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A new genus of Protodikraneurini from Baltic amber shows mixed morphological affinities to modern Typhlocybinae (Hemiptera: Cicadellidae)

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Abstract

Pedioura rotunda **gen. et sp. nov.**, a fossil leafhopper from Eocene Baltic amber, is described, illustrated and placed in the extinct tribe Protodikraneurini. A key for identification of the seven known genera of the tribe is provided. Some morphological traits of the new fossil, including the very short inner apical cell of the forewing and footlike style apex, appear to be transitional between Protodikraneurini and the modern typhlocybine tribe Typhlocybini, suggesting that Protodikraneurini gave rise to both Dikraneurini and Typhlocybini.

Keywords: Homoptera, Auchenorrhyncha, morphology, fossil

Introduction

The microleafhoppers, Typhlocybinae, are presently the second most diverse and abundant subfamily of Cicadellidae, comprising >530 extant genera and >5,100 extant species worldwide (Dmitriev *et al*., 2022 onward). Members of this group are readily distinguishable from other leafhoppers by their small size and delicate appearance, absence of closed preapical cells in the forewing, and acuminate first hind tarsomere. Most typhlocybines also differ from other leafhoppers in feeding preferentially on the contents of leaf parenchyma cells rather than vascular fluids, thus adults and nymphs are usually found on the undersides of leaves rather than on the stems of their host plants (Cao *et al*., 2023).

Recent molecular divergence time analyses place the origin of Typhlocybinae in the lower Cretaceous ~140 Mya, with the six modern tribes (Alebrini, Beameranini, Dikraneurini, Empoascini, Erythroneurini and Typhlocybini) also arising and becoming widespread prior to the end-Cretaceous mass extinction (Cao *et al*., 2023). However, the fossil record of this group is extremely sparse, with fewer than 15 fossil species in nine genera described so far. The oldest undoubted typhlocybine is "*Erythroneura*" *eocenica* Cockerell, 1921, a compression fossil from the early Eocene Green River Formation of western North America that may be confidently included in this subfamily based on forewing shape (Cockerell, 1921: pl. 33, fig. 9) but cannot be placed to tribe with certainty due to poor preservation. Several well-preserved late Eocene Baltic amber inclusions represent four genera belonging to an extinct tribe, Protodikraneurini, species of which share a hind wing venational pattern not found among modern microleafhoppers (Gębicki & Szwedo, 2006; Szwedo & Gębicki, 2008; Szwedo & Gębicki, 2010; Gębicki *et al*., 2023). The similarly-aged late Eocene Rovno amber from Ukraine includes two additional genera of Protodikraneurini and the oldest representatives of the modern tribe Dikraneurini (Dietrich *et al*., 2023). Several species of "*Typhlocyba*" described in older publications are either not sufficiently preserved to confirm their correct placements or the original material has been lost (Heer, 1853; Germar & Berendt, 1856; von Heyden, 1859).

The Baltic amber inclusion described here is important because, although it agrees morphologically with the extinct tribe Protodikraneurini, it exhibits some features characteristic of some modern Typhlocybinae including Typhlocybini, a group still not reported from the fossil record. Baltic amber is deposited in the Prussian Formation of Priabonian (late Eocene) age (Perkovsky *et al*., 2007; Iakovleva, 2023; Ross *et al*., 2025), but amber from this formation has been extensively redeposited and this has complicated the dating process. The Rovno

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amber fauna, primarily from Ukraine, includes a number of species in common with Baltic and Bitterfeld amber (Perkovsky *et al*., 2024; Zakrzewska *et al*., 2025; Eskov *et al*., 2026), strongly suggesting that these amber faunas are of similar age (Mänd *et al*., 2018; Sokoloff *et al*., 2018). Recent geological data on the amber-bearing deposits from Ukraine also confirm their Priabonian age (Matveev *et al*., 2025), *i.e*., 37.7–33.9 Ma.

Although recent phylogenomic analyses have provided well-resolved estimates of relationships among major lineages of modern Typhlocybinae (Cao *et al*., 2023), the phylogenetic position of Protodikraneurini, known only from fossils, remains uncertain. As the tribal name suggests, Protodikraneurini are morphologically similar to modern Dikraneurini in overall body structure and wing venation, having a complete submarginal vein in the hind wing but differing from Dikraneurini in having veins RP and MA free distally and connected by an r-m crossvein. These two hind wing veins are completely confluent in all known modern Dikraneurini. A recently discovered fossil from late Eocene Rovno amber (*Eodikraneura obscura* Dietrich, Simutnik & Perkovsky, 2023) shows a transition between the condition found in *Protodikraneura* Gębicki & Szwedo, 2006 and that of modern Dikraneurini, having RP and MA confluent for a short distance preapically but then divergent distally. This transitional form suggests that Protodikraneurini, as previously defined, is ancestral to Dikraneurini.

Nevertheless, other morphological traits found in some Protodikraneurini are similar to those found in some members of other modern typhlocybine tribes. For example, although the forewing inner apical cell is relatively long and tapered distally in most previously described genera of Protodikraneurini, as in the extant genus *Dikraneura* Hardy, 1850, the recently described protodikraneurine genus *Protoparallaxis* Dietrich, Simutnik & Perkovsky, 2023 has the inner apical cell of the forewing very short, as in the modern dikraneurine genus *Parallaxis* McAtee, 1926 as well as in most modern Typhlocybini.

Here we describe and illustrate a new genus and species of Protodikraneurini from Eocene Baltic amber that exhibits additional traits shared with various modern typhlocybine tribes.

Material and methods

The examined fossil is deposited at the Natural History Museum of Denmark, Copenhagen (NHMD). The specimen was studied and digital images were obtained using a Leica Z16 APO stereomicroscope equipped with Leica DFC450 Digital Camera at the I. I. Schmalhausen Institute of Zoology of the National Academy of Sciences of Ukraine (SIZK). Additional digital images were obtained at NHMD with flash lighting and a P-51Camlift Driver ver. 2.6.1 controlling a Canon EOS K2-SC camera. Morphological terminology follows Dietrich *et al*. (2022).

Systematic palaeontology

Order Hemiptera Linnaeus, 1758
Family Cicadellidae Latreille, 1825
Subfamily Typhlocybinae Kirschbaum, 1868
Tribe Protodikraneurini Szwedo & Gębicki, 2006

Key to Genera of Protodikraneurini

1. Forewing with one or more darkly pigmented false veins near apex of costal margin..... 2
–. Forewing without one or more false veins near apex of costal margin..... 3
2. Forewing vein RA with apex oriented toward wing apex ... .*Retrorsotettix* Dietrich, Simutnik & Perkovsky, 2023
–. Forewing vein RA with apex oriented toward wing base.... .....*Jantarineura* Gębicki, Walczak & Świerczewski, 2023
3. Forewing inner apical cell very short, wider than long, not extended to apical margin of wing 4
–. Forewing inner apical cell as long as or longer than wide, extended to or nearly to apical margin of wing..... 5
4. Forewing with second apical cell enclosing wing apical margin; hind wing vein MP connected to CuA by short m-cu crossvein..... *Protoparallaxis* Dietrich, Simutnik & Perkovsky, 2023
–. Forewing with third apical cell enclosing wing apical margin; hind wing vein MP connected to CuA at single point..... *Pedioura* **gen. nov.**
5. Hind wing with vein MP connected to CuA at single point; male pygofer lobes each with mesally directed distal spine crossing midline.....*Stareono* Gębicki & Szwedo, 2006
–. Hind wing with vein MP either fused with CuA for some distance or connected to CuA by m-cu crossvein..... 6
6. Forewing with third apical cell acutely angulate basally (RP and MA confluent for short distance)..... ..... *Microelectrona* Szwedo & Gębicki, 2010
–. Forewing with third apical cell quadrate basally (RP and MA connected by r-m crossvein) ....*Protodikraneura* Gębicki & Szwedo, 2006

Pedioura gen. nov.

(Figs 1, 2)

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Type species. *Pedioura rotunda* **sp. nov.**, here designated.

Etymology. The genus name combines the Latin word “pedis” (foot) with the Greek word “oura” (tail), referring to the footlike male style. Gender: feminine.

Diagnosis. This genus differs from other Protodikraneurini in having the following combination of traits: head strongly rounded anteriorly with dorsal half

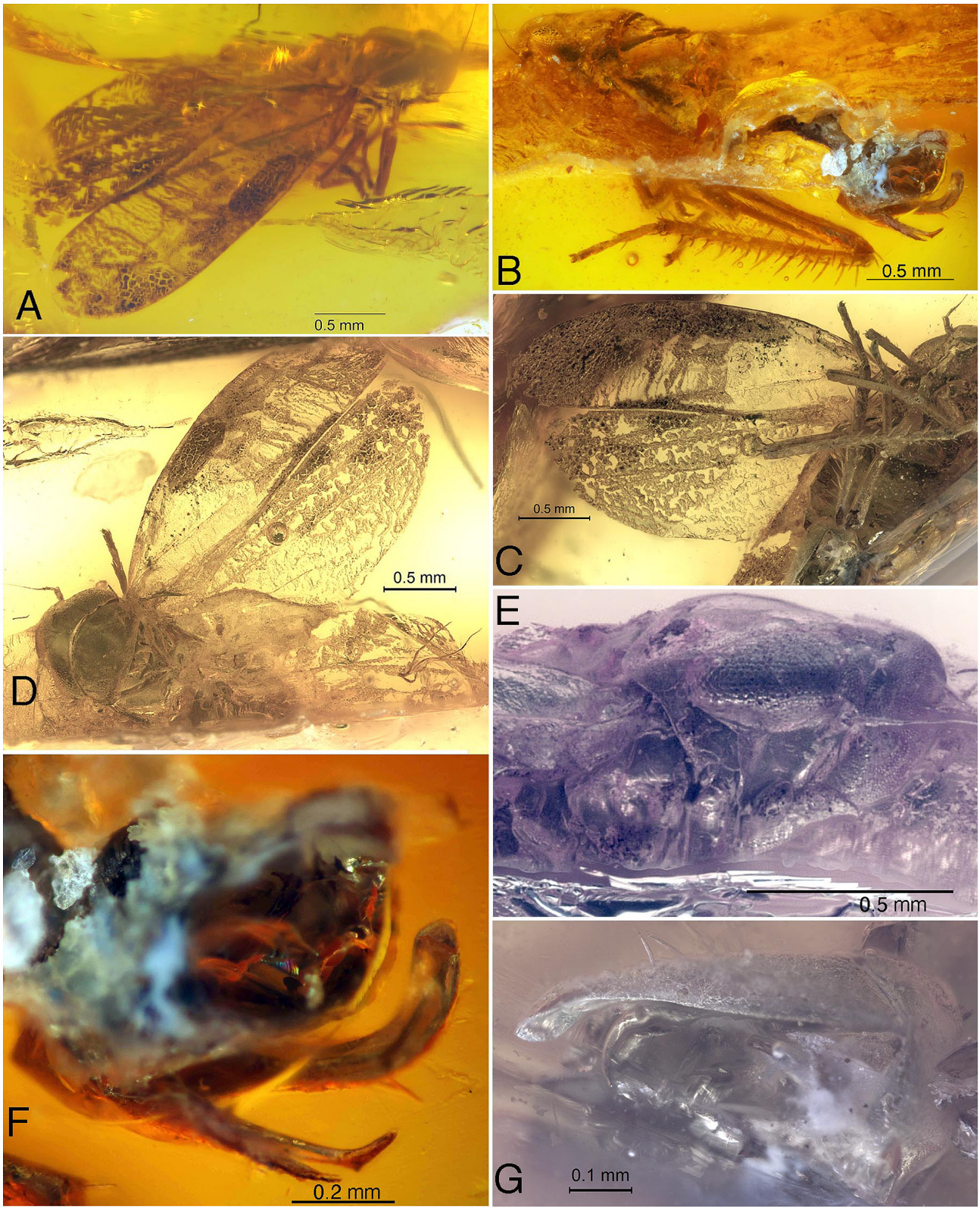

FIGURE 1. *Pedioura rotunda* **gen. et sp. nov.**, holotype male. **A**, Habitus, dorsolateral view. **B**, Habitus, lateral view. **C**, Ventral view. **D**, Dorsal view. **E**, Detail of head and anterior part of thorax, lateral view. **F**, Genital capsule, lateral view. **G**, Genital capsule, ventral view.

nearly vertical in profile; forewing inner apical cell very short and broad, third apical cell enclosing forewing apex; hind wing vein MP connected to CuA at single point; male subgenital plate strongly curved dorsally with oblique row of three macrosetae near midlength; style apophysis elongate with foot-shaped apex.

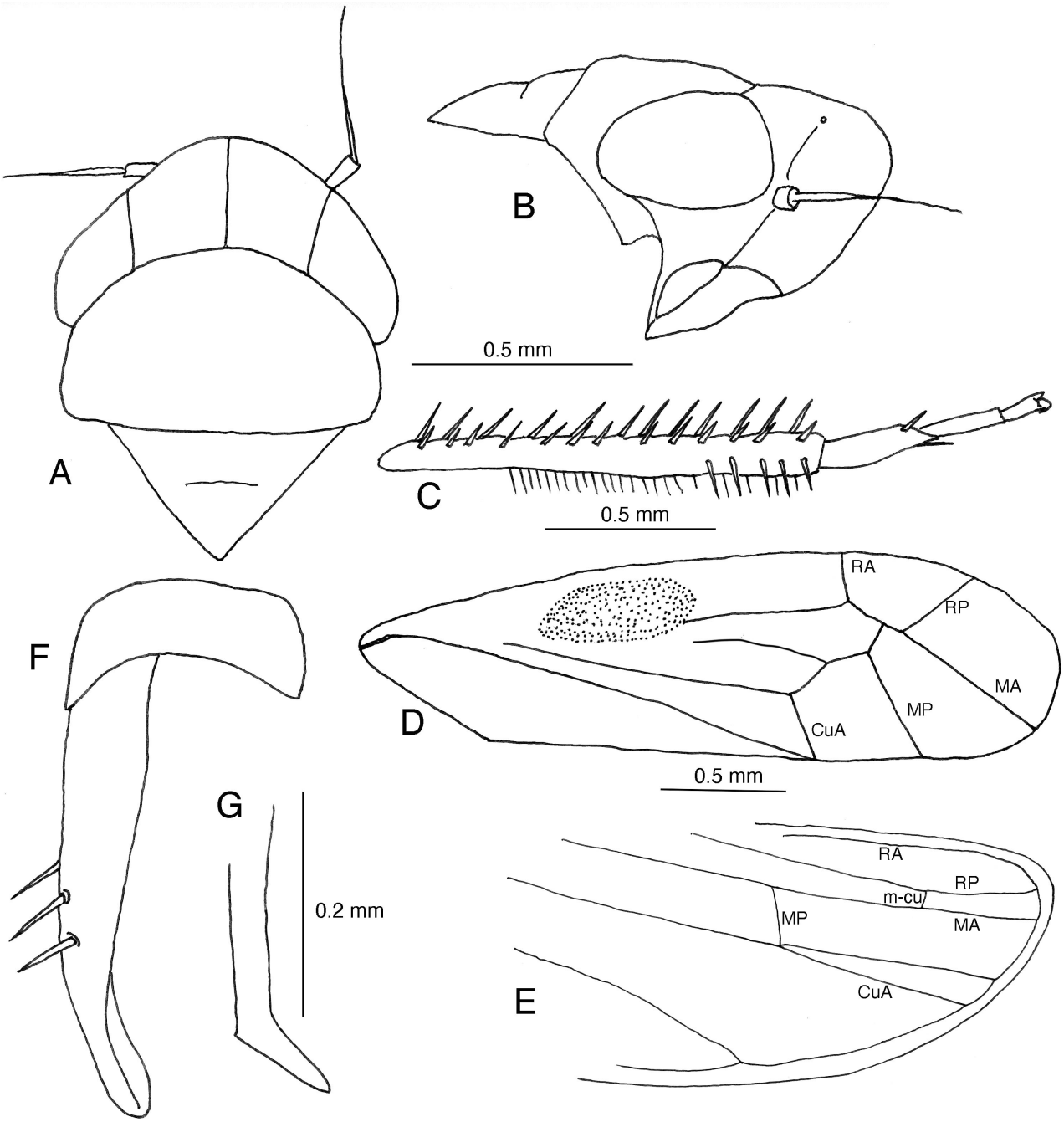

FIGURE 2. *Pedioura rotunda* **gen. et sp. nov. A**, Head, pronotum, mesonotum and scutellum, dorsal view. **B**, Same, lateral view. **C**, Hind tibia and tarsus, anterior view. **D**, Forewing. **E**, Apical part of hind wing. **F**, Valve and left subgenital plate, ventral view. **G**, Style, lateral view.

Pedioura **gen. nov.** resembles *Protoparallaxis* in having the forewing inner apical cell very short and broader than long but differs in having the third apical cell (rather than the second) enclosing the forewing apex.

Remarks. This genus is referable to Protodikraneurini based on the hind wing venation, in which the submarginal vein is complete, extending around the wing apex, and veins RP and MA are separate distally and connected to each other by an r-m crossvein (Gębicki & Szwedo, 2006). Nevertheless, *Pedioura* **gen. nov.** has some peculiar traits not previously reported in this tribe, including a relatively rounded (not produced and depressed) head with distinct ocelli (absent in other Protodikraneurini).

***Pedioura rotunda* sp. nov.**

(Figs 1, 2)

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Material. Holotype male NHMD-677274, Eocene Baltic amber collected at Yantarny, Sambian Peninsula, Kaliningrad, Russia (NHMD).

The holotype inclusion is well preserved with the body intact, showing minimal distortion and some aspects of the color pattern preserved. Syninclusions: stellate hairs.

Etymology. The species name is from the Latin "*rotundus*" (round) referring to the rounded face.

Description. Length including forewing 3.4 mm; body length without wings 2.7 mm, forewing length 2.6 mm. Head and pronotum without distinct markings; forewing mostly pale, translucent with diffuse dark pigmentation especially closer to costal margin and dark elliptical spot corresponding to costal brochosome field; legs and abdomen without distinct color pattern.

Head in dorsal view (Figs 1D, 2A) distinctly wider than pronotum, crown shorter than pronotum, slightly longer medially than next to eye, width between eyes ~1.3× median length, apical margin evenly rounded, coronal suture extended entire length of crown. Head in lateral view (Figs 1A, B, E, 2B) with crown broadly rounded to face; frontoclypeus strongly convex, nearly vertical in profile; anteclypeus relatively broad, tapered apically, slightly concave in profile, base distinctly delimited by transverse suture, in ventral view parallel-sided through most of length; antennae shorter than head width; eyes large, much wider than distance between eyes; ocelli visible on anterior margin of crown well separated from eyes, very small; gena strongly emarginate below eye forming distinct obtuse angle; lorum well delimited, convex, extended close to lateral margin of gena, not extended basad of anteclypeus.

Pronotum ~1.7× (Figs 1D, 2A) longer than crown; lateral margins slightly divergent posterad, slightly shorter than median length of eye in dorsal view. Mesonotum and scutellum together wider at base than median length, slightly shorter than pronotum. Forewing (Figs 1A, C, D, 2D) 3.5× longer than maximum width; vein RP confluent with MA for short distance, both veins then divergent at acute angle and extended straight to wing apex; m-cu crossvein connected slightly beyond midlength of fused portion of RP+MA; inner apical cell slightly shorter than maximum width, vein MP reaching wing margin about midway between apex of clavus and apex of MA; third apical cell enclosing wing apex. Hind wing (Figs 1C, D, 2E) submarginal vein not well visible in fossil but apparently complete, extending around apex onto costal margin, apical cell formed by MP and CuA unusually long and narrow. Front femur with pair of dorsoapical macrosetae, basal seta of intercalary row larger than other setae in row; middle femur with pair of dorsoapical macrosetae. Hind femur distal macrosetae 2+2+1, tibial rows PD, AD, AV and PV with approximately 12, 13, 6 and 23 macrosetae, respectively (Figs 1B, C, 2C); hind tarsus 0.43 times as long as tibia. Male pygofer (Fig. 1F) approximately as long as tall, subgenital plates (Fig. 1F, G) extended beyond pygofer, strongly and evenly curved dorsad in distal half, basal half somewhat depressed, distal half compressed, with oblique row of three macrosetae near midlength; style apophysis elongate, slender, apex footlike with short, angulate ventral heel and longer toe extended dorsad (Fig. 2G).

Discussion

Pedioura rotunda **gen. et sp. nov.** is readily separated from other known Protodikraneurini by the structure of the head, which has the face strongly convex with the dorsal half nearly vertical in profile. Other members of the tribe for which the head has been described have the face relatively flat and more nearly horizontal in profile. The new genus also has visible ocelli, which have not been reported previously in Protodikraneurini but occur commonly in the modern typhlocybine tribes Alebrini and Empoascini, and only rarely in Dikraneurini and Erythroneurini. The parts of the forewing venation of the new genus visible in the fossil resemble those of *Protoparallaxis* Dietrich, Simutnik & Perkovsky in having the inner apical cell very short and broad but the new genus differs in having the third apical cell (rather than the second) enclosing the forewing apex. The head of the only known specimen of *Protoparallaxis* is not well preserved but the new genus differs from *Protoparallaxis* in having forewing crossvein m-cu connected to MP (rather than to MP+RP) and in having the third apical cell (rather than the second) enclosing the forewing apex. The well-delimited and darkly pigmented brochosome field of the new genus resembles that of *Jantarineura* but the latter genus is readily distinguishable by other forewing traits including the relatively long, narrow inner apical cell and the darkly pigmented false veins along the costal margin.

The elongate male style with a footlike apex in the new genus is unlike those of modern Dikraneurini, which tend to be relatively short with a well-developed preapical lobe and strongly curved digitiform apex. Instead, the style of *Pedioura rotunda* **gen. et sp. nov.** closely resembles the styles of some modern genera of Typhlocybini, including *Eupteryx* Curtis, 1837, *Eupterella* DeLong & Ruppel, 1950, *Henribautia* Young & Christian, 1952 and *Ribautiana* Zachvatkin, 1947. Among other known Protodikraneurini, little information is available on the structure of the male genitalia, but *Protodikraneura nasti* Gębicki & Szwedo (2006: fig. 98) also appears to have an elongate style with the apex somewhat footlike. This suggests that Protodikraneurini may be ancestral not only to modern Dikraneurini but also to Typhlocybini.

The hind wing venation of Typhlocybini is more variable than in most other tribes of Typhlocybinae,

including Protodikraneurini. Recent phylogenetic analyses (Cao *et al*., 2023) support a broad concept of Typhlocybini, which includes Eupterygini Kirkaldy and Zyginellini Dworakowska, groups previously considered separate tribes based on differences from "typical" Typhlocybini in the hind wing venation. Young (1952) recognized an even broader definition of Typhlocybini, including Empoascini Distant, which recent analyses have shown is not closely related (Cao *et al*., 2023). Most known genera of Typhlocybini (*s.l.*) have the hind wing submarginal vein absent along the apical wing margin, with the apices of veins RP, MA, and MP free. A few South American genera (*e.g*., *Eualebra* Baker, 1899) have hind wing veins RP and MA separate and connected by a crossvein and also have the submarginal vein extended along the hind wing apex from CuA to RP as in Protodikraneurini but, unlike Protodikraneurini, the submarginal vein of these Neotropical Typhlocybini does not continue basad along the costal margin. Genera of Typhlocybini previously included in Eupterygini have hind wing vein RP separate from MA distally, as in Protodikraneurini, but the submarginal vein is absent at the wing apex, as in most other modern Typhlocybini. The phylogeny of Cao *et al*. (2023) placed the Neotropical genera with nearly complete hind wing submarginal veins as sister to the remainder of the tribe, suggesting that the most plesiomorphic members of the tribe had veins RP and MA separate and retained the submarginal vein along the forewing apex. Thus, if Typhlocybini are derived from Protodikraneurini, then loss of the hind wing submarginal vein along the hind wing costal margin may have occurred in the common ancestor of modern Typhlocybini and fusion of veins RP and MA occurred later. Ancestral character state reconstructions of the two main hind wing characters that vary among modern genera of Typhlocybini show that reduction of the submarginal vein occurred only once, but that derivations and/or losses of the fused RP and MA veins occurred multiple times in the evolution of the tribe (Cao *et al*., 2023).

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