Vestnik zoologii, **50**(2): 111–122, 2016
DOI 10.1515/vzoo-2016-0014

DE GRUYTER
OPEN

UDK 565.796: 551.781.4

This paper is dedicated to memory of Prof. Gennady Dlussky,
who has established a new standard in palaeomyrmecology.

TROPICAL AND HOLARCTIC ANTS IN LATE EOCENE AMBERS

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Tropical and Holarctic Ants in Late Eocene Ambers. Perkovsky, E. E. — Based on representative collections, the ratio of tropical and Holarctic ant species in Priabonian (Late Eocene) Baltic, Bitterfeld (Saxonian), Danish and Rovno ambers is analyzed for the first time. In surveyed representative collections of Baltic amber, the ratios of Holarctic and tropical ant species are from 1.1 to 1.5; with 10 Holarctic and 9 tropical species (out of 31) in the PIN-964 collection, and 9 and 5 species (out of 29) in the Giecewicz collection; the ratio in the representative collection of Saxonian amber is 0.9, 11 Holarctic species vs. 12 tropical species (out of 55); in the representative collection of Rovno amber it is 0.65, 15 vs. 23 species (out of 79); and in the representative collection of Danish amber it is 0.64, 7 vs. 11 species (out of 36). Hence, in representative collections of Baltic amber, Holarctic species clearly prevail not just in terms of the share of their specimens (by 9.8 to 19.6 times), but also by the number of species. In Bitterfeld amber, Holarctic species are somewhat less numerous than tropical ones, but their specimens are 6 times greater. In representative collections of Rovno and Danish ambers, the number of Holarctic species is 1.5 to 1.7 times smaller than that of tropical species, but the number of their specimens is 4.9 to 6.9 times greater. The numbers of tropical and Holarctic species represented by more than one specimen is similar in Priabonian ambers, 25 versus 22, but Holarctic species include four dominants or subdominants. The abundance of temperate elements in the Priabonian amber ant fauna along with the relatively small number of tropical elements greatly distinguishes it from the Middle European Lutetian ant faunas of Messel and Eckfeld in shale, which do not have temperate elements at all. *Formica phaethusa* Wheeler, *Glaphyromyrmex oligocenicus* Wheeler, *Plagiolepis squamifera* Mayr, *Proceratium eocenicum* Dlussky, *Hypoponera atavia* (Mayr), *Ponera lobulifera* Dlussky, *Aphaenogaster mersa* Wheeler, and *Ennaemerus reticulatus* Mayr are new records for Rovno amber, and *Formica gustawi* Dlussky and *Gnamptogenys europaea* (Mayr) for Danish amber.

Key words: Eocene, community structure, Formicidae, fossils, generic diversity, amber, climate.

Ants have dominated insect communities since at least the Eocene, a time of their significant transformation (Wilson, Hölldobler, 2005; Dlussky, Rasnitsyn, 2007; LaPolla et al., 2013; Perkovsky, Wegierek, 2015). Myrmecofaunas of all Priabonian (Late Eocene) ambers have been studied in great detail, and they provide important data on ant biogeography and bear implications for the climate of the Priabonian amber forests (Dlussky, Rasnitsyn, 2009; Perkovsky, 2011).

Recently, several genera of amber ants have been revised, new genera and species described (Dlussky, Radchenko, 2009, 2011; Dlussky, 2010; Dlussky et al., 2014, 2015; Dubovikoff, 2012; Dlussky, Dubovikoff, 2013; LaPolla, Dlussky, 2010; Radchenko, Dlussky, 2012, 2013 a, b, 2015; Radchenko, Perkovsky, 2009), and the list of Rovno species now includes *Formica paleopolonica* Dlussky (Perkovsky, 2015). It was calculated (Penney, Preziosi, 2014), that at least 29 % of Baltic amber ants were unknown in 2009; now number of Batic amber species equals 136 % from their number in 2009 (table 1), so 27 % added already.

The most common tropical ant species have been transferred to the extinct genus *Yantaromyrmex* Dlussky et Dubovikoff (Dlussky, Dubovikoff, 2013), and the extinct species groups *balticus, cornutus, sculpturatus* and *passaloma* of the genus *Dolichoderus* (Dlussky, 2002), were attributed to the tropical extant species groups *thoracicus, scabridus, cuspidatus,* and *sulcaticeps* by Dubovikoff (Dubovikoff, 2012, table 1). Here, we re-evaluate the climatic implications of these ant assemblages based on these advances.

Material and methods

We analysed ants from representative collections of Rovno amber (Schmalhausen Institute of Zoology, Kyiv, SIZK), Baltic amber: PIN-964 (Dlussky, Rasnitsyn, 2009) the Giecewicz collection (Kosmowska-Ceranowicz, 2001), Danish amber (collection of the Zoological Museum of Copenhagen, ZMUC-S), Saxonian amber (Humboldt Museum, Berlin, HMB). All of these ambers are succinites. The Giecewicz collection was used instead of the whole collection of the Muzeum Ziemi (Warszawa) (MZ PAN: Dlussky, Rasnitsyn, 2009), because it is the only part of the whole collection which we considered representative (unbiased with respect to the taxonomic composition of the source fauna, that is, composed with no prior selection either in favour of or against any inclusions) (Kosmowska-Ceranowicz, 2001). The Wheeler collection was excluded from this analysis because it is not confirmed as representative. The share of *Lasius* in this collection (10.2 % of all ants) is 1.5 to 2.3 times smaller than in the representative samples of Baltic amber (1.7 to 2.3 times smaller than in the representative samples of other Priabonian ambers), indicating the strong likelihood that this large collection of ants (9527 specimens) is biased (Dlussky, Rasnitsyn, 2009). The representativeness of other collections is discussed in detail by Dlussky and Rasnitsyn (2009). The representative SIZK collection was collected in the Klesov and the Horyn' river valley (Rovno region, Ukraine), the PIN-964 collection is from Yantarnyi (the former Palmnicken in the Kaliningrad Region, Russia), and the Giecewicz collection is from Gdańsk (Stogi and Górki Zachodnie, Poland). All ants were identified by G. M. Dlussky and A. G. Radchenko. All ants identified to the genus level were used in the analysis, except species of *Dolichoderus* and *Plagiolepis* Mayr, which include both Holarctic and tropical species groups, and those of some species groups that are neither Holarctic nor tropical, and specimens of these genera were not used in the analysis if their species groups were not identified.

In total, there are 193 ant species known from these Priabonian ambers; 56 of them are not found in Baltic amber, which has tens of thousands times more inclusions in collections than other Priabonian ambers combined, and 31 out of these 56 species were found in Rovno amber (table 1).

The reasons of categorising *Formica* L., *Lasius* F., Mayr, *Liometopum* Mayr, the *Plagiolepis pygmaea* group, the *Dolichoderus quadripunctatus* group, and *Stenamma* Westwood as Holarctic taxa were previously discussed in detail by Dlussky and Rasnitsyn (2009) and Perkovsky (2011). All Baltic amber species of the genus *Tetramorium* Mayr belong to the Palaearctic (Radchenko, 1992 a, b) groups *caespitum* and *inerme* (Radchenko, Dlussky, 2015). We consider the following taxa to be tropical: *Acanthomyrmex* Emery, *Carebara* Westwood, *Crematogaster* Lund, *Gesomyrmex* Mayr, *Gnamptogenys* Roger, *Meranoplus* F. Smith, *Oecophylla* F. Smith, *Pachycondyla* Smith, *Platythyrea* Roger, *Pristomyrmex* Mayr, *Proceratium* Roger, *Pseudolasius* Emery, *Tetraponera* F. Smith, and *Vollenhovia* Mayr (table 1), and the *Dolichoderus thoracicus, Dolichoderus scabridus, Dolichoderus cuspidatus* and *Dolichoderus sulcaticeps* species groups (Dubovikoff, 2012, table 1).

It was previously assumed (Perkovsky, 2011) that the genus *Fallomyrma*, known from all Priabonian ambers except Baltic amber, should also be categorised as a tropical element. The recent discovery of an additional three species of this genus in Rovno amber (four species) vs. one species in the more northern Saxonian and Danish faunas (Dlussky, Radchenko, 2006), further supports this hypothesis. We believe that the forest that produced Bitterfeld amber was located at the north-eastern boundary of this genus' range (Perkovsky, 2011) and that this explains *Fallomyrma*'s rarity there. We previously considered amber species of the genus *Myrmica* not to be Holarctic (Perkovsky, 2011), as the majority of these are similar to those of the *ritae* group from the southern part of the genus' distribution. However, it is unclear to what extent this is valid, and whether the similarity of amber species to extant species of the *ritae* group might be a convergence with many dendrobiontic *ritae* species, uncommon for *Myrmica* as a whole (Radchenko et al., 2007; Radchenko, Elmes, 2010). We considered the three extinct genera of Formicini found in Baltic and Bitterfeld amber to be Holarctic sensu lato as well, because all other genera of the tribe are considered so (Dlussky, 2008); *Protoformica* Dlussky was initially described as a subgenus of *Formica* (Dlussky, 2008).

On the other hand, as the authors of *Yantaromyrmex* suggested, "Most likely, the new genus that we describe here should be considered as ancestral for *Anonychomyrma* and *Iridomvrmex*" (Dlussky, Dubovikoff, 2013), and both of these are tropical (Dlussky, Rasnitsyn, 2009). All extant genera of the subfamilies Cerapachyiinae and Myrmeciinae, the tribe Proceratiini (Andrade de, Baroni Urbani, 2003)and the *Leptomyrmex* genus group (Dlussky et al., 2014) are also distributed in the tropics. Therefore, we also decided to compare the portion of tropical species sensu lato including *Yantaromyrmex, Procerapachys* (Cerapachyiinae), *Prionomyrmex* (Myrmeciinae), *Bradoponera* (Proceratiini) (Andrade, de, Baroni Urbani, 2003), *Usomyrma (Leptomyrmex* genus-group), and *Fallomyrma,* with the portion of Holarctic species sensu lato including *Myrmica* and the extinct Formicini.

As demonstrated by Dlussky and Rasnitsyn (2009), the composition of rare species (those not exceeding 1 % of the inclusions in any single collection), in samples up to 1500 specimens is random. Therefore, any accurate comparison of amber faunas based on the composition of the rare species they include would provide misleading results, as in most cases, their absence in a particular amber assemblage is likely an artefact of small sample size. Unfortunately, we found only four tropical species exceeding at least 1 % of the inclusions in one representative collection: *Carebara antiqua* (Mayr), *Gesomyrmex hoernesi* Mayr, *Gnamptogenys europaea* (Mayr), and *Tetraponera simplex* (Mayr), and only two species, *Gesomyrmex hoernesi* and *Tetraponera simplex* (Mayr), which each represent more than 1% in two representative collections. *Gnamptogenys europaea* is not

Table 1. Composition of ant species in Late Eocene European ambers*

Species	Gulf of Gdańsk	Bitterfeld	Jutland	Rovno
ANEURETINAE				
Paraneuretus longipennis Wheeler	+			
Paraneuretus tornquisti Wheeler	+	+		
Pityomyrmex tornquisti Wheeler	+			
Protaneuretus succineus Wheeler	+			
Protaneuretus sp. (undescribed)		+		
DOLICHODERINAE				
Ctenobethylus goepperti (Mayr)	+		+	
Dolichoderus balticus (Mayr)	+	+	+	+
Dolichoderus brevicornis Dlussky	+			
Dolichoderus brevipalpis Dlussky	+			
Dolichoderus brevipennis Dlussky		+		
Dolichoderus cornutus (Mayr)	+	+		
Dolichoderus elegans Wheeler	+			
Dolichoderus granulinotus Dlussky	+			
Dolichoderus kutscheri Dlussky		+		
Dolichoderus longipennis (Mayr)	+			
Dolichoderus longipilosus Dlussky	+		+	
Dolichoderus lucidus Dlussky				+
Dolichoderus mesosternalis Wheeler	+	+	+	
Dolichoderus nanus Dlussky	+			
Dolichoderus passaloma Wheeler	+	+		+
Dolichoderus perkovskyi Dlussky			+	+
Dolichoderus pilipes Dlussky			+	+
Dolichoderus polessus Dlussky	+			+
Dolichoderus polonicus Dlussky	+			
Dolichoderus punctatus Dlussky	+			
Dolichoderus robustus Dlussky	+		+	+
Dolichoderus sculpturatus (Mayr)	+	+		
Dolichoderus tertiarius (Mayr)	+	+	+	+
Dolichoderus vlaskini Dlussky				+
Dolichoderus zherichini Dlussky				+
Dolichoderus sp. A (undescribed)	+			
Eldermyrmex oblongiceps (Wheeler)	+			
Liometopum oligocenicum Wheeler	+			
Tapinoma aberrans Dlussky				+
Tapinoma electrina Dlussky	+	+		+
Tapinoma sp. A (undescribed)		+		
Tapinoma sp. B (undescribed)		+		
Tapinoma sp. C (undescribed)		+		
Usomyrma mirabilis Dlussky, Radchenko et Dubovikoff			+	
Yantaromyrmex constrictus (Mayr)	+	+	+	+
Yantaromyrmex geinitzi (Mayr)	+	+	+	+
Yantaromyrmex intermedius Dlussky et Dubovikoff		+		
Yantaromyrmex mayrianum Dlussky et Dubovikoff	+			+
Yantaromyrmex samlandicus (Wheeler)	+	+		+

Table 1. Continued

Species	Gulf of Gdańsk	Bitterfeld	Jutland	Rovno
Zherichinius sp. A (undescribed)		+		
Genus A sp. A (undescribed)				+
FORMICINAE				
Asymphylomyrmex balticus Wheeler	+			+
Camponotus mengei Mayr	+	+	+	+
Cataglyphoides constrictus (Mayr)	+			
Cataglyphoides intermedius Dlussky	+			
Conoformica bitterfeldiana Dlussky		+		
Drymomyrmex claripennis Wheeler	+			
Drymomyrmex fuscipennis Wheeler	+			
Formica flori Mayr	+	+	+	+
Formica gustawi Dlussky***	+	+	+	+
Formica horrida Wheeler	+			
Formica kutscheri Dlussky		+		
Formica paleopolonica Dlussky	+			+
Formica phaethusa Wheeler**	+	+		+
Formica radchenkoi Dlussky				+
Formica strangulata Wheeler	+			
Formica zherichini Dlussky	+			
Gesomyrmex hoernesi Mayr	+	+	+	+
Glaphyromyrmex oligocenicus Wheeler**	+			+
Lasius edentatus Mayr	+			
Lasius nemorivagus Mayr	+			
Lasius pumilus Mayr	+	+		
Lasius punctulatus Mayr	+			
Lasius schiefferdckeri Mayr	+	+	+	+
Nylanderia pygmaea (Mayr)	+	+	+	+
Oecophylla brischkei Mayr	+	+		
Oecophylla crassinoda Wheeler	+	+		
Plagiolepis klinsmanni Mayr	+	+	+	+
Plagiolepis kuenowi Mayr	+	+	+	+
Plagiolepis paradoxa Dlussky		+		
Plagiolepis singularis Mayr	+			
Plagiolepis solitaria Mayr	+	+		+
Plagiolepis squamifera Mayr**	+	+		+
Plagiolepis wheeleri Dlussky	+			
Plagiolepis sp. A (undescribed)				+
Prenolepis henschei Mayr	+	+	+	+
Prodimorphomyrmex primigenius Wheeler	+			
Protoformica proformicoides Dlussky	+		+	
Pseudolasius boreus Wheeler	+	+		+
MYRMECIINAE				
Prionomyrmex longiceps Mayr	+	+		
PSEUDOMYRMECINAE				
Tetraponera europaea Dlussky		+		+
Tetraponera groehni Dlussky	+			
Tetraponera lacrimarum (Wheeler)	+	+		
Tetraponera klebsi (Wheeler)	+			
Tetraponera ocellata (Mayr)	+	+	+	+

Table 1. Continued

Species	Gulf of Gdańsk	Bitterfeld	Jutland	Rovno
Tetraponera simplex (Mayr)	+	+	+	+
CERAPACHYINAE				
Procerapachys annosus Wheeler	+	+		
Procerapachys favosus Wheeler	+			
Procerapachys sulcatus Dlussky	+			
Procerapachys sp. A (undescribed)				+
Procerapachys sp. B (undescribed)				+
PONERINAE				
Amblyopone groehni Dlussky	+			
Amblyopone electrina Dlussky	+			
Bradoponera electrina Baroni Urbani	+			
Bradoponera meyeri Mayr	+	+		+
Bradoponera similis Dlussky		+		
Bradoponera wunderlichi Baroni Urbani et de Andrade	+			
Cryptopone sp. A (undescribed)				+
Electroponera dubia Wheeler	+			
Gnamptogenys europaea (Mayr)***	+	+	+	+
Gnamptogenys rohdendorfi Dlussky	+			
Hypoponera atavia (Mayr)**	+	+	+	+
Pachycondyla baltica Dlussky	+			
Pachycondyla conservata Dlussky				+
Pachycondyla gracilicornis (Mayr)	+			
Pachycondyla succinea (Mayr)	+	+	+	+
Pachycondyla tristis Dlussky		+		
Platythyrea primaeva Wheeler	+			
Ponera lobulifera Dlussky**	+			+
Ponera mayri Dlussky	+			+
Ponera wheeleri Dlussky		+		
Proceratium eocenicum Dlussky**	+			+
MYRMICINAE				
Acanthomyrmex sp. A (undescribed)	+			
Agroecomyrmex duisburgi (Mayr)	+	+		
Aphaenogaster antiqua Dlussky				+
Aphaenogaster mersa Wheeler**	+			+
Aphaenogaster oligocenica Wheeler	+	+		
Aphaenogaster sommerfeldti Mayr	+	+		
Aphaenogaster sp. A (undescribed)	+			
Aphaenogaster sp. B (undescribed)			+	
Bilobomyrma ukrainica Radchenko et Dlussky				+
Bilobomyrma baltica Radchenko et Dlussky	+			
Boltonidris mirabilis Radchenko et Dlussky				+
Carebara antiqua (Mayr)	+	+		+
Carebara nitida (Dlussky)				+
Carebara sp. A (undescribed)		+		
Carebara ucrainica (Dlussky)				+
Crematogaster sp. A (undescribed)				+
Crematogaster sp. B (undescribed)	+			

Table 1. Continued

Species	Gulf of Gdańsk	Bitterfeld	Jutland	Rovno
Electromyrmex klebsi Wheeler	+			
Electromyrmex sp. A (undescribed)		+		
Ennaemerus reticulatus Mayr**	+			+
Eocenomyrma electrina Dlussky et Radchenko			+	
Eocenomyrma elegantula Dlussky et Radchenko	+			
Eocenomyrma orthospina Dlussky et Radchenko	+			+
Eocenomyrma rugosostriata (Mayr)	+	+		
Eocenomyrma sp. A (undescribed)				+
Eocenomyrma sp. B (undescribed)				+
Fallomyrma transversa Dlussky et Radchenko		+	+	+
Fallomyrma sp. A (undescribed)				+
Fallomyrma sp. B (undescribed)				+
Fallomyrma sp. C (undescribed)				+
Meranoplus sp. A (undescribed)	+			
Monomorium mayrianum Wheeler	+	+		+
Monomorium pilipes Mayr	+	+	+	+
Monomorium kugleri Radchenko et Perkovsky				+
Monomorium sp. A (undescribed)	+			
Monomorium sp. B (undescribed)	+			
Myrmica eocenica Radchenko, Dlussky et Elmes	+		+	
Myrmica intermedia (Wheeler)	+			
Myrmica longispinosa Mayr	+			
Myrmica paradoxa Radchenko, Dlussky et Elmes		+		
Myrmica rudis Mayr	+			
Myrmica sp. A (undescribed)	+			
Myrmica sp. B (undescribed)				+
Myrmica sp. C (undescribed)	+			
Paraneranoplus primaevus Wheeler	+			
Plesiomyrmex tubulatus Radchenko et Dlussky		+		
Pristomyrmex rasnitsyni Dlussky et Radchenko			+	
Pristomyrmex sp. A (undescribed)		+		
Solenopsis sp. A (undescribed)	+			
Stenamma berendti (Mayr)	+			
Stenamma sp. A (undescribed)****	+			
Stigmomyrmex venustus Mayr	+	+		
Stigmomyrmex sp. A (undescribed)	+			
Stiphromyrmex robustus (Mayr)	+			
Stiphromyrmex sp. A (undescribed)	+			
Temnothorax glaesarius (Wheeler)	+			
Temnothorax gracilis (Mayr)	+	+		+
Temnothorax histriculus (Wheeler)	+			
Temnothorax longaevus (Wheeler)	+	+		+

Table 1. Continued

Species	Gulf of Gdańsk	Bitterfeld	Jutland	Rovno
Temnothorax petiolatus (Mayr)	+	+		
Temnothorax placivus (Wheeler)	+			
Temnothorax sp. A (undescribed)		+		
Temnothorax sp. B (undescribed)		+		+
Temnothorax sp. C (undescribed)	+			
Temnothorax sp. D (undescribed)		+		+
Temnothorax sp. E (undescribed)		+	+	+
Temnothorax sp. F (undescribed)	+			
Temnothorax sp. G (undescribed)	+			
Temnothorax sp. H (undescribed)	+			
Tetramorium paraarmatum Radchenko et Dlussky	+			
Tetramorium kulickae Radchenko et Dlussky	+			
Vollenhovia beyrichi (Mayr)	+			
Vollenhovia prisca (Andrė)	+			
Vollenhovia kipyatkovi Radchenko et Dlussky				+
Genus A sp. A (undescribed)				+
Genus B sp. A (undescribed)	+			
Total	**136**	**72**	**35*******	**79**

* The species of the genus *Pheidole* (Dubovikoff, 2011), described from Baltic amber, was actually described from copal (Dubovikoff, personal communication).
** Species, new for Rovno amber.
*** Species, new for Danish amber.
**** *Stenamma* sp. A counted here as Baltic (see Dlussky, Rasnitsyn, 2009, table 2).
***** Two unnamed *Temnothorax* species, mentioned by Dlussky (Dlussky, Rasnitsyn, 2009, table 2), but known only by males, were added to sum.

considered rare only because the single sample of Danish amber that contains it, the ZMUC-S collection, has four male ants of this species, and this collection is the smallest among the representative collections. *Dolichoderus perkovskyi* Dlussky was not categorised as rare by Dlussky and Rasnitsyn (2009), however, following the subsequent substantial growth of the SIZK collection, it does not reach even 1 % of its ants. Half of all tropical species (25 out of 51) are known only by single specimen. There are seven Holarctic species that are not rare: *Dolichoderus polessus* Dlussky, *Dolichoderus tertiarius* (Mayr), *Formica flori* Mayr, *Formica paleopolonica* Dlussky, *Lasius schiefferdckeri* Mayr, *Plagiolepis kuenowi* Mayr, and *Prenolepis henschei* Mayr. *Formica gustawi* Dlussky does not now reach 1 % of ants in the SIZK collection, like *Dolichoderus perkovskyi*, which is also close to 1 % in PIN-964. Four of these seven species are dominants or sub-dominants, five of them are known from all Priabonian ambers. At the same time, 11 out of 32 Holarctic species are presented by single specimens; hence, the number of tropical and Holarctic species represented by more than one specimen is similar in Priabonian ambers, 26 versus 21. Note that the ratio between the number of species of the most

Table 2. Number of specimens of Holarctic and tropical ant species, and number of specimens of modern genera of specialized dendrobionts in the representative collections

Collection	Holarctic	Tropical	Holarctic / Tropical	*Dolichoderus* & *Tetraponera*
PIN-964	166 (37.2 %)	17 (3.8 %)	9.8	21(4.7 %)
Giecewicz	157 (36.9 %)	8 (1.9 %)	19.6	13(3.1 %)
HMB	236 (34.4 %)	40 (5.8 %)	5.9	46(6.7 %)
ZMUC-S	138 (40 %)	28 (8.1 %)	4.9	38(11 %)
SIZK	453 (39.6 %)	66 (5.8 %)	6.9	94(8.2 %)

Table 3. Number of specimens of Holarctic s. l. and tropical s. l. ant species in the representative collections

Collection	Tropical s. l.	Tropical s. l. & *Fallomyrma*	Holarctic & *Myrmica* + *Protoformica* + *Conoformica*
PIN-964	50 (11.2 %)	50 (11.2 %)	167(37.4 %)
Giecewicz	20 (4.7 %)	20 (4.7 %)	157(36.9 %)
HMB	93 (13.6 %)	96 (14 %)	242(35.3 %)
ZMUC-S	54 (15.6 %)	75 (21.7 %)	140(40.5 %)
SIZK	172 (15.1 %)	188 (16.5 %)	454(39.7 %)

common and speciose amber Holarctic genera *Formica* and *Lasius* and the number of species of the most common and speciose species tropical amber genus *Tetraponera* in Baltic amber is 2.4, in Rovno amber it is 2, and in Saxonian and Danish it is 1.5. The number of tropical species increases sharply with the number of ant taxa recorded in the fauna, with the expected maximum in Baltic amber. Therefore, it appears advisable to compare the ratio of Holarctic and tropical species in representative collections and not their total number recorded in different amber faunas.

Results

Comparative composition analysis of representative samples indicates that Baltic amber contains 9.8 to 19.6 times more Holarctic ant specimens than tropical ants, while this is only 4.9 to 6.9 times in other Priabonian ambers (table 2).

In both representative collections of Baltic amber that we examined, the number of Holarctic species is 1.1 to 1.5 times greater than the tropical, 9–10 species (out of 31) in PIN-964; and 5–9 species (out of 29) in the Giecewicz collection. In the representative collection of Saxonian amber (HMB), the number of Holarctic species is 1.1 times smaller, 11 Holarctic species to 12 tropical species (out of 55); in the SIZK collection (Rovno amber) this ratio is 1.5 times smaller (15 to 23, out of 79); and in the ZMUK-S collection (Danish amber) it is 1.6 times smaller, 7 Holarctic species to 11 tropical species (out of 35). Hence, Holarctic species clearly dominate in the representative collections of Baltic amber in terms of both the numbers of specimens and species. In Bitterfeld amber, they have a somewhat smaller number of species, but the number of their specimens is 6 times greater. In the Rovno and Danish representative collections, the number of Holarctic species is 1.5 to 1.7 times smaller but the number of specimens is 4.9 to 6.9 times greater. The ratios between the specimens of Holarctic and tropical species in the representative collections of Baltic amber are 1.4 to 3.5 times higher than that of the representative collections of other Priabonian ambers; the ratios between the numbers of Holarctic and tropical species in the representative collections of Baltic amber are 1.3 to 2.6 times higher. Unexpectedly, the myrmecofauna of Gdańsk appeared much more Holarctic (in the Giecewicz collection) compared with that of the Yantarnyi collection (PIN-964) (table 2).

Note that the ratio between Holarctic and tropical ants is inversely proportional to the share of specialized dendrobionts *Dolichoderus* and *Tetraponera* within the representative samples (table 2).

Table 4. Number of species of Holarctic s. l. and tropical s. l. ant species in the representative collections

Collection	Tropical s. l.	Tropical s. l. & *Fallomyrma*	Holarctic & *Myrmica* + *Protoformica* + *Conoformica*
PIN-964	11	11	11
Giecewicz	7	7	9
HMB	19	20	12
ZMUC-S	14	15	9
SIZK	30	34	16

Considering species of *Yantaromyrmex, Procerapachys*, *Prionomyrmex*, *Bradoponera*, *Usomyrma*, *Myrmica* and all Formicini of the representative collections (table 4), the ratio of tropical species in Baltic amber is 0.8 to 1 times that of the Holarctic species (the number of tropical ant specimens is 3.3 to 7.9 times smaller), in Saxonian amber the number of tropical species is 1.6 times greater than that of Holarctic species (the number of tropical ant specimens is 2.7 times smaller), and in Danish amber the number of tropical species is 1.55 greater than that of Holarctic species (the number of tropical ant specimens is 2.6 times smaller) (table 3, 4). In Rovno amber the number of tropical species is also 1.9 times greater, and the number of tropical specimens is 2.7 times smaller. When *Fallomyrma* species (table 3, 4) are added, the ratio of tropical to Holarctic species in Saxonian amber changes to 1.67 (the number of tropical specimens appears 2.6 times smaller), in Danish amber this equals 1.67 (the number of tropical specimens is 1.8 times smaller), and in Rovno amber it becomes 2.1 (the number of tropical specimens is 2.4 times smaller). As we can see, Holarctic species yet again dominate in terms of the number of specimens in all Eocene ambers, while they also prevail or at least are not less in terms of the number of species in the representative collections of Baltic amber. In Rovno and Danish ambers, the number of tropical species is clearly greater, and the Saxonian amber species ratio is between that of Baltic amber and that of Danish and Rovno ambers. The ratio of specimens of Holarctic and tropical ants in the representative collections of Baltic amber differs by 1.9 to 4 times from that in the representative collections of other Priabonian ambers, the species ratio differs by 1.7 to 2.8 times. The ratios of tropical and Holarctic (sensu lato) ant species of Gdańsk and Yantarnyi ambers (table 4) do not differ less than their respective ratios for ant specimens (table 3).

The surprising coexistence in Priabonian amber of ants that are separated today by climate type as tropical and Holarctic taxa — the so-called "Wheeler dilemma"— can be explained by the equability of the Eocene climate that had low temperature seasonality into higher latitudes, and therefore mild winters even in cooler climates (Archibald, Farrell, 2003). The presence of tropical genera in Priabonian ambers agrees with this model. In the undoubtedly younger Bembridge Marls dated as latest Priabonian (34 Mya; Hooker et al., 2009), which was colder than the first half of Priabonian (the age of the Baltic, Bitterfeld, Danish and Rovno amber forests: Aleksandrova, Zaporozhets, 2008; Dlussky, Perfilieva, 2014) the dominant ant genus was *Oecophylla*, but it occurs together with *Dolichoderus* of the *quadripunctatus* group and other dominants of the Holarctic Formicini and Lasiini (Dlussky, Perfilieva, 2014; Dlussky, personal communication). Among Bembridge Marls caddisflies, the psychrophilic genus *Beraeodes* Eaton (Sukatsheva, 2014) strongly dominates, although it co-occurs in Rovno amber syninclusions with tropical *Yantaromyrmex* ants (Perkovsky, 2013). The ratio between tropical and Holarctic species in other families of amber insects shows a dominance of Holarctic species like that seen in ant specimen ratios; for example, among 28 species of leaf beetles from succinites (Nadein et al., 2015; Legalov, 2016) there are four Holarctic vs. one tropical species.

The dissimilarity of the overwhelmingly tropical fauna of the Lutetian Messel and Eckfeld compression fossil assemblages to the equable fauna of Yantarnyi, Gdańsk, Rovno and Jutland is based on the absence of a notable (far from prevailing) Holarctic element. All common tropical genera of Baltic amber are easily recognizable in the Ypresian and Lutetian myrmecofaunas, whose localities are characterized by a paratropical climate. But there was no evidence of *Lasius* in the Ypresian and Lutetian deposits until last year, and, apart from the Priabonian ambers, the *Dolichoderus quadripunctatus* group is only known from the Priabonian Bembridge Marls in the Eocene (Dlussky, Perfilieva, 2014), whereas the presence of *Formica* in the Lutetian deposits at Messel and Eckfeld is known only from Dlussky's remark (Dlussky, 2008) in his revision of amber Formicini. One specimen of *Formica* and two specimens of Lasius (from 152 determined ants) were found in Lutetian Kishenehn Formation, Montana (LaPolla, Greenwalt, 2015) together with the oldest representatives of two tropical genera (LaPolla, Greenwalt, 2015). The main difference between these faunas and those of Priabonian ambers is the dominance of *Formica* and *Lasius* in the latter. The Messel fauna is dominated (49 % of all ants) by extremely thermophilic Formiciini (not known in Priabonian) of the genus *Titanomyrma* (Archibald et al., 2011), poneromorph ants are quite large in number and extremely diverse (22 species, Dlussky, Wedmann, 2012), whereas Formicinae are apparently 12 species out of 60, and 4 of those are assigned to the tropical genera *Gesomyrmex* and *Oecophylla* (Dlussky et al., 2008, 2009). Conversely, there are at least 18 known species of Holarctic Formicini and *Lasius* in Priabonian ambers, including 15 in Baltic amber. In our opinion, the presence of abundant Holarctic elements in the Priabonian amber faunas of Northern and Eastern Europe is incompatible with the Lutetian age postulated for these ambers (for the Messel Lagerstätte, the estimated MAT is 20–24 °C, Archibald et al., 2011, thus the absence of any notable Holarctic elements is unsurprising), and by combination of tropical and Holarctic elements, the Northern and Eastern European amber assemblage is closest to that of the Bembridge Marls, which is consistent with their being Priabonian.

For the first time, we show that the ratio between Holarctic and tropical species in the representative collections of Priabonian ambers examined is significantly different not only in terms of the number of specimens but also in the number of species, and in Baltic ambers it is substantially greater than in other Priabonian ambers.

Since there appears to be no significant difference in the ages of Gdańsk and Yantarnyi ambers, the Gdańsk amber may have originated either from a more northern part of the Baltic amber forest, or from an interval when the temperatures of Russo-Skandia were somewhat lower than the average temperature of first half of Priabonian.

The author is sincerely grateful to A. G. Radchenko (SIZK) for the unpublished data on Late Eocene Myrmicinae, to A. P. Rasnitsyn (Paleontological Institute, Moscow) for the helpful advice and discussion of the manuscript, and S. B. Archibald (Simon Fraser University, Burnaby, Canada) for editing.

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Received 20 February 2016
Accepted 23 February 2016