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HAEMATOPHAGOUS ARTHROPODS IN BALTIC AMBER

AGATA PIELOWSKA, ELŻBIETA SONTAG
and RYSZARD SZADZIEWSKI*

Laboratory of Evolutionary Entomology and Museum of Amber Inclusions, Department of Invertebrate Zoology and Parasitology, Faculty of Biology, University of Gdańsk, Wita Stwosza 59, PL-80-308 Gdańsk
**Corresponding author: e-mail: ryszardszadziewski@gmail.com*

Abstract.— Haematophagous i.e. blood-feeding or blood-sucking arthropods described from Paleogene Baltic amber are reviewed and commented on. Arthropods feeding on blood from mammals and birds, and occasionally on reptiles and amphibians, are reported as inclusions in fossil resins dated back to the Lower Cretaceous. Eocene Baltic amber from deposits in the Gulf of Gdańsk, Rovno and Bitterfeld, dated from 35 to 50 million years ago, contains 48 fossil species of blood-feeding arthropods placed in extant and extinct genera. Haematophagous fossil arthropods from Acari (1 species), Phthiraptera (+), Siphonaptera (4), and Diptera (43 species) are reported in Baltic amber. Blood-sucking flies are represented by six families: Ceratopogonidae (11), Corethrellidae (5), Culicidae (5), Psychodidae (5), Simuliidae (9), and Tabanidae (8 species). The percentage of species of blood-sucking dipterans in the Baltic amber forest was similar to that in the extant fauna of Poland (3.4%, and 3.2%, respectively). A catalogue of named haematophagous arthropods reported from Baltic amber is provided.

Key words.— amber deposits, Arthropoda, blood feeding, Eocene, fossil flies, fossil resins

INTRODUCTION

Arthropods (phylum Arthropoda) is the most numerous group of animal taxa on the Earth. They represent a great variety of forms, live in all environmental conditions and are spread all over the globe. The number of arthropod species described exceeds one million, which is about $^{3}/_{4}$ of all animals described.

The arthropods include many parasitic species important to human health and the economy. The most important parasites are haematophages, including those arthropods that feed on vertebrate blood, and are of medical and veterinary importance as vectors of many diseases. Haematophagy, or blood feeding (αίμα (*haima*) – blood, and φαγεῖν (*phagein*) – to eat), is rather a rare feeding habit which evolved independently among annelids, arthropods and mammals. Blood-feeding or blood-sucking arthropods belong to three groups: arachnids (Arachnida, subphylum Chelicerata), insects or hexapods (subphylum Insecta or Hexapoda), and to aquatic Crustacea. Among the insects, haematophagy occurs in five orders: Phthiraptera, Hemiptera, Lepidoptera, Siphonaptera and Diptera (Błaszak 2011, 2012).

Blood-feeding arthropods of mammals and birds, and occasionally of reptiles and amphibians, are reported as inclusions in fossil resins dated back to the Lower Cretaceous (Lukashevich & Mostovski 2003). Blood-feeding arthropods are also reported in Eocene Baltic amber from deposits in the Gulf of Gdańsk, Rovno and Bitterfeld, dated from 35 to 50 million years ago (Szadziewski 2018).

The blood-feeding arthropods reported from Eocene Baltic amber belong to four orders: Ixodida, Phthiraptera, Siphonaptera and Diptera. Dipterans (6 families; 9 subfamilies; 20 genera; 43 species) are the most numerous order, making up almost 90% of all haematophagous arthropods in Baltic amber.

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CATALOGUE OF HAEMATOPHAGOUS ARTHROPODS

Phylum: **Arthropoda** Latreille, 1829

Subphylum: **Chelicerata** Heymons, 1901

Class: **Arachnida** Lamarck, 1801

Subclass: **Acari** Leach, 1817

Superorder: **Parasitiformes** Leach, 1815

Order: **Ixodida** Leach, 1815

All Ixodidae, or ticks, are grouped into three, worldwide families: Argasidae (soft ticks), Ixodidae (hard ticks), and the monotypic family Nuttalliellidae with a single species. All developmental stages of ticks are obligate blood-feeding ectoparasites of mammals, birds and reptiles (Błaszak 2011).

Hitherto, almost 900 species of ticks have been described, over 700 of which belong to the family Ixodidae (Guglielmone *et al*. 2010). Fossil ticks are reported from Upper Cretaceous, Eocene and Miocene ambers (de la Fuente 2003).

Family: **Ixodidae** Koch, 1844

The family Ixodidae (Acari: Ixodida: Ixodidae) (Fig. 1A), also known as hard ticks owing to their sclerotized dorsal scutal plate are blood-sucking, obligate temporary external parasites of terrestrial vertebrates. With 702 extant valid species, ixodid ticks make up approximately 80% of the world's tick fauna (Guglielmone *et al*. 2010). The life cycle of Ixodidae consists of one inactive development stage (egg) and three active ones (larva, nymph and adult). A parasitic and a non-parasitic phase occur in the life cycle so ticks feeds only once in each active stage (Sonenshine 1991). Ticks from the family Ixodidae have a worldwide distribution (Guglielmone *et al*. 2014).

Fossil ticks are uncommon in Baltic amber. To date, four hard ticks from two genera (*Ixodes* and *Hyalomma*) have been recorded. Except for the female of *I. succineus*, the three other specimens recorded have not been identified (Szadziewski and Sontag 2001, de la Fuente 2003). It is worth mentioning that Szadziewski and Sontag (2001) found in Baltic amber a larva of an unidentified hard tick feeding on a lizard (Fig. 1A). This is the only fossil record of a parasitic tick on a host.

Subfamily: **Ixodinae** Koch, 1844 (Vitzthum 1941)

Genus: ***Ixodes*** Latreille, 1795: 18.

Type species. *Ixodes ricinus* Linnaeus, 1758.

Ixodes succineus Weidner, 1964

Ixodes succineus Weidner, 1964: 145 (female, amber from Gulf of Gdańsk).

Subphylum: **Tracheata** Haeckel, 1866

Superclass: **Hexapoda** Latreille, 1825

Class: **Insecta** (s. str.) Linnaeus, 1758

Subclass: **Pterygota** Lang, 1888

Order: **Phthiraptera** Haeckel, 1896

Phthiraptera are obligate ectoparasites of birds and mammals. Their larvae (nymphs), males and females feed on the keratin of birds and mammals (Amblycera and Ischnocera) or feed exclusively on the blood of mammals (Anoplura). Only unidentified Phthiraptera eggs on mammalian hairs have been recorded in Baltic amber (Voigt 1952). As these eggs cannot be identified to the suborder level, it is not clear whether they were laid by a blood-sucking Anoplura or by a keratin-feeding mallophagan louse (Amblycera or Ischnocera).

Order: **Siphonaptera** Latreille, 1825

Siphonaptera (Fig. 1B) or fleas are haematophagous, wingless insects with strongly sclerotized laterally compressed bodies including some 2500 species worldwide (Whiting *et al*. 2008). The larvae are free-living. Both sexes of adult fleas lead an ectoparasitic lifestyle: they are associated with warm-blooded vertebrates, mainly of burrowing mammals: only a few families are parasites of birds (Medvedev 1997).

Family: **Ctenophthalmidae** Rothschild, 1915

Ctenophthalmidae are widespread and at the same time the most numerous family of fleas, with around 700 species belonging to 41 genera and 9 subfamilies (Bartkowska 2007). These holometabolous insects are obligate parasites of mammals, mainly rodents (Whiting *et al*. 2008). Members of the family Ctenophthalmidae occasionally take blood from humans and domestic animals. There are four developmental stages in the life cycle — egg, larva, pupa and adult. The mobile larvae are legless, eyeless and strongly elongated with biting mouthparts. In contrast to the adults, larvae and pupae are not parasites. The larvae are usually found in the nests of hosts, in places that are rarely cleaned and where dust gathers: there they feed on organic matter. Adults feed on capillary blood and leave blood-rich faeces which, in turn, are a source of food for the larvae (Krasnov 2008).

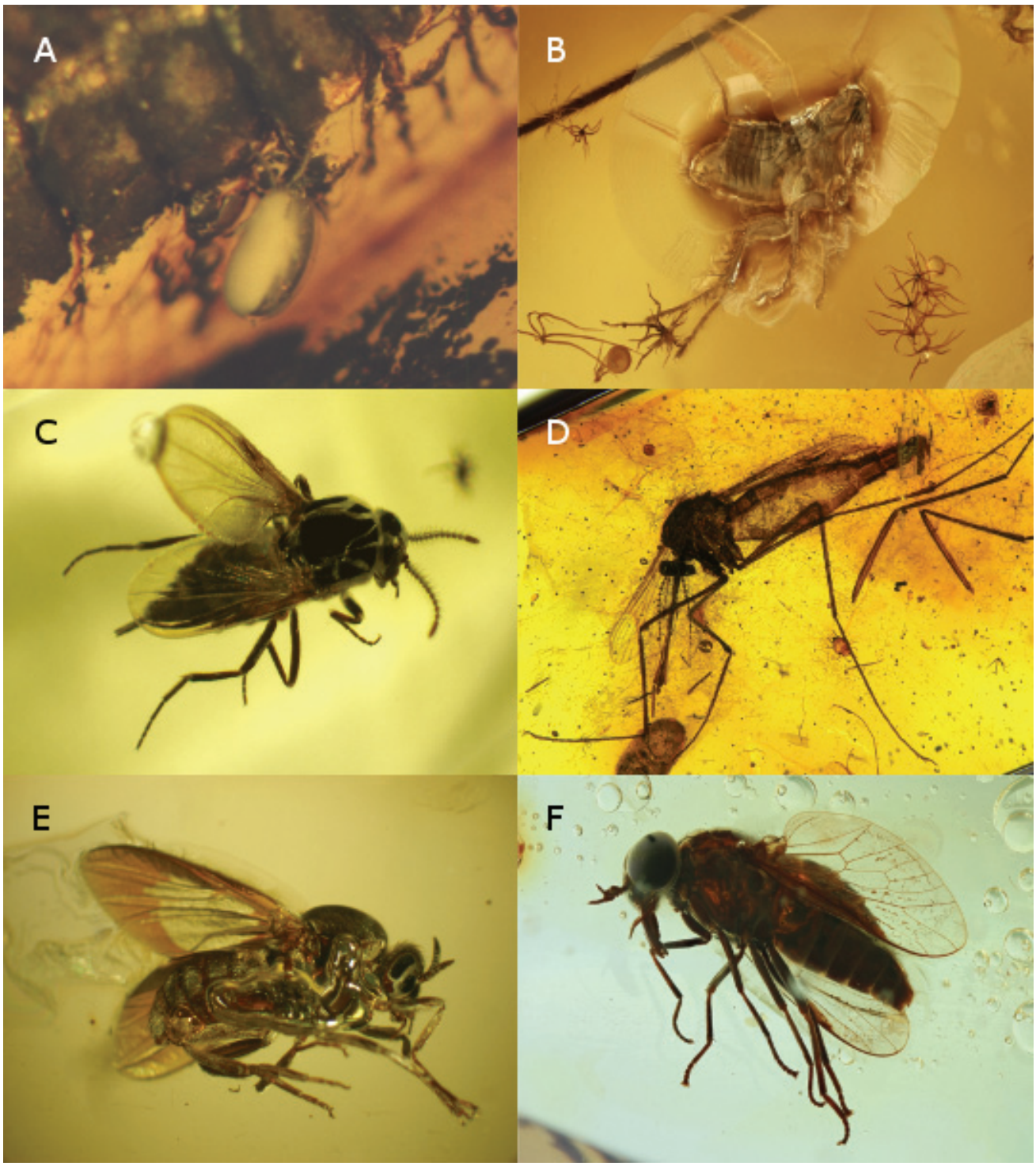

Figure 1. Haematophagous arthropods in Baltic amber: (A) larva of a hard tick (Ixodidae) feeding on a lizard; (B) male of a flea *Palaeopsylla* sp. (phot. by J. Damzen); (C) female biting midge (Ceratopogonidae) *Leptoconops rovnensis* Sontag and Szadziewski, 2011; (D) male mosquito (Culicidae) of the genus *Coquillettidia*; (E) black fly (Simuliidae) in amber from Gulf of 7Gdańsk; (F) horse fly (Tabanidae) in amber from Rovno (phot. by J. Damzen).

Four flea species belonging to the extant Palearctic genus *Palaeopsylla* Wagner have been described from Baltic amber.

Subfamily: **Ctenophthalminae** Rothschild, 1915

Genus: ***Palaeopsylla*** Wagner, 1903: 173

Type species. *Palaeopsylla similis* Dampf, 1910, by designation of ICZN, 1955.

Palaeopsylla baltica Beaucournu et Wunderlich, 2001

Palaeopsylla baltica Beaucournu et Wunderlich, 2001: 296 (female, amber from Gulf of Gdańsk).

Palaeopsylla dissimilis Peus, 1968

Palaeopsylla dissimilis Peus, 1968: 63 (male, amber from Gulf of Gdańsk); Urban 2004: 125 (undetermined specimen, amber from Bitterfeld); Perrichot 2012: 55 (male, amber from Bitterfeld).

Palaeopsylla groehni Beaucournu, 2003

Palaeopsylla groehni Beaucournu, 2003: 217 (male, amber from Gulf of Gdańsk).

Palaeopsylla klebsiana Dampf, 1911

Palaeopsylla klebsiana Dampf, 1911: 253 (female, amber from Gulf of Gdańsk).

Palaeopsylla sp.

Palaeopsylla sp. Hoffeins *et al*. 2018 (male, amber from Gulf of Gdańsk) (Fig. 1B).

Order: **Diptera** Linnaeus, 1758

A characteristic feature of insects from the order Diptera is the presence of one pair of functional wings. Within the order there are two suborders characterized by the presence of short (suborder Brachycera) or long (suborder Nematocera) antennae. The mouthparts of adults are adapted to sucking and licking. Sucking mouthparts specialized for piercing occur in many families of the suborder Nematocera, and the lower and higher Brachycera. To date, about 160 000 extant named species of flies worldwide have been described (Marshall 2012).

Blood-sucking flies are known within the suborder Nematocera (Ceratopogonidae, Corethrellidae, Culicidae, Psychodidae, Simuliidae), the lower Brachycera (Tabanidae), and the higher Brachycera (Hippoboscidae, Nycteribiidae, Glossinidae, Strebliidae, Muscidae, Carnidae). The authors have not included two families of flies (Athericidae and Rhagionidae), which have also been recorded in Baltic amber (2 and 5 species respectively), because their biology associated with haematophagy is unclear and relatively poorly understood. Only nematocerous and lower brachycerous families have been reported from Baltic amber, i.e. Ceratopogonidae, Corethrellidae, Culicidae, Psychodidae, Simuliidae and Tabanidae.

Suborder: **Nematocera** Latreille, 1825

Family: **Ceratopogonidae** Newman, 1834

Ceratopogonidae (Fig. 1C) or biting midges are a family of small nematocerous insects occurring in a wide range of habitats from aquatic, semiaquatic to truly terrestrial. Larvae and pupae develop in a large variety of aquatic habitats like the shallow waters of lakes, ponds, rivers, streams, puddles, margins of water bodies, marshes and moist meadows (Mullen and Hribar 1988, Boorman 1997, Szadziewski *et al*. 1997). The biting habit is limited to the females. Adult females of many species with functional biting mouthparts suck the blood of vertebrates, especially birds and mammals. Blood is a high-energy food that is the source of protein used to produce eggs and can be supplemented with flower nectar, which is the only source of food for males (Szadziewski 2007).

In the world fauna Ceratopogonidae are represented by 6267 extant species classified into 4 subfamilies and 111 genera (Borkent 2016). There are also 283 fossil species belonging to 48 genera: 112 (39.6%) of these species are haematophagous (subfamilies Lebanoculicoidinae, Leptoconopinae, genera *Archiculicoides*, *Culicoides* and the subgenus *Lasiohelea* of *Forcipomyia*) (Szadziewski 2018). 109 species of biting-midges have been described from Baltic amber, 11 (10.1%) of which are blood-suckers.

Subfamily: **Ceratopogoninae** Newman, 1834

Genus: ***Culicoides*** Latreille, 1809: 251

Type species. *Culicoides punctata* Latreille, 1809 [preoccupied, =*Ceratopogon punctatus* Meigen, 1804], by monotypy.

Culicoides balticus Szadziewski, 1988

Culicoides balticus Szadziewski, 1988: 41 (male, female, amber from Gulf of Gdańsk); Szadziewski 1993: 607 (in identification key); Evenhuis 1994: 245 (catalogue); Borkent 2016: 78 (catalogue).

Culicoides ceranowiczi Szadziewski, 1988

Culicoides ceranowiczi Szadziewski, 1988: 45 (male, amber from Gulf of Gdańsk); Szadziewski 1993: 607 (male, amber from Bitterfeld); Evenhuis 1994: 245 (catalogue); Borkent 2016: 80 (catalogue).

Culicoides dasyheleiformis Szadziewski, 1988

Culicoides dasyheleiformis Szadziewski, 1988: 36 (male, amber from Gulf of Gdańsk); Szadziewski 1993: 607 (in identification key); Evenhuis 1994: 245 (catalogue); Borkent 2016: 82 (catalogue).

Culicoides eoselficus Szadziewski, 1988

Culicoides eoselficus Szadziewski, 1988: 43 (male, amber from Gulf of Gdańsk); Szadziewski 1993: 607 (in identification key); Evenhuis 1994: 245 (catalogue); Borkent 2016: 84 (catalogue).

Culicoides gedanensis Szadziewski, 1988

Culicoides gedanensis Szadziewski, 1988: 46 (male, amber from Gulf of Gdańsk); Szadziewski 1993: 607 (in identification key); Evenhuis 1994: 245 (catalogue); Borkent 2016: 86 (catalogue).

Culicoides prussicus Szadziewski, 1988

Culicoides prussicus Szadziewski, 1988: 48 (male, amber from Gulf of Gdańsk); Szadziewski 1993: 607 (in identification key); Evenhuis 1994: 246 (catalogue); Borkent 2016: 99 (catalogue).

Culicoides speciosus (Meunier, 1904)

Ceratopogon speciosus Meunier, 1904: 229 (male, female, amber from Gulf of Gdańsk).
Culicoides speciosus: Kieffer 1906: 1 (combination); Arnaud 1956: 148 (combination); Szadziewski 1988: 33 (redescription, male and female, amber from Gulf of Gdańsk); Szadziewski 1993: 607 (male and female, amber from Bitterfeld); Evenhuis 1994: 245 (catalogue); Sontag and Szadziewski 2011: 784 (male, female, amber from Rovno); Borkent 2016: 103 (catalogue).

Culicoides subgedanensis Szadziewski, 1993

Culicoides subgedanensis Szadziewski, 1993: 608 (male, amber from Bitterfeld); Evenhuis 1994: 246 (catalogue); Borkent 2016: 104 (catalogue).

Subfamily: **Forcipomyiinae** Lenz, 1934

Genus: ***Forcipomyia*** Meigen, 1818: 73

Type species. *Tipula bipunctata* Linnaeus, 1767, automatic (by designation of type species for *Labidomyia*).

Subgenus: ***Lasiohelea*** Kieffer, 1921: 115

Type species. *Atrichopogon pilosipennis* Kieffer, 1919, = *Ceratopogon velox* Winnertz, 1852, by original designation.

Forcipomyia succinea Szadziewski, 1988

Forcipomyia (*Lasiohelea*) *succinea* Szadziewski, 1988: 194 (female, amber from Gulf of Gdańsk); Szadziewski 1993: 643 (in identification key); Evenhuis 1994: 247 (catalogue); Borkent 2016: 46 (catalogue).

Subfamily: **Leptoconopinae** Noé, 1907

Genus: ***Leptoconops*** Skuse, 1889: 288

Type species. *Leptoconops stygius* Skuse, 1889, by monotypy.

Subgenus: ***Leptoconops*** Skuse, 1889: 288

Type species. *Leptoconops stygius* Skuse, 1889, by monotypy.

Leptoconops rovnensis Sontag et Szadziewski, 2011

Leptoconops (*Leptoconops*) *rovnensis* Sontag et Szadziewski, 2011: 780 (female, amber from Rovno) (Fig. 1C); Borkent 2016: 16 (catalogue).

Leptoconops succineus Szadziewski, 1988

Leptoconops (*Leptoconops*) *succineus* Szadziewski, 1988: 233 (female, male, amber from Gulf of Gdańsk); Evenhuis 1994: 249 (catalogue); Sontag and Szadziewski 2011: 783 (in identification key); Borkent 2016: 16 (catalogue).

Family: **Corethrellidae** Edwards, 1932

Corethrellidae or frog-biting midges, are a relatively small family of flies, with 107 extant species placed in the single genus *Corethrella* Coquillett, 1902 (Gil-Azevedo *et al*. 2016). These culicid-like flies are obligate external parasites. In contrast to other blood-sucking flies, they have an unusual way of locating their hosts: adult females are attracted by the vocalizations of male frogs or toads, using Johnston's organ for this purpose (Borkent 2008). The behaviour of males is poorly understood. Lethargic pupae and predaceous larvae are found in aquatic habitats. The occurrence of extant frog-biting midges is limited to warm climates; they are absent from Europe and northern Asia (Borkent 2017). Hitherto, 7 fossil species have been described, 5 of them from Baltic amber.

Genus: ***Corethrella*** Coquillett, 1902: 191

Type species. *Corethrella brakeleyi* Coquillett, 1902, by original designation.

Corethrella baltica Borkent, 2008

Corethrella baltica Borkent, 2008: 200 (male, amber from Gulf of Gdańsk); Borkent 2014: 465 (catalogue); Baranov *et al*. 2016: 538 (in identification key); Wichard *et al*. 2009: 177 (in identification key).

Corethrella miocaenica Szadziewski *et al*., 1994

Corethrella miocaenica Szadziewski *et al*., 1994: 87 (male, amber from Bitterfeld); Borkent 2008: 42 (in identification key); Borkent 2014: 466 (catalogue); Baranov *et al*. 2016: 539 (in identification key); Wichard *et al*. 2009: 177 (in identification key).

Corethrella prisca Borkent et Szadziewski, 1992

Corethrella prisca Borkent et Szadziewski, 1992: 457 (male, amber from Gulf of Gdańsk); Borkent 1993: 18 (catalogue); Evenhuis 1994: 224 (catalogue); Borkent 2008: 42 (in identification key); Borkent 2014: 466 (catalogue); Baranov *et al*. 2016: 539 (in identification key); Wichard *et al*. 2009: 177 (in identification key).

Corethrella rovnoensis Baranov et Kvifte, 2016

Corethrella rovnoensis Baranov et Kvifte in Baranov *et al*. 2016: 536 (female, amber from Rovno).

Corethrella sontagae Baranov et Kvifte, 2016

Corethrella sontagae Baranov et Kvifte in Baranov *et al*. 2016: 533 (male, amber from Rovno).

Family: **Culicidae** Meigen, 1818

Culicidae (mosquitoes) (Fig. 1D) are a family with a worldwide distribution. 3557 valid species have been identified in the extant world fauna: they are currently classified in two subfamilies *Anophelinae* and *Culicinae* (Harbach 2017). The vast majority of mosquitoes are obligate periodic parasites. Females, in particular feed on the blood of homoiothermic vertebrates, but many species attack poikilothermic animals like frogs, snakes and turtles (Service 1993). Some species can produce eggs without a blood meal, e.g. females of the tribe Toxorhynchitini (Coetzee 2017). Males do not bite, even though their mouth-parts form an elongated proboscis. The larvae of most species feed on organic matter (Rueda 2008). Capable of floating, the larvae, pupae and some eggs of Culicidae inhabit a wide range of aquatic areas with both flowing and standing water (Dahl 1997).

Five species have been recorded from Baltic amber. One other species from the genus *Coquillettidia* Dyar, 1905 was recorded by Szadziewski and Giłka (2011) but has not yet been described.

Subfamily: **Culicinae** Meigen, 1818

Genus: †***Aetheapnomyia*** Harbach et Greenwalt, 2012: 33

Type species. *Aedes hoffeinsorum* Szadziewski, 1998.

Aetheapnomyia hoffeinsorum (Szadziewski, 1998)

Aedes hoffeinsorum Szadziewski, 1998: 235 (male, amber from Gulf of Gdańsk); Szadziewski and Giłka 2011: 776 (in identification key); Wichard *et al*. 2009: 201 (in identification key).
Aetheapnomyia hoffeinsorum: Harbach and Greenwalt 2012: 33 (combination).

Genus: ***Culex*** Linnaeus, 1758: 602

Type species. *Culex pipiens* Linnaeus, 1758, by subsequent designation by Latreille [1810: 442].

Culex erikae Szadziewski et Szadziewska, 1985

Culex erikae Szadziewski et Szadziewska, 1985: 515 (female, amber from Gulf of Gdańsk); Evenhuis 1994: 233 (catalogue); Szadziewski 1998: 243 (in identification key); Szadziewski and Giłka 2011: 773 (syn. *Aedes perkunas*; in identification key); Wichard *et al*. 2009: 201 (in identification key).
Aedes perkunas Podenas 1999: 113 (male, amber from Gulf of Gdańsk); Wichard *et al*. 2009: 201 (in identification key).

Genus: ***Culiseta*** Felt, 1904: 391

Type species. *Culex absorbinus* Felt, 1904 [=*Culex impatiens* Walker, 1848], by original designation.

Culiseta gedanica Szadziewski et Giłka, 2011

Culiseta gedanica Szadziewski et Giłka, 2011: 766 (male, amber from Gulf of Gdańsk).

Genus: †***Eoaedes*** Harbach et Greenwalt, 2012: 33

Type species. *Aedes damzeni* Szadziewski, 1998.

Eoaedes damzeni (Szadziewski, 1998)

Aedes damzeni Szadziewski, 1998: 239 (male, amber from Gulf of Gdańsk); Szadziewski and Giłka 2011: 776 (in identification key); Wichard *et al*. 2009: 201 (in identification key).
Eoaedes damzeni: Harbach and Greenwalt 2012: 33 (combination).

Genus: ***Ochlerotatus*** Lynch Arribalzaga, 1891a: 353 [1891b: 143]

Type species. *Ochlerotatus confirmatus* Lynch Arribalzaga, 1891 [=*Aedes scapularis* Rondani, 1848], by subsequent designation of Coquillett [1910: 557].

Ochlerotatus serafini (Szadziewski, 1998)

Aedes (*Finlaya*) *serafini* Szadziewski, 1998: 240 (male, amber from Gulf of Gdańsk); Wichard *et al*. 2009: 201 (in identification key).
Ochlerotatus serafini: Szadziewski and Giłka 2011: 769 (combination; in identification key).

Family: **Psychodidae** Newman, 1834

The family Psychodidae, most often referred to as moth flies, contains more than 3000 described species (Pape *et al*. 2011). These small, densely-haired flies live in a wide range of habitats, from truly aquatic to truly terrestrial (Bejarano and Estrada 2016). Moth flies are wide spread, and the majority of adults are nocturnal. The larvae of most genera are found in

moist conditions, where they feed on rotting organic material. Only two subfamilies in this family are bloodfeeders – Sycoracinae and Phlebotominae (Lane 2003). Adult females feed on the blood of many vertebrates, including mammals, and also humans. Phlebotominae (sand flies) are known vectors of several diseases, especially leishmaniasis in humans (Munstermann 2004), while European *Sycorax* are known to be reservoirs of filariae, which attack green frogs (Desportes 1942).

Five species belonging to three genera of haematophagous Psychodidae have been described from Baltic amber.

Subfamily: **Phlebotominae** Rondani, 1840

Genus: †***Phlebotomiella*** Meunier, 1906: 103

Type species. *Phlebotomus tipuliformis* Meunier, 1905, by monotypy.

Phlebotomiella tipuliformis Meunier, 1905

Phlebotomiella tipuliformis Meunier, 1905: 254 (male, amber from Gulf of Gdańsk); Evenhuis 1994: 193 (catalogue).

Genus: ***Sergentomyia*** França et Parrot, 1920: 699

Type species. *Phlebotomus minutus* Rondani, 1843, automatic, by subsequent designation of França (1920: 234).

Sergentomyia succini (Stuckenberg, 1975)

Phlebotomus succini Stuckenberg, 1975: 456 (female, amber from Gulf of Gdańsk). *Sergentomyia* succini: Evenhuis 1994: 193 (combination, catalogue).

Subfamily: **Sycoracinae** Jung, 1954

Genus: ***Sycorax*** Haliday in Curtis, 1839: 745

Type species. *Sycorax silacea* Haliday in Curtis, 1839, by monotypy.

Sycorax prompta Meunier, 1905

Sycorax prompta Meunier, 1905: 252 (male, amber from Gulf of Gdańsk); Evenhuis 1994: 195 (catalogue).

Sycorax tumultuosa Meunier, 1905

Sycorax tumultuosa Meunier, 1905: 252 (female, amber from Gulf of Gdańsk); Evenhuis 1994: 195 (catalogue).

Sycorax ukrainensis Azar *et al*., 2013

Sycorax ukrainensis Azar *et al*., 2013: 29 (male, female, amber from Rovno).

Family: **Simuliidae** Newman, 1834

The family Simuliidae (black flies) (Fig. 1E) are small, stout nematocerous flies with over 2200 valid species (Adler & Crosskey 2017). These insects inhabit diverse submerged structures in many kinds of lotic environments. All black fly larvae and pupae are aquatic; the larvae in particular can be found in many kinds of flowing water (Currie and Adler 2008). Despite the fact that female black flies require a blood meal from endothermic vertebrates for egg maturation, adults of both sexes acquire floral nectar as a source of energy mainly for flying (Burgin and Hunter 1997). The longevity of bloodsucking and non-bloodsucking adults differs, this variation being closely related to various reproductive strategies (Jensen 1997).

Nine species of black flies belonging to 3 genera and 1 subfamily are represented in Baltic amber.

Subfamily: **Simuliinae** Newman, 1834

Genus: ***Ectemnia*** Enderlein, 1930: 88

Type species. *Cnetha taeniatifrons* Enderlein, 1925, by original designation.

Ectemnia cerberus (Enderlein, 1921)

Nevermannia cerberus Enderlein, 1921: 75 (female, amber from Gulf of Gdańsk); Enderlein 1930: 92 (in species list).
Simulium cerberus: Smart 1945: 502 (combination in catalogue); Crosskey 1988: 485 (checklist, after Smart); Crosskey 1990: 62 (with suggested affinity to *Ectemnia*).
Ectemnia cerberus: Crosskey 1994: 275 (combination); Evenhuis 1994: 239 (catalogue); Wichard *et al*. 2009: 209 (in identification key); Adler and Crosskey 2017: 24 (catalogue).

Ectemnia lithuanica Yankovsky et Bernotiene, 2005

Ectemnia lithuanica Yankovsky et Bernotiene, 2005: Wichard *et al*. 2009: 209 (in identification key); Adler and Crosskey 2017: 24 (catalogue).

Genus: ***Greniera*** Doby et David, 1959: 763

Type species. *Greniera fabri* Doby et David, 1959, by original designation.

Greniera affinis (Meunier, 1907)

Simulium affine Meunier, 1907: 397 (female, amber from Gulf of Gdańsk); Evenhuis 1994: 240 (catalogue).
Simulium meunieri Smart, 1944: 133 (unnecessary new replacement for *affinis* Meunier).
Greniera affinis: Crosskey 2002: 38 (combination); Wichard *et al*. 2009: 209 (in identification key); Adler and Crosskey 2017: 27 (catalogue).

Greniera importuna (Meunier, 1907)

Simulia importuna Meunier, 1907b: 398 (female, amber from Gulf of Gdańsk); Evenhuis 1994: 240 (catalogue).
Greniera importuna: Crosskey 2002: 41 (combination); Wichard *et al*. 2009: 209 (in identification key); Adler and Crosskey 2017: 27 (catalogue).

Greniera pulchella (Meunier, 1907)

Simulium pulchellum Meunier, 1907: 397 (female); Evenhuis 1994: 240 (catalogue).
Greniera pulchella: Crosskey 2002: 40 (combination); Adler and Crosskey 2017: 24 (catalogue).

Greniera ukrainica Perkovsky et Sukhomlin, 2015

Greniera ukrainica Perkovsky et Sukhomlin, 2015: 609 (male, amber from Rovno); Adler and Crosskey 2017: 27 (catalogue).

Greniera yankovskyi Perkovsky et Sukhomlin, 2015

Greniera yankovskyi Perkovsky et Sukhomlin, 2015: 50 (female, amber from Rovno); Perkovsky and Sukhomlin 2016: 80 (syn. *Hellichiella pugach*); Adler and Crosskey 2017: 27 (catalogue).
Hellichiella pugach Perkovsky et Sukhomlin, 2015: 51.

Genus: ***Hellichiella*** Rivosecchi et Cardinali, 1975: 65

Type species. *Hellichiella saccai* Rivosecchi, 1967, by original designation.

Hellichiella oligocenica (Rubtsov, 1936)

Simulium oligocenicum Rubtsov, 1936: 353 (male); Evenhuis 1994: 240 (catalogue); Wichard *et al*. 2009: 209 (in identification key).
Hellichiella oligocenica: Rubtsov 1936 (alternative combination); Adler and Crosskey 2017: 52 (catalogue placement as *Hellichiella oligocenicum*).

Hellichiella polessica Perkovsky et Sukhomlin, 2016

Hellichiella polessica Perkovsky et Sukhomlin, 2016: 80 (female, amber from Rovno).

Suborder: **Brachycera** Zetterstedt, 1842

Family: **Tabanidae** Latreille, 1802

The Tabanidae (Fig. 1F) are a cosmopolitan family of relatively large brachycerous insects, commonly known as horse or deer flies. Approximately 4350 extant species have been described. Tabanids are wide-ranging, and adults are found in open forested habitats. Males with reduced mouthparts are phytophagous, feeding on pollen and nectar, while females, capable of penetrating tissues, have a thick, strong proboscis with which they obtain their blood meals from various vertebrate hosts, including humans. Tabanid flies lay their eggs in moist ground or river sludge. The larval stage can last for more than two years, chiefly in the North. Larvae are predators, mainly of annelids, molluscs and other arthropods, or eat detritus to supplement their diet (Wolff & Miranda-Esquivel 2016).

Eight species from five genera and two subfamilies (Chrysopsinae and Tabaninae) have been recorded in Baltic amber.

Subfamily: **Chrysopsinae** Lutz, 1905

Genus: ***Mesomyia*** Macquart, 1850: 341

Type species. *Mesomyia decora* Macquart, 1850, by original designation.

Mesomyia cuprea Trojan, 2002

Mesomyia cuprea Trojan, 2002: 264 (male, amber from Gulf of Gdańsk).

Mesomyia hoffeinsorum Trojan, 2002

Mesomyia hoffeinsorum Trojan, 2002: 260 (female, amber from Gulf of Gdańsk).

Mesomyia stigmatica Trojan, 2002

Mesomyia stigmatica Trojan, 2002: 261 (female, amber from Gulf of Gdańsk).

Mesomyia yantarophila Trojan, 2002

Mesomyia yantarophila Trojan, 2002: 264 (male, amber from Gulf of Gdańsk).

Genus: ***Pseudotabanus*** Ricardo, 1915: 271

Type species. *Pseudotabanus distinctus* Ricardo, 1915.

Pseudotabanus dereckii Trojan, 2002

Pseudotabanus dereckii Trojan, 2002: 266 (male, amber from Gulf of Gdańsk).

Genus: †***Sznablomyia*** Trojan, 2002: 265

Type species. *Sznablomyia parvula* Trojan, 2002.

Sznablomyia parvula Trojan, 2002

Sznablomyia parvula Trojan, 2002: 265 (female, amber from Gulf of Gdańsk).

Genus: †***Tabanosoma*** Trojan, 2002: 265

Type species. *Tabanosoma tabaniforme* Trojan, 2002.

Tabanosoma tabaniforme Trojan, 2002

Tabanosoma tabaniforme Trojan, 2002: 266 (female, amber from Gulf of Gdańsk).

Subfamily: **Tabaninae** Latreille, 1802

Genus: ***Haematopota*** Meigen, 1803: 267

Type species. *Tabanus pluvialis* Linnaeus, 1758, by monotypy.

Haematopota pinicola Stuckenberg, 1975

Haematopota pinicola Stuckenberg, 1975: 460 (male, amber from Gulf of Gdańsk); Evenhuis, 1994: 288 (catalogue).

Concluding remarks

The terrestrial arthropods feeding on vertebrate blood includes some 1% of all extant species (present calculation). A similar rate (1.1%) has been calculated for 48 named haematophages among 4275 arthropod species living in Eocene amber forest (Szadziewski *et al*. in press).

The extant dipterans in the Polish fauna include 7027 species, 223 of which are blood-suckers (Szadziewski and Giłka 2012), whereas 43 of the 1248 dipteran species from the Baltic amber forest were haematophagous (Szadziewski *et al*. in press). The percentage of blood-feeding flies in the Eocene Baltic amber forest is similar to that in the extant fauna of Poland (3.4%, and 3.2% respectively).

Despite the fact that haematophagous families of higher dipterans in the Calyptratae group had not yet evolved during the Eocene, the percentage of blood feeding arthropods species was similar to that in the extant fauna.

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