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https://doi.org/10.11646/mesozoic.2.4.1

http://zoobank.org/urn:lsid:zoobank.org:pub:73BBE692-C5C2-4DF2-8370-7476D83E5621

The sixth representative of the endemic Cretaceous Burmese amber family Burmaeshnidae (Odonata: Aeshnoptera)

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Abstract

A new species of the aeshnopteran family Burmaeshnidae is described and illustrated based on a pair of well-preserved fore- and hind wings in mid-Cretaceous amber from Kachin, northern Myanmar. *Burmaeshna bechlyi* **sp. nov.** displays all the diagnostic characters of the family and differs from the type species *Burmaeshna azari* Huang, Cai, Nel & Bechly, 2017 in several key features. These include a hind wing with a discoidal triangle crossed by a single vein (vs. two in *B. azari*), an anal loop with four cells (vs. five), and the base of the Mspl is located three cells distal to the discoidal triangle (vs. two). The discovery of *Burmaeshna bechlyi* **sp. nov.**, alongside the recent descriptions of other odonatan species from mid-Cretaceous Kachin amber, highlights the remarkable diversity of true dragonflies in the Burmese amber biota.

Keywords: Anisoptera, diversification, Insecta, mid-Cretaceous, new species

Introduction

Kachin amber is one of the most extensively studied fossiliferous insect deposits worldwide, with over 2,000 arthropod species described to date (Ross, 2025). As of 2025, representatives from nearly all extant insect orders have been identified in this deposit, including Odonata. A recent review of the odonatan fauna from Kachin amber documented at least 38 species across 16 families (Zheng, 2021). While many of these belong to the Zygoptera, perhaps more readily trapped due to their slender and

delicate morphology compared to the more robust and vigorous Anisoptera, true dragonflies are also represented by more than 10 species (Zheng, 2021).

Notably, the assemblage includes extinct families, some of which remain phylogenetically unresolved. Among these is the family Burmaeshnidae, a relatively recent addition assigned to the Aeshnoptera and so far known exclusively from mid-Cretaceous Kachin amber (Huang *et al.*, 2017). Although its placement has not yet been rigorously tested within a phylogenetic framework, preserved wing venation features suggest a possible affinity with extant families such as Telephlebiidae (Cockerell, 1913) and Aeshnidae (Leach, 1815) (Huang *et al.*, 2017a, 2017b; Zheng *et al.*, 2017).

Currently, the family comprises five monospecific genera: Angustaeshna Huang et al., 2017, Burmaeshna Huang et al., 2017, Cretaeshna Zheng et al., 2017, Neoaeschna Liu et al., 2024, and Proaeschna Wei et al., 2019 (Huang et al., 2017a, 2017b; Zheng et al., 2017; Wei et al., 2019; Liu et al., 2024). Here, we describe a sixth species from Kachin amber, attributed to the type genus Burmaeshna. This discovery suggests a potential diversification of the group, possibly driven by insular evolutionary dynamics.

Material and methods

The study is based on a specimen embedded in a piece deriving from the deposits of Noije Bum in the Hukawng Valley (26°29′ N, 96°35′ E), Kachin State, northern

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Myanmar (see detailed map in Grimaldi & Ross, 2017; fig. 2). Radiometric data established an early Cenomanian age $(98.79 \pm 62 \text{ Ma})$ for Kachin amber, based on zircons from volcanic clasts found within the amber-bearing rock (Shi *et al.*, 2012). Some ammonites, found in the amberbearing bed, and within amber, corroborate a late Albian–early Cenomanian age of these sediments (Cruickshank & Ko, 2003). The specimen is housed in the collections of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Science, China (NIGPAS), under the collection number NIGP2208852.

The specimen was examined with a Zeiss Axio Zoom V16 stereomicroscope and photographed with a Zeiss Axiocam 512 colour camera. All images are digitally stacked photomicrographic composites of several individual focal planes, obtained using Helicon Focus 6.7. The figures were composed with Adobe Illustrator CC2018 and Photoshop CC2018.

We followed the wing venation nomenclature of Riek & Kukalová-Peck (1984), emended by Nel et al. (1993) and Bechly (1996), and the higher classification of fossil and extant Aeshnoptera of Bechly et al. (2001) and Bechly (2016). Wing vein abbreviations are as follows: AA = analis anterior; a.l. = anal loop; arc = arculus; Ax0, Ax1, Ax2, Ax3 = primary antenodal crossveins; C = costa; CuA = cubitus anterior; CuP = cubitus posterior (CuP-crossing); IR = intercalary radial vein; MA = media anterior; MAa = anterior-most branch of MA; MAb = posterior branch of MA distally closing discoidal triangle; MP = media posterior; Mspl = supplementary longitudinal vein in post-discoidal area; N = nodus; O = lestine oblique vein; Pt = pterostigma; RA = radius anterior; RP = radius posterior; Rspl = supplementary longitudinal vein posterior to IR2; ScP = subcosta posterior, t = discoidal triangle.

Systematic palaeontology

Order Odonata Fabricius, 1793 Suborder Anisoptera Selys-Longchamps, 1854 Family Burmaeshnidae Huang, Cai, Nel & Bechly, 2017

Type genus. Burmaeshna Huang, Cai, Nel & Bechly, 2017.

Other genera. Angustaeshna Huang, Cai & Nel, 2017, Cretaeshna Zheng, Chang, Jarzembowski & Wang, 2017, Proaeschna Wei, Shi, Ren & Wang, 2019, Neoaeschna Liu, Fang & Zheng, 2024.

Genus Burmaeshna Huang, Cai, Nel & Bechly, 2017

Type species. Burmaeshna azari Huang, Cai, Nel & Bechly, 2017.

Other species. Burmaeshna bechlyi sp. nov.

Burmaeshna bechlyi sp. nov.

(Fig. 1)

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Material. Holotype NIGP208852 (a nearly complete broken forewing and an incomplete hind wing, together with two small crickets, a beetle, a dipteran, and the remains of a probable trichopteran), stored at the Nanjing institute of Geology and Palaeontology, China.

Etymology. Named after our late colleague Dr Günter Bechly, in recognition of his impressive contribution in palaeoentomology and odonatology.

Diagnosis. Wing characters only. Forewing with trigonal planate emerging form MAb in post-discoidal area; discoidal triangle crossed by one vein; base of Mspl situated four cells distad discoidal triangle; IR1 with base located one cell basad pterostigmal brace. Hind wing with secondary antenodal crossveins well aligned; anal loop elongate, narrow, with four cells disposed into two rows; discoidal triangle shorter and broader than in forewing, crossed by one vein; base of Mspl situated three cells distad discoidal triangle; two cells situated below IR2, immediately basal base of Rspl very broad. Both wings with one secondary antenodal vein between Ax1 and Ax2; fork of IR2 situated four cells basad pterostigmal brace.

Locality and horizon. Hukawng Valley, Kachin Province, Myanmar; late Albian to early Cenomanian, mid-Cretaceous.

Description. Forewing broken and deformed but nearly complete, hyaline, wing ca. 30.2 mm long, 6.5mm wide; distance from base to arculus 4.5 mm; from arculus to base of RP3/4 6.2 mm; from arculus to nodus ca. 14.3 mm; five secondary antenodal crossveins of first row and six of second row preserved distal of Ax2; Ax2 between arculus and discoidal triangle; a secondary antenodal crossvein between Ax2 and Ax1; Ax1 well basad arculus; anterior part of arculus slightly curved; RP and MA separated in angle of arculus where posterior part of arculus touches anterior part; hypertriangle 3.6 mm long, free; discoidal triangle 0.9 mm distal of arculus, divided into two smaller cells, elongate and narrow, with basal side 1.0 mm, anterior side 2.5 mm long, and MAb 2.5 mm long, with an angle from which emerges distinct convex trigonal planate, short and zigzagged; post-discoidal area with two rows of cells just distad discoidal triangle and three more distally; Mspl well-defined with one row of cells between it and MAa; base of Mspl four cells distal of discoidal triangle; basal part of area between RA and

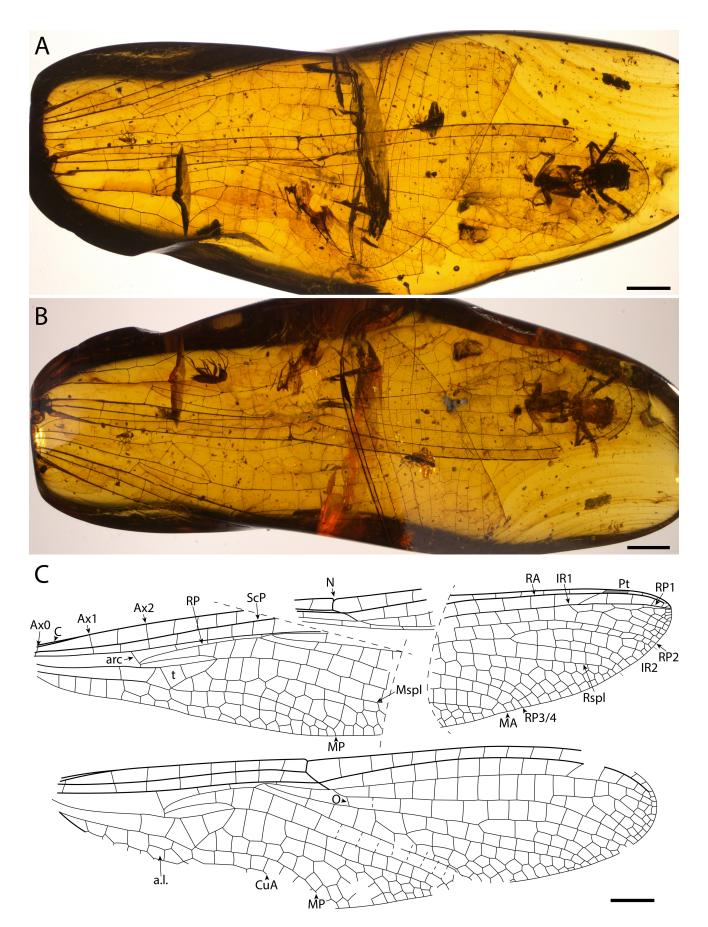


FIGURE 1. Burmaeshna bechlyi **sp. nov.**, holotype NIGP2208852. **A**, Wings in dorsal view. **B**, Wings in ventral view. **C**, Interpretative line drawing of forewing and hind wing venations (doted lines: limits of folded part or broken veins). Scale bars = 2 mm.

RP with four crossveins basal of RP3/4; area between RP and MA with four crossveins basal of RP3/4; median area free; submedian area crossed by curved CuP; subdiscoidal space free; one row of cells between MP and CuA; two rows of cells in a narrow anal area; two rows of cells in area below CuA; CuA without well-defined posterior branches; base of RP2 very slightly distal of subnodus; RP2 nearly straight; one row of cell between RP2 and RP1 basal of Pt-brace; IR2 with a clear distal fork situated four cells basad pterostigmal brace, with two rows of cells between its branches below Pt; Rspl welldefined, straight, with one row of cell between it and IR2; one oblique vein "O" one cell distal of subnodus; eight preserved post-nodal crossveins, not aligned with seven preserved post-subnodal crossveins basal of pterostigma; pterostigma covering one cells; a short IR1 with its base situated one cell basad pterostigmal brace.

Hind wing incomplete, hyaline, 28.7 mm long, width unknown; distance from base to arculus 4.9 mm; from arculus to nodus 7.3 mm; from arculus to base of RP3/4 4.5 mm; two antenodal crossveins of primary type (viz. with a triangular membrane between C, ScP and radius), Ax1 2.7 mm from wing base, Ax2 3.0 mm distally; a complete supplementary antenodal between Ax1 and Ax2, three complete secondary antenodal crossveins distal of Ax2 and most distal one not complete; 10 postnodal crossveins not well aligned with nine post-subnodal crossveins basal of pterostigma; one row of cells between RP1 and RP2; arculus 1.1 mm basal of Ax2; Ax2 aligned with basal side of discoidal triangle; RP and MA separated in angle of arculus where posterior part of arculus touches curved anterior part; hypertriangle 3.3 mm long, free; discoidal triangle 0.7 mm distal of arculus, divided into two smaller cells, shorter and broader than in forewing, with basal side 1.4 mm long, anterior side 2.5 mm long, and MAb 2.5 mm long; post-discoidal area with two rows of cells just after discoidal triangle, distally broadened with 11 rows of cells along posterior wing margin; a distinct convex trigonal planate, short and zigzagged; Mspl welldefined, nearly straight, with one row of cells between it and MAa; base of Mspl three cells distal of discoidal triangle; basal part of area between RA and RP with two crossveins basal of RP3/4, and probably two distal of base of RP3/4 and basal of subnodus; area between RP and MA with two crossveins basal of RP3/4; one oblique vein "O", one cell distal of base of RP2; one row of cells between IR2 and RP3/4 at least till two cells distal of subnodus; base of RP2 aligned with subnodus; Rspl straight with one row of cells between it and IR2; IR2 forked four cells basal of pterostigma, with two rows of cells between its branches; pterostigma not preserved; a short IR1 with its base situated one cell basad pterostigmal brace; anal loop much longer than broad, divided into four cells; CuAb

well-defined; cubito-anal area not preserved but anal area very narrow as discernible by the very close angle between AA and AP at wing base.

Discussion

This fossil can be attributed to the Aeshnoptera because of its narrow one-celled area between RP1 and RP2 and its very long discoidal triangles. It strongly resembles the representatives of the Burmese amber family Burmaeshnidae. The current diagnosis of this family is as follows: discoidal triangles very elongate; well-defined Mspl parallel to MA; very elongate anal area with an anal loop distinctly longer than wide; an accessory anal loop between the two main branches of CuA in hind wing present; IR2 with a distal fork. The presence of two oblique veins "O" between RP2 and IR2, proposed by Huang et al. (2017a), is likely to be erroneous, due to the deformation of the wing of the holotype of Burmaeshna azari Huang, Cai, Nel & Bechly, 2017 in this zone. In the other fossils of the family, described later, there is only one oblique vein "O". The new fossil shows all the diagnostic characters of the family.

Proaeschna zhangi Wei, Shi, Ren & Wang, 2019 shares with the new fossil discoidal triangles divided into two cells by a crossvein, and anal loop four-celled disposed into two rows, but it strongly differs from the new fossil in the presence of only two complete antenodal crossveins in the hind wing vs. six in the new fossil, narrower hind wing discoidal triangle, distinctly broader anal loop, and overall, distinctly broader hind wing anal area (Wei et al., 2019). Neoaeschna kachinensis Liu, Fang & Zheng, 2024 shares with the new fossil a narrow anal loop, even if incompletely preserved, but differs from it in the anal loop only two-celled vs. with four cells disposed into two rows, the presence of incomplete antenodal crossveins between Ax2 and Ax3 in the hind wing and the absence of a trigonal planate emerging form MAb in post-discoidal area of forewing (Liu et al., 2024).

The new fossil shares with Angustaeshna magnifica Huang, Cai & Nel, 2017 a two-celled hind wing discoidal triangle, an anal loop of the same shape even if narrower, but it differs from A. magnifica in the shape of the anal area of hind wing, very narrow and with AA making an acute angle with AP vs. broad with AA making an open angle with AP; the petiole very short vs. very long; three complete secondary antenodal crossveins distal of most distal primary antenodal vs. only three secondary antenodal crossveins of first row not well aligned with the three crossveins of second row; hind wing discoidal triangle shorter and broader than in forewing vs. more elongate and narrower (Huang et al., 2017b).

originally The genus Cretaeshna, in the Telephlebiidae, was transferred by Huang et al. (2017b) into the Burmaeshnidae. Its type species C. lini Zheng, Chang, Jarzembowski & Wang, 2017, is based on an incomplete distal half of a wing. If its venation is typical of the Burmaeshnidae, it shows very few characters that would allow for accurate separation of this taxon from the other genera in the family. The new fossil differs from C. lini in the IR1 situated one cell basad pterostigmal brace vs. below it, and the two cells situated below IR2 and just basal base of Rspl very broad vs. of 'normal' shape (Zheng et al., 2017).

The new fossil and Burmaeshna azari have similar narrow anal area. It differs from B. azari in the hind wing anal loop with only four cells vs. five, discoidal triangle crossed by one vein vs. two, secondary antenodal crossveins well aligned vs. incomplete, and base of Mspl situated three cells distad the discoidal triangle vs. two cells (Huang et al., 2017).

The new fossil differs from all the taxa currently in the Burmaeshnidae. It shows the closest similarities with Burmaeshna azari. We propose to consider it as a new species in this genus. Of course, it is possible that a better knowledge on the body characters of these genera will lead to changes in the taxonomy, currently only based on wing venation characters, known to be subject to more homoplasies than the other body structures in Odonata.

Conclusion

Burmaeshna bechlyi sp. nov. represents the sixth described species within the small and enigmatic family Burmaeshnidae, which remains known exclusively from Burmese amber. A comparable pattern is observed in the damselfly Burmacoenagrionidae or damsel-dragonfly Burmaphlebiidae, also endemic to this deposit, currently comprising seven species and three species, respectively (Liu et al., 2025). The restricted distribution and diversity of the three families suggest a potential case of insular diversification in some Odonata, possibly driven by longterm geographic isolation within an island ecosystem.

Acknowledgements

We thank Dr Daran Zheng and an anonymous reviewer for their useful comments and corrections on the first version of this manuscript. Financial support was provided by the National Key Research and Development Program of China (2024YFF0807601) and the National Science Foundation of China (42288201).

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