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New damselflies (Odonata: Zygoptera: Hemiphlebiidae, Dysagrionidae) from mid-Cretaceous Burmese amber

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Two damselflies, *Burmahemiphlebia zhangi* gen. et sp. nov. and *Palaeodysagrion cretacicus* gen. et sp. nov., are described from the mid-Cretaceous Burmese amber. *Burmahemiphlebia zhangi* is the first record of Hemiphlebiidae from this amber, although the family was cosmopolitan during the Mesozoic. It can be readily distinguished from all other members of Hemiphlebiidae in having very short MP and CuA veins, and in its rectangular discoidal cell. The new fossils support the view that hemiphlebiid damselflies were one of the dominant groups of Zygoptera during the Mesozoic. *Palaeodysagrion cretacicus* is the first dysagrionid damselfly from Burmese amber and the second Mesozoic representative of this predominantly Paleogene group. It differs from other members of Dysagrionidae in having a unique elongate discoidal cell. These new finds increase the diversity of damselflies in mid-Cretaceous Burmese amber.

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Key words: Hemiphlebiidae, Dysagrionidae, Zygoptera, Cenomanian, Cretaceous, Burmese amber.

HEMIPHLEBIIDAE, a family of small damselflies, has only one extant species, *Hemiphlebia mirabilis* Selys-Longchamps, 1869, occurring as a relict taxon in the swamps of Victoria, Australia (Cordero-Rivera 2015). Six fossil genera have been attributed previously to Hemiphlebiidae Kennedy, 1920, *viz*., *Parahemiphlebia* Jarzembowski *et al*., 1998, *Mersituria* Vassilenko, 2005, *Electrohemiphlebia* Lak *et al*., 2009, *Jordanhemiphlebia* Kaddumi in Lak *et al*., 2009, *Pantelusa* Vassilenko, 2014 and *Enteropia* Pritykina & Vassilenko, 2014. The family was one of the dominant zygopteran groups during the Mesozoic, having a global distribution. The earliest member of this family appeared in the Late Jurassic of Mongolia and Transbaikalia, and the group became more widely distributed in the Early Cretaceous, with records from England (Hauterivian–Barremian), Jordan (Barremian), Brazil (late Aptian) and France (latest Albian). The family is also known from the Late Cretaceous of Israel (Turonian) and America (Maastrichtian) (Jarzembowski *et al*. 1998, Bechly 1998, Vassilenko 2005, 2014, Lak *et al*. 2009, Nel *et al*. 2010, Pritykina & Vassilenko 2014).

Dysagrionidae, an extinct damselfly family comprising seven genera, has a distinctive wing venation, especially in the structure of the discoidal cell. Dysagrionidae (Dysagrioninae of Cockerell, 1908) and extant Thaumatoneurinae Tillyard & Fraser, 1938 were regarded as sister subfamilies of Thaumatoneuridae Tillyard & Fraser, 1938 (see Bechly 2016). However, the sister relationship of Dysagrionidae and Thaumatoneurinae is equivocal, and the former was considered a separate family by Garrouste & Nel (2015). Dysagrionidae is currently subdivided into the Mesozoic–Cenozoic Dysagrioninae Cockerell, 1908 and the Cenozoic Eodysagrioninae Rust *et al*., 2008. Dysagrioninae consists of two tribes: Dysagrionini Cockerell, 1908, consisting of the Cenozoic *Dysagrion* Scudder, 1878, *Phenacolestes* Cockerell, 1908, *Electrophenacolestes* Nel & Arillo, 2006 and *Primorilestes* Nel *et al*., 2005, and Petrolestini Cockerell, 1927, consisting of the Cenozoic *Petrolestes* Cockerell, 1927 and the Mesozoic *Congqingia* Zhang, 1992. The Eodysagrioninae comprises a monotypic genus, *Eodysagrion* Rust *et al*., 2008.

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The first report of a dysagrionid damselfly was *Dysagrion* from the early–middle Eocene (Green River Formation) of North America (Scudder 1878). The oldest fossil representative is *Congqingia* from the Early Cretaceous (Laiyang Formation) of Shandong Province, eastern China (Zhang 1992) and it is the only record of dysagrionid damselflies from Mesozoic strata. Dysagrionid damselflies have a relatively wide distribution and high diversity during the Paleogene, with three genera recorded from the early–middle Eocene of America, two genera from the earliest Eocene of Denmark, one genus from the early–middle Eocene of Germany, one undetermined species from the late Eocene of England, one genus from Eocene Baltic amber, and one from the early Oligocene of Russia (Scudder 1878, 1890, Cockerell 1908, 1927, Nel & Paicheler 1994, Nel *et al*. 2005, Nel & Arillo 2006, Rust *et al*. 2008, Nel & Fleck 2014, Garrouste & Nel 2015).

Here we describe two new genera, attributed to Hemiphlebiidae and Dysagrionidae, representing the first discovery of these two groups from mid-Cretaceous Burmese amber. The new discovery enhances knowledge of the diversity of damselflies in Burmese amber.

Material and methods

The specimens described herein were collected in the Hukawng Valley of Kachin Province, Myanmar (locality documented by Kania *et al*. 2015, fig. 1). The age of the Burmese amber is 98.79 ± 0.62 Ma (earliest Cenomanian; Cohen *et al*. 2013) based on U–Pb zircon dating of the volcanoclastic host rock (Shi *et al*. 2012). The amber containing the damselflies is yellow and transparent.

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 were digitally stacked photomicrographic composites of approximately 40 individual focal planes created using the free software Combine-ZP for a better illustration of the 3D structures. Line drawings were prepared from photomicrographs using image-editing software (CorelDraw X7 and Adobe Photoshop CS6). All specimens are housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

The dragonfly venation nomenclature 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 (1996a). The higher classification of fossil and extant Odonatoptera, together with family and generic characters, followed in the present work is based on the phylogenetic system proposed by Bechly (1996a) and Garrouste & Nel (2015) for Dysagrionidae. Wing abbreviations are as follows: AA, anterior anal; AP, posterior anal; 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. All measurements are given in millimetres.

Systematic palaeontology

Order ODONATA Fabricius, 1793
Suborder ZYGOPTERA Selys-Longchamps, 1854
Family HEMIPHLEBIIDAE Kennedy, 1920

Type genus. *Hemiphlebia* Selys-Longchamps, 1869

Burmahemiphlebia gen. nov.

Type species. *Burmahemiphlebia zhangi* sp. nov.

Etymology. A combination of the names Burma and *Hemiphlebia*, gender feminine.

Diagnosis. Based on forewing and hindwing characters. Forewing DC open basally, but hindwing DC closed and quadrangular; IR1 short, originating opposite distal end of Pt; MP extremely short, one cell long, ending on posterior wing margin at mid-distance between Ax2 and N; CuA short, reduced to oblique vein.

Burmahemiphlebia zhangi sp. nov. (Figs 1–4)

Etymology. The specific name is in honour of Dr Junfeng Zhang, palaeoentomologist.

Diagnosis. Based on forewing and hindwing characters. Very small damselfly, estimated complete wing length 7.5–10 mm; four postnodal crossveins present, misaligned with three postsubnodal crossveins; Arc slightly distal of Ax2 in forewing, but aligned with Ax2 in hindwing; midfork basal of N; base of IR2 opposite Sn; base of RP2 at mid-distance between N and Pt; thorax metallic green in colour.

Holotype. NIGP163664, two wings attached to body.

Paratype. NIGP163665, single hindwing attached to body.

Locality and age. Hukawng Valley, Kachin Province, Myanmar; earliest Cenomanian (earliest Late Cretaceous).

Description. Specimen NIGP163298 (Figs 1A, 2A–D, 3A–C, 4A–B) consists of two hyaline wings (one forewing and one hindwing) attached to the body. Preserved length 5.63 mm (head, thorax and basal abdomen). Head dark, with separated eyes (Fig. 2A). Antenna three segmented, with segments 1 and 2 short, and stout and segment 3 long and slim. Legs well developed, profemur 1.17 mm long, protibia 0.89 mm long, tarsus 0.37 mm long (claws excluded); mesofemur 1.32 mm long, mesotibia 1.28 mm long,

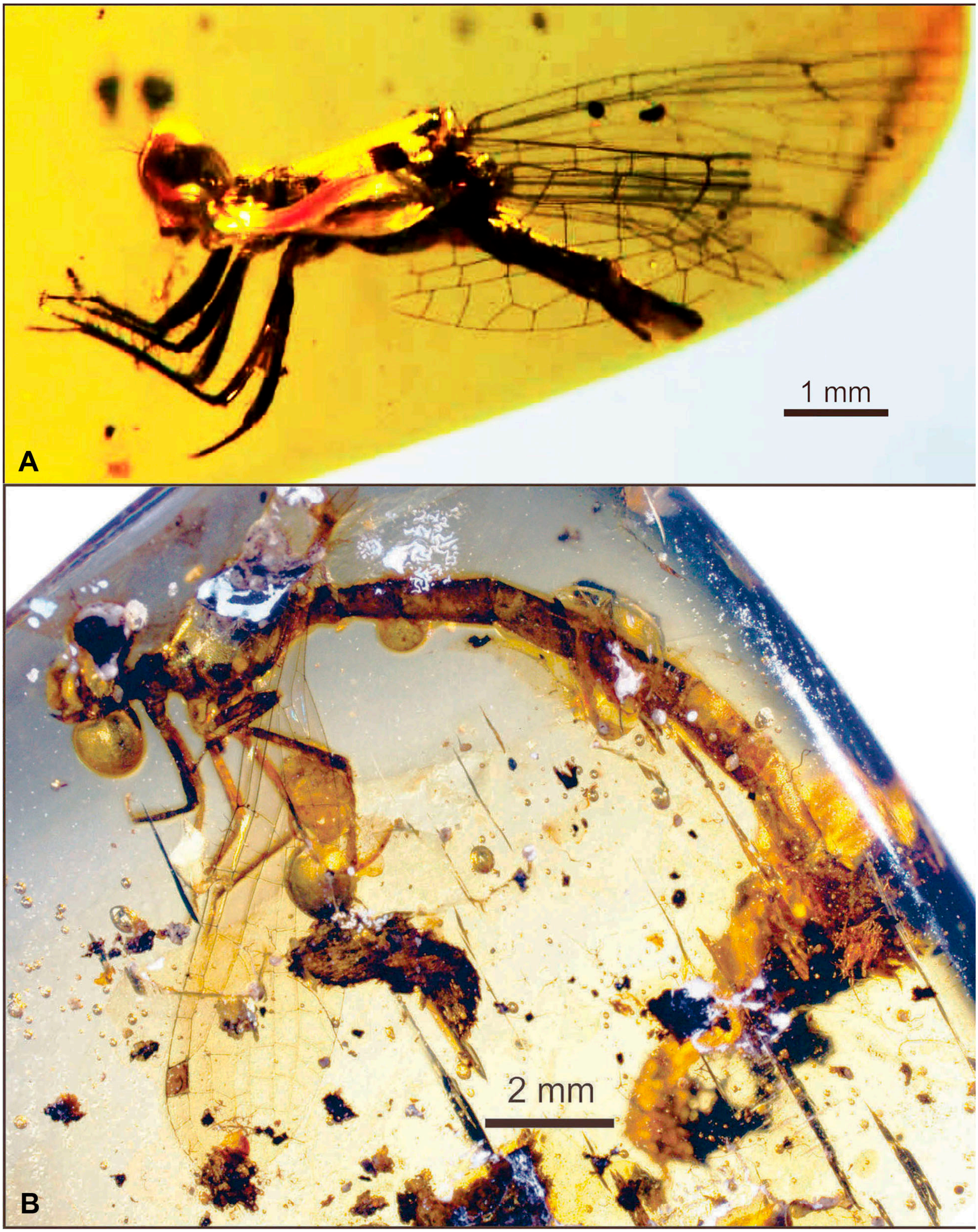

Fig. 1. Burmahemiphlebia zhangi. **A**, Photomicrograph of complete specimen, holotype, NIGP163664; **B**, Photomicrograph of complete specimen, paratype, NIGP163665.

tarsus 0.42 mm long; metafemur 1.33 mm long, metatibia 1.46 mm long, tarsus 0.43 mm long; paired long spines present on tibia and tarsi; tibia armed with about ten pairs of spines; tarsi slightly curved, three segmented, with third tarsomere length equal to first two tarsomeres combined, and armed with about five pairs of spines; apical claws symmetrical, 0.12–0.15 mm long.

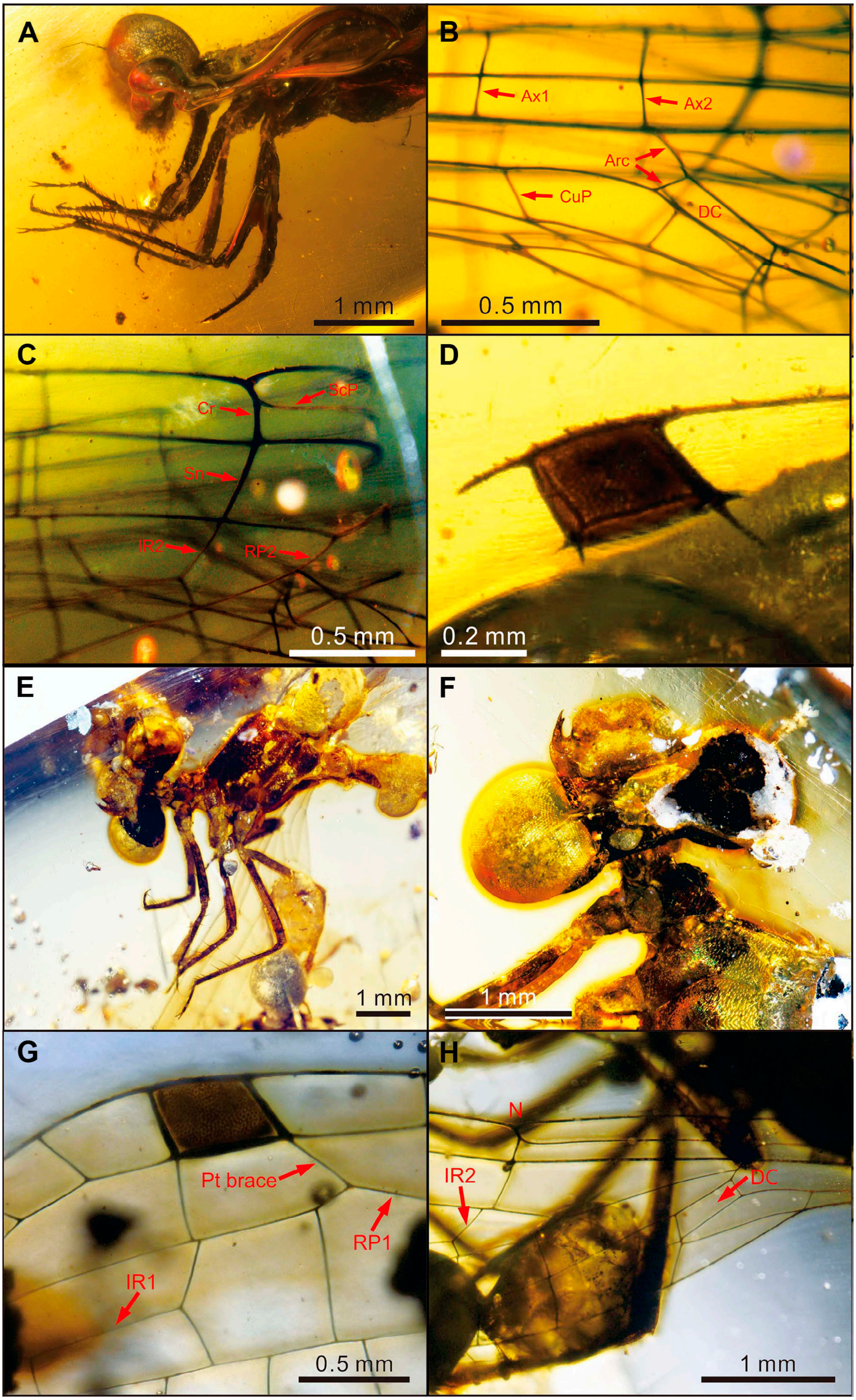

Fig. 2. Photomicrographs of *Burmahemiphlebia zhangi*. **A**, Head and thorax of holotype; **B**, Detail of hindwing base of holotype; **C**, Detail of hindwing nodus of holotype; **D**, Hindwing pterostigma of holotype; **E**, Body of paratype; **F**, Head and metallic green thorax of paratype; **G**, Detail of hindwing apex of paratype; **H**, Detail of basal and middle hindwing of paratype.

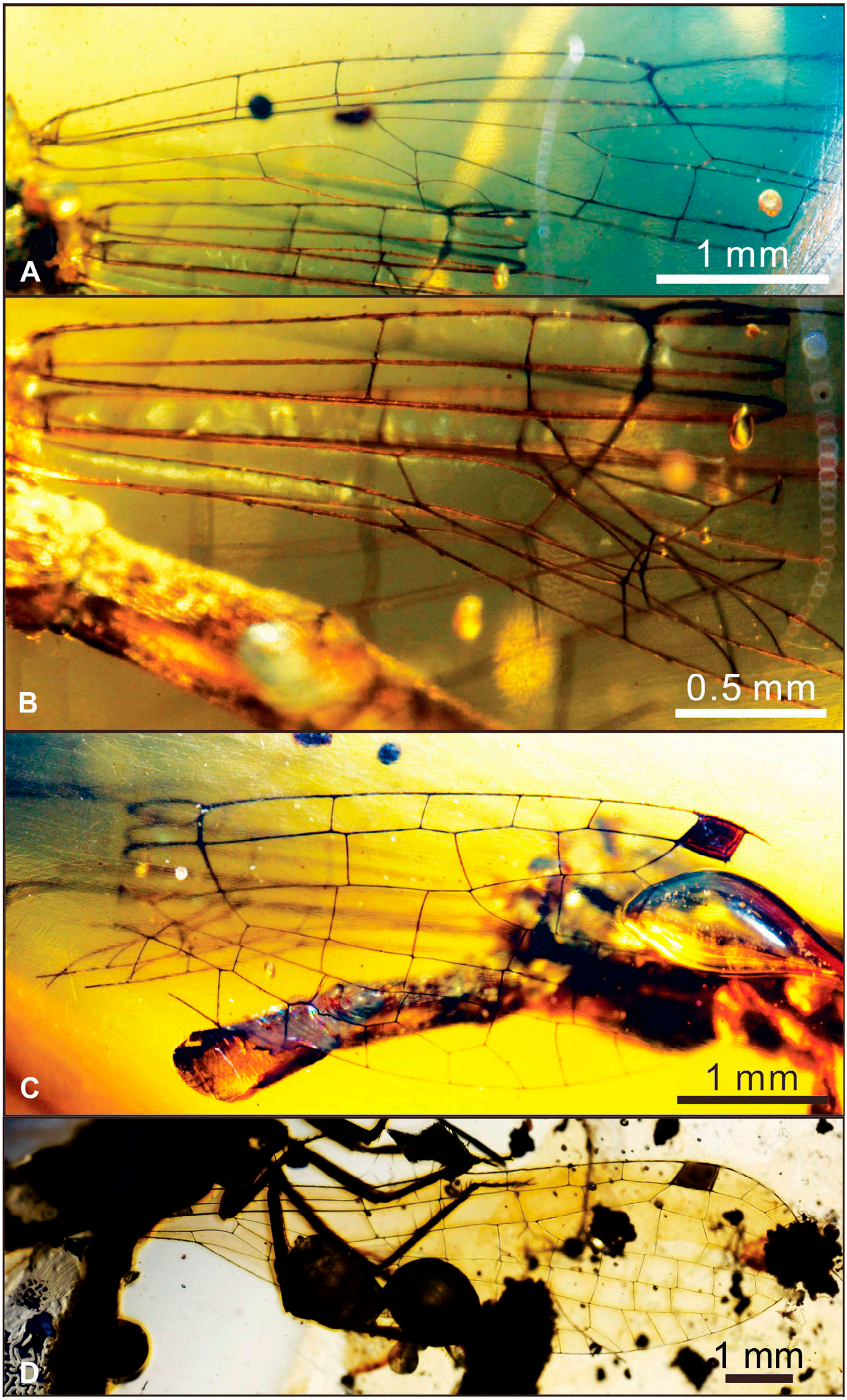

Fig. 3. Photomicrographs of *Burmahemiphlebia zhangi*. **A**, Forewing of holotype; **B**, Basal part of hindwing of holotype; **C**, Distal part of hindwing of holotype; **D**, Hindwing of paratype.

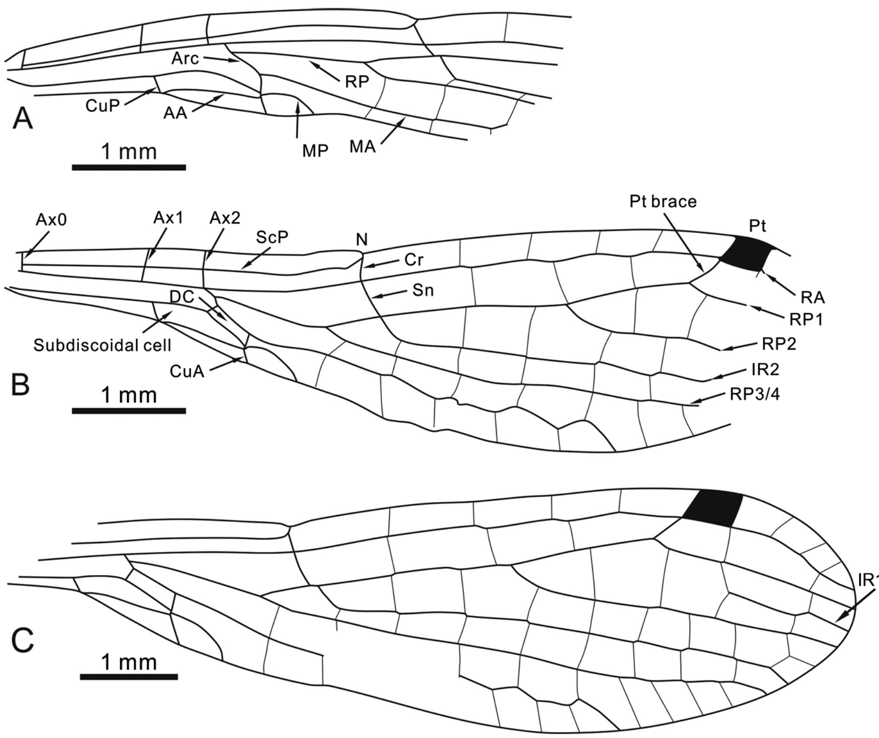

Fig. 4. Burmahemiphlebia zhangi. **A**, Line drawing showing forewing venation of holotype; **B**, Line drawing showing hindwing venation of holotype; **C**, Line drawing showing hindwing venation of paratype.

Forewing (Figs 3A, 4A). Preserved length 4.97 mm, width at level of N 0.99 mm; length from base to Arc 1.93 mm, from Arc to N 1.68 mm. Primary antenodal crossveins preserved, Ax1 1.04 mm distal of Ax0, Ax2 0.6 mm distal of Ax1; no secondary antenodal crossveins present. Arc angular and 0.14 mm distal of Ax2. DC open basally. Subdiscoidal cell free and elongate. CuP almost ending on base of AA. AA separated from AP 0.2 mm distal of Ax1. Nodal structures well preserved, Cr and Sn obliquely aligned. Midfork (base of RP3/4) nearer to N than to Arc, 1.23 mm distal of Arc. Base of IR2 one long cell distal of midfork, lying 0.66 mm distally, almost aligned with Sn. MP curved, very short, 0.46 mm distal of distal angle of DC.

Hindwing (Figs 2B–D, 3B–C, 4B). Preserved length 6.9 mm, estimated complete length 7.5 mm, width at level of N 1.35 mm; length from base to Arc 1.75 mm, from Arc to N 1.39 mm, from N to base of Pt 3.14 mm. Primary antenodal crossveins preserved, Ax1 1.11 mm distal of Ax0, Ax2 0.49 mm distal of Ax1; no subantenodal crossvein present. Arc angular and aligned with Ax2. DC closed basally (Fig. 2B), free, elongate and quadrangular, 0.45 mm long and 0.09 mm wide. Subdiscoidal cell free and elongate. CuP almost ending on base of AA. AA separated from AP 0.16 mm distal of Ax1. Nodal structures well preserved, Cr and Sn aligned slightly obliquely (Fig. 2C). Midfork nearer to N than to DC, 1.07 mm distal of Arc. Base of IR2 aligned with Sn, 0.48 mm distal of midfork. RP2 originating 1.63 mm distal of distal end of Sn, at mid-distance between N and Pt. RP1 with a strong angle below pterostigmal brace. MA distally zigzagged and long, reaching posterior wing margin slightly distal of base of RP2, 5.37 mm distal of wing base. MP curved, very short, ending on posterior wing margin 0.47 mm distal of distal angle of DC. Pt short and broad (Fig. 2D), 0.33 mm long and 0.29 mm wide, covering one cell; pterostigmal brace strong and oblique.

Specimen NIGP163299 (Figs 1B, 2E–H, 3D, 4C) represents a single hyaline hindwing attached to a complete body. The complete body and hindwing provide more characters: body length *ca* 16 mm, with head length *ca* 1 mm, thorax length *ca* 3 mm, and abdomen length *ca* 12 mm; head dark (Fig. 2E–F), broad, 1.36 mm long and 2.66 mm wide; eyes 1 mm wide, well separated by a gap of 0.72 mm; thorax colour metallic green (Fig. 2F); IR1 originating at level of distal end of Pt (Fig. 2G). The hindwing (Figs 3D, 4C) shares all characters of the hindwing of Specimen NIGP163298 apart from the following differences: preserved length 8.66 mm, estimated complete length 9.7 mm; base of IR2 slightly distal of Sn (Fig. 2H); MA ending on posterior wing margin one and half cells distal of base of RP1.

Remarks. Few zygopteran taxa have an open discoidal triangle in the forewing and a closed one in the hindwing, specifically, the Hemiphlebiidae, Chorismagrionidae Tillyard & Fraser, 1938 and Frenguelliidae Petrulevičius & Nel, 2003. The new specimens differ from the Chorismagrionidae in having: 1, the postnodal and postsubnodal crossveins misaligned; 2, the origin of

IR2 being just one cell distal of the midfork; and 3, misalignment between the posterior side of the discoidal cell and the posterior wing margin (Bechly 1996a). Frenguelliidae can also be easily differentiated owing to its characteristically dense vein network (Petrulevičius & Nel 2003). The new specimens share the autopomorphies of the Hemiphlebiidae (Bechly 1996a): lestine oblique vein secondarily absent; wing base with distinctly reduced petiolation; vein RP1 kinked at insertion of pterostigmal brace vein; and all intercalary veins except IR1 and IR2 suppressed. Additionally, the new specimens share two other characters of Hemiphlebiidae, *viz*., tiny size and metallic green structural body colour, seen especially in *Hemiphlebia* and *Parahemiphlebia* (Bechly 2016). However, *Burmahemiphlebia* differs in developing four postnodal crossveins, instead of the 5–7 crossveins generally preserved in the Hemiphlebiidae, although four postnodal crossveins are also present in *Parahemiphlebia mickoleiti* Bechly, 1998.

Among genera of Hemiphlebiidae, *Burmahemiphlebia* shares with *Electrohemiphlebia* the following features: discoidal cell open in the forewing but closed in the hindwing, base of RP3/4 close to Sn, and the base of IR2 opposite Sn. However, *Burmahemiphlebia* differs distinctly in having a short MP and CuA, developing fewer postnodal crossveins, and in its rectangular discoidal cell. *Pantelusa* resembles *Electrohemiphlebia* and can also be excluded from *Burmahemiphlebia* owing to the same differences. Although *Burmahemiphlebia* shares all of the diagnostic characters of *Jordanhemiphlebia*, the very short MP and CuA seen in the former is different enough to exclude placement in the latter genus. *Mersituria* has a long IR1 originating between Sn and Pt, and a long MP and CuA, so it is also distinctly different from *Burmahemiphlebia*. Finally, *Parahemiphlebia* and *Enteropia* both have a long MP and CuA, and a non-rectangular discoidal cell, and can be excluded from further comparison. *Cretarchistigma* Jarzembowski *et al*., 1998, *Cretahemiphlebia* Jarzembowski *et al*., 1998 and an unnamed damselfly described by Nel *et al*. (2010) are all considered to be closely related to Hemiphlebiidae (Jarzembowski *et al*. 1998, Bechly 1998, Nel *et al*. 2010) but differ from *Burmahemiphlebia* in having IR1 originating before, instead of distal of, Pt. The extant genus *Hemiphlebia* differs from *Burmahemiphlebia* in the presence of a long IR1 originating slightly basal of Pt, the long MP and CuA, a short cell between the bases of RP3/4 and IR2 below Sn, and in developing more crossveins between the main veins (Münz 1919). Therefore, the very short MP and CuA, and rectangular discoidal cell are unique to *Burmahemiphlebia* allowing it to be easily distinguished from other members of Hemiphlebiidae.

Family DYSAGRIONIDAE Cockerell, 1908

Type genus. *Dysagrion* Scudder, 1878

Palaeodysagrion gen. nov.

Type species. *Palaeodysagrion cretacicus* sp. nov.

Etymology. Named after the Greek word παλαιός for ‘old’ and *Dysagrion*. Gender masculine.

Diagnosis. Discoidal cell elongate, more or less rectangular; cubital area slightly broadened distally, with one row of cells just below N; Cr and Sn obliquely aligned with same normal orientation.

Palaeodysagrion cretacicus sp. nov. (Figs 5, 6)

Etymology. After the age of the species.

Diagnosis. No antesubnodal or secondary antenodal crossveins present; CuP distinctly oblique; midfork one long cell basal of N, nearer to N than to Arc; base of IR2 aligned with Sn.

Holotype. NIGP163546. The basal third of a single wing.

Locality and age. Hukawng Valley, Kachin Province, Myanmar; earliest Cenomanian (earliest Late Cretaceous).

Description. A fragmentary wing (Fig. 5) that can not be attributed definitively to a forewing or hindwing owing to the similarity of most zygopteran wings. Preserved length 15.81 mm, estimated complete length 26 mm, width at level of N 4.16 mm; length from wing base to Arc 5.5 mm, from Arc to N 4.44 mm. Primary antenodal crossveins distinct, Ax0 near wing base, Ax1 2.82 mm distal of Ax0, Ax2 1.65 mm distal of Ax1, no secondary antenodal crossveins present. Five visible postnodal and five postsubnodal crossveins, with each set well aligned to one another. Arc angular and located close to Ax2 (Fig. 6A), 0.26 mm basal of Ax2, with posterior (basal discoidal) crossvein weak. DC closed basally (Fig. 10), elongate, more or less rectangular; basal side length 0.27 mm, distal side (MAb) length 0.63 mm, anterior side length 1.72 mm, posterior side length 1.69 mm. Subdiscoidal cell undivided (Fig. 6A), elongate, 2.13 mm long and 0.47 mm wide. CuP oblique, ending on AA 0.57 mm distal of separation point of AA from AP. AA separated from AP 0.55 mm distal of level of Ax1, nearer to Ax1 than to Ax2. Nodal structures well preserved (Fig. 6B), Cr and Sn oblique in same orientation and aligned. Midfork nearer to N than to Arc, 2.97 mm distal of Arc. Base of IR2 one long cell distal of midfork, lying 2.16 mm distally, almost aligned with Sn. MA and MP parallel and straight basally; postdiscoidal area with one row of cells below N. CuA basally zigzagged. Cubital area broadened gradually, with one row of cells just below N.

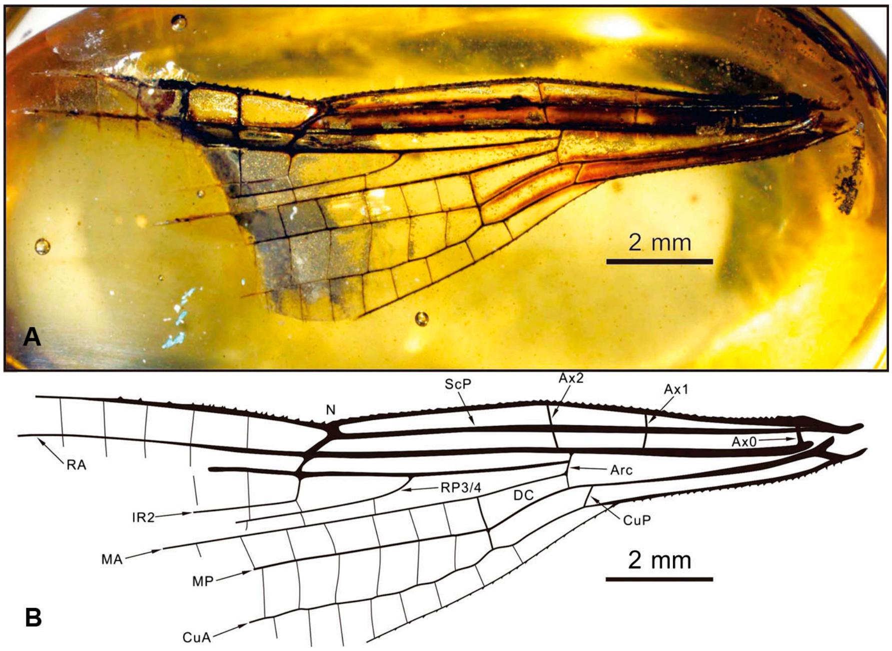

Fig. 5. Palaeodysagrion cretacicus, holotype, NIGP163546. **A**, Photomicrograph of complete specimen; **B**, Line drawing showing wing venation.

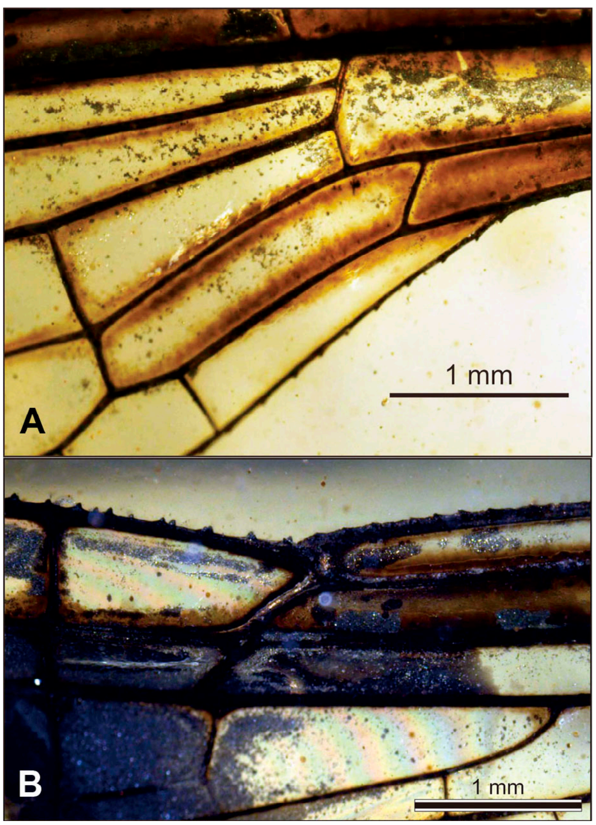

Fig. 6. Palaeodysagrion cretacicus, holotype, NIGP163546. **A**, Photomicrograph showing details of arculus, discoidal and subdiscoidal cells; **B**, Photomicrograph of nodal structures.

Remarks. *Palaeodysagrion* has a combination of characters allowing attribution to the extant family Thaumatoneuridae or the fossil family Dysagrionidae, such as a closed discoidal triangle (more or less rectangular), a non-oblique discoidal vein MAb, a distinctly convexly curved costal margin between the wing base and N, suppression of all secondary antenodal crossveins between ScP and RA distal of Ax2, a free antesubnodal space, and development of the midfork nearer to N than to Arc. Thaumatoneuridae (including *Paraphlebia* Selys-Longchamps, 1862 and *Thaumatoneura* McLachlan, 1897; see Dijkstra *et al*. 2014) has both N and Sn strongly shifted basally, lying between bases of IR2 and RP3/4 (Cr, Sn and base of IR2 aligned in *Palaeodysagrion*), very dense wing venation with high number of cells (normal venation in *Palaeodysagrion*), IR2 arising on RP3/4 (arising on RP2 in *Palaeodysagrion*), and discoidal cell perfectly rectangular (more or less rectangular in *Palaeodysagrion*). *Palaeodysagrion* can, therefore, be attributed to the Dysagrionidae based on the unique shape of the discoidal cell (more or less rectangular with distal side longer than basal side).

Within the Dysagrionidae, *Eodysagrion* is distinguished from *Palaeodysagrion* in having two or three rows of cells in the cubital area below N (only one row in the latter) and Cr poorly aligned with Sn (well aligned in the latter). *Palaeodysagrion* can be excluded from Petrolestini based on its development of the midfork midway between N and Arc. Within Dysagrionini, *Dysagrion* can be differentiated from *Palaeodysagrion* in the following features: Cr and Sn misaligned, four rows of cells in the cubital area below N, two antenodal crossveins present distal of Ax2 between ScP and the costal margin, and discoidal cell not elongate. *Phenacolestes* and *Electrophenacolestes* differ from *Palaeodysagrion* because they have more than one row of cells in the cubital area below N, and in the two antenodal crossveins present distal of Ax2 between ScP and the costal margin. Overall, *Primorilestes* is the most similar genus to *Palaeodysagrion* within the family in that it lacks antenodal crossveins between the costal margin and ScP, has the base of IR2 opposite Sn and has its midfork closer to Sn than to Arc. However, *Palaeodysagrion* differs from *Primorilestes* in having a narrower and more elongate discoidal cell (broader in the latter), in having Cr and Sn oblique in the same orientation and aligned to one another (Sn slightly oblique and not in the same orientation with Cr in the latter), in developing one row of cells between CuA and the posterior wing margin below N (three or four rows in the latter) and in having CuP distinctly oblique (perpendicular to MP + CuA in the latter).

In conclusion, *Palaeodysagrion* is unique in its elongate discoidal cell, a feature lacking in all other genera within this family; further, this feature means the genus can not be attributed to any of the currently defined subfamilies. Other characters of this Burmese amber specimen are shared by members of Dysagrionidae but are not shared in combination by any single genus. Thus, we establish a new genus for this unique specimen from the mid-Cretaceous Burmese amber.

Discussion

Numerous Mesozoic–Cenozoic odonatans have been discovered in laminated clastic strata, but very few have been recorded in amber owing to its scarcity. Odonatans are rare in amber; most previous occurrences are in Cenozoic amber, and very few are from Mesozoic examples (Bechly 1996b, Lak *et al*. 2009, Azar *et al*. 2010, Poinar *et al*. 2010, Bechly & Poinar 2013, Huang *et al*. 2015). The mid-Cretaceous Burmese amber bears abundant insect inclusions, having been studied for a century (Cruickshank & Ko 2003, Shi *et al*. 2012, Kania *et al*. 2015). However, the study of the fossil odonatans has only begun recently (Poinar *et al*. 2010, Bechly & Poinar 2013, Huang *et al*. 2015) and has included the identification of three new damselflies, *Palaeodisparoneura burmanica* Poinar, Bechly & Buckley, 2010, *Mesosticta burmatica* Huang, Azar, Cai & Nel, 2015 and *Cretadisparoneura hongi* Huang, Azar, Cai & Nel, 2015, and the first damsel-dragonfly, *Burmaphlebia reifi* Bechly & Poinar, 2013. In this paper, two new damselflies, *Burmahemiphlebia zhangi* and *Palaeodysagrion cretacicus*, represent the first records of Hemiphlebiidae and Dysagrionidae from Burmese amber. The new finds enhance the known diversity of the damselflies in Burmese amber and extend the palaeogeographic distribution of these two families. *Burmahemiphlebia zhangi* is apparently very common in Burmese amber, since at least 15 more specimens have been observed and checked by the present authors. *Palaeodysagrion cretacicus* is the second dysagrionid damselfly from the Cretaceous deposits and contributes to understanding the evolution and migration of the extinct Dysagrionidae. This family first appeared in the Early Cretaceous of eastern China, was later recorded in Burma from the mid-Cretaceous, and then became widely distributed in America, Denmark, Germany, England and Russia during the Paleocene but disappeared later.

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