



Research article

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A reappraisal of the taxonomy of Neotropical Sialidae (Insecta: Megaloptera): with the description of a new genus from Cuba

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Abstract. The unique Neotropical species of the alderfly genus *Protosialis* van der Weele, 1909, *P. bifasciata* (Hagen, 1861), is herein transferred to the newly described genus *Caribesialis* gen. nov. This new taxon is proposed to be sister to the clade *Protosialis* + *Sialis* Latreille, 1802, after a phylogenetic analysis that included male genital characters scored on a previous morphological matrix of the family. Also, *Ilyobius nigrocephalus* sp. nov., a remarkable new species from Ecuador, is described and its phylogenetic position is discussed. Furthermore, *Ilyobius bimaculatus* (Banks, 1920) from Bolivia, known solely from the female holotype, is redescribed. Based on the present study, the Neotropical fauna of Sialidae is proposed to be constituted by two genera, one insular (Cuba) and one continental (Mexico to Chile and Argentina).

Keywords. Neuropterida, systematics, aquatic insects, morphology, alderflies.

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Introduction

The family Sialidae – commonly known as alderflies – of the order Megaloptera, is a small group of insects currently comprising 97 fossil and living species grouped in 13 genera distributed in all biogeographical realms (Liu *et al.* 2015a; Martins *et al.* (accepted)). This group is easily distinguished from the only other family of Megaloptera, i.e., the Corydalidae, by having smaller adults, absence of ocelli, a short pronotum, and a bilobed fourth tarsomere. The larvae have an elongate caudal filament (New & Theischinger 1993). Tropical America is currently represented by two sialid genera, namely, *Protosialis* van der Weele, 1909 and *Ilyobius* Enderlein, 1910 (Liu *et al.* 2015a; Martins *et al.* (accepted)), but the fauna of this realm was previously classified only within the former genus (Contreras-Ramos 2008; Liu *et al.* 2015b). *Ilyobius* was previously synonymized with *Protosialis* (Penny 1981), but in a recent morphological phylogenetic analysis, this genus was reinstated, and *Protosialis* was relegated to Cuba and the eastern United States (Liu *et al.* 2015a, 2015b). Consequently, of the ten Neotropical extant species of Sialidae, nine are continental and grouped in *Ilyobius*, while a single Cuban species is treated under *Protosialis* (Liu *et al.* 2015a, 2015b). However, the generic affiliation of this Caribbean species remains uncertain, since in the aforementioned phylogenetic analysis, it was scored from a single female. Additionally, the original description is quite general and the male genital structures are unknown (Contreras-Ramos 2008). Furthermore, of the *Ilyobius* species, *I. flavicollis* (Enderlein, 1910) and *I. bimaculatus* (Banks, 1920) lack descriptions of genital structures (Liu *et al.* 2015b). Although this family has received little attention in Tropical America due in part to its presumed rareness, recent contributions have significantly increased our knowledge about its taxonomy and biology (Contreras-Ramos 2008; Azevêdo & Hamada 2014; Liu *et al.* 2015a, 2015b; Archangelsky *et al.* 2017). The present work proposes a new genus, *Caribesialis* gen. nov., based on a phylogenetic analysis in which the male characters were scored onto a morphological matrix of a previous analysis of the entire family (Liu *et al.* 2015a). In addition, a new remarkable species of *Ilyobius* – *I. nigrocephalus* sp. nov. – is described and its phylogenetic affinities are discussed. Finally, *I. bimaculatus*, previously known only from the Bolivian holotype (a female specimen), is herein redescribed after the reexamination of the specimen.

Material and methods

Taxonomic and morphological study

Genitalia preparations were made by clearing the last abdominal segments in a solution of 10% potassium hydroxide (KOH) overnight. Residuals of the alkaline solution were washed with a series of washings of distilled water and 80% ethyl alcohol. Then, the genitalia were stored in microvials filled with glycerin and pinned beneath the specimen. External morphology and cleared genitalia were examined using a stereo microscope. High resolution images were produced using an AxioCam MRc5 digital camera attached to a Zeiss AxioZoom V16 stereo microscope. Series of photographs were stacked and processed with the software ZENpro201. Drawings were initially made using a drawing tube attached to a stereo microscope, which were subsequently vectorized using the program Adobe Illustrator CS®. Morphological terminology generally follows New & Theischinger (1993), except for the genital sclerite terminology, for which the homology hypothesis proposed by Liu *et al.* (2016) was adopted. Terminology for wing venation follows Comstock (1918), but with the modifications of Breitzkreuz *et al.* (2017). Distribution maps were produced with the software ArcMap (ESRI, Redlands, CA, USA).

Specimens studied in the present work are deposited in the following collections:

FSCA = Florida State Collection of Arthropods, Gainesville, Florida, USA

MCZ = Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA

Morphological abbreviations**Wing venation**

A	=	anal veins
CuA	=	cubitus anterior
CuP	=	cubitus posterior
MA	=	media anterior
MP	=	media posterior
RA	=	radius anterior
RP	=	radius posterior
Sc	=	subcosta

Abdomen

Bc	=	bursa copulatrix
ect	=	ectoproct
Gcx 8	=	gonocoxites 8 (light yellow)
Gcx 9	=	gonocoxites 9 (light blue)
Gcx 10	=	gonocoxites 10 (light red)
Gcx 11	=	gonocoxites 11 (light green)
Gph8	=	gonapophyses 8 (dark yellow)
Gst 9	=	gonostyli 9 (dark blue)
Gst 11	=	gonostyli 11 (dark green)
S7–9	=	sternites 7–9
T7–9	=	tergites 7–9

Phylogenetic analysis

The morphological phylogenetic analysis was based on “matrix 3” from Liu *et al.* (2015a), in which the fossil taxa and species lacking male representatives were pruned. This matrix included 108 characters (numbered from 0 to 107) and 69 species representing the eight extant genera of Sialidae, plus *Platychauliodes capensis* Barnard, 1931 (Chauliodinae) and *Sininocellia gigantos* Yang, 1985 (Raphidioptera) as outgroups.

In the present study, the males and females of the enigmatic *Protosialis bifasciata* (now *Caribesialis bifasciata* (Hagen, 1861) comb. nov.), plus a new species of *Ilyobius* were scored in the mentioned matrix through the direct examination of the specimens. Herein, the matrix consisting of the 108 original characters and 71 terminals was handled using the software WinClada® (Nixon 2002), and then it was exported as a nexus file to perform the phylogenetic analysis under the principle of parsimony in the software TNT® 1.5 (Goloboff & Catalano 2016). A first analysis was performed using New Technology search set to 100 employing the algorithms of sectorial search, ratchet, drift and tree fusing, finding the minimum tree 10 times (Liu *et al.* 2015a). For comparison purposes, an analysis of traditional search of TBR (Tree Bisection Reconnection) based on 100 random addition sequences, plus an analysis of New Technology with implied weighting with a value of the constant k of 14.908 calculated by means of the TNT script “setk.run” (Goloboff *et al.* 2008) were conducted. Strict consensus of the most parsimonious trees, as well as optimization and analysis of the evolution of the characters was made using WinClada® (Nixon 2002).

To calculate the support of branches, the Bremer absolute (Bremer 1988, 1994) was used. This index calculates the number of extra steps needed for a consensus branch to collapse. The values of Bremer support were calculated using suboptimal trees of 1–10 extra steps with TBR, on the software TNT® 1.5.

The final topology, including all characters, states and Bremer values, was edited in the Adobe Illustrator CS® software.

Results

Class Insecta Linnaeus, 1758
Order Megaloptera Latreille, 1802
Family Sialidae Leach in Brewster, 1815
Subfamily Sialinae Leach in Brewster, 1815

Caribesialis Ardila-Camacho, Martins & Contreras-Ramos gen. nov.
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Figs 1–6

Type and only species

Sialis bifasciata Hagen 1861: 188.

Diagnosis

Caribesialis gen. nov. is distinguished from other Sialidae genera by the presence of elongated, tubular and digitiform gonostyli 9. Similar structures are also present only in *Sialis nevadensis* Davis, 1903, but in this species these sclerites are short and unguiform. The presence of gonocoxites 10 forming a tiara-shaped sclerite with prominent median hook-shaped process is a unique character of this genus. The gonocoxites 10 are also present in some species of *Sialis* Latreille, 1802 and *Austrosialis* Tillyard, 1919; nevertheless, in these genera they are present as one or a pair of small sclerites. Another autapomorphy of the new genus is the structure of the gonocoxites 11, which form a bar-shaped sclerite fused to the inner region of the ectoproct. Species of *Stenosialis* Tillyard, 1919 and *Sialis navasi* Liu *et al.*, 2009 also have this structure fused to the ectoproct; nevertheless, in *Stenosialis* the gonocoxites 11 are fused only with the ventral region of the ectoproct, while in *S. navasi* the gonocoxites 11 are completely fused with the ectoproct. The new genus has a median, short and straight, caudally projected bifid process (interpreted as gonostyli 11), whose base is fused forming a Y-shaped structure. In other genera of Sialidae, this structure is generally separated into two parts, and when their bases are fused (e.g., *Sialis nigripes* Pictet, 1865 and *Sialis infumata* Newman, 1838) they are elongated and projected posteroventrad or posterodorsad, instead of caudally.

Etymology

The generic epithet is a combination of – *caribe* – in allusion to the native aboriginal people that inhabited a great part of northern South America and the Lesser Antilles, and – *Sialis* – the type genus of the family Sialidae.

Remarks

Caribesialis gen. nov. belongs to the *Sialis* lineage (Liu *et al.* 2015a), which includes the new genus, the extant genera *Protosialis* and *Sialis*, and the fossil genus *Proindosialis* Nel, 1988. The new genus is closely related to *Protosialis*, sharing several characters of wings and female genitalia. Nevertheless, the presence of gonostyli 9, gonocoxites 10 as a tiara-like sclerite and gonocoxites 11 as a bar-like sclerite fused to the inner region of the ectoproct in the new genus clearly separates this group from *Protosialis*, which lacks gonostyli 9 and gonocoxites 10, and gonocoxites 11 are not fused with the ectoproct. The presence of well-developed gonostyli 9 in the new genus is an uncommon character within Sialidae, as it is absent in most of the species. Boudinot (2018) argued that the gonocoxite 9 of *S. nevadensis* is divided into two parts, one ventral and one dorsal, the later fused with the tergite 9. In the new genus, the gonostylus 9 is articulated to the dorsal part of the gonocoxite 9 (in the sense of Boudinot (2018)), a condition observed in Corydalidae. According to Liu *et al.* (2015a), a projection on the tergite 9 is present in *Indosialis* Lestage, 1927, *Haplosialis afra* (Navás, 1936), and the extinct *Ilyobius herrlingi* (Wichard, 2002), which should not be misinterpreted as homologous with the gonostyli 9 expressed in the new taxa described herein.

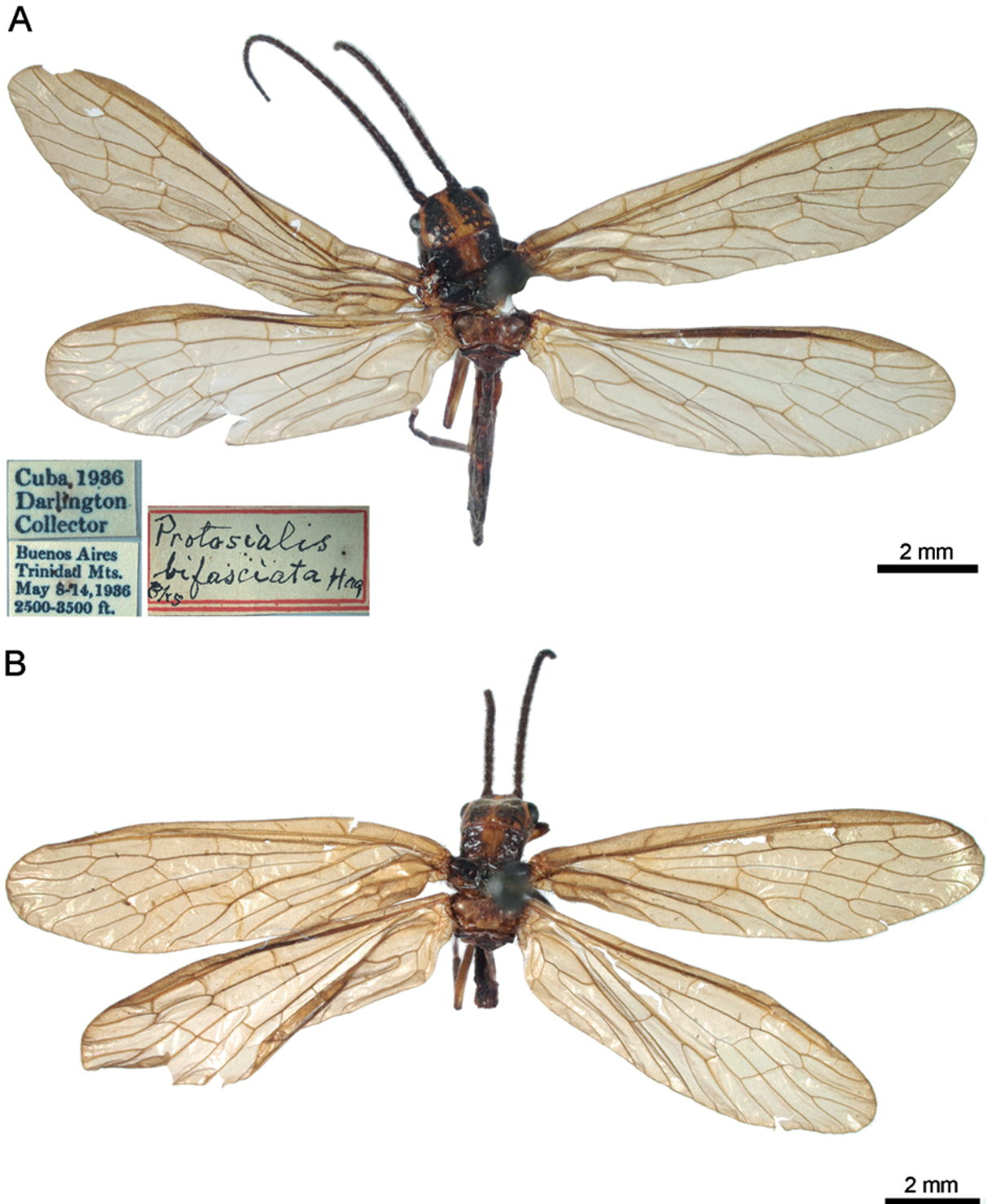


Fig. 1. *Caribesialis bifasciata* (Hagen, 1861) comb. nov., dorsal habitus. **A.** Male. **B.** Female.

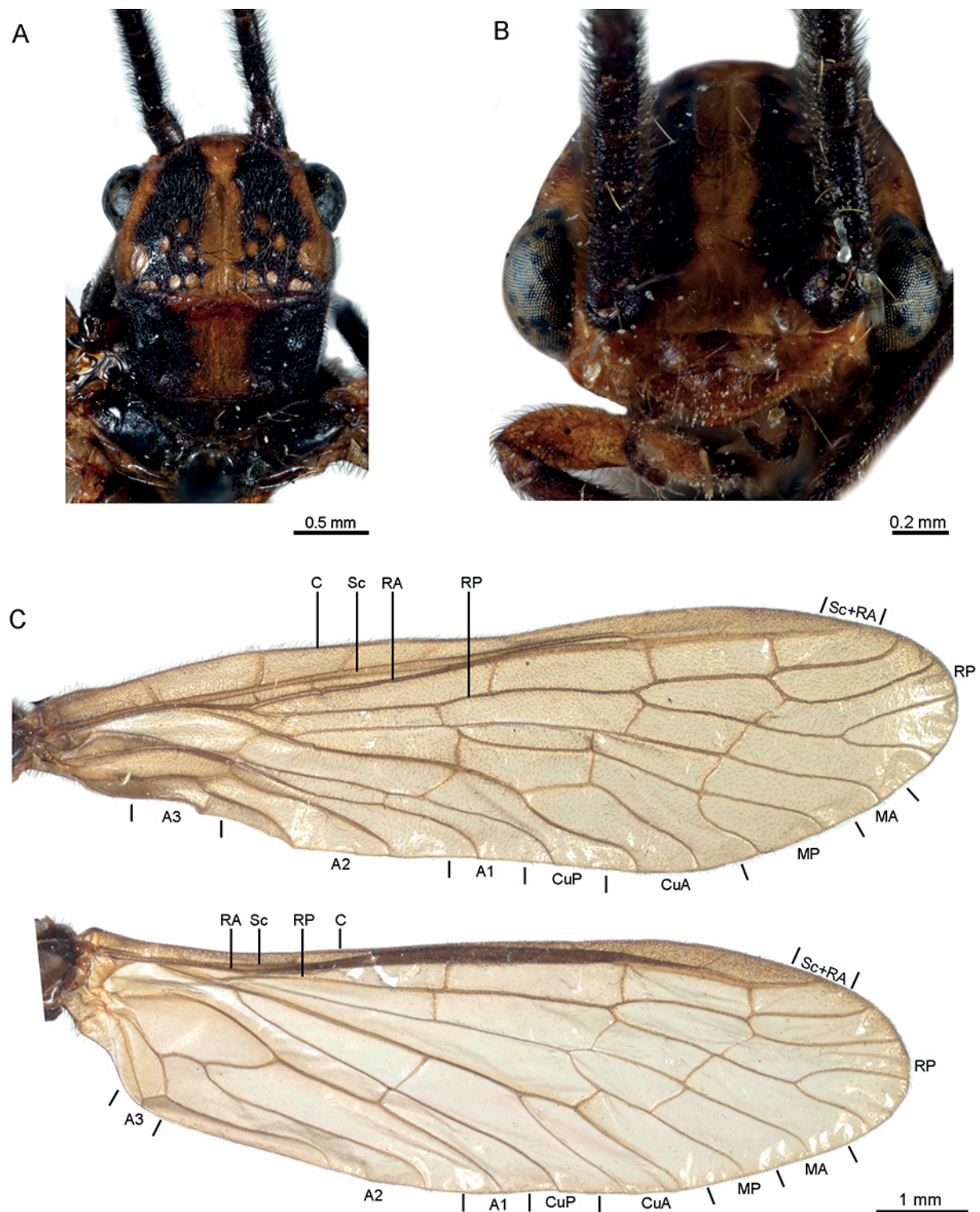


Fig. 2. *Caribesialis bifasciata* (Hagen, 1861) comb. nov. **A.** Head, dorso-frontal view. **B.** Head, frontal view. **C.** Fore- (above) and hindwing (below).

Caribesialis bifasciata (Hagen, 1861) comb. nov.

Figs 1–6

Sialis bifasciata Hagen, 1861: 188.

Protosialis bifasciata – van der Weele 1909: 263.

Revised diagnosis

This species is distinguished by having the head mostly orange, with two lateral, longitudinal, brown bands, extended from antennal sockets to occiput (Fig. 1). The pronotum is orange with wide, lateral, longitudinal, brown bands. Sternite 9 is triangular; gonocoxite 9 is plate-like, and adjacent to sternite 9; gonostylus 9 is adjacent to the base of tergite 9, elongated, tubular, and curved posteromedially. The gonocoxites 10 are plate-like, forming a tiara-like sclerite, medially with a hook-like process, which is distinctively curved ventrad. The gonocoxites 11 form a bar-like structure, that is laterally connected to the ectoprocts; the gonostyli 11 are basally fused and form a bifid projection. The female sternite 8 is subpentagonal, the gonocoxites 8 are narrow, arched, setose, and posteromedially incised, and the gonapophyses 8 are smooth, arched, subtriangular, and glabrous.

Material examined

CUBA • 1 ♂; Santa Clara Prov., Soledad; 25 May 1939; C.T. Parsons leg.; pinned; MCZ • ♀; Buenos Aires, Trinidad Mts.; alt. 2500–3500 ft.; 8–14 May 1936; Darlington leg.; “*Protosialis bifasciata* Hag, BKS.” white label; pinned; MCZ • 1 spec. (probably ♀); Buenos Aires, Trinidad Mts.; alt. 2500–3500 ft.; 8–14 May 1936; Darlington leg.; “*Protosialis bifasciata* Hag, BKS.” white label; pinned; MCZ • ♀; Buenos Aires, Trinidad Mts.; alt. 2500–3500 ft.; 8–14 May 1936; Darlington leg.; “*Protosialis bifasciata* Hag, BKS.” white label; pinned, dissected; MCZ • ♀; Buenos Aires, Trinidad Mts.; alt. 2500–3500 ft.; 8–14 May 1936; Darlington leg.; “*Protosialis bifasciata* Hag, BKS.” white label pinned, dissected; MCZ • ♀; Buenos Aires, Trinidad Mts.; alt. 2500–3500 ft.; 8–14 May 1936; Darlington leg.; “*Protosialis bifasciata* Hag, BKS.” white label; pinned, dissected; MCZ • ♂; Buenos Aires, Trinidad Mts.; alt. 2500–3500 ft.; 8–14 May 1936; Darlington leg.; “*Protosialis bifasciata* Hag, BKS.” white label; dissected; MCZ.

Redescription

HEAD (Fig. 2A–B). Width 1.9 mm, predominantly orange, dorsally with two longitudinal lateral brown bands, extended from antennal sockets to occiput, on occiput with circular orange marks, entire surface covered with minute light brown setae; postocular area with a longitudinal brown stripe and with a semicircular orange muscle scar, stripe posterodorsally extended and connected to dorsal stripe. Compound eyes dark brown. Antenna with scape nearly 1.5 times as long as wide, brown, covered with abundant light brown setae, pedicel brown, nearly as long as wide, flagellum brown with 36–37 flagellomeres, densely covered with brown setae. Frons densely setose, somewhat protuberant between antennae. Clypeus and labrum densely covered with light brown setae, anterior margin of clypeus with median concavity. Maxillary and labial palpi light brown with abundant light brown setae. Occiput with orange muscle scars.

THORAX (Fig. 1). Pronotum rectangular, nearly 1.5 times as wide as long, with wide, lateral, longitudinal brown bands with embedded semicircular orange muscle scars, medially orange, densely covered with minute light brown setae. Mesonotum wider than long, scutum brown, scutellum light brown, entire surface densely covered with minute light brown setae. Metanotum light brown, slightly narrower than mesonotum, glabrous. Pteropleura brown, covered with abundant light brown setae.

LEGS. Brown, all segments densely covered with brown setae; fore femur somewhat expanded and short; mid- and hind femur longer and slightly expanded towards apex. Tibial spurs short, brown. Basitarsus of

fore- and midleg short, as long as second and third tarsomeres together; on hind leg longer than that of fore- and midleg, as long as remainder of tarsomeres together. Pretarsal claws light amber.

WINGS (Fig. 2C). Forewing 9.1–9.6 mm long ($n = 2$), membrane translucent, smoky, densely setose. Venation light brown, densely covered with fine setae of same color as cuticle. Costal field narrow, with four crossveins; pterostigma absent. A single subcostal crossvein. Radial field with three crossveins, RP with two branches, basal one forked near posterior wing margin; a single crossvein between first and second RP branches. Radiomedial space with three crossveins; M forked near mid-length of wing, MA unforked, MP forked near posterior wing margin, intramedial space with two crossveins; mediocubital space with two crossveins; CuA vein forked slightly beyond level of M fork, CuP unforked, intracubital space with single crossvein. Cubitoanal space with two crossveins; area between A1 and A2 with a single crossvein, A2 forked before R fork level; area between A2 and A3 with single crossvein. Hindwing 11 mm long, general aspect similar to forewing. Costal field narrow, with two crossveins; subcostal field with single crossvein. Radial space with three crossveins, RP with two branches, basal one forked near posterior wing margin; a single crossvein between RP branches. Radiomedial space with three crossveins. M vein forked at $\frac{2}{3}$ of wing length; intramedial space with single crossvein. Mediocubital space with single crossvein; Cu forked at $\frac{1}{5}$ of wing length; CuA forked at apex, intracubital space with single crossvein. Cubitoanal space with single crossvein. Area between A1 and A2 with a single sinuous crossvein, A2 forked near wing base; a single crossvein between A2 and A3 is present.

ABDOMEN. Uniformly brown with abundant light brown setae.

MALE GENITALIA (Figs 3–5). Tergite 8 membranous, moderately setose, setae longer on posterior area; sternite 8 semi-membranous, slightly sclerotized posteromedially, uniformly setose. Tergite 9 sclerotized, ring-shaped, laterally slightly widened and sparsely covered with long setae; anal tubercle slightly sclerotized; ectoproct lobe-like, setose. Sternite 9 in ventral view moderately sclerotized, triangular; gonocoxite 9 plate-like, paired, adjacent to sternum, both sternum and gonocoxite 9 uniformly setose; gonostylus 9 separated from gonocoxite 9, articulated to tergite 9 base, elongated, tubular and posteromedially curved inwards. Gonocoxites 10 lower portion plate-like, tiara-shaped, medially with a raised extension and a sclerotized hook-like process distinctively curved ventrad in caudal view. Gonocoxites 11 forming a bar-like sclerite, laterally slightly expanded and connected to ectoprocts; gonostyli 11 basally forming a sclerotized, bifid projection, whose processes appear divergent.

FEMALE. Similar to male, antenna with 35–36 flagellomeres. Forewing length 9.75–11.7 mm ($n = 5$), head width 1.6–1.7 mm.

FEMALE GENITALIA (Fig. 6). Sternite 8 in lateral view posteroventrally somewhat projected, with apex broad, rounded; in ventral view subpentagonal, posteromedially rounded; gonocoxite 8 narrow, bar-shaped, moderately setose, narrow, arched, setose and posteromedially incised in ventral view; gonapophysis 8 in ventral view smooth, arched, subtriangular, glabrous, located just beneath gonocoxite 8. Tergite 9 in lateral view ventrally extended, expanded and articulated to gonocoxite 9, posteroventral margin straight; gonocoxite 9 elongated, ovoid, narrow, with long setae on dorsal $\frac{1}{3}$; gonostylus 9 small, semicircular located at dorsal $\frac{1}{3}$ of the gonocoxite length; ectoproct as a small ovoid sclerite, setose. Bursa copulatrix sac-like.

Distribution

Cuba (Cienfuegos, La Habana, Santiago de Cuba, Sancti Spíritus, Pinar del Río, Villa Clara) (Alayo 1968; Contreras-Ramos 2008) (Fig. 7A–B).

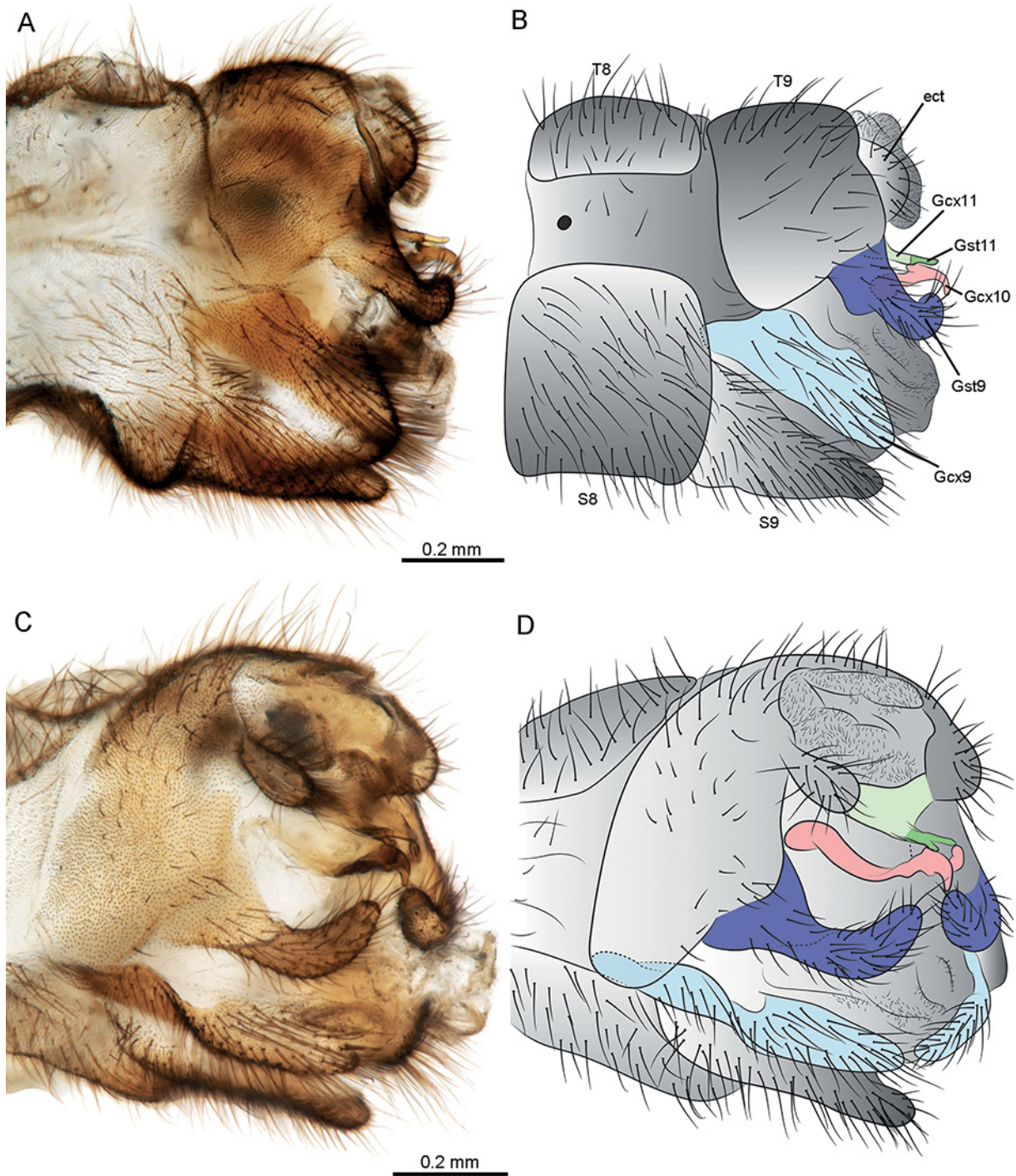


Fig. 3. *Caribesialis bifasciata* (Hagen, 1861) comb. nov., male genitalia. **A.** Lateral view. **B.** Morphological interpretation of genital sclerites in A. **C.** Laterocaudal view. **D.** Morphological interpretation of genital sclerites in C.

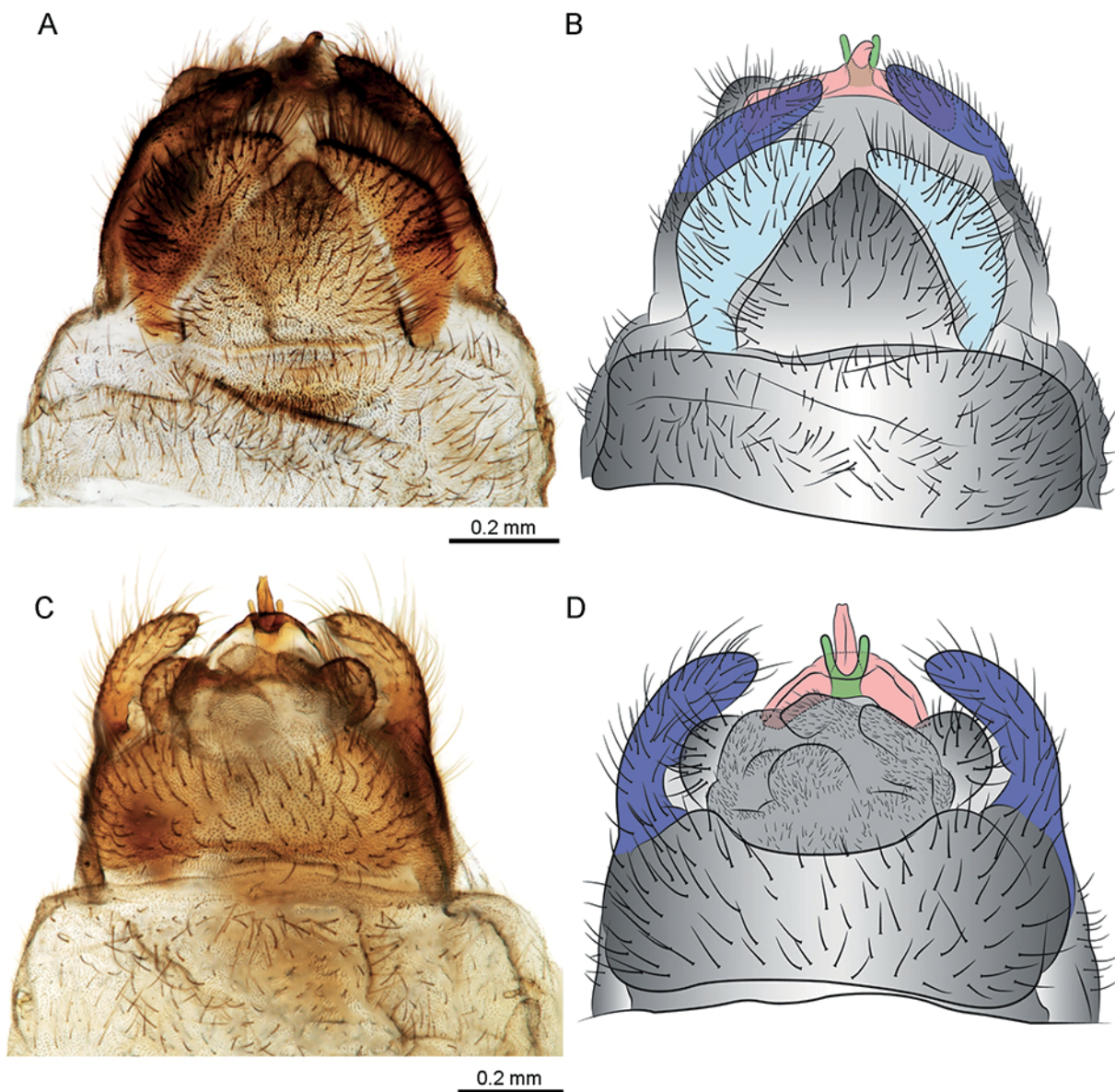


Fig. 4. *Caribesialis bifasciata* (Hagen, 1861) comb. nov., male genitalia. **A.** Ventral view. **B.** Morphological interpretation of genital sclerites in A. **C.** Dorsal view. **D.** Morphological interpretation of genital sclerites in C.

Genus *Ilyobius* Enderlein, 1910

Ilyobius Enderlein, 1910: 381.

Type species

Sialis flavicollis Enderlein, 1910: 380 (by original designation).

Ilyobius bimaculatus (Banks, 1920)

Figs 8–10

Protosialis bimaculata Banks, 1920: 326.

Diagnosis

Ilyobius bimaculatus is known solely from the female holotype, which is in poor condition (Fig. 8). Only few diagnostic characters were observed, which include an area just behind the antennal sockets with a semicircular brown spot. The dorsal area adjacent to the compound eyes has a brown spot, posteriorly extended, flame-shaped, with three-pronged posterior extensions. The gonocoxites 8 appear as small, paired, ovoid sclerites in lateral and ventral view. The gonapophyses 8 are observed as lateral smooth, glabrous, ovoid plates in lateral and ventral view.

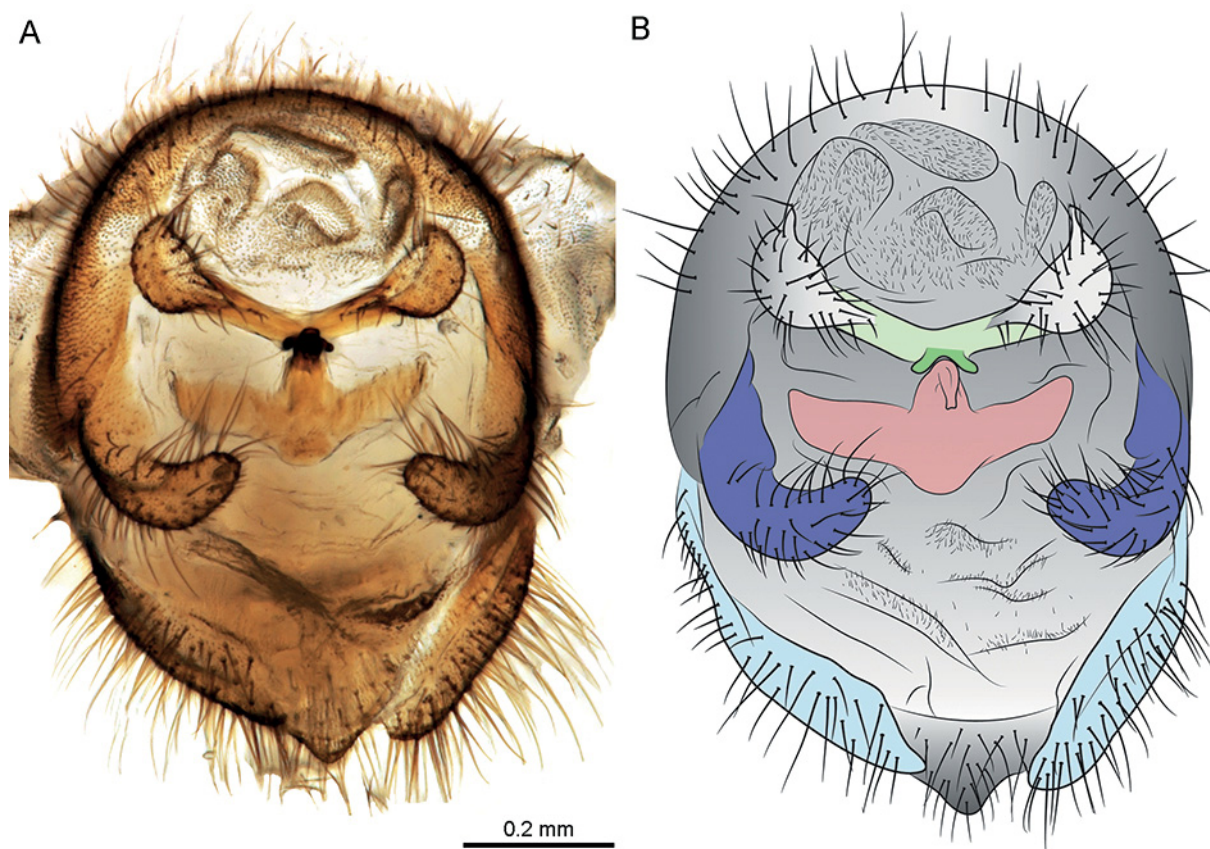


Fig. 5. *Caribesialis bifasciata* (Hagen, 1861) comb. nov., male genitalia. **A.** Caudal view. **B.** Morphological interpretation of genital sclerites in A.

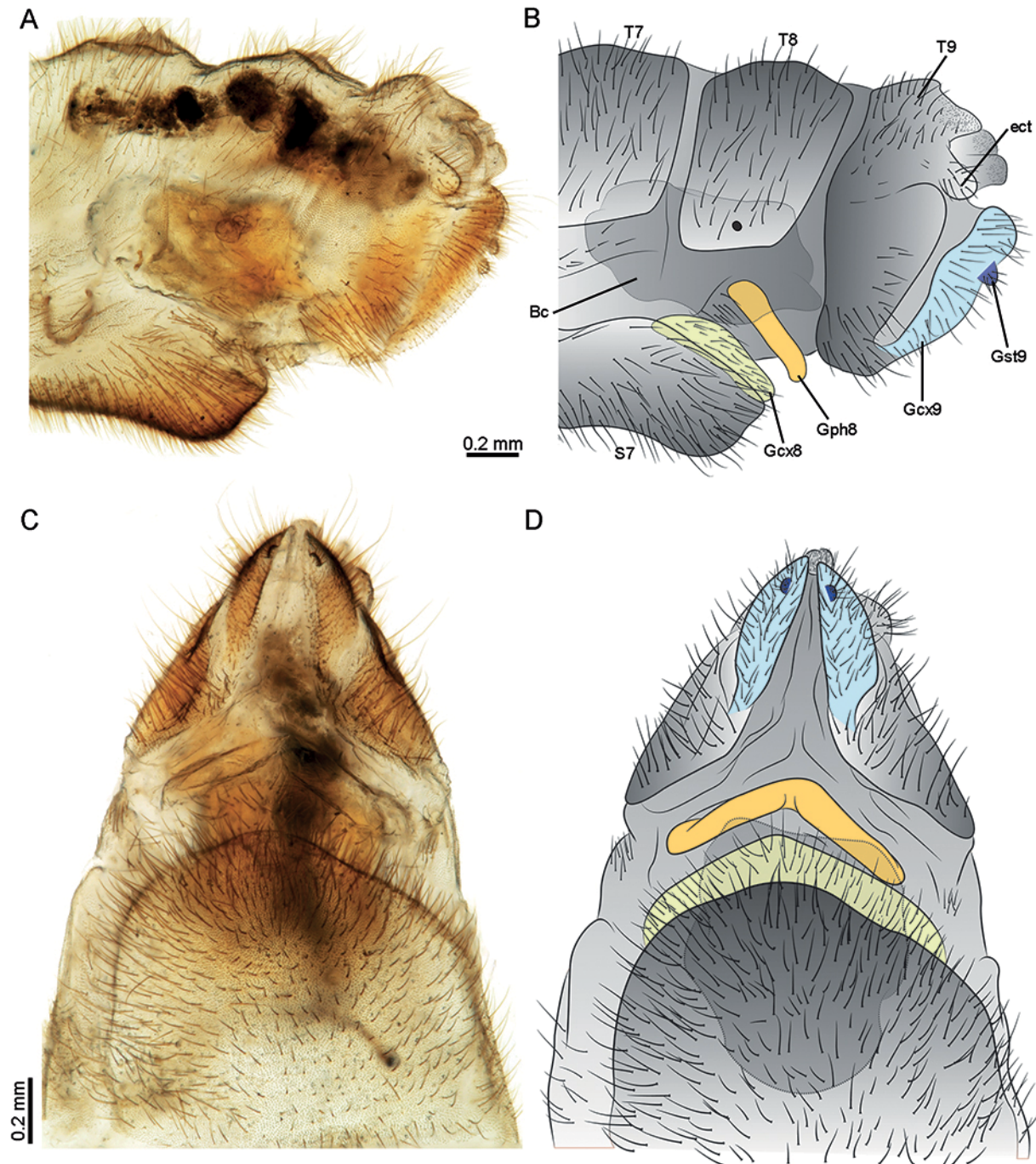


Fig. 6. *Caribesialis bifasciata* (Hagen, 1861) comb. nov., female genitalia. **A.** Lateral view. **B.** Morphological interpretation of genital sclerites in A. **C.** Ventral view. **D.** Morphological interpretation of genital sclerites in C.

Material examined

Holotype

BOLIVIA • ♀; Rio Longo [Río Grande?]; alt. 750 m; Fassel leg. MCZ type 10842.

Redescription

HEAD (Fig. 9A–B). Width 1.9 mm, nearly completely orange. Compound eyes dark brown, dorsal area adjacent to compound eyes with a brown spot, posteriorly extended, flame-shaped, with three-pronged posterior extensions. Antenna with scape subrectangular, enlarged, brown, covered with abundant brown setae, pedicel brown, nearly as long as wide. Area immediately behind antennal sockets with a semicircular brown spot. Frons densely setose, somewhat protuberant between antennae. Clypeus

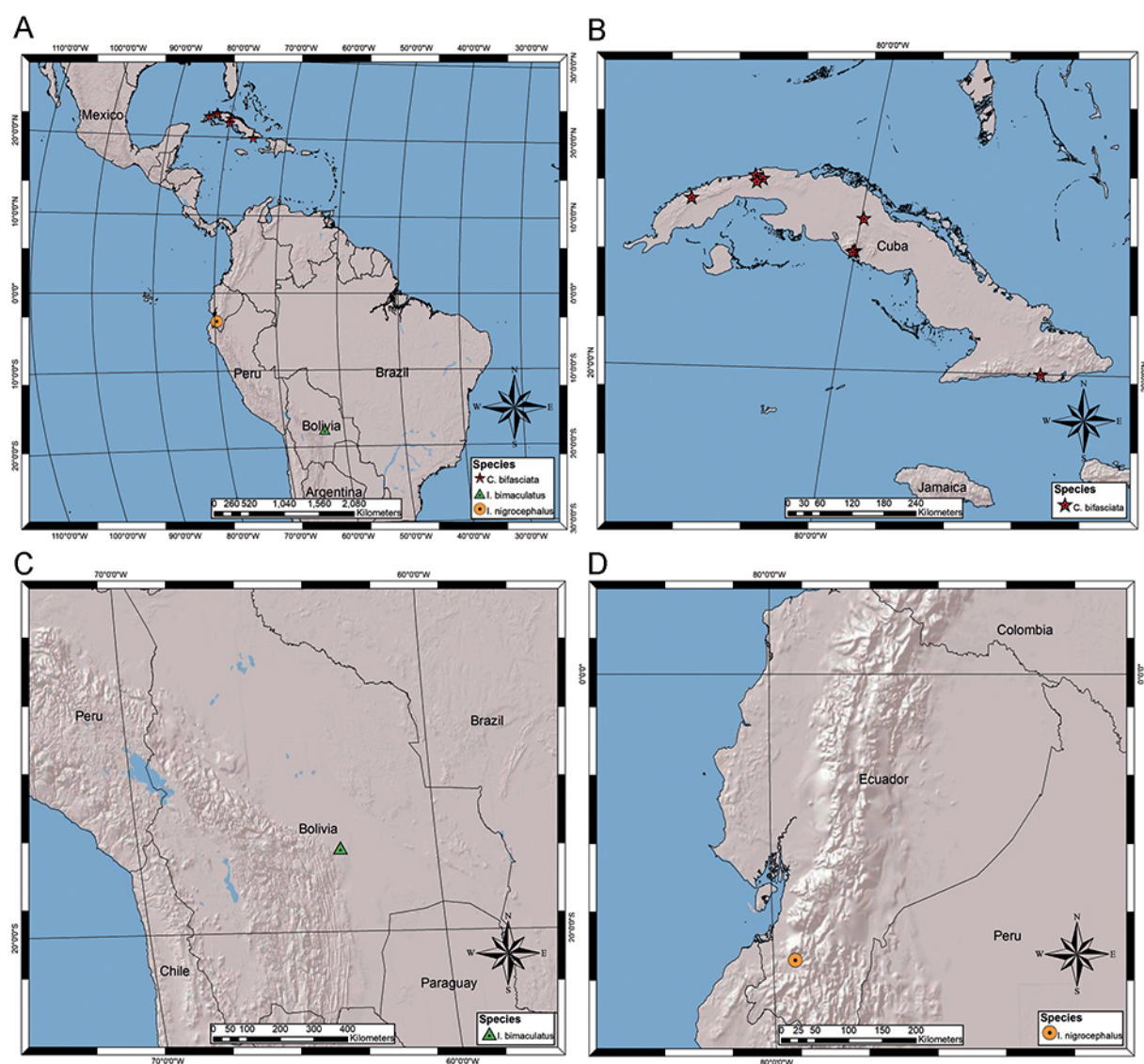


Fig. 7. Distribution of species of Sialidae (Megaloptera) studied herein. **A.** Distribution of *Caribesialis bifasciata* (Hagen, 1861) comb. nov., *Ilyobius bimaculatus* (Banks, 1920), and *I. nigrocephalus* sp. nov. **B.** Distribution of *C. bifasciata* comb. nov. in Cuba. **C.** Distribution of *I. bimaculatus* in Bolivia. **D.** Distribution of *I. nigrocephalus* sp. nov. in Ecuador.

and labrum densely covered with light brown setae, anterior margin of clypeus with median concavity. Maxillary and labial palpi brown with abundant brown setae. Occiput with light orange muscle scars.

THORAX (Fig. 9). Pronotum orange, rectangular, nearly 1.5 times as wide as long, densely covered with minute light yellow setae. Mesonotum wider than long, dark brown, densely covered with minute light brown setae. Metanotum similar to mesonotum, but slightly narrower. Pteropleura brown, covered with abundant setae of same color as cuticle.

LEGS. Brown, all segments densely covered with brown setae; fore femur somewhat expanded and shorter than mid- and hind femur. Tibial spurs short, brown. Basitarsus of fore- and midleg short, as long as the second and third tarsomeres together; on hind leg longer than that of fore- and midleg, as long as remainder of tarsomeres together. Pretarsal claws light amber.

WINGS (Fig. 9C). Forewing 12 mm long, membrane semitranslucent, smoky, densely setose. Venation light brown, densely covered with fine setae of same color as cuticle. Costal field slightly expanded on $\frac{1}{3}$ of wing length, with nine crossveins; pterostigma absent. A single subcostal crossvein. Radial space with three crossveins, RP with two branches, basal one forked near posterior wing margin. Radiomedial space with three crossveins, M forked near mid-length of wing, MA unforked, MP forked near posterior wing margin; intramedial space with two crossveins. Mediocubital space with two crossveins; CuA vein forked slightly beyond level of M fork, CuP unforked; intracubital space with single crossvein. Cubitoanal space with two crossveins; area between A1 and A2 with a single crossvein, A2 forked before R fork level; area between A2 and A3 with single crossvein. Hindwing 11 mm long, costal field narrow, with four crossveins; subcostal field with single crossvein. Radial space with three crossveins, RP with two branches, basal one forked near posterior wing margin. Radiomedial space with three crossveins. M vein forked near mid-length of wing, intramedial space with two crossveins. Mediocubital space with



Fig. 8. Holotype female of *Ilyobius bimaculatus* (Banks, 1920), dorsal habitus.

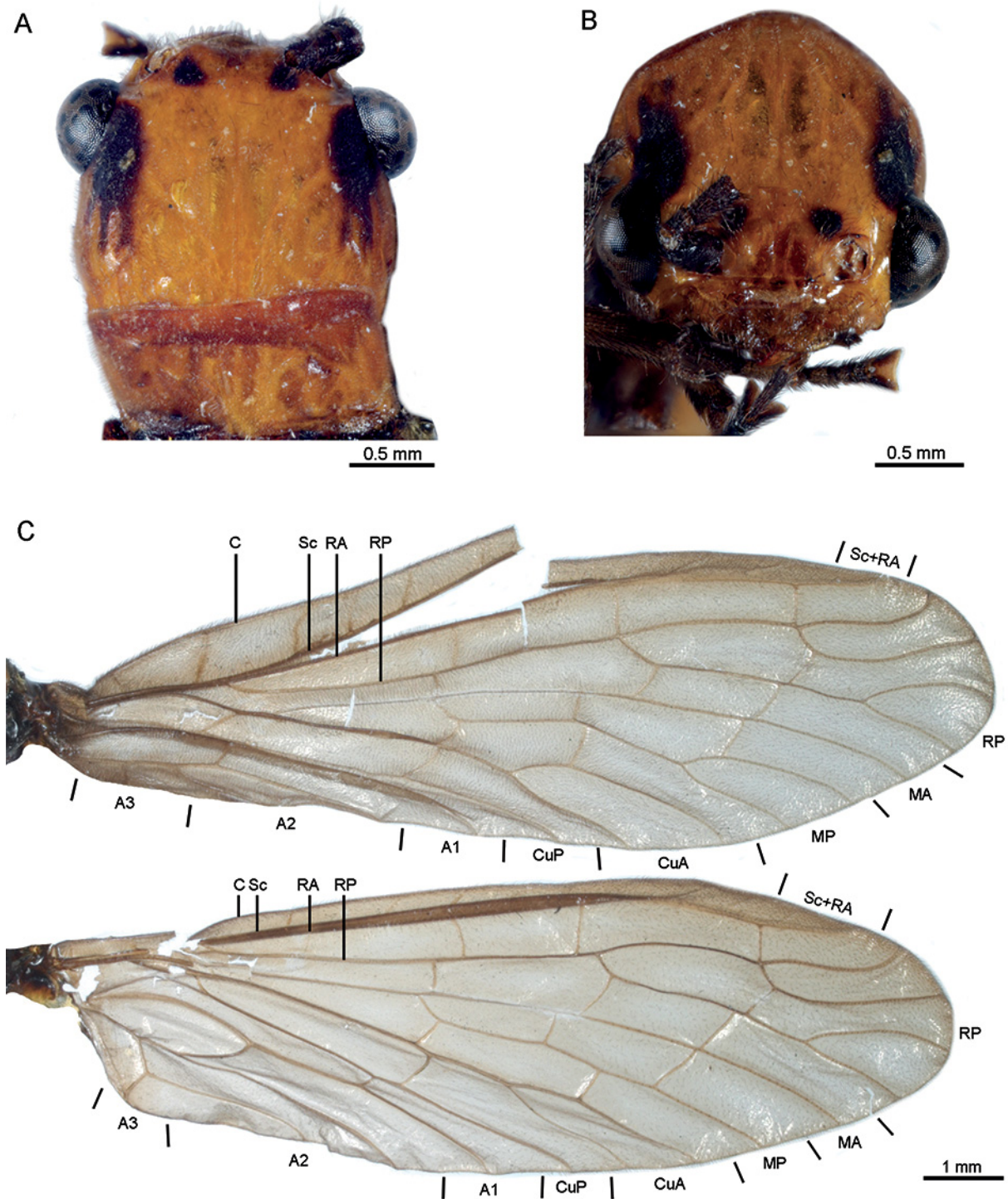


Fig. 9. Holotype female of *Ilyobius bimaculatus* (Banks, 1920). **A.** Head, dorsal view. **B.** Head, dorso-frontal view. **C.** Fore- (above) and hindwing (below).

two crossveins; Cu forked near wing base, CuA forked at apex; intracubital space with single crossvein. Cubitoanal space with single crossvein. Area between A1 and A2 with a single sinuous crossvein, A2 forked near wing base.

ABDOMEN. Dissected and cleared.

MALE GENITALIA. Unknown.

FEMALE GENITALIA (Fig. 10). Sternite 8 unmodified, densely covered by long setae; gonocoxite 8 as small, paired, ovoid sclerites; gonapophyses 8 as lateral smooth, glabrous, ovoid plates. Tergite 9 ventrally extended in lateral view, expanded and articulated to gonocoxite 9, posteroventral margin straight; gonocoxite 9 ovoid, uniformly setose; gonostylus 9 small, semicircular, posterodorsally located on gonocoxite 9; ectoproct as a small ovoid sclerite, setose.

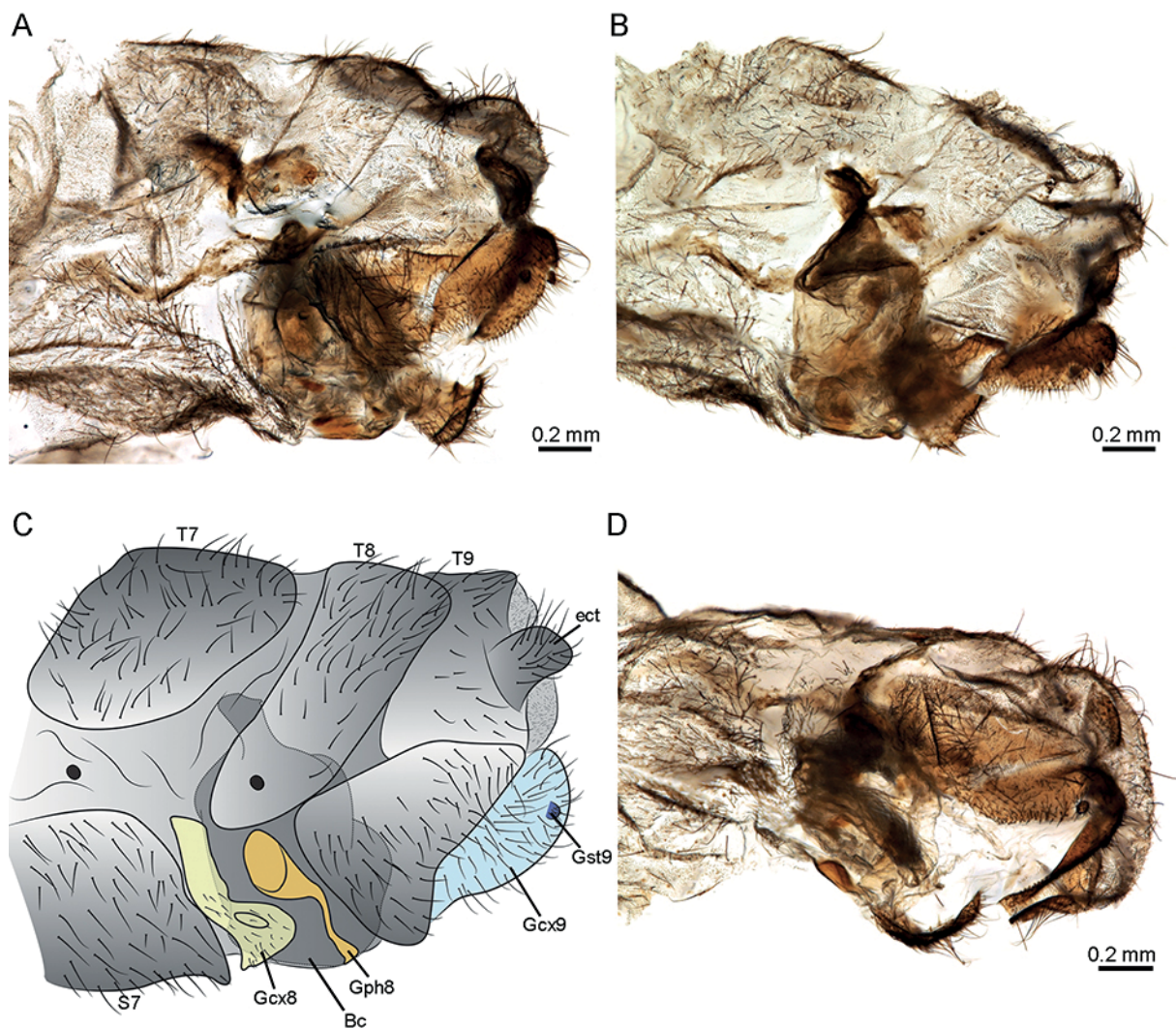


Fig. 10. Holotype of *Ilyobius bimaculatus* (Banks, 1920), female genitalia. **A.** Lateroventral view. **B.** Lateral view. **C.** Morphological interpretation of genital sclerites in B. **D.** Ventral view.

Distribution

Bolivia (probably Santa Cruz) (Fig. 7C).

Remarks

Ilyobius bimaculatus is only known from the holotype female, which is in poor condition. Consequently, understanding the phylogenetic affinities of this species is difficult at present because the primary diagnostic characters are currently limited to the male genitalia. However, the color pattern of this species is similar to that of *I. flammatus* (Penny, 1982), *I. mexicanus* (Banks, 1901) and *I. curvatus* Liu *et al.*, 2015b. In those species, the pronotum is uniformly orange and the head has posteriorly trifurcate dark markings around the compound eyes. *Ilyobius bimaculatus* can easily be distinguished by having the frons possessing a pair of ovoid black spots between the antennal fossae, which are absent in the other species.

Ilyobius nigrocephalus Ardila-Camacho, Martins & Contreras-Ramos sp. nov.

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Figs 11–15

Diagnosis

This species is distinguished from others of the genus by having a dark brown head and orange pronotum (Fig. 11). The male sternite 9 is broadly rounded and shovel-like. The gonocoxites 9 are subtrapezoidal with posterior corners blunt. The gonocoxites 11 are elaborated, with two differentiated portions: the upper portion is posteriorly produced as lateral hook-shaped processes, and the lower portion as two narrow, arched, lateral sclerites, medially fused; in lateral view curved, elongated, and narrow with the distal part representing the gonostyli 11, which are dorsally connected to the upper portion and covered with minute spinulae. The membrane between gonocoxites 11 and sternite 9 is covered with minute spinulae. The female sternite 8 is subpentagonal, posteromedially produced into a short and blunt lobe. The gonocoxites 8 form an ovoid sclerite, located just beneath sternite 8; the bursa copulatrix is bilobed with the distal margin shallowly incised in ventral view.

Etymology

The specific epithet “*nigrocephalus*” is a combination of the Latin *nigrum* which means black, and the Greek κέφαλη (*céfale*) meaning head, alluding to the dark pigmentation of the head of this species. An adjective in the nominative case.

Material examined**Holotype**

ECUADOR • ♂; El Oro, 7 km, E. Piñas; 2 Aug. 1989; L. Stange and R. Miller leg.; FSCA.

Paratype

ECUADOR • ♀; same collection data as for holotype; FSCA.

Description

HEAD (Fig. 12A–B). Width 1.6 mm; nearly completely dark brown, ventrally light brown; compound eyes dark brown. Antenna with scape enlarged, dark reddish brown, covered with abundant light brown setae, pedicel dark brown, nearly as long as wide, flagellum dark brown with 32 flagellomeres, densely covered with dark brown setae. Frons densely setose, somewhat protuberant between antennae. Clypeus and labrum densely covered with light brown setae, anterior margin of clypeus with median concavity. Maxillary and labial palpi dark brown with abundant dark brown setae. Occiput with dark brown muscle scars.

THORAX (Fig. 11). Pronotum orange, rectangular, nearly 1.5 times as wide as long, densely covered with minute, light yellow setae. Mesonotum wider than long, dark brown, densely covered with minute, light brown setae. Metanotum similar to mesonotum, but slightly narrower. Pteropleura dark reddish brown, covered with abundant light brown setae.

LEGS. Dark brown, all segments densely covered with dark brown setae; fore femur somewhat expanded and shorter than mid- and hind femur. Tibial spurs short, dark brown. Basitarsus of fore- and midleg short, as long as second and third tarsomeres together; on hind leg longer, as long as remainder of tarsomeres together. Pretarsal claws dark brown.

WINGS (Fig. 12C). Forewing 9.5 mm long, membrane translucent, smoky, densely setose. Venation light brown, densely covered with fine setae of the same color as cuticle. Costal field slightly expanded on $\frac{1}{3}$ of wing length, with nine crossveins; pterostigma absent. A single subcostal crossvein. Radial space with three crossveins, RP with two branches, basal one forked near posterior wing margin. Radiomedial space with three crossveins, M forked near mid-length of wing, MA unforked, MP forked near posterior wing margin; intramedial space with two crossveins; mediocubital space with two crossveins; CuA vein forked slightly beyond level of M fork, CuP unforked; intracubital space with single crossvein. Cubitoanal space with single crossvein; area between A1 and A2 with a single crossvein, A2 forked before R fork level; area between A2 and A3 with single crossvein. Hindwing 8 mm long, with general

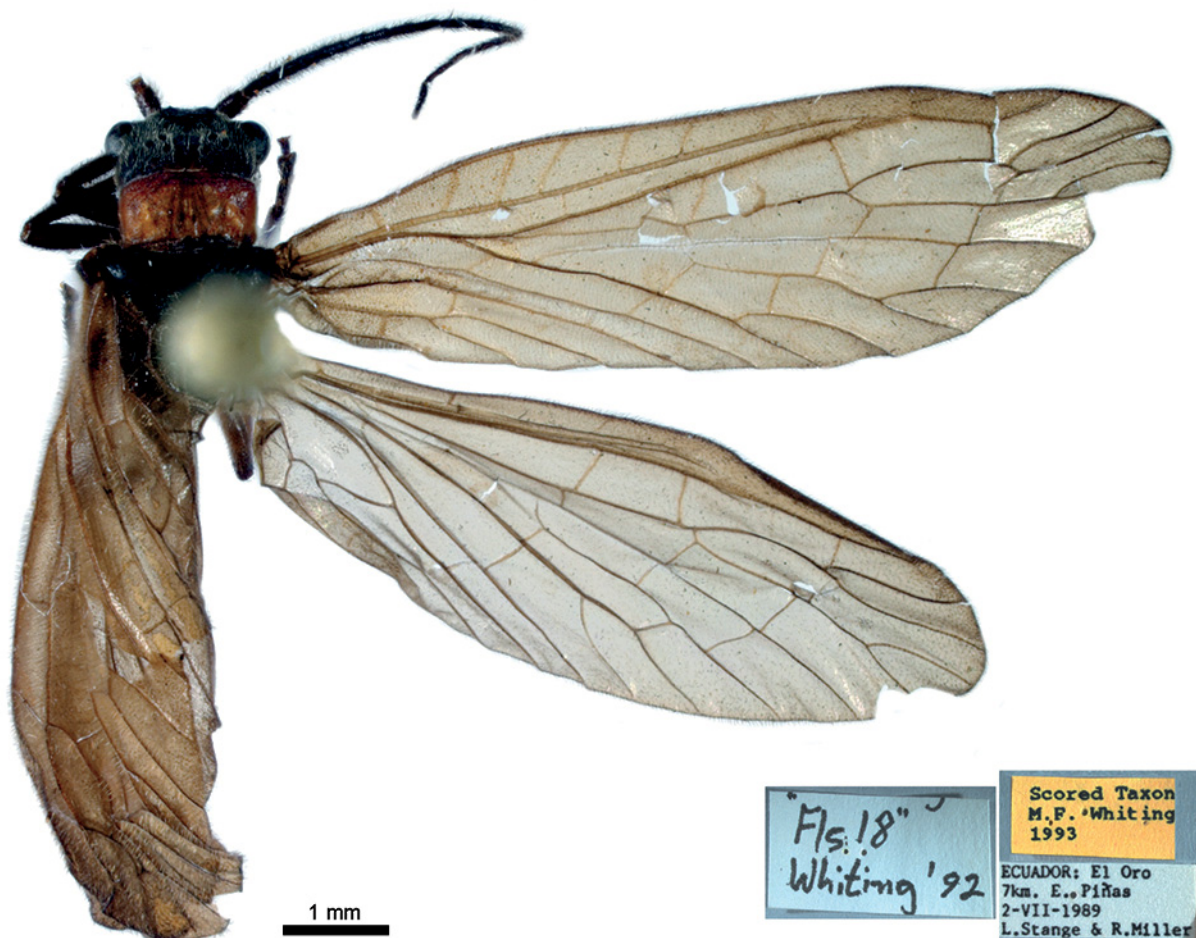


Fig. 11. Holotype male of *Ilyobius nigrocephalus* sp. nov., dorsal habitus.

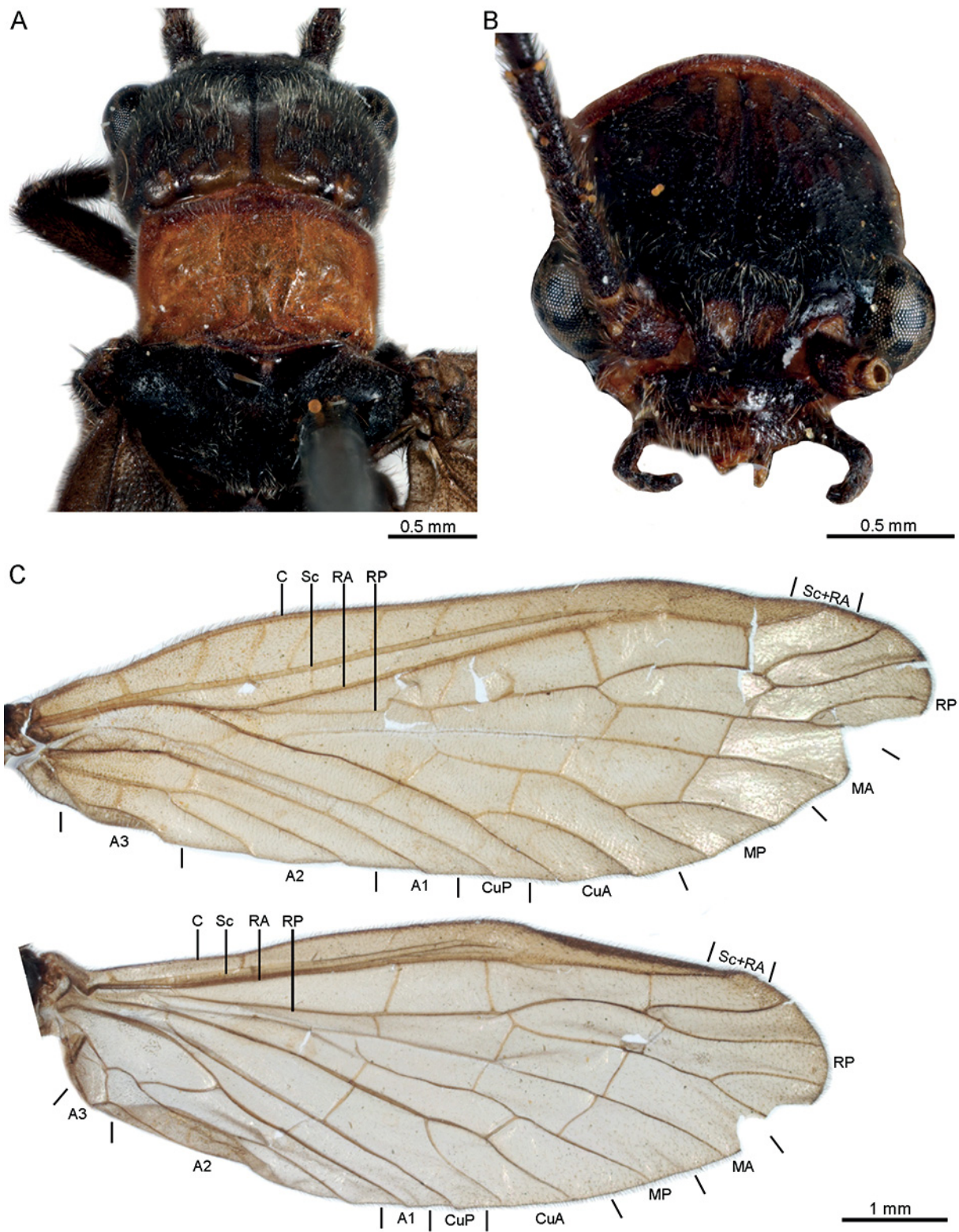


Fig. 12. Holotype male of *Ilyobius nigrocephalus* sp. nov. **A.** Head, dorsal view. **B.** Head, dorso-frontal view. **C.** Fore- (above) and hindwing (below).

aspect similar to forewing. Costal field narrow, with four or five crossveins; subcostal field with single crossvein. Radial space with three crossveins, RP with two branches, basal one forked near posterior wing margin. Radiomedial space with three crossveins. M vein forked near mid-length of wing, intramedial space with two crossveins. Mediocubital space with two crossveins; Cu forked near wing base, CuA forked at apex; intracubital space with single crossvein. Cubitoanal space with single crossvein. Area between A1 and A2 with a single sinuous crossvein, A2 forked near wing base.

ABDOMEN. Dark brown with abundant light brown setae.

MALE GENITALIA (Figs 13–14). Tergite 8 semi-membranous, densely setose; tergite 9 sclerotized, ring-shaped, sparsely covered with long setae, in dorsal view V-shaped around anal tubercle, laterally expanded; in lateral view trapezoidal with ventral half long, posteroventral side oblique, articulated to gonocoxite 9. Anal tubercle membranous; ectoproct mammilliform, elongated, setose, fused to anal tubercle. Sternite 9 sclerotized, broadly rounded in ventral view, densely setose, shovel-like in lateral view, reaching level of gonostyli 11 apex. Gonocoxite 9 sclerotized, adjacent to sternite 9, moderately setose, subtrapezoidal with posterior corners blunt and posterior margin slightly concave; gonostylus 9 absent. Membrane between sternite 9 and gonocoxites 11 covered with minute spinulae. Gonocoxites 11 elaborated, with two distinct portions: upper portion transversely elongated, with ventral margin arched and dorsal margin straight in caudal view; laterally not fused to ectoprocts; medially with fusion line somewhat distinct, in lateral view produced into lateral hook-shaped processes, extended slightly beyond level of ectoproct apex; lower portion as two narrow, arched, lateral sclerites, medially fused, with fusion line distinct; medial part representing the gonostyli 11, caudally produced, covered with minute spinulae and dorsally connected to upper portion.

FEMALE. External morphology and coloration similar to male, head width 1.7 mm; forewing 9.8 mm long, antennae with 29 flagellomeres; costal field with 12 crossveins; radial space with three crossveins. Hindwing 8.5 mm long, costal field with five crossveins; radial space with three crossveins.

FEMALE GENITALIA (Fig. 15). Tergite 9 in lateral view ventrally extended, expanded and articulated to gonocoxite 9, posteroventral margin straight; gonocoxite 9 ovoid, uniformly setose; gonostylus 9 small, semicircular, posterodorsally located on gonocoxite 9; ectoproct as a small ovoid sclerite, setose. Sternite 8 in lateral view posteroventrally projected, with blunt apex, extended on gonocoxite 8 slightly beyond its mid-length; in ventral view subpentagonal, posteromedially produced into short and blunt lobe, entire surface densely covered by long setae; gonocoxite 8 in lateral view narrow, plate-like, densely setose; in ventral view ovoid, located just beneath sternite 8; bursa copulatrix moderately sclerotized, sac-like in lateral view, bilobed, with distal margin shallowly incised in ventral view; gonapophyses 8 as lateral smooth, glabrous, ovoid plates.

Distribution

Ecuador (El Oro) (Fig. 7D).

Remarks

Ilyobius nigrocephalus sp. nov. is related to *Ilyobius ranchograndis* (Contreras-Ramos, 2006) from Aragua, Venezuela because of the complex morphology of the gonocoxites 11 of the male, as well as the structure of the female genitalia (see Contreras-Ramos 2006). Both species lack the posteriorly trifurcate dark marking around the compound eyes, having the head uniformly colored. However, the new species has the head nearly completely dark brown, with some muscle scars on the median area of the vertex, while *I. ranchograndis* has the head orangish brown. Furthermore, the pronotum of *I. nigrocephalus* sp. nov. is uniformly orange, whereas in *I. ranchograndis* it is orangish brown with darker margins. *Ilyobius nigrocephalus* sp. nov. is known from two specimens from El Oro province of

Ecuador, which is located in the geographical area known as the coastal region, with its northwest region limited by the Pacific Ocean. Rivers in El Oro Province originate in the Andean Mountains and flow into the Gulf of Guayaquil. The climate of this mountainous region where the specimens were collected is rainier and colder compared to the coastal region.

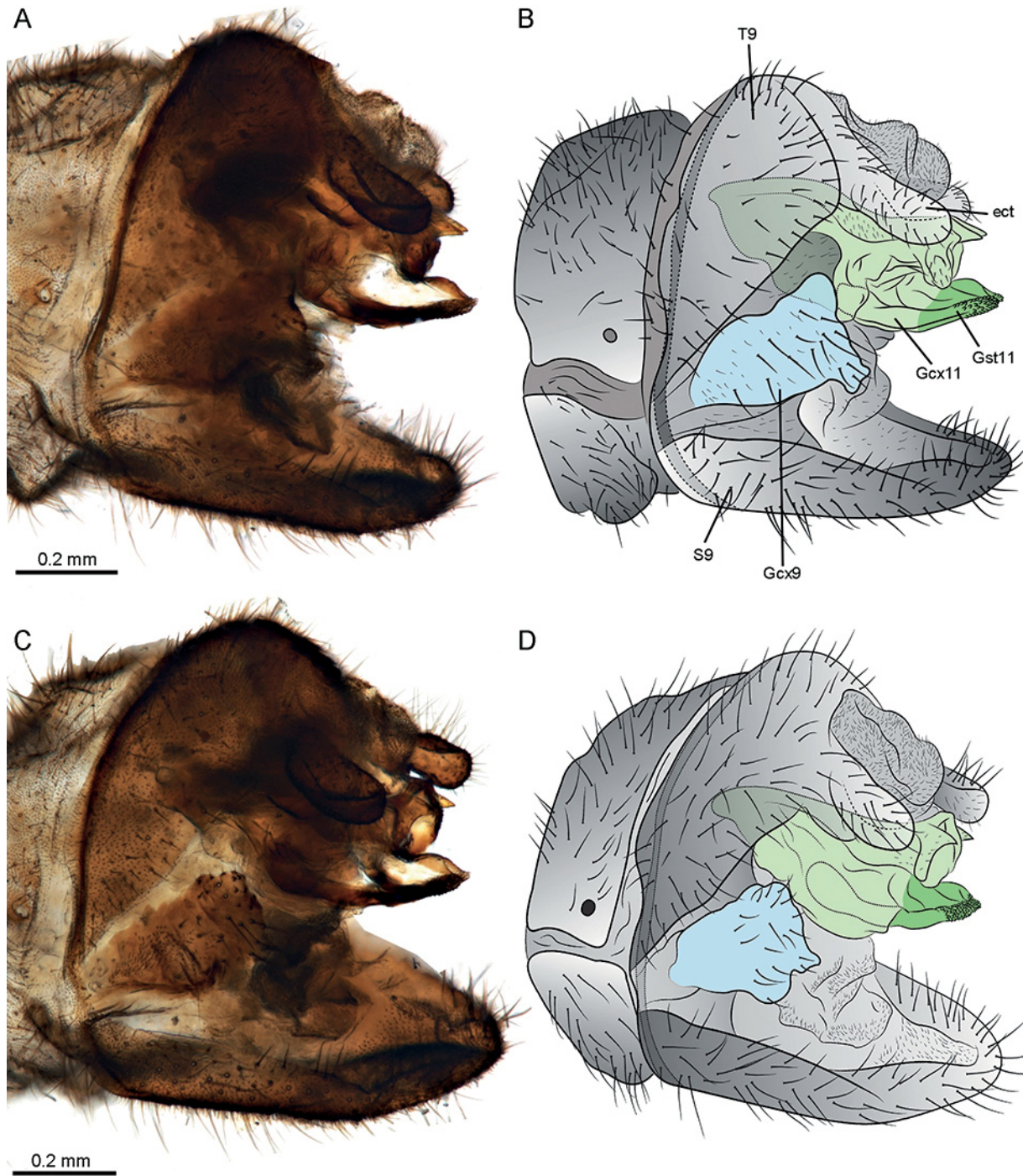


Fig. 13. Holotype of *Ilyobius nigrocephalus* sp. nov., male genitalia. **A.** Lateral view. **B.** Morphological interpretation of genital sclerites in A. **C.** Laterocaudal view. **D.** Morphological interpretation of genital sclerites in C.

Key to world genera of Sialidae

(after Liu *et al.* (2015a) and Martins *et al.* (accepted); adults of †*Sharasialis* Ponomarenko, 2012 are unknown)

Taxa that contain only extinct species are preceded by a dagger (†); taxa that contain both extant and extinct species are followed by “(+†)”; taxa that contain only extant species are unannotated.

1. Forewing: MA 2-branched (Liu *et al.* 2015a: fig. 8a–c) 2
 - Forewing: MA simple (Liu *et al.* 2015a: fig. 8g–i) 6
2. Forewing: costal area only weakly broadened proximally (ca 1–1.5× as wide as distal costal area) (Liu *et al.* 2015a: fig. 8a–b); MA1 and MA2 ca 0.8–1.5× as long as MP1 and MP2 (length from its origin to its end on posterior wing margin) (Liu *et al.* 2015a: fig. 8a–b) 3
 - Forewing: costal area distinctly broadened proximally (ca 2× as wide as distal costal area) (Liu *et al.* 2015a: fig. 8l); MA1 and MA2 ca 2× as long as MP1 and MP2 (length from its origin to its end on posterior wing margin) (Liu *et al.* 2015a: fig. 8l) †*Proindosialis* van der Weele, 1909 (France)
3. Forewing: ra-rp crossveins all more or less perpendicular to RA and RP (Liu *et al.* 2015a: fig. 8a, g); male abdomen: 10th gonocoxites present (as a pair of weakly sclerotized lobes) (Liu *et al.* 2015a: fig. 9a–d) 4
 - Forewing: 1–2 ra-rp crossveins inwardly oblique (i.e., proximal angle with RA >> distal angle with RA) (Liu *et al.* 2015a: Fig. 8b–c); male abdomen: 10th gonocoxites absent (Liu *et al.* 2015a: figs 10a–d, 11a–d) 5
4. Forewing: medio-cubital space with two crossveins (Liu *et al.* 2015a: figs 1a, 8a); CuA 2-branched (Liu *et al.* 2015a: figs 1a, 8a) *Austrosialis* Tillyard, 1919 (Australia)
 - Forewing: medio-cubital space with one crossvein (Liu *et al.* 2015a: fig. 8j); CuA 3-branched (Liu *et al.* 2015a: fig. 8j) †*Dobbertinia* Handlirsch in Schröder, 1920 (Germany)
5. Forewing: costal space with proximal subcostal veinlets not strongly oblique (Liu *et al.* 2015a: fig. 8b); male abdomen: tergite 9 without a digitiform posteroventral process (Liu *et al.* 2015a: fig. 10c); ectoproct with spiniform setae ventrally (Liu *et al.* 2015a: fig. 10d); female abdomen: gonocoxites 8 fused as a single sclerite (Liu *et al.* 2015a: fig. 10f); gonapophyses 8 subtriangular in ventral view (Liu *et al.* 2015a: fig. 10f) *Stenosialis* Tillyard, 1919 (Australia)
 - Forewing: costal space with (most) proximal subcostal veinlets strongly oblique (Liu *et al.* 2015a: fig. 8c); male abdomen: tergite 9 with a digitiform posteroventral process (Liu *et al.* 2015a: fig. 11c); ectoproct without spiniform setae ventrally (Liu *et al.* 2015a: fig. 11c); female abdomen: gonocoxites 8 paired (Liu *et al.* 2015a: fig. 11f); gonapophyses 8 broadly shield-like in ventral view (Liu *et al.* 2015a: fig. 11f) *Leptosialis* Esben-Petersen, 1920 part (*L. necopinata*) (South Africa)
6. Fore and hindwing: RP 4-branched (Liu *et al.* 2015a: fig. 8e, g); male abdomen: 9th gonocoxites widely separated (Liu *et al.* 2015a: fig. 16b, d) 7
 - Fore and hindwing: RP ≥ 5-branched (Liu *et al.* 2015a: fig. 8h–i); male abdomen: 9th gonocoxites closely adjacent medially (Liu *et al.* 2015a: fig. 18h, l) *Sialis* Latreille, 1802 (+†) (Asia, †Europe and North America)
7. Forewing: MP simple (Liu *et al.* 2015a: figs 1c, 8e) 8
 - Forewing: MP 2-branched (Liu *et al.* 2015a: fig. 8f–g) 10

8. Fore and hindwing: RP basal branch simple (Liu *et al.* 2015a: fig. 1c)
..... **Leptosialis** Esben-Petersen, 1920 part (*L. africana*) (South Africa)
– Fore and hindwing: RP basal branch 2-branched (Liu *et al.* 2015a: fig. 8e–f) 9
9. Hindwing: intramedial space with 2 crossveins (Liu *et al.* 2015a: fig. 8e); male abdomen: sternite 9 without an elongate median lobe (Liu *et al.* 2015a: fig. 13b–c); ectoproct without an elongate and weakly sclerotized projection (Liu *et al.* 2015a: fig. 13a, c)
..... **Indosialis** Lestage, 1927 (+†) (Southern Asia, east Pakistan, †Turkey)
– Hindwing: intramedial space with one crossvein (Liu *et al.* 2015a: fig. 8k); male abdomen: sternite 9 with an elongate median lobe (Nel *et al.* 2002: fig. 5); ectoproct with an elongate and weakly sclerotized projection (Nel *et al.* 2002: fig. 5) †**Eosialis** Nel *et al.*, 2002 (France)
10. Male abdomen: gonostyli 9 absent (Liu *et al.* 2015a: fig. 14c–d); gonocoxites 11 not fused laterally with ectoproct (Liu *et al.* 2015a: fig. 14c–d); female abdomen: gonocoxites 8 without longitudinal median incision (Liu *et al.* 2015a: fig. 15d) 11
– Male abdomen: gonostyli 9 present (Figs 3–5); gonocoxites 11 fused laterally with ectoproct (Figs 3–5); female abdomen: gonocoxites 8 with longitudinal median incision (Fig. 6C–D)
..... **Caribesialis** gen. nov. (Cuba)
11. Male abdomen: gonocoxites 9 large, not subtriangular (Liu *et al.* 2015a: fig. 14c); ectoprocts free (Liu *et al.* 2015a: fig. 14c–d); female abdomen: tergite 9 in lateral view with posterodorsal margin not projected, dorsal region straight (Liu *et al.* 2015a: fig. 15c); gonapophyses 8 large and plate-like in ventral view (Liu *et al.* 2015a: fig. 15b, d) 12
– Male abdomen: gonocoxites 9 small, subtriangular (Liu *et al.* 2015a: fig. 16c); ectoprocts fused sagittally and closely surrounding the anus (Liu *et al.* 2015a: fig. 16c–d); female abdomen: tergite 9 in lateral view with posterodorsal margin projected into a convex curvature (Liu *et al.* 2015a: fig. 16e); gonapophyses 8 small and subtriangular in ventral view (Liu *et al.* 2015a: fig. 16f)
..... **Protosialis** van der Weele, 1909 (USA)
12. Forewing: crossvein 1r-m arising from MA (generally from its base) (Liu *et al.* 2015a: fig. 8f); base of CuP clearly distant from A1 base (Liu *et al.* 2015a: fig. 8e); male abdomen: median processes of 11th gonocoxites directed posteroventrad (Liu *et al.* 2015a: fig. 14c–d) 13
– Forewing: crossvein 1r-m arising from stem of M (Liu *et al.* 2015a: fig. 8d); base of CuP close to A1 base (Liu *et al.* 2015a: fig. 8d); male abdomen: median processes of 11th gonocoxites directed posterodorsad (Liu *et al.* 2015a: fig. 12c–d) **Haplosialis** Navás, 1927 (Madagascar)
13. Forewing: costal veinlets absent on pterostigma region (Huang *et al.* 2016: fig. 2a); crossvein 1a2–a3 absent (Huang *et al.* 2016: fig. 2a); male abdomen: ectoproct with a slender, weakly sclerotized projection (Huang *et al.* 2016: fig. 2b) †**Haplosialodes** Huang *et al.*, 2016 (Myanmar)
– Forewing: costal veinlets present on pterostigma region (Liu *et al.* 2015a: fig. 8f); crossvein 1a2–a3 present (Liu *et al.* 2015a: fig. 8f); male abdomen: ectoproct without a slender, weakly sclerotized projection (Liu *et al.* 2015a: fig. 14c)
..... **Ilyobius** Enderlein, 1910 (+†) (Mexico, Central and South America)

Key to world extant species of *Ilyobius*

(after Liu *et al.* 2015b)

1. Thorax: Pronotum pale, uniformly orange to reddish brown (fig. 12A) 2
– Thorax: Pronotum dark, usually black, sometimes with pale markings (Liu *et al.* 2015b: fig. 3) 8
2. Head: without posteriorly trifurcate dark marking around compound eyes (Liu *et al.* 2015b: fig. 3) ... 3

- Head: with posteriorly trifurcate dark markings around compound eyes (Liu *et al.* 2015b: fig. 5) 5
- 3. Head: blackish brown 4
- Head: uniformly orange brown (Contreras-Ramos 2006: fig.1).....
..... *I. ranchograndis* (Contreras-Ramos, 2006)
- 4. Head: dark orange on median portion of vertex (Liu *et al.* 2015b: fig. 3)
..... *I. flavicollis* (Enderlein, 1910)
- Head: completely dark brown, including the median portion of vertex (Fig. 12A–B)
..... *Ilyobius nigrocephalus* sp. nov.
- 5. Head: frons without any dark marking 6
- Head: frons with a pair of ovoid black spots between antennal fossae (Fig. 9A–B)
..... *I. bimaculatus* (Banks, 1920)
- 6. Male abdomen: gonocoxite 9 short, ovoid, not directed posterodorsad (Liu *et al.* 2015b: fig. 8), male gonocoxites 11 with median processes directed posteriad (Liu *et al.* 2015b: fig. 8) 7
- Male abdomen: gonocoxite 9 elongate and strongly directed posterodorsad (Contreras-Ramos 2008: fig. 10), male gonocoxites 11 with median processes directed ventrad (Contreras-Ramos 2008: fig. 10) *I. flammatus* (Penny, 1981)
- 7. Forewing: length more than 11.0 mm in males and 12.0 mm in females; male abdomen: gonocoxites 11 with median processes straightly directed posteriad (Liu *et al.* 2015a: fig. 14g); female abdomen: fused gonocoxites 8 bluntly prominent posteriad (Liu *et al.* 2015a: fig. 15d).....
..... *I. mexicanus* (Banks, 1901)
- Forewing: length less than 9.0 mm in males and 10.0 mm in females; male abdomen: gonocoxites 11 with median processes distinctly curved posteroventrad on distal half (Liu *et al.* 2015b: fig. 8); female abdomen: fused gonocoxites 8 strongly narrowed posteriad (Liu *et al.* 2015b: fig. 11)
..... *I. curvatus* Liu *et al.*, 2015b
- 8. Head: orange with a median black stripe extending from middle of vertex to frons; male abdomen: sternite 9 posteriorly with a long digitiform, median projection and a pair of short lateral projections (Contreras-Ramos *et al.* 2005: fig. 3) 9
- Head: orange with three broad black markings on frons and lateral portions of vertex, but middle of vertex without dark marking (Contreras-Ramos 2008: fig. 3); male abdomen: sternite 9 posteriorly with a long digitiform, median projection, but without any posterolateral projections (Liu *et al.* 2015a: fig. 14b) *I. chilensis* (McLachlan, 1871)
- 9. Head: with median black stripe anteriorly, not approaching compound eyes (Contreras-Ramos *et al.* 2005: fig. 1); female abdomen: gonapophyses 8 posteriorly convex (Contreras-Ramos *et al.* 2005: fig. 6) *I. hauseri* (Contreras-Ramos *et al.*, 2005)
- Head: with median black stripe anteriorly expanded and approaching compound eyes (Liu *et al.* 2015b: fig. 12); female abdomen: gonapophysis 8 posteriorly broadly concave (Liu *et al.* 2015b: fig. 14) ..
..... *I. nubilus* (Navás, 1933)

Phylogeny

The cladistic analyses performed, using equal weight New Technology Search and the Tree Bisection Reconnection method, recovered the same 11 most parsimonious trees with 178 steps in length (L), consistence index (CI) of 0.65 and retention index (RI) of 0.91, which generate a strict consensus tree (Fig. 16) with L = 183, CI = 63, and RI = 90. The New Technology search analysis using implied weighting (k = 14.908) recovered four most parsimonious trees with the same parameters as that of

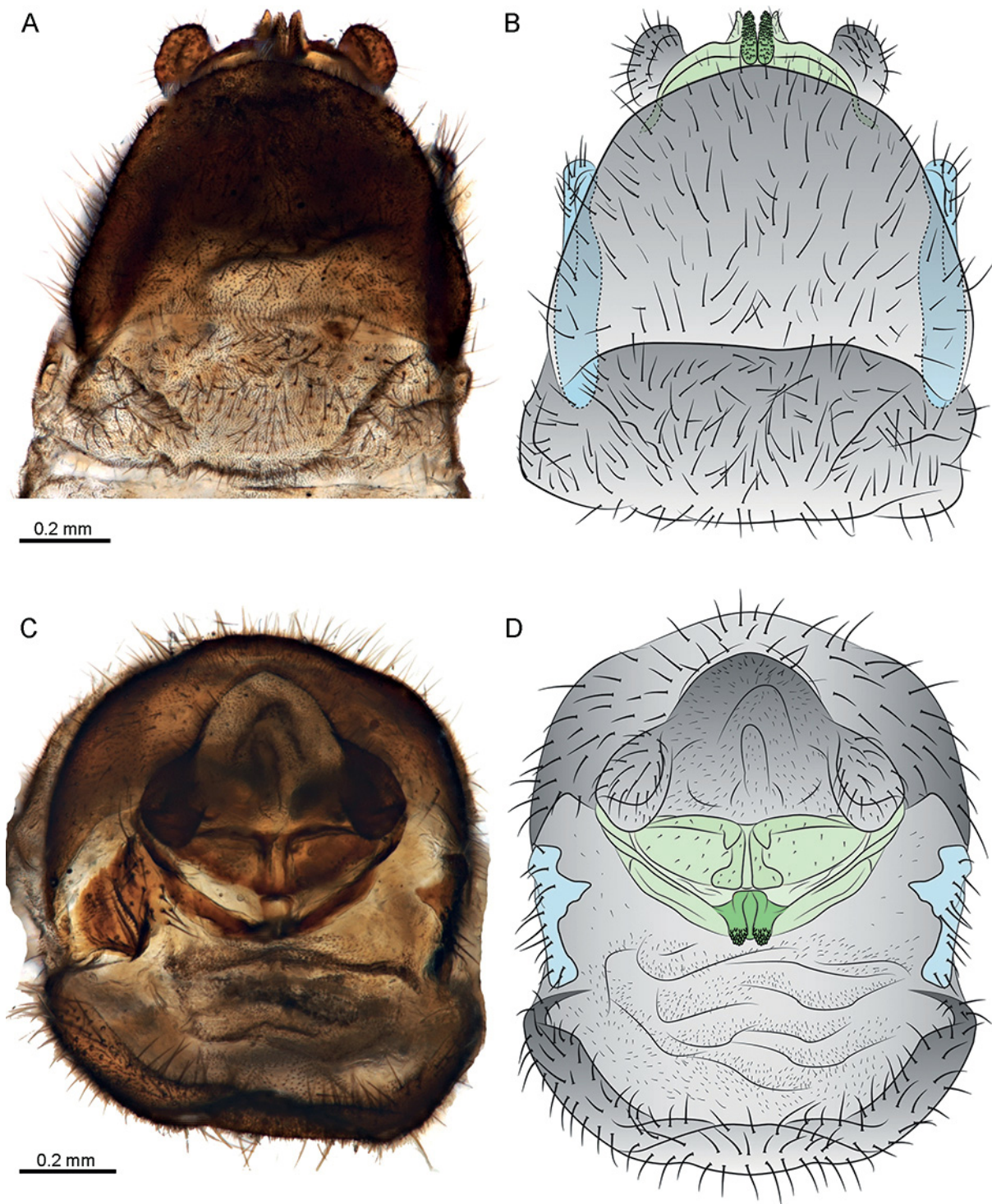


Fig. 14. Holotype of *Ilyobius nigrocephalus* sp. nov., male genitalia. **A.** Dorsal view. **B.** Morphological interpretation of genital sclerites in A. **C.** Caudal view. **D.** Morphological interpretation of genital sclerites in C.

equal weight analysis. All consensus trees (i.e., consensus from each different analysis) possess the same general topology, with no differences on the backbone of the main clades; the only observed difference is within the genus *Sialis*, which has no effects on the position of the new genus *Caribesialis* gen. nov.

Even after inserting the morphological data for *Caribesialis bifasciata* comb. nov. and *Ilyobius nigrocephalus* sp. nov. into the phylogenetic analysis of Sialidae, the family was recovered as monophyletic – similar to the results of Liu *et al.* (2015a) – with eight synapomorphies: forewings with apex of RP possessing two branches (char. 7:0) and with stem of M weak (narrow) (char. 13:1); prothorax wider than long (char. 17:1); legs with fourth tarsomere bilobed (char. 18:1); male with gonocoxites 10 degenerated or absent (char. 58:1); females with gonapophyses 8 sclerotized (char. 100:0); larva without a pair of tracheal gills on abdominal segment 8 (char. 106:1), and with caudal filament on segment 10 (char. 107:1).

All the main Sialidae lineages proposed by Liu *et al.* (2015a) were recovered as monophyletic. *Caribesialis* gen. nov. was recovered as part of the *Sialis* lineage, which was found to be the sister group of the *Ilyobius* lineage by Liu *et al.* (2015a), as well as in the present study. The clade composed of *Ilyobius* lineage + *Sialis* lineage is herein supported by the same three synapomorphies recovered in Liu *et al.* (2015a), i.e., fore (char. 8:1) and hindwing (char. 11:1) with MA simple, also present in the outgroup *P. capensis*; and males with gonocoxites 11 band-like or claw-like, with vertically protruding median process (char. 77:1), which has a unique origin in this clade.

Caribesialis gen. nov. is sister to *Protosialis* + *Sialis* composing the *Sialis* lineage, which herein possesses two synapomorphies – males with bilobed labrum (char. 1:2), which is only deeply concave in *Protosialis*, and tergite 9 nearly as wide as long (char. 19:1), which is more than twice as wide as long in *Protosialis* – and three other plastic characteristics: males with unpaired gonocoxites 10 (char. 57:1), which is absent in most of the species of Sialidae but is present in *Caribesialis* gen. nov. and some species of *Sialis*; females with membranous gonapophyses 8 (char. 100:1), also present in the outgroups *Platychauiodes capensis* and *Sininocellia gigantos*; and bursa copulatrix with irregular shape possessing lateral projection and sclerotized ridges (char. 104:1), which have a parallel origin in *S. gigantos*. In the original study by Liu *et al.* (2015a), the *Sialis* lineage is composed only of *Protosialis* + *Sialis* and was recovered as a monophyletic group supported by the following characters: males with internal apodeme of tergite 9 V-shaped (char. 21:1) and ectoproct largely fused with anus (char. 43:1). This clade was also recovered here as sister to *Caribesialis* gen. nov., supported by these same two synapomorphies, which clearly separates this group from the new genus, which has males with internal apodeme of tergite 9 arched and the ectoproct not fused with the anus. The other two main characteristics considered as synapomorphies of the *Sialis* lineage by Liu *et al.* (2015a) – char. 100: 1 and 104: 1 – also support this lineage in the present study.

The autapomorphies of *Caribesialis* gen. nov. are males with gonostylus 9 present (char. 35:0), only present in this genus and *Sialis nevadensis*; males with ectoproct paired and completely separated (char. 36:2), which is also present in the outgroup *P. capensis* and in some species of *Haplosialis* Navás, 1927, *Indosialis* and *Ilyobius*; ectoproct and gonocoxites 11 of males entirely fused with each other (char. 41:2), which is also present in *Sialis navasi* Liu *et al.*, 2009; males with gonocoxites 10 (char. 56:0), which is considered a reversion; males with anus possessing a setose lobe (char. 91:1), only present in this genus and a small group of *Ilyobius* species; females with gonocoxites 8 without median incision (char. 96:0), considered a reversion; and tergite 9 with distinctly prominent posterodorsal margin (char. 103:1), only present in this genus and in *Protosialis*.

Concerning the new Ecuadorian species *Ilyobius nigrocephalus* sp. nov., it is recovered within the *Ilyobius* lineage, and in the genus *Ilyobius*, which is distinguished by the presence of endophallic thorny setae in the males (char. 90:1). The new species was recovered as sister to a trichotomy

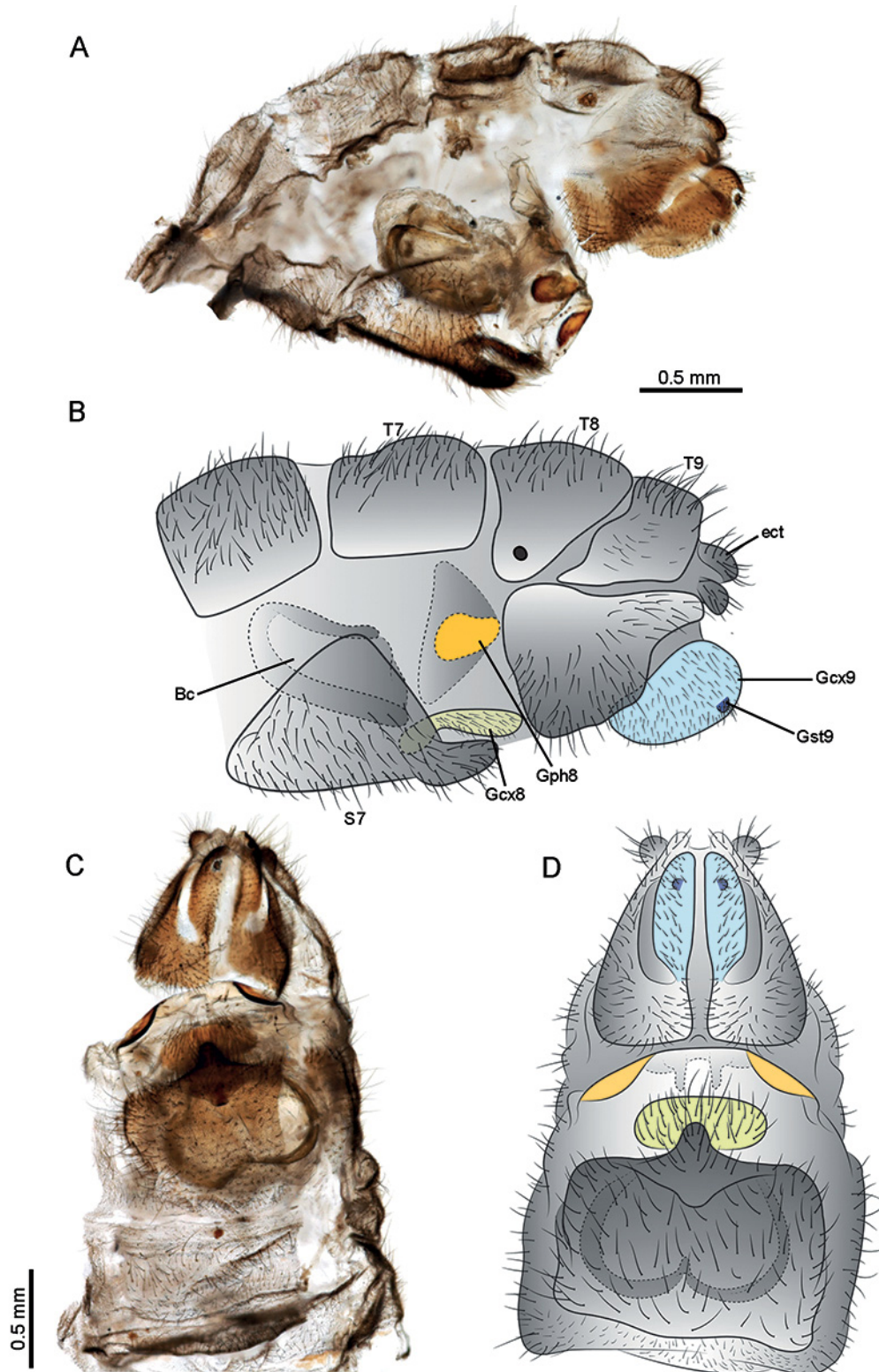


Fig. 15. Paratype of *Ilyobius nigrocephalus* sp. nov., female genitalia. **A.** Lateral view. **B.** Morphological interpretation of genital sclerites in A. **C.** Ventral view. **D.** Morphological interpretation of genital sclerites in C.

composed of *I. flammatus* + *I. mexicanus* + *I. ranchograndis*; the group formed by these four species is supported by males with anus presenting a setose lobe (char. 91:1), also present in *Caribesialis* gen. nov., and females with sternite 7 possessing an obtuse protrusion (char. 93:1), which is only present in this clade.

The new species has six autapomorphies for males: gonocoxites angulated ventrally (char. 30:1), also present in a group of *Sialis* species; ectoproct elongated (char. 46:1), also present in a group of four *Sialis* species; median process of gonocoxites 11 directed posterodorsad (char. 60:1), also present in *Haplosialis* + *Indosialis*; gonocoxites 11 with an additional short lobe beneath the median processes (char. 62:1), with parallel origin in a group of species of *Sialis*; gonocoxites 11 with transparent areas laterally (char. 70:1), with two other independent origins in *Sialis*; gonocoxites 11 with dorsal protrusion (char. 85:1), with independent origin in a group of *Sialis* species. There is an autapomorphy for females, i.e., gonocoxites 8 reduced (char. 97:1), also present in the clade *I. chilensis* + *I. hauseri*.

Discussion

New genus and its effect on the biogeography of the *Sialis* lineage

The Cuban archipelago is considered an important part of the Caribbean Islands, which are classified as a hotspot of biodiversity with a high concentration of endemism of genera and families (Myers *et al.* 2000; Smith *et al.* 2005). Cuba possesses numerous examples of endemic fauna and flora, including species of angiosperms (Morrone 2006), invertebrates, especially insects (Morrone 2006; Holzenthal & Calor 2017), and vertebrates, including fishes, birds, reptiles, amphibians and mammals (Morrone 2006).

Caribesialis gen. nov. is endemic to Cuba and has several uncommon characters to Sialidae, especially the presence of remarkable gonostyli 9 articulated posterolaterally to tergite 9. This structural configuration is present in the family Corydalidae, but typically absent in Sialidae, with the noteworthy exception of *S. nevadensis* in which it originated independently; the gonocoxites 10 composing a tiara-like sclerite and the base of gonocoxites 11 fused on the inner region of the ectoproct are also important characters, unique to the new taxon (see genus diagnosis). The unique morphology of *Caribesialis* gen. nov. is probably related to its isolation from the rest of the *Sialis* lineage (i.e., from *Protosialis* and *Sialis*). The new genus is considered sister to these two genera and may represent a somewhat atavistic relictual taxon. The other genera – which compose a well-supported lineage – have a continental distribution, with *Sialis* widespread in the Holarctic region and *Protosialis* endemic to the eastern United States (Bowles & Sites 2015; Liu *et al.* 2015a).

One of the main attributes that distinguish the order Megaloptera is that their larvae are dependent on lotic and lentic freshwater habitats, and the adults are typically found associated along the terrestrial margins of those same habitats. Some of the oldest fossil records of this adaptation include representatives of Chaulioidinae, such as *Eochauliodes striolatus* Liu *et al.*, 2012 and *Cretochaulus lacustris* Ponomarenko, 1976 from the Middle Jurassic (168.3–166.1 Ma) and Early Cretaceous (139.4–126.3 Ma), respectively (Liu *et al.* 2012; Rivera-Gasperín *et al.* 2019). Among Sialidae, *Sharasialis fusiformis* Ponomarenko, 2012 from the Late Jurassic (163.5–145 Ma), constitutes the oldest larval fossil record of this group, yet adult structures are known from the Early Jurassic (182.7–174.1 Ma) (Liu *et al.* 2015a; Engel *et al.* 2018). Considering this habitat restriction of the larvae, coupled with the low capability of dispersion of the adults, it is logical to think of a low or null capacity of dispersion from continental to insular masses and vice versa of this insect group. Furthermore, at the peak of their evolutionary development there was more freshwater available on the planet, and the present continents were closer together, which may have facilitated their dispersal (Liu *et al.* 2012, 2015a). Herein, we hypothesize that the presence of megalopterans on islands is most likely the product of ancient vicariant events, in which the ancestors of the mainland and insular populations became

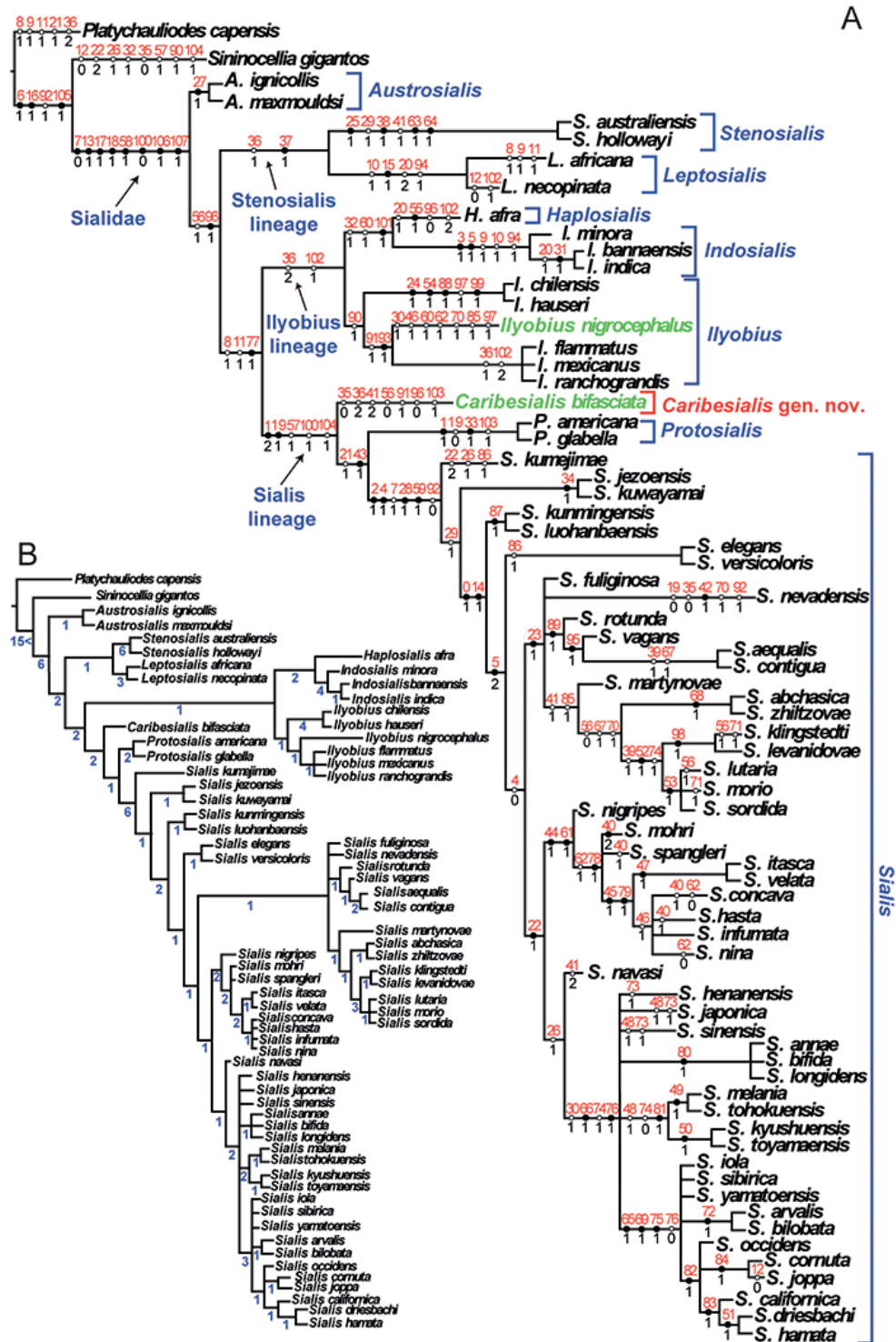


Fig. 16. Phylogenetic relationships of the extant Sialidae (Megaloptera), after Liu *et al.* (2015a). **A.** Strict consensus of 11 most parsimonious trees (number of steps = 183, consistency index = 63, retention index = 90) recovered with New Technology Search and Tree Bisection Reconnection analysis. **B.** Bremer values of branch support, presented below nodes. Character changes are marked on branches, with red characters, number above, and black state, number below each circle. Unequivocal changes (black circles) and reversed or multiple changes (white circles) are shown. Taxa in green are newly inserted into the phylogenetic analysis.

separated after the island formation. *Caribesialis bifasciata* is probably an example of an ancient relictual group that became isolated and survived until the present, as happened with endemic giant shrews (*Solenodon* Brandt, 1833) and Cuban night lizards (*Cricosaura* Gundlach & Peters, 1863), which were proposed as ancient relict populations separated from their continental, North American relatives through proto-Antillean vicariance (Hedges 2006). The divergence times of this remnant fauna were estimated by using molecular data and node dating at 75 Ma for *Cricosaura* as a mean time of origin (Hedges 2006). Similarly, the divergence of the West Indian shrews was estimated with a large molecular data set, yielding a mean of 76 Ma (Roca *et al.* 2004). The interpretation of these results implies that the shrews and the night lizards of the West Indies arose by vicariance in the proto-Antilles in the late Cretaceous and survived the bolide impact at the K/T boundary (Cretaceous/Paleogene, at 65 Ma) (Roca *et al.* 2004; Hedges 2006). This means that besides dry land, freshwater bodies with endemic fauna probably survived since then, including the alderflies. Interestingly, the origin of Sialidae has been estimated between the Lower Cretaceous and Paleogene based on molecular datasets of reduced representation of the genome and mitogenomes (Wang *et al.* 2017; Winterton *et al.* 2018; Vasilikopoulos *et al.* 2020). During the end of the Cretaceous (70–65 Ma) there was a maximum of emerged lands that connected North America with the Antillean archipelago or proto-Antilles, which are originated on the eastern boundary of the Caribbean plate since the Early Cretaceous through volcanic activity (Iturralde-Vinent & MacPhee 1999; Roca *et al.* 2004). There are paleontological data that demonstrate that between the Late Campanian and Paleocene there was an interchange of terrestrial tetrapods between North and South America when the emerged lands were close (Iturralde-Vinent 2005). Consequently, it is hypothesized that an isolation of a sialid population has taken place since then in the proto-Antilles. Such a lineage gradually became separated from their continental relatives (i.e., the ancestors of the remaining *Sialis* lineage) in an ancient cladogenetic event. In this scenario, and given the ecological characteristics of this insect group, a dispersal event through the GAARlandia landspan, i.e., an emerged chain of islands that connected South America with the future Antilles and Central Cuba during the latest Eocene/Early Oligocene (35–33 Ma) (Iturralde-Vinent & MacPhee 1999) is not considered to be a likely explanation for the extant distribution of this group.

The *Sialis* lineage (to which *Caribesialis* gen. nov. belongs) is considered as sister group of the *Ilyobius* lineage. According to Liu *et al.* (2015a), these two lineages have an ancestral area of origin in the Northern Hemisphere. Nevertheless, with the results of the present study, where *Caribesialis* gen. nov. (Neotropical genus) diverges from *Protosialis* + *Sialis* at the base of the *Sialis* lineage, a possible Neotropical origin with subsequent diversification on the Northern Hemisphere is plausible. The ancestral area of origin of the *Sialis* lineage was considered to be North America by Liu *et al.* (2015a); however, with the early cladogenesis originating *Caribesialis* gen. nov., an origin in the Neotropical area is also possible. Despite its earliest fossil record being from Eocene Baltic amber – *Sialis voigti* Wichard & Engel, 2006 and *Sialis groehni* Wichard, 1997 – the origin of the *Sialis* lineage could be much older than the Eocene, and according to Liu *et al.* (2015a) it probably took place after the breakup of Pangaea, thus placing uncertainty on the origin of this new genus in Cuba.

With the description of the new genus, the alderfly fauna from the Neotropics is now composed of two genera, namely *Caribesialis* gen. nov. from Cuba, and *Ilyobius* which occurs in the continental area of the Neotropical region, especially in South America. As far as is known, the unique species of the new genus *Caribesialis* gen. nov. is the only megalopteran known from Cuba (Martins *et al.* (accepted)). Most of these species are known from only a few specimens and locations, and largely only by the type material deposited in collections of Cuba and the United States (Alayo 1968; Contreras-Ramos 2008). Although our knowledge regarding the role of less common species in ecosystems maintenance is limited, conservation of rare taxa may have a relevant impact on the conservation of biological diversity in a broad sense (Lyons & Schwartz 2001; Lyons *et al.* 2005).

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Supplementary files

Supp. file 1. List of morphological characters for Sialidae (Megaloptera) (after Liu *et al.* 2015a). <https://doi.org/10.5852/ejt.2021.782.1587.5539>

Supp. file 2. Matrix of morphological characters for phylogenetic analysis of Sialidae (Megaloptera) (after Liu *et al.* 2015a). <https://doi.org/10.5852/ejt.2021.782.1587.5541>

Supp. file 3. Phylogenetic relationships of the extant Sialidae (Megaloptera), after Liu *et al.* (2015a). **A.** Strict consensus of 4 most parsimonious trees (number of steps = 181, consistency index = 64, retention index = 90) recovered with New Technology Search using implied weighting analysis (k = 14.908). **B.** Bremer values of branch support, presented below nodes. Character changes are marked on branches, with red characters, number above, and black state, number below each circle. Unequivocal changes (black circles) and reversed or multiple changes (white circles) are shown. Taxa in green newly inserted into the phylogenetic analysis. <https://doi.org/10.5852/ejt.2021.782.1587.5543>

Supp. file 4. Matrix of morphological characters for phylogenetic analysis of Sialidae (Megaloptera) (after Liu *et al.* 2015a) in Nexus format. <https://doi.org/10.5852/ejt.2021.782.1587.5545>

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