



Short communication

A new genus and species of Australiphemeridae (Insecta: Ephemeroptera) in mid-Cretaceous Kachin amber of northern Myanmar

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ABSTRACT

Australiphemeridae is an extinct family of mayfly with five Mesozoic genera discovered from Brazil, Siberia, New Jersey, and Myanmar. A new mayfly genus and species, *Crepotamanthus spinitarsus* gen. et sp. nov. (Ephemeroptera: Australiphemeridae), is described based on a well-preserved male imago inside a mid-Cretaceous amber from northern Myanmar. The morphological characters of the head, wings, legs, and genitalia of the new taxa are illustrated. A comprehensive comparison between the extinct taxa and two related extant families, Potamanthidae and Neophemeridae, is present.

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1. Introduction

Ephemeroptera, also known as mayflies, is regarded as one of the earliest winged insect clades and attributed to Palaeoptera together with Odonata. As a common aquatic insect group with a relatively high requirement for water quality, mayflies are widely used for monitoring water quality (Kluge, 2004; Zhou et al., 2015). Their unique metamorphosis model, prometamorphosis, has also been studied in detail (Belles, 2011). Currently, approximately 40 extant mayfly families are recognized, within which, Potamanthidae and Neophemeridae are two remarkable groups and were believed to be closely related (Kluge, 2004; Ogden et al., 2019). These two families share many unique imaginal characters in comparison to other mayflies, both specially with the venation of forewings with MP₂ and CuA strongly curved downward at the base (Kluge 2004; Zhou et al., 2015). However, these two families have entirely different nymphal morphology. The nymphs of Potamanthidae are flat and slender, with mandibular tusks and slender bifurcated hairy gills reminiscent of other burrowing mayfly families, whereas neophemerid nymphs are stout, with a pair of large

gills covering over other ones, which is consistent with Caenidae (Wang et al., 1997; Kluge, 2004; Zhou et al., 2015). Despite this, some molecular studies also support the close relationship between Potamanthidae and Neophemeridae (Ogden and Whiting, 2005; Ogden et al., 2019), but their morphological evolution and cladogenesis remain puzzling (Kluge, 2004; Zhou et al., 2015).

The investigation of related fossil evidence on both nymphal and imaginal stages is essential to resolve the problems regarding Potamanthidae and Neophemeridae. McCafferty (1991) erected the extinct family Australiphemeridae for *Australiphemera* McCafferty, 1990 and *Microphemera* McCafferty, 1990 known from Cretaceous fossil impressions, which are characterized by the similar forewing venation to Potamanthidae but having weakened MP₂ basal arch and without symmetrically bifurcated A₁ vein. Subsequently, another three extinct genera, *Palaeoanthus* Kluge, 1993, *Borephemera* Sinitshenkova, 2000, and *Nanophemera* McCafferty & Santiago-Blay, 2008, were described based on Cretaceous amber inclusions and also assigned to Australiphemeridae (McCafferty and Santiago-Blay, 2008). Probably owing to the poor preservation of these fossils, some crucial characters such as the shape of head, compound eyes, legs, and genitalia were mostly not described in these genera except in *Palaeoanthus* Kluge, 1993. Moreover, the australiphemerid mayflies have always been

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compared with Potamanthidae and are presumed to be closely related to this family (McCafferty, 1991). Nevertheless, the relationships between australiphemerid, potamanthid, and neophemerid genera have not been studied in detail.

To further investigate the fossil taxa, more well-preserved specimens are warranted. The Kachin ambers have provided mid-Cretaceous fossil evidence for many insect lineages, and up to now, five mayfly families including Prosopistomatidae (Lin et al., 2018), Australiphemeridae (McCafferty and Santiago-Blay, 2008), Baetidae (Poinar, 2011), Hexagenitidae (Brandão et al., 2021) and Leptophlebiidae (Chen and Zheng, 2022) have been discovered from Kachin amber. In this study, we found a well-preserved male imago from the mid-Cretaceous Kachin amber. Based on some distinguishable features, we established a new genus and gave a comprehensive comparison between the extinct family and two living allied families.

2. Materials and methods

The Kachin amber specimen herein studied was legally obtained from Kachin State, Hukawng Valley of northern Myanmar (26°20'N, 96°36'E, as in Kania et al., 2015: fig. 1) before June 2017 (see 'Affidavit' and 'Museum Catalogue entry' in Supplementary material). The age of Kachin amber was dated as the earliest Cenomanian (98.79 ± 0.62 Ma) of the mid-Cretaceous, according to Shi et al. (2012) and Yu et al. (2019). Observations of the material were performed with an SDPTOP SZM45 stereomicroscope. Photographs were taken by a Canon EOS 6D digital camera with a Canon MP-E 65 mm 5× macro lens. The holotype is deposited in the Insect

Collection of Jiangsu University of Science and Technology (CZT-EPH-MA2). Terminology follows that of Zhou et al. (2015).

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3. Systematic paleontology

Class: Insecta Linnaeus, 1758
 Order: Ephemeroptera Latreille, 1810
 Suborder: Euplectoptera Tillyard, 1932
 Infraorder: Anteriotorna Kluge, 1993
 Family: Australiphemeridae McCafferty, 1991

Genus *Crepotamanthus* gen. nov.
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Type species. *Crepotamanthus spinitarsus* gen. et sp. nov., by monotypy.

Etymology. The genus name is a combination of the words *Cre* and *potamanthus*. The first word refers to the Cretaceous period; the second is the type genus of Potamanthidae.

Diagnosis. Body slender; head hammer-shaped; compound eyes on lateral sides of head, each width ca. 1/4 head width; antennae slender. Foreleg more than twice the length of midleg and hindleg; paired claws blunt; tarsus five segmented, first tarsomere extremely shortened. Midleg and hindleg similar in length and structure, each with a blunt claw and a hooked claw; tarsus four segmented, each tarsomere with an anteroventral spine, spine of the tarsomere III elongated. Forewings transparent without

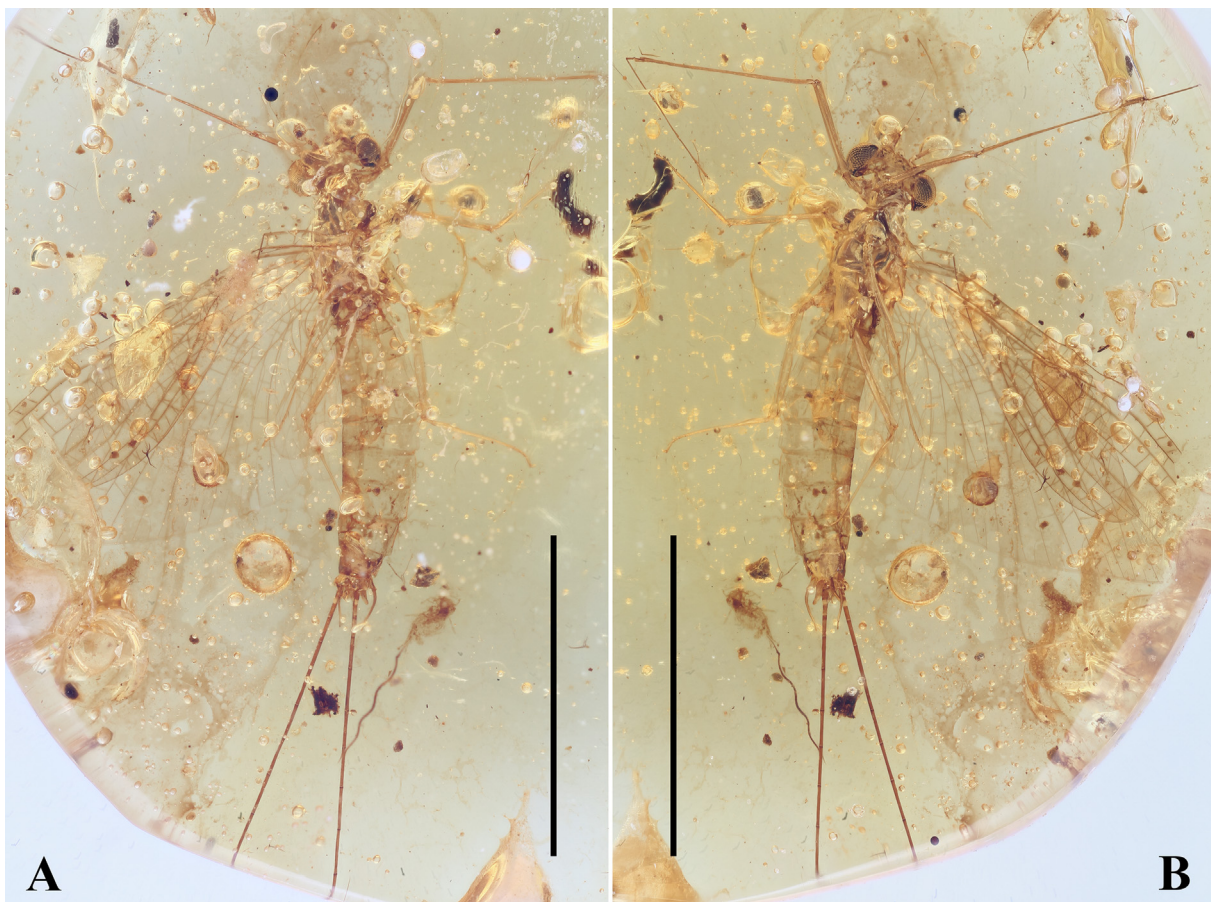


Fig. 1. *Crepotamanthus spinitarsus* gen. et sp. nov., holotype male imago (CZT-EPH-MA2). A. Habitus photo, dorsal view; B. Habitus photo, ventral view. Scale bars = 5.0 mm.

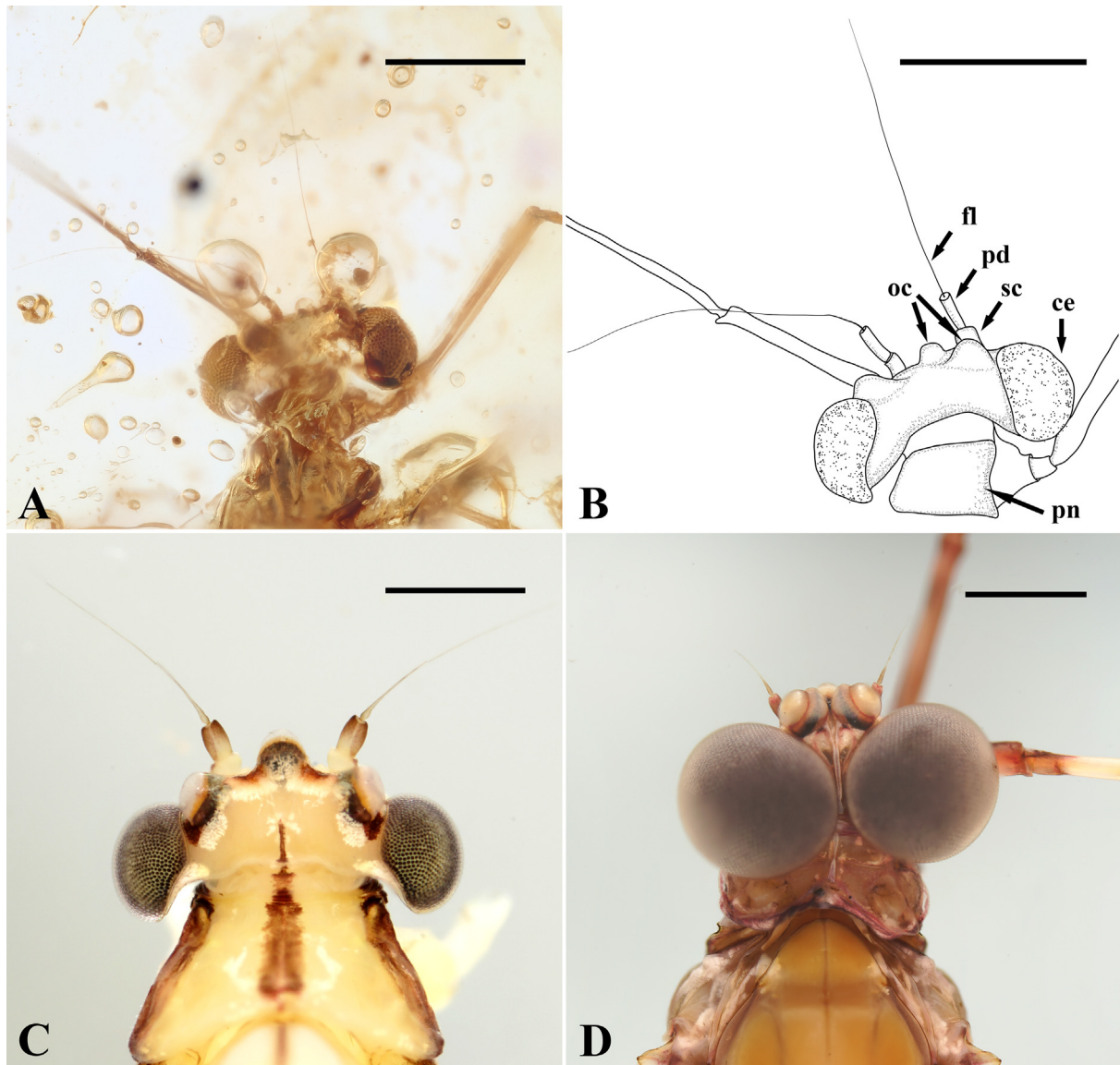


Fig. 2. Head of *Crepotamanthus spinitarsus* gen. et sp. nov., holotype male imago (CZT-EPH-MA2) and extant relatives. A. *C. spinitarsus* gen. et sp. nov., head photo, dorsal view; B. *C. spinitarsus* gen. et sp. nov., drawing of head, dorsal view; C. Head of *Potamanthodes longitibius* (Bae and McCafferty, 1991), dorsal view; D. Head of *Potamanthellus chinensis* Hsu, 1936, dorsal view. Scale bars = 1.0 mm. Abbreviations: ce, compound eye; oc, ocellus; fl, flagella; pd, pedicel; sc, scape; pn, pronotum.

pigment; Rs forked at basal 1/4, in front of the MA fork which at basal 1/2, MP₂ and CuA decurved at base, A₁ single. Forceps four-segmented, segment II longest, segment III and IV ellipsoid shaped; penis flat, forked near base.

***Crepotamanthus spinitarsus* sp. nov.**

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(Figs. 1–5)

Etymology. The specific name is a combination of the words *spini* and *tarsus*, which refers to the spiked mid- and hind-tarsomeres.

Type material. Holotype male imago (No. CZT-EPH-MA2), deposited in the Insect Collection of Jiangsu University of Science and Technology (ICJUST).

Type locality. Hukawng Valley of southwest Maingkhwan, Kachin State (26°20N, 96°36E), Myanmar, lowermost Cenomanian (mid-Cretaceous).

Description of holotype. Body length 7.55 mm (Fig. 1A, B). Head width 1.57 mm, hammerhead shaped; compound eyes on lateral sides of head, width ca. 0.4 mm, three ocelli hemispherical, lateral ocellus nearly attached to compound eye, larger than front ocellus; antennae ca. 2.2 mm, scape and pedicel cylindrical, about 1: 2 in length, flagella longer than head width (Fig. 2A, B). Head shape similar to some extant *Potamanthus* species (Fig. 2C), compound eyes not enlarged as in neoephemerid genera (Fig. 2D). Pronotum significantly narrower and shorter than head (Fig. 2A, B). Foreleg ca. 7.80 mm, mid- and hindleg ca. 3.50 mm (Fig. 3A–C). Femur: tibia: tarsus of foreleg ca. 1.0: 1.6: 3.0, length ratio of tarsomeres ca. 0.1: 1.0: 1.0: 0.7: 0.3, claws paired, both blunt (Fig. 3D, E); midleg and hindleg same in both characters and length, femur: tibia: tarsus ca. 1.1: 1.0: 0.3, tarsus four segmented, 1.3: 1.0: 0.4: 1.8 in length (Fig. 3F–H), each tarsomere with tiny setae on ventral side and an anteroventral spine, spine of the tarsomere III strongly elongated compared with extant relatives (Fig. 3H–J), about 1.8×

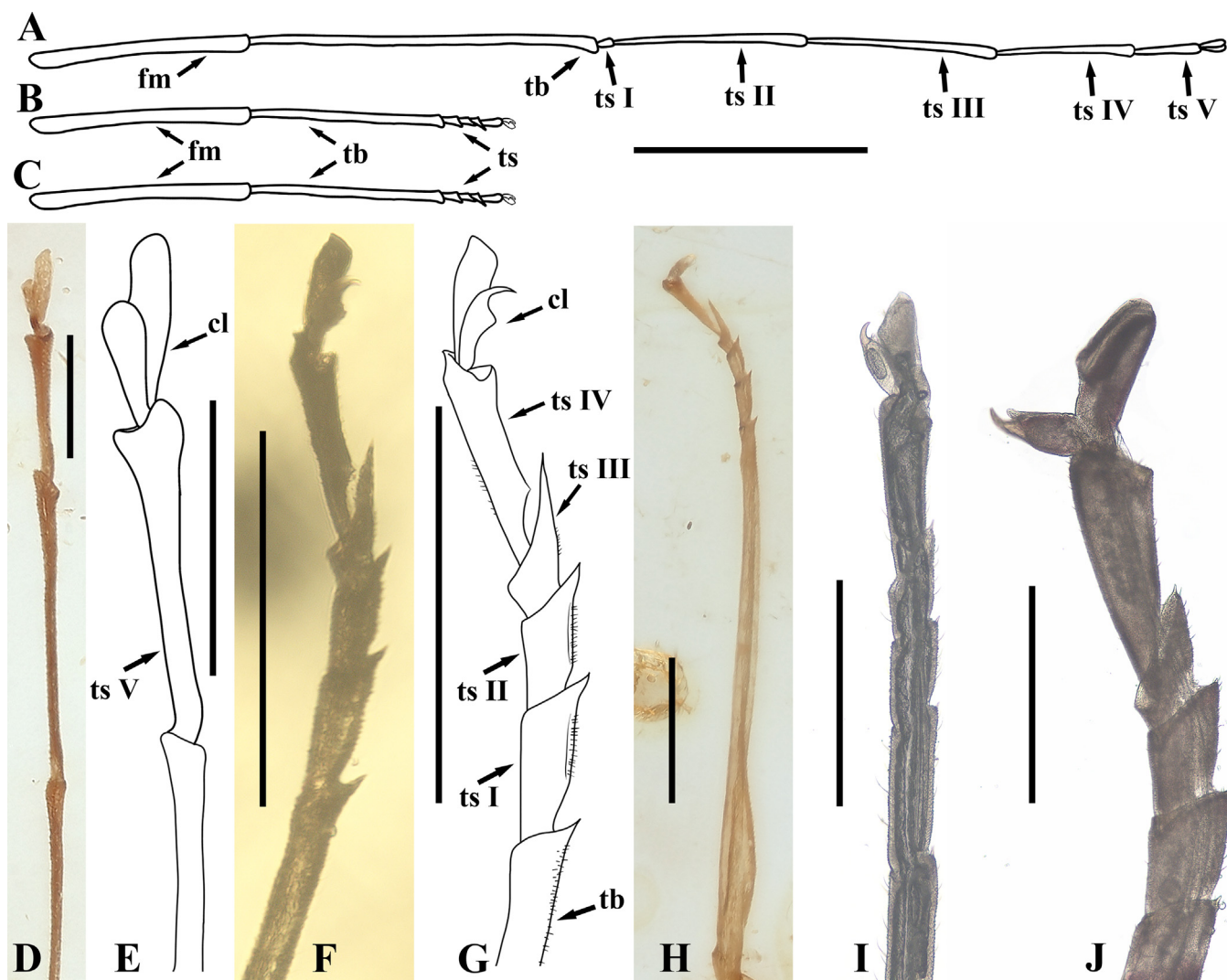


Fig. 3. Legs of *Crepotamanthus spinitarsus* gen. et sp. nov., holotype male imago (CZT-EPH-MA2) and extant relatives. A. *C. spinitarsus* gen. et sp. nov., drawing of foreleg; B. *C. spinitarsus* gen. et sp. nov., drawing of foreleg; C. *C. spinitarsus* gen. et sp. nov., drawing of midleg; D. *C. spinitarsus* gen. et sp. nov., photo of fore-tarsus; E. *C. spinitarsus* gen. et sp. nov., drawing of fore-tarsus; F. *C. spinitarsus* gen. et sp. nov., photo of mid-tarsus; G. *C. spinitarsus* gen. et sp. nov., drawing of mid-tarsus; H. *C. spinitarsus* gen. et sp. nov., photo of mid-tarsus; I. *Potamanthodes longitibius* (Bae and McCafferty, 1991), photo of mid-tarsus; J. *Potamanthellus chinensis* Hsu, 1936, photo of fore-tarsus. Scale bars = 2.0 mm for A–C, 0.5 mm for D–J. Abbreviations: fm, femur; tb, tibia; ts, tarsomere(s); cl, claws.

length of tarsomere III; claws paired, one blunt and one hooked, hooked one has a triangular protuberance in middle.

Costal margin of forewings ca. 6.20 mm, 2.46 mm in hind wings (Fig. 4A), venation generally similar to extant potamanthid and neoephemerid genera, but without any pigment (Fig. 4B, C). One marginal intercalary in each space on forewing outer margin, Rs of forewing forked at basal 1/4, in front of fork of MA which forked near 1/2, MP₂ and CuA running parallel to MP₁ but strongly decurved at base, MP₂ attached to MP₁ and connect with CuA by a basal cross-vein, three sigmoid veins arise from CuA going to hind margin and cubital angle, basal one bifurcated (Fig. 4A), A₁ single (Fig. 4D), without bifurcation or attached veinlets as in extant relatives (Fig. 4E, F). Hindwing has an acute costal angulation, longitudinal and crossveins weak, marginal intercalary undeveloped (Fig. 4A).

Abdomen ca. 5.0 mm, I–VIII abdominal segments transparent, have no posterolateral projection which present in segment IX (Fig. 1A, B). Forceps ca. 0.9 mm, four segmented, segment I: II: III: IV = 1.0: 2.3: 0.3: 0.3 in length, segment II cylindrical, segment III and IV ellipsoid shaped, segment II–IV with small capitate setae covered

on inner margin; penis flat, length subequal to segment II of forceps, forked near base, apex of the deep median cleft blunt (Fig. 5A–D). Caudal filaments covered with tiny setae, median filament lost (Fig. 5A–D) instead of a developed or vestigial filament in extant relatives (Fig. 5E, F).

4. Discussion

The new genus in this study is the sixth genus of Australiphemeridae and the second one discovered in Kachin amber (McCafferty and Santiago-Blay, 2008). *Crepotamanthus* gen. nov. can be assigned to Australiphemeridae by the basally decurved MP₂ and CuA and the single A₁ (Fig. 4A, D). *Crepotamanthus* gen. nov. can be easily distinguished from *Nanophemera*, the other genus known from Kachin amber, by the forewing venation having different connection forms of MP₁ and IMP, fewer crossveins between CuP and A₁, and the presence of a single A₁ (Fig. 4A, D) (See Table 1). Compared with the other two genera, *Australiphemera* and *Microphemera* from Brazilian shale impressions, *Crepotamanthus* gen.

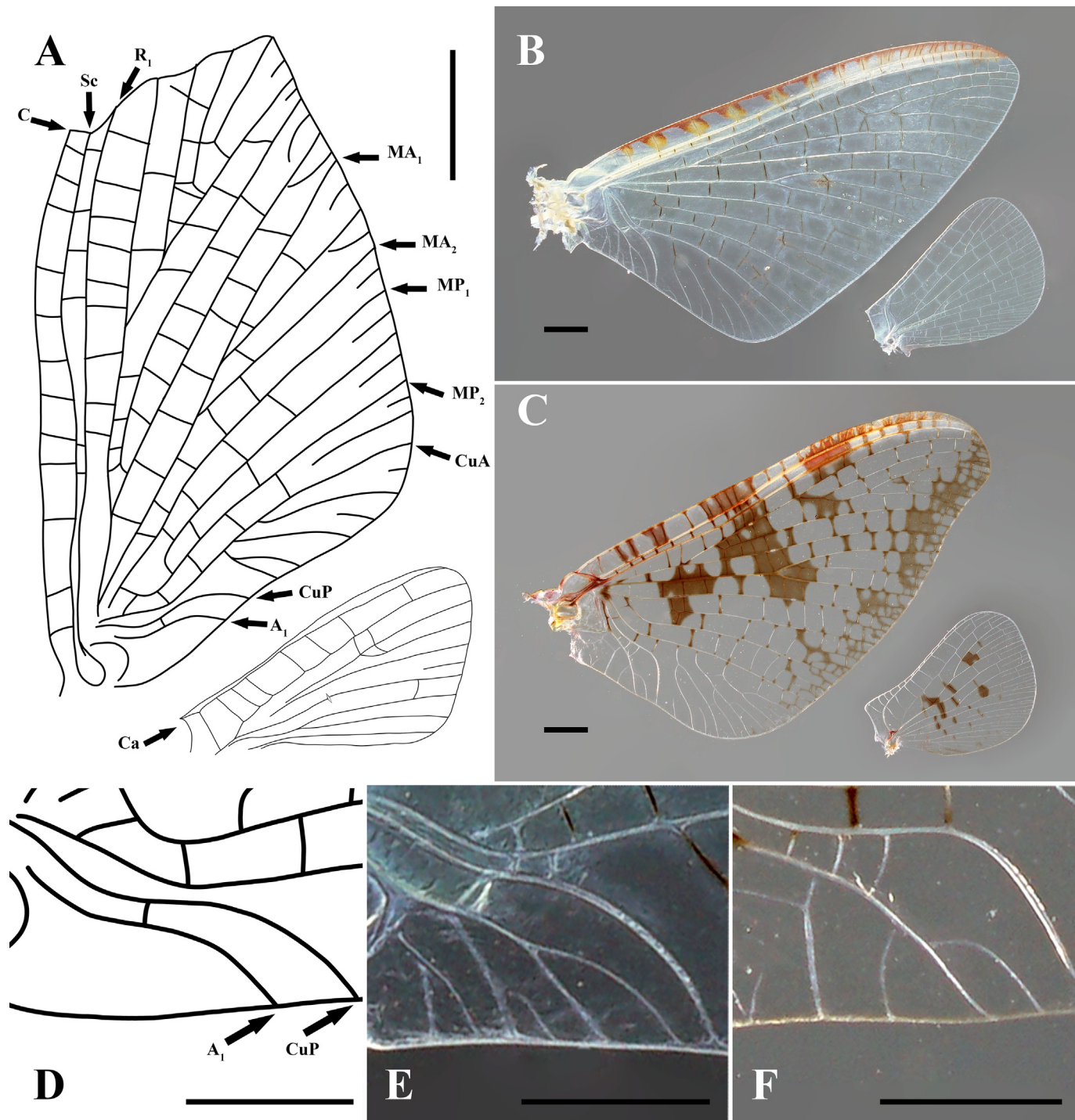


Fig. 4. Wings of *Crepotamanthus spinitarsus* gen. et sp. nov., holotype male imago (CZT-EPH-MA2) and extant relatives. A. *C. spinitarsus* gen. et sp. nov., drawing of wings; B. *Potamanthodes longitibius* (Bae and McCafferty, 1991), photo of wings; C. *Potamanthellus chinensis* Hsu, 1936, photo of wings; D. *C. spinitarsus* gen. et sp. nov., drawing of anal area of forewings; E. *Potamanthodes longitibius* (Bae and McCafferty, 1991), drawing of anal area of forewings; F. *Potamanthellus chinensis* Hsu, 1936, drawing of anal area of forewings. Scale bars = 1.0 mm. Abbreviations: C, costa; Sc, subcostal; R₁, radius; MA, medius anterior; MP, medius posterior; CuA, cubitus anterior; CuP, cubitus posterior; A₁, anal; ca, costal angulation.

nov. can be easily differentiated by single A₁ and single marginal intercalary without marginal crossveins in forewings and undeveloped marginal intercalaries in hindwings (Fig. 4A, D, Table 1). Compared with *Borephemera* from New Jersey amber, *Crepotamanthus* gen. nov. has a single A₁ and no crossveins between marginal intercalaries of forewings (Fig. 4A, D, Table 1). As a result of the poor preservation status of the above fossils, it's difficult to

make comparisons for the other details on the head, legs, and genitalia except for wing venation. The only fossil taxon we can compare with is *Palaeoanthus* Kluge, 1993, from Taimyr Peninsula amber. Male subimago of *Palaeoanthus orthostylus* Kluge, 1993 has big compound eyes almost touching each other, short antennae, conical pedicel, four-segmented forceps touching each other basally, and a pair of slender spine-shaped penis lobes which are

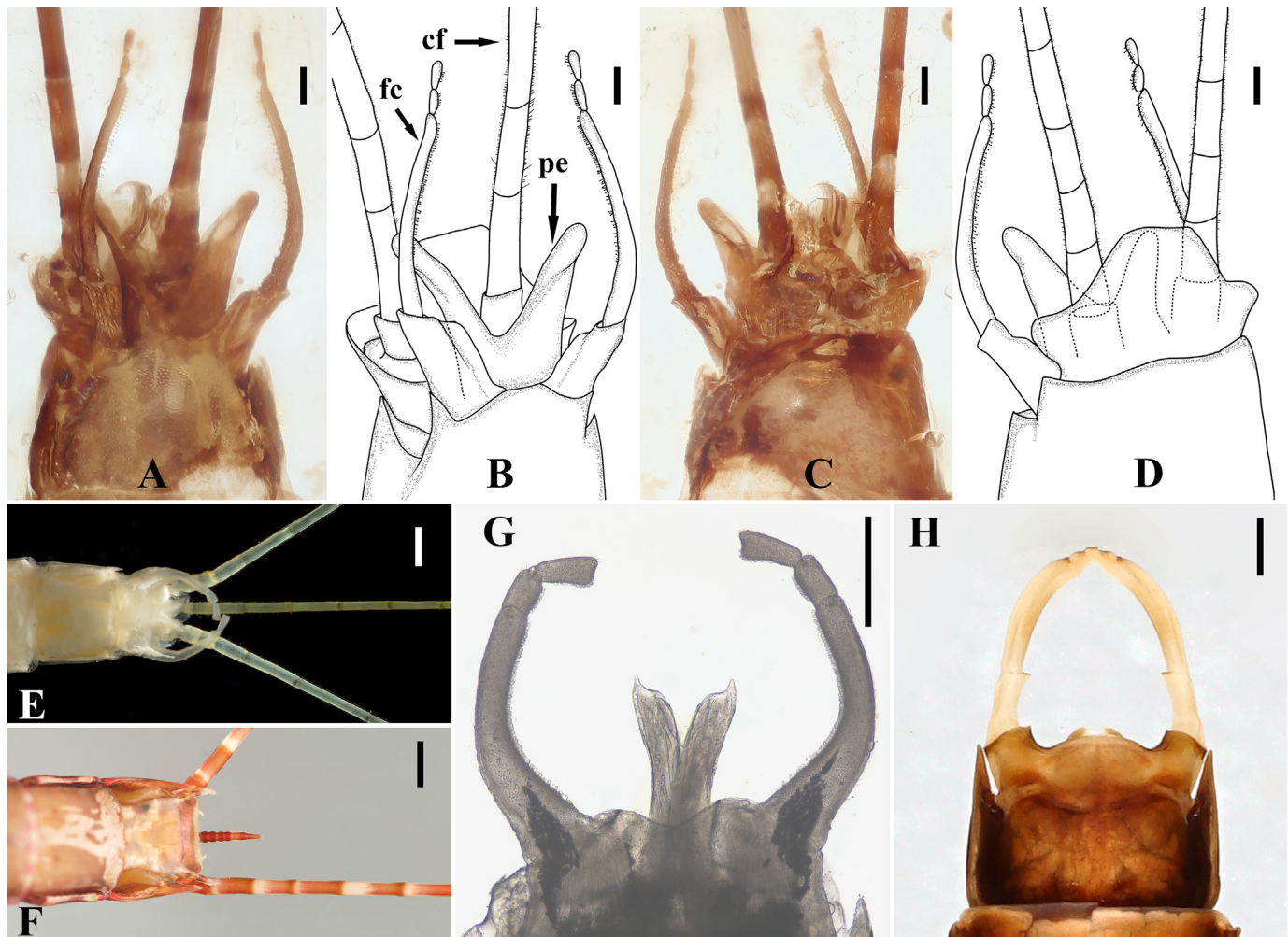


Fig. 5. Genitalia of *Crepotamanthus spinitarsus* gen. et sp. nov., holotype male imago (CZT-EPH-MA2) and extant relatives. A. *C. spinitarsus* gen. et sp. nov., photo of genitalia, ventral view; B. *C. spinitarsus* gen. et sp. nov., drawing of genitalia, ventral view; C. *C. spinitarsus* gen. et sp. nov., photo of genitalia, dorsal view; D. *C. spinitarsus* gen. et sp. nov., drawing of genitalia, dorsal view; E. *Potamanthodes longitibius* (Bae and McCafferty, 1991), photo of terminal abdomen, ventral view; F. *Potamanthellus chinensis* Hsu, 1936, photo of terminal abdomen, ventral view; G. *Potamanthodes longitibius* (Bae and McCafferty, 1991), photo of genitalia, ventral view; H. *Pulchephemera projecta* (Zhou and Zheng, 2001), photo of genitalia, ventral view. Scale bars = 0.1 mm for A–D, 0.5 mm for E–H. Abbreviations: fc, forceps; cf, caudal filament; pe, penis.

entirely different from *Crepotamanthus spinitarsus* sp. nov. (Table 1); the unique spine-shaped tarsi and triangular mid protuberance of the hooked claw (Fig. 3F–H) in *Crepotamanthus spinitarsus* sp. nov. are also absent in *Palaeoanthus*.

Up to now, the two related extant families of Australiphemeridae, i.e., Potamanthidae and Neoephemeridae, each contains five genera (Ma and Zhou, 2021; Li and Zhou, 2022). Differentiation and discussion of these two families are usually based on combined morphological and molecular characters on both imagoes and nymphs that are not available in fossils (Kluge, 2004; Zhou et al., 2015; Ogden et al., 2019). The only distinguishable key character on venation between Potamanthidae and Neoephemeridae is the symmetrically bifurcated A_1 of forewings. McCafferty (1991) established Australiphemeridae for those extinct groups that share similar venation with Potamanthidae and Neoephemeridae but have a weakened MP_2 basal arch, a single A_1 or A_1 with only one attaching veinlet basally. In conclusion, the key character to separate all these three families is restricted to the bifurcation form of A_1 . However, even without considering whether it is stable inside a family and individuals, the definition of symmetrical bifurcation is vague. Moreover, some extant neoephemerid species have a basally attached veinlet to A_1 that completely fits the definition of the

extinct Australiphemeridae, which means that some members of Australiphemeridae may be very close to Neoephemeridae.

Considering the similar venation of the two living families Potamanthidae and Neoephemeridae with the extinct family Australiphemeridae, a comprehensive morphological comparison between the ancient and modern groups might be helpful to analyze the phylogeny and morphological evolution of mayfly families. Given the preservation status of the six extinct genera, we regard *Palaeoanthus orthostylus* Kluge, 1993 and *Crepotamanthus spinitarsus* sp. nov. as the two most informative species inside Australiphemeridae. In *Crepotamanthus spinitarsus* sp. nov., the shape of genitalia, the small and separated compound eyes, and the slender antennae are consistent with some potamanthid members such as *Potamanthodes longitibius* (Bae and McCafferty, 1991) (Figs. 2C, 5E, G), whereas its four-segmented forceps do not exist in potamanthid genera (Bae et al., 1990; Bae and McCafferty, 1991) but are common in neoephemerid genera, such as *Pulchephemera* Ma & Zhou 2021 (Bae and McCafferty, 1998; Ma and Zhou, 2021) (Table 1). In both Potamanthidae and Neoephemeridae, small anteroventral spines of tarsi (Fig. 3I, J) can be found but are not as elongated as in *Crepotamanthus spinitarsus* sp. nov. (Fig. 3F). The mid protuberance of the hooked claw in the new mayfly is another unique structure that

Table 1

Comparison of characteristics between six genera of Australiphemeridae and two extant families, Potamanthidae and Neoephemeridae. Abbreviations: A1f, A₁ of forewings; Cmf, crossveins between marginal intercalaries of forewings; Cah, costal angulation of hindwings; Mih, marginal intercalaries of hindwings; Rde, ratio of distance between compound eyes/diameter of each compound eye; Sf, segmentation of forceps; Dsf, distal segments of forceps.

Family	Genus	A1f	Cmf	Cah	Mih	Rde	Sf	Dsf	References
Australiphemeridae	<i>Australiphemera</i>	Single	Developed	Rounded	Developed	\	\	\	McCafferty (1990)
	<i>Microphemera</i>	Forked asymmetrically	Developed	\	\	\	\	\	McCafferty (1990)
	<i>Nanophemera</i>	Forked nearly symmetrically	Developed	\	\	\	\	\	McCafferty and Santiago-Blay (2008)
	<i>Borephemera</i>	Single	Developed	\	Developed	\	4	Separated	Sinitshenkova (2000)
	<i>Palaeoanthus</i> <i>Crepotamanthus</i> gen. n.	Single Single	Undeveloped Undeveloped	Rounded Sharply acute	Undeveloped Undeveloped	0.05 1.8	4 4	Fused Separated	Kluge (1993)
Potamanthidae	all	Forked symmetrically	Developed	Sharply acute or subacute	Developed	0.1–2.2	3	Separated	Bae and McCafferty (1991), Bae et al. (1990), McCafferty and Bae (1990), Li and Zhou (2022)
Neoephemeridae	all	Forked asymmetrically	Developed	Acute or rounded	Developed	0.04–1.15	3 or 4	Fused or separated	Bae and McCafferty (1998), Ma and Zhou (2021)

differs from the common shape of these two living families. There are only two caudal filaments in the new fossil, but there is always a median filament (Fig. 5E, F) in the 10 extant genera of Potamanthidae and Neoephemeridae (Bae et al., 1990; Bae and McCafferty, 1991; Ma and Zhou, 2021; Li and Zhou, 2022). In *Palaeoanthus orthostylus* Kluge, 1993, the forceps are four-segmented with two fused apical segments, the compound eyes are huge and medially contacted, the antennae are short with conical pedicel, and the hind wings are rounded with blunt costal angulation. Many of these features are consistent with the five extant neoephemerid genera (Figs. 2D, 4C, 5H) (Table 1), which seems to imply that they are closely related genera. Combined with the bifurcation form of A₁ in the other three australiphemerid genera (single in *Australiphemera* and *Borephemera*, significantly asymmetrical bifurcated in *Microphemera*, nearly symmetrical bifurcated in *Nanophemera*) (Table 1), we speculate that Australiphemeridae is not a true monophyletic family, there might be at least two lineages inside the six genera that are related with the ancestral Potamanthidae and Neoephemeridae, respectively. The discovery of more well-preserved fossils of both imagoes and nymphs may prove our hypothesis and inspires us about the early evolution of these three families.

5. Concluding remarks

The present study reports a new genus and species *Crepotamanthus spinitarsus* gen. et sp. nov. of the extinct mayfly family Australiphemeridae, based on a male imago inside a mid-Cretaceous Kachin amber. The new genus can be distinguished from other extinct and extant genera by its forewing venation, the other well-preserved characters on head, legs, and genitalia are also indicated its unique morphology in Australiphemeridae. In addition, we present a comprehensive comparison between the extinct taxa and extant relatives. The discovery of more well-preserved fossils is expected to help us learn more about the relationships between the puzzling taxa.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cretres.2023.105485>.