Cretabaltoraea volsella gen. et sp. nov. (Coleoptera: Nitidulidae) from Cretaceous Kachin amber and its relationship with Eocene *Baltoraea* (Coleoptera: Nitidulidae)

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Abstract

Here we describe *Cretabaltoraea volsella* Peris, Jelínek & Audisio **gen. et sp. nov.** of the family Nitidulidae (Coleoptera). As implied by its generic name, the new species is described after a fossil specimen preserved in the Upper Cretaceous Kachin amber from northern Myanmar. This new species is rather similar to the two fossil nitidulid species of *Baltoraea* Kurochkin & Kirejtshuk, 2010, previously described from the Eocene Baltic amber. The comparison between this group of fossils and the study of *Baltoraea simillima* Kurochkin & Kirejtshuk, 2010 using CT-scanning suggest that *Cretabaltoraea volsella* **gen. et sp. nov.** and the two *Baltoraea* species should be placed in the extinct Apophisandrinae, a basal subfamily of Nitidulidae which until now only includes a group of Cretaceous fossils from the Kachin amber, described as ancient pollinators of both gymnosperms and basal angiosperms.

Keywords: Burmese amber, evolution, fossil, Myanmar, Pinaceae, pollination

Introduction

Nitidulidae is a family of polyphagan beetles constituted by approximately 350 genera and 4500 species (Jelínek *et al.*, 2010; Audisio *et al.*, 2015). The phylogenetic relationship within the family remains controversial due to the high diversity of plesiomorphic characters within the different lineages, the small size of many species, and the need to compare many convergent characters that have undergone similar selective pressures (Cline *et al.*, 2014; Lee *et al.*, 2020; Peris *et al.*, in press). There are nine to ten recent recognized subfamilies in Nitidulidae (Jelínek *et al.*, 2010; Lee *et al.*, 2020) and one additional subfamily (Apophisandrinae) containing only some Cretaceous fossil species preserved in amber from Kachin (Myanmar), representing a morphologically highly diverse group of pollinators (Kirejtshuk *et al.*, 2023; Peris *et al.*, in press).

The fossil record of the family comprises approximately 90 species (Peris *et al.*, in press), the

oldest being known from the Aptian of southern Russia (Baissa) (Kirejtshuk & Ponomarenko, 1990), dated *ca.* 120 Ma (Early Cretaceous). However, it seems that the family diverged from their closest relatives, the family Kateretidae, around 160 Ma (Cai *et al.*, 2022), apparently resulting in a gap of fossils for the first 40 million years. The prolific amber record from Kachin, in Myanmar, dated *ca.* 99 Ma (Shi *et al.*, 2012), preserves Nitidulidae fossils from various extant and extinct linages, extremely well (Peris *et al.*, in press). Many cites about fossil nitidulids have been historically collected also from the equally prolific Baltic amber, 48–34 Ma (Eocene), but their formal descriptions are not so common (Kurochkin & Kirejtshuk, 2010; Kirejtshuk & Bukejs, 2023). Among fossils from Baltic amber, two species *Baltoraea insignis* Kurochkin & Kirejtshuk, 2010 and *B. simillima* Kurochkin & Kirejtshuk, 2010 were described in the subfamily Epuraeinae (Kurochkin & Kirejtshuk, 2010).

Here we describe a monotypic genus *Cretabaltoraea volsella* **gen. et sp. nov.** based on a specimen preserved in the Cretaceous amber from Kachin, that we ascribe to the subfamily Apophisandrinae of Nitidulidae. *Cretabaltoraea* **gen. nov.** owes its name to the similarities that have been detected in its Eocene relative *Baltoraea* (Kurochkin & Kirejtshuk, 2010). In order to offer a comprehensive analysis, we have reviewed both species of *Baltoraea* and have performed a CT-scan of *B. simillima*. This manuscript supports the transfer of *Baltoraea* from Epuraeinae to Apophisandrinae, together with *Cretabaltoraea* **gen. nov.** (Kirejtshuk *et al.*, 2023; Peris *et al.*, in press).

Geological settings

Myanmar is worldwide known by its amber sources, extensively used in jewelry, which contain also bioinclusions in high abundance (Ross, 2024). There are amber deposits from different ages in the country, mostly from the Cretaceous (Zheng *et al.*, 2018), making necessary to differentiate the origin of the amber samples. Amber samples in Myanmar mainly are obtained from the Kachin province, thus being recently known as Kachin amber to differentiate it from other source localities.

We describe in this work a new fossil species from a sample found in the Noije Bum hill amber mines, 18 km to the southwest of Tanai, Hukawng Valley, Kachin Province, Myanmar (Cruickshank & Ko, 2003). The radiometric age of the Kachin amber has been stablished as 98.79 ± 0.62 Ma based on U-Pb dating of zircons (Shi *et al.*, 2012). Nevertheless, some authors called for a more ancient age of the amber based on the polished shape of the amber pieces and marine lifestyle evidence on the pieces surface, suggesting a reworking process before

buried of the amber in the sedimentary rock matrix (*e.g.*, Mao *et al.*, 2018).

We also reanalyzed two amber samples which contain the holotypes of *Baltoraea insignis* and *B. simillima* (Kurochkin & Kirejtshuk, 2010). These two amber pieces are described from the Baltic amber. Baltic amber is a secondary deposit found mainly in glauconitic marine sediments of middle Eocene age, 48–34 Mya, deposited along the paleo-North Sea margin (Wolfe *et al.*, 2016). Although Baltic amber is principally found in Russia (Kaliningrad area), it is also abundant in Poland and Germany, and additional reposited sites are also known in other places.

Material and methods

We examine one new amber sample, NIGP205638, that will be deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS), China.

In addition, we also reexamined the holotypes of *Baltoraea insignis* (Coll. of C. Gröhn, no. 995C) and *B. simillima* (Coll. of C. Gröhn, no. 4243C), described in independent amber samples from the Eocene Baltic amber (Kurochkin & Kirejtshuk, 2010). These specimens are housed at the Geologisch-Paläontologische Museum der Universität Hamburg, Germany.

Amber sample 28 was polished to allow observation of the morphological characters of the specimens. All the amber samples were examined under three different lenses: a Leica MS5 stereomicroscope, an Olympus CX41 compound microscope and a high-resolution Leitz stereomicroscope (40–160×). Photographs were taken using a Moticam 2500 camera attached to the Leica MS5 stereomicroscope. Image stacks were processed using COMBINE ZP (Hadley, 2010) and edited with CorelDraw 2019.

The holotype of *B. simillima* was successfully imaged at the Universitat Politècnica de Catalunya (Spain) with a Bruker Skyscan 1272 X-ray micro-CT system to obtain high-quality 3D images to complement its original description. Images were generated at an X-ray voltage of 50 kV; 200 µA; voxel size 1.601 µm. Four frames per projection were acquired with an exposure time of 1.9 s for a total of 2688 projections. Acquired images were rendered and visualized using Avizo-Lite 2020.2 (Thermo Fisher Scientific, Schwerte, Germany).

All relevant structures were measured from the digitized images. The specific terminology for characters follows that of Jelínek & Cline (2010). The nomenclatural acts established herein are registered under ZooBank LSID: urn:lsid:zoobank.org:pub:D4C76BE7-DB62-421F-84A4-6D5AA193196F.

Systematic palaeontology

Order Coleoptera Linnaeus, 1758
Superfamily Nitiduloidea Latreille, 1802
Family Nitidulidae Latreille, 1802
Subfamily Apophisandrinae Molino-Olmedo, 2017

Genus *Cretabaltoraea* Peris, Jelínek & Audisio, gen. nov.
(Fig. 1)
LSID: urn:lsid:zoobank.org:act:CC6642BC-6719-496C-B973-64AC84E17A02

Type species. *Cretabaltoraea volsella* gen. et sp. nov.

Etymology. The generic name is derived from the prefix '*Creta-*' referring to the Cretaceous age of the amber sample that preserves the holotype, and '*-baltoraea*', after the genus *Baltoraea* Kurochkin & Kirejtshuk, 2010, the most similar-looking genus, described from the Eocene Baltic amber; feminine gender.

Diagnosis. Body surface markedly punctate; head transverse, constricted behind eyes to form wide neck; front strongly depressed; "occipital sulci" surrounding inner dorsal margin of the eyes distinct and complete, converging to middle of head from anterior frontal border; eyes large, protruding outwards, their outer apices separated by *ca*. 0.9× the maximum width of pronotum; antennal insertion hidden under thickening of the "occipital sulci"; antennae 11-segmented, with 3-segmented, distinct but loosely articulated and flattened club; last antennomere with longitudinal cleft along whole antennomere length; labrum emarginated; mandibles very large and narrow, as large as distance between eyes in dorsal view, without punctures, arcuately curved, with blunt, simple apex; each mandible show basal sharp tooth in inner part, near insertion on head; maxillae unilobed, exhibiting only distinct lacinia; pronotum as wide as elytra, subquadrate, parallel at sides, *ca*. 0.7× as long as wide, unciliated at sides; posterior edge markedly bordered; procoxal cavities open; prosternal process moderately long, narrow, subparallel, only slightly widened laterad, acutely triangularly pointed; elytra subparallel at sides, exhibiting irregular longitudinal rows of punctures, approximately as long as wide, markedly truncate, exposing only pygidium and covering all other preceding abdominal tergites; narrowly flattened, disk glabrous; mesocoxal axillary lines on metaventrite rather bluntly and narrowly angulate; tibiae with two big and acute pointed subequal spurs in inner apical angle and a series of pointed spines along outer lateral margin reaching apical angle; tarsi 5-5-5, with three basal tarsomeres subequal in length, long and narrow, almost subcylindrical, indistinctly lobed and not dilated distad, fourth tarsomere slightly shorter, followed by a long and thin last tarsomere, armed distad by long, simple tarsal claws; abdominal ventrite 2 very short, together with ventrite 3 as long as ventrite 1; spinose and hairy apical margin of pygidium.

Description. Description is based on a single male specimen, female unknown. Body short and wide, parallel-sided, body surface rugose; body generally glabrous, except in apex of abdomen, legs and tarsi, with short hairs.

Head prognathous, not covered by pronotum, subquadrate, constricted behind eyes to form wide neck (Fig. 1A, C); frons strongly depressed toward middle; eyes large, protruding outwards, their outer apices separated by distance *ca*. 0.9× width of pronotum; ocular setae not distinct. "Occipital sulci" distinct and complete, converging to middle of head from anterior frontal border; antennal insertion hidden under thickening of "occipital sulci". Antennae 11-segmented, long and thin, *ca*. 1× as long as pronotum, with a 3-segmented, loosely articulated and flattened club (Fig. 1E); scape as long and wide as the pedicel, scape barrel shaped; from pedicel onwards antennomeres cup-shaped; pedicel 1.2× as long as and 2× as wide as antennomere 3; antennomeres 3–8 progressively shorter and wider; antennomeres 9–11 forming club, each 1.2× as long and wide than antennomere 8; last two antennomeres with longitudinal cleft along whole antennomere length, more evident in last antennomere, last segment apically pointing (Fig. 1E). Labrum emarginated in middle (Fig. 1C). Mandibles very large and narrow, as long as distance between eyes in dorsal view, without punctures, arcuately curved, with blunt, simple apex; each mandible with basal sharp tooth in inner part, near insertion on head (Fig. 1C); maxillae unilobed, exhibiting only distinct lacinia; maxillary palpi long, 4-segmented, last maxillary palpomere slightly longer than previous two palpomeres combined, fusiform.

Pronotum as wide as elytra, subquadrate, parallel at sides, *ca*. 0.7× as long as wide; pronotal disk punctured with coarse, dense and shallow punctures, each individual pronotal puncture separated from its closest one by distance of *ca*. 1× diameter; pronotal lateral margins completely carinated, sides narrowly explanate, unciliated at sides; anterior margin straight, with bluntly rounded anterior angles; first half of lateral margins straight, second half roundly converging, showing very roundly posterior angles; posterior margin straight, posterior edge markedly bordered (Fig. 1A).

Scutellar shield large, stout, arrowhead shaped (Fig. 1D). Elytra truncated at apex, exposing only pygidium and covering all other preceding abdominal tergites (Fig. 1A); elytra subparallel at sides, approximately as long as wide, narrowly flattened, disk glabrous; elytra exhibiting
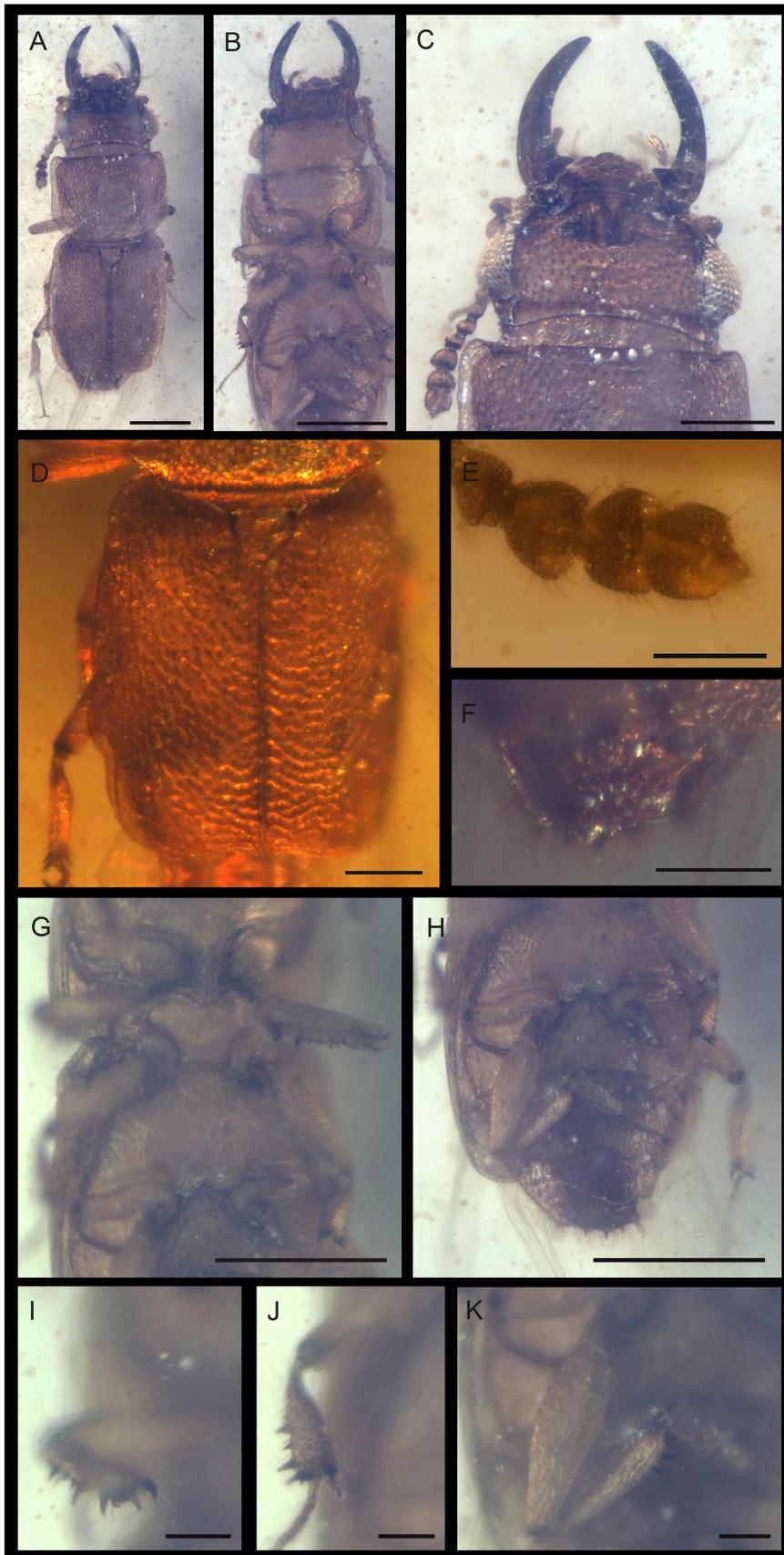
FIGURE 1. Holotype (sample NIGP205638) of *Cretabaltoraea volsella* **gen. et sp. nov.** preserved in Cretaceous Kachin amber. **A**, Dorsal view. **B**, Ventral view. **C**, Head in dorsal view. **D**, Elytra. **E**, Detail of the antenna in dorsal view. **F**, Anal sclerite. **G**, Pro- meso- and metasternum. **H**, Abdomen. **I**, Protibia. **J**, Mesotibia. **K**, Metatibia. Scale bars for **A**–**C** and **G**–**H** = 0.5 mm; for **D** and **F** = 0.2 mm; for **E** and **I**–**K** = 0.1 mm.

irregular longitudinal rows of coarse and shallow punctures (Fig. 1D) similar to punctures in the pronotum.

Procoxal cavities open; notosternal sutures present; prosternal process moderately long, narrow, subparallel, only slightly widened laterad, acutely triangularly pointed (Fig. 1G), slightly protruding over mesosternum. Mesosternum behind procoxae half as long as prosternum, with posterior edge only slightly concave. Mesocoxal axillary lines on metaventrite bluntly and narrowly angulate. Metaventrite with shallow longitudinal median impression; posterior margin of metaventrite shallowly angularly notched between metacoxae.

Procoxae transverse, oval, separated; pro- and mesotrochantins visible, narrow, triangular, attached laterally to coxae (Fig. 1G). Mesocoxae and metacoxae widely separated; mesocoxae circular; metacoxae not reaching the elytra at sides (Fig. 1G, H). Trochanters conspicuous, triangular, attached obliquely to femora; femora caniculate for reception of tibiae. Tibiae gradually widened distad, 0.7× as long as femora; tibiae with two big and acute pointed subequal spurs in inner apical angle and series of pointed spines along outer lateral margin, becoming gradually larger towards apical angle (Figs. 1I–K). All tarsi 5-segmented, with three basal tarsomeres subequal in length, long and narrow, almost subcylindrical, indistinctly lobed and not dilated distad, fourth tarsomere slightly shorter, followed by a long and thin last tarsomere, armed distad by long, simple tarsal claws. Abdomen with five visible abdominal segments; abdominal segment 1 and 5 longest, equal in length, abdominal ventrite 2 very short, together with ventrite 3 as long as ventrite 1; pygidium short, spinose and with hairy apical margin (Fig. 1F, H).

Cretabaltoraea volsella Peris, Jelínek & Audisio, gen. et sp. nov.
(Fig. 1)
LSID: urn:lsid:zoobank.org:act:85172D6C-E1ED-4172-ADB2-7AC8179B1710

Holotype. Sample NIGP205638, a complete specimen, male, preserved isolated in a small piece (*ca.* 1.5×0.8×0.4 cm) of completely transparent amber. The holotype is preserved together with a Thysanoptera and a Diptera in the same amber piece. The type specimen is deposited at the Nanjing Institute of Geology and Paleontology, Chinese Academy of Sciences, Nanjing, China.

Etymology. The specific epithet is derived from the Latin '*volsella*', meaning tweezers in English, in reference to its peculiarly large and narrow mandibles; feminine gender.

Diagnosis. As for the genus (*vide supra*).

Locality and horizon. Kachin Province, near Tanai, northern Myanmar; Late Cretaceous (early Cenomanian) in age (Shi *et al.*, 2012).

Description. Body middle-sized, 2.5 mm in length including mandibles, 2.18 mm excluding mandibles, and 1.79 mm in width at its maximum (measured as maximum width of pronotum), uniformly dark brown in color, markedly flattened dorsoventrally (Fig. 1A, B). Prosternum short and wide, with transverse open procoxal cavities.

Remarks. This new genus is markedly distinct from all other described fossil genera in this group from the Cretaceous Kachin amber (Peris *et al.*, in press) in their diagnostic characters, being significantly denoted in the mandible size and shape. However, the new species seems very closely related to the genus *Baltoraea* (Kurochkin & Kirejtshuk, 2010), described from the Eocene Baltic amber and figured here. Both genera share a list of synapomorphies which include: body dorsal surface glabrous; "occipital sulci" bordering the inner dorsal portion of eyes distinct and complete; frons depressed; mandibles very long and narrow, as long as the distance between the eyes in dorsal view, arcuately curved, with a blunt, simple apex; each mandible with basal sharp tooth in the inner part; basal pronotal border marked; prosternal process moderately long, narrow, subparallel, exceeding procoxae, only slightly widened laterad, acutely triangularly pointed; elytra subparallel at sides, exhibiting irregular longitudinal rows of punctures, markedly truncate, exposing only pygidium dorsally and covering all other preceding abdominal tergites; mesocoxal axillary lines on metaventrite bluntly and narrowly angulate; metaventrite with a shallow longitudinal median impression; posterior margin of metaventrite shallowed angularly notched between metacoxae; tibiae with two big and acute pointed subequal spurs in inner apical angle and series of pointed spines along the outer lateral reaching apical angle. Some of the above listed traits are also present in the partially re-analyzed type specimen of *Apofisandra ammytae* Molino-Olmedo, 2017, the type species of the fossil subfamily Apophisandrinae (also collected in Kachin Amber deposits: Molino-Olmedo, 2017), although in the latter mandibles are wider, flatter, and relatively shorter, eyes protrude more outwards, antennal club markedly looser and longer, and body is less compact (see Fig. 1 in Peris *et al.*, in press).

However, despite the morphological resemblance between both genera, *Cretabaltoraea* **gen. nov.** shows, if compared to *Baltoraea*, half the length (2.5 mm) and much more strongly depressed frons; labrum is emarginated; mandibles do not show apparent punctures; last antennomere has a longitudinal cleft along whole antennomere length; apex of pygidium is spinose and hairy; and tarsi are long and narrow, almost subcylindrical,

indistinctly lobed and not dilated distad. By contrast, the two species of *Baltoraea* nearly are doubled in length (4.8 mm in *B. insignis* and 4.5 mm in *B. simillima*) and show less depressed frons; labrum is transverse and unilobed; mandibles punctured; last antennomere with normal shape; apical margin of the pygidium hairy but not spinose; and tarsi are long and equally narrowly lobed (Kurochkin & Kirejtshuk, 2010).

According to the authors (Kurochkin & Kirejtshuk, 2010), the two species of *Baltoraea* differ in the colouration of the body; which is black in *B. simillima* and browner in *B. insignis* (Fig. 2A–D), being *Cretabaltoraea volsella* **gen. et sp. nov.** more similar to *B. insignis* in colour (Fig. 1A). The impression on the frons is V-shaped and "occipital sulci" (also known as parocular lines) are well developed in *B. simillima* (Fig. 2E), while frons has an arcuate impression and "occipital sulci" are weakly developed in *B. insignis* (Fig. 2A). Frons is strongly depressed in *C. volsella* **gen. et sp. nov.**, differently to *Baltoraea*, but occipital lines are well developed as in *B. simillima* (Fig. 1C). Originally, pronotal border was described as very narrow but distinct in *B. simillima*, while it was distinct and relatively wide in *B. insignis* (Kurochkin & Kirejtshuk, 2010). However, after the reexamination of the two holotypes, no differences have been observed on this character (2A, E), while pronotal border is significantly wider in *C. volsella* **gen. et sp. nov.** (Fig. 1A). Finally, tibiae in *B. simillima* were described wider than in *B. insignis*, being wider than epipleura at base in the former and meso- and metatibia as wide as epipleura at base in the later. In the case of the new species *C. volsella* **gen. et sp. nov.** tibiae are wider than epipleura at base, as well as in *B. simillima.* In addition, we found that *C. volsella* **gen. et sp. nov.** shares with *B. simillima* the very short abdominal ventrite 2 (ventrite 1 as long as ventrites 2 and 3 combined) (Fig. 2D). This character differs from *B. insignis*, whose shortest abdominal ventrites are 3 and 4, being together as long as ventrite 2 (Fig. 2B).

Genus *Baltoraea* Kurochkin & Kirejtshuk, 2010
(Fig. 2)

Type species. *Baltoraea insignis* Kurochkin & Kirejtshuk, 2010

Remarks. The genus *Baltoraea* was erected to fit two fossil species described from the Eocene Baltic amber: *Baltoraea insignis* and *Baltoraea simillima* (Kurochkin & Kirejtshuk, 2010). The genus was originally described as belonging to the subfamily Epuraeinae. However, the authors already stated that this fossil genus shows a list of characters that contrasted to the other species of the subfamily, namely distinct rows of punctures on elytra, unilobed labrum (not divided into lobes), and pronounced posterior basal border of the pronotum (Kurochkin & Kirejtshuk, 2010).

We have reviewed the holotype of both species and found that the genus *Baltoraea* does not seem to belong to the subfamily Epuraeinae based on the following list of observed characters, some of them also indicated in the original descriptions of both included species:

1) "occipital sulci" bordering the inner dorsal portion of eyes distinct and complete, converging to the middle of the head from the anterior frontal border (absent in all known present-day Epuraeinae, although present in other groups of modern Nitidulidae);

2) elytra subparallel at sides, exhibiting irregular longitudinal rows of coarse and shallow punctures (longitudinal rows of punctures absent in all known present-day Epuraeinae, these always bearing only confused elytral punctuation);

3) unilobed labrum (not divided into two distinct lobes, as occurring in all known present-day Epuraeinae);

4) pronounced posterior basal border of the pronotum (not distinct in all known present-day Epuraeinae, although present in other groups of modern Nitidulidae; in a few species of the tropical Epuraeinae genus *Trimenus* Murray, 1864, feeble traces of a posterior pronotal border are otherwise visible towards the sides);

5) tibiae (including the anterior ones) gradually widened distad, only *ca.* 0.7× as long as femora, with two big and acutely pointed subequal spurs in the inner apical angle and a series of pointed and markedly sclerified spurs along their outer edge, bigger in size towards reaching the apical angle (tibiae usually nearly as long as femora in living Epuraeinae, with usually absent pre-distal spurs on their outer edge, at most with only one spur, possibly located at the external outer apex of the anterior tibiae);

6) prosternal process nearly half as long as the anterior portion of prosternum (nearly as long as or even longer than the anterior portion of prosternum in modern Epuraeinae);

7) antennal furrows on ventral side of the head, close to the inner borders of eyes, absent in *Baltoraea*, while being always more or less distinctly impressed (although with very variable length and deepness) in modern Epuraeinae.

By contrast, *Baltoraea* was recently transferred to the subfamily Apophisandrinae in the same family Nitidulidae, based on the diagnostic characters that the genus shares with the rest of Cretaceous fossil species that have been recently integrated within this subfamily (check Table II of the Supporting Information in Peris *et al.*, in press).

Almost all present-day Epuraeinae, and its sister-group Carpophilinae, exhibit in their last antennomere (11th) a medially, large, and distinct inner sensillum (sensillum ampulaceum), normally visible in transparency. It is usually apple-shaped, pear-shaped or worm-shaped,
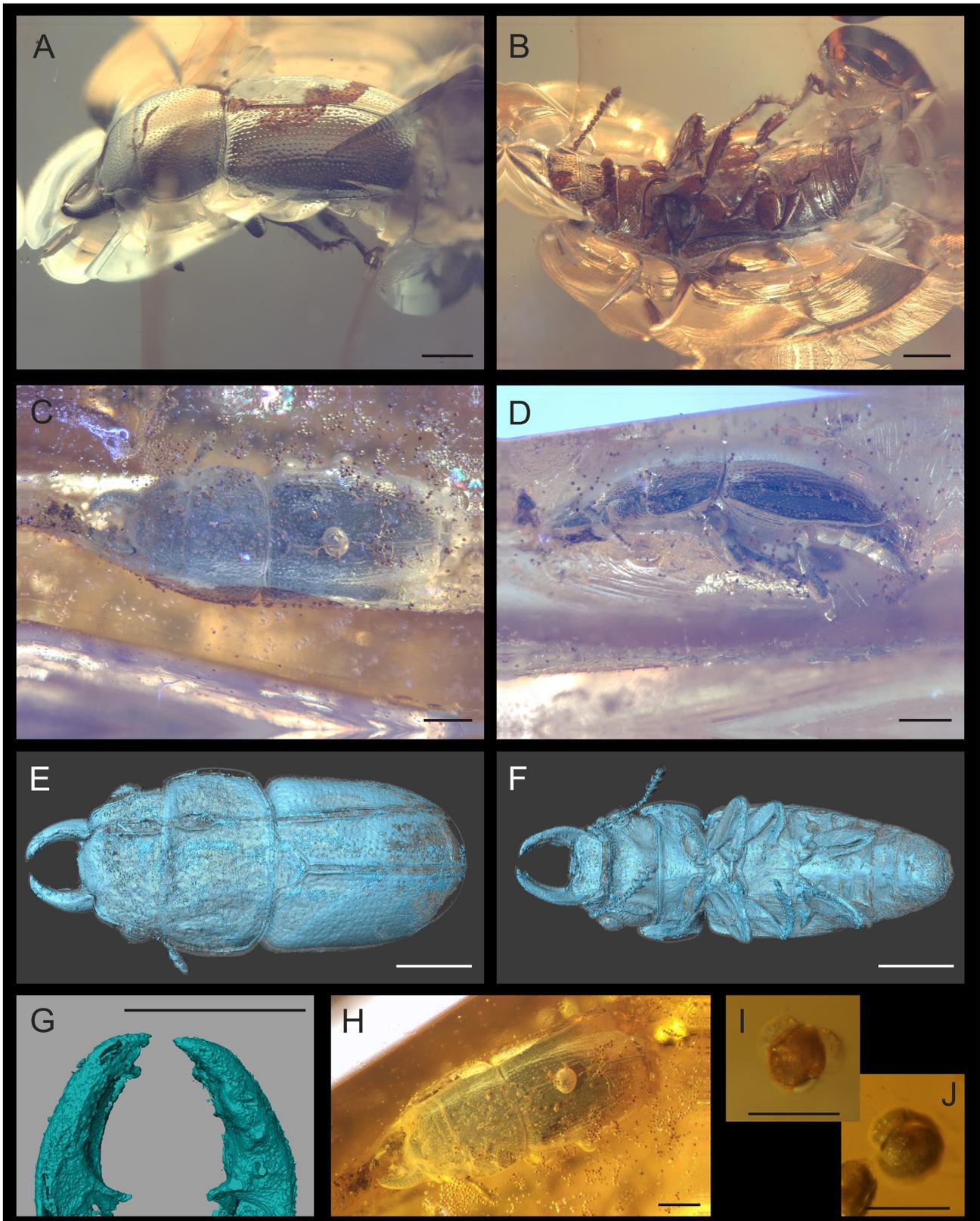
FIGURE 2. Holotypes of *Baltoraea insignis* (Coll. of C. Gröhn, no. 995C) (**A**, **B**) and *B. simillima* (Coll. of C. Gröhn, no. 4243C) (**C–J**), described in independent amber samples from the Eocene Baltic amber (Kurochkin & Kirejtshuk, 2010). **A**, Dorsal view of *B. insignis*. **B**, Ventral view of *B. insignis*. **C**, Dorsal view of *B. simillima*. **D**, Lateral view of *B. simillima*. **E**, 3-D reconstruction of *B. simillima* in dorsal view. **F**, 3-D reconstruction of *B. simillima* in ventral view. **G**, 3-D reconstruction of the mandibles in *B. simillima*. **H**, Pollen grains (probably from Pinaceae) in syninclusion with the holotype of *B. simillima*. **I**, Detail of one pollen grain. **J**, Detail of a second pollen grain. Scale bars for **A–G** = 0.5 mm; for **I–J** = 50 μm.

with an external outlet at the level of a cuticular pore, and clearly manifesting a chemiotactic function (see Gillogly, 1947, 1962; De Marzo, & Porcelli, 1989; Audisio, 1993). Antennal sensilla appear to be absent in both Baltoraea species. It is noteworthy that *Cretabaltoraea* **gen. nov**. exhibits a longitudinal cleft along the whole last (11th) antennomere length that could be maybe a sensillum, but we ignore if it represents a structure with chemotactile functions analogous to the sensillum known in Epuraeinae and Carpophilinae.

Virtual reconstructions of fossils have allowed the description of internal structures (*e.g.*, genitalia, as in Peris *et al.*, in press), but only if the preservation quality allows it. The reconstruction of the male genitalia could be key in defining the taxonomic position of *Baltoraea*, but the attempt to reconstruct the shape of these structures using the data from the scan of *B. simillima*'s type has unfortunately been unsuccessful. Male genitalia appear to differ significantly between the modern Epuraeinae and the very few species of Apophisandrinae in which it has so far obtained some information on their structure. Parameres are fused in a tegmen deeply incised in the Epuraeinae, while being partly mobile distad in the Apophisandrinae; aedeagus is rather strongly elongated, and flattened in lateral view in the Epuraeinae, while being convex and angulate in lateral view, and usually relatively short, wider, triangular in dorsal view in the Apophisandrinae (Peris *et al.*, in press).

Discussion

The family Apophisandridae established by Kirejtshuk *et al.* (2023) for a set of Cretaceous fossil species is suggested to be placed as a basal subfamily within Nitidulidae in Peris *et al.* (in press), as no significant differences are denoted between this group of fossils and the recent Nitidulidae. See Peris *et al.* (in press) for details and discussion about this change. As such, the nitidulid subfamily Apophisandrinae is composed of a total of 16 fossil species described from the Cretaceous Kachin amber and two species of *Baltoraea* described from the Eocene Baltic amber (Kirejtshuk *et al.*, 2023; Peris *et al.*, 2023).

Apophisandrinae were a very morphological diverse group during the Cretaceous, attending to the peculiar list of characters which separately may be found in different current lineages of Nitidulidae or the very close family Kateretidae, but never combined as a defining list of the group (Peris *et al.*, in press). With the inclusion of *Baltoraea* in Apophisandrinae, the evolution of the group is suggested to not be exclusively limited to the Late Cretaceous. Instead, it appears that they successfully passed through the K/Pg mass extinction and persisted at least until the Eocene. This pattern has been similarly observed in other insect groups, such as the genus *Cretoquadratus* Chen, 2019 (Coleoptera: Lymexylidae) and the order Alienopteridae, which went extinct later (Li *et al.*, 2021; Luo *et al.*, 2021).

The Cretaceous is a period of major evolutionary turnover for insects in general and pollinators in particular (Peris *et al.*, 2017; Peris *et al.*, 2020a, b). The evolution of angiosperms (Benton *et al.*, 2022) seems to have significantly influenced the insect diversification (Peris & Condamine, 2024). The coevolution between insects and angiosperms has been suggested (Asar *et al.*, 2022; Renner, 2023), although only co-diversification has been tested (Stephens *et al.*, 2023; Peris & Condamine, 2024). The evolutionary explosion in pollinator diversity launched by the angiosperm dominant position from 50 Mya onwards may have forced the evolutionarily replacement of previous pollinator lineages (Peris & Condamine, 2024). Apophisandrinae, considered as one of the most ancient generalist pollinator groups (Peris *et al.*, 2020a; Peña-Kairath *et al.*, 2023; Peris *et al.*, in press), have been apparently one of the affected groups by the insect increase in diversification and replacement by more modern pollinator lineages.

Indeed, the holotype of *Baltoraea simillima* has been preserved in a piece of transparent amber composed of different resin layers. The external surface of the layer containing the holotype is abundantly covered by a layer of pollen grains, which were transported through the interior of the layer around the beetle's body (Fig. 2H). This situation represents a chance bioinclusion of both a beetle and pollen grains in the same amber piece, which differs from other pollination scenarios described in different amber specimens (reviewed in Peña-Kairath *et al.*, 2023). To be considered as a pollinator, the situation should have been that the pollen grains were being transported by the animal and some of these would have been released along a trail as the animal was engulfed in resin, and not the other way around, as is the case here. Furthermore, the pollen grains embedded in this Eocene amber piece have been identified as saccate pollen of the Pinaceae type (Fridgeir Grimsson, pers. comm.) (Fig. 2I–J), which show characters compatible with wind transportation rather than insect transport.

Species of *Baltoraea* have been suggested to be anthophagous based on their similar morphological characters with current anthophagous groups of nitidulids (Kurochkin & Kirejtshuk, 2010). In addition, the fossil record of this subfamily suggests their implication in the pollination of different plant lineages during the Cretaceous (Peris *et al.*, 2020a; Tihelka *et al.*, 2021). Why *Baltoraea simillima* is preserved together with aerial transported

pollen grains may be answered by the relative abundance of pine at the Eocene resiniferous environment. Pinaceae have been cited in widespread occurrence within northern Europe in Eocene forests and good representation in Baltic amber (Utescher & Mosbrugger, 2007). Thus, the presence of Pinaceae pollen grains preserved in the Baltic amber is not rear. But in addition, many nitidulid species are currently found in or under the bark of fallen or dead pine trees (Majka *et al*., 2008), mostly among Epuraeinae, Cryptarchinae and Nitidulinae (Audisio, 1993).

Conclusion

We describe a new genus and species *Cretabaltoraea volsella* **gen. et sp. nov.**, as a member of Nitidulidae, after the study of a fossil specimen preserved in the Cretaceous Kachin amber from Myanmar. The morphological resemblance between the new species and the two fossil species described in the same family from the Eocene Baltic amber (*Baltoraea insignis* and *Baltoraea simillima*) made necessary the re-examination of the holotypes. We have used CT-scanning to study the holotype of *B. simillima* and to create a reconstruction of the fossil. We confirmed here that all three species belong to the extinct Apophisandrinae (Peris *et al*., in press) of Nitidulidae. The members of this nitidulid subfamily have been identified as ancient pollinators. Despite the inclusion of abundant pollen grains preserved in the Eocene amber piece together with *B. simillima*, the pollen corresponds to aerial transported pollen of Pinaceae. The pollen grains cover part of the surface from a resin layer, suggesting that the pine pollen was trapped on the surface of the resin layer before the beetle became engulfed, while some grains have been dragged together with the specimen as it became encased in resin. This interpretation demonstrates the importance of taphonomy as a paleontological discipline that must be applied correctly in order to obtain ecological conclusions using fossil material.

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