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Phylogenetic analyses provide new insights into systematics of the longhorned beetle tribe Acrocinini (Coleoptera: Cerambycidae: Lamiinae)

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Abstract. Acrocinini is a Neotropical tribe of Lamiinae (Cerambycidae) with a single species: *Acrocinus longimanus* (Linnaeus, 1758). Conspicuous autapomorphic characters in this species have led to divergent interpretations of the morphological body plan of the tribe and its affinities with species of *Macropophora* Thomson, 1864 and some species of *Oreodera* Audinet-Serville, 1835. Therefore, Acrocinini has not always been a monotypic tribe, and its taxonomic composition has changed according to the inclusive or exclusive placement of species of *Macropophora* and *Oreodera*. We carried out phylogenetic analyses, using maximum parsimony and Bayesian criteria, based on 34 morphological characters and 22 taxa in order to evaluate the taxonomic limits of Acrocinini and to infer the relationship among *Acrocinus* Illiger, 1806, *Macropophora* and *Oreodera*. Our results reveal a close relationship among these three genera, supported by six synapomorphies: prothorax with a suture surrounding the lateral tubercle; pronotum with linear coarse punctuation near posterior margin; protibia cylindrical; protibia with a projection near sulcus at inner face; protibia without a pair of apical spurs at inner margin; and protarsomere II longer than wide. New evidence confirms that Acrocinini includes *Acrocinus*, *Macropophora* and *Oreodera*, and increases the number of characters that define the tribe. Additionally, we present new records of *Macropophora accentifer* (Olivier, 1795) for Brazil (Mato Grosso and Mato Grosso do Sul) and of *Macropophora trochlearis* (Linnaeus, 1758) for Venezuela and Northern Brazil (Amapá, Acre and Rondônia).

Key words. *Acrocinus*, cladistic analysis, Harlequin, *Macropophora*, *Oreodera*, phylogeny, taxonomy.

1. Introduction

Acrocinini Swainson, 1840 is a tribe of longhorned beetles (Cerambycidae: Lamiinae) currently composed of a single species: *Acrocinus longimanus* (Linnaeus, 1758), one of the most peculiar and most colourful Neotropical species of Cerambycidae, commonly known as Harlequin or Arlequim-da-mata (in Portuguese) (Fig. 1). Current classifications recognize Acrocinini as a monotypic tribe. However, its taxonomic composition has undergone several changes throughout the history of classification of Lamiinae, reflecting diverse interpretations on the morphological affinities of this species with *Macropophora* Thomson, 1864 and some species of *Oreodera* Audinet-Serville, 1835. Although these genera are currently allocated in Acanthoderini Thomson, 1860, several classification schemes have included some of their species as part of the tribe Acrocinini (e.g., Swainson 1840; Lepesme 1946).

Originally proposed as a subfamily of Prionidae (Swainson 1840), Acrocinini was defined by the following characteristics: body depressed, elytra with spines at

Fig. 1. Male (left) and female (right) of *Acrocinus longimanus* (Linnaeus). Photo kindly provided by Peter Møllmann. Scale bar approximately 5 cm.

their apex, tarsomere I as long as the others and tarsomere III lobed or 'heart-shaped'. Apart from *Acrocinus* Illiger, 1806, Swainson (1840) mentioned other three genera as belonging to the tribe: *Macropus* Audinet-Serville, 1835 (name synonymised under *Macropophora* by Thomson 1864), *Oreodera* and *Microplia* Audinet-Serville, 1835. A few years later, Thomson (1864) redefined the systematic limits of Acrocinini to allocate only genera that have small frons, filiform femora and very elongated forelegs, including two genera in the tribe: *Acrocinus* and *Macropophora*. Following Thomson's (1864) system, Lacordaire (1872) improved the diagnosis of the tribe, adding several characters not mentioned in previous diagnoses (e.g., the median coxal cavities widely opened and metasternum long) and, although without indicating characters, he associated Acrocinini with the tribes Acanthoderini (through *Oreodera*) and Polyrhaphidini Thomson, 1860.

The first taxonomic revision of Acrocinini was published by Lepesme (1946), who delimited the tribe by the scape and femora elongate and subcylindrical (never clavate), fore femur and tibia distinctly elongated in males, and glabrous tarsi. Under this diagnosis, Lepesme (1946) included six species in the tribe: *A. longimanus*, *Macropophora accentifer* (Olivier, 1795), *M. lacordairei* Lepesme, 1946, *M. trochlearis* (Linnaeus, 1758), *M. hoffmanni* (Thomson, 1860) and *M. lateralis* Lacordaire, 1872 (species name synonymised under *M. hoffmanni*, which is currently placed in *Oreodera*). The most recent work dealing with systematics of Acrocinini was undertaken by Néouze & Tavakilian (2003). The authors considered that the diagnostic characters of Acrocinini proposed by Lepesme (1946) were not present in all species of the tribe. They then transferred *Macropophora* to Acanthoderini and left only *A. longimanus* in Acrocinini. The composition of Acrocinini has been particularly unstable with the inclusion or exclusion of *Macropophora* and *Oreodera* species. Both *Macropophora* and *Oreodera*, in addition to *Acrocinus*, are restricted to the Neotropical Region. *Macropophora* is a small genus composed of four species (*M. accentifer*, *M. lacordairei*, *M. trochlearis* and *M. worontzowi* Lane, 1938) and its taxonomy is relatively well-resolved (Lepesme 1946; Néouze & Tavakilian 2003). *Oreodera*, on the other hand, is one of the species-richest genera of the Neotropical Lamiinae with 118 species (Monné 2020) and has never been revised.

The main arguments that defend tribe-level separation of *Macropophora* and *Oreodera* from *Acrocinus* are based on modifications related to the form of the scape and femora (Néouze & Tavakilian 2003). However, in the literature there is mention of characters that associate the morphology of these three genera, suggesting they share the same phylogenetic history, such as the shape of the mesosternal process, tibiae and tarsi (Thomson 1860, 1864; Lepesme 1946; Lacordaire 1872). In this sense, the unsolved systematic issues of Acrocinini may be associated with two factors: (1) misinterpretation of characters and (2) total absence of phylogenetic studies to infer the systematics of the tribe. Thus, considering the historical difficulties concerning the delimitation of Acrocinini, in this manuscript we carried out phylogenetic analyses based on morphological characters in order to define the taxonomic limits of Acrocinini and to infer the relationships among *Acrocinus* and the genera *Macropophora* and *Oreodera*. Additionally, taxonomic notes and new distribution records are provided for species of *Macropophora*.

2. Material and methods

2.1. Material

In order to infer the monophyly of Acrocinini and the phylogenetic relationship among *Acrocinus*, *Macropophora* and *Oreodera,* 21 taxa were sampled, including the sole species of Acrocinini (*A. longimanus*), 18 representatives from 7 genera of Acanthoderini (including 3 species of *Macropophora* and 11 species of *Oreodera*), 1 species of Acanthocinini Blanchard, 1845 (*Acanthocinus aedilis* (Linnaeus, 1758)), and 1 species of Polyrhaphidini (*Polyrhaphis grandini* Buquet, 1853; used to root the trees in the analyses) (see Table 1).

Outgroups were chosen based on the phylogenetic relationships of Lamiinae provided by Souza et al. (2020) and from taxa considered close to *Acrocinus* in previous taxonomic treatments, such as Thomson (1860, 1864), Lacordaire (1872), Lepesme (1946) and Néouze & Tavakilian (2003).

2.2. Characters and analysis procedures

The characters were constructed based on internal and external features of adult specimens. Observations of morphological structures were carried out with a Leica MZ16 stereomicroscope equipped with an ocular graticule for measurements of lengths and ratios. Scanning electron micrographs were produced using a JEOL JSM-6360LV microscope in the Centre of Electron Microscopy of the Federal University of Paraná, Curitiba, Brazil. Illustration of selected structures were produced using digital photographs taken through the compound stereoscopes and then redrawn using the program Inkscape 0.92.3. A list of the 34 characters used in this study with their respective character states (25 binary and 9 multistate) is presented in section 3.1. and the data matrix in Table 1. The description of the characters and their states follows the structural concepts proposed by Sereno (2007). In the matrix, the non-applicability of characters to taxa is indicated by '–'. Following the description of each character, we provide the length, consistency index and retention index based on the topology resulting from the parsimony analysis.

The phylogenetic hypotheses were constructed using two probabilistic methods for phylogenetic reconstruction: maximum parsimony and Bayesian inference. The data matrix for maximum parsimony analysis was produced in Winclada version 1.00.08 (Nixon 2002) and the parsimony analysis was performed in TNT v.1.1 (Goloboff et al. 2008) through a traditional search with 1,000 replications, employing 100 random-addition replicates and saving 10 trees per replication, treating all characters as unordered and non-additive. The statistical support for each clade obtained with maximum parsimony was also calculated in TNT. Bootstrap values (BO) were calculated from an independent analysis using 1,000 pseudoreplicates and Bremer support (BR) was calculated based on the strict consensus topology using 1,000 suboptimal trees up to one step longer. In the trees resulting from the parsimony analysis, only unambiguous character states are shown.

Bayesian inferences were performed in MrBayes v3.2.5 (Huelsenbeck & Ronquist 2001) using two simultaneous Markov Chain Monte Carlo runs, with 8 chains of 100 million generations each, sampling trees every 1,000th generation. In this analysis, the dataset was treated as a single partition and analysed under gamma-distribution variation, considering all state frequencies (change rates) set equal, all topologies with equal probabilities, and with unconstrained branch length. In tree resulting from Bayesian inference, Posterior Probability (PP) was interpreted as statistical support values.

We have also performed a Maximum Likelihood (ML) analysis in RAxML 7.2.6 (Stamatakis 2006), using a bootstraping analysis based on 1,000 pseudoreplicates and the resulting tree was widely congruent with those of the Bayesian and parsimony analyses. All clades statistically supported in the Bayesian and Parsimony trees (as presented in Fig. 31) were also supported in the ML tree. The only difference between ML and the other trees was found in a clade within *Oreodera*, which received support BO > 50% in the ML tree, but was not equally recovered by characters in the parsimony trees. Since our study did not aim at inferring internal relationships of *Oreodera* (indeed, our sampling of *Oreodera* is not suitable for that), we considered not relevant to include the ML analysis in the paper.

2.3. Taxonomic notes

Taxonomic notes and new records on *Macropophora* are provided from examination of material from the following institutions: American Museum of Natural History, New York, New York, United States of America (AMNH) and National Museum, Federal University of Rio de Janeiro, Rio de Janeiro, Brazil (MNRJ).

3. Results

3.1. Character and character states description

Characters and character states used for the morphological phylogenetic assessment of Acrocinini (Cerambycidae: Lamiinae). Values of length (L), consistency index (ci) and retention index (ri) are presented after each character description.

1 Head, coarse punctuation between upper ocular lobes: **(0)** absent; **(1)** present. [L: 3; ci: 33; ri: 60]

2 Head, eyes, connection between upper and lower ocular lobes: **(0)** narrow (anterior and posterior margin touch each other) (Fig. 2); **(1)** wide (anterior and posterior margin do not touch each other) (Fig. 3). [L: 1; ci: 100; ri: 100]

Table 1. Taxon sampling along with data matrix of morphological characters used in the morphological phylogenetic assessment of Acrocinini (Cerambycidae: Lamiinae). * indicates type-species of the tribe. + indicates type-species of the genus. Tribal assignation of each taxon follows current classification, according to Monné (2020).

	Character	0000000001	1111111112	2222222223	3333
Taxon		1234567890	1234567890	1234567890	1234
Acanthocinini	*Acanthocinus aedilis* (Linnaeus, 1758) *+	1111000201	01010-0011	0000000100	1002
Acanthoderini	*Acanthoderes daviesi* (Swederus, 1787) *+	0020011001	1000001200	1000100100	0012
Acanthoderini	*Aegomorphus clavipes* (Schrank, 1781)	1020011001	1000010100	1000000100	0012
Acanthoderini	*Hedypathes betulinus* (Klug, 1825) +	1020011000	1000110110	1000100100	0011
Acanthoderini	*Macropophora accentifer* (Olivier, 1795)	0101100111	1111001211	0101211011	1001
Acanthoderini	*Macropophora lacordairei* Lepesme, 1946	0101100111	1111001211	0001211011	1001
Acanthoderini	*Macropophora trochlearis* (Linnaeus, 1758) +	0101100111	1111001211	0001211011	1001
Acanthoderini	*Oreodera aerumnosa* Erichson, 1847	0111000101	0131021211	0000111001	1100
Acanthoderini	*Oreodera albata* Villiers, 1971	0111000101	1112021211	0000111001	1100
Acanthoderini	*Oreodera charisoma* Lane, 1955	1111000101	1120021211	0010111001	1100
Acanthoderini	*Oreodera exigua* Monné & Fragoso, 1988	0111000101	1131021211	0010111001	1100
Acanthoderini	*Oreodera glauca glauca* (Linnaeus, 1758) +	0111000101	1121021211	0010111001	1100
Acanthoderini	*Oreodera granulifera* Bates, 1872	0111000101	1131021211	0000111001	1100
Acanthoderini	*Oreodera hoffmanni* (Thomson, 1860)	0111010101	1131021211	0011111001	1000
Acanthoderini	*Oreodera jacquieri* Thomson, 1865	0111000101	1121021211	0010111001	1100
Acanthoderini	*Oreodera neglecta* Melzer, 1932	0111000101	0132021211	0000111001	1100
Acanthoderini	*Oreodera quinquetuberculata* (Drapiez, 1820)	0111000101	1131021211	0010111001	1100
Acanthoderini	*Oreodera simplex* Bates, 1861	0111000101	0131021211	0000111001	1100
Acanthoderini	*Steirastoma breve* (Sulzer, 1776) +	1020011000	1000110200	1000100100	0111
Acrocinini	*Acrocinus longimanus* (Linnaeus, 1758) *+	0101100201	1111001211	0111011011	1001
Polyrhaphidini	*Polyrhaphis grandini* Buquet, 1853	1111011001	0020000000	1110000100	0012

3 Head, distance between upper ocular lobe and coronal suture: **(0)** distance = 0 (ocular lobe reaches coronal suture); **(1)** distance ≤ ocular lobe width; **(2)** distance > ocular lobe width. [L: 2; ci: 100; ri: 100]

4 Head, lower ocular lobes, shape, in frontal view: **(0)** rectangular (Fig. 4); **(1)** rounded (Figs. 5, 6). [L: 1; ci: 100; ri: 100]

5 Head, genal suture: **(0)** inconspicuous (Fig. 4); **(1)** conspicuous (Figs. 5–6). [L: 1; ci: 100; ri: 100]

6 Head, posterior margin, shape: **(0)** rounded; **(1)** triangular. [L: 2; ci: 50; ri: 80]

7 Maxilla, length of palpomere II relative to palpomere IV **(0)**; II < IV; **(1)** II > IV. [L: 1; ci: 100; ri: 100]

8 Antennae, scape, shape: **(0)** globose (piriform) (Fig. 7); **(1)** gradually expanded toward apex, with more expanded portion at 1/3 before apex (Fig. 8); **(2)** gradually expanded toward apex, with more expanded portion near apex (Fig. 9). [L: 3; ci: 66; ri: 80]

9 Antennae, scape, coarse granulation: **(0)** absent; **(1)** present. [L: 1; ci: 100; ri: 100]

10 Antennae, antennomere III, length relative to scape: **(0)** III = scape; **(1)** III > scape. [L: 1; ci: 100; ri: 100]

11 Antennae, antennomere III, length relative to antennomere IV: **(0)** III = IV; **(1)** III > IV. [L: 3; ci: 33; ri: 50]

12 Antennae (females), antennomeres V–XI, length: **(0)** gradually decreasing; **(1)** subequal. [L: 1; ci: 100; ri: 100]

13 Prothorax, lateral tubercle, surrounding suture: **(0)** visible only at the base of the tubercle (Figs. 10–15); **(1)** complete (entirely visible) (Figs. 16–19); **(2)** not visible or vestigial (Figs. 20–21); **(3)** visible, reaching superior margin of tubercle (Figs. 22–23). [L: 4; ci: 75; ri: 90]

14 Pronotum, anterior margin, glabrous edge: **(0)** absent; **(1)** present all along the margin; **(2)** present except at median region of the margin. [L: 4; ci: 50; ri: 66]

15 Pronotum, anterior margin, midline, longitudinal elevation: **(0)** absent (Fig. 3); **(1)** present (Figs. 2, 12). [L: 1; ci: 100; ri: 100]

16 Pronotum, paired dorsal tubercles, position: **(0)** on transversal median line; **(1)** at anterior half, with base reaching transversal median line; **(2)** at anterior half, base not reaching transversal median line [L: 3; ci: 66; ri: 85]

17 Pronotum, posterior margin, coarse punctuation: **(0)** irregularly distributed (Figs. 10–13); **(1)** linear (Figs. 14, 15). [L: 2; ci: 50; ri: 75]

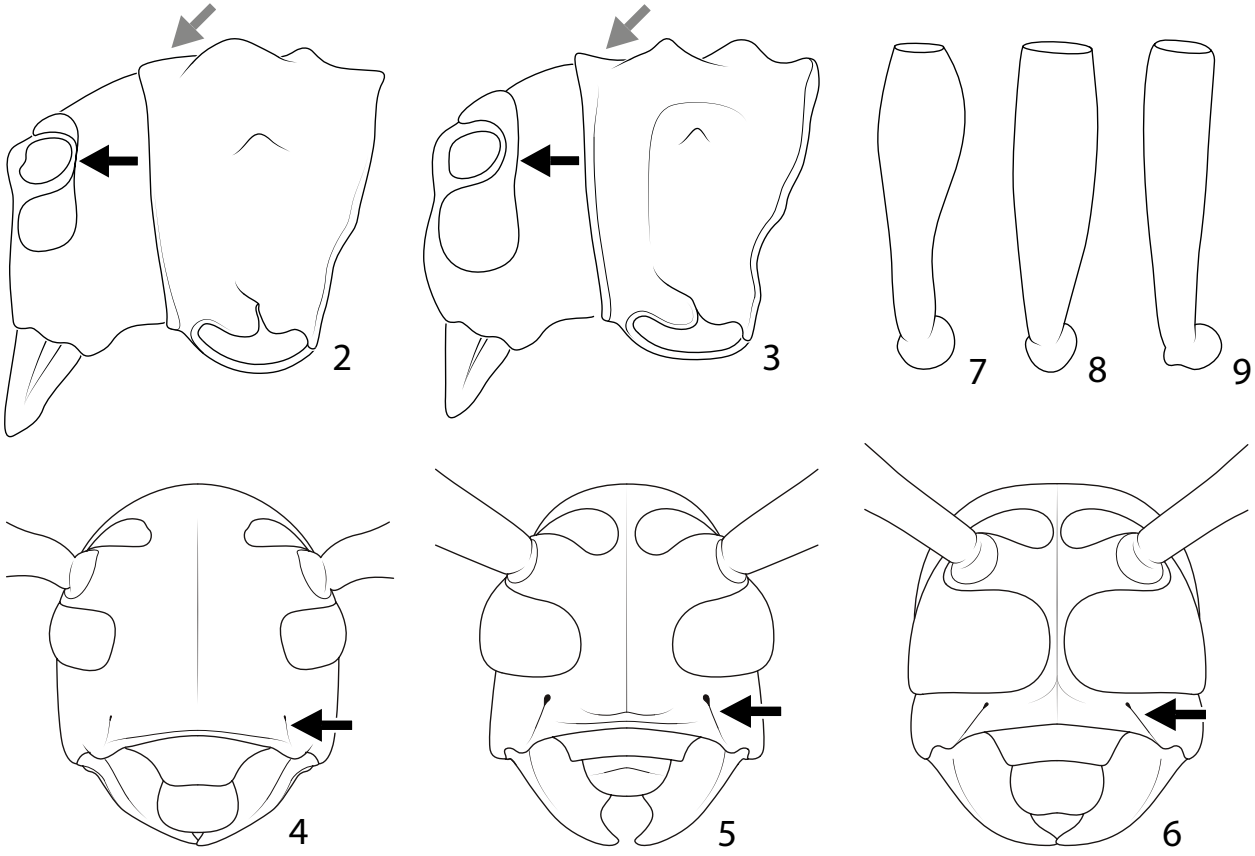
18 Mesosternal process (Mp), length relative to mesocoxa (Mc): **(0)** Mp < Mc; **(1)** Mp = Mc; **(2)** Mp > Mc. [L: 4; ci: 50; ri: 0]

19 Mesoscutum, anterior margin, shape: **(0)** cuspidate; **(1)** rounded. [L: 2; ci: 50; ri: 66]

20 Mesoscutum, stridulatory plate, apexes, shape: **(0)** truncate; **(1)** acuminate. [L: 1; ci: 100; ri: 100]

21 Mesoscutum, stridulatory plate, lateral limits: **(0)** margin well-delimited; **(1)** margin poorly delimited (gradually fading). [L: 1; ci: 100; ri: 100]

22 Elytra, humera, apical spine: **(0)** absent; **(1)** present. [L: 3; ci: 33; ri: 0]



Figs. 2–9. Representation of some character states used in the phylogenetic assessment of Acrocinini (Cerambycidae: Lamiinae). **2**, **3**: head and prothorax in lateral view: **2**: *Acanthoderes daviesi*, connection between upper and lower ocular lobes narrow (2:0; black arrow) and pronotum with longitudinal elevation near anterior margin (15:1; grey arrow); **3**: *Oreodera glauca glauca*, connection between upper and lower ocular lobes wide (2:1; black arrow) and pronotum without longitudinal elevation near anterior margin (15:0; grey arrow). **4–6**: head in frontal view: **4**: *Ac. daviesi*, lower ocular lobes rectangular (4:0) and genal suture short (5:1; black arrow); **5**, **6**: *Macropophora trochlearis* and *Acrocinus longimanus*, respectively, lower ocular lobes rounded (4:1) and genal suture long (5:1; black arrow). **7–9**: shape of scape in dorsal view: **7**: *Ac. daviesi*, globose (8:0); **8**: *M. trochlearis*, gradually expanded toward apex, with more expanded portion at 1/3 before apex (8:1); **9**: *Acanthocinus aedilis*, gradually expanded toward apex, with more expanded portion near apex (8:2).

23 Elytra, apex, inner angle, spine: **(0)** absent; **(1)** present. [L: 3; ci: 33; ri: 71]

24 Femora, shape: **(0)** globose; **(1)** cylindrical. [L: 2; ci: 50; ri: 75]

25 Mesofemur, length relative to metafemur: **(0)** mesofemur shorter than metafemur; **(1)** mesofemur subequal to metafemur; **(2)** mesofemur longer than metafemur. [L: 4; ci: 50; ri: 60]

26 Protibia: **(0)** flatten; **(1)** cylindrical. [L: 1; ci: 100; ri: 100]

27 Protibia, inner face, projection near sulcus: **(0)** absent (Fig. 24); **(1)** present (Figs. 25–28). [L: 1; ci: 100; ri: 100]

28 Protibia, inner margin, pair of apical spurs: **(0)** absent (Fig. 29); **(1)** present (Fig. 30). [L: 1; ci: 100; ri: 100]

29 Protibia (males), inner face, coarse granulation: **(0)** absent; **(1)** present. [L: 1; ci: 100; ri: 100]

30 Protarsomere II, length relative to width: **(0)** wider than long; **(1)** longer than wide. [L: 1; ci: 100; ri: 100]

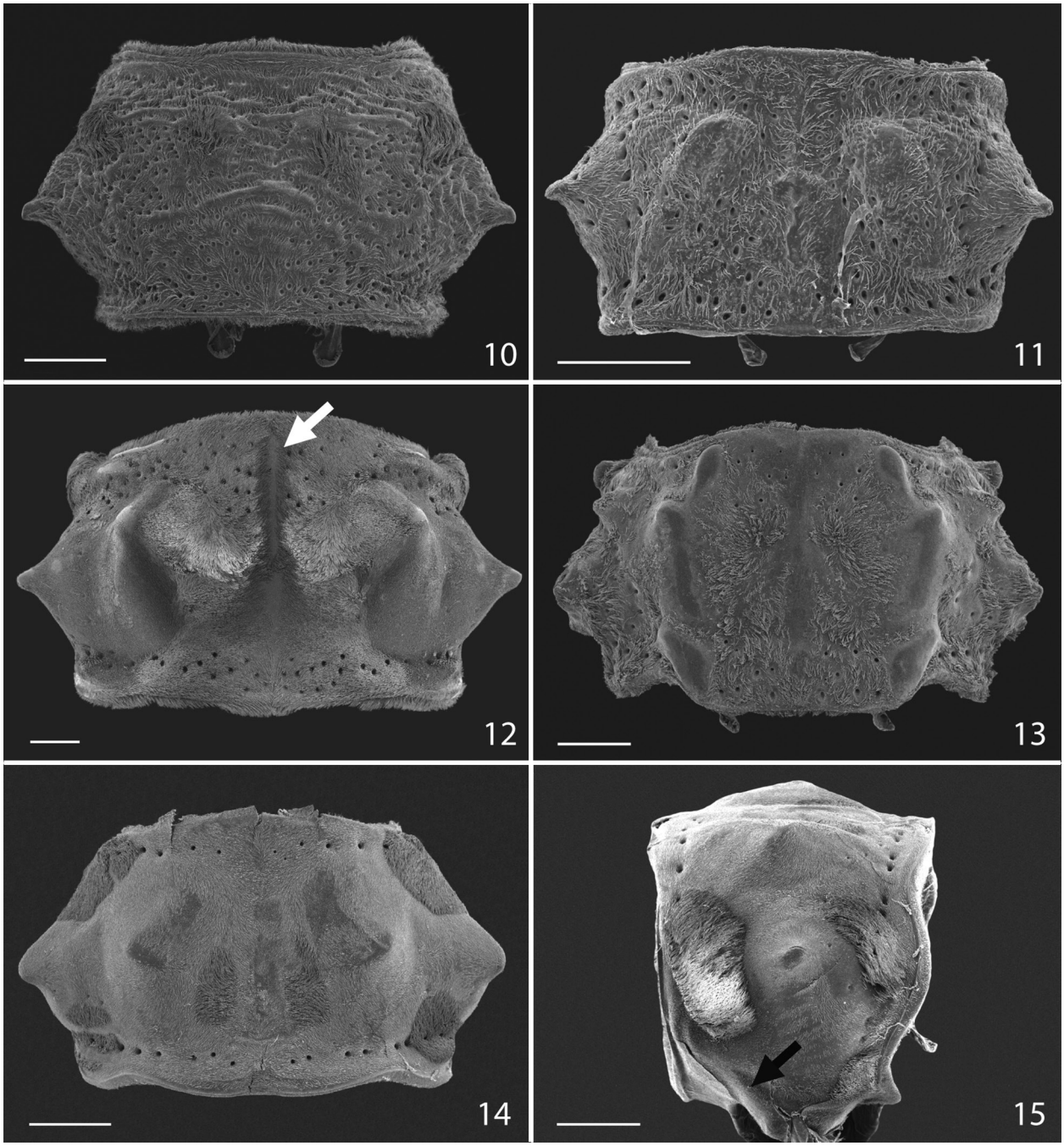
31 Protarsomere I, length relative to protarsomere II: **(0)** I = II; **(1)** I > II. [L: 1; ci: 100; ri: 100]

32 Protarsomere V, lateral face, coverage of setae: **(0)** sparse; **(1)** dense. [L: 3; ci: 33; ri: 77]

33 Protarsomeres I–III, lateral face, coverage of setae (sexual dimorphism in males): **(0)** absent; **(1)** present. [L: 1; ci: 100; ri: 100]

34 Mesotasomere I, length relative to metatarsomere I: **(0)** mesotasomere I < metatarsomere I; **(1)** mesotasomere I = metatarsomere I; **(2)** mesotasomere I > metatarsomere I. [L: 3; ci: 66; ri: 87]

Characters of genitalia were not included in the analyses for two reasons: (1) the unavailability of material for dissection for a large number of the sampled species would increase the number of missing data in the data matrix; and (2) after examining male genitalia of *Polyrhaphis*, *Hedypathes*, *Acanthocinus*, *Acrocinus* and two species of *Macropophora* and *Oreodera*, the main differences we observed were in the apical shape of the median lobe and shape/length of the basal apophysis. The variations in these structures in the species studied seem to be particularly important for taxonomic purposes at species level, but do not express phylogenetic signal to reflect/support tribe divisions (at least not among closely related tribes).

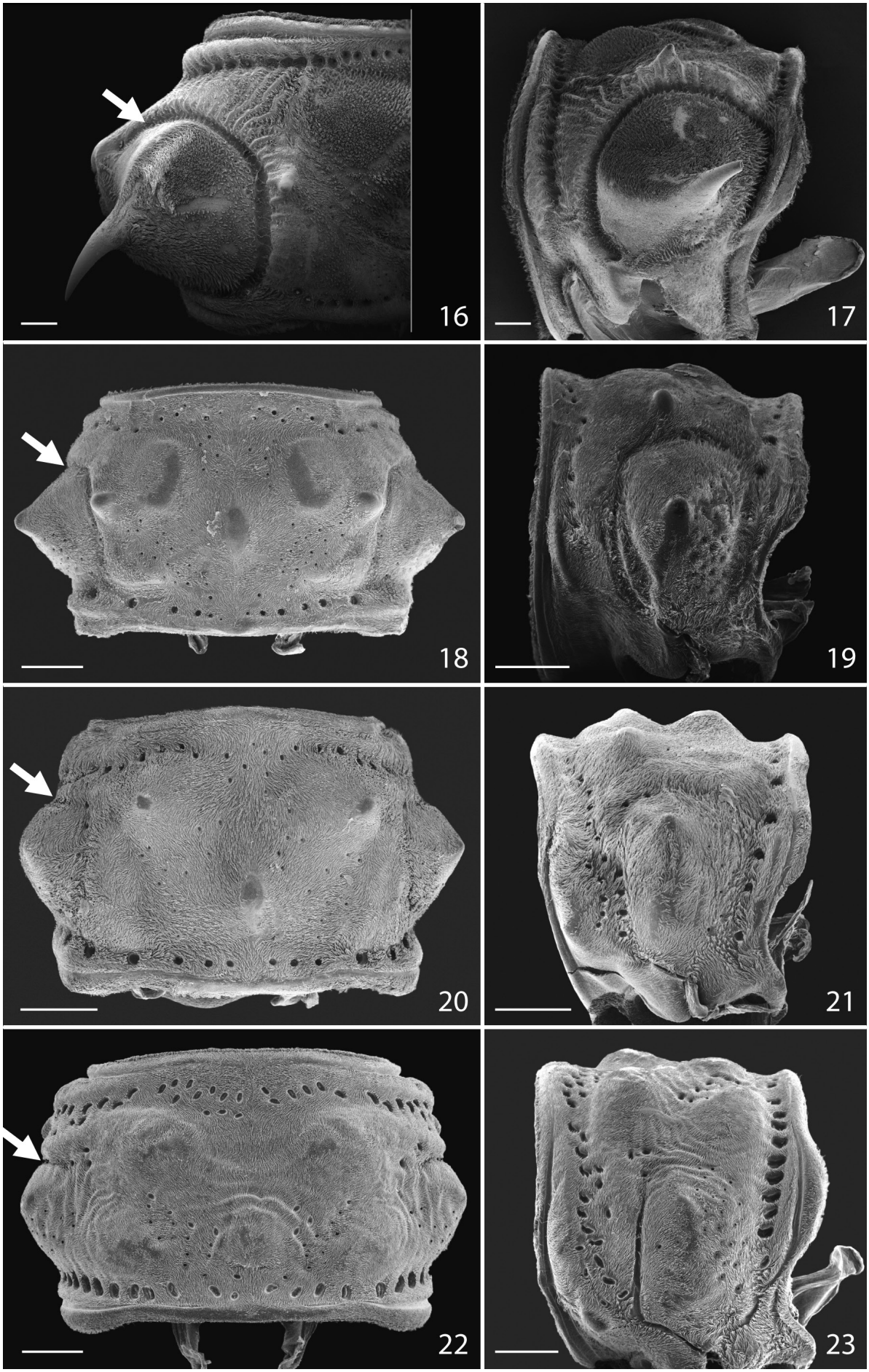


Figs. 10–15. Illustration of some character states used in the phylogenetic assessment of Acrocinini (Cerambycidae: Lamiinae). Prothorax in dorsal view: **10**: *Acanthocinus aedilis*; **11**: *Aegomorphus clavipes*; **12**: *Hedypathes betulinus*; **13**: *Steirastoma breve*; **14**: *Acanthoderes daviesi*. Prothorax in lateral view: **15**: *Ac. daviesi*. White arrow in figure 12 indicates the longitudinal elevation near anterior margin of pronotum (15:1). Black arrow in figure 15 indicates the suture incomplete, visible only at the base of the tubercle (13:0). Scale bars 1 mm.

3.2. Phylogenetic results

Regardless of the analytical method employed, the trees resulting from both Bayesian and maximum parsimony analyses produced entirely congruent results in the well-supported clades and the placement of *Macropophora* and *Oreodera* out of Acanthoderini, which were strongly associated with *A. longimanus* (Fig. 31). Two main clades were recovered with high statistical support in both analyses, although their internal relationships were not clearly resolved: one composed of the species of Acanthoderini sampled in the study (except for *Macropopho-*

→ **Figs. 16–23.** Illustration of some character states used in the phylogenetic assessment of Acrocinini (Cerambycidae: Lamiinae). Prothorax in dorsal and lateral view: **16**, **17**: *Acrocinus longimanus*; **18**, **19**: *Macropophora trochlearis*; **20**, **21**: *Oreodera glauca glauca*; **22**, **23**: *Oreodera hoffmanni*. White arrow indicates the suture surrounding the lateral tubercle of prothorax. Scale bars 1 mm.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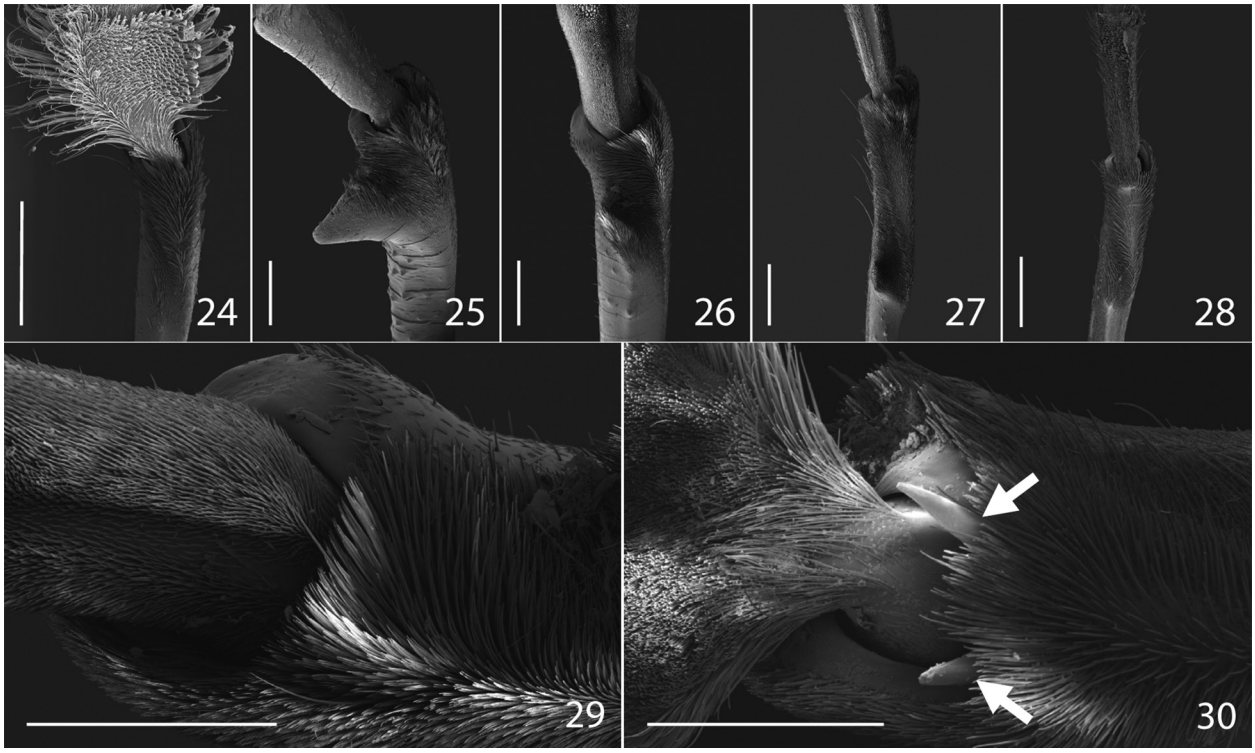

Figs. 24–30. Illustration of some character states used in the phylogenetic assessment of Acrocinini (Cerambycidae: Lamiinae). Apex of left protibia in ventral view, showing the absence or presence of the projection near sulcus (distal at top, anterior to the left): **24**: *Acanthoderes daviesi*; **25**, **26**: *Acrocinus longimanus* (male and female, respectively) **27**: *Macropophora trochlearis*; **28**: *Oreodera glauca glauca*. Detail of apex of left protibia in ventral view, showing the absence or presence (arrows) of the two apical spurs: **29**: *A. longimanus*; **30**: *Hedypathes betulinus*. Scale bars 1 mm.

ra and *Oreodera*); and another composed of *Acrocinus* and all representatives of *Macropophora* and *Oreodera* (which is referred as Acrocinini from now on). Also, in both Bayesian and parsimony inferences, the lineage *Acrocinus* + *Macropophora* + *Oreodera* was strongly supported as sister-group of *Aca. aedilis*, both by unambiguous characters and statistical supports (BR = 7; BO = 93; PP = 1).

Within Acrocinini, both analyses recovered a close relationship between *Acrocinus* and *Macropophora*. However, none of the analyses elucidated the intraspecific relationship within *Macropophora* and *Oreodera*. Discrepancies among the trees resulting from Bayesian and maximum parsimony analyses particularly involve the monophyly of the genus *Oreodera*. Although with low statistical support, trees resulting from the parsimony analysis recovered *Oreodera* as a monophyletic lineage and sister group of the cluster *Acrocinus* + *Macropophora*. In contrast, Bayesian inference was not useful to corroborate the monophyly of *Oreodera* within Acrocinini.
The maximum parsimony analysis resulted in two most parsimonious trees (length = 66, consistency index = 65 and retention index = 84) (Fig. 31). The single difference between the trees resulting from the parsimony analysis is the placement of *Aegomorphus clavipes* (Schrank, 1781) and *Acanthoderes daviesi* (Swederus, 1787) within the clade Acanthoderini. In one of the trees, *Ae. clavipes* was recovered as the most basal lineage of the clade (Fig. 31A), while in the other, *Ac. daviesi* took place as the most basal lineage of the clade (Fig. 31B). This discrepancy was also found in the tree resulting from the Bayesian analysis, where the relationships among these taxa and the clade composed of *Hedypathes betulinus* (Klug, 1825) and *Steirastoma breve* (Sulzer, 1776) remained unresolved.

According to the parsimony analysis, the monophyly of Acrocinini, including *Acrocinus*, *Macropophora* and *Oreodera*, is supported by six synapomorphies: prothorax with a conspicuous suture surrounding the lateral tubercle (13:0) (Figs. 7−9); pronotum with linear coarse punctuation at the posterior margin (17:1); protibia cylindrical (26:1); protibia with a projection near sulcus at inner face (27:1); protibia without a pair of apical spurs at inner margin (28:0) (Fig. 10); and protarsomere II longer than wide (30:1). Accordingly, the monophyly of *Macropophora* is supported by two synapomorphies (scape coarsely granulated (9:1) and mesofemur longer than metafemur (25:2)) and *Oreodera* is supported as a monophyletic group by the following synapomorphies: paired dorsal tubercles of pronotum positioned at anterior half, with base not reaching the transversal median line (16:2); mesofemur subequal to metafemur (25:1); and pretarsomere V densely covered of long setae (32:1).

The relationship between *Acrocinus* and *Macropophora* is supported by four synapomorphies (3:0; 5:1; 24:1; 29:1). Although it was not the goal of this work, the results of the parsimony analysis suggested a series

of characters with potential to define the phylogenetic relationship among Acrocinini and Acanthocinini, for instance: posterior margin of head rounded (6:0), maxillary palpomere II shorter then palpomere IV (7:0), female with antennomeres V–XI subequal (12:1), anterior margin of pronotum with glabrous edge all along the margin (14:1), stridulatory plate with acuminate apexes (20:1), lateral margins of stridulatory plate well-delimited (21:0), protarsomere I longer then protarsomere II (31:1) and protarsomeres I–III without setae on lateral face (33:0).

4. Discussion

4.1. Phylogeny

Our results reveal a close relationship among *Acrocinus*, *Macropophora* and *Oreodera*. This contrasts with the current systematic arrangement of these genera, which consider Acrocinini as a monotypic tribe with *A. longimanus* and classifies *Macropophora* and *Oreodera* in Acanthoderini (e.g., Néouze & Tavakilian 2003). Among the synapomorphies for Acrocinini, containing *Acrocinus, Macropophora* and *Oreodera*, the protibia without spurs (character 28:0; Fig. 29) is the most remarkable diagnostic character of the tribe. This newly discovered character state is unique to this lineage amongst all other Neotropical tribes of Lamiinae (probably unique in the subfamily). Except for character 28, all other synapomorphic characters supporting the relationship among *Acrocinus*, *Macropophora* and *Oreodera* were constructed from features mentioned in previous taxonomic works, such as the suture surrounding the lateral tubercle of the prothorax (character 13; Swainson 1840), the protibia cylindrical (character 26; Thomson 1864) and the protarsomere II longer than wide (character 30; Lepesme 1946).

Similarly, the presence of the suture surrounding the lateral tubercle of the prothorax is an essential character for the taxonomic delimitation of Acrocinini. Although the suture may not be totally evident in some species of *Oreodera* as it is in *Acrocinus* and *Macropophora*, different forms of this character can be observed in this genus. For example, in *Oreodera glauca glauca* (Linnaeus, 1758), *Oreodera charisoma* Lane, 1955 and *Oreodera jacquieri* Thomson, 1865, the suture is almost inconspicuous, but still, it is possible to notice it as a vestigial scar (Figs. 20, 21). Other characters supporting the monophyly of Acrocinini, such as the head without coarse punctuation between the upper ocular lobes (1:0), the pronotum with linear coarse punctuation near posterior margin (17:1) and the protibia cylindrical (26:1) with a projection near sulcus at inner face (27:1), only represent synapomorphies in the context of this study, since several other lineages of Lamiinae not used in the analyses can also exhibit those character states. Nevertheless, these features, in combination with the other synapomorphies mentioned above, allow the identification of species of Acrocinini and, therefore, should be considered as diagnostic characters for the tribe.

Throughout the history of the classification of Lamiinae, several researchers have defended that *Acrocinus* deserves a tribe only for itself (e.g., Audinet-Seville 1835; Néouze & Tavakilian 2003) due to some peculiar characteristics of *A. longimanus*, such as the presence of the suture surrounding the lateral tubercle of the prothorax, the exaggerated elongation of the forelegs and the curvature of the apex of the protibiae of males. However, our analyses demonstrate that, at a more comprehensive scale, some of these features – especially those related with the shape and size of the forelegs – have been misinterpreted. This trait is possibly associated with adaptive evolutionary processes related to sexual selection and does not represent an autapomorphic character for the tribe, since it is also present in other genera of Lamiinae, including *Macropophora* and *Oreodera*.

Regarding the placement of *Macropophora* and *Oreodera* out of Acanthoderini, this result was expected, since several previous classifications and taxonomic works have already associated these genera with *Acrocinus* (e.g., Lepesme 1946; Lane 1938), especially *Macropophora*, which was originally proposed as a genus within Acrocinini by Thomson (1864). *Oreodera*, on the other hand, although morphologically very similar to *Macropophora*, has been recurrently classified in Acanthoderini (e.g., Thomson 1864; Lacordaire 1872) (except for some of its species, which were placed in Acrocinini because at the time they were classified in *Macropophora*, e.g., *O. hoffmanni*).

Historically, the main traits proposed to separate *Oreodera* and *Macropophora* in tribal classification are the shape of the femora, which are cylindrical in *Macropophora* and usually globose in *Oreodera*, and the distinct elongation of the forelegs regarding the other legs, which are distinctly elongated in the species of *Macropophora* (as well as in *Acrocinus*), while in *Oreodera* this form is found only in *O. hoffmanni*. In this study, the proportion between the length of the forelegs with respect the other legs were not codded for the phylogenetic analyses, since it is intrinsically correlated with the shape of the femora (character 24). Nevertheless, our analyses demonstrate that the character 'femora globose' (24:0) by itself is not suitable to support the placement of *Oreodera* in Acanthoderini.

An important initial step toward the systematic delimitation of Acrocinini was given by Néouze & Tavakilian (2003), who impeccably resolved the taxonomic limits of *Macropophora* by transferring *M. hoffmanni* to *Oreodera*. In their work, by considering that *Macropophora* is more closely related to *Oreodera* than to *Acrocinus*, the authors transferred *Macropophora* from Acrocinini to Acanthoderini. Our results partially confirm the statements by these authors in the way that they confirm the position of *O. hoffmanni* in *Oreodera*, recognizing the cylindrical shape of the femora as a homoplasy shared between *O. hoffmanni* and the clade composed of

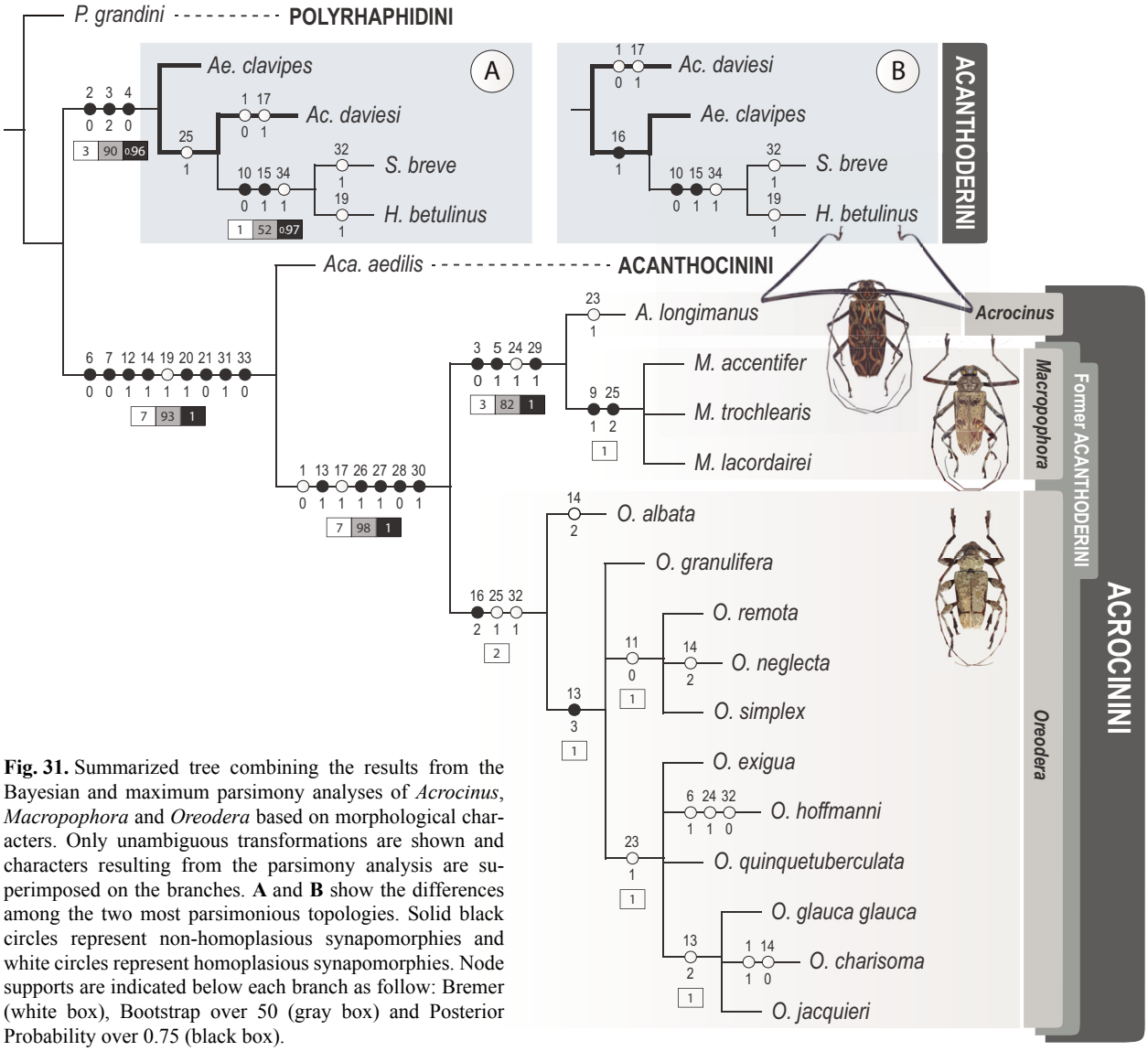

Fig. 31. Summarized tree combining the results from the Bayesian and maximum parsimony analyses of *Acrocinus*, *Macropophora* and *Oreodera* based on morphological characters. Only unambiguous transformations are shown and characters resulting from the parsimony analysis are superimposed on the branches. **A** and **B** show the differences among the two most parsimonious topologies. Solid black circles represent non-homoplasious synapomorphies and white circles represent homoplasious synapomorphies. Node supports are indicated below each branch as follow: Bremer (white box), Bootstrap over 50 (gray box) and Posterior Probability over 0.75 (black box).

Acrocinus and *Macropophora*. However, our results do not validate the placement of *Macropophora* in Acanthoderini.

Acrocinini has been unanimously defended as a distinctive tribe within the Lamiinae classification. Our analyses validate the recognition of the tribe and provide a series of morphological evidence to support its validity. However, Acrocinini is not a monotypic tribe, but rather consists of three genera: *Acrocinus*, *Macropophora* and *Oreodera*. Our taxon sampling includes about 10% of the species that comprise *Oreodera*, including the type-species, *O. glauca*. Certainly, this representation is sufficient to infer the monophyly of the genus and to confirm its placement in Acrocinini. However, bearing in mind that *Oreodera* has never been revised, we highlight the need for a revision and/or phylogenetic analysis to recognize synapomorphies for the genus based on a wider taxon sampling. Also, following the synapomorphies defined for Acrocinini in this study, we emphasize the need for a taxonomic review of the tribe Acanthoderini in order to identify other genera not included in this study that might possibly belong to Acrocinini, such as *Anoreina* Bates, 1861 and *Pyrianoreina* Martins & Galileo, 2008, which are morphologically close to *Oreodera*.

4.2. Systematics of Acrocinini

In the light of the evidence provided in this study, in order to address a phylogenetic classification of Acrocinini, we propose to transfer *Macropophora* and *Oreodera* from Acanthoderini to Acrocinini. Under this new conformation, the tribe Acrocinini is now composed of three genera (number of species according to Monné 2020): *Acrocinus* (monotypic), *Macropophora* (4 species) and *Oreodera* (118 species). Also, in order to avoid future misplacement of species of Acrocinini, we present a diagnosis for the tribe:

Acrocinini Swainson, 1840 — Type-genus: *Acrocinus* Illiger, 1806. — Diagnosis: conspicuous suture surrounding the lateral tubercle of prothorax; linear coarse punc-

tuation at posterior margin of pronotum; protibia cylindrical; salient projection near sulcus at inner face of protibiae; absence of a pair of apical spurs at inner margin of protibiae; tarsal claws divaricate; protarsomere II longer than wide.

4.3. Taxonomic notes

In the revision of *Macropophora*, Néouze & Tavakilian (2003) cited four specimens of *M. worontzowi* in the list of material examined from the MNRJ, identified as two females and two males. We reviewed these specimens and verified that all four specimens mentioned by Néouze & Tavakilian (2003) are actually males. Unlike the other species of *Macropophora*, which usually have forelegs distinctly longer than mid legs, males of *M. worontzowi* have forelegs subequal to mid legs, and this particularity may cause confusion in the recognition of the sexes in this species. After examining material of *Macropophora* from the AMNH and MNRJ, we found new records of *M. accentifer* for Brazil (Mato Grosso and Mato Grosso do Sul) and a new country record of *M. trochlearis* for Venezuela and other records for north of Brazil (Amapá, Acre and Rondônia):

***Macropophora accentifer* (Olivier)**: BRAZIL: Mato Grosso <currently Mato Grosso do Sul>, Rio Caraguata, 1 ♀, 21.48 Lat. 52.27 Lo. 400 m, 17.x.1953, Fritz Plaumann leg. (AMNH); Mato Grosso, Barra do Bugres, Porto Estrela, 1 ♀, xii.1984, P. Magno leg. (MNRJ). — ***Macropophora trochlearis* (Linnaeus)**: VENEZUELA: 1 ♂, 1940 (AMNH); Bolívar, Río Caura, 1 ♂, 14.iv.1957, P. San Martín leg. (MNRJ); BRAZIL: Amapá, Serra do Navio, 1 ♂, x.1995, P. Magno & C.E. Alvarenga leg. (MNRJ); Acre, Porto Walter, 1 ♀, ix.1957, H. Rueth leg. (MNRJ); Rondônia, Vilhena, 1 ♂, xi.1973, Alvarenga & Roppa leg. (MNRJ); Rondônia, Vilhena, 1 ♂, xi.1987, O. Roppa & P. Magno leg. (MNRJ); Porto Velho, Terr. Guaporé, 2 ♂, ii.1944, A. Parko leg. (MNRJ); Porto Velho, Terr. Guaporé, 1 ♀, i.1945, A. Parko leg. (MNRJ); Forte Príncipe do Guaporé, 1 ♂, xi.1952, Walter leg. (MNRJ).

Authors' contributions

D.S.S. and T.A.S. performed the phylogenetic analyses, wrote an earlier version of the manuscript and built the figures. L.M. and M.L.M. meticulously reviewed the text and the characters used in the phylogenetic analyses.

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