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The first larva of the cucujiform superfamily Cleroidea from the Mesozoic and its ecological implications (Coleoptera)

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Abstract

A larva of Cleroidea in Burmese amber is described, which is the first record of an immature beetle of the basal cucujiform superfamily for the Mesozoic. Well-preserved unique specimen is described and illustrated using traditional methods as well as synchrotron-radiation-based micro-computed tomography (SRμCT) to reconstruct the specimen and discern integumental details of cephalic structures, especially the mouthparts. *Cretorhadalus constantini* **gen.** et **sp. nov.** is unambiguously assigned to the melyrid lineage of Cleroidea and tentatively classified within the basal family Rhadalidae. Within this family, this fossil larva has the ancestral cleroid pattern of the stemmata (2+3) and well-developed hooked urogomphi. Based on a comparison with extant rhadalids, as well as most members of the melyrid lineage, the larvae and adults of this new species were probably carnivorous, living on the trunks and branches of trees or in galleries where they foraged for soft xylophagous insects.

Keywords

Coleoptera, Cleroidea, larva, Cenomanian, burmite

1. Introduction

The "melyrid lineage" of Cleroidea is the most species-rich clade of cleroid beetles (Crowson 1964; Peacock 1987; Majer 1994, 1995, 2002). The name of this clade (originally the "melyrid stock" in Majer 1994) was introduced by Bocakova et al. (2011) in their molecular phylogenetic analysis of Cleroidea, which established the monophyletic Rhadalidae and confirmed that Prionoceridae, Mauroniscidae, Dasytidae, Malachiidae and Melyridae are separate cleroid families. Gimmel et al. (2019) support the monophyly of the above taxa but lumped the three latter families within Melyridae (= Melyrinae + Dasytinae + Malachiinae) and classified

former Gietellidae within Rhadalidae like Menier and Constantin (1990), who recorded the genus *Gietella*, suggested. The monotypic Acanthocnemidae that are traditionally considered to be related to Melyridae *sensu lato* (Crowson 1964; Lawrence and Newton 1982; Majer 1994) are excluded from the melyrid lineage by several modern molecular based phylogenies (Bocak et al. 2014; McKenna et al. 2015; Zhang et al. 2018; Gimmel et al. 2019; Kolibáč et al. 2021), which also confirm Phycosecidae from Australasia to be the basal group of the melyrid lineage. Thus, this worldwide distributed lineage includes the families Phycosecidae, Rhadalidae, Mauroniscidae, Prionoceridae and Melyridae (Kolibáč and Huang 2019) and about 7000 species (Mayor 2002; Lawrence and Leschen 2010), which is approximately two thirds of all known cleroids. A more detailed history of its classification is discussed by Kolibáč and Huang (2019).

The Cleroidea is considered to belong among the ancestral superfamilies of Cucujiformia, the largest group of beetles, and sister group to Tenebrionoidea (Robertson et al. 2015; Zhang et al. 2018, McKenna et al. 2019) or to form the very basal group of all Cucujiformia (Cai et al. 2022). The split of Cleroidea is estimated to be relatively old, probably Triassic (210 Mya: Kolibáč et al. 2021; 209–236 Mya: Cai et al. 2022) although some models predict even the end of the Permian/early Triassic (266–237 Mya: Toussaint et al. 2016). The split of the melyrid lineage is estimated on basis of the tip dating procedure as early as in the Lower Jurassic, about 191 Mya (Kolibáč et al. 2021). The oldest cleroid fossils (approx. 165–156 Mya) are known from Callovian deposits (Middle Jurassic) in Inner Mongolia, China. They belong to Cleridae, Prionoceridae, Melyridae and tentatively to Mauroniscidae and Peltidae. Two of these fossils, *Protoclerus korynetoides* Kolibáč and Huang, 2016 (Cleridae) and *Sinomelyris praedecessor* Kolibáč and Huang, 2019 (Melyridae), in particular, are very similar to recent members of these families and the latter could be considered a true "living fossil" as it is difficult to differentiate it from extant species of *Melyris* or *Falsomelyris*. Although members of the melyrid lineage predominate over other cleroids in the recent fauna, their fossils are not so abundant. The reason may be their natural history: these beetles are ecologically mostly connected with flowering plants that appeared in the Cretaceous. That is probably why the first floricolous dasytines are known only from the end of Mesozoic, the late Albian (>100 Mya) from Taimyr amber (Kolibáč and Perkovsky 2020) and early Cenomanian (<100 Mya) from Charente amber (Tihelka et al. 2021). A total of 23 fossil species from the melyrid lineage are described, four from the Mesozoic and 19 from the Cenozoic (Kolibáč and Perkovsky 2020; Tihelka et al. 2021).

Here we describe the oldest larva of the melyrid lineage and first representative of the lineage in Burmese amber and the Mesozoic. We also discuss its implications for phylogeny and palaeoecology and compare it with other extinct and extant taxa in this part of Cleroidea.

2. Material and Methods

2.1. Sample depositories

The material examined is deposited in the following collections:

· The type specimen of the newly described fossil species: Charles University, Faculty of Science, Department of Zoology, Prague, Czechia; registration number PřFUK20.
· All recent species used for morphological study: Moravian Museum, Department of Entomology, Brno, Czechia.

Details above the fossil material record are given under holotype description.

2.2. Preparation, imaging and micro CT reconstruction

The amber piece was polished, allowing improved views of the included specimen, and was not subjected to any supplementary fixation.

Detailed photographs of small, semi-transparent parts of the body of the specimen were taken using an Olympus BX41 fitted with a Canon EOS 1200D digital camera or Leica S9D fitted with a Canon EOS 90D. Photographs of the fossil specimen were taken using a Leica Z16Apo. Body parts were measured using LAS 3.6.0 software. QuickPhoto Camera 2.3 with DeepFocus 3.1 module, LAS 3.6.0 and Helicon Focus (Helicon Soft) programs were used to stack certain images. Adobe CS6 software (Illustrator 16.0.3 and Photoshop 13.0.) was used to assemble the plates and adjust particular images.

Along with traditional optical devices we used synchrotron-radiation-based micro-computed tomography (SRμCT) to reconstruct the specimen and discern otherwise hardly accessible integumental details on cephalic structures. Imaging of amber specimens was done at the Imaging Beamline P05 (IBL) (Greving et al. 2014; Haibel et al. 2010; Wilde et al. 2016) operated by the Helmholtz-Zentrum Hereon at the storage ring PETRA III (Deutsches Elektronen Synchrotron-DESY, Hamburg, Germany) using synchrotron radiation based micro-computed tomography (SRμCT). A photon energy of 18 keV and a sample to detector distance of 50 mm was used for imaging. Projections were recorded using a commercial 50 MP CMOS camera system (Ximea, Germany) with an effective pixel size of 0.46 μm. For each tomographic scan 4001 projections at equal intervals between 0 and π were recorded. Tomographic reconstruction was done using a transport of intensity phase retrieval approach and the filtered back projection algorithm (FBP) implemented in a custom reconstruction pipeline (Moosmann et al. 2014) using Matlab (Math-Works) and the Astra Toolbox (van Aarle et al. 2015; van Aarle et al. 2016; Palenstijn et al. 2011). For the processing, raw projections were binned

twice for further processing resulting in an effective pixel size of the reconstructed volume of 0.92 μm.

The reconstructed 32 bit TIFF image stacks were cropped, converted into 8 bit TIFF files, inverted and exported using the Dragonfly software (Object Research Systems (ORS) Inc, Montreal, Canada). Amira 6.0 software (Visage Imaging GmbH, Berlin, Germany) was used for segmentation of the structures in every 40th slice. The segmentation process was finalised using Biomedisa (Lösel et al. 2020). The segmented data were exported as TIFF image stacks using the plugin „multiExport" in Amira (Engelkes et al. 2018). The final volume renders were created in VG-Studio Max 3.4 software (Volume Graphics GmbH, Heidelberg, Germany).

2.3. Data resources

The raw scan data will be made available at Zenodo repository at https://doi.org/10.5281/zenodo.7701916.

2.4. Classification and LSID registration

We follow the classification of the melyrid lineage of Gimmel et al. (2019), i.e., Phycosecidae, Rhadalidae (= Rhadalinae + Gietellinae), Mauroniscidae, Prioneceridae, Melyridae (= Melyrinae + Dasytinae + Malachiinae).

The publication and the included nomenclatural acts have been registered in ZooBank (www.zoobank.org), the online registration system for the ICZN. The LSID for this publication is: urn:lsid:zoobank.org:pub:8EE85535-FA17-418B-B1BA-6929C4EC7F34.

3. Systematic palaeontology

Order Coleoptera Linnaeus, 1758

Suborder Polyphaga Emery, 1886

Superfamily Cleroidea Latreille, 1802

Melyrid lineage (*sensu* Bocakova et al., 2011)

Family ?Rhadalidae LeConte, 1862

A classification of the fossil larva within Cleroidea is unambiguously based on the shape of its body, sparse but long pubescence, mouthparts, characteristic pattern of thoracic terga (protergal plate + 2 pairs of tergites) and hooked urogomphi (Kolibáč 2018). This fossil belongs undoubtedly in the melyrid lineage as explained in Table 1: i) absence of median endocarina in combination (Fig. 1C) with ii) Y-shaped frontal sutures with long stalk (Figs 1C, 4C), and iii) widely open head capsule (Fig. 1D) with iv) subparallel gular sutures (Fig. 5), unambiguously assign the larva with the lineage (Crowson 1964; Kolibáč et al. 2005).

An assignment to a particular family of the melyrid lineage is based on limited set of known larvae. The families Prioneceridae (Majer 1994; Lawrence and Leschen 2010) and Phycosecidae (Crowson 1964; Beutel and Pollock 2000; Leschen and Beutel 2010) can be excluded as the structure of their antennae, stemmata, terga and urogomphi differ (Table 2). Melyrinae larvae differ in their body vestiture and reduced sclerites on protergum (Majer 1994; Estrada and Solervicens 1997) while Malachiinae have only four stemmata and several fragmented sclerites on protergum (Fiori 1960; Pasqual 1981; Kolibáč et al. 2005).

We tentatively propose attribution of this fossil to Rhadalidae. Such a classification is based on i) the structure of the antenna with 3rd antennomere longer than antennomere 1 or 2, ii) the trapezoidal cranium (Fig. 4C) that is shared with some extant larvae of *Aplocnemus* and *Gietella* (dasytine cranium is rather rounded, Fig. 4B, and iii) the primitive structure of the protergum with a single large tergal plate (Fig. 1A) (Constantin 1990; Constantin and Menier 1990). Two pairs of lateral and dorsal glands occur on the abdominal segments of Dasytinae (Crowson 1964; Lawrence and Leschen 2010); the fossil does not have these glands, which also supports the classification within Rhadalidae. Larvae of four rhadalid genera known to date have only two stemmata on each side while five (2+3) stemmata is the plesiomorphic state (Fig. 2C) within all major cleroid families and subfamilies. Thus, the tentative placement of the fossil in Rhadalidae is partly based on cleroid symplesiomorphies (protergal plate, pattern of meso- and metatergites 2+2) that are unique in the melyrid lineage; the length of the terminal antennomere (Fig. 2D, supposed synapomorphy) is shared with *Aplocnemus*, the slender hooked urogomphi (Fig. 1E), another supposed synapomorphy, are shared with *Pelecophora* larva from Mauricius (Crowson 1964), but not with *Aplocnemus* or *Trichoceble*, in which they are shorter (urogomphi absent in *Gietella*). (The urogomphi formed in such way are unknown in Dasytinae.) Two unclear patches were observed in the fossil, exactly in the place where a pair of membranous appendages are illustrated by Crowson (1964: 309, fig. 72) in *Pelecophora*. The appendages themselves could not be preserved in amber and the structure remains unclear.

It is important to note that no larva of the basal melyrid lineage family Mauroniscidae has been found for comparison, but its presumptive adult is recorded in Callovian deposits in Inner Mongolia (Kolibáč and Huang 2019). The larva is only tentatively assigned to the family Rhadalidae, as we cannot rule out its attribution to Mauroniscidae or some as yet unknown early diverging group of Melyrid lineage.

Table 1. Comparison of larvae of major cleroid families or lineages.

Character	Clerid lineage	Trogossitidae Lophocateridae	Peltidae	Melyrid lineage
Median endocarina	Present/absent	Present	Absent	Absent
Frontal sutures	V/Y/U-shaped, stalk of Y shorter than 1/3 of head	V/Y-shaped, stalk of Y shorter than 1/3 of head	Weakly Y-shaped, reduced in size	Y-shaped, stalk of Y at least 1/3 of head (Figs 3A, C)
Head capsule ventrally	Capsule open but mouth-parts shortened	Capsule closed along anterior margin	Capsule closed along anterior margin	Capsule open or inconspicuously closed
Gula	Gula nearly as long as cranium, sutures subparallel	Gula not exceeding half of cranium, without protrusions; sutures convergent	Gula not exceeding half of cranium, with 2 protrusions; sutures convergent	Gula not exceeding half of cranium, without protrusions; sutures subparallel
Mandible	Unidentate	Bidentate/rarely unidentate	Bidentate	Bidentate
Mandibular mola	Absent	Absent (rudiment rarely present)	Present	Absent
Colour	Pink/red/whitish	Whitish	Whitish	Red/whitish

Table 2. Comparison of larvae of the relevant families of the melyrid lineage.

Character	Phycosecidae	Rhadalidae	Prionoceridae	Melyrinae	Dasytinae	Malachiinae	Fossil larva
Antennomere 3	Longer than 2, weakly longer with sensory appendix	As long as 2 or longer than 2, with 1 long seta	As long as 2	Shorter than 2	As long as 2	As long as 2	Longer than 2, with 1 long seta
Stemmata	6 (2+3+eye spot)	2 (1+1)	5 (2+3)	4 (1+3) or 5 (2+3)	5 (2+3)	4 (1+3)	5 (2+3)
Pronotal tergites	Divided tergal plate	Divided tergal plate	Split into several fragments	Reduced in size/absent	Split into 2 or more tergites/ reduced in size	Split into 3–4 sclerites	Divided tergal plate
Meso- + metathoracic tergites	0+0	2+2	Split into several fragments	2+2	4+4	2+2	2+2
Urogomphi	Present	Present: well-developed, shortened or absent	Present	Present	Present: well-developed or shortened	Present	Present: well-developed
Urogomphi shape	Straight, weakly upturned	Hooked/absent	Straight, divergent	Hooked (Fig. 3D)	Hooked	Hooked (Fig. 3B)	Hooked
Body vestiture	Sparse, short	Sparse, long/ dense and short	Dense, short	Dense, long	Sparse/dense and short/long	Sparse, short	Sparse, long

Cretorhadalus Kolibáč & Prokop gen. nov.

https://zoobank.org/0193AA05-6893-40D4-BF8C-874D02A57167

Type species. *Cretorhadalus constantini* Kolibáč & Prokop **gen.** et **sp. nov.**

Diagnosis. Cranium weakly trapezoidal, approximately as wide as long, its anterior margin wider than base (Figs 1C, 4C); head capsule ventrally open, with long gular sutures (Figs 1D, 5); five stemmata present on each side, with formula 2+3 (Fig. 2C, D); terminal antennomere slender and longer than the previous one (Figs 2D, 5); dorsal side of prothorax with single sclerotized tergal plate divided longitudinally with suture; meso- and metatergum with a pair of distinct tergites (Fig. 1A, C); urogomphi slender, hooked (Fig. 1E), without distinct glandular openings, processes or tubercles (a pair of membranous appendages might be present at centre of abdominal tergite 9).

Etymology. The generic name is composed of the prefix *creto-* (derived from Cretaceous period) and the root *rhadalus* that denotes the supposed affiliation of the new genus with the family Rhadalidae, not a relationship with the nominate genus. Gender of name is masculine.

Cretorhadalus constantini Kolibáč & Prokop gen. et sp. nov.

https://zoobank.org/1D88FD1F-B283-4738-A7FC-BA95C2E-CD61E

Figs 1, 2, 5

Type material. Holotype PřFUK20 preserved in a polished, transparent yellow piece of amber (18.1 × 9.9 × 3.6 mm); deposited in the collection of Charles University, Faculty of Science, Department of Zoology, Prague.
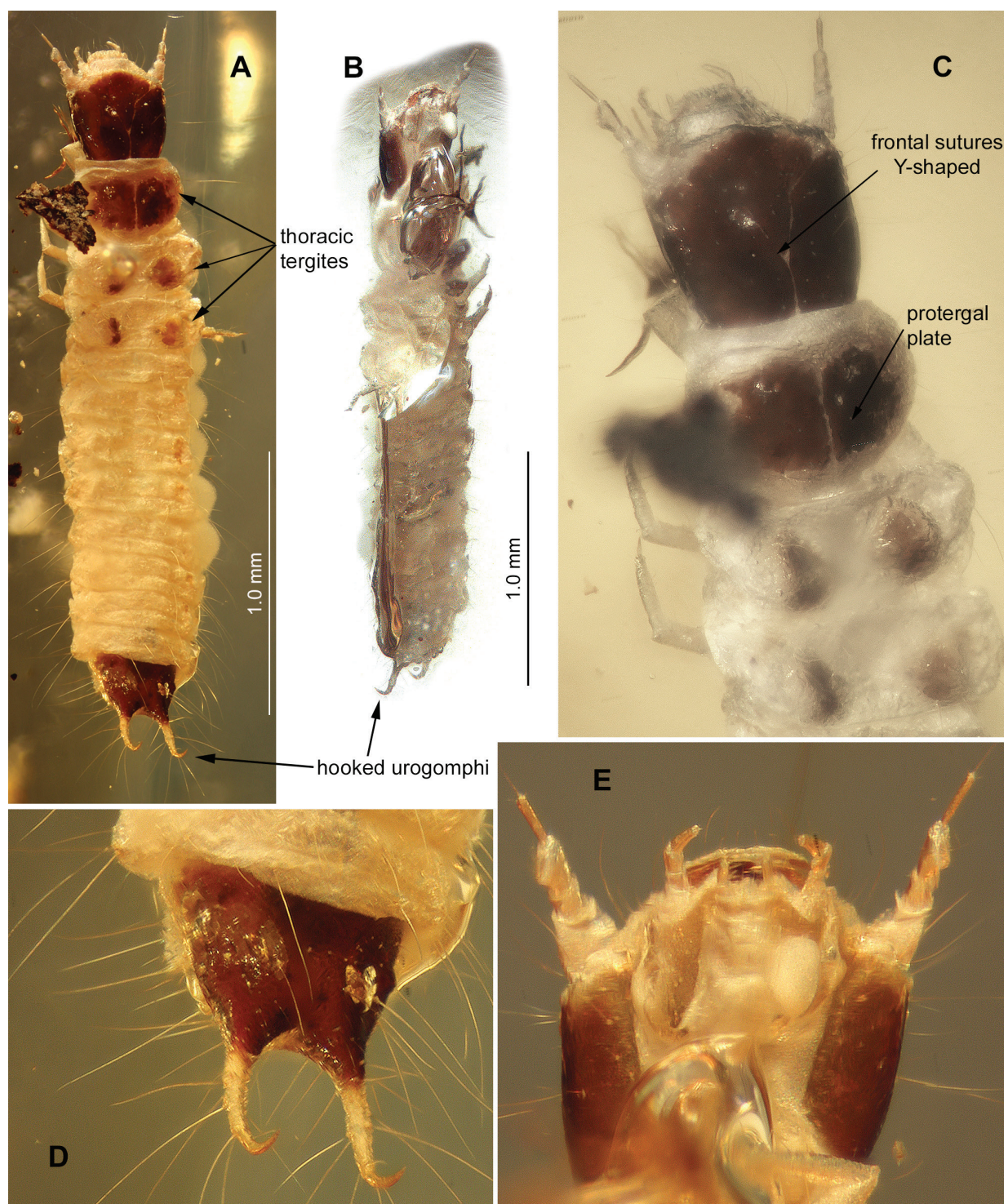
Figure 1. *Cretorhadalus constantini* **gen.** et **sp. nov.**: **A** Habitus, dorsal view. **B** Habitus, ventrolateral view. **C** Head and thorax, dorsal view. **D** Urogomphi, dorsolateral view. **E** Head, ventral view.

Type stratum. Lowermost Cenomanian (Upper Cretaceous); age based on U-Pb dating of zircon crystals from the volcaniclastic matrix (Shi et al. 2012).

Type locality. Hukawng Valley, Kachin State, northern Myanmar.

Description. Body length from clypeus to the last abdominal segment (excluding urogomphi) 2.41 mm. For other measurements see Table 3.

Body habitus and pubescence (Fig. 1A, B): Body elongate, whitish, sclerotized parts brown. Head capsule, urogomphi and dorsal part of abdominal segment IX heavily sclerotized, dark brown (urogomphi lighter than tergite IX); prosternum, protergum and mesotergum with sclerotized brown plates; metathorax and abdomen up to segment VIII whitish. Cranium with long sparse pubescence dispersed irregularly (c. 50–60 setae on dorsal side and c. 20 setae on ventral side); dorsum of thoracic segments with c. 10–15 long setae; legs with
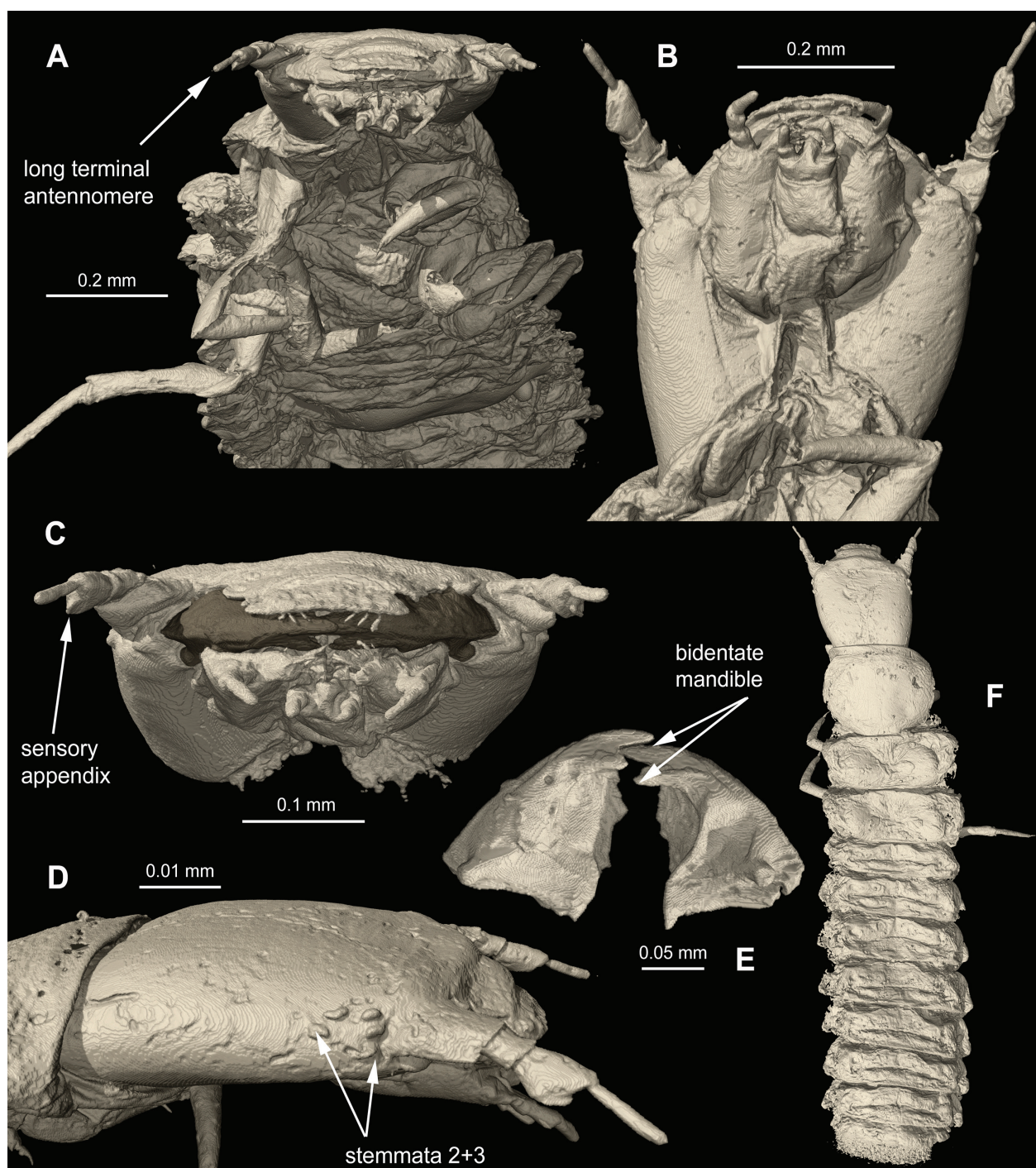
Figure 2. *Cretorhadalus constantini* **gen.** et **sp. nov.**, X-ray μCT renderings: **A** Head and thorax, anterior and/or ventral view. **B** Head, ventral view. **C** Head, anterior view. **D** Head, dorsolateral view. **E** Mandibles, ventral view. **F** Habitus, dorsal view (without segment IX).

few long setae; abdominal segments I–VIII with dorsally about 2–4 long and laterally about 5 setae; sides of abdominal segments IX–X with dense and long pubescence, urogomphi also with long setae. Ventral sides of thoracic and abdominal segments with shorter and sparser pubescence. — **Head**: Cranium approximately as wide as long, lateral sides weakly rounded (convex), its anterior margin wider than base (Table 1; Figs 1C, 4C); five stemmata occur on each side with the formula 2+3 (two posterior and three anterior) (Fig. 2C); frontal arms distinctly Y-shaped, with branches curved at half their length and

divergent (Fig. 4C); median endocarina absent (Fig. 1C); frontoclypeal suture present (Fig. 1A, C); gular sutures widely separated, subparallel, virtually extending to anterior part of cranium (Fig. 5); hypostomal rods absent; paragular sclerites absent. Gular region membranous and pale, its middle part nearly reaching midpoint of cranium so that the maxillolabial complex reaches slightly beyond half of cranium; head capsule is ventrally open, without bridge along anterior margin (Figs 1D, 5). — **Antennae** (Figs 1D; 2B, D): 3-segmented, 1st antennomere shorter than 2nd, the latter obliquely truncated and shorter than
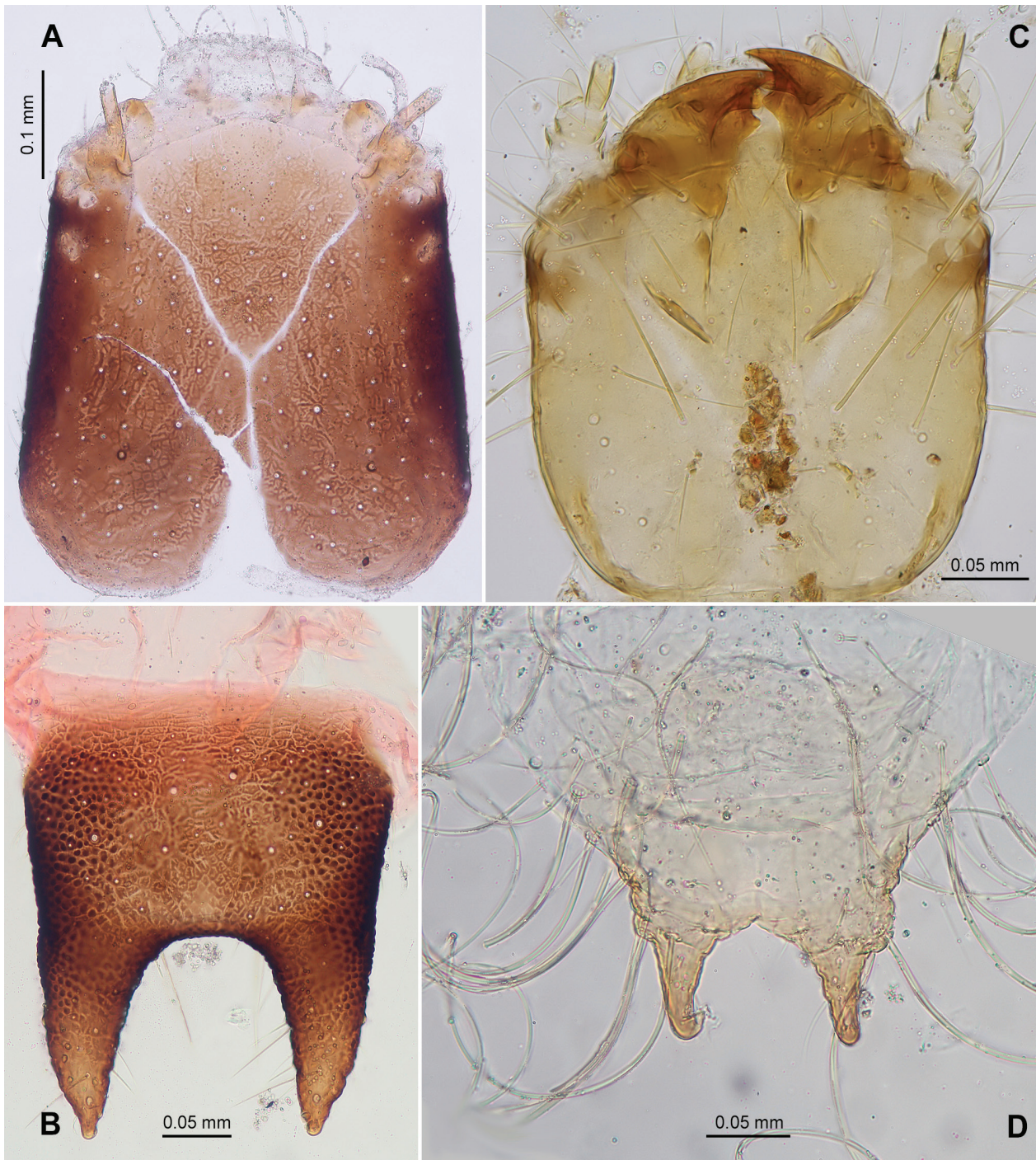
Figure 3. Larva of Malachiidae (cf. *Ebaeus*): **A** Head, dorsal view. **B** Urogomphi. Larva of *Melyris scutellaris*: **C** Head, dorsal view. **D** Urogomphi.

3rd; sensory appendix relatively short and stout, triangular, not extending behind one quarter of 3rd antennomere, which is relatively slender and long, with long seta on apex. — **Mandible** (Figs 1D, 2A): bidentate (Fig. 2A), that is with two apical teeth situated side by side; other mandibular structures not visible in fossil. — **Maxilla** (Figs 2D, 5): mala small, triangular, with at least 3 thick long setae along outer margin; pedunculate seta not observed; palpi 3-segmented, 1st and 2nd palpomeres equal in length, terminal palpomere coniform and longer than 1 or 2; cardo and stipes distinctly separated; cardo narrow and transverse, much smaller than stipes (Fig. 5). — **Labium**

(Figs 1A, 2A, 5): ligula small, pale, membranous, ciliate, rounded; palpi 2-segmented, terminal palpomere cylindrical, about twice as long as basal palpomere; prementum in single part (not divided); border of postmentum not conspicuous. — **Labrum** (Figs 1C, 2E, 5): free; anterior margin wide and convex, with about 6 long setae (Fig. 5); other details not visible. — **Thorax** (Fig. 1A, B, C): protergum heavily sclerotized and pigmented, with single large tergal plate longitudinally divided by medial suture; mesotergum with pair of small but distinctly pigmented and sclerotized tergites; structure of metatergum the same as that of mesotergum, but sclerites slightly smaller (Fig.
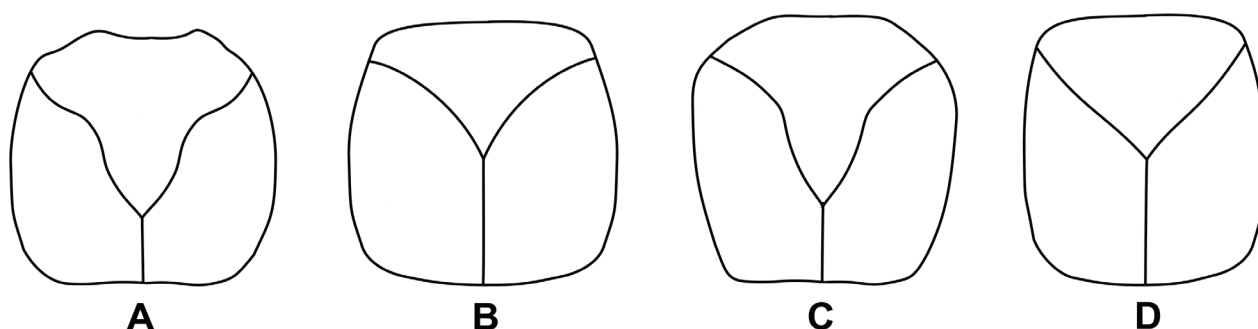
Figure 4. Comparison of frontal sutures and shapes of cranium: **A** *Phycosecis* (Phycosecidae). **B** *Danacea* (Dasytidae). **C** *Cretorhadalus constantini* **gen.** et **sp. nov. D** *Aplocnemus* (Rhadalidae).
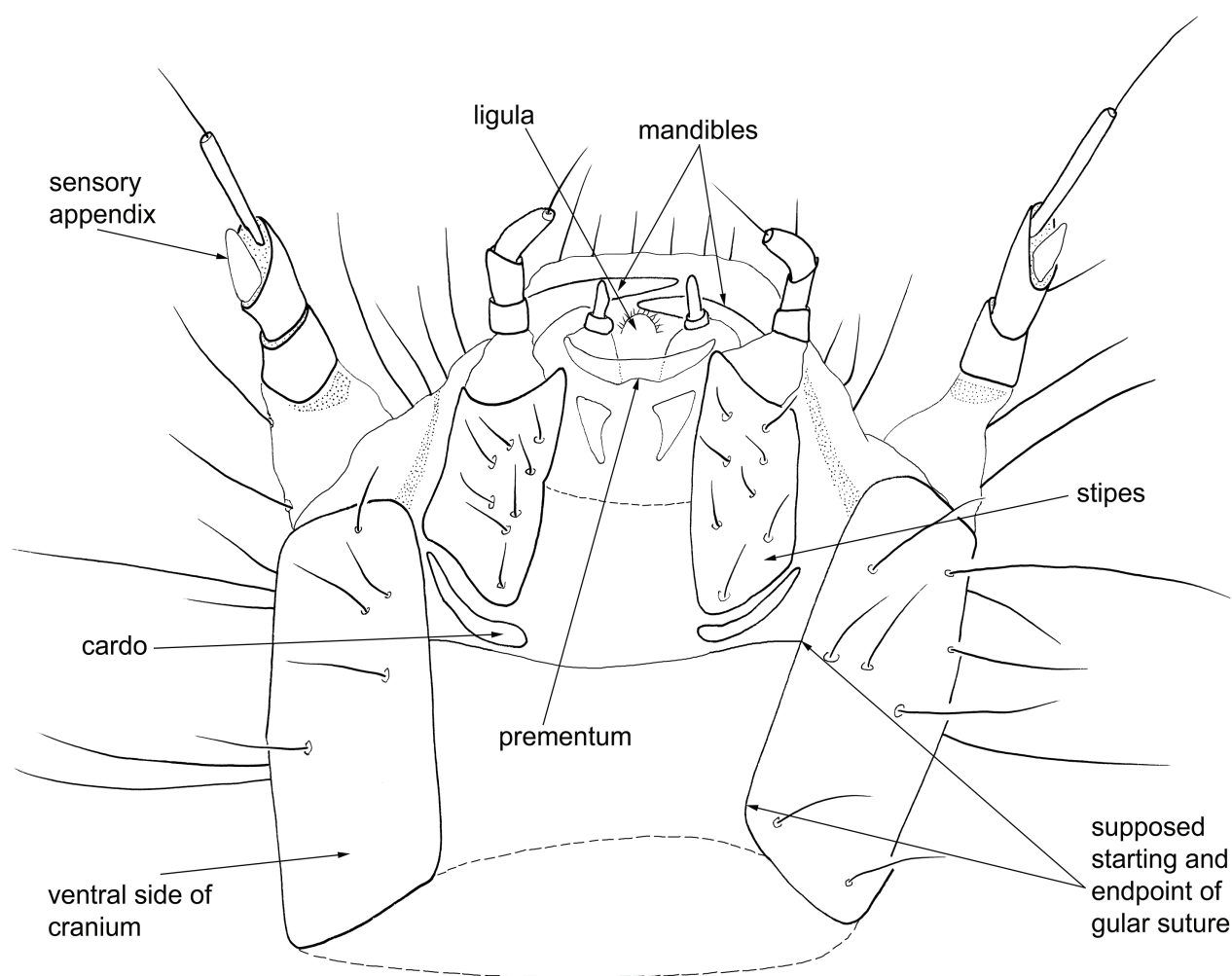

Figure 5. Maxillolabial complex of *Cretorhadalus constantini* **gen.** et **sp. nov.** Dotted lines indicate indistinct margins. Cranium apparently compressed and its ventral side artificially wide open; that is why gular sutures seem divergent and widely separated. The length of the gular sutures is not clear.

1C). Ventral part of pro-, meso- and metathorax without distinctly pigmented sclerites. — **Legs** (Fig. 1B, C): Coxae projecting; trochanters rather triangular; femora longer than tibiae; tarsunguli without visible setae. — **Abdomen**: segments I–VIII membranous, their terga without sclerites (tergites) or pigmented plates (Figs 1A, 2E); segment IX with single tergite (not transversely divided into two parts) bearing a pair of slender hooked urogomphi (Fig. 2E); median process or glandular openings on or between urogomphi not visible, but it is possible that a pair

of membranous appendages are present approximately at the centre of tergite IX; urogomphi without large tubercles, relatively slender, conspicuously turned upwards, well-developed (Fig. 1E; cf. Fig. 3B, D).

Etymology. The specific epithet honours Robert Constantin (Saint Lô, France), the eminent specialist of beetles in the melyrid lineage and leading authority on their larvae.

Table 3. Measurements of some body parts of *Cretorhadalus constantini* **gen.** et **sp. nov.** (in millimetres).

Body part	Measurements
Body length from clypeus, excl. urogomphi	2.41
Body length from clypeus, incl. urogomphi	2.59
Head capsule anterior, max. width	0.36
Head capsule base, width	0.28
Head capsule, max. length	0.34
Antenna, length incl. connecting membrane	0.22
Antennomeres 1+2+3, length	0.03+0.04+0.05
Prothorax, width	0.42
Prothorax, length	0.31
Mesothorax, width	0.47
Mesothorax, length	0.22
Metathorax, width	0.52
Metathorax, length	0.24
Metafemur, length	0.16
Metatibia, length	0.14
Urogomphi, approx. circumference	0.21

4. Discussion

4.1. Systematic placement of the fossil

Although the larva of *Cretorhadalus constantini* **gen.** et **sp. nov.** has distinct features of the melyrid lineage, they are mostly limited to structures of the head. Other parts of the body including the general habitus, morphological structures of the thorax and abdomen, body colour, sculpture and vestiture are shared with basal representatives of other cleroid families including Cleridae, Trogossitidae, Metaxinidae/Chaetosomatidae and Acanthocnemidae, which is why they can be considered symplesiomorphic. In fact, the larva without its cranium could be easily identified within Cleroidea, but not indisputably assigned to the melyrid lineage, however, this may also be the case for larvae of *Phycosecis* (Phycosecidae) or *Aplocnemus* (Rhadalidae). Both of the latter families share with the fossil the single large longitudinally divided protergal plate, which is also present in all the major cleroid families mentioned above outside the melyrid lineage. The prothoracic tergite is always split into several sclerites in Prionoceridae and the former Melyridae *sensu lato* and the structure and/or number of the meso- and metathoracic tergites also differ in the mentioned groups in comparison with *Cretorhadalus constantini* **gen.** et **sp. nov.**, Phycosecidae and Rhadalidae. Both of the latter families are considered to be basal within the lineage in the molecular phylogenies of Bocakova et al. (2011), McKenna et al. (2015), Gimmel et al. (2019) and Kolibáč et al. (2021) (Fig. 6). The fossil moreover shares weakly curved frontal sutures with Australasian littoral *Phycosecis* (Fig. 4A); the strongly curved sutures occur in various cucujiform families and also in the basal cleroid genera *Phloiophilus*, *Protopeltis* and *Byturus* (Crowson 1964;

Kolibáč 2008). It is necessary to note that other phycosecid features, including body size and shape, number of stemmata, structure of urogomphi and its unique biology, are different. The presence of the curved frontal sutures (Fig. 4C) confirms the fossil's position at the base of the melyrid lineage and if the proposed classification is right, a basal position for Rhadalidae (cf. Figs 3A, C; 4A, B, D). The known larvae of four rhadalid genera, *Pelecophora*, *Trichoceble*, *Gietella* and *Aplocnemus* (Crowson 1964; Constantin 1990; Menier and Constantin 1990), have straight frontal sutures. With the exception of *Pelecophora*, the other three extant larvae have a robust and hardly sclerotized tergite 9, but their urogomphi are rather small and minutely hooked (*Aplocnemus*, *Trichoceble*) or absent (*Gietella*). That is why the fossil may be, among known larvae, the most closely related to the extant genus *Pelecophora*, which currently occurs in Réunion, Mauricius and east Africa.

Extant species of the family Rhadalidae are today distributed worldwide except for the Australasian zoogeographical realm and Pacific islands (Peacock 1987; Majer 1994). Fifteen extant and one Cenozoic genus (Majer 1998) are included in the family along with the wingless *Gietella* from Canary and Azores islands (Constantin and Menier 1987, 1990; Menier and Constantin 1988, 1989), which was confirmed as a member of the family by Gimmel et al. (2019). Rhadalids were traditionally classified within Dasytidae or Melyridae. Crowson (1964) recognized their monophyly and established a separate subfamily Haplocneminae for them, which was later treated as Aplocneminae (Majer 1983, 1987) and finally Rhadalinae (Peacock 1987). The molecular phylogeny of Bocakova et al. (2011) revealed their basal position in the melyrid lineage and definitely established the family Rhadalidae (cf. Fig. 6).

The fossil genus *Aploceble* with three species described from Baltic amber is considered to be related to the extant Palaearctic *Trichoceble* while other undescribed but studied rhadalid Eocene fossils (nine specimens) was placed in the extant genera *Xamerpus* (currently distributed from East Africa to India, incl. Madagascar and Seychelles) and *Aplocnemus* (Palaearctic) (Majer 1998).

4.2. Palaeobiology and palaeoecology implications

Palaearctic adults of Rhadalidae, in particular in terms of their habitus, are similar to Melyridae: Dasytinae and it is for this the reason they were classified within the former Dasytidae (Peacock 1987; Majer 1994). Their biology, however, may be different. Larvae of both groups are carnivorous. Rhadalid larvae dwell under bark or in galleries of woodboring insects (for example, Cerambycidae, Buprestidae) where they forage for host larvae or eggs whereas the adults, which are also carnivorous, can be found on branches of shrubs and trees and/or their leaves and cones where they search for insect larvae and eggs (*Aplocnemus*, *Trichoceble*, *Pelecophora*, *Xamerpus*), but some members are floricolous and feed on
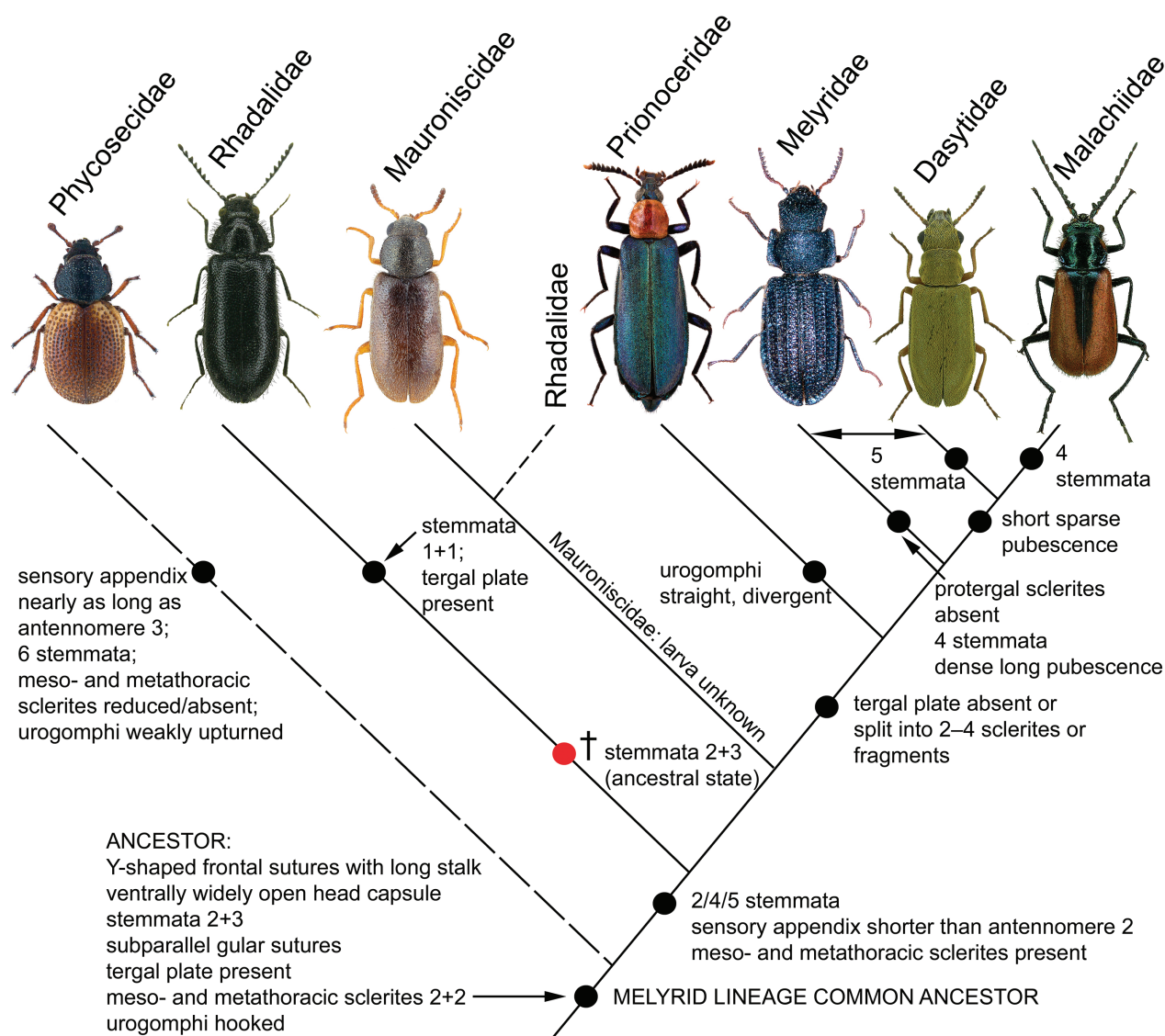
Figure 6. Phylogenetic tree of the melyrid lineage based on the molecular analysis of Kolibáč et al. (2021) with mapping of morphological characters of larvae. Dotted branches (Phycosecidae, Rhadalidae) and the double arrow (between Melyridae and Dasytidae) indicate the results of the molecular phylogeny of Gimmel et al. (2019). Supposed position of *Cretorhadalus constantini* **gen.** et **sp. nov.** denoted by the small cross †.

pollen grains (*Rhadalus*, *Indiodasytes*) (Crowson 1964; Peacock 1987). This way of life is similar to that of other predaceous cleroids, for example Trogossitidae, Cleridae and some Lophocateridae (Kolibáč 2013). Adults of Palaearctic *Aplocnemus* and *Trichoceble* are often found at the base of trees and shrubs, in litter or moss. Some species feed on Coccoidea (*Aplocnemus impressus*), eggs of the moth *Lymantria dispar* (*Trichoceble memnonia*) and aphids (*Trichoceble floralis*) (Kolibáč et al. 2005). The larvae and adults of the island dwelling wingless *Gietella* occur among rocks and under stones and little is known about their biology. On the other hand, dasytinae larvae and adults are often more specialised. Although they can also live under bark or in galleries, they more often dwell and hunt in niches that are not used by other cleroids: cones of conifers or hollow stems of herbaceous plants. Dasytine adults are mostly floricolous and can be found on flowering plants (Kolibáč et al. 2005). These observations also support the placement of Rhadalidae at the base

of the phylogenetic tree of the melyrid lineage. We can only deduce that *Cretorhadalus constantini* **gen.** et **sp. nov.** lived in ancient forests in present day Myanmar and its larvae were carnivorous. It probably hunted for the larvae and eggs of small xylophagous insects like the larvae of modern rhadalids. Unfortunately, it is not possible to conclude anything about the biology of the adults or their relationship with the extant fauna. If the described larva is more related to the extant *Pelecophora* than to the other three Rhadalidae genera for which larvae are known, it might also be floricolous at least for a part of its life. However, this hypothesis is premature as it is dependent on a future record of an adult *Cretorhadalus constantini* **gen.** et **sp. nov.** in burmite or another Cretaceous amber. Due to the limited knowledge of extant cleroid larvae, we are aware that the discovery of *Cretorhadalus* adult may change the opinion on the exact classification of this fossil. The discovery of a recent Mauroniscidae larva would also be important. Even in that case, we assume that *Cre-*

torhadalus constantini **gen.** et **sp. nov.** will remain classified in one of the early diverging groups of the melyrid lineage.

5. Conclusion

Cretorhadalus constantini **gen.** et **sp. nov.** tentatively assigned to Rhadalidae is the earliest described larva of Cleroidea (the only one for the Mesozoic) and the first representative of the melyrid lineage (*sensu* Bocakova et al. 2011) found in Burmese amber. Based on a comparison with the morphological traits of extant relatives we propose that the larva was carnivorous and probably fed on the eggs and larvae of small xylophagous insects.

This contribution demonstrates the potential of studying Cretaceous beetle larvae preserved in amber. These studies are frequently overlooked in recent taxonomic studies mainly due to the lack of diagnostic characters. By using various classical and modern microscopy tools like inverted light microscopy or SRμCT it is possible to see details of their morphology and surface microstructures that reveal larval specializations and lifestyles that can be compared with those of extant species (e.g., Batelka et al. 2018, 2021).

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8. References

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