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Erik TIHELKA
School of Earth Sciences, University of Bristol
Life Sciences Building, Tyndall Avenue, Bristol, BS8 1TQ (United Kingdom)

David PERIS
Section Paleontology, Institute of Geosciences, University of Bonn
53115 Bonn (Germany)

Chenyang CAI
State Key Laboratory of Palaeobiology and Stratigraphy
Nanjing Institute of Geology and Palaeontology, and Center for Excellence in Life and Paleoenvironment, Chinese Academy of Sciences
Nanjing 210008 (China)
and School of Earth Sciences, University of Bristol
Life Sciences Building, Tyndall Avenue, Bristol, BS8 1TQ (United Kingdom)
cycai@nigpas.ac.cn (corresponding author)

Vincent PERRICHOT
Univ. Rennes, CNRS, Géosciences Rennes
UMR 6118, F-35000, Rennes (France)
vincent.perrichot@univ-rennes1.fr (corresponding author)

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ABSTRACT
Jacobsoniidae is a species-poor family of minute polyphagan beetles distributed in tropical and subtropical regions. Both extant representatives of the family as well as fossils are rare. Here we describe a new fossil species, *Derolathrus capdoliensis* n. sp., from latest Albian-earliest Cenomanian Charentese amber from the Cadeuil deposit, Charente-Maritime department in south-western France. The new species is defined by several unusual characters, most notably the co-joined but not fully fused two apical antennomeres. *Derolathrus capdoliensis* n. sp. is approximately contemporaneous with Kachin amber (burmite), filling an important geographical gap in the Mesozoic distribution of the family. The widespread distribution of jacobsoniid beetles in the Cretaceous, encompassing the Tethyan and Austral realms, indicates a more widespread distribution of the family during this time than in the present day and suggests that the current biogeographical range of Jacobsoniidae may be a result of extinction in northern regions. The new species shows remarkable similarity to extant members of the genus and provides further evidence of prolonged morphological, and probably also ecological, stasis in Jacobsoniidae since at least the Cretaceous.

KEY WORDS
Derolathrus,
Mesozoic,
fossil,
Cadeuil,
new species.

RÉSUMÉ
Un coléoptère de Jacobson dans l'ambre crétacé des Charentes (Coleoptera: Jacobsoniidae).
Les Jacobsoniidae sont une famille peu diversifiée de minuscules coléoptères polyphages présents dans les régions tropicales et subtropicales. Les représentants actuels de la famille ainsi que les fossiles sont rares. Nous décrivons ici une nouvelle espèce fossile, *Derolathrus capdoliensis* n. sp., provenant de l'ambre charentais de l'Albien supérieur ou Cénomanien inférieur du gisement de Cadeuil, dans le département de la Charente-Maritime, dans le sud-ouest de la France. La nouvelle espèce est définie par plusieurs caractères inhabituels, notamment ses deux antennomères apicaux co-joints mais pas complètement fusionnés. *Derolathrus capdoliensis* n. sp. est approximativement contemporain de l'ambre birman du Kachin (burmite), comblant ainsi une importante lacune géographique dans la distribution mésozoïque de la famille. La large distribution des coléoptères jacobsoniidés au Crétacé, englobant les provinces téthysienne et australe, indique une distribution plus étendue de la famille à cette période qu'à l'heure actuelle et suggère que l'aire biogéographique actuelle des Jacobsoniidae pourrait résulter d'une extinction dans les régions septentrionales. La nouvelle espèce montre une similarité remarquable avec les membres existants du genre et fournit des preuves supplémentaires d'une stase morphologique, et probablement aussi écologique, prolongée chez les Jacobsoniidae depuis au moins le Crétacé.

MOTS CLÉS
Derolathrus,
Mésozoïque,
fossile,
Cadeuil,
espèce nouvelle.

INTRODUCTION

Jacobson's beetles (Jacobsoniidae Heller, 1926) is a small family of polyphagan beetles with only 24 extant and three extinct described species (Háva & Löbl 2005; Lawrence & Leschen 2010; Peck 2010; Bi *et al.* 2015; Háva 2016; Cai *et al.* 2016, 2017; Yamamoto *et al.* 2017; Yin & Bi 2018). Recent species are distributed in New Zealand, the Indo-Australian region, Sri Lanka, Florida, and tropical islands (Lawrence & Leschen 2010; Peck 2010). All species in this family are small to minute (0.65-2.5 mm long) and little is known about their biology (Lawrence & Leschen 2010). Many jacobsoniids are found in leaf litter and rotten wood, but some were also collected from more specific microhabitats such as fungal fruiting bodies and bat guano (Lawrence & Leschen 2010).

The placement of the family within Coleoptera is controversial. Crowson (1959, 1960) first proposed a relationship between Jacobsoniidae and the superfamily Staphylinoidea although it was provisionally placed in the superfamily Dermestoidea together with Derodontidae, Nosodendridae, and Dermestidae. Subsequently, different authors proposed different classifications and Jacobsoniidae was placed within Cucujiformia (Sen Gupta 1979), Bostrichiformia (Lawrence & Newton 1995; Philips *et al.* 2002), and finally Derodontiformia (Lawrence & Leschen 2010; Bouchard *et al.* 2011). The most recent morphological and molecular phylogenetic studies support a close affinity of the family with Staphylinoidea (Lawrence *et al.* 2011; McKenna *et al.* 2015b, 2019; Toussaint *et al.* 2017; Zhang *et al.* 2018), which resulted in removing Jacobsoniidae from Derodontiformia and the family was treated as taxon *incertae sedis* within Polyphaga (Lawrence 2016), then formally placed in Staphylinoidea (Cai *et al.* 2021). Indeed, an affinity with Staphylinoidea is supported by wing venation characters and the morphology of the maxillary galea of the larvae (Crowson 1959, 1960). A study testing the monophyly of Jacobsoniidae is, however, still lacking.

Jacobsoniidae includes three extant genera with three recently described fossil species. *Derolathrus groehni* Cai, Leschen & Huang, 2016 was the first fossil species belonging to the family to be described from middle Eocene Baltic amber (Cai *et al.* 2016). Later, *D. abyssus* Yamamoto & Parker, 2017 and *Sarothrias cretaceus* Cai, Ślipiński, Leschen, Yin, Zhuo & Huang, 2017 were described from mid-Cretaceous Kachin (Burmese) amber (Yamamoto *et al.* 2017; Cai *et al.* 2017). These fossils indicate that two out of the three current genera, *Derolathrus* Sharp in Sharp & Scott 1908 and *Sarothrias* Grouvelle, 1918, are perfect examples of bradytely ('arrested evolution' *sensu* Simpson 1944); a long morphological stasis is similarly described in many other beetle lineages recorded from Cretaceous ambers (Clarke & Chatzimanolis 2009; Chatzimanolis *et al.* 2013; Peris & Háva 2016, Yamamoto *et al.* 2017; Cai *et al.* 2019). *Derolathrus capdoliensis* n. sp. is described herein as the oldest jacobsoniid species, pushing the definitive record of the family back some millions of years and, as with the rest of the fossil species, provides a new example of bradytely.

MATERIAL AND METHODS

Geological setting

The department of Charente-Maritime in south-western France has several Albian-Cenomanian amber deposits (Perrichot *et al.* 2010). The specimen studied herein was found in the Cadeuil deposit, a quarry near the town of Sainte-Gemme, located about ten kilometers from the Seudre estuary (Fig. 1; Perrichot *et al.* 2010). The alternating sand and clay beds where the amber deposits were discovered belongs to the lithological unit A, which was divided into two subunits (Moreau 1993; Néraudeau *et al.* 2002, 2005): A1, sand of various grain sizes, arranged in large cross beddings, bearing abundant lignite and amber accumulations; and A2, fine sand, mainly arranged in horizontal beds, bearing rare wood remains. In the Cadeuil

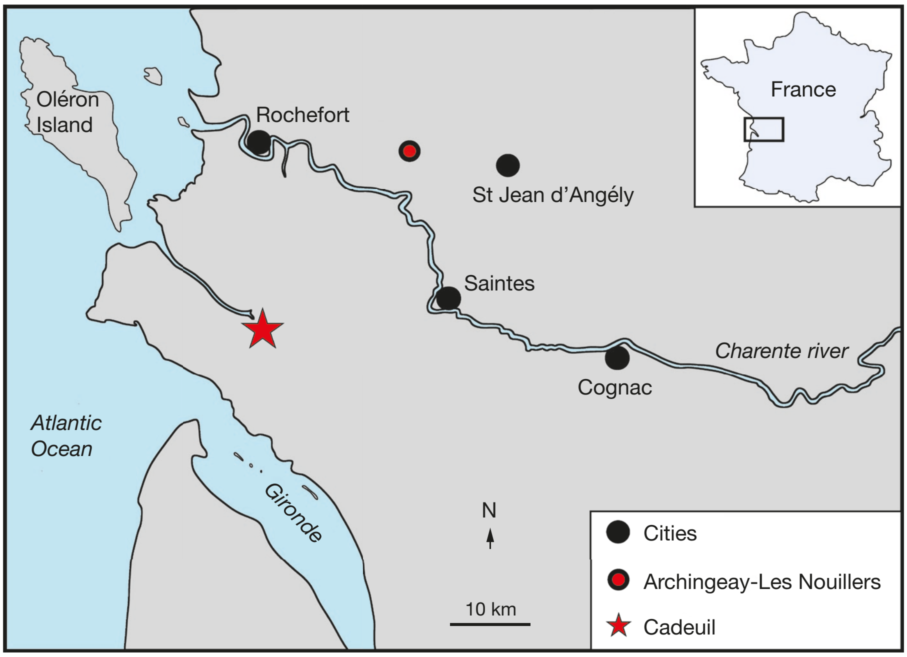

Fig. 1. — Map showing the location of the Cretaceous Charentese amber deposit in Cadeuil near Sainte-Gemme. The location of the largest deposit of Charentese amber, Archingeay-Les Nouillers, is also marked with a red dot.

area, the main amber deposit lies at the top of subunit A1 (Néraudeau *et al.* 2008). This geological section consists of 2 m of coarse sand, which is of brackish to coastal marine origin (Néraudeau *et al.* 2008). The sand includes three remarkable fossiliferous horizons, the amber is found in horizon A1b which is an accumulation of lignite (fossil wood) and horizon A1c which is a hard and coarse sandstone with metric cross beddings, corresponding to a succession of channels (Néraudeau *et al.* 2008). According to palynology, Cadeuil amber may be dated as late Albian in age (Néraudeau *et al.* 2002), but the horizons where the amber is found contain dynocysts, which range from the late Albian to the Cenomanian (Néraudeau *et al.* 2008). Similarly, the palynomorphs from the overlying subunit A2 are indicative of a latest Albian-early Cenomanian age, but ostracod and foraminifer assemblages from the upper part of subunit A1 (A1c) suggest an early Cenomanian age only (Peyrot *et al.* 2019). Thus, the amber from Cadeuil can be dated as latest Albian-earliest Cenomanian, although it was considered reliably dated as early Cenomanian in Perrichot *et al.* (2010). In comparison with other amber deposits from the region, Cadeuil represents a depositional environment which is more strongly influenced by marine conditions (Néraudeau *et al.* 2008). Furthermore, the abundance of algal inclusions suggests that the resin was produced during periods of algal blooms and was probably exuded from submerged conifer roots (Néraudeau *et al.* 2008). Cadeuil is the second largest amber deposit in the Charente-Maritime department, after Archingeay-Les Nouillers. However, only two beetle specimens were found among the about hundred fossil arthropods, mainly insects, from this deposit (VP, pers. data): the specimen studied herein and the sample CDL-2.23 (an isolated elytron).

Studied material, imaging and microtomography

The specimen IGR.CDL-2.42 is included in an irregular, polished prism of amber (Fig. 2). The holotype is slightly distorted, possibly as a result of taphonomic processes after death or later on because of pressure exerted on the amber from the overlying sediment. The head and pronotum are fractured, the pronotum is almost completely separated from the elytra, and the apex of the abdomen is heavily distorted and partly missing. The elytra and wings of the specimen are separated from the body (Fig. 2). The specimen is preserved inside the amber fragment alone, but the fragment was originally part of a larger amber piece ('CDL-2' depicted in Perrichot 2005: fig. 10) containing 47 other arthropods and various microorganisms. This piece was cut into 50 subfragments for access to all inclusions and their detailed morphological features. Several of these insect syninclusions have been described elsewhere already (e.g., Perrichot *et al.* 2006, 2009; Flössner & Fryer 2016). The amber piece containing the specimen is nearly transparent. Amber pieces like this are uncommon since most Cretaceous French ambers are usually translucent to opaque (Lak *et al.* 2008).

Photographs under reflected light were taken with a Zeiss Discovery V16 stereoscope. Photomicrographs with green background were taken under the eGFP mode (Zeiss Filter Set 10; excitation/emission: 450-490/515-565 nm). To uncover additional morphological details in the very small specimen, it was imaged using a propagation phase-contrast X-ray synchrotron (PPC-SRµCT). The scan was conducted at the European Synchrotron Radiation Facility (ESRF) in Grenoble, France. The specimen was imaged at the beamline ID19 using 1999 projections obtained through 360 degrees continuous rotation of the sample, with a multilayer monochromatic beam set at 20.5 keV, an isotropic voxel size of 1.36 µm, 30 mm of propagation distance, and 0.5s of exposure time (see technical details in Lak *et al.* 2008 and Soriano *et al.* 2010). After acquisition, ring artefact correction and 16 bits conversion, the volume was segmented using a filtered back projection algorithm in edge detection mode adapted for local tomography applications (PyHST software, ESRF). The tomographic data were subsequently analyzed using the VG StudioMax (3.0) software and a three-dimensional model was reconstructed from the segmented model.

The map showing the location of the Cadeuil deposit was created in CorelDRAW X8.

SYSTEMATIC PALEONTOLOGY

Order COLEOPTERA Linnaeus, 1758
Suborder POLYPHAGA Emery, 1886
Superfamily STAPHYLINOIDEA Latreille, 1802
Family JACOBSONIIDAE Heller, 1926
Genus *Derolathrus* Sharp in Sharp & Scott, 1908

Derolathrus capdoliensis n. sp. (Figs 2-5)

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HOLOTYPE. — IGR.CDL-2.42, slightly distorted specimen, sex indeterminate (Fig. 2). Deposited in the Geological Department and Museum of the University of Rennes, France.

ETYMOLOGY. — Derived from '*Capdolium*', the latin name of the type locality Cadeuil.

TYPE LOCALITY. — Charentese amber; lithological horizon A1b from Cadeuil quarry at Sainte-Gemme, Charente-Maritime department, France.

AGE. — Early-Late Cretaceous, latest Albian-earliest Cenomanian.

DIAGNOSIS. — Head subglabrous, without deep setiferous punctures. Antennae 11-segmented, apical two antennomeres not completely fused. Antennomere 10 slightly broader and shorter than the following segment, antennomere 11 pointed apically. Eyes large, with *c.* 30 ommatidia, their diameter slightly greater than the distance from their anterior margin to the antennal insertions. Pronotum rather parallel-sided, broadest in the anterior quarter. Pronotal disc with an oval medial depression with a raised longitudinal groove. Femora distinctly clavate.

DESCRIPTION

Body minute, subcylindrical, narrowly elongate. Length from clypeus to apex of the preserved part of abdomen 0.76 mm, 0.22 mm wide across the broadest point of the elytra. Body subglabrous dorsally, dark brown to black (Figs 2; 3).

Head oval, 0.2 mm long from clypeus to distalmost part of the neck, abruptly constricted behind the eyes and with a distinct neck region, slightly fractured. Head surface glabrous, lacking carinae, raised ridges or deep punctures. Mandibles small, slender, curved. Maxillary palpomeres three-segmented, with apical palpomere aciculate and the penultimate palpomere distinctly larger, approximately three times the length of the following segment and broadest in the basal third. Eyes oval, somewhat protruding, multifaceted, and consisting of approximately 30 ommatidia. Antennae 11-segmented, concealed from above and inserted anterior to the eyes, separated by slightly less than the diameter of the eyes. Antennomere 1 (scape) globular, approximately as long as wide, antennomere 2 (pedicel) 0.9 times as long and 0.8 times as wide as the preceding segment, more elongate and barrel shaped; antennomeres 3-9 moniliform, gradually shortening and widening apically, antennomeres 10-11 forming a compact club; antennomere 10 0.9 times as long and 1.1 times as broad as the following segment, widest apically; 11 pointed apically (Figs 4; 5). Temples short, less than a quarter of the length of the eye.

Pronotum slightly distorted, 0.19 mm long, 1.1 times longer than wide, slightly wider than the head, approximately parallel-sided. Widest in anterior quarter. Anterior pronotal angles rounded, posterior pronotal angles obtuse. Pronotal disc with an oval medial depression with a raised longitudinal groove running from the basal quarter to the anterior quarter (Fig. 5A: pd, pg). Ventral side of pronotum strongly deformed. Procoxae globular, separated by approximately a third of their diameter across the broadest point. Mesocoxae rounded, further apart than procoxae, separated by more than half of their diameter. Metaventrite 0.24 mm long, broadening posteriorly and wider than head. Scutellum not visible.

Legs short, slender with the exception of the apically swollen femur. Trochanters distinctly large, trapezoidal. Femora broadened, clavate (Fig. 5B). Tibiae slender, twice as broad in apical half as at base, lacking apical spurs. Tarsus 3-segmented, third tarsomere longer than the basal two segments combined. Claws simple, empodium not apparent.

Elytra incomplete, narrower than pronotum basally, smoothly broadening towards the middle, and narrowing apically. Hind wings present, venation strongly reduced, ventral margin with approximately 30 elongate setae, dorsal margin with about 30 minute setae.

Abdomen poorly preserved, apical portion apparently missing. Intercoxal process of ventrite 1 broadly rounded.

DISCUSSION

SYSTEMATIC POSITION OF *D. CAPDOLIENSIS* N. SP.

The new fossil species can be placed into the family Jacobsoniidae on the basis of its minute size, narrowly elongate body, elongate prothorax, absence of a visible scutellum, concealed antennal insertions, and a distinctly elongate metaventrite (Philips *et al.* 2002; Lawrence & Leschen 2010). It can be placed into the extant genus *Derolathrus* based on its exceptionally small body size (incomplete length of 0.76 mm), 3-3-3 tarsal formula, 11-segmented antennae with a compact two-segmented apical club, and aciculate apical maxillary palpomeres (Sen Gupta 1979; Löbl & Burckhardt 1988; Philips *et al.* 2002; Peck 2010; Lawrence & Ślipiński 2013). In terms of its gross morphology, *D. capdoliensis* n. sp. shows close similarities with extant congenerics as well as with *Derolathrus* fossils known from Cretaceous Kachin amber (Yamamoto

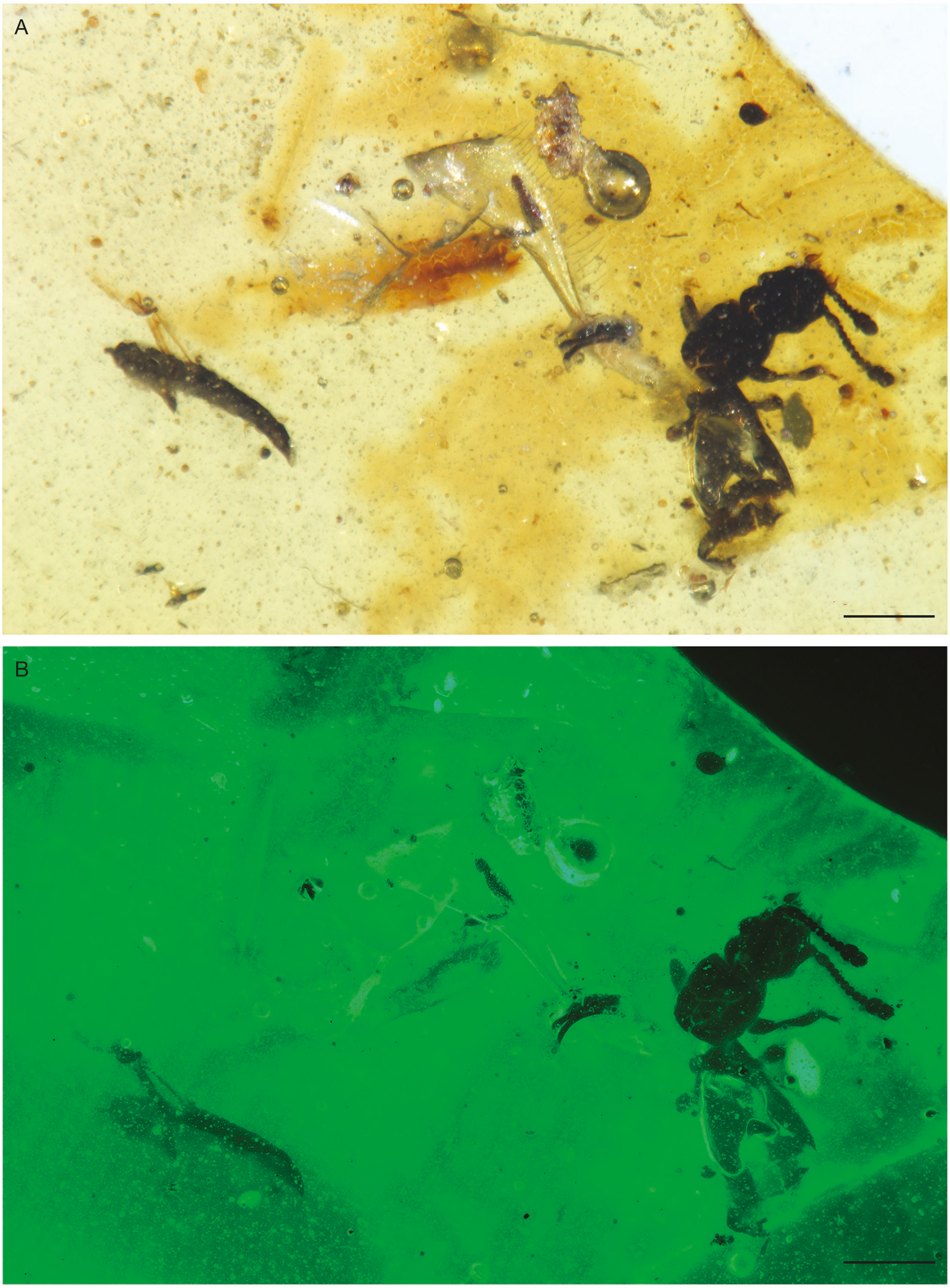

FIG. 2. — Holotype of *Derolathrus capdoliensis* n. sp. (IGR.CDL-2.42) in dorsal view: **A**, under normal reflected light; **B**, under green fluorescence. Scale bars: 200 µm.

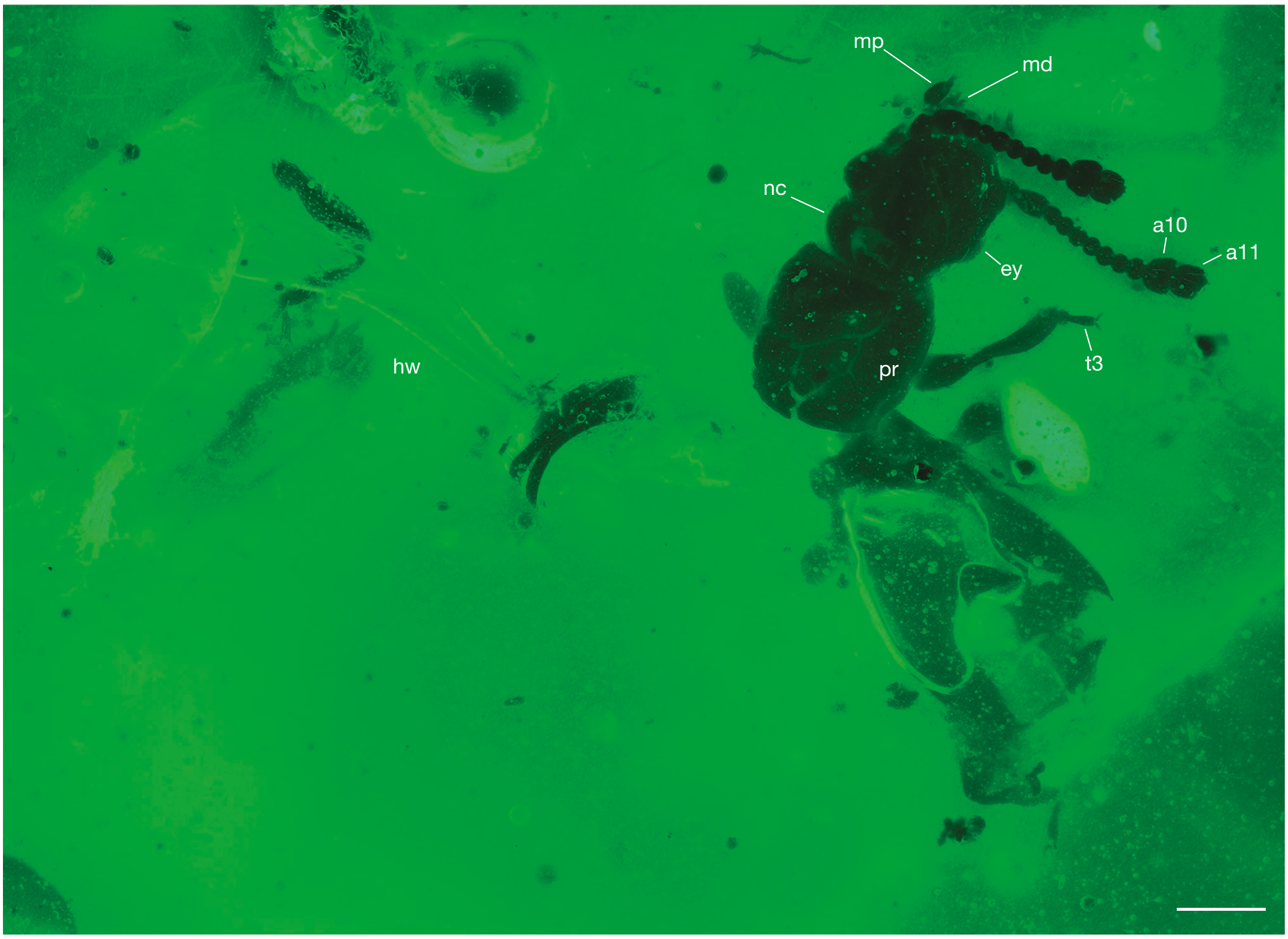

Fig. 3. — Morphological details of the holotype of *Derolathrus capdoliensis* n. sp. (IGR.CDL-2.42) in dorsal view under green fluorescence. Abbreviations: **a10-11**, antennomeres 10-11; **ey**, eye; **hw**, hindwing; **md**, mandible; **mp**, maxillary palpomeres; **nc**, neck region; **pr**, pronotum; **t3**, protarsomere 3. Scale bar: 100 µm.

et al. 2017). It is probable that if the abdominal region of the beetle was complete, the elytra would expose the abdominal apex, similarly to the Cretaceous *D. abyssus* from Kachin amber (Yamamoto *et al.* 2017). Given that the elytra cover the abdomen completely in extant members of the genus, it is possible that this character represent a plesiomorphy.

D. capdoliensis n. sp. differs from the Cretaceous fossil species *D. abyssus* known from Kachin amber in having a more elongate metaventrite, clearly not shorter than the abdomen (Yamamoto *et al.* 2017), and from the Eocene *D. groehni* from Baltic amber in having more finely faceted ommatidia with more than 15 ocelli (Cai *et al.* 2016). Unlike *D. anophthalmus* Franz, 1969, apparently endemic to the Canary Islands, *D. capdoliensis* n. sp. has large eyes and is alate (Franz 1969). The presence of well-developed eyes also separates the new species from *D. parvulus* (Rücker 1983) and *D. troglophilus* (Sen Gupta 1979). It differs from *D. atomus* Sharp in Sharp & Scott 1908, *D. ceylonicus* (Sen Gupta 1979), and an undescribed species from New Zealand in the presence of a pronotal depression (Sharp & Scott 1908; Sen Gupta 1979; Lawrence & Leschen 2010). While it shares with *D. cavernicolus* Peck, 2010 and *D. insularis* (Dajoz 1973) the presence of a medial pronotal depression, it differs from the former in the head lacking densely scattered, large, setiferous punctures and pronotum without a longitudinal subtriangular depression, and from the latter in pronotum more parallel-sided and not expanding anteriorly. The new species differs from *D. sharpi* Grouvelle in Grouvelle & Raffray 1912 in having larger eyes, whose diameter is slightly greater than distance to the base of antennae (Grouvelle & Raffray 1912). *Derolathrus capdoliensis* n. sp. differs from all hitherto described species in the antennal club consisting of two antennomeres that are very closely spaced but nonetheless discrete and not entirely fused.

The new species can be considered as basal within *Derolathrus* based on its antennal structure. While all other congenerics have the apical two antennomeres clearly fused, sometimes appearing as one uniform segment (e.g. *D. insularis*), in *D. capdoliensis* n. sp. the two apical segments are very close but not fused, as indicated by the microtomographs in Figures 4 and 5 showing a slight separation between the two segments. It is thus possible that the distinctly 11-segmented condition is ancestral and that the apical club became progressively more fused in later-diverging species of the genus. However, evaluating whether any given set of characters represent true plesiomorphies depends on resolving the internal phylogeny of Jacobsoniidae and its systematic position within Polyphaga.

FIG. 4. — PPC-SRμCT reconstruction of the holotype of *Derolathrus capdoliensis* n. sp. (IGR.CDL-2.42): **A**, ventral view; **B**, dorsal view. Scale bar: 200 μm.

Hundred million years of morphological stasis in Jacobsoniidae

Derolathrus capdoliensis n. sp. possibly predates the two Cretaceous Jacobson's beetles described to date, *D. abyssus* and *Sarothrias cretaceus* from Kachin amber mined in northern Myanmar (Cai *et al.* 2017; Yamamoto *et al.* 2017). Volcanoclastic matrix from the Kachin amber-bearing horizon was dated radiometrically at 98.79 ± 0.62 Ma (Shi *et al.* 2012), corresponding to the early Cenomanian. Mao *et al.* (2018) pointed out that given the design of the analysis, this radiometric date should be interpreted as the minimum age of the deposit. Even when adhering to this conservative minimum age of Kachin amber, the age of Charentese amber remains uncertain and is either latest Albian or earliest Cenomanian (Néraudeau *et al.* 2002; Perrichot *et al.* 2010). While it is thereby unclear if *D. capdoliensis* n. sp. predates other Jacobson's beetles from Kachin amber, it nonetheless considerably expands the known range of the family during the mid-Cretaceous.

The new species closely resembles its modern and fossil congenerics. It shares the most similarities with the Cretaceous *D. abyssus* and the extant *D. ceylonicus* known from Sri Lanka. *D. capdoliensis* n. sp. thus provides a testimony to a prolonged morphological stasis within Jacobsoniidae since at least the earliest Cenomanian, some 100 Ma ago. A highly conserved morphology within the family is also apparent from the described Cretaceous fossil species (Cai *et al.* 2017; Yamamoto *et al.* 2017) and probably indicates that the ecology of the group has changed little since this time. Similar degrees of morphological stasis have been reported in other Cretaceous beetles inhabiting leaf litter and decaying vegetational matter (e.g. Clarke & Chatzimanolis 2009; Peris *et al.* 2014; Yamamoto & Solodovnikov 2016; Ross 2019, 2020; Liu *et al.* 2020; Yin & Zhou 2020). It is possible that the relative stability of this microhabitat through deep time protected these taxa from strong selective pressures and extinction (Peris & Háva 2016), providing 'refuge niches' (McKenna *et al.* 2015a; Lü *et al.* 2019). Indeed, some of the most diverse groups of beetles such as many ground beetles (Carabidae) and rove beetles (Staphylinidae) occupy predominantly leaf litter, soil, and rotting plant matter, and so the role of refuge niches in acting as a museum of biodiversity may be a more general evolutionary phenomenon across Coleoptera.

Historical biogeography of Jacobson's beetles

Derolathrus capdoliensis n. sp. represents the 11th described species of the genus *Derolathrus*. Members of the genus are rarely collected, which may be in part due to their minute size (most species do not exceed 1 mm in length) and cryptic habits. *Derolathrus* adults and larvae have been collected in fungus-rich and humid microhabitats such as leaf litter, under bark, in rotten

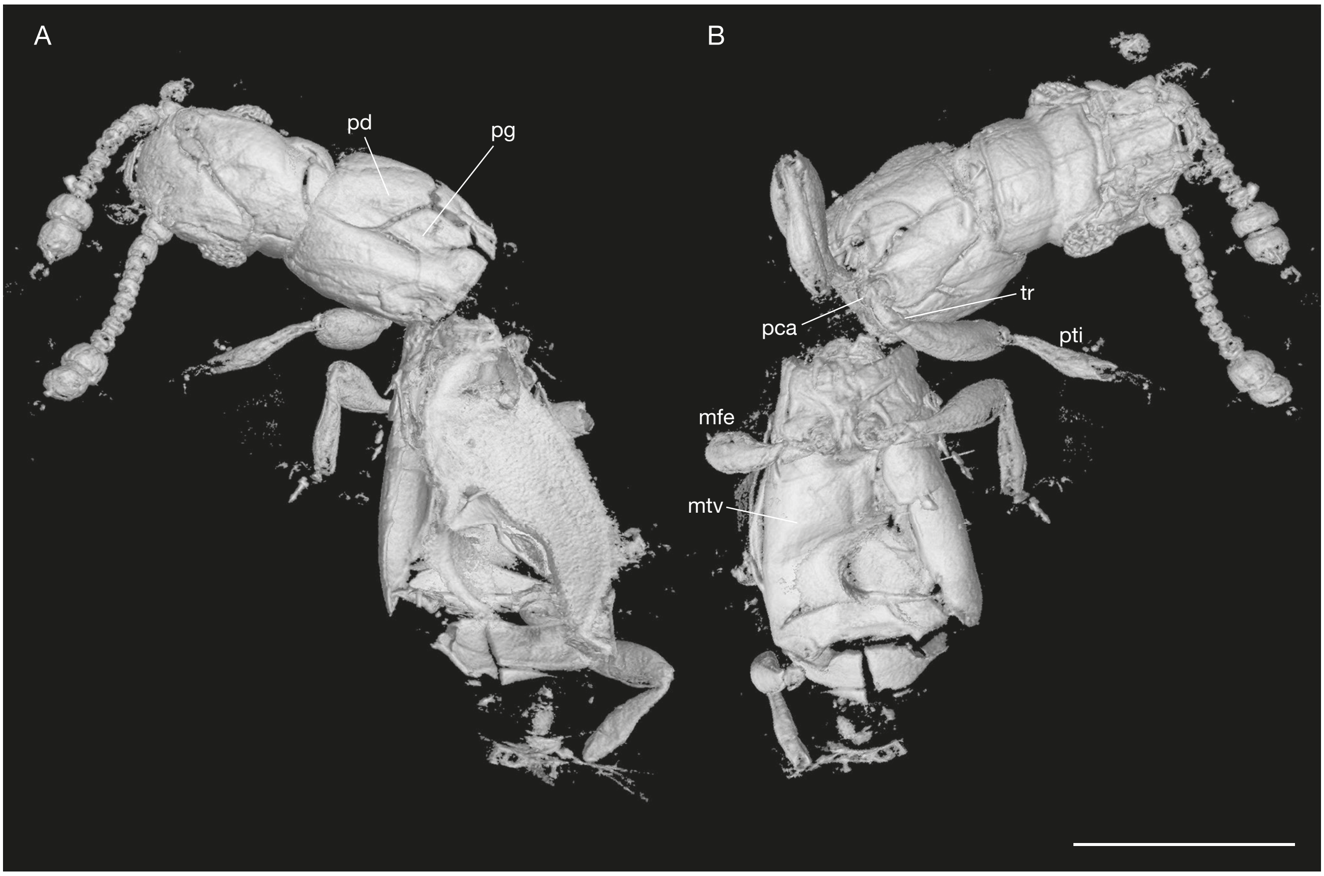

Fig. 5. — Enlargement of the PPC-SRμCT reconstruction details of the holotype of *Derolathrus capdoliensis* n. sp. (IGR.CDL-2.42): **A**, dorsal view; **B**, ventral view. Abbreviations: **mfe**, mesofemur; **mtv**, metaventrite; **pg**, pronotal groove; **pca**, procoxa; **pd**, pronotal depression; **pti**, protibia; **tr**, trochanter. Scale bar: 200 μm.

palm wood, bat guano, and fungal fruiting bodies (Lawrence & Leschen 2010). *Derolathrus* occurs in tropical and subtropical regions throughout the world as well as on isolated landmasses and archipelagos such as the Hawaii Islands, Galapagos Islands, the Solomon Islands, Australia, and New Zealand (Philips *et al.* 2002, Peck 2010). This distributional pattern could have arisen as a result of widespread dispersal. Given their minute size and wing morphology, Jacobson's beetles could be carried by wind currents over long distances (Cai *et al.* 2016). Our discovery in Charentese amber reveals that Jacobsoniidae had a potentially cosmopolitan distribution during the mid-Cretaceous, encompassing the Tethyan and Austral realms. Jacobsoniidae occurred in present-day Europe until at least the Eocene, as evidenced by specimens from Baltic amber (Cai *et al.* 2016). Baltic amber probably formed from resin secreted during the Middle Eocene climatic optimum when northern Europe had a warm and equitable climate, as evidenced by the occurrence of insects such as mantises and stick insects in the deposit (Archibald & Farrell 2003; Brunke *et al.* 2019). It is possible that Jacobsoniidae became extinct in Europe following the cooling after the Eocene climatic optimum that gave the continent the temperate climate with colder winter temperatures that we largely know today (Hren *et al.* 2013).

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