

Paleocene of Menat Formation, France, reveals an extraordinary diversity of orthopterans and the last known survivor of a Mesozoic Elcanidae

THOMAS SCHUBNEL, LAURE DESUTTER-GRANDCOLAS, ROMAIN GARROUSTE,
SOPHIE HERVET, and ANDRÉ NEL



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The orthopteran fauna of the Paleocene of Menat Formation (France) is revised. It comprises at least 12 species in the following clades: Grylloidea (an undescribed species, *Menatgryllus longixiphus* gen. et sp. nov.); Tettigoniidae (*Prophasgonura lineatocollis*); Elcanidae (*Cenoelcanus menatensis* gen. et sp. nov.); two Eumastacoidea (*Paleochina duvergeri* gen. et sp. nov. and *Paleochina minuta* sp. nov., tentatively placed in the extant family Chorotypidae). These two last taxa are compared to the other described fossil Eumastacoidea. As all these Eumastacoidea are represented by tegmina or hindwings, their previous attributions to the Eumastacidae sensu stricto are questionable. All previously described fossil Caelifera from Menat are considered of uncertain position. Those that were previously considered as Acridoidea are excluded from this clade. In consequence, the oldest described Acridoidea are Oligocene, at the time of diversification of the grasses on which these insects predominantly live, in accordance with the most recent molecular dating of the Acrididae. *Cenoelcanus menatensis* is the youngest and first Cenozoic representative of the Mesozoic Elcanidae, showing that this family survived the Cretaceous–Paleocene extinction and became extinct during the Paleogene.

Key words: Insecta, Ensifera, Elcanoidea, Acridoidea, Eumastacoidea, Paleogene, France.

Thomas Schubnel [thomas.schubnel@wanadoo.fr], Laure Desutter-Grandcolas [desutter@mnhn.fr], Romain Garrouste [garrosut@mnhn.fr], and André Nel [anel@mnhn.fr] (corresponding author), Institut Systématique Evolution Biodiversité (ISYEB), Muséum national d'Histoire naturelle, CNRS, Sorbonne Université, Université des Antilles, EPHE, 57 rue Cuvier, CP 50, 75005 Paris, France.

Sophie Hervet [sophie.hervet@yahoo.fr], Association Paléovergne, Musée de Paléontologie de Menat, Place de la Mairie, F-63560 Menat, France.

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Introduction

One of the major problems in paleontology is the incompleteness of the fossil record, complicating the studies in phylogeny and palaeoecology. It is especially the case for the Paleocene insects for which the number of recorded species is less than 300 vs. more than 7000 for the Eocene (internet site Fossilworks at <http://fossilworks.org/>). The current knowledge on the Paleocene Orthoptera is especially very scarce. Kevan and Wighton (1981, 1983) described some Prophalangopsidae from the Paleocene of Alberta (Canada). Petrulevičius (1999) cited the presence of Orthoptera in the Paleocene from Argentina. Ensiferan Gryllidae and Tetti-

goniidae and Caeliferan Eumastacidae and Tetrigidae have been described from the Paleocene–Eocene Fur and Olst formations in Denmark (Rust 1999; Zessin 2017a, b). Lin and Huang (2006) described a Paleocene representative of Prophalangopsidae from the Northern Tibet in China, recently transferred into the Stenopelmatidae by Wang et al. (2019). Therefore, the Paleocene Konservat Lagerstätte of Menat is of great interest because it has led an abundant and diverse orthopteran fauna. From this locality Piton (1936, 1937, 1940) described *Prophasgonura lineatocollis* Piton, 1940 and *Conocephalus martyi* Piton, 1940, two taxa he attributed to the tettigoniids, plus five “Caelifera”, viz. “*Oedipoda* spec.”; *Menatacridium eocenicum* Piton, 1936 (in Acrididae); a fossil genus “*Eremobiites*” with-

out type species; *Orthacanthacris incertus* Piton, 1940 (in “Cyrthacanthacrinae”, sic. for Cyrtacanthacridinae); and *Ochrilidia lineata* Piton, 1940 (in “Truxalinae”). Zeuner (1944) discussed on these fossils but they were never revised. New recent field investigations have given a series of new fossils of great interest, including the youngest Elcanidae and the first accurate Eumastacoidea from this outcrop that we describe herein. We also revise the taxa previously described by Piton (1936, 1937, 1940).

The Elcanoidea is currently a strictly Mesozoic clade, probably of the stem group Caelifera (Béthoux and Nel 2002). The orthopteran superfamily Eumastacoidea Burr, 1899 is one of the most “basal” clades of the extant Caelifera (Song et al. 2015). This group appeared in the fossil record during the Late Jurassic, well before the oldest accurate records of the Acridoidea, dated from the Oligocene (Gorochov and Rasnitsyn 2002; Song et al. 2015; Ataabadi et al. 2017). Nevertheless, only eleven fossil species are currently attributed to the Eumastacoidea (internet sites Fossilworks; Cigliano et al. 2019), ranging between the Upper Jurassic and the Oligocene. Thus these new discoveries of Paleocene Elcanidae and Eumastacoidea are of great interest to determine their evolutionary history, age, and past diversity.

Institutional abbreviations.—MNHN, Muséum national d’Histoire naturelle, Paris, France; MNT, Musée de Paléontologie de Menat, Menat, Puy-de-Dôme, France.

Other abbreviations.—C, costa; CuA/P, cubitus anterior/posterior; CuP α , most anterior branch of CuP; CuP β , median branch of CuP; CuPb, posterior branch of CuP; M, median vein; RA/P, radius anterior/posterior; ScA/P, subcostal anterior/posterior.

Nomenclatural acts.—This published work and the nomenclatural acts it contains, have been registered in ZooBank: urn:lsid:zoobank.org:pub:D395B22A-F1ED-4CD9-862B-384E60BD8B4C

Material and methods

The middle Paleocene Menat fossil site, small outcrop near the southeast of the village of Menat (46°06' N; 2°54' E, Menat Basin, Puy-de-Dôme, France), is a volcanic maar containing a rather small paleolake ca. 1 km in diameter, filled with sedimentary rocks (songo-diatomites) with remains of diverse aquatic and terrestrial flora and fauna (Piton 1940; Nel 1989, 2008; Nel and Roy 1996). The composition of faunal and floral remains suggests that this lake was surrounded by a forest and the palaeoenvironment was warm and humid (Wedmann et al. 2018). Following the pollen, mammalian stratigraphic, and radiometric K/Ar analyses, the age of the Menat outcrop was estimated as 59 Ma. (Kedves and Russel 1982; Nel 2008). However, the new estimate based on macroflora postulated its age within 60–61 Ma (Wappler et al. 2009). Orthoptera are diverse but infrequent at Menat, rep-

resenting only 1% of the very rich and diverse entomofauna, dominated by Coleoptera (78%).

The specimens were studied using a stereomicroscope Olympus SCX9 in MNHN. Photographs were taken with a Nikon D800 and the images treated with graphic software.

We follow the wing venation nomenclature of Béthoux and Nel (2002) for the Orthoptera, as confirmed by Desutter-Grandcolas et al. (2017).

Systematic palaeontology

Orthoptera Latreille, 1793

Ensifera Chopard, 1920

Grylloidea Laicharting, 1781

Grylloidea gen. et sp. indet.

Fig. 1.

Material.—MNT NEL 1681 (small adult female with well-developed ovipositor), Menat, Paleocene.

Measurements.—Fore femur 2.8 mm long; fore tibia 3.0 mm long; hind femur 5.0 mm long, 2.0 mm wide; hind tibia 4.8 mm long; ovipositor 7.5 mm long.

Description.—Body densely covered with strong setae (Fig. 1A₁). Head triangular with small, protruding eyes; last three joints of maxillary palpi about equal in length; joint 5 slightly, but regularly widened toward apex; apex truncated apically; scapes and antennae not visible; pronotum small, with shape not clear; wings and tegmina apparently lacking; right fore leg and both hind legs present; mid legs lacking; right fore tibia with an outer tympanum, elongate, probably obliterate, not slit-like; inner tympanum not visible; at least two apical spurs, one ventral and one dorsal; basitarsomere I long, but less than half tibia I length; both hind legs well-preserved; hind femora thick at base, not filiform at apex; hind tibiae shorter than hind femora; with three inner apical spurs, the dorsal the longest (Fig. 1A₂); outer apical spurs not visible; at least two inner and two outer subapical spurs, short; no spine above and between subapical spurs; basitarsomeres III longer than half hind tibiae; with several dorsal (inner, outer?) spines; tarsomeres II cylindrical, not flattened; tarsomeres III with a pair of claws; abdomen. Cerci long and thin, with very long setae; ovipositor longer than hind femora; apex short, triangular, no ornamentation visible.

Remarks.—The shape of the hind legs, with three-joint tarsi, that of the ovipositor and the presence of acoustic tympanum on fore tibia attest that this fossil belongs to Grylloidea.

?Gryllidae Laicharting, 1781

Genus *Menatgryllus* nov.

Zoobank LSID: urn:lsid:zoobank.org:act:42A274A8-2443-4D8B-A496-598AFBD44B0F

Type species: *Menatgryllus longixiphus* sp. nov., by monotypy, see below.

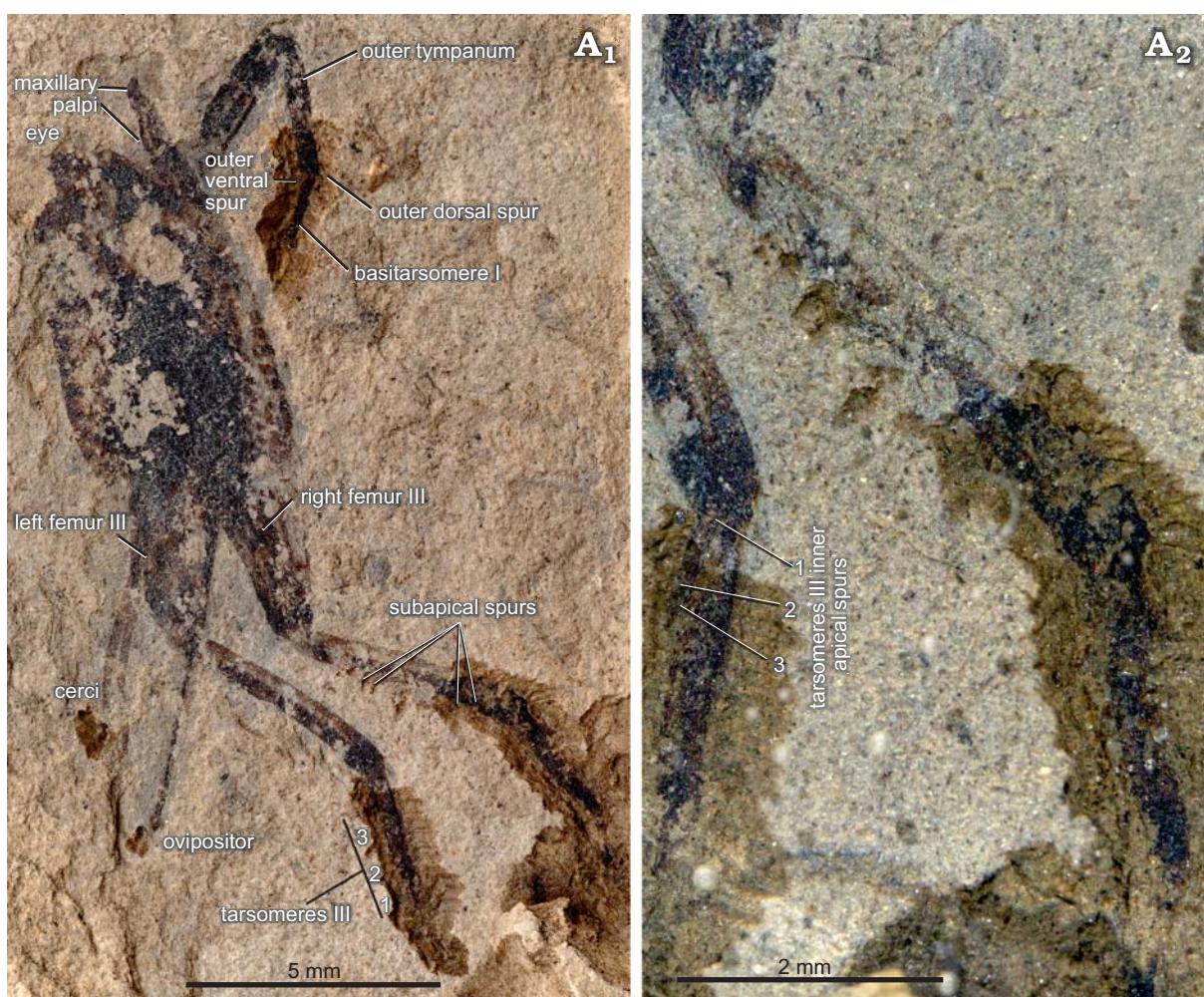


Fig. 1. Orthopteran *Grylloidea* sp., MNT NEL 1681 from Paleocene of Menat, France. A. Habitus. B. Apex of hind tibia.

Etymology: Named after the Menat locality and *Gryllus*, the generic name for a cricket.

Diagnosis.—As for the type species by monotypy.

Remarks.—The presence of forewings and acoustic tympana in females indicates that males possibly had forewings with a stridulatory apparatus.

Menatgryllus longixiphus sp. nov.

Fig. 2.

Zoobank LSID: urn:lsid:zoobank.org:act:DFC23D67-3E7E-4F55-854A-AEBC4F01B39C

Etymology: Named after its very long ovipositor.

Holotype: MNT-1053, female with legs and ovipositor well-preserved, abdomen and hind legs in ventral view, head and thorax in lateral position.

Type locality: New quarry, Menat, Puy-de-Dôme, France.

Type horizon: Middle Paleocene, Menat Basin.

Material.—Holotype only.

Diagnosis.—Acoustic tympanum present on fore tibia; forewings and hindwings both present in females; no serrulation on hind tibiae; tarsomeres 2 flattened; strong setae on the fastigium.

Measurements.—Fore femur 4.2 mm long; fore tibia 2.7 mm long; hind femur 8.0 mm long, 2.9 mm wide; hind tibia 7.5 mm long; ovipositor 17.5 mm long.

Description.—Body densely covered with short setae; head long and narrow in lateral view; scape longer than wide; left eye present but hardly visible, possibly protruding; fastigium distinct, but its shape unclear; with some strong setae (apical?); maxillary palpi hardly distinct; pronotum present in lateral position; lateral lobe probably longer than high, anterior angle longer than posterior one; legs all present; tarsi short with flattened second tarsomere (Fig. 2); left fore leg with a well-developed outer tympanum, elongate and oblique; right fore leg possibly with a smaller elongate inner tympanum; left tibia with three apical spurs; both legs with complete three-joint tarsi; basitarsomere I with two long and subequal apical spurs; mid legs complete, from coxae to tarsi; mid tibiae with four apical spurs (seen in ventral view: Fig. 2); hind femora thick and short, without a filiform apical part; hind tibiae slightly shorter than hind femora; with three inner apical spurs, the dorsal the longest and longer than half basitarsomere, also with three outer apical spurs, shorter than inner spurs, and with at least four inner and four

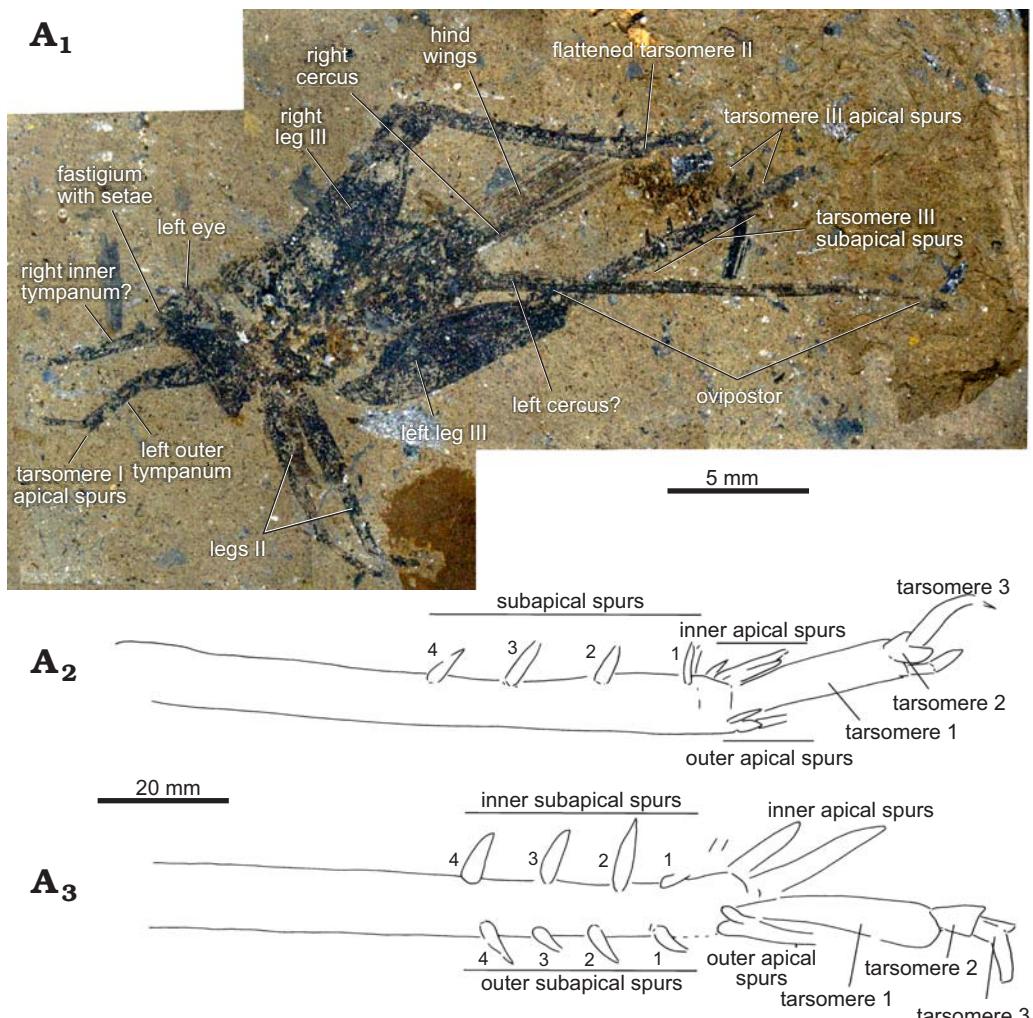


Fig. 2. Grylloidean orthopteran *Menatgryllus longixiphus* gen. et sp. nov., holotype, MNT-1053 from Paleocene of Menat, France. Photograph of habitus (A₁), reconstruction of hind tibiae and tarsus (A₂, left; A₃, right).

outer subapical spurs, with no discrepancy between inner and outer subapical spurs; no serrulation between and above subapical spurs; hind basitarsomeres with several dorsal spines in addition to apical ones; forewings close to left hind femur; wings plicated, colored, except along veins; venation unclear; hind wings much longer than forewings and much longer than body; abdomen complete; subgenital plate small and transverse; distal margin concave; cerci broken, but right only long; ovipositor very long, more than twice hind tibia length; apex small; ornamentation not visible.

Remarks.—The shape of the hindlegs, with three-joint tarsi, the shape of the ovipositor and the presence of acoustic tympanum on tibia I attest that this fossil belongs to Grylloidea. The presence of three apical spurs on fore tibia could fit the synapomorphy of the family Gryllidae (sensu Chintauan-Marquier et al. 2016), but the absence of serrulation on hind tibiae, the flattened shape of tarsomeres 2, and the presence of strong setae on the fastigium make an original combination of characters, supporting a new genus. *Menatgryllus* gen. nov. shares with the Baltic amber genus *Eopenitacentrus* Gorochov, 2010 the presence of four pairs of subapical spurs

on the hind tibiae but it differs from this genus in the fore tibia with three apical spurs instead of two (Gorochov 2010). Some other fossil gryllid genera are described from the Paleocene or the Eocene, but they are based on isolated wings (Gorochov 1992; Rust 1999), impossible to compare to *Menatgryllus* gen. nov.

Stratigraphic and geographic range.—Type locality and horizon.

Tettigoniidae Krauss, 1902

Genus *Prophasgonura* Piton, 1940

Type species: *Prophasgonura lineatocollis* Piton, 1940; Paleocene, Menat, France.

Prophasgonura lineatocollis Piton, 1940

Fig. 3A.

Holotype: MNHN.F. R07050 (coll. Louis Piton), female with wings attached to body.

Type locality: Historical quarry of Menat, Menat, Puy-de-Dôme, France.

Type horizon: Middle Paleocene, Menat Basin.

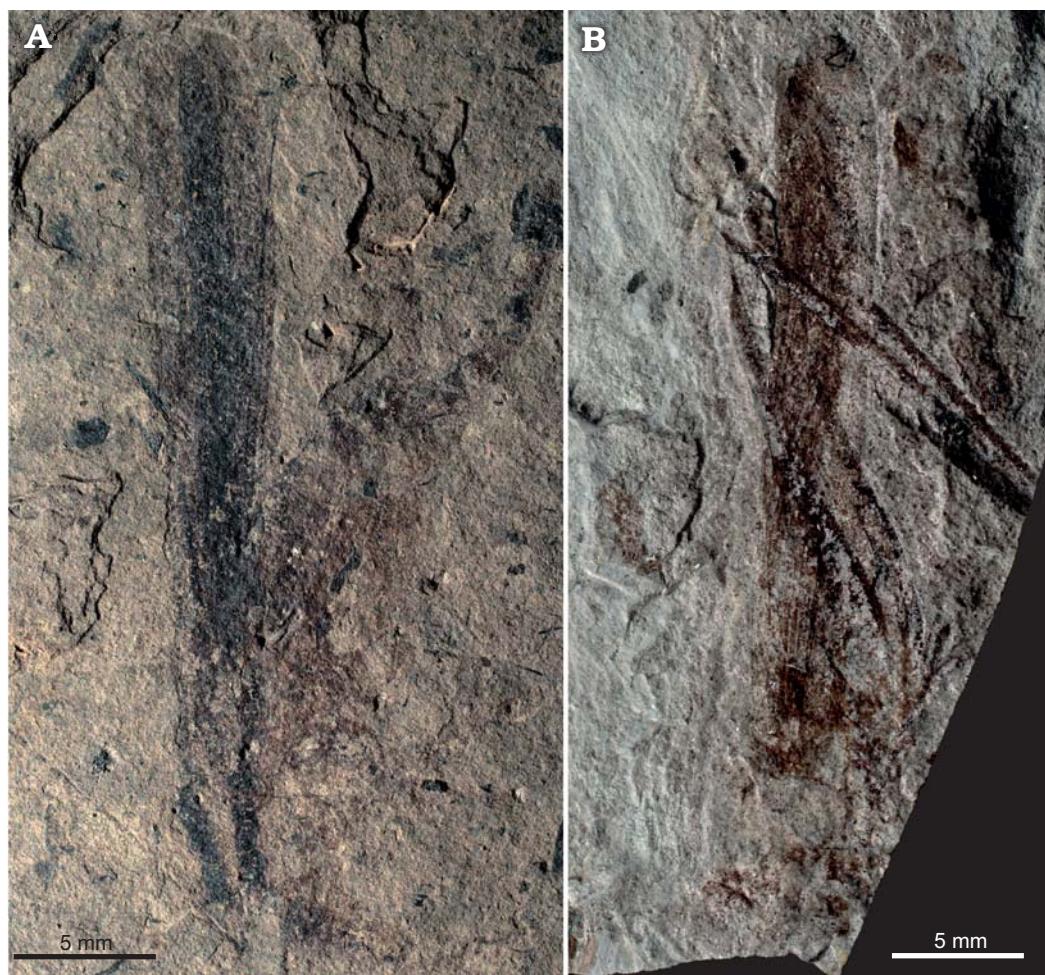


Fig. 3. Habitus of Ensifera from Paleocene of Menat, France. **A.** *Prophasgonura lineatocollis* Piton, 1940, holotype, MNHN.F.R07050. **B.** *Conocephalus martyi* Piton, 1940, holotype, MNHN.F.R07019.

Material.—Holotype only.

Remarks.—This poorly preserved fossil is a Tettigoniidae as shown by its long antennae, long curved ovipositor, and long tegmina, but its exact affinities are impossible to establish because the body structures are poorly preserved and the wing venation cannot be deciphered. *Prophasgonura lineatocollis* is a Tettigoniidae of uncertain affinities.

Stratigraphic and geographic range.—Paleocene, Menat Formation, Menat, France.

Genus *Conocephalus* Thunberg, 1815

Type species: *Conocephalus conocephalus* (Linnaeus, 1767), Recent.

Conocephalus martyi Piton, 1940

Fig. 3B.

Holotype: MNHN.F.R07019 (coll. Louis Piton), an adult Orthoptera with hind legs and wings attached to thorax.

Type locality: Historical quarry of Menat, Menat, Puy-de-Dôme, France.

Type horizon: Middle Paleocene, Menat Basin.

Material.—Holotype only.

Remarks.—The body structures are very poorly preserved

and the venation of tegmen is impossible to decipher. It is only possible to see that there is a dense net of cells covering the tegmen. It is a Tettigoniidae of uncertain affinities, impossible to accurately attribute to the extant genus *Conocephalus*.

Stratigraphic and geographic range.—Paleocene, Menat Formation, Menat, France.

Caelifera Ander, 1936

Acridoidea MacLeay, 1821

Acrididae MacLeay, 1821

Genus *Oedipoda* Latreille, 1829

Type species: *Oedipoda caerulescens* (Linnaeus, 1758); Recent, Europe, Northern Africa, Asia.

Oedipoda sp.

1940 *Oedipoda* spec.; Piton, 1940: 140–141, fig. 16.

Material.—No repository number, currently lost (coll. Louis Piton); basal half of a tegmen from Menat, Paleocene.

Remarks.—This tegmen is very narrow, with a very narrow area between C and ScP, unlike the extant genus *Oedipoda* Latreille, 1829. This pattern is quite strange for an Orthoptera

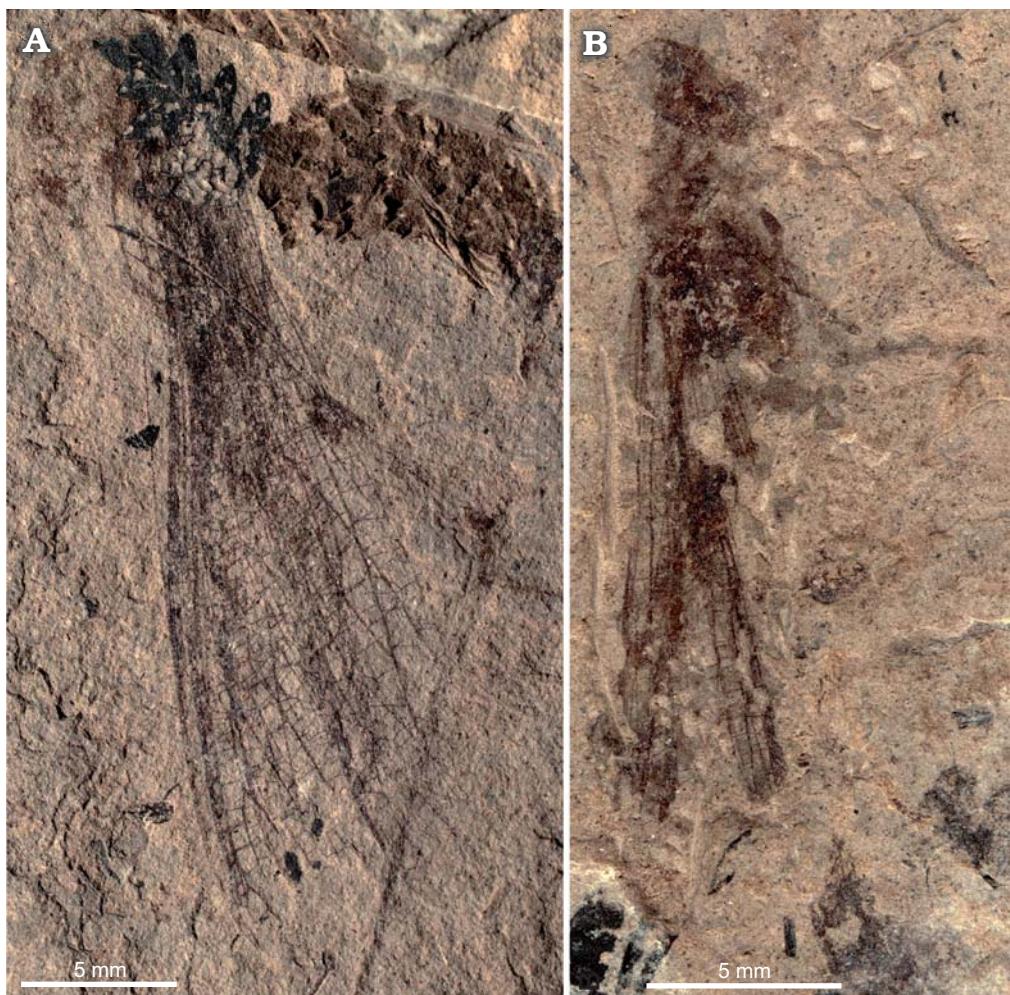


Fig. 4. Habitus of Caelifera from Paleocene of Menat, France. **A.** *Orthacanthacris incertus* Piton, 1940, holotype MNHN.F.R07017. **B.** *Ochrilidia lineata* Piton, 1940, holotype, MNHN.F.R07043.

as Piton (1940: fig. 16) figured because the putative M+CuA would diverge very basally from R and the cubital and anal veins are not distally fused as in the Caelifera. It is a Polyneoptera of uncertain affinities.

Family uncertain

Genus *Orthacanthacris* Karsch, 1896

Type species: *Orthacanthacris humilicrus* (Karsch, 1896), Recent, Afrotropics.

Orthacanthacris incertus Piton, 1940

Fig. 4A.

Holotype: MNHN.F.R07017 (coll. Louis Piton); a very poorly preserved specimen, with fragments of three wings, and dubious remains of thorax and head.

Type locality: Historical quarry of Menat, Menat, Puy-de-Dôme, France.

Type horizon: Middle Paleocene, Menat Basin.

Material.—Holotype only.

Remarks.—It is even not possible to determine which wings are forewing(s) vs. hindwing(s). It is either a Mantodea or an Orthoptera of uncertain affinities.

Stratigraphic and geographic range.—Paleocene, Menat Formation, Menat, France.

Family uncertain

Genus *Ochrilidia* Stål, 1873

Type species: *Ochrilidia tryxalicera* Stål, 1873, Recent, Eastern Africa.

Ochrilidia lineata Piton, 1940

Fig. 4B.

Holotype: MNHN.F.R07043 (coll. Louis Piton); a nearly complete but very poorly preserved specimen.

Type locality: Historical quarry of Menat, Menat, Puy-de-Dôme, France.

Type horizon: Middle Paleocene, Menat Basin.

Material.—Holotype only.

Remarks.—The extant genus *Ochrilidia* belongs to the Acrididae: Gomphocerinae. This fossil has narrow tegmina, with apparently few cells, with a narrow area between C and R and a darkened area between RA and C in distal part of wing. Its hind legs are elongate and with a rather thin femur; the head is orthognathous. The rather reduced number of

cells in distal part of tegmina would exclude this fossil from the Acrididae. It could be an Eumastacoidea. Its attribution to the genus *Ochrilidia* is not supported by any argument. It is a Caelifera of uncertain affinities.

Stratigraphic and geographic range.—Paleocene, Menat Formation, Menat, France.

Family uncertain

Genus *Menatacridium* Piton, 1936

Type species: *Menatacridium eocenicum* Piton, 1936; Menat, Paleocene.

Menatacridium eocenicum Piton, 1936

Holotype: No repository number, currently lost (coll. Louis Piton); a nearly complete tegmen.

Type locality: Historical quarry of Menat, Menat, Puy-de-Dôme, France.

Type horizon: Middle Paleocene, Menat Basin.

Material.—Holotype only.

Remarks.—This taxon was very poorly described and figured by Piton (1936, 1937, 1940: pl. 19: 1). We can only say that it is a Polyneoptera of uncertain affinities, possibly an Orthoptera, but probably not an Acridoidea.

Stratigraphic and geographic range.—Paleocene, Menat Formation, Menat, France.

Orthoptera indet.

Material.—No repository number, currently lost (coll. Louis Piton); a hind femur from Menat, Paleocene.

Remarks.—A hind femur has been ascribed to the new taxon name *Eremobiites* by Piton (1940), but this genus is preoccupied by *Eremobiites* Suassure, 1884. Furthermore, there is no named type species for the genus *Eremobiites* Piton, 1940, thus this genus name, that is based on a taxon in open nomenclature, should be considered invalid. This fossil is an Orthoptera indet.

Caelifera superfamily incertae sedis

Caelifera genus and sp. indet. A

Fig. 5.

Material.—MNHN.F.A71197 (coll. Philippe Olivier); a body with legs and wings attached from Menat, Paleocene.

Description.—Head visible but poorly preserved, 2.0 mm wide; antenna short, 3.0 mm long. Thorax very poorly preserved. Abdomen missing. Fore, mid and hind legs preserved. Hind femur elongate and rather narrow, 15.0 mm long, 1.5 mm wide; hind tibia very long and narrow, with two series of spines, the outer ones of proximal half very short and acute while those of distal half of femur broad and not acute; the inner series of spines all short and acute. Tarsi not preserved. Forewing 17.0 mm long, poorly preserved, hyaline except for two dark longitudinal zones, one along R and one along posterior wing margin, plus two transverse bands. Venation hardly visible, except for the costal area that is very broad,

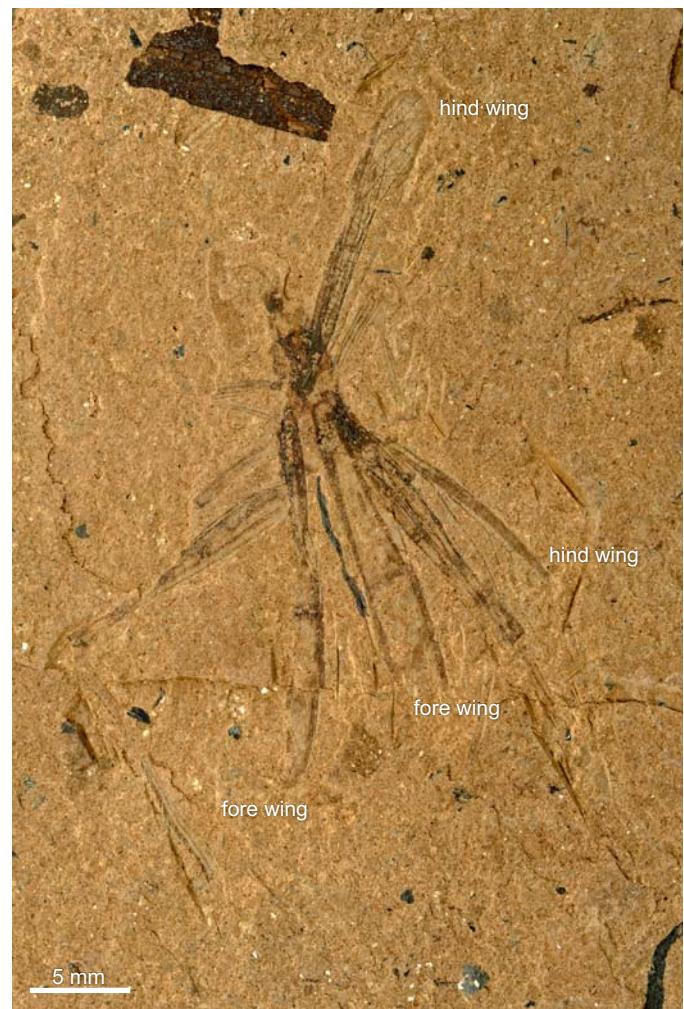


Fig. 5. Habitus of Caelifera genus and sp. indet. A, MNHN.F.A71197 from Paleocene of Menat, France.

2.0 mm wide with a series of ca. 10 curved crossveins. Hind wing hyaline, narrow but partly folded, 16.0 mm long; C very weakly curved basal of apex of ScA; area between C and ScA narrow, 0.4 mm wide, but poorly preserved; area between C and ScP narrow, with a series of short parallel crossveins; ScP and R strongly approximate but not touching; area between C, ScA, ScP, and RA darkened; M simple; a series of broad cells posterior to M; area between RA and RP narrow, with one row of simple crossveins between them; RP with four posterior branches, with one row of cells between them; part of wing posterior to CuP poorly preserved.

Remarks.—This fossil, although nearly complete, has its body and wings poorly preserved, rendering its affinities very uncertain. The presence of a very broad forewing costal area would suggest affinities with the Acridoidea, but some Eumastacoidea Chorotypidae (*Hemicharianthus* spp.) have also such a very broad area. The very particular outer spines of the hind femora are quite unusual among the Caelifera, and remind those of the fossil Elcanidae and the extant Tridactylidae. We cannot accurately name this fossil, even if certainly corresponds to a new taxon.

Eumastacoidea Burr, 1899

Chorotypidae Stål, 1873 (?)

Genus *Paleochina* nov.

Zoobank LSID: urn:lsid:zoobank.org:act:F95A0640-E6B9-41D1-BF8B-667066B2F7E2

Etymology: Named after Paleocene and the extant genus *China*.

Type species: *Paleochina duvergeri* sp. nov. (see below).

Species included: Type species and *Paleochina minuta* sp. nov.

Diagnosis.—Tegmen narrow; few intercalary cells between main veins; narrow area between radial vein and costa; darkened area between RA and C; five branches of RP with two rows of cells between them; C nearly straight along anterior margin; ScA ending on costa well basal of base of RP; narrow area between RA and RP.

Remarks.—This taxon is only tentatively placed in the Chorotypidae because the current classification of the Eumastacoidea is mainly based on the genital structures.

Paleochina duvergeri sp. nov.

Figs. 6, 7A.

Zoobank LSID: urn:lsid:zoobank.org:act:AD7F0C52-16A3-4CDB-A502-C676C84A7F7E

Etymology: Named after M. Bernard Duverger, for his authorization of collect of fossils in the area of Menat.

Holotype: MNT NEL 3267, two fore- and two hind wings, two hind legs.

Type locality: New quarry, Menat, Puy-de-Dôme, France.

Type horizon: Middle Paleocene, Menat Basin.

Material.—Holotype only.

Diagnosis.—M+CuA separating from R well distal of apex of ScA; two rows of cells between CuA+CuPaa and CuPaβ.

Description.—Forewing hyaline, very narrow, 23.3 mm long, 2.7 mm wide in widest part, 1.5 mm in narrowest; posterior margin straight; C very weakly curved basal of apex of ScA; area between C and ScA narrow, 0.3 mm wide, with a series of ca. 10 short parallel crossveins; apex of ScA 6.0 mm from wing base; area between ScA and ScP 0.3 mm wide; area between C and ScP narrow, 0.3 mm wide, with a series of short parallel crossveins; ScP and R strongly approximate but not touching; apex of ScP 6.0 mm distal of that of ScA; area between C and RA darkened, 0.25 mm wide, without visible crossvein, except near apex of RA; apex of RA 1.3 mm from wing apex; M+CuA appressed to R in basal half of wing, separating from R 8.5 mm from wing base; independent stem of M+CuA 2.3 mm long; M simple; CuPaa weak, ending into CuA 0.7 mm from point of separation between M and CuA; CuA+CuPaa simple; two rows of irregular cells between M and CuA+CuPaa; base of RP 12.3 mm distal of wing base; area between RA and RP narrow, 0.3 mm wide, with one row of simple crossveins between them; RP with five posterior branches, with two rows of cells between them; two rows of cells between CuA+CuPaa and CuPaβ; one row of cells between M+CuA and CuPa, and between CuPa and CuPb; CuPb straight, area between CuPb and anal vein very narrow.

Hindwing 22.0 mm long, narrow, with the anal area folded along first anal vein; hyaline, except for a darkened area between C and RA, as in forewing; part of wing anterior to the anal area nearly identical to forewing.

Hind leg long and rather thin: femur 16.7 mm long, 1.3 mm wide, with longitudinal anterior and posterior crests, without spines; tibia 13.2 mm long, 0.3 mm wide; with a series of ca. 28 strong spines, becoming more and more broad distally, apical spines poorly preserved; tarsus also poorly preserved.

Remarks.—The forewings, hindwings, and legs are grouped on a surface of 8 × 7 cm. They clearly belong to the same individual. The body is missing. This locust may have been attacked by a predator that has eaten the body. Wings and legs remained grouped because they have fallen in a surface algal mat (diatoms), and was transported at the lake bottom when the mat has sunk. This scenario is in accordance with what is generally observed in diatom paleolake (Nel 1991).

Stratigraphic and geographic range.—Paleocene, Menat Formation, Menat, France.

Paleochina minuta sp. nov.

Fig. 7B, C.

Zoobank LSID: urn:lsid:zoobank.org:act:C33D57DF-9413-4C75-A312-906D99EC2532

Etymology: Named after the minute size of the tegmen.

Type material: Holotype: MNT NEL 1928. Paratype: MNT BDL 1043, both isolated tegmina.

Type locality: New quarry, Menat, Puy-de-Dôme, France.

Type horizon: Middle Paleocene, Menat Basin.

Material.—Holotype and paratype only.

Diagnosis.—M+CuA separating from R well basal of apex of ScA; one row of cells between CuA+CuPaa and CuPaβ.

Description.—Holotype MNT NEL 1928 (Fig. 7B). Forewing hyaline, very narrow, 14.0 mm long, 2.2 mm wide in widest part; posterior margin straight; C very weakly curved basal of apex of ScA; area between C and ScA narrow, 0.3 mm wide, but poorly preserved; apex of ScA 4.3 mm from wing base; area between ScA and ScP 0.2 mm wide; area between C and ScP narrow, 0.2 mm wide, with a series of short parallel crossveins; ScP and R strongly approximate but not touching; apex of ScP 2.5 mm distal of that of ScA; area between C and RA darkened, 0.2 mm wide, without visible crossvein, except near apex of RA; apex of RA 1.5 mm from wing apex; M+CuA appressed to R in basal half of wing, separating from R 4.0 mm from wing base; independent stem of M+CuA 1.2 mm long; M simple; CuPaa weak, ending into CuA 0.4 mm from point of separation between M and CuA; CuA+CuPaa simple; one row of cells between M and CuA+CuPaa; base of RP 7.3 mm distal of wing base; area between RA and RP narrow, 0.4 mm wide, with one row of simple crossveins between them; RP with five posterior branches, with two rows of cells between them; one row of cells between CuA+CuPaa and CuPaβ; one row of cells



Fig. 6. Wings and hind legs of chorotypid orthopteran *Paleochina duvergeri* gen. et sp. nov., holotype, MNT NEL 3267 from Paleocene of Menat, France.

between M+CuA and CuPa, and between CuPa and CuPb; CuPb straight, area between CuPb and anal vein very narrow.

Paratype MNT BDL 1043 (Fig. 7C). Same pattern of coloration and venation as for holotype, tegmen ca. 14.5 mm long, 2.8 mm wide.

Remarks.—*Paleochina duvergeri* sp. nov. and *Paleochina minuta* sp. nov. have very similar tegmina, that of *P. duvergeri* being longer than that of *P. minuta* and with few differences indicated in the respective diagnoses. We consider that they belong to different species within the same genus. Sexual dimorphism that concern the size and shape of the tegmina can occur in the Caelifera. As we do not know the sex of these insects, it is not totally excluded that they could correspond to male and female of the same species but differences in the venation support a specific non-identity. These tegmina are typical of the Eumastacoidea, viz. reduction of vein CuPaa (Sharov 1968; Dirsh 1975), tegmen very narrow, with few intercalary cells between main

veins and a narrow area between radial vein and costa. Such structures can be found in some Chorotypidae Stål, 1873 and Eumastacidae Burr, 1899 (Dirsh 1975; internet site www.orthopteran.speciesfile.org). Among the Chorotypidae, *Paleochina* gen. nov. differs from *Erucius* Stål, 1875 (Eruciinae Burr, 1899) in the broader radial area and broader and darkened area between RA and C (Dirsh 1975: fig. 2). This last character of *Paleochina* gen. nov. is present in the genus *China* Burr, 1899, but *China mantispoidea* (Walker, 1870), unique species of this genus, has only three branches of RP instead of five in *Paleochina* gen. nov. (Descamps 1974: fig. 30). *Eupatrides* Brunner von Wattenwyl, 1898, second genus of the subfamily Chininae Burr, 1899, has a broader area between C and ScA, with C making a strong curve instead of being straight. Among the winged Chorotypinae Stål, 1873, *Burrinia* Bolívar, 1930 has two rows of cells in area between ScA and C and less developed area of RP (Bolívar 1930). *Chorotypus* Bolívar, 1930,

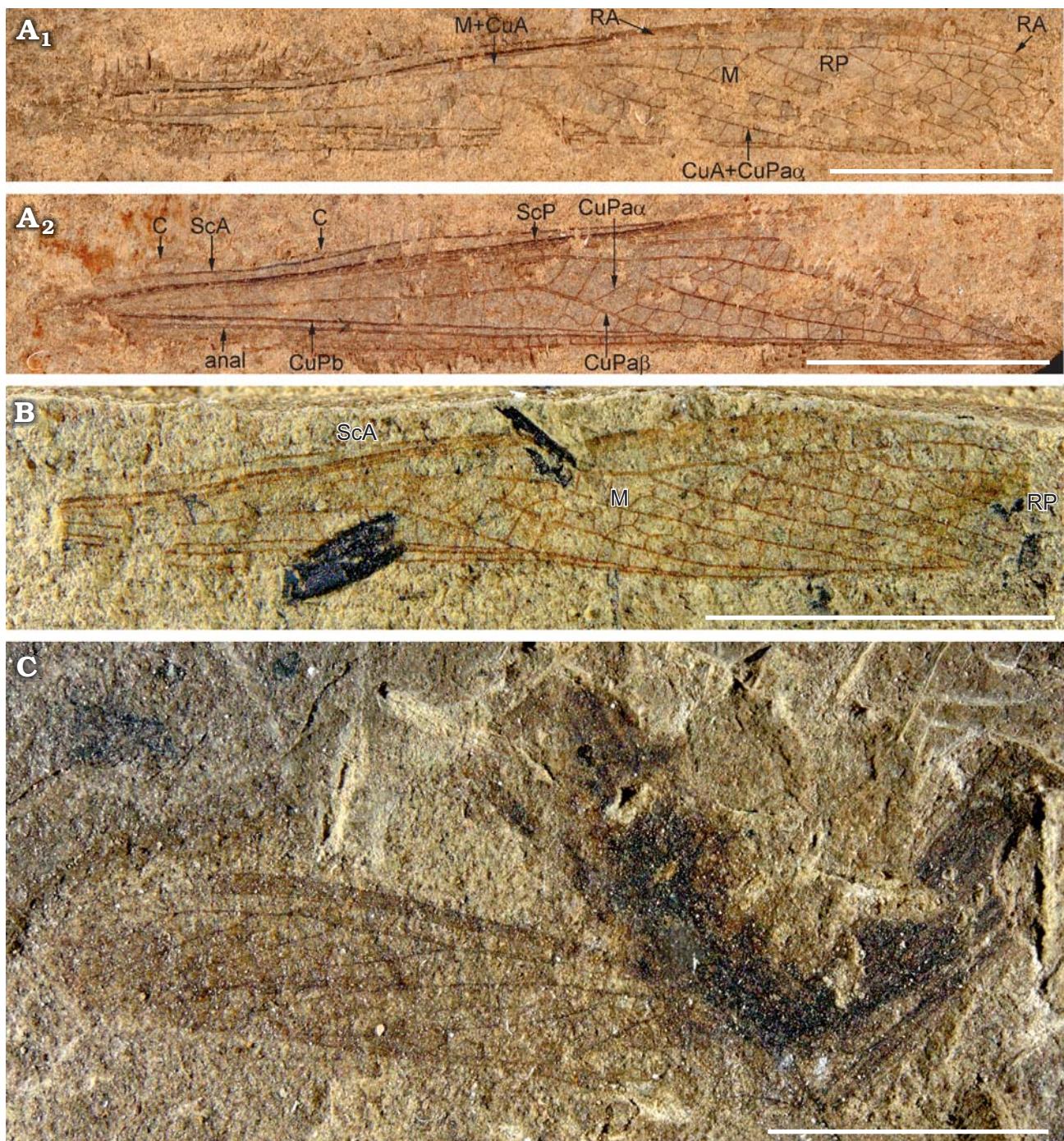


Fig. 7. Tegmina of chorotyrid orthopteran *Paleochina* spp. from Paleocene of Menat, France. A. *Paleochina divergeri* gen. et sp. nov., holotype, MNT NEL 3267; A₁, left wing; A₂, right wing (reversed view). B. *Paleochina minuta* sp. nov., holotype, MNT NEL 1928. C. *Paleochina minuta* sp. nov., paratype, MNT BDL 1043. Scale bars 5 mm. Abbreviations: C, costa; CuA/P, cubitus anterior/posterior; CuPa α , most anterior branch of CuP; CuPa β , median branch of CuP; CuPb, posterior branch of CuP; M, median vein; RA/P, radius anterior/posterior; ScA/P, subcostal anterior/posterior.

Orchetypus Brunner von Wattenwyl, 1898, *Phyllochoreia* Westwood, 1839, and *Hemierianthus* Saussure, 1903 have broader tegmina, with numerous rows of cells between main veins. *Pseudorchetypus* Descamps, 1974 and *Scirtotypus* Brunner von Wattenwyl, 1898 has C making a strong curve instead of being straight in its basal part (Descamps 1974). The extant Erianthinae Karsch, 1889 have a broader area between C and ScP.

Among the extant winged Eumastacidae, several genera, e.g., *Eumastax* Burr, 1899, *Homeomastax* Descamps, 1979, *Hystericomastax* Descamps, 1979, *Helicomastax* Rowell and Bentos-Pereira, 2001, *Paramastax* Burr, 1899, and *Temnomastax* Rehn and Rehn, 1942, among others, have much reduced venation of the tegmina, with three or less branches of RP (Dirsh 1975; Descamps 1974, 1979; internet site [www.orthopteran.speciesfile.org](http://orthopteran.speciesfile.org)). *Paleochina* gen. nov. is prob-

ably not a Eumastacidae and more likely a Chorotypidae, but a more complete specimen with genitalia at least partly preserved will be necessary to better support its exact relationships.

Among the fossil Eumastacoidea, *Promastax archicus* Handlirsch, 1910 (type species of the fossil family Promastacidae Kevan and Wighton, 1981, Paleocene–Eocene, Canada, the distal two-third of a tegmen) has only three branches of RP, ScA ending on costa distal of base of RP, a broad area between RA and RP, unlike *Paleochina* gen. nov. (Handlirsch 1910: fig. 1). Notice that this fossil family is based on few, poor characters (Kevan and Wighton 1981), and should be revised. The second genus and species of this family, *Promastacoides albertae* Kevan and Wighton, 1981 (same outcrop) is based on a nearly complete tegmen. The original description and figure are problematic, but it seems to have M with three branches, and a quite broad wing, unlike the Eumastacoidea. Its phylogenetic relationships are uncertain.

All the described fossil taxa currently placed in Eumastacidae are based on wings, thus their exact positions in the Eumastacoidea are tentative. The Jurassic genus *Archaeomastax* Sharov, 1968 differs from *Paleochina* gen. nov. in the broader area between ScP and RA (Sharov 1968). The Eocene *Eoerianthus* Gorochov in Gorochov and Labandeira, 2012, has only three branches of RP and apices of ScP and RA very close to wing apex (in the type species *E. eocaenicus* Gorochov, 2012). The second species *E.? multispinosa* (Scudder, 1890), originally placed in the fossil genus *Tyrbula* Scudder, 1885 (type species *Tyrbula russelli* Scudder, 1885), and Truxalidae, is rather poorly preserved. The Paleocene–Eocene *Eozaen huepfer* Zessin, 2017 has a two-branched median vein (Zessin 2017b), while it is simple in *Paleochina* gen. nov. The fossil genus *Taphacris* Scudder, 1890 is rather poorly defined (Zeuner 1944; Rehn 1948). Its type species *Taphacris reliquata* Scudder 1890 (Eocene–Oligocene of Florissant, USA) has a simple M but only four branches of RP, unlike *Paleochina* gen. nov. (Scudder, 1890). *Taphacris bittaciformis* Cockerell, 1909 (same outcrop) is poorly described and figured, nevertheless it has a three-branched RP (Cockerell 1909, 1926), unlike *Paleochina* gen. nov. *Taphacris bittaciformis tillyardi* Cockerell, 1926 (same outcrop) is even based on a more fragmentary fossil. The Chinese Paleocene *Taphacris stenosis* Lin, 1977 has also four branches of RP and a simple M, but a distinctly longer ScA than in *Paleochina* gen. nov., reaching mid wing level (Lin 1977). The Chinese Early Cretaceous *Taphacris turgis* Lin, 1980 has apparently the same characters but it would need a revision (Lin 1980). The Miocene *Paleomastacris ambarinus* Pérez-Gelabert, Hierro, Dominici, and Otte, 1997 (from the Dominican amber) is based on an apterous fossil, not comparable to *Paleochina* gen. nov. (Pérez-Gelabert et al. 1997; Pérez-Gelabert 2002). Lastly Lewis et al. (1990) cited a Eumastacidae from the Miocene of Idaho. *Orthacanthacris rhenana* Theobald, 1937 (Oligocene, Germany) could also be an Eumastacoidea

for the narrow tegmina and thin and long hind legs; it differs from *Paleochina* gen. nov. in the more numerous branches of RP (Théobald 1937). This taxon needs to be revised. Lewis (1974) figured undescribed specimens from the Oligocene of Ruby River Basin (Montana) that are attributable to the Eumastacoidea. Lewis (1976) also figured an undescribed eumastacoid tegmen (either in Eumastacidae or Chlorotypidae) from the same outcrop. Its area between C and ScA is broader than in *Paleochina* gen. nov. Martins-Neto (1991a) cited the presence of an Eumastacoidea in the Cretaceous of the Crato Formation in Brazil, that was never described.

Among the other Caelifera described from Menat, only “*Oedipoda* spec.” and *Ochrilidia lineata* are comparable to *Paleochina* gen. nov. “*Oedipoda* spec.” differs from *Paleochina* gen. nov. in the presence of three dark spots on the tegmen. *Ochrilidia lineata* differs from *Paleochina* gen. nov. in the absence of secondary zigzagged longitudinal veins between branches of RP. It also differs from *Paleochina duvergeri* in the distinctly shorter tegmina (ca. 16–17 mm long). The “genus and species A” described above differs from *Paleochina* gen. nov. in the very broad costal area in forewing. Heads (2008) described an apterous Eumastacoidea Proscopiidae from the Lower Cretaceous of the Crato formation in Brazil, showing the antiquity of this superfamily.

Stratigraphic and geographic range.—Paleocene, Menat Formation, Menat, France.

Elcanoidea Handlirsch, 1906

Elcanidae Handlirsch, 1906

Remarks.—The exact phylogenetic relationships of the Elcanoidea within the Orthoptera remain debatable. If Gorochov and Rasnitsyn (2002) considered them as sister group to all other Orthoptera, Béthoux and Nel (2002) considered them as Caelifera on the basis of a phylogenetic analysis.

Genus *Cenoelcanus* nov.

Zoobank LSID: urn:lsid:zoobank.org:act:0745091A-8429-45A2-9B26-A3AF46952577

Type species: *Cenoelcanus menatensis* sp. nov., by monotypy, see below.

Etymology: Named after Cenozoic and genus *Elcanus*.

Diagnosis.—As for the type species by monotypy.

Cenoelcanus menatensis sp. nov.

Fig. 8.

Zoobank LSID: urn:lsid:zoobank.org:act:E1F797A4-4027-472F-A4A8-7622B2EBB123

Etymology: Named after the village of Menat.

Holotype: MNHN.F.A71198 (coll. Philippe Olivier); an incomplete tegmen.

Type locality: Historical quarry of Menat, Menat, Puy-de-Dôme, France.

Type horizon: Middle Paleocene, Menat Basin.

Material.—Holotype only.

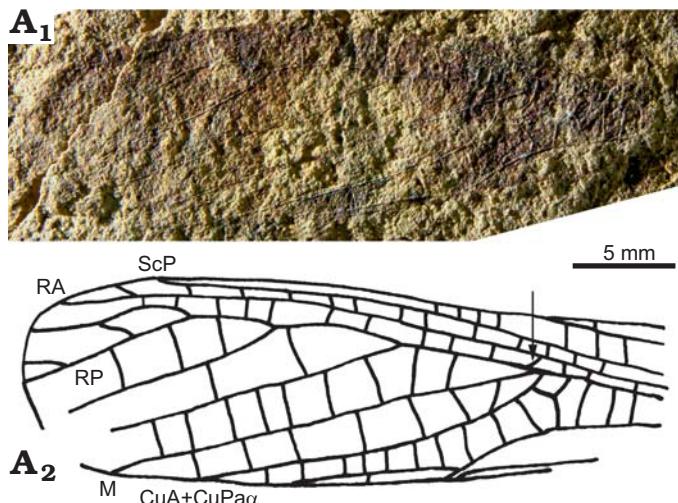


Fig. 8. Tegmen of Elcanid orthopteran *Cenoelcanus menatensis* gen. et sp. nov., holotype, MNHN.F.A71198 from Paleocene of Menat, France. Photograph (A₁), reconstruction (A₂). Abbreviations: CuA/P, cubitus anterior/posterior; CuPaa, most anterior branch of CuP; M, median vein; RA/P, radius anterior/posterior; ScP, subcostal posterior.

Diagnosis.—Forewing characters only. Area between R and M+CuA with a series of short crossveins; distal fusion of of CuPa β , CuPb, and A; base of RP very close to point of separation of M and CuA; M+CuA and RP seem to be aligned; only four branches of RP.

Description.—Distal two-third of a forewing with dark areas along costal part and mid part of tegmen, preserved part 13.0 mm long, 4.2 mm wide in widest part, 3.0 mm in narrowest; posterior margin straight; only distal part of area between C and ScP preserved, 0.7 mm wide, with a series of parallel crossveins; ScP and R not touching, with a series of very short crossveins between them; apex of ScP 8.0 mm distal of that of ScA; area between C and RA 0.3 mm wide, without crossveins; apex of RA 1.3 mm from wing apex; M+CuA not appressed to R, with a series of short crossveins between them, M simple; CuPaa very weak; CuA+CuPaa simple; one row of cells between M and CuA+CuPaa; base of RP as a short oblique veinlet very close to point of separation between M and CuA, 0.15 mm apart; stem of M+CuA aligned with RP; area between RA and RP narrow, 0.4 mm wide, with one row of simple crossveins between them; RP with four posterior branches, with one row of cells between them; one row of cells between CuA+CuPaa and CuPa β ; one row of cells between M+CuA and CuPa, and between CuPa and CuPb; CuPa β distinctly curved, and parallel to posterior wing margin in distal part; CuPb straight, area between CuPb and first anal vein very narrow; anal area not preserved.

Remarks.—The broad area between ScP and costal margin indicates that this fossil is a tegmen and not a hindwing. The presence of long veins parallel to posterior wing margin, the truncate wing apex, the veins M and CuA separating very far from wing base, and the weak CuPaa are characters present in Caelifera. *Cenoelcanus menatensis* gen. et sp. nov. has

a very particular character, viz. the alignment of RP with stem of M+CuA so that RP seems to be a distal branch of M+CuA. This structure is only present in the pre-Cenozoic superfamily Elcanoidea Handlirsch, 1906 (= Permecanidae Sharov, 1962 + Elcanidae Handlirsch, 1906), and considered as the main synapomorphy of this group by Gorochov and Rasnitsyn (2002: fig. 430). The Permecanidae would differ from the Elcanidae by the presence of a better defined origin of RP, which is clearly a plesiomorphic state of character (Sharov 1968). *Cenoelcanus* gen. nov. better falls in the Elcanidae because the base of RP is reduced to a short oblique veinlet. Gorochov et al. (2006) divided the Elcanidae into Elcaninae and Archelcaninae Gorochov et al. 2006, and characterized the Elcaninae on the basis of the more or less narrowed area between tegminal RA and RP, the fused (with each other) distal parts of CuPa β , CuPb, and A, and “possibly the rather small spines of the hind tibiae”. As *Cenoelcanus* gen. nov. has two most important venation characters of the Elcaninae, we consider it belongs to this subfamily. The Archelcaninae would be characterized by the presence of large spines on hind tibia, unknown in our fossil.

Cenoelcanus gen. nov. differs from all the Mesozoic elcanid genera (in which the tegmina are known) by the combination of the two characters: presence of only four branches of RP and a very short vein between M+CuA and RP (Gorochov 1986; Martins-Neto 1991b; Gorochov et al. 2006; Poinar et al. 2007; Fang et al. 2015, 2018a, b). The very long ScP is a character only present in the Permo-Triassic *Meselcana* Sharov, 1968, which could look strange to find in the youngest representative of the Elcanidae. But a reversal is always possible. *Burmelcana* Peñalver and Grimaldi, 2010 and *Hispanelcana* Peñalver and Grimaldi, 2010 are based on nymphs in amber, impossible to compare to *Cenoelcanus* gen. nov. (Peñalver and Grimaldi 2010; Fang et al. 2015). A structure analogous to the “elcanoid” alignment of M+CuA and RP is present in the extant genus *Charilaus* Stål, 1875 (Pamphagodidae Bolívar, 1884) but in this genus, M+CuA is making a thick complex vein together with R, from which CuA, M, and RP successively separate. Thus it is certainly not homologous to the structure of the Elcanoidea and *Cenoelcanus*.

Stratigraphic and geographic range.—Paleocene, Menat Formation, Menat, France.

Discussion

Paleochina duvergeri sp. nov., *Paleochina minuta* sp. nov., and *Cenoelcanus menatensis* sp. nov. are the first Caelifera found in the outcrop of Menat that can be accurately placed in superfamilies. The other fossil Caelifera described by Piton (1940) are all incertae sedis, and cannot be placed in the superfamily Acridoidea. They cannot be used for future dating of this clade. Song et al. (2015) used *Tyrbula*

russelli Scudder, 1885 (lowermost Oligocene of Florissant, Colorado; Scudder 1885, 1890) to calibrate the dating of Acrididae, but Zeuner (1944: 361) indicated that: “Scudder considered *Tyrbula* as an acridine genus on account of the general proportions and the clubbed antennae. Clubbed antennae, however, also occur in the Catantopinae. The smallness of the eyes speaks most emphatically against the Acridinae. The venation, which would settle the point, has not been described.” In fact, this fossil would need a complete revision.

Song et al. (2015) dated the Acrididae origin from the Latest Cretaceous and their diversification from the Paleocene–Eocene, but Song et al. (2018) dated the origin of the family from the Paleocene and the diversification of the majority of the subfamilies from the late Eocene and the Oligocene, which is more in accordance with the Oligocene age of the oldest known Acridoidea (Ataabadi et al. 2017). As these insects frequently live on grasses (Pooideae), these relatively young fossils are in accordance with the major diversification of this clade of plants that happened during the late Eocene–Oligocene (Schubert et al. 2019). The Eumastacoidea, more related to trees, are less and less frequent in the fossil record at the same time. Nevertheless, true grasses of bambusoid type are known in the “mid” Cretaceous Burmese amber (Poinar 2004), thus Acridoidea could have been Cretaceous too. They remain to be discovered. Menat paleolake is a good candidate to search after them.

Cenoelcanus menatensis sp. nov. is the youngest and first Cenozoic representative of the Mesozoic family Elcanidae. The previously youngest Elcanoidea were dated from ca. 100 Myrs in Burmese amber. This discovery shows that this clade survived the Cretaceous/Paleogene extinction event and became extinct during the Paleogene, maybe after the Paleocene. Such situations occur also in other animal clades, such as the multituberculates mammals or some Chrysopoidea (Nel et al. 2005). Li et al. (2019) supposed that some Cretaceous Elcanidae were able to swim under water using leaf-like metatibial spurs. The extant pygmy mole crickets of the genus *Xya* also swim under water using similar structures (Burrows and Sutton 2012). The Elcanidae and Tridactylidae co-existed during the Cretaceous and are both recorded in the “mid” Cretaceous Burmese amber. The reasons of the Cenozoic extinction of the Elcanidae and of the survival of the Tridactylidae remain unknown. Unfortunately the body and leg morphology of *Cenoelcanus menatensis* sp. nov. are still unknown. Future discoveries will possibly help to determine if this Paleocene “survivor” were also able to swim.

Conclusions

The orthopteran fauna of the Menat can be considered as the richest for the Paleocene period. It seems to be dominated by the Caelifera, which could correspond to a fossilization artifact because the locusts are generally more robust with

thicker cuticle than the crickets and katydids. The more remarkable facts concerning this assemblage is the diversity of the Eumastacoidea and the presence of the youngest representative of the extinct superfamily Elcanoidea, while the Acridoidea remain unrecorded. This fauna has an old still “Mesozoic” influence. Further field researches will be necessary to verify these preliminary results.

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