Palaeoentomology 003 (6): 564–568
https://www.mapress.com/j/pe/

Short Communication

ISSN 2624-2826 (print edition)
PALAEOENTOMOLOGY
ISSN 2624-2834 (online edition)

https://doi.org/10.11646/palaeoentomology.3.6.6
http://zoobank.org/urn:lsid:zoobank.org:pub:320A1EB2-73C0-4C4D-B01F-FEA9B75BDC7E

The sixth species of the damselfly family Burmacoenagrionidae (Odonata) endemic to the mid-Cretaceous Burmese amber

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Odonata from the mid-Cretaceous Burmese amber is now one of the best-known fossil assemblages of taxa in this order (Zheng, 2020). It is especially the case for damselflies, which are quite rare in other Mesozoic outcrops, either in amber or as compressions. This assemblage comprises several apparently endemic families, not recorded in any other place. This particularity is possibly related to the situation of the Burma Terrane during the mid-Cretaceous, as an island of the Tethys Ocean. As it happens for endemic clades on islands, some of these families are significantly diversified. It is the case for the Burmacoenagrionidae, already known from four genera and five species. Here we describe a sixth species from the same Burmese amber, attributed to this group, confirming its diversity. The present new taxon allows us to propose a new putative synapomorphy for this group, and an endophytic way of egg laying for these damselflies.

Material and methods

The specimen studied herein derives from the deposits of Noije Bum in the Hukawng Valley (26°29′ N, 96°35′ E), Kachin State, northern Myanmar (see detailed map in Grimaldi & Ross, 2017: fig. 2). Radiometric data established an early Cenomanian age (98.79 ± 0.62 Ma) for Kachin amber, based on zircons from volcanic clasts found within the amber-bearing sediments (Shi *et al*., 2012; Xing & Qiu, 2020). Some ammonites found in the amber-bearing bed and within amber corroborate a late Albian–early Cenomanian age (Cruickshank & Ko, 2003; Yu *et al*., 2019).

The amber piece was polished to facilitate the examination of the specimen using a grinder polisher (Buehler EcoMet 30) and very thin silicon carbide sanding paper and a diamond disk. The specimen was examined and photographed with a Leica MZ APO with an attached Canon EOS 5D Mark II camera. All images were digitally stacked photomicrographic composites of several individual focal planes, which were obtained using Helicon Focus 6.7. The figures were composed with Adobe Illustrator CC2019 and Photoshop CC2019 software.

We follow the higher classification of fossil and extant Odonatoptera based on the phylogenetic system of Bechly (1996, 2016), with the dragonfly wing venation nomenclature used in this paper based on the interpretations of Riek & Kukalová-Peck (1984), as modified by Nel *et al*. (1993), Bechly (1996), and Jacquelin *et al*. (2018).

Venation abbreviations are as follows: AA anterior anal; Arc arculus; Ax primary antenodal crossvein; C costa; CuA anterior cubitus; CuP posterior cubitus; d discoidal cell; IR intercalary radial vein; MAa anterior branch of anterior media; MAb posterior branch of anterior media; MP posterior media; N nodus; Pt pterostigma; RA anterior radius; RP posterior radius; Sn subnodal crossvein; ScP posterior subcostal.

Collection is referred to by the following acronym: NIGP—Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, China.

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 Submitted: 26 Oct. 2020; accepted by D. Azar: 27 Nov. 2020; published: 21 Dec. 2020

Systematic palaeontology

Order Odonata Fabricius, 1793
Suborder Zygoptera Selys Longchamps, 1854
Superfamily Coenagrionoidea Kirby, 1890
Family Burmacoenagrionidae Zheng, Nel, Zhang, Chang, Jarzembowski, Zhuo & Wang, 2019

Type genus. *Burmacoenagrion* Zheng *et al*., 2019.

Included genera. *Burmagrion* Möstel *et al*., 2017, *Burmachistigma* Zheng *et al*., 2019, and *Electrocoenagrion* Zheng *et al*., 2019.

Genus *Burmagrion* Möstel, Schorr & Bechly, 2017

Type species. *Burmagrion marijanmatoki* Möstel *et al*., 2017.

***Burmagrion azari* sp. nov.**
(Figs 1–3)
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Material. Holotype NIGP173729 (female, together with fragments of wings of another specimen of the same species and wings and legs of flies of Mycetophiloidea and Tipuloidea).

Etymology. Named after our friend, Prof. Dany Azar. The specific epithet is treated as a noun in a genitive case.

Diagnosis. Wings *ca*. 20.0 mm long; postnodal crossveins somewhat aligned in distal half of area but not in its basal half; Pt covering only two cells; only 11–14 postnodals; U-shaped structure formed by the pterostigmal part of RA and stigmal crossveins is weakly pronounced; base of RP2 only 3–4 cells distal of that of IR2 instead of six; a series on strong teeth on ovipositor V3.

Locality and horizon. Noije Bum Hill, Hukawng Valley, Kachin State, Myanmar; upper Albian to lower Cenomanian, mid-Cretaceous.

Description. The damselfly is completely dislocated, with the head, abdomen in two parts, part of thorax with two wings attached, and another part of thorax with the two other wings. Head 1.8 mm long, 3.7 mm wide, large compound eyes well-separated; maxillary palps separated from head (fig. 3); general shape of mandible quadrate, with some setae at base of the teeth and several long setae on outer margin; group of apical teeth distally broadened (fig. 2A); thorax with dark lateral bands; fore- and hind wings complete, with same venations (Fig. 1); wing 20.2 mm long, 3.9 mm wide; distance from wing base to arculus 4.9 mm, from arculus to nodus 2.7 mm, from nodus to pterostigma 9.1 mm, from pterostigma to wing apex 1.9 mm; primary antenodal crossveins preserved; Ax0 close to wing base, Ax1 2.0 mm distal of Ax0, Ax2 1.9 mm distal of Ax1; no secondary antenodal and antesubnodal crossveins present; 11 postnodal crossveins and eight postsubnodal crossveins on forewing (respectively 14 and 10 on hind wing) before Pt, partly aligned; 10 postnodals present distal of Pt, non-aligned with postsubnodals; arculus angular and slightly distal of Ax2; discoidal cell basally closed, free, elongate and narrow, somewhat rectangular with weak distal angle; anterior side slightly parallel with posterior side, and distal side longer than basal side; length of basal side 1.0 mm, of anterior side 1.2 mm, of distal side 0.3 mm, of posterior side 1.8 mm; subdiscoidal free and elongate, 2.1 mm long and 0.19 mm wide; CuP 1.4 mm distal of level of Ax1; AA′ originating from AP slightly nearer to Ax2 than to Ax1; subnodus aligned with nodal crossvein; midfork (base of RP3/4) distinctly basal to nodus; base of IR2 aligned with subnodus, one cell and 1.1 mm distal

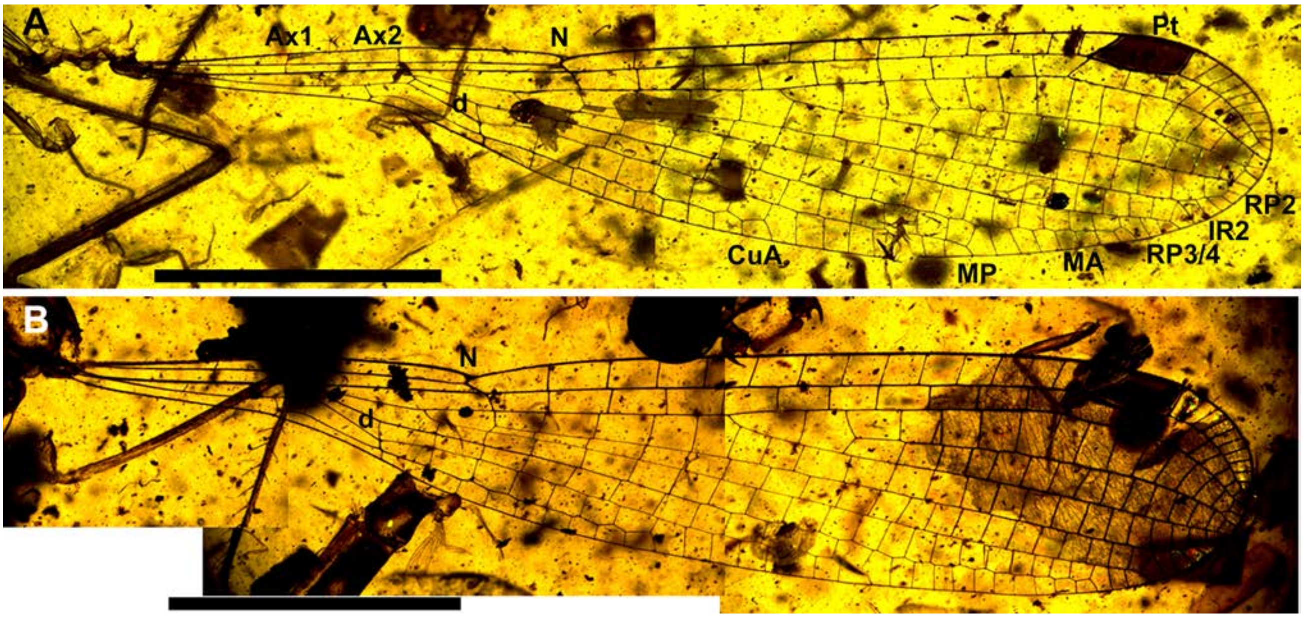

FIGURE 1. *Burmagrion azari* **sp. nov.**, holotype NIGP173729. **A**, Forewing. **B**, Hind wing. Scale bars = 5 mm.

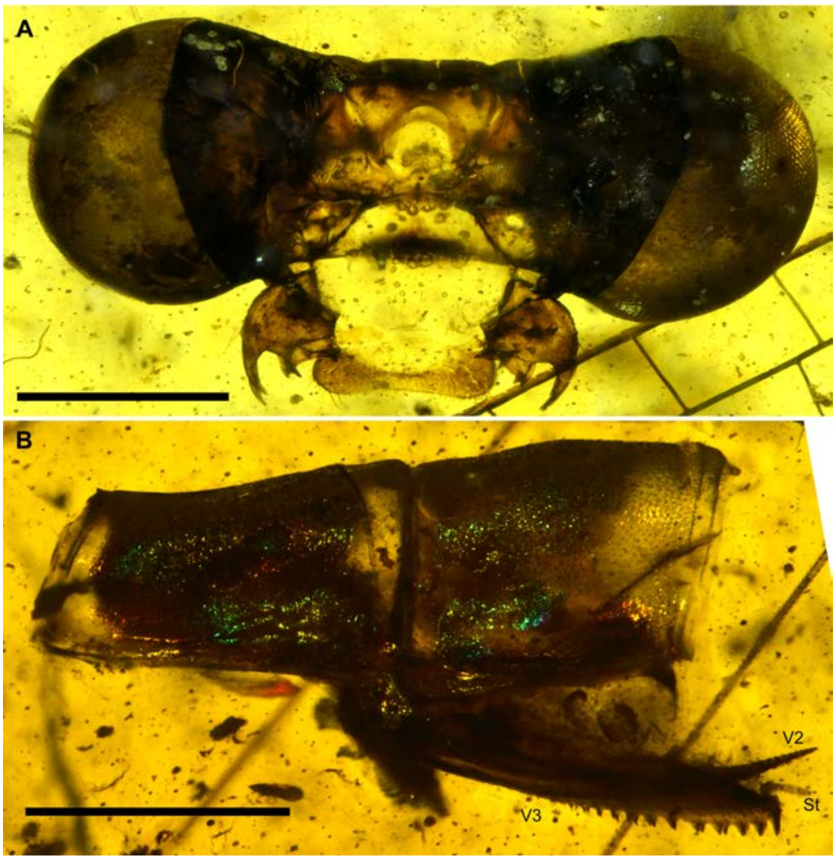

FIGURE 2. *Burmagrion azari* **sp. nov.**, holotype NIGP173729. **A**, Head from below. **B**, Ovipositor; St stylus, V2 and V3 valvula 2 and 3. Scale bars = 1 mm.

FIGURE 3. *Burmagrion azari* **sp. nov.**, holotype NIGP173729. Hind leg and maxillary palp (m.p.). Scale bar = 1 mm.

of midfork; RP2 originating five cells distal of subnodus, nearer to nodus than to pterostigma; IR1 long, originating two-three cells distal of base of RP2 and four-five cells basal of pterostigma; RP1 with weak angle below pterostigmal brace. MA distally zigzagged and long, reaching posterior wing margin just below pterostigma apex; MP long, ending on posterior wing margin one cell distal of base of IR1; CuA long, covering 10–11 cells; all intercalary veins (except IR1 and IR2) suppressed; pterostigma long, hyaline, with basal side and distal side oblique, covering two cells and well braced (Fig. 1), 1.9 mm long and 0.6 mm wide; posterior side of pterostigma thickened and fused with strongly thickened pterostigmal part of RA to form U-shaped structure; pterostigmal brace as oblique as pterostigma base; legs very slender and elongate; tarsi very long, 40% the length of tibiae (Fig. 3); three tarsomeres, second and third very long; abdominal segment I and II dark with a hyaline spot on each sides; segments III to V with a large basal hyaline spot and a smaller distal one on each side; segments VII and VIII dark with a narrow apical hyaline zone; ovipositor (Fig. 2B) with V3 with a protruding narrow elongate apical third, its carina with a series of 12 strong teeth in distal half, apical tooth as large as others; distal stylus elongate and protruding; apex of V2 very sharp and serrate, protruding between the two V3.

Discussion

This damselfly has all the diagnostic characters of the Burmese amber family Burmacoenagrionidae, viz. AA′ originating from AP slightly nearer to Ax2 than to Ax1; DC free, broad, with distal side MAb slightly oblique and longer than basal side; 12–19 postnodal crossveins present distal of N and basal of Pt; Pt long, distinctly braced; pterostigmal part of RA and stigmal crossveins thickened to form U-shaped structure; RP1 with weak angle below Pt-brace; IR1 originating 1–4 cells distal of base of RP2; RA and RP1 sigmoidally curved distal of Pt; numerous sigmoidally curved postnodal crossveins present distal of Pt; RA, RP1, IR1, RP2, IR2 converging near posterior wing margin; one row of cells between CuA and posterior wing margin.

Burmagrion azari **sp. nov.** and *Burmacoenagrion* have very similar legs, very long and slender with elongate tarsi. These structures are putative synapomorphies of the Burmacoenagrionidae, however the legs of the type species of *Burmagrion*, *Burmachistigma*, and *Electrocoenagrion* are unknown.

The main differences between *Burmagrion azari* **sp. nov.** and other Burmacoenagrionidae, except *Burmagrion*, are as follows: the postnodal crossveins are somewhat aligned in distal half of area but not in basal half of area, while it is the contrary in the other Burmacoenagrionidae; base of IR2 below subnodus; Pt covering only two cells instead of 3–5; only 11–14 postnodals instead of 12–21; the U-shaped structure formed by the pterostigmal part of RA and stigmal crossveins is less pronounced than in the other Burmacoenagrionidae except *Burmagrion* (Möstel *et al*., 2017). Difference with *Burmagrion marijanmatoki* are less important, viz. only two cells below pterostigma; base of RP2 only 3–4 cells distal of that of IR2 instead of six; wings larger, more than 20.0 mm long instead of *ca*. 15.0 mm long. These differences justify a separation of our fossil in a different species of *Burmagrion*.

Zheng *et al*. (2019) tentatively proposed to put Burmacoenagrionidae in the superfamily Coenagrionoidea based on wing venation.

The protruding narrow elongate apical third of the V3 of *Burmagrion azari* **sp. nov.** is similar to those of Lestidae, of some Coenagrionidae, but not to the broader V3 of Heteragrionidae (Geijskes, 1976; Matushkina, 2004: figs 3, 5; Machado, 2009; Matushkina & Labret, 2011: fig. 2; Vilela *et al*., 2019: figs 4–6). A strong apical tooth of V3 can be present or absent in different species of the same damselfly genus (Machado, 2009). The presence of strong teeth on V3 would exclude affinities with the Platycnemididae, Protoneuridae, Platystictidae, Philogeniidae (Matushkina, 2004; Vilela *et al*., 2019: fig. 6). The shape and number of these teeth greatly vary among the different genera in a same family (St. Quentin, 1962: fig. 7). *Burmacoenagrion* has teeth of V3 more minute than those of *Burmagrion azari* **sp. nov.** (Zheng *et al*., 2019: fig. 2C). Thus the visible structures of the ovipositor of *Burmagrion azari* **sp. nov.** cannot help much to clarify the phylogenetic relationships of the Burmacoenagrionidae.

The mandibles of the type of *Burmagrion azari* **sp. nov.** are well-visible. Unfortunately, there are very few works on the comparative morphology of the mandibles of adult Odonata. Nevertheless, *Burmagrion azari* **sp. nov.** has a general shape of mandible quadrate and with some setae at base of the teeth, which would rather fit with the Euzygoptera (Lestomorpha and Coenagrionomorpha) rather than in the Caloptera, after the preliminary study of Táborský (1927).

Conclusion

The ovipositor of *Burmagrion azari* **sp. nov.** had certainly an endophytic function, with the V3 used as lever arm to insert the sharp and serrate V2 in the plant cuticle (St. Quentin, 1962: fig. 6; Matushkina & Gorb, 2007). Traces of odonatan endophytic ovipositions remain unknown in the Burmese amber (Ross, 2019, 2020), but these should be found in the near future because of the high diversity and abundant record of the Burmacoenagrionidae in the Burmese amber.

Acknowledgements

We sincerely thank two anonymous referees for their remarks on the first version of the paper. This work was supported by the Second Tibetan Plateau Scientific Expedition and Research (2019QZKK0706), the Strategic Priority Research Program of the Chinese Academy of Sciences (XDB26000000 and XDB18000000), and the National Natural Science Foundation of China (41925008 and 41688103).

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