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New damselflies (†Mesostictinae and Platycnemidinae) from Cretaceous Burmese amber

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Abstract

Damselflies (suborder Zygoptera) are very diverse in extant ecosystems and contain more than 20 fossil species into eleven families in Burmese amber. Here we describe two fossil damselflies from the Cenomanian Burmese amber that we attributed to the families Platystictidae and Platycnemididae. The research focused on specimens housed at the Geominer Museum of the Instituto Geológico y Minero de España, Consejo Superior de Investigaciones Científicas (IGME, CSIC) in Madrid. The results of the study identified two new taxa, *Mesosticta garciavallsi* **sp. nov.** and an undetermined Platycnemididae species, or new morphotype, which have been studied based on their fore- and hind wing venations, being the wings the only parts preserved. These new specimens represent the fifth species described of the extinct genus *Mesosticta* Huang, Azar, Cai & Nel, 2015 and the putative oldest fossil record of Platycnemidinae. Our findings increase the known diversity of damselflies during the mid-Cretaceous.

Keywords: Odonata, Zygoptera, new species, Kachin amber, Cenomanian, Myanmar

Introduction

Odonata are scarce as bioinclusions in amber deposits, particularly when compared to their record as compression fossils. However, Kachin amber from Myanmar is relatively rich in odonates, hosting the majority of mid-Cretaceous bioinclusions of this order (Zheng & Jarzembowski, 2020). From Burmese amber there have been described 46 species placed into 20 families (refer to the list in Zheng, 2021, completed by the works of Huang *et al*., 2021; Bechly & Velten, 2023; Fan *et al*., 2024; Liu *et al*., 2024a, b). Burmese amber damselflies (suborder Zygoptera) are very diverse and contain more than 20 species into eleven families (†Burmacoenagrionidae, †Burmadysagrionidae, †Protohemiphlebiidae, Coenagrionidae, Dysagrionidae, Hemiphlebiidae, †Mesomegaloprepidae, †Paracoryphagrionidae, Perilestidae, Platycnemididae and Platystictidae). The dominant family in that amber is Hemiphlebiidae, representing approximately three-quarters of all damselflies (Zheng, 2021, plus subsequent studies).

The platystictid damselflies are characterized by a long and very slender abdomen, and a unique wing venation with a basally recessed 'CuP' (Jarzembowski *et al*., 1998; Huang *et al*., 2015), a long IR1 and a usually diamond-shaped subdiscoidal cell (Van Tol, 2005). The extinct subfamily Mesostictinae represents the archaic platystictid damselflies showing differences with modern ones such as the number of postnodal and postsubnodal crossveins (less than ten in the genus †*Mesosticta* Huang, Azar, Cai & Nel, 2015), the length of MP, the base of RP2 being more cells distal of the subnodus, and the nodus lying very basally (Zheng *et al*., 2019a). The subfamily †Mesostictinae is represented by only one genus, *Mesosticta*, which currently enclosed four species recorded in the Burmese amber (Huang *et al*., 2015; Zheng *et al*., 2016b, 2019a; Nel *et al*., 2024).

The platycnemidid damselflies are quite diverse in Burmese amber with four species in three genera described to date (Poinar *et al*., 2010; Huang *et al*., 2015; Zheng *et al*., 2017b, c). Three of these four species are represented by the extinct subfamily Palaeodisparoneurinae characterized by the following

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unique autapomorphies: the midfork (the base of RP3/4) originates midway between the arculus and nodus, the pterostigma is of rectangular shape, RP1 is strongly kinked at the pterostigmal brace, and IR1 originates below the pterostigma (Poinar *et al*., 2010).

Here we describe two fossil damselflies from Burmese amber: one new species that we attribute to the Platystictidae; and a new morphotype to the Platycnemididae, this lattermost likely belongs to the subfamily Platycnemidinae.

Material and methods

Two pieces of amber containing the specimens derive from the deposits of Kachin State, Northern Myanmar. Both specimens are permanently deposited in a well-established, public museum, in full compliance with the International Palaeoentomological Society statement (Szwedo *et al*., 2020). We align with the content of Haug *et al*. (2020) regarding the controversy surrounding the ethics of Burmese amber research in relation to the Myanmar armed conflict. We also acknowledge the clarifying publications, such as Peretti (2020), which address misinterpretations of this controversy.

The specimens are housed at the Geominer Museum of the Instituto Geológico y Minero de España, Consejo Superior de Investigaciones Científicas (IGME, CSIC) in Madrid. The specimens were examined with an Olympus BX53 compound microscope equipped with a digital camera. Plates were edited and processed using Adobe Photoshop. Specimens were drawn using a drawing tube Olympus U-DA attached to the Olympus BX53 microscope. The figures were composed with Photoshop CC2018.

The nomenclature of the damselfly wing venation used 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). 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 Zheng, Wang, Nel, Jarzembowski, Zhang & Chang, 2019

Genus *Mesosticta* Huang, Azar, Cai & Nel, 2015

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

***Mesosticta garciavallsi* sp. nov.**
(Figs 1, 2)
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Holotype. Specimen MGM-7910X (a forewing and a hind wing attached to a small portion of the thorax); the wings are complete but slightly deformed by distended movement of the amber material, which implies the breakage and short separation of some veins. Housed at the lithotheque of the Geominer Museum (Instituto Geológico y Minero de España, CSIC) in Madrid.

Etymology. Named in memory of the Valencian Mr. Enrique José García Valls (1960–2022), for his invaluable help in the management of the original amber collection from which the holotype come from, and for his lifelong passion for palaeontology.

Diagnosis. Wing venation characters only; sex unknown. Forewing with eight postnodal and post subnodal crossveins from proximal to Pt, and five and three, respectively, after Pt; RP2 four cells to distal Sn, IR1 originating two cells distal of base of RP2 and three cells basal of Pt base, three cells long in MP, and subdiscoidal cell not crossed in fore- and hind wings; MA ending at level of base of Pt-brace; forewing MP ending one cell distad level of first crossvein between RP3/4 and IR2; subdiscoidal cell free and rhomboidal. Hindwing with seven postnodal and six postsubnodal crossveins from the pterostigma.

Locality and horizon. Kachin amber deposit, northern Myanmar, Cenomanian in age (Shi *et al*., 2012).

Description. Forewing length 11 mm, width at level of N about 1.3 mm; distance from wing base to Arc 2.3 mm, from Arc to N about 1.3 mm, from N to Pt about 5.9 mm, from Pt to wing apex about 0.8 mm. Posterior margin rounded. Ax0 close to the wing base, primary and secondary antenodal crossveins preserved, Ax2 about 0.8 mm distal of Ax1. Eight postnodal crossveins and eight postsubnodal crossveins present proximal to Pt, somewhat aligned. Five postnodal crossveins and three postsubnodal crossveins present distal of Pt, non-aligned. Arc angular and aligned with Ax2. DC basally closed, free, elongate and quadrangular, 0.7 mm long and 0.2 mm maximum wide. Subdiscoidal cell free and rhomboidal,

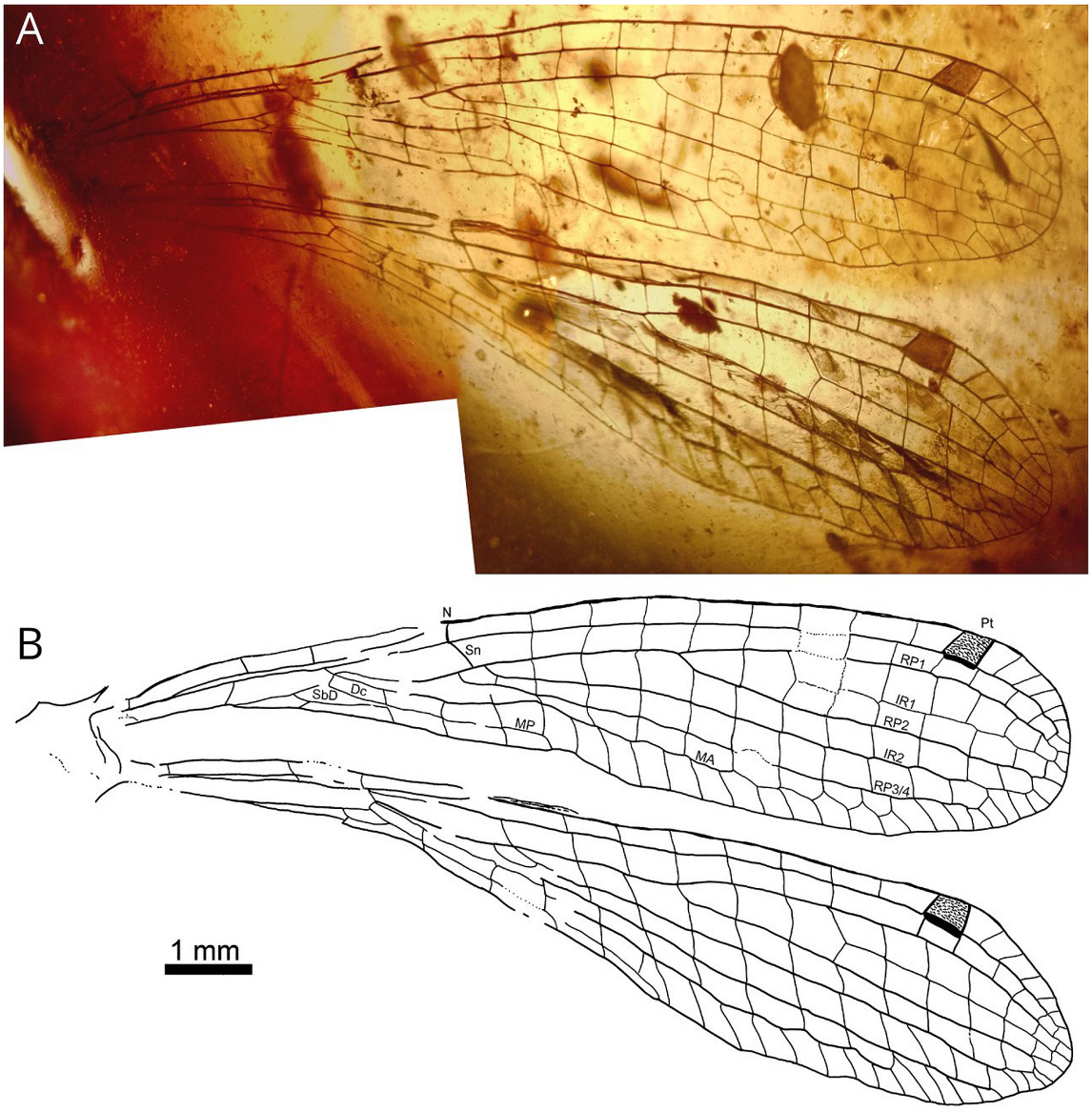

FIGURE 1. *Mesosticta garciavallsi* **sp. nov.**, holotype MGM-7910X. **A**, Composite photograph. **B**, Camera lucida drawing. Abbreviations: DC = discoidal cell; IR = intercalary radial vein; MA = median anterior; MP = median posterior; N = nodus; Pt = pterostigma; RP = radius posterior; SbD = subdiscoidal cell; Sn = subnodal crossvein. Figures at same scale.

1.2 mm long and 0.2 mm maximum wide, and not crossed in fore- and hind wings. AA separated from AP at mid distance between Ax1 and Ax2, ending on distal angle of DC. Nodal structures well preserved, with Sn aligned with Cr. Midfork (base of RP3/4) slightly basal of N. IR2 not aligned with Sn, one cell and 0.6 mm distal of midfork. IR1 long, originating two cells distal of base of RP2 and three cells basal of Pt base. RP1 with a slight angle below Pt-brace. Longitudinal veins RA, RP1, IR1, RP2 and IR2 converging on wing apex. MA distally zigzagged and long, reaching posterior wing margin below to the base of Pt-brace. MP curved, three cells long, ending on posterior wing margin 2 mm distal of distal angle of DC and MP ending on posterior wing margin one cell distad level of first crossvein between RP3/4 and IR2. Pt covering one cell, 0.4 mm long and 0.3 mm wide, thickened and fused with greatly thickened pterostigmal part of RA as a U-shaped structure.

Hind wing about 11.3 mm long, about 0.6 mm wide, length from wing base to Arc 3.8 mm, from Arc to N about 1.3 mm, from N to Pt about 5.3 mm, from Pt to wing apex about 1.9 mm, with nearly the same venation as in forewing, except for the presence of seven postnodal and six postsubnodal crossveins basad pterostigma. Posterior margin pointed. Also, five postnodal crossveins and four postsubnodal crossveins present distal of Pt, non-aligned. Subdiscoidal cell free and subquadrangular. IR2 aligned with Sn. IR1 long, originating three cells distal of base of

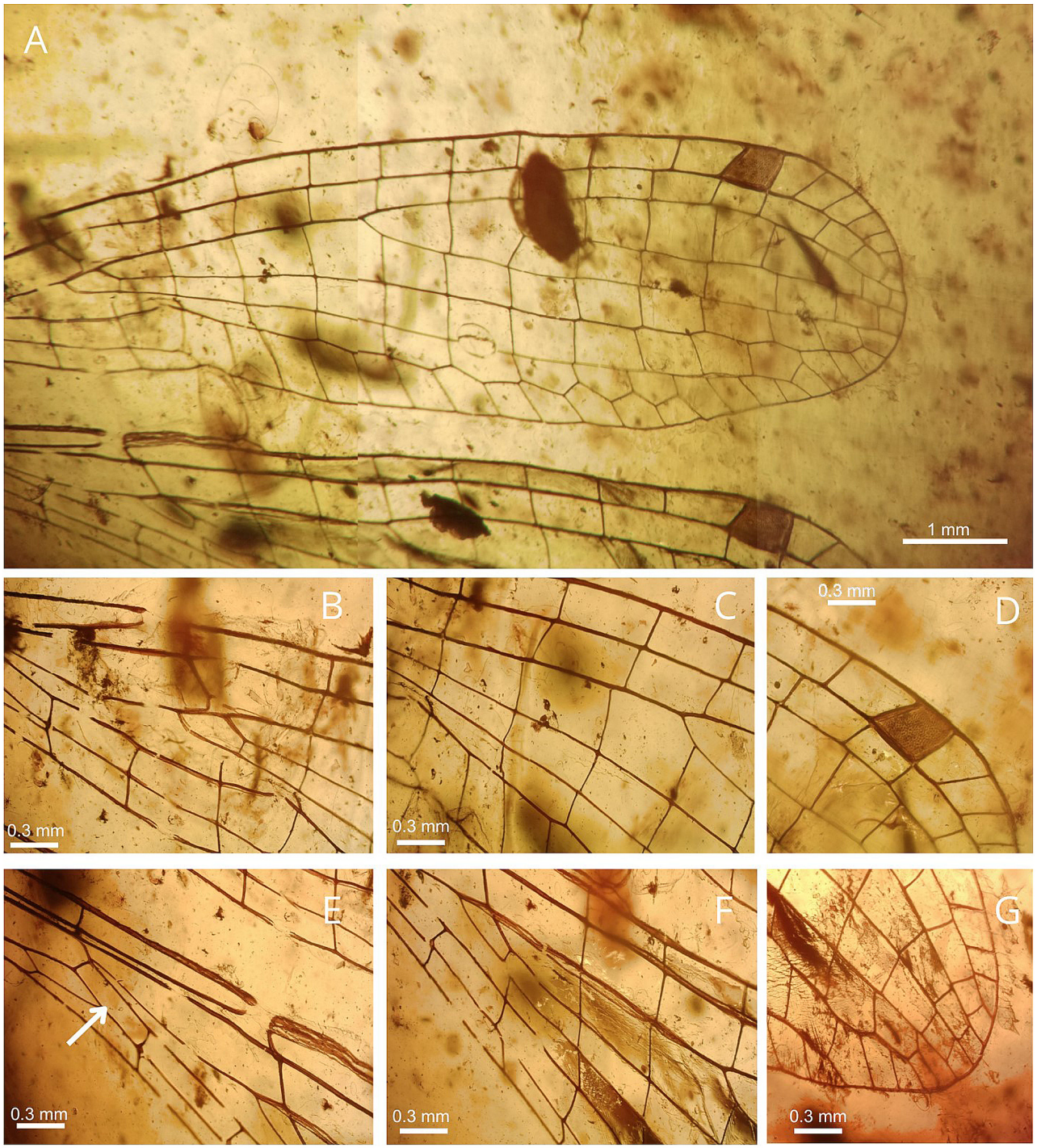

FIGURE 2. Details of *Mesosticta garciavallsi* **sp. nov.**, holotypeMGM-7910X. **A**, Partial view of forewing. **B**–**D**, Details of forewing. **B**, Detail of nodus and subnodal crossvein. **C**, RA and RP veins. **D**, Pterostigma. **E**–**G**, Hind wing. **E**, Wing base (arrow: discoidal cell). **F**, RA and RP veins. **G**, Wing apex.

RP2 and two cells basal of Pt base. MA distally zigzagged and long, reaching posterior wing margin just below base of Pt-brace and MP ending on posterior wing margin one cell distad level of first crossvein between RP3/4 and IR2. MP curved, four cells long, ending on posterior wing margin 3.2 mm distal of distal angle of DC.

Remarks. This new fossil, *Mesosticta garciavallsi* **sp. nov.**, exhibits all the diagnostic characters of the Mesostictinae, according to Zheng *et al*. (2019a): 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; less than 10 postnodal and postsubnodal crossveins, somewhat aligned; 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.

The new fossil shows some differences between venation of the fore- and hind wings, as in †*Mesosticta electronica* and †*M. additicta.* The new fossil represents a medium-sized insect with a forewing length of 11 mm and a width of 1.3 mm, placing it 'between' the species *M. electronica* and †*M. davidattenboroughi* in terms of size. It shares a similar number of postnodal and postsubnodal crossveins with *M. davidattenboroughi*, possessing eight in both categories from proximal to Pt, and five and three, respectively, after the Pt, like *M. additicta* and *M. electronica*. The new fossil shares more characteristics with *M. additicta* than with the other three species, such as: RP2 four cells to distal Sn, IR1 originating two cells distal of base of RP2 and three cells basal of Pt base, three cells long in MP, and subdiscoidal cell not crossed in fore- and hind wings. However, the vein MA is longer in the new fossil, ending at the level of the base of Pt-brace. On the other hand, the vein MP of the forewing of *M. additicta* is considerably shorter than in new fossil, ending at the level of the first crossvein, between IR2 and RP2 (Nel *et al*., 2024). Lastly, the new fossil exhibits a free and rhomboidal subdiscoidal cell similar to *M. electronica*. These differences look sufficient to consider this fossil as representing a new species.

Superfamily Coenagrionoidea Kirby, 1890
Family Platycnemididae Jacobson & Bianchi, 1905
Subfamily Platycnemidinae? Jacobson & Bianchi, 1905

Genus and species undetermined
(Figs 3–5)

Material. Specimen MGM-7912X. Incomplete specimen represented by three wings not totally complete (*e.g*., basal parts absent or very incomplete) due to lost in the amber piece limits. Housed at Geominer Museum (Instituto Geológico y Minero de España, CSIC) in Madrid.

Locality and horizon. Kachin amber deposit, northern Myanmar, Cenomanian in age (Shi *et al*., 2012).

Description. All wings with same shape and venation, but with basal part absent. Preserved part 8.3 mm, maximum width 2.38 mm; length from base of RP3/4 to pterostigma base 5 mm, from pterostigma base to wing apex 0.95 mm. Antenodals not preserved; petiole long (visible in wing B). Five postnodal crossveins and five post-subnodal crossveins present before pterostigma, well aligned, except most distal ones. An alignment of postnodal rows of crossveins between costal margin and hind margin of wing. Three postnodal crossveins and two postsubnodal crossveins present distal of pterostigma, non-aligned. Probably no antefurcal crossveins present in space between RP and MA from arculus to midfork. Nodal structures well preserved; Sn nearly perpendicular to RA and RP and aligned with base of IR2. Midfork one long cell and 0.3 mm basal of Sn. IR2 basally straight but zigzagged in its distal third. Base of RP2 two cells and a half distal of Sn, lying 1.94 mm distally, slightly nearer to N than to pterostigma. No oblique lestine vein. Base of IR1 four cells distal of base of RP2, lying 2.66 mm distally and originating just below pterostigma. RP1 with a very weak angle below pterostigmal brace. MA distally zigzagged and long, reaching posterior wing margin just below Pt-brace. MP straight and reaching a level midway between bases of RP2 and IR1. Pterostigma one cell long, 0.46 mm long and 0.3 mm wide, with basal side not parallel to distal side, basal and distal margin of pterostigma thickened and fused with strongly thickened pterostigmal part of RA, probably slightly longer than costal side; Pt-brace short and less oblique than base of Pt. All intercalary veins (except for IR1 and IR2) suppressed. Longitudinal veins RA, IR1, RP1, IR2 and RP2 not especially converging to wing apex. Discoidal cell very long, and subrectangular, 0.8 mm long and 0.3 mm maximum wide, MAb poorly preserved but perpendicular to MA-MAa, thus not strongly oblique. Subdiscoidal cell very long. CuP situated 0.37 mm distad separation of AA from AP. CuA elongate, zigzagged, with only one row of cells between it and hind margin of wing. Other wings resemble this wing except for following differences: IR1 five cells distal of base of RP2, below mid part of pterostigma, in wing B. A short longitudinal intercalary vein between RP2 and IR2 in wing C.

Remarks. This fossil can be attributed to the Euzygoptera Bechly, 1996 because of the following characters: longitudinal veins rather straight and long (RP3/4 reaching beyond pterostigma, MA reaching level of pterostigma, only one row of cells between CuA and the hind margin of wings). It also has the following putative apomorphies of the Coenagrionomorpha Bechly, 1996: pterostigma shortened; postnodal and postsubnodal crossveins aligned; lestine oblique vein secondarily absent; an alignment of the postnodal rows of crossveins between the costal margin and the hind margin of wing. Affinities with the Hypolestidae Tillyard & Fraser, 1938 are excluded because the basal margin of the pterostigma is not strongly slanting. The Argiolestidae Fraser, 1957 are excluded because the longitudinal veins of the new fossil are not curved.

The new fossil can be attributed to the Coenagrioniformia Bechly, 1996 because of the following characters: short pterostigma, the serrated subnodus aligned with the base of IR2 that is dorsally united with the subnodus by a common sclerotisation (interradial bracket); only two rows of cells present in the total wing space between RP1 and RP2 that are separated by IR1; postnodal crossveins aligned with the rows of crossveins below, forming several pseudo-transverse-veins.

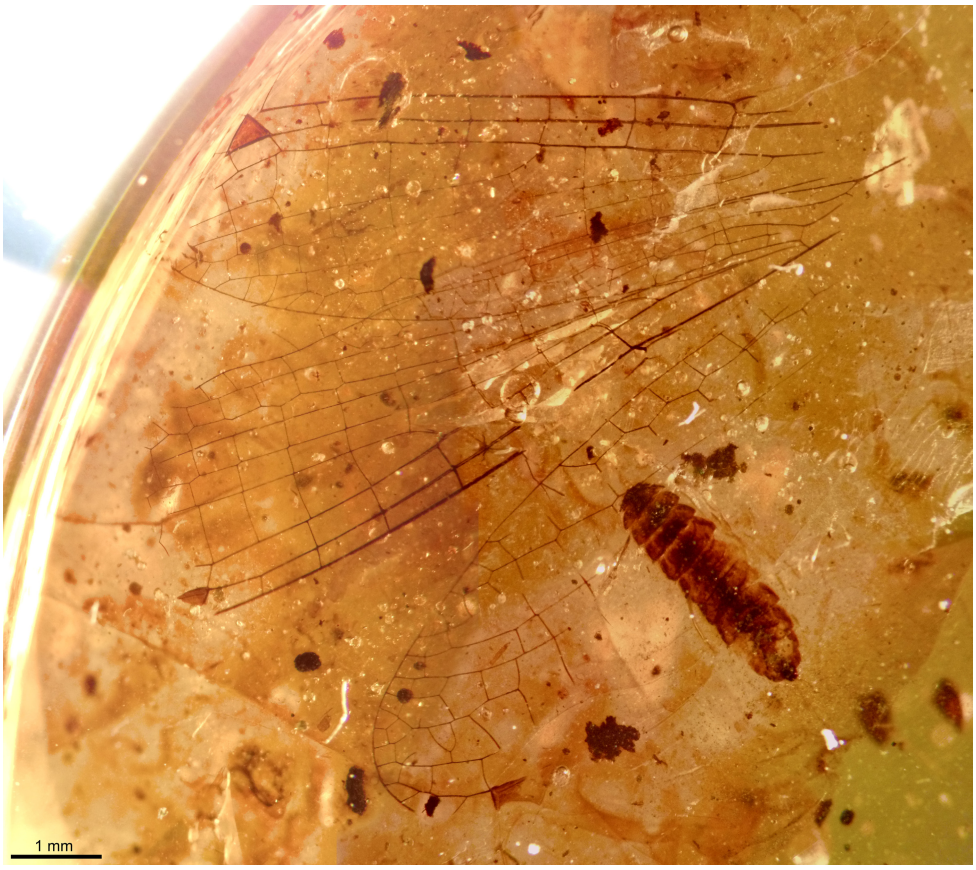

FIGURE 3. Composite image of whole Platycnemidinae? (Platycnemididae) specimen (MGM-7912X) as preserved, from Burmese amber.

The Platystictidae Laidlaw, 1924 are excluded because the wing apex is not falcate. The Pseudostigmatidae Kirby, 1890 and the Coryphagrionidae Pinhey, 1962 are excluded because of the low number of postnodal crossveins, basal wing space between RP3/4 and IR2 not narrowed, and RA and RP1 are not sigmoidally curved at the apex.

Affinities with the †Burmadysagrionidae Zheng *et al*., 2016 (*sensu* Bechly & Velten, 2023) are excluded because of the much shorter RP2 with only four cells between its base and pterostigma *vs*. much longer with 10–12 cells in-between (Zheng *et al*., 2017a; Bechly & Velten, 2023).

The new fossil has the following apomorphies of the Coenagrionidae + Platycnemidoidea: terminal kink of CP at nodus and nodal membrane sclerotisation completely suppressed; basal and distal margin of pterostigma thickened and fused with the strongly thickened pterostigmal part of RA. The Coenagrionidae Kirby, 1890 are excluded because the distal discoidal vein MAb is not oblique, so that the anterior side of the discoidal cell is as long as the posterior side.

Within the Platycnemidoidea *sensu* Bechly (1996), the 'Protoneurinae' *sensu* Dijkstra *et al*. (2014) have shortened CuA and MP.

Dijkstra *et al*. (2014) divided the Platycnemididae into Onychargiinae, Allocnemidinae, Idiocnemidinae, Calicnemiinae, Disparoneurinae, and Platycnemidinae.

The Onychargiinae have an oblique distal discoidal vein MAb (Mitra & Babu, 2010). The Allocnemidinae, Idiocnemidinae, and Calicnemiinae have a perpendicular vein MAb, but a very long IR1, beginning well basad pterostigma. The Disparoneurinae (including the Burmese amber *Cretadisparoneura hongi* Huang, Azar, Cai & Nel, 2015) share with the new fossil a weakly oblique Pt-brace, but they have shortened CuA and MP, and a base of IR1 one to several cells basad pterostigma (Münz, 1919). The Platycnemidinae have discoidal cells similar to that of the new fossil, and elongate CuA and MP (certainly a symplesiomorphy).

The Burmese amber †Palaeodisparoneurinae Poinar, Bechly & Buckley, 2010 (†*Palaeodisparoneura burmanica* Poinar, Bechly & Buckley, 2010, †*Palaeodisparoneura cretacica* Zheng *et al*., 2017 in Zheng *et al*. (2017c), †*Yijenplatycnemis huangi* Zheng *et al*., 2017 in Zheng *et al*. (2017b)) strongly differ from the new fossil in the strongly oblique pterostigmal brace and shortened MP.

The elongate discoidal cell, with distal side MAb slightly longer than basal side, reminds those of some

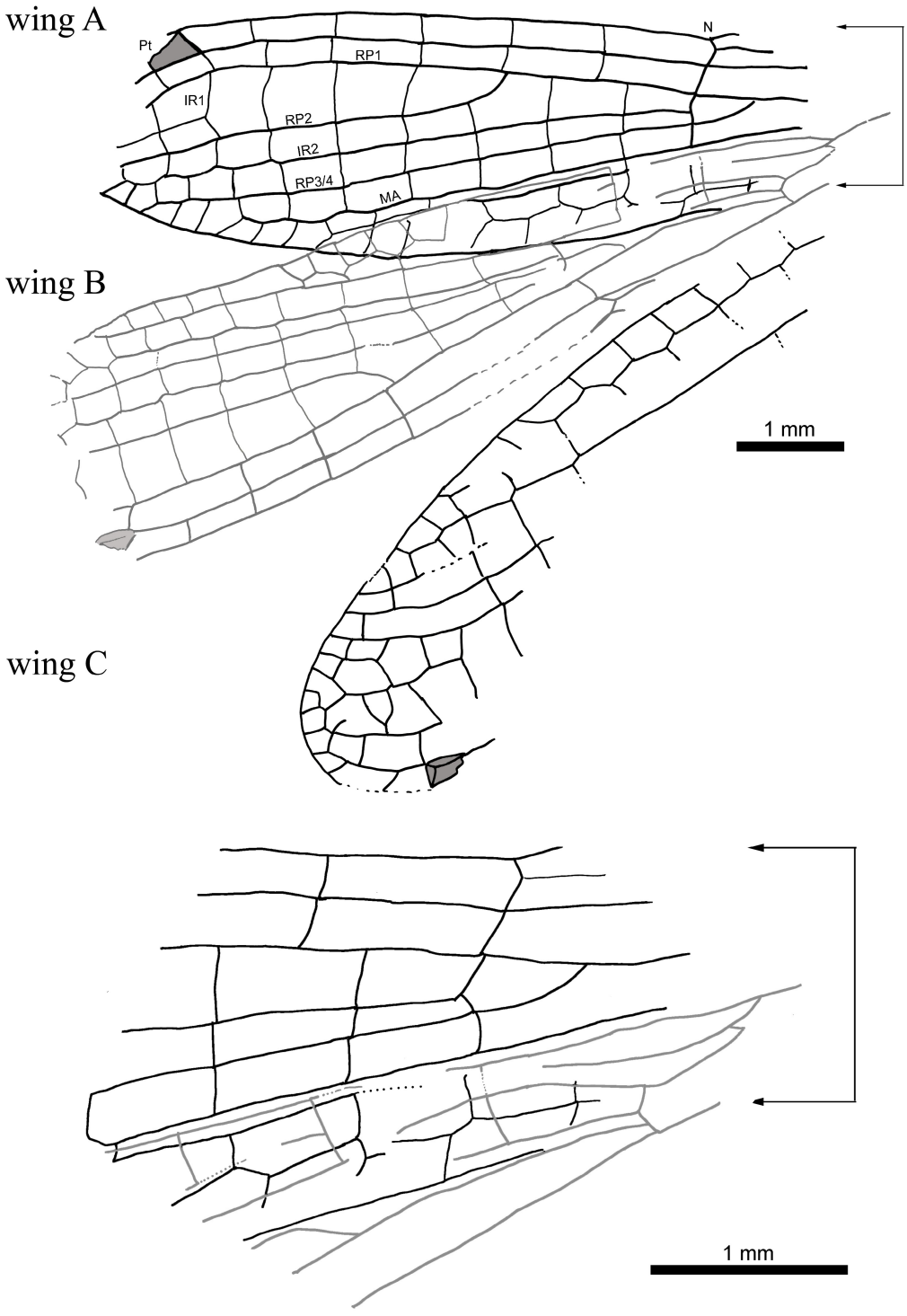

FIGURE 4. Camera lucida drawing of the whole Platycnemidinae? (Platycnemididae) specimen (MGM-7912X) constituted by three incomplete wings, as preserved, from Burmese amber. Below, detailed drawing of wing sections overlapped. Venation of wing B in grey colour to better differentiate its overlapped section. Abbreviations: IR = intercalary radial vein; MA = median anterior; N = nodus; Pt = pterostigma; RP = radius posterior.

Burmadysagrionidae Zheng *et al*., 2016 (*sensu* Bechly & Velten, 2023), *viz*. †*Palaeodysagrion cretacicus* Zheng *et al*., 2017 and †*Pseudopalaeodysagrion youlini* Zheng, Chang & Wang, 2018, but the new fossil strongly differs from the first one in IR1 much shorter and from the second one in the same vein much longer, beginning opposite the base of the pterostigma (Zheng *et al*., 2017a; Bechly & Velten, 2023). The Burmadysagrionidae should be revised

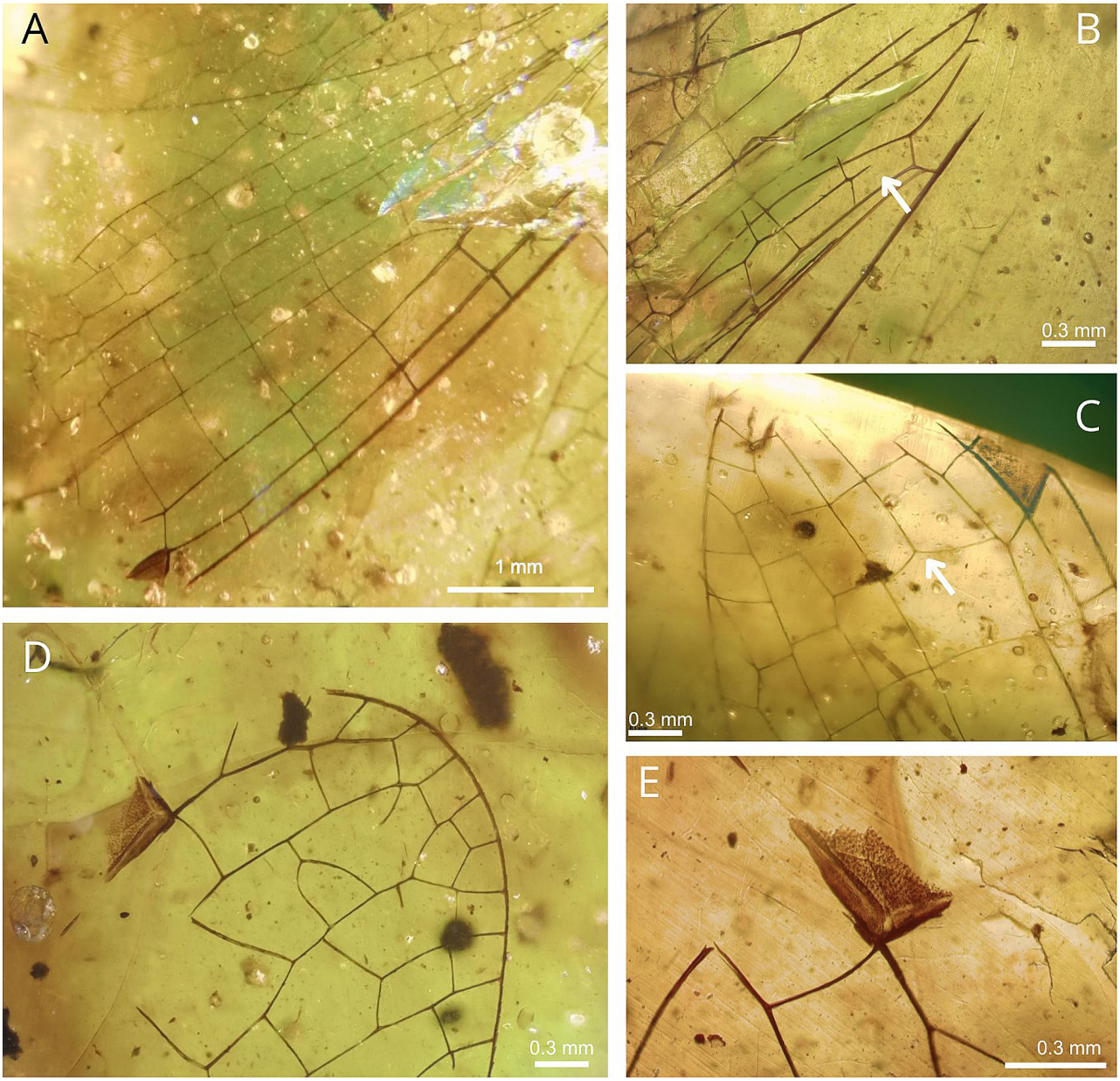

FIGURE 5. Details of the specimen Platycnemidinae? (Platycnemididae) (MGM-7912X). **A**, Detail of most of wing B (see Figure 4 for correspondence). **B**, Overlapping of wings at their bases (wings A and B) (arrow indicates discoidal cell of wing B). **C**, Detail of apex of wing A (arrow indicates vein IR1 originating just below pterostigma). **D**, Detail of apex of wing C. **E**, Detail of pterostigma from image **D**.

because the type genus and species †*Burmadysagrion zhangi* Zheng *et al*., 2016, plus †*Electrodysagrion lini* Zheng *et al*., 2017 and †*Electrodysagrion neli* Zheng, Zhang, Jarzembowski & Wang, 2019 have short and broad discoidal cells unlike *Palaeodysagrion cretacicus* and *Pseudopalaeodysagrion youlini* (Zheng *et al*., 2016a, 2017a, 2018, 2019b; Bechly & Velten, 2023). The new fossil does not correspond to any of these taxa. The discoidal cell of the new fossil differs from those of the Platycnemididae in the distal side MAb slightly longer than its basal side, but the difference is very weak.

We attribute the new fossil to the family Platycnemididae, and possibly to the Platycnemidinae. In that case, it would be the oldest known record of this subfamily. The previous discovery of a Burmese amber Disparoneurinae (sister group of the Platycnemidinae, after Dijkstra *et al*. (2014)) is in accordance with the presence of a representative of this last subfamily in the same amber. But only the discovery of a more complete specimen with wing bases and body structures preserved will possibly allow to precise the position of this new morphotype.

Acknowledgments

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