Евразиатский энтомол. журнал 23(5): 247–251
doi 10.15298/euroasentj.23.05.02

New eusyninclusions of ants in European Late Eocene amber in a view of palaeoecological data

Новые эусининклюзы муравьёв позднеэоценовых янтарей Европы в свете палеоэкологических данных

D.M. Zharkov, D.A. Dubovikoff
Д.М. Жарков, Д.А. Дубовиков

Department of Applied Ecology, Faculty of Biology, Saint Petersburg State University, Universitetskaya nab. 7/9, Saint Petersburg 199034 Russia. E-mail: d.zharkov@spbu.ru; d.dubovikoff@spbu.ru.

Кафедра прикладной экологии, Биологический факультет, Санкт-Петербургский государственный университет, Университетская наб. 7/9, Санкт-Петербург 199034 Россия.

Key words: Syninclusions, Late Eocene amber, Formicidae, palaeoecology, Wheeler's dilemma.

Ключевые слова: синининклюзы, позднеэоценовый янтарь, Formicidae, палеоэкология, дилемма Уилера.

Abstract. We report new interesting findings of ant eusyninclusions in the Late Eocene ambers of Europe (fossil taxa are marked with †). We discuss such findings as, †*Prionomyrmex longiceps* Mayr, 1868 with †*Lasius schiefferdeckeri* Mayr, 1868, †*Agroecomyrmex duisburgi* (Mayr, 1868) with †*L. schiefferdeckeri* Mayr, †*Bradoponera meieri* Mayr, 1868 with †*Formica flori* Mayr, 1868, †*B. meieri* Mayr with †*L. schiefferdeckeri* Mayr, †*Gesomyrmex hoernesi* Mayr, 1868 with †*F. flori* Mayr, †*G. hoernesi* Mayr with †*Yantaromyrmex geinitzi* (Mayr, 1868), and also finding of the four most abundant species in a small piece of Baltic amber.

Резюме. Мы сообщаем о новых интересных находках эусининклюзов муравьёв в познеэоценовых янтарях Европы (ископаемые таксоны отмечены знаком †). Мы обсуждаем такие находки, как, †*Prionomyrmex longiceps* Mayr, 1868 совместно с †*Lasius schiefferdeckeri* Mayr, 1868, †*Agroecomyrmex duisburgi* (Mayr, 1868) совместно с †*L. schiefferdeckeri* Mayr, †*Bradoponera meieri* Mayr, 1868 совместно с †*Formica flori* Mayr, 1868, †*B. meieri* Mayr совместно с †*L. schiefferdeckeri* Mayr, †*Gesomyrmex hoernesi* Mayr, 1868 совместно с †*F. flori* Mayr, †*G. hoernesi* Mayr совместно с †*Yantaromyrmex geinitzi* (Mayr, 1868), а также находку четырёх самых массовых видов в маленьком куске балтийского янтаря.

Introduction

The mixed nature of «tropical» and «temperate» faunal elements in Eocene communities is observed in different parts of the world, including the Baltic, USA, Svalbard, Canada, Great Britain, the Arctic and Australia [Archibald, Farrell, 2003]. It was first noted, more than a hundred years ago, by the great American entomologist William Morton Wheeler (1865–1937) [Wheeler, 1910]. When studying the ant fauna in Baltic Amber, he noted a strange set of ant genera from different climatic zones. Currently, such a combination of «tropical»and «temperate» ant genera in the same biotopes is unknown. Wheeler suggested that either the differences in geographical latitude or height (above sea level) in the amber forests were sufficient for the appearance of two different faunas that coexisted together, or the formation of amber occurred during successive shifts of warmer and earlier Oriental, Australian faunas to colder and later Palaearctic [Wheeler, 1915]. Bruce Archibald and Brian D. Farrell called these assumptions «Wheeler's dilemma» [Archibald, Farrell, 2003].

Brian Daley rejected the first hypothesis, which implied rather high mountains (more than 2000 m) at the site of the amber forest, which contradicts palaeogeomorphological studies. He hypothesised (and proved to be right) about the climate of Central and Northern Europe of the late Eocene, which has no analogues at the present time [Daley, 1972]. In the Eocene, the whole Earth had a special, «extinct» climate, relatively homogeneous, frost-free, hot and humid, which apparently allowed them to coexist [Zachos et al., 2001; Westerhold et al., 2020]. Also, both hypotheses are rejected by numerous findings of syninclusions (inclusions of different organisms or their parts in one piece of amber) of insects and other invertebrates from different climatic zones. Recently, Monica M. Solorzano-Kramer and co-authors [2023] proposed to divide the concept of syninclusions into two terms: «(1) eusyninclusions: prefix (eu-) in its sense «true» — bioinclusions present in a single layer of an amber piece, and (2) parasyninclusions: prefix (para-) in its sense «alongside» — bioinclusions present in different layers of an amber piece in respect to a defined layer that contains eusyninclusions by definition» [Solórzano-Kraemer et al., 2023]. This is a very important division, which contributes to a more accurate analysis of inclusions in amber.

For example, A.G. Radchenko and E.E. Perkovsky [Radchenko, Perkovsky, 2021] described an interesting find eusyninclusions of ants: the recent tropical genus *Oecophylla* Smith F., 1857 (worker †*O. brischkei* Mayr, 1868) with the recent Holarctic *Lasius* Fabricius, 1804 (four workers †*L. schiefferdeckeri* Mayr, 1868), which are not currently found together. Besides the fact that «It is the only evidence that two or more organisms lived in the same time and site» [Koteja, 1996]. In addition, syninclusions s. l. can provide direct evidence of various interactions between such organisms, both intra- and

interspecific [e.g. LaPolla, 2005; Peñalver et al., 2017], which may be the key to understanding their palaeoecology and evolution. The analysis of syninclusions s.l. is one of the key ways to understand the structure of multi-species communities of ancient fossil forests. Here we report about the new interesting findings of ant eusyninclusions in the Late Eocene amber of Europe in view of their significance for the palaeoecological analysis of fauna.

Materials and methods

The studied specimens of fossil ants (Figs 1–7; Supplementary Material 1) originated from the Baltic, Rovno and Bitterfeld ambers, Priabonian age (Late Eocene, 37.8–33.9 Ma) [Wolfe et al., 2016; Perkovsky, 2018; Iakovleva et al., 2022]. The studied specimens are kept in the collection of the Kaliningrad Amber Museum, Kaliningrad, Russia; collection of the Polish Academy of Sciences Museum of the Earth, Warsaw, Poland; collection of the Natural History Museum, Berlin, FRG; Jonas Damzen personal collection, Latvia; Konstantin Andrushchenko personal collection, Kaliningrad, Russia.

The studies were performed using the equipment of the Research Park of St. Petersburg State University («Centre for X-ray Diffraction Studies» project No. 103-23769; «Resource Centre for Microscopy and Microanalysis» project No. 112-23465, «Computing Centre», project No. 110-27449 and «Centre for Molecular and Cell Technologies» project No. 109-34813).

Photography and morphological analysis of samples were performed using a Leica M205C motorised stereomicroscope. Subsequent image processing was carried out using the Helicon Focus Pro 8 software. Arrays of microtomographic sections (for the specimen KAM 8) were obtained using a desktop high-resolution X-ray microtomograph SkyScan 1172. Visualisation, volume rendering, and segmentation of tomographic sections were performed in 3DSlicer 5.1. The sample KAM 8 was scanned with the following parameters: voltage 40 kV, current 250 μA, without a filter, with a pixel size of 4.45 microns and a resolution of 3960 × 3960 pixels per slice with a continuous 360° rotation, and an exposure of 1150 ms per frame (4804 X-ray projections).

Fossil taxa are marked with †.

The present work is registered in ZooBank (www.zoobank.org) under LSID urn:lsid:zoobank.org:pub:DBAFD0DA-C850-4B8E-850F-7546A9386D25

Results and Discussion

†*Prionomyrmex* Mayr, 1868 (Fig. 1) — an extinct genus of ants of the subfamily Myrmeciinae found in Rovno amber together with the recent Holarctic genus *Lasius* Fabricius, 1804. †*Prionomyrmex* Mayr known from the Late Eocene (†*P. longiceps* Mayr, 1868; †*P. janzeni* Baroni Urbani, 2000; †*P. gusakovi* Radchenko & Perkovsky, 2020) and the late Oligocene (†*P. wappleri* Dlussky, 2012). These ants are outwardly very

Fig. 1. †*Prionomyrmex longiceps* Mayr with four workers of †*Lasius schiefferdeckeri* Mayr in Rovno amber. JDC-9597R, J. Damzen collection.

Рис. 1. †*Prionomyrmex longiceps* Mayr совместно с 4 рабочими †*Lasius schiefferdeckeri* Mayr в Ровенском янтаре. JDC-9597R, коллекция Й. Дамзена.

similar to representatives of the recent primitive genus *Nothomyrmecia* Clark, 1934, however, they differ in the presence of a constriction between the III and IV abdominal segments in the first genus. The range of the subfamily Myrmeciinae is currently limited to Australia and New Caledonia. It can be assumed that the lifestyle of †*Prionomyrmex* Mayr was similar to that of modern representatives of the subfamily Myrmeciinae. Workers foraged alone at night on the ground and trees, feeding on honeydew, hunting arthropods, killing them with a sting. Interestingly, *Nothomyrmecia* Clark are most active in the cold season, on cold nights at temperatures of 5–10 °C [Hölldobler, Taylor, 1983], perhaps because at this time they face the least number of competitors, including more numerous species of daytime ants, such as *Camponotus* Mayr, 1861 and *Iridomyrmex* Mayr, 1862. This may explain that †*Prionomyrmex* Mayr continued to exist in Europe until the cooler (compared to the Eocene) in Late Oligocene [Dlussky, 2012], unlike many other «tropical» ant genera. We have studied a sample of JDC-9597R from Rovno amber (Jonas Damzen collection) with 4 workers †*L. schiefferdeckeri* Mayr.

†*Agroecomyrmex duisburgi* (Mayr, 1868) (Fig. 2), an extinct species of ant subfamily Agroecomyrmecinae was also found in the Baltic amber together with the recent Holarctic genus *Lasius* Fabricius. Currently, the Agroecomyrmecinae subfamily is represented by two recent species: *Tatuidris tatusia* Brown & Kempf, 1968, found in the litter of Neotropical forests in Central and South America and *Ankylomyrma coronacantha* Bolton, 1973, presumably arboreal ants from west and central Africa. †*Agroecomyrmex* Wheeler, 1910 is more similar in many morphological features to *Ankylomyrma* Bolton, 1973, than to highly specialised *Tatuidris* Brown & Kempf, 1968, which exhibit some unique features for ants in general. This may indicate the arboreal lifestyle of the fossil †*A. duisburgi* (Mayr), by analogy with *A. coronacantha* Bolton. The obvious signs of this are flat mandibles with 5 teeth, relatively large and complex eyes shifted back, and protective spikes. Bulging eyes on the sides of the head may also indicate a nocturnal lifestyle †*A. duisburgi* (Mayr). In addition, a more open labiomaxillary complex with longer maxillary and labial palps is typical for ants leading an aboveground rather than underground lifestyle. In the course of our work, we studied 4 specimens from Jonas Damzen collection (two of them with syninclusions).

†*Bradoponera meieri* Mayr, 1868 is an extinct species belonging to the so–called poneromorph group of subfamilies, as part of the Proceratiinae subfamily, found in Bitterfeld amber together with †*Formica flori* Mayr, 1868 (MKK, F-101), and in Baltic amber together with †*L. schiefferdeckeri* Mayr (MZ PAN, 10360). Most of the recent taxa of ants from the Proceratiinae subfamily and the poneromorph group as a whole are tropical or subtropical. Although the vast majority of poneromorphs live in the soil and leaf litter, and they almost never climb tree trunks — the exception may be †*Bradoponera* Mayr, 1868. This assumption was put forward by Prof. Gennady M. Dlussky on the basis of the fact that unlike

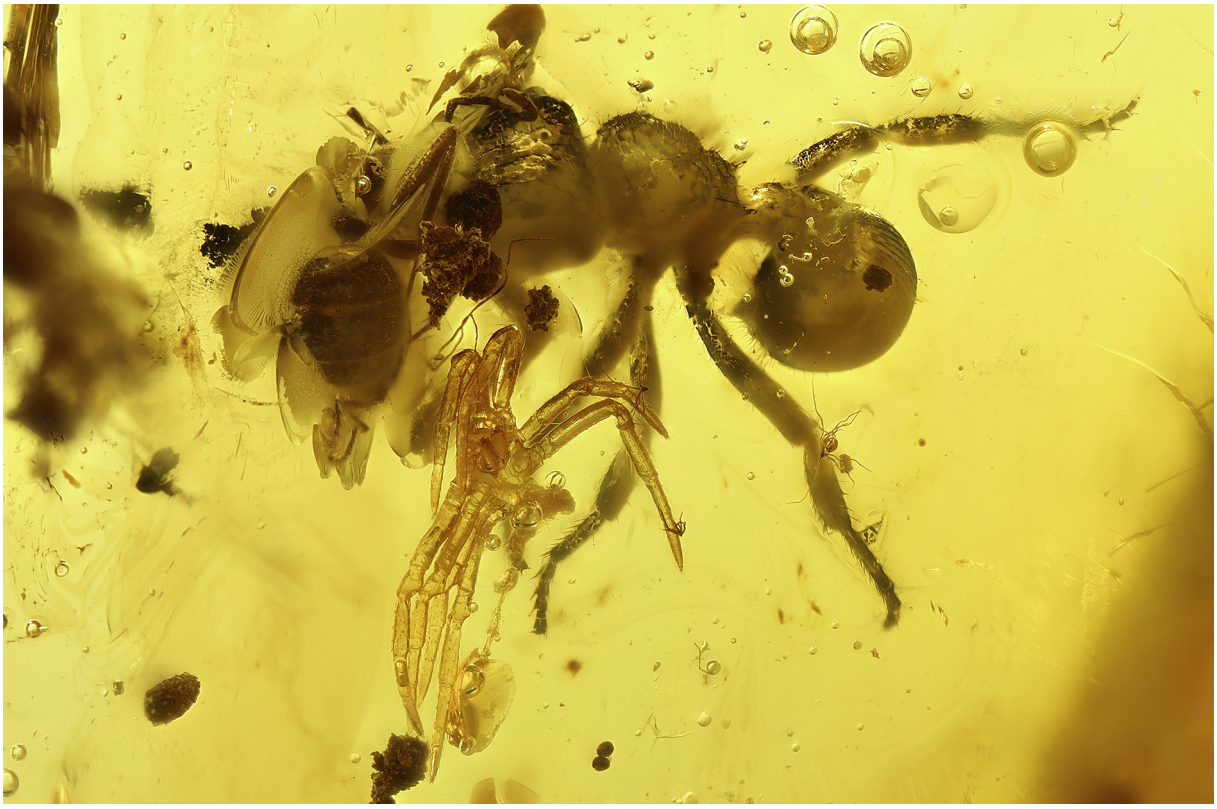
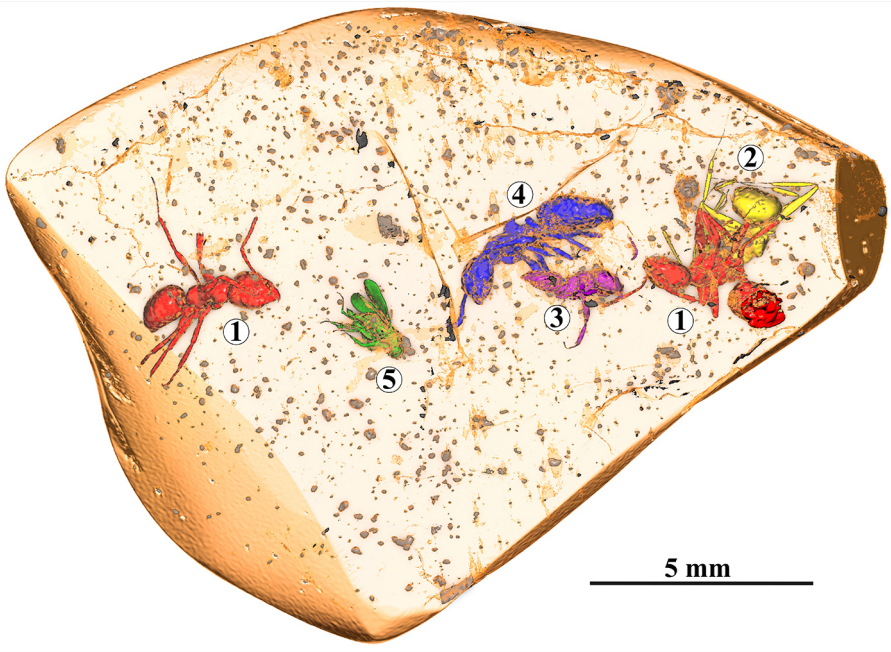


Fig. 2. †*Agroecomyrmex duisburgi* (Mayr) with †*Lasius schiefferdeckeri* Mayr in Baltic amber. JDC-10572, J. Damzen collection.
Рис. 2. †*Agroecomyrmex duisburgi* (Mayr) совместно с †*Lasius schiefferdeckeri* Mayr в Балтийском янтаре. JDC-10572, коллекция Й. Дамзена.

other species of poneromorphs, abundantly represented in amber by winged females and males, †*B. meieri* Mayr are represented in amber mainly by workers and males (30 out of 32 known specimens) [Dlussky, 2009]. The predominance of winged individuals in most fossil finds of the poneromorph group indicates that these ants lived in the forest litter or upper layer of the soil, climbing trees only during nuptial flight. The predominance of wingless individuals in †*B. meieri* Mayr suggests that these ants usually walked on tree trunks. It is likely that they built nests inside natural cavities in dead wood or in suspended soil accumulating on epiphytes, as is the case with some recent tropical Ponerinae. A modern analogue of the extinct †*Bradoponera* Mayr may be a tropical genus of small ants *Discothyrea* Roger, 1863, which is morphologically very similar to the fossil genus. Although they live mainly in the litter, some *Discothyrea* Roger species have been caught during night foraging on the branches of bushes and trees. We studied 4 workers and one male in syninclusions with †*L. schiefferdeckeri* Mayr.

Ants of the genus *Gesomyrmex* Mayr, 1868 — polymorphic mysterious inhabitants of the rainforests of Southeast Asia. As we know from the palaeontological finds, representatives of *Gesomyrmex* Mayr existed in the Early Eocene, were very diverse in the Middle and Late Eocene throughout the Old World, and then disappeared from the palaeontological record in the Early Miocene [Dlussky et al., 2009]. Recent species are relicts and inhabit the rainforests of Southeast Asia [Dubovikoff, 2004]. We have discovered †*Gesomyrmex hoernesi* (Mayr, 1868) with †*Formica flori* (Mayr, 1868) (KAM 4498/7) and with †*Yantaromyrmex geinitzi* (Mayr, 1868) (Ka-69, K. Andrushchenko collection) in the Baltic amber.

There is very poor information about the lifestyle of the recent *Gesomyrmex* Mayr species. In all the few populations studied, living chambers were located in the very center of the core of the tree on living branches of small diameter. As a rule, there are several castes with a brood in all the nests studied, but no females are found. Apparently, mature *Gesomyrmex* Mayr colonies live in several nests at the same time, and nests with females were simply not found. Interestingly, all castes have compound eyes with the same surface area, so workers have disproportionately large eyes due to their much smaller heads. The eyes seem smaller in soldiers, and even more so in supersoldiers and females, whose heads are at least twice as long. Considering that the rectangular head of supersoldiers and females is filled with mandibular muscles, this indicates the ability of both castes to chew hard living wood. On the contrary, workers have thinner elongated mandibles with sharp teeth, which are more adapted to capture prey. Presumably, the female founder chews through the entrance tunnel in the living wood, and then blocks the entrance for a while until the colony gets stronger in order to produce the first soldiers. Soldiers actively forage in the afternoon in the treetops. Supersoldiers have never been seen or collected outside the nests. They exhibit similar behaviour to females: they stay inside the nest chambers and block the entrances,



Figs 3. Four species of ants in one piece of Baltic amber. 1 — †*Yantaromyrmex geinitzi* (Mayr, 1868) (red); 2 — †*Lasius schiefferdeckeri* (Mayr, 1868) (yellow); 3 — †*Ctenobethylus goepperti* (Mayr, 1868) (violet); 4 — †*Dolichoderus* cf. *balticus* (Mayr, 1868) (blue); 5 — Diptera, Brachycera (green) (also see SM 1).

Рис. 3. Муравьи четырёх видов в одном куске Балтийского янтаря. 1 — †*Yantaromyrmex geinitzi* (Mayr, 1868) (красный); 2 — †*Lasius schiefferdeckeri* (Mayr, 1868) (жёлтый); 3 — †*Ctenobethylus goepperti* (Mayr, 1868) (фиолетовый); 4 — †*Dolichoderus* cf. *balticus* (Mayr, 1868) (синий); 5 — Diptera, Brachycera (зелёный) (также смотрите приложение SM 1).

as well as gnaw the entrance holes when building other nests belonging to the same colony. Supersoldiers also store nutrients (trophic eggs) in their abdomen [Peeters et al., 2017].

Formica Linnaeus, 1758 — a large holarctic genus that are common in many northern temperate areas, but unexpectedly we met twice together with †*Gesomyrmex hoernesi* Mayr in the Baltic amber.

An interesting find, shown in Figs 3 and SM 1, is a small piece of Baltic amber (KAM 8, collection of the Kaliningrad Amber Museum) containing ants of four different species, three of which are dominant in the Eocene amber forest (†*C. goepperti*, †*L. schiefferdeckeri*, †*Y. geinitzi*) and one specimen of the most abundant genus in terms of species diversity (26 species) in European Eocene ambers, *Dolichoderus* Lund, 1831. Perhaps, they got into the resin on the trail while visiting the aphid colony.

It is interesting how various recent faunogenetic components coexisted. How did their ecological diversification occur in the Late Eocene? Eusyninclusions of ants in the presented amber indicate a mixed character of biotopes in the late Eocene of Europe.

Supplementary Materials

The following supporting information can be downloaded at Zenodo: https://doi.org/10.5281/zenodo.11536172.

Video S1 of 3D model of a small piece of Baltic amber (KAM 8) containing four different ant species.

Acknowledgements

We dedicate this work to the 300th anniversary of Saint Petersburg State University, to our Alma mater with gratitude for the support of our research. The authors are deeply grateful to Dr. Lyudmila Kryuchkova (Saint Petersburg State University) for permanent help with microtomographic scanning of our specimens. We are grateful to our colleagues Dr. Andranik Manukyan and Dr. Anna Smirnova (Kaliningrad Amber Museum). We are thankful to Konstantin Andrushchenko (Kaliningrad) and Jonas Damzen (Lithuania) for providing fossil specimens for the study. We are thankful to anonymous referees for their useful suggestions and comments to the manuscript.

This work was supported by the Ministry of Science and Higher Education of the Russian Federation in accordance with agreement No. 075-15-2022-322 date 22 April 2022 on providing a grant in the form of subsidies from the Federal budget of Russian Federation. The grant was provided for state support for the creation and development of a World-class Scientific Centre «Agrotechnologies for the Future».

References

Archibald S.B., Farrell B.D. 2003. Wheeler's dilemma // Acta Zoologica Cracoviensia. Vol.46. Supplement Fossil Insects. P.17–23.

Daley B. 1972. Some problems concerning the Early Tertiary climate of southern Britain // Paleogeography, Paleoclimatology, Paleoecology. Vol.11. No.3. P.177–190.

Dlussky G.M. 2009. The ant subfamilies Ponerinae, Cerapachyinae and Pseudomyrmecinae (Hymenoptera, Formicidae) in the Late Eocene ambers of Europe // Paleontological Journal. Vol.43. No.9. P.1043–1086.

Dlussky G.M. 2012. New fossil ants of the subfamily Myrmeciinae (Hymenoptera, Formicidae) from Germany // Paleontological Journal. Vol.46. No.3. P.288–292. https://doi.org/10.1134/S0031030111050054

Dlussky G.M., Wappler T., Wedmann S. 2009. Fossil ants of the genus *Gesomyrmex* Mayr (Hymenoptera, Formicidae) from the Eocene of Europe and remarks on the evolution of arboreal ant communities // Zootaxa. Vol.2031.No.1. P.1–20.

Dubovikoff D.A. 2004. [A new species of the genus *Gesomyrmex* Mayr, 1868 (Hymenoptera: Formicidae) from Vietnam] // Trudy Russkogo Entomologicheskogo Obshchestva. Vol.75. No.9. P.219–221. [In Russian].

Hölldobler B., Taylor R.W. 1983. A behavioral study of the primitive ant *Nothomyrmecia macrops* Clark // Insectes Sociaux. Vol.30. No.4. P.384–401.

Iakovleva A.I., Aleksandrova G.N., Mychko E.V. 2022. Late Eocene (Priabonian) dinoflagellate cysts from Primorsky quarry, southeast Baltic coast, Kaliningrad Oblast, Russia // Palynology. Vol.46 No.2. P.1–40. https://doi.org/10.1080/01916122.2021.1980743

Koteja J. 1996. Syninclusions // Inclusions Wrostek. No.22. P.10–12.

LaPolla J.S. 2005. Ancient trophophoresy: a fossil *Acropyga* from Dominican amber // Transactions of the American Entomological Society. Vol.131. P.21–28.

Peñalver E., Arillo A., Delclòs X., Peris D., Grimaldi D.A., Anderson S.R., Nascimbene P.C., Fuente R.P. 2017. Ticks parasitised feathered dinosaurs as revealed by Cretaceous amber assemblages // Nature Communications. Vol.8. No.1924. P.1–13. https://doi.org/10.1038/s41467-017-01550-z

Perkovsky E.E. 2018. Only half of Rovno amber Hymenoptera fauna is common with Baltic amber // Vestnik Zoologii. Vol.52. No.5. P.353–360. https://doi.org/10.2478/vzoo-2018-0037

Peeters C., Ito F., Wiwatwitaya D., Keller R., Hashim R., Molet M. 2017. Striking polymorphism among infertile helpers in the arboreal ant *Gesomyrmex* // Asian Myrmecology. Vol.9. No.e009015. P.1–15. https://doi.org/10.20362/am.009015

Radchenko A.G., Perkovsky E.E. 2021. Wheeler's dilemma revisited: first *Oecophylla — Lasius* syninclusion and other ants syninclusions in the Bitterfeld amber (late Eocene) // Invertebrate Zoology. Vol.18. No.1. P.47–65. https://doi.org/10.15298/invertzool.18.1.05

Solórzano-Kraemer M.M., Peñalver E., Herbert M.C.M., Delclòs X., Brown B.V., Aung N.N., Peretti A.M. 2023. Necrophagy by insects in Oculudentavis and other lizard body fossils preserved in Cretaceous amber // Scientific Reports. Vol.13. No.2907. https://doi.org/10.1038/s41598-023-29612-x

Westerhold T., Marwan N., Drury A.J., Liebrand D., Agnini C., Anagnostou E., Barnet J.S., Bohaty S.M., Vleeschouwer D., Florindo F., Frederichs T., Hodell D.A., Holbourn A.E., Kroon D., Lauretano V., Littler K., Lourens L.J., Lyle M., Pälike H., Röhl U., Tian J., Wilkens R.H., Wilson P.A., Zachos J.C. 2020. An astronomically dated record of Earth's climate and its predictability over the last 66 million years // Science. No.369. P.1383–1387. https://doi.org/10.1126/science.aba6853

Wheeler W.M. 1910. Ants, their structure, development and behavior // Columbia University Biological Series. New York: Columbia University Press. Vol.9. 663 p.

Wheeler W.M. 1915. The ants of the Baltic Amber // Schriften der Physikalisch-okonotnischen Gesellschaft zu Konigsberg.Vol.55. P.1–142.

Wolfe A.P., MCkellar R.C., Tappert R., Sohdi R.N., Muehlenbachs K. 2016. Bitterfeld amber is not Baltic amber: Three geochemical tests and further constraints on the botanical affinities of succinite // Review of Palaeobotany and Palynology. Vol.225. P.21–32. https://doi.org/10.1016/j.revpalbo.2015.11.002

Zachos J., Pagani M., Sloan L., Thomas E., Billups K. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present // Science. Vol.292. No.5517. P.686–693.

Поступила в редакцию 3.9.2024