

RESEARCH PAPER

The oldest known fossil imago of Ameletopsidae (Ephemeroptera) from 99-million-year-old Kachin amber

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Abstract. A new fossil genus and species of the mayfly family Ameletopsidae, *Paprika atsukochibae* gen. & sp. nov., is described from mid-Cretaceous Kachin amber of northern Myanmar. The specimen represents a female imago and constitutes the oldest known imaginal fossil of the family. *Paprika* gen. nov. exhibits a unique combination of the characters in wing venation that distinguish it from both extant and extinct Ameletopsidae. Although the new genus is assigned to Ameletopsidae based on imaginal morphological characters, it cannot be placed within the existing subfamilies due to the absence of male or caudal appendage characters. This discovery represents the oldest imaginal Ameletopsidae fossil discovered so far and provides the first fossil record of the family in Asia. The finding supports a broader, possibly Pangean, distribution and origin of Ameletopsidae during the Mesozoic and contributes to the understanding of the evolutionary history and paleobiogeography of Siphonuroidea. Moreover, the presence of such a lineage in mid-Cretaceous Myanmar suggests greater ecological and geographical diversity within this mayfly assemblages than previously recognized.

Key words. Ephemeroptera, Siphonuroidea, Ameletopsidae, Burmese amber, Cretaceous, mayfly, morphology, taxonomy

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Introduction

Ameletopsidae Edmunds, 1957 is a relict mayfly family currently comprising six extant species in four genera (*Ameletopsis* Phillips, 1930, *Chaquihua* Demoulin, 1955, *Chiloporter* Lestage, 1931, *Mirawara* Harker, 1954), along with one extinct genus (*Promirara* Jell & Duncan, 1986) from the Southern Hemisphere, and two monotypic extinct genera from the Northern Hemisphere (*Balticophlebia* Demoulin, 1968, *Nebesna* Godunko, Martynov, Damzen & Staniczek, 2025), both described from Eocene Baltic amber (GODUNKO & SROKA 2024, GODUNKO et al. 2025). Additionally, GODUNKO & SROKA (2024) and GODUNKO et al. (2025) mentioned an undescribed female adult from Miocene Dominican amber that may belong to Ameletopsidae.

The family comprises two subfamilies, Ameletopsinae and Chiloporterinae (DOMÍNGUEZ et al. 2006). Ameletopsinae includes *Ameletopsis* (New Zealand), *Balticophlebia* (Baltic Eocene), *Chaquihua* (Chile), and *Mirawara* (Australia), while Chiloporterinae is monogeneric and contains *Chiloporter* (Chile and Argentina). *Nebesna* and *Promirara*

remain unplaced within subfamilies (GODUNKO et al. 2025).

The phylogenetic placement and internal relationships of Ameletopsidae remain unresolved. TOMKA & ELPERS (1991) proposed a close relationship with Acanthametropodidae based on shared synapomorphies, a view later challenged by KLUGE et al. (1995). Combined morphological and molecular analyses by OGDEN et al. (2009) revealed the paraphyly of Ameletopsidae, a result later confirmed by ETHINGTON & OGDEN (2011) using molecular data. However, OGDEN et al. (2019) used anchored hybrid enrichment data and recovered Ameletopsidae as monophyletic, placing it as sister to (Rallidentidae + (Siphlaenigmatidae + Oniscigastridae)), although based on limited sampling of only three ameletopsid genera.

The oldest known fossil of Ameletopsidae is *Promirara* described from the Early Cretaceous Koonwarra Fossil Bed (ca. 115–118 Ma) of Australia (JELL & DUNCAN 1986, GODUNKO & SROKA 2024, GODUNKO et al. 2025). However, *Promirara* was based solely on larval material, limiting our understanding of adult morphology and



diversity during the Mesozoic.

Here, we describe a female imago of Ameletopsidae from mid-Cretaceous Kachin amber (ca. 99 Ma) of northern Myanmar. This fossil represents the oldest known imaginal specimen of the family.

Material and methods

The amber specimen was collected from the Noiye Bum locality (26°21'33.41"N, 96°43'11.88"E) in the Hukawng Valley, Kachin State, northern Myanmar, prior to June 2017. The amber-bearing deposit has been dated to the earliest Cenomanian (98.79 ± 0.62 Ma) based on U–Pb zircon dating and corroborating paleontological evidence (SHI et al. 2012, YU et al. 2019).

Preparation followed standard techniques: the amber piece was trimmed with a mini hand saw, ground with emery paper, and polished using diamond paste. The specimen is deposited in the Insect Collection of Jiangsu University of Science and Technology (ICJUST), Jiangsu Province, China (Curator: Z.-T. Chen).

Morphological observations and measurements were performed under an SDPTOP-SZM45 stereomicroscope. Images under incident light were taken with a Canon EOS 5DSR camera and a Canon MP-E 65 mm macro lens. Transmitted light images were captured using an Olympus CX31 compound microscope. Focus stacking was performed with Zerene Stacker 1.04 (Zerene Systems LLC, Richland, U.S.A.). Illustrations were produced in Adobe Illustrator 2020 and plates were prepared in Adobe Photoshop 2021 (Adobe Inc., San Jose, U.S.A.).

Morphological terminology follows KLUGE (2004). Abbreviations used in the text and figures are as follows:

AA	analis anterior;
An	antenna;
BS	basisternum;
C	costa;
Cl	claw;
CuA	cubitus anterior;
CuP	cubitus posterior;
ey	eye;
fe	femur;
FSp	furcasternal protuberance;
iMA	intercalary vein between branches of media anterior;
iMP	intercalary vein between branches of media posterior;
iRS	intercalary vein between branches of radius sector;
MA	media anterior;
MP	media posterior;
RA	radius anterior;
RSa	radial sector anterior;
RSp	radial sector posterior;
sa	subanal plate;
Sc	subcosta;
st7	sternum VII;
ta1–ta5	tarsomere segments I–V;
ti	tibia.

Results

Family Ameletopsidae Edmunds, 1957

Paprika gen. nov.

Type species. *Paprika atsukochibae* sp. nov., by present designation.

Differential diagnosis. *Paprika* gen. nov. can be distinguished from other genera of Ameletopsidae by the following combination of hind wing characters: MA–RSp fork positioned near mid-length; MA forked near apical 1/4; MP forked at mid-length; iMP present and short.

Etymology. The new genus is named after the fictional character Paprika in the Japanese animated science fantasy movie of the same name, who guides people to create their dreams. Feminine gender.

Species included. Monotypic – *Paprika atsukochibae* sp. nov.

Paprika atsukochibae sp. nov.

(Figs 1–6)

Type material. HOLOTYPE: ♀ imago, inventory number CZT-EPH-MA9, MYANMAR: Kachin State, Myitkyina District, Hukawng Valley, 26°21'33.41"N, 96°43'11.88"E (ICJUST).

Differential diagnosis. As in generic diagnosis.

Etymology. The specific epithet refers to the fictional character Atsuko Chiba, who is the alter ego of Paprika in the same animated film.

Description. *Female imago.* Body length ca. 7 mm (from anterior margin of head to posterior margin of subanal plate); general coloration brown (Fig. 1).

Head widened posteriorly (Fig. 2). Compound eyes large, on lateral sides of head, median space between eyes wide. Antennae length ca. 0.7 mm; scape and pedicel nearly cylindrical, length ratio about 1 : 2; flagellum slender, length ca. 0.5 mm, slightly shorter than eyes.

Thorax. Anterior paracoxal suture of mesothorax complete; basisternum longitudinal, constricted medially; furcasternal protuberances contiguous (Fig. 2). Fore leg length ca. 3.4 mm (Figs 3A, B); length ratio of profemur : protibia : protarsus = 1.0 : 0.6 : 1.0; length ratio of protarsal segments from I to V = 1.0 : 0.9 : 0.5 : 0.3 : 0.3; claws paired and dissimilar. Middle leg length ca. 4.7 mm (Figs 3C–E); length ratio of mesofemur : mesotibia : mesotarsus = 1.0 : 0.5 : 0.8; length ratio of mesotarsal segments from I to V = 1.0 : 0.9 : 0.7 : 0.5 : 0.5; claws paired and dissimilar. Hind leg length ca. 4.9 mm (Fig. 3F); length ratio of metafemur : metatibia : metatarsus = 1.0 : 0.8 : 1.1; length ratio of hind-tarsal segments from I to V = 1.0 : 1.0 : 0.6 : 0.4 : 0.4; claws paired and dissimilar.

Wings hyaline, veins brown. Fore wing length ca. 7.7 mm (Fig. 4); costal brace strongly arched; Sc and RA simple; RS forked at basal 1/4 of fore wing; iRS independent; MA forked at middle of its length; iMA independent; MP forked asymmetrically, approaching basally to RS base; MP₁ with distal veinlets posteriorly; iMP present, independent, with distal veinlet posteriorly; MP₂ with several anterior and three posterior distal veinlets; CuA simple; cubital field with five unforked veins running from CuA to basitornal margins; CuP short, with crossvein with AA and relatively distal crossvein with CuA. AA short, without distal veinlets. Hind wing length ca. 2.4 mm (Fig. 5); costal projection poorly protruded, rounded apically, located near wing base; area between Sc and C broader proximally, abruptly narrowing afterwards; RS forked at basal 1/3 of its length; iRS independent; MA forked distally to RS fork;

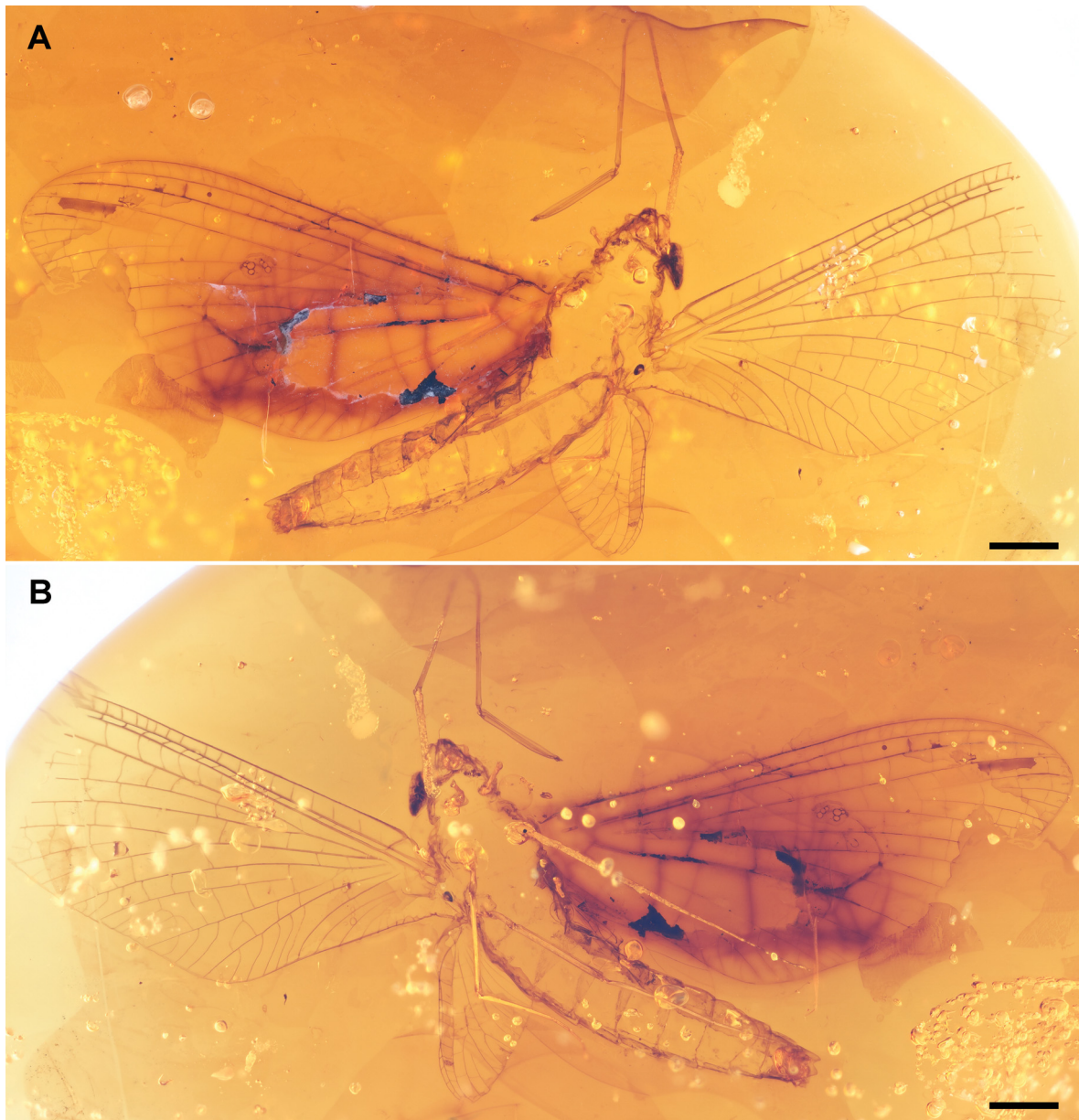


Fig. 1. *Paprika atsukochibae* gen. & sp. nov., holotype, female (CZT-EPH-MA9), habitus. A – dorsal view; B – ventral view. Scale bars: 1 mm.

iMA independent; MP forked at middle of its length; iMP independent; CuA, CuP, and AA simple.

Abdomen. Abdominal segments short, broad (Fig. 6). Sternum VII with subgenital plate rounded apically, extending to half-length of sternum VIII. Subanal plate broad, lateral margins straight, with deep posteromedian emargination. Cerci not preserved, bearing basal remnants of three caudal filaments.

Discussion

The discovery of *Paprika atsukochibae* gen. & sp. nov. provides the oldest definitive record of a female imago of the family Ameletopsidae, predating previously known fossil representatives of this life stage from the Eocene Baltic amber and Miocene Dominican amber. The oldest record of the family was *Promirara*, based on larval material from the Early Cretaceous of Australia (JELL & DUNCAN

1986). However, larval characters observable in fossil material are often inadequate for resolving morphological diversity in mayflies. Thus, imaginal specimens are critical supplements for confirming the taxonomic placements based on larval morphology and understanding the biogeographical and evolutionary history of Ameletopsidae.

Paprika gen. nov. is assignable to the suborder Euplectoptera based on hind wing size, costal brace touching C, shared RS–MA stem in hind wing, and presence of MA fork in the forewing (KLUGE 2004). The genus fits within the infraorder Aneritorna, with the tornus of the forewing located between the apices of CuA and CuP (KLUGE 2004). It clearly belongs to the superfamily Siphonuroidea based on five-segmented tarsi, with the first tarsomere fused to the tibia on middle and hind legs, a narrow cubital field with multiple veins from CuA to the hind margin, and proximally approximated CuA and CuP (KLUGE et al. 1995,

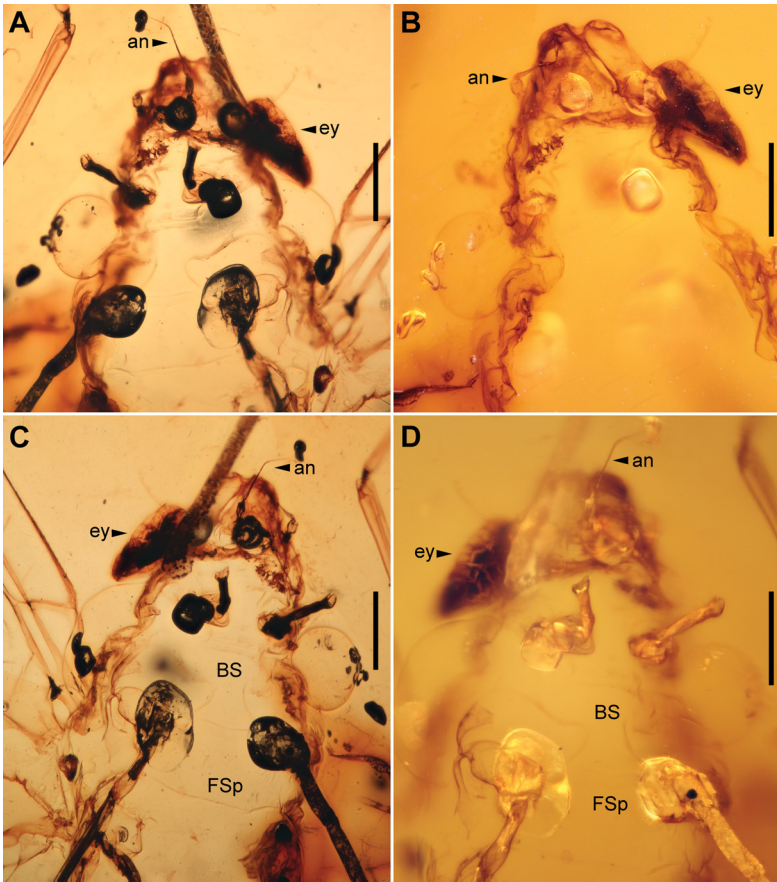


Fig. 2. *Paprika atsukochibae* gen. & sp. nov., holotype, female (CZT-EPH-MA9), head and thorax. A – under transmitted light, dorsal view; B – under reflected light, dorsal view; C – under transmitted light, ventral view; D – under reflected light, ventral view. Abbreviations: an – antenna; BS – basisternum; ey – eye; FSp – furcasternal protuberance. Scale bars: 0.5 mm.

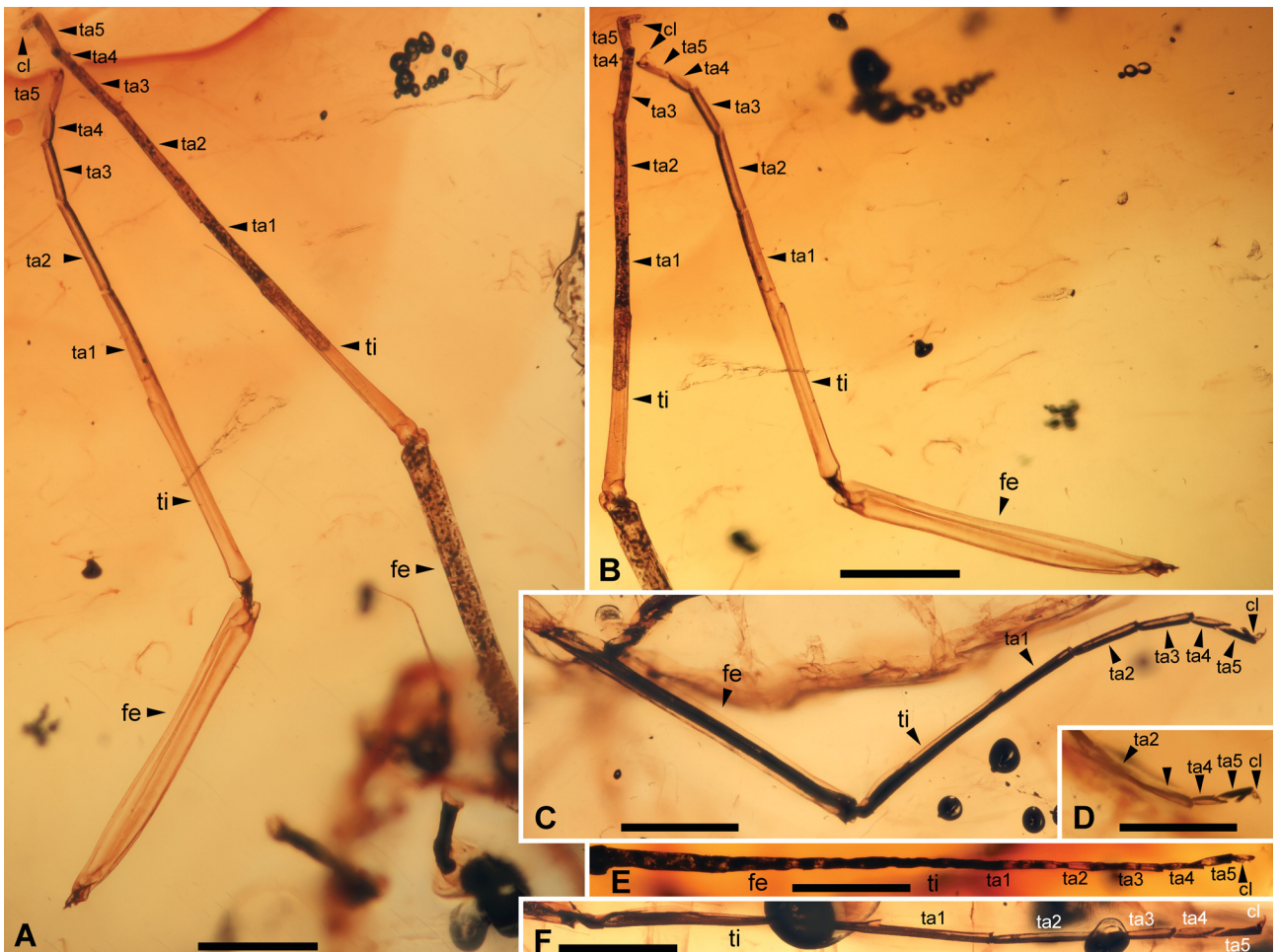


Fig. 3. *Paprika atsukochibae* gen. & sp. nov., holotype, female (CZT-EPH-MA9), legs. A – forelegs, dorsal view; B – forelegs, ventral view; C – right middle leg, ventral view; D – claws of right middle leg, dorsal view; E – left middle leg, ventral view; F – right hind leg, ventral view. Abbreviations: cl – claw; fe – femur; ta1–5 – tarsomeres I–V; ti – tibia. Scale bars: 0.5 mm.

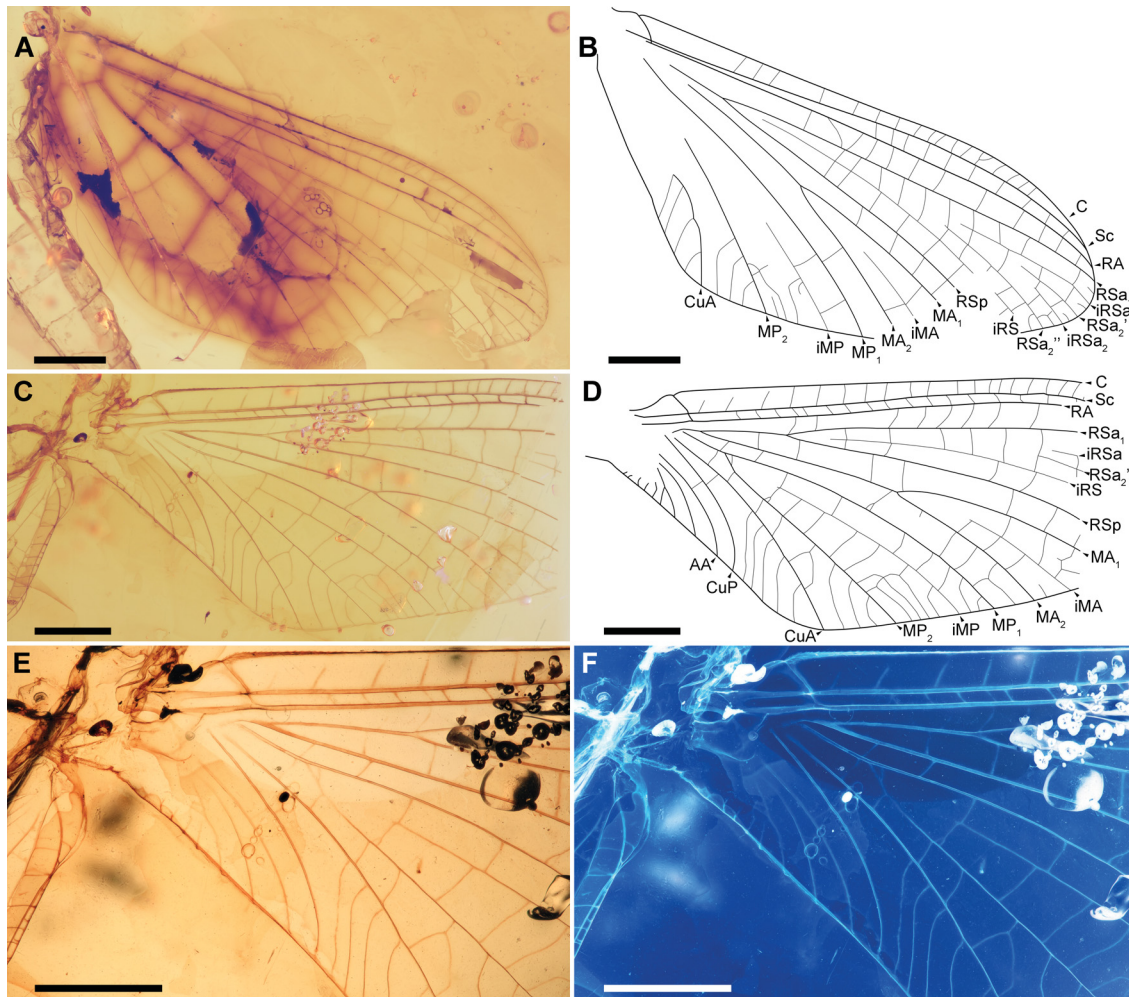


Fig. 4. *Paprika atsukochibae* gen. & sp. nov., holotype, female (CZT-EPH-MA9), forewings. A – photo of left forewing, ventral view; B – drawing of left forewing, ventral view; C – photo of right forewing, dorsal view; D – drawing of right forewing, dorsal view; E – basal area of right forewing, dorsal view; F – basal area of right forewing using reversal processing, dorsal view. Abbreviations: AA – analis anterior; C – costa; CuA – cubitus anterior; CuP – cubitus posterior; iMA – intercalary vein between branches of media anterior; iMP – intercalary vein between branches of media posterior; iRS – intercalary vein between branches of radius sector; MA – media anterior; MP – media posterior; RA – radius anterior; RSa – radial sector anterior; RSp – radial sector posterior; Sc – subcosta. Scale bars: 1 mm.

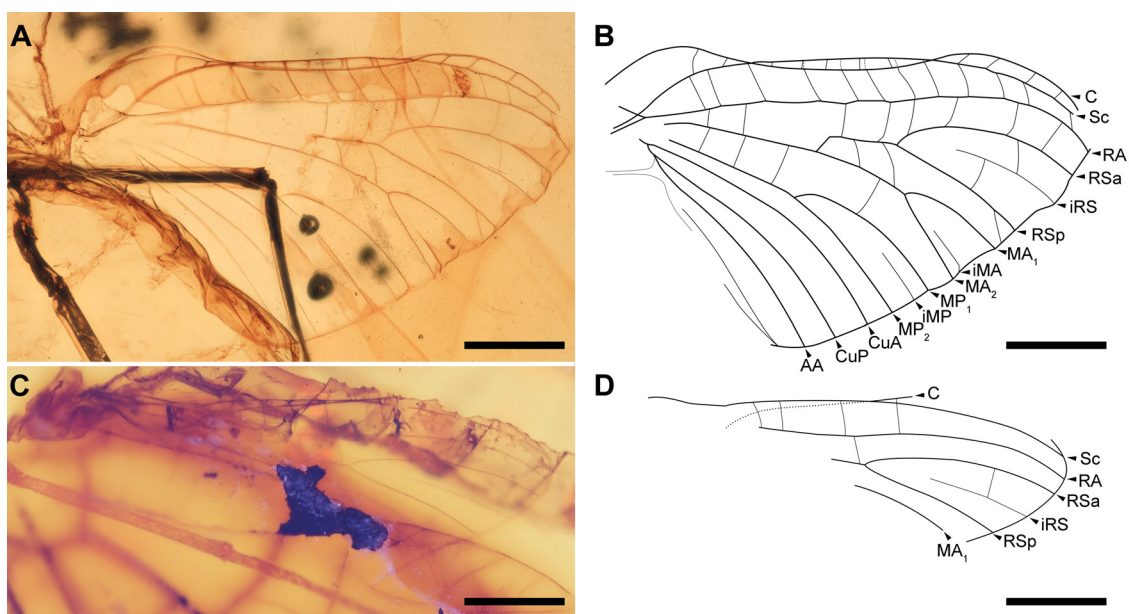


Fig. 5. *Paprika atsukochibae* gen. & sp. nov., holotype, female (CZT-EPH-MA9), hind wings. A – photo of right hind wing, dorsal view; B – drawing of right hind wing, dorsal view; C – photo of left hind wing, ventral view; D – drawing of left hind wing, ventral view. Abbreviations: AA – analis anterior; C – costa; CuA – cubitus anterior; CuP – cubitus posterior; iMA – intercalary vein between branches of media anterior; iMP – intercalary vein between branches of media posterior; iRS – intercalary vein between branches of radius sector; MA – media anterior; MP – media posterior; RA – radius anterior; RSa – radial sector anterior; RSp – radial sector posterior; Sc – subcosta. Scale bars: 0.5 mm.

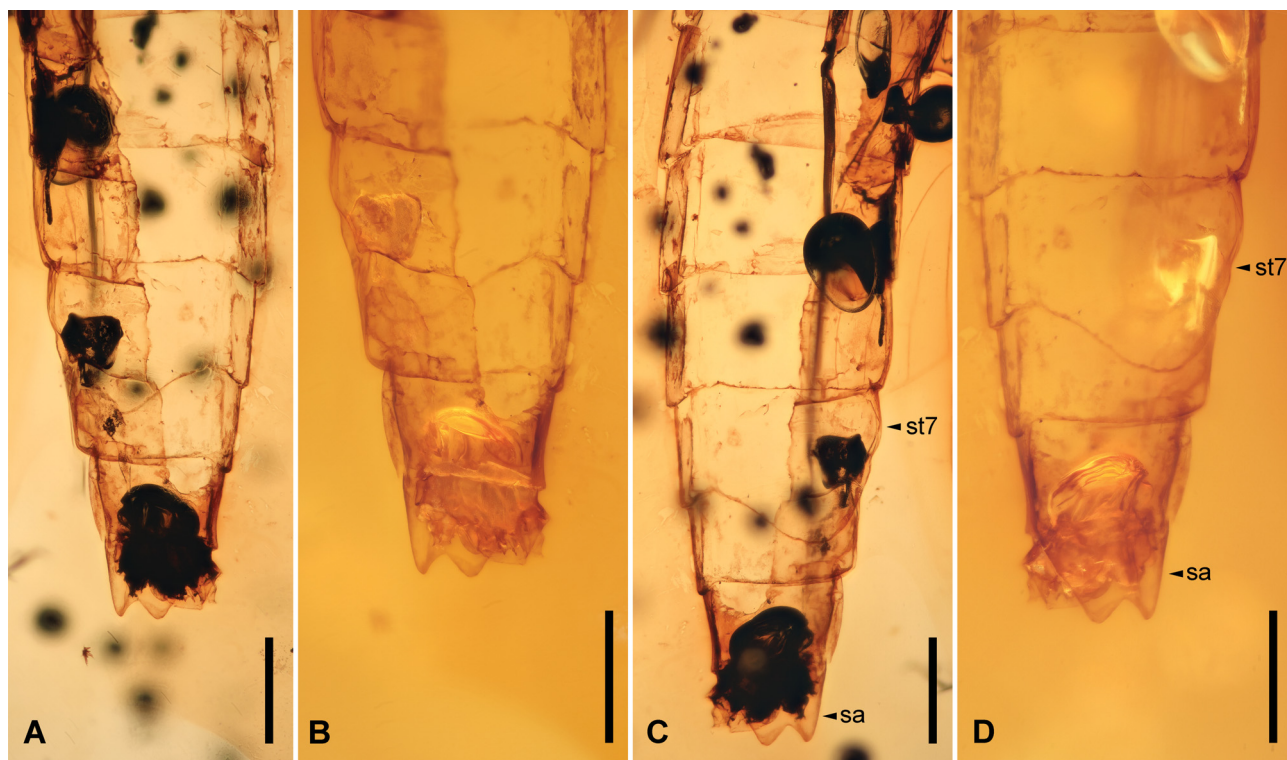


Fig. 6. *Paprika atsukochibae* gen. & sp. nov., holotype, female (CZT-EPH-MA9), abdomen. A – under transmitted light, dorsal view; B – under reflected light, dorsal view; C – under transmitted light, ventral view; D – under reflected light, ventral view. Abbreviations: sa – subanal plate; st7 – sternum VII. Scale bars: 0.5 mm.

GODUNKO et al. 2025). The crossveins between CuP–AA and CuA–CuP in *Paprika* gen. nov. are not numerous, a condition also observed in Ephemerelloidea and in another representative of Siphonuroidea, the family Siphonophemerellidae (KLUGE 2004, CHEN & ZHENG 2023). The small free intercalaries in the forewings of *Paprika* gen. nov. are also typical for Ephemerelloidea. However, the absence of forked cubital veins and the five-segmented tarsi with non-reduced basal tarsomeres preclude attribution to Ephemerelloidea (KLUGE 2004). Within Siphonuroidea, *Paprika* gen. nov. shares key features with Ameletopsidae and Rallidentidae (Table 1), such as dissimilar claws, forewing cubital field structure, and pronounced female genitalia (KLUGE et al. 1995; HITCHINGS & STANICZEK 2003; MERCADO & ELLIOTT 2005, 2006; STANICZEK & HITCHINGS 2014; THRESHER 2016; GODUNKO et al. 2025). It differs from Rallidentidae in the hind wing MP fork, which is not distally placed, and in the complete anterior paracoxal suture (KLUGE et al. 1995, STANICZEK & HITCHINGS 2014, GODUNKO et al. 2025). *Paprika* gen. nov. is closely allied with Ameletopsidae (GODUNKO et al. 2025), yet it shows distinct hind wing features: mid-length MA–RSp fork (vs. basal or absent occurs in remaining Ameletopsidae), apical MA fork (vs. near middle), mid-length MP fork (vs. basal), and short iMP (vs. long/absent). The small body size of *Paprika* gen. nov. is similar to the recently described *Nebesna* from Baltic amber, which differs from the much larger extant representatives of Ameletopsidae. Due to the absence of cerci and lack of known male specimens, further subfamily placement is not possible.

Extant and extinct Ameletopsidae are known from Aus-

tralia (*Mirawara*, *Promirara*), New Zealand (*Ameletopsis*), South America (*Chaquihua*, *Chiloporter*), and Europe (*Balticophlebia*, *Nebesna*) (GODUNKO & SROKA 2024, GODUNKO et al. 2025). *Paprika* gen. nov. represents the first Asian fossil and the oldest known imago of the family, dramatically expanding its spatial range. This discovery contributes further evidence supporting the hypothesis of a Pangean distribution for Ameletopsidae and other related studies on the amphinotic distribution patterns of siphonuroid mayflies (GODUNKO et al. 2025). The addition of *Paprika* gen. nov. demonstrates that Ameletopsidae had a much broader geographic distribution, including Asia, during the Mesozoic. This suggests that the family's diversification may have preceded or occurred alongside the breakup of Gondwana, reinforcing the idea of a more expansive, Pangean-like range for Ameletopsidae prior to the fragmentation of the supercontinent. The morphological continuity and the fossil's age supports the hypothesis that Ameletopsidae has been a distinct and stable family since at least the mid-Cretaceous, further supporting the argument for an ancient and widespread biogeographical history. Two alternative scenarios are possible for *Paprika* gen. nov. that do not contradict the Pangean origin of Ameletopsidae. The first scenario posits that *Paprika* gen. nov. arrived in Asia together with the Burmese Terrane as part of the Gondwanan fragments during continental breakup. The second scenario considers the fossil fauna of Burmese amber to be a distinctive mix of Laurasian and Gondwanan taxa. Accordingly, *Paprika* gen. nov. could represent one of the most ancient northern, Laurasian lineages of Ameletopsidae, having colonized the

Table 1. Comparison of 12 taxa within Siphonuroidea based on characters in KLUGE et al. (1995).

Taxon	Claws	Forewing cubital field	Female subgenital plate	Female subanal plate
<i>Paprika</i> gen. nov.	dissimilar	type S	well developed	well developed
Acanthametropodidae	dissimilar	type S	small	small
Ameletidae	dissimilar	type M and S	small	well developed
Ameletopsidae	dissimilar	type M and S	well developed	well developed
Ametropodidae	dissimilar	type A	small	absent
Dipteromimidae	similar	type S	well developed	projected medially
Metretopodidae	dissimilar	type M	well developed	moderately developed
Nesameletidae	similar	type M and S	well developed	well developed
Oniscigastridae	dissimilar	type M and S	absent	absent
Rallidentidae	dissimilar	type S	well developed	moderately developed
Siphonophemerellidae	similar	type S	?	?
Siphonuridae	similar	type S	small	moderately developed

Burmese Terrane before its collision with Asia, when the terrane existed as an archipelago near the Asian continental margin. Different studies provide varying estimates for the distance between the Burmese Terrane and Asia around 99 million years ago, ranging from several hundred km up to over 2000 km (MITCHELL 1981, MORLEY et al. 2021). In the shorter-distance scenario, such a gap could have been easily crossed by adult mayflies at either developmental stage, supporting the idea that *Paprika* gen. nov. belongs to a Laurasian lineage. In contrast, the longer-distance model suggests a 'younger' lineage that migrated southward, for example during the Jurassic, and later returned northward to Asia with the Burmese Terrane.

This discovery also raises important questions about the role of climatic and environmental factors in shaping the distribution of Ameletopsidae. The family's presence across widely separated regions such as Australia, New Zealand, South America, and now Asia suggests that Ameletopsidae may have been more adaptable to a variety of ecological conditions than previously assumed.

In sum, the new fossil mayfly provides both morphological and biogeographic insights that enhance our understanding of early ameletopsid evolution. Future discoveries, especially of males or larvae associated with the same taxon, will be vital to refining the phylogenetic position of *Paprika* gen. nov. and elucidating the early diversification patterns of Ameletopsidae.

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