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Abstract

A new babinskaiid genus and species, *Paraneliana sennlaubi* **gen. et sp. nov.**, is described and figured from the Lower Cretaceous Crato Formation (Brazil) on the basis of a well-preserved specimen. This new genus is closely related to the genera *Neliana* (also from the Crato Formation) and *Pseudoneliana* (mid-Cretaceous Burmese amber). This new discovery confirms the important diversity of the Babinskaiidae during the early to mid-Cretaceous. We also comment on the original description of the other Crato species *Neliana impolluta* Martins-Neto, 1997 and we conclude that the species has to be treated as *incertae sedis* until a complete revision of the genus or more widely of the family Babinskaiidae.

Keywords: Insecta, Neuroptera, Myrmeleontoidea, taxonomy, wing venation

Introduction

The small Mesozoic myrmeleontoid family Babinskaiidae comprises 13 described species in nine genera known from the Lower Cretaceous Crato Formation of Brazil, the Baissa locality of Siberian Russia, and mid-Cretaceous Burmese amber (Lu *et al*., 2017; Makarkin *et al*., 2017; Hu *et al*., 2018; Huang *et al*., 2019; Makarkin & Staniczek, 2019; Ngô-Muller *et al*., 2020). Makarkin *et al*. (2017) made an extensive revision of these small antlions, and pointed out their morphological proximity with the Nymphidae. However, they could not revise *Neliana impolluta* Martins-Neto, 1997, whose holotype is a poorly preserved specimen. Thus even the generic attribution of this species remained uncertain.

Here we describe a new, well-preserved specimen that we attribute to a new genus and species. We also discuss the original description of *Neliana impolluta*.

Material and methods

The new fossil derives from the Crato Formation, also called Crato Member of the Santana Formation. This deposit is composed of limestone outcropping near Nova Olinda in the north-east Brazilian province of Ceará (7.2° S, 39.4° W: paleocoordinates 12.2° S, 10.8° W) (Barling *et al.*, 2015: fig. 1; Ribeiro *et al.*, 2021: fig. 1). The fossiliferous unit has been dated as Aptian on the basis of its palynology (Pons *et al.*, 1991; Varejão *et al.*, 2021). The fossil is a partly compressed, three-dimension mineralized replica. The cuticle was replaced by dark brown iron hydroxide (goethite).

The specimen was prepared by removing limestone matrix from around the body with fine blades and needles; the limestone dust was then removed with slight puffs of compressed

air. Figures were composed with Adobe Illustrator CC 2019 and Photoshop CC 2019 software.

We follow the wing venation of Makarkin *et al*. (2017). Nevertheless, these authors separated the forewing vein CuP from the zigzagged intercalary longitudinal vein situated between CuA and the posterior wing margin. This alleged secondary vein is in the continuity with CuP and is very difficult to determine where CuP really ends.

Abbreviations: AA1–AA3, first to third anterior anal vein; CuA, anterior cubitus; CuA1, proximal-most branch of CuA; CuP, posterior cubitus; MA and MP, anterior and posterior branches of media; MA1, MP1, proximal-most branches of MA and MP, respectively. RA, anterior radius; RP, posterior sector; RP1, proximal-most branch of RP; ScA, subcosta anterior.

urn:lsid:zoobank.org:pub:9D1C9A1D-3AF0-484E-82A8-BC3465FDD418

Systematic palaeontology

Order Neuroptera Linnaeus, 1758

Superfamily Myrmeleontoidea Latreille, 1802

Family Babinskaiidae Martins-Neto & Vulcano, 1989

Genus *Paraneliana* gen. nov.

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Type species. *Paraneliana sennlaubi* **sp. nov.**

Etymology. Named after ‘para’ for ‘related to’, and the genus name *Neliana*.

Diagnosis. In forewing, presence of four branches of RP; four presectoral crossveins; vein ‘CuP – intercalary vein between CuA and wing margin’ reaching level of base of RP; six

free posterior branches of CuA; posterior margin of wing straight up to apex of CuA; point of fusion between ScP and RA well distal to crossvein between RA and most anterior branch of RP; vein A1 forked; in hind wing, three branches of RP; only two crossveins between stem of RP and M.

***Paraneliana sennlaubi* sp. nov.**

(Fig 1.)

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Material. Holotype specimen 16013 (imprint of a nearly complete specimen in dorsal view), coll. Markus Sennlaub, to be deposited in the future in the Musée d'Histoire Naturelle et d'Ethnographie de Colmar, France.

Etymology. Named after Mr Markus Sennlaub who allowed us to study the holotype.

Diagnosis. As for the genus.

Description. Head transverse (in dorsal view), 0.8 mm long, 1.9 mm wide; as wide as mesothorax; eyes relatively large, 0.8 mm long, 0.4 mm wide; only basal parts of antennae preserved, with *ca.* 15 antenommeres preserved, longest *ca.* 2.0 mm long; scape stout, slightly elongate tapering toward apex; pedicel much thinner than scape, elongate; short flagellomeres. Prothorax very short. Legs not visible, if preserved hidden under the body in the matrix. Abdomen poorly preserved, *ca.* 5.2 mm long as preserved, with terminalia not preserved.

Forewing elongate with apex missing (in both forewings), as preserved *ca.* 9.3 mm long and *ca.* 2.5 mm wide; no visible trichosors; costal space relatively narrow proximad fusion of ScP with RA, dilated thereafter; subcostal veinlets simple, widely spaced in proximal two-thirds; closely spaced, strongly curved with one-two short branches distally; stouter in pterostigmal region; ScP clearly fused with RA, with ScP+RA probably entering margin at

wing apex; its branches (eight-nine in number) mainly once forked; no crossveins between them detected; subcostal space relatively broad; no crossveins detected; area between RA and RP broad basally, narrower distally between upper branch of RP and RA; with four crossveins proximad fusion of ScP with RA, and no crossveins detected distad fusion; RP originating very far from wing base, slightly distally of half of wing length, with four simple branches; only one crossvein in radial space connecting RP1 with RP2; in radiomedial space, four-five presectoral crossveins in both wings, three-four crossveins connecting stem of RP with M; and three crossveins connecting RP1 with M; M with three-four branches (proximal-most branch not pectinate); at most eleven crossveins between M and CuA observed; stem of CuA long, slightly zigzagged distally, almost parallel to hind margin, with at least six simple branches; CuP strictly aligned with an intercalary longitudinal vein between CuA and posterior wing margin, ending opposite base of RP; six crossveins between CuA and vein 'CuP - intercalary longitudinal vein between CuA and posterior wing margin'; AA1 deeply forked; one distal crossvein between CuP and AA1 connects CuP proximad forking with anterior branch of fork of AA1; AA1 dichotomous; AA2 and AA3 simple.

Hind wing elongate, with pointed apex, *ca.* 8.7 mm long, *ca.* 1.9 mm wide; costal space narrow proximad fusion of ScP with RA, slightly dilated after; subcostal veinlets simple, widely spaced in proximal two-thirds; closely spaced, strongly curved with one-two short branches distally; ScP fused with RA; ScP+A entering wing margin at wing apex; no subcostal crossveins detected; area between RA and RP with three-four crossveins proximad fusion of ScP with RA, one short distad fusion; hypostigmal cell long; RP originating very far from base, at midwing length; with four branches; RP1 originating relatively far to origin of RP; only one long crossvein in radial space connecting RP1 with RP2; in radial-medial space, three presectoral; two connecting stem of RP with M, and two connecting RP1 with M; origin

of M poorly preserved, forked into MA and MP probably very near wing base; stem of MA straight, with at least three pectinate branches; MP long, slightly incurved, somewhat zigzagged distally; with six simple branches, not connected by crossveins; in intramedial space at least six crossveins; at least three crossveins between MP and CuA; CuA pectinate, with three simple, widely spaced branches; CuP short, simple; AA1, AA2, AA3 not detected.

Discussion

Following the key to the babinskaiid genera of Makarkin *et al*. (2017), affinities of specimen 16013 with *Burmobabinskaia* Lu *et al*., 2017 are excluded because the hind wing is ovate, not narrowed. Affinities with *Pseudobabinskaia* Makarkin *et al*., 2017 are excluded because the branches of MP are much longer than crossveins between MA and MP in hind wing. Affinities with *Parababinskaia* Makarkin *et al*., 2017 are excluded because of the presence of only two crossveins between stem of RP and M in hind wing. *Electrobabinskaia* Lu *et al*., 2017 has seven branches of RP in hind wing. *Baisonelia* Ponomarenko, 1992 is excluded because of the presence of only three branches of RP, and of only two crossveins between stem of RP and M in hind wing. *Gigantobabinskaia* Makarkin & Staniczek 2019 has much more branches of RP, M, CuA, etc. than specimen 16013.

Affinities with *Babinskaia* Martins-Neto & Vulcano, 1989 are excluded because of the presence of crossveins between the branches of RP in outer gradate series in both wings in specimen 16013. Martins-Neto (2000) separated the genus *Babinskaia* from the genus *Neliana* Martins-Neto, 1992 on the basis of the presence of seven presectoral crossveins in *Neliana* vs. four in *Babinskaia*, but Makarkin *et al*. (2017) indicated the presence of five-six presectoral crossveins in the specimen SMNS 66000/257 they attributed to *Neliana maculata* (Martins-Neto & Vulcano, 1989). Thus this character varies in the genus *Neliana,* and the diffe-

rence concerning this point between the two genera is not so great. The genus *Babinskaia* comprises the two species *B. formosa* Martins-Neto & Vulcano, 1989 and *B. pulchra* Martins-Neto & Vulcano, 1989. Both species are figured in Martins-Neto (2000: figs 9, 22) without crossveins in the outer gradate series. Makarkin *et al*. (2017: 159) considered this character as diagnostic of this genus, but a revision of the type material is necessary to verify it. Nevertheless, if we follow Makarkin *et al*.'s opinion, specimen 16013 is excluded from the genus *Babinskaia*. Also, specimen 16013 differs from the two *Babinskaia* spp. in the point of fusion between ScP and RA well distal to crossvein between RA and most anterior branch of RP, instead of being opposite it. Lastly, specimen 16013 differs from *B. formosa* in the presence of five crossveins between vein 'CuP - intercalary longitudinal vein between CuA and posterior wing margin'. It differs from *B. pulchra* in the vein 'CuP - intercalary longitudinal vein between CuA and posterior wing margin' ending opposite the base of RP instead of one cell distal to it.

Therefore, it remains the two genera *Pseudoneliana* Huang *et al*., 2019 (type species *Pseudoneliana makarkini* Huang *et al*., 2019, mid-Cretaceous Burmese amber) and *Neliana* (Crato Formation, Brazil). *Neliana* currently comprises its type species *Neliana maculata* and a second species, *N. impolluta*. Makarkin *et al*. (2017) revised *N. maculata*, but not *N. impolluta*, which is based on a unique, poorly preserved specimen with incomplete wings (see Martins-Neto, 1997: fig. 6, 2000: fig. 8B, C). Makarkin *et al*. (2017) presented the generic diagnosis based on *N. maculata*. The wing venation of specimen 16013 would fit with the diagnosis of the genus *Neliana*, as revised by Makarkin *et al.* (2017: 153), with the exception of the relative positions of apex of CuP and base of RP in forewings. It is as follows: two to four crossveins between stem of RP and M [in the forewings of *N. maculata* there can be two to three crossveins and three to four in specimen 16013]; no crossveins in radial space in outer

gradate series. In forewing, RP with four to six branches [five-six branches for *N. maculata* while probably four in specimen 16013]. In hind wing, RP with three to five branches; CuP with two pectinate branches.

The main difference of *Neliana* with the other babinskaiid genera would be the base of RP far distal from apex of CuP in the forewings. Indeed, if we follow Makarkin *et al*. (2017: fig. 8), the forewing CuP of *Neliana maculata* would be four cells basal of base of RP; and even if we consider that CuP continues into the intercalary longitudinal vein between CuA and posterior wing margin, this vein ends two cells basal of RP. The situation in specimen 16013 is quite ambiguous as the intercalary longitudinal vein is in the continuation with CuP, and ends opposite the base of RP. Thus the specimen 16013 has not the main character of *Neliana*.

The original diagnosis of *Neliana impolluta* is as follows (Martins-Neto, 1997: 72): 'Similar to *Neliana maculata* Martins-Neto & Vulcano, 1989, but with the forewing smaller and broader, having abundant setae in its veins' (holotype RGMN-T019, collection Martins-Neto, Laboratorio de Paleontologia do Departamento de Biologia da Faculdade de Filosofia, Ciências e Latras, Universidade de Sao Paulo, Brazil). Makarkin *et al*. (2017: 154) separated the two species as follows: 'RP in both wings with five-six branches [two-three branches in *N. impolluta*]'. In fact, four branches are figured in the reconstruction proposed by Martins-Neto (1997: fig. 6B) while this author figured only three 'accurate' branches in the drawing of the specimen (fig. 6A), while there are four branches in specimen 16013. If we consider the characters that are present in the original drawing of the type specimen of *N. impolluta* (and not those added in the reconstruction), specimen 16013 shares with this species the number of branches of CuA and of M. The number of presectoral crossveins would be seven in the holotype (after its hypothetical reconstruction) instead of four in specimen 16013 but it is quite

uncertain for the holotype because Martins-Neto (fig. 6A) did not figured any in the original drawing of the holotype. The relative positions of the point of fusion between ScP and RA and the first crossvein between RA and most anterior branch of RP; and of the base of RP and the apex of CuP are unknown in the holotype of *N. impolluta*. In fact, the holotype of *Neliana impolluta* is so poorly figured and described that it is not possible to determine its exact position. Also, even if specimen 16013 shares some characters with *N. impolluta*, it is not possible to attribute it to this species.

The forewing of *Neliana maculata* is *ca*. 12.7 mm long and 3.4 mm wide, ratio length/width = 3.7; that of the holotype of *N. impolluta* would be *ca.* 10.4 mm long and 2.7 mm wide, ratio length/width = 3.8 (after the reconstruction of Martins-Neto, 1997: fig. 6B), but its wings are incompletely preserved. The forewing of specimen 16013 is 9.3 mm long and 2.5 mm wide, ratio length/width = 3.7). Thus the alleged smaller and broader forewing of *N. impolluta* is not significant.

The diagnosis of the genus *Pseudoneliana* is as follows (Huang *et al.*, 2019): in forewing, three crossveins between stem of RP (before its branching) and MP; four presectorial crossveins; RP originating distal to termination of CuP (one cell); A1 simple; A2 and A3 fused near base of wing, basal of distal bent of A2(+A3); CuA with rather long branches; in hind wing, three crossveins between stem of RP (before its branching) and M; three presectorial crossveins; RP originating far distal to termination of CuA; one crossvein in radial space in outer gradate series; RP with three branches; MP2 with rather long branches. *Neliana impolluta* and specimen 16013 have nearly all these characters, especially the base of RP nearly opposite apex of CuP, except for the presence of only two crossveins between stem of RP and M in hind wing. But this difference is at most of interspecific value. A potentially more important difference with *Pseudoneliana* is the vein A1 forked and A2 and A3 separated in spe-

cimen 16013 (characters unknown in the holotype of *Neliana impolluta*). A forked A1 is present in *Babinskaia pulchra* (but with A2 and A3 basally fused) (Martins-Neto & Vulcano, 1989: fig. 8B), while *Babinskaia formosa* would have a simple A1 (named vein '2A' in the figure in Martins-Neto & Vulcano, 1989: fig. 8A). It is practically not possible to demonstrate that these differences are sufficient to define a new genus for specimen 16013. We can add that *Pseudoneliana* has also the point of fusion between ScP and RA well distal to the first crossvein between RA and most anterior branch of RP, as in specimen 16013, unlike in *Babinskaia*.

A further difference between specimen 16013 and *Pseudoneliana* is the shape of the posterior margin of the forewing, nearly straight up to apex of CuA in specimen 16013, while it is distinctly curved in *Pseudoneliana*.

As a result, we cannot attribute the specimen 16013 to any of the described genera and species of Babinskaiidae.

We propose a new genus and species *Paraneliana sennlaubi* **gen. et sp. nov.** for the specimen 16013. It can be separated from *Neliana maculata* by forewings shorter than in *N. maculata*, presence of four branches of RP in forewing instead of six, of three instead of five in hind wing; of four presectoral crossveins instead of five in forewing; the vein 'CuP – intercalary vein between CuA and wing margin' reaching the level of base of RP instead of terminating well before it; and of only six free posterior branches of CuA instead of 11–12 in forewing. *Paraneliana sennlaubi* **gen. et sp. nov.** can be separated from *Pseudoneliana makarkini* by RP originating opposite termination of 'CuP -– intercalary vein between CuA and wing margin' instead of one cell distally; only two crossveins between stem of RP and M in hind wing instead of three; forewing vein A1 forked; posterior forewing margin straight up to apex of CuA, and A2 and A3 separated.

Conclusion

‘*Neliana*’ *impolluta* was described on a poorly preserved fossil and its original description is too uncertain to be sure of its relationships and attribution to the genus *Neliana*, even if it is probably different from *Neliana maculata*. We need to consider it as a Babinskaiidae *incertae sedis*. We describe a new genus and species *Paraneliana sennlaubi* **gen. et sp. nov.** on the basis of a better-preserved fossil that shares some characters with ‘*Neliana*’ *impolluta*, but that we cannot attribute to this species. The current limits of the genera *Babinskaia*, *Neliana*, and *Pseudoneliana* remain uncertain, mainly because of the poor original descriptions of the *Babinskaia* spp. Only a phylogenetic analysis and a revision of the genus *Babinskia* will help to better define these genera.

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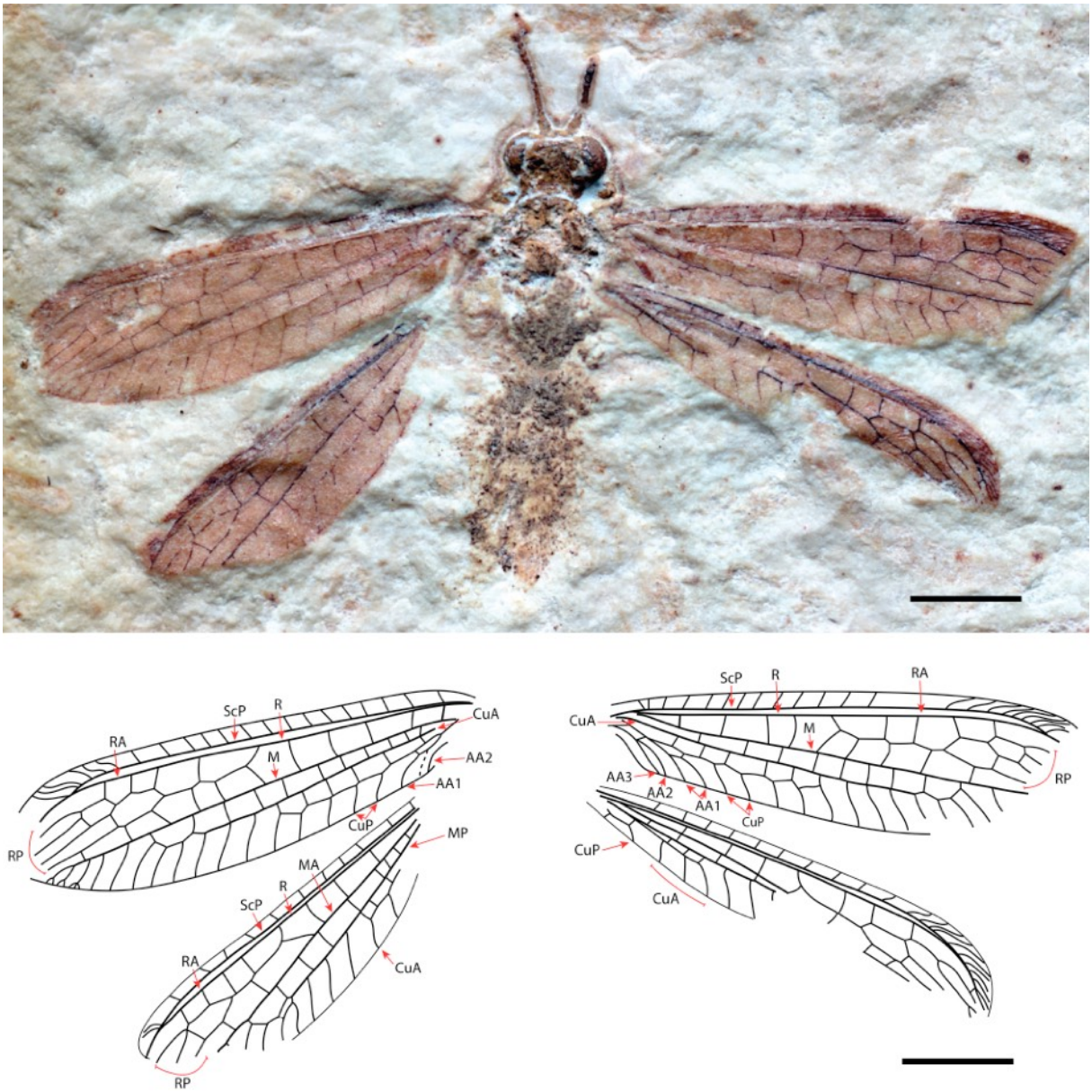

FIGURE 1. *Paraneliana sennlaubi* **gen. et sp. nov.**, holotype 16013. **A**, photograph of habitus. **B**, Reconstruction drawings of fore- and hind wings with vein nomenclature labeled. Scale bars = 2 mm.