First fossil tanaocerid orthopteran insect from the mid-Cretaceous Kachin amber and its palaeogeographic significance

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Desert long-horned grasshoppers (Tanaoceridae) represent a small extant caeliferan group restricted to arid regions of Western North America, particularly the Sonoran Desert. The discovery of the first fossil Tanaoceridae in the mid-Cretaceous Kachin amber from Myanmar provides new insights into the evolutionary history of this relict group. The new fossil Tanaoceridae inhabited warm and humid forest environments, contrasting sharply with the desert habitats of the extant representatives. This suggests an important ecological shift or restriction over time, likely driven by climatic and environmental changes. The pattern of distribution is discussed, indicating that the Sonoran Desert may represent a refugium for Tanaoceridae, a lineage that was once more ecologically diverse and palaeogeographically widespread.

Key words: Insecta, Caelifera, Acridomorpha, Kachin amber, paleoenvironment, calibration point, mid-Cretaceous, Myanmar.

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Introduction

Rehn (1948a) established the eumastacid subfamily Tanaocerinae for the genus *Mohavacris* Rehn, 1948b (type species *Mohavacris timberlakei* Rehn, 1948b) and the closely related genus and species *Tanaocerus koebelei* Bruner, 1906. Dirsh (1955) raised the subfamily to family rank and contested the placement of Tanaoceridae with the family Eumastacidae because of the peculiar stridulatory apparatus proper to the male *Tanaocerus*, plus significant differences in head morphology and appendage structure from the eumastacid typical morphology (Dirsh 1955, 1975; Grant and Rentz 1967). Tinkham (1955) also proposed to erect the Tanaocerinae to

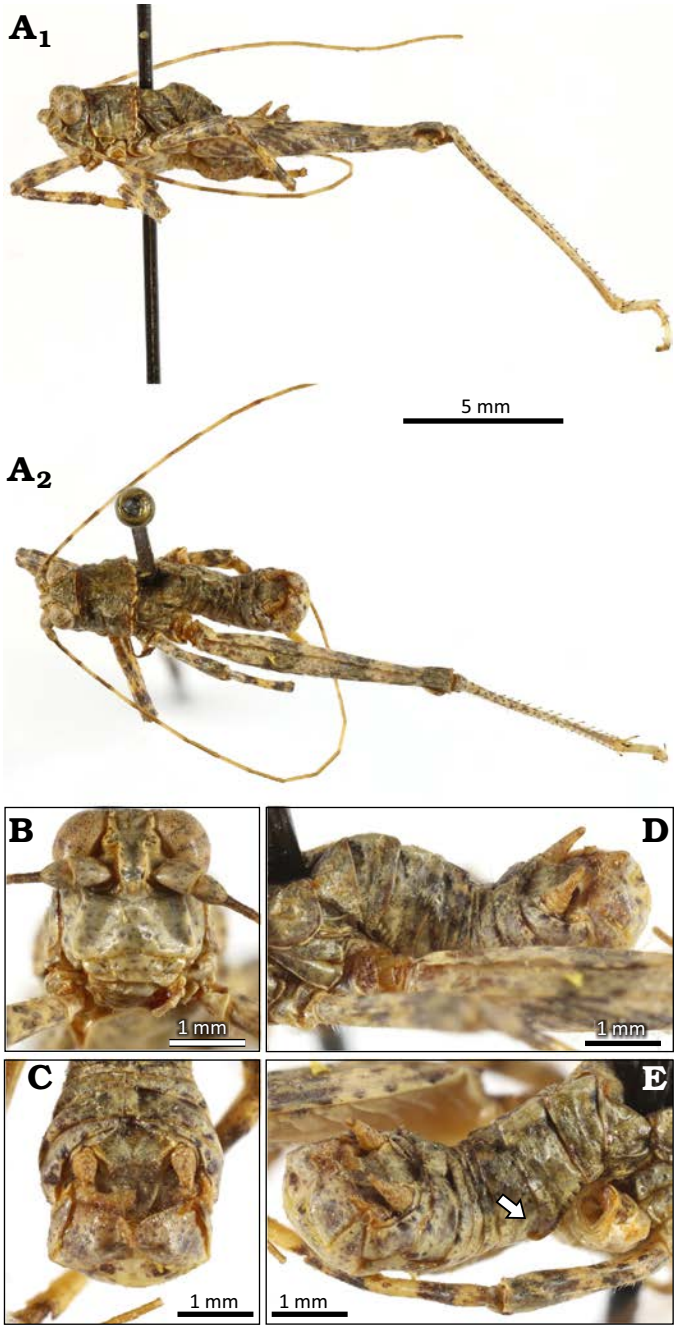


Fig. 1. Tanaocerid orthopteran *Tanaocerus rugosus* Hebard, 1931, MNHN E01226, Recent, Baja California. **A**. Body, lateral (A_1) and dorsal (A_2) views. **B**. Head in anterior view. **C**. Genitalia in posterior view. **D**. Abdomen and genitalia, lateral view. **E**. Abdomen and genitalia, dorso-lateral (arrow stridulatory file). Photographs Christophe Hervé.

family rank and created the new subfamily Mohavacrinae for *Mohavacris* on the basis of morphological revisions of three additional female specimens. Rehn and Grant (1958) confirmed the removal of *Tanaocerus* and *Mohavacris* from the Eumastacidae. Flook et al. (1999, 2000) proposed to erect a separate superfamily Tanaoceroidea within the Acridomorpha, followed by Eades (2000). This hypothesis has been confirmed by molecular phylogenies and is still in use today (Hemp et al. 2025).

Despite their limited diversity, comprising only five described species across two genera, *Mohavacris* and *Tanaocerus*, the Tanaoceridae exhibit a combination of highly distinctive characters: (i) sexual dimorphism in antennal length, with male antennae slightly exceeding body length (Fig. 1A) and female antennae slightly shorter than the body; (ii) a head structure characterized by a deeply concave lateral profile and a flattened facial plane nearly aligned with compound eye area (Fig. 1B) ; (iii) complete wing reduction (apterism, but present in many Caelifera); (iv) external apical spines on lateral margin of hind tibiae; and (v) a stridulatory file made of longitudinal parallel ridges on third abdominal tergite corresponding to a short, sharp ridge (plectrum) near the lower basal margin on the internal side of the hind femur (Fig. $1D_2$) (Dirsh 1955, 1961).

Rehn and Grant (1958) demonstrated that Tanaoceridae are characterized by a male genital complex in which a predominantly membranous ectophallus—featuring moderately sclerotized dorsal regions with distinctly separated large fleshy ventral folds and a cingulum with laterally extending branches—and a disk-shaped epiphallus that is only partially sclerotized on its lateral and ventral surfaces, lacking both lophi and ancorae, yet possessing two hook-like teeth on each lateral plate, thus providing robust morphological evidence to distinguish Tanaoceridae from other Acridoidea families (Hemp et al. 2025).

Tanaoceridae is regarded as an ancient lineage within Acridomorpha, characterized by their diagnostic morphological features and simplified male genital structures (Eades 2000). According to updated studies of comprehensive molecular and morphological analyses (Song et al. 2015; Song 2018), this perspective is further supported by Hemp et al. (2025): Tanaoceroidea is recognized as one of the earliest diverging clades within Acridomorpha, separating from the other Acridomorpha during the Triassic. But up-to-now, no definitive fossil records of this family have been reported.

Here we describe the first fossil representative of this group from the mid-Cretaceous Kachin amber, offering potential insights into its paleogeography and the possibility to perform Total-Evidence dating of this early divergence within Caelifera history.

Institutional abbreviations.—BXAM, Beijing Xiachong Amber Museum, China; MNHN, Muséum national d'Histoire naturelle, Paris, France.

Nomenclatural acts.—This published work and the nomenclatural acts it contains have been registered in ZooBank: urn:lsid:zoobank.org:pub:2702D4E8-53DF-4E2F-A20C-0E3DAFCDF765.

Material and methods

The study is based on one specimen preserved in yellow and transparent amber, collected from mid-Cretaceous Kachin

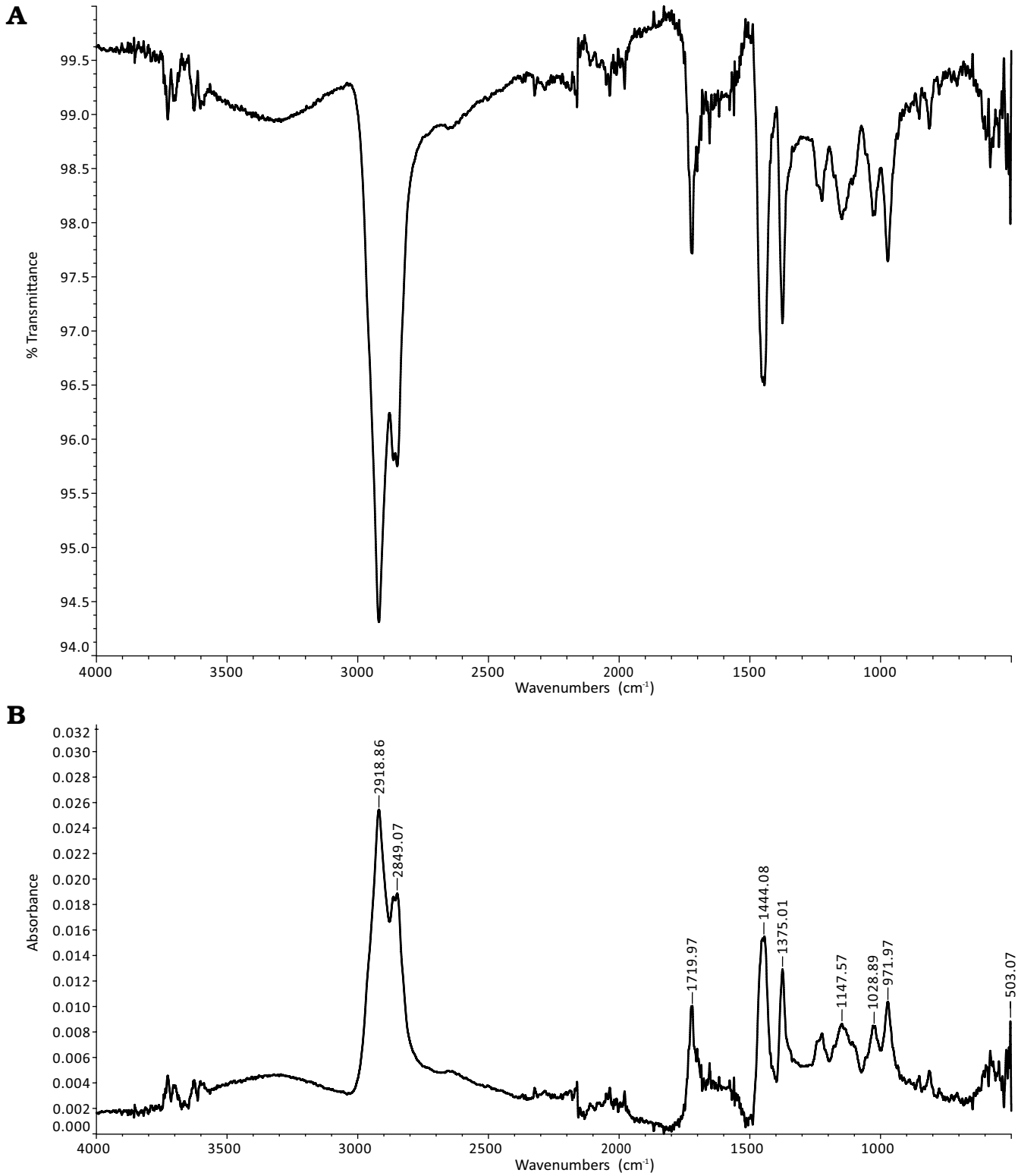


Fig. 2. Analysis of amber matrix of holotype BXAM BA-ORT-201, *Mesotanaocerus yiweizhangae* gen. et sp. nov., Hukawng Valley, Kachin State of northern Myanmar, upper Albian/lower Cenomanian, mid-Cretaceous. **A**. FT-IR spectrum. **B**. ATR corrected FT-IR spectrum with baseline corrected.

amber, from the Hukawng Valley in Kachin State of northern Myanmar (Cruickshank and Ko 2003). According to U-Pb dating of volcanic zircons in the amber-bearing layers, the mid-Cretaceous Kachin amber is estimated to be around 98.79 ± 0.62 million years old (Shi et al. 2012). Additionally, the discovery of an ammonite inclusion further supports that the amber dates back to a period spanning the late Albian to early Cenomanian (Yu et al. 2019).

The Burmese amber insect specimen involved in this study was collected from mid-Cretaceous Kachin amber

(Hukawng Valley, Kachin State of northern Myanmar). This permanent collection item was acquired by the Beijing Xiachong Amber Museum (BXAM) prior to 2016. The specimen is deposited in the Xiachong Amber Museum (BXAM), Beijing, China. Initial observations were conducted using a Zeiss Stemi 508 Microscope; photomicrographs were taken with a Zeiss Stereo Discovery V16 microscope system. To mitigate distortion and minimize unexpected reflections when capturing images of the amber irregular surfaces, the samples were immersed in cedarwood oil. Microphotographs were then processed in depth map mode using Helicon 6 software (https://www.heliconsoft.com/heliconsoft-products/helicon-focus/), and the resulting images were further annotated and measured with CorelDRAW 2021.

Micro-computed tomography (micro-CT) scans were conducted at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS) using a 3D X-ray microscope (3D-XRM), Zeiss Xradia 620 Versa (see the Supplemental Material for detailed specifications). The scanning parameters were set as follows: beam strength of 60 kV/6.5 W, exposure time of 3 s per rotation, voxel size of 2.5134 μm, 1401 projection images acquired per segment, and 1015 slices generated after 3D reconstruction. Radiographs obtained from each scan were saved as .TIFF stacks, and subsequent volume rendering and 3D reconstruction were performed using the open-source software Drishti 3.2 (https://github.com/nci/drishti).

The Fourier transform infrared (FT-IR) spectrum of this amber specimen (Fig. 2) was acquired at the Institute of Soil Science, Chinese Academy of Sciences, Nanjing, China, using a Nicolet iS50 spectrometer equipped with an attenuated total reflectance (ATR) accessory (diamond crystal). Infrared spectra were recorded at a resolution of 4 cm^{-1}, with baseline correction and advanced ATR correction applied.

Morphological terminology for the body used herein generally follows Dirsh (1965a) and Woller and Song (2017) for the male terminalia.

Systematic palaeontology

Order Orthoptera Olivier, 1789

Suborder Caelifera Ander, 1936

Nanorder Acridomorpha MacLeay, 1821

Superfamily Tanaoceroidea Rehn, 1948a

Family Tanaoceridae Rehn, 1948a

Subfamily Tanaocerinae Rehn, 1948a

Genus *Mesotanaocerus* nov.

ZooBank LSID: urn:lsid:zoobank.org:act:9B2CF9E4-F80D-4231-8987-D3F069100E89.

Etymology: Combination of Mesozoic and the genus name *Tanaocerus*. Gender masculine.

Type species: *Mesotanaocerus yiweizhangae* sp. nov., monotypic; see below.

Diagnosis.—As for the monotypic type species.

Stratigraphic and geographic range.—Type locality and horizon only.

Mesotanaocerus yiweizhangae sp. nov.

Figs. 3–5.

ZooBank LSID: urn:lsid:zoobank.org:act:4E9CDF2A-39A7-46D8-B178-24395AD69DF9.

Etymology: Dedicated to Ms Yiwei Zhang, a friend of the collector De Zhuo, who kindly provided the specimen for the present study. Gender masculine.

Type material: Holotype BXAM BA-ORT-201, complete adult male with head preserved with antennae; pro-, meso- and metathoracic legs well preserved; no wing, abdomen preserved with genital appendages, some gas bubbles around ventral part of body render the observation of the mouthparts difficult.

Type locality: Hukawng Valley in Kachin State of northern Myanmar.

Type horizon: Upper Albian/lower Cenomanian, mid-Cretaceous.

Diagnosis.—Body slender (vs. more robust in *Tanaocerus*); 19 antennal flagellomeres, all filiform; the last eight flagellomeres shorter than those more basal, and progressively decreasing in length, vs last eight flagellomeres shorter than those more basal and progressively decreasing in length in *Mohavacris*, and basal and distal ones being shorter than the others in *Tanaocerus*; a low dorsal crest on pronotum vs no dorsal crest in *Tanaocerus*; male subgenital plate in three parts, one median very long triangular and acute and two lateral ones rounded.

Measurements (in mm).—Body 6.22 long (from anterior margin of head to tip of abdomen). Head 1.47 long, 1.70 wide, 0.8 high. Thorax 1.35 long, 0.98 wide. Antenna 6.34 long. Eyes 0.85 long, 0.42 wide. Abdomen 3.45 long, 0.50 wide (near base). Fore leg well-preserved: femur 1.34, tibia 1.45, basitarsus 0.35, second tarsomere 0.08, third tarsomere 0.56; middle legs preserved: femur 1.90, tibia 1.46, basitarsus 0.22, second tarsomere 0.05, third tarsomere 0.51. Hind legs well-preserved: femur 4.20 long, 0.56 wide; tibia 4.06 long, 0.15 wide, basitarsus 0.63, second tarsomere 0.17, third tarsomere 0.85.

Description.—*Head* (Figs. 3, 4A): Well preserved, in lateral profile, deep in breadth so that at least one-third breadth of head projects forward of anterior margin of eye, in facial profile, very broad, almost as broad as deep, with surface strongly convex; gena very long with a crest along its distal margin and a crest between the antennal pit and the anterior angle of subgena, frons and clypeus very long, eyes large and prominent, elongate and oval, located on both sides of top of head, interocular space narrower than eye width; fastigium concave prolonged on frons and on the face by two strong frontal carenules delimiting a deep furrow; antennae located in front of forehead, slightly below mid part of eye, scape twice as long as pedicel, both much shorter than flagellomeres, 19 elongate and thin flagellomeres, the eight most apical shorter than others; flagellomeres alternatively of dark and light colour, three first shorter flagellomeres making a distinctive light ring; maxillary palpi with five

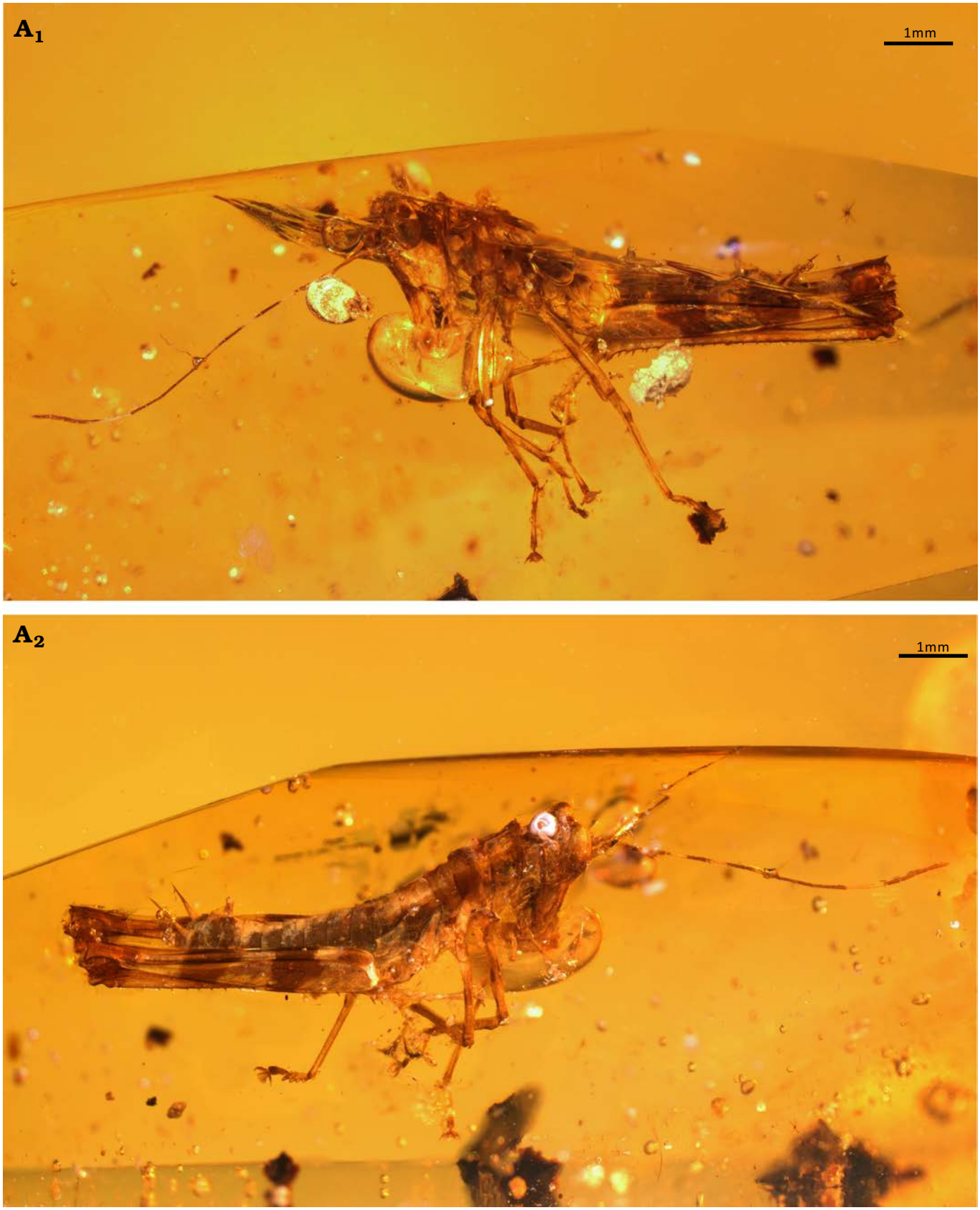


Fig. 3. Tanaocerid orthopteran *Mesotanaocerus yiweizhangae* gen. et sp. nov., holotype BXAM BA-ORT-201, Hukawng Valley, Kachin State of northern Myanmar, upper Albian/lower Cenomanian, mid-Cretaceous. Habitus, left (A_1) and right (A_2) lateral view.

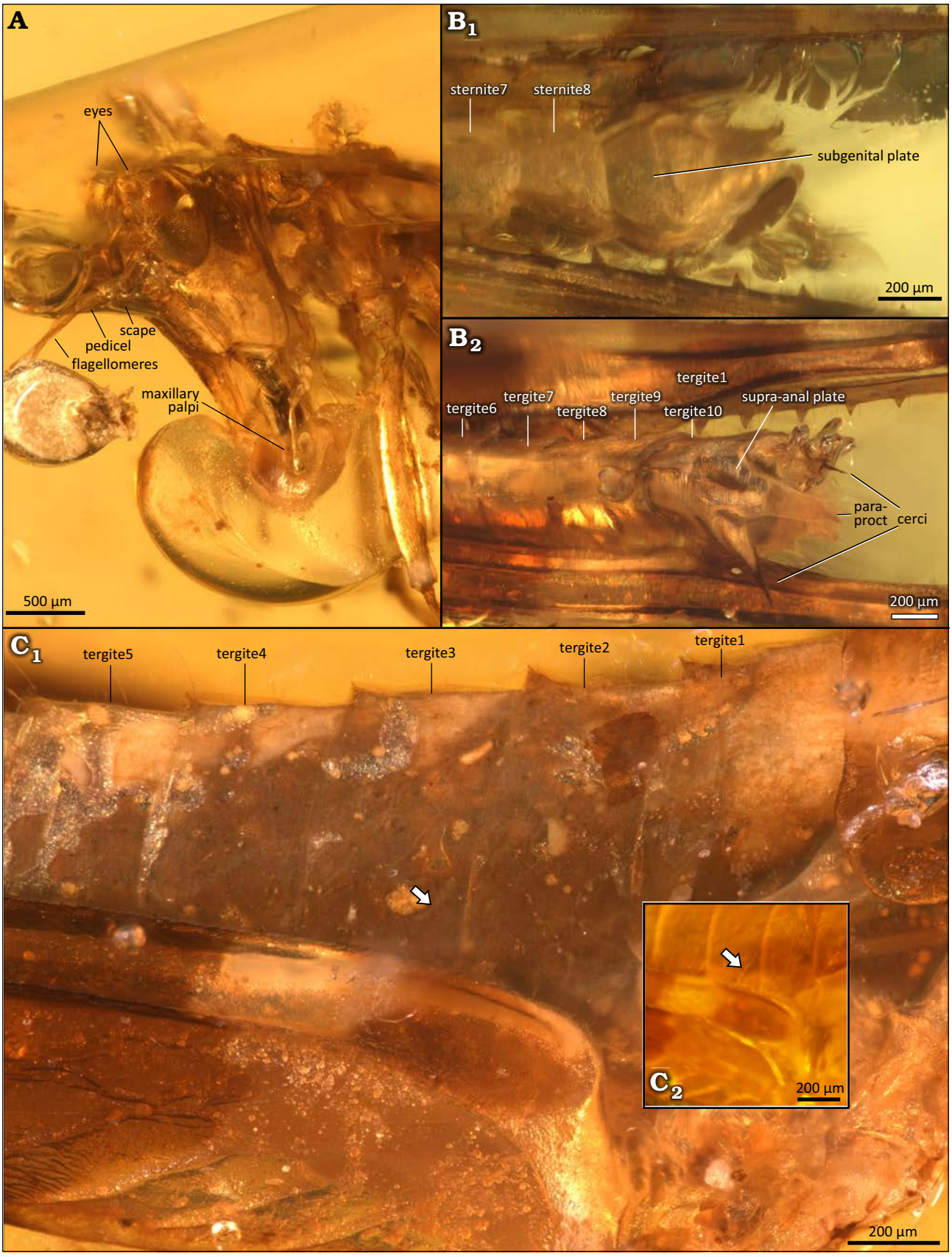


Fig. 4. Tanaocerid orthopteran *Mesotanaocerus yiweizhangae* gen. et sp. nov., holotype BXAM BA-ORT-201, Hukawng Valley, Kachin State of northern Myanmar, upper Albian/lower Cenomanian, mid-Cretaceous. **A**. Head in lateral view. **B**. Genitalia in ventral (B_1) and dorsal (B_2) views **C**. Abdomen in lateral view (C_1, enhanced in C_2) showing stridulatory apparatus with longitudinal ridges on third abdominal tergite (arrows).

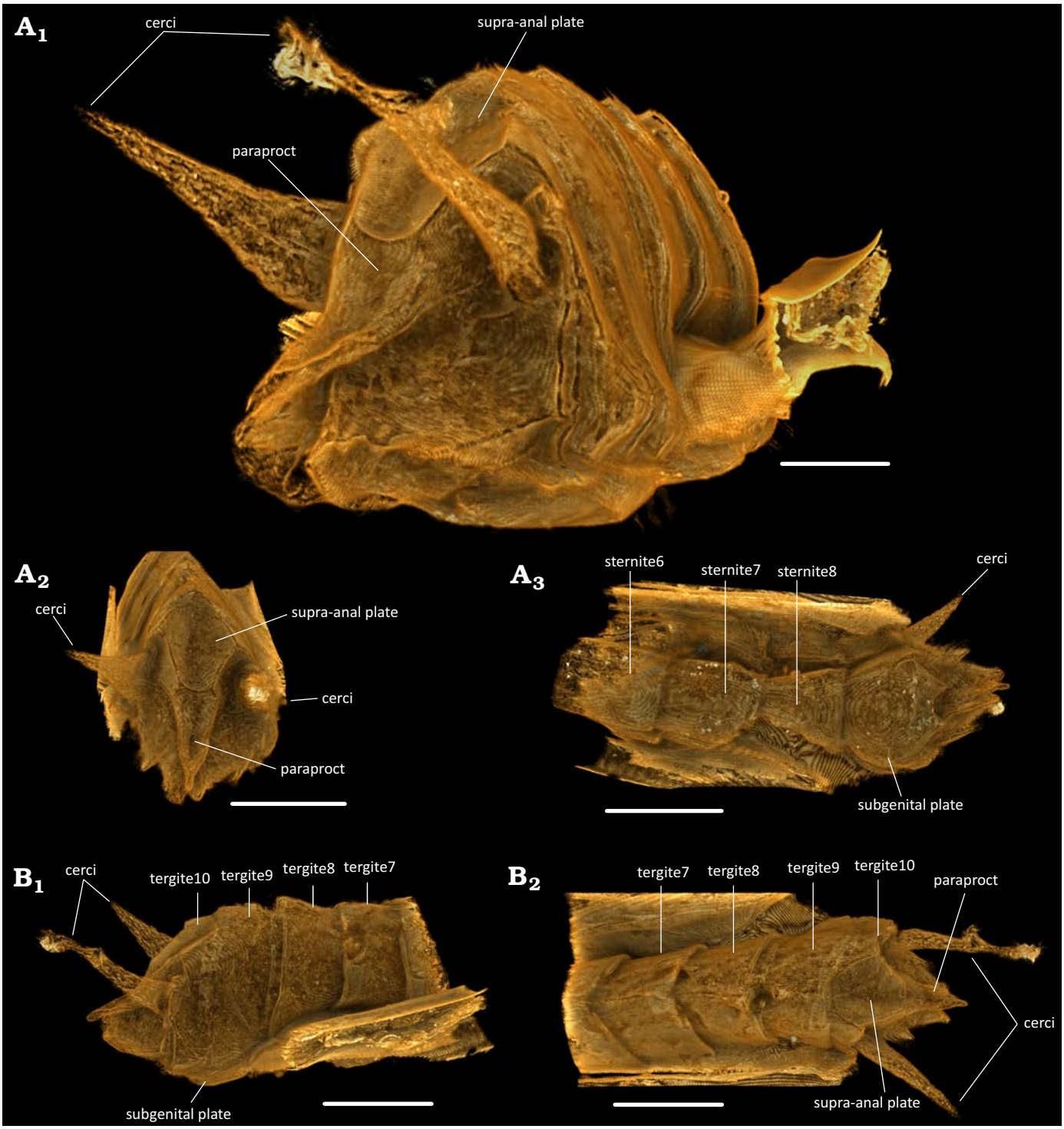


Fig. 5. Tanaocerid orthopteran *Mesotanaocerus yiweizhangae* gen. et sp. nov., holotype BXAM BA-ORT-201, Hukawng Valley, Kachin State of northern Myanmar, upper Albian/lower Cenomanian, mid-Cretaceous. 3D micro-CT scan reconstructions. **A**. Terminalia, general (A_1), detailed (A_2), and ventral (A_3) views. **B**. Genitalia, right lateral (B_1) and dorsal (B_2) views. Scale bars 500 μm.

rather short palpomeres, mandibles apparently strong but obscured by air bubbles.

Thorax (Figs. 2, 3A_1): Pronotum longer than wide, saddle-shaped, with a dorsal longitudinal median crest; no prosternal crest; pronotum with a median transverse furrow at midlength and another near apex; longitudinal median crest of pronotum prolonged on mesonotum, metanotum, and all abdominal tergites except supra-anal plate; metanotum slightly longer than mesonotum. Wings absent.

Fore legs (Fig. 3): Well preserved, coxa as long as wide, columnar, longer than trochanter, slender, cylindrical; femur slightly longer than tibia, slender, covered with fine downy

pilosity; tibia relatively short, with two rows of fine spines developed dorsally; three tarsomeres, tarsomeres 1 and 2 very short, the second the shortest, the third the longest, longer than tarsomeres 1+2 taken together, three euplantulae on tarsomere 1 and one on tarsomere 2; two claws, a large pulvillus.

Mid leg (Fig. 3): Similar to fore leg except for measurements.

Hind leg (Fig. 3): Hind leg with elongate coxa, trochanter shorter than coxa, femur strong, fusiform, with four darkened transverse bands and strong longitudinal crests, lower distal lobe with a short spine, tibia relatively slender, nearly as long as femur, with two rows of small spines on dorsal margins and two apical spines on outer distal margin (inner margin not observable); three tarsomeres, first one longer than second but shorter than third; three euplantulae on tarsomere 1 and one on tarsomere 2.

Abdomen (Figs. 3, $4C_1$): Well preserved, more slender than thorax, slightly raised distally; lateral surface of tergum III with an obliquely oriented row of small, acute spines (absent on adjacent tergites) (Fig. 4D enlargment, arrow).

Male terminalia (Figs. 4B, 5): Long and acute one-segmented cerci, setose; subgenital plate divided into three parts, one median short triangular and acute and two lateral also acute; no visible tympanum; supra-anal plate divided into two distinct parts, with a plicate (folded) region at mid-length. Proximal portion of supra-anal plate elliptical and deeply concave; distal extension triangular and extending posteriorly. Paraprocts short and approximately rectangular, located between supra-anal plate and cerci, with one paraproct positioned on each side of supra-anal plate.

Stratigraphic and geographic range.—Type horizon and locality only.

Discussion

Mesotanaocerus yiweizhangae gen. et sp. nov. is assigned to the family Tanaoceridae primarily based on a suite of diagnostically significant morphological characters: antennae exceeding the body length (an infrequent character in the extant Caelifera, but some Eumastacidae Burr, 1899, of the subfamily Gomphomastacinae Burr, 1899, also have elongate filiform antennae, see below); head displaying a deeply concave and narrow lateral profile, with the dorsal portion being markedly elevated above the pronotal region, thus forming a distinctive head contour. In addition, the face is flat and nearly at level with the region occupied by the large compound eyes; apical spines present on the lateral margin of the hind tibiae, a stridulatory apparatus with longitudinal parallel ridges on third abdominal tergite. The stridulatory ridge on the sides of the third abdominal tergite is shared by the Tanaoceridae, Pneumoridae, and Xyronotidae (Dirsh 1961). The Pneumoridae have shorter antennae and strongly differ from the new fossil in the structure of the thorax among other characters. The Xyronotidae have much shorter antennae than the Tanaoceridae and the new fossil, and the antennal base placed above the level of the compound eye, vs below eye in Tanaoceridae and Pneumoridae (Dirsh 1961; Grant and Rentz 1967). The male subgenital plate in three parts, one median short triangular and two lateral ones acute, is similar to those of the extant Tanaoceridae and constitute a further synapomorphy after Dirsh (1955, 1961), but these structures are much more acute than in the extant Tanaoceridae (Rehn 1948b).

Among Eumastacidae, at least the Gomphomastacinae genus *Gomphomastax* Brunner von Wattenwyl, 1898, has elongate antennae that can be nearly as long as the body, as in the new fossil (Descamps 1973) but the Gomphomastacinae have a subapical antennal organ that is absent in the new fossil (Yamasaki 1983: fig. 3). Also the Eumastacidae have no stridulatory mechanism (Dirsh 1961). Tinkham (1955) moreover listed the many characters that separate Eumastacidae and Tanaoceridae. In particular the shape in profile of the head of the fossil is similar to that of the extant Tanaoceridae.

Based on the overall morphological characteristics (Tinkham 1955), the slender body of the new species shares similarities with the genus *Mohavacris*, as opposed to the broader and more robust body form typical of the genus *Tanaocerus*. All three genera show different lengths and thicknesses of the flagellomeres: in *Mohavacris* the proximal seven flagellomeres are robust, followed by last eight thinner distal ones. *Mesotanaocerus* gen. nov. has 19 thin filamentous flagellomeres, with the last eight flagellomeres shorter than the more basal ones and progressively decreasing in length. *Tanaocerus* has 28–29 flagellomeres and only the median ones are elongate, the basal one and distal one being shorter than the others, even if all have an overall rather filamentous shape (Rehn 1948b; Dirsh 1961). As *Mohavacris*, *Mesotanaocerus* gen. nov. shows a dorsal crest on pronotum and abdomen, but it is very low (higher lobes in *Mohavacris*), and it runs along the whole thorax and abdomen, except the supra-anal plate (present only on thorax and first three abdominal tergites in *Mohavacris*). No dorsal crest exists in *Tanaocerus*. Therefore, considering all these observations, the specimen is assigned to a new genus. No affiliation to a subfamily can however be proposed by now, as the common characters observed between the three tanaocerid genera could be familial plesiomorphies, synapomorphies or parallel character changes. Only a total-evidence phylogeny of basal Acridomorpha could resolve this question, especially as *Mesotanaocerus* gen. nov. offers now the possibility to develop powerful Total Evidence methods (Wright et al. 2022; Ferreira et al. 2024).

The extant Tanaoceridae occur in the modern biota exclusively along the western slopes of the Cordillera in North America, where habitats are primarily located in the ecotonal region between the Upper Sonoran and Lower Sonoran life zones. The geographic range spans from the southern margin of the Great Basin in Utah (approximately 40°N) to Baja California in Mexico (around 28°N) (Rehn

and Grant 1960, 1961; Grant and Rentz 1967). This narrow and confined distribution reflects the ecological adaptation of the family to arid or semi-arid environments, with morphological features such as a slender body and reduced wings representing selective adaptations to locally extreme conditions. The discovery of the new genus and species not only enriches the known diversity of Tanaoceridae but also provides new biogeographic evidence for investigating the persistence and evolution of ancient lineages within Orthoptera in response to environmental changes. It is probably a case of a clade that was living in the deep past under a very different or diverse environment than those of the extant representatives, as the Kachin amber mainly corresponds to a forest palaeoenvironment and not a desert one, even if sand grains have been found in some Kachin amber pieces. But these sand grains are associated to marine fossils such as ammonites (Xing et al. 2025), or to debris-carrying insect larvae (Wang et al. 2016). The palaeoforest was clearly very close to the sea, but nothing indicates a proximity to a desert. As the holotype of *Mesotanaocerus yiweizhangae* gen. et sp. nov. was apterous, it probably did not come from far from the palaeoforest. Kachin amber originated from the Burma terrane or West Burma block, an isolated Gondwana-derived island arc within the Tethys Ocean during the Mid-Cretaceous (Westerweel et al. 2019). This terrane separated from the Gondwana during the Early Cretaceous. As the Tanaoceridae originated during the Triassic (Hemp et al. 2025), they were present in this palaeocontinent before the Early Cretaceous.

Similar situations occur for many families that were much more widespread during the Cretaceous and are now restricted to highly specialized biotas, such as the Grylloblattodea that are now restricted to very cold environments while they were widely distributed in warmer biotas during the Cretaceous, or the family Tettigarctidae Distant, 1905 (Order Hemiptera Linnaeus, 1758) that are now restricted to cold forests in Tasmania. The Sonora desert is possibly also a refugium for the extant relict Tanaoceridae.

Conclusions

In the present paper, we describe the first fossil of the acridomorph Tanaoceridae, from Burmese amber. The new fossil, an adult male specimen, documents the presence of this basal clade within Acridomorpha as early as 98.79 ± 0.62 Ma. As such, it is an important calibration point for dating the Caelifera and adding the Tanaoceroidea in future phylogenomic analyses, because accurate Mesozoic representatives of the different caeliferan clades are quite few to date (Song et al. 2020; Hemp et al. 2025). Hemp et al. (2025: fig. 1) dated the origin of the Tanaoceridae during the Middle Triassic, which is congruent with their presence in the mid-Cretaceous. Also, this new fossil attests that Tanaoceridae had much wider distribution in the past, which parallels what has been documented for Grylloblattodea (Grimaldi and Engel 2005; Wipfler et al. 2014). The drastic changes in distributions of both clades may signify that both have evolved toward particular environmental conditions, making their present states possible evolutionary dead-ends.

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