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Review of true bugs (Insecta: Hemiptera, Heteroptera) from the amber collection of the Museum of the Earth of PAS in Warsaw with some remarks on heteropteran insects from Eocene European amber

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ABSTRACT. From all the information available on Heteroptera in the Palaeogene (European Eocene) amber found in the amber deposits of the Baltic and the Ukrainian (Rovno amber) regions, Central France (Oise), and also the Leipzig area (Saxonian amber), we can conclude that many representatives of true bugs (mainly Miridae, Microphysidae, Anthocoridae and Aradidae) known to us were associated mainly with coniferous vegetation (Early Tertiary European amber forests) and, consequently, were in constant contact with resin. The main findings regarding the taxonomy, number of species, a brief biology, palaeogeography and palaeontology, as well as a review of current literature sources, are given for every family contained in the amber collection of the Museum of the Earth of PAS in Warsaw. A summary table is also included. So far, over 160 genera and more than 240 species belonging to 41 families from all known ambers have been described. About 160 species and 100 genera from 25 modern heteropteran families, described from succinite - Baltic and Ukrainian (Rovno, Klesov) ambers - belong mostly to Miridae, Anthocoridae, Cimicoidea (Electrocoris), Microphysidae, Nabidae, Tingidae and Reduviidae. 12 families (120 inclusions) are represented in the collection of the Museum of the Earth: Saldidae (1), Ceratocombidae (1), Anthocoridae (9), Microphysidae (4), Miridae (73), Reduviidae (2), Nabidae (5), Thaumastocoridae (1), Tingidae (4), Aradidae (2), Piesmatidae (1), Lygaeidae (2), Cimicoidea (7) and Heteroptera incertae sedis (9). About 70% of fossils belong to the plant bugs (Miridae): 26.5% of these are represented by the Isometopinae and 43% by the Cylapinae subfamilies.

KEY WORDS: palaeontology, taxonomy, Hemiptera, Heteroptera, Baltic, Scandinavian, Ukrainian (Rovno, Klesov), French (Oise) and Saxonian (Bitterfeld) ambers, Eocene.

INTRODUCTION

The main purpose of this article is to share new important information about the heteropteran insect (true bugs) inclusions (mainly from Eocene Baltic amber) that are in the excellent large collection of the Museum of the Earth of the Polish Academy of Sciences in Warsaw. Late Eocene Baltic amber h as been studied for over 200 years. Of all the fossil locations, the Baltic is the best-known and best-investigated. Even so, this does not guarantee real knowledge of the Baltic amber fauna and, in particular, of the heteropteran fauna in amber. Hence, it is very important to carry out a comparative study of a representative collection in Poland, such as the richest Baltic amber collection in the Museum of the Earth of PAS (MZ) in Warsaw, the large collection in the Museum of Amber Inclusions at the University of Gdańsk, or the other representative amber collection at the Institute of Systematics and Evolution of Animals of PAS in Kraków.

As far as the amber collection in the Museum of the Earth is concerned, it should be noted first of all that Tadeusz Giecewicz made an invaluable contribution to the creation of this amber collection in the 1950s (KULICKA 1990, KULICKA & KOSMOWSKA-CERANOWICZ 2001b, KOSMOWSKA-CERANOWICZ et al. 2001). The history of the creation and research of the world-famous Baltic amber collection in the Amber Department (MZ) was first described by KULICKA (1990), and subsequently by KULICKA & PIELIŃSKA (2006) and KOSMOWSKA-CERANOWICZ (2001b, 2008a, c). The last-mentioned article was published on the occasion of the 60th anniversary (1948-2008) of the Museum of the Earth (MZ). Recently, another representative collection has been described, namely, the one in the Museum of Amber Inclusions (MAI) at the University of Gdańsk (KOSMOWSKA-CERANOWICZ 2001a, SONTAG 2003, 2004, 2008, SZADZIEWSKI & SONTAG 2008, SONTAG & SZADZIEWSKI 2008). Originally containing some 12 000 specimens, this collection was established in 1998 (SONTAG 2004); in the succeeding 10 years of its existence, MAI has increased the number of inclusions to 13 540 (SONTAG 2008). As far as Heteroptera are concerned, a new microphysid bug *Loricula polonica* from this collection was described by POPOV et al. (2008), who also identified a lace bug Sinalda baltica DRAKE (Tingidae) from the modern genus Sinalda (Popov, pers. comm.).

As of 1996, the collection of amber inclusions at MZ contained (according to Róża Kulicka) no less than 26 thousand specimens within the overall collection of animal inclusions. The most complete data on the amber collection of this Museum was published at the beginning of 2000 (KOSMOWSKA-CERANOWICZ 2001b, KULICKA & PIELIŃSKA 2006).

In recent years, thanks to these authors, the heteropteran collection has grown considerably, especially since 1996 (KULICKA et al. 1996). One of the sources from which specimens were added to the collection stemmed from the authors' long-standing membership (about 15 years) of the International Amber Association, MZ and MAI (Amberif). Symposia on investigations of Baltic amber (succinite) were held at the annual meetings organized by the Museum of Amber Inclusions at the University of Gdańsk (Prof. R. Szadziewski and Dr E. Sontag) and the Museum of the Earth PAS, Warsaw (Prof. B. Kosmowska-Ceranowicz and Dr A. Pielińska). Subsequently, seminars focusing on the study of Baltic amber inclusions were organized, the main outcome of these conferences being publications in the specialist journal "Bursztynisko". Other events at Amberif included the identification of amber inclusions containing numerous animals (mainly insects), and also their purchase, sale and exchange. As a result, the number of heteropteran inclusions (especially types) in the collection of MZ grew significantly. Indeed, during the last fifteen years this collection of true bug inclusions has more than tripled in size: from 38 to 120, from 5 families to 12, from 4 holotypes to 16 and 1 paratype (see the summary Table 1). Foreign heteropterologists also participated in the describing of the type material (CARVALHO & POPOV 1984, GOLUB 2004, HEISS 1998 and P.V. Putshkov & E.E. Perkovsky). In addition, there are 7 true bugs in a new series of Ukrainian amber inclusions from Klesov in the Rovno region, obtained mainly from the private collection of Andrzej Wiszniewski (Bialystok). These inclusions are especially important for establishing the identity and differences, both faunistic and taxonomic, among Baltic and Ukrainian (= Rovno) ambers (Klesov and Dubrovitsa) and also Saxonian (= Bitterfeld) amber. Unfortunately, the problems concerning the relationships, genesis, native amberiferous trees of Baltic resin, and age among Baltic (?Scandinavian), Ukrainian (Rovno), French (Lowermost Eocene) and especially Saxonian ambers, as well as their areas of their origin, are still unresolved. It is well known that amber forests were represented mainly by the amber-rich pine Pinus succinifera, most probably producing resin in large quantities. But although this was the main native plant producing resin, the true origin of the resin is still unknown. For instance, another plant described as a succiniferous tree, the umbrella pine Sciadopitys from the same family, was thought to be a native plant producing Baltic amber resin (WOLFE et al. 2009, SZWEDO 2010). Moreover, we do not know whether one or several different trees were the main source(s) of such a rich accumulation of resin. This problem will be discussed in a subsequent publication.

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THE LATEST KNOWLEDGE OF HETEROPTERAN INSECTS, OR TRUE BUGS, FROM EOCENE EUROPEAN AMBER

Heteroptera, or true bugs, is one of the largest and most diverse groups of insects (about 40 000 species described) with incomplete metamorphosis. They are usually regarded as a suborder of Hemiptera embracing about 75 recent and 12 fossil (besides some undescribed) families widespread on all continents (except Antarctica). So far over 160 genera and more than 240 species belonging to 41 families from all known ambers have been described (Popov, pers. comm.). The Heteroptera are mostly phytophagous and predatory (like most bug families), or zoophytophagous. Today they are successfully occupying the majority of known ecological niches. The oldest extinct Heteroptera are known from the earliest Middle Triassic (ca. 240 Ma) of France (SHCHERBAKOV 2010), represented by the naucoroid water bug (? Triassocoridae), and also from the uppermost Triassic (ca. 220 Ma) of England, Russia, Ukraine, Kazakhstan, China and the USA. They became even more numerous and diverse during the Mesozoic period, especially in the Late Jurassic and Early Cretaceous. During the Cenozoic, the number of extant (sub)families increased further, and most true bugs described from this geological period belong exclusively to these families. It should be emphasized that there has been a trend towards an increase in the relative abundance of the true bugs from the Eocene to the present (ZHERIKHIN et al. 2009). In accordance with the publications of KEILBACH (1982), SPAHR (1988), POPOV & HERCZEK (1993a, 2008), HERCZEK 2011a, ANDERSEN (1998), GOLUB & POPOV (2002), HEISS (1998, 2000a, 2001, 2002 a, b, c), WAPPLER (2003), DAMGAARD (2008), AZAR & NEL (2010), NEL et al. 2004 a, b, c) and some other recent works (see references), about 160 fossil

heteropteran species belonging to the approximately 100 genera and 25 families (Nepidae, Corixidae, Aphelocheiridae, Gerridae, Hydrometridae, Veliidae, Ceratocombidae, Schizopteridae, Hypsipterigidae, Enicocephalidae, Saldidae, Anthocoridae, Nabidae, Plokiophilidae, Microphysidae, Miridae, Reduviidae, Thaumastocoridae, Tingidae, Piesmatidae, Aradidae, Berytidae, Lygaeidae, Cydnidae, and Pentatomidae) that have so far been described or at least named from Baltic, Scandinavian (it is very probable that Baltic and Scandinavian ambers are of identical origin!), Ukrainian (Rovno, Klesov), French (Oise) and Saxonian (Bitterfeld) ambers. Thanks to the activity of one of the authors (JK) during the last fifteen years, this collection has been expanded to include a new type of Eocene amber from Ukraine (Klesov). Most of the information concerning Rovno amber fauna (Ukraine) was supplied by E.E. Perkovsky (see PERKOVSKY 2001, 2007, 2008, PERKOVSKY et al. 2003, 2006). It should also be noted that as a result of some recent publications on fossil insects from the Lowermost Eocene French amber (ca. 53 Ma), a certain similarity among insects from other Eocene ambers has been detected. For instance, the mirid psallopinous bugs of the genus Isometopsallops have been described, which are known from French and Baltic amber (VERNOUX et al. 2010). Moreover, one of the bark bugs (Aradidae) Calisius balticus, previously known from Late (?Middle) Eocene Baltic amber, is recorded in both these ambers, representing a morphological stasis of more than 10 Ma (MARCHAL et al. 2011). One of the causes of such a "long" existence of these heteropteran groups may be due to their relationships with coniferous trees or the fact that they live under bark.

Despite the fact that quite a large number species (over 1000) of fossil true bugs have been described to date (Popov, pers. comm.), they are still quite rare in amber resins. For instance, among the almost 26 thousand inclusions kept at the Museum of the Earth (KULICKA et al. 1996), only 120 contain heteropterans (both imagines and nymphs) belonging to 12 families (see Table 1). Although there are few true bugs in amber, no less than 1500 specimens of Heteroptera have been examined from the leading European and American museums, institutes and private collections (Popov, pers. comm.).

At present there are some 3500 insect species, described from Baltic amber, belonging to over 150 families of almost all the known orders of insects in the fossil condition from the Cenozoic (LARSSON 1978, ZHERIKHIN 1978, POINAR 1992, BACHOFEN-ECHT 1949, WEITSCHAT & WICHARD 1998, RASNITSYN & QUICKE 2002). Among them, aquatic and semiaquatic insects are rather numerous (WICHARD & WEITSCHAT 1996, WICHARD et al. 2009), and nepomorphan and gerromorphan bugs are represented by Corixidae, Nepidae, Notonectidae, Aphelocheiridae (an aphelocheirid nymph was erroneously placed in the Notonectidae, WICHARD et al. 2009), Gerridae, Veliidae and Hydrometridae. It should be noted that the finding of a rheophilous aphelocheirid bug in Eocene amber is so far the oldest one. Yet one cannot rule out the possibility that some aphelocheirids could have become rheophilous Heteroptera by that time. Aphelocheirid bugs in the Pliocene of Willershausen (N. Germany) were reliably redescribed only recently (POPOV 2007), although it is still too early to demonstrate scientifically that they exist in Naucoridae (POPOV 1971). At present most of them are distributed mainly (especially the heteropteran subfamilies) in temperate or (sub)tropical regions. At the beginning of the last century William WHEELER (1910, 1915) drew attention to the strange mixture of thermophiles and temperate ant genera and species (Formicidae) found together in Baltic amber, which are known from different biogeographic provinces, like the Palaearctic, Oriental and Australian ones. ARCHIBALD & FARREL (2003) explain such a surprising mix as the direct consequence of a more equable temperature seasonality. They concluded that the warm/cool organism mixture presumably lasted until some undetermined time later in the Cenozoic, when thermal seasonality increased along with falling MAT (mean annual temperature), and colder winters became generally associated with extra-tropical latitudes, resulting in biotic sorting (ARCHIBALD & FARREL l.c.). According to KOHLMAN-ADAMSKA (1997), such a difference proceeds not only from the morphology of the territory (mountains and lowlands) where amber forests were growing, but also from the fact that in the Eocene these areas lay on the borders of temperate and subtropical zones. Later on, Eocene species of Coniferales and Cupressiaceae were designated as the coniferous amber forests of higher mountain altitudes (KOHLMAN-ADAMSKA l.c.). REID & CHANDLER (1933) considered such a situation to be one of the most vexed climatological problems.

One may presume that the fossil fauna in Baltic amber has a certain similarity with the modern fauna of central America and south-east Asia. The Palaeogene amber-producing forests are similar to modern subtropical assemblages in the mountainous regions of southeast Asia (PIELIŃSKA 1998). In this regard, the opinion of J. Wunderlich, expressed in one of his fundamental works (WUNDERLICH 1986) concerning the faunas of spiders in Baltic and Dominican ambers is quite interesting. He maintains that "there are no close relationships between the fossil Baltic fauna... and the neotropical fauna, but there is a relationship between the fossil Dominican amber fauna... and the recent neotropical fauna as well between the fossil Baltic amber fauna and the recent Oriental, Ethiopian, and Australian faunas". As regards the relationships of the fossil faunas in Baltic and Dominican faunas he seems to be right. Yet we have some real evidence that, for instance, the predatory damsel bug (Nabidae) Metatropiphorus succini (Jordan) from Baltic amber belongs to a recent genus, whose representatives are found only in central America and in the southern USA (KERZHNER 1981). On the other hand, the connection between the fossil Baltic amber fauna and recent Oriental fauna is supported by the discovery of the Eocene reduviid (Emesinae) Collarhamphus mixtus PUTSHKOV et POPOV, which is very close to the recent Oriental genus Stenorhamphus from Sri Lanka (PUTSHKOV & POPOV 1995, POPOV & PUTSHKOV 1998). Moreover, in support of this opinion one may mention the occurrence in

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Baltic amber of other reduviids (see below) from the typical Oriental subfamily Centrocneminae (PUTSHKOV & POPOV 1993, 1995) and also some fossil plant bugs (Isometopinae, Cylapinae and Psallopinae), whose recent relatives have been discovered in the subtropical and tropical faunas of south-east Asia, and central and even South America (see below for other examples). A record of the spider-web bug Pavlostysia wunderlichi POPOV of the tropical Plokiophilidae from Baltic amber (POPOV 2008) is not totally unexpected, as other families known at present only from the Southern Hemisphere also occur there, e.g. Thaumastocoridae (Proxylastodoris gerdae BECHLY et WITTMANN); recent representatives of this family show a discontinuous southerly distribution: South America, Australia, the Caribbean and south India (BECHLY & WITTMANN 2000, HEISS & POPOV 2002). Even one reduviid Proptilocnemis longispinus (Holoptilinae) from Bitterfeld amber was associated with the extant Australian genus Ptilocnemis (HEISS 2009). As noted by GRIMALDI (1996), there are in Baltic amber inclusions of some plants and animals whose recent representatives are distributed in south-east Asia, Australia and even Chile. Another connection between the extinct Heteroptera from Eocene Baltic amber with the tropical regions is demonstrated by the amphibious family Hydrometridae (water measurers). A peculiar group of water measurers belonging to the extinct genera Limnacis GERMAR (L. succini GERMAR et BERENDT, 1856 and L. hoffeinsi POPOV, 1996) and Metrocephala POPOV (M. anderseni POPOV, 1996 and M. schaeferi ZETTEL et HEISS, 2011) have exhibited the greatest similarity to the monotypic genera Chaetometra and Dolichometra (POPOV 1996). The species of these genera are endemic to the Marquesas Islands (South Pacific). The occurrence of abberant hydrometrids in Eocene Baltic amber supports Andersen's hypothesis (ANDERSEN 1977, 1982) of a primitive cosmopolitanism in the family Hydrometridae. Moreover, a very recently described smaller water strider (Veliidae) from Baltic amber was placed in the extant genus Baptista, whose species are nowadays spread throughout south and south-east Asia (ZETTEL & HEISS 2011a). After the recent review of fossil Gerromorpha (34 taxa) by DAMGAARD (2008), some other records need to be added: the hebrid Miohebrus anderseni GARROUSTE et NEL (2010) and Mesovelia dominicana GARROUSTE et NEL (2010) from Dominican amber, the hydrometrid Metrocephala schaeferi ZETTEL et HEISS (2011b), and the gerrids Succineogerris larssoni ANDERSEN (2000) and Succineogerris nilsi ZETTEL et HEISS (2011b) from Baltic amber. At the same time, water bugs of the family Corixidae from Baltic amber (WICHARD & WEITSCHAT 1996) belong to the subfamily Corixinae, widespread in the Palaearctic and Nearctic regions, especially in the temperate zones. Most Palaearctic species of the primitive cosmopolitan dipsocoromorphan family Ceratocombidae (ŠTYS 1989), the representatives of which are not so rare in Baltic amber (Popov, pers. comm.), overwinter in the egg stage (ŠTYS 1990).

The majority of the described and especially the undescribed fossil Heteroptera are

represented by plant bugs of the family Miridae, whose oldest finds are known from the Upper Jurassic of south-western Kazakhstan (BECKER-MIGDISOVA 1962, POPOV 1968, HERCZEK & POPOV 2001) and from the Middle Cretaceous (Cenomanian - Turonian) in eastern Siberia (POPOV & HERCZEK 1998). They are the largest family of the modern Heteroptera, spread all over the world, with about 1400 genera and over 10 000 species known to date (SCHUH 1995, SCHUH & SLATER 1995, KERZHNER & JOSIFOV 1999). They are also generally dominant in the fauna of bugs in the most famous Baltic amber and probably in Ukrainian (s.l.) amber too. About 70% of the described fossil bugs are mirids (Miridae, over 40 genera and more than 60 species); 25% of them are represented by the subfamilies Isometopinae (7 genera and ca. 10 species) and 32% are Cylapinae (over 10 genera and over 20 species) (POPOV & HERCZEK 2008). In fact, among 120 inclusions of true bugs in the collection, 68% of fossils belong to this family. All these plant bugs represent 6 subfamilies: Cylapinae (27 imagines and 4 nymphs), Isometopinae (20 imagines), Psallopinae (3 imagines), Mirinae (4 imagines and 3 nymphs), Phylinae (5 imagines), Orthotylinae (1 imagines) and Miridae incertae sedis (5 imagines and 4 nymphs). Moreover, some other mirids from Baltic amber are known to belong to two other subfamilies: Deraeocorinae (Deraeocoris balticus HERCZEK et GORCZYCA, 1991) and ?Bryocorinae (Mixocapsus eocenicus HERCZEK, 1991). One more member of the subfamily Mirinae was just recently described from Baltic amber as Stenoptera sambiensis HERCZEK et POPOV (2009). It is considered to be a representative of the nearest surmised extant genus Pachypterna inhabiting Coniferaceae, in particular, Pinus cembra (FRANZ & WAGNER 1961, WAGNER & WEBER 1964). A more realistic picture of all fossil mirid finds is given in POPOV & HERCZEK (2008), although it cannot claim to give an absolute real ratio of the subfamily taxa of Miridae.

Nevertheless, such closely-related subfamilies as Cylapinae, Isometopinae and Psallopinae might represent a more practical ratio of their taxa (generic and species level) in the Late Eocene faunas of Baltic and Ukrainian (Rovno) ambers. Our knowledge of the biology of these subfamilies is still very poor, but they are usually associated with fungi and tree bark or rotten logs mainly of Coniferaceae, where they have a predatory mode of life. As is well known, the Pinaceae were widespread in the temperate to subtropical Eocene forest from which the fossil resins originate (GANZELEWSKI 1997). Most probably the source of the resin was originally the open mixed forests of pine (*Pinus succinica*) called *"Pinus succinifera*" and oak (very small "stellate hairs" from oak-tree flowers), a distinguishing feature of Baltic amber, that covered the areas of the Fennoscandian High Shield and also the Volhynian Ukrainian Crystalline Shield during the Eocene. Among other plant inclusions (fungi, lichen, moss and ferns) a large number of deciduous trees were found such as oak, beech, red chestnut, elm, laurel, willow and maple (CZECZOTT 1961, ERICHSON & WEITSCHAT 2008). In addition, there were flowering thuja trees,

cypress, palm trees, magnolias (shrubs) and cinnamon (PIELIŃSKA 1998) with the groups of true bugs clearly associated with them. A later reconstruction of the so called "amber forest" environment was done by KOHLMAN-ADAMSKA (2001), who demonstrated that various trees occupied large areas in the mountain forests, open forest-steppes, and waterlogged riverside forests.

The Cylapinae and Isometopinae take first place as regards the number of inclusions and they are predominant in taxonomic diversity, containing 17 genera and 28 described species (POPOV & HERCZEK 2008, HERCZEK & POPOV, in press). However, they are still poorly investigated and their actual number must have been much greater. Several additional genera and species of these subfamilies that we discovered (HERCZEK & POPOV) await description. The overwhelming majority of recent genera and species of these groups are most typical of tropical and subtropical regions; although a series of Cylapinae and Isometopinae taxa from Baltic amber have so far been described (GERMAR & BERENDT 1856, JORDAN 1944a, b, CARVALHO 1966, CARVALHO & POPOV 1984, HERCZEK & POPOV 1997a, b, 1999, 2000, 2005, HERCZEK 1991a, b, 1993, POPOV & HERCZEK 1992, 1993b, 2003, HERCZEK et al. 2005), the question concerning the original distribution of these subfamilies and their taxonomic composition still remains open. Just recently, an unusual isometopine *Hoffeinsoria robusta* was described from Baltic amber (HERCZEK & POPOV, in press).

The most numerous cylapines in Baltic amber are species of the genus Jordanofulvius and Archeofulvius, along with some isometopinous genera (e.g. Electromyiomma and Metoisops). One undescribed isometopine, described as Metoisops kusiaki, from the collection of the Museum of the Earth was also mentioned in this connection (KULICKA & KUSIAK 1997). They usually prefer cryptic habitats on fallen trees with hard fungi, sometimes they live on soft fungi, under loose bark or in litter (SCHUH & SLATER 1995). Some authors (HERRING 1976, WHEELER & HENRY 1978, WHEELER & WHEELER 1994, AKINGBOHUNGBE 1996, GORCZYCA 2000) believe that cylapines and isometopines feed on fungi or prey on other small mycophagous insects. It is possible that some of these mirids have an alimentary link with certain fossil fungi known from Baltic amber (TIFFNEY & BARGHOORN 1974, WALKER & MINTER 1981, KIRK et al. 2001), like conidial fungus Gonatobotryum picae, which grows on the conifer seedlings of Picea baltica (DÖRFELT & SCHMIDT 2007). The dominance of these two subfamilies in Baltic amber does not mean that they were one of the most abundant subfamilies of Miridae during the Eocene. It is more probable that their occurrence in habitats such as those mentioned above and also their very small size, not exceeding 4 mm, resulted in their being drowned in the resin of coniferous trees. Apart from extinct Cylapinae from Eocene Baltic amber, we also know the authentic cylapine mirid Aragocylapus miocaenicus HERCZEK, POPOV et PEÑALVER from the Miocene of Spain (HERCZEK et al. 2000).

The first fossil Isometopinae was mentioned by HURD, SMITH & DURHAM (1962), also from Mexican amber, which was later on cited by KEILBACH (1982) and SPAHR (1988).

Psallopinae is a very small subfamily of extant plant bugs containing two recent genera - Psallops (4 species) and Isometocoris (1 species) - inhabiting tropical and subtropical regions (SCHUH & SLATER 1995), but unfortunately there is no information about their habitats since most of them were collected in light traps. The extinct Psallopinae are very important for classifying and establishing the relationship with the rather closely related plesiomorphic mirid groups of Isometopinae and Cylapinae. The first fossil psallopinous bug, Isometopsallops schuhi HERCZEK & POPOV, was found in the collection of the Museum of Earth and described from Eocene Baltic amber in 1992. Not long ago a description appeared of the oldest known psallopinous mirid in the same genus Isometopsallops (I. prokopi) from the Lowermost Eocene French amber (VERNOUX et al. 2010). One more psallopine, Epigonomiris skalski HERCZEK et POPOV (1998), initially described in the subfamily Cylapinae, was later on placed in this subfamily (POPOV & HERCZEK 2008). Two other representatives of this group, Cylapopsallops kerzhneri POPOV et HERCZEK (2006) and Epigonopsallops groehni HERCZEK et POPOV (2009), were described from Baltic amber as well. There are some other undescribed Psallopinae bugs (genera and species) including the extant genus Psallops from the Baltic and also from Saxonian amber (HERCZEK 2007). The genus Psallops is most probably a relict mirid group (SCHUH 1976), representatives of which have still not been described. Besides the abovementioned psallopinous mirids, one more undescribed species was recently found in Dominican amber (HERCZEK 2011b, hic). The discovery of fossil psallopine bugs in Baltic, French and Dominican ambers indicates that the appearance and spread of this peculiar group happened during the early Cenozoic (POPOV & HERCZEK 2006).

In the collection of the Museum there are also a few specimens of three other subfamilies of Miridae: Mirinae (7 specimens), Phylinae (5 imagines) and Orthotylinae (1 imago) – all of the largest and most numerous recent groups of plant bugs that are widespread in tropical, subtropical and temperate zones (SCHUH & SLATER 1995). They are considered to be mainly phytophagous (feeding on new foliage, flowers or fruit or even pollen), phytozoophagous and zoophagous insects. It is more probable, that (like Cylapinae) they were not rare and that their recent species are not closely associated with coniferous vegetation. In fact, most fossil species (described and undescribed) belonging to these subfamilies are so far known from numerous Cenozoic insect taphocoenoses of western Europe (e.g. Germany, Poland, Russia, Ukraine, Croatia, Denmark, France and Spain) and also North America (USA, Florissant) (POPOV & HERCZEK 2008).

The first real extinct representatives of Phylinae (*Hallodapomimus elektrinus* HERCZEK and *Hallodapomimus succinus* HERCZEK) from Baltic amber were from the extant tribe Hallodapini (HERCZEK 2000) with about 50 extant genera from the southern Palaearctic,

Africa, the Orient, and North America (SCHUH 1995). Recently (HERCZEK et al. 2010), another new genus *Leptomimoides* with a new species *L. jonasdamzeni* (nr. 26452) was established, as well as a new species from the Eocene genus *Hallodapomimus* (*H. krzeminskiorum* HERCZEK et POPOV). Most probably another mirid of "*Phytocoris*" angustulus GERMAR et BERENDT (1856) from Baltic amber also belongs to this subfamily (HERCZEK & POPOV 1997a).

The second most frequent heteropteran family met with in amber is the modern family Anthocoridae (the flower bugs), containing about 100 recent genera and 600 recent species (PERICART 1996), whose representatives are widespread in all zoogeographical regions. Most members of this family are predatory, feeding on other insects and mites in decaying vegetable matter or under bark; sometimes they feed on pollen. Anthocoridae are probably not rare in amber resins, although as far as Baltic amber is concerned, only the oldest mention by MENGE (1856) of the modern genus Anthocoris is definite. The first representatives of the subfamily Lyctocorinae, from the extant genus Xylocoris (BARTHEL & HETZER 1982), were recorded in Saxonian (Bitterfeld) amber. Recently, some Lyctocorinae were described from Baltic and Ukrainian (Rovno) ambers: one was Persephonocoris kulckae POPOV et HERCZEK (2001), and two others, Lyctoferus kupryjanowiczi POPOV and Lyctoferus similis POPOV (2003b), are at the Museum of the Earth. Later, POPOV (2006) described another anthocorid from Baltic amber as Loricula ablusa: it had been incorrectly placed in Microphysidae and was later tentatively placed in the Oriini tribe (POPOV & HERCZEK 2009). Just recently the first representatives of the Cardiastethini tribe (Lyctocorinae) were described as having an unusually short rostrum (POPOV et al. 2011a, b). The oldest and only known fossil anthocorid from the other subfamily Lasiochilinae (det. R.T. Schuh) was recorded from Late Cretaceous amber of New Jersey (GOLUB & POPOV 2000c). There are 9 specimens (8 imagines and 1 nymph) of flower bugs in the collection of the Museum of the Earth. Also examined were ca. 100 other anthocorid specimens from different collections, among them Lyctocorini, Lyctoferini, Cardiastethini (Lyctocorinae), Anthocorini and Oriini (Anthocorinae) from Baltic, Ukrainian, and Saxonian (Bitterfeld) ambers (Popov, pers. comm.).

The earliest Anthocoridae (flower bugs) are known from the Middle Jurassic of northeastern China (HONG 1983, YAO et al. 2004), from the Early Cretaceous of eastern Transbaikalia (POPOV 1990), and from the Early Cretaceous of north-eastern China (HONG & WANG 1990). There are some undescribed Early Cretaceous anthocorids from central Mongolia and a single anthocorid-like hemelytron from the Lower Cretaceous of Australia (POPOV 2003). Some undescribed flower bugs have been recorded from Upper Cretaceous (Campanian) amber of Canada (MCALPINE & MARTIN 1969, SKIDMORE 1999), northwestern Siberia, the Taimyr Peninsula (ZHERIKHIN & SUKATSHOVA 1973), and also from Lower Cretaceous Lebanese amber from the tribe Lyctoferini (Popov, pers. comm.). Anthocoridae were also reported in Lebanese amber by WHALLEY in 1981 (POINAR 2001). Most probably all Mesozoic anthocorids belong to the ancient Lyctocorinae. In the Earliest Miocene (Aquitanian) of Rott (near Bonn), Germany, the first member of the subfamily Anthocorinae (Anthocorini) *Themnostethus blands* was described by STATZ & WAGNER (1950). From the existence of ancient flower bugs (Anthocoridae) in Cretaceous and the Earliest Cenozoic, one may infer that aphids of the extinct family Palaeoaphididae, one of the most widespread groups of terrestrial insects in North America (USA, Canada), Siberia and northern China in these periods (KANIA & WEGIEREK 2008), most probably constituted the main source of food for anthocorids (POPOV 2003b).

Anthocorids are one of the common bug groups in Eocene Baltic and Ukrainian amber, mostly represented by numerous common specimens of *Electrocoris brunneus* USINGER and *Electrocoris pubescens* USINGER (POPOV 2003b). This genus was tentatively linked to the Mycrophysid-Anthocorid complex USINGER 1942). But after USINGER'S descriptions of 1942, nearly all relevant publications on the family-level classification of the Cimicomorpha were made later on (CARAYON 1961, 1974, ŠTYS & KERZHNER 1975, SCHUH & ŠTYS 1991). Further investigations must reveal the status of *Electrocoris*, i.e. whether it is a microphysid or a cimicoid (POPOV 2008). Here one should take into account the fact that Microphysidae and Cimicoidea are completely separate lineages (SCHUH & ŠTYS I. c. 1). One specimen of this genus in BACHOFEN-ECHT (1949, p. 165, Fig. 158) was erroneously classified by that author as belonging to Lygaeidae (POPOV & HERCZEK 1993a). There are 7 specimens (4 imagines and 3 nymphs) of *Electrocoris* sp. prop. *brunneus* USINGER, 1942 in the collection of the Museum of the Earth.

The family Microphysidae was discovered quite recently (see below). It is a small family (about 30 recent species) of very small bugs (no more than 3 mm), most of them distributed mainly in temperate zones of the Palaearctic and a few in Nearctic regions. Microphysids are found predominantly in leaf litter, on tree bark, on branches and trunks of old trees often covered by mosses or lichens, and also in anthills. They are active predators, sucking small arthropods, like mites, springtails, aphids, psocids, psyllids and some other arthropods. Examination of numerous heteropteran inclusions shows that microphysids are not as rare as expected and that they are probably one of the numerous groups of Heteroptera in Baltic, Ukrainian and Saxonian ambers, like Cylapinae and Isometopinae of the family Miridae (POPOV 2006). Like the above-mentioned mirids, most Microphysidae were also associated with coniferous vegetation.

The first record of a fossil species of Microphysidae, later described as *Loricula ceranowiczae* POPOV from Baltic amber (POPOV 2004), was earlier reported by KULICKA et al. (1996). To date 9 species of the genus *Loricula (L. perkovskyi* PUTSHKOV et POPOV, *L. ceranowiczae* POPOV, *L. damzeni* POPOV, *L. pericarti* POPOV, *L. finitima* POPOV, *L. heissi* POPOV, *L. ocellata* POPOV, *L. samlandi* POPOV, *L. polonica* POPOV et HERCZEK) were

described from Baltic and Ukrainian (Rovno) amber (PUTSHKOV & POPOV 2003, POPOV 2004, 2006, POPOV et al. 2008). One peculiar minute bug of this family was also described recently from Baltic amber as *Tyttophysa sylwiae* POPOV et HERCZEK (2009). There are two microphysid type species (*L. ceranowiczae* and *L. damzeni*) at the Museum of the Earth. There are some more undescribed microphysid species and one new genus from Baltic and Saxonian amber (Popov, pers.comm.). One of the reasons for this poor knowledge of the fossil Microphysidae is their striking resemblance to members of the family Anthocoridae (especially to the Oriini, which are the smallest), to which they have usually been erroneously allocated. For instance, *Loricula ablusa* POPOV was originally described in the family Microphysidae (POPOV 2006) but later transferred to Anthocoridae. Recently, a new cimicomorphan family from the middle Eocene amber of France (PERRICHOT et al. 2006) – Abboidae – was described, which is most probably a coleopteroid form of Microphysidae (Popov & Golub, pers. comm.). Without doubt, the oldest microphysid bug *Popovophysa entzmingeri* MCKELLAR et ENGEL (2011) was found in late Cretaceous (Campanian) amber from Alberta, Canada.

The damsel bugs (Nabidae) are a small family of mainly predatory insects, including about 20 genera and 500 species (KERZHNER 1981, SCHUH & SLATER 1995), whose members are widespread in all zoogeographical regions. They are especially abundant (taxonomically and in number) in the Palaearctic and Nearctic regions. Fossil damsel bugs are very rare in European ambers, including only a few specimens (5) of the extant central American genus *Metatropiphorus* (*M. succini* JORDAN) in the collection of the Museum of the Earth. A series of undescribed specimens are in Dominican amber, which indisputably belong to two new genera and species from the tribe Nabini (Nabidae), which are deposited in the American Museum Natural History of New York (Popov, pers. comm.). All this material is in the process of preparation. One specimen of this nabid is owned by the Museum of the Earth of the Polish Academy of Sciences (Warsaw).

Two type specimens of peculiar true bugs *Aradus frater* POPOV (1978) and *Aradus popovi* HEISS (1998) in the collection belong to the modern family Aradidae (flat bugs or bark bugs), widespread on all continents except Antarctica. The majority of aradids are mycetophagous. Their species are associated mostly with the bark of decaying coniferous trees, especially that of *Pinus succinica*. There are about 2000 described extant species (KORMILEV & FROESCHNER 1987, SCHUH & SLATER 1995), but fossils are quite rare and mostly found in Eocene Baltic amber, where they are represented mainly by species of the recent genus *Aradus*. The oldest aradids are known from the Early Cretaceous of Mongolia – *Aradus nicholasi* (POPOV 1989a), from the Middle Cretaceous of north-eastern Siberia – *Aradus creticus* (KORMILEV & POPOV, 1986), and Burmese amber – *Archearadus burmensis* HEISS (HEISS & GRIMALDI, 2001). To these we should add one *Neuroctenus* sp. from the Miocene in Thailand (ENDO & FUJIYAMA 1966), *Aradus andancensis* MARCHAL,

GUILBERT, BRISAC et NEL (2011) from the Late Miocene of France, and *Calisiopsis* from Dominican amber (FROESCHNER 1992). Until recently, 4 species of the genus *Aradus* (Aradinae), *Mezira succinica* USINGER and *Calisius balticus* USINGER (USINGER 1941) were described from Baltic amber; the last-mentioned was also identified in the Lowermost Eocene French amber (MARCHAL et al. 2011). Now, thanks to the Austrian heteropterologist Ernst Heiss (Innsbruck) the number of fossil aradid species has tripled: he described 10 new species of *Aradus* (Aradinae), 3 species of *Aneurus* (Aneurinae) and 4 *Calisius* species (Calisiinae) from Baltic (HEISS 1997, 1998, 2000 a, b, 2001, 2002 a, b, c), and Dominican amber (HEISS 2000b). Seven new species of Aradidae belonging to the recent genera *Mezira* and *Neuroctenus* from the Middle Eocene of Germany were also described in the work of WAPPLER & HEISS (2006 a, b, c).

In the modern fauna there are approximately 2000 species of the cosmopolitan family Tingidae - cryptic cimicomorphan bugs, or lace bugs - which traditionally comprises two subfamilies (sensu FROESCHNER 1996, PÉRICART & GOLUB 1996), the Cantacaderinae and the Tinginae (DRAKE & RUHOFF 1960, 1965). 40 fossil species of Tingidae have so far been described or recorded, mainly in the last ten years. The oldest fossil tingids Golmonia pater POPOV and Sinaldocader drakei POPOV belonging to the special Mesozoic subfamily, were known from the later Early Cretaceous of central Mongolia (POPOV 1989a). Most of them are from the Cenozoic era (GOLUB & POPOV 1999, 2000 b, NEL 1992, WAPPLER 2003), especially from the Eocene of Western Europe, e.g. Grube Messel of Germany (WAPPLER 2003) and the amber of the Paris basin, France (NEL et al. 2004). The first lace bug, Tingis quinquecarinatus, was described by GERMAR & BERENDT (1856) from Eocene Baltic amber (Prussian Formation); it was subsequently classified as a new cantacaderid genus Paleocader (FROESCHNER 1996). Quite numerous tingids were described much later (especially during the last decade) from Baltic (DRAKE 1950, GOLUB 2001, 2004, GOLUB & POPOV 1998, 2002, 2005a, b, HEISS 2002 c, d). Ukrainian, Saxonian (GOLUB 2004, GOLUB & POPOV 2007) and Dominican ambers (GOLUB & POPOV 2000a, b, 2003, GOLUB et al. 2009). Most of the other fossil tingids are known from western Europe (Oligocene – the Isle of Wight, England; Oligocene – Aix-en-Provence and Luberon-en-Provence, Cereste, France; Miocene - Oeningen, Baden, Germany; Miocene - Crotensee, Bohemia, Czech Republic; Miocene - Radoboj, Croatia) and North America (Oligocene - Florissant, Colorado, U.S.A.). There is also one more tingid from the modern genus Agramma (ZHANG 1989) from the Miocene of western China (Shandong Province). Nearly all the extinct Cenozoic lace bugs belong to the subfamily Cantacaderinae (mostly the Phatnomini tribe), recent members of which are almost exclusively distributed in the tropics and subtropics. The genera Paleocader (Cantacaderini), Sinalda and Intercader, each consisting of several species, are very common in European amber. Another cantacaderid bug was described from the Lowermost Eocene amber of the Paris basin (France) as Parazetekalla eocenica

(NEL et al. 2004a). Recently a peculiar plesiomorphic lace bug from the Late Cretaceous amber of Spain was found. This is probably one of the ancestral forms of the Cantacaderini belonging to a new (sub)family (Golub & Popov, pers. comm.). The collection of the Museum of the Earth also boasts *Paleocader strictus* GOLUB et POPOV (1998), nymphs of *Paleocader* sp. from Baltic amber and *Sinalda baltica* DRAKE (1950) from Ukrainian (Rovno) amber (GOLUB 2004).

The predatory family Reduviidae, or assassin bugs, is one of the largest extant heteropteran groups (about 8000 recent species), comprising 23 subfamilies mainly distributed in the tropical and subtropical regions of both hemispheres (PUTSHKOV 1987, MALDONADO 1990, SCHUH & SLATER 1995). Generally speaking, reduviids in amber are probably not so rare: there are quite a few of them, especially in Eocene Baltic and Ukrainian amber. The earliest description of an assassin bug from Baltic amber, Platymerus insignis (Reduviinae) which most probably belongs to the recent genus Reduvius (PUTSHKOV 1987), was made by GERMAR & BERENDT (1856). Later, WASMANN (1932) described Proptilocerus dolosus (Holoptilinae) from Baltic amber, which is very similar to the recent species P. venosus from Indo-Malaya (PUTSHKOV 1987). Recently a revision of the type P. dolosus WASMANN (5th nymphal stage) together with 5 new inclusions of the macropterous adult of this species was published (HEISS 2009). The author has also described a new holoptilin Proptilocnemus longispinus gen et sp. nov. from Bitterfeld amber, which seems to be related to the extant Australian genus Ptilocnemis (HEISS l.c.). In this connection there is an interesting find of another holoptilin bug - Praecoris dominicana POINAR - from Dominican amber, which is very similar to the extant neotropical genus Neolocoptiris (POINAR 1991).

Judging by the photo in BACHOFEN-ECHT (1949, p. 165, Fig. 159) this reduviid is probably close to the genera *Peirates* or *Ectomocoris* of the subfamily Peiratinae, and another reduviid in the same work (p. 166, Fig. 164) definitely belongs to the subfamily Emesinae (tribe Metapterini). The oldest emesin is recorded from the Later Cretaceous amber of New Jersey (GRIMALDI et al. 1989, Fig. 13e). Members of the latter subfamily are quite common among all other reduviids, especially in Dominican amber (POPOV 1987a, b, 1989b, 1993, MALDONADO & SANTIAGO-BLAY 1993). There are also several undescribed species of Emesinae in the Staatliches Museum für Naturkunde in Stuttgart. Two more emesins were also described from Baltic amber (PUTSHKOV & POPOV 1995, POPOV 2003a): one of them, *Collarhamphus mixtus* PUTSHKOV et POPOV, was identified as belonging to the plesiomorphic tribe Collartidini, which shows characters of two related subfamilies Saicinae and Emesinae. All the other above-mentioned emesins from Dominican, Baltic and Ukrainian amber belong to the Ploiariolini tribe, a rather advanced group of the Emesinae, e.g. *Danzigia christelae* POPOV from Baltic amber, defined as the oldest extinct representative of the largest emesin extant tribe Ploiariolini (POPOV 2003a). The peculiar

reduviid (*Koenigsbergia herczeki* POPOV, imago and nymph) was recently found in Baltic amber, which belongs to the primitive African tribe Themonocorinae of the subfamily Phymatinae (another specimen is also known from the collection of Hans Hoffeins, Hamburg). Its recent representatives are only known from South Africa (POPOV 2003a and Jakobs, pers. comm.). The two other reduviids from Baltic amber, *Redubitus centrocnemarius* PUTSHKOV et POPOV and *Redubinotus liedtke* POPOV et PUTSHKOV (Redubitini), belong to the typical Oriental subfamily Centrocneminae, whose recent representatives appear to be subcorticolous (POPOV & PUTSHKOV 1998). There are two reduviids from Baltic (*Redubitus* sp., Centrocneminae) and Ukrainian (Emesinae, Ploiariolini) amber at the Museum of the Earth.

Other heteropteran families in the collection of the Museum of the Earth are only represented by inclusions in Baltic amber. One of them is the small family Ceratocombidae (about 10 genera and 50 recent species are described), which is represented by a specimen of the recent cosmopolitan genus *Ceratocombus*, which has 25 described and hundreds of undescribed species, particularly from the Indo-Pacific (ŠTYS 1995). This is a little-known family, whose representatives range in length from 1.5 to 3.0 mm. Most of the members of this family inhabit humid leaf litter, decaying wood, mosses and sphagnum in forests and meadows. Ceratocombidae is poor in species in cold and temperate zones, but has a rich diversity in tropical areas. In Europe *Ceratocombus* species live mainly in bracken litter mixed with needles in coniferous woods (ŠTYS, 1.c.). There are also some more specimens of this genus from Baltic amber in different collections (Popov, pers. comm.).

One specimen from Baltic amber (No. 26180), Proxylastodoris gerdae (BECHLY & WITTMANN 2000), belongs to the small tropical family Thaumastocoridae (palm bugs). It is closely related to the extant monotypic genus Xylastodoris (Xylastodorinae) known from Cuba and Florida. Recent Xylastodorinae feed only on palms, e.g. Xylastodoris luteolus BARBER feeds on the developing fronds of the royal palm Roystonea regia (BARBER 1920, BARANOWSKI 1958), where it sometimes causes serious damage (SCHUH & SLATER 1995). Besides other known plants in Eocene Baltic amber, plant inclusions of palm trees were found (PIELIŃSKA 1998, ERICHSON & WEITSCHAT 2008) that undoubtedly served as a habitat for these fossil plant bugs. The oldest undescribed thaumastocorid bug is known from the Late Cretaceous amber of New Jersey (GOLUB & POPOV 2000c). Another old palm bug Protodoris minusculus NEL et al. (2004c) from the Lowermost Eocene amber of Paris basin (France) was described. Two fossil species have so far been described: Palaeodoris lattini POINAR & SANTIAGO-BLAY (1997) in Dominican amber and Xylastodoris gerdae BECHLY et WITTMANN (2000) in Baltic amber. The latter was placed in a new extinct genus Proxylastodoris (HEISS & POPOV 2002). Some specimens of Proxylastodoris gerdae are also found in different collections (Popov, pers. comm.).

There is one particular specimen from Ukrainian (Klesov) amber, belonging to the

family Saldidae (shore bugs), whose two subfamilies (Saldinae and Chiloxanthinae) comprise 26 genera and 335 recent species (SCHUH & SLATER 1995, SCHUH & POLHEMUS 2009). All the members of this family are predators of small invertebrates.

Some of the oldest saldids, recently described from the Early Cretaceous (ca.125 Ma) of north-eastern China (Brevrimatus pulchalifer), belong to Chiloxanthinae (ZHANG et al. 2011). If this is true then they may be considered to be the oldest representatives of this subfamily. Two fossil genera Oligosaldina from the Late Oligocene of Germany (STATZ & WAGNER 1950) and Propentacora (= Oreokora) from the Miocene of the USA (LEWIS 1969) belong to the more generalized subfamily Chiloxanthinae. The latest finding of Saldidae (Salda littoralis L.) was recorded in Recent Late Glacial clay (JESSEN 1923). Only one extinct shore bug (Salda exigua) was known from Baltic amber (GERMAR & BERENDT 1856). The saldid specimen from Klesov (Ukrainian amber), which is at the Museum of the Earth, most probably belongs to the recent genus Pentacora (Chiloxanthinae) (Popov, pers. comm.). COBBEN (1971) also described the unusual fossil Leptosalda chiapensis from Mexican amber (Late Oligocene-Early Miocene), which was placed in a new, separate extinct subfamily Leptosaldinae possessing characters of both Saldidae and Leptopodidae (COBBEN 1980), but SCHUH & POLHEMUS (1980) transferred Leptosalda to Leptopodidae. Subsequently, it was suggested that the extinct Leptosalda and the extant Saldolepta (united on the grounds of their great similarity into the independent subfamily of Leptosaldinae) should be placed within the saldoid family Omaniidae (POPOV 1989c).

Two more unusual specimens of *Heissinia serafini* POPOV, described from Baltic amber (POPOV 2001), are the first ones from Ukrainian amber (Klesov and Rovno). One of them was obtained recently for the Museum of the Earth's collection, and the other one belongs to the Schmalhausen Institute of Zoology of the National Academy of Sciences of Ukraine. It undoubtedly belongs to the small phytophagous family Piesmatidae of the tribe Heissianini, whose modern representatives exhibit a Gondwanan distribution pattern (South America + Australia). Several specimens are also known from different collections; one of them (e.g. coll. J. Serafin, Poland) was illustrated as Piesmatidae (GIERŁOWSKI 1999).

Two specimens represent one of the largest heteropteran families – Lygaeidae (ca. 10 000 species) comprising over 20 subfamilies which are widespread all over the World. They belong to the phytophagous subfamilies Geocorinae and Rhyparochrominae. In spite of the numerous taxa, both fossil and modern, they are generally very rare in amber (e.g. see WEITSCHAT & WICHARD 1998). As far as other fossil lygaeids are concerned, they are numerous and common in the best known Cenozoic insect fossil sites of the in western Europe (Germany, France, Switzerland) and North America (Florissant, Colorado).

There are many undescribed specimens from some other families, e.g. Enicocephalidae, Ceratocombidae, Schizopteridae, Dipsocoridae, Leptopodidae, Gerridae, Miridae, Anthocoridae, Reduviidae, Microphysidae, Coreidae, Lygaeidae, Pentatomidae and some others, which are awaiting study: some heteropteran groups, e.g. the smallest dipsocoromorphan Schizopteridae, occasional specimens of which were only recorded from Cenozoic Dominican, Mexican and Baltic ambers (POINAR 1992, POPOV & HERCZEK 1993, SHCHERBAKOV & POPOV 2002) and also from Neocomian Lebanese amber (GRIMALDI et al. 2002, GRIMALDI & ENGEL 2005). Recently, the first three Mesozoic genera from the Mid-Cretaceous ambers of French, Myanmar (PERICHOT et al. 2007) and from the Lower Cretaceous amber of Lebanon (AZAR & NEL 2010) were described. We also know of several undescribed schizopterids from Eocene Baltic amber (Popov, pers. comm.).

Family/Subfamily	Species	No.
Anthocoridae/Lyctocorinae	Lyctoferus kupryjanowiczi POPOV, 2003	23986 (Holotype)
Anthocoridae/ Lyctocorinae	Lyctoferus similis POPOV, 2003	24121
Anthocoridae/ Lyctocorinae	Lyctoferus sp.	26209
Anthocoridae/Lyctocorinae	Persephonocoris kulickae POPOV et HERCZEK, 2001	22931 (Holotype)
Anthocoridae/Lyctocorinae	?Persephonocoris sp.	26179
Anthocoridae/Lyctocorinae		24000
Anthocoridae inc. sed.		7943
Aradidae/Aradinae	Aradus frater POPOV, 1978	5624 (Holotype)
Aradidae/Aradinae	Aradus popovi HEISS, 1998	14693 (Holotype)
Cimicoidea	Electrocoris brunneus USINGER, 1942	3185,7198, 11486, 16823, 26286
Cimicoidea	Electrocoris sp.	20940
Cimicoidea		26366
Lygaeidae/Geocorinae		13696
Lygaeidae/Rhyparochrominae		10467
Microphysidae/Microphysinae	Loricula (Loricula) ceranowiczae POPOV, 2004	5623 (Holotype)
Microphysidae/Microphysinae	Loricula (Eocenophysa) damzeni POPOV, 2004	24107 (Holotype)
Microphysidae/Microphysinae	Loricula (M.) sp.	26176
Miridae/Cylapinae	Ambocylapus kulickae HERCZEK et POPOV, 2002	2293 (Holotype)
Miridae/Cylapinae	Archeofulvius gulosus (GERMAR et BERENDT, 1856)	14688, 26287, 26362
Miridae/Cylapinae	Balticofulvius kulickae HERCZEK et POPOV, 1997	17356 (Holotype)
Miridae/Cylapinae	Archeofulvius kotejai HERCZEK et POPOV, 2005	24333 (Holotype)
Miridae/Cylapinae	Jordanofulvius punctiger (GERMAR et BERENDT, 1856)	26360, 26361

Table. True bugs (Heteroptera) in Baltic amber in the collection of the Museum of the Earth (PAS) in Warsaw.

POPOV YU.A. et al.: Review of true bugs	(Insecta: Hemiptera, Heteroptera) from the amber 7	17

Miridae/Cylapinae	Archeofulfius indet.	26363
Miridae/Cylapinae	Ambercylapus nigrus CARVALHO et POPOV, 1984	2344/40
		(Holotype)
Miridae/Cylapinae	Jordanofulvius sp.	7247, 9131,
		16496, 19514,
		22241, 26355,
		26356, 26357,
		26358, 26359,
Miridae/Cylapinae/Fulvini		26364 ?, 26365 23116
21		
Miridae/Cylapinae		2293,5629, 8472,
		12232, 16777, 23873, 23984
Miridae/Isometopinae	Archemyiomma sp.	26171
Miridae/Isometopinae	· · ·	26167, 26169,
windae/isometopinae	Clavimyiomma sp.	26173
Miridae/Isometopinae	<i>Electromyiomma polonicum</i> POPOV et HERCZEK,	13098
	1992	(Holotype),
		23988
Miridae/Isometopinae	Myiomma voigti POPOV et HERCZEK, 1992	13670
Miridae/Isometopinae	Metoisops kerzhneri POPOV et HERCZEK, 1992	14646 (Holotype)
Miridae/Isometopinae	Metoisops sp.	23135, 26168,
		26170, 26172
Miridae/Isometopinae	Myiomma sp.	26177
Miridae/Isometopinae	gen. indet.	26178
Miridae/Isometopinae		24519
Miridae/Isometopinae	Heffeinsoria robusta	1560 (Holotype)
Miridae/Mirinae	? Lygus	23942
Miridae/Mirinae		6430, 22101,
		22391, 23073,
		26175
Miridae/Orthotylinae		24009
Miridae/Phylinae/Hallodapini	Hallodapomimus elektrinus HERCZEK, 2000	22918 (Holotype)
Miridae/Phylinae/Hallodapini	Leptomimoides jonasdamzeni HERCZEK et POPOV, 2010	26452 (Holotype)
Miridae/Phylinae		10515, 14681
Miridae/Psallopinae	Epigonomiris skalskii HERCZEK et POPOV, 1998	22932 (Holotype)
Miridae/Psallopinae	Isometopsallops schuhi HERCZEK et POPOV, 1992	23933
Miridae/Psallopinae	<i>Electromyiomma weitschati</i> POPOV et HERCZEK, 1992	26174
Miridae/Psallopinae	gen. et sp. indet.	26166
Miridae inc. sed.		10767, 10773,
		15844, 16235,

		17588, 23805, 23983
Nabidae/Nabinae/Nabini	Metatropiphorus succini (JORDAN, 1952)	26213, 26284
Piesmatidae	Heissiana serafini POPOV, 2001	24713
Reduviidae/Centrocneminae	Redubitus sp.	23989
Saldidae/Chiloxanthinae	Pentacora sp. (? Propentacora) gen. ?	24001
Thaumastocoridae	<i>Proxylastodoris gerdae</i> (BECHLY et WITTMANN, 2000)	26180
Tingidae/Cantacaderinae	Sinalda baltica (DRAKE, 1950)	23985
Tingidae/Cantacaderinae	Paleocader strictus GOLUB et POPOV, 1998	24105 (Paratype)
Tingidae/Cantacaderinae	Paleocader sp.	24106
Heteroptera inc. sed.		14893

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