The first Cheliferidae (Pseudoscorpiones: Cheliferoidea) from mid-Cretaceous Kachin amber

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Abstract

Pseudoscorpiones are a group of small to medium-sized arachnids under the species-rich Chelicerata. They are found in many terrestrial habitats, normally cryptic, including leaf litter and soil, under tree bark or rocks. The fossil record of pseudoscorpiones is mainly composed of species belonging to extinct genera in extant families, with a small number of taxa described from the famous Kachin amber, sometimes referred to as Burmese amber or Burmite (12 species in six families). Here, we describe a well-preserved male specimen of pseudoscorpion from mid-Cretaceous Kachin amber, representing the first fossil record of Cheliferidae from Burmese amber. This new taxon, *Echinochelifer curvatus* gen. et sp. nov., is characterized by elongate tubercle-bearing pedipalps and several trichobothrial features. Based on these, we discuss the systematic placement and palaeoecological implications of the new taxon in Burmese amber.

Keywords: Arachnida; False scorpions; New taxon; Palaeoecology; Taxonomy

1 Introduction

Pseudoscorpiones, a speciose order of small to medium-sized arachnids, are normally referred to as 'false scorpions 'due to their superficial resemblance to true scorpions, and despite their relatively smaller size (Harms & Dunlop, 2017). Unlike true scorpions, pseudoscorpions lack both a sting and a tail-like metasoma (e.g., Geißler et al., 2022). Over 4,384 species of pseudoscorpions are known worldwide, classified into 27 families and 497 genera (World Pseudoscorpiones Catalog, 2024), inhabiting various terrestrial environments, such as leaf litter and soil, under tree bark and rocks (Weygoldt, 1969; Harvey & Muchmore, 2013). Some taxa have evolved complex social behaviour, such as the construction of silken, multi-chambered nests (with moulting within these chambers), raising young, and exhibiting a basic division of labour (Chapin et al., 2022); for example, *Paratemnoides elongatus* (Banks, 1895) is known for its co-operative spinning and synchronised moulting.

Pseudoscorpions are among the oldest groups of terrestrial arthropods, with their fossil record dating back approximately 390 million years (Shear et al., 1989; Schawaller et al., 1991). *Dracochela deprehendor* Schawaller, Shear & Bonamo, 1991, found in the Middle Devonian, represents the stem-group of the order, which also suggests that pseudoscorpions have been integral components of terrestrial ecosystems since at least the Middle Devonian. However, pseudoscorpions are conspicuously absent from other Palaeozoic deposits. It was not until the Mesozoic Era onwards that the fossil record of pseudoscorpions improves, and records become increasingly diverse and abundant (Harms & Dunlop, 2017). The oldest Mesozoic pseudoscorpion originates from the Upper Triassic of Eastern Europe and was placed in the extant family Feaellidae, but in the extinct subfamily Archaeofeaellinae (Kolesnikov et al., 2022; Johnson et al., 2023: fig. 1).

Amber deposits provide critical insights into pseudoscorpion evolution. The Mesozoic era, particularly the Cretaceous Period, was marked by an important phase in the fossil record of pseudoscorpions with a great increase in the number of specimens and taxa (Novák et al., 2024). This coincided with the extensive production of fossiliferous resin, now dubbed the Cretaceous Resinous Interval (Delclòs et al., 2023), combined with other major geological events, such as the Cretaceous Terrestrial Revolution (KTR) and the Angiospermous Terrestrial Revolution (ATR) (Lloyd et al., 2008; Benton et al., 2022). Therefore, the majority of the Mesozoic fossils have been documented from Cretaceous amber deposits (e.g., Harms and Dunlop, 2017; Novák et al., 2024), with mid-Cretaceous Kachin amber standing out as the most significant source of pseudoscorpion fossils (Geißler et al., 2022). To date, 12 species have been reported from this amber biota: most of them are considered early-diverging lineages within extant families (e.g., Cockerell, 1917; Harvey et al., 2018; Henderickx & Boone, 2016; Hagen et al., 2025). However, despite the frequent presence of pseudoscorpions in Kachin amber and as other Mesozoic amber inclusions, only a small proportion have been formally described and studied, greatly limiting our understanding of their diversity and evolutionary history during the KTR.

The family Cheliferidae is a moderately diverse lineage of pseudoscorpions, comprising over 300 species (WPC 2024). Cheliferidae are found all over the world, but they are less diverse in the Australasian and Neotropical regions than in other regions, and include the ubiquitous *Chelifer cancroides* (Linnaeus, 1758), commonly known as House Pseudoscorpion (Harvey, 2014). Recent molecular studies reveal their classification as a relatively recently diverged clade, sister to Atemnidae + Withiidae, with the crown group originating in the mid-Mesozoic (Benavides et al., 2019). The family is currently divided into two subfamilies, Cheliferinae (57 genera) and Philomaoriinae (single genus, *Philomaoria*). The fossil record of Cheliferidae is mainly in amber deposits, with most species described from Eocene Baltic amber (Menge, 1854; Beier, 1937; Beier, 1947; Beier, 1955; Dashdamirov, 2008; Koch & Berendt, 1854).

Here we describe the first fossil record of the family Cheliferidae from mid-Cretaceous Kachin amber. Using micro-CT scanning and laser confocal microscopy, we show detailed morphological characters to support its taxonomic placement. Despite its extant diversity, the fossil record of this family remains sparse, with only a single documented species from the French Cretaceous Charentese amber (see *Discussion*). This new taxon increases the fossil diversity of Cheliferidae and provides additional evidence of their evolutionary history.

2 Material and methods

The specimen (Fig. 1A, B) originates from the deposits of Noije Bum in the Hukawng Valley (26°29′ N, 96°35′ E), Kachin State, northern Myanmar (see Grimaldi and Ross, 2017: fig. 2 for a detailed map). Radiometric U-Pb zircon dating and taphonomic analysis of pholadids have determined that the Kachin amber dates to the early Cenomanian stage, some 98.79 ±0.62 million years ago (Shi et al., 2012). Furthermore, the presence of ammonites in the amber-bearing bed and within the amber itself supports a late Albian or early Cenomanian age for these deposits (Cruickshank and Ko, 2003; Yu et al., 2019).

The amber piece was collected in 2015, before November 2017, when the Myanmar military closed the Kachin amber mining operations. It was collected and bought in full compliance with the laws of Myanmar and China, including regulations on the protection of fossils of China. The specimen is deposited in the Yunnan Key Laboratory for Palaeobiology, Institute of Palaeontology, Yunnan University, Kunming, China. The dimensions of the piece are 11 mm (length), 5 mm (width), and 1.5 mm (height).

To generate a 3D model of the specimen, it was scanned with a Zeiss Xradia 520 Versa X-ray microscope (Fig. 1C, D; made by Carl Zeiss X-ray Microscopy, Inc., Pleasanton, USA). Beam strength was 40kV/3W, with an exposure time at each rotation of 3s. The achieved voxel size was 4.62 µm. Data were collected as the sample rotated from - 96° to + 96°, and the number of projection images acquired was 1201 per segment. The 3D reconstruction generated 2163 slices. Radiographs generated from each scan were saved as TIFF stacks and further processed in Drishti (Version 3.2) software (Limaye, 2012). Screenshots of the 3D models were also saved in Drishti 3.2. The 3D-model of *Echinochelifer curvatus* gen. et sp. nov. is available as Additional File 1.

The amber piece was examined with a Keyence VHX-6000 3D microscope, enabling measurement and high-resolution photography (Fig. 2A; in non-reflective, 3D composition, and image stitching modes). The wide-field fluorescence microscopy image was obtained with a Zeiss Thunder imager DMi8, mainly using the 747 nm laser excitation line. Sketches and explanatory drawings were made in CorelDRAW X8 and Adobe Illustrator CC2019. Published work and nomenclatural acts are registered in ZooBank (http://www.zoobank.org/, last access: 23/07/2025), with the following LSID (reference): urn:lsid:zoobank.org:pub:DD6DEDA2-2C8B-418F-B0AC-B87D998B186C.

Measurements were taken with 3D models using Drishti 3.2. Measurements and terminology largely follow Chamberlin (1931a), with some minor modifications to the terminology of the trichobothria (Harvey, 1992). The following abbreviations are used for the trichobothria: *b* = basal; *sb* = sub-basal; *st* = sub-terminal; *t* = terminal; *ib* = interior basal; *isb* = interior sub-basal; *ist* = interior sub-terminal; *it* = interior terminal; *eb* = exterior basal; *esb* = exterior sub-basal; *est* = exterior sub-terminal; *et* = exterior terminal. Abbreviations for the chelicerae are as follows (Fig. 2B, C, D): *g* = galea; *v* = velum.

3 Systematic palaeontology

Order Pseudoscorpiones de Geer, 1778

Group Homosphyronida Chamberlin, 1929

Remarks. The new fossil possesses the diagnostic characters of the homosphyronids (Fig. 2E, F, G, H): trichobothria *ib* and *isb* located on the lateral face of the chelal fingers, and metatarsi and tarsi of all legs fused, with those of the anterior legs showing the same state as the posterior pair (Benavides et al., 2019).

Suborder Iocheirata Harvey, 1992

Remarks. Benavides et al. (2019) proposed that Iocheiratans are characterised by the presence of venom glands in one or both of the chelal fingers and by the presence of the posterior maxillary lyrifissure. On the new fossil, the presence of venom glands is evident, but the lyrifissure is difficult to discern (Fig. 2G, H and Fig. 3A, B).

Infraorder Panctenata Harvey, 1992

Remarks. The fossil possesses the characteristic velum and lamina exterior, a movable cheliceral finger bears only 1/2 distal teeth/lobes, and a serrula exterior is apparently completely fused to the movable cheliceral finger, as in panctenatans (Benavides et al., 2019).

Superfamily Cheliferoidea Risso, 1827

Remarks. The absence of accessory teeth (or at least their weak development), the presence of a venedens (suggesting a venom duct) on the fixed finger of the chela, and the seemingly reduced eye lenses (Fig. 2A), collectively support the placement of *Echinochelifer* gen. nov. within Cheliferoidea.

Family Cheliferidae Risso, 1827

Remarks. The new specimen is attributed to the family Cheliferidae because it has at least one finger with a venom apparatus and lacks trichobothrium *xs* (Fig. 3; *sensu* Harvey, 1992); the movable cheliceral finger has 2 subapical teeth (Fig. 2B–D); *gs* is subdistal on the movable cheliceral finger

(Fig. 2B–D; *sensu* Harvey, 1992); the serrula exterior is attached along its entire length (on the chelicera) (Fig. 2C); the chelicera has the velum and lamina exterior present (Fig. 2B–D); the carapace is subtriangular (Fig. 2A; see also Chamberlin, 1931a: fig. 10I); the abdomen subrectangular (Fig. 1); the eyes are situated near the anterior magin of the carapace (Fig. 2A); the pseudosternum is absent (Fig. 4A, B; see Harvey, 1985: fig. 10 or Batuwita and Benjamin, 2014: fig. 7f,g for comparison); the pedipalpal femur is without specialised trichobothria in the basal half (Fig. 2E, F); the femur/patella I and II junction is oblique; the male sternites (and tergites; Fig. 4C) are without discrete patches of sensory setae (as preserved); the venom apparatus is present in both chelal fingers (Chamberlin, 1931); as in males generally there are coxal sacs (here clearly visible on coxa IV: Fig. 4A, B).

The family Cheliferidae currently comprises 59 valid genera, distributed between the subfamilies Cheliferinae and Philomaoriinae (WPC, 2024). Based on the diagnostic characteristics outlined by Beier (1976) for the only genus *Philomaoria* Chamberlin, 1931 in the subfamily Philomaoriinae (Chamberlin, 1931b), the new specimen can be easily distinguished from representatives of this subfamily by its elongate pedipalpal fingers (vs. short and stout in *Philomaoria*), the non-clustering of medial tactile setae on the movable finger (vs. more or less clustered basally), and the global tuberculation of the pedipalp (vs. with many bristles but no tubercles).

Genus *Echinochelifer* Feng, Guo et Jouault gen. nov.

(Figs. 1–5)

Type species: *Echinochelifer curvatus* Feng, Guo et Jouault gen. et sp. nov. (by monotypy)

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Etymology. The genus name is a combination of the prefix "*echino*" which derives from the Greek εχινό (echino), meaning thorny (spiny), and the genus name *Chelifer*, type genus of the family. The name refers to the thorny appearance of the type specimen.

Diagnosis. Body with granulation dense, even and low. Carapace longer than broad; carapace covered with raised tubercles, each with one seta; eyes hardly discernible with well-marked median and posterior furrows. Chelicera with *gs*, *ls*, *is*, *sbs*, *bs*, and *es* present, also fixed cheliceral finger with five teeth, setae simple. Pedipalp elongate, covered with raised seta-bearing tubercles (mostly simple setae, but some denticuloclavate); coxal ventrum with one anterolateral spine; trochanter large, without lobes; femur with an inner 'row 'of large, sharp tubercles (resembling shark teeth); femur slightly longer than patella; chelal fingers without accessory teeth, but with venom apparatus and venom teeth, feebly gaping in male when closed; fixed finger with four internal and four external trichobothria, trichobothrium *it* near apex (anteriad of *et*), *ist* located slightly before middle (anteriad of *est*), *est* near midlength, movable finger with four external trichobothria, teeth of chela upright (number impossible to determine). Joint between femur and patella of anterior legs moderately oblique, femur only slightly wider than patella, tarsus I (in male) without dorso-distal process, with subterminal setae simple. Coxa IV with sac. All legs with simple claws, broad bifid arolia, shorter than claws (Fig. 4D–G).

Echinochelifer curvatus Feng, Guo et Jouault gen. et sp. nov.

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Type material. Holotype ♂ (YKLP-AMB-013), complete and well-preserved male specimen, in a piece of amber without syninclusions, housed in the collection of the Yunnan Key Laboratory for Palaeobiology, Institute of Palaeontology, Yunnan University, Kunming, China.

Locality and horizon. Hukawng Valley, Kachin State in northern Myanmar; lowermost Cenomanian (ca. 99 Ma), mid-Cretaceous.

Etymology. The species name is derived from the latin *curvātus*, meaning sickle-like in shape, referring to the pedipalps.

Diagnosis. As for genus (*vide supra*).

Description:

Body brownish yellow, with only chela finger of pedipalps and chelicerae slightly darker; about 3.25 mm long (from tip of chelicera to apex of abdomen) (Fig. 1A, B).

Carapace (Fig. 2A)**:** Subtriangular, not particularly constricting into a cucullus anteriorly; granulate in texture, with numerous small setae (one per tubercle). Eyes located close to pedipalp base and carapace anterior margin.

Chelicerae (Fig. 2B–D)**:** With five acuminate setae on dorsum of palm, seta *es* close to movable finger base, *bs* located below movable finger, seta *sbs* medial-on the dorsal surface, *ls* and *is* grouping at base of fixed cheliceral finger, and *gs* located just below galea base, on the movable finger; lamina exterior, serrula interior and velum present on fixed chelal finger, fixed finger with a preapical row of 5 teeth; serrula exterior present on movable finger, consisting of multiple lamellae (at least 17) ; lamellae longer distally than basally; galea complex, with multiple rami curving ventrally.

Pedipalp (Fig. 2E–H, Fig. 3A, B)**:** Pedipalp slender, coxae with distinct shoulder, setae tapering distally; trochanter rounded with two strong tubercles dorsoexternally and one ventroexternally (somewhat similar to *Chelifer cancroides* (Linnaeus, 1758) or *Metachelifer* Redikorzev, 1938), setae either simple or denticuloclavate; femur and patella granulate, apparently without any sensory trichobothria, setae either simple or denticuloclavate; chelal surface granulate, inner surface with tubercles; both chelal fingers with venom apparatus and poison teeth but without accessory teeth; fixed finger with four trichobothria; movable finger with four trichobothria; trichobothriotaxy as illustrated (Fig. 3).

Legs (Fig. 4D–G)**:** Joint between femur and patella of anterior legs moderately oblique, strongly oblique in posterior legs. Leg I with tarsus of normal shape, but distal setae longer and more numerous than on other tarsi. Junction between femora and patellae I and II strongly oblique to long axis; arolia shorter than claws and fan-shaped. Fourth coxa curved backwards.

Abdomen (Fig. 4A–C)**:** Subrectangular, about 1.83 mm long and 1.44 mm wide; genitalia not observable.

Dimensions (in mm, ratios between parentheses): Pedipalp trochanter (not including protuberance) 0.62/0.29 (2.13×), femur 1.35/0.20 (6.75×), patella 1.24/0.18 (6.89×), chela (with pedicel) 2.15/0.41 (5.24×), chela hand (with pedicel) 0.96/0.41 (2.34×), movable finger 1.10/0.08 (13.75×). Chelicera 0.39/0.15 (2.6×); carapace 1.16/0.96 (1.2×). Leg I trochanter 0.20/0.20 (1×), femur 0.41/0.18 (2.27×), patella 0.34/0.14 (2.42×), tibia 0.58/0.07 (8.28×), tarsus 0.47/0.06 (7.83×). Leg IV trochanter 0.29/0.17 (1.71×), femur+patella 0.82/0.21 (3.90×), tibia 0.74/0.09 (8.22×), tarsus 0.57/0.05 (11.4).

Remarks. The setation of the new genus appears to consist predominantly of simple setae. However, this observation may be influenced by the preservation process in amber, as the resin flow and subsequent engulfment of the specimen can "compact" or distort some setae. Upon closer examination, it seems that a few setae on the pedipalps are denticuloclavate, resembling those observed in certain species of *Ancistrochelifer* (Dashdamirov, 2006: fig. 6). However, their number is difficult to determine (Fig. 5A, B).

4 Discussion

4.1 *Systematic placement and comparisons with other fossil and extant Cheliferidae*

The absence of accessory teeth (or at least their weak development), presence of the venedens (suggesting the presence of a venom duct) on the fixed finger of the chela, and the presence of seemingly reduced eye lenses collectively indicate that *Echinochelifer* gen. nov. falls outside the crown-group of Chernetidae (Judson, 2009). The well-developed venedens on the movable finger exclude *Echinochelifer* gen. nov. from the crown group of Atemnidae, while the slightly oblique articulation between the femur and patella on the anterior legs rules out its placement within the crown group of Withiidae. Consequently, we consider the specimen to belong to Cheliferidae. This classification is further supported by the synapomorphy-based key for the order proposed by Harvey (1992), which readily places the specimen within Cheliferidae.

Attributing the new fossil to one of the tribes within Cheliferinae (i.e., Dactylocheliferini and Cheliferini) is challenging, as these groups are primarily defined by internal characteristics (e.g., Chamberlin, 1932), such as the configuration of the coxal sac and genitalia, both of which are difficult or impossible to discern in this fossil. Additionally, it is worth noting that the group Dactylocheliferini was not recovered as a monophyletic group in a previous molecular study (Harvey et al., 2015), questioning the validity of the group.

The new fossil cannot be assigned to the only Cretaceous genus of Cheliferidae, *Heurtaultia* Judson, 2009, due to its pedipalps bearing an elongated chela (compared to the short chela in *Heurtaultia*), a carapace with marked median and posterior furrows (vs. weakly marked carapace), and a rounded pedipalp trochanter adorned with conspicuous tubercles, some of which are tooth- or spine-like (vs. smooth) (Judson, 2009). Additionally, the chelal fingers are only slightly gaping in males when closed (vs. strongly gaping in *Heurtaultia*), the chelal trichobothrial pattern differs (see **Diagnosis**), coxa IV possesses a sac (vs. being likely absent), and the arolia are bilobed (vs. unilobed) (Judson, 2009).

The Cenozoic fossil record of Cheliferidae is essentially from amber deposits, with most species described from Eocene Baltic amber (Menge, 1854; Beier, 1937; Beier, 1947; Beier, 1955; Dashdamirov, 2008; Koch & Berendt, 1854). Two sizeable genera, *Dichela* Menge, 1854, and *Electrochelifer* Beier, 1937, include four and five species, respectively (Menge, 1854; Beier, 1937). However, meaningful comparisons between the new fossil and these genera are challenging due to their uncertain taxonomic status, the absence of detailed illustrations for many species, and ambiguities in the interpretation of trichobothrial placement and patterns, as emphasized by Dashdamirov (2008).

Based on the illustrations of some *Electrochelifer* species, the new specimen appears to differ notably in having tubercles covering the pedipalps, body and legs; the pedipalps being characterized by an elongated chela and patella, and the elongated femora all being adorned with tubercles, including sharp, tooth-like projections along the inner margin (Beier, 1937; Dashdamirov, 2008).

The new specimen can be readily differentiated from the monotypic genus *Pycnochelifer* Beier, 1937 due to its pedipalps having an elongated patella. However, similar to the genera *Dichela* and *Electrochelifer*, the validity, limits, and diagnosis of *Pycnochelifer* remain uncertain and require further clarification (Koch & Berendt, 1854; Menge, 1855: fig. 9; Beier, 1937; Dashdamirov, 2008).

The most recently described Cenozoic fossil genus attributed to the Cheliferidae is *Trachychelifer* Hong, 1983. Like many other fossil genera within the Cheliferidae, this taxon requires revision. Compared to the illustrations of the holotype specimen, our new specimen differs from *Trachychelifer* in that the chelae are significantly longer than wide, whereas *Trachychelifer* exhibits a triangular shape with equal length and width. Additionally, the new specimen bears an elongated habitus, compared to the stout and robust form of *Trachychelifer* (Hong, 1983: figs. 1–3). It is worth noting that the chelal trichobothrial pattern of *Trachychelifer* has not been illustrated.

The family Cheliferidae currently comprises 59 valid genera (WPC, 2024). Providing a detailed comparison of the new specimen with all of these genera would be counterproductive at this stage, especially given its distinct habitus, which allows for straightforward differentiation from most other genera. However, we offer brief comparisons with genera that superficially resemble *Echinochelifer* gen. nov. Among these, the genus *Metachelifer* Redikorzev, 1938, can be easily distinguished from the new taxon due to the significantly less pronounced tubercles on the carapace and pedipalps. Additionally, the pedipalpal femur of *Metachelifer* lacks the prominent inner ‘row ’of tubercles that is characteristic of the new fossil (Redikorzev, 1938; Li & Shi, 2022).

The shape of the carapace in Cheliferidae can vary significantly, with some species displaying a triangular carapace while others have a more rectangular form (Chamberlin, 1931a: fig. 10). The new genus shares similarities with *Chelifer* Geoffroy, 1762, particularly in the presence of setiferous tubercles on the carapace and pedipalps. In *Chelifer cancroides*, the carapace is slightly longer than wide, and features large posterior tubercles and scattered granules (Harvey, 2014). However, the tuberculation in the new genus appears to be more pronounced and distinct.

This new genus is easily distinguished from *Ancistrochelifer* Beier, 1951 by the absence of the peculiar conformation of the claws on the first pair of male legs (Beier, 1951: fig. 38), differences in the trichobothrial placements (e.g., more proximal arrangement of *et* and *it*), and the stronger tuberculation on the body. Although there are some similarities between the new genus and the extant genera *Dactylochelifer* Beier, 1932, *Hysterochelifer* Chamberlin, 1932 and *Metachelifer* Redikorzev, 1938, the new genus can be differentiated from the latter by its extremely conspicuous tubercles, its simple tarsal claws on leg I (vs. mostly with additional teeth, or processes), the shape of the setae covering the pedipalps being mostly denticuloclavate or simple (vs. often spatulate, bifid or denticuloclavate) and the simple setae on the chelicera (Chamberlin, 1932; Redikorzev, 1938; Dashdamirov, 2006). Finally, the new genus can be easily distinguished from some cheliferid genera that completely lack tuberculation, such as *Aspurochelifer* Benedict and Malcolm, 1979 (Benedict and Malcolm, 1979).

4.2 *Palaeocological considerations*

The pedipalps of pseudoscorpions typically serve three primary functions: predation, defense and in sexual contests, with the relative emphasis varying among species (Simone & Meijden, 2021). These structures bear critical sensory organs and are essential for capturing and manipulating prey, handling small particles used in nest building, and facilitating 'social 'interactions during mating or combat (Weygoldt, 1969; Harvey, 2014; Stemme & Pfeffer, 2022).

The pedipalps of *Echinochelifer* gen. nov. are highly distinctive, resembling the raptorial appendages of certain insects (e.g., mantid flies or mantises). The elongated, scythe-like shape of the pedipalps, combined with pronounced tubercles along the inner edges of the femur, patella, and hand of the chela, suggest a specialization for predation. The sharp, spine-like tubercles may have functioned to immobilize prey by restraining or incapacitating it, significantly reducing its chances of escape.

Additionally, the presence of venom apparatuses in both chelal fingers, which deliver venom, supports the idea that *Echinochelifer* gen. nov. was an active and efficient predator for its size (Harvey, 2014). The combination of venom injection and tuberculate structures on the pedipalps likely worked in tandem to enhance prey capture efficiency, ensuring a high degree of control over captured prey.

The pronounced tubercles on the pedipalps and carapace of *Echinochelifer* gen. nov. may have also served a defensive function, helping the pseudoscorpion resist predation. These sharp, spiky structures could have deterred predators by making the pseudoscorpion more difficult to handle or injure. Additionally, the tubercles might have been utilized as anchoring points, allowing *Echinochelifer* gen. nov. to secure itself beneath bark or within other protective microhabitats, further enhancing its ability to evade or withstand attacks.

5 Conclusions

The discovery of *Echinochelifer* gen. nov. significantly enhances our understanding of the diversity and distribution of the family Cheliferidae during the Cretaceous. The unique morphology of this new taxon allows for clear differentiation from other fossil and extant members of Cheliferidae, while its shared morphology and characteristics suggest it belongs to the crown group of the Cheliferidae. Its distinctive habitus, characterized by numerous sharp tubercles on the pedipalps and carapace, also facilitates behavioural inferences about its lifestyle. In particular, we propose that this species utilized its elongated pedipalps and chelae as raptorial appendages to effectively capture and subdue prey.

While *Echinochelifer* gen. nov. sheds new light on the evolutionary history of Cheliferidae, it is likely that the group's diversity during the Cretaceous is still vastly underestimated. Fossil pseudoscorpions appear to have received relatively limited attention from palaeoarachnologists, especially compared to other groups of Arachnida, perhaps because of their small size. Their diversity in the fossil record remains poorly documented, particularly within the Burmese amber biota. This amber deposit, which has preserved thousands of pseudoscorpions, likely holds critical evidence for unraveling the evolution of the order.

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Figure captions

Fig. 1. *Echinochelifer curvatus* gen. et sp. nov., holotype ♂ (YKLP-AMB-013). **A**, Dorsal view. **B**, Ventral view (white arrows pointing to the coxal spine). **C**, 3D-reconstruction model of dorsal view. **D**, 3D-reconstruction model of ventral view. Scale bars = 1 mm. Abbreviations: Ch, Chelicera; Tr, Trochanter; Fe, Femur; Ti, Tibia; H, Hand; L, Leg; Mf, Movable finger; Ff, Fixed finger; Co, Coxa.

Fig. 2. *Echinochelifer curvatus* gen. et sp. nov., holotype ♂ (YKLP-AMB-013). **A**, Carapace, dorsal view (white arrow pointing to the putative location of the right eye). **B**, Chelicera, dorsal view. **C**, Chelicera, ventral view. **D**, Interpretative drawing of the left chelicera, with names of structures and setae labelled. **E**, Right pedipalpal femur, dorsal view. **F**, Left pedipalpal femur, dorsal

view. **G**, Left chela, lateral view. **H**, Left chela, dorsal view. Scale bars = 0.2 mm (A, E–H), 0.1 mm (B–D).

Fig. 3. *Echinochelifer curvatus* gen. et sp. nov., holotype ♂ (YKLP-AMB-013). **A**, Interpretative line drawing of the dorsal view of the right pedipalp, with names of trichobothria labelled. **B**, Schematic line drawing of the externolateral view of the right chela, with positions of trichobothria labelled. Scale bars = 0.2 mm.

Fig. 4. *Echinochelifer curvatus* gen. et sp. nov., holotype ♂ (YKLP-AMB-013). **A**, Ventral view of coxal bases in fluorescence microscopy (white arrow pointing to the entrance of the left coxal sac). **B**, Ventral view of coxal bases in fluorescence microscopy (white arrow pointing to the entrance of the left coxal sac). **C**, Abdomen in dorsal view. **D**, Tarsus of left leg I (white arrow pointing to elongate setae). **E**, Tarsus of left leg IV, lateral view. **F**, Tarsus of right leg I (white arrow pointing to one elongate seta). **G**, Tarsus of right leg IV. Scale bars = 0.2 mm (A, B), 0.1 mm (C–F).

Fig. 5. *Echinochelifer curvatus* gen. et sp. nov., holotype ♂ (YKLP-AMB-013). **A**, Restored appearance of dorsal view. **B**, Restored appearance of ventral view. Abbreviations: S, Sternite; Ca, Carapace; Ch, Chelicera; Tr, Trochanter; Fe, Femur; Ti, Tibia; H, Hand; T, Tergites; L, Leg; Co, Coxa. Scale bars = 1 mm.