Amber and amber inclusions of planthoppers, leafhoppers and their relatives (Hemiptera, Archaeorrhyncha et Clypaeorrhyncha)

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Abstract

Amber, its origin, deposits and stratigraphic position in the World is presented. The process of amberization and fossilization of an insect in resin is briefly outlined. Data about inclusions of planthoppers, froghoppers, treehoppers and leafhoppers (Hemiptera: Archaeorrhyncha et Clypaeorrhyncha) are given. The fossil record of the relevant families is presented. Families and species described from fossil resins up to the present are listed and some of them additionally commented.

Key words: amber, amber deposits, inclusions, fossils, Fulgoromorpha, Cicadomorpha.

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Introduction

What is amber?

> *"... When the warm kingdom of the amber pine and its seas set, cooled and froze beneath a thick glacial mass, only amber itself survived; the living sap of a dead tree"*
>
> Stefan ŻEROMSKI The Sea Breeze (1922)

Amber is fossilized tree-derived resin that is found in the geological record from the Devonian through the present day (GRIMALDI 1996, KRUMBIEGEL & KRUMBIEGEL 1996a, POINAR 1992). Frequently, resins found in geologically old strata are named amber, while more recent and semi-fossilized resins are not considered proper amber and are known under the name of copal. On the other hand, some authors regard copals as resin of angiosperm plants of the families: Mimosaceae, Caesalpiniaceae, Fabaceae (Fabales) and Dipterocarpaceae (Theales = Hypericales), and amber as fossilized resin of gymnosperm trees of the families Pinaceae and Araucariaceae. Radical "purists" understand amber as referring specifically to the resins of the Baltic amber group, i.e. Baltic amber – also called succinite, Bitterfeld amber (named also Saxonian amber), Danish amber, amber of Oise in France, and Ukrainian amber. Others use copal only of the resin of Caesalpiniaceae, of *Hymenaea* trees, i.e. Mexican amber, Dominican amber and East African copal, copal from Madagascar and Colombian copal (GEINAERT 1998).

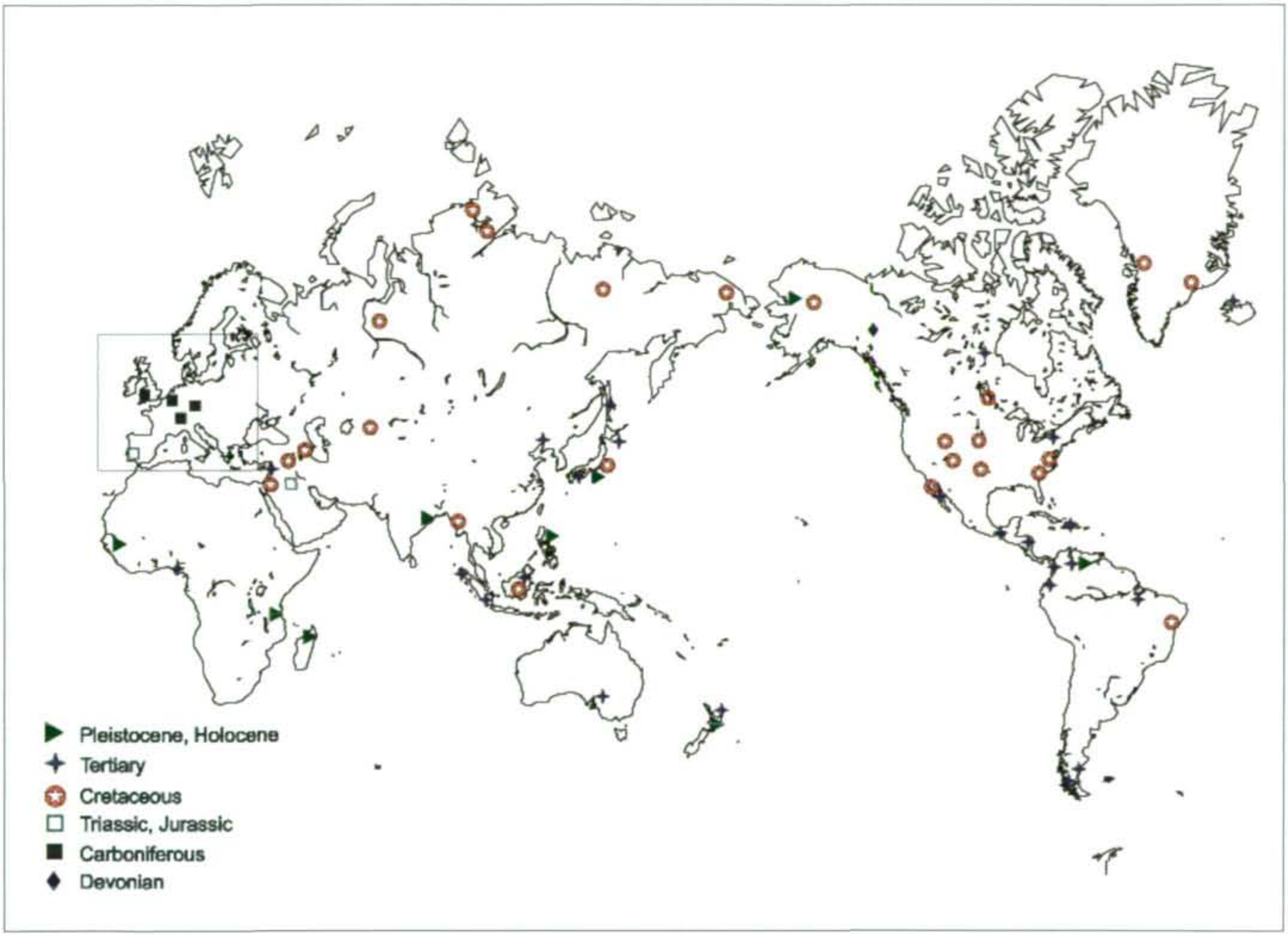
Fossil resins (ambers and copals) are to be found throughout the world (GRIMALDI 1996; KRUMBIEGEL & KRUMBIEGEL 1996a; POINAR 1992, 1999; ROSS 1999; Figs 1 & 2). The total number of amber sites is around 200 (DAHLSTRÖM & BROST 1996).

Mesozoic amber is to be found in various parts of the world (Figs 1 & 2). The oldest inclusions in amber (bacteria, protozoa, fungal spores and unidentified plant spores) are known from the Triassic amber of Raibler Sandstone Formation in Schliersee, Bavaria, Germany (DAHLSTRÖM & BROST 1995; GRIMALDI 1996). The oldest amber deposits containing insects come from the Middle East and are commonly known as Lebanese amber (SCHLEE 1970; ZHERIKHIN 1978), although similar amber occurs in Israel and Jordan (NISSENBAUM & HOROWITZ 1992). They are dated on the Neocomian, Early Cretaceous, which means that they are 130 million years old. The Cretaceous (140 Ma to 65 Ma) is one of the most interesting chapters in the history of the Earth. It was in the Cretaceous that an explosive radiation of flowering plants, angiosperms, occurred, together with many modern families of insects. Several kinds of amber, frequently including a variety of "amberized" insects, are known from the Cretaceous: Lower Cretaceous amber from Alava (Basque Country, Spain), Lower Cretaceous amber found near Vienna and Salzburg, and Lower Cretaceous amber found in Chōshi (Hōnshu, Japan). Many localities of Upper Cretaceous amber are known from North America (DAHLSTRÖM & BROST 1996; GRIMALDI 1996, RICE 1987). These are Cedar Lake, Manitoba, and Medicine Hat and Grassy Lake, Alberta in Canada. Amber — '*omalik*' as called by Inuits — is also found in Alaska Peninsula, in the Yukon delta and on the Fox Islands (part of the Aleutian Archipelago), and in Greenland (KOSMOWSKA-CERANOWICZ 1983; DAHLSTRÖM & BROST 1996). The most famous is New Jersey amber, containing many insect inclusions. Other amber sites in the United States are located in New Mexico, Tennessee, Mississippi, Arizona, Nebraska and North Carolina, along the Atlantic coast in Maryland, on Cape Cod, Long Island and Staten Island. Another famous Cretaceous resin is the amber from Taimyr Peninsula in northern Russia (Fig. 1), of Lower Cretaceous Begichev Formation and Upper Cretaceous Kheta, Khatanga and Dolgan Formations (ZHERIKHIN & SUKACHEVA 1973, ZHERIKHIN 1978, ZHERIKHIN & ESKOV 1999). Upper Cretaceous amber of Asia is amber of Adzhakent in Azerbeijan, Shawarshawan in Armenia, Timmerdiak-Kaja on the Viliuj River in Yakutia (ZHERIKHIN 1978), and Kuji and Iwaki on Hōnshu, Japan (SCHLEE 1990). A very interesting Asian amber is Burmese amber, which is estimated by different authors to be of Miocene, Oligocene, Paleogene, post-Eocene, Eocene, or even Late Cretaceous age (ZHERIKHIN 1978, BOTOSANEANU 1981). The last estimation seems to be correct according to the latest data (ZHERIKHIN & ROSS 2000). Late Cretaceous amber of the Paris and Aquitan Basin in northwestern France, very interesting and rich in inclusions, was reported by SCHLÜTER (1978). Cretaceous amber originated from the resins of the gymnosperm plants of the families Araucariaceae, Taxodiaceae, Cupressaceae and Pinaceae, and angiosperm plants of the family Hamamelidaceae (GRIMALDI 1996).

Most of the known deposits of Tertiary amber are known from Europe (KRZEMIŃSKA et al. 1993; POINAR 1999). The most famous Eocene amber from the Baltic area (Fig. 2) probably represents one of the largest accumulations of amber in the world. It comes from the Tertiary deposits in the Sambian Peninsula and from accumulations in Quaternary deposits. The amber in Sambia is located in layers of the '*blaue Erde*' — the "blue earth"; blue earth is actually grayish 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 Tertiary deposits was transported by glacial, fluvial or fluvoglacial action. This resulted in distribution of the Eocene Baltic amber across Latvia, Lithuania, Belorussia, Poland and Germany, up to the east coast of the British Isles and even as far as Jutland (Denmark) and the southern coast of Scandinavian Peninsula (DAHLSTRÖM & BROST 1996, KOSMOWSKA-CERANOWICZ 1998).

The tree that produced resin which became Baltic amber is the still mysterious "*Pinus succinifera*" (POINAR 1992, GRIMALDI 1996, ROSS 1999) — probably a collective name for resin (amber) producing tree (or trees). Modern methods of analysis of amber have raised some annoying questions. It is surprising, that the infrared spectra (infrared spectroscopy is a successful technique in comparing fossil and recent resins) of Baltic amber are not similar to those of any modern Pinaceae, but more similar to resin of the Araucariaceae tree *Agathis australis* (LAMB.) STEUD. that grows in New Zealand. Further analyses using pyrolysis mass spectrometry have supported the results from IR spectroscopy (POINAR & HAVERKAMP 1985). Additionally, the IR studies demonstrated some heterogeneity, which raises the question 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-western American sugar pine *Pinus lambertiana* DOUGLAS, is marked by a characteristic IR spectrum, with "Baltic amber shoulder" typical of Baltic amber. Some living trees in the pine tree family of the genera *Keteleeria* CARRIÈRE and *Pseudolarix* GORDON do indeed produce resin rich in succinic acid (GRIMALDI 1996). *Pseudolarix* is of particular interest, since resin in 40 Ma old cones from Axel Heiburg Island in Canadian Arctic also contains succinic acid. *Pseudolarix* today is found in Asia. The sole species, *Pseudolarix amabilis* NELSON (REHDER), is closely restricted to some mountains in south-eastern China. This may suggest that *Pseudolarix* might have been connected with the North, with Scandinavia during the Eocene. The *Pseudolarix* hypothesis is also bolstered by the fact that many other plants and insect species fossilized in Baltic amber are closely related to species now living in Asia, Australia and even Chile (GRIMALDI 1996). The "amber tree" could then 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 (LARSON 1978; MILLS, WHITE & GOUGH 1984; BECK 1999). The Pinaceae appeared in the Cretaceous, although certain pine-like ancestral plants have been recorded from the Mid Jurassic; recently 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 none in Baltic amber.

Another famous Tertiary fossil resin is Dominican amber (Fig. 1), which originated from leguminous (Caesalpiniaceae, Fabales) algarrobo trees, although the only one described is *Hymenaea protera* POINAR (POINAR 1991, 1992; CARIDAD 1999, POINAR and POINAR 1999). Dominican amber is aged Oligocene to Lower Miocene, some deposits are regarded as originating from the Middle Eocene (POINAR 1992; KRUMBIEGEL & KRUMBIEGEL 1996a; CARIDAD 1999; POINAR & POINAR 1999). According to ITURRALDE-VINENT & MACPHEE (1996) the amberiferous deposits in the Dominican Republic were formed during the late Early Miocene through the early Middle Miocene. However, mines are scattered throughout portions of the northern mountain range Cordillera Septentrional as well as in the eastern part of the Dominican Republic. Deposits from these diverse localities may have originated from different time periods. Dating attempted by chemical analyses of the amber (LAMBERT, FRYE & POINAR 1985), as well as by an examination of marine microfossils that occur in the bedrock, suggests 15-20 Ma when based on Foraminifera fossils (ITURRALDE-VINENT & MACPHEE 1996). The age of the oldest, based on Coccolithophora fossils, is estimated at 30-45 Ma (SCHLEE 1990). Amber usually occurs in the form of discrete nodules or lumps ranging in size from a few millimeters to masses as large as 20 kilograms.



Figs 1:
Distribution of fossil resins worldwide

Mexican amber, also named "amber of Chiapas", is fossil resin of the same age and origin as Dominican amber, from the *Hymenaea* trees (Caesalpiniaceae). Chiapas amber occurs in primarily marine calcareous sandstone and slit with beds of lignite, in association with the Balumtun Sandstone of the Early Miocene and the La Quinta formation of the Late Oligocene. Radiometric assignation ages the amber bearing strata from 22.5 to 26 Ma (POINAR 1992). It can be found in the lignitic beds or some distance from them. The amber is mined from the lignite or collected from the alluvial deposits (GRIMALDI 1996; RICE 1987).

In recent years a large amount of Miocene fossil resin was found in Merit-Pila Coal Field, Sarawak, Borneo, Malaysia (HILLMER, WEITSCHAT & VĀVRA 1992). This "Bornean amber" is supposed to have deposits far greater than those of Sambia Peninsula (KOSMOWSKA-CERANOWICZ 1998), and rich in inclusions (HILLMER, VOIGT & WEITSCHAT 1992).

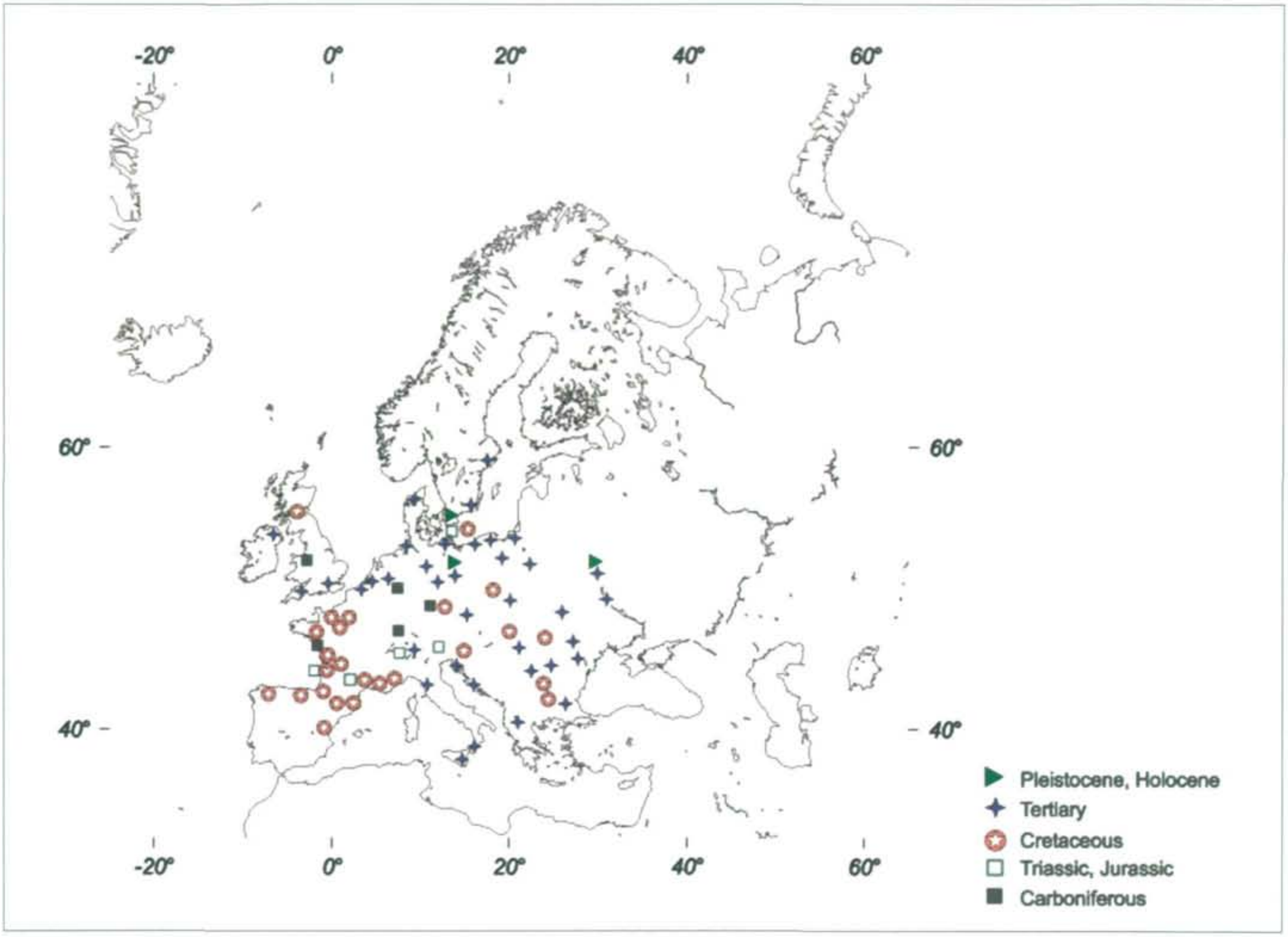


Fig. 2:
Distribution of fossil resins in Europe

Numerous localities of different Tertiary deposits of fossil resins are reported, e.g. Paleocene Sakhalin amber from Russian Far East, Mid Eocene Fu Shun amber from China (ZHERIKHIN 1978, ZHERIKHIN & ESKOV 1999), Eocene Ukrainian amber, Bitterfeld amber from Germany — once believed to be of Miocene age, but recently regarded as Eocene (WEITSCHAT 1997), Danish amber from Jutland, amber of Oise in France, rumanite from Romania and Sicilian amber (simetite) from Sicily, the northernmost in the world localities from Early Eocene of Ellesmere Island and Axel Heberg Island in the northern Arctic Ocean, amber from the Eocene Claiborn Formation in Arkansas, Mid-Eocene amber from Tiger Mountain Formation near Seattle, Washington, Oligocene amber from Chile or amber from Nigeria, from the Ameki Formation of the Eocene (SCHLEE & GLOCKNER 1978; ZHERIKHIN 1978; GRIMALDI 1996; KRUMBIEGEL & KRUMBIEGEL 1996a). All these originate from the resin of various gymnosperm plants of the families Cupressaceae and Pinaceae, as well as of angiosperms: Burseraceae, Dipterocarpaceae and Hamamelidaceae (GRIMALDI 1996, RICE 1987).

The Quaternary fossil and semi-fossil resins also are reported from different parts of the world: Guinea, East Africa, Madagascar, Israel, the Philippines, Japan, Australia, New Zealand and Colombia (SCHLUTER & VON GNIELINSKI 1978; POINAR 1992; KRUMBIEGEL & KRUMBIEGEL 1996a); their origin is also varied (Araucariaceae, Anacardiaceae, Caesalpiniaceae).

The amber trap and inclusions

The Spider, Flye, and Ant, being tender, dissipable substances, falling into Amber are therein buryed, finding therein both a Death and Tombe, preserving them better from Corruption than a Royall Monument

Francis BACON Histoire of Life and Death (1638)

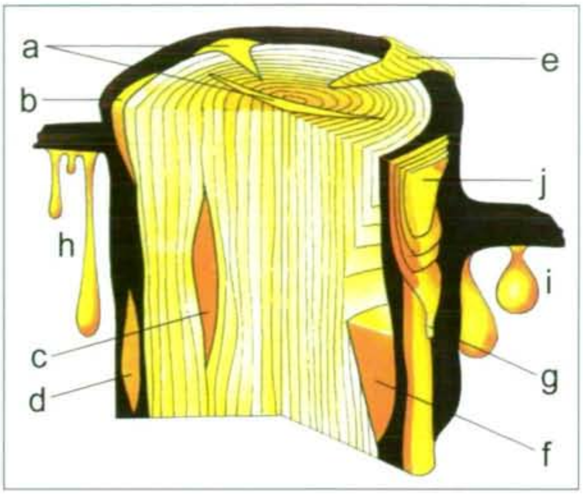
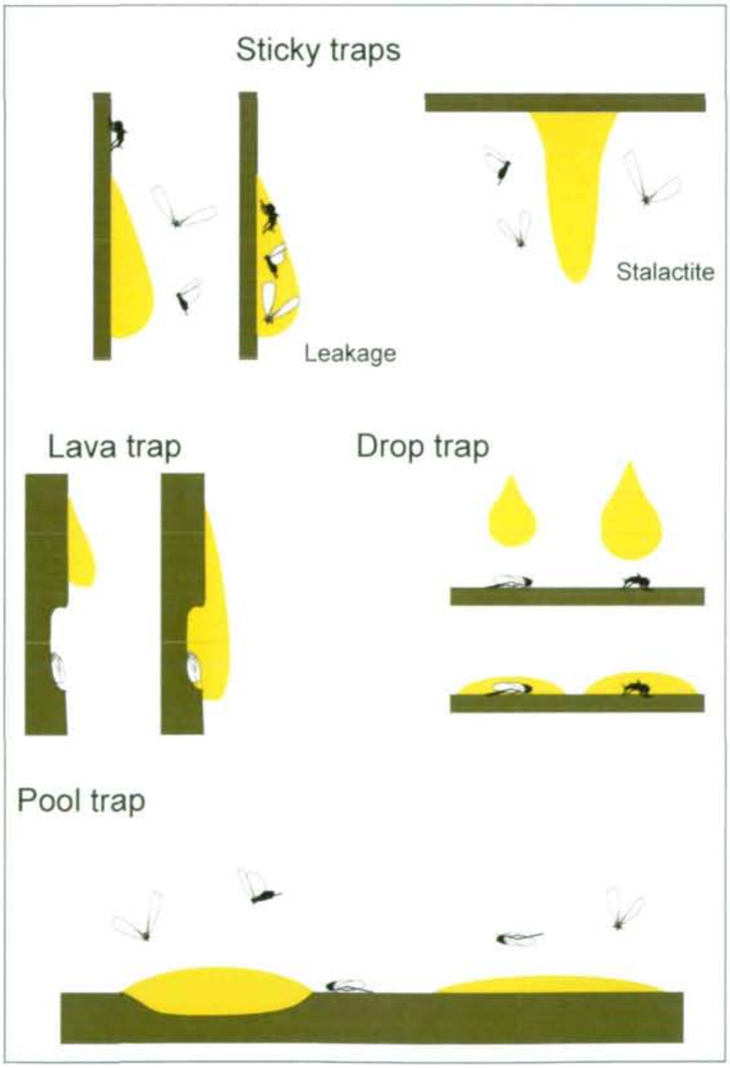


Fig. 3: Places of exudation and accumulation of resin leakage (after Ganzelewski 1996). (a) fill of cracks; (b) under bark; (c) "resin pockets"; (d) fill of cracks in the bark; (e) fill of wounds; (g) fill of emptiness with flat surface (sometimes annual rings are visible); (h) icicle-like and stalactite-like forms; (i) drops and tumescences; (j) stalactites; (k) "baggy" leakage.



Figs 4-7: Kinds of "amber-traps": (4) sticky trap — different types of leakages, icicles and stalactictes; (5) lava trap; (6) drop trap; (7) pool trap.

Amberization – changes involved in the process of forming amber from fresh resin – is a slow, gradual process which leads to the preservation of small, delicate, and soft-bodied insects into inclusion in hardened resin. It is the most complete type of fossilization known for insects. Fossils thus preserved can be easily compared with their extant descendants thanks to the three-dimensional form, colour pattern, and minute details of the exoskeleton (POINAR 1993). Resin originated in different parts of the tree-trunk (KATINAS 1971; KRZEMIŃSKA et al. 1993), so insects living on different parts of trees could be entrapped in resin (Fig. 3). Production of resin differed also according to the season, and time of the day (KRZEMIŃSKA et al. 1993).

The mode of preservation – taphonomy – of amber insects has been discussed many times (BRUES 1933; HENWOOD 1992; PIKE 1993). There were many factors that pre-conditioned the preservation of an organism in resin, so resin was a rather selective trap. The size of an entrapped insect determines its biotic loss: decay and scavenging. Insects living on or near the amber-producing tree had higher fossilization potential than those living far from the forest. Behavior is another important factor affecting the inclusions. Flying insects, insects living on the bark or hiding in the cracks and crannies of the tree bark could be entrapped more easily. Enticing or deterring smell of resin, the colour and glaze of resin are also responsible for the bias of amber trap (KRZEMIŃSKA et al. 1993, KRUMBIEGEL & KRUMBIEGEL 1996b). The "amber trap" in fact comprises four different types of traps (Figs 4-7): sticky trap, lava trap, drop trap and pool trap. Sticky traps – the stalactite-like and icicle-like leakages, rods and "baggy" leakages – entrapped active flyers and passive flyers, as well as forms wandering on the tree-trunk. Lava traps entombed non-moving or slow moving organisms. Drop traps also preserved forms living on branches, leaves, and on the ground, or even in water. Particles of detritus or litter can frequently be found among such inclusions. Pool traps encased dead insects, active and passive flyers, wandering on the ground or in the litter, in some cases also living under the bark or in the wood of "amber tree". In many amber pieces, insect inclusions are preserved in layers, as they were caught in subsequent leakages of resin.

What exactly is an inclusion? An inclusion is an object, which is trapped in amber. It is a three-dimensional, very fine mould of an insect body with all external characters. Only remains of the external skeleton and the rest of the body are to be found inside the inclusion (Fig. 8). Dehydration is the most important process in the insect tissues during creation of an inclusion. All organic remnants are highly changed by acids and other compounds included in resin, by processes of dehydration, polymerization, etc. However, tissue preserved in such a way has many characters of the structure of living tissue. Well-preserved striated muscles of insects, internal organs and hypodermis of spiders in Baltic amber were described (KORNILOVICH 1903; PETRUNKEVITCH 1935, 1950). Using scanning electron microscope exposed surfaces of the insects (MIERZEJEWSKI 1976a, b), and ultrastructure of the preserved tissue in Baltic amber fly of the family Mycetophilidae (POINAR & HESS 1982) were examined. Extracting DNA from amber inclusions is a relatively recent endeavor (POINAR, POINAR & CANO 1994). Several studies have shown that amber provides conditions conducive to the long-term preservation of amino-acids (WANG et al. 1995, POINAR et al. 1996). The first extraction and partial characterization of DNA from amber inclusions of stingless bee from Dominican amber was presented by CANO, POINAR & POINAR (1992). The oldest insect DNA was obtained from the

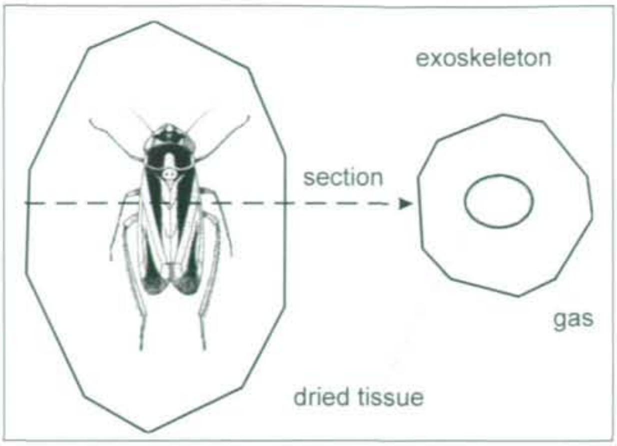
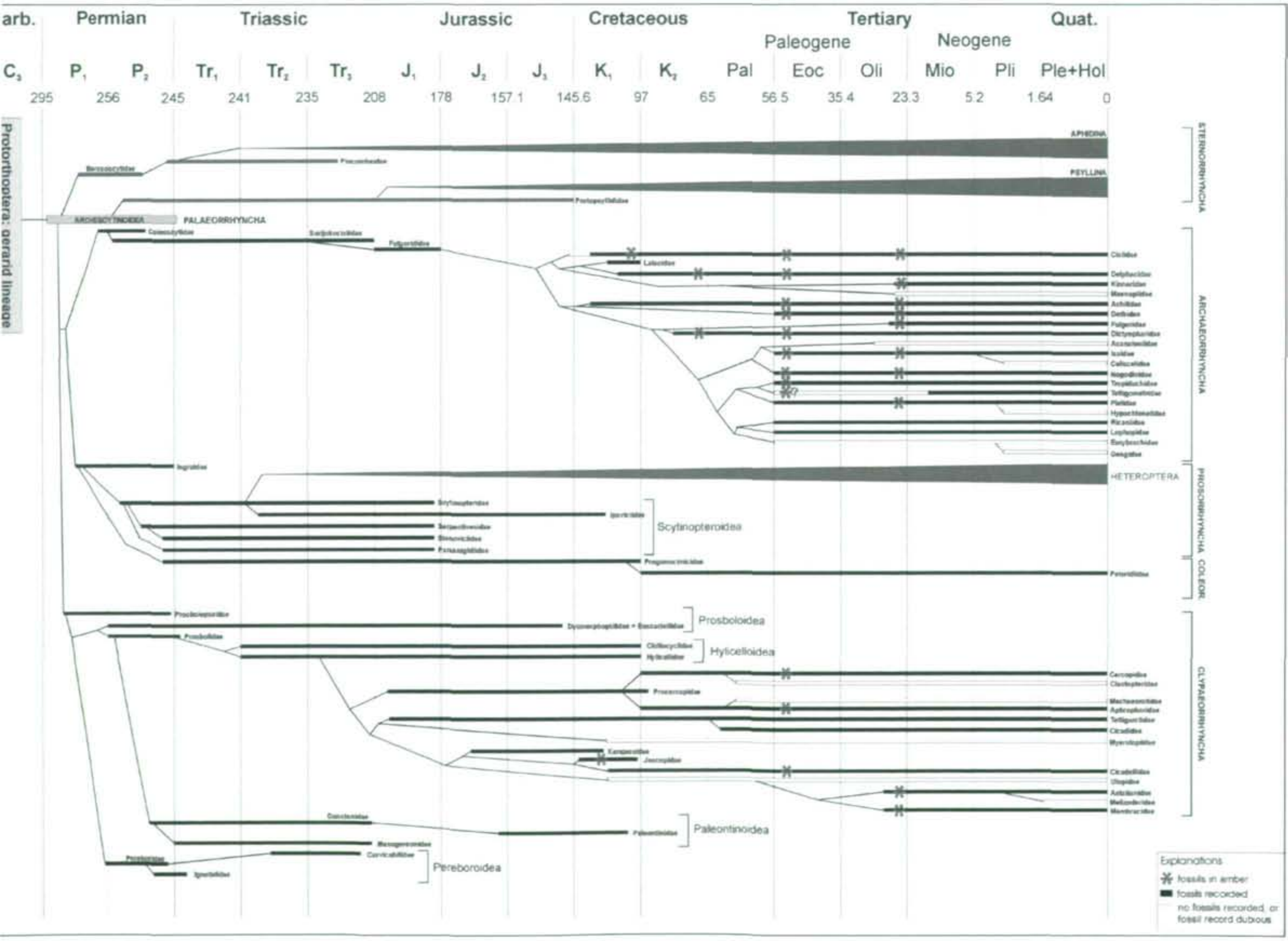


Fig. 8: Structure of an inclusion.

Fig. 9: Simplified phylogram of hemipteran lineages, amber fossils are marked with an asterisk. The relationships adopted mainly after DIETRICH & DEITZ 1993, HAMILTON 1999 and SHCHERBAKOV 1996, 2000.



inclusion of weevil in Lebanese amber, about 125 Ma old (CANO et al. 1993). These data attest the remarkable preservative properties of amber. However, DNA from amber organisms is fragmented, degraded and strongly cross-linked with other molecules in the cell, so it is necessary to take this into consideration. In future, it may be possible to repair some of the 'ancient DNA, which would allow the retrieval of longer, more authentic sequences. Studies with DNA from organisms preserved in amber make it possible to include extinct organisms that existed millions years ago in molecular phylogeny studies.

The amber-trapped planthoppers, froghoppers, treehoppers and leafhoppers

If thou couldst but speak little fly
How much more would we know about the past?
Immanuel KANT (1724-1804)

The study of amber insects was initiated over 250 years ago with the first investigation of the Baltic amber fauna and flora (SENDELIUS 1742). Unfortunately, the collection of the king of Poland August II the Strong, which was the base for this work, was burnt down in Dresden, in the 18th century. Indeed, most of the descriptions of amber insects today pertain to Baltic deposits (KEILBACH 1982, SPAHR 1988, SZWEDO & KULICKA 1999b).

Inclusions of Archaeorrhyncha (planthoppers) and Clypaeorrhyncha (froghoppers, leafhoppers, treehoppers and cicadas) are not very rare in fossil resins (Table 1). First descriptions of delphacid (?) and ricaniid planthoppers come from the beginning of the 19th century (DALMAN 1825). Unfortunately, the original description of the species described – *Asiraca albipuncta* DALMAN 1825 and *Ricania equestris* DALMAN 1825 – only mentions: 'Specimen Copalo inclusum, unicum'. These inclusions probably originated from the '*animè*' or '*gum animè*', as it was called in the 19th century, which is a resinous substance, exuded by *Vateria indica* LINNÉ (Dipterocarpaceae), a gigantic tree of Malabar (HOPE 1836, 1837). This is also suggested by SCHLÜTER & von GNIELINSKI (1987). The resin seems to be rather recent or semi-fossil. HOPE (1836) listed several inclusions from animè and amber, and described another species (HOPE 1837) – Table 1.

In the middle of the 19th century Ernst Friedrich Germar, described 23 representatives of different taxa from Eocene Baltic amber from the famous and rich collection of Gustav Carl Berendt (GERMAR & BERENDT 1856) – Table 1. Later, in the first half of the 20th century, only a few authors described some new species from Baltic amber (BERVOETS 1910, COCKERELL 1910, JACOBI 1938, USINGER 1939). At the same time, the first descriptions of fossils from other types of amber were presented (COCKERELL 1917) – Upper Cretaceous Burmese amber. After a rather long break, a few species of planthoppers from Oligocene/Miocene Mexican amber were described (FENNAH 1963). Other descriptions dealt with Cretaceous amber inclusions: Canadian (HAMILTON 1971) and Lebanese (FENNAH 1987). The renaissance of amber studies began in the last decade of the 20th century, when numerous taxa from Baltic, Mexican and Dominican amber were presented (Table 1). Some inclusions of fulgoromorphan and cicadomorphan insects in the Pleistocene East African copal are reported by STROIŃSKI & SZWEDO (this volume). Apart from formal descriptions, many taxa are listed or mentioned, or even figured in various papers, (for a list of papers up to 1988 see SPAHR 1988, also DIETRICH & VEGA 1995, WU 1996, WEITSCHAT & WICHARD 1998, POINAR & POINAR 1999, SZWEDO & KULICKA 1999a, b).

Most of the taxa described in the 19th and in the beginning of the 20th century call for re-examination. Some species described by GERMAR & BERENDT (1856) should be transferred to other families, e.g. '*Cixius*' *testudinarius* GERM. & BER. to Achilidae, as suggested by USINGER (1939), '*Cixius*' *loculatus* GERM. & BER. seems to represent Tropiduchidae, *Pseudophana reticulata* GERM. & BER. was discussed by EMELJANOV (1983), partly transferred to Achilidae and partly to Tropiduchidae. Unfortunately, type material of the species, ascribed to the genus *Cixius* LATR. by GERMAR & BERENDT (1856), was probably lost during World War II, as it was sent to Königsberg in 1937. Some specimens (described or not) from G.C. Berendt collection are stored in Paläontologisches Museum, Humboldt-Universität zu Berlin and now being examined. Another species – *Oliarus oligocenus* CKLL, ascribed by COCKERELL (1910) to cixiids, also belongs to Achilidae.

Which groups of planthoppers, froghoppers, leafhoppers or treehoppers are reported from fossil resins? Some taxa enter the fossil record for the first time as trapped and preserved in fossil resins – various kinds of amber. It is true both of representatives of the archaeorrhynchan lineage and for bugs of the clypaeorrhynchan line.

Almost all families of Archaeorrhyncha have the fossil record in resins of various ages (Fig. 9).

Cixiidae. Representatives of this group are recorded from Lower Cretaceous Lebanese amber (FENNAH 1987) and Upper Cretaceous Burmese amber (COCKERELL 1917). The family is well-represented in Eocene Baltic amber, a few species are described (Table 1), and many more still wait for formal description. It is very interesting, that representatives of Bothriocerinae (Fig. 10) – subfamily recently widespread in the New World – are found among Baltic amber inclusions (SZWEDO in press), as well as representatives of Cixiinae of the tribes Cixiini s.l. (Fig. 11) and Pentastirini (STROIŃSKI & SZWEDO in prep.). A few species are also reported from Oligocene/Miocene Dominican amber (Table 1). Many formally undescribed species from amber of different age are figured in different sources, e.g. BACHOFEN-ECHT 1949, LARSSON 1978 (Baltic amber), SCHLEE 1990, WU 1996 (Dominican amber).

Delphacidae. In fossil resins these plathoppers are known from Burmese amber (COCKERELL 1917) and from the Eocene Baltic amber (GĘBICKI & SZWEDO 2000b). Undescribed delphacids are also figured in WU (1996) and POINAR & POINAR (1999).

Kinnaridae. This family enter the fossil record in Oligocene/Miocene Dominican amber (EMELJANOV & SHCHERBAKOV 2000). Two species of recent genera are recognized (Table 1)

Meenopliidae. Any representatives of this family, regarded as sister-group of kinnarids are known in fossil state so far.

Achilidae. This highly differentiated, and probably paraphyletic group is well represented in the Eocene Baltic amber (Fig. 12), a few

Fig. 10: Bothriocerinae cixiid in Baltic amber, coll. Gustav Carl Berendt, Paläontologisches Museum des Humboldt-Universität, Berlin, Germany. The colours are false because the piece of amber is dark burgundy, so the filters were used to make the photograph.

Fig. 11: *Kulickamia jantaris* GEB. & SZW. (Cixiidae), holotype, Baltic amber.

Fig. 12: Undescribed yet planthopper of the family Achilidae preserved in Baltic amber.

Fig. 13: *Positrona shcherbakovi* Em. (Derbidae), holotype, Baltic amber. The 'milky veil' is often covering the Baltic amber inclusions.

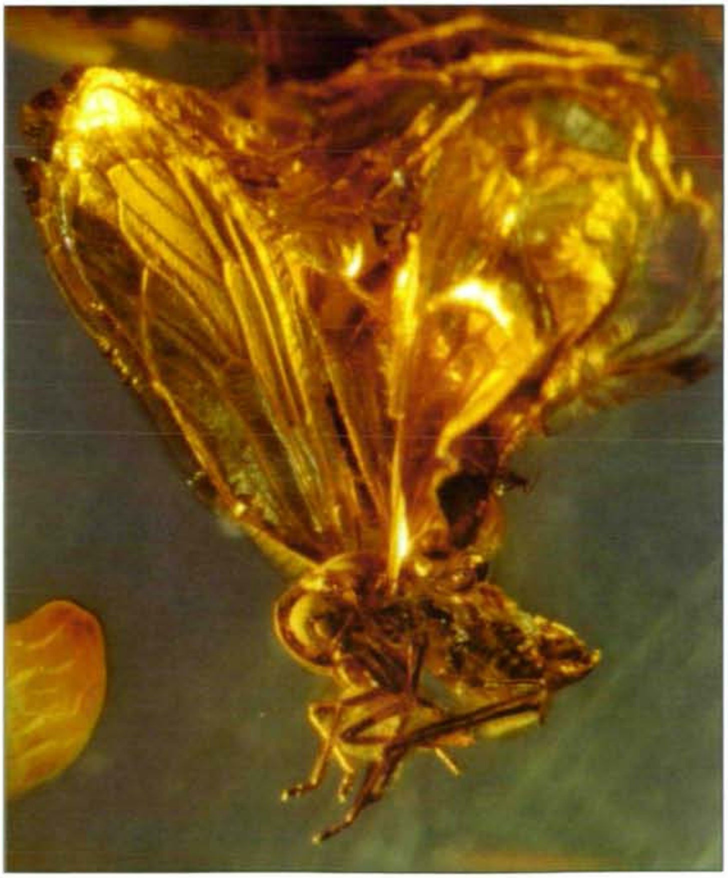


Fig. 14: Specimen of *Positrona* Em. (Derbidae), species not described yet, Bitterfeld amber, coll. Christel and Werner Hoffeins, Hamburg, Germany. The layer on which specimen is placed is disturbed by wings movements during preservation in resin.

species are described, among them representatives of the highly derivative tribe known only from fossils – Ptychoptilini (Table 1). The recent genus *Synecdoche* L. O'Brien is found in Dominican amber (Szwedo in prep.).

Derbidae. For a long time, the fossil record of the family was based on misinterpreted genera, described from imprints and in fact representing other families. The first undoubtful Derbidae have also been found in Baltic amber (Table 1). The identified species, *Positrona shcherbakovi* Em. (Fig. 13), represents the recent tribe Otiocerini, quite advanced in terms of evolution. More derbids of this genus, yet undescribed, have been found in Baltic amber, as well as representative of the tribe Cedusini. It is noteworthy, that also in Bitterfeld (Saxonian) amber a species of the genus *Positrona* Em. has been identified (Fig. 14). In Oligocene/Miocene Dominican amber, two species of Derbidae have recently been described (Emeljanov & Shcherbakov 2000), representing the tribes Cedusini and Derbini. Some other derbids, not yet described, were identified among inclusions in Mexican amber – representatives of the genus *Cedusa* Fowler (Ross & Szwedo in prep) and another form, related to the genus *Cenanges* Fennah. Unnamed derbid inclusions in Dominican amber is figured in Poinar & Poinar (1999).

Dictyopharidae. Emeljanov (1983) presents representative of this family from Upper Cretaceous Taimyrian amber. Szwedo & Kulicka (1999a, b) mention probable nymph of Dictyopharidae in Baltic amber, Wu (1996) and Poinar & Poinar (1999) also mention a few nymphs ascribed to Dictyopharidae from Dominican amber.

Fulgoridae. Representatives of this group preserved in fossil resins are reported only from Oligocene/Miocene Dominican amber. Wu (1996) and Poinar & Poinar (1999) figure two different nymphs in papers.

Acanaloniidae. These planthoppers are not known in fossil record, but Zherikhin (1978) mentions this group from Lower Cretaceous strata of Baissa in Transbaikalia (Russia), from imprints in rocks.

Issidae. The family (Figs 15-17) is also present in the Eocene Baltic amber record (Table 1). Undescribed Issidae in Dominican amber are figured in Wu (1996) and Poinar

Fig. 15:
Nymph of an issid with wax tail, Baltic amber, coll. Mr. Carsten Gröhn, Glinde, Germany

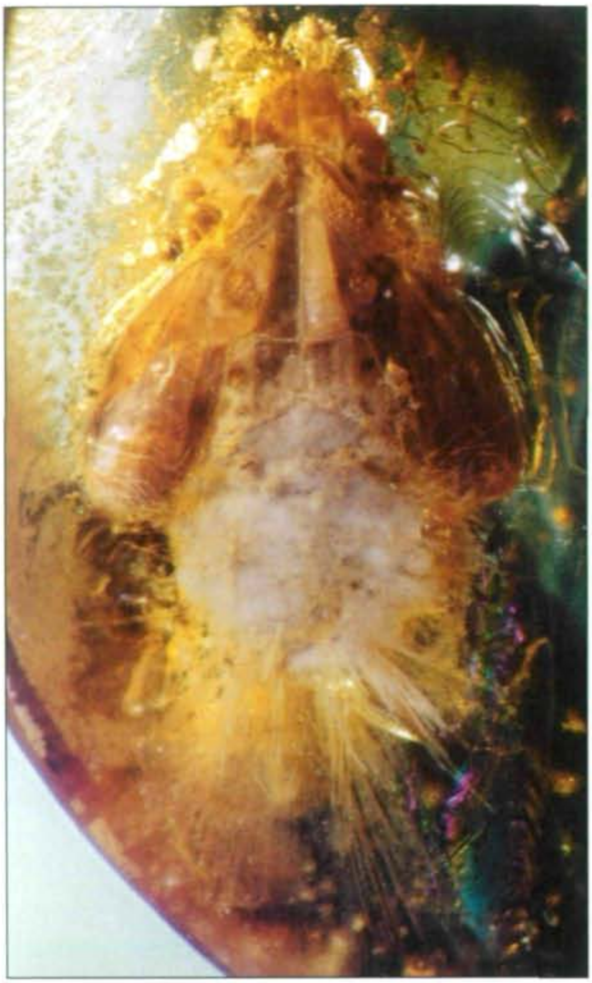


Fig. 16:
Undescribed yet issid, Baltic amber, coll. Adolf Bachofen-Echt, Vienna. This piece of amber in form of cabochon, and probably during the polishing the tarsal segments were destroyed.

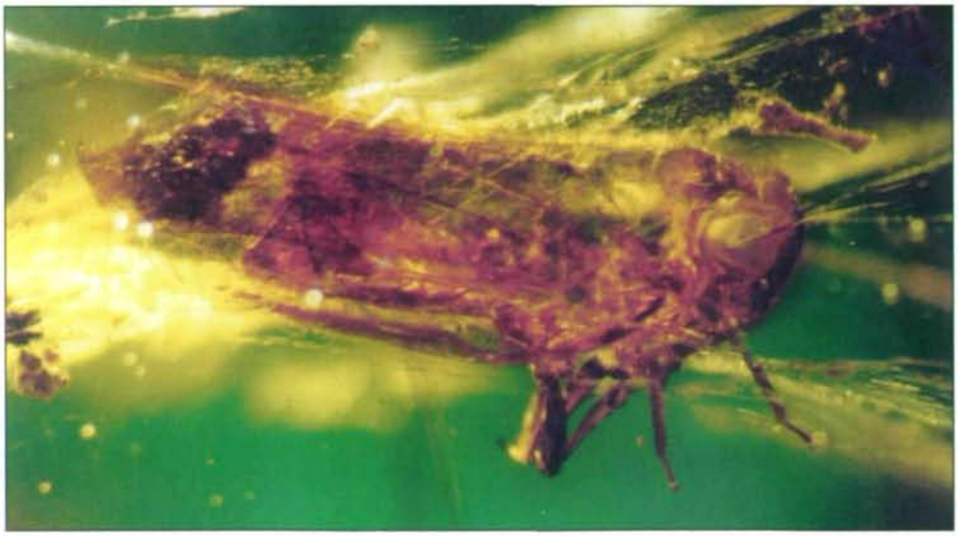


Fig. 17:
This inclusion of an issid in Dominican amber (coll. George Poinar, Oregon State University, Corvallis, U.S.A.) is translucent, such situation is frequently present in New World resins inclusions.

Fig. 18: *Tainosia quisqueyae* SZW. & STR. (Nogodinidae), holotype, Dominican amber. The body of the planthopper is compressed in resin, such situation is quite often among New World ambers inclusions.

Fig. 19: *Jantaritambia serafini* SZW. (Tropiduchidae), holotype, Baltic amber. The body of an insect is partly destroyed, probably by the putrefaction processes and covered with 'milky veil' of the decay gases.

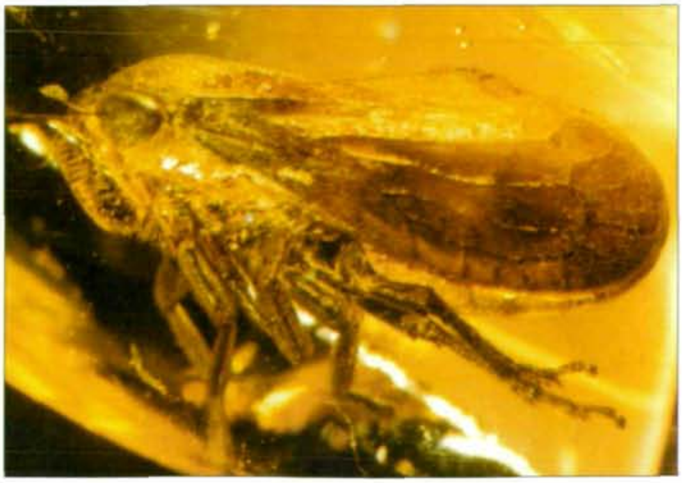


Fig. 20: Not described froghopper (Aphrophoridae) in Baltic amber, coll. Mr. Jacek Serafin, Kasparus, Poland

& POINAR (1999). It is noteworthy that nymphs ascribed to this family are quite numerous both in Baltic and Dominican amber. The waxy 'tails' are frequently preserved with an insect fossilized in resin (Fig. 15).

Caliscelidae. This family was not reported from fossil state yet.

Nogodinidae. A few representatives of this family are known from fossil resins. Members of this family have been reported from Baltic amber, Dominican amber (Fig. 18) and Mexican amber as well (Table 1).

Tropiduchidae. These planthoppers are only recorded from the Eocene Baltic amber. They are represented by few species: a nymph (larva in original description) of '*Pseudophana*' *reticulata* GERM. & BER., discussed by EMELJANOV (1983), and a single form (Fig. 19) representing a fossil tribe (SZWEDO 2000a).

Tettigometridae. The sole report of fossil tettigometrid in Baltic amber is given in LARSSON (1978), but without any more precise data.

Flatidae. FENNAH (1963) briefly describes a nymph from Mexican amber, another nymph has been found in another piece of amber of the same origin.

Hypochtonellidae. Any data about fossil representatives of this family were reported so far. Recently these planthoppers have limited Afrotropical distribution, and their habitat in the litter could be one of the reasons that these insects lack in fossil as well as in subfossil record.

Ricaniidae. Representatives of the family are well known from imprints of various ages, but not recorded from ambers. The only data of Ricaniidae entombed in rather recent resins (animè) are these given by DALMAN (1825). Another report comes from GIEBEL (1862), but without information about the kind of resin. A few Ricaniidae are also known from Pleistocene East African copal.

Scarcely any data of the representatives of the families Lophopidae, Eurybrachidae and Gengidae in fossil resins are available. Apart from a sole lophopid species, these groups are absent from the fossil record.

Representatives of Clypaeorrhyncha are frequently mentioned from fossil resins (Table 1).

Fig. 21:
Nymphs of Cicadellidae are very frequent in Baltic amber inclusions (coll. Mr. Carsten Gröhn, Glinde, Germany)

Fig. 22:
This nymph of leafhopper, with extremely long antennae, exceeding the length of the body, is well preserved in Baltic amber (coll. Museum of the Earth, PAS, Warsaw)

Fig. 23:
Even 40 Ma ago the parasitic insects (Oryinidae) attacked leafhoppers, Baltic amber (coll. Amber Museum, University of Gdańsk, thanks of courtesy Mrs. Elżbieta Sontag)

Fig. 24:
Brachypterous forms are to be found among Baltic amber inclusions (coll. Museum of the Earth PAS, Warsaw)

Fig. 25:
Yet undescribed cicadellid, with uncertain subfamilial assignment. Forms with well preserved colour pattern are to be found among Baltic amber inclusions also (coll. Mr. Carsten Gröhn, Glinde, Germany).

Cercopidae and **Aphrophoridae.** Representatives of these families are recorded from Baltic amber (Table 1), a few yet undescribed species (Fig. 20) are also known, e.g. these figured in WEITSCHAT & WICHARD (1998). A single froghopper from Dominican amber is also figured in WU (1996). Other Cercopoidea: Clastopteridae and Machaeortidae are not reported from fossil resins or imprints.

Tettigarctidae and Cicadidae. The cicadas are quite frequent in fossil record, but amberized 'cicadas' are in fact representatives of other groups. A nymph of a true cicada is figured in POINAR & POINAR (1999).

Jascopidae. This fossil family was described from the Upper Cretaceous Canadian amber (HAMILTON 1971). The taxonomic status of this unit, as intermediate between cicadellid and cercopid lineages was postulated by HAMILTON (1971). EVANS (1978) argued with such statement and placed *Jascopus notabilis* HAMILTON 1971 in Cicadellidae. Similar point of view was presented by SHCHERBAKOV (1992), who discussed the characters of Jascopidae and Lower Cretaceous Paracarsonini and postulated to include these fossils into Ledrinae (Cicadellidae).

Myerslopiidae. This recently established family is not recorded from fossil resins, but their representatives may perhaps be found in fossilized resin of kauri-pine (Araucariaceae).

Cicadellidae. Leafhoppers are numerous in Baltic amber inclusions (Figs 21-26), but only a few species have been described (Table 1). Representatives of various lower taxa of Cicadellidae are known, representing groups with a very limited recent distribution, e.g. some forms similar to Cicadellinae: Errhomenini and Euacanthellinae. Representatives of Mileewinae have been identified (GĘBICKI & SZWEDO 2001). Also taxa absent from recent fauna are known from Baltic amber, among them some Typhlocybinae, well differentiated during the Eocene, with a few genera and species recognized in Baltic amber and belonging to a new fossil tribe (GĘBICKI & SZWEDO in prep.). It is noteworthy that Baltic amber abounds in nymphs (Figs 21-23). Dominican amber Cicadellidae, representing recent genera and a fossil one as well, have been described quite recently (DIETRICH & VEGA 1995), some others are figured in papers by WU (1996) and POINAR & POINAR (1999).

Ulopidae. These insects are widespread in the Old World, are not recorded in fossils. It can perhaps be attributed, among other things, to their habits – most of recent Ulopidae live in concealment. Nevertheless, a nymph with a mosaic of ulopid and cicadellid characters has been found among Baltic amber inclusions.

Aetalionidae. These treehoppers have been found among inclusions of Oligocene /Miocene Mexican amber (Fig. 27) and Dominican amber. These new, fossil genera differ in many characters from recent ones (Szwedo in prep.). Paradoxically, the fossil aetalionid described from the Upper Oligocene strata of Germany (STATZ 1950) seems to be very similar to recent forms. This report is of particular interest, because Aetalionidae are recently restricted in distribution to the New World, with the exception of two species of the genus *Darthula* DISTANT from India and southern China (MCKAMEY 1998). Aetalionid planthopper is also figured in WU (1996), but wrongly assigned to Eurymelidae.

Membracidae. Recently numerous and highly differentiated treehoppers are not recorded in the Eocene Baltic amber, only a poorly preserved nymph with some characters similar to membracids is known. Treehoppers are represented in great numbers in Dominican amber, but not a single species is formally described. A few different genera and species are figured in papers by SCHLEE (1990), WU (1996) and POINAR & POINAR (1999).

Amber inclusions are our "windows to the past". The studies of amber inclusions are vital not only for taxonomic and phylogenetic purposes, but in taphonomy, palaeoecology and palaeoclimatology as well. They can also help reconstruct interactions that occurred among organisms. A few examples of host-parasite interactions are known from fossil resin, which is a very important source of information on such associations. Some behavioral data can also be obtained from an analysis of amber inclusions. A detailed study of amber inclusions may assist in the reconstruction of host-plant-insect associations. From plant and animal remains in amber, it is possible to reconstruct the past biota and their conditions. Moreover, amber inclusions are informative of the pattern of past climatic conditions. Recent distribution of many insects can be properly understood only after comprising the data obtained from inclusions in fossil resins. Verification of old amber collections kept in different institutions, their detailed attestation, addition of new specimens and their detailed description will greatly contribute to the development of our knowledge about amber and its inclusions.

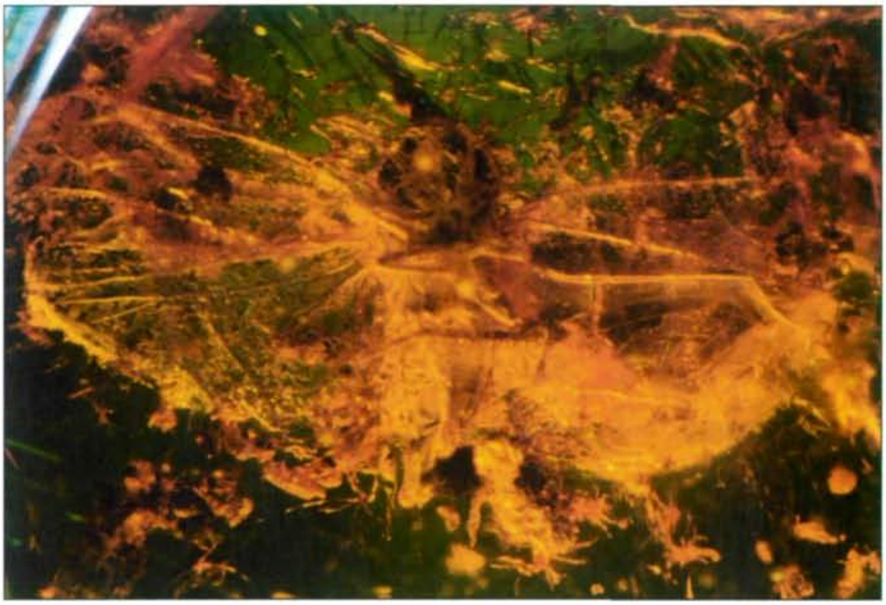


Fig. 26:
Sometimes inclusions are hardly visible because of cracks, particles of detritus and stairy hairs of *Quercus* spp. trees. (Cicadellidae: Typhlocybinae; coll. Museum of the Earth PAS, Warsaw).

Fig. 27:
This treehopper of the family Aetalionidae is preserved in Mexican amber (coll. George Poinar, Oregon State University, Corvallis, U.S.A.). It strongly differs from recent aetalionids and represents a new genus.

Table 1. Described inclusions of Archaeorrhyncha and Clypaeorrhyncha in fossil resins

Name	**Higher categories**	**Author**	**Kind of resin**	**Comments**
Names of species, genera and family assignation presented as in original papers. Only original data are listed. If a species was transferred to another taxon, the fact is mentioned in column "Comments", together with other data.				
Asiraca albipuncta Dal.	Delphacidae	Dalman 1825	Indian animè	
Ricania equestris Dal.	Ricaniidae	Dalman 1825	Indian animè	
Cercopis strongii Hope	Cercopidae	Hope 1837	Indian animè	
Typhlocyba encaustica Germ. & Ber.	'Cicadellina'	Germar & Berendt 1856	Baltic amber	Cicadellidae: Typhlocybinae
Typhlocyba resinosa Germ. & Ber.	'Cicadellina'	Germar & Berendt 1856	Baltic amber	Cicadellidae: Typhlocybinae
Bythoscopus homousius Germ. & Ber.	'Cicadellina'	Germar & Berendt 1856	Baltic amber	Cicadellidae: Macropsinae
Jassus immersus Germ. & Ber.	'Cicadellina'	Germar & Berendt 1856	Baltic amber	Cicadellidae: Coelidiinae (Metcalf & Wade 1966)
Jassus spinicornis Germ. & Ber.	'Cicadellina'	Germar & Berendt 1856	Baltic amber	Cicadellidae
Tettigonia proavia Germ. & Ber.	'Cicadellina'	Germar & Berendt 1856	Baltic amber	Cicadellidae
Tettigonia terebrans Germ. & Ber.	'Cicadellina'	Germar & Berendt 1856	Baltic amber	Cicadellidae
Aphrophora electrina Germ. & Ber.	'Cicadellina'	Germar & Berendt 1856	Baltic amber	Aphrophoridae (Metcalf & Wade 1966)
Aphrophora vetusta Germ. & Ber.	'Cicadellina'	Germar & Berendt 1856	Baltic amber	Aphrophoridae (Metcalf & Wade 1966)
Aphrophora (Ptyela) carbonaria Germ. & Ber.	'Cicadellina'	Germar & Berendt 1856	Baltic amber	Aphrophoridae (Metcalf & Wade 1966)
Cercopis melaena Germ. & Ber.	'Cicadellina'	Germar & Berendt 1856	Baltic amber	Cercopidae (Metcalf & Wade 1966)
Cixius vitreus Germ. & Ber.	'Cicadellina'	Germar & Berendt 1856	Baltic amber	Cixiidae (Metcalf & Wade 1966)
Cixius testudinarius Germ. & Ber.	'Cicadellina'	Germar & Berendt 1856	Baltic amber	Cixiidae (Metcalf & Wade 1966)
Cixius insignis Germ. & Ber.	'Cicadellina'	Germar & Berendt 1856	Baltic amber	Cixiidae (Metcalf & Wade 1966)
Cixius Sieboldtii Germ. & Ber.	'Cicadellina'	Germar & Berendt 1856	Baltic amber	Cixiidae (Metcalf & Wade 1966)
Cixius fraternus Germ. & Ber.	'Cicadellina'	Germar & Berendt 1856	Baltic amber	Cixiidae (Metcalf & Wade 1966)
Cixius longirostris Germ. & Ber.	'Cicadellina'	Germar & Berendt 1856	Baltic amber	Cixiidae (Metcalf & Wade 1966)
Cixius succineus Germ. & Ber.	'Cicadellina'	Germar & Berendt 1856	Baltic amber	Cixiidae (Metcalf & Wade 1966)
Cixius loculatus Germ. & Ber.	'Cicadellina'	Germar & Berendt 1856	Baltic amber	Cixiidae (Metcalf & Wade 1966)
Cixius gracilis Germ. & Ber.	'Cicadellina'	Germar & Berendt 1856	Baltic amber	Cixiidae (Metcalf & Wade 1966)
Pseudophana reticulata Germ. & Ber.	'Cicadellina'	Germar & Berendt 1856	Baltic amber	Achilidae (pars) and Tropiduchidae (pars) (Emeljanov 1983)
Poeocera nasata Germ. & Ber.	'Cicadellina'	Germar & Berendt 1856	Baltic amber	Issidae
Poeocera pristina Germ. & Ber.	'Cicadellina'	Germar & Berendt 1856	Baltic amber	Fulgoridae (?)
Poeocera venulosa Gieb.	'Fulgorinen'	Giebel 1862	?	Fulgoridae [?]
Ricania multinervis Gieb.	'Fulgorinen'	Giebel 1862	?	
Cercopis aurata Gieb.	'Cicadellinen'	Giebel 1862	?	
Issus reticulatus Berv.	'Fulgoridae'	Bervoets 1910	Baltic amber	Issidae
Bythoscopus punctatus Berv.	'Jassidae'	Bervoets 1910	Baltic amber	Cicadellidae: Macropsinae
Pediosis minuta Berv.	'Jassidae'	Bervoets 1910	Baltic amber	Cicadellidae
Eupteryx minuta Berv.	'Jassidae'	Bervoets 1910	Baltic amber	Cicadellidae
Acocephalus resinosus Berv.	'Jassidae'	Bervoets 1910	Baltic amber	Cicadellidae
Oliarus oligocenus Ckll	'Fulgoridae: Cixiinae'	Cockerell 1910	Baltic amber	Achilidae
Plecophlebus nebulosus Ckll	'Odontoceridae' [Trichoptera, sic!]	Cockerell 1917	Burmese amber	Cixiidae (Botosaneanu 1981)
Liburnia (s.lat) *burmitinia* Ckll.	'Fulgoridae: Delphacinae'	Cockerell 1917	Burmese amber	Delphacidae
Tritophania patruelis Jac.	Ricaniidae	Jacobi 1938	Baltic amber	Nogodinidae (Carpenter 1992); Nogodinidae: Bladinini, Gaetulina (Szwedo & Stroiński 1999)
Protepiptera kaweckii Usg.	Achilidae	Usinger 1939	Baltic amber	Achilidae
Oeclixius amphion Fenn.	Cixiidae	Fennah 1963	Mexican amber	
Mnemosyne sp.	Cixiidae	Fennah 1963	Mexican amber	Pentastirini: Mnemosynina
Jascopus notabilis Hmlt.	Jascopidae	Hamilton 1971	Canadian amber	
Netutela annunciator Em.	Dictyopharidae: Netutelini	Emeljanov 1983	Taimyrian amber	
Mundopoides aptianus Fenn.	Cixiidae	Fennah 1987	Lebanese amber	Original genus name *Mundopoides* Fenn. is praeoccupied (Szwedo 2001).
Ptychoptilum major Em.	Achilidae: Ptychoptilini	Emeljanov 1990	Baltic amber	Ptychoptilini - fossil tribe
Ptychoptilum minor Em.	Achilidae: Ptychoptilini	Emeljanov 1990	Baltic amber	Ptychoptilini - fossil tribe
Oligocixia electrina Geb. & Weg.	Cixiidae	Gebicki & Wegierek 1993	Dominican amber	Cixiinae
Positrona shcherbakovi Em.	Derbidae: Otiocerini	Emeljanov 1994	Baltic amber	
Krisna garciamarquezi Dietr. & Vega	Cicadellidae: Iassinae: Krisnini	Dietrich & Vega 1995	Dominican amber	
Krocarites reflexa Dietr. & Vega	Cicadellidae: Nirvaniinae: Nirvanini	Dietrich & Vega 1995	Dominican amber	
Jassoqualus hispaniolensis Dietr. & Vega	Cicadellidae: Nirvaniinae: Nirvanini	Dietrich & Vega 1995	Dominican amber	
'Agallia' sp.	Cicadellidae: Agallinae: Agallini	Dietrich & Vega 1995	Dominican amber	
Xestocephalus sp.	Cicadellidae: Xestocephalinae: Xestocephalini	Dietrich & Vega 1995	Dominican amber	
Ambericarda skalskii Szw. & Geb.	Cicadellidae: Cicadellinae: Proconiini	Szwedo & Gebicki 1998	Baltic amber	
Camptelasmus sp.	Cicadellidae: Ledrinae: Petalocephalini	Szwedo & Gebicki 1999	Baltic amber	
Camptelasmus sp.	Cicadellidae: Ledrinae: Petalocephalini	Szwedo & Gebicki 1999	Baltic amber	
Oeclidius salaco Em. & Shch.	Kinnaridae: Propleromini	Emeljanov & Shcherbakov 2000	Dominican amber	
Quilessa stolida Em. & Shch.	Kinnaridae: Prosotropini	Emeljanov & Shcherbakov 2000	Dominican amber	
Cedusa credula Em. & Shch.	Derbidae: Cedusini	Emeljanov & Shcherbakov 2000	Dominican amber	
Dysimia imprudens Em. & Shch.	Derbidae: Derbini	Emeljanov & Shcherbakov 2000	Dominican amber	
Kulickamia jantaris Geb. & Szw.	Cixiidae: Cixiinae	Gebicki & Szwedo 2000a	Baltic amber	
Serafinana perperunae Geb. & Szw.	Delphacidae: Asiracinae: Ugyopini	Gebicki & Szwedo 2000b	Baltic amber	
Tonacatecutlius gibsoni Str. & Szw.	Nogodinidae: Nogodinini: Nogodinida	Stroiński & Szwedo 2000	Mexican amber	
Oliarus kulickae Szw.	Cixiidae: Cixiinae: Pentastirini	Szwedo 2000a	Dominican amber	
Jantaritambia serafini Szw.	Tropiduchidae: Jantaritambini	Szwedo 2000b	Baltic amber	Jantaritambini - fossil tribe
Ptychogroehnia reducta Szw. & Str.	Achilidae: Ptychoptilini	Szwedo & Stroiński 2001a	Baltic amber	Ptychoptilini - fossil tribe
Tainosia quisqueyae Szw. & Str.	Nogodinidae: Nogodinini: Nogodinina	Szwedo & Stroiński 2001b	Dominican amber	
Youngeawea bicolorfata Geb. & Szw.	Cicadellidae: Mileewinne			
Youngeawea bicolorfata Geb. & Szw.	Cicadellidae: Mileewinne	Szwedo & Stroiński 2001	Baltic amber	
Eomileewaeridani Geb. & Szw.	Cicadellidae: Mileewinne	Szwedo & Stroiński 2001	Baltic amber	

Zusammenfassung

Bernstein, seine Herkunft, stratigraphische Lagen und Lagerstätten der Welt werden dargestellt. Der Vorgang der Fossilisierung von Insekten in Harz wird erläutert. Daten zu Einschlüssen von Zikaden (Hemiptera: Archaeorrhyncha und Clypaeorrhyncha) in Bernstein werden zusammengefasst, Fossilfunde wichtiger Arten und Familien werden diskutiert und zum Teil kommentiert.

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