



The first larval record of Migadopinae (Coleoptera: Adephaga: Carabidae) from mid-Cretaceous Kachin amber, northern Myanmar

Hua Liu ^{a, b}, Rolf G. Beutel ^c, Kirill V. Makarov ^d, Edmund A. Jarzembowski ^b,
Chuantao Xiao ^{a, *}, Cihang Luo ^{b, e, **}

^a School of GeoSciences, Yangtze University, Wuhan, Hubei 430100, China

^b State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology and Center for Excellence in Life and Palaeoenvironment, Chinese Academy of Sciences, 39 East Beijing Road, Nanjing 210008, China

^c Institut für Zoologie und Evolutionsforschung, Friedrich-Schiller-Universität Jena, 07743 Jena, Germany

^d Moscow State Pedagogical University, Zoology & Ecology Department, Kibalchicha Str. 6, Build. 3, Moscow 129164, Russia

^e University of Chinese Academy of Sciences, Beijing 100049, China

ARTICLE INFO

Article history:

Received 28 July 2022

Received in revised form

16 October 2022

Accepted in revised form 29 October 2022

Available online 3 November 2022

Keywords:

Coleoptera

Carabidae

Migadopinae

Mid-Cretaceous

Myanmar

New species

ABSTRACT

A new genus and species of Carabidae (Coleoptera: Adephaga), *Cretomigadops bidentatus* gen. et sp. nov., is described based on a well-preserved specimen from mid-Cretaceous Kachin amber from northern Myanmar. It is a first instar shortly after hatching, with distinct, elongate frontal eggburst and a disproportionately large head. *Cretomigadops bidentatus* gen. et sp. nov. displays typical adephagan features and is classified as a larva of Carabidae based on a strongly sinuate frontal suture. It is assigned to Migadopinae based on characters of the head, especially the presence of two acute subapical mandibular teeth. It differs from other known genera of this small subantarctic subfamily by its long urogomphus, elongate legs with equal pretarsal claws and a long abdominal segment X. It is the first definite Mesozoic larval record of Carabidae from amber. Differences between *C. bidentatus* gen. et sp. nov. and four other fossil caraboid larvae are also discussed. The mandibles with a falcate apical tooth and two additional sharp subapical teeth indicate that *C. bidentatus* gen. et sp. nov. was a specialized active predator and good at grasping and piercing small arthropods. The elongate and articulated urogomphi, the long legs, the well-developed stemmata and the pigmented cuticle indicate that the larva was a surface runner, moving mostly on the soil surface and hunting more or less fast-moving prey. In contrast to the subantarctic distribution of Migadopinae, *C. bidentatus* gen. et sp. nov. preserved in Burmite shows that the distribution range of the subfamily was wider in the Mesozoic.

© 2022 Elsevier Ltd. All rights reserved.

1. Introduction

Adephaga is the second-largest suborder within Coleoptera with more than 45,000 described species (Beutel et al., 2020). It is traditionally divided into the aquatic Hydradephaga (Gyrinidae, Haliplidae, Meruidae, Noteridae, Amphizoidae, Aspidytidae, Hygrobiidae, Dytiscidae) and the terrestrial Geadephaga (Trachypachidae, Carabidae). The monophyly of the latter is firmly

established (e.g. Beutel et al., 2020; Vasilikopoulos et al., 2021), whereas Hydradephaga is likely paraphyletic (McKenna et al., 2015, 2019; Zhang et al., 2018; Beutel et al., 2020; Brandmayr, 2021), with Gyrinidae forming the sistergroup to all remaining adephagan families (Beutel and Roughley 1988; Vasilikopoulos et al., 2021).

Carabidae (ground beetles), by far the largest family within Adephaga, together with the relictual Trachypachidae, constitutes the superfamily Caraboidea (Beutel et al., 2020). The phylogenetic position and taxonomic status of Rhysodinae, Cicindelinae and Paussinae are controversial. All of them were considered separate families at a certain stage by some authors (e.g. Beutel, 1992; Makarov, 2008; Bousquet, 2012; Duran and Gough, 2020; Brandmayr, 2021). In contrast, recent research based on genomic data shows that they are part of the Carabidae, and this opinion is

* Corresponding author.

** Corresponding author. State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology and Center for Excellence in Life and Palaeoenvironment, Chinese Academy of Sciences, 39 East Beijing Road, Nanjing 210008, China.

E-mail addresses: ctxiao@yangtzeu.edu.cn (C. Xiao), chluo@nigpas.ac.cn (C. Luo).

widely accepted today (e.g. López-López and Vogler, 2017; Baehr and Will, 2019; McKenna et al., 2019; Beutel et al., 2020).

The predacious and campodeiform adepagan larvae are characterized by a distinctly prognathous head, four-segmented antennae, a fused labrum, six-segmented thoracic legs with paired pretarsal claws, and preoral digestion. Carabid larvae differ from the adepagan groundplan in several features: the antennae are anteriorly directed, the mandibles display only a single cutting edge, the maxillary grooves are absent, the maxillae are antenna-like, and the cardo is subdivided into two elements (Beutel, 1993). Plesiomorphic features preserved in the family are the well-developed abdominal segments IX and X (in contrast to Dytiscoidea) and the presence of well-developed functional spiracles I–VIII (e.g. Emden, 1942; Thompson, 1979; Arndt, 1993; Makarov, 1994; Beutel et al., 2006, 2020; Brandmayr, 2021). Presumptive apomorphies of the family are the sinuate frontal suture, a distinctly protracted prementum, and a distinctly developed hypopharyngeal filter formed by long microtrichia (Beutel, 1993, 1997). Despite the abundant fossils of adult beetles, the fossil record of beetle larvae is extremely sparse, particularly in Caraboidea. There are only four reliable records of fossil caraboid larvae in the Mesozoic so far, and all of them predate the Cretaceous period (Zhao et al., 2019).

Migadopinae is a small but distinctive subfamily of ground beetles comprising the two tribes Amarotypini and Migadopini (Larochelle and Larivière, 2001, 2007; Johns, 2010; Bouchard et al., 2011; Bousquet, 2012). The subfamily has a subantarctic distribution, mainly occurring in South America, Australia, and New Zealand (Gourlay, 1950; Johns, 1974, 2010; Erwin, 2011; Roig-Juñent and Rouaux, 2012; Lawrence and Ślipiński, 2013; Baehr and Will, 2019). The tribe Amarotypini currently consists of four genera (i.e. *Amarotypus* Bates, 1872; *Migadopiella* Baehr, 2009; *Amarophilus* Larochelle et Larivière, 2022; *Amaroxenus* Larochelle et Larivière, 2022) (Larochelle and Larivière, 2022). The other tribe Migadopini comprises 16 genera. However, the number of species in each genus is low, and there are likely many more genera and species to be discovered and described (Baehr, 2009; Martin Baehr, 2013; Roig-Juñent and Rouaux, 2012). Like the sparse research on migadopine species generally, morphological descriptions of larvae are almost completely lacking (Johns 1974; see also Arndt 1993: p. 25). Presently all generic diagnoses are purely based on adults (Larochelle and Larivière, 2001, 2007; Johns, 2010).

There is no fossil record of Migadopinae so far. Herein we describe a novel new larva, *Cretomigadops bidentatus* gen. et sp. nov., from mid-Cretaceous Kachin amber, which can be attributed to the subfamily Migadopinae of Carabidae. It is the first carabid larva embedded in amber and the first record of Migadopinae from the Mesozoic.

2. Material and methods

The specimen described herein is from the Cretaceous deposits of the Hukawng Valley, Tanai/Danai Township, Myitkyina District of Kachin State, northern Myanmar; see the locality in fig. 1 of Yu et al. (2019). The amber from pits near Tanai/Danai in Kachin State is called Kachin amber, or Burmese amber *sensu stricto* (Zheng et al., 2018). The geological age of Kachin amber is considered to be earliest Cenomanian (ca. 99 Ma) (Shi et al., 2012).

The amber piece was collected in 2015, before the Myanmar military closed the Kachin amber mining in November 2017. It is now deposited in the School of GeoSciences, Yangtze University, Wuhan, Hubei, China (see 'Museum Catalogue Entry' in Supplementary Material).

Observations were made using a Zeiss Stemi 508 microscope and photographs were taken with a Zeiss Stereo Discovery V16 microscope system; measurements were obtained using Zen software. In most instances, incident and transmitted light were used simultaneously. All images are digitally stacked photomicrographic composites of approximately 10–60 individual focal planes obtained using the software Helicon Focus 6.7.1 for a better illustration of 3D structures. Photographs and drawings were adjusted and combined into plates using CorelDraw X8 graphic software.

For 3-dimensional reconstruction we scanned fossils at the micro-CT laboratory of NIGPAS, using a 3D X-ray microscope (3D-XRM), Zeiss Xradia 520 versa. Unlike conventional micro-CT, which relies on maximum geometric magnification and a flat panel detector to achieve high resolution, 3D-XRM uses a charge-coupled device (CCD)-based objective to achieve higher spatial resolution. Based on the size of the fossil specimen, a CCD-based 4× objective was used, providing isotropic voxel sizes of 2.0902 μm with the help of geometric magnification. During the scan, the acceleration voltage for the X-ray source was 40 kV (power 3W), and a thin filter (Air) was used to avoid beam hardening artefacts. To improve the signal-to-noise ratio, 2601 projections over 360° were collected, and the exposure time for each projection was 3s. Volume data were processed with VGStudio Max software (version 3.0, Volume Graphics, Heidelberg, Germany).

The morphological terminology of the specimen in this study follows Arndt (1993), Beutel (1993) and Lawrence and Ślipiński (2013).

3. Systematic palaeontology

Order Coleoptera Linnaeus, 1758
 Family Carabidae Latreille, 1802
 Subfamily Migadopinae Chaudoir, 1861a,b
 Tribe *incertae sedis*

***Cretomigadops* gen. nov.** (Figs 1–7)
 urn:lsid:zoobank.org:act:6B502DBE-D024-4309-8B41-90305B0672B9

Etymology. The generic epithet combines the prefix 'creto-' (Latin for chalky as in Cretaceous), in reference to the geological period of the new genus, and 'migadops', referring to the type genus of Migadopinae.

Type species. *Cretomigadops bidentatus* Liu, Beutel, Makarov & Luo sp. nov. by original designation and monotypy.

Included species. Type species only.

Diagnosis (larva). Body campodeiform. Head large, prognathous, without appendages almost half as long as thorax, about as wide as pronotum. Head capsule slightly longer than wide, distinctly narrowing posteriorly, with weak neck region. Labrum completely fused with clypeal region. Anterior part of frontale (=clypeofrons, frontoclypeolabrum) with moderately prominent trapezoid or subtriangular nasale, only partly visible and possibly with indistinct teeth, and shallow rounded adnasalia laterally. Any vestiges of clypeofrontal strengthening ridge lacking. Elongate eggburstors present on narrowed posterior part of frontale. Stemmata well-developed, with convex lens, six on each side, arranged in two vertical rows, with size slightly decreasing from ventral to dorsal. Coronal suture about half as long as head capsule; frontal sutures sinuate, enclosing U-shaped frontal region posteromedially, then abruptly bent laterad. Antenna inserted on oblique articulatory membrane, four-segmented, about as long as head capsule; all antennomeres elongate, cylindrical, of subequal length; penultimate antennomere with three long setae (=chaetae) and a conical



Fig. 1. Microphotographs of *Cretomigadops bidentatus* gen. et sp. nov., holotype, YU-CO-2022-001. A, dorsal view. B, lateral view. Scale bars = 1 mm.

sensorium inserted posterolaterally; terminal antennomere with three long setae. Mandibles falcate and symmetrical, widely separated, with single cutting edge; penicillum not visible; apical tooth elongate and slender, distinctly curved inwards, acute apically and distinctly serrated mesally; retinaculum or first subapical tooth prominent, triangular, slightly curved, with sharply pointed apex and serrated; additional second subapical tooth separated from retinaculum by distinct gap, smaller but also triangular and apically pointed. Maxilla long and narrow, strongly protracted, apparently inserted without maxillary groove; cardo not distinctly visible; stipes elongate, curved basally, six times longer than wide; galea articulated apicomeresally on stipes, slender, palp-like, two-segmented; galeomere II 1.3 times shorter than I and slenderer, slightly narrowing towards apex; maxillary palpus four-segmented, about as long as stipes; terminal maxillary palpomere shorter and narrower than proximal segments, almost peg-like; lacinia absent. Labium only partly visible; prementum wide, protracted, bearing two-segmented, elongated palps.

Thorax with distinctly sclerotized tergites. Prothorax larger than meso- and metathorax. Pronotum subrectangular, with acute angle anterolaterally, rounded posterolaterally; long seta inserted on

each of four corners. Meso- and metanotum shorter and slightly narrower than pronotum; mesonotum with nearly straight lateral margin, metanotum more rounded laterally; each with a seta inserted posterolaterally. Median ecdysial sutures not recognizable. Thoracic legs strongly developed, elongate, longer than thorax, six-segmented. Coxae and trochanters of most legs not distinctly recognizable, but metacoxae apparently elongate and conical, moderately narrowing distally. Metatrochanter only slightly shorter than metacoxa, tube-like, distinctly curved. Metafemur slightly longer than metacoxa, with short and separate proximal portion; slightly curved and very slightly widened proximally and distally. All tibiae distinctly shorter than femora, slightly widened distally and rounded apically. Tarsi elongate and slender, ca. 1.5 times as long as femora; slightly curved proximally, otherwise straight, slightly narrowing towards apex. Paired slender claws inserted apically.

Abdomen ten-segmented, only about as long as thorax, tapering posteriorly. Tergites slightly less sclerotized than thoracic ones. Abdominal segments I–VIII well-developed, similar in general structure. Dorsum mainly formed by moderately sclerotized, laterally rounded tergites. Nearly transparent paired epipleurites I–VIII, about as wide as length of tergites I–VIII, each of

them bearing a long seta and an annular spiracle. Abdominal ventrites very weakly sclerotized, with numerous bristles. Abdominal segment IX represented by very short, transverse, sclerotized tergite, distinctly narrower than tergite VIII, posteriorly bearing pair of elongate and articulated urogomphi, at base together as wide as tergite; base of urogomphi as long as rest of body excluding cephalic appendages and abdominal segment X. Abdominal segment X tubular, elongate, with at least five pairs of long setae.

Comparative notes. The attribution of the newly described larva to Migadopinae is first of all supported by the structure of the mandible, notably the presence of two sharp subapical teeth, a condition which is not known in any other carabid subfamily (see Discussion below). The new genus differs in larval characteristics from all known consubfamilial genera by its leg proportions, symmetric claws and the long urogomphi. By its mandibular structure, shape and, in part, cephalic chaetotaxy, the new genus seems to be particularly similar to the *Migadopinae* gen. et sp. indet. larva described by Johns (1974). Unfortunately, it is impossible to properly trace several characters in the inclusion, notably the exact structure of the nasale. The micro-tomographic reconstruction of the head reveals a subtriangular nasale devoid of teeth. However, transmission microscopy shows that the right margin of the nasale forms a distinct step or a small tooth. In addition, the remaining frontal margin is apparently nearly straight, a condition that only rarely corresponds with a strongly protruding nasale in carabid larvae. This allows us to suggest that *Cretomigadops* gen. nov. could have had an indistinctly quadridentate nasale, possibly with a rather strongly protruding hypodon. However, confirmation of this is required.

Occurrence. Burmese amber from Kachin State, northern Myanmar; mid-Cretaceous (lowermost Cenomanian).

***Cretomigadops bidentatus* sp. nov.** (Figs 1–7)

urn:lsid:zoobank.org:act:DOC54669-21FD-474E-B9BF-E61BBF89165F

Etymology. The specific epithet refers to the two subapical mandibular teeth.

Material. Holotype, first instar larva. Specimen No. YU-CO-2022-001, deposited in the School of GeoSciences, Yangtze University, Wuhan, Hubei, China. The specimen embedded in a piece of amber is nearly intact. The dorsal side of the thorax is largely obscured by a bubble.

Locality and horizon. Burmese amber, from deposits near Tanai Village in the Hukawng Valley of northern Myanmar; lowermost Cenomanian (mid-Cretaceous).

Diagnosis (larva). As for genus.

Description (larva). Body length ca. 3.01 mm (mouthparts and urogomphi not included) (Fig. 1). Head capsule ca. 0.85 mm long, 0.69 mm wide (Fig. 2A–B). Moderately prominent anteromedian nasale without distinctly visible individual teeth; anterior edge of frontale straight between this structure and shallowly rounded lateral adnasalia (Fig. 3A). Coronal suture ca. 0.27 mm long. One pair of long setae (PA₇) inserted on epicranial plates, ca. 0.52 mm long (Fig. 2A, B). Antenna ca. 0.78 mm long; antennomere I ca. 0.20 mm long, 0.05 mm wide; antennomere II ca. 0.22 mm long, 0.05 mm wide; antennomere III ca. 0.18 mm long, 0.04 mm wide; antennomere IV ca. 0.18 mm long, 0.03 mm wide (Fig. 2C, D).

Mandibles ca. 0.58 mm long. Distal subapical tooth about 0.12 mm long and proximal one ca. 0.06 mm long; apical tooth finely serrated along mesal edge; distal subapical tooth with fine serration along anterior edge and few minute teeth on posterior margin (Fig. 2E). Maxillary stipes ca. 0.28 mm long, 0.08 mm wide (Fig. 2F). Maxillary palpomere I ca. 0.07 mm long, 0.05 mm wide;

palpomere II ca. 0.06 mm long, 0.04 mm wide; palpomere III ca. 0.04 mm long, 0.03 mm wide; palpomere IV, ca. 0.07 mm long, 0.03 mm wide (Fig. 2G).

Pronotum ca. 0.42 mm long, 0.66 mm wide. Meso- and meta-thorax each ca. 0.24 mm long, 0.65 mm wide (Fig. 4A, B).

Forelegs shortest, femora ca. 0.43 mm long, 0.07 mm wide; tibiae ca. 0.24 mm long, 0.08 mm wide; tarsus ca. 0.54 mm long, 0.04 mm wide. Midlegs intermediate, femora ca. 0.47 mm long, 0.10 mm wide; tibiae ca. 0.29 mm long, 0.08 mm wide; tarsus ca. 0.66 mm long, 0.04 mm wide. Hindlegs longest, femora ca. 0.55 mm long, 0.11 mm wide; tibiae ca. 0.32 mm long, 0.10 mm wide; tarsus ca. 0.77 mm long, 0.04 mm wide. Paired pretarsal claws of equal length, very slender, without additional hook, ca. 0.14 mm long (Fig. 4C–F).

Abdominal segments I–VIII similar in general structure, with dorsum consisting of tergum and paired epipleurites; venter membranous with numerous bristles (Fig. 5A, B); distinct spiracles present on abdominal segments I–VIII, similar in size (Fig. 5C). Paired urogomphi inserted posterodorsally on abdominal segment IX, elongate (Fig. 5D, E), ca. 2.46 mm long, almost five times as long as abdominal segment X. Abdominal segment X tubular (Fig. 5F), ca. 0.52 mm long, 0.09 mm wide, with long setae.

Chaetotaxy. The good preservation condition of the larva allows us to identify a considerable number of setae and thus to reconstruct the chaetom.

Setae on frontal sclerite (Fig. 6) only discernible on basal part, macroseta FR₂ and microsetae FR₁ and FR₃ visible, and both FR₂ and FR₃ located at about same level. Parietal sclerites with macrosetae PA₇, PA₁₁ and PA₁₄; seta PA₉ long, about 1/3rd as long as PA₇. Basal complex PA₁–PA₄ only fragmentarily discernible, but appears very similar to standard set typical of Carabidae.

Antennae (Fig. 6) with macrosetae AN₁–AN₅ and AN₇ subequal in length, AN₆ short, less than diameter of antennomere IV. Sensory complex of antennomere III consisting of large and rounded sensorium, as well as trichoid sensillum and subconical sensillum. In addition to AN₆ on apex of antennomere IV, single conical sensillum placed on high socket.

Mandibles (Fig. 6) with distinct placoid sensilla MN_a and MN_c; MN₁ seta missing but base clearly visible.

Stipes of maxilla with macrosetae MX₂ and MX₃ at outer edge, and inner margin with group of small and straight setae gMX and large MX₅; lacinia and MX₆ indistinguishable. Sensilla on galea only partially visible, apex of galeomere II with conical sensilla, long centrally and short peripherally. Seta MX₁₀ about as long as palpomere I. Only one seta, ventral MX₁₁, discernible on palpomere III. Last palpomere girded with large conical sensilla; this zone poorly sclerotized, appearing like separate pseudosegment (Fig. 6).

Setae on labium poorly visible, gLA₃ absent from prementum, LA₂ rather long, slightly shorter than palpomere I. Neither ligula nor ligular setae discernible. Apical labial palpomere poorly visible; based on shape probably with annular group of sensilla on apical third, similar to those on apex of maxillary palp; probably with differentiation of one or two pseudosegments (Fig. 6).

Only few setae discernible on thoracic segments: lateral macrosetae PR₆, PR₁₁ and ME₁₂; short and spiniform ME₉ and ME₁₃ also distinguishable. Setae on disk short or reduced, and macrosetae absent.

Leg chaetom (Fig. 7A) almost fully reconstructed, except for some coxal setae, trochanteral placoid sensilla, and small setae on tarsal apex. Almost identical to generalized pattern, but frontal femoral and tibial setae (FE_{2,3}, TI_{3,4}) much longer than posterior ones (FE_{4,5}, TI_{5,6}).

Abdominal tergites with several setae, especially discal ones, greatly reduced in size or missing. TE₉ and TE₁₀ distinctly visible,

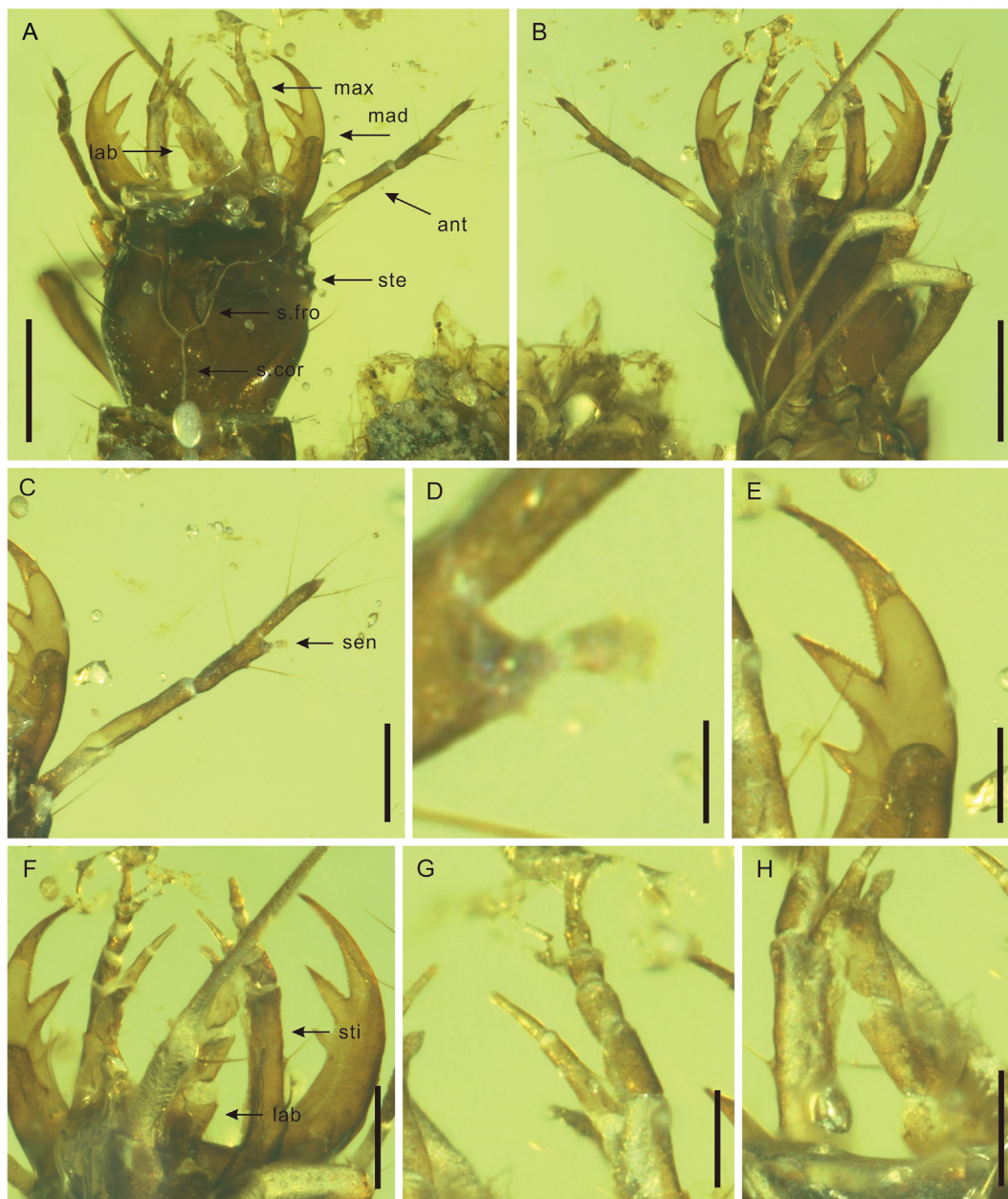


Fig. 2. Photographs showing details of *Cretomigadops bidentatus* gen. et sp. nov., holotype, YU-CO-2022-001. A, head, dorsal view. B, head, ventral view. C, antenna, dorsal view. D, sensorium on the penultimate antennomere. E, mandible, dorsal view. F, maxilla, ventral view. G, maxillary palpus and galea, dorsal view. H, Labium, dorsal view. Abbreviations: ste, stemma; ant, antenna; sen, sensorium; mad, mandible; max, maxilla; lab, labium; sti, stipes; s.cor, coronal suture; s.fro, frontal suture. Scale bars for A–B = 0.4 mm; C, F = 0.2 mm; D = 0.03 mm; E, G, H = 0.1 mm.

and microseta distinguishable near anterior margin, probably TE₁ (Fig. 7B). Size and shape of setae TE₉ and E₁₀ varying from segment to segment, TE₉ on tergite VIII large (length ca 0.94 mm) and spiniform, but TE₁₀ small and fusiform (Fig. 7C). Sternites and pleurites (Fig. 7D) both with ordinary sets of setae (only ST₁ not visible), with sizes and proportions similar to condition typical for Carabidae.

Long and slender urogomphi with full set of setae UR₄–UR₉ (Fig. 7E), UR₁–UR₃ not visible on specimen. Macrosetae UR₄–UR₈ similar in size, but UR₉ only half as long as UR₈.

Segment X (Fig. 7F) with rather long dorsal (PY_{2,3}) and ventral (PY_{4,6,7}) setae, with neither PY₁ nor PY₅ visible. Additional setae missing.

Thus, *Cretomigadops bidentatus* gen. et sp. nov. is characterized by oligochaetosis (see Makarov, 1996): the setae are strongly

differentiated in size (macrosetae at least 4 times longer than microsetae) and partly in shape, with some of them thickened and spiniform.

4. Discussion

The combination of a campodeiform body, prognathous head, six-segmented thoracic legs, a ten-segmented abdomen without leglets, and articulated urogomphi on abdominal segment IX unambiguously indicate that *Cretomigadops bidentatus* gen. et sp. nov. is an adephagan larva. This new genus can be excluded from Myxophaga and Polyphaga based on the presence of six-segmented legs with two tarsal claws (legs have five or fewer segments and a single claw in Myxophaga and Polyphaga) and four-segmented

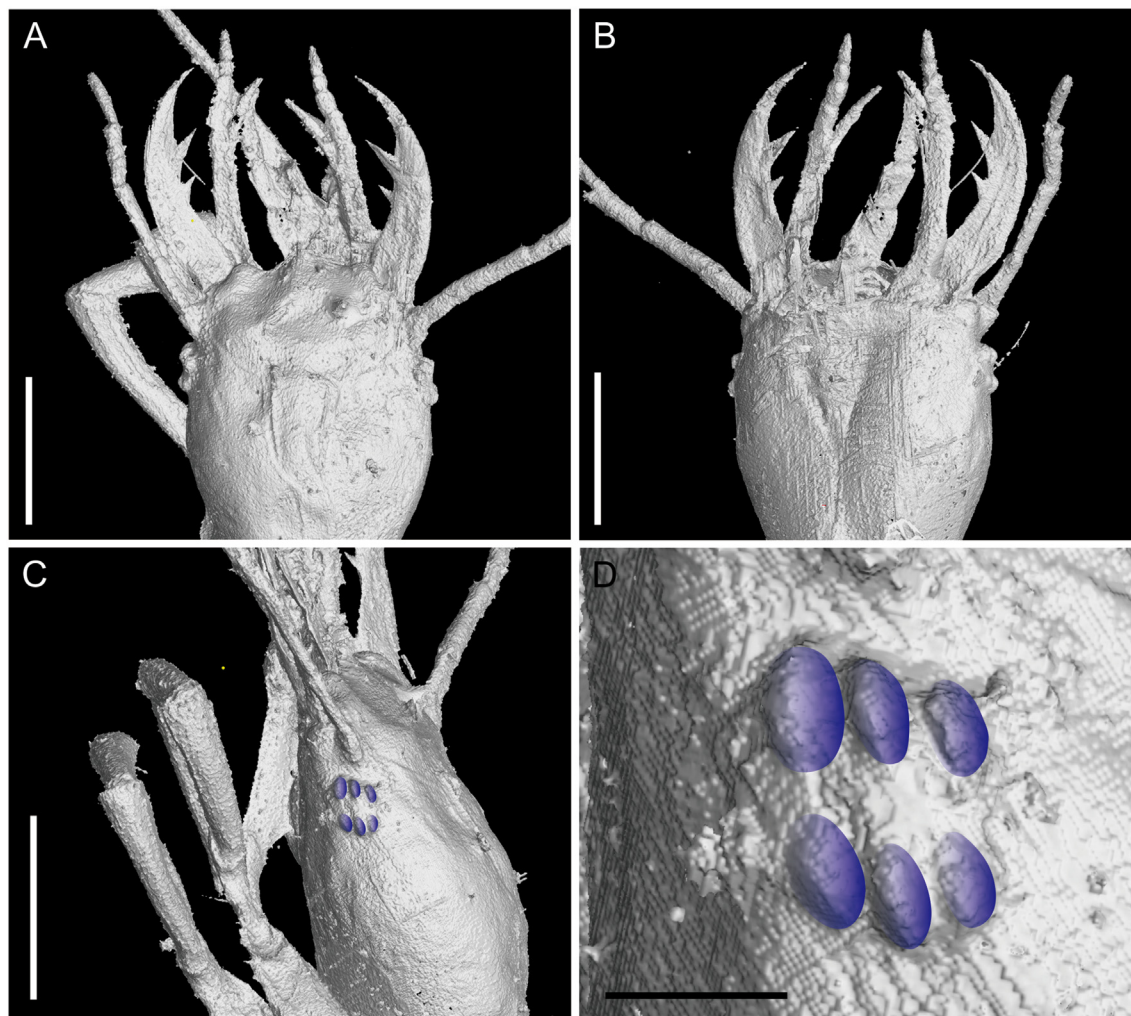


Fig. 3. Micro-tomographic reconstruction of *Cretomigadops bidentatus* gen. et sp. nov., holotype, YU-CO-2022-001. A, head, dorsal view. B, head, ventral view. C, head, lateral view. D, Stemmata, lateral view. Scale bars for A–C = 0.4 mm; D = 0.1 mm.

antennae (never occurring in Myxophaga and only very rarely and secondarily in Polyphaga). It is distinguished from Archostemata by its slender postcephalic body, the lack of mandibular molae and of the ligular sclerome, the fused labrum, and the protracted slender maxillae (Thompson, 1979; Beutel, 1993; Beutel and Haas, 2000; Alekseev, 2013). Aside from the unambiguous placement in Adephaga, *C. bidentatus* gen. et sp. nov. can be reliably assigned to the megadiverse Carabidae. An apomorphic condition characterizing this family, i.e. Geadephaga excluding Trachypachidae, is the distinctly sinuate frontal suture (Beutel, 1992b, 1993; see also Thompson, 1979). An additional feature of carabid larvae is the presence of three apical setae on antennomere III (e.g. Arndt, 1993). The larva can be easily excluded from Rhyssodinae, Cicindelinae, Paussinae, Pseudomorphinae, and Carenina of Scaritinae due to the slender postcephalic body, presence of articulated urogomphi on abdominal segment IX, absence of hooks on abdominal segment X, and absence of a terminal disk on abdominal segments VIII–IX (Lawrence and Ślipiński, 2013; Brandmayr, 2021).

We assign *C. bidentatus* gen. et sp. nov. to the subfamily Migadopinae based on the presence of two distinct and acute subapical mandibular teeth, with the posterior one smaller than the anterior one (Johns, 1974; see also Arndt, 1993). Bidentate mandibles also occur in Omophronini, but they are blunt in larvae of this group (Beutel, 1992a). Moreover, the entire cephalic morphology differs

strongly (Beutel, 1992a), and the pretarsal claws in Omophronini are unequal (Thompson, 1979). Several characteristics of larvae of Migadopinae cannot be observed in our fossil specimen. This includes pleural glands and pores on abdominal segments I–VIII (Johns, 1974). Two additional features tentatively support a placement in this subfamily, the posteriorly narrowed head and the absence of postocular and cervical ridges. However, both features also occur in other groups (Thompson, 1979). The postocular and cervical ridges are a derived feature characterizing a large subunit of ‘higher’ Carabidae including Scaritinae, Broscinae, Trechinae and Harpalinae (Beutel, 1993). This indicates that the larva described here belongs to a ‘middle grade’ of the family.

Cretomigadops bidentatus gen. et sp. nov. resembles the larvae of the migadopine genus *Loxomerus* Chaudoir, 1842, but is distinguished by its elongated legs with equal claws. In addition, the urogomphi of *C. bidentatus* gen. et sp. nov. are about five times as long as abdominal segment X, versus a similar length in *Loxomerus* (Johns, 1974).

It is noteworthy that the composition of the sensory antennal complex is quite different in the described larvae of Migadopinae (Larsson, 1943; Johns, 1974) and in *Cretomigadops* gen. nov. In carabid larvae, such variability is likely a plesiomorphic syndrome, as the stabilization of the number and types of antennal sensilla is typical for ‘higher Carabidae’ (Makarov, 1999). In addition, in the

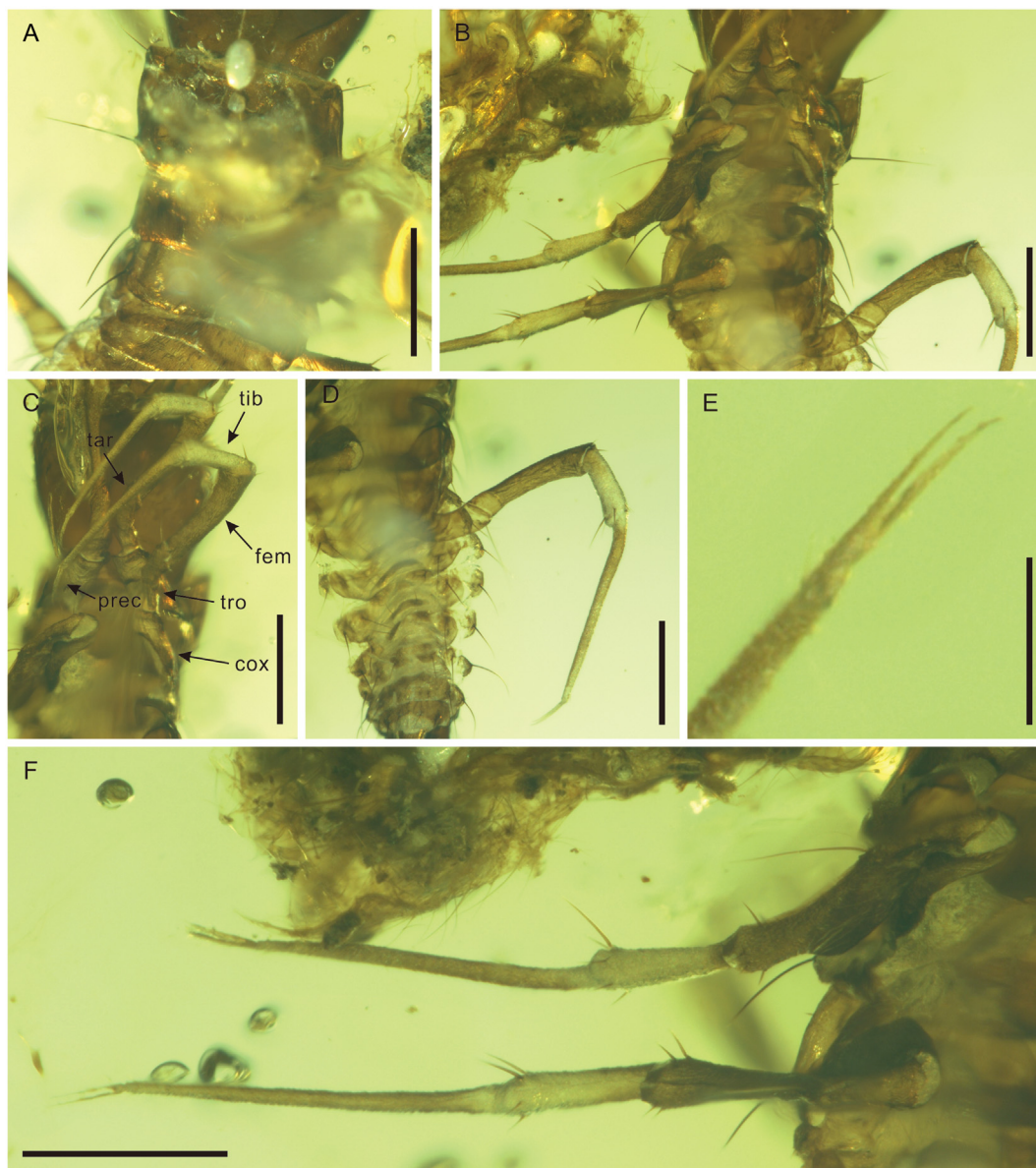


Fig. 4. Detailed photographs of thorax and legs of *Cretomigadops bidentatus* gen. et sp. nov., holotype, YU-CO-2022-001. A, thorax in dorsal view. B, thorax and legs in ventral view. C, foreleg and midleg, ventral view. D, hindleg, ventral view. E, pretarsal claws of foreleg, dorsal view. F, midleg and hindleg, ventral view. Abbreviations: cox, coxa; tro, trochanter; fem, femur; tib, tibia; tar, tarsus; prec, pretarsal claws. Scale bars for A–D, F = 0.4 mm; E = 0.1 mm.

larva of *Cretomigadops* gen. nov., the gMX setae are straight and simple, without a more or less sharp bend, outgrowths or a serration, a plesiomorphic state of the maxillary filter (Makarov, 1996). In this way, despite the significant specialization of the *Cretomigadops* gen. nov. larva, it has apparently preserved plesiomorphic features, indicating the proximity of Migadopinae to the 'basal grade' of Carabidae.

The presence of a strongly serrated retinaculum and long urogomphi resembles conditions observed in Loricerinae. However, *C. bidentatus* can be easily set apart from larvae of this group by the presence of a second subapical mandibular tooth, and the absence of a unique type of galea, with the second segment covered by a hyaline substance and used for prey catching. Besides this, abdominal segment X in *C. bidentatus* is distinctly longer than that of larvae of *Loricera* Latreille, 1802 (Makarov, 1994). Ball and Erwin (1969) suggested that the similarities between Loricerinae and

Migadopinae are the result of convergence, failing to reflect common ancestry. Yet this remains unclear.

There are only four reliable records of fossil caraboid larvae in the Mesozoic so far, all of them assigned to the genus *Carabilarva*: *Carabilarva jurassica* Ponomarenko, 1985, *Carabilarva robusta* Makarov, 1995, *Carabilarva triassica* Makarov and Prokin, 2013, and *Carabilarva gongi* Zhao et al., 2019. All of them are compression fossils and the first three are in a poor condition of preservation (Ponomarenko, 1985; Makarov, 1995; Prokin et al., 2013; Zhao et al., 2019). *Carabilarva jurassica* is the earliest fossil larval record of Caraboidea, but a clear family or even subfamily assignment is not possible due to its lack of observable morphological features. It was speculated that *C. robusta* is closely related to Trachypachidae, based on its long coronal suture and wide and laterally rounded head. However, these are rather vague and plesiomorphic features not suitable for a phylogenetic placement. *Carabilarva triassica* is

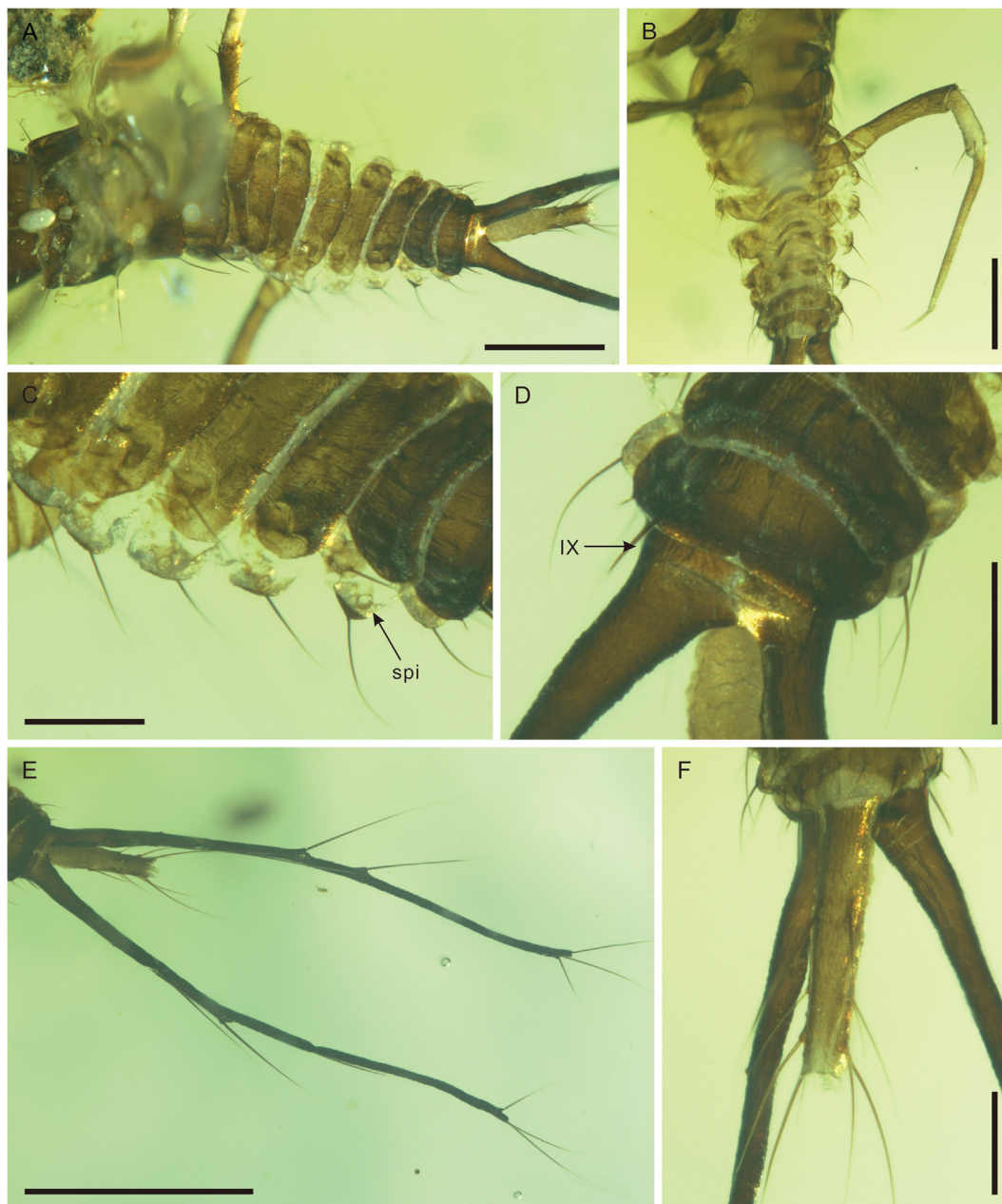


Fig. 5. Abdomen of *Cretomigadops bidentatus* gen. et sp. nov., holotype, YU-CO-2022-001. A, abdomen, dorsal view. B, abdomen, ventral view. C, abdominal spiracles, dorsal view. D, abdominal segment IX, dorsal view. E, urogomphi, dorsal view. F, abdominal segment X, ventral view. Scale bars for A = 0.5 mm; B = 0.4 mm; C, D, F = 0.2 mm; E = 1 mm.

the earliest known larva of Caraboidea. Its head is wider than long, the coronal suture is short, the mandible bears a single subapical tooth, and the legs display elongate trochanters and femora. The comparatively well-preserved and large *C. gongi* is ca. 20 mm long and equipped with a pair of short urogomphi. However, even in this case the recognizable features are insufficient for a reliable placement in Carabidae (or Caraboidea).

Whereas the preservation of larvae assigned to the genus *Carabilarva* is not sufficient for their systematic placement at the subfamily level, their description as part of one collective appears justified. In contrast, the larva of *Cretomigadops* gen. nov. shows nearly all of the taxonomically relevant features, allowing us to assign this genus to Migadopinae based on an unambiguous apomorphy and to establish a new genus in this family.

Like in other groups of Holometabola, unusual morphological structures of larvae can be considered as indicators of a specialized lifestyle (Brandmayr, 2021). Comparing structural features of the larva of *Cretomigadops* gen. nov. with suggested morphological adaptations of other ground beetle larvae (Sharova, 1981, 2008), a number of conclusions can be drawn about its life habits.

The distinctly pigmented head and tergites, well-developed eyes, long antennae, and urogomphi bearing macrosetae, indicate that such larvae, at least the first instar, mainly moved on the surface of the substrate. The very long coronal suture and the proportions of the frontal sclerite suggest that the head could assume a moderately declined orientation (approximately so as in the larvae of Nebriini, Notiophilini, Loricerini and, especially Dryptini and Galeritini), in this way hunting small and mobile arthropods and grasping them with the mandibles from above.

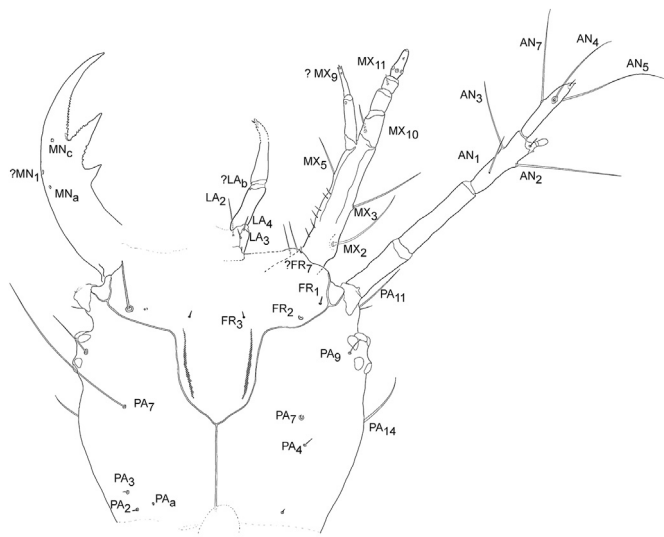


Fig. 6. Head of *Cretomigadops bidentatus* gen. et sp. nov., holotype, YU-CO-2022-001, reconstruction with chaetotaxy, not in scale.

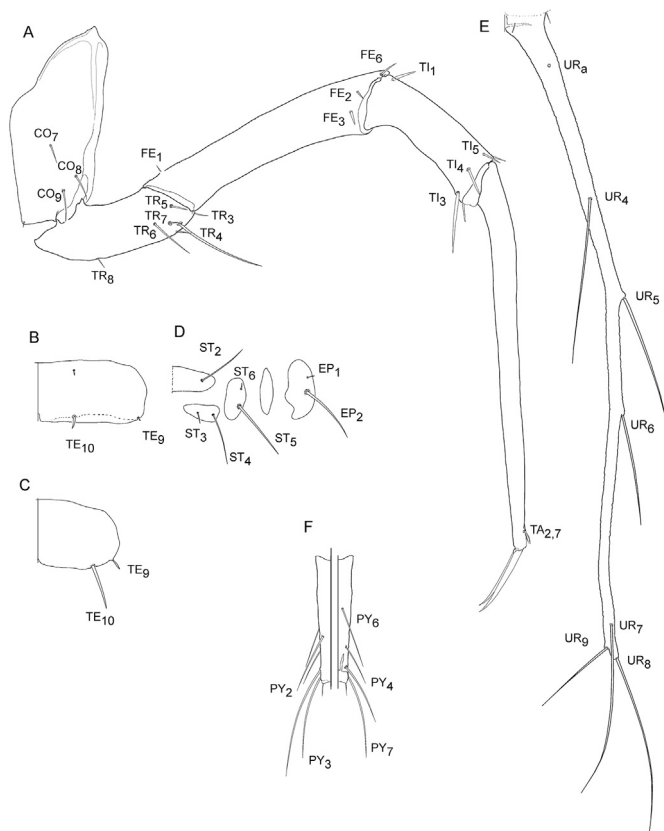


Fig. 7. *Cretomigadops bidentatus* gen. et sp. nov., holotype, YU-CO-2022-001, reconstruction with chaetotaxy, not in scale. A, hindleg, frontal view. B, abdominal tergite VI, right half. C, abdominal tergite VIII, right half. D, abdominal ventrite and pleurite VI, right half. E, right urogomphus. F, abdominal segment X, left-dorsal view, right-ventral view.

Strongly elongated tarsi (2.0–2.45 times the length of the tibia) and slender and long claws indicate an ability to run fast on the surface. However, the large anterior setae at the apex of the femur and tibia, combined with the long segment X and large ventral

spiracles, also suggest that the larva was able to squeeze through rather narrow cavities/spaces. This conclusion is tentatively confirmed by the peculiarities of the chaetotaxy, as shortened and/or reduced discal chaetae on the dorsal surface of the body are typical of larvae regularly moving in dense substrates. Thus, recent larvae assigned to the functional category of the hemicyptobionts series of the subclass Stratobionts-runners in the lifestyle system of Sharova (2008) can be considered as the closest analogue to *Cretomigadops* gen. nov.

A combination of features of *C. bidentatus* is not only characteristic of larvae of Carabidae, but also of ‘higher’ Staphylinidae (Staphylininae, Polyphaga) (e.g. Thayer, 2016), obviously a case of parallel evolution: a campodeiform body, prognathous head with fused labrum, well-developed thoracic legs, and a pair of articulated urogomphi on abdominal segment IX, composed of several segments. This larval configuration also suggests an active and predacious lifestyle as suggested above. In the case of *C. bidentatus*, this is also strongly supported by the elongate, falcate mandibles with a distinct serration and an additional subapical tooth, highly suitable not only for catching agile prey, like for instance spring-tails, but also for holding it in a secure grip, and for perforation of the cuticle and thus enabling preoral digestion. A dense preoral filter formed by long microtrichia as is characteristic of Carabidae, is likely present in *C. bidentatus*, but not visible in the fossil. Another characteristic of *C. bidentatus* and other carabid larvae is the slender and strongly protracted maxilla, resembling a ventrally inserted accessory antenna. These specialized paired ventral mouthparts are not suitable for mechanically processing food, but very likely screening the underground and are probably also involved in detecting prey. Another feature that can be considered in this context is the length and shape of the urogomphi. In the case of *C. bidentatus* and carabid larvae with similar appendages on segment IX, it can be assumed that the typical environment is the surface of the ground or loose leaf litter. The urogomphi with their long sensorial setae apparently function as sensorial apparatuses, mainly as a complex mechanoreceptive device. Larvae inhabiting narrow spaces beneath bark or burrowing in soil or other substrates tend to have solid and recurved urogomphi, assisting in locomotion; short and non-articulated urogomphi occur in larvae living in seasonally arid soils, for instance in Trachypachidae. It is likely that these robust structures facilitate digging in the substrate (Lawrence and Ślipiński, 2013; Brandmayr, 2021). In contrast, it is likely that *C. bidentatus* with its long legs, urogomphi and long and tubular abdominal segment X was a surface runner as pointed out above, mainly but not only moving on the soil surface.

A conspicuous feature of the fossil larva is the small size of the postcephalic body, in contrast to the strongly sclerotized head capsule. This suggests that the larva was enclosed in amber shortly after molting. Whereas the size and shape of the head are generally constant within one stage of beetle larvae, the postcephalic body, especially the abdomen with its weakly sclerotized or membranous lateral and ventral areas, can strongly expand after the larvae start taking up food. This usually results in a postcephalic body several times longer than the head (e.g. Arndt, 1993; fig. 1). Even though our larva is undoubtedly a first instar, the size of the head and known size correlations between adults and larvae (Emden, 1942: 8–13) allow for a tentative estimate of the size of adults of *Cretomigadops* gen. nov. It could have averaged 8.6 mm (7.4–10.6 mm), which is smaller than most recent species of the subfamily.

The present distribution of the Migadopinae is restricted to the subantarctic areas (e.g. Gourlay, 1950; Johns, 1974, 2010; Roig-Juñent and Rouaux, 2012; Lawrence and Ślipiński, 2013; Baehr and Will, 2019). The tribe Amarotyptini was formerly found only in New Zealand with only one genus (*Amarotyptus* Bates, 1872) until the discovery of another genus (*Migadopielia* Baehr, 2009) in

Tasmania (southern Australia) (Larochelle and Larivière, 2001; Johns, 2010; Martin Baehr, 2013). Recently, two additional genera from New Zealand were described by Larochelle and Larivière (2022). The other tribe Migadopini has a geographic distribution in South America, Australia, and New Zealand, summarily, eight genera occur in South America, i.e. *Aquilex* Moret, 1989 in the Andean region, *Rhytidognathus* Chaudoir, 1861a,b on the shores of the La Plata river, *Pseudomigadops* Jeannel, 1938, and *Migadopidius* Jeannel, 1938, *Migadops* Waterhouse, 1842, *Lissopterus* Waterhouse, 1843, *Monolobus* Solier, 1849, and *Antarctonomus* Chaudoir, 1861a,b in the sub-Antarctic region in Chile and Argentina (Roig-Juñent, 2012; Roig-Juñent and Rouaux, 2012); five genera occur in Australia, i.e. *Nebriosoma* Laporte de Castelnau, 1867, *Stichonotus* Sloane, 1910, *Decognmus* Sloane, 1915, *Calyptogonia* Sloane, 1920, *Dendromigadops* Baher, 2013 (Martin Baehr, 2013); and three genera are described from New Zealand and circum-Antarctic islands, i.e. *Loxomerus* Chaudoir, 1842, *Taenarthrus* Broun, 1914, *Calathosoma* Jeannel, 1938 (Larochelle and Larivière 2001; Johns, 2010). No migadopine species was hitherto recorded from the northern hemisphere. The discovery of *C. bidentatus* gen. et sp. nov. preserved in Burmite shows that the subfamily Migadopinae might have had a wider distribution in the Mesozoic.

5. Concluding remarks

The discovery of this specimen provides an important glimpse into the deep evolutionary history of Migadopinae, an isolated and phylogenetically crucial group of Carabidae, and will hopefully inspire new research on this exceptional group of Carabidae. The discovery of additional fossil specimens and of adults of Migadopini should have high priority.

Data availability

No data was used for the research described in the article.

Acknowledgements

We express our sincere thanks to the anonymous reviewers for their thoughtful comments on the manuscript. This research was supported by the Strategic Priority Research Program of the Chinese Academy of Sciences (XDB26000000), National Natural Science Foundation of China (42125201, 42288201), the Second Tibetan Plateau Scientific Expedition and Research (2019QZKK0706) and the CAS President's International Fellowship Initiative (PIFI). This is a contribution to UNESCO-IUGS IGCP Project 679.

References

Alekseev, V.I., 2013. The beetles (Insecta: Coleoptera) of Baltic amber: the checklist of described species and preliminary analysis of biodiversity. *Zoology and Ecology* 23, 5–12.

Arndt, E., 1993. Phylogenetische Untersuchungen larvalmorphologischer Merkmale der Carabidae (Insecta: Coleoptera). *Stuttgarter Beiträge zur Naturkunde (A)* 488, 1–56.

Baehr, M., 2009. A new genus and two new species of the subfamily Migadopinae from Tasmania (Coleoptera: Carabidae). *Folia Heyrovskyana (Series A)* 17, 95–103.

Baehr, M., Will, K., 2019. Carabidae Latreille 1802. In: Ślipiński, A., Lawrence, J.F. (Eds.), *Australian Beetles, Archostemata, Myxophaga, Adephaga, Polyphaga* (part), vol. 2. CSIRO Publishing, pp. 61–220.

Ball, G.E., Erwin, T.L., 1969. A taxonomic synopsis of the tribe Loricerini (Coleoptera: Carabidae). *Canadian Journal of Zoology* 47, 877–907.

Bates, H.W., 1872. Notes on Cicindelidae and Carabidae, and descriptions of new species (No. 16). *Entomologist's Monthly Magazine* 9, 49–52.

Beutel, R.G., 1992a. On the morphology of the head of the larva of *Omoglymmius hamatus* (LeConte) and the systematic position of Rhysodidae (Coleoptera: Adephaga). *Entomologica Scandinavica* 23, 169–184.

Beutel, R.G., 1992b. Study on the systematic position of Metriini based on characters of the larval head (Coleoptera: Carabidae). *Systematic Entomology* 17, 207–218.

Beutel, R.G., 1993. Phylogenetic analysis of Adephaga (Coleoptera) based on characters of the larval head. *Systematic Entomology* 18, 127–147.

Beutel, R.G., 1997. Über Phylogenese und evolution der Coleoptera (Insecta), insbesondere der Adephaga. *Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg (NF)* 31, 1–164.

Beutel, R.G., Haas, F., 2000. Phylogenetic relationships of the suborders of Coleoptera (Insecta). *Cladistics* 16, 103–141.

Beutel, R.G., Roughley, R.E., 1988. On the systematic position of the family Gyrinidae (Coleoptera: Adephaga). *Journal of Zoological Systematics and Evolutionary Research* 26, 380–400.

Beutel, R.G., Balke, M., Steiner, W.E., 2006. On the systematic position of Meruidae (Coleoptera, Adephaga) and the phylogeny of the smaller hydradephagan families. *Cladistics* 22, 102–131.

Beutel, R.G., Ribera, I., Fikáček, M., Vasilikopoulos, A., Misof, B., Balke, M., 2020. The morphological evolution of the Adephaga (Coleoptera). *Systematic Entomology* 45, 378–395.

Bouchard, P., Bousquet, Y., Davies, A.E., Alonso-Zarazaga, M.A., Lawrence, J.F., Lyal, C.H., Newton, A.F., Reid, C.A., Schmitt, M., Slipiński, S.A., Smith, A.B., 2011. Family-group names in Coleoptera (Insecta). *ZooKeys* 88, 1–972.

Bousquet, Y., 2012. Catalogue of Geadephaga (Coleoptera, Adephaga) of America, north of Mexico. *ZooKeys* 245, 1–1722.

Brandmayr, P., 2021. An outlook on the evolutionary history of Carabid beetles (Coleoptera, Adephaga). *Memorie della Società Entomologica Italiana* 97, 15–46.

Broun, T., 1914. Descriptions of new genera and species of Coleoptera. *Bulletin of the New Zealand Institute* 1, 79–142.

Chaudoir, M.de., 1842. Description de quelques genres nouveaux de la famille des carabiques. *Bulletin de la Société Impériale des Naturalistes de Moscou* 15, 832–857.

Chaudoir, M.de., 1861a. Matériaux pour servir à l'étude des cicindélètes et des carabiques (continuation). *Bulletin de la Société Impériale des Naturalistes de Moscou* 34, 491–576.

Chaudoir, M.de., 1861b. Matériaux pour servir à l'étude des cicindélètes et des carabiques (1-e partie). *Bulletin de la Société Impériale des Naturalistes de Moscou* 33, 269–337.

Duran, D.P., Gough, H.M., 2020. Validation of tiger beetles as distinct family (Coleoptera: Cicindelidae), review and reclassification of tribal relationships. *Systematic Entomology* 45, 723–729.

van Emden, F.V., 1942. A key to the genera of larval Carabidae. *Transactions of the Royal Entomological Society of London* 92, 1–99.

Erwin, T.L., 2011. *A Treatise on the Western Hemisphere Caraboidea (Coleoptera): Their Classification, Distributions, and Ways of Life*, 3. Pensoft series faunistica. Coronet Books Incorporated, p. 412.

Gourlay, E.S., 1950. Auckland Island Coleoptera. *Transactions of the Royal Society of New Zealand* 78, 171–202.

Jeannel, R., 1938. Les Migadopides (Coleoptera, Adephaga), une lignee sub-antarctique. *Revue Française d'Entomologie* 5, 1–55.

Johns, P.M., 1974. Arthropoda of the subantarctic islands of New Zealand (1) Coleoptera: Carabidae southern New Zealand, Patagonian, and Falkland Islands insular Carabidae. *Journal of the Royal Society of New Zealand* 4, 283–302.

Johns, P.M., 2010. Migadopini (Coleoptera: Carabidae: Migadopinae) of New Zealand. *Records of the Canterbury Museum* 24, 39–63.

Laporte de Castelnau, F.L., 1867. Notes on Australian Coleoptera. *Royal Society of Victoria* 8, 1–94.

Larochelle, A., Larivière, M.C., 2001. Carabidae (Insecta: Coleoptera): catalogue. *Fauna of New Zealand* 43, 1–285.

Larochelle, A., Larivière, M.C., 2007. Carabidae (Insecta: Coleoptera): synopsis of supraspecific taxa. *Fauna of New Zealand* 60, 1–188.

Larochelle, A., Larivière, M.C., 2022. Synopsis of the tribe Amarotyptini in New Zealand (Coleoptera: Carabidae). *Insecta Mundi* 0942, 1–30.

Larsson, S.G., 1943. Une larve de *Loxomerus* des îles Auckland (Carabidae: Migadopini). *Entomologiske Meddelelser* 23, 420–431.

Latreille, P.A., 1802. *Histoire naturelle: générale et particulière des crustacés et des insectes: Familles Naturelles des Genres*. F. Dufart, Paris, pp. 16–37 pls.

Lawrence, J.F., Ślipiński, A., 2013. *Australian Beetles* volume 1: Morphology, Classification and Keys. CSIRO Publishing, Melbourne, p. 561.

Linnaeus, C., 1758. *Systema Naturae*. Editio Decima, reformata, p. 824.

López-López, A., Vogler, A.P., 2017. The mitogenome phylogeny of Adephaga (Coleoptera). *Molecular Phylogenetics and Evolution* 114, 166–174.

Martin Baehr, 2013. A revision of the carabid tribe Migadopini in Australia (Insecta: Coleoptera: Carabidae: Migadopini). *Memoirs of the Queensland Museum/Nature* 56, 279–304.

Makarov, K.V., 1994. A key to the genera of the groundbeetle larvae (Coleoptera, Carabidae) of the Palearctic region. *Bollettino del Museo Regionale di Scienze Naturali di Torino* 12, 221–254.

Makarov, K.V., 1995. New data on the larvae of the Jurassic Carabomorpha (Coleoptera, Adephaga). *Journal of Paleontology* 29, 167–171.

Makarov, K.V., 1996. Patterns of chaetome modifications in ground-beetle larvae (Coleoptera: Carabidae). *Acta Societatis Zoologicae Bohemicae* 60, 391–418.

Makarov, K.V., 1999. Morphological evolution of the antennal sensorial complex of ground-beetle larvae (Coleoptera, Carabidae). In: *Problems of Soil Zoology (Proceedings of the II (XII) All-Russian Conference on Soil Zoology)*. KMK, Moscow, pp. 84–85.

- Makarov, K.V., 2008. Larval chetotaxy in the genus *Rhysodes* Dalman, 1823 and the position of Rhysodidae within Adephaga (Coleoptera). In: Back to the Roots and Back to the Future. Towards a New Synthesis amongst Taxonomic, Ecological and Biogeographical Approaches in Carabidology (Proceedings of the XIII European Carabidologists Meeting). Pensoft, Sofia-Moscow, pp. 101–124.
- McKenna, D.D., Wild, A.L., Kanda, K., Bellamy, C.L., Beutel, R.G., Caterino, M.S., Farnum, C.W., Hawks, D.C., Ivie, M.A., Jameson, M.L., Leschen, R.A.B., Marvaldi, A.E., McHugh, J.V., Newton, A.F., Robertson, J.A., Thayer, M.K., Whiting, M.F., Lawrence, J.F., Ślipiński, A., Maddison, D.R., Farrell, B.D., 2015. The beetle tree of life reveals Coleoptera survived end Permian mass extinction to diversify during the Cretaceous terrestrial revolution. *Systematic Entomology* 40, 835–880.
- McKenna, D.D., Shin, S., Ahrens, D., Balke, M., Beza-Beza, C., Clarke, D.J., Donath, A., Escalona, H.E., Friedrich, F., Letsch, H., Liu, S., Maddison, D., Mayer, C., Misof, B., Murin, P.J., Niehuis, O., Peters, R.S., Podsiadlowski, L., Pohl, H., Scully, E.D., Yan, E.V., Zhou, X., Ślipiński, A., Beutel, R.G., 2019. The evolution and genomic basis of beetle diversity. *Proceedings of the National Academy of Sciences* 116, 24729–24737.
- Moret, P., 1989. Un Migadopidae sans strie surnuméraire des Andes de l'équateur: *Aquilex diabolica* gen. nov. sp. nov. (Coleoptera, Caraboidea). *Nouvelle Revue d'Entomologie* 6, 245–257.
- Ponomarenko, A.G., 1985. Coleoptera from the Jurassic of Siberia and western Mongolia. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR* 211, 47–87.
- Prokin, A.A., Makarov, K.V., Ponomarenko, A.G., Bashkuev, A.S., 2013. New beetle larvae (Coleoptera: Coptoclavidae, Caraboidea, Polyphaga) from the Upper Triassic of Germany. *Russian Entomological Journal* 22, 259–274.
- Roig-Juñent, S., Rouaux, J., 2012. A new species of *Rhytidognathus* (Carabidae, Migadopini) from Argentina. *ZooKeys* 247, 45–60.
- Sharova, I.Kh., 1981. Zhiznennyye formy zhuzhelits (Carabidae). *Nauka, Moscow*, p. 360 (in Russian).
- Sharova, I.Kh., 2008. Adaptive radiation of carabid larvae (Coleoptera, Carabidae). In: Back to the Roots and Back to the Future. Towards a New Synthesis amongst Taxonomic, Ecological and Biogeographical Approaches in Carabidology (Proceedings of the XIII European Carabidologists Meeting). Pensoft, Sofia-Moscow, pp. 285–304.
- Shi, G., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Yang, M., Lei, W., Li, Q., Li, X., 2012. Age constraint on Burmese amber based on U–Pb dating of zircons. *Cretaceous Research* 37, 155–163.
- Sloane, T.G., 1910. Studies in Australian entomology. No. XVI. New species of Carabidae. *Proceedings of the Linnean Society of New South Wales* 35, 378–406.
- Sloane, T.G., 1915. Studies in Australian entomology. No. XVII. New genera and species of Carabidae. (Pamborini, Migadopini, Broscini, Cunepectini, Nomoni, Pterostichini, Platynini, Oodini, Harpalini, Lebini). *Proceedings of the Linnean Society of New South Wales* 40, 438–446.
- Sloane, T.G., 1920. The Carabidae of Tasmania. *Proceedings of the Linnean Society of New South Wales* 45, 113–178.
- Solier, A.J.J., 1849. Orden III. Coleópteros Pentámeros. In: Gay, C. (Ed.), *Historia Física y Política de Chile* 4 (Zoología), Paris, pp. 105–507.
- Thayer, M.K., 2016. Staphylinidae Latreille, 1802. In: Beutel, R.G., Leschen, R.A.B. (Volume eds.), *Coleoptera, Beetles. Volume 1: Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim)*. In *Handbook of Zoology*, Walter de Gruyter Berlin, 394–442.
- Thompson, R.G., 1979. Larvae of North American Carabidae with a key to the tribes. In: *Carabid Beetles*. Springer, Dordrecht, pp. 209–291.
- Vasilikopoulos, A., Balke, M., Kukowka, S., Pflug, J.M., Martin, S., Meusemann, K., Hendrich, L., Mayer, Ch., Maddison, D.R., Niehuis, O., Beutel, R.G., Misof, B., 2021. Phylogenomic analyses clarify the pattern of evolution of Adephaga (Coleoptera) and highlight phylogenetic artifacts due to model misspecification and excessive data trimming. *Systematic Entomology* 46, 991–1018.
- Waterhouse, G.R., 1842. Carabideous insects collected by Charles Darwin, Esq., during the voyage of Her Majesty's ship Beagle. *The Annals and Magazine of Natural History* 9, 134–139.
- Waterhouse, G.R., 1843. XLIII.—Description of a new genus of Carabideous Insects brought from the Falkland Islands by Charles Darwin, Esq. *The Annals and Magazine of Natural History* 11, 281–283.
- Yu, T.T., Kelly, R., Mu, L., Ross, A., Kennedy, J., Broly, P., Xia, F.Y., Zhang, H.C., Wang, B., Dilcher, D., 2019. An ammonite trapped in Burmese amber. *Proceedings of the National Academy of Sciences of the United States of America* 116, 11345–11350.
- Zhang, S.Q., Che, L.H., Li, Y., Dan, L., Pang, H., Ślipiński, A., Zhang, P., 2018. Evolutionary history of Coleoptera revealed by extensive sampling of genes and species. *Nature Communications* 9, 205.
- Zhao, X., Zhao, X., Fang, Y., Chen, L., Wang, B., 2019. A new caraboid larva from the Middle Jurassic of China (Insecta: Coleoptera). *Proceedings of the Geologists' Association* 130, 242–246.
- Zheng, D.R., Chang, S.C., Perrichot, V., Dutta, S., Rudra, A., Mu, L., Kelly, R.S., Li, S., Zhang, Q., Zhang, Q.Q., Wong, J., Wang, J., Wang, H., Fang, Y., Zhang, H.C., Wang, B., 2018. A Late Cretaceous amber biota from central Myanmar. *Nature Communications* 9, 3170.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cretres.2022.105413>.