European Journal of Taxonomy 921: 136–157
https://doi.org/10.5852/ejt.2024.921.2423

ISSN 2118-9773
www.europeanjournaloftaxonomy.eu
2024 · Nel A. *et al.*

Research article

urn:lsid:zoobank.org:pub:45D0E738-77BA-49EA-8B9F-4828E919AAD8

A 'giant' Paleocene cerambycid (Coleoptera) from Menat Konservat-Lagerstätte, France

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Abstract. *Palaeosphryon menatensis* gen. et sp. nov., first unambiguous representative of the longhorn beetle subfamily Prioninae from the Paleocene of Menat (France), is described and illustrated. The new fossil is placed into the tribe Prionini, showing some similarities with some species of the extant genera *Osphryon* (Papua New Guinea) and *Titanus* (Brazil, Colombia, Guianas, Ecuador, Peru), viz. in general body shape, antennomere 3 as long as first and second together but shorter than the length of fourth plus fifth, elongate elytra, and small spines on the lateral margin of the pronotum disposed in a relatively similar way as in *Osphryon*. Nevertheless, the exact affinities of the new fossil within the Prionini remain uncertain because of the lack of a recent phylogenetic analysis in which it could be integrated. This fossil beetle is exceptional for its very large size, with a body 70 mm long. Some other large longhorn beetles have been found in the same outcrop, and are awaiting description. The positions of the previously described Cerambycidae from Menat are also discussed. This exceptional fauna of Cerambycidae is in accordance with the current palaeoenvironmental reconstruction for the Menat Konservat-Lagerstätte, as a small maar lake surrounded by a warm and humid, probably evergreen forest.

Keywords. Insecta, Prioninae, Prionini, paleodiversity, Menat fauna.

Nel A., Kirejtshuk A. & Garrouste R. 2024. A 'giant' Paleocene cerambycid (Coleoptera) from Menat Konservat-Lagerstätte, France. *European Journal of Taxonomy* 921: 136–157. https://doi.org/10.5852/ejt.2024.921.2423

Introduction

Cerambycids or longhorn beetles are Coleoptera Linnaeus, 1758 with principal predominance of adaptations to xylophagy, root- or stem-boring (Gymnosperms, Monocots, Dycotiledones). The oldest accurate identification of Cerambycidae Latreille, 1802 are lower Cretaceous compression fossils in China and inclusions in Burmese amber (Wang *et al.* 2014; Yu *et al.* 2015; etc.). The older *Cerambycinus dubius* Germar, 1839 (upper Jurassic of Solnhofen, Germany) is based on a very incomplete and poorly preserved specimen, even its attribution to a beetle is dubious, judging from the original figure of Germar (1839: pl. 22 fig. 9). Vitali (2019: 217) indicated that "Giebel (1856) described this species again as *Mesosa germari*", and that "the fossil shows unequivocal long antennae supporting its belonging to the Cerambycoidea". But Giebel (1856: 129) did not figure again this fossil. The presence of rather long antennae in an insect (or even a beetle) is not sufficient for an attribution to the Cerambycidae. Thus, the attribution of *Cerambycinius* Germar, 1839 to the Cerambycidae is uncertain.

The most impressive and largest cerambycids usually belong to the subfamily Prioninae Latreille, 1802. Despite their strong bodies, these beetles are rare in the known fossil record, mostly because this family in general seemed to become rather abundant only in the Cenozoic forests, and also because it is frequently represented in deposits by body fragments that are difficult for a reliable identification (AN pers. obs.). Rather few fossils are currently attributed to the Prioninae. The oldest known Prioninae is *Cretoprionus liutiaogouensis* described by Wang *et al.* (2014) from the lower Cretaceous Yixian Formation of China. From the same formation *Sinopraecipuus* Yu, Ślipiǹski, Reid, Shih, Pang, Hong & Ren, 2015 with unclear subfamily attribution, is also known (Yu *et al.* 2015). Lin & Bai (2017) described the cerambycid *Qitianniu zhihaoi* from the mid-Cretaceous Burmese amber assigned by Vitali (2019) to the prionine tribe Meroscelisini Thomson, 1860. There are some other prionine species recorded from Cenozoic fossils whose systematic position in most cases needs to be revised. Piton (1940) described two alleged prionine *Megopis lineolatus* and *Prionus sinuatus* from the Paleocene of Menat. Haupt (1950) described *Xyleoconites proavus* from the Eocene of Geiseltal (Germany) on the basis of fragments of abdomen, leg and elytra. Vitali (2008) attributed the latter to the prionine tribe Macrotomini Thomson, 1860. Wickham (1914: 263, pl. 8 fig. 19) described the prionine *Scaptolenopsis wilmattae* from the lower Oligocene of Florissant (USA), but Linsley (1942) transferred it into the Dascillidae Guérin-Méneville, 1843. Germar (1837: fig. 19) described *Prionus umbrinus* from the Oligocene of Rott (Germany). From the lower Miocene of Oeningen (Germany), Cockerell (1922) described the prionine *Ergates atavellus* and attributed the two species *Prionus polyphemus* Heer, 1865 and *Prionus spectabilis* Heer, 1865 to the same genus *Ergates* Audinet-Serville, 1832 (Heer 1865: 402, figs 292–293). Heer apparently never proposed a formal description of these two species. Riou (1999) described *Prionus rhodanensis* from the upper Miocene maar paleolake of Montagne d'Andance (Ardèche, France). Schmidt (1967) cited a Prioninae, close to *Ergates* or *Megopis* Audinet-Serville, 1832, from the Pliocene of Willershausen (Germany).

Here is described a new very large Cerambycidae attributable to the Prioninae, from the outcrop of Menat. The Cerambycidae from the Paleocene outcrop of Menat are already well diversified, as Piton & Théobald (1937) and Piton (1940) listed eight species from Menat, viz. the two Prioninae listed above plus the alleged lamiine *Palaeoncoderes eocenicus* Piton & Théobald, 1937, *Palaeoncoderes piacentini* Piton, 1940, *Prolamioides bituminosus* Piton & Théobald, 1937, *Prolamioides brunneus* Piton, 1940 and *Monohammus orientalis* Piton, 1940. The alleged Cerambycinae *Chlorida magnifica* Piton, 1940 is here transferred to Chrysomelidae Latreille, 1802. The putative affinities of these taxa are also discussed.

Material and methods

Sampling of specimen

The type fossil was found during field research by Sophie Hervet. It was prepared using a sharp spine to remove the small fragments of rocks that were partly covering the margin of body. It is stored at the Musée de Paléontologie, Menat, Puy-de-Dôme, France.

Imaging

Photographs with normal light were taken using a Nikon SMZ 25 microscope with a Nikon Z7II camera. UV light photographs were taken with Nikon D850 FX camera with a 60 mm/2.8 Micro-Nikkor. UV light (365 nm) has been used to find differential chemical/morphological composition with different visible fluorescence contrast with sedimentary matrix and revealed putative ornamentations or patterns on the body surface. High definition images (45 MP sensor) permitted cropping into images. UVA (365 nm rather than 390 nm) used for fossil insect studies is a new useful and promising technique for enhancing observation with a simple, portable and economic device (Nel *et al.* 2023). It is a useful way to select specimens of interest for chemical analysis and imaging by more sophisticated techniques (e.g., X-ray synchrotron fluorescence, Georgiou *et al.* 2019) or looking for special anatomical/morphological adaptation of the cuticles.

Geological setting

The middle Paleocene site of Menat, near the south of the village of Menat (46°06′ N; 2°54′ E, Menat Basin, Puy-de-Dôme, France) is a volcanic maar corresponding to a rather small paleolake (ca 1 km in diameter), filled with spongo-diatomites. This paleolake contains numerous remains of diverse aquatic and terrestrial flora and fauna (Piton 1940; Nel 1989, 2007, 2022; Nel & Roy 1996; Nel & Auvray 2006; Nel & Jouault 2022; etc.). The composition of faunal and floral remains suggests that this lake was surrounded by a forest and that the paleoenvironment was warm and humid (Wedmann *et al.* 2018). Following the pollen, mammalian stratigraphy, and radiometric K/Ar analyses, its age was estimated as 59 Ma (Kedves & Russel 1982; Nel 2007); vs an age within 60–61 Ma, based on macroflora (Wappler *et al.* 2009). Some previous reviews of coleopterous fossils from Menat were published, in addition to publications of Piton (1940), in some recent papers (Kirejtshuk *et al.* 2010, 2016, 2019; Legalov *et al.* 2017, 2019; Nabozhenko & Kirejtshuk 2017; Kirejtshuk & Nel 2018; etc.).

We follow the catalogue of extant prionine genera and species as proposed in the internet site https://www.prioninae.eu/fr/. The comparisons between the new fossil and the extant taxa have been done after this site and in some cases after the direct examination of the concerned publications.

Results

Class Insecta Linnaeus, 1758
Order Coleoptera Linnaeus, 1758
Family Cerambycidae Latreille, 1802
Subfamily Prioninae Latreille, 1802
Tribu Prionini Latreille, 1804

Genus ***Palaeosphryon*** gen. nov.
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Type species

Palaeosphryon menatensis gen. et sp. nov.

Diagnosis

Body very large, 70 mm long; antennomere 3 as long as first and second together but shorter than length of fourth plus fifth; elytra elongate, gently narrowing posteriorly, at apices rounded and with two very small processes; eyes very shallowly emarginate anteriorly; no apical spine on protibia; pronotum subtrapezoid, with subrectilinear anterior margin, three rather short spines with blunt apex at each side, without spine at antero-lateral shoulder.

Etymology

The name of new genus is created from the Greek ‘palaiós’ (παλαιός) ‘old, ancient’ and the genus name *Osphryon*. Masculine gender.

Palaeosphryon menatensis sp. nov.

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Figs 1–3

Diagnosis

As for the genus, by monotypy.

Etymology

Named after the type locality Menat.

Material examined

Holotype

FRANCE • compression fossil of a body with left antenna, right fore and hind legs, basal part of right antenna and left mid leg, elytra preserved; Menat, Puy-de-Dôme; middle Palaeocene, Menat Basin; BDL 1828 Musée de Paléontologie, Menat, Puy-de-Dôme, France.

Notes

The holotype is represented by the print of the specimen with many deformations. Its head seems longer than what it should be by comparison with extant relatives – this means that this head in the print is somewhat turned by its anterior part while its anterior part was probably oriented almost downwards, thus appearing not so long from above. The pronotum was probably rather convex. During fossilization it was compressed and became flat and much wider than in a living specimen. The same deformation happened with the elytra that in the print seem much wider than in the present-day relatives.

Description

Appearance. Body 70.0 mm long (measured from anterior edge of head to elytral apices), 30.0 mm wide (measured across humeri). Head 12.0 mm long, 11.0 mm wide. Dorsal integument apparently dark brown to blackish (left elytron noticeably lighter), with comparatively small and rather dense punctures on upper surface of head and pronotum and interspaces between them apparently alutaceous, about diameter of punctures on head and somewhat sparser on pronotum; elytra with distinctly coarser punctures separated by smaller than puncture diameter and alutaceous on interspaces and punctures becoming finer and sparser toward apex. Very fine and long hairs traced on integument of base of head, pronotum, and elytra (visible under UV light).

Head. Subtriangular, widest at base and declined downwards (can be traced in long frons on print); mandibles ca 2.0 mm long, moderately strong and short, but without visible inner tooth, with pubescence at base visible under UV light, separated from frons by line (probably suture); eyes emarginate, not surrounding antennal socket; antennae ca 38.0 mm, black, with 11 antennomeres, last antennomere incompletely preserved, but reaching two thirds of body; scape widened apically, subtriangular, slightly longer than antennomere 4; antennomere 2 (pedicel) very short and third almost double as long as antennomere 4; following antennomeres starting from antennomere 4 gradually decreasing in length; part of head behind compound eyes short, ca 2.0 mm long.

Pronotum. About 9.0 mm long, 18.0 mm wide, narrower than elytra, with anterior margin shallowly emarginate, setose (visible under UV light), no spine on antero-lateral shoulder; three minute spines on

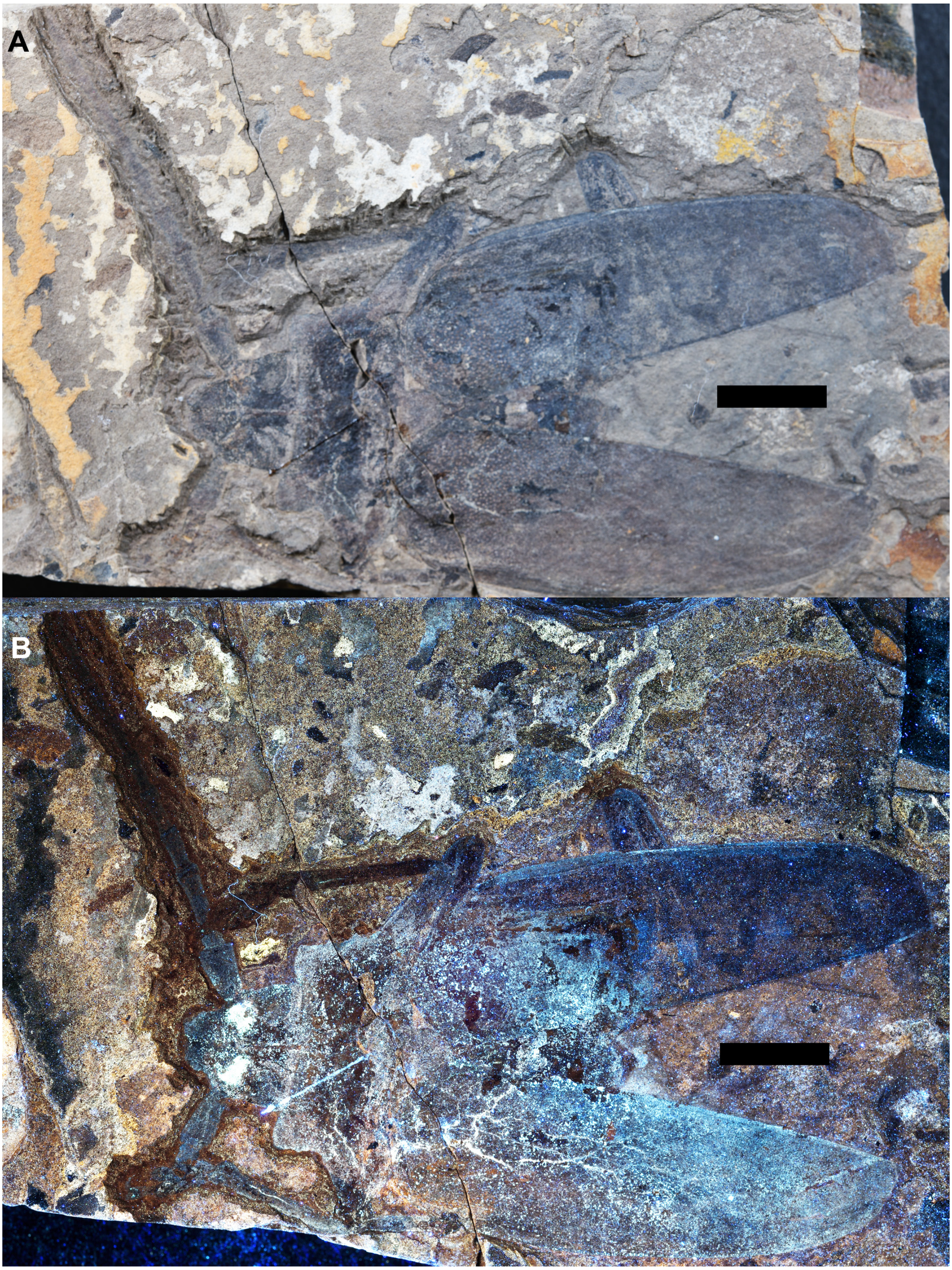

Fig. 1. *Palaeosphryon menatensis* gen. et sp. nov., holotype (BDL 1828). Photographs of general habitus. **A**. Under normal light. **B**. Under UV light. Scale bars = 10 mm.

each side of pronotum. Scutellum large triangular, about twice as wide as long and widely rounded at apex, 5.0 mm long, 7.0 mm wide; thorax 27.0 mm long (ventral side partly visible under elytra).

Elytra. 48.0 mm long, 15.0 mm wide, widest at anterior third, broadly arcuate at sides, slightly narrowing to subtruncate (widely rounded) apex with very small processes (clear under binocular but

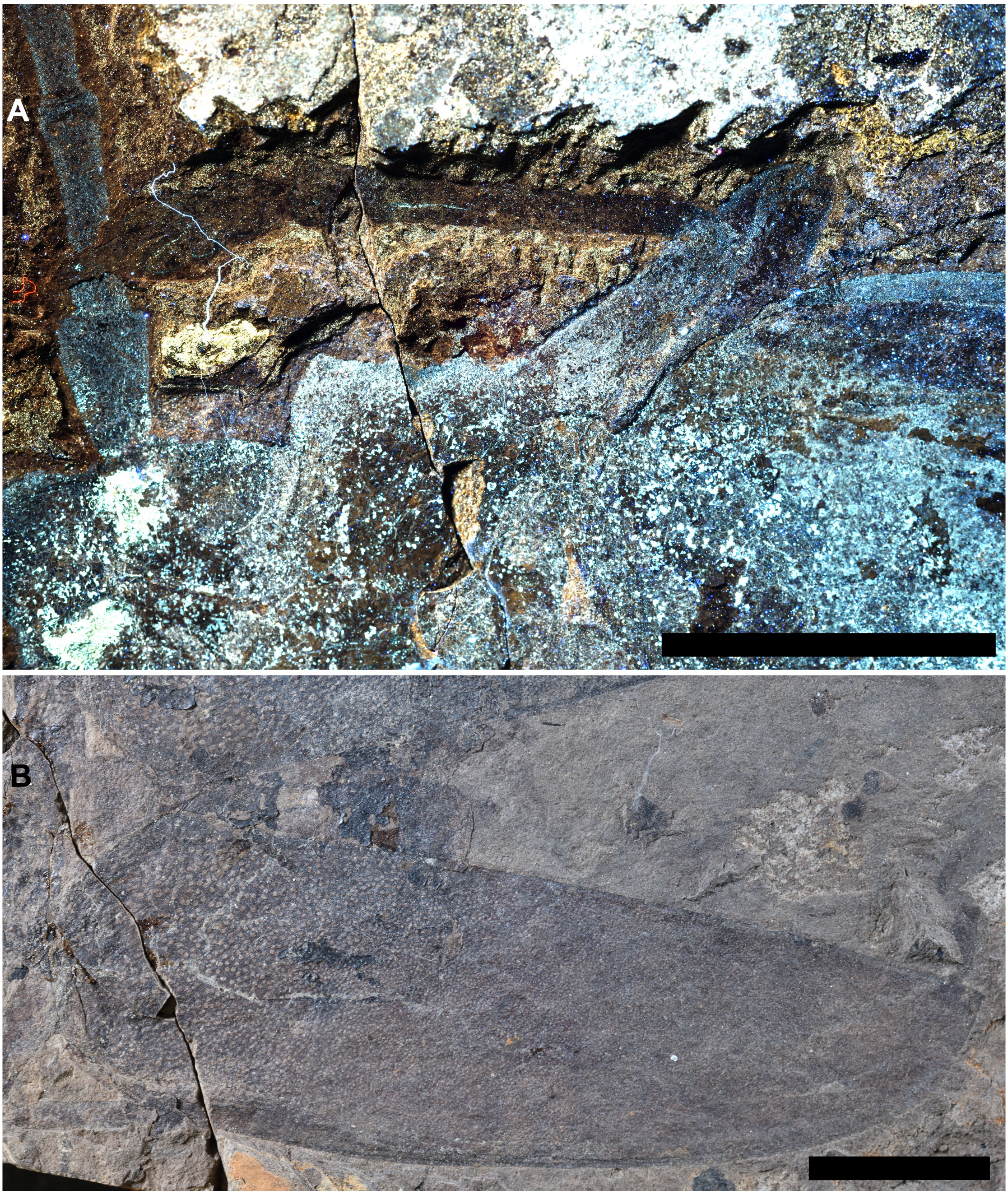

Fig. 2. *Palaeosphryon menatensis* gen. et sp. nov., holotype (BDL 1828). Photographs. **A**. Head, base of antenna, fore leg and pronotum, under UV light. **B**. Elytra, under normal light. Scale bars = 10 mm.

scarcely visible in many photographs); elytral surface with unclear and irregular longitudinal furrows; apex rounded with smooth sutural spine and with small apico-lateral projection.

Procoxa. Transverse, profemur 14.0 mm long, 2.5 mm wide, protibia without mesal sinus, 14.0 mm long, 1.5 mm wide, without apical spine; protarsus 6.0 mm long, pseudo-tetramerous with tarsomere 3 dilated and covering tarsomere 4. Mesofemur 18.0 mm long. Metafemur 16.0 mm long, metatibia 18.0 mm long.

Abdomen. Not preserved.

Discussion

This fossil cerambycid certainly is a member of the subfamily Prioninae because of the following character (Monné *et al.* 2017): pronotum carinate at sides and with four short and blunt processes (dentate) at each side; plus these: tarsi pseudo-tetramerous with tarsomere 3 dilated and covering tarsomere 4; antennae surpassing base of pronotum; head subtriangular; protibia without mesal sinus; procoxa transverse; no external groove or notch on mesotibia. Lameere (1919: 4) characterized the Prioninae as follows: "Languette cornée ; dernier article des palpes tronqué à son extrémité ; espace situé entre l'insertion des antennes et celle des mandibules court ; rebord latéral du prothorax présent au moins en avant ou en arrière ; hanches antérieures très fortement transversales ; cavités cotyloïdes intermédiaires largement ouvertes en dehors ; mésonotum sans appareil de stridulation ; ailes inférieures à nervure cubitale antérieure simple", confirming the carinate pronotum and a transverse procoxa as main characters of the subfamily, present in the new fossil (see also Gahan 1906 and Linsley 1962).

Lameere (1901, and several papers between 1902 and 1919) proposed a classification of the Prioninae, Linsley (1961) also proposed some hypotheses on the phylogeny of the Cerambycidae. Nevertheless, there is no recent phylogenetic analysis in the modern sense of this subfamily, except for the regional one proposed by Jin *et al.* (2020) for the Australian fauna, in which these authors showed that at least some of the tribes are probably non monophyletic. Gahan (1906), Lameere (1919), and Linsley (1962)

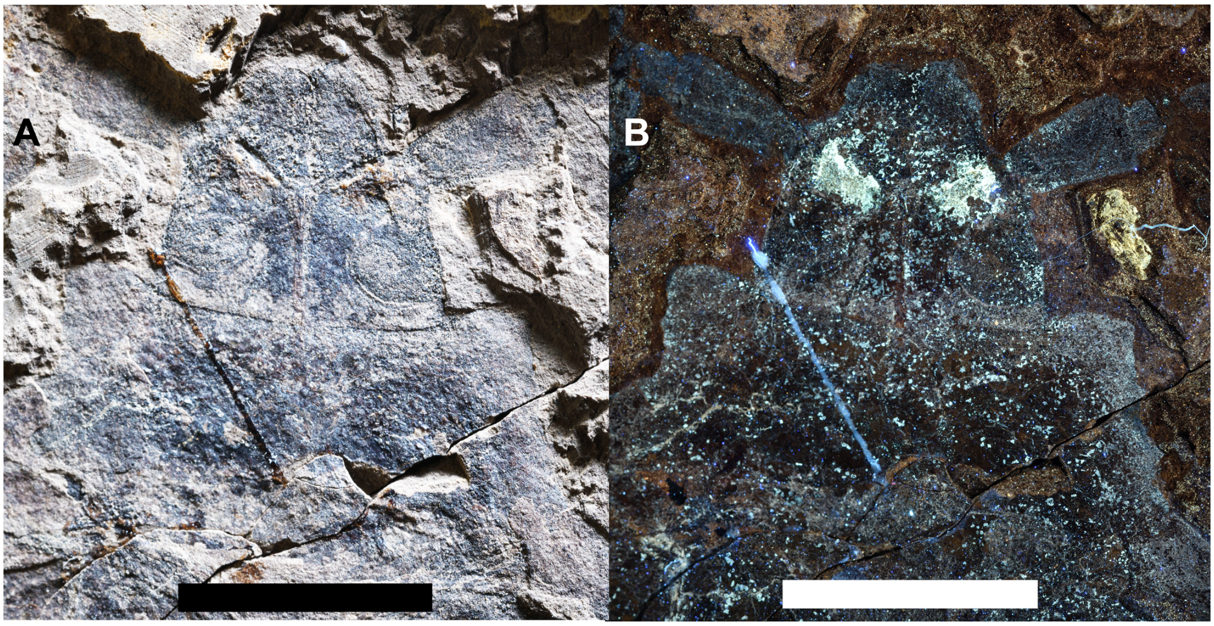

Fig. 3. *Palaeosphryon menatensis* gen. et sp. nov., holotype (BDL 1828). Photographs of head and pronotum. **A**. Under normal light. **B**. Under UV light. Scale bars = 10 mm.

proposed keys to the tribes available at that time, but there is no recent key to the tribes at the world level. Also, some recent molecular 'phylogenetic' analyses of the Cerambycidae (Liu *et al.* 2018; Nie *et al.* 2021; Ashman *et al.* 2022; etc.) gave contradictory results. Thus, the phylogeny of the Cerambycidae clearly needs further investigations, although some promising ideas on probable phylogenetic relations have been already proposed (Napp 1994; Haddad *et al.* 2018, 2023; etc.).

One important character proposed by Gahan (1906: 3–4) to separate two groups of prionine tribes is the "episterna of metathorax with posteriorly converging sides, narrowly truncate or obtusely pointed at apex" vs "episterna of metathorax parallel-sided for the greater part of their length or nearly so; broadly truncate behind". Unfortunately, this structure is not discernable in the new fossil.

Nevertheless, the pronotum with only three spines on its sides excludes affinities with the Eurypodini Gahan, 1906 and Macrotomini (sensu Gahan 1906), or the Ergatini LeConte, 1873 and Macrotomini (sensu Linsley 1962). Also, the eyes scarcely emerginate exclude affinities with the Macrotomini and Mallodontini Thomson, 1860 that have a straight anterior margin of the eye (Gilmour 1960; Quentin & Villiers 1981; Bouyer & Susini 2009; Santos-Silva & Galileo 2010; Santos-Silva *et al.* 2010; etc.). The eye not surrounding the antennal socket and the tibiae not dentate externally exclude affinities with the Anacolini Lameere, 1802 (Lameere 1919; Galileo 1987b; Drumont *et al.* 2000).

The large triangular scutellum excludes affinities with the Solenopterini LeConte, 1873 (Galileo & Martins 1993a). The solenopterins also have different shapes of the pronotal margin, either smooth, denticulate, or with very strong spines (Galileo & Martins 1993a, 1993b, 1993c, 1994a). The elytra not strongly truncate at the apex and the anterior part of the lateral margin of the pronotum not rounded but straight exclude affinities with the Calocomini Galileo & Martins, 1993 (Galileo & Martins 1994b). The Ergatini, Remphanini Lacordaire, 1869, and *Paulhutchinsonia* Jin, de Keyzer & Ślipiński, 2020 are excluded because the pronotum of the new fossil is tridentate at the sides, instead of being entire, crenulate, or multispinose (Gilmour 1956; Linsley 1962; Quentin & Villiers 1977; Jin *et al.* 2020; etc.). The Aegosomatini Thomson, 1860 (including Megopini Lameere, 1912), Callipogonini Thomson, 1860, Eurypodini, and Mallaspini Thomson, 1860 are excluded because they have an elongate part of the head posteriorly from the compound eyes and an antennomere 3 much longer than first, unlike in the new fossil (Galileo & Martins 1992; Komiya 2002, 2003a, 2003b, 2004a, 2004b, 2005; Drumont 2006; Vives *et al.* 2008; Komiya & Drumont 2001, 2007, 2009, 2010, 2011, 2012, 2013; Santos-Silva 2004a, 2004b; Perger & Santos-Silva 2010; Audureau 2011; Drumont & Do 2013; Delahaye & Santos-Silva 2016; Haller & Delahaye 2018; An 2019; Zubov & Titarenko 2019; Jin *et al.* 2020; etc.; internet site Prioninae of the World at https://www.prioninae.eu/fr/). The eyes coarsely faceted also exclude the Mallaspini (Linsley 1962).

The new fossil has no elevated ridges on the elytra unlike many Aegosomatini Thomson, 1860. The Hopliderini Quentin & Villiers, 1975 have typically five spines on the lateral sides of the pronotum and an antennomere 3 distinctly longer than the scape, unlike the new fossil (Quentin & Villiers 1972; Bouyer 2012; Bjørnstad *et al.* 2016).

The Cantharocnemini Bouchard *et al.*, 2011 have the antenna only slightly longer than the head plus pronotum, with a short antennomere 3 (McKeown 1938; Drumont 2004). The Tereticini Lameere, 1912 and the Erichsoniini Thomson, 1861 also have the antenna only slightly longer than the head plus pronotum (Quentin & Villiers 1975). The Closterini Quentin & Villiers, 1974 share with the new fossil a part of the head posterior of the compound eyes shortened and an antennomere 3 only slightly longer than first one, but have ridges on the elytra unlike the new fossil (Quentin & Villiers 1974; Fragoso & Monné 1982). The Macrodontiini Thompson, 1860 have longer and larger mandibles and a different body shape with a stronger spine on the thorax (Peña & Vidal 1976; Bleuzen 1990). The Meroscelisini

Thompson, 1860 have the antennomere 3 distinctly longer than the antennomere 1 and very different patterns of the spines on the thorax, also their pronotum is generally strongly pubescent (Galileo 1987a).

The antennomere 3 longer than all the others, but not very much longer than antennomere 4, is also a characteristic feature of the 'group Prionini' sensu Lameere (1919) (see also Komiya & de Keyzer 2011). Lameere (1919) subdivided the 'group Prionini' into four subgroups, the 'Nothophysies Lameere, 1912', the 'Acanthophori Lacordaire, 1869', the 'Derobrachi Lameere, 1913', and the 'Prioni Lameere, 1912'. The 'Acanthophori' are currently considered as Acanthophorini Thomson, 1864. The Prionini sensu stricto comprise the 'Derobrachi' and the 'Prioni'. After Lameere (1919), the 'Nothophysies' are currently considered Cacoscelini Thomson, 1860 and comprise the two genera *Nothophysis* Audinet-Serville, 1832 and *Cacosceles* Newman, 1838. They have the lateral margin of the pronotum without marked teeth, unlike the new fossil.

The lateral border of the pronotum with three spines shows affinities with the Acanthophorini or Prionini. The scape of the antenna much longer than broad supports an attribution to the Prionini while the Acanthophorini have the scape nearly as long as wide (Lameere 1919; Santos Ferreira 1980; Delahaye *et al.* 2006).

The 'Derobrachi' are characterized by longitudinal striations on the antenna, at least in the apical antennomeres, while the 'Prioni' have no such striations. No striation is visible on the antenna of the new fossil, but these could not be preserved.

In addition to the absence of striation of the antenna, Lameere (1912: 258–259) proposed to separate the two genera *Dorysthenes* Vigors, 1826 and *Prionus* Geoffroy, 1762 from the group of genera that he (Lameere 1919) put in his 'Derobrachi' on the basis of the lateral teeth of the pronotum weakly developed, generally short and triangular. But at least some 'Derobrachi' (e.g., *Osphryon elina* Voitsekhovskii, 2020) have rather short triangular teeth on the pronotum (Voitsekhovskii 2020: fig. 3). Thus, these differences seem to be somewhat uncertain.

Thus, we need to compare the new fossil with all the genera in the Prionini.

Also within the Prionini, the genera *Apterocaulus* Fairmaire 1864, *Callistoprionus* Tippmann, 1953, *Microarthron* Pic, 1900, *Miniprionus* Danilevsky, 2000, *Prionacalus* White, 1845, *Prionoblemma* Jakovlev, 1887, *Emphiesmenus* Lansberge, 1884, and *Psalidocoptus* White, 1856 are excluded because of their very different shapes of the pronotum and body. *Braderochus* Buquet, 1852 has, in contrast to the new species, a much longer antennomere 3, very large eyes, close to the bases of the antennae, a narrow anterior margin of the pronotum and more arcuate elytral sides (Santos-Silva & Martins 2005a, 2005b). Species of the genus *Derobrachus* Audinet-Serville, 1832 have strong spines at an antero-lateral angle of the pronotum and usually much longer elytra (Santos-Silva 2007), unlike the new fossil species. The antenna not serrate in the new fossil excludes affinities with the genera *Prionus* (some species in this genus have a very weak serration, but a very long third antennomere, e.g., *Prionus mexicanus* Bates, 1884), *Bifidoprionus* Komiya & Keyzer, 2011, *Dorysthenes*, *Macroprionus* Semenov, 1900, *Mesoprionus* Jakovlev, 1887, and *Trichoprionus* Fragoso & Monné, 1982 (Fragoso & Monné 1982; Komiya & de Keyzer 2011). *Prionocornis* Pic, 1928 differs from *Palaeosphryon* gen. nov. in the presence of three strong ridges on the elytra (Komiya 2001).

The males of *Lobarthron* Semenov, 1900, *Polylobarthron* Semenov, 1900, *Polyarthron* Audinet-Serville, 1832, *Mesoprionus* Jakovlev, 1887, *Prionomma* White, 1853, *Priotyrannus* Thomson, 1857, *Monocladum* Pic, 1898, *Psilotarsus* Motschulsky, 1860, *Unilaprionus* Lin & Danilevsky, 2017, *Pseudoprionus* Pic, 1898 have serrate to pectinate antennae, while the females have rather short antennae with shorter antennomeres than in the new fossil genus (Lorenc & Drumont 2013; Lin & Danilevsky

2017; Jin *et al.* 2020). The male of *Pogonarthron* Semenov, 1900 a so have pectinate antennae while the females have serrate ones (Danilevsky 2004; Danilevsky & Komiya 2014).

Opisognathus Thomson, 1861 has the pronotum narrowing posteriorly, the elytra only five times as long as the pronotum vs seven times and thicker antennomeres in contrast to those in *Palaeosphryon* gen. nov. *Psalidosphryon* Komyia, 2001 has also much stronger spines on the pronotum and usually longer and thinner antennomeres (Komiya 2001; Delahaye *et al.* 2021). The species of the genus *Psalidognathus* Gray, 1832 have stronger spines on the pronotum and markedly longer and stronger mandibles than in the new fossil genus (Santos-Silva & Komiya 2012).

Orthosoma Audinet-Serville, 1832 shares with *Palaeosphryon* gen. nov. the presence of three small spines on the lateral margin and narrowing posteriorly of the pronotum, antennomere 3 as long as the first plus second but shorter than the fourth plus fifth, and very long elytra (Linsley 1940). *Orthosoma* differs from the new fossil genus also in the elytra parallel-sided from base to apex (see Linsley 1962: fig. 11). Besides, the latter is quite smaller than in the new fossil genus (body length 24 to 48 mm vs 70 mm in the new fossil).

The Neotropical genus *Titanus* Audinet-Serville, 1832 shares with *Palaeosphryon* gen. nov. a very large body size (body 70 mm long in the new fossil genus vs 140 mm in *Titanus*), the long median keel on the head, relatively short spines on the lateral side of the pronotum, antennomere 3 as long as the first plus second, very robust legs and antennae, antennae not serrate. However, the new fossil genus differs from *Titanus* in the strong tooth on the left mandible (see https://www.galerie-insecte.org/galerie/ref-117120.htm), the pronotum not rather narrowing posteriorly and considerably narrower tarsomeres 1–3. Besides, the longitudinal folds on the elytra are very distinct in *Titanus*, while in *Palaeosphryon*, the elytra have scarcely expressed longitudinal furrows.

The genus *Osphryon* Pascoe, 1869 (in Derobrachi sensu Lameere, Papua New Guinea) shares with the new fossil genus some similarity in general body shape, sometimes antennomere 3 as long as the first plus second but shorter than the fourth plus fifth, a long elytra, and, in some species (e.g., *O. delahayei* Voitsekhovskii, 2020), small spines on the margin of the pronotum disposed in a relatively similar way (Voitsekhovskii 2020: fig. 3). The new fossil also has two very small processes along the elytral apex. The pronotum of *Palaeosphryon* gen. nov. is, in contrast to the species of *Osphryon*, more or less quadrangular, and its elytra are usually markedly longer. Also, the antenna of the new fossil species reaches to two thirds of the body, as frequently is the case in the some extant species of *Osphryon*, although most modern congeners have antennomere 3 much longer than in the new fossil species (Komiya 2020).

Remarks on the other Cerambycidae from Menat

Palaeoncoderes eocenicus is based on a body compression stored at the Muséum national d'histoire naturelle (MNHN, Paris) MNHN (MNHN-F-R06992) (Fig. 4A); *Palaeoncoderes piacentini* is based on a body compression stored at the MNHN (MNHN-F-R06683) (Fig. 4B). Both belong to the extinct genus *Palaeoncoderes* Piton & Théobald, 1937, supposedly close to the extant genus '*Oncoderes*' (= *Oncideres* Lacordaire, 1830). The Onciderini have a strongly pronounced basal shoulder of the elytra, unlike in both *P. eocenicus* and *P. piacentini* (Dillon & Dillon 1945, 1946). Thus, their attribution to this tribe is quite uncertain.

Monohammus orientalis is based on a body compression stored at the MNHN (MNHN-F-R07237) (Fig. 5A). This fossil is probably a Cerambycidae, but it is not possible to attribute it to a precise subfamily because of the poor preservation of the head, and the absence of the legs and antennae.

Chlorida magnifica is based on a body compression stored at the MNHN (MNHN.F.R06997) (Fig. 5B). it does not resemble the extant genus *Chlorida* Audinet-Serville, 1834 that has small spines on the pronotum and on the apex of the elytra, and a posterior constriction of the pronotum, unlike this fossil (Piton 1940: fig. 75; Monné & Napp 2005: fig. 165). Indeed, it more closely resembles a Chrysomelidae than a Cerambycidae in the pattern of the body and elytral coloration. Its second antennomere is as long as the third, which is a character of Chrysomelidae rather than Cerambycidae.

Prolamioides bituminosus Piton & Théobald, 1937 is based on a body compression stored at the MNHN (MNHN.F.R07016, Fig. 6A). *Prolamioides brunneus* Piton, 1940 is based on a body compression stored at the MNHN (MNHN.F.R07031, Fig. 6B). Piton (1940) put both of them in the Lamiinae Latreille,

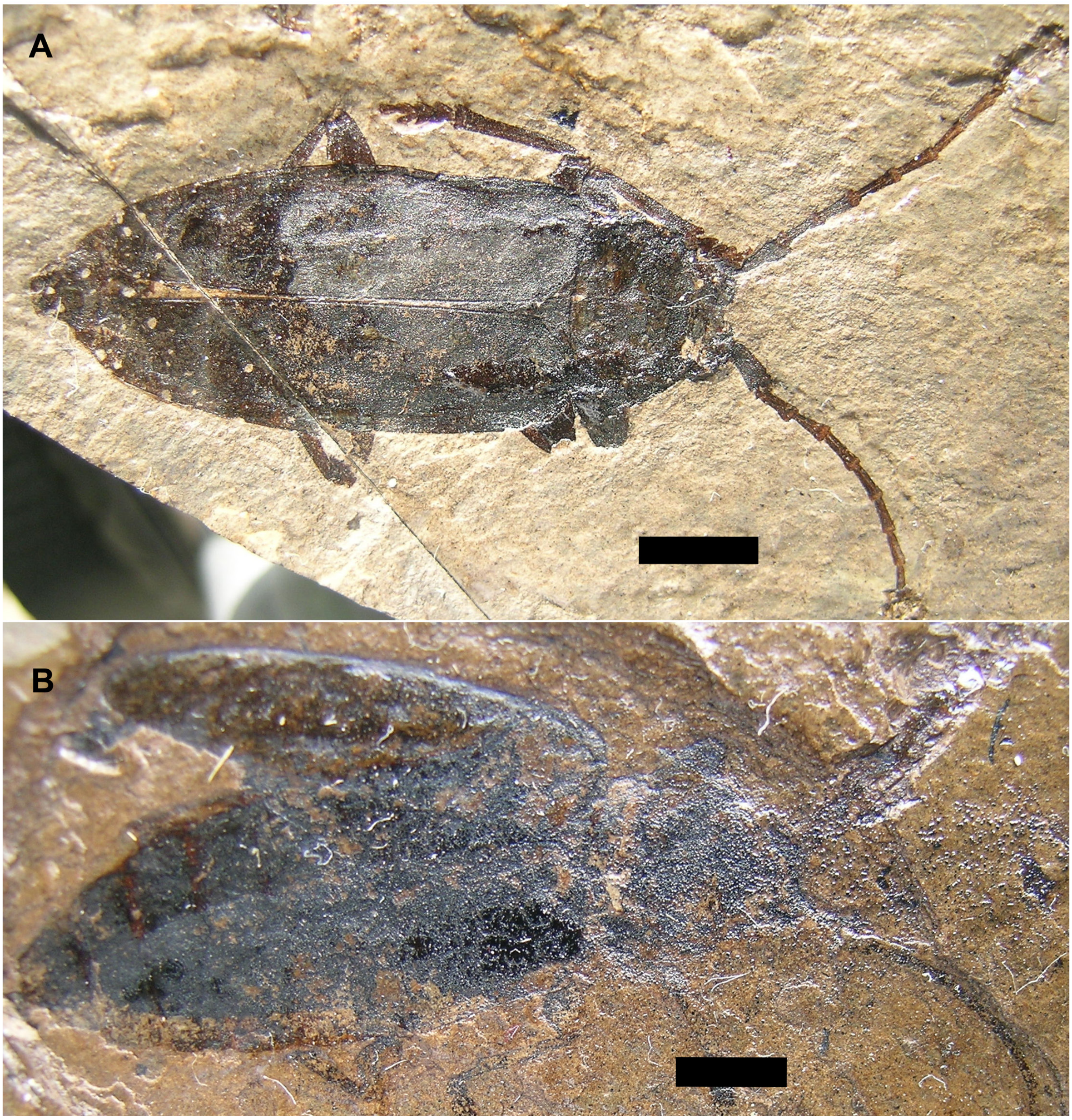

Fig. 4. A. *Palaeoncoderes eocenicus* Piton & Théobald, 1937, holotype (MNHN-F-R06992). **B**. *Palaeoncoderes piacentini* Piton, 1940, holotype (MNHN-F-R06683). Scale bars = 5 mm.

1825, supposedly with tropical Indo-Malayan affinities. Their preservation does not allow to propose a more precise affinity than possibly with the Lamiinae.

Megopis lineolatus is based on a single elytron with 15 longitudinal striae (Piton 1940: fig. 76). The author indicated that it has strong affinities with the extant species *Megopis sinica*, but the latter has very few longitudinal ridges and no striae on the elytra. Thus, *Megopis lineolatus* can only be considered as a Coleoptera of uncertain family as there is not argument for a placement in the Cerambycidae, although Vitali (2008: 4) indicated, without argument, it could be 'possibly' a Macrotomini. Its type seems to be lost.

Prionus sinuatus is based on two overlapping elytra stored at the MNHN (MNHN-F-R07045) (Fig. 7). Its attribution to the Cerambycidae is not evident. It could belong to this family, but possibly to the Chrysomelidae, for instance.

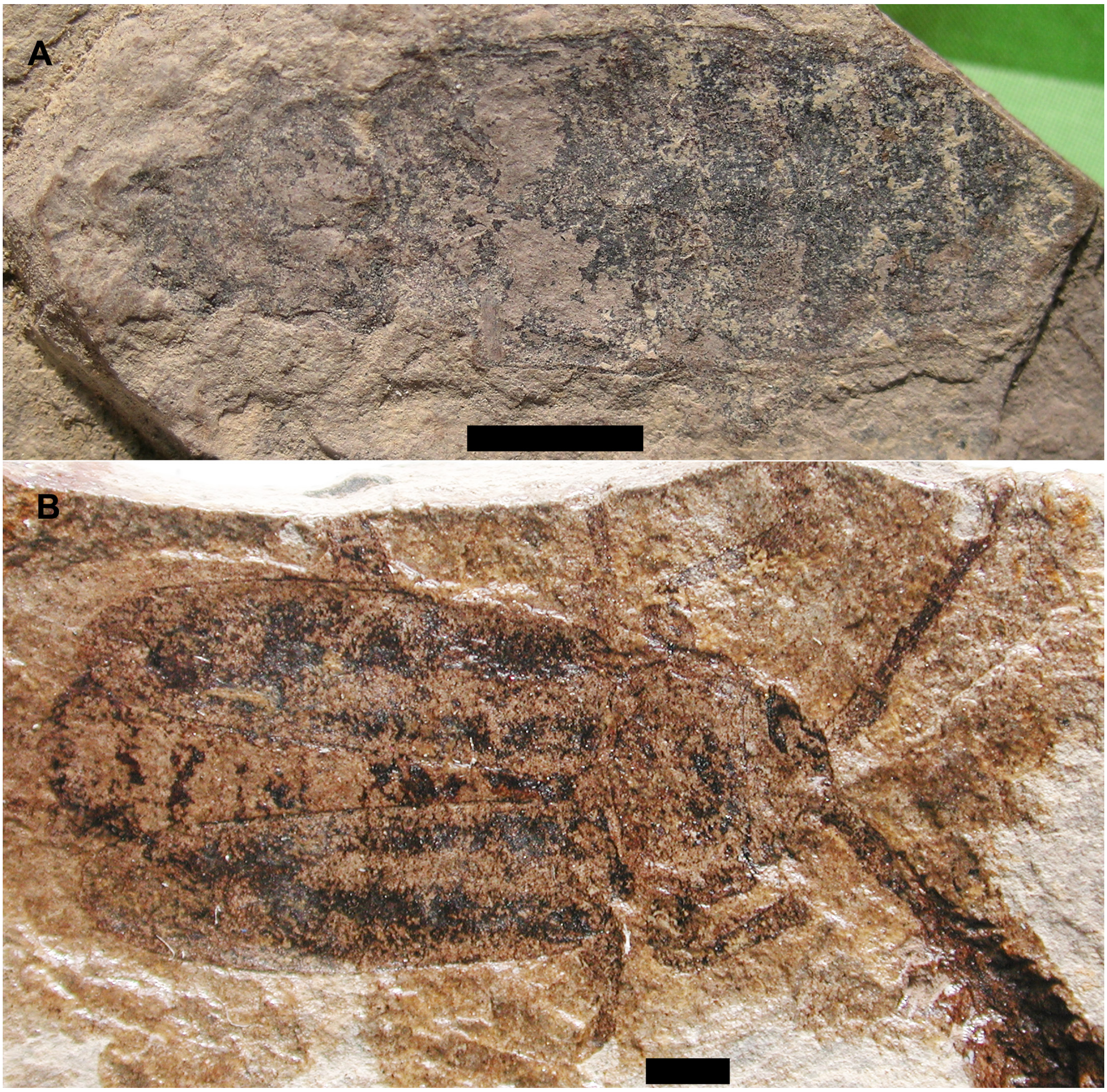

Fig. 5. **A**. *Monohammus orientalis* Piton, 1940, holotype (MNHN-F-R07237). **B**. *Chlorida magnifica* Piton, 1940, holotype (MNHN.F.R06997). Scale bars: A = 5 mm; B = 2 mm.

Conclusion

Palaeosphryon menatensis gen. et sp. nov. is the first accurately assigned Prioninae from the Paleocene of Menat, and the third oldest record of this subfamily. The presence of the Macrotomini *Xyleoconites proavus* in the Eocene of Geiseltal together with the attribution of a new fossil to the Prionini suggest that the subfamily was already well diversified during the Paleocene–Eocene.

Fig. 6. **A**. *Prolamioides bituminosus* Piton & Théobald, 1937, holotype (MNHN.F.R07016). **B**. *Prolamioides brunneus* Piton, 1940, holotype (MNHN.F.R07031). Scale bars = 5 mm.

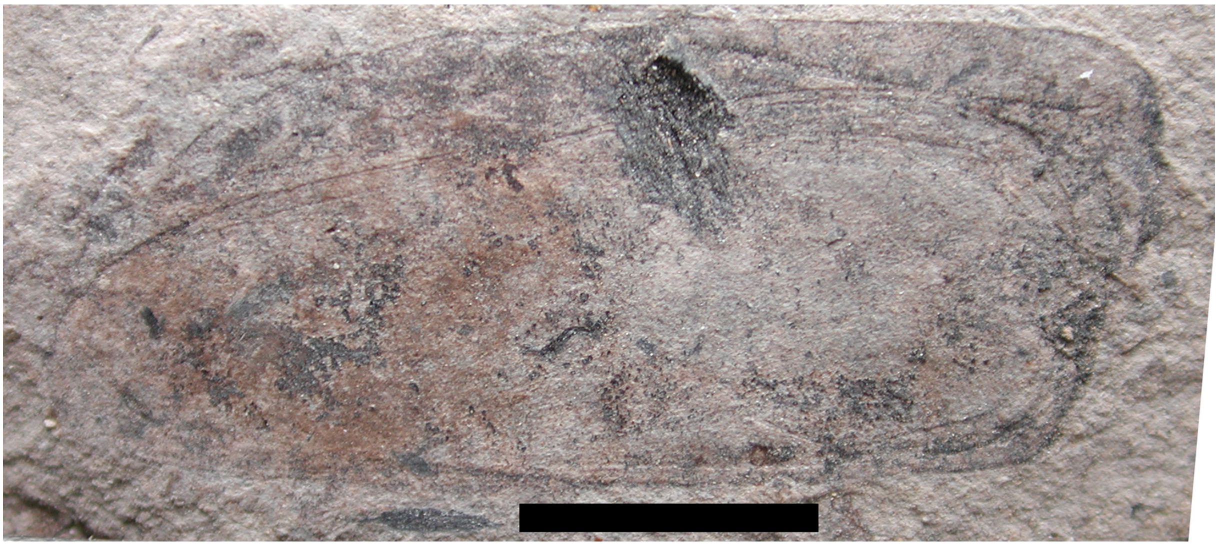

Fig. 7. *Prionus sinuatus* Piton, 1940, holotype (MNHN-F-R07045). Scale bar = 5 mm.

The Cerambycidae are quite diverse and not infrequent in the Menat paleolake, but clearly rarer than the Curculionidae Latreille, 1802, Elateridae Leach, 1815, or Buprestidae Leach, 1815. But they remain much more frequent than in the other Cenozoic Konservat-Lagerstätte compression deposits (e.g., only two specimens in the uppermost Oligocene of Aix-en-Provence for more than 60 000 fossil insects). This diversity and abundance is in accordance with the current reconstruction of a small lake surrounded by an important forest with an important diversity of trees. The large size of some of these Cerambycidae supports a warm and humid climate (Wedmann *et al.* 2018). Also, the exceptional preservation of such large insects (e.g., very large cockroach with wings over 8 cm long) is possibly linked to the presence of surface diatom and microbial mats embedding the insects that went in the water.

Acknowledgments

We thank two anonymous referees for their useful remarks on the first version of the paper. We sincerely thank Sophie Hervet, curator of the Musée de Paléontologie of the Village of Menat, for the loan of the type specimen. The studies of AGK were carried out within the framework of the Russian state research project No. 122031100272-3. We thank a lot for Dr Gaelle Doitteau (RECOLNAT) for the photograph of the holotypes of Piton.

References

An S. 2019. Revision of the genus *Eurypoda* Saunders (Coleoptera: Cerambycidae: Prioninae) with a new record from Korea. *Journal of Asia-Pacific Biodiversity* 12: 558-560. https://doi.org/10.1016/j.japb.2019.09.012

Ashman L.G., Shin S., Zwick A., Ślipiński A. & McKenna D.D. 2022. The first phylogeny of Australasian Lamiinae longhorn beetles (Coleoptera: Cerambycidae) reveals poor tribal classification and a complex biogeographic history. *Systematic Entomology* 47: 213–230. https://doi.org/10.1111/syen.12526

Audureau A. 2011. Révision du genre *Orthomegas* Audinet-Serville, 1832 (Coleoptera, Cerambycidae, Prionidae). *Les Cahiers Magellanes* (N.S.) 6: 63–96.

Bjørnstad A., Grobbelaar E. & Perissinotto R. 2016. Review of *Afraustraloderes rassei* Bouyer, 2012: description of its female and a new species of *Pixodarus* Fairmaire, 1887 (Coleoptera, Cerambycidae, Prioninae). *ZooKeys* 558: 77–93. https://doi.org/10.3897/zookeys.558.6112

Bleuzen P. 1990. Révision du genre *Macrodontia* Serville 1832 (Coleoptera, Cerambycidae, Prioninae, Ancistrotini). *Bulletin de la Société Sciences Nat* 67: 8–11.

Bouyer T. 2012. Description d'un nouveau genre et d'une nouvelle espèce d'Hopliderini d'Afrique du Sud (Coleoptera, Cerambycidae, Prioninae). *Lambillionea* 112: 213–217.

Bouyer T. & Susini A. 2009. Description d'un nouveau genre de Macrotomini du Gabon (Coleoptera, Cerambycidae, Prioninae). *Entomologia Africana* 14: 28–32.

Cockerell T.D.A. 1922. A new fossil longicorn beetle. *The Entomologist* 55: 176–178.

Danilevsky M.L. 2004. Review of genus *Pogonarthron* Semenov, 1900 with a description of a new species (Coleoptera, Cerambycidae). *Les Cahiers Magellanes* 40: 1–14.

Danilevsky M.L. & Komiya, Z. 2014. *Pogonarthron* (*Multicladum* subgen. n.) and a female of *Pogonarthron* (*Pseudomonocladum* Villiers, 1961, stat. nov.) *minutum* (Pic, 1905) (Coleoptera, Cerambycidae). *Humanity Space International Almanac* 3: 267–271.

Delahaye N. & Santos-Silva A. 2016. Nouveau genre et nouvelle espèce de Callipogonini du Pérou (Coleoptera, Cerambycidae, Prioninae). *Les Cahiers Magellanes* (N.S.) 24: 1–4.

Delahaye N., Drumont A. & Sudre J. 2006. Catalogue des Prioninae du Gabon (Coleoptera, Cerambycidae). *Lambillionea* 106 (1, suppl. 1): 1–29.

Delahaye N., Komiya Z., Drumont A. & Shapovalov A. 2021. A new species of the genus *Psalidosphryon* Komiya, 2001 from West Papua, Indonesia (Coleoptera, Cerambycidae, Prioninae). *Faunitaxys* 9: 1–7.

Dillon L.S. & Dillon E.S. 1945. The tribe Onciderini (Coleoptera: Cerambycidae) Part I. *Scientific Publications, Reading Public Museum and Art Gallery* 5: 1–186.

Dillon L.S. & Dillon E.S. 1946. The tribe Onciderini (Coleoptera: Cerambycidae) Part II. *Scientific Publications, Reading Public Museum and Art Gallery* 6: 189–413.

Drumont A. 2004. Complements à l'étude du genre *Cantharocnemis* (1ere note): revalidation du sous-genre *Paracantharocnemis* Plavilstshikov, 1933 et premières captures de *Cantharocnemis* (*Cantharocnemis*) *spondyloides* Audinet-Serville, 1832 en Afrique du Sud et au Sultanat d'Oman (Coleoptera, Cerambycidae, Prioninae). *Entomologia Africana* 9: 29–37.

Drumont A. 2006. Description d'une nouvelle espèce de *Palaeomegopis* Boppe originaire de Chine (Coleoptera, Cerambycidae, Prioninae). *Lambillionea* 106: 281–285.

Drumont A. & Do C. 2013. Description of a new genus and species of the tribe Aegosomatini Thomson, 1861 from Vietnam (Coleoptera, Cerambycidae, Prioninae). *Les Cahiers Magellanes* (N.S.) 12: 95–107.

Drumont A., Galant M. & Huedepohl K.-E. 2000. Contribution à l'étude des Prioninae asiatiques. Notes taxonomiques (Coleoptera, Cerambycidae). *Lambillionea* 100: 489–493.

Fragoso S.A. & Monné M.A. 1982. Notas sobre Prioninae neotropicais (Coleoptera, Cerambycidae). *Pesquisa Agropecuaria Brasileira* 17: 519–523.

Gahan C.J. 1906. Cerambycidae. *Fauna of British India, including Ceylon and Burma, Coleoptera* 1: i–xviii + 1–329. https://doi.org/10.5962/bhl.title.9452

Galileo M.H.M. 1987a. Sistemática das tribos Meroscelisini e Anacolini (Coleoptera, Cerambycidae, Prioninae) nas Américas. 1. Meroscelisini. *Revista Brasileira de Entomologia* 31: 141–367.

Galileo M.H.M. 1987b. Sistemática das tribos Meroscelisini e Anacolini (Coleoptera, Cerambycidae, Prioninae) nas Américas. 2. Anacolini. *Revista Brasileira de Entomologia* 31: 481–705.

Galileo M.H.M. & Martins U.R. 1992. Revisão da tribo Mallaspini Thomson, 1860 (Coleoptera, Cerambycidae, Prioninae). *Revista Brasileira de Entomologia* 36: 293–422.

Galileo M.H.M. & Martins U.R. 1993a. Revisão da tribo Solenopterini (Coleoptera, Cerambycidae, Prioninae). Parte I. Transferência de *Poekilosoma* A.-Serville, 1832 e *Calocomus* A.-Serville, 1832; os gêneros *Prosternodes* Thomson, 1860 e *Derancistrodes*, gen. n. *Revista Brasileira de Entomologia* 37: 79–99.

Galileo M.H.M. & Martins U.R. 1993b. Revisão da tribo Solenopterini (Coleoptera, Cerambycidae, Prioninae). Parte II. Gêneros *Derancistrus* A.-Serville, 1832; *Holonotus* Thomson, 1860 e *Sphenostethus* Haldeman, 1845. *Revista Brasileira de Entomologia* 37: 199–222.

Galileo M.H.M. & Martins U.R. 1993c. Revisão da tribo Solenopterini (Coleoptera, Cerambycidae, Prioninae). Parte III. Gênero *Solenoptera* A-Serville, 1832. *Revista Brasileira de Entomologia* 37: 425–458.

Galileo M.H.M. & Martins U.R. 1994a. Revisão da tribo Solenopterini (Coleoptera, Cerambycidae, Prioninae). Parte IV. Gênero *Elateropsis* Chevrolat, 1862 e distribuição geográfica da tribo. *Revista Brasileira de Entomologia* 38: 109–153.

Galileo M.H.M. & Martins U.R. 1994b. Revisão da tribo Calocomini (Coleoptera, Cerambycidae, Prioninae). *Revista Brasileira de Entomologia* 38: 489–505.

Georgiou R., Gueriau P., Sahle C.J., Bernard S., Mirone A., Garrouste R., Bergmann U., Rueff J.-P. & Bertrand L. 2019. Carbon speciation in organic fossils using 2D to 3D x-ray Raman multispectral imaging. *Science Advances* 5 (8): eaaw5019. https://doi.org/10.1126/sciadv.aaw5019

Germar E.F. 1837. Insectorum Protogaeae specimen, sistens Insecta carbonum fossilium. *Fauna Insectorum Europae* 19: 27 pp.

Germar E.F. 1839. Die versteinerten Insecten Solnhofens. *Nova Acta Academica Leopoldina-Caroliniense* 19: 189–222.

Giebel C.G. 1856. *Fauna der Vorwelt mit steter Berücksichtigung der lebenden Thiere. Band II: Gliederthiere. Abt. I: Insekten und Spinnen*. F.A. Brockhaus, Leipzig. https://doi.org/10.5962/bhl.title.24938

Gilmour E.F. 1956. Revision of the "Prioninae" of Tropical and South Africa. *Longicornia* 3: 1–252.

Gilmour E.F. 1960. On some African Macrotomini (Coleop. Ceramb.). *Bulletin de l'Institut royal des Sciences naturelles de Belgique* 36: 1–6.

Haddad S., Shin S., Lemmon A.R., Lemmon E.M., Svacha P., Farrell B., Ślipiński A., Windsor D. & McKenna D.D. 2018. Anchored hybrid enrichment provides new insights into the phylogeny and evolution of longhorned beetles (Cerambycidae). *Systematic Entomology* 43: 68–89. https://doi.org/10.1111/syen.12257

Haddad S., Clarke D.J., Jeong S., Mitchell R.F. & McKenna D.D. 2023. Antennal sensilla in longhorn beetles (Coleoptera: Cerambycidae). *Annals of the Entomological Society of America* 116: 83–113. https://doi.org/10.1093/aesa/saac026

Haller P. & Delahaye N. 2018. The genus *Scatopyrodes* Galileo & Martins, 1992 with description of a new species from Mexico (Coleoptera, Cerambycidae, Prioninae). *Les Cahiers Magellanes* (N.S.) 29: 97–105.

Haupt H. 1950. Die Käfer (Coleoptera) der Eozänen Braunkohle des Geiseltales. *Geologica* 6: 1–168.

Heer O. 1865. *Die Urwelt der Schweitz*. F. Schultheß, Zürich.

Jin M., Zwick A., Ślipiński A., Dekeyzer R. & Pang H. 2020. Museomics reveals extensive cryptic diversity of Australian prionine longhorn beetles with implications for their classification and conservation. *Systematic Entomology* 45: 745–770. https://doi.org/10.1111/syen.12424

Kedves M. & Russell D.E. 1982. Palynology of the Thanetian layers of Menat. The geology of the Menat Basin, France. *Palaeontographica B* 182: 87–150.

Kirejtshuk A.G. & Nel A. 2018. Nitidulidae (Coleoptera) from the Paleocene of Menat (France). *Zootaxa* 4402: 1–41. https://doi.org/10.11646/zootaxa.4402.1.1

Kirejtshuk A.G., Nel A. & Collomb F.-M. 2010. New Archostemata (Insecta, Coleoptera) from the French Paleocene and Early Eocene, with a note on the composition of the suborder. *Annales de la Société entomologique de France* (N.S.) 46: 216–227. https://doi.org/10.1080/00379271.2010.10697661

Kirejtshuk A.G., Nel A. & Kirejtshuk P.A. 2016. Taxonomy of the reticulate beetles of the subfamily Cupedinae (Coleoptera, Archostemata), with a review of the historical development. *Invertebrate Zoology* 13: 61–190. https://doi.org/10.15298/invertzool.13.2.01

Kirejtshuk A.G., Kovalev A.V. & Nel A. 2019. The oldest Cenozoic passandrid (Coleoptera: Cucujoidea: Passandridae) from the Paleocene of Menat (France). *Comptes Rendus Palevol* 18: 178–185. https://doi.org/10.1016/j.crpv.2019.10.005

Komiya Z. 2001. Prioninae cerambycid beetles with degenerate hind wings of the world (Coleoptera, Cerambycidae). *Gekkan-Mushi* 366: 29–37.

Komiya Z. 2002. A synopsis of the prionine cerambycid of the genus *Megobaralipton*, new status (Coleoptera, Cerambycidae, Prioninae). *Elytra* 30: 219–234.

Komiya Z. 2003a. Notes on the genus *Baralipton* (Coleoptera, Cerambycidae), with description of a new species. *Elytra* 31: 43–54.

Komiya Z. 2003b. Description of a new genus close to *Baralipton* (Coleoptera: Cerambycidae). *Elytra* 31: 307–320.

Komiya Z. 2004a. Notes on the genus *Aerogrammus* Gahan, with description of a new species (Coleoptera, Cerambycidae, Prioninae) (Revisional studies of the genus *Megopis* sensu Lameere, 1909-4). *Elytra* 32: 187–193.

Komiya Z. 2004b. A new prionine genus erected for *Aegosoma metallicum* Aurivillius (Coleoptera, Cerambycidae, Prioninae). *Elytra* 32: 421–424.

Komiya Z. 2005. A synopsis of the prionine genus *Aegolipton*, new status (Coleoptera, Cerambycidae). *Elytra* 33: 149–181.

Komiya Z. 2020. New or little known *Osphryon* species from Sulawesi, Sangihe and Papua State of Indonesia (Coleoptera, Cerambycidae, Prioninae). *Trends in Entomology* 16: 63–70.

Komiya Z. & de Keyzer R. 2011. A new genus and species of the subfamily Prioninae (Coleoptera, Cerambycidae) from Australia. *In*: Kawai S. (ed.) *Masamushi. Entomological Papers Dedicated to Dr Kimio Masumoto on the oOccasion of his Retirement*. *Special Publication of the Japanese Society of Scarabaeoidology* 1: 317–323.

Komiya Z. & Drumont A. 2001. Description of a new prionine genus intermediate between *Megopis* and *Eurypoda* (Coleoptera, Cerambycidae, Prioninae) from Indochina and Borneo. *Elytra* 29: 391–400.

Komiya Z. & Drumont A. 2007. A synopsis of the prionine genus *Spinimegopis* stat. nov. (Coleoptera, Cerambycidae, Prioninae). (Revisional studies of the genus *Megopis* sensu Lameere, 1909-8). *Elytra* 35: 345–384.

Komiya Z. & Drumont A. 2009. Study on prionine cerambycid *Megopis* (Coleoptera, Cerambycidae). (Revisional studies on the genus *Megopis* sensu Lameere, 1909-9). *Elytra* 37: 313–342.

Komiya Z. & Drumont A. 2010. A revision of the genus *Nepiodes* (Coleoptera, Cerambycidae, Prioninae) (Revisional studies of the genus *Megopis* sensu Lameere, 1909-10). *Elytra* 38: 169–192.

Komiya Z. & Drumont A. 2011. Note préliminaire sur le genre *Hystatus* Thomson avec la description d'une nouvelle espèce de l'ile de Bornéo (Coleoptera, Cerambycidae, Prioninae). *Les Cahiers Magellanes* (N.S.) 6: 109–113.

Komiya Z. & Drumont A. 2012. Description of a new genus close to *Aegosoma* (Coleoptera, Cerambycidae, Prioninae) (Revisional studies of the genus *Megopis* sensu Lameere, 1909-11). *Elytra New Series* 2: 181–187.

Komiya Z. & Drumont A. 2013. Notes on the genera *Dandamis*, *Paradandamis* and *Rhineimegopis* (Coleoptera, Cerambycidae, Prioninae) (Revisional studies of the genus *Megopis* sensu Lameere, 1909-11). *Elytra New Series* 3: 149–159.

Lameere A. 1901. Etude sur la phylogénie des Longicornes. *Annales de la Société entomologique de Belgique* 45: 314–323. Available from https://www.biodiversitylibrary.org/page/36148279 [accessed 25 Jan. 2024].

Lameere A. 1912. Révision des Prionides. Vingtième mémoire: Prionines VII. *Annales de la Société entomologique de Belgique* 56: 185–260.
Available from https://www.biodiversitylibrary.org/page/12848075 [accessed 25 Jan. 2024].

Lameere A. 1919. Coleoptera Longicornia Fam. Cerambycidae Subfam. Prioninae. *Genera Insectorum* 172: 1–189. Available from https://www.biodiversitylibrary.org/page/33621325 [accessed 25 Jan. 2024].

Legalov A.A., Kirejtshuk A.G. & Nel A. 2017. New and little known weevils (Coleoptera: Curculionoidea) from the Paleocene of Menat (France). *Comptes Rendus Palevol* 16: 248–256.
https://doi.org/10.1016/j.crpv.2016.10.007

Legalov A.A., Kirejtshuk A.G. & Nel A. 2019. The oldest genus of the subfamily Sagrinae (Coleoptera: Chrysomelidae) from the Paleocene of Menat (France). *Comptes Rendus Palevol* 18: 178–185.
https://doi.org/10.1134/S0013873818070084

Lin M. & Bai M. 2017. *Qitianniu zhihaoi* gen. et sp. nov.: the first cerambycid beetle found in Cretaceous Burmese amber (Coleoptera: Chrysomeloidea). *Cretaceous Research* 75: 173–178.
https://doi.org/10.1016/j.cretres.2017.03.030

Lin M. & Danilevsky M.L. 2017. Two new Prioninae (Coleoptera, Cerambycidae) genera from China. *Humanity Space. International Almanac* 6: 46–56.

Linsley E.G. 1940. Notes and descriptions of West American Cerambycidae. IV (Coleoptera). *Entomological News* 51: 253–258 + 285–290.

Linsley E.G. 1942. A review of the fossil Cerambycidae of North America. *Proceedings of the New England Zöological Club* 21: 17–42.

Linsley E.G. 1961. The Cerambycidae of North America. Part 1. Introduction. *University of California Publications in Entomology* 18: 1–97.

Linsley E.G. 1962. The Cerambycidae of North America. Part 2. Taxonomy and classification of the Parandrinae, Prioninae, Spondylinae and Aseminae. *University of California Publications in Entomology* 19: 1–120.

Liu Y., Chen D., Liu H., Hu H., Bian H., Zhang R., Yang R., Jiang X. & Shi S. 2018. The complete mitochondrial genome of the longhorn beetle *Dorysthenes paradoxus* (Coleoptera: Cerambycidae: Prionini) and the implication for the phylogenetic relationships of the Cerambycidae species. *Journal of Insect Science* 18: 21. https://doi.org/10.1093/jisesa/iey012

Lorenc J. & Drumont A. 2013. Contribution to the knowledge of the bionomics of some steppe Westpalaearctic species belonging to tribe Prionini Latreille, 1802, with the description for the first time of the females of *Polylobarthron margelanicum* (Thery, 1896) and *Mesoprionus petrovitzi* (Holzschuh, 1981) (Coleoptera, Cerambycidae, Prioninae). *Les Cahiers Magellanes* (N.S.) 11: 82–90.

McKeown K.C. 1938. Notes on Australian Cerambycidae. IV. *Records of the Australian Museum* 20: 200–216. https://doi.org/10.3853/j.0067-1975.20.1938.569

Monné M.L. & Napp D.S. 2005. Cladistic analysis of the tribe Torneutini Thomson (Coleoptera: Cerambycidae: Cerambycinae: Trachyderoinia). *Zootaxa* 1062: 1–56. https://doi.org/10.11646/zootaxa.1062.1.1

Monné M.L., Monné M.A. & Wang Q. 2017. Chapter 1. General morphology, classification, and biology of Cerambycidae. *In*: Wang Q. (ed.) *Cerambycidae of the World: Biology and Pest Management*: 1–76. CRC Press.

Nabozhenko M.V. & Kirejtshuk A.G. 2017. The oldest opatrine terrestrial darkling beetle (Coleoptera: Tenebrionidae: Tenebrioninae) from the Paleocene of Menat (France). *Palaeontologische Zeitschrift* 91: 307–313. https://doi.org/10.1007/s12542-017-0368-2

Napp D.S. 1994. Phylogenetic relationships among the subfamilies of Cerambycidae (Coleoptera, Chrysomeloidea). *Revista Brasileira de Entomologia* 38: 265–419.

Nel A. 1989. Les Gyrinidae fossiles de France (Coleoptera). *Annales de la Société entomologique de France* (N.S.) 25: 321–330. https://doi.org/10.1080/21686351.1989.12277593

Nel A. 2007. Les Bibionidae du Paléocène de Menat (Puy-de-Dôme, France) (Diptera). *Bulletin de la Société entomologique de France* 112: 369–370. https://doi.org/10.3406/bsef.2007.16447

Nel A. 2022. The oldest fossil of the sawfly subfamily Nematinae (Hymenoptera: Tenthredinidae) from the Paleocene of Menat (France). *Palaeoentomology* 5: 289–293. https://doi.org/10.11646/palaeoentomology.5.3.13

Nel A. & Auvray F. 2006. The oldest Vespinae from the Paleocene of Menat (France) (Hymenoptera: Vespidae). *Zootaxa* 1344: 59–62. https://doi.org/10.11646/zootaxa.1344.1.5

Nel A. & Jouault C. 2022. The odonatan insects from the Paleocene of Menat, central France. *Acta Palaeontologica Polonica* 67: 631–648. https://doi.org/10.4202/app.00960.2021

Nel A. & Roy R. 1996. Revision of the fossil "mantid" and "ephemerid" species described by Piton from the Palaeocene of Menat (France) (Mantodea: Chaeteessidae, Mantidae; Ensifera: Tettigonioidea). *European Journal of Entomology* 93: 223–234.

Nel A., Garrouste R., Kaya M., Licht A., Legal S. & Coster P. 2023. The second oldest representative of the genus Aeshna (Odonata: Aeshnidae) found in the lowermost Oligocene of Luberon (France) and revealed by UV light. *Historical Biology* 36: 261–265. https://doi.org/10.1080/08912963.2022.2157274

Nie R., Vogler A.P., Yang X. & Lin M. 2021. Higher-level phylogeny of longhorn beetles (Coleoptera: Chrysomeloidea) inferred from mitochondrial genomes. *Systematic Entomology* 46: 56–70. https://doi.org/10.1111/syen.12447

Peña L.E.G. & Vidal G.H.P. 1976. Algunas observaciones sobre especies poco conocidas de Cerambycidae (Coleoptera). 3. *Acalodegma servillei* (Bl.). *Revista Chilena de Entomología* 9: 45–47.

Perger R. & Santos-Silva A. 2010. A new genus and species of Callipogonini, description of the male of *Strongylaspis boliviana* Monné & Santos-Silva, 2003, and a new distributional record for *Chorenta reticulata* (Dalman, 1817) (Coleoptera, Cerambycidae). *ZooKeys* 48: 29–38. https://doi.org/10.3897/zookeys.48.417

Piton L. 1940. Paléontologie du gisement éocène de Menat (Puy-de-Dôme), flore et faune. *Mémoire de la Société d'Histoire naturelle d'Auvergne* 1: 1–303.

Piton L. & Théobald N. 1937. Part 2. Les insectes fossiles de Menat. *In*: Marty P., Piton L. & Théobald N. (eds) *Les Lignites et Schistes bitumineux de Menat*: 76–88. *Revue des Sciences naturelles d'Auvergne* 3.

Quentin R.M. & Villiers A. 1972. Révision des Hopliderina africains et malgaches. *Annales de la Société entomologique de France* (N.S.) 8: 257–289. https://doi.org/10.1080/21686351.1972.12278101

Quentin R.M. & Villiers A. 1974. Révision des Closterini de Madagascar (Col. Cerambycidae Prioninae). *Annales de la Société entomologique de France* (N.S.) 10: 249–341. https://doi.org/10.1080/21686351.1974.12278151

Quentin R.M. & Villiers A. 1975. Insectes Coléoptères Cerambycidae Parandrinae et Prioninae. *Faune de Madagascar* 40: 1–251.

Quentin R.M. & Villiers A. 1977. Genera et catalogue raisonné des Prioninae africains. 1. Ergatini (1) (Coleoptera, Cerambycidae). *Annales de la Société entomologique de France* (N.S.) 13: 509–523. https://doi.org/10.1080/21686351.1977.12278654

Quentin R.M. & Villiers A. 1981. Les Macrotomini de l'ancien monde (région éthiopienne exclue). Genera et catalogue raisonné (Col. Cerambycidae Prioninae). *Annales de la Société entomologique de France* (N.S.) 17: 359–393. https://doi.org/10.1080/21686351.1981.12278290

Riou B. 1999. Descriptions de quelques insectes fossiles du Miocène supérieur de la Montagne d'Andance (Ardèche, France). *Travaux de l'École pratique des hautes Études, Biologie et Evolution des Insectes* 11–12: 123–133.

Santos Ferreira G.W. 1980. The Parandrinae and the Prioninae of Southern Africa (Cerambycidae, Coleoptera). *Memoirs van die Nasionale Museum* 13: i–iii + 1–335.

Santos-Silva A. 2004a. Nova espécie de *Anacanthus* do Brasil (Coleoptera, Cerambycidae, Prioninae, Callipogonini). *Iheringia Série Zoologica* 94: 281–283. https://doi.org/10.1590/S0073-47212004000300010

Santos-Silva A. 2004b. Descrição de *Hephialtes mourei* sp. nov. e notas em *Hephialtes* Thomson e *Braderochus mundus* (White) (Coleoptera, Cerambycidae, Prioninae). *Revista Brasileira de Entomologia* 48: 35–38. https://doi.org/10.1590/S0085-56262004000100006

Santos-Silva A. 2007. Revisão do gênero *Derobrachus* Audinet-Serville, 1832 (Coleoptera, Cerambycidae, Prioninae). *Arquivos de Zoologia do Estado de São Paulo* 38: 1–94. https://doi.org/10.11606/issn.2176-7793.v38i1p1-94

Santos-Silva A. & Galileo M.H.M. 2010. A new genus of Macrotomini (Coleoptera, Cerambycidae, Prioninae). *ZooKeys* 35: 65–75. https://doi.org/10.3897/zookeys.35.312

Santos-Silva A. & Komiya Z. 2012. Contribution towards the knowledge of *Psalidognathus* Gray, 1831 (Coleoptera, Cerambycidae, Prioninae). *Insecta Mundi* 247: 1–28. Available from https://digitalcommons.unl.edu/insectamundi/755 [accessed 15 Jan. 2024].

Santos-Silva A. & Martins U.R. 2005a. Novos táxons e notas taxonômicas em Prioninae (Coleoptera, Cerambycidae). *Iheringia Série Zoologica* 95: 393–403. https://doi.org/10.1590/S0073-47212005000400009

Santos-Silva A. & Martins U.R. 2005b. Nova espécie e sinonímia em *Braderochus* Buquet, 1852 (Coleoptera, Cerambycidae, Prioninae). *Revista Brasileira de Entomologia* 49: 237–239. https://doi.org/10.1590/S0085-56262005000200006

Santos-Silva A., Swift I.P. & Nearns E.H. 2010. Division of the genus *Nothopleurus* Lacordaire, 1869 (Coleoptera: Cerambycidae: Prioninae). *Zootaxa* 2643: 1–44. https://doi.org/10.11646/zootaxa.2643.1.1

Schmidt G. 1967. Die Bockkäfer (Cerambycidae, Coleoptera) des Pliozäns von Willershausen. *Berichte der Naturhistorischen Gesellschaft zu Hannover* 111: 113–120.

Vitali F. 2008. Systematic revision of the fossil cerambycids from Geiseltal (Coleoptera Cerambycidae). *Entomapeiron* (P. S.), 3: 1–10.

Vitali F. 2019. Systematic notes on the Cerambycidae (Insecta: Coleoptera) described from Burmese amber. *Palaeoentomology* 2: 215–218. https://doi.org/10.11646/palaeoentomology.2.3.3

Vives E., Drumont A., Komiya Z. & Heffern D. 2008. The New Caledonian genus *Acideres* Guérin-Méneville, 1858: systematic notes, sexual dimorphism and geographic distribution (Coleoptera, Cerambycidae). *Les Cahiers Magellanes* 84: 1–20.

Voitsekhovskii V. 2020. Two new species of the genus *Osphryon* (Pascoe, 1869) (Coleoptera: Cerambycidae, Prioninae) from Papua, Indonesia. *Suara Serangga Papua* 12: 102–111.

Wang B., Ma J., McKenna D.D., Yan E.V., Zhang H. & Jarzembowski E.A. 2014. The earliest known longhorn beetle (Cerambycidae: Prioninae) and implications for the early evolution of Chrysomeloidea. *Journal of Systematic Palaeontology* 12: 565–574. https://doi.org/10.1080/14772019.2013.806602

Wappler T., Currano E.D., Wilf P., Rust J. & Labandeira C.C. 2009. No post-Cretaceous ecosystem depression in European forests? Rich insect-feeding damage on diverse middle Palaeocene plants, Menat, France. *Proceedings of the Royal Society B* 276: 4271–4277. https://doi.org/10.1098/rspb.2009.1255

Wedmann S., Uhl D., Lehman T., Garrouste R., Nel A., Gomez B., Smith K. & Schaal S.F.K. 2018. The Konservat-Lagerstätte Menat (Paleocene; France) – an overview and new insights. *Geologica Acta* 16: 1–31. https://doi.org/10.1344/GeologicaActa2018.16.2.5

Wickham H.F. 1914. Twenty new Coleoptera from the Florissant shales. *Transactions of the American Entomological Society* 40: 257–270. Available from https://www.biodiversitylibrary.org/page/6468195 [accessed 15 Jan. 2024].

Yu Y., Šlipiǹski A., Reid C., Shih C., Pang H. & Ren D. 2015. A new longhorn beetle (Coleoptera: Cerambycidae) from the Early Cretaceous Jehol Biota of Western Liaoning in China. *Cretaceous Research* 52: 453–460. https://doi.org/10.1016/j.cretres.2014.02.019

Zubov A.S. & Titarenko A.Yu. 2019. A new species of a new subgenus of *Toxeutes* Newman, 1840 (Coleoptera, Cerambycidae) from Australia. *Humanity Space. International Almanac* 8 (9): 1184–1192.

Manuscript received: 10 June 2023
Manuscript accepted: 25 September 2023
Published on: 7 February 2024
Topic editor: Marie-Béatrice Forel
Desk editor: Pepe Fernández