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From Priabonian to Selandian: a new species of *Eocenostenus* (Coleoptera: Staphylinidae: Steninae) from the Paleocene Menat Formation of France

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Abstract

A new species of the extinct genus *Eocenostenus* Cai, Clarke, Huang & Nel, 2014, is described from the middle Paleocene (Selandian) of Menat (France). *Eocenostenus vanja* **sp. nov.** is the second known species of the genus, the first being *Eocenostenus fossilis* Cai *et al.* described from the late Eocene (Priabonian) of Monteils, France. The discovery of *E. vanja* has implications for our understanding of the evolution of *Eocenostenus* because it pushes back the origin of the genus by several tens of millions of years (i.e., from the Priabonian to the Selandian). Additionally, it possibly sheds light on the cuticular colouration of this genus, which is putatively similar to some extant Steninae, particularly those from the tropical regions of the world. An updated checklist of fossil Steninae is provided.

Introduction

The rove beetle subfamily Steninae (Coleoptera: Staphylinidae) includes one of the most diverse animal genera on Earth, *Stenus* Latreille, 1796 which comprises 3,128 described species. The extant diversity of the subfamily also includes the genus *Dianous* Leach, 1819 with 265 described species, and an undescribed genus from Australia containing several undescribed species (Clarke & Grebennikov, 2009; Newton, 2022). Steninae are represented by 21 described fossils species known from several amber inclusions and imprint/compression fossils from the mid-Cretaceous to the Oligocene (Table 1).

The Paleocene and early Eocene represent a significant gap in rove beetle (Staphylinidae) palaeontological knowledge, with almost no fossils known from these epochs. Despite a number of beetles described from the Paleocene Menat Formation (*e.g.*, Piton, 1940; Kirejtshuk & Nel, 2008; Legalov *et al.*, 2017, 2019), merely a single rove beetle has been described: *Oxyporus impressus* Piton, 1940 (Oxyporinae), which likely does not belong to this genus or even subfamily and will be revised later (Jenkins Shaw *et al.*, in prep). Other Paleocene/early Eocene rove beetles are known from the Ølst and Fur Formations ('Mo-clay') (Denmark) but have not yet been formally described (Rust, 1999; J.J.S. personal observation). Discovery and description of Paleocene/early Eocene fossils are important for our understanding of the temporal evolution of rove beetles but also because at this time the Paleocene–Eocene Thermal Maximum (PETM), an abrupt global warming event, occurred (Zachos *et al.*, 2008).

Recently, several rove beetle fossils have been found in the Menat Formation, renewing interest in the beetle fauna of this important deposit. Whilst their preservation is not perfect,

several subfamilies are represented, including Xantholininae, Paederinae, and Steninae. The single Steninae specimen is here described as a new species of *Eocenostenus* Cai, Clarke, Huang & Nel, 2014 (Cai *et al.*, 2014), a genus that was established for *Eocenostenus fossilis* Cai, Clarke, Huang & Nel, 2014 from the late Eocene of Alès-Montels (France).

Materials and methods

The Menat Formation is a Paleocene unit, from the Puy-de-Dôme (France), deposited in a lacustrine environment. The outcrops, from the city of Menat, are renowned for their abundant and well-preserved paleofauna (*e.g.*, Nel, 2007; Wedmann *et al.*, 2018; Jouault & Nel, 2022; Nel & Jouault, 2022) and palaeoflora (*e.g.*, Laurent, 1912; Piton, 1940), and are composed of spongo-diatomites deposited in a small maar paleolake (ca. 1 km in diameter). The study of the palaeoflora and paleofauna suggested that the lake was surrounded by a forest developing in a warm and humid palaeoenvironment (Wedmann *et al.*, 2018).

It is currently accepted that the age of the Menat outcrops is ca. 59 Ma (Selandian). This age resulted from palynological studies, mammalian stratigraphy, and radiometric K/Ar analyses, (Kedves & Russel, 1982; Nel, 2007). Interestingly, the study of the macroflora suggested that the deposit may be slightly older with an age between 60–61 Ma (Wappler *et al.*, 2009).

The material described herein is housed in the Musée de Paléontologie de Menat, Menat, Puy-de-Dôme, France (MNT). The specimen was prepared with an air scribe and studied using a stereomicroscope Nikon SMZ25 in the Muséum National d'Histoire Naturelle, Paris, France (MNHN). Photographs were taken using a Canon 50D camera and a Canon MP-E 65mm f/2.5 1-5x Macro lens mounted on an automated stacking rail (StackShot). All images are digitally stacked using Helicon Focus. The figures were composed with Adobe Illustrator CC2019 and Adobe Photoshop CC2019 software. The following measurements are taken using ImageJ (Schneider *et al.*, 2012) but should be taken with caution due to the imperfect preservation of the fossil which is slightly distorted: TL = total body length; HW = head width; PW = pronotum width; PL = pronotum length; EL = elytron length; EW = elytron width; AbL = abdomen length.

Systematic palaeontology

Order Coleoptera Linnaeus, 1758

Family Staphylinidae Latreille, 1802

Subfamily Steninae Macleay, 1825

Genus *Eocenostenus* Cai *et al.*, 2014

Type species. *Eocenostenus fossilis* Cai, Clarke, Huang & Nel, 2014, by original designation.

Eocenostenus vanja Jenkins Shaw **sp. nov.**

(Figs 1A–C, 2A–D, 3)

LSIDurn:lsid:zoobank.org:act:2DE5A656-30DF-4805-8D69-69B7B7454C11

Material. Holotype MNT-staph.169 (part and counterpart), Musée de Paléontologie de Menat.

Locality and horizon. Lagerstätte of Menat (Puy-de-Dôme, France), middle Paleocene (59–61 Ma).

Comparative diagnosis. *Eocenostenus vanja* **sp. nov.** can be separated from *E. fossilis* Cai *et al.* based on its larger size (total body length 5.4 mm in *E. vanja* **sp. nov.** vs. 4.60 mm in *E. fossilis*), distinctly longer head, lack of distinct pronotal anterolateral projections, putative elytral spots more elongate situated closer to elytra suture, and tergites III to V with inverted 'U-shaped' carinae.

Table 1. Measurements of *Eocenostenus fossilis* Cai *et al.* and *E. vanja* sp. nov.

	TL	HW	HL	PW	PL	EL	EW	AbL
<i>E. fossilis</i>	4.6	0.82	0.52	1.04	0.78	1.08	0.64	2.36
<i>E. vanja</i> sp. nov.	5.4	0.89	0.66	0.93	0.78	0.97	0.58	2.93

Etymology. The new species is dedicated to the wife of the first author, Vanja Eillertsen Gomo in recognition of her continued support of his research on rove beetles and is to be treated as a noun in a genitive case.

Description. Body stout of medium-large size, length 5.4 mm (probably slightly longer, due to preservation), coarsely punctate except medial oval area on each elytron (Figs 1A–C, 3). Head triangular, narrower than pronotum, ca. 0.75 mm long from apex of mandibles to anterior margin of pronotum, ca. 0.73 mm wide (including eyes). Eyes large and long (ca. 0.45 mm long) (Figs 2A, 3), protruding laterally, reniform, occupying most of head lateral surface. Antenna poorly preserved; antennal socket exposed (*i.e.*, not concealed under ridge or protuberance) in broad concavity (Figs 2A, 3) between anterior eye margin and labrum; antennal insertion located anterior lower margin of eyes; first antennomere widening toward apex (Figs 2A, 3). Vertex with two putative longitudinal grooves virtually reaching nuchal groove, slightly diverging anteriorly (maybe due to preservation) (Figs 2A, 3; *Lg*). Labrum with anterior margin broadly convex (not lobed or dentate). Gular sutures widely separated, parallel-sided (Fig. 2B; *Gs*). Mouthparts and mandibles not preserved.

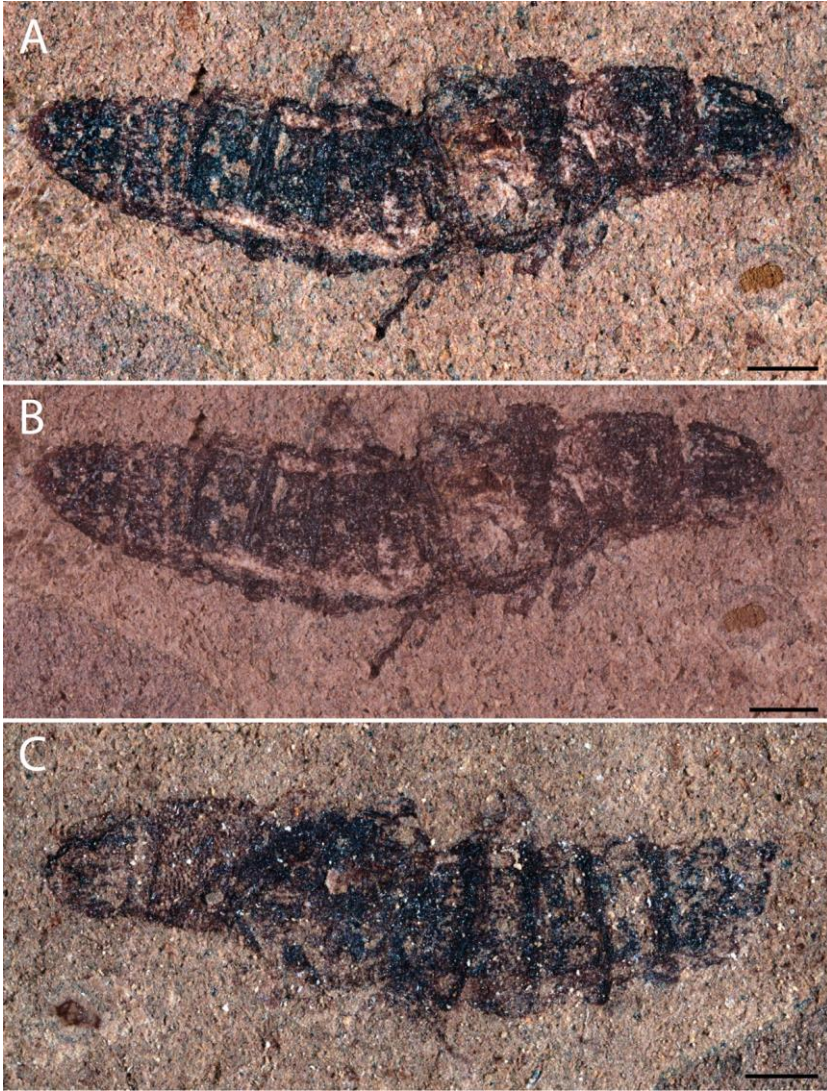


FIGURE 1. *Eocenostenus vanja* **sp. nov.**, holotype (MNT-staph.169). **A**, Dorsal view (enhanced contrasts). **B**, Dorsal view (natural lighting). **C**, Ventral view. Scale bars = 0.5 mm.

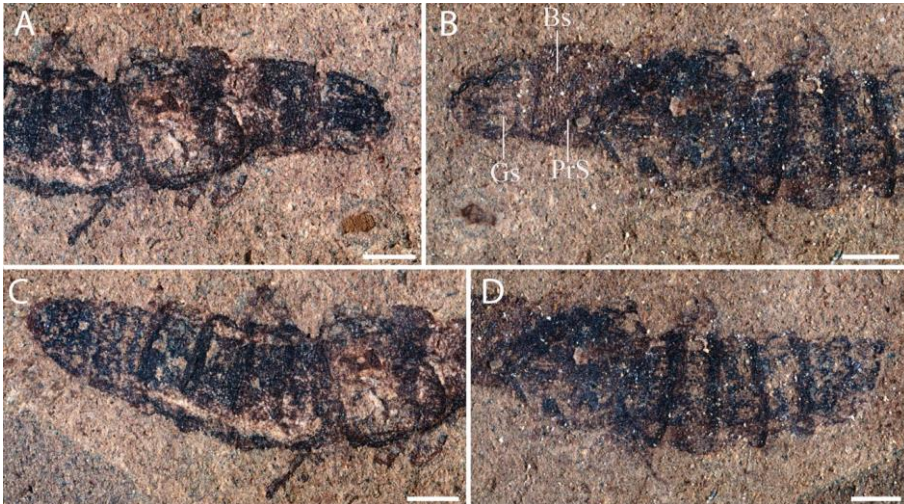
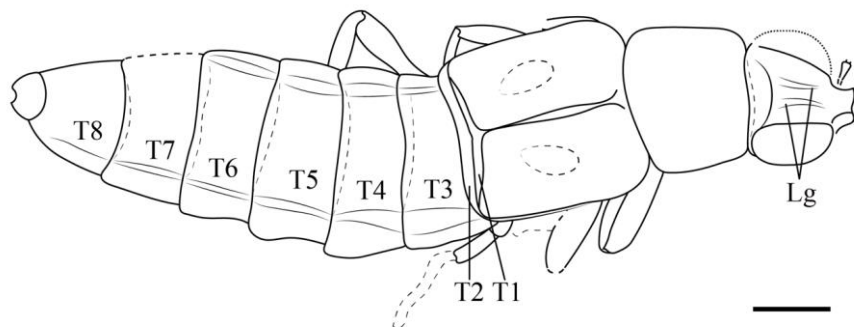


FIGURE 2. *Eocenostenus vanja* sp. nov., holotype (MNT-staph.169). **A**, Anterior part of body, dorsal view. **B**, Elytra and abdomen, dorsal view. **C**, Anterior part of body, ventral view. **D**, Abdomen, ventral view. Bs = basisternum; Gs = gular sutures; Prs = Pronotosternal suture. Scale bars = 0.5 mm.

Pronotum transverse (slightly deformed), with rounded hind angles, ca. 0.78 mm long medially, 0.93 mm wide medially, evenly, densely and coarsely punctate; without any visible impressions or sculpturing (Figs 1A, B, 2A). Antero-lateral corners rounded; lateral margins slightly curved (somewhat sinusoidal, with concavity at 1/3rd), posterolateral corners rounded, posterior margin convex. Basisternum coarsely punctate (Fig. 2B; *Bs*). Pronotosternal suture present (Fig. 2B; *Prs*); procoxal cavities closed anteriorly. Scutellum not discernible. Elytron rectangular, truncate, ca. 0.97 mm long and ca. 0.58 mm wide; width of elytra combined wider than pronotum; elytral disc with densely and coarsely punctate, possibly with one smoother oval spot (visible on left elytron) (Figs 1A, 2A, 3). Legs apparently long, poorly preserved. Femora long, widening toward mid-lengths then tapering toward apices (*i.e.*, junction with tibiae), wider than tibiae. Tibiae elongate, thin slightly widened toward apices. Tarsi poorly preserved. Abdomen relatively broad, gradually tapering to apex, with eight visible abdominal tergites (Figs 1A–C, 2C, D, 3). Tergites I and II short and fused, slightly protruding from underneath elytra (Figs 2C, 3); tergites III–VIII form main part of abdomen; genital capsule



present after tergite VIII but poorly visible/preserved. Tergites III to V each with inverted ‘U-shaped’ carina before posterior margin.

FIGURE 3. *Eocenostenus vanja* **sp. nov.**, holotype (MNT-staph.169). Line drawing. T1–8 = tergites 1 to 8. Lg = longitudinal groves. Scale bar = 0.5 mm.

Remarks. *Eocenostenus vanja* **sp. nov.** is assigned to the genus *Eocenostenus* of the subfamily Steninae based on the densely punctate dorsal and ventral surfaces of the body, the large eyes occupying almost the whole lateral surface of the head, antennal insertions exposed and narrowly separated, more anteriorly placed than in extant Steninae, and the strongly transverse pronotum (Cai *et al.* 2014). Cai *et al.* (2014) noted the pronounced anterolateral projections as diagnostic of *Eocenostenus*. They do not seem so well developed in *Eocenostenus vanja* **sp. nov.**, however, they do seem to be visible in ventral view (Fig. 2B).

Discussion

The discovery of the new species has several implications: 1) it extends the origin and occurrence of this genus back to the Paleocene, 2) provides support that *Eocenostenus* is a valid genus, whose diagnostic characters were questioned by earlier authors and suggested to be the result of preservation, and 3) preservation of the ‘cuticular colour’ suggests that this species was shiny blue-dark green, which among extant Steninae is mostly encountered in tropical species of the subfamily. An updated checklist of fossil Steninae is provided.

The earliest fossil records of Steninae dates to the Early/Late Cretaceous (Albian/Cenomanian): *Stenus inexpectatus* Schlüter, 1978 and *Stenus imputribilis* Ryvkin, 1988, from the Cretaceous of France and Russia respectively, are confidently placed in Steninae (Żyła *et al.*, 2017). Several species closely resembling *Stenus* are known from mid-Cretaceous amber from Myanmar but are thus far undescribed (J.J.S. pers. obs.). Three species of †*Festenus* Żyła *et al.*, 2017 are known from mid-Cretaceous amber from northern Myanmar (Żyła *et al.*, 2017; Cai *et al.*, 2019; Maında, 2023) and they are rather commonly encountered in amber pieces from this deposit. Mnguni *et al.* (2023) recently described *Afristenus orapensis* from the Upper Cretaceous Orapa Diamond Mine, Botswana. The poor preservation of this fossil makes it difficult to be certain of its placement in Steninae or the justification for the description of a new genus. Several inconsistencies can be observed in the photos and line drawings provided: the “antennal stem” (annotated “as” in fig. 4B of the bottom row) appears more likely to be pronotal margins where the pronotum and hypomeron of the prothorax are joined. Such a character state is absent in Steninae. In addition, the ‘harpoon-like’ mouthparts, consisting of the labium and paired paraglossae (fig. 3A, B and fig. 4B in the top row, and fig. 4A in the bottom row in Mnguni *et al.*, 2023) could equally be the result of emesis during preservation. The overall body shape and proportion are more reminiscent of the subfamily Aleocharinae. Re-study of this specimen would be highly desirable.

The majority of fossil Steninae (Table 1) are from Cenozoic deposits, and most are placed in the genus *Stenus*. Nine species are known from Baltic amber that morphologically conform to the accepted diagnosis of the genus. Five species of *Stenus* are described based on rock fossils from the Eocene (USA) and Oligocene (France and Germany). These Cenozoic rock fossils are rather poorly preserved but also resemble recent *Stenus* (Heer, 1856; Heyden & Heyden, 1866; Oustalet, 1874; Förster, 1891).

The only stenine fossils from the Cenozoic not placed in *Stenus* are *Eocenostenus fossilis* Cai, Clarke, Huang & Nel, 2014 from the late Eocene of Alès-Monteils (France) and *Eocenostenus vanja* **sp. nov.** from the middle Paleocene of Menat (France) described herein. Żyła *et al.* (2017) noted that *Eocenostenus* strongly resembles *Stenus* and only really differs in the strongly transverse prothorax with anterolateral projections, and anteriorly placed antennal

insertions. Żyła *et al.* (2017) posited that the shape of the prothorax and the position of the antenna insertions could be an artifact of preservation. The discovery here of *Eocenostenus vanja* **sp. nov.**, which overall fits the diagnosis of the genus, supports the diagnostic value of these characters, especially the transverse prothorax, and therefore supports that these characters are not simply caused by preservation. Despite this, the discovery and study of more specimens of *Eocenostenus* is desirable.

Eocenostenus vanja **sp. nov.** is not as well preserved as *Eocenostenus fossilis* in terms of structural detail. Even so, *E. vanja* is particularly noteworthy and informative due to the apparent preservation of cuticular colour. The fossil indicates that *E. vanja* was a shiny blue-dark green beetle. It is notable that among extant species of Steninae, such colouration is typically associated with warmer, tropical climates. The European fauna of Steninae is dominated by species that are entirely black (either matt or shiny) (*Stenus*), except the single species of *Dianous* (*D. coerulescens* (Gyllenhal, 1810)) which is matt dark blue.

Our discovery prompted us to provide an updated list of fossil Steninae (Table 1). Readers are referred to this list for further details and references.

Table 1. Fossil record of Steninae, adapted from Clarke & Chatzimanolis (2009)

Taxon	Subgenus	Preservation	Deposit	Time period	Reference
<i>Stenus prodromus</i> Heer	-	limestone laminites	Niveau du gypse d'Aix Formation, Aix-en- Provence, France	Late Oligocene	Heer (1856)
<i>Stenus gypsi</i> Oustalet	-	limestone laminites	Niveau du gypse d'Aix Formation, Aix-en- Provence, France	Late Oligocene	Oustalet (1874)
<i>Stenus scribai</i> Heyden & Heyden	-	Brown coal	Rott Formation, Germany	Oligocene	Heyden and Heyden (1866)
<i>Stenus ornatus</i> Förster	-	limestone laminites	Brunnstatt bei Mülhausen, France	Oligocene	Förster (1891)
<i>Stenus morsei</i> (Scudder)	-	shale	Florissant Formation, Colorado USA	late Eocene	Scudder (1900), Wickham (1913)
<i>Eocenostenus fossilis</i>	-	limestone laminites	Monteils Formation, France	late Eocene: Priabonian	Cai <i>et al.</i> (2014)
<i>Stenus priscus</i> Benick	Hemistenus (orig. Parastenus)	amber	Europe: Baltic region	Eocene	Benick (1943)
<i>Stenus abraham</i>	-	amber	Europe: Baltic region	Eocene	Puthz, 2010
<i>Stenus archetypus</i>	-	amber	Europe: Baltic region	Eocene	Puthz, 2010
<i>Stenus atavus</i>	-	amber	Europe: Baltic region	Eocene	Puthz, 2010
<i>Stenus avus</i>	-	amber	Europe: Baltic	Eocene	Puthz, 2010

			region		
<i>Stenus groehni</i>	-	amber	Europe: Baltic region	Eocene	Puthz, 2010
<i>Stenus ketura</i>	-	amber	Europe: Baltic region	Eocene	Puthz, 2010
<i>Stenus methusalem</i>	-	amber	Europe: Baltic region	Eocene	Puthz, 2010
<i>Stenus noach</i>	-	amber	Europe: Baltic region	Eocene	Puthz, 2010
<i>Eoceneostenus vanja</i> sp. nov.	-	diatomite	Menat Formation, France	middle Palaeocene	This paper
<i>Afristenus orapensis</i> Mnguni <i>et al.</i>		limestone laminites	Orapa Diamond Mine, Botswana	Turonian/Cenomanian/Campanian	Mnguni <i>et al.</i> (2023)
<i>Stenus inexpectatus</i> Schlüter	Tesnus	amber	Bezonnais, France	Cretaceous: Cenomanian/Albian	Schlüter (1978)
<i>Stenus imputribilus</i> Ryvkin	Stenus (orig. Nestus)	limestone laminites	Magadanskaia obl., Russia	Cretaceous: Cenomanian/Albian	Ryvkin (1988)
<i>Festenus gracilis</i> Żyła, Yamamoto, Wolf-Schwenninger & Solodovnikov, 2017	-	amber	Myanmar	Cretaceous: Cenomanian	Żyła <i>et al.</i> (2017)
<i>Festenus robustus</i> Żyła, Yamamoto, Wolf-Schwenninger & Solodovnikov, 2017	-	amber	Myanmar	Cretaceous: Cenomanian	Żyła <i>et al.</i> (2017)
<i>Festenus amodutt</i> Mainda, 2023	-	amber	Myanmar	Cretaceous: Cenomanian	Mainda (2023)

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Figure legends

FIGURE 1. *Eocenostenus vanja* **sp. nov.**, holotype (MNT-staph.169). **A**, Dorsal view (enhanced contrasts). **B**, Dorsal view (natural lighting). **C**, Ventral view. Scale bars = 0.5 mm.

FIGURE 2. *Eocenostenus vanja* **sp. nov.**, holotype (MNT-staph.169). **A**, Anterior part of body, dorsal view. **B**, Elytra and abdomen, dorsal view. **C**, Anterior part of body, ventral view. **D**, Abdomen, ventral view. Bs = basisternum; Gs = gular sutures; Prs = Pronotosternal suture. Scale bars = 0.5 mm.

FIGURE 3. *Eocenostenus vanja* **sp. nov.**, holotype (MNT-staph.169). Line drawing. T1–8 = tergites 1 to 8. Lg = longitudinal groves. Scale bar = 0.5 mm.