

New genus *Microticus* from Upper Cretaceous of Taymyr (Coleoptera: Cryptophagidae), oldest silken fungus beetle with sexually dimorphic tarsal formula

Новый род *Microticus* из верхнего мела Таймыра (Coleoptera: Cryptophagidae), находка скрытноеда с древнейшим случаем проявления полового диморфизма в строении лапок

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КЛЮЧЕВЫЕ СЛОВА. Cryptophagidae, *Microticus khatanga*, Верхний Мел, Таймырский янтарь, Россия

ABSTRACT. *Microticus khatanga* Lyubarsky et Perkovsky **gen. et sp.n.** is described based on an inclusion in Upper Cretaceous (Santonian) amber from Taymyr (Russia). The new genus is similar to the extant *Mnioticus*, both differing from other genera of the tribe Cryptophagini by absence of tooth and callosity on sides of pronotum. The new species differs from *Mnioticus* by shape of sides of pronotum (parallel-sided in *Mnioticus*, convex in *Microticus*); length of ventrite 1 (equal to any of the remaining ventrites in *Mnioticus*, longer than those in *Microticus*); and tarsal formula of male (5–5–4 in *Microticus*, 5–5–5 in *Mnioticus*). The new genus is the first Mesozoic representative of Cryptophaginae. It is shown for the first time that sexual dimorphism in the tarsal formula was present in Cryptophaginae already in the Cretaceous.

РЕЗЮМЕ. *Microticus khatanga* Lyubarsky et Perkovsky **gen. et sp.n.** описан из верхнемелового (сантонского) янтаря с Таймыра (Россия). Новый род относится к трибе Скрытофагини, и похож на рецентный род *Mnioticus* отсутствием мозолей и зубцов на переднеспинке. Новый род отличается от *Mnioticus* формой переднеспинки, суженной к вершине, первым стернитом брюшка, более длинным, чем последующие (у *Mnioticus* равен им по длине), и формулой лапок самца 5–5–4 (у *Mnioticus* 5–5–5). Новый род — первый мезозойский представитель криптофагин. Впервые показано, что половой диморфизм по формуле лапок был свойственен им уже в мелу.

Introduction

The family Cryptophagidae includes two subfamilies, Cryptophaginae and Atomariinae, each with three

tribes [Leschen, 1996]. The family is one of the basal lines of the superfamily Cucujoidea and includes about 60 genera and 600 described species. The Cryptophagidae are distributed in all biogeographic realms.

The natural history of the family is described in detail [Leschen, 1996, 2010; Lyubarsky, 2002]. These beetles are often found in forest litter, it is a common group met within bird nests and burrows of animals in the burrow litter. The silken-fungus beetles are best known as pests of agricultural products in storage. Many species of cryptophagids are pyrophilic, i.e. fly to the smell of smoke. Some members of the family live in the nests of social insects (bees, ants, wasps, and termites), as well as in collective nests of caterpillars. Most species feed on the hyphae and spores of fungi. Apparently, many species are able to carry the spores and conidia of fungi in mycangia on their body. Few genera feed on pollen of vascular plants (*Cryptothelypteris* Leschen et Lawrence 1991, *Micrambe* C.G. Thomson, 1863, *Mnioticus* Coombs et Woodroffe, 1962, *Telmatophilus* Heer, 1841, *Paratomaria* Leschen, 1996). Some *Atomaria* Stephens, 1829 and *Ootypus* Ganglbauer, 1899 are found in horse and moose manure at a specific stage of decay. Ancestral diet of Cryptophagidae is apparently microphagy [Leschen, Buckley, 2007].

Most paleontological findings of Cryptophagidae are from Late Eocene and Miocene [Kirejtshuk, Ponomarenko, 2014]. Cryptophagidae are recorded in the Baltic and Rovno amber [Spahr, 1981; Hieke, Pietrzeniuk, 1984; Lyubarsky, Perkovsky, 2010, 2011, 2012, 2013, 2014; Perkovsky, Lyubarsky, 2014], and also in impression fossils [Scudder, 1876; Wickham, 1913, 1914, 1916; Cockerell, 1926; Piton, Theobald, 1935; Zhang, 1989]. These findings belong to recent genera *Atomaria*, *Cryptophagus* Herbst, 1792, and *Micrambe*. Thus, at the

genus level the fauna observed in Late Eocene is modern.

Atomaria cretacea has been described from the Lower Cretaceous of southern China [Cai, Wang, 2013]. Otherwise the Mesozoic fossils include genera not represented in the modern fauna: known from the Upper Cretaceous of Taymyr are *Nganasania khetica* Zherikhin, 1977 [Zherikhin, 1977] and *N. taymyrica* [Lyubarsky, Perkovsky, 2014]. The latter genus belongs to subfamily Atomariinae; the other major subfamily, Cryptophaginae, has not been otherwise recorded in the Mesozoic. Besides, there are reports about the findings of Cryptophagidae from Lebanese amber dated within the late Barremian to lowermost Aptian [Kirejtshuk, Azar, 2008].

At the family level, the fauna of beetles assumed its modern shape long ago. Ponomarenko [1977]; Arnoldi et al. [1977/1992] presented a general characterization of the Upper Cretaceous beetles. According to him, that time was dominated by the Cenozoic forms. The replacement of Mesophytic flora by the Caenophytic one had already occurred, and gymnosperms were widely replaced by angiosperms. The reshaping of the beetle fauna had already been completed by that time, although there are some relict groups that appeared on the background of a possible crisis of Upper Cretaceous communities. In fact, the Late Cretaceous insect faunas are more similar to the Tertiary than to the Early Cretaceous assemblages, at least at the family level [Zherikhin, 1978; Labandeira, Eble, 2001; Gratshev, Zherikhin, 2003]. Now this view dominates, although much more details have been discovered [Wang et al., 2013]. The angiosperm radiations provided new food resources and habitats, and had a profound effect on beetles and other insects. However, in spite of the essentially modern appearance of composition of the Mesozoic beetle families, the generic level demonstrates a considerable difference from the modern fauna. Meanwhile, among the silken fungus beetles the only extinct Mesozoic genus found so far is *Nganasania* Zherikhin, 1977.

In this paper, we describe a new fossil belonging to the silken fungus beetles from the Santonian amber of Taymyr (Russia). Judging by the cladogenesis of Cryptophagidae [Leschen, 1996], the new genus originated after the formation of the basal tribes of the family.

Material and methods

The fossil studied represents an inclusion in the fossil resin of a mineralogical variety called retinite (not true amber) collected in deposits of the Kheta Formation (Santonian Stage of Upper Cretaceous) at Yantardakh 3 km upstream of mouth of Maimecha River, a tributary of Kheta River, Khatanga basin, Taymyr Peninsula, northernmost Siberia.

Based on the study of collections of the expeditions organized by Paleontological Institute of Academy of Sciences of USSR in 1970 and 1971, a small number of beetle specimens have been recorded from Yantardakh [Zherikhin, 1978]. The expedition of PIN RAS in 2012 collected another 80 kg of retinite from Yantardakh.

This material included several relatively well-preserved, more or less complete beetle specimens. One of them is described in this article.

The specimen is partially obscured by the opacities in the resin, so some details of the structure can not be seen. The type specimen is stored at the PIN RAS, Moscow.

Photographs were taken at the Paleontological Institute, Russian Academy of Sciences (PIN RAS) in Moscow by Alexandr P. Rasnitsyn using a Leica M 165 microscope and Leica DFC 425 camera.

Taxonomical part

Family Cryptophagidae Kirby, 1837

Microticus Lyubarsky et Perkovsky **gen.n.**

Figs 1–4.

Type species. *Microticus khatanga* Lyubarsky et Perkovsky **sp.n.**

DIAGNOSIS. Body shape parallel-sided, moderately convex. Antenna clubbed. Pronotum with anterior margin straight. Lateral margin unmodified, without teeth and not serrate. Ventrite 1 longer than other ventrites. Tarsal formula 5–5–4 in male. Elytra with incomplete epipleuron extending to posterior margin of metathorax.

DESCRIPTION. Body moderately convex, body setae moderately elongate. Punctuation of body confused, punctures present on prosternum. Eyes normal in size, well developed, with facets small in size. Width of labial palpomere 1 subequal to that of palpomere 2. Antenna inserted near the eye, distance between antennal insertions larger than between insertion and eye. Antennae clubbed, 1st joint of antenna elongate, cylindrical in shape, antennal club 3-segmented. Pronotum transverse, with sides converging anteriorly. Anterior margin of pronotum straight. Pronotal sides without teeth or callosity, not serrate. Shape of tibia parallel-sided. Tarsal formula 5–5–4. Tarsi without lobes. Elytra long oval, moderately arched, without elytral depressions, weakly curved at sides. Width of mesosternal process greater than that of mesocoxa. Epipleuron present beyond level of posterior margin of metasternum. Metasternum long and punctured, longitudinal metasternal median line present. Femoral lines absent. Metacoxal cavities located close to each other. Ventrite 1 longer than any of remaining ventrites. Ventrite 5 arcuate, not lobed, without thickened setae.

Male. Antennal segments not compact. Tibia unmodified. Tarsal formula 5–5–4, tarsomeres not dilated. Ventrite 5 unmodified.

Etymology. The generic name is a combination of the Greek words *micros*, meaning ‘small’, and the common part of the generic names *Henoticus* C.G.Thomson, 1868, *Mnioticus* (both belong to Cryptophagini).

TAXONOMIC POSITION. The specimen belongs to family Cryptophagidae. The specimen has characteristic features of the family: the incomplete epipleuron, which extends to the anterior edge of the 1 ventrite, and the length of ventrite 1, which is longer than the other ventrites.

The specimen belongs to subfamily Cryptophaginae: tarsal formula 5–5–4, width of the mesosternal process greater than that of mesocoxa, longitudinal metasternal line present, femoral lines absent. Unfortunately, the upper side is not preserved, and some important characters are not visible: presence or absence of frontoclypeal suture, presence or absence of boss of frons of head, the temporal ridge behind the eye, the ridge surrounding antennal concavity.

The specimen differs from tribe Caenoscelini: femoral lines absent, tibia parallel-sided, width of labial palpomere 1 subequal to that of palpomere 2, ventrite 5 without thickened setae.

The specimen differs from tribe Cryptosomatulini: longitudinal metasternal line present, tibia parallel-sided.

The specimen belongs to tribe Cryptophagini: tarsal formula 5-5-4, width of labial palpomere 1 subequal to that of palpomere 2, longitudinal metasternal line present, width of the mesosternal process greater than that of mesocoxa, femoral lines absent, tibia parallel-sided.

The specimen differs from many taxa of tribe Cryptophagini by lateral margin of pronotum unmodified, teeth and callosity absent, therefore its pronotum is similar to that of *Mnioticus*.

The genus *Microticus* **gen.n.** is known from a single species, which is described in this article. The new genus is similar to the extant *Mnioticus*, both differing from other

genera of the tribe Cryptophagini by absence of tooth and callosity on sides of pronotum. The new species differs from *Mnioticus* by shape of sides of pronotum, which is parallel-sided in *Mnioticus* and convex in *Microticus* **gen.n.**; and length of ventrite 1, which is equal to each of the remaining ventrites in *Mnioticus*, as well as by tarsal formula of male, which is 5-5-5 in *Mnioticus*.

Microticus khatanga Lyubarsky et Perkovsky **sp.n.**

MATERIAL. Holotype: PIN 3311/1999, Yantardakh, 3 km above the mouth of Maimecha river, eastern Taymyr. Kheta formation, Santonian.

DESCRIPTION. Male. Body unicolorous, testaceous, parallel-sided, elytra with some elevated pubescence. Eyes normal prominent. Antenna elongate, extending to base of pronotum. 1st joint of antenna elongate, cylindrical in shape, antennomeres 3-8 elongated, 3rd antennomere up to 1.5x the



1



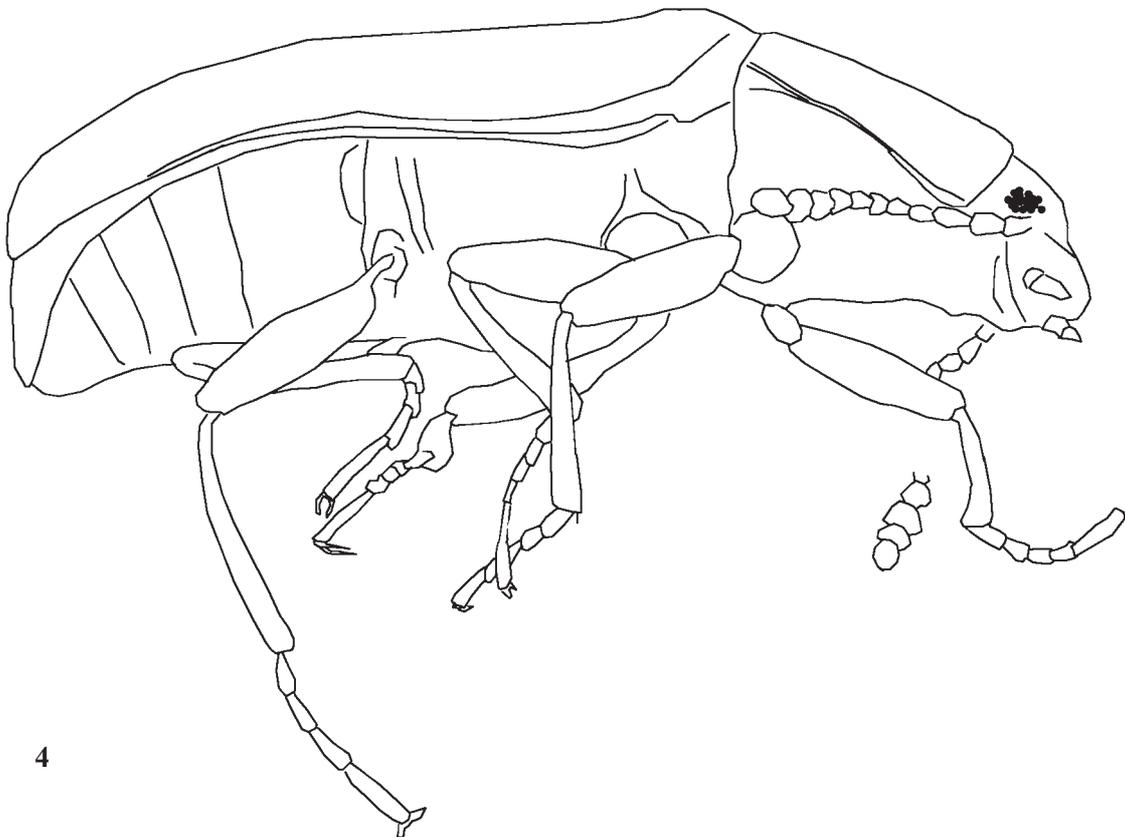
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Figs 1-2. *Microticus khatanga* **gen. et sp.n.**, ventral view: 1 — photo; 2 — tracings.

Рис. 1-2. *Microticus khatanga* **gen. et sp.n.**, снизу: 1 — фотография; 2 — прорисовка.



3



4

Figs 3–4. *Microticus khatanga* gen. et sp.n., lateral view: 3 — photo; 4 — tracings.
Рис. 3–4. *Microticus khatanga* gen. et sp.n., сбоку: 3 — фотография; 4 — прорисовка.

length of the 4th antennomere, 5th and 7th slightly elongated, antennal club 3-segmented. 9th, 10th antennomeres strongly transverse. 11th antennomere elongate, symmetrical and more or less flattened.

Pronotum distinctly transverse, about 0.7x as long as wide, converging anteriorly, broadest in first third of length of pronotum, sides unmodified. Posterior angles obtuse. Prosternal process equal in length to anterior portion of prosternum. Pronotum and metanotum strongly punctured.

Crown of thorns and spurs of tibia are not visible. Tarsi not dilated.

Elytra broadest approx. at first third of length, 2.9 times as long as pronotum, 1.3 times as long as broad combined. Elytral humeri not toothed.

Length 1.6 mm. Maximal breadth 0.7 mm.

ETYMOLOGY. The species name is derived from the name of the Khatanga River.

DISCUSSION. Now, from the Cretaceous period, we know four specimens of Cryptophagidae, belonging to the genera *Atomaria*, *Nganasania*, and *Microticus gen.n.* While the described taxa are not numerous enough to draw conclusions on the comparison of the Cretaceous fauna with the modern one, we can assume that in general the generic composition of the Cretaceous fauna is much different from the present, in contrast with the Eocene fauna of Cryptophagidae where most genera are modern.

However, further studies are required to estimate the validity of attributing Cai and Wang's findings to the genus *Atomaria*. Cai and Wang wrote: "Owing to the lack of sufficient detailed characters (e.g., tarsal formula, glandular ducts, maxillary palpi) of the tiny impression, the fossil can be only tentatively assigned to the modern widespread genus *Atomaria* based on its parallel-sided body, and general habitus, including three-segmented antennal club, parallel pronotum and prosternum lacking parallel lines" [Cai, Wang, 2013]. These characters, however, are not sufficient for a reliable attribution to the genus. It can be suggested that in fact we deal with an extinct genus here.

Some comments can be made concerning the similarity of the new genus with *Mnioticus*. Body length is 2.5–4 mm in *Mnioticus*, and only 1.6 mm in the new genus. Posterior tarsi of *Mnioticus* male are composed of 5 joints, and tarsi of male *Microticus gen.n.*, of 4 joints. The change of tarsal formula can be connected to a decrease in overall size; a similar hypothesis has been put forward based on examples from Cecidomyiidae (Diptera) and Leiodidae (Coleoptera) [Perkovsky, Fedotova, 2008]. The reduction of size is often achieved via an earlier molt to adults, and juvenalization often leads to a change in the formula of tarsi [Tichomirova, 1991].

While a connection between body size and tarsal formula may appear plausible in general, this hypothesis can raise some objections in discussing the cryptophagid material. Firstly, the tarsal formula remains constant in females, 5–5–5. Secondly, in some species, intraspecific variation includes variable number of segments in the hind legs of the male. Thus, N. Bruce [1951] described *Micrambe alberti*, whose males have either 5–5–5 or 5–5–4 as their tarsal formula, with unstable number of segments in the hind tarsi. Therefore, even in intraspecific variation the number of segments in hind tarsi of the male may be not related to body size. The species in question, *Micrambe alberti*, is a very interesting example of a character of great significance, normally stable at the family level in beetles, being affected by intraspecific variation.

The genus *Micrambe* includes several tens of species with stable sexual dimorphism by the tarsal formula as well as several African species which are not dimorphic [male tarsi

5–5–5; Otero, 2012]. The same is observed in the genus *Henoticus*, where among several tens of African species there are several species with male tarsal formula 5–5–5. These observations suggest that the loss of sexual dimorphism could be a result of secondary feminization of males. The sexual dimorphism in the tarsal formula might be characteristic of Cryptophagidae since the Late Cretaceous perhaps except for the lineage leading to *Mnioticus*.

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References

- Arnoldi L.V., Zherikhin V.V., Nikritin L.M., Ponomarenko A.G. 1977. [Mesozoic Coleoptera] // Trudy Paleontol. Inst. AN SSSR. Moscow: Nauka Publ. Vol.161. 204 p. (Translation: Mesozoic Coleoptera. Smithsonian Institution Libraries and National Science Foundation, Washington, D.C., xii + 285 p., 1992).
- Bruce N. 1951. Cryptophagidae (Coleoptera, Polyphaga) // Exploration du Parc National Albert. Mission G.F. de Witte (1933–1935). Fasc.75. Bruxelles. P.1–26.
- Cai C.-Y., Wang B., 2013. The oldest silken fungus beetle from the Early Cretaceous of southern China (Coleoptera: Cryptophagidae: Atomariinae) // Alcheringa. Vol.37. P.452–455.
- Cockerell T.D.A. 1926. Some Tertiary fossil insects // Annals and Magazine of Natural History (series 9). Vol.18. P.313–324.
- Gratshev V.G., Zherikhin V.V. 2003. The fossil record of weevils and related beetle families (Coleoptera, Curculionoidea) // Acta zoologica cracoviensia. Vol.46 (suppl.– Fossil Insects). P.129–138.
- Hieke F., Pietrzeniuk E. 1984. Die Bernstein-Käfer des Museums für Naturkunde, Berlin (Insecta, Coleoptera) // Mitteilungen aus dem Zoologischen Museum in Berlin. Bd.60. S.297–326.
- Kirejtshuk A.G., Ponomarenko A.G. 2014. [Systematic list of fossil beetles of the suborder Scarabaeina (3rd part of catalogue)]. <http://www.zin.ru/animalia/coleoptera/rus/paleosy2.htm> [in Russian]
- Kirejtshuk A.G., Azar D. 2008. New taxa of beetles (Insecta, Coleoptera) from Lebanese amber with evolutionary and systematic comments // Alavesia. Vol.2. P.15–46.
- Labandeira C.C., Eble G.J. 2001. The Fossil Record of Insect Diversity and Disparity // Gondwana Alive. Johannesburg: Witwatersrand University Press. Santa Fe Institute Working Paper. Vol.121. P.1–54. <http://www.santafe.edu/media/workingpapers/00-08-044.pdf>
- Leschen R.A.B. 1996. Phylogeny and revision of the genera of Cryptophagidae (Coleoptera: Cucujoidea) // Kansas Science Bull. Vol.55. P.549–634.
- Leschen R.A.B. 2003. Erotylidae (Insecta: Coleoptera: Cucujoidea): phylogeny and review // Fauna of New Zealand. Vol.47. 108 p.
- Leschen R.A.B. 2010. Cryptophagidae Kirby, 1837 // Coleoptera, Beetles. Volume 2: Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia partim). R.A.B. Leschen, R.G. Beutel, J.F. Lawrence (eds.). Handbook of Zoology. Volume IV. Arthropoda: Insecta. Part 38. Berlin: Walter de Gruyter. 786 p.
- Leschen R.A.B., Buckley T.R. 2007. Multistate characters and diet shifts: evolution of Erotylidae (Coleoptera) // Systematic Biology. Vol.56. No.1. P.97–112.
- Lyubarsky G.Yu. 2002. [Cryptophaginae (Coleoptera: Cucujoidea: Cryptophagidae): diagnostics, arealogy, ecology]. Moscow: MSU Publishers. 421 p. [in Russian]
- Lyubarsky G.Yu., Perkovsky E.E. 2010. First Eocene species of the genus *Micrambe* (Cryptophagidae: Coleoptera, Clavicornia) // Vestnik zoologii. Vol.44. No.3. P.275–279.

- Lyubarsky G.Yu., Perkovsky E.E. 2011. Third contribution on Rovno amber silken fungus beetles: a new Eocene species of *Cryptophagus* (Coleoptera, Clavicornia, Cryptophagidae) // ZooKeys. Vol.130. P.255–261.
- Lyubarsky G.Yu., Perkovsky E.E. 2012. The first Eocene species of the genus *Cryptophagus* (Coleoptera, Clavicornia, Cryptophagidae) // Vestnik zoologii. Vol.46. No.1. P.83–87.
- Lyubarsky G.Yu., Perkovsky E.E. 2013. Fourth contribution on Late Eocene amber silken fungus beetles: a new Baltic amber species of *Atomaria* (Coleoptera, Clavicornia, Cryptophagidae) // Vestnik zoologii. Vol.47. No.3. P.273–276.
- Lyubarsky G.Yu., Perkovsky E.E. 2014. New species of the genus *Nganasania* from Upper Cretaceous of Taymyr (Coleoptera: Cryptophagidae) // Russian Entomological Journal. Vol.23. No.3. P.191–194.
- Otero J.C. 2012. The species of the genus *Micrambe* Thomson 1863, from South Africa (Coleoptera: Cryptophagidae) // Ann. soc. entomol. Fr. (n.s.). Vol.48. Nos.3–4. P.407–438.
- Perkovsky E.E., Fedotova Z.A. 2008. [On the Systematics of the Gall-Midge Supertribe Heteropezidi (Diptera, Cecidomyiidae) from the Rovno Amber. New Taxa and Combinations of the Tribes Heteropezini and Miastorini] // Vestnik zoologii. Vol.42. No.5. P.403–425 [in Russian].
- Perkovsky E.E., Lyubarsky G.Yu. 2014. Fifth contribution on silken fungus beetles from Late Eocene amber: a second Baltic amber species of *Atomaria* (Coleoptera: Clavicornia: Cryptophagidae) // Russian Entomological Journal. Vol.23. No.1. P.41–44.
- Piton L.E., Theobald N. 1935. La faune entomologique des gisements miopliocènes du Massif central // Revue des Sciences Naturelles d'Auvergne. Vol.1. P.65–104.
- Ponomarenko A.G. 1977. [Composition and ecological characteristics of Mesozoic Coleoptera] // Mezozoiskie zhestkokrylye. Trudy Paleontol. Inst. AN SSSR. Moscow: Nauka. T.161. P.8–16 [in Russian].
- Scudder S.H. 1876. Fossil Coleoptera from the Rocky Mountain Tertiaries // Bulletin of the United States Geological and Geographical Surveys of the Territories. Vol.2. P.78–87.
- Spahr U. 1981. Systematischer Katalog der Bernstein- und Kopalpäpfer (Coleoptera) // Stuttgarter Beitr. Naturk. (Series B: Geologie und Paläontologie). Bd.80. S.1–107.
- Tichomirova A.L. 1991. [Ontogenesis remodelling as a mechanism of insect evolution]. Moscow: Nauka Publ. 168 p. [in Russian].
- Wang B., Zhang H., Jarzembowski E.A. 2013. Early Cretaceous angiosperms and beetle evolution // Frontiers in Plant Science. Vol.4. P.360.
- Wickham H.F. 1913. The Princeton collection of fossil beetles from Florissant // Annals of the Entomological Society of America. Vol.6. P.359–366.
- Wickham H.F. 1914. New Miocene Coleoptera from Florissant // Bulletin of the Museum of Comparative Zoology, Harvard University. Vol.58. P.423–494.
- Wickham H.F. 1916. New fossil Coleoptera from the Florissant beds // Bulletin from the Laboratories of Natural History of the State University of Iowa. Vol.7. P.3–20.
- Zhang J.-F. 1989. Fossil Insects from Shanwang, Shandong, China // Shandong Science and Technology Publishing House, Jinan. 459 p. [in Chinese with English summary].
- Zherikhin V.V. 1977. [Family Cryptophagidae] // Mezozoiskie zhestkokrylye. Trudy Paleontol. Inst. AN SSSR. Moscow: Nauka Publ. T.161. P.138–139 [in Russian].
- Zherikhin V.V. 1978. [Development and change of the Cretaceous and Cenozoic faunal assemblages (Tracheata and *Chelicerata*)] // Trudy Paleontol. Inst. AN SSSR. Vol.165. 198 p. [in Russian]