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A brief review of Odonata in mid-Cretaceous Burmese amber

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Odonatans are rare as amber inclusions, but quite diverse in Cretaceous Burmese amber. In the past two years, over 20 new species have been found by the present authors after studying over 250 odonatans from 300,000 amber inclusions. Most of them have now been published, and here we provide a brief review. Three suborders of crown Odonata have been recorded, including the damselfly families or superfamilies Platycnemididae, Platystictidae, Perilestidae, Hemiphlebiidae, Coenagrionoidea, Pseudostigmatoidea, Mesomegaloprepidae and Dysagrionidae, plus the dragonfly families Lindeniidae, Gomphaeschnidae and Burmaeshnidae, and the damsel-dragonfly family Burmaphlebiidae.

Keywords: Anisoptera; Anisozygoptera; Zygoptera; Cretaceous; Burmese amber; dragonfly

Introduction

Dragonflies have an excellent fossil record on account of their large size and association with water-laid geological sedimentary deposits. Moreover, the ready preservation of the complex wing venation provides systematically useful features including the appearance of the pterostigma, nodus and arculus. Dragonflies *sensu lato* – in the broad, palaeontological sense or odonatopterans – date back to the earliest-known, late Palaeozoic radiation of the pterygotes (winged insects) in the mid-Carboniferous, circa 320 million years ago. The Carboniferous geropterans resemble some other contemporary insects (palaeodictyopteroids) that did not habitually fold their wings. The Carboniferous-Permian meganisopterans (protodonatans, griffenflies), by contrast, included the celebrated giant dragonflies which were the top aerial predators of their time in well-oxygenated, low-latitude, coal-forming forests. Smaller, narrow-winged protozygopterans (archizygopterans) were, however, also present by the Late Carboniferous; these and other extinct lineages survived the Permo-Triassic crisis.

Modern dragonflies in the entomological sense made their debut in the Mesozoic Era (age of the dinosaurs). True (anisopteran) dragonflies arose in the Jurassic Period, accompanied by diverse anisozygopterans (damsel-dragonflies) unlike today. One of the most exciting discoveries of the past few years has been the recovery of numerous odonatans in mid-Cretaceous Burmese amber (circa 100 million years old). The inclusions, especially true damselflies (zygopterans), were entrapped in a resinous, coniferous woodland amidst the burgeoning angiospermous flowering plants along the north-eastern fringe of the Tethyan ocean. Questions remain, however, such as what the forest palaeoecology was really like.

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Figure 1. Burmese amber mines in Hukawng Valley, Kachin Province, Myanmar.

Odonata have a relatively high diversity in Burmese amber, with 21 species in 18 genera representing 13 families having been described; more new species will be described in the future, especially rare ones. All these specimens are based on the adult stage, but there are still many immature insect inclusions (nymphs/larvae) which need to be studied. Over 250 odonatans have been examined by the present authors, representing the most abundant dragonfly assemblage so far discovered in any amber inclusions. Here we give a review of the odonatans from Burmese amber. The most diverse odonatans, especially damselflies, can help us evaluate the origin, evolution, and palaeobiogeography of the modern families of Odonata.

Material and methods

The specimens reviewed herein were collected in the Hukawng Valley of Kachin Province, Myanmar (Figure 1), and the age of Burmese amber is considered to be Late Albian (Zheng, Nel, Chang, Jarzembowski, Zhang, et al., 2018). The amber containing the dragonflies is normally yellow or red and transparent. 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, Martinez-Delclòs, Paicheler, and Henrotay (1993) and Bechly (1996). Photographs were taken using a Zeiss Stereo Discovery V16 microscope system (Jena, Germany) and Zen software (Carl Zeiss Microscopy, Jena). All the specimens are housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS).

Odonata in Burmese amber

Anisoptera

True dragonflies are normally not well present as amber inclusions due to their large size and they normally fly in more open habitats. Six true dragonflies have been described from Burmese amber, including Lindeniidae (Schädel & Bechly, 2016), Gomphaeschnidae (Zheng,

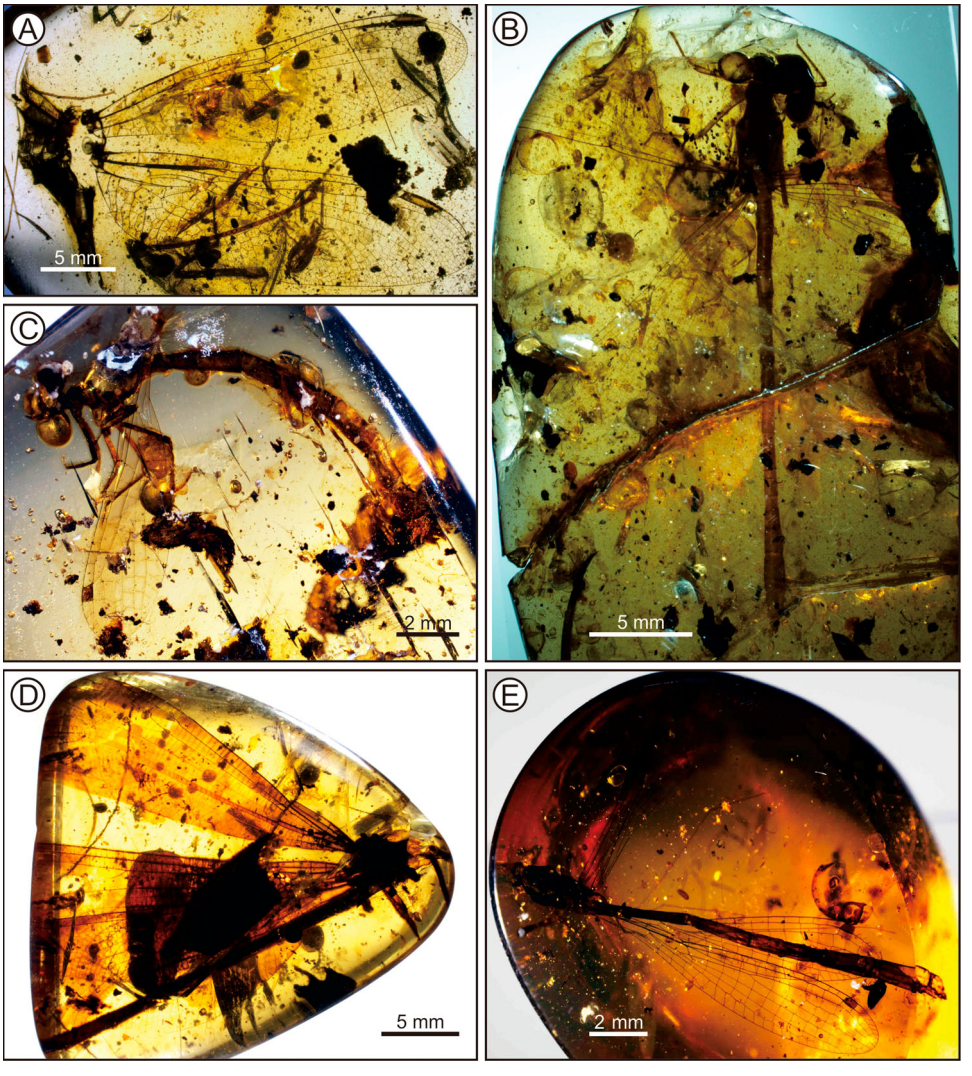

Figure 2. Typical odonatans from Burmese amber. (A) *Burmagomphides electronica* (Burmagomphidae); (B) *Burmaphlebia* sp. nov. (Burmaphlebiidae); (C) *Burmahemiphlebia zhangi* (Hemiphlebiidae); (D) *Mesomegaloprepus magnificus* (Mesomegaloprepidae); (E) *Mesosticta electronica* (Platystictidae).

Jarzembowski, Chang, & Wang, 2016), Burmaeshnidae (Zheng, Chang, Wang, & Jarzembowski, 2017; Huang, Cai, Nel, & Bechly, 2017; Huang, Cai, & Nel, 2017), and Burmagomphidae (Zheng, Nel, Chang, Jarzembowski, Zhang, et al., 2018). Almost all the recorded dragonflies are preserved with fragmentary wings, except a recently found specimen with complete forewing and hindwing, viz, *Burmagomphides electronica* (Figure 2A). *B. electronica* has a wing length of *c*.26 mm, sharing mixed characters of Hagenioidea and Brevicubitalia. *Cretaeshna lini* Zheng, Chang, Wang, et al., 2017 and *Burmaeshna azari* Huang, Cai, & Nel, 2017b are considered to have a close relationship with Telephlebiidae Cockerell, 1913.

Anisozygoptera

Burmaphlebia reifi Bechly & Poinar 2013 (Burmaphlebiidae) is the only damsel-dragonfly recorded in the amber inclusions. Thirty-six specimens attributed to *Burmaphlebia* have been

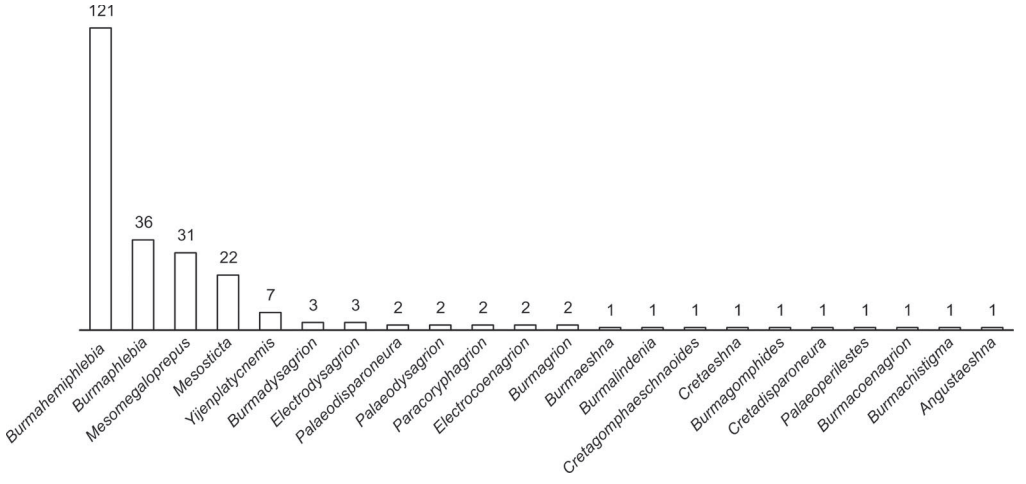

Figure 3. Histogram chart showing number of odonatan specimens vs. genus in Burmese amber.

examined by the present authors (Figure 3). *Burmaphlebia* has a small wing size of 11–13 mm and a pronounced anal angle in the hindwing (Figure 2B), which is quite frequent among other Mesozoic damsel-dragonflies.

Zygoptera

The recent family Hemiphlebiidae Kennedy, 1920 contains the relict *Hemiphlebia mirabilis* Selys Longchamps, 1869 found in the swamps of Victoria, Australia (Cordero-Rivera, 2016). However, the fossil record is more diverse, including seven fossil genera recorded from the Mesozoic of England, Jordan, Brazil, France, Israel, America as well as Burmese amber (Zheng, Zhang, et al., 2017). *Burmahemiphlebia zhangi* Zheng, Zhang, et al., 2017 (Figure 2C) is the dominant damselfly inclusion, numbering over 100 specimens and comprising *c*.60% of all odonatans observed by the present authors. *Burmahemiphlebia* is comparatively small with a wing length of 7.5–10 mm, differing from *Hemiphlebia* in the presence of a short vein IR1 (first interradial) originating below Pt (the pterostigma), short veins MP (posterior median) and CuA (anterior cubitus), and in having few crossveins between the main veins.

The family Platystictidae Kennedy, 1920 is commonly called the forest damselflies or shadow damsels, preferring to hang from trees along streams. It currently consists of about 250 extant species in eight genera and four tropical subfamilies and is restricted to central and northern South America (subfamily Palaemnematinae) and tropical Southeast Asia (subfamilies Platystictinae, Protostictinae and Sinostictinae) (Dijkstra, Kalkman, Dow, Stokvis, & van Tol, 2014; Schorr & Paulson, 2015; Suhling et al., 2015; van Tol, Reijnen, & Thomassen, 2009). The subfamily Mesostictinae Zheng, Wang, et al., 2019 contains three species in mid-Cretaceous Burmese amber (Figures 2E, 4B; Huang, Azar, Cai, & Nel, 2015; Zheng, Zhang, Chang, & Wang, 2016; Zheng, Wang, et al., 2019), sharing the typical characters of platystictid damselflies: a long and very slender abdomen and a unique wing venation comprising a basally recessed "CuP" (posterior cubitus), a long IR1, and the usual diamond-shaped subdiscoidal cell. Mesostictinae, however, differ from modern Platystictidae by the presence of fewer postnodal and postsubnodal crossveins, a short MP (posterior median), the base of RP2 (second posterior radius) being nearer to the subnodus, and the nodus lying more distally. Platystictid damselflies are comparatively frequent as amber inclusions. They were previously considered to have originated in the

Late Cretaceous in the northern hemisphere (van Tol & Müller, 2003; van Tol et al., 2009), while *Mesosticta* puts the appearance of Platystictidae back to at least the mid-Cretaceous.

The Family Perilestidae Kennedy, 1920 is normally called shortwings or twigtails. It has short wings (20–25 mm) and very long, slender and colour-banded abdomens (40–56 mm) (Williamson and Williamson 1924; Haber and Wagner, 2014). It is a small family, now comprising two Neotropical genera (*Perilestes* Hagen in Selys Longchamps, 1862 and *Perissolestes* Kennedy, 1941) and 19 species (Dijkstra et al., 2011, 2014; Machado, 2015; Schorr & Paulson, 2015). The adults of recent Perilestidae often perch on plant stems or dead twigs near streams and frequent the understory and glades within dense forest, thus making them easily overlooked in the field. *Palaeop*erilestes *electronicus* Zheng, Wang, Jarzembowski, Chang, & Nel, 2016a (Figure 4D) from Burmese amber is the first fossil perilestid, identified by the midfork being distal of the subnodus and the base of IR2 (second interradial) being near to the base of RP2, but having a strongly zigzagged IR1 unlike recent species. *P. electronicus* puts the origin of Perilestidae back to at least the mid-Cretaceous.

The recent superfamily Coenagrionoidea Kirby, 1890 comprises three-fifths of all extant damselfly species (over 1800 species). It currently includes Isostictidae, Platycnemididae and Coenagrionidae (Dijkstra et al., 2014). Coenagrionoid damselflies are frequent in Mesozoic-Cenozoic strata, having been recorded from Baltic, Dominican and Mexican ambers and the USA, Germany, France and Brazil as adpressions (Bechly, 2000, 2012; Carle & Wighton, 1990; Jarzembowski et al., 1998; Nel & Jarzembowski, 1999; Nel & Paicheler, 1993; Poinar, 1996; Ross et al., 2016). Coenagrionoidea are quite diverse in Burmese amber and are typically represented by the earliest Platycnemididae (Figure 4A; Poinar, Bechly, & Buckley, 2010; Huang et al., 2015; Zheng, Nel, et al., 2017; Zheng, Wang, & Chang, 2017). The first coenagrionoid damselfly described from Burmese amber was *Burmagrion marjanmakoki* Möstel, Schorr & Bechly, 2017 but lacked detailed discussion and accurate attribution: it was recently attributed to a new coenagrionoid family established and based on four new species in three new genera (Zheng, Nel, et al., 2019). The Family Platycnemididae Yakobson and Bianchi, 1905 is quite diverse in Burmese amber with four species in three genera having been described (Poinar et al., 2010; Huang et al., 2015; Zheng, Nel, et al., 2017; Zheng, Wang, et al., 2017). There have been few previous records of fossil Platycnemididae: the recent family, on the other hand, consists of over 400 species widely distributed in the Old World (Dijkstra et al., 2014; Schorr & Paulson, 2015; Theischinger, Gassmann, & Richards, 2015). A fossil subfamily Palaeodisparoneurinae Poinar, Bechly & Buckley, 2010 was attributed to Platycnemididae based on a well-preserved damselfly from mid-Cretaceous Burmese amber. Three species in two genera were included in this subfamily: *Palaeodisparoneura burmanica* Poinar, Bechly & Buckley, 2010, *P. cretacica* Zheng, Wang, et al., 2017 and *Yijenplatycnemis huangi* Zheng, Nel, et al., 2017. *Y. huangi* (Figure 4A) has extremely expanded, pod-like or plate-like tibiae interpreted as probably helping to fend off other suitors as well as attract mating females, thus increasing the chances of successful mating (as in the living *Platycnemis foliacea*). This is the first fossil evidence of courtship behaviour in fossil odonatans, although it must have impeded directional flight.

The superfamily Pseudostigmatoidea consists of Coryphagrionidae and Pseudostigmatidae according to Bechly (2007) (see also Dijkstra et al., 2014). Coryphagrionidae contains the monotypic genus *Coryphagrion grandis* Morton, 1924, which is normally called the "East Coast Giant" distributed in the fragmented coastal forests of Kenya and Tanzania (Clausnitzer, 2010). The Neotropical family Pseudostigmatidae contains the largest extant odonatan, *Megaloprepus caerulatus* Drury, 1782, with a wingspan of over 190 mm (Dijkstra et al., 2014; Ingley, Bybee, Tennessen, Whiting, & Branham, 2012). *Paracoryphagrion deltoides* (Figure 4F; Zheng, Nel, Chang, Jarzembowski, Zhuo, & Wang, 2018b) has a wing length of *c*.30 mm. It is attributed to the superfamily Pseudostigmatoidea due to the presence of an extremely long, slightly zigzagged vein CuA (anterior cubitus) covering numerous cells parallel to the hindwing margin, and

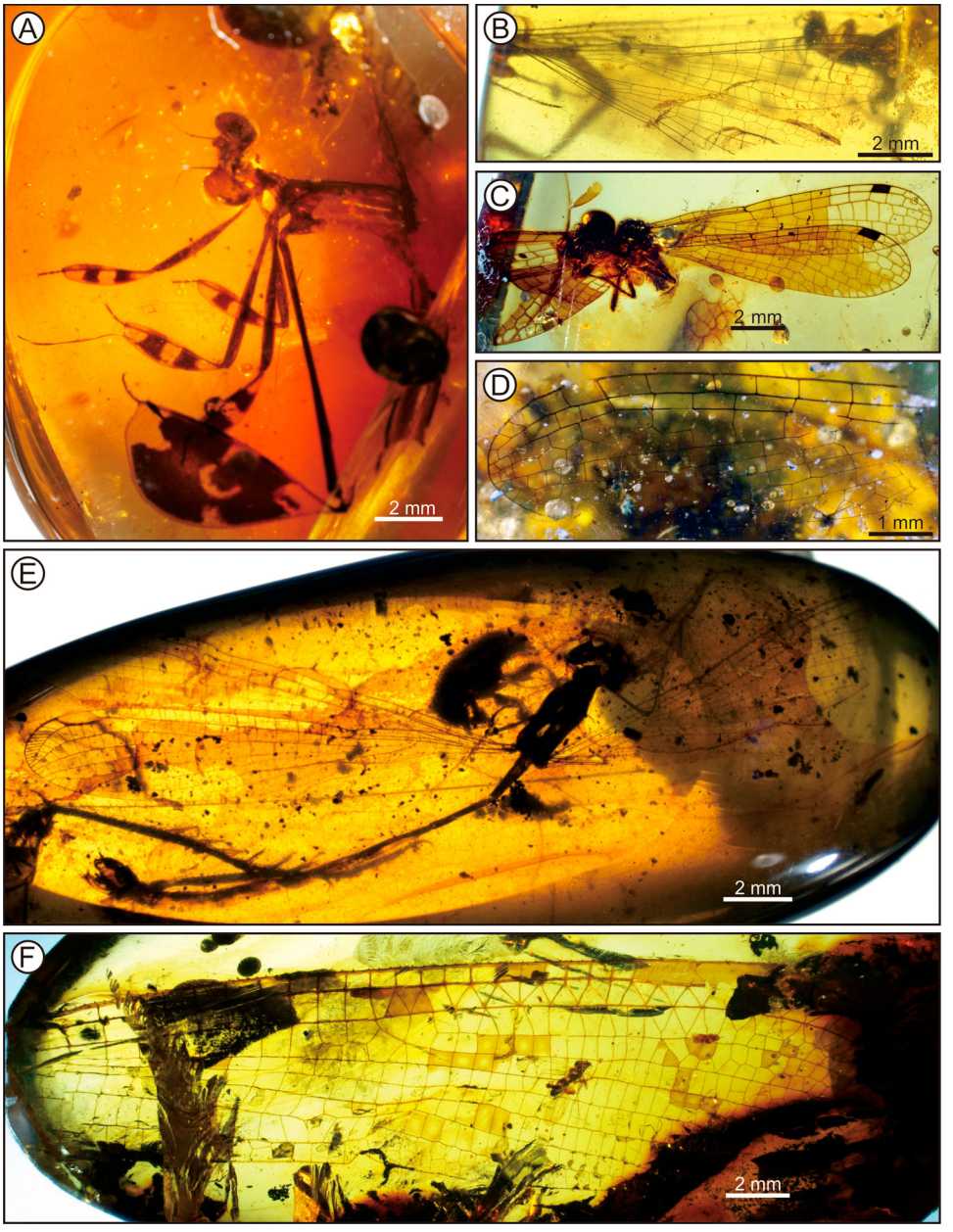

Figure 4. Typical odonatans from Burmese amber. (A) *Yijenplatycnemis huangi* (Platycnemididae); (B) *Mesosticta burmatica* (Platystictidae); (C) *Burmadysagrion zhangi* (Dysagrionidae); (D) *Burmacoenagrion preciosus* (Coenagrionoidea); (E) *Paracoryphagrion deltoides* (Pseudostigmatoidea).

numerous trigonal cells like *C. grandis*. It differs, however, from other pseudostigmatoid families in characters near the unique pterostigmal area: *P. deltoides* is unique within Zygoptera due to the presence of a very elongate pterostigma and many triangular cells in the postsubnodal area.

Dysagrionidae (Dysagrioninae Cockerell, 1908) is an extinct damselfly family and sister to the extant Thaumatoneurinae Tillyard & Fraser, 1938 (Bechly, 2007). While this relationship is debatable, the former has been considered as a separate family (Garrouste & Nel, 2015).

Dysagrionidae now comprise three subfamilies and 10 genera. The oldest fossil representative is *Congqingia* from the Lower Cretaceous Laiyang Formation of Shandong Province, eastern China (Zhang, 1992) and it is the only adpression of dysagrionid damselflies known from the Mesozoic. Other dysagrionid damselflies are widely recorded from the Cenozoic of America, Denmark, Germany, England, Russia, as well as in Burmese and Baltic amber (Zheng et al., 2017b). They are quite diverse in Burmese amber with three genera and species including *Burmadysagrion zhangi* Zheng, Wang, Jarzembowski, Chang, & Nel, 2016b, *Palaeodysagrion cretacicus* Zheng, Zhang, et al., 2017 and *Electrodysagrion lini* Zheng, Chang, Nel, et al., 2017. Dysagrionidae are characterised by a somewhat rectangular discoidal cell normally with the distal side longer than the basal side. However, the discoidal cells of the dysagrionid damselflies are diverse in detail: very elongate and somewhat rectangular in *P. cretacicus*; anterior and posterior sides not parallel and basal side longer than distal side in *B. zhangi* (burmadysagrionine type); anterior and posterior sides not parallel and distal side longer than basal side in *E. lini* (sieblosiid-dysagrionine type). Thus fossil dysagrionid damselflies can help us appreciate the diversity and evolution of the discoidal cell. New discoveries will be reported at future congresses.

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