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First thaneroclerid beetle from Cretaceous Charentese amber (Coleoptera: Cleroidea: Thanerocleridae)

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Abstract

Thanerocleridae is a small family of predaceous cleroid beetles with a cosmopolitan distribution. Here we describe a new genus and species, *Mesozenodosus insularis* **gen. et sp. nov.**, from early Cenomanian Charentese amber from the Fouras deposit, Charente-Maritime department in south-western France. The new genus belongs to the relictual subfamily Zenodosinae represented in the Recent fauna by a single Nearctic species, *Zenodosus sanguineus* (Say). *Mesozenodosus* **gen. nov.** can be differentiated from *Zenodosus* and the two fossil zenodosine genera from the approximately contemporaneous Burmese amber by its smaller body size, more elongate body, non-carinate pronotal margins, and apical antennomere with an oval depression. The new fossil confirms a wider diversity and distribution range of Zenodosinae in the mid-Cretaceous than in the present day and provides further evidence of the relictual status of the subfamily.

Keywords: Thanerocleridae, Zenodosinae, Mesozoic, fossil, Cretaceous amber, French amber

Introduction

With thirty-four described species placed in ten extant genera distributed worldwide, Thanerocleridae constitutes one of the smaller families of the superfamily Cleroidea (Kolibáč, 1992, 1998; Kolibáč & Leschen, 2010; Opitz, 2010). The beetles are small, either uniformly brown-black

or black-yellow with stripes. All thaneroclerids appear to be predators of small beetles associated with wood and fungi such as members of Ptinidae, Tenebrionidae, and Curculionidae (Kolibáč & Leschen, 2010). They can be collected under tree bark, by beating tree branches, or on fungi growing on trees. The species *Thaneroclerus termiticola* Corporaal was collected inside termite nests with abundant ptinid beetles. Members of the genera *Thaneroclerus* Lefebvre and *Isoclerus* Lewis have been recorded from bales of stored tobacco, coffee, tea, and rice. As a result of the worldwide trade with these commodities, *T. buquet* (Lefebvre) is the only thaneroclerid with a truly cosmopolitan distribution (Kolibáč *et al.*, 2005; Kolibáč, 2018). Most thaneroclerids are endemic to southern and southeastern Asia, although native species also occur in Americas, tropical Australia, Africa, Madagascar, New Guinea, and the Fiji islands (Kolibáč & Leschen, 2010). There are no extant thaneroclerids native to Europe, although populations of *T. buquet* are being continuously introduced with foodstuffs trade (Kolibáč *et al.*, 2005).

Thanerocleridae was first recognised as a subfamily of the more diverse Cleridae (checkered beetles) by Chapin (1924), before being elevated to family rank by Kolibáč (1992). Thaneroclerids can be differentiated from clerids most notably by having non-emarginate eyes, tegmen lacking median and lateral struts, and expanded protarsomeres 1–4 (Kolibáč, 1992). Most recent analyses of morphological and molecular data have recovered the two families as sister to each other, forming the informal

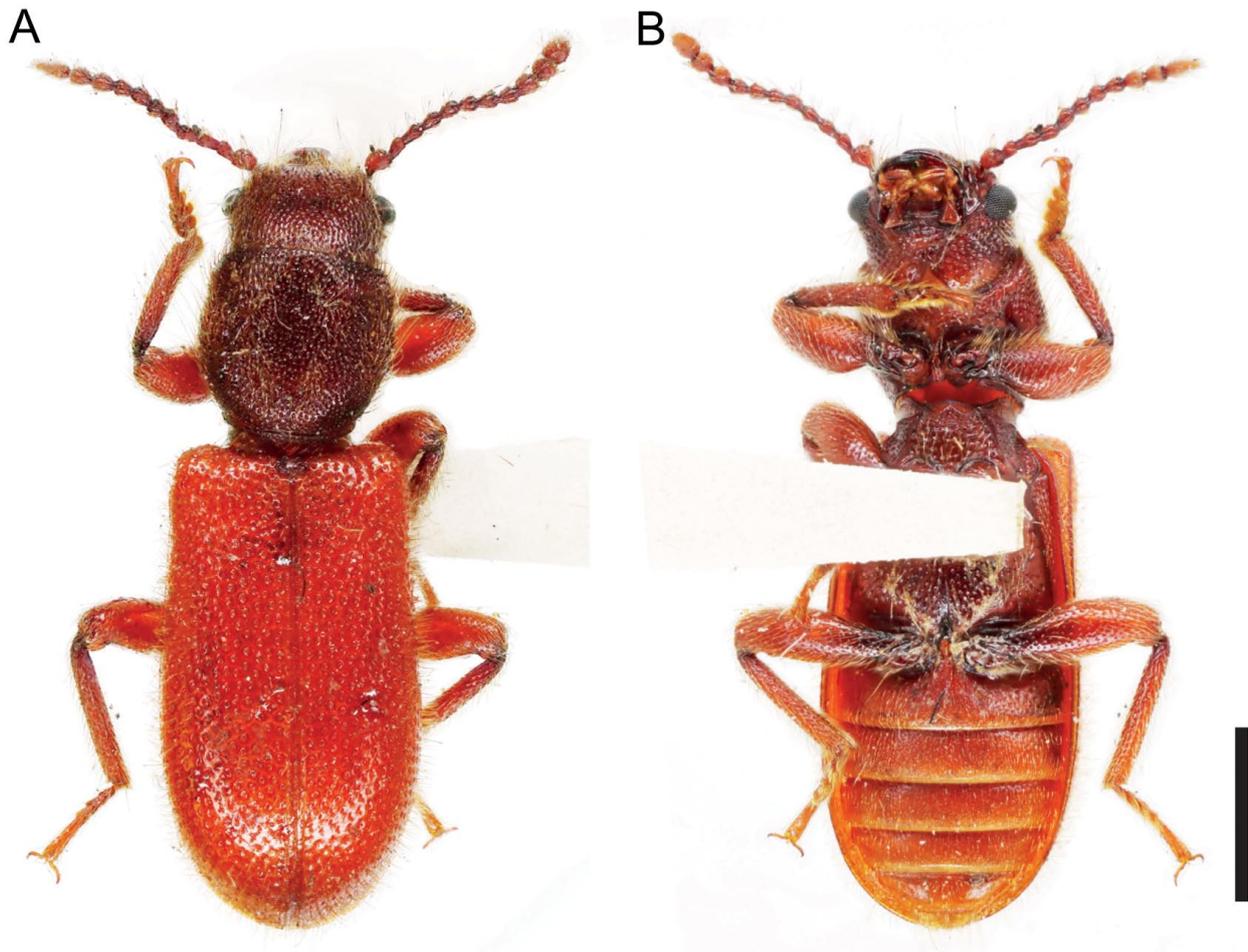


FIGURE 1. The sole extant species of Zenodosinae, *Zenodosus sanguineus*, from USA. **A**, Dorsal view. **B**, Ventral view. Scale bar = 1 mm.

‘clerid group’ together with the closely related small family Chaetosomatidae (Opitz, 2010; Lawrence *et al.*, 2011; McKenna *et al.*, 2015, 2019; Kolibáč & Huang, 2016; Zhang *et al.*, 2018; Gimmel *et al.*, 2019). Notably, the three gene analysis of Gunter (2013) recovered Thanerocleridae as nested within Cleridae, although as Gimmel *et al.* (2019) pointed out this relationship may be artificial and caused by limited gene sampling and unbalanced inclusion of taxa.

Thanerocleridae is divided into two subfamilies with all but one genus belonging to the subfamily Thaneroclerinae. The subfamily Zenodosinae includes the single extant species *Zenodosus sanguineus* (Say) (Fig. 1) occurring in southeastern Canada and the eastern, central, and southern United States (Kolibáč & Leschen, 2010). Kolibáč (1992) provided a list of plesiomorphic morphological characters supporting *Zenodosus* Wolcott (Say) as the earliest-diverging member of the family. Two fossil zenodosine genera are known from Albian–Cenomanian Burmese amber mined in northern Myanmar: *Archaeozenodosus* Yu & Kolibáč, and *Cretozenodosus* Cai & Huang (Yu *et al.*, 2017; Cai & Huang, 2018). Here

we describe the first Cretaceous thaneroclerid beetle from outside Myanmar, *Mesozenodosus insularis* **gen. et sp. nov.**, from mid-Cretaceous Charentese amber from south-western France.

Material and methods

Geological background

The amber inclusion originates from a lignitic deposit exposed occasionally during low tides on the ‘Plage de la Vierge’ at Fouras, Charente-Maritime department, south-western France (Néraudeau *et al.*, 2003: fig. 1). Specifically, amber pieces are sparsely preserved with lignitic debris and vertebrate remains within a glauconitic sand and clay. The location and stratigraphy of the deposit have been described in detail in a number of previous publications, with the amber bed being named ‘lithological subunit B2ms’ (Néraudeau *et al.*, 2003, Perrichot, 2005; Perrichot *et al.*, 2010; Cockx *et al.*, 2016), or alternatively ‘B2c/d’ in an updated stratigraphic section of the locality

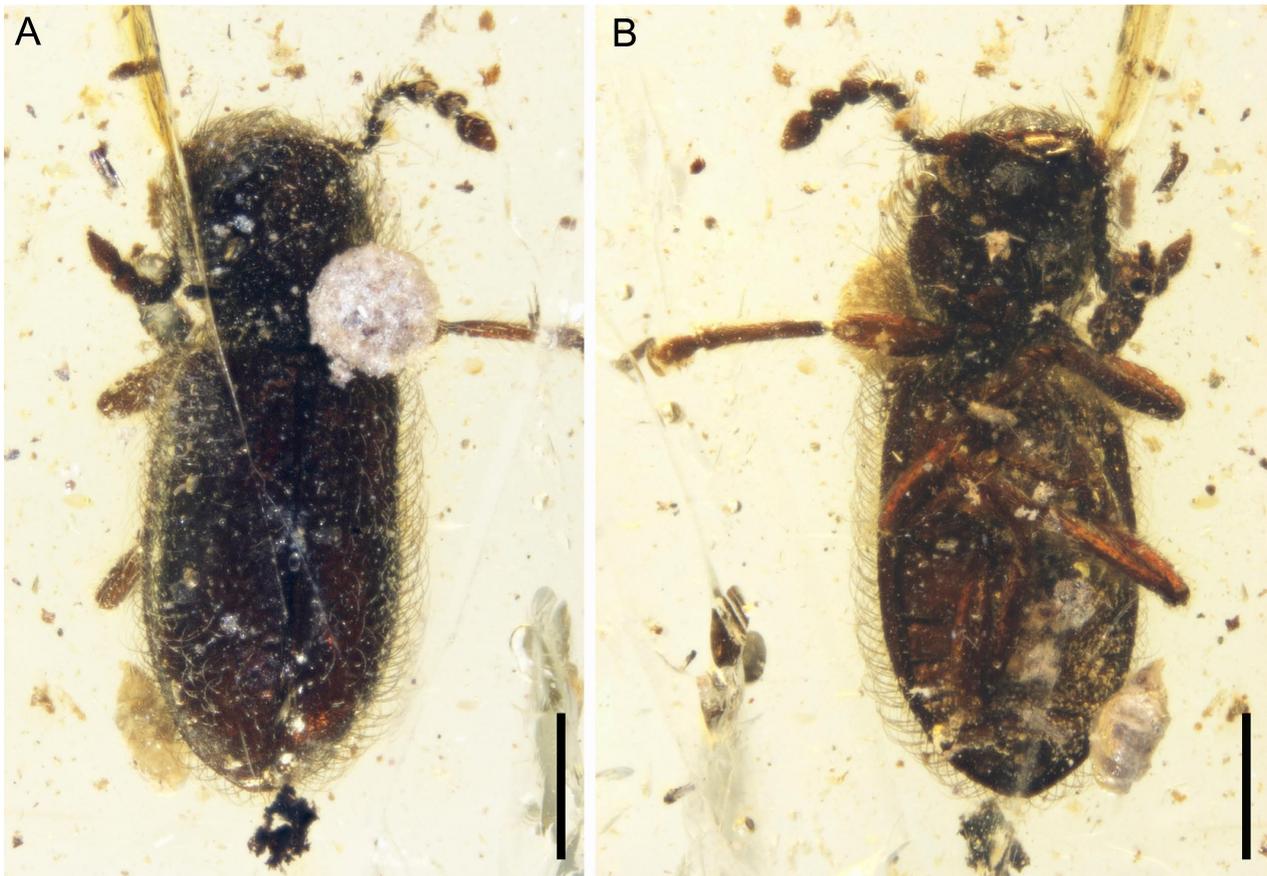


FIGURE 2. Habitus view of *Mesozenodosus insularis* gen. et sp. nov. (holotype, IGR.FRS-7.6) under normal reflected light. **A**, Dorsal and **B**, Ventral views. Scale bars = 500 μ m.

and study of the associated palynomorphs (Peyrot *et al.*, 2019). From this latest account, Fouras amber is considered early Cenomanian in age (96–100.5 Ma). The depositional environment is considered to be lagoonal, with a storm-induced deposit from a proximal coastal or riparian forest dominated by gymnosperms (mostly Cheirolepidiaceae and Cupressaceae), abundant ferns, and with rare aquatic angiosperms (Peyrot *et al.*, 2019).

The shore exposes one of the several deposits in the region yielding fossiliferous Cretaceous amber. To date, Fouras amber has yielded about 110 organismic inclusions, mostly arthropods, including a beetle originally assigned to the family Trogossitidae (Peris *et al.*, 2014) and now considered to belong to Thymalidae (Peris, 2020). It is worth noting that the piece of amber containing the Thanerocleridae specimen described herein is highly fossiliferous and has yielded nearly half of all inclusions from this deposit, with a total of 53 arthropods and three conifer fragments, as listed in Cockx *et al.* (2016: table 1 – amber piece #IGR.FRS-7, in which the present thaneroclerid is reported as a member of the family Cleridae). Among these, a few wasps have been described in the chrysidoid families Bethyridae and Sclerogibbidae (Cockx *et al.*, 2016; Perkovsky *et al.*,

2020), and the conifer remains have been assigned to the presumably resin-producing genus *Pagiophyllum* Heer, a member of the extinct family Cheirolepidiaceae (Moreau *et al.*, 2020). The same piece also contains four other undescribed beetles, including a Melyridae and three undetermined, fragmentary specimens.

The type specimen is deposited in the amber collection of the Geological Department and Museum of the University of Rennes, France.

Specimen preparation and photography

Because the original piece was highly fossiliferous and comprised multiple resin layers, polishing of its outer surface was not sufficient for a clear view of all inclusions deep into the amber matrix. The piece was thus cut into several fragments using a scalpel blade as a microsaw. Each fragment containing at least one organic inclusion was then embedded into mineralogical-grade epoxy Epotek 301-2 using a vacuum chamber, and the resulting blocks were polished for an optimal view of the fossils. A total of 34 fossiliferous fragments were prepared, and collection numbers IGR.FRS-7.1 to IGR.FRS-7.34 were assigned. The thaneroclerid described herein is now preserved

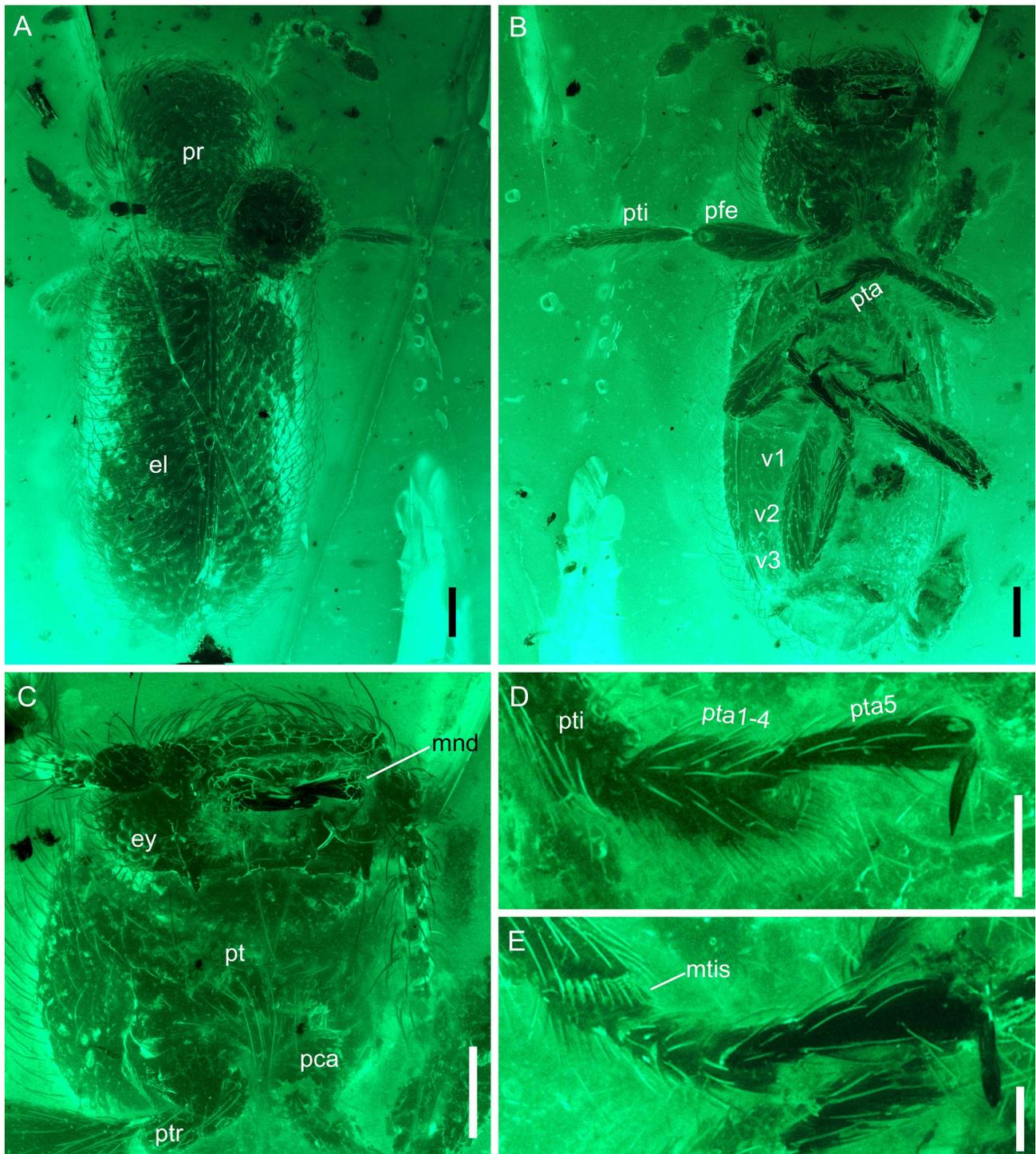


FIGURE 3. *Mesozenodosus insularis* **gen. et sp. nov.** (holotype, IGR.FRS-7.6) under green fluorescence. **A**, Dorsal view. **B**, Ventral view. **C**, Head and prothorax in ventral view. **D**, Protarsus. **E**, Metatarsus. Abbreviations: cl, claws; el, elytra; ey, eye; mnd, mandible; mtis, metatarsal apical setae; pca, procoxa; pfe, profemur; pr, pronotum; pt, prothorax; pta 1–5, protarsomeres 1–5; pta, protarsus; pti, protibia; ptr, prothorax v1–3, ventrites 1–3. Scale bars = 200 μ m (**A–C**), 50 μ m (**D** and **E**).

isolated in fragment IGR.FRS-7.6. A Zeiss Discovery V20 stereomicroscope was used for observation and photography. Green fluorescence microphotographs were taken using the Zeiss Axio Imager 2 light microscope under the eGFP mode.

X-ray microtomography

Given the small size of the specimen and the limited transparency of the amber piece, which is characteristic of French amber, it was imaged using high-resolution

X-ray microtomography (micro-CT) to uncover fine morphological detail. The specimen was scanned using Zeiss Xradia 520 versa at the micro-CT laboratory of Nanjing Institute of Geology and Palaeontology, CAS. Considering the comparatively small size of the fossil, a CCD-based 4× objective was used, providing isotropic voxel sizes of 2.6887 µm with the help of geometric magnification. During the scanning, the acceleration voltage for the X-ray source was 40 kV. To improve signal-to-noise ratio, 2801 projections over 360° were collected, and the exposure time for each projection was 5 s. The tomographic data were analysed using VG Studio (version 3.0; Volume Graphics).

Systematic palaeontology

Order Coleoptera Linnaeus, 1758
 Superfamily Cleroidea Latreille, 1802
 Family Thanerocleridae Chapin, 1924
 Subfamily Zenodosinae Kolibáč, 1992

Genus *Mesozenodosus* gen. nov.

Included species. *Mesozenodosus insularis* sp. nov.

Etymology. The generic name is a combination of ‘Mesozoic’ and ‘Zenodosus’, referring to the age and systematic placement of the fossil.

Diagnosis. Body small, approximately 2.3 mm long, rather elongate, 2.6 times longer than wide. Dorsal surface with dense and elongate setae. Head strongly declined. Antennal insertions not covered by edge of frons. Antennae 11-segmented with apical three segments forming a loose club. Antennomere 11 with an apical oval depression. Pronotum constricted at base, without dorsal depressions, margins non-carinate. Elytra somewhat arching laterally, broadest medially, deeply punctate dorsally. Humeral angles not protuberant, smoothly rounded.

Mesozenodosus insularis sp. nov.

(Figs 2–5)

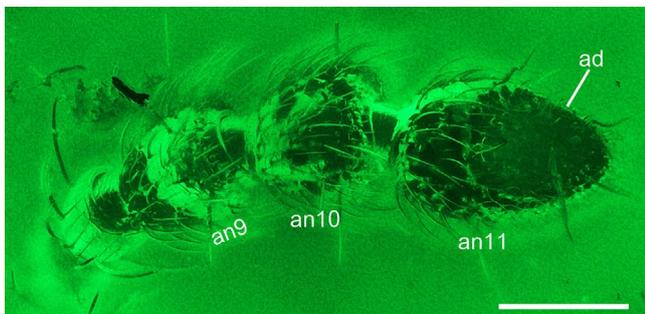


FIGURE 4. Antennal apex of *Mesozenodosus insularis* gen. et sp. nov. (holotype, IGR.FRS-7.6) under green fluorescence. Abbreviations: ad, depression of apical antennomere; an9–11, antennomeres 9–11. Scale bar = 100 µm.

Type material. IGR.FRS-7.6, sex indeterminate. Deposited in the Geological Department and Museum of the University of Rennes, France.

Etymology. The specific epithet is derived from the Latin ‘*insularis*’ (insular) in reference to the paleogeography of the Charentese region in the mid-Cretaceous; the area was part of an archipelago on the eastern rim of the Atlantic Ocean.

Diagnosis. As for genus with additional characters: antennomere 8 wider than long; apical antennomere spindle-shaped with a rounded apex; metatarsus as long as two thirds of the metatibia; claws almost as long as half of tarsomere 5.

Locality and horizon. Charentese amber; early Cenomanian; lithological subunit B2ms from the ‘Plage de la Vierge’ at Fouras, Charente-Maritime department, south-western France.

Description. Body small, 2.31 mm long from labrum to abdominal apex, 0.88 mm wide across the broadest point of elytra. Body elongate, 2.6 times longer than wide. Dorsal body surface with erect elongate setae bending mid-way, deeply punctate. Body uniformly dark-coloured, appendages mahogany brown (Figs 1, 2).

Head strongly declined, narrower than prothorax, lacking temples and dorsal impressions. Mandibles robust, broad basally, abruptly curved, apparently with two apical teeth. Ventral mouth parts not well visible. Frontoclypeal region not wrinkled, frons straight. Eyes large and protuberant, coarsely setose, with interfacetal setae (Fig. 3C). Medial distance between eyes 1.7 times the eye diameter. Antennal insertions not visible from above, not covered by edge of frons. Subantennal grooves absent. Antennae reaching to the elytral base, 11-segmented, moniliform, with loose but distinct 3-segmented apical club. Basal antennomere barrel-shaped, approximately 1.25 times wider than the following segments, antennomeres 2–8 subequal in width with antennomere 8 wider than long, antennomeres 9–11 abruptly widened, 2.0 times broader than the preceding segment; antennomeres 9–10 broadest apically; antennomere 11 spindle-shaped, rounded apically, with elongate oval depression extending two third the length of the segment (Figs. 4, 5d: ad). Temples not developed.

Pronotum 0.47 mm long, weakly convex, constricted at base, broadest medially, 1.3 times wider than long. Pronotal margin smooth, without serrations. Pronotal disc without marked depressions, densely setose, with deep circular punctures. Procoxae transverse and oval, maximum width approximately equal to precoxal length of prothorax. Procoxal cavities externally open. Prosternal process narrow, about 0.2 times the maximum width of the coxa. Scutellum strongly transverse, with posterior margin straight. Mesocoxal cavities circular, narrowly separated by about 0.2 times their width. Subtriangular anterior process of the metaventricle extending midway

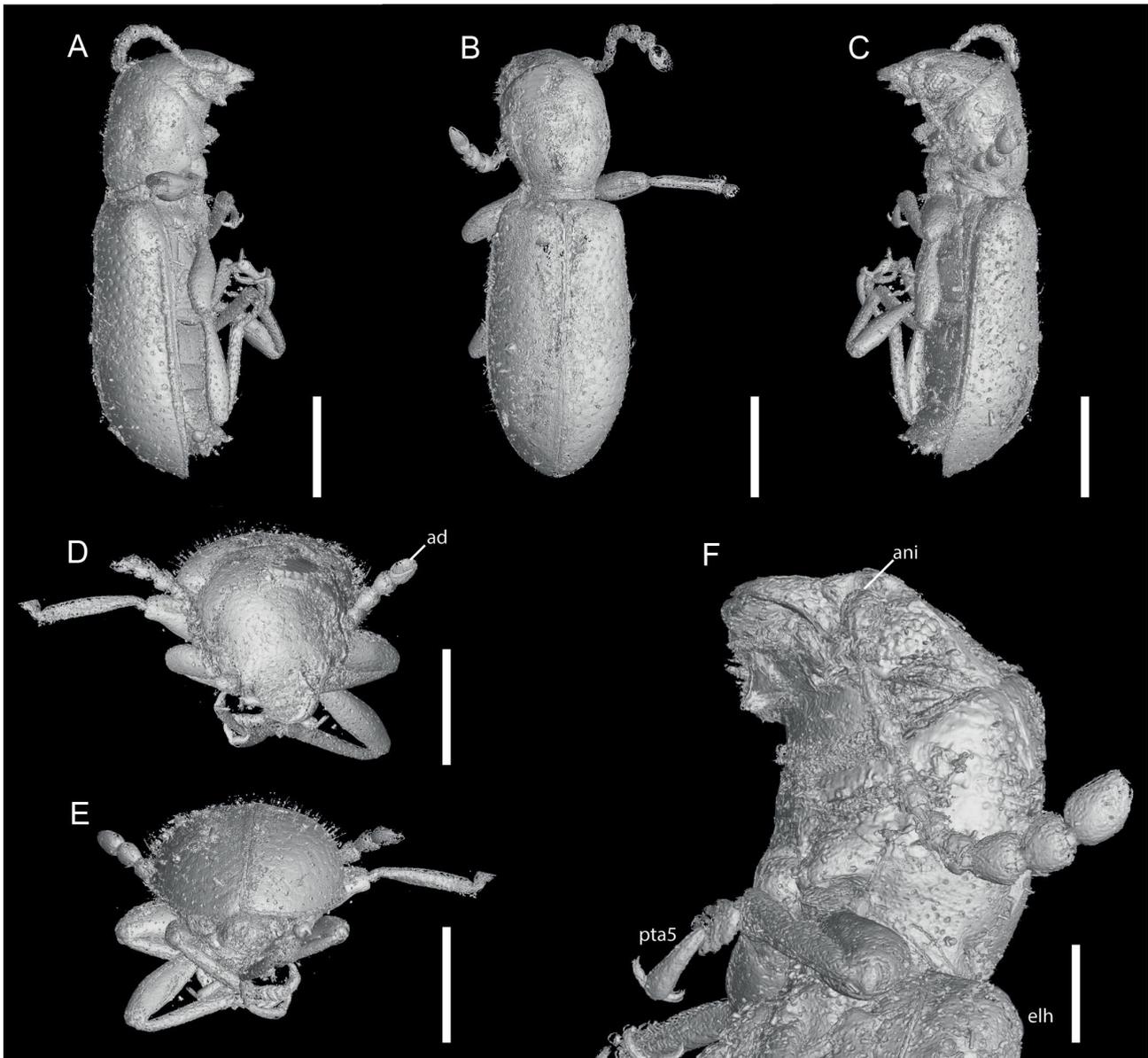


FIGURE 5. Micro-CT reconstruction of the holotype of *Mesozenodosus insularis* **gen. et sp. nov.** (holotype, IGR.FRS-7.6). **A**, Lateral view. **B**, Dorsal view. **C**, Lateral view. **D**, Anterior view. **E**, Posterior view. **F**, Detail of head and prothorax in lateral view. Abbreviations: ad, depression of apical antennomere; ani, antennal insertion; elh, elytral humerus; pta5, protarsomere 5. Scale bars = 500 μ m (**A–E**), 200 μ m (**F**).

between mesocoxae. Metaventricle flattened. Metacoxae flat, transverse, narrowly separated and extending laterally to meet the elytra.

Elytra elongate, 1.57 mm long, 1.8 times longer than collective width, at base about as broad as widest point of pronotum. Medial area at base of elytra forming roughly triangular indistinct depression. Humeral angles not protuberant, smoothly rounded. Lateral margin of elytra slightly arched such that elytra are broadest medially. Elytral surface with dense setae stemming from regularly arranged deep circular pits no closer than one times pit diameter. Epipleura complete, widest basally and narrowing posteriorly.

Legs slender and long, setose. Trochanters small and

lachrymiform. Femora with basal grooves for reception of tibiae. Tibiae apparently with apical spurs and row of strong setae or spines. Tarsi 5-5-5. Basal four protarsomeres forming compact unit, short and densely setose, each segment wider than long, protarsomere 5 longer than preceding four segments together (Fig. 3d). Mesotarsi reaching to basal third of mesotibia, mesotarsomeres 1–4 as long as mesotarsomere 5. Metatarsomeres 1–4 as long as metatarsomere 5, metatarsomere 1 shorter than metatarsomere 2, metatarsi 3 and 4 subequal in length, metatarsi not distinctly lobed beneath (Fig. 3e). Claws simple, not serrated. Empodium apparently prominent and bisetose, projecting between pretarsal claws.

Abdomen with five seemingly freely articulated

ventrites. Ventricle 1 broadest and 2.3 times longer than the following segment, ventrite 2 1.1 times longer than the following segment, ventrites 3–5 each slightly shortening apically. Abdominal setae shorter and finer than dorsal setae, arranged in smaller irregularly distributed pits.

Discussion

The new genus can be unambiguously assigned to the family Thanerocleridae based on its general habitus, prognathous head, eyes lacking an emargination, antennae with a 3-segmented club, all coxae narrowly separated, mesocoxal cavities circular, metacoxae extending laterally to meet the elytra, tibiae with two apical spurs, tarsal formula 5-5-5, protarsomeres 1–4 distinctly widened and compacted, tarsal claws simple, empodium apparently bisetose, and abdomen with five visible ventrites (Kolibáč, 1991; Kolibáč & Leschen, 2010; Opitz, 2010; Yu *et al.*, 2017). It can furthermore be placed into the subfamily Zenodosinae based on the externally open procoxal cavities and transverse procoxae (Kolibáč, 1992). *Mesozenodosus* gen. nov. is differentiated from the extant *Z. sanguineus* as well as the fossil species *Archaeozenodosus bellus* Yu & Kolibáč and *Cretozenodosus fossilis* Cai & Huang by a combination of its minute size, presence of dense and long setae, elongate body with laterally arched elytra, and non-carinate pronotal margins. The presence of an oval depression on antennomere 11 (Figs 4, 5d: ad), which may have fulfilled a sensory function, appears to be unique within Thanerocleridae and thus represents a putative apomorphy of *Mesozenodosus* gen. nov.

The fossil record of Thanerocleridae is limited to three members of the subfamily Zenodosinae known from mid-Cretaceous ambers: *Archaeozenodosus* and *Cretozenodosus* from Burmese (Kachin) amber, and *Mesozenodosus* gen. nov. from Charentese amber. Both ambers are currently dated as early Cenomanian (Smith & Ross, 2018; Peyrot *et al.*, 2019; Yu *et al.*, 2019), thus *M. insularis* gen. et sp. nov. can be considered as roughly contemporaneous with the Burmese amber fossils. The high diversity of Cretaceous Zenodosinae supports the idea that the subfamily was more diverse in the Mesozoic than today, and represents a relict lineage (Cai & Huang, 2018).

The first record of a thaneroclerid beetle in Charentese amber adds to our understanding of the distribution of the family in the Mesozoic. Burmese amber was secreted on an island in the Tethys Ocean with a near-equatorial climate and a mostly Gondwanan fauna (Cai *et al.*, 2018; Gimmel *et al.*, 2019; Westerweel *et al.*, 2019). The discovery of a Cretaceous thaneroclerid beetle in Fouras shows that the family inhabited modern-day Europe

during the generally warm mid-Cretaceous period (Huber *et al.*, 2018) and suggests that the range of the subfamily Zenodosinae was much wider in the Albian–Cenomanian than in the present. Given that the Recent *Z. sanguineus* is restricted to North America, *M. insularis* gen. et sp. nov. demonstrates that present-day distribution patterns of endemic taxa do not necessarily indicate that the taxon originated in the given region.

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