

THE OLDEST TENEBRIONIDAE (COLEOPTERA)
OF THE SUBFAMILY DIAPERINAE AND
THE TRIBE SCAPHIDEMINI
FROM THE PALEOCENE OF MENAT (FRANCE)

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The oldest tenebrionid beetle *Palaeobasanus neli* gen. et sp. n. of the tribe Scaphidemini (subfamily Diaperinae) is described from the Paleocene of Menat (Thanetian) in France. The new extinct genus shows a distinct complex of characters of the tribe Scaphidemini, such as modified procoxal cavities, modified prosternal “cowling” and mesocoxal cavities partly closed by mesepimera. *Palaeobasanus* gen. n. differs from the extant Scaphidemini in the narrowly separated coxae, structure of prosternal process, which is moderately narrow at middle but strongly widened at apex and rounded (not truncate), abdominal intercoxal process, antennomeres 4–7 clearly covered by simple trichoid sensilla but without round sensory complexes as in recent Scaphidemini and Diaperini. All these mentioned characters seem to be symplesiomorphies within the tenebrionoid lineage, including oldest Mesozoic ‘tenebrionoid’ darkling beetles. It is thought that *Palaeobasanus* gen. n. could be a basal group within Scaphidemini, closely related to Diaperini, which probably existed at least in the border of the Mesozoic and Cenozoic.

Key words: diversification of Diaperini and Scaphidemini, new species and genus, fossil tenebrionids, Tenebrionidae.

INTRODUCTION

Fossil Tenebrionidae were recently intensively investigated; however, many tenebrionids, superficially described during 19th and partly 20th centuries, need reexamination and revision. Here, we consider only the taxa undoubtedly belonging to the family Tenebrionidae. The oldest taxa of the family are known from the middle/late Jurassic of Karatau, Kazakhstan (Alleculinae Laporte, 1840: *Jurallecula grossa* Medvedev, 1969) (MEDVEDEV 1969) and the early Cretaceous of Yixian Formation, China (Alleculinae: *Platycteniopus diversoculatus* Chang, Nabozhenko, Pu, Xu, Jia et Li, 2016 and *Calcarocistela kirejtshuki* Nabozhenko in Nabozhenko, Chang, Pu, Xu, Jia et Li, 2015; Tenebrioninae: *Alphitopsis initialis* Kirejtshuk, Nabozhenko et Nel, 2011) (KIREJTSHUK

et al. 2012, NABOZHENKO *et al.* 2015, CHANG *et al.* 2016). Most Tenebrionidae were described and partly obtained from Paleogene deposits: the Paleocene of Menat (NABOZHENKO & KIREJTSHUK 2014, 2017), earliest Eocene Oise amber (KIREJTSHUK *et al.* 2010), Eocene Baltic amber (KIREJTSHUK *et al.* 2008, ALEKSEEV & NABOZHENKO 2015, 2017, NABOZHENKO *et al.* 2016*a, b*, SOLDATI & NABOZHENKO 2017, NABOZHENKO & CHIGRAY 2018, NABOZHENKO *et al.* 2019*a, b*, TELNOV *et al.* 2019), and late Eocene of Florissant Formation, Colorado (WICKHAM 1912, 1913).

The majority of fossil darkling beetles belongs to forest groups in tenebrioid and lagrioid lineages apparently adapted to humid environments. The pimeloid arid-adapted tenebrionids (at least the subfamily Pimeliinae Latreille, 1802) are scarce in the fossil record due to taphonomic reasons (SOLDATI & NABOZHENKO 2017, NABOZHENKO & KIREJTSHUK 2017). The tenebrioid lineage is represented by the subfamilies Tenebrioninae, Alleculinae, Diaperinae Latreille, 1802 and Stenochiinae Kirby, 1837 (KIREJTSHUK *et al.* 2008). The first two mentioned groups have the greatest diversity in the fossil record. Diaperinae is represented by ten extinct species from eight extant genera. The oldest one is *Ceropria messelense* Hörnschemeyer, 1994 (Diaperini), described from the Messel paleolake, Germany (middle Eocene, 48.6–40.4 Ma) (HÖRNSCHEMEYER 1994). Other Paleogene species are known from the middle-late Eocene (37.2–33.9 Ma): *Pentaphyllus cioides* Kirejtshuk, Merkl et Kernegger, 2008 (Diaperini) from the Baltic amber (KIREJTSHUK *et al.* 2008) and two species of *Platydema* Laporte et Brullé, 1831 (Diaperini) from the late Eocene of Florissant (WICKHAM 1912, 1913). The Neogene taxa (early Miocene) from tribes Diaperini (subtribes Diaperina and Adelina Dejean, 1835) and Hypophlaeini were predominantly described from the Dominican amber (KASZAB & SCHAWALLER 1984, DOYEN & POINAR 1994, VITALI 2007, 2008).

Here, a new extinct diaperine genus and species of the small tribe Scaphidemini from the Paleocene of Menat, France, is described. This group also includes four extant genera, distributed mainly in the Old World (Palaeartic, Indo-Malayan and Australian regions) (DOYEN *et al.* 1990). Only one species is known in the New World (BOUSQUET *et al.* 2018).

MATERIAL AND METHODS

The holotype examined is deposited in the Menat Town Museum, Menat, Puy-de-Dôme, France (further MNT). It was studied using a stereomicroscope Olympus SCX9 in Muséum national d'Histoire naturelle, Paris (further MNHN) with different modes of light and color filters. The specimen was also examined with a Tescan Vega LSU scanning electron microscope in the Laboratory of Minéralogy and Cosmochemistry, MNHN. MNHN to test the characters not clearly visible in the usual optic stereomicroscope (punctuation, outlines of legs, pronotum, pterothorax 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, NEL & AUVRAY 2006, WAPPLER *et al.* 2009, etc.). The Menat Pit fossil site is located in France, Department of Puy-de-Dôme (near Gannat) (46°06'N, 02°54'E). The age of the site, according to pollen, paleomammalian stratigraphic and radiometric K/Ar analyses was estimated as 59 Ma (KEDVES & RUSSEL 1982, NEL 2008). The estimation based on macroflora postulated its age within 60–61 Ma (WAPPLER *et al.* 2009).

Paleobiotic circumstances of Menat were briefly reviewed by NABOZHENKO and KIREJTSHUK (2017). In addition, the diversity of beetles and birds from this deposit was discussed in further publications (LEGALOV *et al.* 2017, 2019, KIREJTSHUK & NEL 2018, MAYR *et al.* 2019, etc.).

Palaeobasanus gen. n.

Family Tenebrionidae Latreille, 1802

Subfamily Diaperinae Latreille, 1802

Tribe Scaphidemini Reitter, 1922

Type species: *Palaeobasanus neli* sp. n.

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

Description. Body oval and medium-sized (body length nearly 7.5 mm). Mouth parts of tenebrioid type, with open basal parts (cardo and stipes); mentum transverse, trapezoidal; gula with rounded margins, not reaching submentum. Antennomeres 5–7 elongate; apical antennomeres (beginning from antennomere 8) forming an unclear club. Pronotum trapezoidal, widest at base; anterior margin twice narrower than base; each side of pronotum with deep furrow along edge. Prosternum moderate before coxae, about twice as long as postcoxal bridge, with cleft lateral margin of the procoxal cavities. Prosternal process narrow between coxae and strongly widened behind coxae. Mesocoxal cavities partly closed by mesepimera and mesotrochantin. Elytra with eight visible distinct striae, each with one row of dense and distinct punctures (elytra with indistinct lateral striae in extant scaphidemins) and scutellary striola; interstriae convex; epipleura narrow, terminating before apex. Abdomen with distinct intersegmental membranes between ventrites 3–5; abdominal intercoxal process widely rounded. Legs (at least hind ones) moderately long, with tibiae subequal in length with femora. Metatarsomere 1 long, but slightly shorter than metatarsomere 4.

Comparison. *Palaeobasanus* gen. n. clearly belongs to the tribe Scaphidemini due to the following characters: tarsi heteromeric; base of scape concealed by gena; tenebrioid mouthparts (open cardo and stipes); cleft lateral margin of

procoxal cavities; present scutellary striola; mesocoxal cavities partly closed by mesepimeron and trochantine; tenebrionoid hinging of abdomen with visible intersegmental membranes (defensive glands present).

The new genus is externally similar to extant species of the genus *Basanus* Lacordaire, 1859 but clearly differs from all Scaphidemini in the structure

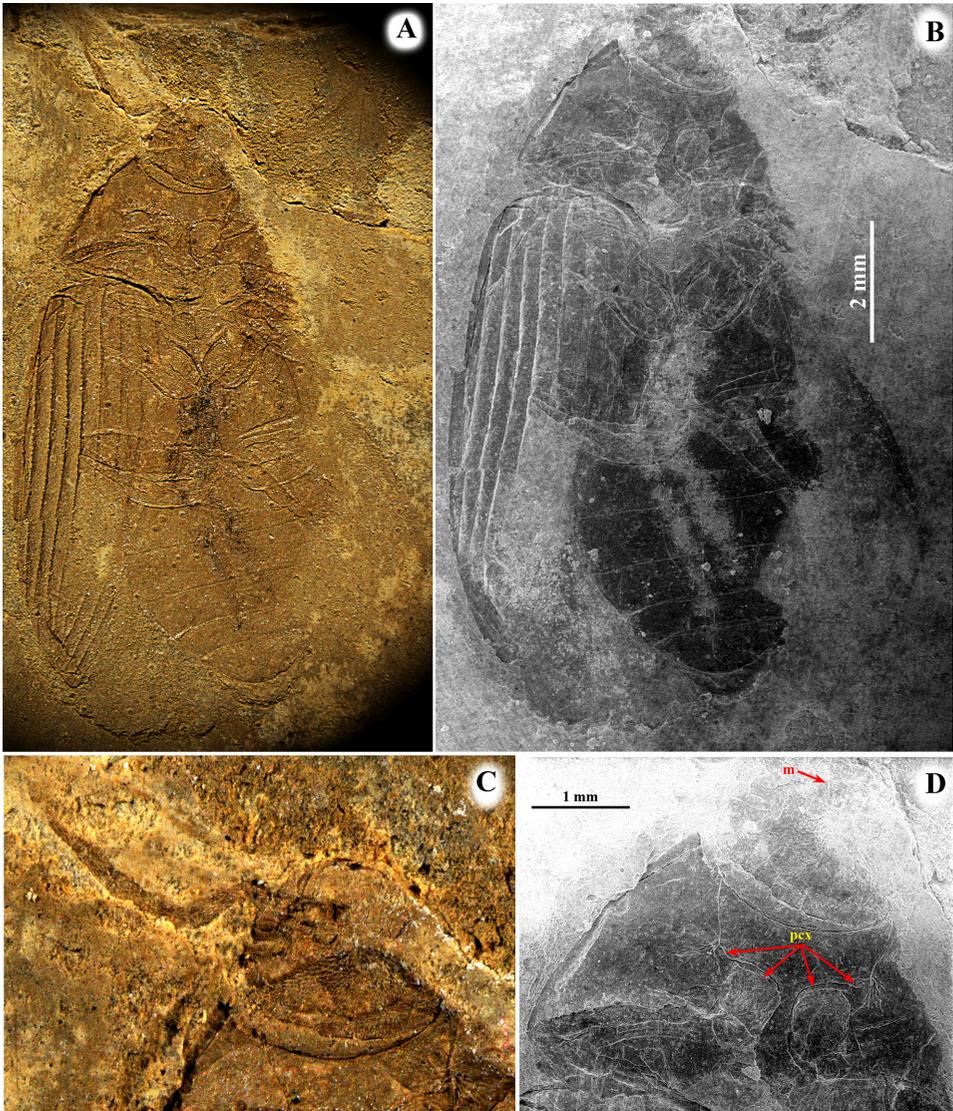


Fig. 1. *Palaeobasanus neli* gen. et sp. n. holotype, Paleocene of Menat (France) imprint: A = imprint, general view, optic microscope, B = the same, SEM, C = head, optic microscope, D = prosternum and head, SEM, m = mentum, pcx = procoxae

of the abdominal intercoxal process, which is widely rounded unlike widely truncate. The genus additionally differs from

– *Scaphidema* Redtenbacher, 1848 and *Spiloscapa* Bates, 1873 in the antennomeres 4–7 not elongate (gradually or abruptly widening distally) and the large body (in extant genera, the body length is within 3.5–5 mm)

– *Basanus* Lacordaire, 1859 in the narrower antennomeres and the metatarsomere 1 slightly shorter than metatarsomere 4 (in *Basanus*, the metatarsomere 1 is clearly longer than metatarsomere 4).

– *Laoscapha* Schawaller, 2016 in the antennomeres 4–7 not elongate and the metatarsomere 1 clearly longer than metatarsomere 2.

***Palaeobasanus neli* sp. n.**
(Figs 1–2)

Type material: holotype MNT 06 3415 (sex unknown)

Description. Body length about 7.5 mm. Head about half as wide as pronotum; mentum with longitudinal median elevation (Fig 1D); Head underside with dense and coarse subcircular punctures around throat emargination; other ventral sclerites with undulate

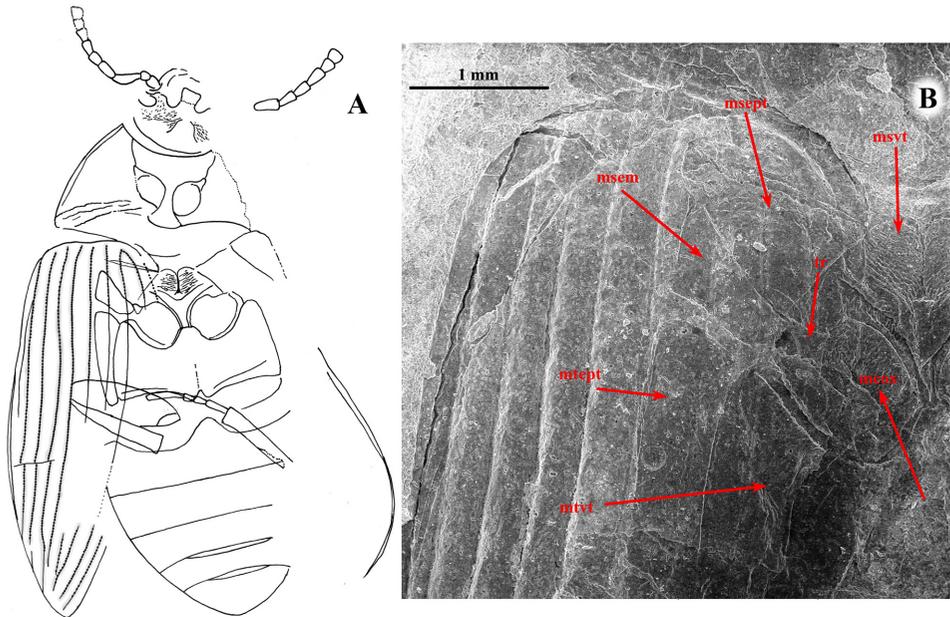


Fig. 2. *Palaeobasanus neli* gen. et sp. n. holotype, Paleocene of Menat (France), details of the structure: A = reconstruction, B = right half of pterothorax, msvt = mesoventrite, msept = mesepisternum, msem = mesepimeron, tr = trochantine, mtept = metaepisternum, mtvt = metaventrite, mcox = mesocoxa

transverse wrinkle-like foveae (Fig. 1D); gula short, with weakly rounded margins. Antennomeres 4-7 elongate, with dense simple trichoid sensillae (Fig. 1C), without sensory complexes; apical antennomeres (beginning from antennomere 8) subquadrate and short.

Pronotum transverse (Figs 1A, B, D; 2A), nearly 3.5 times as wide as long, widest at base; lateral margins and base evenly weakly arcuate; anterior margin shallowly emarginated; lateral margins strongly beaded (Fig. 1B, D); anterior angles subacute, weakly projected; posterior angles subacute but rounded at tip.

Elytra at base little wider than base of pronotum, with eight striae and scutellary striola; humeri rounded, not projected; striae deep, bearing a row of circular punctures at bottom (Figs 1A, 2A). Mesoventrite with median elevation and transverse wrinkles, strongly depressed before mesocoxae; mesocoxae transversely suboval; metaventrite transverse (2.6 times as wide as long, with median impressed furrow in basal part and groove along metacoxal cavities; intercoxal process of metaventrite rounded and beaded.

Legs moderately long; femora not strongly protruded beyond body lateral edges; tibiae straight; metatarsi with long metatarsomeres 1 and 4; metatarsomere 4 the longest (longer than metatarsomeres 2 and 3 combined).

Etymology. The species is named in honor of Prof. André Nel (MNHN), the famous paleoentomologist, who made a great contribution to the study of the paleofauna of Menat.

Comparative diagnosis is the same as for the genus *Palaeobasanus* gen. n.

DISCUSSION

DOYEN *et al.* (1990) resurrected the tribe Scaphidemini in a new sense from Diaperini, based on the following imaginal synapomorphies: (1) structures of female genital tubes, (2) tentorium, (3) prosternal process, (4) modified procoxal cowling. This tribe includes five genera: *Scaphidema*, *Basanus*, *Spiloscapa*, *Laoscapa* and *Pseudoscapidema* Pic, 1926. According to the original description, this last genus, monotypic from Kamchatka, distinctly belongs to the genus *Phaleromella* Reitter, 1916 (Diaperinae Phaleriini Blanchard, 1845), as well with only one species – *P. subhumeralis* (Marseul, 1876) – from Kamchatka. This should be confirmed only after study of the type material. The range of Scaphidemini occupies Holarctic, Indo-Malayan and Australian regions, but the greatest diversity of the tribe is observed in Palaearctic Eastern Asia and Indo-Malayan Region (SCHAWALLER 1995, 1997, 2003, 2004, 2006, 2008, 2011, 2012, 2016, MASUMOTO & MERKL 2003, ANDO & SCHAWALLER 2006, SCHAWALLER & ANDO 2006, GRIMM 2010). Only one species of *Spiloscapa* reaches Australia (MATTHEWS & BOUCHARD 2008) and one *Scaphidema* occurs in North America (SCHAWALLER 2003).

DOYEN *et al.* (1990, note 27) indicated the phylogenetic position as “the less derived sister clade to the Nilionini-Leiochrini”. The last two tribes were combined by WATT (1974). Among the listed characters, the third and fourth ones are clearly visible on the imprint of *Palaeobasanus* gen. n. Such structures

of the procoxal cavities, as the anterior and posterior lobes of the cowlings that meet at an acute angle leaving the coxa exposed along about half its length, are typical for Scaphidemini, Nilionini Oken, 1843 and Leiochrini Lewis, 1894, and distinctly distinguish these groups from the other Tenebrionidae. Within these tribes, the very wide prosternal process, as wide as diameter of the procoxa, is peculiar for Scaphidemini.

MATTHEWS and BOUCHARD (2008) stated that Scaphidemini are difficultly separable from Diaperini based on external characters, but they mentioned differences, as the cleft lateral margins of the procoxal cavities, the somewhat more widely separated coxae and the wide truncate intercoxal process of abdomen.

Palaeobasanus neli sp. n. shows a distinct set of characters of Scaphidemini, such as the modified procoxal cavities, the modified prosternal cowling and the mesocoxal cavities partly closed by mesepimera (Fig. 2B) (unlike Leiochrini, which show coxae closed by meso- and metaventrites). Similar type of cavities and 'open' mesocoxal cavities are also typical for Nilionini, but this tribe, as well Leiochrini, shows hemispherical body and epipleura notched at the level of metacoxae, which is unique within the Tenebrionidae (DOYEN *et al.* 1990).

Palaeobasanus gen. n. differs from the extant Scaphidemini in the narrowly separated coxae, structure of the prosternal process, which is moderately narrow at middle but strongly widened at apex, and rounded (not truncate) abdominal intercoxal process. All these characters seem to be symplesiomorphies within the tenebrionoid lineage, including the oldest Mesozoic tenebrionoid darkling beetles as Alleculinae and Tenebrioninae (Alphitobiini Reitter, 1917). The prosternal process strongly widened at apex is probably a 'transitional' character between the typical 'tenebrionoid' and the 'scaphidemin' types. The abdominal intercoxal process of *Palaeobasanus* gen. n. also shows 'transitional' features between the widely truncate type of the extant Scaphidemini and the triangular type of Diaperini and most of other darkling beetles of the tenebrionoid lineage. In addition, the antennomeres 4–7 of *Palaeobasanus* gen. n. are clearly covered by simple trichoid sensilla, without round sensory complexes, as in the recent Scaphidemini and Diaperini. This is also typical for most extant darkling beetles of the tenebrionoid lineage (MEDVEDEV 1977). These characters suggest that *Palaeobasanus* gen. n. apparently is a 'basal' group within Scaphidemini, closely related to Diaperini and evolved possibly at the border of Mesozoic and Cenozoic.

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REFERENCES

- ALEKSEEV, V. I. & NABOZHENKO, M. (2015): A new fossil tenebrionid beetle of the tribe Palorini (Coleoptera: Tenebrionidae) from Eocene Baltic amber. – *The Coleopterists Bulletin* **69**: 127–130. <http://dx.doi.org/10.1649/0010-065X-69.mo4.127>
- ALEKSEEV, V. I. & NABOZHENKO, M. V. (2017): *Palorus platycotyloides* sp. n., the second fossil representative of the tribe Palorini (Coleoptera: Tenebrionidae) from Baltic amber. – *Acta Zoologica Bulgarica* **69**: 167–170.
- ANDO, K. & SCHAWALLER, W. (2006): Two new species of the genus *Spiloscapa* (Coleoptera, Tenebrionidae) from Laos and Vietnam. – *Japanese Journal of Systematic Entomology* **12**: 127–131.
- BOUSQUET, Y., THOMAS, D. B., BOUCHARD, P., SMITH, A. D., AALBU, R. L., JOHNSTON, M. A. & STEINER, W. E. JR. (2018): Catalogue of Tenebrionidae (Coleoptera) of North America. – *ZooKeys* **728**: 1–455. <https://doi.org/10.3897/zookeys.728.20602>
- CHANG, H. L., NABOZHENKO, M., PU, H. Y., XU, L., JIA, S. H. & LI, T. R. (2016): First record of fossil comb-clawed beetles of the tribe Cteniopodini (Insecta: Coleoptera: Tenebrionidae) from the Jehol Biota (Yixian Formation of China), Lower Cretaceous. – *Cretaceous Research* **57**: 289–293. <http://dx.doi.org/10.1016/j.cretres.2015.09.001>
- DOYEN, J. T., MATTHEWS, E. G. & LAWRENCE, J. F. (1990): Classification and annotated checklist of the Australian genera of Tenebrionidae (Coleoptera). – *Invertebrate Taxonomy* **3** (1989): 229–260. <https://doi.org/10.1071/IT9890229>
- DOYEN, J. T. & POINAR, G. O. (1994): Tenebrionidae from Dominican amber (Coleoptera). – *Entomologica Scandinavica* **25**: 27–51. <https://doi.org/10.1163/187631294X00027>
- GRIMM, R. (2010): New and little known species of Tenebrionidae (Coleoptera) from Borneo. – *Stuttgarter Beiträge zur Naturkunde A, Neue Serie* **3**: 257–267.
- HÖRNSCHEMEYER, T. (1994): Ein fossiler Tenebrionide *Ceropria?* messelense n. sp. (Coleoptera: Tenebrionidae: Diaperinae) aus dem Mitteleozän der Grube Messel bei Darmstadt. – *Courier Forschungsinstitut Senckenberg* **170**: 75–83.
- KEDVES, M. & RUSSEL, D. E. (1982): Palynology of the Thanetian layers of Menat. The Geology of the Menat Basin, France. – *Palaeontographica B* **182**: 87–150.
- KASZAB, Z. & SCHAWALLER, W. (1984): Eine neue Schwarzkäfer-Gattung und -Art aus Dominikanischem Bernstein (Coleoptera, Tenebrionidae). – *Stuttgarter Beiträge zur Naturkunde Serie B (Geologie und Paläontologie)* **109**: 1–6.
- KIREJTSHUK, A. G., MERKL, O. & KERNEGGER, F. (2008): A new species of the genus *Pentaphyllus* Dejean, 1821 (Coleoptera, Tenebrionidae, Diaperinae) from the Baltic amber and checklist of the fossil Tenebrionidae. – *Zoosystematica Rossica* **17**: 131–137.
- KIREJTSHUK, A. G., NABOZHENKO, M. V. & NEL, A. (2010): New genus and species of the tribe Opatrini (Coleoptera, Tenebrionidae, Tenebrioninae) from the Lowermost Eocene

- amber of Paris Basin. – *Proceedings of the Zoological Institute of the Russian Academy of Science* **314**: 191–196.
- KIREJTSHUK, A. G., NABOZHENKO, M. V. & NEL, A. (2011): First Mesozoic representative of the subfamily Tenebrioninae (Coleoptera, Tenebrionidae) from the Lower Cretaceous of Yixian (China, Liaoning). – *Entomologicheskoe Obozrenie* **90**: 548–552. [in Russian] [English translation (2012): *Entomological Review* **92**: 97–100.] <https://doi.org/10.1134/S0013873812010101>
- KIREJTSHUK, A. G. & NEL, A. (2018): Nitidulidae (Coleoptera) from the Paleocene of Menat (France). – *Zootaxa* **4402**: 1–41. <https://doi.org/10.11646/zootaxa.4402.1.1>
- LEGALOV, A. A., KIREJTSHUK, A. G. & NEL, A. (2017): New and little known weevils (Coleoptera: Curculionoidea) from the Paleocene of Menat (France). – *Comptes Rendus Palevol* **16**: 248–256. <http://dx.doi.org/10.1016/j.crpv.2016.10.007>
- LEGALOV, A. A., KIREJTSHUK, A. G. & NEL, A. (2019): The oldest genus of the subfamily Sagarinae (Coleoptera: Chrysomelidae) from the Paleocene of Menat (France). – *Comptes Rendus Palevol* **18**: 178–185. <http://dx.doi.org/10.1134/S0013873818070084>
- MATTHEWS, E. G. & BOUCHARD, P. (2008): *Tenebrionid beetles of Australia: descriptions of tribes, keys to genera, catalogue of species*. – Australian Biological Resources Study, Canberra. 410 pp.
- MAYR, G., HERVET, S. & BUFFETAUT, E. (2019): On the diverse and widely ignored Paleocene avifauna of Menat (Puy-de-Dôme, France): new taxonomic records and unusual soft tissue preservation. – *Geological Magazine* **156**: 572–584. <https://doi.org/10.1017/S0016756818000080>
- MEDVEDEV, G. S. (1977): Taxonomic significance of antennal sensilla of darkling beetles (Coleoptera, Tenebrionidae). Pp. 61–86. In: MEDVEDEV, G. S. (ed.): *Trudy vsesoyuznogo entomologicheskogo obshchestva. Vol. 58. Morphological bases of the systematics of insects*. – Nauka, Leningrad. [in Russian]
- MEDVEDEV, L. N. (1969): New Mesozoic beetles (Cucujoidea) of Asia. – *Paleontologicheskii Zhurnal* **1**: 119–125. [in Russian]
- NABOZHENKO, M., BUKEJS, A. & TELNOV, D. (2019a): Gonialaenini, a new tribe of Lagriinae (Coleoptera: Tenebrionidae) from Eocene Baltic Amber. – *Zootaxa* **4565**: 253–260. <https://doi.org/10.11646/zootaxa.4565.2.9>
- NABOZHENKO, M. V. & CHIGRAY, I. A. (2018): New and little known species of Alleculini (Coleoptera: Tenebrionidae: Alleculinae): extinct from Eocene Baltic amber and extant from Lebanon. – *Caucasian Entomological Bulletin* **14**: 171–176. <https://doi.org/10.23885/181433262018142-171176>
- NABOZHENKO, M. V. & KIREJTSHUK, A. G. (2014): *Cryptohelops menaticus* – a new genus and species of the tribe Helopini (Coleoptera: Tenebrionidae) from the Palaeocene of Menat (France). – *Comptes Rendus Palevol* **13**: 65–71. <http://dx.doi.org/10.1016/j.crpv.2013.09.005>
- NABOZHENKO, M. V. & KIREJTSHUK, A. G. (2017): The oldest opatrine terrestrial darkling beetle (Coleoptera: Tenebrionidae: Tenebrioninae) from the Paleocene of Menat (France). – *Palaöntologische Zeitschrift* **91**: 307–313. <https://doi.org/10.1007/s12542-017-0368-2>
- NABOZHENKO, M. V., KIREJTSHUK, A. & MERKL, O. (2016): *Yantaroxenos colydioides* gen. and sp. n. (Tenebrionidae: Lagriinae) from Baltic Amber. – *Annales Zoologici* **66**: 563–566. <https://doi.org/10.3161/00034541ANZ2016.66.4.008>
- NABOZHENKO, M. V., CHANG, H., XU, L., PU, H. & JIA, S. (2015): A new species and a new genus of comb-clawed beetles (Coleoptera: Tenebrionidae: Alleculinae) from Lower

- Cretaceous of Yixian (China, Laoning). – *Paleontological Journal* **49**: 1420–1423. <https://doi.org/10.1134/S0031030115130079>
- NABOZHENKO, M., CHIGRAY, I. & BUKEJS, A. (2019b): Taxonomic notes on the Eocene Helopini, and a review of the genus *Isomira* Mulsant, 1856 from Baltic amber (Coleoptera: Tenebrionidae). – *Insect Systematics and Evolution*. 15 pp. <https://doi.org/10.1163/1876312X-00002302>
- NABOZHENKO, M. V., PERKOVSKY, E. E. & CHERNEI, L. S. (2016): A new species of the genus *Nalassus* Mulsant (Coleoptera: Tenebrionidae: Helopini) from the Baltic amber. – *Paleontological Journal* **50**: 947–952. <https://doi.org/10.1134/S0031030116090082>
- NEL, A. (2008): The oldest bee fly in the French Paleocene (Diptera: Bombyliidae). – *Comptes Rendus Palevol* **7**: 401–405. <https://doi.org/10.1016/j.crpv.2008.08.001>
- NEL, A. & AUVRAY, F. (2006): The oldest Vespinae from the Paleocene of Menat (France) (Hymenoptera: Vespidae). – *Zootaxa* **1344**: 59–62. <https://doi.org/10.11646/zootaxa.1344.1.5>
- PIC, M. (1926): Entomologische Ergebnisse der Schwedischen Kamtschatka-Expedition 1920–1922. 7. Coleoptera. – *Arkiv för Zoologi* **18B**: 1–5.
- PITON, L. (1940) Paléontologie du gisement éocène de Menat (Puy-de-Dôme), flore et faune. – *Mémoire de la Société d'Histoire Naturelle d'Auvergne, Clermont-Ferrand* **1**: 1–303.
- SCHAWALLER, W. (1995): The genus *Basanus* Lacordaire (Coleoptera. Tenebrionidae) in continental south-eastern Asia. – *Acta Zoologica Academiae Scientiarum Hungaricae* **41**: 327–334.
- SCHAWALLER, W. (1997): The genus *Spiloscapa* Bates (Coleoptera: Tenebrionidae), with descriptions of new species from the Oriental and Papuan regions. – *Stuttgarter Beiträge zur Naturkunde, Serie A (Biologie)* **566**: 1–15.
- SCHAWALLER, W. (2003): Two new species of *Scaphidema* Redtenbacher (Coleoptera: Tenebrionidae) from Nepal and China. – *Stuttgarter Beiträge zur Naturkunde Serie A (Biologie)* **653**: 1–7.
- SCHAWALLER, W. (2004): New species and records of the genus *Spiloscapa* Bates (Coleoptera: Tenebrionidae) from the Oriental and Papuan Regions. – *Stuttgarter Beiträge zur Naturkunde Serie A (Biologie)* **661**: 1–10.
- SCHAWALLER, W. (2006): New species and records of the genus *Basanus* Lacordaire (Insecta: Coleoptera: Tenebrionidae). – *Revue suisse de Zoologie* **113**: 239–246. <https://doi.org/10.5962/bhl.part.80347>
- SCHAWALLER, W. (2008): Three new species of *Scaphidema* Redtenbacher (Coleoptera: Tenebrionidae) from China. – *Stuttgarter Beiträge zur Naturkunde Serie A (Biologie)* **1**: 381–385.
- SCHAWALLER, W. (2011): New species and records of the genus *Basanus* Lacordaire (Coleoptera: Tenebrionidae), part 3. – *Special Bulletin of the Japanese Society of Scarabaeoidology (Masumushi)* **1**: 285–292.
- SCHAWALLER, W. (2012): New species and records of the genus *Spiloscapa* Bates (Coleoptera: Tenebrionidae) from the Oriental and Papuan Regions (part 2). – *Zootaxa* **3336**: 62–68. <https://doi.org/10.11646/zootaxa.3336.1.4>
- SCHAWALLER, W. (2016): *Laoscapa phoupanense* gen. et sp.nov. (Coleoptera: Tenebrionidae: Diaperinae) from Laos. – *Entomologica Basiliensia et collectionis Frey* **35**: 439–442.
- SCHAWALLER, W. & ANDO, K. (2006): New species and records of the genus *Basanus* Lacordaire (Coleoptera, Tenebrionidae), part 2. – *Japanese Journal of systematic Entomology* **12**: 215–223.
- SOLDATI, F. & NABOZHENKO, M. (2017): *Asida groehni* sp. nov., the first and the oldest fossil representative of the subfamily Pimeliinae from Eocene Baltic amber (Coleoptera:

- Tenebrionidae: Asidini). – *Annales Zoologici* **67**: 555–559. <https://doi.org/10.3161/00034541ANZ2017.67.3.003>
- TELNOV, D., BUKEJS, A. & MERKL, O. (2019): Description of a new fossil Statira Lepeletier et Audinet-Serville, 1828 (Coleoptera: Tenebrionidae: Lagriinae) from Baltic amber of the Sambian Peninsula. – *Zootaxa* **4683**: 508–514. <https://doi.org/10.11646/zootaxa.4683.4.2>
- VITALI, F. (2007): A new species of *Corticeus* Piller & Mitterpacher, 1783 from Dominican amber (Coleoptera Tenebrionidae). – *Entomapeiron (P.S.)* **2**: 1–6.
- VITALI, F. (2008): A new species of *Tyrtaeus* Champion, 1913 from Dominican amber (Coleoptera Tenebrionidae). – *Entomapeiron (P.S.)* **3**: 11–16.
- WAPPLER, T., CURRANO, E. D., WILF, P., RUST J. & LABANDEIRA, C. C. (2009): No post-Cretaceous ecosystem depression in European forests? Rich insectfeeding damage on diverse Middle Palaeocene plants, Menat, France. – *Proceedings of the Royal Society B* **276**: 4271–4277. <https://doi.org/10.1098/rspb.2009.1255>
- WATT, J. C. (1974): A revised subfamily classification of Tenebrionidae (Coleoptera). *New Zealand Journal of Zoology* **1**: 381–452. <https://doi.org/10.1080/03014223.1974.9517846>
- WICKHAM, H. F. (1912): The Princeton collection of fossil beetles from Florissant. – *Annals of the Entomological Society of America* **6**: 359–366. <https://doi.org/10.1093/aesa/6.3.359>
- WICKHAM, H. F. (1913): Fossil Coleoptera from Florissant in the United States National Museum. – *Proceedings of the United States National Museum* **45**: 283–303. <https://doi.org/10.5479/si.00963801.45-1982.283>

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