Title: Invertebrates in contemporary coniferous resins – an insight into the ecosystem?

Author: Natalia Kaszyca, Angelina Kubusiak, Bartosz Baran, Arkadiusz Imiela, Artur Taszakowski, Piotr Węgierek, Łukasz Depa

Citation style: Kaszyca Natalia, Kubusiak Angelina, Baran Bartosz, Imiela Arkadiusz, Taszakowski Artur, Węgierek Piotr, Depa Łukasz. (2019). Invertebrates in contemporary coniferous resins – an insight into the ecosystem? "Fragmenta Faunistica" T. 62, z. 2 (2019), s. 117-134, DOI 10.3161/00159301FF2019.62.2.117

FRAGMENTA FAUNISTICA 62 (2): 117–134, 2019
PL ISSN 0015-9301 © MUSEUM AND INSTITUTE OF ZOOLOGY PAS
DOI 10.3161/00159301FF2019.62.2.117

Invertebrates in contemporary coniferous resins – an insight into the ecosystem?

Natalia KASZYCA[1,2], Angelina KUBUSIAK[1,2], Bartosz BARAN[1,2], Arkadiusz IMIELA[1,2], Artur TASZAKOWSKI[1], Piotr WEGIEREK[1] and Łukasz DEPA[1]*

[1]*University of Silesia in Katowice, Faculty of Biology and Environmental Protection, Department of Zoology, Bankowa 9, 40-007 Katowice, Poland; *corresponding author: lukasz.depa@us.edu.pl*
[2]*Students' Scientific Association "Faunatycy", University of Silesia in Katowice, Faculty of Biology and Environmental Protection, Department of Zoology, Bankowa 9, 40-007 Katowice, Poland*

Abstract: A study aiming at the description of invertebrate fauna trapped in contemporary, coniferous resins was undertaken in a mixed forest of Central Europe (Southern Poland). Resins were collected predominately from spruce (*Picea abies*), but also from pine (*Pinus sylvestris*) and larch (*Larix decidua*), the cadavers were extracted from the ethanol solution of resin. As many as 394 specimens were extracted, consisting mainly of insects, but also arachnids, crustaceans and single mollusc were found. Among the collected specimens, some were identified to species, and a few mutual, ecological interrelationships could be traced. Although the amount of collected resins is far from being comparable with the amount of particular types of amber studied in the world so far, the Discussion focuses on similarities and differences in insect inclusions composition in resins and known amber collections.

Key words: resin, amber, paleoecology, fauna, insects, forests

INTRODUCTION

Amber is considered as one of the best media for the fossilization of organic soft tissues such as arthropods, plant remains, and microorganisms (Grimaldi & Agosti 2000, Wier et al. 2002, Schmidt et al. 2006, Poinar & Poinar 2008, Zherikhin et al. 2008, Penney 2010, Hart 2018, Szadziewski et al. 2018) and thus, it represents an original opportunity to document past ecosystems (Antoine et al. 2006, Schmidt et al. 2006; Girard et al. 2009) and palaeoenvironmental conditions (Azar et al. 2003, Aquilina et al. 2013). Inclusions in fossil resins may also serve studying the changes in plaeobiota over the evolutionary history of various taxonomic groups e.g. arthropods (Rasnitsyn et al. 2016). Such studies may reach as far back in the past as to the Triassic period (ca. 230 mya) (Schmidt et al. 2012) and have served such purpose for many distinct geological periods in various geographical areas.

However, such inclusions cannot be considered a representative sampling of the environment in which they originated (Poinar & Poinar 2008, Solórzano Kraemer et al. 2018). First losses of information occur during the process of fossilization, when specimens trapped in the resin may be removed from it by other animals or by atmospheric phenomena (Zherikhin 2002, Martinez-Delclós et al. 2004). What is preserved, not always is an outright representation of the ecosystem and interpretation of the findings may pose some difficulties (Szwedo & Sontag 2009). Among the taxa entrapped in resins, and later in amber, arthropods prevail, with an only minority of vertebrates or vertebrates remains. Furthermore, tree-surface foragers are more common than species having other movement patterns e.g. winged ones, which nonetheless, are quite common. Winged species may be blown with wind even from distant habitats and thus, may give insight into the ecosystems of areas surrounding the amber forest, but their presence may also disrupt proper recognition of the amber fauna and their ecosystem.

It is thus crucial to know, to what extent the taphofauna of amber/resin represents the zooceonosis of the forest ecosystem in which it originated (Zherikhin & Sukatsheva 1989, Schmidt & Dilcher 2007). Such studies were previously conducted by Zherikhin & Sukatsheva (1989) in various areas of Eastern Europe and Far Eastern Asia. The aim of the presented study was to examine the composition of the taphofauna taphocoenosis of inclusions in recent coniferous resins, collected in forests of Central Europe. We further wanted to describe the ecological components trapped in resins, and search for ecological relationships between particular taxa. Such data could further help to predict, how accurate the reconstructions of ecosystems based on amber inclusions may be.

MATERIAL AND METHODS

Study area

The research was carried out in south-eastern Poland, in the Low Beskidy Mts. This geographic region (Fig. 1A) consists of drainage dividing montane range arranged from east to west and it is divided by a few low mountain passes. The total length of the Low Beskidy Mts. from east to west is ca. 100 km and width reaches 40 km. The highest peak on the Polish territory (Mount Lackowa) is elevated 997 m a. s. l. (Kondracki 2013).

In respect of the vegetation type, it is intermediate between the Western and Eastern Beskidy Mountains. The montane flora is poorly represented, but a few thermophilous plant species from the Pannonian Basin occur. The forests are of foothill and montane altitudinal zone, but there occur spots with relic forests from earlier periods of other climatic conditions (Kondracki 2013). Among the deciduous trees, the most abundant is beech (*Fagus sylvatica*). Among the conifers, the dominant tree species is fir (*Abies alba*), but also spruce (*Picea abies*), pine (*Pinus sylvestris*) and larch (*Larix decidua*) are very often. Apart from the forests, there are also pastures, barren fields and shrublands.

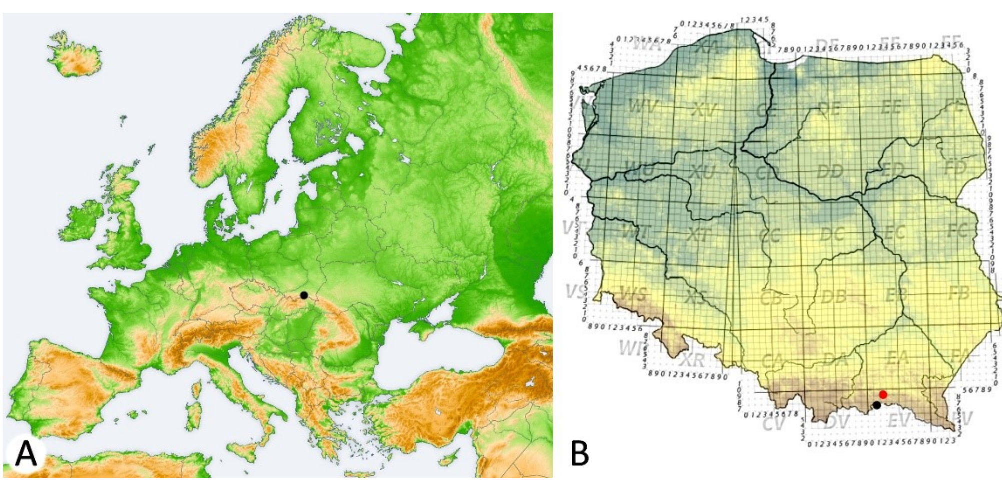

Fig. 1. Locations of both study sites: A – in Europe, B – in Poland: ● – Bartne,● – Wysowa-Zdrój.

Sites and methods of collection

Bartne (municipality of Sękowa), UTM (Universal Transverse Mercator): EV28, EV29, 49°34′06″N 21°19′32″E, ca. 600 m a. s. l., collection date: 09 – 12 VII 2013 (Fig. 1B).

The resin was collected in a single vegetation type – the Carpathian beech forest (*Dentario glandulosae–Fagetum* Klika 1927 em. Mat. 1964). This is a fertile type of forest, with dominant beech and fir, typical for the Carpathian Mountains, with other typical species being: *Dentaria glandulosa*, *Symphytum cordatum* and *Polystichum braunii* (Matuszkiewicz 2007). Among tree species, there were also *Betula pendula*, *Acer pseudoplatanus*, *Populus tremula*, *Picea abies*, *Larix decidua* and *Pinus sylvestris* and in the lower forests layers *Salix caprea*, *Corylus avellana*, *Sambucus nigra*, *Rubus* sp. *Pteridium aquilinum*, *Salvia glutinosa* and *Tussilago farfara*.

The resin was collected from living, standing trees (larch, pine and spruce), of an approximate trunk diameter of 0.25 – 0.4 m . The resin was solid, extruded naturally from the trunk and in case of spruce, its extrusion was connected with the feeding behaviour of the European spruce bark beetle *Ips typographus* (Linnaeus, 1758).

Wysowa-Zdrój (municipality of Uście Gorlickie) UTM: EV17, 49°26′30″N 21°10′26″E, ca. 600 m a. s. l., collection date: 01 – 03 V 2014 (Fig. 1B).

The resin was collected in the Carpathian beech forest (*Dentario glandulosae–Fagetum*) – from spruce (Fig. 2A) and pine (in a clearing) and also in a young spruce monoculture (ca. 20 years old) in the direct neighbourhood of a beech forest. The resin was collected from living, standing trees (pine and spruce), from 0.3 m above soil level up to the height of 1.8 m. The resin was solid, extruded either naturally from the trunk or from mechanical damage resulting from forest management.

In all cases the resin was carefully collected from the surface of the trunk with a knife, often with small pieces of bark, to the plastic containers (Fig. 2B). The pieces of bark were not removed from the resin not to damage the insects trapped in the resin inclusions.

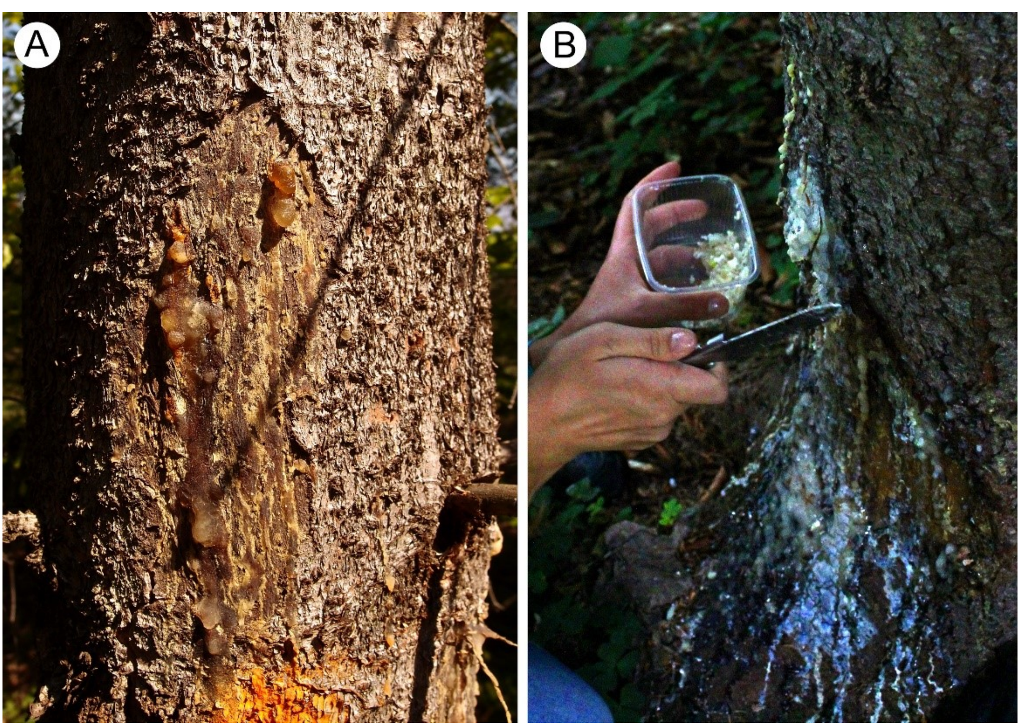

Fig. 2. Resin extruding from wounded trunk (A) and the collection of resin from the tree trunk of spruce (B).

Extraction and identification of extracted invertebrates

The collected resin (Fig. 3) was dissolved in ethanol in the laboratory. The small portions of resin (ca. 40 g) were put in round, polypropylene containers (Ø 90 mm, 250 ml) and poured with 200 ml of 92% ethanol per 1 portion. To dissolve 100 g of resin ca. 500 ml of ethanol was required. The shaking incubator IKA KS 4000 ic control (45°C, 80 r/min) was applied to completely dissolve the resin in ethanol and extract the remains of invertebrates (Fig. 4).

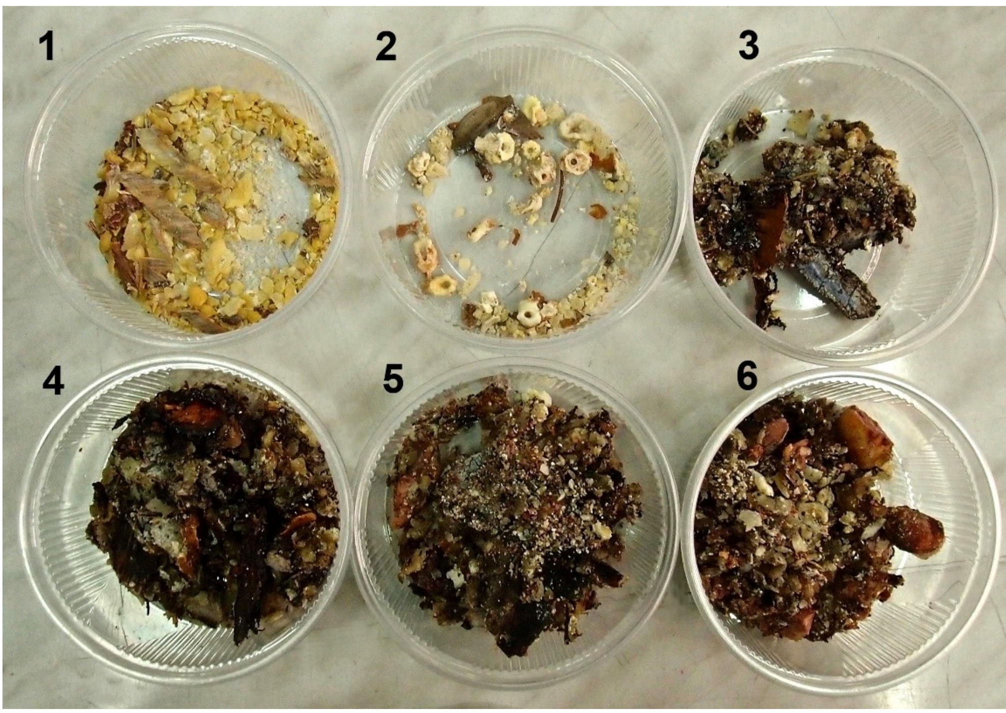

Fig. 3. The whole collected resin samples directly before dissolving in denaturated ethanol (1, 2 – pine, 3–6 – spruce).

After dissolving, the remains of insects were carefully extracted from the solution, under stereoscopic microscope Optek SZM, at magnification 7x–90x. Either whole insect bodies were extracted or odd body parts, so it was possible to count the number of individuals of particular taxa trapped in the resin (e.g. head capsule, thorax, whole abdomen, shell). Single legs or antennae were not extracted. The remains were preserved in 70% ethanol and consecutively identified to the taxon of the lowest possible rank, depending on the condition of the extracted remains. We did not present the degree of disarticulation of entrapped specimens as we could not differentiate if it was caused by extraction or entrapment in resins with methodology applied . The material was deposited in the collection of the Department of Zoology of the University of Silesia in Katowice. The following keys were applied for identification: Pławilszczikow 1972, Cmoluchowa 1978, Blackman & Eastop 2018, Mertlik & Leseigneur 2007, Löbl 1970, Szujecki 1965, Burakowski 2003, Nunberg 1976, 1981, Mroczkowski 1954, Freude et al. 1965, 1979, Czechowski et al. 2012, Heie 1980, 1992 and also the online catalogue of beetles by Borowiec (2018).

Fig. 4. Dissolved resin directly before extracting the invertebrates from the sedimentresidue. The surplus ethanol was removed before taking the photo.

Terminology

In this study, we have applied the two terms: retinotaphofauna and retinotaphocoenosis. Both are new, however, we feel there is a strong need for diversification the two points of view on our results. Firstly, the term taphocoenosis was already applied by Lutz (1997) and the term taphofauna by Lawfield & Pickerill (2006) to name the set of animal cadavers buried in the sand by flood waters. We have partly changed the term and modified its meaning for purpose of this work. The prefix retino-, used in both terms, originates from Greek "ρητίνη" which means resin, while infix tapho- is widely applied for designating preserved remnants of living organisms, as e. g. in word taphonomy – a general discipline studying the process of fossilisationall aspects of fossilization process (Efremov 1940) and whole extinct biota (Fraser & Sues 2017). Thus, both, the first and second part of both terms indicate remnants of organisms preserved in resins.

The last parts of the names require further explanation:

- retinotaphofauna – under this term we understand all animals trapped in resins. In other words, it is a set of all species (or other determinable taxa) extracted from the sample of resin representative for particular type of resin in particular type of ecosystem;
- retinotaphocoenosis – by applying the ending -coenosis, we indicate some ecological aspects (Weiher et al. 2011) revealed by the extracted invertebrate specimens, especially their mutual ecological relationships. The term describes only a set of species which in life remained in a defined and recognized mutual relationship, such as: symbiosis, host-parasite relationship, prey-predator relationship etc.

Both terms are of course tentative and their further implementation, as well as the definitions themselves, may undergo some modifications.

RESULTS

In Bartne, the total number of 199 specimens were extracted from 591 g of resin: spruce (*Picea abies*) resin [S] – 486 g, pine (*Pinus sylvestris*) resin [P] – 48 g, larch (*Larix decidua*) resin [L] – 57 g. Among the remains, a cadaver of single crustacean was identified, 40 cadavers of chelicerates and a predominant number of 158 specimens of various groups of insects (mainly hymenopterans and dipterans) (Table 1, Fig. 5).

Fig. 5. Cadavers extracted from the resin: A – C – various Acari (A – tick; B, C – various Oribatida); D, E – spiders, F – representative of Oniscidea.

At Wysowa-Zdrój, the total number of 195 specimens were extracted from 675 g of resin: spruce (*Picea abies*) resin [S] – 610 g, pine (*Pinus sylvestris*) resin [P] – 40 g, larch (*Larix decidua*) resin [L] – 25 g. Among the remains, cadavers of 6 crustaceans were identified, 32 cadavers of chelicerates and a predominant number of 156 specimens of various groups of insects. Also, single remain of a mollusc (gastropod) was detected (Table 1).

Table 1. List of specimens extracted in the present study.

Taxon	Bartne	Wysowa Zdrój
Crustacea:		
Malacostraca:		
Isopoda: Oniscidea	[S] 1	[S] 6
Cheliceromorpha:		
Arachnida:		
Pseudoscorpionida	[S] 1	
Acari	[S] 15	[S] 13, [P] 12
Aranae	[S] 21	[S] 3, [P]] 3, [L} 1
Entognatha	[S] 8	
Ectognatha:		
Thysanoptera:	[S] 1	
Hemiptera: Aphididae: *Phyllaphis fagi* (Linnaeus , 1767)	[L] 3	
Anoecia corni (Fabricius, 1775)	[S] 1	[S] 1
Elatobium abietinum (Walker, 1849)	[S] 2	
Euceraphis sp.	[S] 1	
Cinara sp.	[S] 8, [P] 3, [L] 2	[S] 13, [L] 2
Reduviidae: *Empicoris vagabundus* (Linnaeus, 1758)	[S] 1	
Cicadellidae: *Populicerus populi* (Linnaeus, 1761)	[S] 1	
Eupelix cuspidata (Fabricius, 1775)	[S] 1	
Aphrophoridae: *Aphrophora alni* (Fallén, 1805)		[S] 3
Dermaptera:	[S] 3, [P] 1	
Neuroptera:	[S] 1	
Coleoptera:	[P] 1	[P] 1
Derodontidae: *Laricobius erichsoni* Rosenhauer, 1846	[S] 1	
Omalisidae: *Omalisus fontisbellaquaei* Geoffroy, 1785	[S] 1	
Latridiidae:		[S] 5
Leiodidae: Leiodinae	[S] 2	
Staphylinidae:		[P] 4
Tachyporinae	[S] 1e	
Aleocharinae	[S] 1	
Staphylininae	[S] 1	
Poederinae: *Paederus brevipennis* Lacordaire, 1835		[S] 1
Scaphidiinae: *Scaphisona* sp.		[P] 1
Throscidae: *Trixagus carinifrons* (Bonvouloir, 1859)		[S] 6
Hydrophilidae: *Cercyon* sp.	[S] 3	
Nitidulidae: *Epuraea* sp.	[S] 2	
Curculionidae:	[S] 1	
Scolytinae: *Phloeosinus thujae* (Perris, 1855)	[S] 1	
Pityogenes chalcographus (Linnaeus, 1761)		[S] 1, [P] 1
Xyleborinus saxesenii (Ratzeburg, 1837)		[P] 1
Ips typographus (Linnaeus, 1758)		[S] 1
Chrysomelidae: Alticinae: *Plyllotreta* sp.		[S] 1
Chrysomelinae		[S] 1
Elateridae:	[S] 1	
Dermestidae: *Attagenus smirnovi* Zhantiev, 1973		[S] 1
Cantharidae		[S] 1
Cryptophagidae		[S] 1
Apionidae		[L] 1

Table 1 continued on the next page

Continuation of the Table 1.

Hymenoptera:	[S] 6, [P] 3, [L] 3	[S] 6, [P] 3
Formicidae: *Formica* sp.	[S] 1	
Myrmica sp.	[S] 1	[S] 2
Myrmica rubra (Linnaeus, 1758)	[S] 1	[S] 50, [P] 1, [L] 9
Myrmica ruginodis Nylander, 1846		[S] 1
Lasius sp.		[S] 5
Lasius brunneus (Latreille, 1798)	[S] 36	
Lasius flavus (Fabricius, 1782)	[S] 2	
L. platythorax Seifert, 1991 / *L. niger* (Linnaeus, 1758)	[S] 8, [P] 4	
Lasius platythorax Seifert, 1991		[S] 1
Diptera:	[S] 33, [L] 3	[S] 16, [P] 9, [L] 3
Psocoptera:	[L] 4	
Lepidoptera:		[P] 1
Blattodea:		[L] 1
Mollusca:		
Gastropoda:		[S] 1

Some of the collected taxa, despite small quantity of the collected resins, comprised a quite significant number of species. Many of the extracted cadavers were preserved in good condition, allowing their credible identification. This allowed us to analyze some of groups with respect to their ecological/behavioral requirements or their characteristics.

Aphidotaphofauna

The most abundant were aphids belonging to the genus *Cinara* (Lachninae) Curtis, 1835 (Fig. 6E), feeding exclusively on coniferous trees (Szelegiewicz 1978) – on needles, twigs and branches of all three species from which the resin was collected (Table 2). Also, the presence of *Elatobium abietinum* (Aphidinae) and *Phyllaphis fagi* (Phyllaphidinae) cannot be surprising, as the first feeds on fir (*Abies alba*) and the second on beech (*Fagus sylvatica*) (Heie 1982, 1992), which were dominant tree species in the area of collection. Next two species are also very common in adjacent areas and habitats, as *Euceraphis* sp. is connected with birches (*Betula* spp.) and *Anoecia corni* (Fig. 6F) with dogwoods (*Cornus sanguinea*) and various grasses (*Poaceae*) (Heie 1980, 1982). It is also very characteristic that apterous individuals trapped in resins belonged exclusively to genera trophically associated with conifers, while winged individuals to genera feeding on deciduous trees (Table 3). Although dogwoods do not contribute to the tree composition of the montane beech forests, the alate individuals of *A. corni* in huge numbers fly in late summer from grasses to dogwoods, hence the presence of alate *A. corni* in resins.

Table 2. Biocharacteristic of aphid fauna trapped in resins in two study sites (al. – alate female, apt. – apterous female, viv. – viviparous female, nym. – nymph, l – larva).

Bartne			**Wysowa-Zdrój**		
Resin	Species	Individuals	Resin	Species	Individuals
spruce	*Anoecia corni*	1 exx. al. viv.	spruce, young spruce forest	*Cinara* sp	13 exx. apt. viv
pine	*Cinara* sp.	3 exx. apt. viv.	spruce, beech forest	*Cinara* sp.	2 exx. apt. viv.
larch	*Cinara* sp.	2 exx. apt. viv.			

Table 3. Comparison of the number of alate and apterous specimens of aphids in respect of their trophic relations.

Aphids	Trophically connected with coniferous trees	Trophically connected with deciduous trees
Alate females	0	5
Apterous females	30	1

Myrmecotaphofauna

The most abundant ant species recovered from resins were representatives of the genus *Myrmica*, predominately *Myrmica rubra*, and also representatives of the genus *Lasius*, mainly *Lasius brunneus* (Fig. 6G-I).

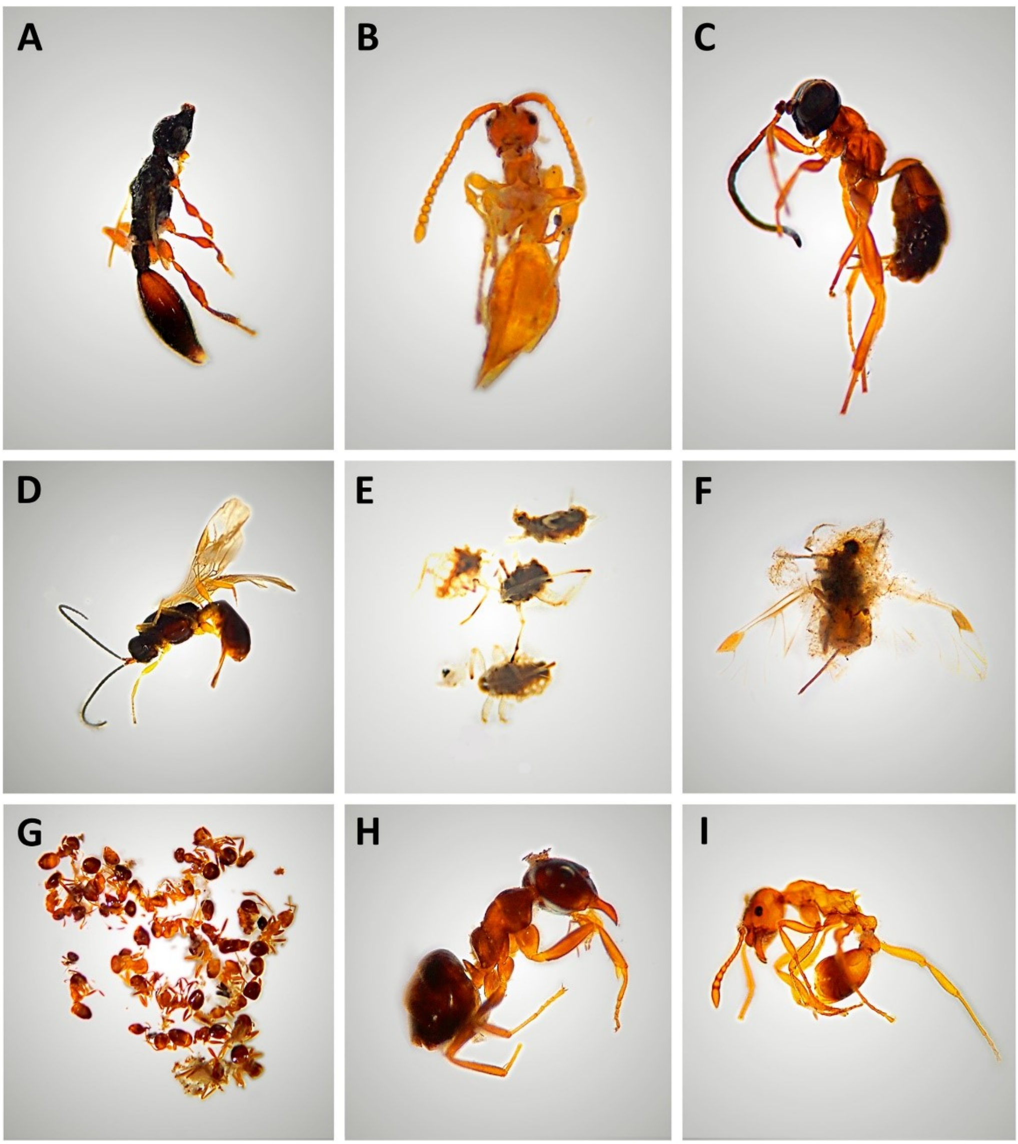

Fig. 6. Various insects extracted from resins: A–D – Hymenoptera, E – aphids of the genus *Cinara* (Lachninae), F – winged specimen of aphid *Anoecia corni* (Anoeciinae), G – ants of the genus *Lasius* (Formicinae) H – ant worker of *L. brunneus* (Formicinae), I – ant worker of *Myrmica rubra* (Myrmicinae).

M. rubra is one of the most common ant species, of a very wide range of habitat tolerance, eurytopic, ground nesting and constituting the core of the ant fauna of Poland. It is less frequent in the woods, where it is replaced by *M. ruginodis* (Czechowski et al. 2012), which was very rare in the collected resins. The presence of *M. rubra* was significant in spruce resins from Wysowa Zdrój, in both types of forest – young and beech forest, despite a very small amount of resin in the latter. Its presence in pine resin may also be explained by their food requirements – this species is known to utilize pine pollen as a source of food.

The second most common ant species was *Lasius brunneus*, a typical inhabitant of forests, with preference to deciduous and mixed forests. It is an arboreal species, nesting in trunks of deciduous trees, and foraging mainly on trees, hence its significant presence in the resins collected in well-developed Carpathian beech forest (Czechowski et al. 2012). In this habitat also other species of this genus were present in resins – either *L. platythorax* or *L. niger*. The two species differ only with minute morphological features, which did not preserve in resins, hence the difficulty of their credible determination. However, *L. platythorax* is a typical forest inhabitant, while *L. niger* prefers open habitats, so rather the presence of *L. platythorax* is expected.

Other ant species were either rare or their cadavers were in bad condition, disabling their credible determination.

Coleopterotaphofauna

Among the collected beetles, trapped in resins, a few specimens were in a condition enabling their determination (Fig. 7). Among them, there are species which are common in Central Europe and are trophically connected with coniferous trees, such as *Pityogenes chalcographus* or *Ips typographus* or common, but preferably feeding on deciduous trees as *Xyleborinus saxesenii* (Burakowski et al. 1992). There are also rare species, connected with forests, such as *Phloeosinus thujae* (Burakowski et al. 1992) or *Omalisus fontisbellaquaei* (Szczepański et al. 2013). Interesting is the presence of the rarely found beetle – *Laricobius erichsoni*, which is most often collected on coniferous trees, preferably firs, where it feeds on aphids such as e. g. *Cinara piceae* (Panzer, 1801) (Burakowski et al. 1986). Also, some species which are not connected with forests, but with open habitats, such as meadows, pastures or shrubs, were collected: *Paederus* (*Harpopaederus*) *brevipennis* and *Trixagus carinifrons* (Burakowski et al. 1979, 1985).

A special case concerns *Attagenus* (*Attagenus*) *smirnovi* which is suspected to originate from Africa, where it is very common in nests of birds and bats, probably feeding on their feathers or remnants of skin. Its presence was also confirmed in Europe in the second half of the XX century, mainly in strictly synanthropic habitats. In Poland, it was so far only recorded indoors, and reports begin since the year 2000. Hence, it is regarded as an alien invasive species, most probably introduced with zoological material brought to Europe with museum collections (Pawłowski 2014). Its specimen trapped in resin is, therefore, the first report of this species occurring outdoors in Poland.

Retinotaphocoenosis

Among the identified species of invertebrates, despite very scarce and fragmentary data, we may detect some mutual ecological relationships. We can distinguish three groups of insects, which are trophically connected with coniferous trees: aphids (especially *Cinara* spp.), various Scolytinae beetles and pollen-feeding ant *Myrmica rubra*. However, ants from both genera – *Myrmica* and *Lasius*, utilize aphids of the genus *Cinara* as a source of food, in their mutualistic relationship. Aphids of the genus *Cinara* also serve as a source of food for the predatory beetle *L. erichsoni*. Spiders extracted from the resin, although unidentified, were most probably feeding also on ants, beetles and other insects living on the surface of the trunk.

Another case is the true bug – *Empicoris vagabundus* (Fig. 8D), which inhabits trees, where it searches for prey on living or dead branches and perhaps also on the trunk, but mainly

Fig. 7. Various Coleoptera extracted from the resins: A – *Laricobius erichsoni* (Derodontidae), B – *Omalisus fontisbelleaquaei* (Omalisidae), C – representative of Staphylinidae, D – *Paedurus brevipennis* (Staphylinidae), E – representative of Nitidulidae, F – *Trixagus carinifrons* (Throscidae).

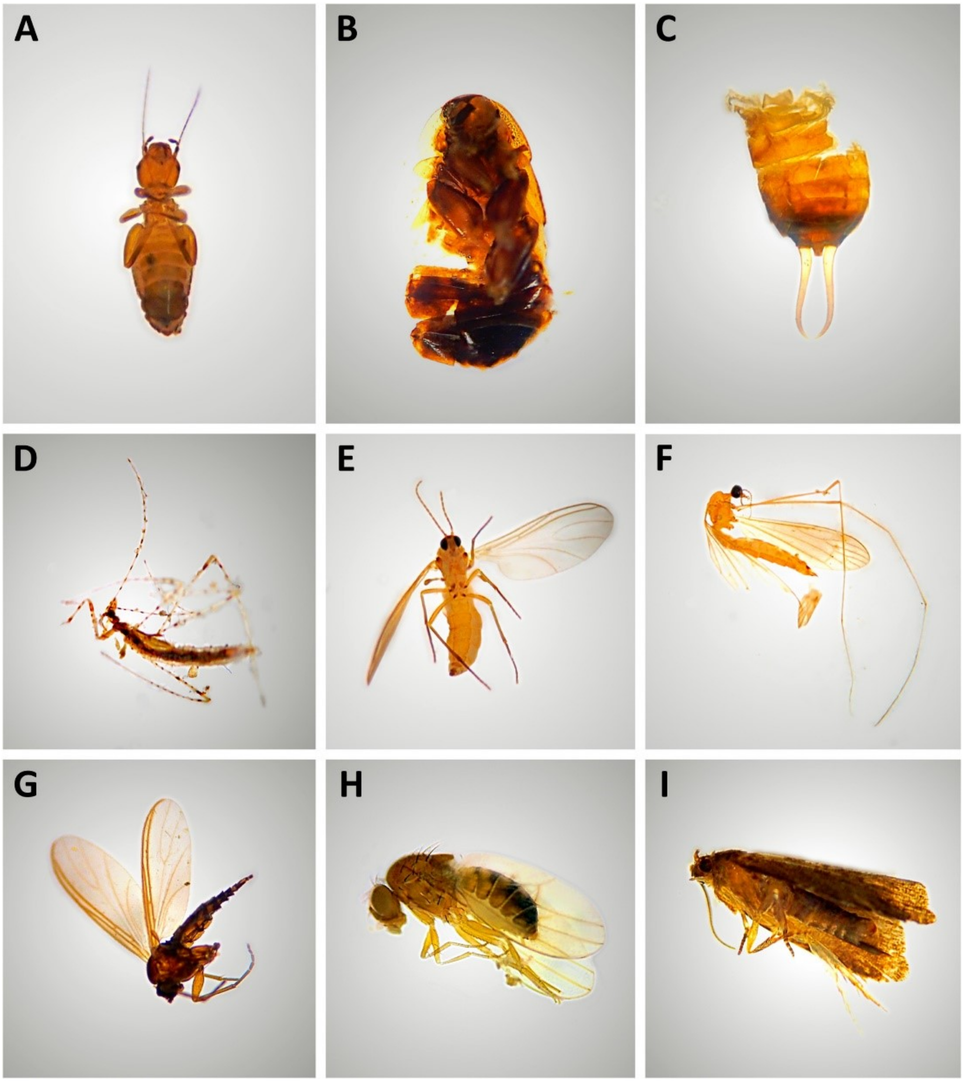

Fig. 8. Various insects extracted from resins: A – Psocoptera, B – Blattodea, C – Dermaptera, D – *Empicoris vagabundus* from Hemiptera, E–H – various Diptera, I – Lepidoptera

of deciduous trees (Wachmann et al. 2006). It preys on small insects, such as flies (Diptera) or bark lice (Psocoptera) (Fig 8 a, e–i), which were also extracted from the collected resins in the beech forest. Barklice use the bark crevices and the surface of the tree trunk to forage in search for food (organic remnants, algae or fungi). Being scavengers, they are not connected trophically with trees, but the trees serve as their place of living, where *E. vagabundus* feeds on them. The presence of well flying dipterans is rather accidental, although they are quite numerous.

Thus, in the small sample of resins, we could identify three levels of trophic chain: trophic level II (primary consumers) – herbivorous beetles and aphids, trophic level III (secondary consumers) – predators e. g. *L. erichsoni* and ants feeding on aphids and trophic level IV (tertiary consumers) – spiders, feeding on other predators, such as ants. Possibly, collected mites (Acari) and barklice (Psocoptera) belonged to the level of decomposers.

DISCUSSION

Presented results indicate, that even a small quantity of resin may contain a quite diverse and complex fragment of the ecosystem. The mean quantity of resin required to trap a single invertebrate was in this study 2.77 g (SD 1.33), ranging from 1.17 g to 4.36 g, being the number comparable to mean quantity of amber/per inclusion in the collection of Museum of Amber Inclusions, University of Gdańsk, Sonntag Collection of Baltic Amber (Perkovsky et al. 2007), but significantly higher than amber nodules with inclusions in studies by Pike (1993) on Alberta ambers from late Cretaceous. This also means that contemporary resins have high efficiency of trapping insects, but it may also depend on its type and place of origin (Zherikhin 1978; Solórzano Kraemer et al. 2015, 2018). The total amount of slightly more than 1 kg (exactly 1266 g) contained as many as 394 specimens of invertebrates, from 2 types: Mollusca and Arthropoda. Within arthropods, there were representatives of all three subtypes: Cheliceromorpha, Hexapoda and Crustacea. Mites (Acari) are quite numerable (8.75% of collected cadavers) and outnumber spiders (Araneae), but their presence in collected resins is twice lower than in e.g. Baltic or Rovno ambers (Perkovsky et al. 2007). Presence of crustacean, represented by Oniscoidea, results from the biology of terrestrial crustaceans, which are soil foragers, exploiting also bark crevices. They were recorded in Dominican but not Baltic or Rovno ambers (Poinar & Poinar 2006, Perkovsky et al. 2007), but these two types of amber differ significantly in their ability to represent contemporaneous fauna (Penney & Jepson 2014).

Among insects, trapped in resins, we recorded representatives of 10 orders, from 15 living in Poland, but they were very unevenly represented in the collected material (Fig. 9). This could be due to material limited to specific stratocoenosis and microhabitat. Some specimens were significantly fragmented, due to various processes of necrolysis after entrapment in the resin (Martinez-Delclòs et al. 2004) but many were in very good condition, allowing determination not only to the taxonomic order, but even to species level.

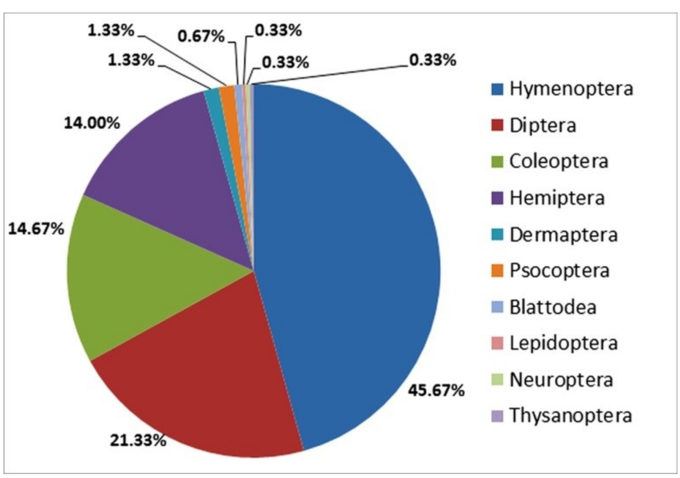

Fig. 9. Shares of specimens of particular orders of Insecta in the collected resins.

The abundance of Hymenoptera (Fig. 6 e–h) is predominately connected with the high number of ants trapped in resins – 89% of collected hymenopteran cadavers were ant workers. Ants comprise ca. 31% of collected invertebrates – an amount similar to resins from the far east of Russia (Zherikhin & Sukatsheva 1989) but more than collected in resins from Madagascar (Solórzano Kraemer et al. 2018). Surprisingly, among the extracted ants there were only two winged specimens – *Myrmica* males, while in e. g. Dominican amber (Poinar & Poinar 2006) the winged ants comprise ca. one-third of the trapped specimens of ants. This could be explained by avoidance of forest by winged adult ants during nuptial flight. However, even if they swarm in open areas, they need to fly through the forest from their nest to the place of swarming, unless they behave otherwise during their flight. It is also possible that the frequency of trapping winged ants is higher on trees growing close to the swarming place. All of our resins were collected from dense tree stands, while usually singly standing trees over scarcely vegetated area serve ants as a swarming place (Hölldobler & Wilson 1990). Unless reproductive, alate individuals of ants were more abundant than workers, in the period when Dominican amber originated, or were attracted to fossil resins.

We were also able to distinguish between the two types of habitats where resins were collected, on the basis of species composition of ants. Because *L. brunneus* is an inhabitant of older, deciduous trees and *L. platythorax* prefers to nest in decaying logs (Czechowski et al. 2012), it indicates that the resins in Bartne were collected in mature, mixed forest. Accordingly, lack of *L. brunneus* and predominance of *M. rubra*, preferring open and sunny habitats, suggests young coniferous forests, well sunlit, with lack of old trunks serving as a nesting place for *L. brunneus*.

Dipterans are the second most common group of insects trapped in resins, although they are slightly less than half as numerous as hymenopterans, while in Dominican amber they constitute comparable amounts (1017 dipterans and 1107 hymenopterans – Poinar & Poinar 2006). During the research on resins by Zherikhin et al. (2009), they also noted a relatively low number of dipterans in contemporary resins, which occurred mainly as puparia. However, such differences may strongly depend on the type of habitat and the type or resin – Zherikhin et al. (2009) inform that Trichoptera (caddisflies) are more common in ambers than Lepidoptera (butterflies), while the Dominican amber (Poinar & Poinar, 2006) gives 60 moths and 8 caddisflies per 3017 pieces of amber. Also in data presented by Zherikhin & Sukatsheva (1989) butterflies outnumber the caddisflies. In our study, we found only 1 lepidopteran (Fig. 6i) per 394 cadavers and no caddisfly. Similarly, in Dominican amber barklice are fairly frequent, while in our study only 4 specimens occurred, which is a result similar to Zherikhin & Sukatsheva (1989). Other groups found in our study in single specimens, such as Dermaptera and Blattodea (Fig. 8 b, c), are also rare in fossilised resins (Zherikhin & Sukatcheva, 1989) and in e.g. Dominican amber (Poinar & Poinar, 2006). Studies by Solórzano Kraemer et al. (2018) indicate also very high proportions of Lepidoptera and Neuroptera in resins of Madagascar, but in our research these taxa are represented by negligible number of specimens, but this may be explained by differences in ecosystem or even biome type.

The cadavers of most common aphids in resins – *Cinara* spp. were very abundant, but low on the trunk, while these aphids feed on needles and/or young twigs (Blackman and Eastop, 2018), which in case of the trees from which the resin was collected were rather high (at least 2–3 meters above ground level). This indicates, that apterous aphids trapped in resins, collected at the height of 0.5–1.5 m above ground level, were most probably taken by ant workers as a source of food (apart from honeydew rich in saccharides, ants also eat aphids, as a source of proteins). Species of the genus *Cinara* were not recorded in neither Baltic nor Rovno ambers (Perkovsky et al.2007). When we consider their significant presence in contemporary resins, it may strengthen the conclusions, that the representatives of this genus were either absent or only scarcely abundant in the forest of origin of Baltic and Rovno ambers. It may further indicate their recent radiation (despite this genus is one of the most species-rich and Holarctic in its geographical distribution) (Chen et al. 2015).

Furthermore, interesting data on the ecosystem may be revealed from the differences in the species composition of aphid cadavers and their morphs (Tab. 2). All apterous aphids belonged to species directly feeding on trees building the habitat in which resins originated, as they were all feeding on conifers. Alate aphids, however, give us information on the general type of ecosystem, not necessarily neighbouring with the place of collection. These are *Cornus*, *Betula* and *Fagus* feeding aphids, which may have been brought even from a significant distance. Among these aphids, there is *A. corni*, which has its life cycle alternating between *Cornus* and grasses, so its presence is also an indicator of grassy habitats being near.

Similarly, the fauna of beetles could provide a broader view of the ecosystem. Apart from species living directly within the tree trunk, such as those from the genus *Ips*, or generally connected with the habitat of coniferous forests e.g. *Laricobius erichosni*, the species of another habitat could have been found. These were connected with various ecotone or shrubby habitats.

Thus, aphids and partly, also beetles, may serve as indicators at multilevel resolution: tree type within the ecosystem (in this case conifers), ecosystem (Carpathian beech forest) and a biome (nemoral forests or temperate broadleaf and mixed forests). Still, however, must be remembered, that resin is a selective medium as it entraps selectively animals from various strata of biocoenosis and it accumulates them during long time.

Finally, a minute but representative fragment of the zoocoenosis existing in the site of resin collection could have been reconstructed. Mainly, it is a piece of life taking place around the tree, whose trunk served either as a place of living, foraging and hunting, its bark as a place of hiding and its branches and flowers as a source of food. Similar results have been suggested by studies by Perkovsky et al. (2010) on syninclusia in Rovno ambers . However, in our case, ants seem to be definitely connected with on-trunk foraging, while some of the collected dipterans and e.g. alate aphids may be also a part of aerial plankton, trapped in resins by accident.

Conclusions

Despite fragmentary and scarce data, if we have in mind the whole species diversity of the forest being a place of the study, significant interrelationships between trapped insects could be revealed. Nonetheless, the collected amount of resins is far from being comparable with the preserved and well-studied collections of amber e.g. Baltic amber and definitely too small to trap a representative set of specimens for forest fauna. Further research (such as by Solórzano Kraemer et al. 2015, 2018) should focus on collecting a significantly higher amount of resins from various trees and various types of forests. Such studies could provide knowledge on the possible selectiveness of particular types of resins in trapping invertebrates.

Acknowledgements

Members of the Students Scientific Association “Faunatycy” wish to thank the Students’ Union of the University of Silesia for the financial support of the project. All authors wish to thank Małgorzata Tomecka, Miłosz Morawski, Miłosz Obrzut for help during the field research and also Wojciech Szczepański for identifications of beetles.

We also thank anonymous reviewers for constructive criticism which helped to significantly improve the manuscript.

References

Antoine P. O., De Franceschi D., K J. J., Nel A., Baby P., Benammi M., Calderón Y., Espurt N., Goswami A. & Salas-Gismondi R. 2006. Amber from western Amazonia reveals Neotropical diversity during the middle Miocene. Proceedings of the National Academy of Sciences 103: 13595–13600.

Aquilina L., Girard V., Henin O., Bouhnik-Le Coz M., Vilbert D., Perrichot V. & Néraudeau D. 2013. Amber inorganic geochemistry: New insights into the environmental processes in a Cretaceous forest of France. Palaeogeography, Palaeoclimatology, Palaeoecology 369: 220–227.

AZAR D., NEL A. & GÈZE R. 2003. Use of Lebanese amber inclusions in paleoenvironmental reconstruction, dating and paleobiogeography. Acta Zoologica Cracoviensia 46 (Suppl. – Fossil Insects): 393–398.

BLACKMAN R. L. & EASTOP V. F. 2018. Aphids on the World's Plants. An online information and information guide. Available at http://www.aphidsonworldsplants.info (15 Oct 2018).

BOROWIEC L. 2018. Iconographia Coleopterorum Poloniae. Chrząszcze Polski. World Wide Web electronic publication: http://www.colpolon.biol.uni.wroc.pl/index.htm (16 Sep 2018).

BURAKOWSKI B. 2003. Ślimacznikowate – Drilidae, Rozgniotkowate – Omalisidae. Klucze do oznaczania owadów Polski. 19, 32–33. Muzeum i Instytut Zoologii PAN, Warszawa, 16 pp.

BURAKOWSKI B., MROCZKOWSKI M. & STEFAŃSKA J. 1979. Chrząszcze – Coleoptera. Kusakowate Staphylinidae. 1. Katalog Fauny Polski 6, Instytut Zoologii PAN, Warszawa, 310 pp.

BURAKOWSKI B., MROCZKOWSKI M. & STEFAŃSKA J. 1985. Chrząszcze – Coleoptera. Buprestoidea, Elateroidea i Cantharoidea. Katalog Fauny Polski 10. Instytut Zoologii PAN, Warszawa, 401 pp.

BURAKOWSKI B., MROCZKOWSKI M. & STEFAŃSKA J. 1986. Chrząszcze – Coleoptera. Dermestoidea, Bostrichoidea, Cleroidea i Lymexyloidea. Katalog Fauny Polski 11. Instytut Zoologii PAN, Warszawa, 243 pp.

BURAKOWSKI B., MROCZKOWSKI M. & STEFAŃSKA J. 1992. Chrząszcze Coleoptera. Ryjkowcowate prócz ryjkowców – Curculionoidea prócz Curculionidae. Katalog Fauny Polski 23. Muzeum i Instytut Zoologii PAN, Warszawa, 323 pp.

CHEN R., FAVRET C., JIANG L., WANG Z. & QIAO G. 2015. An aphid lineage maintains a bark-feeding niche while switching to and diversifying on conifers. Cladistics 32: 555–572. DOI: https://doi.org/10.1111/cla.12141

CMOLUCHOWA A. 1978. Nabidae, Reduviidae, Phymatidae. Klucze do oznaczania owadów Polski 18 (7). PWN, Warszawa, 43 pp.

CZECHOWSKI W., RADCHENKO A., CZECHOWSKA W. & VEPSÄLÄINEN K. 2012. The ants of Poland with reference to the myrmecofauna of Europe. Fauna Poloniae. Vol. 4. New Series. Muzeum Museum and Institute of Zoology of the Polish Academy of Sciences and Natura optima dux Foundation, Warszawa, 496 pp.

EFREMOV J. A. 1940. Taphonomy: a new branch of paleontology. Pan-American Geologist 74: 81–93.

FRASER N. C., SUES H.-D. 2017. Terrestrial Conservation Lagerstätten: Windows into the Evolution of Life on Land. Dunedin Academic Press Ltd. Edinburgh, 450 pp.

FREUDE H., HARDE K. W. & LOHSE G. A. 1965. Die Käfer Mitteleuropas. Band 1: Einführung in die Käferkunde. Goecke and Evers, Krefeld, 214 pp.

FREUDE H., HARDE K. W. & LOHSE G. A. 1979. Die Käfer Mitteleuropas. Band 6. Diversicornia. Goecke and Evers, Krefeld. 367 pp.

GIRARD V., SCHMIDT A. R., STRUWE S., PERRICHOT V., BRETON G. & NÉRAUDEAU D. 2009. Taphonomy and palaeoecology of mid-Cretaceous amber-preserved microorganisms from southwestern France. Geodiversitas 31: 153–162.

GRIMALDI D. & AGOSTI D. 2000. A Formicine in New Jersey Cretaceous amber (Hymenoptera: Formicidae) and early evolution of the ants. Proceedings of the National Academy of Sciences 97: 13678–13683.

HEIE O.E. 1980. The Aphidoidea (Hemiptera) of Fennoscandia and Denmark. I. General Part. The Families Mindaridae, Hormaphididae, Thelaxidae, Anoeciidae, and Pemphigidae. Fauna Entomologica Scandinaviaca 9: 1–236.

HEIE O.E. 1982. The Aphidoidea (Hemiptera) of Fennoscandia and Denmark. II. Family Drepanosiphidae. Fauna Entomologica Scandinavica 11: 1–169.

HEIE O.E. 1992. The Aphidoidea (Hemiptera) of Fennoscandia and Denmark. IV. Fauna Entomologica Scandinavica 25: 1–189.

HÖLLDOBLER B. & WILSON E.O. 1990. The ants. Springer-Verlag, Berlin, 732 pp.

KONDRACKI J. 2013. Geografia regionalna Polski. Wydawnictwo Naukowe PWN, Warszawa, 440 pp.

LAWFIELD A. M. W. & PICKERILL R. K.. 2006. A novel contemporary fluvial ichnocoenose: Unionid bivalves and the Scoyenia-Mermia ichnofacies transition. PALAIOS 21: 391–396.

LÖBL I. 1970. Scaphidiidae. Klucze do oznaczania owadów Polski. 19 (23). PWN, Warszawa, 16 pp.

LUTZ H. 1997. Taphozönosen Insekten in aquatischen Sedimenten – ein Beitrag zur Rekonstruktion des Paläoenvironments. Neues Jahrbuch für Geologie und Paläontologie – Abhandlungen 203 (2): 173–210. DOI: 10.1127/njgpa/203/1997/173

MARTÍNEZ-DELCLÒS X., BRIGGS D. E. G. & PEÑALVER E. 2004. Taphonomy of insects in carbonates and amber. Palaeogeography, Palaeoclimatology, Palaeoecology 203: 19–64.

MATUSZKIEWICZ W. 2007. Przewodnik do oznaczania zbiorowisk roślinnych Polski. Wydawnictwo Naukowe PWN, Warszawa, 537 pp.

MERTLIK J. & LESEIGNEUR L. 2007. Druhy čeledi Throscidae (Coleoptera: Elateroidea) České a Slovenské republiky. Elateridarium 1: 1–55.

MROCZKOWSKI M. 1954. Skórniki – Dermestidae. Klucze do oznaczania owadów Polski 19 (52). PWN, Warszawa, 48 pp.

NUNBERG M. 1976. Łyszczynkowate – Nitidulidae. Klucze do oznaczania owadów Polski 19 (65). PWN, Warszawa, 92 pp.

NUNBERG M. 1981. Korniki – Scolytidae, Wyrynniki – Platypodidae. Klucze do oznaczania owadów Polski 19 (99–100). PWN, Warszawa, 116 pp.

PAWŁOWSKI J. 2014. *Attagenus smirnovi* Zhantiev, 1973. In: Gatunki obce w faunie Polski. Publikacja internetowa: Instytut Ochrony Przyrody PAN, Kraków 2008–2012. Available at http://www.iop.krakow.pl/gatunkiobce (3 Feb 2018).

PENNEY D. 2010. Dominican amber. In: PENNEY D. (ed.), Biodiversity of fossils in amber from the major world deposits. Siri Scientific Press. Manchester 304 pp.

PENNEY D. & JEPSON J. E. 2014. Fossil Insects. An introduction to palaeoentomology. Siri Scientific Press. Manchaster 224 pp.

PERKOVSKY E. E., RASNITSYN A.P., VLASKIN A.P. & RASNITSYN S. P. 2010. Community structure in the amber forest: study of the arthropod syninclusia in the Rovno amber (Late Eocene of Ukraine). Acta Geologica Sinica 84: 954–958.

PERKOVSKY E. E., RASNITSYN A. P., VLASKIN A. P. & TARASCHUK M. V. 2007. A comparative analysis of the Baltic and Rovno amber arthropod faunas: representative samples. African Invertebrates 48: 229–245.

PIKE E. M. 1993. Amber taphonomy and colelcting biases. Palaios 8: 411–419.

PŁAWILSZCZIKOW N. 1972. Klucz do oznaczania owadów. PWRiL, Warszawa, 756 pp.

POINAR G. O. Jr & POINAR R. 2008. The Amber Forest. A Reconstruction of a Vanished World. Princeton University Press, Princeton 239 pp.

RASNITSYN A. P., BASHKUEV A. S., KOPYLOV D. S., LUKASHEVICH E. D., PONOMARENKO A. G., POPOV Yu. A., RASNITSYN D. A., RYZHKOVA O. V., SIDORCHUK E. A., SUKATCHEVA I. D. & VORONTSOV D. D. 2016. Sequence and scale of changes in the terrestrial biota during the Cretaceous (based on materials from fossil resins). Cretaceous Research 61: 234–255.

SCHMIDT A. R., JANCKE S., LINDQUIST E. E, RAGAZZI E., ROGHI G., NASCIMBENE P. C., SCHMIDT K., WAPPLER T. & GRIMALDI D. A. 2012. Arthropods in amber from the Triassic Period. Proceedings of the National Academy of Sciences 109: 14796–14801.

SCHMIDT A. R. & DILCHER D. L. 2007. Aquatic organisms as amber inclusions and examples from a modern swamp forest. Proceedings of the National Academy of Sciences of the United States of America 104 (42) 16581–16585; https://doi.org/10.1073/pnas.0707949104

SCHMIDT A. R., RAGAZZI E., COPPELLOTTI O. & ROGHI G. 2006. A microworld in Triassic amber. Nature 444: 835.

SOLÓRZANO KRAEMER M. M., KRAEMER A. S., STEBNER F., BICKEL D. J., RUST J. 2015. Entrapment bias of arthropods in Miocene amber revealed by trapping experiments in a tropical forest in chiapas, Mexico. PLoS ONE 10(3): e0118820, doi:10.1371/journal.pone.0118820

SOLÓRZANO KRAEMER M. M., DELCLÒS X., CLAPHAM M. E., ARILLO A., PERIS D., JÄGER P., STEBNER F., PEÑALVER E. 2018. Arthropods in modern resins reveal if amber accurately recorded forest arthropod communities. PNAS 115: 6739–6744. https://doi.org/10.1073/pnas.1802138115

SZADZIEWSKI R., SZWEDO J., SONTAG E. 2018. Fauna lasu bursztynowego / Fauna of the amber forest. Pp. 38–75, 216–217. In: SZADZIEWSKI R., PYTLOS R., SZWEDO J. (eds), Bursztyn bałtycki – skarb Zatoki Gdańskiej / Baltic amber – trasure of the Bay of Gdańsk. Związek Miast i Gmin Morskich, Gdańsk, 222 pp.

Szelegiewicz H. 1978. Pluskwiaki równoskrzydłe – Homoptera. Mszyce – Aphidodea. Wstęp i Lachnidae. Klucze do oznaczania owadów Polski 17 (5a). PWN, Warszawa, 107 pp.

SZCZEPAŃSKI W. S., KARPINSKI L. & TASZAKOWSKI A. 2013. Nowe stanowiska *Omalisus* (*Omalisus*) *fontisbellaquaei* Geoffroy, 1785 (Coleoptera: Omalisidae) w południowej Polsce. Acta Entomologica Silesiana 21: 73.

SZUJECKI A. 1965. Kusakowate – Staphylinidae. Kiepurki – Euasthetinae i żarlinki – Paederinae. Państwowe Wydawnictwo Naukowe, Warszawa, 74 pp.

SZWEDO J. & SONTAG E. 2009. The traps of the "amber trap". How inclusions could trap scientists with enigmas. Denisia 26: 155–169.

WACHMANN E., MELBER A. & DECKERT J. 2006. Wanzen. Band 1. Dipsocoromorpha, Nepomorpha, Gerromorpha, Leptopodomorpha, Cimicomorpha (Teil 1). Die Tierwelt Deutschlands 77, Goecke & Evers, Keltern, 263 pp.

WEIHER E., FREUND D., BUNTON T., STEFANSKI A., LEE T. & BENTIVENGA S. 2011. Advances, challenges and a developing synthesis of ecological community assembly theory. Philosophical Transactions of the Royal Society B 366: 2403–2413.

WIER A., DOLAN M., GRIMALDI D., GUERRERO R., WAGENSBERG J. & MARGULIS L. 2002. Spirochete and protist symbionts of a termite (*Mastotermes electrodominicus*) in Miocene amber. Proceedings of the National Academy of Sciences of the United States of America 99: 1410–1413. https://doi.org/10.1073/pnas.022643899

ZHERIKHIN V. V. 1978. Development and changes of the Cretaceous and Cenozoic faunal assemblages (Tracheata and Chelicerata). Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR 165. Nauka, Moscow, 198 pp. [In Russian]

ZHERIKHIN V. V. 2002. Patterns of insect burial and conservation. Pp. 17–63. In: RASNITSYN A. P. & QUICKE D. L. J. (eds), History of insects. Kluwer Academic Publishers, New York, 516 pp.

ZHERIKHIN V. V., PONOMARENKO A. G. & RASNITSYN A. P. 2008. Introduction into Palaeoentomology. KMK Press. Moscow 371 pp.

ZHERIKHIN V. V. & SUKATSHEVA I. D. 1989. Zakonomernosti zakhoroneniya nasekomyh v smolah [Patterns of the insects burial in resins]. Pp. 84–92. In: SOKOLOV B. S. (ed.), Osadochnaya obolochka Zemli v prostranstve i vremeni. Stratigraphiya i palaeontologiya [Sedimentary cover of the Earth in space and time. Stratigraphy and paleontology]. Nauka, Moskva: [in Russian]

ZHERIKHIN V. V., SUKATSHEVA I. D. & KULICKA R. 2009. Inclusions in fossil and extant resins (taphonomic and palaeontological aspects. Acta entomologica Silesiana 17: 5–10. [In Polish with English abstract]

STRESZCZENIE

[**Bezkręgowce we współczesnej żywicy – spojrzenie na ekosystem?**]

Wyniki badań prezentowane w niniejszej pracy opisują faunę bezkręgowców uwięzionych we współczesnych żywicach drzew iglastych. Terenem badań był las mieszany w Europie Środkowej (Polska południowa). Żywice zbierano z następujących drzew: świerku (*Picea abies*), sosny (*Pinus sylvestris*) i modrzewia (*Larix decidua*). Szczątki zwierzęce wyekstrahowano z roztworu żywicy przy pomocy etanolu (98%). Zebrano 394 okazy zwierząt. Najliczniej reprezentowaną grupą były owady, ale znaleziono również pajęczaki, skorupiaki i pojedyncze mięczaki. Zebrany materiał starano się oznaczyć do jak najniższej rangi; część do gatunku (w zależności od stanu zachowania próbki). Dyskusja skupia się na podobieństwach i różnicach składu owadów w żywicach i znanych kolekcjach bursztynu.

Accepted: 20 Aug 2019