

The oldest opatrine terrestrial darkling beetle (Coleoptera: Tenebrionidae: Tenebrioninae) from the Paleocene of Menat (France)

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Received: 8 August 2016 / Accepted: 27 May 2017 / Published online: 7 July 2017
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Abstract The oldest terrestrial darkling beetle of the opatrine lineage, *Palaeosclerum pohli* gen. et sp. nov. (subfamily Tenebrioninae) is described from the Middle Paleocene of Menat (France). The complex of characters, combining the peculiar shape of body (robust, adapted to a fossorial lifestyle), structure of fossorial protibia, 5-segmented antennal club demonstrates a considerable similarity of the new genus to the extant representatives of the ‘sclerina’ generic group of the subtribe Opatrina. *Palaeosclerum* gen. nov. is compared with recent genera *Sclerum* Dejean, 1834, *Platynosum* Mulsant and Rey, 1859 and *Eurycaulus* Fairmaire, 1868.

Keywords Coleoptera · Tenebrionidae · gen. et sp. nov. · Paleocene · France

Kurzfassung Der älteste terrestrische Schwarzkäfer (der Abstammungslinie Opatrini), *Palaeosclerum pohli* gen. et

sp. nov. (Unterfamilie Tenebrioninae), wird aus dem mittleren Paläozän von Menat in Frankreich beschrieben. Verschiedene Charaktermerkmale, einschließlich der eigentümlichen Form des Körpers (robust, angepasst an eine grabende Lebensweise), der Ausbildung der Grab-Protibia und die fünfgliedrigen Fühler, zeigen eine große Ähnlichkeit der neuen Gattung zu rezenten Vertretern der “Sclerina”-Gattungsgruppe des Subtribus Opatrina. *Palaeosclerum* gen. nov. wird mit den heutigen Gattungen *Sclerum* Dejean, 1834, *Platynosum* Mulsant und Rey, 1859 und *Eurycaulus* Fairmaire, 1868, verglichen.

Schlüsselwörter Coleoptera · Tenebrionidae · gen. et sp. nov. · Paläozän · Frankreich

Introduction

Darking beetles (Tenebrionidae Latreille, 1802) are one of the largest families of the order Coleoptera, including about 20,000 species in the recent world fauna. More than half of the extant members of the family are xerophilous and spread in arid and semiarid landscapes of all continents, including subantarctic islands (but not actually Antarctica). Arid-adapted terrestrial species are poorly represented in known fossils for taphonomic reasons. Therefore, most extinct species belong to dendrobiontic groups (Kirejtshuk et al. 2008). Most extinct tenebrionids are known from Baltic amber (late Eocene), Geiseltal (Middle Eocene) and Dominican amber (early Miocene). The oldest Paleogene Helopini (Tenebrioninae) genus and species was recently described from the Middle Paleocene of Menat (Nabozhenko and Kirejtshuk 2014). Mesozoic Tenebrionidae are poorly represented in the fossil record. At present, we have descriptions of only two Jurassic

Handling editor: Mike Reich.

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comb-clawed beetles (Alleculinae), and three early Cretaceous tenebrionids (two species of subfamily Alleculinae and one of the tribe Alphitobiini, Tenebrioninae) (Kirejtshuk et al. 2012; Nabozhenko and Kirejtshuk 2014; Nabozhenko et al. 2015; Chang et al. 2016). The other Cretaceous taxa described in the beginning of the twentieth century, after studies of imprints of beetles represented by separated elytra or very incomplete insect bodies and classified as Alleculinae, are doubtful and need further revision (Nabozhenko et al. 2015). Among all described Jurassic, Cretaceous and Paleocene darkling beetles, till now terrestrial arid-adapted species were absent.

Materials and methods

The holotype examined is deposited in Musée Lecoq d'Histoire Naturelle in Clermont-Ferrand (France). It was studied using a stereomicroscope Olympus SCX9 in Muséum National d'Histoire Naturelle (Paris), and a stereomicroscope Leica MZ 16.0 in the Zoological Institute (St. Petersburg) with different modes of light and color filters. The specimen was also examined with a Tescan Vega LSU scanning electron microscope in MNHN to test the characters not clearly visible in the usual optic stereomicroscope (puncturation, outlines of legs, pronotum, elytra, etc.) with the Low Vacuum Secondary Electron TESCAN Detector (LVSTD).

Geological setting and locality

Geological setting and stratigraphy, depositional environment as well as maps of Paleocene volcano-sedimentary maar are reviewed and summarized in many works (Piton 1940; Wappler et al. 2009; Nel and Auvray 2006; etc.). The Menat Pit fossil site is located France, Department Puy-de-Dôme (near Gannat) (46°06'N, 02°54'E). The age of Menat according to the pollen, paleomammalian stratigraphic, and radiometric K/Ar analyses was estimated as 59 Ma (Kedves and Russel 1982; Nel 2008). The estimation based on macroflora postulated its age within 60–61 Ma (Wappler et al. 2009).

Brief information about paleobiota of Menat

The paleomacroflora of the Menat locality was very rich, including diverse coniferous (*Pinus*, *Abies*, *Sequoia*, *Thuja*, etc.) and deciduous (many species of *Quercus*, *Populus*, etc.) trees. Consequently, dendrobiontic insects dominate among insect fossils from this outcrop. Blattodea and Coleoptera are the most numerous and most diverse insects of Menat (Piton 1940; Nel and Auvray 2006). Most beetles are identified only to the family level, which is partly

related to poor preservation of fossils due to peculiar taphonomic reasons. Among beetles, Buprestidae, Carabidae, Cerambycidae, Elateridae, and Staphylinidae have been described in greater number than other groups (Piton 1940). The current studies show a considerable representation of Cupedidae consisting of some genera as remains of the Mesozoic fauna (for example, members of the Cenozoic subgenus *Caenomerga* Kirejtshuk, Nel and Kirejtshuk, 2016, of the genus *Mesocupes* Martynov, 1926 and apparently *Mesocupes* Kirejtshuk, Nel and Kirejtshuk, 2016), although at the same time some close relatives to the modern fauna were present (at least by probable members of the *Cupes* Fabricius, 1801). The general composition of beetles in the outcrops of Menat includes a significant proportion of weevils (more than half of beetle remains), many specimens of Buprestidae, Cerambycidae, Elateridae, Nitidulidae, and some other arboreal groups (Balazuc and Descarpentries 1964; Nabozhenko and Kirejtshuk 2014; Kirejtshuk et al. 2016). Before the current studies, Tenebrionidae were known only after one species of the genus *Cryptohelops* Nabozhenko and Kirejtshuk, 2014, which is rather similar to recent *Stenohelops* Reitter, 1922 (Tenebrionidae, Helopini) (Piton 1940; Nabozhenko and Kirejtshuk 2014). This representation of beetles should be associated with forest ecosystems around the place of their deposition and it is in accordance with other invertebrate groups (Piton and Théobald 1937; Piton 1940; Stroński and Szewo 2012; etc.).

Systematic palaeontology

Phylum **Arthropoda** von Siebold, 1848

Class **Insecta** Linné, 1758

Order **Coleoptera** Linné, 1758

Family **Tenebrionidae** Latreille, 1802

Subfamily **Tenebrioninae** Latreille, 1802

Tribe **Opatrini** Brullé, 1832

Genus ***Palaeosclerum*** gen. nov.

Etymology. The name of the new genus is formed from the Greek “palaeo” (παλαιός—old, ancient) and generic name “*Sclerum*” Gender neutral.

Type species. *Palaeosclerum pohli* sp. nov.

Diagnosis. Body robust, comparatively small. Head with median deep triangular emargination at anterior margin. Head and pronotum with coarse and dense puncturation. Antennae short, with 5-segmented club. Pronotum transverse, massive, with shallowly bi-emarginate anterior margin and slightly projecting anterior angles, which closely contacted with lateral sides of head. Lateral margins of pronotum serrate in basal third. Elytra robust, subparallel sided, with nine sparsely punctured interstriae and eight

striae. Strial punctures deep, depressed. Protibiae strongly dilated with edges subparallel in distal half, without large teeth, but crenellate along outer edge. Meso- and metatibiae short, moderately wide, not widened from base to apex. Tarsi slightly shorter than tibiae.

Comparison. See “Discussion” and Table 1.

Remarks. The new genus is included in the family Tenebrionidae based on the following combination of characters: presence of scutellary striole; tarsal formula 5-5-4; strongly widened and fossorial protibia, but without large teeth; triangularly and rather deeply excised anterior margin of head (character of the opatrine branch, tribes Opatrini, Pedinini).

Palaeosclerum pohli gen. et sp. nov.

Figures 1, 2, 3

Etymology. The epithet of the new species is dedicated to Burkhard Pohl, who collected many interesting fossil specimens in the Menat outcrop.

Holotype. D.MHLCLFE.2016.1.1 (“M622”, collector’s number), imprint and counterimprint with the incomplete specimen (dorsum of body with some sclerites of appendages: left tibiae and tarsi), deposited in the rather hard and somewhat calcined rock. It originated from a new, small outcrop near to and south–east of the village of Menat.

Locality and horizon. The Menat Pit fossil site is located France, Department Puy-de-Dôme (near Gannat) (46°06’N, 02°54’E). The Middle Paleocene; approximately 60–61 Ma. Type locality is situated around the small lake near the village of Menat. Map is given in Stroiński and Szwedo (2012).

Diagnosis. See the diagnosis above for the new genus with the single new species under description.

Description. Body length 4.3 mm, width 2.5 mm. Body short oval and rather convex dorsally. Head transverse, widest on genal level. Anterior margin of head widely rounded. Genae large, projected, head without sinuation between frontoclypeus and genae. Puncturation of head comparatively fine and sparser than on other dorsal sclerites, each puncture bearing short setae (stout hairs). Antennae with 5-segmented club of transverse antennomeres. Pronotum transverse (near 2.5 as wide as long), subcordiform, widest before middle, nearly 1.6 times as wide as head on the genal level. Anterior margin of pronotum shallowly bi-emarginate but slightly convex in the middle. Lateral edges of pronotum somewhat S-outlined: arcuately rounded in anterior two-thirds and widely sinuate and serrate in the basal third. Base of pronotum widely regularly arcuately convex, not beaded. Anterior edge of pronotum near 1.5 times as wide as posterior one. Puncturation of pronotum strongly coarse and dense; punctures large, deep, longitudinally elongate, each with

Table 1 Characters of *Palaeosclerum* gen. nov. and recent genera of ‘sclerina’ generic group sensu Iwan (2004)

Character	<i>Palaeosclerum</i>	<i>Sclerum</i>	<i>Eurycaulus</i>	<i>Platynosum</i>
Ratio elytral/pronotal length	Near 2	2.3–2.6	2–2.1	1.9–2
Ratio elytral length/width	Near 1.2	1.4–1.6	1.1–1.3	1.3
Narrow deep emargination of frontoclypeus	Present	Present	Present	Present
Protibiae	Fossorial	Fossorial	Fossorial	Fossorial
Outer margin of protibia	Dilated	Dilated	With distinctly protruding denticle	With distinctly protruding denticle
Dentation of lateral pronotal margin	Present	Present	Present	Present
Antennal club	5-Segmented	5-Segmented	4-Segmented	3-Segmented
Elytra	Short, oval	Long, subparallel	Short, oval	Short, oval
Pronotal base	Arcuate	Bisinate	Arcuate	Arcuate
Lateral margins of pronotum	Serrated (at least in basal half)	Serrated	Serrated	Serrated
Setation of body surface	Not visible on holotype	Yes	Yes (long)	Yes
Pronotal disc sculptured	Not	Yes	Slightly	Yes
Head sculptured	Not	Yes	Yes	Yes
Meso- and meta tibiae	Slightly widened	Distinctly widened at apex	Distinctly widened at apex	Fossorial
Elytral stria punctures	Small, slightly depressed	Foveolate	Foveolate	Foveolate
Elytral intervals 1, 3, 5, 7	Visibly not convex	Strongly convex	Strongly convex	Strongly convex

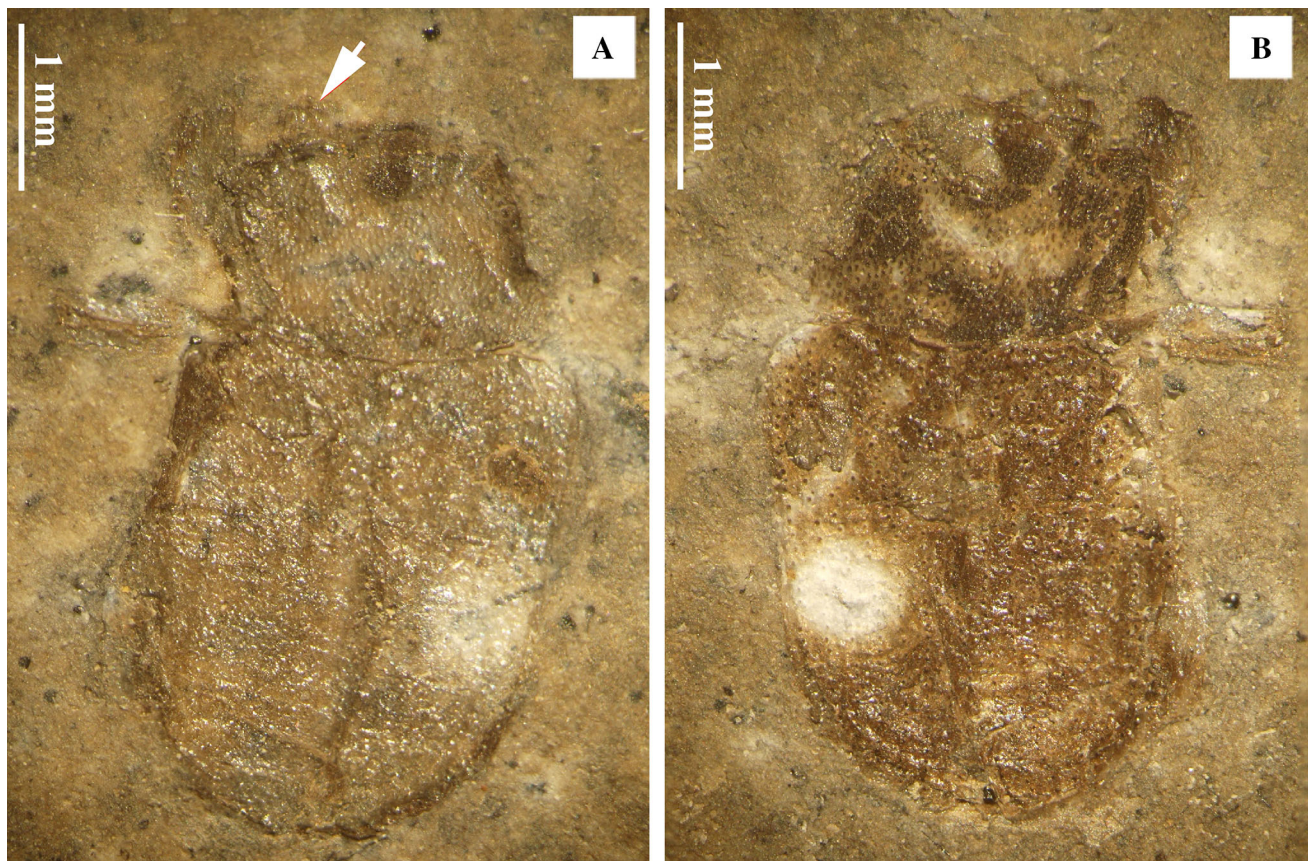


Fig. 1 *Palaeosclerum pohli* gen. et sp. nov., holotype, Middle Paleocene of Menat (France), optic microscope. **A** Habitus, part (arrow shows clubbed left antenna); **B** Habitus, counterpart

short seta (stout hair); diameter of punctures 2–4 times as great as distance between them. Scutellum triangular, moderately sized.

Elytra rather short (about 1.2 times as long as wide combined), widest in the middle. Strial punctures oval, apparently moderately depressed. Each stria with near 30 punctures. Interstriae with sparse and very fine but distinct puncturation (diameter of punctures more than 5–6 times as short as distance between them). Protibiae regularly widening in proximal half and strongly dilated and subparallel sided in distal one, with very coarse and dense punctures, probably foveae). Each fovea (puncture) with short strong seta. Meso- and metatibiae apparently slightly widened from base to apex. Metatibiae apparently slightly longer than mesotibiae. Tarsi about 3/5 as long as corresponding tibiae, tarsomeres narrow, moderately short and somewhat elongate.

Discussion

Classification of opatrine beetles has been rather disputable for a long time. Iwan (2001, 2004) significantly clarified the classification of “opatrine lineage” and

divided the subfamily Opatrinae sensu G. S. Medvedev (1968) into two main tribes, Opatrini and Pedinini, based on the characters of structure of the male genitalia and coxa/trochanter/femur complex. The tribe Pedinini includes the species with ‘small’ trochanter and large process at the femoral base, while the species with large trochanter (including the process of the trochanter base) and reduced or small process of the femoral base belong to the tribe Opatrini. Unfortunately, this character is not observable in the examined holotype of *Palaeosclerum* gen. n., therefore it is impossible to use these features to attribute the new genus to one of these two groups. The emarginate anterior edge of the head supports assignment of the new genus to the ‘opatrine lineage’, but this character is strongly variable and could independently develop in various groups (Iwan 2004). Therefore, it has a restricted phylogenetic meaning as additional evidence in a complex of characters.

Externally, *Palaeosclerum pohli* gen. et sp. nov. is similar to modern species of the tribe Cnemeplatiini (subfamily Pimeliinae): *Cnemeplatia* A. Costa, 1847 and *Philhammus* Fairmaire, 1871 (in having rather wide and dilated fossorial protibia), but it distinctly differs from the

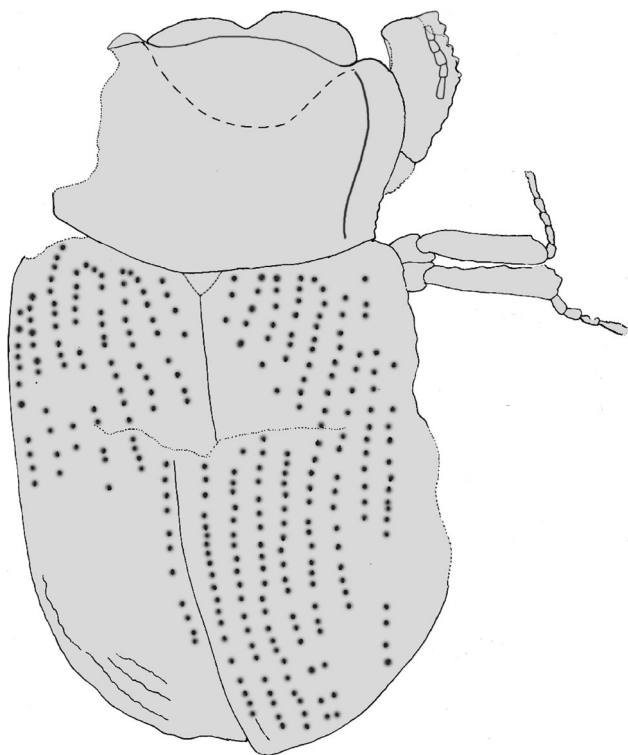


Fig. 2 *Palaeosclerum pohli* gen. et sp. nov., holotype, Middle Paleocene of Menat (France), habitus, reconstruction (after part and counterpart)

members of this fossorial group in the comparatively narrow deep emargination of anterior margin of head and absence of large strong spurs on protibiae. The complex of

characters, combining the peculiar shape of body (robust, adapted to fossorial lifestyle), structure of fossorial protibia and serrate lateral margins of pronotum, demonstrates a considerable similarity of the new genus to the extant representatives of the ‘sclerina’ generic group (sensu Iwan 2004) of the subtribe Opatrina: *Sclerum* Dejean, 1834, *Platynosum* Mulsant and Rey, 1859 and *Eurycaulus* Fairmaire, 1868. The modern species of the genus *Sclerum* is widely distributed from South Europe (including France), North Africa and Asia (Palearctic Region) to Afrotropical and Oriental Regions, *Platynosum* is distributed in the Near East, Transcaucasia (Nakhichevan) and Europe (Rodos), *Eurycaulus* occurs the Middle East (Syria, Israel, Arabian and Sinai peninsulas), Afghanistan, Tajikistan and North Africa (Iwan and Löbl 2008; Grimm 2005). The first two genera lastly mentioned unite specialized myrmecophilous species with the dilated triangular protibia. According to G. S. Medvedev (1965), the function of such triangularly dilated protibia could be to protect the vertex and mouth-parts during situations when the beetles are in a state of thanatosis. *Eurycaulus* includes psammobiontic, probably also myrmecophilous species with oval and a more or less small body covered by setae. *Palaeosclerum pohli* gen. et sp. nov. has a very similar structure of protibia (Fig. 1a, c) and shape of body, which makes it possible to suggest a peculiar mode of life, analogous to that of myrmecophilous in *Eurycaulus*. Taking into consideration the above mentioned circumstances, some level of close relationship of the new fossil species with species of three modern genera from the ‘sclerina’ generic group (subtribe

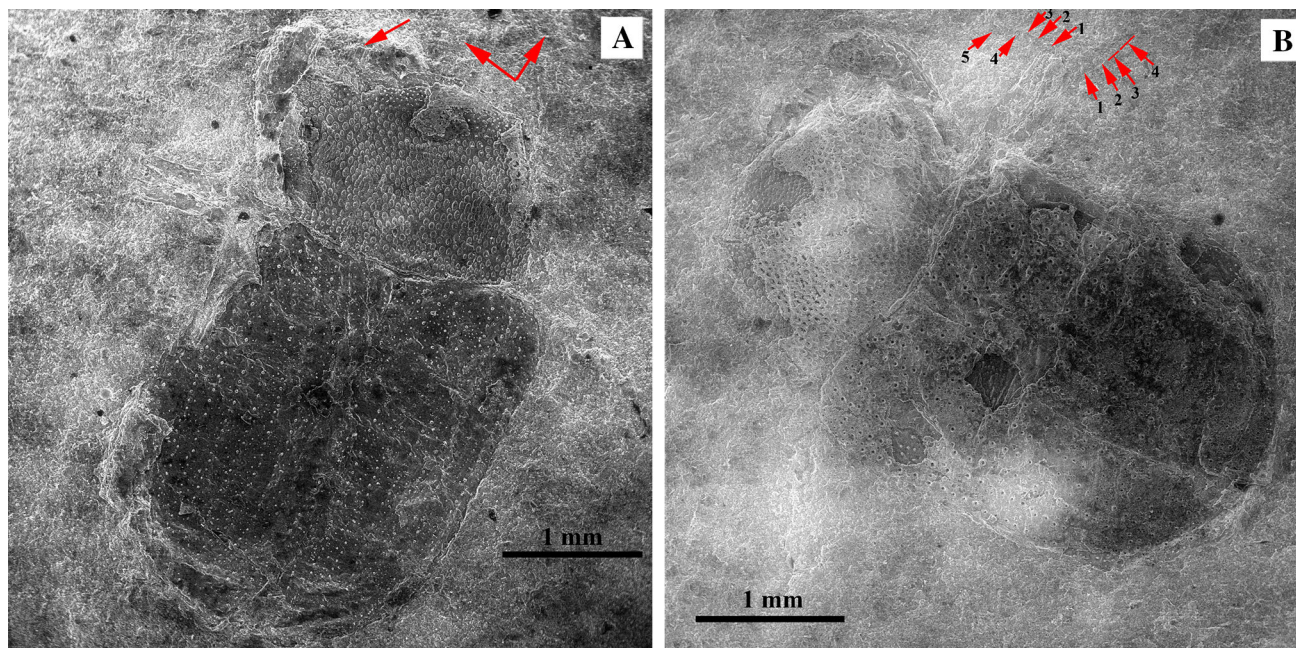


Fig. 3 *Palaeosclerum pohli* gen. et sp. nov., holotype, Middle Paleocene of Menat (France), SEM. **A** Habitus, part (arrows show antennae); **B** Habitus, counterpart (arrows show meso- and metatarsomeres)

Opatrina) can be admitted. Differences between *Palaeosclerum* gen. nov. and the three recent genera of these generic group are given in Table 1.

Palaeosclerum pohli gen. et sp. nov. is the oldest representative of the opatrine darkling beetles. Members of the Recent genera of the opatrine lineage were known in the Cenozoic fossil record: four species of the tribe Opatrini from *Gonocephalum* Solier, 1834 (Oligocene of Rott, Germany), *Ephalus* LeConte, 1862 (late Eocene of Florissant, USA), *Ulus* Horn, 1870 (late Eocene of Florissant, USA) and *Eupachypterus* Kirejtshuk, Nabozhenko and Nel, 2010 (Oise earliest Eocene amber, France) and one species of Pedinini from *Leichenum* Dejean, 1834 (late Eocene Baltic amber) (Kirejtshuk et al. 2008, 2010).

Conclusions

The finding of fossil terrestrial tenebrionids in the Paleocene deposits (Menat of France) is very important for the understanding the evolutionary history of Tenebrionidae. The oldest opatrine species demonstrates that in the Middle Paleocene this tribe was represented by forms that were rather similar to the recent specialized myrmecophilous ones, supporting the concept of late Mesozoic differentiations of the subfamily Tenebrioninae, most of which seem to have been completed before the Cenozoic (L. N. Medvedev 1969; Kirejtshuk 1994; Kirejtshuk et al. 2010; Nabozhenko et al. 2015; Chang et al. 2016). Ants are present in the Menat outcrop by at least two species (one very large and one smaller).

Acknowledgements This study was impossible without the enthusiasm of Burkhard Pohl (Le Bourg, Menat, France) in collecting of fossils in the Menat outcrop and the very efficient assistance of Jean-Marc Pouillon (Nivolas-Vermelle, France) in providing the authors with the specimens for their study. In addition, very valuable assistance in carrying out the study and preparation of this paper was received from André Nel (Laboratoire de Entomologie, MNHN), including very valuable comments to the manuscript. Sylvain Pont (Laboratoire de Minéralogie et de Cosmochimie, MNHN) essentially assisted in providing the authors with the possibility to study the holotype by electronic microscopy. The authors extend thanks to Dariusz Iwan, Vitalii Alexeev and Mike Reich for valuable comments and additions to the MS. This work was supported by a grant from the Russian Foundation for Basic Research 15-04-02971A and the study of the second author was partly carried out under the framework of the Russian state research project no. 01201351189, programmes of the Presidium of the Russian Academy of Sciences “Evolution of the organic world and planetary processes” and Sorbonne Universités (programme d’Accueil de chercheurs de haut niveau).

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