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RESEARCH PAPER

New species of Burmese amber Elcanidae (Insecta: Orthoptera) suggest Gondwanan origin and demonstrate ovipositor diversity

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Abstract

A new genus of Elcaninae Handlirsch, 1906 (Orthoptera: Elcanidae) with three new species is described from mid-Cretaceous Burmese amber. The type species is *Elcanodentes alatus* gen. et sp. nov., described from an almost completely preserved female specimen. *Elcanodentes cretaceus* gen. et sp. nov. is described based on the male holotype and a female paratype. *Elcanodentes thanatos* gen. et sp. nov. is reported from a partly preserved female specimen. The genus is characterised by a wing venation similar to *Panorpidium* Westwood, 1854, however, differs from the latter by featuring a pterostigma without cross veins, an anal forewing margin between CuA + CuPaα and MP making up 26–33% of the total wing length and the name giving small teeth along the lateral margins of the metatibial spurs. A proportionally much longer tegminal margin between CuA + CuPaα and MP of Burmese-amber Elcanidae compared with most Laurasian species suggests a descent from Gondwanan predecessors, such as *Cratoelcana* Martins-Neto, 1991. The diversity of ovipositors in the Elcanidae is discussed and three different morpho-types for this structure are suggested: sword-shaped, scythe-shaped and saber-shaped. Some previously described taxa of Burmese amber Elcanidae are taxonomically revised: *Panorpidium maculosum* Zhou et al., (Cretaceous Research 136, 2022) is moved to *Pseudopanorpidium* gen. nov. *Probaisselcana oculata* Hu and He, (Cretaceous Research 151, 2023) is moved to *Pseudoprobaisselcana* gen. nov. *Hukawnelca gracile* and *Caelielca spinocrus* both Uchida, (Cretaceous Research 131, 2022) are assigned to the Archelcaninae Gorochov et al., (Cretaceous Research 27:641–662, 2006).

Keywords Metatibial spurs · *Elcanodentes* · *Pseudopanorpidium* · *Pseudoprobasselcana* · Burma Terrane · Kachin

Introduction

The Elcanidae Handlirsch, 1906 are an orthopteran family found in the fossil record of the early Permian to the Paleocene (ca. 255–60 mya) (Béthoux & Nel, 2002; Gorochov et al., 2006; Grimaldi & Engel, 2005; Schubnel et al., 2020; Sharov, 1968). Due to their contradictory morphological features, their phylogenetic position within the order of Orthoptera Olivier, 1789 remains unclear (Béthoux & Nel, 2002; Gorochov & Rasnitsyn, 2002; Peñalver & Grimaldi, 2010; Poinar et al., 2007; Tian et al., 2019a, 2019b; Zhou et al., 2022). Elcanidae are characterized by a unique combination of traits, such as their large movable spurs, large ovipositors, as well as their antennae, which are longer than their bodies (Handlirsch, 1906; Zessin, 1987). These morphological features indicate a close link to the suborder Ensifera Chopard, 1921 (Zessin, 1987). In contrast, their wing venation and the shape of the forewings would place them in the suborder Caelifera Ander, 1936 (Béthoux & Nel, 2002). Some authors suggested the Elcanidae may represent

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an extinct sister group to Caelifera and Ensifera at the base of Orthoptera (Béthoux & Nel, 2002). The Elcanidae have been divided into two subfamilies by Gorochov et al. (2006), the Elcaninae Handlirsch, 1906 and the Archelcaninae Gorochov et al., 2006, which are mainly differentiated by the state of the forewing veins 1A, CuPb and CuPaβ being fused (Elcaninae) or not (Archelcaninae) (Gorochov et al., 2006).

Findings of Elcanidae have been reported both as compression fossils as well as amber inclusions (e.g. Kim et al., 2021; Poinar et al., 2007). Their distribution ranges from Central Europe, England, Spain, Myanmar, China and North America to Brazil with the singular suggested Permian species, *Elcanopsis sydneiensis* Tillyard, 1918, from Australia (Fang et al., 2015, 2018; Gorochov et al., 2006; Heads et al., 2022; Martins-Neto, 1991; Peñalver & Grimaldi, 2010; Poinar et al., 2007; Tillyard, 1918). In recent years, amber found in the mines of northern Myanmar has revealed an especially rich diversity of Elcanidae species (Poinar et al., 2007; Peñalver & Grimaldi, 2010; Heads & Thomas, 2018; Kočárek, 2020; Gu et al., 2022; Uchida, 2022; Xu et al., 2022; Zhou et al., 2022; Hu & He, 2023; Schall et al., 2024). As of September 2024, 18 species of Elcanidae are known from Burmese amber representing 15 different genera (*Panorpidium* sp. Fang et al., 2015 not counted as separate species) (Cigliano et al., 2024; Schall et al., 2024). These species have added important knowledge to our understanding of Elcanidae ecology, as many of the morphologic features are often more exquisitely preserved in amber than in compression fossils. Studies concerning the ecology of Elcanidae have discussed the use of the pterostigma, a specialized cell in the forewing of these animals which has been speculated upon by Fang et al. (2018) and Kočárek (2020) to have facilitated a unique method of flight in Elcanidae different from all other Orthoptera. Tian et al., (2019a, 2019b) and Kim et al. (2021) suggested an aquatic affiliation due to the large metatibial spurs of Elcanidae, which may have been used to jump over water surface when trying to avoid predation. In this study we aim to take a closer look at ovipositor diversity in Elcanidae, which allows for conclusions on different habitat use of these enigmatic orthopterans.

Another aspect of the Burmese amber fauna is the peculiar history of their habitat, the Burma Terrane (BT). Several studies have dealt with the geological history of the BT with latest findings suggesting a rifting from Gondwana alongside the Greater Indian plate during the Early Cretaceous (ca. 140 mya; da Silva Schmitt et al., 2023) and an isolated position in the Mesotethys at around 95 mya during the formation of the amber (Westerweel et al., 2019; Licht et al., 2020; Bolotov et al., 2022). According to these studies, the BT would have either been connected to Greater India during this time or have resided as part of a Trans-Tethyan island arc in an isolated position (Westerweel et al., 2019). Due to this, it is possible that the BT has promoted the evolution of an endemic fauna (Westerweel et al., 2019). Other studies have found apparent evidence for Gondwanan influence on the Burmese amber biota (e. g. Bolotov et al., 2022; Wood & Wunderlich, 2023). The new species presented in this study support a Gondwanan origin of BT Elcanidae. However, this hypothesis is to be taken with caution for as long as very little is known about Gondwanan representatives of the family which so far are only known from three species of the one genus *Cratoelcana* Martins-Neto, 1991 (Martins-Neto, 1991; Nel & Jouault, 2022).

Materials and methods

The taxonomy in this study follows the Orthoptera Species File (OSF) (https://orthoptera.speciesfile.org/, Cigliano et al., 2024). Wing venation nomenclature follows Béthoux and Nel (2002). Abbreviations are as follows: CP posterior costa; ScA, ScP = anterior/posterior subcosta; R = radius; RA, RP = anterior/posterior radius; MA, MP = anterior/posterior media; CuA, CuP = anterior/posterior cubitus; CuPaα = anterior branch of first posterior cubitus; CuPaβ = posterior branch of first posterior cubitus; CuPb = second posterior cubitus; 1A = anterior anal vein.

The amber pieces used in this study are deposited in the amber collection of the LIB (Leibniz Institute for the Analysis of Biodiversity Change, Hamburg, Germany). They originated from Myanmar and were discovered in the mining sites near the city of Tanai in the Hukawng Valley of the Kachin State, Myanmar. Their age is estimated to be 98.79 ± 0.62 mya placing it in the mid-Cretaceous era, earliest Cenomanian (Shi et al., 2012). We are aware of the ethical implications connected to Burmese amber, especially that obtained post 2017. We hope our work—along with other research on Burmese amber—contributes to spreading that awareness and highlights the importancy of local mining workers of Myanmar in deepening our understanding of life on our planet. A thorough discussion about the Burmese amber situation is given in Haug et al. (2020).

Images were taken with a DUN. Inc. stacking system holding a Canon EOS 5Dsr Camera with a 65 mm lens and a magnification of 1.5x. The individual pictures were taken with a combination of VD Passport and the Capture-One-program (Capture One A/S, Denmark). Following this, the pictures were stacked with Zerene Stacker (Zerene Systems LLC, Washington, USA), resulting in high-resolution multilayered images. The images were edited with Photoshop CS6 Extended by Adobe Inc. (USA). Further modifications, creation of image plates and scale bars were done in Inkscape (v. 1.3.2) (Moini et al., 2024, https://inkscape.org/).

Drawings were made using Procreate Version 5.3.1. (Savage Interactive, Hobart, Australia) and an Apple iPad Air 2020 together with an Apple Pencil (2nd Generation).

The bar charts visualizing the findings from the analysis of anal margin length of the forewing between CuA + CuPaα and MP were created in OpenOffice Calc (https://de.libreoffice.org/discover/calc/). To perform the analysis, the undersides of the forewing (length from base to apex) of several Elcanidae species were measured. Values of species not described in the present study were obtained by calculation based on published material of Elcanidae with well-preserved forewings. The relative length forewing margin between CuA + CuPaα and MP was given in % of the total wing length (measured along the underside).

Systematic palaeontology

Order **Orthoptera** Olivier, 1789

Superfamily **Elcanoidea** Handlirsch, 1906

Family **Elcanidae** Handlirsch, 1906

Subfamily **Elcaninae** Handlirsch, 1906

Genus ***Elcanodentes*** gen. nov. Willmott, Schall, Kotthoff & Husemann.

Type species. *Elcanodentes alatus* sp. nov. Willmott, Schall, Kotthoff & Husemann.

Zoobank-ID. urn:lsid:zoobank.org:act:8B7E5133-A29C-44C6-B9AB-42A7D07A5B06.

Etymology. The generic name is derived from the Latin word "dentes" meaning "teeth", referring to the serration of spines.

Diagnosis. The genus can be recognized by a forewing venation similar to *Panorpidium* Westwood, 1854, however, with a pterostigma without cross veins and an anal wing margin between CuA + CuPaα and MP being significantly longer than in *Panorpidium*. Further, it is defined by a row of small teeth-like structures along the lateral margins of the metatibial spurs.

Remarks. The genus is assigned to the subfamily Elcaninae Handlisch, 1906 based on the fusion of 1A + CuPb + CuPaβ (visible in *E. cretaceus* and *E. thanatos*) as well as the space between RA and RP being rather narrow. It exhibits some resemblance to *Panorpidium* Westwood, 1854 in having three branches of M between CuA + CuPaα and the stem of RP (MP, MA2, MA1), however, differs from the latter by featuring a pterostigma without cross veins as well as a much longer anal forewing margin between CuA + CuPaα and MP.

Elcanodentes alatus sp. nov. Willmott, Schall, Kotthoff & Husemann.

Figure 1

Zoobank-ID. urn:lsid:zoobank.org:act:7CE52F94-CAC9-422D-96B2-D759E35DB96C.

Etymology. The species name derives from the Latin word "ala" meaning "wing", referring to the special wings of this species.

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. Lowermost Cenomanian, middle Cretaceous, 98.8 ± 0.6 Ma.

Holotype. Adult female; deposited in the amber collection of Leibniz Institute for the Analysis of Biodiversity Change, Hamburg, Germany (coll. no. GPIH 7016, ex. Collection Martin Husemann, Fossil 0047).

Diagnosis. The species can be recognized by the presence of prolonged veins which are protruding from the forewings. Forewing tapered towards the top distal part of the wing. Eyes large, protruding from head. Pronotum saddle-shaped, shortened distally. Metatibial spurs leaf-like with lateral margins bearing a row of small teeth.

Description. Body length 8.2 mm, including wings 14.8 mm.

Forewings. Approximate length 12.19 mm. Basal part of wing not visible due to density and darkness of the amber. Shape of forewing tapered distally. Three branches of M between CuA + CuPaα and the stem of RP. Anal margin between CuA + CuPaα and MP very long (estimated to make up 32.8% of total wing length). RP with five branches. Pterostigma narrow, only taking up an estimated 2.5% of total wing surface (the lowest value of all known Elcanidae species). Pterostigma without cross veins. Forewing without spots, however, with a rather conspicuous darkened distal margin.

Head. Compound eyes protruding from the head, one eye partially visible due to the position in the amber, second eye only partly visible due to some damage on the surface. Part of one antenna visible, bent backwards, with small spines covering the antenna, at least 3.67 mm long. Parts of head and mouth preserved, frons, clypeus, mandible, labrum as well as the maxillary or labial palps visible.

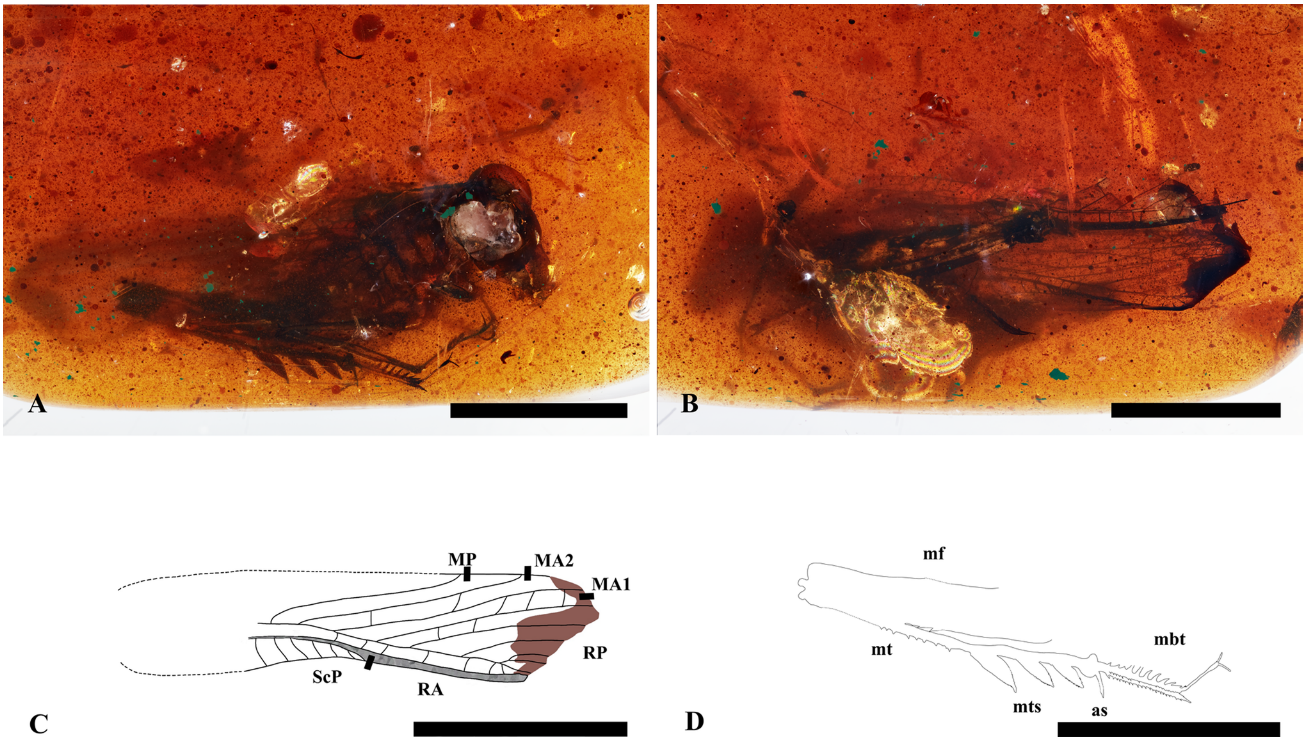

Fig. 1 *Elcanodentes alatus* gen. et sp. nov. holotype male GPIH 7016 **A** Right view of the specimen. **B** Left view of the specimen. **C** Interpretative drawing of the forewing. **D** Interpretative drawing of the specimens right metathoracic leg. as = apical spur; mbt = metabasitarsus; mf = metafemur; mt = metatibia; mts = metatibial spurs. *Scale bars:* 5 mm

Thorax. Pronotum saddle-shaped. Length 3.40 mm, height 2.8 mm. Shape similar to *Ellca nevelka* Kočárek, 2020, *Caelielca spinocrus* Uchida, 2022 and *Hukawnelca gracile* Uchida, 2022, shorter distally compared to the other species; covering wing bases.

Legs

Prothoracic leg. Leg slightly obscured, only outline of joints visible. Length 3.20 mm. Profemur, -tibia and -tarsus without denticles or hairs. Protarsus with one claw preserved.

Mesothoracic leg. Mesofemur 3.8 mm long. Mesotibia 4.2 mm long, ventrally covered with small denticles proximally and short hairs apically. Mesobasitarsus 1.5 mm long, making up more than 50% of total mesotarsal length (2.6 mm); ventrally with a row of prominent denticles and an apical oar-like lobe which features denticles or hairs too. Second tarsal segment very short. Third tarsal segment apically with two curved claws.

Metathoracic leg. Metafemur 7.6 mm long, featuring distinct dark blotches on its surface and a ring of prominent denticles on the connection to metatibia. Metatibia 7.1 mm long, proximal half with a row of small denticles, followed by the metatibial spurs which are leaf-like with very small teeth along the lateral margins apically. Three metatibial spurs present, ranging in size from 1.2 mm to 0.9 mm (proximal to apical); no paired spur visible. Metatibia ending in at least one prominent apical spine, pointing orthogonally away from the leg, 0.7 mm long. Metabasitarsus 2.1 mm long, with seven very prominent spines ventrally and two ridges of much thinner spines dorsally. Apically with at least two spine-like lobes, setulose. Rest of metatarsus unusually thin, 1.4 mm long, somewhat setulose with rather long hair and two not claw-like appendages at the end.

Abdomen. Ovipositor slender, ca. 2.8 mm long and saber-like, slightly S-curved. Two valvulae visible.

Remarks. The new species differs from all previously described genera of Elcanidae by its unique metatibial spur morphology, namely a row of tiny teeth along the lateral margins of the spurs. Based on this feature, a new genus *Elcanodentes* gen. nov. is erected. Because three other specimens of Elcanidae share the metatibial spur morphology of *E. alatus* gen. et sp. nov., which are described below and have their forewings more clearly visible, *Elcanodentes* belongs to the subfamily Elcaninae Handlirsch, 1906. It is placed in this taxon due to its 1A + CuPb + CuPaβ of the

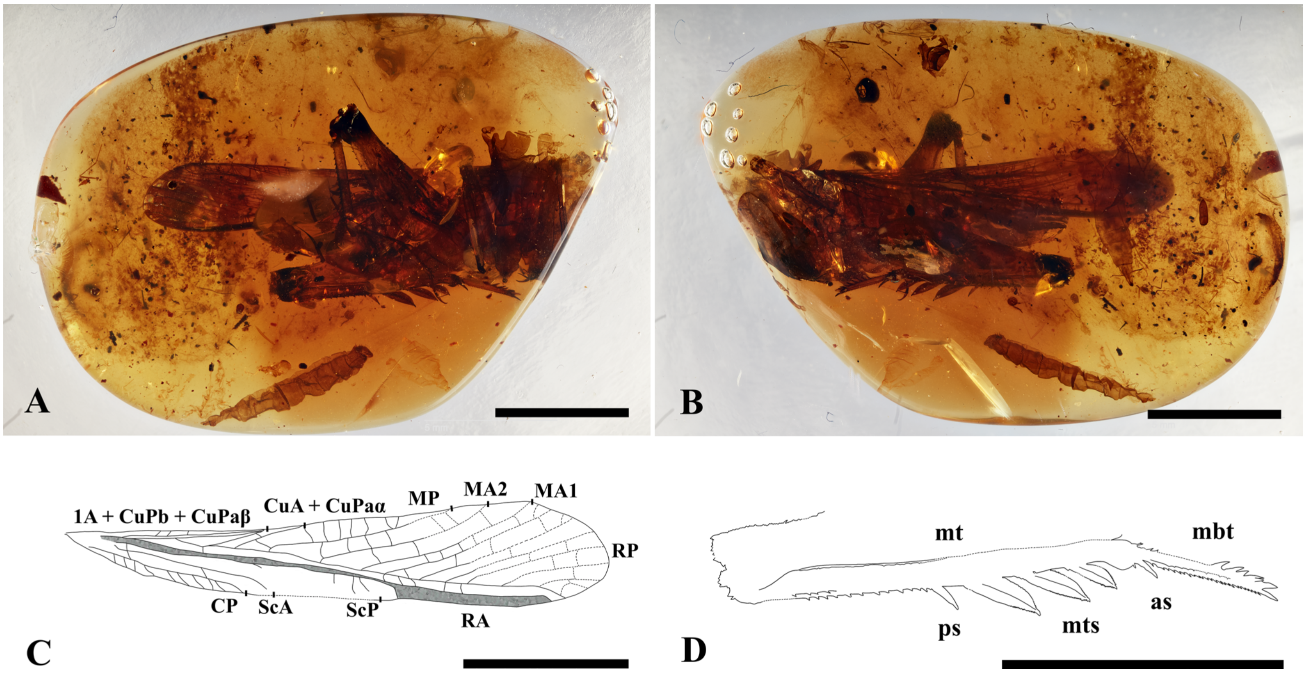

Fig. 2 *Elcanodentes cretaceus* gen. et sp. nov. holotype male GPIH 7017. **A** Right view of the specimen. **B** Left view of the specimen. **C** Interpretative drawing of the specimen's forewing. **D** Interpretative drawing of the specimens right metathoracic leg. *Abbreviations:* as = apical spur; mbt = metabasitarsus; mt = metatibia; mts = metatibial spurs; ps = proximal spur. *Scale bars:* 5 mm

forewing being fused. *Elcanodentes alatus* further differs from previously described species of Elcanidae in the unique shape of its forewing which is tapered towards the top distal part, a pterostigma which is very narrow and only makes up 2.5% of the entire forewing surface area and an ovipositor that is saber-shaped as so far only known from *Probaisselcana oculata* Hu & He, 2023.

Elcanodentes cretaceus sp. nov. Willmott, Schall, Kotthoff & Husemann.

Figures 2, 3

Zoobank-ID. urn:lsid:zoobank.org:act:75839869-164C-44F0-9B50-FA88FEBF4F41.

Etymology. The species name derives from the Latin word "cretaceus" meaning "Cretaceous", referring to the age of this species.

Locality and horizon. Specimens were included in separate amber pieces found in Hkamti, Sagaing Division, Myanmar or Tanai, Kachin State Burma, Myanmar, two nearby amber mining locations. Lowermost Cenomanian, middle Cretaceous, 98.8 ± 0.6 Ma.

Type material. Male holotype and female paratype (PT); deposited in the amber collection of Leibniz Institute for the Analysis of Biodiversity Change, Hamburg, Germany (holotype coll. no. GPIH 7017, ex. Collection Martin Husemann, Fossil 0049 and paratype GPIH 07208, ex. Collection Martin Husemann, Fossil_0010).

Diagnosis. Anal margin of forewing between CuA + CuPaα and MP estimated to make up ca. 1/3 of the total wing length. RP with seven branches. Pterostigma making up 4.4% of total wing surface. At least female forewing with at least one dark spot. Metatibial spurs leaf-like with small teeth along almost the entire length of lateral margins. Ovipositor sword-like, more than 6 mm long. Cerci with moveable hair-like appendage.

Description of Holotype GPIH 7017. Male. Preservation of a complete specimen with only the antennae missing; head region significantly damaged and hardly visible. Body-length approximately 11.25 mm (not including wings).

Forewing. Forewing length 13.7 mm. 1A + CuPb + CuPaβ fused. CuA + CuPaα very narrow. Anal margin between CuA + CuPaα and MP makes up about 33.5% of total wing length. M with three branches. All three branches of M between CuA + CuPaα and the stem of RP. Branches of M, especially MP, with numerous cross veins. RP with seven

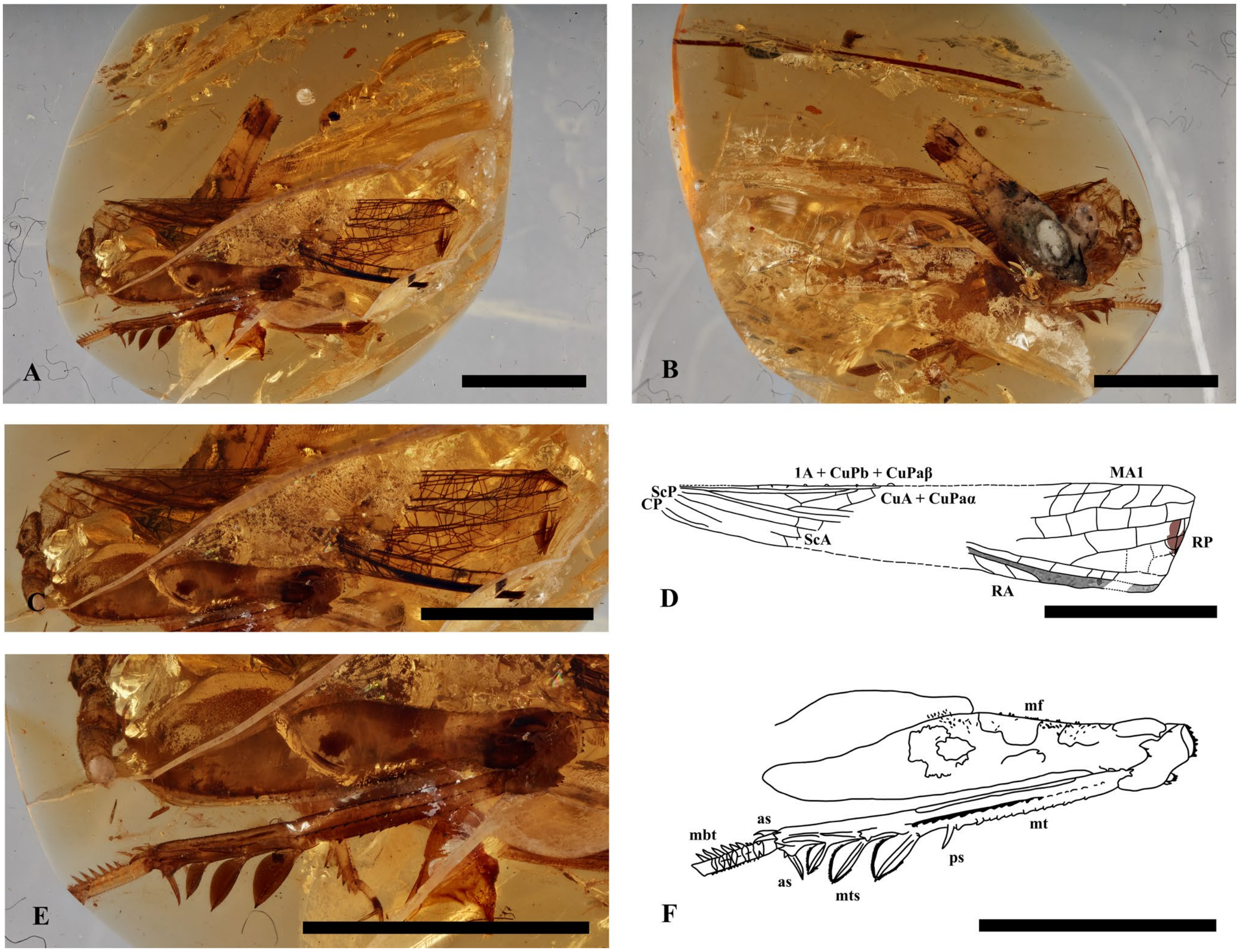

Fig. 3 *Elcanodentes cretaceus* gen. et sp. nov. paratype female GPIH 07208. **A** Left view of the specimen. **B** Right view of the specimen. **C** Close-up of the paratypes left forewing. **D** Interpretational drawing of C. **E** Close-up of the metathoracic leg. **F** Drawing of E. *Abbreviations:* as = apical spur; mbt = metabasitarsus; mf = metafemur; mt = metatibia; mts = metatibial spurs; ps = proximal spur. *Scale bars:* 5 mm

branches. ScP broad (5 times as broad as ScA). CP with numerous cross veins. Pterostigma without cross veins.

Pronotum. Only most posterior part visible. With an upwards slope of an about 30° angle. Setulose on dorsal surface.

Legs

Prothoracic leg. Profemur 3.7 mm long, ventrally with two rather prominent edges. At genicular joint rounded lobes with few small to medium spines. Protibia only proximal part preserved, with one rather sharp-looking dorsal ridge and few fine spines ventrally.

Mesothoracic leg. Mesofemur 3.8 mm long. Mesotibia 4.4 mm long. Very similar built to prothoracic extremity.

Metathoracic leg. Metafemur 7.5 mm long. Metafemur with short fine hair ventrally and several larger blotches of light to dark brown coloration (color pattern may deviate from live animal). Insertion of metatibia to metafemur with a crown of small dark spines, reminiscent in shape of the teeth of *Carcharodon* sharks, on the apical margin of metafemur. Metatibia 6.6 mm long, significantly less broad than metafemur. Various types of spines and spurs are located on the metatibia. Proximal half of metatibia occupied by two rows of previously mentioned shark teeth like spines, running parallelly. Distal half occupied by large metatibial spurs, with one proximal ensiform spur about half the size of main spurs (0.54 mm long). Main metatibial spurs leaf-like with small teeth running along the margin; teeth going deeper on the more convex side of spurs. Spine like stem of the spur clearly visible with a slightly darker tip at the top. Metatibial spurs are arranged in (probably) 3 pairs (however, for the most proximal spur only the toothed leaf like can be seen). Paired spurs are of significantly different structure, however, being ensiform and of different angular orientation, i.e. not erected at about a 60° angle to the leg as is the leaf like variation, but parallel to it and kept close to its side. These ensiform spurs do not feature teeth. In the holotype the ensiform spurs are erected as usual on one metatibia where the leaf-like spurs appear to have gone missing. On the opposing metatibia of the holotype the ensiform spurs are not visible, however, this might be due to their close orientation to the leg as seen in the paratype. Leaf-like metatibial spurs 1.2 mm/1.2 mm/0.7 mm (proximal to distal) long. Ensiform spurs 0.68 mm long. Metatibia apically with 3 (probably 4) spine like spurs which are again of different angular orientation. A larger one (0.54 mm) erected at almost a 90° angle from the leg and two slightly smaller, pointing downwards (0°). Metatarsus three-segmented with two claws (0.4 mm long) at the end. Metabasitarsus with beige colored stripes, short hair on the ventral and a row of at least six prominent spines on the dorsal side. Metabasitarsus apically with three visible spines arranged in a crown. Total length of metabasitarsus can only be assumed, as the full length can only be added together by the preserved/visible pieces of right and left metabasitarsus, but likely around 1.8 mm. Second metatarsal segment very short. Third metatarsal segment 0.77 mm long with a light colored proximal and a dark colored distal half.

Abdomen. Cerci 1.8 mm long, with long and evenly spaced hair across entire length and a hair-like tip of 0.6 mm.

Description of non-mentioned characters found in paratype GPIH 07208. Female. Preservation of forewing, metathoracic leg and ovipositor; forewing partly obscured in the medial region. Body length approximately 12.3 mm (not including wings).

Forewing. In the PT estimated 16.7 mm; distal part missing. Forewing of PT with one dark spot towards the distal margin of which only the most anterior part is preserved in the specimen.

Metathoracic leg. Metafemur 9 mm long. Metatibia 6.8 mm long. Proximal metatibial spur spine-like.

Abdomen. Ovipositor sword-like, broad and almost straight with just a subtle bend. Broken off at the tip, preserved part about 6 mm in length.

Remarks. The new species is placed in the genus *Elcanodentes* gen. nov. based on its wing venation features and the toothed lateral margins of the metatibial spurs. *Elcanodentes cretaceus* gen. et sp. nov. differs from the other two species of *Elcanodentes* in the relative size of the pronotum to total wing surface (*E. alatus* 2.5%, *E. cretaceus* 4.4%, *E. thanatos* 7.7%), the presence of at least one wing spot on the forewing of the female, and an ovipositor that is sword-shaped. The paratype female specimen of *E. cretaceus* is very similar to the male holotype, however, two features stand out as different. First, the forewing of the female shows part of a dark colored wing spot towards the distal part of the wing. Such a wing spot might be seen on the tegmen of the male too. Yet, as the amber which includes the female is much brighter in coloration than that which holds the male, it is far more conspicuous in the female. A definite difference between the holotype and the allotype is the metatibial spur proximal to the big leaf-like spurs. It is ensiform in the holotype, yet spine-like in the paratype. This variation could be due to sexual dimorphism in Elcanidae. It is also possible, that the two specimens are not from the same species. However, the similarities between holotype and female paratype are very apparent and suggest a very close affinity of the two. Maybe, future studies investigating sexual dimorphism in Elcanidae can shed light on this case and *E. cretaceus* will be revised.

Elcanodentes thanatos sp. nov. Schall, Willmott, Kotthoff & Husemann.

Figure 4

Zoobank-ID. urn:lsid:zoobank.org:act:696444C8-1975-45D8-AE0D-FE3F8649C7B8.

Etymology. The species name refers to the ancient Greek deity of death, Thanatos. It is based on the very prominent ovipositor of this species, remindful of a scythe's blade as commonly depicted on images of reapers.

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. Lowermost Cenomanian, middle Cretaceous, 98.8 ± 0.6 Ma.

Holotype. Adult female; deposited in the amber collection of Leibniz Institute for the Analysis of Biodiversity Change, Hamburg, Germany (coll. no. GPIH 7018, ex. Collection Martin Husemann, Fossil 0047).

Diagnosis. The species can be recognized by its forewing without wing spots and a prominent pterostigma without cross veins. 1A + CuPb + CuPaβ are fused and CuA + CuPaα is narrow. 3 branches of M between CuA + CuPaα and the

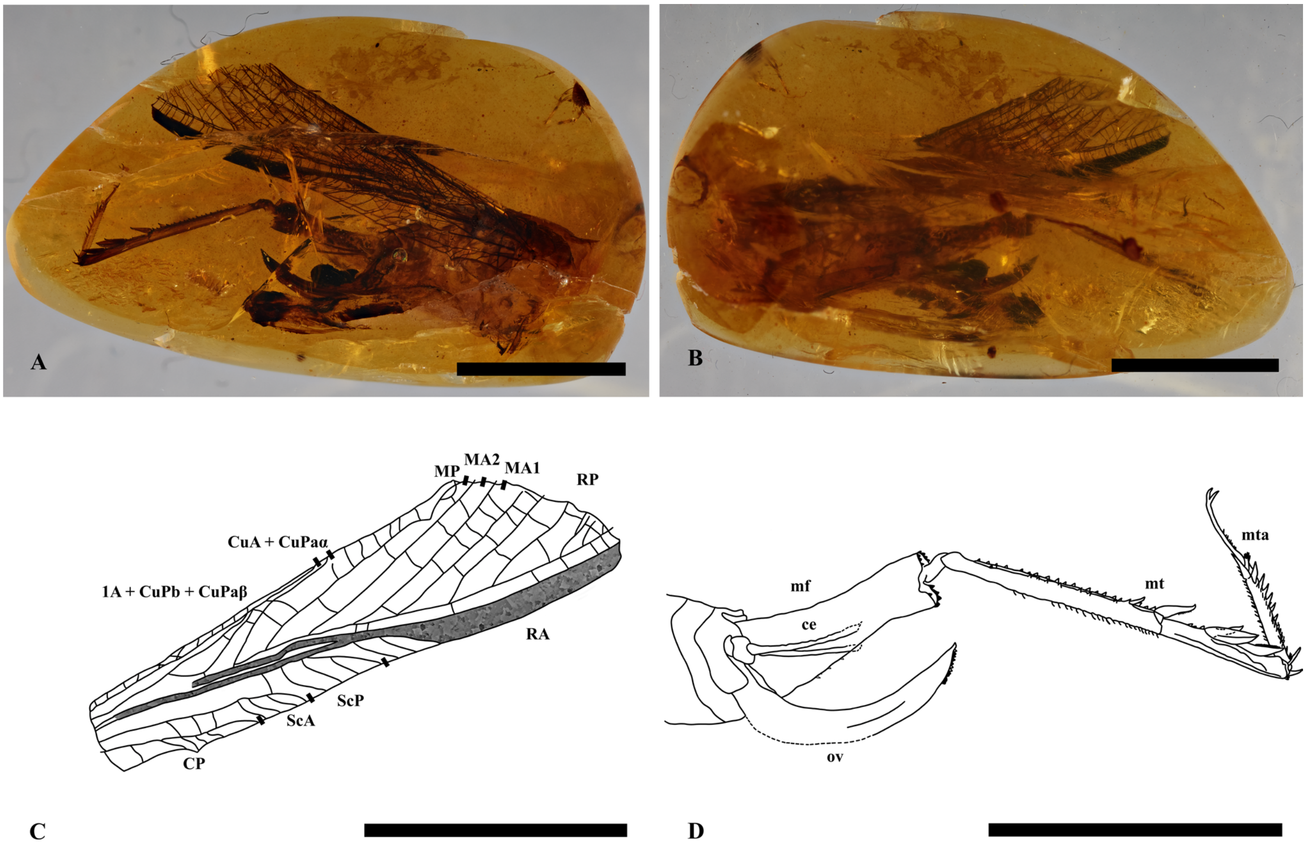

Fig. 4 *Elcanodentes thanatos* holotype female GPIH 7018. **A** Right view of the specimen. **B** Left view of the specimen. **C** Interpretational drawing of the preserved right forewing. **D** Interpretational drawing of metathoracic leg and abdominal region with scythe-like ovipositor. *Abbreviations:* ce = cercus; mf = metafemur; mt = metatibia; mta = metatarsus; ov = ovipositor. *Scale bars:* 5 mm

stem of RP. Metatibial spurs are a combination of short ensiform and toothed leaf-like. The ovipositor is prominent, broad and scythe blade-shaped with a row of ventral teeth apically.

Description. Female. Posterior part of pronotum up to abdomen including ovipositor, forewing and metathoracic leg preserved.

Forewing. Forewing well preserved, except for most distal part. Preserved wing length 10.5 mm. 1A + CuPb + CuPaβ fused. CuA + CuPaα narrow. 3 longitudinal branches between the stem of RP and CuA + CuPaα. Length of anal margin between CuA + CuPaα and MP making up 26.5% of total reconstructed wing length. ScP relatively broad. ScP, ScA and CP all sporting numerous cross veins. Pterostigma long and broad without cross veins. Preserved length (most distal part missing) 4 mm. No wing spots present.

Pronotum. Pronotum relatively long, covering wing base, saddle-shaped and with rather high lateral margins. Posterior end triangularly pointed. Small hairs can be seen on the surface.

Metathoracic leg. Metafemur 4.86 mm long. Setulose and with a couple of small teeth-like denticles ventrally. Surface probably light in coloration with dark blotches, one big and in prominent position. Joint to metatibia looks like an opened can with the metatibia inserted and the apical margin with a ring of several, evenly spaced dark denticles. Apical end of metafemur 0.9 mm high whereas beginning of metatibia is much shorter, 0.27 mm. Metatibia long and slender, 6.5 mm long. First part up to metatibial spurs ventrally with equally spaced hairs, dorsally with two rows of darkly colored denticles (similar to those on apical margin of metafemur). Between fourth and third to last of those denticles small ensiform spur about the double the size of denticles, yet significantly smaller than main metatibial spurs. Main metatibial spurs bimorph; supposedly one short ensiform spur paired with one toothed leaf-like spur (a row of very small denticles along the outer margin). However, this coupling is only visible/preserved for the middle pair. Main spurs ranging from 0.7 mm to 0.88 mm in length with ensiform spurs ca. of same length as toothed leaf-like ones (in other Elcanidae, e.g. *Panorpidium longirostris* (Peñalver & Grimaldi, 2010), the ensiform spurs are relatively much longer). At least two apical spines are visible at the joint of metatarsus to metatibia, both slender and pointed, 0.23–0.33 mm long. Metatarsus three-segmented. Metabasitarsus 1.8 mm long with short, but rather thick evenly spaced hairs on ventral and two rows of equally shaped hairs dorsally. Hairs of one row are replaced before reaching half the length of basitarsus by rather prominent spines of around 0.14 mm in length. At least three apical spines on transition to second tarsal segment, slightly longer than previous spines. Second tarsal segment bears a setulose elongated lobe about the same length as apical spines of basitarsus. Third tarsal segment 1.3 mm long including two curved claws forming the foot. Dorsally with two rows of either very distinct hairs or very fine spines.

Abdomen. About 10 tergites visible (however, partly obscured anteriorly by forewing so exact number unsure). Cerci 1.7 mm long, unsegmented and possibly featuring a hair like tip (obscured). Ovipositor very prominent, scythe-shaped, 3.6 mm long (not factoring in the curve) and about 0.55 mm broad at highest point. A row of 11–12 very small denticles are featured towards the tip.

Remarks. The new species is placed in the genus *Elcanodentes* gen. nov. based on its wing venation features and the toothed lateral margins of the metatibial spurs. It differs from the previously described *E. alatus* gen. et sp. nov. and *E. cretaceus* gen et. sp. nov. in a forewing showing no coloring (i.e. neither wing spots nor darkened margin), a unique combination of leaf-like and short ensiform metatibial spurs and a broad scythe-shaped ovipositor.

Genus ***Pseudopanorpidium*** gen. nov. Schall, Willmott, Kotthoff & Husemann.

Type species. Pseudopanorpidium maculosum (Zhou et al., 2022).

Zoobank-ID. urn:lsid:zoobank.org:act:B9B34509-6F98-4A32-B722-5011F06862CA.

Etymology. The generic name refers to the close resemblance of this genus to the wing venation of *Panorpidium* Westwood, 1854.

Diagnosis. The genus can be recognized by a forewing venation similar to *Panorpidium* Westwood, 1854, however, with an anal wing margin between CuA + CuPaα and MP being significantly longer than in *Panorpidium*. In species of *Panorpidium* the mean value for this character is ca. 9% of the total forewing length. In *Pseudopanorpidium maculosum* it is 20% (Fig. 5A).

Remarks. The genus is assigned to the subfamily Elcaninae Handlisch, 1906 based on the fusion of 1A + CuPb + CuPaβ as well as the space between RA and RP being rather narrow. It differs from other genera of Elcaninae *Probaisselcana* Gorochov, 1989, *Minelcana* Gorochov et al., 2006 and *Ellca* Kočárek, 2020 by featuring three branches of M between CuA + CuPaα and the stem of RP instead of two. It differs from *Elcanodentes* gen. nov., by having a pterostigma with cross veins. It differs from *Panorpidium* by having its anal margin of the forewing between CuA + CuPaα and MP much longer.

Genus ***Pseudoprobaisselcana*** gen. nov. Schall, Willmott, Kotthoff & Husemann.

Type species. Pseudoprobaisselcana oculata (Hu & He, 2023).

Zoobank-ID. urn:lsid:zoobank.org:act:6A858EE2-F553-4038-9E67-45588EF76A87.

Etymology. The generic name refers to the close resemblance of this genus to the wing venation of *Probaisselcana* Gorochov, 1989.

Diagnosis. The genus can be recognized by a forewing venation similar to *Probaisselcana* Gorochov, 1989, however, with an anal wing margin between CuA + CuPaα and MP being significantly longer than in *Probaisselcana*. In species of *Probaisselcana* the mean value for this character is ca. 11% of the total forewing length. In *Pseudoprobaisselcana oculata* it is 21% (Fig. 5B). It is further characterized by a derived wing coloration consisting of two wing spots and a colored wing margin.

Remarks. The genus is assigned to the subfamily Elcaninae Handlisch, 1906 based on the fusion of 1A + CuPb + CuPaβ as well as the space between RA and RP being rather narrow. It differs from other genera of Elcaninae *Panorpidium* Westwood, 1854 and *Elcanodentes* gen. nov., by featuring two branches of M between CuA + CuPaα and the stem of RP instead of three. It differs from *Ellca* Kočárek, 2020 by having a pterostigma with cross veins. It differs from *Probaisselcana* Gorochov et al., 1989 by having its anal margin of the forewing between CuA + CuPaα and MP much longer and from *Probaisselcana zhengi* Gu et al., 2022 due to the cross veins in its pterostigma; *P. zhengi* does not have cross veins in that wing cell and will have to be revised in a future publication. Lastly, it differs from *Minelcana* Gorochov et al., 2006 by its pattern of wing coloration. The tegmen of *M. membranacea* Gorochov et al., 2006 shows coloration typical for members of Jurassic Elcanidae, an irregular pattern of darker and lighter areas. *Pseudoprobaisselcana* instead exhibits the possibly more derived coloration found in many species of Cretaceous Elcanidae, two dark wing spots and a darkened wing margin.

Comment on the subfamily placement

Based on the free tegminal veins 1A, CuPb and CuPaβ correctly recognized by the author, it seems more conclusive to place *Hukawnelca gracile* and *Caelielca spinocrus* in the subfamily Archelcaninae Gorochov et al., 2006. This makes them the first members of this subfamily reported from Kachin amber.

Discussion

In this study we report three new species of Burmese amber Elcanidae from the new genus *Elcanodentes*. *Hukawnelca gracile* and *Caelielca spinocrus* both Uchida, 2022 as well as *Panorpidium maculosum* Zhou et al., 2022 and *Probaisselcana oculata* Hu & He, 2023 are taxonomically revised. Based on the reported findings, a new hypothesis regarding the geographic origin of the Burma Terrane (BT) Elcanidae is proposed. Further, the diversity of ovipositors in Elcanidae is discussed, as every ovipositor type currently known in the family is represented by one of the new *Elcanodentes*-species.

In part 1 of the discussion one yet undescribed specimen of Elcanidae from Burmese-amber is mentioned: Elcanidae spec. 1. A description of this species is currently under review and will hopefully be published soon.

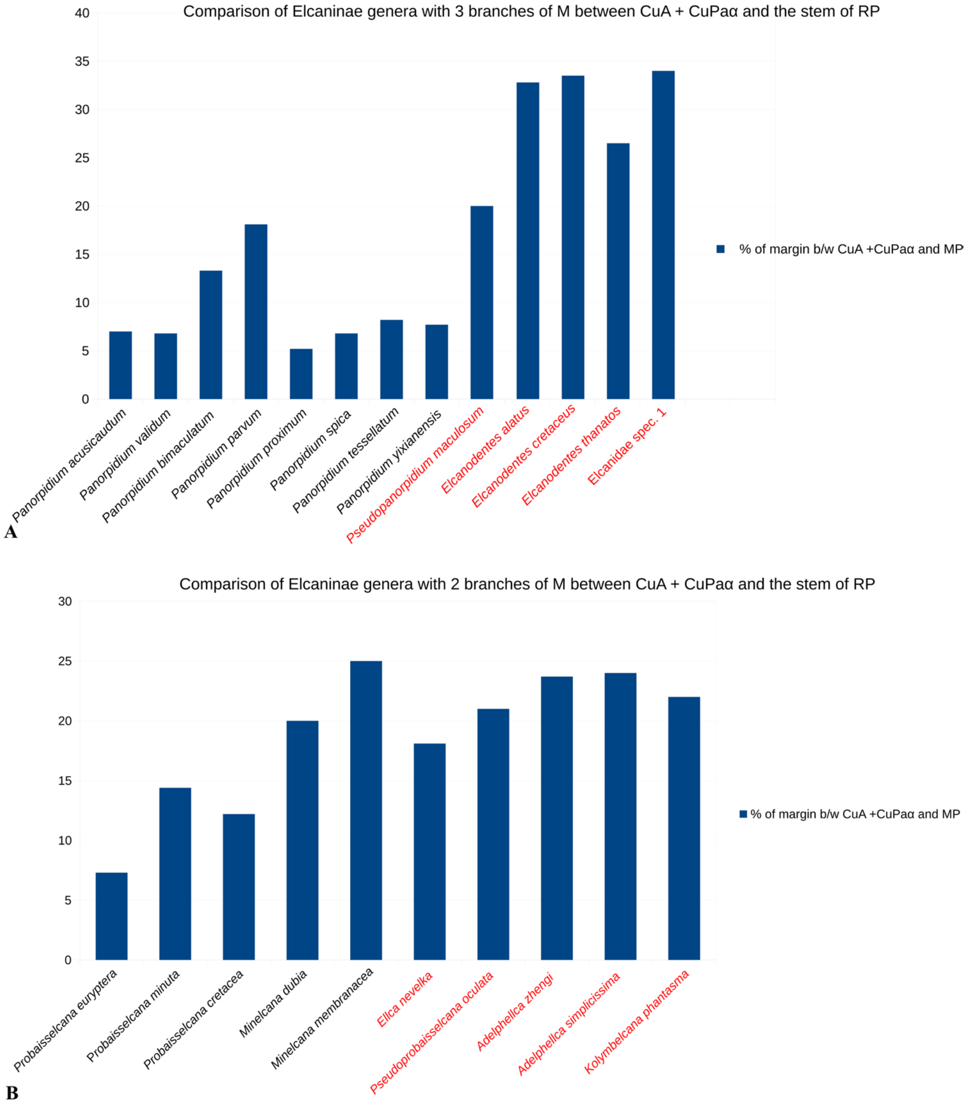

Fig. 5 **A** % of anal margin length of the forewing of the total wing length in several well-known Elcaninae Handlirsch, 1906 species with three branches of M between CuA + CuPaα and the stem of RP. Red species names indicate a Burma Terrane origin. Species from the Burma Terrane have a relatively much longer anal margin between CuA + CuPaα and MP than species from elsewhere. **B** % of anal margin length of the forewing of the total wing length in several well-known Elcaninae species with two branches of M between CuA + CuPaα and the stem of RP. Red species names indicate a Burma Terrane origin. Species from the Burma Terrane have a relatively much longer anal margin between CuA + CuPaα and MP than species from elsewhere

Anal margin length of the forewing between CuA + CuPaα and MP—a new characterising feature of Burmese amber Elcanidae

Figure 5

The three new species of *Elcanodentes* gen. nov. described in this study have revealed an important new characteristic of Burmese amber Elcanidae which is featured in most species known from this origin: a relatively much longer anal margin of the forewing between CuA + CuPaα and MP. Measurements of this character were taken for several known species of Elcanidae both from Burmese material as well as other regions. Figure 5A shows the relative length of the anal margin in Elcaninae Handlirsch, 1906 species with three branches of M between CuA + CuPaα and the stem of RP, such as *Panorpidium* Westwood, 1854 and *Elcanodentes* gen. nov. In this assemblage the species with the shortest relative margin is *Panorpidium proximum* Gorochov et al., 2006 from Southern England, where the length between CuA + CuPaα and MP only makes up 5.2% of the entire wing length. The longest relative margin has a currently undescribed species of Elcanidae from Burmese amber, Elcanidae sp. 1 (a description of this specimen is currently under review), with 34%. The range for Burmese amber species is 20–34% and 5.2–18.1% for species from other regions. The mean value for Burmese amber species is 29% and only 9% for other regions. Figure 5B shows the same as before, except here the species included feature two branches of M between CuA + CuPaα and the stem of RP which comprises representatives of *Probaisselcana* Gorochov, 1989, *Minelcana* Gorochov et al., 2006, *Ellca* Kočárek, 2020, *Adelphellca* Schall et al., 2025 and *Kolymbelcana* Schall et al., 2025. Here, the difference in anal margin length is not as significant. The species with the lowest value (i e. the shortest relative margin) is *Probaisselcana euryptera* Tian et al., 2019a, 2019b (7.3%). The highest value has *Minelcana membranacea* Gorochov et al., 2006 (25%). The range for Burmese amber species is 18.1–24% and 7.3–25% for species from other regions with a mean value of 22% and 16%, respectively. It should be noticed however, that the high average value of the non-Burmese amber species has a strong bias due to the two members of *Minelcana* Gorochov et al., 2006 of which a long margin between CuA + CuPaα and MP is the defining character for the genus. The three species of *Probaisselcana* included in the analysis only have a mean value of 11%. Generally speaking, species from Burmese amber have a much longer anal margin between CuA + CuPaα and MP than their counterparts from other regions. Based on this new finding we propose that former species of *Panorpidium* and *Probaisselcana* from Burmese amber should be placed into separate genera. We suggest that *Panorpidium maculosum* Zhou et al., 2022 should be placed into *Pseudopanorpidium* gen. nov. Similarly, *Probaisselcana oculata* Hu & He, 2023 ought to be placed into *Pseudoprobaisselcana* gen. nov.

Geographic origin of Burmese amber Elcanidae

The proportionally much longer tegminal margin between CuA + CuPaα and MP of some Burmese amber Elcanidae in comparison with most mainland members of the family raises questions regarding the phylogenetic affiliations of the BT Elcanidae and their geographic origin. Westerweel et al. (2019) proposed the BT was an isolated island in the Tethys during the formation of the amber that had travelled along with Greater India from Gondwana and would have collided with South-East Asia during the Early Paleogene. Bolotov et al. (2022) suggested that Greater India and the BT served as a”biotic ferry” for Gondwanan fauna based on findings of freshwater mussels. Zessin (1987) and Ansorge (2003) pointed out the potential use of the metatibial spurs of Elcanidae for resting periods on the water during long distance travel overseas (this was suggested for the Central European Jurassic Elcanidae). Therefore, the BT Elcanidae may have originated on Gondwana or have reached the island via long distance dispersal from Laurasia. The elongated tegminal margin between CuA + CuPaα and MP of Burmese amber Elcanidae suggests the former option as more likely, as most Laurasian Elcanidae do not share this character. On the other hand, the three species of *Cratoelcana* Martins-Neto, 1991, which are the only Gondwanan Elcanidae known so far, seem to all show similar tegminal morphology (MP called “CuP” in Martins-Neto, 1991, Fig. 2–32D) (Martins-Neto, 1991; Nel & Jouault, 2022). Unfortunately, knowledge of the Crato-Elcanidae is rather limited and the venation patterns can be hard to interpret due to overlapping fore- and hindwings (which is why they were not included in the comparison above). Of course, a descent of BT Elcanidae from *Minelcana* Gorochov et al., 2006 cannot be ruled out either, but this appears less likely as *Minelcana* was only found in Great Britain, whereas Elcanidae from Asia such as *Panorpidium acusicaudum* (Tian et al., 2022) or *Probaisselcana euryptera* (Tian et al., 2019a, 2019b) that are putatively much more likely candidates for a Laurasian invasion of the BT did not have an elongated margin. The description of additional material from the Crato-Formation will show whether this type of tegminal morphology is common amongst Gondwanan Elcanidae and answer the question of geographical origin of the Burmese-amber species.

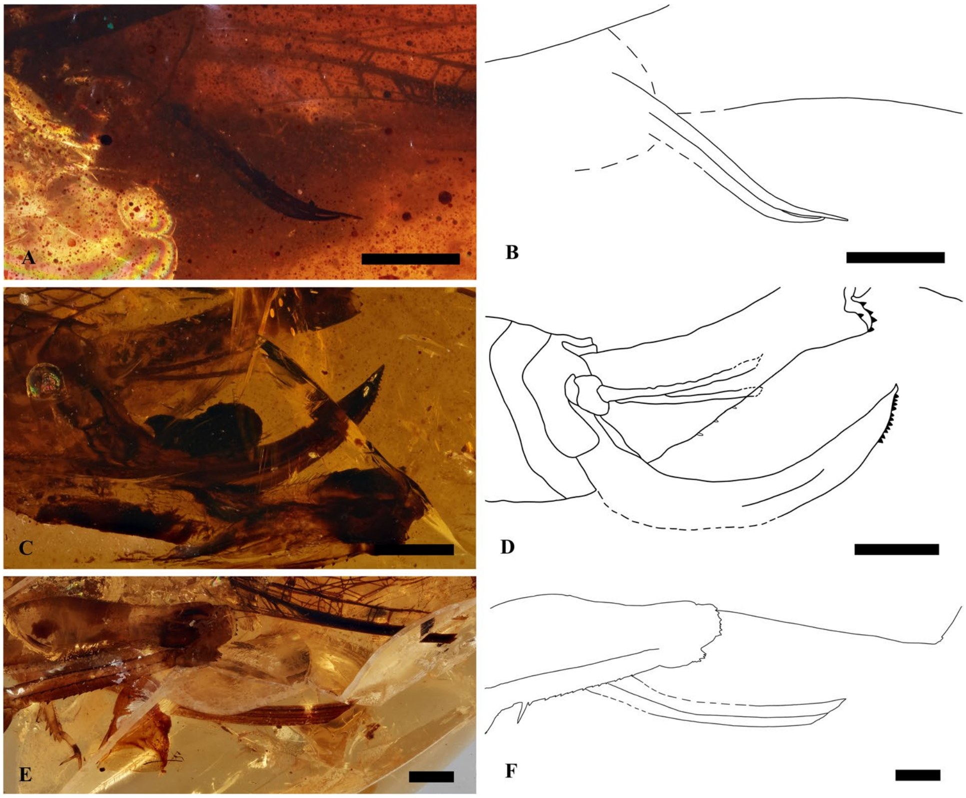

Fig. 6 Ovipositor types found in Elcanidae. **A** Saber ovipositor of *Elcanodentes alatus* gen. et sp. nov. This type is characterised by being short and slightly S-curved. **B** Scythe ovipositor of *E. thanatos* gen. et sp. nov. This type is broader, slightly longer than the saber and curved like a scythe-blade. **C** Sword ovipositor of *E. cretaceus* Coll_MH_0010 gen. et sp. nov. This type is long and almost straight, sometimes exhibiting a slight curve however, much less than the scythe

Ovipositor morphology in Elcanidae

Of the 78 species of Elcanidae known to date (Cigliano et al., 2024; this study) the ovipositor is known of only 19 species (Table 1). The type of ovipositor is associated with the site of oviposition in Orthoptera (e.g. Turner, 1916). Accordingly, based on the different ovipositors of the 19 species, hypotheses can be made regarding possible oviposition sites used by Elcanidae. The typeQuery of ovipositor most common in the 19 species is a long and straight structure which can sometimes be slightly curved and most closely resembles the appearance of a two-edged sword. It is found in *Elcanodentes cretaceus* gen. et sp. nov. (Fig. 6C), *Cratoelcana damianii* Martins-Neto, 1991, *C. zessini* Martins-Neto, 1991, *Kolymbelcana phantasma* Schall et al., 2025, *Letoelcana artemisapollonque* Schall et al., 2024, *Panorpidium acusicaudum* Tian et al., 2019a, 2019b, *P. lithophilum* (Germar, 1842), *P. magnum* (Handlirsch, 1906), *P. minimum* (Handlirsch, 1906), *P. spica* Kim et al., 2021, *P. validum* Tian et al., 2022, *Probaisselcana euryptera* Tian et al., 2019a, 2019b and *P. minuta* Gu et al., 2022. This means ca. 68% of the species with a known type of ovipositor had a sword-type (Table 1). A long and rather straight ovipositor is usually associated with an oviposition in soil as exhibited for example by the Tettigoniid *Monocerophora longispina* (Burmeister, 1838) (Barbosa & Fianco, 2024). Additionally, egg laying in grass stalks is known from katydids with a sword ovipositor, too, such as *Conocephalus fuscus* (Fabricius, 1793) (Fischer et al., 2016). The second most common type of ovipositor in Elcanidae, shared by four species, is the scythe. This one, most impressively seen in *Elcanodentes thanatos* gen. et sp. nov. (Fig. 6B), is shorter than the sword and much more curved, similar to the blade of a scythe. This type is also found in *Ellca nevelka* Kočárek, 2020, *Adelphellca zhengi* (Gu et al., 2022) and *Sinoelcana minuta* Gu et al., 2020. A scythe-like ovipositor is used for oviposition in the pith of stems with a modern-day example being *Eriolus acutipennis* Saussure & Pictet, 1898 (Barbosa & Fianco, 2024). The rarest type of ovipositor to date is the saber found in *Elcanodentes alatus* gen. et sp. nov. (Fig. 6A) and *Pseudoprobaisselcana oculata* (Hu & He, 2023). This one is the shortest of all types, much thinner than sword and scythe and slightly S-curved. It is unclear to what oviposition site this type of ovipositor relates to, as to our knowledge no species of modern-day Orthoptera is known to exhibit such a saber-shaped ovipositor as seen in

Table 1 Known ovipositor types of Elcanidae

Sword	Scythe	Saber
Elcanodentes cretaceus gen. et sp. nov.	*Elcanodentes thanatos* sp. nov.	*Elcanodentes alatus* sp. nov.
Cratoelcana damianii Martins-Neto, 1991	*Ellca nevelka* Kočárek, 2020	*Pseudoprobaisselcana oculata* (Hu & He, 2023)
Cratoelcana zessini Martins-Neto, 1991	*Adelphellca zhengi* (Gu et al., 2022)	
Kolymbelcana phantasma Schall et al., 2025	*Sinoelcana minuta* Gu et al., 2020	
Letoelcana artemisapollonque Schall et al., 2024		
Panorpidium acusicaudum Tian et al., 2022		
Panorpidium lithophilum (Germar, 1842)		
Panorpidium minimum (Handlirsch, 1906)		
Panorpidium spica Kim et al., 2021		
Panorpidium validum Tian et al., 2022		
Probaisselcana euryptera Tian et al., 2019a, 2019b		
Probaisselcana minuta Gu et al., 2022		
Panorpidium magnum (Handlirsch, 1906)		

E. alatus and *P. oculata*. It is possible the 'saber ovipositor' is related to those depicted in Figs. 4A or 5A in Barbosa and Fianco (2024) as it bears some resemblance to both. If so, it could be either associated with an oviposition in soil or the pith of stems (Barbosa & Fianco, 2024). However, maybe these Elcanidae species had an oviposition site not occupied by any extant members of Orthoptera.

Except for *Sinoelcana minuta* from the Middle Jurassic of China, all Elcanidae species with a scythe or saber ovipositor have been found in Burmese amber (and are thus of Cretaceous age). On the other hand, a sword-like ovipositor has been found in Elcanidae from Burmese amber, Brazil, China, Korea and Germany and corresponding species are of Cretaceous and Jurassic age (*Panorpidium lithophilum, P. magnum* and *P. minimum* are Jurassic) (Kim et al., 2021; Martins-Neto, 1991; Tian et al., 2022; Zessin, 1987). This suggests the sword type to have been the ancestral state of ovipositor morphology in Elcanidae and it further underlines the peculiar diversity of the Burmese amber species.

Conclusions

A new genus with three new species of Elcaninae Handlirsch, 1906 from Burmese amber is described: *Elcanodentes alatus, E. cretaceus* (including a male holotype as well as female paratype) and *E. thanatos*. The new genus has a wing venation similar to *Panorpidium* Westwood, 1854. However, it differs from the latter by featuring a pterostigma without cross veins, a much longer anal margin of the forewing between CuA + CuPaα and MP as well as lateral margins of the metatibial spurs with a row of small teeth. An anal margin between CuA + CuPaα and MP that makes up more than 18% of the total wing length is suggested as a defining character for Burmese amber Elcanidae. Based on this character, former *Panorpidium maculosum* (Zhou et al., 2022) and *Probaisselcana oculata* (Hu & He, 2023) are placed in new genera, *Pseudopanorpidium* gen. nov. and *Pseudoprobaisselcana* gen. nov.

Hukawnelca gracile Uchida, 2022 and *Caelielca spinocrus* Uchida, 2022 are moved to the Archelcaninae. The presence of the longer anal margin led to the suggestion that Burmese-amber Elcanidae have originated from Gondwana. Burma Terrane Elcanidae also feature a greater diversity of ovipositor types than genera from any other region. Three types of ovipositors are known in Elcanidae: the sword (long and rather straight; most common type found in Elcanidae species from all regions), the scythe (medium length, distinctly curved and rather broad; found only in Burmese amber Elcanidae and *Sinoelcana minuta* Gu et al., 2020) and the saber (short, thin and slightly S-curved; the rarest type, known only from two species from Burmese amber, *Pseudoprobaisselcana oculata* (Hu & He, 2023) and *Elcanodentes alatus* gen. et sp. nov.). The greater ovipositor diversity of Burmese amber Elcanidae suggests an adaptation to more habitat types of this family on the Burma Terrane and further highlights the numerous forms that were present in this exceptional ecosystem. The publication of four additional Elcanidae specimens currently in progress by us is going to shed new light on possible aspects of the family's ecology.

Table 2 Genera and species of Burmese amber Elcanidae with respect to the findings of this study

Subfamily	Species	Pronotum	Wing spots	Wing venation	Metatibial spurs	Publication
Elcaninae	*Panorpidium longirostris*	Posterio-lateral margin flat and straight	?	?	Ensiform	Peñalver & Grimaldi, 2010
	Panorpidium sp.	?	?	?	Ensiform	Fang et al., 2015
	Ellca nevelka	Postero lateral margin convexely curved	None	2 Branches of M between CuA + CuPaα and stem of RP; margin between CuA + CuPaα and MP 18.1%; pterostigma without cross veins	Spine-like with hairs	Kočárek, 2020
	Pseudopanorpidium maculosum	Postero lateral margin convexely curved	Two	3 Branches of M between CuA + CuPaα and stem of RP; margin between CuA + CuPaα and MP 20%; pterostigma with cross veins	Leaf-like	Zhou et al., 2022
	Adelphellca zhengi	Postero lateral margin convexely curved	None	2 Branches of M between CuA + CuPaα and stem of RP; margin between CuA + CuPaα and MP 23.7%; pterostigma without cross veins	?	Gu et al., 2022
	Adelphellca simplicissima	?	None	2 Branches of M between CuA + CuPaα and stem of RP; margin between CuA + CuPaα and MP 24%; pterostigma without cross veins	Leaf-like	Schall et al., 2025
	Kolymbelcana phantasma	?	Two	2 Branches of M between CuA + CuPaα and stem of RP; margin between CuA + CuPaα and MP 22%; pterostigma without cross veins	Leaf-like	Schall et al., 2025
	Pseudoprobaisselcana oculata	Posterolateral margin with straight decline (convex curve only very subtle)	Two	2 Branches of M between CuA + CuPaα and stem of RP; margin between CuA + CuPaα and MP 21%; pterostigma with cross veins	Leaf-like	Hu & He, 2023
	Elcanodentes alatus	Postero lateral margin convexely curved (curvature less pronounced)	None	3 Branches of M between CuA + CuPaα and stem of RP; margin between CuA + CuPaα and MP 32.8%; pterostigma without cross veins	Leaf-like with toothed margins	Herein
	Elcanodentes cretaceus	?	One?	3 Branches of M between CuA + CuPaα and stem of RP; margin between CuA + CuPaα and MP 33.5%; pterostigma without cross veins	Leaf-like with toothed margins	Herein

Table 2 (continued)

Subfamily	Species	Pronotum	Wing spots	Wing venation	Metatibial spurs	Publication
	Elcanodentes thanatos	?	None	3 Branches of M between CuA + CuPaα and stem of RP; margin between CuA + CuPaα and MP 26.5%; pterostigma without cross veins	Leaf-like with toothed margins + short ensiform	Herein
Archelcaninae	*Hukawnelca gracile*	Postero lateral margin convexely curved	Two	2 Branches of M between CuA + CuPaα and stem of RP; margin between CuA + CuPaα and MP 25.8%; pterostigma with cross veins	Leaf-like	Uchida, 2022
	Caelielca spinocrus	Postero lateral margin convexely curved	None	2 Branches of M between CuA + CuPaα and stem of RP; margin between CuA + CuPaα and MP 32.1%; pterostigma with cross veins	Leaf-like	Uchida, 2022
Incertae sedis	*Longioculus burmensis*	Uncertain; perhaps with very slight convex curve of posterolateral margin	None	Unsure; possibly 3 branches of M between CuA + CuPaα and stem of RP; margin between CuA + CuPaα and MP ca. 31%; pterostigma with cross veins	?	Poinar et al., 2007
	Elcanonympha diana	Posterolateral margin with straight decline	?	?	Ensiform	Heads and Thomas, 2018
	Monitelcana penalveri	Posterolateral margin with straight decline	?	?	Spine-like with hairs	Xu et al., 2022
	Letoelcana artemisapollonque	Posterolateral margin with straight decline	Two	Pterostigma without cross veins	Leaf-like	Schall et al., 2024
	Paraxelcana coronakanthodis	Postero lateral margin convexely curved	None	Margin between CuA + CuPaα and MP 29.8%; pterostigma without cross veins	Leaf-like	Schall et al., 2024
	Trigonelca jennywinterae	Postero lateral margin convexely curved	None	Pterostigma without cross veins	Ensiform	Schall et al., 2024

One can only imagine what more spectacular findings the amber forest of Myanmar will unearth in the future.

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Data availability All data presented in this study can be found in the text and figures of the present or referenced papers.

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