Mesostictinae subfam. nov., an archaic group of platystictid damselflies (Odonata: Zygoptera) from mid-Cretaceous Burmese amber

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Odonatans are quite rare in the fossil record compared with the other insects, especially in Cretaceous amber inclusions. The extant family Platystictidae is one of the most diverse Zygoptera, but short of fossil records. In this paper, a new species, *Mesosticta davidattenboroughi* sp. nov., is described from mid-Cretaceous Burmese amber, representing the third-known fossil species of Platystictidae. *Mesosticta davidattenboroughi* sp. nov. has a long IR1 beginning one cell distal of the base of RP2, confirming the previous attribution of *Mesosticta* Huang, Azar, Cai & Nel, 2015 to Platystictidae. It differs from other species of *Mesosticta* in having a long IR1 and a basally crossed subdiscoidal cell. The fossil genus *Mesosticta* shares the diagnostic characters of the modern platystictid genera, viz. a basally recessed 'CuP' (shared by all species), a very long IR1 (only in *Mesosticta davidattenboroughi* sp. nov.), and a specialized subdiscoidal area mostly rhomboidal in shape (only in *Mesosticta electronica* Zheng, Zhang, Chang & Wang, 2016). Based on the platystictid damselflies from Burmese amber, a new subfamily Mesostictinae subfam. nov. is established. Mesostictinae subfam. nov. represents the first fossil group of modern platystictid damselflies, documenting the appearance of Platystictidae as early as mid-Cretaceous. It differs from modern Platystictidae by the presence of fewer postnodal and postsubnodal crossveins, a short MP, the base of RP2 being nearer to the subnodus and the nodus lying more distally.

http://zoobank.org/urn:lsid:zoobank.org:pub:6669DBCD-F2EF-4C84-9623-BD33142AD36B

Keywords: Platystictidae; Zygoptera; Odonata; Cenomanian; Cretaceous; Burmese amber

Introduction

Platystictidae (shadowdamsels) currently consist of about 250 extant species in eight genera and four tropical subfamilies (Wilson 1997; Van Tol 2005; Van Tol *et al*. 2009; Dow & Orr 2012; Dijkstra *et al*. 2014; Haber & Wagner 2014; Schorr & Paulson 2015; Suhling *et al*. 2015; Dow *et al*. 2016; Phan & Kompier 2016; Bedjanič *et al*. 2016), and two fossil species of the genus *Mesosticta* Huang, Azar, Cai & Nel, 2015 from mid-Cretaceous Burmese amber (Huang *et al*. 2015; Zheng *et al*. 2016a). The subfamily Palaemnematinae (*Palaemnema* Selys, 1860) is confined to central and north-western South America, while Sinostictinae (*Sinosticta* Wilson, 1997), Platystictinae (*Platysticta* Selys, 1860, *Ceylonosticta* Fraser, 1931) and Protostictinae (*Protosticta* Selys, 1885, *Drepanosticta* Laidlaw, 1917, *Telosticta* Dow & Orr, 2012 and *Sulcosticta* van Tol, 2005) are restricted to South-East Asia. Platystictidae were hypothesized to have originated from eastern Africa during the Late Cretaceous, then later migrated to South America, Asia and New Guinea (van Tol & Müller 2003; van Tol *et al*. 2009; Sánchez-Herrera & Ware 2012). The recently discovered *Mesosticta*, however, puts the appearance of Platystictidae back to at least the mid-Cretaceous (Zheng *et al*. 2016a).

The platystictid damselflies are characterized by a long and very slender abdomen, and a unique wing with a basally recessed 'CuP' (Fraser 1957; Jarzembowski *et al*. 1998; Huang *et al*. 2015), a long IR1 and a usually diamond-shaped subdiscoidal cell (Haber & Wagner 2014). The platystictid genus *Mesosticta* (*M. burmatica* Huang, Azar, Cai & Nel, 2015 and *M. electronica* Zheng, Zhang, Chang & Wang, 2016) was tentatively attributed to this family due to a basally recessed CuP-crossing (Huang *et al*. 2015) and the rhomboidal shape of the subdiscoidal triangle (only present in the hindwing of *M. electronica*;

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Zheng *et al*. 2016a). Both species, however, do not have a very long IR1, which is present in all recent platystictid damselflies. In this paper, we describe a new platystictid species of *Mesosticta* from mid-Cretaceous Burmese amber. The new species has a very long IR1, so it confirms the previous attribution of *Mesosticta* to the Platystictidae. Based on three species of *Mesosticta*, a new subfamily is established.

Geological background

The piece of amber containing the new 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). Abundant insect inclusions have been described from Burmese amber (Cruickshank & Ko 2003; Shi *et al*. 2012; Kania *et al*. 2015), with rare odonatans including true dragonflies (Schädel & Bechly 2016), damsel-dragonflies (Bechly & Poinar 2013) and damselflies (Poinar *et al*. 2010; Huang *et al*. 2015; Zheng *et al*. 2016a, b, c, d). The age of the Burmese amber was considered to be Late Albian to Cenomanian based on palynology and ammonite stratigraphy (Cruickshank & Ko 2003; Ross *et al*. 2010), while it was radiometrically dated at 98.79 ± 0.62 Ma (earliest Cenomanian) based on U-Pb zircon dating of the volcanoclastic matrix (Shi *et al*. 2012). The real depositional age of the amber is probably earlier than this radiometric age since the amber shows evidence of redeposition (Wang *et al*. 2015). Here we follow the age given by Shi *et al*. (2012), but we treat it as minimal.

Material and methods

The piece of amber containing the damselfly is yellow and transparent. The damselfly is near the amber surface, and well preserved with complete forewings. The abdomen and hindwings were polished away. Photographs were taken using a Zeiss Stereo Discovery V16 microscope system and Zen software. In most instances, incident and transmitted light were used simultaneously. All images are digitally stacked photomicrographic composites of approximately 40 individual focal planes obtained using the free software Combine ZP for a better illustration of the three-dimensional structures. The line drawings were

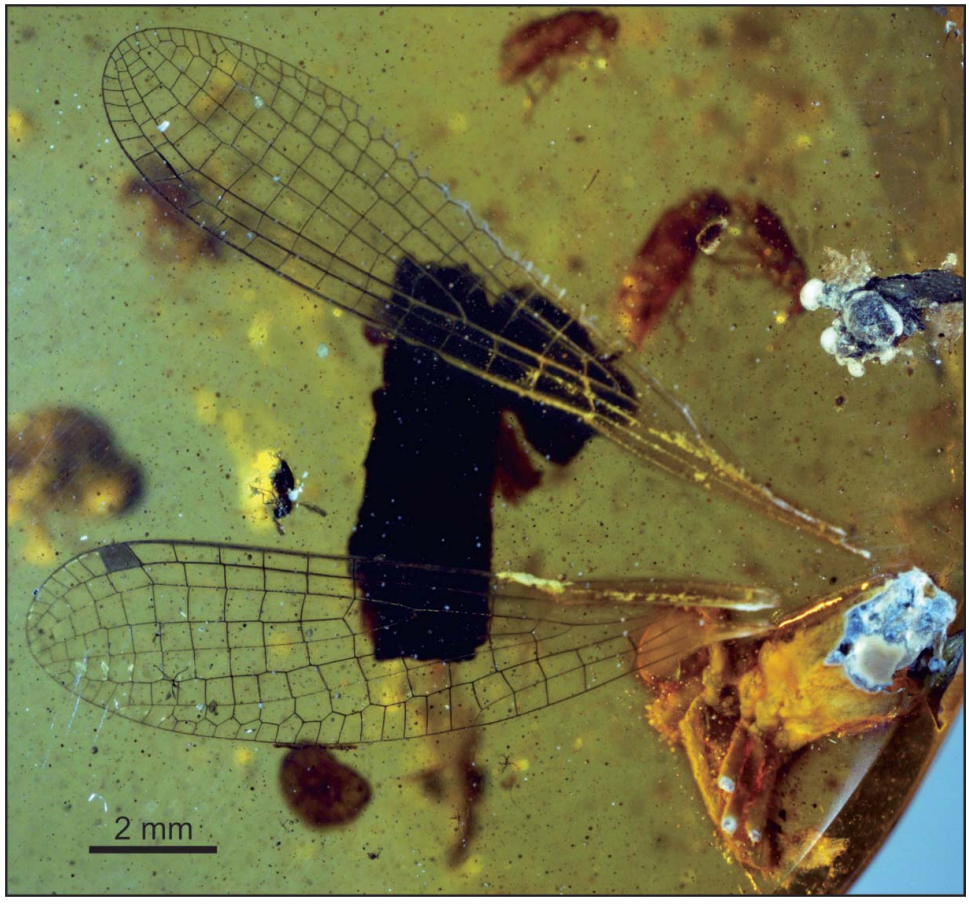

Figure 1. *Mesosticta davidattenboroughi* sp. nov., holotype, NIGP164541, photograph of specimen.

prepared from photographs using image-editing software (CorelDraw X7 and Adobe Photoshop CS6). The specimen is housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (**NIGPAS**).

The nomenclature of the dragonfly wing venation used in this paper is based on the interpretations of Riek (1976) and Riek & Kukalová-Peck (1984), as modified by Nel *et al*. (1993) and Bechly (1996). The phylogeny of extant Zygoptera followed in the present work is based on Dijkstra *et al*. (2014), while the generic characters of *Mesosticta* are after Zheng *et al*. (2016a). Wing abbreviations are as follows: **AA**, anal anterior; **AP**, anal posterior; **Arc**, arculus; **Ax**, primary antenodal crossvein; **Cr**, nodal crossvein; **CuA**, cubitus anterior; **CuP**, cubitus posterior; **DC**, discoidal cell; **IR**, intercalary radial vein; **MA**, median anterior; **MP**, median posterior; **N**, nodus; **Pt**, pterostigma; **RA**, radius anterior; **RP**, radius posterior; **ScP**, subcosta posterior; **Sn**, subnodal crossvein.

Systematic palaeontology

Order **Odonata** Fabricius, 1793
Suborder **Zygoptera** Selys-Longchamps, 1854
Superfamily **Platystictoidea** Kennedy, 1920
Family **Platystictidae** Kennedy, 1920
Subfamily **Mesostictinae** subfam. nov.

Type genus. *Mesosticta* Huang, Azar, Cai & Nel, 2015.

Diagnosis. Base of RP3/4 just basal of Sn; base of RP2 three or four cells distal of Sn; MA long and ending on posterior wing margin just below Pt brace; MP three or four cells long; CuP in basal position; crossvein present basally closing subdiscoidal cell, seperate from CuP; subdiscoidal cell posteriorly closed by AA and not by posterior wing margin; RP1 with slight angle below pterostigmal brace; few postnodal and postsubnodal crossveins (less than 10), somewhat aligned; nodus not in very basal position, at least at 35% of wing length; longitudinal veins RA, RP1, IR1, RP2 and IR2 strongly converging on wing apex; Pt one cell long, thickened and fused with greatly thickened pterostigmal part of RA as U-shaped structure.

Mesosticta Huang, Azar, Cai & Nel, 2015

Type species. *Mesosticta burmatica* Huang, Azar, Cai & Nel, 2015.

Included species. *Mesosticta electronica* Zheng, Zhang, Chang & Wang, 2016; *Mesosticta davidattenboroughi* sp. nov.

Revised diagnosis. As for subfamily diagnosis.

Mesosticta davidattenboroughi sp. nov.
(Figs 1–7)

Type species. NIGP164541, two complete forewings attached to body.

Diagnosis. Forewing characters: IR1 long, originating one cell distal of base of RP2, nearer to N than to Pt; Arc aligned with Ax2; subdiscoidal cell basally crossed by one vein.

Etymology. In honour of Sir David Attenborough, on his 90th birthday, for his appreciation of dragonflies.

Locality and horizon. Hukawng Valley, Kachin Province, Myanmar; lowermost Cenomanian, lowermost Upper Cretaceous.

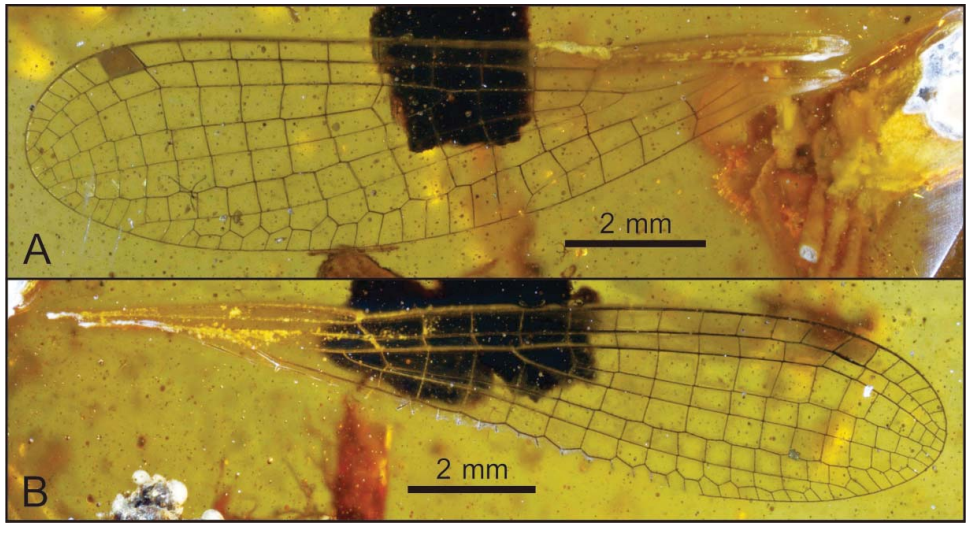

Figure 2. *Mesosticta davidattenboroughi* sp. nov., holotype, NIGP164541. **A,** photograph of left forewing; **B,** photograph of right forewing.

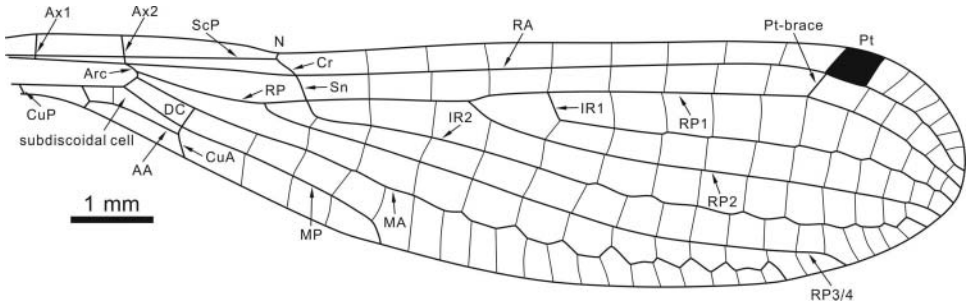

Figure 3. *Mesosticta davidattenboroughi* sp. nov., holotype, NIGP164541, line drawing showing venation of left forewing.

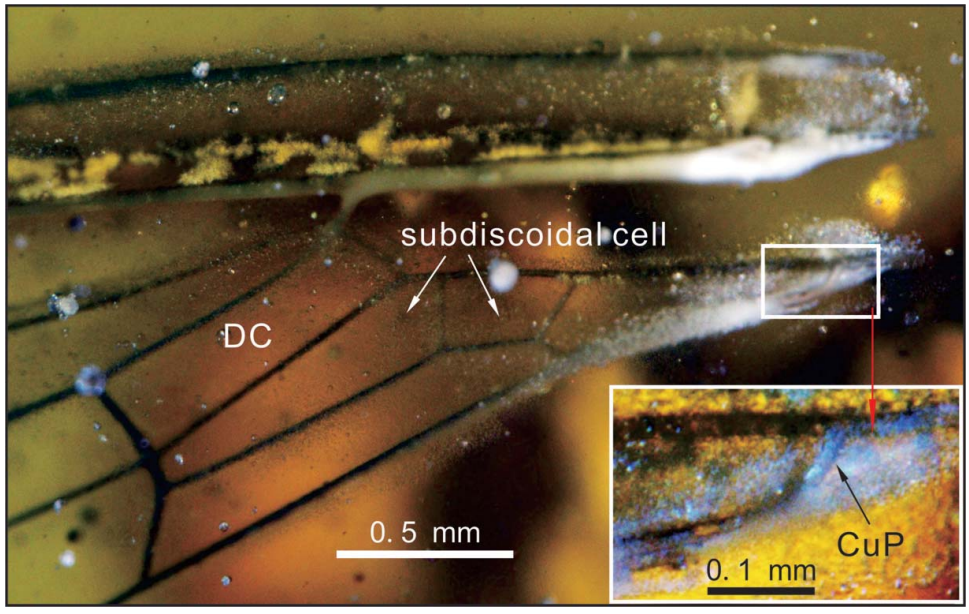

Figure 4. *Mesosticta davidattenboroughi* sp. nov., holotype, NIGP164541, photograph showing detail of left forewing base.

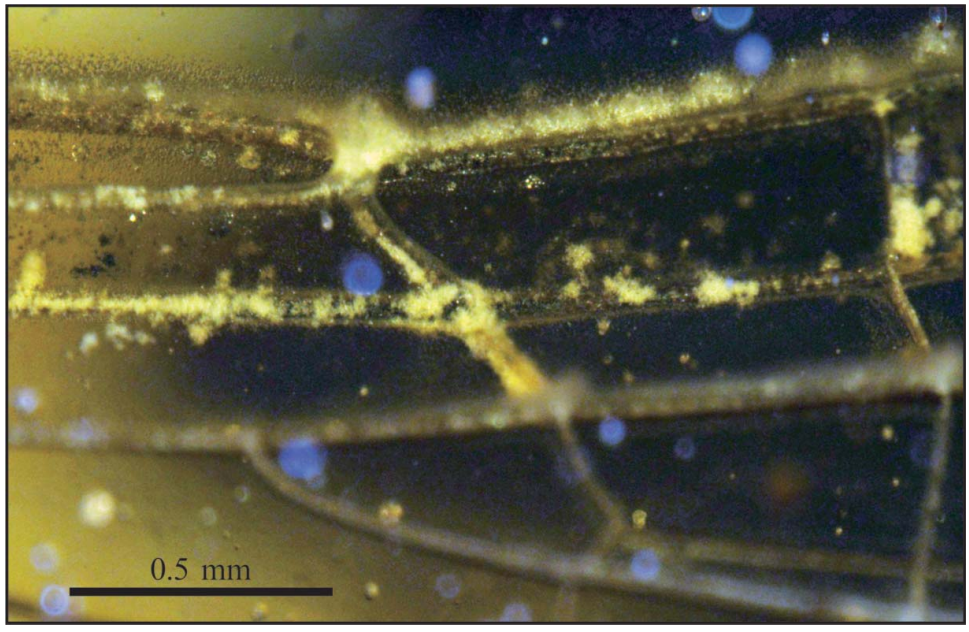

Figure 5. *Mesosticta davidattenboroughi* sp. nov., holotype, NIGP164541, photograph of right forewing nodus.

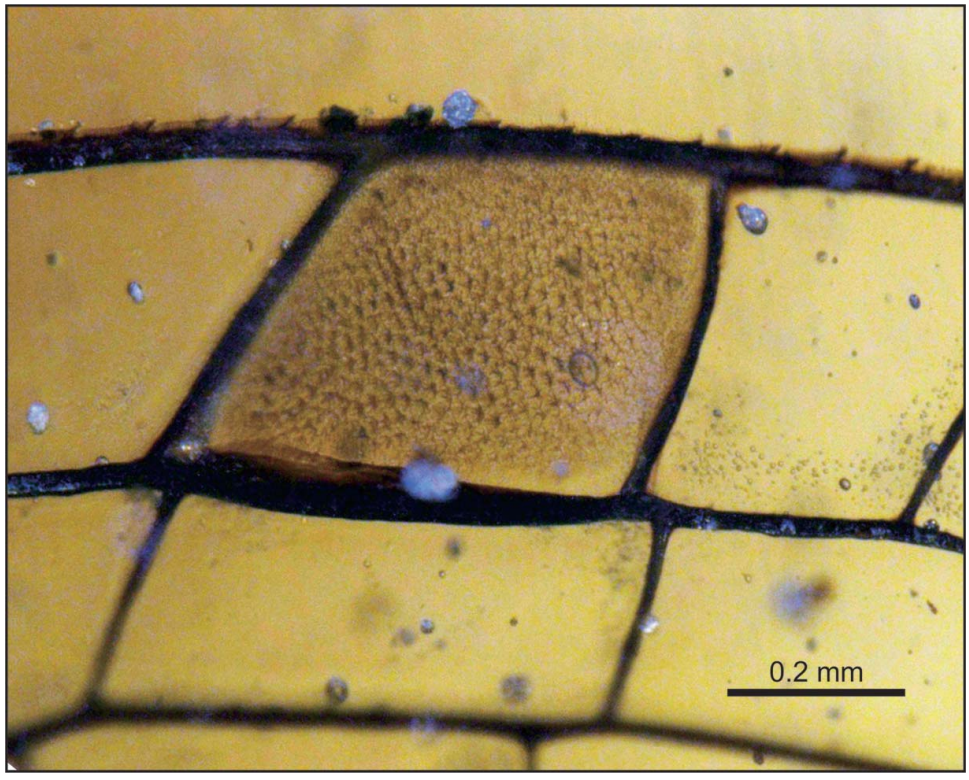

Figure 6. *Mesosticta davidattenboroughi* sp. nov., holotype, NIGP164541, photograph of right forewing pterostigma.

Description. Forewings complete (Figs 2, 3). Wing length 11.62 mm, width at level of N 1.85 mm; length from wing base to Arc 1.46 mm, from Arc to N 1.85 mm, from N to Pt 6.62 mm, from Pt to wing apex 1.69 mm. Primary antenodal crossveins preserved, Ax2 1.09 mm distal of Ax1; no secondary antenodal crossveins present. Eight postnodal crossveins and eight postsubnodal crossveins present proximal to Pt, somewhat aligned. Six postnodal crossveins and five postsubnodal crossveins present distal of Pt, non-aligned. Arc angular and aligned with Ax2. DC basally closed, free, elongate and quadrangular, 0.79 mm long and maximum 0.27 mm wide. Subdiscoidal cell free and elongate, 1.29 mm long and maximum 0.24 mm wide, crossed by one vein slightly basal of Arc. AA separated from AP at mid distance between Ax1 and Ax2, ending on distal angle of DC (Fig. 4). Nodal structures well preserved (Fig. 5), with Sn aligned with Cr. Midfork (base of RP3/4) slightly basal of N. IR2 aligned with Sn, one cell and 0.51 mm distal of midfork. RP2 three cells distal of Sn, lying 1.95 mm distally, nearer to N than to Pt. IR1 long, originating one cell distal of base of RP2 and five cells basal of Pt base. RP1 with a slight angle below Pt brace. Longitudinal veins RA, RP1, IR1, RP2 and IR2 strongly converging on wing apex. MA distally zigzagged and long, reaching posterior wing margin just below base of Pt-brace. MP curved, four cells long, ending on posterior wing margin 2.38 mm distal of distal angle of DC. Pt covering one cell (Fig. 6), 0.52 mm long and 0.44 mm wide, thickened and fused with greatly thickened pterostigmal part of RA as a U-shaped structure.

Discussion

Mesosticta davidattenboroughi has nearly all the characters of the genus *Mesosticta* Huang, Azar, Cai & Nel, 2015, after Zheng *et al*. (2016a), listed here: (1) base of RP3/4 just basal of Sn; (2) base of RP2 three or four cells distal of Sn; (3) MA long but ending two cells distal of level of base of IR1; (4) MP three or four cells long; (5) CuP in basal position; (6) basal crossvein present closing subdiscoidal cell, seperate from CuP; (7) subdiscoidal cell posteriorly closed by AA and not by posterior wing margin; (8) RP1 with slight angle below pterostigmal brace; (9) IR1 three cells distal of base of RP2, nearer to Pt than to base of RP2; (10) postnodal and postsubnodal cossveins aligned slightly distal of N and basal of base of IR1; (11) longitudinal veins RA, RP1, IR1, RP2 and IR2 strongly converging on wing apex; and (12) Pt covering one cell, thickened and fused with greatly thickened pterostigmal part of RA as U-shaped structure. *Mesosticta davidattenboroughi* shares all the above characters except (3) and (9) due to the long IR1. In fact, MA reaches the posterior wing margin just below the pterostigmal brace in *M.*

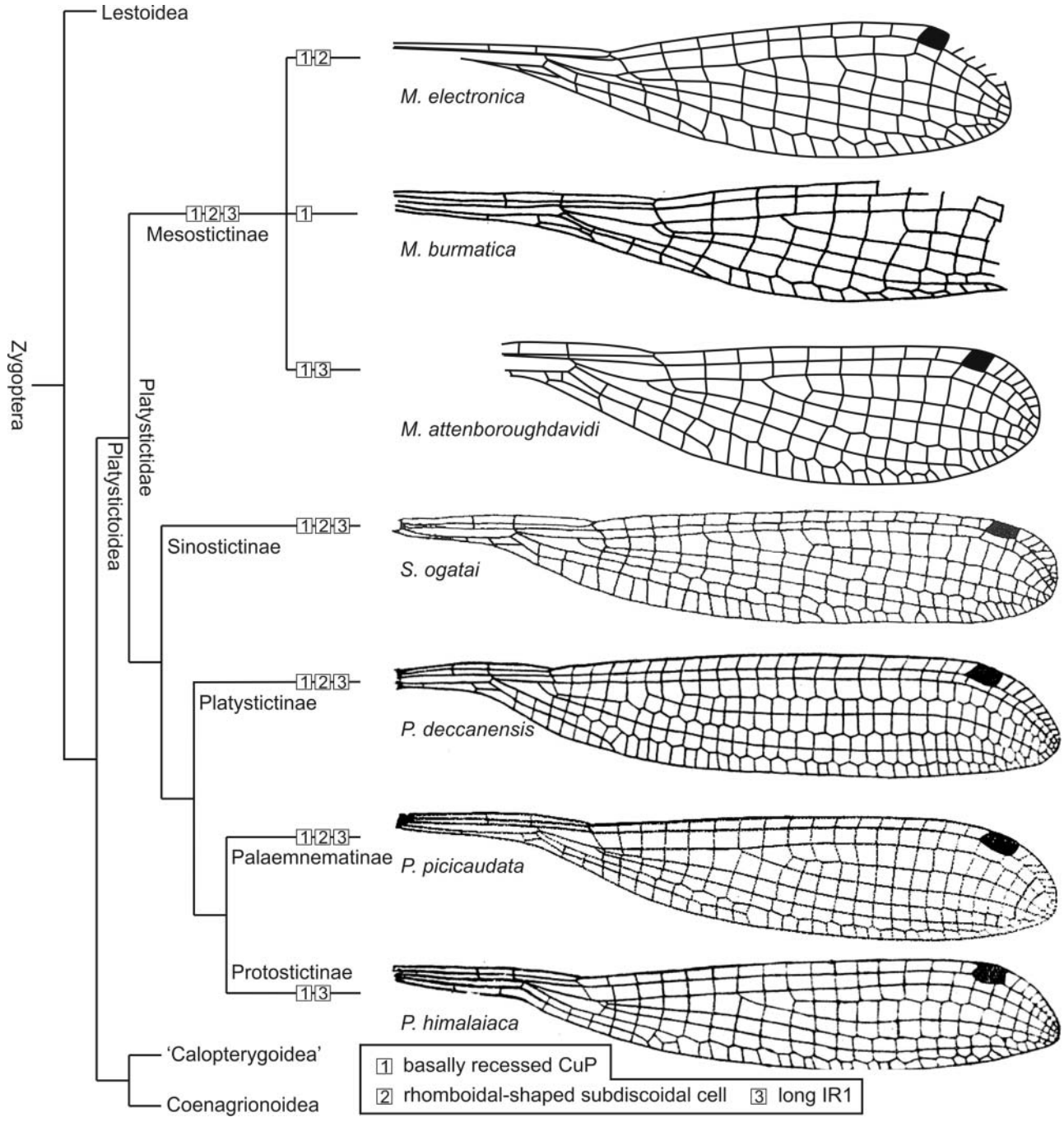

Figure 7. Hypothetical position of *Mesosticta davidattenboroughi* sp. nov. in phylogenetic tree of Zygoptera. All line drawings are based on forewings (phylogeny based on Dijkstra *et al*. 2014; line drawing of *Sinosticta ogatai* Matsuki & Saito, 1996 after Wilson 1997; line drawing of *Palaemnema picicaudata* Kennedy, 1938 after Kennedy 1938; line drawings of *Platysticta deccanensis* Laidlaw, 1915 and *Protosticta himalaiaca* Laidlaw, 1917 after Fraser 1933).

davidattenboroughi and two previously described species of *Mesosticta*. *M. davidattenboroughi* has the base of IR1 shifted basally and only one cell distal of base of RP2, closer to the nodus than to the pterostigma, while the other species of *Mesosticta* have the base of IR1 three cells distal of the base of RP2 and nearer to the pterostigma. Due to the similarity with the other *Mesosticta*, we attribute *M. davidattenboroughi* to *Mesosticta* by revising the generic character (3) as 'MA long and reaching posterior wing margin just below pterostigmal brace' and removing

character (9) to differentiate the species. Within *Mesosticta* (Fig. 7), *M. davidattenboroughi* has a crossvein across the basal part of the subdiscoidal cell, differing from *M. burmatica* which has a crossvein in the distal part of the subdiscoidal cell, and *M. electronica* which has a free, rhomboidal subdiscoidal cell. *M. davidattenboroughi* also has the arculus aligned with Ax2, as in *M. burmatica* but unlike *M. electronica* which has Ax2 slightly basal of the arculus.

The fossil genus *Mesosticta* has the diagnostic characters of the modern platystictid genera (Fig. 7), viz. a basally recessed 'CuP' (shared by all species), a very long IR1 (in *M. davidattenboroughi*), and a specialized subdiscoidal area mostly rhomboidal in shape (rhomboidal shape shared with *M. electronica*). The presence of these characters confirms the previous attribution of *Mesosticta* to Platystictidae. However, all these characters are not shared by one species as in most recent Platystictidae. Also, *Mesosticta* shares with the extant platystictid damselflies the following characters: vein RP1 with a very slight angle below the pterostigmal brace; postnodal and postsubnodal crossveins somewhat aligned; longitudinal veins RA, RP1, IR1, RP2 and IR2 strongly converging on wing apex; pterostigma one cell long, thickened and fused with greatly thickened pterostigmal part of RA to form a U-shaped structure.

The differences between the modern platystictid damselflies and *Mesosticta* (Fig. 7) are that the former have more postnodal and postsubnodal crossveins (over 15 compared to 10 or fewer in *Mesosticta*), a long MP (at least five cells long in Protostictinae to over half the wing length in Sinostictinae, compared with three or four cells long in *Mesosticta* – the shortening of the vein MP being a potential synapomorphy of the Mesostictinae), the base of RP2 being more cells distal of the subnodus (at least four cells compared to only three or four cells in *Mesosticta*) and the nodus lying very basally (23–30% of the wing length compared to at least 35% in the latter). Due to the above differences, we establish a new subfamily Mesostictinae for the fossil platystictid damselflies from Burmese amber, representing the archaic platystictid damselflies.

Acknowledgements

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