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Short communication

Two new kateretid beetle species (Coleoptera: Kateretidae) with specialized antennal scapes in males from mid-Cretaceous Kachin amber

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ABSTRACT

Kateretidae is a beetle family with 15 reported fossil species, four of them with specialized antennal scape. Specialized scape represents a rare form of sexual dimorphism in Kateretidae. Here we report two new species with a special scape in males of *Protokateretes* Zhao, Huang and Cai, 2023, and one female individual of an unnamed species of *Protokateretes*. The discovery of new species provides a supplementary diagnosis of *Protokateretes*, and increases the biodiversity of the fossil genus. The high diversity of species in *Protokateretes* provides new insights into sexual dimorphism of Kateretidae in mid-Cretaceous, enriching the knowledge of potential courtship strategy of kateretid beetles in the late Mesozoic.

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1. Introduction

Kateretidae is a small family of polyphagan beetles (Coleoptera), including over 90 extant species and 15 reported fossil species (Jelínek and Cline, 2010; Zhao et al., 2023c). Most extant kateretid beetles are widely distributed in temperate and subtropical zones globally, inhabiting various biotypes from forests to semideserts (Jelínek and Cline, 2010). Kateretidae are typically anthophagous, feeding on and developing in flowers of angiosperms (Jelínek and Cline, 2010). Besides, Kateretidae are classified into the Nitidulidae group in superfamily Nitiduloidea, not in Cucujoidea anymore, and the closest sister relationship between Kateretidae and Nitidulidae has been strongly proved, according to the latest molecular phylogenetic analysis (Cai et al., 2022).

Most fossil kateretids have been discovered from amber deposit, except *Amartus petrefactus* Wickham, 1912 from the Oligocene Florissant shales (Wickham, 1912). *Heterhelus expressus* Kirejtshuk

* Corresponding author. *E-mail address:* cycai@nigpas.ac.cn (C. Cai). and Nel, 2008 and *Eoceniretes yantaricus* Kirejtshuk and Nel, 2008 are two ancient species found in the Eocene French amber (Kirejtshuk and Nel, 2008). *Heterhelus buzina* Kupryjanowicz, Lyubarsky and Perkovsky, 2021 is the only fossil record of Kateretidae in the late Eocene Rovno amber (Kupryjanwicz et al., 2021; Perkovsky et al., 2007). Kateretid beetles from the Cretaceous period are preserved in the Early Cretaceous Lebanese amber, with *Lebanoretes andelmani* Kirejtshuk and Azar, 2008, and the mid-Cretaceous Kachin amber (Myanmar), including 10 species (Kirejtshuk and Azar, 2008; Zhao et al., 2023c).

Among the 10 kateretid species preserved in the mid-Cretaceous Kachin amber, the variation in pollen grains associated with *Electrumeretes birmanicus* Peris and Jelinek, 2019, *Cretaretes minimus* Peris and Jelínek, 2020, *Protokateretes antiquus* (Peris and Jelínek, 2020), and *Polliniretes penalveri* Peris and Jelinek, 2019, implied that Kateretidae may be a pollinator family generally involved in pollinating both gymnosperms and basal angiosperms during early Late Cretaceous (Peris and Jelinek, 2019, 2020; Peris et al., 2020; Peña-Kairath et al., 2023). Besides, the pollinator lineage to which *Pelretes vivificus* Tihelka, Li, Fu, Su, Huang and Cai, 2021 belongs, and the pollen grain in contact with this fossil directly proved that some







of ancient Kateretidae are anthophagous (Tihelka et al., 2021; Peña-Kairath et al., 2023). *Pelretes bicolor* Zhao, Huang and Cai, 2022 is also known from the same amber deposit (Zhao et al., 2022). *Furcalabratum burmanicum* Poinar and Brown, 2018 occupied enlarged mandibles (Poinar and Brown, 2018), a character also shared with *Cr. minimus* (Peris and Jelínek, 2020). Four of the fossil species in two genera, *Scaporetes rectus* Zhao, Huang and Cai, 2023, and *Pr. antiquus*, *Protokateretes megacephalus* Zhao, Huang and Cai, 2023, and *Protokateretes longiscapus* Zhao, Huang and Cai, 2023, show differentiated scape between males and females as sexual dimorphism (Peris and Jelínek, 2020; Zhao et al., 2023a, b, c).

In extant Kateretidae, sexual dimorphism displayed as modified antennal scape is rare; it is only observed in some species of *Kateretes* Herbst, 1793 (Jelínek and Cline, 2010). Here we report two new species with different shapes in the male scape. *Protokateretes magnascapulae* sp. nov. and *Protokateretes rectangulum* sp. nov., and one female individual in an unnamed species in *Protokateretes Zhao*, Huang and Cai, 2023 are newly described. The male scapes in *Pr. magnascapulae* sp. nov. and *Pr. rectangulum* sp. nov. are different from those of previously reported species of *Protokateretes* (Peris and Jelínek, 2020; Zhao et al., 2023b, c). The morphological differences in females among species of *Protokateretes* are too subtle to establish a new taxon based on the female individual (Peris and Jelínek, 2020; Zhao et al., 2023c). Our discovery of new species provides a supplementary diagnosis of *Protokateretes*, and increases the biodiversity of the fossil genus.

2. Material and methods

We have studied four specimens preserved in three different amber pieces, all of them housed in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences, Nanjing, China. The ambers were collected from an amber mine near Noije Bum Hill summit site, 20 km southwest of Tanai, in the Hukawng Valley, Kachin State of northern Myanmar (26150N, 96330E) (Cruickshank and Ko, 2003; Yin et al., 2018). Zircon SIMS U-Pb dating has constrained the age of the Kachin amber to the Late Cretaceous, Cenomanian (around 98.79 ± 0.62 Ma), but the palaeontological data indicated that the age may be earlier (Shi et al., 2012; Mao et al., 2018). Therefore, the actual age of Kachin amber would be from the latest Albian to the earliest Cenomanian, the Early to Late Cretaceous boundary (Shi et al., 2012; Mao et al., 2018). The studied specimens of Kachin amber were legally acquired before June 2017 (See 'NIGP203317-NIGP203320, Museum Catalogue Entry' in Supplementary Material).

The four specimens belonging to two species are derived from three Kachin amber pieces, a male of the species Protokateretes rectangulum sp. nov. with a female individual in one amber piece, and two males of the species Protokateretes magnascapulae sp. nov. in two independent amber samples. All amber pieces were ground with sandpapers of different grit sizes, and polished with diatomite mud (Sidorchuk and Vorontsov, 2018). The sample holotype NIGP203319 was included between two coverslips in a Canada balsam, and the remain part between coverslips is filled with AB glue to achieve an adhesion and fixation effect (Azar et al., 2003). Photographs were taken using four devices: a Zeiss Stereo Discovery V16 microscope system with an incident light and a transmitted light, a Zeiss Axio Imager 2 light microscope, a Leica DM 1000 light microscope, and a Zeiss LSM 710 confocal laser scanning microscope (CLSM) with digital cameras attached (Cai and Huang, 2014; Fu et al., 2021). The images were rendered for a better 3D effect with the Extend Depth of Field in Helicon Focus 8.0.3, and figure plates were compiled and arranged in Adobe Photoshop 2021. The nomenclatural acts established herein are registered under LSID urn:lsid:zoobank.org:pub:EF3A3E8C-1145-4669-AE09-DA3334A76EA8.

3. Systematic palaeontology

Order: Coleoptera Linnaeus, 1758. Superfamily: Nitiduloidea Latreille, 1802. Family: Kateretidae Erichson in Agassiz, 1846.

Genus Protokateretes Zhao, Huang and Cai, 2023. Type species. Protokateretes antiquus (Peris and Jelínek, 2020)

Modified diagnosis. Head subrectangular or quadrate in males. Scape in males highly modified, in most species enlarged and curved, with lateral attachment of pedicel and with an inner conical extension behind the insertion of pedicel, in less species scape more or less longer than head; enlarged in females, with antennomeres 2–3 elongate; antennal club loose. Pronotum transverse, without explanate sides in most species; head subequal with pronotum in most species. Elytra shortened and complete; three or four (less species) last abdominal segments remaining completely uncovered. Tibial spurs paired. Metatibiae armed by one (less species) or two (more species) rows of spines dorsally.

Protokateretes magnascapulae Zhao, Huang and Cai, sp. nov. (LSID urn:lsid:zoobank.org:act:3F48CD2B-8BB0-4F04-B43B-5C7077ACE3EC) Figs. 1–2.

Etymology. The specific epithet is derived from two Latin words 'magna-' and 'scapulae', meaning the large and thin scape in the species.

Diagnosis. The differences of females between different species in Protokateretes is relatively subtle, and the most distinguishable character in Protokateretes is the morphology of scape in males, when other characters in males are not unique enough to distinguish species in *Protokateretes* completely. The new specie is mainly different from other Protokateretes species in scape in male elongated and concaved ventrally, with small round bumps dorsoventrally. New specie also differs from other species in Protokateretes by four abdominal segments exposed. And the new specie could be identified by following characters: antennomere 11 oblong oval; mandibles bidentate; pronotal angles rounded, and lateral sides arcuate; scutellar shield stout; elytra separately rounded apically, as wide as pronotum; metafemora wider than pro- and mesofemora; pro- and mesotibiae without row of spines; metatibiae wrapped by two rows of spines on outer sides and long setae on inner edge; claws dentate.

Type material. Holotype, NIGP203317, Male.

Paratype. NIGP203318, Male. The paratype specimen was preserved in an independent amber, with thrips.

Type locality and horizon. Amber obtained in the Hukawng Valley, Myitkyina District, Kachin State, Myanmar; late Albian to early Cenomanian (mid-Cretaceous) (Shi et al., 2012; Mao et al., 2018). *Description.* Body elongated, flattened; elytra short, leaving four abdominal segments exposed; body length 2.24 mm (from apex of frons to end of pygidium), width 0.58 mm (measured from medial elytra) in Holotype; length 1.93 mm (from apex of frons to end of pygidium), width 0.69 mm (measured from medial elytra) in Paratype (Fig 1A–1C).

Antennae 11-segmented with loosely 3-segmented club, sparsely setose, and all antennomeres gradually dilated apically except from the last one (Fig 1D); scape specialized, antennomeres 2–7 subequal in length and width, slightly larger than antennomeres 8 (Fig 1D); antennomeres 9–10 subequal in length and width, shorter and wider than oblong oval antennomere 11 (Fig 1D); scape elongated,



Fig. 1. Photomicrographs of *Protokateretes magnascapulae* sp. nov. from mid-Cretaceous Kachin amber; images are from the holotype specimen NIGP203317 except C, H and I that are from the paratype specimen NIGP203318; A–C under ordinary reflected light; D–I under confocal laser scanning microscopy (CLSM). A, dorsal view. B, ventral view. C, dorsal view. D, antennae. E, dorsal edge of scape. F, ventral view of scape. G, dorsal view of head. H, dorsal view of mandibles. I, ventral view of head. Abbreviations: a1–11, antennomeres 1–11; ey, eye; he, head; lbp, labial palp; ma, mandible; mt, mentum; mxp, maxilla palp; pr, pronotum; to, tooth. Scale bars: 500 µm in A–C; 100 µm in others.

as long as head, and concaved ventrally, with small round bumps dorsoventrally (Fig 1E, 1F). Antennal insertion concealed by projecting lobe of frons (Fig 1G). Head prognathous, transverse, length 0.4 mm (measured from anterior margin of frons to that of pronotum), dorsum rough, with recumbent pubescence (Fig 1G); anterior margin of head emarginated slightly, occipital ridge distinct; compound eyes small, situated laterally (Fig 1G). Mandibles bidentate, maxilla palpomeres narrow, with terminal segment subconical (Fig 1H, 1I). Mentum transverse, over half the width of the head (Fig 1I).

Pronotum transeverse, over 1.4 times as wide as long, lateral sides arcuate and obtusely angulate at midlength; anterior margin nearly paralleled with posterior sides; anterior and posterior angles broadly rounded (Fig 2A). Prosternal process subconical, narrow, shorter than length of procoxae (Fig 2B). Procoxal cavities transverse and open (Fig 2B).



Fig. 2. Detail photomicrographs of *Protokateretes magnascapulae* sp. nov. (holotype, NIGP203317) from mid-Cretaceous Kachin amber; under confocal laser scanning microscopy (CLSM). A, pronotum. B, prosternal process. C, elytra. D, abdomen. E, overall view of leg. F, dorsal view of protibiae. G, dorsal view of mesotibiae. H, dorsal view of metatibiae. I, tarsi. J, claw. Abbreviations: cl, claw; el, elytra; fe, femora; msb, mesotibiae; mtb, metatarsi; pp, prosternal process; pr, pronotum; ptb, protibiae; si, spine; sm, scutellum; sp, spur; ts 1–5, tarsomeres 1–5; v1–5, ventrites 1–5. Scale bars: 200 µm in A, C–E, 50 µm in J, 100 µm in others.

Scutellar shield triangular, and stout, half the width of elytron (Fig 2C). Elytra shortened but complete, separately rounded apically (Fig 2C); length around 0.9 times combined width, and dorsum with densely recumbent pubescence (Fig 2C). Abdomen with five ventrites, gradually elongating and narrowing, with ventrite 1 widest (Fig 2D); ventrite 5 subtriangular, and longest (Fig 2D); abdomen with densely recumbent pubescence (Fig 2D).

Femora flattened, and meta-femora wider than pro- and meso-femora; canaliculate for reception of tibiae, and densely setose (Fig2E). Tibiae widened posteriorly, with tibial spurs (Fig 2E); lateral edges of pro- and mesotibiae without row of spines (Fig 2F, 2G); metatibiae armed by two rows of spines dorsally and long setae ventrally (Fig 2H). Tarsi 5-5-5, tarsomeres 1–3 bilobed and gradually smaller, densely setose; tarsomere 4 smallest, with tarsomere 5 longest (Fig 2I). Claws dentate (Fig 2I).

Protokateretes rectangulum Zhao, Huang and Cai, sp. nov. (LSID urn:lsid:zoobank.org:act:12A90AF8-5E5F-46E0-AE82-584F 891B97DF)

Figs. 3-4.

Etymology. The specific epithet is derived from the Latin word 'rectangulum', to indicate the thin scape bent at a right angle, in males of the species.

Diagnosis. In new specie, scape in male is slender and extremely elongated, curved in the middle, approximately at right angles, with densely long setae ventrally. This unique scape could distinguish the new specie from other species in *Protokateretes*. Besides, *Protokateretes rectangulum* possesses a row of short and coarse spines on dorsal side of protibiae, which is different from other *Protokateretes* species. And the type specimen of this new specie differs from other species in following characters: mandibles simple; anterior pronotal angles obtusely angulate and posterior angles rounded; prosternal process longer than procoxal cavities; elytra short with three abdominal segments exposed; mesotibiae abruptly widened nearly base, without spines; metatibiae armed by two rows of long and thin spines on outer edge, and spines nearly apex; tarsomeres 1–3 bilobed; claw simple.

Type material. Holotype, NIGP203319, male.

Type locality and horizon. Amber obtained in the Hukawng Valley, Myitkyina District, Kachin State, Myanmar; late Albian to early Cenomanian (mid-Cretaceous) (Shi et al., 2012; Mao et al., 2018). *Description.* Body elongated, flattened; length 2.4 mm (measured from apex of anterolateral angle of frons, to end of pygidium), and body width 1.0 mm (measured from widest pronotum); color brown black (Fig 3A, 3B).

Head prognathous, length around 0.5 mm (measured from apex of frons to anterior margin of pronotum), width larger than 0.7 mm, across eyes (Fig 3C). Occipital ridge transverse, slightly narrower than anterior margin of pronotum (Fig 3C). Compound eyes small, situated at the sides (Fig 3C). Straight part of scape longer than head (Fig 3D); scape slender and extremely elongated, curved in the middle, approximately at right angles, with densely long setae ventrally (Fig 3D); antennomere 2 as long as antennomere 3, but nearly twice wider than antennomere 3, and antennomere 3 dilated apically (Fig 3E); antennomere 4-8 subequal in width; 3segmented antennal club loose, antennomere 10 wider than antennomere 9 (Fig 3E). Mandible simple and small, concealed by anterior margin of frons (Fig 3F). Mentum nearly square (Fig 3F). Pronotum transverse, 1.5 times as wide as long; widest near posterior, almost as wide as elytra; lateral sides arcuate, without explanate margin; anterior angles obtusely angulate, and posterior angles broadly rounded; dorsum with recumbent short pubescence (Fig 3G). Prosternal process short and narrow, longer than length of

procoxal cavities; procoxal cavities open (Fig 4A).

Elytra short, with three abdominal segments exposed (Fig 4B); elytra complete, and separately rounded apically, length about 0.9 times combined width (Fig 4C); disc densely short setose (Fig 4C); scutellum triangular and large (Fig 4C). Abdomen with five ventrites, and metacoxal cavities narrowly separated, no longer than 0.1 mm (Fig 4D); ventrites 1–5 narrow in turn, and pygidium triangular and longest (Fig 4D).

Femora flattened, meta-femora slightly larger than others, and canaliculate for reception of tibiae (Fig 4D). Claws simple (Fig 4D). Tibiae densely long setose, tibial spur concealed by impurities in amber; protibiae armed by one row of short and coarse spines dorsally (Fig 4E); mesotibiae abruptly widened nearly base, without spines (Fig 4F); metatibiae armed by two rows of long and thin spines on outer edge, and spines nearly apex (Fig 4G). Tarsi 5-5-5, tarsomeres 1–3 bilobed, densely setose; tarsomere 4 smallest and triangular, with tarsomere 5 longest (Fig 4F–4G).

Protokateretes sp.

Material examined. NIGP203320, female.

Figs. S1–S2

Type locality and horizon. Amber obtained in the Hukawng Valley, Myitkyina District, Kachin State, Myanmar; late Albian to early Cenomanian (mid-Cretaceous) (Shi et al., 2012; Mao et al., 2018). Description. body elongated, length 1.4 mm (measured from anterior margin of frons to end of pygidium), width around 0.4 mm (measured from medial combined elytra) (Figs. S1A and S1B). Head nearly trapezoidal, almost as wide as long; compound eyes nearly half the length of head, and situated at the sides (Fig. S2A). Pronotum nearly oblong oval horizontally, anterior and posterior angles broadly rounded (Fig. S2A). Antennae 11-segmented, with 3segmented loosely club; scape straight, nearly twice larger than pedicel, no longer than 0.1 mm; antennomere 2 as long as antennomere 3, but nearly twice wider than antennomere 3, and antennomere 3 dilated apically (Fig. S2B); antennomere 4-8 subequal in width; antennal club loose, antennomere 10 wider than antennomere 9 (Fig. S2B). Prosternal process short and narrow (Fig. S2C). Elytra short, complete, with four abdominal segments exposed (Figs. S2D and S2E). Abdomen with five ventrites, pygidium triangular and longest, and ventrite 1 as long as pygidium medially (Fig. S2F). Visible terminal of internal genitalia (Fig. S2F). Tibiae slender, densely setose, with two tibial spurs (Figs. S2G–S2I); metatibiae armed by two rows of spines dorsally (Fig. S2I). Tarsi 5-5-5; tarsomeres 1-3 concaved, and tarsomere 1 largest. Claw simple (Fig. S2]).

4. Discussion

4.1. Morphological comparisons

We have described two new species in the fossil genus *Protokateretes* based on three male specimens preserved in three different amber pieces: *Pr. magnascapulae* sp. nov. and *Pr. rectangulum* sp. nov. In addition, an unnamed female of the same genus is also cited in syninclusion with the holotype of *Pr. rectangulum* sp. nov. *Protokateretes magnascapulae* sp. nov. and *Pr. rectangulum* sp. nov. possess special morphology of antennal scape in males, significantly different with other fossil genera, which possess a normal scape. The new female described in this work, although with normal scape, shares with the holotypes of *Pr. magnascapulae* sp. nov. and *Pr. rectangulum* sp. nov. the elytra short and complete, with at least three abdominal segments exposed dorsally, the gular suture absent, posterior pronotal angles widely round, prosternal process narrow, tibiae slender, densely setose,

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Fig. 3. Photomicrographs of *Protokateretes rectangulum* sp. nov. (holotype, NIGP203319) from mid-Cretaceous Kachin amber; A and B under ordinary reflected light, others under confocal laser scanning microscopy (CLSM). A, dorsal view. B, ventral view. C, dorsal view of head. D, scape. E, antennae except scape. F, ventral view of head. G, pronotum. Abbreviations: a2–11, antennomeres 2–11; he, head; ma, mandibles; mt, mentum. Abbreviations: a1–11, antennomeres 1–11; he, head; ma, mandible; mt, mentum. Scale bars: 500 µm in A and B, 200 µm in F and G, 100 µm in others.



Fig. 4. Detail photomicrographs of *Protokateretes rectangulum* sp. nov. (holotype, NIGP203319) from mid-Cretaceous Kachin amber; under confocal laser scanning microscopy (CLSM). A, prosternal process. B, exposed abdominal segments. C, elytra. D, abdomen. E, protibiae. F, mesotibiae. G, metatibiae. Abbreviations: cl, claw; el, elytra; msb, mesotibiae; mtb, metatibiae; pp, prosternal process; ptb, protibiae; py, pygidium; si, spine; ts 1–5, tarsomeres 1–5; v1–4, ventrites 1–4. Scale bars: 200 μm in A–D, 100 μm in E–G.

with two tibial spurs, mesotibiae without row of spines dorsally, metatibiae armed by two rows of spines dorsally, and tarsomeres 1–3 bilobed. Thus, all the new specimens are described in *Protokateretes*, but the holotype of *Pr. rectangulum* sp. nov. differs from the female specimen in syninclusion in the three abdominal segments exposed, protibiae armed by one row of spines dorsally, mesotibiae abruptly widened nearly base, without spines, and metatibiae armed by two rows of spines on outer edge. By contrast, there are four abdominal segments exposed, and only metatibiae armed by two rows of spines dorsally in the female specimen.

Therefore, we suggest that this female illustrate a new example of sexual dimorphism in *Protokateretes*.

- 2a. Mandibles bidentate; prosternal process narrow; pygidium terminal without tooth; tibiae armed by

two rows of long stiff setae dorsally.....Furcalabratum burmanicum Poinar and Brown, 2018

- 2b. Mandibles simple; prosternal process wide; pygidium with small teeth apically; tibiae armed by a row of five spines dorsally......Polliniretes penalveri Peris and Jelinek, 2019

- 4a. Body wrapped by long setae densely; metatibiae armed by one row of thick spines dorsally; scape elongated and fourth times larger than pedicel......Scaporetes rectus Zhao, Huang and Cai, 2023
- 5a. Elytral disc unfirmly coloured without markings; anterior pronotal angles broadly rounded......Pelretes vivificus Tihelka, Li, Fu, Su, Huang and Cai, 2021
- 5b. Elytral disc decorated by bilaterally symmetrical trapezoidal white markings; anterior pronotal angles obtusely angulate......Pelretes bicolor Zhao, Huang and Cai, 2022
- 6a. Mandibles prominent, straight and longer than scape dorsally; protibiae with a pair of unequal thick spurs in inner sub-apical angle.....*Cretaretes minimus* Peris and Jelínek, 2020
- 7a. Gular suture distinct; mesotibiae armed by one longitudinal row of long setae or spines on dorsal side approximately.......*Electrumeretes birmanicus* Peris and Jelinek, 2019
- 8a. Scape in males straight and elongated, with small round bumps ventrally......9
- 8b. Scape in males curved and enlarged, without small round bumps......10
- 9a. Mandibles bidentate (Fig. S3A); scape in males moderately long, nearly equal with the length of head (Figs. S4A and S4B); pedicel attached at the terminal of scape (Figs. S4A and S4B)......Protokateretes magnascapulae sp. nov.
- 9b. Mandibles simple without tooth (Fig. S3B); scape in males extremely long, much longer than head (Fig. S4C); pedicel attached at the lateral sides of center of scape (Fig. S4C)......Protokateretes longiscapus Zhao, Huang and Cai, 2023
- 10a. Mandibles bidentate (Fig. S3C); curved tooth distinct on inner side of scape in males, with a conical extension (Fig. S4D).....Protokateretes megacephalus Zhao, Huang and Cai, 2023
- 10b. Mandibles simple without tooth (Figs. S3D and S3E); tooth absent on inner side of scape in males, with an inner flat extension.......11
- 11a. Scape in males dorsal border smooth; the second half of scape nearly as long as head, and nearly horizontal; long pubescence densely present on inner sides of second half of scape (Fig. S4E)......Protokateretes rectangulum sp. nov.
- 11b. Scape in males dorsal border reticulate; the second half of scape shorter than length of head, and not horizontal; setae or pubescence absent on inner sides of scape (Fig. S4F)......Protokateretes antiquus (Peris and Jelínek, 2020)

It is noticed that the differences of females between different species in *Protokateretes* is relatively subtle. And the distinguishing features between different females are more likely to focus on various small characters, such as the distribution pattern of setae on body, pronotal angles, ratio of head/pronotum, etc. For example, female in *Protokateretes* sp. is different from *Pr. antiquus* and *Pr. longiscapus* by pronotal and elytral sides without densely long setae, pronotal angles round, four abdominal segments exposed, and ratio of head/pronotum around 1 (Peris and Jelínek, 2020; Zhao et al., 2023c). Therefore, the contents about different species from *Protokateretes* in above key table are developed based on the striking and easy-to-distinguish scape in males.

4.2. Specialized antennal scape in beetles

Long antennal scape in some species of Laemophloeidae (Cucujoidea), including Laemophloeus Dejean, 1836, Cryptolestes Ganglbauer, 1899, Microbrontes Reitter, 1874, Dysmerus Casey, 1884, and Placonotus Macleay, 1871 (Lefkovitch, 1958; Thomas, 1988, 1995) and some species of Histanocerus Motschulsky, 1858 in Pterogeniidae (Tenebrionoidea) (Lawrence, 2010), have been discussed as a form of sexual communication or stereotyped display, as a type of courtship strategy (Peris and Jelínek, 2020). This manifestation of specialized scape as sexual dimorphism is rare in extant Kateretidae, only present in some Kateretes (Jelínek and Cline, 2010). But there are 5 species in the genus Protokateretes (Peris and Jelínek, 2020; Zhao et al., 2023b, c), and 1 species in genus Scaporetes (Zhao et al., 2023a), with specialized scape, among the currently known 10 fossil species of Kateretidae during the Cretaceous (Kireitshuk and Azar, 2008; Peris and Jelinek, 2019, 2020: Poinar and Brown, 2018: Tihelka et al., 2021: Zhao et al., 2022, 2023a, b, c). In addition, the scape in males of the above cited five species are different, with various morphologies (Fig. S3), which indicates that *Protokateretes* is a highly diverse fossil genus. The diversity of kateretids with specialized scape is decreased since the Cretaceous, which indicates that sexual communication or special display activity operated by the singular scape went through a significant declination since the Cretaceous.

4.3. Associated pollen grains and paleoecology

Fossil Kateretidae preserved with pollen grains include the species *Electrumeretes birmanicus*, *Cretaretes minimus*, *Proto-kateretes antiquus*, *Polliniretes penalveri*, and *Pelretes vivificus*. The first three pollinated gymnosperms (including cycads, ginkgoa-leans, or bennettitaleans), while the remaining two were likely angiosperm pollinators (Peris et al., 2020; Tihelka et al., 2021). It has been observed that both male specimens of Protokateretes magnascapulae sp. nov. from the samples NIGP203317 and NIGP203318 are also preserved in syninclusion with pollen grains.

In the holotype of *Pr. magnascapulae* sp. nov. (NIGP203317) there are two pollen grains observed in syninclusion with the fossil beetle. One grain was observed attached to the elytra, and another one was found close to the antennae dorsally (Fig 5A). The pollen grain near the antennae is compressed with a circular outline, with 29 μ m in diameter and 17 μ m in width (Fig 5B–5D). The grain is heteropolar and monoaperturate, with trichotomocolpate aperture, seeming as trisyncolpate in polar view (Fig 5B, 5D). The pollen grain is reticulate, with muri about 0.5 µm wide (Fig 5C, 5D). This pollen grain is similar to Asteropollis trichotomosulcatus Singh, 1983, and their aperture are all trichotomocolpate, but pentachotomocolpate, tetrachotomocolpate and hexachotomocolpate aperture are common in other species of Asteropollis Hedlund and Norris, 1968; Song et al., 2000; Friis et al., 2019; Korasidis and Wagstaff, 2020). Genus Asteropollis is common and distributed early in the history of angiosperms, and even the age of Asteropollis trichotomosulcatus dates back to Early late Albian (Friis et al., 2019;



Fig. 5. Detail photomicrographs of particles around *Protokateretes magnascapulae* sp. nov. from the holotype (NIGP203317) and the paratype (NIGP203318). A, general view of *Protokateretes magnascapulae* (holotype, NIGP203317) and pollen grain, under normal reflected light. B, enlargement of pollen grain, under reflected light and transmitted light. C, enlargement of pollen grain, lateral view, under confocal laser scanning microscopy (CLSM). D, enlargement of pollen grain, dorsal view, under confocal laser scanning microscopy (CLSM). F, legs unilaterally, under confocal laser scanning microscopy (CLSM). F, legs unilaterally, under confocal laser scanning microscopy (CLSM). G, enlargement of particle near the tibiae, under confocal laser scanning microscopy (CLSM). H, general view of *Protokateretes magnascapulae* (paratype, NIGP203318) dorsally, under ordinary reflected light. I, enlargement of gathering pollen grains, under confocal laser scanning microscopy (CLSM). J, enlargement of pollen grains, under transmitted light by Leica DM 1000 microscope. Scale bars: 500 µm in A and H, 200 µm in F, and 20 µm in others.

Korasidis and Wagstaff, 2020). The closet allied species of *Asteropollis* pollen are related to Chloranthaceae, and pollen grains of *Asteropollis* are found linked to flowers and fruits of fossil genus *Hedyflora* Friis, Crane and Pedersen, 2019 in Chloranthaceae, which confirmed that *Asteropollis* is closely related to Chloranthaceae, the only member of Chloranthales (Walker and Walker, 1984; Angiosperm Phylogeny Group IV, 2016; Friis et al., 2019). Chloranthales

is one of the earliest diverging lineages of extant angiosperms, sister to magnoliids, and the fossil records extend the differentiation of Chloranthaceae back to the mid Early Cretaceous (Angiosperm Phylogeny Group IV, 2016; Friis et al., 2019; Guo et al., 2021). The pollen grain mentioned here is likely from the crown group of Chloranthaceae in the mid-Cretaceous. The grain attached to the elytra is not clearly discernible for identification, primarily due to the preservation angle of *Pr. magnascapulae* sp. nov. (Fig 5E). Moreover, a potential third grain is found in contact with the metatibiae, whose outline is compressed into a circular, with vaguely trichotomocolpate (Fig 5F, 5G). Regrettably, this particle is not clear enough to determined its similarity to the aforementioned pollen grain, due to its preservation depth (Fig 5G). Therefore, *Pr. magnascapulae* sp. nov. is likely to be a vector of *Asteropollis* pollen, but more evidence is needed.

There are five gathering together pollen grains preserved in the same amber piece that the paratype of *Pr. magnascapulae* sp. nov. (NIGP203318), closing to its pygidium (Fig 5H). These pollen grains are spindle-shaped on equatorial view, prolate, and tricolpate, vaguely visible, and their average measurements (N = 5) include polar axis length of 17.8 μ m (15–20 μ m) and an equatorial diameter of 8.5 μ m (7.5–8.5 μ m) (Fig 5I, 5J). Unfortunately, the quantity of these pollen grains is limited, and their preservation is unclear, allowing only a rough determination that these pollen grains likely originate from angiosperms.

There are two conditions to be met to classify a fossil insect as a pollinator: pollen grains are attached to the body of insect and some extant descendants of the insect are pollinators (Peña-Kairath et al., 2023). Protokateretes magnascapulae sp. nov. belongs to Kateretidae, and extant short-winged flower beetles are pollinivorous as larvae and adults, visiting various angiosperms, which satisfies the second criterion (Jelínek and Cline, 2010). However, the pollen grains preserved in syninclusion with Pr. magnascapulae sp. nov. in two amber samples, are not directly attached to the body except for one badly preserved grain attached to the elytra and a putative grain attached to the metatibia in one of the specimens. This fact makes it impossible to confirm the relationship between Pr. magnascapulae sp. nov. and the plants more than they coexisted in the same Cretaceous environment. Therefore, the syninclusion of pollen grains with the holotype and paratype of Pr. magnascapulae sp. nov. suggest that Pr. magnascapulae sp. nov. might have been acted as a pollinator at the beginning of the Late Cretaceous, although we cannot determine this function because lack of enough evidence (Peña-Kairath et al., 2023).

5. Conclusion

Protokateretes is a fossil genus of Kateretidae with special antennal scape in males, which is rare in extant kateretids. Here we report two new species belonging to Protokateretes: Pr. magnascapulae sp. nov. and Pr. rectangulum sp. nov. based on one male in the first species and two males in the second species. Additionally, a female of Protokateretes sp. is in syninclusion with the holotype of Pr. rectangulum sp. nov. Our discovery suggests that Protokateretes is a diverse genus in the Cretaceous. The morphology of specialized scape in males is a useful feature to determine new species in Protokateretes, whereas the morphological differences among females are subtle. In addition, some sexual communication or displayed activities is inferred in males with such specialized scape, which may have gone through a phase of decline from mid-Cretaceous to the present. Pollen grains preserved together with the two specimens of Pr. magnascapulae may increase the possibility that the species could be a potential pollinator in the Cretaceous, although more robust evidence is needed.

CRediT authorship contribution statement

Qian Zhao: Writing – review & editing, Writing – original draft, Software, Methodology. **David Peris:** Writing – review & editing. **Jia Liu:** Supervision. **Diying Huang:** Resources, Funding acquisition, Conceptualization. **Chenyang Cai:** Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

We declare that we have no conflicts of interest to this work. We declare that we do not have any commercial or associative interest that represents a conflict of interest in relation to the submitted work.

Data availability

Data will be made available on request.

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References

- Azar, D., Perrichot, V., Néraudeau, D., Nel, A., 2003. New Psychodids from the Cretaceous Ambers of Lebanon and France, with a Discussion of Eophlebotomus connectens Cockerell, 1920 (Diptera, Psychodidae). Annals of the Entomological Society of America 96 (2), 117–126. https://doi.org/10.1603/0013-8746(2003) 096[0117:NPFTCA]2.0.CO, 2.
- Cai, C.Y., Huang, D.Y., 2014. The oldest micropepline beetle from Cretaceous Burmese amber and its phylogenetic implications (Coleoptera: Staphylinidae). Naturwissenschaften 101, 813–817. https://doi.org/10.1007/s00114-014-1221-z.
- Cai, C.Y., Tihelka, E., Giacomelli, M., Lawrence, J.F., Slipinski, A., Kundrata, R., Yamamoto, S.H., Thayer, M.K., Newton, A.F., Leschen, R.A., Gimmel, M.L., Lü, L., Engel, M.S., Bouchard, P., Huang, D.Y., Pisani, D., Donoghue, P.C., 2022. Integrated phylogenomics and fossil data illuminate the evolution of beetles. Royal Society Open Science 9, 211771. https://doi.org/10.1101/2021.09.22.461358.
- Cruickshank, R., Ko, K., 2003. Geology of an amber locality in the Hukawng Valley, northern Myanmar. Journal of Asian Earth Sciences 21, 441–455b. https:// doi.org/10.1016/S1367-912000044-5.
- Friis, E.M., Crane, P.R., Pedersen, K.R., 2019. *Hedyosmum*-like fossils in the Early Cretaceous diversification of angiosperms. International Journal of Plant Sciences 180, 232–239. https://doi.org/10.1086/701819.
- Fu, Y.Z., Li, Y.D., Su, Y.T., Cai, C.Y., Huang, D.Y., 2021. Application of confocal laser scanning microscopy to the study of amber bioinclusions. Palaeoentomology 4, 266–278. https://doi.org/10.11646/palaeoentomology.4.3.14.
- Guo, X., Fang, D., Sahu, S.K., Yang, S., Guang, X., Folk, R., Smith, S.A., Chanderbali, A.S., Chen, S., Liu, M., Yang, T., Zhang, S., Liu, X., Xu, X., Soltis, P.S., Soltis, D.E., Liu, H., 2021. Chloranthus genome provides insights into the early diversification of angiosperms. Nature Communications 12, 6930. https://doi.org/10.1038/ s41467-021-26922-4.
- Jelinek, J., Cline, A.R., 2010. Chapter 10.25 Kateretidae Erichson in Agassiz, 1846. In: Leschen, R.A.B., Beutel, R.G., Lawrence, J.F. (Eds.), Handbook of Zoology, Arthropoda: Insecta, Coleoptera, Beetles Morphology and Systematics. De Gruyter, Berlin, pp. 386–390. https://doi.org/10.1515/9783110911213.386.
- Kirejtshuk, A.G., Azar, D., 2008. New taxa of beetles (Insects, Coleoptera) from Lebanese amber with evolutionary and systematic comments. Alavesia 2, 15–46.
- Kirejtshuk, A.G., Nel, A., 2008. New beetles of the suborder Polyphaga from the Lowermost Eocene French amber (Insecta: Coleoptera). Annales de la Société Entomologique de France 44, 419–442.
- Korasidis, V.A., Wagstaff, B.E., 2020. The rise of flowering plants in the high southern latitudes of Australia. Review of Palaeobotany and Palynology 272, 104126. https://doi.org/10.1016/j.revpalbo.2019.104126.
- Kupryjanwicz, J., Lyubarsky, G., Perkovsky, E., 2021. Heterhelus buzina sp.n. (Coleoptera: Kateretidae) from Rovno amber: the first proxy for Sambucus in the

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Eocene of Eastern Europe. Invertebrate Zoology 18, 16–24. https://doi.org/ 10.15298/invertzool.18.1.02.

- Lawrence, J.F., 2010. Chapter 11.3. Pterogeniidae Crowson, 1953. In: Kükenthal, W., Leschen, R.A.B., Beutel, R.G., Lawrence, J.F. (Eds.), Volume 2 Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia partim). De Gruyter, Berlin, New York, pp. 501–504. https://doi.org/10.1515/9783110911213.501.
- Lefkovitch, L.P., 1958. Unusual antennal characters in some Laemophloeinae (Coleoptera: Cucujidae) and their taxonomic importance. Proceedings of the Royal Entomological Society, London (B) 27, 93e100.
- Mao, Y.Y., Liang, K., Su, Y.T., Li, J.G., Rao, X., Zhang, H., Xia, F.Y., Fu, Y.Z., Cai, C.Y., Huang, D.Y., 2018. Various amberground marine animals on Burmese amber with discussions on its age. Palaeoentomology 1, 91–103. https://doi.org/ 10.11646/palaeoentomology.1.1.11.
- Peña-Kairath, C., Delclòs, X., Álvarez-Parra, S., Peñalver, E., Engel, M.S., Ollerton, J., Peris, D., 2023. Insect pollination in deep time. Trends in Ecology & Evolution 38, 749–759. https://doi.org/10.1016/j.tree.2023.03.008.
- Peris, D., Jelínek, J., 2019. Atypical short elytra in Cretaceous short-winged flower beetles (Coleoptera: Kateretidae). Palaeoentomology 2, 505–514. https:// doi.org/10.11646/palaeoentomology.2.5.14.
- Peris, D., Jelínek, J., 2020. Syninclusions of two new species of short-winged flower beetle (Coleoptera: Kateretidae) in mid-Cretaceous Kachin amber (Myanmar). Cretaceous Research 106, 104264. https://doi.org/10.1016/j.cretres.2019.104264.
- Peris, D., Labandeira, C.C., Barron, E., Delclos, X., Rust, J., Wang, B., 2020. Generalist pollen-feeding beetles during the mid-Cretaceous. iScience 23, 100913. https:// doi.org/10.1016/j.isci.2020.100913.
- Perkovsky, E.E., Rasnitsyn, A.P., Vlaskin, A.P., Taraschuk, M.V., 2007. A comparative analysis of the Baltic and Rovno amber arthropod faunas: representative samples. African Invertebrates 48, 229–245.
- Poinar Jr., G., Brown, A.E., 2018. Furcalabratum burmanicum gen. et sp. nov., a shortwinged flower beetle (Coleoptera: Kateretidae) in mid-Cretaceous Myanmar amber. Cretaceous Research 84, 1–5. https://doi.org/10.1016/ j.cretres.2017.11.010.
- Shi, G., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Yang, M.C., Lei, W.Y., Li, Q.L., Li, X.H., 2012. Age constraint on Burmese amber based on U-Pb dating of zircons. Cretaceous Research 37, 155–163. https://doi.org/10.1016/ i.cretres.2012.03.014.
- Sidorchuk, E.A., Vorontsov, D.D., 2018. Preparation of small-sized 3D amber samples: state of the technique. Palaeoentomology 1, 80–90. https://doi.org/ 10.11646/palaeoentomology.1.1.10.
- Song, Z.C., Shang, Y.K., Liu, Z.S., Huang, P., Wang, X.F., Qian, L.J., Du, B.A., Zhang, D.H., 2000. Fossil spores and pollen of China. Vol. 2. The Mesozoic spores and pollen. Science Press, Beijing, p. 710.

- Tihelka, E., Li, L.Q., Fu, Y.Z., Su, Y.T., Huang, D.Y., Cai, C.Y., 2021. Angiosperm pollinivory in a Cretaceous beetle. Nature Plants 7, 445e451. https://doi.org/10.1038/ s41477-021-00893-2.
- The Angiosperm Phylogeny Group, 2016. An update of the angiosperm phylogeny group classification for the orders and families of flowering plants: APG IV. Botanical Journal of the Linnean Society 181, 1–20. https://doi.org/10.1111/boj.12385.
- Thomas, M.C., 1988. A revision of the new world Species of Cryptolestes Ganglbauer (Coleoptera: Cucujidae: Laemophloeinae). Insecta Mundi 2, 43–65.
- Thomas, M.C., 1995. A remarkable new species of Placonotus Macleay from Malaysia (Coleoptera: Laemophloeidae [Cucujidae, Sens. Lat.]). The Coleopterists Bulletin 49, 53–57.
- Walker, J.W., Walker, A.G., 1984. Ultrastructure of Lower Cretaceous angiosperm pollen and the origin and early evolution of flowering plants. Annals of the Missouri Botanical Garden 464–521.
- Wickham, H.F., 1912. A report on some recent collections of fossil Coleoptera from the Miocene shales of Florissant. Bulletin from the Laboratories of Natural History of the State University of Iowa 6, 3–38.
- Yin, Z.W., Cai, C.Y., Huang, D.Y., 2018. Last major gap in scydmaenine evolution filled (Coleoptera: Staphylinidae). Cretaceous Research 84, 62-68. https://doi.org/ 10.1016/j.cretres.2017.10.026.
- Zhao, Q., Huang, D.Y., Cai, C.Y., 2022. Pelretes bicolor sp. nov., a new short-winged flower beetle (Coleoptera: Kateretidae) from mid-Cretaceous amber of northern Myanmar. Cretaceous Research 140, 105330. https://doi.org/10.1016/ i.cretres.2022.105330.
- Zhao, Q., Huang, D., Cai, C., 2023a. A new genus of short-winged flower beetles with an enlarged antennal scape in mid-Cretaceous amber from Northern Myanmar (Coleoptera: Kateretidae). Diversity 15, 19. https://doi.org/10.3390/d15010019.
- Zhao, Q., Huang, D., Cai, C., 2023b. A new short-winged flower beetle with exaggerated head and antennal scape in mid-Cretaceous amber from northern Myanmar (Coleoptera: Kateretidae). Cretaceous Reasearch 149, 105567. https:// doi.org/10.1016/j.cretres.2023.105567, 2023.
- Zhao, Q., Huang, D., Cai, C., 2023c. A new short-winged flower beetle with sexual dimorphism in antennal scape (Coleoptera: Kateretidae) in Cretaceous amber form northern Myanmar. PalZ (under revision).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10. 1016/j.cretres.2024.105848.