Review of the Neotropical Genus *Sparnia* Stål (Hemiptera, Fulgoroidea: Delphacidae)

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Abstract—The South American planthopper genus *Sparnia* Stål has been revised. For the three species accommodated here, supplementary descriptions and detailed illustrations of the male genital structures are provided. The phylogenetic relationships of *Sparnia* to other genera of Delphacini and of the species within the genus are briefly discussed. At least for one species, *S. praecellens*, a potential role as a pest on sugar cane cannot be ruled out.

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INTRODUCTION

The Neotropical Region is generally considered as one of the most species-rich and diverse floral and faunal areas of the World (e.g., Foottit and Adler, 2009). The insect order Hemiptera is well represented there and covers a significant portion of the taxa described worldwide (e.g., McKamey, 1999).

In the Neotropics, the hemipteran suborder Auchenorrhyncha has been referred to by many authors, mostly concerning the taxa of the subgroup Cicadomorpha (e.g., Linnavuori, 1959; Young, 1968, 1977; de Remes Lenicov, 1973; Deitz, 1975). The Fulgoromorpha with the recent superfamily Fulgoroidea (*planthoppers*), however, has only received fragmentary attention mostly devoted to single families (e.g., Broomfield, 1985; see also the list of Fulgoromorpha taxa in FLOW, Bourgoin, 2015). A comprehensive overview of the planthoppers of the Neotropics similar to that recently presented for the United States by Bartlett et al. (2014) does not exist.

One of the planthopper families which must still be regarded as insufficiently known in South America is the Delphacidae. Distributed worldwide, this family comprises more than 2000 described species (e.g., Asche, 1985b; Ding, 2006). From the vast area of land south of the United States covering Central and South Americas as well as the Caribbean, nearly 300 species have been reported (e.g., Fowler, 1905; Crawford, 1914; Muir, 1926; Metcalf, 1938; Fennah, 1945, 1959, 1963, 1964, 1965a, 1965b, 1967, 1969a, 1971; Caldwell and Martorell, 1951); however, some 150 species are known from the South American continent *sensu strictu*. Recent publications deal with some taxa from South America like the delphacine genus *Pissonotus* Van Duzee (Bartlett and Deitz, 2000) and the subfamily Asiracinae (Barringer and Bartlett, 2011). Many other delphacid taxa, some of them described nearly a century ago (e.g., by Muir, 1926), remain enigmatic or taxonomically obscure as only sketchy descriptions with no or rather superficial illustrations provided.

One of these little known endemic South American genera is Sparnia Stål, 1862, established as monotypical with Sparnia praecellens Stål, 1862, based on a single specimen from Brazil (Rio de Janeiro: Stål, 1862). Muir (1915) discussed this genus but commented that he knew it only from the literature; however, he included Sparnia in his key to the tribe Delphacini sensu Lambertie, 1910. Later, Muir and Giffard (1924), as well as Muir (1926), placed Sparnia together with the New World genera Burnilia Muir et Giffard, 1924 and Stobaera Stål, 1859 in the tribe Alohini Muir. Muir (1926) also associated the monotypical genus Synpteron Muir, 1926 with this tribe. Surprisingly, Metcalf (1943) placed Sparnia (together with the taxonomically unclear Synpteron) in the tribe Tropidocephalini Muir. Finally, Fennah (1959) returned all the South American genera mentioned above to Alohini (giving no comment on the Metcalf's placement of *Sparnia* and *Synpteron* in Tropidocephalini). Asche (1985b) synonymized the Alohini with Delphacini, and listed *Sparnia* within the latter.

Sparnia remained monotypical with Sparnia praecellens for more than 60 years, and was known only from the type specimen from Brazil until Muir and Giffard (1924) and Muir (1926) reported a "long series" of specimens of this species collected in 1922 by the American entomologist F.X. Williams (Bishop Museum, Honolulu) on sugar cane in Ecuador. Based on Williams' samples, Muir (1926) described the second Sparnia species, viz., Sparnia williamsi from Ecuador. Only one year later Muir (1927) added the third species to this genus, Sparnia edwardsi from Chile (Chiloe Island) collected by the British entomologists F. and M. Edwards in 1926, and for the first time provided illustrations of the undissected male genitalia in left lateral and caudal view for a species of this genus. He also referred to the presence of nymphs in his material. Fennah (1959) reported S. praecellens from Venezuela (based on a single female); otherwise no further records of any of the three Sparnia species have been published. Thus, we take the recent findings of S. edwardsi in Chile by A.F. Emeljanov and E.D. Lukashevich (Palaeontological Institute of the Russian Academy of Sciences, Moscow) as a welcome occasion to revise the genus, to provide detailed illustrations for each species, and to discuss its generic placement in the Delphacini.

MATERIALS AND METHODS

Measurements and illustrations (line drawings and photographs) of the external body parts were taken from dry specimens. An A Leitz stereomicroscope with *camera lucida* was used for morphological examinations and for producing line drawings. For studying the male genitalia the abdomina were removed from the specimens and macerated in 10% KOH for 24 hours at room temperature, then transferred to glycerin for storage and/or to glycerin-jelly for preparing drawings. Photographs were taken with a Canon EOS 650 D camera attached to a Leica MZ 16 stereo microscope.

The terminology of body structures, including male genitalia, with slight modifications follows Asche (1985b), that of female genital structures is adjusted to Bourgoin (1993); terminology of tegminal and hind wing venation follows Bourgoin et al. (2014), also discussing the interpretation by Anufriev and Emeljanov (1988).

The specimens examined are deposited in the following collections (the acronyms following Evenhuis and Samuelson, 2005, resp. Evenhuis, 2012):

BMNH, The Natural History Museum, London, UK;

BPBM, Bernice P. Bishop Museum, Honolulu, Ha-wai'i, USA;

NCSU, North Carolina State University Insect Collection, Raleigh, USA;

NHRS, Naturhistoriska Riksmuseet, Stockholm, Sweden;

SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany;

UDCC, University of Delaware, Newark, Delaware, USA;

ZIN, Zoological Institute RAS, St. Petersburg, Russia.

TAXONOMY

SPARNIA Stål, 1862 (Figs. 1–16)

Sparnia Stål, 1862 : 6, type species: Sparnia praecellens Stål, 1862 : 6 [Brazil], by monotypy.

Sparnia: Stål, 1866 : 175 [Key].

Sparnia: Ashmead, 1889 : 25 [Key].

Sparnia: Muir, 1915 : 296 [Key].

Sparnia: Muir and Giffard, 1924 : 4 [Key].

Sparnia: Muir, 1926 : 6 [listed].

Sparnia: Metcalf, 1943 : 108 [listed].

Sparnia: Fennah, 1959 : 250 (Key), 252 [listed].

Stål (1862 : 6) described the genus in Latin, and characterized only the external characters of the head including antennae as well as the thorax including tegmina and legs. He mentioned a short and narrow vertex (coryphe) (*"caput vertice parvo, antrorsum angustato, latitudine vix longiore"*), a narrow and elongate frons (metope) with foliately ridged lateral carinae (*"fronte … angusta, elongata, … marginibus lateralibus carinato-elevatis"*); furthermore, elongate, parallel-sided and compressed antennae (*"Antennae*



Fig. 1. Sparnia spp., left antenna, front view: (A) S. praecellens Stål; (B) S. williamsi Muir; (C) S. edwardsi Muir. Scale bar 0.1 mm.

longae, ..., compressae, parallelae, ..."), and a tricarinate mesonotum with carinae parallel to each other ("Thorax cum scutello parallele tricarinatus"). He described the tegmina as fully developed and distinctly surpassing the apex of the abdomen ("Tegmina completa, abdomen multo superantia, ..."); he clearly referred to the shape of the claval vein (Pcu+A1), "Y-vein") ("corio venis tribus longitudinalibus, furcates, pone medium convergentibus, ...") and to the apical cells of which the median one is the longest and widest ("areolis apicalibus longis, media longiore, latiore."). Finally he characterized the legs as elongate, slender and simple ("Pedes longiusculi, graciles, spimplices."). Stål (1862) stated an affinity of Sparnia to the genus Araeopus Spinola, 1839 ("Genus Araeope affine.").

Diagnosis. The genus Sparnia Stål can readily be distinguished from other South American delphacid genera by the following combination of characters: head distinctly narrower than pronotum, vertex (eucoryphe with areolet) subtriangular, compartimention absent or faint; frons (eumetope) very elongate and narrow, at least apically deeply concave, frontal carinae elevated; antennae extremely elongate, partly surpassing anteclypeus, scape foliately compressed, in two species with a distinct longitudinal median rib; legs slender, elongate; post-tibial spur slender, terete in cross-section, posterior margin with separated coneshaped teeth ("alohinoid"). Male genitalia with rather elongate genital styli which are basoventrally furnished with a spinose process and apically with two projections pointing medially; with a short anal segment which ventrocaudally displays a single spinose process; with a rather short tubular aedeagus which is bent ventrally and furnished on both sides with minute teeth; with a suspensorium which consists of a sclerotized ring surrounding the aedeagal base and a dorsal flange.

Distribution. Endemic to South America from Venezuela in the North to Chile in the South.

Key to the Species of Sparnia Stål

For comparison of shape and proportions of the antennal joints of the three *Sparnia* species see Fig. 1.



Fig. 2. Sparnia praecellens Stål, head: (A) dorsal view; (B) left lateral view; (C) ventral view. Scale bar 0.5 mm.

Sparnia praecellens Stål, 1862 (Figs. 2–5; 15*A*, 16*A*)

Sparnia praecellens Stål, 1862 : 6 (Brazil).

Sparnia praecellens: Muir and Giffard, 1924 : 7.

Sparnia praecellens: Muir, 1926 : 6.

Sparnia praecellens: Muir, 1927: 297.

Sparnia praecellens: Fennah, 1959 : 252.

In the original description Stål (1862 : 6–7) mentioned color and color patterns of the head including antennae, thorax including tegmina and legs, and abdomen. He provided measurements of the total length and width, but did not mention number and sex of the specimens examined. The only specimen available in the collections of the Swedish Museum of Natural History, Stockholm ("*Mus. Holm.*") is a macropterous male from Brazil which was designated as type, probably by Stål. It is likely that this is the only specimen which was available to Stål. After more than 150 years the specimen is still intact, i.e., it is not dissected or otherwise damaged. In addition, we have examined specimens from Ecuador (partly those mentioned in Muir and Giffard, 1924; Muir, 1926), Columbia, Peru, and Venezuela (mentioned by Fennah, 1959) which

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Fig. 3. Sparnia praecellens Stål, thorax: (A) left hind tibia and tarsus, dorsal view; (B) left forewing; (C) left hind wing; (D) male sound producing organ, posterior view. Scale bars 0.5 mm (A-C) and 0.1 mm (D).

appeared to be conspecific; thus we use the opportunity to provide a supplementary description of the external features as well as the first description of the genital structures.

Supplementary description. Slender, mediumsized delphacid with predominating orange-brownish color.

Body length (measured from apex of head to tip of tegmina; macropterous individuals): males (n = 5, including holotype): 4.3–4.7 mm, holotype: 4.5 mm (5.0 mm according to Stål, 1862); females: (n = 4): 4.8–5.3 mm.

Brachypterous individuals unknown.

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Head and thorax. Vertex (coryphe with areolet) subtriangular, shallowly concave, lateral carinae strongly ridged and anteriorly converging to pointed apex, compartment vestigial, median carina absent or faint, vanishing toward apex. Frons (eumetope) very elongate and narrow, medially about 3.5 times as long as wide, widest near frontoclypeal suture, about 1.35 times as long as post- and anteclypeus combined; lateral carina foliately ridged, converging toward apex, median carina sharply ridged, enclosed frontal surface concave; postclypeus medially about 1.2 times as long as anteclypeus, lateral carinae foliately ridged, median carina of post- and anteclypeus weakly developed. Antennal joints elongate, distinctly surpassing anteclypeus, scape strongly compressed and dilated, ante-



Fig. 4. Sparnia praecellens Stål, male genitalia: (A) male genital capsule, undissected, left lateral view; (B) genital segment, left lateral view; (C) genital segment, ventral view; (D) genital capsule, undissected, caudal view; (E) genital segment, caudal view. Scale bar 0.1 mm.

riorly along midline strongly ridged; pedicel compressed at dorsal base, forming a short ridge, then terete, on all sides furnished with numerous sensory plaques arranged in rows. Compound eyes relatively small, flat, kidney-shaped, above antennal base with deep elongate incision separated from dorsal margin of eye by narrow area; ocelli well developed, close to lower anterior margin of compound eyes; transition of coryphe to metope in lateral view smoothly rounded; genal carina slightly arched, ridged; *lamina maxillaris* with lower margin concave. Pronotum about 1.5–1.6 times as wide as head including compound eyes, about 4 times as wide as long medially, posterior margin slightly concave; carinae of disk strongly ridged, enclosed area nearly flat, lateral carinae slightly arched, reaching posterior margin; sublateral part of pronotum with faint and incomplete carina. Mesonotum medially about triple as long as pronotum; carinae ridged, lateral carinae subparallel to median one, not reaching posterior margin; enclosed area of disk nearly flat. Tegulae large, about as long as dorsally wide. Tegmina (macropterous form) elongate, about 3.15 times as long as wide, widest at level of entering CuA2 into commissural margin; in both sexes surpassing tip of abdomen with nearly half of their length; apically slightly pointed at



Fig. 5. Sparnia praecellens Stål, male genitalia: (A) anal segment, aedeagus, suspensorium, connective and genital styles in situ, left lateral view; (B) aedeagus, left lateral view; (C) aedeagus and suspensorium, ventrocaudal view; (D) aedeagus, right lateral view; (E) anal segment, ventral view; (F) genital styles, caudal view. Scale bars 0.1 mm.

level of M2; outer subapical cell (C1) distinctly larger than inner cell (C5); M basally of nodal line sinuately curved; M distally branched into M1 and M2, CuA1 straight, unbranched, CuA2 branched shortly beyond nodal line; basal cell present but distally weakly limited. Hind wings with short distal branch of M.

Legs. Hind tibia about twice as long as hind tarsal joints combined, laterally with two spines: one short very close to base, the other one longer, below midlength in distal third; distally with 5 spines: 3 longer ones forming an oblique row on outer margin, 2 short ones on inner margin. Post-basitarsus about 1.6 times as long as 2nd and 3rd post-tarsal joints combined, about 1.45 times as long as post-tibial spur; distally with 6 spines grouped into 3 outer and 3 inner ones. 2nd post-tarsal joint distally with 4 spines in a row. Post-tibial spur very slender, convex on both sides, posterior margin furnished with 8 or 9 coneshaped teeth well separated from each other ("alohinoid" configuration). Male sound-producing organ with sternal apodemes weakly developed, apodemes of first abdominal sternite subtriangular, those of second abdominal sternite forming short spinose processes.

Coloration. Surface of vertex (coryphe with areolet) including median carina pale yellow, posteriorly on both sides of median carina in some individuals (including holotype) with oblong-ovate brown mark, in others with faint orange spot, apex of coryphe with areolet at transition to eumetope (frons) brown; lateral carinae pale yellow, anteriorly, in middle part and posteriorly interrupted by short brown stretches. Frons (eumetope) orange-brown to chestnut-brown, lateral carinae concolorous with brownish crest, position of ocelli on inner sides of lateral carinae marked dark; median carina creamy-white. Postclypeus chestnutbrown, lower part darker; lateral and median carinae creamy-white. Anteclypeus dark brown, median carina creamy-white, crested brown; laterally with pale yellow spot. Head laterodorsally above compound eyes pale yellow with two narrow transverse brown stripes; genae orange-brown, oblique genal carina and antennal base creamy-white; lamina maxillaris dorsally pale yellow, ventrally dark brown. Rostrum brown with black tip. Antennae: scape chestnut-brown with lower margin creamy-white; pedicel dark brown, dorsal crested base whitish. Pronotum orange-brown with lateral parts creamy-white; disk in some individuals (including holotype) chestnut-brown; carinae creamywhite, finely fringed brown. Mesonotum orange- to chestnut-brown, laterally lighter, lateroposterior angles creamy-white; carinae creamy-white, fringed brown; scutellum dark brown. Tegulae creamy-white with lateral parts brown. Sides of pro- and mesonotum as well as median part of tegulae forming continuous arched creamy-white longitudinal stripe. Tegmina semitranslucent, basal half until nodal line faded orange-brown in midlength with hyaline fenestra between costal margin and M; between CuA and CuP partly a dark brown stripe; M and claval "Y-vein" fringed white; other veins brownish or in hyaline parts pale yellow, pustules on veins brown; commissural margin anterior of junction with Pcu and A1 brown; nodal line from commissural margin to level of outer subapical cell (C1) whitish; membrane largely hyaline, furnished with two arched brown stripes: one posteriorly along nodal line broadly fringing inner and apical margin until the level of apical M-branchesaltogether forming a nearly semicircular band; the other stripe narrower, parallel to first one and filling the space between apical branches of *RP*. Hind wings translucent, veins sordid yellowish brown.

Legs: fore and middle coxae dark brown, posterior coxae orange-brown. Fore femur dark brown, anterior margin yellowish, medially on anterior side with narrow longitudinal pale yellow stripe; middle femur dark brown, anterior margin yellowish, median longitudinal stripe on anterior surface not obvious; posterior femur dark brown, upper anterior margin yellowish, underside distally with faint median yellow stripe. Tibiae mostly stramineous, somewhat brownish at inner margin. Fore and middle tarsi chestnut- to blackish brown; posterior tarsi as well as post-tibial spur stramineous. Abdominal tergites and sternites fuscous; male genitalia brown; female genitalia with ovipositor mostly light stramineous, bases of gonoplacs brownish, gonocoxae VIII brown with yellowish inner margin.

Male genitalia. Genital segment in lateral view trapezoidal, ventrally about 2.6 times as long as dorsally, caudal margin nearly straight, vaulted ventrocaudally; in ventral view subquadrangular with caudal edges inflecting medially, mediocaudal margin slightly concave; in caudal view high ovate, dorsal margin of dorsal foramen straight, dorsally a flat bridge with a shallow furrow on each side, diaphragm narrow with a few transverse wrinkles, foramen for genital styli flat, ovate with dorsal margin slightly convex, surrounding parts sclerotized; lateral margins gently rounded toward middle. Aedeagus slender, finger-shaped, gently curved ventrally, from broad base narrowing toward rounded apex; left laterally with continuous row of about 30 minute teeth from basal third to lower apex, right laterally with continuous row of about 29 teeth from dorsal level of bending to lower apex; phallotreme caudally exposed, elongate and narrow, slit-like. Suspensorium pull-tab-like, i.e., flat dorsal y-shaped base connecting to sclerotized ring which entirely surrounds the aedeagal base. Connective slightly compressed, dorsally almost straight, ventrally slightly curved caudally. Anal segment short, mediocaudally on ventral side with a single sturdy spinose process which is curved subrectangularly ventrad; ventral surface membranous; lateral parts of ventral base lobate. Anal stylus slightly compressed, ventrally largely membranous, slightly longer than anal segment; epiproct small, in lateral view hardly visible. Genital styli elongate, directed dorsally, in repose attaining base of anal segment; in lateral view from narrow base widening toward subtriangular apex reminding on a snout, ventromedially at base with distinct subtriangular projection; in caudal view subapically on inner margin at level of dilated distal part with pair of spinose processes or lobate projections, resp., directed medially, lower one relatively long, heavily sclerotized and apically pointed, upper one shorter and apically rounded.

Female genitalia. Ovipositor distinctly surpassing anal segment; gonocoxae VIII caudally narrow, roundly dilated toward base; gonapophyses IX (*sensu* Bourgoin, 1993; = "mediane gonapophyse IX" *sensu* Müller, 1942; = "second valvae" *sensu* Emeljanov, 2014) dorsally in caudal half very finely serrate, nearly smooth.

Nymphs unknown.

Diagnosis. Sparnia praecellens is similar to S. williamsi in the shape of the antennae and the terminally pointed tegmina; they also share the anastomosis between M and Cu in the hind wing; these characters are different in the third species S. edwardsi. Sparnia praecellens differs from S. williamsi in the proportions of the tegmina (membrane dilated beyond nodal line in S. praecellens versus that not dilated in S. williamsi); in the proportions of the antennal scape (4.8 times as long as wide in S. praecellens versus 5.8 times that in S. williamsi); in genital styli with an elongate spinose process on the ventral base and a short subapical lobe versus short spinose process and elongate subapical lobe in S. williamsi); in the genital segment with shallowly concave caudal margin in S. praecellens versus triangularly excavated margin in S. williamsi).

Distribution (Fig. 14, *3*). Brazil (type locality: Rio de Janeiro), Columbia, Ecuador, Peru, Venezuela.

Host plants and ecology. Label data of the specimens collected in Ecuador say that S. praecellens is associated with sugar cane (Muir and Giffard, 1924 : 7, "...living on sugar cane;" Muir, 1926 : 6, "...it can be considered as a sugar cane species."). In his list of sugar-cane insects worldwide known at that time Box (1953 : 40) mentioned this record; however, he did not indicate any pest status or name any potential parasitoids and predators. In the later literature this record on sugar cane found no mention either in Fennah's "Pests of Sugar cane" (Fennah, 1969b), or in the "Survey of planthopper pests of economically important plants" by Wilson and O'Brien (1987), or in the faunistic contribution to Auchenorrhyncha on sugar cane by Wilson (1988). As Muir and Giffard (1924) and Muir (1926) reported a large number of specimens collected from sugar cane its role as a potential pest species cannot be excluded. Since in the New World sugar cane is an introduced plant (from Asia) the primary host plants of this species remain unknown.

Remarks. Muir and Giffard (1924) enumerated delphacid genera from the New World known at that time (not only North American ones as could be assumed from the title of their paper); they gave a brief generic description of Sparnia Stål which was most likely based on the specimens from Ecuador collected by F.X. Williams (see above) and identified by them as Sparnia praecellens. Muir and Giffard (1924) described only external characters. There is no mention of re-examination of the type from Brazil, and most likely, it was not available to them at that time. Muir (1926) listed this species from Ecuador as Sparnia praecellens without describing specific features including genitalia. A few characters of the male genitalia of the Ecuadorian S. praecellus can be only indirectly deduced from the comparison with the second Sparnia species, S. williamsi Muir, for which a brief description of the male genitalia (without illustrations) was provided (Muir 1926 : 6): "The genitalia are similar, but the arrangements of small spines or teeth along the penis are quite distinct."

Material. Holotype: ♂, macropterous, examined, pinned through base of abdomen, otherwise intact; labelled: "Brazil" (white rectangular, printed); "F. Sahlb." (white rectangular, printed), "Typus" (red rectangular, printed); NHRS.

Additional material. 1 3, macropterous, Ecuador, Banos Or. 6000 ft., 26.X.1922, F.X. Williams, sugarcane, with Muir's handwritten label "Sparnia praecellens (Stal)" (sic); left forewing missing right forewing damaged: distal membrane missing; 1 Å, macropterous, same locality data and collector, 31.XII.1922, with handwritten label "Sparnia praecellens" (not Muir's handwriting); genitalia dissected by M. Asche in 1984, preserved in glycerin in genital vial attached to specimen; both in BMNH: accession-number 1928-293. 1 Q, macropterous, Venezuela, Rancho Grande, E. do Aragua, Marcuzzi, III.(19)49, "Sparnia praecellens Stål" (probably handwritten by Fennah), R.G. Fennah collection, B.M. 1951-511, BMNH. 1 \mathcal{E} , macropterous, Peru, Tingo Maria, forested eastern foothills of the Andes, shrubs on hillside 1 mile NE of the town, 2000 ft., 5.VIII.1971, P.S. & H.L. Broomfield, B.M. 1971-486, genitalia dissected by M. Asche in 1984, preserved in glycerin in genital vial attached



Fig. 6. Sparnia williamsi Muir, head: (A) dorsal view; (B) left lateral view; (C) ventral view. Scale bar 0.5 mm.

to specimen, labelled "*Sparnia praecellens* Stål, det. M. Asche 1984," BMNH. 1 ♂, Columbia, Medellin, La Estrella, 1720 m, Seminar, 21.X.1972, P.A.B. Schneble, SMNS.

> *Sparnia williamsi* Muir, 1926 (Figs. 6–9, 15*B*, 16*B*)

Sparnia williamsi Muir, 1926 : 6 (Ecuador).

Sparnia williamsi: Muir, 1927: 297.

In the original description of *Sparnia willamsi* Muir (1927) states an external similarity with *S. praecellens* in the structural body parts and provides information on coloration and color patterns, especially those of the head and tegmina. For the first time the male genitalia of a *Sparnia* species were addressed, although without illustrations. Muir (1926) described as most notable the anal segment with a single spinose medioventral process, also the narrow and elongate genital styli each with an inner marginal spine at base, as well

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Fig. 7. Sparnia williamsi Muir, left forewing. Scale bar 0.5 mm.

as a short, curved, subtubular aedeagus with minute spines in a row.

Here we provide supplementary information, especially on the morphological configuration of the male genitalia.

Supplementary description. Medium-sized, slender delphacid with predominantly brownish color.

Body length: macropterous individuals (from apex of head to tip of tegmina): males (n = 2, including holotype): 4.0 mm.

Females, nymphs, and brachypterous individuals unknown.

Head and thorax. Vertex (coryphe with areolet) as in S. praecellens acutely triangular with surface deeply concave, lateral carinae strongly ridged, median carina only posteriorly faintly visible. Frons (eumetope) elongate and narrow, medially about 4.2 times as long as wide, widest shortly above frontoclypeal suture, about 1.45 times as long as post- and anteclypeus combined; lateral carinae strongly ridged, ventrally slightly convex, then straight and converging toward apex, median carina sharply ridged; frontal surface, especially in dorsal part, shallowly to deeply concave. Antennal joints elongate, rather narrow, distinctly surpassing tip of anteclypeus; scape strongly compressed, anteriorly with elevated mid-rib, about twice as long as pedicel; pedicel compressed at base with short dorsal ridge, then conical, beset with numerous sensory plaques, mostly arranged in rows. Compound eyes relatively small, as in S. praecellens, medioanteriorly with deep incision ventrally sparing the antennal base; ocelli large, at lower anterior margin of compound eyes; transition of vertex to frons in lateral view rounded, lateral frontal carinae slightly sinuate; genal carina sharply ridged, slightly arched; lamina maxillaris slender, its lower margin concave. Pronotum about 1.4 times as wide as head including compound eyes, about 4 times as wide as medially long, posteriorly shallowly concave; disk slightly elevated, carinae sharply ridged, enclosed area nearly flat, lateral carinae convex, reaching posterior margin; sublaterally pronotum dorsally with faint ridge. Mesonotum medially about 2.8 times as long as pronotum, carinae ridged, nearly straight and parallel to each other, not reaching posterior margin; area of disk plane. Tegulae large, in dorsal view slightly longer than wide. Tegmina (macropterous form) elongate and very slender, about 3.8 times as long as wide, widest shortly distad of nodal line, surpassing tip of abdomen by almost half of their length; outer subapical cell (C1) distinctly larger than inner cell (C5); M in basal part straight; in membrane with short anastomosis between M and RP, M apically branching into M1 and M2, inner branch of CuA2 not reaching margin. Hind wings as in S. praecellens. Legs: post-tibia very slender, about 2.3 times as long as post-tarsal joints combined, laterally with 2 spines, a short one at base and longer one submedially, distally with 5 spines: 3 longer ones at outer, 2 very short ones at inner side; post-basitarsus about 1.8 times as long as 2nd and 3rd post-tarsal joints combined, distally with 5 spines, median one slightly shifted toward base; 2nd post-tarsal joint with 3 spines in a row. Post-tibial spur slender, terete in crosssection, posterior margin with 7 or 8 sturdy coneshaped teeth.

Coloration. Vertex (coryphe with areolet) pale yellow, posteriorly light brownish, lateral carinae posteriorly, medially and anteriorly with dark brown fringe, transition to frons (eumetope) brown. Metope, postand anteclypeus chestnut-brown, median frontal carina creamy-white, lateral carinae brownish with darker crest. Rostrum basally brown, then stramineous; tip blackish. Antennal joints chestnut-brown, scape with dorsal and ventral margins fringed narrowly yellow, base of pedicel dorsally with a yellow-brown rim. Lateral parts of head largely chestnut-brown, with



Fig. 8. Sparnia williamsi Muir, male genitalia: (A) male genital capsule, undissected, left lateral view; (B) genital segment, left lateral view; (C) genital segment, ventral view; (D) genital capsule, undissected, caudal view; (E) genital segment, caudal view. Scale bar 0.1 mm.

small transverse yellowish stripe between compound eyes and lateral carina of coryphe; genal carina creamy-white, area posterior to it pale yellow; *lamina maxillaris* entirely dark brown. Pro- and mesonotum with disk dark brown, carinae concolorous except for median pronotal carina yellowish brown; lateral parts of pro- and mesonotum largely orange-brown. Tegulae pale yellow with brown posterior margin; lateroposterior margin of mesonotum, tegulae and anterior sides of pronotum forming continuous oblique pale yellow stripe. Tegmina semitranslucent, mostly dark brown except for narrow hyaline stripe along cells flanking

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Fig. 9. Sparnia williamsi Muir, male genitalia: (A) anal segment, aedeagus, suspensorium, connective and genital styles in situ, left lateral view; (B) aedeagus, left lateral view; (C) aedeagus and suspensorium, ventrocaudal view; (D) aedeagus, right lateral view; (E) anal segment, ventral view; (F) genital styles, caudal view. Scale bars 0.1 mm.

costal margin and for narrow subtriangular hyaline spot between M1 and M2; Pcu pale yellow at base. Hind wings hyaline, veins brownish. Legs: femora

chestnut-brown with yellowish fringe at upper anterior margin; tibiae light brown to stramineous, pro- and mesotarsi dark brown, metatarsi stramineous to pale yellow; post-tibial spur light stramineous. Abdominal tergites and sternites fuscous, epipleurites yellowish brown. Male genitalia chestnut-brown.

Male genitalia. Genital segment in lateral view trapezoidal, caudodorsal margin straight, then bent ventrally in blunt angle, ventrally about 2.3 times as long a dorsally; in ventral view subrectangular, caudal margin medially triangularly excavated; in caudal view high ovate, dorsal foramen large, subcircular with dorsal margin shallowly concave; dorsal part converging, forming shallowly depressed bridge. Diaphragm narrow, shallowly concave, medially with a few transverse furrows; foramen for genital styli flat, ovate, dorsal margin medially distinctly projected, surrounding area heavily sclerotized; lateral margins obtusely rounded. Aedeagus slender, finger-shaped, slightly compressed, from broad base narrowing toward apex, in lateral view dorsally at about midlength bluntly bent ventrally; left laterally, mainly exposed to ventral margin with about 26 minute teeth in slightly curved row; right laterally with about 28 minute teeth in curved row from mediodorsal margin to apex; in caudal view almost parallel-sided with rounded apex; phallotreme elongate, slit-like. Suspensorium pull-tablike as in S. praecellens. Connective compressed, slightly curved caudally. Anal segment short, in ventral view flat, rectangular, mediocaudal margin projected to a single relatively short and sturdy spinose process, laterovental edges lobe-like dilated, medioventral surface membranous. Genital styli elongate, widening toward apex, distal part in lateral view snout-like (as in S. praecellens); at medioventral base with rather short spinose projection directed mediocaudad; dilated part in ventral view with two subapical processes on inner margin, basal one tooth-like and pointed, upper one lobe-like; the processes almost equally long.

Females and nymphs unknown.

Diagnosis. Sparnia williamsi shares with S. praecellens the apically pointed tegmina; however, this is much more pronounced in S. williamsi. Also it shares the anastomosis between M and Cu in the hind wing. Differences between these two species were already mentioned above in the diagnosis for S. praecellens. It should be mentioned that in S. williamsi the mediocaudal spinose process of anal segment is relatively short as compared to the congeners.

Distribution (Fig. 14, 2). Ecuador (type locality: Naranjapata) (Muir, 1926).

Host plants and ecology. Unknown.

Remarks. Sparnia williamsi is apparently the closest relative of *S. praecellens*. It appears to be a rare species confined to Ecuador.

Material. Holotype: \Diamond , macropterous, glued on pointed cardboard mount, examined; labelled: "Naranjapata, 1850 FT., Ecuador, Dec. 1922" (white, rectangular, printed); "F.X. Williams" (white, rectangular, printed); "*Sparnia williamsi* Muir, \Diamond , Type 1205" (handwritten by Muir on rectangular white label with red fringe with print "Holotype"); small rectangular white label with number "1033" [handwritten; in BPBM; originally indicated by Muir (1926) as "*Type No.1205*," in actual Bishop Museum list: Type 4955].

Additional material. 1 ♂, macropterous, Ecuador, Pichincha, Union del Rio Toachi, Otongachi, 15.VII.2005, P. Lenhart, PL02826, 00°19′05″S, 78°57′15.9″W, 770 m, tropical rainforest, on hillside along trail, UDCC.

> *Sparnia edwardsi* Muir, 1927 (Figs. 10–13, 15*C*, 16*C*)

Sparnia edwardsi Muir, 1927 : 296 (Chile: Chiloe Island).

Of the three known *Sparnia* species *S. edwardsi* has been described in greatest detail, not only concerning external structural characters like the head and antennae and coloration. For the first time for a *Sparnia* species the male genitalia in left lateral and caudal views have been illustrated (Muir, 1927 : 297: figs 1, 2). As Muir (l.c.) did not dissect the genitalia, we provide here a more detailed description of the genital structures, describe the female genitalia, and add some further notes on external characters.

In the original description 5 nymphs are mentioned, which have been compared with adults concerning their antennal proportions ("....not so long and the two segments more uniform than in the adult, ...") and the configuration of the median frontal carina ("...median carinae of frons separate for their whole length."). Three of these nymphs (5th instar) were examined by us and are described below.

Supplementary description. Medium-sized, slender delphacids with contrasting pale yellow and blackish brown color, especially expressed in the metope with three transverse blackish stripes.



Fig. 10. Sparnia edwardsi Muir, head: (A) dorsal view; (B) left lateral view; (C) ventral view. Scale bar 0.5 mm.

Body length: macropterous individuals (from apex of head to apex of tegmina): males (n = 3): 3.9–4.3 mm, females (n = 2): 4.7–4.8 mm; brachypterous individuals (from apex of head to posterior end of abdomen): males: (n = 3): 2.1–2.4 mm, females (n = 8): 3.1–3.3 mm; nymphs (5th instar, n = 3): 1.9–2.1 mm.

Head and thorax. Vertex (coryphe with areolet) triangular, lateral carinae ridged, strongly converging toward apex and continuing as medially as ridged frontal carina, area concave and compartimented into two large posterior cells separated by ridged median carina and rather small anterior cell (areolet) with weakly developed but distinct posterior carinae; laterodorsal parts of eumetope (frons) deeply concave. Eumetope narrow, about 2.9 times as long as wide, widest shortly dorsally of frontoclypeal suture, about

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1.3 times as long as post- and anteclypeus combined; lateral carinae ridged, convex in lower part close to frontoclypeal suture, then straight and converging toward apex, median carina strongly pronounced, enclosed frontal area concave; post- and anteclypeus with faint median carina, surfaces smooth. Antennal joints elongate; scape about 1.5 times as long as pedicel, slightly compressed, anteriorly vaulted, dorsally with fine ridge; pedicel with short dorsal ridge at base, otherwise terete, furnished with numerous sensory plaques, mostly in longitudinal rows. Compound eyes comparatively large, mediobasal incision above antennal base relatively short, merely surpassing midlength of eye; ocelli as in the other congeners at lower anterior margin of eyes; transition of vertex to frons in lateral view broadly rounded; genal carina sharply



Fig. 11. *Sparnia edwardsi* Muir, thorax: (*A*) left forewing, macropterous male; (*B*) left forewing, brachypterous female (light color); (*C*) same, brachypterous female (dark color); (*D*) male sound producing organ, posterior view. Scale bars 0.5 mm (A–C) and 0.1 (D).

ridged; lamina maxillaris with ventral margin nearly straight. Pronotum about 1.4 times as wide as head including compound eyes, about 4.3 times as wide as medially long; posterior margin very shallowly concave; disk elevated, carinae sharply ridged, reaching posterior margin, enclosed area flat; sublaterally on each side an oblique edge. Mesonotum medially about 2.9 times as long as pronotum, surface smoothly rounded, carinae faint, not reaching posterior margin, lateral carinae posteriorly slightly diverging. Tegulae large, in dorsal view about as long as wide. Tegmina of macropterous form elongate, about 3 times as long as wide, widest in membrane shortly beyond nodal line; anterior part until nodal line about 1.6 times as long as posterior part (membrane); posterior margin broadly rounded; subapical cells (C1 and C5) almost equal in size and length; in membrane only Mbranched into M1 and M2, all other terminal veins unbranched. Tegmina of brachypterous form relatively broad and stout, apically rounded, about 2.4-2.5 times as long as wide, widest at level of nodal line, anterior part about 2.5–2.6 times longer than membrane; subapical cells either equally long, or inner cell (C5) slightly longer, M posteriorly branched or unbranched; in some individuals terminal branch of RP. Legs: Posttibia about 1.7 times as long as post-tarsal joints combined, laterally with 2 spines: a very small one at base, a longer one infra midlength, distally with 5 spines (3 longer outer and 2 smaller inner ones). Postbasitarsus with 7 spines in a shallowly concave row; 2nd post-tarsal joint distally with 4 spines in row. Post-tibial spur terete in cross-section, posterior mar-



Fig. 12. Sparnia edwardsi Muir, male genitalia: (A) male genital capsule, undissected, left lateral view; (B) genital segment, left lateral view; (C) genital segment, ventral view; (D) genital capsule, undissected, caudal view; (E) genital segment, caudal view. Scale bar 0.1 mm.

gin with 10–12 cone-shaped teeth well separated from each other.

Male sound-producing organ with short subtriangular apodemes of the first abdominal sternite pointing medially, with sturdy, medium-sized pike-like apodemes of the second abdominal sternite pointing laterodorsally.

Coloration. Vertex (coryphe with areolet) pale to orange-yellow, posteriorly at both sides of median carina with sordid brown depression, lateral margins at level of anterior compartment (areolet) with dark brown spot, transition to frons (eumetope) marked by narrow brown cross-band. Eumetope (frons) pale yellow with 3 blackish brown transverse stripes: a very narrow w-shaped one at apex (transition to coryphe), a slightly wider one at level of compound eyes, and a broad one crossing below compound eyes and laterally continuing onto genae; in some individuals latter cross-band in metopal part orange (Figs. 15*C*, 15*D*);



Fig. 13. Sparnia edwardsi Muir, male genitalia: (A) anal segment, aedeagus, suspensorium, connective and genital styles in situ, left lateral view; (B) aedeagus, left lateral view; (C) aedeagus, right lateral view; (D) aedeagus and suspensorium, ventrocaudal view; (E) anal segment, ventral view; (F) left genital style, caudal view. Scale bars 0.1 mm.

lateral and median carinae at level of ocelli with small brown spot. Postclypeus blackish brown; anteclypeus pale yellow, laterally with dark brown spot. Rostrum stramineous with blackish tip. Antennae: scape pale yellow, on both sides with broad dark brown stripe from base to apex; pedicel brownish, anteriorly at base medially with short blackish stripe, dorsal base with yellowish rim. Pronotum mostly blackish brown; disk with carinae and anterior and posterior margins pale yellow, framing on either side subquadrangular blackish area; lateral parts shiny blackish brown, at level of tegulae with narrow yellowish margin; sides medially blackish, laterally pale yellow. Mesonotum including carinae uniformly blackish brown. Tegulae pale yellow, posterior margin slightly infuscate; tegulae and lateral pronotal parts forming oblique pale yellow

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Fig. 14. Location of species of the genus Sparnia Stål: (1) S. edwardsi Muir; (2) S. williamsi Muir; (3) S. praecellens Stål.

stripe. Tegmina translucent; in macropterous form angle between Pcu and A1 and commissural margin dark brown; clavus anteriorly slightly infuscate; nodal line and inner apical margin of membrane framed brownish; veins pale yellow, pustules within contrasting dark brown dots. Hind wings hyaline, veins sordid brown. In brachy-pterous form tegmina translucent with stippled veins, either entirely devoid of color pattern, or apex of membrane fuscous (applying to both sexes). Legs: femora stramineous, anterior and posterior side with a broad brown stripe; pro- and mesotibiae in proximal two thirds sordid brown, in distal third pale yellow; post-tibia stramineous, at base and towards distal spines slightly darkened; pro- and mesotarsi blackish brown, 1st and 2nd post-tarsal joints stramineous, 3rd post-tarsal joint blackish brown; post-tibial spur pale stramineous. Abdominal tergites and sternites of males as well as male genitalia blackish brown; in females abdominal sternites anteriorly fringed yellow, ovipositor fuscous, gonocoxae VIII medially fringed sordid yellow, anal stylus blackish.

Male genitalia. Genital segment in lateral view trapezoidal with caudal margin slightly concave, ventrally about 2.4 times as long as dorsally; in ventral view caudal margin shallowly concave, dorsal bridge of foramen for genital styli subtriangularly elevated; in caudal view high ovate, slightly higher than wide, dorsal margin of diaphragm deeply concave, diaphragm medially wrinkled, foramen for genital styli subquadrangular, surrounded by stronger sclerotization; laterocaudal margins gently rounded. Aedeagus short, tubular, bent ventrally, from a broader base continuously narrowing toward apex; left laterally with double row of small teeth, median row of 7-9 teeth, parallel ventral row with 12-15 teeth; right laterally with ventral row of up to 15 small teeth, dorsally of this row with varying number of irregularly scattered teeth (15-18); phallotreme elongate, slit-like, exposed



Fig. 15. (*A*) Sparnia praecellens Stål, head, front view; (*B*) S. williamsi Muir, head, front view; (*C*) S. edwardsi Muir, head ("dark" form), front view; (*D*) S. edwardsi, head ("light" form), front view; (*E*) S. edwardsi, habitus, macropterous male/female; left lateral view; (*F*) S. edwardsi, habitus, brachypterous male/female, dorsal view.

dorsocaudally; suspensorium, as in the other *Sparnia* species, pull-tab-like; connective slightly sinuate. Anal segment short, with mediocaudal margin projected into single, rather elongate and sturdy process slightly compressed at tip; anal stylus short, subcylindrical. Genital style elongate, in repose reaching dorsal margin of anal segment, in ventral view apically slightly converging; base narrow, ventrally with comparatively

long and slender spinose process pointing dorsocaudally; styli subapically dilated, apically tapering, in lateral view snout-like, subapically on inner side with small and slender spinose process.

Female genitalia. Ovipositor gently curved dorsally, reaching posteroventral margin of anal segment; gonoplacs not particularly dilated; gonocoxae VIII relatively broad, widening toward base, medially

Fig. 16. (*A*) Sparnia praecellens Stål, left forewing, macropterous; (*B*) S. williamsi Muir, left forewing, macropterous; (*C*) S. edwardsi Muir, left forewing, macropterous; (*D*) S. edwardsi, left forewing, brachypterous female ("light" form); (*E*) S. edwardsi, left forewing, brachypterous male ("dark" form).

rounded; gonapophyses IX dorsally in caudal half furnished with 9–12 sturdy, rounded teeth.

Diagnosis. Sparnia edwardsi can easily be distinguished from the other two congeners by a much shorter antenna with scape devoid of a median ridge, by the presence of a compartimented coryphe, by a broad blackish band across metope and genae, by apically broadly rounded tegmina with dark pustules on veins, by a "normal" configuration of veins in the hind wing devoid of anastomosis; in male genitalia by very long and slender spinose processes at the ventral base of the genital styles, and by an aedeagus which on each side is multiply furnished with small teeth (not with teeth in a single row as in *S. praecellens* and *S. williamsi*). **Distribution** (Fig. 14, 1). Chile: Chiloe Island (type locality), mainland opposite of Chiloe Island (new record)

Host plants and ecology. In the original description no indication of any host plant(s) was provided; however, both nymphs and (brachypterous) adults were collected in December. This coincides very well with the recent finding of S. edwardsi by A.F. Emeljanov (December, January). It is assumed that in the part of Chile with a mild temperate climate the species is univoltine. Oviposition may proceed in spring or in the short south Chilean summer, and hibernation either occurs at the egg or at nymphal stages. On Chiloe Island the macropterous female of S. edwardsi examined by us was swept from grasses and shrubs in a Sphagnum bog; in mainland Chile in the National Parc of Alerce Andino a macropterous male individual was swept from grasses in a bog in the middle of the forest; in both cases a particular host plant could not be recognized (information of A.F.E.).

Remarks. Among the *Sparnia* species, *S. edwardsi* appears to be the most plesiomorphic one because of the shape of antennae (much less elongate than in the other two species), the rounded apex of the tegmina, and of the normal configuration of hind wing venation devoid of anastomosis.

Material examined. Holotype: ♂, brachypterous, examined; intact, non-dissected specimen mounted with a minute pin on a strip of white cardboard labeled: "♂" (white rectangular label, printed), "Type" (circular BMNH-label with red edging, printed), "Ancud, 17.–19.XII.1926" (white rectangular label, printed), "S. Chile, Chiloe I., F. & M. Edwards, B.M. 1927–63" (white rectangular label, printed), "Holotype" (printed on red cross border of white label), "*Sparnia edwardsi* Muir" (handwritten by Muir on the same white rectangular label); BMNH.

Paratypes: 2 \Im , brachypterous, same data as holotype (1 \Im dissected by M. Asche in 1984, genitalia in glycerin transferred to a genital vial), BMNH.

Additional material. Chile. 3 nymphs (1 nymph lacking abdomen), 5th instar, same data as holotype BMNH; 1 \Im macropterous, Chile, Parque Nac. Alerce Andino cordun Sargaza, 35 km E Puerto Montt., 41°30'S, 72°37'W, 11.I.2014; 1 \Im , macropterous, Chile: Chiloe Island, Senda Darwin, 10 km E Ancud, 41°25'S, 73°39'W, 29.XII.2013; both A.F. Emeljanov; 2 \Im , brachypterous, ibid., near Villa Cerro Castillo,

46°06'S, 72°11'W, 31.XII.2014–2.I.2015, E.D. Lukashevitch; all ZIN. 1 \Diamond , brachypterous, Chile: Chiloe Island, Dalcahue, 20.I.1962, R. Usinger, UDCC. 1 \bigcirc , brachypterous, Prov. de Arauco, Butamalal, 12.– 20.II.1953, L.E. Pena, NCSU. 2 \Diamond , macropterous, 1 \bigcirc , macropterous, 1 \Diamond , brachypterous, 4 \bigcirc , brachypterous, 1 nymph (5th instar), Chile, Region X Los Lagos, 3 km E Punta Curinaca, 39°42′15.5″S, 73°20′44.9″W, Alt. 485 m, 27.I.2006, L.R. Donovall, sweeping, degraded Valdivian evergreen deciduous forest, UDCC; 3 \bigcirc , brachypterous, ibid., J.R. Cryan, Loc. 12; Assoc. material in NYSM Genome Bank, Num. 11-02-04-63, identified as "*Sparnia* sp." by C.R. Bartlett, UDCC.

DISCUSSION

Within the South American Delphacini the genus Sparnia Stål is unique in the combination of characters not found in other taxa: "alohinoid" post-tibial spur, significantly compressed and elongate antennal joints, coryphe with faint median carina, narrow and elongate metope, in hind wing anastomosis between M and CuA (at least in 2 species), unispinose anal segment, very elongate genital styles with mediobasal spinose projection, and a relatively small tubular aedeagus pointing ventrally. However, in the Neotropical delphacid fauna, the "alohinoid" post-tibial spur is also present in the genera Burnilia Muir et Giffard, 1924, Stobaera Stål, 1859, and, according to Muir (1926), in the Brazilian genus Synpteron Muir, 1926. Burnilia was transferred to a separate subfamily, Plesiodelphacinae, by Asche (1985), and, due to fundamental structural differences, especially in the male and female genitalia, can by no means be regarded as a close relative of Sparnia. Stobaera species share the general shape of the post-tibial spur and an anal segment which is similarly furnished with a single medioventral process (see Kramer, 1973); however, the head- and antennal morphology is quite different; nevertheless, in all the aspects both genera belong to the Delphacinae: Delphacini. The examination of the (parasitized) male holotype of Synpteron brazilensis Muir (Bishop Museum, type number 4969) has revealed the presence of a "normally" dentate (not "alohinoid") post-tibial spur and other bodily and genital characters which do not suggest a close relationship to Sparnia, and also not attribution to Tropidocephalini as suggested by Metcalf (1943). Muir's placement of Sparnia in the tribe Alohini erected by Muir (1915) was questioned by Asche (1985b, 1990, 1997, 1998) who assumed the polyphyly of that tribe and subsumed it under Delphacini by means of the presence of advanced oviduct gland of the females *sensu* Strübing (1956a, 1956b). Thus, "Alohini" are multiple lineages of not necessarily closely related taxa of the highly evolved and apparently monophyletic Delphacini.

Consequently, the "*alohinoid*" Sparnia remains isolated amongst the Delphacini.

The paradoxical direction of ecological and geographical evolution of the genus *Sparnia* "against the stream" from the less favorable conditions to the more favorable ones, from geologically younger, cooler, lying closer to the pole (South) to more ancient, warm, tropical ones, in conjunction with the isolated position of this genus in the tribe Delphacini, gives us a ground to look for *Sparnia*'s motherland and ancestors in the ancient Antarctic fauna devastated by glaciations.

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