

# Differences in Ant (Hymenoptera, Formicidae) Species Composition between Weight Fractions of Rovno Amber

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**Abstract**—Arboreal specialists (including *Ctenobethylus goepperti*) comprise 54% of all ant inclusions in Rovno amber pieces weighing up to 1.5 g and 43% of those in larger pieces. In the small-size amber fraction, syninclusions containing more than a single worker ant are represented exclusively by the arboreal *Dolichoderus* spp. and *C. goepperti*, while syninclusions in larger amber pieces often contain workers of *Lasius* spp., which are not associated with trees. Species of *Lasius* comprise 15% of ants in the smaller and 28% in the larger amber pieces. It seems that the smaller pieces of amber have formed on the thinner branches of the amber-producing trees and, consequently, contain a larger proportion of arboreal ant species. Comparison of composition of inclusions between different weight fractions of amber is a promising tool to study fossil faunas and environments.

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In recent decades the ants of the Late Eocene amber were intensively studied by G.M. Dlussky (see Dlussky and Rasnitsyn, 2009, pp. 1024–1042, this volume). Because comparing ant faunas is crucial for understanding relationships between different Late Eocene ambers, it is important to find out whether the ant species composition is similar between amber pieces of different size (the importance of this factor has been pointed out by Zherikhin and Eskov, 2006). The results presented here demonstrate that the comparative analysis of different weight fractions of amber provides an important tool for reconstructing the ecology of ants in amber forests and may also be of use in other studies.

The examined material has been acquired by the Institute of Zoology, National Academy of Sciences of Ukraine, at the Ukryantar factory in Rovno. The vast majority of the examined amber specimens came from the Pugach quarry in Klesov (Rovno region). This fossil locality and its fauna have been characterized in detail in a recent review by Perkovsky et al. (2007).

When amber is processed at the factory, it loses about one-third of its original weight (A.P. Vlaskin, personal communication). In the present study the net weight of amber was determined directly after the amber was purchased from the factory, prior to cutting and subsequent processing. The amber containing ant inclusions was divided by weight into two fractions: the smallest pieces (net weight up to 1.5 g) and the rest. All the material was identified by A.G. Radchenko and G.M. Dlussky. We included some material acquired

after the manuscript on the Late Eocene amber ants (Dlussky and Rasnitsyn, 2009, pp. 1024–1042, this volume) was prepared. On the other hand, some of the previously described material (Dlussky and Perkovsky, 2002) could not be used in the present study because the net weight of many amber pieces acquired by the Institute between 2001 and 2002 is unknown. The total of 576 ants, enclosed in 424 pieces of Rovno amber and identified to subfamily, were included in the analysis.

The results are presented in Table 1. For comparison, data on the relative abundance of ant taxa in other Late Eocene amber collections are included (for details, see Dlussky and Rasnitsyn, 2009, pp. 1024–1042, this volume). Records of *Anonychomyrma* Donisthorpe and *Iridomyrmex geinitzi* (Mayr) are combined under “*Iridomyrmex*.” The Giecwicz collection is housed in the Museum of Earth of the Polish Academy of Sciences, Warsaw, Poland, and comprises amber from the Gulf of Gdansk (Kulicka et al., 2001).

In the small-size amber, the relative abundance of *Dolichoderus* Lund is 2 times, of Pseudomyrmicinae (*Tetraponera* F. Smith) 3.5 times, and of all Dolichoderinae 1.3 times higher and that of the genus *Lasius* F. is 1.8 times, of Myrmicinae 2.7 times, and of Formicinae 1.3 times lower than in the large-size amber (Table 1). In small amber pieces Dolichoderinae are 1.8 times as abundant as Formicinae and 23.5 times as abundant as Myrmicinae. In larger amber pieces Dolichoderinae and Formicinae are equally abundant, and

**Table 1.** Proportion (%) of ant taxa in different weight fractions of Rovno amber and in other collections of Late Eocene amber

	Danish amber	Rovno amber		Baltic amber	
		small, ≤1.5 g	large, >1.5 g	PIN-964	Giecewicz collec- tion, MZ PAN
<i>Dolichoderus</i>	7.7	11.5	4.7	4.1	3.0
" <i>Iridomyrmex</i> "	7.1	4.5	4.4	7.1	2.3
<i>Ctenobethylus</i>	23.5	38.5	35.3	49.9	47.1
<i>Tapinoma</i>	0	1.3	0.3	0.5	0.7
Other Dolichoderinae	1.3	3.2	1.7	5.5	0.2
<b>All Dolichoderinae</b>	<b>39.6</b>	<b>58.9</b>	<b>46.3</b>	<b>67.1</b>	<b>53.3</b>
<i>Lasius</i>	21.1	14.1	25.5	14.6	22.9
<i>Formica</i>	4.0	7.1	7.6	11.2	4.1
<i>Paratrechina</i>	3.4	1.3	3.9	0.5	4.8
<i>Prenolepis</i>	6.0	3.2	3.9	0.5	6.0
<i>Plagiolepis</i>	3.0	5.8	1.5	0.2	2.1
<i>Gesomyrmex</i>	1.3	0	0.3	0.7	0.9
<i>Oecophylla</i>	0	0	0	0	0.2
<i>Camponotus</i>	0.7	1.3	1.0	0.5	0.2
Other Formicinae	2.7	0.6	1.2	1.6	0.5
<b>All Formicinae</b>	<b>34.1</b>	<b>33.3</b>	<b>44.9</b>	<b>32.9</b>	<b>41.7</b>
<i>Fallomyrma</i>	6.4	0.6	1.1	0	0
<i>Monomorium</i>	2.0	1.3	1.3	0	0.2
<i>Temnothorax</i>	1.3	0.6	1.7	1.0	0
Other Myrmicinae	3.8	0	2.9	1.6	2.8
<b>All Myrmicinae</b>	<b>13.5</b>	<b>2.6</b>	<b>6.9</b>	<b>2.6</b>	<b>2.8</b>
<b>Pseudomyrmecinae</b>	<b>2.7</b>	<b>2.6</b>	<b>0.8</b>	<b>0.5</b>	<b>0</b>
<b>Ponerinae</b>	<b>2.0</b>	<b>2.6</b>	<b>1.2</b>	<b>0</b>	<b>1.8</b>

Myrmicinae are only 7 times less abundant than Dolichoderinae.

Among amber ants G.M. Dlussky recognized specialized arboreal species and species associated with soil and/or litter (Dlussky and Rasnitsyn, 2009, pp. 1024–1042, this volume). Based on the ecology of the recent representatives and the close morphological similarity between those and the amber species, he classified the following amber genera as arboreal specialists: *Dolichoderus*, *Camponotus* Mayr, *Dryomyrmex* Wheeler, *Oecophylla* F. Smith, *Gesomyrmex* Mayr, and *Tetraaponera*. Terrestrial species (associated with soil or/and litter) were recognized by the characteristic large proportion of sexuals. While most ant species are represented in amber inclusions predominantly by workers (>90%), some are represented almost exclusively by alate sexuals (Dlussky and Rasnitsyn, 2009, pp. 1024–1042, this volume). Apparently, in those species, alate males and gynes climbed the trees during the nuptial flight, while workers never left the ground. Based on this characteristic, *Paratrechina pygmaea* (Mayr) and all Ponerinae were classified as terrestrial.

In Rovno amber pieces weighing up to 1.5 g the proportion of arboreal species was 15.1% and that of terrestrial species was 3.8%. In the large-size fraction the proportion of arboreal species was 8.2% and that of terrestrial species was 5.0%. Therefore, in smaller amber pieces, arboreal ants are 4 times and in larger pieces only 1.6 times as abundant as terrestrial ants.

Because the distribution of worker ants among different amber fractions is of particular interest, the data on workers were analyzed separately (Table 2). The small-size amber contains less Formicinae (just slightly over one-quarter of all workers) and more Dolichoderinae. Comparison with other collections of Late Eocene amber demonstrates that, in the small-size Rovno amber, the abundances of *Dolichoderus* and Dolichoderinae are the overall maximum and those of *Lasius* and Formicinae are the overall minimum. In the large-size fraction (>1.5 g), the abundance of *Formica* is higher than in any non-Rovno collection, and the abundance of Myrmicinae not belonging to the genus *Fallomyrma* Dlussky et Radchenko is only slightly less

**Table 2.** Number of individuals (*n*) and proportion (%) of worker ants in different weight fractions of Rovno amber and in other collections of Late Eocene amber

	Danish amber		Rovno amber				Baltic amber Giecwicz collection, MZ PAN	
			small, ≤1.5 g		large, >1.5 g			
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
<b>Dolichoderinae</b>	<b>114</b>	<b>42.9</b>	<b>91</b>	<b>64.1</b>	<b>185</b>	<b>49.5</b>	<b>225</b>	<b>57.4</b>
<i>Dolichoderus</i>	21	7.9	18	12.7	17	4.6	13	3.3
“ <i>Iridomyrmex</i> ”	19	7.1	7	4.9	18	4.8	10	2.6
<i>Ctenobethylus</i>	72	27.1	60	42.3	143	38.2	202	51.5
<b>Formicinae</b>	<b>102</b>	<b>38.4</b>	<b>43</b>	<b>30.3</b>	<b>159</b>	<b>42.5</b>	<b>157</b>	<b>40.1</b>
<i>Lasius</i>	61	22.9	21	14.8	103	27.6	99	25.3
<i>Formica</i>	11	4.1	8	5.6	29	7.8	17	4.4
<i>Prenolepis</i>	9	3.4	4	2.8	13	3.5	26	6.6
<i>Plagiolepis</i>	9	3.4	8	5.6	5	1.3	6	1.5
<i>Gesomyrmex</i>	4	1.5	0	–	1	0.3	4	1
<i>Oecophylla</i>	0	–	0	–	0	–	1	0.3
<i>Camponotus</i>	2	0.8	1	0.7	3	0.8	1	0.3
<b>Myrmicinae</b>	<b>40</b>	<b>15.0</b>	<b>4</b>	<b>2.8</b>	<b>26</b>	<b>7.0</b>	<b>10</b>	<b>2.6</b>
<i>Fallomyrma</i>	19	7.1	1	0.7	4	1.1	0	–
Other Myrmicinae	21	7.9	3	2.1	22	5.9	10	2.6
<b>Pseudomyrmecinae</b>	<b>8</b>	<b>3.0</b>	<b>3</b>	<b>2.1</b>	<b>3</b>	<b>0.8</b>	<b>0</b>	–
<b>Ponerinae</b>	<b>2</b>	<b>0.8</b>	<b>1</b>	<b>0.7</b>	<b>2</b>	<b>0.6</b>	<b>0</b>	–
Total	266		142		374		392	

than that in the Danish amber, in which the abundance of Myrmicinae is maximal.

Separately, for each of the two weight fractions, we quantified the number of amber pieces containing representatives of each ant taxon (Table 3). Among the amber pieces below 1.5 g in net weight, pieces containing arboreal specialists (see above) are 1.4 times more numerous and those containing Myrmicinae are 3.2 times less numerous.

Other differences in the relative abundance of worker ants between the small-size and the large-size amber reflect not only differences in the proportion of amber pieces containing representatives of a given taxon, but also the abundance of syninclusions and the average number of individuals per syninclusion. In the small-size amber, 65% of *Dolichoderus* and 44% of *Ctenobethylus goepperti* (Mayr) were found in syninclusions, containing an average of 3.7 and 2.5 ants per amber piece. In this fraction *C. goepperti* (Mayr) was found only in syninclusions with conspecifics, while workers of *Dolichoderus* were found in two syninclusions with other *Dolichoderus* workers and one syninclusion with two ponerines (a worker and a gyne). The only other ant species represented in syninclusions in the small-size amber was *Plagiolepis klinmanni* Mayr (two workers together). Within the large-size fraction of amber only 28% of the *Dolichoderus* workers and

28% of the *Ctenobethylus* workers were found in syninclusions (2 and 15, respectively). Among the *Lasius* workers, 46% were found in syninclusions with conspecifics (12). On average, the large-size amber pieces containing *C. goepperti* contain 1.21 and the small-size pieces 1.35 workers of that species. The large-size amber containing *Lasius* contain an average of 1.44 workers.

Therefore, the relatively high abundance of the *Dolichoderus* workers in the small-size compared with the large-size Rovno amber reflects two phenomena: the proportion of amber pieces containing *Dolichoderus* being in that fraction 1.4 times higher (2.6 times higher for *Tetraoponera*) and a large number of such pieces containing syninclusions with multiple *Dolichoderus* specimens. The high abundance of *Ctenobethylus* in the same amber fraction is explained by the large number of *Ctenobethylus* syninclusions. At the same time, the relatively high abundance of the *Lasius* workers in the large-size Rovno amber is explained by such amber containing 1.3 times more pieces with *Lasius* as well as by that genus being well represented in syninclusions. The relatively high abundance of Myrmicinae in the larger-size amber is not associated with the abundance of this subfamily in syninclusions.

**Table 3.** Number of Rovno amber pieces of different weights containing inclusions of worker ants (no./percent)

	Small, ≤1.5 g	Large, >1.5 g
<i>Dolichoderus</i>	10/8.7	15/5.0
" <i>Iridomyrmex</i> "	7/6.1	18/6.0
<i>Ctenobethylus</i>	45/39.1	119/39.5
Other Dolichoderinae	6/5.2	7/2.4
<b>Dolichoderinae</b>	<b>68/59.1</b>	<b>158/52.5</b>
<i>Lasius</i>	21/18.3	72/24.0
<i>Formica</i>	8/7.0	26/8.7
<i>Prenolepis</i>	4/3.5	11/3.7
<i>Plagiolepis</i>	7/5.3	5/1.7
<i>Gesomyrmex</i>	0	1/0.3
<i>Camponotus</i>	1/0.9	3/1.0
Other Formicinae	1/0.9	4/1.3
<b>Formicinae</b>	<b>40/34.8</b>	<b>122/40.5</b>
<i>Fallomyrma</i>	1/0.9	4/1.4
<i>Monomorium</i>	2/1.7	5/1.7
<i>Temnothorax</i>	1/0.9	6/2.0
Other Myrmicinae	0	11/3.7
<b>Myrmicinae</b>	<b>4/3.5</b>	<b>26/8.6</b>
<b>Pseudomyrmecinae</b>	<b>3/2.6</b>	<b>3/1.0</b>
<b>Ponerinae</b>	<b>1/0.9</b>	<b>2/0.7</b>
Total	117	301

Dlussky (2008, p. 514) pointed out that "the higher abundance and higher species diversity of arboreal specialists from the genera *Dolichoderus* and *Tetraponera* may reflect the larger number of niches suitable for nesting by these ants. The majority of the modern representatives of these genera build their nests in dead branches or under tree bark." In the case of Rovno and possibly also Scandinavian ambers this explanation is additionally supported by a relatively high abundance of syninclusions of *Dolichoderus*. Among syninclusions in the small-size Rovno amber are individuals of *D. polessus* Dlussky (which is a subdominant in the Rovno fauna and the analogue of *D. tertiarius*) and the type series of *D. robustus* Dlussky (Dlussky, 2002). Among syninclusions in the large-size amber are paratypes of *D. perkovskyi* Dlussky (8 individuals of this species have been already discovered in Rovno amber, but only one of them in a piece weighing less than 1.5 g). For Danish amber data on syninclusions are limited, but the distribution of the *Dolichoderus* individuals among records allows making some indirect inferences. The Danish amber ants in Copenhagen collection are recorded under 68 different acquisition dates. Only in two cases more than a single *Dolichoderus* ant entered the collection on the same day. On one occasion these were five workers (from the total of 9 ants), two of which remain in the same piece of

amber. On another occasion these were two workers and a gyne (from the total of 42 ants). All of those 8 individuals were identified as *D. tertiarius* (Mayr); they represent 52.3% of all the ants of this species known from Scandinavian amber. Because *D. tertiarius* comprises mere 5.30% of the ants recorded from Scandinavian amber, this high percentage indicates that, originally, many of these ants were part of syninclusions, later cut into smaller pieces.

Because colonies of *Dolichoderus* are small, ants of that genus did not preserve in Baltic amber in such large numbers as *C. goepperti* (Mayr), *I. geinitzi* (Mayr), *L. schiefferdeckeri* Mayr, and *F. flori* Mayr, together comprising 79% of all the ant individuals in that amber, of which *Dolichoderus* ants comprise only 5% (Dlussky, 2008). For this reason, it is not surprising that the collections of Giecewicz and PIN-964, containing together 1.5 times as many ants as the Danish amber collection, contain only a single syninclusion (Giecewicz collection, 3 workers of *D. tertiarius*) or no syninclusions containing ants of that genus (PIN-964). The Berlin collection of Bitterfeld amber, which is 2.3 times larger than the Danish collection, contains only two syninclusions of *Dolichoderus*, each with two workers (*D. tertiarius* and *Dolichoderus* sp.) (Dlussky, personal communication). We believe that the fact that the most common *Dolichoderus* species of the corresponding faunas are better represented in syninclusions indirectly corroborates the idea 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" (Dlussky and Rasnitsyn, 2009, pp. 1024–1042, this volume).

Most inclusions, particularly those in private collections, are enclosed in "layered" amber, i.e., chunks formed by multiple effluxes of resin. Such amber specimens are often contaminated with tree dust and sand and most probably formed on lower parts of tree trunks or on thick branches. Syninclusions are particularly common in such amber. Small, transparent pieces of amber, devoid of contaminants and tree dust, are more likely to have formed on upper parts of tree trunks and on thin branches. In such amber syninclusions are relatively rare. We believe that most of the small Rovno amber, below 1.5 g in net weight, formed in such conditions. The obligately arboreal ant species should be more common on thin branches and upper parts of tree trunks, which is exactly what the Rovno material demonstrates (Table 3). In contrast, the ants not directly associated with amber trees, including Myrmicinae, are rare in the small-size pieces of Rovno amber. The three species of Dolichoderinae, syninclusions of which are found in small-size amber, account for 53% of all the workers. In contrast, the two species of Dolichoderinae, syninclusions of which are found in large-size amber, account for only 40% of all the workers. The relative abundance of those Formicinae species the workers of which are recorded in syninclusions is rather similar to

that of Dolichoderinae: the four species of Formicinae, found in syninclusions with conspecific workers, account for 33% of all the workers.

Judging from its morphology and characteristics of burial (Dlussky and Rasnitsyn, 2007), *Ctenobethylus goepperti* was also an arboreal species. This is additionally confirmed by larvae and pupae of *C. goepperti* having been found in amber (Wheeler, 1915). The relative abundances of workers of *C. goepperti* are similar between the small-size and the large-size Rovno amber, suggesting that, at least in the Rovno amber forest, this ant uniformly colonized the entire amber tree. Taken together, arboreal specialists (including *C. goepperti*) comprise 54% of the ant inclusions in the small-size and 43% of those in the large-size amber. Unlike *C. goepperti*, *Lasius schiefferdeckeri* Mayr, which is the second most abundant species in the Rovno amber, in which its larvae and pupae were also found (Perkovsky, 2007; Perkovsky, 2008), was obviously more closely associated with lower parts of tree trunks and with thick branches. The proportion of small-size inclusions containing this species is 1.3 times lower than that of the large-size inclusions. Numerous syninclusions of *L. schiefferdeckeri*, including those containing the larvae and pupae, were found in large-size but not in small-size amber pieces.

Conclusions about the general character of the ant fauna of a particular amber type may be strongly affected by which size fraction dominates in the examined collection. For example, the proportions of individual ants representing "Palearctic" and "tropical" genera (see Dlussky and Rasnitsyn, 2009, pp. 00–00, this volume) in our sample of Rovno amber are, correspondingly, 21.2% and 7.1% of all the ants identified to subfamily in the small-size amber and 33.1% and 6.3%, correspondingly, in the large-size amber. The difference is explained primarily by the lower abundance of *Lasius* in small-size amber. The relative abundances of arboreal and terrestrial species in small-size and large-size ambers have been discussed above.

Therefore, there undoubtedly exists a correlation between the size of amber and the composition of ant inclusions, and it can be interpreted in ecological terms with considerable confidence. Consequently, the analysis of distribution of inclusions among size fractions of amber is a promising tool to study fossil faunas and environments.

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