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Archaeomegalomus gen. nov.: A remarkable new brown lacewing from mid-Cretaceous Kachin amber from northern Myanmar (Neuroptera: Hemerobiidae)

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Abstract

A new fossil species of Hemerobiidae, *Archaeomegalomus burmiticus* **gen**. **et sp**. **nov**., is described from mid-Cretaceous Kachin amber of northern Myanmar. This new genus is the third Mesozoic Hemerobiidae with a single stem of the radius posterior (RP) in the forewing. This suggests that *A. burmiticus* is one of the specialized side branches within the basal Hemerobiidae. Our study sheds more light on the Cretaceous diversity of Mesozoic brown lacewings, suggesting potentially higher generic and species paleodiversity of the hemerobiids in Burmese amber.

Key words: Cenomanian, Burmese amber, wing venation, radius posterior, paleodiversity

Introduction

The Hemerobiidae or brown lacewings is a relatively large group of Neuroptera that includes 591 extant species in 28 genera found worldwide except for Antarctica (Breitkreuz *et al.* 2017; Engel *et al.* 2018). Oswald (1993) published a comprehensive taxonomic revision of Hemerobiidae based on morphological data. Recently, Garzón-Orduña *et al.* (2016) presented the phylogeny of this family using both morphological and molecular data, showing the divergence time estimates of the intrafamilial relationships of Hemerobiidae. The phylogenetic relationships among Hemerobiidae and related groups are controversial. Hemerobiids are recognized as a sister taxon to Chrysopidae (Winterton *et al.* 2010; Aspöck *et al.* 2012; Engel *et al.* 2018), (Mantispoidea + [Myrmeleontoidea + Chrysopidae]) (Winterton *et al.* 2018), or Myrmeleontoidea (Vasilikopoulos *et al.* 2020).

To date, 29 fossil Hemerobiidae species have been described from the Late Jurassic to the Miocene (Yang *et al.* 2018; Makarkin & Gröhn 2020; Makarkin & Perkovsky 2020; Perkovsky & Makarkin 2020; Liu *et al.* 2022). Although they are relatively abundant in the Cenozoic, only seven species have been described from the Mesozoic: *Promegalomus anomalus* Panfilov, 1980 from Late Jurassic, Kazakhstan; *Purbemerobius medialis* Jepson, Makarkin & Coram, 2012 from Early Cretaceous, Barremian, England, United Kingdom; *Cretomerobius disjunctus* Ponomarenko, 1992 from Early Cretaceous, Mongolia; *Hemeroberotha sinefurca* Makarkin & Gröhn, 2020 and *Cretoneuronema jarzembowskii* Liu, Chen & Zhuo, 2022 from mid-Cretaceous, earliest Cenomanian, Myanmar (Kachin) amber; *Plesiorobius sibericus* Makarkin, 1994 from Late Cretaceous, Cenomanian, northeastern Russia; and *Plesiorobius canadensis* Klimaszewski & Kevan, 1986 from Late Cretaceous, Campanian, Canadian amber. Makarkin & Gröhn (2020) suggested including *Protohemerobius perexiguus* Jepson, Makarkin & Jarzembowski, 2009 from Early Cretaceous, Barremian, England in Hemerobiidae, but we treat it as family *incertae sedis*. The multiple radial veins in the forewing (also called oblique radial branches [ORBs] *sensu* Oswald 1993) are considered a synapomorphy of Hemerobiidae and differ from the condition in all other extant Neuroptera, but the Cretaceous *Hemeroberotha* and *Plesiorobius* have the single stem of the radius posterior (RP) in the forewing.

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This paper describes a remarkable new genus and species of Hemerobiidae from mid-Cretaceous Kachin amber of northern Myanmar, as the third record of this family from this amber deposit. This new genus is the third Mesozoic Hemerobiidae with a single stem of RP in the forewing. We also record an undetermined hemerobiid specimen from Kachin amber. Our study sheds light on the potential diversity of brown lacewings in Burmese amber.

Material and methods

All fossil specimens used in this study are deposited in the American Museum of Natural History (New York, NY, USA; D. Grimaldi).

The amber pieces were from deposits in Hukawng Valley, Kachin State, northern Myanmar (26° 20′ N, 96° 36′ E; Cruickshank & Ko 2003; Grimaldi & Ross 2017). This amber deposit was dated to 98.79 ± 0.62 Ma by U-Pb dating of zircons from the amber matrix (Shi *et al.* 2012), equivalent to the earliest Cenomanian. However, Cruickshank and Ko (2003) and Balashov (2021) suggest older ages, from the late Albian to the Albian–Cenomanian stage boundary.

The second (SY) and third (YT) authors polished the amber fossil using waterproof sandpaper of different grain sizes, and then with plastic buffing cloths. We observed the specimen using a Nikon SMZ 800 stereomicroscope (Nikon, Tokyo, Japan). Images were obtained using a Canon 80D digital camera with a Canon MP-E 65 mm macro lens (F2.8, 1–5×) and a Canon MT-24EX twin flash as a light source (Canon, Tokyo, Japan). The amber specimen was immersed in clove oil when it was photographed to increase the visibility of the inclusion. Helicon Focus 7.6.4 (Helicon Soft, Kharkiv, Ukraine) was used for image stacking. All figures were prepared with Adobe Photoshop and Illustrator CC 2020 (Adobe, San Jose, CA, USA).

The morphological terminology follows Oswald (1993). The wing venation terminology generally follows Oswald (1993) and Breitkreuz *et al.* (2017). Although some authors describe MA (media anterior) as the posterior-most vein of the RP (radius posterior) field in both fore- and hindwing (*sensu* Kukalová-peck 1991; Kukalová-peck & Lawrence 2004), we have identified it as a separate field from the RP, following such treatment by Garzón-Orduña *et al.* (2016) and Breitkreuz *et al.* (2017). Wing venation abbreviations are as follows: A1–A3, first to third anal vein; CuA, cubitus anterior; CuP, cubitus posterior; MA, media anterior; MP, media posterior; RA, radius anterior; RP, radius posterior; Sc, subcosta.

Systematic palaeontology

Order Neuroptera Linnaeus, 1758

Superfamily Hemerobioidea Latreille, 1802

Family Hemerobiidae Latreille, 1802

Genus *Archaeomegalomus* gen. nov.

(Figs. 1–3, 5)

Type species. *Archaeomegalomus burmiticus* **sp. nov.**, here designated.

Diagnosis. *Archaeomegalomus* **gen. nov.** can be distinguished from the other hemerobiid genera by the combination of the following characters: Antennae, relatively long; in forewing, costal space broad, narrowed distally; humeral veinlets recurrent, pectinately branched, most subcostal veinlets once to twice forked; Sc fused with RA at distal fourth; RP stemmed single origin; MP deeply forked; CuP deeply forked. In hind wing, basal crossvein connecting RP and M (1r-m) long, slightly sigmoidal; CuP present, branched.

Species included. *Archaeomegalomus burmiticus* **sp. nov.**

Etymology. Combination of the Greek '*archaios*' [ἀρχαῖος], meaning 'ancient', and *Megalomus*, a genus-group name of Hemerobiidae, in reference to the similarities in wing venation. Gender masculine.

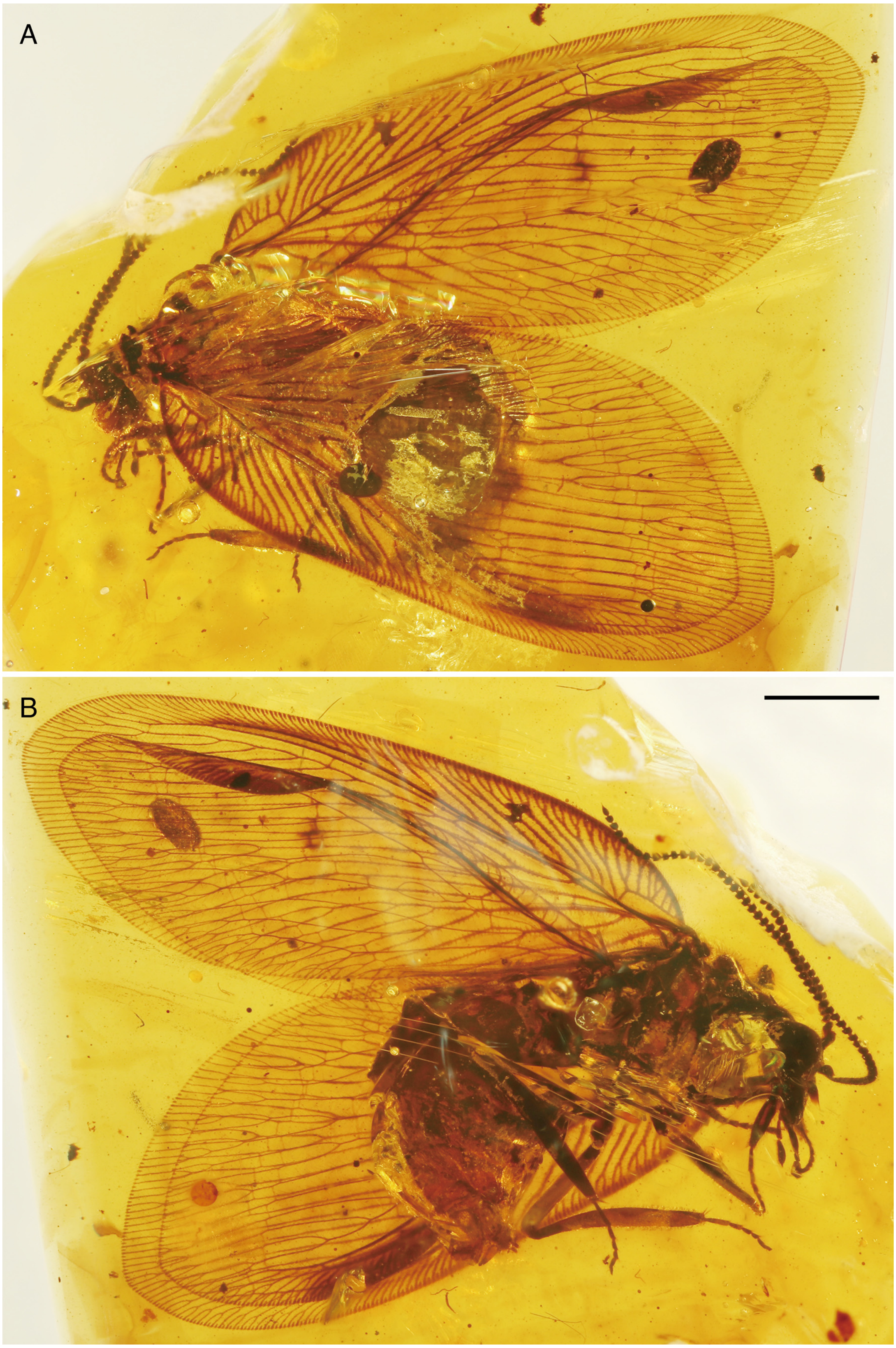

FIGURE 1. Habitus and wing detail of *Archaeomegalomus burmiticus* **gen. et sp. nov.**, holotype (AMNH Bu-SY31) in mid-Cretaceous Kachin amber. A, left lateral view; B, right lateral view. Scale bar: 1.0 mm.

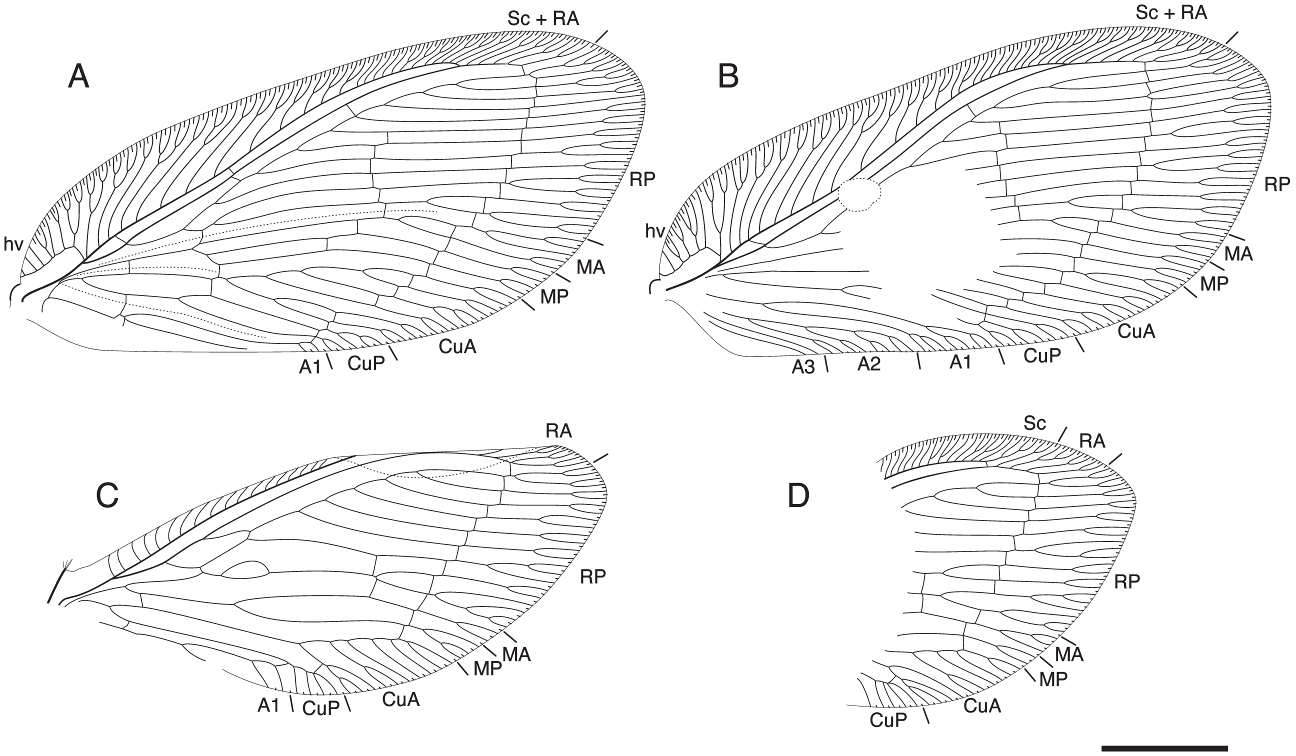

FIGURE 2. Wing venation of *Archaeomegalomus burmiticus* **gen. et sp. nov.**, holotype (AMNH Bu-SY31) in mid-Cretaceous Kachin amber. A, right forewing; B, left forewing; C, right hind wing; D, left hind wing. Abbreviations: A1–A3: first to third anal vein; CuA: cubitus anterior; CuP: cubitus posterior; hv: humeral vein; MA: media anterior; MP: media posterior; RA: radius anterior; RP: radius posterior; Sc: subcosta. Scale bar: 1.0 mm.

Remarks. We assign this new genus to Hemerobiidae because of the presence of a pair of tibial spurs (absent or very short in Berothidae), slightly swollen tibia at the middle (usually not swollen in Berothidae), well developed recurrent and branched humeral vein in the forewing (usually undeveloped in Berothidae), and the hind wing CuA have long pectinate branches (long with short to very short branches in Berothidae) (see further details in Makarkin & Gröhn 2020).

Archaeomegalomus burmiticus sp. nov.

(Figs. 1–3, 5)

Diagnosis. As for the genus (*vide supra*).

Description. Body. Length ca. 3.7 mm as preserved (measured from vertex to apex of the abdomen).

Head. Eyes large, protruding laterally. Antennae: scapus relatively short, ca. 2 times as long as wide; pedicellus one-half length of scape; both scattered with thin setae; flagellum moniliform, relatively long, composed of 38 flagellomeres, with scattered fine setae on each segment. Maxillary palpi 4 or 5 segmented; labial palpi 3 segmented.

Thorax. Pronotum rather short, poorly preserved, covered with thin setae. Mesothorax and metathorax covered with thin setae.

Legs. Foreleg slender; procoxa poorly preserved, relatively long; profemur ca. 0.8 mm long, scarce setae; protibia ca. 0.5 mm long, slightly swollen at the middle, covered with dense thin setae, paired tibial spurs; protarsus five segmented, all tarsomeres covered with thin setae, pretarsal claws thin, small. Midleg slender; mesocoxa short; mesofemur ca. 0.9 mm long, scarce setae; mesotibia ca. 0.9 mm long, only slightly swollen at the middle to apex, covered with dense thin setae, paired tibial spurs; mesotarsus five segmented, all tarsomeres covered with thin setae, pretarsal claws thin, small. Hindleg slender; metacoxa short; metafemur ca. 0.9 mm long, scarce setae; metatibia ca. 1.5 mm long, slightly curved, only slightly swollen at the middle to apex, covered with dense thin setae, paired tibial spurs (Fig. 3E); metatarsus five segmented, all tarsomeres covered with thin setae, pretarsal claws thin, small.

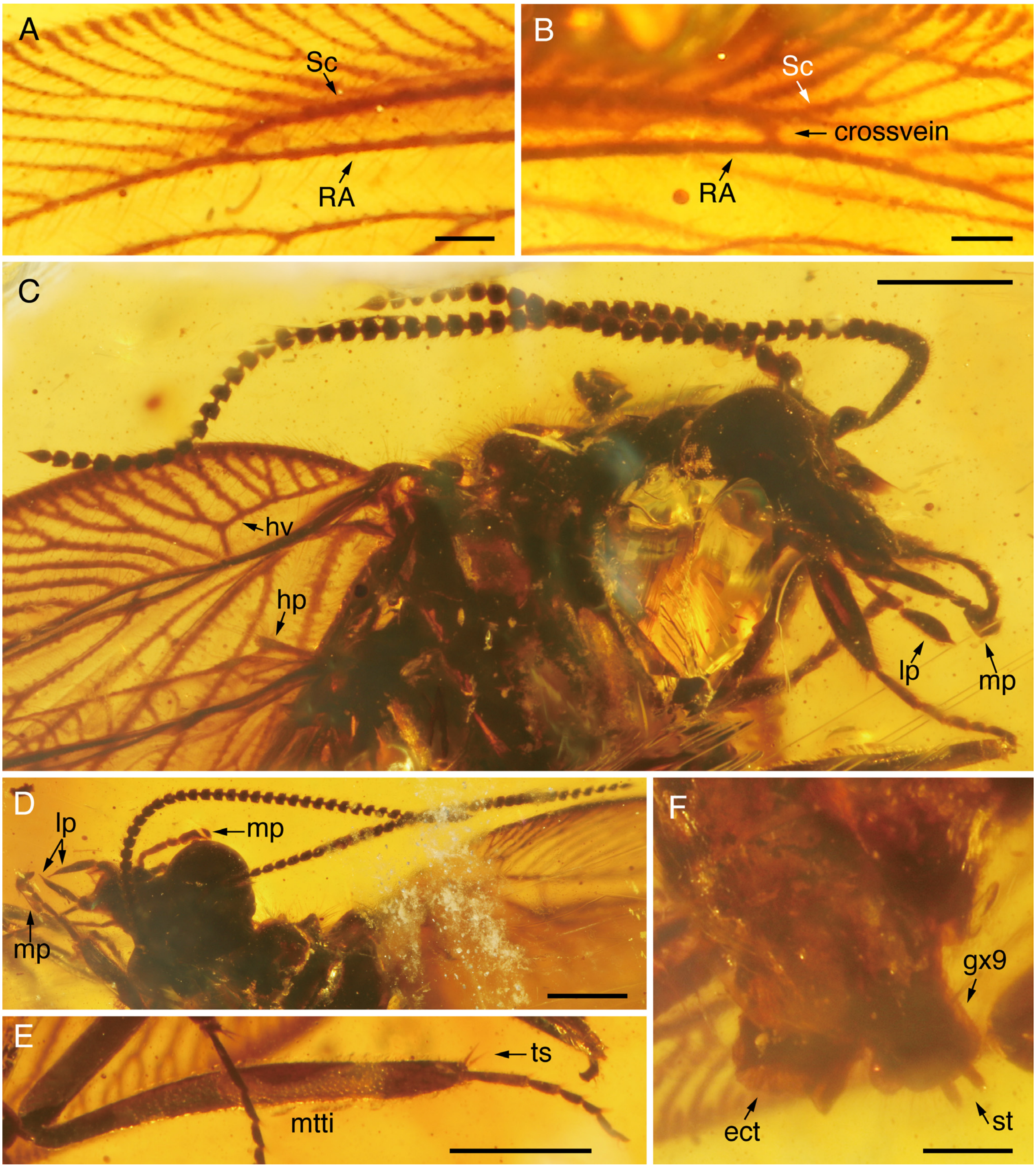

FIGURE 3. Details of *Archaeomegalomus burmiticus* **gen. et sp. nov.**, holotype (AMNH Bu-SY31) in mid-Cretaceous Kachin amber. A, Sc and RA on right forewing; B, Sc and RA on left hind wing; C, right lateral view of head and thorax; D, dorsal view of head and thorax; E, left metatibia and tarsus; F, right lateral view of terminalia. Abbreviations: ect: ectoproct; gx9: gonocoxite 9; hp: humeral plate; hv: humeral veinlet; lp: labial palpus; mp: maxillary palpus; mtti: metatibia; RA: radius anterior; Sc: subcosta; st: gonostylus of gonocoxite 9; ts: tibial spurs. Scale bars: 0.1 mm for A and B; 0.5 mm for C–E; 0.2 mm for F.

Wings. Forewing hyaline (Fig. 2A, B), oval with subacute apex, ca. 5.5 mm long, ca. 2.3 mm wide (right forewing); ca. 5.3 mm long, ca. 2.0 mm wide (left forewing). Trichosors present along the entire wing margin, one trichosor between adjacent veins; marginal portions of veins and trichosors with tufts of thin setae; thin setae sparsely present on dorsal and ventral surfaces of longitudinal veins, but absent on crossveins. Costal space broad, narrowed distally; humeral veinlets recurrent, pectinately branched, most subcostal veinlets once to twice forked. Sc fused with RA at distal fourth (Fig. 3A). Subcostal space, proximal crossvein (1sc-r) located at origin of RP, intermediate crossvein (2sc-r) present. RP stemed single origin, with nine branches, most proximal branch deeply forked at the near stem, all branches terminally forked rather shallowly once or twice; five (right forewing) or six (left forewing) third series intra-crossveins and ten (left forewing) or eleven (right forewing) forth series intra-crossveins present. Three ra-rp crossveins (2ra-rp, 3ra-rp, and 4ra-rp) present. M divided into MA and MP, MP deeply forked; two third series intra-crossveins and three fourth series intra-crossveins present. Three r-m crossveins (2r-m, 3r-m, and 4r-m) present. Long radiomedial flexion line clearly discernible. Cu divided into CuA and CuP, CuP close to wing base; CuA pectinately branched, with four branches, most proximal branch deeply forked; CuP deeply forked; all branches terminally forked shallowly once or twice; one second series intra-crossvein and six fourth series intra-crossveins present. Three m-cu crossveins (1m-cu, 2m-cu, and 4m-cu) present. Short mediocubital flexion line clearly discernible. Three anal veins present, poorly preserved; A1 deeply forked. Two cu-a crossveins (1cu-a and 4cu-a) present. Cubitoanal flexion line clearly discernible.

TABLE 1. Venation in Mesozoic Hemerobiidae.

Taxon	Deposit	Distal part of Sc and RA in the forewing	Number of stem of RP in the forewing	Reference
Promegalomus anomalus Panfilov, 1980	Late Jurassic, Kazakhstan	? (probably fused)	three	Panfilov 1980: fig. 91
Purbemerobius medialis Jepson, Makarkin and Coram, 2012	Early Cretaceous, late Berreiasian, Durlston Formation, England, United Kingdom	?	?	Jepson *et al.* 2012: fig. 16
Cretomerobius disjunctus Ponomarenko, 1992	Early Cretaceous, Mongolia	fused	three	Ponomarenko 1992: fig. 4
Hemeroberotha sinefurca Makarkin and Gröhn, 2020	Mid-Cretaceous, earliest Cenomanian, Myanmar	separated	single	Makarkin & Gröhn 2022: fig. 4
Cretoneuronema jarzembowskii Liu, Chen and Zhuo, 2022	Mid-Cretaceous, earliest Cenomanian, Myanmar	fused	two	Liu *et al.* 2022: fig.3
Archaeomegalomus burmiticus gen. et sp. nov.	Mid-Cretaceous, earliest Cenomanian, Myanmar	fused	single	this study
Plesiorobius sibericus Makarkin, 1994	Late Cretaceous, Cenomanian, northeastern Russia	fused	single	Makarkin 1994: figs. 9–12
Plesiorobius cf. *canadensis* Klimaszewski and Kevan, 1986	Late Cretaceous, Santonian, Taymyr amber, northern Siberia	?	single	Makarkin 1994: fig. 13
Plesiorobius canadensis Klimaszewski and Kevan, 1986	Late Cretaceous, Campanian, Canadian amber	fused	single	Klimaszewski & Kevan 1986: figs. 1, 2

Hind wing hyaline (Fig. 2C, D), elongate-ovoid, ca. 4.6 mm long, ca. 1.8 mm wide (right hind wing); dark brown on pterostigmal area. Trichosors present from the pterostigmal area of costal margin to along the entire wing margin, one trichosor between adjacent veins; marginal portions of veins and trichosors with tufts of thin setae; thin setae sparsely present on dorsal and ventral surfaces of longitudinal veins, but absent on crossveins. Costal space narrowed; humeral lobe triangular, humeral plate bears dense bristles; almost subcostal veinlets simple, five veinlets forked at distal (left hind wing). Subcostal space one crossvein (3sc-r) present (Fig. 3B). RP divided into seven branches; most proximal branche (RP1) loop like vein at the near stem (right hind wing), deeply forked; one second series intra-crossvein and eight third series intra-crossveins present. Two ra-rp crossveins (1ra-rp and 3ra-rp) present, 1ra-rp long and slightly sinuate. M divided into MA and MP, one intra-crossvein (3ma-mp) present. Three r-m crossveins (1r-m, 2r-m, and 3r-m) present, basal 1r-m long and sinuate. Cu divided into CuA and CuP; CuP close to wing base: CuA pectinately branched, with six (right hind wing) or five (left hind wing) branches; one third series intra-crossvein present. Two m-cu crossveins (1m-cu and 3m-cu) present. Anal vein poorly preserved; A1 deeply forked. Two cu-a crossveins (1cu-a and 3cu-a) present.

Abdomen. Visible in right lateral view (Fig. 3F), poorly preserved, but posterior part rather well preserved. Tergite 6 and 7 developed each posterior margin. Terminal segment unclear. Gonocoxite 9 visible, scattered setae on surface; gonostylus of gonocoxite 9 well developed. Ectoproct poorly preserved.

Material. HOLOTYPE: a nearly complete female adult (Fig. 1), partly unobservable due to cracks, preserved in approximately 14 mm × 7.5 mm × 4 mm flat drop-shaped, yellow, transparent amber piece; specimen accession number AMNH Bu-SY31.

Type locality and horizon. Hukawng Valley (26° 20′ N, 96° 36′ E), Kachin State, northern Myanmar; mid-Cretaceous, upper Albian to lower Cenomanian.

Etymology. The specific epithet '*burmiticus*', noun in apposition, refers to the occurrence of the fossil in Burmese amber (burmite) from northern Myanmar.

Remarks. The distal parts of Sc and RA in the forewing are separated in nearly all extant Hemerobiidae, except for *Adelphohemerobius* Oswald, 1994 (see Oswald 1994: fig. 1; Monserrat 1997: fig. 116). In contrast, in the Mesozoic Hemerobiidae, *Hemeroberotha sinefurca* Makarkin, 2020 is the only species in which the distal part of Sc and RA in the forewing are definitely separated, while the others are fused (Table 1). This trait is probably a plesiomorphic condition in the Hemerobiidae.

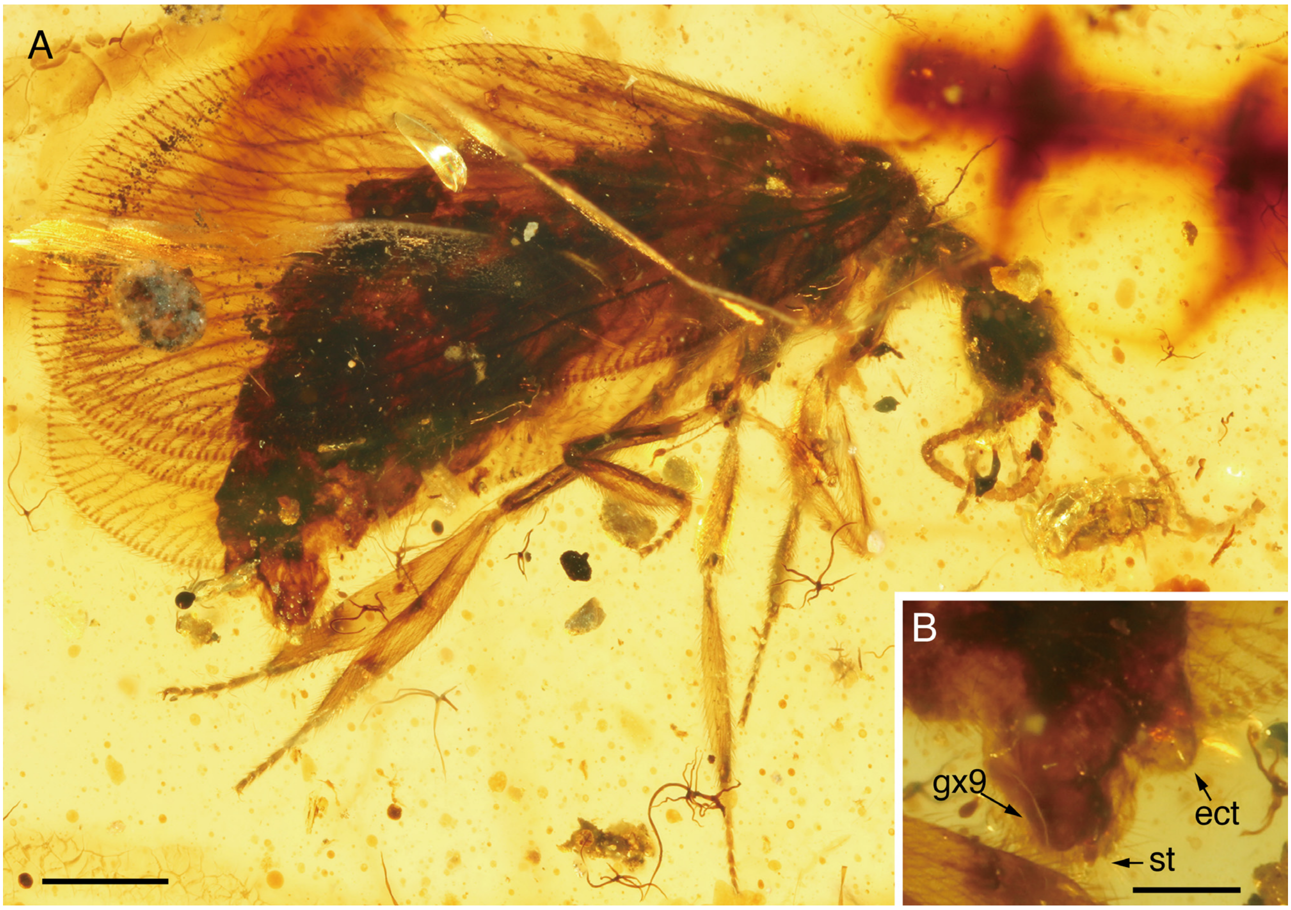

FIGURE 4. Habitus and Detail of Hemerobiidae gen. et sp. indet. (AMNH Bu-SY32) in mid-Cretaceous Kachin amber. A, right lateral view; B, left lateral view of terminalia. Abbreviations: ect: ectoproct; gx9: gonocoxite 9; st: gonostylus of gonocoxite 9. Scale bars: 0.5 mm for A; 0.2 mm for B.

Hemerobiidae gen. et sp. indet.

(Fig. 4)

Description. The body and wings are not clearly visible due to many cracks. Length ca. 3.6 mm as preserved (measured from vertex to apex of the abdomen). Head poorly preserved; eyes large; antennae composed at least

27 flagellomeres with scattered fine setae on each segment. Thorax covered with dense thin setae; pronotum rather short. All legs slender, covered with dense thin setae; all tibia slightly swollen at the middle with paired tibial spurs. Wings poorly preserved; forewing hyaline, oval, ca. 3.5 mm long; trichosors present along the entire wing margin, one trichosor between adjacent veins, marginal portions of veins and trichosors with tufts of thin setae, humeral veinlets recurrent, costal space rather broad; hind wing hyaline, oval, ca. 3.0 mm long. Abdomen poorly preserved; terminal segment scattered with thin setae; gonostylus of gonocoxite 9 developed.

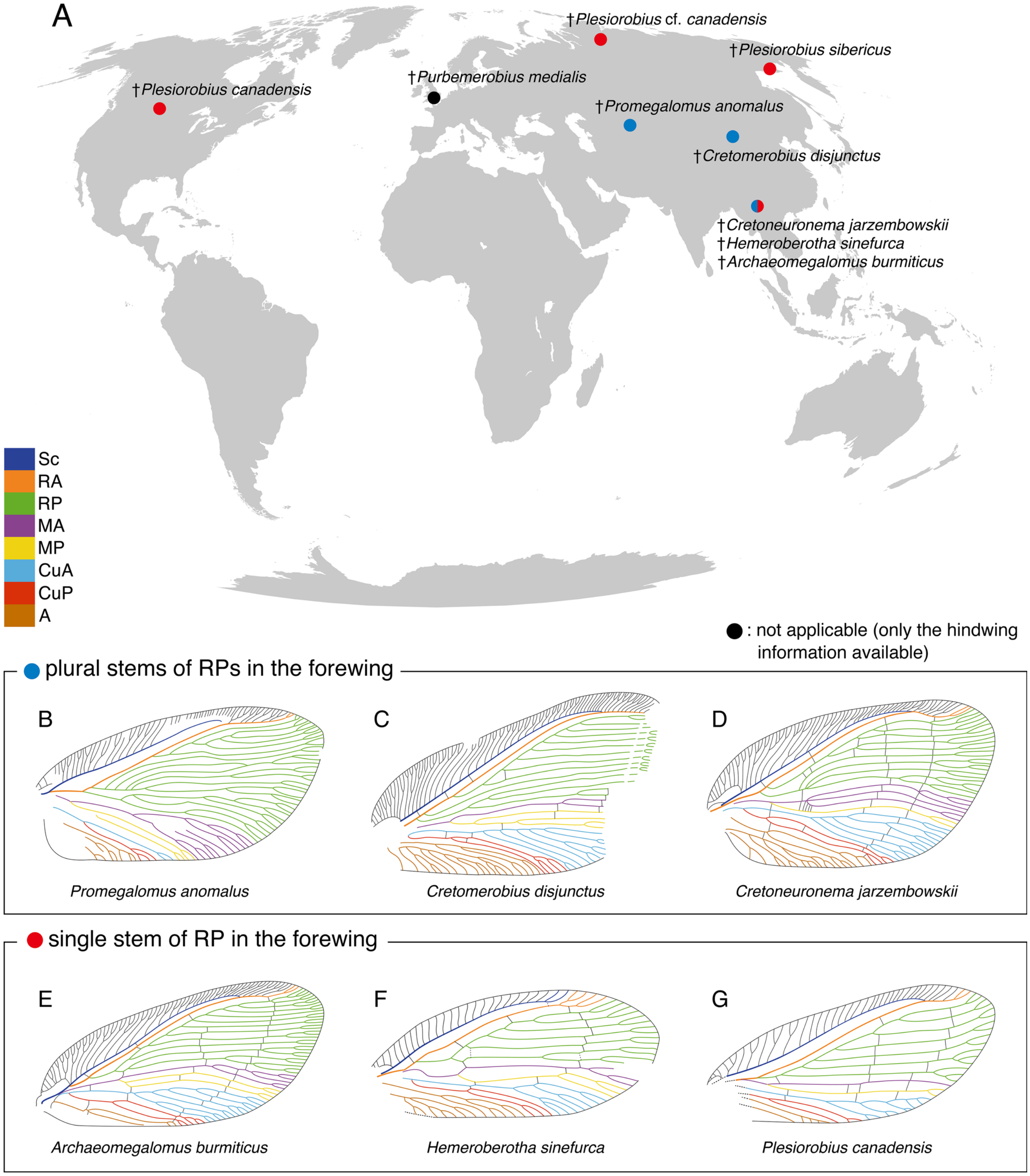

FIGURE 5. Distribution map and forewing venation of Mesozoic Hemerobiidae. A, distribution map of Mesozoic Hemerobiidae; B, *Promegalomus anomalus* (modified after Panfilov 1980, fig. 91); C, *Cretomerobius disjunctus* (modified after Ponomarenko 1992, fig. 4); D, *Cretoneuronema jarzembowskii* (modified after Liu *et al.* 2022, fig. 3); E, *Archaeomegalomus burmiticus* gen. et sp. nov.; F, *Hemeroberotha sinefurca* (modified after Makarkin & Gröhn 2020, fig. 4); G, *Plesiorobius canadensis* (modified after Klimaszewski & Kevan 1986, fig. 2).

Material. Incomplete female adult (Fig. 4), indiscernible many morphological details due to numerous cracks and overlapping wings and body, preserved in approximately 15 mm × 11 mm × 2.5 mm flat arcwise, dark yellow, somewhat transparent amber piece with mumerous debris and pigmentation; specimen accession number AMNH Bu-SY32.

Remarks. We assign this undetermined specimen to the Hemerobiidae because of the presence of a pair of tibial spurs, slightly swollen tibia at the middle, and recurred humeral veinlets. This undetermined specimen can be distinguished from the three burmite hemerobiids by the number of flagellomeres (this specimen has at least 27 or 28 flagellomeres, whereas there are 38 in *Archaeomegalomus*, 19 in *Hemeroberotha*) and the costal space in the forewing (this specimen is rather broad, whereas it is very broad in *Cretoneuronema*). Thus, we withheld identification of the specimen as we could not confirm the important traits of the wing venation, although we were able to differentiate it from the three previously recorded fossil species found in Burmese amber.

Discussion

To date, only three genera of all described Hemerobiidae, the Cretaceous *Archaeomegalomus*, *Hemeroberotha*, and *Plesiorobius*, have a single stem of RP in the forewing. These three genera were widely distributed in the Northern Hemisphere (Table 1, Fig. 5). The fossil localities of the genus *Plesiorobius* are of Laurasian origin, whereas the Burmese amber was recently suggested to have originated from Gondwana (Poinar 2019; Westerweel *et al.* 2019). These backgrounds suggest a wider distribution on Pangea before the continental breakup, as already seen in thorny lacewings (Neuroptera: Rhachiberothidae: Paraberothinae) (Nakamine *et al.* 2020). Oswald (1994) described *Adelphohemerobius enigmaramus* from Chile as the only extant species with a single stem of RP in the forewing and considered it to be the putative sister of all other Hemerobiidae. However, Garzón-Orduña *et al.* (2016) and Makarkin & Gröhn (2020) subsequently suggested that the forewing crossvein 2ir1 (= 2ra-rp) reported by Oswald (1994) could be a second radial vein. In the future, male genitalia morphology and DNA sequence data are needed to determine the taxonomic position of *A. enigmaramus*. Although *A. enigmaramus* may still have a single stem of RP in the forewing, we presently agree with the interpretations of Garzón-Orduña *et al.* (2016) and Makarkin & Gröhn (2020).

Garzón-Orduña *et al.* (2016) recovered a total-evidence phylogeny of Hemerobiidae and noted that four or more radial veins in the forewing are the typical plesiomorphic condition with transformations to fewer veins occurring independently. However, a single stem of RP in the forewing is considered a symplesiomorphic character state in Hemerobiidae (Makarkin & Gröhn 2020). The three genera—Jurassic *Promegalomus* and Cretaceous *Cretomerobius* and *Cretoneuronema*—have two or three separated stems of radial veins in the forewing (Table 1, Fig. 5). This suggests that the group with a single stem of RP in the forewing is actually a specialized side branch within the basal Hemerobiidae (Makarkin & Gröhn 2020).

Studies suggest that Hemerobiidae diversified during the Cretaceous (Winterton *et al.* 2018; Vasilikopoulos 2020), and our results reinforce this scenario. However, the details of the origin and early evolution of Hemerobiidae remain an interesting unresolved question. Future discoveries, such as Jurassic hemerobiid fossils, are expected to solve this issue and to add more insight into the morphological evolution and diversification of the brown lacewings.

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