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Hymenopteran insects in Baltic amber with respect to the overall history of the order

ABSTRACT. Hymenopterous insects in Baltic amber are discussed.

The data relating to the percentage representation of Hymenoptera in different assemblages of fossil and recent resins are presented.

The assemblages of Baltic amber Hymenoptera differ strongly from the Late Cretaceous fauna in that they consist mostly of parasitic forms, with the aculeates being a minor component, while sawflies and horntails are absent. The leading family was invariably *Scelionidae*, followed by the *Serphitidae* and *Mymaromatidae* since the Santonian stage.

The families *Stigmaphroridae*, *Cretevanidae*, *Austroniidae*, *Chrysididae* and *Falsiformicidae* decreased in their representation, often up to extinction, during the first half of the Late Cretaceous. Some other groups underwent increasing representation in the assemblages and probably in the parental faunas.

Hymenopterans as a whole began to play a more important role in fossil insect assemblages during the Miocene.

The insects assemblages in Baltic amber are essentially intermediate in composition between Late Cretaceous and contemporary ones.

Several groups such as *Megalyridae*, *Evaniidae*, *Dipriidae*, *Bethylidae* and *Dolichoderinae* (*Formicidae*), which were more common in Baltic amber than in both older and younger assemblages are thermophilic and their relative abundance there was probably environmentally determined.

The hymenopteran assemblages from Baltic amber seem to be more similar to the extant fauna than to the Late Cretaceous one.

The hymenopterans (order Hymenoptera, earlier Vespida) are insects of great general and applied interest. The number of species is high, 108,000 having been described up to the middle of the 20th century (Borror, Delong, Triplehorn 1976), and the total number of existing species being roughly estimated as half a million, based on published figures of 70,000 for *Aculeates* (Brothers 1975), 40–50,000 for *Braconidae* (Achterberg 1976), 100,000 for *Chalcidoidea* (Noyes 1978), and 100,000 for *Ichneumonidae* (Heinrich 1978). The important role of Hymenoptera in the life of natural and man-affected communities is well appreciated. Various aspects of morphology, genetics, social organization, and fossil history of hymenopterans are really instructive for the general view on what living systems

are, one example being the meaning of the haplo-diploid genetic system for sociobiology.

Hymenopterans tell us much about past environments too. For example, a proportion of the sawflies belonging to the families *Xyelidae* (in the Mesozoic era) and *Tenthredinidae* (in the Cenozoic era) can be used to characterize the thermic conditions of the respective era (Rasnitsyn 1980; Zherikhin 1980). A member of the family *Cephidae* found in the Lower Cretaceous period deposits in Transbaikalia allowed one of us to predict the presence of the oldest Angiosperm plants there (Rasnitsyn 1969, p. 14), and this prediction was found to be correct (Vakhromeev and Kotova 1977).

Baltic amber is one of the best sources of our knowledge about ancient insects and their environments (Larsson 1978). Due to the abundance and excellent state of preservation of their inclusions and the long history of their study, the insects of Baltic amber are comparatively well known. R. Keilbach (1982) cited ca. 2200 described species belonging to 266 families, whereas V. V. Zherikhin (1978) estimated ca. 3000 species, both described and mentioned in Baltic amber. Three hundred and seventy hymenopteran species are described or at least named from Baltic amber up to now (Spahr 1987, and additional descriptions by Lelej 1986; Tobias 1987; Kasparyan 1988 a, b; Nemkov 1988, Dlussky 1988). These figures are very high, taking into account that they include only a part of the entomofauna of the amber forest, because the insects populating water and grass communities had little chance to become amber inclusions (Zherikhin and Sukatcheva 1988).

In respects other than numerical our knowledge of Baltic amber insects is still modest, because most species were described long ago (late 19th and early 20th centuries) and are badly in need of revision. However,

an important step in exploring palaeoecology of the amber forest was made several years ago (Larsson 1978).

The purpose of the present paper is to place the accumulated information of Baltic amber hymenopterans into the general perspective on the evolution of the order. It is paradoxical at first sight, though natural on more close examination that the Mesozoic history of the Hymenoptera is presently better known than the Cenozoic history. This is partly because most descriptions and lists of Cenozoic era Hymenoptera are old and unreliable. The other reason is that the Cenozoic history of the order is rather slow, not very rich in striking events and thus more difficult to elucidate.

The Mesozoic segment of the history of the Hymenoptera is presented here as a short version of the last chapter in A. P. Rasnitsyn (1980), corrected according to A. P. Rasnitsyn (1988a,b). Comparable data for the Cenozoic era are non-existent. We have gathered information about the family-level composition of ancient insect assemblages, because this sort of data is more reliable and easier to check and correct. We have additionally reduced the issue of uncertainty by taking into consideration only the assemblages originating in fossil resins because these assemblages are essentially uniform taphonomically and, in part, ecologically. This considerably reduced the number of comparable assemblages. Nevertheless, we still have a reasonably long succession of assemblages covering all the late Cretaceous period and Cenozoic era up to the assemblage of insects from the resin of living trees (described by Zherikhin and Sukatcheva 1988). The Early Cretaceous period is not covered because comparable data for the Lebanon insect assemblage are unfortunately not available.

History of the Hymenoptera is documented palaeontologically since the Late or, possibly, Middle Triassic period. The oldest forms belonged to the family *Xyelidae* which flourished during the Mesozoic era (albeit mostly in more temperate regions) and which still exist as a relic group in Holarctic forests. The Triassic representatives come from Madygen clays on the northern slopes of the Zeravshan mountain range in Kirghizia and from the Ipswich deposits in Queensland, Australia.

Not later than the very beginning of the Jurassic period the *Xyelidae* gave rise to the evolutionary lines leading to other groups. Ten families are now known to have existed during the Early Jurassic period, belonging to both suborders, Siricina and Vespina (the suborders largely corresponding to though not identical with the former suborders Symphyta and Apocrita, respectively). Among these families only three survived until now: *Pamphilidae*, *Xyelidae* and *Megakyridae*, the last two as relicts.

The Middle Jurassic fauna is little known yet. In contrast, the rich and diverse Late Jurassic assemblage is known at present from the famous locality in the Karatau mountain range, southern Kazakhstan.

Listed in a dominance order, the leading Karatau families were *Praeaulacidae* (extinct), *Megalyridae* (8 relic genera still extant in the Southern Hemisphere), *Ephialtitidae* (extinct), *Mesoserphidae* (extinct), *Heloridae* (two relic genera still extant), *Anaxyelidae* (single extant relic species) and *Xyelidae* (five relic genera living). The first five families belong to the suborder Vespina, the last two to Siricina.

Ecologically the Karatau assemblage was similar to other Mesozoic thermophilous assemblages in abundance of the xylophilous groups — wood-bores (*Anaxyelidae* and other Siricoidea, as well as some beetles) and their parasites (the first four families in the above list, many other representatives of Vespina, and the parasitic fly family *Nemestrinidae*).

On crossing the Jurassic-Cretaceous periods border the hymenopteran assemblages retained the above ecological pattern without change, with the thermophilous, assemblages having been rich in xylophilous forms. The taxonomic turnover has been great, however, so that only *Xyelidae* kept their dominant position in more temperate environments. The remaining families in the above list became subordinate groups, and many minor components of the Karatau assemblage also were strongly affected in one way or another.

Many new groups appeared during the first half of the Early Cretaceous period, including those so characteristic of present-day communities, e. g. *Tenthredinidae*, *Ichneumonidae*, *Braconidae*, *Proctotrupidae*, *Scelionidae*, *Cynipidae*, *Chalcidoidea*, *Sphecidae*, *Pompilidae*, *Vespidae*, and many others.

Many new families appeared later during the Cretaceous period, including those now among the dominant groups (*Cynipidae*, *Diapriidae*, *Scoliidae*, several new Chalcidoid families) while still other families born in the Cretaceous period failed to cross the upper boundary of the period (*Maimetshidae*, *Stigmaphronidae*, *Cretevaniidae*, *Archaeocynipidae*, *Serphitidae*, the primitive ants *Armaniidae* and *Sphecomyrmae* and some others). In general, the Late Cretaceous hymenopteran assemblages had already acquired considerable similarity with the Tertiary and modern ones.

The processes of the taxonomic turnover during the Late Cretaceous and Tertiary periods are the main objective of the present paper. The available relevant data are compiled in Tables 1 and 2, which serve as a base for further considerations. As has already been stated, the evolutionary stage documented by the Baltic amber assemblage is of most interest in the framework of the present paper.

Table 1 shows that the hymenopteran representa-

Table 1
Representation (%) of Hymenoptera in insect assemblages from Baltic amber, and non-Baltic fossil and present-day resins
Procentowy udział Hymenoptera w zbiorowiskach owadów z bursztynu bałtyckiego i z niebałtyckich kopalnych i współczesnych żywic

Region Locality	Tajmyr Agapa	Tajmyr Jantar-dakh	Alberta Medicine Hat	Tajmyr Baikura	Sakhalin Starodubsk	Poland	BALTIC REGION						Dominic	Sicily	New England (USA)	Moscow Region (USSR)	Maritime Province (USSR)
Age	K ₂ c	K ₂ s	K ₂ cp	K ₂ m	P ₁		Upper Eocene P ₂ ³						N ₁ aq	N ₁		present-day	
Owner	PIN	PIN	CNC	PIN	PIN	ME	ZM	GC	AU	PI	MW	MC	MW	AC	HU	PIN	PIN
Number of insects	580	3000	1280	246	945	11850	6249	707	>50000	433	—	189	243	227	21600	1460	1220
Parasit. ins.	21%	12	11	19	11	3	10	4	1	9	—	—	15	2	5	7	5
Hymenoptera:	23%	13	12	22	16	11	15	12	5-7	21	—	18	28	60	5,4	49	41
<i>Phytophaga</i>																	
<i>siricina</i>	0	0	0	0	0	+	0	0	—	0	0	0	0	0	0,9	0,7	2
Parasitica	93	91	93	87	95	31	70	31	19	41	—	—	55	3	92	15	11
<i>Aculeata</i> excl.																	
(excl. ants)	7	8	3	2	1	3	2	5	1	3	—	—	7	6	2	1	+
<i>Apidae</i> s.l.	0	0	0	0	0	+	—	—	—	0	—	0	10	>50	0	0	1
<i>Formicoidea</i>	0	1	3	11	4	66	28	64	~80	56	—	62	38	91	6	84	87
<i>Formicinae</i>	0	0	0	0	+	38	—	—	33	—	41	—	—	15	—	81	54
<i>Dolichoderina</i>	0	0	+	0	+	57	—	—	64	—	51	—	—	10	—	0	8
<i>Myrmicinae</i>	0	0	0	0	0	3	—	—	2	—	4	—	—	55	—	19	0
Other ants	0	100	+	100	+	2	—	—	1	—	4	—	—	20	—	0	0

HYMENOPTERAN INSECTS IN BALTIC AMBER

Depositories: PIN — Paleontological Institute, Moscow; CNC — Canadian National Collection, Ottawa; ME — Museum of the Earth, Warsaw; ZM — Zoological Museum, Copenhagen; GC — Gyllen Collection, Uppsala; AU — Albertus University, Königsberg (now one part in Göttingen); PI — Paleontological Institute, Wien; MC — Mayr Collection, Wien; MW — Natural History Museum, Wien; AC — private collection of Alvolio family, Bologna; HU — Harvard University, Cambridge.

Data sources: Agapa, Jantardakh — Rasnitsyn, 1975; Baikura — Rasnitsyn, 1980; Baltic region: ZM — Larsson, 1978; AU — Klebs, 1910 for insects, Brues, 1933 for Hymenoptera, Dlussky, 1981 for ants; New England — Brues, 1933. Other data are original by A. P. Rasnitsyn and, for ants, G. M. Dlussky, except for GC — from the unpublished census by I. -B. Selberg, 1963, MW and MC — by A. G. Ponomarenko.

Present-day assemblages: New England — data by Brues, 1933, other — insects extracted from the resin of *Picea excelsa* L. in various sites in the Moscow Region, and of *Picea*, *Abies* and *Larix* spp. in various sites of the Maritime province of the USSR.

Age symbols: K₂c — Upper Cretaceous, Cenomanian, K₂s — the same, Santonian, K₂cp — the same, Campanian, K₂m — same, Maestrichian, P₁ — Paleocene, N₁aq — Miocene, Aquitanian, N₁ — Miocene unspecified.

Table 2

Representation (%) of hymenopteran families in amber and resin assemblages. Source of data as in Tabl. 1. Sawflies and ants are excluded.

Extinct families are marked with a cross

Procentowy udział rodzin błonkówek w zespołach z bursztynu i żywic. Źródło danych jak w tabeli 1. Muchówki i mrówki są wyłączone.

Rodziny wymarłe — oznaczone krzyżykami

Locality	Agapa	Jantar-dakh	Medicine Hat	Baikura	Starodubsk	Baltic ME	Amber AU	PIN	Present-day New England (USA)	Moscow	Maritime
Number of specimens	125	366	147	65	171	450	1817	296	1088	106	57
<i>Orussidae</i>	1	0	0	0	0	0	0	0	0	0	0
<i>Stephanidae</i>	0	0	0	0	0	0	+	0	0	0	0
<i>Megalyridae</i>	0	0	0	3	0	1	2	3	0	0	0
+ <i>Maimetshidae</i>	0	+	1	0	0	0	0	0	0	0	0
<i>Megaspilidae</i>	0	+	1	2	1	3		+		1	2
<i>Ceraphronidae</i>	0	0	0	0	0	+	3	+	5	1	5
+ <i>Stigmaphronidae</i>	10	1	1	0	0	0	0	0	0	0	0
<i>Trigonalidae</i>	1	0	0	0	0	0	0	0	0	0	0
<i>Evanidae</i>	0	0	0	0	0	1	2	2	0	1	0
+ <i>Cretevanidae</i>	3	1	0	0	0	0	0	0	0	0	0
<i>Gasteruptiidae</i>	0	0	1	3	0	0	+	0	0	0	0
<i>Cynipidae</i>	0	1	3	2	1	0		0		0	2
<i>Figitidae</i> s. l.	0	0	0	0	0	0	+	+	8	0	0
<i>Ibaliidae</i> s. l.	0	1	0	0	0	0		0		0	0
<i>Proctotrupidae</i>	0	0	0	0	1	2	4	+	+	5	0
<i>Pelecniidae</i>	0	0	0	0	1	0	+	0	0	0	0
<i>Roproniidae</i>	0	0	0	0	0	0	0	0	+	0	0
<i>Austroniidae</i> s. l.	1	+	0	0	0	0	0	0	0	0	0
<i>Diapriidae</i>	0	1	1	6	1	12	14	5	14	1	5
<i>Scelionidae</i>	57	38	37	29	11	22	16	20	2	3	5
<i>Platygasteridae</i>	0	0	0	0	3	5	1	1	10	4	5
+ <i>Serphitidae</i>	6	30	18	12	0	0	0	0	0	0	0
<i>Mymaromatidae</i>	10	4	17	14	1	+	1	0	0	0	0
<i>Mymaridae</i>	0	+	4	0	4	1	1		1	0	0
<i>Chalcidoidea varia</i>	1	8	10	23	30	16	11	18	4	46	7
<i>Ichneumonidae</i>	1	1	1	3	1	9	16	13	45	21	30
										+5	+5
<i>Bracconidae</i> s. l.	3	5	2	2	46	18	18	27	12	15	30
<i>Chrysididae</i>	1	3	1	0	0	+	+	+	0	0	0
	+2	+3									
<i>Bethylidae</i>	1	1	2	2	0	5	10	6	0	0	0
<i>Dryinidae</i>	1	+	1	0	0	+	1	0	+	1	2
<i>Embolemidae</i>	0	0	0	0	0	0	+	+	0	0	0
<i>Sphecidae</i> s. l.	2	+	0	0	0	1	—	2		0	2
<i>Apidae</i> s. l.	0	0	0	0	0	1	—	0		0	2
<i>Pompilidae</i>	0	0	0	0	0	1	—	1	2	0	0
<i>Mutillidae</i>	0	0	0	0	0	+	1	+		0	0
+ <i>Falsiformicidae</i>	2	+	0	0	0	0	0	0	0	0	0
<i>Vespoidea</i>	0	0	0	0	0	0	—	0	+	0	0

tion in the older assemblages in question is usually about 12–13% rising considerably during the Miocene epoch due to the ant explosion (Dlussky and Fedoseeva 1988). As a result, nearly a half of the insects included in the Miocene epoch and present resins belongs to the Hymenoptera. There are deviations from this pattern, however. Some of them are evidently artifacts, e. g. varying figures for Baltic amber which depend on the personal approach of the collectors and owners of the collections. The tanglefoot figure is ab-

normally low, probably because this method strongly underestimates ants. The moderately high percentage found in the oldest and youngest Late Cretaceous assemblages are more realistic, especially if we take into account the data on additional assemblages not studied enough to be included in Table 1 (Fig. 1).

Also noteworthy seem to be the dynamics of the abundance of ants and their subgroups. The subject was already discussed in detail by G. M. Dlussky and E. B. Fedoseeva (1988). Our data confirm their results

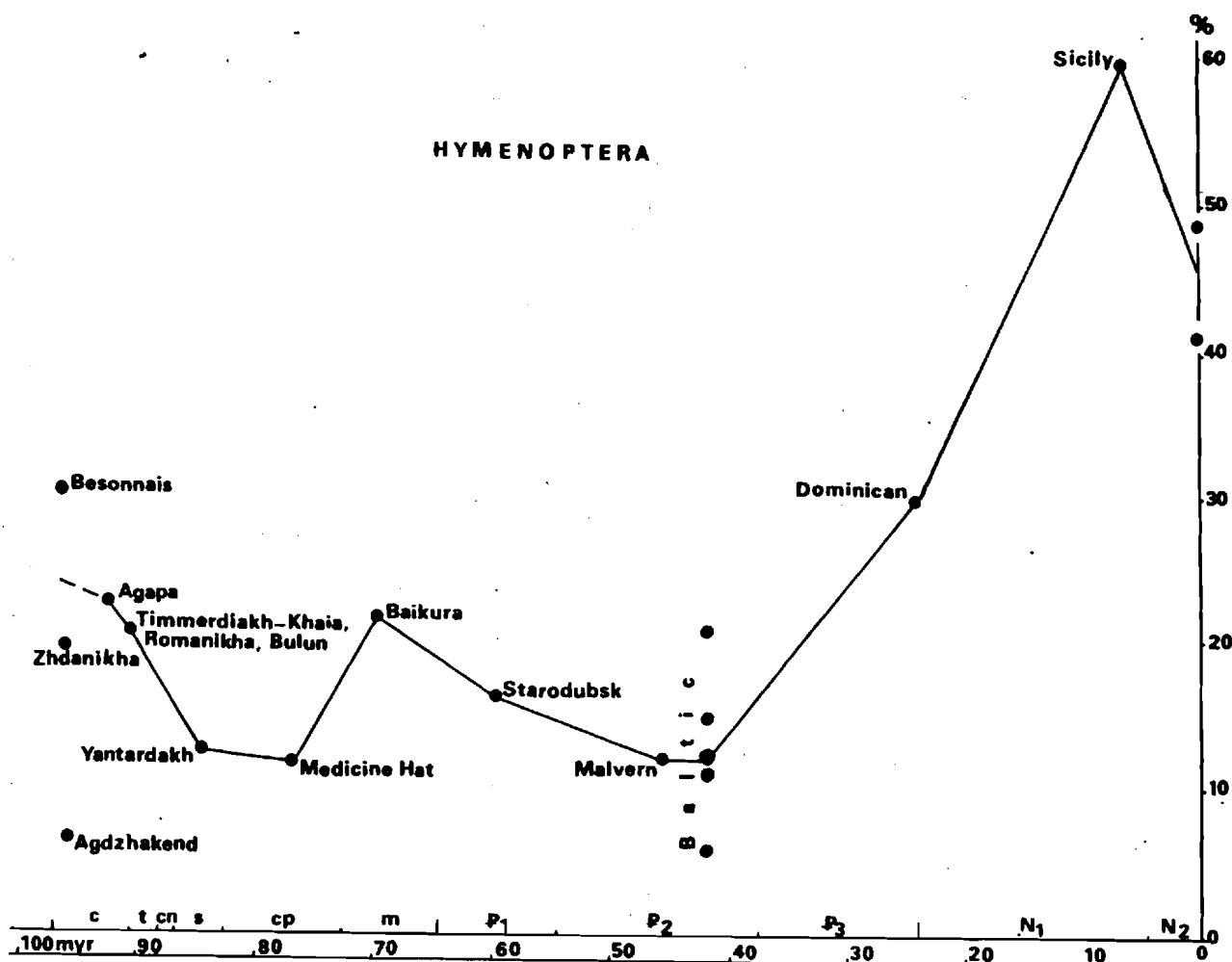


Fig. 1

Representation of Hymenoptera in Late Cretaceous and Cenozoic insect assemblages. Data for assemblages from Besonnais (NW France, Early Cenomanian age) after Schlüter (1978); from Agdzhakend (Azerbaijan, the same age), Zhdanikha (Taimyr, probably the same age), Timmerdiakh-Khaia (Yakutia, Turonian age), Romanikha and Bulun (Taimyr, probably the same age) after Rasnitsyn (1980); from Malvern (Arkansas, Middle Eocene) after Saunders *et al.* (1974); other data from Table 1. Age symbols in Figs. 1–7: c – Cenomanian; t – Turonian; cn – Coniacian; s – Santonian; cp – Campanian; m – Maestrichtian (Late Cretaceous); P₁ – Paleocene; P₂ – Eocene; P₃ – Oligocene; N₁ – Miocene; N₂ – Pliocene

Występowanie błonkówek w górnokredowych i kenozoicznych zespołach owadów. Dane z zespołu z Besonnais (NW Francja, wczesny cenoman) według T. Schütera (1978), z Agdzhakend (Azerbejdżan, tego samego wieku), Zhdanikha (Tajmyr, prawdopodobnie tego samego wieku), Timmerdiakh-Khaia (Jakucja, turon), Rumanikha i Bulun (Tajmyr, prawdopodobnie tego samego wieku) według A. Rasnitsyna (1980), z Malvern (Arkansas, środkowy eocen) według Saundersa i in. (1974), inne dane z tabeli 1. Oznaczenia wieku na fig. 1–7: c – cenoman; t – turon; cn – santon, cp – kampan, m – mastrycht (górna kreda); P₁ – paleocen; P₂ – eocen, P₃ – oligocen, N₁ – miocen; N₂ – pliocen

and further develop some details. Table 1 shows low ant abundance before the time of Baltic amber formation followed by the ant explosion which proceeded in two steps: prior to the Late Eocene epoch (up to more than half of Hymenoptera) and early in the Miocene epoch (Fig. 2). The first event is explainable by the appearance of dolichoderine and, to a lesser extent, formicine ant species which form large colonies. The second, Miocene, ant explosion depended most probably on the further development of *Formicinae* and especially *Myrmicinae* in the same direction. The above data illustrate only the dynamics of ant abundance and not the time of origin of their subfamilies. In fact,

Ponerinae and *Dolichoderinae* are known since the Late Cretaceous period (recent findings in Canadian amber, Medicine Hat locality, Canadian National Collection in Ottawa, Canada), *Formicinae*, *Dolichoderinae* and *Aneuritinae* since the Paleocene and the remaining subfamilies since the Late Eocene epoch (Dlussky and Fedoseeva 1988).

Other interesting events indicated by Table 1 are the increasing role of bees in the Miocene epoch and of sawflies in present-day samples. These events were most probably environmentally and not evolutionarily governed, because the Miocene assemblages concerned came from supposedly tropical regions while the

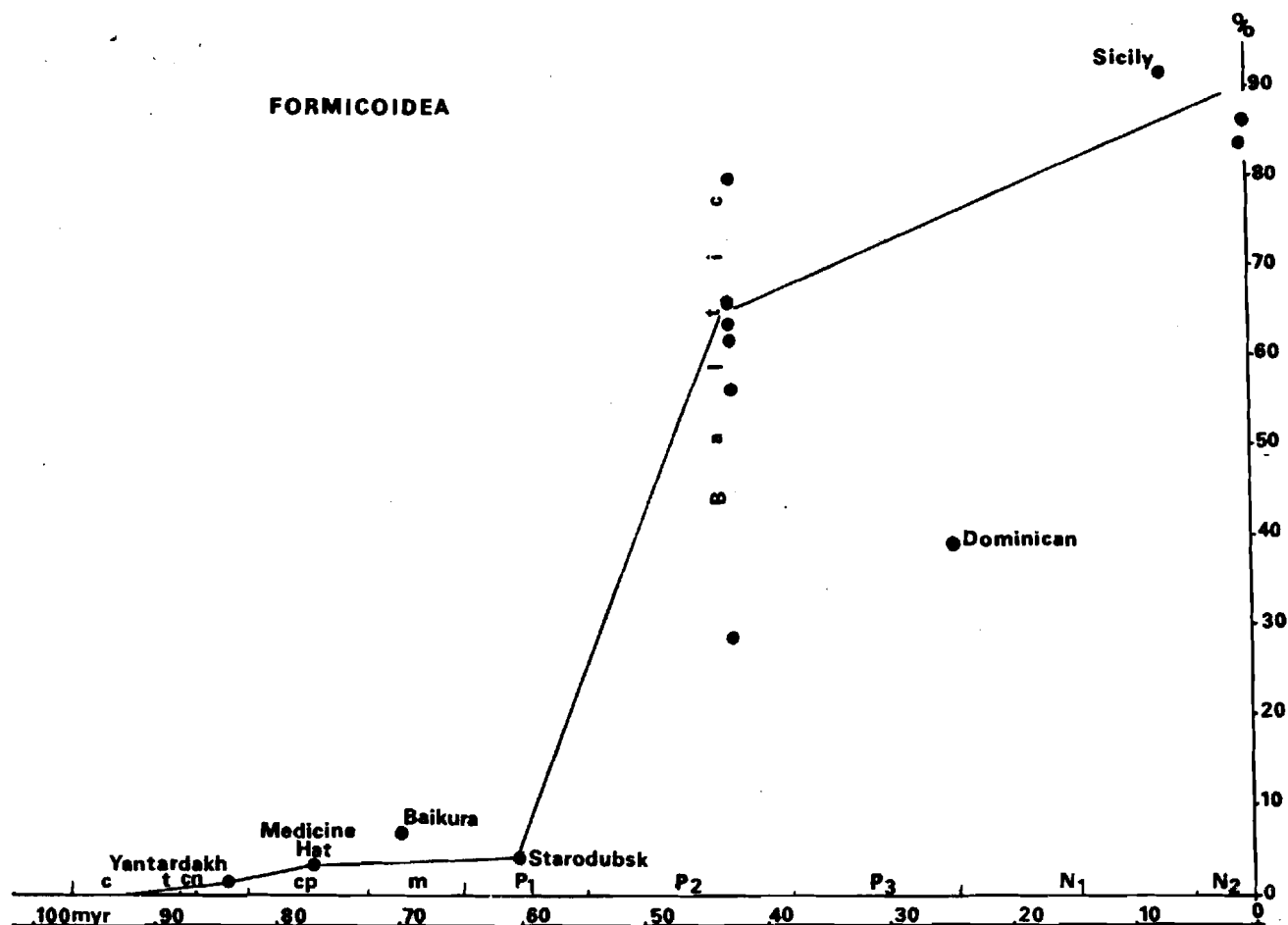


Fig. 2

Representation of ants in the hymenopteran assemblages. Lettering as in Figure 1
 Udział mrówek w zespołach błonkówek. Oznaczenia jak na fig. 1

present-day samples are collected in temperate climates. Similarly, the bees from the Dominican and Sicilian Miocene resin belonged to the tropical subfamily *Meliponinae*, and the sawflies found in the resin of extant trees belong to the predominantly temperate families *Xyelidae*, *Tenthredinidae*, *Pamphiliidae* and *Siricidae*. Again, all these groups originated long before the mentioned time intervals. In particular, meliponine bees are known since the Late Cretaceous period (Michener and Grimaldi 1988).

Further, Table 1 shows the wasps as a stable minor component of the studied assemblages, except for their moderately high abundance early in the Late Cretaceous period. The parasitic wasp component is seen to regress strongly during the time interval concerned, though this decrease is mostly apparent, because of the ant explosion. Some real reduction in their abundance was probably involved, however, because representation of the Parasitica in the assemblages of all insects was also decreasing to some extent.

The family-level turnover in composition of the assemblages of Hymenoptera (except sawflies and ants) is shown in Table 2. The Late Cretaceous assemblages

were invariably dominated by the *Scelionidae*, though their leading position became less expressed during the era (Fig. 3). The second-ranked groups were in turn the *Stigmaphronidae* (Fig. 4), *Serphitidae* (Fig. 4) and *Chalcidoidea* (Fig. 5). The third-ranked family was always the *Mymaromatidae* (Fig. 5). Representation of the *Mymaromatidae* and *Chalcidoidea* was increasing, of *Stigmaphronidae* — decreasing during the Late Cretaceous period, of *Serphitidae* — increasing from the Cenomanian to Santonian stages and decreasing after that.

Among the minor groups noteworthy for the Late Cretaceous period were decreasing representation (sometimes even extinction) of the *Cretevaniidae*, *Austroiniidae*, *Chrysididae*, *Falsiformicidae* and possibly even *Sphecidae*, and the reverse processes for the *Megaspilidae*, *Cynipidae* and *Diapriidae* (Fig. 6). Decreasing representation of the *Austroiniidae*, *Chrysididae* and *Sphecidae* is confirmed by observations that the impression fossils of these groups are much more common in Early Cretaceous deposits than in Tertiary ones (Late Cretaceous impression fossils are not numerous enough to be used in the present analysis).

The Paleocene stage is not the best one to be il-

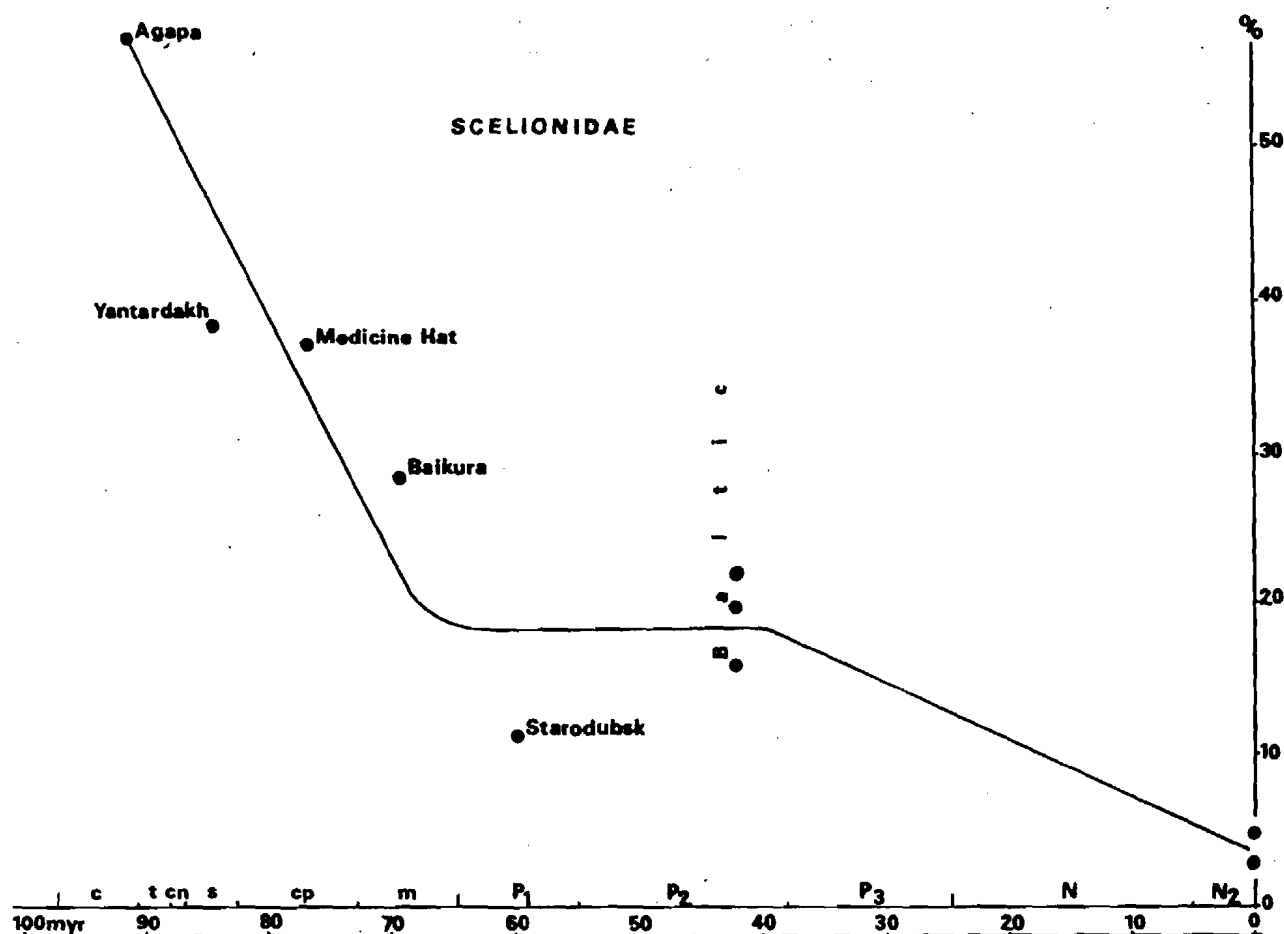


Fig. 3

Representation of *Scelionidae* in assemblages of Apocrita other than ants (after Table 2)Udział *Scelionidae* w zespołach Apocrita poza mrówkami (jak w tabeli 2)

luminated with our favourite method. The only assemblage of that age that originated from fossil resin (Sakhalin amber) was paradoxical in its composition due to the extreme abundance of aphidiine *Braconidae* (and their aphid hosts). This deviation (Fig. 7) most probably reflects a peculiarity of the local environments. The next most abundant group was the *Chalcidoidea* (Fig. 5), while *Scelionidae* were rare (Fig. 3). Rarity of *Scelionidae* was probably also environmentally induced, because the proportion of *Scelionidae* was much higher in both Cretaceous and Eocene assemblages.

The next epoch in our succession is the Late Eocene one, and is exemplified by the Baltic amber assemblage. Unfortunately various Baltic amber collections are not completely mutually consistent with respect to their composition. The most abundant groups are invariably *Braconidae*, *Scelionidae* and *Chalcidoidea*, though their dominance order varies from one collection another. These families are followed in order of abundance by *Ichneumonidae*, *Diapriidae* and *Bethylidae* (Figs. 3, 5–7).

Comparing these data with those for the Late Cretaceous period, it can be seen that several leading groups

were reduced in their representation (*Scelionidae*, *Myrmecommataidae*) or even died out (*Serphitidae*), while some minor groups were increased in their representation and became dominant (*Ichneumonidae*, *Braconidae*, *Diapriidae*, *Bethylidae*). Other subordinate families also became more common in Baltic amber assemblages though to a lesser extent (*Megalyridae*, *Ceraphronidae*, *Evaniidae*, *Proctotrupidae*, *Platygastridae*). Not all of these processes necessarily reflect evolutionary tendencies. Some of them could be induced environmentally or might even have no real counterpart in the parental fauna, being determined taphonomically, i. e. by some special features of the mode of burial. Indeed, pieces of Cretaceous fossil resins are on average of small size compared to pieces of Baltic amber. The same is typical for the insect inclusions, and this may be the reason why *Ichneumonidae*, *Braconidae*, *Bethylidae*, *Evaniidae* and *Proctotrupidae*, insects of comparatively large size, are more common in Baltic amber. This does not exclude, however, that the respective processes actually took place and that the taphonomic factors only exaggerated them. The latter possibility can be testified using independent evidences, particularly tho-

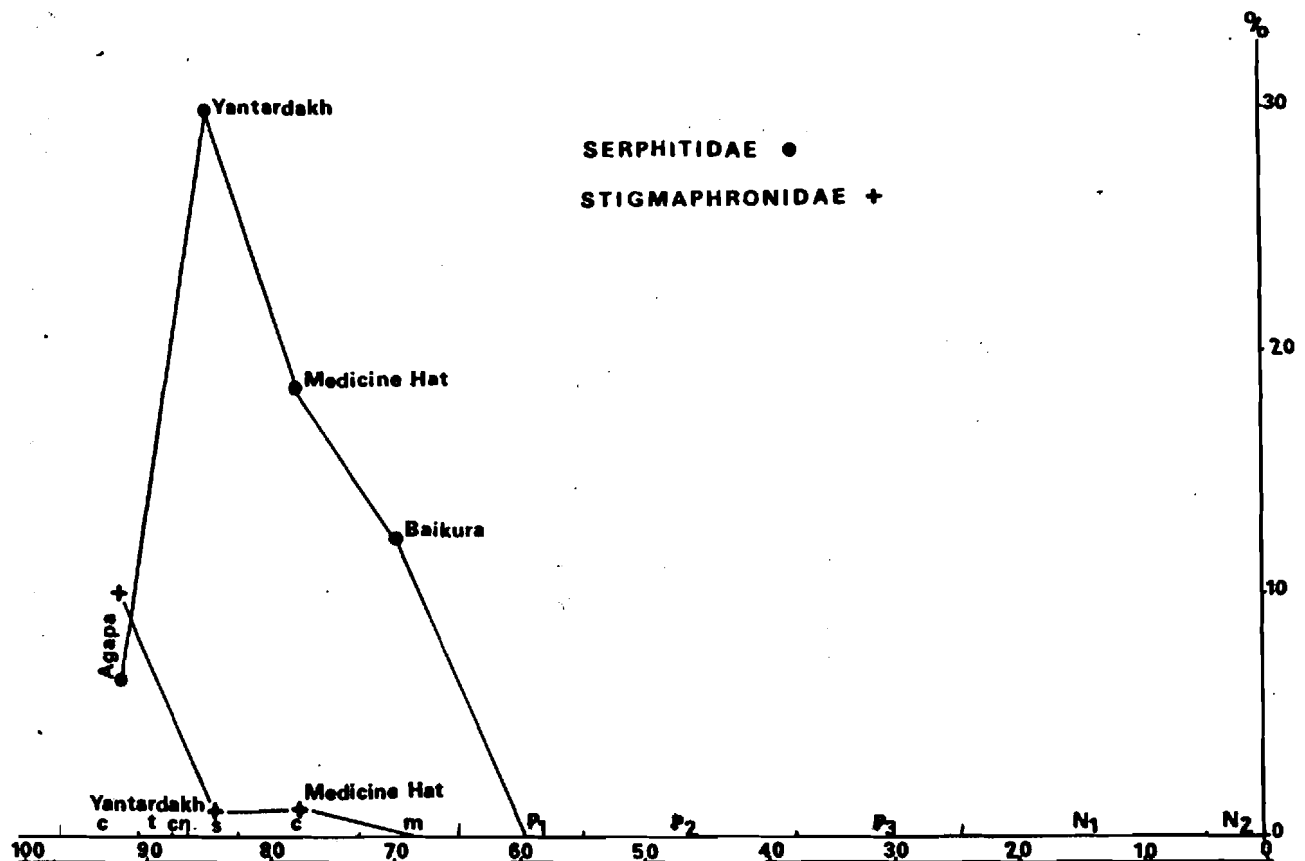


Fig. 4

Representation of *Serphitidae* and *Stigmaphronidae* in assemblages of Apocrita other than ants (after Table 2)
 Udział *Serphitidae* i *Stigmaphronidae* w zespołach Apocrita poza mrówkami (według tabeli 2)

se concerning either other parts of the time succession or other types of fossils. For example, further increase of the ichneumonid representation in the samples from present-day resin points in favour of the evolutionary nature of changes in their abundance in the Eocene period, whereas the observation that the Early Cretaceous assemblages of the impression fossils were richer in *Proctotrupidae* than the Tertiary ones makes a similar hypothesis concerning that group less probable. Abundance of the megalyrids among the Jurassic, and to a lesser extent, among the Cretaceous impression fossils, as well as presence of megalyrid inclusions in the Late Cretaceous fossil resin from the Caucasus (Rasnitsyn 1977a) and Taimyr (new date) equally indicates that the *Megalyridae* were rather common in Baltic amber due to their thermophily and the warm climate of the amber forest, and not because of the general increase of their role during the Eocene.

The following step in our succession is the present-day time level. Unfortunately, we have to miss assemblages of intermediate age (from the Mexican, Dominican, Sicilian and Saxonian amber), because their composition is not known in sufficient detail. Even for the present-day assemblages the available figures are not fully reliable, because the samples are either small

(those from resin) or deviant taphonomically and thus difficult to compare with other samples (the tanglefoot sample). This permits us to rely only on the best expressed trends.

Interpretation of the results by comparison is additionally hindered by the environmental discrepancy between the assemblages, the extinct ones coming from subtropical or even tropical climates and the extant ones from temperate climates. Here we again strongly depend on the independent information in evaluating the meaning of the trends derivable from Table 2. These trends are the decreasing role of the *Megalyridae*, *Scelionidae* and *Bethylidae* and increasing role of *Ichneumonidae* and *Cynipidae*. The case of the *Megalyridae* was already discussed. The *Bethylidae* seem to be thermophilic enough to explain climatically their absence from present-day samples. For the other groups listed it is less evident that the suggested trends are fully explainable environmentally. Their evolutionary nature seems possible though much more investigation is needed.

The above observations can be summarized as follows. The assemblages of the Hymenoptera preserved in resin differ strongly from ordinary assemblages of impression fossils due to the deviant mode of burial

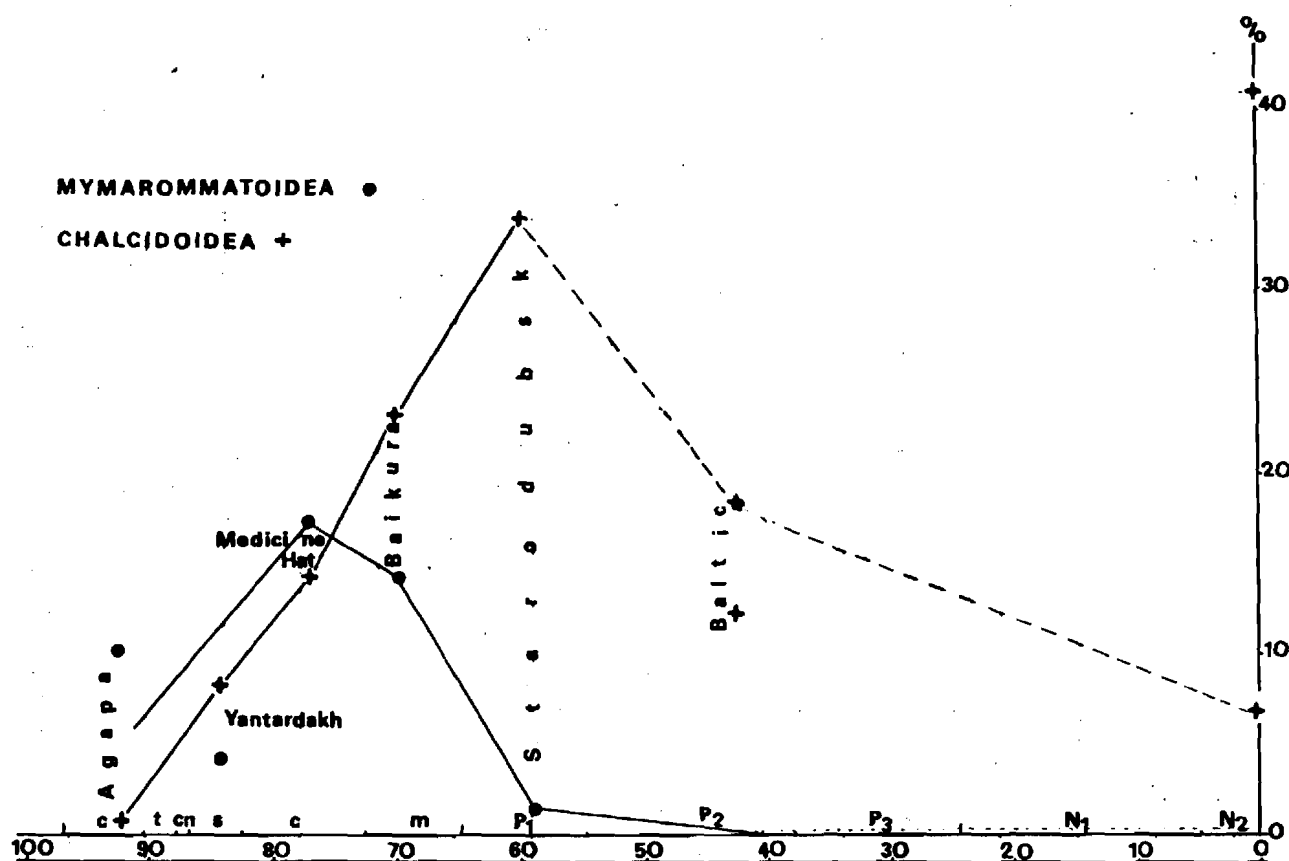


Fig. 5

Representation of *Mymaromatidae* and *Chalcidoidea* in assemblages of Apocrita other than ants (after Table 2)
 Udział *Mymaromatidae* i *Chalcidoidea* w zespołach Apocrita poza mrówkami (według tabeli 2)

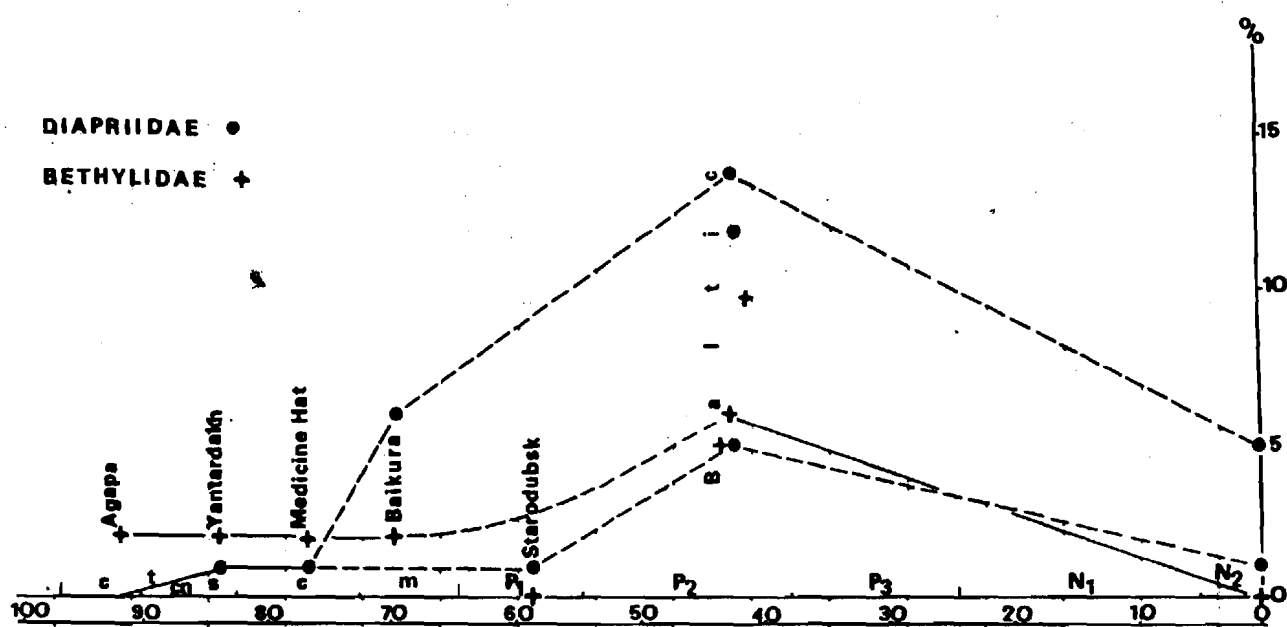


Fig. 6

Representation of *Diapriidae* and *Bethylidae* in assemblages of Apocrita other than ants (after Table 2)
 Udział *Diapriidae* i *Bethylidae* w zespołach Apocrita poza mrówkami (według tabeli 2)

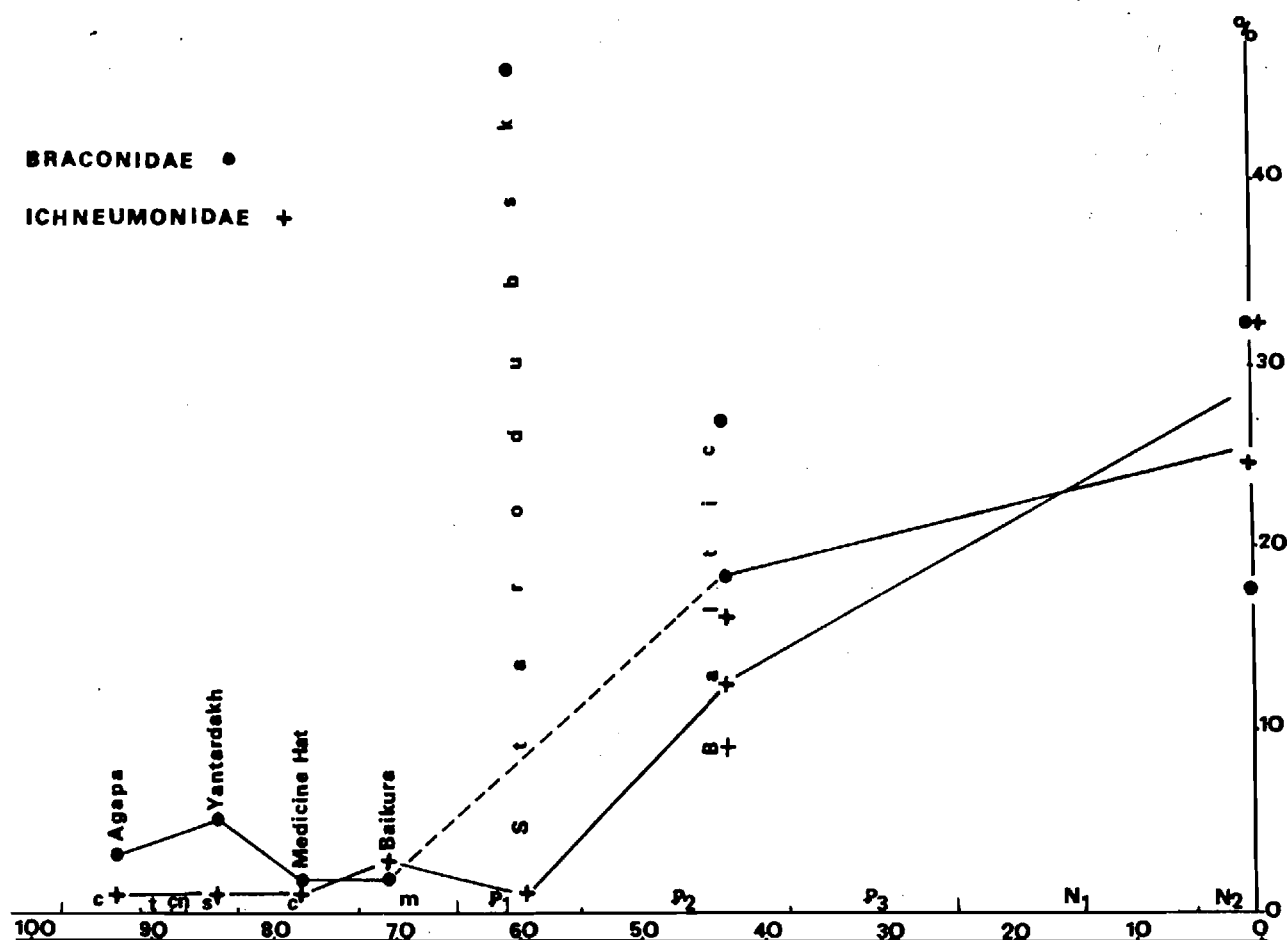


Fig. 7

Representation of Braconids and Ichneumonids in assemblages of Apocrita other than ants (after Table 2)
 Udział *Braconidae* i *Ichneumonidae* w zespołach Apocrita poza mrówkami (według tabeli 2)

and thus they need to be considered separately. The oldest studied inclusion assemblages of the Late Cretaceous period consisted mostly of parasitic forms, with the aculeates being a minor component, and sawflies and horntails being absent. The leading family was invariably *Scelionidae*, followed by the *Serphitidae*, *Chalcidoidea*, *Mymaromatidae*, and *Stigmaphronidae*, listed in order of maximal representation in the Late Cretaceous assemblages.

The main evolutionary trends during the Late Cretaceous period and the following time were mostly simply increase and decrease in representation of particular groups in the succeeding assemblages. More complex processes were less common. *Stigmaphronidae*, *Cretevaniidae*, *Austroniidae*, *Chrysidae* and *Falsiformicidae* underwent reduction in their representation, often to the point of extinction, during the first half of the Late Cretaceous period. *Serphitidae* and *Mymaromatidae* disappeared from the assemblages or became very rare toward the end of the Cretaceous period, and this event in each case was preceded by the increasing representation earlier in the Late Cretaceous period. *Scelionidae* were decreasing in abundance the

whole time from the Cenomanian stage until now. Some other groups underwent an increase in representation in the assemblages and presumably in the parental faunas — *Diapriidae* and *Chalcidoidea* during the Late Cretaceous period and possibly later in the Paleocene and Eocene, ants the entire period from the Santonian until now (more strongly so in the Eocene and Miocene), *Platygastridae* in the Paleocene, *Evaniidae* in the Eocene, *Ichneumonidae* possibly during or after the Miocene. Hymenoptera as a whole began to play a more important role in the insect assemblages during the Miocene.

The above evidences and considerations permit us to draw the following conclusion concerning Baltic amber. This assemblage is essentially intermediate in composition between the Late Cretaceous and present-day ones, as it can be seen on examination of virtually every hymenopteran group. The exceptional groups which were more common in Baltic amber than in both older and younger assemblages (*Megalyridae*, *Evaniidae*, *Diapriidae*, *Bethylidae* and dolichoderine ants) are thermophilic and their relative abundance in Baltic amber is generally explainable by the warm climate of the

amber forest. The contrary explanation seems acceptable only in the case of *Dolichoderinae* where exists independent evidence in favour of evolutionary rather than environmentally governed dynamics of their participation in the ant assemblages (Dlussky, Fedoseeva 1988).

At the same time, the Baltic amber assemblage seems more similar to the present-day fauna than to the Late Cretaceous one. Indeed, it includes only one extinct family, the extremely rare *Electrotomidae*, known from a single specimen found in an assemblage not used in this study (Rasnitsyn 1977b). In contrast, the Late Cretaceous assemblages are rather rich in extinct families (*Maimetshidae*, *Stigmaphronidae*, *Cretevanidae*, *Serphitidae*, *Falsiformicidae*, *Sphecomyrmae*) in spite of being much more weakly explored. The dominant

Late Cretaceous families are either absent or weakly represented in Baltic amber, except for the *Scelionidae*. Abundance of the ants and the list of their subfamilies are similar to present-day ones, though the role of each subfamily differs considerably.

We realize that this conclusion is based on data which are rather small quantitatively and less sound and comparable than we would like. Future studies will surely correct or may even alter our suggestions profoundly. However, it is our major objective to stimulate further investigations in the fossil history of our beloved group using the qualitative data on the composition of fossil and living assemblages. We hope to achieve this.

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Hymenoptera z bursztynu bałtyckiego na tle ogólnej historii rzędu

Streszczenie

Hymenoptera to jeden z najliczniejszych rzędów owadów obejmujących ponad 108 000 opisanych współczesnych gatunków (Borner *et al.* 1976). Również w bursztynie bałtyckim owady te są bardzo licznie reprezentowane. Żerichin (1978) doliczył się 3000 opisanych lub wzmiankowanych gatunków owadów w bursztynie, wśród których aż 370 gatunków należy do Hymenoptera.

Historia mezozoicznych Hymenoptera jest obecnie lepiej poznana niż kenozoicznych. Jest to związane głównie z tym, że większość dawnych spisów i opisów kenozoicznych owadów należących do tego rzędu jest już obecnie nieaktualna. Ponadto, zmiany ewolucyjne zachodzące w obrębie tego rzędu w kenozoiku były tak powolne, że trudne do zauważenia i interpretacji.

W powyższej pracy mezozoiczna historia Hymenoptera przedstawiona została za Rasnitsynem (1980, 1988a). Dane o wczesnokredowych Hymenoptera występujących w bursztynie libańskim nie były dostępne autorom.

Dotychczas nie ma porównań kenozoicznych Hymenoptera ze starszymi ani młodszymi, toteż jest to celem niniejszej publikacji. W pracy zostały zebrane i przedstawione wyniki badań rodzin Hymenoptera występujących w bursztynie bałtyckim ze zbiorów Muzeum Ziemi PAN oraz analogiczne dane z literatury. W tabeli 1 i na

figurze 2 zamieszczono dane o procentowym udziale grup Hymenoptera w zespołach owadów kopalnych i współczesnych. W tabeli 2 i na figurze 1, 3–7 podano procentowe dane o udziale poszczególnych rodzin Hymenoptera w zespołach kopalnych i współczesnych.

Na podstawie przedstawionego materiału wyciągnięto następujące wnioski:

— zespół Hymenoptera z bursztynu bałtyckiego jest ogniwem pośrednim pomiędzy owadami późnokredowymi i współczesnymi. Wyjątkiem są rodziny powszechniej reprezentowane w bursztynie bałtyckim niż w osadach wcześniejszych okresów (*Megalyridae*, *Scolionidae*, *Bethylidae*, *Ichneumonidae*, *Cynipidae*). Te ostatnie są owadami termofilnymi, a ich względna obfitość w bursztynie może być wyjaśniona ciepłym klimatem lasu bursztynowego;

— zespoły Hymenoptera z bursztynu bałtyckiego wydają się bardziej podobne do współczesnych zespołów tych owadów niż do tych samych z okresu późnej kredy. Dominujące późnokredowe rodziny są nieobecne lub nielicznie reprezentowane w bursztynie bałtyckim (z wyjątkiem *Scolionidae*).

Zdajemy sobie sprawę, że wnioski powyższe mogą być uściślane w miarę gromadzenia nowych materiałów badawczych.