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Copelatus diving beetles (Coleoptera, Dytiscidae) from early Miocene Mexican amber, with description of a new species displaying distinct sexual dimorphism

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Non-technical Summary.—Sexual dimorphism in surface sculpture as a result of sexual conflict in mating systems is well known in many extant diving beetles but was never recorded from fossils. We record two species of diving beetles from early Miocene Mexican amber and assign them to the hyperdiverse extant genus *Copelatus*. One of them, *Copelatus chiapas* new species, represents the first fossil diving beetle with documented sexual dimorphism in sculpture on elytra. We hypothesize that those species lived in freshwater habitats, such as swamps or pools/puddles, in a Tertiary rain forest about 20 million years ago.

Abstract.—Two diving beetle species (Coleoptera, Dytiscidae) from the extant genus *Copelatus* Erichson are documented from early Miocene Mexican amber. *Copelatus chiapas* new species is described based on a series of specimens of both sexes. *Copelatus chiapas* n. sp. is the third species of the subfamily Copelatinae described from amber and the first fossil diving beetle for which distinct sexual dimorphism is documented. The other species remains identified to genus level only, due to poor structural visibility. Key morphological characters of the species are illustrated.

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Introduction

The extant genus *Copelatus* Erichson, 1832, represents the most speciose genus of the family Dytiscidae, known as predaceous diving beetles. To date, 440 species, predominantly from forested areas of the tropics, have been described (Nilsson and Hájek, 2024). Despite their diversity, *Copelatus* species are morphologically rather homogenous, mainly of oval and dorsoventrally weakly convex body shape and about 3–10 mm in length. Many species possess conspicuous longitudinal striae on the dorsal side of the elytron of both sexes. *Copelatus* species inhabit a large variety of both running and stagnant waters, including caves (Caetano et al., 2013), ephemeral forest-floor depressions (Ranarilalatiana and Bergsten, 2019), and water tanks in bromeliads (Hájek et al., 2024).

At present, there are still several competing hypotheses regarding the phylogenetic placement of the subfamily Copelatinae within Dytiscidae. Morphological analyses suggest either a position of Copelatinae as the sister to all other Dytiscidae (e.g., Beutel et al., 2020) or subordinated within the family, as the sister of Hydrodytinae + Hydroporinae (Miller, 2001). The latter placement was also suggested by a recent molecular phylogenetic analysis (Baca et al., 2021). Alternative molecular phylogenetic analyses suggest topologies such as Copelatinae (Laccophilinae + Cybistrinae) (Désamore et al., 2018) or Copelatinae (Matinae [Hydrodytinae + Hydroporinae]) (Vasilikopoulos et al., 2021).

Based on a molecular clock analysis, Copelatinae are estimated to have originated between 85 and 95 million years ago (Ma); *Copelatus* itself is estimated to be from about 55 Ma (Balke et al., 2004; see also Désamore et al., 2018) to around 90 Ma (Baca et al., 2021). This is in accordance with the few hitherto known *Copelatus* fossils. The oldest one is a fossil from Eocene Baltic amber; without precise locality information,

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its age is estimated to be circa 55–40 Ma. The other amber fossil *Copelatus* is known from the La Toca Formation, Dominican Republic amber (Miocene, ca. 20–14 Ma) (Miller and Balke, 2003). There are also compressed *Copelatus* fossils that have been discovered: one from the Upper Rhine Graben Formation in Alsace, France (Eocene–Oligocene boundary, ca. 34 Ma) (Förster, 1891; Fikáček et al., 2011), and three species described from Vishnevaya Balka in Russia (Middle Miocene, ca. 16–11.6 Ma) (Říha, 1974).

The paleontological site near Simojovel de Allende, Chiapas, Mexico, is well known for its rich Tertiary biota. The amber can be found in three lithostratigraphic units there. The oldest amber is found in the La Quinta Formation, dated to early Miocene (amber deposit began ca. 23 Ma); its fossiliferous resin came from two legume (*Fabaceae*) tree species of the genus *Hymenaea* (Calvillo-Canadell et al., 2010), whose communities developed in estuarine environments near the ancient coast, very similar to mangroves (Poinar, 1992; Serrano-Sánchez et al., 2015). This stratum is overlaid by Mazantic Shale containing amber pieces that were originally deposited in a humid forest (Solórzano-Kraemer, 2010). The Balumtum Sandstone is the uppermost unit that occasionally bears some amber (Serrano-Sánchez et al., 2015). The insect fauna from Simojovel was revised by Solórzano Kraemer (2007), who reported about 2400 specimens, predominantly from the order Diptera, followed by Hymenoptera and Heteroptera. Additional organisms recently described from the area represent such taxa as Blatodea (Vršanský et al., 2011), Dermaptera (Estrada-Álvarez et al., 2023), semiaquatic Heteroptera (Cifuentes-Ruiz et al., 2021), Neuropterida (Engel and Grimaldi, 2007), and curculionoid Coleoptera (Poinar and Brown, 2007; Peris et al., 2015; Legalov and Poinar, 2016; Poinar and Legalov, 2016; Legalov et al., 2019).

A review of aquatic and semiaquatic biota was published by Serrano-Sánchez et al. (2015), who mentioned a syninclusion with seven unidentified "aquatic coleopterans," apparently belonging to the genus *Copelatus*, deduced from the presence of elytral striae on one specimen illustrated in dorsal view. Another unidentified species of *Copelatus*, in the *C. consors* Sharp, 1882a, species group, was diagnosed and illustrated by Solórzano Kraemer (2007). Here we contribute to the known diversity of Tertiary biota in Chiapas by describing a highly characteristic new diving beetle species preserved in amber pieces from that area. Because a series of specimens from both sexes is available, we also reveal the remarkable sculptural sexual dimorphism of the new species, well known in extant species, but for the first time documented in a fossil diving beetle. In addition, we present two more specimens that cannot be assigned to any of these taxa due to poor structural visibility; both will require further investigation.

Materials and methods

The specimens were examined using a Leica M205 C stereomicroscope. Measurements were made with an ocular graticule. Photographs were taken with a Canon EOS R camera, and Mitutoyo 5× and 10× ELWD Plan Apo objectives were used for photographing the habitus. These were attached to a Carl Zeiss Jena Sonnar 3.5/135 MC. Illumination was accomplished with three LED segments SN-1 from Stonemaster. Image stacks were generated using the Stackmaster macro rail (Stonemaster), and images were assembled with Helicon Focus v. 7.61 on a MacPro 2019 with a Radeon Pro 6800X MPX GPU. We also used a Keyence VHX-6000 digital microscope equipped with a ZST 20×–2000× objective for photographing of morphological details.

The following abbreviations were used in the descriptions: TL = total length, measurement of length from clypeal margin to apex of elytra; TL−h = total length minus head length, measurement of length from anterior margin of pronotum to apex of elytra; TW = maximum width of body measured at right angle to TL.

Repositories and institutional abbreviations.—Specimens examined in this study are deposited in the following collections: Staatliches Naturhistorisches Museum, Braunschweig, Germany (SNHMB) and Zoologische Staatssammlung, Munich, Germany (ZSMG).

Systematic paleontology

Order Coleoptera Linnaeus, 1758
Suborder Adephaga Schellenberg, 1806
Family Dytiscidae Leach, 1815
Subfamily Copelatinae Branden, 1884
Genus *Copelatus* Erichson, 1832

Type species.—*Dytiscus posticatus* Fabricius, 1801, by monotypy.

Copelatus chiapas new species
Figures 1–3

Type material.—Holotype ♂ (SNHMB, Inventory # SNHMB.G 8199); Mexico, Chiapas State, Simojovel de Allende (MEX004). Paratypes 1♂ 5♀♀, same locality and stratigraphic interval as holotype (SNHMB, Inventory # MEX005 with two individuals = SNHMB.G 8200; MEX010 = SNHMB.G 8201; MEX PS MEX34 = SNHMB.G 8202; MEX035 with two individuals = SNHMB.G 8203).

Diagnosis.—Elongate oval species; dorsal surface coarsely punctured in male, in female with dense long longitudinal striolae on pronotum and elytra; striae on elytral disc absent; appendages long, antennae filiform reaching nearly 0.4 of body length; metatarsomeres rectangular, well separated (not forming compact "scull"-like piece).

Occurrence.—All specimens are from early Miocene amber collected near Simojovel de Allende, Chiapas State, Mexico. Precise location (mine) and formation are not known.

Description.—Male holotype (Figs. 1, 2). Measurements (in mm): TL = 5.0; TL−h = 4.5; MW = 1.8. The whole beetle appears slightly compressed laterally; this is best seen in the compressed prosternal process, metaventrum, and metatibiae. Habitus elongate oval; sides almost parallel-sided, only slightly attenuated proximally and distally; dorsally slightly convex, ventrally flat (Fig. 1). Base of pronotum slightly broader than base of elytra; broadest posteriorly to elytral

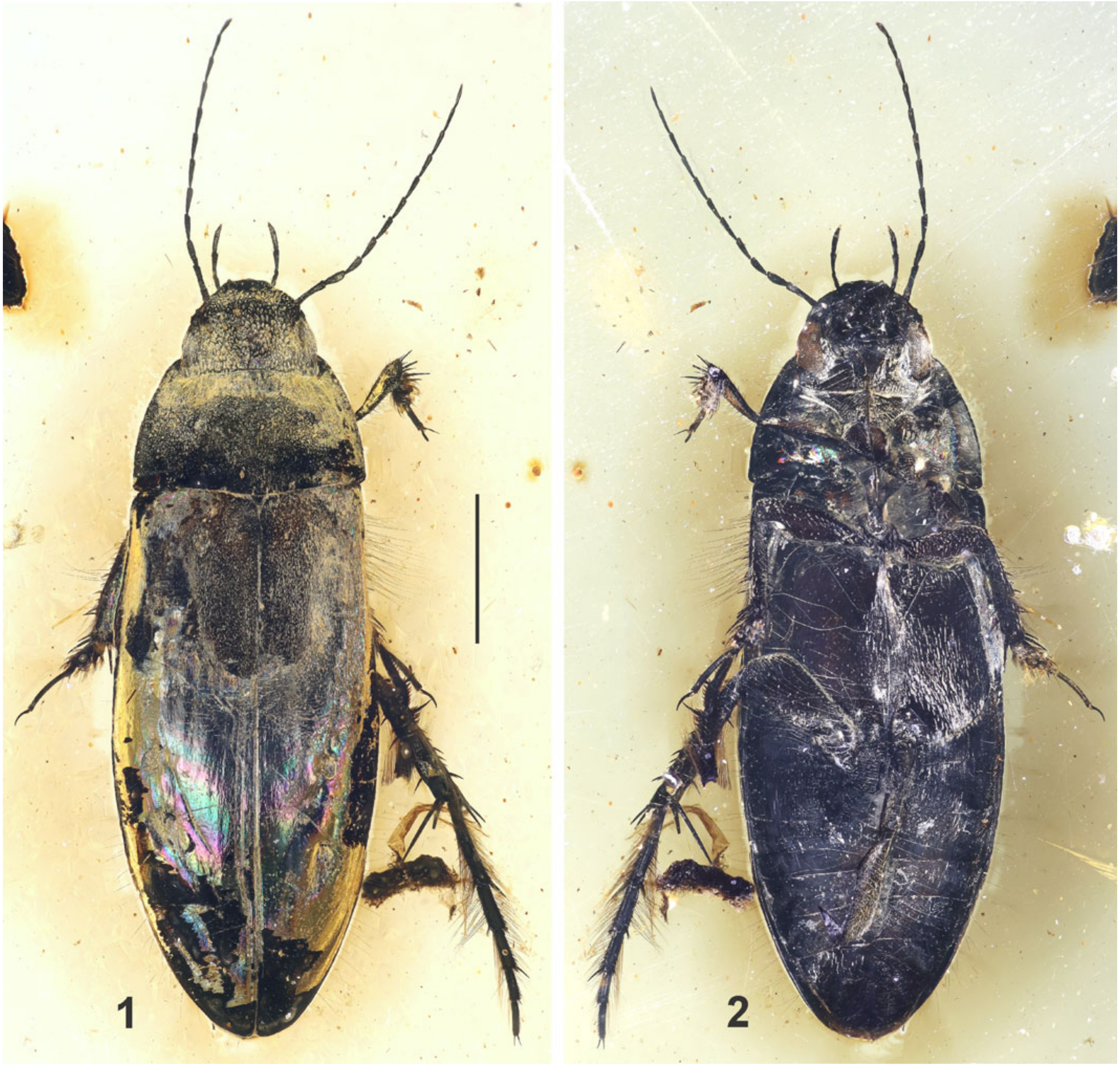

Figure 1. *Copelatus chiapas* n. sp., male holotype (# SNHMB.G 8199): (**1**) dorsal habitus; (**2**) ventral habitus. Scale bar = 1 mm.

mid-length. Coloration of body brownish black; elytra with indistinct transverse orange brownish band at base. Head elongate, ~0.59× width of pronotum, almost semi-circular; anterior margin of clypeus slightly convex; antennae with antennomeres club-shaped, long and slender (antennomeres II–X ~3× longer than wide); eyes small (eye width/interocular distance ratio = 0.25), emarginate antero-laterally; reticulation consisting of fine, well-impressed isodiametric polygonal meshes; punctation consisting of coarse punctures. Pronotum transverse, broadest at posterior angles; anterior angles acute, posterior angles obtuse; sides moderately and evenly curved; reticulation imperceptible; punctation consisting of dense punctation smaller than those on head (Fig. 2.1).

Scutellar shield small, triangular. Elytra without longitudinal striae but disc in basal half covered with short longitudinal striolae (Fig. 2.1); reticulation consisting of very fine, superficially impressed polygonal meshes; meshes isodiametric, hardly perceptible in basal half, but transverse and more apparent in apical half; punctation double, large setigerous punctures present along lateral margin of elytra, fine punctures distributed on whole surface of elytra.

Legs with metafemora without distinct linear series of setae near anteroapical angle; all tibiae with numerous long spines; protibia distinctly broadened distally, club-shaped; all tarsi pentamerous; pro- and mesotarsomeres 1–3 strongly broadened, ventrally with four transverse rows of adhesive setae; apical

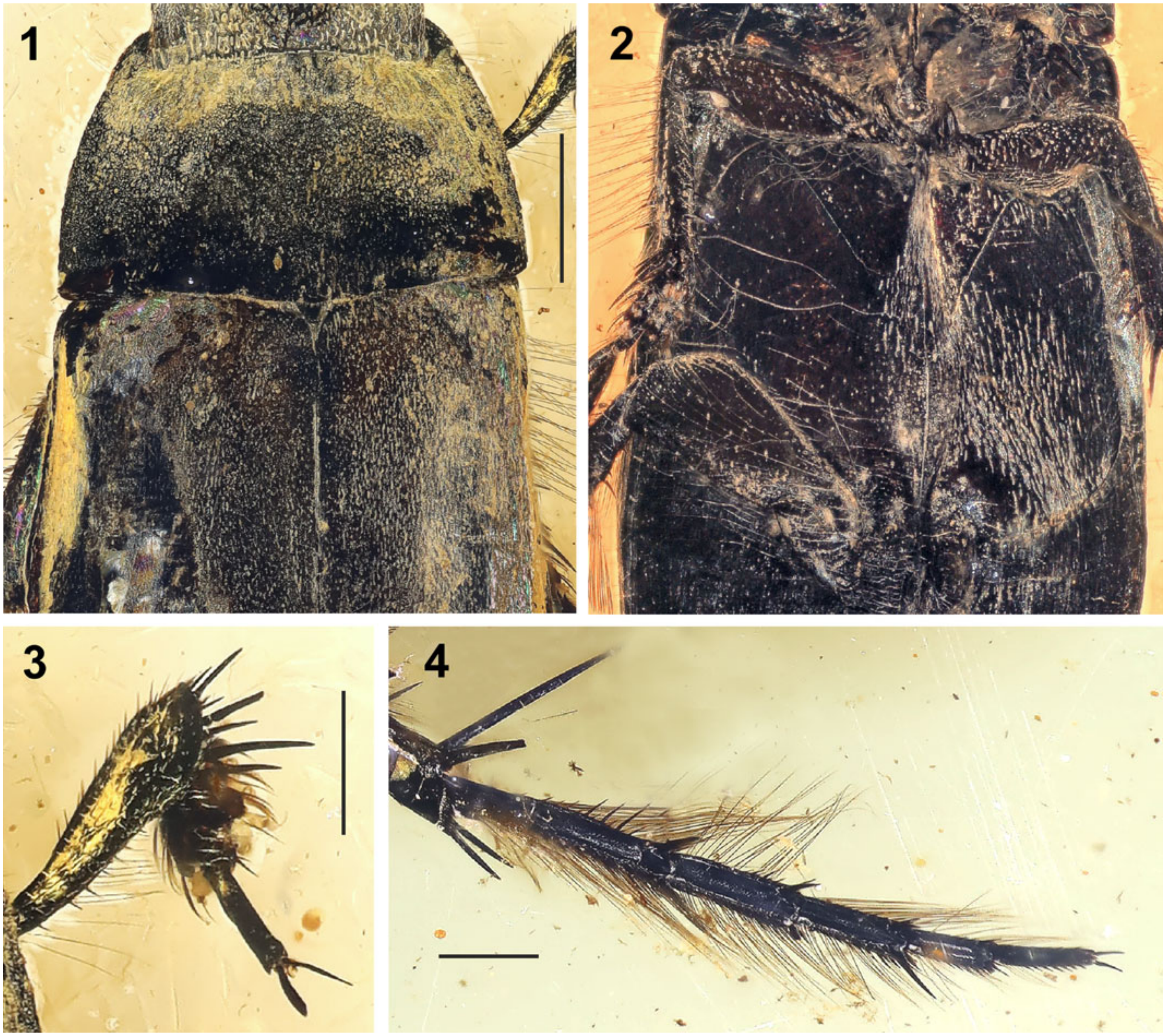

Figure 2. *Copelatus chiapas* n. sp., male holotype (# SNHMB.G 8199): (**1**) pronotum and base of elytra; (**2**) metaventrite and metacoxae; (**3**) protarsus; (**4**) metatarsus. Scale bars = 0.5 mm (**1, 2**), or 0.25 mm (**3, 4**).

pro- and mesotarsomere as long as preceding tarsomeres together; protarsal claws unequal, anterior claw slender and strongly curved, posterior claw broadened medially, straight (Fig. 2.3); metatarsomeres long, rectangular to slightly club-shaped, well separated (not forming compact "scull"-like piece), with numerous spines on edges (Fig. 2.4.); metatarsal claws equal; long natatorial setae well developed on dorsal side of pro- and mesotibia, and on both sides of metatibia and metarsomeres. Ventral side with prosternum keeled medially; prosternal process lanceolate, in most specimens artificially laterally compressed, apex obtuse; lateral parts of metaventrite ("metasternal wings") tongue-shaped, slender; metacoxal lines closely approximated, well impressed, anteriorly abbreviated; metacoxal plates covered with long longitudinal strioles; reticulation not perceptible (Fig. 2.2); metacoxal processes rounded at posterior margin; abdominal ventrites I–II with longitudinal strioles; ventrites III–V with oblique strioles laterally; apical ventrite bordered on posterior margin.

Female.—Similar to male in habitus (Fig. 3.1). Pro- and mesotarsomere 1–3 not broadened; protarsal claws equal, thin. Dimorphic in dorsal surface sculpture: one female similar to male in structure, remaining four females with pronotum and elytra (except for apical part) covered with densely distributed long longitudinal striolae (Fig. 3.2).

Variation.—TL = 4.1–5.1 (mean = 4.6 ± 0.3); TL−h = 3.9–4.5 (mean = 4.2 ± 0.2); MW = 1.6–2.0 (mean = 1.8 ± 0.1).

Etymology.—The species is named after the Chiapas State (Mexico), where the type locality is situated. The specific epithet is a noun in the nominative singular.

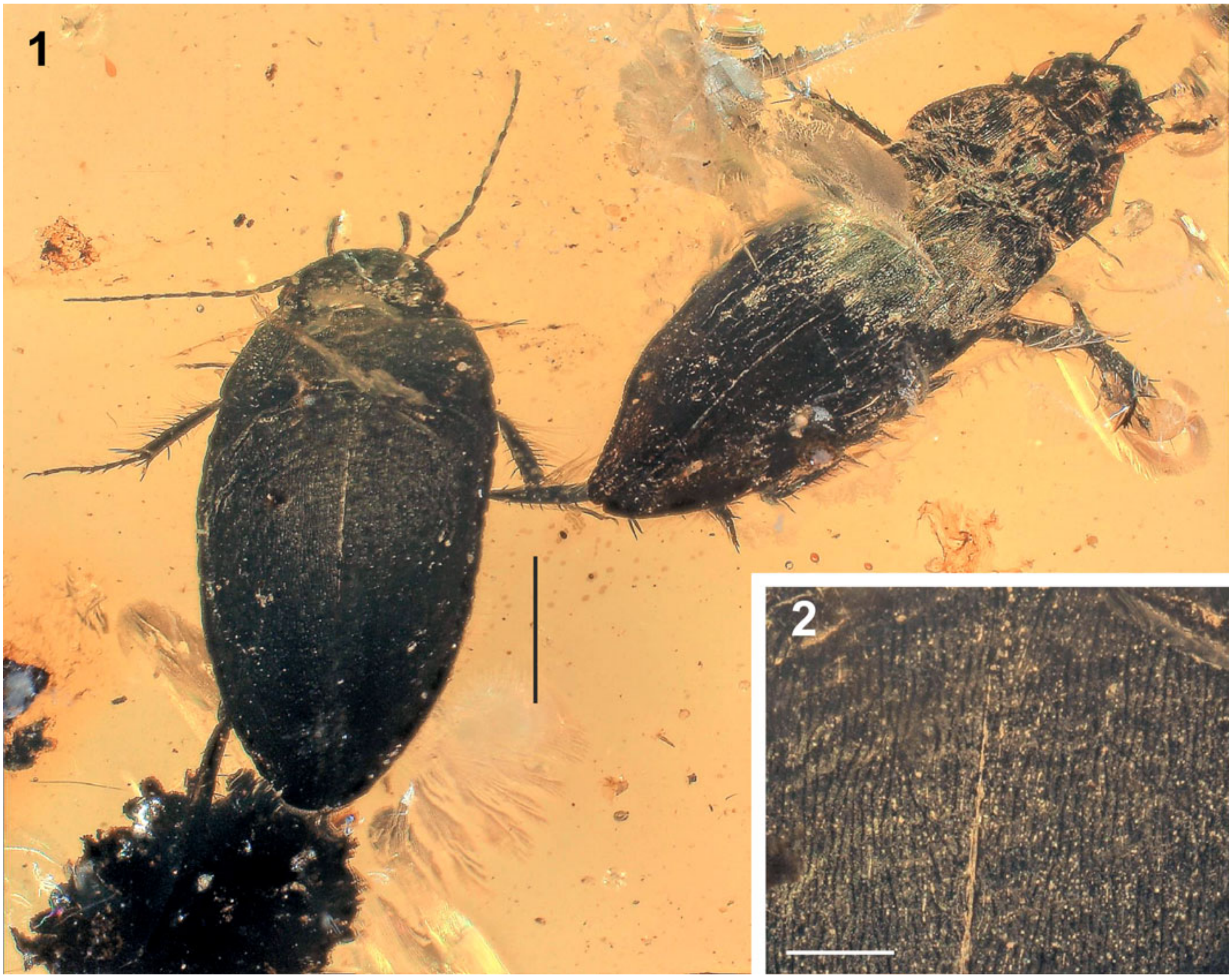

Figure 3. *Copelatus chiapas* n. sp., female paratypes (# SNHMB.G 8200): (**1**) dorsal habitus; (**2**) detail of elytral microsculpture. Scale bars = 1 mm (**1**), or 0.25 mm (**2**).

Taxonomic remarks.—We can undoubtedly classify this species within the subfamily Copelatinae based on the following characters: (1) elongate habitus, (2) eyes emarginate antero-laterally, (3) exposed scutellum, (4) metacoxal lines very closely approximated, (5) metafemur without distinct linear series of setae near anteroapical angle, (6) all tarsi pentamerous, and (7) equal metatarsal claws. This subfamily is found in Central and North America represented solely by the genus *Copelatus*—a large and variable taxon for which no morphological synapomorphy can be postulated at present.

The intrageneric classification of *Copelatus* is unsatisfactory; species are clustered based on the presence of longitudinal striae on elytra into informal species groups (Sharp, 1882a; Guignot, 1961), which usually do not delineate monophyletic units (Balke et al., 2004). *Copelatus chiapas* n. sp. possesses no regular striae on its elytra, which places it in the *Copelatus hydroporoides* (Murray, 1859) species group. This group comprises 57 extant species, occurring in all zoogeographical regions, 25 of which occur in the Neotropics. In the review of Neotropical species of this group (Young, 1942), the new species keys with *C. biformis* Sharp, 1882b, from Veracruz, Mexico. However, the latter species is characterized by a broadly oval habitus, the male elytra with distinct lines of serial punctures that are deeply impressed to form two short striae, and the female elytra with four regular striae. *Copelatus chiapas* n. sp. also can be easily distinguished from all hitherto described fossil *Copelatus* species, including the one previously recorded from Simojovel (Solórzano Kraemer, 2007), because they all have elytra with distinct longitudinal striae.

Copelatus sp.
Figure 4

Diagnosis.—Elongate oval species (Fig. 4.1, 4.2), TL = 3.9–4.0 mm; dorsal surface with longitudinal strioles close to pronotal basal angles (Fig. 4.3), elytra tentatively with 11 dorsal striae and submarginal stria; appendages long, antennae filiform reaching nearly 0.4 of body length; metatarsomeres rectangular, forming compact “scull”-like metatarsus.

Figure 4. *Copelatus* sp. from Mexico, Chiapas State, Simojovel de Allende: (**1**) dorsal habitus (# MexAmb 001); (**2**) dorsal habitus (# MexAmb 002); (**3**) detail of structure on lateral part of pronotum (# MexAmb 001). Scale bars = 1 mm (**1, 2**), or 0.25 mm (**3**).

Occurrence.—All specimens are from the early Miocene amber collected near Simojovel de Allende, Chiapas State, Mexico. Precise locality (mine) and formation are not known.

Material examined.—Two ♂♂, labelled: "2201/-5/29 Mexican amber, Adult, Copelatinae, Prorhinopsenius 0.9 mm, 20–15 ma" // "MEXICAN AMBER, Simojovel, Chiapas, Mexico" (ZSMG, Inventory # MexAmb 001, 002).

Remarks.—The two additional male specimens cannot be assigned to a species known from Mexican amber due to poor structural visibility. Based on the tentative presence of 11 dorsal elytral striae and a submarginal stria, they may belong to the *Copelatus erichsoni* Guérin-Méneville, 1847, species group—one of the largest groups worldwide—containing currently 145 species, 35 of them occurring in Latin America (Nilsson and Hájek, 2024). Further investigation would require µCT scanning as well as comparison with the other existing *Copelatus* species from Chiapas amber.

Discussion

Based on a review of aquatic and semiaquatic fauna from the La Quinta Formation, Serrano-Sánchez et al. (2015, p. 243) characterized the Miocene landscape in Simojovel as an "estuarine environment similar to modern mangrove communities." This opinion was corroborated by subsequent studies on various arthropod groups, predominantly various crustaceans such as Brachyura (Serrano-Sánchez et al., 2016), Copepoda (Huys et al., 2016), and Ostracoda (Matzke-Karasz et al., 2019), and most recently insects (Heteroptera) as well (Cifuentes-Ruiz et al., 2021). In contrast, studies of predominantly terrestrial fossils from the later Mazantic Shale Formation suggest the presence of a humid forest (Solórzano-Kraemer, 2010; Estrada-Álvarez et al., 2023).

The precise formation is not known for our *Copelatus* specimens. However, a mangrove habitat with brackish water and regular fluctuation of water level is rather an unsuitable environment for most aquatic beetles; and in fact, we are not aware of any diving beetles that live in mangroves today. We suggest freshwater habitats, such as swamps or pools/puddles in a rain forest—the environment documented from the study area (e.g., with palynological studies; Graham, 1999)—as the most probable place where the newly described *Copelatus* lived.

Sexual dimorphism, which is well known in the majority of diving beetle groups, is interpreted as the result of sexual conflict. Because multiple prolonged matings may reduce overall fitness in females, they are thought to resist mating attempts under certain circumstances, while males are thought to attempt to force copulation. In terms of morphology, the most apparent adaptations in the males are the expansion of male pro- and, to a lesser extent, mesotarsomeres, with the presence of adhesive setae on the ventral side, and sometimes the modification of protarsal claws. Female adaptations most frequently comprise modification of the cuticle sculpture on the pronotum and elytra to create various striolae, striae, or grooves, or reticulate patterns. Those structures appear to interfere with the male grasping device, giving the females greater control over the decision to mate. In many Dytiscinae species with modified elytra, females are dimorphic, with some modified and others not, and the proportion of modified females appears to vary among populations (for review of Dytiscidae sexual systems, see Miller and Bergsten, 2014).

Although we expect that sexual dimorphism exists in extinct diving beetles, their limited fossil records prevent us from confirming this. Here, we document sexual dimorphism in the newly described *Copelatus* species. The male has distinctly broadened pro- and mesotarsi with adhesive setae on their ventral side, and a modified, medially broadened posterior protarsal claw. The female is dimorphic; one preserved female is identical to the male in its dorsal surface sculpture, while the other four females have the surface of their pronotum, and elytra covered with densely distributed, long longitudinal striolae. While this is the first fossil diving beetle for which a distinct sexual dimorphism has been documented, we expect additional examples will be found in the fossil record as more new species are discovered.

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Declaration of competing interests

The authors declare none.

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