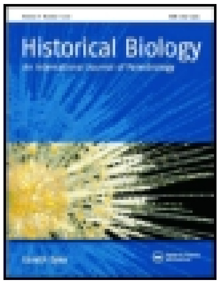

Historical Biology: An International Journal of Paleobiology
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/ghbi20

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To cite this article: Günter Bechly & George Poinar Jr (2013): Burmaphlebia reifi gen. et sp. nov., the first anisozygopteran damsel-dragonfly (Odonata: Epiophlebioptera: Burmaphlebiidae fam. nov.) from Early Cretaceous Burmese amber, Historical Biology: An International Journal of Paleobiology, DOI:10.1080/08912963.2012.753884

To link to this article: http://dx.doi.org/10.1080/08912963.2012.753884

Historical Biology
iFirst article, 2012, 1–5

Burmaphlebia reifi gen. et sp. nov., the first anisozygopteran damsel-dragonfly (Odonata: Epiophlebioptera: Burmaphlebiidae fam. nov.) from Early Cretaceous Burmese amber

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(*Received 23 October 2012; final version received 26 November 2012*)

A new family, genus and species of damselfly, *Burmaphlebia reifi* **gen.** et **sp. nov.** (Burmaphlebiidae **fam**. **nov**.), is described as the second fossil odonate from Early Cretaceous Burmese amber. Its phylogenetic position is discussed and the fossil is attributed to a new family at the base of the anisozygopteran grade, probably closely related to the Recent relict group Epiophlebiidae. It is the first record of the 'anisozygopteran' grade from amber and the smallest known representative of this group.

http://zoobank.org/6EFE7288-BD89-42F9-BFA5-804CE6B904A6

Keywords: Burmese amber; Early Cretaceous; Odonata; Anisozygoptera; fossil insect; phylogeny

Introduction

Many fossil Odonata have been described from various sedimentary deposits of Cretaceous age, including representatives of at least 16 families from the Lower Cretaceous Crato Formation in Brazil (Bechly 2007, 2010). However, only few fossil odonates are yet known from inclusions in Cretaceous amber. Three species of the primitive damselfly family Hemiphlebiidae (Lestomorpha) have been described from French, Jordan and South Dakota amber (Kaddumi 2007: 66–67, figures 53B,C; Lak et al. 2009; Nel et al. 2010), and one damselfly species of disparoneurine Platycnemididae (Coenagrionoidea) from Burma amber (Poinar et al. 2010). Dejax et al. (1996) mentioned an undescribed damselfly wing fragment from Lebanon amber, while Azar et al. (2010) recently described *Libanolestes flecki* (Lestomorpha) as the first damselfly from Lebanon amber.

This study describes the second Odonata from Burmese amber, which also represents the very first record of an anisozygopteran damsel-dragonfly from amber and the smallest representative of this grade as well as the first putative fossil relative of the Recent relict group Epiophlebiidae.

Materials and methods

The fossil is in a small piece of Burmese amber, 13 mm in length and 6 mm in width (Figure 1). The specimen has been embedded in a small block of polyester resin to protect it from oxidation and to improve visibility of the wing venation.

It was obtained from a mine first excavated in 2001, in the Hukawng Valley, south-west of Maingkhwan in Kachin State (26°20′N, 96°36′E) in Burma (Myanmar). This amber site, known as the Noije Bum 2001 Summit Site, was assigned to the Early Cretaceous, Upper Albian to Lower Cenomanian, on the basis of paleontological evidence from insect inclusions and the ammonite *Mortoniceras* (Cruickshank and Ko 2003), and recently dated by U–Pb dating of zircons (Shi et al. 2012), placing the absolute age at 98.79 ± 0.62 mya (earliest Cenomanian). Nuclear magnetic resonance spectra and the presence of araucaroid wood fibres in amber samples from the Noije Bum 2001 Summit site indicate an araucarian (possibly *Agathis*) tree source for the amber (Poinar et al. 2007).

The fossil was studied with a Leica M80 stereomicroscope and 1.6 × Plan Achromat lens. The drawing was made with a camera lucida, and subsequently scanned with a Canon CanoScan 4200F flatbed scanner and digitised with Adobe Photoshop™ CS3. Photographs were taken with a Leica DFC490 digital macro camera on a Leica Z16-Apo Macroscope and processed with Leica Application Suite 3.8.0 for focus stacking. All figures have been enhanced with Adobe Photoshop™ CS3 image processing software.

Wing venation terminology follows that of Riek and Kukalová-Peck (1984), and the phylogeny is mainly based on Bechly (1996).

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ISSN 0891-2963 print/ISSN 1029-2381 online

http://dx.doi.org/10.1080/08912963.2012.753884
http://www.tandfonline.com

Figure 1. *B. reifi* **gen.** et **sp. nov.**, holotype I-PO 9, Early Cretaceous Burmese amber. Scale: 2 mm.

Abbreviations

Ax, primary antenodal cross vein; arc, arculus; dc, discoidal cell; sn, subnodus; C, Costa; RA, Radius anterior; RP, Radius posterior; IR, Interradius; Rspl, Radial supplement; MA, Media anterior; MP, Media posterior; Mspl, Median supplement; CuA, Cubitus anterior.

Systematic paleontology

Order Odonata Fabricius, 1793
Suborder Epiophlebioptera Bechly, 1996
Superfamily Epiophlebioidea Muttkowski, 1910
Family Burmaphlebiidae **fam. nov**
Type genus: *Burmaphlebia* **gen. nov.**
Diagnosis: Same as type genus since monotypic.

New genus: *Burmaphlebia* **gen. nov.**
Type species: *Burmaphlebia reifi* **sp. nov.**
Derivation of name: Named after Burma and the Greek word phleps (gen. phlebos) for vein.
Diagnosis: Same as type species since monotypic.
New species: *B. reifi* **sp. nov.** (Figures 1–5).

Holotype: Specimen no. B-OD-1 (old no. I-PO 9) in coll. Poinar, Oregon State University.

Derivation of name: Named in honour of the late Wolf-Ernst Reif, who was influential teacher and PhD supervisor of the first author (GB).

Type horizon and locality: Burmese amber (Burmite), Lower Cretaceous, earliest Cenomanian; Noije Bum 2001 Summit Site, Hukawng Valley, south-west of Maingkhwan in Kachin State (26°20′N, 96°36′E) in Burma (Myanmar).

Diagnosis: Very small damsel-dragonfly species characterised by the following set of characters: wing length only about 13 mm (autapomorphy); secondary antenodals present in both rows (plesiomorphy); arculus (arc) only slightly distal of A×1 (autapomorphy); nodus and subnodus (sn) very oblique (autapomorphy); postnodals not aligned with subnodals (plesiomorphy); pterostigma very short (1.5 cells) (autapomorphy), but distinctly braced (plesiomorphy); discoidal cell (dc) basally closed (at least in one of the wing pairs), undivided and with acute distal angle (plesiomorphy); first branching of RP and origin of IR2 recessed midway between arculus and nodus (plesiomorphy); RP2 originates two cells distal of nodus (autapomorphy); lestine oblique vein absent (autapomorphy); IR1 long and straight (plesiomorphy); shorter convex intercalary vein between IR1 and RP2; a longer concave and a shorter convex intercalary vein in the distal expanded area between IR2 and RP3/4; cubito-anal field not expanded and with a single row of cells (autapomorphy); wing slender and wing base only briefly stalked.

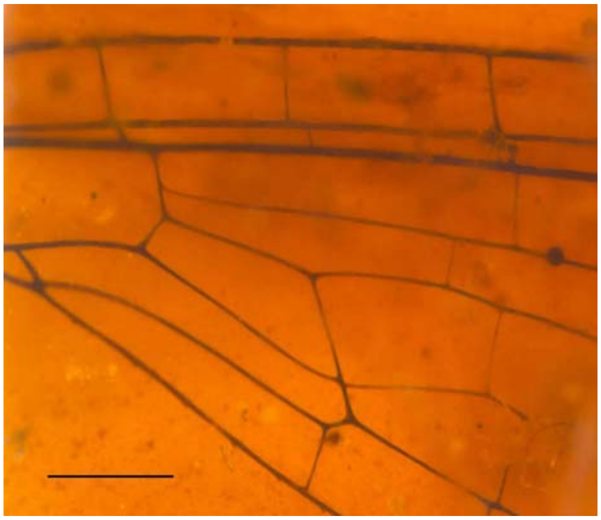

Figure 2. *B. reifi* **gen.** et **sp. nov.**, holotype I-PO 9, Early Cretaceous Burmese amber, wing base. Scale: 0.5 mm.

Description

A nearly complete isolated wing of a fossil damsel-dragonfly, most probably a forewing (Figure 5). Only wing base and apex are missing. Wing hyaline except for

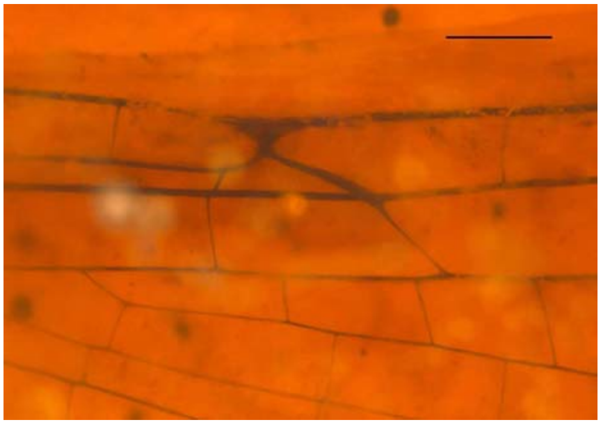

Figure 3. *B. reifi* **gen.** et **sp. nov.**, holotype I-PO 9, Early Cretaceous Burmese amber, nodus. Scale: 0.5 mm.

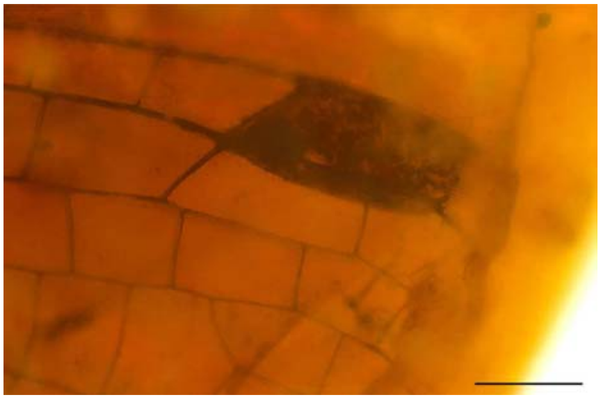

Figure 4. *B. reifi* **gen.** et **sp. nov.**, holotype I-PO 9, Early Cretaceous Burmese amber, pterostigma. Scale: 0.5 mm.

pterostigma. Preserved part of wing 12.4 mm long, estimated complete length about 13.5 mm; maximum width 3.5 mm. Nodus closer to wing base than to apex with very oblique nodal veinlet and oblique subnodus (Figure 3). Two primary antenodal cross veins A×1 and A×2 with a single non-aligned secondary antenodal in-between (Figure 2); two secondary antenodals between A×2 and nodus in the first row and a single one in the second row. Three antesubnodal cross veins between arculus and subnodus. Eight postnodals and six postsubnodals non-aligned. Pterostigma short and broad (1.1 mm long, 0.6 mm wide), covering 1.5 cells, and strongly braced (Figure 4). Discoidal cell basally closed, free (not divided by cross veins), small, quandrangular with acute distal angle (Figure 2). Subdiscoidal cell elongate, narrow and free (Figure 2). Arculus angulate and very close to A×1 (Figure 2); sectors of arculus (RP and MA) separated at origin. Only a single antefurcal cross vein basal of midfork. Midfork (first branching of RP) recessed midway between discoidal cell and nodus. Origin of IR2 one cell distal of RP3/4 and two cells basal of subnodus. Origin of RP2 two cells distal of subnodus. No lestine oblique vein between RP2 and IR2. No Rspl. IR1 distinct, long and parallel to RP1; short convex intercalary vein between IR1 and RP2. Space between IR2 and RP3/4 distally widened with two intercalary veins in-between (a longer concave one and a shorter convex one). Postdiscoidal space between MA and media posterior (MP) narrow with a single row of cells in-between, except near wing margin where it is divided by a short concave intercalary Mspl? parallel to MA. Cubito-anal area narrow, with a single row of cells and without posterior branches of CuA.

Considering the identification as ‘anisozygopteran’ and the putative affinity to Epiophlebiidae, the narrow shape of the fossil wing with a single row of cells in the cubito-anal area suggests that it is a forewing. The sex cannot be determined. The point of fusion of the hind margin with CuA and MP basal of A×1 indicates that the wing base was only briefly stalked.

Discussion

Phylogenetic relationship

The very small size of this new taxon (less than half the wing length of *Epiophlebia*) implies several reductions in the wing venation that make it somewhat more difficult to distinguish between a small zygopteran and a miniaturised anisozygopteran odonate. The presence of a basally closed discoidal cell at least in one of the wing pairs, but most probably in both (because it seems to be a forewing and all odonates with a closed cell in the forewing also have a closed hind wing discoidal cell), clearly shows that this damselfly-like insect belongs to the crown group of modern Odonata.

The recessed arculus that is situated close to A×1 is a derived character of Epiprocta (‘Anisozygoptera’ + Anisoptera), which is absent in all stem group Odonata, and all Zygoptera (Bechly 1996), except as convergence in the two highly derived calopterygoid families Epallagidae

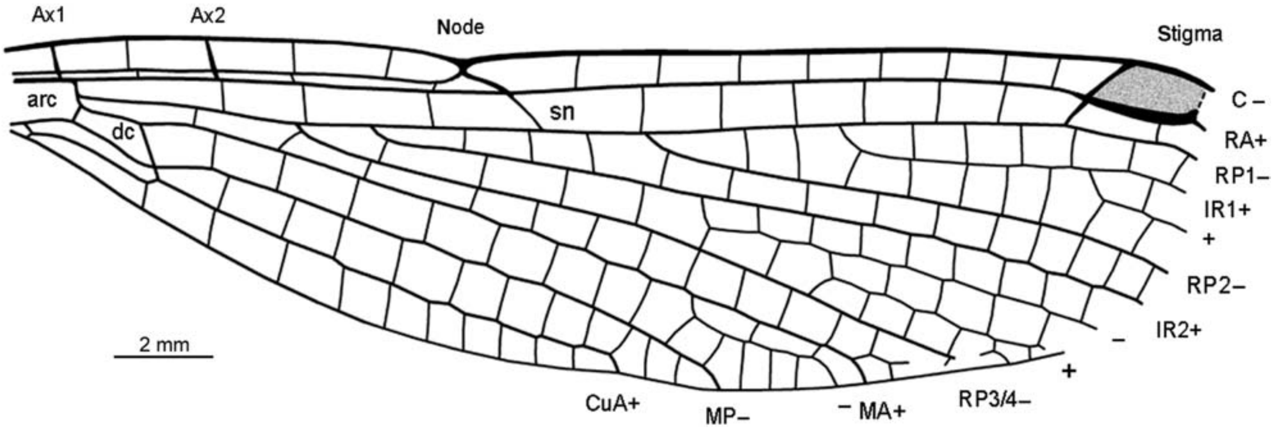

Figure 5. *B. reifi* **gen.** et **sp. nov.**, holotype I-PO 9, Early Cretaceous Burmese amber, drawing of wing venation. Scale: 2.0 mm.

(= Euphaeidae) and Heliocharitidae (= Dicteriadidae), which clearly have no affinities with this fossil.

The recession of the midfork (first branching of RP) midway between arculus and nodus is a further putative synapomorphy with Epiprocta, which is present as convergence in some Zygoptera like Caloptera, Lestinoidea and Hypolestinae (Bechly 1996). The plesiomorphic presence of a pterostigmal brace vein excludes a position in crown group Caloptera. The presence of secondary antenodals, antesubnodals and antefurcal cross veins excludes a position in Lestinoidea and Hypolestinae.

The absence of a division of the discoidal cell into hypertriangle and triangle demonstrates that the new taxon cannot belong to Trigonoptera (Stenophlebioptera + Pananisoptera). It also lacks the autapomorphies and diagnostic features of the more basal Heterophlebioptera and Isophlebioptera. The structure of the nodus, with distinctly oblique nodal and subnodal veinlets, excludes a position in Sieblosiidae. The position of nodus and midfork, as well as the shape of the discoidal cell and pterostigma, excludes a relationship with Frenguellidae. This only leaves Epiophlebiidae as putative relative among the basal groups of Epiprocta.

The reduced nodal furrow corresponds to the character state in Zygoptera and Epiophlebiidae. The new taxon also shares with Epiophlebiidae the IR1 that is closely parallel to RP1. This could be considered as weak evidence in favour of a sister group relationship with Epiophlebiidae, even though none of the other diagnostic autapomorphies of Epiophlebiidae are visible in this fossil. All other fossil dragonflies that had been previously considered as members or relatives of Epiophlebiidae (see Nel et al. 1993), such as *Mesoepiophlebia veronicae* Nel and Henrotay, 1993 and *Ensphingophlebia undulata* Bode, 1993, have been shown to be isophlebioid Sphenophlebiidae rather than Epiophlebiidae by Bechly (1997).

Consequently, the new taxon does not share any significant synapomorphies with any of the known families of the anisozygopteran grade, but it has several distinct autapomorphies listed in the diagnosis above. Because the differences in primitive and derived characters of the new taxon to any known family of fossil or Recent odonates are as large as the differences between the known families, the erection of a new family is well justified, and in fact required as obligatory rank by the international rules of zoological nomenclature.

For a taxonomic name for the putative subordinal clade formed by Epiophlebiidae and Burmaphlebiidae, there are two possibilities: either the name Epiophlebioptera Bechly, 1996 could be used, which would be analogous to the fossil 'anisozygopterous' suborders Isophlebioptera, Heterophlebioptera and Stenophlebioptera, or the old name Anisozygoptera could be redefined in a phylogenetic way as the clade that includes all odonates that are closely related to Epiophlebiidae than to either Zygoptera or Anisoptera. However, the latter option would be a strong renunciation from the traditional usage of the name 'Anisozygoptera' for a paraphyletic grade of fossil stem group Anisoptera and Epiophlebiidae. Therefore, we here prefer to use Epiophlebioptera and to reject the paraphyletic taxon 'Anisozygoptera', but we are open to any other solutions that may be favoured by a consensus of the odonatological community (Dijkstra et al. in press).

Paleobiogeography and paleoecology

The Recent relict genus *Epiophlebia* (Epiophlebiidae) is restricted to cold mountain forest streams and occurs in four species in Japan (*E. superstes*), Nepal, India and Bhutan (*E. laidlawi*), northern China (*E. sinensis*) and southern China (*E. diana*) (Carle 2012). A minimum age of Epiophlebiidae lineage can be estimated as Lower Jurassic based on the oldest fossil record of its sister group (Anisoptera and their stem group representatives like Heterophlebioptera from the Liassic of Europe; Nel et al. 1993; Carle 2012). Thus, the occurrence of a possible sister group of Epiophlebiidae in the Mesozoic of Burma is not to be considered as a big surprise. The absence or rarity of fossils of epiophlebiid relationship could be explained with the adaptation to a highland stream habitat (Carle 2012) that makes fossilisation very unlikely.

Acknowledgements

We are most grateful to Karin Wolf-Schwenninger (SMNS, Stuttgart) for the preparation of the holotype specimen and help with the macro photos. We thank two anonymous reviewers for helpful comments that improved the manuscript.

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