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How many species of alderflies are in southern Brazil? On the taxonomy of Ilyobius Enderlein, 1910 and the names Protosialis nubila, P. brasiliensis, and P. hauseri (Megaloptera: Sialidae)

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How many species of alderflies are in southern Brazil? On the taxonomy of *Ilyobius* Enderlein, 1910 and the names *Protosialis nubila, P. brasiliensis*, and *P. hauseri* (Megaloptera: Sialidae)

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Running title: Atlantic Forest *Ilyobius*

Abstract

In this study, we revisited the taxonomy of three southern endemic Brazilian species of alderflies of the genus *Ilyobius* Enderlein, 1910. Our investigation was based on specimens of *Ilyobius nubilus* (Navás, 1933) collected from a recently discovered population from state of Paraná, which is the first record of the family Sialidae for that state. The specific limits between *Protosialis nubila* Navás, 1933, *P. brasiliensis* Navás, 1936 and *P. hauseri* Contreras-Ramos *et al*., 2005—all now combined in *Ilyobius*—were evaluated based on a comparative morphological study. In light to the new data, we judge *Protosialis brasiliensis* and *P. nubila* represent the same species, and therefore, *Protosialis brasiliensis* is therefore reinstated as the junior synonym of *P. nubila* with *Ilyobius nubilus* (Navás, 1933) the valid name to be applied to this species. A reviewed diagnosis for *I. nubilus*, including a key to Brazilian species of genus are presented and the specific status of *I. hauseri* is also discussed.

Keywords: Aquatic insects, Atlantic Forest, Neotropical region, new record, Systematics

Introduction

Taxonomy practices in the twenty-first century are largely dynamic, integrating multiple data sources and inference criteria. Many tasks of taxonomy have been recognized as limitations, which were highlighted in the last decade. Among them are the so-called “Linnean shortfall”, characterized by the absence of formal species descriptions, which is a significant challenge that affects our ability to understand global biodiversity and accurately identify specimens (Hortal *et al*. 2015). This gap has implications for scientific research, collections management, conservation, evolutionary studies, and ecology, and it is exacerbated in

Southern Hemisphere countries by the Latitudinal Taxonomic Gradient phenomenon (see Diniz-Filho *et al*. 2023). Although molecular analyses have the potential to improve species identification, accurate and reliable implementation of molecular approaches remains a barrier (see Wilkins *et al.* 2022). For the Sialidae (alderflies), lack of information is especially troublesome as many of the species were described based on only a few specimens, brief diagnoses, with insufficient illustrations and incomplete data. Part of these constraints can be explained because alderflies tend to be rarely collected in the field (Contrera-Ramos 2008; Mendes *et al.* 2024). Thus, these limitations, combined with the high similarity between recognized species, present challenges for the classification and identification of alderflies.

The Sialidae encompass about 100 known species, divided into two subfamilies, Sialinae (13 genera and 98 species) and the exclusively fossil †Sharasialinae (1 genus and 1 species) from Ulan Malgait Formation in Shar-Teg Sequence in Mongolia, dated as Late Jurassic 163.5–145 Mya (see Martins *et al*. 2022). The center of diversity for the living alderflies is located in the temperate areas of Holarctic with at least 50 species, while in the Neotropical and Andean regions, they are poorly represented with a single species of *Caribesialis* Ardila-Camacho, Martins & Contreras-Ramos *in* Ardila-Camacho *et al*., 2021, a genus endemic to Cuba, and fourteen species of *Ilyobius* Enderlein, 1910 (Cover & Resh 2008; Martins *et al*. 2022). The later genus has been targeted for many studies during the last decade that helped to better understand its morphology, biology, taxonomy, and phylogenetic relationships (e.g., Liu *et al*. 2015a, b; Pereira 2019; Mendes *et al.* 2022, 2024). However, the identity and characterization of a few species, particularly those distributed in the Brazilian southern Atlantic Forest, remains problematic.

Based on results of phylogenetic analysis supported by morphology of male and female genitalia, Liu *et al*. (2015a) transferred all Neotropical species of *Protosialis* to *Ilyobius* and proposed two groups, *I. chilensis* (McLachlan, 1871) group and *I. mexicanus* (Banks, 1901) group. All five species occurring in Brazil belong to the *I. chilensis* group: *I. brasiliensis* (Navás, 1936), *I. flammatus* (Penny, 1981), *I. hauseri* (Contreras-Ramos *et al.*, 2005), *I. nubilus* (Navás, 1933) and *I. erebus* Mendes *et al.*, 2022 (Liu *et al*. 2015a, Mendes *et al*. 2024). In general, they are all strongly similar in appearance and poorly known species, identified based by minor differences in the general coloration, shape of sternite 9 of the male having an elongated median protrusion, hook-like ectoproct of the male, gonocoxite 11 of the male with the median processes short, and the female gonocoxite 8 reduced and fused with gonapophysis 8 (Liu *et al*. 2015a).

Protosialis nubila and *Protosialis brasiliensis* were the first two *Ilyobius* species recorded from Brazil, described by the Jesuit priest and naturalist Longino Navás in 1930s. He based his descriptions on single specimens, made short diagnoses, and only depicted a single wing of each species (see Navás 1933, 1936). Such limited descriptions hamper the actual understanding of the concept of each name and species identity. Many decades later Contreras-Ramos (2006) redescribed *I. brasiliensis* and stated that the holotype was in poor condition of preservation, lacking many parts and appendages, and it consisted only of the head, thorax and left forewing, making it impossible to determine its sex. Liu *et al*. (2015b) reexamined the holotype of this species judging it as an invalid name and treated *I. brasiliensis* as a junior synonym of *I. nubilus*. They supported their decision based on similar coloration on the head and pronotum, the markedly dilated costal area on the wing, and sympatric distribution—São Paulo State. However, Mendes *et al*. (2024) challenged the conclusion of Liu *et al*. (2015b), suggesting that the characters were not robust enough to synonymize *I. nubilus* and *I. brasiliensis*, especially considering the precarious state of the holotype. Furthermore, the absence of additional material from the type locality of *I. brasiliensis* further added to the debate over whether these names represent two or a single species thus confusing taxonomic knowledge of the genus.

When introduced to the most recent *Ilyobius* species, Mendes *et al.* (2022) offered an updated point of view on the taxonomy and biology of the genus *Ilyobius*, including the rediscovery of *I. hauseri* based on specimens collected from the type locality. *Ilyobius hauseri* was described based on single male and female collected in the state of Rio Grande do Sul, southern Brazil (Contreras-Ramos *et al*. 2005). The morphology of terminalia of this species has been reinterpreted a few times (i.e., Liu *et al*. 2015a; Mendes *et al*. 2022), and some structures were putatively lost, such the ectoproct of the male (see Liu *et al*. 2015b). Additionally, Mendes *et al.* (2024) discussed similarities between *I. hauseri* and *I. nubilus* and suggested three main characters to differentiate them: (1) dark dorsal mesial stripe on the head narrower in *I. hauseri* than in *I. nubilus* than; (2) tip of female gonapophysis 8 in ventral view distally convex and without a posterior notch in *I. hauseri* while the distal margin is putatively not convex and with a broad and arched posterior notch in *I. nubilus*; (3) male tergite 9 subtriangular, gonocoxite 9 without concavity, and gonostyli 11 in lateral view, projected distally downwards in *I. hauseri*; while the tergite 9 subrectangular, distal margin of gonocoxite 9 with a concavity, and gonostyli 11 projected distally upwards in *I. nubilus*.

Despite of recent advances in the knowledge of these three southern Brazilian species—*I. brasiliensis*, *I. hauseri*, and *I. nubilus*—the taxonomic status of these names remains disputed, because either *I. brasiliensis* was previously judged to be a junior synonym of *I. nubilus* or, more recently, *I. brasiliensis* as a valid name can be considered justified. Furthermore, the striking similarity between *I. brasiliensis*, *I. hauseri* and *I. nubilus* justifies a closer look at these species to see if they are valid.

Addressing these issues, our objective in this study is to report the very first record of Sialidae for the state of Paraná, together with a critical review of *Protosialis nubila*, *Protosialis brasiliensis* and *Protosialis hauseri*. Therefore, we conducted a detailed comparative morphological analysis of the three species, in particular reinterpreting the small differences in the genitalia of the females and males, and in the coloration of the head and wing venation.

Material and methods

Collections. The specimens examined are deposited in the Entomological Collection Padre Jesus Santiago Moure, Departamento de Zoologia, Setor de Ciências Biológicas, Universidade Federal do Paraná, Curitiba, PR, Brazil (DZUP – https://doi.org/10.15468/ukqvdu). Paraná's specimens (Fig. 1a) were collected using a variety of combined techniques, ranging from active collection—a standard light sheet trap with a 250 W lamp and a beating sheet- to passive collection—Pennsylvania light traps and double lightweight (Townes 1972), and 6 m long Malaise traps (Gressit & Gressit 1967), each either with a white or black roof (Fig. 2b). About 90% of Parana's specimens were collected with Malaise traps crossing streams such as discussed by De Almeida *et al*. (2013).

General procedures and terminology. The abdomen of both males and females were sectioned between segments VII and VIII with the aid of dissecting needles, after they were macerated in a 10% potassium hydroxide (KOH) solution at room temperature during two to five hours. To neutralize the reaction, the genitalia was transferred and kept on a plate containing water and a few drops of glacial acetic acid for 30 minutes. After the examination, the pieces were preserved in microvials with ethanol (80%) next to the specimen. The homology and terminology for male and female genitalia were based in Liu *et al.* (2016). Wing venation nomenclature follows Breitkreuz *et al.* (2017).

Taxonomy and nomenclature. The available diagnostic characters listed in the original descriptions and redescriptions (Navás 1933, 1936; Contreras-Ramos *et al*. 2005; Mendes *et al*. 2022, 2024) were critically analyzed and compared with examined specimens. Nomina and nomenclatural acts were taken in accordance with the International Code of Zoological Nomenclature (ICZN 1999, 2012).

Measurements, figures and maps. Measurements in millimeters were made with the aid of a micrometer eyepiece coupled in a stereomicroscope. Specimens were photographed or digitized using various techniques.

Original drawings published by Navás (1933; 1936); Contreras-Ramos *et al.* (2005); Liu *et al.* (2015b); Mendes *et al.* (2022, 2024) have been adapted and presented here with permission granted by Creative Commons 3.0 CC BY-NC-SA, 4.0 CC BY-NC-SA, CC BY 4.0, CC BY-NC-ND 3.0 BR and Magnolia press. Focus stacking images were generated using either Helicon Remote and Helicon Focus or using a Leica Stereomicroscope using Leica Application Suite (LAS). All images were edited in a dedicated image editor software. The illustrations were created with Inkscape (Inkscape Project 2022).

The map was produced using the freeware QGIS 3.32.0 with the biogeographical regionalization of the Neotropical region and accompanying shapefiles from Morrone *et al.* (2022).

Results and Discussion

Diagnostic characters and species delimitation

We analyzed previously proposed diagnostic characters (Table 1) using photographs and additional material, totaling 25 characters from a set of 29 examined specimens. We did not find any individual character or set of characters that justify *Protosialis brasiliensis* Navás, 1936 as a valid species, therefore it is restored as a junior synonym of *Protosialis nubila* Navás, 1933, in its current combination, *Ilyobius* *nubilus* (Navás, 1933), as previously championed by Liu *et al*. (2015b). A key to Brazilian species of *Ilyobius* and an amend diagnosis of *Ilyobius nubilus* **stat. rev.** are presented below.

Our analysis also revealed subtle differences in head coloration patterns, with significant inter- and intraspecific variations in the width and size of dark marks among the three species from the southern Atlantic Forest (Figs. 3, 4). Additionally, we observed that male (Fig. 6) and female genitalia (Figs. 7, 8), show notable similarities between *I. nubilus* and *I. hauseri* (Figs. 6–8), which raises doubts about the specific status of *I. hauseri* and suggests it may be a junior synonym of *I. nubilus*. However, insufficient material of *I. hauseri* exists to formalize that assessment.

Similarly, there were no clear-cut differences either in the shape and size of markings on the head and pronotum between *I. brasiliensis* and *I. nubilus*, as considerable variation was observed in the putative diagnostic character (Figs. 3a–j; 4 a–g). Specimens located in more southern regions, such as those associated with *I. hauseri* (Figs. 3k–l), may have narrower dark markings on the head compared to those found in more northern regions, such as *I. nubilus* (Fig. 1a) and *I. brasiliensis* (Fig. 1c). These morphological variations must be considered in the context of phenotypic plasticity, which may be related to ecological or environmental conditions along the latitudinal gradient, temperature fluctuations, or the availability of ecological resources. We hypothesize that these differences represent intraspecific variations and may correspond to be associated with patterns of variation of features related to geographic latitude, known as latitudinal clines (see Lancaster *et al*. 2017).

Recently, significant variation in the coloration of the head and pronotum of *I. nubilus* was demonstrated, with some specimens largely darkened and others paler (Mendes *et al*. 2024). These variations include pronotum coloration patterns very similar to those reported for *I. hauseri* and *I. brasiliensis* (Contreras-Ramos 2005, 2006). Furthermore, the head coloration in darker specimens is very similar to that observed in the holotype of *P. brasiliensis* (see Mendes *et al*. 2024; and Figs. 1b–d). Both these characters were previously mentioned by Liu *et al*. (2015b) to support the synonymization of *P. brasiliensis* with *P. nubilus*. Therefore, when considered independently, dark markings on the head and pronotum may not be useful characters to distinguish these species, as previously argued in recent studies (e.g., Liu *et al*. 2015b; Mendes *et al*. 2024).

Key for Brazilian species of *Ilyobius* (modified from Ardila-Camacho *et al*. 2021).

Some couplets in this key are largely based on the coloration because many specific diagnostic characters rely on this data. Dark markings and other characters can sometimes be misleading, so accurate identification can be achieved by consulting the diagnosis presented here, as well as the descriptions and redescriptions of these species available elsewhere.

1. Head with a pair of furcated dark marks around compound eyes, forming a mask; pronotum pale, uniformly orange to reddish-brown. Male, posterior margin of sternite 9 projected into a single acute process. Female unknown .... *I. flammatus* (Amazonas State)

1’. Head entirely black or orange with a dark longitudinal mesial stripe; pronotum dark, sometimes with ill-defined pale markings. Male, posterior margin of sternite 9 projected into a three thumb-like processes. Female gonocoxite 8 reduced into setose sclerite, gonapophysis 8 short, 2x wider than long (length ≤ 0.4 of width) 2

2. Head and pronotum almost entirely black. Female gonapophysis 8 in lateral view with dorsal margin regularly convex, lacking a process .... *I. erebus* (Minas Gerais State)

2’. Head orange to yellow with a dark longitudinal stripe, pronotum black, with ill-defined pale markings. Female gonapophysis 8 in lateral view with dorsal margin concave, forming an acute process distally 3

3. Head with a longitudinal black stripe short, not reaching the clypeus or labrum anteriorly; narrower, not approaching the compound eyes (Figs. 3k–l). Male tergite 9 subtriangular (Fig. 6a). Female, distal margin of gonapophysis 8 convex without medial notch in ventral view (Fig. 7d) .... *I. hauseri* (Rio Grande do Sul State)

3’. Head with a longitudinal black stripe long, reaching the clypeus and labrum anteriorly; wider, near to the compound eyes (Figs. 3a–j). Male tergite 9 subrectangular (Fig. 6b–d). Female, distal margin of gonapophysis 8 regularly curved, with a small mesial notch in ventral view (Fig. 7a–c) .... *I. nubilus* (São Paulo and Paraná States)

On taxonomic status of Longino Navas’s species of *Ilyobius*

Protosialis nubila was described by Navás (1933) based on a single female, holotype by monotypy. Navás (1933) indicates “Matto Grosso? (no se lee bien)…”, as the type locality, with uncertainty about handwriting in the label. Today, Navás’ (1933) description is insufficient to species recognition even though he mentioned characters of the whole insect body, including wings and detailed description of the coloration of head. However, he presented a single illustration of a wing. A similar treatment occurred when he described *Protosialis brasiliensis* from “São Paulo: Ypiranga” and the unique illustration was also a wing of the holotype (Navás 1936). With the reinstatement of *Ilyobius* after a phylogenetic study (see Liu *et al.* 2015a), both *Protosialis nubila* and *P. brasiliensis* were transferred to that genus. In the same year Liu *et al.* (2015b) proposed the synonymization between *I. brasiliensis* with *I. nubilus*, based on the chance of both species sharing the same geographic distribution and due to the strong similarities in the coloration of the head and thorax. Liu *et al.* (2015b) also observed that the type locality of *I. nubilus* was based on the handwritten data, but on the back of the specimen label is printed a clear indication of São Paulo as provenance locality, most likely referring to the capital of São Paulo State. Therefore, there is a possibility that *I. nubilus* was collected in the same locality as *I. brasiliensis*. Contreras-Ramos (2006) re-examined the holotype *P. brasiliensis* and provided a photograph of the label. It is important to highlight that both holotypes are severely damaged, making it difficult to access detailed information about morphology and type localities. Such limitations also apply to the original descriptions and more recent, the redescriptions published in the last two decades (Contreras-Ramos 2006, Liu *et al*. 2015b, Mendes *et al*. 2024).

Based on specimens of *I. nubilus* collected in the state of São Paulo, Mendes *et al*. (2024) redescribed the female, and described the male genitalia and larva for the first time (Figs. 6b, g; 7c; 8a–d). In the same study, they proposed to distinguish *I. brasiliensis* from *I. nubilus*, arguing that the characteristics mentioned by Liu *et al*. (2015b) were insufficient to justify the synonym. Their hypothesis relies mainly on minor different aspects of wing venation, but there are a few taxonomic inconsistencies in the wing characters. For example, the fusion between Sc and RA is considered a synapomorphy of Sialidae (Liu *et al*. 2015b), however, the quality of the illustrations and shape of the wings of *P. brasiliensis* and *P. nubila* poses difficulties in comparing this character and other venational aspects between the two holotypes. Moreover, there is doubt about the consistency of the fusion of Sc + RA in *I. nubilus*. The unfused Sc and RA is clearly observed in the wing depicted by Navás (1933) and in the photograph of this species by Liu *et al.* (2015b) (Fig. 5d). However, these veins are merged in the illustrations and photographs of *I. brasiliensis* (Navás 1936; Contreras-Ramos 2006; Mendes *et al.* 2024), of *I. hauseri* (Contreras-Ramos *et al*. 2005; Pereira 2019), as well as in all specimens from Paraná in this study identified as *I. nubilus*. There is some question as to whether Navás (1936) and Contreras-Ramos (2006) depicted the same wing of the holotype of *I. brasiliensis* (Figs. 5e–f), because of the differences in the number of crossveins between the two studies. Considering that Contreras-Ramos (2006) redescription was based on the holotype, the differences may be due to asymmetric number of crossveins between the wing pairs. It is likely that one author pictured the right wing and another the left one. Nonetheless, Longino Navás’ work on neuropteran species sensu lato, which encompasses various insect orders, has been source of taxonomic challenges. These difficulties arise from several aspects, including the lack of types specimens, laconic descriptions, and inaccuracies in both descriptions and illustrations (e.g., Monserrat 1986).

When Liu *et al*. (2015b) proposed the synonymization of *I. nubilus* and *I. brasiliensis,* they did not discuss wing venation, except by the link between MA and MP by a small vein (veinlet) in the hindwing of *I. nubilus* (Figs. 1a–b), a character not possible to observe in the holotype of *I. brasiliensis* because it lacks hindwings. Mendes *et al*. (2024) believe that the lack of a veinlet linking MA with MP in hindwing of *I. brasiliensis* serves as a distinctive character to differentiate it from *I. nubilus*, suggesting that would prevent the synonymy between the two species. Upon examining the descriptions of other *Ilyobius* species, we found that other species also display a distinct proximal veinlet linking MA to MP in the hindwing, such as those in *I. erebus* (see Mendes *et al.* 2022), *I. flammatus* (K. Justi unpubl. data), and *I. curvata* (see Liu *et al.* 2015b). This tiny vein can also be seen in the sole available photograph of the hindwing of *I. hauseri* (Pereira 2019; and Fig. 5c). As this character is shared by other species in the genus, it therefore cannot be considered diagnostic of *I. nubilus.*

Mendes *et al.* (2024) considered the overall shape of the forewing as another key taxonomic feature to distinguish these two species. In the case of *I. nubilus*, the wing is 3x longer than it is width along its entire length, with posterior margin slightly rounded (Fig. 5a). In contrast, in *I. brasiliensis* the forewing is 4x longer than it is width proximally and 3x longer than it is width distally, with the posterior margin almost straight (Figs. 5e–f). However, there are specimens from Paraná with wider wings like those of *I. nubilus*, and specimens with narrower wings similar to those of *I. brasiliensis* (Fig. 5b). In addition, Mendes *et al.* (2024) showed that the previous diagnostic character of the forewings varied for two different specimens of *I. nubilus* with one being narrow as in *I. brasiliensis*. The posterior wing margin also exhibits variations in shape, with some specimens having a slightly rounded margin (Fig. 5b) and others within the same population showing a straighter margin (Fig. 5a). Such variation is also observable in *I. hauseri* (Figs. 5c, g). Because of these noted variations within the same population, it is not possible to reliably distinguish between these species using wing size and shape as diagnostic traits. It is important to note that dry preserved specimens tend to show deformations in the wings due to the drying process and preservation. This causes the wings to not align correctly, resulting in distorted proportions.

Another character questioned in the separation between *I. brasiliensis* and *I. nubilus* is the coloration pattern on the vertex. Although the pattern is well conserved within the *Ilyobius* species groups, as proposed by Liu *et al*. (2015a), there is a large variation within *I. nubilus*, as demonstrated by specimens collected from the state of Paraná, and illustrated in the literature. The dark stripe ranges from a relatively narrow band in the medial region of the vertex, as shown in the holotype of *I. nubilus* (Liu *et al.* 2015b) and a specimen from Paraná (Figs. 3h, j), to a broad, continuous stripe, observed in specimens from São Paulo (Mendes *et al.* 2024; and Fig. 3a). The latter resembles the illustration by Contreras-Ramos (2005) for *I. brasiliensis*, and also the specimens considered in this study as *I. nubilus* (Fig. 3f). Another similarity is the concave dark spot on the head with an abrupt margin at eye level, which can be observed both in the holotype of *I. brasiliensis* (Fig. 3c–d) and in specimens of *I. nubilus* from São Paulo (Fig. 3b) and Paraná (Fig. 3f–g).

We conclude that all these minor differences in coloration, wing shape and venation are due to inaccuracies in illustrations, missing body structures, and intraspecific variation among specimens examined. *Ilyobius brasiliensis* is still known only by its holotype, but considering the characters presented, it cannot be supported as a distinct species and it must be treated as a synonym of *I. nubilus*.

Ilyobius nubilus **(Navás, 1933) stat. rev.**

Zoobank: https://zoobank.org/NomenclaturalActs/3A14CCAE-AD76-40F4-BE00-CD0A29F02B98

(Figures 1–3a–j; 4; 5a–b, d–f; 6b–d, g–h; 7a–c; 8a–d)

Protosialis nubila Navás, 1933: 36, fig. 88 (description of holotype female “Brasil <<Matto Grosso? Melzer>> Mus. De Berlín-Dahlem”, illustration of forewing of holotype); —Penny 1977: 9 (checklist to Neotropical region); —Penny 1981: 845

(mention); —Contreras-Ramos *et al.* 2005: 269 (taxonomic notes); —Contreras-Ramos 2006: 978 (mention); —Hamada & Azêvedo 2012: 549 (mention); —Liu *et al.* 2015a: 21, 48 (phylogenetic analysis); —Heckman 2017: 78 (key).

Protosialis brasiliensis Navás, 1936**:** 725, fig. 15 (description of the holotype "<<São Paulo: Ypiranga, Luederwaldt. 9.XI.1909>>. Mus. Paulista, illustration of forewing); —Penny 1977: 9 (checklist to Neotropical region); —Penny 1981: 845 (mention); —Contreras-Ramos *et al.* 2005: 268 (taxonomic notes); —Contreras-Ramos 2006: 977, 978, 980–982, fig. 3–5, 8, 10 (redescription and illustration of the head, forewing and labels of the holotype); —Hamada & Azêvedo 2012: 549 (mention); —Liu *et al.* 2015a: 20 (mention); —Heckman 2017: 78 (key).

Ilyobius nubila (Navás, 1933): —Liu *et al.* 2015a: 36, 48 (comb. nov.; phylogenetic analysis); —Liu *et al.* 2015b: 56, 57, 59, 61, 62, 63 figs. 4, 12-15 (key, redescription and illustrations the head, pronotum, genitalia and labels of the female holotype, map).

Ilyobius nubilus (Navás, 1933): —Ardila-Camacho *et al.* 2021: 44 (key); —Martins *et al.* 2022: 51 (catalog); —Mendes *et al.* 2022: 346, 360, 362 (taxonomic notes);—Martins *et al.* 2022: 51 (catalog); —Hamada & Azevêdo 2024: 551 (mention); —Mendes *et al.* 2024: 123, 124, 126-129, 131–139, fig. 2–11, 12 (taxonomic notes, description of male, female and larvae); —Martins 2025 (catalog); —Oswald 2025 (catalog).

Ilyobius brasiliensis (Navás, 1936): —Liu *et al.* 2015b: 59, 60, 62 (taxonomic notes, as junior synonym of *P. nubila*); —Martins *et al.* 2022: 51 (catalog); —Mendes *et al.* 2024: 123, 124, 138, 139, fig. 12 (taxonomic notes, reinstatement as valid name); —Martins 2024 (online catalog).

Material examined (24 females and 5 males).

BRAZIL. Paraná State: **2 females**, Piraquara municipality, Parque Estadual Pico do Marumbi, Mananciais da Serra (SANEPAR), Caixa do Iporã -25.4800, -48.9689, 1053 m a.s.I., malaise, 28.XI.2018–11.XII.2018. Lic. IAP 04.18. AP Pinto & BR Araujo leg. (DZUP 516245–516246); **3 females**, same data but Caixa do Urú -25.4844, -48.9728, 1051 m a.s.I., Malaise sobre riacho, 22.XII.2023–10.I.2024, AP Pinto, E Denck, L Polizeli & RC Varella leg. (DZUP 516286); **1 female**, same data but 07–22.XII.2023 (DZUP 516287); **2 males and 7 females**, same data but 17.XI.2023–07.XII.2023 (DZUP 516288); **3 males and 8 females**, same data but 19.X–17.XI.2023 (DZUP 516289–516290); **1 female**, same data but Reservatório do Carvalho -25.4964, -48.9817, 1021 m a.s.I., light sheet, 07.XII.2023, AP Pinto, J Ehlert, MJM de Almeida & RC Varella leg. (DZUP 516291); **1 female**, Telêmaco Borda municipality, Reserva Biológica Klabin, lâmpada, 28.II.1987, PROFAUPAR, Luminosa (DZUP 516247); **1 female**, Reserva, Gichuva [beating tray], XI.[19]46, Coleção F[elipe] Justus Jr. (DZUP 381189).

Diagnosis. Based on the male having the posterior margin of sternite 9 projected posteriorly into an elongated process (Fig. 6) and the female having gonocoxite 8 reduced to a very small setose sclerite (Figs. 7, 8), *I. nubilus* belongs to the *I. chilensis*-group in addition to the also Brazilian Atlantic Forest species *I. erebus* and *I. hauseri*, and the exclusively Andean *I. chilensis* (Argentina and Chile). These characters help to separate those species from the remaining species of *Ilyobius* belonging to the *I. mexicanus*-group (*I. mexicanus*, *I. curvatus*, *I. flammatus*, *I. nigrocephalus* and *I. ranchograndis*), in which the male has the posterior margin of sternite 9 regularly convex, and the female the gonocoxite 8 is well-developed (see Liu *et al*. 2015a,b; Ardila-Camacho *et al*. 2021). The status of species in the *I. chilensis*-group is doubtful because they lack clear-cut diagnostic characters, and they are currently distinguished by minor differences in coloration, and shape of structures of the genitalia. The head background color in the I. chilensis-group is orange with a dark brown to black longitudinal stripe in both sexes (Fig. 3a–j), and the female gonapophysis 8 has the anterior margin posteriorly recessed, forming a closed v- or open u-shaped (Fig. 7a–d), are shared only with *I. hauseri* and will allows to distinguish *I. nubilus* from *I. erebus* and *I. chilensis* (head uniformly dark brown in *I. erebus* and three spotted with broad black markings in *I. chilensis*; anterior margin of gonapophysis 8 almost truncated or slightly concave lacking a mesial incision in both *I. erebus* and *I. chilensis*).

Ilyobius nubilus is most similar to *I. hauseri*, and a recent study has suggested characters in male and female genitalia as diagnostic between these two species (Mendes *et al*. 2024). We found these characters to be inconsistent among examined specimens and we did not identify any other distinguishing character other than the larger longitudinal dark stripe on the head. For example, in *I. nubilus*, the head stripe occupies 40–55% of head width and reaching anteriorly the labrum and clypeus while it occupies only 30% of head width and anteriorly is limited to the frons in *I. hauseri* (Figs. 3k–l).

Measurements (mm). *Male* (n = 5): Body length: 9.3–12.0 ($\bar{X}$ = 10.4); Forewing length: 10.0–11.5 ($\bar{X}$ = 10.7); head maximum width: 1.0–1.6 ($\bar{X}$ = 1.2). *Female* (n = 5): Body length: 14.2–16.0 ($\bar{X}$ = 15.0); Forewing length: 12.5–15.2 ($\bar{X}$ = 13.6); head maximum width: 2.3–2.6 ($\bar{X}$ = 2.4).

Distribution and biology. This species appears to be endemic to the Brazilian Atlantic Forest, and it was previously known only from the state of São Paulo (Navás 1933, 1936; Mendes et al. 2024). Here, we report it for the first time from the state of Paraná. It is distributed at north from the municipalities of São Luiz do Paraitinga (Serra do Mar State Park, Núcleo Santa Virgínia -23.3619, -45.1375), Salesópolis (Estação Biológica de Boracéia -23.6521, -45.8759) and São Paulo, Ypiranga (Ipiranga district -23.5853, -46.6097) in the state of São Paulo (Navás 1936, Mendes *et al*. 2024), and at south from the municipalities of Piraquara (Pico do Marumbi State Park, Caixa do Iporã -25.4800, -48.9689; Caixa do Urú -25.4844, -48.9728; and Caixa do Carvalho -25.4964, -48.9817), Telêmaco Borba (-24.3239, -50.6158), and Reserva (-24.6500, -50.8508). Specimens were collected in Araucaria and Tropical Atlantic Forests associated to typical shaded streams of Brazilian Atlantic Forest, which typically have muddy substrates with large amount of leaf litter, sand, gravel and pebbles. Elevation ranges from 730 m a.s.l. (Telêmaco Borba) to 1053 m a.s.l. (Pico do Marumbi State Park) (Fig. 2a).

Is *I. hauseri* a well-supported species?

Since its description by Contrera-Ramos *et al*. (2005), the poorly known *I. hauseri* has been shown to be strongly similar to *I. nubilus*. The original description of *I. hauseri* was based on a male and female from the state of Rio Grande do Sul (Floresta Nacional de São Francisco de Paula; Fig. 3l; 5g; 6e; 7d; 8e–f).

Subsequently, both male and female, with additional ten specimens from the type locality, were redescribed (see Mendes *et al*. 2022; Fig. 6a, f). In the original description of the male, the ectoproct was considered absent, however it is the sternite 10 described by Contreras-Ramos *et al.* (2005; see Liu *et al.* 2015b; Mendes *et al*. 2022). This species is mainly identified by a smaller dark dorsal-medial stripe on the head, not extended close to the eyes, nor over the clypeus and labrum. The male tergite 9 is subtriangular in lateral view, the central projection of sternite 9 slightly longer than the lateral projections, and the gonocoxite 11 with a "L"-shape in lateral view. In addition, the female gonapophysis 8 in ventral view has a convex distal margin in the medial region, and lacks an apical incision.

Specimens of *Ilyobius* from Paraná we examined exhibit characteristics that superimpose to the current diagnosis for both *I. hauseri* and *I. nubilus*. We identified three characteristics that overlap for these species: (1) the size and shape of the dorsal-medial dark stripe on the head (assumed be narrow and less extended in *I. hauseri* and wide and more extended in *I. nubilus*, Fig. 1); (2) the distal margin of male gonocoxite 9 (lacking a concavity n *I. hauseri* while in *I. nubilus*, has a small concavity, Fig. 6); (3) and the shape of female gonapophysis 8 (considered with a strongly convex posterior margin, without apical notch in *I. hauseri* and depressed ventrally with an apical incision and enlargement in the posterior half in *I. nubilus*; Figs. 7, 8).

Coloration of the head and pronotum in *I. nubilus* are variable, ranging from almost entirely dark brown to, most commonly, orange with a dark longitudinal stripe as demonstrated in previous studies and corroborated with the specimens from the state of Paraná examined in this study. These variations raise doubts about the reliability of this character as a diagnostic for the Atlantic Forest species. For example, a specimen from the municipality of Reserva in Paraná has a narrow stripe at the vertex (Fig. 3j), similar to that of *I. hauseri*. Therefore, a narrow head stripe is a diagnostic character that overlaps with that of *I. hauseri*. However, the overall length of the stripe appears to be consistent between *I. nubilus* and *I. hauseri*. In *I. nubilus*, this stripe extends anteriorly up to the labrum (Figs. 3a–j), while in *I. hauseri*, the stripe is limited anteriorly to the frontal suture (Fig. 3k). Furthermore, the variation in coloration of the pronotum—which ranges from uniformly dark to lighter with ill-defined orange spots—also reinforces the perception that coloration, by itself, is not a consistent diagnostic feature. The specimen of *I. nubilus* from the municipality of Reserva has spots that most closely resemble those illustrated by Contreras-Ramos (2005) for *I. hauseri*. Specimens from Pico do Marumbi State Park (also in Paraná) exhibit darker pronotum spots, similar to specimens from the state of São Paulo (see Mendes *et al.* 2024).

The similarity between these species is also clear in both male and female genitalia. Although we found superimposition of genitalia characters within the Paraná population, they potentially remain more consistent characters to the distinguish between *I. nubilus* and *I. hauseri*. Mendes *et al*. (2024) cited three useful characters from the male genitalia to differentiate *I. nubilus* from *I. hauseri*. For example, the distal margin of the male gonocoxite 9 has the distal margin concave in *I. nubilus*, (Fig. 6b), while in *I. hauseri* this margin is straight (Fig. 6a). However, in the specimens from Paraná, it is possible to observe variation in both characters (Fig. 6c–d). This makes the character doubtful for distinguishing between *I. hauseri* and *I. nubilus*.

The main proposed diagnostic feature for female genitalis is on the gonapophysis 8. In *I. hauseri*, the posterior margin is convex and does not have an apical incision (Fig. 7d); in *I. nubilus*, on the other hand, the posterior margin is wide and almost straight, presenting an apical incision (Figs. 7a, c). The female genitalia of *I. nubilus* were first illustrated by Liu *et al*. (2015b). However, that illustration led to confusion because the structures are not regularly oriented in ventral view. We believe that the tergite 9 is open, exposing the gonapophysis 8 in almost as in a caudal view, which makes distal margin concave. Recently, the female genitalia was re-illustrated to show these differences. We note that specimens with terminalia macerated in KOH solution tend to expand and, depending on the angle of view, can lead to distinct interpretation of its overall shape. In the ventral view the distal margin of the gonapophysis 8 is regularly curved, with a small mesial concavity. However, when analyzing specimens from Paraná, we observed that the shape of posterior margin varies, being the margin either with low or higher levels of convexity or concavity (Figs. 7a–b). This aspect associated to the changes due to the angle of observation can also lead to misinterpretations, for example, the distal margin of gonapophysis 8 in the specimen from Telêmaco Borba is mesially arched and lacking a fissure (Fig. 7b), which resembles the plate described for *I. hauseri* (Fig. 7d). On the other hand, specimens from Pico do Marumbi State Park is less arched, with a straight mesial region (Fig. 7a), resembling the plate described for *I. nubilus* (Fig. 7c).

Currently, the three characters used to distinguish between *I. hauseri* and *I. nubilus* are: (1) the extension of the dark stripe on the head, which reaches the clypeus in *I. nubilus*, while in *I. hauseri* the spot does not reach the clypeus, it is interrupting in the region of the epicranial suture. However, this character is variable, since environmental factors and conditions of preservation can affect both size and shape of the spot; (2) the shape of the tergite 9 in lateral view, which is subtriangular in *I. hauseri* and subrectangular in *I. nubilus*; and (3) the orientation of the male gonocoxite 11, which projects downward in *I. hauseri* and upward in *I. nubilus*. However, it is important to highlight that the gonocoxite 11 is an extremely reduced and probably membranous structure, whose orientation also may vary. Therefore, it should be interpreted with caution, due to the difficulty of its observation.

Accurate identification of males and females for the species of *Ilyobius* requires careful and detailed analysis of multiple characteristics. The variations observed in the specimens from Paraná highlight the complexity of genital morphology in *I. nubilus* and *I. hauseri*, suggesting that factors such as preservation techniques and intraspecific variation should be considered when identifying these species.

Conclusion

The specimens from the state of Paraná present features that overlap and are intermediate between the proposed diagnostic characters of the three nominal species, *P. brasiliensis*, *P. nubila* and *P. hauseri*, which significantly weakens the hypothesis that they represent distinct species. It is possible that *I. nubilus* and *I. hauseri* represent extreme phenotypes in a clinal variation of a widely distributed population in the southern Atlantic Forest. Thus, it is plausible to consider *I. nubilus* as the northernmost phenotype, *I. hauseri* as the southernmost phenotype, and the previously unknown population from Paraná as intermediate between these extreme phenotypes. Although we did not perform, for example, molecular-based species delimitation analyses, we highlight the importance of future studies with integrative approaches using multiple sources of data such as championed nowadays elsewhere (Schlick-Steiner *et al*. 2010, Pinto *et al*. 2023). Possibly a phylogeographic analysis to investigate genetic distances between known populations will help resolve this problem. This reinforces the need to consider both morphological and molecular data, as well as expanding data collection, especially in strategic geographic locations.

In this work we show that *I. brasiliensis* and *I. nubilus* represent the same species, resuming the synonymy first proposed by Liu *et al*. (2015b), with *Ilyobius nubilus* (Navás, 1933) being the valid name for the species. *Ilyobius hauseri* was retained as distinct species from *I. nubilus*, despite of the overlapping characters with the Paraná specimens.

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Conflicts of interest. The authors declare there are no conflicts of interest.

Author contributions. KJ and APP conceived the study, compiled, organized, measured, and analyzed the data, wrote the manuscript, revised, and approved its definitive version.

Data available. The entire data set supporting the results of this study was published in the article itself.

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Figures, captions and tables

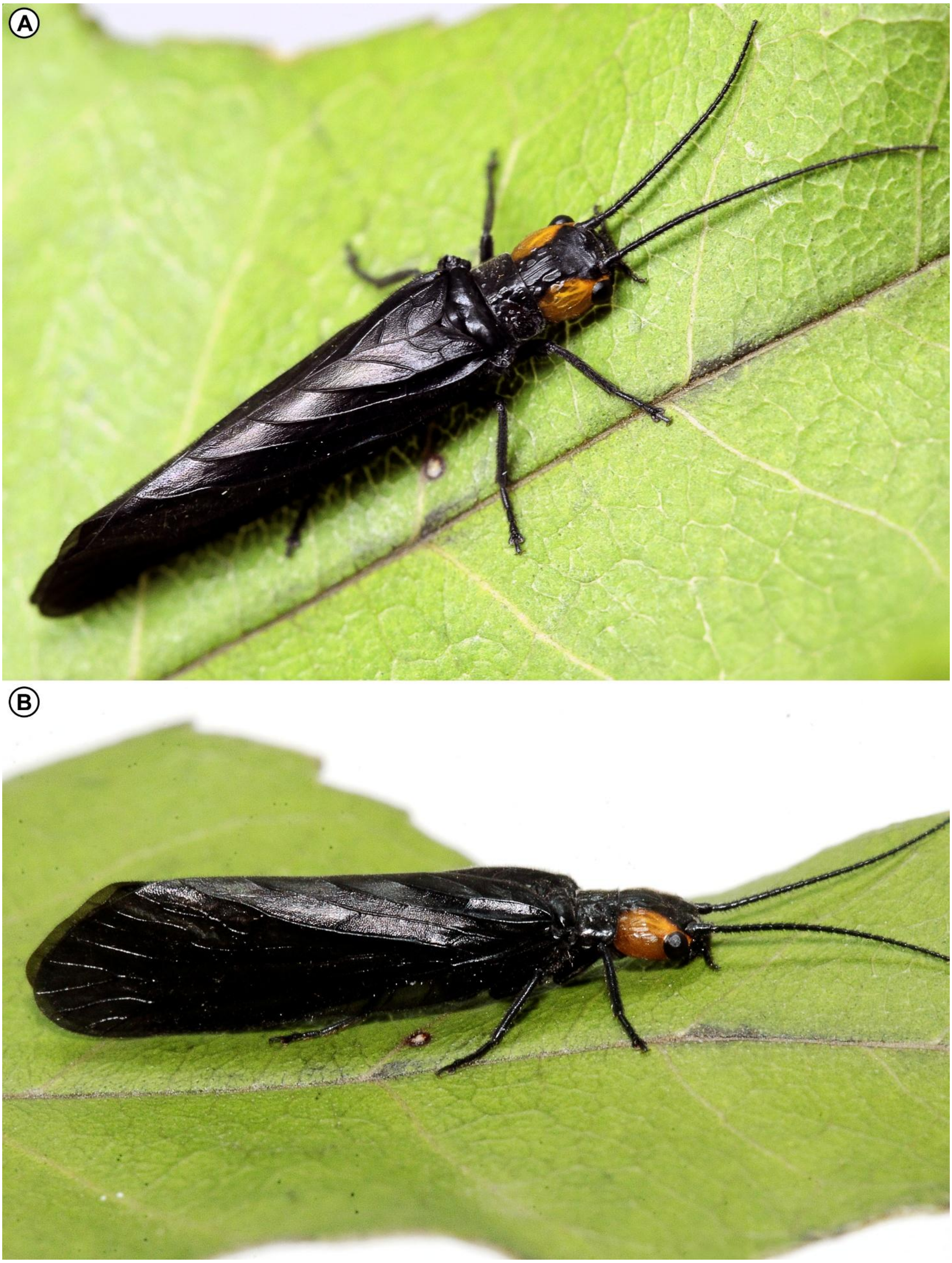

FIGURE 1. Habitus of *Ilyobius nubilus* (Navás, 1933) from the protected area Mananciais da Serra, Piraquara municipality, state of Paraná, Brazil: (a) Dorsal view; (b) Lateral view. Photos APP in 2023.

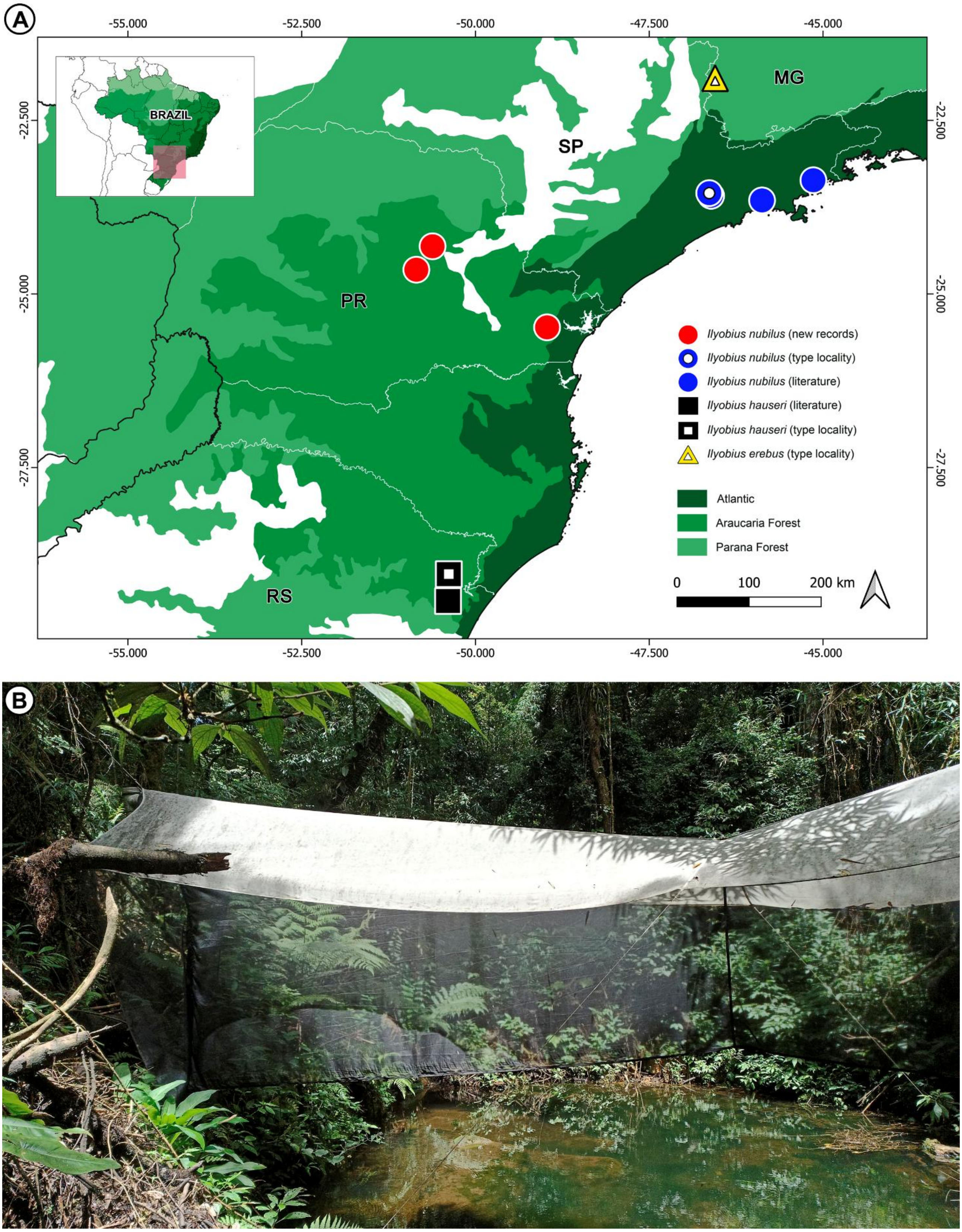

FIGURE 2. Map of southeastern Brazil and habitat of the Atlantic Forest species of *Ilyobius*. (a) Distribution records; (b) Malaise traps crossing in the Mananciais da Serra, Caixa do Urú. Abbreviation: MG = Minas Gerais, PR = Paraná, RS = Rio Grande do Sul, SP = São Paulo. Biogeographic regionalization of dominions based on Morrone *et al.* (2022). Photo (b) LP in 2024.

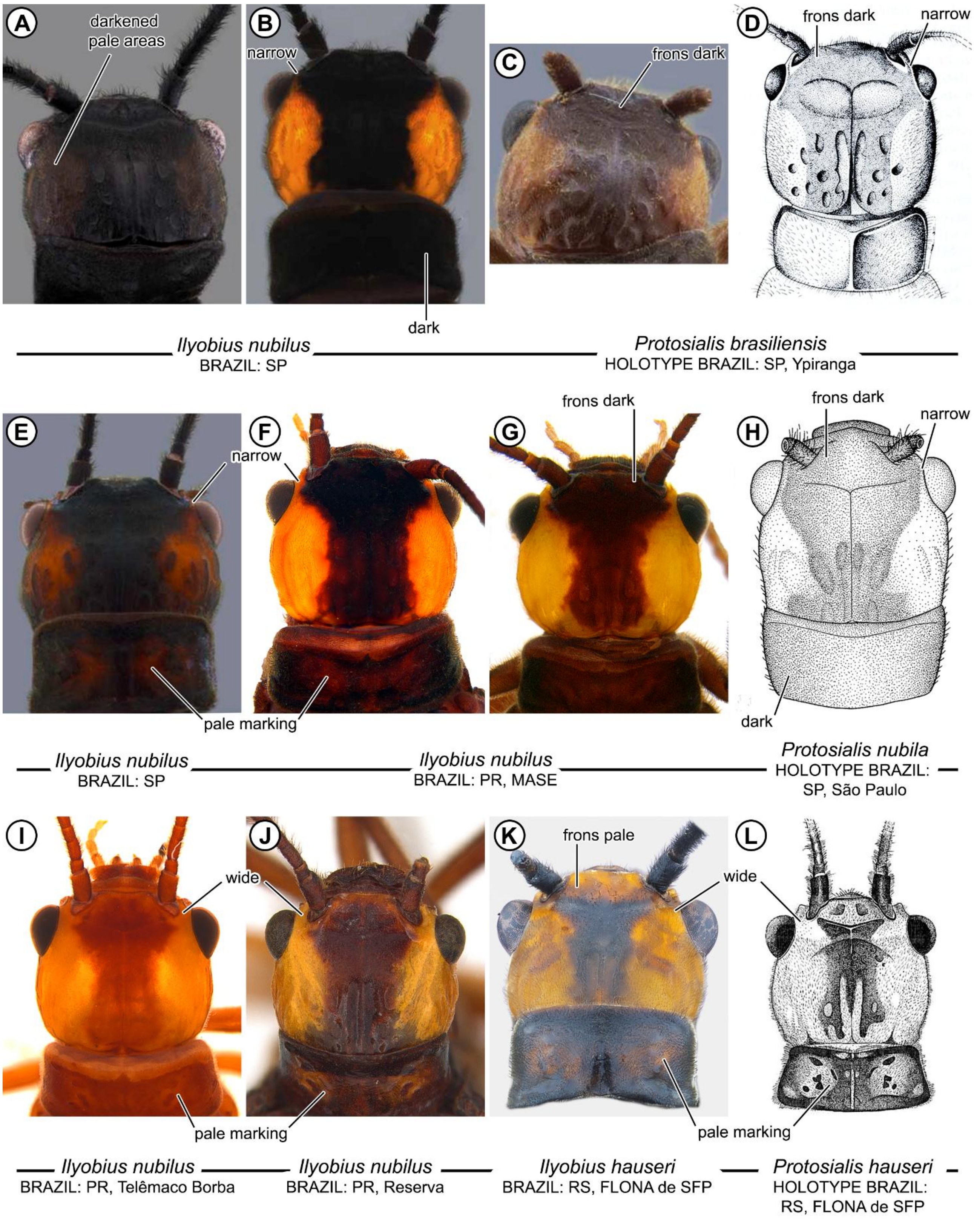

FIGURE 3. Head and prothorax in dorsal view of *Ilyobius* species. **a–b, e:** *Ilyobius nubilus* (adapted from Mendes *et al*. 2024, figs. 3); **c–d:** holotype of *Protosialis brasiliensis* (c, adapted from Mendes *et al*. 2024, fig. 12; d, adapted from Contreras-Ramos 2006, figs. 8); **f–g, i–j:** *Ilyobius nubilus*; **k:** *Ilyobius hauseri* (adapted from Pereira 2019, fig. 81); **h:** holotype of *Protosialis nubila* (adapted from Liu *et al*. 2015a, fig. 12); **l:** holotype of *Protosialis hauseri* (adapted from Contreras-Ramos *et al*. 2005, fig. 1). Copyright: a–b, c, e = Magnolia press, d = CC BY-NC-SA 3.0, h = license CC BY 4.0, k–l = CC BY-NC-ND 3.0 BR.

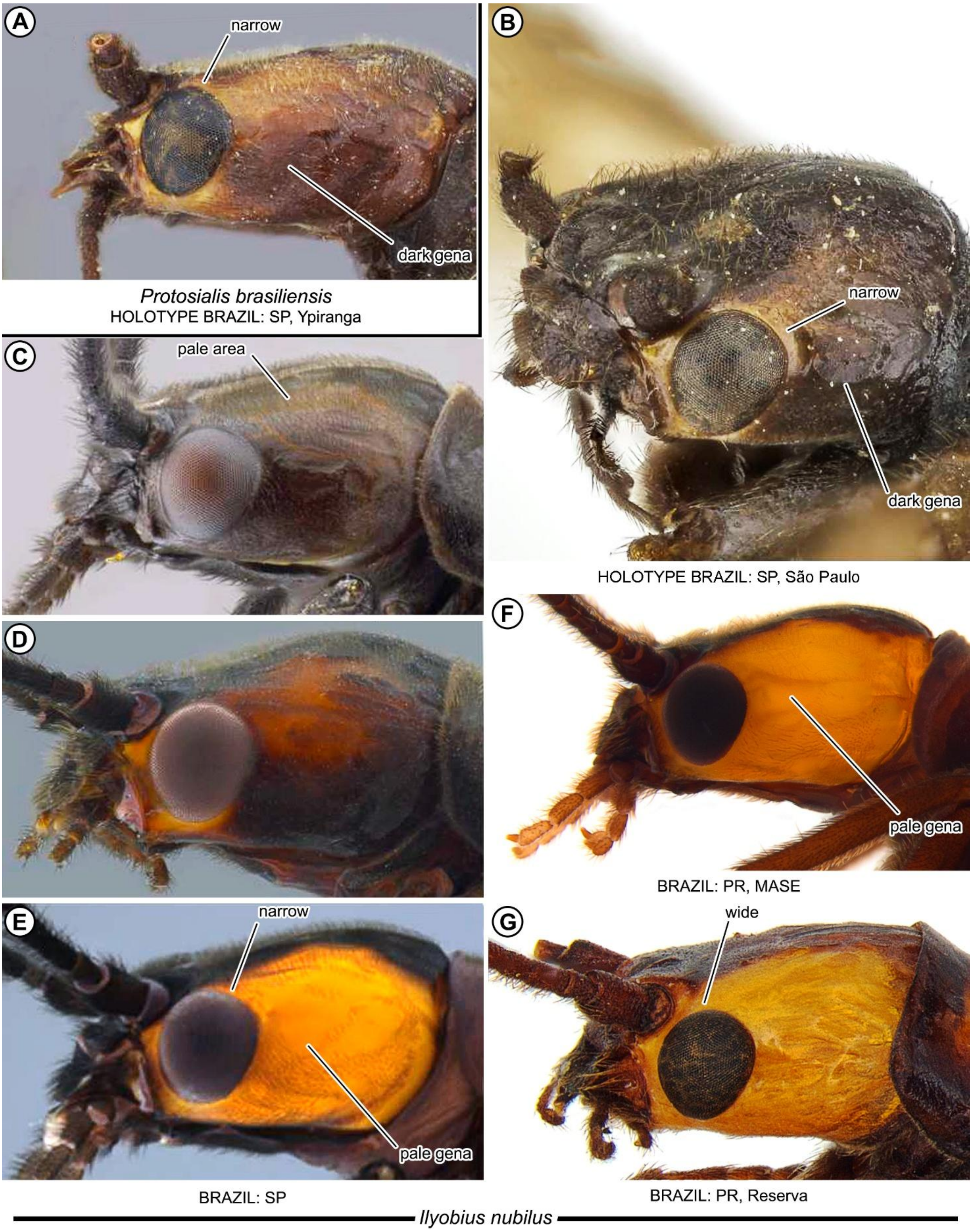

FIGURE 4. Head and prothorax in lateral view of *Ilyobius nubilus* (Navás, 1933). **a**: holotype of *Protosialis brasiliensis* (adapted from Mendes *et al*. 2024, figs. 12); **b:** holotype of *Protosialis nubila* (adapted from Mendes *et al*. 2024, figs. 3); **c–e:** *Ilyobius nubilus* (adapted from Mendes *et al*. 2024, figs. 3); **f–g:** *Ilyobius nubilus*. Copyright: a–e = Magnolia press.

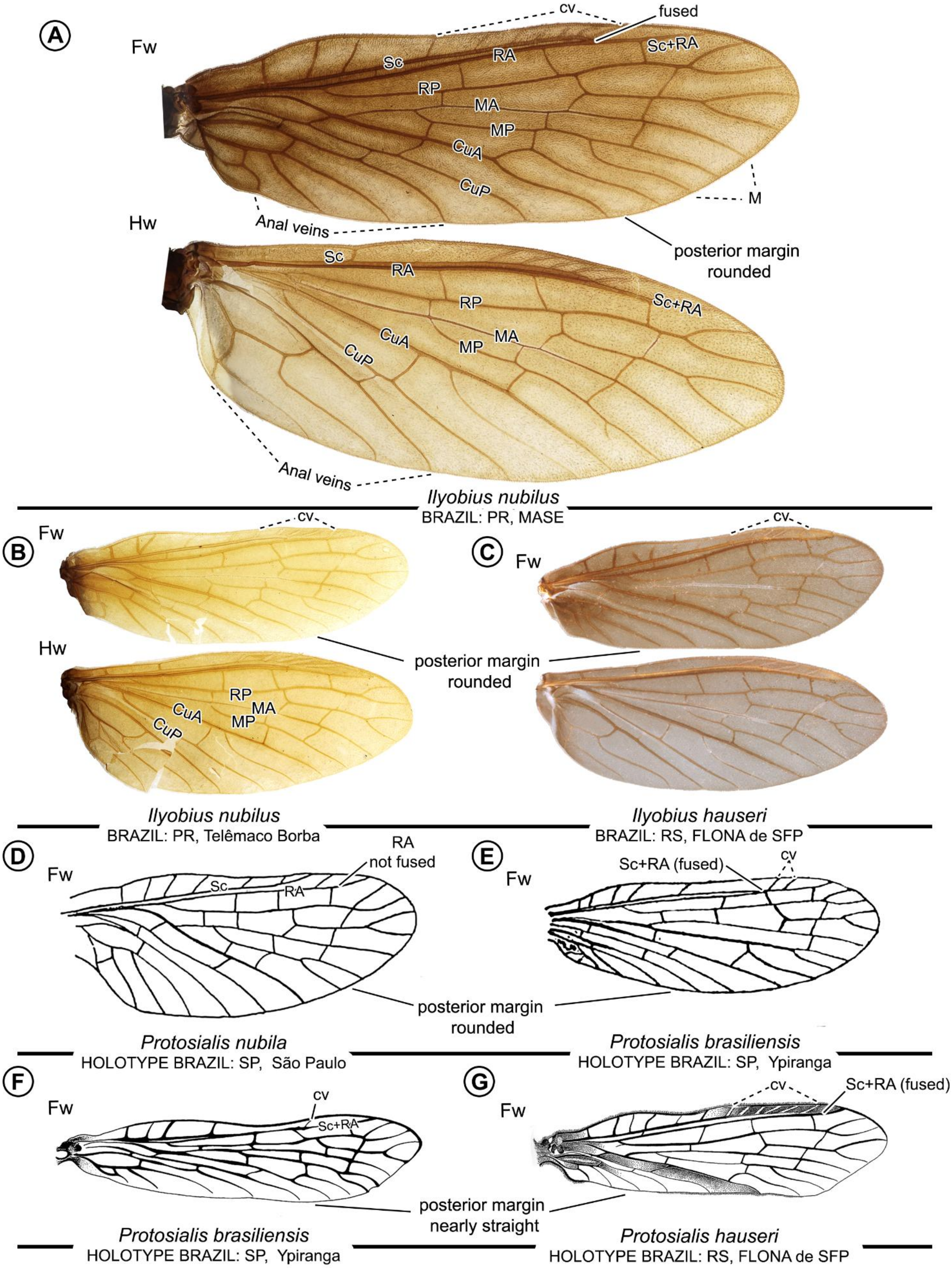

Figure 5. Wings of *Ilyobius* species. **a–b:** *Ilyobius nubilus*; **c:** *Ilyobius hauseri* (adapted from Pereira 2019, fig. 81); **d:** holotype of *Protosialis nubila* (adapted from Navás, 1933, fig. 88); **e–f:** holotype of *Protosialis brasiliensis*, left forewing (e, adapted from Navás, 1936, fig. 15; f, adapted from Contreras-Ramos, 2006, fig. 10); **g:** holotype of *Protosialis hauseri* (adapted from Contreras-Ramos *et al*. 2005, fig. 2). Copyright: c, g = CC BY-NC-ND 3.0 BR, d–e = CC BY-NC-SA, f = CC BY-NC-SA 3.0.

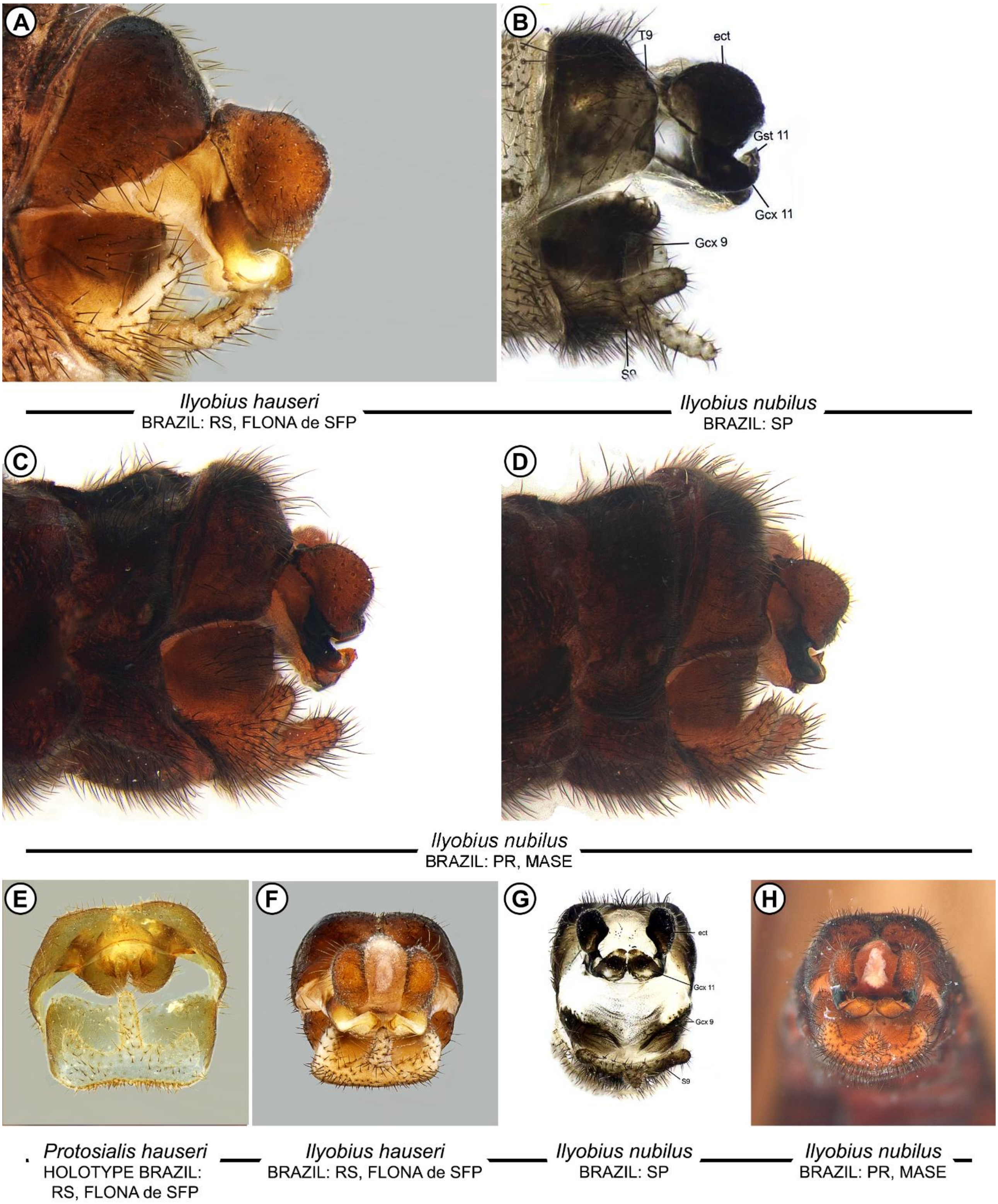

FIGURE 6. Terminalia in lateral (**a–d**) and caudal (**e–h**) views of males of *Ilyobius* species. **a, f:** *Ilyobius hauseri* (adapted from Mendes *et al*. 2022, figs. 11); **b, g:** *Ilyobius nubilus* (adapted from Mendes *et al*. 2024, figs. 3); **c–d, h:** *Ilyobius nubilus*; **e:** holotype of *Protosialis hauseri* (adapted from Mendes *et al*. 2022, fig. 11). Copyright: a–b, e–g = Magnolia press.

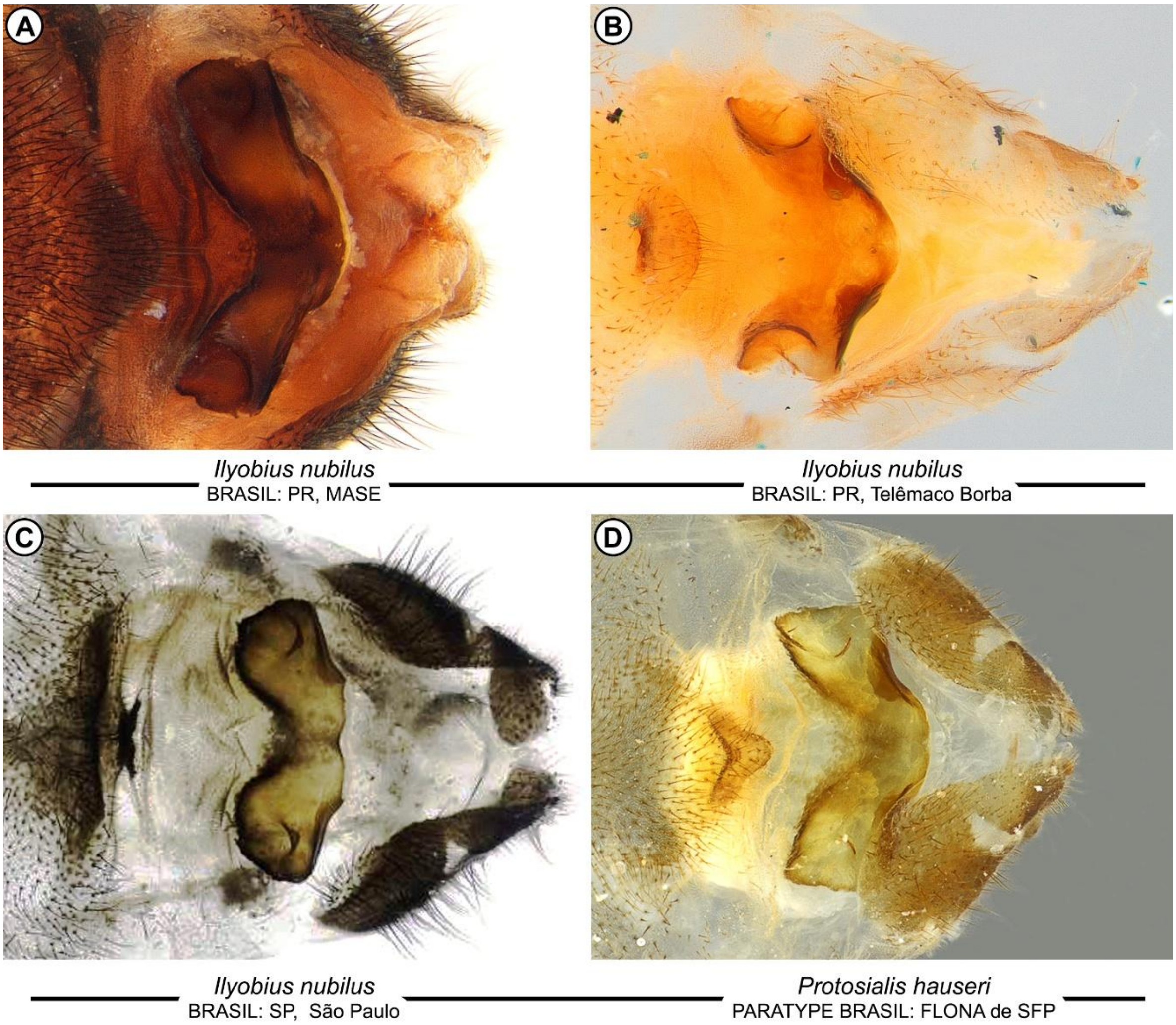

FIGURE 7. Terminalia in ventral (**a–d**) views of female of *Ilyobius* species. **a–c:** *Ilyobius nubilus*; **c:** *Ilyobius nubilus* (adapted from Mendes *et al*. 2024, figs. 5); **d:** paratype of *Protosialis hauseri* (adapted from Mendes *et al*. 2022, figs. 12). Copyright: c, d = Magnolia press.

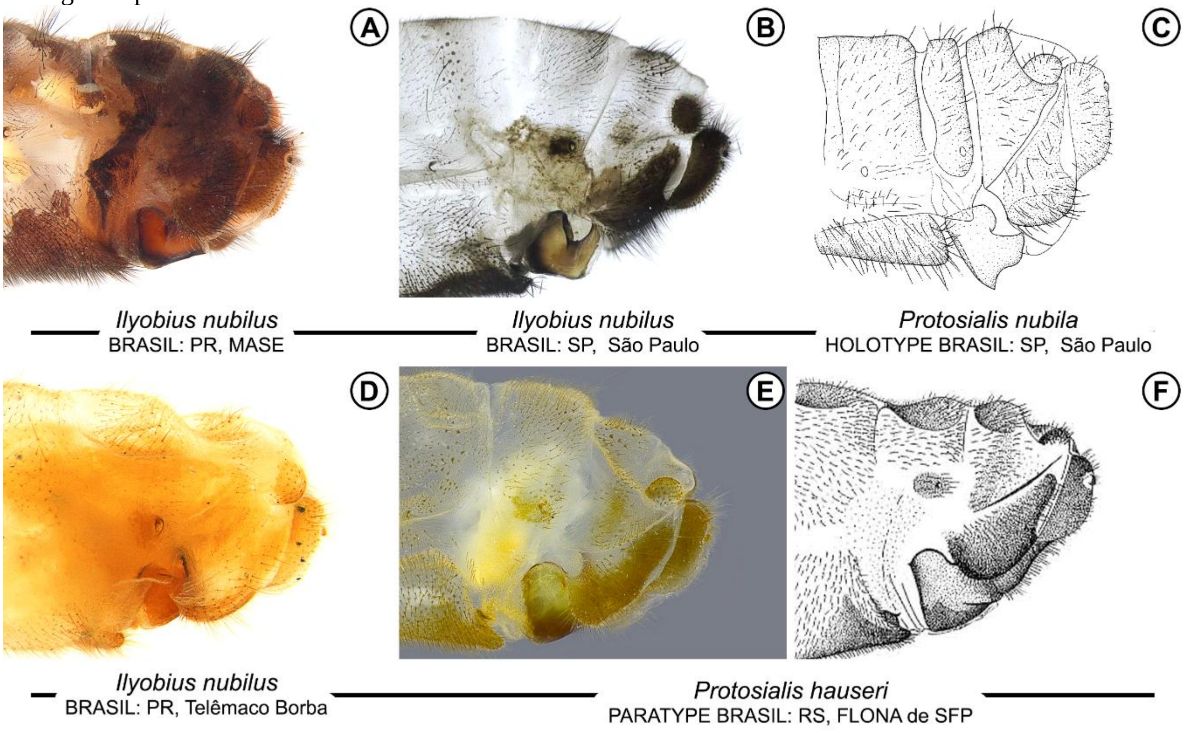

FIGURE 8. Terminalia in lateral (**a–f**) views of female of *Ilyobius* species. **a–d:** *Ilyobius nubilus*; **b:** *Ilyobius nubilus* (adapted from Mendes *et al*. 2024, figs. 5); **c:** holotype of *Protosialis nubila* (adapted from Liu *et al*. 2015a, fig. 12). **e–f:** paratype of *Protosialis hauseri* (**e**, adapted from Mendes *et al*. 2022, figs. 12; **f**, adapted from Contreras-Ramos *et al*. 2005, fig. 7). Copyright: b, e = Magnolia press; c = license CC BY 4.0; f = CC BY-NC-SA 3.0.

Table 1. Comparative characters of male and female based on literature for *I. brasiliensis*, *I. hauseri* and *I. nubilus*. Additional specimens are from this study. Type series data were compiled from Navás (1933, 1936), Contreras-Ramos *et al.* (2005), Liu *et al.* (2015b), Pereira (2019) and Mendes *et al.* (2022, 2024). Not applicable = "—"; MASE = Mananciais da Serra, PR; Paraná = PR; Rio Grande do Sul = RS; São Paulo = SP; Forewing = Fw; Hindwing = Hw; Gonocoxito = Gcx; Gonostyle = Gst; Gonapophysis = Gph; Sternite = S; Tergite = T.

		Species type			DZUP specimens (29)
	Caracter / Species	*Ilyobius brasiliensis* (SP)	*Ilyobius hauseri* (RS)	*Ilyobius nubilus* (SP)	*Ilyobius nubilus* (PR)
1.	Body length (mm)	Male [?] = 7.0 (Navás 1936, Contrera-Ramos 2006)	—	Male = 9.1 (Mendes *et al*. 2024) Female = 8.0–9.6 (Navás 1933, Liu *et al.* 2015b)	Male = 9,3–12,0 Female: 14,2–16,0
2.	Fw length (mm)	Male [?] = 9.0–10.0 (Navás 1936, Contreras-Ramos 2006, Mendes *et al.* 2024)	Male = 10.0–12.0 Female = 12.8–13.0 (Contreras-Ramos *et al*. 2005, Pereira 2019)	Male = 9.8 (Mendes *et al*. 2024) Female = 10.0–11.3 (Navás 1933, Liu *et al.* 2015b, Mendes *et al.* 2024)	Male = 10–11,5 Female = 12,5–15,2
3.	Fw width (mm)	2.7 (Mendes *et al.* 2024)	—	3.5 Mendes *et al.* 2024)	—
4.	Hw length (mm)	—	—	Male = 8.6–9.2 Female = 8.3–9.6 (Navás 1933, Liu *et al*. 2015b, Mendes *et al*. 2024)	—
5.	Hw width (mm)	—	—	3.5 (Mendes *et al.* 2024)	—
6.	Width of the dark area on the dorsal region of the head (at the level of the	Wide (0.90)	**Narrow** (0.50—0.65)	Wide (0.91)	Intermediate (0.70–0.90)

	frontal suture between the eyes)				
7.	Width of the spot in the medial region of the head	Wide (0.85)	**Narrow** (0.30)	Wide (0.50)	Wide (0.45–0.70)
8.	Width of the spot in the posterior region of the head (near the pronotum)	Wide (0.85)	**Narrow** (0.30)	Wide (0.65)	Wide (0.55–0.70)
9.	Labrum color	Present	**Absent**	Present	Present
10	Lateral margin of the pronotum	Slight rounded	**Straight**	Slight rounded	**Straight and Slight rounded**
11	Measurement of the pronotum (median region, height X length)	0.45	0.50	0.45	0.55
12	Light spots on the pronotum	Absent	**Present**	Absent (Navas 1933; Liu *et al*. 2015b) Present (Mendes *et al*. 2024).	**Present (Reserva) and absent (MASE)**
13	FW: Transverse veins in the costal space	5 (Navas, 1936 7 (Contreras-Ramos, 2006) 8 (Mendes *et al*. 2024)	12 (Contreras-Ramos *et al*., 2005)	6 (Navas, 1933; Liu *et al*. 2015b) 10–12 Mendes *et al*. 2024)	6–10
14	FW: Apex of RA	Fused with ScP in 0.33—0.25 distal wing (Navas, 1936; Mendes *et al*. 2024)	Fused with ScP in 0.33—0.25 distal wing (Contreras-Ramos *et al*. 2005)	**Not fused** (Navas, 1933; Liu *et al*. 2015b) Fused with ScP in 0.33—0.25 distal wing (Mendes *et al*. 2024)	Fused with ScP in 0.33—0.25 distal wing

15	HW: Transverse veins in the costal space	—	6 (Pereira, 2019)	6—9 (Mendes *et al*. 2024)	5–10
16	HW: Small vein between MA and MP	—	Present (Pereira, 2019)	Present (Mendes *et al*. 2024)	Present
	Female				
17	S7 shape in ventral view	—	**Subquadrate**—subpentagonal (Pereira, 2019; Mendes *et al*. 2022)	**Subtriangular** (Mendes *et al*. 2024)	Subtriangular
18	Ratio between female Gph 8 (length X height in the median region)		0.2	0.1–0.2	0.1–0.3
19	Median region of the distal margin of the female Gph 8	—	**Convex without notch** (Pereira, 2019; Mendes *et al*. 2022)	Concave (Liu *et al*. 2015b) Straight with notch (Mendes *et al*. 2024)	**Straight with notch (MASE) and Convex without notch (Telêmaco Borba).**
	Male				
20	Shape of the T9 in lateral view	—	**Subtriangular** (Mendes *et al*. 2022)	Subrectangular (Mendes *et al*. 2024)	Subrectangular
21	The S9 center projection size	—	Central projection is longer than the sides (Mendes *et al.* 2022)	Central projection is longer than the sides (Mendes *et al.* 2024)	Central projection is longer than the sides
22	Gcx 9 shape in lateral view	—	Subtriangular (Mendes *et al.* 2022)	**Subrectangular** (Mendes *et al.* 2024)	Subtriangular
23	Notch central in Gcx 9 in lateral view		Absent	**Present**	Absent

24	Internal margin the Gcx 11 in lateral view	—	Straight (Mendes *et al.* 2022)	**Curved** (Mendes *et al.* 2024)	Straight
25	Direction of the Gst 11 in lateral view	—	**Projected downwards** (Mendes *et al.* 2022)	Projected upwards (Mendes *et al.* 2024)	Projected upwards