white with well-delimited dark brown to black spots on apices and forks of all veins except R_1 , one medial spot on each $R+M+Cu_1$, apical portion of R_s , M_{1+2} , M_{3+4} and Cu_{1a} , respectively, as well as two medial spots on anal vein (Figs 1, 7). Hind wing membrane clear, vein $C+Sc$ infuscate. Abdominal tergites orange brown, laterally and on posterior margin darker brown; sternites pale ochreous, dark brown laterally (especially on first visible sternite) to almost entirely dark brown (Fig. 1). Male terminalia uniformly pale yellow; female terminalia ochreous, apex of female proctiger dark brown (Fig. 1).

Morphology. Body with microsculpture, matt. Head, in frontal view, about twice wider than high (Fig. 5). Vertex dorsally with raised median ridge and two lateral bulges on either side in front; median epicranial suture completely reduced; lateral ocelli lying on small tubercles slightly above the plane of vertex. Eyes hemispherical; occiput and anteoccipital sclerite narrow. Genae small, weakly swollen, tubercle below torulus small and acute (Fig. 5). Antenna short, robust, serrate, segments strongly widening from base to apex (Fig. 25); one large elliptic rhinarium subapically on each of segments 4–9; rhinaria bordered with wreath



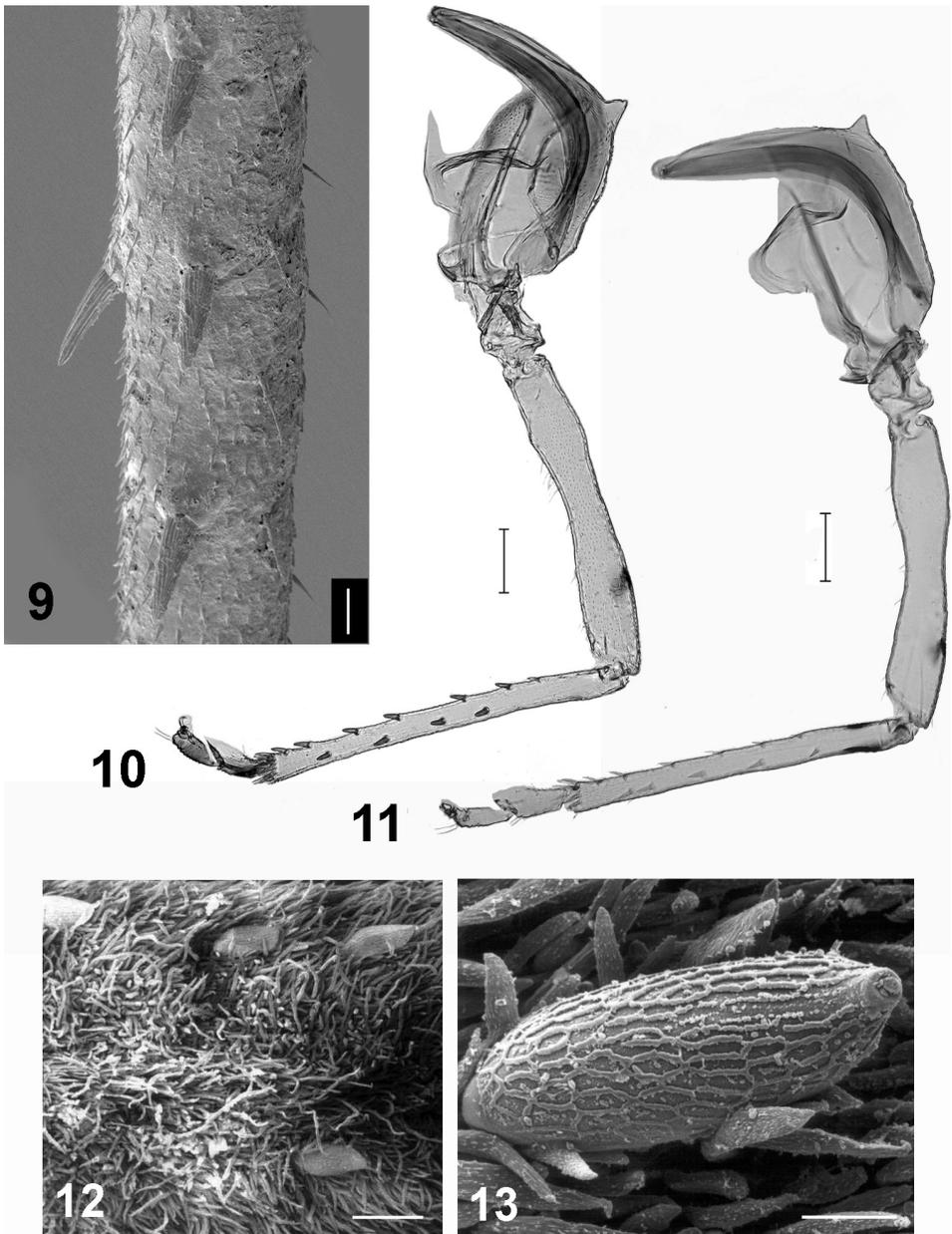
Figs 1–6. Habitus of *Pseudophacopteron* spp. 1, 3, 5 – *P. aspidospermi* sp. nov., paratype female; 2, 4, 6 – *P. longicaudatum* sp. nov., paratype female. 1, 2 – habitus, lateral view; 3, 4 – habitus dorsal view; 5, 6 – habitus, frontal view (red arrow: tips of genal tubercles).

of long cuticular spines; terminal setae subequal, more than twice longer than segments 9 and 10 together (Fig. 23). Fore wing (Fig. 7) pyriform, apex broadly rounded; costal break situated in distal fifth of vein C+Sc; membrane with fields of sparse surface spinulation in all cells except c+sc, leaving wide spinule-free bands along veins. Mesotibia with a comb composed of five stout setae on outer side subapically. Metafemur relatively long and slender, medially distinctly constricted, with a row of several evenly short setae along ventral margin (Fig. 10). Metatibia bearing open crown of ten tightly packed sclerotised spurs apically and two rows of seven and four similar, stout and sclerotised spurs laterally (Figs 9, 10). Metabasitarsus about 1.5 times longer than broad, conical, lacking sclerotised spurs laterally (Fig. 10). Abdominal tergites 3–4 with large dorsal tubercles (Fig. 1). Male subgenital plate with dorsal margin slightly convex. Male proctiger relatively slender, cylindrical (Fig. 14). Paramere shorter than

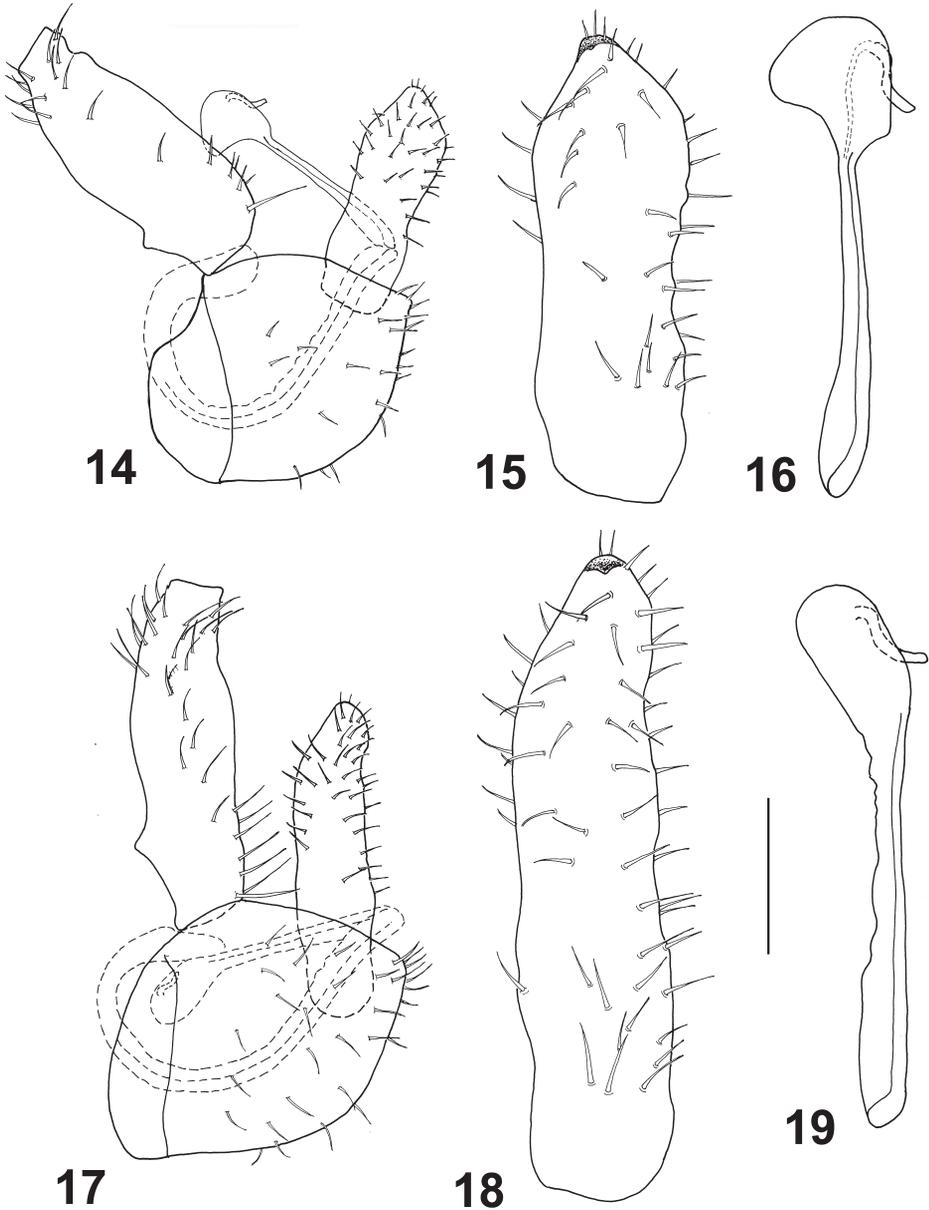


Figs 7–8. Fore wings of *Pseudophacopteron* spp. 7 – *P. aspidospermi* sp. nov.; 8 – *P. longicaudatum* sp. nov.

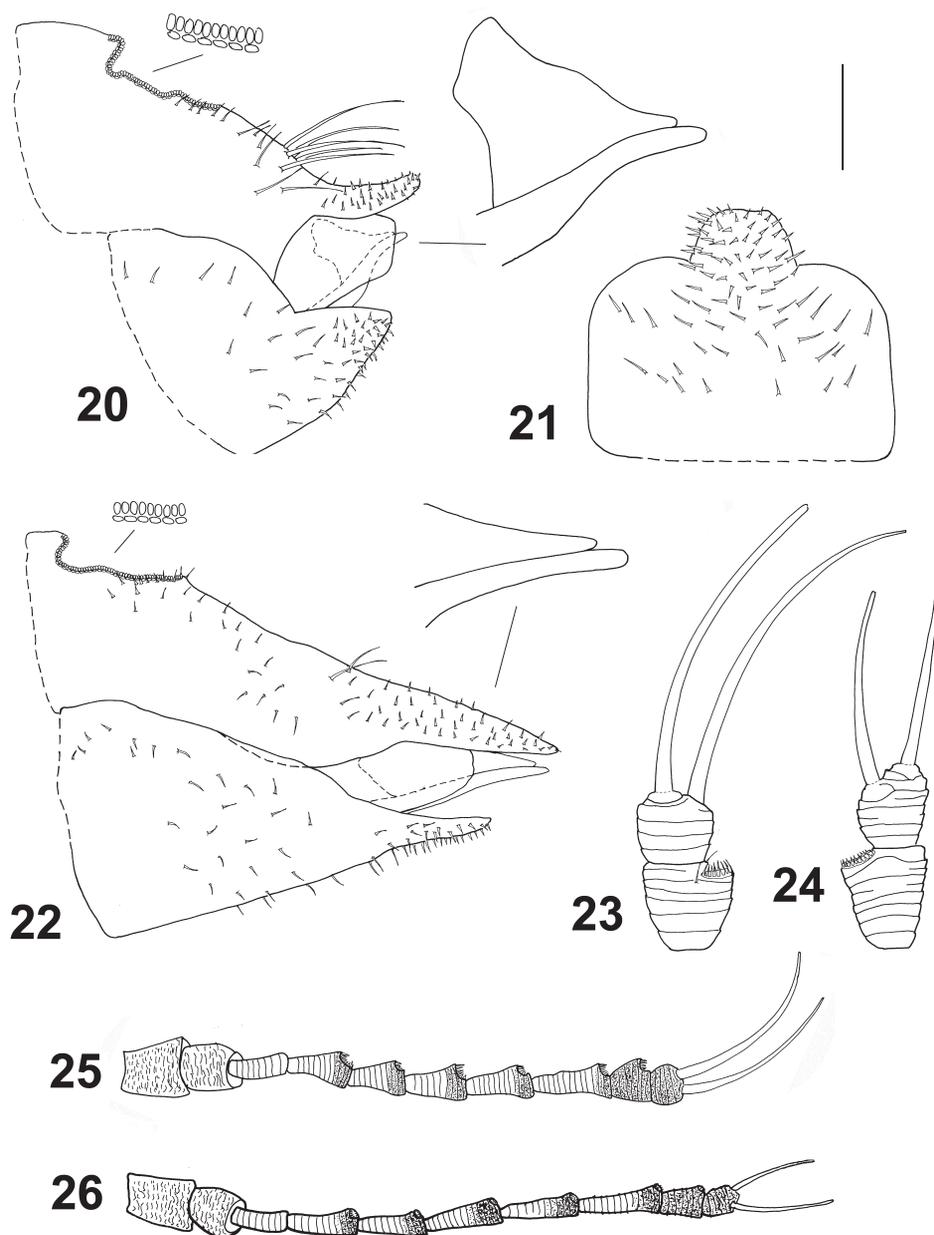
proctiger; in lateral view, abruptly narrowing in apical fourth to a subacute apex; inner side bearing approximately 15 fine setae (Fig. 15). Distal segment of aedeagus with long shaft, apical dilation relatively short and broad, hooked; sclerotised end tube of ductus ejaculatorius relatively long and sinuate (Fig. 16). Female proctiger and subgenital plate with moderately long apical extensions covered with short and stout setae; dorsal margin of proctiger posterior to circumanal ring, in lateral view, strongly concave; circumanal pore ring with two rows of pores, pores of outer row contiguous; subgenital plate, in lateral view, with ventral margin



Figs 9–13. Hind legs and eggs of *Pseudophacopteron* spp. 9, 10, 12, 13 – *P. aspidospermi* sp. nov.; 11 – *P. longicaudatum* sp. nov. 9 – detail of metatibia, inner side; 10, 11 – hind leg, inner side; 12, 13 – eggs on *Aspidosperma australe* (reprinted from CHRISTIANO 2002, with permission). Scale bars: 9 – 0.01 mm; 10, 11 – 0.1 mm; 12 – 0.2 mm; 13 – 0.05 mm.



Figs 14–19. Male terminalia of *Pseudophacopteron* spp. 14–16 – *P. aspidospermi* sp. nov.; 17–19 – *P. longicaudatum* sp. nov. 14, 17 – male terminalia outer face, lateral view; 15, 18 – paramere inner face, lateral view; 16, 19 – distal segment of aedeagus, lateral view. Scale bar: 14, 17 – 0.1 mm; 15, 16, 18, 19 – 0.05 mm.



Figs 20–26. Female terminalia and antennae of *Pseudophacopteron* spp. 20, 21, 23, 25 – *P. aspidospermi* sp. nov.; 22, 24, 26 – *P. longicaudatum* sp. nov. 20, 22 – female terminalia with details of circumanal pore ring and dorsal and ventral valvulae, lateral view; 21 – female subgenital plate, ventral view; 23, 24 – antennal segments 9 and 10; 25, 26 – antenna. Scale bar: 20–22 – 0.1 mm; 23, 24 – 0.025 mm; 25, 26 – 0.05 mm.

convex, apex pointed (Fig. 20); in ventral view, broadly rectangular basally, with a truncate apical extension (Fig. 21). Dorsal and ventral valvulae lacking distinct lateral teeth (Fig. 20).

Measurements and ratios in Table 1.

Fifth instar immature (Fig. 27). Uniformly pale yellow, eyes grey. Body dorsally flat, ventrally strongly inflated. Body outline broadly ovoid, with convex lateral margins. Whole dorsal surface almost evenly covered with coarse microsculpture consisting of densely arranged small irregular (more or less round or square) cuticular granules; one larger quadrate cuticular scale on first visible abdominal tergite at posterior margin of hind wing pad on each side of midline. Whole body margin with pointed lanceolate setae in following numbers (one side only): head in front of insertion of antenna: 6–8, cephaloprothorax behind eye: 8–11, fore wing pad: 26–34, hind wing pad: 7–8, abdomen: (5–6) + (31–36); lanceolate setae absent from body dorsum except for a group of ca. 20 submarginal setae on each side of midline in subapical area of caudal plate. Antenna inserted on ventral side, oriented obliquely outwards and backwards over the body, extending beyond eye, gradually narrowing to a pointed apex, lacking distinct divisions and bearing two rhinaria posteriorly. Tarsal arolium membranous, hardly visible on slide-mounted specimens, sessile, pad-like, small, extending approximately to half of length of claws. Abdomen dorsally with four large free sclerites and caudal plate (incompletely fused in some specimens); caudal plate margin broadly rounded. Anus small, rhomboid, in ventral position. Circumanal ring moderately large, with fore and hind margins close together; outer ring composed of a single row of pores, hardly sinuate laterally. Measurements and ratios in Table 2.

Egg (Figs 12, 13). Elongate, ca. 0.25 mm long, asymmetrical with subacute apex and reticulated surface.

Diagnosis. Adults of *Pseudophacopteron aspidospermi* sp. nov. are similar to *P. longicaudatum* sp. nov. in size and the absence of sclerotised lateral spurs on the metabasitarsus (the latter are well-developed in all other described Neotropical species of the genus). *Pseudophacopteron aspidospermi* differs from *P. longicaudatum* as well as from all the other known Neotropical *Pseudophacopteron* species in the robust antenna with very long terminal setae (more than twice longer than antennal segments 9 and 10 together), the dark coloured spurs on the metatibia, as well as the shape of the paramere, aedeagus and the female terminalia. It also differs from *P. longicaudatum* in the generally darker coloration of the body, particularly the head, the absence of oval light brown infuscations on the fore wing membrane on the apices of veins Rs, M_{1+2} , M_{3+4} and the touching point of Rs and M_{1+2} , the smaller number of small dark brown spots on fore wing veins, the relatively broader fore wing with shorter apical section of Rs, the larger distance between apices of Rs and M_{1+2} , and the smaller (narrower) cell cu_1 of fore wing.

The fifth instar immature of *P. aspidospermi* generally resembles other *Pseudophacopteron* spp. living in intralaminar galls (see the Discussion). It is similar to *P. longicaudatum* in the unsegmented antenna oriented backwards and outwards over the body, the coarse microsculpture of the body dorsum, the presence of pointed lanceolate setae along whole body margin, and the structure of the circumanal pore ring. It differs from *P. longicaudatum* in the shorter and relatively broader body, the more evenly shaped and distributed granulous microsculpture on whole body dorsum, the more numerous and densely arranged lanceolate setae on the wing pad margins, the lack of isolated lanceolate setae on the abdominal dorsum,

Table 1. Measurements (in mm) and ratios of adults of *Pseudophacopteron aspidospermi* sp. nov. and *P. longicaudatum* sp. nov.

	<i>P. aspidospermi</i>		<i>P. longicaudatum</i>	
	♂♂ (n = 2)	♀ (n = 1)	♂♂ (n = 4)	♀♀ (n = 4)
Head width (HW)	0.48	0.54	0.53–0.56	0.55–0.61
Antenna length (AL)	0.49–0.54	0.57	0.51–0.63	0.54–0.62
Longer antennal terminal seta length	0.17	0.15	0.08–0.10	0.09–0.11
Shorter antennal terminal seta length	0.15	0.14	0.06–0.09	0.06–0.09
Fore wing length (WL)	1.31–1.33	1.54	1.31–1.43	1.49–1.58
Fore wing width (WW)	0.61–0.62	0.72	0.55–0.62	0.64–0.71
Rs apical portion length (a)	0.29–0.30	0.35	0.33–0.36	0.38–0.41
Distance between apices of Rs and M ₁₊₂ on fore wing (b)	0.44–0.46	0.51	0.29–0.33	0.34–0.36
Fore wing cell cu _{1a} width (c)	0.22–0.24	0.28	0.28–0.30	0.32–0.35
Fore wing cell cu _{1a} height (d)	0.12–0.13	0.15	0.12–0.15	0.14–0.16
Metafemur length	0.43	0.52	0.42–0.46	0.45–0.47
Metatibia length (TL)	0.52	0.60	0.44–0.53	0.51–0.55
Male proctiger length (MP)	0.18–0.19	–	0.19–0.22	–
Male paramere length (PL)	0.15–0.16	–	0.17–0.19	–
Aedeagus distal segment length (DL)	0.14–0.16	–	0.14–0.17	–
Female proctiger length (FP)	–	0.43	–	0.54–0.59
Female subgenital plate length (SL)	–	0.20	–	0.37–0.39
AL/HW ratio	1.02–1.13	1.06	0.96–1.15	0.90–1.11
WL/HW ratio	2.73–2.77	2.85	2.47–2.56	2.52–2.82
WL/WW ratio	2.15	2.14	2.26–2.38	2.16–2.43
a/b ratio	0.71–0.73	0.78	0.85–0.95	0.86–0.91
c/d ratio	1.69–2.00	1.87	1.93–2.50	2.00–2.50
TL/HW ratio	0.94–1.08	1.11	0.83–0.96	0.84–0.98
MP/HW ratio	0.38–0.40	–	0.36–0.41	–
PL/HW ratio	0.31–0.33	–	0.30–0.35	–
DL/HW ratio	0.29–0.33	–	0.25–0.31	–
FP/HW ratio	–	0.80	–	0.92–1.00
SL/FP ratio	–	0.47	–	0.63–0.72

the presence of submarginal groups of lanceolate setae on the caudal plate subapically, the longer and less robust antenna, the larger circumanal pore ring, and the smaller tarsal arolium. Another species with similar fifth instar immatures are *P. electum* Capener, 1973 and *P. sodalis* Malenovský & Burckhardt, 2009 from Africa with which *P. aspidospermi* shares similar body shape, antenna, circumanal pore ring and pointed lanceolate setae on body margin but differs in the arrangement of the latter (both Afrotropical species lack the subapical groups of setae on caudal plate; *P. electum* also completely lacks lanceolate setae on cephaloprothorax and wing pad margins) and some other details (MALENOVSKÝ et al. 2007, MALENOVSKÝ & BURCKHARDT 2009). The only other Neotropical species of the genus with described fifth instar

immatures, *P. punctinervis* Brown & Hodkinson, 1988, associated with *Protium tenuifolium* (Burseraceae) and known from Panama, differs from all the aforementioned species in the shape of the marginal lanceolate setae which are truncate, and the obliquely forwards-directed antenna with 3–5 indistinct divisions (BURCKHARDT & BROWN 1992).

Etymology. Derived from the host plant genus *Aspidosperma*; noun in genitive case.

Host plant and biology. Inducing intralaminar lenticular galls (*sensu* ISAIAS et al. 2013) on the leaf lamina of both young and mature leaves of *Aspidosperma australe* Müll. Arg. (Apocynaceae) (Figs 29, 30). Mature galls are green, glabrous, forming a slight projection of the adaxial surface and a more prominent projection of the abaxial surface of its host leaf, 5.0 ± 0.5 mm wide, with a central inner chamber lined with wax and enclosing one individual of *P. aspidospermi* from the first immature instar until the adult stage (Fig. 31–35). The gall is parenchymatic, with vascular tissues only at the top of the chamber, which is permanently opened through an ostiole to the abaxial leaf surface. Two tissue zones, an inner cortex, around the inner chamber, and an outer cortex with larger cells, can be distinguished within the gall (ISAIAS et al. 2000, CHRISTIANO 2002, CHRISTIANO et al. 2003, OLIVEIRA & ISAIAS 2010, OLIVEIRA et al. 2011). Feeding of *P. aspidospermi* immatures alters the metabolism of the host plant during the gall development, particularly in both reserve substances (storage of starch in cells close to the inner chamber) and enzyme activity (related to carbohydrate metabolism and reactive oxygen species production), even though a nutritive tissue *per se* is not differentiated (CAMPOS et al. 2010, OLIVEIRA & ISAIAS 2010, OLIVEIRA et al. 2011). Senescent galls open with a wide aperture on the gall surface (CAMPOS et al. 2010; Fig. 43). The galls can be frequent and numerous on the host; there are 5.35 ± 4.97 (mean \pm standard deviation, $n = 204$) galls per leaf (FERNANDES et al. 1988). Developing galls were observed over the entire year, indicating *P. aspidospermi* is a multivoltine species (CAMPOS et al. 2010). In 2006, the highest percentage (80 %) of galled leaves was recorded in December, after the peak of leaf flushing, which occurred in September and when most galls were concomitantly induced on the young leaves. However, another peak of occurrence of galled leaves (77 %) occurred in July 2007, independently of new leaf production, which indicates *P. aspidospermi* might use mature leaf tissues as alternative oviposition sites (CAMPOS et al. 2010).

Distribution. Brazil (Minas Gerais, Rio de Janeiro, Santa Catarina). The host plant, *Aspidosperma australe*, is widely distributed in the Midwest, Southeast and South of Brazil (Distrito Federal, Goiás, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Rio de Janeiro, São Paulo, Paraná, Rio Grande do Sul, Santa Catarina), Bolivia, Argentina (Corrientes, Misiones), and Paraguay (HASSLER 2014).

Pseudophacopteron longicaudatum sp. nov.

(Figs 2, 4, 6, 8, 11, 17–19, 22, 24, 26, 28, 36–40)

Pseudophacopteron sp.: BURCKHARDT & QUEIROZ (2012), CASTRO et al. (2013).

Type locality. Brazil, Minas Gerais: Vazante, Fazenda Bainha, 17°53.4'S 46°55.5'W, 662 m a.s.l.

Type material. HOLOTYPE: ♂, BRAZIL: MINAS GERAIS: 'Vazante, Fazenda Bainha, around the house and in eucalypt plantation, S17°53.4' W46°55.5', 662 m, 11 September 2014, *Aspidosperma tomentosum* Apocynaceae, remnants of cerrado forest and eucalypt plantation, sweeping vegetation, D. Burckhardt & D. L. de Queiroz leg., #147(5)' (MZSP, dry mounted). PARATYPES: BRAZIL: DISTRITO FEDERAL: 12 ♀♀, 1 adult without abdomen, Brasilia, 3–11

August 1991, *Aspidosperma tomentosum*, emerged ex galls, VFE 19288 [V. F. Eastop leg.]; 2 skins of fifth instar immatures, same data but 27 July 1991 (BMNH, dry- and slide-mounted). **GOIÁS:** 2 ♂♂ 3 ♀♀, Serra Dourada, March 2010, *Aspidosperma tomentosum*, T. M. Silva leg.; 1 ♀, same data but *Aspidosperma macrocarpon* (NHMB, preserved in 70% ethanol). **MINAS GERAIS:** 4 ♂♂ 12 ♀♀, same data as holotype (NHMB, dry-mounted and preserved in 70% ethanol); 1 ♂ 1 ♀ in LEEF, dry-mounted; 1 ♂ 1 ♀ in MZSP, dry-mounted; 2 ♀♀, same but Fazenda Bainha, 17°53.1'S 46°55.0'W, 660 m, 23 September 2011, #19 (NHMB, no. 00002949, preserved in 70% ethanol); 1 ♀, same but Vazante, near Fazenda Maria Olivia, 17°53.8'S 46°56.9'W, 650 m, 14 July 2012, disturbed forest along river, #42 (NHMB, preserved in 70% ethanol); 2 ♀♀, same but Três Marias, BR 040, km 280, Casa do Caminhoneiro, 18°13.7'S 45°13.2'W, 740 m, 10 July 2012, scrub along road, #36(5) (NHMB, preserved in 70% ethanol); 16 ♂♂ 10 ♀♀ 26 skins of fifth instar immatures, Uberlândia, 8 km S, Reserva Ecológica do Clube Caça et Pesca Itororó (CCPIU), approx. 18°59'S, 48°18'W, 855 m, July 2013, on *Aspidosperma tomentosum*, D. C. Oliveira leg.; 9 fifth and 6 fourth instar immatures, same data but March 2013 (MMBC, dry- and slide-mounted and preserved in 70% ethanol); 1 ♂ 1 ♀ in NMPC, dry-mounted). **MATO GROSSO DO SUL:** 1 ♂ 2 ♀♀, Município Campo Grande, near BR 163, 20°53.7'S 54°34.3'W, 440–450 m, 16 September 2012, cerrado edge along unpaved road, D. Burckhardt & D. L. Queiroz leg., #74(8) (NHMB, no. 00002948, preserved in 70% ethanol). **PARANÁ:** 1 ♀, Jaguariaíva, Parque do Cerrado, 24°09.878'S 49°39.610'W, 807 m, 10 July 2013, cerrado vegetation, D. L. Queiroz leg., #530 (NHMB, dry-mounted). **SÃO PAULO:** 4 ♂♂ 4 ♀♀, Mogi Guaçu, 1 October 1981, *Aspidosperma tomentosum*, M. Cytrynowicz leg. (BMNH, dry- and slide-mounted).

Description. Adult. Coloration. Vertex orange brown to dark brown with pale yellow markings on median ridge, lateral bulges in front and near posterior margin of vertex pale yellow with orange brown and dark brown markings; genae, frons and clypeus brown to dark brown, tips of genal tubercles below toruli pale yellow (Figs 4, 6). Pronotum and mesopraescutum brown to dark brown with midline and lateral corners pale yellow; mesoscutum brown to dark brown with four pale yellow stripes; mesoscutellum pale yellow; pleural sclerites dark brown with pale yellow markings (Figs 2, 4). Antenna off-white, segments 1–2 basally, segments 4–8 apically, and segments 9–10 entirely dark brown (Figs 6, 26). Legs pale yellow with two dark brown transverse streaks on pro- and mesofemora, and small dark brown patches on all tibiae basally; metafemur with a small dark brown patch on dorsal side subapically; metacoxa extensively dark brown ventrally (Figs 2, 6, 11). Fore wing membrane transparent, clear with oval light brown infuscations around apices of veins Rs, M_{1+2} , M_{3+4} , Cu_{1a} and Cu_{1b} , around touching point of Rs and M_{1+2} and across M+Cu fork. Veins off-white with well-delimited dark brown to black spots on apices and forks of all veins except R_1 fork, one medial spot on each R+M+ Cu_1 , apical portion of Rs, M_{3+4} and Cu_{1a} , respectively, and one or two medial spots on M, two medial spots on anal vein, and two or three small spots on R and M_{1+2} (Fig. 8). Hind wing membrane clear, veins off-white. Abdomen uniformly pale yellow or tergites laterally brownish. Male and female terminalia pale yellow, apex of female proctiger dark brown (Figs 2, 4).

Morphology. Body with microsculpture, matt. Head, in frontal view, about twice wider than high (Fig. 6). Vertex dorsally with raised median ridge and two lateral bulges on either side anteriorly; median epicranial suture completely reduced; lateral ocelli lying on small tubercles slightly above the plane of vertex. Eyes hemispherical; occiput and anteoccipital sclerite narrow. Genae small, weakly swollen, tubercle below torulus distinct and acute (Fig. 6). Antenna moderately long, robust, slightly serrate, segments 4–9 distinctly widening to apex (Fig. 26); one large elliptic rhinarium subapically on each of segments 4–9; rhinaria bearing wreath of long cuticular spines; terminal setae subequal, approximately 1.5 times longer

than segments 9 and 10 together (Fig. 24). Fore wing pyriform, apex broadly rounded; costal break situated in apical fifth of vein C+Sc (Fig. 8); membrane with fields of sparse surface spinulation in all cells except c+sc, leaving wide spinule-free bands along veins. Mesotibia with subapical comb on outer side reduced to 1–2 stout setae. Metafemur relatively long and slender, medially distinctly constricted, with a row of several evenly short setae along ventral margin (Fig. 11). Metatibia bearing open crown of 7–8 unsclerotised spurs apically and two rows of 6 and 4–5 similar spurs laterally (Fig. 11). Metabasitarsus about twice longer than broad, conical, lacking sclerotised lateral spurs (Fig. 11). Abdominal tergites 2–4 with distinct dorsal tubercles. Male subgenital plate with dorsal margin slightly convex. Male proctiger relatively slender, very long, cylindrical (Fig. 17). Paramere long but slightly shorter than proctiger; in lateral view, nearly straight and parallel-sided in basal four fifths, apex slightly turned posteriorly, blunt; inner side covered with fine setae (Fig. 18). Distal segment of aedeagus with long shaft, apical dilation relatively short and narrow with apex broadly rounded; sclerotised end tube of ductus ejaculatorius relatively long and sinuate (Fig. 19). Female proctiger and subgenital plate with very long apical extensions covered with short and stout setae; dorsal margin of proctiger posterior to circumanal ring, in lateral view, almost straight; circumanal ring with two rows of pores, pores of outer row contiguous; subgenital plate, in lateral view, with ventral margin straight, apex pointed (Fig. 22); in ventral view, narrowly triangular and gradually narrowing to subacute apex. Dorsal and ventral valvulae lacking distinct teeth laterally (Fig. 22).

Measurements and ratios in Table 1.

Fifth instar immature (Fig. 28). Yellowish, specimens preserved in alcohol pale off-white, tergites hardly darker pale brown, eyes red. Body elongate, more or less parallel-sided. Dorsal surface with coarse microsculpture: cephaloprothorax, fore and hind wing pads medially and abdominal tergites (including caudal plate) entirely covered with small irregular (mostly round) granules, anterior margins of free abdominal tergites and caudal plate (including anterior margins of fused segments in some specimens) each with a row of larger, irregularly quadrate cuticular scales; lateral portions of cephaloprothorax and wing pads smooth or at least with a less pronounced microsculpture. Whole body margin with pointed lanceolate setae in following numbers (one side only): head in front of insertion of antenna: 3–5, cephaloprothorax behind eye: 8–10, fore wing pad: 14–19, hind wing pad: 3–5, abdomen: (4–6) + (7–9) + (34–42); a few isolated lanceolate setae also in submarginal region and on dorsum of free abdominal tergites and caudal plate. Antenna inserted on ventral side, oriented obliquely outwards and backwards over the body, short and robust, not extending beyond eye posterior margin, lacking distinct divisions and bearing two rhinaria posteriorly. Tarsal arolium membranous, hardly visible in slide-mounted specimens, sessile, broadly fan-shaped, as large as claws. Abdomen dorsally with four large free sclerites and caudal plate (incompletely fused in some specimens); caudal plate margin broadly rounded. Anus small, rhomboid, in ventral position. Circumanal ring small, with fore and hind margins close together; outer ring composed of a single row of pores, hardly sinuate laterally. Measurements and ratios in Table 2.

Diagnosis. *Pseudophacopteron longicaudatum* sp. nov. is probably closely related to *P. aspidospermi* sp. nov. (see the comments under the latter). Adult resembles *P. nervosum* Brown & Hodkinson, 1988, *P. punctinervis* Brown & Hodkinson, 1988, and *P. vitivenis* Brown &

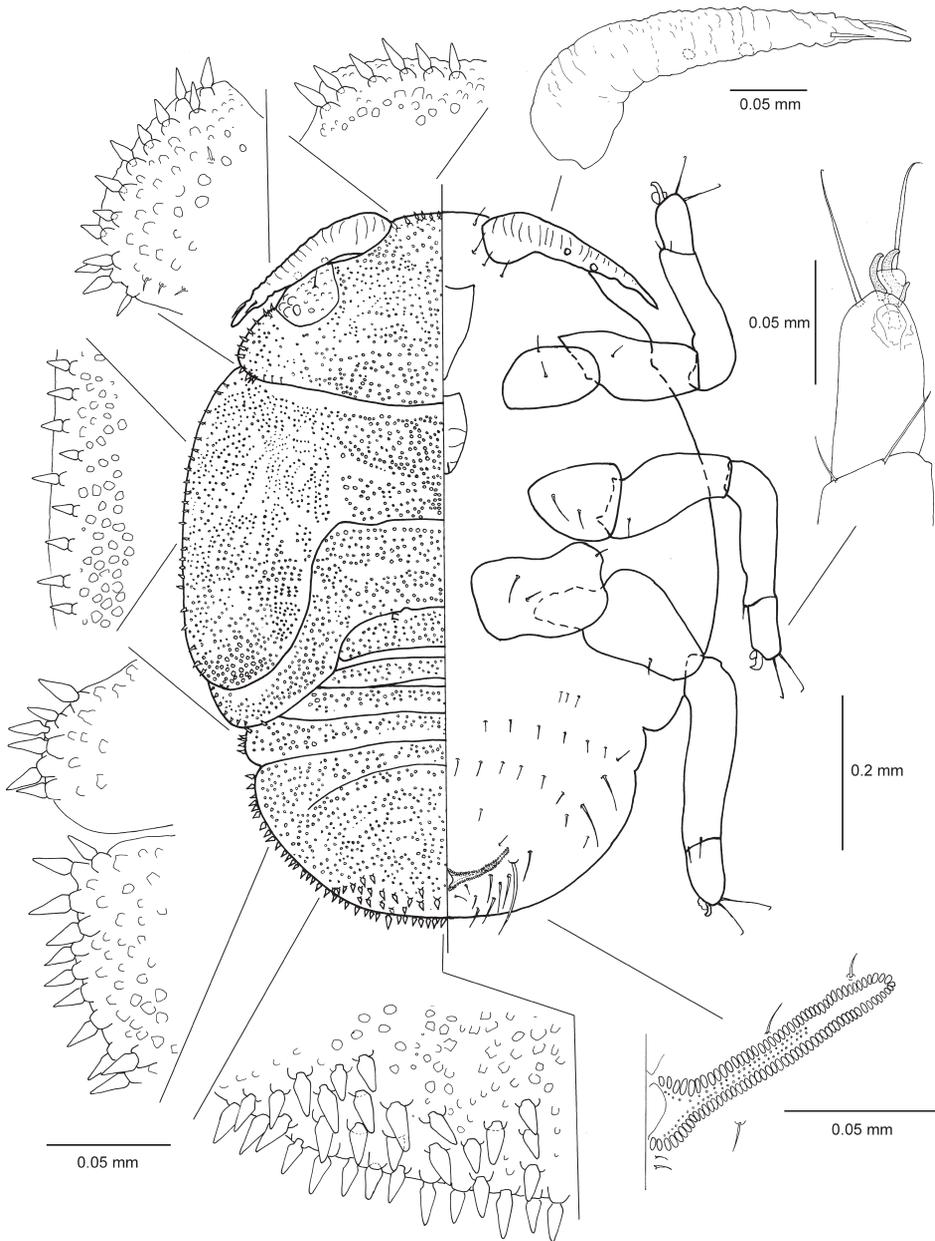


Fig. 27. Fifth instar immature of *Pseudophacopteron aspidospermi* sp. nov., left dorsal side, right ventral side, with details of setae and microsculpture on body margin, antenna, tarsus, and circumanal pore ring.

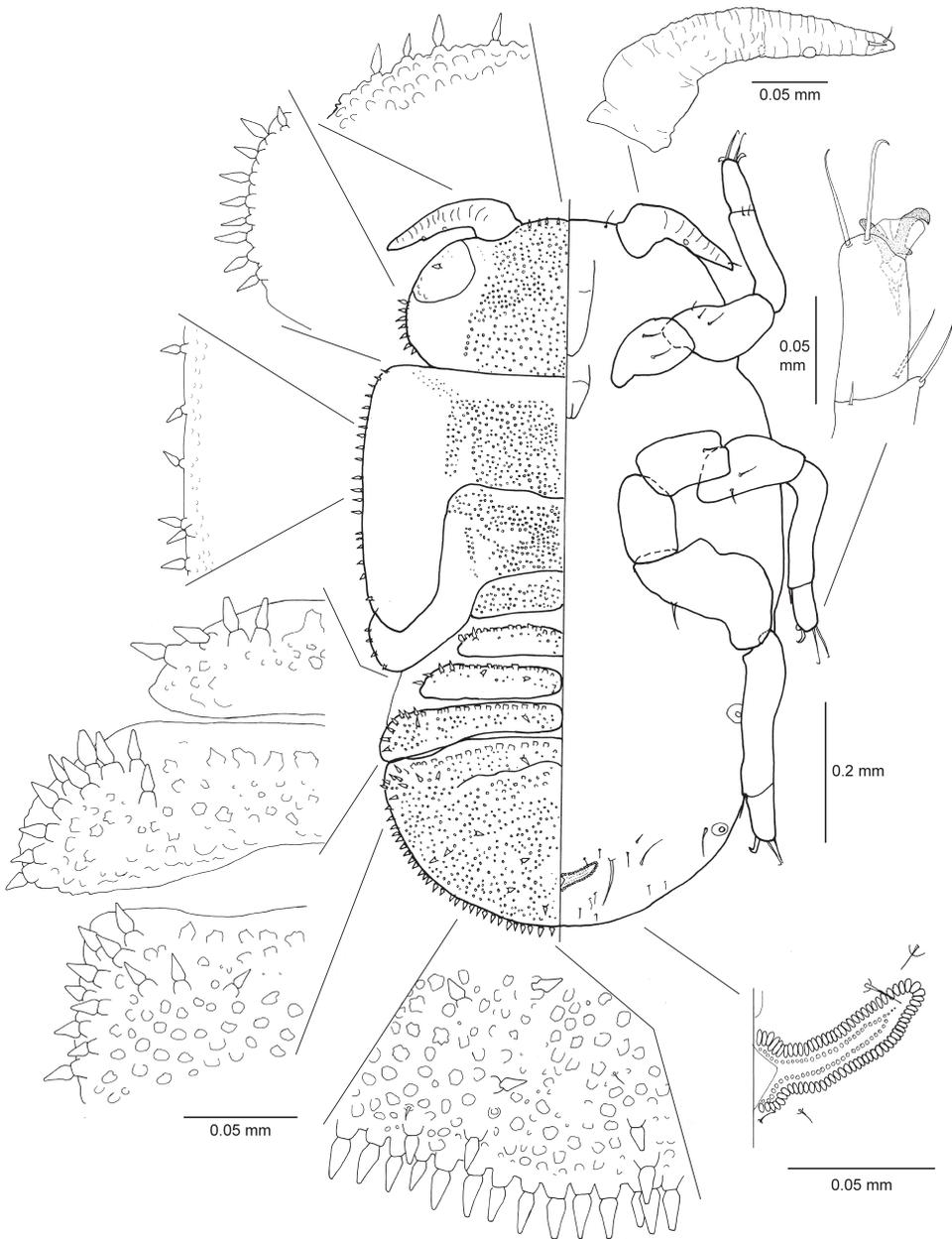


Fig. 28. Fifth instar immature of *Pseudophacopteron longicaudatum* sp. nov., left dorsal side, right ventral side, with details of setae and microsculpture on body margin, antenna, tarsus, and circumanal pore ring.

Table 2. Measurements (in mm) and ratios of fifth instar immatures of *Pseudophacopteron aspidospermi* sp. nov. and *P. longicaudatum* sp. nov.

	<i>P. aspidospermi</i> (n = 3)	<i>P. longicaudatum</i> (n = 6)
Body length (BL)	0.83–0.96	0.98–1.16
Body width (BW)	0.64–0.73	0.62–0.81
Antenna length (AL)	0.26–0.29	0.19–0.22
Forewing pad length (FL)	0.41–0.47	0.39–0.44
Metatibiotarsus length (TL)	0.28–0.36	0.26–0.31
Caudal plate length (CL)	0.23	0.26–0.33
Caudal plate width (CW)	0.46–0.52	0.53–0.59
Circumanal pore ring width (RW)	0.15–0.16	0.10–0.12
BL/BW ratio	1.30–1.32	1.43–1.68
AL/FL ratio	0.60–0.66	0.45–0.53
CW/CL ratio	2.22–2.26	1.79–2.04
RW/CW ratio	0.29–0.35	0.19–0.23

Hodkinson, 1988 in the fore wing pattern with light brown infuscations on the membrane on apices of most veins and several dark dots on veins, it is, however, generally larger (see BROWN & HODKINSON 1988). From the known Neotropical *Pseudophacopteron* spp., it can be reliably differentiated by the very long male and female terminalia. The adults also differ in the reduced mesotibial comb of setae.

The fifth instar immatures of *P. longicaudatum* differ from *P. aspidospermi* (and partly also from the immatures of other similar species discussed in the Diagnosis section under *P. aspidospermi*) in the more elongate and parallel-sided body shape, the microsculpture of dorsal surface (more or less smooth cuticle of lateral portions of cephaloprothorax and wing pads, presence of rows of quadrate scale-like projections of cuticle near anterior margins of abdominal tergites), the shorter and more robust antenna, the smaller number of lanceolate setae on the wing pad margins, the presence of several isolated lanceolate setae on the abdominal dorsum, the smaller circumanal pore ring, and the larger tarsal arolium.

Etymology. Adjective derived from Latin *longus* = long and *cauda* = tail, referring to the long female terminalia.

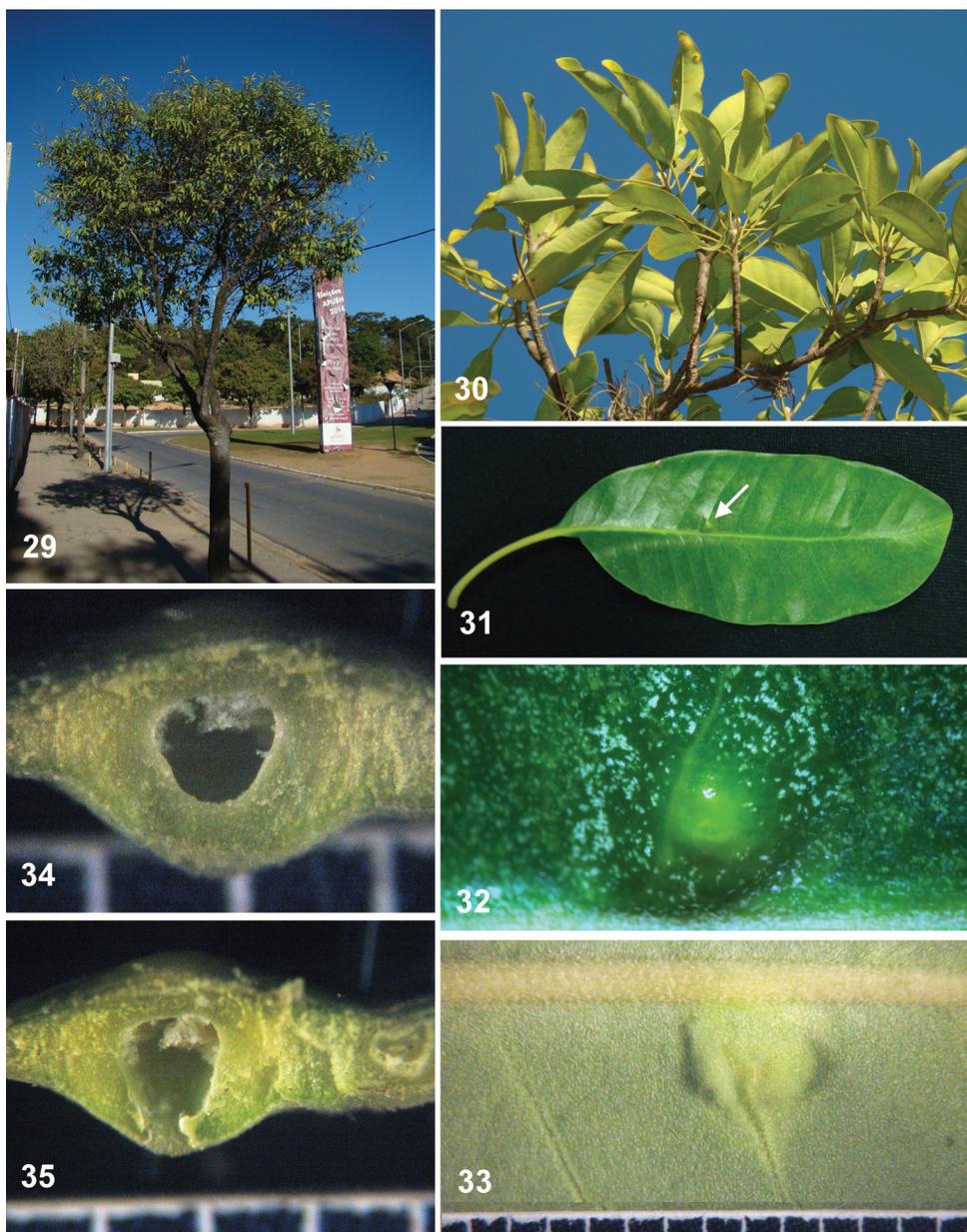
Host plant and biology. Gall-inducer on leaf lamina of *Aspidosperma macrocarpon* Mart. and *A. tomentosum* Mart. (Apocynaceae) (Figs 36, 37). The intralaminar lenticular galls (*sensu* ISAIAS et al. 2013) on *A. macrocarpon* were described by CASTRO et al. (2013): they are induced on the abaxial surface of the leaf by the feeding action of the first-instar immatures of *P. longicaudatum*; mature galls are green, 5.3 mm large in diameter and 1.3 mm high, slightly protruding to the adaxial leaf surface with a higher prominence to the abaxial surface, with a single inner central chamber opening to the abaxial surface through a narrow ostiole (Fig. 40). They occur on the leaves of *A. macrocarpon* in large numbers (in average, there are 18.1 galls per leaf; SD = 14.6, n = 40). The period of induction coincides with the

appearance of young tissues, with the highest numbers of galls recorded in January (62.8 % leaves infested) and July (65.2 %) following two peaks of leaf flushing and highest nitrogen content of the host in October and June. In Brazil: Goiás, gall senescence takes place in the dry season from March to September, together with that of the host leaves. The beginning of *A. macrocarpon* leaf falling in March causes the interruption of *P. longicaudatum* life cycle by premature abscission of immature galls (CASTRO et al. 2013). The galls on *A. tomentosum* have the same structure, being 3.8 mm large in diameter and 1.6 mm high (Figs 38, 39), and occur on the leaves with an infestation index of 75 %. The gall induction occurs exclusively on young leaves (unpublished data). On both host plant species *P. longicaudatum* sp. nov. presents a univoltine life cycle.

Distribution. Brazil (Distrito Federal, Goiás, Minas Gerais, Mato Grosso do Sul, Paraná and São Paulo). Psyllid galls on *Aspidosperma tomentosum* which involve this species were also recorded from Brazil: Goiás by ARAÚJO et al. (2007) and SANTOS et al. (2012). The host plants, *A. macrocarpon* and *A. tomentosum*, are widely distributed in all regions of Brazil (Acre, Tocantins, Bahia, Maranhão, Pernambuco, Piauí, Distrito Federal, Goiás, Mato Grosso do Sul, Mato Grosso, Espírito Santo, Minas Gerais, Rio de Janeiro, São Paulo, Paraná, Santa Catarina), Bolivia, and Paraguay; *A. macrocarpon* is also present in Peru and Venezuela (WOODSON 1951, HASSLER 2014).

Discussion

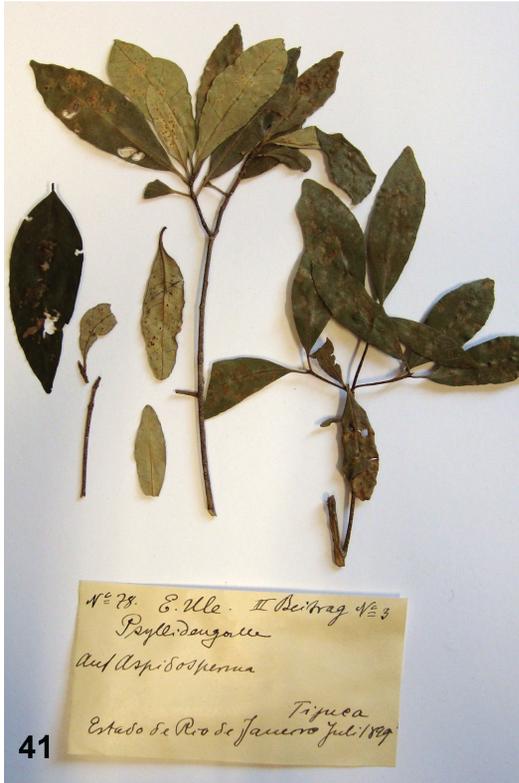
With the two new taxa associated with *Aspidosperma*, the number of formally described Neotropical Phacopteronidae species increases to eight. Besides the monotypic *Phacosemoides* Costa Lima & Guitton, 1962 (including *Phacosemoides sicki* Costa Lima & Guitton, 1962 from Brazil: Pará), there are five previously described species of *Pseudophacopteron* from Panama (BROWN & HODKINSON 1988). *Pseudophacopteron aspidospermi* sp. nov. and *P. longicaudatum* sp. nov. are similar to *P. nervosum* Brown & Hodkinson, 1988, *P. punctinervis* Brown & Hodkinson, 1988, *P. vitivenis* Brown & Hodkinson, 1988, and *P. antennatum* Brown & Hodkinson, 1988 from Panama in the head morphology (particularly in the weakly inflated genae with small, acute tubercle under the insertion of antenna), antenna (with a single, large, elliptic rhinarium bordered with a wreath of cuticular spines on apices of each of segments 4–9), fore wing venation, and hind leg (the medially constricted metafemur and the presence of lateral spurs on metatibia along its length). These characters are shared also with the Afrotropical *P. zimmermanni*-group as defined in MALENOVSKÝ & BURCKHARDT (2009; the group includes *P. zimmermanni* Aulmann, 1912 and additional 25 species), as well as *Pseudophacopteron* species described from the Oriental Region including the type of the genus, *P. tuberculatum* (Crawford, 1912) (MATHUR 1975, YANG et al. 2009, LI 2011). The remaining Neotropical species, *P. perlucidum* Brown & Hodkinson, 1988 from Panama, is similar in the head and hind leg structure but differs from the aforementioned phacopteronids in the fore wing venation (in the absence of the cu_1 cell) and details of the rhinaria (BROWN & HODKINSON 1988; Malenovský & Burckhardt, unpublished data). *Phacosemoides sicki* is distinct in having the genae more markedly swollen, forming prominent projections oriented ventrally, in the robust unstricted metafemur, and the lack of lateral spines on the metatibia (COSTA LIMA & GUITTON 1962, Malenovský & Burckhardt, unpublished data). Within *Pseudophacopteron*,



Figs 29–35. Host plant and galls of *Pseudophacopteron aspidospermi* sp. nov. 29 – *Aspidosperma australe* tree on the street of the Pampulha Campus of Universidade Federal de Minas Gerais, Belo Horizonte, the type locality of *P. aspidospermi*; 30 – vegetative branch of *A. australe* with some leaves showing galls of *P. aspidospermi*; 31 – leaf of *A. australe* with a gall of *P. aspidospermi* (white arrow); 32 – detail of the gall, seen on the adaxial leaf surface; 33 – detail of the gall, seen on the abaxial leaf surface; 34, 35 – hemi-sections of a mature gall showing the inner chamber and the ostiole.



Figs 36–40. Host plant and galls of *Pseudophacopteron longicaudatum* sp. nov. 36 – *Aspidosperma tomentosum* tree in a cerrado area near Uberlândia (Reserva Ecológica do Clube Caça e Pesca Itororó); 37 – vegetative branch of *A. tomentosum* with leaves showing galls of *P. longicaudatum*; 38 – detail of the galls on *A. tomentosum*, seen on the adaxial leaf surface; 39 – hemi-section of a gall on *A. tomentosum* showing an immature of *P. longicaudatum* in central chamber; 40 – hemi-section of a gall on *A. macrocarpon*.



Figs 41–43. Herbarium specimen of *Aspidosperma australe* with galls of *Pseudophacopteron aspidospermi* in the Rübsaamen collection, ZMHB. 41 – twig with original label; 42 – detail of the adaxial leaf surface; 43 – detail of the abaxial leaf surface with senescent galls.

P. aspidospermi and *P. longicaudatum* may be closely related: besides sharing the host plant genus, they both lack lateral spurs on the metabasitarsus, which is probably an apomorphic character state within the Psylloidea and the Phacopteronidae.

Pseudophacopteron galls on *Aspidosperma* are similar in structure to the intralaminar galls induced by *P. zimmermanni* on *Khaya anthotheca* Welw. C. DC. and *K. senegalensis* Desr. A. Juss. (Meliaceae), *P. electum* on *Ekebergia capensis* Sparrm. (Meliaceae), *P. fuscivenosum* Malenovský, Burckhardt & Tamesse, 2007 on *Deinbollia* sp. (Sapindaceae) and *P. lecaniodisci* Malenovský, Burckhardt & Tamesse, 2007 on *Lecaniodiscus cupanioides* Planch. (Sapindaceae) in Africa (AULMANN 1911, 1912; HOUARD 1922; SCHABEL 2006; MALENOVSKÝ et al. 2007; OLMÍ & CORREIA 2008), and *P. tuberculatum* on *Alstonia scholaris* (L.) R. Br. (Apocynaceae) in tropical south-eastern Asia (HOUARD 1923, MANI 1964, ALBERT et al. 2011). The immatures of these species share a similar morphology: an elongate, cylindrical, weakly sclerotised body, short antenna, and simply structured ventral anus surrounded by a single row of wax pores (RAHMAN 1932, MALENOVSKÝ et al. 2007; generally, the immature morphology of Psylloidea reflects largely the immature biology: BURCKHARDT 2005). Some other species of the Phacopteronidae and *Pseudophacopteron* induce different types of galls (open pit galls or closed nut galls) or are free-living on their host plants (RAMAN 1987, MALENOVSKÝ et al. 2007, MALENOVSKÝ & BURCKHARDT 2014).

In general, biology of the Phacopteronidae is poorly known. Details provided on the galls and phenology of *P. aspidospermi* and *P. longicaudatum* by ISAIAS et al. (2000), CHRISTIANO (2002), CHRISTIANO et al. (2003), OLIVEIRA & ISAIAS (2010), OLIVEIRA et al. (2011), CAMPOS et al. (2010), and CASTRO et al. (2013) make them the best studied species of the family, apart from the Indian *Phacopteron lentiginosum* Buckton, 1896, inducing conspicuous galls on *Garuga pinnata* Roxb. (Burseraceae) in India, for which the cecidogenetic process and life cycle has been studied in detail (MATHUR 1946, RAMAN 1987). More field and laboratory work is, however, needed to determine the number of generations, the host plant ranges and natural enemies of *P. aspidospermi* and *P. longicaudatum*.

CAMPOS et al. (2010) hypothesized that in Minas Gerais *P. aspidospermi* is multivoltine, while CASTRO et al. (2013) suggested a single generation per year for *P. longicaudatum* based on the distinct phenological cycle of the host plant due to the alternation of dry and wet seasons in Goiás.

In the Campus of Pampulha of the Universidade Federal de Minas Gerais in Belo Horizonte, galls of *P. aspidospermi* are common on *Aspidosperma australe* while no galls have been observed on the related *A. cylindrocarpon* Müll. Arg., commonly occurring at the same locality. ISAIAS et al. (2000) suggested that the resistance of *A. cylindrocarpon* to the galling activity of *P. aspidospermi* may be related to structural differences in the leaf epidermis and mesophyll as well as to a higher content of phenolic compounds in *A. cylindrocarpon*. In contrast, *P. longicaudatum* is recorded from two different host plant species. The populations of *A. macrocarpon* studied by CASTRO et al. (2013), and that of *A. tomentosum* (field observation) are sympatric in Minas Gerais and Goiás. In addition, these plant species are phylogenetically very close (WOODSON 1951), and the psyllids may not recognize them as different species. Currently it is not known whether there are other *Pseudophacopteron* spp. that are associated with any of the many other *Aspidosperma* species known in South and Central America.

As far as known, *P. aspidospermi* and *P. longicaudatum* are restricted to dry woodland and savanna (cerrado) habitats of south-central and south-eastern Brazil, which are very diverse with a high percentage of endemic plant and animal species. For this reason the cerrado zone has recently been recognised as a biodiversity hotspot (MYERS et al. 2000, PENNINGTON et al. 2006, WERNECK 2011). As data on the psyllid fauna of Brazil and neighbouring countries are still scarce (BURCKHARDT & QUEIROZ 2012), the exact distribution, habitat requirements and status of endemism of *P. aspidospermi* and *P. longicaudatum* are difficult to evaluate at the moment.

According to HODKINSON (1989), the pantropical genus *Pseudophacopteron* represents a tropical Guyano-Brazilian element in the Neotropical fauna and is distributed from Brazil in the south to lowland Mexico in the north. Based on unidentified material in several museum collections (mainly BMNH, NHMB and USNM), there are many undescribed species of the genus from tropical and subtropical South, Central and North America. *Pseudophacopteron* appears, however, to be absent from the temperate and subantarctic South America south of 30°S, where the psyllid fauna is better explored (BURCKHARDT 1987a,b, 1988). So far, the record of *P. aspidospermi* from Santa Catarina in Brazil represents the southernmost occurrence of the genus in South America.

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