

First record of Odonata and a new subfamily of damselflies from Early Cretaceous Burmese amber

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Abstract

A new subfamily, genus and species of damselfly, *Palaeodisparoneura burmanica* n. gen., n. sp. (Platycnemididae; Palaeodisparoneurinae n. subfam.) is described as the first fossil odonate from Early Cretaceous Burmese amber. This fossil taxon is tentatively considered as sistergroup of Recent Disparoneurinae. The remains of a lizard in the same piece of amber suggest that the damselfly may have been targeted as prey.

Key words: Burmese amber, Early Cretaceous, fossil damselfly, Odonata, Zygoptera, Platycnemididae, Protoneturidae, Disparoneurinae.

Zusammenfassung

Eine neue Unterfamilie, Gattung und Art von Kleinlibellen, *Palaeodisparoneura burmanica* n. gen., n. sp. (Platycnemididae; Palaeodisparoneurinae n. subfam.), wird als erster Fund einer fossilen Libelle aus dem frühkretazischen Burma-Bernstein beschrieben. Dieses fossile Taxon wird vorläufig als Schwestergruppe der rezenten Disparoneurinae angesehen. Die Überreste einer Eidechse im selben Bernsteinstück legen nahe, dass die Kleinlibelle deren Beutetier gewesen sein könnte.

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1. Introduction

Dragonflies are well represented in Tertiary amber deposits, with about 50 specimens known (BECHLY 1993, 1996, 1998a, 1998b, 2000; BECHLY & WICHARD 2008), however descriptions in Cretaceous amber are limited to two species of Hemiphlebiidae in French and Jordanian amber (KADDUMI 2007: 66–67, figs. 53B–C; LAK et al. 2009). DEJAX et al. (1996) mention an undescribed damselfly wing fragment from Lebanon amber. Numerous Odonata have been described from sedimentary deposits of this age, including representatives of at least 16 families from the Lower Cretaceous Santana Formation in Brazil (BECHLY 1996, 2007, 2010), as well as numerous taxa from Lower Cretaceous deposits in England (JARZEMBOWSKI et al. 1998), France (NEL et al. 2008) and China (Liaoning). The present study describes the first Odonata from Burmese amber in a new subfamily Palaeodisparoneurinae.

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2. Material and methods

The fossil is in an oval piece of Burmese amber 33 mm in length and 22 mm in width. The specimen was obtained from a mine first excavated in 2001, in the Hukawng Valley, southwest of Maingkhwan in Kachin State (26°20'N, 96°36'E) in Burma (Myanmar). This amber site, known as the Noiye Bum 2001 Summit Site, was assigned to the Early Cretaceous, Upper Albian, on the basis of palaeontological evidence (CRUICKSHANK & KO 2003), placing the age at 97 to 110 mya. Nuclear magnetic resonance (NMR) spectra and the presence of araucaroid wood fibers in amber samples from the Noiye Bum 2001 Summit Site indicate an araucarian (possibly *Agathis*) tree source for the amber (POINAR et al. 2007).

Observations, drawings, and photographs were made with a Nikon SMZ-10 R stereoscopic microscope and Nikon Optiphot compound microscope with magnifications up to 600X. Wing venation terminology follows that of RIEK & KUKALOVÁ-PECK (1984).

3. Systematic palaeontology

Order Odonata FABRICIUS, 1793

Suborder Zygoptera SELYS, 1854

Family Platycnemididae JACOBSON & BIANCHI, 1905

Subfamily Palaeodisparoneurinae n. subfam.

Typus familiaris: *Palaeodisparoneura* n. gen.

Diagnosis. – Same as type genus since monotypic.

Genus *Palaeodisparoneura* n. gen.

Typus generis: *Palaeodisparoneura burmanica* n. sp.

Derivatio nominis: Named after the greek word παλαιός for “old” and after the related Recent damselfly genus *Disparoneura*.

Diagnosis. – Same as type species since monotypic.

Palaeodisparoneura burmanica n. sp.

Figs. 1–6

Holotype: Male specimen no. E17 in coll. BUCKLEY, Oregon State University.

Derivatio nominis: Named after Burma, the country of origin.

Stratum typicum: Burmese amber, Early Cretaceous, Upper Albian.

Locus typicus: Noiye Bum 2001 Summit Site, Hukawng Valley, southwest of Maingkhwan in Kachin State (26°20'N, 96°36'E) in Burma (Myanmar).

Diagnosis. – Small damselfly species characterized by greatly shortened veins MP (only one cell long) and CuA (only an oblique crossvein) (synapomorphy with *Disparoneurinae*, but autapomorphic in extent); rectangular discoidal cell (synapomorphy with *Caconeurinae* and *Disparoneurinae*); well-developed sub-rectangular subdiscoidal cell not fused to wing margin (plesiomorphy); rela-

tively basal position of origin of midfork halfway between arculus and subnodus (autapomorphy); aligned postnodal and postsubnodal crossveins (synapomorphy with *Coenagrionoidea*); rectangular (autapomorphy) and distinctly braced (plesiomorphy) pterostigma; RP1 strongly kinked at stigmal brace (synapomorphy with *Coenagrionoidea*, but autapomorphic in extent); very short intercalary vein IR1 originating beneath pterostigma (autapomorphy); male terminalia short (synapomorphy with *Caconeurinae* and esp. *Disparoneurinae*).

Description (Figs. 1–6). – A male fossil damselfly, dark brown in color. Most of the specimen is preserved, including all four wings. However, the head is missing and only four legs are present, one of which is detached. Body length about 17 mm. Wings hyaline except for pterostigmata; forewing (right) 11.5 mm long, with only distal 7.2 mm clearly visible; venation similar to that of hind wing; right hind wing 11.6 mm long, with only distal 6.9 mm clearly visible; left hind wing entirely visible (Fig. 2), 12 mm long. Only two primary antenodal crossveins Ax1 and Ax2; Ax2 aligned with arculus; nodus in basal position; subnodus aligned with origin of IR2; postnodal and postsubnodal crossveins aligned; pterostigma rectangular, only a single cell long, and strongly braced; RP1 strongly kinked at stigmal brace; IR1 very short (only 5 cells long), originating beneath pterostigma; discoidal cell rectangular; subdiscoidal cell well developed, subrectangular, not fused to wing margin; midfork (anterior sector of arculus RP forking into RP1/2 and RP3/4) about midway between arculus to subnodus; MP extremely short, only a single cell long; CuA reduced to an oblique crossvein. Foreleg complete; femur narrow, swollen at distal end, 3.6 mm in length; tibia narrow, bearing inner spines on distal portion; tibial length 3.3 mm; tarsus short, 5-segmented, 0.83 mm long; middle leg with straight setae at base of femur, length of femur 3.5 mm; tibia long and narrow, with spines on inner distal surface, length of tibia 3.7 mm; tarsus bearing double claws (Fig. 5). Abdomen complete, terminalia short and not forcipate, with moderate-sized superior appendages (cerci) and relatively small inferior appendages (paraprocts) (Fig. 6). The absence of an ovipositor at the sternites of segments 8 and 9 clearly shows that this is a male specimen.

Systematic position. – The aligned postnodal and postsubnodal crossveins, the absence of intercalary veins (except IR1 and IR2), and the kink of RP1 at the stigmal brace suggest that this fossil belongs to the coenagrionid clade that includes the families *Isostictidae*, “*Protoneuridae*”, *Platycnemididae*, *Coenagrionidae*, and *Pseudostigmatidae* (Fig. 7).

The fossil is tentatively placed in the family *Platycnemididae* as the putative sister group to the Recent subfamily *Disparoneurinae*, that was previously classified as a subfamily of “*Protoneuridae*”, but had to be transferred



Fig. 1. *Palaeodisparoneura burmanica* n. gen., n. sp., holotype E17, Early Cretaceous Burmese amber. – Scale: 2 mm.

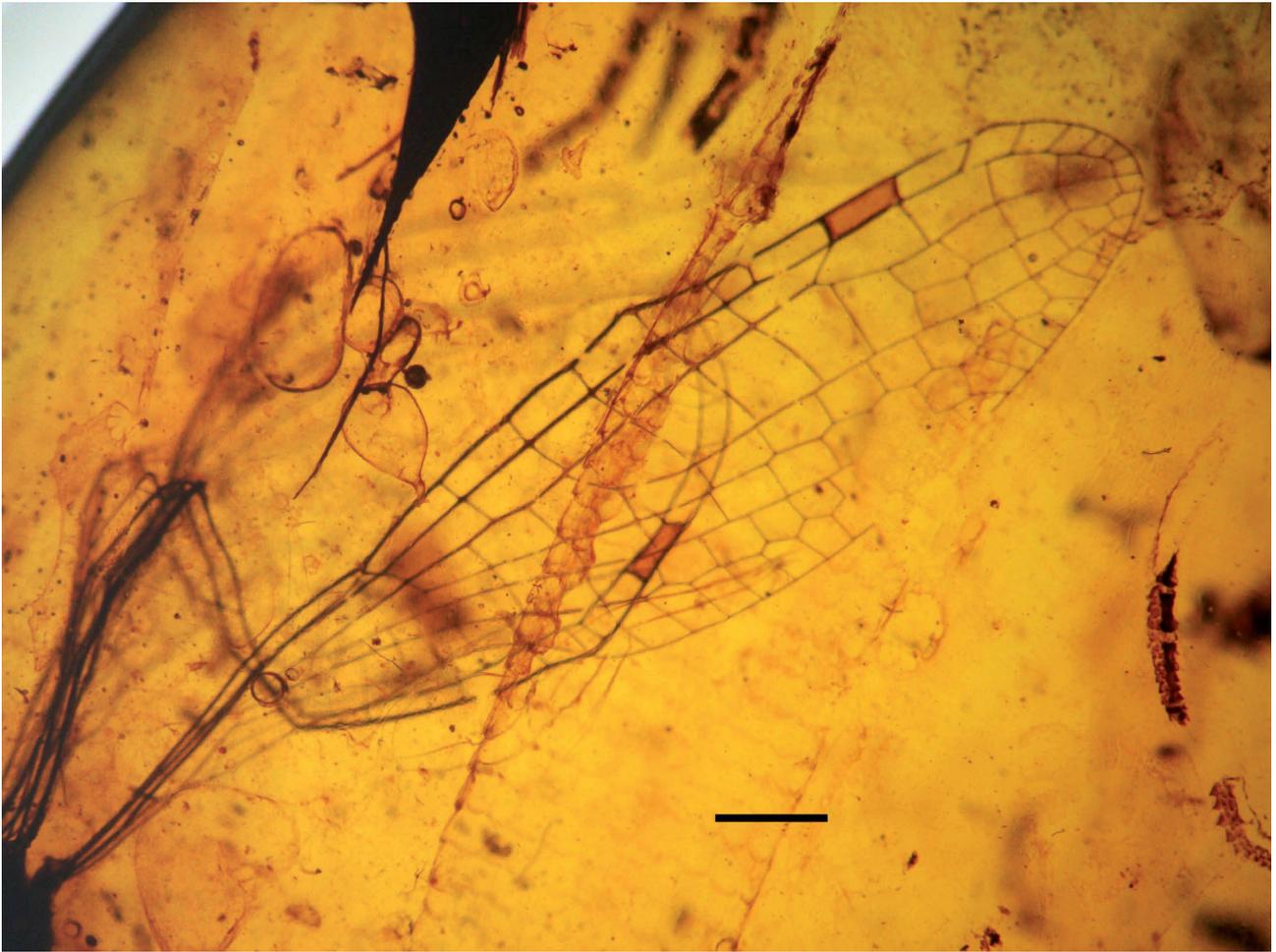


Fig. 2. *Palaeodisparoneura burmanica* n. gen., n. sp., holotype E17, hind wing; Early Cretaceous Burmese amber. – Scale: 1 mm.

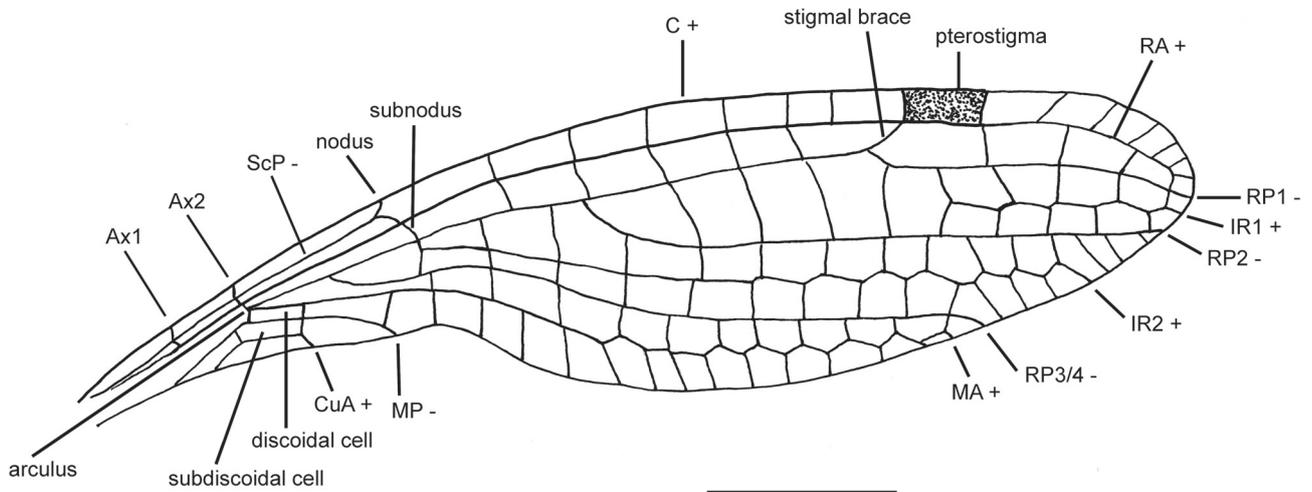


Fig. 3. *Palaeodisparoneura burmanica* n. gen., n. sp., holotype E17, drawing of hind wing venation; Early Cretaceous Burmese amber. – Scale: 2 mm.

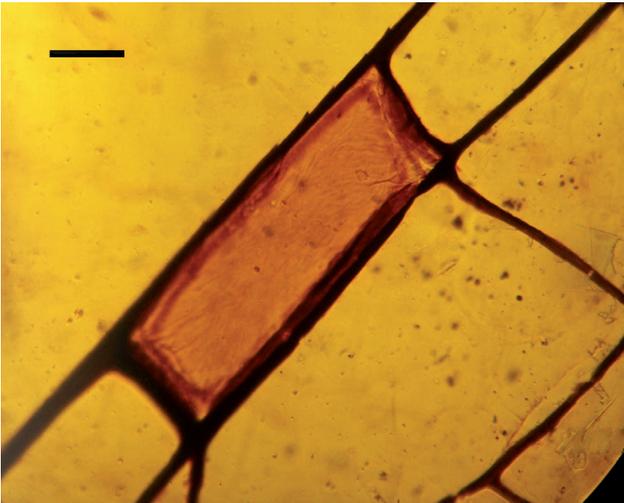


Fig. 4. *Palaeodisparoneura burmanica* n. gen., n. sp., holotype E17, detail of pterostigma; Early Cretaceous Burmese amber. – Scale: 0.25 mm.



Fig. 5. *Palaeodisparoneura burmanica* n. gen., n. sp., holotype E17, terminal mesotarsum and claws; Early Cretaceous Burmese amber. – Scale: 0.2 mm.

from the Protoneuridae to the Platyncnemididae based on cladistic and phylogenomic studies (REHN 2003; BYBEE et al. 2008; CARLE et al. 2008; DUMONT et al. 2005) that demonstrated the polyphyly of the traditional “Protoneuridae”. The Protoneuridae was downsized to the subfamily Protoneurinae and is now restricted to Neotropical genera (former monophyletic subfamily Protoneurinae of Protoneuridae) within the family Coenagrionidae. Within Platyncnemididae the former Old World “protoneurid” subfamilies Caconeurinae and Disparoneurinae constitute a subclade (REHN 2003) that is characterized by a derived

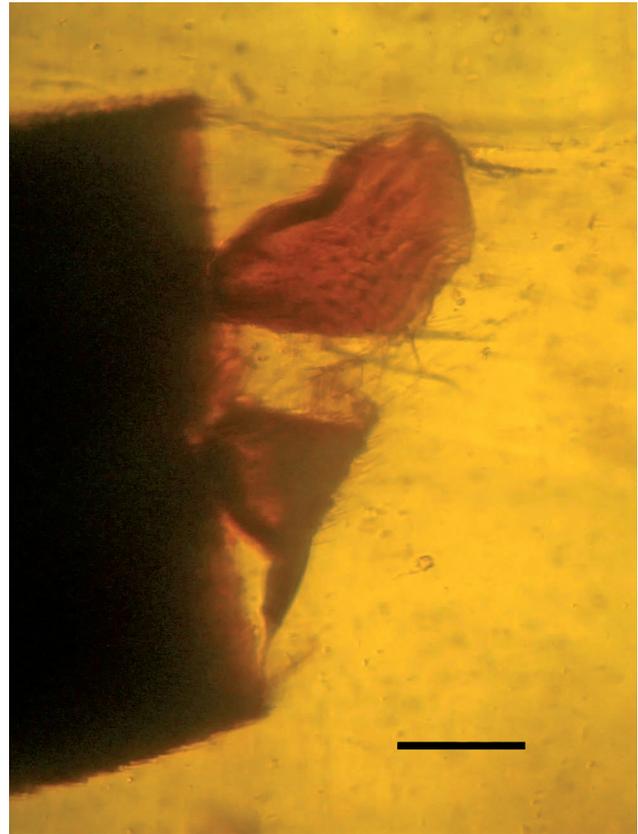


Fig. 6. *Palaeodisparoneura burmanica* n. gen., n. sp., holotype E17, male terminalia; Early Cretaceous Burmese amber. – Scale: 0.2 mm.

protoneurid-like wing venation that was convergently developed to Protoneurinae and Isostictidae.

Palaeodisparoneura n. gen. clusters with groups that have strongly shortened veins MP and CuA and a rectangular discoidal cell (viz. Protoneurinae, Eoprotoneurinae, Caconeurinae, Disparoneurinae, Isostictidae, Platystictidae, and Lestoideidae).

Protoneurinae can be excluded because they are endemic to the Neotropics. Within Protoneurinae there are some genera that have a greatly shortened MP, but this vein still extends at least over 2–3 cells. A few genera of Protoneurinae, like *Junix*, also have a distinctly kinked RP1 at the stigmal brace, but differ in other characters (e. g. origin of RP3/4 very close to subnodus). The fossil Eoprotoneurinae (*Eoprotoneura hyperstiogma*) from the Lower Cretaceous Crato Formation of Brazil either belong to Isostictidae (BECHLY 2007) or to the stemgroup of Neotropical Protoneurinae. *Eoprotoneura* shares with *Palaeodisparoneura* n. gen. the extremely shortened vein MP that is only a single cell long and the CuA that is reduced to an oblique crossvein, but these are homoplastic features

(see below) and *Eoprotoptera* strongly differs in other important characters (Ax2 basal of arculus, subdiscoidal cell fused to hind margin, RP3/4 aligned with subnodus, pterostigma 1.5 cells long, IR1 long).

Isostictidae can be excluded because they have Ax2 basal of the arculus, the distal side of the pterostigma very oblique, and the subdiscoidal cell is completely reduced. Furthermore, in most Isostictidae the subnodus is aligned with the origin of RP3/4 rather than IR2, IR1 is longer, and the males have very elongate claspers as terminalia. However, some Isostictidae do also have a greatly shortened vein MP that is only a single cell long and a CuA that is reduced to an oblique crossvein, but this is most probably a convergence.

Platystictidae can be excluded because they have much longer wings with a falcate apex, a very long IR1, and unbraced pterostigmata (except in Neotropical Palaemnematinae) of very different shape, as well as a very different subdiscoidal area (rhomboid, triangular, or reduced), longer MP, and Ax2 basal of the arculus. Furthermore, Platystictidae have very different and elongate male terminalia. According to the phylogenomic studies mentioned above, the Platystictidae are a very basal group of Zygoptera that is certainly unrelated to the Coenagrionidae (incl. Pseudostigmatinae and Protoneurinae) and Platycnemididae (incl. Caconeurinae and Disparoneurinae), while Isostictidae could be the sistergroup to the coenagrionoid clade.

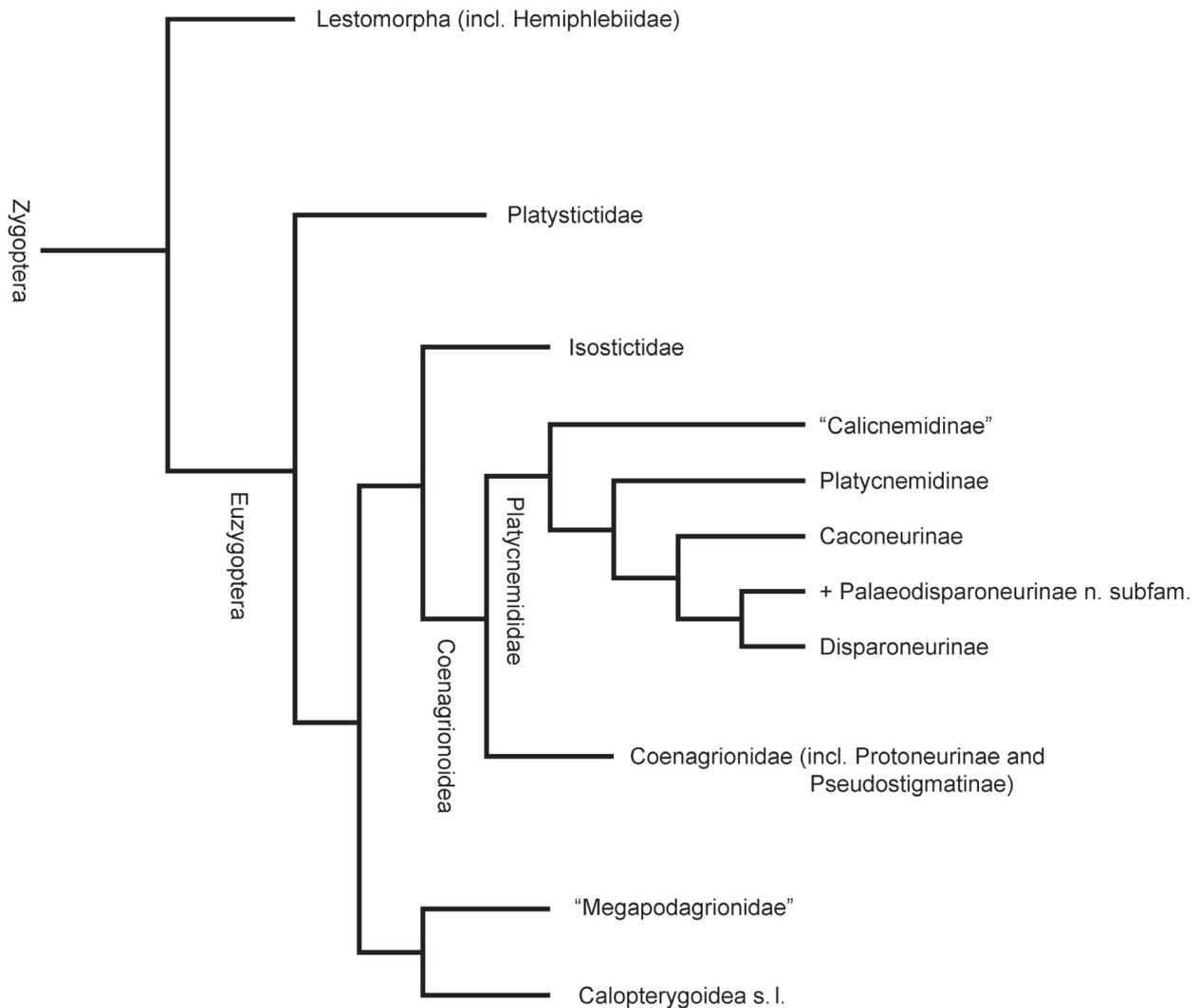


Fig. 7. Cladogram of Zygoptera (with probable position of the new fossil taxon) based on recent cladistic and phylogenomic studies mentioned in the text.

Lestoideidae (only including the Australian endemic genus *Lestoidea*) can be excluded because they have much different pterostigmata (2.5 cells long, unbraced, and with oblique basal side) and a totally different branching pattern of the veins in the radial area (the nodus is midway between the recessed midfork and the origin of RP2, and there are three long intercalary veins between RP1 and RP2), as well as a completely reduced subdiscoidal cell. The greatly shortened vein MP that is only 1–2 cells long is most probably another convergence of this feature.

Caconeurinae can be excluded because they have a venation that is very similar to Platystictidae, with long falcate wings, very long IR1, a longer vein MP, and longer pterostigmata (1.5–2 cells long) with oblique sides.

Palaeodisparoneura n. gen. agrees with Disparoneurinae (e. g. *Nososticta*) in many characters, including the shape of the short male terminalia (also short in Caconeurinae), especially the superior appendages that are shaped like the hammer of a revolver. The shape of the

male terminalia is the best evidence for an attribution of *Palaeodisparoneura* n. gen. to the Caconeurinae-Disparoneurinae clade within Platycnemididae, even though the wing venational characters show a heterogeneous pattern that would not allow an attribution to any of the mentioned Recent groups.

Differences like the relatively basal position of the midfork or origin of RP3/4 (midway between arculus and nodus), a rectangular pterostigma, strongly kinked RP1 at stigmal brace, and the very short IR1 that originates beneath the pterostigma seem to represent unique autapomorphies of *Palaeodisparoneura* n. gen. fossil that justify the erection of a new subfamily, especially because the character combination falls outside the range of the Recent taxa and the attribution to the crown group of any Recent taxon is not supported by the evidence. A similarly short IR1 is an extremely rare feature among extant Zygoptera and is only found in the unrelated genus *Perilestes* (Perilestidae). The greatly shortened vein MP and the CuA that

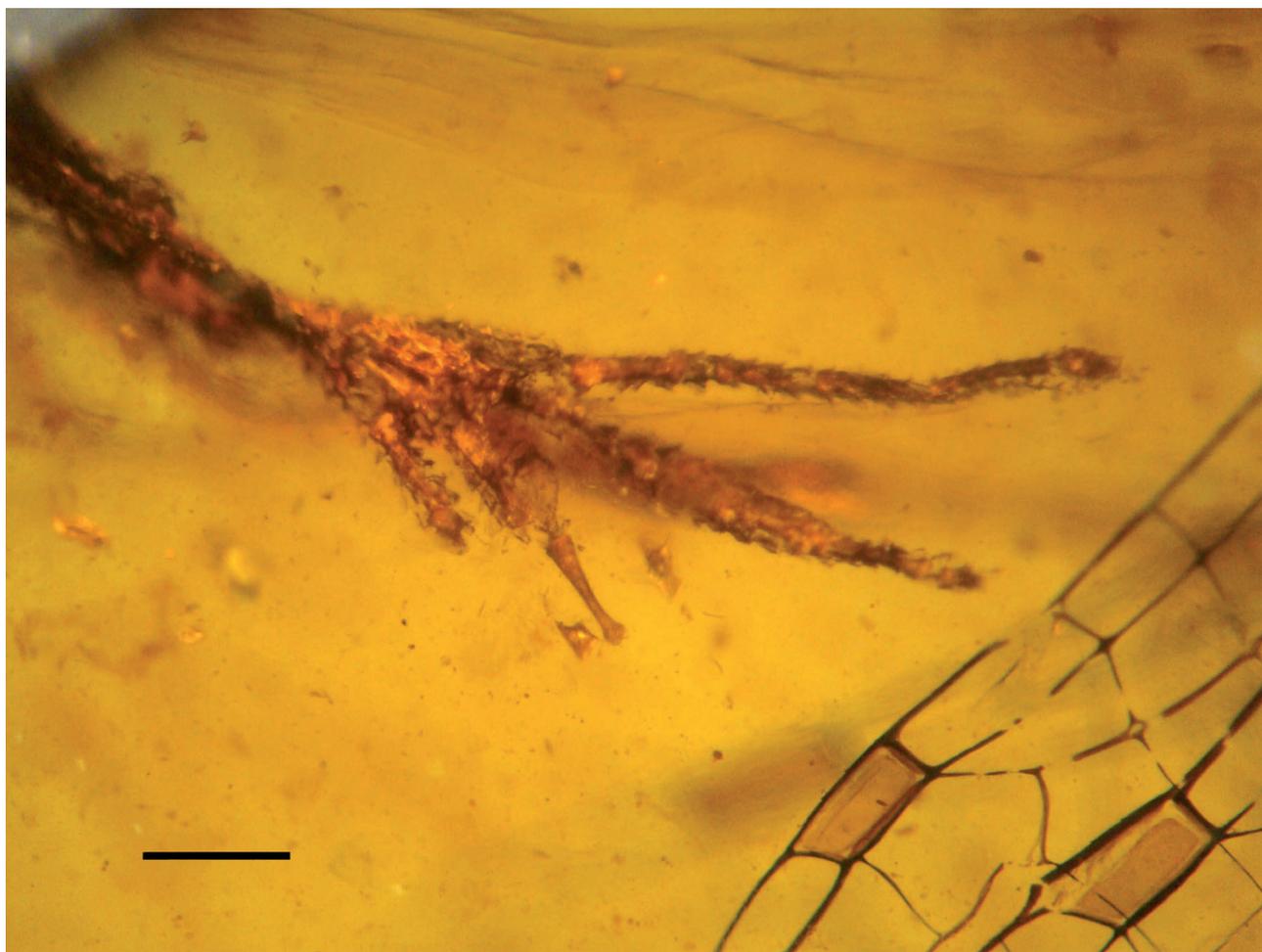


Fig. 8. Lizard foot adjacent to the holotype of *Palaeodisparoneura burmanica* n. gen., n. sp.; Early Cretaceous Burmese amber. – Scale: 1 mm.

is reduced to an oblique crossvein are probably further autapomorphies of *Palaeodisparoneura* n. gen., convergent to the fossil Eoprotoneurinae, Lestoideidae, some Isostictidae, and the Recent disparoneurine genus *Nososticta*.

D i s c u s s i o n . – Platynemididae (incl. Caconeurinae and Disparoneurinae) are an Old World group with tropical or subtropical climatic preferences. Breeding locations range from spring-fed seepages and marginal trickles to slow, moderate and fast lotic habitats (CORBET 1999). South African forms are found near streams and small rivers, often those that flow through woods and ravines (PINKEY 1985). It is likely that *Palaeodisparoneura* n. gen. bred in streams that passed through stands of resin-producing araucarians in the Burmese amber forest. It appears that the adults rested on the trunks of these trees, possibly during their emergence period.

Palaeodisparoneura n. gen. is the first described odonate in Burmese amber and its discovery with the remains of a lizard in the same piece of amber suggests a predator-prey scenario. It is possible that *Palaeodisparoneura* n. gen. was on the trunk of a tree when a nearby lizard lunged at it, grabbing the damselfly by the head but then falling into a resin deposit and taking the odonate with it. All that remains of the lizard is the tail, which extends the length of the amber piece, and the posterior right foot (Fig. 8).

Odonates are selected as food items by extant lizards and CORBET (1999) lists lizards of the genera *Lacerta* and *Sceloporus* as preying on Odonata during their emergence phases. REINHARD & MÖLLER (1996) noted that 5% of the lizards they examined fed on odonates. In their studies on the biology of the waterfall associated damselfly *Thaumatoneura* in Costa Rica, CALVERT & CALVERT (1917) noted that the damselflies occurred at waterfalls where lizards were absent but when lizards were present, the damselflies were absent. They suggested that the lizards were the cause for the absence of *Thaumatoneura* at some of the preferred habitats. The fossil record provides many examples of past behavioral patterns of ancient animal life, including predator-prey associations (BOUCOT & POINAR 2010).

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