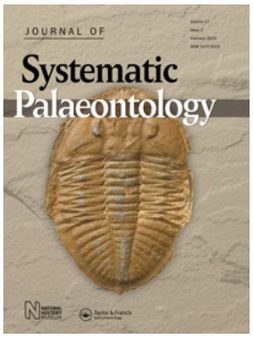

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A highly diverse coenagrionoid damselfly group (Odonata: Zygoptera: Burmacoenagrionidae fam. nov.) from mid-Cretaceous Burmese amber

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The damselfly superfamily Coenagrionoidea is the largest zygopteran group, comprising three-fifths of all extant damselfly species. The Mesozoic fossil record of this superfamily is sparse, whilst it is relatively common in Burmese amber. A new coenagrionoid family, Burmacoenagrionidae Zheng *et al*., fam. nov., is established here based on four new species in three new genera: *Burmacoenagrion pretiosus* Zheng *et al.* gen. et sp. nov., *Burmachistigma cheni* Zheng *et al.* gen. et sp. nov., *Electrocoenagrion elongatum* Zheng *et al.* gen. et sp. nov. and *Electrocoenagrion forficatum* Zheng *et al.* gen. et sp. nov. The previously described damselfly genus, *Burmagrion* Möstel *et al*., 2017, is transferred to this family. Burmacoenagrionidae Zheng *et al.* fam. nov. has a long pterostigma covering 3–5 cells, pigmented wings and a sigmoidally curved RA and RP1 distal of the pterostigma, differing from other coenagrionoid damselflies. Until now, this is the most diverse damselfly family reported from Burmese amber, showing that the Coenagrionoidea were already highly diversified 100 million years ago.

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Keywords: Coenagrionoidea; Zygoptera; Odonata; Albian; Cretaceous; Burmese amber

Introduction

The superfamily Coenagrionoidea Kirby, 1890 consists of three-fifths of all extant damselfly species (over 1800 species) currently including three families: Isostictidae, Platycnemididae and Coenagrionidae (Dijkstra *et al*. 2014). Coenagrionoidea is considered monophyletic, but can include Coenagrionidae, Platycnemididae, Protoneuridae and Pseudostigmatidae *sensu* Silsby (2001) (Bybee *et al*. 2008; Carle *et al*. 2008) with Isostictidae as the sister group (Bybee *et al*. 2008). This view is similar to that of Bechly (2007a), i.e. the Coenagrionida including Pseudostigmatoidea and Coenagrionoidea (Platycnemididae, Protoneuridae and Coenagrionidae).

The coenagrionoid damselflies are frequent in Cenozoic deposits, viz. Eocene Baltic amber (Bechly 2012), upper Eocene of the Isle of Wight, UK (Nel & Jarzembowski 1999; Nel & Fleck 2014), Oligocene and Miocene of Germany and France (Nel & Paicheler 1993), Miocene Dominican (Poinar 1996; Bechly 2000) and Mexican amber (Ross *et al*. 2016). The Mesozoic fossil record is scarcer, mainly from the Lower Cretaceous of the UK (Jarzembowski *et al*. 1998) and Brazil (Carle & Wighton 1990). In Burmese amber, Coenagrionoidea are quite diverse, typically represented by the earliest Platycnemididae (Poinar *et al*. 2010; Huang *et al*. 2015; Zheng *et al*. 2017a, b). Another coenagrionoid damselfly, *Burmagrion marjanmatoki* Möstel *et al*., 2017, was recently reported from Burmese amber (Möstel *et al*. 2017) but short of detailed discussion and accurate attribution. In the present paper, we described a new coenagrionoid family based on four new species in three new genera. The genus *Burmagrion* Möstel *et al.*, 2017 is transferred to this family. The new family is the most diverse damselfly group in Burmese amber.

Material and methods

All samples containing the damselflies were collected in the Hukawng Valley (26° 29′ N, 96° 35′ E) in Kachin

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Province, Myanmar (locality in Kania *et al*. 2015, fig. 1). The age of Burmese amber is 98.79 ± 0.62 Ma (Shi *et al*. 2012), but this is a re-deposition age (Zherikhin & Ross 2000; Ross *et al*. 2010; Ross 2015). Palynology and an ammonite from the amber-bearing layers suggest a late Albian age (Cruickshank & Ko 2003) which we adopt herein.

The amber pieces containing the damselfly are either red or 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 are digitally stacked photomicrographic composites of approximately 40 individual focal planes obtained using the free software Combine ZP for a better illustration of the 3D structures. The line drawings were prepared from photographs 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 (**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 classification of the clade Coenagrioniformia is after Bechly (2007a). Wing venation 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; **SdC**, subdiscoidal cell; **Sn**, subnodal crossvein.

Systematic palaeontology

Order **Odonata** Fabricius, 1793
Suborder **Zygoptera** Selys Longchamps, 1854
Superfamily **Coenagrionoidea** Kirby, 1890
Family **Burmacoenagrionidae** Zheng *et al.* fam. nov.

Type genus. *Burmacoenagrion* Zheng *et al.* gen. nov.

Other genera. *Burmagrion* Möstel *et al.*, 2017, *Burmachistigma* Zheng *et al.* gen. nov. and *Electrocoenagrion* Zheng *et al.* gen. nov.

Diagnosis. AA' originating from AP slightly nearer to Ax2 than to Ax1; DC free, broad, with distal side MAb slightly oblique and longer than basal side; 12–19 postnodal crossveins present distal of N and basal of Pt, somewhat aligned in basal half of area but not in distal part; Pt long, covering 3–5 short cells, distinctly braced; pterostigmal part of RA and stigmal crossveins thickened to form U-shaped structure; RP1 with weak angle below Pt-brace; IR1 originating 1–4 cells distal of base of RP2; RA and RP1 sigmoidally curved distal of Pt; numerous sigmoidally curved postnodal crossveins present distal of Pt; RA, RP1, IR1, RP2, IR2 converging near posterior wing margin; one row of cells between CuA and posterior wing margin.

Genus ***Burmacoenagrion*** Zheng *et al.* gen. nov.

Type species. *Burmacoenagrion pretiosus* Zheng *et al.* sp. nov.

Diagnosis. Wing hyaline; Arc slightly distal of Ax2; IR2 aligned with Sn in forewing but originating one cell distal of Sn in hind wing; Pt hyaline, well braced; MA long, ending on posterior wing margin just below Pt brace; MP long, ending on posterior wing margin one cell distal of RP2 base; CuA short, covering four or six cells.

Etymology. Named after Burma and *Coenagrion*. Gender male.

Burmacoenagrion pretiosus Zheng *et al*. sp. nov.
(Figs 1–3)

Holotype. NIGP 165219, complete left forewing and hind wing, right forewing lost, right hind wing with basal two-thirds preserved, all wings attached to complete body.

Diagnosis. As for genus.

Etymology. Named after the Latin word for great-value '*pretiosus*', for the well-preserved, beautiful specimen.

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

Description. Body length *c.* 17 mm, head length *c.* 1 mm, thorax length *c.* 3 mm and abdominal length *c.* 13 mm; head dark (Fig. 2A), broader than long. Eyes not well preserved, separated by gap of 0.8 mm. One foreleg, two mid legs and two hind legs preserved (Fig. 2B).

Left forewing complete (Fig. 1B). Wing length 14.18 mm; length from wing base to Arc 2.78 mm, from Arc to N 1.88 mm, from N to Pt 7.78 mm, from Pt to wing apex 1.75 mm. Primary antenodal crossveins preserved (Fig. 2D), Ax0 close to wing base, Ax1 1.33 mm distal of Ax0, Ax2 1.17 mm distal of Ax1; no secondary antenodal and antesubnodal crossveins present. Fourteen postnodal crossveins and 12 postsubnodal crossveins present before Pt, partly aligned. Eleven postnodal and five postsubnodal crossveins present distal of Pt, non-aligned. Arc angular and slightly distal of Ax2. DC basally closed (Fig. 2E), free, long and narrow, somewhat rectangular with weak distal angle; anterior side slightly parallel with posterior side, and distal side longer than basal side; length of basal side

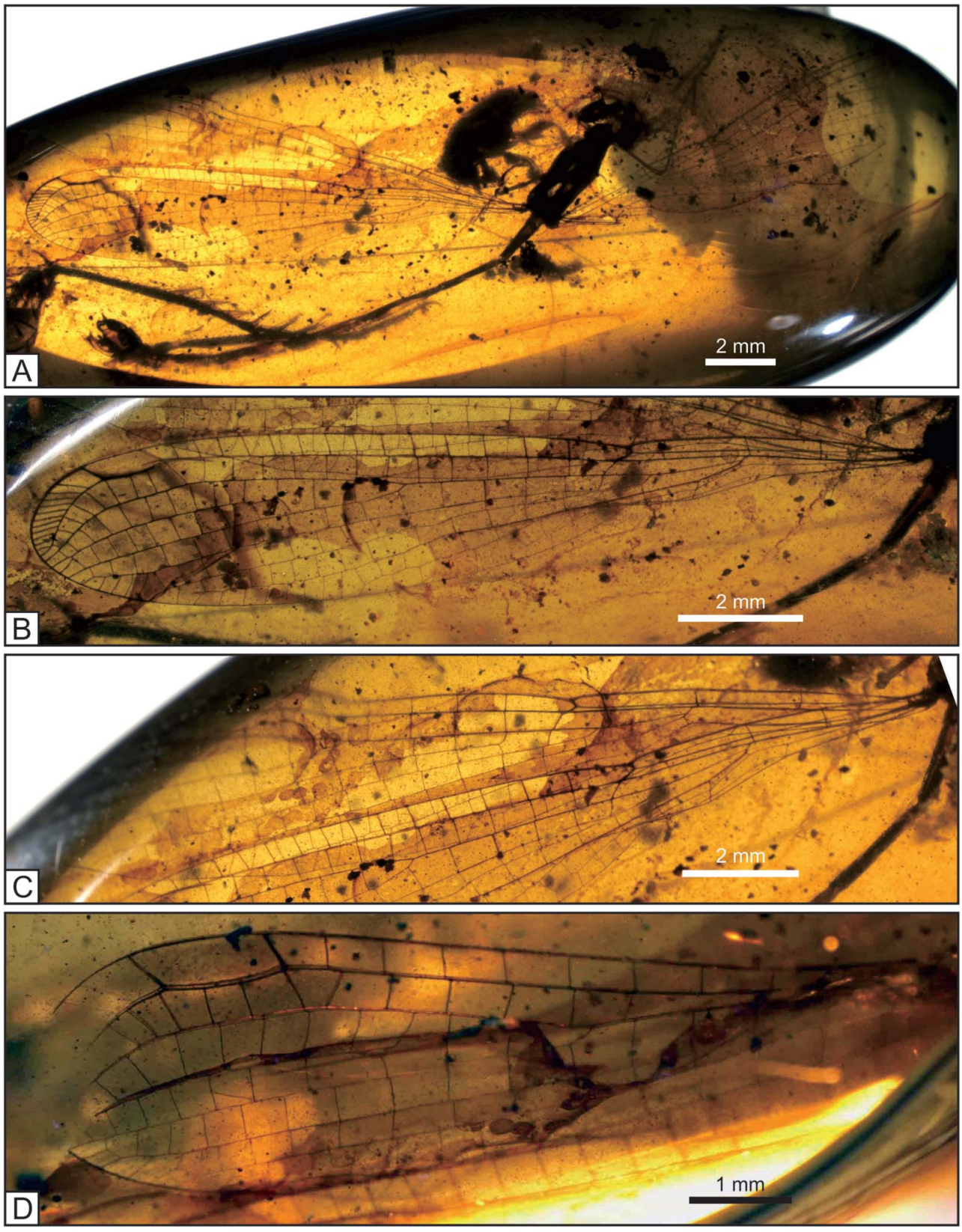

Figure 1. *Burmacoenagrion pretiosus* Zheng *et al.* gen. et sp. nov., holotype, NIGP 165219. Photographs of **A,** entire specimen; **B,** left forewing; **C, D,** left hind wing.

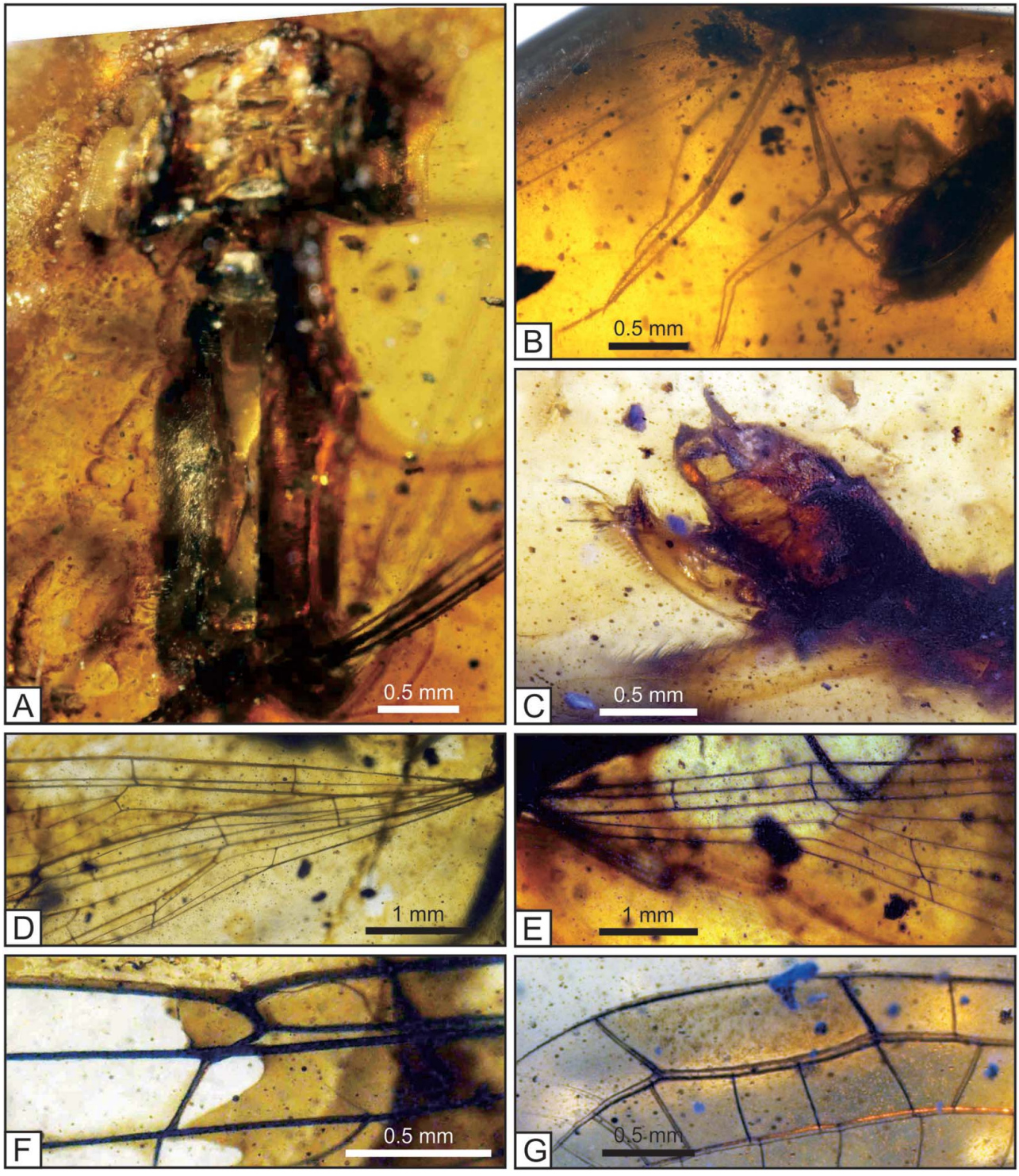

Figure 2. *Burmacoenagrion pretiosus* Zheng *et al.* gen. et sp. nov., holotype, NIGP 165219. Photographs of **A,** head and thorax; **B,** legs; **C,** anal terminalia; **D,** left forewing and hind wing base; **E,** right hind wing base; **F,** left forewing nodus; **G,** left hind wing pterostigma.

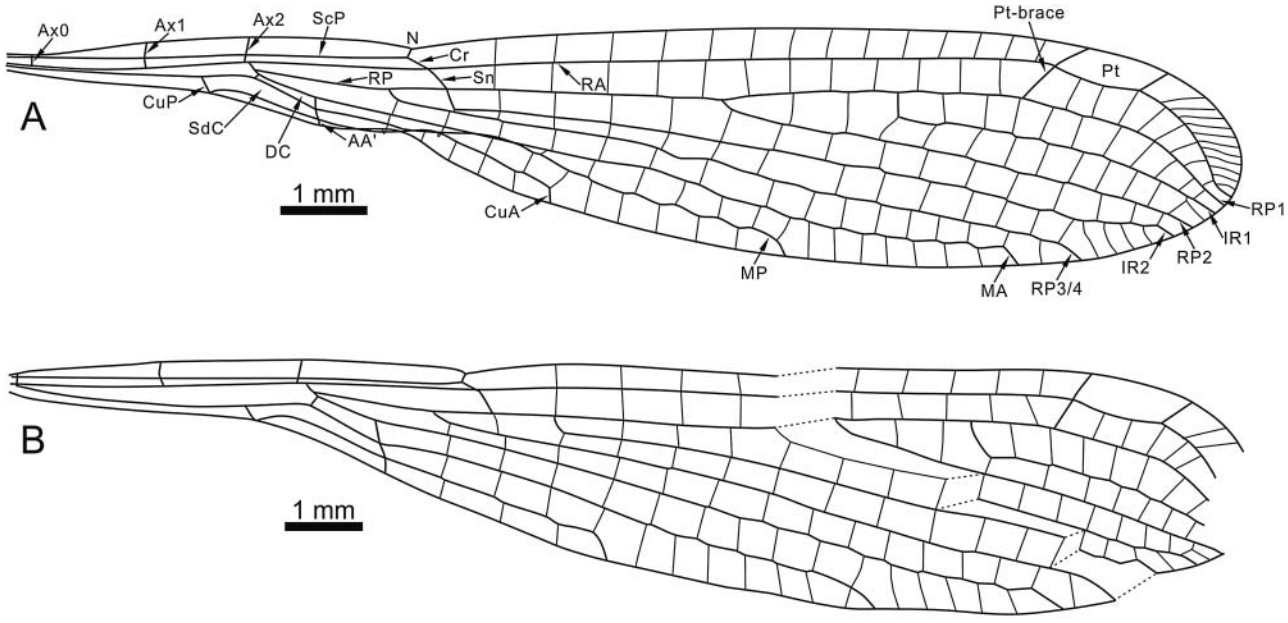

Figure 3. Line drawing showing wing venation of *Burmacoenagrion pretiosus* Zheng *et al.* gen. et sp. nov., holotype, NIGP 165219, **A,** forewing; **B,** hind wing.

0.06 mm, of anterior side 0.7 mm, of distal side 0.14 mm, of posterior side 0.77 mm. SdC free and elongate, 1.38 mm long and maximum 0.2 mm wide. CuP 0.63 mm distal of level of Ax1. Nodal structures well preserved (Fig. 2F), Sn aligned with Cr. Midfork (base of RP3/4) just under N. Base of IR2 aligned with Sn, one cell and 0.66 mm distal of midfork. RP2 originating five cells distal of Sn, lying 3.17 mm distally, nearer to N than to Pt. IR1 long, originating three cells distal of base of RP2 and three cells basal of Pt, lying 2.02 mm distal of base of RP2. RP1 with weak angle below Pt-brace. MA distally zigzagged and long, reaching posterior wing margin just below Pt brace. MP distally zigzagged and long, ending on posterior wing margin one cell distal of base of RP2. CuA long, covering six cells. All intercalary veins (except IR1 and IR2) suppressed. Pt long, hyaline, with basal side and distal side oblique, covering three cells and well braced (Fig. 2G), 0.96 mm long and 0.48 mm wide; posterior side of Pt thickened and fused with strongly thickened pterostigmal part of RA to form U-shaped structure; Pt-brace less oblique than Pt base.

Remarks. *Burmacoenagrion* differs from *Burmachistigma* in having a hyaline pterostigma and wing, the midfork being not as much basal of Sn, IR2 originating one cell distal of Sn in the hind wing, RP2 originating more cells distal of Sn, IR1 originating at mid level between RP2 and the Pt-brace, and MA ending on the posterior wing margin just below the Pt-brace. *Burmacoenagrion* differs from *Electrocoenagrion* in having a hyaline pterostigma and wing, a short pterostigma, a straight Pt-brace, IR2 originating one cell distal of Sn in the hind wing, IR1 originating at the level of the mid-area between RP2 and the Pt-brace, and only one row of postnodal crossveins distal of Pt. *Burmacoenagrion* differs from *Burmagrion* in having a hyaline pterostigma, IR2 originating one cell distal of Sn in the hind wing, a broader postpterostigmal area between C and RA with more sigmoidally curved postnodal crossveins distal of Pt, and a shorter CuA ending only two cells distal of Sn level in the hind wing.

Genus ***Burmachistigma*** Zheng *et al.* gen. nov.

Type species. *Burmachistigma cheni* Zheng *et al.* sp. nov.

Diagnosis. Forewing dark but hind wing hyaline; hind wing obviously broader than forewing; Pt dark, covering three or four cells, well braced; hind wing Pt broader and shorter than that of forewing; RP2 originating three cells distal of Sn in forewing; MA long, ending on posterior wing margin below distal side of Pt; 11–13 cells between MA and MP along wing margin.

Etymology. Named after Burma and its unique pterostigma.

Burmachistigma cheni Zheng *et al*. sp. nov.
(Figs 4, 5)

Holotype. NIGP 165220, a forewing and hind wing, with distal two-thirds present, gender unknown.

Diagnosis. As for genus.

Etymology. Named after the Chinese geologist Peiji Chen.

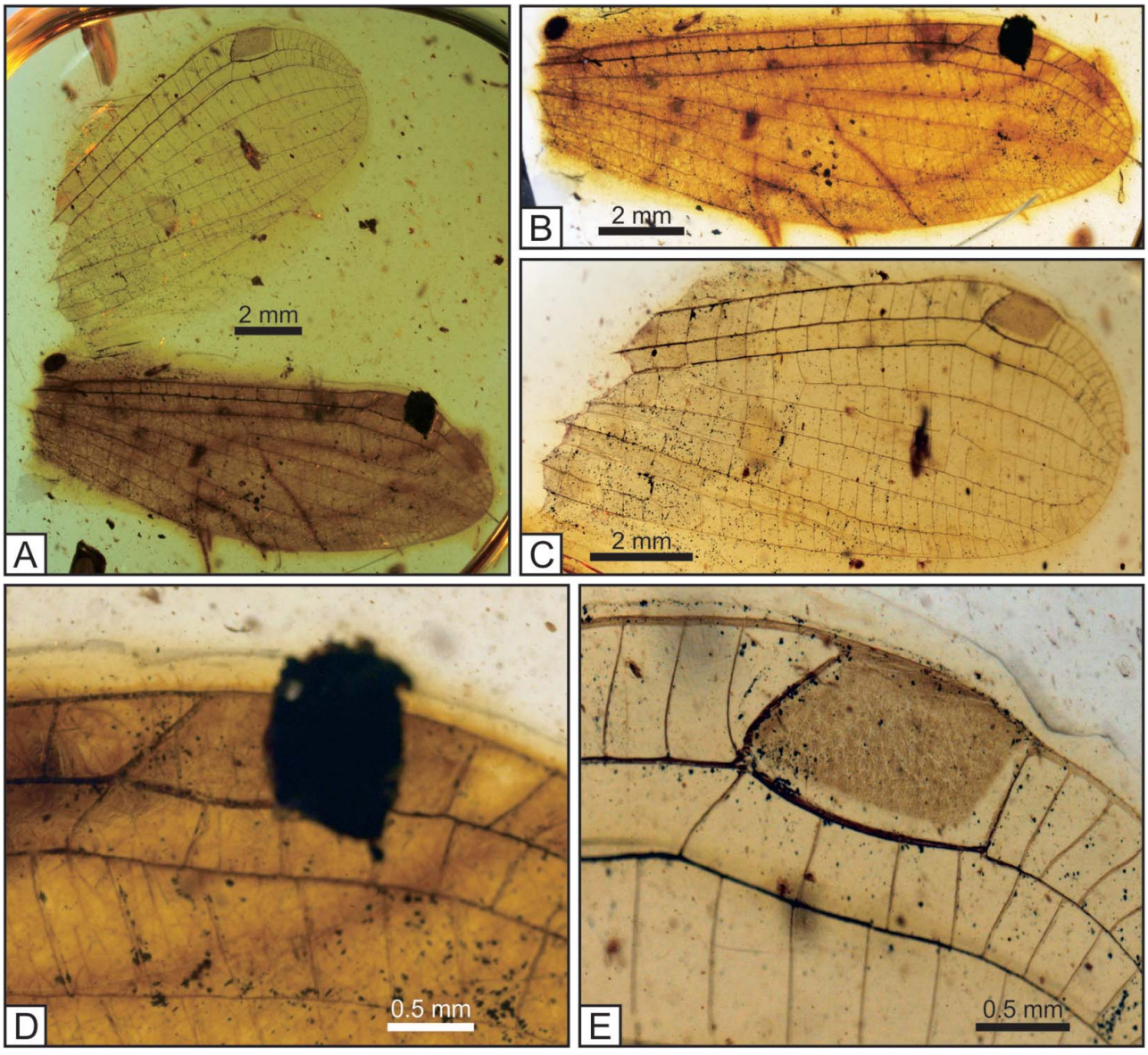

Figure 4. *Burmachistigma cheni* Zheng *et al.* gen. et sp. nov., holotype, NIGP 165220. Photographs of **A,** specimen; **B,** forewing; **C,** hind wing; **D,** forewing pterostigma; **E,** hind wing pterostigma.

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

Description. Forewing preserved length 13.88 mm (Fig. 4B), width at level of N 2.39 mm; length from N to Pt 8.8 mm, from Pt to wing apex 3.97 mm. Twelve postnodal crossveins and 10 postsubnodal crossveins present before Pt, partly aligned. Twelve postnodal crossveins and nine postsubnodal crossveins present distal of Pt, non-aligned. Midfork 0.75 mm basal of N. Nodal structures well preserved, Sn aligned with Cr. Base of IR2 aligned with Sn, one cell and 1.34 mm distal of midfork. RP2 originating three cells distal of Sn, lying 2.22 mm distally, nearer to N than to Pt. IR1 long, originating three cells distal of base of RP2 and six cells basal of Pt, lying 2.15 mm distal of base of RP2. RP1 with weak angle below Pt-brace. MA distally zigzagged and long, reaching posterior wing margin just below distal side of Pt. MP distally zigzagged and long, ending on posterior wing margin slightly basal of Pt base. CuA covering nine cells, ending on posterior wing margin slightly basal of IR1 base. Two cells present between IR1 and RP2 along wing margin. Four cells present between IR2 and RP2 along wing margin. Pt long, dark, with basal side more oblique than distal side, covering four cells and well braced (Fig. 4D), 1.77 mm long and 0.71 mm wide; posterior side of Pt thickened and fused with strongly thickened pterostigmal part of RA to give U-shaped structure; Pt brace oblique like Pt base.

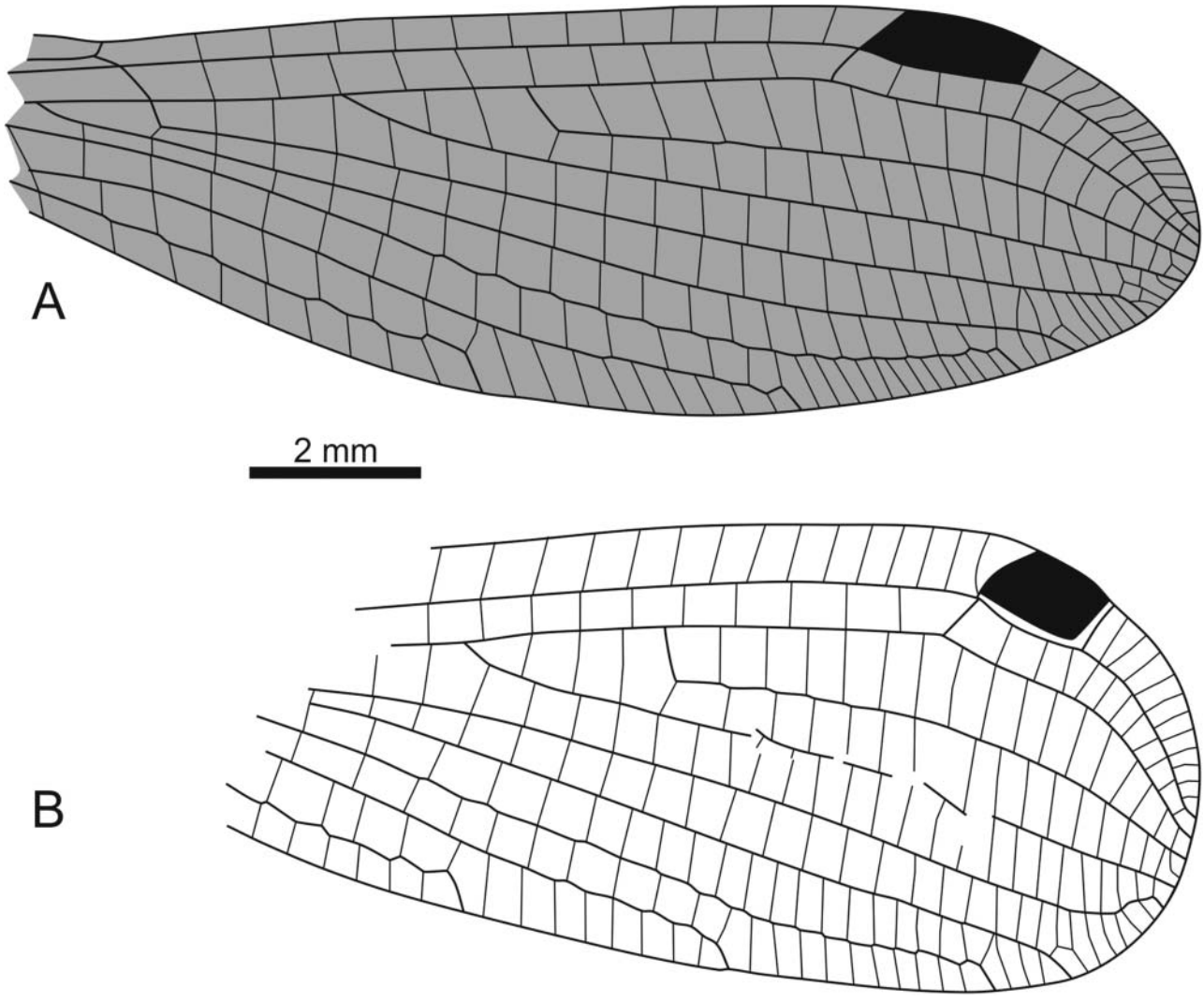

Figure 5. Line drawing showing wing venation of *Burmachistigma cheni* Zheng *et al.* gen. et sp. nov., holotype, NIGP 165220, **A,** forewing; **B,** hind wing.

Hind wing preserved length 11.32 mm (Fig. 4C). Fifteen postnodal crossveins and 10 postsubnodal crossveins present before Pt, partly aligned. Eleven postnodal crossveins and eight postsubnodal crossveins present distal of Pt, non-aligned. IR1 long, originating four cells distal of base of RP2 and seven cells basal of Pt, lying 2.34 mm distal of base of RP2. RP1 with weak angle below Pt-brace. MA distally zigzagged and long, reaching posterior wing margin nearly level with distal side of Pt. MP distally zigzagged and long, ending on posterior wing margin one or two cells distal of IR1. CuA long, covering more than seven cells, ending on posterior wing margin just below base of RP2. Pt broad and dark with basal side more oblique than distal side, covering three cells and distinctly braced (Fig. 4E), 1.21 mm long and 0.85 mm wide; posterior side of Pt thickened and fused with strongly thickened pterostigmal part of RA to form U-shaped structure; Pt brace oblique like Pt base.

Remarks. *Burmachistigma* is well differentiated from *Electrocoenagrion* and *Burmagrion* in having a pigmented forewing and a hyaline hind wing instead of pigmented wing apices or completely hyaline wings, RP2 originating three cells distal of the subnodus instead of 6–8 cells in *Electrocoenagrion* and six cells in *Burmagrion*, and a long MA ending on the posterior wing margin nearly opposite the distal side of the pterostigma, and a broader hind wing shape. Also, *Burmachistigma* has a straight Pt-brace instead of a curved one, unlike *Electrocoenagrion*.

Genus ***Electrocoenagrion*** Zheng *et al.* gen. nov.

Type species. *Electrocoenagrion elongata* Zheng *et al.* sp. nov.

Other species. *Electrocoenagrion forficatum* Zheng *et al.* sp. nov.

Diagnosis. Wing apex dark; Pt dark, covering four or five cells, well braced; Pt-brace sigmoidally curved, slightly distal of side of Pt base; two rows of cells present in postnodal area distal of Pt; IR1 nearer to base of RP2 than to Pt base, lying two or three cells distal of base of RP2.

Etymology. Named after the combination of the Greek term 'electron' (meaning amber) and *Coenagrion*.

Remarks. *Electrocoenagrion* differs from *Burmagrion* in the pigmented wing apex and a sigmoidally curved Pt-brace slightly distal of basal side of Pt.

Electrocoenagrion elongatum Zheng *et al.* sp. nov. (Figs 6, 7)

Holotype. NIGP 165221, one complete wing and one fragmentary wing, gender unknown.

Diagnosis. Arc aligned with Ax2; midfork basal of N; 19 postnodal crossveins present basal of Pt; RP2 originating eight cells distal of RP2.

Etymology. Named after the elongate shape.

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

Description. Complete wing with apex coloured (Figs 6B, 7A–C). Wing length 17.21 mm, width at level of N 1.81 mm; length from wing base to Arc 2.79 mm, from Arc to N 1.92 mm, from N to Pt 9.53 mm, from Pt to wing apex 2.96 mm. Primary antenodal crossveins preserved, Ax2 1.61 mm distal of Ax1; no secondary antenodal and antesubnodal crossveins present. Nineteen postnodal crossveins and 18 postsubnodal crossveins present before Pt, partly aligned. Thirteen postnodal crossveins and seven postsubnodal crossveins present distal of Pt, non-aligned. Arc angular and aligned with Ax2. DC basally closed (Fig. 7A), free and long, somewhat rectangular with distal angle; anterior side nearly parallel with posterior side, and distal side longer than basal side; length of basal side 0.15 mm, of anterior side 0.74 mm, of distal side 0.35 mm, of posterior side 1 mm. SdC free and elongate, 1.83 mm long and maximum 0.3 mm wide. CuP 0.95 mm distal of level of Ax1 and closer to Ax2. Nodal structures well preserved, Sn aligned with Cr. Midfork (base of RP3/4) just under N. Base of IR2 aligned with Sn, one cell and 0.91 mm distal of midfork at base of RP3/4. RP2 originating eight cells distal of Sn, lying 3.88 mm distally. IR1 long, originating three cells distal of base of RP2 and seven cells basal of Pt, lying 1.47 mm distal of base of RP2. RP1 with weak angle below Pt-brace. MA distally zigzagged and long, reaching posterior wing margin below mid-area of Pt. MP distally zigzagged and long, ending on posterior wing margin just below IR1 base. CuA long, covering nine cells. Two rows of cells present between RP1 and IR1 basal of Pt. Pt long, dark, with distal side more oblique than basal side, covering four cells and well braced (Fig. 7B, C), 1.41 mm long and 0.48 mm wide; posterior side of Pt thickened and fused with strongly thickened pterostigmal part of RA to form U-shaped structure; Pt-brace sigmoidally curved, slightly distal of Pt base.

Another fragmentary wing has the following differences (Figs 6C, 7D): IR1 two cells distal of base of RP2 and six cells basal of Pt; one row of cells between RP1 and IR1; Pt five cells long; Pt brace slightly curved; seven cells between MP and CuA.

Remarks. *Electrocoenagrion elongatum* differs from *E. forficatum* in having the Arc aligned with Ax2 instead of distal of Ax2, more postnodal crossveins basal of the pterostigma (19 instead of 15), and one row of cells just below Pt base instead of two rows.

Electrocoenagrion forficatum Zheng *et al*. sp. nov. (Figs 8, 9)

Holotype. NIGP 165222, one overlapped wing attached to body, gender unknown.

Diagnosis. Arc distal of Ax2; midfork well basal of N; 15 postnodal crossveins present basal of Pt; RP2 originating six cells distal of Sn; two rows of cells present between RA and RP1 just below Pt base.

Etymology. Named after the Latin word *forficatus*, reflecting the shape of the partly overlapped wings.

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

Description. Wings overlapped (Fig. 8C, D). Wing length 15.84 mm; length from wing base to Arc 3.41 mm, from Arc to N 1.64 mm, from N to Pt 8.1 mm, from Pt to wing apex 2.7 mm. Primary antenodal crossveins preserved (Fig. 9B), Ax0 close to wing base, Ax1 1.22 mm distal of Ax0, Ax2 1.68 mm distal of Ax1; no secondary antenodal and antesubnodal crossveins present. 15 postnodal crossveins and 15 postsubnodal crossveins present before Pt, partly aligned. 11 postnodal crossveins and seven postsubnodal crossveins present distal of Pt, non-aligned; two rows of cells present in postnodal area distal of Pt. Arc angular and 0.21 mm distal of Ax2. DC closed basally (Fig. 9C), free, long and narrow, somewhat rectangular with weak distal angle; anterior side nearly parallel with posterior side, and distal side longer than basal side; length of basal side 0.15 mm, of anterior side 0.6 mm, of distal side 0.31 mm, of posterior side 0.77 mm. SdC free and very elongate, 1.66 mm long and maximum 0.18 mm wide. CuP 0.89 mm distal of level of Ax1. Nodal structures well preserved (Fig. 9C), Sn aligned with Cr. Midfork (at base of RP3/4) 0.61 mm basal of N. Base of IR2

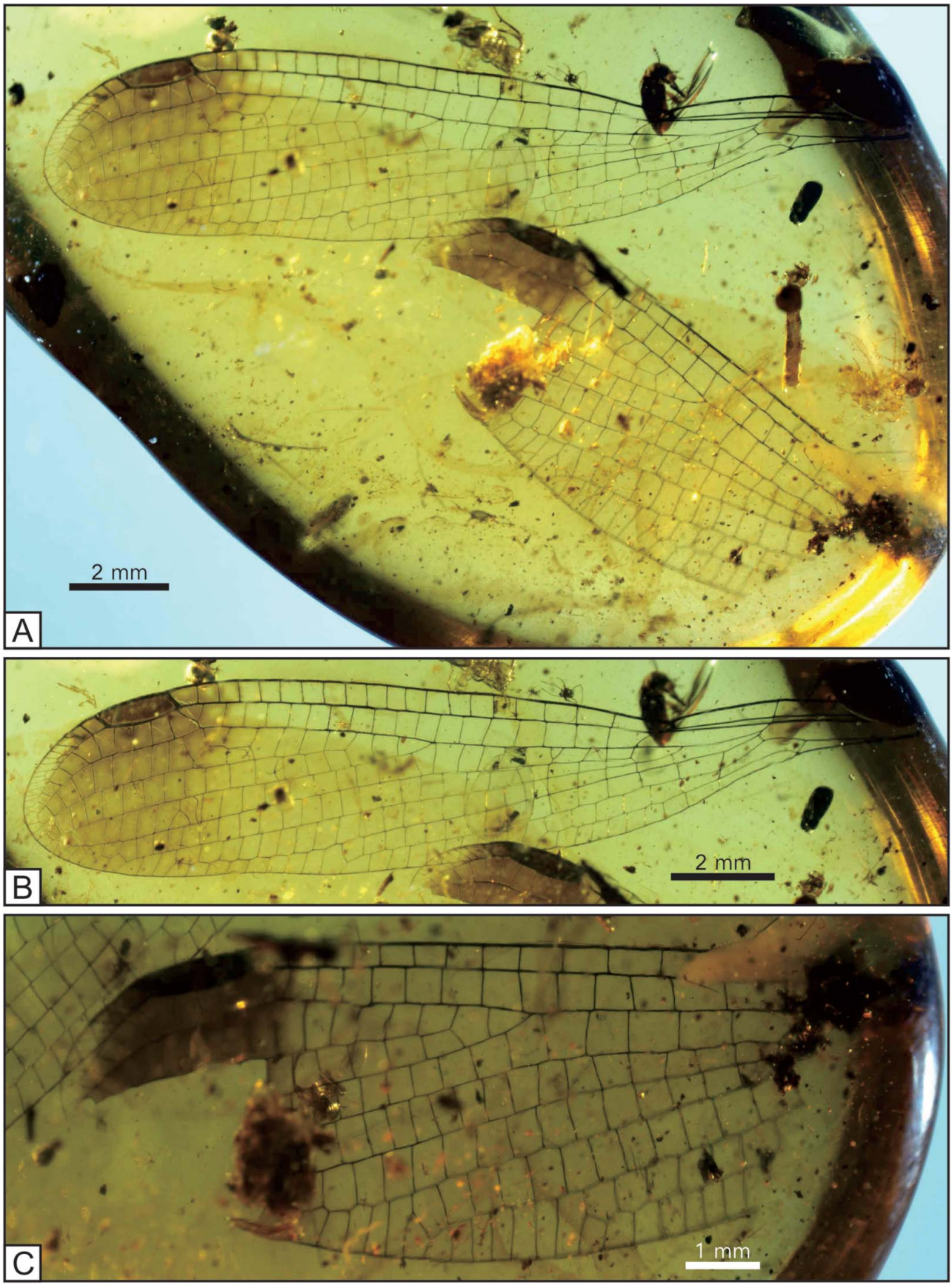

Figure 6. *Electrocoenagrion elongatum* Zheng *et al.* gen. et sp. nov., holotype, NIGP 165221. Photographs of **A,** specimen; **B,** complete wing; **C,** fragmentary wing.

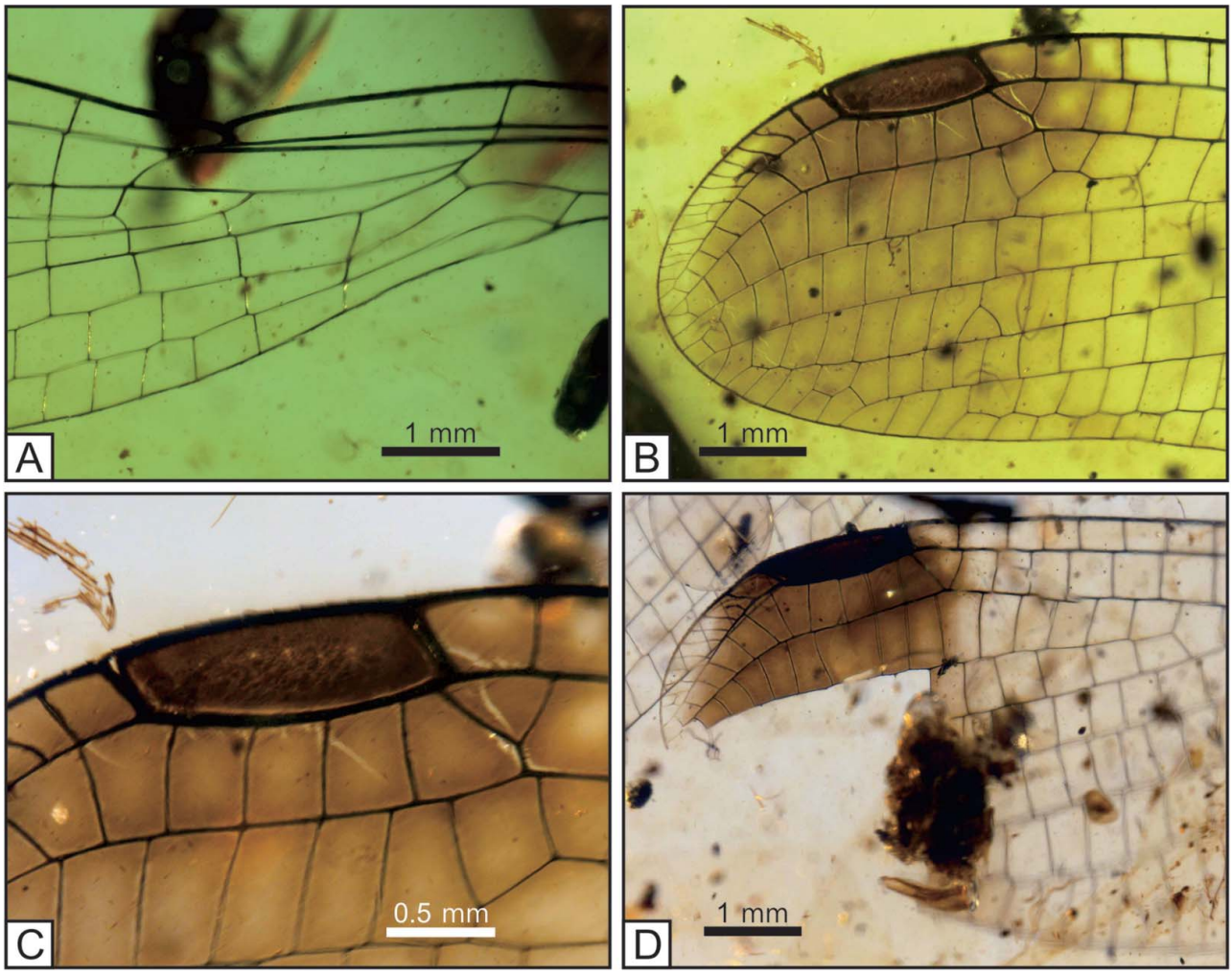

Figure 7. *Electrocoenagrion elongatum* Zheng *et al.* gen. et sp. nov., holotype, NIGP 165221. Photographs of **A,** wing base; **B,** apex; and **C,** pterostigma of complete wing, **D,** wing apex of fragmentary wing.

aligned with Sn, one cell and 1.05 mm distal of midfork. RP2 originating six cells distal of Sn, lying 3.2 mm distally, nearer to N than to Pt. IR1 long, originating two cells distal of base of RP2 and seven cells basal of Pt, lying 1.14 mm distal of base of RP2. RP1 with weak angle below Pt-brace. Pt long, dark, with distal side more oblique than basal side, covering four cells and well braced (Fig. 9E), 1.37 mm long and 0.55 mm wide; Pt-brace slightly distal of basal side; two cells below Pt base; pterostigmal part of RA and stigmal crossveins thickened to form U-shaped structure; Pt-brace oblique like Pt base.

Genus ***Burmagrion*** Möstel *et al*., 2017
Burmagrion marjanmatoki Möstel *et al*., 2017

Emended diagnosis. Wing hyaline; Arc slightly distal of Ax2; Pt dark, 3 or 4 cells long; RP2 originating five or six cells distal of Sn.

Remarks. Möstel *et al*. (2017) proposed the following characters for this genus: (1) wings strongly petiolate; (2) Ax1 and Ax2 very widely separated; (3) Arc slightly distal of Ax2; (4) *c*. 15 postnodal crossveins present, of which only the most basal three are aligned and connected to incipient pseudo-transverse veins; (5) pterostigmata 2.5–3.5 cells long and distinctly braced; (6) no lestine oblique vein present; (7) no intercalary veins except IR1 and IR2 present; (8) DC basally closed, elongate, free, and distally acute; (9) SdC elongate and free; (10) CuP-crossing at origin of AA' + CuA; (11) about six cells between subnodus and origin of RP2, and three cells between origins of RP2 and IR1; and (12) only one row of cells between CuA and hind margin.

Regarding these characters, (8), (10) and (12) are transferred to the family diagnosis. Characters (1), (2), (6), (7) and (9) are shared by all Coenagrionoidea, and removed

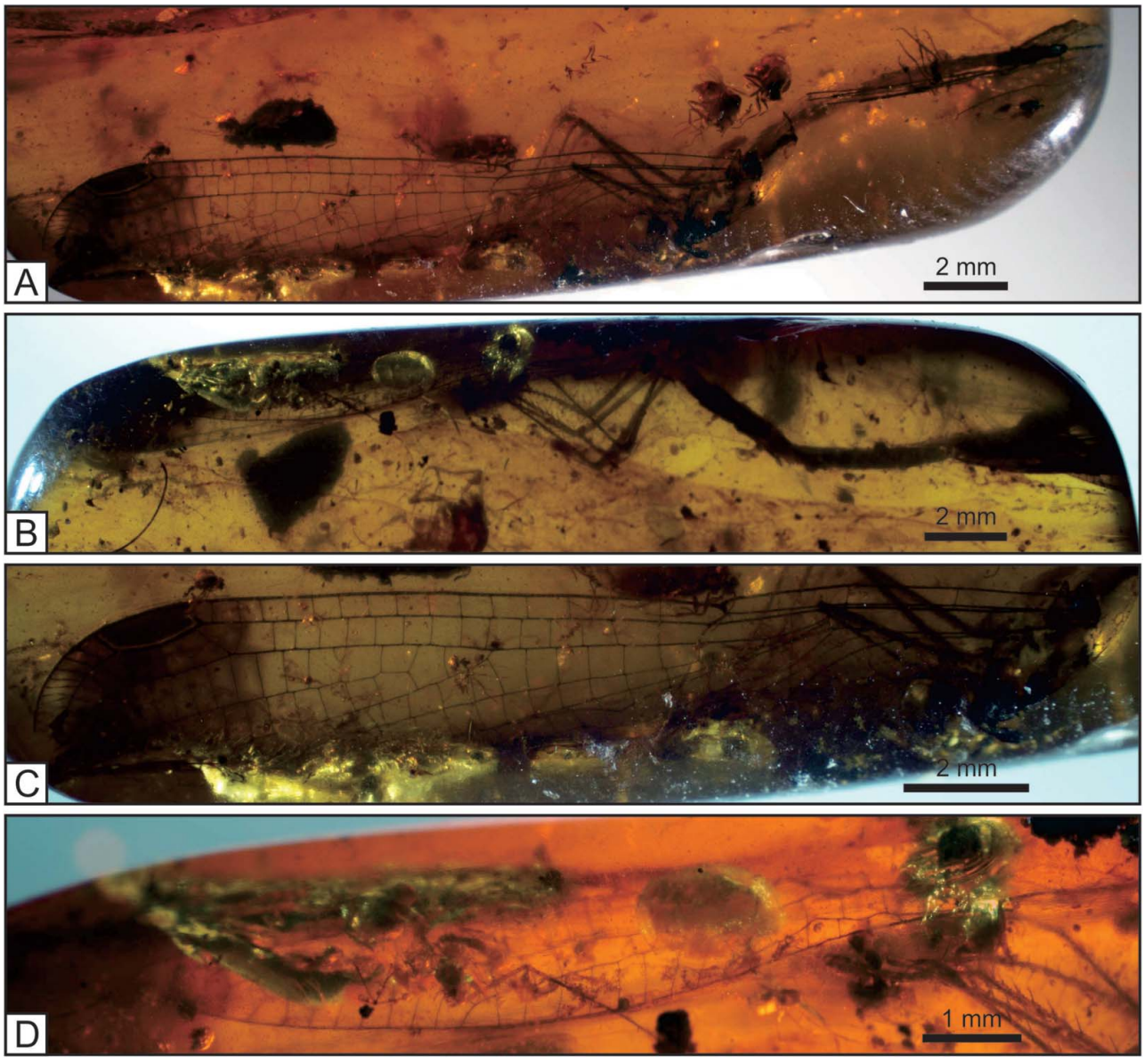

Figure 8. *Electrocoenagrion forficatum* Zheng *et al.* gen. et sp. nov., holotype, NIGP 165222. Photographs of **A, B,** specimen; **C, D,** forewing.

herein; (4), (5), and (11) are correct for this genus, but were inaccurately illustrated. Notably, *Burmagrion marjanmatoki* has *c*. 11–15 postnodal crossveins before the pterostigma, instead of *c*. 15 postnodal crossveins: the most basal three are shown aligned and connected to incipient pseudo-transverse veins, which is wrongly illustrated since there are four basally aligned but not connected crossveins (Möstel *et al*. 2017, fig. 9). This latter character is revised as follows: 'postnodal crossveins are somewhat aligned with postsubnodals in basal half of area but not in distal part' as a family character. The pterostigma is three or four cells long (Möstel *et al*. 2017, fig. 5). There are five or six cells between the subnodus and the origin of RP2 (Möstel *et al*. 2017, fig. 9), and 1–3 cells between the bases of RP2 and IR1. Character (3), 'arculus slightly distal of Ax2', is retained as a generic character, which is also shared by *Burmacoenagrion pretiosus* and *Electrocoenagrion forficatum*.

Discussion

Burmacoenagrionidae can be attributed to the clade Coenagrioniformia Bechly, 1996 (= Coenagrionida Bechly, 1996 + Platystictidae Kennedy, 1920) due to the following characters: pterostigma rather short with only

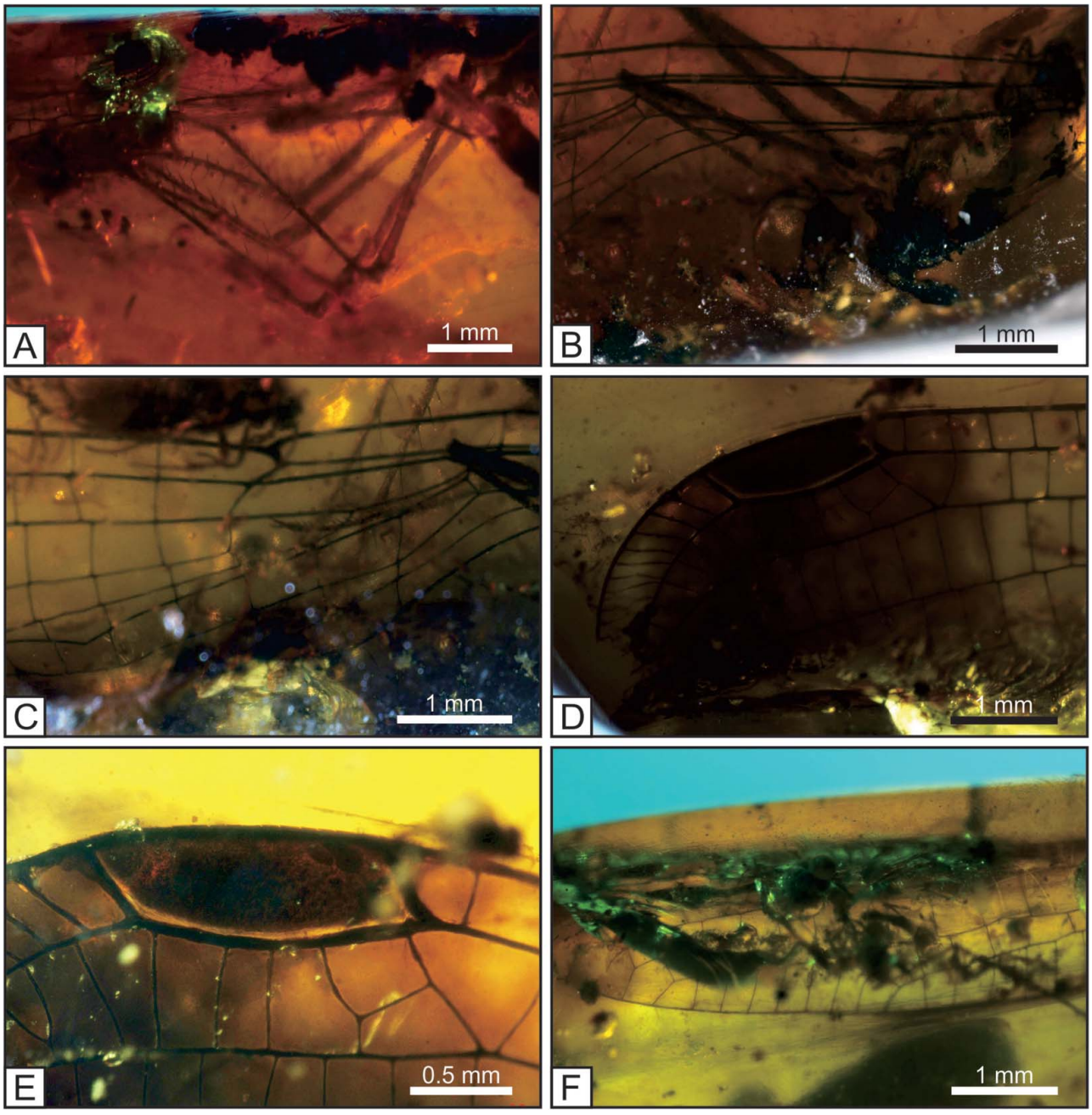

Figure 9. *Electrocoenagrion forficatum* Zheng *et al.* gen. et sp. nov., holotype, NIGP 165222. Photograph of **A,** legs; **B,** wing base; **C,** centre; **D,** apex; **E,** pterostigma; **F,** posterior wing.

two (rarely three) crossveins beneath it; pterostigmal brace ventrally serrated like RP1; subnodus aligned with base of IR2 (reversed in several subordinate taxa), at least somewhat strengthened and dorsally united with the subnodus by the common sclerotization (interradial bracket), usually serrated; number of hexagonal and pentagonal cells greatly reduced; postnodal crossveins aligned with rows of crossveins below forming several pseudo-transverse veins (reversed within Platystictinae); all intercalary veins (except IR1 and IR2) suppressed.

Within Coenagrioniformia, Burmacoenagrionidae shares with the Platystictidae the following apomorphies: wings with falcate apex; longitudinal veins RA, RP1, IR1, RP2 and IR2 strongly converging to wing apex; discoidal cell rather rectangular; MA very long (in the groundplan also including MP), at least reaching up to 90% of wing length from base. Nevertheless, the family Burmacoenagrionidae do not have the following synapomorphies of Platystictidae: costal border of pterostigma much shorter than radial border; nodus in very basal position (at about 22% of wing

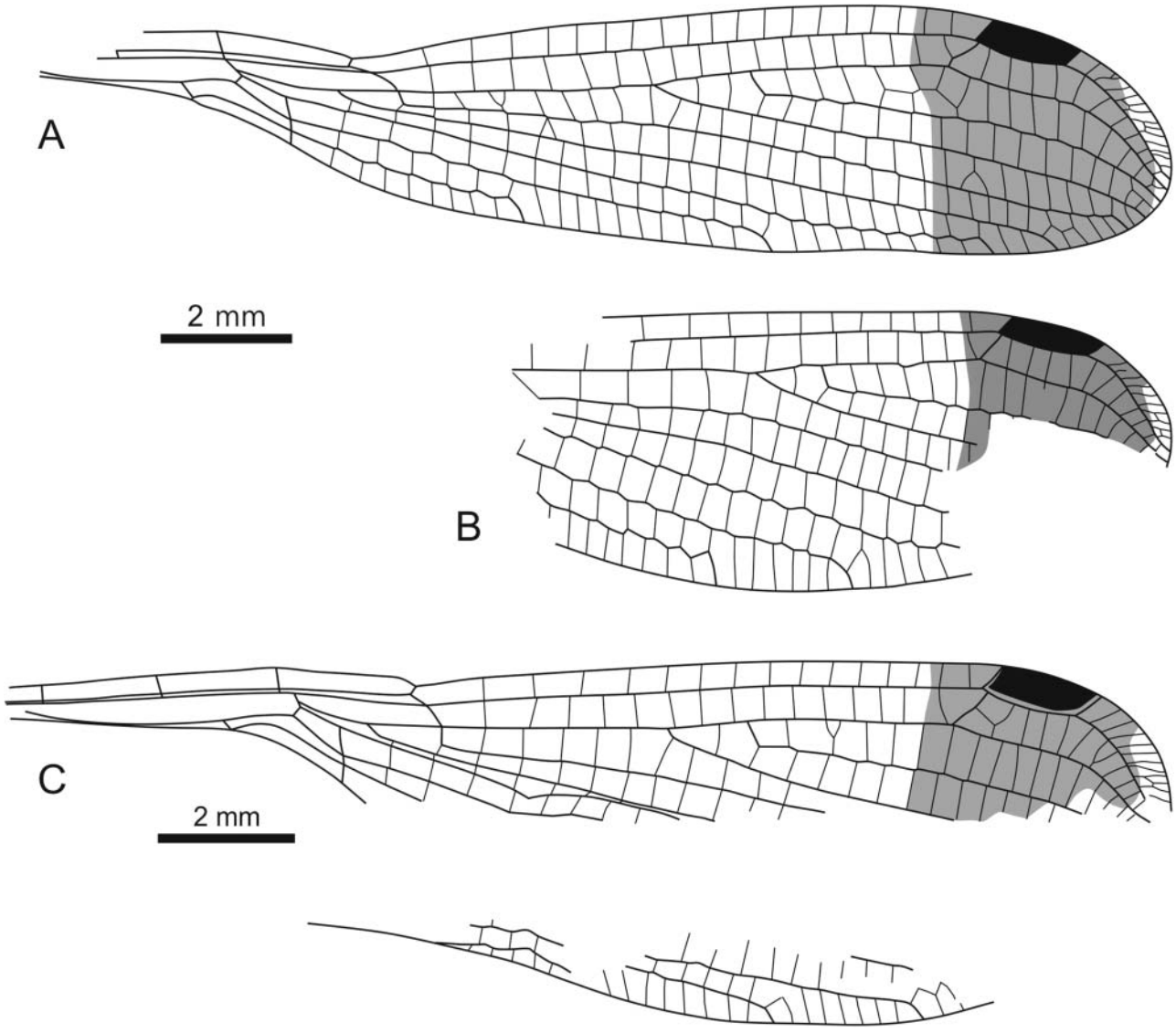

Figure 10. Line drawing showing wing venation. **A, B,** *Electrocoenagrion elongatum* Zheng *et al.* gen. et sp. nov., holotype, NIGP 165221, **A,** complete; **B,** fragmentary wings. **C,** *Electrocoenagrion forficatum* Zheng *et al.* gen. et sp. nov., holotype, NIGP 165222, forewing.

length); CuP-crossing recessed in a very basal position; subdiscoidal cell traversed by three crossveins that delimit a pseudo-subdiscoidal cell; and CuA completely fused with hind margin, thus only retained as subdiscoidal vein. In contrast, Burmacoenagrionidae can be attributed to the Coenagrionida following Bechly (2007a) because of the following synapomorphies: longitudinal veins rather straight and long, with branches of RP distally converging; only one row of cells present between CuA and hind wing margin; only two primary antenodal crossveins Ax1 and Ax2 retained; no antesubnodal and antefurcal crossveins; pterostigma rather short (three cells long); postnodal and postsubnodal crossveins somewhat aligned; oblique vein absent; basal closure of discoidal cell in forewings includes development of dorsal arcular bracket; Sn aligned with base of IR2; number of hexagonal and pentagonal cells greatly reduced; and all intercalary veins (except IR1 and IR2) suppressed.

The clade Coenagrionida (= Coenagrionoidea Kirby, 1890 in Dijkstra *et al*. 2014) consists of Pseudostigmatoidea Kirby, 1890 and Coenagrionodea Bechly 1996 (Bechly 2007a). Burmacoenagrionidae have a sigmoidally curved RA and RP1 distal of the pterostigma, a character present in Pseudostigmatidae (including *Coryphagrion* Morton 1924 except *Anomisma* McLachlan, 1877), *Euarchistigma* Carle and Wighton, 1990 (currently in Thaumatoneuridae Bechly, 2007b), and *Cretarchistigma* Jarzembowski *et al*., 1998 (currently considered as 'Zygoptera family *incertae sedis*, probably Hemiphlebiidae', Bechly 2007b). However, the new

family differs from recent Pseudostigmatoidea in having the nodus not lying in an extremely basal position (32% compared to 16–23% of wing length in the latter), few postnodal crossveins (14 instead of around 40), short CuA (four or six cells long instead of ending near the wing apex), and a 3–5 cell-long pterostigma with a well-defined pterostigmal brace (especially in the case of *Coryphagrion* that otherwise shares with the fossils a relatively long, sclerotized and braced pterostigma), and CuP not so basally recessed. Affinities between Burmacoenagrionidae and *Cretarchistigma* can also be excluded since the latter has fewer postnodal crossveins, a short pterostigma covering one or two cells, a long MP, a more acute distal angle of the discoidal cell, and CuP not ending on the base of AP. Burmacoenagrionidae closely resembles *Euarchistigma* in having a much broadened apex with numerous cells, an elongate and free discoidal cell with a more or less oblique distal side; but the latter has a larger wing size (23–35 mm), IR2 not aligned with the subnodus, more than two rows of cells between the main longitudinal veins near the wing apex, the pterostigma is not braced, the nodus is in a very basal position (at 25% of wing length from base), and has a long CuA covering *c*. 20 cells, all differing from the former.

Burmacoenagrionidae possess the following characters of Coenagrionodea (= Platycnemididae & [Protoneurinae & Isostictinae (= Protoneuridae)] & Coenagrionidae) (Bechly 2007a): terminal kink of CP at nodus and nodal membrane sclerotization suppressed; basal and distal margin of pterostigma thickened and fused with strongly thickened pterostigmal part of RA to form a U-shaped structure; and all intercalary veins (except IR1 and IR2) suppressed. Nevertheless, RP1 is not distinctly kinked at the Pt brace in Burmacoenagrionidae, unlike in many modern Coenagrionodea.

Extant Protoneurinae and Isostictinae can easily be excluded because these groups have a more rectangular discoidal cell, the discoidal bracket (dorsal sclerotization on MAb and the subdiscoidal vein) is strongly reduced, and CuA is completely fused with the hind margin, thus only being retained as a subdiscoidal vein. In contrast, Coenagrionidae and Platycnemididae have a long, distally zigzagged CuA and acute discoidal triangle, more like Burmacoenagrionidae. The discoidal cell of the Coenagrionidae has a very acute distal angle with a very oblique MAb, so that the anterior side of the discoidal cell is much shorter than the posterior side (convergent with Lestinae), different from Burmacoenagrionidae. Also, Burmacoenagrionidae have a long pterostigma covering 3–5 cells, pigmented wings, and CuP just on the origin of AA', distinguishing them from extant and fossil Coenagrionidae. Platycnemididae have the distal angle of the discoidal cell not so acute, resembling Burmacoenagrionidae, but differ from the latter in the presence of a short pterostigma (less than two cells long), hyaline wings, well aligned, transverse crossvein series between the main longitudinal veins distal of the nodus, and CuP not on the origin of AA'.

In conclusion, Burmacoenagrionidae differ from all Coenagrioniformia due to the presence of a long pterostigma (3–5 cells long), pigmented wings, and sigmoidally curved RA and RP1 distal of the pterostigma, while the last character is shared only with Pseudostigmatidae. Möstel *et al*. (2017) suggested that *Burmagrion marjanmakoki* Möstel *et al.*, 2017 is a member of Coenagrionodea, but did not attribute it to any family. Here we introduce a new family, Burmacoenagrionidae, based on the above fossil damselflies. The phylogenetic affinities of Burmacoenagrionidae remain uncertain within the Coenagrionodea. A new phylogenetic analysis based on molecular and morphological characters, including fossil taxa, will be necessary to solve this question.

Conclusions

The new damselfly family Burmacoenagrionidae Zheng *et al.* fam. nov. is established based on four new species in three new genera plus the previously described *Burmagrion* Möstel *et al.*, 2017. Burmacoenagrionidae Zheng *et al.* fam. nov. resembles Pseudostigmatidae and Platystictidae, but differs from all Coenagrioniformia in having a long pterostigma covering 3–5 cells, pigmented wings, and sigmoidally curved RA and RP1 distal of the pterostigma. The new family is the most diverse one among the damselflies recorded in Burmese amber.

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