



Vicariance drove the speciation in the Pan-American genus *Achradocera* Becker (Diptera: Dolichopodidae): insights from Geographically Explicit Event Model analysis

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Abstract

Understanding the biogeographic patterns that explain species distribution in the Americas is a long and challenging endeavor. Insects represent a potentially promising group for these kinds of investigations, but deficits in basic taxonomic and systematic knowledge hinder the development of many studies. In this context, a cladistic analysis of the Pan-American genus *Achradocera* Becker (Diptera: Dolichopodidae: Diaphorinae) was conducted using a morphology-based matrix comprising 54 characters and 18 terminal taxa, including all 12 known species of the genus and six outgroup taxa. The analysis yielded two topologies under equal weighting and one under implied weighting of characters. *Achradocera* was recovered as monophyletic, and two species groups are proposed: the *barbata* group (Nearctic: *A. barbata* and *A. arcuata*) and the *femoralis* group (Neotropical: *A. excavata*, *A. femoralis*, *A. meridionalis*, and *A. tuberculata*). Biogeographic analyses were performed using the Geographically Explicit Event Model (GEM) method, which identified vicariance as the primary driver of speciation events in *Achradocera*, with founder events playing a secondary role. The results provide insights into the patterns that may explain the evolutionary history of the genus across the Americas, and potentially contributing to the understanding of patterns observed in other taxa with similar distributions, while also fostering discussions that can be integrated into broader frameworks, such as insect biogeography and studies of other taxa.

Keywords

Biogeography, Brachycera, cladistics, Empidoidea, insect biogeography, Nearctic region, Neotropical region, New World

1. Introduction

The American continent comprises a complex and heterogeneous area, encompassing two major zoogeographical regions (Nearctic and Neotropical) divided by the Mexican transition zone (Morrone 2015a), and all cor-

responding subregions. The species within each region reflect this heterogeneity: while Nearctic taxa often display phylogenetic affinities with Palearctic counterparts, some Neotropical taxa tend to have closer relatives in the

tropical regions of the Old World or, for the Andean species, with Australasian taxa (Morrone 2006, 2013, 2015), patterns associated with the ancient continents Laurasia and Gondwana.

Insects are particularly valuable for elucidating biogeographic patterns, and numerous studies have contributed to our understanding of biogeography in the Americas across the years (Antonelli et al. 2018; Fittkau 1969; Halfter 1974, 1987; Müller 1973; Rivas-Martins et al. 2011; Oberski 2025; Savage 1982). However, while the high insect diversity provides great potential for biogeographic studies, it also presents substantial difficulties—many taxa remain poorly known, and basic taxonomic information is still lacking for a significant portion of this group. The Dipteran family Dolichopodidae perfectly fits this scenario, being at the same time highly diverse, with over 8,000 species worldwide (Yang et al. 2006; Bickel 2009a; Grichanov and Brooks 2017; Grichanov 2016), and poorly understood regarding its phylogenetic and biogeographical relationships, resulting in Linnean, Darwinian, and Wallacean shortfalls (Diniz-Filho et al. 2023).

Similarly to several other insect groups, taxonomy of dolichopodid generic and suprageneric taxa were historically based on Palearctic and Nearctic faunas, which led to considerable discrepancies when applied to the tropical and temperate forms of the southern hemisphere (Bickel 2009a). The first cladistic analyses dealing with Dolichopodidae using computational methods began more recently, either with morphological (Yang et al. 2006; Sinclair and Cumming 2006) or molecular data (Bernasconi et al. 2007—comparing both morphological and molecular cladograms; Germann et al. 2011; Lim et al. 2010). Nevertheless, several non-algorithm analyses have been published in the past (Bickel 1985, 1987, 1994, 2006; 2009b, 2013; Naglis 2001a,b). Just a few phylogenetic studies have aimed to resolve the internal relationships of the subfamilies through computational methods (Brooks 2005 and Pollet et al. 2010 for Dolichopodinae; Cumming and Brooks 2019 for Parathalasiinae; Capellari 2013 for Diaphorinae; Pollet et al. 2011 for *Medetera*; Quevedo et al. 2025 for *Dactylomyia*; and Silva et al. 2025 for *Mberu*), and more comprehensive phylogenetic studies on Dolichopodidae lack a broad representative sampling of the subfamilies (Bernasconi et al. 2007; Germann et al. 2011; Lim et al. 2010).

The scenario is even worse when we analyze the biogeographical knowledge about the group, which is virtually restricted to geographical records from descriptive articles, checklists or catalog compilations. Biogeographical studies of long-legged flies using computational methods are hence scarce and can be summarized by a few contributions (e.g., Goodman et al. 2014, 2016; Grichanov et al. 2021). The lack of historical biogeographic works probably reflects the primary need of descriptive taxonomic papers and the poorly known phylogenetic relationships in the family (Lim et al. 2010), but also of the wandering pattern observed for many species of long-legged flies. However, it is important to emphasize that this is not a general rule. For example, it has been doc-

umented that a large number of European species have more restricted distribution ranges (e.g., Pollet 2011).

In this study, we use the recently reviewed dolichopodid genus *Achradocera* Becker as a model, which includes 12 nominal species spread throughout the Americas, as well as an updated distribution map (Quevedo et al. 2024). We present for the first time a morphology-based phylogeny for the group and an event-based biogeography using the GEM (Geographically Explicit Event Model) method. The combination of a revised taxon, studied in a phylogenetic and biogeographic perspective renders *Achradocera* an excellent group for elucidating the biogeographical patterns in the New World, minimizing shortfalls and contributing to the debates of insect biogeography on the continent.

2. Materials and methods

2.1. Taxon sampling and abbreviations

The specimens examined belong to the following institutions: American Museum of Natural History, New York, USA (AMNH); Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil (INPA); Montana Entomology Collection, Bozeman, USA (MTEC); Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP); Museum für Naturkunde, Berlin, Germany (MfN); National Museum of Natural History, Smithsonian Institute, Washington, D.C., USA (USNM); Natural History Museum, United Kingdom, London, England (NHMUK); Senckenberg Naturhistorische Sammlungen Dresden, Dresden, Germany (MTD); and Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany (SNMS).

Terminology follows Cumming and Wood (2017) for general morphology. The abbreviation list used in this paper follows: I, II, III: fore-, mid-, hind legs; CI: consistency index; Cx: coxa; F: femur; L: length; MSSC: male secondary sexual character; RI: retention index; T: tibia; t_{1-5} : tarsomeres 1 to 5. Photos were taken using an Axio-Cam MRC 5 camera attached to a Zeiss Discovery V20 stereomicroscope and stacked with ZEISS AxioVs40 v. 4.8.2.0 software and assembled in Helicon Focus 6. For examination under microscope, the terminalia were treated with lactic acid following the procedure described by Cumming (1992), and after examination transferred to a microvial with glycerin attached to the same pin of the dissected specimen. The final images were worked on Adobe Illustrator CS6 for the separate pictures and Adobe Photoshop CS6 for the plates.

2.2. Phylogenetic data and analysis

Parsimony analyses were carried out in the TNT version 1.6 program (Goloboff 1993; 1995; Goloboff et al. 2008; Farris 2008; Goloboff and Morales 2023) through heuris-

tic searches using equal weighting (EW) and differential weighting of characters by implied weighting (IW). The following parameters were used for traditional search: maximum of 20000 trees in memory; random seed = 0; repls. = 1000; trees saved per replication = 20, the trees collapsed after analysis. Bremer support was established using the command prompt “sub 1 hold 6000; bb = tbr filonly; unique*”, changing the value of suboptimal trees. The ordering of the transformation series was carried out by rooting with outgroups (Nixon and Carpenter 1993).

The dataset transposed into the matrix comprised morphological characters of adult males and females (Table S1), meticulously curated using Morphobank (O’Leary and Kaufman 2007) version 3.0. New characters were coded following appointments of Fitzhugh (2006) and Sereno (2007) (see Results: Character List). The in-group includes all 12 known nominal species of the genus *Achradocera* (Quevedo et al. 2024): *A. angustifacies* Becker; *A. apicalis* (Aldrich); *A. arcuata* (Van Duzee); *A. balin* Quevedo, Capellari and Lamas; *A. barbata* (Loew); *A. excavata* (Van Duzee); *A. femoralis* Becker; *A. gimli* Quevedo, Capellari and Lamas; *A. insignis* Parent; *A. longiseta* Parent; *A. meridionalis* Becker; and *A. tuberculata* (Van Duzee). Species from three different genera of the same subfamily (Diaphorinae) as *Achradocera* composed the outgroup: *Chrysotus* Meigen [4 spp.]; *Diaphorus* Meigen [1 sp.] (root); and *Lyroneurus* Loew [1 sp.]. The program WinClada ASADO 1.61 (Nixon 1999–2002) was used to analyze the trees. Brackets are used to indicate the numbers of characters from the character list, and points are used after the numbers to indicate the character status (e.g., [2.1] indicates character 2, state 1).

2.3. Biogeographical data and analysis

The analysis incorporated data from a total of 204 localities (Table S2), sourced from the labels of the specimens under study. One record was used from iNaturalist [photographic record: <https://www.inaturalist.org/observations/108430413>] and another was provided by personal communication [Mexico. 1m#, “Ciudad de México, Universidad Nacional Autónoma de México, Cantera Oriente, La grieta, 19.31639, -99.17179, 06.iii.2024, L. R. P. Gomes”]. *Achradocera* specimens from Hawaii, Tonga and French Polynesia were probably accidentally introduced in those islands (Bickel 2000; Evenhuis 2012) and the data was not plotted to avoid noise in the analysis. All collected data were plotted on a New World shapefile and edited in QGIS 3.4 (QGIS Development Team 2020).

Event-based analysis was conducted employing the Geographically explicit Event Model (GEM) method, facilitated through the EVS software package (Arias 2017). EVS configuration adhered to the author’s guidelines, employing a raster grid with 1x1 degree pixels and a fill value of 1. Each of the four events (vicariance, sympatry, founder event, and point sympatry) carried an equal cost of 1. To penalize ancestral distributions and deter extensive ancestors, a value of $Z = 10$ was employed, where

Z denotes the size of ancestral ranges. The analysis employed a flipping algorithm with 10 independent runs, each comprising 10,000 replicates.

3. Results

3.1. Character List

Head

- 0 Shape of first flagellomere ($L = 1$; $CI = 1,0$; $RI = 1,0$): (0) rounded; (1) with broad base constricted into short or long narrow tip (Fig. 1A, C).
- 1 Length of first flagellomere ($L = 2$; $CI = 1,0$; $RI = 1,0$): (0) very small, about as long as scape plus pedicel; (1) small, about 2x longer than scape plus pedicel (Fig. 1A); (2) long, about 4x longer than scape plus pedicel (Fig. 1C).
- 2 Configuration of ventral postocular setae ($L = 3$; $CI = 0,33$; $RI = 0,5$): (0) weak and sparse, or even absent setae; (1) strong and multiseriate, forming prominent stiff white “beard” (Fig. 1A, C).
- 3 Shape of ventral postocular setae ($L = 1$; $CI = 1,0$; $RI = 1,0$): (0) not flattened; (1) flattened (Fig. 1J).
- 4 Insertion of antennal stylus ($L = 2$; $CI = 0,5$; $RI = 0,66$): (0) superior (“dorsal”); (1) medial (“apical”) (Fig. 1A, C). – **Remarks.** In his thesis, Capellari (2013) pointed out that in most cases the use of the terms medial (rather than “apical”) and superior (rather than “dorsal”) better reflects the position of the antennal stylus. The appearance of a “dorsal” insertion of the stylus is often associated with an enlargement of the lower part of postpedicel. Similarly, the term apical is accurate, as there are both medial apical stylus (as in the genus *Achradocera*) and superior apical stylus (as in the genus *Trigonocera* Becker).
- 5 Inner margin of male eyes at frons level ($L = 2$; $CI = 0,5$; $RI = 0$): (0) holoptic, almost or totally connected; (1) dicoptic, divergent (Fig. 1A).
- 6 Pruinosity on face ($L = 4$; $CI = 0,5$; $RI = 0,71$): (0) dense grey pruinosity covering the entire face; (1) grey pruinosity restricted to the area close to the eye margin; (2) face without grey pruinosity. – **Remarks.** We preferred to treat this character as multistate (and others ahead: char15, 16, 18, 21, 22 and 31), instead of splitting it into two contingent characters. Although there is phylogenetic information regarding pruinosity (or darkening pattern of the podomeres, on the following other indicate characters), we assume a priori that the signal is weaker compared to “structure” characters, and contingent coding could further bias some results. Moreover, this character, together with characters 7, 11, and 14, can be considered “imprecise” for a phylogenetic analysis. To test this, we performed an analysis excluding these four characters, which resulted in a consensus tree based on six MPTs (Figs S1, S2). However, this only produced a polyto-

my in the outgroup; the monophyly of *Achradocera* as well as its internal relationships remained unaffected in all MPTs, and all corroborated the topology of *Achradocera* recovered in T1.

- 7 Shining pattern on face (L = 4; CI = 0,25; RI = 0,4): (0) dark green; (1) dark green with coppery reflection below antenna.
- 8 Shape of palpus in lateral view (L = 2; CI = 0,5; RI = 0): (0) rounded; (1) subtriangular (Fig. 1A, C).
- 9 Length of palpus (L = 2; CI = 0,5; RI = 0): (0) short, shorter than proboscis; (1) medium, about as long as proboscis (Fig. 1A, C); (2) long, longer than proboscis.
- 10 Size of marginal setae of palpus (L = 2; CI = 0,5; RI = 0,75): (0) short, shorter than 1/5 the length of palpus; (1) long, at least 1/5 the length of palpus or longer (Fig. 1A, C).

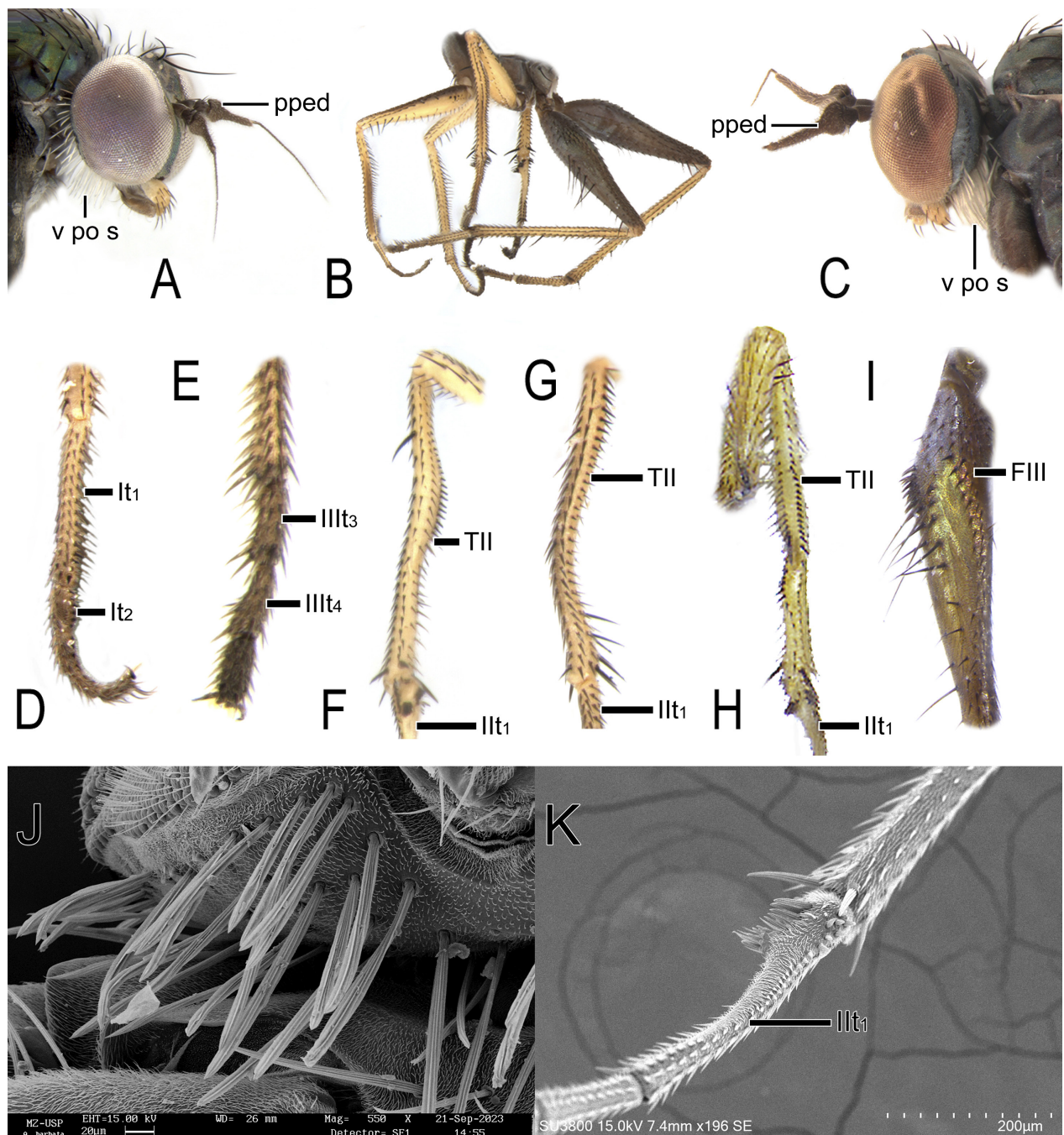


Figure 1. Main characters of external morphology. **A** *Achradocera apicalis*, head and postpedicel. **B** *A. excavata*, legs. **C** *A. angustifacies*, head and postpedicel. **D** *A. barbata*, tarsomeres of foreleg. **E** *A. meridionalis*, tarsomeres of hind leg. **F** *A. meridionalis*, tibia of the mid leg. **G** *A. insignis*, tibia of mid leg. **H** *A. tuberculata*, tibia of mid leg. **I** *A. tuberculata*, femur of hind leg. **J** *A. barbata*, scanning electron microscope (SEM) of ventral postocular setae. **K** *A. tuberculata*, SEM of the midleg tarsomere. Abbreviation list: FIII, Femur of Leg III; It₁, first tarsomere of Leg I; It₂, second tarsomere of Leg II; III t₁, first tarsomere of Leg II; III t₂, second tarsomere of Leg II; III t₃, third tarsomere of Leg III; III t₄, fourth tarsomere of Leg III; pped, postpedicel (= first flagellomere); TII, tibia of leg II; v po s, ventral postocular setae.

Thorax

- 11 Pruinosity on lateral sclerites of thorax ($L = 3$; $CI = 0,33$; $RI = 0,66$): (0) densely coated by pruinosity; (1) barely coated by pruinosity, highly visible metallic coloration.
- 12 Number of acrostical setae ($L = 6$; $CI = 0,33$; $RI = 0,33$): (0) few, about five; (1) many, about ten.

Wing

- 13 Number of setae on lower calypter ($L = 2$; $CI = 0,5$; $RI = 0,5$): (0) few, about five; (1) many, about ten.

Legs

- 14 Coating of frontal side of CxI ($L = 3$; $CI = 0,33$; $RI = 0,5$): (0) background color totally visible; (1) pruinose, mostly or entirely silver.

- 15 Infuscated pattern on FI ($L = 5$; $CI = 0,8$; $RI = 0,66$): (0) entirely yellow; (1) entirely blackish; (2) yellow, infuscate at basal 3/4; (3) yellow, infuscate at basal 1/2; (4) yellow, infuscate along the entire dorsal side (Fig. 1B). — **Remarks.** Characters based on color are controversial in cladistic analyses (Areekul and Quicke 2006) and the color or darkening observed on the podomeres may be substantially affected by subjective interpretation, not to mention the effect of time and preservation of specimens. However, the infuscation patterns are easily identified on the podomeres and seem to remain visible in the same relative positions regardless of the preservation method, only becoming darker or more subtle. Infuscation on the dorsal surface of FI was already considered differential and diagnostic for *Achradocera*, here, other patterns of infuscation have been added to better delimit the

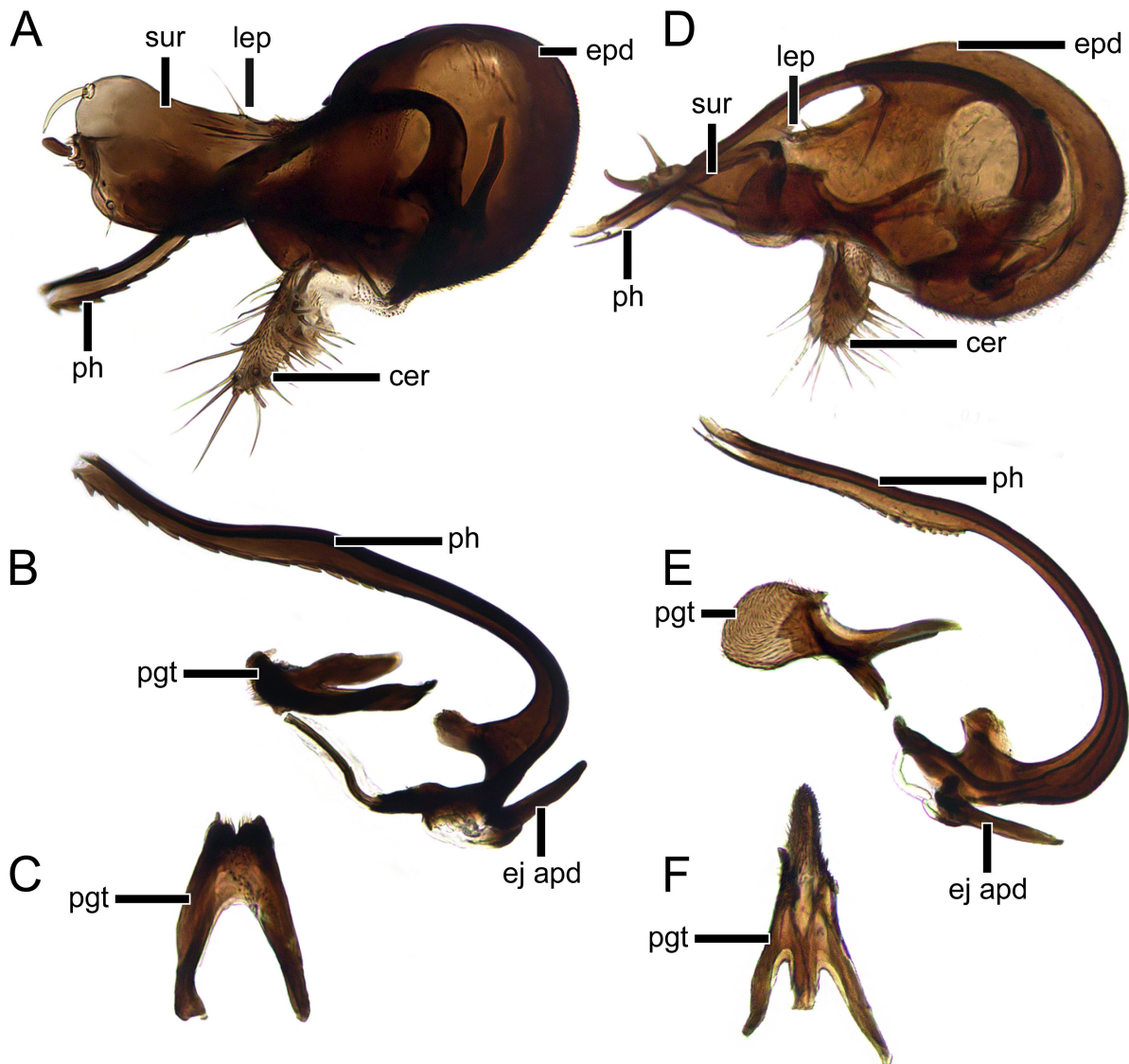


Figure 2. Main characters from internal morphology. *Achradocera barbata*: **A** Hypopygium, left lateral view. **B** internal structures of the epandrium, left lateral view. **C** postgonite, ventral view. *Achradocera tuberculata*: **D** Hypopygium, left lateral view. **E** internal structures of the epandrium, left lateral view. **F** postgonite, ventral view. Abbreviation list: cer, cercus; ej apd, ejaculatory apodeme; epd, epandrium; lep, lateral epandrial lobe; pgt, postgonite; ph, phallus; sur, surstylus.

relationship between species within the genus. Leg infuscation patterns for each *Achradocera* species are extensively illustrated and described in Quevedo et al. (2024).

- 16 Infuscated pattern on TI (L = 3; CI = 0,66; RI = 0,66): (0) entirely yellow; (1) yellow, infuscate at apical half of dorsal side (Fig. 1B); (2) yellow, with two infuscate spots, in the middle and in the apex.
- 17 Chaetotaxy of TI (L = 2; CI = 0,5; RI = 0,5): (0) podomere without any modified seta; (1) podomere bearing a conspicuous ventral row of setae (Fig. 1B).
- 18 Infuscated pattern on It (L = 1; CI = 1,0; RI = 1,0): (0) wholly yellow; (1) mostly blackish, It₁ ranges from yellow at the base to brown at the apex (Fig. 1D); (2) mostly blackish, It₁ wholly yellow (Fig. 1B).
- 19 Chaetotaxy of It₁ (L = 1; CI = 1,0; RI = 1,0): (0) uniform setae; (1) with a conspicuous row of ventral setae (Fig. 1D).
- 20 Shape of It₂ (L = 1; CI = 1,0; RI = 1,0): (0) longer than It₃; (1) about as long as It₃ (Fig. 1D).
- 21 Infuscated pattern on FII (L = 7; CI = 0,57; RI = 0,57): (0) entirely yellow; (1) entirely blackish; (2) yellow, infuscate at basal 3/4; (3) yellow, infuscate at basal half; (4) yellow, infuscate along the entire dorsal side.
- 22 Infuscated pattern on TII (L = 4; CI = 0,25; RI = 0,4): (0) entirely yellow; (1) dorsal infuscation at dorsal apical half (Fig. 1B).
- 23 Shape of TII (L = 2; CI = 0,5; RI = 0,75): (0) straight; (1) excavated in the middle (Fig. 1F–H).
- 24 Chaetotaxy of anterior surface of TII (L = 1; CI = 1,0; RI = 1,0): (0) uniform setae; (1) with a strong seta on basal 1/3 (Fig. 1F).
- 25 Chaetotaxy of ventral surface of TII (L = 1; CI = 1,0; RI = 1,0): (0) uniform setae; (1) with 2 ventral rows of strong setae near to the middle of podomere (Fig. 1F, H).
- 26 Shape of IIIt₁ (L = 1; CI = 1,0; RI = 1,0): (0) straight; (1) bent (Fig. 1K).
- 27 IIIt₁ relief on basal 1/3 (L = 1; CI = 1,0; RI = 1,0): (0) plain; (1) bearing a small tubercle (Fig. 1F, H, K).
- 28 Chaetotaxy of IIIt₁ (L = 1; CI = 1,0; RI = 1,0): (0) uniform setae; (1) a ring of strong bristles at basal 1/3 of podomere (Fig. 1F).
- 29 Width of FIII (L = 1; CI = 1,0; RI = 1,0): (0) about same width along FIII; (1) swelled at basal half (Fig. 1I).
- 30 Chaetotaxy of FIII (L = 1; CI = 1,0; RI = 1,0): (0) uniform setae; (1) with a clutch of strong and long setae in the middle of podomere (Fig. 1I).
- 31 Infuscated pattern on TIII (L = 5; CI = 0,6; RI = 0,71): (0) entirely blackish; (1) entirely yellow; (2) yellow, infuscate at apex; (3) yellow, infuscate at apex and basal 1/4 (Fig. 1B).
- 32 Shape of tarsomeres on hind leg (L = 1; CI = 1,0; RI = 1,0): (0) straight; (1) IIIIt₃₋₄ concave (Fig. 1E).

Abdomen

- 33 Length of abdomen (L = 2; CI = 0,5; RI = 0,5): (0) shorter or about the same length of head plus thorax; (1) longer than head plus thorax.

- 34 Colour of setae on sternites (L = 3; CI = 0,66; RI = 0,66): (0) all setae black; (1) white setae between the sternites 1–5, then black; (2) white setae restricted to the sternites 1–2, then black.
- 35 Chaetotaxy on sternite 5 (L = 4; CI = 0,25; RI = 0,25): (0) all setae with the same size and length; (1) bearing both weak and few distinct strong setae posteriorly.

Hypopygium

- 36 Position of the foramen on the vertical axis (L = 1; CI = 1,0; RI = 1,0): (0) peripheral; (1) central (Fig. 2A, D).
- 37 Shape of surstylus (L = 4; CI = 0,75; RI = 0,66): (0) digitiform; (1) elongate subtriangle; (2) small subtriangle (Fig. 2D); (3) subrectangular (Fig. 2A).
- 38 Chaetotaxy of surstylus (L = 2; CI = 1,0; RI = 1,0): (0) all setae equal in length and width; (1) bearing one distinct and strong seta on apex; (2) bearing two distinct and strong setae on apex (apical and ventral) (Fig. 2A, D).
- 39 Shape of apical setae of surstylus (L = 1; CI = 1,0; RI = 1,0): (0) spine-like (Fig. 2D); (1) thumb-like (Fig. 2A).
- 40 Shape of surstylus on apex (L = 1; CI = 1,0; RI = 1,0): (0) plain (2D); (1) folded up (2A).
- 41 Relative position of surstylus on anterior margin of epandrium (L = 1; CI = 1,0; RI = 1,0): (0) approximately equidistant between ventral and dorsal surfaces (Fig. 2A, D); (1) closer to the ventral surface.
- 42 Size of lateral lobe of epandrium (L = 3; CI = 0,66; RI = 0,75): (0) projected forward, as long as surstylus; (1) projected forward, shorter than surstylus; (2) not projected, appressed on epandrium posterior margin (2A, D).
- 43 Number of outer setae on lateral lobe of epandrium (L = 2; CI = 0,5; RI = 0): (0) 2 (Fig. 2A, D); (1) 3.
- 44 Size of inner seta of lateral lobe of epandrium (L = 1; CI = 1,0; RI = 1,0): (0) long, about four times bigger than outer setae of lateral lobe of epandrium (1) short, about as long as the outer setae of lateral lobe of epandrium.
- 45 Coating of lateral lobe of epandrium (L = 1; CI = 1,0; RI = 1,0): (0) bare; (1) coated by microtrichia.
- 46 Shape of anterodorsal margin of epandrium (L = 1; CI = 1,0; RI = 1,0): (0) diagonal; (1) vertical, forming a subtriangular projection.
- 47 Shape of phallus out of the epandrium (L = 1; CI = 1,0; RI = 1,0): (0) plain; (1) tumescent (2B, E).
- 48 Ventral surface of phallus (L = 1; CI = 1,0; RI = 1,0): (0) entirely plain; (1) grooved on apical half (Fig. 2B, E).
- 49 [Conditional on character 49] Shape of the grooves on phallus (L = 2; CI = 1,0; RI = 1,0): (0) small grooves; (1) lump-like grooves (2E); (2) saw-like grooves (2B).
- 50 [Conditional on character 49] Extension of grooves on phallus (L = 1; CI = 1,0; RI = 1,0): (0) restricted to apical third (2E); (1) covering the entirely apical half (2B).

- 51 Shape of frontal part of postgonite (L = 2; CI = 1,0; RI = 1,0): (0) thin and tubiform; (1) swollen, rounded laterally, and projected forward (2E, F); (2) narrow and excavated ventrally (2B, C).
- 52 Curvature of postgonite arms (L = 3; CI = 0,33, RI = 0): (0) curved out (Fig. 2F); (1) curved inward (Fig. 2C).
- 53 Length of the left postgonite arm (L = 3; CI = 0,33, RI = 0): (0) similar to right postgonite arm (Fig. 2C); (1) shorter than right postgonite arm (Fig. 2F).

3.2. Phylogeny

The EW analysis yielded two Most Parsimonious Trees (MPTs) with a length of 117 steps, CI of 0.62 and RI of 0.71 (Fig. 3, T1 and T2). The strict consensus tree exhibits a length of 118 steps, CI of 0.61 and RI of 0.71 (Fig. 3, T0). All searches utilizing IW resulted in only one topology (Fig. 3, T1), regardless of the value employed k. This suggests that any minimal weighting against homoplasy favors T1 as the most parsimonious topology. Therefore,

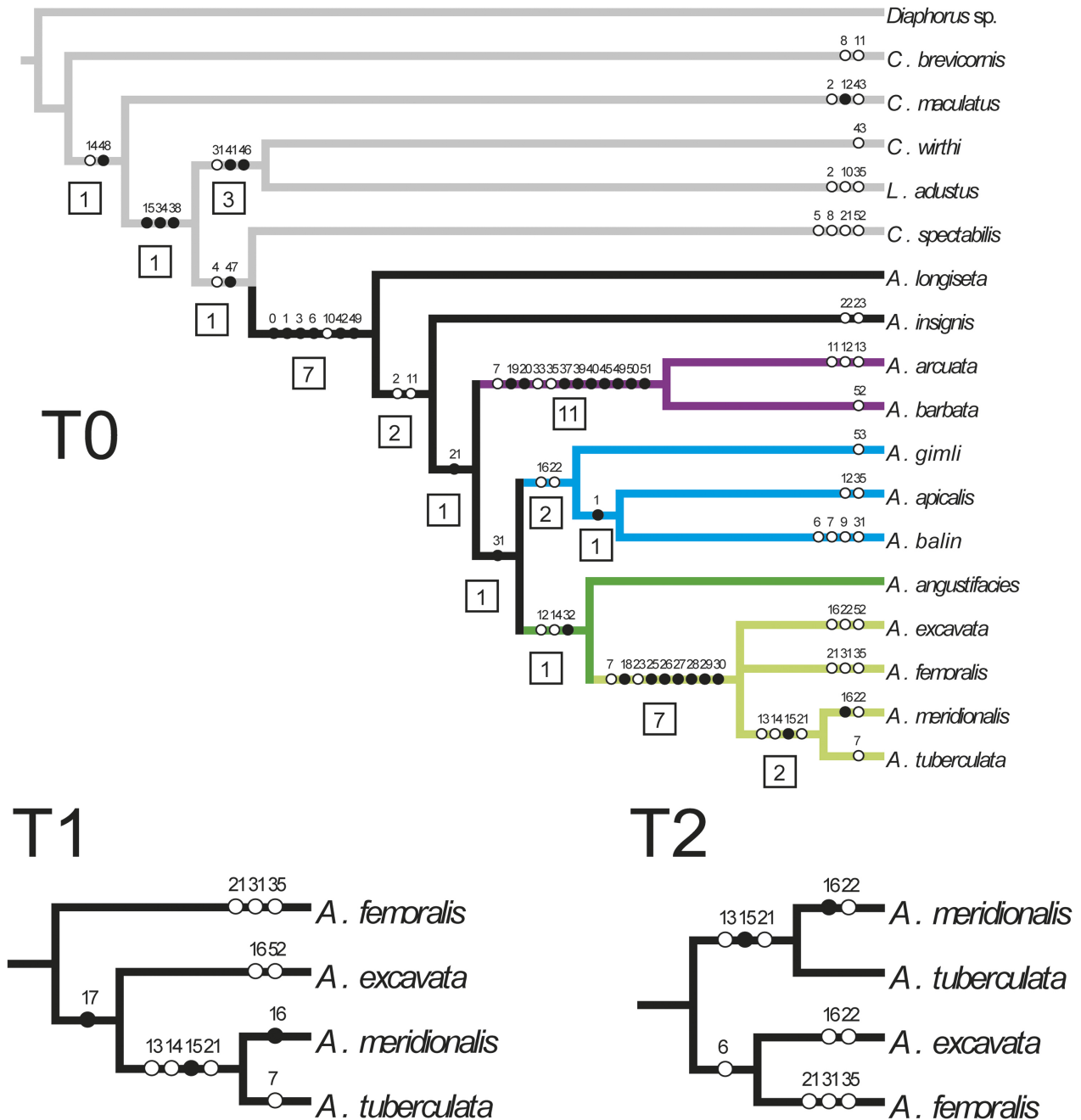


Figure 3. Phylogenetic analysis of *Achradocera*. T0, Consensus tree (L = 118; CI = 0.61; RI = 0.71) derived from an Equal Weighting (EW) analysis, reconciling two topologies. T1, (L = 117; CI = 0.62; RI = 0.71) represents the primary hypothesis in the EW analysis and the sole outcome in the Implied Weighting (IW) searches. T2, (L = 117; CI = 0.62; RI = 0.71) denotes the secondary hypothesis from the EW analysis. Grey clades depict the outgroup; the purple clade corresponds to the *barbata*-group; the blue clade represents the (*A. gimli* (*A. apicalis* *A. balin*)); and the green clade represents the *femoralis*-group plus *A. angustifacies* (with light green indicating only the *femoralis*-group). Black circles denote unique homologies, while white circles signify homoplasy. The number above the circles indicates the character.

it serves as the primary evolutionary hypothesis for this study. However, T2 will also be considered in the discussions.

Achradocera is robustly supported as a monophyletic group, characterized by six synapomorphies: enlarged postpedicel with a broad base constricted into a long narrow tip [0.1]; postpedicel length slightly longer than arista [1.2]; flattened ventral postocular setae [3.1]; grey pruinosity restricted to the area close to the eye margin [6.1]; lateral lobe of epandrium appressed on the margin of the epandrium [42.2]; and phallus with conspicuous lump-like grooves on dorsal surface [49.1]. The high Bremer's support (7) further corroborates the strength of this clade.

Within *Achradocera*, it is also possible to delineate smaller lineages of species. The *femoralis*- and *barbata*-groups are easily recognizable due to their morphological traits. The *barbata*-group comprises *A. barbata* and *A. arcuata*, both displaying numerous synapomorphies on the tarsomeres of the male foreleg [19.1 and 20.1] and hypopygium [37.3, 39.1, 40.1, 45.1, 49.2, 50.1, and 51.2] (see Figs 1D and 2A–C). Similarly, the *femoralis*-group—consisting of *A. excavata*, *A. femoralis*, *A. meridionalis* and *A. tuberculata*—is well supported, sharing many synapomorphies on the male legs [18.2, 25.1, 26.1, 27.1, 28.1, 29.1, and 30.1] (Fig. 1B, E, F, H, I). The *femoralis*-group is sister of *A. angustifacies* and both share the apomorphic state of character 32.1 (III₃₋₄ concave) as a synapomorphy with all the other species (see Fig. 1E). However, species of the *femoralis*-group accumulated many other synapomorphies after cladogenesis with *A. angustifacies*, and maintenance of the *femoralis*-group remains more applicable due to the ease species recognition associated with those characters that appears during the anagenesis of the group.

The last lineage that deserves further attention is composed by *A. apicalis*, *A. gimli* and *A. balin*. The primary challenge is that this clade lacks any exclusive synapomorphy and is solely grouped based on the infuscated pattern on TI and TII (see remarks of character 15). Moreover, Bremer's support for this clade was low, and is preferable to avoid the use of “species group” for this assemblage of species. Ultimately, *A. longiseta* was recovered as the sister-group of the remaining species and, in this latter group, *A. insignis* is the sister of all other species. The apomorphic dense white “beard” composed by the ventral postocular setae [3.1] is distinctive of the entire genus, yet in *A. longiseta* this trait is not remarkably developed. Additionally, this species also exhibits rather simple legs, which justifies its position as the sister group of all the other *Achradocera* species.

The analysis recovered *Chrysotus spectabilis* as the sister group of *Achradocera*. However, assigning this relationship is challenging given the complexity of the genus *Chrysotus*, which comprises over 300 species and is likely to be polyphyletic (Capellari and Amorim 2010, 2012, 2014) and even in our current analysis, we recovered *Chrysotus* as paraphyletic. Hypopygial characters favored those results, nesting *C. wirth* and *Lyroneurus adustus* [41 and 46] and placing *C. spectabilis* as the sister-group of *Achradocera* [47]. Van Duzee (1924) formal-

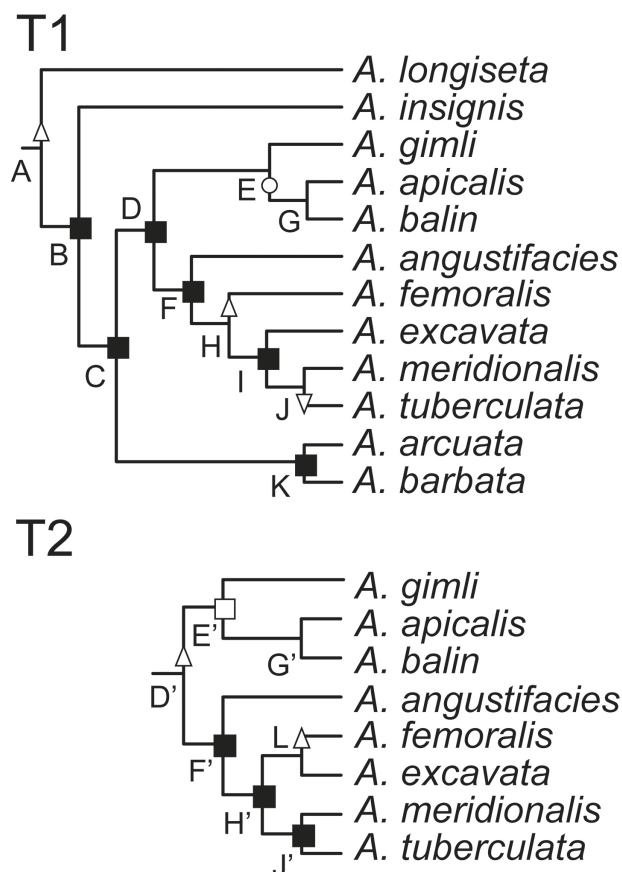


Figure 4. Comparison between results on GEM using both topologies, T2 displays only those clades that differ in their event hypotheses from T1. Symbols on the nodes indicate the events of the GEM method: black square, vicariance; white square, sympatry; white circle, sympatry punctual; white triangle, founder event (triangle's orientation indicates the direction of the founder event).

ly split *Chrysotus* into smaller species-groups to enhance our understanding of the genus, but his units are a mix of shared overall similarities and not necessarily reflect true homologies between species (see examples in: Capellari 2015; Capellari and Almeida 2024). Although the taxonomic delimitation of *Chrysotus* is entangled with *Achradocera*, a clear-cut definition of *Chrysotus* is beyond the scope of this work and was preliminary discussed by Capellari and Amorim (2012).

3.3. Biogeography

The GEM method was applied for the two MPTs, with the same parameters. Both analyses yielded only one reconstruction each (Fig. 4, T1 and T2). The cost of T1 was 37, with six vicariances (Fig. 4, nodes B, C, D, F, I, and K), one point sympatry (Fig. 4, node E), three founder events (Fig. 4, nodes A, H, and J) and zero sympatries. Conversely, T2 exhibited a cost of 31, with six vicariances (Fig. 4, nodes B, C, K, F', H', and J'), one sympatry (Fig. 4, node E'), three founder events (Fig. 4, nodes A, D', and G'), and zero point-sympatry. However, despite T2 displaying a lower cost, the primary hypothesis to be

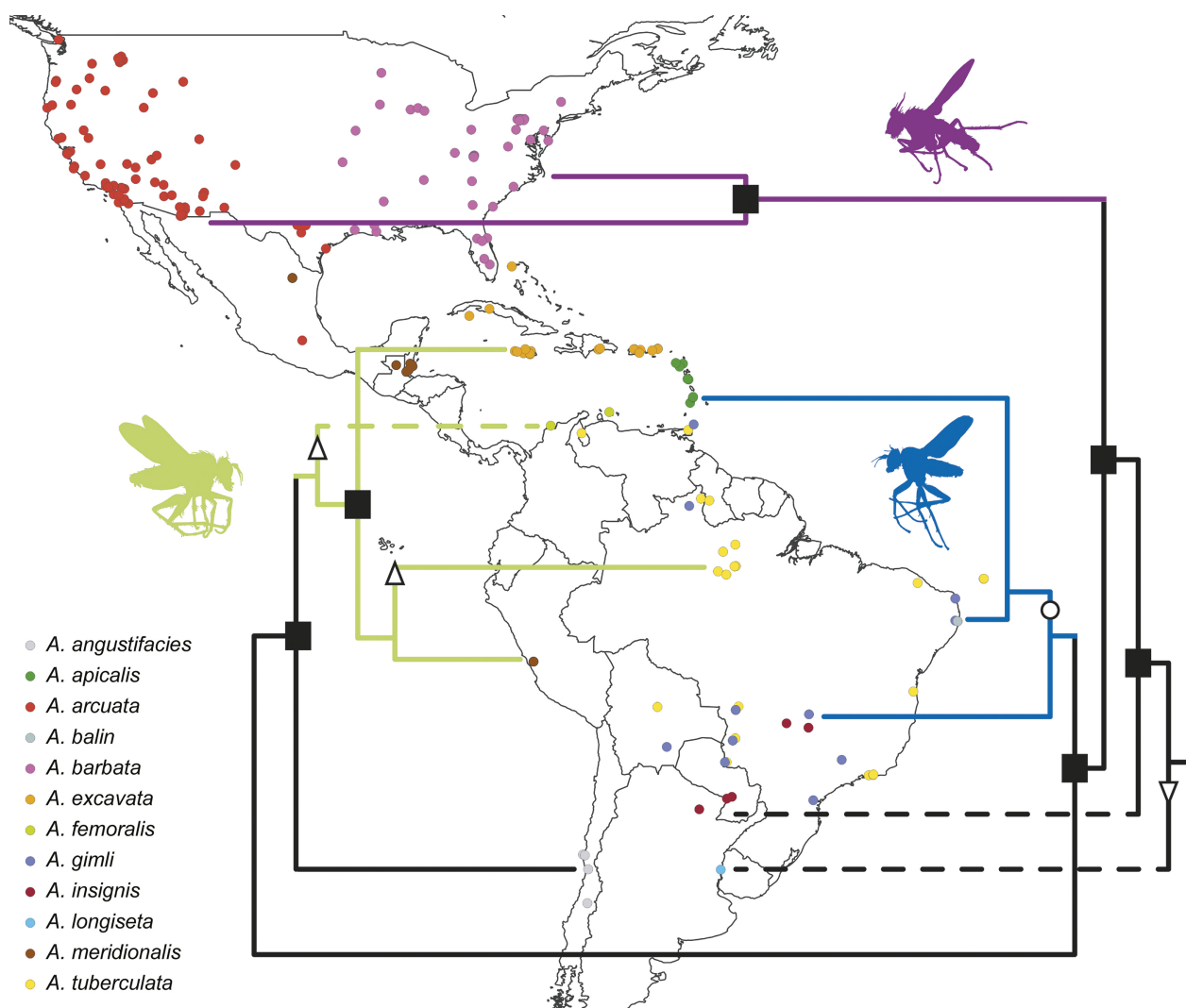


Figure 5. Association between the distribution map and cladistic T1 of the genus *Achradocera*. Colored dots indicate the locations where specimens were collected/found. The association between color and species is indicated in the image's bottom left corner. The purple, blue and green clades represent the *barbata*, *apicalis* and *femoralis* groups respectively. Dashed lines are used when the lines overlapping each other. Symbols on the nodes indicate the events of GEM method: black square, vicariance; white circle, sympatry punctual; white triangle, founder event.

considered will be T1. This determination stems from the phylogenetic analysis of the taxa, where T1 was the sole topology recovered in the IW analysis and demonstrates greater robustness compared to T2.

Given the current biogeographical scenario (Fig. 5), it is evident that vicariance played a significant role in driving the majority of speciation events in *Achradocera*. Many species within the genus exhibit extensive distribution ranges, overlapping several areas commonly utilized as biogeographical boundaries (Morrone 2017). This phenomenon underscores both the remarkable resilience of these species across diverse biomes and their exceptional dispersion capabilities. The first vicariant event on phylogeny divides *A. insignis* from the ancestor of the clade C (Fig. 4). Subsequently, we can observe the fragmentation between the ancestors of the species from node D and the Nearctic clade (node K), which species were also originated by vicariance. Notably, *A. arcuata* is restricted to the western side, whereas *A. barbata* occurs on the eastern side of North America (Fig. 5).

It is noteworthy to observe the reconstruction depicted in clade D (Fig. 6). Following the separation from Nearctic species, the subsequent vicariant event delineates the ancestor of the *femoralis*-group (Fig. 6D: yellow squares) on the west side of the Andes, while the hypothetical ancestor of the clade (*A. gimli* (*A. apicalis* *A. balin*)) (Fig. 6D: red squares) remains restricted to the east side of the Andes. While the clade (*A. gimli* (*A. apicalis* *A. balin*)) exhibited only point sympatric speciation, the *femoralis*-group undergoes alternations between vicariances and founder events.

Examining Figure 6, we note that the subsequent vicariant event isolates the ancestor of *A. angustifacies* in Chile [clade F]. Following this, a founder event drives the evolution of *A. femoralis* in the northern region of South America [H]. Another vicariance event then fragments the ancestor of clade I, leading to the scenario where *A. excavata* evolves isolated on the Greater Antilles. Finally, a founder event results in the speciation of *A. tuberculata*, which re-colonizes the eastern side of the Andes in South America

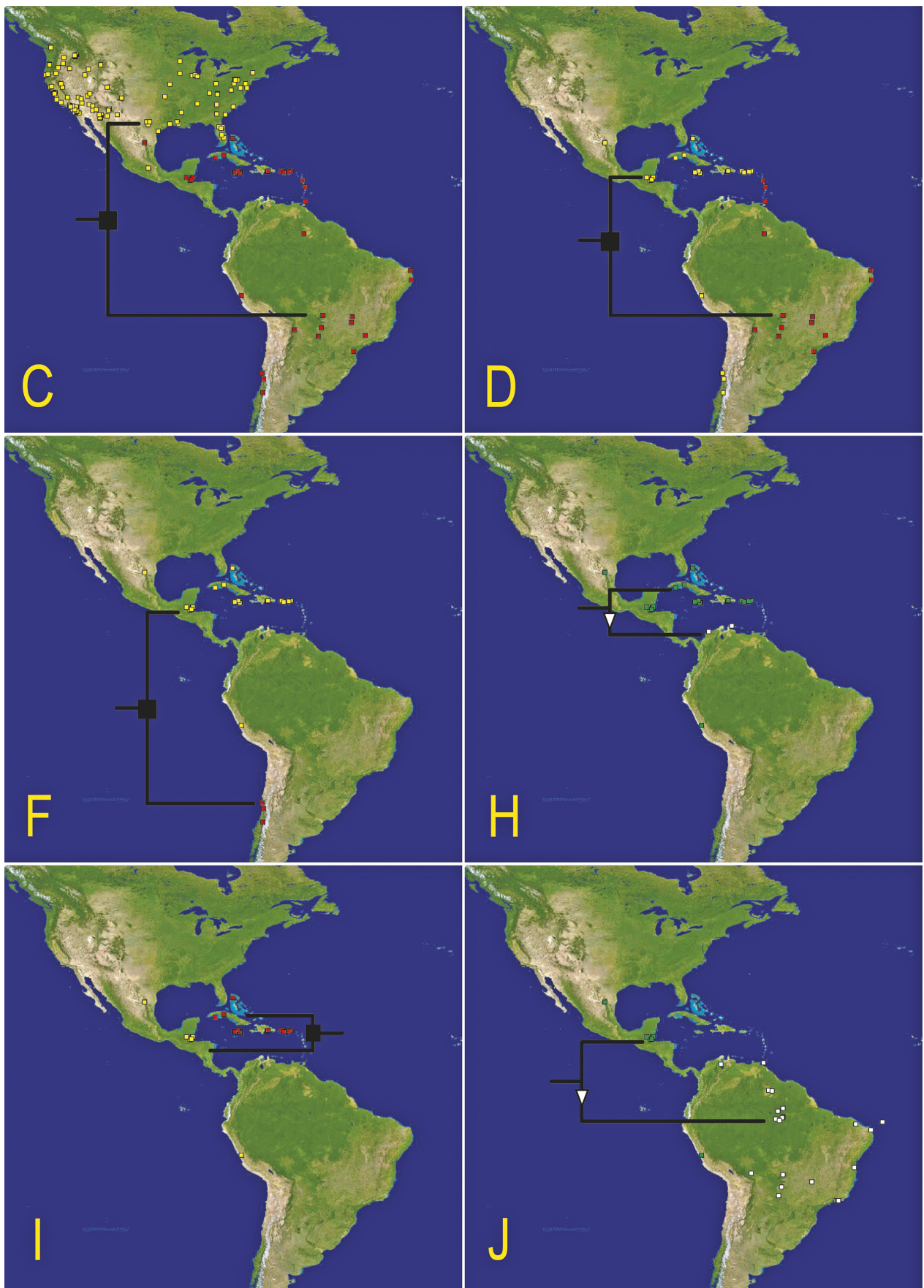


Figure 6. Reconstruction of the primary hypothesis regarding the evolutionary scenario of the *femoralis*-group. Letters on the Figure correspond to the clades labeled with the same letter in Figure 4. Yellow and red dots represent species originating after a vicariant event, while green and white dots indicate founder events (green signifies the ancestral distribution, while white dots represent newly colonized areas). Symbols on the nodes indicate the events of GEM method: black square, vicariance; white triangle, founder event.

[J], while *A. meridionalis* evolves across the western side of the Andes and the Neotropical regions of Mexico.

The GEM analysis reconstructed the ancestral distribution of *Achradocera* as encompassing the entire New World. However, we posit that this conclusion may have been influenced by the lack of information regarding the sister group of *Achradocera*, as mentioned earlier. *Chrysotus*, being a vast and imprecisely delimited genus, imposes a challenge to elucidate the biogeographical relationships of *Achradocera* at this point. As such, determining the ancestral distribution of the genus was not the primary objective of this study, given the surrounding uncertainties. Nonetheless, we can still speculate that the genus likely originated in the Neotropical region, known for its high species richness and hosting species exhibiting ancestral states of the hypopygium (Quevedo et al. 2024). In any case, a better understanding of *Chrysotus* is necessary for a more accurate analysis of the ancestral distribution of *Achradocera*.

4. Discussion

4.1. Phylogeny

The results of the phylogenetic analysis shed light on the evolutionary relationships within the genus *Achradocera*, which emerges as a monophyletic group, characterized by six morphological apomorphies pointing to a robustly defined group. The placement of *C. spectabilis* as the sister-group of *Achradocera* underscores the importance of analyzing hypopygial structures for a better understanding of the relationships between the *Chrysotus* groups and related genera. Certainly, the statement of the species *Chrysotus spectabilis* as sister-group of *Achradocera* should not be seen as definitive, since many other *Chrysotus* were not included in the analysis, even so, the hypopygial similarity of this species (Capellari and Amorim 2010) with the plesiomorphic condition of the hypopygium of *Achradocera* (Fig. 2D) is striking. However, the application of the same treatment to hypopygial structures may not be as useful for separating species within *Achradocera*—or perhaps even for the entire Diaphorinae—compared to other groups such as the *longipalpus*-group (Capellari 2015; Runyon and Capellari 2018), where hypopygial structures show minimal variation. This contrasts with other subfamilies of Dolichopodidae, such as Neurigoninae (Naglis 2001a,b, 2002a,b, 2003), Dolichopodinae (Soares et al. 2023; Brooks 2005), some Sympycninae lineages (Bickel 1992, 1999), and others, where hypopygial structures exhibit more pronounced differences between congeneric species.

Furthermore, our understanding of the biology and behavior of long-legged flies remains limited, particularly when contrasted with the taxonomic diversity within the group. However, the significance of their legs in courtship is apparent, as evidenced by the abundance of morphological specializations observed across various genera and

species (Land 1993a,b; Lunau 1992, 1996; Zimmer 2000, 2003). In the case of *Achradocera*, it appears that certain convergent traits have emerged over the course of species evolution, this observation may suggest the utilization of these podomeres since their more basal lineages.

For instance, similar variations are observed in different species: *A. excavata*, *A. meridionalis* and *A. tuberculata* exhibit distinct setae on TI [char 17.1], while the *barbata*-group displays modified It_{1-2} [19.1, 20.1]. Additionally, *A. insignis* (see Fig. 1G) independently developed an arching on TII [char 23.1], differing from the excavation observed in the *femoralis*-group (see Fig. 1F–H), and these characters clearly evolved independently: the excavation within the *femoralis*-group occurs initially with a bulge near the middle of TII, and gets more pronounced in *A. tuberculata*, which bears a secondary bulge more apically, forming a deep excavation. In contrast, the excavation in *A. insignis* is formed by an arching of the podomere, with no visible bulge, indicating the homoplasy. *Achradocera balin* demonstrates an arching on III t_2 , whereas the *femoralis*-group and *A. angustifacies* display arched III t_{3-4} . Moreover, *A. arcuata* exhibits a modified FIII with protrusions and special setae, contrasting with the bulged FIII and special setation observed in the *femoralis*-group (see Fig. 1I). These observations suggest that each of these podomeres likely plays a fundamental role in courtship behavior across various species within the genus.

Due to Dolichopodidae being a highly diverse family, the focus of study on the family has traditionally been the taxonomic description of new taxa (as pointed by Lim et al., 2010—see Discussion section), which indeed is crucial, especially considering the gaps in knowledge about the fauna of naturally megadiverse regions, such as the Neotropical and Afrotropical regions (Yang et al., 2006; Grichanov and Brooks, 2017). However, some studies involving phylogeny and biogeography may represent an important tool to resolve some historically problematic groups (as advocated by Capellari and Santos, 2012), such as *Chrysotus*, *Sympycnus* Loew or various other cosmopolitan and imprecisely delimited genera.

4.2. Biogeography

As for the biogeographical results, although there is no known fossil of *Achradocera*, it is presumable that it is a fairly recent group, considering that it is a derived lineage within *Chrysotus* (Capellari 2013), which has Baltic fossils dated from the Eocene/Oligocene (Evenhuis 2017). Due to the locality of its most basal species (southern South America), *Achradocera* potentially has a Neotropical origin, later spreading to the Nearctic. According to Sanmartín and Ronquist (2004), these regions connected twice in the last 40 Myr: first with the formation of the Panamá Island Arc (15 Myr), and subsequently through the Isthmus of Panama (3.5 Myr), in a process known as the Great American Biotic Interchange. Considering that cladogenesis in clade C occurred after one of these events, it leads us to presuppose an older (h1, hypothesis 1) or

more recent (h2, hypothesis 2) diversification origin of the species.

It is plausible to assume that the vicariant event observed in clade C is related to the Mexican Transition Zone (MTZ) (Morrone 2004, 2006), causing a spatial disjunction between the Nearctic clade and the other species of clade D. Linking this vicariant event associated with the MTZ to a precise time frame is challenging. Morrone (2015b) recognizes five stages in the development of the MTZ: (1) Jurassic–Cretaceous, (2) Late Cretaceous–Palaeocene, (3) Oligocene–Miocene, (4) Miocene–Pliocene, and (5) Pleistocene. Considering hypotheses *h1* and *h2*, the vicariance of clade D may be associated with stages 3, 4, or 5. This pattern was also observed in analyses with the genus *Heterostylum* Macquart (Lamas et al. 2014), potentially being congruent. In the Nearctic, the vicariant event in clade K promotes segregation between the western side for *A. arcuata* and eastern for *A. barbata*. Sanmartín et al. (2001), in a biogeographical analysis involving numerous Holarctic clades for different periods of time, separate the Nearctic areas into East Nearctic (EN) and West Nearctic (WN), a pattern commonly observed, where EN and WN are often more associated with Palaearctic areas than between each other. However, considering that the *barbata*-group is a strictly Nearctic clade, as far as we know, it is valid to consider Halffter's (1987) proposition, in which this distribution pattern (EN and WN) is recurrent in recently speciated insect groups, suggesting time *h2*, where the achradoceran species have undergone a fairly recent radiation.

In South America, the divisions observed between transandine (= west of Andes) species, such as *A. meridionalis* and *A. angustifacies*, and cisandine (= east of Andes) species, such as *A. longiseta*, *A. insignis*, *A. tuberculata*, *A. gimli*, and *A. balin*, indicate a strong Andean influence on the genus distribution. Andean radiations are complex to analyze; geological reconstructions indicate that uplift events occurred at various periods throughout time, advancing from south to north and from west to east (Hoorn et al. 1995; Gregory-Wodzicki 2000; Taylor 1991; Garzone 2008). Following the interpretation of time *h2*, the vicariant event recovered in clade D must be related to some more recent uplifting, followed by subsequent isolation in Chile of the species *A. angustifacies*, possibly through an event related to the South American Transition Zone (SATZ) (Morrone 2004). The transandine recolonization by *A. tuberculata* may have also been caused by some vicariant event related to SATZ, for clade J' in T2 (Fig. 4)—we consider that founder events are not viable for a more detailed explanation, due to multiple factors and stochastic events that may be involved, so most of them will not be addressed. This is also the case for the founder event hypothesis of *A. tuberculata* in clade J in T1, but also in H or L for *A. femoralis* and A for *A. longiseta*. Although it is not possible to directly detect their causes, founder events—which promotes speciation through a rapid bottleneck effect resulting from a small, and isolated population (Barton, 1984)—have been widely supported in biogeographical studies (Matzke, 2014). The founder event was incorporated into the method of Arias (2017)

based on the following principle: one descendant inherits the whole ancestor's range, and the other descendant starts as a founder population outside the ancestral range.

The vicariant event recovered for *A. excavata* is controversial. The current position of the Greater Antilles was reached in the Miocene (about 25 Myr), when the Caribbean Plate collided with the Bahamas Block (Buck 1990). These islands have no recent connection with continental landmasses, having been separated from South America in the Cretaceous (Anderson and Schmidt 1983). Nevertheless, due to fluctuations in sea level, it is difficult to determine exactly how much land remained above water during prehistoric times, if any (Buck 1990). Therefore, we can speculate about some land connection between Cuba and Mexico that might justify this result. However, it is also plausible that it could be some analytical noise in the GEM, and a founder event, like the one that originated *A. apicalis* in the Lesser Antilles, may have also promoted the speciation of *A. excavata*. One plausible explanation for these cases could be dispersal through air masses or surface debris (Bickel 1996). An alternative hypothesis for the current distribution pattern of *A. excavata* and *A. apicalis* is the GAARlandia hypothesis (GAAR = Greater Antilles + Aves Ridge), introduced by Iturralde-Vinent and MacPhee (1999), but which has gained strength recently (Alonso et al. 2011). In this hypothesis, land masses connected South America with the Caribbean Islands about 34 Myr, resulting from a combination of tectonic compression factors and a rapid sea-level fall, due to a fast ice-sheet growth in Antarctica (Ali 2012). However, taking this hypothesis into account pushes the time of cladogenesis of *Achrado-cera* even further in the past. In time, stating anything would be premature, especially since we lack “branching clock” data, let alone a minimum fossil record. Nevertheless, considering that this is a seminal work for the biogeographical patterns of Dolichopodidae in the New World, we believe that raising some historical possibilities may stimulate future discussions in the field.

In general, the lowland Pan-American Dolichopodidae fauna commonly presents species with wide distribution areas, disregarding “areas” traditionally used for biogeographical studies (Morrone 2017). Thus, biogeography methods that do not rely on areas (Hovenkamp 1997, 2001, 2002; Arias et al. 2011) and, alternatively, emphasize the processes generating cladogenesis, may be potentially favorable for future research with this taxon. Despite being recent and still presenting evident limitations, GEM (Arias 2017) has proven to be a very promising tool. Finally, this study was only possible thanks to a previous and extensive review of the genus (Quevedo et al. 2024) and the morphological study that provided the phylogeny, thus reducing Linnaean, Darwinian, and Wallacean shortfalls. Still, some data noises were unfeasible to resolve for now, we highlight two: (1) the lack of systematic knowledge about *Chrysotus* made it not possible to confidently choose a sister group for *Achrado-cera* for the biogeographical analysis, creating noise in the reconstruction of the genus's ancestral distribution; (2) collection bias, where many areas in the interior of

Brazil and entire countries in South and Central America, lacked occurrence records.

5. Declarations

Data Availability Statement (DAS). The data that support this study are available in the supplementary material of this article and in the examined material listed in Quevedo et al. (2024) [<https://doi.org/10.11646/zootaxa.5519.3.1>].

Conflict of Interest Statement. We declare that we have no conflict of interest.

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Supplementary Material 1

Figures S1, S2

Authors: Quevedo L, Capellari RS, Lamas CJE (2026)

Data type: .pdf

Explanation notes: **Figure S1.** Tree 1 with character states under the circles to indicate polarization of characters. — **Figure S2.** Strict consensus tree (L = 124; CI = 0.58; RI = 0.67) of six MPTs (L = 118; CI = 0.61; RI = 0.71) after a new analysis inactivating characters 6, 7, 11 and 14.

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Supplementary Material 2

Table S1, S2

Authors: Quevedo L, Capellari RS, Lamas CJE (2026)

Data type: .pdf

Explanation notes: **Table S1.** Morphological matrix used for cladistic analysis, including all species of the genus *Achradocera*, as well as all outgroup species. Characters and character states correspond to the list of characters presented in the Results section. — **Table S2.** Coordinates of *Achradocera* species used on the biogeographical analyses. The “GEM coordinates” column corresponds to the format required to run the analyses in the GEM program (Geographically Explicit Event Model analysis).

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