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A new fossil species of the reticulated beetle genus *Cupes* (Coleoptera: Archostemata: Cupedidae) from Eocene Baltic amber

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Abstract

The single extant species of the reticulated beetle genus *Cupes* Fabricius is confined to North America. In contrast, a diverse and abundant fossil record of the genus has been documented in Cenozoic deposits in Europe, especially in Eocene Baltic amber. This paper describes another species, *Cupes balticus* **sp. n.**, as the eighth named species of the genus from Baltic amber. The discovery of an additional *Cupes* species further evidences the hidden paleodiversity of reticulated beetles in European Eocene forests.

Key words: new species, fossiliferous resin, Europe, paleoentomology, zoogeography, paleodiversity

Introduction

Cupedidae, also known as reticulated beetles, represent the most species-rich family within the small coleopteran suborder Archostemata (Ślipiński *et al*. 2011). The family comprises ~40 species across nine extant genera, distributed worldwide in regions including the Nearctic, Neotropical, Oriental, Palearctic, Australasian, Oceanic, Afrotropical, and Madagascan (Neboiss 1984; Hörnschemeyer 2009; Hörnschemeyer & Yavorskaya 2016; Rodríguez-Mirón & López-Pérez 2019; Bukejs *et al*. 2021). Interestingly, many genera within each genus exhibit disjunct distributions (e.g., Neboiss 1984), likely indicating relictual distribution patterns.

The type genus of the family, *Cupes* Fabricius, 1801, underwent recent revision by Rodríguez-Mirón and López-Pérez (2019), who synonymized the African-endemic genus *Rhipsideigma* Neboiss, 1984 under *Cupes*, along with transferring a species from *Tenomerga* Neboiss, 1984 to this genus. This resulted in several new generic combinations. Nonetheless, some researchers have not adopted these taxonomic changes (e.g., Li *et al*. 2019, 2023; Bukejs *et al*. 2021). Excluding the adjustments made by Rodríguez-Mirón and López-Pérez (2019), *Cupes*, which is known for having only one extant species in eastern North America (Canada and the USA), encompasses a significant number of fossil species. To date, fossil records have consistently reported 20 fossil species, with the majority of the paleodiversity discovered in Europe, particularly in the Paleocene of Menat in France and Eocene Baltic amber (Kirejtshuk 2005; Kirejtshuk *et al*. 2016; Kirejtshuk 2020). Excluding *Cupes motschulskyi* Kirejtshuk, 2005, which was later transferred to the newly established genus *Taxopsis* Kirejtshuk, Nel & Kirejtshuk, 2016, seven *Cupes* species have been recorded from Baltic amber (Kirejtshuk *et al*. 2016). The species *Cupes groehni* Kirejtshuk, 2005, has also been reported from Eocene Rovno amber in Ukraine (Bukejs *et al*. 2021).

This study introduces a new species of *Cupes* from Baltic amber, *Cupes balticus* **sp. n.**, contributing to our understanding of the paleodiversity of both this genus and the Cupedidae.

Materials and Methods

The new species described here is based on an adult individual encased in Baltic amber, sourced near the Baltic Sea coast of Yantarny, Kaliningrad Oblast, in the westernmost region of Russia. The type specimen is relatively

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well-preserved and appears to be complete. However, the ventral details of the beetle are largely obscured by a milky layer of micro-bubbles on its surface, referred to as 'Verlumung', which is a characteristic commonly found in authentic Baltic amber. The specimen is housed at the Laboratory of Systematic Entomology (SEHU, curator Dr. M. Ôhara) within the Hokkaido University Museum (HUM), Hokkaido University, Sapporo, Japan, and has been assigned the accession number SEHU-0000121237. The precise age of Baltic amber is controversial and remains unsettled. A middle Eocene (Lutetian) age for the Baltic amber-bearing sediments has been estimated through K–Ar dating, as reported by Ritzkowski (1997), with a similar conclusion reached by Bukejs *et al*. (2019). Conversely, several other studies have proposed a younger upper Eocene (Priabonian) age based on palynological evidence and faunal comparisons (e.g., Perkovsky *et al*. 2007; Aleksandrova & Zaporozhets 2008). Consequently, the age of Baltic amber is tentatively assigned to the upper–middle Eocene in this study.

Observations were conducted using Nikon SMZ1500 and SMZ800 stereomicroscopes. For photographic documentation, the entire amber piece was submerged in clove oil to enhance clarity. Habitus images were captured with a Canon EOS 90D digital camera equipped with a Canon MP-E 65 mm F2.8 1–5× macro lens, supported by a Canon MT-24EX twin flash. The image of the left metatarsus was taken using an EOS 90D digital camera paired with a LAOWA Aurogon FF 10× NA0.5 Supermicro APO lens and a MT-24EX twin flash. Additional images were taken with a Canon EOS 6D Mark II digital camera attached to a Leica M205C stereomicroscope, illuminated by four Hayashi-Repic SPA2-10SW lighting devices. A series of images were compiled using Helicon Focus 8.2.0 software and refined with Adobe Photoshop Elements 15. The terminology for morphological descriptions generally follows the works of Kirejtshuk (2005), Yamamoto (2017), and Hörnschemeyer and Yavorskaya (2016). The classification of Archostemata adheres to Cai *et al*. (2022).

Systematic paleontology

Order Coleoptera Linnaeus, 1758

Suborder Archostemata Kolbe, 1908

Superfamily Cupedoidea Laporte, 1838

Family Cupedidae Laporte, 1836

Subfamily Cupedinae Laporte, 1838

Genus *Cupes* Fabricius, 1801

(Type species: *Cupes capitatus* Fabricius, 1801: 66).

Cupes balticus sp. n.

Figs. 1–4.

Type material. Holotype, a complete adult of undetermined sex, preserved in a yellowish-transparent, flattened rectangular parallelepiped piece (dimensions, ca. 18.0 × 10.6 × 3.7 mm) of Baltic amber, with the accession number SEHU-0000121237, deposited at the Laboratory of Systematic Entomology (SEHU), the Hokkaido University Museum (HUM), Hokkaido University, Sapporo, Japan. Syninclusion: a tiny Collembola.

Type locality and horizon. Russia: Kaliningrad Oblast; middle to upper Eocene.

Etymology. The specific epithet *balticus* refers to the occurrence of the type material in Baltic amber from near the Baltic Sea Coast, also emphasizing the potentially higher diversity and abundance of *Cupes* beetles in this amber deposit.

Diagnosis. Body of relatively large size (9.3 mm long) as *Cupes* species in Baltic amber, with a peculiar bi-colored pattern on elytra by scales, consisting of brownish and yellowish grey spots (head, median longitudinal stripe on pronotum, and elytral apex brownish); head with 2 pairs of dorsal paramedian tubercles well raised, with temples only slightly shorter than eyes; antenna with antennomere 3 almost twice as long as antennomere 2, as well as moderately narrowly elongate terminal antennomere (about 3.8 times as long as thick); pronotum wider than head, anterolaterally projecting and laterally broadly angulate, with an anteriorly widened medial elevated stripe without a clear longitudinal furrow; hind leg with comaratively short metatarsomere 5 (metatarsomere 1 distinctly less than twice as long as metatarsomere 5).

Description. Body (Fig. 1) narrowly elongate, relatively large, 9.32 mm long, moderately convex dorsally, flattened ventrally, widest at posterior part of elytra. Surface with extremely dense scales, masking coloration of body surface; scales on head, pronotum (including pronotal median longitudinal stripe) dark brown; elytra bicolored, with a characteristic pattern of brownish and yellowish grey spots, with brownish apex (both subapical and apical bands without interruption); body ventrally with extremely dense, yellowish grey scales; surface on antennae and legs scales gradually transforming into subrecumbent, rather stout setae.

Head (Figs. 2A, B, 3A, B) weakly transverse, widest across eyes, 1.06 mm long, 1.60 mm wide (including eyes), moderately narrower than pronotum. Surface of head with 2 paramedian pairs of dorsal tubercles, both well raised dorsally and swollen; anterior tubercles or protuberances (*p1*) rather rectangular, transverse, with their base closed; posterior protuberances (*p2*) elongate-oval, with more raised anterior half, their bases separated by a relatively wide and elevated median stripe divided by a longitudinal furrow (*fv*). Eyes (Figs. 2A, B, 3A, B, *ey*) rather small, as wide as scape, only slightly longer than temples, moderately protuberant laterally. Temples (Figs. 2A, B, 3A, B, *tmp*) long, prominent. Gular sutures apparently subparallel-sided, narrowly separated. Antennal insertions divided by distance about as wide as length of scape (Fig. 3A, B). Antennae (Figs. 1, 2F, 4C) 11-segmented, filiform, somewhat slender, about 0.6 time as long as body (5.53 mm, left), barely reaching to middle of elytra; scape (antennomere 1, *a1*) approximately oval, 1.5 times as long as thick; pedicel (antennomere 2) short, as long as thick, wider than scape; antennomere 3 narrowly elongate, moderately dilated towards apex, nearly about twice as long as 2nd, slightly longer than 4th; antennomeres 4–10 each narrowly elongate, subcylindrical, gradually narrowing distally; ultimate antennomere less than 4 times as long as thick (3.8 times as long as thick on left side). Labrum scarcely visible.

Pronotum (Figs. 2A, C, 3C, D, *pn*) subtrapezoidal, moderately transverse, widest at about half length, narrower than elytra, 1.29 mm long (along midline), 1.94 mm wide; lateral edges broadly angulate, strongly narrowed in anterior 2/5; anterolateral angles right to obtuse, slightly projecting; posterolateral corners broadly arcuate; posterior margin weakly bisinuate, slightly projecting posteriorly, with a small and weak emargination medially; disc moderately convex dorsally (medial area only, outer areas somewhat explanate), with a median elevated ridge, or stripe, along entire length (Fig. 3C, D, *mrp*), as well as a pair of shallow paramedian fossae at anterior edge (Fig. 3C, D, *fs*), but lacking a longitudinal furrow along midline. Prosternal process seemingly narrow. Scutellum minute, subquadrangular.

Elytra (Figs. 1A, 2D) narrowly elongate, gradually divergent posteriorly, widest in posterior 1/3 (right and left elytron 6.70 mm long from base to apex, right elytron 1.48 mm wide, left elytron 1.79 mm; the distinct difference of the width of the elytra must be an artefact), with acute elytral apices (not emarginate); surface each with 9 longitudinal rows of sub-oval to rounded window-punctures (window-punctures regularly arranged; some punctures rather transverse near base of elytra); 5 interval elevations present, all distinctly raised from base or subbase to apex.

Legs (Figs. 1, 2E, 4B, D, E) moderately long, relatively thick; femora stout, clavate, metafemora not extending beyond lateral edge of posterior body; tibiae slender, bar-like, gradually slightly widened toward apex, much thinner than corresponding femora (but not less than half as wide), with metatibial length of 0.64 mm (left). Tarsi (Figs. 1, 2E, 4B, D, E) 5-segmented, slightly narrower than corresponding tibiae; protarsi (Fig. 4B, D) shortened and robust; protarsomere 1 slightly longer than wide, protarsomeres 2–4 subequal in length, each shorter than 1st, ventrally expanded; protarsomere 5 apparently as long as 1st, but apical part not well visible due to milky coarting of micro airbubbles; mesotarsi (Fig. 4D, E) slender; mesotarsomere 1 elongate, about twice as long as wide, mesotarsomeres 2–3 subequal in length, each wider than long, shorter than 1st, mesotarsomere 4 slightly longer than 3rd but shorter than 1st, as wide as two preceding segments, mesotarsomere 5 seemingly as long as 1st; metatarsi (Figs. 2E, 4D, E) slender; metatarsomere 1 (Fig. 2E, *mtt1*) elongate, about 2.9 times as long as wide, about 1.6 times as long as 5th, metatarsomere 2 elongate, sub-cylindrical, about 1.6 times as long as wide, about half as long as 1st, metatarsomere 3 short, very slightly wider than long, distinctly shorter than 2nd, metatarsomere 4 short, widest, bilobed ventrally, moderately longer than 3rd, as long as 2nd, metatarsomere 5 narrowly elongate, slender, strongly dilated apically, widest near apex, about 2.7 times as long as wide. Claws short, simple.

Abdomen (Figs. 1, 4D, E) elongate, apex acute, with five visible ventrites; tergite VIII well sclerotized, semicircular, closely covered with minute setae; ventrite 5 twice as long as 4th; all ventrites except the 1st markedly depressed anteriorly and overlapping the anterior margin of each successive ventrite.

FIGURE 1. General habitus of *Cupes balticus* **sp. n.**, holotype, SEHU-0000121237. **A**, Dorsal view. **B**, Ventral view. Scale bars: 3.0 mm.

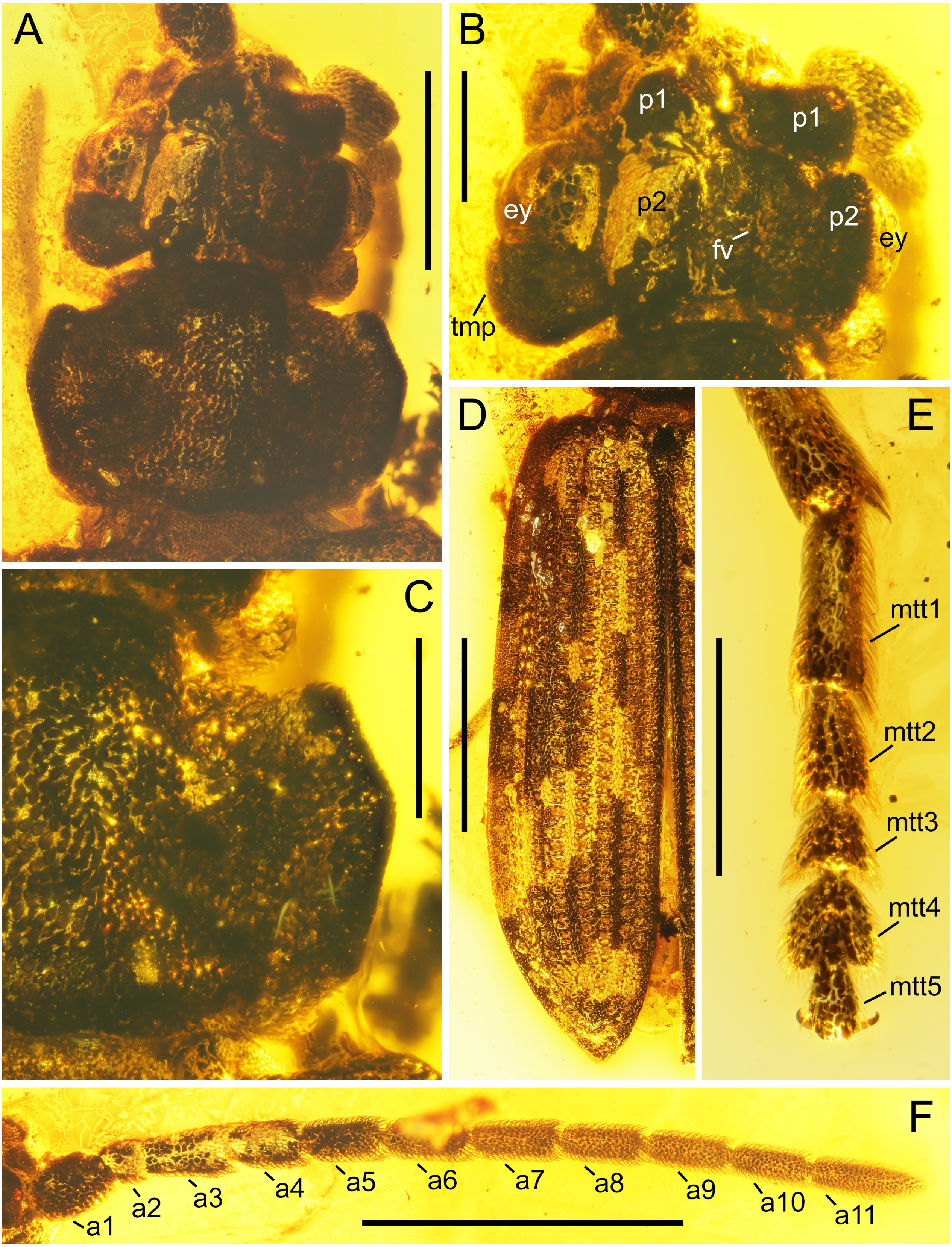

FIGURE 2. Morphological details of *Cupes balticus* **sp. n.**, holotype, SEHU-0000121237. **A**, Head and pronotum, dorsal view. **B**, Head, dorsal view. **C**, Right lateral half of pronotum, dorsal view. **D**, Left elytron and scutellum, dorsal view. **E**, Right metatarsus, dorsal view. **F**, Left antenna, dorsal view. Abbreviations: a1–11, antennomeres 1–11; ey, eyes; fv, longitudinal median furrow on vertex; mtt1–5, metatarsomeres 1–5; p1, supraantennal tubercle; p2, supraocular tubercle; tmp, temple. Scale bars: 1.0 mm (A); 0.5 mm (B, C, E); 2.0 mm (D, F).

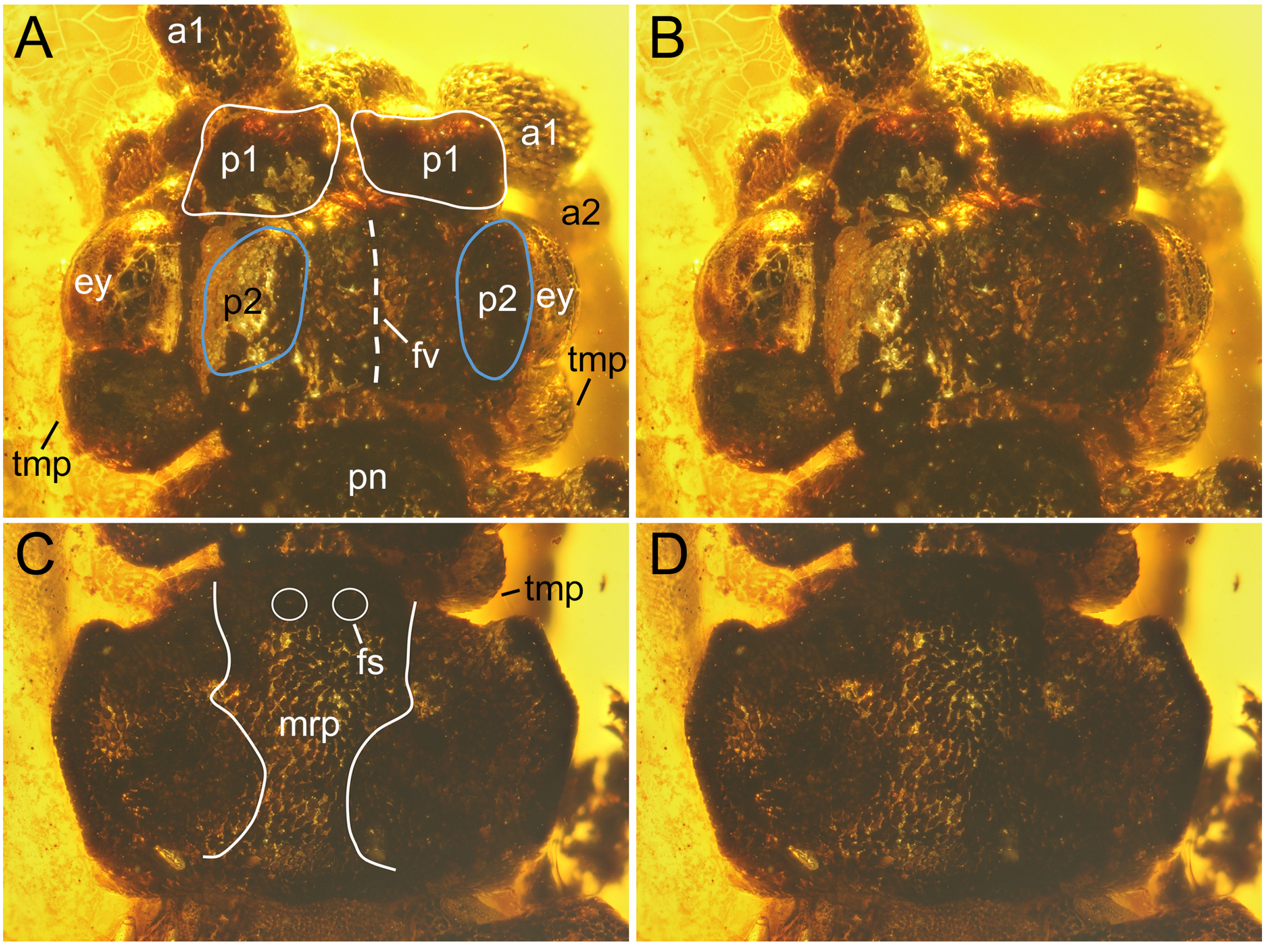

FIGURE 3. Morphological details of *Cupes balticus* **sp. n.**, holotype, SEHU-0000121237. **A**, Head with morphological interpretations, dorsal view. **B**, Head without morphological interpretations, dorsal view. **C**, Pronotum with morphological interpretations, dorsal view. **C**, Pronotum without morphological interpretations, dorsal view. Abbreviations: a1–2, antennomeres 1–2; ey, eyes; fs, paramedian fossae at anterior pronotal edge; fv, longitudinal median furrow on vertex; mrp, median elevated ridge of pronotum; p1, supraantennal tubercle; p2, supraocular tubercle; pn, pronotum; tmp, temple.

Comparative notes. The new species is most closely related to *Cupes weitschati* Kirejtshuk, 2005, characterized by two paramedian pairs of similar dorsal tubercles on the head, comparable eye size, and bi-colored elytra with a distinct pattern. It is differentiated by its anteriorly pointed pronotal corners with angulate lateral margins, uniformly brownish head and pronotum, the presence of two interrupted bands in the apical and subapical parts of the elytra, and a more narrowly elongate ultimate antennomere. Among the Baltic amber cupedid taxa, *Cupes balticus* **sp. n.** does not align with the monospecific extinct genus *Taxopsis* due to its much smaller body size (body length 16.1–18.1 mm in *Taxopsis vs.* 9.3 mm in the new species), narrowly separated procoxae, and more or less oval-to-polygonal elytral cells (compared to strongly transverse subquadrangular cells in *Taxopsis*) (Kirejtshuk 2005; Kirejtshuk *et al*. 2016). Distinguished from the other six species of *Cupes* in Baltic amber, the new species is differentiated by a combination of the following character states (Kirejtshuk 2005; Kirejtshuk *et al*. 2016):

—From *Cupes rohdendorfi* Iablokoff-Khnzorian, 1960, by having only two paramedian pairs of suboval tubercles on the head dorsum, distinctly smaller eyes, much longer temples, a less elongate terminal antennomere, and the absence of a longitudinal division of the pronotoum by a furrow;

—From *Cupes komissari* Kirejtshuk, 2005, by the bi-colored scales on the elytra, only two paramedian prominent pairs of suboval tubercles on the head dorsum, smaller eyes, longer temples, and the absence of a median longitudinal furrow on the pronotum;

—From *Cupes kerneggeri* Kirejtshuk, 2005, by much more prominent protuberances on the head dorsum, a large scape as wide as the eye, a more narrowly elongate terminal antennomere, and a prontum with a rounded posterior edge with a weakly sinuate median part;

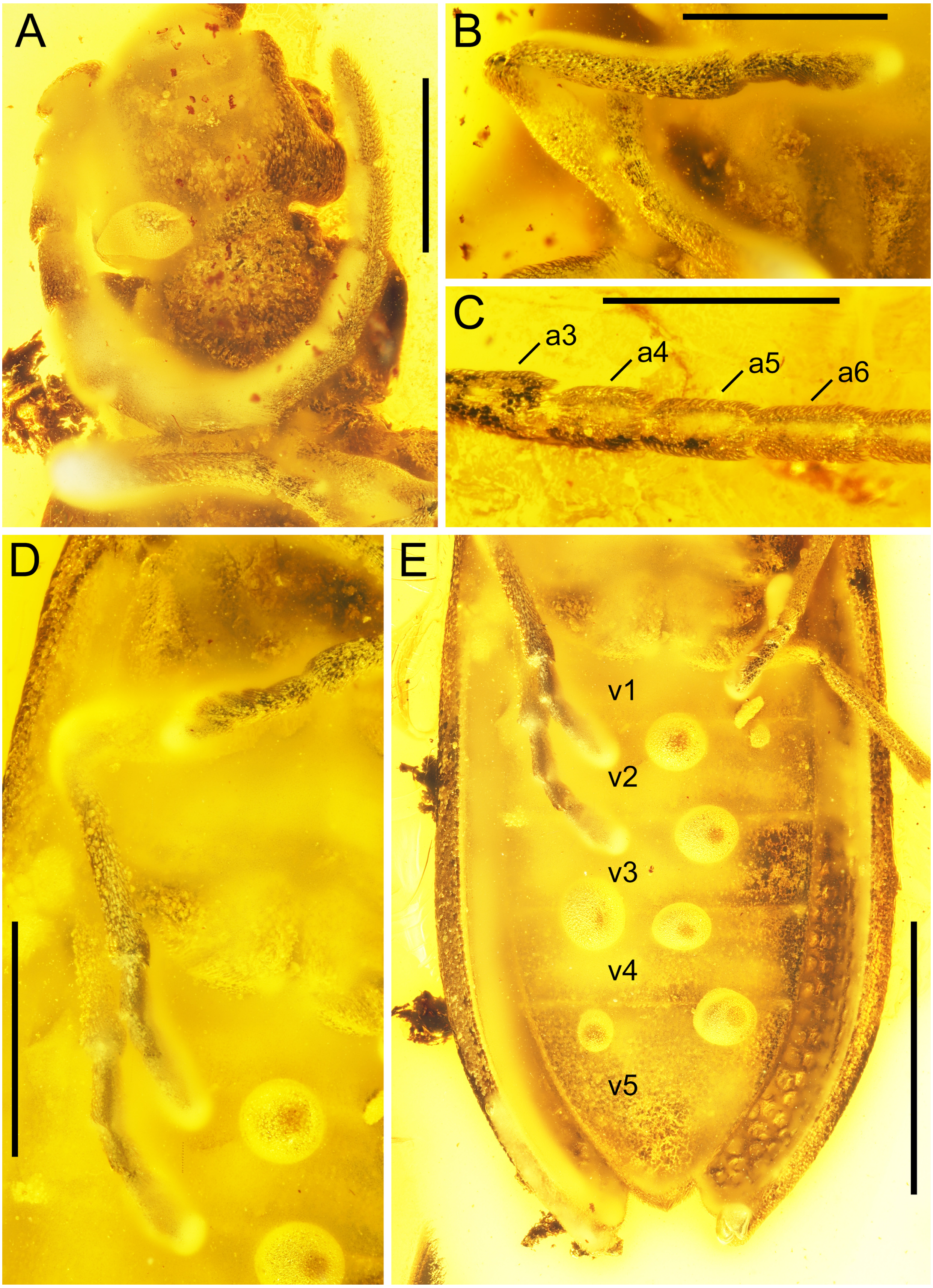

FIGURE 4. Morphological details of *Cupes balticus* **sp. n.**, holotype, SEHU-0000121237. **A**, Head, right antenna, and prothorax, ventral view. **B**, Forelegs, ventral view. **C**, Basal part of left antenna, ventral view. **D**, Mid- and hindlegs, ventral view. **E**, Abdomen, ventral view. Abbreviations: a3–6, antennomeres 3–6; v1–5, ventrites 1–5. Scale bars: 1.0 mm (A–D); 2.0 mm (E).

—From *Cupes groehni* Kirejtshuk, 2005, by smaller eyes and longer temples, a shorter and less elongate third antennomere compared to the second, a much less narrowly elongate ultimate antennomere (paratype), an anteriorly projecting pronotal margin, a less elongate first protarsomere, and a less elongate first metatarsomere;

—From *Cupes hoffeinsorum* Kirejtshuk, 2005, by partially lighter scales, smaller eyes, longer temples, a vertex with a median longitudinal furrow, a shorter and less elongate third antennomere compared to the second, a much less elongate terminal antennomere, a pronotum wider than the head at temples, and a much shorter fifth metatarsomere compared to the first;

—From *Cupes tesselatus* (Motschoulsky, 1856), by the uniformly brownish head and pronotum, smaller eyes with longer temples, a shorter and less elongate third antennomere compared to the second, a more elongate terminal antennomere, a wider pronotum compared to the head at temples, a curved posterior pronotal edge weakly protruding medially, a more narrowly elongate first metatarsomere, and a much shorter fifth metatarsomere compared to the first.

Therefore, the specimen described here differs distinctly from any cupedids previously described from Baltic amber and is thus recognized as a new species.

Discussion

To date, the paleofauna of reticulated beetles from Eocene Baltic amber has been known to comprise seven species of *Cupes* and a monotypic fossil genus, *Taxopsis* (Kirejtshuk 2005, 2020; Kirejtshuk *et al*. 2016). The the generic status and validity of *Taxopsis* should be evaluated critically in the future, preferably checking whether this is only an aberrant species in fact nested within an existing genus, namely *Cupes*, using a formal phylogenetic approach (see Komarek & Beutel 2007). However, as this subject is out of the scope of the present study, I provisionally accept the generic status of *Taxopsis* here based on its wide prosternal process with a rounded apex and unusually transverse subquadrangular cells of the elytra as potential autapomorphies. Likewise, the monophyly of *Cupes* (including the fossil species) also needs to be assessed with appropriate phylogenetic methods, using a representative taxon sampling. The morphology-based phylogenetic analyses of Hörnschemeyer (2009) and Li *et al*. (2019) have consistently recovered that the peculiar South African species *Tenomerga leucophaea* (Newman, 1839) forms a clade together with the single extant species of *Cupes* and the African *Rhipsideigma*. In both studies, a sister group relationship between the extant *Cupes* and *Rhipsideigma* was supported, resulting in polyphyletic *Tenomerga* (Hörnschemeyer 2009; Li *et al*. 2019). To resolve this issue, Rodríguez-Mirón and López-Pérez (2019) made several taxonomic changes and expanded *Cupes* to include also "*T*." *leucophaea* (Newman, 1839) and *Rhipsideigma*. Nevertheless, these taxonomic treatments were not accepted in some later works (Bukejs *et al*. 2021; Li *et al*. 2023). Therefore, additional investigations on the status of "*T*." *leucophaea* are necessary. Furthermore, including the extinct species of *Cupes* into phylogenetic evaluations should have high priority, to assess the limits of *Cupes* and allied genera.

The identification of an additional species, described herein as *Cupes balticus* **sp. n.** from Baltic amber, underscores the potential for a previously unrecognized paleodiversity, suggesting a possibly greater species diversity and abundance of Cupedidae in European amber deposits. This inferred diversity of *Cupes* species is of particular interest with respect to the historical biogeography of these beetles in Europe, given that no extant species of *Cupes* (or Cupedidae) are found in contemporary Europe, with the sole existing species of the genus, *Cupes capitatus* Fabricius, 1801, being native to eastern North America (Young 2000). Moreover, fossils of *Cupes* have also been prevalent in other European fossil deposits (summarized in Kirejtshuk 2020), as documented in France, within the lowermost Eocene Oise amber and the Paleocene of Menat; and in Germany, from the Eocene of the Eifel (Eckfeld Maar) and the Pliocene of Niedersachsen (Willershausen clay pit). Additionally, a specimen of *Cupes groehni*, previously known only from Baltic amber, has recently been identified in Eocene Rovno amber from Ukraine, demonstrating the spatial and temporal proximity of Baltic and Rovno amber deposits (Bukejs *et al*. 2021). These discoveries provide profound insights into the evolutionary history and complex historical distribution of *Cupes* beetles throughout the Cenozoic.

The extinction of cupedids in Europe is thought to have been driven by climatic changes and biotic factors within the continent (Kirejtshuk 2020). Notably, despite the absence of *Cupes* fossils in Mesozoic deposits, the North American-endemic extant cupedid genus *Priacma* LeConte, 1861, has been reported from mid-Cretaceous Kachin amber in northern Myanmar (Li *et al*. 2019). Continued exploration of Eocene European ambers (Baltic, Bitterfeld, Rovno, and Danish) is crucial for uncovering additional *Cupes* species that inhabited amber-producing forests, offering valuable insights into terrestrial entomofauna and woodland ecosystems during that era.

Data Availability

The original images and higher-resolution figure plates are available in the Zenodo repository (https://doi.org/10.5281/zenodo.10705445).

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