UNIVERSIDADE FEDERAL DO RIO DE JANEIRO

TAXONOMIC REVIEW AND PHYLOGENETIC ANALYSIS OF *AULACIZES* AMYOT & SERVILLE, 1843 (HEMIPTERA: CICADELLIDAE: CICADELLINAE: PROCONIINI)

NATHALIA HILUY PECLY

2025

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Nathalia Hiluy Pecly

Doctoral Thesis presented to the Programa de Pós-graduação em Ciências Biológicas (Zoologia), Museu Nacional, Universidade Federal do Rio de Janeiro, as part of the requirements for obtaining the title of Doctor in Biological Sciences (Zoology).

Advisors: Prof. Dr. Gabriel Mejdalani and Prof. Dr. Daniela Maeda Takiya.

Rio de Janeiro
May 2025

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Advisors: Prof. Dr. Gabriel Mejdalani (Departamento de Entomologia, Museu Nacional, UFRJ) and Prof. Dr. Daniela Maeda Takiya (Departamento de Zoologia, Instituto de Biologia, UFRJ).

Cover photo: *Aulacizes persistans* Walker, 1858 (kindly provided by André Almeida Alves).

WARNING

THIS DISSERTATION SHOULD NOT BE CONSIDERED AS A PUBLICATION IN THE SENSE OF THE **ARTICLE 9 OF ICZN**. THEREFORE, ANY NOMENCLATURAL ACTS HEREIN PROPOSED ARE CONSIDERED VOID FOR THE PRINCIPLES OF PRIORITY AND HOMONYMY.

INDEX CARD

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Dedicated to my dad, my mother, and my brother.

There's something good coming
There's something happening
And it doesn't matter what I suffered
What matters is that I survived
- Sarah Farias

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ABSTRACT

Taxonomic revision and phylogenetic analysis of *Aulacizes* Amyot & Serville, 1843 (Hemiptera: Cicadellidae: Cicadellinae: Proconiini)

Nathalia Hiluy Pecly

Advisors: Prof. Dr. Gabriel Mejdalani and Prof. Dr. Daniela M. Takiya

This thesis is divided into two scientific papers: the first addresses species delimitation within the *Aulacizes conspersa* Walker, 1851 complex; the second consists of a taxonomic revision and a morphological and molecular phylogenetic analysis of the Neotropical genus *Aulacizes* Amyot & Serville, 1843. The first article (and chapter) aims to understand and define the boundaries among distinct evolutionary lineages of *A. conspersa* through single-locus molecular species delimitation methods, in conjunction with a detailed morphological analysis. Mitochondrial (COI) and nuclear (ITS2) DNA sequences were used and analyzed using various delimitation approaches, including ABGD, ASAP, GMYC, bPTP, mPTP, and PTP. The second article (and chapter) presents a taxonomic revision of *Aulacizes*, along with phylogenetic analyses based on morphological data (92 characters) and molecular data (four genes: 16S, H3, COI, and COII). According to the results, *Aulacizes* still includes nine valid species, albeit with a new taxonomic arrangement: *A. conspersa* Walker, 1851, *A. erythrocephala* (Germar, 1821), *A. insistans* (Walker, 1858), *A. nigriceps* Schmidt, 1928 **stat. nov.**, **sp. rev.**, *A. obsoleta* Melichar, 1926, *A. persistans* (Walker, 1858) **sp. reval.**, *A. quadripunctata* (Germar, 1821) (type species), *A. repanda* (Signoret, 1855) **sp. reval.**, and *A. similata* (Signoret, 1855). The phylogenetic analyses recovered *Aulacizes* as a monophyletic group, with *Proconosama* + (*Paraulacizes* + *Pseudometopia*) as its sister group, partially corroborating previous studies.

Key-words: Atlantic Forest. Morphology. Neotropical Region. Phylogeny. Species delimitation. Taxonomy.

Rio de Janeiro – May 2025

RESUMO

Revisão taxonômica e análise filogenética de *Aulacizes* Amyot & Serville, 1843 (Hemiptera: Cicadellidae: Cicadellinae: Proconiini)

Nathalia Hiluy Pecly

Orientadores: Prof. Dr. Gabriel Mejdalani e Profa. Dra. Daniela M. Takiya

Esta tese foi estruturada em dois artigos científicos: o primeiro trata da delimitação de espécies no complexo *Aulacizes conspersa* Walker, 1851; o segundo consiste em uma revisão taxonômica e análise filogenética morfológica e molecular do gênero neotropical *Aulacizes* Amyot & Serville, 1843. No primeiro artigo (e capítulo), o objetivo é compreender e definir os limites entre linhagens evolutivas distintas de *A. conspersa* por meio de métodos moleculares de delimitação de espécies baseados em lócus único, em conjunto com uma análise morfológica detalhada. Foram utilizadas sequências de DNA mitocondrial (COI) e nuclear (ITS2), analisadas por meio de diferentes abordagens de delimitação, incluindo ABGD, ASAP, GMYC, bPTP, mPTP e PTP. No segundo artigo (e capítulo), é apresentada uma revisão taxonômica de *Aulacizes*, acompanhada de análises filogenéticas baseadas em dados morfológicos (92 caracteres) e moleculares (quatro genes: 16S, H3, COI e COII). De acordo com os resultados, *Aulacizes* permanece com nove espécies válidas, mas com uma nova organização: *A. conspersa* Walker, 1851, *A. erythrocephala* (Germar, 1821), *A. insistans* (Walker, 1858), *A. nigriceps* Schmidt, 1928 **stat. nov.**, **sp. rev.**, *A. obsoleta* Melichar, 1926, *A. persistans* (Walker, 1858) **sp. reval.**, *A. quadripunctata* (Germar, 1821) (espécie-tipo), *A. repanda* (Signoret, 1855) **sp. reval.** e *A. similata* (Signoret, 1855). As análises filogenéticas recuperaram *Aulacizes* como um grupo monofilético, tendo *Proconosama* + (*Paraulacizes* + *Pseudometopia*) como grupo-irmão, corroborando parcialmente estudos anteriores.

Palavras-chave: Mata Atlântica. Morfologia. Região Neotropical. Filogenia. Delimitação de espécies. Taxonomia.

Rio de Janeiro – Maio de 2025

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LIST OF ABREVIATIONS

ACRONYMS OF INSTITUTIONS

DZRJ: Coleção Entomológica Prof. José Alfredo P. Dutra, Departamento de Zoologia, Instituto de Biologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil.

DZUP: Coleção Entomológica Pe. Jesus Santiago Moure, Departamento de Zoologia, Setor de Ciências Biológicas, Universidade Federal do Paraná, Curitiba, Brazil.

IFNU: Ivan Franko National University, Lviv, Ukraine.

MNRJ: Departamento de Entomologia, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil.

MELQ: Museu de Entomologia "Luiz de Queiroz", Escola Superior de Agricultura "Luiz de Queiroz", Universidade de São Paulo, Piracicaba, São Paulo, Brazil.

MMBC: Moravské Zemské Muzeum (Moravian Museum), Brno, Czech Republic.

MZSP: Serviço de Invertebrados, Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil.

NHM: Natural History Museum, London, UK.

NHMW: Zoologische Abteilung, Naturhistorisches Museum Wien, Austria.

NHRS: Naturhistoriska Riksmuseet, Stockholm, Sweden.

ZMPA: Museum and Institute of Zoology, Polish Academy of Sciences, Warszawa, Poland.

INTRODUCTION

The order Hemiptera is the fifth largest group of insects and the most diverse among the hemimetabolous forms, with more than 106,000 species worldwide (Forero 2008; Bartlett *et al.* 2018; Grazia *et al.* 2024). Their diversity is probably related to the radiation of angiosperms and their efficiency as plant feeders is a consequence of the structure of the piercing-sucking mouthparts (Grimaldi & Engel 2005). Many species are important pests of cultivated plants and some are vectors of human diseases, with their feeding habits ranging from phytophagy to predation, including ectoparasitism and hematophagy (Forero 2008). The monophyly of the order is supported by molecular and morphological data (Yoshizawa & Saigusa 2001; Cryan & Urban 2011) and the following morphological characters are diagnostic: absence of maxillary and labial palps; the mandibles and maxillary laciniae are modified into concentric stylets (mandibles surround the laciniae, with the latter forming the alimentary and salivary canals); and forewing anterior axillary fold line forming a bifurcation (Forero 2008; Yoshizawa & Saigusa 2001). It currently comprises four suborders: Coleorrhyncha (32 species), Sternorrhyncha (18,000 species), Auchenorrhyncha (43,000 species), and Heteroptera (45,300 species) (Cryan & Urban 2011; Bartlett *et al.* 2018).

The infraorders Fulgoromorpha and Cicadomorpha constitute the suborder Auchenorrhyncha (true hoppers). They are all plant feeders with exception of Achilidae and Derbidae that feed on fungi as nymphs (Dietrich 2009). According to Bartlett *et al.* (2018), the most striking characters separating the Cicadomorpha from the Fulgoromorpha are the proportions or parts of the head (in most Cicadomorpha the clypeus [frons] occupies the largest portion of the face, and in the Cicadoidea and Cercopoidea even reaches the crown – head dorsum – while in the Fulgoromorpha the clypeus [frons] is small and restricted to the lower half – or less – of the face; the antennae of the Cicadomorpha are segmented or distally annulated – when segments of flagellum are fused –, but lack the bulbous basal segments seen in Fulgoromorpha). The Fulgoromorpha are divided into three superfamilies: Fulgoroidea (2,635 species in 21 families), Coleoscytoidea, and Surijokocixioidea (the last two extinct) (Bartlett *et al.* 2018); this infraorder is characterized by the antennae located below the eyes, well-developed antennal pedicel that bears conspicuous sensilla, distinct tegulae located at the base of forewings, and Y-shaped claval veins of the forewings; they are also known for behavioral characters such as phloem-feeding and efficient jumping (O'Brien 2002). The Cicadomorpha are divided into three superfamilies: Cicadoidea (two

families, 428 genera, and 2,900 species), Cercopoidea (five families, 366 genera, and 2,612 species), and Membracoidea (five families, including Cicadellidae, 2,989 genera, and 24,882 species) (Dietrich 2009; Bartlett *et al.* 2018); this infraorder can be recognized by the enlarged frontoclypeus, antennal pedicel poorly developed in comparison with that of the Fulgoromorpha and without conspicuous sensilla, tegulae reduced, and forewing anal veins usually separated from base to wing margin (Dietrich 2005); they can be phloem-, xylem-, or mesophyll-feeders and most of them are also excellent jumpers.

The Cicadellidae (leafhoppers), in terms of species richness and abundance of individuals in tropical ecosystems, is among the dominant groups of herbivorous insects, with approximately 22,000 described species (Dietrich 1999; Bartlett *et al.* 2018). However, based on a study of the Amazon rainforest canopy carried out in Ecuador, it was estimated that the actual number of leafhopper species could reach more than 200,000 (Dietrich & Wallner 2002). These insects are distributed in all continents, except for Antarctica (Dietrich 2009). They range in length from 2 to 32 mm and feed on a surprising variety of vascular plants, being phloem-, xylem-, or mesophyll-feeders (Bartlett *et al.* 2018). The family can usually be recognized by the presence of four rows of enlarged, spine-like setae on the hind tibia and a distinct suture at the mesothorax separating the anepisternum from the katepisternum; also, they are the only insects whose Malpighian tubules produce brochosomes (see details below). Cicadellidae was recovered as a monophyletic taxon only by the cladistic analysis of Dietrich & Deitz (1993) based on morphological data. In other phylogenetic studies, it was repeatedly recovered as a paraphyletic group in relation to other membracoids such as Membracidae, Aetalionidae, and Melizoderidae; this paraphyletic condition was indicated, for instance, by the morphological and behavioral studies of Hamilton (1983, 1999) and Rakitov (1997) and by the molecular analyses of Dietrich *et al.* (2001) and Cryan (2005). The number of subfamilies recognized within Cicadellidae is currently a matter of considerable contention; Deltocephalinae (circa 6,900 species) is the largest subfamily, followed by Typhlocybinae (circa 5,000 species) and Cicadellinae (circa 2,300 species) (Dietrich 2005; Bartlett *et al.* 2018).

The subfamily Cicadellinae (sharpshooters) is very large and diverse, being thus somewhat difficult to characterize (Young 1968; Mejdalani 1998). According to Young (1968), it can be distinguished from other Cicadellidae by the following combination of characteristics: body usually not flattened dorsoventrally; ocelli located on crown, nearly always closer to the posterior margin than to apex or to anterolateral margin (exception:

some species of *Mesogonia* Melichar); lateral clypeal sutures [= frontogenal sutures] extending onto crown and almost always attaining ocelli; proepisternum [= lateral lobe of the pronotum] exposed; forewing with outer margin of inner apical cell parallel to long axis of wing; posterior tibiae with macrosetae in four regular rows. Sharpshooters range in length from very large (circa 22 mm) to forms measuring just 3.4-4.5 mm; many are quite colorful, with a great diversity of contrasting spots or stripes, sometimes forming complex patterns (Young 1968; Mejdalani 1998). They are distributed in all zoogeographic regions, being especially rich in the Neotropics (Young 1968; Linnavuori 1979; Mejdalani 1998; Nielson & Knight 2000). About 320 genera and 2,300 species are currently known (Bartlett *et al.* 2018), being all of them, as far as is known, xylem-feeders (Young 1968). Some species have considerable economic importance because they are vectors of the phytopathogenic bacterium *Xylella fastidiosa* (Redak *et al.* 2004; Nielson 1968; Freytag & Sharkey 2002).

According to Young (1968, 1977, 1986), the Cicadellinae is divided into two tribes: Cicadellini and Proconiini; the latter includes the genus treated here (*Aulacizes* Amyot & Serville; Figure 1). In the first part of his comprehensive taxonomic revision of the Cicadellinae, Young (1968) provided an identification key to these tribes; he differentiated the Proconiini from the Cicadellini by the following combination of characteristics: antennal ledges usually protuberant in dorsal aspect; posterior legs at rest with knees (femur-tibia articulations) not attaining the posterior proepimeral margins [= lateral lobes of the pronotum] (exception: *Splonia* Signoret); and male pygofer and subgenital plates both usually with numerous evenly dispersed microsetae (occasionally with a few interspersed macrosetae). The Proconiini comprises approximately 400 species and 60 genera (Young 1968; Cavichioli & Sakakibara 1989; Nielson & Knight 2000; Godoy 2005; Rakitov & Godoy 2005; Takiya & Dmitriev 2007; Carvalho *et al.* 2011; Silva *et al.* 2018). They are restricted to the New World, being more diversified in the Neotropics (Mejdalani 1998; Nielson & Knight 2000). The length of adult individuals varies from 10 to 22 mm (Evans 1947). Some members of this tribe are among the largest or most morphologically peculiar leafhoppers; their morphology shows quite curious features, such as the elongate head process of *Raphirhinus* Laporte, the keeled pronotum of *Proconia* Peletier & Serville, and the greatly flattened and expanded anterior tibiae of *Peltocheirus* Walker (Mejdalani *et al.* 2019).

Phylogenetic relationships among the genera of the Cicadellinae were studied for the first time, in a more comprehensive way, by Takiya (2007) in her Ph.D. thesis; in this study,

in which morphological and molecular data were included from a broad sampling of taxa, the Proconiini was not recovered as a monophyletic taxon. Furthermore, taxonomic changes for the subfamily were suggested, such as inclusion of the Phereurhinini (previously treated as a separate subfamily by Kramer 1976) and the division of the Proconiini into two lineages, *viz.*, Proconiini (*sensu stricto*) and a new tribe for *Oncometopia* Stål and related genera. More recently, Feng *et al.* (2024) performed a new phylogenetic analysis based on molecular data and with an even more comprehensive sampling of the Cicadellinae; this study recovered the subfamily as monophyletic and corroborated Takiya's (2007) proposals regarding the non-monophyly of the Proconiini and its division into two groups, as well as the treatment of the Phereurhinini as a tribe of the Cicadellinae.

Brochosomes are peculiar submicron proteinaceous secretory particles produced in the Malpighian tubules of leafhoppers (Rakitov & Gorb 2013; Day & Briggs 1958; Hix 2001); they are generally released after molting in almost all leafhopper species and are actively spread, especially by the setae of the hind legs, onto the integument of females and males as a particulate hydrophobic coating (Rakitov 2004). The function of brochosomes is not entirely clear; however, their hydrophobic nature suggests that they could perhaps protect leafhoppers against excessive environmental humidity and adhesion of honeydew to the body (sticky exudates – filtered plant sap) (Rakitov & Gorb 2013). Rakitov (2004) described a unique behavior of some Proconiini females (of the *Oncometopia*-related group) that cover their egg nests with a special type of brochosomes; the exact function of these egg brochosomes is unknown, but suggested possibilities include reduction of egg desiccation, protection against ultraviolet (UV) light, reduction of attacks by parasitoids and predators, signaling to other females that a certain leaf already has eggs laid in it, or some kind of antimicrobial activity (Hix 2001).

The genus *Aulacizes* Amyot & Serville, 1843

Amyot & Serville (1843), in the "Hémiptères" part of the "*Histoire Naturelle des Insectes*," treated ten genera of the "*Tettigonides*," a group roughly similar to the Cicadellinae. The genus *Aulacizes* was included in this group (p. 571) and diagnosed; *Tettigonia quadripunctata* Germar, 1821 was the only species included in *Aulacizes* and its diagnosis was also provided; hence, the latter is considered the type-species by monotypy (Young 1968). Subsequently, species that are currently included in *Aulacizes* were described by a few authors (Walker 1851, 1858; Signoret 1855; Schmidt 1928; Melichar 1926). Young

(1968), in his detailed review of the Proconiini, redescribed *Aulacizes* considering features of the head, thorax, male and female terminalia; he recognized seven valid species, *viz.*, *A. basalis* Walker, 1851, *A. clypeata* (Signoret, 1855), *A. conspersa* Walker, 1851, *A. conspurcata* Melichar, 1926, *A. divergens* Schmidt, 1928, *A. insistans* (Walker, 1858), *A. obsoleta* Melichar, 1926, and *A. quadripunctata* (Germar, 1821). Mejdalani *et al.* (2006) revalidated *A. erythrocephala* (Germar, 1821) from the synonymy of *A. quadripunctata* (see details below), so that *Aulacizes* currently includes nine species. The genus was catalogued, among others, by Metcalf (1965), Oman *et al.* (1990), McKamey (2007), Wilson *et al.* (2009), and Dmitriev *et al.* (2022 onward).

Aulacizes is distributed in Southeastern and Southern Brazil and Argentina, with a record from Venezuela (for *A. basalis*) that is most probably erroneous (Young 1968; Mejdalani *et al.* 2006). Specimens of this genus are quite common in the Brazilian Atlantic Forest (Figure 1). Some *Aulacizes* species were associated in Brazil with the transmission of the phytopathogenic bacterium *Xylella fastidiosa* Wells *et al.*, 1987 (Azevedo-Filho & Carvalho 2006; Ringenberg *et al.* 2010; Paris *et al.* 2012; Schneider *et al.* 2017): *A. conspersa*, *A. obsoleta*, and *A. quadripunctata* in citrus orchards (*Citrus sinensis* (L.) Osbeck, Rutaceae); *A. clypeata*, *A. conspersa*, *A. obsoleta*, and *A. quadripunctata* in grapevine orchards (*Vitis* spp., Vitaceae); and *A. obsoleta* in plum orchards (*Prunus salicina* Lindl., Rosaceae).

Fig. 1. Diversity of *Aulacizes* Amyot & Serville, 1843 species from the Brazilian Atlantic Forest. A, *A. erythrocephala* (Germar, 1821); B, *A. obsoleta* Melichar, 1926; C, *A. quadripunctata* (Germar, 1821); D, *A. conspersa* Walker, 1851; E, *A. insistans* (Walker, 1858). Photographs A and C by D.M. Takiya, B by A.C. Domahovski, D by F.F. Salles, and E by A.A. Alves.

The available taxonomic comparative information on *Aulacizes* species is somewhat fragmentary. For instance, Young (1968) provided more complete sets of illustrations only for *A. quadripunctata* and *A. obsoleta* (including the head and pronotum in dorsal view, pygofer and aedeagus in lateral view, connective and style in dorsal view, and female sternite VII in ventral view). However, unfortunately, little information and illustrations were provided for other species of the genus such as *A. conspersa* (only the pygofer and aedeagus in lateral view), *A. basalis* (only the head, pronotum, and mesonotum in dorsal view and female sternite VII in ventral view), and *A. insistans* (only the aedeagus in lateral view). After studying the male terminalia and female sternite VII within *Aulacizes*, Young (1968) concluded that these structures do not appear to offer conclusive specific characters and that external characters are variable. For these reasons, he did not attempt to develop a taxonomic key to the species of the genus.

Tettigonia erythrocephala Germar, 1821 was regarded by Young (1968) as a junior synonym of *A. quadripunctata*. However, he did not examine the types of these taxa because efforts on the part of European taxonomists have failed to reveal the location of the Ernst F. Germar collection (Mejdalani *et al.* 2006). Subsequently, the Germar collection has been located in the Ivan Franko National University, Lviv, Ukraine. Specimens of Cicadellinae deposited in this collection were studied by Dr. Daniela M. Takiya. Based on her study, Mejdalani *et al.* (2006) were able to designate lectotypes for *Tettigonia erythrocephala* and *T. quadripunctata* and to revalidate the former from the synonymy of the latter; the authors described in detail the head, thorax, male and female terminalia of *A. erythrocephala*, as well as the color pattern; they showed that the two species have very similar male and female terminalia, but can be consistently distinguished by color features (Figure 1A, C).

Concerning generic relationships within the Proconiini, Young (1968) considered *Aulacizes* as closely related to *Paraulacizes* Young, 1968 and *Pseudometopia* Schmidt, 1928 on the basis of general morphology. According to him, *Aulacizes* could be distinguished from these two genera by the incomplete hind wing vein R_{2+3} and the aedeagus, which is not inflated and bears a ventral scoop-shaped apical process (Young 1968; Mejdalani *et al.* 2006). Indeed, the scoop-shaped process is apparently a unique feature of *Aulacizes*, but an uninflated aedeagus also occurs in *Paraulacizes* and other similar genera, such as *Depanana* Young, 1968, *Depanisca* Young, 1968, *Procama* Young, 1968, and *Proconosama* Young, 1968. Furthermore, the presence of a process on the male pygofer, of dorsal origin, is apparently a homologous feature shared by these genera; this process shows a considerable

variation in shape and size (Young 1968), which can be useful for generic diagnoses. Thus, currently, the boundaries of these genera are not entirely clear, so that in-depth morphological and molecular comparative studies are necessary.

After the publication of Young's (1968) monograph, members of the genus *Aulacizes* were treated in a few publications, such as Mejdalani *et al.* (2006) (see above), Azevedo-Filho & Carvalho (2006), Takiya (2007), and Dellapé (2016). In her Ph.D. thesis, Takiya (2007) carried out a morphological and molecular phylogenetic analysis of the Proconiini, including two *Aulacizes* terminals (*A. quadripunctata* and *Aulacizes* sp.). In her combined hypothesis, *Aulacizes* appeared as the sister group of *Pseudometopia* + *Proconosama*, this clade being the sister group of *Paraulacizes*, with high branch support values. These results partially corroborate Young's (1968) suggestions based on raw morphology. Dellapé (2016) described the female terminalia of twelve species of Proconiini and provided a key to the identification of genera recorded from Argentina, including male and female characters. In this article, the structures of the female terminalia of four species of *Aulacizes* (*A. basalis*, *A. conspersa*, *A. insistans*, and *A. quadripunctata*) were described and illustrated, including the abdominal sternite VII (ventral view), apex of the first valvula of the ovipositor (lateral view), and teeth and apex of the second valvula of the ovipositor (lateral view). The diagnoses provided for the four species included a few features of the color pattern.

Despite the relatively small number of *Aulacizes* species considered valid, one of them, *A. conspersa*, has currently seven synonyms (Young 1968), *viz.*, *affinis* Signoret, 1855, *annuligera* Walker, 1858, *maculata* Walker, 1851, *maculata* var. *nigriceps* Schmidt, 1928, *persistans* Walker, 1858, *repanda* Signoret, 1855, and *terminalis* Walker, 1851. This high number of synonyms is related to an apparently large and complex variation in the color pattern and possibly to small differences in the male terminalia, which were not studied in detail by Young (1968). Other species of the genus are poorly known (*A. basalis*, *A. clypeata*, and *A. conspurcata*). The identification of most *Aulacizes* species remains difficult because detailed comparative redescriptions are still needed, including complete sets of drawings of the male and female terminalia. Therefore, a formal taxonomic revision of *Aulacizes* is necessary to ensure the correct identification of its species, including those of possible economic importance (see above). A new diagnosis of the genus is also necessary.

GOALS

This study aims to contribute to our knowledge of the subfamily Cicadellinae in the Neotropical Region. Specific goals are as follows:

1. To produce a taxonomic review of *Aulacizes*, including an identification key to males and females.
2. To test the monophyly of *Aulacizes* and estimate its relationships to related genera (*Depanana*, *Depanisca*, *Paraulacizes*, *Proconosama*, and *Pseudometopia*) based on morphological and molecular characters.
3. To estimate phylogenetic relationships among species of the genus based on morphological and molecular characters.
4. To understand the limits of the nominal species *A. conspersa*, using molecular species delimitation methods combined with a detailed study of morphology in an integrative approach.

This thesis is divided into two scientific articles, which were prepared in collaboration with Prof. Dr. Daniela M. Takiya and Prof. Dr. Gabriel Mejdalani:

1. **When the male genitalia do not provide useful taxonomic characters: species delimitation of *Aulacizes conspersa* Walker, 1851 complex (Hemiptera: Cicadellidae).**
2. **Taxonomic review and phylogenetic analysis of the genus *Aulacizes* Amyot & Serville, 1843 (Hemiptera: Cicadellidae: Proconiini).**

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ARTICLE I*

When the male genitalia do not provide useful taxonomic characters: species delimitation of *Aulacizes conspersa* Walker, 1851 complex (Hemiptera: Cicadellidae)

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Abstract

The genus *Aulacizes* Amyot & Serville is recorded from Southeastern and Southern Brazil and Argentina, with nine species. Among them, *A. conspersa* Walker, with seven synonyms due to an apparently considerable variation of color pattern, is a taxon of complex taxonomy and unclear boundaries. This study seeks to understand the boundaries among distinct evolutionary lineages of *A. conspersa*. Molecular methods of species delimitation are employed together with a morphological study. We applied single-locus species delimitation methods (ABGD, ASAP, GMYC, bPTP, mPTP, and PTP) to mitochondrial (COI) and nuclear (ITS2) DNA sequences. The analyses included specimens previously identified as *A. conspersa* and of the similar *A. insistans* (Walker), as well as two outgroups (one for COI and one for ITS2). COI analyses recovered a group including only specimens previously identified as *A. conspersa* and delimited from three to five putative species within it, whereas ITS2 delimited from two to fifteen putative species and was not able to distinguish *A. conspersa* from *A. insistans*. Discordant results provided by COI and ITS2 are likely caused by low variability in ITS2 sequences, confounding the distinction between interspecific and intraspecific processes. Based on COI results and type specimen studies, we revalidate and redescribe *A. repanda* (Signoret) **sp. reval.** and *A. persistans* (Walker) **sp. reval.**, and synonymize *A. conspurcata* Melichar with *A. persistans* and *A. divergens* Schmidt with *A. conspersa*. Although molecular methods delimited at least three species within *A. conspersa sensu stricto*, no consistent morphological differences were found, a situation that supports its treatment as a cryptic species complex. This study highlights the limited interspecific variation in the terminalia of both sexes within *Aulacizes*. Homogeneity of male terminalia hinders species delimitation, explaining the longstanding challenges in resolving *Aulacizes* taxonomy based on morphology. Formal taxonomic treatments are provided for *A. conspersa*, *A. repanda*, and *A. persistans*.

Key words: COI, cryptic species, DNA barcoding, integrative taxonomy, ITS2, leafhopper, Proconiini

Introduction

The subfamily Cicadellinae is divided into two tribes, Cicadellini and Proconiini. Cicadellini is a cosmopolitan and diverse tribe, comprising about 2,000 species and 260 genera. Proconiini is restricted to the New World and comprises approximately 400 species and 60 genera (Young, 1968; Cavichioli & Sakakibara, 1989; Nielson & Knight, 2000; Godoy, 2005; Rakitov & Godoy, 2005; Carvalho et al., 2011; Dellapé, 2016; Silva et al., 2018); members of this tribe are among the largest leafhoppers, with adults usually varying in length from 10 to 22 mm (Evans, 1947). According to Young (1968), the Proconiini can be distinguished from the Cicadellini by the following combination of features: (1) posterior legs at rest with knees (femoral-tibial articulation) not attaining the lateral lobe of the pronotum (except in *Splonia* Signoret, 1891); (2) male pygofer and subgenital plates both usually with numerous evenly dispersed microsetae (occasionally with a few interspersed macrosetae); and (3) antennal ledges usually protuberant in dorsal aspect. Recent phylogenetic analyses based on DNA sequences (Feng et al., 2024) have shown that both Proconiini and Cicadellini, as currently delimited, are not monophyletic, and most Proconiini are divided into two unrelated clades, the *Proconia* and the *Oncometopia* groups.

The genus *Aulacizes* Amyot & Serville, 1843 belongs to the *Proconia* group and is recorded from Venezuela (most likely an error), Argentina, and Southern and Southeastern Brazil (Young, 1968; Dellapé, 2016). The following nine species are currently considered valid (Young, 1968; Mejdalani et al., 2006): *A. basalis* Walker, 1851, *A. clypeata* (Signoret, 1855), *A. conspersa* Walker, 1851, *A. conspurcata* Melichar, 1926, *A. divergens* Schmidt, 1928, *A. erythrocephala* (Germar, 1821), *A. insistans* (Walker, 1858), *A. obsoleta* Melichar, 1926, and *A. quadripunctata* (Germar, 1821) (type species). In Brazil, three of these species were associated with the transmission of *Xylella fastidiosa* Wells et al., 1987 in citrus and grape orchards and one in plum orchards (Azevedo-Filho & Carvalho, 2006; Ringenberg et al., 2010; Paris et al., 2012; Schneider et al., 2014).

Young (1968) treated the genus *Aulacizes* in his detailed revision of the Proconiini. He provided more complete sets of illustrations only for *A. quadripunctata* and *A. obsoleta* (including the head and pronotum in dorsal view, male pygofer and aedeagus in lateral view, connective and style in dorsal view, and female sternite VII in ventral view). However, unfortunately, little information and illustrations were provided for other species of the genus such as *A. conspersa* (only the male pygofer and aedeagus in lateral view), *A. basalis* (only the head, pronotum, and mesonotum in dorsal view and female sternite VII in ventral view),

and *A. insistans* (only the aedeagus in lateral view). After studying the male genitalia and female sternite VII within *Aulacizes*, Young (1968) concluded that these structures do not appear to offer conclusive specific characters and that external characters are variable. For these reasons, he did not attempt to develop a taxonomic key to the species of the genus.

According to the original description provided by Walker (1851), *A. conspersa* could be recognized by the following characteristics: (1) head yellow with two black lines starting from the base of the crown, diverging anteriorly, involving the ocelli, and reaching the antennal ledges; (2) black stripe on the lower portion of the face, over the epistomal suture, extending laterally to the genae and reaching the eyes; (3) pronotum yellow with two black transverse bands, the first thin, forked on each side, connected by a black band to the second, which is wider, includes yellow spots and occupies the posterior portion; and (4) reddish-brown forewings with various scattered rounded yellow spots of various sizes and with a large preapical transverse spot (similar to a stripe). However, these characters do not allow an accurate identification and the limits of *A. conspersa* (Figs. 1–5) have never been clear, so that Young (1968) listed seven taxa as synonyms: *affinis* Signoret, 1855, *annuligera* Walker, 1858, *maculata* Walker, 1851, *maculata* var. *nigriceps* Schmidt, 1928, *persistans* Walker, 1858, *repanda* Signoret, 1855, and *terminalis* Walker, 1851. This high number of synonyms is related to a large variation in color patterns and, possibly, to small differences in the male genitalia, which were not studied in detail by Young (1968). Therefore, it appears to us that *Aulacizes* is a genus of complex taxonomy and that the status of these nomina should be reevaluated. In addition, there is apparently significant intraspecific color variation within *A. conspersa* (see Wilson et al., 2009).

Considering the aforementioned taxonomic uncertainties concerning *A. conspersa* and related *Aulacizes* species, the main goal of this study is to increase our understanding about the limits among the evolutionary lineages of these taxa, using molecular species delimitation methods combined with a detailed study of morphology in an integrated approach. Currently, there are few works on the delimitation of leafhopper species based on molecular data and they deal mainly with some groups of the Deltocephalinae (Gao et al., 2021; Yan et al., 2022; Wang et al., 2024; Zhang et al., 2024). Therefore, we hope that the present work will serve as a model for the treatment of other genera that present similar taxonomic problems in the Cicadellinae, as well as in other leafhoppers and hemipterans.

Materials and methods

Taxon sampling and material examined

Leafhoppers included in this study were collected directly in ethanol 93%-100% recently (2021-2023) and during previous collaborative projects (2012-2020); these samples were stored in ethanol at Laboratório de Entomologia (LabEnt), Universidade Federal do Rio de Janeiro (UFRJ). Individuals putatively belonging to a single species were collected from different sites with the aim of covering as much geographic and morphological variation as possible (Fig. 6). Identification of each individual was based on examination of external morphology and male genitalia, using the most recent contributions on *Aulacizes* (Young, 1968; Mejdalani et al., 2006; Dellapé, 2016), original descriptions (Walker, 1851, 1858; Signoret, 1855; Schmidt, 1928; Melichar, 1926), and, most importantly, photographs of type specimens.

In addition to the samples used for DNA extraction, a total of 114 specimens of *A. conspersa* and 50 of *A. insistans* were analyzed from the following collections: Coleção Entomológica Pe. Jesus Santiago Moure, Departamento de Zoologia, Universidade Federal do Paraná, Curitiba (DZUP); Coleção Entomológica Prof. José Alfredo Pinheiro Dutra, Departamento de Zoologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro (DZRJ); Departamento de Entomologia, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro (MNRJ); Museu de Entomologia "Luiz de Queiroz", Escola Superior de Agricultura "Luiz de Queiroz", Universidade de São Paulo, Piracicaba (MELQ); and Museu de Zoologia, Universidade de São Paulo, São Paulo (MZSP). Photographs of type specimens were provided by the following institutions: Naturhistorisches Museum, Vienna (NHMW); Museum and Institute of Zoology, Warsaw (ZMPA); and The Natural History Museum, London (NHM).

DNA extraction, PCR amplification, purification, sequencing, and alignment

Genomic DNA extraction was carried out from one hind leg of adult specimens using the DNeasy Blood & Tissue extraction kit (Qiagen Inc., Hilden, Germany), optimizing the original protocol by incubating the tissue for lysis in Proteinase K for 48 hours and generating two separate 50µL elutions of DNA extract, instead of 100µL. Voucher specimens were pinned and deposited in DZRJ, DZUP, MELQ, and MNRJ (Table 1).

All PCR reactions had a total volume of 25µL and contained 12.9µL of H_2O DEPC, 5µL of Green Taq Buffer (Promega), 3.5µL of $MgCl_2$ (25mM, Promega), 1µL of BSA

(10mg/mL, Promega), 0.5 µL of dNTP (20mM, Promega), 1µL of each primer (10pmol/L), 0.1µL of Taq Polymerase (5U/µL, Promega), and 2µL of genomic DNA; for ITS2, BSA was not employed in PCR reactions. Amplification of COI was performed with a thermocycling profile that consisted of 3 min at 94°C; followed by 35 cycles of 1 min at 94°C, 1 min at 48°C, 50°C, or 52°C, 2 min at 72°C; and a final step of 7 min at 72°C. Amplification for ITS2 was performed with a thermocycling profile that consisted of 3 min at 94°C; followed by 35 cycles of 1 min at 94°C, 1 min at 50°C, 2 min at 72°C; and a final step of 7 min at 72°C. PCR and sequencing primers used are given in Table 2. PCR products were stained with GelRed™ diluted 1000X (Biotium) and underwent agarose gel electrophoresis in 1.0% TBE; these products were visualized under UV light. Successfully amplified PCR samples were purified using ExoSAP-IT® (USB Affymetrix) and were subsequently sent for sequencing at Macrogen (Seoul, South Korea).

Sequences obtained by PCR were assembled and edited using GeneStudio™ Professional v.2.2.0.0 software; they were tested for contamination using BLAST in GenBank. COI consensus sequences (~383bp) were aligned with ClustalW (Thompson et al., 1994), which is implemented in the MEGA11 software (Tamura et al., 2021). Amino acid translations were conducted to check for the absence of stop codons. ITS2 consensus sequences (~616bp) were aligned with the MAFFT v.7.222 program (Katoh et al., 2019) on its online platform (https://mafft.cbrc.jp/alignment/server/), with the E-INS-i alignment algorithm. Alignments included sequences of specimens identified as *A. conspersa sensu lato*, *A. insistans*, *A. quadripunctata*, and *A. erythrocephala*, the last two used for rooting trees of ITS2 and COI, respectively.

Phylogenetic inference and species delimitation

The molecular evolution model with the best fit, based on the Bayesian Information Criterion (BIC) (Akaike, 1974), was chosen using the jModeltest 2 program (Darriba et al., 2012). According to the analyses, the model with the best fit was HKY+I for both sets of data (COI and ITS2). Datasets aligned in FASTA format were employed as input files for the generation of ultrametric phylogenetic trees, using the BEAST v.2.7.6 program (Bouckaert et al., 2019). Phylogenetic analyses were performed using an optimized relaxed molecular clock and a birth-death model. Single runs of Markov Chain Monte Carlo (MCMC) analyses were performed for 100 million generations, sampling every 10,000. Proper mixing of parameters was evaluated in Tracer v.1.7 (Rambaut et al., 2018), seeking to achieve effective

sample size values of at least 200, after the 10% burn-in. Subsequently, TreeAnnotator v.2.7.6 (Bouckaert et al., 2019) was used to generate a consensus tree. The obtained ultrametric phylogenetic trees were visualized in the software Fig Tree v.1.4.4 (Rambaut, 2018) and converted into Newick format.

Aulacizes species were delimited using six different methods for the analyses of the COI and ITS2 datasets: Automatic Barcode Gap Discovery (ABGD; Puillandre et al., 2012), Assemble Species by Automatic Partitioning (ASAP; Puillandre et al., 2021), Generalized Mixed Yule Coalescent (GMYC; Fujisawa & Barraclough, 2013), Bayesian Poisson Tree Processes (bPTP; Zhang et al., 2013), Multi-rate Poisson Tree Processes (mPTP; Kapli et al., 2017), and Poisson Tree Processes (PTP; Zhang et al., 2013). For species delimitation analyses, the recently developed SPdel pipeline was used based on the ultrametric phylogenetic trees; this pipeline is a tool for visualizing and comparing single-locus species delimitation methods; it was designed to calculate indices, compare, and generate consensus MOTUs obtained by different methods (Ramirez et al., 2023).

A maximum likelihood (ML) analysis was performed in IQ-TREE2 2.2.2.7 (Minh et al., 2020) for the concatenated dataset of COI + ITS2 genes. Each individual codon position of the protein-coding gene (COI) and ITS2 was treated as separate partitions in the phylogenetic analyses. The selection of the best evolutionary model for each partition was carried out considering the Bayesian information criterion (BIC) through ModelFinder (Kalyaanamoorthy et al., 2017). For the first two codon positions of COI + ITS2, the best evolutionary model was K2P+I, whereas for the third codon position of COI the best model was K3Pu+F. A total of 1,000 ultrafast bootstrap approximations (UFBoot) (Minh et al., 2013; Hoang et al., 2018) and 1,000 replicates of SH-aLRT (Guindon et al., 2010) were performed to evaluate branch supports. The obtained phylogenetic tree was visualized in Fig Tree v.1.4.4 (Rambaut, 2018). Ultrametric BEAST2 phylogenetic trees and log results of SPdel are available in the Supplementary Material.

Morphological studies

Descriptive terminology followed mainly Young (1968, 1977, 1986), except for the facial areas of the head (Hamilton, 1981; Mejdalani, 1993, 1998) and the female genitalia (Nielson, 1965; Hill, 1970). Use of the term gonoplac (= third ovipositor valvula) and the names of the sculptured areas of the first ovipositor valvula followed Mejdalani (1998). Techniques for preparation of genital structures followed mainly those of Oman (1949) for males and

Mejdalani (1998) for females. Dissected parts were stored in small vials with glycerin that were pinned beneath the specimens (Young & Beirne, 1958). Total length of specimens was measured from the apex of the crown to the tips of the forewings at rest position (Young, 1977). Photographs of the body at different focal planes were taken using a Leica M205 automated stereomicroscope and processed (stacked) with Leica LASX software, whereas photographs of male and female genitalia were taken using a ZEISS SmartZoom5 automated digital microscope. A map of distribution of *Aulacizes* vouchers employed in this study was created using QGIS 3.34.14-Prizren.

Results

Phylogenetic analysis

PCR and sequencing from the available samples (Table 1) yielded alignments of 44 COI sequences (11 of *A. insistans*, 32 of *A. conspersa sensu lato*, and one of *A. erythrocephala*) and 41 ITS2 sequences (10 of *A. insistans*, 31 of *A. conspersa sensu lato*, and one of *A. quadripunctata*). The resulting maximum likelihood tree (-logL = 1892.769) based on the concatenated dataset (COI + ITS2) of *Aulacizes* species is shown in Fig. 7 and is divided into four clades with moderate to high support, each corresponding to a distinct species treated herein.

Species delimitation

The six species delimitation methods employed (ABGD, ASAP, GMYC, bPTP, mPTP, and PTP) generated different numbers of putative species (Fig. 7). For COI data, considering the above-mentioned samples preliminarily identified as *A. conspersa* (except for *A. insistans* and *A. erythrocephala*), ABGD retrieved three putative species, whereas ASAP retrieved four. GMYC retrieved three and seven putative species, under the single-threshold model and multiple-threshold model, respectively, with confidence intervals of 3–24 and 5–21, excluding the outgroup. Three different types of tree-based PTP analyses (bPTP, mPTP, and PTP) retrieved the same results, recognizing five putative species, excluding *A. insistans* and *A. eryhtrocephala*.

For ITS2 data, ABGD and ASAP retrieved two putative species (except for *A. quadripunctata*), treating *A. insistans* as the same species as *A. conspersa* (only distinguishing *A. repanda*). GMYC retrieved 15 and 21 putative species, under the single-threshold model and multiple-threshold model, respectively, with confidence intervals of 1–

41 and 18–27, excluding *A. insistans* and *A. quadripunctata*. The bPTP, mPTP, and PTP analyses retrieved divergent results. The bPTP found 13, mPTP three, and PTP seven putative species. These results can be compared to each other in Fig. 7, which shows the topology of the tree reconstructed by ML based on the concatenated data, with rectangles representing results of each analysis of species delimitation and of each molecular marker.

Taxonomic implications

Considering 12 species delimitation molecular results, we identify the following most significant taxonomic implications: *Aulacizes insistans* (supported by 11 results), *A. erythrocephala*, and *A. quadripunctata* (these two supported by all results) are each separate species from the *A. conspersa* complex. Specimens initially identified as *A. conspersa* were recovered as five distinct species (based on the results of three methods applied to the COI gene). Of these five delimited species, only three can be distinguished and diagnosed by morphological characters. *Aulacizes repanda* **sp. reval.** (supported by 11 results) and *A. persistans* **sp. reval.** (supported by six results), previously considered *A. conspersa* junior synonyms, are morphologically distinct from the *A. conspersa* type; therefore, they are herein regarded as valid species. However, the remaining *A. conspersa* specimens (segregated into one to three species) cannot be reliably distinguished morphologically; thus, they are treated as belonging to a cryptic species complex. Accordingly, formal taxonomic treatments of *A. conspersa*, *A. repanda*, and *A. persistans* are provided below.

Taxonomy – species redescriptions

***Aulacizes conspersa* Walker, 1851**

(Figs. 1, 2, 8–13, 22, 25, 28, 31–39, 40–44, 50–54, 58–60)

Aulacizes conspersa Walker, 1851: 792.

Tettigonia affinis Signoret, 1855: 60.

Proconia annuligera Walker, 1858: 231.

Aulacizes maculata Walker, 1851: 794.

Aulacizes terminalis Walker, 1851: 793.

Aulacizes divergens Schmidt, 1928: 78. **New synonym.**

Type locality: Brazil.

Length. ♂♂ 11.67–13.40 mm (n = 3); ♀♀ 14.07–14.11 mm (n = 3).

Description. Head. Crown (Figs. 22, 40, 42, 50–54), in dorsal view, well produced anteriorly, its median length approximately 6/10 of interocular width and 4/10 of transocular width; anterior margin carinate; ocelli located approximately on imaginary line between anterior angles of eyes, each approximately equidistant between median line of crown and adjacent eye angle; crown with M-shaped elevation bordering posterior margin; with short longitudinal carina laterad of each ocellus; with median fovea that is broadened anteriorly; disc without conspicuous pubescence. Antennal ledge, in dorsal view, protuberant, with longitudinal sulcus; in lateral view, slightly carinate dorsally, directed forward and digitiform. Face with setae, especially on lower portion. Frons (Figs. 58–60), in anterior view, convex and protuberant, slightly pubescent; with depression at central portion; muscle impressions distinct; epistomal suture obsolete; clypeus, in lateral view, convex, continuing inferior contour of frons.

Thorax. Pronotum (Figs. 22, 40, 42, 50–54), in dorsal view, with width approximately equal to transocular width of head; lateral margins convergent anteriorly; posterior margin concave; posterior ¾ of disc transversely rugose and with punctures; dorsolateral carina complete, declivent anteriorly. Mesoscutellum finely transversely striate. Forewing not strongly coriaceous; without distinct apical membranous area; punctures concentrated mostly close to costal margin and on clavus; veins elevated and distinct; bases of inner and median anteapical cells located more basally than that of outer anteapical cell; with four apical cells, base of fourth more proximal than base of third; without anteapical discal plexus of veins; without supernumerary anteapical crossveins to costal margin; female forewings at rest concealing apex of ovipositor. Hind wing at rest extending almost as far posteriorly as forewing; vein R2+3 incomplete. Hind leg with femoral setal formula 2:0:0; first tarsomere distinctly shorter than combined length of second and third.

Color. Ground color of crown and pronotum yellow to orange (Figs. 22, 40, 42, 50–54). Crown, in dorsal view, with somewhat variable dark brown to black lines positioned as follows: along coronal suture and its arms, a pair of oblique lines extending from central portion of posterior margin, over ocelli, to antennal ledges, each one bifurcated anteriorly, the inner branch directed medially and connected to line over arm of coronal suture, from this connection point, on each side, a line extends to apex of crown, where a transverse line is formed over apical coronal carina, enclosing apical concavity; this pattern of lines delimits

large yellow to orange symmetrical areas. Pronotum with narrow dark brown to black line along anterior margin, bifurcated laterally behind eye, the arms (or at least the inner one) connected posteriorly to an irregular transverse arc on anterior third of pronotal disc; this pattern of lines delimits a broad central anterior area and often a pair of ovoid areas behind eyes; posterior portion of pronotal disc with broad dark brown to black transverse stripe that forms medially a line directed anteriorly to arc on anterior third, delimiting pair of large yellow to orange areas; posterior pronotal stripe including yellowish-brown maculae. Mesonotum dark brown to black, with three spots on anterior portion and one spot on scutellum, yellow to orange; scutellar apex brown. Forewing brown, with large number of well-delimited yellow spots, of distinct sizes, on corium and clavus; with large yellow spot extending from inner anteapical cell to costal margin. Ground color of face yellow to orange (Figs. 1, 2, 41, 43, 58–60); inferior portion of frons with broad transverse stripe, adjacent to marking on gena, dark brown to black; superior portion of frons with dark brown to black dots on muscle impressions; dark brown to black dot on maxillary plate, adjacent to lorum; sometimes with small dark marking on apical portion of clypeus. Lateral and ventral portions of thorax yellow to orange, with some dark brown to black lines and maculae; legs mostly yellow to orange, with tarsi and pretarsi darker. Abdomen (Figs. 40, 41) mostly yellow to orange ventrally and dark brown to black dorsally.

Male terminalia. Pygofer (Fig. 8), in lateral view, not strongly produced posteriorly; posterior margin convex; dorsal margin with extremely long and slender process arising near middle, extending ventrally and then curved dorsally; disc with dispersed microsetae, concentrated mostly on posteroventral portion and extending anteriorly along ventral margin. Valve fused with pygofer laterally. Subgenital plates (Figs. 8, 12), in ventral view, separated from each other throughout their length; subtriangular; with short dorsal dentiform projection on lateral margin at basal half (Fig. 13); surface with numerous scattered microsetae; in lateral view, plate extending posteriorly approximately as far as pygofer apex. Style (Fig. 12), in dorsal view, extending farther posteriorly than apex of connective; with distinct outer preapical projection; outer margin beyond projection with few small setae; apex obtuse. Connective (Fig. 12), in dorsal view, narrowly Y-shaped; arms not widely divergent; stem weakly keeled, longer than arms. Aedeagus symmetrical, short; shaft, in lateral view (Fig. 9), forming dorsal elevation, obtuse at apex; with apical ventral scoop-shaped process (Fig. 10, 11) that exceeds apex of shaft, lateral portions of process curved dorsomesally and acute apically; with pair of lateral longitudinal projections extending from

inferior portion of aedeagal shaft to scoop-shaped process (Fig. 10); gonopore with small associated projection. Paraphyses absent.

Female terminalia. Abdominal sternite VII (Fig. 25), in ventral view, with lateral margins convergent posteriorly; posterior margin deeply emarginate and with inconspicuous, slightly projected median lobe; surface with numerous dispersed microsetae. "Internal" sternite VIII, in dorsal view, forming poorly sclerotized arch located above sternite VII just before valvifers I and ovipositor base; this arch distinctly expanded medially. Pygofer (Fig. 28), in lateral view, moderately produced posteriorly; posterior margin broadly rounded; surface with numerous dispersed microsetae, distributed mostly at posterior third and near ventral margin. Valvifer I (Fig. 31), in lateral view, subrectangular. Valvula I (Fig. 31), in ventral view, expanded at base, forming distinct outer lobe; in lateral view, blade with apex acute; dorsal sculptured area extending from basal portion to apex, formed by scale-like processes arranged in oblique lines at apical half and more horizontal lines at basal half (Figs. 32, 33); ventral sculptured area restricted to apical portion, formed by scale-like processes; surface with setae/pores on basal portion and extending posteriorly below ramus; ventral interlocking device located on basiventral half of valvula. Valvifer II, in lateral view, subpentagonal, narrowed inferiorly; with distinct sensory field of small setae adjacent to articulation point (Fig. 39); denticuli densely distributed on inferior half. Valvula II (Fig. 34), in lateral view, distinctly broadened beyond basal curvature and then narrowing gradually toward obtuse apex; basidorsal hyaline area distinct; preapical prominence inconspicuous (Fig. 37); dorsal margin of blade with approximately 35-40 triangular or subtriangular, non-contiguous small teeth (Figs. 35–37); denticles distributed on teeth (except for those located at basal ascending portion of dorsal margin) and on dorsal and ventral apical margins of blade (except on apex); valvula with ducts extending toward teeth and apex. Gonoplac (Fig. 38) extending slightly beyond pygofer apex; in lateral view, with basal half narrow and apical half distinctly expanded; apex obtuse; surface with group of setae located ventroapically and extending anteriorly along ventral margin; denticuli also present, forming more distinct group near dorsoapical margin.

Material examined. Brazil. Bahia State: Pico do Barbado, DZUP: 1 ♂. **Mato Grosso State:** Chapada dos Guimarães, DZUP: 1 ♀. **Minas Gerais State:** Juiz de Fora, DZRJ: 2 ♂; Serra do Cipó, DZRJ: 1 ♂ (voucher ENT5973); Itamonte, DZRJ: 3 ♀. **Espírito Santo State:** Brejetuba, DZRJ: 1 ♀. **Rio de Janeiro State:** Petrópolis, DZRJ: 3 ♂ and 3 ♀; Teresópolis,

DZRJ: 2 ♂ (vouchers ENT5986 and ENT6278) and 1 ♀; Nova Friburgo, DZRJ: 3 ♂ and 1 ♀; Itatiaia, DZRJ: 13 ♂ and 4 ♀ (vouchers ENT5970 ♂, ENT5971 ♂, ENT5980 ♂, ENT5981 ♂, ENT5982 ♂, ENT5983 ♂, ENT5984 ♂, ENT5985 ♂, ENT6287 ♂, and ENT6288 ♂), MZSP: 2 ♂; Engenheiro Paulo de Frontin [Morro Azul do Tinguá], DZRJ: 1 ♂ and 1 ♀; Rio de Janeiro [Parque Estadual da Pedra Branca], DZRJ: 5 ♂ and 1 ♀ (vouchers ENT5991 ♂, ENT5992 ♂, and ENT5993 ♂); Rio de Janeiro [Parque Nacional da Tijuca], DZRJ: 2 ♂ and 4 ♀ (vouchers ENT6538 ♀ and ENT6539 ♂); Rio de Janeiro [Jardim Botânico], DZRJ: 1 ♀ (voucher ENT5990); Rio de Janeiro, DZUP: 1 ♀. **São Paulo State:** Atibaia, DZRJ: 2 ♀; São Paulo, MZSP: 7 ♂ and 2 ♀; Caraguatatuba, MZSP: 1 ♂; Barueri, MZSP: 1 ♂; São José do Barreiro [Serra da Bocaina], DZUP: 2 ♂; Pilar do Sul, MELQ: 2 ♂ (voucher 6350 ♂); Águas de Lindóia, DZRJ: 1 ♀ (voucher ENT6291). **Paraná State:** São José dos Pinhais, DZUP: 1 ♂, DZRJ: 1 ♂ and 3 ♀ (vouchers ENT5995 ♀, ENT5996 ♀, and ENT5997 ♀); Morretes, DZUP: 2 ♂ and 2 ♀; Guaratuba, DZUP: 3 ♂; Antonina, DZUP: 3 ♂ and 1 ♀. **Santa Catarina State:** Nova Teutônia, MZSP: 1 ♂, DZUP: 1 ♂; Blumenau, MZSP: 2 ♂ and 1 ♀; Timbó, MZSP: 4 ♂ and 2 ♀; Joinville, DZUP: 2 ♂; Praia Grande, DZUP: 1 ♂ and 1 ♀. **Argentina. Misiones:** Loreto, MZSP: 1 ♀.

Taxonomic notes. After a careful study of the photographs of type specimens, we agreed with Young (1968), who synonymized three species with *A. conspersa*, viz., *Proconia annuligera*, *A. maculata*, and *A. terminalis*; additional details are provided above in the list of synonyms of *A. conspersa*; concerning this list, we observe that Signoret (1855) proposed the name *affinis* as a replacement for *terminalis* Walker, 1851, which was preoccupied. Here we propose an additional synonym, *A. divergens* (Figs. 42–44), whose type has the same morphological and color characteristics as those of *A. conspersa* (Figs. 40, 41). Based on the results of the species delimitation analyses (Fig. 7), it appears to us that *A. conspersa* could constitute a complex of cryptic species, whose individuals share three characteristics (Figs. 1, 2, 22, 50–54, 58–60): (1) rounded and relatively short crown, its median length corresponding to approximately 6/10 of the interocular distance, (2) apex of clypeus without a distinct black spot, and (3) forewings with widely spaced rounded yellow spots. This combination of characteristics distinguishes this putative complex from *A. persistans* **sp. reval**.

***Aulacizes persistans* (Walker, 1858), sp. reval.**

(Figs. 3, 4, 14–17, 23, 26, 29, 45–49, 55–57, 61–63)

Proconia persistans Walker, 1858: 232.

Aulacizes conspurcata Melichar, 1926: 306. **New synonym.**

Type locality: Petrópolis, Rio de Janeiro, Brazil.

Length. ♂♂ 13.04–14.37 mm (n = 3); ♀♀ 14.66–14.81 mm (n = 3).

Description. Head. Crown (Figs. 23, 45, 48, 55–57), in dorsal view, strongly produced anteriorly, its median length approximately 7/10 of interocular width and 5/10 of transocular width; anterior margin carinate; ocelli located slightly before imaginary line between anterior angles of eyes, each slightly closer to median line of crown than to adjacent eye angle; crown without distinct M-shaped elevation bordering posterior margin; with short longitudinal carina laterad of each ocellus; with median fovea that is broadened anteriorly; disc without conspicuous pubescence. Antennal ledge, in dorsal view, protuberant, with longitudinal sulcus; in lateral view, slightly carinate dorsally, directed forward and digitiform. Face with setae, especially on lower portion. Frons (Figs. 61–63), in anterior view, convex and protuberant, slightly pubescent; with depression at central portion; muscle impressions distinct; epistomal suture obsolete; clypeus, in lateral view, convex, continuing inferior contour of frons.

Thorax. Pronotum (Figs. 23, 45, 48, 55–57), in dorsal view, with width slightly greater than transocular width of head; lateral margins convergent anteriorly; posterior margin concave; posterior ¾ of disc transversely rugose and with punctures; dorsolateral carina complete, declivent anteriorly. Mesoscutellum finely transversely striate. Forewing not strongly coriaceous; without distinct apical membranous area; punctures concentrated mostly close to costal margin and on clavus; veins elevated and distinct; bases of inner and median anteapical cells located more basally than that of outer anteapical cell; with four apical cells, base of fourth more proximal than base of third; without anteapical discal plexus of veins; irregular supernumerary anteapical crossveins to costal margin may be present; female forewings at rest concealing apex of ovipositor. Hind wing at rest extending almost as far posteriorly as forewing; vein R_{2+3} incomplete. Hind leg with femoral setal formula 2:0:0; first tarsomere distinctly shorter than combined length of second and third.

Color. Ground color of crown and pronotum yellow to orange (Figs. 23, 45, 48, 55–57). Crown, in dorsal view, with somewhat variable dark brown to black lines positioned as follows: along coronal suture and its arms, a pair of oblique lines extending from central portion of posterior margin, over ocelli, to antennal ledges, each one bifurcated anteriorly, the inner branch directed medially and connected to line over arm of coronal suture, from this connection point, on each side, a line extends to apex of crown, where a transverse line may be formed over apical coronal carina, enclosing apical concavity; this pattern of lines may or may not enclose well-defined large yellow to orange symmetrical areas. Pronotum with narrow dark brown to black line along anterior margin, bifurcated laterally behind eye, the inner branch connected posteriorly to an irregular transverse arc on anterior third of pronotal disc; this pattern of lines delimits a broad central anterior area; posterior portion of pronotal disc with broad dark brown to black transverse stripe that forms medially a line directed anteriorly to arc on anterior third, delimiting pair of large yellow to orange areas; posterior pronotal stripe including yellowish-brown maculae. Mesonotum dark brown to black, with three spots on anterior portion and one spot on scutellum, yellow to orange. Forewing brown, with large number of yellow spots, of distinct sizes, on corium and clavus, often fused to each other; large posterior yellow spot not strongly developed. Ground color of face yellow to orange (Figs. 61–63); inferior portion of frons with broad transverse stripe, adjacent to marking on gena, dark brown to black; superior portion of frons with dark brown to black dots, or pair of stripes, on muscle impressions; dark brown to black dot on maxillary plate, adjacent to lorum; with dark marking on apical portion of clypeus. Lateral and ventral portions of thorax yellow to orange, with some dark brown to black lines and maculae; legs mostly yellow to orange, with tarsi and pretarsi darker. Abdomen (Figs. 45, 46) mostly yellow to orange ventrally and dark brown to black dorsally.

Male terminalia. Pygofer (Fig. 14), in lateral view, not strongly produced posteriorly; posterior margin convex; dorsal margin with extremely long and slender process arising near middle, extending ventrally and then curved dorsally and posteriorly; disc with dispersed microsetae, concentrated mostly on posteroventral portion and extending anteriorly along ventral margin. Valve fused with pygofer laterally. Subgenital plates (Fig. 14), in ventral view, separated from each other throughout their length; subtriangular; with short dorsal dentiform projection on lateral margin at basal half; surface with numerous scattered microsetae; in lateral view, plate extending posteriorly slightly beyond pygofer apex. Style, in dorsal view, extending farther posteriorly than apex of connective; with

distinct outer preapical projection; outer margin beyond projection with few small setae; apex truncate. Connective, in dorsal view, narrowly Y-shaped; arms not widely divergent; stem weakly keeled, longer than arms. Aedeagus symmetrical, short; shaft, in lateral view (Fig. 15), forming dorsal elevation, obtuse at apex; with apical ventral scoop-shaped process (Figs. 16, 17) that exceeds apex of shaft, lateral portions of process curved dorsomesally and acute apically; with pair of lateral longitudinal projections extending from inferior portion of aedeagal shaft to scoop-shaped process (Fig. 16); gonopore with small associated projection. Paraphyses absent.

Female terminalia. Characters as in *A. conspersa* (Figs. 26, 29, 31–39).

Material examined. Brazil. Rio de Janeiro State: Teresópolis, DZRJ: 14 ♂ and 5 ♀ (vouchers ENT6275 ♂, ENT6276 ♂, ENT6277 ♂, ENT5987 ♀, and ENT5988 ♀). **São Paulo State:** Caraguatatuba, MZSP: 1 ♂ and 1 ♀; Salesópolis, MZSP: 3♂; Itatiba, MZSP: 1 ♂; São Paulo, MZSP: 1 ♂. **Paraná State:** São José dos Pinhais, DZUP: 2 ♂ and 1 ♀; Piraquara, DZUP: 3 ♂ and 1 ♀; Antonina, DZRJ: 1 ♀. **Santa Catarina State:** São Bento do Sul, DZUP: 2 ♂ and 2 ♀, MZSP: 2 ♂.

Taxonomic notes. Photographs of the type specimens of *A. persistans* (Figs. 45, 46) and *A. conspurcata* (Figs. 47–49) were carefully compared. This study showed that these types share the same morphological and color characteristics. Based on this comparison and the results of the species delimitation analyses (Fig. 7), we revalidate *A. persistans* **sp. reval.** and treat *A. conspurcata* as its junior synonym (additional details are provided above in the list of synonyms of *A. persistans*). Individuals of *A. persistans* have the following combination of diagnostic characteristics (Figs. 3, 4, 23, 55–57, 61–63) that distinguishes them from *A. conspersa*: (1) crown triangular and more pronounced anteriorly, its median length corresponding to 7/10 or more of the interocular distance, (2) apex of clypeus distinctly black, and (3) forewings with numerous rounded yellow spots often fused to each other.

***Aulacizes repanda* (Signoret, 1855), sp. reval.**

(Figs. 5, 18–21, 24, 27, 30, 64–72)

Tettigonia repanda Signoret, 1855: 60.

Type locality: São Paulo, Brazil.

Length. ♂♂ 10.92–11.29 mm (n = 3); ♀♀ 11.80–12.20 mm (n = 3).

Description. Head. Crown (Figs. 24, 64–66, 69–72), in dorsal view, strongly produced anteriorly, its median length approximately 7/10 of interocular width and 4/10 of transocular width; anterior margin carinate; ocelli located slightly before imaginary line between anterior angles of eyes, each slightly closer to median line of crown than to adjacent eye angle; crown without distinct M-shaped elevation bordering posterior margin; with short longitudinal carina laterad of each ocellus; with median fovea that is broadened anteriorly; disc without conspicuous pubescence. Antennal ledge, in dorsal view, protuberant, with longitudinal sulcus; in lateral view, slightly carinate dorsally, directed forward and digitiform. Face with setae, especially on lower portion. Frons (Figs. 65, 66), in anterior view, convex and protuberant, slightly pubescent; with slight depression at central portion; muscle impressions distinct; epistomal suture obsolete; clypeus, in lateral view, convex, continuing inferior contour of frons.

Thorax. Pronotum (Figs. 24, 64–66, 69–72), in dorsal view, with width approximately equal to transocular width of head; lateral margins convergent anteriorly; posterior margin concave; posterior ¾ of disc transversely rugose and with punctures; dorsolateral carina complete, declivent anteriorly. Mesoscutellum finely transversely striate. Forewing not strongly coriaceous; without distinct apical membranous area; punctures concentrated mostly close to costal margin and on clavus; veins elevated and distinct; bases of inner and median anteapical cells located more basally than that of outer anteapical cell; with four apical cells, base of fourth more proximal than base of third; without anteapical discal plexus of veins; irregular supernumerary anteapical crossveins to costal margin may be present; female forewings at rest concealing apex of ovipositor. Hind wing at rest extending almost as far posteriorly as forewing; vein R_{2+3} incomplete. Hind leg with femoral setal formula 2:0:0; first tarsomere distinctly shorter than combined length of second and third.

Color. Ground color of crown and pronotum yellow to red (Figs. 5, 24, 64–66, 69–72). Color pattern somewhat variable. Crown, in dorsal view, with triangular marking on coronal suture, with or without pair of lines extending from posterior margin to ocelli, and with or without marking on apical carina, dark brown to black. Pronotum anteriorly with

median macula and pair of linear markings behind eyes, dark brown to black; posterior portion of pronotal disc with broad dark brown to black transverse stripe that forms medially a line directed anteriorly to median marking at anterior margin (this line often incomplete or variably interrupted); transverse pronotal stripe bordered posteriorly by irregular yellowish-brown area. Mesonotum with ground color yellow to red; lateral portions and scutellar suture mostly dark brown to black. Forewing brown to dark brown, with large, variable greenish-yellow spots, of distinct sizes, on corium and clavus, often with transcommissural spot at apical portion of clavus. Ground color of face mostly pale yellow to red; without broad transverse dark brown to black stripe on inferior portion of frons and adjacent marking on gena; superior portion of frons without dark brown to black dots or stripes on muscle impressions; other markings on face usually also absent but sometimes with extensive brown area on clypeus and inferior portion of frons. Lateral and ventral portions of thorax mostly pale yellow to red, usually without extensive dark brown to black markings, except for a stripe on anepisternum; legs mostly yellow to red, sometimes with darker portions, including tarsi and pretarsi. Abdomen with ground color yellow to red, with extensive dark brown areas ventrally and dorsally; apical portion of gonoplacs contrastingly dark brown.

Male terminalia. Pygofer (Fig. 18), in lateral view, not strongly produced posteriorly; posterior margin convex; dorsal margin with extremely long and slender process arising on apical portion, extending ventrally, and then curved dorsally; disc with dispersed microsetae, concentrated mostly on posteroventral portion and extending anteriorly along ventral margin. Valve fused with pygofer laterally. Subgenital plates (Fig. 18), in ventral view, separated from each other throughout their length; subtriangular; with short dorsal dentiform projection on lateral margin at basal half; surface with numerous scattered microsetae; in lateral view, plate extending posteriorly slightly beyond pygofer apex. Style, in dorsal view, extending farther posteriorly than apex of connective; with distinct outer preapical projection; outer margin beyond projection with few small setae; apex truncate. Connective, in dorsal view, narrowly Y-shaped; arms not widely divergent; stem weakly keeled, longer than arms. Aedeagus symmetrical, short; shaft, in lateral view (Fig. 19), forming dorsal elevation, obtuse at apex; with apical ventral scoop-shaped process (Figs. 20, 21) that exceeds apex of shaft, lateral portions of process curved dorsomesally and acute apically; with pair of lateral longitudinal projections extending from inferior portion of aedeagal shaft to scoop-shaped process (Fig. 20); gonopore with small associated projection. Paraphyses absent.

Female terminalia. Abdominal sternite VII (Fig. 27), in ventral view, with lateral margins convergent posteriorly; posterior margin shallowly emarginate and with inconspicuous, slightly projected median lobe; surface with numerous dispersed microsetae. "Internal" sternite VIII, in dorsal view, forming poorly sclerotized arch located above sternite VII just before valvifers I and ovipositor base. Pygofer (Fig. 30), in lateral view, slightly produced posteriorly; posterior margin broadly rounded; surface with numerous dispersed microsetae, distributed mostly at posterior third and near ventral margin. Valvifer I, valvula I, valvifer II, valvula II, and gonoplac as in *A. conspersa* (Figs. 31–39) and *A. persistans*.

Material examined. Brazil, Minas Gerais State: Maria da Fé, MELQ: 3 ♂ (vouchers ENT6345, ENT6347, and ENT6348). **São Paulo State:** São Bento do Sapucaí, MELQ: 1 ♀ (voucher ENT6352); Barueri, DZUP: 1 ♂; São Paulo, MELQ: 1 ♂. **Paraná State:** Curitiba, DZUP: 6 ♂ and 4 ♀ (voucher ENT6821 ♀); São José dos Pinhais, DZUP: 2 ♀; Piraquara, DZUP: 1 ♀. **Santa Catarina State:** São Bento do Sul, DZUP: 1 ♂, MSZP: 1 ♂ and 1 ♀; Ponte Alta, DZUP: 1 ♂. **Rio Grande do Sul State:** Passo Fundo, MELQ: 1 ♂.

Taxonomic notes. Based on the results of the species delimitation analyses (Fig. 7), *A. repanda* is herein revalidated and redescribed in detail. It can be distinguished from other *Aulacizes* species by the following features: (1) ground color of crown and pronotum yellow to red; (2) crown with a triangular dark brown to black marking on the coronal suture; (3) forewing brown to dark brown, with large, variable greenish-yellow spots, of distinct sizes, on corium and clavus, often with a transcommissural spot at the apical portion of the clavus. Both male and female specimens show some color variation, especially on the forewings (Figs. 69–72). Our comparisons of specimens, descriptions, and photographs of males and females of *A. repanda* **sp. reval.** with those of *A. conspersa* and *A. persistans* **sp. reval.** revealed a few differences among these species. In males, minor differences are only observed in the scoop-shaped process of the aedeagus and the posterior margin of the pygofer, whereas the subgenital plates, connective, and styles are conservative in these species. In females, differences occur in the sternite VII (Fig. 27) and pygofer (Fig. 30), whereas other structures are also conservative (Figs. 31–39).

Discussion

The external morphology of most *Aulacizes* species remains relatively poorly known. For instance, Young (1968) provided only illustrations of the aedeagus and pygofer of a male of *A. conspersa*. His interpretation of this species was based on the comparison of a single male specimen with the teneral female lectotype. He also observed that the terminalia of the male lectotype of *A. divergens*, which is here considered a junior synonym of *A. conspersa*, were similar to those of *A. obsoleta*. Subsequently, Mejdalani et al. (2006) provided more detailed descriptions and illustrations of the male and female terminalia of *A. erythrocephala*, which they revalidated from the synonymy of *A. quadripunctata*. Dellapé (2016) presented detailed descriptions and illustrations of the female terminalia of *Aulacizes* species recorded from Argentina (*A. basalis*, *A. conspersa*, *A. insistans*, *A. obsoleta*, and *A. quadripunctata*). Therefore, previous taxonomic studies on *Aulacizes* have focused only on partial morphological information (Young, 1968; Mejdalani et al., 2006; Dellapé, 2016), whereas previous phylogenetic analyses of the Proconiini have not included sufficient samples of species or specimens of the genus to explore relationships within it or evaluate species boundaries (Feng et al., 2024). Although the taxonomy of the Cicadellidae is traditionally mainly based on the great diversity of form observed in the male terminalia, whereas the female terminalia are usually less studied due to their supposedly conservative nature (Carvalho & Mejdalani, 2014), our observations suggest that within *Aulacizes* the terminalia of both sexes present few interspecific variations. This is the reason why delimiting *Aulacizes* species using morphology alone has been a challenge since the 19th century. Therefore, we employed mitochondrial and nuclear loci data for the first time to address the problem of delimiting *Aulacizes* species.

Young (1968) synonymized *Tettigonia repanda* with *A. conspersa*. Nevertheless, most results of our species delimitation analyses (Fig. 7), considering both COI and ITS2, as well as comparisons of photographs of type specimens (Figs. 64–68), suggest the distinction of *T. repanda* from *A. conspersa* (Figs. 40, 41). Accordingly, *A. repanda* **sp. reval.** is herein revalidated based on molecular and morphological data and redescribed. This species can be differentiated from other *Aulacizes* species by the following combination of characteristics (Figs. 5, 24, 64–66, 69–72): (1) ground color of crown and pronotum yellow to red; (2) crown with a triangular dark brown to black marking on the coronal suture; (3) forewing brown to dark brown, with large, variable greenish-yellow spots, of distinct sizes, on corium and clavus, often with a transcommissural spot at the apical portion of the clavus.

Likewise, individuals from the lineage from Teresópolis and Itatiaia at Rio de Janeiro State (six specimens, green vertical bars in Fig. 7) have the crown more produced anteriorly, with an average length corresponding to 7/10 or more of the interocular distance, and triangular in shape (Figs. 23, 55–57); the clypeus is black apically (Figs. 61–63); and forewings have a great number of rounded yellow spots, which are almost fused to one another (Figs. 3, 4, 23, 55–57). These specimens share these characteristics with the types of *A. conspurcata* (Figs. 47–49) and *A. persistans* (considered by Young, 1968 as a synonym of *A. conspersa*) (Figs. 45, 46), both with type locality in Petrópolis (Rio de Janeiro State). Here, this lineage is treated and redescribed as *A. persistans* **sp. reval.**, with *A. conspurcata* being its junior synonym. Therefore, our molecular analysis corroborates the morphological interpretation of a taxonomist (Walker, 1858) who worked in the 19th century.

However, individuals from the remaining lineages (*A. conspersa sensu stricto*; blue vertical bars in Fig. 7) apparently do not present morphological characteristics that allow a clear distinction of these lineages from one another. Therefore, they are treated here tentatively as a complex of cryptic species, the *A. conspersa* complex. Specimens of this complex share characteristics with the types of *A. conspersa* (Figs. 40, 41) and *A. divergens* (Figs. 42–44), both of which are currently considered valid species. We propose, also taking into account a careful comparison of the photographs of lectotypes, that *A. divergens* be considered a junior synonym of *A. conspersa*. Individuals of the *A. conspersa* complex have the crown rounded and relatively short, corresponding to approximately 6/10 of the interocular distance (Figs. 22, 50–54), the apex of the clypeus has no distinct black spot (Figs. 58–60), and the forewing rounded yellow spots are more widely spaced (Figs. 1, 2, 22, 50–54). These features distinguish the complex from *A. persistans* **sp. reval.**

In addition to apparently not having distinct morphological characteristics, lineages from Serra do Cipó (Minas Gerais State) and Itatiaia (Rio de Janeiro State) were recognized as separate species only by the bPTP, mPTP, and PTP methods, in disagreement with the GMYC and ABGD, which included them in a single group together with other individuals (Fig. 7). The lineage from Serra do Cipó is based on a single sample; therefore, this is the group that has the greatest sampling asymmetry in our work. Unfortunately, to date, no additional specimens of this lineage have been obtained.

Zhang et al. (2013) conducted several tests comparing species delimitation methods; they considered different scenarios and concluded that their PTP method outperformed GMYC. Specifically, tests with simulated datasets were performed with uniform and uneven

sampling and, overall, PTP produced the best results (Zhang et al., 2013). The better performance of PTP was perceived when the evolutionary distances between species were small, showing that this method is more sensitive and can detect subtle evolutionary differences. Perhaps it is for this reason that, in the present study, PTP was able to separate the lineages from Serra do Cipó (Minas Gerais) and Itatiaia (Rio de Janeiro) (Fig. 7). Kapli et al. (2017) stated that mPTP outperforms PTP and other popular distance-based methods, as it produces substantially smaller numbers of putative species, as well as delimitations that are closer to traditional taxonomy; here, mPTP generated the same results as PTP and bPTP.

GMYC and ABGD, despite being quite distinct methods, generated similar results that are closer to the number of species detected by morphology. GMYC is considered more conservative than PTP; it may have difficulty in detecting species separated by small evolutionary differences. Furthermore, some studies have also indicated that the GMYC performance is affected not only by the ratio of population size to species divergence times, but also by variation in population size and numbers of species involved and unique samples (Talavera et al., 2013; Luo et al., 2018). These are some of the factors that may, in the present study, be related to the non-separation of the lineages of the *A. conspersa* complex by GMYC. Whereas ABGD is a genetic distance method based on a phenetic approach (similar sequences are simply grouped together in the same group/species) and works when the speciation events are radiations, bifurcations, or a mixture of both (Puillandre et al., 2021), GMYC, PTP, bPTP, and mPTP are explicitly based on a phylogenetic approach. The ASAP (also based on a phenetic approach) result was the only one distinct from the other methods, as it recovered three lineages within *A. conspersa*, discriminating a second lineage with six individuals from Itatiaia (Rio de Janeiro State) and one from Serra do Cipó (Minas Gerais State) (Fig. 7).

The ITS2 gene constitutes a rapidly evolving fragment of nuclear DNA that has been considered useful for inferring phylogenetic relationships of closely related species in groups of plants and fungi (Coleman, 2007; Wiemers et al., 2009). In addition, more recent studies, dealing mainly with insects, indicated that ITS2 was a promising candidate for barcode approaches (species delimitations) and, consequently, for the discovery of cryptic species, as shown by Wiemers et al. (2009, Lepidoptera: Lycaenidae), Li et al. (2010, Hymenoptera: Eurytomidae), Gebiola et al. (2012, Hymenoptera: Eulophidae), Haarto & Ståhls (2014, Diptera: Syrphidae), Schwarzfeld & Sperling (2014, Hymenoptera: Ichneumonidae), Jürgenstein et al. (2015, Diptera: Mycetophilidae), and Zhang et al. (2021, Odonata:

Coenagrionidae). In the present study, unlike COI, ITS2 results were not very informative, except for one well-delimited species, *A. repanda*, as mentioned previously (Fig. 7). Distance and tree-based methods were unable to distinguish *A. conspersa* from *A. insistans*. ABGD and ASAP grouped these species in a single lineage. These results could likely be due to the relatively small number of variable and informative nucleotide positions (i.e., the molecular divergence is relatively low). Only two lineages were delimited by mPTP, one including only individuals of *A. conspersa* and another grouping *A. conspersa* plus *A. insistans*. GMYC, bPTP, and PTP splitted these two species into a great number of lineages as detailed in the results. Such discordant results could be due to imbalance between speciation and coalescence, a situation that poses a challenge for identifying transition points between inter- and intraspecific processes, resulting in incorrect species delimitations and false positives (excessive division) (Luo et al., 2018). Our ITS2 results did not even delimit the *A. conspersa* complex, contradicting the morphological data; this gene is perhaps unable to distinguish species within *Aulacizes*.

Cryptic species are taxa that cannot be easily distinguished morphologically; however, other kinds of evidence indicate that they are separated from closely related forms and thus have their own evolutionary trajectories (Struck et al., 2018). Pfenninger & Schwenk (2007) observed that an exponential growth in publications dealing with cryptic species (genetically divergent but morphologically enigmatic lineages) occurred during the last two decades; discovery of many cryptic species occurred during the course of phylogenetic, phylogeographic, or population genetics studies, in association with technical advances in PCR and DNA sequencing. Identification and description of cryptic species have important implications for the quantification of biological diversity, conservation, protection and management of natural resources, human health, pest management, and studies on coevolution and species interactions (Bickford et al., 2007). Studies on cryptic species are vital for a more precise estimation of the global diversity of insects (Li & Wiens, 2023). Few studies reporting cryptic species within the Cicadellinae are available (e.g., Valderrama, 2023). The present result is even more significant because members of the *A. conspersa* complex are potential vectors of the bacterium *Xylella fastidiosa* in citrus, grape, and plum orchards (Azevedo-Filho & Carvalho, 2006; Ringenberg et al., 2010; Paris et al., 2012).

Conclusions

In general, the mitochondrial COI gene was more effective than the nuclear ITS2 gene for distinguishing *Aulacizes* species. Furthermore, the delimitations indicated by COI were corroborated by morphological data. Thus, this gene was useful for improving our knowledge about species delimitation within the genus. However, we emphasize that the species limits inferred here based on sequence data and external morphology are approximate. More information should be taken into account for an in-depth evaluation of the initial proposals, such as additional morphological characters, morphometry, ecology, behavior, geographic distribution, etc., establishing thus an integrative taxonomic framework (Dayrat, 2005; Padial et al., 2010). In situations in which morphological characters are complex and of somewhat uncertain significance (Puillandre et al., 2012), as in the present case, results of delimitation analyses, if interpreted naively, can lead to an artificial inflation of species numbers (Luo et al., 2018).

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Disclosure statement

No potential conflict of interest was reported by the authors.

Supplementary data

Appendix S1. Ultrametric tree of COI sequences (~383 bp) of *Aulacizes* obtained with BEAST2 and used in species delimitation analyses with the SPdel pipeline.

Appendix S2. Ultrametric tree of ITS2 sequences (~616 bp) of *Aulacizes* obtained with BEAST2 and used in species delimitation analyses with the SPdel pipeline.

Appendix S3. Log of species delimitation analyses of SPdel pipeline, with ultrametric tree obtained with BEAST using COI alignment.

Appendix S4. Log of species delimitation analyses of SPdel pipeline, with ultrametric tree obtained with BEAST using ITS2 alignment.

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Table 1. Specimens of *Aulacizes* included in the molecular species delimitation analyses; voucher code, depository, locality data from Brazil, and GenBank accession numbers are given.

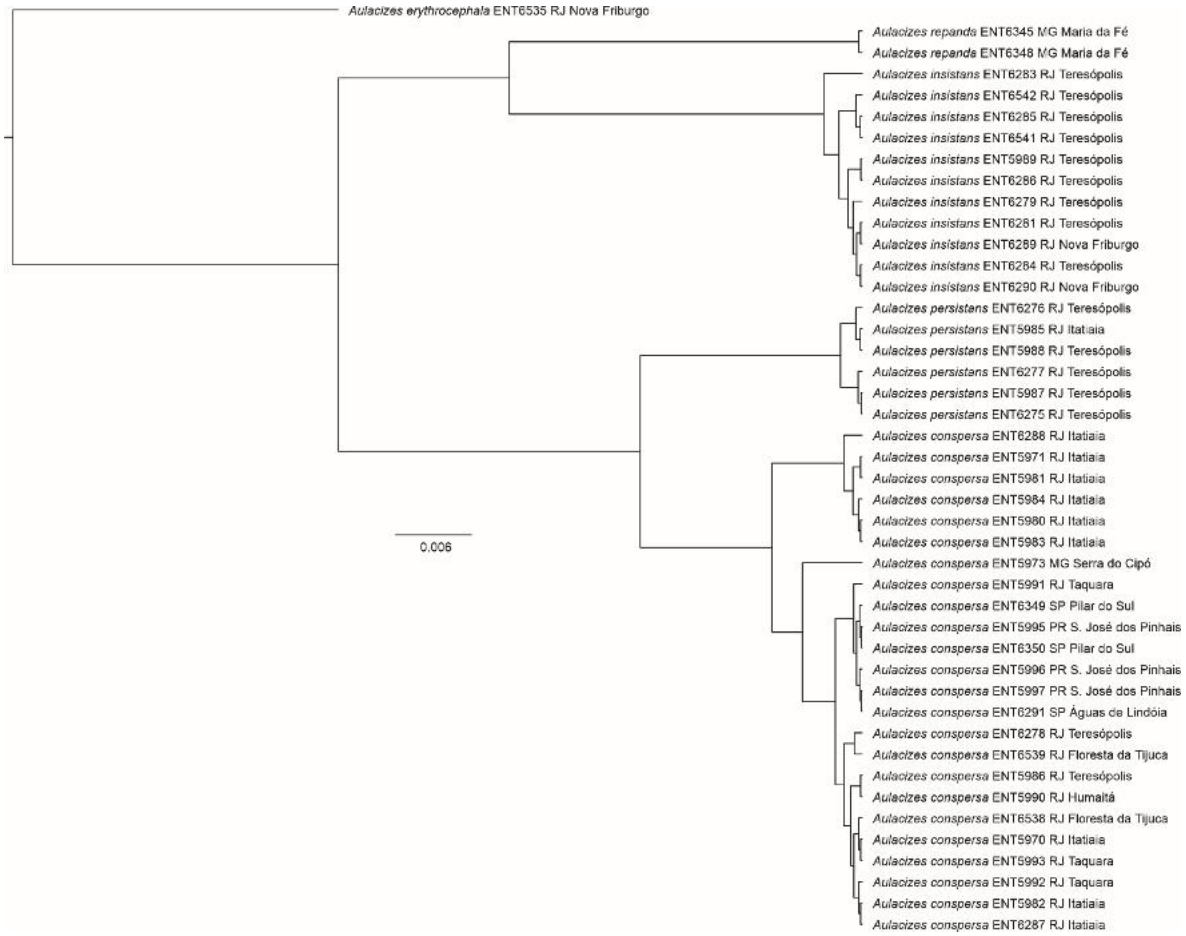
Species	Voucher	Depository	Locality	COI	ITS-2
Aulacizes conspersa	**ENT5970**	DZRJ	RJ: Itatiaia	PV176399	PV185424
Aulacizes conspersa	**ENT5971**	DZRJ	RJ: Itatiaia	PV176398	-
Aulacizes conspersa	**ENT5973**	DZRJ	MG: Serra do Cipó	PV176397	PV185445
Aulacizes conspersa	**ENT5980**	DZRJ	RJ: Itatiaia	PV176396	-
Aulacizes conspersa	**ENT5981**	DZRJ	RJ: Itatiaia	PV176395	PV185446
Aulacizes conspersa	**ENT5982**	DZRJ	RJ: Itatiaia	PV176394	PV185425
Aulacizes conspersa	**ENT5983**	DZRJ	RJ: Itatiaia	PV176393	PV185449
Aulacizes conspersa	**ENT5984**	DZRJ	RJ: Itatiaia	PV176392	PV185447
Aulacizes conspersa	**ENT5986**	DZRJ	RJ: Teresópolis	PV176390	PV185427
Aulacizes conspersa	**ENT5990**	MNRJ	RJ: Humaitá	PV176387	PV185428
Aulacizes conspersa	**ENT5991**	DZRJ	RJ: Taquara	PV176386	PV185429
Aulacizes conspersa	**ENT5992**	DZRJ	RJ: Taquara	PV176385	PV185437
Aulacizes conspersa	**ENT5993**	DZRJ	RJ: Taquara	PV176384	PV185440
Aulacizes conspersa	**ENT5995**	DZUP	PR: São José dos Pinhais	PV176383	PV185430
Aulacizes conspersa	**ENT5996**	DZUP	PR: São José dos Pinhais	PV176382	PV185441
Aulacizes conspersa	**ENT5997**	DZUP	PR: São José dos Pinhais	PV176381	PV185431
Aulacizes conspersa	**ENT6278**	DZRJ	RJ: Teresópolis	PV176377	PV185450
Aulacizes conspersa	**ENT6287**	DZRJ	RJ: Itatiaia	PV176376	PV185433
Aulacizes conspersa	**ENT6288**	DZRJ	RJ: Itatiaia	PV176375	PV185448
Aulacizes conspersa	**ENT6291**	DZRJ	SP: Águas de Lindóia	PV176374	PV185434
Aulacizes conspersa	**ENT6349**	MELQ	SP: Pilar do Sul	PV176373	PV185435
Aulacizes conspersa	**ENT6350**	MELQ	SP: Pilar do Sul	PV176372	PV185419
Aulacizes conspersa	**ENT6538**	MNRJ	RJ: Rio de Janeiro	PV176370	PV185438
Aulacizes conspersa	**ENT6539**	MNRJ	RJ: Rio de Janeiro	PV176371	PV185443

Aulacizes persistans **sp. reval.**	**ENT5985**	DZRJ	RJ: Itatiaia	PV176391	PV185426
Aulacizes persistans **sp. reval.**	**ENT5987**	DZRJ	RJ: Teresópolis	PV176389	PV185412
Aulacizes persistans **sp. reval.**	**ENT5988**	DZRJ	RJ: Teresópolis	PV176388	PV185439
Aulacizes persistans **sp. reval.**	**ENT6275**	DZRJ	RJ: Teresópolis	PV176380	PV185421
Aulacizes persistans **sp. reval.**	**ENT6276**	DZRJ	RJ: Teresópolis	PV176379	PV185444
Aulacizes persistans **sp. reval.**	**ENT6277**	DZRJ	RJ: Teresópolis	PV176378	PV185442
Aulacizes insistans	**ENT5989**	DZRJ	RJ: Teresópolis	PV176357	PV185413
Aulacizes insistans	**ENT6279**	DZRJ	RJ: Teresópolis	PV176358	PV185414
Aulacizes insistans	**ENT6281**	DZRJ	RJ: Teresópolis	PV176359	PV185415
Aulacizes insistans	**ENT6283**	DZRJ	RJ: Teresópolis	PV176360	PV185416
Aulacizes insistans	**ENT6284**	DZRJ	RJ: Teresópolis	PV176361	PV185417
Aulacizes insistans	**ENT6285**	DZRJ	RJ: Teresópolis	PV176362	PV185422
Aulacizes insistans	**ENT6286**	DZRJ	RJ: Teresópolis	PV176363	PV185432
Aulacizes insistans	**ENT6289**	MNRJ	RJ: Nova Friburgo	PV176364	PV185418
Aulacizes insistans	**ENT6290**	MNRJ	RJ: Nova Friburgo	PV176365	PV185423
Aulacizes insistans	**ENT6541**	DZRJ	RJ: Teresópolis	PV176366	PV185436
Aulacizes insistans	**ENT6542**	DZRJ	RJ: Teresópolis	PV176367	PV185420
Aulacizes repanda **sp. reval.**	**ENT6345**	MELQ	MG: Maria da Fé	PV176368	PV185451
Aulacizes repanda **sp. reval.**	**ENT6348**	MELQ	MG: Maria da Fé	PV176369	PV185452
Aulacizes erythrocephala	**ENT6535**	MNRJ	RJ: Nova Friburgo	PV176356	-
Aulacizes quadripunctata	**ENT6537**	DZRJ	RJ: Teresópolis	-	PV190392

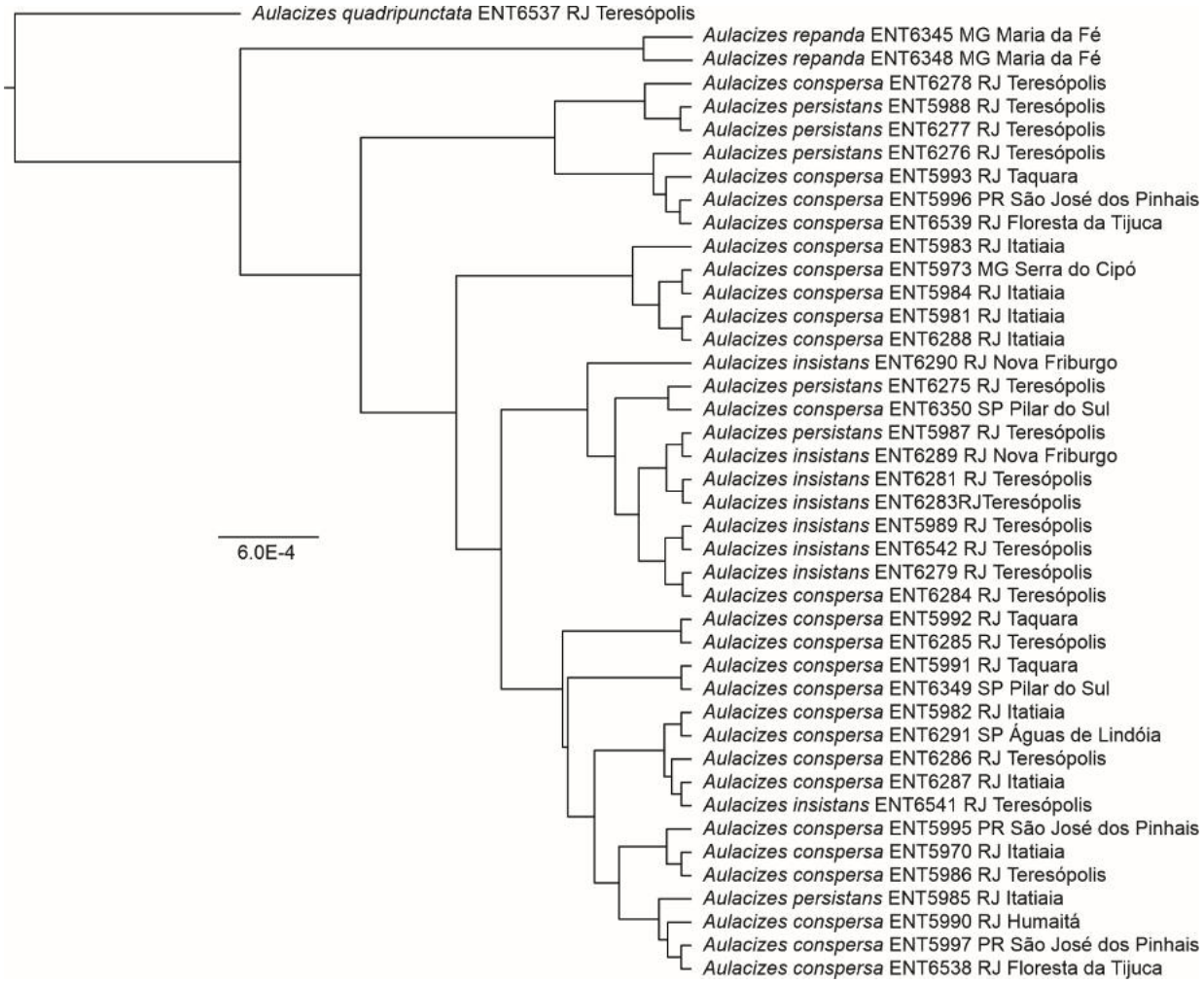
Brazilian states. MG: Minas Gerais; PR: Paraná; RJ: Rio de Janeiro; SP: São Paulo.

Table 2. Primer sequences for PCR amplification and sequencing.

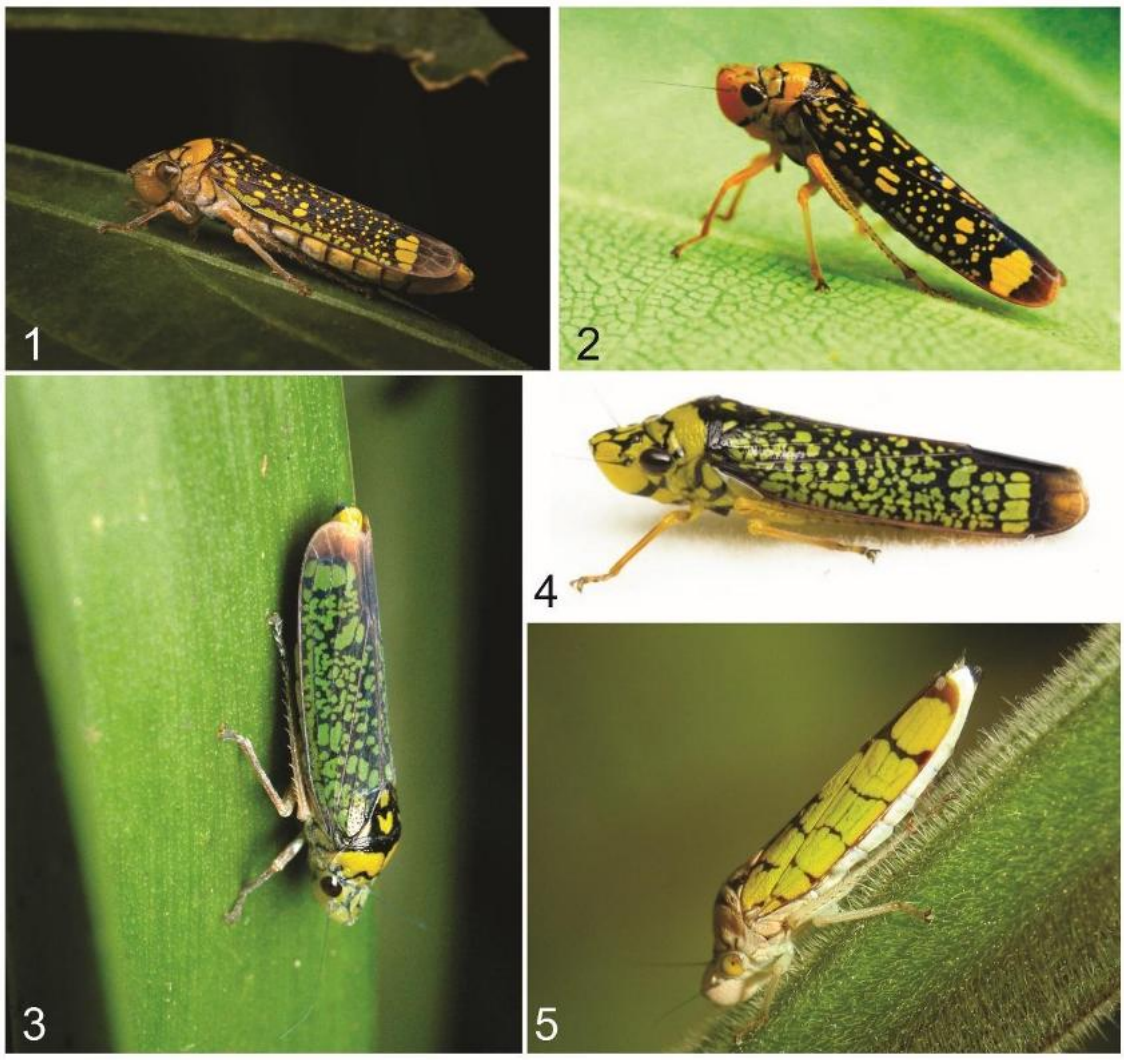
Gene segment	Primer name	Primer sequence (5'–3')	Reference
COI	LCO1490	GGTCAACAAATCATAAAGATATTGG	Folmer et al., 1994
	HCO2198	TAAACTTCAGGGTGACCAAAAAATCA	Folmer et al., 1994
	Ron	GGATCACCTGATATAGCATTCCC	Monteiro & Pierce, 2001
	Nancy	CCCGGTAAAATTAAAATATAAACTTC	Monteiro & Pierce, 2001
	COIa+ (C1-J-1718)	GGAGGATTTGGAAATTGATTAGTTCC	Simon et al., 1994
ITS2	58F (CAS5p8sFc)	TGAACATCGACATTTYGAACGCACAT	Jie et al., 2003
	28B (CAS28sB1d)	TTCTTTTCCTCCSCTTAYTAATATGCTTAA	Jie et al., 2003



Appendix S1. Ultrametric tree of COI sequences (~383 bp) of *Aulacizes* obtained with BEAST2 and used in species delimitation analyses with the SPdel pipeline.



Appendix S2. Ultrametric tree of ITS2 sequences (~616 bp) of *Aulacizes* obtained with BEAST2 and used in species delimitation analyses with the SPdel pipeline.



Figs. 1–5. Live individuals of *Aulacizes conspersa*, *A. persistans* **sp. reval.**, and *A. repanda* **sp. reval.** (1) *A. conspersa* (Viçosa, Minas Gerais State); (2) *A. conspersa* (Parque Estadual da Pedra Branca, Rio de Janeiro, Rio de Janeiro State); (3–4) *A. persistans* **sp. reval.** (Parque Nacional da Serra dos Órgãos, Teresópolis, Rio de Janeiro State); (5) *A. repanda* **sp. reval.** (São José dos Pinhais, Paraná State). Photographs taken by Frederico F. Salles (1), André Luis D. Ferreira (2), André A. Alves (3 and 4), and Alexandre C. Domahovski (5).

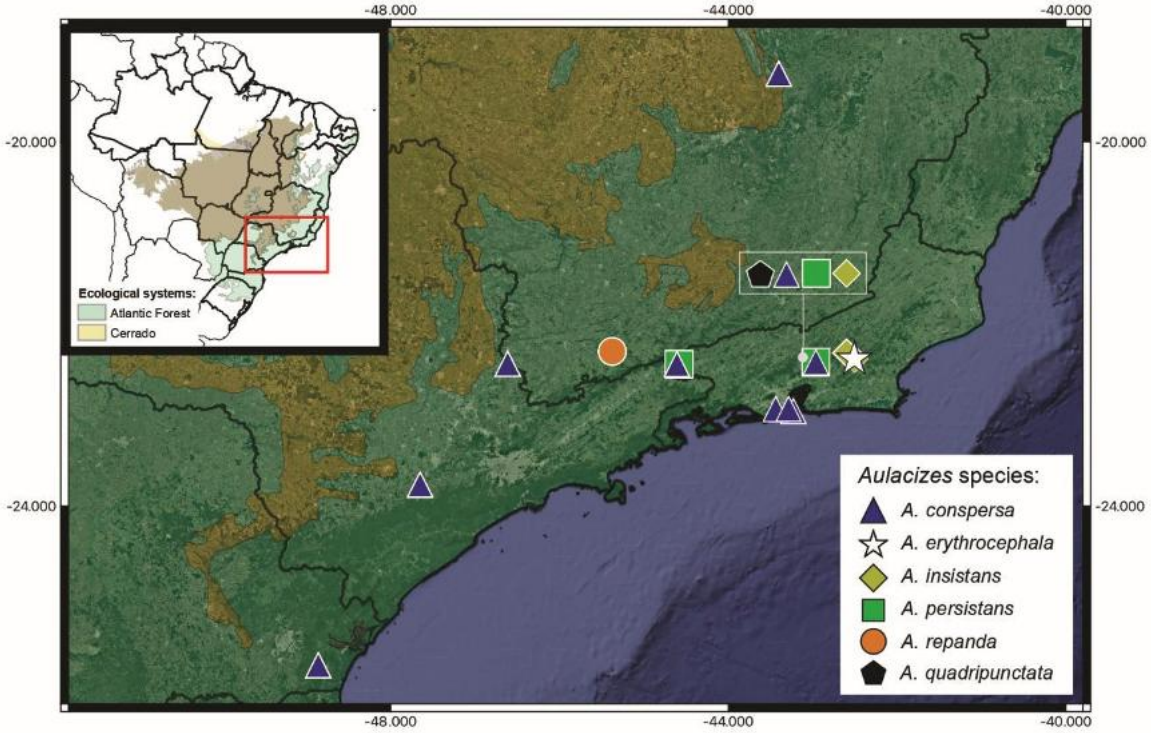


Fig. 6. Distribution of sampled *Aulacizes* specimens (vouchers) in the Atlantic Forest of Southeastern and Southern Brazil.

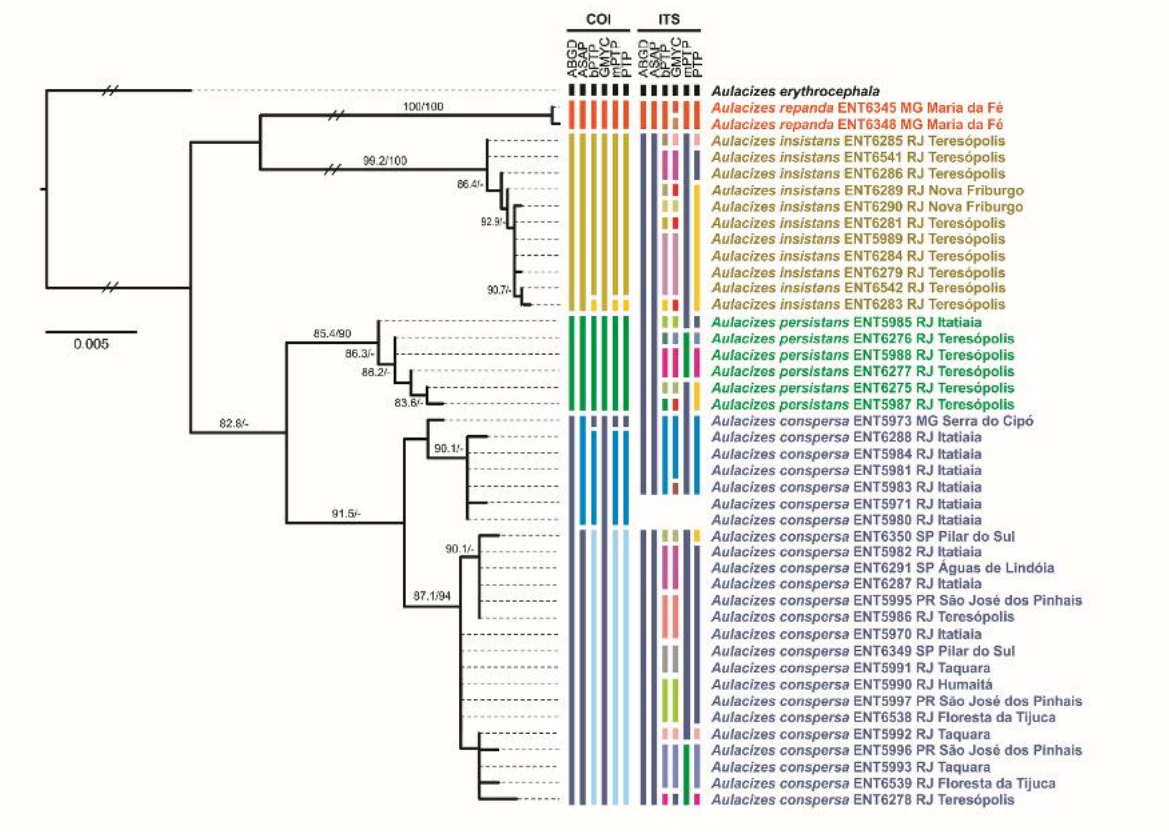
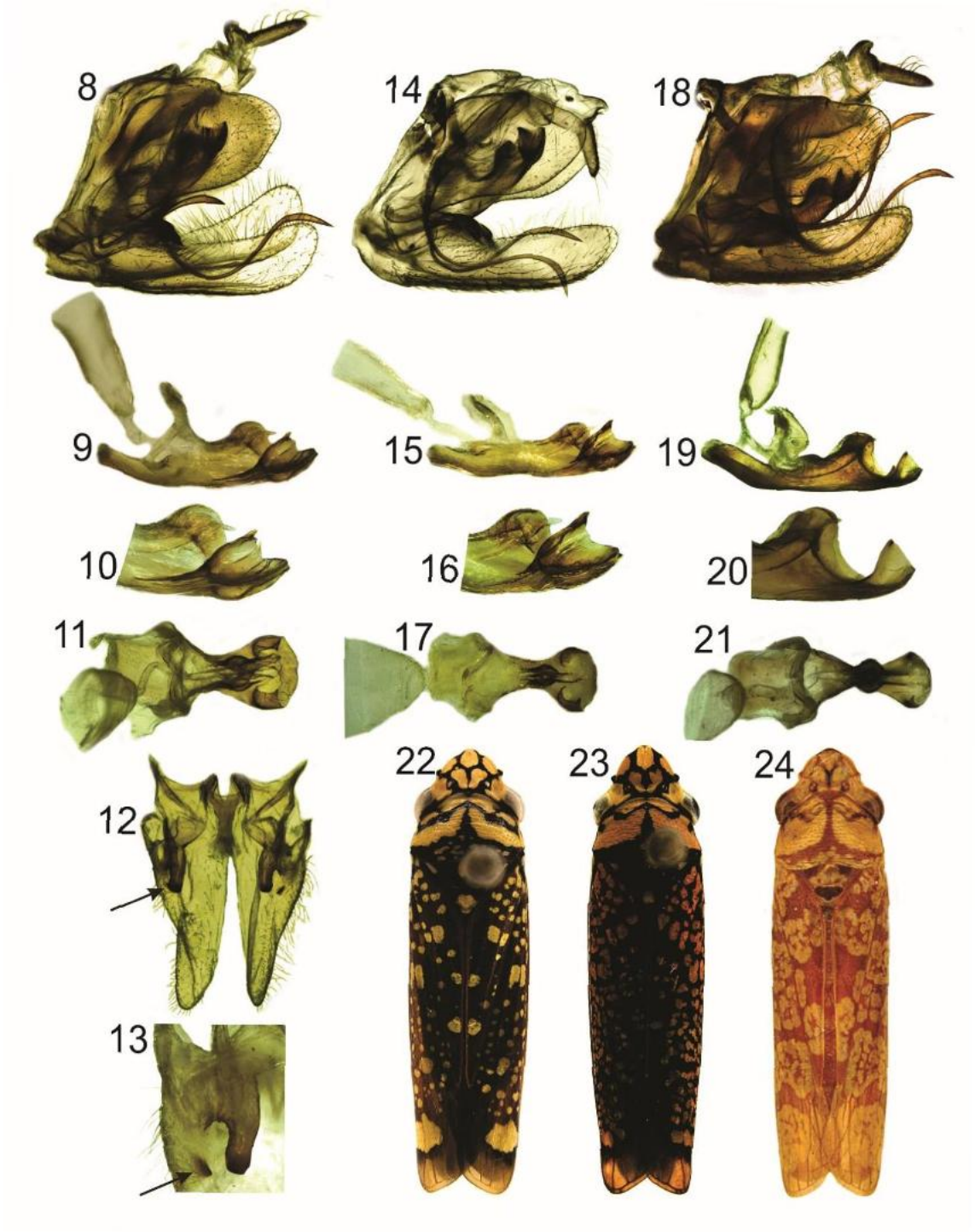
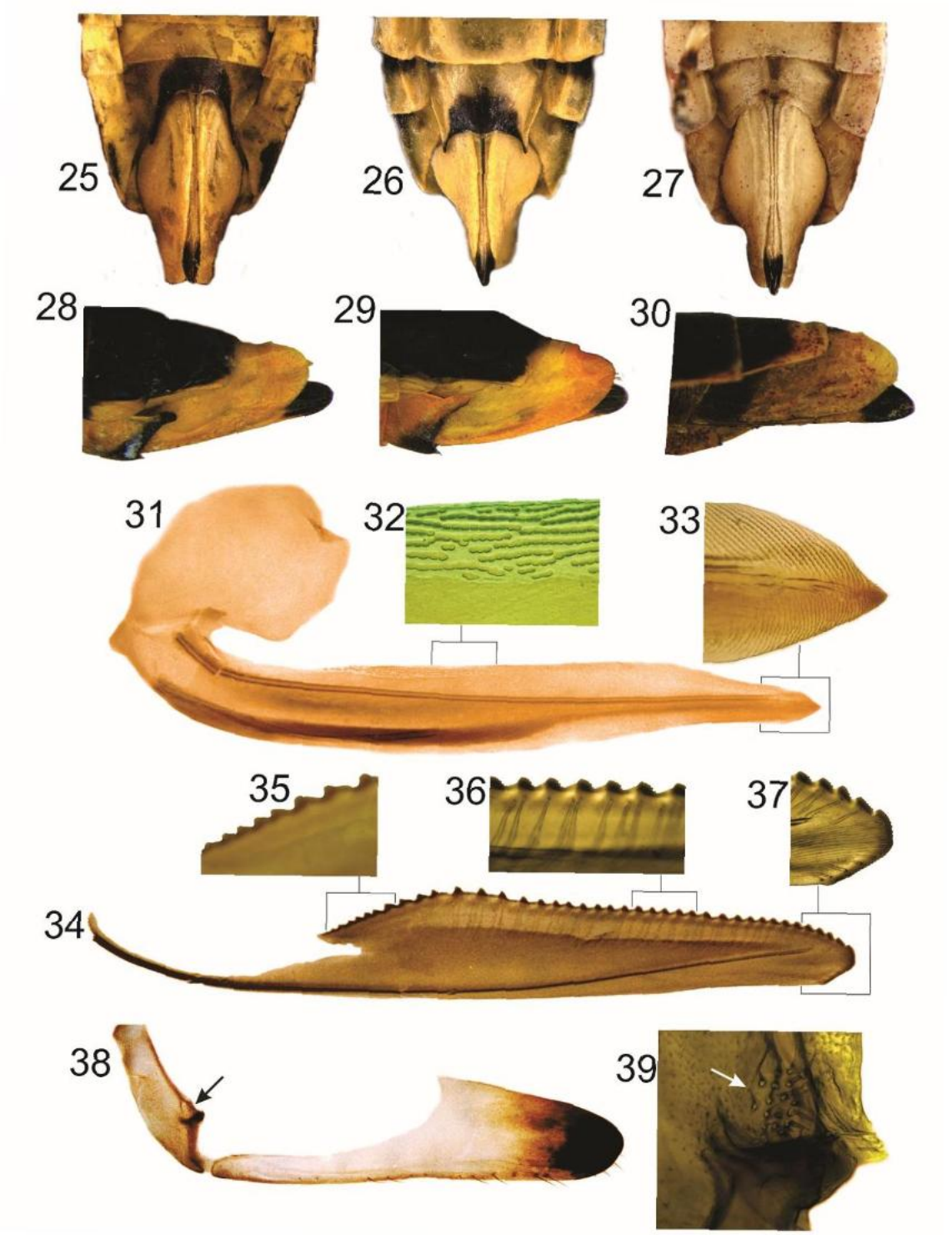


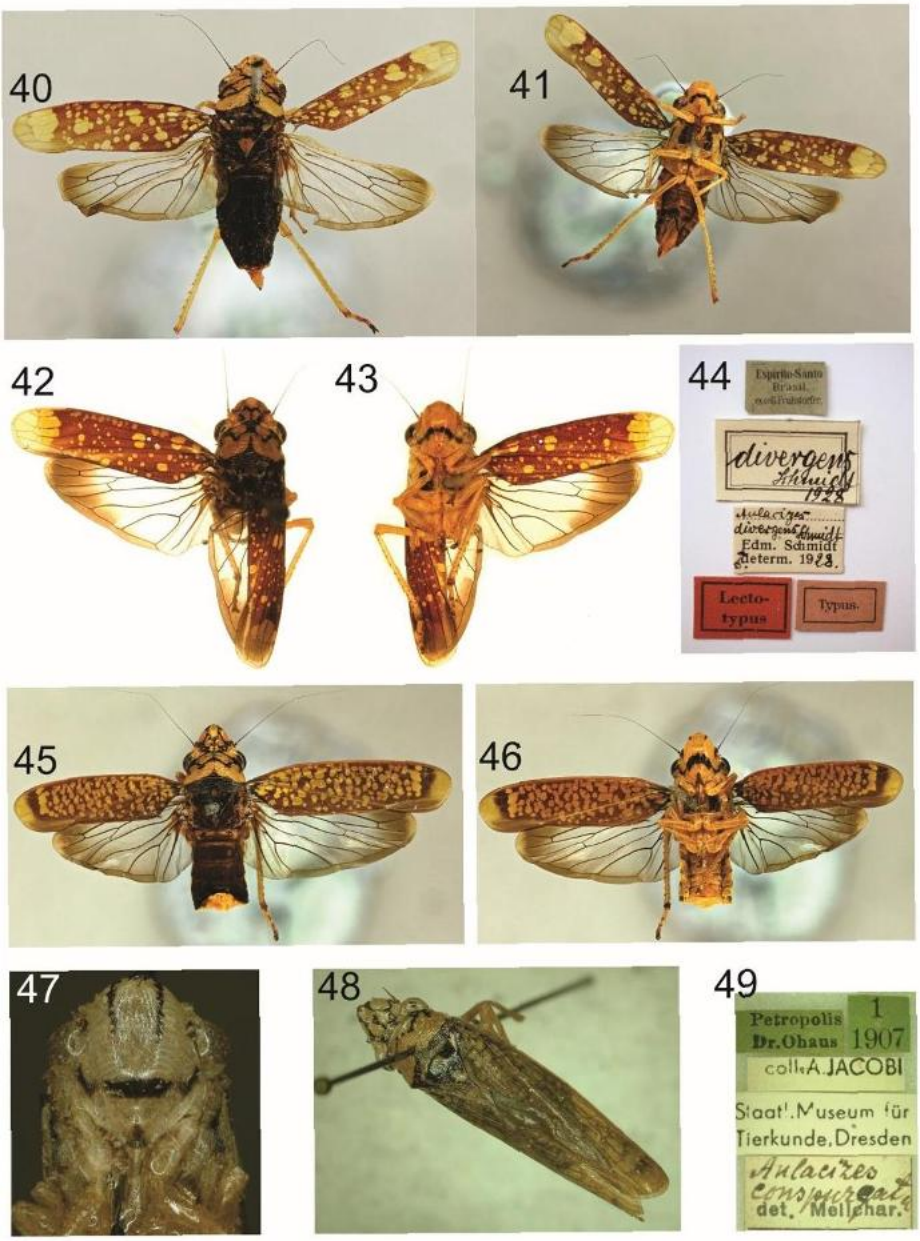
Fig. 7. Maximum likelihood tree (-lnL = 1892.769) of the concatenated dataset based on the mitochondrial cytochrome c oxidase subunit I (COI) (~383 bp) and nuclear ribosomal ITS2 (~616 bp) of *Aulacizes* species. Support values are above branches (SH-aLRT / UFBoot). The results of the six species delimitation methods employed are associated with the tree in a comparative way. Each vertical bar corresponds to the summary of the results of a method as follows: ABGD: Automatic Barcode Gap Discovery; ASAP: Assemble Species by Automatic Partitioning; GMYC: Generalized Mixed Yule Coalescent; bPTP: Bayesian Poisson Tree Processes; mPTP: multi-rate Poisson Tree Processes; PTP: Poisson Tree Processes.



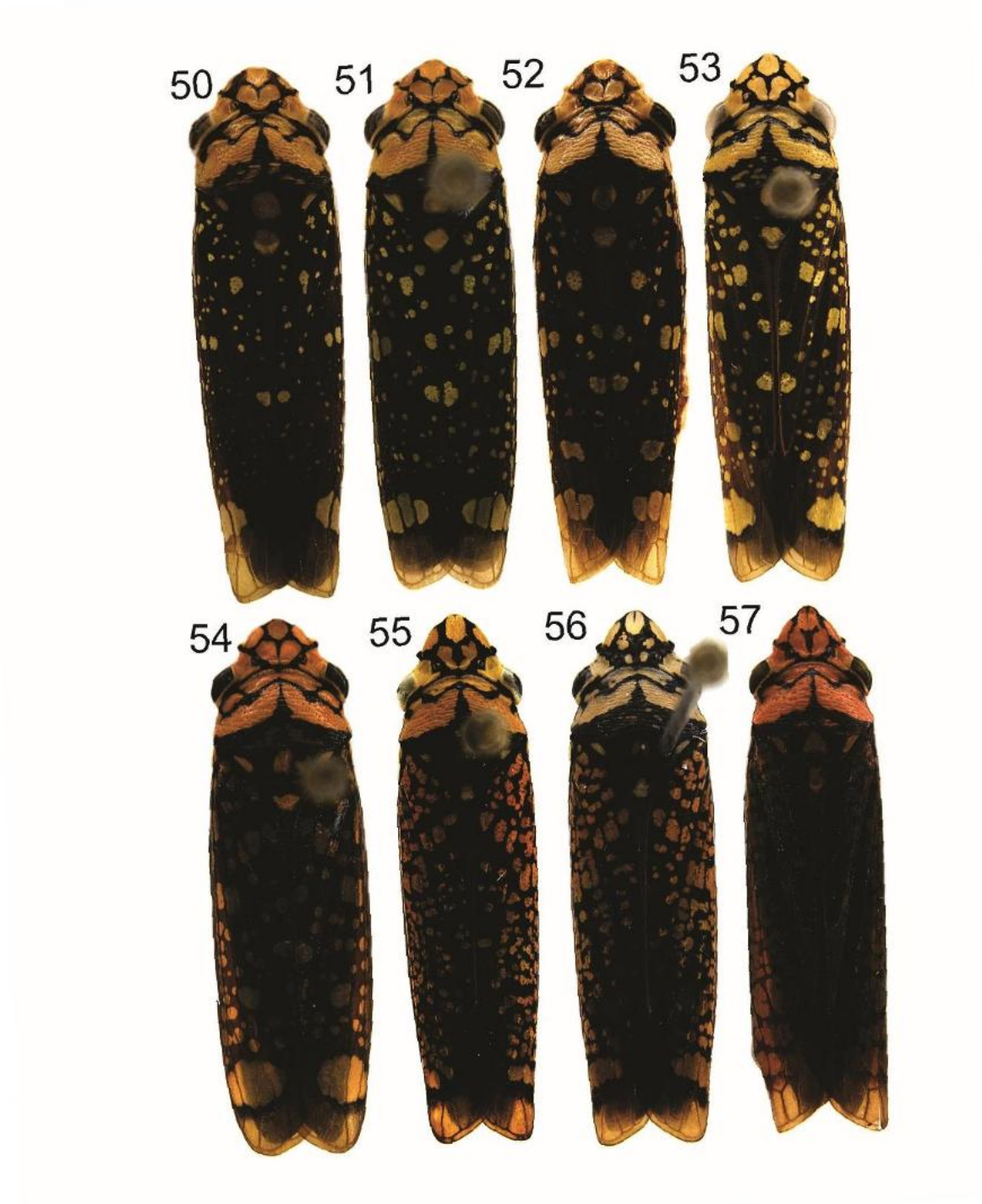
Figs. 8–24. Male terminalia and body (dorsal view) of *Aulacizes conspersa* (8–13, 22, length: ♂♂ 11.67–13.40, ♀♀ 14.07–14.11 mm), *A. persistans* (14–17, 23, length: ♂♂ 13.04–14.37, ♀♀ 14.66–14.81 mm), and *A. repanda* (18–21, 24, length: ♂♂ 10.92–11.29, ♀♀ 11.80–12.20 mm). Terminalia: (8, 14, 18) genital capsule, lateral view; (9, 15, 19) ejaculatory bulb and aedeagus, lateral view; (10, 16, 20) apical portion of aedeagus, lateral view; (11, 17, 21) ejaculatory bulb and aedeagus, dorsal view; (12) subgenital plates, connective, and styles, dorsal view; (13) dorsal dentiform projection at basal half of subgenital plate associated with style apex. Arrows indicate location of dentiform projection.



Figs. 25–39. Female terminalia of *Aulacizes conspersa* (25, 28, 31–39), *A. persistans* (26, 29), and *A. repanda* (27, 30). (25–30) Apical portion of abdomen in ventral and lateral views; (31) valvifer I and valvula I, lateral view (ramus of valvula I damaged); (32) dorsal sculptured area at basal portion; (33) apical portion, showing dorsal and ventral sculptured areas; (34) valvula II, lateral view (ramus incomplete); (35–37) teeth at basal, median, and apical portions, respectively (denticles and ducts shown in Figs. 36 and 37); (38) valvifer II and gonoplac, lateral view; (39) sensory field adjacent to articulation point of valvifer II. Arrows indicate location of sensory field.

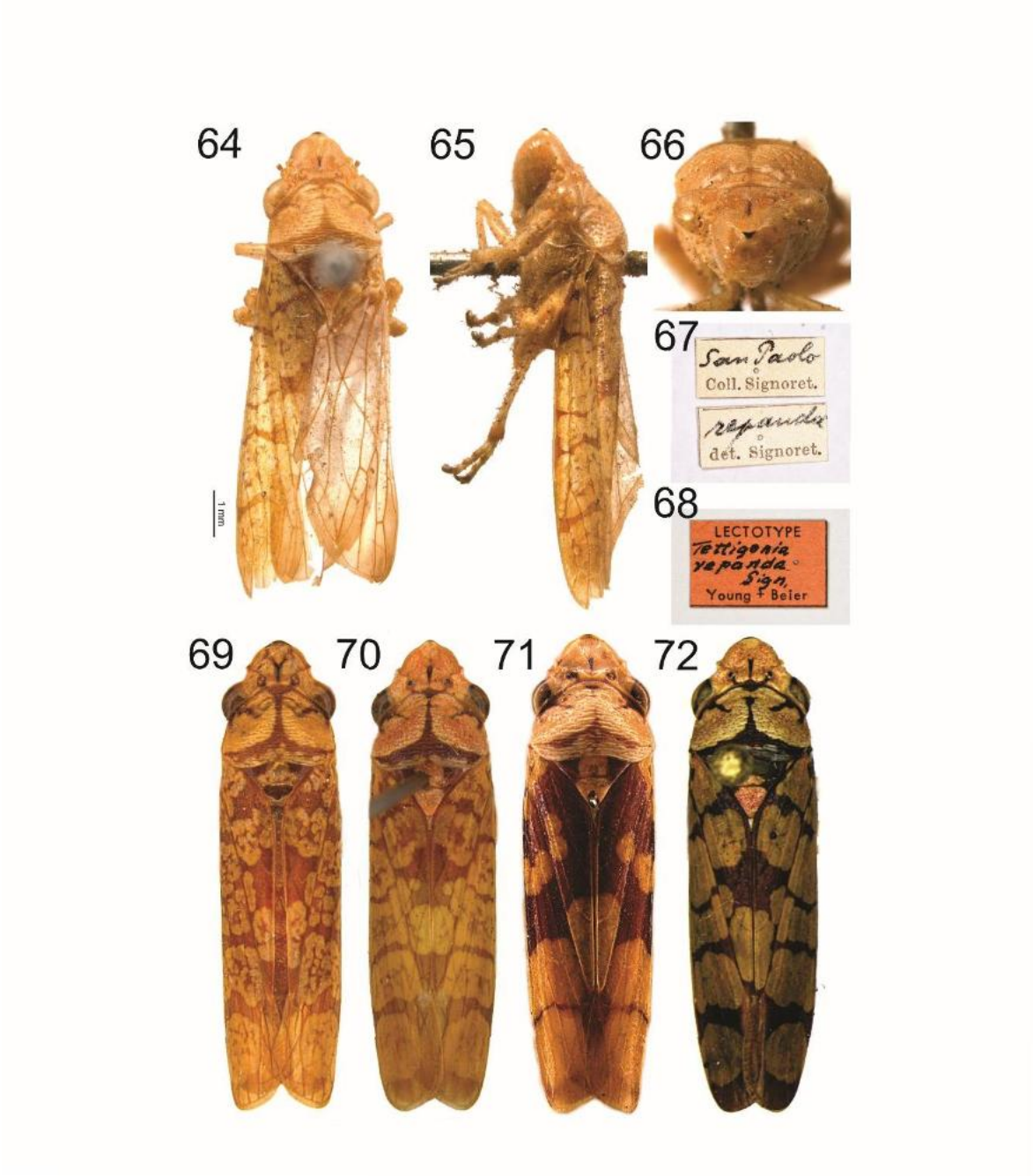


Figs. 40–49. Photographs of type specimens. (40–41) Dorsal and ventral views of female lectotype of *Aulacizes conspersa* Walker, 1851 (©The Natural History Museum, London; Michael D. Webb and Valerie Lemaitre); (42–44) dorsal and ventral views, and labels, of male lectotype of *A. divergens* Schmidt, 1928 (©Museum and Institute of Zoology, Polish Academy of Sciences, Warsaw; Przemysław D. Szymroszczyk); (45–46) ventral and dorsal views of male lectotype of *Proconia persistans* Walker, 1858 (©The Natural History Museum, London; M. D. Webb and V. Lemaitre); (47–49) face in ventral view, body in dorsal view, and labels of female holotype of *A. conspurcata* Melichar, 1926 (©Senckenberg Museum, Dresden; Christian Schmidt). The present study indicates that *A. divergens* is a junior synonym of *A. conspersa*, whereas *A. conspurcata* is a junior synonym of *A. persistans*.



Figs. 50–57. Dorsal habitus of individuals of *Aulacizes conspersa* and *A. persistans* **sp. reval.** Interspecific difference in the distribution of spots on forewings, which is in accordance with the result of the species delimitation analysis (see Fig. 7). (50–54) *A. conspersa* (Minas Gerais, São Paulo, Paraná, and Rio de Janeiro states, including Teresópolis); (55–57) *A. persistans* (Teresópolis, Rio de Janeiro State). (50) ENT5973; (51) ENT6288; (52) ENT5971; (53) ENT5992; (54) ENT6278; (55) ENT6276; (56) ENT6275; (57) ENT5987.

Figs. 58–63. Face of *Aulacizes conspersa* and *A. persistans* **sp. reval.** Interspecific difference at the clypeus apex (with or without black spot), which is in accordance with the result of the species delimitation analysis (see Fig. 7). (58–60) *A. conspersa* (Minas Gerais, São Paulo, Paraná, and Rio de Janeiro, including Teresópolis); (61–63) *A. persistans* **sp. reval.** (Teresópolis, Rio de Janeiro State). (58) ENT5992; (59) ENT6278; (60) ENT6288; (61) ENT6275; (62) ENT6276; (63) ENT5987.



Figs. 64–72. (64–68) Male lectotype of *Tettigonia repanda* Signoret, 1855 (©Natural History Museum, Hemiptera Image Collection, Vienna; Harald Bruckner); (64) dorsal view; (65) lateral view; (66) anterior view; (67) labels of the specimen; (68) lectotype label added by David A. Young. (69–72) dorsal habitus of males (69–70) and females (71–72) of *Aulacizes repanda* **sp. reval.** showing variation in the distribution of spots on the forewings. The results of the present study support the revalidation of this species.

ARTICLE II*

Taxonomic review and phylogenetic analysis of the genus *Aulacizes* Amyot & Serville, 1843 (Hemiptera: Cicadellidae: Cicadellinae: Proconiini)

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*Manuscript not yet submitted.

Abstract

Aulacizes Amyot & Serville, 1843 is a genus of Neotropical sharpshooters recorded from Northeastern, Southeastern, and Southern Brazil and Argentina, with nine recognized species, whose taxonomy remains poorly understood. In this study, we performed a comprehensive taxonomic revision of the genus, together with a phylogenetic analysis based on morphological (92 characters) and molecular (four genes: 16S, H3, COI, and COII) data. The taxonomic revision resulted in the removal of three species from *Aulacizes* (*A. basalis* Walker, 1851, *Tettigonia clypeata* Signoret, 1855, and *Tettigonia maculifrons* Signoret, 1855), proposing the tentative new combinations *Pseudometopia basalis* **comb. nov.** and *Deselvana clypeata* **comb. nov.**, reinterpretation of *A. nigriceps* Schmidt, 1928 **stat. nov., sp. rev.**, which was previously synonymized with *A. conspersa* Walker, 1851, establishment of generic limits, and updating of the number of known species. Phylogenetic analyses recovered *Aulacizes* as monophyletic and the clade *Proconosama* + (*Paraulacizes* + *Pseudometopia*) as its sister group, partially corroborating previous studies. This is the first detailed study dedicated to the genus; the analyses revealed new relationships among species and highlighted the importance of specific morphological characters in defining taxa. The male terminalia of *Aulacizes* species are useful for the genus recognition when compared with those of *Paraulacizes*, *Proconosama*, and *Pseudometopia*. However, the identification of *Aulacizes* species based on the male and female terminalia remains somewhat difficult, since they are very similar to each other, presenting few interspecific variations. Therefore, it is easier to identify *Aulacizes* species by their color pattern. In addition to detailed redescriptions of *Aulacizes* species, a key to species, new geographic records, and distribution maps are provided.

Keywords: Atlantic Forest, Neotropical region, leafhoppers, morphology, systematics.

Introduction

Amyot & Serville (1843), in the "Hémiptères" part of the "*Histoire Naturelle des Insectes*," treated ten genera of the "*Tettigonides*," a group roughly equivalent to the Cicadellinae. The South American genus *Aulacizes* was included in this group (p. 571) and diagnosed; *Tettigonia quadripunctata* Germar, 1821 was the only species included in *Aulacizes* and its diagnosis was also provided; hence, the latter is considered the type-species by monotypy (Young 1968, McKamey 2007). Subsequently, species assigned to *Aulacizes* were described by a few authors (Walker 1851, 1858, Signoret 1855, Schmidt 1928, Melichar 1926). Young (1968), in his detailed revision of the Proconiini, redescribed *Aulacizes* considering features of the head, thorax, male and female terminalia; he recognized eight valid species, viz., *A. basalis* Walker, 1851, *A. clypeata* (Signoret, 1855), *A. conspersa* Walker, 1851, *A. conspurcata* Melichar, 1926, *A. divergens* Schmidt, 1928, *A. insistans* (Walker, 1858), *A. obsoleta* Melichar, 1926, and *A. quadripunctata* (Germar, 1821).

Mejdalani et al. (2006), based on consistent color pattern differences, revalidated *A. erythrocephala* (Germar, 1821) from the synonymy of *A. quadripunctata*. Pecly et al. (2025), employing molecular and morphological data, carried out a species delimitation study of the "*A. conspersa* complex" and proposed several nomenclatural changes, including the revalidation of *A. repanda* (Signoret, 1855) and *A. persistans* (Walker, 1858), previously synonymized with *A. conspersa* (see Young 1968). Also, *A. conspurcata* was synonymized with *A. persistans* and *A. divergens* was synonymized with *A. conspersa*. Therefore, the following nine *Aulacizes* species are currently recognized as valid: *A. basalis*, *A. clypeata*, *A. conspersa*, *A. erythrocephala*, *A. insistans*, *A. obsoleta*, *A. persistans*, *A. quadripunctata*, and *A. repanda*. The genus was catalogued or listed, among others, by Metcalf (1965), Zanol & de Menezes (1982), Oman et al. (1990), McKamey (2007), Wilson et al. (2009), Dmitriev et al. (2022 onward), and Takiya et al. (2024).

Aulacizes is distributed in Northeastern, Southeastern, and Southern Brazil and Argentina, with a record from Venezuela (*A. basalis*) that is most probably erroneous (Young 1968, Mejdalani et al. 2006). Specimens of this genus are quite common in the Brazilian Atlantic Forest. Some *Aulacizes* species were associated in Brazil with the possible transmission of the phytopathogenic bacterium *Xylella fastidiosa* Wells et al., 1987 (Azevedo-Filho & Carvalho 2006, Ringenberg et al. 2010, Paris et al. 2012, Schneider et al. 2017): *A. conspersa*, *A. obsoleta*, and *A. quadripunctata* in citrus orchards (*Citrus sinensis* (L.) Osbeck, Rutaceae); *A. conspersa*, *A. obsoleta*, and *A. quadripunctata* in grapevine

orchards (*Vitis* spp., Vitaceae); and *A. obsoleta* in plum orchards (*Prunus salicina* Lindl., Rosaceae).

Despite the above-mentioned studies, the taxonomic comparative information on *Aulacizes* species remains somewhat fragmentary. For instance, Young (1968) provided more complete sets of illustrations only for *A. quadripunctata* and *A. obsoleta* (including the head and pronotum in dorsal view, pygofer and aedeagus in lateral view, connective and style in dorsal view, and female sternite VII in ventral view). However, unfortunately, little information and illustrations were provided for other species of the genus such as *A. conspersa* (only the pygofer and aedeagus in lateral view), *A. basalis* (only the head, pronotum, and mesonotum in dorsal view and female sternite VII in ventral view), and *A. insistans* (only the aedeagus in lateral view). After studying the male terminalia and female sternite VII within *Aulacizes*, Young (1968) concluded that these structures do not appear to offer conclusive specific characters and that external characters are variable. For these reasons, he did not attempt to develop a taxonomic key to the species of the genus.

After the publication of Young's (1968) monograph, members of the genus *Aulacizes* were treated in a few publications, such as Mejdalani et al. (2006) (see above), Azevedo-Filho & Carvalho (2006), and Dellapé (2016). Azevedo-Filho & Carvalho (2006) described in detail and illustrated three *Aulacizes* species associated with citrus orchards in Southern Brazil (*A. conspersa*, *A. obsoleta*, and *A. quadripunctata*). Dellapé (2016) described the female terminalia of twelve species of Proconiini and provided a key to the identification of genera recorded from Argentina, including male and female characters; in her article, the structures of the female terminalia of four species of *Aulacizes* were described and illustrated (*A. basalis*, *A. conspersa*, *A. insistans*, and *A. quadripunctata*).

Concerning generic relationships within the Proconiini, Young (1968) considered *Aulacizes* as closely related to *Paraulacizes* Young, 1968 and *Pseudometopia* Schmidt, 1928 based on general morphology. According to him, *Aulacizes* could be distinguished from these two genera by the incomplete hind wing vein R_{2+3} and the aedeagus, which is not inflated and bears a ventral scoop-shaped apical process (Young 1968, Mejdalani et al. 2006). Indeed, the scoop-shaped process is apparently a unique feature of *Aulacizes*, but an uninflated aedeagus also occurs in *Paraulacizes* and other similar genera, such as *Depanana* Young, 1968, *Depanisca* Young, 1968, *Procama* Young, 1968, and *Proconosama* Young, 1968. Furthermore, the presence of a process on the male pygofer, of dorsal origin, is apparently a homologous feature shared by these genera; this process shows a considerable

variation in shape and size (see Young 1968), which can be useful for generic diagnoses. More recently, Feng et al. (2024), in their study on the molecular phylogeny and biogeography of the Cicadellinae, included two *Aulacizes* terminals (*A. quadripunctata* and *Aulacizes* sp.) and recovered *Aulacizes* as the sister group of *Pseudometopia* + *Proconosama*, this clade being the sister group of *Paraulacizes*, with high branch support. These results partially corroborate Young's (1968) suggestions based on raw morphology. Currently, it appears to us that the boundaries of *Aulacizes* and related genera are not entirely clear, so that in-depth morphological and molecular comparative studies are still necessary.

The identification of most *Aulacizes* species remains difficult because detailed comparative redescriptions are still needed, including complete sets of drawings of the male and female terminalia. Therefore, a formal taxonomic revision of *Aulacizes* is necessary to ensure the correct identification of its species, including those of possible economic importance (see above). A new diagnosis of the genus is also necessary. Accordingly, here we redescribe *Aulacizes* and its known species (with the exception of those recently treated by Mejdalani et al. 2006 and Pecly et al. 2025). An updated list of species and a dichotomic key to their identification are provided, as well as distribution maps. In addition, we assembled morphological and molecular data to investigate the phylogenetic relationships within *Aulacizes* and of this genus with related taxa (*Depanana*, *Depanisca*, *Paraulacizes*, *Procama*, *Proconosama*, and *Pseudometopia*).

Material and methods

Specimens sampling

A total of 384 specimens of *Aulacizes* was studied here. These specimens belong to the following collections: Coleção Entomológica Pe. Jesus Santiago Moure, Departamento de Zoologia, Universidade Federal do Paraná, Curitiba (DZUP); Coleção Entomológica Prof. José Alfredo Pinheiro Dutra, Departamento de Zoologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro (DZRJ); Departamento de Entomologia, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro (MNRJ); Museu de Entomologia "Luiz de Queiroz", Escola Superior de Agricultura "Luiz de Queiroz", Universidade de São Paulo, Piracicaba (MELQ); and Museu de Zoologia, Universidade de São Paulo, São Paulo (MZSP). Identification of specimens was based on examination of the external morphology and male terminalia, using the most recent contributions on *Aulacizes* (Young 1968, Mejdalani et al. 2006, Dellapé 2016, Pecly et al. 2025), original descriptions (Walker 1851,

1858, Signoret 1855, Schmidt 1928, Melichar 1926), and, most importantly, photographs of type specimens. The latter were provided by the following institutions: The Natural History Museum, London (NHM), Naturhistoriska Riksmuseet, Stockholm (NHRS), Museum and Institute of Zoology, Warsaw (ZMPA), and Ivan Franko National University, Lviv (IFNU).

Terminology and techniques for preparation of specimens

Techniques for preparation of genital structures followed mainly those of Oman (1949) for males and Mejdalani (1998) for females. Dissected parts were stored in small vials with glycerin, as suggested by Young & Beirne (1958). The morphological terminology adopted here followed mainly Young (1968, 1977, 1986), except for the head (Hamilton 1981, Mejdalani 1993, 1998) and female terminalia (Nielson 1965, Hill 1970). Use of the term gonoplac followed Mejdalani (1998). The total length of specimens was measured from the apex of the crown to the tips of the forewings at rest position (Young 1977). Photographs of the body in different focal planes were taken using a Leica M205 stereomicroscope and stacked with Leica LASX software, whereas photographs of male and female terminalia were taken using a ZEISS SmartZoom5 automated digital microscope. Using the online tool SimpleMappr (Shorthouse 2010), we prepared maps to show the distribution of species of *Aulacizes*. Records were obtained from specimens deposited in DZRJ, DZUP, MELQ, MNRJ, and MZSP, as well as from the literature (Azevedo-Filho 2004, Mejdalani et al. 2006, Mejdalani et al. 2009, Ringenberg et al. 2010, Paris et al. 2012, Paradell et al. 2012, Tolotti et al. 2012, Peruzo et al. 2013, Olizeski 2013, Azevedo-Filho et al. 2016, Dellapé 2016, Froza 2017, Czeikoski et al. 2017, Schneider et al. 2017).

Sequence data

Genomic DNA extraction was carried out from one hind leg of adult specimens using the DNeasy Blood & Tissue extraction kit (Qiagen Inc., Hilden, Germany), optimizing the original protocol by incubating the tissue for lysis in Proteinase K for 48 hours and generating two separate 50µL elutions of DNA extract, instead of a single 100µL elution. Twelve specimens collected from 2012 to 2023, pinned or preserved in ethanol, representing a total of eleven *Aulacizes* species and one out group, had their DNA extracted and subsequently PCR and sequencing were performed. Voucher specimens were pinned and deposited in DZRJ, DZUP, MELQ, and MNRJ (Table 1).

The same molecular markers studied by Takiya (2007) were employed here, viz., the nuclear gene histone H3 subunit and three mitochondrial genes (16S rDNA, cytochrome oxidase subunit I (COI), and cytochrome oxidase subunit II (COII)). All PCR reactions had a total volume of 25µL and contained 12.9µL of DEPC water (Ambion), 5µL of Green Taq Buffer (Promega), 3.5µL of $MgCl_2$ (25mM, Promega), 0.5 µL of dNTP (20mM, Promega), 1µL of each primer (10pmol/L), 0.1µL of Taq Polymerase (5U/µL, Promega), and 1 µL of genomic DNA. Amplifications of COI, COII, 16S, and H3 were performed with a thermocycling profile that consisted of 3 min at 94°C, followed by 35 cycles of 1 min at 94°C, 1 min at 50°C, 2 min at 72°C, and a final step of 7 min at 72°C. PCR and sequencing primers used are given in Table 2. PCR products were stained with GelRed™ diluted 1000X (Biotium) and underwent agarose gel electrophoresis in 1.0% TBE; these products were visualized under UV light. Successfully amplified PCR samples were purified using ExoSAP-IT® (USB Affymetrix) and were subsequently sent for sequencing at Macrogen (Seoul, South Korea).

Electropherograms obtained were assembled and edited using GeneStudioTM Professional v.2.2.0.0 software. Consensus sequences were tested for correct marker amplification and rule out contamination using BLAST (Basic Local Alignment Search Tool) in GenBank. Sequences generated here were deposited in GenBank. Alignments were obtained using the consensus sequences generated and including outgroups available from Feng et al. (2024) (Table 1). COI (749bp), COII (588bp), and H3 (294bp) sequences were aligned with ClustalW (Thompson et al. 1994) implemented in MEGA11 (Tamura et al. 2021). Amino acid translations were conducted to check for the absence of stop codons. 16S (488bp) sequences were aligned with the MAFFT v.7.222 program (Katoh et al. 2019) on its online platform with the FFT-NS-i alignment algorithm (https://mafft.cbrc.jp/alignment/server/). Unfortunately, we were not able to obtain representatives of *A. nigriceps* Schmidt, 1928 **stat. nov., sp. rev.** for molecular analyses. The software SequenceMatrix v1.6.7 (Vaidya et al. 2011) was used to concatenate alignments. Alignments are available in the Supplementary Material.

Matrices were partitioned by marker and codon position (for COI, COII, and H3). Bayesian inference (BI) and maximum likelihood (ML) analyses were run for two different datasets: concatenated (molecular) and combined (molecular + morphology). The selection of the best evolutionary model for each partition was carried out considering the Bayesian information criterion (BIC) through ModelFinder (Kalyaanamoorthy et al. 2017), which is

implemented in IQ-TREE 2.2.2.7 (Minh et al. 2020) for ML. The substitution models selected and applied for each partition of the concatenated (molecular) and combined (molecular + morphology) data matrices in the ML analyses were as follows: (1) 16S: K3Pu+F+G4; (2) COI_pos1 + COII_pos1: TN+F+G4; (3) COI_pos2 + COII_pos2 + H3_pos1 + H3+pos2: HKY+F+I; (4) COI_pos3 + COII_pos3: TPM2u+F+R2; (5) H3_pos3: TPM2u+F+G4; and (6) morphology: MK+ASC+G4. For BI analysis, the command reference "-mset mrbayes" was used, which restricted the selection of models to the MrBayes program as follows: (1) 16S: GTR+F+G4; (2) COI_pos1 + COII_pos1: GTR+F+G4; (3) COI_pos2 + COII_pos2 + H3_pos1 + H3_pos2: HKY+F+I; (4) COI_pos3 + COII_pos3: HKY+F+R2; (5) H3_pos3: HKY+F+G4; and (6) morphology: MKv+G.

Morphological data

Morphological characters of the head, thorax, and male terminalia were studied. Hypotheses of primary homology (De Pinna 1991) were generated and subsequently coded in a data matrix using the software Mesquite (Maddison & Maddison 2023). Characters were composed considering the four fundamental functional components proposed by Sereno (2007). Missing data were coded as '?' and non-comparable conditions were coded as "-". The codification of *Proconosama takiyae* Mejdalani, Cavichioli & Carvalho, 2012 was conducted based on photographs of the holotype and the original species description (Mejdalani et al. 2012).

Phylogenetic analyses

Phylogenetic analyses were conducted based on three different data matrices: (1) morphological dataset with 21 terminal taxa analyzed with parsimony (MP); (2) concatenated molecular dataset with 17 terminal taxa analyzed with maximum likelihood (ML) and Bayesian inference (BI); and (3) combined molecular and morphological dataset with 24 terminal taxa analyzed with ML and BI. The combined matrix included 9 species of *Aulacizes* (Table 1) and 15 species employed as outgroups, 14 of them from the tribe Proconiini stricto sensu (*Depanana bugabensis* (Fowler, 1898), *Depanisca sulcata* (Signoret, 1855), *Paraulacizes figurata* (Fowler, 1898), *P. irrorata* (Fabricius, 1794), *P. mutans* (Signoret, 1855), *Proconosama alalia* (Distant, 1908), *P. columbica* (Signoret, 1855), *P. takiyae* Mejdalani, Cavichioli & Carvalho, 2012, *Pseudometopia amblardii* (Signoret, 1855), *P. appendiculata* Schmidt, 1928, *P. irenae* Young, 1968, *P. latifascia*

(Walker, 1851), *P. phalaesia* (Distant, 1908), and *P. transversa* Young, 1968); *Oncometopia orbona* (Oncometopiini sensu Takiya 2007) was used for rooting the trees. These outgroups were selected based on the results of a combined analysis (morphological + molecular data) containing all genera of the Proconiini (Takiya 2007) and of the concatenated analysis (H3, cox1, cox2, 16S, and 28S) of the Cicadellinae (Feng et al. 2024).

Parsimony (MP) analysis was conducted in TNT 1.5 (Goloboff & Catalano 2016) using the traditional search algorithm, with 10,000 replicates for estimating most parsimonious trees (Goloboff et al. 2008). All characters were treated with equal weights and unordered. The strict consensus method was employed to summarize all resulting most parsimonious trees from the equal weights analysis. Branch support was calculated using the non-parametric bootstrap method with 10,000 pseudoreplicates (Felsenstein 1985). Morphological characters, as well as their consistency index (ci) and retention index (ri) based on the parsimony results, are listed in the results of the phylogenetic analysis. The optimization of morphological characters was carried out in the program WinClada, ver. 1.00.08 (Nixon 2002), using the parsimony criterion. One of the 78 equally most parsimonious trees obtained from the phylogenetic analysis was selected as a representative for character mapping.

Maximum likelihood (ML) analyses were conducted in IQ-TREE (Minh et al. 2020) for the concatenated and combined matrices, with a total of 1,000 ultrafast bootstrap approximations (UFBoot) (Minh et al. 2013) and 1,000 replicates of SH-aLRT (Guindon et al. 2010) for evaluating branch supports. Bayesian inference (BI) was carried out in MrBayes 3.2.6 (Ronquist et al. 2012) for the concatenated and combined matrices, with ten million generations with two independent runs of four Markov chain Monte Carlo (MCMC) chains, a sampling frequency of 1,000, and a burn-in of 25%. The convergence of the runs was assessed in Tracer 1.7 (Rambaut et al. 2018) (ESS > 200). Topological robustness was assessed using posterior probabilities (PP). Support values considered reliable herein were SH-aLRT ≥ 80, UFboot ≥ 95, and PP ≥ 95 (Guindon et al. 2010, Ronquist et al. 2012, Minh et al. 2013). The obtained phylogenetic trees were visualized in Fig Tree v.1.4.4 (Rambaut 2018) and subsequently edited in CorelDraw.

Results

Data matrices for phylogenetic analyses

A total of 92 morphological characters of the head, thorax, abdomen, and male terminalia were coded for 9 terminal taxa of *Aulacizes* and 11 outgroup species (see Appendix S1). Final alignments of the individual molecular markers were as follows: 16S rDNA (488 bp), COI (749 bp), COII (558 bp), and histone H3 (294 bp), each with 17 terminal taxa. The concatenated molecular matrix included a total of eight terminal species of *Aulacizes* and nine outgroup taxa.

List of morphological characters

Head:

1. Crown, ground coloration: (0) yellow; (1) light brown; (2) brown; (3) orange; (4) black; (5) red; (6) brownish-yellow. (ci: 0.857; ri: 0.667).

2. Crown, rugosity: (0) absent; (1) present. Non-informative.

3. Crown, pubescence: (0) present; (1) absent. (ci: 0.333; ri: 0.333).

4. Crown, anterior margin: (0) not carinate; (1) carinate. (ci: 0.333; ri: 0.714).

5. Crown, anterior margin, median sulcus: (0) absent; (1) present. (ci: 0.500; ri: 0.000).

6. Crown, apex, macula: (0) absent; (1) present. (ci: 0.250; ri: 0.571).

7. Crown, apex, macula, reaching facial depression at central portion of frons: (0) absent; (1) present. (ci: 0.333; ri: 0.500).

8. Crown, pair of maculae, near posterior margin including ocelli: (0) absent; (1) present. (ci: 0.500; ri: 0.000).

9. Crown, pair of black bands originating from antennal ledges, extension to posterior margin: (0) not extended; (1) extended over ocelli. (ci: 0.250; ri: 0.400).

10. Crown, coronal suture, triangular brown marking: (0) absent; (1) present. (ci: 0.500; ri: 0.000).

11. Crown, apical area, irregular yellow spots: (0) absent; (1) present. (ci: 0.500; ri: 0.500).

12. Crown, posterior margin, M-shaped elevation: (0) absent; (1) present. (ci: 0.333; ri: 0.714).

13. Crown, dorsal view, frontogenal suture, extension: (0) attaining ocellus; (1) not attaining ocellus. (ci: 0.500; ri: 0.000).

14. Crown, area adjacent to ocelli, longitudinal carina: (0) absent; (1) present. (ci: 0.500; ri: 0.500).

15. Crown, ocelli, position: (0) on imaginary line between anterior angles of compound eyes; (1) before imaginary line. (ci: 0.250; ri: 0.000).

16. Antennal ledge, longitudinal sulcus: (0) absent; (1) present. (ci: 0.333; ri: 0.333).

17. Antennal ledge, dorsal carina, lateral view: (0) present; (1) absent. (ci: 0.500; ri: 0.500).

18. Antennal ledge, apex, direction: (0) distinctly directed ventrally; (1) slightly directed ventrally. (ci: 0.333; ri: 0.500).

19. Frons, profile, shape: (0) rounded; (1) rectilinear. Non-informative.

20. Frons, development: (0) protuberant; (1) not protuberant. (ci: 0.500; ri: 0.000).

21. Frons, superior portion, surface aspect: (0) not medially depressed; (1) medially depressed. (ci: 0.333; ri: 0.333).

22. Frons, superior portion, slight transverse arcuate carina: (0) absent; (1) present. (ci: 0.333; ri: 0.500).

23. Frons, ground color: (0) yellow; (1) light brown; (2) brown; (3) orange; (4) black; (5) red; (6) brownish-yellow. (ci: 0.857; ri: 0.667).

24. Frons, superior portion, yellow maculae: (0) absent; (1) present. Non-informative.

25. Frons, inferior portion, black broad transverse stripe: (0) present; (1) absent. (ci: 0.167; ri: 0.444).

26. Frons, inferior portion, black broad transverse stripe, extension: (0) interrupted medially; (1) continuous. (ci: 0.500; ri: 0.000).

27. Frons, median area, large black spot: (0) absent; (1) present. Non-informative.

28. Clypeus, lateral view, shape: (0) convex; (1) angulate. Non-informative.

29. Clypeus, inferior portion, black macula: (0) present; (1) absent. (ci: 0.143; ri: 0.250).

30. Clypeus, ground color:(0) yellow; (1) light brown; (2) orange; (3) black; (4) red. (ci: 0.500; ri: 0.200).

31. Gena, black macula: (0) absent; (1) present. (ci: 0.200; ri: 0.500).

32. Gena, black maculae, extension: (0) not continuous over frons; (1) continuous over frons. (ci: 0.250; ri: 0.500).

33. Gena, inferior portion, black spot: (0) absent; (1) present. (ci: 0.500; ri: 0.000).

34. Lorum, black macula: (0) absent; (1) present. (ci: 0.333; ri: 0.000).

Thorax:

35. Pronotum, ground color: (0) yellow; (1) light brown; (2) brown; (3) orange; (4) black; (5) brownish-yellow; (6) red. (ci: 0.750; ri: 0.333).

36. Pronotum, surface, punctures: (0) present; (1) absent. (ci: 0.500; ri: 0.000).

37. Pronotum, lateral margins, orientation: (0) slightly divergent anteriorly; (1) convergent anteriorly; (2) parallel. Non-informative.

38. Pronotum, pair of anterior foveae: (0) present; (1) absent. (ci: 0.167; ri: 0.286).

39. Pronotum, posterior margin, shape: (0) slightly concave; (1) distinctly concave; (2) rectilinear. (ci: 0.667; ri: 0.000).

40. Pronotum, anterior margin, narrow transverse line bifurcated laterally behind each eye: (0) absent; (1) present. (ci: 1.000; ri: 1.000).

41. Pronotum, median longitudinal line: (0) absent; (1) present. (ci: 0.333; ri: 0.333).

42. Pronotum, median longitudinal line, color: (0) black; (1) brown. Non-informative.

43. Pronotum, median area, longitudinal line and transverse anterior line bifurcated behind each eye, connection: (0) absent; (1) present. (ci: 1.000; ri: 1.000).

44. Pronotum, anterior third of disc, median black macula: (0) absent; (1) present. Non-informative.

45. Pronotum, posterior margin, black or brown transverse band: (0) absent; (1) present. (ci: 0.250; ri: 0.500).

46. Pronotum, posterior margin, black or brown transverse band, aspect: (0) broad; (1) narrow. (CI: 0.500; RI: 0.000).

47. Pronotum, posterior margin, dark transverse band, color: (0) concolorous to remainder; (1) bordered by irregular yellowish-brown area. (ci: 0.500; ri: 0.000).

48. Pronotum, irregular yellow spots of variable sizes: (0) absent; (1) present. Non-informative.

49. Pronotum, pair of dark brown to black linear markings behind compound eyes: (0) absent; (1) present. (ci: 0.333; ri: 0.000).

50. Pronotum, dorsolateral carina, shape: (0) approximately rectilinear; (1) strongly curved near eye; (2) curved near eye. (ci: 0.500; ri: 0.500).

51. Mesonotum, pubescence: (0) absent; (1) present. (ci: 0.200; ri: 0.000).

52. Mesonotum, ground color: (0) yellow; (1) light brown; (2) brown; (3) black. (ci: 0.500; ri: 0.500).

53. Mesonotum, anterior portion, three yellow spots: (0) absent; (1) present. (ci: 1.000; ri: 1.000).

54. Mesonotum, laterally, black marking: (0) absent; (1) present. (ci: 0.500; ri: 0.000).

55. Scutellum, single yellow spot: (0) absent; (1) present. (ci: 1.000; ri: 1.000).

56. Forewings, pubescence: (0) small quantity (sparse); (1) great quantity (dense). (ci: 0.500; ri: 0.000).

57. Forewings, apical membrane: (0) distinct; (1) indistinct. (ci: 0.167; ri: 0.167).

58. Forewings, apical membrane, extension: (0) apical cells and distal portion of anteapical cells; (1) inner apical cell; (2) distal portion of apical cells. (ci: 0.400; ri: 0.400).

59. Forewings, costal margin, shape of basal portion: (0) almost rectilinear; (1) distinctly curved. Non-informative.

60. Forewings, cross veins between outer anteapical cell and costal margin: (0) absent; (1) present. (ci: 0.167; ri: 0.167).

61. Forewings, claval veins: (0) close to each other or fused to each other at median portion; (1) parallel. Non-informative.

62. Forewings, ground color: (0) bluish-grey; (1) brown; (2) black; (3) dark green. (ci: 1.000; ri: 1.000).

63. Forewings, corium and clavus, yellow spots of distinct sizes: (0) absent; (1) present. (ci: 0.250; ri: 0.500).

64. Forewings, yellow spots: (0) well-delimited; (1) often fused to each other. (ci: 0.500; ri: 0.000).

65. Forewings, large yellow spot from inner anteapical cell to costal margin: (0) absent; (1) present. (ci: 1.000; ri: 1.000).

66. Hind wings, vein R_{2+3}, extension: (0) incomplete; (1) complete. (ci: 0.333; ri: 0.714).

67. Hind legs, femoral setal formula: (0) 2:0:0; (1) 2:1:1. Non-informative.

Abdomen (male terminalia):

68. Pygofer, posterior margin, shape: (0) broadly rounded; (1) narrowly rounded; (2) subtruncate. (ci: 0.667; ri: 0.000).

69. Pygofer, disc, chaetotaxy, macrosetae: (0) present; (1) absent. Non-informative.

70. Pygofer, ventral margin, process: (0) present; (1) absent. (ci: 0.500; ri: 0.000).

71. Pygofer, conjunctiva IX-X, process: (0) absent; (1) present. (ci: 0.500; ri: 0.500).

72. Pygofer, dorsal margin, process: (0) absent; (1) present. (ci: 1.000; ri: 1.000).

73. Pygofer, distal half of process of dorsal margin, aspect: (0) thick; (1) slender or filiform. (ci: 0.500; ri: 0.500).

74. Pygofer, process of dorsal margin, size: (0) short; (1) moderately elongate; (2) extremely elongate. (ci: 1.000; ri: 1.000).

75. Pygofer, process of dorsal margin, origin: (0) apex of dorsal margin; (1) middle of dorsal margin. (ci: 1.000; ri: 1.000).

76. Pygofer, dorsoapical margin, aspect: (0) continuous; (1) with emargination. (ci: 0.500; ri: 0.833).

77. Subgenital plates, fusion to each other: (0) basally fused; (1) separated along their entire length. (ci: 0.500; ri: 0.000).

78. Subgenital plates, lateral margin, short dorsal dentiform projection: (0) absent; (1) present. (ci: 0.500; ri: 0.500).

79. Subgenital plates, apex in relation to pygofer, extension: (0) not reaching pygofer apex; (1) extending as far posteriorly as pygofer apex. (ci: 0.333; ri: 0.333).

80. Subgenital plates, macrosetae: (0) present; (1) absent. (ci: 0.500; ri: 0.000).

81. Styles, relation to stalk of connective, extension: (0) extending beyond stalk; (1) not extended beyond stalk. Non-informative.

82. Styles, preapical lobe: (0) absent; (1) present. (ci: 0.333; ri: 0.778).

83. Styles, apex, shape: (0) obtuse; (1) foot-shaped; (2) truncate. (ci: 0.400; ri: 0.000).

84. Connective, keel of stalk: (0) present; (1) absent. (ci: 0.500; ri: 0.889).

85. Connective, arms, dorsal view: (0) strongly divergent; (1) slightly convergent; (2) moderately divergent. (ci: 0.286; ri: 0.375).

86. Aedeagus, ventral process: (0) absent; (1) present. (ci: 0.333; ri: 0.714).

87. Aedeagus, ventral process, aspect: (0) paired and slender; (1) paired and dentiform; (2) scoop-shaped. (ci: 1.000; ri: 1.000).

88. Aedeagus, caudoventral aspect, inflation: (0) not inflated; (1) inflated. (ci: 1.000; ri: 1.000).

89. Aedeagus, shaft, length: (0) short; (1) elongate. Non-informative.

90. Aedeagus, shaft apex, direction: (0) directed dorsally; (1) directed posterodorsally. (ci: 1.000; ri: 1.000).

91. Aedeagus, paired apical processes: (0) absent; (1) present. Non-informative.

92. Gonoduct, distal portion, projection: (0) not projected beyond shaft; (1) projected beyond shaft. (ci: 1.000; ri: 1.000).

Phylogeny

Both maximum likelihood (lnL = -11521.166) and Bayesian inference analyses of the combined data matrix (Fig. 10) recovered *Aulacizes* as monophyletic with high support values (SH-aLRT = 96.1, UFboot = 97, and PP = 98). This result was also obtained in the ML and BI analyses of the molecular matrix and in the morphological analysis (Figs. S1 and S2), with high support of SH-aLRT (= 91.3) and PP (= 100), but with low support of UFboot (= 89) and parsimony bootstrap (= 22). In the ML and BI results of the concatenated and combined datasets, the clade *Proconosama* + (*Paraulacizes* + *Pseudometopia*) was

recovered as the sister group of *Aulacizes* (Fig. S1) with high support in the concatenated datasets (SH-aLRT = 99.9, UFboot = 97, and PP = 100) and with medium to high support in the combined datasets (SH-aLRT = 96.9, UFboot = 93, and PP = 78). However, the morphological parsimony trees recovered *Pseudometopia* or *Proconosama* as possible sister groups of *Aulacizes* (Fig. S2), both possibilities with low support (bootstrap = 30).

Aulacizes repanda was recovered as the sister group of the remaining species of the genus. However, this relationship was not recovered in the morphological MP analyses. The sister clade of *A. repanda* was divided into three major clades (Fig. 10) with medium to high support (SH-aLRT = 81.6, 90, UFBoot = 56, 86, and PP = 61, 73). The first and second clades included, respectively, *A. erythrocephala* + *A. quadripunctata* (SH-aLRT = 79.3, 98.3, UFboot = 77, 100, and PP = 99, 100, concatenated and combined, respectively) and *A. conspersa* + *A. persistans* (SH-aLRT = 99.3, 100, UFBoot = 100, 100, and PP = 100, 100, concatenated and combined, respectively), both groups showing thus medium to high support. These two clades were also recovered in morphological MP analyses (Fig. S2), but supports were low (parsimony = 57, 68, respectively). The third clade included *A. obsoleta*, *A. similata*, *A. insistans*, and *A. nigriceps*, but relationships among these species were unstable. In the concatenated ML and BI analyses (Fig. S1), the clade *A. obsoleta* + (*A. insistans* + *A. similata*) appeared with high support (SH-aLRT = 100, UFboot = 100, and PP = 100). In the combined ML (Fig. S1), the clade *A. obsoleta* + (*A. similata* + (*A. insistans* + *A. nigriceps*)) was recovered with medium to high support (SH-aLRT = 99.9, UFboot = 98). In the combined BI, the clade *A. nigriceps* + (*A. obsoleta* + (*A. insistans* + *A. similata*)) was recovered with medium to low support (PP = 50). In the morphological MP analyses (Fig. S2), unlike observed in the results of ML and BI, the clade *A. nigriceps* + (*A. insistans* + (*A. persistans* + *A. conspersa*)) was recovered, but with low support (bootstrap = 29), whereas *A. repanda*, *A. similata*, and *A. obsoleta* had unstable positions.

Taxonomic revision

Genus *Aulacizes* Amyot & Serville

(Figs. 1–9; 11–98)

Aulacizes Amyot & Serville, 1843: 571 [gen. nov.]. Metcalf 1965: 620 [catalogue]; Young 1968: 89 [species list; species synonymies]; Oman et al. 1990: 193 [listed]; Mejdalani et al. 2006 [revalidation of species]; McKamey 2007: 272 [catalogue].

Type-species. *Tettigonia quadripunctata* Germar, 1821: 59, by monotypy.

Total length (mm). ♂♂ 10.92–14.78 mm; ♀♀ 11.80–15.48 mm.

Description. Head. Crown, in dorsal view, well to strongly produced anteriorly (Figs. 11–19); anterior margin slightly elevated and carinate; position of ocelli variable in relation to imaginary line between anterior angles of eyes; crown with M-shaped elevation bordering posterior margin; short longitudinal carina laterad of each ocellus; median fovea broadened anteriorly; disc with or without pubescence. Antennal ledge, in dorsal view, protuberant, with longitudinal sulcus; in lateral view, slightly carinate dorsally, directed anteriorly and digitiform. Face with setae, especially on lower portion. Frons, in anterior view, convex and protuberant, slightly pubescent; with depression at central portion; muscle impressions distinct; epistomal suture obsolete; clypeus, in lateral view, convex, continuing inferior contour of frons.

Thorax. Pronotum (Figs. 11–19), in dorsal view, width equal to or greater than transocular width of head; lateral margins convergent anteriorly; posterior margin concave; posterior ¾ of disc transversely rugose and sometimes with punctures; dorsolateral carina complete, declivent anteriorly. Mesoscutellum finely transversely striate. Forewing strongly coriaceous or not; with or without distinct apical membranous area; punctures concentrated mostly close to costal margin and on clavus; veins elevated and distinct; position of bases of inner and median anteapical cells variable; with four apical cells, base of fourth more proximal than base of third or their bases approximately aligned; without anteapical discal plexus of veins; usually without supernumerary anteapical crossveins to costal margin; female forewing, at rest position, concealing apex of ovipositor. Hind wing, at rest position, extending almost as far posteriorly as forewing; vein R2+3 incomplete. Hind leg with femoral setal formula 2:0:0, first tarsomere distinctly shorter than combined length of second and third.

Male terminalia. Pygofer (Figs. 21, 45, 65, 74, 91), in lateral view, not strongly produced posteriorly; posterior margin convex; dorsal margin with extremely long and slender process arising near middle, extending ventrally and then curved dorsally or sometimes posteriorly; disc with dispersed microsetae, concentrated mostly on posteroventral portion and extending anteriorly along ventral margin. Valve fused with

pygofer laterally. Subgenital plate (Figs. 22, 46, 47, 66, 75, 92), in ventral view, separated from the other throughout length; subtriangular; with short dorsal dentiform projection on lateral margin at mid-length (Fig. 67); surface with numerous scattered microsetae; in lateral view, each plate extending posteriorly approximately as far as pygofer apex or slightly farther. Style (Figs. 22, 46, 66, 75, 76, 92), in dorsal view, extending farther posteriorly than apex of connective; with distinct outer preapical projection; outer margin beyond projection with few small setae; apex obtuse or truncate. Connective (Figs. 22, 46, 66, 75, 76, 92), in dorsal view, narrowly Y-shaped; arms not widely divergent; stem weakly keeled, longer than arms. Aedeagus symmetrical (Figs. 23, 48, 68, 77, 93), short; shaft, in lateral view, forming dorsal elevation, obtuse at apex; with apical ventral scoop-shaped process (Figs. 24, 49, 69, 78, 94), which exceeds apex of shaft, lateral portions of process curved dorsomesally (Figs. 25, 50, 70, 86, 79, 95); with pair of lateral longitudinal projections extending from inferior portion of aedeagal shaft to scoop-shaped process; gonopore with small associated projection. Paraphyses absent.

Female terminalia. Abdominal sternite VII (Figs. 26, 71, 80, 96), in ventral view, with lateral margins convergent posteriorly; posterior margin variable interspecifically; surface with numerous dispersed microsetae. “Internal” sternite VIII, in dorsal view, with pair of slightly striated lobed sclerotized areas, which may be connected to each other. Pygofer (Figs. 27, 72, 81, 97), in lateral view, moderately produced posteriorly; posterior margin rounded; surface with numerous dispersed microsetae. Valvifer I (Fig. 82), in lateral view, variable interspecifically. Valvula I (Fig. 82), in ventral view, expanded at base, forming distinct outer lobe; in lateral view, blade with acute apex (Fig. 84); dorsal sculptured area extending from basal portion to apex, formed mostly by scale-like processes arranged in oblique lines at apical half and more horizontal lines at basal half (Fig. 83); ventral sculptured area restricted to apical portion, formed by scale-like processes; surface with setae/pores on basal portion and extending posteriorly below ramus; ventral interlocking device located on basiventral half of valvula. Valvifer II (Fig. 85), in lateral view, subpentagonal, narrowed inferiorly; with distinct sensory field of small setae adjacent to articulation point; denticuli densely distributed on inferior half. Valvula II (Fig. 85), in lateral view, distinctly broadened beyond basal curvature and then narrowing gradually towards obtuse apex; basidorsal hyaline area distinct; preapical prominence inconspicuous (Fig. 88); dorsal margin of blade with approximately 35-40 triangular or subtriangular, non-contiguous small teeth; denticles distributed on teeth (except for those located at basal ascending portion

of dorsal margin) and on dorsal and ventral apical margins of blade (except at apex) (Figs. 86, 87); valvula with ducts extending toward teeth and apex (Figs. 87, 88). Gonoplac (Fig. 89), in lateral view, with basal half narrow and apical half distinctly expanded; apex obtuse; surface with group of setae located ventroapically and extending anteriorly along ventral margin; denticuli also present, forming more distinct group near dorsoapical margin.

Distribution. Brazil (Bahia, Mato Grosso, Minas Gerais, Espírito Santo, Rio de Janeiro, São Paulo, Paraná, Santa Catarina, and Rio Grande do Sul) and Argentina (Missiones).

Systematic notes. *Aulacizes* was recovered as monophyletic in our phylogenetic analyses (Figs. 10, S1, S2). Results obtained from the combined matrix (Fig. 10) agree with those from the molecular matrix (Fig. S1), recovering the genus as the sister group of *Proconosama*, *Paraulacizes*, and *Pseudometopia*. However, in the morphological analyses, *Aulacizes* was recovered as the sister group of only *Pseudometopia* and *Proconosama* (Fig. S2).

Specimens of *Aulacizes* are more similar to those of *Proconosama* in the external morphology and male terminalia. At least four synapomorphic male terminalia features distinguish *Aulacizes* from *Proconosama*, *Paraulacizes*, and *Pseudometopia* (Fig. S3), viz., (1) inferior portion of frons with black broad transverse stripe (character 25, state 0); (2) styles with preapical lobe (c. 82, s. 1); (3) stalk of connective with keel (c. 84, s. 0); and (4) distal portion of gonoduct projected beyond aedeagal shaft (c. 92, s. 1).

Young (1968), in his review of the Proconiini, included *Aulacizes basalis* Walker, 1851 (Figs. 99–102) and *Tettigonia clypeata* Signoret, 1855 (Figs. 103–106) in *Aulacizes*. The study of their female types shows that these species definitely do not belong in *Aulacizes* and should thus be transferred out. In addition, *Tettigonia maculifrons* Signoret, 1855 was catalogued by Metcalf (1965) under *Aulacizes* without justification and is herein also removed from the genus. See the discussion below for proposed positions. Given this new circumscription of *Aulacizes*, we limit the genus distribution from Northeastern Brazil south to Argentina, with no records from the Amazonian biome.

List of valid species of *Aulacizes*

Previous distributional records from Young (1958), Azevedo-Filho (2004), Mejdalani et al. (2006, 2009), Ringenberg et al. (2010), Paris et al. (2012), Paradell et al. (2012),

Tolotti et al. (2012), Peruzo et al. (2013), Olizeski (2013), Azevedo-Filho et al. (2016), Dellapé (2016), Froza (2017), Czeikoski et al. (2017), Schneider et al. (2017), and Pecly et al. (2025).

A. conspersa Walker, 1851 (Figs. 4, 11). Brazil: Bahia, Mato Grosso, Minas Gerais, Espírito Santo, Rio de Janeiro, São Paulo, Paraná, and Santa Catarina states. Argentina. Misiones Province.

A. erythrocephala (Germar, 1821) (Figs. 1, 12). Brazil: Bahia **[new record]**, Espírito Santo, and Rio de Janeiro states.

A. insistans (Walker, 1858) (Figs. 8, 13). Brazil: Minas Gerais **[new record]**, Rio de Janeiro, and São Paulo states.

A. nigriceps Schmidt, 1928 **stat. nov., sp. rev.** (Figs. 5, 14). Brazil: São Paulo **[new record]**, Paraná **[new record]**, and Santa Catarina **[new record]** states.

A. obsoleta Melichar, 1926 (Figs. 2, 15). Brazil: Minas Gerais **[new record]**, São Paulo, Paraná **[new record]**, Santa Catarina **[new record]**, and Rio Grande do Sul **[new record]** states.

A. persistans (Walker, 1858) (Figs. 9, 16). Brazil: Rio de Janeiro, São Paulo, Paraná, and Santa Catarina states.

A. quadripunctata (Germar, 1821) (Figs. 5, 17). Brazil: Minas Gerais **[new record]**, Rio de Janeiro, São Paulo, Paraná **[new record]**, Santa Catarina **[new record]**, and Rio Grande do Sul states.

A. repanda (Signoret, 1855) (Figs. 3, 18). Brazil: Minas Gerais, São Paulo, Paraná, Santa Catarina, and Rio Grande do Sul states.

A. similata (Signoret, 1855) (Figs. 7, 19). Brazil: Rio de Janeiro State **[new record]**.

Key to species of *Aulacizes*

1 Forewing with yellow spots (Figs. 11, 13, 14, 16, 18) ……. 2

1' Forewing without yellow spots (Figs. 12, 15, 17, 19) ...……... 6

2 Pronotum with pair of dark brown to black linear markings behind compound eyes…...…….. *A. repanda* (Signoret) (Fig. 18)

2' Pronotum not as above (Figs. 11, 13, 14, 16) ……..…..……...…… 3

3 Mesonotum with three yellow spots on anterior portion and scutellum with additional yellow spot (Figs. 11, 13, 16) ...……. 4

3' Mesonotum without three yellow spots on anterior portion and scutellum without additional yellow spot …… *A. nigriceps* Schmidt **stat. nov., sp. rev.** (Fig. 14)

4 Forewings with great number of well-delimited yellow spots, of distinct sizes, on corium and clavus; pronotum without yellow spots; crown mostly yellow to orange (Figs. 11, 16) ……..... 5

4' Forewings with small number of well-delimited yellow spots, of distinct sizes, on corium and clavus; sometimes pronotum with yellow spots; crown mostly black with three yellow spots at apex …… *A. insistans* (Walker) (Fig. 13)

5 Crown triangular; apex of clypeus with distinct black spot; forewings with numerous rounded yellow spots often fused to each other …… *A. persistans* (Walker) (Fig. 16)

5' Crown rounded; apex of clypeus without distinct black spot; forewings with widely spaced rounded yellow spots ……... *A. conspersa* Walker (Fig. 11)

6 Crown and frons red, mesonotum black (Figs. 12, 17) …… 7

6' Crown and frons yellow or brownish-yellow, mesonotum yellow or brownish-yellow (Figs. 15, 19) ……..... 8

7 Clypeus and pronotum black ……..… *A. erythrocephala* (Germar) (Fig. 12)

7' Clypeus and pronotum red …...…… *A. quadripunctata* (Germar) (Fig. 17)

8 Pronotum with thin black longitudinal line on median area of disc ……...……... *A. obsoleta* Melichar (Fig. 15)

8' Pronotum with dark brown to black horizontal band along posterior margin ……..…….. *A. similata* (Signoret) (Fig. 19)

Species redescriptions and notes

***Aulacizes erythrocephala* (Germar, 1821) (Figs. 1, 12, 20)**

Tettigonia erythrocephala Germar, 1821: 59 [sp. nov.]. Metcalf 1965: 627 [catalogue]; Young 1968: 93 [syn. nov. of *Aulacizes quadripunctata*]; Mejdalani et al. 2006 [revalidation]; McKamey 2007: 274 [catalogue; syn. of *A. quadripunctata*].

Type-locality. Brazil.

Length. ♂♂ 13.57–14.78 mm (n = 3); ♀♀ 13.44–14.19 mm (n = 3).

Type material. Male lectotype, Brazil, IFNU [studied based on photographs provided by Mejdalani et al. 2006].

Material examined. Brazil. Bahia State [new record]: Amargosa, DZUP: 5 ♂ and 2 ♀; Camacã, Serra Bonita [Reserva Particular do Patrimônio Natural Serra Bonita], DZRJ: 3 ♂ and 6 ♀, DZUP: 8 ♂ and 2 ♀. **Espírito Santo State:** Santa Tereza, DZRJ: 1 ♀, DZUP: 58 ♂ and 79 ♀, MZSP: 1 ♂ and 2 ♀; Colatina, DZUP: 1 ♂ and 2 ♀. **Rio de Janeiro State:** Nova Friburgo, MNRJ: 2 ♂ (vouchers ENT6535 and ENT6699) and 1 ♀.

Taxonomic notes. Young (1968) treated this species as a synonym of *A. quadripunctata* (Fig. 17). However, Mejdalani et al. (2006), based on the study of the lectotypes of both species, concluded that they can be easily distinguished by the color pattern and thus are not synonyms. Therefore, *A. erythrocephala* was revalidated. According to Mejdalani et al. (2006), besides the distinct coloration of the crown and pronotum, the clypeus is mostly black in *A. erythrocephala*, whereas in *A. quadripunctata* it is red. Both the male and female terminalia are very similar in the two species.

Here, in all our phylogenetic analyses (morphological MP, ML, and BI), *A. erythrocephala* was recovered as sister of *A. quadripunctata* (Figs. 10, S1, and S2), but only in the combined analysis this relationship was well supported. The synapomorphies that support the clade *A. erythrocephala* + *A. quadripunctata* are the following: (1) crown red (character 1, state 5); (2) coronal surface with pubescence (c. 3, s. 1); (3) frons red (c. 23, s. 5); (4) mesonotum black (c. 52, s. 3); and (5) forewings black (c. 62, s. 2). The present work corroborates the revalidation of *A. erythrocephala* proposed by Mejdalani et al. (2006). Autapomorphies of *A. erythrocephala* indicated by the morphological MP analysis are the following: (1) crown with pair of black bands extending from the antennal edges, over ocelli, to the posterior margin (c. 9, s. 1); (2) frons not protuberant (c. 20, s. 1); (3) absence of black or brown transverse band on posterior margin of pronotum (c. 45, s. 0); and (4) forewings with apical membrane indistinct (c. 57, s. 1). The species is herein recorded for the first time from Bahia State, Northeastern Brazil (Fig. 20).

***Aulacizes insistans* (Walker, 1858) (Figs. 8, 13, 21–44)**

Proconia insistans Walker, 1858: 232 [n. sp.]. Metcalf 1965: 630 [catalogued under *Aulacizes maculata* Walker, 1851: 794]; Young 1965: 180 [lectotype designated]; Young 1968: 93 [implicit reinstatement]; McKamey 2007: 273 [catalogue].

Aulacizes obtusa Walker, 1858: 239 [n. sp.]. Metcalf 1965: 630 [catalogued under *Aulacizes maculata* Walker, 1851: 794]; Young 1965: 186 [holotype clarified]; Young 1968: 93 [syn. nov. of *Aulacizes. insistans*]; McKamey 2007: 273 [catalogue; syn. of *A. inquieta* Melichar, 1926 {error}].

Aulacizes inquieta Melichar, 1926: 304 [n. sp.]. Metcalf 1965: 629 [catalogue]; not treated by Young 1968; McKamey 2007: 273 [catalogue]. **New synonym**.

Type locality. Rio de Janeiro, Brazil.

Length. ♂♂ 12.38–13.52 mm (n = 4); ♀♀ 13.65–13.75 mm (n = 3).

Description. Head. Crown (Figs. 13, 32–39), in dorsal view, well produced anteriorly, its median length approximately 8/10 of interocular width and 4/10 of transocular width; ocelli located on imaginary line between anterior angles of eyes, each slightly closer to adjacent eye angle than to median line; disc without conspicuous pubescence. Face with longer setae, especially on lower portion. **Thorax.** Pronotum, in dorsal view (Figs. 13, 32–39), width approximately equal to transocular width of head; posterior ¾ of disc with punctures. Forewing not strongly coriaceous; without distinct apical membranous area; bases of inner and median anteapical cells approximately aligned, located more basally than that of outer anteapical cell.

Color. Ground color of head and pronotum yellow to orange (Figs. 13, 32–39). Head, in dorsal view, usually with large black spot starting from posterior margin and reaching apex (form and development of this spot variable intraspecifically); this black spot often delimiting three spots on apex of crown and pair of spots adjacent to eyes, yellow to orange (smaller additional spots on median portion of crown may also be present). Pronotum with narrow dark brown to black line along anterior margin, usually bifurcated laterally behind eye, this pattern of lines often delimiting a pair of central anterior yellow to orange areas and often a pair of ovoid yellow to orange areas behind eyes; posterior portion of pronotal disc with broad dark brown to black irregular transverse stripe that forms medially a line directed

anteriorly to arc on anterior third (additional irregular lines originated from transverse stripe may also be present). Mesonotum dark brown to black, usually with one median spot on anterior portion and one spot on scutellum, yellow to orange (variable basilateral spots may also be present); scutellar apex brown. Forewing brown, usually with a small number of large well-delimited yellow spots on corium and clavus (greatly variable intraspecifically, sometimes entirely absent). Ground color of face yellow to orange (Figs. 42, 43); inferior portion of frons with broad transverse dark brown to black stripe, central portion of frons with large dark brown to black area delimiting variable yellow to orange spots. Clypeus (Figs. 42, 43) with dark brown to black spot. Labium dark brown. Gena yellow to orange, with dark brown to black macula that extends to superior portion of lorum. Lorum yellow to orange. Lateral and ventral portions of thorax mostly yellow to orange with dark brown to black areas; legs mostly yellow to brown. Ground color of abdomen dark brown with extensive light brown to light yellow areas (Figs. 40, 41).

Male terminalia. Style, in dorsal view, with apex obtuse (Fig. 22). Aedeagus, in lateral view, with concavity more accentuate at median portion of apical ventral scoop-shaped process, and not irregularly serrated at lateral portions of process (Figs. 23, 24).

Female terminalia. Abdominal sternite VII (Fig. 26), in ventral view, with posterior margin deeply emarginate and with slightly projected median lobe.

Type material. *Aulacizes insistans*: male lectotype, Rio de Janeiro, Brazil, NHM [studied based on photographs]; *Aulacizes obtusa*: male holotype, Rio de Janeiro, Brazil, NHM [studied based on photographs]; *Aulacizes inquieta*: male, Brazil [studied based on original description].

Material examined. Brazil. Minas Gerais State [new record]: Itamonte, DZRJ: 2 ♂. **Rio de Janeiro State:** Nova Friburgo, DZUP: 4 ♂, DZRJ: 8 ♂ and 6 ♀; Itatiaia, MZSP: 2 ♂; Teresópolis, DZRJ: 11 ♂ and 6 ♀; Teresópolis [Parque Nacional da Serra dos Órgãos], DZRJ: 18 ♂ (voucher ENT6279) and 4 ♀; Petrópolis [Reserva Biológica de Araras], DZRJ: 1 ♂ and 3 ♀. **São Paulo State:** Barueri, MZSP: 2 ♂; São José do Barreiro [Serra da Bocaina], MZSP: 2 ♂, DZUP: 1 ♂.

Taxonomic notes. *Aulacizes inquieta* was described by Melichar (1926) and catalogued by Metcalf (1965). Later, Young (1977) stated that he was unable to associate specimens with

this species, which thus became a taxon of uncertain position within the Cicadellinae. Here we studied the original description and concluded that is possibly a synonym of *A. insistans* (Figs. 28–30). Furthermore, based on the study of the photograph of the type (Fig. 31), we agree with the synonym of *A. obtusa* Walker, 1858 proposed by Young (1968).

In the morphological MP analysis (Fig. S2), *A. insistans* was recovered as the sister of *A. persistans* + *A. conspersa*, with moderate support. The clade is supported by three synapomorphies: (1) anterior margin of pronotum with narrow dark brown to black line bifurcated laterally behind eye (character 40, state 1); (2) mesonotum with three yellow spots on anterior portion (c. 53, s. 1); and (3) scutellum with a yellow spot (c. 55, s. 1). In the concatenated analysis (Fig. S1), *A. insistans* was recovered as the sister group of *A. similata*, with high support. In the combined analysis (Fig. 10), it was recovered as the sister group of *A. nigriceps*, with good support of SH-aLRT in the ML. Finally, in the BI, it was recovered as the sister group of *A. similata*, but with moderate support. This species can be recognized by the following autapomorphic characteristics: (1) median area of frons with large black spot (c. 27, s. 1); (2) pronotum with irregular yellow spots of variable sizes (c. 48, s. 1); (3) pronotal dorsolateral carina approximately rectilinear (c. 50, s. 0); and (4) pronotal disc with pubescence (c. 51, s. 1). *Aulacizes insistans* shows considerable variation of coloration in the crown, pronotum, mesonotum, and forewings (Figs. 32–39). New distribution records were herein provided (Fig. 44).

***Aulacizes nigriceps* Schmidt, 1928 stat. nov., sp. rev. (Figs. 6, 14, 45–64)**

Aulacizes maculata var. *nigriceps* Schmidt, 1928: 79 [new variety]. Metcalf 1965: 630 [catalogue]; Young & Nast 1963: 268 [lectotype designated]; Young 1968: 92 [syn. nov. of *Aulacizes conspersa*]; McKamey 2007: 273 [catalogue; treated as subspecies; syn. of *A. conspersa*].

Type locality: Brazil.

Length. ♂♂ 13.1–13.4 mm (n = 4).

Description. Head. Crown (Figs. 14, 54–60), in dorsal view, well produced anteriorly, median length approximately 7/10 of interocular width and 4/10 of transocular width; ocelli located slightly behind imaginary line between anterior angles of eyes, each approximately

equidistant between median line of crown and adjacent eye angle; disc with sparse pubescence. Face with setae, especially on lower portion. **Thorax.** Pronotum (Figs. 14, 54–60), in dorsal view, width greater than transocular width of head; posterior ¾ of disc with punctures. Forewing not strongly coriaceous; without distinct apical membranous area; bases of inner and median anteapical cells aligned to each other and more proximal than that of outer anteapical cell; without supernumerary anteapical crossveins to costal margin or with few irregular such veins.

Color. Ground color of head and pronotum brown (Figs. 14, 54–60); crown with irregular yellow spots located mainly basally and apically; pronotal disc with irregular yellow spots of variable sizes. Mesonotum almost entirely brown. Forewing brown with irregular yellow spots, of various sizes, on corium and clavus, including large transverse preapical spot extending from costal margin to inner anteapical cell. Face with frons largely dark brown to black, with central yellow area of variable size; clypeus almost entirely yellow; gena with brown marking extending from lorum to eye (Figs. 62, 63). Lateral and ventral portions of thorax yellow with brown markings; legs mostly yellow with pretarsi brown (Fig. 61). Abdomen mostly brownish-yellow; posterior area of tergites brown.

Male terminalia. Style, in dorsal view, with apex obtuse (Fig. 46, 47). Aedeagus, in lateral view, with pair of lateral longitudinal projections shorter; with concavity more accentuate from median portion to posterior portion of apical ventral scoop-shaped process; irregularly serrated at lateral portions of process (Figs. 48, 49).

Female unknown.

Type material. Male lectotype, Brazil, ZMPA [studied based on photographs].

Material examined. Brazil. São Paulo State [new record]: Caraguatatuba, MZSP: 1 ♂. **Paraná State [new record]**: Guaratuba [Estrada dos Castelhanos], DZUP: 5 ♂. **Santa Catarina State [new record]**: Timbó, MZSP: 1 ♂.

Taxonomic notes. Schmidt (1928) described *nigriceps* (Figs. 51–53) as a variety of *A. maculata* Walker. Subsequently, Young (1968) synonymized this variety with *A. conspersa* (Fig. 11). McKamey (2007) treated it as a subspecies in his catalogue. However, the study of the original descriptions and photographs of the lectotypes revealed differences, especially in the coloration of the head, pronotum, and forewings. These differences

indicated that *A. conspersa* and *A. nigriceps* are distinct biological entities; thus, the latter is herein considered a valid species.

In the morphological MP analysis (Fig. S2), *A. nigriceps* was recovered as the sister group of *A. insistans* + (*A. persistans* + *A. conspersa*), but with low support. This clade was supported by characters: (1) gena with black maculae (character 31, state 1); (2) black macula at gena extending to the frons (c. 32, s. 1); (3) corium and clavus of forewings with yellow spots of distinct sizes (c. 63, s. 1); and (4) yellow spot extending from inner anteapical cell to costal margin of forewings (c. 65, s. 1). In the combined analysis (molecular + morphology) (Fig. 10), *A. nigriceps* was recovered as the sister group of *A. insistans*, with good support of SH-aLRT, but with low support of UFBoot. Our phylogenetic analyses corroborate the treatment of *A. maculata* var. *nigriceps* as a species, although, unfortunately, no molecular information was obtained for this taxon. Here we described *A. nigriceps* for the first time in detail and provided precise data on its geographic distribution (Fig. 64). Furthermore, we noticed that specimens of this species show color variations in the crown, pronotum, and forewings (Figs. 54–60).

Aulacizes nigriceps (Figs. 51, 52, 54–60) can be recognized by the following autapomorphic features: (1) crown dark brown (c. 1, s. 2); (2) with irregular yellow spots located mainly basally and apically (c. 11, s. 1); (3) ocelli located before the imaginary line between the anterior angles of compound eyes (c. 15, s. 0); (4) frons black (c. 23, s. 4); (5) yellow macula at superior portion of frons (c. 24, s. 1); (6) inferior portion of frons without black broad transverse stripe (c. 25, s. 1); (7) black spot at inferior portion of gena (c. 33, s. 1); (8) pronotum brown (c. 35, s. 2); and (9) absence of black band at posterior margin of pronotum (c. 45, s. 0).

Aulacizes obsoleta Melichar, 1926 (Figs. 2, 15, 65–73)

Aulacizes obsoleta Melichar, 1926: 306 [sp. nov.]. Metcalf 1965: 637 [catalogue]; Young & Lauterer 1966: 267 [lectotype designated]; Young 1968: 93 [listed]; McKamey 2007: 274 [catalogue].

Type locality: São Paulo, Brazil.

Length. ♂♂ 11.08–11.49 mm (n = 3); ♀♀ 11.75–12.96 mm (n = 3).

Description. Head. Crown (Fig. 15), in dorsal view, well produced anteriorly, median length approximately 6/10 of interocular width and 4/10 of transocular width; ocelli located on imaginary line between anterior angles of eyes, each slightly closer to adjacent eye angle than to median line; disc without conspicuous pubescence. Face with longer setae, especially on lower portion. **Thorax.** Pronotum (Fig. 15), in dorsal view, width greater than transocular width of head. Forewing not strongly coriaceous; without distinct apical membranous area; bases of inner and median anteapical cells approximately aligned, located more basally than that of outer anteapical cell.

Color. Ground color of head and pronotum light brown (Figs. 2, 15). Head, in dorsal view, sometimes with posteromedian black spot. Pronotum with complete narrow black longitudinal line at median area of disc, connected with narrow black band located along posterior margin. Mesonotum entirely light brown. Forewing entirely brown (mostly green when alive, Fig. 2). Face with clypeus black; labium dark brown to black. Lateral and ventral portions of thorax mainly dark brown with light brown areas; legs mainly light brown. Ground color of abdomen dark brown with extensive light yellow areas.

Male terminalia. Style, in dorsal view, with apex truncate (Fig. 66). Aedeagus, in lateral view, with apical ventral scoop-shaped process narrower, with concavity slightly accentuate and irregularly serrated apically at median portion of process (Figs. 68, 69).

Female terminalia. Abdominal sternite VII (Fig. 71), in ventral view, with posterior margin deeply emarginate and with slightly projected median lobe.

Type material. Female lectotype, São Paulo, Brazil, MMBC [studied based on photographs].

Material examined. Brazil. Minas Gerais [new record]: Itamonte, DZRJ: 1♂ and 1♀. **São Paulo State**: Barueri, MSZP: 2 ♂ and 2 ♀. **Paraná State [new record]**: Foz do Iguaçu, DZUP: 2 ♀; São José dos Pinhais, DZUP: 2 ♂ and 6 ♀ (1 ♀ voucher ENT6819); Ponta Grossa [Parque Estadual de Vila Velha], DZUP: 1 ♂ and 1 ♀; Curitiba, DZUP: 10 ♂ and 15 ♀; Curitiba [Centro Politécnico da Universidade Federal do Paraná], DZUP: 1 ♂ and 3 ♀ (1 ♀ voucher ENT6820); Colombo, DZUP: 2 ♀; Tijucas do Sul, DZUP: 2 ♂ and 4 ♀; Piraquara, DZUP: 2 ♂ and 4 ♀. **Santa Catarina State [new record]**: Lages, DZUP: 3 ♂ and 1 ♀; São Bento do Sul, DZUP: 4 ♂ and 4 ♀; Nova Teutônia, DZUP: 7 ♂ and 8 ♀;

MZSP: 1 ♂ and 1 ♀; Ponte Alta, DZUP: 1 ♂ and 2 ♀. **Rio Grande do Sul [new record]**: Passo Fundo, DZUP: 2 ♂.

Taxonomic notes. In the morphological MP analysis (Fig. S2), relationships of *A. obsoleta* with other species of the genus were unstable. In the concatenated analysis (Fig. S1), *A. obsoleta* was recovered as the sister group of *A. insistans* + *A. similata*, with high support. In the combined analysis (Fig. 10), it was recovered as the sister group of *A. similata* + (*A. insistans* + *A. nigriceps*), with good support in ML. *Aulacizes obsoleta* can be recognized by the following autapomorphies: (1) ground color of crown, frons, and pronotum brownish-yellow (characters 1, 23, and 35, states 6, 6, and 5, respectively); (2) clypeus black (c. 30, s. 3); (3) presence of black maculae on gena (c. 31, s. 1); (4) black maculae of gena extending to frons (c. 32, s. 1); (5) median longitudinal line on pronotal disc (c. 41, s. 1); (6) posterior margin of pronotum with transverse band narrow (c. 46, s. 1); (7) pronotal dorsolateral carina approximately rectilinear (c. 50, s. 0); (8) pubescence on pronotum (c. 51, s. 1); (9) mesonotum with black marking laterally (c. 54, s. 1); (10) apical membrane of forewings including apical cells and distal portion of antapical cells (c. 58, s. 0); and (11) apex of styles truncate (c. 83, s. 2). Distribution records of this species were here expanded (Fig. 73).

***Aulacizes quadripunctata* (Germar, 1821) (Figs. 5, 17, 74–90)**

Tettigonia quadripunctata Germar, 1821: 59 [sp. nov.]. Metcalf 1965: 639 [catalogue]; Young 1968: 93 [listed]; McKamey 2007: 274 [catalogue].

Diestostemma terminalis Walker, 1851: 798 [sp. nov.]. Metcalf 1965: 639 [catalogued under *Aulacizes quadripunctata*]; Young 1965: 196 [holotype clarified]; Young 1968: 93 [listed under *A. quadripunctata*]; McKamey 2007: 273 [catalogue; syn. of *A. quadripunctata*].

Type locality: São Paulo, Brazil.

Total length. ♂♂ 14.35–14.58 mm (n = 3); ♀♀ 15.09–15.90 mm (n = 3).

Description. Head. Crown (Fig. 17), in dorsal view, strongly produced anteriorly, median length approximately 8/10 of interocular width and 5/10 of transocular width; ocelli located on imaginary line between anterior angles of eyes, each slightly closer to median line than

to adjacent eye angle; disc without conspicuous pubescence. Face with longer setae, especially on lower portion. **Thorax.** Pronotum (Fig. 17), in dorsal view, width greater than transocular width of head; posterior ¾ of disc with punctures. Forewing not strongly coriaceous; without distinct apical membranous area; bases of inner and median anteapical cells approximately aligned, located more basally than that of outer anteapical cell.

Color. Ground color of head and pronotum red (Figs. 5, 17). Head, in dorsal view, with black macula at apex of crown, reaching facial depression at central portion of frons, and pair of black maculae close to posterior margin, including ocelli. Pronotum with median black macula at anterior third of disc and black transverse band along posterior margin. Mesonotum entirely black. Forewing almost entirely black, with narrow apical brown area. Frons with pair of black maculae on inferior portion. Clypeus with small dark brown to black apical spot. Labium dark brown to black. Lateral and ventral portions of thorax mostly red with dark brown to black areas; legs mostly dark brown to black. Ground color of abdomen red with extensive dark brown to black areas.

Male terminalia. Style, in dorsal view, with apex obtuse (Figs. 75, 76). Aedeagus, in lateral view, with pair of lateral longitudinal projections more elongate, extending from inferior portion of aedeagal shaft to scoop-shaped process; without concavity at scoop-shaped process, rectilinear at apex; irregularly serrated at lateral portions of process (Figs. 77, 78).

Female terminalia. Abdominal sternite VII (Fig. 80), in ventral view, with posterior margin deeply emarginate and with distinct, slightly projected median lobe. Valvifer I (Fig. 82), in lateral view, subquadrangular. Valvula I (Fig. 82), in lateral view, with blade slightly curved dorsally. Gonoplac (Fig. 89) extending slightly beyond pygofer apex.

Type material. Male lectotype, St. Paul [São Paulo], Brazil, IFNU [studied based on photographs in Mejdalani et al. 2006].

Material examined. Brazil. Minas Gerais State [new record]: Itamonte, DZRJ: 1 ♂ and 2 ♀; Brumadinho, DZUP: 1 ♂. **Rio de Janeiro State**: Resende, MNRJ: 1 ♂; Nova Friburgo, MNRJ: 1 ♂ and 3 ♀, DZUP: 2 ♂ and 4 ♀; Teresópolis [Parque Nacional da Serra dos Órgãos], DZRJ: 2 ♂ and 2 ♀, MNRJ: 1 ♂ (voucher ENT6537); Teresópolis [Vale da Revolta], DZRJ: 3 ♀, DZUP: 1 ♂; Teresópolis, DZRJ: 1 ♂ and 1 ♀; Teresópolis [Serra do Subaio], DZRJ: 1 ♀; Petrópolis [Araras], DZRJ: 1 ♀; Rio de Janeiro [Parque Nacional da

Tijuca], MNRJ: 1 ♀. **São Paulo State**: Bananal, MNRJ: 1 ♀; Cantareira [Horto de São Paulo], MNRJ: 1 ♀; São José do Barreiro [Serra da Bocaina], DZUP: 5 ♂; Salesópolis [Estação Biológica da Boracéia], DZUP: 2 ♀; Campos do Jordão, DZUP: 1 ♂. **Paraná State [new record]**: Piraquara, DZRJ: 1 ♀, DZUP: 4 ♂ and 6 ♀; Ponta Grossa, DZUP: 2 ♀; Ponta Grossa [Parque Estadual de Vila Velha], DZUP: 1 ♂ and 2 ♀; São José dos Pinhais, DZUP: 2 ♂; Curitiba, DZUP: 1 ♂ and 1 ♀; Tijucas do Sul, DZUP: 2 ♂ and 4 ♀; Guarapuava, DZUP: 1 ♀; Guaratuba, DZUP: 1 ♂ and 3 ♀; Castro, DZRJ: 1 ♀, DZUP: 2 ♀. **Santa Catarina State [new record]**: Praia Grande, DZUP: 1 ♂ and 2 ♀; Lages, DZUP: 4 ♂ and 5 ♀; São Bento do Sul [Rio Vermelho], DZUP: 3 ♀; São Bento do Sul [Rio Natal], DZUP: 4 ♂ and 8 ♀; Santa Cecília, DZUP: 2 ♀; Urubici, DZUP: 1 ♀. **Rio Grande do Sul State**: Gramado, DZRJ: 1 ♀; Tenente Portela, DZUP: 2 ♂; Campo Novo, DZUP: 1 ♂ and 2 ♀; São Francisco de Paula, DZUP: 1 ♀.

Taxonomic notes. See notes above on *A. erythrocephala* for information on the phylogenetic position of *A. quadripunctata*. The latter can be recognized by the following autapomorphies: (1) black macula at apex of crown present (character 6, state 1) and (2) reaching the facial depression at central portion of frons (c. 7, s. 1); (3) pair of black maculae near posterior margin of crown, including ocelli (c. 8, s. 1); (4) black macula at inferior portion of clypeus (c. 29, s. 1); and (5) median black macula at anterior third of pronotal disc (c. 44, s. 1). Distribution records of this species were here expanded (Fig. 90).

***Aulacizes similata* (Signoret, 1855) (Figs. 7, 19, 91–98)**

Tettigonia similata Signoret, 1855: 236 [sp. nov.]. Metcalf 1965: 640 [catalogued under *Aulacizes*]; not treated by Young 1968; Young 1977: 1106 [incertae sedis]; McKamey 2007: 274 [catalogued under *Aulacizes*].

Type locality: Brazil.

Length. ♂♂ 11.46–12.76 mm (n = 4); ♀♀ 13.25–13.75 mm (n = 4).

Description. Head. Crown (Fig. 19), in dorsal view, well produced anteriorly, median length approximately 6/10 of interocular width and 4/10 of transocular width; ocelli located slightly before imaginary line between anterior angles of eyes, each slightly closer to

adjacent eye angle than to median line; disc without conspicuous pubescence. Face with longer setae, especially on lower portion. **Thorax.** Pronotum (Fig. 19), in dorsal view, with width greater than transocular width of head; posterior ¾ of disc with punctures. Forewing coriaceous; with distinct apical membranous area; bases of inner and median anteapical cells approximately aligned or irregular, their positions variable in relation to that of outer anteapical cell.

Color. Ground color of head, pronotum, and mesonotum yellow (Fig. 19). Pronotum with posterior 2/3 of disc yellowish-orange, with dark brown to black narrow stripe along posterior margin. Mesonotum with black markings laterally associated with scutellar suture. Forewing with corium and clavus green; apical membrane and narrow area along costal margin brown; some veins partially yellow. Face with frons yellow; inferior portion with pair of dark brown to black short stripes; clypeus yellow medially and pale yellow laterally, its distal half with central dark brown to black marking; gena, lorum, and maxillary plate pale yellow, with inconspicuous brown markings; labium mostly brown to dark brown. Lateral and ventral portions of thorax mostly pale yellow with few brown markings; legs pale yellow, apex of tibiae, tarsi, and pretarsi dark brown. Abdomen pale yellow ventrally with brown markings at bases of sternites and laterotergites, tergites dark brown. Female sternite VII with distinct dark brown marking posteriorly; gonaplac dark brown at apex.

Male terminalia. Style, in dorsal view, apex obtuse (Fig. 92). Aedeagus, in lateral view, pair of lateral longitudinal projections shorter; with concavity more accentuate at anterior portion of apical ventral scoop-shaped process; not irregularly serrated at lateral portions of process (Figs. 93, 94).

Female terminalia. Abdominal sternite VII (Fig. 96), in ventral view, with posterior margin deeply emarginate and with distinct, slightly projected median lobe. Valvifer I (Fig. 82), in lateral view, subpentagonal. Valvula I (Fig. 82), in lateral view, with blade approximately rectilinear. Gonoplac (Fig. 89) extending approximately as far posteriorly as pygofer apex.

Type material. Unfortunately, photographs of the type material of *Tettigonia similata* were not available for study.

Material examined. Brazil. Rio de Janeiro State [new record]: Teresópolis [Parque Nacional da Serra dos Órgãos], DZRJ: 8 ♂ (vouchers ENT6536 and ENT6700) and 15 ♀,

MNRJ: 2 ♂ and 7 ♀; Nova Friburgo, DZRJ: 1 ♂ [Alto da Cascatinha]; Nova Friburgo [Pico do Caledônia], DZUP: 1 ♀.

Taxonomic notes. *Tettigonia similata* was described by Signoret (1855) with Brazil as the type locality. Subsequently, Young (1977) stated that he was unable to associate specimens with this species. Metcalf (1965), McKamey (2007), and Wilson et al. (2009) included *T. similata* in *Aulacizes*, the latter providing photographs of the body (dorsal and lateral views) of a Brazilian female specimen deposited in ZMHB. According to Signoret (1855), the type of *T. similata* belonged to the Spinola Collection (Turin, Italy). However, it was not located there and, thus, is perhaps lost, unfortunately. Here, with have been able to associate our specimens with this species based on the original description and photographs provided by Wilson et al. (2009). Accordingly, we confirmed the assignment of *similata* to *Aulacizes*, described it for the first time in detail, and provided precise data on its distribution (Fig. 89).

In the morphological MP analysis (Fig. S2), relationships of *A. similata* with other species of the genus were unstable. In the concatenated analyses (ML and BI) (Fig. S1), it was recovered as the sister group of *A. insistans*, with good support. In the combined analysis (ML) (Fig. 10), *A. similata* was recovered as the sister group of *A. insistans* + *A. nigriceps*, with good support only of SH-aLRT; in BI, it was recovered as the sister group of *A. insistans*, but with low support. This species can be recognized by the following autapomorphies: (1) inferior portion of frons with black broad transverse stripe interrupted (character 26, state 0); (2) black macula at inferior portion of clypeus (c. 29, s. 0); (3) posterior margin of pronotum with transverse band narrow (c. 46, s. 1); (4) pronotum with a pair of linear markings behind compound eyes (c. 49, s. 1); (5) ground color of mesonotum yellow (c. 52, s. 0); (6) mesonotum with a black marking laterally (c. 54, s. 1); and (7) forewings mostly dark green (c. 62, s. 3).

Discussion

This is the first comprehensive taxonomic study of *Aulacizes* published after Young's (1968) preliminary review of the genus, in the present case combined with a phylogenetic analysis based on morphological and molecular data. These data were assembled for the study of the phylogeny within the genus, as well as its relationships with *Depanana*, *Depanisca*, *Paraulacizes*, *Proconosama*, and *Pseudometopia*. We provided redescriptions of *Aulacizes* and its known species (except for those recently treated by Mejdalani et al. 2006 and Pecly

et al. 2025), including photographs and diagnostic characters. Additionally, a key to males and females of all species is given. *Aulacizes nigriceps* was here regarded as a valid species (Figs. 6, 14, 45–63), whereas *Tettigonia similata* (Figs. 7, 19), considered of uncertain position within the Cicadellinae (see Young 1977), was confirmed as a member of *Aulacizes*. The female terminalia of four species (*A. insistans*, *A. obsoleta*, *A. quadripunctata*, and *A. similata*) were studied and described.

The study of the female types of *Aulacizes basalis* Walker, 1851 (Figs. 99–102, holotype) and *Tettigonia clypeata* Signoret, 1855 (Figs. 103–106, lectotype), which were treated by Young (1968) in *Aulacizes*, shows that these species definitely do not belong in the genus. Young (1968) examined the type of *A. basalis*, a specimen from "Venezuela" (a genus record considered by him as possibly erroneous). This type has the external morphology very similar to species of *Aulacizes*, *Paraulacizes*, and *Pseudometopia*, which can only be more precisely distinguished based on male terminalia features. However, considering the distribution of the type ("Venezuela") and the redescription of the species by Signoret (1855) (from "Bolivia"), *basalis* most likely does not belong in *Aulacizes*, whose distribution is restricted to Northeastern Brazil south to Argentina. The twelve species of *Paraulacizes* are mostly distributed in North and Central America, with only two species reaching Panama, whereas the nine species of *Pseudometopia* are mostly distributed in Amazonian countries with a single species widespread in South America. Considering these distributions, we tentatively propose the following new combination: *Pseudometopia basalis* (Walker, 1851) **comb. nov.** *Tettigonia clypeata* was described from Brazil and its female lectotype was studied by Young (1968), who noted that the abdominal sternite VII was similar to that of *A. quadripunctata*, and that a male specimen, similar to the lectotype, had an angular head and male terminalia as in *A. obsoleta*. Based on similarities of the type's external morphology to species of *Deselvana*, we tentatively propose the new combination *Deselvana clypeata* (Signoret, 1855) **comb. nov.** Finally, a third species, *Tettigonia maculifrons* Signoret, 1855, described from a specimen from Cayenne based on material from the Spinola collection, was catalogued by Metcalf (1965) under the genus *Aulacizes* without justification. Young (1977) was not able to associate any specimen to this name and left the species as incertae sedis in the Cicadellinae. Based on the original description and illustration (Signoret 1855, plate 12, figure 12), it is not possible to associate this species to a particular genus, given that several Proconiini *sensu lato* from Amazonia have produced heads. However, we can certainly exclude it from *Aulacizes*, given its Amazonian

distribution. Thus, we agree with Young and treat this species as incertae sedis in the subfamily.

After the present review and another recent study by Pecly et al. (2025), nine valid species are now recognized within *Aulacizes*, viz., *A. conspersa*, *A. erythrocephala*, *A. insistans*, *A. nigriceps*, *A. obsoleta*, *A. persistans*, *A. quadripunctata*, *A. repanda*, and *A. similata* (Figs. 1–9; 11–19). Features of the male terminalia of *Aulacizes* are useful for distinguishing the genus from *Paraulacizes*, *Proconosama*, and *Pseudometopia*. However, the identification of *Aulacizes* species remains difficult when performed by means of the examination of the male and female terminalia, as they show little interspecific variation (Pecly et al. 2025). Therefore, it is easier to identify *Aulacizes* species by means of comparisons of their color patterns; this is the reason why our key is based almost entirely on color characters.

We herein expanded the records of *Aulacizes* species (Figs. 20, 44, 64, 73, 90, 98) within Southeastern and Southern Brazil based on specimens deposited in scientific collections and data from the literature (Azevedo-Filho 2004, Mejdalani et al. 2006, 2009, Ringenberg et al. 2010, Paris et al. 2012, Paradell et al. 2012, Tolotti et al. 2012, Peruzo et al. 2013, Olizeski 2013, Azevedo-Filho et al. 2016, Dellapé 2016, Froza 2017, Czeikoski et al. 2017, Schneider et al. 2017). We also studied specimens from the Northeastern and Central-Western Brazilian regions (Pecly et al. 2025). The records from the Northeastern, Southeastern, and Southern regions are within the Atlantic Forest, whereas that from the Central-Western region is within the Cerrado (Pecly et al. 2025).

As aforementioned, the first phylogenetic study that included *Aulacizes* was the unpublished doctoral thesis of Takiya (2007). In this thesis, the monophyly of the Cicadellinae was tested and phylogenetic relationships within this subfamily were estimated based on morphological and molecular data. In her study, only two species of *Aulacizes* were included in the morphological analyses (*Aulacizes* sp. and *A. quadripunctata*) and a single one in the molecular analyses (*Aulacizes* sp.). The parsimony strict consensus of her morphological phylogeny recovered *Aulacizes* as monophyletic, forming a polytomy with *Paraulacizes*, *Proconosama*, and *Pseudometopia*. In her analyses of the concatenated molecular dataset (16S, COI, COII, and H3), *Aulacizes* sp. was recovered as the sister group of *Pseudometopia* + *Proconosama* in the statistically supported BI tree. The second phylogenetic study that included *Aulacizes* was conducted by Feng et al. (2024), aiming to provide improved molecular phylogenetic and biogeographic inferences of the Cicadellinae;

this study, which included the same *Aulacizes* terminals of Takiya (2007), also positioned the genus as the sister group of *Pseudometopia* + *Proconosama*. The present study, which included all recognized *Aulacizes* species, corroborates these two previous works, as it recovered the genus as a monophyletic group with strong to medium support in all analyses (Figs. 10, S1, S2). The results of the combined (morphology + molecular) and concatenated (molecular) datasets partially corroborate those of Takiya (2007) and Feng et al. (2024), as they recovered *Proconosama* + (*Paraulacizes* + *Pseudometopia*) as the sister group of *Aulacizes*. However, the MP morphological results recovered *Pseudometopia* or *Proconosama* as possible sister groups of *Aulacizes* (Fig. S2). All results cited and compared above also corroborate to a certain extent the suggestions of Young (1968) on *Aulacizes* relationships based on raw morphological data.

Specimens of *Aulacizes* are more similar to those of *Proconosama* in external morphology and male terminalia, sharing the following characteristics: (1) anterior margin of crown carinate (not carinate in *Pseudometopia*); (2) posterior margin of crown with M-shaped elevation (absent in *Pseudometopia*); (3) apex of antennal ledges slightly directed ventrally (distinctly directed ventrally in *Pseudometopia*); (4) vein R2+3 incomplete (complete in *Pseudometopia*); (5) process of pygofer inserted at middle of dorsal margin (at apex of dorsal margin in *Pseudometopia*); (6) ventroapical process of aedeagus present (absent in *Pseudometopia*); and (7) aedeagus not inflated in caudoventral aspect (inflated in *Pseudometopia*). Similarities shared by *Aulacizes* and *Pseudometopia* are the following: (1) sulcus of antennal ledges present (absent in *Proconosama*); (2) carina of antennal ledges present (absent in *Proconosama*); (3) carina at superior portion of frons present (absent in *Proconosama*); (4) arms of connective moderately divergent (slightly convergent in *Proconosama*); and (5) apex of shaft of aedeagus directed dorsally (posterodorsally in *Proconosama*).

According to the MP morphological results, species of *Aulacizes* can be distinguished from those of *Paraulacizes*, *Proconosama*, and *Pseudometopia* by the following synapomorphies: (1) inferior portion of frons with black broad transverse stripe (character 25, state 0); (2) styles with preapical lobe (c. 82, s. 1); (3) presence of a keel on the stalk of the connective (c. 84, s. 0); and (4) distal portion of gonoduct projected beyond aedeagal shaft (c. 92, s. 1). In addition to these apomorphies, *Aulacizes* can be recognized by the combination of the following features: (1) anterior margin of crown slightly elevated and carinate; (2) M-shaped elevation bordering posterior coronal margin; (3) short longitudinal

carina laterad of each ocellus; (4) clypeus depressed beneath apex of head; (5) posterior two-thirds of pronotal disc transversely rugose and punctate; (6) forewings with veins elevated and distinct; (7) dorsal margin of pygofer with extremely long and slender process arising near middle, extending ventrally and then curved dorsally and sometimes posteriorly; and (8) aedeagus with scoop-shaped process.

This study contributes to the advance of our knowledge of the taxonomy and phylogeny of the Cicadellinae, especially of *Aulacizes*. The taxonomic revision allowed a redefinition of the limits of *Aulacizes*, including the exclusion of two species previously attributed to this genus and revalidation of another one that has been considered a junior synonym of *A. conspersa*. The phylogenetic analyses, based on morphological and molecular data, partially corroborated available phylogenies, but also unraveled previously unknown relationships among the species of the genus, highlighting the importance of morphological and molecular characters in the delimitation of taxa. Furthermore, the results obtained can be useful for future taxonomic and phylogenetic investigations on other genera of the Cicadellinae, contributing to a better understanding of the evolution and classification of this subfamily, since there are currently few phylogenetic studies on the Proconiini (e.g., Ceotto & Mejdalani 2005, Ceotto et al. 2007, Carvalho et al. 2011, Krishnankutty et al. 2015, Sauceda-V. et al. 2025). As Sauceda-V. et al. (2025) pointed out, such studies demonstrate the importance of investigating little-known taxa in order to better quantify biodiversity, especially in the case of abundant and diverse insect groups, such as Neotropical leafhoppers.

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Supplementary data

Figure S1. Maximum likelihood tree of *Aulacizes* based on 2,089 bp of 16S, COI, COII, and H3 (-lnL = 9715.736). Thick branches are those also recovered in the Bayesian inference. Values associated with branches are likelihood SH-aLRT ≥ 80 / ultrafast bootstrap support ≥ 95 / Bayesian posterior probabilities (in percentages) ≥ 95. Green rectangle indicates *Aulacizes*.

Figure S2. Strict consensus tree obtained from 78 equally most parsimonious trees (L = 254, CI = 0.484, and RI = 0.511) based on the morphological dataset of *Aulacizes*. Bootstrap support values are given above branches. Green rectangle indicates *Aulacizes*.

Figure S3. Character optimization on one of the 78 equally most parsimonious trees, based on 92 morphological characters (L = 238, CI = 0.517, and RI = 0.571). Tree rooted with *Oncometopia orbona*. Character numbers shown above circles; character states below.

White circles (○) indicate homoplastic transformations and black circles indicate (●) non-homoplastic transformations.

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Table 1. Species of *Aulacizes* and outgroups included in the morphological and molecular phylogenetic analyses, with DNA voucher specimen codes and locality information, except for terminals obtained from GenBank. GenBank accession codes are given for each molecular marker (those generated herein are in bold).

Species	Voucher	Depository	Locality	Morphology	COI	COII	16S	H3
Aulacizes conspersa	ENT5981	DZRJ	Brazil/RJ	X	X	X	X	X
A. erythrocephala	ENT6535*/6699**	MNRJ	Brazil/RJ	X	X*	X**	X*	X*
A. insistans	ENT6279	DZRJ	Brazil/RJ	X	X	X	X	X
A. nigriceps		DZUP	Brazil/SP	X				
A. obsoleta	ENT6819*/6820**	DZUP	Brazil/PR	X	X*	X*	X**	X*
A. quadripunctata	ENT6537	DZRJ	Brazil/RJ	X	X	X	X	X
A. repanda	ENT6345	MELQ	Brazil/MG	X	X	X	X	X
A. similata	ENT6536*/6700**	DZRJ	Brazil/RJ	X	X*	X**	X**	X*D
A. persistans	ENT6275	DZRJ	Brazil/RJ	X	X	X	X	X
Depanisca sulcata		GenBank	--	X	MH618950.1	MH619057.1	MH656545.1	MH619164.1
Depanana bugabensis		GenBank	--		MH618949.1	MH619056.1	MH656490.1	MH619163.1
Paraulacizes figurata		GenBank	--		MH618999.1	MH619103.1	MH656498.1	MH619211.1
P. irrorata		GenBank	--	X	AY869737.1	AY869788.1	AY869815.1	AY869762.1
P. mutans		MELQ	Honduras	X				
Proconosama alalia		GenBank	--	X	AY869742.1	AY869794.1	AY869812.1	AY869768.1
P. columbica		GenBank	--		AY869731.1	AY869781.1	AY869816.1	AY869757.1
P. takiyae		MNRJ	Ecuador	X				
Pseudometopia amblardii	ENT6546	DZRJ	Peru	X	MK907397.1	MH619115.1	X	X
P. appendiculata		DZUP	Bolivia	X				
P. irenae		DZUP	Peru	X				
P. latifascia		DZRJ	Brazil/RJ	X				
P. phalaesia		DZRJ	Peru	X	MH619011.1	MH619115.1	MH656497.1	MH619222.1
P. transversa		DZUP	Brazil/AM	X				
Oncometopia orbona		GenBank	--	X	AY869736.1	AY869787.1	AY869811.1	AY869761.1

Brazilian states: AM: Amazonas, MG: Minas Gerais, PR: Paraná, RJ: Rio de Janeiro, and SP: São Paulo.

Table 2. Primer sequences for PCR amplification and sequencing.

Molecular marker	Primer name	Primer sequence (5'–3')	Reference
Cytochrome Oxidase I	C1 (F)	TTGATTTTTTGGTCAYCCWGAAGT	Takiya et al. 2006
	3014 (R)	TTCATTGCACTAATCTGCCATACTA	Takiya et al. 2006
Cytochrome Oxidase II	C2 (F)	CCRCAAATTTCWGARCATTGACCA	Takiya et al. 2006
	TL2 (=3037) (R)	TAGTATGGCAGATTAGTGCAATGAA	Takiya et al. 2006
16S rDNA	16S+ (F)	CCGGTYTGAACTCARATCA	Takiya et al. 2006
	16S- (R)	CRMCTGTTTAWCAAAAACAT	Takiya et al. 2006
Histone (H3)	HF (F)	ATGGCTCGTACCAAGCAGACGGC	Ogden & Whiting 2003
	HR (R)	ATATCCTTGGGCATGATGGTGAC	Ogden & Whiting 2003

Appendix S1. Morphological data matrix assembled for the phylogenetic study of *Aulacizes*.

										10									20									30									40					
Oncometopia orbona	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0
Depanisca sulcata	1	1	1	1	1	0	0	0	0	0	0	1	0	0	0	1	0	1	1	1	0	0	1	0	1	-	0	1	1	1	0	0	0	0	1	0	1	0	1	0	0	-	0
Paraulacizes irrorata	2	0	0	1	1	0	0	0	0	0	0	1	1	1	1	0	1	1	0	0	1	1	2	0	1	-	0	0	0	1	0	0	0	1	2	0	2	0	0	0	0	-	0
Paraulacizes mutans	3	0	1	0	0	0	0	1	0	0	0	0	0	0	1	1	0	1	0	0	0	0	3	0	0	1	0	0	0	2	1	1	0	0	3	0	1	0	0	0	0	-	0
Proconosama alalia	4	0	0	1	1	0	0	0	0	0	1	1	0	1	1	0	1	1	0	0	1	0	4	0	1	-	0	0	1	3	0	0	0	0	4	0	1	0	0	0	0	-	0
Proconosama takiyae	4	0	0	1	1	0	0	0	0	0	1	1	1	1	1	0	1	1	0	0	1	0	4	0	1	-	0	0	1	3	0	0	0	0	4	0	1	0	0	0	0	-	0
Pseudometopia amblardii	0	0	0	0	1	1	1	0	0	0	0	0	0	1	1	1	0	0	0	0	1	1	0	0	1	-	0	0	1	0	0	0	0	0	0	1	1	0	1	0	0	-	0
Pseudometopia appendiculata	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	1	0	0	1	-	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	-	0
Pseudometopia irenae	0	0	0	0	1	1	0	0	1	1	0	0	0	1	1	1	0	1	0	0	1	1	0	0	0	1	0	0	1	3	1	1	0	0	0	1	1	0	2	0	0	-	0
Pseudometopia latifascia	0	0	0	0	1	1	1	0	1	0	0	0	0	1	1	1	0	0	0	0	1	1	0	0	1	-	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	-	0
Pseudometopia phalaesia	0	0	0	0	1	1	1	0	0	0	0	0	0	1	1	1	0	0	0	0	1	1	0	0	1	-	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	-	0
Pseudometopia transversa	0	0	0	0	1	1	1	0	1	0	0	0	0	1	1	1	0	0	0	0	1	1	0	0	1	-	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	-	0
Aulacizes conspersa	0	0	0	1	1	0	0	0	1	0	0	1	0	1	1	1	0	1	0	0	1	1	0	0	0	1	0	0	1	0	1	1	0	0	0	0	1	1	0	1	1	0	1
Aulacizes erythrocephala	5	0	1	1	1	0	0	0	1	0	0	1	0	1	1	1	0	1	0	1	1	1	5	0	0	1	0	0	1	3	0	0	0	0	4	0	1	0	0	0	0	-	0
Aulacizes insistans	0	0	0	1	1	0	0	0	0	0	0	1	0	1	1	1	0	1	0	0	1	1	0	0	0	1	1	0	0	0	1	1	0	1	0	0	1	0	0	1	0	-	0
Aulacizes nigriceps	2	0	0	1	1	0	0	0	0	0	1	1	0	1	0	1	0	1	0	0	1	1	4	1	1	-	0	0	1	0	1	1	1	1	2	0	1	1	0	0	0	-	0
Aulacizes obsoleta	6	0	0	1	1	0	0	0	0	0	0	1	0	1	1	1	0	1	0	0	1	1	6	0	0	1	0	0	1	3	1	1	0	0	5	0	1	1	0	0	1	0	0
Aulacizes persistans	0	0	0	1	1	1	0	0	1	0	0	1	0	1	1	1	0	1	0	0	1	1	0	0	0	1	0	0	0	0	1	1	1	0	0	0	1	1	0	1	1	0	1
Aulacizes quadripunctata	5	0	1	1	1	1	1	1	0	0	0	1	0	1	1	1	0	1	0	0	1	1	5	0	0	1	0	0	0	4	0	0	0	0	6	0	1	0	0	0	0	-	0
Aulacizes repanda	0	0	0	1	1	1	0	0	0	1	0	1	0	1	0	1	0	1	0	0	1	1	0	0	1	-	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0
Aulacizes similata	0	0	0	1	1	0	0	0	0	0	0	1	0	1	1	1	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	-	0

							50										60										70										80	
Oncometopia orbona	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	-	-	-	0	0	0	0	0	0
Depanisca sulcata	0	0	-	0	0	0	1	1	1	0	0	0	0	1	-	1	1	1	1	0	-	0	0	1	1	1	1	1	0	-	-	-	0	1	1	1	0	1
Paraulacizes irrorata	0	0	-	0	0	0	0	1	2	0	0	0	1	0	1	1	1	1	1	0	-	0	1	0	1	1	1	1	0	-	-	-	0	1	1	0	1	0
Paraulacizes mutans	0	0	0	0	0	0	0	0	2	0	0	0	1	0	0	1	1	1	1	0	-	0	1	0	1	1	1	1	0	-	-	-	0	1	1	0	1	0
Proconosama alalia	0	0	-	0	0	0	2	0	3	0	0	0	0	1	-	1	0	1	1	1	0	0	0	0	1	1	1	0	1	0	0	0	1	1	1	0	1	0
Proconosama takiyae	0	1	0	0	0	0	2	0	3	0	0	0	0	1	-	1	0	1	1	0	-	0	0	0	0	1	1	0	1	0	0	0	1	0	1	1	1	0
Pseudometopia amblardii	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	1	0	1	1	1	0	1	1	1	1	1	1	0	1	1	0
Pseudometopia appendiculata	0	1	0	0	0	1	2	0	2	0	0	0	0	1	-	1	0	1	1	0	-	0	1	0	1	1	1	0	1	1	2	0	0	1	1	1	1	0
Pseudometopia irenae	0	1	0	0	0	0	2	1	2	0	0	0	0	?	?	1	?	1	1	0	-	0	1	0	2	1	1	0	1	0	0	1	1	1	1	1	1	0
Pseudometopia latifascia	0	1	0	0	0	0	2	0	2	0	0	0	0	0	2	1	0	1	1	0	-	0	1	0	1	1	1	0	1	0	0	1	1	1	1	1	1	0
Pseudometopia phalaesia	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	-	0	1	0	1	1	1	0	1	1	1	1	1	1	0	1	1	0
Pseudometopia transversa	0	1	0	0	0	0	2	0	2	0	0	0	0	0	2	1	0	1	1	0	-	0	1	0	1	1	1	0	1	0	0	1	1	1	1	1	1	0
Aulacizes conspersa	0	1	0	1	0	0	2	0	2	1	0	1	0	0	0	1	0	1	1	1	0	1	0	0	1	1	1	0	1	0	0	0	0	1	1	1	1	0
Aulacizes erythrocephala	0	0	-	0	0	0	2	0	3	0	0	0	0	1	-	1	0	1	2	0	-	0	0	0	1	1	1	0	1	0	0	0	0	1	1	1	1	0
Aulacizes insistans	0	1	0	0	1	0	0	1	2	1	0	1	0	1	-	1	0	1	1	1	0	1	0	0	1	1	1	0	1	0	0	0	0	1	1	1	1	0
Aulacizes nigriceps	0	0	-	0	0	0	2	0	2	0	0	0	0	1	-	1	1	1	1	1	0	1	0	0	1	1	1	0	1	0	0	0	0	1	1	1	1	0
Aulacizes obsoleta	0	1	1	0	0	0	0	1	2	0	1	0	0	0	0	1	1	1	1	0	-	0	0	0	1	1	1	0	1	0	0	0	0	1	1	1	1	0
Aulacizes persistans	0	1	0	0	0	0	2	0	2	1	0	1	0	0	2	1	0	1	1	1	1	1	0	0	1	1	1	0	1	0	0	0	0	1	1	1	1	0
Aulacizes quadripunctata	1	1	0	0	0	0	2	0	3	0	0	0	0	0	2	1	1	1	2	0	-	0	0	0	1	1	1	0	1	0	0	0	0	1	1	1	1	0
Aulacizes repanda	0	1	0	1	0	1	2	0	2	0	0	0	0	0	2	1	0	1	1	1	1	0	0	0	1	1	1	0	1	0	0	0	0	1	1	1	1	0
Aulacizes similata	0	1	1	0	0	1	2	0	0	0	1	0	0	0	2	1	1	1	3	0	-	0	0	0	1	1	1	0	1	0	0	0	0	1	1	1	1	0

Oncometopia orbona	0	0	0	0	0	-	0	0	0	0	0
Depanisca sulcata	1	0	1	1	0	-	0	1	0	1	0
Paraulacizes irrorata	0	1	1	1	1	0	0	0	0	0	0
Paraulacizes mutans	1	1	1	1	1	0	0	0	0	0	0
Proconosama alalia	0	0	1	1	1	1	0	0	1	0	0
Proconosama takiyae	0	2	1	1	1	1	0	0	1	0	0
Pseudometopia amblardii	0	0	1	2	0	-	1	0	0	0	0
Pseudometopia appendiculata	0	0	1	2	0	-	1	0	0	0	0
Pseudometopia irenae	0	0	1	2	0	-	1	0	0	0	0
Pseudometopia latifascia	0	0	1	1	0	-	1	0	0	0	0
Pseudometopia phalaesia	0	0	1	1	0	-	1	0	0	0	0
Pseudometopia transversa	0	0	1	2	0	-	1	0	0	0	0
Aulacizes conspersa	1	0	0	2	1	2	0	0	0	0	1
Aulacizes erythrocephala	1	0	0	2	1	2	0	0	0	0	1
Aulacizes insistans	1	0	0	2	1	2	0	0	0	0	1
Aulacizes nigriceps	1	0	0	2	1	2	0	0	0	0	1
Aulacizes obsoleta	1	2	0	2	1	2	0	0	0	0	1
Aulacizes persistans	1	0	0	2	1	2	0	0	0	0	1
Aulacizes quadripunctata	1	0	0	2	1	2	0	0	0	0	1
Aulacizes repanda	1	2	0	1	1	2	0	0	0	0	1
Aulacizes similata	1	0	0	1	1	2	0	0	0	0	1

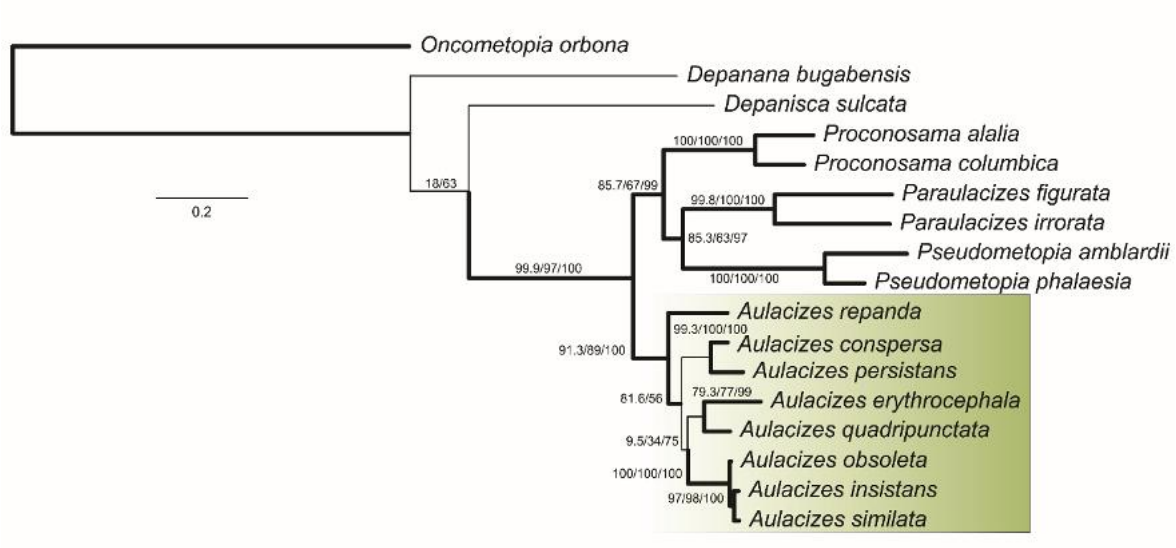


Figure S1. Maximum likelihood tree of *Aulacizes* based on 2,089 bp of 16S, COI, COII, and H3 (-lnL = 9715.736). Thick branches are those also recovered in the Bayesian inference. Values associated with branches are likelihood SH-aLRT ≥ 80 / ultrafast bootstrap support ≥ 95 / Bayesian posterior probabilities (in percentages) ≥ 95. Green rectangle indicates *Aulacizes*.

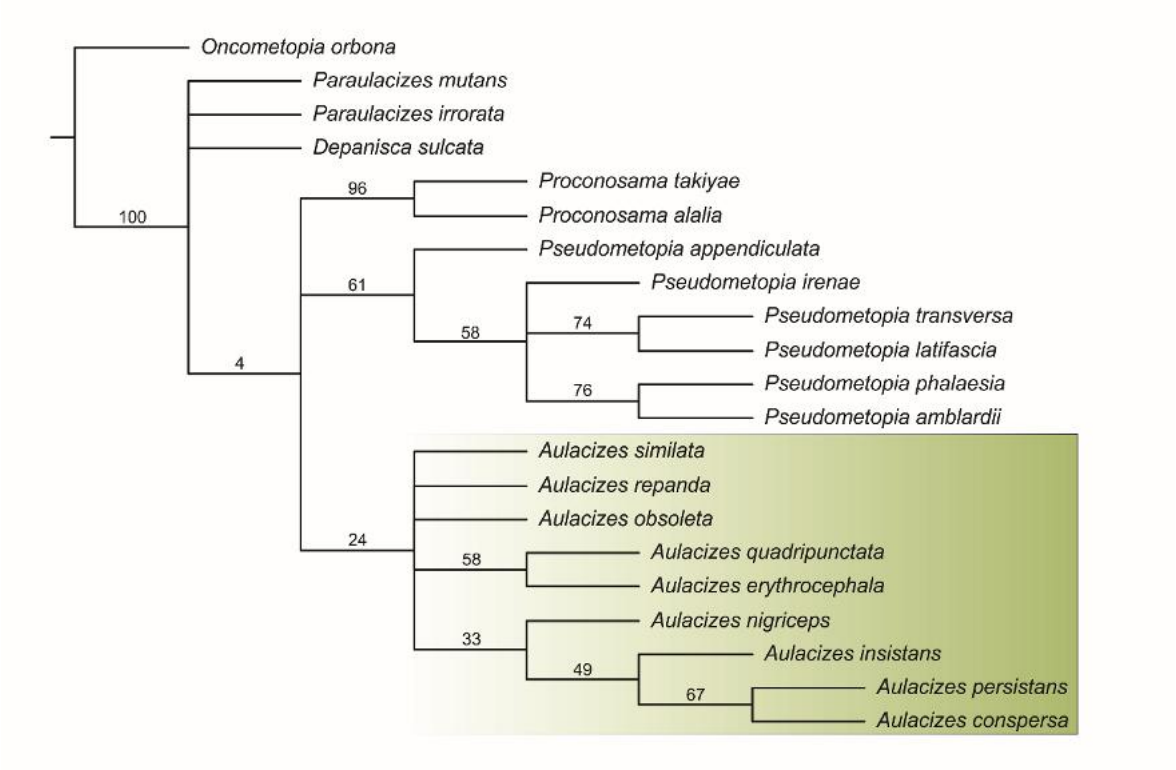


Figure S2. Strict consensus tree obtained from 78 equally most parsimonious trees (L = 254, CI = 0.484, and RI = 0.511) based on the morphological dataset of *Aulacizes*. Bootstrap support values are given above branches. Green rectangle indicates *Aulacizes*.

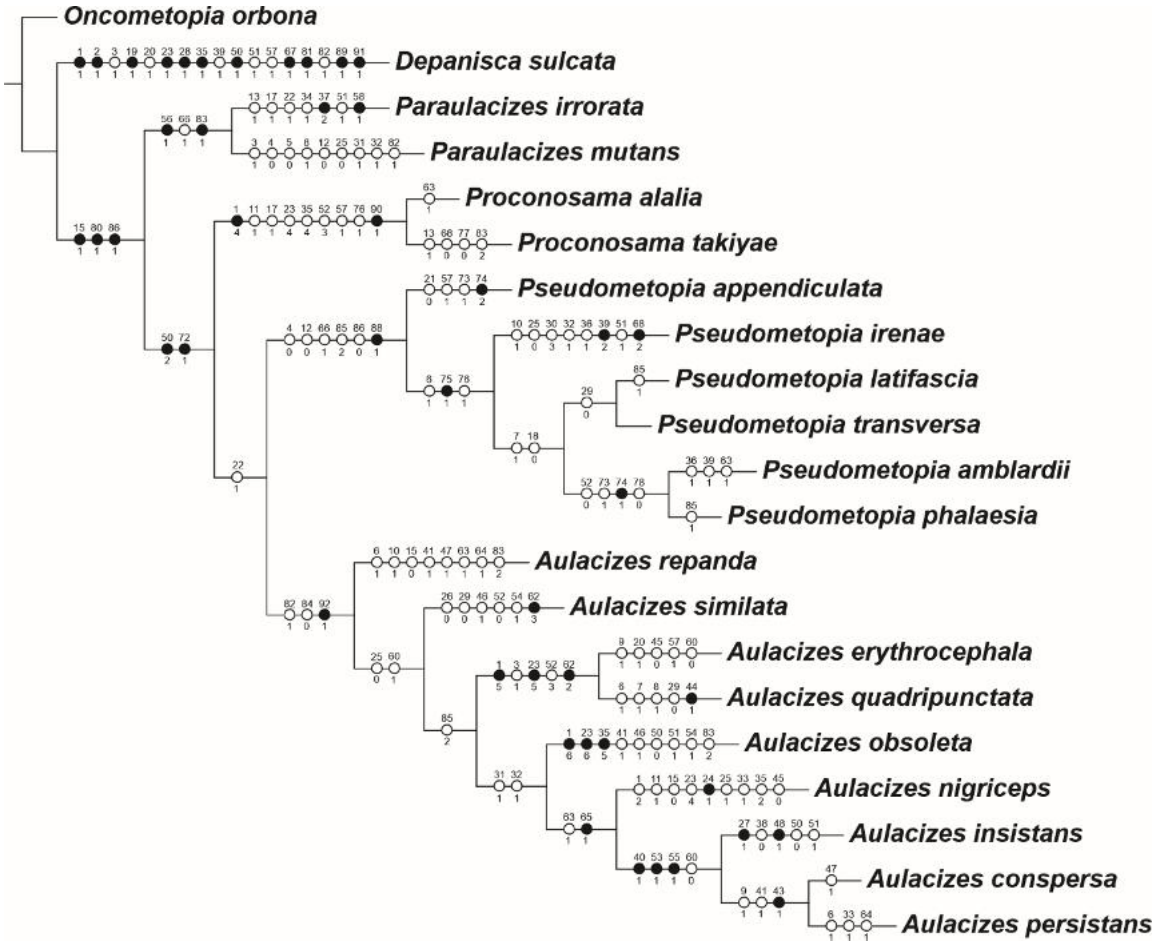


Figure S3. Character optimization on one of the 78 equally most parsimonious trees, based on 92 morphological characters (L = 238, CI = 0.517, and RI = 0.571). Tree rooted with *Oncometopia orbona*. Character numbers shown above circles; character states below. White circles (○) indicate homoplastic transformations and black circles indicate (●) non-homoplastic transformations.

Figs. 1–9. Live *Aulacizes* individuals. (1) *A. erythrocephala* (RPPN Serra Bonita, Camacan, Bahia State); (2) *A. obsoleta* (São José dos Pinhais, Paraná State); (3) *A. repanda* (São José dos Pinhais, Paraná State); (4) *A. conspersa* (Viçosa, Minas Gerais State); (5) *A. quadripunctata* (Parque Nacional do Itatiaia, Itamonte, Minas Gerais State); (6) *A. nigriceps* (Jardim Botânico de São Paulo, São Paulo State); (7) *A. similata* (Parque Nacional da Serra dos Órgãos, Teresópolis, Rio de Janeiro State); (8) *A. insistans* (Nova Friburgo, Rio de Janeiro State); (9) *A. persistans* (Parque Nacional da Serra dos Órgãos, Teresópolis, Rio de Janeiro State). Photographs taken by Daniela M. Takiya (1 and 5), Alexandre C. Domahovski (2 and 3), Frederico F. Salles (4), Carlos A. Raposo (6), and André A. Alves (7, 8, and 9).

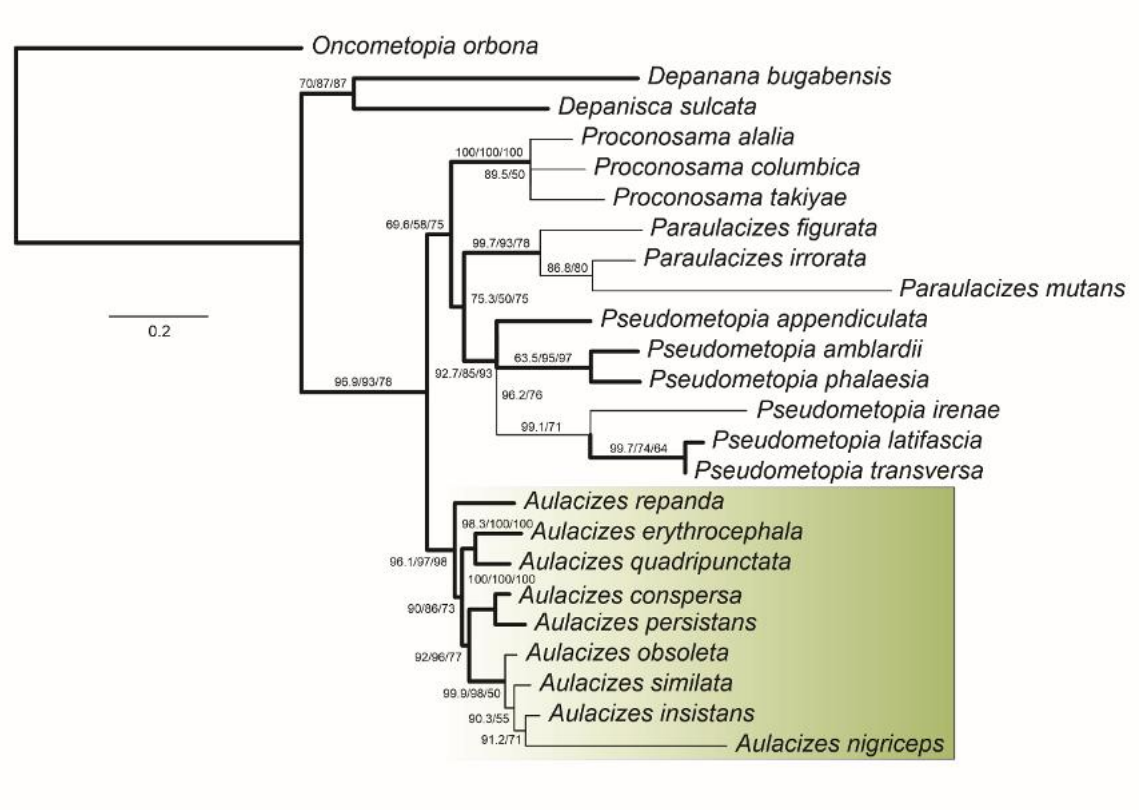
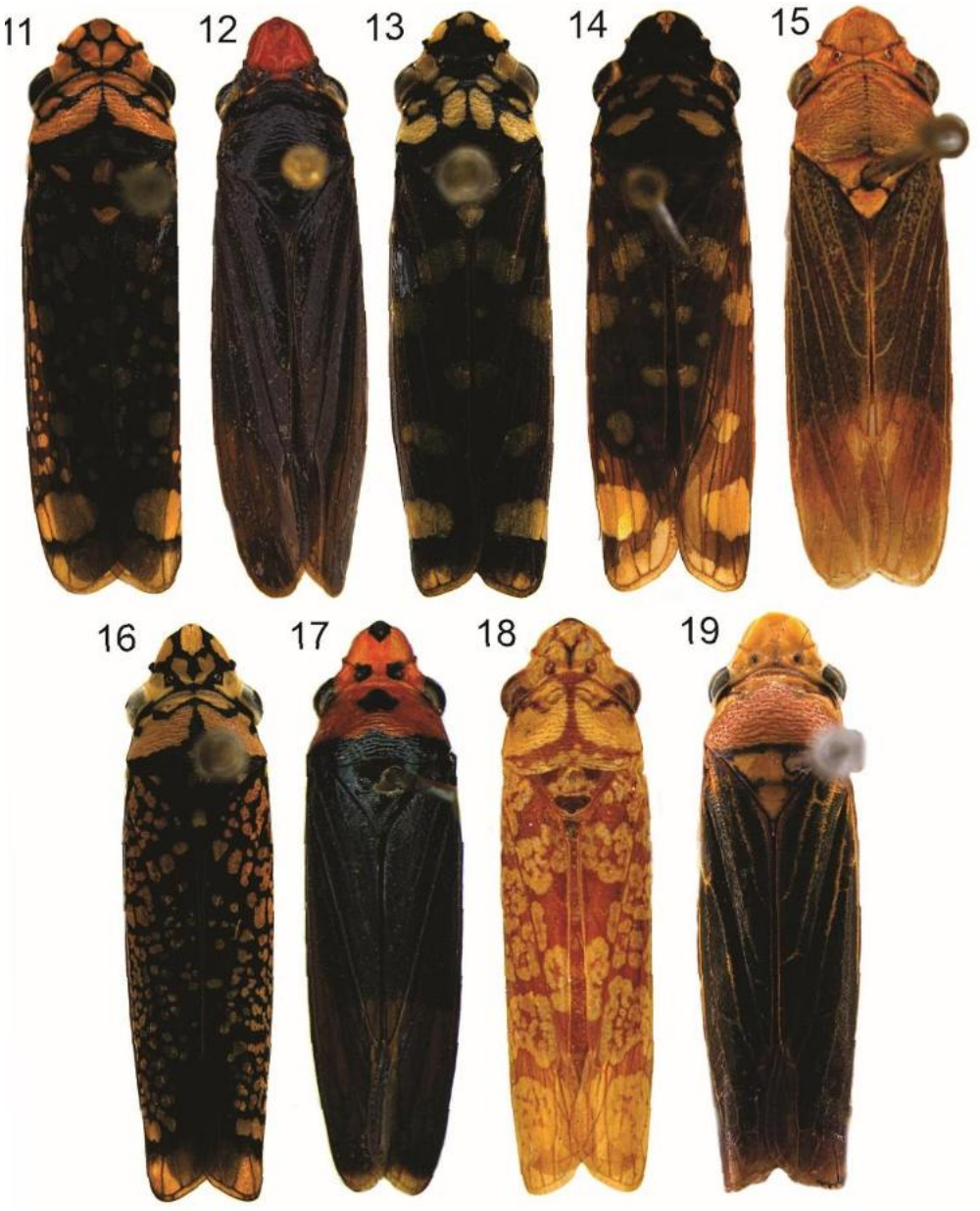


Fig. 10. Maximum likelihood phylogenetic tree of *Aulacizes* based on combined morphological (92 characters) and molecular data (2,089 bp of 16S, COI, COII, and H3) (lnL = -11521.166). Thick branches are those also recovered in the Bayesian inference. Support values associated with branches are SH-aLRT > 80 / ultrafast bootstrap >95 / Bayesian posterior probabilities (in percentages) > 95. Green rectangle indicates *Aulacizes*.



Figs. 11–19. Dorsal habitus of *Aulacizes* specimens. (11) *A. conspersa* Walker, 1851 (Parque Nacional da Serra dos Órgãos, Teresópolis, Rio de Janeiro State, DZRJ); (12) *A. erythrocephala* (Germar, 1821) (RPPN Camacan, Bahia State, DZRJ); (13) *A. insistans* (Walker, 1858) (Parque Nacional da Serra dos Órgãos, Teresópolis, Rio de Janeiro State, DZRJ); (14) *A. nigriceps* Schmidt, 1928 **stat. nov., sp. rev.** (Estrada dos Castelhanos, Guaratuba, Paraná State, DZUP); (15) *A. obsoleta* Melichar, 1926 (Passo Fundo, Rio Grande do Sul State, DZUP); (16) *A. persistans* (Walker, 1858) (Parque Nacional da Serra dos Órgãos, Teresópolis, Rio de Jsaneiro State, DZRJ); (17) *A. quadripunctata* (Germar, 1821) (Teresópolis, Rio de Janeiro State, DZRJ); (18) *A. repanda* (Signoret, 1855) (Rio Vermelho, Santa Catarina State, MZSP); (19) *A. similata* (Signoret, 1855) (Parque Nacional da Serra dos Órgãos, Teresópolis, Rio de Janeiro State, DZRJ).

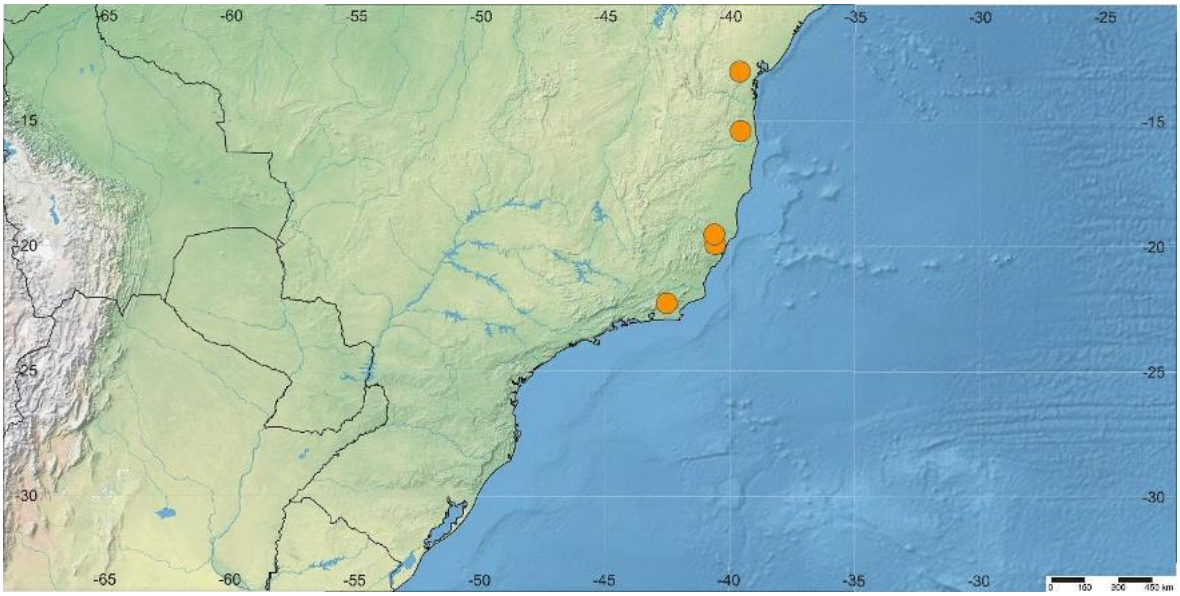
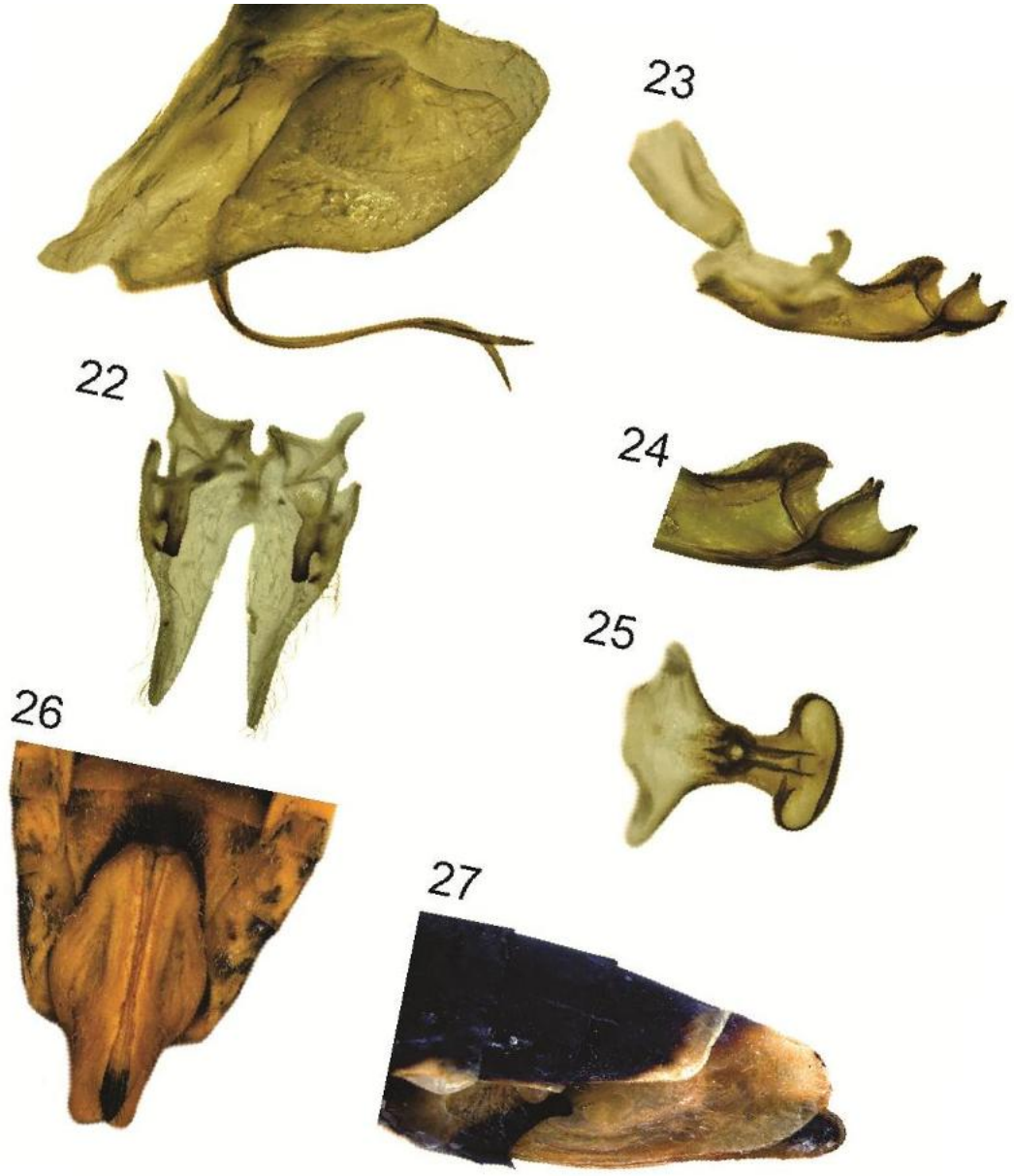


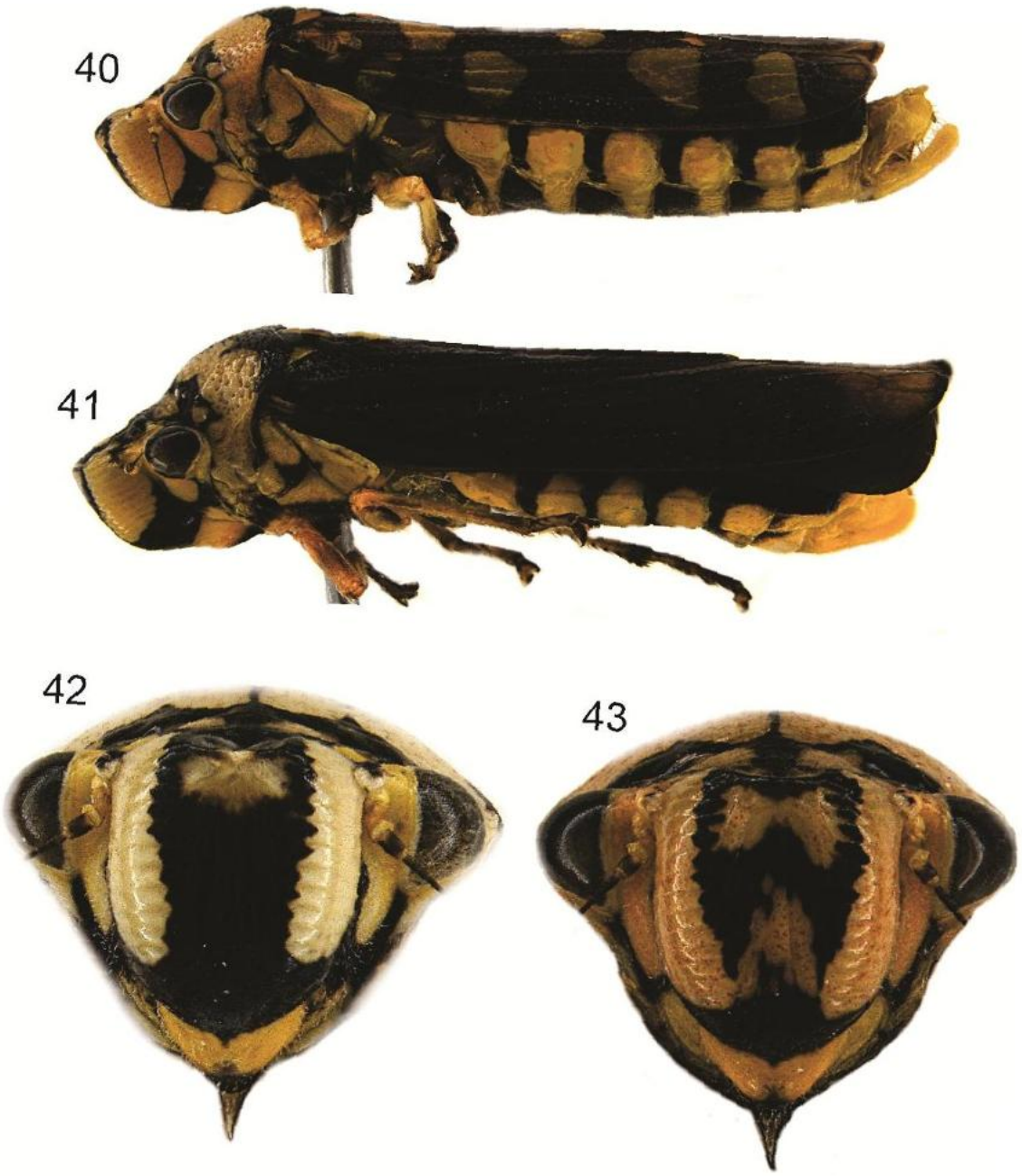
Fig. 20. Distribution map of *Aulacizes erythrocephala* (Germar, 1821).



Figs. 21–27. Male and female terminalia of *A. insistans* (Walker, 1858). Male from Teresópolis, Rio de Janeiro State, DZRJ; female from Itamonte, Minas Gerais State, DZRJ. (21) male pygofer, lateral view; (22) subgenital plates, styles, and connective, dorsal view; (23) ejaculatory bulb and aedeagus, lateral view; (24) apical portion of aedeagus, lateral view; (25) aedeagus, dorsal view; (26) apical portion of female abdomen, ventral view; (27) apical portion of female abdomen, lateral view.

Figs. 28–31. Photographs of type specimens (©The Natural History Museum, London; M. D. Webb and V. Lemaitre). (28–30) Dorsal, ventral, and face views of male lectotype of *Aulacizes insistans* (Walker, 1858); (31) Dorsal view of holotype of *A. obtusa* Walker, 1858.

Figs. 32–39. Dorsal habitus of males of *Aulacizes insistans* (Walker, 1858) showing variation in the distribution of spots on the crown, pronotum, and forewings. (32–35, 37–39) Parque Nacional da Serra dos Órgãos, Teresópolis, Rio de Janeiro State, DZRJ; (36) Nova Friburgo, Rio de Janeiro State, DZRJ.



Figs. 40–43. Lateral habitus and face of males of *Aulacizes insistans* (Walker, 1858) showing variation in the distribution of spots on forewings. Parque Nacional da Serra dos Órgãos, Teresópolis, Rio de Janeiro State, DZRJ.

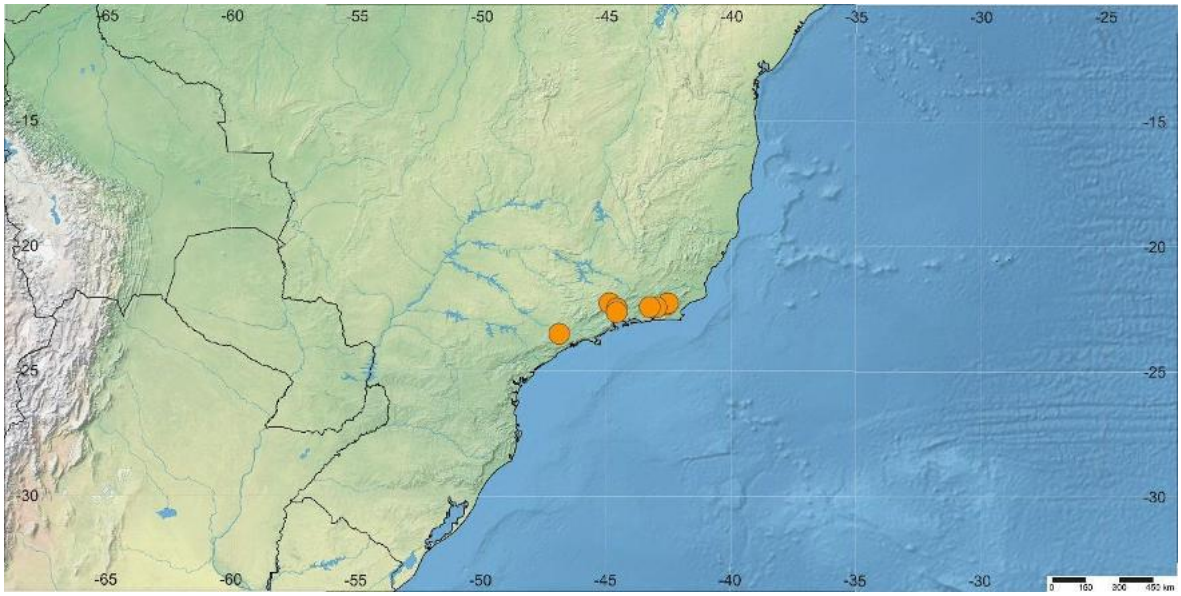
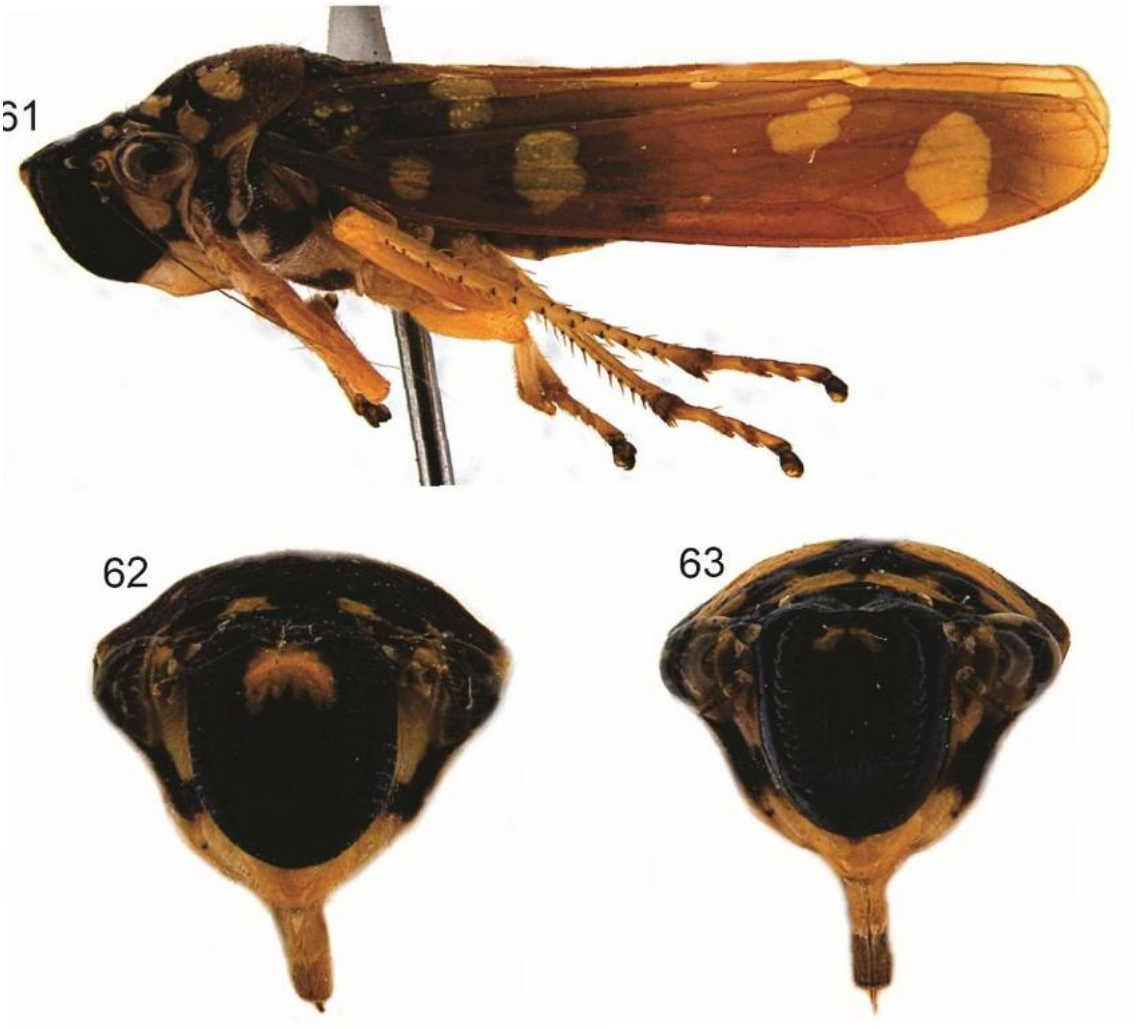


Fig. 44. Distribution map of *Aulacizes insistans* (Walker, 1858).

Figs. 45–50. Male terminalia of *Aulacizes nigriceps* Schmidt, 1928 **stat. nov., sp. rev.** Caraguatatuba, São Paulo State, MZSP. (45) genital capsule, lateral view; (46) subgenital plates, styles, and connective, dorsal view; (47) subgenital plate, style, and aedeagus, lateral view; (48) aedeagus, lateral view; (49) apical portion of aedeagus, lateral view; (50) aedeagus, dorsal view.

Figs. 51–53. Male lectotype of *Aulacizes maculata* var. *nigriceps* Schmidt, 1928 (©Museum and Institute of Zoology, Polish Academy of Sciences, Warsaw; P. D. Szymroszczyk). (51) dorsal view; (52) ventral view; (53) labels. Results of the present study support the revalidation of *nigriceps* and its new status as a distinct species.

Figs. 54–60. Dorsal habitus of males of *Aulacizes nigriceps* Schmidt, 1928 **stat. nov., sp. rev.** showing variation in the distribution of spots on the crown, pronotum, and forewings. (54–58) Estrada dos Castelhanos, Guaratuba, Paraná State, DZUP; (59) Caraguatatuba, São Paulo State, MZSP; (60) Timbó, Santa Catarina State, MZSP.



Figs. 61–63. Lateral habitus and face of males of *Aulacizes nigriceps* Schmidt, 1928 **stat. nov., sp. rev.** showing variation in the distribution of spots on the crown, face, pronotum, and forewings. (61 and 63) Estrada dos Castelhanos, Guaratuba, Paraná State, DZUP. (62) Caraguatatuba, São Paulo State, MZSP.

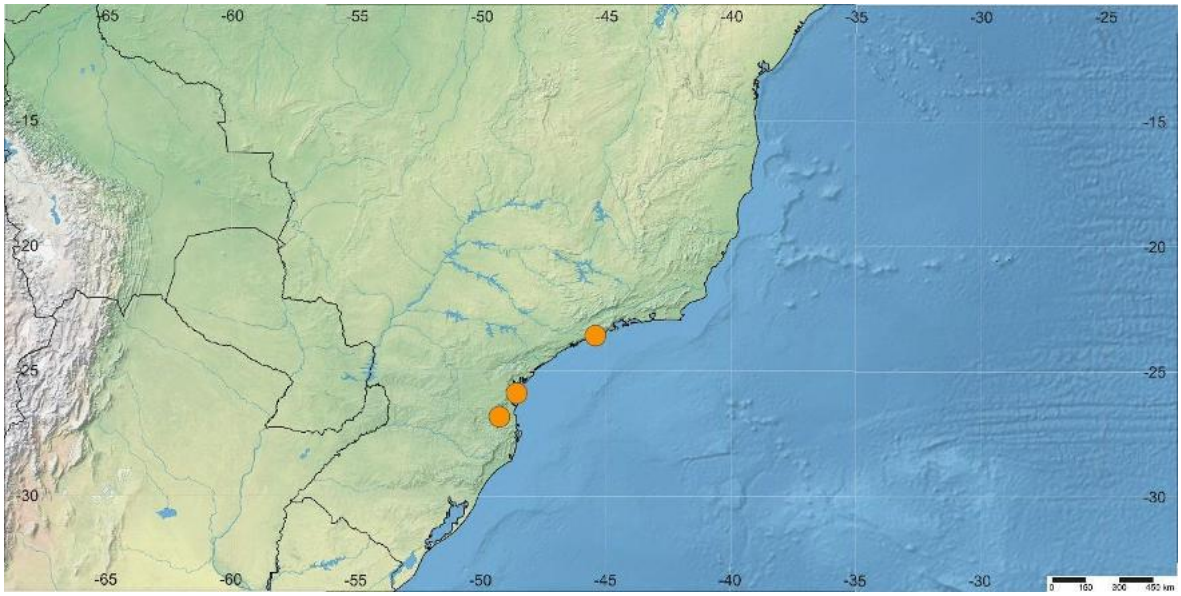
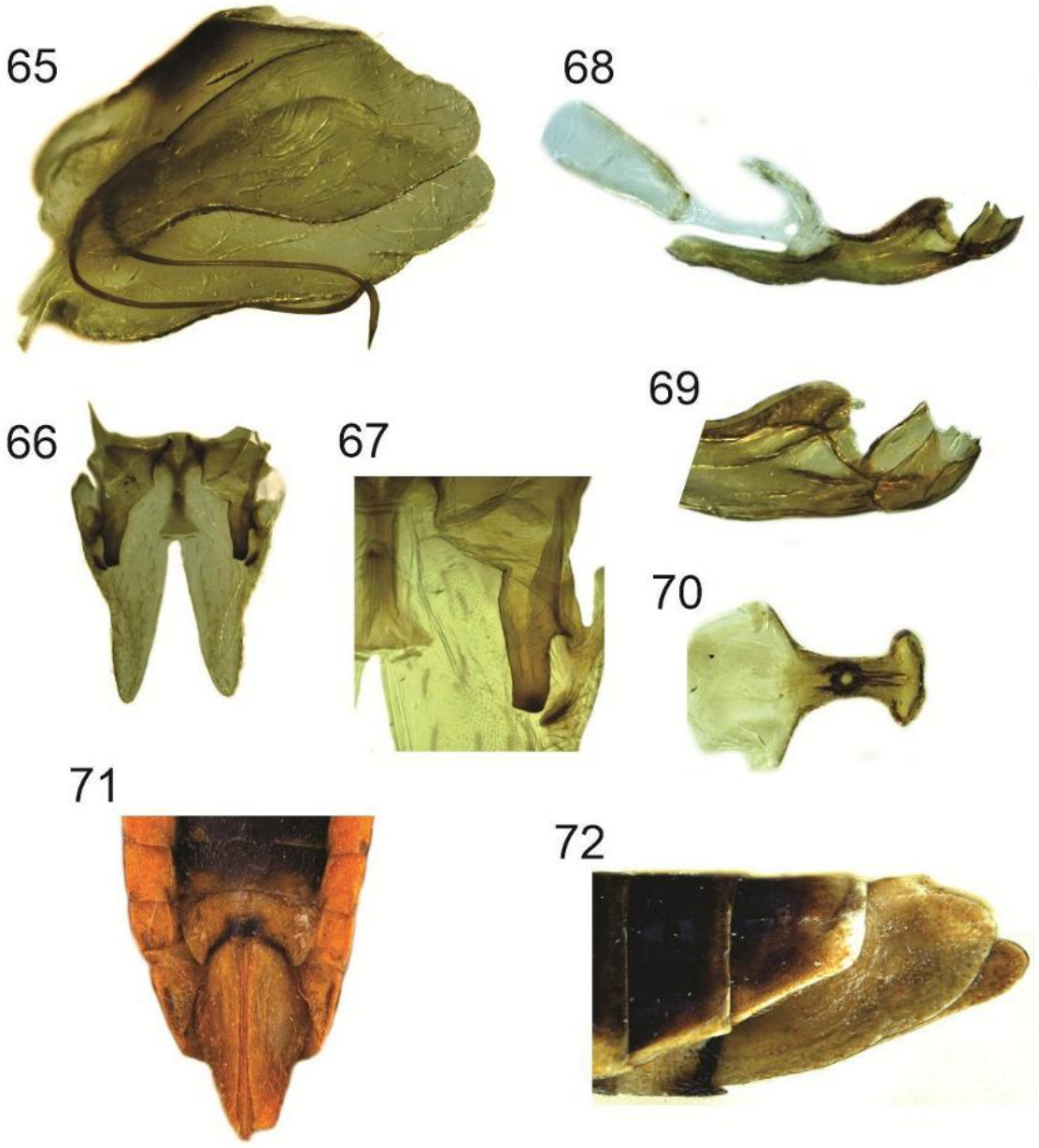


Fig. 64. Distribution map of *Aulacizes nigriceps* Schmidt, 1928 **stat. nov., sp. rev.**



Figs. 65–72. Male and female terminalia of *Aulacizes obsoleta* Melichar, 1926. Male from Passo Fundo, Rio Grande do Sul State, DZUP; female from Curitiba, Paraná State, DZUP. (65) male pygofer, lateral view; (66) subgenital plates, styles, and connective, dorsal view; (67) dorsal dentiform projection at basal half of subgenital plate associated with style apex; (68) ejaculatory bulb and aedeagus, lateral view; (69) apical portion of aedeagus, lateral view; (70) aedeagus, dorsal view; (71) apical portion of female abdomen, ventral view; (72) apical portion of female abdomen, lateral view.

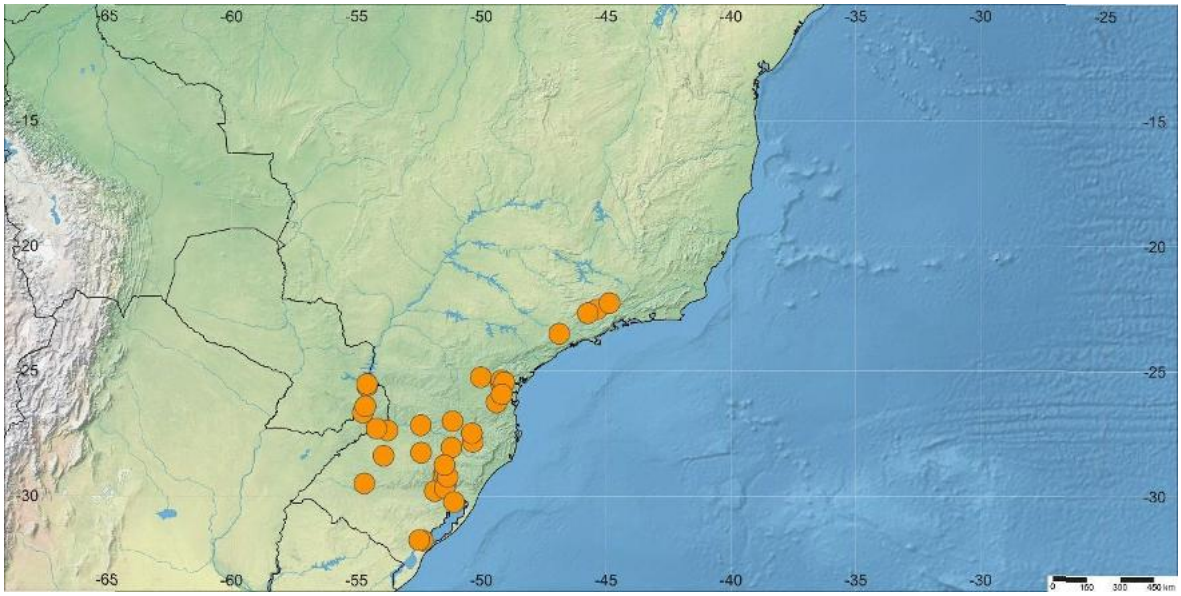
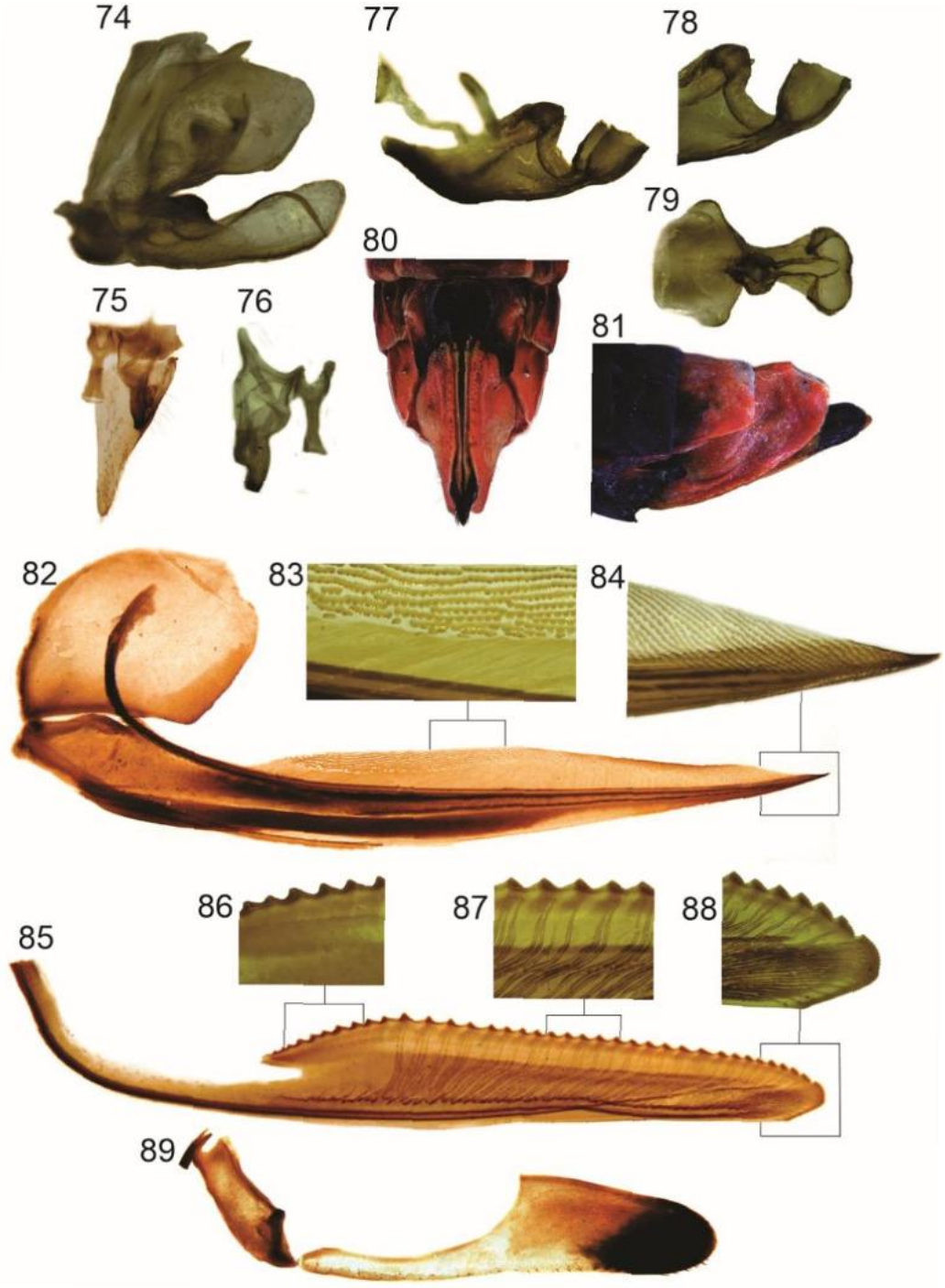


Fig. 73. Distribution map of *Aulacizes obsoleta* Melichar, 1926.



Figs. 74–89. Male and female terminalia of *Aulacizes quadripunctata* (Germar, 1821). Teresópolis, Rio de Janeiro State, DZRJ. (74) male genital capsule, lateral view; (75) subgenital plate, style, and connective, dorsal view; (76) style and connective, dorsal view; (77) distal part of ejaculatory bulb and aedeagus, lateral view; (78) apical portion of aedeagus, lateral view; (79) aedeagus, dorsal view; (80) apical portion of female abdomen, ventral view; (81) apical portion of female abdomen, lateral view; (82) valvifer I and valvula I, lateral view; (83) dorsal sculptured area at median portion; (84) apical portion showing dorsal and ventral sculptured areas; (85) valvula II, lateral view; (86–88) teeth at basal, median, and apical portions, respectively; (89) valvifer II and gonoplac, lateral view.

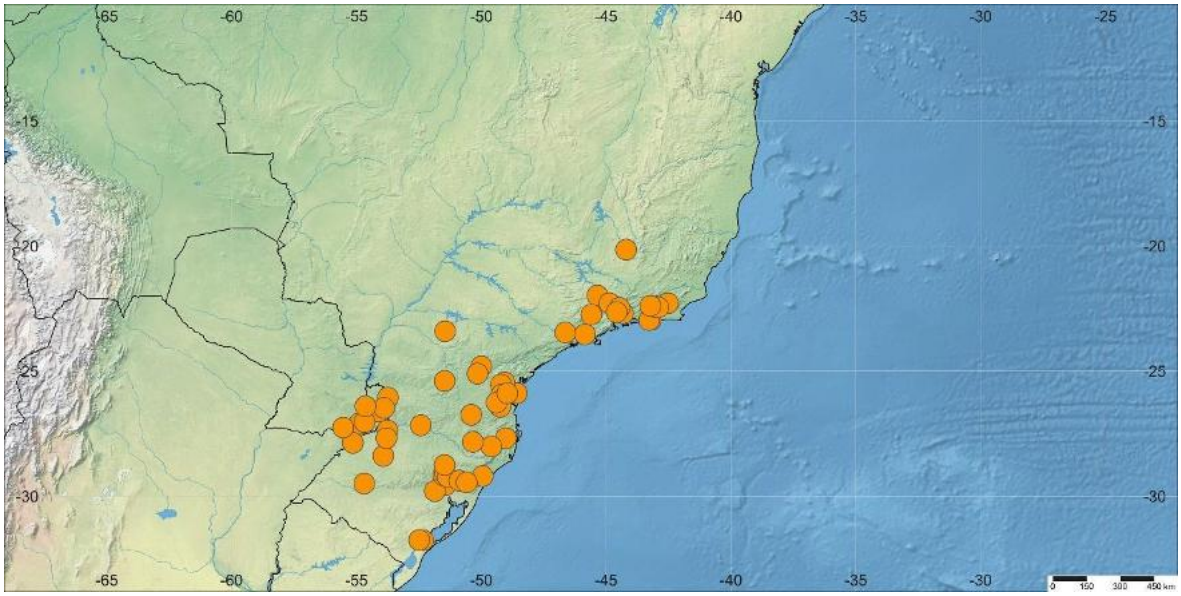
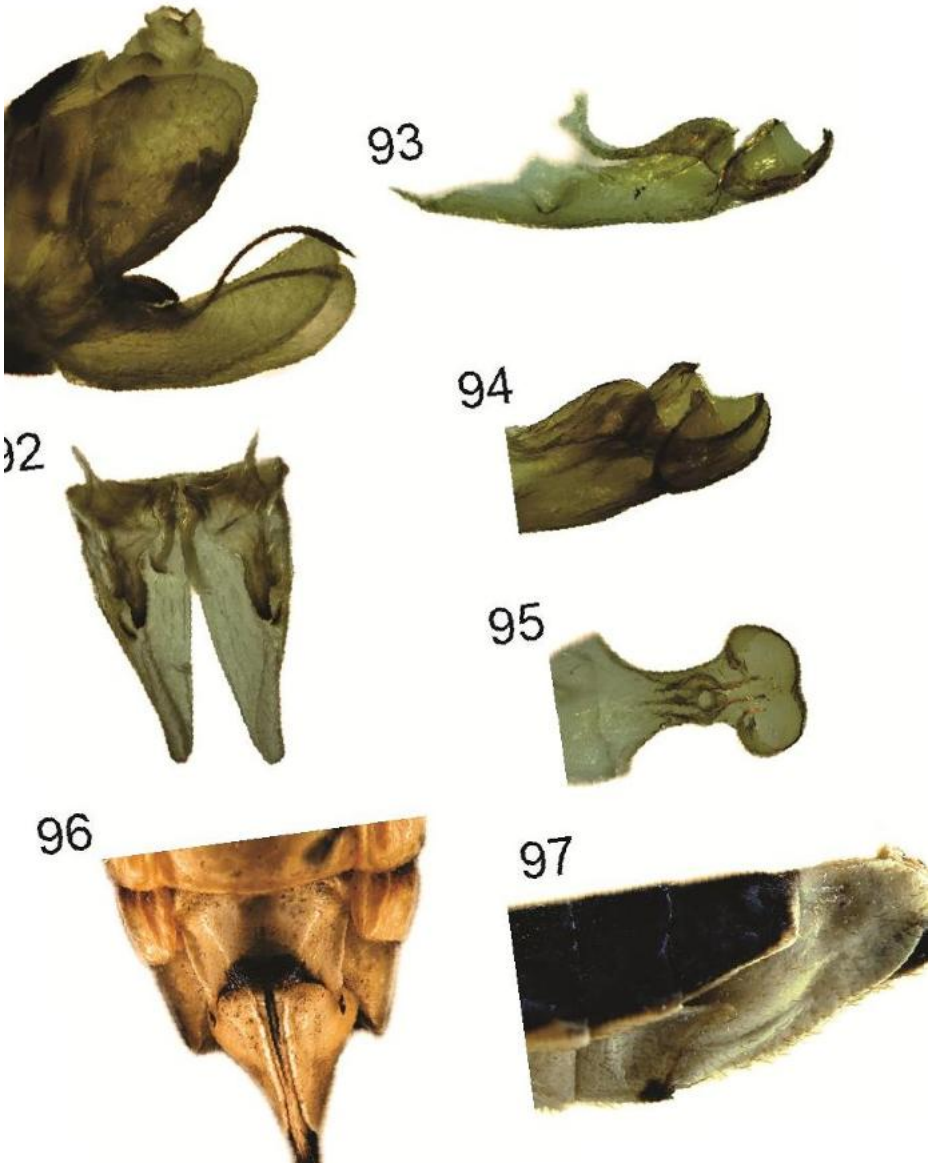


Fig. 90. Distribution map of *Aulacizes quadripunctata* (Germar, 1821).



Figs. 91–97. Male and female terminalia of *Aulacizes similata* (Signoret, 1855). Parque Nacional da Serra dos Órgãos, Teresópolis, Rio de Janeiro State, DZRJ. (91) male genital capsule, lateral view; (92) subgenital plates, styles, and connective, dorsal view; (93) aedeagus, lateral view; (94) apical portion of aedeagus, lateral view; (95) aedeagus, dorsal view; (96) apical portion of female abdomen, ventral view; (97) apical portion of female abdomen, lateral view.

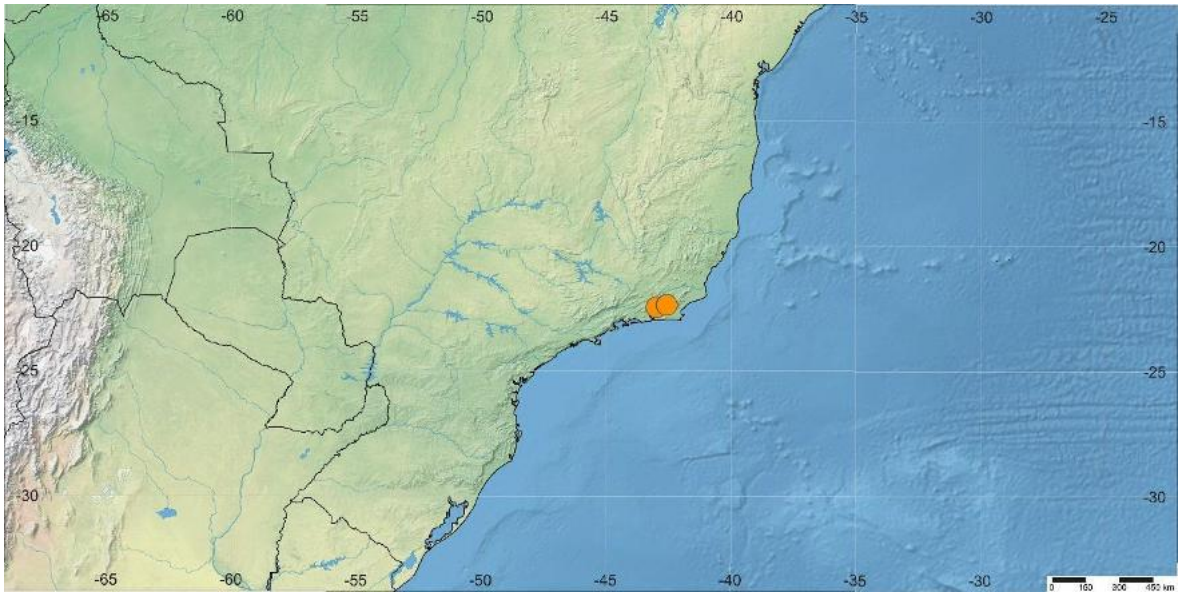
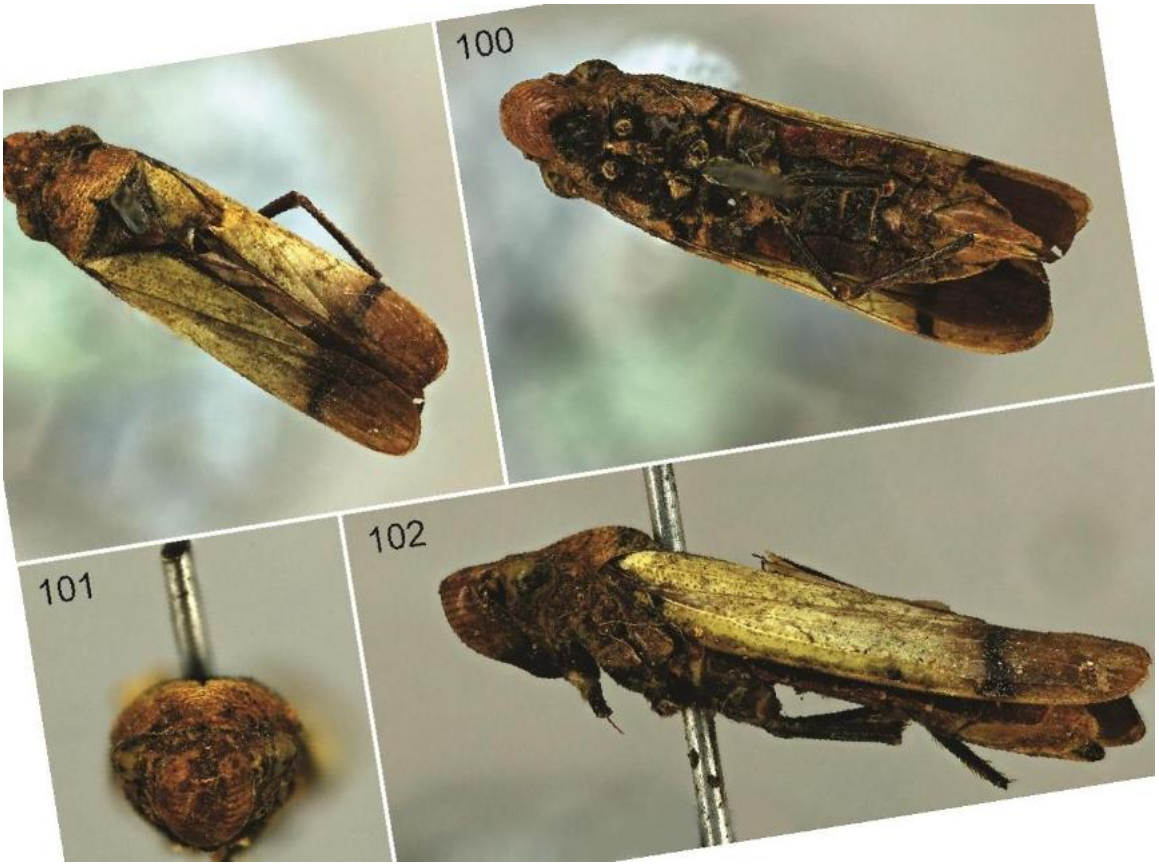


Fig. 98. Distribution map of *Aulacizes similata* (Signoret, 1855).



Figs. 99–102. Female holotype of *Aulacizes basalis* Walker, 1851 (©The Natural History Museum, London; M. D. Webb and V. Lemaitre). (99) habitus, dorsal view; (100) habitus, ventral view; (101) face, anterior view; (102) habitus, lateral view. The present study proposes the transference of this species to *Pseudometopia* Young, 1968.

Figs. 103–106. Female lectotype of *Tettigonia clypeata* Signoret, 1855 (©Naturhistoriska Riksmuseet, Stockholm; Gunvi Lindberg). (103) habitus, dorsal view; (104) habitus, lateral view; (105) habitus, ventral view; (106) labels. The present study proposes the transference of this species to *Deselvana* Young, 1968.

GENERAL CONCLUSIONS

This study provides a significant contribution to our knowledge of the taxonomy and phylogeny of *Aulacizes* Amyot & Serville, 1843 (Hemiptera: Cicadellidae: Cicadellinae: Proconiini), including species delimitation analyses, taxonomic revision, and investigation of the evolutionary relationships of the group. Results obtained highlight the importance of integrating different approaches for the advancement of systematic studies on the Cicadellidae. Thus, this work provides a basis for future research on the diversity and evolution of *Aulacizes* and other members of this family, contributing to the resolution of taxonomic problems.

The use of both morphological and molecular data allowed an assessment of the limits among species and contributed to the taxonomic reinterpretation of *Aulacizes*. The review allowed the delimitation of the genus and redefinition of species. Complementary species descriptions with information on the morphology of the male and female terminalia were added. Phylogenetic analyses based on morphological and molecular characters, including new DNA sequence data, contributed to the advance of our understanding of the evolutionary history of *Aulacizes*, including its internal relationships and position within the Proconiini. In addition, data on the geographic distribution of *Aulacizes*, including various new species records, reinforce the need for more comprehensive reviews of the group, contributing to a better understanding of the biogeography of the Proconiini from South America.

After this study, *Aulacizes* remains with nine recognized species, but with a new configuration, viz., *A. conspersa* Walker, 1851, *A. erythrocephala* (Germar, 1821), *A. insistans* (Walker, 1858), *A. nigriceps* Schmidt, 1928 **stat. nov., sp. rev.**, *A. obsoleta* Melichar, 1926, *A. persistans* (Walker, 1858), *A. quadripunctata* (Germar, 1821), *A. repanda* (Signoret, 1855), and *A. similata* (Signoret, 1855). The apparently limited interspecific variation in the terminalia of both sexes within the genus was highlighted. The homogeneity of the male terminalia makes identification and delimitation of species difficult, explaining the long-standing challenges in resolving the taxonomy of *Aulacizes* based solely on morphology. For the first time, a taxonomic key to the species of the genus was elaborated.