



Nitidulidae (Coleoptera) from the Paleocene of Menat (France)

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Abstract

This paper is devoted to the study of the first Palaeocene Nitidulidae, all from the lacustrine outcrop of Menat (France), viz. *Nitoraeopsis mixta* **gen. et sp. nov.** (Eपुरaeinae, first fossil member of Taenioncini); ?*Soronia* spp. (*S. menatensis* **sp. nov.** and *S. sp.*) of the *Soronia*-complex of genera (Nitidulinae, Nitidulini); *Menatoraea* **gen. nov.** (*M. typica* **sp. nov.** (type species), *M. angustitibialis* **sp. nov.**, *M. laticollis* **sp. nov.**, and *M. gracilis* **sp. nov.**) of the *Pocadius*- or *Thalycra*-complexes, and *Palaeolydra palaeocenica* **gen. et sp. nov.** of the *Thalycra*-complex (Nitidulinae, Nitidulini); and ?*Cryptarcha subglobosa* **sp. nov.**, oldest fossil record of the tribe Cryptarchini sensu stricto (Cryptarchinae). A key to the species of *Menatoraea* **gen. nov.** and a review of the fossil record of the family Nitidulidae are provided.

Key words: Nitidulinae, Eपुरaeinae, Cryptarchinae, fossil record

Introduction

Fossil insects, especially beetles, are very common in the Paleocene maar of Menat (several small outcrops occur near the Village of Menat, Puy-de-Dôme, France) (Nabozhenko & Kirejtshuk 2014, 2017; Kirejtshuk *et al.* 2016; Legalov *et al.* 2017; etc.). The current fossil record of the Nitidulidae Latreille, 1802 comprises two genera (four species) from the Mesozoic, and 29 genera (40 species) from the Cenozoic (Kirejtshuk & Ponomarenko 1990, 2017; etc.). No nitidulid species were known from the Paleocene before this contribution. The present paper introduces several species that can be regarded as obvious members of the family Nitidulidae. They provide a first view on the diversity of this family in the Palaeocene.

Materials and methods

The studied specimens are deposited in Muséum national d'Histoire naturelle, Paris (MNHN), and in the Menat Town Museum (Village of Menat, Puy-de-Dôme) (MNT). Comparisons with modern species were based on specimens from MNHN and the Zoological Institute of the Russian Academy of Sciences, St Petersburg.

The specimens were studied using an Olympus SCX9 stereomicroscope with an Olympus camera and a Nikon SMZ1500 with Microscope Eyepiece Camera 9.0MP Aptina Color CMOS MU900, at MNHN; a Leica MZ 12.0 stereomicroscope with a DFC290 camera, at the Zoological Institute of the Russian Academy of Sciences. Most illustrations for the paper were made using a Nikon SMZ25 stereomicroscope with a Nikon D800 camera. Selected specimens were also examined with a Tescan Vega LSU scanning electron microscope, at MNHN (Low Vacuum Secondary Electron TESCAN Detector, LVSTD), to test the characters not readily visible with optic equipment (punctuation, margins of legs, shape of large sclerites, scales on elytra).

Insect specimens available for study from Menat outcrops are mostly disarticulated and even the proportion of such fossils is markedly much greater than in other collections of Cenozoic fossils. Besides, the consistence of the matrix in different regions of Menat is rather coarse. In most cases outlines of sclerites are more or less deformed or unclear. Frequently, insect remains are deposited in a soft spongo-diatomite matrix. In other cases insect specimens under study are fossilized in rather hard, more silicified layers. Many of them have been rather carbonized and, therefore, are difficult to study because most structural details are unclear.

Another peculiarity of insect fauna in Menat is the predominance of beetles, mostly belonging to different groups of Curculionoidea (Legalov *et al.* 2017), which rather frequently demonstrate various superfamily peculiarities, represented even by separate elytra (pers. obs.). The Curculionoidea are followed by Cerambycidae and Buprestidae, while the Archostemata are represented by ca. 30 fossils (Kirejtshuk *et al.* 2016). Nevertheless, the most abundant beetle group are the Curculionoidea. According to general appearances a considerable proportion among other beetles corresponds to nitidulid-like forms. Most of these however, have not enough diagnostic characters to be sure of their family and even infraorder attribution, because in most cases the outlines of the body sclerites are not traceable and the sclerites of appendages are missing. Many other families have similar nitidulid-like features, including representatives of hydrophiloids, cleroids, cucujoids, tenebrionoids, kateretids and even chrysomeloids. Nevertheless, some remains examined show enough characters to suggest their attribution to Nitidulidae.

Finally, the specimens of Nitidulidae examined and other comparatively small beetles from Menat possess a uniform very fine microgranulation along their outlines in the stone matrix that could be caused by certain conditions of fossilization. An examination of organic matter at these areas (when they are present) shows that they do not correspond to sculptures of insect integument. Such conditions could be caused by the chemical composition of the clay where these small specimens were deposited or/and to the peculiar structure of microorganisms that were involved in the partial decay during fossilization.

Geological setting and locality information for Menat biota

The Middle Paleocene Menat fossil site (Menat Basin, Puy-de-Dôme, France) is a volcanic maar containing a lake ca. 700 m in diameter, which at present contains sedimentary rocks (spongo-diatomites) with remains of diverse aquatic and terrestrial flora and fauna (Piton 1940; Nel 1989, 2008; Wappler *et al.* 2009; Nabozhenko & Kirejtshuk 2014, 2017; Kirejtshuk *et al.* 2016; etc.). This locality has been well known since the beginning of the 20th century (Fritel 1903; Laurent 1912; etc.) and a general preliminary overview of its biota was published by Piton (1940). According to Wappler *et al.* (2009), the plant and insect diversity in the lacustrine outcrop of Menat is comparatively high, confirming the results of Piton (1940). Recent field investigations made by our team strongly suggest that it is even higher than originally thought. The composition of faunal and floral remains makes it possible to conclude that this lake was surrounded by a subtropical evergreen forest. The palaeoenvironment was comparatively warm and humid, supporting a high diversity of insects. However, traces of paleofires on wood fragments in several layers suggest the presence of dry periods. According to the pollen analysis, paleo-mammalian stratigraphic, and radiometric K/Ar analyses, the age of Menat was estimated at 59 Ma (Kedves & Russel 1982; Nel 2008). However, the newest estimates based on macroflora postulate its age at 60–61 Ma (Wappler *et al.* 2009). Beetles dominate the animal biodiversity in terms of species number and abundance of specimens, as they represent more than 80% of the animals collected in this outcrop (after the collection of ca. 1,200 animals made during the years 2013–2014).

Systematics

Family Nitidulidae Latreille, 1802

Notes. The specimens were sorted after selection of the beetles demonstrating a suboval and not strongly convex, typical “nitidulid body, transverse procoxae, and also moderately separated coxae in each pair. A somewhat similar configuration of the thoracic structures can also be found in Trogossitidae Latreille, 1802 and some other cleroids (Acanthocnemidae Crowson, 1969, Cleridae Latreille, 1802, Melyridae Leach, 1815 *sensu lato*, Phloeostichidae Reitter, 1911), bostrichiods (Dermestidae Latreille, 1804), Derodontidae LeConte, 1861, cucujoids (Byturidae Jacquelin du Val, 1858), chrysomeloids (Cerambycidae Latreille, 1802, Chrysomelidae Latreille, 1802, Megalopodidae Latreille, 1802, Orsodacnidae Thomson, 1859). But in all these cases metacoxae are more or less (sub)-conjoining. On the other hand, some nitidulids have very narrowly separated or almost (sub)-conjoining metacoxae. Therefore it is difficult to discriminate them from the other above-mentioned groups, especially those with the open mesocoxal cavities. Because of such complexities, all small nitidulid-like fossils with (sub) conjoining metacoxae were not included in this study. The chrysomeloids with similar configuration of thoracic structures, general body outline, particularly in wide prohypomera and elytral epipleura (although wide members of Cassidinae Gyllenhal, 1813 frequently have these thoracic sclerites rather wide), differ from the specimens under study in usually having (sub)-conjoining metacoxae and never have such transverse procoxae (Shin & Chaboo 2012). Tenebrionidae Latreille, 1802 with similar outlines of body and somehow coxae have widely externally closed and not strongly transverse procoxal cavities and externally by meso- and metaventrites (pimeliine and most branches) or partly closed by trochantine (tenebrionine branch) mesocoxal cavities mesocoxal cavities (Matthews & Bouchard 2008). Kateretidae Erichson, 1843, in contrast to the new species described here, have more or less shortened elytra with transverse apices and widely separated metacoxae (see also below *Nitoraeopsis mixta* **gen. et sp. nov.**) (Hisamatsu S. 2011). Finally, similar outlines of thoracic sclerites could also

be found in some groups of Coccinellidae Latreille, 1807, although most members of the latter family have oval or slightly transverse (not wider than mesocoxae), widely separated metacoxae and characteristic submeso- and submetacoxal lines (Gordon 1985). Nevertheless some comparatively narrow chilocorines demonstrate comparatively narrowly separated metacoxae and their discrimination from fossil nitidulids could be quite problematic (see also below *?Cryptarcha subglobosa* sp. nov.).

Subfamily Epuraeinae Kirejtshuk, 1986

Notes. The print and counterprint “NEL 2978” assigned to the subfamily Epuraeinae shows the exposed male anal sclerite projecting far posteriorly from the posterior edge of the hypopygidium, which is mostly characteristic of Epuraeinae and Carpophilinae Erichson, 1843 (both from carpophiline-lineage) rather than other nitidulid groups. This print has the narrowly separated mesocoxae as in both Epuraeinae and Carpophilinae, while these are widely separated in the subfamily Amphicrossinae Kirejtshuk, 1986 from the carpophiline-lineage. Rather important characters of this print are the shortened elytra with truncate apices so that the abdominal apex of the beetles is remained uncovered as in many epuraeines, in contrast to most carpophilines usually having 2–3 posterior abdominal segments (but only abdominal apex). Besides, the anal sclerite of “NEL 2978” is exposed extending posteriorly beyond the abdominal apex as in Epuraeinae and few Carpophilinae (*Nitops* Murray, 1864 and few *Urophorus* Murray, 1864). At the same time, the hypopygidium of this specimen has a clear median depression at the posterior edge which resembles that in most members of Carpophilinae and Amphicrossinae. Thus, “NEL 2978” can be regarded as a member of Epuraeinae, although it has some features of other groups of the carpophiline-lineage. Similar outlines of the body sclerites can be found in some members of Kateretidae. Nevertheless, “NEL 2978” has a prosternal process widened at the apex (unknown in the kateretids), distinct hemicircular median depression at apex of hypopygidium (also unknown in the kateretids) and rather long elytra (quite rare in kateretids).

Tribe ?Taenioncini Kirejtshuk, 1998

Genus *Nitoraeopsis* gen. nov.

Type species. *Nitoraeopsis mixta* sp. nov.

Etymology. The name of the new genus is formed from the generic names “*Nitops*”, “*Epuraea*” and Greek “*opsis*” translated as “resembling a (specified) thing”. Gender feminine.

Diagnosis. Body elongate, oval, and medium-sized (3.4 mm); apparently moderately convex dorsally and ventrally. Integument usually with fine and rather sparse punctures, without longitudinal rows on elytra. Head apparently transverse, with comparatively large eyes. Pronotum with arcuate sides and without explanations along edges. Prosternal process widened before apex with rounded posterior edge. Pro- and mesocoxae narrowly separated and metacoxae moderately widely separated: distance between mesocoxae somewhat smaller than that between procoxae and about fourth as great as that between metacoxae. Posterior edge of metaventricle shallowly angularly excised between metacoxae. Elytra truncate at apices, leaving abdominal apex uncovered; without expressed adsutural lines. Epipleura moderately wide. Pro- and mesofemora of usual subelliptic shape. Protibiae subtriangular, apparently very finely crenulate at outer edge.

Comparison. This genus is characterized by some structures that make it distinct from all extant genera of Epuraeinae: broadly rounded narrowing pronotal sides and a clear median depression of the male hypopygidium. This depression is unknown among other Epuraeinae. Representatives of most epuraeine genera are characterized by having the pronotum widest at base and frequently with the posterior angles slightly projecting posteriorly (or if not widest, then the posterior angles of the pronotum with a distinct top), although in some members of the tribe Epuraeini sensu stricto (of the genera *Amystrops* Grouvelle, 1906, *Ceratomeidia* Kirejtshuk, 1990, and *Epuraea* Erichson, 1843) the posterior pronotal angles are more or less rounded. In most genera of the tribe Taenioncini the pronotal posterior angles are at least narrowly rounded. Finally, most Epuraeini have explanate pronotal sides while

the Taenioncini are characterized by more or less steeply sloping and not explanate pronotal sides. *Nitoraeopsis mixta* **sp. nov.** in its general appearance and outlines of the body sclerites is more similar to some species of the genus *Carpocryraea* Kirejtshuk, 1998 (including *Csiromenus* Kirejtshuk et Kvamme, 2001) from the latter tribe. However, in addition to the lack of the median depression on their hypopygidium, all other known species of Taenioncini have the posterior pronotal angles narrowly rounded or rarely with a more or less distinct top.

The new genus is similar to the fossil genus *Baltoraea* Kurochkin et Kirejtshuk, 2010 with unclear position from Baltic amber and differs from it not only in absence of depression on the hypopygidium, but also in the smaller head, pronotal shape, diffuse elytral puncturation and shorter precoxal part of prosternum. The members of the Lower Cretaceous genus *Crepuraea* Kirejtshuk, 1990 (= *Nyujwa* Perkovskiy, 1990) can be split at least into two groups. Note that the two fossil taxa *Crepuraea archaica* Kirejtshuk, 1990 and *Nyujwa zherichini* Perkovskiy, 1990 apparently should be regarded in the same genus (Kirejtshuk 2008). All species of *Crepuraea* differ from *Nitoraeopsis mixta* **sp. nov.** at least in outline of their pronotum, although the pronotum of *Crepuraea zherichini* Kirejtshuk, 1990 (not *Crepuraea zherichini* Perkovskiy, 1990 seems to have pronotal sides not explanate with a nearly distinct top of the posterior angles of the pronotum. The genus *Epanuraea* Scudder, 1900 (drawn by Scudder in 1893, and described in by Scudder in 1900) is usually regarded as a probable member of Epuraeini (Kirejtshuk 2008); however, the new genus is distinguished from the latter by a more elongate body, lacking a subquadrangular pronotum (with not subrectilinear sides) and much shorter elytra.

Nitoraeopsis gen. nov. presumably represents the first fossil Taenioncini, because all others fossils of this tribe have been reinterpreted as members of Epuraeini (Kirejtshuk & Ponomarenko 2017) (see also Discussion and Conclusions below).

***Nitoraeopsis mixta* sp. nov.**

Figs 1–7

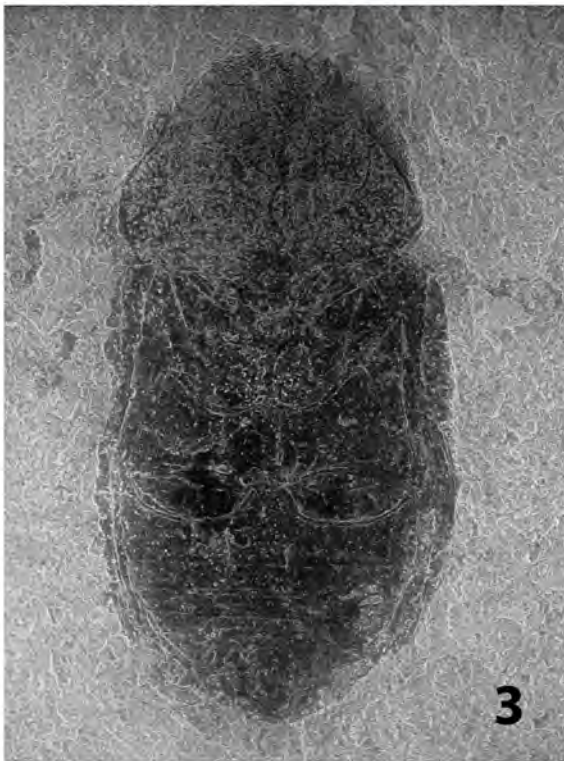
Holotype. “NEL 2978” (MNT), print with remains of organic matter and counterprint of a beetle body, male; in comparatively soft and somewhat smoothed rock represented by a mixture of the partly obliterated outlines of the body dorsal (mostly in counterprint) and ventral (mostly in print) sclerites, coxae and parts of both protibiae, outlined depressions of both profemora and right mesofemur, but with missing distal part of counterprint and without seriation in elytral puncturation.

Locality and stratigraphy. Paleocene, Menat (see *Geological setting section*).

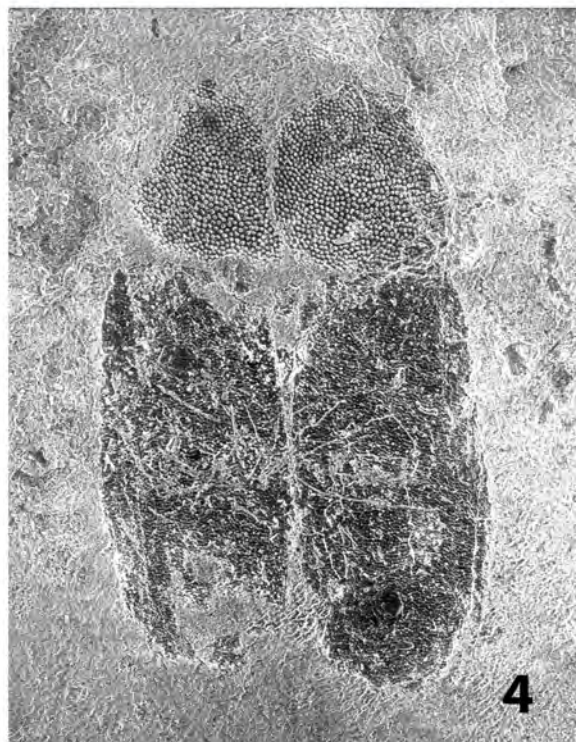
Etymology. The epithet of this new species means mixed, complex and composite. It is a reference to the combination of the characters of this new species, including peculiarities of Epuraeinae and Carpophilinae.

Description. Holotype. Body length 3.4 mm, width 2.1 mm. Integument of upper surface apparently with rather fine and sparse punctures and without trace of longitudinal rows on elytra; underside with fine and markedly denser punctures.

Head apparently subtriangular. Prothorax moderately short; pronotum less than twice as wide as long, sides seemingly gently sloping and not explanate arcuate at sides, anterior edge shallowly emarginate, anterior and posterior angles comparatively broadly rounded; prosternum before procoxae apparently shorter than procoxae, procoxae moderately narrowly separated by prosternal process, latter strongly widened at widely rounded apex. Mesocoxae moderately large and about as narrowly separated as procoxae and metacoxae. Metaventrite markedly more than twice as long as prosternum before coxae. Submetacoxal lines invisible. Elytra about as wide as prothorax, with somewhat emarginate sides, somewhat longer than wide combined, apparently moderately convex, with sides not explanate and apices subtruncate forming sutural angle. Abdomen with ventrite 1 longest (only slightly longer than hypopygidium), each of ventrites 2–4 much shorter than hypopygidium (ventrite 5); hypopygidium shallowly emarginate at apex and with subsemicircular median depression. Male anal sclerite rather far posteriorly extending beyond apex of hypopygidium. Protibiae rather narrow, apparently very finely crenulate along outer edge.

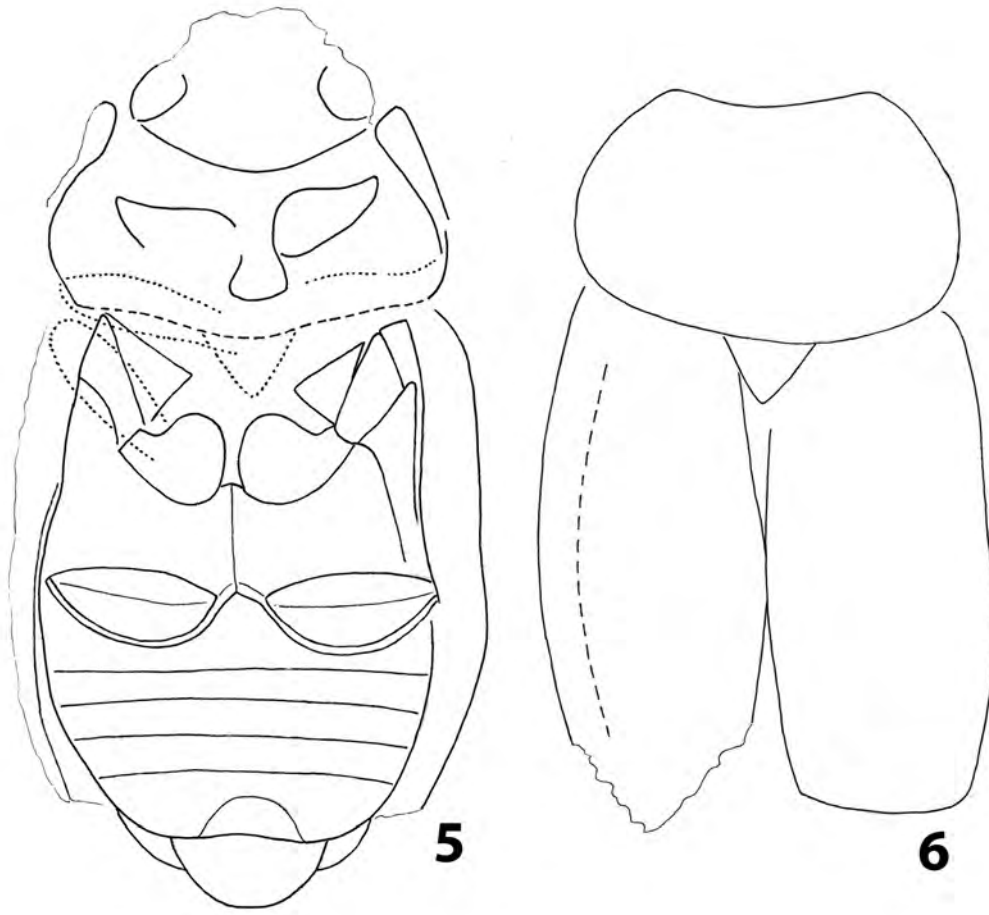
**1****2****3**

SEM HV: 15.00 kV Vac: LowVac, 34 Pa
View field: 4.37 mm Det: LVSTD 1 mm

**4**

SEM HV: 15.00 kV Vac: LowVac, 30 Pa
View field: 3.95 mm Det: LVSTD 1 mm

I FIGURES 1–4. *Nitoraeopsis mixta* gen. et sp. nov., holotype “NEL 2978” (MNT), print and counterprint. 1, body, print; photographed under Nikon SMZ25 stereomicroscope with a Nikon D800 camera. 2, body, counterprint, photographed under Olympus SCX9 with camera Olympus camera. 3, print, micrograms, photographed under scanning electron microscope (SEM). 4, counterprint, micrograms, photographed under scanning electron microscope (SEM). Length of body 3.4 mm.



II FIGURES 5–7. *Nitoraeopsis mixta* **gen. et sp. nov.**, holotype “NEL 2978” (MNT). 5, body, reconstructed drawing of print with broken lines for outline of posterior edge of pronotum, and dotted lines for outlines of depressed places of pro- and mesofemora, and scutellum. 6, body, reconstructed drawing of counterprint with broken lines for outline of inner edge of epipleuron. 7, distal part of body, print, photographed under Nikon SMZ25 stereomicroscope with a Nikon D800 camera. Length of body 3.4 mm.

Subfamily Nitidulinae Latreille, 1802

Tribe Nitidulini sensu stricto

Genus ?*Soronia* Erichson, 1843

Type species. *Nitidula grisea* Linnaeus, 1758; Recent.

Notes. The outlines of the body sclerites visible in the print “R 63912 N” demonstrate a considerable similarity to those in both extant species of *Soronia* and Eocene representatives of *Microsoronia* Kirejtshuk et Kurochkin, 2010. However, the body size of the new species (*Soronia menatensis* sp. nov) fits within the range reported for the members of the first rather than those of the second genus (Kirejtshuk & Kurochkin 2010). Besides, the diffuse puncturation of elytra, which can be clearly traced on metacoxae, support this assumption (Fig. 10). A less probable alternative interpretation of this print could be an assumption that it represents remains of a member of *Cryptarcha* Shuckard, 1839 (*Cryptarchinae* C.G. Thomson, 1859); however, the pronotum narrowing at base and coarse dorsal puncturation are somewhat similar to those of *Soronia* than *Cryptarcha* or any other cryptarchine group. There are no remains of appendages in this print except a stripe along left side of the head which could be remains of an anterior leg sclerite (femur). It would be important for a reliable discrimination to determine if the attribution of this print is either *Soronia* or *Cryptarcha* to observe the posterior edge of the metaventricle between the metacoxae, which remain invisible in the print “R 63912 N” here named as ?*Soronia menatensis* sp. nov., but clearly visible in the print “NEL 1811” here named as ?*Soronia* sp. But the first one has traces of explanate sides of its pronotum (characteristic of a member of *Soronia*), while the second one does not show them.

In conclusion, R 63912 represents the first fossil records of the genus *Soronia* (see also below Discussion and conclusions).

The attempts to study the print of R 63912 under the Tescan Vega LSU scanning electron microscope were unsuccessful because the SEM images of the specimens obtained are rather unclear.

?*Soronia menatensis* sp. nov.

Figs 8–10

Holotype. “R 63912” (MNHN), print, sex unknown; deposited in rather hard rock and represented by a mixture of the somewhat obliterated outlines of body dorsal and ventral sclerites, and also coxae and one mandibles, but without traces of other parts of appendages (mouthparts, antennae, legs).

Locality and stratigraphy. Paleocene, Menat (see *Geological setting section*).

Etymology. The epithet of this new species is formed from the name of the locality of its origin.

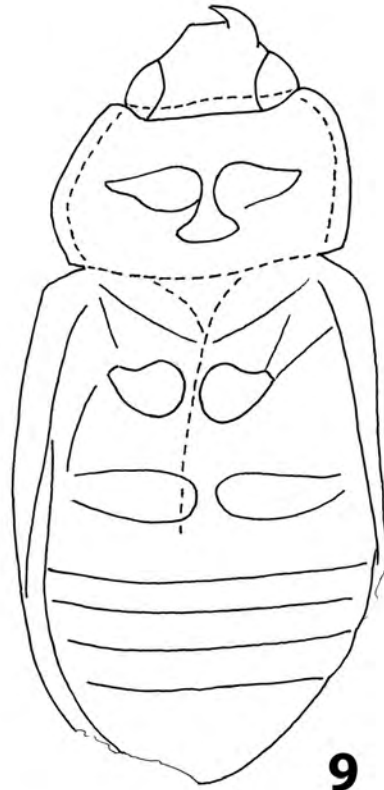
Diagnosis. This new species is similar to some extant Indo-Malayan members of *Soronia*, but seem to be different from them by having coarse and dense dorsal puncturation (particularly traced coarse elytral punctures). The head of (?) *Soronia menatensis* sp. nov., in contrast to most extant congeners, is characterized by rather large eyes and the distance between metacoxae being not wider than that between pro- and mesocoxae. The last abdominal ventrite (hypopygidium) of the new species is only slightly shorter than ventrite 1, while in the case of extant species this sclerite is considerably shorter. Besides, the distance between pro- and mesocoxae appears abnormally great and that between meso- and metacoxae is rather small and not characteristic of the genus. The proportions between the pairs of coxae visible in the print examined could be a result of fossilization (probable shifting of mesocoxae). However it is necessary to take into consideration that the mesoventrites in most members of *Soronia* are comparatively longer (sometimes almost as long as the metaventricle).

Description. Holotype. Body length 6.0 mm, width 3.2 mm. Body elongate oval; apparently slightly to moderately convex dorsally. Integument of upper surface apparently with extremely coarse and rather dense punctures and without a trace of longitudinal rows on elytra, less coarse and very dense on epipleura; underside with fine and rather dense punctures (with puncture diameter less than half as great as that on dorsal surface).

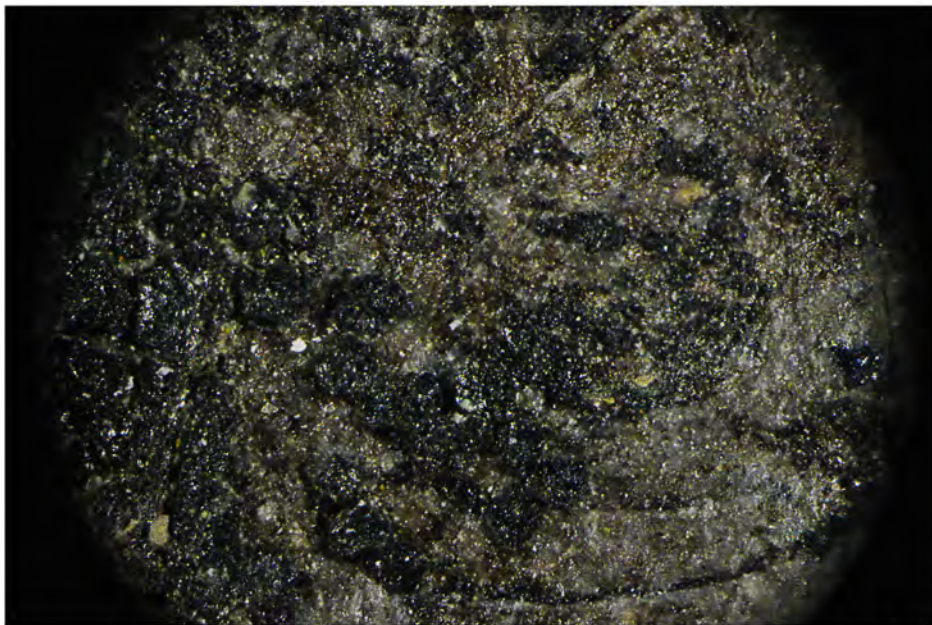
Head subtriangular, somewhat shorter than distance between relatively large eyes. Mandibles apparently moderately developed, far exposed beyond anterior edge of frons, with gently curved outer edge. Prothorax moderately short; pronotum about 1 2/5 as wide as long, its sides moderately widely (sub) explanate and arcuate at



8



9



10

III FIGURES 8–10. *?Soronia menatopsis* sp. nov., holotype “NEL 1811” (MNT), print. 8, body, photographed under Nikon SMZ25 stereomicroscope with a Nikon D800 camera. 9, body, reconstructed drawing of print with broken lines for outlines of anterior and posterior edges, and explanate sides of pronotum, and also inner edges of elytra. 10, place around left metacoxa of print, photographed under Nikon SMZ25 stereomicroscope with a Nikon D800 camera. Length of body 6.0 mm.

sides, anterior edge shallowly emarginate, anterior angles widely rounded, and posterior ones stump and with distinct top; prosternum before procoxae longer than procoxae, procoxae moderately narrowly separated by prosternal process with apex strongly widened and widely rounded at posterior edge. Mesocoxae moderately large and about as narrowly separated as procoxae and metacoxae. Metaventrite about twice as long as prosternum before coxae. Submetacoxal lines invisible. Abdomen with ventrite 1 longest (only slightly longer than hypopygidium), each of ventrites 2–4 much shorter than hypopygidium; hypopygidium apparently rounded at apex. Elytra slightly wider than prothorax, with broadly arcuate sides, about 1.5 times as long as wide, apparently moderately convex; moderately wide (slightly narrower than apex of prosternal process).

(?) *Soronia* sp.

Figs 11–12

Specimen examined. “NEL 1811” (MNT), print, sex unknown; deposited in comparatively soft rock and represented by a mixture of the somewhat obliterated outlines of body dorsal and ventral sclerites, and also coxae, but without traces of other parts of appendages (mouthparts, antennae, legs).

Locality and stratigraphy. Paleocene, Menat (see *Geological setting section*).



SEM HV: 15.00 kV Vac: LowVac, 42 Pa View field: 4.53 mm Det: LVSTD 1 mm

11

12

IV FIGURES 11–12. ?*Soronia* sp., “NEL 1811” (MNT), print. 11, body, photographed under Nikon SMZ25 stereomicroscope with a Nikon D800 camera. 12, body, micrograms, photographed under scanning electron microscope (SEM). Length of body 3.7 mm.

Notes. The specimen “NEL 1811” is 3.7 mm long and 2.3 mm wide. It demonstrates many characters similar to those observed in the holotype of (?) *Soronia menatensis* **sp. nov.** (i.e., the general outlines of all visible sclerites, course and dense punctures on dorsum. However, the lack of clear explanations of the pronotal sides and wider epipleura make it impossible to join this print and the holotype of (?) *Soronia menatensis* **sp. nov.** as probable members of the same species. Nevertheless the angulate posterior edge of its metaventricle can be evidence that the print “NEL 1811” can be assigned to this genus.

Genus *Menatoraea* gen. nov.

Type species. *Menatoraea typica* sp. nov.

Etymology. The name of this genus is formed from the name of the type locality of its type species and the end of generic name *Eपुरaea*.

Diagnosis. Body elongate oval and medium-sized (4.0–6.3 mm); apparently slightly to moderately convex dorsally and ventrally. Integument usually with very dense punctures on pronotum, coarse or rather fine, dense or sparse punctures arranged in more or less distinct longitudinal rows usually associated with longitudinal furrows on elytra or elytral puncturation fine and nearly diffuse. Head moderately large, transversely subtriangular, with medium-sized to rather large eyes. Pronotum with arcuate sides and evenly sloping along edges or at most narrowly (sub) explanate. Prosternal process slightly widened before apex with rounded posterior edge. Distance between coxae in each pair of coxae subequal or those between meso- and metacoxae somewhat greater than that between procoxae. Posterior edge of metaventricle angularly excised between metacoxae. Elytra with not explanate or (sub) explanate and broadly arcuate sides, completely covering the abdomen; apices conjointly rounded or somewhat subangular. Epipleura moderately wide. Protibiae subtriangular, finely crenulate at outer edge. Protarsi rather wide.

Comparison. The longitudinal rows of punctures on elytra are known only in modern representatives of subfamily Nitidulinae Latreille, 1802 and Cillaeinae Kirejtshuk et Audisio, (in Kirejtshuk, 1986), although this new genus cannot be placed within the latter group because of the complete elytra covering the entire abdomen. The species of *Menatoraea* **gen. nov.** are characterized by the elongate oval and slightly to moderately convex dorsum with (sub) explanate pronotal and elytral sides, moderately wide epipleura, subequally separate coxae in each pairs, crenulate outer edge of protibiae and wide protarsi. The mentioned characters exclude attribution of this group to the nitiduline tribes Amborotubini Lesche et Carlton, 2004, Cychramini Lacordaire, 1854, Cychramptodini Kirejtshuk et Lawrence, 1992, Cyllochini Everts, 1898, Lawrenceosini Kirejtshuk, 1990, Mystropini Murray, 1864, and also the *Aethina*-, *Megauchenia*-, *Pocadius*- and *Thalycra*-complexes of the tribe Nitidulini sensu stricto. As to other complexes of Nitidulini sensu stricto, the seriate sculpture and puncturation of elytra of *Menatoraea* species make the new genus joining them very different from any genus of the *Nitidula*-, *Perilopsis*- *Prometopia*- and *Soronia*-complexes. In conclusion, *Menatoraea* **gen. nov.** can be compared with the genera representing the *Ipedia*- and *Phenolia*-complexes of genera. However the members of these taxonomic entities have protibiae without distinct crenellation of the outer edge and rather narrow in almost all cases. The new genus is similar to *Perilopa* Erichson, 1843 by the metacoxae and posterior edge of metaventricle, but differs from it in the not widened apex of prosternal process, posterior pronotal angles not projecting posteriorly and widely explanate pronotal and elytral sides. *Menatoraea typica* **sp. nov.** differs from other members of *Ipedia*- and *Phenolia*-complexes in the more or less larger and wider body, posterior pronotal angles projecting posteriorly and angularly excised posterior edge of metaventricle between metacoxae and; also from *Platychora* Erichson, 1843 in the seriate elytral puncturation and wide apex of prosternal process.

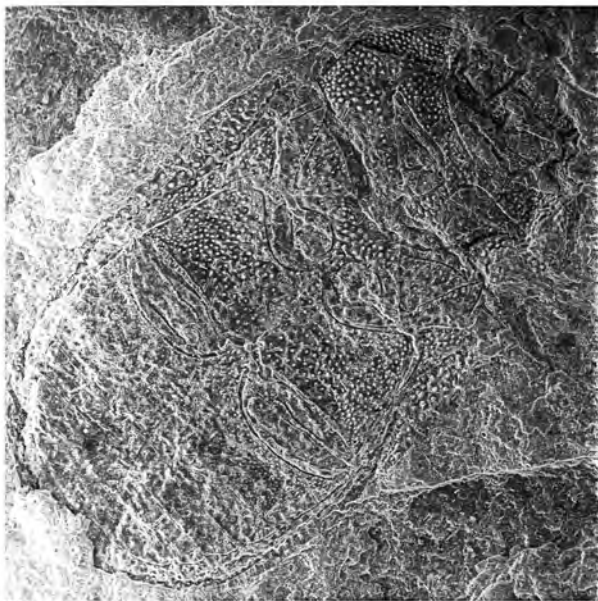
It is impossible to define a strict placement of this new genus in the system of the tribe Nitidulini. According to the above comparison and taking into consideration the general appearance, disposition of coxae and peculiarities of elytral sculpture, including adsutural lines, it is thought that the more probable relation of *Menatoraea* **gen. nov.** can belong to the *Pocadius*- and *Thalycra*-complexes of genera, which sometimes are considered together as one complex, see Kirejtshuk (2008). If so, these species together with *Palaeolydra palaeocenica* **sp. nov.** can be regarded as the oldest representatives of these complexes or the joined complex (see also below Discussion and conclusions).



13

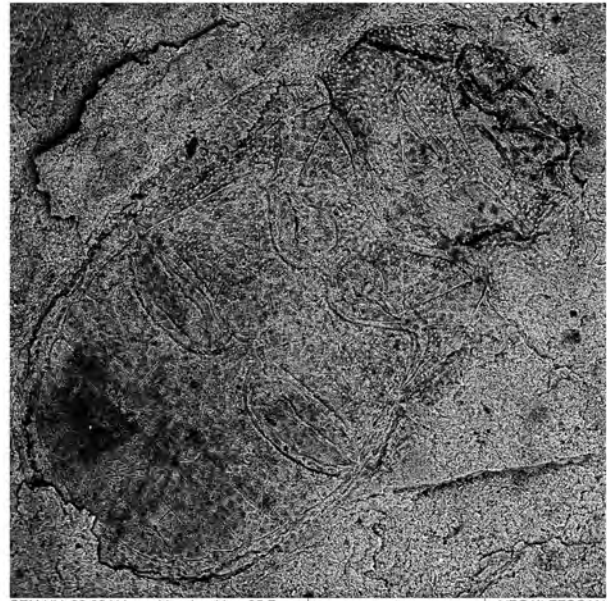


14



SEM HV: 20.00 kV Vac: LowVac, 35 Pa
View field: 3.37 mm Det: LVSTD

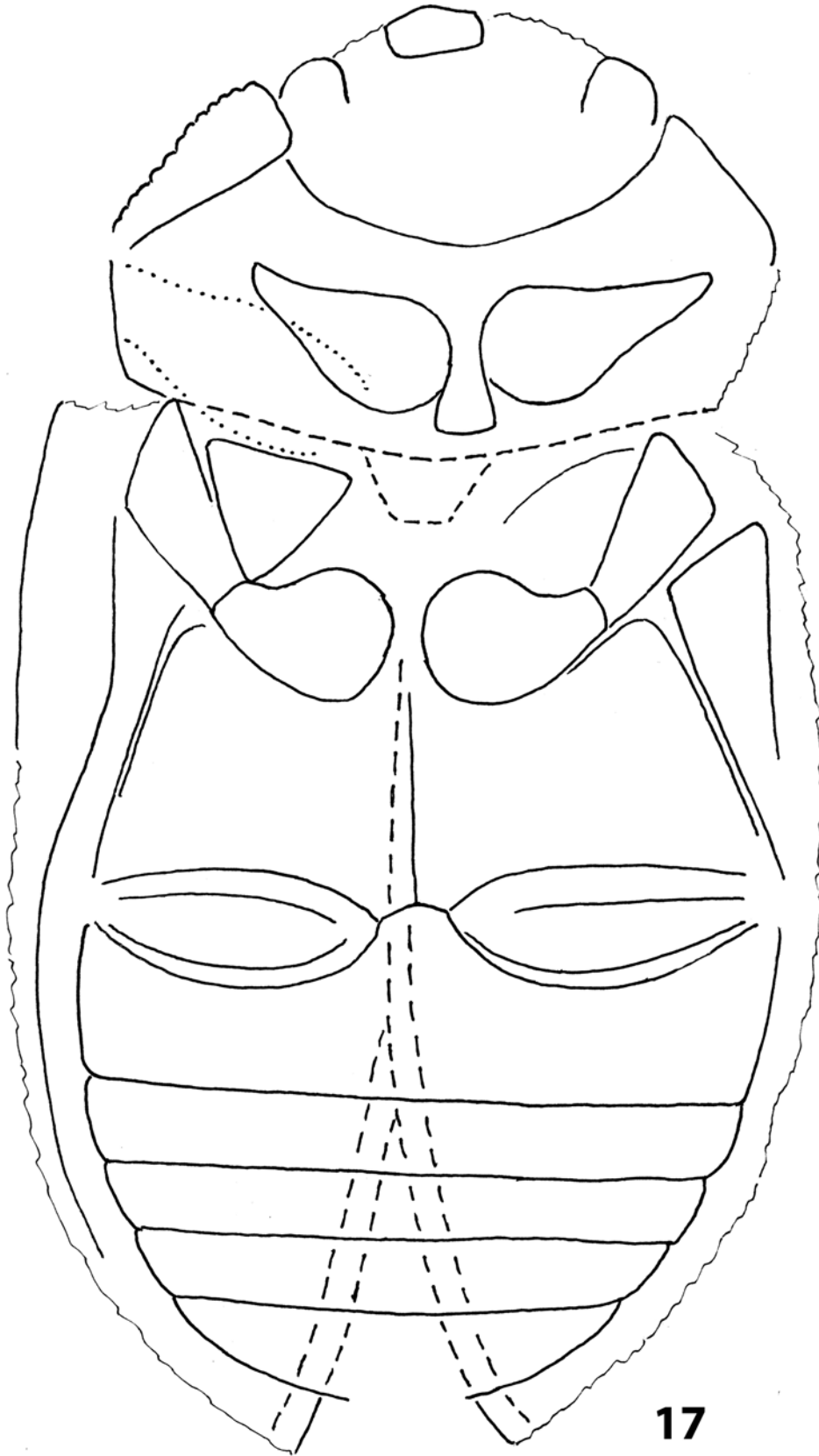
VEGA\\ TESCAN
MNHN 
15



SEM HV: 20.00 kV Vac: LowVac, 35 Pa
View field: 3.37 mm Det: BSE

VEGA\\ TESCAN
MNHN 
16

V FIGURES 13–16. *Menatoraea typica* gen. et sp. nov., holotype, print “MNT 06-3459A” (MNT) and counterprint “MNT 06-3459B” (MNT). 13, body, print, photographed under Nikon SMZ25 stereomicroscope with a Nikon D800 camera. 14, body, counterprint, photographed under Nikon SMZ25 stereomicroscope with a Nikon D800 camera. 15, body, print, micrograms, photographed under scanning electron microscope (SEM). 16, body, print, micrograms, photographed under scanning electron microscope (SEM). Length of body 4.1 mm.



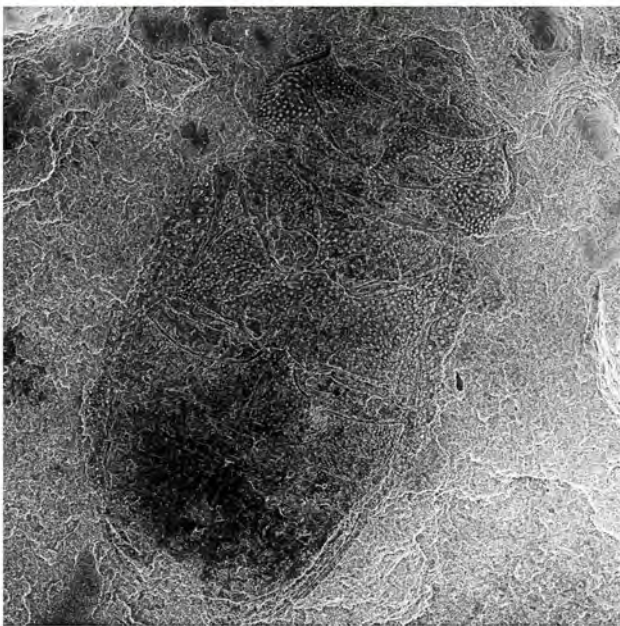
VI FIGURE 17. *Menatoraea typica* **gen. et sp. nov.**, holotype, print “MNT 06-3459A” (MNT). 17, body, reconstructed drawing of print with broken lines for outline of posterior edge of pronotum, scutellum, sutural edges and adsutural lines of elytra, and dotted lines for outlines of right profemur. Length of body 4.1 mm.



18

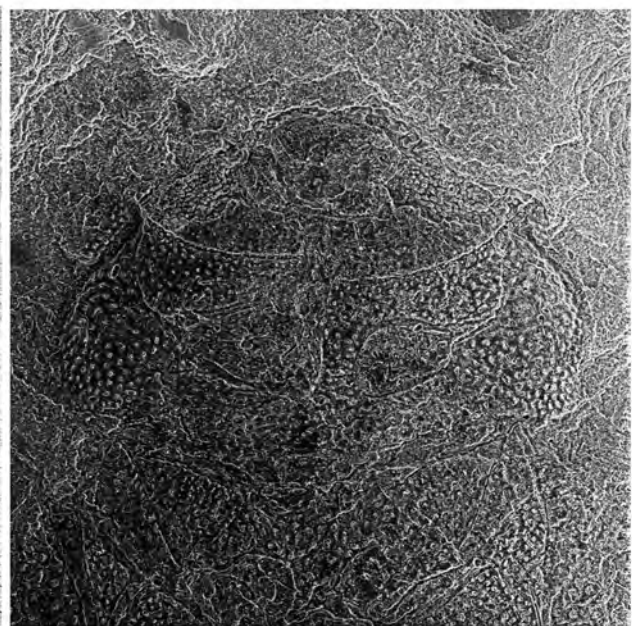


19



SEM HV: 15.00 kV Vac: LowVac, 46 Pa
View field: 4.19 mm Det: LVSTD 1 mm

20



SEM HV: 15.00 kV Vac: LowVac, 46 Pa
View field: 2.17 mm Det: LVSTD 500 µm

21

VII FIGURES 18–21. *Menatoraea typica* gen. et sp. nov., paratype, print “NEL 135” (MNT). 18, body, photographed under Nikon SMZ25 stereomicroscope with a Nikon D800 camera. 19, distal part of body, photographed under Nikon SMZ25 stereomicroscope with a Nikon D800 camera. 20, print, micrograms, photographed under scanning electron microscope (SEM). 21, anterior part of body, print, micrograms, photographed under scanning electron microscope (SEM). Length of body 4.6 mm.



22



23



SEM HV: 15.00 kV Vac: LowVac, 42 Pa
View field: 4.65 mm Det: LVSTD



24



SEM HV: 15.00 kV Vac: LowVac, 42 Pa
View field: 4.04 mm Det: LVSTD

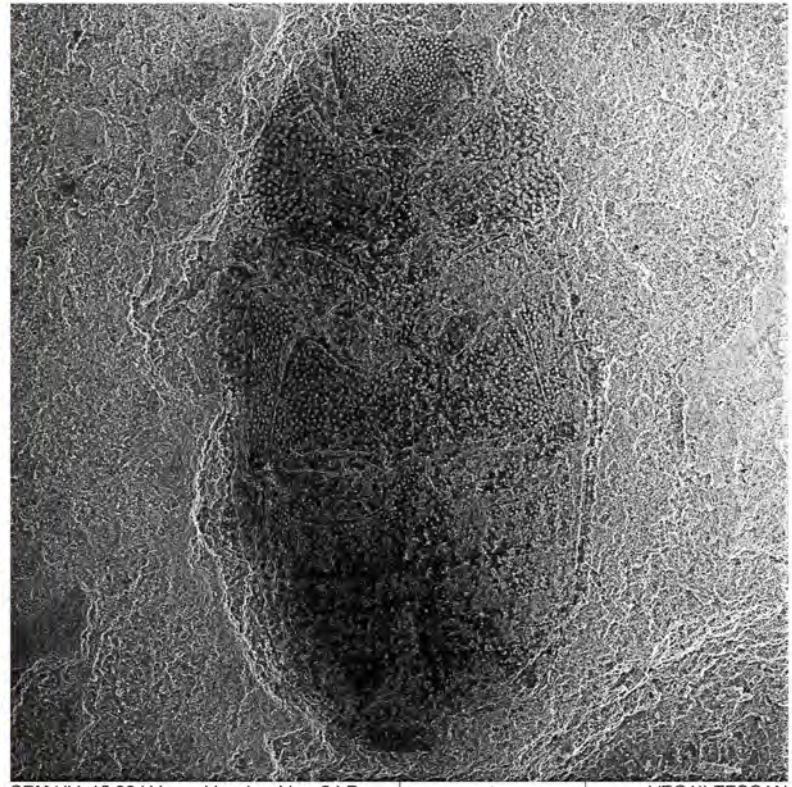


25

VIII FIGURES 22–25. *Menatoraea typica* gen. et sp. nov., paratype, print and counterprint “NEL 2294” (MNT). 22, body, print; photographed under Nikon SMZ25 stereomicroscope with a Nikon D800 camera. 23, ibid., counterprint, photographed under Nikon SMZ25 stereomicroscope with a Nikon D800 camera. 24, print, micrograms, photographed under scanning electron microscope (SEM). 25, anterior part of body, counterprint, micrograms, photographed under scanning electron microscope (SEM). Length of body 4.6 (without missing posterior part of body) mm.



26



SEM HV: 15.00 kV Vac: LowVac, 34 Pa View field: 4.19 mm Det: LVSTD 1 mm VEGA\\ TESCAN

27

MNHN

IX FIGURES 26–27. *Menatoraea typica* **gen. et sp. nov.**, additional specimen, print “NEL 2895” (MNT). 26, body; photographed under Nikon SMZ25 stereomicroscope with a Nikon D800 camera. 27, body, micrograms, photographed under scanning electron microscope (SEM). Length of body 4.6 (without missing posterior part of body) mm.

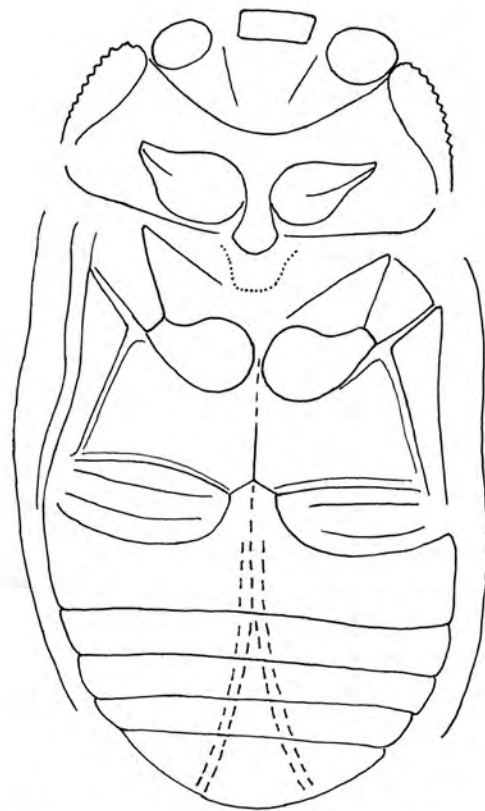
***Menatoraea typica* sp. nov.**

Figs 13–36

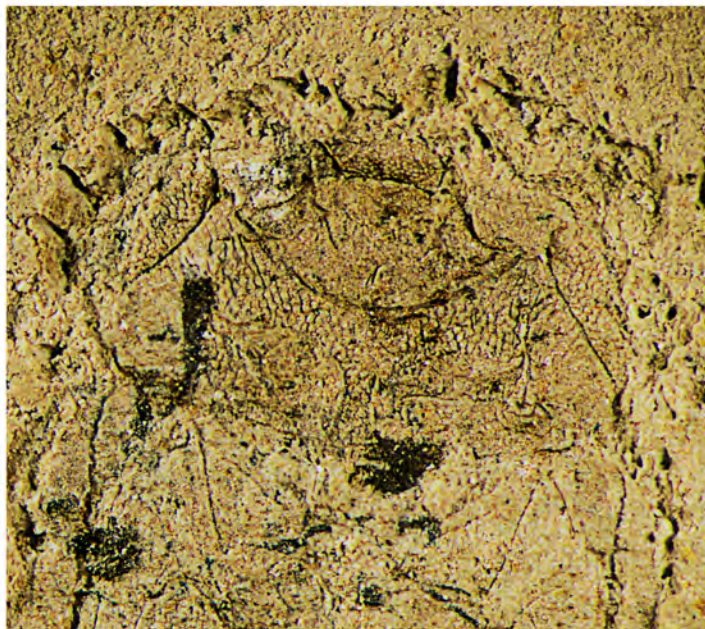
Holotype. Print “MNT 06-3459A” (MNT) and counterprint “MNT 06-3459B” (MNT) of beetle body (both with few remains of organic matter), sex unknown, deposited in rather soft and somewhat smoothed rock and represented by a mixture of the slightly obliterated outlines of body dorsal and ventral sclerites, and also coxae and right protibia, with trace of seriate elytral puncturation and depressions of both left part of the mesofemora and the femur in the counterprint; **paratype** “NEL 135” (MNT), print of beetle body with few remains organic matter on head and prothorax, sex unknown; deposited in comparatively soft and somewhat smoothed rock and represented by a mixture of the slightly obliterated outlines of body dorsal and ventral sclerites, and also coxae, but clear traces of visible seriate elytral puncturation (visible under optic microscope but not in SEM image); **paratype** “NEL 2294” (MNT), print and counterprint of beetle body with a large portion of organic matter and missing posterior part, sex unknown; deposited in rather hard rock and represented by a mixture of the obliterated outlines of body dorsal and ventral sclerites, and also coxae, with trace of seriate elytral puncturation in SEM picture; **additional specimen** “NEL 2895” (MNT), print of beetle body with some amount of remains of organic matter on head and prothorax, sex unknown; deposited in comparatively soft and somewhat smoothed rock and represented by a mixture of the slightly obliterated outlines of body dorsal and ventral sclerites, and also coxae and small parts of protibiae, and with coarse seriate elytral puncturation (visible in usual optics, but not on SEM picture); **additional specimen** “MNT-05-233” (MNT), print of beetle body, sex unknown; deposited in rather soft and somewhat smoothed rock and represented by a mixture of the slightly obliterated outlines of body dorsal and ventral sclerites, and also coxae and two protibiae, with trace of seriate elytral puncturation; **additional specimen** “MNT 06-3354”



28

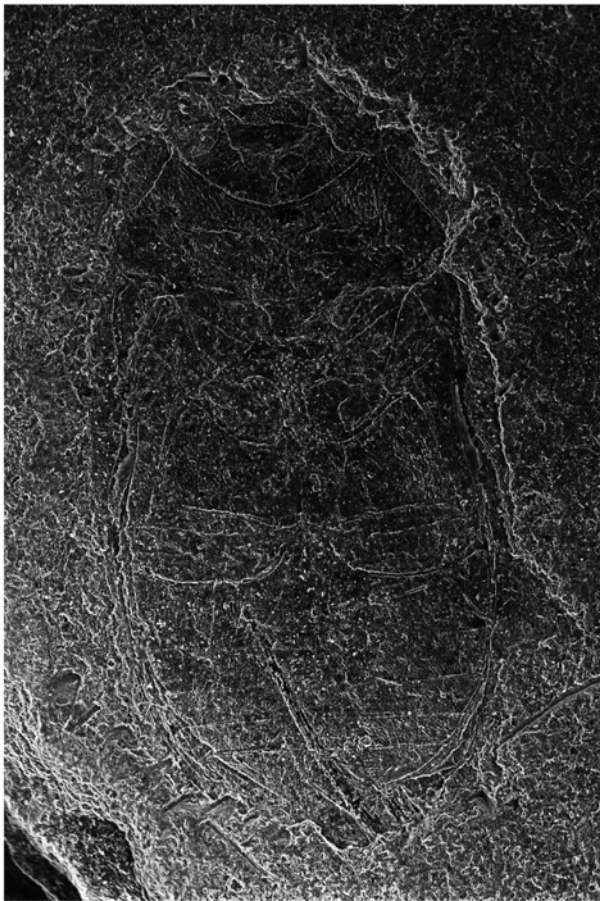


29

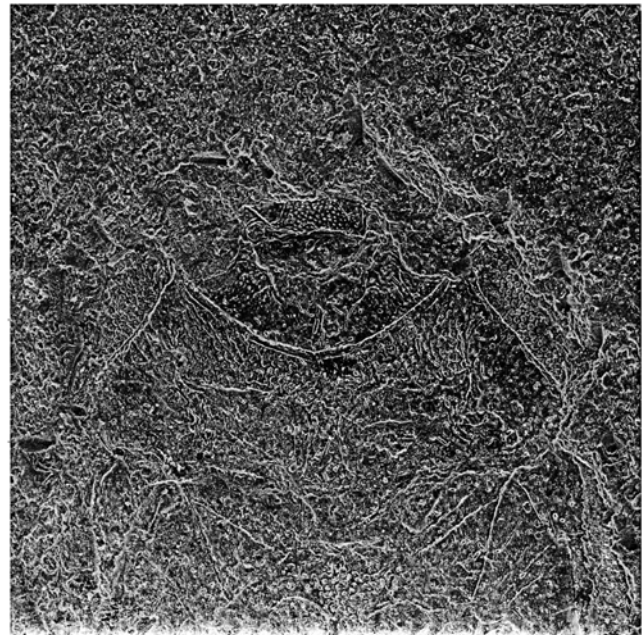


30

X FIGURES 28–30. *Menatoraea typica* gen. et sp. nov., additional specimen, print “MNT 05-233” (MNT). 28, body; photographed under Nikon SMZ25 stereomicroscope with a Nikon D800 camera. 29, body, reconstructed drawing of print. 30, anterior part of body, photographed under Olympus camera. Length of body 4.6 mm.



SEM HV: 20.00 kV Vac: LowVac, 38 Pa
View field: 5.20 mm Det: LVSTD 1 mm



SEM HV: 20.00 kV Vac: LowVac, 38 Pa
View field: 2.59 mm Det: LVSTD 500 µm
VEGA\\ TESCAN
MNH

32

31

XI FIGURES 31–32. *Menatoraea typica* **gen. et sp. nov.**, additional specimen, print “MNT 05-233” (MNT). 31, body, micrograms, photographed under scanning electron microscope (SEM). 25, anterior part of body, micrograms, photographed under scanning electron microscope (SEM). Length of body 4.6 mm.

(MNT), print with few remains of organic matter on head and prothorax of beetle body, sex unknown; deposited in moderately soft rock and represented by a mixture of the slightly obliterated outlines of body mostly dorsal and some ventral sclerites (mostly as depressions), with traces of seriate elytral puncturation. **additional specimen** “NEL 2851” print of beetle body, sex unknown; deposited in hard rock and represented by outlines of body mostly ventral sclerites, and also coxae, with trace of seriate elytral puncturation on epipleura (under usual optics).

Locality and stratigraphy. Paleocene, Menat (see *Geological setting*).

Etymology. The epithet of this new species means “typical”, “characteristic”, “model” referring that this species includes all diagnostic characters of the genus *Menatoraea* **gen. nov.**

Diagnosis. This new species is distinct among congeners due to its pronotum moderately wide and more or less strongly narrowing at base, comparatively wide protibia, distinctly seriate elytral puncturation with dense punctures in longitudinal rows and lack of submetacoxal line following the posterior edge of metacoxa (see the below key to species).

Description. Holotype. Body length 4.1, width 2.2 mm. Integument of upper surface apparently with median-sized punctures: apparently rather dense and diffuse on pronotum and arranged into longitudinal rows of dense punctures on elytra; punctures on epipleura somewhat finer and denser than those on elytral disc; underside with rather fine and moderately dense punctures. Integument covered with rather short hairs.

Head apparently with medium-sized to moderately large eyes. Prothorax moderately short; pronotum about twice as wide as long, sides seemingly gently sloping, not explanate arcuate at sides, anterior edge apparently very shallowly emarginate, anterior angles apparently very broadly rounded and posterior angles with distinct top; prosternum before procoxae apparently shorter than procoxae, procoxae moderately narrowly separated by

prosternal process strongly widened at widely rounded apex. Mesocoxae moderately large and about as narrowly separated as procoxae. Distance between metacoxae almost twice as great as that between pro- and mesocoxae. Metaventricle markedly more than twice (almost 2.5 times) as long as prosternum before coxae. Submetacoxal lines invisible. Elytra somewhat wider than prothorax, about one and third as long as wide combined, apparently moderately convex, with sides not explanate. Abdomen with ventrite 1 longest (only slightly longer than hypopygidium), each of ventrites 2–4 much shorter than hypopygidium (ventrite 5); hypopygidium very broadly rounded at apex. Protibiae comparatively wide (about three times as long as wide), uniformly and finely crenulate along outer edge. Pro- and mesofemora apparently about twice as wide as protibia, with gently arcuate both anterior and posterior edges.



33

34

XII FIGURES 33–34. *Menatoraea typica* **gen. et sp. nov.**, additional specimen “MNT 06-3354” (MNT), print, photographed under Nikon SMZ25 stereomicroscope with a Nikon D800 camera. 33, body. 34, anterior part of body. Length of body 5.1 mm.

Variations. Length of body 3.2–5.1 mm. Many specimens have the pronotum rather narrowing at the posterior angles. This could be because of differences in conditions of fossilization. The specimen “NEL 2895” has coarse and very dense punctures in longitudinal rows (visible in usual optics, but not on SEM picture) which could be either a sequence of specific fossilization or because of its attridution to another species. Other distinguishing peculiarities of additional specimens can be interpreted without a certain level of doubt and therefore all of them are temporarily regarded as *Menatopsis typica* **sp. nov.**

The specimens examined in addition to the holotype:

paratype “NEL 135”, length 4.6, width 2.3 mm;

paratype “NEL 2294”, length 4.6 (without missing posterior part of body), width 2.5 mm; in SEM longitudinal rows of punctures apparently associated with short scales;

additional specimen “NEL 2895”, length 4.6, width 2.3 mm;

additional specimen “MNT-05-233”, length 4.6, width 2.4 mm; distance between mesocoxae has a different comparable proportion than that in other specimens considered as conspecific ones;

additional specimen “MNT 06-3354”, length 5.1, width 2.6 mm; pronotum evenly convex and most widest at base with rounded posterior angles;

additional specimen “NEL 2851”, length 3.2, width 1.8 mm; Print somewhat turned along longitudinal body axis during fossilization and therefore completely comparable with other specimens here regarded as conspecific.



35



SEM HV: 15.00 kV Vac: LowVac, 40 Pa
View field: 3.83 mm Det: LVSTD

1 mm

36

XIII FIGURES 35–36. *Menatoraea typica* **gen. et sp. nov.**, additional specimen, print “NEL 2851” (MNT). 35, body, photographed under Nikon SMZ25 stereomicroscope with a Nikon D800 camera. 36, *ibid.*, micrograms, photographed under scanning electron microscope (SEM). Length of body 3.2 mm.

***Menatoraea angustitibialis* sp. nov.**

Figs 37–45

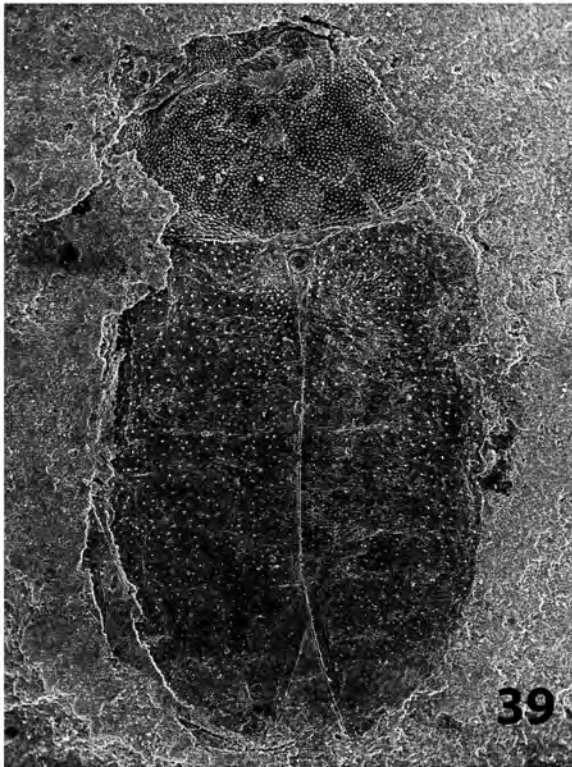
Holotype. Print “MNT 05-253a” (MNT) and counterprint “MNT 05-253b” (MNT) of beetle body (both with few and very small remains of organic matter), sex unknown, deposited in rather soft and somewhat smoothed rock and represented by a mixture of the somewhat obliterated outlines of body dorsal (mostly in the print) and ventral (mostly in the counterprint) sclerites, and also coxae and right protibia, with few trace of slightly seriate elytral puncturation in the SEM picture and depressions of both profemora and the left mesofemora in the print; abdomen somewhat crushed and viewed wider than elytra; **paratype**, print “MNT 05-29A” (MNT) and counterprint “MNT 05-29B” (MNT) of beetle body without remains organic matter, sex unknown; deposited in rather soft and somewhat smoothed rock and represented by a mixture of the somewhat obliterated outlines of body dorsal (mostly in the print) and ventral (mostly in the counterprint) sclerites, and also coxae and right protibia, with few traces of slightly seriate elytral puncturation in the SEM picture and depressions of both profemora in the print and right mesofemur in the counterprint.



37



38



39

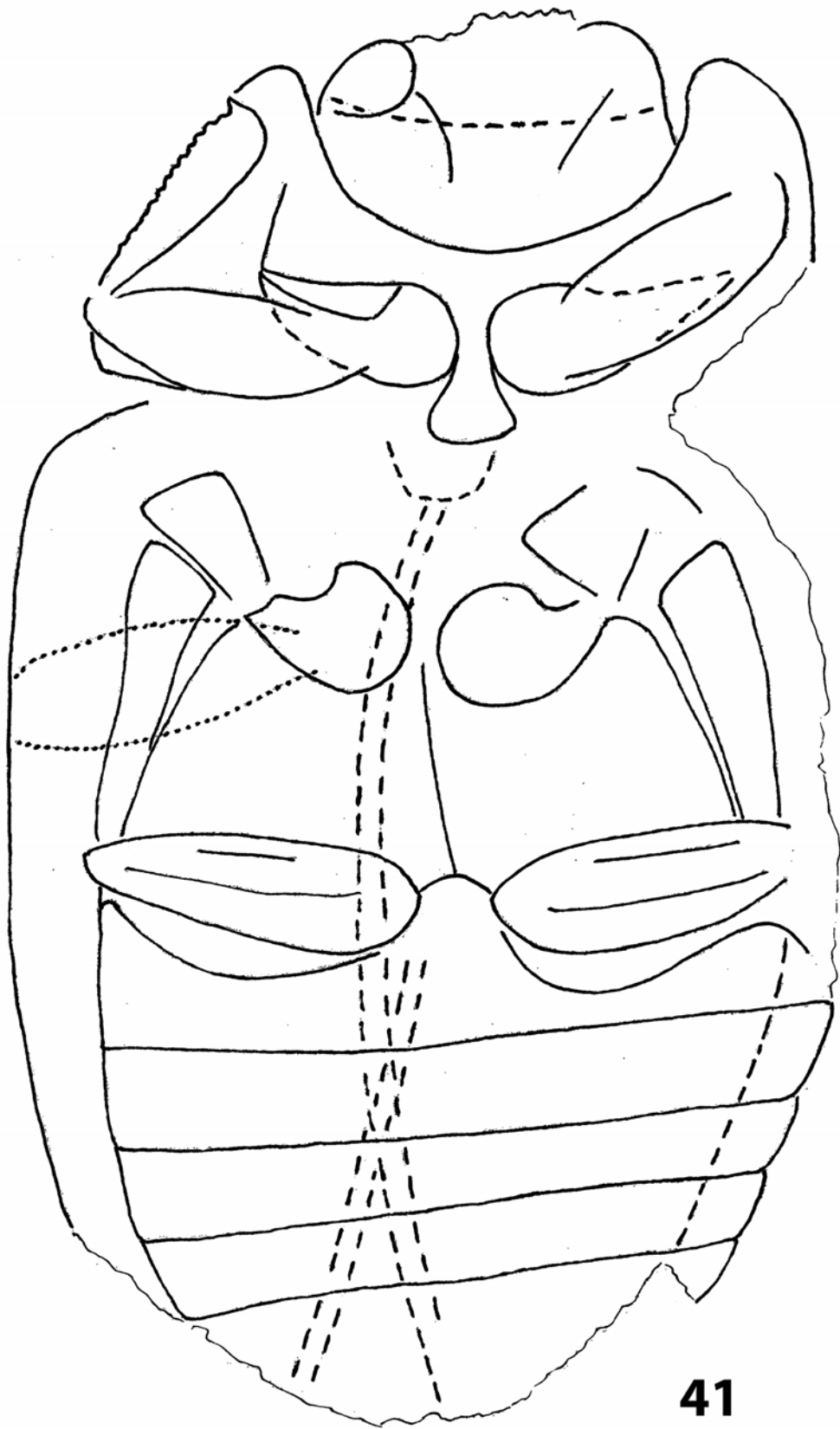
SEM HV: 20.00 kV Vac: LowVac, 45 Pa
View field: 5.40 mm Det: LVSTD 1 mm



40

SEM HV: 20.00 kV Vac: LowVac, 45 Pa
View field: 5.45 mm Det: LVSTD 1 mm

XIV FIGURES 37–40. *Menatoraea angustitibialis* gen. et sp. nov., holotype, print “MNT 05-253a” (MNT) and counterprint “MNT 05-253b” (MNT). 37, body, print; photographed Olympus SCX9 stereomicroscope with an Olympus camera; 38, counterprint, photographed under Nikon SMZ25 stereomicroscope with a Nikon D800 camera. 39, print, micrograms, photographed under scanning electron microscope (SEM). 40, counterprint, micrograms, photographed under scanning electron microscope (SEM). Length of body 6.0 mm.



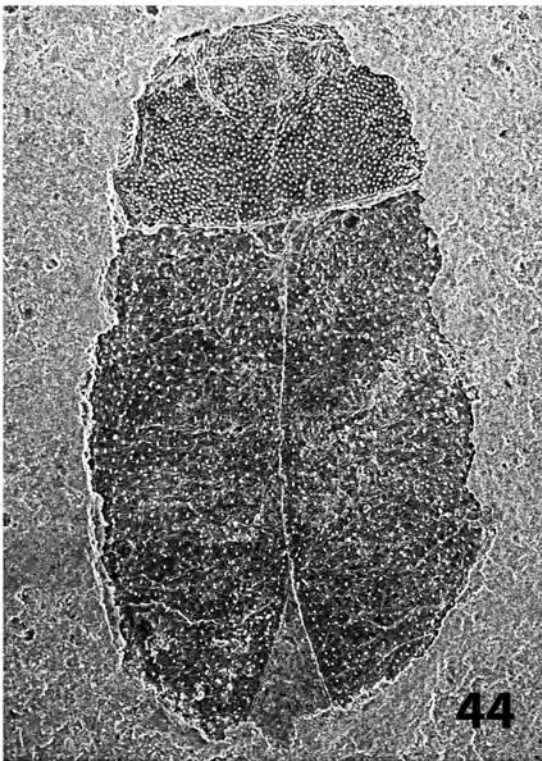
XV FIGURE 41. *Menatoraea angustitibialis* **gen. et sp. nov.**, holotype, counterprint “MNT 05-253b” (MNT). Reconstructed drawing with broken lines for outline of elytral edges and adsutural lines, and dotted lines for outlines of depressed place of right mesofemur. Length of body 6.0 mm.



42

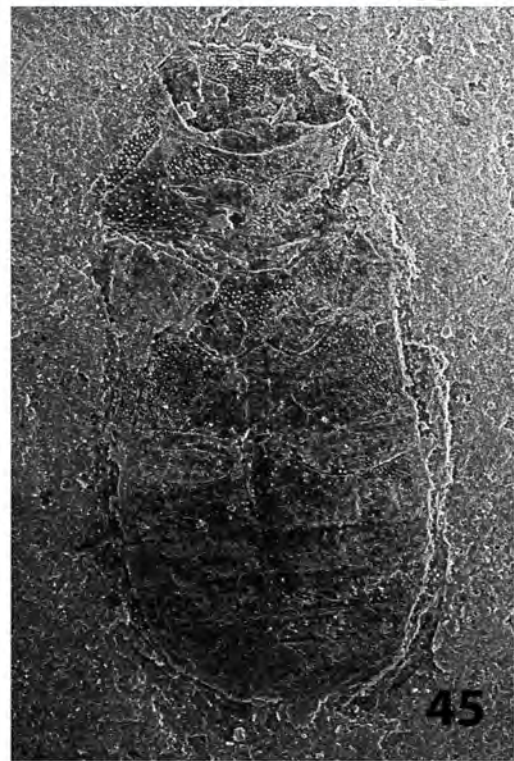


43



44

SEM HV: 20.00 kV Vac: LowVac, 36 Pa
View field: 5.47 mm Det: LVSTD 1 mm



45

SEM HV: 20.00 kV Vac: LowVac, 45 Pa
View field: 5.79 mm Det: LVSTD 1 mm

XVI FIGURES 42–45. *Menatoraea angustitibialis* gen. et sp. nov., paratype, print “MNT 05-29A” (MNT) and counterprint “MNT 05-29B” (MNT). 42, body, print; photographed under Nikon SMZ25 stereomicroscope with a Nikon D800 camera. 43, ibid., counterprint; photographed under Nikon SMZ25 stereomicroscope with a Nikon D800 camera. 44, print, micrograms, photographed under scanning electron microscope (SEM). 45, anterior part of body, counterprint, micrograms, photographed under scanning electron microscope (SEM). Length of body 5.6 mm.

Locality and stratigraphy. Paleocene, Menat (see *Geological setting*).

Etymology. The epithet of this new species is formed from the Latin “*angustus*” (narrow, thin) and “*tibialis*” (adjective from “*tibia*”).

Diagnosis. This new species is distinct within congeners due to its comparatively large body, pronotum moderately wide and widest at base, comparatively large head, rather narrow protibia, only with weak traces of seriate elytral puncturation and submetacoxal line deviating from the posterior edge of metacoxa (see the below key to species).

Description. Holotype. Body length 6.0, width 3.4 mm. Integument of upper surface apparently with small punctures: rather dense and diffuse on pronotum and very sparse punctures on elytra with trace of longitudinal rows; punctures on epipleura somewhat finer and denser than those on elytral disc; underside with rather fine and moderately dense punctures (denser on prosternum). Integument covered with rather short and thick hairs (probably scales).

Head large and apparently with large eyes. Prothorax moderately short; pronotum about twice as wide as long, sides seemingly gently sloping, not explanate and arcuate at sides, anterior edge apparently subtruncate very shallowly emarginate, anterior angles apparently very broadly rounded and posterior angles with rounded top; prosternum before procoxae apparently shorter than procoxae, procoxae moderately narrowly separated by prosternal process strongly widened at widely rounded apex. Mesocoxae moderately large and slightly more widely separated than procoxae. Distance between metacoxae almost twice as great as that between pro- and mesocoxae. Metaventricle more than three times as long as prosternum before coxae. Submetacoxal lines clearly arcuately deviated. Elytra about as wide as prothorax, about one and third as long as wide combined, apparently moderately convex, with sides not explanate. Abdomen with ventrite 1 about as long as hypopygidium, each of ventrites 2–4 much shorter; hypopygidium apparently very broadly rounded at apex. Protibiae rather narrow (about four times as long as wide), uniformly and finely crenulate along outer edge. Pro- and mesofemora apparently more than twice as wide as protibia, with gently arcuate anterior and posterior edges.

Variations. Length of body 5.6–6.0 mm (paratype “MNT 05-29A” and “MNT 05-29B” (MNT), length 5.6, width 3.0 mm. Another specimen is rather similar to the holotype.

***Menatoraea laticollis* sp. nov.**

Figs 46–51

Holotype. “NEL 80” (MNT) print and counterprint of beetle body (both with many remains of organic matter), sex unknown, deposited in moderately soft and somewhat smoothed rock and represented by a mixture of the somewhat obliterated outlines of body dorsal (mostly in the counterprint) and ventral (mostly in the print) sclerites, and also with coxae, mesofemora, deep longitudinal furrows (striae) on elytra and short scales on dorsal sclerites (visible under normal optics).

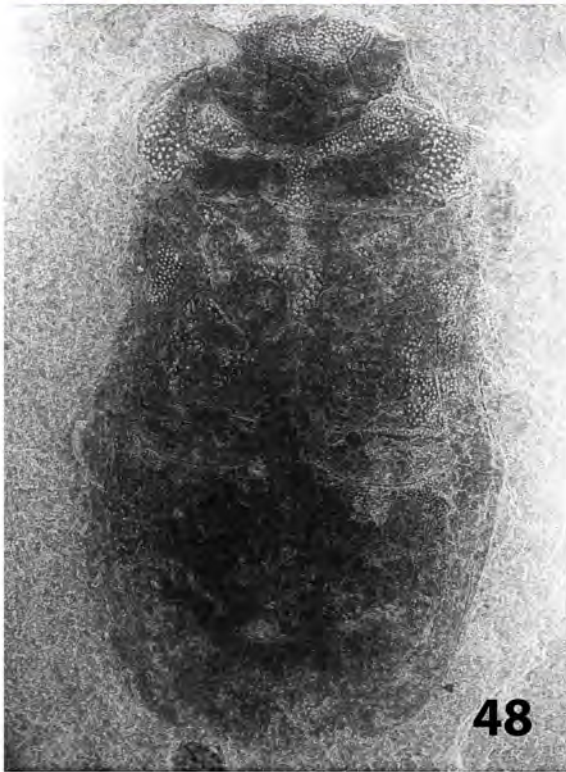
Locality and stratigraphy. Paleocene, Menat (see *Geological setting*).

Etymology. The epithet of this new species is formed from Latin “*latus*” (wide, broad) and “*collis*” frequently used as adjective from “*pronotum*”.

Diagnosis. This new species is quite distinct among congeners due to its rather wide pronotum, very short prosternum, deep longitudinal furrows on elytra and sparse punctures on elytra (see the below key to species).

Description. Holotype. Body length 4.0, width 2.4 mm. Integument of upper surface apparently with small punctures: rather dense and diffuse on pronotum and somewhat sparser punctures on elytra with trace of longitudinal rows of punctures associated with longitudinal furrows; punctures on epipleura somewhat finer and denser than those on elytral disc; underside with rather fine and rather dense punctures (denser on prosternum). Integument covered with rather short and thick hairs (probably scales).

Head moderately large and apparently with large eyes. Prothorax rather short; pronotum about three times as wide as long, sides seemingly gently sloping and narrowly (sub) explanate along arcuate sides, anterior edge apparently subtruncate to very shallowly emarginate, anterior and posterior angles very broadly rounded; prosternum before procoxae apparently about half as short as procoxae, procoxae moderately narrowly separated by prosternal process particularly strongly widened at almost transverse apex. Mesocoxae moderately large and slightly more widely separated than procoxae. Distance between metacoxae almost twice as great as that between

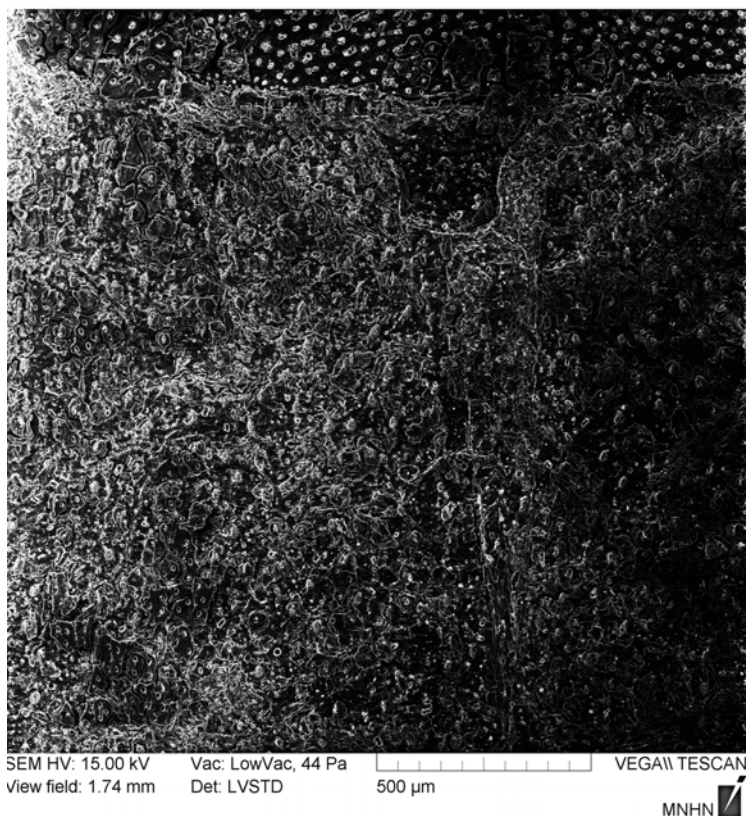


SEM HV: 15.00 kV Vac: LowVac, 44 Pa
View field: 5.20 mm Det: LVSTD 1 mm

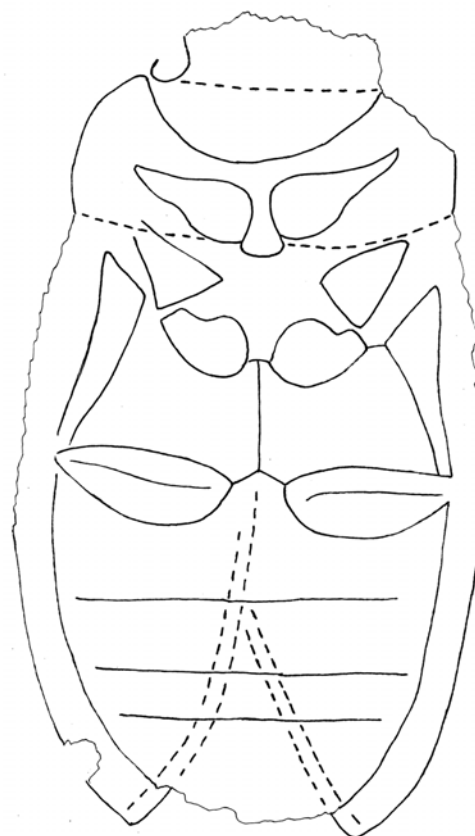


SEM HV: 15.00 kV Vac: LowVac, 44 Pa
View field: 4.96 mm Det: LVSTD 1 mm

XVII FIGURES 46–49. *Menatoraea laticollis* gen. et sp. nov., “NEL 80” (MNT) print and counterprint. 46, body, print; photographed under Nikon SMZ25 stereomicroscope with a Nikon D800 camera. 47, ibid., counterprint; photographed under Nikon SMZ25 stereomicroscope with a Nikon D800 camera. 48, print, micrograms, photographed under scanning electron microscope (SEM). 49, anterior part of body, counterprint, micrograms, photographed under scanning electron microscope (SEM). Length of body 4.0 mm.



50



51

XVIII FIGURES 50–51. *Menatoraea laticollis* **gen. et sp. nov.**, “NEL 80” (MNT) print and counterprint. 50, base of pronotum, scutellum and elytra, counterprint, micrograms, photographed under scanning electron microscope (SEM). 51, body, reconstructed drawing with broken lines for outline of posterior edge of pronotum, sutural edges and adsutural lines of elytra. Length of body 4.0 mm.

pro- and mesocoxae. Metaventricle almost four three times as long as prosternum before coxae. Submetacoxal lines invisible. Elytra about as wide as prothorax, widest at midlength, about one and third as long as wide combined, apparently moderately convex, with sides not explanate. Abdomen with ventrite 1 about as long as hypopygidium, each of ventrites 2–4 much shorter; hypopygidium apparently very broadly rounded at apex. Mesofemora markedly less than twice as long as wide, with gently arcuate anterior and posterior edges.

***Menatoraea gracilis* sp. nov.**

Figs 52–59

Holotype. “NEL 2944” (NMT), print of beetle body, sex unknown, deposited in moderately rather hard rock and represented by outlines of dorsal side of body with almost not exposed seriate puncturation and pubescence, and also with depressions of some scleriters of underside (pro- and metacoxae); **Paratype** “NEL 1981” (NMT), print of beetle body (with missing elytral apices), sex unknown, deposited in moderately rather hard rock and represented by a outlines of dorsal side of body with scarcely exposed seriate puncturation and pubescence, and also with depressions of some scleriters of underside (coxae).

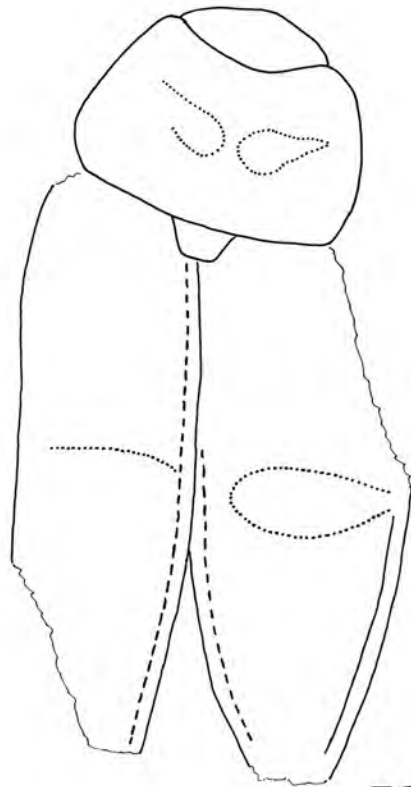
Locality and stratigraphy. Paleocene, Menat (see *Geological setting*).

Etymology. The epithet of this new species means graceful.

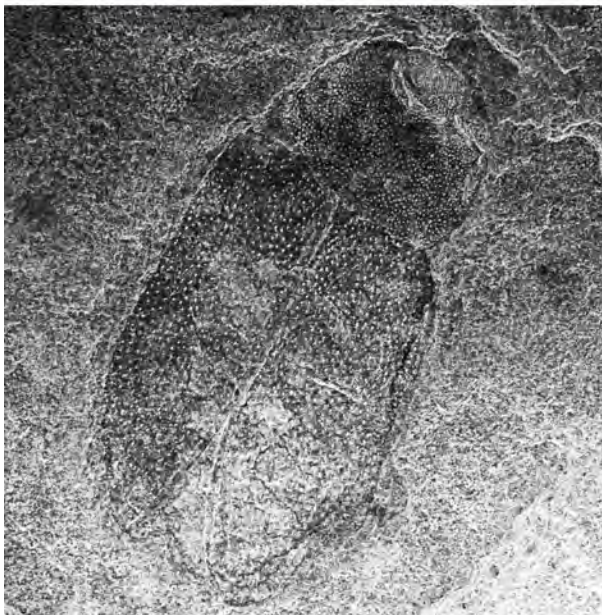
Diagnosis. This new species is distinct from the other congeners by its comparatively long pronotum with very broadly arcuate sides, longer and more acuminate elytral apices (see the below key to species). It is also characterized by slightly expressed longitudinal rows of punctures and scales on its elytra.



52

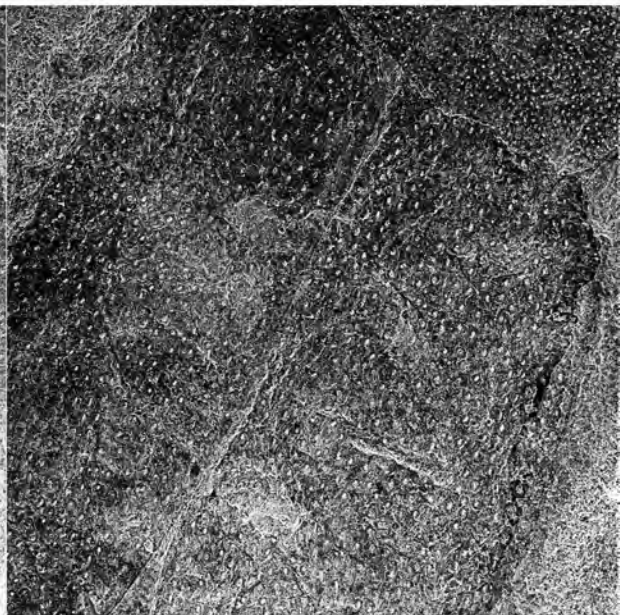


53



EM HV: 15.00 kV Vac: LowVac, 40 Pa
View field: 5.56 mm Det: LVSTD 1 mm

54



VEGAII TESCAN SEM HV: 15.00 kV Vac: LowVac, 36 Pa
View field: 2.92 mm Det: LVSTD 500 µm

55

XIX FIGURES 52–55. *Menatoraea gracilis* **gen. et sp. nov.**, holotype, print “NEL 2944” (NMT). 52, body, photographed under Olympus SCX9 stereomicroscope with an Olympus camera. 53, *ibid.*, reconstructed drawing with dotted lines outlined depressed places of pro- and metacoxae. 54, *ibid.*, micrograms, photographed under scanning electron microscope (SEM). 55, base of pronotum, scutellum and elytra, micrograms, photographed under scanning electron microscope (SEM). Length of body 6.3 mm.



56

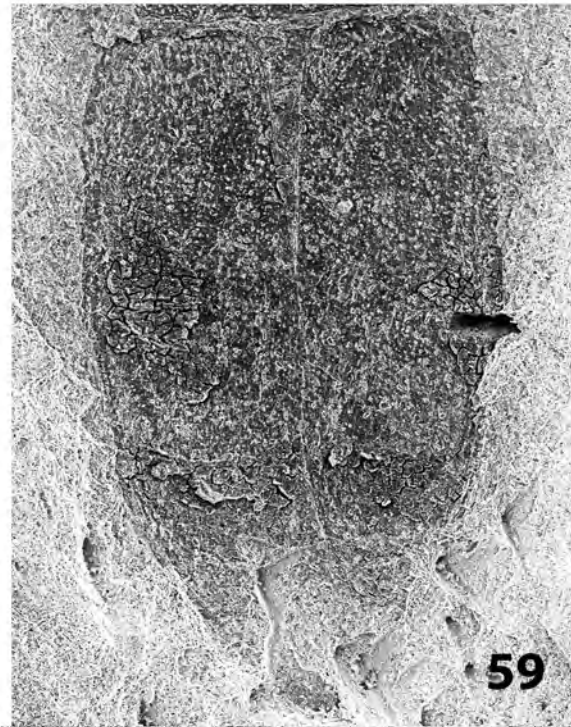


57



58

SEM HV: 15.00 kV Vac: LowVac, 29 Pa
View field: 4.90 mm Det: LVSTD 1 mm



59

SEM HV: 15.00 kV Vac: LowVac, 36 Pa
View field: 3.25 mm Det: LVSTD 1 mm

XX FIGURES 56–59. *Menatoraea gracilis* gen. et sp. nov., paratype, print “NEL 1981” (MNT). 56, body, photographed under Nikon SMZ25 stereomicroscope with a Nikon D800 camera. 57, posterior part of body, photographed under Olympus SCX9 stereomicroscope with an Olympus camera. 58, body, micrograms, photographed under scanning electron microscope (SEM). 59, posterior part of body, micrograms, photographed under scanning electron microscope (SEM). Length of body 4.8 mm.

Description. Holotype. Body length 6.3, width 3.2 mm. Integument of upper surface apparently with small punctures: rather dense and diffuse on pronotum and sparser punctures on elytra with slight trace of longitudinal rows. Integument covered with rather short and thick hairs (probably scales).

Head large and apparently with moderately large eyes. Pronotum comparative about 1.5 times as wide as long, sides seemingly gently sloping, not explanate and broadly arcuate at sides, anterior edge shallowly emarginate, anterior angles apparently very broadly rounded and posterior angles apparently with stump top. Elytra about as wide as prothorax, about 1.5 times as long as wide combined, apparently moderately convex, with sides not explanate. Outlines of depressions of coxae are very similar to those in other congeners.

Variation. Length of paratype body 4.8 mm.

Key to species of the genus *Menatoraea* gen. nov. from Menat

1. Pronotum about 1.5 times as wide as long; elytra about 1.5 times as long as wide combined. 4.8–6.3 mm. Figs 52–59 *M. gracilis* sp. nov.
- Pronotum at least twice as wide as long; elytra at most one and third as long as wide combined 2
2. Pronotum about 3 times as wide as long; precoxal part of prosternum about half as long as procoxae. 4.0 mm. Figs 46–51 *M. laticollis* sp. nov.
- Pronotum at least twice as wide as long; precoxal part of prosternum longer – only slightly shorter than procoxae 3
3. Pronotum widest at base; protibiae very narrow; elytra with hardly visible puncturation and with weakly expressed longitudinal rows of punctures. 5.6–6.0 mm. Figs 37–45 *M. angustitibialis* sp. nov.
- Pronotum widest before base; protibiae moderately narrow; elytra with moderately coarse puncturation and with well expressed longitudinal rows of punctures. 4.1–5.1 mm. Figs 13–36 *M. typica* sp. nov.

Menatoraea sp. 1

Figs 60–61

Specimen examined. “NEL 1481” (MNT), print of beetle prothorax and abdomen, sex unknown; deposited in hard rock and represented by outlines of posterior part of the body mostly ventral sclerites, and also coxae; with depressions of mesofemora and without trace of seriate elytral puncturation. Available characters of this print is as in other species of *Menatoraea* but not enough to determine species, although its body about as large as in *M. angustitibialis*. Length of print 4.7 mm.

Menatoraea sp. 2

Figs 62–63

Specimen examined. “NEL 3085” (MNT), print of somewhat deformed beetle body, sex unknown; deposited in hard rock and represented by a mixture of the somewhat obliterated outlines of body dorsal and ventral sclerites, coxae and right protibia, with traces seriation in elytral puncturation. All characters are deformed and not comparable, but all of them more or less fit those in other species of *Menatoraea* gen. nov. Length of body 3.7 mm, width 2.0 mm.

Genus *Palaeolycra* gen. nov.

Type species. *Palaeolycra palaeocenica* sp. nov.

Etymology. The name of the new genus is formed from the Greek “*palaeos*” (ancient, old) and one of root of the generic names “*Thalycra*”, “*Thalycrodes*”, etc. Gender feminine.

Diagnosis. Body elongate oval and convex, medium-sized (length 4.0 mm). Integument with rather fine and diffuse punctures; without visible hairs. Head transverse, apparently with moderately large eyes. Prothorax short; pronotum strongly narrowing anteriorly, sides seemingly steeply sloping at arcuate unbordered sides, anterior and

posterior angles more or less distinct; prosternum rather short before procoxae, procoxae narrowly separated, and metacoxae somewhat more widely separated. Metaventricle moderately short, with raised submesocoxal lines and without discripen. Scutellum apparently rather large and transversely triangular. Elytra about as wide as prothorax, apparently rather convex, widest at base and somewhat longer than wide combined, with clear adsutural line reaching elytral base. Protibia very wide and subflattened and with strongly projecting outer apical angle. Protarsus strongly widened.

Notes. The very wide protibia with a long apical process is characteristic of some nitidulines with pubescent dorsum, mostly from the *Thalycra*-complex of genera (or *Thalycra*-like genera of the *Pocadius*-complex), although few representatives of these groups with fine and almost inconspicuous hairs on integument (up to completely bald on the dorsum), however, the groups of these complexes have not very wide protarsi. Nevertheless, some genera of this complex have the adsutural lines on elytra and comparable separations of coxae in every pair, and, therefore, the new genus seems to be a member of this complex. A significant similarity of *Palaeolycra* **gen. nov.** with some other genera of *Pocadius*-complex concerns distances between coxae, body shape and structure of tibiae, but these members have more oval bodies with (sub)explanate pronotal and elytral sides and narrow tarsi that make assignment of the new genus to this complex less probable. The very wide protibia and wide protarsus are also characteristic of many Meligethinae Thompson, 1859, but the groups of the latter subfamily have widely separate metacoxae with nearly straight posterior edge of metaventricle between metacoxae, tibiae without strong apical process and, if they have expressed adsutural lines, these lines are present only in distal pat of elytra. On the other hand, the oval and convex body with the shallowly emarginated posterior edge of metaventricle between metacoxae and lack of raised pubescence occur in the tribes Cyllodini that are currently spread on all zoogeographic regions (except Antarctic Region) and endemic Australian Cychramptodini Kirejtshuk et Lawrence, 1992. The second tribe seems to have had a comparatively recent origin in Australia during the Cenozoic, while the first was recorded in the Obeshtshayushtshiy (Magadanskaya region) of the Cenomanian age (Kirejtshuk & Ponomarenko 1990). Besides, the cychramptodin meso- and metacoxae are very narrowly separated to subcontiguous, while those in Cyllodini are more or less separated. Thus, the relationships of *Palaeolycra* **gen. nov.** to Meligethinae and tribes Cyllodini and Cychramptodini is not so close as that to the mentioned complexes of genera of Nitidulini.

Comparison. The oval convex body, long adsutural lines, diffuse elytral puncturation and wide flattened tibiae with long apical process are known in the extant genus *Quadriprons* Blatchley, 1916, but the new genus differs from it in the adsutural lines reaching elytral base, lack of pubescence and apparently triangular scutellum. *Palaeolycra* **gen. nov.** differs from other genera of *Thalycra*-complex in either seriate sculpture of elytra (*Australycra* Kirejtshuk et Lawrence, 1992; *Pocadiolycra* Kirejtshuk et Leschen, 1998; *Rixerodes* Kirejtshuk et Lawrence, 1992; *Tagmolycra* Kirejtshuk et Leschen, 1998; *Thalycrodes* Blackburn, 1891), shape of pronotum (*Pleuroneces* Olliff, 1891; *Pocadionta* Lucas, 1920; *Pseudothalycra* Howden, 1962; *Rixerodes*; *Thalycra* Erichson, 1843; *Thalycrodes*), or very wide protibiae with strong apical process (*Pleuroneces*, *Pocadiolycra*, *Pocadionta*, *Pseudothalycra*, *Tagmolycra*, *Thalycra*, *Thalycrodes*).

This new genus shows a clear attribution to the *Thalycra*-complex of genera and a probable close relation to *Quadriprons* and, maybe also, to *Menatoraea* **gen. nov.** (see also the above Diagnosis of the latter genus and below Discussion and conclusions).

***Palaeolycra palaeocenica* sp. nov.**

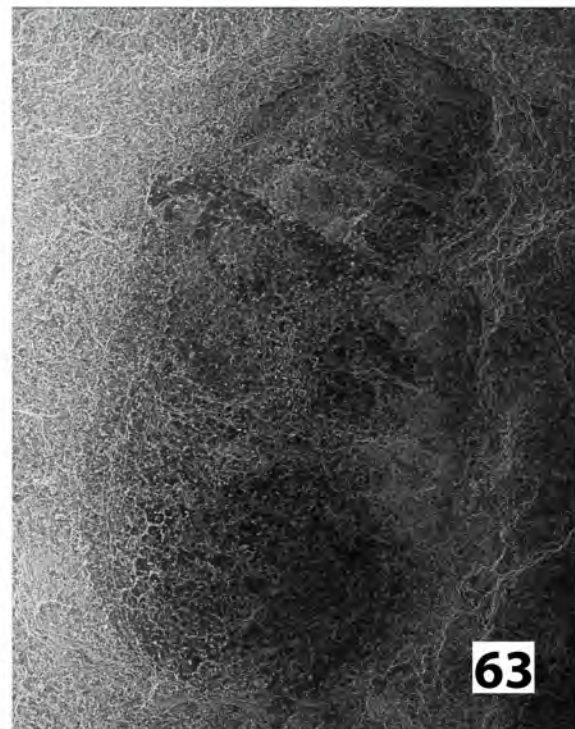
Figs 64–69

Holotype. “MNT 06-3520A” (MNT), print and “MNT 06-3520B” (MNT), counterprint of beetle body (both without organic matter), male, deposited in moderately soft and somewhat smoothed rock and represented by a mixture of the somewhat obliterated outlines of body dorsal (mostly in the print) and ventral (mostly in the counterprint) sclerites, and also with coxae, right protibia and protarsus.

Locality and stratigraphy. Paleocene, Menat (see *Geological setting*).

Etymology. The epithet of this new species refers to age of this species.

Description. Holotype. Body length 4.0, width 2.4 mm. Integument of with rather small punctures, moderately dense and diffuse, somewhat sparser on elytra; without visible hairs.



SEM HV: 15.00 kV Vac: LowVac, 40 Pa
View field: 4.02 mm Det: LVSTD 1 mm

SEM HV: 15.00 kV Vac: LowVac, 42 Pa
View field: 3.76 mm Det: LVSTD 1 mm

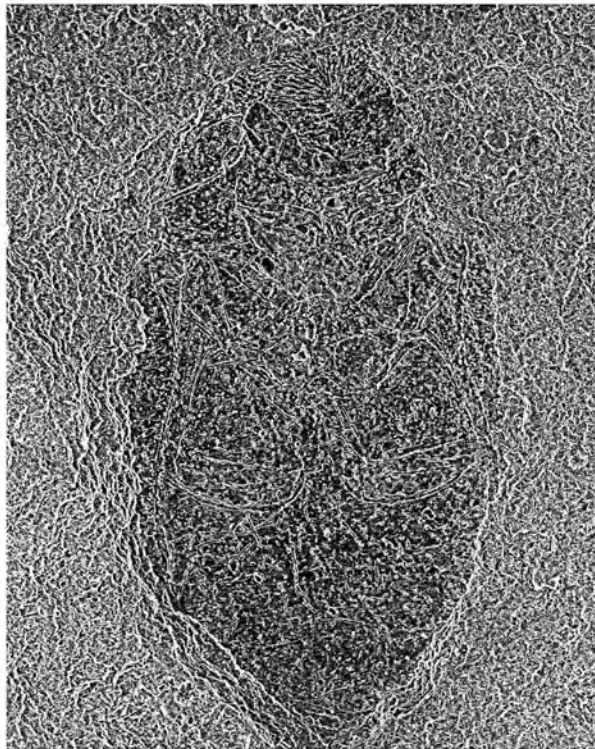
XXI FIGURES 60–63. *Menatoraea* spp. 60, posterior part of body *M.* sp. 1, print “NEL 1481” (MNT); photographed under Nikon SMZ25 stereomicroscope with a Nikon D800 camera. 61, body *M.* sp. 2, print “NEL 3085” (MNT); photographed under Olympus SCX9 stereomicroscope with an Olympus camera. 62, posterior part of body of print “NEL 1481”, micrograms, photographed under scanning electron microscope (SEM). 63, body of print “NEL 3085”, micrograms, photographed under scanning electron microscope (SEM). Length of posterior part of body of print “NEL 1481” 4.7 mm and length of body of print “NEL 3085” 3.7 mm.



64



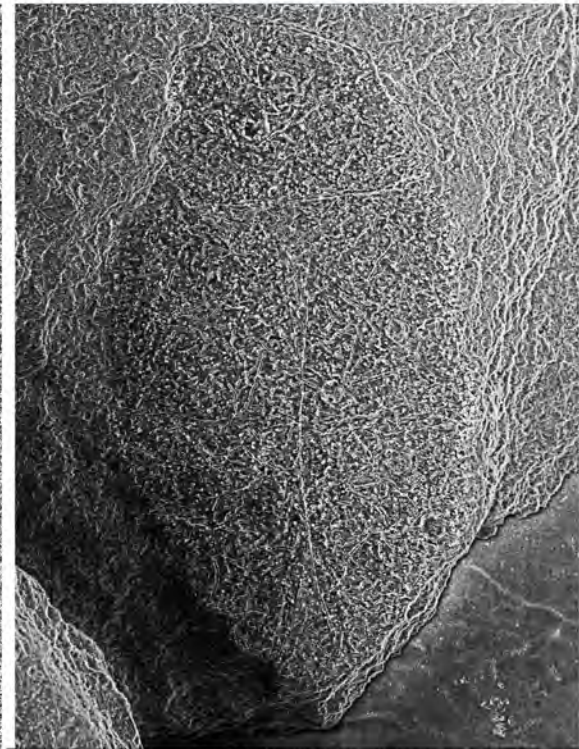
65



SEM HV: 20.00 kV Vac: LowVac, 35 Pa
View field: 3.71 mm Det: LVSTD

1 mm

66



SEM HV: 20.00 kV Vac: LowVac, 36 Pa
View field: 3.77 mm Det: LVSTD

1 mm

67

XXII FIGURES 64–67. *Palaeolydra palaeocenica* **gen. et sp. nov.**, holotype, print “MNT 06 3520A” (MNT) and counterprint “MNT 06 3520B” (MNT). 64, body, print; photographed under Nikon SMZ25 stereomicroscope with a Nikon D800 camera. 65, *ibid.*, counterprint; photographed under Olympus SCX9 stereomicroscope with an Olympus camera. 66, body, print, micrograms, photographed under scanning electron microscope (SEM). 67, *ibid.*, counterprint, micrograms, photographed under scanning electron microscope (SEM). Length of body 4.0 mm.



68



69

XXIII FIGURES 68–69. *Palaeolydra palaeocenica* **gen. et sp. nov.**, holotype. 68, anterior part of body, print “MNT 06 3520A” (MNT), photographed under Olympus SCX9 stereomicroscope with an Olympus camera. 69, body, reconstructed drawing with broken line for outline of scutellum. Length of body 4.0 mm.

Head moderately large and apparently with moderately large eyes. Prothorax rather short; pronotum apparently about twice as wide as long, sides seemingly steeply sloping at arcuate sides, anterior edge apparently subtruncate, anterior and posterior angles apparently with distinct top; prosternum before procoxae apparently about half as short as procoxae, procoxae moderately narrowly separated by prosternal process somewhat widened at almost transverse apex. Mesocoxae moderately large and as widely separated as procoxae. Distance between metacoxae somewhat greater than that between pro- and mesocoxae. Metaventricle about 2.5 times as long as prosternum before coxae. Submesocoxal lines following closely to posterior edge of mesocoxae and inner edge of metepisterna. Submetacoxal lines invisible. Elytra about as wide as prothorax, about one and third as long as wide combined. Abdomen with ventrite 1 somewhat longer than hypopygidium, each of ventrites 2–4 much shorter; hypopygidium apparently shallowly emarginate at apex. Protibia about twice as wide as long and with thick outer subapical process. Protarsus slightly wider than distance between procoxae or distance between mesocoxae and about half as wide as protibia. Male anal sclerite somewhat exposed behind apex of hypopygidium.

Subfamily ?Cryptarchinae Thomson, 1859

Tribe ?Cryptarchini Thomson, 1859

?*Cryptarcha* Shuckard, 1839

Notes. The specimen (print and counterprint) “NEL 1758” shows a combination of the characters that can be linked with some recent species of the genus *Cryptarcha*: oval and rather convex body with distinct posterior angles of

pronotum, fine and very sparse diffuse puncturation, and also short diffuse hairs on elytra, comparatively long prosternal process narrowing at apex, moderately narrowly separated procoxae and slightly more widely separated meso- and metacoxae, shallowly emarginate posterior edge of metaventrite. Almost all mentioned characters, except such long prosternal process, can be observed in different taxa of the *Pocadius*- and *Thalycra*-complexes of genera of the tribe Nitidulini (Nitidulinae), but the combination of whole set of characters of the specimen under consideration is not present in these complexes.

The convexity of the elytra of specimen “NEL 1758” can be inferred after the outline of the lateral and sutural edges, and after the narrow explanate stripe along their lateral edge and sculpture. It seems that these elytra are somewhat crushed. Therefore their outlines are wider than in the former living insect. The outlines of pronotal sides are not clear and the width of pronotum and combined width of elytra could be comparable, as characteristic of the modern cryptarchines. Similar outlines of thoracic sclerites are found in some comparatively narrow coccinellids. However the prosternal process, lack of discripen on metaventrite and submeso- and submetacoxal lines of this fossil are rather characteristic of nitidulids and different from those in coccinellids. After the counterprint, it seems that the scutellum could be similar to that of *Menatoraea* **gen. nov.** However the analysis of the outlines of both print and counterprint shows that this impression seem to be false. Scutellum of “NEL 1758” is similar to those of most nitidulids, including most cryptarchines.

This finding is the first fossil record of the subfamily Cryptarchinae (see also below Discussion and conclusions).

(?) *Cryptarcha semiglobosa* sp. nov.

Figs 70–75

Holotype. “NEL 1758”, print and counterprint of a body (both without organic matter), male, fossilised in moderately soft and somewhat smoothed rock, and represented by a mixture of the somewhat obliterated outlines of body dorsal (mostly in the print) and ventral (mostly in the counterprint) sclerites, and also with coxae, right profemur and protibia.

Locality and stratigraphy. Paleocene, Menat (see *Geological setting*).

Etymology. The epithet of this new species refers to its characteristic body shape.

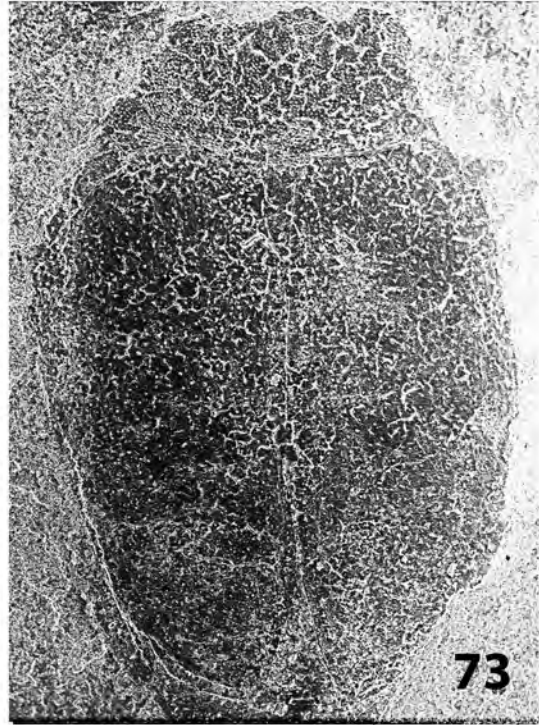
Diagnosis. This new species seems to be distinct from all congeners in the extant fauna in the sub-trapezoid scutellum and dense and fine punctures on pronotum but with markedly sparser and fine punctures on elytra. Most Recent *Cryparcha* species are characterized by longer and denser hairs on dorsum, and also only few extant species of this genus have a rather convex body shape. Besides, most Recent species have more widely separate metacoxae, and not infrequently their posterior edge of metaventrite is very shallowly emarginated, but some species (like *C. concinna* Reitter, 1873) have the proportions in separation of each pair of coxae quite comparable with those in *C. semiglobosa* **sp. nov.**

Description. Body length 5.2, width 3.1 mm. Integument of upper surface apparently with small punctures: rather dense and diffuse on pronotum, and very sparse and diffuse on elytra. Integument covered with rather short and apparently thin hairs.

Head moderately large and apparently with large eyes. Prothorax short; pronotum somewhat more than 2.5 times as wide as long, apparently with gently sloping and broadly arcuate sides, anterior edge apparently subtruncate to very shallowly emarginate, anterior angles very broadly rounded and posterior angles narrowly rounded; prosternum before procoxae slightly shorter than procoxae, procoxae moderately narrowly separated by prosternal process slightly widened before subangular apex. Mesocoxae moderately large and about as widely separated as procoxae. Distance between metacoxae somewhat greater than that between pro- and mesocoxae. Metaventrite about 2.5 times as long as prosternum before coxae, with posterior edge between metacoxae shallowly emarginated and without discripen. Submetacoxal lines distinct and arcuately deviated from posterior edge of metacoxae. Scutellum moderately large and subtriangular. Elytra about as wide as prothorax, widest at anterior third, about one and fourth as long as wide combined, apparently moderately convex, with sides narrowly (sub)explanate. Abdomen with ventrite 1 longest, ventrites 2–4 much somewhat shorter and subequal in length; hypopygidium shortest and apparently very broadly rounded to subtruncate at apex. Male anal sclerite strongly projecting behind pygidial apex. Legs comparatively long. Profemur less than twice as long as wide, with gently arcuate anterior and posterior edges. Protibia rather narrow.

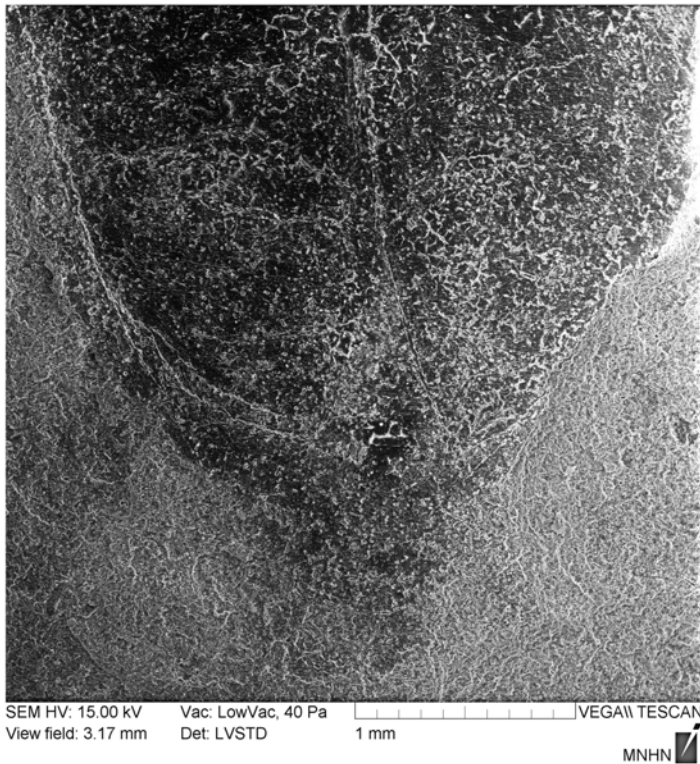


SEM HV: 15.00 kV Vac: LowVac, 35 Pa
View field: 5.44 mm Det: LVSTD 1 mm

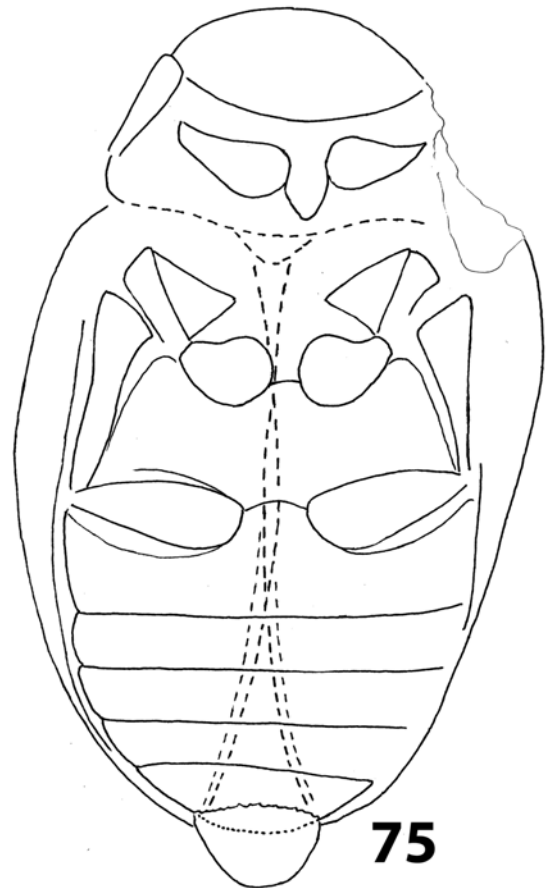


SEM HV: 15.00 kV Vac: LowVac, 40 Pa
View field: 5.02 mm Det: LVSTD 1 mm

XXIV FIGURES 70–73. *?Cryptarcha subglobosa* sp. nov., holotype, print and counterprint “NEL 1758” (MNT). 70, body, print; photographed under Olympus SCX9 stereomicroscope with an Olympus camera. 71, ibid., counterprint, photographed under Olympus SCX9 stereomicroscope with an Olympus camera. 72, print, micrograms, photographed under scanning electron microscope (SEM). 73, ibid., counterprint, micrograms, photographed under scanning electron microscope (SEM). Length of body 5.2 mm.



74



75

XXV FIGURES 74–75. *?Cryptarcha subglobosa* **sp. nov.**, holotype. 74, posterior part of body, counterprint, photographed under scanning electron microscope (SEM). 75, body, reconstructed drawing with broken lines for outline of posterior edge of pronotum, scutellum, sutural edges and adsutural lines of elytra. Length of body 5.2 mm.

?Nitidulidae

Genus et species incertae sedis

Figs 76–79

Specimen examined. Print “MNT 05 703A” (MNT) of body without apical portion and counterprint “MNT 05 703B” (MNT) of pterothorax and abdomen, both without organic matter, sex unknown; deposited in rather soft rock and represented by a mixture of the somewhat obliterated outlines of body dorsal (in the print) and ventral (in the counterprint) sclerites, and also coxae, without trace of seriate elytral puncturation in the SEM picture. Body length 6.2 mm, width 3.2 mm. This species is very similar in most available characters to the members of *Menatoraea* **gen. nov.** (particularly to *M. angustitibialis* **sp. nov.**), but its head is markedly larger with very large eyes and nearly absent temples, scutellum is subtriangular rather than subtrapezoid, elytral sculpture and pubescence are diffuse, adsutural line are not so distinct as in the species of *Menatoraea* **gen. nov.** The procoxae of the specimen under consideration (MNT 05 703) can be traced only by the depressions on prothorax and looking like transverse (as those in nitidulids), all its tibiae are missing. Moreover, the shape of the head of this specimen and particularly the proportion of the head to the prothorax make it very difficult to link it with most taxa of Nitidulidae. Its pronotum has a subrectilinear to nearly convex anterior edge and rounded posterior angles, i.e. features not characteristic of nitidulids in general. This specimen can be scarcely assigned to the family Nitidulidae and it is one of the typical examples of the difficulties encountered in trying to determine the majority of the small specimens examined from outcrops of Menat.

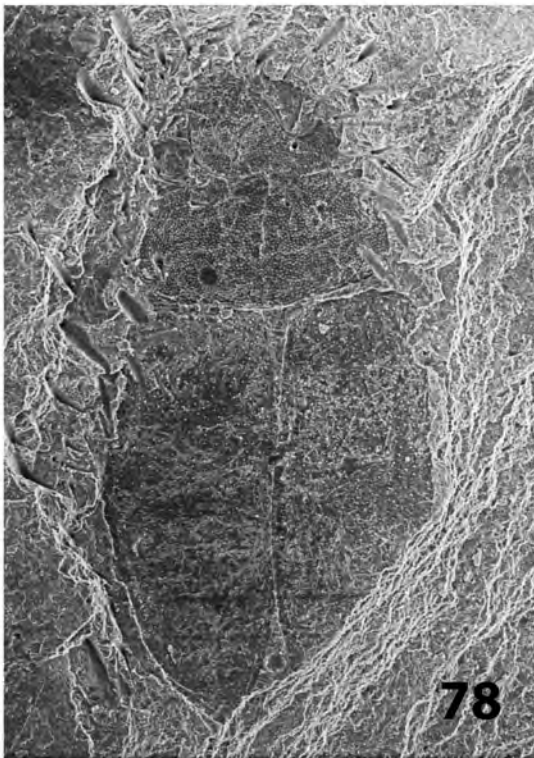
Locality and stratigraphy. Paleocene, Menat (see *Geological setting*).



76

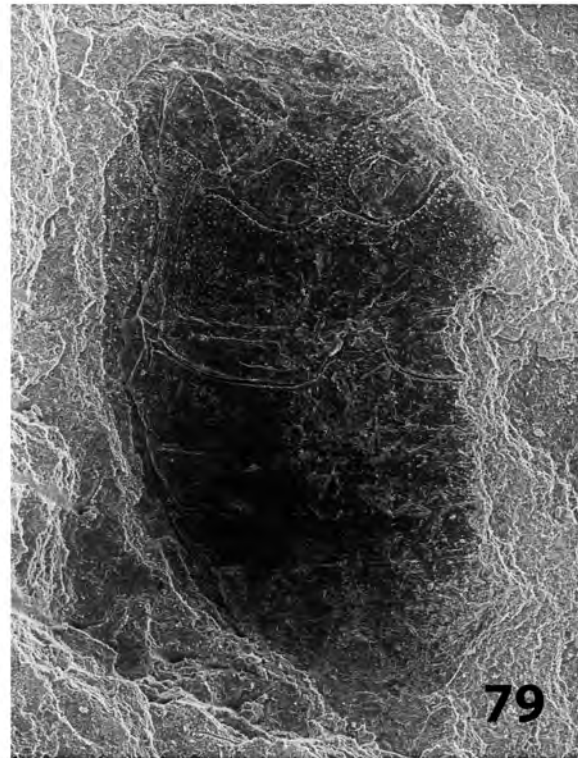


77



78

SEM HV: 20.00 kV Vac: LowVac, 45 Pa
View field: 6.11 mm Det: LVSTD 1 mm



79

SEM HV: 20.00 kV Vac: LowVac, 45 Pa
View field: 4.31 mm Det: LVSTD 1 mm

XXV FIGURES 76–79. ?Nitidulidae: gen. et sp. incertae sedis, print “MNT 05-703A” (MNT) and counterprint “MNT 05-703B” (MNT). 76, body, print; photographed under Nikon SMZ25 stereomicroscope with a Nikon D800 camera. 77, *ibid.*, counterprint; photographed under Nikon SMZ25 stereomicroscope with a Nikon D800 camera. 78, print, micrograms, photographed under scanning electron microscope (SEM). 79, anterior part of body, counterprint, micrograms, photographed under scanning electron microscope (SEM). Length of body 6.2 mm.

Probable Trogossitidae rather than Nitidulidae

Genus et species incertae sedis

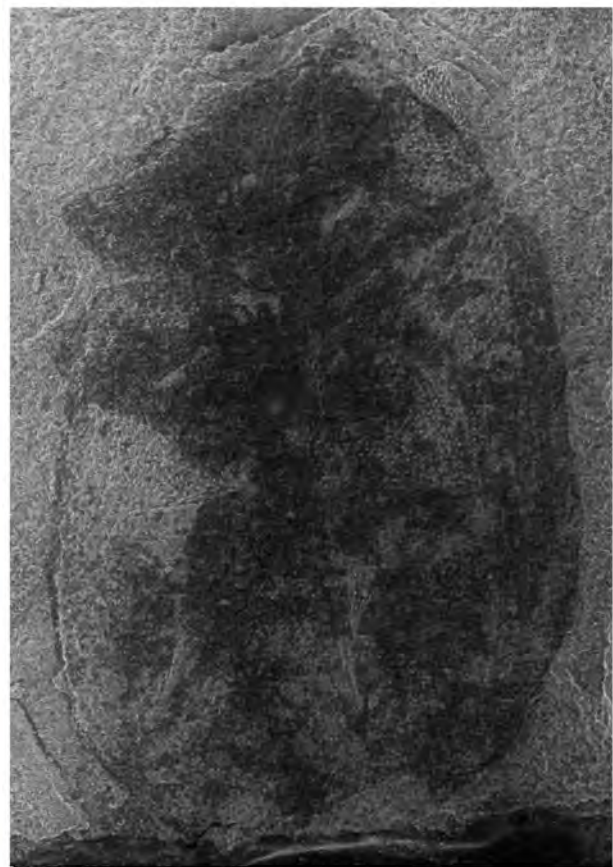
Figs 80–81

Specimen examined. “Oli 092” (MNHN), print of beetle body (with large amount of organic matter covering outlines of print), sex unknown, deposited in rather hard rock and represented by a mixture of the somewhat obliterated outlines of body ventral sclerites, and also with coxae, right protibia and left mesotibia, depressions with organic matter of right profemur and mesofemur. Body length 6.6 mm, width 4.6 mm. Procoxae transverse and slightly visible, meso- and the shape of metacoxae as those in species of *Menatoraea* **gen. nov.**, but mesocoxae are very narrowly separated and metacoxae are apparently almost contiguous. This combination of characters is rather characteristic of the trogossitid Peltinae Kirby, 1837 rather than nitidulids, although it is also impossible to be sure that such an attribution is more probable than a link of this species to nitidulids. Besides, this print demonstrates the rather wide epipleura, and narrow and comparatively long legs.

Locality and stratigraphy. Paleocene, Menat (see *Geological setting*).



80



SEM HV: 15.00 kV Vac: LowVac, 48 Pa
View field: 6.00 mm Det: LVSTD 1 mm

81

XXVII FIGURES 80–81. Nitidulidae or Trogossitidae gen. et sp. incertae sedis, print “Oli 092” (MNHN). 80, body, photographed under Olympus SCX9 stereomicroscope with an Olympus camera. 25, *ibid.*, micrograms, photographed under scanning electron microscope (SEM). Length of body 6.6 mm.

Discussion and conclusions

The nitidulids recovered in the Menat outcrops are not only the first members of the family from the Paleocene,

they also correspond to one of the largest numbers of members of this family in the same fossil locality. The composition of this assemblage shows a certain accordance with other data from these outcrops that indicated a forested habitat. Included are *Nitoraeopsis mixta* **gen. et sp. nov.** (Eपुरaeinae, first fossil member of Taenioncini); also species of ?*Soronia* spp. (*S. menatensis* **sp. nov.** and *S. sp.*), *Menatoraea* **gen. nov.** (*M. typica* **sp. nov.**, *M. angustitibialis* **sp. nov.**, *M. laticollis* **sp. nov.**, *M. gracilis* **sp. nov.**), and *Palaeolydra palaeocenica* **sp. nov.**, which seem to be first fossils of the *Thalycra*-complex (Nitidulinae, Nitidulini), and ?*Cryptarcha subglobosa* **sp. nov.**, the oldest fossil of Cryptarchinae (Cryptarchini sensu stricto). These results provide an important contribution to the knowledge on the evolution of the family, its dynamics in time and particularly the appearance of each concrete group considered in this paper.

However, the nitidulids have a greater representation in the fauna of the Middle-Upper Eocene Baltic amber, mostly still waiting description: genera and species of Eपुरaeinae, Nitidulinae (for now exclusively from different complexes of Nitidulini sensu stricto and questionable members of Cyllodini), Meligethinae C.G. Thomson, 1859, Cillaeinae, Cryptarchinae (Cryptarchini and Platyarchini Kirejtshuk, 1998) and Cybocephalinae (Hieke & Pietrzeniuk 1984; Kirejtshuk & Poinar 2007; Kirejtshuk & Kurochkin 2010; Kurochkin & Kirejtshuk 2010; Kirejtshuk 2011; etc.). A rather considerable portion of fossil nitidulids can be expected to be found among rich inclusions in Cretaceous Burmese amber, as this family was mentioned by Rasnitsyn & Ross (2000). At least some eपुरaeines and nitidulines are now under description by the first author of this paper. Other resources of Cenozoic fossil nitidulids are Lowermost Eocene Oise amber (Eपुरaeini sensu stricto, Nitidulini sensu stricto and Cybocephalinae: Kirejtshuk & Nel 2008, 2013 and undescribed); Middle Eocene outcrops of Messel (still undescribed Nitidulini sensu stricto) and Green River (questionable Nitidulini sensu stricto: Scudder 1890); Lower Oligocene outcrops of Quesnel (questionable Nitidulini: Scudder 1877, 1891) and Kleinkembs (questionable Nitidulini: Theobald 1937); probably Lower Oligocene outcrop of Florissant (Eपुरaeini, Carpophilinae, Nitidulini, Cychramini, Cillaeinae: Scudder 1900; Wickham 1913; 1916; although some fossils described as nitidulids indeed belong to other families and their generic attributions are rather doubtful); Oligocene outcrop of Rott (questionable Nitidulini: Meunier 1922); Oligocene outcrop of Brunnstatt (questionable Meligethinae: Forster 1891; Theobald 1937); outcrop of Kaja well (Djirah oilfield on Sumatra) at the boundary between Oligocene and Miocene (Carpophilinae: de Jong 1953); Lower Miocene Radoboj (Questionable Nitidulini: Heer 1847); Lower Miocene outcrop of Wishnevaya Balka (Nitidulini: Kirejtshuk & Ponomarenko 1990); Middle Miocene outcrop of Mule canyon (Cybocephalinae: Palmer *et al.* 1957); Lower Miocene Dominican amber (Eपुरaeini sensu stricto, Eपुरaeinae), and also Mystropini Murray, 1864 and Cyllodini from Nitidulinae sensu stricto, all still undescribed, but some information was published in Kirejtshuk & Poinar 2007); Upper Miocene outcrop of Oeningen (Heer 1847, 1862); and also the Upper Pliocene outcrop of Willershausen (only with family attribution: Gersdorf 1969). Beyond Burmese amber, Mesozoic fossil Nitidulidae were described from the Lower Cretaceous outcrops of Baisa (Eपुरaeini sensu stricto: Kirejtshuk & Ponomarenko 1990), Upper Cretaceous outcrop of Obeshtshayushtshiy (Cyllodinae: Kirejtshuk & Ponomarenko 1990) and Lower Cretaceous outcrops of Montsec (Carpophilinae, Nitidulini sensu stricto, and Cyllodinae; unpublished). Thus, only the nitidulid subfamilies Calonecrinae Kirejtshuk, 1982, Maynipeplinae Kirejtshuk, 1998 and Amphicrossinae still remain unknown in the fossil record. However, it is necessary to keep in mind that most of old indications of any nitidulid genus or even of the family Nitidulidae need to get further substantiation by re-examining the specimens to give a reason for these attributions. For example, many mentions of the genus *Nitidula* Fabricius, 1775 (Heer 1847, 1862; Scudder 1900; Meunier 1922; and many others) are doubtful. The more detailed published data on fossil nitidulids could be found in the catalogue of fossil beetles (Kirejtshuk & Ponomarenko 2017).

The new data on fossil nitidulids from the lacustrine outcrop of Menat give the first information on representation of this group in the Paleocene faunas and support the viewpoint that its most basal diversifications have happened before the Cenozoic (Kirejtshuk & Ponomarenko 1990, 2017; Kurochkin & Kirejtshuk 2010; etc.). The most important finding among the studied species from Menat is *Nitoraeopsis mixta* **gen. et sp. nov.** from the tribe Taenoncini, which is known only from the modern fauna of the Eastern Hemisphere (mostly from Indo-Malayan and Australian Regions), while the 'archaic' Eपुरaeini sensu stricto were recorded from the early Cretaceous (see above). The subfamily Nitidulinae is represented in the Mesozoic fossil record by only cyllodins and nitidulins from the early Cretaceous (see above). Nevertheless the genus *Soronia*, which seems to have been well present in the Cenozoic deposits, was recorded only from the Eocene Baltic amber. It spreads in the modern fauna mostly in the Eastern Hemisphere, with few members occurring in the Western Hemisphere, although other

genera of the *Soronia*-complex are endemic to South America (Kirejtshuk 2003). Other genera of this complex are also known not earlier than the late Eocene (Kirejtshuk & Kurochkin 2010: Baltic amber). The genera *Menatoraea* **gen. nov.** and *Palaeolydra* **gen. nov.** apparently belong to the *Pocadius*- and/or *Thalycra*-complex (Nitidulini), which are now widely distributed in all zoogeographic regions except Antarctica. The genus *Cryptarcha* (Cryptarchini sensu stricto) and subfamily Cryptarchinae in general were known in fossils not earlier than the Eocene Baltic amber, although both are now also distributed in all zoogeographic regions except Antarctica.

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