

## Short communication

# The extant genus *Eutheia* (Coleoptera: Staphylinidae: Scydmaeninae) discovered in Upper Cretaceous Taimyr amber

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## ABSTRACT

The Eutheini includes over 90 extant species classified in seven genera and distributed predominantly in the Northern Hemisphere. So far only one extinct genus and species unambiguously placed in this tribe has been known, *Archeutheia*, from Albian of Spain. We report the discovery of *Eutheia*, a member of the largest extant genus of Eutheini, in Santonian of northern Siberia. Extant species of *Eutheia* are primarily defined on the basis of male genital characters, and the specimen discovered in Taimyr amber is a female; consequently it is described as *Eutheia* sp. The new finding remarkably extends the known range of Eutheini during Cretaceous over the area of about 6 thousand kilometers, from the Iberian Plate to northern Siberia. A long morphological stasis in *Eutheia* suggests that this genus was associated with stable mesic microhabitats of the upper soil layers or rotten wood for at least 83 my.

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## 1. Introduction

Eutheini is a relatively small tribe of morphologically conspicuous Scydmaeninae, or ant-like stone beetles. It comprises over 90 extant species in seven genera distributed on all continents (Jałoszyński, 2014a). This is predominantly a Northern Hemisphere group, with only one genus, *Paraneseuthia* Franz, 1986, known to occur also south of equator. Moreover, the majority of species belong to two genera, *Eutheia* Stephens, 1830 and *Veraphis* Casey, 1897, both distributed mostly in the Holarctic region (Newton & Franz, 1998; Jałoszyński, 2014a). Species of Eutheini are minute (typically 0.7–2 mm), elongate and flattened; only *Paraneseuthia* and *Euthiconus* Reitter, 1881 include strongly convex beetles. Very little is known about biology of Eutheini; these are rare scydmaenines usually collected by sifting surface layers of forest leaf litter or rotten wood, and infrequently also by flight intercept traps. Despite the rarity, Eutheini is one of the best studied tribes of Scydmaeninae. Morphological structures of all genera were

described and illustrated in detail (Jałoszyński, 2010a, 2011, 2014a), the tribe was a subject of a phylogenetic analysis which resulted in placing it within Cephenniitae, Reitter, 1882, as a sister group of a clade composed of Cephenniini, Reitter, 1882 and Marcepaniini Jałoszyński, 2014a (Jałoszyński, 2014a), and although only one extinct taxon is known, it also was included in a phylogenetic analysis and its placement in Eutheini is well-supported (Jałoszyński & Peris, 2016).

Schaufuss (1890) described two new genera, each including one species, from the upper Eocene Baltic amber, and suggested that they were similar to the extant *Eutheia*. These are *Hetereuthia* Schaufuss, 1890 and *Palaeothia* Schaufuss, 1890. However, the descriptions are vague and lack details that could be used to confirm the placement within Eutheini. Schaufuss' paper is not illustrated, and the current depository of his type specimens remains unknown. In the world catalog of the genera of Scydmaeninae (Newton & Franz, 1998) *Hetereuthia* and *Palaeothia* are listed as *incertae sedis*, and this view seems most reasonable at the current stage of knowledge. Consequently, the only species known in a fossil form and unambiguously placed in Eutheini is *Archeutheia magnifica* (Peris, Chatzimanolis and Delclòs, 2014) from the lower Albian of Spain. This species was originally placed in *Kachinus* Chatzimanolis, Engel and Newton, 2010, genus described from the Upper Cretaceous Burmese amber and treated as *incertae sedis* within Scydmaenitae. Jałoszyński and Peris (2016) re-examined the

Abbreviations: PIN, Paleontological Institute of the Russian Academy of Sciences, Moscow; SIZK, Schmalhausen Institute of Zoology, National Academy of Sciences of Ukraine, Kiev.

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type material, incorporated characters of *K. magnificus* in a phylogenetic analysis and concluded that this species should be placed in Eutheini, as a sister group of *Eutheia*. It was therefore demonstrated for the first time that Eutheini is an old group whose members, morphologically very similar to the extant *Eutheia*, were present on the Iberian Plate over 105 Ma.

In the present study we report a discovery of Eutheini in the Upper Cretaceous amber of Taimyr Peninsula. This finding is the oldest definite *Eutheia* known so far, and represents the first member of the Staphylinidae determined to the generic level from the Taimyr amber.

## 2. Geographic and geological context

The specimen used in this study comes from Yantardakh, situated at the base of Taimyr Peninsula, northern Siberia (Fig. 1). The locality is a cliff on the right bank of the Maimecha River, three km upstream from its confluence with the Kheta River (Yantardakh Hill, about 200 m long and 30 m high; 71°18'26.54"N 99°33'46.51"E). The amber piece was collected in 2012 during a PIN expedition by D. S. Kopylov, E. A. Sidorchuk and D. D. Vorontsov, near the water level (Fig. 3 in Rasnitsyn et al., 2016).

The amber at Yantardakh is deposited in the Kheta Formation of Coniacian-Santonian age (Saks et al., 1959). All amber in Yantardakh comes from the upper horizons of the formation, and is consequently thought to be Santonian (Zherikhin, 1978) or even upper Santonian, based on the presence of marine bivalves of the genus *Inoceramus* Sowerby, 1814 (Praecardioida: Inoceramidae) in the overlying (upper Santonian-lower Campanian) Mutino formation (Saks et al., 1959; Zherikhin & Sukacheva, 1973; Zherikhin & Eskov, 1999). The Mutino Formation conformably overlays the amber-bearing horizon without visible breaks (Rasnitsyn, 1980). Geological and palaeontological data concerning the Kheta formation and Yantardakh were recently summarized by Rasnitsyn et al. (2016); the available biostratigraphic evidence indicates the late Santonian age of the horizon.

A warm-temperate, humid climate was reconstructed for the Mutino and Turonian/Coniacian Ledyanaya formations that overlay and underlay the Kheta Formation, respectively (Golovneva, 2012). Inclusions of Taimyr Santonian localities are hypothesized to have been rapidly buried in deltaic sediments and reflect the fauna that inhabited an area directly adjacent to the river bank (Zherikhin & Sinitshenkova, 2002).

## 3. Material and methods

The fossil specimen here described is housed in the Paleontological Institute of the Russian Academy of Sciences (PIN) and was assigned a collection number 3311/1086. The inclusion is in a polished flat pentagonal piece of retinite 4.35 × 3.8 × 0.65 mm; it was observed under a Leica stereomicroscope M165C in the center of the collective usage of the scientific equipment 'Animalia' (SIZK). Photographs were taken using a Leica DFC 425 digital camera mounted to a Leica M165 microscope in PIN. Images were edited with Corel PhotoPaint 9.397. Morphological structures were figured by freehand drawing, with exact proportions and general shapes sketched from photographs. Measurement convention and the terminology of morphological structures follow those of Jałoszyński (2011, 2014a). The map in Fig. 1 is based on that published previously by Perkovsky and Makarkin (2015).

## 4. Systematic palaeontology

Suborder Polyphaga Emery, 1886

Superfamily Staphylinoidea Latreille, 1802

Family Staphylinidae Latreille, 1802

Subfamily Scydmaeninae Leach, 1815

Tribe Eutheini Casey, 1897

Genus *Eutheia* Stephens, 1830

**Remarks.** The specimen is unambiguously placed in Eutheini on the basis of the following synapomorphies (Jałoszyński, 2014a): the body only weakly constricted between the head and pronotum and between pronotum and elytra; the head prognathous, lacking deep occipital constriction, maxillary palp (Fig. 2 D; *mxp*) with palpomere 4 short and broad, with blunt apex; prothorax with sharp lateral edges, complete notosternal sutures (Fig. 2D; *nss*) and long basisternal part of prosternum (Fig. 2D; *bst*); mesanepisterna (Fig. 2D; *aest2*) and mesepimera (Fig. 2D; *epm2*) exposed in ventral view; and broadly separated metacoxae. The taxon is unambiguously identified as belonging to the branch of Eutheini comprised of *Veraphis*, *Eutheia* and *Archeutheia* (Jałoszyński & Peris, 2016) on the basis of strongly elongate, slender and flattened body; sub-triangular intercoxal area; weakly elevated mesoventral intercoxal process (Fig. 2D; *msvp*); and truncated elytral apices that leave the pygidium and propygidium (Fig. 2B; *pg*, *ppg*) exposed. The specimen has the mesoventral intercoxal process broad and

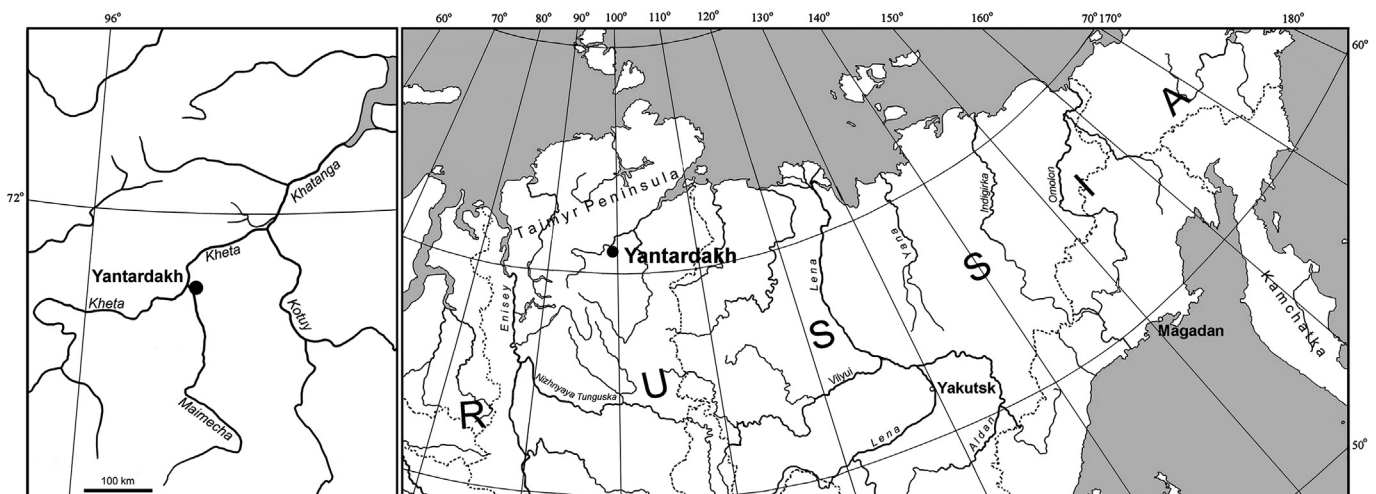
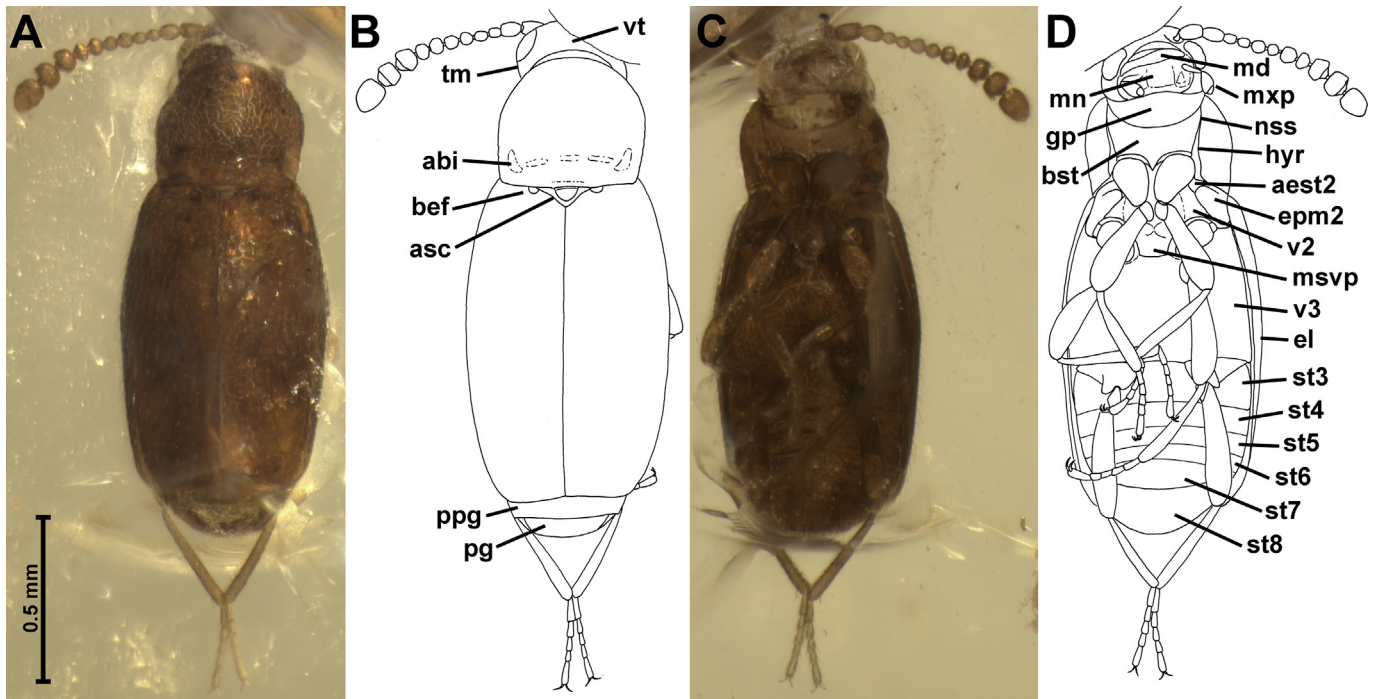


Fig. 1. The location of Santonian amber deposits of Yantardakh in Taimyr Peninsula, northern Siberia.



**Fig. 2.** Studied specimen (PIN 3311/1086) of *Eutheia* sp. **A.** Dorsal habitus, photograph. **B.** Dorsal habitus, schematic. **C.** Ventral habitus, photograph. **D.** Ventral habitus, schematic. Abbreviations: abi, antebasal impression; aest2, mesanepisternum; asc, adscutellar carina; bef, basal elytral fovea; bst, basisternal part of prosternum; el, elytron; epm2, mesepimeron; gp, gular plate; hyr, hypomerite; md, mandible; mn, mentum; msvp, mesoventral intercoxal process; mxp, maxillary palp; nss, notosternal suture; pg, pygidium; ppg, propygidium; st3–8, abdominal sternite 3–8; tm, temple; v2, mesoventrite; v3, metaventrite; vt, vertex.

subtrapezoidal, the basal elytral foveae asetose (Fig. 2B; bef), and the vertex lacking a pair of lateral pits or grooves; these characters exclude *Veraphis*, which has the mesoventral process narrowly carinate, setose elytral foveae, and the vertex always with two conspicuous pits or longitudinal grooves (Jałoszyński, 2014a). *Archeutheia*, which lacks hypomerite ridges (Jałoszyński & Peris, 2016) can also be excluded; the studied specimen has distinct and complete hypomerite ridges (Fig. 2D; hyr). All characters of the specimen agree with those of *Eutheia* (Jałoszyński, 2014a); no differences in character states were found. Consequently, the specimen is identified as *Eutheia*.

Species: *Eutheia* sp.

#### Fig. 2

**Material studied.** Female PIN 3311/1086, Taimyr amber, collected in 2012 during a PIN expedition. Well-preserved, nearly complete specimen with only the right anterolateral portion of the head and right antenna missing.

**Locality and horizon.** Russia: Krasnoyarsk Krai: Taymyrsky Dolgano-Nenetsky District: Taimyr Peninsula: right bank of the Maimecha River 3 km upstream of its confluence with the Kheta River (a left source of the Khatanga River), Yantardakh Hill; Upper Cretaceous, Santonian (Kheta Formation).

**Description.** Body (Fig. 2A–D) elongate, slender, strongly flattened, light brown; body length <1.5 mm (length of head not possible to measure; length of pronotum + length of elytra = 1.30 mm). Body covered with short and nearly recumbent vestiture of setae; only antennae with longer and suberect setae.

Head with broad posterior part ('neck' region) largely retracted into prothorax, only part of gular plate (Fig. 2D; gp) visible; tempora (Fig. 2B; tm) slightly shorter than compound eyes; eyes large, finely faceted and distinctly projecting from the head silhouette; vertex

(Fig. 2B; vt) transverse and evenly, weakly convex, anteriorly confluent with frons; frons only partly visible, evenly and weakly convex between eyes. Mouthparts only partly visible; maxillary palps (Fig. 2D; mxp) exposed except for palpomere 1; mentum (Fig. 2D; mn) subrectangular; mandibles (Fig. 2D; md) closed and only their outer surface visible. Width of head 0.35 mm. Antenna (Fig. 2A–D) with scape and pedicel strongly elongate; antennomeres 3 and 4 each slightly elongate, 5 and 6 about as long as broad, 7–10 each slightly transverse, 11 elongate, distinctly shorter than 9–10 combined, rounded at apex, unmodified. Length of antenna 0.60 mm.

Prothorax (Fig. 2A–D) strongly flattened, in dorsal view semi-elliptical, with sharp lateral edges which are finely microserrate in posterior half. Pronotum (Fig. 2A, B) with anterior margin strongly rounded; sides rounded in anterior third and nearly straight in posterior third, where lateral margins are slightly convergent towards indistinctly obtuse-angled and blunt posterior pronotal corners; posterior margin very weakly arcuate with indistinct median flattening in front of mesoscutellum. Pronotal base with five shallow and diffused antebasal impressions (Fig. 2B; abi): one lateral pair of large elongate impressions near each hind pronotal corner; one pair of transverse impressions; and faint transverse impression at middle. Length of pronotum 0.375 mm, width 0.425 mm.

Elytra (Fig. 2A, B) elongate, suboval with truncate apices. Basal elytral foveae (Fig. 2B; bef) located slightly closer to mesoscutellum than to humeri, adjacent to distinct adscutellar carinae (Fig. 2B; asc). Length of elytra 0.925 mm, width 0.60 mm.

Two terminal abdominal tergites exposed, propygidium (Fig. 2B; ppg) and subtriangular pygidium (Fig. 2B; pg).

Legs (Fig. 2B, D) moderately slender, all tibiae nearly straight, unmodified.

Abdomen partly translucent, unclear outline of valvifers seen in the terminal segments.



## 5. Discussion

The currently known forty-two extant species of *Eutheia* (Jałoszyński, 2014b) are distributed throughout Holarctic and in the northern part of Neotropical regions; most of them can be identified on the basis of comprehensive regional revisions and recent descriptions (Franz, 1971; Kurbatov, 1990, 1991; Jałoszyński, 2004, 2008a,b, 2010b,c, 2011, 2013, 2014b; Hoshina, 2007). Notable exceptions are Nearctic species, whose aedeagi have never been illustrated. Morphological structures of *Eutheia* were recently described and illustrated in detail (Jałoszyński, 2011, 2014a), which facilitated identification of the specimen reported in the present paper. Species of *Eutheia* show very uniform appearance, and differences between them are weakly expressed in external characters, whereas the male genitalia (the aedeagus) differ remarkably. Species complexes are known that differ only in male genital characters, and females cannot be distinguished at all (e.g., Jałoszyński, 2011). It is, therefore, not a good practice to describe a new species based solely on females, as the primary (and often only reliable) diagnostic characters are associated with the unique and often complicated aedeagus. Some species groups can be distinguished within *Eutheia*, but they are evident only when the aedeagal structures are considered. For instance, some eastern Palaearctic and Taiwanese species share complicated, bifurcate apex of the median lobe showing variously shaped lateral lobes and projections (Jałoszyński, 2008b), whereas western Palaearctic species have the apical region invariantly simple and undivided (e.g., Jałoszyński, 2014b). Mesoamerican species, in turn, share hyaline lateral subapical lobes bearing sensilla (either setae or pores) on their margins (Jałoszyński, 2011). The amber inclusion described in the present study does not have any unique external characters that could unambiguously distinguish this species from its extant congeners, and structures resembling valvifers visible through the abdomen prove this is a female. Consequently, a species diagnosis cannot be given. Nonetheless, a discovery of the extant genus *Eutheia* in Santonian deposits of Siberia is a valuable contribution to the knowledge of the evolution and biogeography of Eutheini.

As summarized previously (Jałoszyński, 2011), extant species of *Eutheia* are predominantly Palaearctic. Thirty-five of them are known to occur in this region (including Taiwan), only three in North America and four in Central America. All known species seem to be associated with cool or temperate climate zones and those recorded from subtropical regions have been collected in high mountains, often above 2000 m. They inhabit isolated mountainous 'islands' located on borders of the currently known geographic range of *Eutheia* and surrounded by subtropical areas. The most striking example is a group of five Taiwanese species, all known to occur only above 2100 m in the Alishan range (Jałoszyński, 2008b), while their geographically closest congeners inhabit the Russian Far East, Japan, Yunnan and Sichuan (Kurbatov, 1990, 1991; Jałoszyński, 2004, 2008a, 2010b,c, 2013). The warm-temperate, humid climate suggested for the Mutino and Turonian/Coniacian Ledyanaya formations that overlay and underlay the Kheta Formation (Golovneva, 2012) is clearly within the ecological plasticity of *Eutheia*, as in Europe this genus reaches the Mediterranean Basin.

The only unambiguously identified fossil Eutheini recorded so far was *Archeutheia magnifica* from the early Albian of Spain (105 Ma). *Archeutheia* is strikingly similar to extant *Eutheia*; according to the recent study these are sister groups (Jałoszyński & Peris, 2016). It is not, therefore, surprising to find Eutheini in nearly 20 my younger Santonian deposits. An important finding is that during the Cretaceous the geographical range of Eutheini, represented by sister taxa *Archeutheia* and *Eutheia*, extended from

the Iberian Plate to at least northern Siberia, spanning a distance of about six thousand kilometers from west to east. The long morphological stasis of Eutheini, and *Eutheia* in particular, is also an interesting phenomenon. Several species of Staphylinidae placed in extant genera were recorded from Cretaceous deposits, belonging to the subfamilies Euaesthetinae (*Octavius electrospinosus* Clarke and Chatzimanolis, 2009), Oxyporinae (*Oxyporus yixianus* Solodovnikov and Yue, 2011, in Yue, Ren and Solodovnikov (2011); but the placement suggested as problematic by Cai and Huang (2014)), Phloeocharinae (*Phloeocharis agerata* Chatzimanolis, Newton and Engel, 2013, in Chatzimanolis, Newton, Soriano and Engel (2013)), Megalopsidiinae (*Megalopinus extinctus* Yamamoto and Solodovnikov, 2016) and Steninae (*Stenus* spp. (Schlüter, 1978; Ryvkin, 1988)). Therefore, a long morphological stasis in various lineages of rove beetles seems to be a well-established fact and a stability of mesic habitats was hypothesized as the main reason for this phenomenon (e.g., Clarke & Chatzimanolis, 2009; Chatzimanolis et al., 2013; Yamamoto & Solodovnikov, 2016). The Cretaceous *Eutheia*, reported in the present paper, supports the role of the stable habitat of soil, leaf litter and rotten wood, which is typical of extant Eutheini, as a factor responsible for the observed morphological stability.

A male of Cretaceous *Eutheia* with the aedeagus (or at least its apical region) visible would be the most desired finding; this would make it possible not only to provide a formal diagnosis of a new species, but, more importantly, to infer relationships of the fossil of *Eutheia* to the currently known species groups.

## 6. Conclusions

For the first time, the extant genus *Eutheia* is recorded from Cretaceous (Santonian) deposits, representing the second known genus of fossil Eutheini. This is also the first Scydmaeninae species known from the Taimyr amber. This finding demonstrates a relatively wide geographic distribution of Eutheini during Cretaceous (from the Iberian Plate to northern Siberia), and a long morphological stasis of *Eutheia*. The latter phenomenon suggests that stable mesic microhabitats of the upper soil layers and rotten wood, where species of this genus can be found today, were inhabited by *Eutheia* for over 83 my.

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## References

- Cai, C., Huang, D., 2014. Diverse oxyporine rove beetles from the Early Cretaceous of China (Coleoptera: Staphylinidae). *Systematic Entomology* 39 (3), 500–505.
- Casey, T.L., 1897. Coleopterological notices, VII. *Annals of the New York Academy of Science* 9, 285–684.
- Chatzimanolis, S., Engel, M.S., Newton, A.F., Grimaldi, D.A., 2010. New ant-like stone beetles in mid-Cretaceous amber from Myanmar (Coleoptera: Staphylinidae: Scydmaeninae). *Cretaceous Research* 31, 77–84.

- Chatzimanolis, S., Newton, A.F., Soriano, C., Engel, M.S., 2013. Remarkable stasis in a phloeocharine rove beetle from the Late Cretaceous of New Jersey (Coleoptera: Staphylinidae). *Journal of Paleontology* 87 (2), 177–182.
- Clarke, D.J., Chatzimanolis, S., 2009. Antiquity and long-term morphological stasis in a group of rove beetles (Coleoptera: Staphylinidae): description of the oldest *Octavius* species from Cretaceous Burmese amber and a review of the “*euaesthetine* subgroup” fossil record. *Cretaceous Research* 30 (6), 1426–1434.
- Emery, C., 1886. Über Phylogenie und Systematik der Insekten. *Biologisches Zentralblatt* 5, 648–656.
- Franz, H., 1971. Untersuchungen über die paläarktischen Arten der Gattungen *Euthia* Steph. und *Veraphis* Casey (Col. Scydmaenidae). *Eos, Revista Española de Entomología* 46, 57–84.
- Franz, H., 1986. Zweiter Beitrag zur Kenntnis der Scydmaenidenfauna der Fiji-Inseln. *Entomologische Blätter* 82, 147–178.
- Golovneva, L.B., 2012. The Late Cretaceous flora of the Khatanga depression (northern Siberia). *Paleobotanika* 3, 32–61 (in Russian, English summary).
- Hoshina, H., 2007. Discovery of the third species of the genus *Euthia* (Coleoptera: Scydmaenidae) from Shikoku, Japan. *Memoirs of the Faculty of Education and Regional Studies, University of Fukui, Series II: Natural Science* 58, 7–10.
- Jatoszyński, P., 2004. Two new species of *Euthia* Stephens (Coleoptera, Scydmaenidae, Scydmaeninae) from Japan. *Bulletin of the National Science Museum Tokyo* 30, 129–135.
- Jatoszyński, P., 2008a. *Euthia puetzi* n. sp. from China (Coleoptera, Scydmaenidae). *Genus* 19, 33–36.
- Jatoszyński, P., 2008b. Revision of *Euthia* Stephens of Taiwan (Coleoptera, Scydmaenidae). *Genus* 19, 177–190.
- Jatoszyński, P., 2010a. *Paraneseuthia* Franz, 1986 of Australo-Oriental region, with notes on Palearctic species (Coleoptera, Staphylinidae, Scydmaeninae). *Annales Zoologici* 60, 181–193.
- Jatoszyński, P., 2010b. *Euthia nujianglisuana* n. sp. from China, and an updated checklist of Palearctic *Euthia* Stephens (Coleoptera, Staphylinidae, Scydmaeninae). *Genus* 21, 21–29.
- Jatoszyński, P., 2010c. *Euthia sculpturata* n. sp. from Sichuan, China (Coleoptera, Staphylinidae, Scydmaeninae). *Genus* 21, 489–493.
- Jatoszyński, P., 2011. *Euthia* Stephens (Coleoptera, Staphylinidae, Scydmaeninae) of Central America. *Studies on Neotropical Fauna and Environment* 46, 121–130.
- Jatoszyński, P., 2013. Three new species of *Euthiini* (Coleoptera, Staphylinidae, Scydmaeninae) from China. *Zootaxa* 3609, 495–503.
- Jatoszyński, P., 2014a. Phylogeny of a new supertribe Cephenniitae with generic review of *Euthiini* and description of a new tribe Marcepaniini (Coleoptera: Staphylinidae: Scydmaeninae). *Systematic Entomology* 39, 159–189.
- Jatoszyński, P., 2014b. *Euthia bekchievi* sp. n. (Coleoptera, Staphylinidae, Scydmaeninae) from Bulgaria. *Zootaxa* 3779, 493–496.
- Jatoszyński, P., Peris, D., 2016. Cretaceous amber inclusions of Spain and Myanmar demonstrate early diversification and wide dispersal of Cephenniitae (Coleoptera: Staphylinidae: Scydmaeninae). *Cretaceous Research* 57, 190–198.
- Kurbatov, S.A., 1990. More on the tribe *Euthiini* (Coleoptera, Scydmaenidae) in the USSR Far East. *Zoologicheskii Zhurnal* 69, 136–140 (in Russian).
- Kurbatov, S.A., 1991. New data for the fauna of beetles tribe *Euthiini* (Coleoptera, Scydmaenidae) from the Far East of the USSR. *Zoologicheskii Zhurnal* 70, 153–155 (in Russian).
- Latreille, P.A., 1802. *Histoire naturelle, générale et particulière des Crustacés et des Insectes. Familles Naturelles des Genres* 3. Paris: F. Dufart, xii + 13–467 pp.
- Leach, W.E., 1815. *Entomology*. In: Brewster, D. (Ed.), *Brewster's Edinburgh Encyclopedia*. Volume 9 [part I]. W. Blackwood, J. Waugh, etc, Edinburgh, pp. 57–172.
- Newton, A.F., Franz, H., 1998. World catalog of the genera of Scydmaenidae (Coleoptera). *Koleopterologische Rundschau* 68, 137–165.
- Peris, D., Chatzimanolis, S., Delclòs, X., 2014. Diversity of rove beetles (Coleoptera: Staphylinidae) in Early Cretaceous Spanish amber. *Cretaceous Research* 48, 85–95.
- Perkovsky, E.E., Makarkin, V.N., 2015. First confirmation of spongillaflies (Neuroptera: Sisyridae) from the Cretaceous. *Cretaceous Research* 56, 363–371.
- Rasnitsyn, A.P., 1980. *Origin and Evolution of Hymenoptera*. Nauka, Moscow, 192 pp. (in Russian).
- Rasnitsyn, A.P., Bashkuev, A.S., Kopylov, D.S., Lukashevich, E.D., Ponomarenko, A.G., Popov, Yu.A., Rasnitsyn, D.A., Ryzhkova, O.V., Sidorchuk, E.A., Sukatsheva, I.D., Vorontsov, D.D., 2016. Sequence and scale of changes in the terrestrial biota during the Cretaceous (based on materials from fossil resins). *Cretaceous Research* 61, 234–255.
- Reitter, E., 1882. Bestimmungs-Tabellen der europäischen Coleopteren. V. Entaltend die Familien: Pausidae, Clavigeridae, Pselaphidae und Scydmaenidae. *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien* 31, 443–593.
- Ryvkin, A.B., 1988. New Cretaceous Staphylinidae (Insecta) from the Far East. *Paleontologicheskii Zhurnal* 4, 103–106 (in Russian).
- Saks, V.N., Gramberg, I.S., Ronkina, Z.Z., Aplonova, E.N., 1959. The Mesozoic deposits of the Khatanga depression. *Trudy Nauchno-issledovatel'skogo Instituta Geologii Arktiki* 99, 246 pp. (in Russian).
- Schaufuss, L.W., 1890. *Die Scydmaeniden des baltischen Bernsteines*. *Nunquam Otiosus* 3, 561–586.
- Schlüter, T., 1978. Zur Systematic und Palökologie harzkonserverter Arthropoda einer Taphozönose aus dem Cenomanium von NW-Frankreich. *Berliner Geowissenschaftliche Abhandlungen, Reihe A, Geologie und Paläontologie* 9, 1–150.
- Sowerby, J., 1814. *The Mineral Conchology of Great Britain; or Coloured Figures and Descriptions of those Remains of Testaceous Animals or Shells, which have been Preserved at Various Times and Depths in the Earth*, vol. 1. Benjamin Meredith, London, pp. 45–78.
- Stephens, J.F., 1830. *Illustrations of British Entomology; or, a Synopsis of Indigenous Insects: Containing Their Generic and Specific Distinctions; with an Account of their Metamorphoses, Times of Appearance, Localities, Food, and Economy, as far as Practicable*. In: *Mandibulata*, Vol. 3. Baldwin & Cradock, London, 374 pp.
- Yamamoto, S., Solodovnikov, A., 2016. The first fossil Megalopsidiinae (Coleoptera: Staphylinidae) from Upper Cretaceous Burmese amber and its potential for understanding basal relationships of rove beetles. *Cretaceous Research* 59, 140–146.
- Yue, Y., Ren, D., Solodovnikov, A., 2011. The oldest fossil species of the rove beetle subfamily Oxyporinae (Coleoptera: Staphylinidae) from the Early Cretaceous (Yixian Formation, China) and its phylogenetic significance. *Journal of Systematic Palaeontology* 9 (4), 467–471.
- Zherikhin, V.V., 1978. Development and Changes in Cretaceous and Cenozoic Faunistic Complexes (Tracheates and Chelicerates). Nauka Press, Moscow, 200 pp. (in Russian).
- Zherikhin, V.V., Eskov, K.Yu., 1999. Mesozoic and Lower Tertiary resins in former USSR. In: *Estudios del Museo de Ciencias Naturales de Álava* 14 (núm. espec. 2), pp. 119–131.
- Zherikhin, V.V., Sinitshenkova, N.D., 2002. Ecological history of the aquatic insects. Cretaceous. In: Rasnitsyn, A.P., Quicke, D.L.J. (Eds.), *History of Insects*. Kluwer Academic Publishers, Dordrecht, pp. 400–417.
- Zherikhin, V.V., Sukacheva, I.D., 1973. On the Cretaceous insect-bearing “amber” (retinite) of northern Siberia. In: Narchuk, E.P. (Ed.), *Problems of Paleontology of the Insects*. Reports of the 24 Annual Reading in Memory of N.A. Kholodkovsky (1–2 April 1971). Nauka Press, Leningrad, pp. 3–48 (in Russian).