

Wheeler’s dilemma revisited: first *Oecophylla*–*Lasius* syninclusion and other ants syninclusions in the Bitterfeld amber (late Eocene)

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ABSTRACT. The first syninclusions of extant tropical and Holarctic ant genera are reported from Bitterfeld amber: the tropical *Oecophylla* F. Smith (*O. brischkei* Mayr, 1868) with the Holarctic genus *Lasius* F. (four workers of *L. schiefferdeckeri* Mayr, 1868), and others. The ratio of tropical and Holarctic ants in Bitterfeld, Baltic, Rovno and Danish ambers is analyzed; Holarctic ants dominate in all ambers, consistent with late Eocene climate. *Oecophylla*, *Lasius* and the temperate extant Palaearctic caddisfly genus *Beraeodes* Eaton are dominant as compression fossils in the terminal Eocene Bembridge Marls, UK. Syninclusions of *Oecophylla* with *Lasius*, as well as syninclusions of *Beraeodes* with *Yantaromyrmex* Dlussky et Dubovikoff, 2013 in Rovno amber, are consistent with an equable climate of the late Eocene amber forests of Europe. The cooccurrence of *Oecophylla*, *Lasius* and *Beraeodes* at the terminal Eocene in the Bembridge Marls supports a late Eocene age of European ambers. The coexistence of *Oecophylla* and *Lasius* in Europe was possible only from the late Eocene to the late Miocene: until the late Eocene, the climate in European middle latitudes was too hot for aphids, the obligate symbionts of *Lasius*, but after the late Miocene it became too cold for *Oecophylla*. The dominance of *Oecophylla* in the periodically flooded terminal Eocene Bembridge environment might be explained by its arboreal lifestyle providing a competitive advantage over terrestrial *Formica* species, for which nesting places were quite limited under these conditions.

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KEY WORDS: age of Baltic amber, Priabonian, paleoclimate, Europe, palaeontology, Bembridge, *Formica*, *Beraeodes*.

Возвращение к дилемме Вилера: первый сининклюд *Oecophylla* и *Lasius* и другие сининклюды муравьёв в саксонском янтаре

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РЕЗЮМЕ. Впервые приведены сведения о сининклюдзах современных тропических и голарктических родов муравьёв из саксонского янтара: тропического *Oecophylla* F. Smith (рабочий *O. brischkei* Mayr, 1868) с голарктическим *Lasius* F. (четыре рабочих *L. schiefferdeckeri* Mayr, 1868), а также из других родов. Проанализировано соотношение тропических и голарктических муравьёв в саксонском, балтийском, ровенском и датском янтарях; голарктические муравьи доминируют во всех янтарях, что соответствует климату позднего эоцена. *Oecophylla*, *Lasius* и ныне живущий в палеарктических регионах с умеренным климатом род ручейников *Beraeodes* Eaton доминируют в отпечатках из терминального эоцена Бембриджа, Великобритания. Сининклюды *Oecophylla* с *Lasius*, а также *Beraeodes* с *Yantaromyrmex* Dlussky et Dubovikoff, 2013 в ровенском янтаре говорит об эквабельном климате янтарных лесов Европы в позднем эоцене. Совместное обитание *Oecophylla*, *Lasius* и *Beraeodes* в Бембридже также свидетельствует в пользу позднеэоценового возраста европейских янтарей. Существование *Oecophylla* и *Lasius* в Европе было возможным только с позднего эоцена до позднего миоцена: до позднего эоцена климат в европейских средних широтах был слишком жарким для тлей, облигатных симбионтов *Lasius*, но после позднего миоцена стал слишком холодным для *Oecophylla*. Преобладание *Oecophylla* в периодически затопляемых местообитаниях Бембриджа в самом конце эоцена может быть объяснено древесным образом жизни экофилл, обеспечивающим конкурентные преимущества перед наземными видами *Formica*, места для гнездования которых в этих условиях были весьма ограничены.

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КЛЮЧЕВЫЕ СЛОВА: возраст балтийского янтара, приабон, палеоклимат, Европа, палеонтология, Бембридж, *Formica*, *Beraeodes*.

Introduction

More than century ago Wheeler (1910) drew attention to the unusual mixed character of the ant fauna of Baltic amber, which includes both modern temperate and tropical genera. He later divided the amber ant genera into two groups: “those which are today represented in Europe and Siberia and those either belonging to the Indomalayan and Australian fauna, or with more or less pronounced affinities to this latter fauna... we are able to recognize at least four different faunas, the palearctic, the Indian, the Malayan and the Australian” (Wheeler, 1915: 12). Such a combination of temperate (“Holarctic” according Dlussky, Rasnitsyn, 2009; Perkovsky, 2011a, 2016) and tropical genera in the same habitats is not known today.

Wheeler (1915) proposed two hypotheses to explain these cooccurrences: 1) the amber was created over a long interval during the late Eocene, and tropical ant genera existed there earlier, when the climate was warmer, and temperate ones later, after the climate cooled; 2) the amber has the same geological age, but the tropical genera lived in hot lowlands and temperate ones in cooler regional uplands, from where resin was carried down by streams and then redeposited on the same territory as “lowland” resin. Both hypotheses are rejected now.

The second hypothesis assumes the presence of rather high mountains in the places where amber forests grow. However, such regional mountains at that time were only in Scandinavia, and these were much lower than now, as their secondary uplift wasn't until the Neogene (Ollier, Pain, 2019). Daley (1972), examining this climatic mixture in the late Eocene flora of southern England, rejected the two elevations hypothesis as such mountains would have had to exceeded 2000 m above sea level, incompatible with paleotopographic reconstructions.

Daley (1972) hypothesized a late Eocene central and northern European climate with no present day analogue. Late Eocene global mean annual temperatures (MAT) were around 5 °C warmer than today (Westerhold *et al.*, 2020).

The climate had much less seasonal temperature fluctuation, lacking winter frost, rainfall was higher than that of today, and MAT were higher, though not as high as those in modern tropical rain forests (Daley, 1972). Archibald & Farrell (2003) called such climate “more equable”, i.e., not completely seasonless, but with reduced thermal seasonality compare to modern temperate regions, with higher mean temperature of cold months allowing plant and animal taxa excluded from extra-tropical regions today by cold winters, not by lack of heat, to extend their ranges into milder mid-latitudes.

The hypotheses that the amber was formed in the same place at different geological times or at different elevations are refuted by the cooccurrences (syninclusions) of insects and other invertebrates in the same piece of amber. The term syninclusions was proposed by Koteja (1989), who proposed their usefulness as an instrument of scientific inquiry. Syninclusion analysis has come to be widely used by paleobiologists as a key means for studying the structure of the biocenoses of ancient amber forests (Kutscher, Koteja, 2000; Sontag, 2003; Perrihot, Girard, 2009; Weitschat, 2009; Wichard, 2009; Coty *et al.*, 2014). We have widely used this approach, especially in the study of ant-homopteran syninclusions first from Rovno amber, then from Bitterfeld, Baltic and Danish ambers (Perkovsky *et al.*, 2007, 2010, 2012; Perkovsky, 2006, 2007a, b, 2008a, b, 2009a, b, 2010, 2011b, 2013a).

Material and Methods

We investigated ants from Bitterfeld amber from the collection of Zoological Museum of Humboldt University, Berlin, and collection of Mr. Manfred Kutscher, Sassnitz, Rügen, Germany, preserved at the Geowissenschaftlicher Zentrum der Georg-August-Universität Göttingen. Detailed data on these ant collections are given by Dlussky & Rasnitsyn (2009).

The original photographs were taken with Leica Z16 APO stereomicroscope equipped with Leica DFC 450 camera and processed by LAS Core software (E.V. Martynova) and Leica

M165C stereomicroscope equipped with Leica DFC 420 camera and processed by LAS Core software (A.P. Rasnitsyn).

Results

Thirty-five of the 68 ant genera known from the late Eocene European ambers are extant, and 17 of 41 (Dubovikoff *et al.*, 2020) are extinct in Bitterfeld amber (61 species, all are extinct). The characterization of ants in Baltic, Rovno, Bitterfeld and Danish ambers as Holarctic or tropical was partially considered by Dlussky & Rasnitsyn (2009) and Perkovsky (2011a, 2016).

The extant ant genera and species groups found in Bitterfeld amber that we classed as Holarctic are (number of species in species group in parentheses): *Formica* Linnaeus, 1758, *Lasius* Fabricius, 1804, *Camponotus mengei* Mayr, 1858, *Prenolepis* Mayr, 1861, *Plagiolepis pygmaea* species-group (three) (Formicinae), *Dolichoderus quadripunctatus* species-group (two) (Dolichoderinae), *Aphaenogaster* Mayr, 1853, *Temnothorax* Mayr, 1861, *Myrmica* Latreille, 1804 (Myrmicinae).

We grouped the following extant genera or species-groups as tropical: *Gesomyrmex* Mayr, 1868, *Oecophylla* F. Smith, 1869, *Pseudolasius* Emery, 1887 (Formicinae), *Tapinoma* Foerster, 1850, *Technomyrmex* Mayr, 1872, *Dolichoderus thoracicus* species-group, *D. scabridus*, *D. cuspidatus*, and *D. sulcaticeps* species-groups (Dolichoderinae), *Carebara* Westwood, 1840, *Pristomyrmex* Mayr 1866 (Myrmicinae), *Tetraponera* F. Smith, 1852 (Pseudomyrmecinae), *Gnamptogenys* Roger, 1863 (Ectatomminae), *Pachycondyla* F. Smith, 1858 (Ponerinae).

Temnothorax is among the most speciose extant ant genera, comprising more than 400 species today, distributed worldwide except for Australia, most of which are Holarctic. Only six species are known from the Afrotropical Region, all belonging to the Mediterranean species groups (Prebus, 2015); *Temnothorax* species inhabit southern China, the Himalayas and in northern mountains of Vietnam and Myanmar; though they are very diverse in Central Ameri-

ca, they do not penetrate into South America except in the extreme north-western edge of Columbia (Prebus, 2017). *Temnothorax* species are nearly absent in the vast Eurasian taiga (except in the southern Russian Far East). They are found north to southern Sweden and Finland, and are most diverse and abundant in much warmer deciduous and mixed forests, and in regions of Mediterranean vegetation from the Atlantic to Central Asia. They generally avoid true deserts. Therefore, Palearctic *Temnothorax* species are characterized as mesophylic or meso-thermophilic dwellers of various types of warm forests or open landscapes. They nest in soil, under stones, in rock crevices, leaf litter, and many are typically arboreal.

Six fossil *Temnothorax* species have been previously described in Baltic amber (see Wheeler, 1915), and at least 10 new species have not yet been described in Baltic and other late Eocene European ambers (Radchenko, unpublished data). All of these belong to, or are at least potentially related to extant species from various Palearctic species-groups of the genus, but in any case they are not more closely related to the Central America species. Therefore, here we consider *Temnothorax* species from European ambers to be Holarctic.

Camponotus Mayr, 1861 is one of the most diverse of ant genera, with more than 1000 species, second only to *Pheidole* Westwood, 1839 (Bolton, 2020). It has a worldwide distribution (except Antarctica), both in the Temperate Zone and in the tropics. Nevertheless, only one described species, *C. mengei*, is known from all late Eocene European ambers. Mayr (1868) assumed that it is related to extant *C. sylvaticus* (Olivier, 1792) from the subgenus *Tanaemyrmex* Ashmead, 1905 distributed in South Europe, but Wheeler (1915) questioned this. We agree with Wheeler and suppose that *C. mengei*, by the shape of the head, mesosoma and especially clypeus, more closely resembles species of the modern subgenus *Camponotus* s.str., which are distributed in the Holarctic Subboreal Zone.

The genus *Aphaenogaster* includes more than 200 extant species, distributed in the south-

ern Palaearctic, the Oriental Region, Australia, the Nearctic, the Neotropics (Mexico and Central America), and Madagascar, but it is absent in the Afrotropical Region. About half of them are known from the Palaearctic. More than 20 fossil species were previously attributed to this genus, but Radchenko and Perkovsky (2016) reduced this number to nine, and proposed to transfer the other eleven to the morphogenus *Paraphaenogaster* Dlussky, 1981. Recently, Jessen (2020) described a further *Aphaenogaster* species from the late Oligocene deposits of Enspel (Germany). All of these *Aphaenogaster* fossils were found in Eurasia and America, mostly from the late Eocene (European ambers and Florissant) and middle Miocene (Dominican and Mexican ambers). The oldest described *Aphaenogaster* (and oldest described Myrmicinae species) is from middle Eocene Sakhalinian amber (Radchenko, Perkovsky, 2016). All *Aphaenogaster* species from late Eocene European ambers and Florissant (latest Eocene) are similar to those of the extant Holarctic former subgenus *Attomyrma* Emery, 1915 (Radchenko, Perkovsky, 2016), and so we consider the European amber *Aphaenogaster* species Holarctic.

In the generic revision of modern Ponerinae (Schmidt, Shattuck, 2014), the taxonomic status of *Pachycondyla* was reassessed and many generic names were restored from synonymy. As a result, *Pachycondyla* is now considered Neotropical with some species in the southern Nearctic. The taxonomic position of all fossil species previously attributed to *Pachycondyla* (Dlussky, 2009; see also Schmidt, Shattuck, 2014) need thorough revision.

The cosmopolitan genus *Tapinoma* has more than 70 extant species, 17 of which are distributed in the Palaearctic, and only two in the Nearctic. Two fossil species described from late Eocene European ambers are close to modern Oriental species (Dlussky, Perkovsky, 2002; Dubovikoff, 2012), and we consider amber *Tapinoma* tropical.

We find it somewhat difficult to attribute extinct amber species of the extant genera *Nylanderia* Emery, 1906, *Ponera* Latreille, 1804,

Hypoponera Santschi, 1938 and *Monomorium* Mayr, 1855 as well as two *Plagiolepis* Mayr, 1861 species, to Holarctic or tropical groups for the following reasons.

Nylanderia is cosmopolitan, with 125 extant and two extinct species: *N. pygmaea* (Mayr, 1868) from late Eocene European ambers, and one from Miocene Dominican amber. Most of its extant species are distributed in tropical regions; some are typical tramp species, introduced to all continents. Seventeen native species are known from the Nearctic and five from the Palaearctic (North Africa, Transcaucasia, the Middle East, China, Korea, and Japan), but no native *Nylanderia* species are known from Europe (Pisarski, 1960; LaPolla *et al.*, 2010; LaPolla, Dlussky, 2010; Kallal, LaPolla, 2012; Messer *et al.*, 2016; Bolton, 2020). Since the internal phylogeny of *Nylanderia* has not yet been examined, it is difficult to characterize *N. pygmaea* as tropical or Holarctic, only that it is not related to extant Nearctic species-groups. However, the ecological preferences of most modern tropical species appear analogous to that of *N. pygmaea* in the amber forests. Based on this assumption as well by zoogeographic data, we place *N. pygmaea* in the tropical group.

Hypoponera is one of the most diverse ponerine genera, with more than 150 described extant species, but there may be many more. They are distributed predominately in all tropical regions, but eight native species are found in the Palaearctic (four in the Mediterranean Region from the Atlantic to the Transcaucasia, and four in China, Korea and Japan), and one in the Nearctic (Schmidt, Shattuck, 2014). Its single known fossil species, *H. atavia* (Mayr, 1868), is one of 19 ant species found in all late Eocene European ambers (Perkovsky, 2016). Its affinities to modern species remain unknown, but we tentatively place it in the tropical group.

The genus *Ponera* presents a similar situation. It currently has 60 extant species, mostly distributed in the Oriental Region and Australia, but absent in the Afrotropical and Malagasy Regions and in the Neotropics (but some species penetrating Central America from the north). Only six species are known in the Palaearctic

(three from Europe, the Mediterranean Region, the Near East and Transcaucasia, and three from China, Korea and Japan), and two species from the Nearctic. Three species from late Eocene European ambers were recently described by Dlussky (2009) based exclusively on males. Nothing can be said about the relationship of these fossil species to extant species, but by analogy with *Hypoponera*, we propose to consider them as tropical.

Dlussky (2010) attributed *Plagiolepis* species from late Eocene European ambers to two species-groups: the modern Palaearctic *pygmaea*-group (we considered them Holarctic, see above), and the extinct *klinsmanni* species-group. Members of the latter group are characterized by their nodiform petiole, unique among all known *Plagiolepis* species. Most likely they represent an extinct specialized branch of the genus, adapted to conditions of the amber forests, and we doubt they can be assigned to either the tropical or Holarctic groups.

Monomorium is among the most speciose of myrmicine genera, with more than 300 extant species (Bolton, 2020). Its greatest diversity occurs in the Afrotropical and Malagasy Regions (more than half of known species), and in Australia; they are also abundant in the Oriental Region, as well in the southern, semiarid, arid and subtropical parts of Palaearctic (about 50 species are recorded from here, see Radchenko, 2016), but their Neotropical and Nearctic faunas are much less diverse (Bolton, 1987). Three extinct species were described from late Eocene European ambers (Radchenko, Perkovsky, 2009), two of them among the most common amber ants. Nevertheless, it is impossible at this time to make a definitive conclusion on the relatedness of these species with any modern ones, and so we cannot attribute any of them to either the “Holarctic” or “tropical” group.

It is often much more difficult or even impossible to classify extinct amber genera as tropical or Holarctic.

Nevertheless, Dlussky & Rasnitsyn (2009) and Perkovsky (2011a, 2016) provided justifications for including the genera *Yantaromyrmex* Dlussky et Dubovikoff, 2013 (Dolichoderinae),

Procerapachys Wheeler, 1915 (Dorylinae), *Paraneuretus* Wheeler, 1915, *Protaneuretus* Wheeler, 1915 (Aneuretinae), *Prionomyrmex* Mayr, 1868 (Myrmeciinae), *Fallomyrma* Dlussky et Radchenko, 2006 (Myrmicinae) and *Bradoponera* Mayr, 1868 (Proceratiinae) in the tropical group.

Here we consider the genera *Conoformica* Dlussky, 2008 (Formicinae) and *Eocenomyrma* Dlussky et Radchenko, 2006 (Myrmicinae) as Holarctic by the following reasons: *Conoformica* belongs to the tribe Formicini, all extant members of which are distributed almost exclusively in the Holarctic (Dlussky, 2008), and *Eocenomyrma* is related to the genus *Temnothorax* (Radchenko, Dlussky, 2016).

Finally, we find it difficult to attribute fossil *Ctenobethylus* Brues, 1939, *Eldermyrmex* Shattuck, 2011, *Zherichinius* Dlussky, 1988 (Dolichoderinae), *Electromyrmex* Wheeler, 1915, *Enneamerus* Mayr, 1868, *Stigmomyrmex* Mayr, 1868 and *Plesiomyrmex* Dlussky et Radchenko, 2009 to either groups.

As above, the study of ant (and other invertebrate) syninclusions is very important for analyses of the taxonomic and ecological structures of amber faunas, and are especially important in understanding their implications as tropical and Holarctic taxa.

Already Wheeler (1915) reported 10 ant syninclusions from Baltic amber and stressed that “simultaneous inclusion could only have occurred in the case of forms living at precisely the same time and place” (op. cit.: 15). Though they did not include a mix of definitely tropical and Holarctic ant genera, five syninclusions with *Ctenobethylus goepperti* (Mayr, 1868) contain Holarctic *Dolichoderus tertiaris* (Mayr, 1868), *Myrmica rudis* (Mayr, 1868), *Lasius schiefferdeckeri* Mayr, 1868, *Formica flori* Mayr, 1868 and *Cataglyphoides constrictus* (Mayr, 1868), while two other include *C. goepperti* with tropical *Yantaromyrmex geinitzi* (Mayr, 1868) and *Gesomyrmex hoernesi* Mayr, 1868 (names of species and genera are given according to modern taxonomy). The remaining three syninclusions contain only Holarctic or only tropical genera.

Table 1. Ant syninclusions in Bitterfeld amber.
Таблица 1. Сининклюзы муравьёв в саксонском янтаре.

Museums, numbers	Species	Castes, specimens	Species	Castes, specimens
HMB 7/235	<i>Ctenobethylus goepperti</i>	1 w	<i>Lasius schiefferdeckeri</i>	1 w
HMB 10/205	<i>Ctenobethylus goepperti</i>	1 w	<i>Lasius schiefferdeckeri</i>	1 w
HMB 12/201	<i>Yantaromyrmex geinitzi</i>	1 w	<i>Temnothorax gracilis</i>	1 g, 1 m
HMB 12/225	<i>Myrmica</i> sp.n.	1 w	<i>Plagiolepis kuenowi</i>	1 w
HMB 12/227	<i>Temnothorax</i> sp.n.	1 w	<i>Yantaromyrmex geinitzi</i>	2 w
HMB 14/208	<i>Monomorium pilipes</i>	1 w	<i>Tapinoma electrinum</i>	1 w
HMB 14/211	<i>Formica flori</i>	1 w	<i>Lasius schiefferdeckeri</i>	1 w
HMB 15/222	<i>Formica flori</i>	1 w	<i>Monomorium mayrianum</i>	1 w
HMB 16/215	<i>Ctenobethylus goepperti</i>	1 w	<i>Monomorium mayrianum</i>	1 w
HMB 16/266	<i>Ctenobethylus goepperti</i>	1 w	<i>Plagiolepis squamifera</i>	1 w
HMB 7/235	<i>Ctenobethylus goepperti</i>	1 w	<i>Lasius schiefferdeckeri</i>	1 w
GZG.BST.27.016	<i>Gnamptogenys europea</i>	1 m	<i>Nylanderia pygmaea</i>	6 m
GZG.BST.27.040	<i>Ctenobethylus goepperti</i>	1 w	<i>Nylanderia pygmaea</i>	5 m
GZG.BST.27.053	<i>Formica flori</i>	1 w	<i>Ctenobethylus goepperti</i>	3 w
GZG.BST.27.063	<i>Lasius schiefferdeckeri</i>	4w	<i>Oecophylla brischkei</i>	1 w
GZG.BST.27.090	<i>Monomorium pilipes</i>	1 w	<i>Yantaromyrmex geinitzi</i>	1 w
GZG.BST.27.101	<i>Bradoponera meyeri</i>	1 w	<i>Formica flori</i>	1 w
GZG.BST.27.157	<i>Ctenobethylus goepperti</i>	2 w	<i>Tetraponera simplex</i>	1 w

More than 60 ant syninclusions are known in late Eocene European ambers, including those with *L. schiefferdeckeri* reported by Dlussky (2011); 20 of these are from Bitterfeld amber (Dlussky, pers. comm., 2013) (Table 1).

Five syninclusions from Bitterfeld amber contain both tropical and Holarctic ants: two of

Y. geinitzi with *Temnothorax gracilis* (Mayr, 1868), *Y. geinitzi* with *Temnothorax* sp. nov., *Oecophylla brischkei* Mayr, 1868 with *L. schiefferdeckeri* (Fig. 1), and *Bradoponera meyeri* Mayr, 1868 with *F. flori*. Two contain only Holarctic species: a *F. flori* with *L. schiefferdeckeri* and *Myrmica* sp.n. with *Plagiolepis*

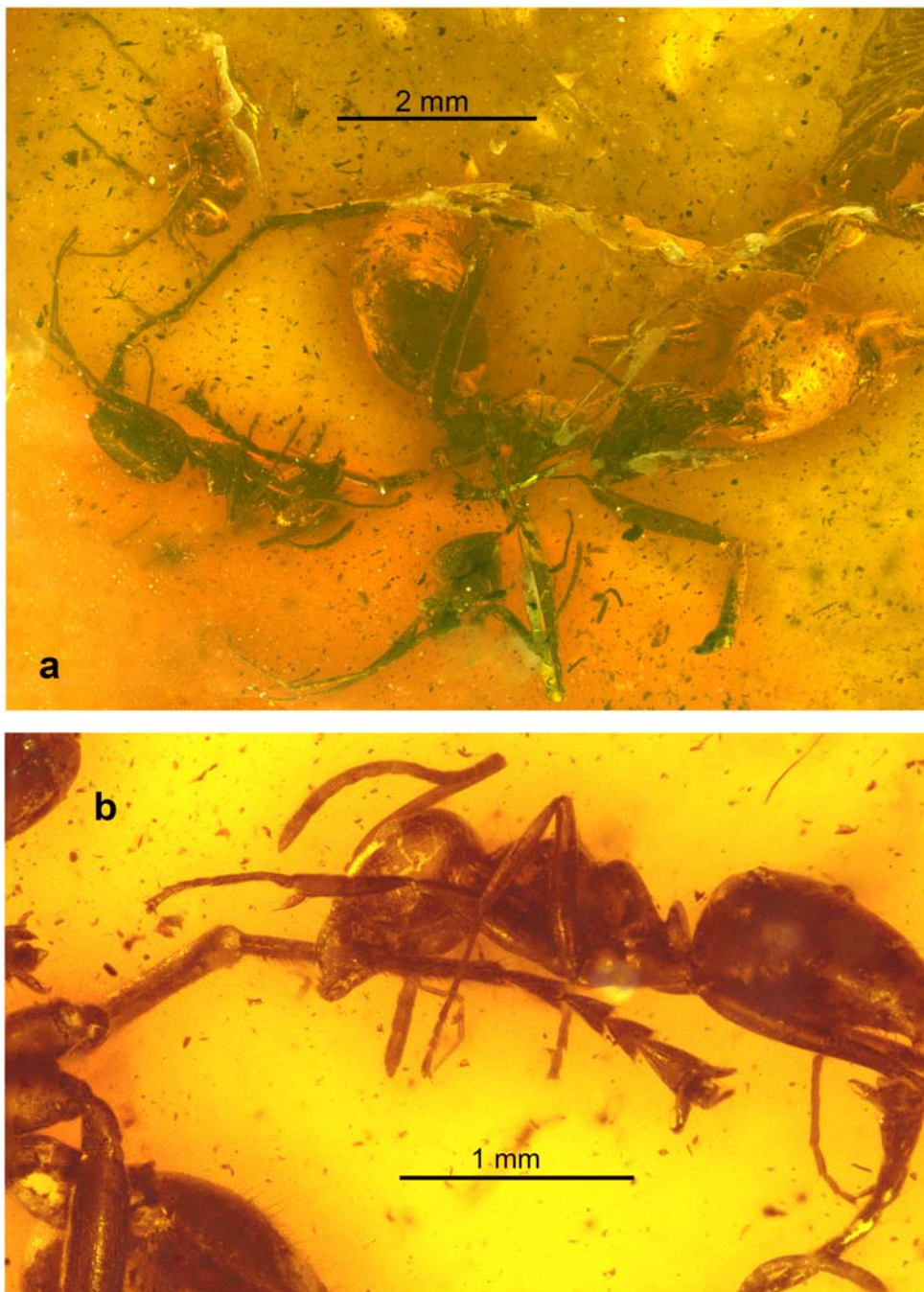


Fig. 1. Photo of syninclusion of *Oecophylla brischkei* and *Lasius schiefferdeckeri*; a — general appearance (photo by E.V. Martynova), b — detail, *L. schiefferdeckeri*, biting leg of *Oecophylla* (photo by A.P. Rasnitsyn); Bitterfeld amber, No. GZG.BST.27.063a.

Рис. 1. Фото сининклюдоза *Oecophylla brischkei* и *Lasius schiefferdeckeri*; а — общий вид (фото Е.В.Мартыновой), б — деталь, *L. schiefferdeckeri*, кусающий *Oecophylla* за ногу (фото А.П. Расницына); саксонский янтарь, No. GZG.BST.27.063a.

Table 2. Number of specimens of Holarctic and tropical s.l. ants in the representative amber collections.
Таблица 2. Число экземпляров голарктических и тропических s.l. муравьёв в репрезентативных янтарных коллекциях.

Amber	Collection	Holarctic	Tropical s.l.	Holarctic/ Tropical
Baltic (Russia)	PIN-964	186 (41.7%)	64 (14.4%)	2.90
Baltic (Poland)	Giecwicz	157 (36.9 %)	41 (9.6%)	3.83
Bitterfeld	HMB	244 (35.4%)	111 (16.2%)	2.21
Danish	ZMUC-S	142 (41%)	64 (18.5%)	2.22
Rovno	SIZK	457 (40%)	194 (17%)	2.36

kuenowi Mayr, 1868. One contains only tropical ants: *Gnamptogenys europea* (Mayr, 1868) with *N. pygmaea*.

As in the syninclusions with *Ctenobethylus* reported by Wheeler (1915) (see above), four pieces of amber contain *C. goepperti* with Holarctic species: three with *L. schiefferdeckeri* and one with *F. flori*, but three include *C. goepperti* with the tropical species *N. pygmaea*, *Tetraponera simplex* (Mayr, 1868) and *Dolichoderus passaloma* Wheeler, 1915. Two syninclusions with *Monomorium pilipes* Mayr, 1868 contain tropical genera: *Tapinoma electrinum* Dlussky, 2002 and *Y. geinitzi*, and one of *M. mayrianum* Wheeler, 1915 is with *F. flori* and another one is with *C. goepperti*.

Thus, regardless of whether *Ctenobethylus* and *Monomorium* are considered Holarctic or tropical, they occur in syninclusions with species of both groups, which not only emphasizes the mixed nature of the amber fauna, giving strong support for the cooccurrence of tropical and Holarctic species at the same time and place, and these syninclusions are no less important than those containing definitely Holarctic and tropical species.

The ratio of Holarctic and tropical taxa is important for a better understanding the climatic conditions in amber forests and the age of amber biota as a whole.

After adding *Aphaenogaster*, *Temnothorax*, *C. mengei*, *Eocenomyrma* and *N. pygmaea* the ratio of Holarctic to tropical s.l. elements for representative collections is 2.8–3.5 for Baltic amber, 1.6 for Danish amber and 2.1 for both Bitterfeld and Rovno ambers (Table 2). It is

interesting that at least for two amber faunas with the same (Danish, 1.6) or very similar (Rovno, 1.9) ratios were calculated for biting midges (Ceratopogonidae): predominance of Holarctic biting midges in the representative collections from other ambers is even higher than for Holarctic ants (Perkovsky, 2017).

In the early Eocene at Messel and middle Eocene at Eckfeld, tropical taxa absolutely dominate, nearly as much as in tropical climate Oligocene Sicilian amber (Emery, 1891; Wappler, 2003; Dlussky *et al.*, 2008, 2009; Archibald *et al.*, 2011; Dlussky, 2012; Dlussky, Wedmann, 2012). The prevalence of Holarctic species in all representative amber ant collections is associated with decreasing of temperature in the late Eocene (see below). The ratio of Holarctic and tropical specimens in the former private amber ant collection of M. Kutscher from Bitterfeld amber (now in the collection of Geowissenschaftlicher Zentrum der Georg-August-Universität Göttingen) is only 0.98, but it is highly biased, containing mainly rare and ‘exotic’ ants (Dlussky, Rasnitsyn, 2009).

Discussion

Oecophylla–Lasius syninclusion is of great importance, as both genera are widely represented in both amber and compression fossils. Despite modern areas where the ranges of both genera partly overlap in the Himalaya and China, we did not find any records of their coexistence at the same site. The northern limit of *Oecophylla smaragdina* (Fabricius, 1755) extends to 34.1°N in China and 32.7°N in India,

and the vast majority of its records come from sites classified as having tropical climates (Wetterer, 2017). The highest altitudinal records of *Oecophylla* in the Himalayas reported by different authors vary from 900 (Supriya *et al.*, 2020) to 1200 (Wetterer, 2017) or even to 1150–1450 m a.s.l. (Collingwood, 1970). At the same time, *Lasius* s. str. species are distributed in southern China and in the Himalayas at higher altitudes than *Oecophylla* (Seifert, 2020). Wetterer (2017) suggested that more cold-tolerant *Oecophylla* populations from higher altitudes with subtropical climates could represent a separate species. It is interesting to note that the modern distribution of *O. smaragdina* in subtropical conditions fits well with the discovery of numerous fossil *Oecophylla* in European Oligocene and Miocene deposits (Dlussky *et al.*, 2008; Dlussky, Perfilieva, 2014; Perfilieva *et al.*, 2017). In general, 16 fossil *Oecophylla* species have been reported; as well as in Europe, one species was described from the Miocene of Kenya, and another from the early Eocene of the U.S.A. (Dlussky *et al.*, 2008; Perfilieva *et al.*, 2017).

Close mutualistic relations of not only extant but also extinct *Lasius* species with aphids and other homopteran insects are well-known: syninclusions of *Lasius* species with numerous aphids have been reported from Bitterfeld amber (Perkovsky, 2006, 2010). Modern *Oecophylla* species also actively tend homopterans (Crozier *et al.*, 2010), and one may suppose that fossil ones had similar behavior. In the syninclusion GZG.BST.27.063 (Table 1) we observe for the first time three *Lasius schiefferdeckeri* workers attacking a worker of *Oecophylla brischkei*, stretching it spread-eagle, while a fourth bites the antennal funiculus of the *Oecophylla* (and see Fig. 1). Stellate hairs in the syninclusion (Fig. 1) prove that ants got to the resin in spring. This piece of amber contains wood particles (Fig. 1), so it is likely that there may have been old fissured bark with longirostred aphids on the tree trunk nearby, which may support the idea of competition between mentioned species for honeydew.

It is necessary to discuss in more detail the presumed role of *Oecophylla* species in ecosys-

tems since Priabonian. Dlussky & Rasnitsyn (2007) suggested that they may be strongly underrepresented in late Eocene European ambers (0.95% specimens in the representative collection of Bitterfeld amber and much less in all others). They provided two possible explanations for this.

First, these ants are large, with long legs and would be more rarely trapped in the resin than smaller ants. *Oecophylla* is arboreal; its workers build nests from living broad-leaved trees, while amber was formed from the resin of conifers, where its workers are very unlikely to be found.

Secondly, while alate specimens of *Oecophylla* can be dispersed far from nests, they are very large, which may decrease their representation in amber like their workers. The forewings of gynes and males of extant species reach 8–9 mm in length, and forewings of Bitterfeld amber *O. brischkei* males were even larger (10 mm), similar to those of gynes and males of *O. megarche* Cockerell, 1915 from the UK Bembridge Marls, which have wing lengths of 20–23 and 10–16 mm, respectively (Dlussky, Perfilieva, 2014). So, the chance of their being trapped in resin would be even lower than that of the workers. Only two males of *Oecophylla* are known from the Baltic amber (Wheeler, 1915) vs. about 60 workers (Dlussky, Rasnitsyn, 2009).

However, the amber was formed in the humid and moderately well-illuminated temperate mixed forests (Sadowski *et al.*, 2017; Kaasalainen *et al.*, 2017) and *Oecophylla* could use leaves of deciduous trees for nest building. Even when the leaves become dry and detach, these nests remain attached to the branch and continue to function (Lokkers, 1990; Radchenko, personal observations).

Hypotheses explaining the presumed strong underrepresentation of *Oecophylla* in European ambers of gymnosperm origin are based mostly on their dominance as compression fossils in the Bembridge Marls. At the same time, even in the tropical-climate Oligocene Sicilian amber of angiosperm origin, *Oecophylla* comprise only 4.9% of ants (Emery, 1891), even less than in the Miocene compression fossils of Radoboj (7.4%) (Dlussky, Putyatina, 2014). *Oecophylla*

has not yet been found in Danish and Rovno ambers, and as more than 1800 amber ant specimens are now known in Rovno amber (vs. ca 1100 in Bitterfeld amber), it can be assumed that this genus was absent in the Rovno amber forests. *Oecophylla* is represented by single specimens in all European compression localities except the Bembridge Marls and at Radoboj. It seems especially important that only two specimens of *Oecophylla* (0.7% of 278 ants identified to subfamily level) are known from the localities almost coeval with Bembridge Marls, the Upper Rhine Graben of Kleinkems (Baden-Württemberg, Germany) and at Brunstatt (Alsace, France) taken together (Théobald, 1937), and only a single specimen of *Oecophylla* has been found in the late Eocene deposits of Kučhlin (Czechia) (Deichmüller, 1881).

Ants form multispecies associations (= ant assemblages) in any habitats, and the structure of these depends to a great extent on their inter- and intraspecific relations (Demchenko, 1975; Dlussky, 1981b). This is very often based on interspecific competition, and dominant species are usually decisive in setting the structure of these associations (Vepsäläinen, Pisarski, 1982; Reznikova, 1983). Dominant species as a rule have very big colonies with tens or even hundreds of thousands of workers; they have a protected foraging area (often quite large one), high dynamic density on the territory, and are usually aggressive towards other dominants (Zakharov, 1991).

Extant *Oecophylla* species are typical territorial dominant species in ant assemblages, and absence of other dominant ant species is optimal for them (Hölldobler, 1983). Furthermore, weaver ants are also quite vulnerable in extratropical regions because nests made from leaves of deciduous plants there are less durable and often need repair (Lokkers, 1990). The inability to repair a nest or build a new one due to the low activity of workers or the death larvae in winter can lead to the death of the colony.

The most important competitors of fossil *Oecophylla* in Europe (other than in the Bembridge Marls) may have been various ant species, but it is difficult to define which of them

may have been obligate or facultative territorial dominants. For example, extant *Lasius emarginatus* (Olivier, 1792) is a facultative dominant in many ant associations (Stukalyuk, 2015, 2017), and one may assume that extinct *L. schiefferdeckeri* might have been so, too. Species of the modern subgenus *Formica* s. str. are typical territorial dominants, but *F. flori*, one of the most abundant ants in late Eocene European ambers, most probably belongs to the subgenus *Serviformica* Forel, 1913. Most extant species of this subgenus are subordinate in ant communities, but some are facultative dominants (Stukalyuk, 2015) or obligate territorial dominants like *F. cinerea* Mayr, 1853 (Dlussky, 1965). Another kind of domination in ant associations is “numerical dominance”, i.e. dominance not by behavior, but exhibit territorial aggression as numerical dominants with high biomass and so increased frequency of interactions (Segev, Ziv, 2012). Such numerically dominant species have a high foraging efficiency, negatively affecting other species that utilize the same food sources.

Fossil *Oecophylla* probably consumed the honeydew of aphids and other homopterans as well as the numerous invertebrates which they hunted, and their competitors in amber forests could have been the most numerous ants: *C. goepperti*, *Y. geinitzi*, probably some *Dolichoderus*, *F. flori* (and other *Formica* species) and *L. schiefferdeckeri*.

Oecophylla species comprise 69.8% of ant specimens identified to genus level in the Bembridge Marls, and are at least 4.1 times more common there than *Lasius* (Dlussky, Perfilieva, 2014). Species of the morphogenus *Emplastus* Donisthorpe, 1920 make up 7.9% of all ants determined to the genus level, the most common species, *E. gurnetensis* (Donisthorpe, 1920), is 5% of ant specimens, and *Dolichoderus* species 0.7%. This morphogenus may include species of various dolichoderine genera, particularly *Yantaromyrmex* and *Ctenobethylus* (Dlussky, Dubovikoff, 2013; Dlussky, Perfilieva, 2014). The formicine ant *Leucotaphus gurnetensis* Cockerell, 1915 is the third most abundant species among ants of the Bembridge Marls. It comprises 25% of all ants identified to the

species level, but the second species of this genus there, *L. donistorpei* Dlussky et Perfilieva, 2014, is only a tenth as common as *L. gurnetensis*. The majority of ants in the Bembridge Marls are attributed to the morphogenus *Leucotaphus* Cockerell, 1915 most probably belong to the genus *Lasius* (Dlussky, Putyatina, 2014); e.g., *L. gurnetensis*, which is similar in general appearance to modern species of *Lasius* s.str. (Dlussky, Perfilieva, 2014).

Formica specimens outnumber those of *Oecophylla* 17 times at Brunstatt and Kleinkems, *Dolichoderus* 17.5 times, and *Ctenobethylus* and *Yantaromyrmex* taken together 11 times (Théobald, 1937). *Formica* comprise 20.9% of all ant specimens determined to species at Radoboj, 2.82 times more than *Oecophylla*, and *Lasius* specimens are 49.2%, or 6.65 times more common than *Oecophylla* specimens. The most common Dolichoderinae specimens are those of *Liometopum* Mayr, 1861, almost as plentiful as *Oecophylla* (Dlussky, Putyatina, 2014).

Formica makes up 11–12% of ants, *Dolichoderus* 4.7–5%, *L. schiefferdeckeri* Mayr 9.5–16.4%, *Ctenobethylus* and *Yantaromyrmex* together 60–69%, *Oecophylla* 0.2–0.5% in representative amber collections from Kaliningrad Province of Russia (Wheeler, 1915; our unpublished data). In the unbiased collection of Bitterfeld amber *Formica* comprises only 5.5%, *Dolichoderus* 5.3%, *L. schiefferdeckeri* 22.8%, *Ctenobethylus* and *Yantaromyrmex* together 44.9%, *Oecophylla* 0.7%. Accordingly, there are 22–64 times more *Formica* specimens than those of *Oecophylla* and *Lasius* is 21–73 times more common than *Oecophylla* in the unbiased amber collections of the Kaliningrad Region; in Bitterfeld amber *Formica* is eight times more common than *Oecophylla* and *Lasius* is 33 times more common than *Oecophylla*.

The reason for the absence of *Formica* and the relative rarity of *Lasius* in the Bembridge Marls could be ecological character of the biotope: wetland elements are abundant in the Bembridge flora and non-wetland elements infrequent (Hayes, Collinson, 2014).

Under conditions of periodic flooding, arboreal ants have an obvious advantage. Hooker

(1994) indicated that by many reasons the best analogue for the Bembridge Marls Limestone Formation is freshwater marsh environments of the Florida Everglades. The upper strata of the Bembridge Limestone Formation is thought to have been deposited 10,000 years earlier (Hooker *et al.*, 2009) than the Insect Beds, where all insects of this Lagerstätte are found (Ross, Self, 2014). If it is true and periodic flooding continued during the formation of Insect Beds, this would well explain the abundance of *Oecophylla*.

Oecophylla colonies form polycalic systems with one or a few large central nests and several peripheral smaller ones. In the winter, workers from peripheral nests move to central ones, and trees controlled by them show significant consumption even in the tropics. The opposite process occurs with the rising of temperature (Lokkers, 1990); for terminal Eocene of Bembridge it must be more pronounced.

The cold month mean temperature (CMMT) for the northernmost locality of extant *Oecophylla* in Zhoukou (Henan, China) is 1.3 °C. *Sabal* palms leaves have been found in the Bembridge Marls above the Insect Beds; CMMT for the northernmost extant locality of palms in the eastern North America (Tripp, Dexter, 2006) equals 6.1 °C. Although palms can be somewhat cold tolerant (Kupryjanowicz *et al.*, 2019 and references therein), their northern distribution is affected by the number of days between the first and last with freezing temperatures to zero (Tripp, Dexter, 2006). We presume that in equable climates the number of such days must be less than in an extant seasonal climate with palms and the same CMMT. We estimate CMMT for the Bembridge Marls as 2–5 °C (with MAT 13.3 °C, Sheldon *et al.* (2009)). Even a CMMT of 5 °C is low for a WMMT (warm month mean temperature) of 21.6 °C, but this corresponds well with an estimated CMMT of 0–3 °C for a more northern terminal Eocene site east of Iceland in the Norwegian Sea (Eldrett *et al.*, 2009). A WMMT not higher than 24.5 °C is consistent with the abundance of the caddisfly *Beraeodes* Eaton (see below), unknown from regions with a WMMT higher than 25 °C; *Beraeodes* can't

survive even in shallow running water a temperature higher than 25 °C (Ivanov, pers. com.). We presume winter activity of *Oecophylla* was very limited at Bembridge, and that attacks on them by *Lasius* likely took place on aphid colonies in the spring, when *Oecophylla* presumably would have been increasing their foraging territory after restricted winter activity.

Colonies of *Oecophylla* have so-called “no-ant land” along the borders of their protected area (Lokkers, 1990 and references therein). It is interesting to note that among 63 amber specimens of *Oecophylla*, only three are known as syninclusions: one described here, one with *Gesomyrmex* in Baltic amber (our unpublished data), and one with a minor worker of *Camponotus* (which are common prey of modern *Oecophylla*), as well as several ant fragments (Wheeler, 1915).

Oecophylla and *Lasius* as syninclusions (as well as *Yantaromyrmex* and *Beraeodes* McLachlan, 1879) are also important for confirming the Priabonian age of European ambers of gymnosperm origin.

Perkovsky (2013b) reported the syninclusion of the thermophilous ant *Iridomyrmex geintzi* (Mayr, 1868) and temperate beraeid caddisflies *Beraeodes pectinatus* Ulmer, 1912 in a piece of Rovno amber. *I. geintzi* was transferred to the extinct genus *Yantaromyrmex* (Dlussky, Dubovikoff, 2013), which we consider here also as tropical (see above). *Beraeodes* is a West Palearctic genus, comprised of a single extant species with a mostly northern distribution.

Yantaromyrmex geintzi is a quite common species in Rovno and Baltic ambers, comprising 4–6% of ant specimens in unbiased collections (Dlussky, Rasnitsyn, 2009), but only a few specimens of *B. pectinatus* are found there. *Beraeodes* dominates as 90% of caddisfly specimens in the late Eocene Bembridge Marls (Sukatsheva, 2014), where *Oecophylla* strongly dominates ants (Dlussky, Rasnitsyn, 2007; Dlussky, Perfilieva, 2014). The single extant *Beraeodes* species inhabits cold streams, the inflow to lakes, and other water bodies (Czachorowski, 1998; Corallini *et al.*, 2015), where its larvae live on exposed underwater roots of plants along

river banks and in lakes (Ivanov *et al.*, 2001). This abundance of *Beraeodes* in the Bembridge Marls does not contradict the idea of periodic flooding of soils in these habitats where *Oecophylla* dominated. Interestingly, in one of the southernmost localities of extant *Beraeodes*, the MAT is the same as is estimated for the Bembridge Marls (Corallini *et al.*, 2015).

The climate at the end of the early Eocene at Messel and middle Eocene at Eckfeld and the Oligocene in Sicily was much warmer than today with MAT estimated as 11–12 °C higher (Westerhold *et al.*, 2020). Such a climate would have been quite suitable for *Oecophylla*, but too hot for *Lasius* and its obligate symbiotic aphids (Perkovsky, Wegierek, 2018 and references therein). The climate of Messel and Eckfeld would have been too hot for *Beraeodes* as well, with an estimated MAT at least 6 °C higher than in the warmest modern locality where *Beraeodes* was found. The Priabonian climate was probably more appropriate for *Beraeodes*: its syninclusion with ants are known from Rovno amber; at least seven *Beraeodes* specimens have been found from Baltic amber (Wichard, 2013; Perkovsky, 2013b). The Bembridge Marls has a single known locality, where two *Oecophylla* and two *Beraeodes* species are found (Dlussky, Perfilieva, 2014; Sukatsheva, 2014), suggesting a combination of climatic and environmental factors unknown anywhere else.

Some tropical elements of the Bembridge Marls fauna were very peculiar. For example, two specimens of the thermophilic subfamily Gumillinae (Neuroptera) have been found there (Perkovsky, Makarkin, 2020), the single locality of where Gumillinae has been found in the Cenozoic. This subfamily is represented today by only two species known by two specimens from northern South America (Martins *et al.*, 2016). At the same time only one specimen of aberrant mastotermitid is known from Baltic amber, which is in a syninclusion with *Liometopum* (Engel *et al.*, 2007), though size of the Ypresian and Miocene *Mastotermes* Froggatt, 1897 would not have prevented their being trapped in resins (Perkovsky, Vasilenko, 2020). That is, the abundance of *Mastotermes* in Bem-

bridge (81% of all termites) (Jarzembowski, 1980) may indicate that winters there were milder in the Bembridge Marls forest than in the somewhat older Priabonian amber forests (Colombo *et al.*, 2021, fig. 26).

MAT in the middle latitudes of the North America apparently decreased by 5–9 °C from the end of the Ypresian to the end of the Priabonian (Allen *et al.*, 2020), while that of the latest Ypresian at Messel differs by 5 °C from that of Priabonian at Kučhlin (where *Oecophylla* is known) (Grein *et al.*, 2011; Kvaček, Teodoridis, 2011), and differs by 9 °C from the Bembridge Marls (latest Priabonian).

The Bembridge flora in general is an analogue of Kučhlin's, but devoid of some thermophilic elements (Hayes, Collinson, 2014). The mostly temperate Palaearctic genus *Beraeodes*, which dominates at Bembridge, also could not have spread to Ukraine before the Priabonian.

Besides in European ambers and the Bembridge Marls, *Oecophylla* and *Lasius* coexisted in Radoboj (late Serravallian, middle Miocene) and Stavropol (Vishnevaya Balka, middle Miocene) (Dlussky, Putyatina, 2014; Perfilieva *et al.*, 2017). *Oecophylla* are the most numerous ants in the Bembridge Marls assemblage with 69.8% of all ants identified to the genus level, in Radoboj *Oecophylla obesa* (Heer, 1849) it is 7.4%, but *Formica* and *Lasius* taken together are 72% of all ants identified to genus (Dlussky, Putyatina, 2014). *Oecophylla* is also several times less abundant than *Lasius* in Stavropol (Dlussky, 1981a; Perfilieva *et al.*, 2017). The coexistence of *Oecophylla* and *Lasius* appears possible when winters were mild and summers were not very hot, i.e. when the climate was equable. Since two *Oecophylla* species coexisted only in the Baltic and Bitterfeld amber forests and Bembridge, Priabonian climate seemed to provide opportunities for diversification of *Oecophylla*.

Both *Oecophylla* and *Beraeodes* dominated in the latest Eocene Bembridge Marls (Ross, Self, 2014) and *Lasius* was also common there (Dlussky, Perfilieva, 2014). The coexistence of *Oecophylla* with *Beraeodes* and *Lasius* was possible only in the equable Priabonian climate

in both European ambers and Bembridge Marls.

LaPolla & Greenwalt (2015) described the oldest named *Lasius* from the middle Eocene shale (Lutetian, 44–45 Ma, Dawson, Constenius (2018)) of Kishenehn Formation in north-western Montana, USA based on two males, 1.3% of all determinable ants. The Kishenehn megaflora is moderately diverse, but dominated by the platanoid *Macginitea augustiloba*, which indicates a humid, subtropical paleoclimate (Dawson, Constenius, 2018). *Oecophylla*, the thermophile giant Formiciinae (dominant ants in Messel and Eckfeld, present in the terminal Ypresian Green River Formation), and Myrmeciinae (dominant ants in the Ypresian Mo-Clay, details of Eocene distribution in Radchenko, Perkovsky, 2020) are all absent in the Kishenehn Formation.

The Kishenehn Formation is interpreted as early Uintan (Uintan North American land mammal age: 41.3–46.2 Ma) based on twenty-six mammal taxa (Dawson, Constenius, 2018). Faunal diversity loss (the 'Bridgerian Crash') before the early Uintan is associated with climatic deterioration: relative mammalian abundance shifted from very diverse and evenly represented communities to those dominated by the condylarth *Hyopsodus* when regional MAT shifted from megathermal to a mesothermal 15 °C and even lower (Woodburne *et al.*, 2009). This is consistent with the presence of *Lasius* in this Lagerstätte.

Assignment of this species to *Lasius* raises certain doubts, however, as available specimens do not show a single clearly diagnostic feature of this genus. In addition, their heads appear to be suboval with barely marked occipital corners while the position of the hind coxae seems characteristic of the tribe *Lasiini* (op. cit., Fig. 8). We can only assume that *Lasius glom* LaPolla et Greenwalt, 2015 may represent a new, extinct genus, probably related to *Lasius*.

Some other insect taxa, e.g. Chrysopinae (Neuroptera, Chrysopidae) and Hybrizoninae (Hymenoptera, Ichneumonidae) also first appeared in Baltic amber and the Bembridge Marls (Makarkin, Perkovsky, 2020); in Baltic, Bitterfeld and Rovno amber; in the Bembridge Marls

(Tolkanitz, Perkovsky, 2015); or are only known from European ambers of gymnosperm origin and the Bembridge Marls, e.g. Townesitinae (Hymenoptera, Ichneumonidae) (Tolkanitz, Perkovsky, 2018). Another important insect that first appeared in Baltic amber and the Bembridge Marls is the extant avian malaria vector *Coquillettidia* Dyar, 1905 (Culicidae), now represented in Europe by a single species (Szadziewski *et al.*, 2019). The optimal biotope for *Coquillettidia* includes the larval host plants such as *Typha* sp., *Phragmites* sp., and *Juncus* sp.; the spread of semi-submerged helophytes appears to have been facilitated by the appearance of macrophyte lakes during Priabonian climatic cooling (Lyubarsky, Perkovsky, 2020 and references therein).

A Priabonian age for Bitterfeld and Baltic ambers is supported by the syninclusions of *Oecophylla* and *Lasius*, *Temnothorax* and *Yantaromyrmex*, and other tropical and Holarctic ant combinations mentioned above, as well as by the co-occurrence of various other insect taxa mentioned above that are also found in the confidently dated Bembridge Marls, and by the abundance of Baltic amber taxa unknown as compression fossils until Priabonian.

Thus, the coexistence of *Oecophylla* and *Lasius* in Europe was possible only from the late Eocene to the late Miocene: before this, the climate of European middle latitudes was too hot for aphids, the obligate symbionts of *Lasius*, but after the late Miocene it became too cold for *Oecophylla*. In general, the coexistence of Holarctic and tropical species on the same territory can be explained by the equable climate of the late Eocene, which has no analogues in modern times, except in limited areas in higher elevations of tropical mountains (Archibald, Farrell, 2003).

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