

A revision of the Cretaceous antlion subfamily Pseudonymphinae (Neuroptera: Myrmeleontidae) highlights the complicated taxonomy of *Blittersdorffia* Martins-Neto & Vulcano

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Abstract

The Crato Formation (Lower Cretaceous, Brazil) represents one of the most significant fossil deposits for unravelling the early evolutionary history of Myrmeleontoidea (Neuroptera). This study provides a comprehensive taxonomic revision of the problematic subfamily “Pseudonymphinae”, which includes the genera *Pseudonymphes* Martins-Neto & Vulcano, *Bleyeria* Martins-Neto, and *Blittersdorffia* Martins-Neto & Vulcano. With access to previously unavailable holotypes and new material, we reassess these genera, refine their diagnoses, and resolve long-standing ambiguities. We propose *Pseudonymphes araripensis* Martins-Neto & Vulcano as the valid name, designating *P. ponomarenkoi* Martins-Neto and *P. brunherottae* Martins-Neto as junior synonyms, thereby reducing species overestimation in *Pseudonymphes*. We reinterpret the wing venation of *Bleyeria nordestina* Martins-Neto and describe *Blittersdorffia vulcanoae* sp. nov., highlighting the generic polyphyletic character and its taxonomic challenges. Our findings confirm that Pseudonymphinae, as traditionally defined, is not monophyletic and highlight the need for a simpler, more stable taxonomic framework for Crato Formation fossil Myrmeleontidae. This revision establishes a foundation for future phylogenetic analyses and advances our understanding of the diversity and evolutionary relationships of early antlion lineages.

Keywords: Antlions, Fossil insects, Crato Formation, new species

Introduction

The Crato Formation (Lower Cretaceous, Aptian) in

northeastern Brazil is one of the most important sites for understanding the early evolution of several neuropteran lineages. Currently, over 90 valid species in 49 genera of Neuroptera have been described from this deposit (Martins *et al.*, 2022; Bueno *et al.*, 2025a, b). This palaeodiversity covers at least eight extant and many extinct families (e.g., Babinskaiidae, Kalligrammatidae), as well as several subfamilies of extant families (Martins *et al.*, 2022). The superfamily Myrmeleontoidea is the best represented group of Neuroptera in the Crato Formation. Together, the myrmeleontoid families Nemopteridae, Myrmeleontidae, Nymphidae, and the two fossil families Palaeoleontidae and Babinskaiidae represent nearly 60% of the described species and genera in the Crato Formation (Martins *et al.*, 2022; Bueno *et al.*, 2025a).

Pseudonymphinae was initially proposed by Martins-Neto (1992) as a subfamily of Myrmeleontidae to include the genus *Pseudonymphes* Martins-Neto & Vulcano. It was defined by its short, clavate antennae; unforked forewing MA, with the radial sector originating relatively far from the wing base and the presectorial crossveins absent; a small cubital area; and M, CuA, and CuP stems subparallel at the prefork area. The group was later expanded to include *Bleyeria* Martins-Neto and *Blittersdorffia* Martins-Neto & Vulcano after the author’s main phylogenetic work on the Crato Formation Neuropterida (Martins-Neto, 2002).

Despite initial support from phylogenetic analysis, the validity of this subfamily has been consistently questioned in recent discussions concerning fossil Myrmeleontoidea. This is mainly due to the lack of clear apomorphic diagnostic features, leading to its classification as a paraphyletic stem group of

Myrmeleontidae (Makarkin *et al.*, 2018; Lu *et al.*, 2019). Debates have been worsened by the long inaccessibility of Crato Formation holotypes—once kept in private collections—and by inadequate original descriptions and illustrations (Makarkin *et al.*, 2018; Lu *et al.*, 2019; Bueno *et al.*, 2025a).

The genus *Pseudonymphes*, composed of four species, was revisited by Makarkin *et al.* (2018) through additional materials from the Crato Formation, contributing to the generic stability and renewed diagnosis, and raising some concerns about its species overestimation. However, the impossibility of accessing the original types makes some species identification and potential synonymy only putative. *Bleyeria* is a monotypic genus that has never been revisited since its description, and many of its features remain to be reevaluated. *Blittersdorffia* was recently revisited, in part, and was considered highly problematic (Bueno *et al.*, 2025a). Although some considerations were suggested to stabilize *Blittersdorffia*, proposing a potential monophyletic "core", there are still many open questions. The genus is now considered highly polyphyletic given the highly variable wing venation, and many future taxonomic modifications are necessary (Bueno *et al.*, 2025a).

Recently, parts of the two most important collections regarding Crato Formation Neuroptera were found and incorporated into public Brazilian Institutions, which has allowed access to important specimens (Martins *et al.*, 2022; Bueno *et al.*, 2025a, b). The present work revisits the genera and species of Pseudonymphinae through the evaluation of key holotypes and new materials. We propose new synonyms, a new diagnosis and a new interpretation of the wing venation of *Bleyeria*. Also, we describe a new species of *Blittersdorffia*. With these new findings, we contribute to stabilize the taxonomy of these genera, providing a foundation for future phylogenetic analysis.

Geological setting

The fossil specimens described herein originate from the Crato Formation, a world-renowned Lower Cretaceous (Aptian) Konservat-Lagerstätte located in the Araripe Basin, northeastern Brazil (Martill *et al.*, 2007; Ribeiro *et al.*, 2021). The Araripe Basin is an intracratonic basin whose sedimentary record reflects the complex tectonic events associated with the breakup of West Gondwana and the opening of the South Atlantic Ocean (Assine *et al.*, 2014; Varejão *et al.*, 2021). The Crato Formation is the basal unit of the Santana Group and is characterized by finely laminated limestones that facilitated the exceptional

preservation of a diverse terrestrial and aquatic biota (Neumann *et al.*, 2003; Martill *et al.*, 2007).

The palaeoenvironment of the fossil-rich Crato Formation interval (Crato Konservat-Lagerstätte CKL) was recently reinterpreted by Ribeiro *et al.* (2021). Their comprehensive study proposes that the CKL represents an equatorial, semi-arid, shallow lacustrine wetland. This ecosystem featured seasonal water-level changes, with a central shallow water body bordered by periodically flooded mesophytic zones and more distant xeric habitats (Ribeiro *et al.*, 2021; Santos *et al.*, 2023). The exceptional preservation of allochthonous terrestrial arthropods, such as the insects studied here, is attributed to rapid burial and entombment by microbial mats that thrived in the shallow, and at times likely hypersaline, waters of the wetland (Varejão *et al.*, 2019; Ribeiro *et al.*, 2021). This model provides a crucial framework for understanding the palaeoecology of the fauna, including the likely habitats of the Pseudonymphinae in the terrestrial environments surrounding the depositional site.

Material and methods

The specimens analyzed in this study are from three Brazilian public institutions. The holotypes of *Pseudonymphes araripensis* Martins-Neto & Vulcano (CV-1542) and *Pseudonymphes ponomarenkoi* Martins-Neto (CV-214) are stored at the Vulcano Collection, which was recently acquired by the Museu de Zoologia da Universidade de São Paulo (MZUSP). The holotype of *Bleyeria nordestina* Martins-Neto & Vulcano (GP/1T-1676) and the additional specimen of *Blittersdorffia vulcanoae* **sp. nov.** (GP-1E 5238) are held in the palaeontological collection of the Instituto de Geociências da USP (IGc/USP). The holotype of *Blittersdorffia vulcanoae* **sp. nov.** (CCNH 856) and additional material CCNH 38 are kept at the palaeontological collection of the Centro de Ciências Naturais e Humanas (CCNH), Universidade Federal do ABC. The new specimens deposited in the CCNH collection were collected at Pedreira Três Irmãos (Brazil: Ceará: Nova Olinda) with the help of local mining workers, under authorization from the Brazilian National Mining Agency (ANM). As the specimens came from mining debris, their exact stratigraphic level cannot be determined.

Photographs were taken with a Zeiss Discovery V20 stereomicroscope and a Zeiss AxioCam Mrc5 camera. The images of each fossil were edited using Adobe Photoshop, while illustrations were created in Adobe Illustrator with the aid of a graphic tablet (XP-PEN Artist Pro 24). Morphological terminology follows mostly New (1985) and Stange (1994). Wing terminology

follows Breitkreuz *et al.* (2017), except for the forewing MP+CuA sector in *Bleyeria nordestina*, which follows Makarkin *et al.* (2018). The abbreviations for wing veins and cells used in the text are as follows: A = anal, CuA = cubital anterior, CuP = cubital posterior, MA = medial anterior, MP = medial posterior, RA = radial anterior, RP = radial posterior, Sc = subcostal, *irc* = infra radial cell, *ps* = presectoral crossveins, *h cell* = hypostigmal cell.

Systematic palaeontology

Class Insecta Linnaeus, 1758

Order Neuroptera Linnaeus, 1758

Family Myrmeleontidae Latreille, 1802

Subfamily Pseudonymphinae Martins-Neto, 1992

Genus *Pseudonymphes* Martins-Neto & Vulcano, 1989

Type species. *Pseudonymphes araripensis*, Martins-Neto & Vulcano 1989, by original designation.

Diagnosis (emended). The genus is characterized by the following features: (1) wings elongate (14–15 mm), with fore- and hind wings similar in size and shape; (2) forewing RP originating relatively far from wing base (around the end of wing basal fourth); (3) absence of presectoral crossveins on both wings; (4) *h cell* long and broad; (5) M forked distal to RP origin; (6) MP separated from CuA but connected through a small crossvein; (7) CuA dichotomously branched; (8) trichosors present along the apical margin before apex on both wings; (9) hind wing MP pectinate with several branches; (10) hind wing CuA strongly pectinate, with at least eight branches.

Species included. *Pseudonymphes araripensis* Martins-Neto & Vulcano, 1989.

Remarks. We propose a complementary diagnosis to that provided by Makarkin *et al.* (2018), highlighting additional diagnostic features such as the broad hypostigmal cell. The holotype of *Pseudonymphes zambonii* Martins-Neto was described based solely on a fragmentary wing, initially interpreted as a forewing but more likely to be a hind wing (see Martins-Neto, 2001: fig. 1D). As the holotype is currently considered lost and the original description and illustration are insufficient to confidently assign the specimen to *Pseudonymphes* or to any other genus, we regard *P. zambonii* as a *nomen dubium*.

Pseudonymphes zambonii Martins-Neto, 1998—*nomen dubium*

Material. Holotype (RGMN-T10, mould and counter-mould) was reportedly deposited in the R.G. Martins-Neto private collection (Martins-Neto, 1998; Martins *et al.*,

2022). Unfortunately, the material is currently considered lost and could not be located in the recently recovered RGMN personal collection.

Remarks. The holotype of *Pseudonymphes zambonii* was originally described based on a highly fragmentary specimen, with limited preservation of diagnostic features. Both the description and the accompanying illustration are notably incomplete, lacking sufficient morphological detail to confidently determine the generic placement of the species (Martins-Neto, 1998). Makarkin *et al.* (2018) had already expressed doubts regarding the validity and placement of this species, even suggesting that it might belong to a different, undescribed genus. However, at the time, the authors had not examined the type specimen, which is now confirmed lost. Given the current absence of the holotype and the inadequacy of the original documentation, it is impossible to verify the identity of this species or assign it unambiguously to *Pseudonymphes* or any other genus. For these reasons, we are treating *Pseudonymphes zambonii* as a *nomen dubium*.

Pseudonymphes araripensis Martins-Neto & Vulcano, 1989

(Figs 1–3)

1989 *Pseudonymphes araripensis* Martins-Neto & Vulcano, p. 376, figs 4, 18.

1992 *Pseudonymphes ponomarenkoi* Martins-Neto, p. 134, fig. 11A, B, F. (new synonym)

1994 *Pseudonymphes brunherottae* Martins-Neto, p. 274, fig. 2B, C; pl. II, fig. C. (new synonym)

Material. Holotype (Fig. 1): Sex unknown, CV-1542, NE Brazil, Crato Formation, Aptian, Lower Cretaceous. Housed at MZUSP, Brazil. Specimen partially preserved in dorsal view, with collateral wings partially preserved and overlaid. Left forewing only partially preserved, lacking many costal and Sc + RA veinlets, most RP and terminal portions MA and CuA branches. Left hind wing almost complete, except for the costal veinlets, some CuA and A sector. Both right wings poorly preserved. Antennae well-preserved, head well-preserved, thorax partially preserved without legs, thorax partially preserved but terminalia not clear.

Additional material: CV-214 (Fig. 2), holotype of *P. ponomarenkoi*. NE Brazil, Crato Formation, Aptian, Lower Cretaceous. Housed at MZUSP, Brazil. Specimen preserved in dorsal view with collateral wings overlaid. Right hind wing partially preserved, especially in the apical region, CuP and A sectors poorly preserved. Right forewing poorly preserved. Left hind wing partially preserved, missing the anterior margin, some CuA branches, CuP and A. Left forewing poorly preserved. Antennae partially preserved, head preserved with one

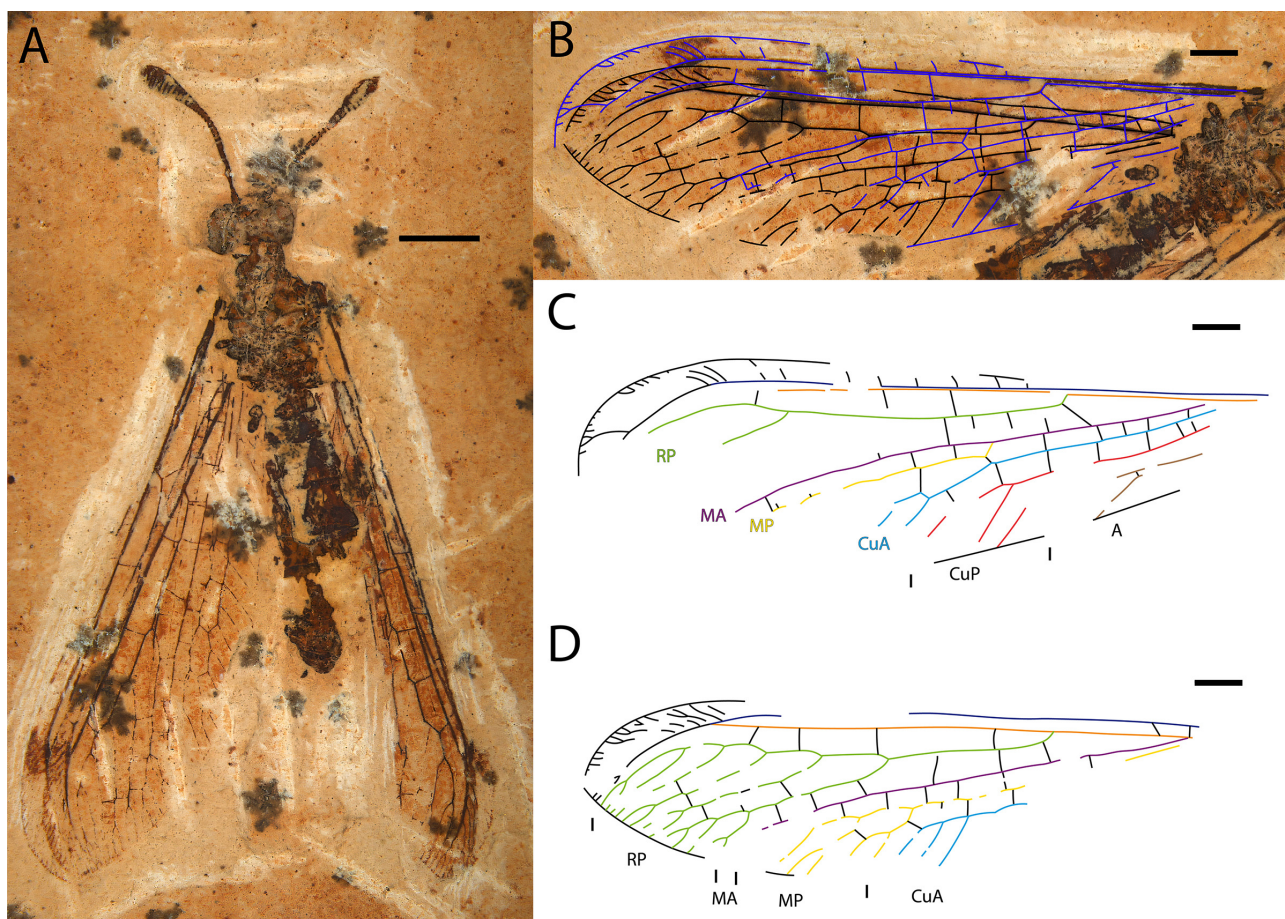


FIGURE 1. *Pseudonymphes araripensis*, holotype (CV-1542). **A**, Habitus. **B**, Overlaid fore- and hind wings (blue and black, respectively). **C**, Forewing drawing. **D**, Hind wing drawing. Scale bars: 2 mm (**A**), 1 mm (**B–D**).

compound eye discernible, thorax partially preserved with some fragments of forelegs, abdomen relatively complete but terminalia uncertain.

Diagnosis. As for the genus.

Description (revised). Antennae clavate, *ca.* 4.5 mm long; compound eyes large, *ca.* 1.1 mm large. Thorax relatively short and robust, *ca.* 4 mm long and *ca.* 2.3 mm wide; prothorax *ca.* 0.7 mm long. Forewing elongate, *ca.* 14.2–15.8 mm long and *ca.* 4.2–4.6 mm wide (length/width ratio 3.38–3.46). Costal space narrow, slightly widening near apex. Subcostal veinlets simple, Sc and RA fused far from wing apex. Veinlets of Sc+RA are relatively long, forked one to twice distally; subcostal space narrow basally, relatively broad near fusion of Sc and RA. RA space broad, slightly narrowing at most distal crossvein before fusion of Sc and RA with 5 straight crossveins proximal to fusion of Sc and RA; a single crossvein distal to fusion of Sc and RA, delimiting a long and broad hypostigmal cell. Presectoral crossveins absent. RP originates moderately far from wing base (approximately at basal fourth of wing length), with five main branches. RP1 originates relatively far from RP origin (near wing midpoint), dichotomously branching up to three times, *irc*

moderately long and broad; RP2 relatively close to RP1 in nearly half the relative distance between RP origin and RP1, forked once near wing margin. Other RP branches similarly distant to each other. Crossveins between RP branches scarce, three between RP1 and RP2, two between RP2 and RP3, a single between RP3 and RP4. Three crossveins between stem of RP and M. Stem M and CuA with five crossveins preserved. M forked distal to the RP origin. MP unfused to CuA, but linked to it through a small crossvein. MA relatively close and parallel to MP, single forked near the wing margin. Five crossveins between MA and MP. MP with three main branches. CuA with 4 pectinate branches, with only two crossvein between CuA and MP. Seven crossveins preserved between CuA and CuP. CuP sector relatively short, with five pectinate branches. Anal sector poorly preserved, but A1 seems long and connected to CuP through a crossvein. Hindwing similar to forewing in shape but slightly shorter (*ca.* 13.3–14.5 mm) and narrower (*ca.* 3.7–3.9 mm), with a slightly large length/width ratio (3.59–3.71). Costal space slightly narrower than in forewing. Subcostal veinlets single. Subcostal veinlets mostly single. Sc and RA fused far from wing apex, reaching wing margin after wing

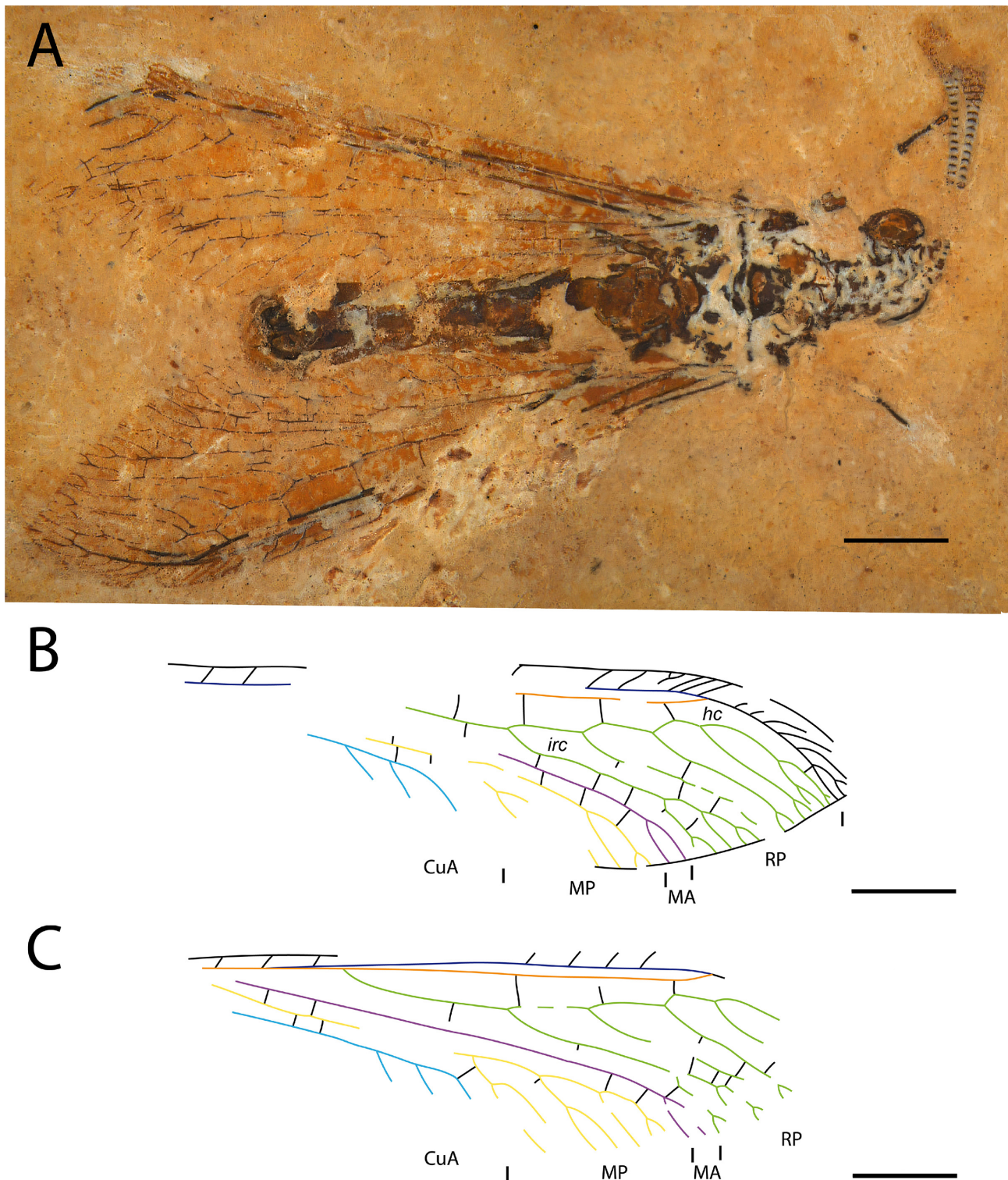


FIGURE 2. *Pseudonymphes ponomarenkoi* (Martins-Neto) holotype (CV-214). **A**, Habitus. **B**, Left hind wing drawing. **C**, Right hind wing drawing. Scale bars: 2 mm.

apex. Sc-RA veinlets mostly forked once. Subcostal space similar to forewing. RA space broad, slightly narrowing at the most distal crossvein before fusion of Sc and RA, with four crossveins preserved proximal to fusion of Sc and RA, a single crossvein distad delimiting the long and broad hypostigmal cell. Presectoral crossveins absent. RP

originates relatively far from wing base, slightly distad the end of basal fourth, with five main branches. RP1 originates moderately far from RP origin, near wing midpoint, branching dichotomously up to three times. Branching pattern of other RP branches similar to forewing, mostly single forked near wing margin. Crossveins between

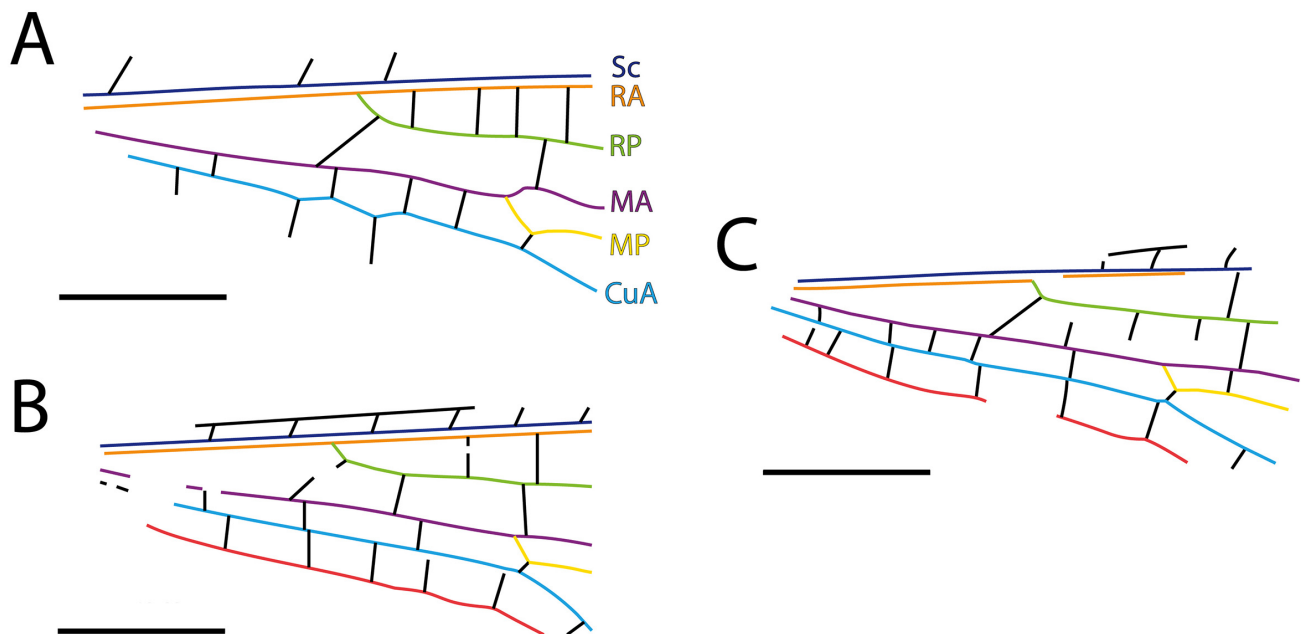


FIGURE 3. Forewing basal region comparison. **A**, *Pseudonymphes brunherottae*, holotype (modified from Martins-Neto, 1994). **B**, *P. brunherottae*, additional material (modified from Makarkin *et al.*, 2018). **C**, *P. araripensis*, holotype (CV-1542). Scale bars: 2 mm.

RP branches scarce as in forewing: four between RP1 and RP2, two between RP2 and RP3, two between RP3 and RP4, and a single crossvein between RP4 and RP5. Three crossveins between stem RP and MA. MA long and reticulate, single forked near wing margin. MP forking slightly proximad wing midpoint, with four to five main branches, MP1 and MP2 once forked. Eight crossveins between MA and MP branches. Six crossveins between MP and CuA sector, with the most distal one connecting CuA to MP1. CuA sector long, reaching wing midpoint with eight pectinate branches single branches. CuP and A sector not preserved.

Remarks. We propose the synonym between *P. araripensis*, *P. brunherottae*, and *P. ponomarenkoi*. The consulted materials show no differences justifying separation into distinct species, aside from minor size variation. The original species distinctions were based mainly on thorax proportions, but these variations are insignificant or unreliable given the preservation state.

The wing venation of these species is indistinguishable. Although the holotype of *P. brunherottae* is currently lost and was originally incomplete, the published illustration clearly shows the forewing MP configuration (see Fig. 3A), which served as the main character for uniting these specimens. The forewings of *P. ponomarenkoi* are poorly preserved, but its hind wings show no significant differences compared to those of the other specimens.

The specimen recently identified as *P. araripensis* by Makarkin *et al.* (2018) (figs 12, 13; INHSP 1525)

likely represents a new species, given the forewing MP configuration (fused to CuA proximal to the cubital fork). This configuration is similar to additional material of *P. araripensis* to which we did not have access (Martins-Neto, 1992, figs 11C, 12E). Given our reevaluation of the *P. araripensis* holotype, this material could belong to the potential new species mentioned above.

As we did not have access to either of these materials, this feature was not included in the genus diagnosis, pending a formal description of this potential new species.

Genus *Bleyeria* Martins-Neto, 1992

Type species. *Bleyeria nordestina* Martins-Neto, 1992, by monotypy.

Diagnosis (emended). The genus is characterized by the following features: (1) Forewing slightly falcate; (2) forewing RP originating relatively far from wing base (around the end of wing basal fifth); (3) absence of presectoral crossveins; (4) RP with only three main branches; (5) RP branches with distinct zigzagged pattern and very broad polygonal cells in RP sector; (6) MP fused to CuA proximal to the cubital fork; (7) (MP+CuA)1 pectinately branched; (8) short CuP sector with only four pectinate branches; (9) anal sector very large, with A1 and A2 deeply forked dichotomously.

Species included. *Bleyeria nordestina* Martins-Neto, 1992.

***Bleyeria nordestina* Martins-Neto, 1992**

(Figs 4, 5)

1992 *Bleyeria nordestina* Martins-Neto, p. 127 fig. 8; pl. II, fig. C.

Material. Holotype: Sex unknown, GP/1T-1676 (part and counterpart), NE Brazil, Crato Formation, Aptian, Lower Cretaceous. Housed at Instituto de Geociências da USP (IGc/USP), Brazil. Material preserved in dorsal view, with collateral wings at least partially overlaid. Both forewings are nearly complete, but left hindwings poorly preserved. Head unpreserved, thorax partially preserved but without leg fragments. Abdomen partially preserved, but terminalia uncertain.

Diagnosis (emended). As for the genus.

Redescription. Thorax *ca.* 2.25 mm (prothorax missing) long and *ca.* 1.12 mm wide. Abdomen long and thin, *ca.* 11 mm long and *ca.* 1.5 mm wide. Forewing elongate, falcate, with rounded apex, *ca.* 18.2 mm long and 5.9 mm wide (length/width ratio 3.08). Costal space

narrow, slightly widening near apex. Subcostal veinlets single and mostly straight. Sc and RA fused far from wing apex. Veinlets of Sc + RA not very long and mostly unbranched (forked once in some cases); subcostal space narrow. RA space relatively broad, slightly narrowing at distalmost crossvein before fusion of Sc and RA, with eight straight crossveins proximal to the fusion; no crossveins traceable after fusion of Sc and RA, hypostigmal cell narrow and likely long. Presectorial crossveins absent. RP originates relatively far from wing base (around 0.2 from total wing length), with only three main branches. RP1 originates moderately far from wing base (*ca.* 0.42 from wing length), branching twice dichotomously, *irc* short and broad; RP2 origin present far from RP1 in a slightly shorter distance from RP and RP1, unbranched. RP3 origin forking dichotomously twice very distal, after Sc and RA fusion. RP branches form a distinct “zigzagged” pattern that resembles those in Chrysopoidea, with many crossveins between main branches, forming multiple, very wide and polygonal cells in RP sector. Four crossveins

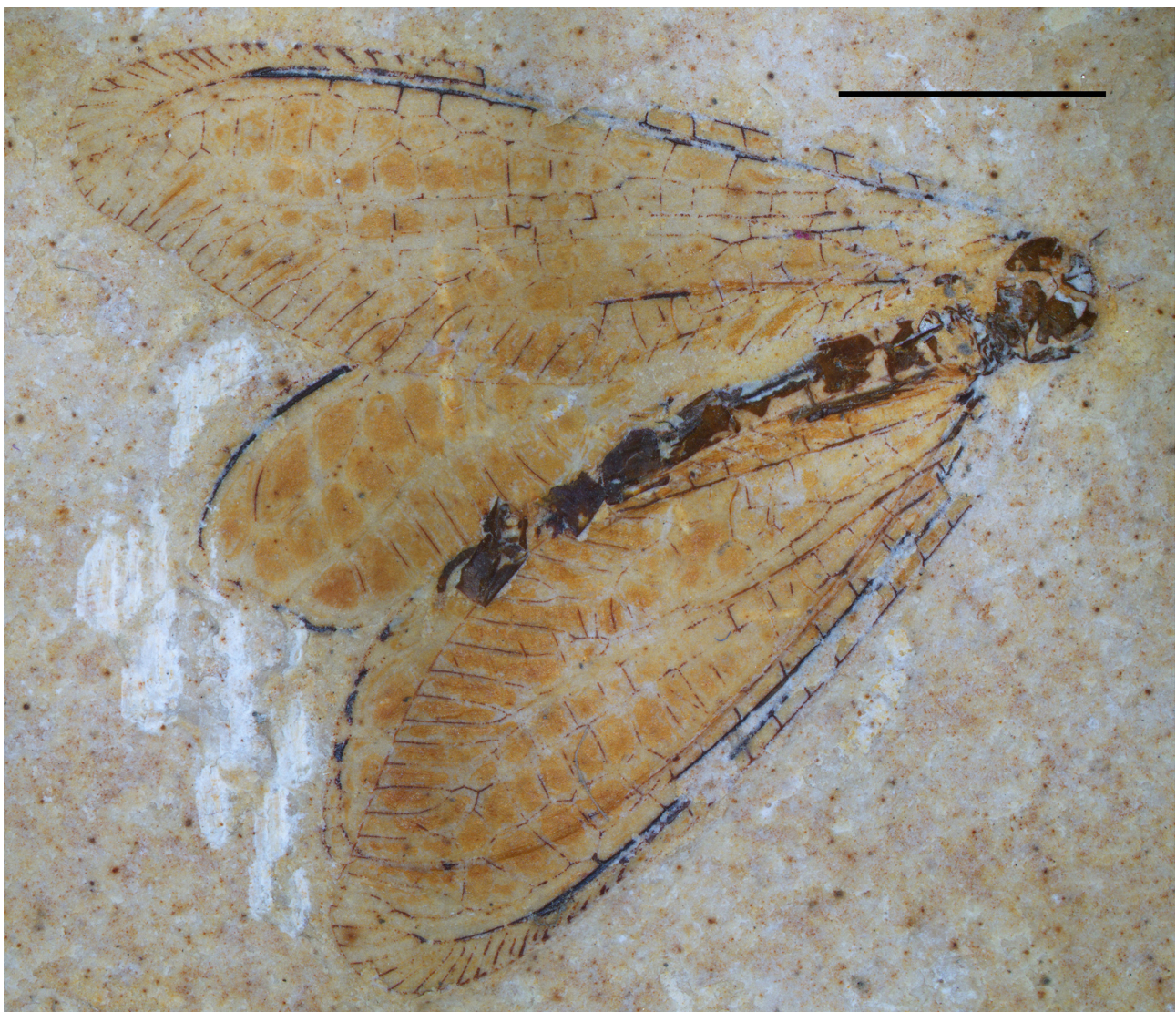


FIGURE 4. Habitus of *Bleyeria nordestina*, holotype (GP/1T-1676). Scale bar: 5 mm.

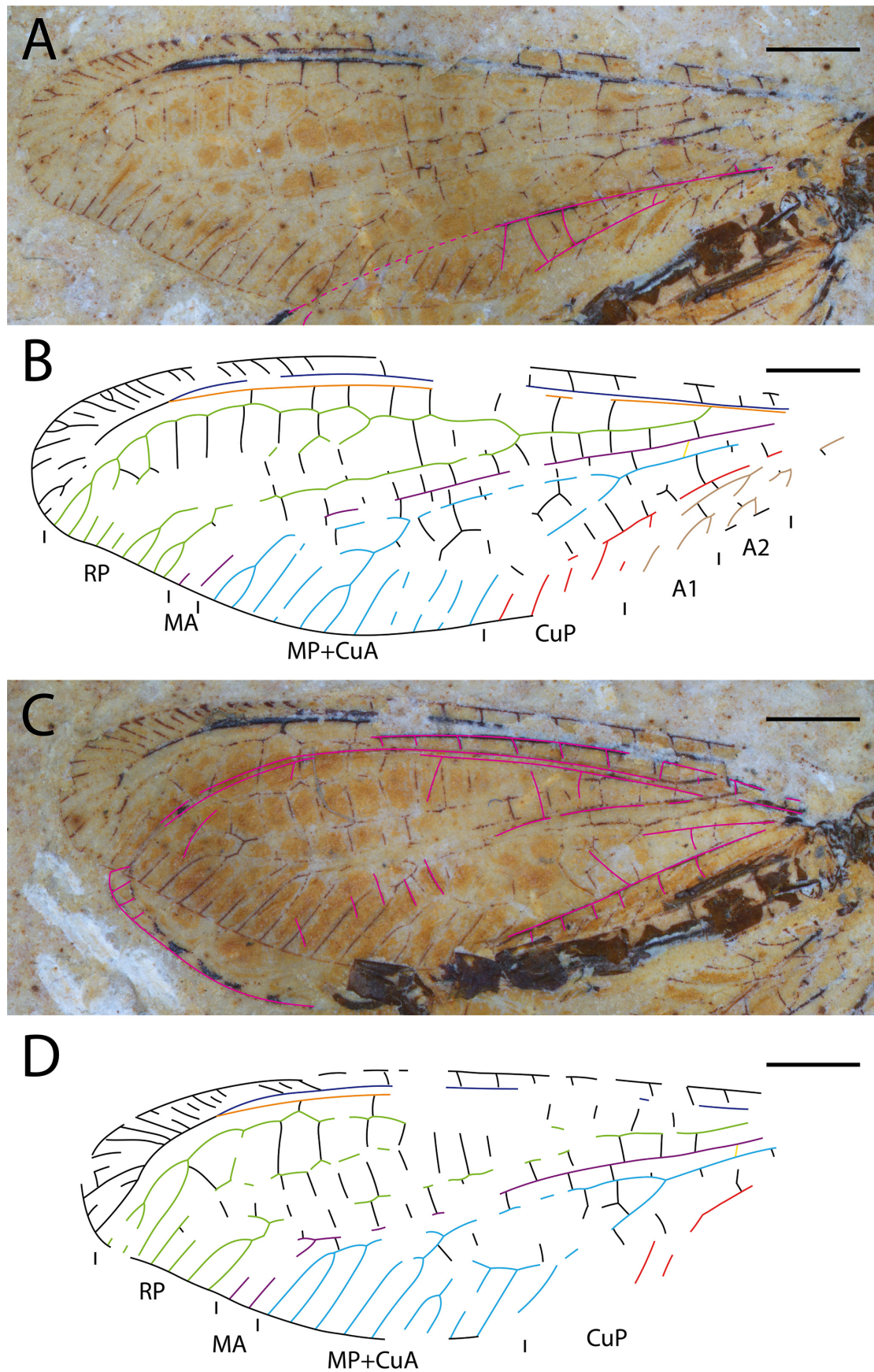


FIGURE 5. *Bleyeria nordestina*, holotype (GP/1T-1676). **A**, Left forewing (hind wing venation in pink). **B**, Left forewing drawing. **C**, Right forewing (hind wing venation in pink). **D**, Right forewing drawing. Scale bars: 2 mm.

between stem of RP and MA and at least eight after RP first fork. M forked proximal to cubital fork and MP present as an oblique vein fused with CuA proximal to the fork. Stem M (and MA after its fork) relatively close and parallel to MP + CuA, MA single forked near wing margin. Multiple crossveins between MA and CuA, particularly after cubital fork. MP + CuA forking very distal RP origin, (MP + CuA)1 pectinately branched in at least four (even five in left forewing) branches. Other three to four MP+CuA branches present, mostly unforked, except for (MP + CuA)2 that is forked dichotomously once to twice (variable on right and left wings). CuP sector short, with only four short, straight and single branches. Eight crossveins preserved between CuA and CuP. A1 very long and dichotomously deeply forked, linked to stem CuP through a crossvein. A2 deeply forked, A3 poorly preserved. Hind wing shape seemingly quite different from forewing, oval-like, slightly shorter and similar in width, *ca.* 15.8 mm long and 5.8 mm wide (length/width ratio 2.72). Costal space narrower than forewing, subcostal veinlets single and straight. The remaining hind wing venation cannot be clearly depicted.

Remarks. The reassessment of *Bleyeria nordestina* holotype helps to solve some uncertainties about forewing venation, especially concerning some controversial or uncommon features. The supposedly short hypostigmal cell, unique among the fossil Myrmeleontoidea, could not be confirmed, and is considered to be a mistake in the original description. The forewing MP merge point is another crucial uncertainty that is now cleared as being present far basal to the cubital fork. The very unusual forewing RP sector with very few “zigzagged” branches and broad polygonal cells is confirmed. The hind wing, despite not being very clear, seems to have a very odd venation pattern with strongly curved crossveins and with an apparent very broad RA space. Although those features seem very singular and curious, we prefer not to use those interpretations in generic diagnosis because of the lack of clarity in hind wing morphology. We hope that some new and more complete materials belonging to *Bleyeria* can be found in the future to solve these uncertainties and provide reliable information for the hind wing characters of this genus.

Genus *Blittersdorffia* Martins-Neto & Vulcano, 1989

Type species. *Blittersdorffia pleoneura* Martins-Neto & Vulcano, 1989, by monotypy.

Species included. *Blittersdorffia pleoneura* Martins-Neto & Vulcano, 1989; *Blittersdorffia polyplusia* Martins-Neto, 1997; *Blittersdorffia evanescens* Bueno *et al.*, 2025a; *Blittersdorffia dicotomica* Martins-Neto, 1990 and *Blittersdorffia volkheimeri* Martins-Neto & Vulcano, 1989; *Blittersdorffia vulcanoae* **sp. nov.**

Remarks. The inclusion of *B. dicotomica* and *B. volkheimeri* in the genus remains provisional, since a more detailed evaluation with phylogenetic support is needed to address these species' taxonomic future (for a detailed discussion, see Bueno *et al.*, 2025a). Additional discrepancies in wing venation among core *Blittersdorffia* species also highlight the need for a comprehensive revision of the genus.

Blittersdorffia vulcanoae **sp. nov.**

(Figs 6, 7)

Material. Holotype (Fig. 6): Sex unknown, CCNH 856 (mould and counter-mould). NE Brazil, Crato Formation, Aptian, Lower Cretaceous. Housed at CCNH–UFABC, Brazil. Specimen preserved in dorsal position, with both left wings partially preserved, right forewing well preserved except for the terminal parts of RP and CuA + MP. Right hindwing partial, preserving most of RP, RA and costal region. The right wings are partially preserved and overlapped. Head well preserved with compound, antennae absent. Thorax partially preserved, abdomen partially preserved with terminalia missing.

Additional material: GP-1E 5238 (Fig. 7). NE Brazil, Crato Formation, Aptian, Lower Cretaceous. Housed at the collection of Instituto de Geociências da USP (IGc/USP), Brazil. Specimen preserved in dorsal view with four wings at least partially preserved. Right forewing well-preserved, except for the most apical region and most of its basal fifth. Right hind wing partially preserved, missing most posterior margin, CuA, CuP and A sectors. Left forewing poorly preserved, left hindwing partial, preserving mainly the wing distal half. Antennae partially preserved, head unpreserved, thorax and abdomen poorly preserved. Additional material CCNH38 (Fig. 8). NE Brazil, Crato Formation, Aptian, Lower Cretaceous. Housed at CCNH–UFABC, Brazil. Specimen preserved in lateral view, both hind wings partially preserved with some apical portions missing, forewings not preserved. Other body parts unpreserved except for a partial tibia and tarsus.

Etymology. In honor of the entomologist Maria Aparecida Vulcano, an important researcher of the Crato Formation palaeoentomofauna, and author of many Neuroptera fossil species.

Diagnosis. Differs from other “core” *Blittersdorffia* species (*sensu* Bueno *et al.*, 2025a) by the forewing CuA2 pectinate pattern, which is dichotomous in remaining species and the presence of two presectoral crossveins in forewings, absent in other *Blittersdorffia*.

Description. Antennae at least 5.2 mm long, shape uncertain but likely clavate. Tarsi *ca.* 2.75 mm long, t1 relatively long, *ca.* 1.05 mm long, t2–t4 short, each *ca.* 0.25 mm long, t5 *ca.* 0.95 mm long, with setae preserved

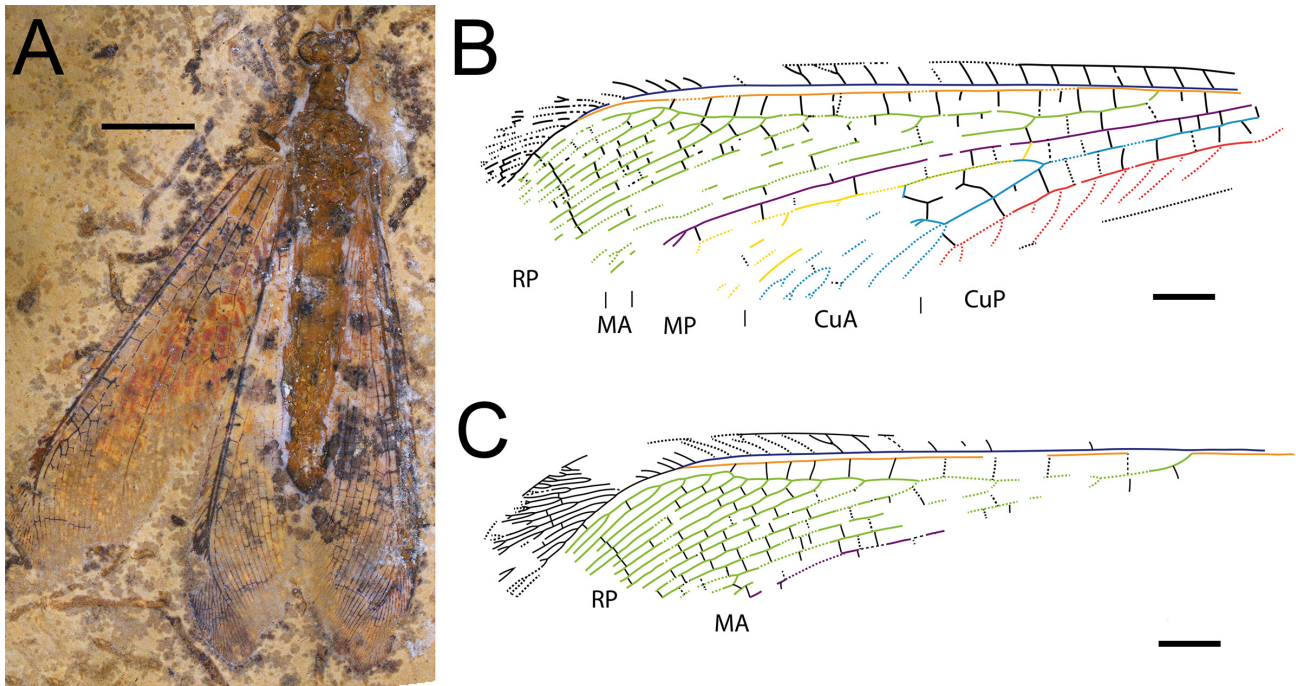


FIGURE 6. *Blittersdorffia vulcanoae* sp. nov., holotype (CCNH 856a). **A**, Habitus. **B**, Left forewing drawing. **C**, Left hind wing drawing. Dotted lines represent counter-mould contributions to the final wing drawings. Scale bars: 5 mm (**A**), 2 mm (**B**, **C**)

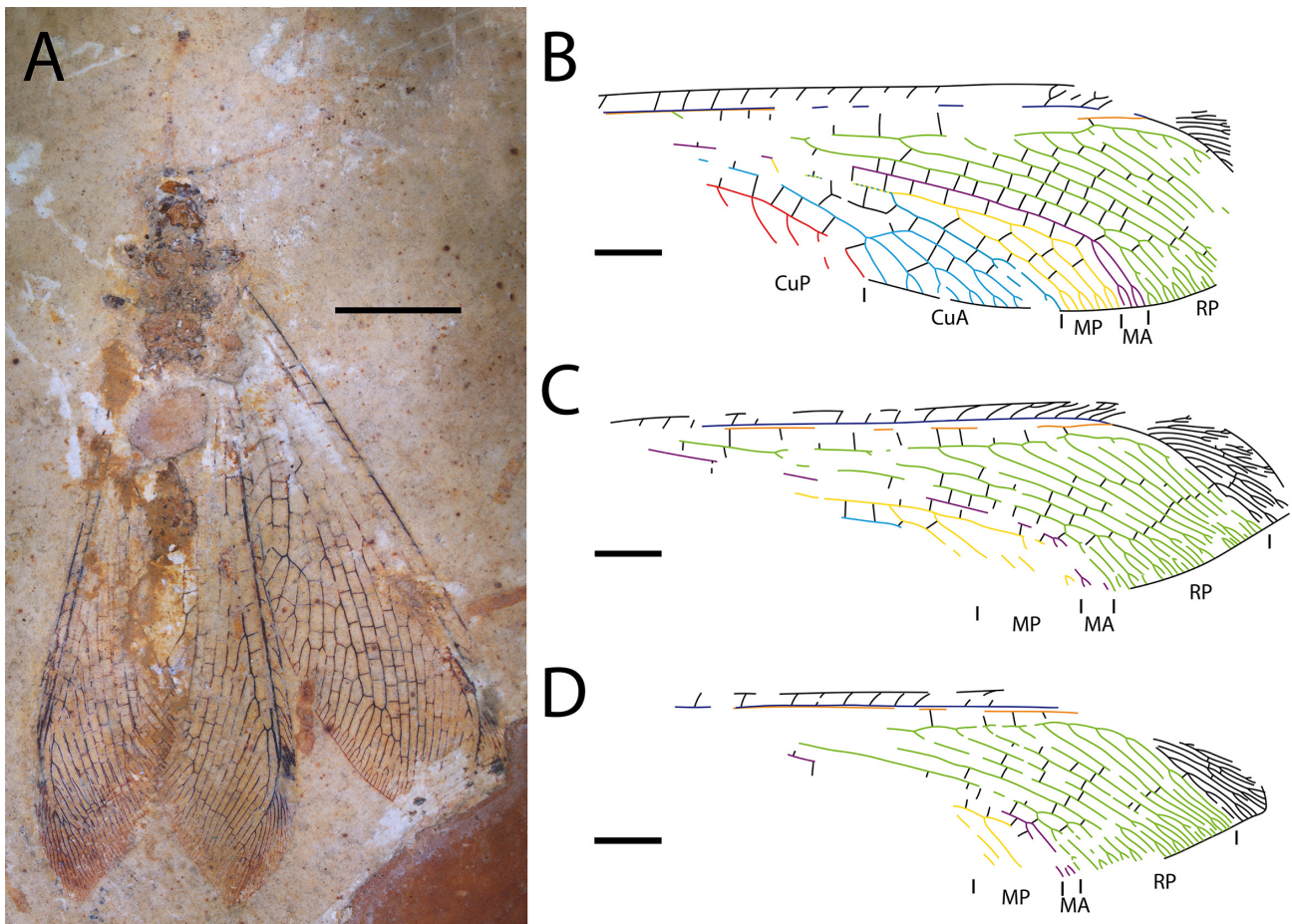


FIGURE 7. *Blittersdorffia vulcanoae* sp. nov., additional material (GP/1E-5238). **A**, Habitus. **B**, Right forewing drawing. **C**, Right hind wing drawing. **D**, Left hind wing drawing. Scale bars: 5 mm (**A**), 2 mm (**B**, **C**).

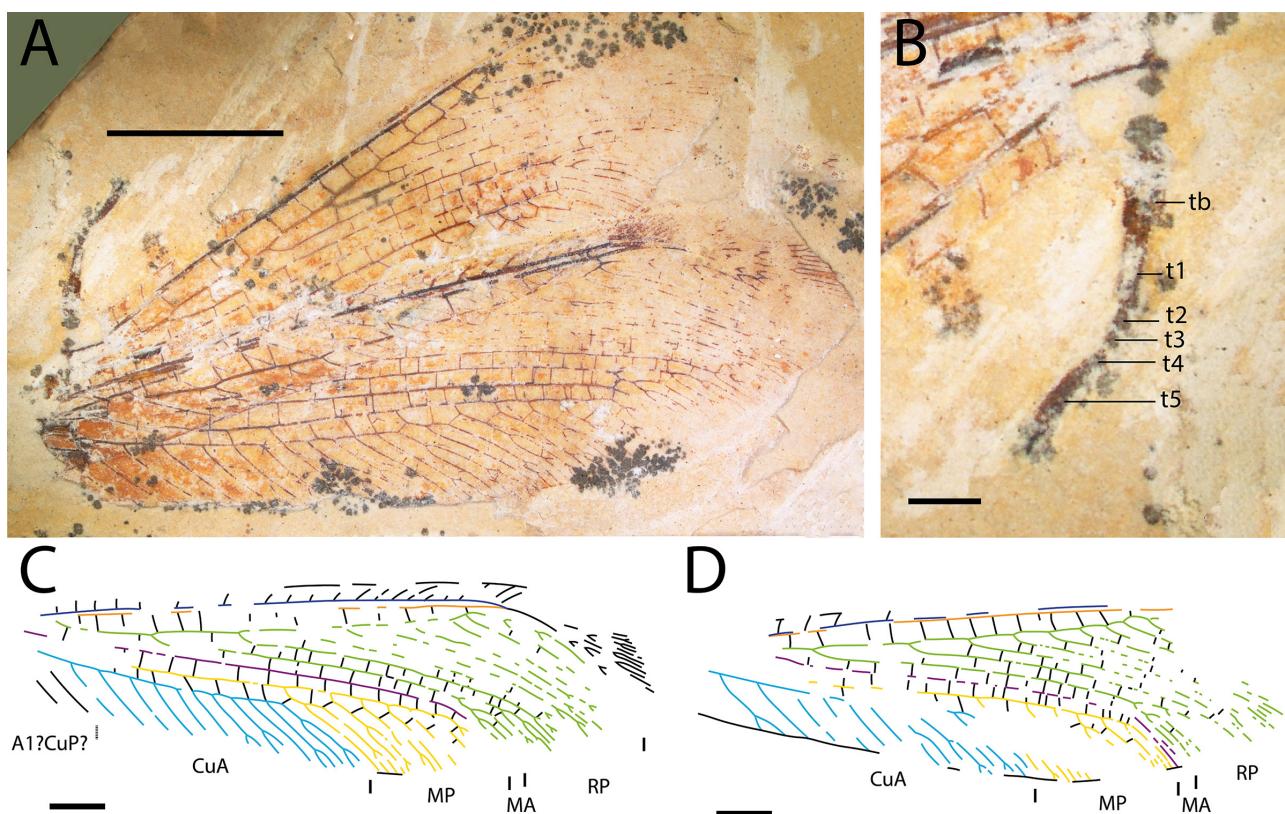


FIGURE 8. *Blittersdorffia vulcanoae* sp. nov., additional material (CCNH38). **A**, Habitus. **B**, Detail of preserved leg. **C**, Right hind wing drawing. **D**, Left hind wing drawing. Scale bars: 5 mm (**A**), 1 mm (**B**), 2 mm (**C**, **D**).

ventrally, pretarsal claw not preserved. Forewing elongate-oval, *ca.* 28.9 mm long and 7.8 mm wide (length/width ratio 3.7). Costal space narrow, widening near apex. Subcostal veinlets simple in the first half, some dichotomous after wing midpoint. Sc and RA fused far from wing apex. Veinlets of Sc + RA poorly preserved, but likely long and at least twice forked, subcostal space narrow. RA space relatively broad, narrowing at distal-most crossvein before fusion of Sc and RA, with at least 15 straight crossveins proximal to Sc and RA fusion; a single crossvein thereafter, delimiting a long and narrow hypostigmal cell. Two presectoral crossveins present. RP originates moderately far from wing base, approximately the end of wing basal fifth of total wing length, with 12 main branches. RP1 originates moderately close to RP origin, extensively branched (forked up to four times), *irc* slightly elongate; RP2 origin occurring distant from RP1 in a slightly short distance from relative distance between RP and RP1. Remaining branches originate close to each other, without RP7 deep bifurcations. Multiple crossveins between RP branches, presenting a gradate series of crossveins between RP branches. Three crossveins preserved between stem of RP and M. M forked distad RP origin, very close to RP first fork. MP fused to CuA1 distal to cubital fork. MA mostly single, forking dichotomously near wing margin. Multiple crossveins

between MA and MP. MP with four to five main branches, each one forking at least once near wing margin, multiple crossveins between MP branches. CuA pectinately forked into four branches, some of them secondarily forking once to twice. CuP sector large, terminating slightly proximad wing midpoint, with at least nine simple, straight and dichotomous branches preserved. Six crossveins present between CuA and CuP sector. Anal sector unpreserved. Hindwing similar to forewing in shape, but proportionally narrower with a more acute apex, *ca.* 27 mm long and *ca.* 6.9 mm wide, length/width ratio 3.9. Costal space width similar to forewing. Subcostal veinlets mostly simple, but some distal-most dichotomously branched. Sc and RA fused far from wing apex, reaching wing margin after wing apex. Sc-RA veinlets long, up to three times branched. RA space broad, slightly narrowing at distal-most crossvein before fusion of Sc and RA, with up to 14 crossveins preserved proximal to Sc and RA fusion, a single crossvein distad delimiting a long and narrow hypostigmal cell. Presectoral crossveins absent. RP originates relatively far from wing base (*ca.* 0.16 of total wing length), with 14 main branches. RP branching pattern similar to forewing, with branches originating near each other, terminal portions of RP branches mostly forked near wing margin. Many crossveins between RP branches present, including a similar series of gradate

crossveins. Two crossveins preserved between stem RP and MA. MA forked near wing margin. MP single until slightly proximal wing midpoint, then bifurcating in seven main branches (all of them once to twice branched secondarily). Multiple crossveins preserved between MA and MP. CuA sector long, reaching wing midpoint, with at least 11 straight pectinate branches, some of the distal-most branches secondarily branched. CuP probably simple, A sector not preserved.

Remarks. The placement of this new species in *Blittersdorffia* is putative, as the genus remains poorly defined with many complexities to be solved in the future. The new species reveals some significant variation in forewing such as CuA2 pectinate pattern, raising questions about the genus integrity, even when considering only the “core *Blittersdorffia*” group as proposed in Bueno *et al.* (2025a) (see Discussion). We choose not to revise the generic diagnosis at this time and provisionally retain the species in *Blittersdorffia*, pending future phylogenetic analysis. The materials CCNH 38 and GP-1E 5238 do not preserve some key diagnostic features (such as the *ps* in the forewing). However, given the highly similar wing venation, we decided to describe them as additional material, putatively considered *B. vulcanoae* **sp. nov.** specimens.

Discussion

The Crato Formation is a central fossil site for understanding the early evolution of Myrmeleontidae. If we consider only Myrmeleontidae (*sensu* Lu & Liu, 2022), not including Palaeoleontidae, there are more than 30 fossil species across 12 genera in the Crato Formation (Martins *et al.*, 2022). This represents over 50% of all known Myrmeleontidae fossil diversity, and more than 70% of the Mesozoic species of the family.

Recent evaluations of the recovered holotypes reiterate the validity of most Crato Formation genera (Bueno *et al.*, 2025a, b; this paper), demonstrating the reality of the group's high diversity in this past ecosystem. On the other hand, the species delimitation for many Myrmeleontidae from the Crato Formation need reevaluation and the number of species in some genera could be potentially overestimated (see Makarkin *et al.*, 2018). Two cases appear as the most urgent: *Pseudonymphes* (four valid species, prior to this paper) and *Araripeneura* Martins-Neto & Vulcano (6 valid species, five in the Crato Formation).

The present work confirms this suspicion, at least for *Pseudonymphes*, proposing the synonymy for two of its species and a *nomen dubium* to *P. zambonii*. The diagnosis for most species of the genus relies on

features that cannot be confidently verified on the type materials due to taphonomic reasons. Despite being useful for species delimitation in extant species, features such as proportions of thorax regions, leg segments, or the abdomen are, in most cases, not reliable for fossils, especially for materials preserved as impressions (not necessarily the case for amber specimens). In the Crato Formation fossils, it is preferable to rely on wing venation or proportion as primary diagnostic features, using other morphological observations only as a complement when these characteristics are evident (as for *Caririneura* Martins-Neto & Vulcano in Makarkin *et al.*, 2018).

The taxonomic revision of these supposedly diverse genera is very important in order to delimit a more concise and stable framework to study Myrmeleontidae in a broader evolutionary context. The excess of extinct taxa names frequently generates much noise in fossil groups, and efforts to establish synonyms when there is no strong evidence to support a specific name's validity are welcome. The case of *Araripeneura* seems to be similar and future synonyms are expected given the highly conserved wing features among the materials (Makarkin *et al.*, 2018; Khramov & Nam, 2025).

The forewing MP issue in Pseudonymphinae

The configuration of the forewing MP vein in Myrmeleontoidea is a character of considerable taxonomic and phylogenetic significance. Plesiomorphically, the forewing M in Neuroptera is deeply forked near the wing base, with MP free along most of its length—a condition widespread across the order, including in lineages related to Myrmeleontoidea such as Psychopsidae. This plesiomorphic state is retained in most fossil and extant Nymphidae (Shi *et al.*, 2015), with notable exceptions in *Myiodactylus* Brauer, *Austronymphes* Esben-Petersen and some *Nymphes* species (e.g., *N. apertus*, New, 1982; *N. nigrescens* New, 1982), where M remains single for much of its course and forks only close to the wing margin (New, 1981).

In other myrmeleontoid lineages, forewing M shows greater variation. In Babinskaiidae, M is typically unforked, except in *Paradoxoleon*, which retains a deep fork (Lu *et al.*, 2022). The genera formerly placed in Cratosmylidae, a group closely related to Babinskaiidae, also retain the putatively plesiomorphic deep fork (Myskowiak *et al.*, 2015; Lu *et al.*, 2022). In contrast, extant Nemopteridae and Myrmeleontidae display a short, oblique MP fused to CuA in the forewing (Breitkreuz *et al.*, 2017), a consistent feature across all known lineages and a strong venational synapomorphy uniting Nemopteridae + Myrmeleontidae.

Among fossils, an oblique MP is likewise documented in Nemopteridae (e.g., *Cratonemopteryx speciosa*; Makarkin *et al.*, 2018, fig. 15). In Myrmeleontidae-like

fossils, MP fusion with CuA is also common, though the position of fusion varies: proximad to the cubital fork in Araripeneurinae (Makarkin *et al.*, 2018, figs 2, 7; Bueno *et al.*, 2025b, figs 4, 6) and *Bleyeria* (Fig. 5), proximad or aligned with the fork in most Palaeoleontidae (Shi *et al.*, 2012, fig. 2; Myskowiak & Nel, 2016, figs 4, 5), or distad to the fork in forms resembling extant taxa as in *Diegopteryx* (Bueno *et al.*, 2025a, fig. 6) and in some *Blittersdorffia* as in *B. vulcanoae* **sp. nov.** (Fig. 6) and possibly in *B. pleoneura* (Martins-Neto & Vulcano, 1989, fig. 3).

However, interpretation of MP in some fossil Myrmeleontidae remains contentious, notably in *Blittersdorffia polyplusia* and *Pseudonymphes*. In *Blittersdorffia*, MP not fused to CuA was proposed as a key diagnostic feature separating *B. polyplusia* from other congeners (Martins-Neto, 1997). In *Pseudonymphes brunherottae*, Makarkin *et al.* (2018) described MP as unfused to CuA, linked only by a short crossvein (Fig. 3B). In the original description, Martins-Neto (1994) noted that the “oblique vein” differed from that of *P. araripensis*, possibly alluding to lost additional material, which may represent an undescribed species.

The interpretation of *Pseudonymphes* MP as unfused to CuA warrants caution. If the additional *P. araripensis* material—with MP fused to CuA proximad to the cubital fork (Makarkin *et al.*, 2018, figs 12, 13)—indeed belongs to a distinct species, it would be less parsimonious to assume a non-forked CuA with MP fusing and splitting in such a short span. Given that nearly all fossil and extant Myrmeleontidae exhibit a forked CuA with MP fused to the sector (varying only in position), MP fused to CuA emerges as a reasonable alternative interpretation for *Pseudonymphes* and *Blittersdorffia polyplusia* forewing venation.

Nonetheless, in the absence of more definitive evidence, we retain the published interpretations for *Pseudonymphes* (Makarkin *et al.*, 2018) and *B. polyplusia* (Martins-Neto, 1997) pending re-evaluation with additional material and a more robust phylogenetic framework.

The controversial genus Blittersdorffia

In the diverse fauna of Neuroptera in the Crato Formation, the genus *Blittersdorffia* is certainly one of the most controversial. In his last revision of *Blittersdorffia*, Martins-Neto (1997) highlights the main forewing features supporting the genus: short *irc*, a large number of RPs (7 to 12), and small radial cells. As discussed previously, these characters are quite generalized and some may be more sensitive to fossilization (Bueno *et al.*, 2025a).

Recently, the genus underwent some taxonomic modifications, including the transfer of *Blittersdorffia pulcherrima* (Martins-Neto & Vulcano) to *Diegopteryx*

Martins-Neto & Rodrigues, which highlights the polyphyletic character of its original proposition. Furthermore, *Blittersdorffia dicotomica* and *B. volkheimeri* probably belong to other genera as well, and their placement in the genus is provisional (Bueno *et al.*, 2025a). In summary, *Blittersdorffia* was used as a “wastebasket genus” within the Crato Myrmeleontoidea, including a morphologically heterogeneous assemblage of species lacking clear synapomorphies. Its broad diagnosis and generalized wing morphology have historically attracted numerous poorly preserved or ambiguous specimens.

In an attempt to stabilize this scenario, Bueno *et al.* (2025a) proposed a “monophyletic core” composed of *B. pleoneura* Martins-Neto & Vulcano, *B. polyplusia* Martins-Neto, and *B. evanescens* Bueno *et al.* (now including *B. vulcanoae* **sp. nov.**). The proposed diagnosis includes: absence of *ps* on both wings; fore- and hindwings of similar size and shape; forewing RP origin near the wing base, within its basal fifth; forewing with at least 10 RP branches; absence of wing pattern; and CuA2 dichotomously branched (Bueno *et al.*, 2025a). However, even considering the renewed diagnosis, there is still some controversy regarding its taxonomic status.

First and foremost, it should be highlighted that the diagnostic features are all likely plesiomorphic and two of them are not present in *B. vulcanoae* **sp. nov.**: absence of *ps* and CuA2 dichotomous in forewing. Despite being more detailed than the original diagnosis, the new proposition still holds many generalized features. The lack of terminalia preservation in the Crato Formation fossils, which could potentially help in establishing additional diagnostic features, restricts the reliable characters mostly to wing features.

Additionally, we can highlight at least three key morphological distinctions between the “core” species:

—*Forewing MP*: In *B. evanescens*, the MP is untraceable, while in the other species, it is present either forking very close to the cubital fork (*B. polyplusia*) or fused to CuA after the fork (*B. pleoneura* and *B. vulcanoae* **sp. nov.**). Although an untraceable MP occurs in other fossil Myrmeleontidae (e.g., *Xiaoleon* Lu & Liu and *Burmanaura* Huang *et al.*), this degree of variation within a single genus has not been reported in any other Myrmeleontoidea fossil genera.

—*Forewing CuA2 forking pattern*: *B. vulcanoae* **sp. nov.** possesses a pectinately branched pattern in the forewing, diverging from the remaining species (dichotomous). This variation is also uncommon within a single genus, being usually stable in fossil genera.

—*Hind wing CuA and MP sectors*: Although not preserved in *B. pleoneura* and *B. polyplusia*, there is a significant difference in the proportion of these sectors between *B. evanescens* (reduced CuA, very long MP) and *B. vulcanoae* **sp. nov.** (long CuA and reduced MP).

There are some cases of presence and absence of *ps* in the same genus as in *Cratoalloneura* Martins-Neto, *Caririneura* Martins-Neto & Vulcano and likely *Cratopteryx* Martins-Neto & Vulcano (Bueno *et al.*, 2025b). So, despite being very interesting and rare in the Cretaceous Myrmeleontidae, the presence of presectoral crossveins in *B. vulcanoae* **sp. nov.**, does not directly challenge the placement of *B. vulcanoae* in the genus.

The loss of type materials, including the type-species holotype *B. pleoneura*, and the poor descriptions and illustrations further complicates the proposition of a reliable diagnosis, particularly regarding the evaluation of features like the forewing CuA2 branching pattern. The lack of hind wing preservation in both *B. polyplusia* and *B. pleoneura* holotypes also contributes to these uncertainties.

Given the aforementioned complexity, we choose not to make any major modifications to the generic diagnosis for now, to avoid causing even more instability. We recognize that many taxonomic revisions are still needed to solve this tricky taxonomic puzzle that *Blittersdorffia* has become since its description. We expect that a future phylogenetic analysis will help us to better circumscribe the genus and make the necessary taxonomic treatments to clean up its taxonomic framework.

The systematics of Pseudonymphinae

The current configuration of Pseudonymphinae was proposed by Martins-Neto (2002) in his comprehensive revision of Crato Formation Neuroptera, comprising *Pseudonymphes*, *Bleyeria*, and *Blittersdorffia*. In the same work, this group is referred to for the first and only time as family Pseudonymphidae, although it was listed as “Myrmeleont. Pseudonymphinae” (Martins-Neto, 2002: p. 39). Despite the informal familial rank, no formal diagnosis was ever published. However, based on Martins-Neto’s results a few shared traits could be

inferred: short and clavate antennae, a short CuA2 in the forewing, absence of *ps*, and the forewing MP fused to CuA posterior to the cubital fork.

Subsequent works, however, never corroborated monophyly of this group. Makarkin *et al.* (2018) refer to the group as “stem group Pseudonymphidae,” tentatively including members such as *Choromyrmeleon* Ren & Guo and *Burmaneura* (at that time, the only genus described from Kachin amber). *Bleyeria* was not evaluated in detail, but was suggested to be more closely related to the Araripeneurinae (referred to as Araripeneuridae by the author). *Diegopteryx* is not discussed, but after the recent revision (Bueno *et al.*, 2025a), it is potentially also related to the “Pseudonymphinae” genera. The species reunited under Pseudonymphinae have highly distinctive wing venation, and lack any well-defined synapomorphy.

The phylogenetic analysis by Lu *et al.* (2019) also could not find support for a monophyletic Pseudonymphinae, neither in Martins-Neto’s original composition nor in the new composition proposed by Makarkin *et al.* (2018). Lu *et al.* (2022) recovered a monophyletic Pseudonymphinae (*Bleyeria* + *Pseudonymphes* + *Pseudonymphes*) but with very weak support, sustained by a single non-exclusive synapomorphy: the pectinate 3–4 branches of CuA2 in the forewings.

Based on our reassessment, especially concerning the new interpretation of *Bleyeria nordestina* wing venation and the complicated status of *Blittersdorffia* (also discussed in Bueno *et al.*, 2025a), the monophyly of Pseudonymphinae becomes even more difficult to support. Table 1 summarizes the main supposedly shared characters that support the subfamily (*sensu* Martins-Neto, 2002) and their controversies.

It is now more difficult than ever to support a monophyletic Pseudonymphinae in any of its historical configurations. Nevertheless, some forewing traits, such as the MP fused to CuA distad of the cubital fork,

TABLE 1. Proposed characters supporting the monophyly of Pseudonymphinae and their recent assessments.

Proposed character	Source	Recent assessment / Considerations
Short and clavate antenna	Martins-Neto, 2002	Not very distinct from the relative size observed in Araripeneurinae genera.
Forewing short CuA2	Martins-Neto, 2002	Similar to the Palaeoleontidae species, not very distinctive.
Absence of <i>ps</i> in forewing	Martins-Neto, 2002	Plesiomorphic condition; similar to most Cretaceous Myrmeleontidae-like groups, except for <i>Cratoalloneura verdandia</i> Martins-Neto, <i>Nanoleon wangae</i> Hu, Lu & Liu, <i>Caririneura macrothoracica</i> Makarkin <i>et al.</i> ; and <i>Blittersdorffia vulcanoae</i> sp. nov.
MP posterior to cubital fork in forewing	Martins-Neto, 2002	Anterior or untraceable in several cases: <i>Bleyeria nordestina</i> ; potential new species of <i>Pseudonymphes</i> (Makarkin <i>et al.</i> , 2018: INHSP 1525); <i>Blittersdorffia evanescens</i> .
CuA2 with 3–4 pectinate branches in forewing	Lu <i>et al.</i> , 2022	Likely dichotomic in <i>Blittersdorffia pleoneura</i> and <i>B. polyplusia</i> , dichotomic in <i>B. evanescens</i> .

might indicate that some genera like *Diegopteryx*, *Pseudonymphes*, and at least part of *Blittersdorffia* could be relatively close to extant species as inferred by previous hypothesis (Lu *et al.*, 2019).

Conclusion

This study, based on renewed access to Crato Formation holotypes and new materials, advances the reassessment of neuropteran fossil diversity. It stabilizes the taxonomy of *Pseudonymphes* by synonymizing *P. ponomarenkoi* and *P. brunherottae* with *P. araripensis* and proposing *P. zambonii* as a *nomen dubium*, thus mitigating species overestimation. The redescription of *Bleyeria nordestina* provides a revised diagnosis and reinterpretation of its wing venation, facilitating precise character coding in future phylogenetic analyses. The description of a new species of *Blittersdorffia* offers a more comprehensive context for this intricate genus. This work reinforces the apparent lack of monophyly of the subfamily Pseudonymphinae, as previously suggested, and integrates recent taxonomic advancements into a comprehensive evolutionary framework, aiding in the understanding of the early evolution of Myrmeleontidae and allied lineages.

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