

AMERICAN MUSEUM NOVITATES

Number 3962, 12 pp.

October 6, 2020

First known extant species of *Alavesia* (Diptera:
Atelestidae) in the Neotropical region:
Alavesia leukoprosopa, sp. nov.,
from the southern Atlantic Forest, Brazil

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ABSTRACT

A first known extant Neotropical species of the atelestid genus *Alavesia*—*Alavesia leukoprosopa*, sp. nov.—is described from southeastern Brazil. The holotype (and only specimen so far) was collected with a Malaise trap in an area with strongly impacted semideciduous seasonal forest (dry forest) and open, entirely secondary vegetation. It was collected in mid spring, but has not been collected again so far. *Alavesia leukoprosopa* shares some derived features with the only two other extant species of the genus, known from the Brandberg Massif in Namibia, suggesting that all three extant species may compose together a small clade separate from the bulk of the Cretaceous diversity of *Alavesia*.

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INTRODUCTION

Five extant genera are now gathered under the family Atelestidae—*Atelestus* Walker, *Acarteroptera* Collin, *Meghyperus* Loew, *Nemedina* Chandler, and *Alavesia* Waters and Arillo. A subfamily Atelestinae was originally proposed by Hennig (1970) within the Empididae s.l., later raised to family rank by Chvála (1983). There is still no consensus about position of the atelestids among the empidoids. Chvála (1983) proposed a sister group relationship between Atelestidae and the Cyclorrhapha. Collins and Wiegmann (2002), Moulton and Wiegmann (2004, 2007), and Wahlberg and Johanson (2018) proposed Atelestidae to be sister of the remaining Empidoidea based on molecular data, while Sinclair and Cumming (2006) accepted the family as sister to the Hybotidae based on morphological data. In Sinclair and Kirk-Spriggs' (2010) phylogenetic study of the atelestids, *Nemedina* is proposed as sister to the remaining genera of the family and was kept in a subfamily of its own, Nemedininae Sinclair and Cumming. *Alavesia* is sister to the other three genera within a subfamily Atelestinae.

Alavesia was first described based on a middle Albian–upper Aptian amber fossil from Spain (Waters and Arillo, 1999), to which a second species also from the Spanish Cretaceous amber was later added (Peñalver and Arillo 2007). The original hypothesis by Waters and Arillo (1999) and Peñalver and Arillo (2007) was that *Alavesia* would belong to the Ocydromiinae hybotids. Grimaldi et al. (2002) referred to undescribed species of the genus in Myanmar mid-Cretaceous amber. Sinclair and Kirk-Spriggs (2010) transferred *Alavesia* to the family Atelestidae. Besides the phylogenetic consideration of the Atelestidae, Sinclair and Kirk-Spriggs (2010) also described the first two extant species known in the genus, from Namibia. The description of the extant species brought a better understanding of the general morphology of the genus, including the details of the male terminalia.

There were recent additions to the knowledge of the atelestids by Poinar and Vega (2020), Jouault et al. (2020), and Zhang et al. (2020). Poinar and Vega (2020) described a Cretaceous Myanmar amber species, placed in a new genus *Neoalavesia* Poinar and Vega—in the paper assigned to the atelestids, but also referred to as an empidid. Jouault et al. (2020) described another Cretaceous species of *Alavesia* of Myanmar amber and raised some hypotheses for the origin of the genus. Zhang et al. (2020) described an additional species of *Alavesia* from Myanmar amber and the female of *A. myanmarensis* Jouault, Ngô-Muller, and Nel; they also discuss the homology of sclerites of the male and female terminalia in the genus.

We now have a great expansion of our understanding of the diversity of *Alavesia* genus with the description of nine additional species of the genus from Myanmar Cretaceous amber material by Sinclair and Grimaldi (2020). They also synonymized *Neoalavesia* Poinar and Vega (Poinar and Vega, 2020) to *Alavesia*.

To our initial amazement, we collected an additional extant species of *Alavesia* in southeastern Brazil. The discovery of a Neotropical species of the genus in South America is considered, nevertheless, consistent with an old clade with prior wide distribution in the world, now with a relict distribution (Sinclair and Grimaldi, 2020). The presence of *Alavesia* in South America adds a second genus to the diversity of Atelestidae in South America, the family also including *Acarteroptera* from Chile (Collin, 1933). In this paper, we describe and illustrate this

first known Neotropical species of the genus and forward some initial comments on the position of this species in *Alavesia*.

MATERIAL AND METHODS

The holotype is deposited in the Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP). Pictures were taken with LAS software coupled to a stereomicroscope and assembled in Helicon Focus 6. The terminalia were treated with 10% KOH at 40° C for 20 minutes, then neutralized in 1% acetic acid, and transferred to a microvial with glycerin. The wing was mounted in Euparal between cover slips, then pinned beneath the specimen together with the terminalia microvial. The morphological nomenclature follows Cumming and Wood (2017), except for the ventral apodeme, referred to by Sinclair and Cumming (2006). Costal sections also in Cumming and Wood (2017): section 1, between h and R₁; section 2 between R₁ and R₂₊₃; section 3 between R₂₊₃ and R₄₊₅; section 4 between R₄₊₅ and M₁. Abbreviations are provided in the legend of illustrations.

RESULTS

Alavesia Waters and Arillo, 1999

TYPE SPECIES: *Alavesia subiasi*† Waters and Arillo, 1999: 60, by original designation.

DIAGNOSIS (from Sinclair and Kirk-Spriggs, 2010): Diminutive cell dm, M₁₊₂ and M₄ greater than half the length of wing and widely divergent, postpedicel very long and lanceolate, stylus three-articled, legs with parallel rows of minute setulae.

Alavesia leukoprosopa, new species

Figures 1–4

DIAGNOSIS: Postpedicel slightly longer than scutum; face with whitish pruinosity; thorax dark, with a whitish pruinosity; head and thorax setulae pale; legs yellow; M₁₊₂ slightly sinuose along its length; ventrolateral of epandrium longitudinally sclerotized (fig. 4D, arrow); hypoproct longer than cercus; postgonites not jointed mesally, long, curved anteriorly; hypandrium indistinct.

DESCRIPTION: *Male*. Body length, 2.2 mm (fig. 1A). **Head** (figs. 1B–C): Frons black, with some grayish pruinosity, face whitish with dense white pruinosity, occiput black on dorsal half, thinly pruinose, grayish on ventral half, more densely pruinose. Gena very narrow. Ocelli on slightly projected vertex, mid ocelli only slightly displaced anteriorly in relation to lateral ocelli. Frons without setae, occiput with crown of yellowish postocular setae, face without setae. Eye bare; eyes dichoptic, large, with a rather metallic reddish color. Scape whitish, pedicel pale yellow, postpedicel dark brown. Postpedicel greatly lengthened, longer than scutum; stylus short, postpedicel about 5.8 length of stylus (fig. 3B). Maxillary palpus whitish, close to each other at

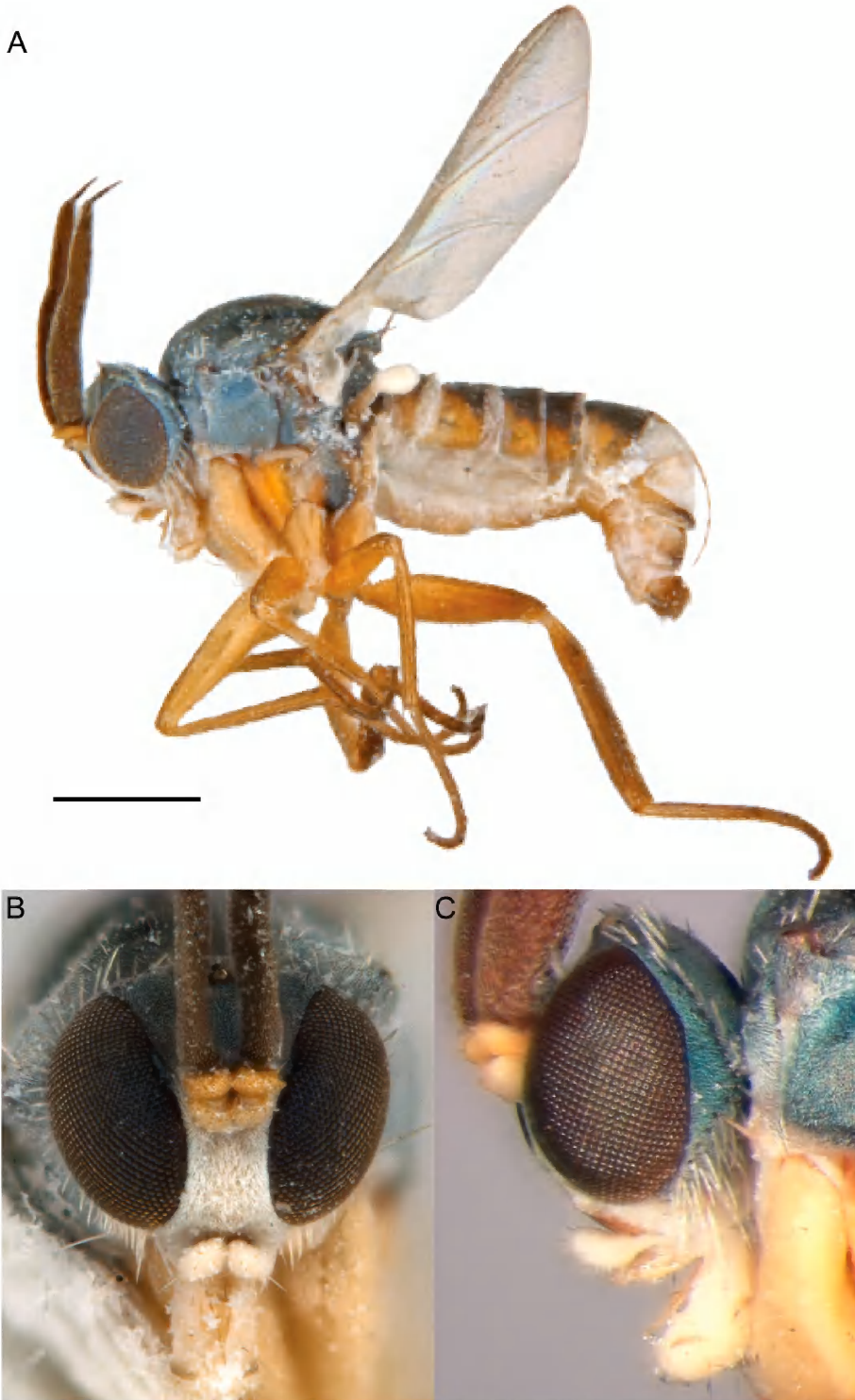


FIGURE 1. *Alavesia leukoprosopa*, sp. nov., holotype. **A.** Habitus (scale bar = 0.1 mm). **B.** Head, frontal view. **C.** Head, lateral view.

tip; labellum light brownish yellow at base, whitish toward apex; labrum slender, elongate. Prementum well developed, whitish, setose.

Thorax (figs. 2A–B): Scutum and scutellum black, entirely covered with scattered pruinosity, denser on postpronotal lobe; 3–5 rows of short acrostichals clearly separated from 4–6 rows of short dorsocentral setae; pair of strong notopleurals, pair of long postalars, and an irregular row of stronger postsutural. Antepronotum blackish, proepisternum ochre-yellow. Anepisternum blackish; katepisternum mostly ochreous yellow, with small dorsoposterior brownish mark. Anepimeron blackish, with brownish area along meso-dorsal suture, katepimeron reaching ventral margin of thoracic pleura, weakly sclerotized, cream-yellow. Meron brownish yellow, dark brown along contact with metepisternum. Metepisternum blackish brown, metepimeron dirty yellow, darker dorsally. Laterotergite and mediotergite blackish brown. Elongate membranous area between anepisternum and katepisternum (fig. 2A, seta). Postpronotum densely microtrichose. One pale proepisternal seta present. Anepisternum densely pruinose, bare of setae; katepisternum shiny, no pruinosity or setae. Anepimeron, katepimeron, metepisternum, metepimeron, laterotergite and mediotergite pruinose, devoid of setae. Meron thinly pruinose, without setae. Halter stalk light brown, knob whitish, without setae.

Legs (fig. 1A, 3C–D): Coxae whitish yellow, forecoxa lighter, femora light brownish yellow, front and mid tibiae light brownish yellow, hind tibia darker, tarsi brownish yellow, darker towards apex. Femora with longitudinal area devoid of setulae, but no furrow; tibiae with rows of palisades with furrows in between. Hind tibia modified, more sclerotized than front and mid tibiae, with conspicuous sensorial organ dorsally on basal fourth, bearing ellipsoidal opening (fig. 3D).

Wing (fig. 3A): Length, 1.5 mm. Rather short compared to other congeneric species, oval shaped. Costal sections 1–4: 10; 1.5; 6; 3. C without spines. H present, weakly developed, Sc relatively long, extending beyond level of r-m, but incomplete; R_1 ending at distal third of wing, with one basal (fig. 3A, arrow) and two distal sensorial pits; R_{2+3} ending at C slightly beyond tip of R_1 . R_{4+5} reaching C well before tip of wing, with three distal sensorial pits; M_{1+2} almost as sclerotized as R_{4+5} , slightly sinuous along its length; cell dm present, small, restrict to basal third of wing, cells br and bm also short; dm-cu connecting M_{1+2} to M_4 , nearly transverse. Cell cua short, CuA+CuP reaching wing margin; long conspicuous anal fold almost reaching wing margin.

Abdomen (fig. 1A): Tergites 1–5 blackish brown medially, yellowish at lateral margins, sternites 1–5 pale brownish yellow. Tergites 6–7 more sclerotized along posterior margin, rather dark brown; tergite 8 membranous, slender, bare of setation.

Terminalia (figs. 4A–D): Hypandrium not discernible. Gonocoxal apodeme slender and greatly lengthened rod-like process, as long as ejaculatory apodeme, narrow in ventral view. Postgonites not joined medially, striplike, very long and bent anteriorly. Phallus tube-like, short, apex arched ventrally; ejaculatory apodeme long, articulated at base of phallus, posterior end slightly broadened. Epandrium U-shaped, with slender dorsal bridge anteriorly to cerci; setae concentrated along ventro-lateral margin; ventrolateral edge longitudinally sclerotized (fig. 4D, arrow), basally attached to epandrium, projected apically. Surstylus subapical, divided into pair

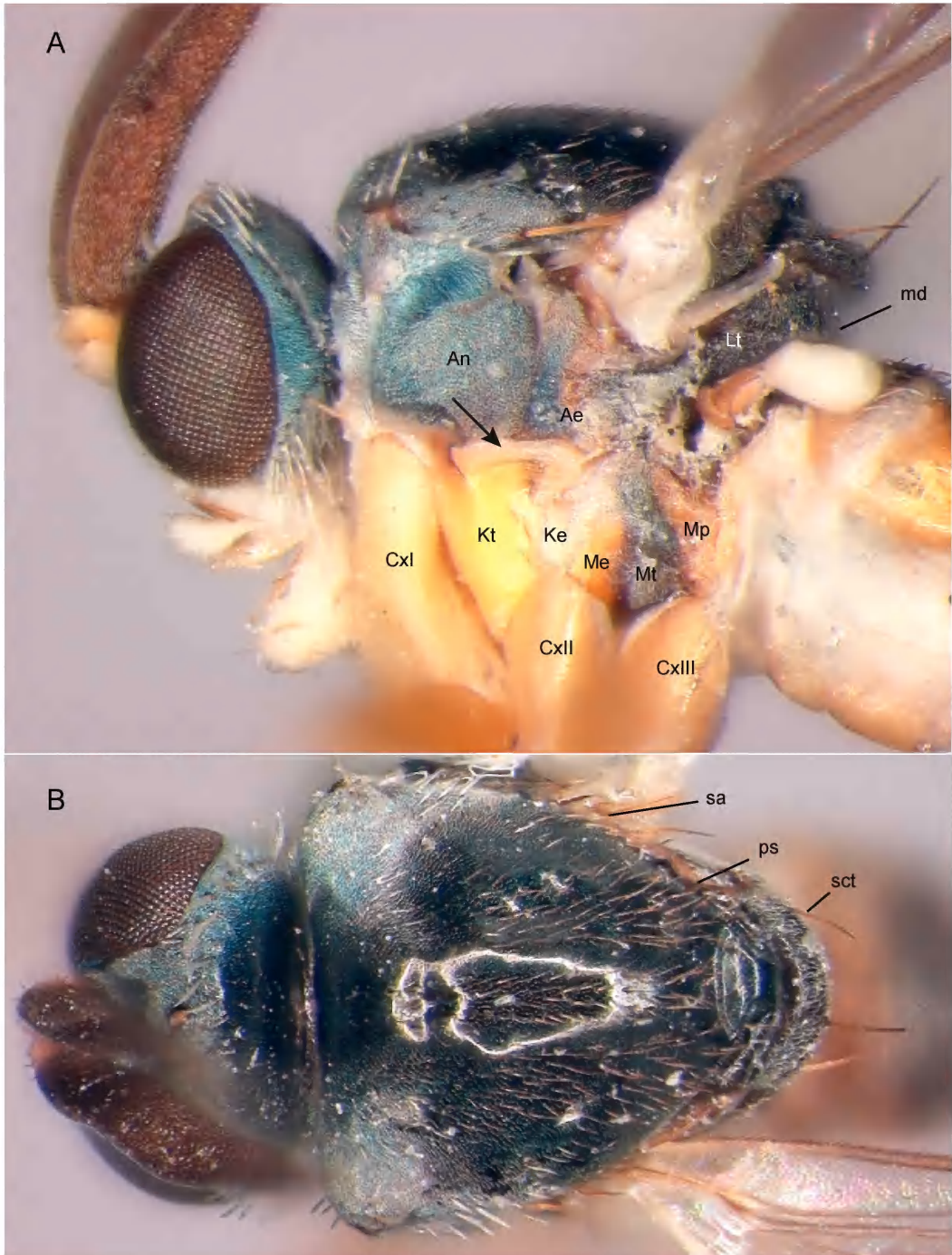


FIGURE 2. *Alavesia leukoprosopa*, holotype. **A.** Thorax, lateral view. **B.** Thorax, dorsal view. Abbreviations: **Ae**, anepimeron; **An**, anepisternum; Cx I-III, front, mid, hind coxae; **Kt**, katepisternum; **Ke**, katepimeron; **Lt**, laterotergite; **Md**, mediotergite; **Me**, meron; **Mp**, metepimeron; **Mt**, metepisternum; **ps**, prescutellar setae; **sa**, supraalar setae; **sct**, marginal scutellar setae. Arrow points membranous area between the anepisternum and the anepimeron, dorsally, and the katepisternum and the katepimeron, ventrally.

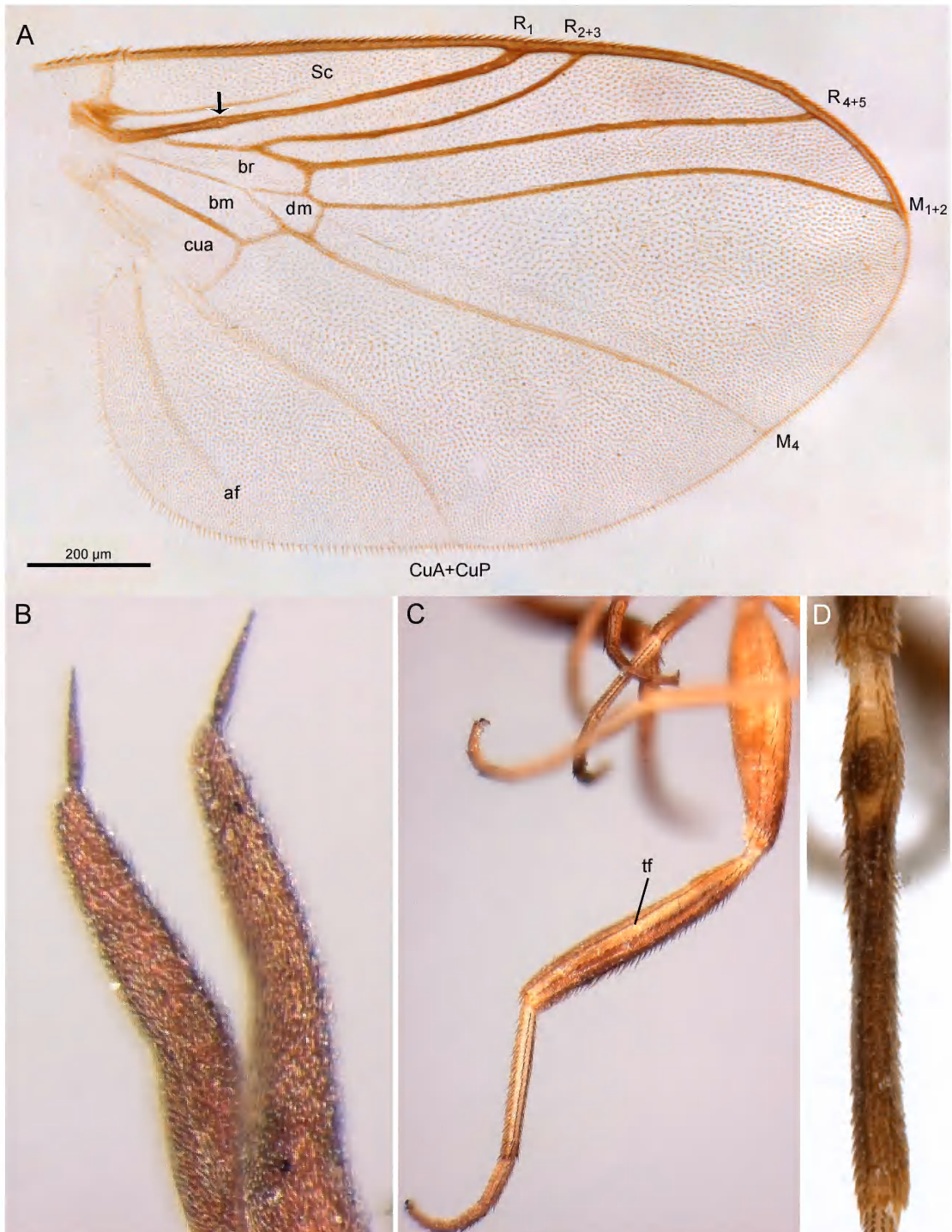


FIGURE 3. *Alavesia leukoprosopa*, holotype. **A.** Wing (abbreviations following Cumming and Wood, 2017). **B.** Postpedicel and stylus. **C.** Hind leg, inner lateral view. **D.** Hind tibia, dorsal view, with tibial organ on basal fourth. Arrow point basal R_1 sensorial pit. Abbreviation: **af**, anal fold; **tf**, tibial furrow.

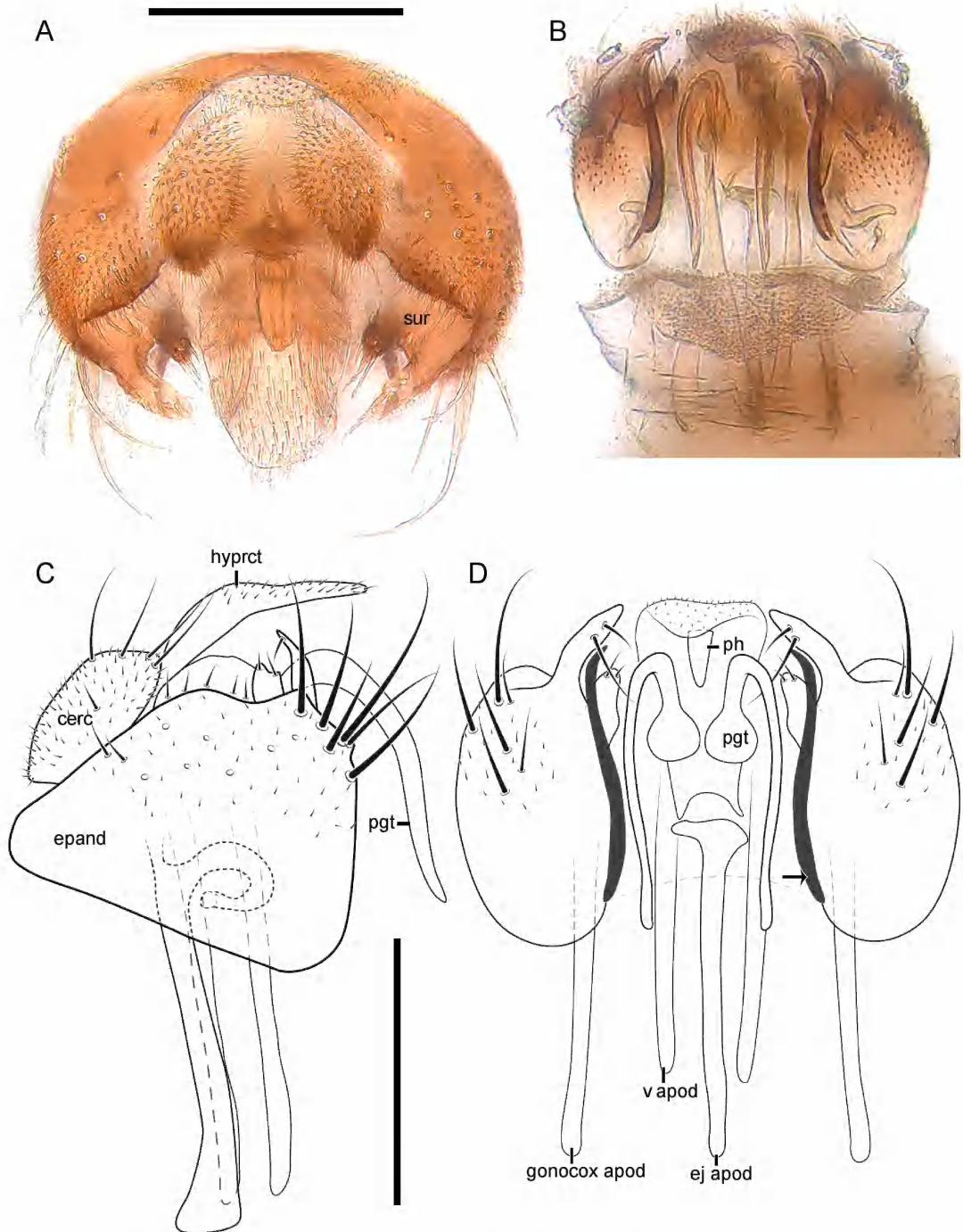


FIGURE 4. *Alavesia leukoprosopa*, holotype. Male postabdomen. **A.** Dorsal view. **B.** Ventral view. **C.** Lateral view. **D.** Ventral view (arrow points to heavily sclerotized blade at margin of epandrial ventral margin) (scale bar 0.1 mm). Abbreviations: **cer**, cercus; **ej apod**, ejaculatory apodeme; **epand**, epandrium; **gonocox apod**, gonocoxal apodeme; **hyprct**, hypoproct; **pgt**, postgonite; **ph**, phallus; **sur**, surstylus; **v apod**, ventral apodeme.

of pointed lobes, each dorsal lobe with pair of setae along inner margin. Hypoproct longer than cercus, with setulae. Cercus sclerotized, ovoid, setose.

Female: Unknown.

TYPE MATERIAL: Holotype male, BRAZIL, São Paulo, Ribeirão Preto, University of São Paulo – campus of Ribeirão Preto, in front Guest House, S21°09'54" W47°50'56", 593 m, Malaise trap, 19.xi-3.xii.2019, P.R. Riccardi and H.F. Flores leg. [MZUSP].

ETYMOLOGY: The specific epithet of the species name refers to the face (Greek, *prosopa*) with white (Greek, *leukos*) pruinosity in the described species.

REMARKS: This Neotropical representative of *Alavesia* differs in significant details from both known extant species described from Namibia. The postpedicel is longer than in both extant species of the genus. The scutum is yellow in *A. brandbergensis*, and black in *A. daura* and *A. leukoprosopa*, sp. nov. As in *A. brandbergensis*, the legs in *A. leukoprosopa* are yellowish, without the dark apex of mid and hind tibiae in *A. daura*. Compared to *A. daura*, the wing shape is more rounded and the venation of the Neotropical species has a slightly wider cell c and a more slender cell r_1 . Although Tergite 8 is about the same width, it is more membranous than in *A. brandbergensis*, and without setulae. The male terminalia has the same general pattern in the three extant species, but with some differences. The epandrium in *A. leukoprosopa* is wider than in the remaining extant species. Also, the hypoproct and the postgonite in *A. leukoprosopa* are much longer than in *A. brandbergensis*, bent ventrally in this latter species. The connection between the gonocoxal apodemes and the hypandrium is indistinct in *A. leukoprosopa*, while these structures are visible in *A. brandbergensis*. *Alavesia leukoprosopa* seems to be the only known species in the genus, extant or extinct, with a dorsal sensory organ at the basal fourth of the hind tibia.

DISCUSSION

Sinclair and Kirk-Spriggs (2010) performed a phylogenetic study to place *Alavesia* using as background the phylogenetic study of the empidoidea by Sinclair and Cumming (2006) and by redefining characters used earlier by Wiegmann et al. (1993) and Sinclair (1995). In the study by Sinclair and Kirk-Spriggs (2010), *Alavesia* was used as a terminal, differently from other terminals in the same analysis, which are species of the remaining atelestid genera and outgroups.

Alavesia leukoprosopa shares two synapomorphies established for *Alavesia*: dichoptic males and discal cell shorter than the basal cells. A third feature taken as a synapomorphy of the genus, a truncate CuA, is now known to be absent in some of the Myanmar amber *Alavesia* species. A long postpedicel is present in different empidoidea clades. In *Meghyperus* the postpedicel is wide at the basal half and longer than twice the pedicel length. *Nemedina* and *Acarteroptera* also have the postpedicel more than twice the pedicel length, but not as long as in *Meghyperus* and not even close to the condition seen in *Alavesia* species. The species from Myanmar amber described by Sinclair and Grimaldi (2020) also show a variety of conditions of the antenna, all with a long postpedicel. In this sense, the short postpedicel in *Atelestus* may be secondary among the atelestids.



FIGURE 5. Collecting site (with Malaise trap) of *Alavesia leukoprosopa*, campus of the Universidade de São Paulo at Ribeirão Preto, Brazil.

The holotype of *A. leukoprosopa* was collected in the northwest of the State of São Paulo, an area that has intersections between the semideciduous seasonal forest (also referred to as a dry forest) and cerrado elements (see, e.g., Amorim and Santos, 2018). The collecting site is at the university campus and has a mix of highly impacted original forest patches and exotic vegetation. One single male was collected mid spring of 2019 on the campus in a Malaise trap. No other specimens of the species have been collected to the second half of the summer of 2020. It may be the case that the species has a very restricted phenology. This will be verified by continued collecting through 2020. The two extant known Afrotropical species of *Alavesia*, on the other hand, were collected in Namibia, on the Brandberg Massif, which is a transition between savannah and semidesert. This area is actually home to extant species of scorpions that hardly could have questioned their Gondwanan origin (Prendini, 2003). The clade of Afrotropical bothriurid scorpions are also related to a South American / Australian lineage living in dry environments (Prendini, 2003).

The species of *Alavesia* now known from the Cretaceous of Spain (Waters and Arillo, 1999; Peñalver and Arillo, 2007), from the Cretaceous of Myanmar, and the extant Namibia and Neotropical species show an impressive array of morphological variation. Not only are there innumer-

able patterns of antennal length and shape, but there is also a considerable variation of wing-vein patterns: the shape itself of the wing varies considerably, as well as the size of cells dm and cua , the extension of R_{4+5} , the position of M_{1+2} , etc. Among the distinguishing features of *A. leukoprosopa* is the sinuosity of M_1 , its distal half gently curved towards posteriorly. This is a feature also seen in the Afrotropical species of *Alavesia* (see Sinclair and Kirk-Spriggs, 2010: fig. 4C). The extant species of the genus also agree in the size and shape of the closed wing cells, the relative position of R_1 , R_{2+3} and R_{4+5} , etc. It could be the case that the extant Neotropical and Afrotropical species compose a small clade within the genus. A formal phylogenetic study of the relationships between Recent and extinct species of *Alavesia* would be particularly interesting to show how a small group of relict species derived from an earlier, much more diverse Cretaceous clade.

The inclusion of South America in the geographic range of *Alavesia*, despite initially surprising, is not properly in conflict with evidence of other atelestids. Sinclair and Grimaldi (2020) consider the taxonomic and geographic diversity of the Atelestidae, showing that the family is clearly a relict group that had its diversity and distribution strongly impacted by extinction since the Early Cretaceous, now with scattered extant representatives in different parts of the world.

ACKNOWLEDGMENTS

The authors benefitted from CNPq Protax II grants 440.423/2015-5 (J.A.R.) and 88887.176040/2018-00 (P.R.R.) and from FAPESP/CNPq Protax II grant 2016_50369-9 (D.S.A.). Brad Sinclair made comments and suggestions to an early draft of the manuscript and we are also thankful to Emma Wahlberg and an anonymous reviewer for their useful contribution to the polishing of the paper.

REFERENCES

- Amorim, D.S., and C.M.D. dos Santos. 2018. Flies, endemism, and the Atlantic Forest: a biogeographical study using topographic units of analysis. *Australian Systematic Botany* 30: 439–469.
- Chvála, M. 1983. The Empidoidea (Diptera) of Fennoscandia and Denmark, 2: General part, the families Hybotidae, Atelestidae and Microphoridae. *Fauna Entomologica Scandinavica* 12: 1–279.
- Collin, J.E. 1933. Empididae. *Diptera of Patagonia and South Chile* 4: 1–334.
- Collins, K.P., and B.M. Wiegmann. 2002. Phylogenetic relationships and placement of the Empidoidea (Diptera: Brachycera) based on 28S rDNA and EF-1 α sequences. *Insect Systematics and Evolution*, 33: 421–444.
- Cumming, J.M., and D.M. Wood. 2017. [Chapter] 3. Adult morphology and terminology. In A.H. Kirk-Spriggs and B.J. Sinclair (editors), *Manual of Afrotropical Diptera*, vol. 1. Introductory chapters and keys to Diptera families: 89–133. Pretoria: Suricata 4, South African National Biodiversity Institute.
- Grimaldi, D.A., M.S. Engel, and P.C. Nascimbene. 2002. Fossiliferous Cretaceous amber from Myanmar (Burma): its discovery, biotic diversity, and paleontological significance. *American Museum Novitates* 3361: 1–72.
- Hennig, W. 1970. Insektenfossilien aus der unteren Kreide. II. Empididae (Diptera, Brachycera). *Stuttgarter Beiträge zur Naturkunde* 214: 1–12.

- Jouault, C., V. Ngô-Muller, Q.Q. Zhang, and A. Nel. 2020. New empidoid flies (Diptera: Atelestidae; Dolichopodidae) from mid-Cretaceous Burmese amber. *Palaeoentomology* 3: 204–211.
- Moulton, J.K., and B.M. Wiegmann. 2004. Evolution and phylogenetic utility of CAD (rudimentary) among Mesozoic-aged Eremoneuran Diptera (Insecta). *Molecular Phylogenetics and Evolution* 31: 363–378.
- Moulton, J.K., and B.M. Wiegmann. 2007. The phylogenetic relationships of flies in the superfamily Empidoidea (Insecta: Diptera). *Molecular Phylogenetics and Evolution* 43 (3): 701–713.
- Peñalver, E., and A. Arillo. 2007. A new species of the family Hybotidae in the Lower Cretaceous amber of El Caleyú (Asturias, Spain); *Alavesia prietoi* n. sp. *Alavesia* 1: 63–68.
- Poinar, G.O., and F.E. Vega. 2020. A new genus of Empididae (Diptera) with enlarged postpedicels in mid-Cretaceous Burmese amber. *Historical Biology*, 6 pp. [doi.org/10.1080/08912963.2020.1743700]
- Prendini, L. 2003. A new genus and species of bothriurid scorpion from the Brandberg Massif, Namibia, with a reanalysis of bothriurid phylogeny and a discussion of the phylogenetic position of *Liposoma* Lawrence. *Systematic Entomology* 28: 149–172.
- Sinclair, B.J. 1995. Generic revision of the Clinocerinae (Empididae), and description and phylogenetic relationships of the Trichopezinae, new status (Diptera: Empidoidea). *Canadian Entomologist* 127: 665–752.
- Sinclair, B.J., and J.M. Cumming. 2006. The morphology, higher-level phylogeny and classification of the Empidoidea (Diptera). *Zootaxa* 1180 (1): 1–172.
- Sinclair, B.J., and D.A. Grimaldi. 2020. A Cretaceous diversity of the relict genus *Alavesia* Waters and Arillo (Diptera: Empidoidea: Atelestidae). *American Museum Novitates* 3961: 1–40.
- Sinclair, B.J., and A.H. Kirk-Spriggs. 2010. *Alavesia* Waters and Arillo - a Cretaceous-era genus discovered extant on the Brandberg Massif, Namibia (Diptera: Atelestidae). *Systematic Entomology* 35: 268–276.
- Wahlberg, E., and K.A. Johanson. 2018. Molecular phylogenetics reveals novel relationships within Empidoidea (Diptera). *Systematic Entomology* 43: 619–636.
- Waters, S.B., and A. Arillo. 1999. A new genus of Hybotidae (Diptera, Empidoidea) from Lower Cretaceous amber of Alava (Spain). *Studia Dipterologica* 6: 59–66.
- Wiegmann, B.M., C. Mitter, and F.C. Thompson. 1993. Evolutionary origin of the Cyclorrhapha (Diptera): tests of alternative morphological hypotheses. *Cladistics*, 9, 41–81.
- Zhang, H.Q., C. Shih, D. Ren, and Y. Wang. 2020. New *Alavesia* species from mid-Cretaceous Burmese amber highlight genital structural homology (Diptera: Empidoidea: Atelestidae). *Cretaceous Research*. [doi.org/10.1016/j.cretres.2020.104573]