

Arthropods in Contemporary and Some Fossil Resins

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Abstract—More than 4800 arthropod inclusions were isolated and identified from resin of various contemporary conifer trees in various parts of northern Eurasia. Their composition is compared with that in representative collections of Baltic and Rovno ambers (Upper Eocene) and with that in Dominican amber (Lower Miocene). The original composition of inclusions of Dominican amber is reconstructed for the first time using a procedure intended to reduce the effect of human bias. Taphonomical characteristics of resins and their effects on the composition of inclusions are studied. The actual paleontological approach reveals a trend towards a decrease in the relative abundance of arboreal springtails and nematoceran dipterans and an increase in that of the true bugs, beetles, lepidopterans, and hymenopterans (especially ants) between the Eocene and the present. Relative abundances of spiders and mites show no clear trend. The available data on other arthropods are still insufficient for elucidating evolutionary trends. Surprisingly, a small contemporary sample from Taimyr (N. Siberia) was inexplicably more similar to the Eocene amber than to other contemporary resins. No other significant differences in composition of inclusions, compared across different conifer genera or geographic areas, have been revealed. A more detailed comparison between contemporary and fossil hymenopteran and beetle inclusions reveals correlations with both age (= evolutionary change) and geography. The absolute dominance of ants, particularly Formicinae and Myrmicinae, and, among solitary hymenopterans, Ichneumonidae, Braconidae, and Pteromalidae, and a corresponding decline in the abundance of Scelionidae and Dolichoderinae in contemporary resins compared to amber reflect evolutionary changes. In contrast, the overwhelming abundance of Formicinae and consistent occurrence of sawflies in contemporary resins of northern Eurasia appear to be explained by geography. The Eocene assemblages of beetle inclusions are characterized by a wider and more variable set of dominant families, in sharp contrast to contemporary resins, which are uniformly dominated by Curculionidae, Chrysomelidae, and Staphylinidae. Additional analyses are needed to explain this difference.

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INTRODUCTION

The composition of inclusions in fossil resins has long attracted researchers as a window into the biota and environments of the past, as well as their dynamics. Yet, building historical reconstructions upon such data is a difficult task, because the composition of arthropod taxa in inclusions differs dramatically from the fauna of the ancient habitats where these inclusions originated. Numerous reasons of these differences are studied by a particular branch of paleontology, taphonomy. The taphonomy of fossil resins has been elucidated in several publications (Zherikhin and Sukacheva, 1989, 1992, 2003; Zherikhin, 2002; Martínez-Delclòs et al., 2004). In brief, the major reasons of the resin inclusions giving a biased picture of the original fauna are as follows.

Getting trapped in resins is a highly selective process: the larger and stronger the organism, the better its chances of getting away. Resin is produced, particularly in large quantities, by only a few tree species, mostly conifers. The arthropods not frequenting trunks and

branches of such trees are unlikely to get trapped in resin. Moreover, resin can be attractive for some species and repellent for others. In different environments resins of different tree species have different chances of becoming polymerized, transported to places of burial, and preserved. Yet, even those inclusions that survived to our days vary strongly in their chances of ending up in museum collections, because both collectors and museum curators are highly picky and regularly discard not only poorly preserved inclusions but also common (“banal”) forms and everything else deemed by them uninteresting for whatever reason.

The latter, human source of bias can be avoided to some degree by use of so-called representative collections, currently becoming popular. These are assembled with special precautions to avoid both intentional and unintentional selection of material (*Bursztynowy...*, 2001; Sontag, 2003; Hoffeins and Hoffeins, 2004; Zherikhin and Eskov, 2007; Perkovsky et al., 2007). Yet, the selective character of the burial and fossilization processes cannot be avoided, and, therefore, it has to be corrected for during reconstruction of past biotas.

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This requires a detailed understanding of how various arthropods become trapped in resin and how the resin containing such inclusions becomes buried and eventually turns into amber.

To better understand the process of preservation of arthropods in fossil resins, one can use the actual paleontological approach and, in particular, seek out a contemporary faunal assemblage close in its selectivity to taphonomical characteristics of ancient resins in order to use it as a reference. As a first such standard, it has been suggested to use the assemblage of arthropods collected in sticky traps placed on tree trunks in New England, the United States (Brues, 1933). Yet, the sticky traps and resins turned out rather dissimilar in their taphonomical characteristics. In particular, Hymenoptera account for 5.4% of the total number of insects collected by the sticky traps, thus approximating their relative abundance in the Eocene (see Table 2), which does not seem realistic because both paleontological and actualistic data indicate that the presence of that insect order in terrestrial communities has considerably increased since the Eocene (Rasnitsyn and Kulicka, 1990). The relative abundances of parasitoid groups and ants in the assemblages of Hymenoptera collected by the traps (92% and 6%, respectively) are close to the pre-Eocene levels (87–95% and 0–11%, respectively), which again is contrary to the general trend (Rasnitsyn and Kulicka, 1990).

It seems more promising to use as a reference the composition of arthropod inclusions in contemporary tree resins (Skalski, 1975; Zherikhin and Sukacheva, 1989, 1992). The work on creating such a reference set, based on conifer resins mostly from European Russia and the Russian Far East, was started by V.V. Zherikhin and I.D. Sukacheva in the 1970–1980s. However, only partial and most general results of this study have been published so far (Zherikhin and Sukacheva, 1989, 1992, 2003; Rasnitsyn and Kulicka, 1990). In the present paper we begin a more detailed publication of these results. The composition of contemporary arthropod inclusions is being compared here with that in representative collections of fossil resins (see below).

MATERIAL AND METHODS

We examined more than 13 kg of resin, collected from various conifer species at many localities across northern Eurasia and containing a total of more than 4800 arthropod inclusions (Table 1). The amber was dissolved in ethanol, and the arthropod remains were extracted from the sediment, washed, and preserved in ethanol for identification. Each particular sample was relatively small, only rarely containing more than a hundred arthropod specimens (maximum 238). (By a sample we understand here resin collected from several closely located trees of one conifer species, rarely from a single tree). With exception of *Picea excelsa* in the Moscow Region, no sample exceeded 300 arthropods from one conifer species, even if pooled across a large

territorial unit (Region or Krai). Consequently, we grouped samples into larger batches, each combining samples from one conifer genus across a relatively large territory (mid-Europe, Crimea, Russian Far East, etc., see Table 2). A number of samples were excluded because of their small size (e.g., from spruce in Poland, fir in the Russian Far East, etc.).

The differences between Tables 1 and 2 in the total number of inclusions reported for each locality are due to inclusions not identified to order and puparia of resinicolous flies (i.e., normally developing within resin) from the families Syrphidae and Anthomyidae being excluded. Such puparia, extremely common in contemporary resins, are completely absent from amber collections. Apparently, resinicolous flies are evolutionarily young. Because, for obvious reasons, they are overrepresented in contemporary resins, comparison with fossil faunas is complicated unless they are excluded from the record (Zherikhin and Sukacheva, 2003).

Preliminary sorting of arthropod remains into groups was done by V.V. Zherikhin, A.G. Ponomarenko, Yu.A. Popov, and A.P. Rasnitsyn. A more detailed identification was done by experts on the systematics of particular taxa. Such detailed data are used below in the parts dedicated to particular orders, while in the analysis of the composition of insect inclusions in general mostly the preliminary identifications are used (Zherikhin and Sukacheva, 1989, 1992, 2003).

Data on the composition of inclusions in representative collections of fossil amber were taken from literature (*Bursztynowy...*, 2001; Perkovsky et al., 2007). The Dominican amber was an exception and needs to be discussed here in more detail.

As previously mentioned, collections of fossil resins represent the actual relative abundances of various inclusions with a bias, which may be quite large. Because the direct approach to avoiding this bias (through creation of special, representative collections, see above) is laborious and not always practical, other approaches to its corrections are of significant interest. In the case of Dominican amber we were able to partly solve this problem by using two sources of data, obtained independently. One of the sources was Brodzinski and Lopez-Penha personal collection, acquired by the Smithsonian Institution (Washington, United States) and studied by one of the authors (A.P.R.) in October 1989. Partly because of the shortage of time and partly because some taxa were on loan to other researchers (e.g., caddisflies and some ant taxa) or missing for other reasons, only approximately two-thirds of the collection were examined (Table 3). This collection is also biased due to the well-known phenomenon of selectivity of collection managers and curators, who discard the “less interesting” (usually the most abundant) taxa. Davis (1989, p. 549) directly indicated that numerous ant inclusions were discarded during the assembly of this collection; one can suspect the same for stingless Meliponinae bees and several other taxa.

Table 1. Examined samples of arthropod inclusions in contemporary conifer tree resins

Tree species	Geographical Region	Admin. region/Krai	Admin. district	Locality	Sample no.	Inclusion no.	Collectors
<i>Picea excelsa</i> L.	mid-Europe	Moscow	Odintsovskii	Mozzhinka	13	Σ2398	IDS, VVZh, EDSH
<i>Picea excelsa</i> L.	mid-Europe	Moscow	Odintsovskii	Pokrovskoe	18		APR
<i>Picea excelsa</i> L.	mid-Europe	Moscow	Odintsovskii	Uspenskoe	18		AZSh
<i>Picea excelsa</i> L.	mid-Europe	Moscow		Moscow and environs	3		IDS, APR
<i>Pinus sylvestris</i> L.	mid-Europe	Moscow	Odintsovskii	Mozzhinka	4		IDS, VVZh
<i>Pinus sylvestris</i> L.	mid-Europe	Moscow	Odintsovskii	Pokrovskoe	7	Σ87	APR, IDS
<i>Pinus sylvestris</i> L.	mid-Europe	Moscow		Moscow and environs	6		IDS, APR
<i>Pinus sylvestris</i> L.	mid-Europe	Moscow	Sepukhov	Oka Terrace Reserve	1		APR
<i>Larix</i> sp.	mid-Europe	Moscow		Moscow and environs	1	11	LNP
<i>Picea excelsa</i> L.	mid-Europe	Kirov	near Kotelnich	Viatka River at Rvachi Village	1	195	IDS
<i>Pinus sylvestris</i> L.	mid-Europe	Estonia	Tallinn	Rocca-al-Mare	1	4	APR
<i>Picea excelsa</i> L.	mid-Europe	Poland	Tatra Mts.	near Zakopane	1	40	IDS
<i>Picea excelsa</i> L.	mid-Europe	Poland	East Poland	near Lomzha and Belovezhskaya Pushcha		67	RK
<i>Pinus sylvestris</i> L.	mid-Europe	Poland	East Poland	near Lomzha and Belovezhskaya Pushcha		176	RK
<i>Pinus stankewiczii</i> (Sukacz.)	SE Europe	Crimea	Yalta	Nikitskii Botanical Garden	1	135	IDS
<i>Larix dahurica</i> Turcz.	N Siberia	Taymyr Peninsula	Khatangskii	Katyryk		Σ50	IDS, VVZh, APR, NNK
<i>Larix dahurica</i> Turcz.	N Siberia	Taymyr Peninsula	Khatangskii	Zhdanikha and others	8		
<i>Pinus sylvestris</i> L.	E Siberia	Chita	Shelopuginskii	Daya River	5	1	APR
<i>Picea excelsa</i> L.	E Siberia	Buryatia	Zaigraevskii	Staraya Bryan'	1	182	APR
<i>Larix</i> spp.	Far East	Amur	Zeyskii	Tukuringra Ridge	1	37	SPR
<i>Pinus</i> spp.	Far East	Amur	Zeyskii	Upper Zeya depression	1	17	SPR
<i>Abies holophylla</i> Maxim.	Far East	Primorskii Krai	Khasanskii	Nezhino	1	43	IDS, VVZh
<i>Pinus koraiensis</i> Sieb. et Succ.	Far East	Primorskii Krai	Khasanskii	Nezhino	1	49	IDS, VVZh
<i>Pinus funebris</i> Kom.	Far East	Primorskii Krai	Khankaiskii	Khanka Lake	1	238	IDS, VVZh
<i>Pinus koraiensis</i> Sieb. et Succ.	Far East	Primorskii Krai	Vladivostok	Shamora	1	44	IDS, VVZh
<i>Larix</i> spp.	Far East	Primorskii Krai	Vladivostok	Shamora	2	93	IDS, VVZh
<i>Abies holophylla</i> Maxim.	Far East	Primorskii Krai	Vladivostok	Shamora	1	6	IDS, VVZh

Table 1. (Contd.)

Tree species	Geographical Region	Admin. region/Krai	Admin. district	Locality	Sample no.	Inclusion no.	Collectors
<i>Picea</i> spp.	Far East	Primorskii Krai	Kavalerovskii	Olga-Kavalerovo Pass	1	199	IDS, VVZh, AGP
<i>Pinus koraiensis</i> Sieb. et Succ.	Far East	Primorskii Krai	Kavalerovskii	Olga-Kavalerovo Pass	1	1	IDS, VVZh, AGP
<i>Larix</i> spp.	Far East	Primorskii Krai	Kavalerovskii	Vysokogorsk	1	20	APR
<i>Pinus koraiensis</i> Sieb. et Succ.	Far East	Primorskii Krai	Kavalerovskii	Vysokogorsk	1	0	APR
<i>Picea</i> spp.	Far East	Primorskii Krai	Kavalerovskii	Uglovoi spring	1	88	APR
<i>Pinus koraiensis</i> Sieb. et Succ.	Far East	Primorskii Krai	Dalnegerskii	Uglovoi Spring	1	1	APR
<i>Pinus koraiensis</i> Sieb. et Succ.	Far East	Primorskii Krai	Dalnegerskii	Kamenskii Spring	1	68	APR
<i>Picea</i> spp.	Far East	Khabarovskii Krai	River Bikin basin	Bol'shaya Svetlovodnaya River	8	98	VVZh
<i>Larix</i> spp.	Far East	Khabarovskii Krai	River Bikin basin	Bol'shaya Svetlovodnaya River	9	224	VVZh
<i>Larix dahurica</i> Turcz.	Far East	Khabarovskii Krai	Okhotskii	Khetana River	4	81	VVZh, APR
<i>Larix dahurica</i> Turcz.	Far East	Khabarovskii Krai	Okhotskii	Amka River	1	52	IDS
<i>Picea</i> spp. (+ <i>Abies</i> sp.?)	Far East	Sakhalin Is.	Dolinskii	Sokol	3	Σ139	IDS, VVZh
<i>Larix curilensis</i> May	Far East	Sakhalin Is.	Dolinskii	Sokol	1		IDS, VVZh
<i>Picea</i> spp.	Far East	Sakhalin Is.	Dolinskii	Starodubskii	1	3	IDS, VVZh
<i>Pinus</i> sp.	Japan	Honshu Is.	Inuyama	Rain Park	1	44	AGP
Total					133	4891	

Note: Collectors are designated as follows: (AGP) A.G. Ponomarenko, (AZSh) A.Z. Shilkin, (APR) A.P. Rasnitsyn, (VVZh) V.V. Zherikhin, (EDSh) E.D. Shnitnikova, (IDS) I.D. Sukacheva, (LNP) L.N. Pritykina, (NNK) N.N. Kalandadze, (RK) Róża Kulicka, (SPR) S.P. Rasnitsyn.

Another source of data on the Dominican amber were unpublished data on the composition of inclusions in 12000 pieces of Dominican amber, compiled by Mr. Robert Woodruff, San Francisco, the United States, and kindly provided for our study (Table 4). According to Woodruff (personal communication), the material was studied without any preliminary selection; therefore, it matches the criteria of a representative collection. It served as the source from which the collection acquired by the Smithsonian Institution was selected. Yet, Woodruff's material has its own shortcoming: small-size inclusions, such as those of thrips, springtails, and also possibly scale insect males, particularly abundant in the Dominican amber, and some other hard-to-see groups are clearly underrepresented. Moreover, it appears that, in many cases, the quality of identification was lower

than for the Smithsonian sample studied by us. During our visit to San Francisco, we quantified Woodruff's records for the first 1961 amber pieces he examined (containing 3900 arthropod specimens) for use in subsequent analyses; the rest of his records could not be processed due to time limitations.

Taking into account advantages and shortcoming of each data source, one of the authors (A.P.R.) successfully attempted using both for more accurate estimation of the original composition of inclusions in the Dominican amber. In order to do it, it was necessary to identify a group of arthropods the relative abundance of which was accurately reflected by both samples. Such a group had to satisfy the following criteria: it had to be common enough without being "banal," which would

Table 2. Composition of arthropod inclusions in the examined contemporary and some fossil resins

Taxa	Ambers						Contemporary resins						Japan		
	Baltic		Warsaw (3)	Bitterfeld	Rovno	Domi-nian	mid-Europe		Crimea	Taymyr	Buryatia			Far East	
	Brighton (1)	Hamburg (2)					Picea	Pinus			Larix	Pinus		Picea	Pinus
Pseudoscorpiones	2/0.3%	6/0.1%	9	21/0.1%	1/0.1%	0.2%	7/0.4%	-	19/16%	-	21.5%	1	-	1	-
Opliones	3/0.4%	10/0.1%	7	25/0.2%	4/0.3%	+	1	-	-	-	-	-	-	-	-
Aranei	24/3.3%	359/5.0%	5377/1.1%	909/6.1%	39/3.2%	3.1%	41/2.6%	3/5.4%	6/5%	2/5.4%	21.5%	10/2.9%	2/0.6%	30.8%	2/4.5%
Acar	192/26.2%	998/13.9%	316/4.2%	2492/16.8	196/15.9%	2.5%	181/11.5%	3/5.4%	-	13/21.6%	64.4%	52/14.9%	37/11.2%	39/10.4%	-
Myriapoda	3/0.4%	17/0.2%	18/0.2%	29/0.2%	2/0.2%	0.5%	2/0.1%	-	-	-	-	-	1	-	-
Collembola	39/5.3%	68/9.6%	338/4.5%	1213/8.2%	86/7.0%	2.3%	4/0.2%	1	12/10%	3/8.1%	61.7%	6/1.7%	2/0.6%	-	5/11.4%
Archaeognatha	1	15/0.2%	2	16/0.1%	5/0.4%	-	-	-	-	-	-	-	-	-	-
Thysanura	-	3	1	9	2/0.2%	0.4%	-	-	-	-	-	-	-	-	-
Ephemeroptera	-	1	2	1	2/0.2%	0.1%	-	-	-	-	-	-	-	-	-
Odonata	-	1	0	1	-	+	-	-	-	-	-	-	-	-	-
Psocoptera	4/0.5%	37/0.5%	36/0.5%	62/0.4%	5/0.5%	2.1%	7/0.4%	1	2/1.8%	-	-	-	-	-	1
Thysanoptera	3/0.4%	33/0.5%	51/0.7%	44/0.3%	6/0.5%	0.8%	11/0.7%	-	-	-	-	-	-	1	-
Hemiptera total	42/5.8%	321/4.5%	422/5.5%	673/4.5%	47/3.9%	3.1%	104/6.6%	5/8.9%	3/2.7%	-	11/8.1%	46/13.1%	8/2.4%	57/15.2%	4/9.1%
Homoptera total	42/5.8%	321/4.5%	400/5.3%	673/4.5%	44/3.6%	2.5%	48/3.1%	4/7.1%	-	-	6/4.4%	34/9.7%	6/1.8%	55/14.7%	2/4.5%
Sternorrhyncha	40/5.4%	68/9.6%	358/4.7%	400/5.3%	32/2.6%	0.7%	17/1.1%	3/5.4%	-	-	21.5%	3/0.9%	-	50/13.4%	2/4.5%
Aphidoidea	32/4.4%	15/0.2%	313/4.1%	24/2.0%	24/2.0%	-	8/0.5%	1	-	-	1	3/0.9%	-	49/13.1%	1
Psyllomorpha	-	-	3	-	-	-	5/0.3%	2/3.6%	-	-	1	-	-	-	-
Auchenorrhyncha	2/0.3%	37/0.5%	42/0.5%	-	11/0.9%	2.5%	9/0.6%	1	-	-	4/3%	25/7.1%	4/1.2%	4/1.1%	-
Other Homoptera	10/1.4%	33/0.5%	51/0.7%	44/0.3%	23/1.9%	0.6%	56/3.6%	1	3/2.7%	-	5/3.7%	12/3.4%	2/0.6%	20.5%	2/4.5%
Heteroptera	-	2	4	-	4/0.3%	0.6%	-	-	-	-	-	-	-	-	-
Strepsiptera	-	4	2	6	-	-	20/12.9%	11/19.6%	8/7.3%	5/13.5%	20/14.8%	64/18.3%	18/5.4%	83/22.2%	16/36.4%
Coleoptera	14/1.9%	312/4.4%	382/5.0%	693/4.7%	64/5.2%	8.6%	5/0.3%	2/3.6%	-	-	5/3.7%	-	-	-	-
Neuroptera s.l.	-	-	2	1	-	+	-	-	-	-	-	-	-	-	-
Mecoptera	1	-	1	1	9/0.7%	0.1%	2/0.1%	-	1	-	-	-	-	-	-
Trichoptera	2/0.3%	48/0.7%	88/1.2%	81/0.5%	7/0.6%	1.9%	30/1.9%	2/3.6%	2/1.8%	-	-	-	3/0.9%	8/2.1%	3/6.8%
Lepidoptera	7/1.0%	23/0.3%	32/0.4%	70/0.5%	62/5.0%	25.9%	75/4.8%	1	87.3%	6/16.2%	13/9.6%	32/9.1%	7/2.1%	53/14.2%	-
Diptera	339/46.2%	367/5.2%	4498/59.2%	7128/48.1%	518/42.1%	20.7%	12/0.8%	-	21.8%	5/13.5%	-	-	-	4/1.1%	-
Nematocera	277/37.7%	2929/40.8%	3651/48.1%	5685/38.4%	104/8.5%	5.2%	39/2.5%	1	5/4.5%	-	9/6.7%	5/1.4%	-	46/12.3%	-
Brachycera	58/7.9%	738/10.3%	847/11.1%	1426/9.6%	37/3.0%	36%	71/45.3%	22/39.3%	46/41.8%	1	63/46.7%	73/20.9%	245/74%	93/24.9%	11/25%
Formicidae	22/3.0%	44/5.8%	444/5.8%	55/0.4%	50/4.1%	8%	177/11.3%	5/8.9%	87.3%	7/18.9%	13/9.6%	54/15.4%	3/0.9%	31/8.3%	2/4.5%
Other Hymenoptera	28/3.8%	556/7.7%	407/5.4%	1205/8.1%	87/7.1%	42%	888/56.6%	27/48.2%	54/49.1%	8/21.6%	76/56.3%	127/36.3%	248/75%	124/33.1%	13/29.5%
All Hymenoptera	50/6.8%	310/4.4%	819/10.8%	33/0.2%	5/0.4%	0.3%	2/0.1%	-	-	-	-	-	-	-	-
Blattoptera	2/0.3%	16/0.2%	13/0.2%	3	3	1.9%	-	-	-	-	-	-	-	-	-
Isoptera	1	1	-	-	-	+	-	-	-	-	-	-	-	-	-
Mantodea	-	4	3	2	-	+	2/0.1%	-	-	-	-	-	1	5/1.3%	-
Plecoptera	1	1	1	1	1/0.1%	+	-	-	-	-	-	-	-	-	-
Embiodera	1	1	3	1	-	+	5/0.3%	-	-	-	-	-	-	-	-
Dermoptera	1	1	2	11/0.1%	-	0.7%	-	-	-	-	-	-	-	-	-
Orthoptera	1	8/0.1%	1	-	-	+	-	-	-	-	-	-	-	-	-
Phasmatida	1	1	1	1	-	+	-	-	-	-	-	-	-	-	-
Total	734	7177	7596	14808	1233	96.7%	1569	56	110	37	135	350	330	374	44

Note: Original data, unless indicated otherwise. Amber collections: (1) representative collection of Baltic amber, Brighton, England (Perkovsky et al., 2007); (2) representative collection of Baltic amber of Christel and Hans Hoffeins, Hamburg, Germany (Hoffeins and Hoffeins, 2004); (3) representative collection of Baltic amber of Tadeusz Giecwicz, Museum of Earth PAN, Warsaw (Bursztynowy, ... 2001); (4) representative collection of Bitterfeld amber of Christel and Hans Hoffeins, Hamburg, Germany (Hoffeins and Hoffeins, 2004); (5) representative collection of Rovno amber, Institute of Zoology, NASU, Kiev, Ukraine (Perkovsky et al., 2007).

Table 3. List of inclusions in the collection of Dominican amber of the Smithsonian Institution (Washington, United States), identified by A.P. Rasnitsyn

unidentified wormlike creature 1	Ceraphronidae 14
Mollusca Gastropoda 4	Evaniidae 13
Isopoda 5	Proctotrupidae 1
Scorpiones 1	Diapriidae 28
Amblypygi 1	Scelionidae 271
Pseudoscorpiones 35	Platygastridae 103
Opiliones 1	Mymaromatidae 13
Araneae 193	Mymaridae 130
Acari 439 (the number is arbitrary because countless newborn mites in one amber piece were nominally recorded as 200, including:	Trichogrammatidae 14
Oribatei 18 (Galumnidae 5)	Agaonidae 4
Eriophyidae 2	other Chalcidoidea 298
Bdellidae 1	Figitidae Eucoilinae 3
Argasidae 1	Ichneumonidae 9 (Cryptinae 3)
Ixodidae 2	Braconidae 36 (Cheloninae 3)
Chilopoda 12 (Geophilidae 6)	solitary Aculeata 103, including:
Diplopoda 72 (<i>Polyxenus</i> 7)	Bethyidae 81
Collembola 408	Chrysididae Amiseginae 1
Archaeognatha 54	Sclerogibbidae 1
Zygentoma 16	Embolemidae 2
Thysanura indet. 5	Dryinidae 10 (Anteoninae 2, <i>Thaumatodryinus</i> 3)
Odonata Zygoptera 4	Pompilidae 1
Ephemeroptera 24	Sphecidae 7, including:
Psocoptera 375	Crabroninae 2
Thysanoptera 142	Psenini 1
Hemiptera 682, including:	Ammoplanini 1
Psylloidea 28	<i>Pison</i> 1
Aleurodoidea 11	<i>Trypoxylon</i> 2
Coccoidea (mostly males) 96	social Aculeata 1041, including:
Sternorrhyncha indet. 1	Apidae 181 (<i>Trigona dominicana</i> 180)
Cicadelloidea 148	Vespidae Polistinae 1
Fulgoroidea 236	Formicidae 924, including:
Homoptera indet. 4	Ponerinae 124 (Odontomachini 7)
Heteroptera 104	Pseudomyrmicinae 18
Coleoptera 1163 (Platypodidae 128)	Myrmicinae 214
Neuroptera 3 (Coniopterygidae 2)	Dolichoderinae 437
Trichoptera 2	Formicinae 45
Lepidoptera 336	Blattodea 52
Diptera 2,682, including:	Isoptera 342, including:
Tipuloidea 16	Mastotermitidae 6
Psychodidae 203	Termitidae: "long-nosed" workers 16
Culicidae 7	Mantodea 5
Chironomidae 169	Plecoptera 1
Ceratopogonidae 141	Dermaptera 36
Mycetophilidae s.l. 136 (Keroplastidae 5)	Embioptera 12
Cecidomyiidae s.l. 623	Orthoptera 126, including:
Sciaridae 184	Gryllidae 117, including:
Scatopsidae 166	Gryllinae 8
Bibionidae 3	Nemobiinae 8
Anisopodidae (? <i>Valeseguya disjuncta</i> Grimaldi) 5	Oecanthinae 11
Nematocera indet. 382	Mogoplistinae 48
Phoridae 219	Stenopelmatidae 1
Empididae 18	Raphidophoridae 1
Brachycera indet. 273	Tettigonioidea indet. 1
Hymenoptera 2154, including:	Ensifera indet. 2
Argidae 1	Tridactylidae 1
Parasitica 941, including:	Caelifera indet. 1
Megaspilidae 3	Phasmatodea 3
	Insecta indet. 6
	Total 9368

Table 4. List of Dominican amber inclusions identified by R.E. Woodruff (first 1961 amber pieces only)

Nematoda 5	Trichoptera 4
Vermes indet. 1	Lepidoptera 12
Isopoda 2	Diptera 795
Pseudoscorpiones 2	Hymenoptera 1392, including:
Opiliones 1	Parasitica 52
Araneae 98	solitary Aculeata 6
Acari 64	Formicidae 1105
Diplopoda 10	Apidae Meliponinae 66
Collembola 11	Blattodea 7
Thysanura 9	Isoptera 53
Ephemeroptera 1	Mantodea 1
Psocoptera 35	Zoraptera 1
Thysanoptera 6	Dermaptera 7
Homoptera 82, including:	Embioptera 1
Sternorrhyncha 5	Orthoptera 22
Auchenorrhyncha 36	Insecta indet. 1014
Heteroptera 15	Amphibia Anura 1
Coleoptera 264	Total 3918
Neuroptera 2	

prompt the Smithsonian Institution to screen it out during the assembly of its collection. At the same time, the organisms had to be relatively large and easy to identify, so that the probability of their discovery and accurate identification were equally high for the Smithsonian and for Woodruff samples. The order Orthoptera satisfied the above criteria, mostly due to abundance of various small crickets in the Dominican amber, and was used as a reference.

For each of the two amber samples, as they are presented in Tables 3 and 4, we calculated the “orthopteran ratio” of each taxon, i.e., the number of recorded individuals of that taxon divided by the number of orthopteran individuals in the same sample (Table 5). Comparison of these indices has confirmed that relatively large, easily identifiable, and not overly abundant forms, such as diplopods, thysanurans, true bugs, beetles, lepidopterans, termites, and earwigs are approximately equally well represented in our Smithsonian records and Woodruff’s records. In contrast, small-size and obscure arthropods, such as collembolans, barklice, thrips, homopterans (apparently due to scale insect males neglected), and parasitic and solitary aculeate Hymenoptera (the latter apparently due to abundant small Bethyridae ignored) were underrepresented in Woodruff’s records. On the other hand, mass inclusions of ants and stingless bees, caddisflies (loaned out), and, for more obscure reasons (but possibly also in part due to loans), spiders and dipterans, were underrepresented in our records on the Smithsonian sample.

Table 5. Relative abundance of various taxa among Dominican amber inclusions, calculated in “orthopteran ratios”

Taxa	Smithsonian collection	Woodruff’s data
Pseudoscorpiones	0.28	*0.09
Araneae	*1.5	4.4
Acari	3.5	2.9
Diplopoda	0.57	0.45
Collembola	3.2	*0.5
Thysanura	0.59	0.41
Psocoptera	3.0	*1.6
Thysanoptera	1.1	*0.27
Homoptera	4.6	*3.0
Heteroptera	0.8	0.68
Coleoptera	9.2	12.0
Trichoptera	*0.02	0.18
Lepidoptera	2.7	2.4
Diptera	*20.7	36.1
Hymenoptera	*17.1	63.3
Parasitica	7.5	*2.4
solitary Aculeata	0.78	*0.27
Formicidae	*7.4	50.2
Apidae Meliponinae	*1.4	3.0
Blattodea	0.41	*0.13
Isoptera	2.7	2.4
Dermaptera	0.29	0.32
Orthoptera	1.0	1.0

Note: Asterisks indicate taxa clearly underrepresented in the collections. Rare taxa are excluded.

Because our hypotheses on the character of the bias have been mostly confirmed, for the ultimate comparison for each taxon we used the maximum of the two “orthopteran ratios” (both shown in Table 5). The sum of these (maximum) ratios across all the taxa was taken as 100%, based on which the relative abundance of each group in the composition of the Dominican amber inclusions was calculated (Table 2).

RESULTS AND DISCUSSION

1. Arthropods in General

To discuss our data on contemporary resins (Table 2), we first have to point out a few instances of drastic variation in the composition of inclusions, which can be currently explained by neither geographical differences, nor different characteristics of the corresponding conifer species and their resins. This is primarily the abundance of pseudoscorpions in the resin of the only examined specimen of *Pinus stankewiczi* (Sukacz.) Fomin in Crimea and, to a lesser degree, the abundance

of collembolans in the same sample and in the resin of *Pinus* sp. from Japan. Also noteworthy is variation, although not as drastic, of the relative abundance of some groups even within better studied resin assemblages, such as those of *Picea* resin in Central Russia and Primorye, as well as *Pinus* and *Larix* resins in Primorye: Homoptera (3–15%), Coleoptera (5–22%), Diptera (2–14%), Formicidae (21–74%), and other Hymenoptera (1–15%). Relative abundances of some other groups are less variable: Acari (10–15%), Lepidoptera (1–3%).

In general, the composition of inclusions in contemporary resins is more variable than that in amber. It is not surprising because our samples (assemblages of inclusions) reflect the contents of resins collected from a low number (1 to 100) of trees of each genus in each of the studied regions over a period of just a few years. In Central Russia and Primorye collecting was done over a period of six field seasons and in other regions in the course of a single field season. Because it is unlikely that inclusions within pieces of resin found on trees remain identifiable for longer than two or three years, our samples represent local assemblages of inclusions that formed not longer than 10 years. In contrast, amber assemblages reflect the composition of inclusions in fossil resins from a vast number of trees having grown over vast territories in the course of thousands if not millions of years (Zherikhin, 2002). In those assemblages all the local and geologically short-term fluctuations of the corresponding regional faunas have been thoroughly averaged and smoothed out, just as in sedimentary fossil deposits (Ponomarenko and Rasnitsyn, 1967). This important difference should always be kept in mind when the compositions of the recent and fossil organisms are compared.

Unfortunately, due to considerable variation in the composition of inclusions in contemporary resins, our material is insufficient to reliably identify differences between assemblages of inclusions from different conifer species or different geographical regions. Among the exceptions are an unusual composition of a small assemblage of larch resin inclusions from the Taimyr Peninsula, discussed below, and some additional data not included in Table 2 but published previously (Zherikhin and Sukacheva, 1989, 1992, 2003). The most remarkable among the latter is a virtual absence of grassland insects from both the contemporary and fossil resins, once again confirming the fact that the absence of any given group of organisms even in rich paleontological collections does not necessarily mean it was actually absent in the area in question during the period under examination. Our data also demonstrate that samples from trees growing near water contain a larger proportion of aquatic insects. This observation parallels available data on a considerably higher abundance of aquatic insects in Cretaceous retinites, in comparison with true ambers, such as succinities and rumanites. These results were interpreted as corroborating the hypothesis of Savkevich (1970, 1983), who suggested

that true ambers had formed in deep forests and spent a long time maturing in soil, while retinites had formed from resin quickly fallen into water. Yet, because the perceptible presence of undoubtedly aquatic organisms, such as mollusks and aquatic insect larvae, in true amber is a well-known fact, the above hypothesis can be accepted only tentatively.

Now we can turn to comparison of the compositions of inclusions in the contemporary and fossil resins. Only those numbers that appear at least minimally reliable will be used.

Pseudoscorpions are rare everywhere, except the already mentioned specimen of *P. stankewiczi* in Crimea. Opilionids, myriapods, and many insect taxa (Archaeognatha, Thysanura, Ephemeroptera, Odonata, Thysanoptera, Mecoptera, Trichoptera, Blattodea, Mantodea, Embioptera, Dermaptera, Orthoptera, and Phasmatodea) are also extremely rare. Spiders consistently account for 3–7% of inclusions, except the anomalous cases of the *Pinus* and *Larix* resins from the Russian Far East (0.6–0.8%). The *Pinus* resin from the Far East was also unusual in the high average abundance of ants (74%), explained by their enormous number in one of the six studied samples (*Pinus funebris*, Lake Khanka). The relative abundance of ants in the other five samples was only 22%, approximately as high as in *Picea* and *Larix* resins from the Russian Far East. If we treat that record as an outlier and count only 20–25% of ants in it, pretending that the rest are nonexistent, the size of the sample will be halved and the relative abundances of all taxa other than ants will double, in most cases approaching figures typical of other resins. Even if we count 40–45% of ants in that sample (as typical of more western regions), so that the sample will be reduced to two-thirds its previous size instead of one-half, then the relative abundances of other groups in the sample will still be much closer to figures typical of contemporary resins. Besides spiders, this consideration is very important for homopterans, beetles, lepidopterans, and dipterans. Yet, this explanation does not work in the case of the Far East *Larix* resin, because this resin contains an inexplicably small proportion of spiders.

The relative abundance of mites in most collections varies between 11 and 26% (4–5% in some small samples obviously being artifacts of the small sample size); only in the Warsaw collection of Baltic amber it is 4.2% and in Dominican amber, 2.5%. This drastic difference suggests that the Warsaw collection is not perfectly representative with regard to the smallest arthropods (mites and, to a lesser degree, collembolans), which probably were simply overlooked by the collector. In the case of Baltic amber, such explanation is less convincing. Therefore, it seems possible that the abundance of tree mites may actually be lower in the tropics than in the temperate zone. Collembolans are not particularly rare in the Eocene European ambers (4.5–9.6%), relatively rare in the Miocene Dominican amber (2.3%), and extremely rare in contemporary resins

(except the already mentioned small samples from *Pinus* from Crimea and Japan, *Larix* resin from Taymyr, and, to a lesser degree, *Picea* samples from the Russian Far East). The observed decrease in the relative abundance of collembolans in the Neogene and, particularly, contemporary resins may indicate a gradual decrease in the actual abundance of arboreal Collembola. Psocoptera are rare in all resins, except Dominican amber, which agrees well with the general opinion that this insect order is particularly abundant in the tropics. Considerable variation in the relative abundances of Homoptera in contemporary resins precludes seeing any clear trend: they account for 3.6–5.8% of all inclusions in the Eocene, 2.5% in the Miocene, and (1.8–)3–15% in contemporary resins (here and below, the figures in parentheses refer to the Far East *Pinus* sample, in which the actual abundance is underestimated due to the unusually large number of ants in the sample, see above). One can only suspect a possible decrease in the abundance of Homoptera in the tropics. It is possible that the abundance of Heteroptera increases: they are extremely rare in the Eocene (0–0.3%), perhaps only slightly more common in the Miocene (0.6%), but they form a small yet perceptible proportion (about 3.5%) in two of the four most representative assemblages of contemporary resin inclusions (mid-Europe and Primorye, *Picea*), while being rare in two others (0.5%, Primorye, *Pinus* and *Larix*). The abundance of beetles is not too high in European ambers (2–5%), higher in Dominican amber (8.6%), and much higher yet in contemporary resins (5–)13–22% (36.4% in a small sample from Japan). In other words, the participation of beetles increases considerably from the Eocene to the Miocene, and then to the present. The relative abundance of Lepidoptera also seems to be gradually increasing: 0.3–1% in the Eocene, 1.9% in the Miocene, and (1–)2–3% in the present. In contrast, the abundance of Diptera is dropping sharply: from 46–59% in the Eocene to 26% in the Miocene and (2–)5–16% at the present. This is due to an inexplicable disappearance of Nematocera: in ambers they are four to five times more abundant than Brachycera, while in contemporary resins, except the sample from Taymyr, they are less abundant (even when puparia of resinicolous flies, not found in amber but common in contemporary resins, are excluded from the count). A sharp increase in the abundance of ants from the Eocene (3–6%) to the Miocene (36%) and to the present (21–45(–74%)) (the last value being a chance outlier, see above) has also been observed in a different data set (Dlussky and Rasnitsyn, 2007). Other Hymenoptera also appear becoming more common (3.8–5.4% in the Eocene, 8% in the Miocene, and (1–)8–15% in the contemporary resins). The extreme rarity of termite records everywhere except the tropics (1.9% in Dominican amber) is not surprising. The abundance of stoneflies, extremely rare in fossil resins, appears to increase (0.1–1.5%), but the available material is too scarce to draw a definite conclusion. Zherikhin and

Sukacheva (1989, 1992) explain the increased participation of stoneflies in modern assemblages by a colder climate of the regions where contemporary resin was collected in comparison to the climates in which amber had formed.

In summary, our data indicate a possible decrease in the abundance of arboreal Collembola and of Nematocera towards the present and a parallel increase in the abundance of Heteroptera, Coleoptera, Lepidoptera, and Hymenoptera, particularly ants. The relative abundances of spiders and mites in resin inclusions do not demonstrate any significant changes. Data for other taxa are still insufficient for revealing any evolutionary trends.

As previously mentioned, the assemblage of larch resin inclusions collected on the Taymyr Peninsula turned out unique. Unfortunately, the low rate of resin production did not allow obtaining a more representative sample. However the available data, unreliable as they are, are extremely intriguing. First of all, half of the inclusions of Hymenoptera in that sample are members of the family Tenthredinidae, which is extremely rare both in the fossil and in all other contemporary resins. This phenomenon is not too surprising: the abundance of true sawflies in the Far North is well known. However, what is inexplicable at the current state of knowledge is the relative abundances of collembolans, beetles, ants and, to a lesser degree, nematocerans in that sample being approximately at the Eocene levels! This similarity is somewhat superficial because the Nematocera inclusions in the contemporary sample are represented mostly by Culicidae, very rare in the Eocene. Nevertheless the phenomenon definitely requires testing and confirmation on a sample of greater size.

Other results presented here are also preliminary, but they nevertheless show a significant promise of the actuapaleontological method in the study of past biotas, which left their traces as inclusions in fossil resins.

2. Hymenoptera

The data on Hymenoptera inclusions in amber and contemporary resins are presented in Tables 6–8. First, it needs to be noted that the composition of inclusions needs to be analyzed separately for solitary hymenopterans and social hymenopterans (primarily ants) because the patterns of fossilization and especially the pattern of their selection during assembly of amber collections differ for these two groups profoundly. Raw data on the number of Hymenoptera inclusions in contemporary resins are given in Table 6, while Tables 7 and 8 present data on relative abundances of both fossil and contemporary resin inclusions for solitary Hymenoptera families and ant subfamilies, respectively. More detailed data on the composition of ants in amber inclusions can be found in the article by Dlussky and Rasnitsyn (2009, pp. 38–56 this volume).

An important characteristic is the proportion of ants in the total number of Hymenoptera inclusions. In the

Table 6. Hymenoptera inclusions in contemporary resins

Taxa	mid-Europe		Crimea	Taymyr	Burya- tia	Far East			Japan	Total
	<i>Picea</i>	<i>Pinus</i>		<i>Larix</i>	<i>Picea</i>	<i>Picea</i> , <i>Abies</i>	<i>Pinus</i>	<i>Larix</i>	<i>Pinus</i>	
Xyelidae										
<i>Xyela ussuriensis</i> Rasn.						2				2
Tenthredinidae										
Diprioninae	1									1
Nematinae	2							3		5
<i>Anoplonyx</i> sp.				2						2
<i>Pikonema montana</i> (Zadd.)						1				1
indet.				1	3					4
Argidae										
<i>Arge</i> sp.						1				1
Pamphiliidae										
<i>Cephalcia</i> sp.	1					1				2
indet.								1		1
Siricidae										
<i>Sirex</i> sp.	1									1
<i>Urocerus tardigradus</i>						1				1
Megaspilidae										
<i>Conostigmus</i> sp.	1					1				2
Ceraphronidae										
<i>Aphanogmus dolichocerus</i> Dess. et Hel.	1					1				2
<i>Aphanogmus fumipennis</i> (Thoms.)						1				1
indet.								1		1
Evaniidae										
<i>Brachygaster minuta</i> Olivier	1	1								2
Proctotrupidae										
<i>Proctotrupes gravidator</i> L.	2									2
<i>Phaenoserphus</i> sp.	3									3
indet.	1									1
Diapriidae										
<i>Trichopria</i> sp.	1									1
<i>Psilus</i> sp.						1				1
<i>Spilomicrus</i> sp.						2				2
<i>Loxotropa</i> sp.						1				1
indet.					1					1
Cynipidae						1	1			2
Scelionidae										
<i>Telenomus</i> sp.	1					1		1		3
<i>Trissolcus flavipes</i> (Thoms.)						1				1
<i>Trissolcus grandis</i> Thoms.	1									1
Telenominae indet.	1									1
Platygastridae										
<i>Platygaster</i> sp.	1		1				1			3
<i>Synopeas</i> sp.	1	2								3
Platygastrinae indet.	1									1
Platygastridae indet.							2			2
Chalcidoidea										
Pteromalidae										
<i>Asaphes vulgaris</i> Walk.	1									1
<i>Melancistrus mucronatus</i> Thoms.	16									16

Table 6. (Contd.)

Taxa	mid-Europe		Crimea	Taymyr	Buryatia	Far East			Japan	Total
	<i>Picea</i>	<i>Pinus</i>		<i>Larix</i>	<i>Picea</i>	<i>Picea, Abies</i>	<i>Pinus</i>	<i>Larix</i>	<i>Pinus</i>	
<i>Trichomalus</i> sp.	3									3
indet.	17	1				1		1		20
Aphelinidae										
<i>Azotus celsus</i> Walk.			2							2
Torymidae										
<i>Megastigmus seitneri</i> Hoffm.								1		1
Encyrtidae										
<i>Syrphophagus?</i> sp.	1									1
indet.	8		1					1		10
Eurytomidae										
Eurytomidae indet.						1				1
Trichogrammatidae										
<i>Trichogramma</i> sp.	1									1
Chalcidoidea indet.	8		1		1	1				11
Ichneumonidae										
<i>Campoplex</i> sp.	1									1
<i>Hyposoter?</i> sp.	2									2
<i>Exenterus</i> sp.	1									1
<i>Exochus</i> sp.	2									2
<i>Scambus?</i> sp.	1									1
<i>Pimpla turionellae</i> L.	1									1
<i>Pimpla</i> sp.						1				1
Pimplinae indet.	1									1
<i>Hybrizon</i> sp.	1									1
<i>Orthocentrus</i> sp.	1					2				3
<i>Stenomactrus</i>						1				1
<i>Eusternix</i> sp.	1									1
<i>Plectiscus?</i> sp.				1						1
<i>Cylloceria</i> sp.						2				2
Diplazontinae								2		2
<i>Gelis ruficornis</i> Retzius	1					1				2
<i>Gelis instabilis</i> Förster						1				1
<i>Gelis</i> sp.	1									1
<i>Endasys</i> sp.	1									1
<i>Hemiteles</i> sp.						1				1
<i>Cubocephalus</i> sp.						1				1
Cryptinae indet.					2					2
Phaeogenini indet.	3					2				5
<i>Tycherus</i> sp.	1					1				2
<i>Aethecerus discolor</i> Wesmael						1				1
Platylabini									1	1
cf. <i>Cratichneumon</i>	1									1
<i>C. rufifrons</i> Grav.						2				2
Ichneumonidae indet.	6	1		1		5				13
Braconidae										
<i>Bracon (Sculptobrabon) burjaticus</i> Tobias	1					2		2		5
<i>Bracon</i> sp.	1					2				3
<i>Rhogas</i> sp.						1				1
<i>Macrocentrus (Amphicroplus)</i> sp.	7									7

Table 6. (Contd.)

Taxa	mid-Europe		Crimea	Taymyr	Burya- tia	Far East			Japan	Total
	<i>Picea</i>	<i>Pinus</i>		<i>Larix</i>	<i>Picea</i>	<i>Picea</i> , <i>Abies</i>	<i>Pinus</i>	<i>Larix</i>	<i>Pinus</i>	
Cheloninae indet.	1					1				2
<i>Ascogaster</i> sp.	3									3
<i>Apanteles</i> sp.	1									1
<i>Adelius</i> ? <i>subfasciatus</i> Hal.	1									1
Alysiidae indet.						1		1		2
<i>Synaldis</i> sp.	1									1
Braconidae indet.	1					8				9
Ichneumonoidea indet.	3					1		1		5
Parasitica indet.	1									1
Bethyloidea										
Bethylidae indet.			1							1
Dryinoidea										
<i>Aphelopus atratus</i> Dalman						1				1
Gonatopodinae m.	1									1
Sphecidae s.l.										
Pemphredoninae indet.			1				1	1		2
Apidae										
<i>Apis</i> sp.						1				1
Vespidae										
<i>Vespula germanica</i>					1					1
Formicidae										
<i>Myrmica rubra</i> L.	33						3		7	43
<i>M. scabrinodis</i> Nylander	1									1
<i>M. lobicornis</i> Nylander	1									1
<i>M. ruginodis</i> Nylander	1									1
<i>M. e.g. sulcinodis</i> Nylander	1							5		6
<i>M. saposchnikovi</i> Ruzsky							1			1
<i>Myrmica</i> sp.	9	1	1		4	1				16
<i>Leptothorax</i> sp.			1	1						2
<i>Pristomyrmex</i> ? <i>pungens</i> Mayr									4	4
Myrmicinae indet.	1									1
<i>Dolichoderus sibiricus</i> Emery						1	1			2
<i>Lasius niger</i> L.	107	1				1	4			113
<i>L. flavus</i> F.	1									1
<i>L. alienus</i> Forster			4							4
<i>Lasius</i> sp.	1	2			47	1				51
<i>Formica rufa</i> L.	65									65
<i>F. fusca</i> L.	15									15
<i>Formica</i> sp.	2	2			8	2				14
<i>Camponotus fallax</i> Nylander			44							44
<i>Camponotus</i> sp.					4					4
Formicidae indet.	174	1	1			73	1	75		325
Total	536	12	58	6	71	137	15	96	12	943

Note: Material was identified by Tenthredinoidea and Pamphilioidea, A.G. Zinov'ev, ZIN, Russian Academy of Sciences, St. Petersburg; Ceraphronoidea, A.V. Alekseev, Orekhovo-Zuevo Pedagogical Institute, Orekhovo-Zuevo; Chalcidoidea, S. Glogowski, Institute of Zoology PAN, Warsaw; Proctotrupeoidea and Platygastroidea, M.A. Kozlov, ZIN, Russian Academy of Sciences, St. Petersburg; Ichneumonidae, D.R. Kasparyan, ZIN, Russian Academy of Sciences, St. Petersburg; Braconidae, V.I. Tobias, ZIN, Russian Academy of Sciences, St. Petersburg; Formicidae, G.M. Dlussky, Moscow State University, Moscow; other groups, A.P. Rasnitsyn. All identifications were made in 1985–1990.

Table 7. Relative abundance of families of solitary Hymenoptera in assemblages of inclusions in contemporary and fossil resins. Percents are calculated from the total number of solitary Hymenoptera inclusions in each category

Taxa	Contemporary resins										Ambers				
	mid-Europe		Crimea	Taymyr	Buryatia	Far East			Japan	total	%	Baltic	Rovno	Scandinavian	Dominican
	<i>Picea</i>	<i>Pinus</i>	<i>Larix</i>	<i>Picea</i>	<i>Picea, Abies</i>	<i>Pinus</i>	<i>Larix</i>	<i>Pinus</i>				%	n/%	n/%	
Xyelidae															
Tenthredinidae	3/2.5%		3	3	2/3.6%		3/20%			2	0.9				
Argidae					1/1.8%					13	5.9				0.1
Pamphiliidae	1				1/1.8%		1/6.7%			1	0.4				
Siricidae	1				1/1.8%					3	1.4				
Megalyridae										2	0.9		2/0.5		
Megaspilidae	1				1/1.8%					2	0.9		9/2.2	?	0.3
Ceraphronidae	1				2/3.6%		1/6.7%			4	1.8		7/1.7	?	1.3
Evaniidae	1	1								2	0.9		2/0.5	2/0.5	1.2
Proctotrupidae	6/5%									6	2.7		4/1.0	?	0.1
Diapriidae	1			1	4/7.1%					6	2.7		57/14.2	?	2.7
Proctotrupoidea indet.													3/0.7	?	
Cynipoidea					1/1.8%			1		2	0.9		1/0.2	1/0.2	0.2
Scelionidae	3/2.5%				2/3.6%					6	2.7		120/30	?	25.9
Platygasteridae	3/2.5%	1						3		9	4.1		19/4.7	?	9.9
Platygastroidea indet.													1/0.2	?	
Mymarommatidae															
Proctoidea s.l. indet.															
Mymaridae															
Pteromalidae	37/30.8%	1			1/1.8%		1/6.7%			40	18.1		22/5.5	21/5.2	
Torymidae							1/6.7%			1	0.4		12/3.0	4/1.0	
Encyrtidae	9/7.5%						1/6.7%			11	5		6/1.5	27/6.7	

Table 7. (Contd.)

Taxa	Contemporary resins										Ambers			
	mid-Europe		Crimea	Taymyr	Buryatia	Far East		Japan	total	%	Baltic	Rovno	Scandinavian	Dominican
	<i>Picea</i>	<i>Pinus</i>		<i>Larix</i>	<i>Picea</i>	<i>Picea, Abies</i>	<i>Pinus</i>	<i>Larix</i>	<i>Pinus</i>		%	n/%	n/%	
Eulophidae											0.2	1/0.2	4/1.0	
Signiphoridae									1	0.4				
Tetracampidae						1/1.8%			2	0.9	2/0.5	5/1.2		
Eurytomidae		2/3.4%							1	0.4	2/0.5	15/3.7		
Aphelinidae									1	0.4	11/2.7	12/3.0		
Trichogrammatidae	1								11	5		34/8.5		
Chalcidoidea indet.	8/6.7%	1/1.7%			1	1/1.8%			55	24.9	28/7.0	44/11		0.9
Ichneumonidae	26/21.7%		2		2	21/37.5%	1/6.7%	1	35	15.8	39/9.7	93/23.2		3.4
Braconidae	17/14.2%					15/26.8%	3/20%				1/0.2			
Ichneumonoidea indet.									1	0.4	13/3.2	14/3.5		7.7
Bethylidae		1/1.7%									0.2	1/0.2	1/0.2	0.1
Chrysididae														
Embolemyidae									2	0.9		1/0.2		1
Dryinidae	1					1/1.8%						2/0.5	3/0.7	0.1
Pompilidae									3	1.4	0.5	2/0.5	3/0.7	0.7
Sphecidae		1/1.7%					1	1/6.7%			0.5	2/0.5	2/0.5	
Apidae											0.2	1/0.2	2/0.5	
Mutillidae											0.2	2/0.5	2/0.5	
TOTAL	120	5	7	5	7	56	5	15	221	30	400	401		
Chalcidoidea total											19.2	58/14.5	124/31	42.6

Note: Data on the Baltic amber refer to T. Giecwicz collection in Museum of Earth PAN, Warsaw (after Kosmowska-Ceranowicz in *Burszynowy...*, 2001), and those on the Rovno amber to representative collection of the Institute of Zoology, NASU, Kiev (E.E. Perkovsky, unpublished). Other data original (see text for details).

Table 8. Abundance of various ant subfamilies in contemporary and fossil resins

Taxa	Contemporary resins									Ambers						
	mid-Europe		Cri- mea	Tay- myr	Bury- atia	Far East			Japan	total	%	Scandina- vian	Baltic	Bitterfeld	Rovno	Dominican
	<i>Picea</i>	<i>Pinus</i>	<i>Larix</i>	<i>Picea</i>	<i>Picea, Abies</i>	<i>Pinus</i>	<i>Larix</i>	<i>Pinus</i>								
Dolichoderinae						1	1			2	0.5	39.8	58.4	55.4	52.7	51.2
Formicinae	191	5	48		59	4	4			311	79.9	43.2	37.8	36.3	41.1	4.9
Ponerinae											0	1.8	1.4	1.6	1	13.4
Pseudomyrmicinae											0	2.8	0.2	0.9	1.9	1.9
Myrmicinae	47	1	2	1	4	1	4	5	11	76	19.5	12.5	2.1	5.7	12.5	23.2
Total	238	6	50	1	63	6	9	5	11	389						

Note: Original data, except on the Eocene amber, after Dlussky and Rasnitsyn (2009, this volume). Percents are calculated from the total number of ant inclusions in each category.

better studied contemporary resins (Table 6) the proportion of ants varies between 60 and 90% (75% on average), i.e., it is much higher than in amber. Their share in the Baltic amber (the collection of Giecewicz in Warsaw, described by Kosmowska-Ceranowicz in *Bursztynowy...* (2001) is 52%; in the Rovno amber (E.E. Perkovsky, unpublished data), 56%; and in the Dominican amber (data of A.P.R., see above), 47%. As previously mentioned, the proportion of ants varies widely in different assemblages from contemporary resins, but the material available is insufficient for revealing any clear trends. The conclusion that the abundance of ants was steadily growing from the Cretaceous to the present is neither surprising nor new (Rasnitsyn, 1980; Dlussky and Rasnitsyn, 2003; Wilson and Hölldobler, 2005; Dlussky and Rasnitsyn, 2007). What is surprising is such an overwhelming abundance of ants in the cold-temperate zone of Central Russia, while tropical conditions are usually considered optimal for these insects.

Therefore, solitary Hymenoptera account for only the remaining 10–40% of contemporary resin inclusions. Within that share the proportions of different taxa are markedly different (Tables 6 and 7). Three groups dominate consistently: Ichneumonidae (22–37%, average 22%), Pteromalidae (2–31%, average 18%), and Braconidae (14–27%, average 16%). Other families, in representative samples, usually do not exceed 5% each (maximum 7.5%), and their combined share does not exceed 35% of the total number of solitary Hymenoptera. Some of those families still deserve special mention. First of all, one has to mention Tenthredinidae, accounting for 6% of the inclusions of solitary Hymenoptera, and occasional yet consistent records of Pamphiliidae. Tenthredinidae (like all Symphyta) are very rare in amber, and Pamphiliidae are not positively known from amber, which is explained by these two

families being mostly boreal in their distribution. It is known that the abundance of Tenthredinidae approximates that of Lepidoptera in the temperate forest zone and is much higher than that in tundra (Rasnitsyn, 1969).

Records of Xyelidae stuck to resin have already been pointed to as evidence that the complete absence of these insects from vast collections of amber inclusions cannot be explained by their alleged resistance to such entrapment (Zherikhin and Sukacheva, 1989). The total absence of this family from amber is particularly puzzling given the records, sometimes numerous, of rock impressions of Xyelidae in Cenozoic deposits from various continents (in the Mesozoic this family was among the dominant groups of Hymenoptera, see *History...*, 2002).

Comparing compositions of solitary Hymenoptera between contemporary resins and fossil ambers in a wider context reveals some additional important characteristics. First of all, these are different sets of dominant taxa. In both Baltic and Rovno ambers, the most abundant within this category are Scelionidae (36 and 30% of all inclusions of solitary Hymenoptera, respectively), followed by Chalcidoidea (19 and 14.5%), despite Pteromalidae chalcidoids not being particularly common (4 and 3%). These two dominant groups are followed, in Baltic amber, by Ichneumonidae and Braconidae (12–13%), and, in Rovno amber, by Diapriidae (14%), Braconidae (10%), Mymaromatidae, and Ichneumonidae (7% each). In the Miocene Dominican amber, the most abundant in this category are Chalcidoidea (43%), the proportions of specific families are not known, followed by Scelionidae (26%) and Platygasteridae (10%). These data support the hypothesis put forward during preliminary study of the same material (Rasnitsyn and Kulicka, 1990) that the abundance of

Table 9. Abundance of beetles in contemporary and fossil resins

Taxa	Contemporary resins							Ambers			
	mid-Europe	Crimea	Buryatia	Far East			total	%	Rovno	Baltic	
	<i>Picea</i>	<i>Pinus</i>	<i>Picea</i>	<i>Picea</i>	<i>Pinus</i>	<i>Larix</i>				(1)	(2)
Cupedidae									7/0.4%		
Gyrinidae	11/9.2%			1			12	5.4	2/0.1%		8/2.2%
Carabidae									76/3.9%		2/0.6%
Dytiscidae							1	0.4	1		2/0.6%
Hydrophilidae			1						5/0.2%		
Histeridae									2/0.1%		1/0.3%
Ptiliidae			1	1			2	0.9	3/5.7%		7/1.9%
Leiodidae							1	0.4	5/9.4%		36/10%
Seydmenidae	1										
Sylphidae									9/0.4%		
Staphylinidae	8/6.7%		3/17.6%	4/10%	3/23.1%	2/7.1%	20	8.9	93/4.7%		11/3.1%
Lucanidae							3	1.3	1		22/6.1%
Scarabaeidae	3/2.5%								1		
Clambidae									2/0.1%		
Scirtidae	2/1.7%	5/83%					7	3.1	376/19.4%		46/12.8%
Dascillidae									5/0.2%		
Buprestidae									3/0.1%		
Byrridae	1						1	0.4	2/0.1%		1/0.3%
Artematopodidae											1/0.3%
Eucleridae				1			1	0.4	48/2.4%		3/0.8%
Throscidae				1	1		2	0.9	17/0.8%		1/0.3%
Elateridae	6/5%		1	2/5%	1	1	11	4.9	286/14.7%		20/5.6%
Lycidae									1		1/0.3%
Cantharidae						1	1	0.4	91/4.6%		3/0.8%
Dermestidae	3/2.5%			6/15%		3/10.7%	12	5.4	5/0.2%		2/0.6%
Anobiidae				5/12.5%	2/15.3%		7	3.1	236/12.2%		32/8.9%
Lymexylophoridae									5/0.2%		
Trogossitidae									4/0.2%		
Cleridae	1						1	0.4	15/07%		1/0.3%
Trogossitidae vel Lophocateridae											
Melyridae				1	1		2	0.9			5/1.4%
Monotomidae											2/0.6%

Table 9. (Contd.)

Taxa	Contemporary resins										Ambers	
	mid-Europe	Crimea	Buryatia	Far East			total	%	Rovno	Baltic		
	<i>Picea</i>	<i>Pinus</i>	<i>Picea</i>	<i>Picea</i>	<i>Pinus</i>	<i>Larix</i>				(1)	(2)	
Nitidulidae	1					1	2	0.9	10/0.4%		10/0.4%	
Cucujidae	2/1.7%						3	1.3	17/0.8%		17/0.8%	
Cryptophagidae				1					16/0.7%		16/0.7%	
Phalacridae									1		1	
Languriidae									1		1	
Erotylidae									2/0.1%		2/0.1%	
Bothrideridae												
Cerylonidae												
Endomychidae												
Coccinellidae	5/4.2%						5	2.2	16/0.7%		16/0.7%	
Corylophidae									12/0.6%		12/0.6%	
Latridiidae	8/6.7%	1	1	1		2/7.1%	13	5.8	1		1	
Mycetophagidae							4	1.8	41/2.1%		41/2.1%	
Ciidae			4/23.5%						31/1.5%		31/1.5%	
Melandriidae									3/0.1%		3/0.1%	
Mordellidae									44/2.3%		44/2.3%	
Rhipiphoridae									115/5.8%		115/5.8%	
Colydiidae				1			1	0.4	2/0.1%		2/0.1%	
Zopheridae									14/0.7%		14/0.7%	
Tenebrionidae									31/1.5%		31/1.5%	
Salpingidae												
Oedemeridae				1			1	0.4	4/0.2%		4/0.2%	
Pythidae									1		1	
Pyrrhocroidae									49/2.5%		49/2.5%	
Anthicidae									53/3%		53/3%	
Aderidae	2/1.7%								39/2.3%		39/2.3%	
Scaptiidae	1								30/1.5%		30/1.5%	
Cerambycidae	14/11.7%		3/17.6%			2/7.1%	1	0.4	10/0.4%		10/0.4%	
Chrysomelidae	7/5.8%			2/5%		4/30.7%	25	11	85/4.3%		85/4.3%	
Anthribidae	44/36.7%		3/17.6%	12/30%		16/57.1%	76	34	1946		1946	
Curculionidae	120	6	17	40	13	28	224		53		53	
T total												

Note: Data on Rovno amber after Perkovsky et al. (2007). Percents are calculated from the total number of beetle inclusions in each category. Data on the Baltic amber: (1) Königsberg collection, after Klebs (1910); (2) T. Giecwicz collection in Museum of Earth PAN, after *Bursztynowy...* (2001). Other data original.

Scelionidae has considerably decreased and that those of Ichneumonidae and Braconidae have increased.

In combination, the three most abundant groups account for 68% of all solitary Hymenoptera in the Baltic amber, 48.5% in the Rovno amber, and 79% in the Dominican amber. In this characteristic, the Baltic and Dominican ambers do not differ significantly from contemporary resins (71%, treating Chalcidoidea as a single group, with a 30% abundance), while Rovno amber turns out the most diverse (i.e., the dominance of a few groups here is the least prominent).

In the composition of ant inclusions, contemporary resins of northern Eurasia differ from amber even more strongly than in the composition of solitary Hymenoptera (Table 8). On average, 80% of ant inclusions in such resins are members of Formicinae, and 20% are Myrmicinae (Dolichoderinae occur sporadically). The relative abundance of myrmecines in different assemblages varies profoundly. The composition of European amber ant assemblages is much more diverse: 40–60% of all ant inclusions comprise Dolichoderinae, 36–43% Formicinae, and 2–12% Myrmicinae. In the Dominican amber, the relative abundance of Dolichoderinae is approximately the same (51%), followed by Myrmicinae (23%), Ponerinae (13%), and only then Formicinae (5%). These differences reflect both evolutionary changes (decline of Dolichoderinae and rise of Myrmicinae) and geographical differences between the faunas (superdominance of Formicinae in temperate and particularly in cold-temperate climates). The evolution of the role of ants in terrestrial ecosystems has been discussed in more detail by Dlussky and Rasnitsyn (2007), and the composition of ant inclusions in the Late Eocene ambers is discussed in detail by Dlussky and Rasnitsyn (2009) in this volume.

3. Coleoptera

Despite their obvious scarcity, our records of beetle inclusions in contemporary resins (Table 9) are of interest for comparison with data on the composition of beetles in the Eocene ambers. Unfortunately, the available data are too limited to make separate comparisons for each particular assemblage of contemporary resins. Moreover, the available list of beetles from Scandinavian amber (Larsson, 1978) is not sufficiently detailed, and for Dominican amber no data exist that could be used for a comparison. Therefore, the data at hand give little opportunity for comparative analysis.

It is immediately seen from Table 9 that in all the samples of contemporary resins that contain over 20 beetles the dominant family is Curculionidae (30–57%), followed by Chrysomelidae (5–12%), and then Staphylinidae (7–10%). Across the entire material, curculionids account for 34%, chrysomelids for 11%, and staphylinids for 9% of all the beetle inclusions. This does not contradict intuitive ideas of the leading role

played by these three families of beetles in terrestrial communities of northern Europe.

For the Eocene amber the picture is completely different. First, no beetle family dominates profoundly, none accounting for more than 20% of beetle inclusions in any of the three amber collections. This may be a consequence of a warmer climate and, correspondingly, higher diversity of the original amber forest fauna. Yet, more abundant and reliable material is required to draw a more definite conclusion. Secondly, different amber faunas are dominated by different beetle families. Three families, Scirtidae, Elateridae, and Mordellidae, each account for more than 5% of all beetle inclusions in each of the three amber collections. Scirtidae, a clear dominant in the Baltic amber, ranks fifth in the Rovno amber. Conversely, Staphylinidae, dominating in the Rovno amber, ranks very low in the Baltic amber (3.1–4.7%). Elateridae ranks second in the Rovno amber and the Baltic amber collection described by Klebs (1910), while ranking only sixth in the Baltic amber collection of Gieciwicz. The second and third positions in the latter collection are shared by Scydmenidae and Aderidae, while in Klebs (1910) Anobiidae ranks third, and in Rovno amber Scydmenidae and Aderidae share the third and fourth positions. It seems likely that all the above seven families of beetles were prominent in the amber forest faunas, but their abundance has significantly decreased since. Further studies are needed to find out whether their decline was limited to northern Eurasia or it occurred over a wider geographic range.

CONCLUSIONS

The actual paleontology of inclusions in fossil resins is still making its first, modest steps. The material collected so far is scarce and limited, both in terms of diversity of resin-producing plant taxa and geographic scope. Because the compositions of inclusions in contemporary resins are highly variable in comparison with those of amber assemblages, which have been averaged across vast territories and long time intervals, our results can be considered only as a first approximation, serving as a basis for planning further, wider and more robust studies. It is even more important than that these strictly preliminary results in general agree well with intuitive expectations and, in some respects, supplement these. In particular, the general taphonomical similarity between the compositions of inclusions in the recent and fossil resins was confirmed. Also confirmed was the trend towards the increase of the relative abundances of true bugs, beetles (particularly curculionids, chrysomelids, and staphylinids), lepidopterans, ants (particularly Formicinae and Myrmicinae), and ichneumonoids. Other phenomena and trends discovered were less expected, such as the decrease in the abundance of nematocera, scelionids, collembolans, and some beetle families (Scirtidae, Elateridae, Mordellidae, and some others). Further studies of inclusions in contemporary resins, particularly in addi-

tional regions and on additional resiniferous plants, will undoubtedly yield highly important and interesting results.

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