



A new enigmatic lineage of Dascillidae (Coleoptera: Elateriformia) from Eocene Baltic amber described using X-ray microtomography, with notes on Karumiinae morphology and classification

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Abstract. Dascillidae are a species-poor beetle group with a scarce fossil record. Here, we describe *Baltodascillus seraticornis* gen. et sp. nov. based on a well-preserved specimen from Eocene Baltic amber. It differs from all known Dascillidae by its reduced mandibles. After studying the specimen using light microscopy and X-ray microtomography, we tentatively place this genus in the poorly defined subfamily Karumiinae based on the large eyes, serrate antennae, and lack of prosternal process. This is the first representative of the Dascillidae formally described from Baltic amber and the first described fossil member of the subfamily Karumiinae. We briefly discuss the problematic higher classification of Dascillidae, along with the morphology and biogeography of the group.

1 Introduction

Dascillidae are a small beetle family with about 100 extant species classified in 11 genera distributed in all zoogeographic realms (Ivie and Barclay, 2011; Jin et al., 2013b; Lawrence, 2016; Johnston and Gimmel, 2020). Together with the still-smaller family Rhipiceridae, they form the superfamily Dascilloidea within the series Elateriformia (Lawrence, 2016; Kundrata et al., 2017). Dascillidae are further divided into two subfamilies with unclear limits, i.e., Dascillinae (six genera, about 80 species) and Karumiinae (five genera, about 20 species) (Lawrence and Newton, 1995; Ivie and Barclay, 2011; Lawrence, 2016). There has been no

worldwide taxonomic revision of Dascillidae. However, the subfamily Dascillinae has received particular attention during the last decade. The worldwide genera and Asian species of Dascillinae were revised by Jin et al. (2013b), with additional species described in several subsequent papers (Jin et al., 2015, 2016, 2017; Li et al., 2017; Fang et al., 2020; Wang et al., 2020a, b). The only Australian genus of the family, *Notodascillus* Carter, 1935, was revised by Jin et al. (2013a), and Terzani et al. (2017) revised the Western Palearctic species of *Dascillus* Latreille, 1797. Most recently, Johnston and Gimmel (2020) reviewed the North American Dascillidae of both subfamilies and also provided a species checklist for the New World. Although Karumiinae were included in the latter study, issues of higher classification did not receive much attention. Ivie and Barclay (2011) revised the status of certain genera associated with *Karumia* Escalera, 1913, but a comprehensive revision of Karumiinae in the modern sense is missing.

The fossil record of Dascillidae is rather scarce and was critically reviewed by Jin et al. (2013c). Two Australian Upper Triassic genera, *Apheloodes* Dunstan, 1923 and *Leioodes* Dunstan, 1923, described based on a single elytron each, were removed from Dascillidae and placed in Coleoptera *incertae sedis*, and the North American Miocene *Protacnaeus* Wickham, 1914 and *Miocyphon* Wickham, 1914 were transferred to Psephenidae and Scirtidae, respectively. The monotypic genus *Mesodascilla* Martynov, 1926 from the Jurassic Karatau locality in Kazakhstan, which was originally assigned to Dascillidae (Martynov, 1926), has been re-

cently treated either as a member of Eulichadidae (Kirejtshuk and Azar, 2013) or Lasiosynidae (Yan et al., 2014). Jin et al. (2013c) kept only three genera which contain fossil species in Dascillidae. The genus *Lyprodascillus* Zhang, 1989, with two described species from the Miocene of China, has remained tentatively in Dascillidae, although authors could not confirm its systematic placement based on the available descriptions and illustrations (Jin et al., 2013c). The only Mesozoic dascillid genus is the monotypic *Creto-dascillus* Jin, Slipinski, Pang & Ren, 2013 from the Cretaceous Yixian Formation in China (Jin et al., 2013c). Most fossil species are classified in the extant genus *Dascillus*, which currently contains six species from the Miocene Shandong Formation of China (Zhang, 1989; Zhang et al., 1994), one from the Miocene Latah Formation of the USA (Lewis, 1973), and one from the Eocene Florissant Formation of the USA (Wickham, 1911). However, at least some of these species probably do not belong to Dascillidae and are kept there only tentatively until the type material is examined in detail (Jin et al., 2013c). Some fossil taxa attributed to Dascillidae, and usually to *Dascillus* (sometimes as its synonym *Atopa* Paykull, 1799), remain unnamed, as for example the specimens found in the Oligocene Aix-en-Provence in southern France (Hope, 1847) or specimens reported from Baltic amber (Helm, 1886, 1896; Klebs, 1910; Larsson, 1978; Spahr, 1981).

In this study, we describe an enigmatic new genus based on a well-preserved specimen from Eocene Baltic amber. This is the first described representative of Dascillidae from amber. We discuss its systematic placement as well as the higher classification and biogeography of Dascillidae.

2 Material and methods

The amber piece was polished by hand, allowing improved views of the included specimen, and was not subjected to any additional treatment. For the purpose of light microscopic image capture, the amber specimen was fixed at a suitable angle of view to a Petri dish with gray plasticine modeling clay (Pelikan, Germany, model number 601492). It was photographed submersed in glycerol to prevent reflections and to reduce visibility of small scratches on the surface of the amber piece. Images were taken with a Leica MC 190 HD camera attached to a motorized Leica M205 C stereo microscope equipped with the flexible dome Leica LED5000 HDI or the conventional ring light Leica LED5000 RL-80/40 as an illuminator, applying the software Leica Application Suite X (version 3.7.2.22383, Leica Microsystems, Switzerland). Stacks of photographs were combined with the software Helicon Focus Pro (version 7.6.4, Kharkiv, Ukraine), applying the rendering method “depth map” or “weighted average”.

The X-ray micro-CT (μ CT) observations were conducted at Daugavpils University, Daugavpils, Latvia (DU), using a Zeiss Xradia 510 Versa system. In order to achieve the

best results possible, three scans were conducted: habitus, head/prothorax and abdomen. For prothorax/head and abdomen scans, the parameters were mostly identical with the exception of exposure time. For both scans, sample-detector and source-sample distances were set to 37.4 and 38 mm, respectively, the source X-ray beam energy was set to 30 kV and power of 2 W. Tomographic slices were generated from 2401 slices through 360-degree rotation, using 4 \times objective. Achieved voxel size during scan was 3.3 μ m. Exposure times were set to 8 s for the abdomen scan and 9 s for the head/prothorax scan. The overall scan was carried out at X-ray beam energy of 40 kV and power of 3 W, source-sample distance was set to 24.4 mm and sample-detector distance was set to 117.7 mm. Tomographic slices were generated from 1601 slices through 360-degree rotation using a 0.4 \times objective and exposure set to 17 s. Achieved voxel size during overall scan was 11.7 μ m. All three scans had binning set to 2 times as well as variable exposure time set to 2 at the thickest part of the sample. Prior to each scan a warm-up scan was conducted that lasted 25 min. Acquired images were imported into Dragonfly PRO (version 2020.2) software platform for interactive segmentation and 3D visualization. Final image plates were assembled using Adobe Photoshop CC (version 2019-20.0.5).

Body length of the examined specimen was measured from the clypeus to apex of elytra, body width at the widest part of the body, pronotal length at midline, and pronotal width at the widest part. Morphological terminology follows Jin et al. (2013b) and Johnston and Gimmel (2020). The holotype is deposited in the collection of the Department of Palaeontology of the National Museum, Prague, Czech Republic (NMPC). The ZooBank LSID number for this publication is urn:lsid:zoobank.org:pub:F55CA75B-AF7C-4F1F-BD65-DCBEAAC75410 (12 March 2021).

3 Systematic paleontology

Order **Coleoptera** Linnaeus, 1758

Suborder **Polyphaga** Emery, 1886

Series **Elateriformia** Crowson, 1960

Superfamily **Dascilloidea** Guérin-Méneville, 1843

Family **Dascillidae** Guérin-Méneville, 1843

Subfamily **Karumiinae** Escalera, 1913

Genus *Baltodascillus* gen. nov.

Type species *Baltodascillus serraticornis* sp. nov., here designated

urn:lsid:zoobank.org:act:A2B037D4-8951-4BE2-8263-4891CCD03E3B; Figs. 1–4, Video supplements 1–4

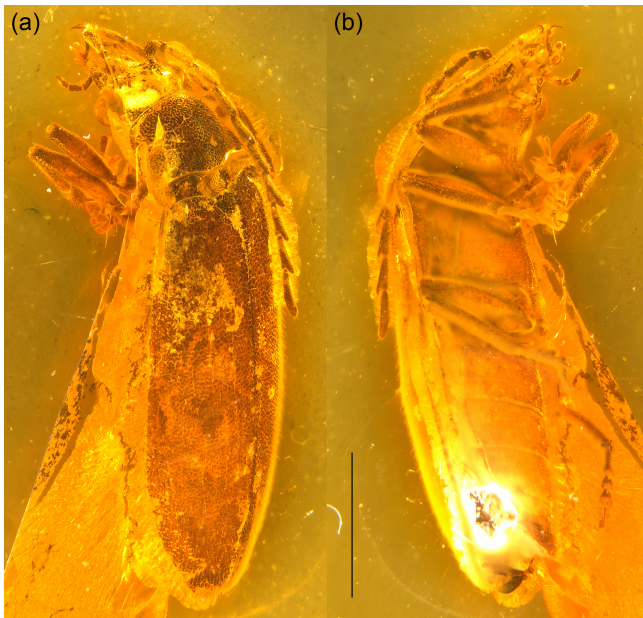


Figure 1. *Baltodascillus serraticornis* gen. et sp. nov., holotype: (a) habitus, dorso-frontal view; (b) habitus, ventro-lateral view. Scale bar = 2.0 mm.

Etymology

Derived from the words “Baltic” (referring to Baltic amber) and “*Dascillus*” (a genus name in Dascillidae). Gender: masculine.

Diagnosis

Baltodascillus gen. nov. can be recognized among other genera of Dascillidae by the reduced mandibles (Figs. 2a, 3d). Additionally, the following combination of characters serves to distinguish it from all other genera: strongly serrate antennae, a fusiform terminal maxillary palpomere, large eyes, pronotum widest posteriorly and with a strongly developed lateral carina, lack of a developed prosternal process, complete elytra, confused elytral punctation, a weakly developed elytral epipleuron, and abdomen with five ventrites (Figs. 1–4).

Description

Body (Fig. 1) narrowly elongate. Eyes large, strongly protuberant. Frontoclypeal suture distinctly impressed. Labrum wider than long, distinctly sclerotized, anteriorly slightly concave. Antenna (Figs. 1–3) serrate, almost reaching middle of elytra; antennomeres 3–10 with prominent, acute serrations; terminal antennomere simple, elongate, apically rounded. Mandible (Figs. 2a, 3d) considerably reduced, very short, subtriangular, without teeth, apically narrowly rounded. Maxillary and labial palpi (Figs. 2c, d; 3; 4a, b)

each with terminal palpomere fusiform, apically flattened and narrowly rounded.

Pronotum (Figs. 2b, c; 3a, d) transverse, widest near posterior angles; sides weakly arcuate; lateral carinae distinct, complete; posterior angles weakly acute; posterior edge weakly crenulate. Hypomeron with postcoxal process obtuse. Prosternal process (Figs. 3b; 4b, c) not developed, forming short right-angled denticle. Elytra (Figs. 1a; 2a, b) elongate, lateral edges more or less straight, widest at apical third, then gradually narrowed towards apex; elytral surface without costae or striae; elytral punctures irregular, only partially in weakly defined rows; elytral epipleuron narrow and oblique behind humeral area. Leg (Figs. 1b; 2d; 4a, b) with tibia about as long as femur in fore- and midlegs, and slightly longer than femur in hind legs; tibial spurs paired, approximately equal in length, serrate. Tarsomeres (Figs. 2e, f; 4f, g) 1–4 each with membranous ventral lobe; lobes gradually larger from tarsomere 1 to tarsomere 4, those on tarsomeres 2–4 strongly bilobed.

Abdomen (Figs. 1b; 4d, e) with five ventrites; ventrites 1–4 gradually shorter towards apex; ventrite 1 without delimited hind coxal cavities, and with intercoxal process indistinct; ventrite 5 slightly longer than 4, triangular, narrowly rounded apically.

Composition and distribution

Baltodascillus gen. nov. is a monotypic genus and is known exclusively from Eocene Baltic amber.

Baltodascillus serraticornis sp. nov.

urn:lsid:zoobank.org:act:1839A0BD-37DB-4F9A-ABB9-12C8300682E1; Figs. 1–4, Video supplements 1–4.

Type material

Holotype, adult male, NM-T 3470 (NMPC, ex coll. R. Kundrata, Olomouc, No. BAL0012, ex coll. J. Damzen, Lithuania, No. 8751). A complete beetle is included in an elongate, transparent, yellow amber piece with dimensions of $32 \times 15 \times 4$ mm, weighing approximately 1.7 g, without any syninclusions.

Type stratum and age

Mid-late Eocene, 48–34 Ma (Seyfullah et al., 2018; Bukejs et al., 2019; Kasiński et al., 2020; Sadowski et al., 2017, 2020).

Type locality

Baltic Sea coast, Yantarny mine, Sambian (Samland) Peninsula, Kaliningrad Oblast, Russia.

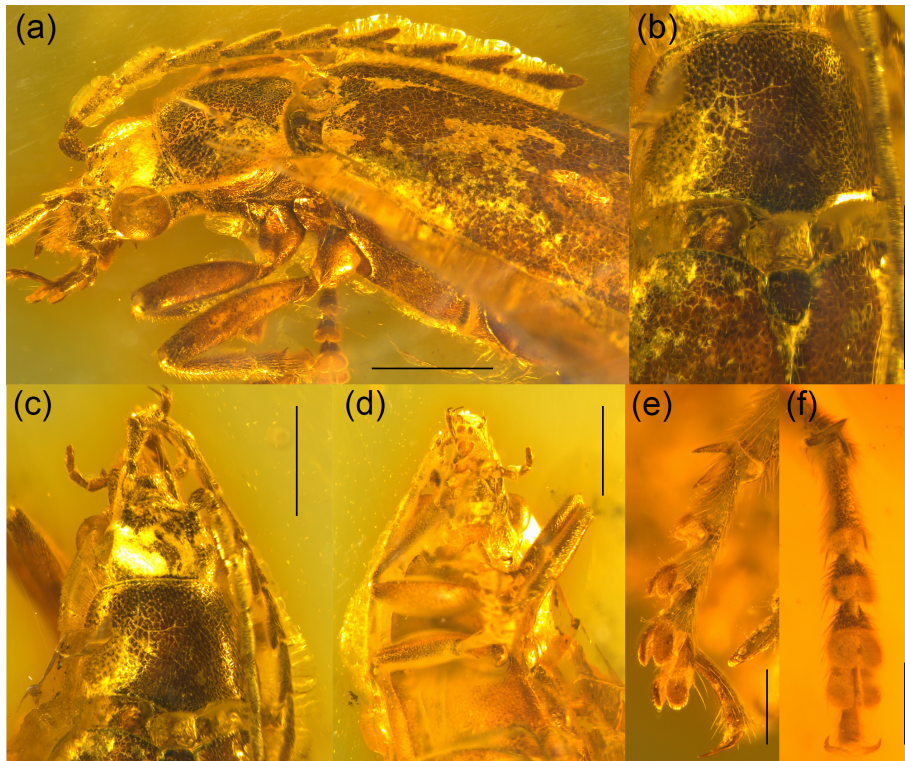


Figure 2. *Baltodascillus serraticornis* gen. et sp. nov., holotype: (a) habitus, lateral view; (b) pronotum and scutellar shield, dorsal view; (c) head and pronotum, dorsal view; (d) head and thorax, ventral view; (e) tarsus, ventro-lateral view; (f) tarsus, ventral view. Scale bars = 1.0 mm (a–d), 0.3 mm (e, f).

Etymology

The specific epithet “*serraticornis*” is a Latin adjective referring to the shape of the antennae.

Diagnosis

As for the genus (vide supra).

Description

Adult male. Body (Fig. 1) about 7.5 mm long and 2.5 mm wide, narrowly elongate, about 3 times as long as wide, weakly convex; dorsally moderately densely setose.

Head (Figs. 2a, c, d; 3; 4a, b) 1.5 mm wide, subquadrate, 0.8 times as wide as pronotum width. Eyes large, strongly protuberant. Frontoclypeal suture distinctly impressed, more or less straight; clypeus short and strongly transverse. Labrum wider than long, distinctly sclerotized, anteriorly slightly concave, with discal setae longer than length of exposed portion of labrum. Antenna (Figs. 1–3) serrate, almost reaching middle of elytra; scape slightly longer than pedicel; pedicel slightly longer than wide; antennomeres 3–10 elongate, with prominent, acute serrations; terminal antennomere simple, slightly curved, elongate, about 1.4 times as long as antennomere X, apically rounded. Mandible

(Figs. 2a, 3d) considerably reduced, very short, subtriangular, without teeth, apically narrowly rounded. Maxillary palpus (Figs. 2c, d; 3; 4a, b) moderately long; penultimate palpomere elongate, shorter than preceding one, about twice as long as wide; terminal palpomere fusiform, slightly longer than penultimate palpomere, about 2.5 times as long as wide, apically flattened and narrowly rounded. Labial palpus distinctly shorter than maxillary palpus, with terminal palpomere fusiform.

Pronotum (Figs. 2b, c; 3a, d) transverse, about 1.7 times wider than long (1.9 mm wide, 1.1 mm long), widest just anterior to posterior angles; sides weakly arcuate; lateral carinae distinct, complete, slightly explanate; anterior angles obtuse, not projecting, posterior angles weakly acute; posterior edge tri-emarginate and weakly crenulate along entire length; disk slightly convex, with rather smooth surface. Hypomeron with postcoxal process obtuse. Prosternum (Figs. 3b; 4b, c) in front of coxa about as long as procoxal diameter; prosternal process not developed, forming short right-angled denticle. Pronotosternal suture complete. Scutellar shield (Figs. 1a; 2b; 3a) slightly longer than wide, weakly rounded anteriorly, narrowly rounded posteriorly. Elytra (Figs. 1a; 2a, b) together about 2.4 times as long as wide (5.9 mm long, 2.5 mm wide) and 5.0 times as long as pronotum; weakly convex, more or less straight, widest at apical third, then gradually narrowed

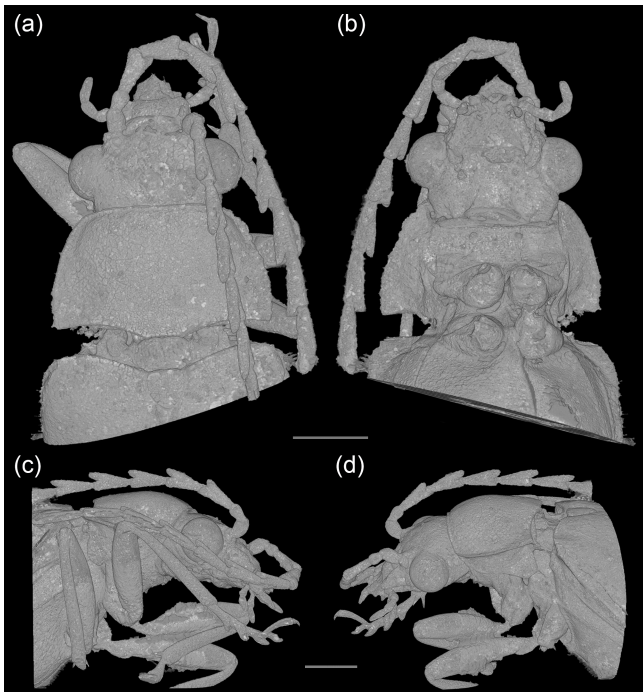


Figure 3. *Baltodascillus serraticornis* gen. et sp. nov., holotype, X-ray micro-CT renderings: (a) head and thorax, dorsal view; (b) head and thorax, ventral view; (c) head and thorax, right lateral view; (d) head and thorax, left lateral view. Scale bars = 1.0 mm.

towards apex; elytral surface without costae or striae; elytral punctures irregular, only partially in weakly defined rows; elytral intervals flat; elytral epipleuron narrow and oblique behind humeral area. Mesoventrite (Figs. 3b; 4b, c) with anterior edge medially on the same plane as metaventrite, forming short triangular projection laterally bordered by procoxal rests. Mesocoxal cavities separated by narrow mesoventral process. Metaventrite wider than long, moderately convex. Metacoxae contiguous, extending laterally to level of elytral epipleuron; metacoxal plate well developed mesally. Hind wing fully developed. Leg (Figs. 1b; 2d; 4a, b) slender, femur robust, elongate; tibia about as long as femur in fore- and midlegs, and slightly longer than femur in hind legs; each tibia with pair of distinctly serrate spurs approximately equal in length. Tarsomere 1 distinctly longer than tarsomere 2, tarsomeres 2–4 gradually shorter towards apex, each of tarsomeres 1–4 with membranous ventral lobe; lobes gradually larger from tarsomere 1 to tarsomere 4, those on tarsomeres 2–4 strongly bilobed (Figs. 2e, f; 4f, g); claws simple, moderately curved; empodium absent.

Abdomen (Figs. 1b; 4d, e) with five ventrites, with surface moderately densely covered by fine punctures; ventrites 1–4 gradually shorter towards apex; ventrite 1 without delimited hind coxal cavities, and with intercoxal process indistinct; ventrite 5 slightly longer than 4, triangular, narrowly rounded apically, apical half of ventrite in slightly different plane from

basal half. Tergite X triangular, apically narrowly rounded. Aedeagus with only parameres visible but not median lobes.

Remark

We conclude that the examined specimen is a male based on the shape of the body, serrate antennae, a long, narrowly rounded abdominal ventrite 5, and aedeagal structure (parameres) detected in X-ray micro-CT imaging.

4 Discussion

In order to understand the placement of the newly discovered fossil genus within Dascillidae, it is important to acknowledge the currently problematic situation with the subfamilial classification of the group. As currently delimited, Dascillidae contain two vaguely defined subfamilies with a divergent taxonomic history (Lawrence and Newton, 1995; Lawrence, 2016). Free-living and non-modified Dascillinae occur in non-arid areas of western North America, the Greater Antilles, Palearctic and Oriental regions, western Africa, and Australia. Karumiinae, which contain morphologically modified lineages of which at least some are associated with subterranean termites, are mostly distributed in arid and semi-arid regions of western North America, northern Africa, central Asia and southern South America (Lawrence and Newton, 1995; Jin et al., 2013b; Lawrence, 2016). The latter group had long been treated as a separate family, Karumiidae, associated with the families of former Cantharoidea (i.e., roughly the soft-bodied Elateroidea) and originally included only the morphologically highly modified groups near *Karumia* Escalera, 1913 with an apparently soft cuticle, variously reduced elytra and unknown females (Crowson, 1955; Arnett, 1964; Paulus, 1972). Crowson (1971) first associated Karumiidae with Dascillidae based on a number of morphological characters, although he still kept the family status for both groups. He also transferred the genera *Anorus* LeConte, 1859, *Pleolobus* Philippi and Philippi, 1864 (Fig. 5), *Genecerus* Walker, 1871 and *Emmita* Escalera, 1914 from Dascillidae to Karumiidae and provided updated diagnoses for both groups. Based on his key, the Karumiidae contained taxa with a simple galea, the ligula with two short lobes, the ventral tarsal lobes absent or not basally articulated, the corpotentorium very broad, the male antenna pectinate or flabellate, and females wingless (apparently referring to known females of *Anorus* sp. with shortened elytra and reduced hind wings). However, Crowson's characters for separating the two subfamilies have been largely problematic since they do not apply to all included genera, and especially certain intermediate groups like *Genecerus* violate the diagnosis of Karumiinae (Lawrence and Newton, 1995; Lawrence, 2016). For example, both subfamilies share a very broad corpotentorium, the ventral lobes on tarsomeres of *Genecerus* and *Anorus* are similar to those in Das-

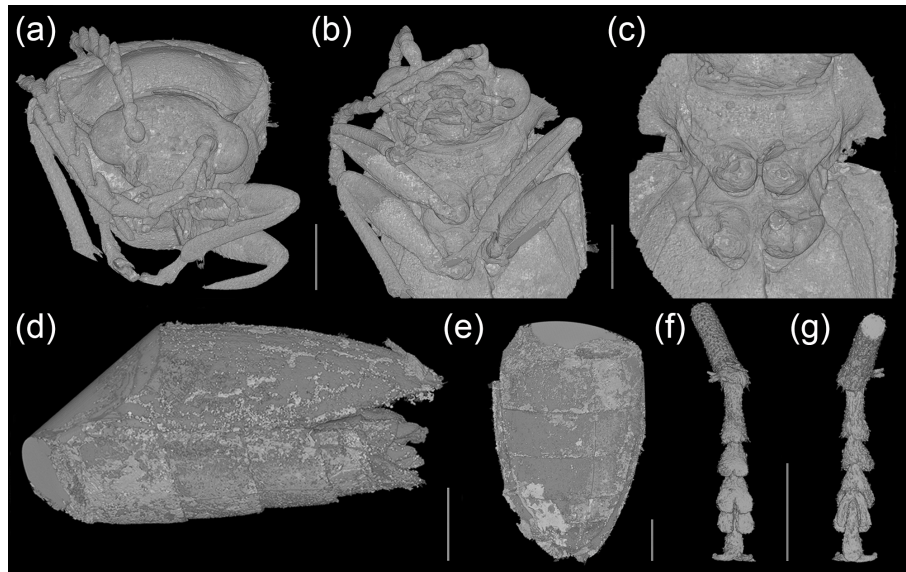


Figure 4. *Baltodascillus serraticornis* gen. et sp. nov., holotype, X-ray micro-CT renderings: (a) head, frontal view; (b) head and thorax, fronto-ventral view; (c) pro- and mesothorax, ventral view; (d) abdomen (ventrites 2–5), lateral view; (e) abdomen (ventrites 2–5), ventral view; (f) tarsus, ventral view; (g) tarsus, dorsal view. Scale bars = 1.0 mm.

cillinae, at least females of *Genecerus* have well-developed hind wings (Lawrence, 2016), and serrate to pectinate antennae are known only in *Emmita* and *Genecerus* but not in any other karumiine genus. Additionally, Grebennikov and Scholtz (2003) concluded that the larval morphology of *Pleolobus* is highly similar to that of Dascillinae, with the primary difference being that the latter possess molar ridges on the mandible. Unfortunately, the relationships among the dascillid genera have never been tested using a focused molecular approach. The only available molecular phylogenetic analyses, although either preliminary or focused on broader issues, have nonetheless called into question the current subfamilial classification (Kunderata et al., 2017; Johnston and Gimmel, 2020).

Representatives of Dascillidae display a graded series of morphological modifications connected with possible neoteny and soft-bodiedness, similar to the situation in various Elateroidea (Cicero, 1988; Kunderata and Bocak, 2019). In Dascillidae, the modifications represent a continuum from the well-sclerotized groups with adults of both sexes fully developed (although at least some females might have slightly less developed hind wings than their counterparts) (traditional Dascillinae), through more or less soft-bodied groups with males with complete elytra and females with variously shortened elytra and reduced hind wings (*Anorus* spp., *Pleolobus*, probably also *Emmita*) (Fig. 5) to the soft-bodied forms with males with greatly shortened elytra and females unknown but probably even more dramatically modified, termitiform (most *Karumia*) (Paulus, 1972; Solervicens, 1991; Ivie and Barclay, 2011; Johnston and Gimmel, 2020). Such modifications also affect the morphology of the thorax, such

that the hard-bodied groups have a well-developed, spine-like prosternal process, whereas the soft-bodied forms have the prosternal process dramatically reduced to form a short triangle-shaped denticle. It is probable that the modifications of morphology connected with the independent evolution of soft-bodiedness have influenced the formal classification of Dascillidae, similar to many cases in the Elateroidea (Kunderata and Bocak, 2019). This hypothesis, however, needs to be tested using a well-sampled molecular phylogenetic analysis.

Under the current state of knowledge, we tentatively place the newly described *Baltodascillus* gen. nov. in Karumiinae based on the large eyes, serrate antennae, and lack of a spine-like prosternal process. This fossil genus is morphologically similar to the New World genera *Anorus* and *Pleolobus* (Fig. 5) or the African/Middle Eastern genus *Genecerus* but differs from these in the strongly serrate (but not pectinate) antennae, crenulate hind margin of the pronotum, and confused elytral punctation. It differs from all known Dascillidae by the highly reduced mandibles which do not overlap and are apparently non-functional. Given the unusual nature of this character, further specimens of this genus will be critical in determining whether this is a stable character or the result of a single teratological specimen. This is the first representative of the Dascillidae formally described from Baltic amber and also the first described fossil member of the subfamily Karumiinae since *Semenoviola obliquotruncata* Martynov, 1925, originally described in that group, was determined to be a dermapteran (Bolívar y Pieltain, 1926). Also, *Baltodascillus* gen. nov. is the first karumiine known from Europe and, therefore, sheds light not only on the paleodi-

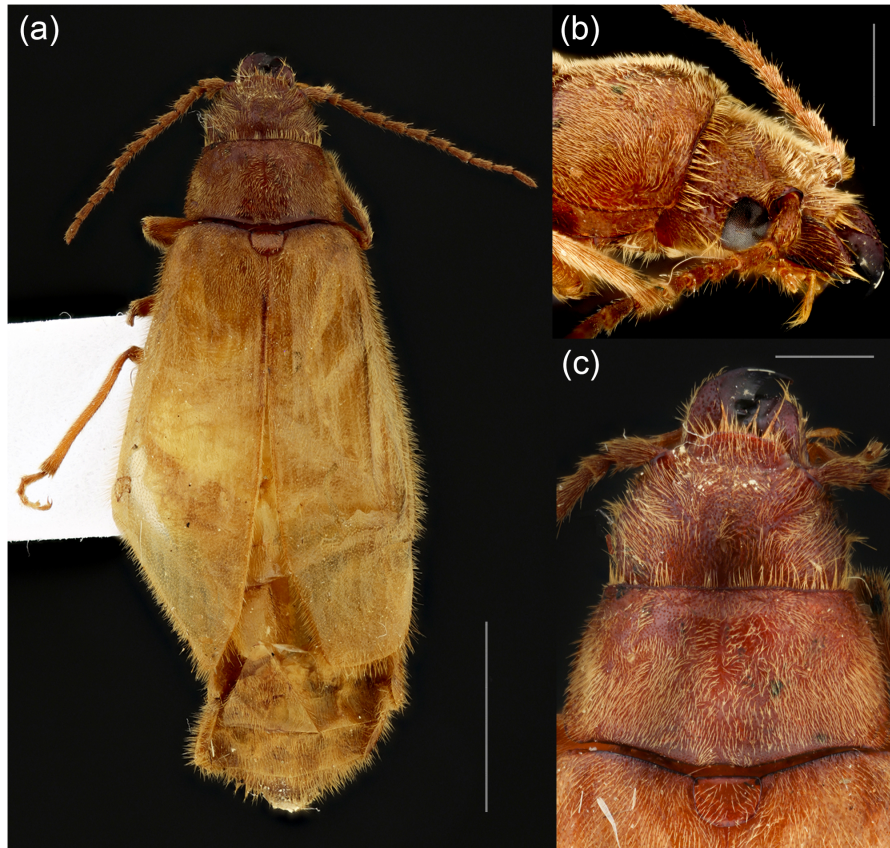


Figure 5. *Pleolobus fuscescens* Philippi et Philippi, 1864, female from Chile: (a) habitus, dorsal view; (b) head, lateral view; (c) head, pronotum and scutellar shield, dorsal view. Scale bars = 4.0 mm (a), 1.0 mm (b, c). All images by Jorge Jensen.

versity and systematics of the group but also on its biogeography.

Data availability. The holotype of *Baltodascillus serraticornis* gen. et sp. nov. is deposited in the collection of the Department of Palaeontology of the NMPC. Volume renderings of X-ray microtomography of habitus, head/prothorax, hind tarsus, and abdomen are available as Video supplements 1–4, respectively.

Video supplement. X-ray micro-CT volume renderings of the habitus, head/pterothorax, hind tarsus, and abdomen of *Baltodascillus serraticornis* gen. et sp. nov. are available at <https://doi.org/10.5446/52211> (Video supplement 1, Kunderata et al., 2021a), <https://doi.org/10.5446/52212> (Video supplement 2, Kunderata et al., 2021b), <https://doi.org/10.5446/52213> (Video supplement 3, Kunderata et al., 2021c), <https://doi.org/10.5446/52214> (Video supplement 4, Kunderata et al., 2021d).

Author contributions. RK conceived and designed the study. MLG and RK carried out the morphological investigation. AB conducted the micro-CT scanning. SMB prepared microphotographs.

GP and RK prepared figure plates. RK and MLG wrote the initial manuscript with help of GP, AB, and SMB. All authors performed the literature search, discussed the results, and edited, reviewed, and approved the manuscript.

Competing interests. The authors declare that they have no conflict of interests.

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