The traps of the "amber trap".
How inclusions could trap scientists with enigmas

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Abstract: Studies of Baltic amber and its inclusions give the unique opportunity to take a look into the past. However, interpretation of the data obtained during studies confronts the student with some problems and traps. Problems facing the researchers dealing with taxonomy, phylogenetic analyses, and biogeographic as well as ecological analyses and reconstructions are discussed.

Key words: Baltic amber, inclusions, taxonomy, phylogeny, biogeography, ecology.

Santrauka: Baltijos gintaro ir jame esančių inkliuzų studijos suteikia unikalią galimybę pažvelgti į praeitį. Tačiau interpretuodami studijų metu gautus duomenis mokslininkai susiduria su tam tikrais klausimais ir spąstais. Aptariamos problemos, su kuriomis susiduria mokslininkai, dirbantys taksonomijos, filogenetinės analizės, biogeografijos ir ekologinės analizės bei rekonstrukcijos srityse.

Raktiniai žodžiai: Baltijos gintaras, inkliuzai, taksonomija, filogenija, biogeografija, ekologija.

Introduction

Eocene Baltic amber is unequalled as Konservat-Lagerstätte, as a place of exceptionally rich and well preserved fossil organisms. Its importance for scientific study is not to be overestimated. The results of Baltic amber investigations are used in the taxonomy and phylogenetics of plants and animals, palaeobotany, palaeobiogeography, palaeoecology, palaeoclimatology, etc.

The richness of data from the inclusions "trapped" in amber is enormous; however, the number of questions arising during amber studies is not decreasing.

The deposits of Baltic amber are to be found along the Baltic coast from Denmark to Russia (KRZEMIŃSKA et al. 1992, 1993; KOSMOWSKA-CERANOWICZ 2005). However, the richest ones are placed on the Sambian (Samland) Peninsula in Russia, north of Kaliningrad (formerly Königsberg). The amber deposits in the vicinity of Chłapowo, district Gdańsk, Poland are also rich although placed deeper underground. Deposits of Baltic amber probably represent the largest accumulations of amber in the world. Baltic amber is common in the Eocene deposits and in accumulations of the Quaternary deposits. The amber in Sambia is located in layers of "blaue Erde" – "blue earth"; blue earth is actually greyish, with traces of green when dry or black when wet, and composed mainly of clay, not blue-clay but rather glauconite-rich clay. During the Pleistocene, amber from Paleogene deposits was transported by glacial,

fluvial or fluvioglacial action. This resulted in distribution of the Eocene Baltic amber across Latvia, Lithuania, Byelorussia, Poland and Germany, up to the east coast of the British Isles and even as far as Jutland (Denmark) and the southern coast of the Scandinavian Peninsula (DAHLSTRÖM & BROST 1996; KOSMOWSKA-CERANOWICZ & KONART 1989; KOSMOWSKA-CERANOWICZ 2005). Sambian amber-bearing deposits are placed in the lower portion of the Prussian Formation, aged Late Eocene (Priabonian). Their absolute age was estimated c. 37±1.5 Ma (KAPLAN et al. 1977). Chłapowo deposits are estimated to be Late Eocene (Priabonian), c. 37.5±3 Ma (PIWOCKI et al. 1985). Small amounts of Baltic amber are recorded from the earliest Eocene sediments of North Jutland (Ypresian, c. 55 Ma) (LARSSON 1978), as well as in younger deposits of Sambia, the Early Oligocene (Rupelian, c. 34±3.7 Ma) (KAPLAN et al. 1977).

Amber-bearing strata could be the accumulations of the fossil resins of the biogenic-sedimentary (primary, autochthonous) and placer (secondary, allochthonous) deposits. Originally amber occurred in ancient soils, where the resin underwent the diagenetic processes. Due to erosion the ancient soils with amber were removed and the amber re-deposited in the coastal zones by rivers. Baltic amber is today no longer found at the site where the resins were originally produced and deposited in the forest floor (WEITSCHAT & WICHARD 1998, 2002). The amber deposit of the Sambian Peninsula and Chłapowo consists of a mixture of different al-
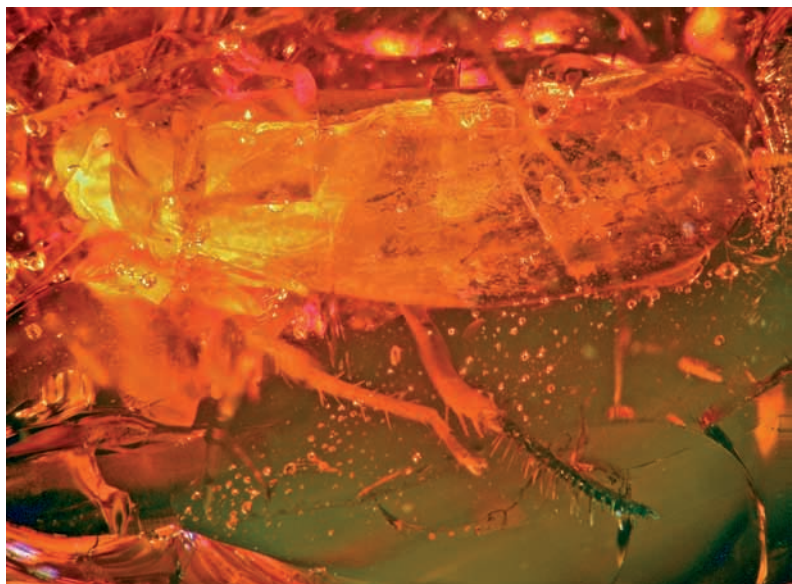
Fig. 1: *"Jassus" immersus* GERMAR & BERENDT, 1856 (Hemiptera: Cicadomorpha: Cicadellidae), Holotype, MB.I. 1991, Geologisch-Paläontologisches Museum der Humboldt-Universität, Berlin. This specimen focuses several questions: state of preservation of the amber and the inclusion, incompleteness of data available, unclear systematic position. The generic name *"Jassus"* was widely used for various Cicadellidae. This generic name is placed on the List of Rejected and Invalid Names in Zoology, ICZN Opinion 612. The fossil species very probably represents the subfamily Coelidiinae.
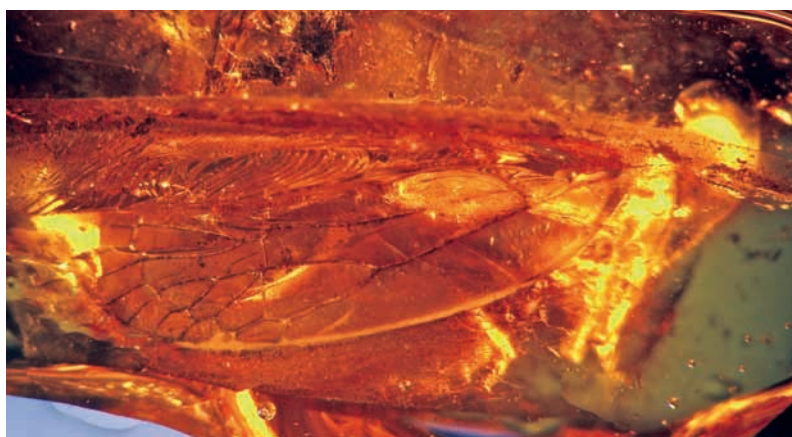

Fig. 2: *Jantaritambia* sp. (Hemiptera: Fulgoromorpha: Tropiduchidae), No. 149. Coll. Janusz KUPRYJANOWICZ. The genus is placed in the extinct tribe Jantaritambini, known from the Paleogene of Europe. The range of Tropiduchidae is now under investigation, the definition, tribal classification and relationships of the family are going to be revised, then fossils could give insight to the evolution of the group.

Fig. 3: Representatives of the Bothriocerinae (Hemiptera: Fulgoromorpha: Cixiidae) are recently distributed in the New World, with most species in Central America. Fossils of the subfamily are known from the Paleogene of Europe and the Miocene Dominican amber. Coll. Jonas DAMZEN, deposited in the Museum of Amber Inclusions, University of Gdańsk.

lochthonous (not indigenous, the resin did not originate at that location but was introduced by some processes) fossil resins transported to one site from various parts of the huge ancient river(s) basins differing in relief, climate and biota. Rich findings of "Baltic amber group fossil resins" in other areas: Parczew delta (Poland), Klesovo delta (Ukraine) suggest transport from southern areas of origination. Deposits of Bitterfeld amber (Saxony) also are allochthonous, re-deposited in the Lower Miocene. The most massive re-deposi-

tions of Baltic amber certainly took place during the Pleistocene (KRUMBIEGEL & KRUMBIEGEL 1996; WEITSCHAT & WICHARD 1998, 2002; KOSMOWSKA-CERANOWICZ 2002; KOSMOWSKA-CERANOWICZ & GIERŁOWSKI 2006).

The age of Baltic amber itself has been widely discussed. It is generally dated as Eocene (55.8-33.9 Ma), but there were doubts about the exact age, as this fossil resin has an age range between 38-47 Ma (RITZKOWSKI 1997; PERKOVSKY et al. 2007). Absolute dating analyses of glauconites from Sambia Peninsula show that the "blue earth" formation (amber-bearing Prussian Formation) is allocated to the Middle Eocene (Lutetian: 44.1±1.1 Ma) and is thus significantly older than previously assumed (WAPPLER 2003, 2005). This is partly revealed by insect groups, in particular by genera of the Coleoptera, Hymenoptera, and Hemiptera. Mounting evidence for a possible Middle Eocene origin of Baltic amber now comes from limnic sediments within the Eckfeld Maar, which correlate perfectly in age with the K-Ar radiometric data from the Kaliningrad district. Biostratigraphically, Eckfeld Maar corresponds to the

Middle Eocene mammal reference level MP 13 of the ELMA. In the maar crater, basalt fragments could be recovered by drilling. The ^{40}Ar/^{39}Ar dating of the basalt presents for the first time a direct numerical calibration mark for an Eocene European mammal locality. The Eckfeld basal isochron has an age of 44.3±0.4 Ma. Comparing taxa exclusively from the Eckfeld taphocoenosis with their occurrence in Baltic amber, the Eckfeld Maar insects are found to contain an interesting mix of palaeofaunal elements that shows a strong alliance with groups currently known only from the roughly contemporaneous and geographically close Baltic amber (WAPPLER 2005). However, assumptions on the Middle Eocene age of Baltic amber are challenged by PERKOVSKY et al. (2007), who prefer the Late Eocene (Bartonian/Priabonian: 37.7±3 Ma) age of the Prussian Formation.

The Middle Eocene was the period of the most massive sea transgression, with the maximum in the Late Eocene. The North-West European Basin, developing at this time, achieved the connection with the Boreal province of the Donetsk-Caspian Basin through the Baltic Sea and with the Alpine-Carpathian forefield of the Mediterranean Basin through the Moravian Gate (ZIEGLER 1990). The sea appeared in the present Baltic Sea area at the border of the Late Eocene/Early Oligocene. The most characteristic feature of palaeogeographic conditions of the area at this time was the Chłapowo-Sambia delta. This river delta was supported by the terrigenous material, mainly from the north, transported by the hypothetical Eridanos River (KOSMOWSKA-CERANOWICZ & KONART 1989). It could be assumed that this delta was comparable the Recent deltas of the Danube or even the Mississippi and formed by the fluvial processes modified by sea wave processes (JAWOROWSKI 1987). The amber concentrations were formed on the distal slopes of submerged, under water river mouth embankments during suitable, long and stable conditions (KRAMARSKA 2007).

The global climate during the Cretaceous and the early Cenozoic is thought to have been warmer than the present climatic conditions, and for at least the first 10 Ma of the Eocene a large part of the Earth, including continental interiors, had climates with winter temperatures much higher than today (GREENWOOD & WING 1995). It is worth noting that the northern parts of North America, the southern parts of Greenland, and the Scandinavian Peninsula were covered with vegetation of the warm temperate zone during the Eocene. During the warm periods it was the paratropical forest on the south and the microphyllous (with leaf size 25-75 mm long, 225-2025 mm^2 in area) broad-leaved evergreen forest to the north, in the cool intervals it was the

Fig. 4: Two mites (Arachnida: Acarina), identified by acarologist as predators, were caught feeding on long-legged fly (Diptera: Dolichopodidae). Such inclusions, inclusions "in action", are not very common, and sometimes are over-interpreted as proofs of the relationships between organisms trapped in resin. Coll. Museum of Amber Inclusions, University of Gdańsk.


Fig. 5: This mite trapped together with a long-legged fly (Diptera: Dolichopodidae) could be predator or phoretic. The answer could be found after examination of the mite alimentary tract, which is not possible yet. Coll. of Amber Inclusions, University of Gdańsk.

mixed coniferous forest on the north, the microphyllous broad-leaved evergreen forest and notophyllous (with leaf size 75-125 mm long, 2025-4500 mm^2 in area) broad-leaved evergreen forests (WOLFE J.A. 1985; WILLIS & MCELWAIN 2002).

The Earth was much warmer in the Eocene. The equatorial sea currents which reached the southern part of Fennoscandia gave it a very warm subtropical climate; palm trees grew up to 60° of latitude. Further north there were conditions appropriate for warm-tem-

Fig. 6: The mite on the lizard's skin is most probably a parasite of this animal. Photo: E. SONTAG.
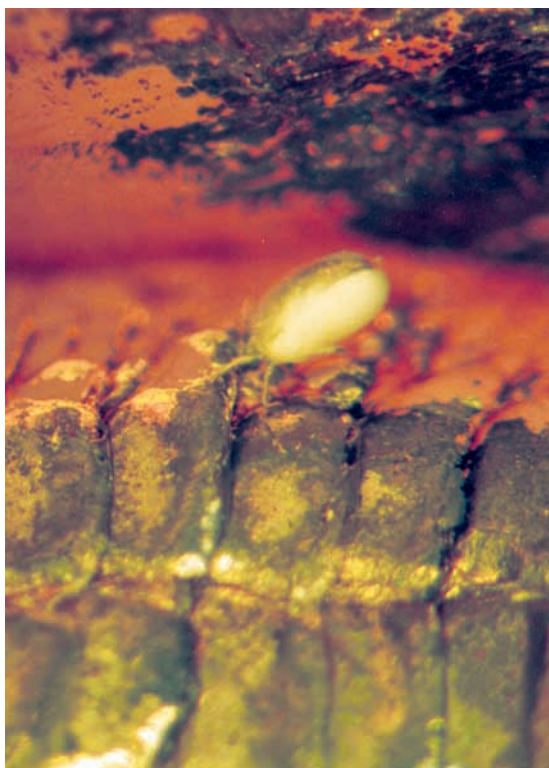
perate and temperate climate plants. The rivers flowing through these forests would carry smaller and larger dripstone resin forms and entire tree trunks with resin accumulated in all kinds of cracks inside and under the bark, and inside the tree. All this resinous material accumulated in the deltaic deposits of today's southern Baltic, and underwent gradual physical and chemical transformations, producing the amber nuggets we find today (PIELIŃSKA 2008a).

The trap

The "amber trap" and its mechanisms described indicate that the resin could entrap animals from various habitats (SZADZIEWSKI & SONTAG 2001; SZWEDO 2002a). Amber (resin) trapping may be biased toward certain organisms. A number of factors promote preservation of some groups of insects and not others (MARTÍNEZ-DELCLÓS et al. 2004). Resin viscosity, stickiness, and drying depend on its volatile content, which controls the effectiveness and longevity of the resin as a trap – these properties of the resin are influenced by its position on the tree. The behaviour of insects influences the likelihood of their entrapment in amber. The location of resin production affects the trapping of insects. Insects that live around resin-producing trees are most prone to entombment. Volatile resin products may deter or attract groups of insects. Environmental factors, such as light, temperature, moisture, and nutrients play an important role in controlling the nature and quantity of resins, and of insect inclusions (see review in

MARTÍNEZ-DELCLÓS et al. 2004). Therefore, the "amber traps" in the Eocene amber forest were selective and more effective for the animals which had the chance to be entombed in amber, inhabited or visited the "amber forest" habitats, had no possibility to escape from the resin, and got through the fossilisation processes. The fossilisation potential was higher for the smaller organisms, actively penetrating the "amber forest" habitats or passively moved there. The opposite situation occurs, when selected pieces of amber, usually with a bigger size and thus more easily identified during macroscopic selection, are subjects of research. This "double selection" makes the samples available for study presenting a bias in taxonomic composition. Only a small portion of the organisms present in the "amber forest" habitats was entrapped in resin (SONTAG 2003).

Thinking about the "amber trap" several points must be taken into consideration. The time span of the amber producing forest – the "amber trap" could be active for a few million years during the Eocene. The geographical distribution of the amber producing forest – the area covered by this type of vegetation comprised thousands of square kilometres, thus the distance between particular "amber traps" could be several hundreds of kilometres. The intensity of resin production was not equal depending of season and environmental conditions – the victims of the "amber trap" were caught at different vegetational seasons, trees exude more resin during spring and summer than in autumn and winter. For this reason the majority of insects in Tertiary ambers are spring and summer taxa (MARTÍNEZ-DELCLÓS et al. 2004).

The victims of the "amber trap", the specimens entombed in amber, are the very rich material for the scientific investigation, the material of great importance. However, this material is simultaneously of unknown precise age, originating from various areas with imprecisely known climatic and environmental conditions, is "double selected", and often interpreted as originates from a single "amber forest". Therefore, making investigations into amber and its inclusions we are jeopardised to fall into various traps.

The taxonomy traps

Fossils, i.e. remains of living organisms, provide unique information concerning the past. Fossils allow statements to be made about morphological features that would otherwise remain unknown; fossils could help clarify morphological disparity of taxa, and taxonomic diversity as well. Amber inclusions offer (sometimes) perfect preservation of the fossil with all the features of external morphology well preserved and available for study.

The early descriptions of Baltic amber inclusions usually placed the species found in extant genera (see e.g. BERENDT 1848-1856; KEILBACH 1982; SPAHR 1981-1993; EVENHUIS 1994; SZWEDO et al. 2004). Numerous taxa of various groups are reported at the family or genus level rather than at the species level; others call for revision and/or re-description. The data about the presence of particular taxa (genera, families) in the fossil record from the Eocene Baltic amber are of limited credibility in numerous papers. The reasons for this are various taxonomic impediments, i.e. general decrease of taxonomic research and students in "classic" taxonomy, lack of fossil specialists working with the group, lack of interest in fossils among specialists working with Recent faunas, misinterpretation of fossil specimens, identification problems of fossils in respect to knowledge on Recent taxa, incompleteness or poor preservation of fossils, but also rapid changes in classification schemes thanks to molecular research, sometimes contradicting the data from the fossil record, the necessity of revisions and re-definitions of taxa in respect to new morphological and molecular data, etc. All of these factors result in the repeated (but not verified) use of doubtful data even in the excellent manuals, books and monographs on amber fossils (CARPENTER 1992; WEITSCHAT & WICHARD 1998, 2002; JANZEN 2002; GRIMALDI & ENGEL 2005).

The traps (or problems in interpretation) during studies of amber inclusions are several: Is it possible that morphological features presented by the fossil remain unchanged for 40 Ma when compared with morphology of extant taxa? Is it possible that the species remain unchanged since the Eocene? What is the generic placement of the amber fossil – could it be placed in a genus of the Recent fauna? Do we have fossils of the extinct higher taxa (tribes, families, orders)? There are no simple answers for these questions. The first question is an estimation of the lifespan for the species (ZHERIKHIN 1999). For example, mammals are among the fastest-radiating orders, being characterised by a lifespan in the Recent orders of some 40 Ma, and c. 2.5 Ma to 600,000 years for the species lifespan (ALROY 2000; VRBA & DEGUSTA 2004; VAN DAM et al. 2006), while insect orders could be over 300 Ma old, with species lifespans of c. 2 Ma (LABANDEIRA 1995; RASNITSYN & QUICKE 2002; GRIMALDI & ENGEL 2005). Then studying amber trapped insects means dealing with extinct species, but sometimes it is very difficult to differentiate the extinct species from the Recent ones. Generic placement is another question with a number of answers – in some groups, e.g. among some Diptera (Ceratopogonidae), we can trace genera back to the Early Cretaceous, while among some Hemiptera lineages (Fulgoromorpha and Cicadomorpha) the Recent genera are no older than Miocene (SZADZIEWSKI & SZWEDO 2007), but

Fig. 7: Stellate hairs. These inclusions are believed to be the indicator of spring and early summer intense exudation of the resin from the trees, which is, however, disputable. Coll. Museum of Amber Inclusions, University of Gdańsk.

Fig. 8: The co-occurrence of stellate hairs and leafhopper nymphs (Hemiptera: Cicadomorpha: Cicadellidae). The question if it is related to seasonal changes is still open, as unselected samples must be analysed. Collection of the Museum of the Earth, Polish Academy of Sciences, Warsaw, MZIE 20516.

we have Recent genera among the Eocene Baltic amber inclusions of another hemipteran lineage – aphids (HEIE & WEGIEREK 1998). There could be several reasons for such patterns, morphological disparity and, in consequence, definitions of the genera, their range and species content. It could be particularly tricky if the generic definitions are based on the characters not accessible or very difficult to access during amber inclusion studies. Thorough descriptions and up-to-date revisions based on morphological characters, and comparative morphological studies are the tools necessary for future amber inclusion studies. Another trap is the common assumption
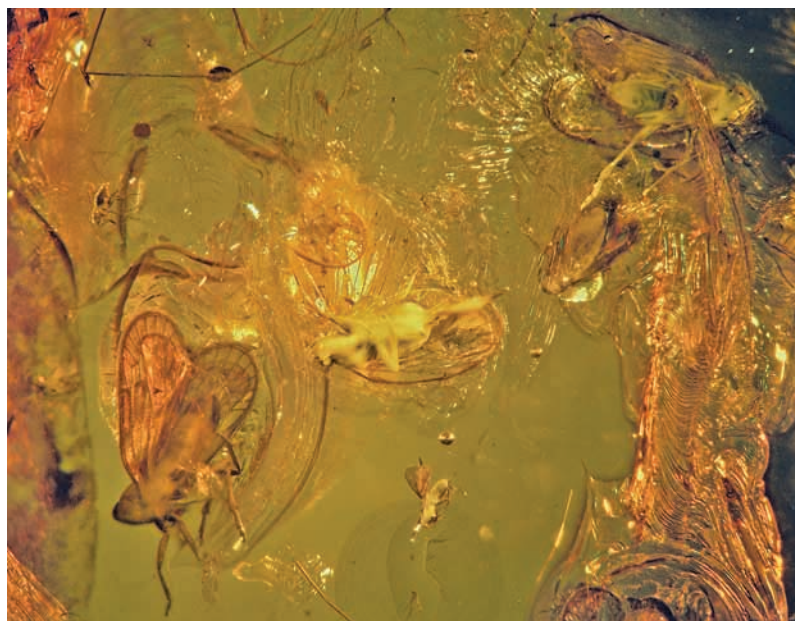
Fig. 9: The aggregation of these planthoppers (Hemiptera: Fulgoromorpha: Cixiidae) is very particular. This piece of amber contains 6 males and a single female, other syninclusions (Diptera, Coleoptera, Opiliones) also occur. The question if it is a proof of gregarious behaviour of the planthoppers remains unanswered. Coll. Hans-Werner and Christel HOFFEINS, No. 1171, Hamburg.
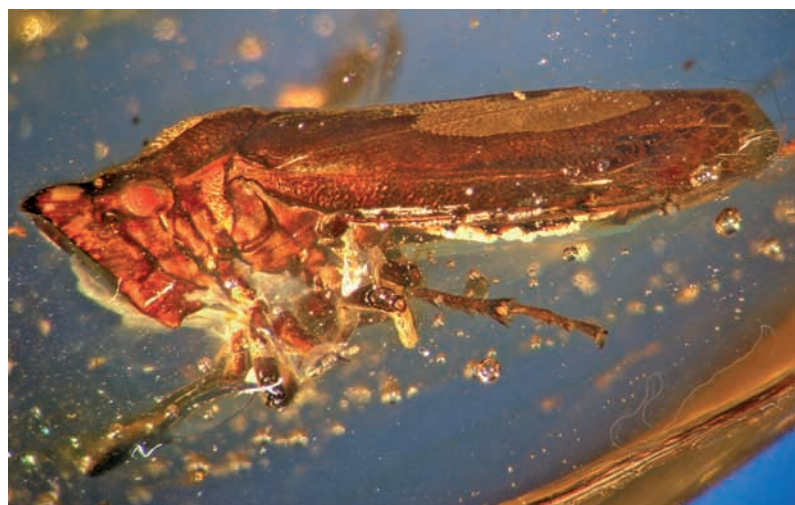

Fig. 10: Inclusion of leafhopper (Hemiptera: Cicadomorpha: Cicadellidae) in Colombian copal, coll. Jacek SERAFIN, Piaseczno. Such inclusions (after treatment) are sometimes offered as Baltic amber inclusions.

that fossils must present more "primitive", more "basal" sets of characters, which is definitely not true. It must be taken into consideration that the taxa we are now studying as a fossil had been living in a particular habitat, at a particular time, in particular conditions. Those specimens of organisms preserved in amber represent taxa well adapted to the conditions of their habitats and times, and have a set of adaptation features, sometimes more derived than found among Recent species. Specimens caught in amber and studied now as inclusions could represent the crown groups of particular evolutionary lineages, or blind branches of highly specialised lineages. We cannot exclude that very particular, exceptional taxa having no equivalents in the Recent faunas or exceptional specimens (mutated, parasitised or attacked by diseases, presenting teratological changes) were trapped in amber. Such findings make the interpretations more difficult, being unique and particular.

Similar questions arise when higher taxa are considered, i.e. tribes, families, etc. The case of Mantophasmatodea is one of the most striking. The first mention of these insects appears to have been by ARILLO et al. (1997), who provided the description of an enigmatic insect in Baltic amber, but did not name it. ARILLO et al. (1997) left the fossil unassigned as to its order, discussing its apparent affinities to Phasmatodea and other lineages. ZOMPRO (2001) later described, albeit inadequately, additional material that was clearly allied to ARILLO et al.'s (1997) species, assigning the taxon to the then new genus *Raptophasma*. Although ZOMPRO (2001) formally considered *Raptophasma* as Orthoptera incertae sedis, he noted that the acquisition of modern species similar to the fossil indicated the possibility of a distinct ordinal assignment and even provided a name for the group as Raptophasmatodea. More recently, a third species was established and placed in a new, putatively basal family (ZOMPRO 2005). Recently the Baltic amber Mantophasmatodea were reviewed (ARILLO & ENGEL 2006), followed by new data tracking them back to the Middle Jurassic (HUANG et al. 2008), new behavioural data (EBERHARD & PICKER 2008) and new molecular phylogeny interpretations (DAMGAARD et al. 2008).

Another trap possibly biasing the taxonomic interpretation occurs if the inclusion has been treated in autoclave. This procedure of amber treatment is used e.g. for removing the "milky veil" covering many inclusions in order to make the amber clearer and the inclusion better visible. During processing of the amber in an autoclave, the combination of temperature and pressure used has an effect not only on the resin itself but also on the inclusions inside the piece of amber. In many cases the inclusions are distorted or damaged after autoclave processing. Such specimen, an "autoclaved inclusion", could be a potential trap, in particular if it is designated as typespecimen. One cannot be sure if during autoclave processing the delicate external elements, e.g. palps or genital structures, were deformed, or if the hairs or setae were destroyed or removed. It could be that the chaetotaxy scheme found on treated inclusion is an effect of autoclave processing and not a species-characteristic feature. Moreover, the general measures and ratios of particular elements of body structures are often distorted during the autoclave processing, in which case measurements of such inclusions are unreliable (see also VON TSCHIRNHAUS & HOFFEINS 2009: p. 172).

The phylogeny trap

Combining data received from studies of amber inclusions with data on Recent representatives of the group could lead to another trap of interpretation. Some authors say that the fossil record is too fragmentary to be accurate (for discussion see e.g. NELSON & PLATNICK 1981; RIDLEY 1986; FOREY et al. 2002). Evaluation of the congruence between phylogeny and stratigraphy raised questions about the adequacy of the fossil record and the value of the temporal information in phylogenies. Several answers have been proposed, some of them summarised and discussed by LELIÈVRE et al. (2008).

Other problems and interpretation traps arise if cladistic methods are applied to fossils. Cladistics was developed originally as a method of analysis of the taxonomic pattern in a phylogenetic aspect (HENNIG 1966; SCOTT-RAM 1990; FOREY et al. 2002). In a few decades it has become the dominating methodology in phylogenetics as well as in taxonomy. Palaeontological data, the data coming from the discipline dealing with phenomena which can be discovered only in fossil record, were largely ignored in the basic concept of cladistics. In cladistic analyses fossils are usually taken as equivalent to the modern taxa or are omitted (ZHERIKHIN 1999). There are two important difficulties in using cladistic methodology for analysis of fossil data:

- the different time scales (a phylogenetic scale in cladistics, geological or physical scales in palaeontology where neither paraphyletic taxa nor chronotaxa can be excluded accurately);
- the different basic levels for establishment of terminal branches (the single present-day level in cladistics and numerous successive levels in palaeontology).

However, a modified version of cladistics, a modern approach to cladistics and complementary methods could be the tools to describe fossil diversity and disparity in an adequate manner. The original Hennigian cladistics, referred to as manual cladistics, is considered outdated and is uncommon in use (but see BECHLY 2000; KLUGE 2000). The current dominating version, computer cladistics, is essentially different. The methodological aspects of treatment of fossil data were discussed recently by RASNITSYN (2002a,b, 2006) and ZHERIKHIN et al. (2008).

Phylogeny is interpreted as a history of a particular group of organisms, with their history described in terms of both diminishing genealogical relationships between its subgroups and their changing similarity (RASNITSYN 2006). The relationships between fossil species and Recent representatives are usually not simple ancestor-descendant relationship, as often interpreted. We should consider any similarity between organisms as inherited from a common ancestor and not gained independently (as homoplasy), unless and until strong contrary evidence is presented (RASNITSYN 2002a). It could be presumed that the fossil species of a particular group living in the particular moment of the Eocene should present a similar range of morphological variability (disparity) as the Recent species. However, only a small portion of them were entrapped in amber, presenting a limited portion of the real disparity available for study.

If fossil data present a set of characters very close to that found in the Recent representative it could be a sign of close relationship, but not necessarily so. The observable features of the amber inclusion could be analogous not homologous (a homoplastic nature of these features cannot readily be excluded). In this case a good knowledge of, the detailed morphological comparative analyses of Recent taxa is necessary for the true interpretation of fossil data. The second case, when the fossil species present a mixture of characters found among Recent representatives of the genus, seems to be easier for interpretation. It could be proof of the presence of a common ancestor of the Recent and fossil species; yet again, the fossil species is not necessarily the ancestor (in most cases it is not). It must be taken into consideration that the fossils preserved in amber must have been adapted to the conditions in which they lived, therefore a mixture of ancestral plesiomorphic conditions and autapomorphic derived conditions is often present. HENNIG (1981: 20-21) claimed that the taxonomic position of a fossil has to be argued with constitutive characters (the autapomorphic characters of the taxon) while for living organisms we may use both isomorphic and plesiomorphic characters as the diagnostic features. This requirement seems to be too rigid, and hypotheses on the relationships between the taxa (classification) have to be argued on the basis of available evidence and falsifiable hypotheses (ZHERIKHIN 1999). The easiest situation for interpretation (but also bearing problems) seems to be the case of fossil species (taxon) uniting features of species (taxa) believed to be remotely related. Such "intermediate links" are of great value for phylogenetic reconstructions and evolutionary approaches (KRZEMIŃSKA et al. 1992). The fossils preserved in the Eocene amber were the crown taxa (in the sense of terminal taxa) for the period of their presence and fossilisation. It is possible that some of the extinct lineages from the Baltic amber fauna are the final Paleogene survivors of Mesozoic lineages. Therefore the treatment of them for phylogenetic analysis purposes should be done with special attention to avoid confusion. The analyses of extinction patterns, often criticised as based on paraphyletic taxa, are based in fact on taxa not paraphyletic at the time of their extinction (ZHERIKHIN 1999).

The biogeography trap

The geographical distribution of any taxon in any period of its history has been formed by two main factors: by the actual climatic gradients (equatorial-temperate, humid-arid etc.), and by the previous dispersal routes (sea barriers for the terrestrial groups, continents for the marine ones). The significance of each component in these two factors seems to be quite different for various groups (ESKOV 2002). The first serious study to discuss insect distributional patterns, based on Baltic amber inclusions, is a comprehensive but neglected paper of ANDER (1942). A general pattern of affinity between the Eocene fauna of Europe and the present day faunas of other parts of the world is documented for various groups (ANDER 1942; ZHERIKHIN 1970; LARSSON 1978; SZADZIEWSKI 1988; ENGEL 2001; SZWEDO 2002b, 2005; GRIMALDI & ENGEL 2005). For example, the famous Baltic amber lizard has affinities to groups in Africa and was even assigned, until recently, to the living African genus *Nucras* (BÖHME & WEITSCHAT 1998). Likewise, the Baltic amber scorpion *Palaeolychras balticus* LOURENÇO & WEITSCHAT has as its nearest relative a genus presently occurring in Africa and southern Asia (LOURENÇO & WEITSCHAT 1996). The living relatives of above-mentioned Mantophasmatodea are now restricted in distribution to South Africa (DAMGAARD et al. 2008).

Groups evolve in their distributional routes, so the distributional history of a group could correlate in a way with its genealogy, so phylogenetics may benefit from biogeography. There are problems, however. The classic, dispersalist biogeography considers distribution of a group as a result of its individual dispersal through various barriers. The major factors of the distribution are thus supposed to be (1) the geographic structure of the space, (2) the dispersal potential of the group, (3) chance. In contrast, the cladistic concept of biogeography (summarised by HUMPHRIES & PARENTI 1986) considers the distribution of plants and animals as a result, both phylogenetic and geographical, of barriers imposed by various physical agents (primarily connected with continental drift, but also of climatic nature, etc.) on a continuous ancestral distribution. The dispersalist biogeography (mobilistic biogeography) attempts to fit the cladogram of the taxon to the sequence drawn by geophysics for dispersal of plate fragments. This approach seems now to be a basic paradigm of historical biogeography. However, it ignores the opposite side of the coin, because just as geological and climatic change can sometimes cause barriers to form, at other times, they may cause barriers to fall, allowing many taxa to simultaneously expand their range (LIEBERMAN 2005). The "ousted relicts" hypothesis implies the discoveries of fossil representatives of the taxon well outside of its present range and regarding transoceanic disjunctions as result of extinction of a taxon over the main part of its initially pan-continental range. Recent advances in biogeographical theory suggest that the current focus on vicariance versus dispersal is too narrow because it ignores "geodispersal" (i.e. expansion of species into areas when geographical barriers disappear), extinction and sampling errors. Geodispersal produces multiple, conflicting vicariance patterns, and extinction and sampling errors destroy vicariance patterns (UPCHURCH 2007).

An important question concerns parsimony. OCCAM's razor is one of the basic scientific principles; but, like any principle, it has to be used correctly. It seems that the parsimony principle in biogeographic interpretations is inappropriate because of an inadmissibly high probability of misinterpretation, perhaps about 50% or more, as a result of numerous local extinction events (RASNITSYN 2006). Even in the course of the last 100,000 years the distribution of many taxa changed quite radically more than once, in Eurasia practically from the Pacific to the Atlantic and back (COOPE 1994). There are data about rapid Asia-Europe-North America geographic dispersal of small primates during the Paleocene-Eocene Thermal Maximum (SMITH et al. 2006; BEARD 2008). For instance, the famous "southern" or "Gondwanan" distribution pattern is very often only the pattern of survival of the groups which are only relics of a broader, probably global distribution in the Mesozoic and Paleogene. Attempts to consider their places of origin as being the same as their present-day distribution seem to be inadequate and may not manifest the past restriction of a taxon to the Gondwanaland (ESKOV 1984, 1987, 1992, 2002; ESKOV & GOLOVATCH 1986).

The (palaeo)habitat and (palaeo)ecology traps

Finally, the question of the origin of Baltic amber remains unanswered to date. Various trees are believed to be the source of the resin transformed into amber. PLINY THE ELDER (PLINIUS SECUNDUS) related it to pines, cedars and poplars (PLINIUS SECUNDUS, Liber 37); HACZEWSKI (1838) named the source *Abies bituminosa*; it was formally described under the name *Pinites succinifer* GÖPPERT, 1836 and later *Pinus succinifera* (GÖPPERT, 1836) CONWENTZ, 1890; MENGE (1858) named it *Taxoxylum electrochyton*. Other trees supposed to be sources of amber producing resin were species of the genus *Agathis* SALISBURY, *Cedrus atlantica* LINNÉ (sic!; KATINAS 1987), and *Pseudolarix* GORDON (ANDERSON & LEPAGE 1995; GRIMALDI 1996; KOSMOWSKA-CERANOWICZ 2001), all species belonging to gymnosperm conifers.

Modern methods for the analysis of amber raised some annoying questions. Infrared spectra – a successful technique in comparing fossil and Recent resins (IR spectroscopy) – of Baltic amber are not similar to those of any modern Pinaceae, but more similar to resin of the Araucariaceae tree *Agathis australis* (LAMBERT) STEUDEL that grows in New Zealand. Further analyses using pyrolysis mass spectroscopy have supported the results from IR spectroscopy (POINAR & HAVERKAMP 1985). Additionally, the IR studies demonstrated some heterogeneity, which raises the questions of whether a single tree species was the amber-producing tree (POINAR 1992). Baltic amber lacks abietic acid, which chemically distinguishes pine resin; and araucarian resin does not have the succinic acid, which is distinctive of most Baltic amber. On the other hand, Recent pine species, the North American sugar pine *Pinus lambertiana* DOUGLAS, is marked by a characteristic IR spectrum, with the "Baltic amber shoulder" typical of Baltic amber. Some living trees in the family Pinaceae of the genera *Keteleeria* CARRIÈRE and *Pseudolarix* GORDON do indeed produce resin rich in succinic acid (GRIMALDI 1996). The genus *Pseudolarix* is of particular interest, since resin in 40 Ma old cones of *Pseudolarix wehri* GOOCH from Axel Heiberg Island in the Canadian Arctic also contains succinic acid (ANDERSON & LEPAGE 1995). The amber was found on primary deposit (a primary deposit indicates the amber occurrence is still at the original location or at the place of formation), together with organic remnants of the tree. Palaeobotanical, physical and chemical analyses, including IR spectra, were done and the geographic position of this amber corresponds more to the position of Fennoscandia in the Palaeogene (J.A. WOLFE 1985) than to the distribution of *Agathis* forests. *Pseudolarix* trees are to be found today in Asia. The sole species, *Pseudolarix amabilis* NELSON (REHDER), is strictly restricted to some mountains in south-eastern China. This may suggest that *Pseudolarix* might have been connected with the North, with the Scandinavian Peninsula during the Eocene, being one of the components of the "amber forest". The *Pseudolarix* hypothesis is also bolstered by the fact that many other plants and insect species fossilised in the Baltic amber are closely related to the Recent forms living in Asia, Australia and even Chile (GRIMALDI 1996). Another tree – *Sciadopitys* SIEBOLD & ZUCCARINI is postulated as related to the amber producing tree (A.P. WOLFE 2007), presenting a solid-state Fourier-transform infrared spectroscopy (FTIR) spectrum very similar to these of the Baltic amber. The tree was placed in its own family by STEFANOVIAC et al. (1998), related to Cupressaceae. Araucariaceae and Podocarpaceae are related, while Pinaceae is a sister group to other Coniferales (STEFANOVIAC et al. 1998), an interpretation supported by others (CHAW et al. 1997; MILLER 1999; GUGERLI et al. 2001). The Pinaceae appeared in the Cretaceous although certain pine-like ancestral plants have been recorded from the Middle Jurassic; now the family is restricted to the northern hemisphere, with a sole exception. The Araucariaceae date back to the Mesozoic, when the family was abundant both in northern and southern hemispheres. There are few araucarian fossils in the northern hemisphere, and apparently not in the Baltic amber.

Thus, the currently accepted view is that several extinct Pinaceae species have contributed to the formation of the Baltic amber. Neither examination using infra-red spectral examination nor other chemical and physical analyses could solve the difficulties in the diagnoses and descriptions of these species (CZECZOTT 1961; ZALEWSKA 1974; LARSSON 1978; POINAR 1992; GRIMALDI 1996; LANGENHEIM 2003). The amber producing tree(s) could be considered a rather primitive type, an early stage of developmental history of the Pinaceae, which still retained archaic characteristics in common with the Araucariaceae (LARSSON 1978; MILLS et al. 1984; BECK 1999).

There are numerous traces of plants found in the Eocene Baltic amber, small fragments of plant tissue and plant organs, which – fresh or already decomposing – fell into the aromatic resin flowing out profusely from the amber-bearing trees. Attempts to identify such specimens usually prove unsuccessful. Very rarely found inclusions of whole small plant organisms, such as liverworts and mosses, are the most rewarding for researchers of amber flora. Such plant parts as flowers, fruit, seeds, needles, leaves, branches and resin-permeated wood can also be identified down to their genus or species. Pollen and spores, just as micro-organisms in amber, have yet to garner serious attention in the studies. The most numerous angiosperm remains are the stellate hairs torn off young leaves or leaf buds of oak which are ubiquitous in Baltic amber. Morphological research has allowed palaeobotanists to identify over 200 species of spore-bearing, herbaceous and arborescent plants from the amber-bearing forest. These include plants from diverse habitats: mountain, lowland and swamp plants. This diversity indicates, among other things, the diverse area of the amber-bearing forests. Furthermore, the co-existence of temperate climate species alongside subtropical and tropical elements has been found. Contemporary plant species, which are comparable to the fossil plants found in Baltic amber, occur in Africa, America, South Eastern Asia, China, Indonesia, Japan and Oceania (KOHLMAN-ADAMSKA 2001; PIELIŃSKA 2008a, b).

In 1997, palaeobotanist Aleksandra KOHLMAN-ADAMSKA distinguished three main amber-bearing for-

est communities (KOHLMAN-ADAMSKA 2001). Coniferous forests in the higher mountains were composed of sequoias *Sequoia* ENDLICHER, umbrella pines *Sciadopitys verticillata* (THUNBERG) SIEBOLD & ZUCCARINI, firs *Abies* MILLER, spruces *Picea* A. DIETRICH, larches *Larix* MILLER, and numerous representatives of the cypress family (Cupressaceae): the Californian incense-cedar *Calocedrus decurrens* TORREY (FLORIN), *Thujopsis* SIEBOLD & ZUCCARINI ex ENDLICHER, *Chamaecyparis* SPACH, and the *Thuja* LINNÉ. In the lightly forested steppes, which covered lower parts of mountains, there were mainly species of pines *Pinus* LINNÉ, palms, and numerous species of oaks *Quercus* LINNÉ, both evergreen and with falling leaves; other trees grew there as well: beeches *Fagus* LINNÉ, chestnuts *Castanea* MILLER, maples *Acer* LINNÉ, cycads from the genus *Zamia* LINNÉ; shrubs, such as the magnolia, holly and some laurel family (Lauraceae) plants; grasses dominated the undergrowth. Swamp forests grew in the damp river valleys, and in them grew the exotic Chinese swamp cypress *Glyptostrobus pensilis* (STAUNTON ex D. DON) K. KOCH, shrubs from the Salicaceae, Myricaceae and Clethraceae families, as well as herbaceous plants from the family Commelinaceae.

The most famous "trap" in interpretation of the data obtained from the analyses of the Eocene Baltic amber inclusions is known as WHEELER's dilemma, which was reviewed by ARCHIBALD & FARRELL (2003). They concluded that the mixture of thermophilic and temperate ants seen in Baltic amber is most likely a direct consequence of more equable temperature seasonality: expectable, not anomalous. This theory could be adapted also to other groups of insects. The presence of fossil organisms with closely related modern representatives that have clear tropical affinities in the high latitudes may be a consequence of raised Cold Month Mean in cool climates (increased equability), not necessarily an indicator of raised Mean Annual Temperature (subtropical or tropical climates). In light of this, ascribing tropical or subtropical climates to early Paleogene sites by the presence of thermophilic organisms should take such considerations into account. The comparison revealed an immense diversity of the floral elements recorded in the "amber forest". The plants were recorded from various habitats, montane and lowland, as well as wetlands, all of very different climatic requirements, from temperate through warm and subtropical climates. This diversity results not only from the varied topography of the area where the forests grew, but mainly from the fact that in the Eocene the area was located on the border of two climatic zones: temperate and subtropical also called "paratropical" (J.A. WOLFE 1985; MEYEN 1987; COLLINSON & HOOKER 2003; AKHMETIEV 2004). Two geofloras intermingled in the area: an Arcto-Tertiary geoflora associated with a circumboreal, temperate

climatic zone, with the prevalence of deciduous trees; and a Palaeotropical geoflora, evergreen with numerous palms, migrating from southern into northern areas during warmer climatic phases (J.A. WOLFE 1985). Baltic amber could have originated anywhere in an enormous region from the eastern edge of the Eocene ocean on the west to the Turgai Strait (the Recent Ural Mts) on the east (WEITSCHAT & WICHARD 1998, 2002; COLLINSON & HOOKER 2003; AKHMETIEV 2004; ERICHSON & WEITSCHAT 2008). These botanical changes influenced also insects and other organisms inhabiting the "amber forests", therefore they could be one of the factors influencing the composition of faunal elements entombed in amber.

Analyses of the faunistic and taxonomic composition of the "Baltic amber forest" could lead to another interpretation trap. Studies on inclusions are usually based on material from museum or private collections, and this has previously undergone multiple selections by amber workers, collectors and museum curators resulting in collections of highly selected and compiled specimens (SONTAG 2003). There are several reports comparing unselected samples of Baltic amber and other ambers of similar age (HOFFEINS & HOFFEINS 2004; ZHERIKHIN & ESKOV 2006; PERKOVSKY et al. 2007). The "systematic deviations" which might have artificially affected the collections (museum collections in particular) could be one of the sources of errors. The expertise of collectors and their working conditions in general, including the quality of instruments used, could be other sources of mistakes. However, most probably the differences in the taxonomic composition of various samples could reflect the real heterogeneity of amber samples as well.

Additional sources of uncertainty could include the highly seasonal occurrence of some groups or biotopic aggregated distributions of others (ZHERIKHIN & ESKOV 2006; PERKOVSKY et al. 2007). The new challenges facing amber researchers are syninclusions and co-occurrence of organisms entrapped in amber and their palaeoethology (SONTAG 2003; ARILLO 2007). The term "syninclusion" was added to the scientific vocabulary and literature in 1986 (KOTEJA 1986, 1989). The problem of co-occurrence has been known for 150 years while the relations of co-occurring inclusions are still weakly known (SONTAG 2003). For example, LARSSON (1978) postulated that stellate hairs (the most common plant inclusions; the hairs covering buds flowers and leaves of the *Quercus* spp. and related plants) are indicators of spring and early summer exudation of resin. The insects and other organisms were caught at different vegetational seasons; however, trees usually exude more resin during spring and summer than in autumn

and winter. For this reason the majority of insects in the Paleogene ambers are believed to be spring and summer taxa (Martínez-Delclós et al. 2004). This opinion was used to support Borkent & Groogan's (1995) hypothesis. They stated that the co-occurrence of stellate hairs and Ceratopogonidae flies of the genus *Ceratopogon* Meigen, 1803 in amber is proof for the spring activity of these flies, as well as the reason for the dominating role of *Ceratopogon* among Ceratopogonidae. However, after the detailed analysis of inclusions and syninclusions in unselected samples of the Baltic amber this hypothesis must be rejected. Thus, the competitive hypothesis, proposed by Szadziewski (1988) and rejected by Borkent & Grogan (1995), stated that the dominance of the genus *Ceratopogon* among Ceratopogonidae inclusions in the Eocene Baltic amber is a result of their numerous presence in the area and time. Arillo (2007) discussed palaeobehaviours preserved in amber in three sections: 1) intraspecific relations, 2) interspecific relations and 3) interactions with fresh resin. Still unanswered is the question of whether two organisms embedded in the same resin flow lived and died at the same time, the same day, and lived in the same habitat thus belonging to the same palaeoecosystem, or were only contemporaneous and ended up together by accident so that the association between them is not real.

Last but not least – the forgeries

One particular danger with insects enclosed in fossil resins, particularly amber fossils, is the existence of numerous forgeries. Grimaldi et al. (1994) described the main kinds and diagnostics of amber forgeries. Most extant insect species recorded from Baltic amber were shown to be either fakes (Palmer 1993) or misidentified (Röschmann 1998). Another problem to be considered is the origin of the amber piece. It is particularly important in case of the holotypes. Receiving the piece of amber from the collector or museum, in many cases we are not sure about the origin of the material. It could be other than Baltic amber fossil resin, or copal. This case is quite common in the old, historical collections. The modern methods of thermal modification, commonly used for the jewellery making purposes, allow to produce forgeries that can be recognised only by Infrared Spectroscopy (IRS). Therefore, especially in the case of an unusual inclusion when an assignment to a certain amber source is difficult, simply trusting the museum label may not be sufficient.

Conclusions

Studying amber and its inclusions means facing particular problems, interpretation traps, and doubts. Forgeries, the identification of amber and its physical and chemical features, estimations of the age of Baltic amber and its origin, as well as taxonomic, phylogenetic, biogeographic or ecological questions concerning the inclusions are to be taken into consideration. Anyway, it means that studies of amber and its inclusions are fascinating, and that all difficulties encountered only make it more interesting and a bigger challenge.

Zusammenfassung

Der Baltische Bernstein hält, nicht nur für die im eozänen Bernsteinwald lebenden Organismen, sondern auch für die heutigen Bernsteinforscher, zahlreiche Fallen bereit. Obwohl der Bernstein und seine Inklusen die Möglichkeit bieten, einen einzigartigen Blick in die Vergangenheit zu werfen, muss bei der Interpretation der Daten beachtet werden, dass auf verschiedenen Ebenen Probleme auftauchen. In dieser Arbeit werden die folgenden Bernsteinfallen diskutiert: Bernstein-Fälschungen sowie die Identifikation von Bernstein und seiner chemischen und physikalischen Besonderheiten, wie auch Fragen nach dem Alter und der Herkunft des Baltischen Bernsteins, und solcher, die bei taxonomischen, phylogenetischen, biogeographischen und ökologischen Analysen und Rekonstruktionen der Inklusen stellen können.

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