The first Cretaceous Eumastacoidea (Orthoptera, Caelifera) from Burmese amber

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Abstract

A new genus and species of fossil Eumastacoidea Burr, 1899 from Kachin amber is described. *Burmeumastax lexiae* **gen. et sp. nov.** is the 14th member of this superfamily known from fossil material and only the third to predate the Cretaceous-Paleogene (K-Pg) extinction event, following *Archaeomastax jurassicus* Sharov, 1968 and *Taphacris turgis* Lin, 1980. Most fossil species of Eumastacoidea were reported based mainly on wings, with *B. lexiae* being only the second species with most parts of the body well preserved, predating the only other species in this condition by ca. 80 Myr. *Burmeumastax lexiae* is brachypterous with a body morphology similar to extant species of apterous Eumastacoidea. However, its last abdominal tergite consists of seven separate plates, whereas this structure is made up of only one or two plates in modern-day species. Because Eumastacoidea taxonomy based on morphology relies heavily on internal genital structures, the position of *B. lexiae* within the Eumastacoidea is uncertain. Since the orthopteran fauna of the Burma Terrane appears to be influenced by South American-Gondwana (based on the high diversity of Tridactyloidea Brullé, 1835 and the Elcanidae Handlirsch, 1906 found in Burmese amber compared to deposits of the Crato-Formation from Brazil), it is speculated that *B. lexiae* may belong to Eumastacidae Burr, 1899, as this is the only family of Eumastacoidea with a wide distribution across South America. The new species provides remarkable insights into the early evolution of Eumastacoidea and further highlights the insect diversity of the Burma Terrane.

Keywords

Acrididea, burmite, fossil record, monkey hoppers

Introduction

Eumastacoidea Burr, 1899 is a relatively small superfamily of short-horned grasshoppers with a largely tropical distribution. Currently, 1,078 species, 281 genera, and 8 families are considered valid (Cigliano et al. 2024) with just 13 fossil species (this does not count *Taphacris tillyardi* Cockerell, 1926 as a valid species, as Cockerell had only suggested a second specimen of *Taphacris bittaciformis* Cockerell, 1926 as a variety of the type specimen, which he called *T. b. tillyardi*). Fossil Eumastacoidea are known from deposits in North America, Europe, and Asia (Fig. 1) (Scudder 1890, Handlirsch 1910, Cockerell 1926, Sharov 1968, Lin 1977, Lin 1980, Kevan and Wighton 1981, Gorochov 2012, Zessin 2017, Schubnel et al. 2020). Thus far, no members of the superfamily have been described from pre-Neogene amber, while specimens from Dominican amber have been known for decades (Perez-Gelabert et al. 1997).

Based on DNA evidence, the Eumastacoidea Burr, 1899 have been dated to the Early Jurassic at approximately 180 Mya (Toarcian), with most families estimated to be around 150 My old (Late Jurassic, Kimmeridgian) (Song et al. 2015). Fossil specimens are mainly known from preserved wings (Cockerell 1926, Scudder 1890, Zessin 2017) (Table 1). Only the Eocene *Eoerianthus eocaenicus* Gorochov, 2012 has most major parts of the body preserved, with the abdominal apex missing (Gorochov 2012). The external and internal genitalia of Eumastacoidea are a key reference point for their diagnosis, and thus, the generic assignment of fossil members of the family is difficult (Rowell and Bentos-Pereira 2001, Gorochov 2012). Specimens preserved in amber can provide unique opportunities for understanding past Eumastacoidea morphology due to the sometimes-outstanding quality of preservation. In this study, we present the first record of a Cretaceous member of Eumastacoidea from Burmese amber. The specimen's entire body is preserved, allowing for a description of the external genitalia of a fossil member of this taxon for the first time.

According to paleogeographic analyses conducted by Westerweel et al. (2019), Burmese amber reflects an ecosystem during the Cretaceous (earliest Cenomanian) that was situated on an isolated terrane. This so-called Burma Terrane broke off from Gondwana in

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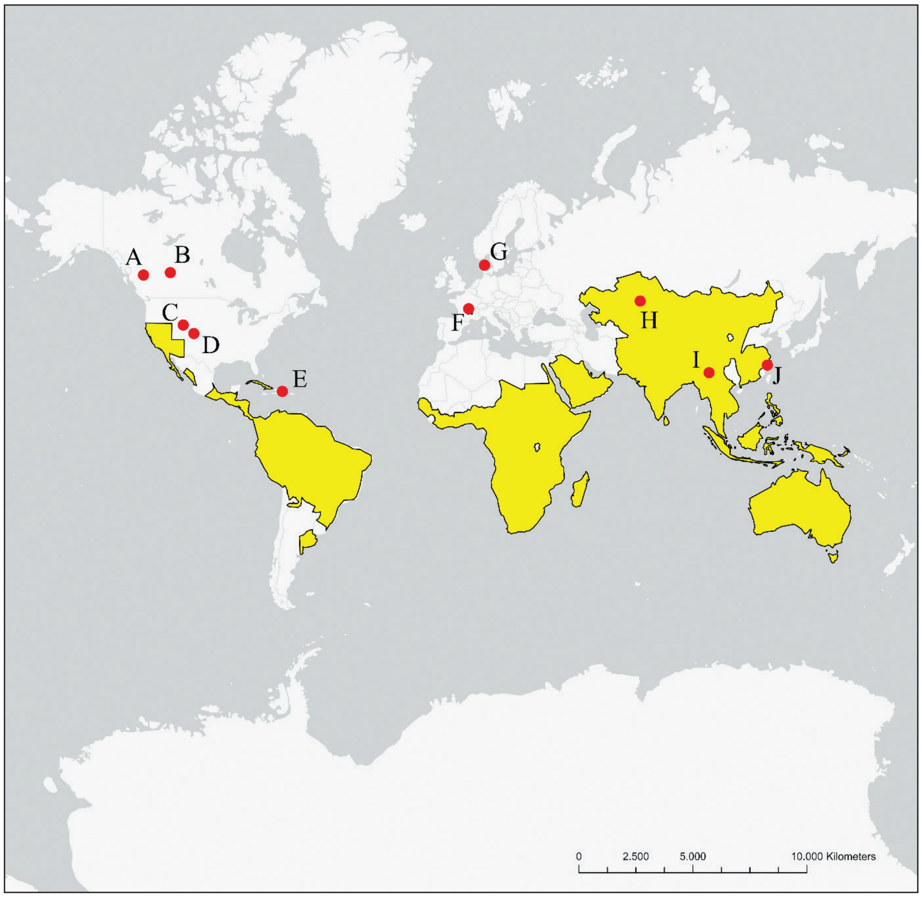

Fig. 1. Map showing the geographical distribution of Eumastacoidea (yellow) with findings of fossil Eumastacoidea marked by red dots. **A.** *Promastax archaicus* Handlirsch, 1906; **B.** *Promastacoides albertae* Kevan & Wighton, 1981; **C.** *Eoerianthus eocaenicus* Gorochov, 2012; *E. multispinosus* (Scudder, 1890); **D.** *Taphacris reliquata* Scudder, 1890; *T. bittaciformis* Cockerell, 1926; (*T. tillyardi* Cockerell, 1926); *E. multispinosus*; **E.** *Paleomastacris ambarinus* Perez-Gelabert et al., 1997; **F.** *Paleochina duvergeri* Schubnel et al., 2020; *P. minuta* Schubnel et al., 2020; **G.** *Eozaenhuepfer erteboellei* Zessin, 2017; **H.** *Archaeomastax jurassicus* Sharov, 1968; **I.** *Burmeumastax lexiae* gen. et sp. nov.; **J.** *Taphacris stenosis* Lin, 1977; *T. turgis* Lin, 1980. Map created with ArcGIS Pro and modified in Inkscape. Data of Eumastacoidea distribution from the Orthoptera Species File (Cigliano et al. 2024; accessed on 10.07.2024).

the Late Jurassic–Early Cretaceous (Heine et al. 2004, Heine and Müller 2005) and drifted northward, becoming part of an island arc in the Meso-Tethys at around 120 Myr (Westerweel et al. 2019) (Fig. 3). The Burmese amber found in Kachin in Myanmar today developed around 20 million years later (Shi et al. 2012). The orthopteran fauna of the Burma Terrane was apparently strongly influenced by the parts of Gondwana belonging to South America today. This was tentatively proposed by Nel and Jouault (2022) for the Elcanidae Handlirsch, 1906 and is further evidenced by the rich diversity of Ripipterygidae Ander, 1939, members of which are otherwise only known from South America (Xu et al. 2020a, Xu et al. 2020b, Gu et al. 2022, Zhao et al. 2023, Zhao et al. 2024). The possible connection between the two faunas (i.e., Burmese amber and South America, e.g., the Crato-Formation) may hold implications for the taxonomic placement of the new species of Eumastacoidea described herein.

Materials and methods

The taxonomy in this study follows the Orthoptera Species File (OSF) (Cigliano et al. 2024).

The amber piece discussed in this study is deposited in the amber collection of the LIB (Leibniz Institute for the Analysis of Biodiversity Change, Hamburg, Germany, accession number: GPIH07011). It originated from Myanmar where it was discovered in a mining site near either Tanai village or Hkamti village. The age of the two amber sites differs by ca. 10 My: Amber from Tanai is estimated to be 98.79 ± 0.62 My old (Shi et al. 2012), and amber from Hkamti is ca. 110 My old (Xing and Qiu 2020). The exact origin is currently unknown.

Images were taken with a DUN. Inc. stacking system holding a Canon EOS 5Dsr Camera with a 65 mm lens and a magnification of 2×. Individual pictures were taken using VD Passport and the Capture One program (Capture One A/S, Denmark). Pictures were stacked using a Zerene Stacker (Zerene Systems LLC, Washington, USA). The resulting high-resolution images were edited with Photoshop CS6 Extended application by Adobe Inc. (USA), where a scale bar was added as reference. Further modifications and the creation of image plates were done in Inkscape v. 1.3.2 (https://inkscape.org). Drawings were created in GIMP v. 2.10.30 (GIMP Team 2024) and redrawn with PITT artist pens by FABER-CASTELL to improve quality.

A map of the geographical distribution of Eumastacoidea (Fig. 1) was created in ArcGIS Pro by Esri (California, USA, https://www.esri.com/en-us/home) and modified in Inkscape. Eumastacoidea distribution data were obtained from OSF (Cigliano et al. 2024).

Table 1. Fossil record of Eumastacidae. *Taphacris tillyardi* Cockerell, 1926 is not a valid species, but was suggested as a variety of *T. bittaciformis* Cockerell, 1926 by Cockerell (1926) after Tillyard had suggested a second specimen of *Taphacris* Scudder, 1890 to be a different species than the type specimen in a personal conversation with Cockerell. The age of *T. stenosis* Lin, 1977 is debated to be Cretaceous or Cenozoic (Li et al. 2015).

Family (as suggested)	Genus and Species	Publication	Locality and horizon	Preservation
Eumastacidae	*Archaeomastax jurassicus*	Sharov 1968	Karatau: Michailowka (166–157 Mya)	Forewing, hindwing
Eumastacidae	**Burmeumastax lexiae*	herein	Myanmar: Kachin State Burma (99 Mya)	Almost complete body (brachypterous)
Eumastacidae	*Eoerianthus eocaenicus*	Gorochov 2012	Colorado: Green River Formation (50–46 Mya)	Imprint of almost complete body, including forewing
Eumastacidae	*Eoerianthus multispinosus*	(Scudder 1890)	Colorado: Florissant (37–34 Mya)	Isolated hind wing; isolated hind leg
Eumastacidae	*Eozaenhuepfer erteboellei*	Zessin 2017	Denmark: Ertebølle (56–48 Mya)	Forewing
Chorotypidae	*Paleochina duvergeri*	Schubnel et al. 2020	France: Menat Formation (61–59 Mya)	Forewing, hindwing, partial hind leg
Chorotypidae	*Paleochina minuta*	Schubnel et al. 2020	France: Menat Formation (61–59 Mya)	Forewing, very badly preserved body imprint
Episactidae	*Paleomastacris ambarinus*	Perez-Gelabert et al. 1997	Dominican Republic: Cordillera Septentrional (20 Mya)	Almost complete body (apterous)
Promastacidae	*Promastacoides albertae*	Kevan and Wighton 1981	Alberta: Paskapoo Formation (62.5–58.5 Mya)	Forewing
Promastacidae	*Promastax archaicus*	Handlirsch 1910	British Columbia: Horsefly Shale (49 Mya)	Wing
Eumastacidae	*Taphacris bittaciformis*	Cockerell 1926	Colorado: Florissant (37–34 Mya)	Hindwing
Eumastacidae	*Taphacris reliquata*	Scudder 1890	Colorado: Florissant (37–34 Mya)	Wings, compressed body
Eumastacidae	*Taphacris stenosis*	Lin 1977	China: Lanping (66–56 Mya)	Forewing
(Eumastacidae)	*Taphacris tillyardi*	Cockerell 1926	Colorado: Florissant (37–34 Mya)	Folded hindwing
Eumastacidae	*Taphacris turgis*	Lin 1980	China: Zhejiang (125–113 Mya)	Forewing

Results

Systematic paleontology

Order Orthoptera Olivier, 1789
Suborder Caelifera Ander, 1936
Superfamily Eumastacoidea Burr, 1899
Family ?Eumastacidae, Burr, 1899

Genus *Burmeumastax* gen. nov.
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Figs 3, 4

Type species.—*Burmeumastax lexiae* sp. nov., by monotypy.

Etymology.—The genus name derives from a combination of the words "Burma" and "Eumastacidae" in reference to its geographical and phylogenetic affiliations, respectively.

Diagnosis.—Pronotum with two distinct grooves. Anterior groove smooth, posterior groove sharp. Brachypterous. Last abdominal tergite consisting of 5–7 plates. Supraanal plate elongate, triangular. Sub-genital plate bulbous with apical central fold and lateral cercus-like lobes. Cercus slender, same length as supra-anal plate. Cercus and sub-genital plate setulose. Only dorsal (= middle) plate of last abdominal tergite setulose.

Remarks.—Systematic placement of *Burmeumastax* inside Eumastacoidea is difficult. As *Burmeumastax* is a brachypterous genus, a comparison with most other fossil genera of the superfamily is impossible. The only two fossil genera that can be compared with *Burmeumastax* are *Eoerianthus* Gorochov, 2012 and *Paleomastacris* Perez-Gelabert et al., 1997. The type and only species of the first genus, *E. eocaenicus* Gorochov, 2012, is from the Eocene (56–33.9 Mya) of North America (Wyoming, Green River Formation) (Gorochov and Labandeira 2012), thus separated from *Burmeumastax* by at least 40 My. Morphologically, *Eoerianthus* differs from *Burmeumastax* in having a body three

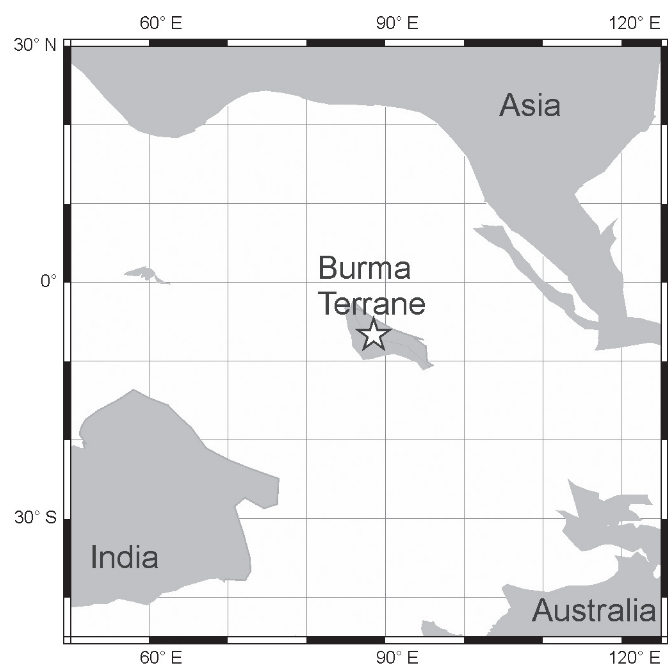

Fig. 2. Map showing the position of the Burma Terrane at about 95 mya (after Westerweel et al. 2019).

times longer, featuring fully developed wings, a very different pronotum morphology with no dorsal grooves, and no small spines on the metafemur (Gorochov and Labandeira 2012). The abdominal apex and external genitalia were not preserved in the specimen of *Eoerianthus*. *Paleomastacris ambarinus* Perez-Gelabert et al., 1997, type and only species of the second genus, differs from *Burmeumastax* by being completely apterous, a pronotum without dorsal grooves, and external genitalia of alternate shape. The supraanal plate of *P. ambarinus* is diamond-shaped, while it is triangular in *B. lexiae*. The sub-genital plate consists of two ventrally separated triangle-shaped parts in *P. ambarinus* but is bulbous with a ventral fold in *B. lexiae*.

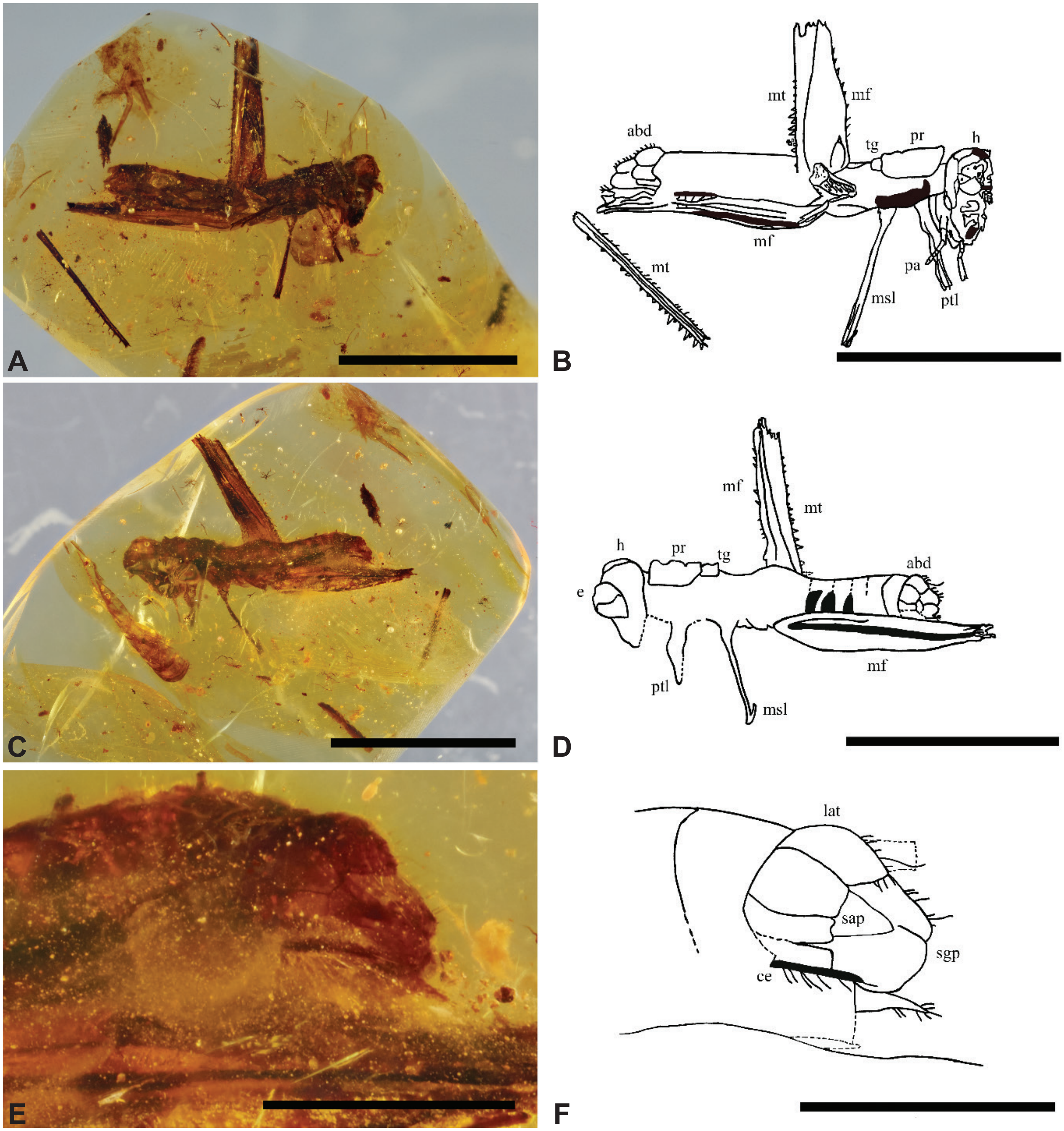

Fig. 3. *Burmeumastax lexiae* gen. et sp. nov. holotype male GPIH_07011. **A, B.** Image and drawing of specimen's right side, respectively. **C.** and **D.** Image and drawing of specimen's left side, respectively. **E, F.** Image and interpretative drawing of the abdominal region including external genitalia. **Abbreviations:** abd = abdomen; tg = forewing; mt = metatibia; mf = metafemur; pr = pronotum; h = head; ptl = prothoracic leg; pa = palpus; msl = mesothoracic leg; e = eye; lat = last abdominal tergite; ce = cercus; sap = supra-anal plate; sgp = sub-genital plate. Scale bars: 5 mm (**A, B, C, D**); 1 mm (**E, F**).

Without knowledge of the internal genitalia and specifically the phallic complex, attribution of *Burmeumastax* to one of the seven extant families of Eumastacoidea is problematic, as other morphological characters that could be used for diagnosis are lacking in this understudied group. *Burmeumastax* differs from modern-day Eumastacoidea by its last abdominal tergite consisting of several (5–7) separate parts. In extant species, this structure is made up of one joint or two lateral plates with just a small space dorsally (Dirsh 1966, Descamps 1979, Rowell and Bentos-Perreira 2001).

Burmeumastax lexiae sp. nov.

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Figs 3, 4

Holotype.—Male; possibly nymph. Deposited in the amber collection of the LIB (GPIH07011), Leibniz Institute for the Analysis of Biodiversity Change, Hamburg, Germany.

Etymology.—The species is named after Lexi Husemann, the daughter of the first author of the study.

Locality and horizon.—The specimen was included in amber found in Hkamti, Sagaing Division, Myanmar or Tanai, Kachin State Burma, Myanmar, two nearby amber mining locations. The amber from Hkamti is ca. 110 My old, and the amber from Tanai is ca. 99 My old.

Diagnosis.—Same as for genus, since this is the only species.

Description.—Body long and slender, about seven times as long as high. Body length (tip of head to tip of abdomen) 7.53 mm; 1.03 mm high (measured right in front of metathoracic leg).

Head.—Twice as high as wide and twice as high as body height. Top of head capsule to bottom tip of mouth parts, 2.05 mm; 1.03 mm width at widest point (eye level). Fastigium not elongated. Eyes large, ellipsoid, and laterally protruding from head. Eyes take up almost half the head height and are about twice as high as wide. Eye top to bottom 0.87 mm long, 0.45 mm wide. Distance from bottom of the eye to bottom of the head, 1.2 mm. Interocular distance (measured at top of head), 0.32 mm. Antennae missing except antennal bud, which is 0.32 mm long and reminiscent of a pinecone with scales closed. Antennal bud located right in front of the bottom of the eyes. Lower face slightly oblique in profile with mouthparts forming a cone or almost triangular shape. Right maxillary palpus 7-segmented, 0.87 mm long in total.

Thorax.—Thoracic height 1.06 mm, of which 0.58 mm is covered by the pronotum. Pronotum 1.31 mm long dorso-laterally, slightly shorter at 1.12 mm ventro-laterally. Pronotum saddle-like, covering the thorax with distinct elevation. Pronotum marked by two distinct grooves on its dorsal surface, one smooth anteriorly, second sharp posteriorly.

Wings.—Brachypterous. Short wing buds can be seen sticking out from under the posterior margin of the pronotum. Wing buds ca. 0.42 mm long.

Legs.—Prothoracic leg: only preserved up to femur. Long and slender. Preserved part 1.64 mm long. Mesothoracic leg: only preserved up to femur. Long and slender. Preserved part 2.36 mm long. Metathoracic leg: femur very long, length/width ratio 4.2 mm/0.77 mm = 5.5; thinning distally. Tibia thinning further along its length of more than 4 mm (metatibia not fully preserved) until it shares a width similar to pro- and mesofemur. Dorsal margin of metafemur on proximal half with spaced short fine hairs, which are replaced by small spines on distal half. Spines continuing along the dorsal margin of metatibia and getting larger distally (0.03 mm–0.12 mm). Dislocated object in bottom left area probably left metatibia: 4.04 mm long (including three spines at distal end; these spines may be the apical spines of the metatibia).

Abdomen.—Abdomen with a distinct hump at the position of metathoracic legs. Last abdominal tergite made up of five to seven individual plates that cover the dorsal part of the genitalia like a ring. Dorsal (= middle) plate setulose. Supra-anal plate elongate, triangular. Sub-genital plate bulbous with central fold apically and lateral cercus-like lobes. Real cercus slender, ca. 0.47 mm long. Sub-genital plate and cercus setulose.

Remarks.—Based on the short wing buds and the small body size, *Burmeumastax lexiae* may be a nymph. This is further supported by the abdomen not being curved upwards, as is the case in several male Eumastacoidea, for example *Paralethus insolitus* Rowell and Perez-Gelabert, 2006 or *Episactus tristani* Rehn & Rehn, 1934. However, in other species, such as *Teicophrys robertsi* (Rehn & Rehn, 1939), the male abdomen is straight.

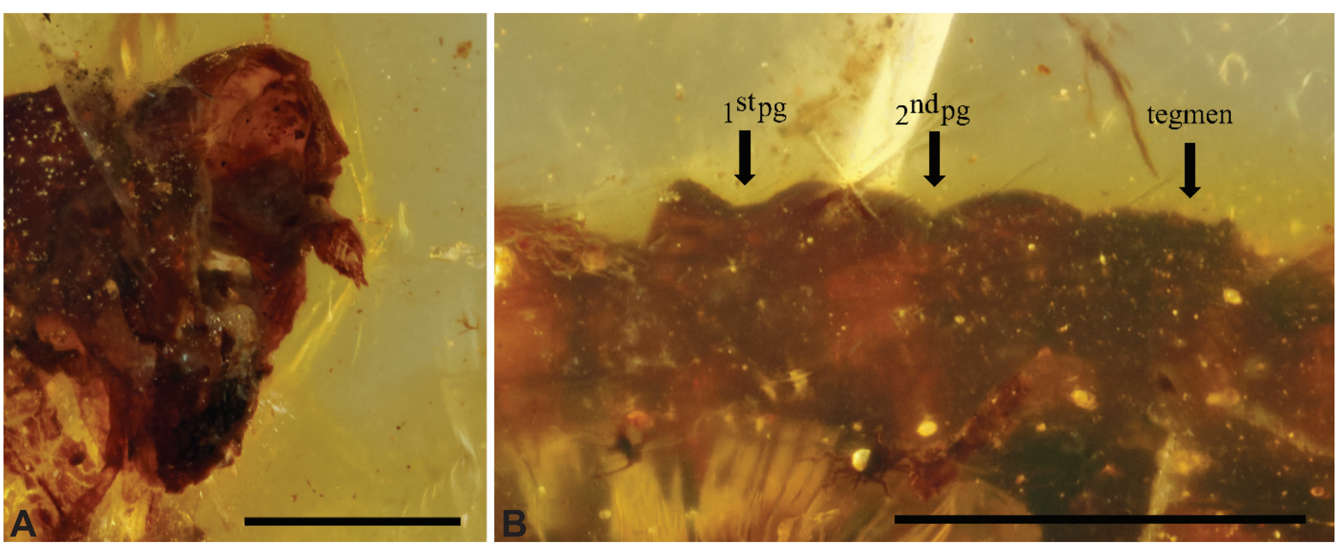

Fig. 4. *Burmeumastax lexiae* gen. et sp. nov. holotype male GPIH_07011. **A.** Detail of the head. **B.** Detail of the pronotum. Abbreviations: pg = pronotal groove. Scale bars: 1 mm.

Discussion

A new genus and species of Eumastacoidea Burr, 1899 is described based on an almost completely preserved specimen from mid-Cretaceous Kachin amber. As the fossil record for this superfamily is relatively poor and most species are only known from hind- or forewings, it is difficult at this time to make any taxonomic suggestions as to the position of the new taxon. Its brachypterous state separates it from all known species of Eumastacoidea in the fossil record (Scudder 1890, Handlirsch 1910, Cockerell 1926, Sharov 1968, Lin 1977, Lin 1980, Kevan and Wighton 1981, Gorochov and Labandeira 2012, Zessin 2017). *Burmeumastax lexiae* differs from modern-day Eumastacoidea in the morphology of its last abdominal tergite consisting of five to seven separate plates; in extant species, there are usually one or two plates (Descamps 1979).

Despite the difficulties of placing *B. lexiae* in one of the families of Eumastacoidea, the new species may belong to Eumastacidae Burr, 1899 based on two arguments: most other fossil Eumastacoidea were placed in this family (see Table 1) based on their wing venation features. This suggests that Eumastacidae may have been more diverse earlier on in the diversification of Eumastacoidea, and it would be more likely for *B. lexiae* to also be part of this family. Furthermore, the orthopteran fauna of the Burma Terrane appears to have been majorly influenced by South American Gondwana. Nel and Jouault (2022) suggested that Elcanidae Handlirsch, 1906 (a family of Mesozoic Ensifera-like Orthoptera) from the Burma Terrane may have originated from predecessors such as those found in the deposits of the Crato-Formation from Brazil (122–113 Mya). This hypothesis is supported by the high abundance of Tridactyloidea Brullé, 1835, especially of the family Ripipterygidae Ander, 1939, in Burmese amber, as these cricket-like Caeliferans exclusively occur in South and Middle America in modern times (Cigliano et al. 2024).

The presence of an Eumastacoidea on the Burma Terrane has implications for the evolutionary origin of the superfamily. The earliest fossil attributed to Eumastacoidea is ca. 160 My old and was found in Karatau, Kazakhstan (*Archaeomastax jurassicus* Sharov, 1968). Carbonell (1977) suggested that these pioneering Caelifera invaded the Americas via Beringia, reaching South America during the Late Cretaceous. However, if *B. lexiae* derived from ancestors in South America prior to the breakup of the Burma Terrane from Gondwana in the Late Jurassic-Early Cretaceous, Eumastacoidea must have been present in the area much earlier than previously assumed and only shortly after their evolutionary origin estimated at around 180 Mya (Song et al. 2015).

Conclusions

The first completely preserved specimen of Mesozoic Eumastacoidea *Burmeumastax lexiae* gen. et sp. nov. is described from mid-Cretaceous Kachin amber. Its discovery provides important insights into the early morphological features of this superfamily, which is generally scarce in the fossil record, especially from the Mesozoic. The new species differs from modern-day Eumastacoidea by its last abdominal tergite consisting of five to seven separated plates; in extant species, the structure is made up of only one or two plates. The presence of a member of Eumastacoidea on the Burma Terrane suggests that ancestors of *B. lexiae* may have been present in South American Gondwana much earlier than previously assumed, shortly after the estimated evolutionary origin of Eumastacoidea ca. 180 Mya.

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