



The earliest evidence of Omophroninae (Coleoptera: Carabidae) from mid-Cretaceous Kachin amber and the description of a larva of a new genus

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Abstract

Omophroninae is a distinctive monogeneric group of Carabidae, presumably placed relatively close to the root of the megadiverse adaphagan family. In the present study we describe a larva belonging to Omophroninae from mid-Cretaceous Burmese amber and erect a new genus †*Cretomophron*. Several features support the placement in this small but distinctive subfamily, such as the wedge-shaped head, the large triangular nasale, the elevated antennae with the apical segment directed sideways, the large and bidentate mandibular retinaculum, the enlarged hexagonal prothorax, legs with a distinct armature of spines, and the relatively narrow and posteriorly tapering abdomen. In contrast to larvae of the extant genus *Omophron* Latreille, the posterior tentorial grooves are not shifted backwards, apparently a plesiomorphic feature, the 2nd antennomeres are markedly longer, and the legs bear long setae rather thin and long spike-like setae. †*Cretomophron* also differs in the presence of numerous setae arranged in transverse rows on abdominal segment VI. Lateral lobe-like expansions of abdominal tergites are a conspicuous feature of the new genus but similar structures occur in later instars of *Omophron*. Structural specializations of the head, prothorax and legs strongly suggest that the larvae were burrowing in sand, like adults and larvae of the extant genus, and that they were efficient predators, detecting prey with the unusually shaped antennae and long maxillae, grasping it with the elongate apical mandibular tooth, and squeezing and piercing it between the bidentate retinaculum and large and triangular nasale.

Key words

Coleoptera, Adephaga, burrowing behavior, Myanmar, new species

1. Introduction

The fossil record of the megadiverse Carabidae (ca. 40.000 described spp.; e.g., Raupach et al. 2022) is relatively rich, with impression fossils dating back to the

Triassic (Ponomarenko 1977; Liu et al. 2023). However, larvae are extremely scarce in any deposits, with a total of only five specimens from the Mesozoic (Ponomaren-

ko 1985; Makarov 1995; Prokin et al. 2013; Zhao et al. 2019), four of them preserved as impression fossils from the Late Triassic and Jurassic, and one larva of Migadopinae embedded in mid-Cretaceous Burmite from Myanmar (Liu et al. 2023).

The discovery of a conspicuous larva embedded in Burmite, apparently belonging to Carabidae but with an unusual morphology, inspired us to carry out the present study. The single well-preserved specimen was examined using light microscopy and synchrotron μ -computed tomography (SR μ CT). The identification of fossil beetle larvae can be an enormous challenge (e.g. Batelka et al., 2019; see also misidentification in Zippel et al. 2022). However, in this case an identification as a species of the small and very distinctive ground beetle subfamily Omophroninae appeared as a well-founded working hypothesis, suggested for instance by a very unusual shape of the antennae, a wedge-shaped head capsule, and an enlarged prothorax. Presently Omophroninae comprise one genus with slightly less than 80 extant species (Valainis 2010; Kavanaugh et al. 2021). It is very widely distributed on the northern hemisphere, where it even reaches the Arctic circle (Valainis 2010). It also occurs in Guatemala and on Hispaniola, in South Africa and Madagascar, and in Malaysia and on the Philippines, but is not recorded from South America and Australia (Valainis 2010, 2016). The adults are fairly small but conspicuous beetles, with a rounded rather than elongated body and a yellowish coloration with green metallic markings (e.g. Valainis 2010; Arndt et al. 2016). Superficially they resemble ladybirds rather than “normal” carabids, for instance of the megadiverse Harpalinae (e.g. Arndt et al. 2016). They are characterized by a number of apomorphic features, including a short and transverse head, an unusual type of externally closed procoxal cavities, a very broad prosternal process covering the entire mesoventrite, and a protibial burrowing spur (Beutel 1991). Shores of lakes and small ponds are the typical environment, and larvae and adults burrow efficiently in the sandy substrate (Landry and Bousquet 1984; Arndt et al. 2016).

The primary aim of the present study is a detailed morphological documentation of the larva, using light microscopy, microphotography, and also synchrotron μ -CT scanning and computerbased 3D reconstruction. The observed features are entered in a data matrix and analysed cladistically, and also interpreted with respect to the possible habitat and life style.

2. Material and methods

2.1. Sample origin and depository

The specimen described herein is from the lowermost Cenomanian (Cretaceous) deposits of the Hukawng Valley in Myanmar (Kachin). The age of deposits has been confirmed as 98.79 ± 0.62 Ma by radiometric analysis of zircons (Shi et al. 2012). The rough amber piece was

trimmed and polished. The described holotype is deposited in the Charles University, Faculty of Science, Department of Zoology collection, Prague (prefix PĚFUK) and is available for study upon request addressed to J. Prokop.

2.2. Preparation, imaging and SR μ CT data reconstruction

The specimen was examined by transmitted light microscopy using a Leica S9 stereomicroscope and Olympus BX40 microscope with UIS2 objectives. The habitus and detailed photographs of the holotype specimen were taken using an Olympus BX40 fitted with a Canon EOS 550D digital camera or Leica S9D fitted with a Canon EOS 90D. The original photographs were processed using Adobe Photoshop CS (Adobe Systems Incorporated, San Jose, CA, USA). Some images were prepared as a series of focal layers, and then combined using the focus stacking software Helicon Focus (Helicon Soft, Kharkiv, Ukraine) or Zerene Stacker (Zerene systems LLC, Richland, USA).

Line drawings of the specimen were prepared using camera lucida equipment and based on photographs using the Clip Studio Paint (CELSYS, Inc., Tokyo, Japan) and Adobe Photoshop CS software. Where the parts of the specimen were not visible the shape was completed according to the volume renders of the segmented SR μ CT data.

Along with traditional optical microscopy we used synchrotron radiation based micro-computed tomography (SR μ CT) to reconstruct the 3D habitus of the specimen and discern otherwise hardly accessible integumental details of cephalic, thoracic and abdominal structures. Imaging of amber specimen was performed at the Imaging Beamline P05 (IBL) (Greving et al. 2014; Haibel et al. 2010; Wilde et al. 2016) operated by the Helmholtz-Zentrum-Geesthacht at the storage ring PETRA III (Deutsches Elektronen Synchrotron – DESY, Hamburg, Germany) using SR μ CT. A photon energy of 18 keV and a sample to detector distance of 50 mm has been used for imaging. Projections were recorded using a commercial 50 MP CMOS camera system (Ximea GmbH, Münster, Germany) with an effective pixel size of 0.46 μ m. For the tomographic scan 4001 projections at equal intervals between 0 and π have been recorded. Tomographic reconstruction has been done by applying a transport of intensity phase retrieval approach and using the filtered back projection algorithm (FBP) implemented in a custom reconstruction pipeline (Moosmann et al. 2014) using Matlab (The MathWorks, Inc., Natick, USA) and the Astra Toolbox (van Aarle et al. 2015, 2016; Palenstijn et al. 2011). For the processing raw projections were binned for further processing two times resulting in an effective pixel size of the reconstructed volume of 0.92 μ m.

The resulting 32-bit TIFF image stack was cropped, converted to 8-bit TIFF images and exported using Dragonfly software (Object Research Systems (ORS) Inc,

Montreal, Canada). Segmentation of the whole larva was performed in Amira 6.0 software (Visage Imaging GmbH, Berlin, Germany). Parts of the larval body were marked in every 20th slice, in the region of mouthparts and pretarsus the structures were marked in every second to 10th slice. The segmentation process was then completed using Biomedisa (Lösel et al. 2020). The semiautomatic segmentation of the mouthparts provided insufficient results, therefore some structures were then segmented manually in Amira software. Still, parts of the mouthparts are missing from the final volume renders because of the little to no contrast of the structures in the image slices. The segmented data were exported as TIFF image stack using the plugin “multiExport” (Engelkes et al. 2018) in Amira software and imported into VG-Studio Max 3.4 software (Volume Graphics GmbH, Heidelberg, Germany) to create the final volume renders of the specimen.

2.3. Morphology, morphological terminology and cladistic analysis

The main aim of this study is to document the general morphological configuration of the larva and structures that can be related with specific functions. This includes the shape of the head capsule, the condition of the antennae and mouthparts, the general configuration of the post-cephalic body, and features of the legs and urogomphi. Chaetotaxy, which can be useful in a taxonomic context, is not in the main focus of our contribution. Some features are included (partly based on personal communication with K. Makarov). However, we did not attempt a full treatment of the chaetotaxy. As our specimen is not a first instar the interpretation of the pattern of setae, sensilla and pores would have been difficult.

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

Characters were entered in a matrix with Winclada (Nixon 1999) and parsimony analyses were carried out with NONA (ratchet, 1000 replicates) (Goloboff 1995). The branch support value (Bremer 1994) of *Omophron* + †*Cretomophron* was calculated with NONA. The taxon sampling was limited as the primary aim was to confirm the placement of the fossil larva. A full scale analysis of Carabidae would have been far beyond the scope of this contribution. Moreover, larval characters alone would certainly be insufficient to reveal the phylogenetic pattern in the megadiverse family. A solid phylogeny of Geadephaga based on transcriptomic data is presently not available (Vasilikopoulos et al. 2021).

2.4. Data resources

The raw scan data, original unedited photos, and reconstructions will be made available at Zenodo repository at <https://doi.org/10.5281/zenodo.8151974>.

3. Results

3.1. Systematic palaeontology

Order Coleoptera Linnaeus, 1758

Family Carabidae Latreille, 1802

Subfamily Omophroninae

†*Cretomophron* Rosova, Prokop & Beutel, gen. nov.

<https://zoobank.org/B7D03034-E81C-41C9-B407-262A5B21C864>

Type species. †*Cretomophron mutilus* Rosova, Prokop & Beutel, gen. et sp. nov. — sp. nov. by original designation and monotypy. — Included species. Type species only.

Diagnosis (larva). The specimen described here differs from larvae of all holometabolan groups outside of Coleoptera and from Archostemata by the presence of distinctly developed urogomphi on abdominal tergite IX (Figs 1B, 4). It can be distinguished from all carabid groups outside of Omophroninae by a pronouncedly wedge-shaped head, antennae directed upwards (Fig. 3B), and a laterally oriented terminal 4th antennomere (Figs 2A, 5A). The prothorax appears proportionally larger than in other carabid larvae, but this is a gradual modification only. Additional unusual diagnostic features are the large triangular nasale (Figs 1A, 5A), antennae with the 2nd antennomere markedly elongated, legs with a very short tibia and long setae UN1, UN2 on claws (Fig. 2D), and abdominal segment VI with numerous setae collected in transverse rows (Figs 1A, 2B, 4), and large trochanters with distal projections (Figs 3B, C). Posterior tentorial grooves not shifted to the posterior margin of the ventral head capsule distinguish it from larvae of *Omophron* (Figs 2A, 5B).

Etymology. The generic epithet combines ‘creto-’ (Latin for chalky as in Cretaceous), referring to the geological period, and ‘omophron’, the single extant genus of Omophroninae.

†*Cretomomophron mutilum* Rosova, Prokop & Beutel, sp. nov.

<https://zoobank.org/53D8F3BA-7280-4FBF-B5E4-BF2ECCD97461>

Figs 1–5

Material. Holotype no. P̄FUK46, third(?) instar larva preserved in transparent yellow piece of amber

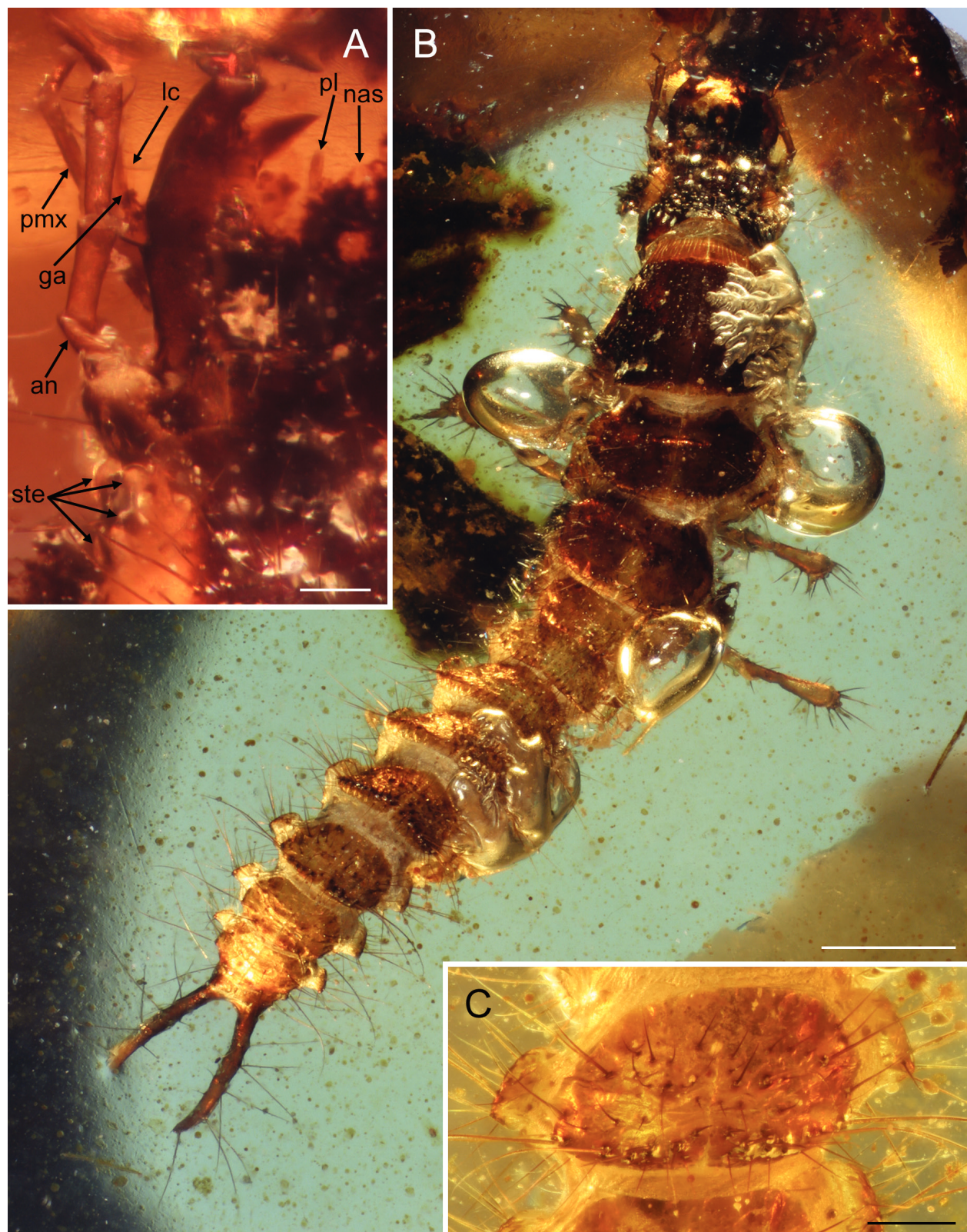


Figure 1. †*Cretomophron mutilus* Rosova, Prokop & Beutel, gen. et sp. nov.: **A** detail of head and mouthparts, dorsal view; **B** habitus, dorsal view; **C** abdominal segment VI, dorsal view. Scale bars: (A) 0.1 mm, (B) 0.8 mm, (C) 0.2 mm. Abbreviations: an – antenna, ga – galea, lc – lacinia, nas – nasale, pl – labial palpus, pmx – maxillary palpus, ste – stemmata.

(10.9 × 11.2 × 3.2 mm), deposited in the collection of Department of Zoology collection, Faculty of Science, Charles University in Prague. The specimen embedded in a piece of amber is almost completely intact, but some damage is visible on the anterior head region (e.g., apical

tooth of left mandible missing). Parts of the dorsal and lateral surface are covered with bubbles.

Age and occurrence. Mid-Cretaceous (late Albian–early Cenomanian, 99 million years ago) amber; age based on

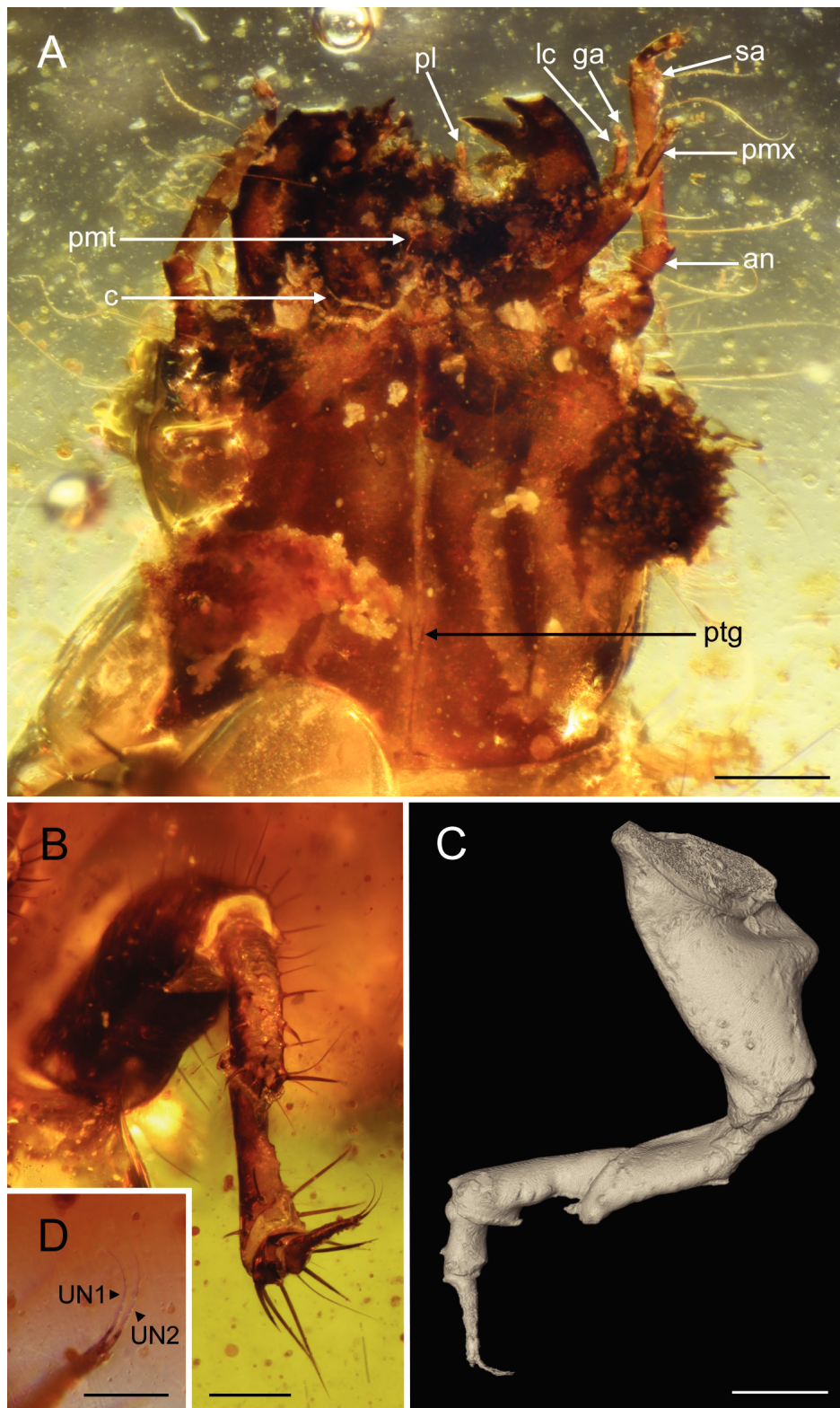


Figure 2. †*Cretomophron mutilus* Rosova, Prokop & Beutel, gen. et sp. nov.: **A** head and mouthparts, ventral view; **B** mesothoracic leg, ventral view; **C** volume render of prothoracic leg from the segmented SR μ CT data, lateral view; **D** detail of the pretarsus of the metathoracic leg. Scale bars: (A, B) 0.2 mm, (C) 0.8 mm, (D) 0.1 mm. Abbreviations: an – antenna, c – cardo, ga – galea, lc – lacinia, pl – labial palpus, pmt – prementum, pmx – maxillary palpus, ptg – posterior tentorial bridge, sa – sensorial appendage.

U-Pb dating of zircon crystals from the volcaniclastic matrix (Shi et al. 2012).

Locality and horizon. Hukawng Valley, Kachin State in northern Myanmar.

Measurements. Length of the inclusion from the tip of the right antenna to the tip of right urogomphus 7.2 mm.

Etymology. The specific epithet refers to the damaged (mutilated) mandibles.

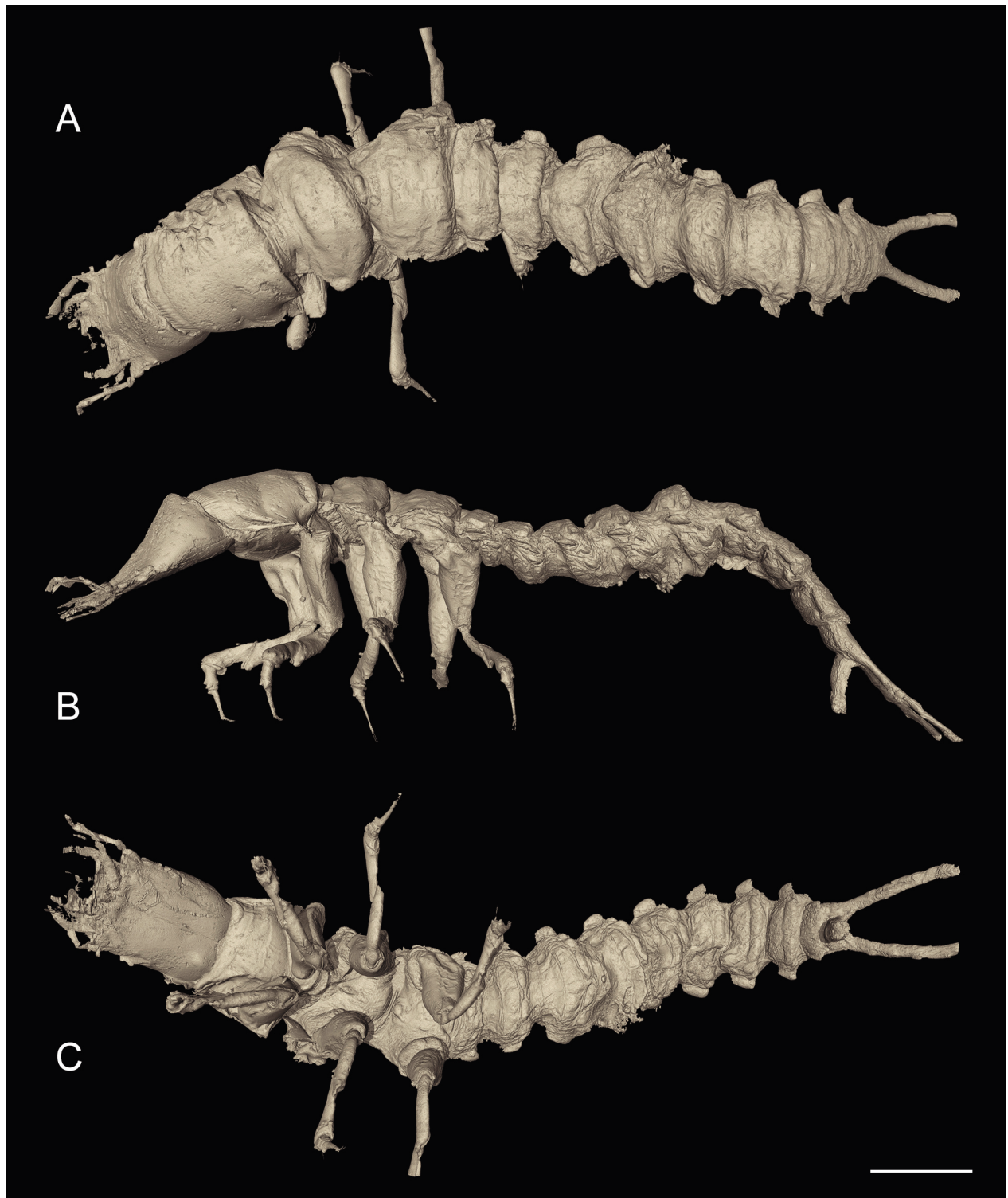


Figure 3. †*Cretomophron mutilus* Rosova, Prokop & Beutel, gen. et sp. nov., volume renders of the segmented SR μ CT data: **A** dorsal view, **B** lateral view, **C** ventral view. Scale bar 0.8 mm.

Description. Habitus (Figs 1B, 3, 4): Campodeiform larva, with a wedge-shaped head, a large prothorax hexagonal in dorsal view, strongly developed legs with a distinct armature of spines, and a relatively slender abdomen tapering posteriorly.

Coloration. Sclerotized areas such as thoracic tergites, coxae or parts of the head middle brown to dark brown. Other parts with some degree of sclerotization like legs

and abdominal tergites light brown. Membranous or semimembranous regions, e.g., pleural areas, cream-colored.

Setation. Body surface with a well-developed vestiture of long setae, especially inserted on the dorsal side of the head, on the tergites, and on the pleural areas of the abdominal segments, and urogomphi. Legs with pattern of long chaetae and long, rather thin spike-like setae.

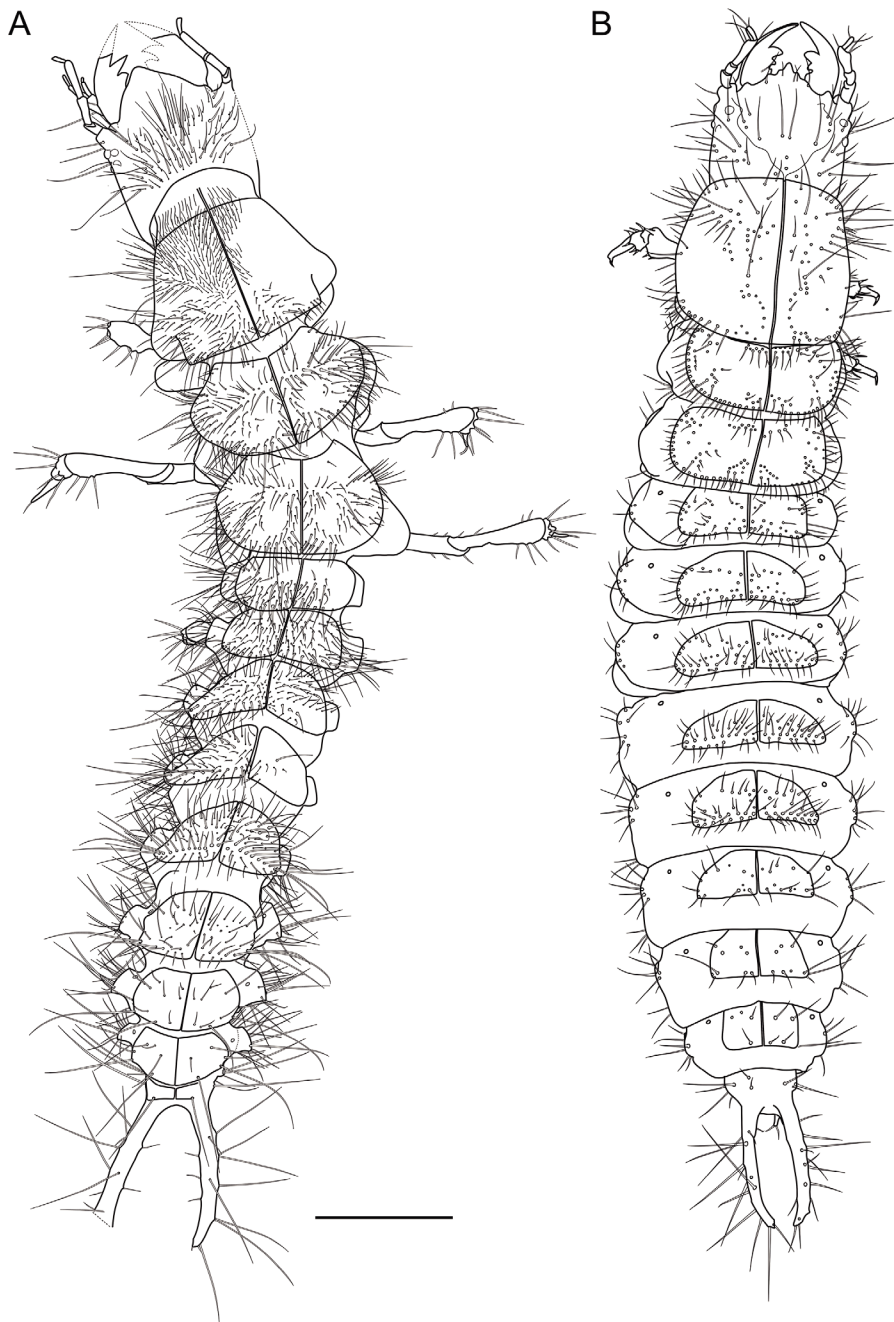


Figure 4. (A) Habitus of †*Cretomophron mutilus* Rosova, Prokop & Beutel, gen. et sp. nov., dorsal view. Dashed lines show missing or poorly visible structures. Scale bar 0.8 mm; (B) Habitus of larva of *Omophron limbatum* (Fabricius, 1776), adapted from Luff 1993, modified.

Head: Distinctly prognathous, wedge-shaped or shovel-shaped in lateral view, anteriorly strongly flattened (Fig. 3B). Strongly sclerotized and dark brown, almost black on dorsal side (Fig. 1B). Ventral side less strongly pigmented, brownish (Fig. 2A). Dorsally with a set of long setae (Figs 1A, B). Coronal suture about 1/3 as long as head capsule and distinct, but frontal sutures only partly visible (obscured by small bubbles) (Fig. 5A). Nasale large and roughly triangular, with small, rounded protuberances (Fig. 1A; not clearly recognizable in μ -CT data set). Four large stemmata recognizable in dorsal view behind antennae (ventral stemmata not visible; Figs 1A, 5A). **Antennae:** Four-segmented (Figs 1A, 5A), held upward (Fig. 3B); 1st antennomere markedly shorter than others; 2nd antennomere distinctly longer than in *Omophron*; apical 4th antennomere narrower than proximal segments, cylindrical, about half as long as 3rd antennomere, and distinctly turned outwards, with three apical setae (broken off)

(Figs 2A, 5A, B). **Mandibles** (Figs 1A, 2A, 5A, B): Incomplete (apparently damaged, apical tooth broken off), curved inwards, with retinaculum well-developed and bidentate; penicillum not visible, probably absent. **Maxillae** (Figs 2A, 5B): Maxillary cardo transverse, undivided; stipes elongate, almost twice as long as wide, slightly narrowing distally; with at least two long setae; palpifer not recognizable as a separate element; palp very likely four-segmented but only three palpomeres preserved; 1st palpomere about half as wide as distal edge of stipes, slightly longer than broad; 2nd palpomere cylindrical, elongate, narrower than 1st but more than twice as long; 3rd palpomere slightly narrower than 2nd and shorter than 1st; apical palpomere apparently broken off. Galea two-segmented; proximal galeomere slender, elongate and slightly curved; distal galeomere narrower and less than half as long, apically rounded; lacinia elongate, spine-like, straight or nearly straight, slightly longer than basal ga-

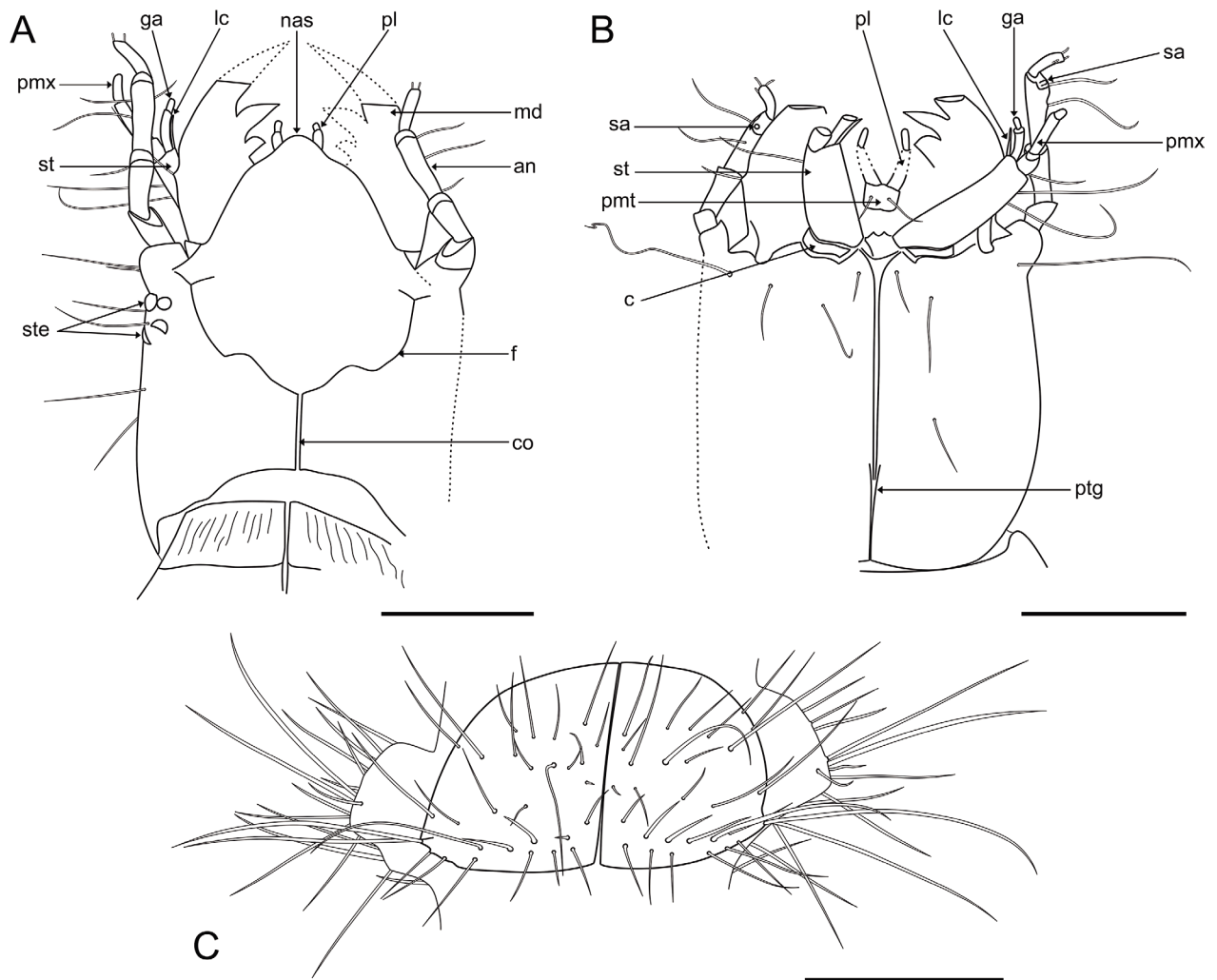


Figure 5. †*Cretomophron mutilus* Rosova, Prokop & Beutel, gen. et sp. nov.: **A** head, dorsal view, chaetotaxy simplified; **B** head, ventral view; **C** abdominal segment VI, dorsal view. Dashed lines show missing or poorly visible structures. Scale bars 0.4 mm. Abbreviations: an – antenna, c – cardo, co – coronal suture, f – frontal suture, ga – galea, lc – lacinia, md – mandible, nas – nasale, pl – labial palpus, pmt – prementum, pmx – maxillary palpus, ptg – posterior tentorial bridge, sa – sensorial appendage, st – stipes, ste – stemmata.

leomere. **Labium** (Figs 2A, 5B): Labial submentum fully integrated into ventral wall of head capsule, medially divided by ventral ecdysial line; mentum short, trapezoid, membranous; prementum small, roughly quadrangular; distinctly protracted but covered by distal part of enlarged nasale in dorsal view; ligula not clearly visible, possible much shorter than in *Omophron*; palps two-segmented; elongate 1st palpomere nearly twice as long as prementum and very slightly curved, slightly narrowing distally; 2nd palpomere distinctly shorter, cylindrical, apically rounded. **Thorax**: Slightly more than 1/3 of total body length (excl. urogomphi) (Figs 1B, 4). In lateral view appearing moderately compressed dorsoventrally (Fig. 3B). Segments distinctly larger and broader than those of abdomen. Prothorax about half as long as all three segments combined; anteriorly with distinct collar with densely set longitudinal ruffles. Pronotum well-sclerotized, with dark brown tergal halves separated by distinct median ecdysial suture; distinctly widening posteriorly, almost twice as wide posteriorly than at anterior edge; lateral edges straight, evenly diverging posteriorly; posterolateral cor-

ners not clearly visible. Meso- and metathorax similar except for longer hind legs. Mesonotum slightly wider than metanotum and more distinctly rounded laterally; both sclerotized and divided by median ecdysial suture; both distinctly concave anteriorly and very slightly convex posteriorly. **Legs** (Figs 2B, C): Six-segmented, strongly developed, robust, almost as long as the thorax (Fig. 3B). With long chaetae and rather thin spike-like setae, mainly concentrated on distal femur. Hind legs slightly longer than two other pairs. Coxa elongated-conical, almost as long as the pronotum (Fig. 3B). Trochanter unusually large, especially on foreleg, with distinct lateral projection on distal apical region (Fig. 2C). Femur slightly shorter than trochanter, also distally widened, Tibia cylindrical, about half as long as femur. Tarsus slender, elongated, narrowing towards apex, with apical setae about three times longer than thin paired claws (Fig. 2D). **Abdomen**: Composed of ten segments and narrower than thorax (Figs 1B, 4). Lateral appendages like gills absent. Segments I–IX with distinctly developed tergites with long setae. Segments III–VI with many setae arranged in trans-

verse rows, in contrast to *Omophron* where such a pattern is found on segments I–V (K. Makarov, pers. comm.) (Figs 1C, 4, 5C). Epipleurites present, forming conspicuous lateral projections with long setae on segments I–VIII (Figs 1C, 5C). Segment IX distinctly narrower than VIII and slightly shorter. Fixed urogomphi present on tergite IX, unsegmented, 0.95 mm long, slightly curved inwards, each with at least eight long outer setae and three shorter inner setae (Figs 1B, 4). Slender, tube-shaped pygopod formed by segment X, shorter than urogomphi (Fig. 3B), covered with short setae.

3.2. List of characters for the systematic placement of †*Cretomophron*

Orientation of head: (0) subprognathous; (1) prognathous; (2) hyperprognathous; (3) almost at right angle to longitudinal body axis. The head is prognathous in the larva of †*Cretomophron* like in almost all groups of Adephaga (Beutel 1993) (Fig. 3B). It is hyperprognathous in larvae of *Metrius*, and almost at a right angle to the longitudinal body axis in Cicindelinae, forming a lid-like structure (Breyer 1989; Beutel 1992a; Arndt 1993; Arndt et al. 2016).

Shape of head in lateral view: (0) dorsal and ventral side more or less parallel-sided; (1) wedge shaped. Distinctly wedge-shaped in extant Omophroninae (Landry and Bousquet 1984; Beutel 1991; Arndt et al. 2016) and also in the larva of †*Cretomophron* (Fig. 3B). The dorsal and ventral side are usually parallel-sided in Adephaga or the dorsal side is more or less convex (e.g., Arndt 1993; Beutel 1993).

Labrum: (0) free; (1) fused. Fused in in the larva of †*Cretomophron* like in all known adephagan larvae (Arndt 1993; Beutel 1993; Beutel and Haas 1996) (Fig. 1A).

Shape of nasale: (0) with several teeth; (1) without teeth and more or less rounded; (2) median triangular projection. A single large triangular nasale is very likely an autapomorphy of Omophroninae (Landry and Bousquet 1984; Beutel 1991; Arndt et al. 2016). This condition is also present in the larva of †*Cretomophron* (Fig. 1A). Four teeth are present in most genera of Gyrininae (Beutel and Roughley 1993), in the dytiscid genus *Hydrotrupes* Sharp (Beutel 1994), and in many groups of Carabidae (e.g., *Metrius*, *Carabus*, *Nebria*, *Leistus*; Thompson 1979; Arndt 1993; Beutel 1992a, 1992b, 1993), and six or eight in Trachypachidae (Lindroth 1960; Beutel 1993; Beutel and Arndt 1995). Nasal teeth are missing in Rhyssodinae, Haliplidae, and almost all groups of Dytiscoidea (Jaboulet 1960; Beutel 1986, 1992c, 1993).

Frontal suture: (0) straight or evenly curved; (1) with indistinct indentation; (2) sinuate; (3) v-shaped posteriorly, with parallel-sided middle region, anteriorly diverging towards antennal groove; (4) largely or completely reduced

in 3rd instars. Distinctly sinuate in almost all subgroups of Carabidae including *Omophron* Latreille (e.g. Thompson 1979; Erwin 1981; Beutel 1991, 1992a, 1992b, 1992c; Arndt 1993). Also is sinuate in †*Cretomophron* (Fig. 5A). V-shaped in Trachypachidae and *Mystropomus* and most of the aquatic groups (Bertrand 1972; Beutel 1993; Beutel and Arndt 1995; Beutel et al. 2020).

Cervical ridge: (0) absent; (1) present. Absent in †*Cretomophron* like in extant Omophroninae and some other groups of Carabidae (e.g., *Gehringia*, *Metrius*, *Carabus*, Cicindelinae; Beutel 1991, 1993). Usually present in larvae of Harpalinae and related groups (e.g., Bembidiini, Pterostichini; Thompson 1979; Tröster 1987; Arndt 1993). Missing in the aquatic groups and Trachypachidae (Lindroth 1960; Beutel 1993; Beutel and Arndt 1995), and also in some Brachininae and Pseudomorphiini (Erwin 1967; Thompson 1979; Arndt 1993).

Postocular ridge: (0) absent; (1) present (Beutel 1993). Missing in †*Cretomophron* and in extant Omophroninae (Beutel 1991). Similar character state distribution as in the case of the cervical ridge (Thompson 1979; Arndt 1993; Beutel and Haas 1996; Arndt et al. 2016).

Gula: (0) not present as a sclerotized structure; (1) sclerotized, about as broad as long or broader; (2) not suture-like, less than half as broad as long; (3) narrow, suture-like; (4) sclerotized gular halves separated by semi-membranous area. Strongly narrowed and suture-like in †*Cretomophron* like in most other groups of Adephaga (e.g., Gyrininae, Trachypachidae, Carabidae [with few exceptions]; Beutel 1991, 1992a–c, 1993) (Fig. 5B). Moderately broad in Hygrobiidae, Amphizoidae and Dytiscidae (Beutel 1991; Alarie et al. 2004), and as broad as long or broader in larvae of Haliplidae, Noteridae, Aspitytidae (Jaboulet 1960; Beutel 1986; Michat et al. 2014; Toussaint et al. 2016), and few genera of Carabidae (Arndt 1993; Beutel 1993).

Position of posterior tentorial grooves: (0) central region of ventral wall of head capsule; (1) posterior head region, at anterior margin of short gula or adjacent to foramen occipitale. Usually located in the central region of the head capsule in adephagan larvae, as for instance in †*Cretomophron* (Arndt 1993; Beutel 1993) (Figs 2A, 5B) or *Sinaspidytes* Balke, Beutel et Ribera (Michat et al. 2014; Toussaint et al. 2016). Slightly shifted posteriorly in larvae of *Aspidytes* (Alarie and Bilton 2005; Balke et al. 2005; coded as 0), but adjacent with foramen occipitale in extant *Omophron* (Beutel 1991), *Omoglymmius* (Beutel 1992b), and Noteridae (Uéno 1957; Bertrand 1972; Ruhnau 1985; Beutel 1993).

Caudal tentorial arm: (0) absent; (1) very short; (2) elongate and slender; (3) thin arms dorsally attached to head capsule. The caudal arms are usually absent in adephagan larvae, and not visible in the fossil included here. They are short in *Trachypachus* and *Noterus* (Ruhnau 1985; Beutel 1993; Beutel and Arndt 1995), but strong-

phaga (Lindroth 1960; Landry and Bousquet 1984; Arndt 1993; Beutel and Arndt 1995) but missing in the aquatic groups (Beutel 1993; Balke et al. 2005; Beutel et al. 2020). The three setae are partially broken off in the specimen of †*Cretomophron* but clearly present (Figs 2A, 5A, B).

Mola: (0) present; (1) absent. Absent in larvae of extant groups of Adephaga (Beutel 1993; Beutel et al. 2006). Very likely also missing in †*Cretomophron* but mandibular base not clearly visible.

Penicillus: (0) present; (1) absent. Usually present in larvae of anisochaetous groups of Carabidae with the noteworthy exception of Omophroninae and some other taxa (e.g., Bembidiini partim [coded as 1], Brachininae; Thompson 1979; Erwin 1967, 1981; Landry and Bousquet 1984; Beutel 1991, 1992a, b; Arndt 1993; Arndt et al. 2016). Not visible in †*Cretomophron* (coded as ?).

Retinaculum: (0) single prominence; (1) bidentate; (2) vestigial or absent. Usually present in Adephaga, but absent in several aquatic groups (Beutel 1993; Balke et al. 2005). A single prominence is found in most groups of Carabidae (Arndt 1993), whereas a bidentate retinaculum is present in extant *Omophron* and †*Cretomophron* (Figs 1A, 5A), and also in Migadopinae (Landry and Bousquet 1984; Arndt 1993; Arndt et al. 2016; Liu et al. 2023). The retinaculum is very small or vestigial in Haliplidae and Amphizoidae but still recognizable (Beutel 1986, 1993) (coded as 1).

Mesal mandibular edge in mature larvae: (0) without distinct cutting edge; (1) one cutting edge; (2) two cutting edges delimiting a mesal groove; (3) mandibular sucking channel. One mesal edge is present in mature larvae of Carabidae including †*Cretomophron* (Figs 1A, 2A), and in Hygrobiidae (Ruhnau 1986; Beutel 1993). An upper and a lower edge are developed in Trachypachidae (Beutel and Arndt 1995) and larvae of several aquatic groups (Beutel 1993). Mandibular sucking channels are present in Gyrininae, Haliplidae, in the noterid genera *Hydrocanthus* and *Canthydrus* (Ruhnau 1986; Beutel 1993), and in almost all groups of Dytiscidae (Bertrand 1972; De Marzo and Nilsson 1986).

Maxillary articulation: (0) present; (1) absent, maxilla articulates at anterior margin of ventral wall of head capsule. The maxillary groove is absent in Carabidae including †*Cretomophron* (Fig. 2A), and is also missing in most other groups of Adephaga. The maxillae articulate at the anterior margin of the ventral head capsule (Beutel 1991, 1992, a, b, 1993; Beutel and Haas 1996). The groove is deep in many non-adephagan groups (e.g. Beutel et al. 1999, 2020; Beutel and Haas 2000; Beutel and Hörschemeyer 2002a, b) and partly preserved in Gyrinidae and Haliplidae (Jaboulet 1960; Beutel and Roughley 1988; Beutel 1993; Beutel et al. 2013, 2020).

Intramaxillary movability: (0) fully retained; (1) absent. The intramaxillary movability is fully retained in

Gyrinidae (Noars 1956; Beutel 1993), but largely reduced or absent in other adephagan larvae, including the fossil described here (e.g. Beutel 1993; Beutel et al. 2006, 2020).

Subdivision of cardo: (0) absent; (1) lateral and mesal sclerite; (2) three sclerotized elements. The cardo is represented by a mesal and a lateral sclerite in most larvae of Carabidae (Beutel 1992a, b, 1993; Arndt 1993). It is a undivided in †*Cretomophron* (Figs 2A, 5A), apparently a plesiomorphic condition.

Lacinia: (0) present; (1) absent. Absent in larvae of Trachypachidae (Lindroth 1960; Beutel and Arndt 1995) and Dytiscoidea, and in larvae of some groups of Carabidae (e.g., Brachininae) (Erwin 1967, 1981; Arndt 1993; Beutel 1993; Beutel and Arndt 1995; Beutel et al. 2006). The lacinia is well-developed in †*Cretomophron* (Figs 2A, 5A, B).

Shape of lacinia: (0) large, hook-shaped, broadly fused with stipes; (1) elongated and apically pointed; (2) hook-shaped, articulated, (3) small, peg-like; (4) strongly reduced and fused with stipes; (5) membranous. Elongated and apically pointed in †*Cretomophron*, *Omophron*, and *Metrius*, but not articulated basally (e.g., Landry and Bousquet 1984; Beutel 1991, 1992a, 1993; Arndt 1993). Hook-shaped, articulated and movable in Gyrinidae (Noars 1956; Beutel and Roughley 1988). Peg-like in many carabid larvae (Thompson 1979; Beutel 1992b; Arndt 1993). Absent in other carabid groups such as e.g. Bembidiini or Brachininae (Thompson 1979; Erwin 1967). Strongly reduced and fused with stipes in Haliplidae (Jaboulet 1960; Beutel 1986) and strongly modified and unsclerotized in Rhysodinae (Beutel 1992c).

M. craniolacinalis: (0) present and attached to the base of the lacinia; (10) replaced by *M. craniostipitalis*. The muscle with a typical attachment on the lacinia is present in Cupedidae and various groups of Polyphaga, but missing in all groups of Adephaga with the noteworthy exception of Gyrinidae (Noars 1956; Beutel 1991, 1992a–c, 1993).

Position of prementum: (0) not protracted; (1) protracted and usually protruding beyond clypeolabral edge. The prementum of larvae of Carabidae is protracted and usually protrudes beyond the anterior clypeolabral margin (e.g. Tröster 1987; Beutel 1991, 1992a, b, 1993). It is also protracted in *Omophron* and †*Cretomophron* (Figs 2A, 5B), but not visible in dorsal view due to the enlarged triangular nasale.

Ligula: (0) distinctly developed as a median ligular node; (1) not present as a well-defined ligular node; (2) broad and setose; (3) elongated. The ligula is present as a short elevation in most groups of Carabidae (Moore 1974; Thompson 1979; Arndt 1993; Arndt et al. 2016), but distinctly elongated in *Omophron*, *Metrius* and *Mythropomus* Chaudoir (Landry and Bousquet 1984; Bousquet

1986; Beutel 1991, 1992a; Di Giulio and Moore 2009). It is not recognizable in the larva of †*Cretomophron* (coded as ?). The ligula is absent or fused with prementum in the aquatic groups and Trachypachidae (Beutel 1993), and also missing in some groups of Carabidae (Thompson 1979; Arndt 1993). It is broad and setose in Cicindelinae (Breyer 1989).

Preoral filter formed by long microtrichia: (0) absent; (1) present. Not visible in the larva of †*Cretomophron*. Usually present in carabid larvae (Landry and Bousquet 1984: fig. 19; Tröster 1987; Beutel 1992b, 1993). Absent in Rhysodinae (Beutel 1992c), Trachypachidae (Beutel 1993; Beutel and Arndt 1995) and the aquatic groups.

Pronotum: (0) shorter than meso- and metanotum combined; (1) as long as meso- and metanotum combined. The pronotum of larvae of *Omophron* and †*Cretomophron* is about as long the meso- and metanotum combined and rounded laterally or widening towards the posterior margin (Landry and Bousquet 1984) (Figs 1A, 4). It is usually more or less parallel-sided in Carabidae and less long than the combined posterior thoracic tergites (Arndt 1993: fig. 1; Arndt et al. 2016).

Number of larval leg segments: (0) six; (1) five. Six in the larva of †*Cretomophron* (Figs 2B, C) like in other groups of Adephaga with few exceptions (e.g. Beutel and Haas 1996, 2000). Five-segmented in Polyphaga and Myxophaga (e.g. Lawrence et al. 2011).

Setation of the distal legs: (0) normally developed; (1) well-developed armature of spines distally on femur and tibia. Larvae of †*Cretomophron* and *Omophron* display an armature of strengthened spines on their distal leg region, especially distally on the femur and tibia (Landry and Bousquet 1984: figs 1, 12, 13) (Fig. 2B).

Segment IX: (0) well-developed; (1) small but distinct; (2) vestigial or absent. Normally developed in †*Cretomophron* (Figs 1A, 4) like in other geadephagan larvae (e.g. Beutel et al. 2006). Small but still distinctly visible in dorsal view in larvae of *Aspidytes* (Balke et al. 2005). Vestigial or absent in larvae of the other groups of Dytiscoidea (Beutel and Haas 1996; Alarie et al. 2011).

Segment X: (0) present; (1) absent. Present in †*Cretomophron* (Fig. 3B) and the groundplan of Adephaga. Absent in larvae of Dytiscoidea and the haliplid genus *Peltodytes* (Jaboulet 1960; Beutel et al. 2006; Alarie et al. 2011; Arndt et al. 2016).

Hooks of segment X (pygopodium): (0) absent; (1) present. Only present in larvae of Gyrinidae (Noars 1956; Bertrand 1972; Beutel et al. 2006).

Spiracle VIII: (0) normally developed; (1) enlarged, terminal; (2) reduced. The spiracle is normally developed in †*Cretomophron* and other groups of Geadephaga (Beutel et al. 2006; Arndt et al. 2016). It is distinctly enlarged and

terminal in larvae of Amphizoidae and Dytiscidae, and reduced in Hygrobiidae, Gyrinidae and Haliplidae (e.g. Beutel et al. 2006, 2013, 2020).

Terminal disc formed by segments VIII and IX: (0) absent; (1) present. Missing in the larva of †*Cretomophron*. Only present in Metriinae and Paussinae (e.g. Bousquet 1986; Di Giulio and Moore 2009; Arndt et al. 2016).

Urogomphi: (0) absent; (1) present, articulated; (2) present, fixed. Urogomphi are distinctly developed in †*Cretomophron* and almost all other groups of Adephaga, but absent in Gyrinidae, Haliplidae (excl. *Peltodytes*; Jaboulet 1960), Rhysodinae, *Systolosoma* (Beutel and Arndt 1995), and few groups of Carabidae (e.g., Cicindelinae) (Thompson 1979; Arndt 1993; Arndt et al. 2016). They are fixed in †*Cretomophron* (Figs 1B, 4) like in most other groups of Geadephaga, but articulated in Dytiscoidea and few groups of Carabidae (e.g., *Metrius* [antler-shaped], *Nebria*, *Loricera*) (Bousquet 1986; Arndt 1993; Beutel et al. 2006; Arndt et al. 2016).

Epipleurites of abdominal tergites III–VIII: (0) not elevated; (1) distinctly prominent. Distinctly prominent epipleurites III–VIII are present in larvae of †*Cretomophron* (Figs 1B, C, 3, 4). They are probably homologous with densely setose pad-like abdominal epipleurites of later instars of *Omophron* (R.G. Beutel pers. obs.).

3.3. Results of the phylogenetic analysis

The analysis of our limited larval data set with 38 larval characters and 28 terminal taxa yielded only two minimum length trees with 95 steps (consistency index 0.68, retention index 0.85). It clearly confirms the placement of †*Cretomophron* as sister to the extant genus *Omophron*, with four unambiguous apomorphies shared by both taxa and a branch support value of 6. The monophyly of Adephaga, of Adephaga excl. Gyrinidae, of Dytiscoidea, Geadephaga, and Carabidae (Fig. 6) is in agreement with previous studies (e.g. Beutel et al. 2020).

4. Discussion

4.1. Phylogeny

The larvae we examined can be unambiguously assigned to the species-rich coleopteran suborder Adephaga. The slender body with elongate legs clearly indicates a placement in Neuropteroidea (Coleoptera [=Strepsiptera + Coleoptera] + Neuroptera [=Raphidioptera, Megaloptera, Neuroptera]). The presence of well-developed urogomphi on abdominal tergite IX is a derived feature occurring only in Coleoptera (excl. Archostemata). The four-segmented antennae, six-segmented legs, and dou-

ble claws are plesiomorphic features excluding a placement in the hyperdiverse Polyphaga and the species-poor Myxophaga (e.g. Beutel and Haas 2000; Lawrence et al. 2011). The campodeiform configuration of the larva, the pattern of sclerotization of the postcephalic body, and the presence of urogomphi and a distinct pygopod formed by abdominal segment X distinguish it clearly from Archostemata (Beutel and Hörschemeyer 2002a, b). The pronouncedly prognathous head with protracted ventral mouthparts and a fused labrum are apomorphies placing it in Adephaga (e.g. Beutel 1993; Beutel and Haas 1996, 2000). The presence of ten well-developed segments and the absence of tracheal or microtracheal gills indicate that the larva belongs to Geadephaga. Elongate urogomphi and various other characteristics differ from conditions found in the relict family Trachypachidae (Lindroth 1960; Beutel and Arndt 1995). An entire series of features supports a placement in the specialized basal grade carabid subfamily Omophroninae (Landry and Bousquet 1984; Arndt et al. 2016): this includes the distinct wedge shape of the head in lateral view, a large triangular nasale, the highly unusual elevated posture of the antenna, the large bidentate retinaculum, an enlarged prothorax and pronotum, and legs with a distinct vestiture of spines. An additional potential synapomorphy is the presence of distinct lateral projections of abdominal segments I–VIII, formed by setose epipleurites, still absent in first instars of *Omophron* described by Landry and Bousquet (1984) but present in later stages (R.G. Beutel, pers. obs.). Despite of the clear phylogenetic assignment, †*Cretomophron* differs in several features from its sister genus *Omophron*. The thorax is not distinctly hump-shaped (Fig. 3B) as in larvae of the extant genus, even though this is possibly an artefact of preservation. In contrast to *Omophron* larvae, the posterior tentorial grooves are not shifted to the hind margin of the ventral wall of the head capsule (Figs 2A, 5B), apparently a plesiomorphic condition. The 2nd antennomere is distinctly longer than in *Omophron* and the ligula is possibly much shorter. Whereas the elongate lacinia of *Omophron* is curved, it appears straight and spine-like in †*Cretomophron* (Figs 2A, 5B). A distinct lobe-like projection is present on the apical region of the large trochanters of the fossil (Fig. 2C). This structure was not observed in larvae of *Omophron* (Landry and Bousquet 1984), but may have been overlooked. Abdominal segments III–VI of *Cretomophron* displays many setae arranged in transverse rows, whereas such a pattern is present on tergites I–V in *Omophron* (K. Makarov, pers. comm.; Fig. 4A,B).

A large, triangular nasal projection as it is characteristic for Omophroninae (Beutel 1991), is also found in few other groups of Carabidae, as for instance in Elaphrini (Makarov 1994: fig. 51), very likely the result of parallel evolution. A bidentate retinaculum is also present in larvae of extant and extinct species of Migadopinae (Thompson 1979; Liu et al. 2023). However, the specific shape is different, and a close relationship between both small subfamilies appears unlikely (Beutel 1991, 1992), even though a robust phylogeny of Carabidae with an

extensive molecular data set and taxon sampling is still lacking (Maddison et al. 2009; Vasilikopoulos et al. 2021; Raupach et al. 2022). The elongate lacinia and ligula are features shared with Paussinae (e.g. Beutel et al. 1992a; Arndt et al. 2016). However, considering distant placements of *Omophron* and this specialized subfamily in a recent transcriptomic analysis (Vasilikopoulos et al. 2021), this is also rather due to homoplasy, or possibly a symplesiomorphy in the case of the lacinia.

The presented taxon sampling is too limited to resolve the phylogeny of Carabidae. Moreover, larval characters alone will not be sufficient to reconstruct the evolutionary history of this extremely species-rich family. A robust phylogeny will require a dense sample of taxa and an extensive molecular data set, i.e., transcriptomes or ultraconserved elements (UCE) (see e.g. Vasilikopoulos et al. 2021).

4.2. Habitat and life style

Larvae of *Omophron* dig burrows in sand or clay in the direct vicinity of fresh- or saline aquatic habitats, and leave them at night to hunt prey (Landry and Bousquet 1984; Brandmayr et al. 1998; Arndt et al. 2016; Brandmayr 2020). As the entire configuration of the body of the larva we describe here and also various specific parts are very similar to conditions observed in *Omophron*, we assume that they are also similar in their biology and habitat preference. However, the legs of †*Cretomophron* clearly differ from *Omophron*, bearing long chaetae and rather thin and long spike-like setae, suggesting that *Cretomophron* may have lived on beaches with finer sand. Other adaptations to burrowing in sandy substrates are the wedge-shaped head and the enlarged prothorax.

It is very likely that the larval instars of †*Cretomophron* were active predators like almost all carabid larvae. Even though the mandibles are not fully preserved, it is apparent that they were suitable for grasping agile prey. It is likely that small arthropods and insect larvae were detected by the antennae and the slender maxillae functioning like accessory ventral tactile organs. The prey was likely fixed between the large triangular nasale and the mesal mandibular edge, and its body wall then pierced by the sharp teeth of the bidentate retinaculum. Even though the preoral hypopharyngeal filter is not visible in the fossil (Landry and Bousquet 1984; Beutel 1991, 1992a–c;), it is very likely that the larva ingested preorally liquefied food.

5. Conclusions

The fossil documents the presence of Omophroninae in the Cretaceous. The placement of †*Cretomophron* in this small but very distinctive carabid subfamily is unambiguously confirmed. The morphology suggests burrowing and predaceous habits, similar to larvae (and adults) of the extant genus *Omophron*.

6. Declaration of Interest

The authors declare no conflict of interest.

7. Acknowledgements

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