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Ants (Insecta: Vespida: Formicidae) in the Upper Eocene Amber of Central and Eastern Europe

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Abstract—A total of 5754 ant inclusions from 13 European collections of Baltic, Bitterfeld, Rovno, and Scandinavian ambers are studied and identified as belonging to 147 species, 57 genera, and 9 subfamilies. The taxonomic composition and relative species abundances of species in representative collections are analyzed and considerable differences between the above four types of amber are shown. These differences appear to reflect differences in ecological conditions rather than in age. The Baltic and Bitterfeld ant assemblages are shown to be most similar, the Scandinavian assemblage turns out to be most dissimilar to these, and the Rovno assemblage is shown to be intermediate.

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INTRODUCTION

The Baltic and similar ambers are widespread on the territories of the Central and Eastern Europe and for a long time attracted attention of geologists, entomologists, and other researchers. The age and sources of amber from different regions of Europe have been a subject of discussion for many decades. Because amber easily withstands repeated redeposition and because its mineralogical characteristics are variable, an important role in settling these issues is played by organic inclusions, particularly the relatively well-studied inclusions of ants.

The Late Eocene age of the best studied Baltic amber has not been called into question for a long time, until radiometric analysis of glauconite suggested its Middle Eocene age (Ritzkowski, 1997). This hypothesis, however, is not well supported and contradicts a large body of available data (for details, see Perkovsky et al., 2007). For this reason, here we accept the Late Eocene age of the Baltic amber. The main deposits of Baltic amber are on the southern shores of the Baltic Sea.

The first hypothesis of a non-Baltic origin was put forward for the Scandinavian amber, which had long been collected mostly from the Danish shore (Larsson, 1978). The reason was the taxonomic composition of inclusions, different from that of the Baltic amber. The hypothesis appeared plausible, but, as far as we know, until our study, nobody attempted testing it more rigorously. The second candidate for a non-Baltic origin became the Bitterfeld amber, discovered in the Miocene deposits near the town of Bitterfeld (Saxony-Anhalt, Germany) and originally dated as Miocene (Barthel and Hetzer, 1982). Later it was identified as redeposited. While some authors interpret it as redeposited Baltic amber (Weitschat, 1997; Perkovsky et al., 2007), others treat it as a separate type of amber, of a considerably different, Oligocene age (Knuth et al., 2002; Fuhrmann, 2005). The third type of amber of a supposedly non-Baltic origin is the Rovno amber (also called Ukrainian, Byelorussian, or Polesye amber), mined from the Upper Eocene and Lower Oligocene deposits of the northern margin of the Ukrainian Crystalline Shield on the territories of northern Ukraine, southern Byelorussia, and western Poland (for details, see Perkovsky et al., 2007). An independent origin of the Rovno amber remains debatable (Zherikhin and Eskov, 2007).

It appears that the controversies about the origin of these amber types cannot be currently solved by geological methods only. As some of the above authors suggested, the rapidly accumulating paleontological data on the amber inclusions can facilitate the solution. Among the groups most promising in this respect are ants. The amber ants are abundant (4–5% of all the amber arthropods, see Zherikhin et al., 2009, this volume), diverse (171 species in total, see below), ecologically informative, and relatively well-studied in all the amber types.

The first descriptions of ants from Baltic amber appeared in the first quarter of the 19th century, and already by 1868 as many as 11 ant species had been described (Presl, 1822; Holl, 1829; Giebel, 1856). Their types have been lost, and their descriptions are poor and give no clues as to their placement in species or even genera. Based on the drawings provided in the original descriptions, Mayr (1868) suggested that *Formica cordata* Holl, 1829 most probably belonged to the genus *Pheidole*, and *F. lucida* Giebel, 1856 was a member of the family Braconidae, but he made no comments on the other descriptions. Later publications did not list these species as *Formica* (Wheeler, 1915; Dlussky, 1967, 1997; Burnham, 1978). Dlussky (2008a) suggested treating them as Formicidae incertae sedis.

The first thorough revision of the Baltic amber ants was undertaken by Mayr (1868). He studied 1461 specimens from various collections and described 7 new genera and 50 new species, some of which were eventually synonymized. Dalla Torre (1893) revised some of the previously published descriptions but added no new taxa. André (1895) examined 690 inclusions in Baltic amber, identified 24 species previously described by Mayr, and described two new species. Emery (1905) studied the collection of A. Thery and described one species, later synonymized. Twenty-three specimens from Thery's collection identified by Emery are deposited in the British Museum. It needs to be emphasized that there is no clarity as to whether all the inclusions described prior to Wheeler were actually in Baltic amber. Mayr (1868) suggested that *F. cordata (?= Pheidole)* had in fact been included in copal, and Wheeler suspected the same about *Plagiolepis succini* André.

The fundamental study of the Baltic amber ants was produced by Wheeler (1915), who studied 9527 inclusions from the collection of Königsberg Geological Institute and several private collections, corrected some errors of Mayr, redescribed the majority of Mayr's species, added descriptions of 10 new genera and 40 new species, and provided superb drawings, made from actual individual inclusions. The latter is particularly important because Mayr's work contains drawings of reconstructions (sometimes containing obvious errors) instead of drawings of actual specimens. Until recently it was assumed that the collection studied by Wheeler became lost during World War II. Ritzkowski (1990) was the first to report that a part of this collection is actually preserved in Göttingen. The preserved specimens have been catalogued. Unfortunately, not all the types have survived.

For a long period after the publication of Wheeler's study, no new descriptions were published, his monograph remaining the sole source of information on the Baltic amber ants. Only in two short papers Wheeler (1922, 1929) made a few synonymic changes to his earlier publication. Much later Wilson (1955) redescribed the fossil *Lasius,* including *L. schiefferdeckeri* Mayr, based on a small amber collection gathered by W. Haren and identified by Wheeler, preserved at the Museum of Comparative Zoology at Harvard University. A few years later a revision of the Baltic amber *Formica* was published by Dlussky (1967). It contained several errors, that were subsequently corrected by the author (Dlussky, 2002b).

During the most recent ten-year period Dlussky published a series of papers on the Late Eocene ants of Europe (Dlussky, 1997, 2002a, 2002b, 2008a, 2008b, and in press; Dlussky and Perkovsky, 2002; Dlussky and Radchenko, 2006a, 2006b, and in press; Radchenko et al., 2007). The first list of ants from the Rovno amber (Dlussky and Perkovsky, 2002) was based on a relatively small collection (108 specimens). Intensive collecting by E.E. Perkovsky and A.P. Vlaskin in recent years has expanded the examined sample of Rovno ants to a total of 738 specimens. No lists of ants have been previously published for the Scandinavian and Bitterfeld ambers.

Besides the above-mentioned publications, three additional species were recently described from Baltic amber, *Prionomyrmex janzeni* Baroni Urbani (Baroni Urbani, 2000) and *Bradoponera electrina* De Andrade et Baroni Urbani and *Bradoponera wunderlichi* Baroni Urbani et De Andrade (De Andrade and Baroni Urbani, 2003).

MATERIAL

The following collections were examined (Table 1):

Paleontological Institute, Russian Academy of Sciences, Moscow (PIN): two collections of Baltic amber, a small old collection, no. 364 (PIN-364, 44 specimens) and no. 964 (PIN-964, 486 specimens). This material has been sorted out in 1948, by A.G. Sharov, directly on the amber processing factory in the town of Yantarnyi, and undoubtedly represents a random sample.

Schmalhausen Institute of Zoology, National Academy of Sciences of Ukraine (SIZK): Rovno amber.

Muzeum Ziemi PAN, Warsaw, Poland (MZ PAN): Baltic amber (571 specimens).

Natural History Museum, London (BMNH): Baltic amber (163 specimens), a small collection including some material from Thery's collection, identified by Emery (1905).

Naturhistorische Museum in Wien (NHMW): includes a part of Mayr's (1868) types from Baltic amber (31 specimens examined).

Geowissenschaftlicher Zentrum der Georg-August-Universität Göttingen (GZG.BST): Baltic amber, a collection formerly housed in the Geological Institute of Königsberg. One part of this collection (GZG-W) (1136 specimens) includes ants identified by Wheeler (1915), and another part (GZG-K) (368 specimens) comprises unidentified material.

Humboldt Museum, Berlin, Germany (HMC): Bitterfeld amber (740 specimens).

Table 1. Examined material

	Total	Identified to			Identified	
		subfamily	genus	species	genera	species
Literature data						
Mayr, 1868	1461				31	51
Andre, 1895	690				18	26
Wheeler 1915	9527				45	79
Original data						
Baltic amber						
GZG-K	368	365	363	356	16	20
GZG-W	1136	1135	1135	1122	27	48
NHMW	31	30	29	25	5	9
PIN 364	44	44	44	41	10	12
PIN 964	486	449	435	420	18	29
Gusakov	71	69	68	66	11	12
MZ PAN	971	952	939	919	31	44
Gröhn	102	102	102	102	27	36
NHML	163	160	156	149	20	25
ZMUC	50	45	42	37	12	13
Total	3421	3350	3313	3236	43	99
Bitterfeld amber						
Gröhn	28	28	26	26	5	5
HMC	740	710	680	634	34	51
Kutscher	396	392	389	379	32	53
Total	1164	1130	1095	1039	40	71
Rovno amber						
Rovno	571	531	520	484	26	50
Scandinavian amber						
ZMUC	317	299	280	271	24	34
Amber of unknown origin						
ZMUC	70	68	66	63	10	13
Wisz	23	19	18	17	5	5
Total (original data)	5566	5397	5292	5109	54	144
TOTAL	17244				61	173

Note: For data taken from the literature, the reported numbers of genera and species are based on the most recent nomenclature, i.e., corrected for synonymy. The original data include some undescribed species, currently being prepared for description. The last line takes into account species described in Baroni Urbani (2000) and De Andrade and Baroni Urbani (2003), which are not counted elsewhere in the table (see text for details).

Zoological Museum, University of Copenhagen (ZMUC): a mixture of ant inclusions in Scandinavian (317 specimens, ZMUC-S) and Baltic (50 specimens, ZMUC-B) ambers and ambers of unknown origin (70 specimens).

A personal collection of Carsten Gröhn, Glinde, Germany (CGC): ant inclusions in Baltic (102 specimens) and Bitterfeld ambers (28 specimens).

A personal collection of Manfred Kutscher, Sassnitz, Rügen, Germany (MKC), recently acquired by the Geoscience Centre of the University of Göttingen, Germany: Bitterfeld amber (396 specimens).

A personal collection of V.A. Gussakov, Korolev, Moscow Region (VGC): Baltic amber (71 specimens).

A personal collection of A. Wiszniewski, Warsaw, Poland: Rovno amber (23 specimens).

A personal collection of S.A. Suvorkin, Kiev, Ukraine: Rovno amber (14 specimens).

Details on the number of ant inclusions examined in each collection are given in Table 1.

We examined a total of 5754 inclusions but, because some of them were poorly preserved, only 5465 were identified to genus and 5282 to species. A total of 147 species, belonging to 57 genera of 9 subfamilies, were recorded. In the collections examined we did not find 25 previously described species (Mayr, 1868; André, 1895; Wheeler, 1915; Baroni Urbani, 2000; De Andrade and Baroni Urbani, 2003); in particular we did not find any species from the genera *Electroponera* Wheeler, *Liometopum* Mayr, *Pityomyrmex* Wheeler, *Platythyrea* Roger, *Prodimorphomyrmex* Wheeler, and *Vollenhovia* Mayr. On the other hand, we discovered 8 new genera and 83 new species. Descriptions of 7 new genera and 52 new species have been published or are in press; the rest of descriptions are in preparation. Representatives of the following 9 recent genera were found in the Late Eocene ambers for the first time: *Amblyopone* Erichson, *Meranoplus* F. Smith, *Pheidologeton* Mayr, *Ponera* Latreille, *Pristomyrmex* Mayr, *Proceratium* Roger, *Tapinoma* Förster, *Technomyrmex* Mayr, and *Tetramorium* Mayr. Additionally, a representative of the extinct genus *Zherichinius* Dlussky, previously known only from the Sakhalin amber (Paleocene), was recorded.

Statistical analysis of the results was performed using Microsoft Excel 2000.

SELECTION OF COLLECTIONS FOR COMPARATIVE ANALYSIS OF FAUNAS

The number of ant species found in a particular collection depends on its size. For larger collections of Baltic amber (examined by us or described in the literature) this relationship is most closely described by the equation $S = 17.244\ln(N) - 78.949$, where N is the number of specimens identified to species in the collection, and S is the number of identified species (Fig. 1). However, the leveling out of the species accumulation curve, visible in Fig. 1, is observed in practice only when the number of examined specimens becomes very high. For collections not exceeding 1500 specimens the relationship is almost linear. For the majority of the examined collections of Baltic amber it can be most closely described as $S = 0.0269N + 12.251$ (Fig. 2). It is clear from Fig. 2 that the personal collection of Gröhn (KGC) and the NHML collection are outliers, containing significantly more species than expected. The first collection is obviously not a random sample, because Gröhn acquired only those specimens that he considered "interesting." The most common amber species are represented in it by only a few specimens (*Ctenobethylus goepperti* (Mayr), 8, *Lasius schiefferdeckeri* Mayr, 4). On the other hand, as many as 14 specimens (14% of the sample) turned out undescribed species. Apparently, the NHML collection should also be considered nonrandom, because its core comprises the personal collection of Thery, identified by Emery. The

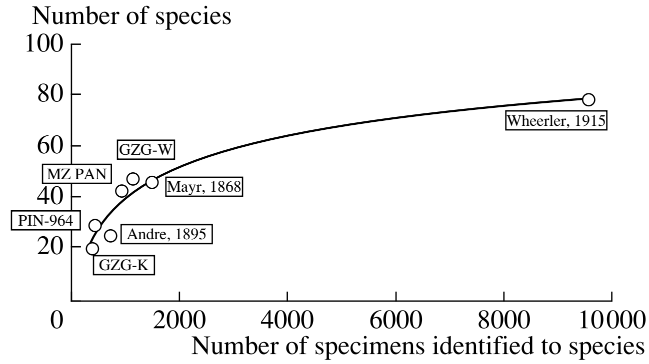

Fig. 1. Relationship between the number of ant inclusions examined and the number of species identified in the largest studied collections of Baltic amber. The trend line equation: $S = 17.244\ \ln(N) - 78.949$.

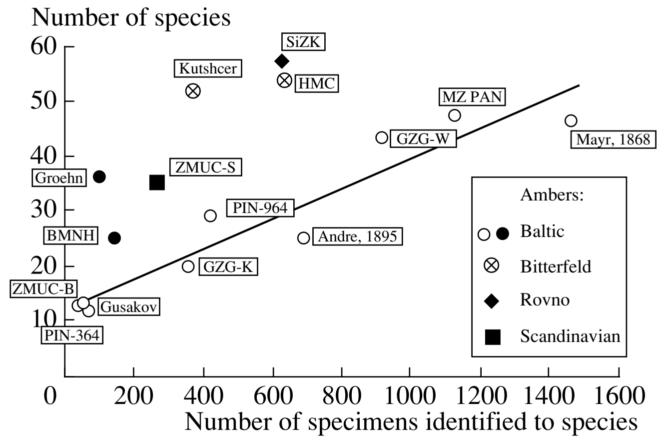

Fig. 2. Relationship between the number of ant inclusions examined and the number of species identified. The trend line ($S = 0.0269N + 12.251$) was calculated for only those Baltic amber collections that represent random samples.

personal Bitterfeld amber collection of Kutscher is most probably also nonrandom. Although it is almost half as large as the HMC collection (396 and 736 specimens, respectively) both contain an approximately equal number of species (52 and 54 species, respectively). Naturally, such collections do not reflect the actual relative abundances of species in the fossil faunas and cannot be used for their comparison. Small (less than 100 specimens) collections cannot be used either, because the relative abundances of species they represent may be strongly affected by stochastic factors.

Likewise, we could not use for comparison the collection of the University of Göttingen, which comprises about 10% of the collection that had previously belonged to the Geological Institute of Königsberg. Although the actual numbers of species, both in the collection identified by Wheeler (GZG-W) and the unidentified collection (GZG-K), agree relatively well with those expected, neither collection is in fact a random sample. The subfamilies Myrmicinae and Ponerinae are

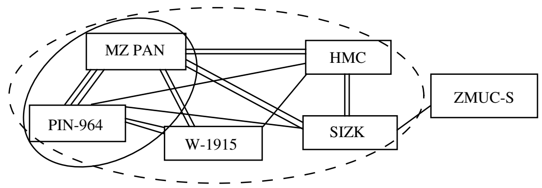

Fig. 3. The structure of similarity (after Smirnov, 1969) between reference amber collections, based on data from Table 4 (all ant species included). W-1915 designates the collection studied by Wheeler (1915). Degrees of similarity: triple line, 86%, double line, 78–82%, simple line, 72–75%. Solid and dashed ovals circumscribe the collections displaying similarity of the two highest degrees. See the text and Table 4 for details.

represented in both by only a few specimens, while Cerapachyinae and Myrmeciinae are completely absent. No type of any species described by Wheeler in those subfamilies has been preserved. At the same time, the collection contains almost all the types and rare species of Formicinae and Dolichoderinae. Most probably the Königsberg collection was arranged by subfamilies, and during evacuation only part of the specimen boxes were rescued.

Some difficulties also arise when literature data are used. Early authors did not recognize some of the species recognized currently. Wheeler (1915) corrected some of the errors made by Mayr (1868), but he had only seen those type specimens of Mayr that were deposited in Königsberg. Examination of Mayr's types at the NHMW demonstrated that the syntypes of *Formica flori* Mayr in fact belong to three species of two genera (*F. flori, F. gustawi* Dlussky, and *Pseudolasius boreus* Wheeler), and the syntypes of *Ponera atavia* Mayr belong to two genera (*Hypoponera* and *Pachycondyla*) (Dlussky, 2002b). Therefore, use of Mayr's data does not seem justified. For the same reason we decided not to use the data of André (1895). The situation with Wheeler's data is different. We examined 1139 ant inclusions, determined by Wheeler (ca. 12% of the collection he described), and the vast majority of our identifications agreed with his. Only in ten cases (less than 1%) our decisions were different. Four specimens identified by Wheeler as *Formica flori* turned out *F. gustawi* Dlussky, described after Wheeler's publication. One specimen, identified as *Dolichoderus balticus* (Mayr), turned out *D. robustus* Dlussky. Two specimens, identified as *Prenolepis henschei* Mayr, turned out *Dolichoderus polessus* Dlussky and *Tapinoma aberrans* Dlussky, and three specimens identified as *Ponera atavia* Mayr turned out two yet-undescribed species of *Ponera.* Because all the above species are rare and because the collection studied by Wheeler was vast (9527 specimens), his published data on the relative abundance of different species reflect the real situation.

Therefore, for our comparative analyses we used: for Baltic amber, published data on the ants of Königsberg collection (Wheeler, 1915) as well as PIN-964 and MZ PAN collections we examined; for Bitterfeld amber, the HMC; for Scandinavian amber, the ZMUC-S; and for Rovno amber, the SIZK collections. These will be referred to below as the *reference* collections. It needs to be noted that only for the PIN-964 and SIZK collections we can be absolutely sure that these are random samples, because it is known that the material came directly from the amber processing factories without any prior sorting.

COMPARISON METHODS

The most common metric used for comparison of modern faunas is Jaccard's index (i.e., the ratio of the number of species shared by two samples to the combined number of species in these samples, expressed as a percentage). Yet, this index is only applicable when the species composition of the faunas is exhaustively known. Our data indicate that none of the collections that we examined represents the fauna exhaustively. In particular, this is indicated by the linear relationship between the number of identified species and the collection size in the range between 100 and 1500 specimens. Another evidence is the fact that more than half of the species are represented in these collections by only one or two specimens: 20 out of 29 (69%) in PIN-964, 27 out of 43 (63%) in MZ PAN, 32 out of 54 (59%) in HMC, 21 out of 35 (60%) in ZMUC-S, and 34 out of 57 (60%) in SIZK. For these reasons we decided that it would not be appropriate to use Jaccard's index for comparison between collections.

It seems more adequate to compare collections using frequency spectra of the species. We used Shorygin's index (Shorygin, 1939), also known as Schoener's overlap index (Schoener, 1974). It is calculated as the sum of the minimum values of relative abundance across all the species represented in both compared habitats, expressed in percents:

$$PS = \Sigma \min|P_{ki}, P_{kj}|,$$

where P_{ki} is the proportion of the species k in the total number of specimens in the sample i, P_{kj} is its proportion in the sample j, and min $|P_{ki}, P_{kj}|$ is the minimum of the two values P. Our results are presented as upper triangular matrices (Tables 4–8) and visualized as taxonomic structure diagrams (Figs. 3–7), introduced by Smirnov (1969).

RESULTS

The full list of ant species found in Late Eocene ambers, including the number of specimens, is presented in Table 2. Not included are *Prionomyrmex janzeni* Baroni Urbani (Baroni Urbani, 2000), *Bradoponera electrina* De Andrade et Baroni Urbani, and *Bradoponera wunderlichi* Baroni Urbani et De Andrade (De Andrade and Baroni Urbani, 2003), as well as the data of Emery (1905), who described *Dimorphomyrmex theryi* (= *Gesomyrmex hoernesi* Mayr) and

Table 2. Composition of ant species in collections of Late Eocene European ambers

Authors	Mayr, 1868	Andre, 1895	Wheeler, 1915	Dlussky, original data					
Ambers	Baltic				Bitter-feld	Scandi-navian	Rovno	Unknown	All
ANEURETINAE									
Paraneuretus longipennis Wheeler			1						
Paraneuretus tornquisti Wheeler			24	6	1				7
Pityomyrmex tornquisti Wheeler			1						
Protaneuretus sp. (undescribed)					1				1
Protaneuretus succineus Wheeler			5						
DOLICHODERINAE									
Anonychomyrma constricta (Mayr)	10	3	57	16	7	1	6	1	31
Anonychomyrma samlandica (Wheeler)			82	12	2		3		17
Asymphylomyrmex balticus Wheeler			10	8			1		9
Ctenobethylus goepperti (Mayr)	580	309	4539	1355	405	70	194	23	2047
Ctenobethylus oblongiceps (Wheeler), comb. n.			1	1					1
Dolichoderus balticus (Mayr)	11	1	18	21	4	1	1	1	28
Dolichoderus brevicornis Dlussky				1					1
Dolichoderus brevipalpis Dlussky				1					1
Dolichoderus brevipennis Dlussky					1				1
Dolichoderus cornutus (Mayr)	9	3	16	12	1			1	14
Dolichoderus elegans Wheeler			1						
Dolichoderus granulinotus Dlussky				2					2
Dolichoderus kutscheri Dlussky					1				1
Dolichoderus longipennis (Mayr)	2			1					1
Dolichoderus longipilosus Dlussky				1		1			2
Dolichoderus lucidus Dlussky							2		2
Dolichoderus mesosternalis Wheeler			11	1	1	1			3
Dolichoderus nanus Dlussky				1					1
Dolichoderus passaloma Wheeler			10	8	4		1		13
Dolichoderus perkovskyi Dlussky						1	7		8
Dolichoderus pilipes Dlussky						1	1		2
Dolichoderus polessus Dlussky			+	1			12		13
Dolichoderus polonicus Dlussky				2					2
Dolichoderus punctatus Dlussky				1					1
Dolichoderus robustus Dlussky			+	1		1	3		5
Dolichoderus sculpturatus (Mayr)	2	4	13	7	3				10
Dolichoderus tertiarius (Mayr)	87	38	369	78	20	15	2	5	120
Dolichoderus vlaskini Dlussky							1		1
Dolichoderus zherichini Dlussky							1		1
Dolichoderus sp. (undescribed)				1					1
Iridomyrmex geinitzi (Mayr)	168	80	1041	259	62	16	26	5	368
Liometopum oligocenicum Wheeler			2						
Tapinoma aberrans Dlussky							1		1
Tapinoma electrinum Dlussky			+	11	9		4		24
Tapinoma sp. A (undescribed)					7				7
Tapinoma sp. B (undescribed)					24				24
Technomyrmex sp. (undescribed)					1				1
Zherichinius sp. (undescribed)					1				1
gen et sp. undescribed						2			2

Table 2. (Contd.)

Authors	Mayr, 1868	Andre, 1895	Wheeler, 1915	Dlussky, original data					
Ambers	Baltic				Bitter-feld	Scandi-navian	Rovno	Unknown	All
FORMICINAE									
Camponotus mengei Mayr	12	12	105	32	7	2	3		44
Camponotus sp. (undescribed)							1		1
Cataglyphoides constrictus (Mayr), comb. n.	5	2	12	10					10
Cataglyphoides intermedius Dlussky				3					3
Conoformica bitterfeldiana Dlussky					1				1
Drymomyrmex claripennis Wheeler			1						
Drymomyrmex fuscipennis Wheeler			4	4					4
Formica flori Mayr	189	99	1022	281	43	8	27	7	366
Formica gustawi Dlussky	+		+	23	3		5	1	32
Formica horrida Wheeler			2						
Formica kutscheri Dlussky					2				2
Formica paleopolonica Dlussky				5					5
Formica phaethusa Wheeler			3	1	4				5
Formica radchenkoi Dlussky							1		1
Formica strangulata Wheeler			2	1					1
Formica zherichini Dlussky				1					1
Gesomyrmex hoernesi Mayr	19	7	172	39	12	4	1		56
Glaphyromyrmex oligocenicus Wheeler			1	3					3
Lasius edentatus Mayr	1								
Lasius nemorivagus Mayr			1						
Lasius pumilus Mayr	3	1	67	6	2				8
Lasius punctulatus Mayr	4		8	1					1
Lasius schiefferdckeri Mayr	174	96	902	504	237	64	116	8	929
Lasius sp. (undescribed)				1					1
Oecophylla brischkei Mayr	5		45	6	7				13
Oecophylla crassinoda Wheeler			1	1	1				2
Paratrechina pygmaea (Mayr), comb. n.	23	1	49	85	32	10	18		145
Plagiolepis balticus Dlussky	1	1	12	1					1
Plagiolepis klinsmanni Mayr	8	3	85	25	2	1	5		33
Plagiolepis kuenowi Mayr	1	2	10	7	4	8	3		22
Plagiolepis minutissima Dlussky				2			2		4
Plagiolepis singularis Mayr	1								
Plagiolepis solitaria Mayr	1			1	3		1		5
Plagiolepis squamifera Mayr	2		4	2	2				4
Plagiolepis succini Andre		1							
Plagiolepis sp. A (undescribed)					1				1
Plagiolepis sp. B (undescribed)							1		1
Prenolepis henschei Mayr	69	18	524	209	3	17	17		246
Prodimorphomyrmex primigenius Wheeler			1						
Protoformica proformicoides Dlussky				1		1			2
Pseudolasius boreus Wheeler	+		33	26	1		2		29
MYRMECIINAE									
Prionomyrmex longiceps Mayr	1		9	1	1				2

Table 2. (Contd.)

Authors	Mayr, 1868	Andre, 1895	Wheeler, 1915	Dlussky, original data					
Ambers	Baltic				Bitter-feld	Scandi-navian	Rovno	Unknown	All
PSEUDOMYRMECINAE									
Tetraponera europaea Dlussky					1		1		2
Tetraponera groechni Dlussky				1					1
Tetraponera klebsi (Wheeler)			1	1					1
Tetraponera lacrimarum (Wheeler)			1	1	1				2
Tetraponera ocellata (Mayr)	5		5	2	2	3	1		8
Tetraponera simplex (Mayr)	7		10	8	6	4	7	3	28
CERAPACHYINAE									
Procerapachys annosus Wheeler			8	9	3				12
Procerapachys favosus Wheeler			1						
Procerapachys sulcatus Dlussky				1					1
PONERINAE									
Amblyopone groehni Dlussky				1					1
Amblyopone electrina Dlussky				1					1
Electroponera dubia Wheeler			1						
Gnamptogenys europaea (Mayr)	1		3	4	5		1	4	14
Gnamptogenys rohdendorfi Dlussky				1					1
Bradoponera meyeri Mayr	5	2	11	7	2		2		11
Bradoponera similis Dlussky					1				1
Proceratium eocenicum Dlussky				2					2
Hypoponera atavia (Mayr)	13		29	14	4	4			22
Pachycondyla baltica Dlussky	+			1					1
Pachycondyla gracilicornis (Mayr)	1								
Pachycondyla succinea (Mayr)	3		21	4	3	1	1		9
Pachycondyla tristis Dlussky					1				1
Pachycondyla conservata Dlussky							1		1
Platythyrea primaeva Wheeler			2						
Ponera lobulifera Dlussky			+	3					3
Ponera mayri Dlussky			+	3			1		4
Ponera wheeleri Dlussky					3				3
MYRMICINAE									
Agroecomyrmex duisburgi (Mayr)	2		4	1	1				2
Aphaenogaster antiqua Dlussky							1		1
Aphaenogaster mersa Wheeler			1	2					2
Aphaenogaster oligocenica Wheeler			1	1	1				2
Aphaenogaster sommerfeldti Mayr	6	2	15	7	5				12
Aphaenogaster sp. A (undescribed)				1					1
Aphaenogaster sp. B (undescribed)						2			2
Electromyrmex klebsi Wheeler			1						
Electromyrmex sp. A (undescribed)					1				1
Ennaemerus reticulatus Mayr	3		10	5					5
Eocenomyrma electrina Dlussky et Radchenko						1			1
Eocenomyrma elegantula Dlussky et Radchenko				1					1
Eocenomyrma orthospina Dlussky et Radchenko				1			1		2
Eocenomyrma rugosostriata (Mayr)	2		10	5	5				10

Table 2. (Contd.)

Authors	Mayr, 1868	Andre, 1895	Wheeler, 1915	Dlussky, original data					
Ambers	Baltic				Bitter-feld	Scandi-navian	Rovno	Unknown	All
Eocenomyrma sp. A (undescribed)							1		1
Fallomyrma transversa Dlussky et Radchenko					5	19	6	3	33
Monomorium mayrianum Wheeler	5		23	5	9		1		15
Monomorium pilipes Mayr	3	1	22	23	23	6	1		53
Myrmica eocenica Radchenko, Dlussky, Elmes				1		1			2
Myrmica intermedia (Wheeler)			1	1					1
Myrmica longispinosa Mayr	1		1						
Myrmica paradoxa Radchenko, Dlussky, Elmes					3				3
Myrmica rudis Mayr	2	1	10	1					1
Myrmica sp. A (undescribed)				1					1
Oligomyrmex antiquus (Mayr)	3		9	8	2				10
Oligomyrmex nitidus Dlussky							1		1
Oligomyrmex sp. A (undescribed)					1				1
Oligomyrmex ucrainicus Dlussky							1		1
Paraneranoplus primaevus Wheeler			1						
Paraneranoplus sp. A (undescribed)				1					1
Pheidole ? sp. A (undescribed)						1			1
Pheidologeton sp. A (undescribed)					5				5
Pristomyrmex sp. A (undescribed)						1			1
Pristomyrmex sp. B (undescribed)					2				2
Stenamma berendti (Mayr)	1		1						
Stenamma sp. A (undescribed)								1	1
Stigmomyrmex venustus Mayr	2	1	3	1	5				6
Stiphromyrmex robustus (Mayr)	1		2	1					1
Stiphromyrmex sp. A (undescribed)				1					1
Temnothorax glaesarius (Wheeler)			1	2					2
Temnothorax gracilis (Mayr)	3		31	7	9		2		18
Temnothorax histriculus (Wheeler)			1	1					1
Temnothorax longaevus (Wheeler)			1		1		1		2
Temnothorax petiolatus (Mayr)	2		6	1	2				3
Temnothorax placivus (Wheeler)			1						
Temnothorax sp. A (undescribed)					1	1			2
Temnothorax sp. B (undescribed)						1			1
Temnothorax sp. C (undescribed)						1			1
Temnothorax sp. D (undescribed)					2				2
Tetramorium sp. A (undescribed)				1					1
Tetramorium sp. B (undescribed)				1					1
Tetramorium sp. C (undescribed)							1		1
Vollenhovia beyrichi (Mayr)	2	1	2						
Vollenhovia prisca (Andre)		1							
Genus A sp. A (undescribed)					1				1
Genus B sp. A (undescribed)				1					1
No. specimens identified to species	1461	690	9527	3237	1039	271	501	63	5111
No. species identified	51	26	86	100	71	34	51	13	146

Note: Only inclusions identified to species are counted. Data taken from the literature were corrected for synonymy. The following species are excluded from the list: *Prionimyrmex janzeni* Baroni Urbani, 2000, *Bradoponera electrina* De Andrade et Baroni Urbani, 2003, and *Bradoponera wunderlichi* Baroni Urbani et De Andrade, 2003. (+) species identified in the examined collections, but not previously listed by Mayr or Wheeler.

Table 3. Relative abundance of ant species in reference collections, %

Ambers	Baltic			Bitterfeld	Scandinavian	Rovno
Collections	Wheeler, 1915	PIN 964	MZ PAN	HMC	ZMUC-S	SIZC
Paraneuretus longipennis	0.01	0.00	0.00	0.00	0.00	0.00
Paraneuretus tornquisti	0.25	0.00	0.00	0.16	0.00	0.00
Pityomyrmex tornquisti	0.01	0.00	0.00	0.00	0.00	0.00
Protaneuretus succineus	0.05	0.00	0.00	0.00	0.00	0.00
Anonychomyrma constricta	0.60	0.00	0.00	0.79	0.37	1.24
Anonychomyrma samlandica	0.86	0.48	0.00	0.00	0.00	0.62
Asymphylomyrmex balticus	0.10	0.48	0.22	0.00	0.00	0.21
Ctenobethylus goepperti	47.64	52.14	50.27	42.27	25.83	37.81
Ctenobethylus oblongiceps	0.01	0.00	0.00	0.00	0.00	0.00
Dolichoderus balticus	0.19	0.48	0.22	0.63	0.37	0.21
Dolichoderus brevicornis	0.00	0.24	0.00	0.00	0.00	0.00
Dolichoderus cornutus	0.17	0.00	0.11	0.00	0.00	0.00
Dolichoderus elegans	0.01	0.00	0.00	0.00	0.00	0.00
Dolichoderus granulinotus	0.00	0.00	0.22	0.00	0.00	0.00
Dolichoderus longipilosus	0.00	0.24	0.00	0.00	0.37	0.00
Dolichoderus lucidus	0.00	0.00	0.00	0.00	0.00	0.41
Dolichoderus mesosternalis	0.12	0.00	0.00	0.00	0.37	0.00
Dolichoderus nanus	0.00	0.00	0.11	0.00	0.00	0.00
Dolichoderus passaloma	0.10	0.24	0.00	0.47	0.00	0.21
Dolichoderus perkovskyi	0.00	0.00	0.00	0.00	0.37	1.45
Dolichoderus pilipes	0.00	0.00	0.00	0.00	0.37	0.21
Dolichoderus polessus	0.00	0.00	0.00	0.00	0.00	2.48
Dolichoderus polonicus	0.00	0.00	0.11	0.00	0.00	0.00
Dolichoderus robustus	0.00	0.00	0.00	0.00	0.37	0.62
Dolichoderus sculpturatus	0.14	0.48	0.22	0.32	0.00	0.00
Dolichoderus tertiarius	3.87	2.62	2.83	2.84	5.54	0.41
Dolichoderus vlaskini	0.00	0.00	0.00	0.00	0.00	0.21
Dolichoderus zherichini	0.00	0.00	0.00	0.00	0.00	0.21
Iridomyrmex geinitzi	10.93	5.95	3.81	6.31	5.90	5.37
Liometopum oligocenicum	0.02	0.00	0.00	0.00	0.00	0.00
Tapinoma aberrans	0.00	0.00	0.00	0.00	0.00	0.21
Tapinoma electrinum	0.00	0.48	0.44	1.26	0.00	0.83
Technomyrmex sp.	0.00	0.00	0.00	0.16	0.00	0.00
Zherichinius sp.	0.00	0.00	0.00	0.16	0.00	0.00
gen et sp. undescribed	0.00	0.00	0.00	0.00	0.74	0.00
Camponotus mengei	1.10	0.48	0.44	0.79	0.74	0.62
Camponotus sp.	0.00	0.00	0.00	0.00	0.00	0.21
Cataglyphoides constrictus	0.13	0.00	0.00	0.00	0.00	0.00
Conoformica bitterfeldiana	0.00	0.00	0.00	0.16	0.00	0.00
Drymomyrmex claripennis	0.01	0.00	0.00	0.00	0.00	0.00
Drymomyrmex fuscipennis	0.04	0.00	0.00	0.00	0.00	0.00
Formica flori	10.73	7.86	5.44	4.57	2.95	4.96
Formica gustawi	0.00	0.95	0.00	0.16	0.00	1.03
Formica horrida	0.02	0.00	0.00	0.00	0.00	0.00
Formica kutscheri	0.00	0.00	0.00	0.16	0.00	0.00

Table 3. (Contd.)

Ambers	Baltic			Bitterfeld	Scandinavian	Rovno
Collections	Wheeler, 1915	PIN 964	MZ PAN	HMC	ZMUC-S	SIZC
Formica paleopolonica	0.00	0.00	0.54	0.00	0.00	0.00
Formica phaethusa	0.03	0.24	0.00	0.63	0.00	0.00
Formica radchenkoi	0.00	0.00	0.00	0.00	0.00	0.21
Formica strangulata	0.02	0.00	0.00	0.00	0.00	0.00
Formica zherichini	0.00	0.24	0.00	0.00	0.00	0.00
Gesomyrmex hoernesi	1.81	0.71	1.31	1.42	1.48	0.21
Glaphyromyrmex oligocenicus	0.01	0.00	0.22	0.00	0.00	0.00
Lasius nemorivagus	0.01	0.00	0.00	0.00	0.00	0.00
Lasius pumilus	0.70	0.00	0.44	0.16	0.00	0.00
Lasius punctulatus	0.08	0.00	0.00	0.00	0.00	0.00
Lasius schiefferdckeri	9.47	15.24	19.48	24.45	23.62	23.76
Oecophylla brischkei	0.47	0.00	0.22	0.79	0.00	0.00
Oecophylla crassinoda	0.01	0.00	0.00	0.16	0.00	0.00
Paratrechina pygmaea	0.51	0.71	3.59	1.26	3.69	3.72
Plagiolepis balticus	0.13	0.00	0.00	0.00	0.00	0.00
Plagiolepis klinsmanni	0.89	0.00	1.20	0.32	0.37	1.03
Plagiolepis kuenowi	0.10	0.24	0.11	0.16	2.95	0.62
Plagiolepis minutissima	0.00	0.24	0.00	0.00	0.00	0.41
Plagiolepis solitaria	0.00	0.00	0.00	0.32	0.00	0.21
Plagiolepis sp.	0.00	0.00	0.00	0.00	0.00	0.21
Plagiolepis squamifera	0.04	0.00	0.00	0.32	0.00	0.00
Prenolepis henschei	5.50	6.67	4.79	0.32	6.27	3.31
Prodimorphomyrmex primigenius	0.01	0.00	0.00	0.00	0.00	0.00
Protoformica proformicoides	0.00	0.00	0.00	0.00	0.37	0.00
Pseudolasius boreus	0.35	0.00	0.00	0.16	0.00	0.41
Prionomyrmex longiceps	0.09	0.00	0.00	0.16	0.00	0.00
Tetraponera europaea	0.00	0.00	0.00	0.16	0.00	0.21
Tetraponera klebsi	0.01	0.00	0.00	0.00	0.00	0.00
Tetraponera lacrimarum	0.01	0.00	0.00	0.00	0.00	0.00
Tetraponera ocellata	0.05	0.24	0.00	0.32	1.11	0.21
Tetraponera simplex	0.10	0.24	0.22	0.47	1.48	1.45
Procerapachys annosus	0.08	0.00	0.00	0.32	0.00	0.00
Procerapachys favosus	0.01	0.00	0.00	0.00	0.00	0.00
Procerapachys sulcatus	0.00	0.00	0.11	0.00	0.00	0.00
Electroponera dubia	0.01	0.00	0.00	0.00	0.00	0.00
Gnamptogenys europaea	0.03	0.00	0.22	0.47	0.00	0.21
Bradoponera meieri	0.12	0.00	0.33	0.16	0.00	0.41
Bradoponera similis	0.00	0.00	0.00	0.16	0.00	0.00
Proceratium eocenicum	0.00	0.00	0.11	0.00	0.00	0.00
Hypoponera atavia	0.30	0.00	0.33	0.00	1.48	0.00
Pachycondyla conservata	0.00	0.00	0.00	0.00	0.00	0.21
Pachycondyla succinea	0.22	0.00	0.22	0.16	0.37	0.21
Platythyrea primaeva	0.02	0.00	0.00	0.00	0.00	0.00
Ponera mayri	0.00	0.00	0.11	0.00	0.00	0.21
Ponera wheeleri	0.00	0.00	0.00	0.32	0.00	0.00

Table 3. (Contd.)

Ambers	Baltic			Bitterfeld	Scandinavian	Rovno
Collections	Wheeler, 1915	PIN 964	MZ PAN	HMC	ZMUC-S	SIZC
Agroecomyrmex duisburgi	0.04	0.00	0.00	0.16	0.00	0.00
Aphaenogaster antiqua	0.00	0.00	0.00	0.00	0.00	0.21
Aphaenogaster mersa	0.01	0.00	0.00	0.00	0.00	0.00
Aphaenogaster oligocenica	0.01	0.24	0.00	0.16	0.00	0.00
Aphaenogaster sommerfeldti	0.16	0.00	0.44	0.47	0.00	0.00
Aphaenogaster sp. A	0.00	0.00	0.11	0.00	0.00	0.00
Aphaenogaster sp. B	0.00	0.00	0.00	0.00	0.74	0.00
Electromyrmex klebsi	0.01	0.00	0.00	0.00	0.00	0.00
Electromyrmex sp.	0.00	0.00	0.00	0.16	0.00	0.00
Ennaemerus reticulatus	0.10	0.00	0.11	0.00	0.00	0.00
Eocenomyrma electrina	0.00	0.00	0.00	0.00	0.37	0.00
Eocenomyrma orthospina	0.00	0.00	0.11	0.00	0.00	0.00
Eocenomyrma rugosostriata	0.10	0.00	0.22	0.16	0.00	0.00
Eocenomyrma sp.	0.00	0.00	0.00	0.00	0.00	0.21
Fallomyrma transversa	0.00	0.00	0.00	0.47	7.01	1.24
Monomorium mayrianum	0.24	0.00	0.00	0.95	0.00	0.21
Monomorium pilipes	0.23	0.00	0.33	1.89	2.21	0.21
Myrmica eocenica	0.00	0.24	0.00	0.00	0.37	0.00
Myrmica intermedia	0.01	0.00	0.00	0.00	0.00	0.00
Myrmica longispinosa	0.01	0.00	0.00	0.00	0.00	0.00
Myrmica rudis	0.10	0.00	0.11	0.00	0.00	0.00
Oligomyrmex antiquus	0.09	1.19	0.11	0.16	0.00	0.00
Oligomyrmex nitidus	0.00	0.00	0.00	0.00	0.00	0.21
Oligomyrmex ucrainicus	0.00	0.00	0.00	0.00	0.00	0.21
Paraneranoplus primaevus	0.01	0.00	0.00	0.00	0.00	0.00
Paraneranoplus sp.	0.00	0.00	0.11	0.00	0.00	0.00
Pheidole ? sp.	0.00	0.00	0.00	0.00	0.37	0.00
Pristomyrmex sp.	0.00	0.00	0.00	0.00	0.37	0.00
Stenamma berendti	0.01	0.00	0.00	0.00	0.00	0.00
Stigmomyrmex venustus	0.03	0.00	0.00	0.47	0.00	0.00
Stiphromyrmex robustus	0.02	0.00	0.11	0.00	0.00	0.00
Stiphromyrmex sp.	0.00	0.00	0.11	0.00	0.00	0.00
Temnothorax glaesarius	0.01	0.24	0.00	0.00	0.00	0.00
Temnothorax gracilis	0.33	0.00	0.00	0.47	0.00	0.41
Temnothorax histriculus	0.01	0.24	0.00	0.00	0.00	0.00
Temnothorax longaevus	0.01	0.00	0.00	0.00	0.00	0.21
Temnothorax petiolatus	0.06	0.00	0.00	0.00	0.00	0.00
Temnothorax placivus	0.01	0.00	0.00	0.00	0.00	0.00
Temnothorax sp. A	0.00	0.00	0.00	0.16	0.37	0.00
Temnothorax sp. B	0.00	0.00	0.00	0.00	0.37	0.00
Temnothorax sp. C	0.00	0.00	0.00	0.00	0.37	0.00
Tetramorium sp. A	0.00	0.00	0.11	0.00	0.00	0.00
Tetramorium sp. B	0.00	0.00	0.00	0.00	0.00	0.21
Tetramorium sp. C	0.00	0.00	0.11	0.00	0.00	0.00
Vollenhovia beyrichi	0.02	0.00	0.00	0.00	0.00	0.00
Total no. of inclusions	9527	420	919	634	271	482

Table 4. Similarity (after Shorygin, 1939) between reference amber collections: all ant species

	PIN-964	MZ PAN	HMC	ZMUC-S	SIZC
Wheeler, 1915	82%	80%	73%	58%	67%
PIN-964		86%	76%	62%	72%
MZ PAN			80%	67%	77%
HMC				70%	80%
ZMUC-S					72%

Note: For explanation of collection acronyms, see Material. Amber types: Baltic (Wheeler, 1915, PIN-964, MZ PAN), Bitterfeld (HMC), Scandinavian (ZMUC-S), and Rovno (SIZK). Different shades of background correspond to the degrees of similarity shown in Fig. 3 by the lines of variable thickness.

a pseudogyne of *Camponotus igneus* Mayr (= *C. mengei* Mayr). These data were excluded because the authors of the descriptions did not report the number of ants in the collections they studied. The nomenclature has been brought up to date according to Bolton et al. (2005) and publications by Dlussky after 2005. Additionally, some new changes are introduced:

1. *Iridomyrmex oblongiceps* Wheeler was placed in the genus *Ctenobethylus* Brues (comb. n.) because it displays all the diagnostic characters of that genus.

2. The genus *Pityomyrmex* Wheeler was transferred from the subfamily Dolichoderinae to Aneuretinae (comb. n.). Wheeler (1915) placed it in a separate tribe Dolichoderinae. However, he also treated Aneuretinae as a tribe in the same subfamily. Judging from the drawing (the type is lost), *Pityomyrmex* is more similar to *Paraneuretus* Wheeler than typical Dolichoderinae.

3. *Prenolepis pygmaea* Mayr was transferred to the genus *Paratrechina* Motschoulsky (comb. n.). At the time when the studies of Mayr and Wheeler were published, these genera were treated as one. Later they were separated by Emery (1925). In all of its characters, *P. pygmaea* is a typical representative of *Paratrechina.*

4. In an earlier study, Dlussky (1997) synonymized *Drymomyrmex* Wheeler to *Camponotus* Mayr, based exclusively on the description. After examination of the types of *Drymomyrmex fuscipennis* Wheeler, it became obvious that the species does not belong to the tribe Camponotini and is only convergently similar to the subgenus *Colobopsis* Mayr of the genus *Camponotus.* Therefore, the former name is being restored here.

5. Recently, Bolton (2003) divided the subfamily Ponerinae into subfamilies Amblyoponinae, Ponerinae, Ectatomminae, Heteroponerinae, Paraponerinae, and Proceratiinae and the subfamily Myrmicinae into Agroecomyrmecinae and Myrmicinae. Without going into details, it needs to be mentioned here that we do not consider that division justified. In this publication we treat Ponerinae and Myrmicinae in their traditional, undivided scopes, i.e., as was until recently accepted by the majority of authors, including Bolton (1994, 1995) himself.

In total, including data from the literature and newly discovered by us yet-undescribed species, and correcting for synonyms, 171 ant species were recorded from the Late Eocene ambers. These represent 63 genera of 9 subfamilies. One hundred and twenty-four species of 53 genera were found in Baltic amber; 71 species of 40 genera, in Bitterfeld amber; 35 species of 24 genera, Scandinavian amber; and 58 species of 27 genera, in Rovno amber. Seventeen species (10% of the total) were found in all the amber types: *Anonychomyrma constricta* (Mayr), *Camponotus mengei* Mayr, *Ctenobethylus goepperti* (Mayr), *Dolichoderus balticus* (Mayr), *D. tertiarius* (Mayr), *Formica flori* Mayr, *Gesomyrmex hoernesi* Mayr, *Iridomyrmex geinitzi* (Mayr), *Lasius schiefferdckeri* Mayr, *Monomorium pilipes* Mayr, *Pachycondyla succinea* (Mayr), *Paratrechina pygmaea* (Mayr), *Plagiolepis klinsmanni* Mayr, *Plagiolepis kuenowi* Mayr, *Prenolepis henschei* Mayr, *Tetraponera ocellata* (Mayr), and *Tetraponera simplex* (Mayr). In all the representative collections the ants of these species comprise the vast majority of inclusions. In the reference collections of Baltic amber their relative abundances were nearly identical: 94.0% in Wheeler's collection, 93.3% in PIN-964, and 94.2% in MZ PAN. In the reference collections of Bitterfeld (HMC), Scandinavian (ZMUC-S), and Rovno (SIZK) amber, the relative abundances of these species were lower: 88.7%, 84.6%, and 85.4%, respectively.

At the same time, the ant faunas of these amber types are different, especially in the relative abundances of particular species (Table 3). The above data are already sufficient to see that the proportion of low-abundance species in Bitterfeld amber is 1.7 times and that in Rovno and Scandinavian ambers 2.2–2.3 times as large as on average in Baltic amber (6.7%). The higher diversity of these amber faunas is also evidenced by the data on the relationship between the sample size and the number of identified species (Fig. 2). For most Baltic amber collections containing less than 1500 specimens, the relationship between the collection size and the number of identified species is approximated by the linear equation $S = 0.0269N + 12.251$, where N is the number of specimens identified to species, and S is the number of identified species. The actual number of species varied among representative collections between 0.9 and 1.2 times the value estimated using this formula. At the same time, the actual number of species in Bitterfeld (HMC) and Scandinavian (ZMUC) ambers was 1.8 and in Rovno amber (SIZK) 2 times as large as the value estimated for Baltic amber samples of the same size. Any accurate comparison of amber faunas based on the composition of rare species they include is impossible, because, in most cases, such species are represented by only a few individuals, and their absence in a particular amber type is likely to be an artifact of the small sample size. Yet, in one case the difference is unquestionable. One of the species we described, *Fallomyrma transversa* (Dlussky and Radchenko, 2006a), comprised 20 out of the 273 (7.3%) Scandinavian amber inclusions, 8 out of the 628 (1.3%) Rovno inclusions, and 3 out of the 636 (0.5%) Bitterfeld inclusions (HMC), but it was never found among the 3239 Baltic inclusions. Considering the extremely high qualification of Wheeler, one can be reasonably confident that this species had also been absent from the large Baltic amber collection he examined (9527 inclusions).

Table 4 and Fig. 3 present our results concerning the structure of similarity in species composition between the reference collections. The Moscow and Warsaw collections turned out the most similar and the Scandinavian amber the most isolated from the rest.

When only the 11 species shared by all the reference collections are considered, all the Baltic amber collections group together, the Bitterfeld and Rovno ambers are most close to these, and the Scandinavian amber is, again, the most isolated (Table 5, Fig. 4). This picture is similar to the above-described distribution of the proportion of rare species, maximal in the Scandinavian and minimal in the Baltic ambers. When 22 most abundant species (i.e., those which comprised >1% in at least one sample) are included in the analysis, the result is the same (Table 6, Fig. 5). When the two most abundant species, *Ctenobethylus goepperti* and *Lasius schiefferdeckeri*, are excluded from the analysis, both the Scandinavian and the Rovno ambers turn out the most isolated (Table 7, Fig. 6). However, when we attempted comparing our samples based only on rare species (those not exceeding 1% of the inclusions in any single collection), the result was uninterpretable. The composition of the Scandinavian amber remains the most peculiar, but the most isolated among other samples turn out Baltic amber collections in Moscow and Warsaw, instead of the Bitterfeld and Rovno ambers (Table 8, Fig. 7).

These results indicate that the Baltic, Bitterfeld, Scandinavian, and Rovno amber faunas differ in their ant species compositions. The most distinct is the ant species composition of the Scandinavian amber, that of the Rovno amber is slightly less distinct, while the Bitterfeld amber is significantly closer in this respect to the Baltic amber. The bulk of these differences is contributed by the most abundant species, primarily, *Ctenobethylus goepperti* and *Lasius schiefferdeckeri.* The first

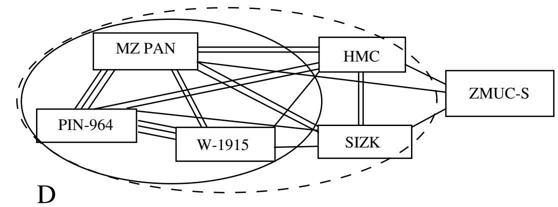

Fig. 4. The structure of similarity (after Smirnov, 1969) between reference amber collections, based on data from Table 5 (16 ant species, shared by all reference collections). Degrees of similarity: triple line, 81–84%, double line, 73–76%, simple line, 65–70%; other designations as in Fig. 3.

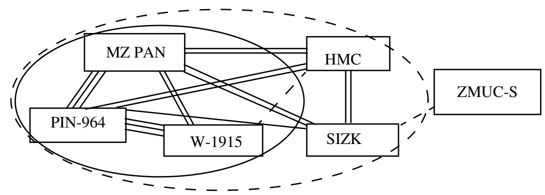

Fig. 5. The structure of similarity (after Smirnov, 1969) between reference amber collections, based on data from Table 6 (22 most abundant ant species). Degrees of similarity: triple line, 81–85%, double line, 77–79%, simple line, 74%, dashed line, 70–71%; other designations as in Fig. 3.

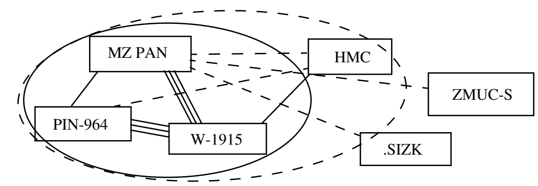

Fig. 6. The structure of similarity (after Smirnov, 1969) between reference amber collections, based on data from Table 7 (all ant species, except *Ctenobethylus goepperti* and *Lasius schiefferdeckeri*). Degrees of similarity: triple line, 69–72%, double line, 65%, simple line, 61%, dashed line, 54–56%; other designations as in Fig. 3.

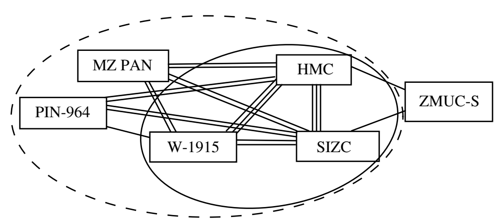

Fig. 7. The structure of similarity (after Smirnov, 1969) between reference amber collections, based on data from Table 8 (rare species only). Degrees of similarity: triple line, 2.7–2.9%, double line, 1.6–2.1%, simple line, 1.0–1.2%; other designations as in Fig. 3.

dominates in all collections, but, among Baltic ambers, its share in the reference collections varies from 47.6% in Wheeler's sample to 52.1% in PIN-964. The relative abundance of this species in the Bitterfeld amber is not

Table 5. Similarity (after Shorygin, 1939) between reference amber collections: 16 ant species shared by all reference collections

	PIN-964	MZ PAN	HMC	ZMUC-S	SIZC
Wheeler, 1915	81%	78%	70%	58%	65%
PIN-964		84%	74%	61%	69%
MZ PAN			77%	66%	76%
HMC				69%	77%
ZMUC-S					69%

Note: Different shades of the background correspond to the degrees of similarity shown in Fig. 4 by the lines of variable thickness. Other designations as in Table 4.

Table 6. Similarity (after Shorygin, 1939) between reference amber collections: 22 most abundant ant species (i.e., accounting for >1% of inclusions in at least one collection)

	PIN-964	MZ PAN	HMC	ZMUC-S	SIZC
Wheeler, 1915	81%	78%	70%	58%	65%
PIN-964		85%	74%	61%	71%
MZ PAN			78%	66%	76%
HMC				69%	78%
ZMUC-S					71%

Note: Different shades of the background correspond to the degrees of similarity shown in Fig. 5 by the lines of variable thickness. Other designations as in Table 4.

Table 7. Similarity (after Shorygin, 1939) between reference amber collections: without the two most abundant species, *Ctenobethylus goepperti* and *Lasius schiefferdeckeri*

	PIN-964	MZ PAN	HMC	ZMUC-S	SIZC
Wheeler, 1915	72%	69%	61%	49%	50%
PIN-964		65%	55%	48%	51%
MZ PAN			56%	56%	56%
HMC				47%	51%
ZMUC-S					50%

Note: Different shades of the background correspond to the degrees of similarity shown in Fig. 6 by the lines of variable thickness. Other designations as in Table 4.

Table 8. Similarity (after Shorygin, 1939) between reference amber collections (139 rare species only, i.e., species not exceeding 1% of inclusions in any one collection)

	PIN-964	MZ PAN	HMC	ZMUC-S	SIZC
Wheeler, 1915	1.1%	2.0%	2.9%	0.5%	2.1%
PIN-964		0.7%	1.4%	0.8%	1.1%
MZ PAN			1.9%	0.3%	1.0%
HMC				0.7%	1.9%
ZMUC-S					0.8%

Note: Different shades of the background correspond to the degrees of similarity shown in Fig. 7 by the lines of variable thickness. Other designations as in Table 4.

significantly different (HMC, 42.3%), while in the Rovno and, particularly, the Scandinavian ambers it is considerably lower (SIZK, 37.8%; ZMUC-S, 25.8%). In contrast, the relative abundances of *L. schiefferdeckeri* in the Bitterfeld (HMC, 24.4%), Rovno (SIZK, 23.4%), and Scandinavian (ZMUC-S, 23.4%) ambers are approximately equal, considerably exceeding those for the Baltic amber (9.5% in Wheeler's sample, 15.0% in PIN-964, and 19.5% in MZ PAN).

There exist other differences, too. For example, the relative abundance of *Prenolepis henschei* in the Bitterfeld amber (0.3%) is significantly lower than in other ambers, where it varies between 4.1 and 6.7%. In the Scandinavian amber the participation of *Formica flori* (3.0%) is lower than in other ambers (4.1–10.7%). The relative abundance of *Dolichoderus tertiarius* in the Baltic and Bitterfeld ambers varies between 2.6% and 3.9%, reaches 5.5% in the Scandinavian amber, and comprises only 0.5% in the Rovno amber. In the latter amber type the species is substituted by a close one, *D. polessus*, which comprises 2.2% of all the inclusions there. A single specimen of this species was also found in the Baltic amber. The relative abundance of *Tetraponera simplex* is 0.1–0.2% in the Baltic, 0.5% in the Bitterfeld, 1.0% in the Rovno, and 1.5% in the Scandinavian ambers. The abundance of *Gesomyrmex hoernesi* in the Rovno amber is 0.3%, while in other ambers it varies between 0.7 and 1.8%.

Three explanations of these faunal differences can be put forward: (1) minor differences in age, (2) origin in different climatic zones, and (3) differences between environments.

In order to test the first hypothesis, we calculated relative abundances of species belonging to extant versus extinct genera in different amber types. So far, 26 extinct genera have been described (including papers in press) from the Late Eocene amber: *Agroecomyrmex* Mayr, *Asymphylomyrmex* Wheeler, *Bradoponera* Mayr, *Cataglyphoides* Dlussky, *Conoformica* Dlussky, *Ctenobethylus* Brues, *Drymomyrmex* Wheeler, *Electromyrmex* Wheeler, *Electroponera* Wheeler, *Ennaemerus* Mayr, *Eocenomyrma* Dlussky et Radchenko, *Fallomyrma* Dlussky et Radchenko, *Glaphyromyrmex* Wheeler, *Parameranoplus* Wheeler, *Paraneuretus* Wheeler, *Pityomyrmex* Wheeler, *Plesiomyrmex* Dlussky et Radchenko, *Protomyrmica* Dlussky et Radchenko, *Prionomyrmex* Mayr, *Procerapachys* Wheeler, *Prodimorphomyrmex* Wheeler, *Protaneuretus* Wheeler, *Protoformica* Dlussky, *Stigmomyrmex* Mayr, *Stiphromyrmex* Wheeler, and *Zherichinius* Dlussky. Two additional genera, discovered by us, currently await description. These genera represent 28 (42%) of the 63 genera recorded from these ambers. However, because each of these genera was represented by only a handful of species, the total proportion of the corresponding species is considerably lower: 27% (34 out of 124) in the Baltic, 20% (15 out of 71) in the Bitterfeld, 14% (5 out of 35) in the Scandinavian, and 12% (7 out of 58) in the Rovno amber. At first glance, the proportion of representatives of extinct genera in the total number of ant inclusions identified to genus in reference collections seems rather large: Wheeler (1915), 48.9%; PIN-964, 52.6%; MZ PAN, 51.8%; HMC, 44.8%; ZMUC-S, 34.4%; and SIZK, 41.1%. Thus, the Baltic amber fauna appears somewhat more archaic than those of other amber types. However, it needs to be taken into consideration that the bulk of inclusions representing extinct genera belong to *Ctenobethylus goepperti,* while the abundance of other representatives of extinct genera is low. If this species is excluded from the comparison, the picture changes drastically: Wheeler (1915), 2.4%; PIN-964, 1.0%; MZ PAN, 3.1%; HMC, 4.6%; ZMUC-S, 11.8%; and SIZK, 3.6%. Now the fauna of Scandinavian amber appears the most archaic, in this case due to the large proportion of *Fallomyrma transversa.* As previously mentioned, the composition of rare species in samples up to 1500 specimens is always purely random. Because nearly all species of the extinct genera are represented in collections by only a few individuals (except the excluded *C. goepperti*), the observed differences should also be treated as accidental. The observed higher species diversity of the extinct genera from the Baltic and Bitterfeld ambers, compared to the Scandinavian and Rovno ambers, is most probably explained by the larger sizes of the examined samples and, consequently, the increased probability of encountering rare species. Therefore, the examined material did not allow revealing statistically reliable differences in the relative abundances of extinct versus recent genera between different types of amber.

To test the hypothesis that the observed differences between the amber faunas reflect their origin in different climatic zones, we calculated the relative abundances of species in the genera the recent representatives of which are associated with different climates. If the samples under consideration indeed originated in different geographical zones, then it is logical to assume that the sources of the Baltic and Scandinavian ambers were located farther north than those of the Bitterfeld and Rovno ambers. Therefore, we can expect that, in those amber faunas, the proportion of recent genera currently associated predominantly with the temperate climate will be larger and that of genera currently associated with the tropics will be lower. In the modern fauna, the vast majority of species from the genera *Formica* L., *Lasius* Fabricius, and *Myrmica* Latreille occur in the Palearctic and Nearctic, with only few extending into tropical areas, where they are restricted exclusively to mountains. In contrast, recent species of the genera *Anonychomyrma* Donisthorpe, *Carebara* Westwod, *Gesomyrmex* Mayr, *Gnamptogenys* Roger, *Iridomyrmex* Mayr, *Meranoplus* F. Smith, *Oecophylla* F. Smith, *Pheidologeton* Mayr, *Platythyrea* Roger, *Pristomyrmex* Mayr, *Pseudolasius* Emery, *Technomyrmex* Mayr, *Tetraponera* F. Smith, and *Vollenhovia* Mayr (all these genera are represented in the Late

Eocene ambers of Europe) occur in the tropics or the southern parts of subtropical regions. Other genera contain both Palearctic and tropical species, although in most genera the latter dominate. In all the amber types the "tropical" genera are more diverse. The "Palearctic" and "tropical" genera accounted, respectively, for 16 (13%) and 19 (15%) out of the 124 species in the Baltic, 7 (10%) and 16 (23%) out of the 71 species in the Bitterfeld, 3 (9%) and 6 (18%) out of the 35 species in the Scandinavian, and 4 (7%) and 11 (19%) out of the 58 species in the Rovno ambers. In the reference collections, relative abundances of the "Palearctic" and "tropical" genera in the total number of ant inclusions identified to genus were, respectively, 21.2 and 15.4% (Wheeler, 1915), 24.8 and 8.8% (PIN-964), 26.0 and 6.0% (MZ PAN), 30.0 and 11.3% (HMC), 26.7 and 10.6% (ZMUC-S), and 28.5 and 10.0% (SIZK).

These data indicate that different amber faunas, indeed, differ in relative abundances of the genera presently associated predominantly with the temperate or the tropical climates, but these differences do not correlate with the latitude of the amber deposits.

Therefore, there remains only the last hypothesis, which explains the observed differences between the amber ant faunas by differences between the habitats where these had formed. This hypothesis can be evaluated by comparing relative abundances of various ecological types of ants in the examined collections. It is known that nearly all species of *Dolichoderus* Lund and all *Tetraponera* F. Smith are specialized to arboreal living and build their nests under bark or in dead tree branches. A close morphological similarity between recent and fossil representatives of these genera gives no reasons to suspect that in the Eocene their life style was different. The relative abundances of *Dolichoderus* inclusions in the Baltic amber were 4.6% in Wheeler's sample, 4.1% in PIN, and 3.7% in MZ PAN. In the Bitterfeld amber the share of this species (HMC, 5.3%) was close to the one observed in the Baltic faunas, but in the Scandinavian and Rovno ambers it was almost twice as large (ZMUC-S, 8.2%, SIZK, 7.3%). The relative abundances of *Tetraponera* in various ambers follow the same pattern but exhibit even more pronounced differences. The share of this genus is very small in the Baltic amber (0.2% in both Wheeler's sample and MZ PAN, 0.5% in PIN-964), 1.5% in the Bitterfeld amber (HMC), 1.2% in the Rovno amber, and 2.8% in the Scandinavian amber, which is almost six times its abundance in the Baltic samples. Interestingly, an opposite pattern of distribution is observed in the case of *Ctenobethylus goepperti*, which, based on the morphology and taphonomic characteristics, was also arboreal (Dlussky and Rasnitsyn, 2007). As previously mentioned, its relative abundance in the Baltic (47.6–52.1%) and Bitterfeld (42.1%) ambers is considerably higher than in the Rovno (38.9%) and, particularly, the Scandinavian (25.6%) ambers.

It seems logical to think that, in the forests where Rovno and Scandinavian ambers had formed, trees suitable for nesting of *Dolichoderus* and *Tetraponera* were more abundant, and those suitable for *C. goepperti* were less abundant, than where Baltic ambers had formed. Apparently, the conditions where Bitterfeld ambers had formed were intermediate.

When the relative abundances of terrestrial species (i.e., living in litter and upper soil) are compared, the resulting picture is less distinct. As a criterion indicating whether a particular species belongs to this ecological type one can use the ratio of workers to alate sexuals in inclusions. For the vast majority of ant species, inclusions are dominated by workers, while the relative abundance of alates does not exceed 10%. However, more than 90% of inclusions of *Paratrechina pygmaea* and the ponerine genera *Gnamptogenys* Roger, *Hypoponera* Santschi, *Pachycondyla* F. Smith, *Ponera* Latreille, and *Proceratium* Roger are alates. This is because workers of terrestrial species only extremely rarely climb the trees. On the other hand, during nuptial flight, the males and alate gynes of the same species climb up the stems of grass or tree trunks and, thus, the probability of their getting trapped in resin is much higher. In the collections of Baltic amber (Wheeler's sample and PIN-964), the relative abundance of terrestrial species is low. In the collection examined by Wheeler (1915), Ponerinae comprised 0.56%, and *P. pygmaea*, 0.51% of all the ants identified to genus. In the PIN-964 collection, inclusions of *P. pygmaea* comprised 0.71%, while Ponerinae were completely absent. The share of these ants in the Bitterfeld amber (HMC) was only slightly larger, 0.94% of Ponerinae and 1.26% of *P. pygmaea.* The relative abundance of these ants in the Rovno amber (SIZK: Ponerinae, 0.64%, *P. pygmaea*, 3.03%) and, particularly, the Scandinavian amber (ZMUC-S: Ponerinae, 1.83%, *P. pygmaea*, 3.66%) was significantly higher. Yet, the MZ PAN collection of Baltic amber does not fit this pattern, because the relative abundance of terrestrial species in it (Ponerinae, 0.98%, *P. pygmaea*, 3.59 %) does not significantly differ from that in the Scandinavian amber. It is possible that the ant fauna composition may be affected by the humidity of the habitat. Perkovsky et al. (2007) pointed out that the Rovno amber fauna appears more xerophilous compared to those of the Baltic and Bitterfeld ambers. However, the Scandinavian amber has not yet been studied in this respect, and no methods of predicting the humidity of a habitat from the composition of ant species have yet been developed.

CONCLUSIONS

Therefore, because ant faunas of the Baltic, Bitterfeld, Scandinavian, and Rovno ambers share 17 species and, moreover, in each representative collection these species account for more than 80% of the total number of inclusions, these faunas appear to be of similar age. On the other hand, these ambers differ in relative abundances of common as well as rare species, species representing recent and extinct genera, genera currently occurring in different climates, and ecological types of ants. Our data do not allow correlation of the observed differences between the ant faunas with the age or geographical origin of these ambers. Therefore, it seems most likely that these faunas had formed autochthonously in different habitats of an approximately equal (on the geological scale) age. The most similar are the ant faunas of the Baltic and Bitterfeld ambers, while the fauna of the Scandinavian amber is the most peculiar.

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