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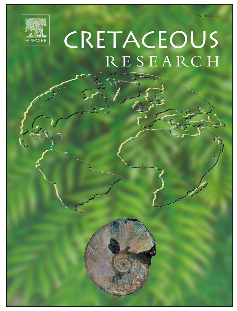

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PII: S0195-6671(16)30092-1

DOI: 10.1016/j.cretres.2016.05.002

Reference: YCRES 3400

To appear in: *Cretaceous Research*

Received Date: 25 March 2016

Revised Date: 5 May 2016

Accepted Date: 8 May 2016

Please cite this article as: Zheng, D., Wang, B., Jarzembowski, E.A., Chang, S.-C., Nel, A., The first fossil Perilestidae (Odonata: Zygoptera) from mid-Cretaceous Burmese amber, *Cretaceous Research* (2016), doi: 10.1016/j.cretres.2016.05.002.

The first fossil Perilestidae (Odonata: Zygoptera) from mid-Cretaceous Burmese amber

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A B S T R A C T

Palaeoperilestes electronicus gen. et sp. nov. is the first perilestid damselfly described from mid-Cretaceous Burmese amber. This new damselfly can be attributed to the family Perilestidae by the midfork being distal of the subnodus and the base of IR2 quite near to the base of RP2, both features found in the extant genera *Perilestes* and *Perissolestes*. *Palaeoperilestes electronicus* gen. et sp. nov. has a strongly zigzagged IR1, however, differing from *Perilestes* and *Perissolestes* which have a straight IR1. The discovery not only adds to the diversity of damselflies in Burmese amber, but also puts the origin of Perilestidae back to at least the mid-Cretaceous.

Key words: Perilestidae, Zygoptera, Odonata, Cenomanian, Cretaceous, Burmese amber

1. Introduction

The Perilestidae Kennedy, 1920 is a family of small damselflies, often called shortwings or twigtails, characterized by short wings (20–25 mm) and very long, slender and colour-banded abdomens (40–56 mm) (Williamson and Williamson 1924; Haber and Wagner, 2014). The adults 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. Perilestidae now consists of two Neotropical genera: *Perilestes* Hagen in Selys-Longchamps, 1862 and *Perissolestes* Kennedy, 1941, with the former consisting of eight species while the later comprises 11 species (Dijkstra et al., 2011, 2014; Schorr and Paulson, 2015; Machado, 2015). The African endemic genus *Nubiolestes* Fraser, 1944 was previously attributed to this family (Bechly, 1996; Neiss and Neusa, 2010); however, it is the sister genus of the Perilestidae sensu stricto in the phylogenetic analysis of Dijkstra et al. (2014). In the present paper, a new damselfly, *Palaeoperilestes electronicus* gen. et sp. nov., is described from the mid-Cretaceous Burmese amber. This is the first fossil representative of the extant family Perilestidae. The new discovery increases our knowledge about these unique damselflies.

2. Material and methods

The specimen described herein was collected from the Hukawng Valley of Kachin Province, Myanmar (locality in Kania et al., 2015: fig. 1). The age of Burmese amber is radiometrically dated at 98.79 ± 0.62 Ma (earliest Cenomanian; Cohen et al., 2013) based on U–Pb zircon dating of the volcanoclastic matrix (Shi et al., 2012).

The amber containing the damselfly is yellow and transparent. The damselfly is preserved together with a big horsefly. The damselfly wings are close to the amber surface and are slightly curved towards the horsefly. This makes it difficult for further polishing and obtaining clear photomicrographs. Photomicrographs 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). The specimen is housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS). All taxonomic acts established in the present work have been registered in ZooBank (see below), together with the electronic publication LSID: urn:lsid:zoobank.org:pub:28289195-14CB-4434-92CD-6D6F5865ABBF.

The nomenclature of the odonatan wing venation used in this paper is based on the interpretations of Riek (1976) and Riek and Kukalová-Peck (1984), as modified by Nel et al. (1993) and Bechly (1996). The higher classification of fossil and extant Odonatoptera, as well as family and generic characters followed in the present work, are based on the phylogenetic system proposed by Bechly (1996) and Dijkstra et al. (2014) for the phylogeny of extant Zygoptera. Wing abbreviations are as follows: CuA, cubitus anterior; IR, intercalary radial veins; MA, median anterior; MP, median posterior; N, nodus; Pt, pterostigma; RA, radius anterior; RP, radius posterior; Sn, subnodal crossvein. All measurements are given in mm.

3. Systematic palaeontology

Order: Odonata Fabricius, 1793

Suborder: Zygoptera Selys-Longchamps, 1854

Family: Perilestidae Kennedy, 1920

Type genus. *Perilestes* Hagen in Selys-Longchamps, 1862

New genus. *Palaeoperilestes* gen. nov.

(urn:lsid:zoobank.org:act:08EA6631-83A4-4EBA-8BEC-A6932257A86B)

Type species. *Palaeoperilestes electronicus* sp. nov.

Etymology. Named from the Greek word παλαιός for 'old' and the type genus *Perilestes*. Gender unknown.

Diagnosis. Wing characters: hindwing midfork (base of RP3/4) shifted distal of N; IR1 strongly zigzagged and shortened, originating basal of Pt base; IR2 distinctly shortened, arising on base of RP2 in forewing but one cell basal of that in hindwing; IR2 two cells distal of midfork in hindwing; hindwing MP long and reaching posterior wing margin slightly distal of base of IR1; CuA short and ending on posterior wing margin near base of IR2; postnodal and postsubnodal crossveins somewhat aligned; all intercalary veins (except IR1 and IR2) suppressed; longitudinal veins RA, IR1, RP1, IR2, and RP2 strongly converging to wing apex; Pt one cell long and well braced.

Palaeoperilestes electronicus sp. nov.

(urn:lsid:zoobank.org:act:15000F2A-E86C-451F-8857-45BA86B873F6)

Figs. 1–5

Etymology. Named after the Greek word electron for 'amber'.

Holotype. NIGP163955. The distal two third of two wings, probably a forewing and a hindwing because of their respective positions; deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

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

Diagnosis. As for genus.

Description. Forewing incomplete (Figs 2A, 3A). Preserved wing length 6.81 mm, maximum width 2.36 mm, length from base of RP2 to Pt 3.8 mm, from Pt to wing apex 1.87 mm. Five postnodal crossveins and six postsubnodal crossveins present distal of N and basal of Pt, with two basal rows aligned but three distal rows not aligned. Three postnodal and postsubnodal crossveins present distal of Pt, not aligned. IR2 slightly zigzagged, arising from RP2 and slightly distal of base of RP2, lying 0.25 mm distally. IR1 strongly zigzagged, three cells and 2.45 mm distal of base of RP2, and two cells basal of Pt base. RP1 with a slight angle below Pt brace. MA distally zigzagged and long. CuA ending on posterior wing margin just below base of IR2. Pt one cell long (Fig. 4), 0.6 mm long and 0.35 mm wide, well braced; star- or pyramid-like microstructures distributed on Pt suface; Pt brace in same orientation to base of Pt. All intercalary veins (except IR1 and IR2) suppressed. Longitudinal veins RA, IR1, RP1, IR2, and RP2 strongly converging to wing apex.

Hindwing incomplete (Figs 2B–C, 3B), resembling forewing except for following differences. Preserved wing length 9.01 mm, maximum width 2.37 mm, length from base of RP3/4 to base of RP2 2.7 mm, from base of RP2 to Pt 3.32 mm, from Pt to wing apex 1.57 mm. Seven postnodal crossveins and eight postsubnodal crossveins present before Pt, somewhat aligned. Five postnodal crossveins and five postsubnodal crossveins present distal of Pt, non-aligned. Midfork present distal of N.

Base of IR2 two cells and 1.99 mm distal of midfork. Base of RP2 one cell distal of base of IR2, lying 0.7 mm distally. IR1 strongly zigzagged, two cells and 1.38 mm distal of base of RP2, and two cells basal of Pt base. MA long, basally straight but strongly zigzagged distally, ending on posterior wing margin slightly basal of Pt brace. MP long, basally straight but slightly zigzagged distally, ending on posterior wing margin slightly distal of base of IR1. CuA ending on posterior wing margin slightly basal of base of IR2.

Three fragmentary legs preserved (Fig. 5), paired long spines present on tibia and tarsi; tibia armed with about seven or eight pairs of spines; tarsi three segmented with third tarsomere length equal to first two tarsomeres, and armed with about five or six pairs of spines; apical claws symmetrical.

4. Discussion

The absence of the wing bases makes the attribution of this damselfly rather difficult. However, *Palaeoperilestes* has a star like microstructures distributed on the surface of the pterostigma (Fig. 4), a derived type for the superfamily Lestoidea Calvert, 1901 (Bechly, 2016), indicating the strong relationship between *Palaeoperilestes* and Lestoidea. Besides, *Palaeoperilestes* has the base of IR2 shifted several cells distal of the midfork. This unique character is only shared by a few zygopteran taxa, i.e., Chorismagrionidae Tillyard and Fraser, 1938, Perilestidae Tillyard and Fraser, 1938, Nubiolestinae Bechly, 1996 and the "megapodagrionid" genus *Arrhenocnemis* Lieftinck, 1933 (according to Bechly, 2016).

Arrhenocnemis was reassigned to Megapodagrionidae by Lieftinck, (1971); however, it was later attributed to the Paltycnemididae: Calicnemiinae (see Gassmann, 2005; Orr and Kalkman, 2010). *Arrhenocnemis* consists of three species, viz., *A. sinuatipennis* Lieftinck, 1933, *A. amphidactylis* Lieftinck, 1949, and *A. parvibullis* Orr and Kalkman, 2010, all from New Guinea. *Palaeoperilestes* resembles *Arrhenocnemis* in having the base of RP2 one cell distal of the base of IR2, and the base of IR1 being three cells distal of the base of RP2. However, any affinity of *Palaeoperilestes* with *Arrhenocnemis* can be excluded by the presence of crenulated distal wing margins, the midfork being aligned with Sn, and a non-zigzagged IR1 in *Arrhenocnemis*.

Chorismagrionidae comprise the relict species *Chorismagrion risi* Morton, 1914 (Fig. 6), only recorded in Australia. Fraser (1957) considered the Chorismagrionidae as ‘an annectent between the families Perilestidae and Chlorolestidae’, but Dijkstra et al. (2014) placed *Chorismagrion* in the Synlestidae. The open discoidal cell in *Chorismagrion* cannot indicate affinities between these two groups, since this character has evolved several times within Zygoptera and Epiproctophora (Bechly, 2016). The absence of wing base characters makes it more difficult to distinguish *Palaeoperilestes* from *Chorismagrion*. The new specimen shares with *Chorismagrion* a strongly zigzagged IR1. However, *Chorismagrion* has a midfork aligned with Sn, the base of IR2 more cells basal of the base of RP1, the base of IR1 nearer to the base of RP2 than to the base of Pt, and Pt covering two cells, obviously differing from the new specimen.

Nubiolestinae Bechly, 1996 comprises the relict genus *Nubiolestes* (type species: *Nubiolestes diotima* (Schmidt, 1943, Fig. 6), recorded in tropical Africa and restricted to Cameroon (Dijkstra and Vick, 2004). *Palaeoperilestes* resembles *Nubiolestes* in the base of IR2 being near to the base of RP2 and the base of IR1being basal of Pt. The differences of *Palaeoperilestes* from *Nubiolestes* are: the midfork is distal of the subnodus instead of being aligned as in *Nubiolestes*, IR1 is quite zigzagged instead of being straight, and the base of IR2 is two cells distal of the midfork instead of six cells (Schmidt, 1943; Fraser, 1944).

Palaeoperilestes has IR2 distinctly shortened, arising on RP2 in the forewing and one cell basal of base of RP2 in the hindwing. These structures resemble the situation in the extant family Perilestidae. *Palaeoperilestes* shares with *Perilestes* and *Perissolestes* (Fig. 6) the midfork distal of the subnodus, the base of IR2 quite near to the base of RP2, but differs from them in having a quite zigzagged IR1 (straight IR1 in *Perilestes* and *Perissolestes*).

In conclusion, *Palaeoperilestes electronicus* cannot be attributed to any known genus. However, *Palaeoperilestes* resembles *Perilestes* and *Perissolestes* more than any of the other genera discussed above. Thus we suggest a new genus provisionally attributed to the family Perilestidae (Fig. 6).

It should be noted that the family Austroperilestidae Petrulevičius and Nel, 2005 (*Austroperilestes hunco* Petrulevičius and Nel, 2005), described from the Lower Eocene of Argentina, was considered to be related to Perilestidae (Petrulevičius and Nel, 2005). However, *A. hunco* can be easily differentiated from *P. electronicus* by the presence of a 'lestine' oblique vein, IR2 being opposite the subnodus, RP3/4 being basal of the nodus, a long pterostigma and a very dense wing venation.

5. Conclusions

The first fossil representative of the extant family Perilestidae, *Palaeoperilestes electronicus* gen. et sp. nov., is described from mid-Cretaceous Burmese amber. The new discovery adds to the diversity of damselflies in the mid-Cretaceous amber. Gondwana was considered to be the ancestral area of the Lestoidea (van Tol et al., 2009), and the recent Perilestidae only occurs in the Neotropical region. The new discovery puts the appearance of perilestid damselfly back to at least the mid-Cretaceous in India.

Acknowledgements

This research was supported by the National Basic Research Program of China (2012CB821900), National Natural Science Foundation of China (41572010, J1210006), Youth Innovation Promotion Association of Chinese Academy of Sciences (No. 2011224), the Chinese Academy of Sciences President's International Fellowship Initiative (2011T2Z04), Open projects of Key Laboratory of Economic Stratigraphy and Palaeogeography, Chinese Academy of Science (Grant no. 2016KF05), and the HKU Seed Funding Program for Basic Research (Grant no. 201210159058). We offer our sincere gratitude to Dr. Eduardo Koutsoukos for editing, and two anonymous reviewers for the very useful comments on the earlier version of the manuscript.

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Figure captions

Fig 1. *Palaeoperilestes electronicus* gen. et sp. nov., holotype, NIGP163955, photomicrograph of specimen.

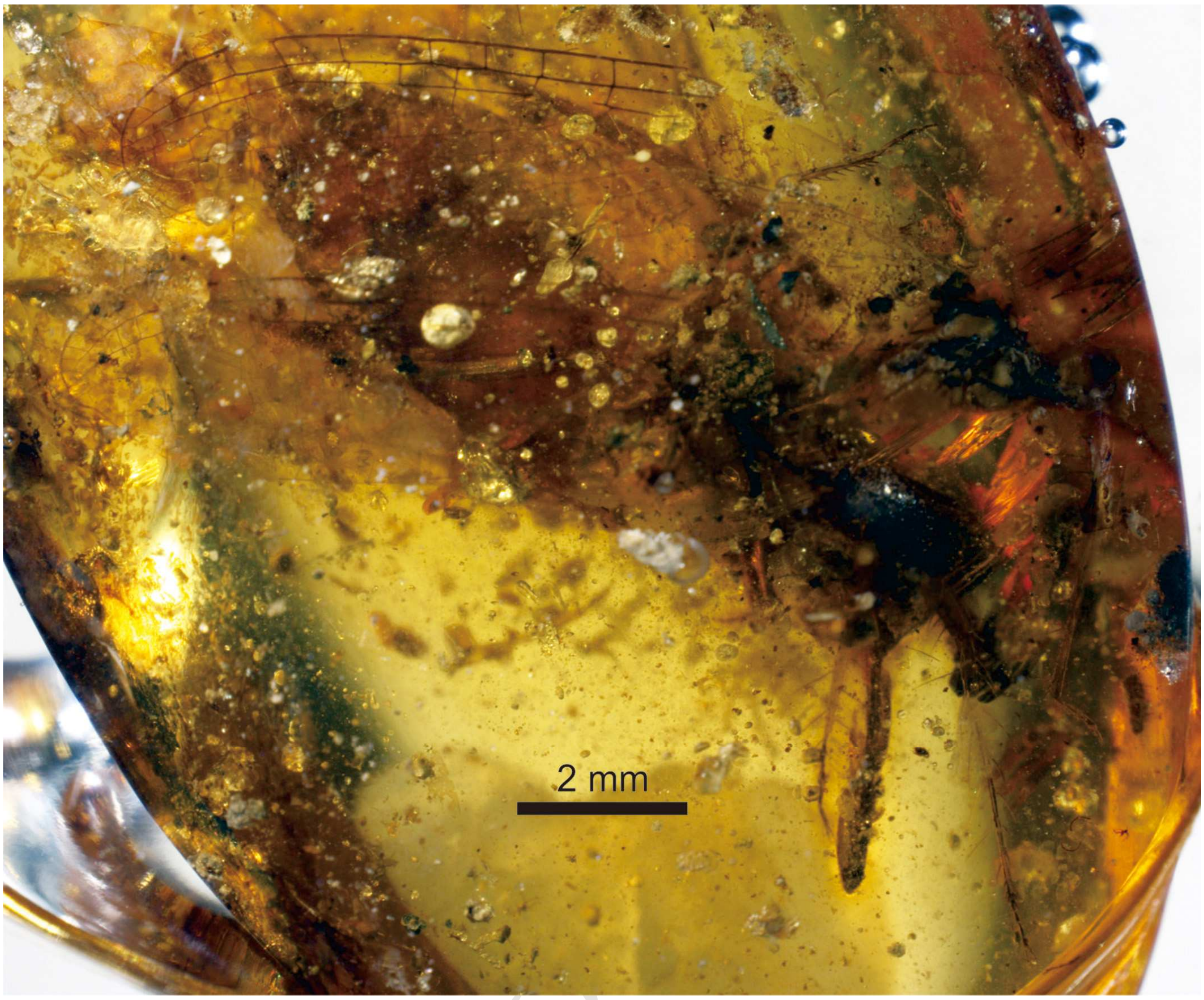
Fig 2. *Palaeoperilestes electronicus* gen. et sp. nov., holotype, NIGP163955. A, photomicrograph of forewing; B, photomicrograph of mid hindwing; C, photomicrograph of distal part of hindwing.

Fig 3. *Palaeoperilestes electronicus* gen. et sp. nov., holotype, NIGP163955, line drawing showing wing venation.

Fig 4. *Palaeoperilestes electronicus* gen. et sp. nov., holotype, NIGP163955, photomicrograph showing details of Pt.

Fig 5. *Palaeoperilestes electronicus* gen. et sp. nov., holotype, NIGP163955, photomicrograph showing leg details.

Fig 6. Putative position of *Palaeoperilestes* gen. nov. in phylogenetic tree of Zygoptera. All line drawings are based on forewings except for *Palaeoperilestes* gen. nov. from a more complete hindwing (Cladogram based on Dijkstra et al. 2014, line drawing of *Chorismagrion risi* Morton, 1914 after Fraser, 1960; line drawing of *Nubiolestes diotima* Schmidt, 1943 after Fraser, 1944; line drawings of *Perilestes gracillimus* Kennedy, 1941 and *Perissolestes remotus* Williamson & Williamson, 1924 after Kennedy, 1941).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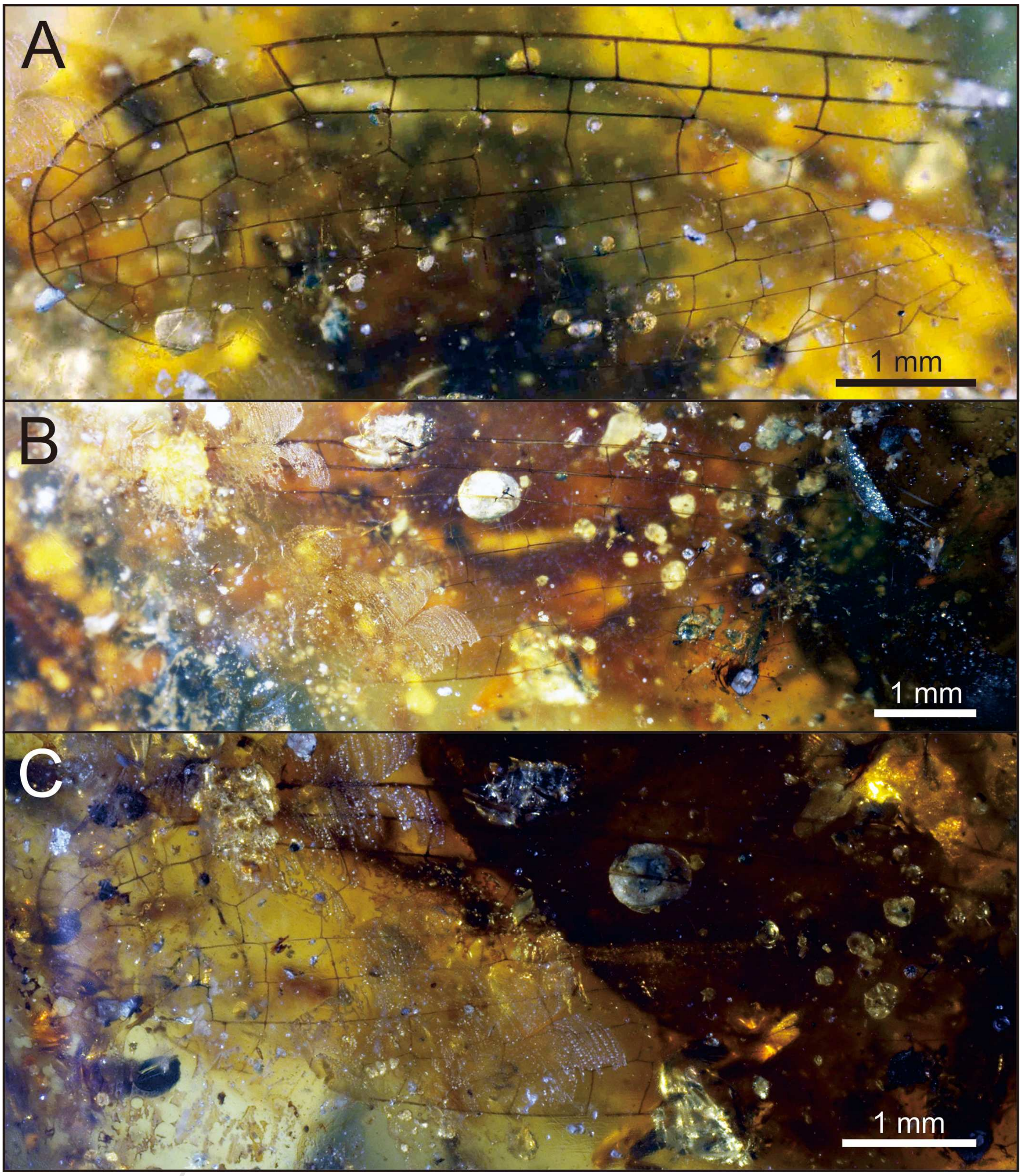
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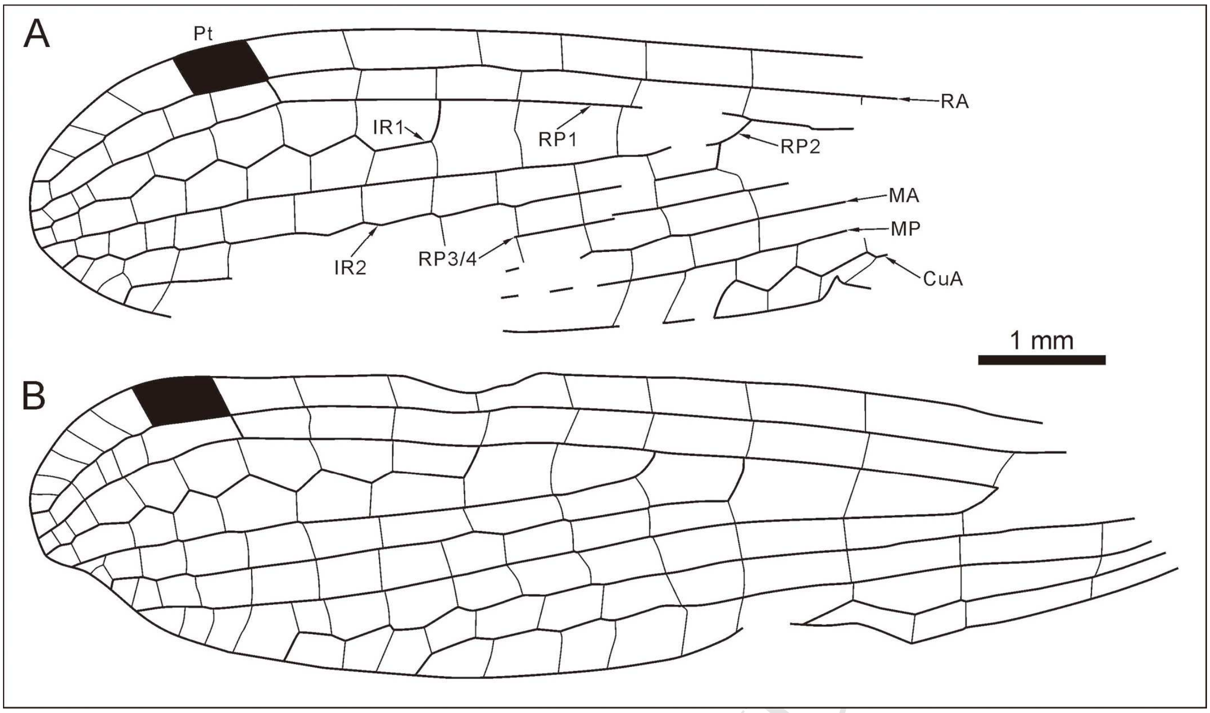
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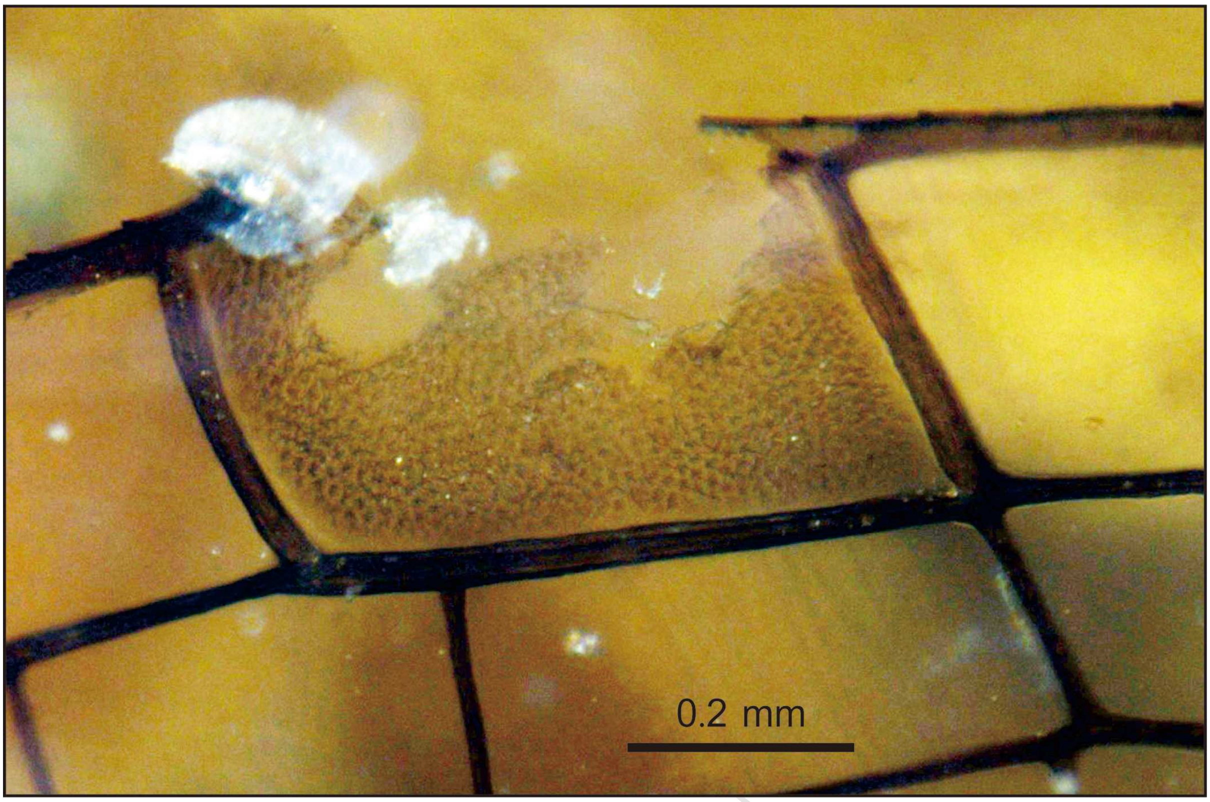
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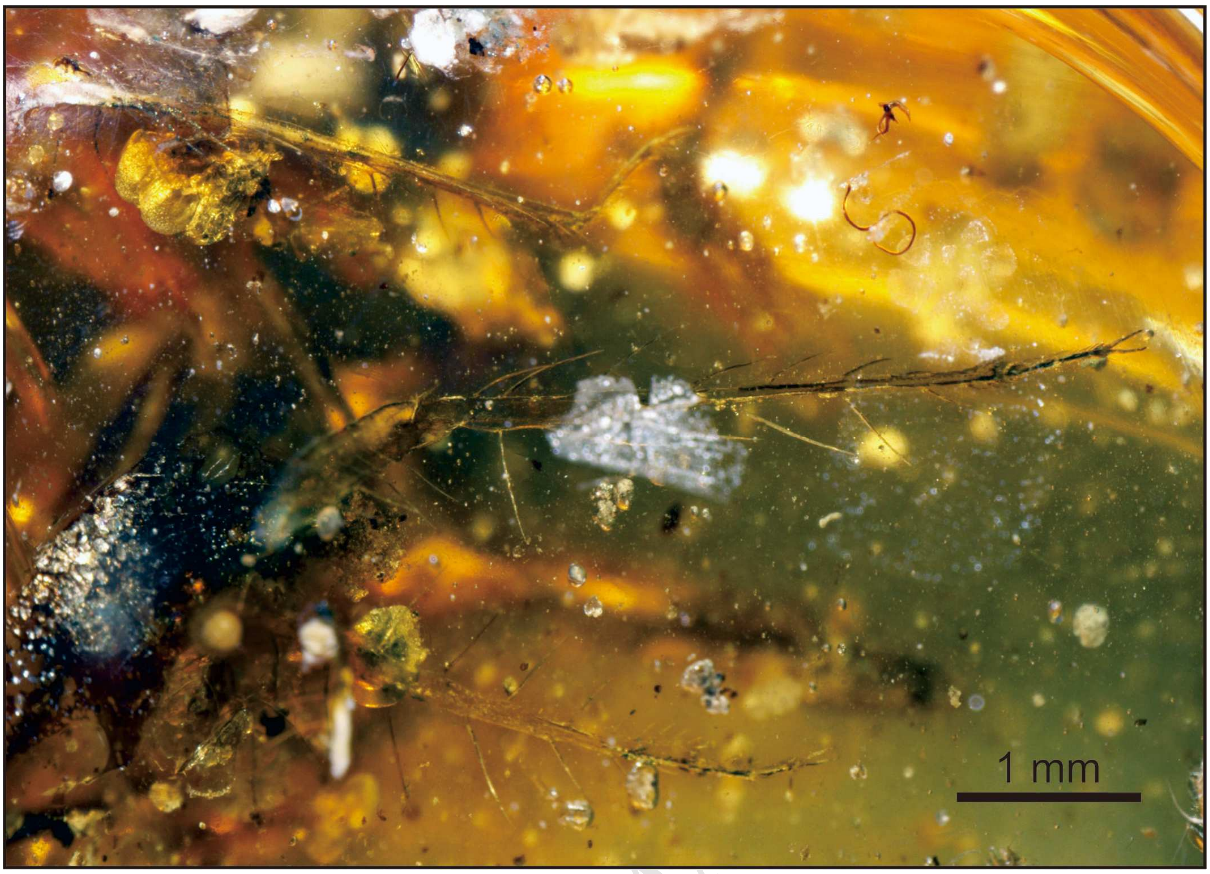
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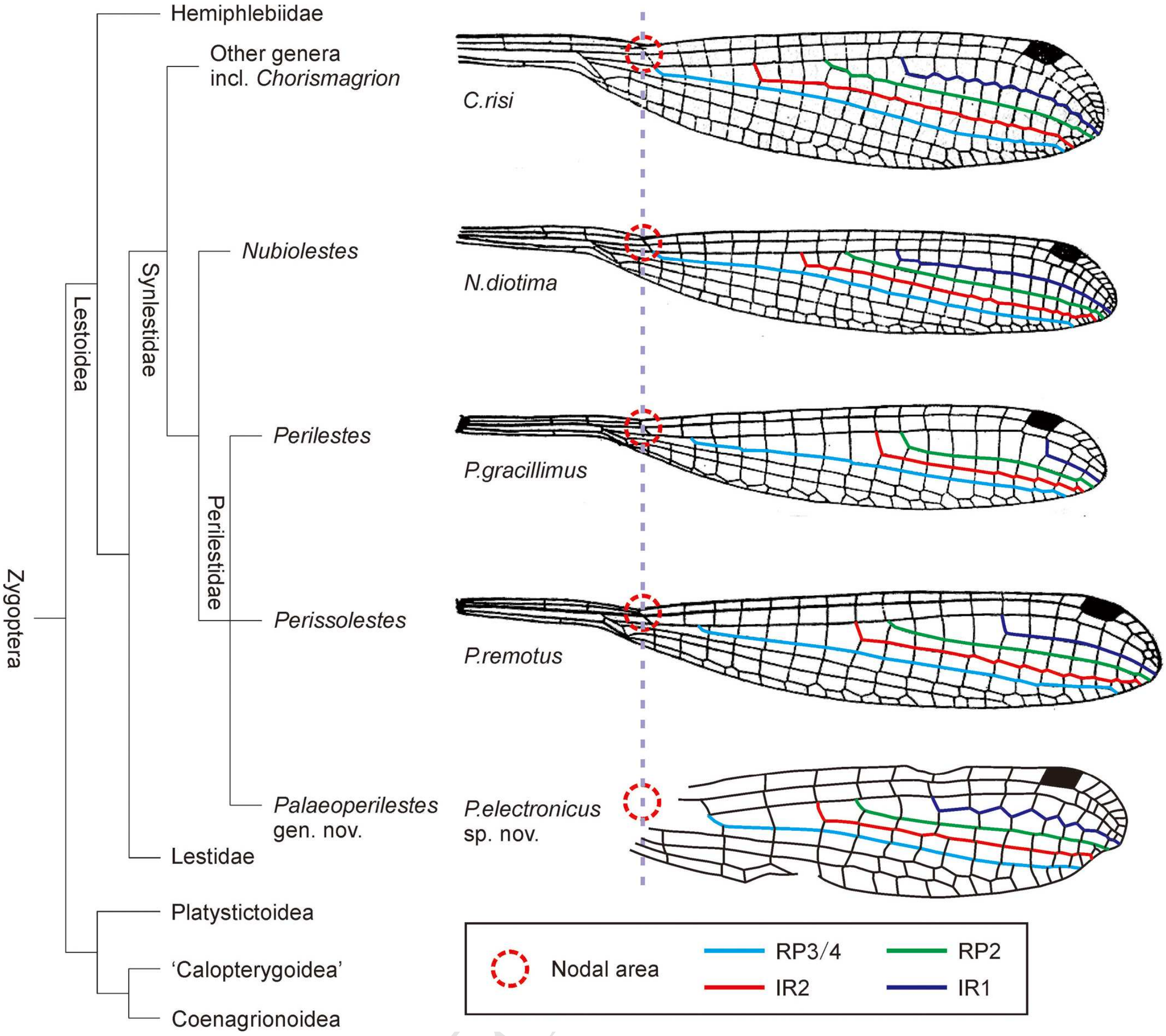
Hemiphlebiidae
Other genera
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Nubiolestes
Perilestes
Perissolestes
Palaeoperilestes
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Lestidae
Platystictoidea
'Calopterygoidea'
Coenagrionoidea
Zygoptera
Lestoidea
Synlestidae
Perilestidae
C.risi
N.diotima
P.gracillimus
P.remotus
P.electronicus
sp. nov.
Nodal area
RP3/4
RP2
IR2
IR1