The first amber stenophlebiid damsel-dragonfly (Odonata, Epiproctophora, Stenophlebiidae) from mid-Cretaceous amber of northern Myanmar

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ABSTRACT

Burmastenophlebia flecki gen. et sp. nov., first stenophlebiid damsel-dragonfly in mid-Cretaceous Burmese amber is described and illustrated. It allows to show structures proper to this family, previously unknown. In particular, the subnodus is enforced by a dorsal chitinous bracket and the nodal furrow is very weak, suggesting that the stenophlebiid nodal complex is very particular and did not functioned as in other Odonata.

Keywords: Insecta; Odonata; Stenophlebiidae; Burmese amber; gen. et sp. nov.

1. Introduction

Burmese amber is currently the most important source of knowledge on the insects from the mid-Cretaceous. It is especially the case for the Odonata (for a catalogue of described inclusions in this amber see Ross, 2018). The Zygoptera clearly dominate this assemblage, probably in part because of their smaller sizes and lower capacities to escape the fresh resin than the larger and stronger Anisoptera. Few more 'basal' Epiproctophora (former 'Anisozygoptera' or damsel-dragonflies are also recorded, viz. the Epiophlebioidea Burmaphlebiidae (Bechly and Poinar, 2013). The discovery of any new taxon of this clade in this amber is of interest because they can give new characters not observable in the numerous Mesozoic Epiproctophora preserved as compression fossils. Among these, the Stenophlebioptera are especially important because they are currently considered as the sister group of the Pananisoptera (Bechly, 2016), but up to now no fossil stenophlebioid in amber has been recorded. This clade is strictly Mesozoic but it was clearly widespread in the Jurassic of Europe and Asia, and the Lower Cretaceous of Europe, Asia, and Brazil. Here we describe the first Stenophlebiidae from the mid-Cretaceous Burmese amber. Although incomplete, the fossil shows some wing structures that were unknown.

2. Material and methods

The amber containing the damselfly was collected in the Hukawng Valley (26° 29' N, 96'° 35' E) of Kachin Province, Myanmar (locality in Kania et al., 2015: fig. 1). The re-deposition age of Burmese amber was considered to be 98.79 ± 0.62 Ma (Shi et al., 2012), but palynology and an ammonite from the amber-bearing layers suggest a late Albian age (Cruickshank and Ko, 2003) which we adopt herein. The amber containing the damselfly is yellow and transparent. The individual shows a nearly complete fore wing (basal section missing) and fragments of a hind wing, of thorax, a complete fore leg, a nearly complete middle leg, and two incomplete hind legs. Photographs were taken using a Zeiss Discovery V20 microscope system. Photomicrographs with a green or red backgrounds were taken using fluorescence as a light source attached to the Zeiss Axio Imager 2 light microscope. Six small neuropterans, two beetles, one dipteran, one psocopteran wing, and one spider co-occurred with this damsel-dragonfly. The specimen is housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, China. All taxonomic acts established in the present work have been registered in Zoo-Bank (see below), together with the electronic publication LSID: xxxx We follow the wing venation nomenclature of Riek and Kukalová-Peck (1984), amended by Nel et al. (1993) and Bechly (1996). The higher classification of fossil and extant Odonatoptera, as well as familial and generic characters followed in the present work are based on the phylogenetic system proposed by Bechly (1996, 2016) and Fleck et al. (2003) for the revision of the Stenophlebioptera. Abbreviations for wing venation are as follow: IR = intercalary radial vein; MA = media anterior; MP = media posterior; N = nodus; Cr = nodal crossing; Pt = pterostigma; RP = radius posterior; ScP = subcostal posterior; Sn = subnodus.

3. Systematic Palaeontology

Order Odonata Fabricius, 1793

Infrasuperorder Stenophlebioptera Bechly, 1996

Superfamily Stenophlebioidea Pritykina, 1968

Family Stenophlebiidae Needham, 1903

Genus *Burmastenophlebia* gen. nov.

(urn:lsid:zoobank.org:act:E656B6E7-3F01-46E5-9165-64A0DB80BC08)

Type species: *Burmastenophlebia flecki* sp. nov.

Etymology. Named after Burma, ancient name for Myanmar, and *Stenophlebia*.

Diagnosis. Wing venation characters only. No secondary longitudinal vein just basal of base of RP2, between RP1/2 and IR2; pterostigma covering two cells and a half, nodal Cr receiving one postnodal crossvein and one antenodal crossvein, subnodus receiving no antesubnodal crossveins; IR1 basally quite straight; three antenodal crossveins of first row between nodus and level of base of RP3/4; a straight Mspl; a straight supplementary longitudinal vein of postdiscoidal space.

***Burmastenophlebia flecki* sp. nov.**

(urn:lsid:zoobank.org:act:128A9528-0465-45BE-8E94-6AA989E5CFE3)

Fig. 1

Diagnosis. Ratio length/width of pterostigma = 5; wing 5.7 mm wide, rather small. *Burmastenophlebia flecki* is among the smallest Stenophlebiidae, its wing dimensions being comparable to those of *Gallostenophlebia incompleta* Nel et al., 2015.

Etymology. Named after Dr. Günther Fleck, for his numerous contributions to Odonatology.

Holotype. NIGP168834, Nanjing Institute of Geology and Paleontology, Chinese Academy of Sciences, China.

Locality and Horizon. Hukawng Valley, Kachin Province, Myanmar; late Albian, late Lower Cretaceous.

Description. Four legs (two hind legs are incomplete), a fragment of the base of the abdomen and posterior part of thorax and two incomplete wings with base missing; three pair of legs very similar in shape and size; fore coxae rather small, trochanter thin, femora (3.0 mm long) slightly longer than tibia, almost straight, slightly protruding at median section, armed with two series of moderately long, asymmetric ventral spines, spines of one side obviously larger than those of the other side, sizes of spines increasing from basal section to middle and posterior sections, several long spines alternatively arranged with short spines in distal third; tibia (2.9 mm long) armed with two series of spines, nearly symmetrical, spines of median section larger than basal and distal spines, long spines and short spines alternatively arranged in one side only; tarsi (0.7 mm long) three-segmented, armed with two series of spines, each tarsomere armed with two spines in one side, the basal one distinctly smaller than distal one, first tarsomere short and oblique apically, third tarsomere longer than second one; tarsal claws moderately large, curved and sharp, with a tiny tooth near apex; middle femora (4.0 mm long) distinctly longer than tibia, clearly protruding at median section, long and short ventral spines alternatively arranged in basal section, long spines rather sparse in middle and distal sections, characters of tibia and tarsi similar to those of fore legs, middle tibia (2.7 mm long) slightly shorter than fore tibia, middle tarsi 0.7 mm long; hind femora (5.0 mm long) nearly straight, distinct longer than middle femora, two series of spines nearly symmetrical, long and short ventral spines alternatively arranged, longest spines in middle section, rather sparse in distal section; the basal two abdominal segments are preserved, no trace of secondary genital structures on segment 2; length of preserved part of wing 22.6 mm; wing ca. 30-33 mm long, width 5.7 mm; pterostigma 2.5 mm long, 0.5 mm wide; covering two cells and a half; pterostigmal ornamentation apparently wrinkled-like (sensu Bechly, 1996); basal side of pterostigma with a crossvein ending in it, and much more oblique than distal side; no pterostigmal brace; a vein Mspl and a long secondary longitudinal convex vein in postdiscoidal area beginning near or on MAb; vein ScP clearly fused with costal margin; nodal furrow very weak; nearly no interruption of costal margin; vein Cr very oblique and directly aligned with general trend of ScP; one postnodal crossvein and one antenodal crossvein of second row reaching Cr; subnodus (Sn) very oblique and aligned with Cr, with no crossvein reaching it; base of RP2 slightly distal to Sn; no secondary longitudinal 'stenophlebiid veinlet' between RP1+2 and IR2 below subnodus; antenodal area only partly preserved; primary antenodal cross-vein Ax1 and Ax2 not preserved, 10 secondaries between C and ScP not aligned with the 10 preserved antenodal crossveins of second row between ScP and RA; 20 postnodal crossveins, not aligned with the 15 postsubnodals; bases of RP3/4 and IR2 close together, between nodus and arculus, probably closer to nodus (only three cells basal to nodus) than to arculus; a very long and narrow bridge space; oblique vein "O" absent; IR1 well defined, straight and proximally parallel to RA; numerous secondary longitudinal veins between the main veins; all longitudinal veins curved near posterior wing margin; veins with fine and short spines.

4. Discussion

This fossil is attributable to the Stenophlebiidae because of the following synapomorphies (Fleck et al., 2003): IR2 and RP3/4 arising close together; a very long and narrow bridge space; a long and not zigzagged (or slightly zigzagged) secondary longitudinal convex vein in postdiscoidal area, parallel to MP, its base being close to discoidal triangle; a long and not zigzagged concave Mspl; wings elongate and slender; nodal veinlet extremely oblique and very long; nodal furrow reduced; numerous intercalary veins with a characteristic pattern between MA and MP (described in Fleck et al., 2003); presence of numerous antenodal crossveins distal of Ax2.

The Stenophlebioptera Bechly, 1996 comprise some other families: affinities with the Liassostenophlebiidae Fleck et al., 2003 are excluded because of the absence of the oblique vein 'O', the long pterostigma, the long and straight IR1, and the long convex secondary longitudinal vein in postdiscoidal area. The presence of numerous secondary antenodal crossveins of first row distal of Ax2, the long nodal Cr and subnodus exclude affinities with the Prostenophlebiidae Fleck et al., 2003. Bechly (1996, 2016) included the Gondwanogomphidae Bechly, 1996 in the Stenophlebioptera, but Fleck et al. (2003) discussed this hypothesis and considered it as weakly supported. *Burmastenophlebia* gen. nov. is definitely not related to *Gondwanogomphus* Schlüter and Hartung, 1982.

Among the Stenophlebiidae, *Burmastenophlebia* differs from *Yixianstenophlebia* Nel and Huang, 2015, *Stenophlebia* Hagen, 1866, *Hispanostenophlebia* Fleck et al., 2003, *Sinostenophlebia* Hong, 1984, and *Gallostenophlebia* Nel et al., 2015 in the absence of a secondary longitudinal vein just basal of base of RP2, between RP1/2 and IR2 (Fleck et al., 2003; Bechly et al., 2003; Nel et al., 2015; Nel and Huang, 2015; Zheng et al., 2016a,b).

Cretastenophlebia Fleck et al., 2003 and *Mesostenophlebia* Fleck et al., 2003 also lack this secondary longitudinal vein. The pterostigmata of *Cratostenophlebia* and *Cretastenophlebia* cover much more cells than in *Burmastenophlebia*, their nodal Cr receive several antenodal and postnodal crossveins, their subnodus receive two antesubnodal crossveins, and the IR1 of *Cretastenophlebia* is basally zigzagged instead of being quite straight in *Burmastenophlebia* (Fleck et al., 2003; Bechly, 2007; Zheng et al., 2018). *Mesostenophlebia* has 11 antenodal crossveins of first row between the nodus and the level of the base of RP3/4, instead of only three in *Burmastenophlebia* (Fleck et al., 2003). *Burmastenophlebia* is difficult to compare to *Liaostenophlebia* Zheng et al., 2016 because there are very few comparable preserved parts (*Burmastenophlebia* is known by distal wing structures, while *Liaostenophlebia* is known by basal structures). Nevertheless, *Burmastenophlebia* has straight Mspl and supplementary longitudinal vein of postdiscoidal space while these veins are slightly zigzagged in *Liaostenophlebia* (Zheng et al., 2016a).

5. Concluding remarks

This fossil is the first amber record of the clade Stenophlebioptera. Thus it is of interest for some morphological structures not discernable in compression fossils. In particular, the subnodus of *Burmastenophlebia* is enforced by a dorsal chitinous bracket and the nodal furrow is very weak, suggesting that the stenophlebiid nodal complex is very particular and did not functioned as in other Odonata. Possibly the nodus of *Burmastenophlebia* could not be bent as in modern Libellulidae (Fauziyah et al., 2014), and the nodal Cr and subnodus had a more important function in the strengthening of the whole nodal complex than in other Odonata.

Burmastenophlebia has long ‘L spines’ on the main veins and crossveins in dorsal view but no ‘S spine’ is visible on the veins. The spines of the costal edge are looking like those of an Anisoptera Petaluridae, viz. long scale-like structures separated by indentations of the margin (see Bechly, 1996: 303, fig. 54). This character would support the current attribution of the Stenophlebioptera as sister-group of the Pananisoptera (Bechly, 2016).

The Stenophlebiidae were clearly widespread during the Lower Cretaceous, as they have been found in Brazil, Europe, and Central Asia. The region of Myanmar was probably an island during the mid-Cretaceous, period of deposition of the Burmese amber (Rasnitsyn and Öhm-Kühnle, 2018). This island separated from the Gondwana during the Lower Cretaceous. This is congruent with the presence of the Stenophlebiidae in the central part of Gondwana (Brazil) during the Aptian. The Stenophlebiidae were probably present also in Africa at that time but they remain to be found. The whole clade was no longer recorded after the Cenomanian.

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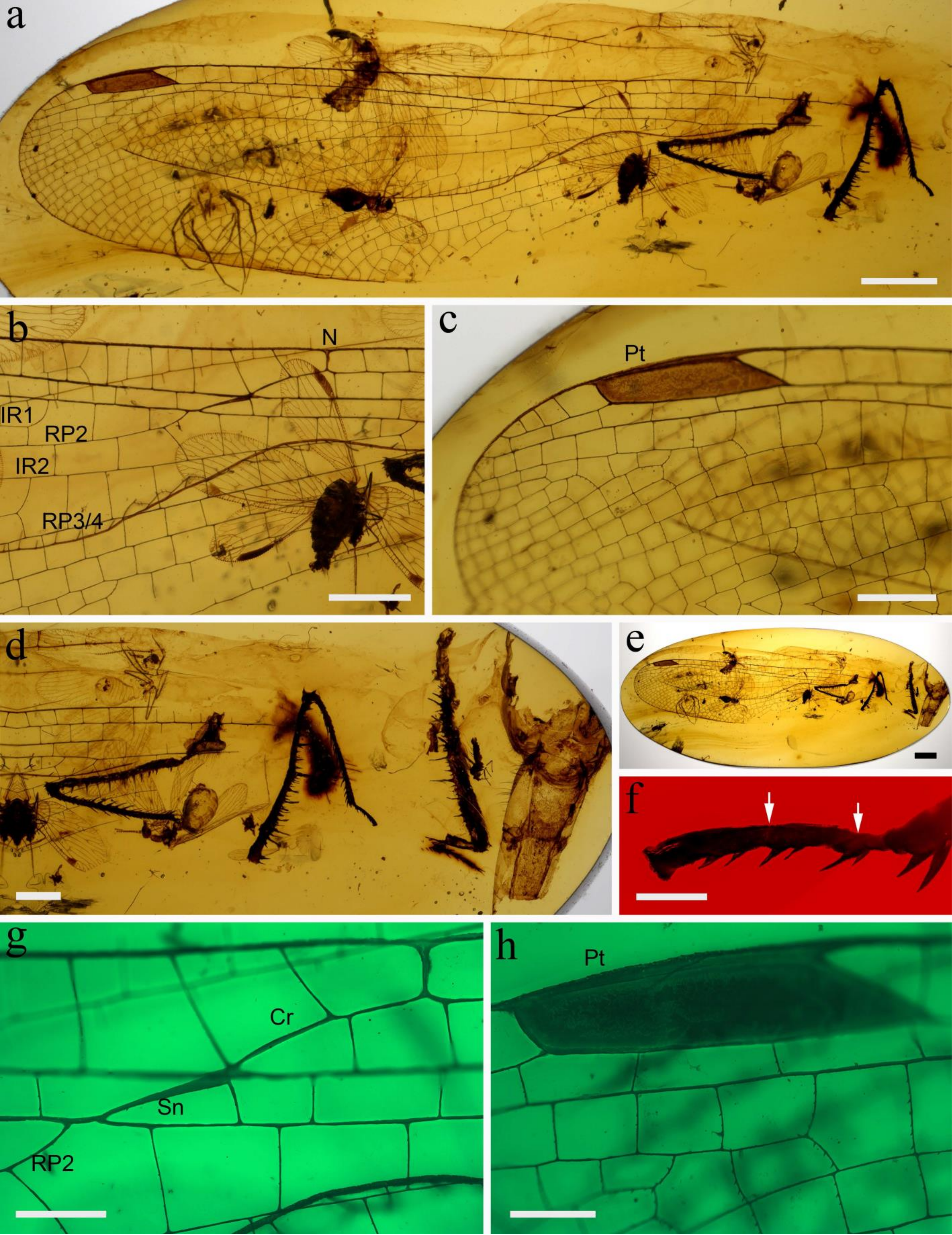
Fig. 1. *Burmastenophlebia flecki* gen. et sp. nov. Holotype NIGP168834. a, general view of wing; b, mid part of wing; c, pterostigmal region; d, wing base, legs and body fragments; e, general view of amber piece, f, middle tarsi with arrow indicating the joints under fluorescence light; g, detail of nodus under fluorescence light; h, pterostigma under fluorescence light. Scale bars = 2.0 mm (a, e), 1 mm (b, c, d), 0.5 mm (g, h), 0.2 mm (f).



a
b
N
IR1
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IR2
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